INVESTIGATIONS INTO SOME IMPORTANT FISH LARVAE IN THE SOUTH EAST ATLANTIC IN RELATION TO THE HYDROLOGICAL ENVIRONMENT

By

MICHAEL JOHN O'TOOLE

Sea Fisheries Branch and Zoology
Department, University of Cape Town

Thesis presented for the Degree of Doctor of Philosophy
at the University of Cape Town

SUPERVISORS AND PROMOTORS: Dr. J. Field (UCT)
Dr. G. Branch (UCT)
Dr. A.H.B. de Decker (SFB)

SUBMITTED: MARCH 1977

CONTENTS

A DISCUSSION ON THE RESULTS OF PAPERS I - 7 ENTITLED: ECOLOGICAL INTER-RELATIONSHIPS BETWEEN LARVAL POPULATIONS AND WITH HYDROLOGY

SUPPORTING PAPERS

I.	LOUW, A.E. AND M.J.O'TOOLE	I977	LARVAL DEVELOPMENT OF SARDINOPS OCELLATA(PISCES:CLUPEIDAE) ANN. S. AFR. MUS. 72, (7),I25-I45.
2.	AHLSTROM,E.H., H.G.MOSER AND M.J.O'TOOLE	I976	DEVELOPMENT AND DISTRIBUTION OF LARVAE AND EARLY JUVENILES OF THE COMMERCIAL LANTERN FISH, LAMPANYCTODES HECTORIS (GUNTHER) OFF THE WEST COAST OF SOUTHERN AFRICA WITH A DISCUSSION OF THE PHYLOGENETIC RELATIONSHIPSOF THE GENUS. BULL. STH. CALIF. ACAD. SCI, 75, (2), I38-I52.
3.	O'TOOLE, M.J. AND D.P.F. KING	I974	EARLY DEVELOPMENT OF THE ROUND HERRING ETRUMEUS TERES (DEKAY) FROM THE SOUTH EAST ATLANTIC VIE MILIEU, 24, FASC.3, SER.A, 443-452.
4.	O'TOOLE, M.J.	I976	INCIDENTAL COLLECTIONS OF SMALL AND JUVENILE FISHES FROM EGG AND LARVAL SURVEYS OFF SOUTH WEST AFRICA. FISH. BULL. S. AFR. (8), 23-33.
5.	O'TOOLE, M.J.	I974	FISH LARVAL INVESTIGATIONS OFF SOUTH WEST AFRICA. S. AFR. SHIPP. NEWS FISH. IND. 29, (II),53-59.

6. O'TOOLE, M.J. 1977 IN PRESS A NOTE ON THE RELATIONSHIP BETWEEN THE VERTICAL DISTRIBUTION OF MAASBANKER LARVAE (*TRACHURUS TRACHURUS*) AND ENVIRONMENTAL PARAMETERS OFF SOUTH WEST AFRICA *FISH*. *BULL*. *S*. *AFR*. (9) .

7. O'TOOLE, M.J. 1976 A NOTE ON THE PRESENCE OF RIPE ANCHOVY OFF CAPE POINT *FISH*. *BULL*, *S*. *AFR.* (8), P.35.

INTRODUCTION

The waters off South West Africa constitute a rich commercial fishing area and is the focus of a sizeable international multi-species fishery. In 1973, catches of pelagic and demersal species taken by all vessels operating off the coast exceeded two million metric tons (.F.O.A. 1974). The most sought-after pelagic fish are the pilchard Sardinops ocellata Pappe, anchovy Engraulis capensis Gilchrist and the Cape horse mackerel or maasbanker Trachurus trachurus Linnaeus. The hakes, Merluccius capensis Castelnau and M. paradoxus Franca are the most important demersal species. Pilchard and anchovy stocks are mainly exploited by fishing vessels based at Walvis Bay, whereas, the maasbanker and hake populations are heavily fished by large fleets from U.S.S.R., Spain, South Africa, Japan, Bulgaria, Cuba and Poland. In a commercial fishery of this magnitude, it is desirable to detect changes and predict trends taking place within the populations to facilitate proper management of the resources. Fish populations are not only sensitive to increased fishing effort but also to changes in oceanographic conditions which can cause marked fluctuations in abundance, availability and year-class strength.

During the last decade, the rapid depletion of the stocks of some species of marine food fish in various parts of the world have been well-documented. The pilchard or sardine fisheries are typical examples. The decline of the Californian sardine Sardinops caerulea has been attributed to a reduction in the parent stock due to heavy exploitation severe enough to upset the rate of recruitment (Murphy 1966, Sette 1969). Intensive fishing and recruitment failure was the cause of the collapse of the South African pilchard fishery (Stander and Le Roux 1968) whereas the decline of the Japanese sardine Sardinops melanosticta was caused by unfavourable environmental conditions affecting recruitment (Nakai 1960). Parallel with the reduction of pilchards in the various fisheries, the availability of other pelagic species, especially the anchovy increased noticeably. Moreover, the exploited stock usually showed changes in reproductive behaviour as indicated by variations in egg and larval abundance, alterations in spawning seasons as well as localities.

Studies on ichthyoplankton have contributed in many ways to the detection and appraisal of fish resources, to population dynamics and to the general biology and systematics of fishes. One of the most useful methods of monitoring fluctuations in fish stocks is to compare the variation in abundance of the pelagic eggs and larvae between years through regular routine ichthyoplankton surveys (Ahlstrom I965, I971, I972). Seasonal distribution of eggs and larvae are particularly useful in detecting changes in the spawning behaviour of the adults in respect of shortening or lengthening of the spawning season and geographical shifting of the breeding areas.

It is generally believed that year-class strength is determined during the egg and larval phase (Hjort I9I4, I926, Walford I938, Wilborg I957). For several species there is evidence of a high mortality rate during certain development stages (critical phase). High mortalities have been reported between hatching and absorption of the yolk-sac in the Californian sardine (Ahlstrom I954, Farris I961) and in the Japanese sardine (Nakai et al I955), from yolk-sac absorption to a length of 16 - 20 mm in the herring larvae Clupea harengus (Blaxter and Hempel I961) and from 30 - 40 days after hatching in the Atlantic mackerel Scomber scombrus (Sette I943, Marr I956). The causes of these mortalities during the early larval phase are thought to be due to a variety of physical and biological factors. Fluctuations in hydrological and biological conditions such as temperature, currents, nutrients and plankton have a profound influence on spawning, development and survival of larvae. For example, larval abundance and in some cases recruitment of marine fish has been correlated with specific oceanographic parameters, including wind, currents and plankton distribution (Walford I938, Carruthers et al I951, Rae I957, Corlett I958, I964, Cushing I967, Bainbridge and Cooper I973, Hart I974). However, the influence of these parameters are likely to be felt more as a complex of interactions rather than one factor operating in isolation. Temperature perhaps can be singled out as one of the more important physical parameters as it controls the migration of fish populations, the rate of metabolism and also the development of the pelagic eggs and larvae.

Many species of marine fish larvae need certain thermal requirements where the body metabolism can presumably operate with maximum efficiency. Above and below these limits, the effects may be lethal, causing heavy mortalities. Temperature also indirectly affects larval survival by regulating the period over which the developing larvae are vulnerable to predation (Murphy I961). Rapid changes in temperature during the spawning season can have drastic consequences, as shown by Dannevig and Hansen (I952) for the Norwegian cod and by Colton (I959) for several species of larval fish off Georges Bank. The production of food organisms for developing larvae also depends largely upon abiotic factors such as temperature.

During the planktonic phase, developing larvae are carried passively by water currents and consequently dispersal patterns could play a vital part in determining the fate of a year-class. Transportation of larvae into areas which may have favourable or unfavourable environments would ultimately affect their growth rate and survival. It is desirable, therefore, to understand the movement of water masses in the spawning grounds and to trace the direction in which larvae are carried.

Despite the fact that the waters off South West Africa may be classified as one of the major world fishing areas there is surprisingly little information on the ichthyoplankton of the region. Previous investigations have mainly been concerned with the seasonal occurrence of pilchard eggs (Hart and Marshall I951, Matthews I963, Stander I963, King I977 in press). Information on the eggs and larval stages of other species of fish is sparse. Sciaenid eggs and early larvae have been recorded and described by Meyer-Rochow (I972). King (I975) reported on the relationship between egg development of the pilchard and temperature, salinity and oxygen and in a later paper (King I977, in press) outlined the distribution of anchovy eggs off the coast. The occurrence of eggs and larvae of the hake was listed by Porebski and Koronkiewicz (I975) and of the frostfish Lepidopus candatus by Porebski and Bielaszewska (I975).

Because of the sudden decline in pilchard availability from 1,5 million tons in 1968 to 450000 tons in 1970 (F.A.O. 1971), the Sea Fisheries Branch embarked on a major research project in 1972 The Cape Cross Programme, to investigate the state of the fishery. (Cram and Visser 1972). Part of the overall research commitment was an extensive quantitative ichthyoplankton study which became known as SWAPELS (South West African Pelagic Egg and Larvae Survey) in the region between Cape Frio (18°20'S) and Hollam's Bird Island (24°40'S) during the months August to March/April. The period and the area was selected because they covered the known spawning season and the geographic range of the South West African pilchard population. The first survey was carried out between August 1972 (late winter) and March 1973 (early autumn) and the second between August 1973 and March/April 1974. Unfortunately, no sampling was conducted during the intermediate period.

The primary purpose of SWAPELS was to estimate the pilchard adult stock size from its spawning production. Additional objectives were an investigation of the planktonic stages of other commercially exploited species. Findings on the larvae are presented here for the pilchard S.ocellata, anchovy E. capensis, Cape horse mackerel T.trachurus, hake M.capensis, West Coast sole Austroglossus microlepis and bearded goby, Sufflogobius bibarbatus. The latter was of interest as its larvae constituted 62 percent of all fish larvae taken on the surveys.

The following objectives are covered in the study:

(i) the description of the seasonal hydrological changes in the survey area and a comparison between years.

(ii) an examination of the seasonal distribution and abundance of the larval stages in relation to hydrological conditions.

(iii) the determination of the preferential temperature and salinity ranges for the larvae.

(iv) an examination of seasonal shift in location and intensity of spawning from the geographic distribution, abundance and size composition of the larvae.

(v) the establishment of dispersal trends of developing larvae from the spawning grounds.

(vi) the provision of information on the identity and development of important fish eggs and larvae

(vii) the determination of diurnal changes in abundance and size composition of various larval species.

The results reported are regarded as scientifically significant in view of the paucity of basic information on the early life history of any fish species off South West Africa. Many aspects such as identity, development, distribution, abundance, hydrological affinities, diurnal variation and dispersal are given for the first time. The findings make a positive contribution not only to knowledge of the early stages and biology of the species but also provide an insight into the general ecology of fish larvae in what is probably the most productive and lucrative fishing grounds in the South East Atlantic.

In this work information is given only on the larvae of selected species. However, numerous other kinds of fish larvae were also collected on the surveys. It may therefore be useful at this stage to give an overview of the general larval composition and seasonality of all the species.

Fish larval composition

During SWAPELS, a total of 80,428 larvae representing 24 families of fish were collected in the plankton. These belonged to the Clupeidae, Engraulidae, Carangidae, Merluccidae, Gobiidae, Soleidae, Myctophidae Blennidae, Gonostomatidae, Triglidae, Scorpaenidae, Lepidopidae, Syngnathidae, Callionymidae, Ophidiide, Coryphaenoididae, Scomberescidae, Sciaenidae, Gempylidae and Lophiidae.

Eleven kinds of larvae constituted over 96 percent of all those collected during the two year investigation. The bearded goby was the dominant species and formed 66,8 percent and 58,8 percent of all the larvae taken during Survey 1 and 2 respectively. Although this species is of no economic significance, its striking dominance suggests that it is of cardinal importance in the food web.

Larvae of commercial species such as the anchovy, pilchard, hake, maasbanker and sole ranked amongst the ten most abundant species. However, pronounced differences in the order of rank were noticeable between years which perhaps indicated natural fluctuations in populations abundance. For example, anchovy larvae were three times as abundant during 1972/73 compared with 1973/74 whereas these of the pilchard were almost nine times more plentiful during the second survey.

Of the bathypelagic fish larvae, the myctophid Lampanyctodes hectoris and the maurolicid, Maurolicus muelleri were the most numerous and were an important component of the offshore plankton. Another myctophid of the genus Symbolophorous was consistently taken in hauls at offshore stations and ranked 11th and 9th in abundance during survey 1 and 2 respectively.

A species of blenny, provisionally identified as Chalaroderma capito was an important constituent of the was an important constituent of the offshore plankton in the northern part of the research area.

The remaining 13 kinds of larvae and those which could not be identified formed only 3,0 percent and 2,2 percent of all those collected during Survey 1 and Survey 2.

Abundance of the more common species and genera is summarised in Table 1.

Seasonality of larvae

The seasonal abundance of the eleven most common kinds of fish larvae collected on the SWAPELS cruises is shown in Table II and III. It may be seen that the larvae of some species occurred predominantly in late winter/spring whereas others were collected only during summer and early autumn months. The general pattern of seasonal abundance amongst the various species was consistent between years. For example over 85 percent of bearded goby larvae were collected in the plankton during late winter and spring. The larvae of the West Coast sole and the lanternfish L. hectoris also occurred mostly during winter and spring. Hake larvae were found mainly during the months of October, November and December (mid spring to early summer).

In contrast, larvae of such species as the anchovy, maasbanker and Senegal sole were found to occur mostly in the summer and early autumn. The pilchard appeared to spawn continuously from late winter to autumn but the larval abundance showed a late winter and a summer/autumn spawning peak. A comparison of the seasonal abundance of larvae between years indicates that the intensity of spawning can change from month to month and season to season.

For example over 67 percent of all pilchard larvae captured during 1972/73 were taken in September whereas over 70 percent occurred during March/April 1973/74. Sixty three percent of maasbanker larvae were collected in January during Survey 1 but on Survey 2 most of the larvae (70 percent) were captured two months later in March/April.

TABLE I COMPARISON OF RELATIVE ABUNDANCE OF FISH LARVAE COLLECTED OFF SOUTH WEST AFRICA DURING THE SWAPELS CRUISE OF 1972 - 1974.

	SURVEY 1 1972/73			SURVEY 2 1973/74		
Species	No. taken	% of total	Rank	No. taken	% of total	Rank
Sufflogobius bibarbatus	17 825	66,83	1	31 173	58,82	1
Engraulis capensis	4 316	15,70	2	1 034	1,95	5
Sardinops ocellata	986	3,59	3	9 065	17,10	2
Trachurus trachurus	802	2,92	4	2 574	4,90	4
Merluccius capensis	673	2,45	5	911	1,72	6
Austroglossus microlepis	358	1,30	9	178	0,33	10
Dicologlossa cuneata	385	1,40	8	420	0,89	7
Lampanyctodes hectoris	449	1,63	7	5 785	10,92	3
Maurolicus muelleri	580	2,11	6	349	0,65	8
Symbolophorous spp.	105	0,38	11	214	0,40	9
Chalaroderma capito	184	0,67	10	114	0,21	11
Diaphus spp.	46	0,17	12	62	0,11	12
Hogophum macahir	235	0,08	14	18	0,03	15
Pterothrissus belloci	12	0,04	15	8	0,01	17
Vinciguerria spp.	10	0,04	16	12	0,02	16
Chauliodius spp.	6	0,02	17	4	0,01	19
Lepidopus caudatus	35	0,13	13	28	0,05	13
Stomias boa	4	0,01	18	6	0,01	18
Trigla spp.	12	0,04	15	22	0,04	14
All others	687	2,50		924	1,93	
Total	27 497	100,0		52 931	100,0	

TABLE II PERCENTAGE SEASONAL ABUNDANCE OF THE MORE COMMON KINDS OF LARVAE COLLECTED DURING 1972/73.

Species	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar
S. bibarbatus	0,9	10,3	3,7	37,6	32,6	8,8	5,9	0,3
E. capensis	–	–	–	0,2	4,5	40,1	25,9	32,2
S. ocellata	0,2	67,7	5,1	6,5	0,8	4,9	6,6	8,2
T. trachurus	–	–	2,9	2,2	7,0	63,1	17,5	7,4
M. capensis	–	–	1,5	18,3	76,1	2,8	–	1,3
A. microlepis	–	54,5	7,5	34,1	3,9	–	–	–
D. cuneata	–	–	–	–	77,2	10,3	10,6	1,8
L. hectoris	8,7	28,1	9,7	39,0	13,6	0,7	–	–
M. muelleri	–	0,67	1,0	51,9	36,6	9,1	0,7	–
Symbolophorous sp.	–	–	9,5	21,9	45,7	12,3	2,8	7,6
C. capito	–	5,1	11,7	13,1	12,6	22,0	32,2	3,3

TABLE III PERCENTAGE SEASONAL ABUNDANCE OF THE MORE COMMON KINDS OF LARVAE COLLECTED DURING 1973/74

Species	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar/Apr
S. bibarbatus	0,4	0,5	21,6	27,2	36,2	7,1	3,8	3,2
E. capensis	–	–	0,5	3,0	6,5	20,1	46,9	24,9
S. ocellata	0,1	1,1	1,7	1,9	0,1	18,4	5,9	70,9
T. trachurus	–	–	–	1,2	1,0	11,1	38,7	47,8
M. capensis	–	–	9,2	27,1	53,8	2,9	2,2	5,8
A. microlepis	1,1	7,3	59,9	10,7	10,2	10,2	–	–
D. cuneata	66,5	–	–	6,2	9,3	3,1	11,4	70,0
L. hectoris	–	4,5	13,1	13,1	2,7	1,2	0,3	0,2
M. muelleri	–	–	0,9	53,6	48,7	–	–	–
Symbolophorous sp.	4,7	6,0	22,8	33,9	24,2	3,3	2,9	6,0
C. capito		9,4	9,4	23,5	–	–	–	52,9

SUMMARY OF CONTRIBUTIONS

This thesis is presented in the form of a series of papers. The first seven manuscripts comprising the main part of the dissertation are unpublished. A discussion follows intergrating the main findings and general conclusions. Seven publications which may be regarded as supporting documents are also included. For convience, literature cited is given at the end of individual papers.

I. Distribution of temperature and salinity off South West Africa I972 - I974.

A description of the seasonal hydrological features off the coast of South West Africa between I8°20'S (Cape Frio) and 24°40'S (Hollam's Bird Island) during the survey periods August I972 to March I973 and August I973 to March/April I974 is given. The interpretations are based on the monthly distribution of temperature in the upper 50 m layer and surface salinity. Gross seasonal changes in water movement from temperature and salinity data are discussed. Particular attention is given to upwelling and frontal systems between warm and cold bodies of water. Comparisons are made for both periods and the differences emphasized.

2. Investigations into the early life history of the South West African pilchard *Sardinops ocellata* Pappe.

Previous work on the biology and early life history of the pilchard *S. ocellata* is briefly reviewed and an account is given on larval seasonality, distribution, abundance, size composition and diurnal variation in catches. Spawning and the occurrence of larvae is discussed in relation to temperature, salinity and seasonal movements of water masses off the coast. Dispersal trends and larval growth are also examined. In addition to the larvae, some information is provided on the depth distribution of pilchard eggs and the relationship between depth of occurrence and environmental parameters.

3. Investigations into the early life history of the South West African anchovy Engraulis capensis Gilchrist.

4. Investigations into the early life history of the Cape horse mackerel Trachurus trachurus L. off South West Africa.

5. Aspects of the early life history of the hake, Merluccius capensis off South West Africa.

Papers 3, 4 and 5 are similar to Paper 2 but concern the larval stages of anchovy, Cape horse mackerel and hake. Such aspects as seasonality, distribution, abundance, diurnal variation in catches, hydrological relationships and dispersal are discussed. In the case of Paper 4, egg development and the yolk-sac larva is described.

6. The development and distribution ecology of the larvae of the West Coast sole Austroglossus microlepis (Bleeker) from the South East Atlantic.

This paper describes the larval development of the West Coast sole A. microlepis and gives an account on larval seasonality, distribution, abundance and relationships with hydrological parameters.

7. Description of the larvae and early juveniles of the bearded goby. Sufflogobius bibarbatus (von Bonde) with notes on its distribution, abundance and ecology in the South East Atlantic.

The larval development of the bearded goby S. bibarbatus is described and illustrated. The geographic distribution, abundance, seasonality, diurnal variation in catches and relationships of the larvae to temperature and salinity is also given. Possible explanations for the large concentrations of larvae of this species in the plankton are discussed.

8. The ecological inter-relationships between the larval populations and with hydrology.

This paper integrates the results of the preceeding 7 manuscripts and discusses some broad inter-relationships between larval populations and the environment. The time of spawning and the formation of separate spawning areas are examined in relation to seasonal hydrological change and plankton production cycles. Competition and predation between adult and larval populations is given as a possible explanation for the dominance of certain species.

9. Louw, A.E. and M.J. O'Toole 1977
Larval development of Sardinops ocellata (Pisces: Clupeidae)
Ann. S. Afr. Mus. 72 (7), 125-145.

This paper describes and illustrates the development of the yolk-sac, larval and metamorphic stages of the South West African pilchard S. ocellata. Emphasis is placed on the changes in body proportion, pigmentation, fin development and fin positions relative to myotomes during the course of development. The findings are briefly compared with larval development of other Sardinops species.

10. Ahlstrom, E.H., H.G. Moser and M.J. O'Toole 1976
Development and distribution of larvae and early juveniles of the commercial lanternfish, Lampanyctodes hectoris (Günther), off the west coast of southern Africa, with a discussion on phylogenetic relationships of the genus.
Bull. Sth. Calif. Acad. Sci., 75 (2) 138-152.

The larvae, transitional and early juvenile stages of the commercial lantern fish L. hectoris are described and illustrated for the first time. Information on the relative abundance of larvae and occurrence in relation to temperature is given. Larval characters are used in combination with selected adult characters to elucidate the phylogenetic affinities of the genus.

11. O'Toole, M.J. and D.P.F. King 1974

Early development of the round herring Etrumeus teres (De Kay) from the South East Atlantic. Vie Milieu, 24 fasc. 3, Ser.A, 443 - 452.

The eggs and early larval development of the round herring E. teres collected off the Cape Peninsula is described. Incubation rates for egg development from blastocap stage to hatching is given for a variety of temperatures. A short comparison is made between Etrumeus egg characters and other clupeid eggs encountered in Cape waters.

12. O'Toole, M.J. 1976

Incidental collections of small and juvenile fishes from egg and larval surveys off South West Africa (1972-1974) Fish. Bull. S. Afr. 8 23 - 33.

This paper provides an annotated list of juvenile and small fish species captured in the plankton nets during the routine SWAPELS cruises. The general distribution, number of occurrences, length range, time of capture and temperature ranges at which specimens were taken are given. The importance of two species, the bearded goby S. bibarbatus and the commercial lanternfish L. hectoris is emphasized.

13. O'Toole M.J. 1974

Fish larval investigations off South West Africa. S. Afr. Shipp. News. Fish. Ind. Rev. 29 (11) 53-59.

This paper briefly summarizes the results of the first SWAPELS cruised (August 1972 - March 1973). The report is of a general nature and deals with catch composition of various larval species, overall distribution, seasonality, diurnal variation in catches and temperature/salinity relationships.

14. O'Toole, M.J. 1977

A note on the relationship between the vertical distribution of maasbanker larvae (Trachurus trachurus L) and environmental parameters off South West Africa. <u>Fish. Bull. S. Afr.</u> <u>9</u>

The depth distribution of maasbanker larvae is given in relation to temperature, salinity, oxygen and chlorophyll in the upper 50 m of water. Observations were based on one hour long stratified tow using Miller nets in an area where the larvae were particularly abundant. The results are compared briefly with the larvae of other species of <u>Trachurus</u>.

15. O'Toole, M.J. 1976

A note on the presence of ripe anchovy off Cape Point. <u>Fish. Bull. S. Afr.</u> <u>8</u>, p. 35

Freshly eaten anchovy <u>E. capensis</u> in a ripe and running condition were disgorged by some long-fin tuna <u>Tunnus alalunga</u> caught off Cape Point. Spawning anchovy are noticeably rare in the commercial catches and suggestions are made regarding the depth at which spawning occurs.

Presentation of this dissertation in the form of separate papers inevitably results in some repetition and also tends to disrupt the continuity of the thesis. Nevertheless, since the candidate was employed by the Sea Fisheries Branch during the course of this work, speedy publication was encouraged and thus aided by presenting the results in this way. Apologies are made for the poor reproduction quality of some illustrations.

The work reported in this thesis is original except where otherwise stated and acknowledged in the text. In Paper 2, vertical distribution studies on pilchard eggs were conducted and analysed with Mr D.P.F. King, Sea Fisheries Branch. Much of Paper 8 was written and illustrated by the senior author. I wrote some of the text and aided in the measurement of larvae and in the analyses of the morphometric data. In Paper 9, the candidate was responsible for the field work, drafting distributional figures and writing some of the text. The senior authors wrote most of the paper, including the phylogenetic discussion. The field work in Paper 10 was jointly carried out with Mr D.P.F. King, however, the candidate described and illustrated the eggs and early larvae and wrote the majority of the text. The incubation experiments on the eggs were conducted by Mr King.

In general, the candidate participated in and helped jointly organise many of the ichthyplankton cruises with his fellow colleague Mr King.

ACKNOWLEDGEMENTS

I am sincerely grateful to the following persons without whose help, the completion of this study would have been very difficult if not impossible.

The Director of Sea Fisheries, Dr. B.V.D. de Jager and Assistant Director Mr. D.L. Cram whose active support for the SWAPELS programme made this study possible. I am much indebted to fellow colleague Mr. D.P.F.King, Sea Fisheries Branch for his help and encouragement in many aspects of the work and to Mr. A.A.Robertson for the excellent way he ensured the smooth running of the survey cruises. The advise and assistance recieved from Dr. A.H.B. de Decker and Mr. L. Hutchings, Sea Fisheries Branch and Dr. N. Bang, Oceanographic Department, University of Cape Town, with the hydrological interpretations is greatly appreciated. I also gratefully acknowledge the technical assistance given by Mr. J. Giddey, Mrs. S. Payne, Mr. B. Rose and Mr. D. Alexander in sorting and enumeration of the ichthyoplankton, staining of larval specimens and photographic reductions.

My two supervisors, Dr. J. Field and Dr. G. Branch, Zoology Department, University of Cape Town and Mr. A.I.L. Payne, Sea Fisheries Branch are due special thanks for the valuable suggestions and criticism recieved.

Finally, I wish to thank Miss Marie Meaney for her patience in typing the thesis and for her continuous support and encouragement during all phases of this work.

LITERATURE CITED

AHLSTROM, E.H. 1954 Distribution and abundance of egg and larval populations of the Pacific sardine. Fish. Bull.U.S. Fish Wildl. Serv., 56, (93) 83-140.

AHLSTROM, E.H. 1965 Kinds and abundance of fishes in the Californian Current region based on egg and larval surveys. Rep. Calif. coop. oceanic Fish. Invest. IO : 31-52

AHLSTROM, E.H. 1971 Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. Fish. Bull. U.S. Fish Wildl. Serv. 69, (I) : 3-77.

AHLSTROM, E.H. 1972 Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey and observations on the annual cycle of larval abundance. Fish. Bull. U.S. Fish Wildl.Serv. 70 , (4) : II53 - I242.

BAINBRIDGE, V. AND COOPER, G.A. 1973 The distribution and abundance of the larvae of the blue whiting Micromesistius poutassou (Risso) in the northeast Atlantic, I948-I970. Bull. Mar. Ecol. 8, (2); 99-II4.

BLAXTER, J.H.S. AND G. HEMPEL. 1961 Biologische Beobachtungen bei der Aufzucht von Heringsbrut. Helgoland wiss, Merresunters. 7 (5) : 260 - 283.

CARRUTHERS, J.N., A.N. LAWFORD, & V.F.C. VELEY 1951 Fishery Hydrography: Brood-Strength fluctuations in various North Sea fish, with suggest methods of prediction. Kieler Meeresforch. 8 (I) : 5-15.

COLTON, J.B. 1959 A field observation of mortality of marine fish larvae due to warming. Limnol, and Oceanogr. 4 : 219-222.

CORLETT, J. 1958 Plankton in the western Barents Sea and the year-class strength of the Arcto-Norwegian cod. J.du Cons. 23 : 354-356.

CORLETT, J. 1965 Wind, current, plankton and year-class strength of cod in the western Barents Sea. ICNAF, Environmental Symposium (6), FAO, Rome. 373-378.

CRAM, D.L. AND G.A. VISSER. 1972 Cape Cross Research Programme, phase II , a summary of results. S.Afr. Shipp. News Fish. Ind. Rev. 27 , (2) : 40-43

CUSHING, D.H. 1967 The grouping of herring populations. J.mar. biol. Ass. U.K., 47 : 193-208.

DANNEVIG A. AND S. HANSEN. 1952 Faktorer av betydning for fiskeeggenes og fiskeyngelens opp vekst. Fiskeridir. Skr., 10 (I).

FAO 1971 Catches and Landings Year book of fishery statistics, 1970, 32 : Food and Agricultural Organization of the United Nations, Rome.

FAO 1974 Catches and Landings Year book of fishery statistics, 1973, 34: Food and Agricultural Organization of the United Nations, Rome.

FARRIS, D.A. 1961 Abundance and distribution of eggs and larvae and survival of larvae of jack mackerel *Trachurus symmetricus*. *Fish. Bull. U.S. Fish. Wildl. Serv.* *61*, (I87) : 247-279.

HART, T.J. AND N.B. MARSHALL. 1951 Breeding ground of pilchard off the coast of South West Africa. *Nature, Lond.* *I68* : p.272

HART, P.J.B. 1974 The distribution and long term changes in abundance of larval *Ammodytes marinus* (Raitt) in the North Sea. Reprint from " *The Early Life History of Fish*"(*Ed. by J.H.S. Blaxter*). *Springer-Verlag, Berlin, New York*.

HJORT, J. 1914 Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P-V. Reun. Cons. Perm. Int. Explor. Mer.* *20* :1-228.

HJORT, J. 1926 Fluctuations in the year classes of important food fishes. *J.du. Cons.* *I* : 5-38.

KING, D.P.F. 1975 Influence of salinity,temperature and dissolved oxygen on embryonic development of the South West African pilchard , *Sardinops ocellata*. *Msc thesis, Univ.of Stellenbosch, South Africa*.

KING, D.P.F. 1977 in press The distribution and abundance of eggs of the South West African pilchard (*Sardinops ocellata*) and anchovy (*Engraulis capensis*) I971-1972. *Fish. Bull. S.Afr.* *9*.

MARR, J.C. 1956 The "critical period" in the early life history of marine fishes. J. du Cons. 2I, (2) : I60-I69.

MATTHEWS, J.P. 1963 The pilchard of South West Africa (Sardinops ocellata). Sexual development, condition factor and reproduction. Investl Rep. mar. Res. Lab. S.W. Afr. IO ; 96 pp.

MEYER-ROCHOW, V.B. I972 Pelagic sciaenid eggs and early larval stages from off Luderitz Bay (South West Africa). Vie et Milieu, 23, fasc. I, ser.A: II-I9.

MURPHY, G.I. I96I Oceanography and variations in the Pacific sardine population. Rep. Calif. coop. oceanic Fish. Invest., 8, 55-64.

MURPHY, G.I. I966 Population biology of the Pacific sardine (Sardinops caerulea). Proc. Calif. Acad. Sci. 34, (I):88pp.

NAKAI, Z. I960 Changes in the populations and catches of the Far East sardine area. Proceedings of the world scientific meeting on the biology of sardines and related species. Food and Agricultural Organization of the United Nations, Rome, 3: 807-853.

NAKAI, Z, S. USAMI, S. HATTORI, ET AL I955 Progress report of the cooperative iwashi resources investigation, April I949- December I95I. Fish Agency Tokai Reg. Fish. Res. Lab. Tokyo, p. II6.

POREBSKI, J. AND E. BIELASZEWSKA I975 The occurrence of eggs and larvae of the frost fish Lepidopus caudatus (Euphrasen) in the waters of the S.W. African shelf, based on the investigation conducted from the R.V."Professor Siedlecki". ICSEAF, Coll. Sc. Pap. 2 :I07-II2.

PORE BSKI, J. AND A. KORONKIEWICZ	1975	Distribution of eggs and larvae of Merluccius spp. in south east African waters according to the materials collected by R.V. "Professor Siedlecki" in November-December I972 and January-February I973. ICSEAF. Coll. Sc. Pap. 2 : 92-IOI.
RAE, K.M.	1957	Relationship between wind, plankton distribution and haddock brood. Bull. Marine Ecology, 4 (38) : 247-269.
SETTE, O.E.	1943	Biology of the Atlantic mackerel (Scomber scombrus) of North America. Pt I. Early life history including the growth, drift and mortality of the egg and larval populations. Fish. Bull. U.S. Fish Wildl. Serv. 50,(38) : 149-237.
SETTE, O.E.	1969	A prespective of a multispecies fishery. Rep. Calif. oceanic Fish. Invest. I3 : 81-87.
STANDER, G.H.	1963	The pilchard of South West Africa. Temperature: Its annual cycles and relation to wind and spawning. Investl Rep.mar.Res.Lab. S.W.Afr. 9 : 57 pp.
STANDER, G.H. AND P.J. LE ROUX.	1968	Notes on fluctuations of the commercial catches of the South African pilchard (Sardinops ocellata) I950-I965. Investl. Rep. Div. Sea Fish S.Afr. 65 : I4 pp.

WALFORD, L.A. 1938 Effects of currents on the distribution and survival of eggs and larvae of haddock (Melanogrammus aeglefinus) on Georges Bank. Bull. U.S. Bur. Fish., 49 (29) : 73 pp.

WIBORG, K.F. 1957 Factors influencing the size of the year-classes in the Arcto-Norwegian tribe of cod. Fiskeridir. Skr. II, (8) : 5 - 22.

SEASONAL DISTRIBUTION OF TEMPERATURE AND SALINITY OFF SOUTH WEST AFRICA
1972 - 1974

by

MICHAEL J. O'TOOLE,
SEA FISHERIES BRANCH,
BEACH ROAD,
SEA POINT,
CAPE TOWN.

The seasonal distribution, migration, spawning behaviour and early life history of many pelagic fish are known to be closely related to oceanographic conditions. A know= ledge of the characteristics and movements of associated water masses is often useful in understanding the fluctuations in fish availability, migration and spawning patterns.

Apparent overexploitation of the South West African pilchard stocks induced the Sea Fisheries Branch to initiate a study into the distribution and ecology of ichthyoplankton in the upper 50 metre layer during 1972 - 1974. Surveys were operated on a monthly basis between latitudes 18°20'S and 24°40'S from August 1972 to March 1973 and from August 1973 to March/April 1974 (Fig. 1).

During the course of the routine ichthyoplankton collections, surface termperature, salinity and temperature to a depth of 50 m were recorded at each station.

The chief contributions to knowledge of the Benguela Current are the hydrological studies of Hart and Currie (1960) and Stander (1964). In these reports, the general features of the current i.e. water circulation, origin of water masses, upwelling and seasonal distribution of temperature, salinity and oxygen are described and discussed. Subsequent investigations based on various smaller-scale physical observations (duPlessis) 1967; Yelizariv, 1967; Filippov and Kolesnikov, 1971; Hobson, 1971; Visser _et al_, 1973; Wessels _et al_, 1974; Piechura and Wozniak, 1975) agree in general with the findings of Hart and Currie _op cit_.and Stander _op cit_. Most hydrological representations of the Benguela Current in the past, however, have been based on the results of stations on widely - scattered grids visited at several-month intervals. The results of the present study are therefore particularly useful in that eight consecutive months of intensive measure= ments were made over a two year period on a closely - spaced fixed grid. This allowed a more detailed examination and comparison of seasonal changes in hydrological events than was previously possible.

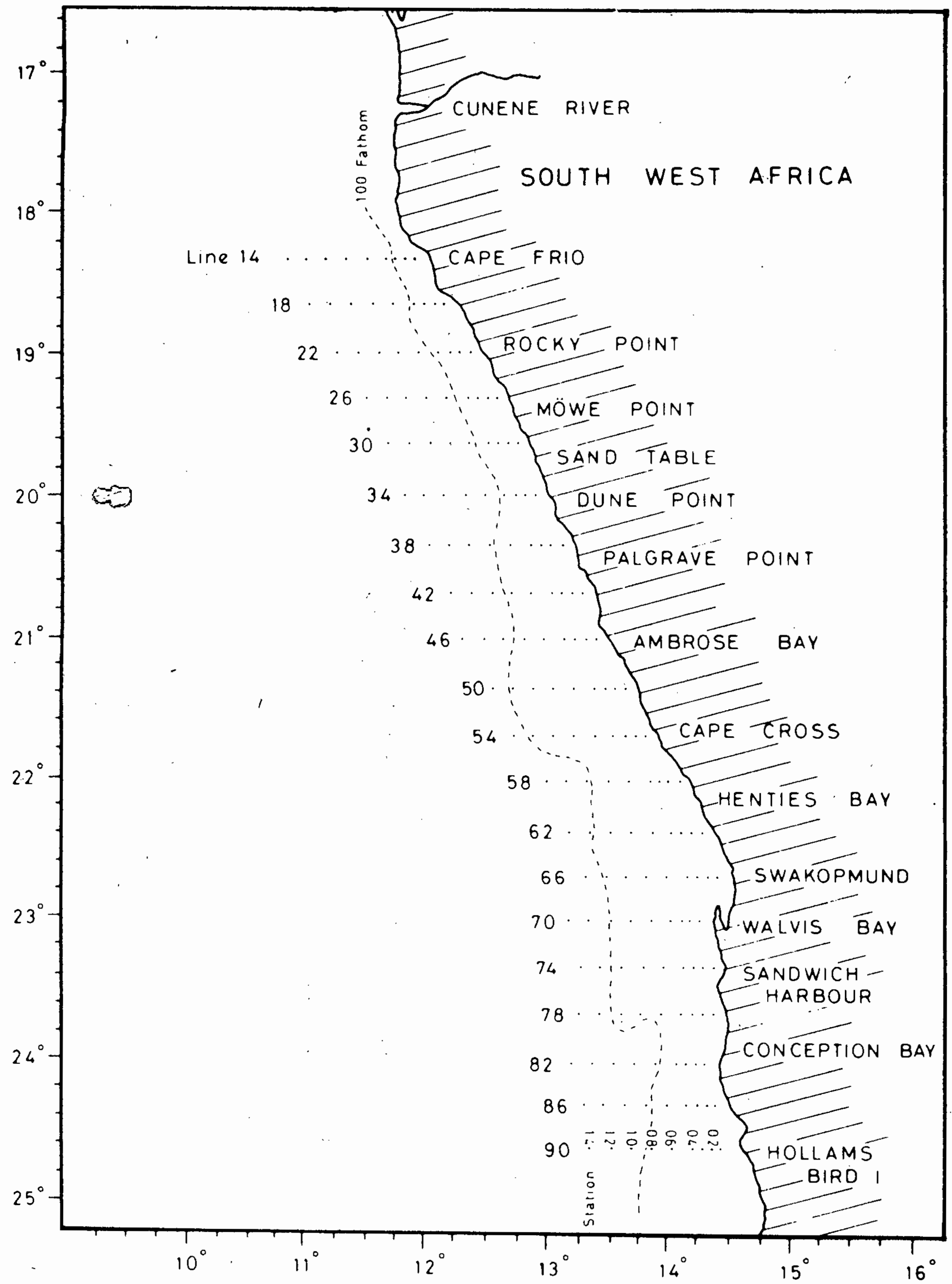


Fig. 1 Location of routine stations occupied during the SWAPELS cruises in 1972/73 and 1973/74

The purpose of this report is to broadly describe the basic seasonal changes in the hydrology of the region as a background to future papers relating the distribution of fish larvae to hydrological change. A detailed analysis of the mechanisms involved is not attempted.

GENERAL CHARACTERISTICS OF THE BENGUELA CURRENT SYSTEM OFF SOUTH WEST AFRICA.

Marked seasonal variation in temperature and salinity occurs off South West Africa both parameters being directly influenced by the intensity of upwelling activity along the coast. (Hart and Currie, 1960; Stander, 1964).

Upwelling is at its maximum during spring when the velocities of the South east Trade and South/South west coastal winds are more constant. This results in the widespread distribution of homogenous cold low salinity water. As summer approaches the South Atlantic high pressure system responsible for the S E trade winds moves south, causing a decrease in wind intensity. The coastal winds, which depend on the interaction between the South Atlantic high pressure zone and the continental pressure system, become more variable. Up=welling diminishes to reach a minimum during late summer and autumn. During this period, warm saline oceanic water invades the zone normally occupied by the cool coastal (Hart and Currie, 1960; Stander, 1964).

The stability of the water increases and strong temperature gradients form, particularly in the shallow coastal areas (du Plessis, 1967).

Towards the end of autumn the South Atlantic high pressure system moves north and the prevailing winds simultaneously increase in speed. Upwelling intensifies and the movement of cold upwelled coastal water seaward displaces the warm oceanic water offshore.

Temperature gradients become less pronounced and are eventually destroyed by the uplift of water near the coast. The phenomenon of upwelling is characteristic of several localities along the coast but is more intense in the area between Luderitz (26°25'S) and the Orange River (28°30'S), (Stander, 1964). A substantial reduction of the upwelling process occurs north of Walvis Bay (23°S).

Accounts of the general patterns of water movements have been given by Stander (1964), Yelizarov (1967), Filippov and Kolesnikov (1971) and Wessels et al (1974). Water normally flows along the coast in a northward direction particularly in the southern region. The flow is more pronounced during periods of active upwelling i.e. late winter and spring. Onshore movement and sometimes a complete reversal of flow occurs in lower latitudes (Hart and Currie, 1960; Stander, 1964; Wessels et al, 1974).

The movement of water off the northern coast of South West Africa is more complex and variable. Where the northward-flowing Benguela Current turns offshore to meet the southward-flowing Angola Current between latitudes 17° and 18° S, large eddies frequently form at the surface and in deeper layers (Stander, 1964; Yelizarov, 1967; Filippov and Kolensnikov, 1971). The flow of the Angola Current may vary from southwards inshore to northwards offshore or vice versa depending on whether the eddies are cyclonic or anticyclonic. Evidence of a subsurface counter current beneath the Benguela has been identified by Hart and Currie (1960), Stander, (1964), Yelizarov (1967) and Filippov and Kolesnikov (1971).

Another notable feature of the Benguela Current System is the presence of water of low oxygen content off the coast, particularly during summer months when conditons are relatively calm and little vertical mixing takes place. A detailed analysis of the distribution of oxygen is given by Stander (1964).

GEOGRAPHIC FEATURES.

The coastline of South West Africa runs in a N N W direction from the Orange River until at 18^{o}S it deflects north and then N N E into Angola. Much of the coast is characterized by a narrow belt of low-lying land and sand dunes. The land is arid and dominated by the Namib desert. Annual rainfall is low. Heavy coastal mists produced as a result of interaction of the cold Benguela Current and the warm desert air periodically enshroud the coastal areas giving a cool damp climate. The territory is bordered by two large rivers, the Cunene in the North and the Orange in the South. The catchment areas of these rivers are extensive in the interior but drainage to the sea is slight and usually confined to periods of heavy summer rains. At these times however, the rivers may discharge large volumes of flood water into the sea. A few smaller rivers, the Ugab, Swakop and Kuiseb are situated between the Cunene and the Orange but water from summer rains rarely reaches the Atlantic.

BOTTOM TOPOGRAPHY

The dominant feature of the bottom topography (Fig. 2) is a wide shelf bounded by the 200 m isobath extending some 90 km offshore between Cape Cross (21^{o}50') and Conception Bay (23^{o}50'). The shelf narrows north of Cape Cross tapering to within 24 km of the coast at Cape Frio (18^{o}20'S) South of Conception Bay, the shelf narrows but widens again towards Hollam's Bird Island (24^{o}40'S). The isobaths run approximately parallel to the coastline over much of the region. However, the comparatively gently slope of the sea floor changes suddenly between 18^{o} - 19^{o}S.

A sharp increase in depth occurs to the west of Cape Frio, where the Walvis Ridge joins the African continent. The shelf in this region slopes steeply from 300m to 3000 m over a short distance of 50 Km. Another fairly sharp

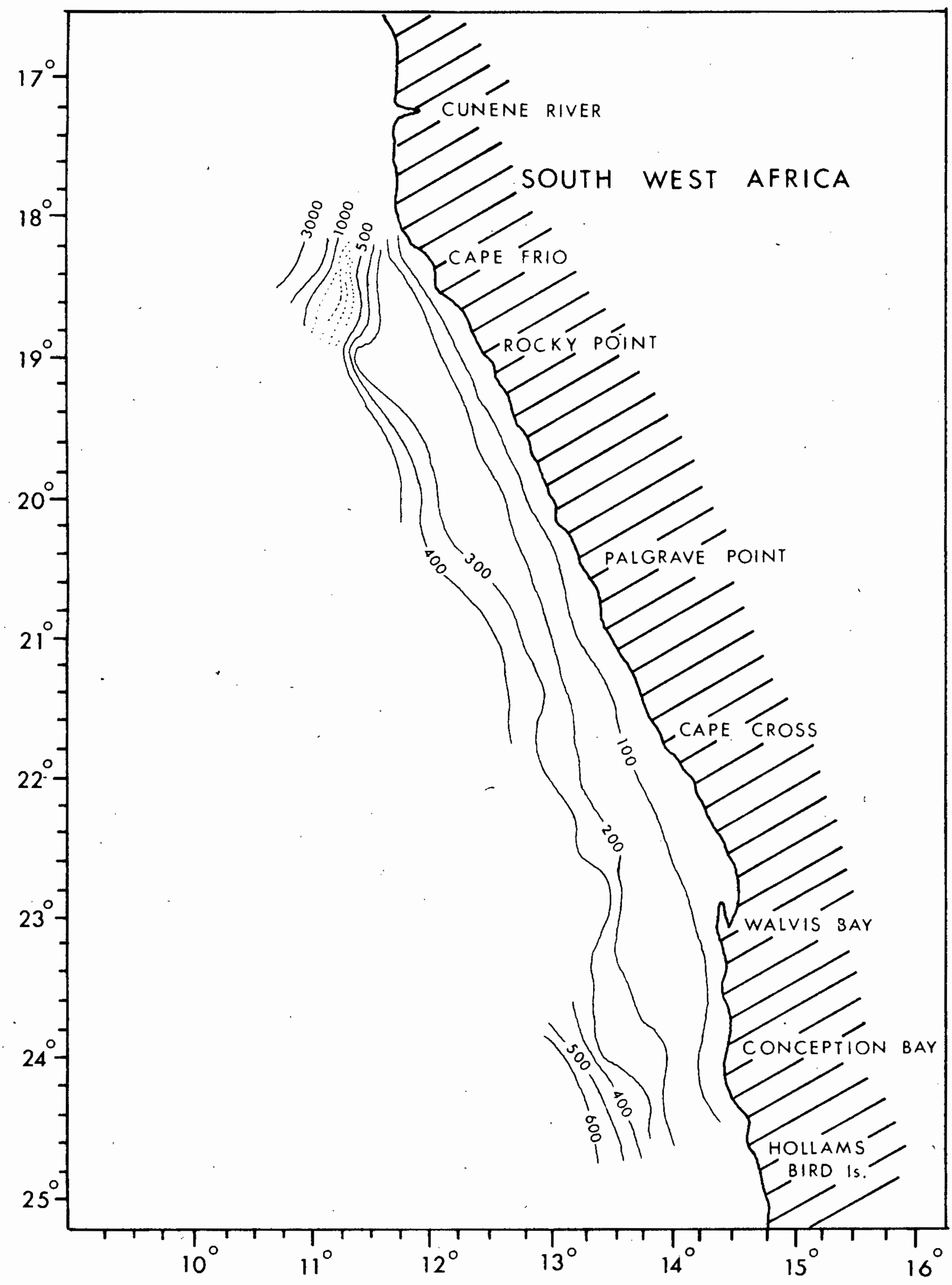


Fig. 2 Bottom topography of survey area
(isobaths in metres)

increase in depth occurs about 120 km west of Hollams Bird Island. A slight coastward deflection of the 300 m isobath is evident between Palgave Point ($20^{o}25$'S) and Walvis Bay.

STATION GRID

An area of approximately 82,000 sq.km between Cape Frio and Hollams Bird Island was selected for study. The samp= ling grid consisted of twenty parallel lines of stations running east-west, spaced about 32 km apart. Nine stations were located on each line, the four inshore stations at 8 km intervals and the outer five stations at 16 km intervals. The inshore station on each line was 8 km from the coast and the outer station approximately 117 km offshore.

The survey grid was initially designed to accommodate extra stations and additional lines between the existing ones, to allow for an expansion of the grid to the north, south or seaward of the research area. The design of the sampling grid is outlined in more detail by King and Robertson (1973). The original grid (line 14, 18, 22 etc) with stations (01, 02, 03, 04, 06, 08, 10, 12, 14) was adhered to throughout the surveys, except for the expansion of the grid to the north of the area in October 1973 to include lines 2, 6, and 10. The lines of stations were sampled from north to south on a continuous 24 hour basis by the Sea Fisheries Branch research vessels, R.S. Benguela or R.S. Sardinops.

Sampling operations commenced at the inshore station on line 14 i.e. 14-01 and progressed seaward until the last station (14-14) on the line had been occupied. The vessel then moved south to the outer station on the second line (18-14) and worked inshore along the line. The other lines of stations were occupied in a similar sequence until the entire grid had been surveyed. The grid usually took from 8 - 10 days to complete with approximately two lines of stations being occupied every twenty four hours. Some stations were omitted during certain months because of poor weather conditions or technical difficulties. The geographical position of each station, the mean station depth and the dates of each cruise are given by O'Toole (1976). The precise positions of a number of key coastal localities frequently referred to in the text are listed below.

GEOGRAPHIC NAMES	LATITUDE
Cape Frio	18°20'S
Rocky Point	19°00'S
Mowe Point	19°50'S
Palgrave Point	20°25'S
Cape Cross	21°50'S
Henties Bay	22°00'S
Swakopmund	22°50'S
Walvis Bay	23°00'S
Sandwich Harbour	23°25'S
Conception Bay	23°50'S
Hollams Bird Island	24°40'S

MATERIALS AND METHODS.

Surface temperature was measured to the nearest 0,1° C using a Crawford surface temperature bucket (Crawford, 1968). The bucket was trailed over the stern of the vessel for approximately 10 minutes at each station. A sample for salinity determination was taken and the chlorinity later estimated in the laboratory by an inductively coupled salinometer. In addition, a thermo/salinograph was operated throughout the cruise giving a reference picture of surface temperature and salinity. When the sampling operation was complete, a vertical bathythermograph dip was made to record sub-surface temperature in the upper 50 metres. No temperature/depth profiles were taken in February 1974 because of instrumentation difficulties but for all other months, the distribution of temperature and salinity were drawn at 1°C and 0,1 °/oo intervals. Stander (1964) showed that salinity generally does not fluctuate much between the surface and 50 m consequently the depth distribution of salinity was not monitored during the routine cruises. For the purpose of this report, monthly vertical temperature sections were made only along five lines i.e. Cape Frio (line 14), Palgrave Point (line 38), Cape Cross (line 54), Walvis Bay (line 70) and Hollams Bird Island (line 90).

RESULTS

Because of the general sequence of hydrological events were similar for both survey periods, surface and sub=surface observations are described in detail only for the first survey. A comparison of these findings is made with the results of the second survey emphasizing the more noticeable differences. The monthly distribution of temperature and salinity for Survey I are illustrated in figures 3 - 6. Those for Survey 2 are given in figures 7 - 10.

HYDROLOGICAL FEATURES DURING SURVEY I.

Late winter and Spring (August - November 1972)

In August, a belt of cool water (12° - 14°C) lay adjacent to the coast with warmer water present further offshore (Fig. 3A). The lowest temperature (12°C) occurred inshore south of Walvis Bay and highest (16°C) offshore west of Palgrave Point. Low salinity water (35,1 $^{\circ}/oo$ - 35,2 $^{\circ}/oo$) was found over much of the southern region but in the northern offshore area, a tongue of highly saline water (35,3$^{\circ}/oo$ - 35,9$^{\circ}/oo$) corresponding with the warmer 15° - 16°C water was present along the outer stations west of Palgrave Point (Fig. 4A). Intermediate salinity values of 35,2 $^{\circ}/oo$ to 35,3 $^{\circ}/oo$ were recorded over the rest of the area. Isolines in the north and south were orien=tated approximately parallel to the coast. However, in the central region off Walvis Bay, a deflection of the 14°C isotherm and the 35,2 $^{\circ}/oo$ - 35,3$^{\circ}/oo$ isohalines away from the coast indicated an offshore movement of water. Over much of the area, the vertical slopes of the isotherms (Fig. 5A) indicated the existence of a body of well-mixed isothermal water characteristic of strong upwelling. The warmest water (16°C) on the Palgrave Point line was present only as a shallow layer some 20 m deep. To the south, the vertical sections indicated that the warmer water was being pushed further offshore reaching maximum displacement at Walvis Bay. A small incursion of warm water from the south-west was apparent off Hollams Bird Island.

During September, a pronounced eastward movement of warm offshore water (15° - 16° C) occurred between Cape Cross and Walvis Bay and off Hollams Bird Island (Fig. 3B). The lowest temperatures were found inshore near Palgrave Point and just south of Walvis Bay. Surface salinities were somewhat lower in the north than in August (Fig. 4B). Upwelling was still occurring at Palgrave Point and south of Walvis Bay, apparently uninfluenced by the warm water intrusions between Cape Cross and Walvis Bay and off Hollams Bird Island. Figure 5B showed marked vertical sloping of the isotherms with little thermal stratification. The absence of active upwelling and the subsequent intrusions of oceanic water on the Cape Cross line and to a lesser extent on the Hollams Bird Island line had the effect of bending the isotherms towards the coast. Where this happened, the cooler 13°C coastal water sank to deeper layers and there was a tendency for weak thermoclines to form inshore in the upper 10 metres. The warm water intrusions were present as a shallow surface layer not exceeding 20 m in depth. In contrast, the upward slope of the isotherms on the Palgrave Point and Walvis Bay lines indicated that upwelling was intense at these localities especially off Walvis Bay where the 13°C isotherm was markedly displaced offshore.

Hydrological conditions in October showed little difference from the previous month. Warm water intrusions were more marked in the north than in the south especially with depth (Figs. 3C, 5C). A core of warm, highly saline water approached the coast from the north-west. Vertical temp= erature sections showed that upwelling was still occurring at the coast on the Palgrave Point line but had weakened off Walvis Bay compared with September (Fig. 5C). A significant increase in upwelling occurred on the Hollams Bird Island line resulting in the displacement of warm water offshore and a wider distribution of low salinity in the south. The depth of the warm water intrusion (16°C) ranged from 30 - 40 m but it was further offshore in the south.

The distribution of temperature in November indicated that warm water had moved closer to the coast in the north, up= welling having become reduced in the south (Fig. 3D). Surface salinity values were similar to those of October except that the 35,0 °/oo isohaline withdrew further south and an intrusion of high salinity water occurred corresponding with 18°C isotherm off Cape Cross (Fig. 4D). Vertical sections indicated that considerable stratification of the isotherms occurred over much of the area (Fig. 5D). Sharp thermoclines formed at depths of 15 - 20 metres particularly inshore in the northern region. Further south, thermoclines were not as marked and were least developed off Walvis Bay. Beneath the thermoclines, cool 13° - 14°C water was invariably present at depths of 10 - 15 metres.

At Cape Frio, 14°C water was only a few metres below the warmer 16°C surface water. The direction of surface isotherms and isohalines in the northern offshore area suggested an east to south-east movement of water towards the coast. Conditions during this month were typical of the end of spring and announced the onset of more stable conditions character= istic of the summer months.

Summer and early Autumn (December 1972 - March 1973)

In December, warm water extended further southwards so that all water north of Cape Cros was warmer than 19°C (Fig. 3E).

Surface salinities were highest in the north (35,6 $^{o}/_{oo}$) and became progressively lower further south, reaching 35,2 $^{o}/_{oo}$ at Palgrave Point (Fig. 4E). An increase in upwelling activity was evident at Hollams Bird Island. Thermal structures in the upper 50 metres (Fig 6A) showed that isotherms were more or less horizontally stratified in the north. Thermoclines were most marked at depths of 10 - 20 m inshore on the Palgrave Point and Cape Cross Lines. Further south, isotherms were more steeply inclined due to the uplift of cooler water at the coast associated with a slight renewal of upwelling activity. The distribution of surface isolines suggested a southerly movement of warm water from the north along the coast and a northerly flow of cooler water from the south.

During January, water was 2 - 3 degrees cooler over much of the northern area. A belt of relatively cold water (15^{o} 17^{o}C) with intermediate salinity values (35,2 $^{o}/_{oo}$ - 35,4 $^{o}/_{oo}$ lay adjacent to the coast (Figs. 3F and 4F). A reduction in upwelling occurred in the south compared with the previous month. The water off Cape Frio was well mixed and a sharp front separated the warmer offshore water from the cooler inshore water (Fig. 6B). The almost vertical orientation of isotherms with depth in this region suggested that renewed coastal upwelling between December and January pushed cold water offshore disrupting the relatively stable conditions found in December. Further south, the front weakened and warm water advanced inshore as a shallow surface layer 20 - 30 m deep overlying the cooler subsurface water. Thermocline formation was marked in the upper 20 m at inshore stations. In general, the surface temperature showed isotherms being almost linear and parallel to the coast. In the vertical temperature sections, an uplift of cool water occurred in the north and a corresponding downward movememt of cold water in the south.

In February, warm saline water invaded much of the region (Fig. 3G, 4G). Surface temperatures were 2^{o} - 3^{o} higher in the north and 3^{o} - 4^{o} higher in the south

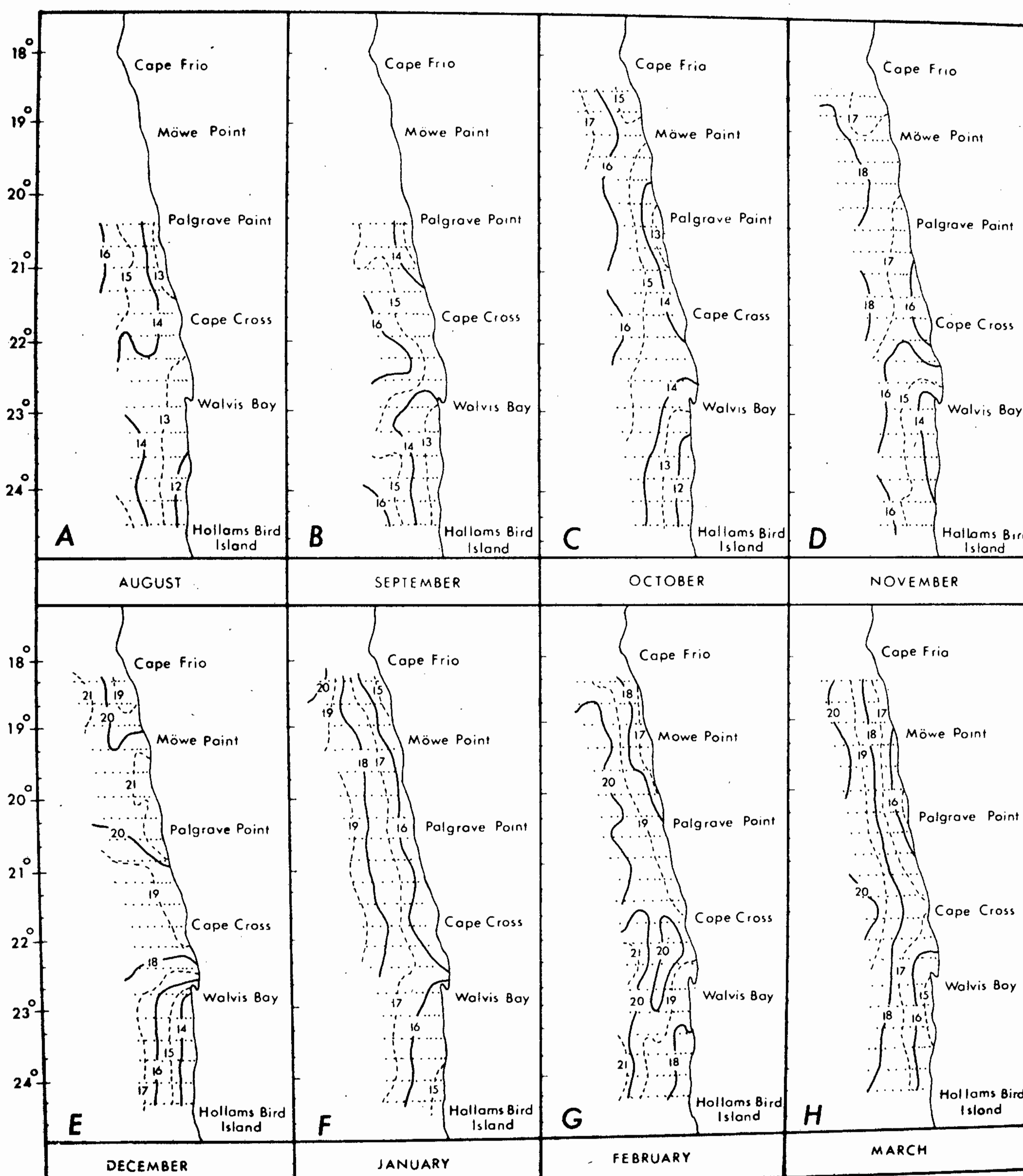


Fig. 3, A - H Horizontal distribution of surface temperature, August 1972 to March 1973

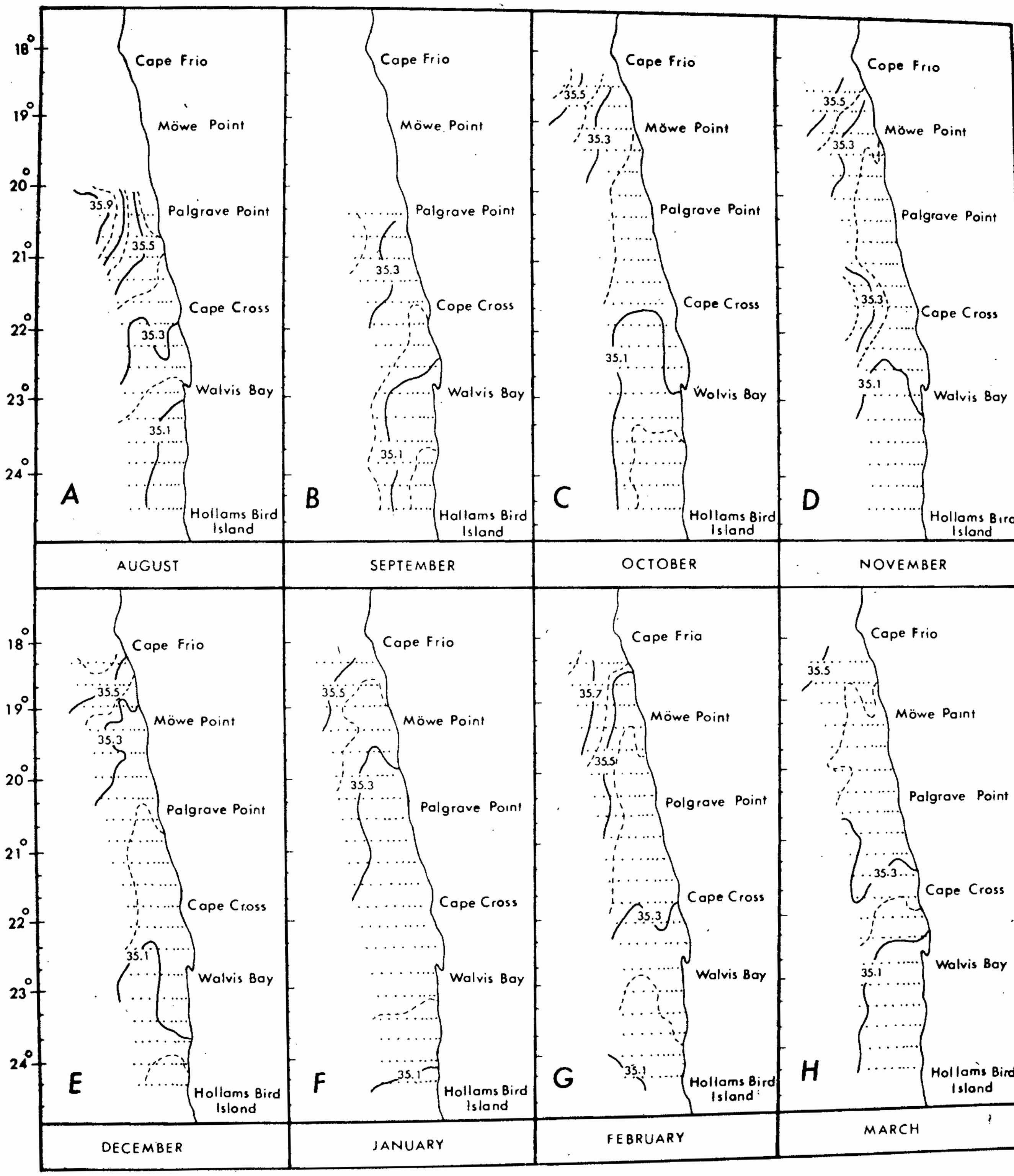


Fig. 4, A - H Horizontal distribution of surface salinity, August 1972 to March 1973

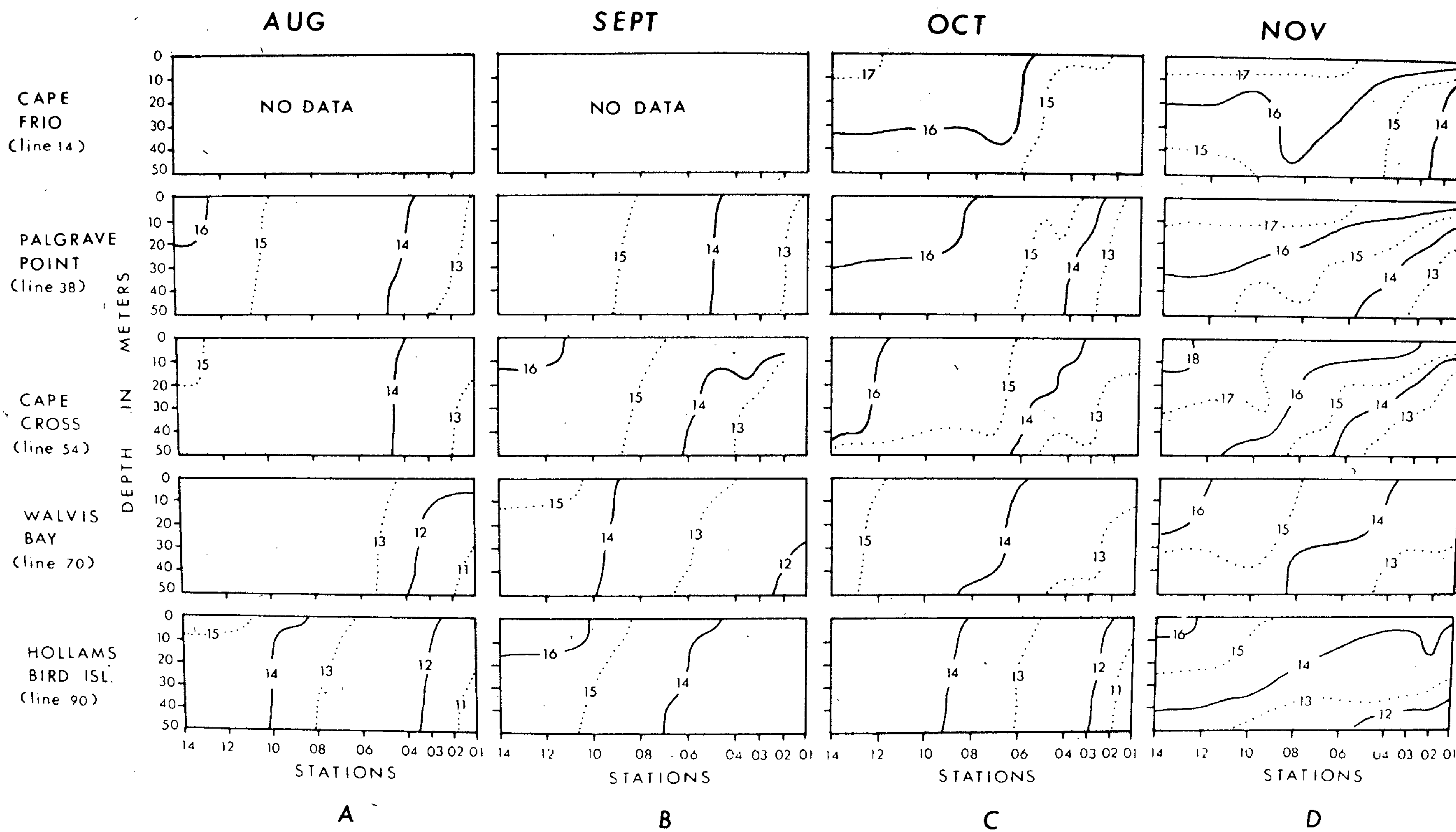


Fig. 5 A-D Vertical temperature profiles at five selected lines of stations, August to November 1972

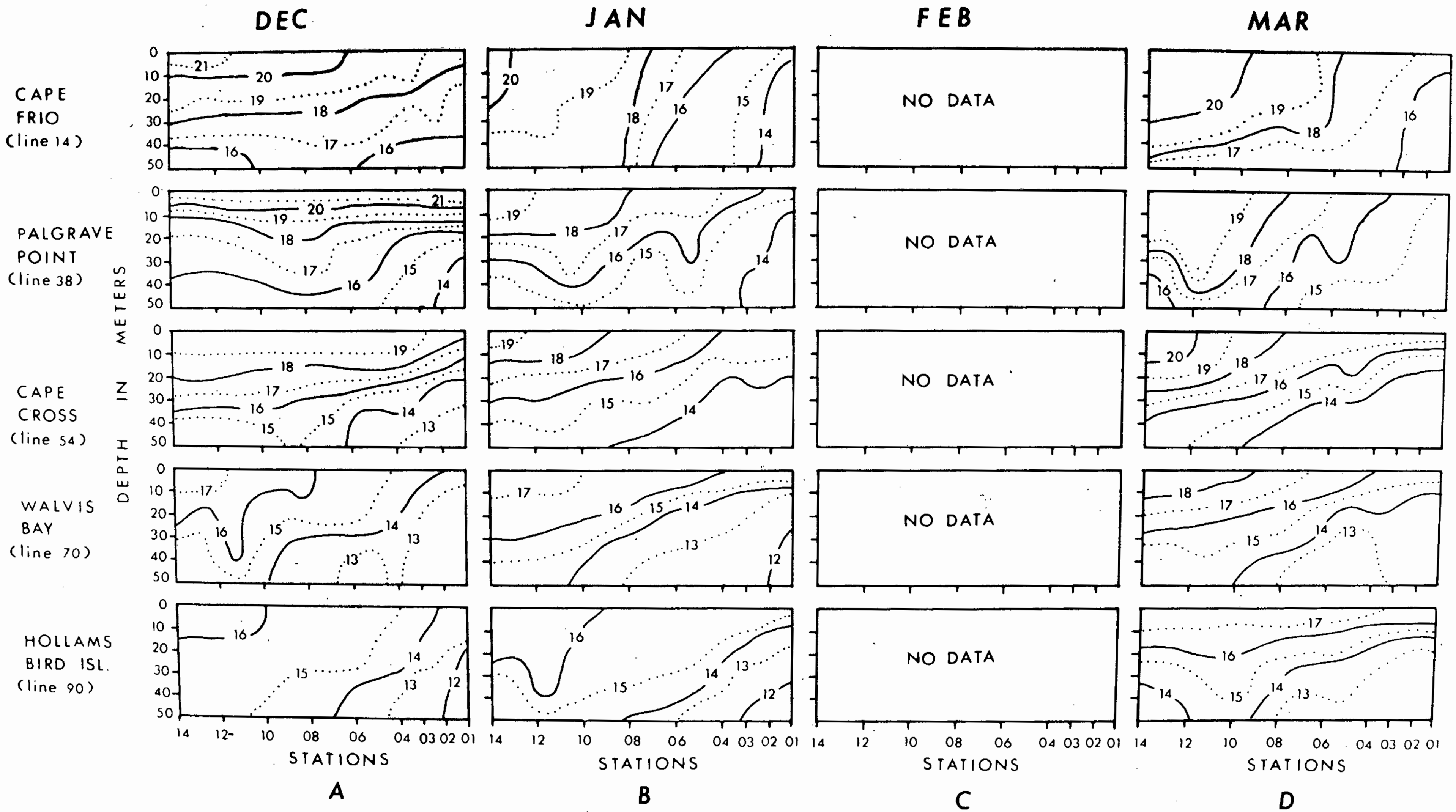


Fig. 6 A-D Vertical temperature profiles at five selected lines of stations, December 1972 to March 1973

compared with January. The distribution of salinity showed a southeasterly movement of high salinity water (35,3 ^{o}/oo - 35,5^{o}/oo) towards the coast from the north west. The oceanic front had been pushed further south and intensified in the region of Mowe Point. Although no vertical sections were taken during February, it was apparent from surface features that mixing was occurring associated with the front in the north, whereas more stable conditions prevailed in the south.

Surface temperatures in the north during March varied little from those of February (Fig. 3H). In the south, however, temperatures were 2-4^{o} colder. Renewed upwelling activity occurred south of Walvis Bay pushing the warmer offshore. The distribution of salinity showed a northward movement of 35,1 ^{o}/oo isohaline and a corresponding withdrawal of high salinity water (35,5^{o}/oo) to the extreme northwest (Fig 4H). Intermediate salinites were found over much of the area north of Cape Cross. The oceanic front was still well defined between Cape Frio and Palgrave Point. Vertical sections across the frontal system showed that water temp= erature was fairly uniform with depth particularly near the coast (Fig. 6D). However, thermal stratification occurred on the oceanic side of the front at depths of 20 - 40 metres. The front became less pronounced further south and moved offshore. Compared with the northern region, conditions appeared to be relatively stable in the south. Marked temperature gradients occurred especially inshore at depths of 10 - 20 metres. A slight uplift of cooler water at Walvis Bay suggested an increase in upwelling activity.

HYDROLOGICAL FEATURES DURING SURVEY 2.

The general cycle of events were basically similar to the observations during Survey 1. However, the timing of water movement and the intensity of upwelling showed marked variations. The distribution of temperature and salinity is given in figures 7 to 10.

Late winter and spring (August - November 1973)

In August and September, cold low salinity water occurred over much of the area, but was particularly noticeable south of Walvis Bay (Figs. 7A, B, 8A, B). Warmer more saline water was present offshore further north. Temperature sections showed marked upward sloping of the isotherms indicative to active upwelling. (Fig. 9A, B). Warm water intrusions were not as pronounced during these months as during the same months in 1972.

Upwelling weakened during October 1973 and warmer more saline water moved inshore (Fig. 7C, 8C). The movement shorewards of the 16°C isotherm was most prominent between Cape Cross and Hollams Bird Island. The influx of warm water tended to stabilize conditions and temperature gradients were well established at depths of 10 - 15 m inshore (Fig. 9C) In the north, conditions were less stable and little thermal stratification was evident. Higher surface temperatures and well developed thermoclines in the south indicated that upwelling appeared to have declined a month earlier in 1973 than in 1972. In contrast, upwelling was more evident at Cape Frio in 1973 than in 1972.

The 16°C isotherm advanced further inshore in November reaching the coast south of Walvis Bay (Fig 7D). Considerable mixing of water masses occurred in the north as seen from the upward slope of the isotherms (Fig. 9D). A deep mass of 16° - 17° C water pushed the oceanic front towards the coast and high salinities (35,3 ‰ - 35,5 ‰) were associated with this warm water intrusion (Fig. 8D). Further south, conditions were essentially similar to the month of October. The front moved offshore and stable conditions with well defined thermoclines were found. In general, the uplift of water was stronger and thermal stratification more pronounced in the north than in November 1973.

Summer to mid autumn (December 1973 March/April 1974)

Warm saline water advanced further inshore in December (Figs. 7E, 8E). The intrusion was particularly strong between Palgrave Point and Cape Cross where the 18°C isotherm reached the coast. Thermal structures in the upper 50 m layer showed that the front was still well established off Cape Frio (Fig. 10A). Southward from Cape Frio the front weakened and warm saline water pushed coastward overlying the cooler subsurface water. Strong thermoclines formed near the coast at depths of 10 - 15 metres. Offshore on the Palgrave Point and Cape Cross lines, marked oscillations of isotherms occurred at depths of 20 - 30 metres. These upthrusts of cooler bottom water and the sinking of warmer subsurface water possible re= presented cyclonic and anticyclonic eddies formed by the interaction of different water masses. Thermoclines were well-developed on either side of these disturbances. In the north, temperatures were 2 - 3°C lower, thermoclines less well established and conditions generally more unstable than in 1972. The hydrology in the south, however, remained basically similar to those found during December 1972.

In January and February 1974, warm oceanic water (19°-20°) moved further inshore from the west and northwest (Figs. 7F, G). An influx of high-salinity water (35,3°/oo - 35,8°/oo) associated with the warm water intrusion was particularly noticeable in the north during February (Fig. 8G). The water was strongly stratified over most of the region (Fig. 10B) and thermoclines were well-developed, especially inshore at depths of 10-15 metres. Hydrological conditions were generally more stable than during January 1973.

Although no vertical sections are available during February 1973 for comparison with thermal profiles of February 1974, the surface features of both months showed similar conditions.

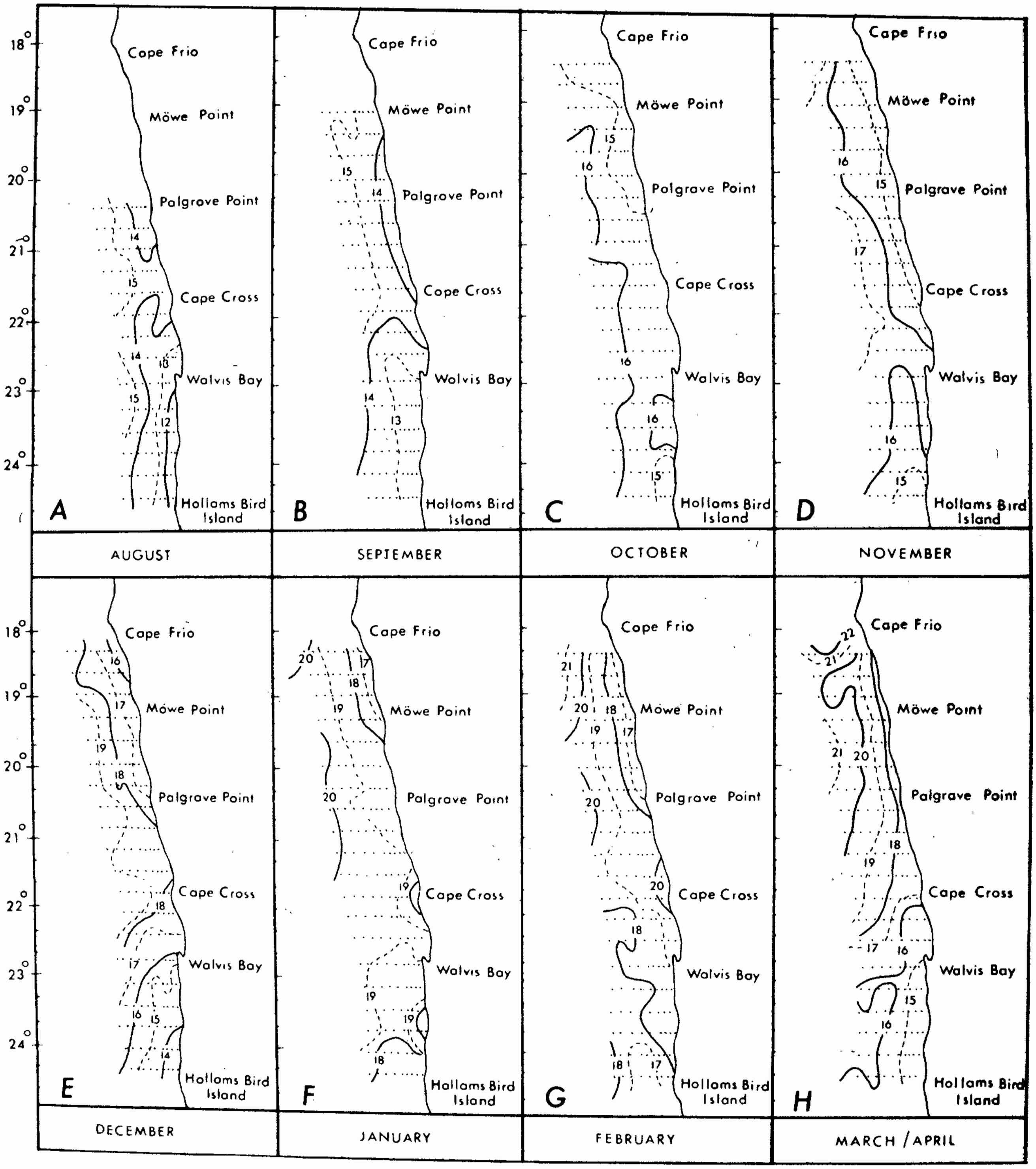


Fig. 7 A - H Horizontal distribution of surface temperature, August 1973 to March / April 1974

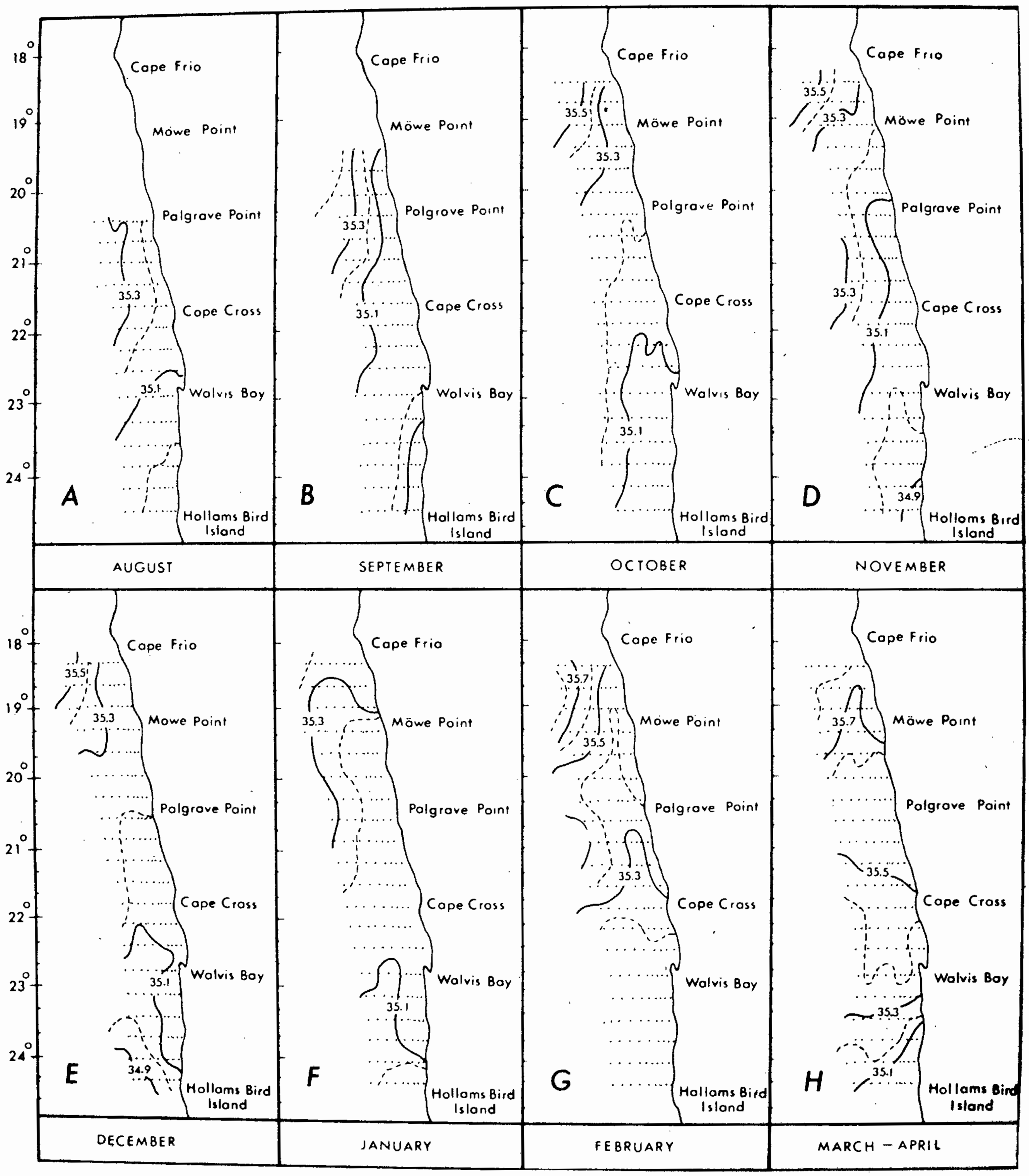


Fig. 8 A - H Horizontal distribution of surface salinity, August 1973 to March / April 1974

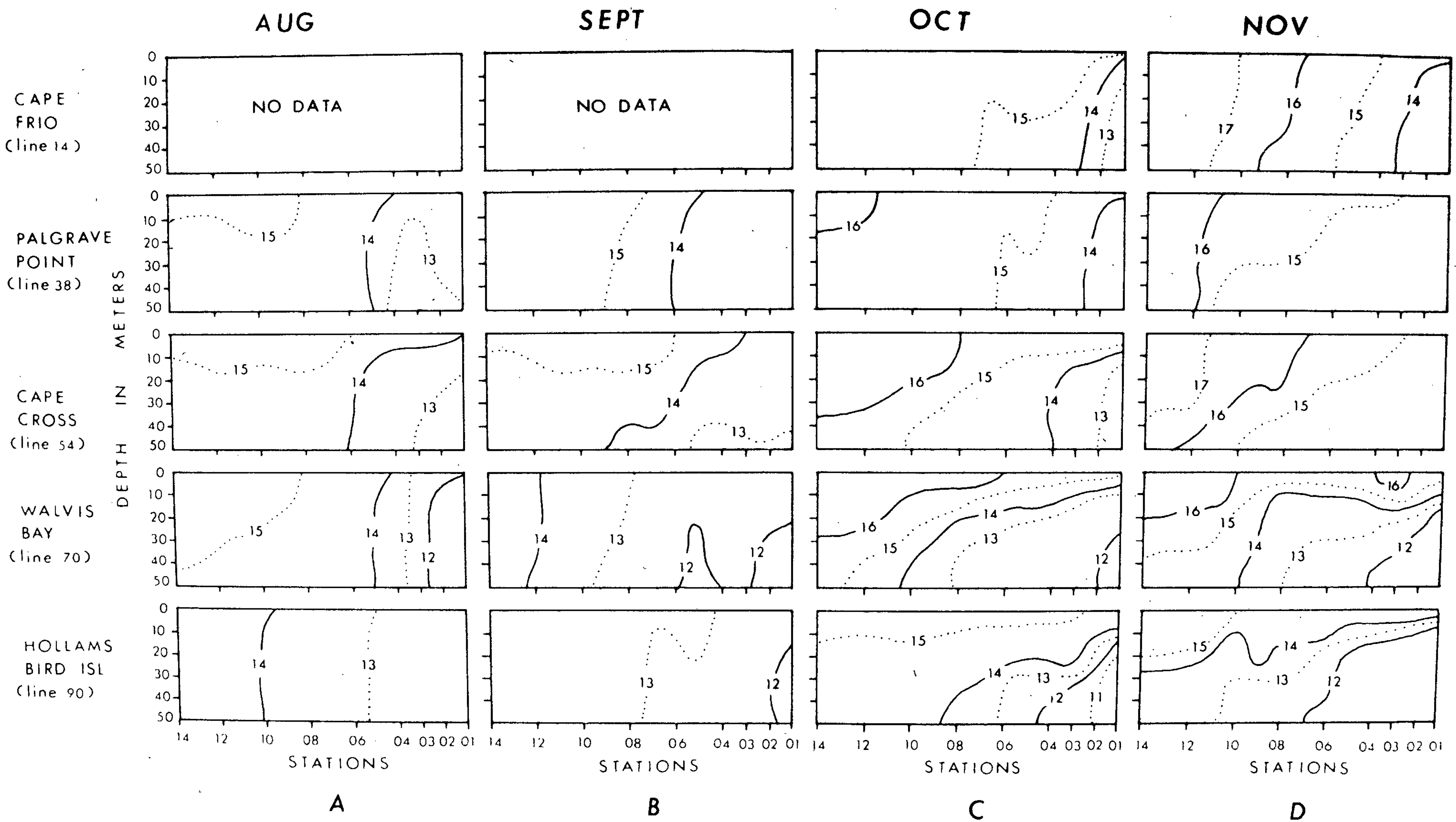


Fig. 9 A - D Vertical temperature profiles at five selected lines of stations, August to November 1973

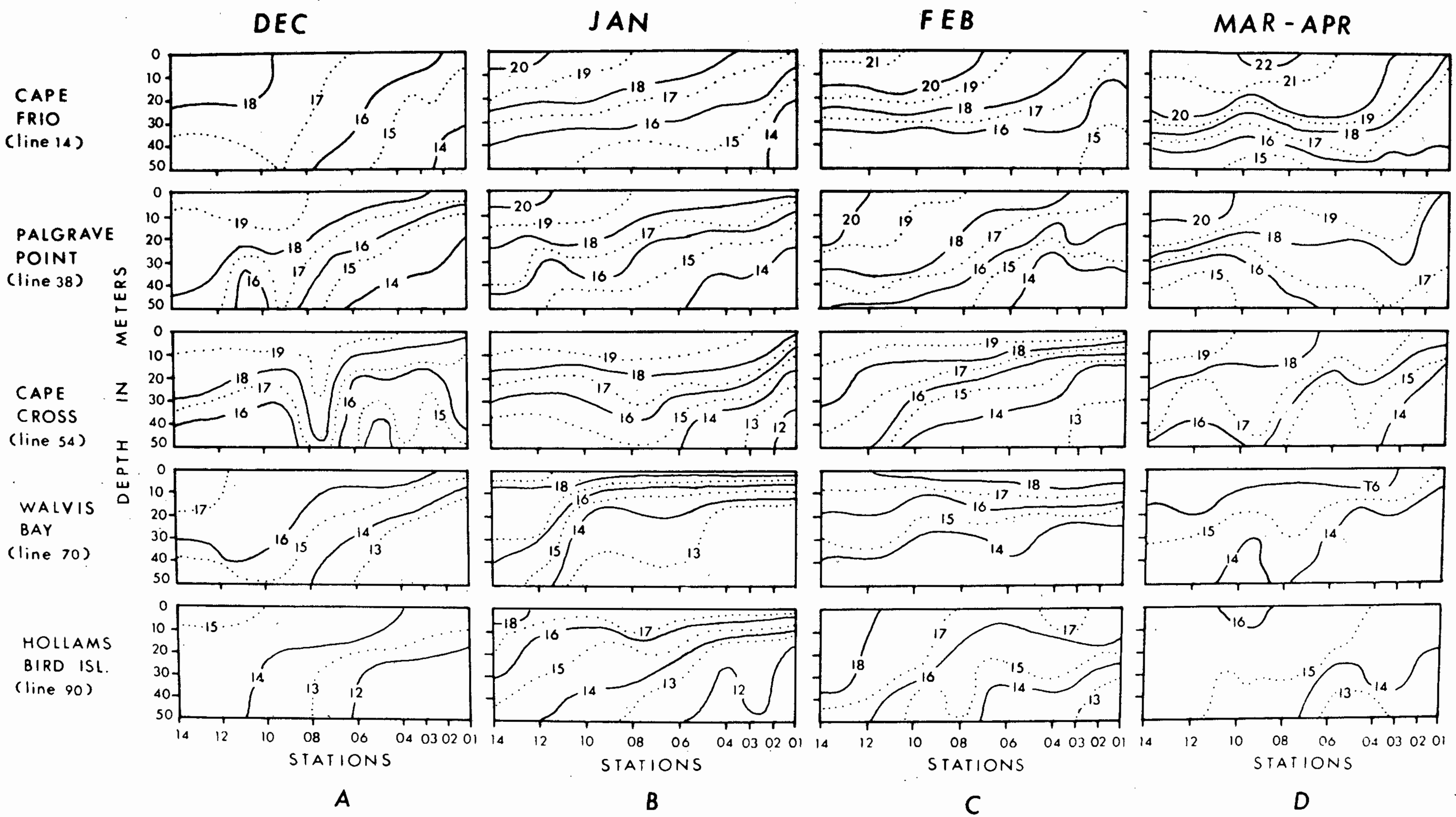


Fig. 10 A - D Vertical temperature profiles at five selected lines of stations, December 1973 to March / April 1974

During March/April, further incursions of warm saline water occurred from the west and north west (Fig. 7H, 8H). A core of very warm highly saline water with temperature of 20° - $22^{\circ}C$ and salinities of $35,7^{\circ}/oo$ - $35,9^{\circ}/oo$ advanced southwards from Angola. The temperature profile at Cape Frio (Fig. 10D) showed a deep layer of warm water over much of the section with sharp temperature gradients at depths of 20 - 30 meters. The upward slope of the isotherms near the coast indicated a certain amount of vertical water movement. At Palgrave Point, there was an upthrust of cooler water offshore and a corresponding sinking of warmer water inshore. Further south, marked oscillations of the isotherms and the absence of the well-defined thermoclines characteristic of the previous month indicated that mixing was more widespread. There was evidence of a slight increase in upwelling activity at Hollams Bird Island. In contrast to March 1973, hydrological conditions were more stable at Cape Frio and Palgrave Point, but, uplifting of subsurface water and mixing was more pronounced in the south. The higher surface salinities encountered in the south during March/April 1974 could indicate a more southerly displacement of the intermixing zone between the Angola and Benguela Current.

DISCUSSION

The gross seasonal movement of water masses and the distribution of surface temperature and salinity appeared to be consistent for both surveys. The findings in general agreed with those outlined by Hart and Currie (1960) and Stander (1964) summarized in the introductory review. However, a closer examination of the hydrological features showed that considerable variations occurred in the timing of seasonal events. The zones of upwelling were subject to monthly change both in location and intensity. For example, strong spring upwelling ceased a month earlier in the south during October 1973 than in October 1972. In contrast, upwelling persisted in the north until

December 1973, but in 1972, upwelling ceased in November (Figs 6A, 10D). During survey 1, the oceanic front was weaker and developed two months earlier, in November (Fig. 9D). It is also significant that when upwelling occurred in the south, warm water invariably advanced towards the coast in the north. Conversely, if cooler water upwelled in the north, an influx of warmer oceanic water resulted in the south. When upwelling occurred at two locations simultaneously, as in September 1972 (Fig. 3B), warm water was drawn inshore between the two centres to replace the upwelled water. Regional oscillations between upwelling and warm water intrusions appeared con= sistently in both horizontal and vertical sections.

Currie (1953) and Stander(1964) noted that two distinct surface water masses with relatively sharp boundaries, occurred off the South West African coast. The surface water inshore was cold with salinities of 34,9^{0}/oo - 35,1^{0}/oo and the offshore water was warm with salinities greater than 35,2^{0}/oo. A certain amount of mixing between the two water masses was suggested. In this investigation, surface termperature and salinity patterns showed the existence of three fairly distinct bodies of surface water.

1.

Cold low salinity surface water characteristic of upwelled or recently upwelled water occurred mainly in the south= ern region. In spring, surface temperatures ranged from 12^{0} - 16^{0}C and in Summer they varied from 14^{0} - 18^{0}C. Salinities were invariably low (34,9^{0}/oo - 35,1^{0}/oo.

In January 1973, exceptionally high surface temperatures (19^{0} - 20$^{0C)}$ and low salinities (35,1^{0}/oo - 35,2^{0}/oo were encountered inshore south of Walvis Bay (Fig. 7F). However, the vertical termperature section at Walvis Bay (Fig. 10B) showed that cooler water 13^{0} - 15^{0} C was present a few metres below the surface. The high surface temperature in the south during this month could have been caused by increased solar radiation warming the surface layers.

2.

In the north-west sector of the research area off Cape Frio, a warm highly saline water mass, periodically advanced towards the south-east and retreated to the north-west. The water had temperature and salinity properties of 17° - 22° C and $35{,}5^{\circ}/oo$ - $35{,}9^{\circ}/oo$. The incursions were most pronounced during summer months and its north/south displacement appeared to be related to the intensity of upwelling in the south (Figs. 3F,G, 4F,G).

3.

The remaining body of surface water had intermediate temperature and salinity properties ranging from approximately 16° - 20°C and $35{,}2^{\circ}/oo$ - $35{,}5^{\circ}/oo$. The water mass usually advanced towards the coast from the west between 19° and 22°S. The surface termperature and salinity characteristics suggest that the water could be South Atlantic surface water. These intermediate properties could also result from mixing between the cold Benguela Current from the south and the warmer Angola Current from the north.

Although intrusions of this surface water occurred during spring months (Figs. 3B, 7C, D), the greatest inshore movement took place in summer (Figs, 3E,F, 7E,F). Again, the degree of movement inshore was related to the intensity of upwelling near the coast.

To summarize, the general water movements off the coast consisted of a rather complex series of advances and withdrawals by three water masses with a possible mixing at the boundaries. Off Cape Frio, warm highly-saline water was present offshore in spring, but advanced in a south/south-easterly direction in summer. In spring, oceanic water with intermediate properities lay offshore over much of the northern area, but pushed towards the coast during summer. In the south, Benguela Current water advanced northward in spring and retreated towards the south in summer. Because of the general uniformity in bottom topography it was difficult to relate the movement of water to any noticeable feature on the sea floor. However, it was noteworthy that off Cape Frio, the warm saline oceanic water intruded over the region where the continental shelf sloped steeply. Furthermore, the orientation of surface isolines in the north-west sector, particularly the isohalines, were remarkably similar to those of the isobaths (Figs 1, 4, C-H,8,C-H). In the south, a similar situation was observed offshore between Conception Bay and Hollams Bird Island, although not as pronounced as at Cape Frio. In this region, periodic intrusions of offshore water took place in a north easterly direction over an area where a significant increase in depth occurred (Figs. 1, 3,AB, 4A,B, 8E).

Cyclonic and anticyclonic eddies were prominent features during the summer months, particularly off Palgrave Point and Cape Cross. (Figs. 6B,D, 10A).

It can be concluded that the localized short term effects of upwelling and mixing, govern to a large extent, the thermal structures in the upper 50 m layer. The seasonal intrusions and withdrawals of offshore water are in turn apparently related to the dynamics of upwelling and the intensity of the interaction between the northward-flowing Benguela Current and the southward-flowing Angola Current.

Although it is not known how much variation in temperature occurred between cruises, the overall seasonal pattern suggested a gradual thermal change rather than the often extremely rapid and short term variations characteristic of the Cape upwelling system. (W.R.H. Andrews, Sea Fisheries Branch. pers comm.)

The results of the investigation show the need for further studies on the mechanisms and dynamics responsible for the gross seasonal fluctuations in hydrological conditions. Regular systematic temperature, salinity and current measurements throughout the water column, particularly off Cape Frio, and in the upwelling area south of Walvis Bay would contribute greatly to the oceanography of the region.

LITERATURE CITED

CRAWFORD, A.B., 1968 - Sea surface termperature bucket. Department of Transport, Weather Bureau. Youngsfield, South Africa.

CURRIE, R.I. 1953 - Upwelling in the Benguela Current. Nature, Lond. 171, (4351): 497 - 500.

DU PLESSIS, E., 1967 - Seasonal occurrence of thermoclines off Walvis Bay, South West Africa, 1959 - 1965. Investl Rep. mar. Res. Lab. S.W. Afr. 13: 28 pp.

FILLIPPOV, E.A. and G.I. KOLESNIKOV, 1971 - On the origin of the southern components in the Benguela Current System. Atlantic Ocean Fisheries Research, Proceedings. 23, Kaliningrad; 42 - 49.

HART, T.J. and R.I. CURRIE, 1960 - The Benguela Current. "Discovery" Rep. 31: 123 - 298.

HOBSON, L.A., 1971 - Relationships between particualte organic carbon and micro-organisms in upwelled areas of South West Africa. Investigación pesq. 35 (1): 195 - 208.

KING, D.P.F. and A.A. ROBERTSON, 1973 - Methods of pelagic fish egg and larval research off South West Africa. S. Afr. Shipp. News Fish. Ind. Rev. 28, (5): 57 - 61.

O'TOOLE, M.J., 1976 - Incidental collections of small and juvenile fishes from egg and larval surveys off South West Africa (1972 - 1974). Fish. Bull. S. Afr. 8: 23 - 33.

PIECHURA, J. and S. WOZNIAK, 1975 - Environmental research during the first trip of the Polish research vessel. "Professor Siedlecki". ICSEAF Collection of Scientific Papers, 2: 152 - 161.

STANDER, G.H., 1964 - The Benguela Current off South West Africa. Investl Rep. mar. Res. Lab. S.W. Afr. 12: 143 pp.

VISSER, G.A., KRUGER, I., COETZEE, D.J. and CRAM, D.L. 1973 - The environment. Cape Cross Programme, Phase III, Sea Fisheries Branch, South Africa, 9pp.

WESSELS, G.F. and D.J. COETZEE, 1974 - The environment. Cape Cross Programme, Phase IV, Sea Fisheries Branch, South Africa, 8pp.

YELIZAROV, A.A., 1967 - Some results of oceanic research in fisheries areas off South=west Africa. Oceanology, 7, (3): 344 - 347.

INVESTIGATIONS INTO THE EARLY LIFE HISTORY OF THE SOUTH WEST AFRICAN PILCHARD _SARDINOPS OCELLATA_ PAPPE

B Y

MICHAEL J.O'TOOLE,
SEA FISHERIES BRANCH,
BEACH ROAD,
SEA POINT,
CAPE TOWN.

INTRODUCTION

The pilchard, Sardinops ocellata Pappe, is widely distributed around the coast of Southern Africa, from Baia dos Tigres in Angola to Durban (Natal) on the east coast of South Africa (Davies 1956). The species is the basis of an important pelagic fishing industry, particularly in South West African waters where large shoals are heavily exploited by local fishing vessels from Walvis Bay.

Other smaller fishing centres are located in southern Angola (Mossamedes) and off the west coast of South Africa (St. Helena Bay). In recent years, landings of pilchard at Walvis Bay have fluctuated considerably, increasing from 637,675 metric tons in 1964 to 1,5 million tons in 1968, then decreasing sharply to 450,000 tons in 1970 (Schülein 1971). In 1974 the catch amounted to 561,558 metric tons.

Extensive research has been carried out on many aspects of the general biology of the pilchard. Davies (1954, 1956, 1957) studied the biology, sexual maturity and reproduction of the South African pilchard. The age composition and growth of the South West African pilchard was investigated by Nawratil (1961, 1962). Matthews (1963) studied the sexual development, condition factor and reproduction of the pilchard from the Walvis Bay fishing grounds. The relation between temperature and spawning was analysed by Stander (1963) and Le Clus (1976) reported on the fecundity of the South West African pilchard.

The stocks from South West Africa and South Africa are generally considered to be separate entities. Stander and Le Roux (1968) found no evidence of large scale movement between the two regions and tagging work by Newman (1970) showed the independent nature of the two stocks, although a very slight southward migration was suggested by some returns. A more recent study by Thompson and Mostert (1974) concluded that the pilchard population around the coast of Southern Africa consisted of several stocks breeding in isolation.

Research work on the early life history of the South West African pilchard has been mainly concerned with the seasonality and distribution of eggs (Matthews I963, Stander I963, King I977 in press). However, other aspects, such as, egg development in relation to temperature, salinity and oxygen have recently been studied by King (I975). In contrast to the egg, there is little known about the distribution and ecology of the larval stages.

The South West African Pelagic Egg and Larval Survey (SWAPELS) was carried out between August I972 and March I973 and from August I973 to March/April I974. The research area and the approximate location of stations are shown on Figure 1. Additional information on the depth and precise positions of the stations is given by O'Toole (I976). Pilchard larvae were common in the plankton collections, constituting I2,~~8~~5 percent of all species taken on the two-year survey and ranking second in order of abundance. The larvae comprised 3,75 percent and I7,48 percent of all fish larvae collected on Survey 1 and Survey 2 respectively. Some preliminary findings on egg distribution and seasonality of pilchard eggs taken during the same surveys have already been outlined by King (I975). This report is mainly concerned with the larval stages and deals with such aspects as seasonal distribution, abundance, diurnal variation in catches, hydrological relationships, growth and dispersal. Some information is also given on the vertical distribution of the eggs based on a series of separate observations conducted in I975.

M A T E R I A L   A N D   M E T H O D S

Collecting Gear

Routine ichthyoplankton samples were collected with cylindro-conical paired Brown-Mc Gowan bongo nets similar to that described by Posgay <u>et al</u> (I968). Each unit had a mouth diameter of 57 cm, giving a convenient mouth area (0,5m^2) for calculating the volume of water filtered. During Survey I, the frames were equipped with 0,940 mm monofilament Nitex

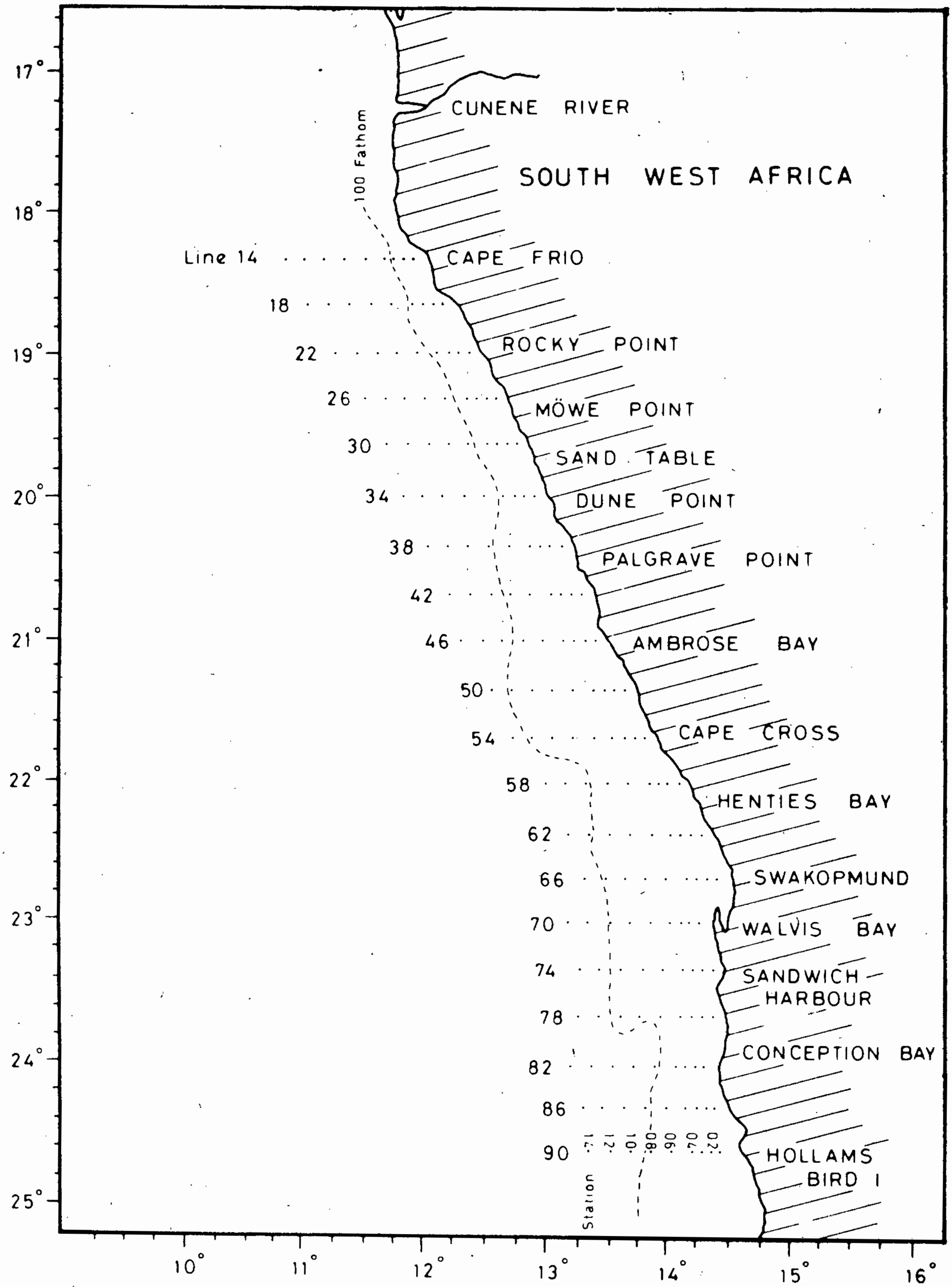


Fig. 1 Location of routine stations occupied during the SWAPELS cruises in 1972/73 and 1973/74

nets, but on Survey 2, 0,940 mm mesh was used on the left unit and 0,500 mm mesh on the right unit.

A digital flowmeter+ was suspended in the mouth of each sampler to measure the volume of water filtered during the tow.

A detailed description and illustration of the bongo assemblage used in this investigation is given by King and Robertson (I973a). A bathykymograph was attached to the towing cable immediately above the sampling unit to measure the time-depth profile of each haul. The temperature profile within the sampled depth was measured with a bathythermograph suspended beneath the bongo unit. The net assemblage was submerged to the required depth with a 45 kg weight attached at the end of a wire of IO mm diameter cross-section.

A smaller bongo unit of similar construction, but equipped with 0,300 mm mesh was used at selected stations together with the larger sampler. This net was designed to collect anchovy eggs but proved to be only of limited value because of the small mouth area and the frequent clogging of the fine meshes with phytoplankton. The results of this survey are based on the catches from the larger 57 cm bongo nets.

Sampling Procedure

It is a known fact that the eggs and larvae of mainly marine fish lie in the upper 50 metres of the water column,(Silliman I943, Sette I943, Ahlstrom I959, Miller et al I963, Ida I972), thus, only this surface layer was sampled.

A double oblique tow to a depth of 50 m was made at each station except where the depth at inshore stations was less than 50 m. Hauls were then taken to within a few metres of the bottom. The net assemblage was lowered over the stern of the research vessel and seventy-five metres of cable was paid out at a rate of 0,3 m/sec. Thirty seconds was allowed for stabilization before the gear was hauled to the surface at the same rate.

+ General Oceanics Inc, San Diego, Calif.

Throughout the tow, the wire angle was maintained at about 45° and the ship's speed at approximately 2 knots. The duration of each haul was timed with a stop watch and averaged between eight and ten minutes. Samples of sea water were collected at all stations for surface temperature and salinity measurements. An account of the methods used in the collection and analysis of physical parameters is given by O'Toole (I977a).

Treatment of Samples.

The nets were washed after each tow to remove any plankton adhering to the meshes. Samples were transferred to a IO litre bucket containing seawater where large zooplankters, such as medusae and salps, were washed and removed. The remaining plankton was concentrated by filtering through a 0,500 mm mesh sieve and transferred to storage jars. Plankton samples were topped up with seawater, labelled and preserved with IO% buffered formalin. In the laboratory fish eggs and larvae were extracted from each sample with the aid of a stereo microscope and pilchard and anchovy eggs separated from other fish eggs and counted. Where the number of eggs in the sample was excessively large, a Folsom Splitter (Mc Ewen _et al_ I954) was used to obtain a subsample. All fish larvae were counted.

Larvae of the commercially important species were identified and measured to the nearest millimetre, using a binocular microscope equipped with an ocular micrometer. Larger larvae and juveniles were usually measured on a finely-graduated millimetre rule with the unaided eye. During preservation in formalin, fish larvae are known to shrink about 10-12 percent in length (Blaxter I968), but this was not corrected for during length measurements. Since the larvae were preserved and measured in the same way during each month, the lengths are assumed to be comparable.

Quantification of Samples.

In order to quantify the results, the number of eggs and larvae collected at each station was standardized to the number under IO m^2 of sea surface. Such a procedure is usually recommended to obtain a meaningful integration over an area. The method for standardization is given in greater detail by Kramer <u>et al</u> (I972), but it is briefly summarized below.

The actual catch for each unit of the bongo net was multiplied by a standard haul factor using the mean value for both nets to represent the numbers per IO m^2 at that station.

The standard haul factor (SHF) was derived for each tow as follows:-

$$SHF = \frac{IOD}{V}$$

where D = average depth of haul (in metres)

V = total volume of water filtered (in cubic metres)

The total volume of water filtered was determined by multiplying the number of revolutions of the flowmeter during the haul by the mouth area of the net (in square metres) and the length of the water column needed to effect one revolution of the flowmeter at an average speed of 2 knots. The latter parameter was obtained from calibration charts drawn up for individual flowmeters before each cruise.

The mean volume of water filtered by the left and right nets varied between 27 m^3 at some inshore stations and I35 m^3 at an offshore station , but averaged I03 m^3 (Standard deviation 30 m^3).

Net Clogging

Clogging rarely occurs in nets constructed of meshes with operture openings of 0,500 mm or larger, provided the nets have a ratio of operture area to mouth area of 5 to 1 or greater (Smith et al, 1968).

The nets used on the SWAPELS cruises had meshes of 0,940 mm and 0,500 mm and the ratio of aperture area to mouth area was approximately 14 to 1 for both nets. The estimated filtration efficiency of the 0,940 mm mesh net used during Survey 1 was approximately 95 percent (King and Robertson, 1973 a). Since one of the 0,940 mm mesh nets was substituted by a net with a finer mesh (0,500 mm) on the second survey, it was possible that differential filtration efficiency between nets could have taken place while sampling.

To test whether the volume of water filtered by the left and right units of the net differed significantly, the data from 180 hauls selected at random was compared using the two-tailed paired-sample t test (Zar, 1974). The results were as follows:-

$$\bar{d} = 0{,}68 \quad ; \quad S\bar{d} = 0{,}5938 \quad ; \quad t = 1{,}145 \quad ; \quad .2 < p < .3$$

The test shows that filtration or clogging did not differ significantly at a probability level of between 0,2 and 0,3.

Extrusion

Small fish larvae often pass through the aperture of netting material causing the numbers of larvae to be underestimated. The rate of escapement depends directly on the speed of the tow as well as the size of the meshes (Vannucci 1968, Lenarz 1972). In order to reduce extrusion and at the same time to prevent net avoidance of larger larvae during routine sampling, a towing speed of about 2 knots is generally recommended. (Ahlstrom et al 1973).

Extrusion is often high for thin-bodied larvae, such as pilchard and anchovy, which would pass more easily through the meshes. Consequently, a greater underestimation of abundance of these species is to be expected. In the SWAPELS collections, pilchard and anchovy larvae less than 5 mm in length were poorly represented in the samples, while small hake and maasbanker larvae, of the same size range, were better retained, presumably because of their deeper and more robust bodies. For example, of all the larvae collected during the two year survey, only 15,5 percent of pilchard and 8,6 percent of anchovy measured less than 5 mm. In contrast, over 46 percent of maasbanker larvae and 50,8 percent of hake specimens taken in the samples were smaller than 5 mm. This indicates that many of the smaller larval stages of pilchard and anchovy were probably lost due to extrusion through the meshes.

Since a finer 0,500 mm meshed net was substituted for one of the coarser 0,940 mm nets during the second survey, it was expected that greater numbers of smaller larvae would be reflected in the combined catches compared with Survey 1. However, the number of small larvae captured by the 0,940 mm and 0,500 mm meshed nets during tows did not show any constant differences. Large collections of small stages were often captured by the coarse meshed net, while low numbers were recorded simultaneously in the finer meshed net and vice versa.

To determine whether there were significant differences in catches of small larvae between the meshes, a two-tailed paired-sample t test (Zar 1974) was applied to catch data for four species from 20 independent hauls. The samples for analysis were selected at random from areas of high concentration of larvae. The results were as follows:-

Pilchard : $d = 3{,}45$; $Sd = 1{,}89$; $t = 1{,}7424$; $.1 < P < .5$

Anchovy : $d = 4{,}15$: $Sd = 3{,}92$; $t = 1{,}0585$; $.3 < P < .4$

Maasbanker: $d = 1{,}64$; $Sd = 1{,}84$; $t = 1{,}0585$; $.3 < P < .4$

Hake : $d = 2{,}68$; $Sd = 2{,}43$; $t = 1{,}1029$; $.2 < P < .3$

The test showed that the catches of small larvae (those less than 5,0 mm) did not differ significantly at the 0,05 level. The catches of pilchard larvae, however, were close to the set significant level (0,05). A possible explanation for the large fluctuations in catch rate of the two different meshed-nets of the Bongo unit could be a patchiness or random spatial distribution of newly hatched larvae in the plankton. King and Robertson (I973 b) also attributed the variation in pilchard egg numbers between nets to patchiness in egg distribution.

Distribution Charts

Seasonal distribution of larvae is presented as contoured shaded charts. Isopleths were prepared in the standard manner assuming a linear density gradient existed between pairs of stations. Logarithmic contour intervals were used to minimise any differences between stations caused by variability in numbers and net performance.

Identification of the Egg

Davies (I954) described the egg and general development from Cape waters. Hart and Marshall (I951) illustrated pilchard ova collected off South West Africa and King (I975) recently described pilchard egg development from the same region.

The egg is spherical with a smooth transparent membrane, a large perivitelline space and a single oil globule. The yolk is small and irregularly segmented. Measurements of eggs given by the above authors range from I,17 to 1,91 mm with a mean diameter of approximately I,70 to I,82 mm. The oil globule measures approximately 0,18 mm in diameter.

Identification of the Larvae

Pilchard larvae were identified during the course of the investigation from the diagnostic characters outlined by E.H. Haigh and A.E. Louw (South African Museum personal communication).

The most useful distinguishing features are the position of the anal fin in relation to the dorsal fin and the location of the mandible and maxilla in relation to the eye. The origin of the anal fin is well behind the posterior end of the dorsal fin. The mandible extends no further than the middle third of the eye and the maxilla terminates vertically below the anterior border of the eye. Myomeres usually number between 48 and 50 although complete counts are difficult to obtain in the newly-hatched specimens.

These characters are most useful when identifying larvae longer than 6,0 mm. Newly hatched pilchard larvae are typically elongated and thread-like with a posterior anus. The smaller specimens can sometimes be confused with recently hatched anchovy larvae, especially if individuals have been damaged during collection. Nevertheless, since pilchard and anchovy spawning was found to differ considerably, both in time and locality, confusion over the identity of the smaller stages may be regarded as minimal. Generally larvae less than 5,0 mm were poorly represented in the samples and consequently there was little possibility of large numbers of newly hatched specimens of both species occurring together

The development of pilchard larvae from the Cape Peninsula has been briefly described and illustrated by Davies(I954). Hart and Marshall (I951) illustrate a newly-hatched larva and post-larva from South West Africa. A more complete description of pilchard larval development from the yolk-sac stage to the juvenile is given by Louw and O'Toole (I977).

R E S U L T S

Depth Distribution of Eggs

It was assumed during the course of the routine collections that pilchard eggs occurred predominantly in the upper 50 metres and that those taken within this column were representative of the vertical distribution of the eggs. This assumption was based on the results of Silliman (I943) and Ahlstrom (I959) who observed that the eggs of the

Pacific sardine S. caerulea occurred mainly in the 0-50 m layer.

Analysis of the depth distribution of pilchard eggs was not attempted until later. On January I5 1975, large concentrations of pilchard eggs were taken in a surface tow net by the R.S. Benguela approximately 35 km west of Swakopmund. The location of capture roughly corresponds to station 66-04 on the routine SWAPELS grid (Fig. I). A free drifting drogue was launched on the spawning site in order to stay with the same water mass during the experiment. Pilchard eggs were collected simultaneously at a series of depths from the surface to 75 m, using nine samplers similar to those described by Miller (I961). A description of the nets and the methods of operation is given by O'Toole (I977).

A total of thirty hauls were taken over a period of three days, samples being collected at three-hourly intervals. Nets were towed at a speed of 2 knots for the duration of one hour in random directions within 1 km of the buoy. Every six hours, temperature, salinity, oxygen and chlorophyll were measured at depths of 0, 5, I0, 20, 30, 40, 50 and 75 metres.

At the end of each haul, eggs were extracted from the samples and counted. The average depth range fished by each net was interpreted from the bathykymograph traces.

A total of 472 pilchard eggs were collected from thirty hauls. Eggs were found over the entire depth range from the surface to 75 metres. The numbers of eggs found at various depth ranges are given for each haul in Table 1. Although pilchard eggs were taken at all depths, approximately 75 percent of the total collected were found in the upper 20 metres of water. (Fig. 2A). Egg abundance showed a sharp decline with increased depth, only 6 percent of the total being taken below 50 metres.

TABLE I: Depth distribution of pilchard eggs collected off Swakopmund between I5-18 January, 1975.

Station series	Depth Range (in metres) 0-5	5-10	10-20	20-30	30-40	40-50	50-75	Total
1	2	5	5	4	9	4	1	30
2	17	9	14	0	0	0	0	40
3	13	3	0	1	3	0	0	20
4	9	0	1	0	4	0	0	14
5	6	7	1	0	0	6	4	24
6	25	30	12	0	2	0	2	71
7	0	0	0	0	1	2	0	3
8	0	0	3	0	0	1	3	7
9	4	1	12	0	0	4	0	21
10	3	0	13	4	7	2	0	29
11	4	17	6	4	0	3	1	35
12	2	0	1	3	1	0	0	7
13	2	0	0	0	1	1	0	4
14	4	0	0	0	0	0	4	8
15	0	0	0	0	0	0	0	0
16	10	1	4	2	0	1	1	19
17	3	1	1	0	0	0	1	6
18	15	0	1	3	1	0	0	20
19	0	6	1	1	0	0	5	13
20	1	0	1	2	1	2	0	7
21	2	1	3	0	1	0	0	7
22	1	1	2	1	1	1	1	8
23	5	0	2	0	0	2	0	9
24	2	1	7	1	0	0	2	13
25	8	13	13	2	2	0	1	39
26	-	3	3	0	0	0	0	6
27	3	4	2	1	0	0	0	10
28	0	0	0	0	0	1	1	2
29	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0
TOTAL:	141	103	108	28	34	30	28	472

The complete depth distribution of eggs was not covered but it may be assumed that some eggs would have been found deeper than 75 metres. Nevertheless, the decrease in egg abundance with depth at most stations suggested that pilchard eggs were less abundant in the deeper layers.

The observed depth distribution was similar to the vertical distribution of Pacific sardine eggs. Silliman (1943) reported that sardine eggs were taken almost exclusively in the upper 50 metres of water but were most abundant in the top 20 metres. Ahlstrom (1959) also found that Pacific sardine eggs were most numerous in the 0-50 m layer and were sometimes taken in large quantities close to the surface.

Depth Distribution and Hydrology

Environmental parameters were generally similar at the ten hydrological stations which suggested that all the sampling was carried out in the same water mass. Salinity showed little variation with depth and ranged from 35,00^{o}/oo at the surface to 34,90^{o}/oo at 75 metres. In contrast, the mean values for temperature, oxygen and chlorophyll "a" dropped sharply with depth (Figs. 2 B - D). Above the thermocline (approximately 20 m), the water was relatively warm, well-oxygenated and with a high chlorophyll "a" content, while in the region of the thermocline temperature, oxygen and chlorophyll "a" decreased rapidly. Pilchard eggs were also most abundant above the thermocline but decreased in numbers below the thermocline and chlorophyll maximum layer, where the cooler less-oxygenated water was encountered. Most of the eggs occurred over the following range of environmental parameters: temperature 14,5^{o}-15,8^{o}C; oxygen 3,8-7,4 ml/l; chlorophyll 3,8-5,8ml/m^{3}.

King (1975) observed the effects of temperature, salinity and oxygen on the development of South West African pilchard eggs in the laboratory and reported that optimal conditions for successful incubation were within the temperature and salinity ranges of 16-21^{o}C and 33-35^{o}/oo respectively, where the oxygen content exceeded 1,5 ml/l. A decrease in oxygen associated with high temperatures was found to cause retardation of development.

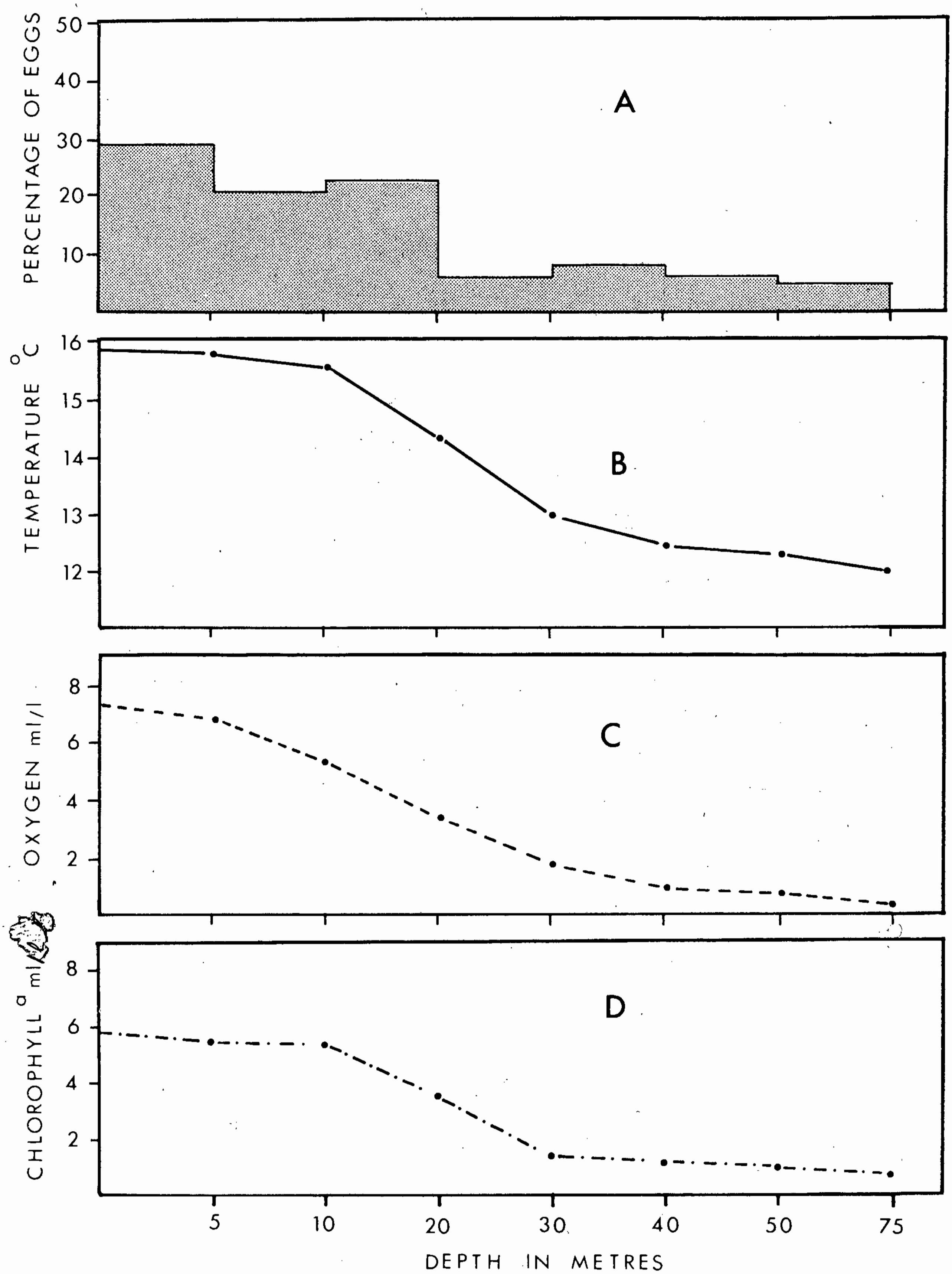


Fig. 2 Depth distribution of pilchard eggs in relation to hydrological parameters

Ahlstrom (1959) showed that the depth of the thermocline was an important factor in determining the vertical distribution of pacific sardine eggs. High numbers of eggs were taken close to the surface when the thermocline was shallow, while eggs were more abundant over a greater depth range if the thermocline was deeper.

The results of the present investigation indicated that conditions in the upper 20 m were apparently favourable for developing eggs. Temperatures were relatively high, and the water was well-oxygenated. In addition, there was a high chlorophyll "a" content, which suggested that adequate food was available for newly hatched larvae.

If the depth distribution of pilchard eggs is closely related to the depth of the thermocline then the absence of a thermocline may result in a wider and, perhaps, deeper distribution within the water column. Thermal stratification is a seasonal feature off the South West African coast and is usually pronounced in summer months (du Plessis 1967; O'Toole 1977 a). During late winter and spring, the water is generally isothermal with depth and considerable pilchard spawning takes place during this period (King, 1977 in press). It is possible therefore that eggs spawned during spring may be more abundant at deeper levels than those resulting from summer spawning.

Distribution and Seasonality of the Larvae

Pilchard larvae were common and widely distributed over the whole research area during both surveys. The geographic distribution of the larvae closely resembled the egg distribution described by King (1975).

Approximately 98 percent of all the larvae collected during the two-year investigation were taken between Mowe Point and Sandwich Harbour (lines 30 to 74). Abundance decreased to the north and south of this area. The percentage of the total number of larvae taken in the different sectors of the survey are summarized in Table II.

TABLE II : The percentage of larvae collected in the different sectors of the research area.

Area	Station line	I972/73	1973/74	I972/74
Cape Frio - Mowe Point	14 - 26	11,7	1,2	2,2
Mowe Point - Palgrave Point	30 - 42	10,2	51,1	47,2
Palgrave Point - Henties Bay.	46 -58	66,8	27,0	30,8
Henties Bay - Sandwich Hb.	62 - 74	10,7	20,6	19,6
Sandwich Hb - Hollam's Bird Island	78 - 90	0,3	0,1	0,2

Pilchard larvae were caught within 6 km from shore and up to II2 km offshore but 98 percent were taken at distances greater than 20 km from the coast. Greatest concentrations were found between 30 and 50 km offshore.

The regional distribution of larvae was adequately covered to the north and south but the seaward distribution was not entirely encompassed. However, the occurrence of larvae to the west of the research area was probably low, since larval abundance generally fell off towards the outer limit of the sampling grid. The percentage occurrence of pilchard larvae in relation to distance from the shore is given in Table III.

TABLE III : The percentage occurrence of pilchard larvae in relation to distance from the shore.

Distance from shore	I972/73	I973/74	I972/74
IO km or less	0,7	0,1	0,1
10 - 20 km	9,5	0,6	1,4
20 - 30 km	55,9	12,9	16,9
30 - 50 km	21,9	35,3	34,0
50 - 100 km	10,9	42,4	39,4
100 km or more	1,1	8,8	8,1

The overall distribution was similar for both years (Figs. 3 and 4), but larvae were much more common in the plankton during the second survey. The centre of abundance in I973/74 also extended over a much larger area to the north and south than in I972/73.

Pilchard larvae occurred in the plankton from September to March during Survey 1 and from August to March/April in Survey 2. Over 70 percent of the total number of larvae collected in I972/73 were taken in spring (September to November), whereas approximately 80 percent of all larvae were found in summer months and early autumn (December to March/April) during I973/74.

SURVEY 1 (August I972 to March I973)

Monthly distribution and abundance charts of pilchard larvae, together with surface temperature features, from the period August I972 to March I973 are shown in Figure 5. A summary of the monthly hauls and abundance of larvae is given in Table IV. The size composition of specimens collected for each month is shown in Figure 6.

In August, only two larvae were taken in the plankton, approximately IO km west of Cape Cross. The specimens were 6 mm and 8 mm in length and probably hatched from isolated eggs spawned in early August.

Large numbers of pilchard larvae were captured during September in coastal waters north of Walvis Bay making up more than 50 percent of the total collected during the eight month survey. Greatest concentrations were found north west of Cape Cross about 30 km offshore. Larvae measured between 3 and 25 mm in length but consisted mainly of the larger size classes. Ahlstrom (I954), roughly estimated that larvae of the Pacific sardine Sardinops caerulea required I-2 months to complete development, depending on temperature. He also suggested that a larva of 24 mm in length was approximately 45 days old.

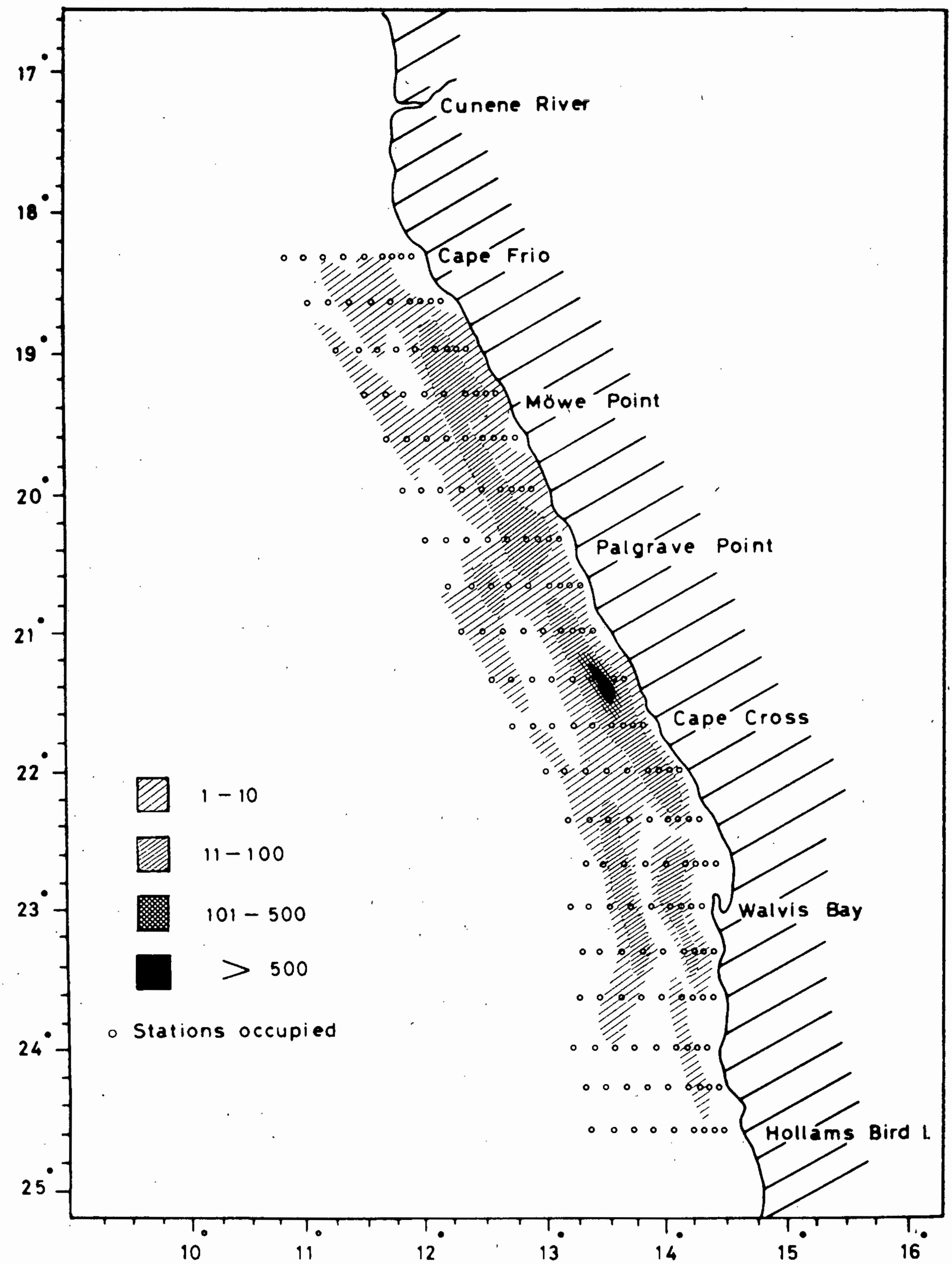


Fig. 3 Distribution and abundance of pilchard larvae during Survey 1 (values represent cumulative standard haul totals for all cruises)

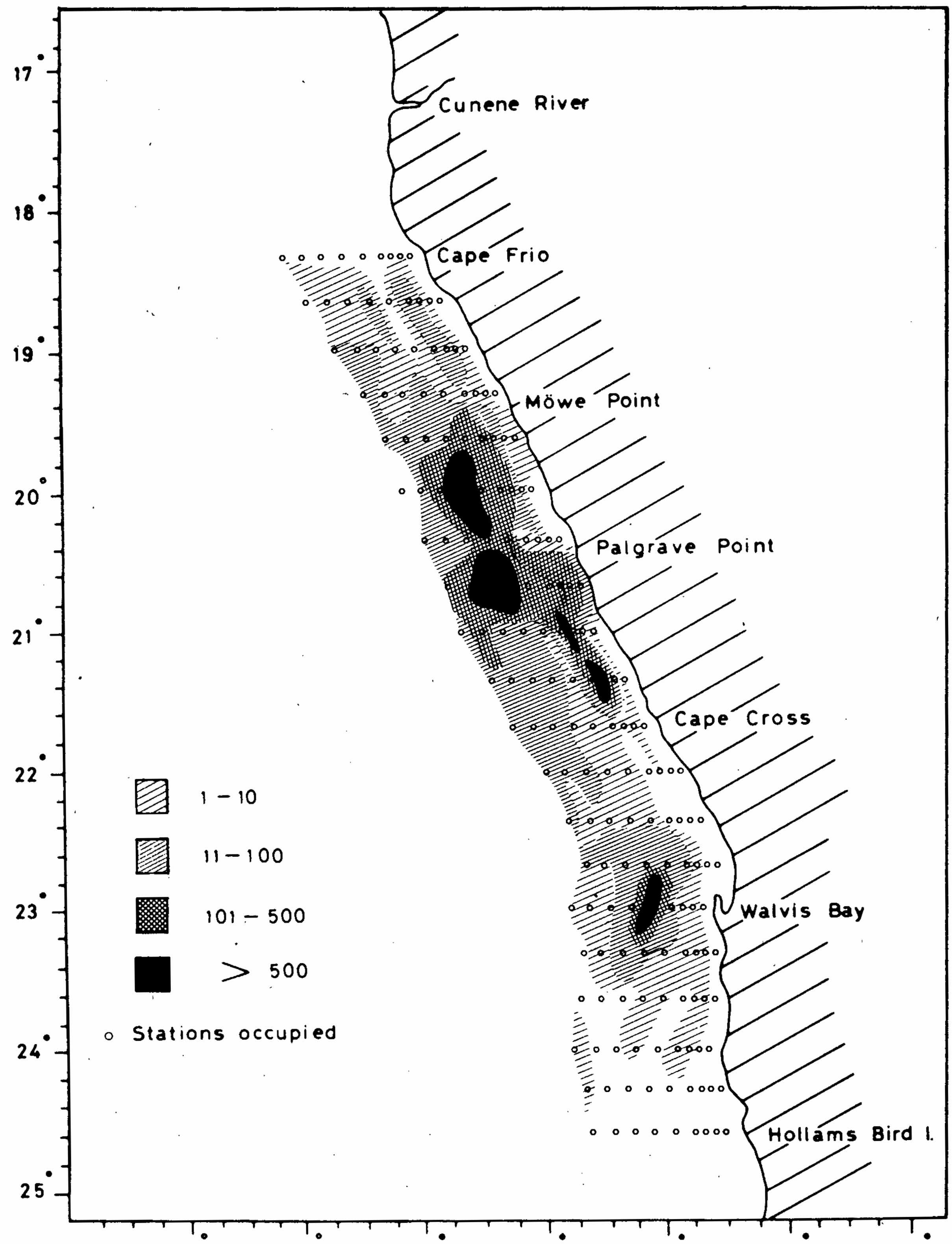


Fig. 4 Distribution and abundance of pilchard larvae during Survey 2 (values represent cumulative standard haul totals for all cruises)

Assuming a similar developmental rate, then pilchard larvae collected in September were between I and 4 weeks old and resulted from considerable spawning in August.

During October, larvae were less numerous in the plankton and were found in scattered patches further north, between Mowe Point and Cape Cross. The larvae were predominantly from the larger length groups (I2 - 26 mm) some of which probably represented the same population sampled during September.

In November, larvae were found further south in coastal waters between Palgrave Point and Walvis Bay. The length composition ranged from 8 to 26 mm and indicated renewed spawning in October.

Pilchard larvae were scarce in the plankton during December. Only eight specimens of mixed sizes (5 - 21 mm) were taken on the entire cruise and were found in offshore waters to the north of Palgrave Point.

In January, larvae were slightly more common and occurred mainly in the north between Cape Frio and Mowe Point. Some scattered individuals were found in the south at both inshore and offshore stations. The presence of smaller length groups suggested renewed spawning in the north some time in late December.

Pilchard larvae were again common in the north during February and consisted mainly of small specimens between 4 and I2 mm in length. The centre of abundance occurred 30 to 80 km offshore, between Mowe Point and Palgrave Point.

In March, the reappearance of recently hatched specimens around Walvis Bay indicated renewed spawning in the south during late February/early March. A few isolated larvae were captured in the north but they consisted primarily of larger length groups.

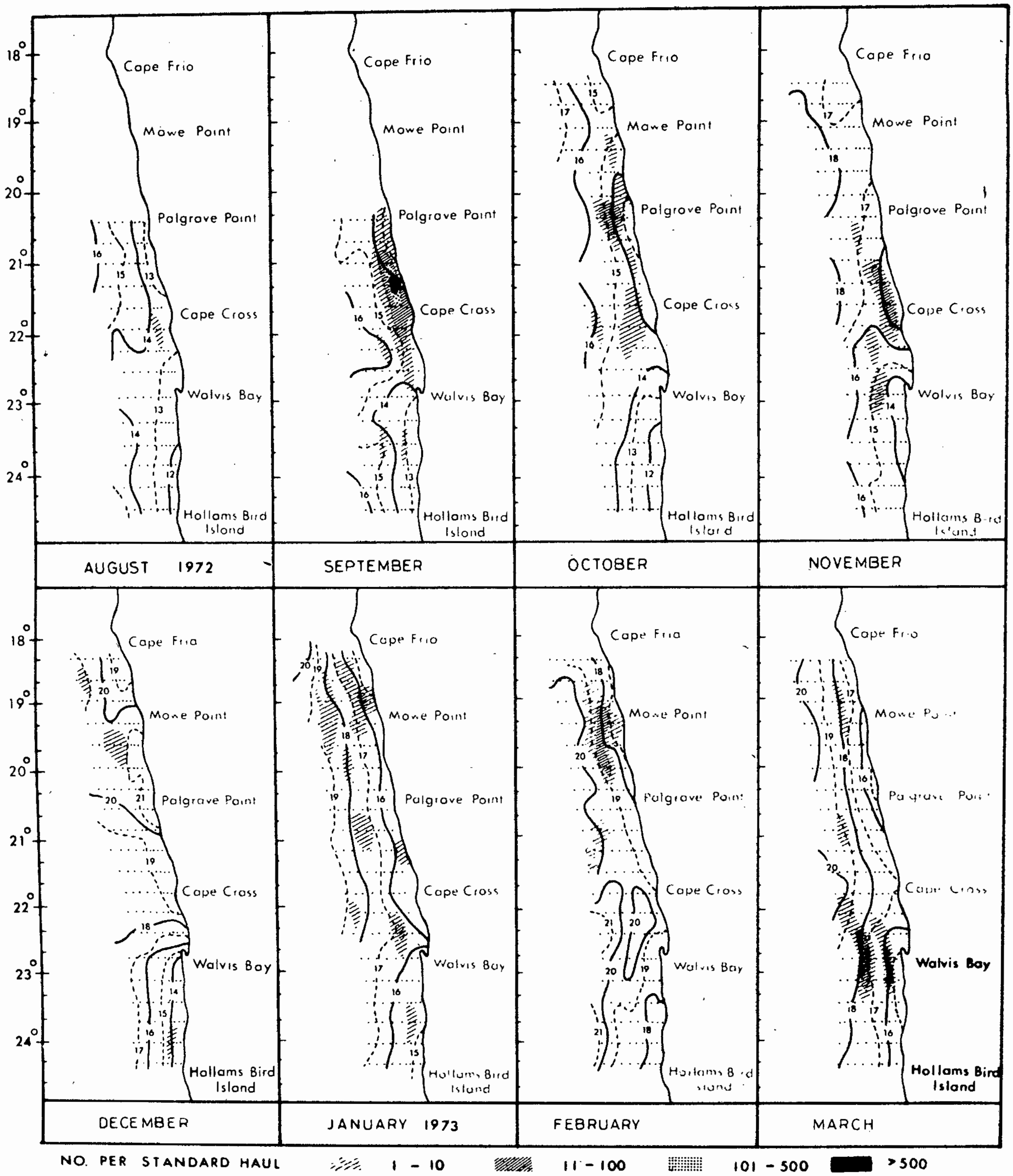


Fig 5. Monthly distribution and abundance of pilchard larvae, August 1972 to March 1973

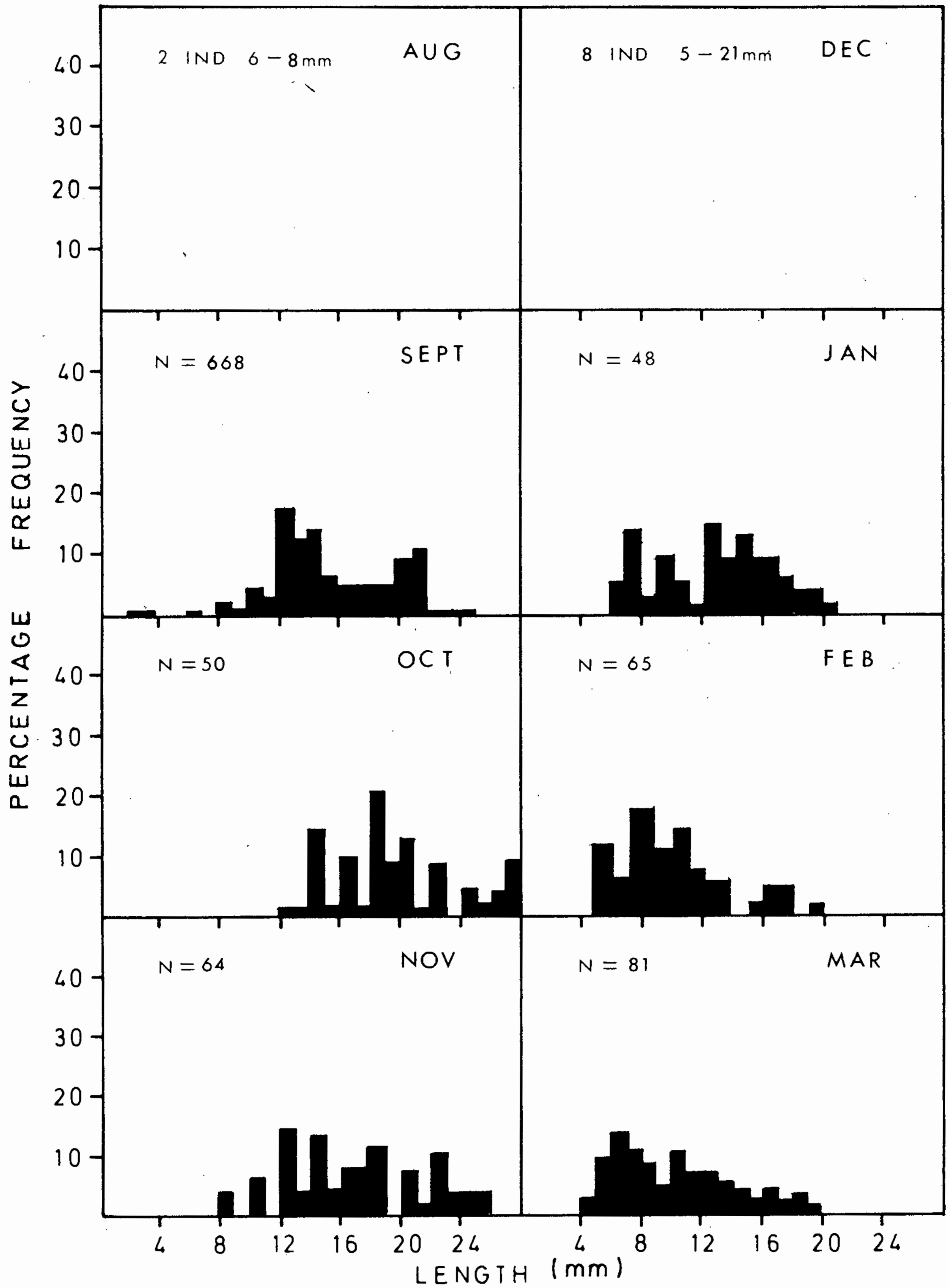


Fig. 6 Length composition of pilchard larvae collected during the survey cruises August 1972 to March 1973

TABLE IV : A summary of the monthly hauls and abundance of pilchard larvae I972 - I973.

Cruise Dates	No. of hauls taken	No. of positive hauls	No. of larvae collected.	Mean no of larvae per IO m^2	% of total collected.
August 21-31	126	2	2	5,2	0,2
September 15-20	126	19	668	104,5	67,7
October 15-22	156	15	50	18,3	5,1
November 11-19	180	11	64	22,8	6,5
December 5-14	180	5	8	4,1	0,8
January 13-21	180	26	48	11,3	4,9
February 14-24	177	18	65	16,5	6,6
March 11-19	177	13	81	22,8	8,2

SURVEY 2 (August I973 to March/April I974)

Pilchard larvae were collected in the plankton throughout the survey period but were more abundant and widespread during summer and early autumn. Larval distribution, abundance and temperature for each month is illustrated in Figure 7 and abundance in relation to monthly hauls is summarized in Table V. Length composition of the larvae caught during each cruise are shown in Figure 8.

In August, a few isolated individuals ranging from IO to 20 mm in length were taken in samples north of Cape Cross.

Pilchard larvae were more common in the plankton during September and again occurred in the north between Mowe Point and Cape Cross. Approximately 80 percent of the specimens were newly-hatched, probably resulting from eggs spawned in late August-early September.

During October, larvae were taken further north, between Mowe Point and Palgrave Point. The majority consisted of younger stages derived from late September/early October spawning.

Distribution in November was similar to that of October. Larger size groups were, however, more plentiful and may have represented the same cohort of larvae sampled in October.

A noticeable decrease in abundance was evident during the month of December. Only eleven specimens (6 - 15 mm) were caught at scattered offshore localities between Mowe Point and Walvis Bay. The decline in larval abundance in December suggested that spawning was at a minimum between late November and early December.

In January, pilchard larvae were very abundant, especially south of Cape Cross, and were caught in the whole inshore/offshore range. Highest densities were found approximately 45 km west of Walvis Bay and 90-112 km offshore between Mowe Point and Palgrave Point. Some newly-hatched individuals were present in the samples, but the majority consisted of I2-16 mm specimens, probably resulting from an increase in spawning activity towards the end of December.

Larvae were not as plentiful in February but were found mainly offshore over a wide area from Mowe Point to Conception Bay. Specimens collected during this month were predominantly larger forms measuring from I2 to I6 mm in length resulting from eggs spawned in early January.

The March/April cruise produced the largest catches of the eight month survey. Larvae were exceptionally abundant and widely distributed in the offshore waters between Mowe Point and Cape Cross. Dense concentrations of pilchard larvae were found over a wide area to the west of Palgrave Point. Isolated individuals were also taken offshore south of Walvis Bay. Most of the specimens captured during March/April were newly-hatched from heavy egg production during mid-March.

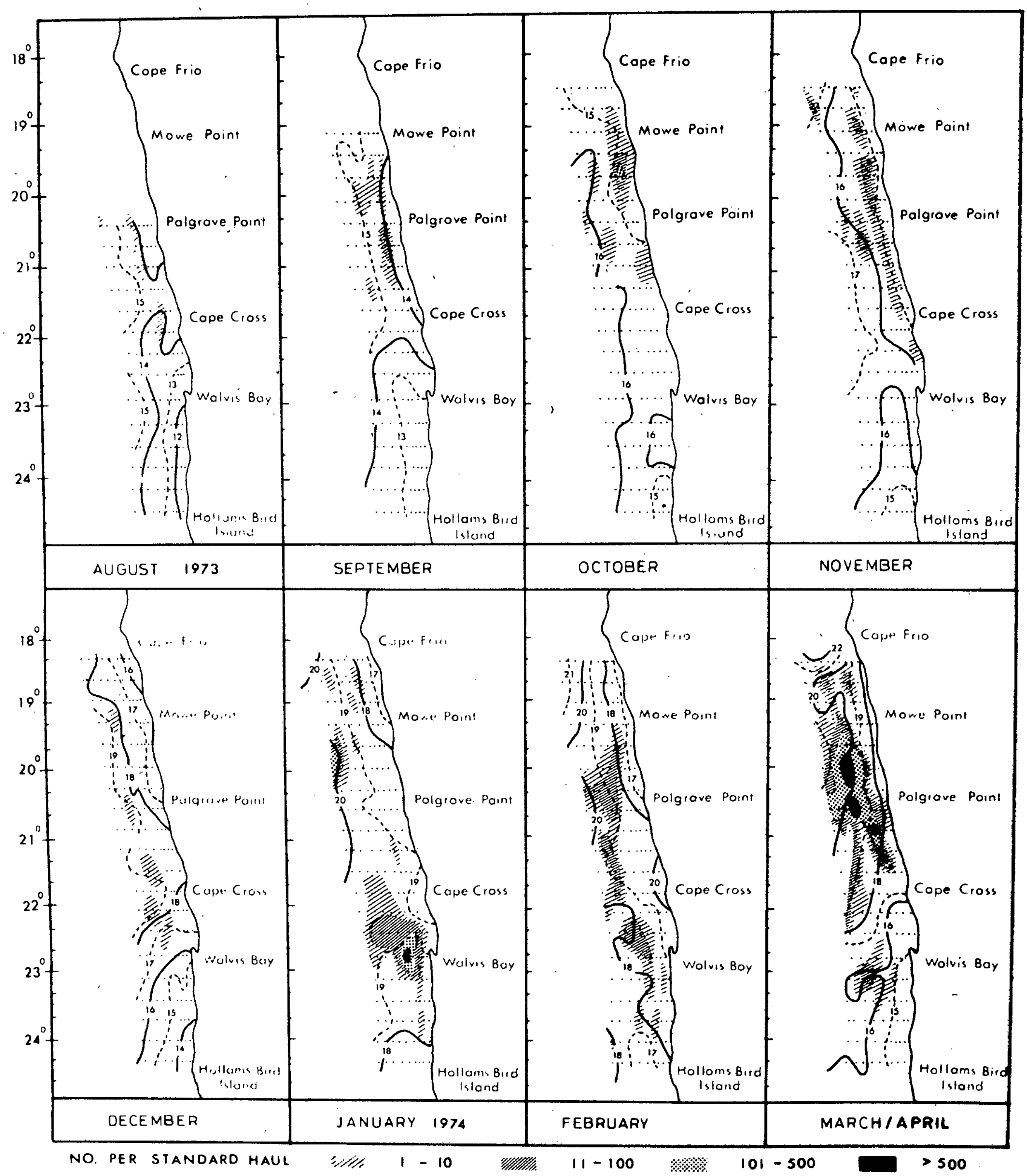


Fig 7 Monthly distribution and abundance of pilchard larvae, August 1973 to March / April 1974

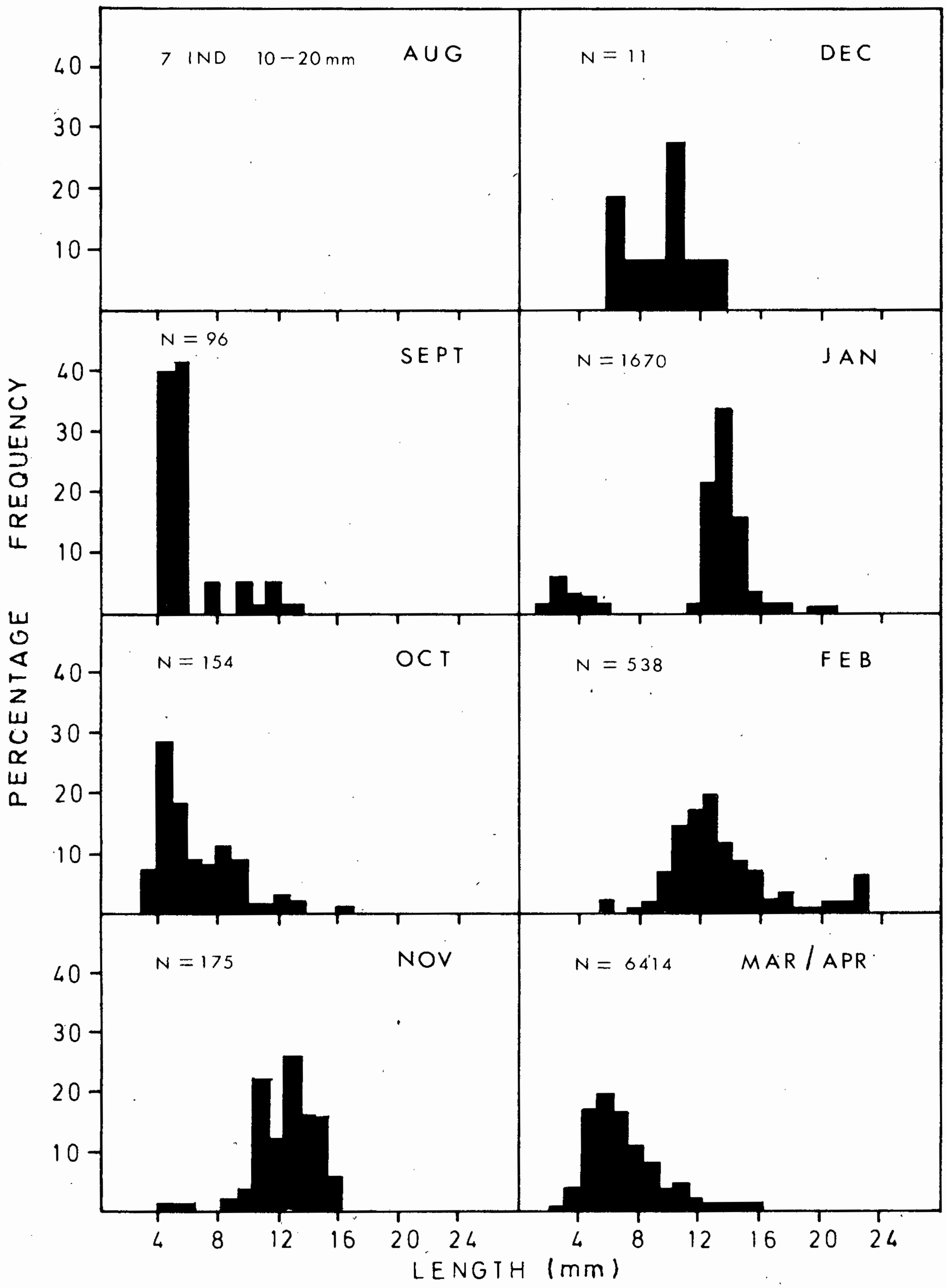


Fig. 8 Length composition of pilchard larvae collected during the survey cruises August 1973 to March / April 1974

TABLE V : A summary of the monthly hauls and abundance of pilchard larvae I973 - I974.

Cruise dates	No.of hauls	No.of positive hauls	No.of larvae collected	Mean no. of larvae per IO m^2	% of total collected.
August I4-19	126	6	7	6,1	0,1
September 9-15	135	8	96	66,8	1,1
October 17-23	180	19	154	36,9	1,7
November 10-18	180	23	175	27,8	1,9
December 10-18	180	7	11	6,4	0,1
January 12-20	180	28	1670	224,3	18,4
February 6-14	169	29	538	55,2	5,9
March 27/ April 4	175	60	6414	287,9	70,7

Spawning Seasonality

The seasonal occurrence, distribution and size composition of pilchard larvae suggested that spawning was continuous during the period August to March of both years. However, seasonal differences in the geographic location and intensity of spawning were apparent. During Survey 1, spawning was heaviest in the south during late winter/spring while a secondary spawning, of perhaps equal or lesser intensity, took place in the offshore waters north of Cape Cross during summer months. Spawning also occurred in the south between February and March. In late winter/spring of Survey 2, spawning was not as heavy in the south and the breeding population evidently moved further north than during the same period in I972/73. Summer/autumn spawning, in contrast, was apparently heavier and more widespread over the entire region during the second survey.

Sampling was not carried out from April to July in 1973 or after March/April 1974 and consequently the duration of the spawning season could not be determined. However, Matthews (1963) found that pilchard egg production decreased towards the end of autumn and eggs were virtually absent from the plankton during winter months. King (1975, 1977 in press) showed that spawning can be substantial during early/mid autumn. The abundance and size composition of the larval stages, particularly in March/April 1974, also suggested that the spawning season could extend into late autumn.

In general, the main breeding period is between August and April, with peak spawning taking place in late winter/spring and summer/early autumn. Presumably the later spawning season could extend into late autumn or even into winter, if favourable environmental conditions existed.

Diurnal Variation in Catches

A comparison of the number of pilchard larvae captured during day and night hauls showed that over four times as many specimens were taken in night collections. Analysis of the day/night catch ratio of larvae of different size categories demonstrated that the increased incidence of the larger size groups accounted for the high numbers in the night hauls (Table VI).

TABLE VI : Day and night differences in catches of pilchard larvae according to size. (all positive stations).

	Day Hauls(I45)		Night Hauls(I51)		
Size group (mm)	No.of larvae	Percentage	No.of larvae	Percentage	D/N Ratio
5,0	510	29,8	1961	26,4	1:3,8
5,1 - 10,0	315	18,4	2010	27,0	1:6,4
10,1 - 15,0	750	43,9	2710	36,5	1:3,6
I5,0	I34	7,8	746	10,0	1:5,5
TOTAL	1709	18,7	7427	81,3	1:4,3

The percentage of the total number of pilchard larvae of various length groups collected at different times of the day and night hauls were plotted at 2-hourly intervals over a period of 24 hours. (Fig. 9). The diurnal variation in abundance was essentially similar for all stages of development. Larvae were more plentiful in hauls after dusk but decreased in number between midnight and 02h00. Maximum catches were made in the early morning hours between 02h00 and 08h00. Larvae became progressively less abundant after dawn and were relatively scarce during daytime collections. Occasional hauls yielded both large and small larvae during the day, especially between I2h00 and I6h00.

The larvae of the Pacific sardine, S. caerulea, also exhibits marked diurnal variation in catch-rates. Silliman (I943) observed that night samples contained many more larvae than day samples, and that larger larvae were found more commonly after dusk. Moreover, he found that the larger larvae were not only less numerous during the day, but also appeared to be distributed at deeper levels.

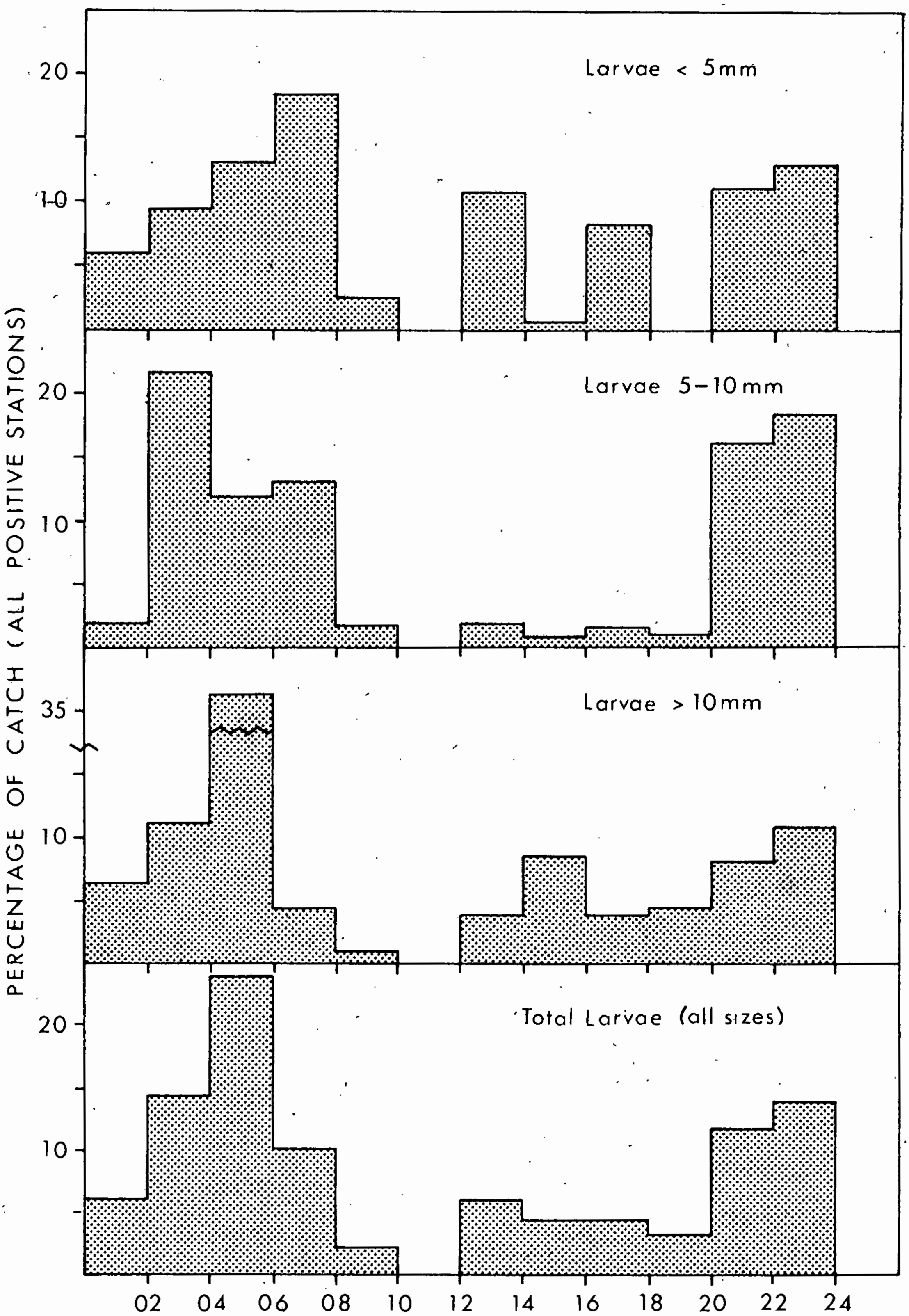


Fig. 9 Diurnal variation in catch rates of pilchard larvae according to size categories (all cruises)

Ahlstrom (I959) reported in a separate investigation that the larger size larvae of the Pacific sardine were generally more numerous in night hauls and found some evidence of larger larvae moving to deeper levels in the daytime. Both authors, however, attribute the differences in the day/night ratio of larval catches to avoidance of the net by the more advanced larvae during the day, rather than a migration to to deeper levels.

Occurrence of Larvae in Relation to Temperature

Pilchard larvae were found at surface temperatures ranging from I3,2^{o} to 21,0^{o}C. Larvae resulting from late winter/spring spawning occurred at relatively low temperatures, between I3,1^{o}-I7,0^{o}C. Almost 70 percent of the occurrences were at temperatures of I4,1^{o} to I6,0^{o}C. During summer and early autumn, pilchard larvae were collected at higher surface temperatures ranging from I6,0^{o} to 22,0^{o}C. Approximately 65 percent of the hauls containing larvae during this later spawning period were at surface temperatures of I7,I^{o} to 20,0^{o}C, with only 10 percent and 23 percent occurring above and below this range. Fifty percent of the hauls with catches greater than 250 larvae per I0m^{2} were taken at surface temperatures of between I8,1^{o}and I9,0^{o}C.

The depth distribution of fish larvae often varies with physical and biological conditions. In this investigation, the depth distribution was not studied. The routine hauls only provide information on the occurrence of larvae in the upper 50 metres and therefore the larvae could have been captured at any depth stratum within this layer. Since sharp temperature changes occur with increased depth, particularly during summer months (O'Toole I977a), larvae probably inhabit water with lower thermal characteristics than that indicated by surface patterns.

The only information on the depth distribution of pilchard larvae off South West Africa is that of d'Arcangues (1974) who found several larvae at a depth of 25 m near the thermocline. The vertical distribution of pilchard eggs also suggested that newly-hatched individuals were more likely to occur in the upper layers near the thermocline, rather than in deeper layers.

Silliman (1943) found that larvae of the Pacific sardine S. caerulea were taken mainly in the upper 30 m, above the thermocline. Ahlstrom (1959) also reported that sardine larvae occurred in greatest abundance above the thermocline in the upper 23 m of water. He further observed that the position of the thermocline was an important factor in determining larval depth distribution. Assuming that the pilchard larvae collected during this study were most abundant in the upper layers above the thermocline, then temperatures at a depth of 20 m would be more representative of thermal conditions in the larval environment.

The relationship between larval abundance and temperature at 20 m showed that most of the larvae were found between 12,1^{o} and 21,0^{o}C, which was generally similar to the overall surface temperature range. Nevertheless, larvae derived from late winter/spring spawning were collected at lower temperatures (12,1^{o} to 17,0^{o}C) with 76 percent occurring at temperatures between 13,1^{o} and 15,0^{o}C. This represents a drop of about one degree compared with the optimal surface temperature range.

During summer/early autumn, larvae were common over a wider temperature range (14,0^{o} to 21,0^{o}C). Approximately 45 percent of occurrences were at 16,1^{o} to 18,0^{o}C, about 80 percent of the hauls with more than 250 larvae per 10 m^2 being captured within this temperature range.

The relationship between temperature, at surface and at 20 m, and the frequency of occurrence of pilchard larvae at a level of abundance greater than 10 per haul is shown in Figure 10. The two peaks on the left and right hand sides of the diagram represent temperatures in late winter/spring and summer/early autumn respectively.

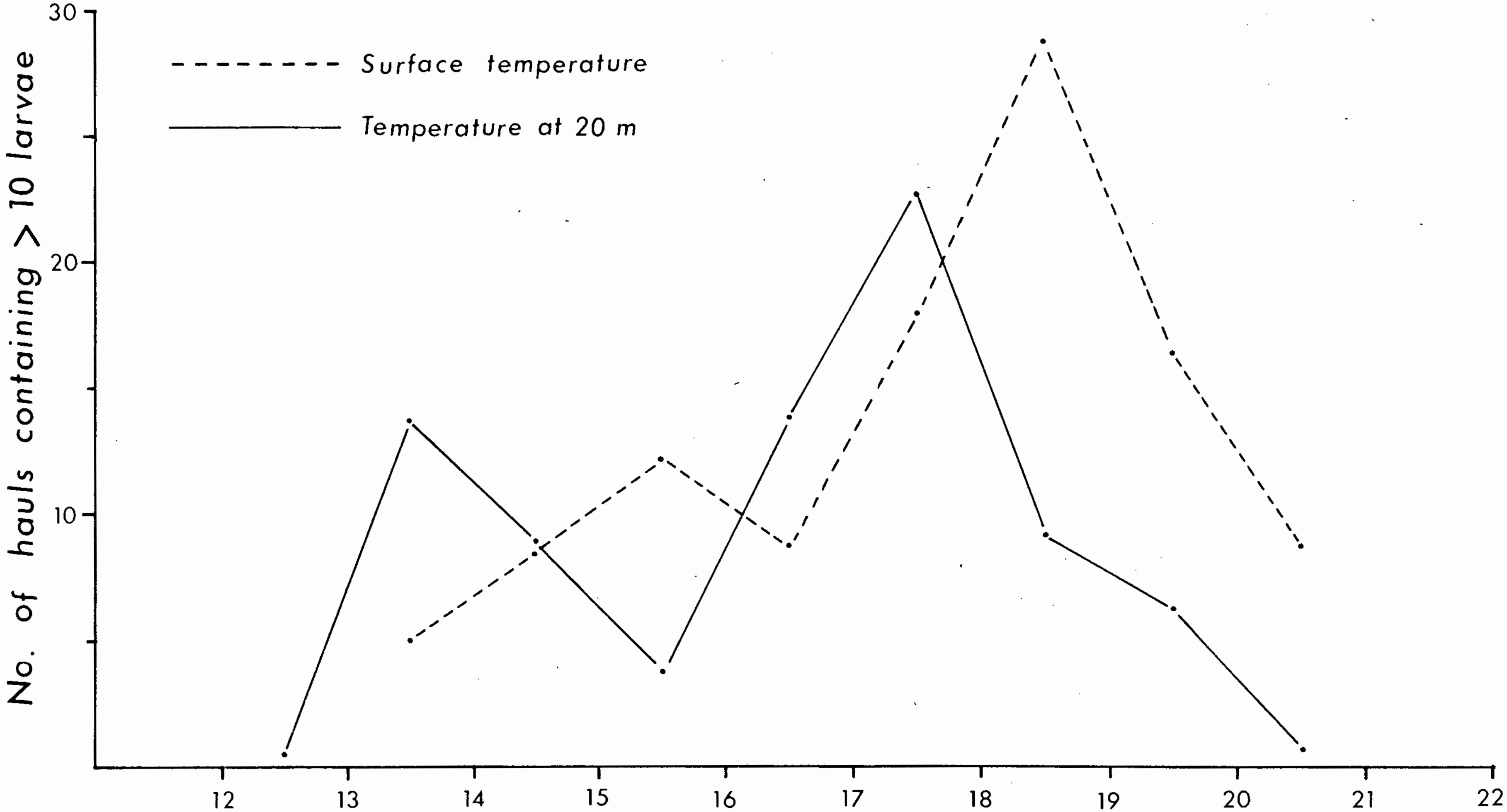


Fig. 10. Relationship between the frequency of occurrence of pilchard larvae (> 10) and temperature

The Kruskal-Wallis one way analysis of variance by rank (Siegel, I956) was used to test whether there were significant differences in larval abundance between temperature classes. The analysis was applied to the number of larvae taken for each positive haul at the various temperature classes. Values of H^o for temperature at the surface and at 20 m were I8 ,58 and 20,42 respectively both being significant at the 1% level. The fact that H - values give a better temperature-dependence at 20 m than at surface temperatures is possibly an indication that larvae are mainly at about 20 m depth.

It may be concluded that pilchard larvae hatched from spring-spawned eggs were associated with significantly lower temperatures and that the optimal range within the 0-20 m layer was between I3,0^o and I6,0^{o}C. In contrast, most of the larvae resulting from eggs spawned during summer/early autumn were found at consistently higher and within wider temperature ranges, but were more abundant between I6,0^o and I9,0^{o}C.

Occurrence of Larvae in Relation to Salinity

Pilchard larvae were collected over a wide range of surface salinities (34,90^o/oo to 35,80^o/oo. However, larvae hatched from eggs spawned in late winter/spring were found at a lower salinity range (34,90^o/oo - 35,40^o/oo) than those resulting from summer/early autumn spawning. Approximately 95 percent of the hauls containing larvae during spring were taken at surface salinities of 35,00^o/oo to 35,30^o/oo.

During the later spawning larvae were found over a much higher and wider salinity range (35,00^o/oo - 35,80^o/oo). Approximately 60 percent of the occurrences were noted at salinities ranging between 35,30^o/oo and 35,60^o/oo.

The abundance of pilchard larvae in relation to surface salinity (late winter and spring) is summarized in Table VII.

TABLE VII : Abundance of pilchard larvae in relation to surface salinity during late winter and spring (Survey 1 & 2)

Surface salinity	Numbers of standard hauls that collected:- I - 5 larvae	6 - 10 larvae	11 - 100 larvae	101 - 250 larvae	250+ larvae	Total
34,91-35,00	2	0	0	0	0	2
35,01-35,10	9	1	0	0	1	11
35,11-35,20	27	9	12	0	0	48
35,21-35,30	20	1	10	1	1	33
35,31-35,40	3	0	0	0	0	3

Table VIII reflects the abundance of larvae in relation to surface salinity during the summer and early autumn of both years.

The Kruskal-Wallis test was applied to the number of larvae collected per positive station at the various salinity ranges during the late winter/spring and the summer/early autumn periods. These data are summarized in Tables VII and VIII , Values of $H^o = 13,58$ and $H^o = 3,48$ were obtained for the two seasons respectively. This showed that the relationship between larval abundance and surface salinity was significant at the 0,1 level for larvae collected in late winter/spring but was not significant for those found during summer/early autumn. The greater range of salinity encountered in the north during summer months together with the more widespread spawning may explain the absence of a significant relationship during the latter period.

TABLE VIII : Abundance of pilchard larvae in relation to surface salinity during summer and early autumn (Survey 1 & 2).

Surface salinity (°/oo)	Number of standard hauls that collected:-					
	I-5 larvae	6-IO larvae	II-I00 larvae	I0I-250 larvae	250+ larvae	Total
35,01-35,10	3	1	4	0	1	9
35,11-35,20	20	5	12	0	0	27
35,21-35,30	14	3	3	0	1	21
35,31-35,40	27	9	9	1	0	47
35,41-35,50	9	3	4	1	2	19
35,51-35,60	5	1	9	4	15	35
35,61-35,70	0	1	3	1	1	6
35,71-35,80	1	1	3	0	0	5

Hydrological Affinities

Hydrological features off South West Africa show marked seasonal variations in temperature and salinity. Intense upwelling in the south during late winter/early spring results in the widespread distribution of homogenous cold low salinity water over much of the region. As summer approaches, upwelling diminishes and warm saline oceanic water invades the zone normally occupied by the cooler coastal water. The hydrological features of the survey area has been described and illustrated, for both years, by O'Toole (I977 a).

In general pilchard spawning is continuous during most of the year and takes place over such widely contrasting hydrological conditions that it is difficult to relate the timing of spawning to any particular sequence of hydrological events. However, if it is assumed that two breeding populations exist, one in the north and another in the south, then seasonal environmental changes may play a more direct role in the timing of spawning groups.

During late winter/spring, the pilchard population in the south spawn in relatively cold low salinity water, characteristic of active upwelling. Larvae were found in waters where temperatures and salinities ranged from I4^{o} to I6^{o}C and 35,10^{o}/oo to 35,30^{o}/oo respectively. Since temperatures in the south during late winter/early spring period remain relatively low and is often uniform with depth (Fig.5 and 7, O'Toole, I977a), it is unlikely that temperature could trigger spawning of the southern population. It is possible that other factors such as the start of food production may play a more direct role in the timing of spawning.

In contrast, spawning in summer/early autumn occurred in warmer mixed waters following the intrusions of oceanic water towards the coast. Larvae were widely distributed along the zone of intermixing and were often abundant where the barriers between the cold and warm water masses were well-developed. Temperatures and salinities in the spawning grounds during summer were invariably high and ranged from I6^{o} to 21^{o}C and 35,20^{o}/oo to 35,80^{o}/oo. In this case the stimulation of summer spawning may be enhanced by a rapid rise in temperature associated with the influx of warm oceanic water.

A comparison of the distribution and abundance of pilchard larvae for both years suggested that the intensity and the regional extent of spawning varied from year to year. During spring of I973, spawning in the south was not as intense compared with I972. The distribution of larvae also showed that the spawning population moved further north.

The northern displacement of the spring spawners may have been caused by changes in environmental conditions in the south during I973. In August and September of both surveys, temperatures in the south were generally similar but warmer water was more widespread in October and November of I973. In addition, water was cooler in the north during the spring of I973 which may have stimulated the breeding population to move further north.

Another factor which may have contributed towards unfavourable conditions in the south was the abnormally high concentrations of medusae (<u>Dactylometra</u> <u>sp.</u>) in the plankton, particularly in August and September.

Medusae are important predators of pelagic eggs and larvae and areas where these organisms are abundant would undoubtedly be unfavourable for spawning fish.

The most striking difference between years was that spawning during the summer of 1974 was heavier and more widespread than during the same period in 1973. This was particularly evident during March/April. Hydrological conditions during March/April 1974 indicated a deep core of warm water occupying much of the area north of Cape Cross. The depth distribution of temperature indicated that in the upper 20 m, water was relatively well mixed whereas below this level thermoclines were generally sharp. Further south, thermoclines were not as developed and water was cooler and more mixed (O'Toole, 1977a). In contrast, temperatures were colder during March 1973, and warm water intrusions were less extensive and shallower.

Thus pilchard spawn predominantly in cold upwelled water in spring. During summer and early autumn spawning takes place on the seaward side of the boundary between the warm oceanic water and the cooler coastal water. A greater penetration of oceanic water into the summer spawning grounds is apparently more favourable for widespread spawning. This is presumably because the more extensive mixing effect between the water masses may stimulate a larger area of production of phytoplankton and small zooplankters which would be suitable for larval feeding and survival.

Development, Growth and Dispersal

Development

King (1975) determined the developmental rate of eggs of the South West African pilchard from blastocap stage to hatching for a variety of temperatures. Although no pre-blastodisc eggs were used in the experiment, he assumed an age of 13 hrs for the eggs to develop from fertilization to the blastodisc stage based on the results of Miller (1952) for the Pacific sardine S.caerulea. Developmental rates shown in Figure 11 indicate that the eggs of S.ocellata may require anything from one to four days to complete development depending upon the temperature at which incubation takes place.

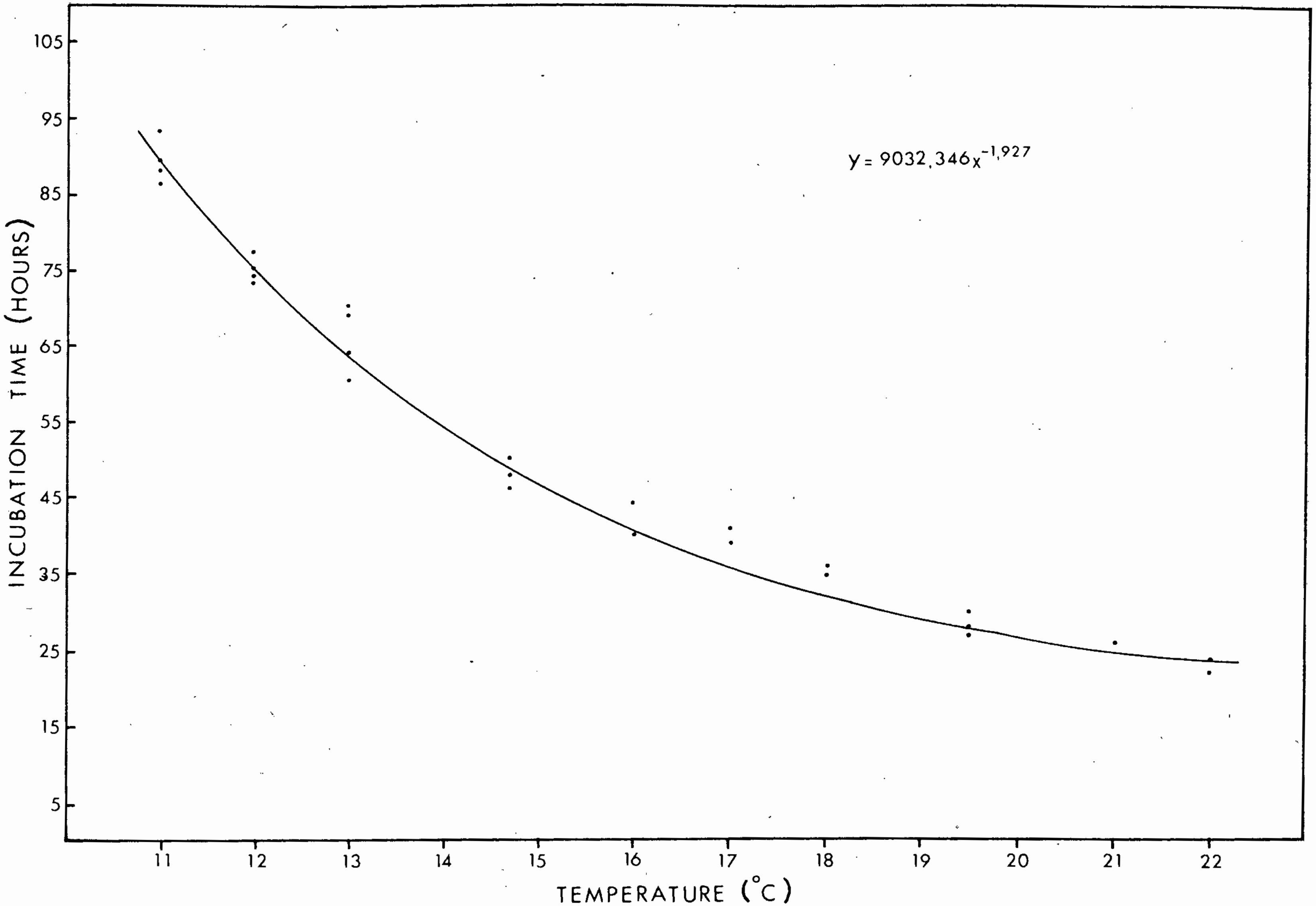


Fig. 11 Development rates of pilchard eggs (after King 1976)

Since pilchard eggs spawned in the south during late winter/ spring must usually develop at temperatures ranging between I3° and I6,5°C (King I975, I977 in press) it can be assumed from Figure II that hatching would take place approximately 2 to 2½ days after spawning. In contrast, eggs spawned during summer/autumn in the northern area are found within a higher temperature range (I6,5° to 22°C) and would require between 1 and 2 days to complete development. Thus the developmental rate of the eggs may differ by as much as 1 day, depending upon the time and locality of spawning. King (I975) also demonstrated that the growth rate of newly-hatched larvae was linear, being more rapid at higher temperatures. For example, live newly-hatched larvae (mean standard length 3,59 mm) required 3 and 5 days to complete yolk-sac absorption at temperatures of I8° and I3°C respectively and increased in length by between 2 and 2,3 mm. These findings therefore suggest that specimens measuring between 5,0 and 6,0 mm long collected in the south during the earlier spawning season were probably about 6 to 6½ days old from the time of fertilization. Larvae of the same size range and at a similar stage of development, but taken in the northern area during summer/autumn would be somewhat younger and approximately 4 to 4½ days old.

Growth

To assess the growth rate of specimens caught at sea, it is necessary to identify a cohort of larvae or group of cohorts by comparing sizes collected on successive cruises. This is often a difficult task, due to the time interval between cruises, the continuous nature of spawning in some species and the progressive decrease in the number of larger specimens due to mortality and net avoidance. Environmental factors, such as, currents, eddies and storms may lead to additional confusion by breaking up identifiable patches of larvae. For these reasons, the growth of pilchard larvae could only be roughly calculated in this study. Two cohorts were satisifactorily identified between successive cruises. One group was followed from September to October I972 in the coastal region between Palgrave Point and Cape Cross (see Fig.5) while another patch of larvae was identified in both January and February I974 offshore north west of Palgrave Point (see Fig.7). Larval abundance

According to size classes from these areas are illustrated in Figure 12. During September 1972 larvae measuring between 12,25 and 14,25 mm in length (mean 13,25 mm) dominated the catches (Fig 12 A). In October, a full 30 days later, larvae of between 18,25 and 20,25mm (mean 19,25mm) were the most abundant size class. If these larger forms were derived from the September population then larvae increased in length by about 6,0mm in the intervening period. This represented an increase of approximately 0,20mm per day in water with a temperature of between 14,0 and 15,0°C. A similar analysis of a larval patch found between Möwe Point and Palgrave Point on the January and February cruises of 1974 (Fig. 12B) suggested that the growth rate of larvae derived from summer spawning was more rapid increasing to about 8,0mm in 24 days (0,33mm per day) in water which averaged 19°C. It is possible to roughly estimate the age of pilchard larvae collected at sea using the growth rate of laboratory reared newly hatched larvae (King 1975) and the conclusions drawn from Figure 12. Thus, a larva of 10,0mm in length hatched from spring spawning in the south would be between 25 and 27 days old from the time of fertilization. In contrast, a similar sized larva hatched from summer/autumn spawning in the north would be 20 to 21 days old. These ages are based on the assumption that larval growth is linear which may not always be the case since food availability and temperature variations can cause short term fluctuations in growth. Ahlstrom (1954) estimated the age of a Pacific sardine larva of the same length as approximately 26 days old, and Blaxter (1969) showed that a 10,0mm Sardina pilchardus larva was 4 weeks old from the time of fertilization when reared at temp= eratures of 16,0° to 19,5°C.

Dispersal

It has already been pointed out by Hart and Currie (1960), Stander (1964) and O'Toole (1977a) that the direction of water movement off the South West African coast during late winter/ spring is largely influenced by the process of upwelling. The flow is usually parallel to the shore in a north to north-easterly direction. Therefore, one would expect that pilchard eggs spawned in the south during this period would be carried northwards along the coast.

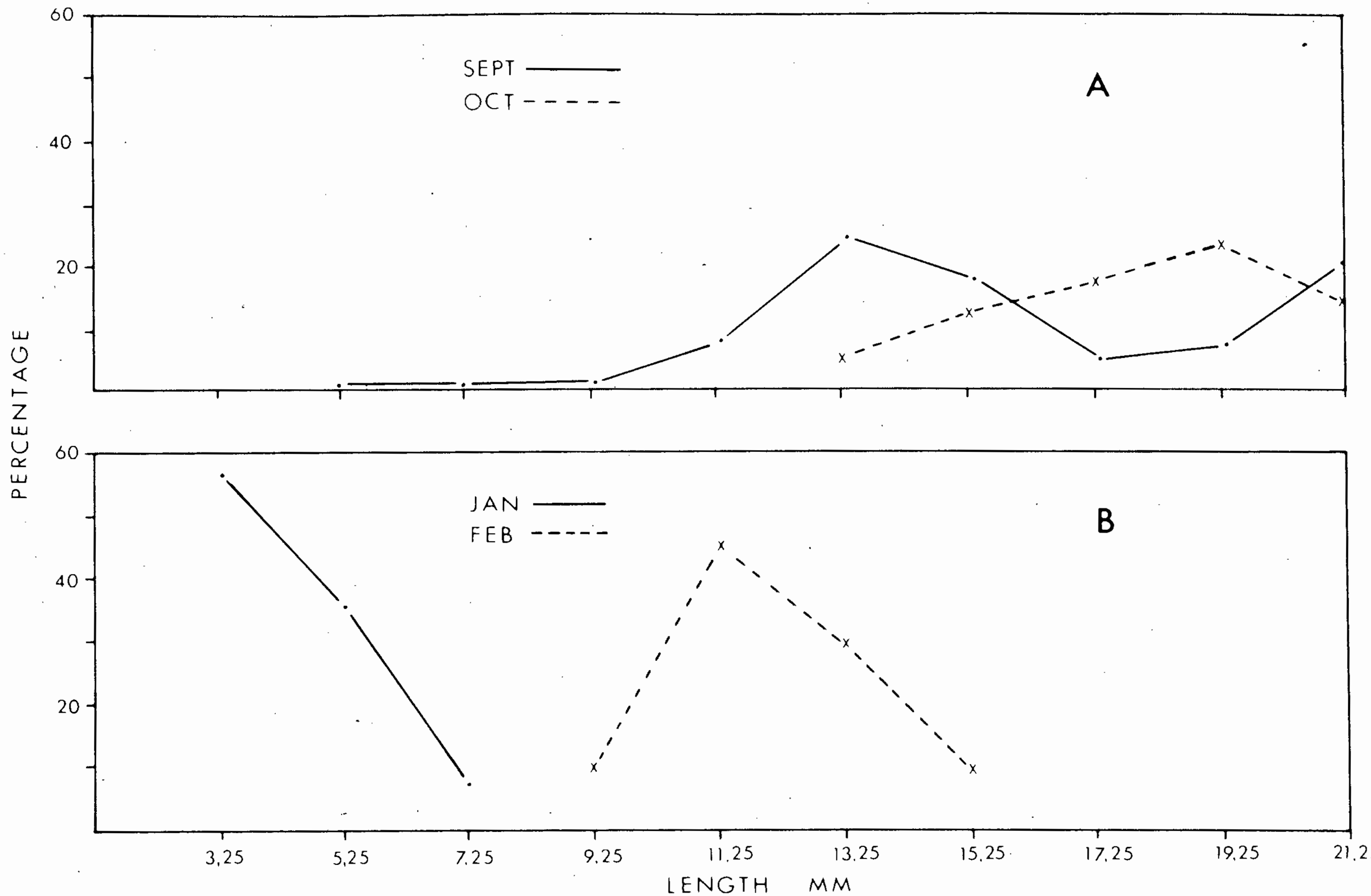


Fig. 12 A: The size composition of larvae collected between Palgrave Point and Cape Cross during September and October cruises 1972

B: The size composition of larvae collected between Mowe Point and Palgrave Point during January and February cruises 1974

A comparison of the horizontal distribution of small and large larvae during September and October 1972 (Fig.13) demonstrates this. In September, pilchard larvae less than 12,0 mm in length were concentrated inshore along a narrow belt between Palgrave Point and Walvis Bay. By October, the more advanced stages (those greater than 20,0 mm) were found north of Palgrave Point closer inshore. It may be assumed that the larger larvae collected in October represented the offspring of the same spawning as the smaller forms captured in September as an increment of 8-10 mm over a period of 30 days is not unreasonable (see Fig.12). Furthermore, an apparent drift northwards between months is supported by hydrological evidence which showed that upwelling was marked and isolines were orientated parallel to the coast (Fig.5).

In contrast, larval dispersal between January and February 1974 (also illustrated in Figure 14) showed a different pattern. Pilchard larvae less than 10,0 mm in length were plentiful in the offshore plankton north west of Palgrave Point in January. The distribution of the larger size groups (greater than 15,0 mm) during February indicated an inshore southward drift which was presumably caused by water movement in this direction over these months (see Fig.7).

In general, the examples given appear to be quite typical of spring and summer conditiond. Newly-hatched larvae from the late winter/spring spawning in the south are normally carried northwards along the coast by the Benguela Current. Larvae resulting from offshore summer spawning are probably carried inshore and southwards by the seasonal influxes of oceanic water from the north and west. However, movements offshore can sometimes occur during summer as happened between December 1972 and January 1973 (Fig.5). Such a process might well transport developing larvae away from the coast into unfavourable areas where food scarcity and excessively high temperatures may affect larval survival.

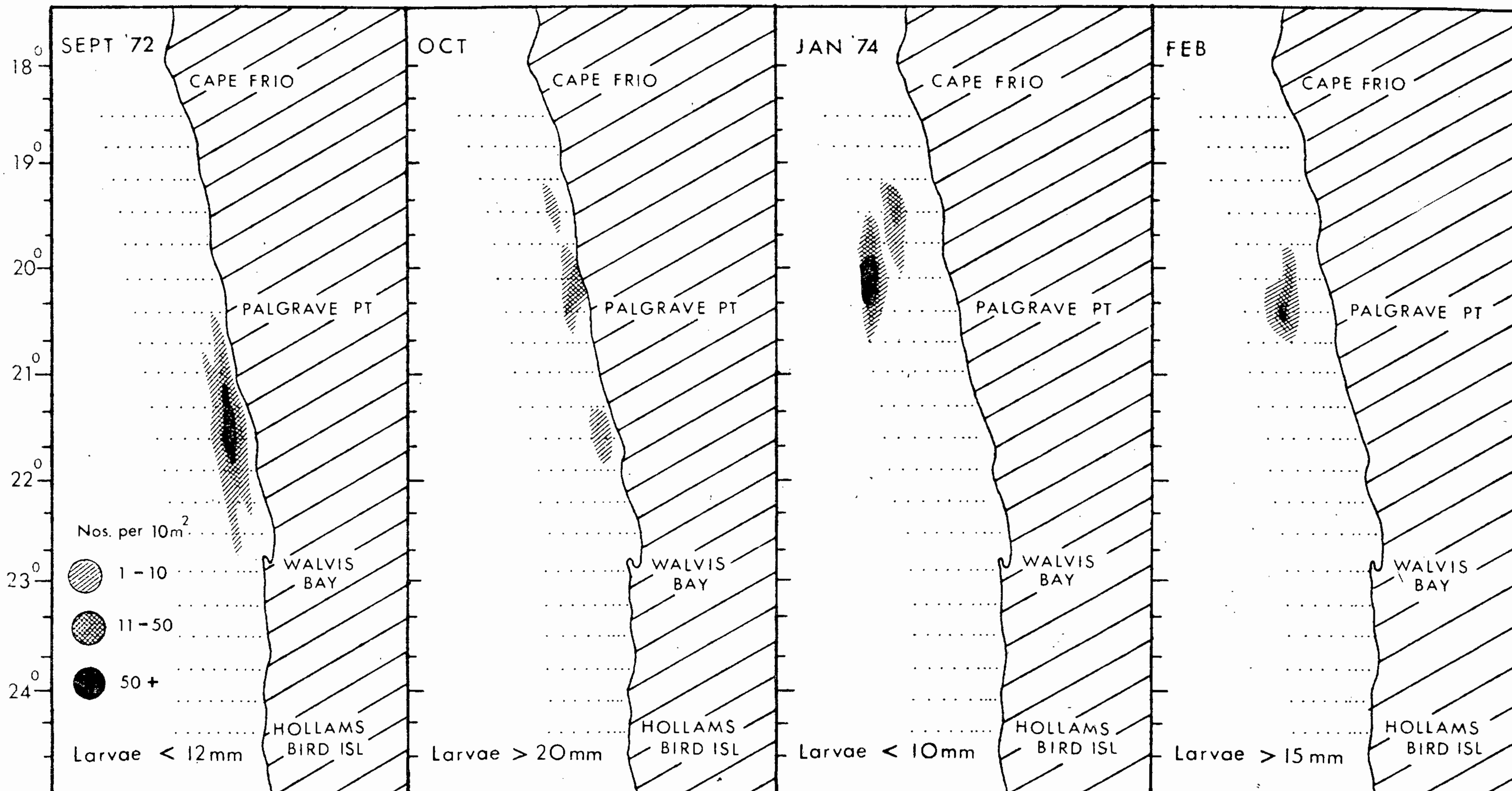


Fig. 13 Dispersal trends of delveloping pilchard larvae between September and October 1972 and between January and February 1974

DISCUSSION

The seasonal distribution, abundance and size composition of pilchard larvae collected on the SWAPELS survey showed that spawning occurred continuously from August to April between Cape Frio and Hollam's Bird Island. Two major spawning seasons were evident, one in late winter/spring and another in summer/early autumn, both taking place at different localities and in contrasting hydrological environments. The earlier spawning in the south was associated with cold upwelled waters near the coast where temperatures and salinities ranged from 13,0° to 16,0°C and 35,10°/oo to 35,30°/oo respectively. In contrast, spawning in summer/ early autumn was predominantly in the north, although a minor renewal of spawning was still evident in the south. Larvae from summer/autumn spawning fish were found in warm saline water ranging from 16,0° to 21,0°C and 35,20°/oo to 35,80°/oo.

These findings agree closely with previous investigations into pilchard spawning off South West Africa. Matthews (1963) studied the southern area between Cape Cross and Conception Bay and reported that spawning was widespread within 80 km of the coast. Two spawning seasons were noted, one in August/September and another in February/March, both coinciding with peak gonad weight in adult fish. Little spawning activity was evident during winter months. The results of a more extensive exploratory survey in 1971 (King 1977 in press) showed that pilchard spawned over a larger area than indicated by the earlier investigation of Matthews (1963). In addition to the main spring spawning peak and the smaller summer peak in the south, heavy spawning was also evident offshore between Cape Frio and Cape Cross during summer/autumn. The northern boundary of egg occurrence was established at Cape Frio and the southern limit at Hollam's Bird Island. Preliminary results on pilchard egg distribution from the SWAPELS cruises (King 1975) also substantiates these findings and the conclusions drawn from the larval data.

As in the case of the larvae, pilchard eggs were found over two temperature ranges. Stander (1963) showed that in spring, eggs were most abundant at temperatures of between 13° and 14°C, while in summer, spawning was most intense at higher temperatures and over a wider variation (14°-22°C). King (1975, 1977 in press) similarily found that pilchard spawned over two distinct temperature ranges. Eggs from spring spawning fish occurred at surface temperatures of 13,0°-16,5°C whereas those from summer spawning were found at higher temperatures (16,5°-22°C). These seasonal ranges are almost identical to those obtained for the larvae.

Since samples were not collected between April and July 1973 or from May 1974, it is possible that spawning could have continued into late autumn or even winter. Indeed, the abundance of newly-hatched larvae in the plankton during March/April 1974 suggested this. In general, one can conclude that the period between August and April covers the main breeding seasons of the South West African pilchard. However, some clupeids are known to spawn outside the main breeding periods if conditions are temporarily favourable. The Pacific sardine, S.caerulea can mature several batches of eggs during the year and release ova at anytime when the environment is suitable (J.Mc Gregor, NMFS, La Jolla, personal communication). The South West African pilchard S. ocellata is also a serial spawner and developing ovaries contain different size modes of yolked eggs (Le Clus, 1976). It is, therefore, possible that the species could similarly extend its spawning season if environmental conditions continued to be favourable. Fluctuation in pilchard spawning and intensity were evident from the SWAPELS larval collections. For example, larvae were more plentiful in the south during late winter/spring 1972 whereas in 1973, larvae were less numerous and occurred further north. This apparent shift in spawning cannot be explained from hydrological data since the thermal patterns during August and September of both years were similar. However, higher temperatures in the south and colder water in the north during October and November 1973 may have caused a northward movement. Alternatively, a combination of other abiotic or biotic factors during the spawning season could have resulted in unfavourable conditions in the south during 1973.

Pilchard spawning in the north during summer could apparently be linked with a rapid increase in temperature associated with the seasonal influx of warm oceanic water. Greater incursions of warm mixed water seemed to enhance more widespread and heavier spawning. This was especially noticeable during March/April I974 when a southward extension of warmer water corresponded with an enlargement of the spawning area. Such conditions brought about by the mixing of warm oceanic water and cool coastal water may have caused a wider distribution of food organisms.and thus an expansion in the larval distribution.

The fact that pilchard eggs and larvae are found in geographically separate areas at different seasons and contrasting hydrological conditions strongly suggests that two separate breeding groups or independent stocks may inhabit the area between Cape Frio and Hollam's Bird Island. The southern population is apparently limited to the region between Palgrave Point and Hollam's Bird Island and spawns continuously from August to March. The peak spawning, however, takes place in late winter and spring (August to November) whereas spawning in the south during summer months can be regarded as a secondary peak by the same group of fish. This hypothesis is supported by Matthews (I963) who investigated pilchard spawning south of Palgrave Point. Although, he suggested the possibility of two spawning groups in this area to account for the late winter/ spring and summer peaks, he concluded, probably correctly, that the earlier peak was the result of the ripeness of the largest part of the gonad while the secondary summer spawning was the termination of continual spawning by the same population. Additional evidence for the single breeding stock in the south is supported by Le Clus (I976) who found no significant difference in relative fecundity, length or weight of fish in the area. A northern spawning population was first suggested by King (I977 in press) when egg searches were expanded northwards to the Cunene River. In contrast to the southern spawning stock, the breeding season is apparently shorter but nevertheless intense during summer/early autumn. Spawning characteristically occurs in warm saline water at considerable distance from the coast.

Further evidence for the separate northern stock is given by Thompson and Mostert (I974) who found some genetic variation between the pilchards examined from Ambrose Bay (21°03') and Walvis Bay. With the present available data, it can be tentatively suggested that two breeding stocks exist off the South West African coast. The separation of these stocks may have been caused by adaption to specific hydrological conditions and the timing of plankton production cycles in both regions.

Dispersal trends suggest that larvae from late winter/spring spawning in the south are carried northwards by the Benguela Current while larvae from the summer/autumn spawning population in the north tend to be transported southwards by the Angola Current and inshore. The boundary zone between the coastal and oceanic water in the north probably serves as an important nursery area for developing larvae and juvenile stages of both stocks. During winter, when the temperature drops and upwelling commences, some of the juvenile pilchards presumably migrate southwards to recruit into the southern population whereas others return to the northern waters to supplement the northern stock. Schulein (I971), reported a southerly movement of juvenile pilchard based on the fact that smaller fish were more frequently encountered in catches made in the north. However, recent findings (F. Schulein, Sea Fisheries Branch, personal communication) show that juveniles also occur in the southern area.

In the final analysis, it is probable that some intermingling of larvae, juveniles and adult fish from both stocks occurs and that hydrological conditions may determine the geographic area, the time of spawning, dispersal and adult migration.

LITERATURE CITED

AHLSTROM, E.H. 1954 Distribution and abundance of egg and larval populations of the Pacific sardine. U.S. Fish Wildl. Serv., Fish. Bull. (56), 93: 83-140

AHLSTROM, E.H. 1959 Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. (161), 60; 107-146.

AHLSTROM, E.H., K. SHERMAN AND P.E. SMITH 1973 Seagoing operations in ichthyoplankton surveys. "Fish egg and larval surveys" (contribution to a manual). F.A.O. Fish. Tech. Paper, 122 (3): 14-26.

BLAXTER, J.H.S. 1968 Feeding and conditions of Clyde herring larvae. The Biology of early stages and recruitment mechanisms of herring. Int. Coun. Explor. Sea, Symp. Copenh., (14); 1-7 (mimeo).

BLAXTER, J.H.S. 1969 Experimental rearing of pilchard larvae. J. mar. biol. Ass. U.K. 49 (3), 557-575.

DAVIES, D.H. 1954 The South African pilchard (Sardinops ocellata). Development, occurrence and distribution of eggs and larvae. Investl Rep. Div. Sea Fish. S. Afr. 15: 28 pp.

DAVIES, D.H. 1956 The South African pilchard (Sardinops ocellata). Sexual maturity and reproduction 1950-1954. Investl Rep. Div. Sea Fish. S. Afr. 22: 155 pp.

DAVIES, D.H. 1957 The South African pilchard (Sardinops ocellata) and maasbanker (Trachurus trachurus). Young fish survey. Investl Rep. Div. Sea Fish S. Afr. 29: 1-36

DU PLESSIS, E. 1967 Seasonal occurrence of thermoclines off Walvis Bay, South West Africa, 1959-1965. Investl Rep. mar. Res. Lab. S.W. Afr. 13: 28pp

HART, T.J. AND N.B.MARSHALL 1951 Breeding ground of pilchards off the coast of South West Africa. Nature, Lond. 168 : p.272.

HART, J.J AND R.I. CURRIE 1960 The Benguela Current.'Discovery' Rep. 31 : 123 - 298.

IDA, H. 1972 Some ecological aspects of larval fishes in waters off Central Japan. Bull. Jap. Soc. scient. Fish., 38,(9): 981-994.

KING, D.P.F AND A.A.ROBERTSON 1973 a Methods of pelagic fish egg and larval research in South West Africa. S.Afr.Shipp.News Fish. Ind. Rev. 28, (5) : 57-61.

KING, D.P.F AND A.A.ROBERTSON 1973b Variability in Bongo net catches of South East Atlantic pilchard (Sardinops ocellata) eggs. S.Afr.Nat.Oceanogr.Symposium Abstracts. P.35.

KING, D.P.F. 1975 Influence of salinity,temperature and dissolved oxygen on embryonic development of the South West African pilchard, Sardinops ocellata. Msc.thesis, Univ.of Stellenbosch, South Africa.

KING, D.P.F. 1977 in press. The distribution and abundance of eggs of the South West African pilchard (Sardinops ocellata)and anchovy (Engraulis capensis),1971-1972. Fish.Bull.S.Afr. 9.

KRAMER, D. M.J.KALIN, E.G.STEVENS, J.R.THRAILKILL & J.R. ZWEIFEL. 1972 Collecting and processing data on fish eggs and larvae in the California Current region. NOAA Tech. Rep. CIRC - 370 38 pp.

LE CLUS, F. 1976 Fecundity of the South West African pilchard, Sardinops ocellata. Msc.thesis, Univ.of Stellenbosch, South Africa.

LENARZ, W.H. 1972 Mesh relention of larvae of Sardinops caerulea and Engraulis mordax by plankton nets. Fish.Bull.Natl.Oceanic Atmos. Admin. Seattle, 70 (3) : 839-848.

LOUW, A.E. AND M.J. O'TOOLE. 1977 Larval development of Sardinops ocellata (Pisces : Clupeidae). Ann. S.Afr. Mus. 72, (7), 125-145.

MC EWEN, G.F., M.W. JOHNSON & T.R.FOLSOM 1954 A statistical analysis of the performance of the Folsom plankton sample splitter, based upon test observations. Arch. Meteorol.Geophys. Bioklimatol., (7) : 502-527.

MATTHEWS, J.P. 1963 The pilchard of South West Africa (Sardinops ocellata). Sexual development, condition factor and reproduction. Investl Rep. mar.Res. Lab. S.W.Afr. 10 : 96 pp.

MILLER, D.J. 1952 Development through the prolarval stage of artifically fertilized eggs of the Pacific sardine (Sardinops caerulea). Calif. Fish. Game. 38, 587-595.

MILLER, D. 1961 A modification of the small Hardy plankton sampler for simultaneous high-speed plankton hauls. Bull. Mar. Ecol. 5, (45) : 165-172.

MILLER,D., J.B. COLTON JR., & R.R. MARAK 1963 A study of the vertical distribution of larval haddock. J.Cons.int. Explor.Mer.28,(1),37-49

NAWRATIL, O. 1961 Age studies and age composition of Sardinops ocellata in the commercial catches, I952-58, and a new method for the determination of the age of Sardinops ocellata. Investl Rep.mar.Res.Lab.S.W.Afr. 2 : 43 pp.

NAWRATIL, O. 1962 Age composition of Sardinops ocellata in the commercial catches I958 and I959 with reference to a change in rate of growth. Investl Rep. mar. Res. Lab. S.W.Afr. 6 : 33 pp.

NEWMAN, G.G. 1970 Migration of the pilchard Sardinops ocellata in Southern Africa. Investl Rep. Div. Sea Fish. S.Afr. 86 : 6pp.

O'TOOLE, M.J. 1976 Incidental collections of small and juvenile fishes from egg and larval surveys off South West Africa (I972 - I974). Fish.Bull.S.Afr. 8 : 23-33.

O'TOOLE, M.J. 1977a Distribution of temperature and salinity off South West Africa, I972-I974. PhD thesis, University of Cape Town, section I, 3I pp.

POSGAY, J.A., R.R.MARAK AND R.C.HENNEMUTH 1968 Development and test of new zooplankton samplers. Annual Meeting Int.Comm.Northwest.Atl. Fish. Res. Doc. 85 (mimeo).

SCHULEIN, F.H. 1971 Rekrutering studies oor die Suidwes-Afrikaanse Sardyn (Sardinops ocellata),I954-I968. Msc.thesis, Univ.of Stellenbosch, South Africa.

SIEGEL, S. 1956 Non parametric statistics for the behavioural sciences. Mc Graw-Hill, New York, 312 pp.

SILLIMAN, R.P. 1943 Studies on the Pacific pilchard or sardine (Sardinops caerulea). 6. Thermal and diurnal change in the vertical distribution of eggs and larvae. Spec.Sci.Rep. U.S. Fish Wildl. Serv. (Fish)., 22 : I7 pp.

SMITH, P.E., R.C. COUNTS & R.I. 1968 Changes in filtering efficiency of plankton nets under tow due to clogging. J.Cons.int.Explor. Mer. 32 , (1) : I-13.

STANDER, G.H. 1963 The pilchard of South West Africa (Sardinops ocellata). Temperature : Its annual cycles and relation to wind and spawning. Investl Rep. mar.Res.Lab. S.W. Afr. 9 : 57 pp.

STANDER, G.H. 1964 The Benguela Current off South West Africa. Investl Rep. mar. Res.Lab. S.W.Afr. I2 : 43 pp.

STANDER, G.H. AND P.J. LE ROUX. 1968 Notes on the fluctuations of the commercial catches of the South African pilchard (Sardinops ocellata)I950-I965. Investl Rep. Div. Sea.Fish.S.Afr. 65 : I4 pp.

THOMPSON, D. AND S. MOSTERT. 1974 Muscle esterase genotypes in the pilchard, Sardinops ocellata. J.Cons.int. Explor. Mer, 36 (I): 50-53.

VANNUCCI, M. 1968 Loss of organisms through meshes. Unesco Monogr. Oceanogr.Methodal., (2) : 77-86.

ZAR, J.H. I974 Biostatistical Analysis . Printers Hall Press, London.

INVESTIGATIONS INTO THE EARLY LIFE HISTORY OF THE SOUTH WEST AFRICAN ANCHOVY *ENGRAULIS CAPENSIS* GILCHRIST

By

MICHAEL J. O'TOOLE,
SEA FISHERIES BRANCH,
BEACH ROAD,
SEA POINT,
CAPE TOWN.

INTRODUCTION

The anchovy, *Engraulis capensis* Gilchrist, occurs from the Cunene River on the northern borders of South West Africa to Cape St. Sebastian on the south coast of South Africa (Pollock I970). The species forms the basis of an important pelagic fishery along the west coast of South Africa (Baird and Geldenhuys I973) and off South West Africa (Ratte I973).

Since the introduction of purse-seine nets with finer meshes in I968, anchovy landings have increased dramatically in South West African waters. The total catch for the territory rose from I78300 metric tons in I965 to 579600 metric tons in I973 (F.A.O. I974) accounting for between 30 and 50 percent of the pelagic fish landed in Walvis Bay. Only landings of the pilchard, *Sardinops ocellata*, are greater.

The biology of *E.capensis* is generally well-known and has been the subject of a number of investigations. The fish form large shoals in the upper layers and feed on a variety of phytoplankton and zooplankton. (Robinson I966, King and Mc Leod I976). Growth is rapid during the first year of life and individuals frequently attain 50 per cent sexual maturity at lengths of 9,0 cm. Gonad development usually reaches a peak between November and January, with activity declining again during autumn and early winter (Robinson I966, Ratte I972). Anchovy eggs occur in Cape waters from early spring to late summer (Anders I965, I975) but are uncommon or absent from the plankton during autumn and winter. King (I977 in press) reported anchovy eggs off the South West African coast from October (spring) to April (autumn) and noted heaviest spawning during the month of February. The general biology of the populations from the Cape and South West Africa are regarded as essentially similar but no morphological differences have been found to suggest any subspecific division. Ratte (I973) however, pointed out that the mean length/age of the northern stock was slightly larger than that off the Cape. No migration between the two more or less geographically separate populations has been identified.

Little is known about the pelagic egg and larval stages of the species, especially off South West Africa. Some information on the seasonal occurrence of eggs is given by King (I977 in press) but the distribution and ecology of the larvae is poorly understood.

During a two-year ichthyoplankton investigation conducted off South West Africa between I972 and I974, anchovy eggs and larvae were collected in considerable numbers in the plankton. The area between Cape Frio (I8^{o}20'S) and Hollam's Bird Island (26^{o}40'S) (Fig.1) was sampled monthly from August I972 to March I973 and from August I973 to March/April I974. Information on the depth and position of stations together with an account of the methods of collection are given by O'Toole (I976a) and O'Toole (I977b). Anchovy larvae accounted for 6,7 percent of all the fish larvae captured and were the fourth most abundant species collected.

This report is mainly concerned with the distributional ecology of the larvae and deals with such aspects as seasonality, geographic distribution, diurnal variation in abundance, relation to temperature and salinity, hydrological affinities, growth and dispersal. Some information is also given on the distribution of anchovy eggs and occurrence in relation to temperature and salinity.

RESULTS

Identification of the eggs

Like all other members of the family Engraulidae, the eggs of E. capensis are elongated, ellipsoid, with a narrow perivitelline space and no oil globule. The yolk is segmented in the manner characteristic of clupeid eggs. Anchovy eggs collected during this investigation had the following dimensions: Long axis I,20 - I,47mm (mean I,38mm); short axis 0,57 - 0,67mm (mean 0,59mm). These measurements were based on approximately 300 eggs selected randomly from samples taken during the cruises of January I973 and February I974 from between Cape Frio and Palgrave Point and compare favourably with egg measurements given

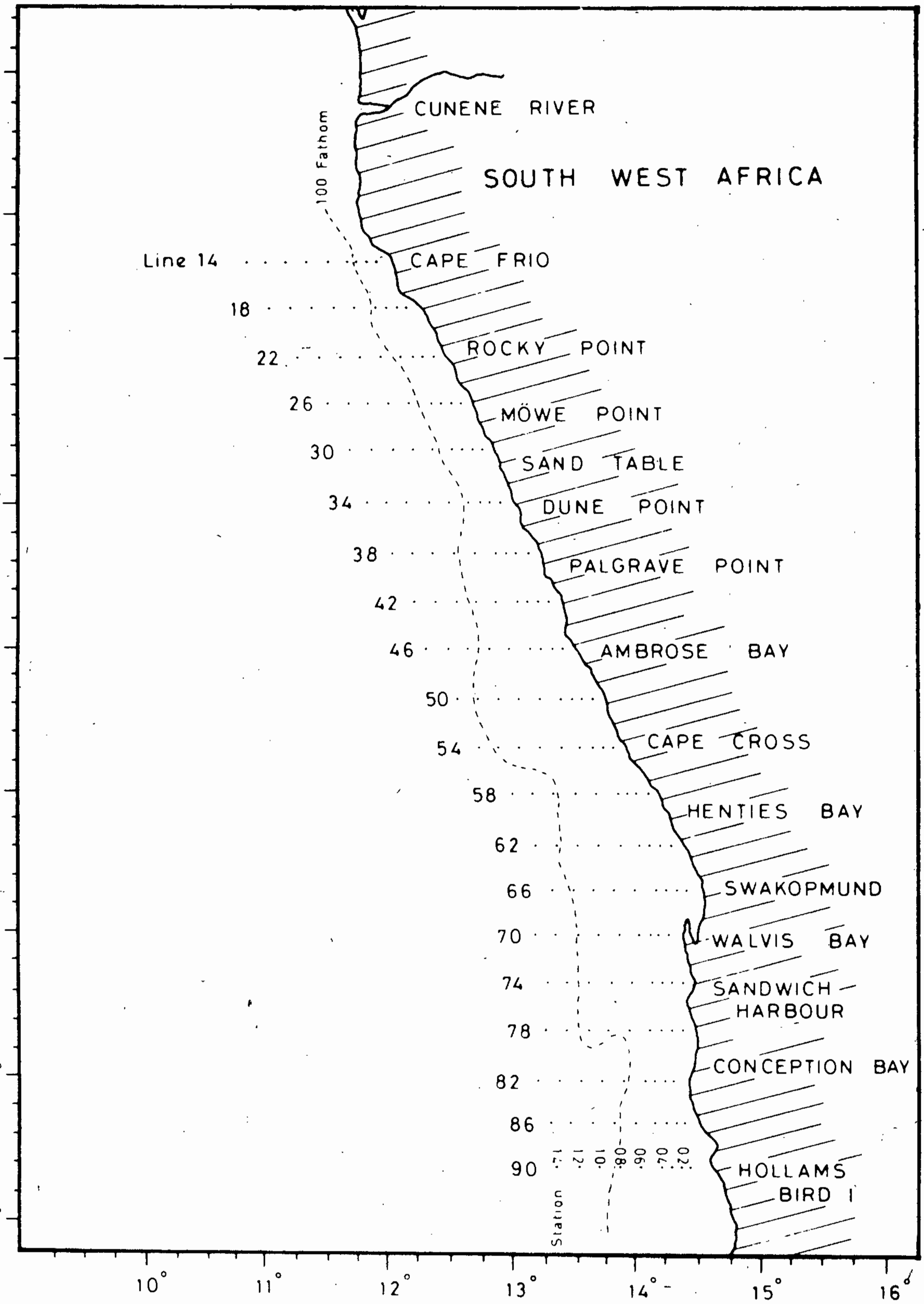


Fig. 1 Location of routine stations occupied during the SWAPELS cruises in 1972/73 and 1973/74

by Ratte (1973) from Walvis Bay and Anders (Sea Fisheries Branch personal communication) from the Cape Peninsula.

The size range of some eggs collected from various localities around Southern Africa is outlined below. The egg of *E. capensis* has been illustrated by Anders (1975).

	Cape Peninsula	Walvis Bay	Cape Frio - Palgrave Point.
Nos.measured	unknown	unknown	305
long axis	1,25 - 1,58mm	1,18 -1,60mm	1,20 - 1,47mm
short axis	0,53 - 0,64mm	0,40 - 0,60mm	0,57 - 0,67mm
month	December	December	January/February
source	Anders (pers. comm.)	Ratte (1973)	this study

Identification of the Larvae

The larval stages of *E.capensis* were identified in this study from descriptions given by E.H. Haigh and A.E. Louw of the South African Museum (unpublished). The larvae are typically clupeid, being elongated and slender with a posterior anus. Preserved newly-hatched larvae measured between 2,52 and 2,95 mm.

The larvae of anchovy and pilchard are similar in many respects and their identity can sometimes be confused. Differences in the position of the mandible in relation to the eye, the location of the dorsal fin in relation to the anal fin and the number of myomeres can be used in most cases to distinguish between the two larval forms. Some of these distinguishing characters are listed below (after E. H. Haigh, unpublished).

Anchovy *E. capensis*	Pilchard *S. ocellata*
Mandible extending well beyond the posterior border of eye and maxilla to posterior third of eye.	Mandible extending at the most to the middle third of eye and maxilla terminating vertically below anterior border of eye.

Anchovy *E. capensis*	Pilchard *S. ocellata*
Posterior end of dorsal fin and anterior end of anal fin usually overlapping in smaller larvae and situated at least opposite each other in larger larvae.	Origin of anal fin well behind posterior end of dorsal fin.
The number of myomeres range from 44 - 45.	The number of myomeres range from 49 - 50.

These larval characteristics were particularly useful in distinguishing between anchovy and pilchard larvae larger than 6,0mm SL. Smaller anchovy larvae were sometimes more difficult to identify precisely because larval characteristics were not clearly differentiated. The dorsal and anal fins were usually undeveloped at this early stage and damage to newly-hatched specimens during the collections sometimes made it difficult for larval characters to be positively identified. However, since larvae of both species were uncommon in the same haul and the seasonality, spawning and geographic distribution of the larvae of the pilchard and anchovy differed, confusion over the identity of recently-hatched anchovy larvae may be regarded as negligible.

The Distribution and Seasonality of Anchovy Eggs.

The collection of anchovy eggs posed some problems. During the first survey, a small paired bongo unit with a mouth diameter of I8cm and a 300 micron mesh was used specifically to sample anchovy eggs at stations 02, 04, 06, 08 and IO on each line. However, it proved unsatisfactory due to frequent clogging of the meshes with dense concentrations of phytoplankton (*Fragilaria* sp.). The mouth area of the units was also considered to be too small to provide reliable information on egg abundance (King and Robertson I973). During the second survey, the mouth opening of the sampling units was increased to 30cm diameter, but phytoplankton again caused frequent clogging of the meshes, to the extent that sampling for anchovy eggs had to be periodically discontinued.

Anchovy eggs, therefore, were not collected reliably or in sufficient number to provide a good indication of monthly abundance or horizontal distribution. In general, the egg collection data suggested that spawning occurred continuously from October to March/April with isolated spawning evident in the south during late spring. However, most of the eggs were found in northern waters during summer/early autumn. (December - March/April).

An earlier report on anchovy spawning off South West Africa (King I977 in press) also showed that eggs were found from October to April but occurred in greatest quantities from December to March. King (op.cit.), however, noticed that anchovy eggs were more abundant in the south whereas in this investigation, eggs were more numerous in the north.

Occurrence of Anchovy Eggs in Relation to Temperature and Salinity.

Anchovy eggs were collected only at surface temperatures ranging from I3,4°C to 20,8°C. (Table I). Approximately 70 percent of the eggs were taken at surface temperatures between I8,1° and 20,0°C. Less than one per cent of the eggs were collected at surface temperatures greater than 20,0°C and approximately 29 percent of the eggs occurred at surface temperatures lower than 18,I°C.

TABLE 1 : The relative abundance of anchovy eggs in relation to surface temperature.

Temperature Range °C	No.of eggs	No.of hauls containing eggs	Mean no.of eggs per haul	Percentage of egg occurrence
12,1 - 13,0	0	0	0	0
I3,1 - 14,0	344	4	86,8	7,2
I4,1 - 15,0	70	7	10,5	1,5
15,1 - 16,0	232	9	25,7	4,8
16,1 - 17,0	482	12	40,1	10,1
17,1 - 18,0	342	12	28,5	7,2
18,1 - 19,0	1384	12	115,3	29,9
19,1 - 20,0	1861	8	232,6	39,2
20,1 - 21,0	31	4	7,7	0,6

The oblique hauls taken in the 0-50m layer only indicate that eggs were present within the water column. No information on the vertical distribution of anchovy eggs was gathered during the course of the investigation. However, in studies on the vertical distribution of a variety of fish eggs and larvae, Ahlstrom (I959) showed that the egg of the northern anchovy *E.mordax* occurred predominantly in the upper 20 metres.

In the Cape waters, Anders (I975) found large numbers of anchovy eggs at various stages of development at or close to the surface. Further evidence that anchovy spawn close to the surface in the Cape is given by O'Toole (I976 b). Since temperature to a depth of 50m was routinely measured at SWAPELS stations (O'Toole, I977a), it is possible to relate egg occurrence to temperature at selected depths within this column of water. If 20 metres is chosen as the zone of greatest concentration then eggs occurred at temperatures ranging from 11,5 to I9,0°C (Table II). Nevertheless, approximately 73 percent of the anchovy eggs were taken at temperatures of between I6,1 and I9,0°C. The remainder were found at temperatures less than I6,0°C.

TABLE II : The relative abundance of anchovy eggs in relation to temperature at 20m.

Temperature Range °C.	No.of eggs	No.of hauls containing eggs.	Mean no.of eggs per haul.	Percentage of egg occurrence.
11,1 - 12,0	10	1	10,0	0,21
12,1 - 13,0	107	4	26,7	2,2
13,1 - 14,0	451	11	41,0	9,4
14,1 - 15,0	310	12	20,6	6,5
15,1 - 16,0	376	15	25,0	7,8
16,1 - 17,0	1243	11	113,0	26,0
17,1 - 18,0	1646	9	182,8	34,4
18,1 - 19,0	643	4	160,7	13,4
19,1 - 20,0	0	0	0	0

The results are in general agreement with the temperature ranges of anchovy egg presence given by other workers. King (I977 in press) found anchovy eggs off South West Africa at surface temperatures ranging from 12,3° to 21,8°C.

In the Cape, Baird and Geldenhuys (I973), recorded anchovy eggs over a surface temperature range of 9,5° to 22,0°C with the optimum temperatures between I5° and 21°C.

Anchovy eggs were taken within a surface salinity range of between 35,05°/oo and 35,75°/oo, indicating a tolerance to wide variations in salinity. The relative abundance of eggs in relation to surface salinity is shown in Table III.

TABLE III : Occurrence of anchovy eggs in relation to surface salinity.

Salinity range °/oo	No.of eggs.	No.of hauls containing eggs.	Mean no.of eggs per haul.	Percentage of egg occurrence.
35,05 - 35,15	347	7	49,5	7,3
35,16 - 35,25	636	7	90,8	13,4
35,26 - 35,35	214	14	15,2	4,51
35,36 - 35,45	616	15	41,0	12,9
35,46 - 35,55	1083	16	67,6	22,8
35,56 - 35,65	1629	7	232,7	34,3
35,66 - 35,75	225	2	112,5	4,7

Eggs occurred in relatively large numbers at both high and low salinities but were more abundant at salinities greater than 35,35°/oo. Again, as in the case of temperature, the optimum salinity range is difficult to determine because eggs were not representatively sampled during the surveys. Eggs are however likely to be found at relatively high salinity when associated with warmer water. In general, anchovy eggs occurring in the north would usually be found at a surface salinity greater than 35,30°/oo. Anchovy spawning in the south would take place where the salinity was less than 35,20°/oo. Anders (I975) reported that anchovy eggs taken off the south east coast of South Africa were associated with low salinity water and were scarce or absent at high surface salinity (35,55°/oo). In contrast, anchovy spawning in South West Africa apparently takes place over a greater salinity range.

Distribution and Seasonality of Larvae.

Anchovy larvae were common and widely distributed in the northern part of the research area during both surveys. Approximately 98 percent of all the larvae collected during the investigation were found between Cape Frio ($18^{\circ}20'$S) and Palgrave Point ($20^{\circ}20'$S). Less than 2 percent of the total numbers were taken south of Palgrave Point and only a few specimens were recorded in the plankton south of Walvis Bay (23°S). The percentage of the total number of larvae taken in the different parts of the survey area during both surveys is summarized below:-

Area	Station line	Percentage of Total.
Cape Frio - Mowe Point	14 - 26	90,2
Mowe Point - Palgrave Point	30 - 42	8,0
Palgrave Point - Henties Bay	46 - 58	1,7
Henties Bay - Sandwich Hb.	62 - 74	0,1
Sandwich Hb. - Hollams Bird Is.	78 - 90	0

Anchovy larvae were found over the entire inshore/offshore range, but over 85 percent of the total were taken from offshore waters at distances greater than 30km from the coast. Maximum concentrations of larvae were taken at distances of 60 - 112 km offshore (Table IV). The northern and seaward extent of the larval distribution was not determined in either of the surveys but the presence of high densities at the northern and offshore stations suggested a considerable extention of distribution north and west of the survey area.

TABLE IV : The percentage occurrence of the total number of anchovy larvae (1972 - 74) in relation to distance from shore.

Distance from shore	Percentage occurrence	1972/73	1973/74
10km or less	0,2	0,1	0,8
10 - 20km	0,5	0,6	0,4
20 - 30km	3,1	2,9	6,2
30 - 50km	13,2	11,4	19,0
50 - 100km	63,9	69,3	46,7
100km or more	18,9	16,5	26,8

The overall distribution and the main centre of larval abundance were remarkably similar for both survey periods (Figs. 2 & 3) but the larvae were four times more numerous in the collections of I972/73 than in I973/74.

Larvae were found in the plankton from November to March in Survey 1 and October to April in Survey 2. During I972/73, 99 percent of the total number of larvae were collected between December and March. In comparison, 96 percent were taken during the same period in I973/74.

Survey 1 (August 1972 - March 1973)

The horizontal distribution and abundance of anchovy larvae together with surface isotherms for each survey cruise are illustrated in Figure 4. The monthly hauls and larval abundance are summarized in Table V and larval length frequencies for each cruise are shown in Figure 5.

Anchovy larvae were first taken in the plankton during November when three specimens were captured offshore in the south of the research area. The larvae measured from I4 to I7 mm and probably resulted from eggs spawned as early as September. Larvae were more common in December but were found only in the north, between Cape Frio and Mowe Point. The centre of abundance was 24 to 80km offshore. The larvae consisted of mixed size groups ranging from 3 to 26 mm in length. Specimens measuring between I2 and 20 mm were the dominant size classes. It is assumed that these larger forms were at least 2 - 3 weeks old and hatched from eggs spawned in the north during November. In addition the presence of some smaller larvae, although few in number, indicated more recent spawning.

Anchovy larvae were most abundant during the month of January and formed 40 percent of the total number of larvae collected on all the survey cruises. Larvae distribution extended further south to Palgrave Point but was generally similar to December. Larvae were plentiful in offshore waters at distances of 80 to II2 km from the coast. The greatest number of larvae were taken at stations I4 - 10, approximately 80 km west of Cape Frio.

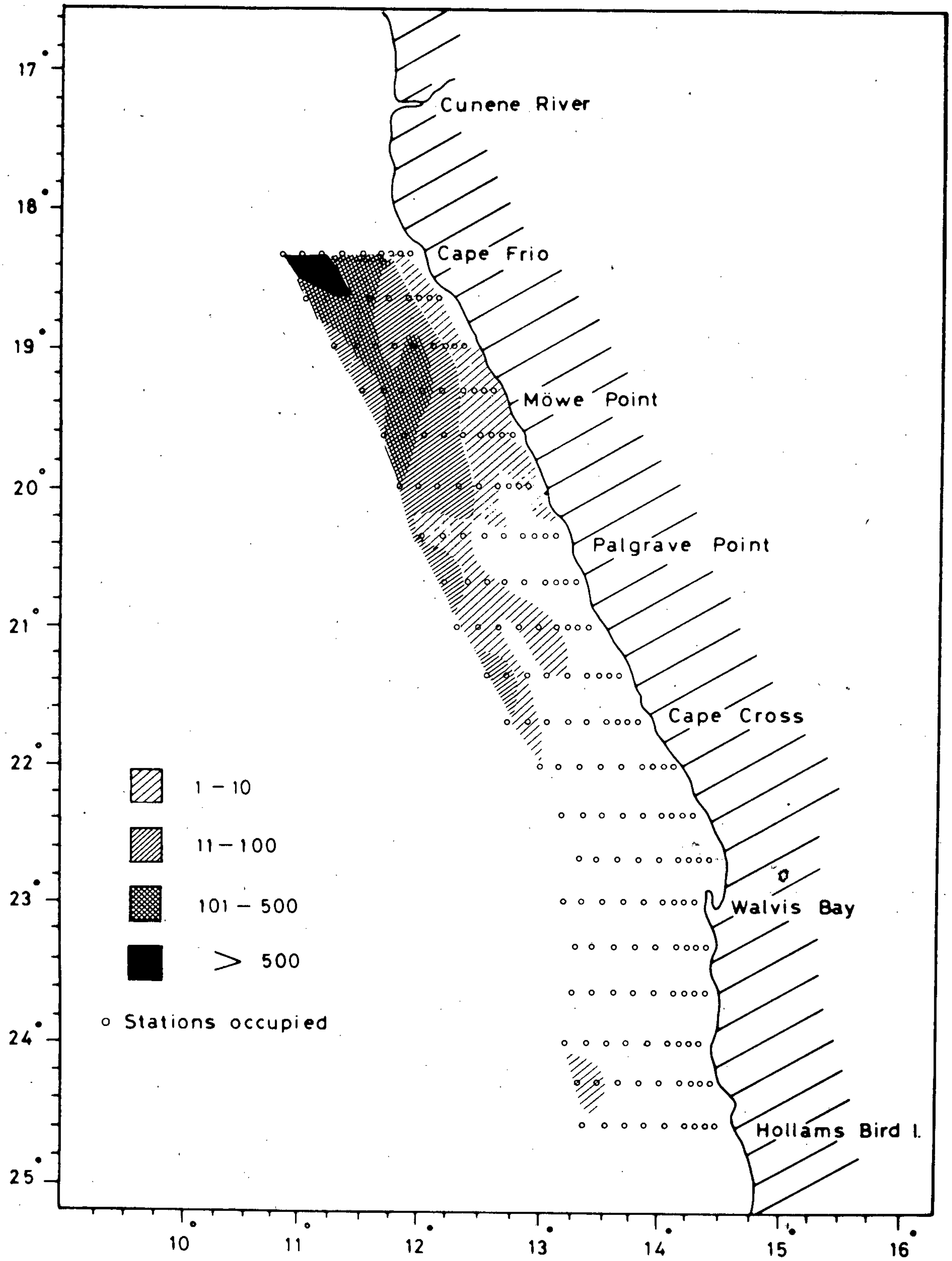


Fig. 2 Distribution and abundance of anchovy larvae during Survey 1 (values represent cumulative standard haul totals for all cruises)

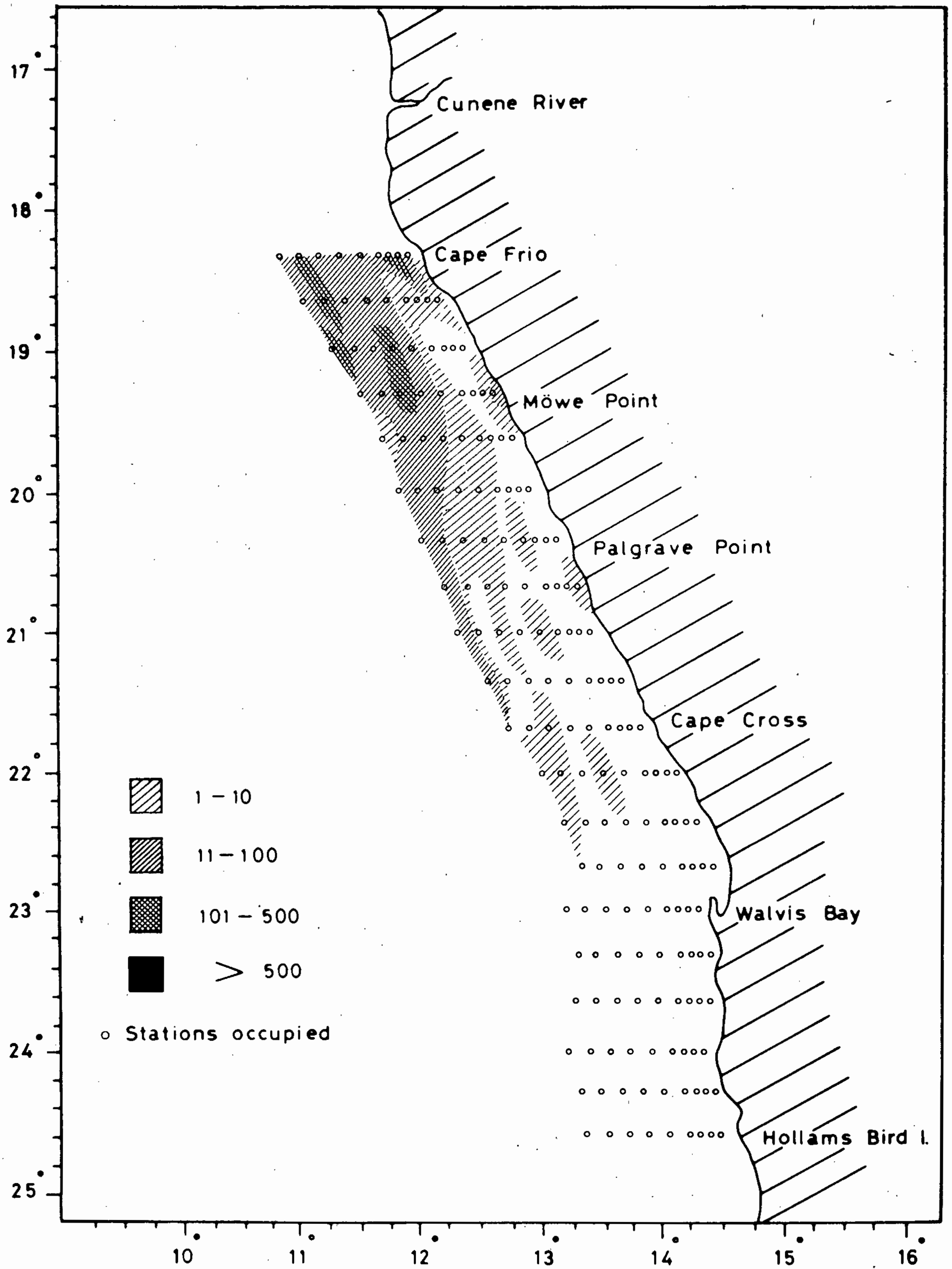


Fig. 3 Distribution and abundance of anchovy larvae during Survey 2 (values represent cumulative standard haul totals for all cruises)

The length of the specimens ranged from 5 - 23 mm with over 75 percent of the larvae measuring between I3 and 20 mm. The size composition and increase in numbers suggested that spawning intensified in December.

In February, anchovy larvae were still common in the plankton and were widely distributed over the whole area north of Palgrave Point. Specimens were most numerous 50-80 km from the coast off Cape Frio and Mowe Point. Approximately 85 percent of the specimens captured during the February cruise were recently hatched (3 - 12 mm) which showed that spawning was widespread in the north between January and early February.

The number of larvae increased slightly in March and consisted of mixed size groups ranging from 4 to 23 mm. All the larvae were caught in offshore waters between Cape Frio and Palgrave Point. The centre of greatest larval abundance was 80-112 km from the coast west and south-west of Cape Frio. Specimens measured between 4 and 23 mm, but larvae with lengths of 8-16mm formed 75 percent of the sizecomposition. The distribution and size frequency of larvae collected in March suggested that anchovy spawning continued into late February and early March.

TABLE V : A summary of the monthly hauls and abundance of anchovy larvae I972 - I973.

Month	No.of hauls	No.of positive hauls	No.of larvae collected	Mean no. of larvae per 10m ^{2}	Percentage of total collected
August	126	0	0	0	0
September	I26	0	0	0	0
October	156	0	0	0	0
November	180	2	3	3,4	0,2
December	I80	20	153	20,3	4,5
January	180	24	1733	237,7	40,I
February	I77	54	1077	60,2	25,9
March	177	28	1350	252,4	32,2

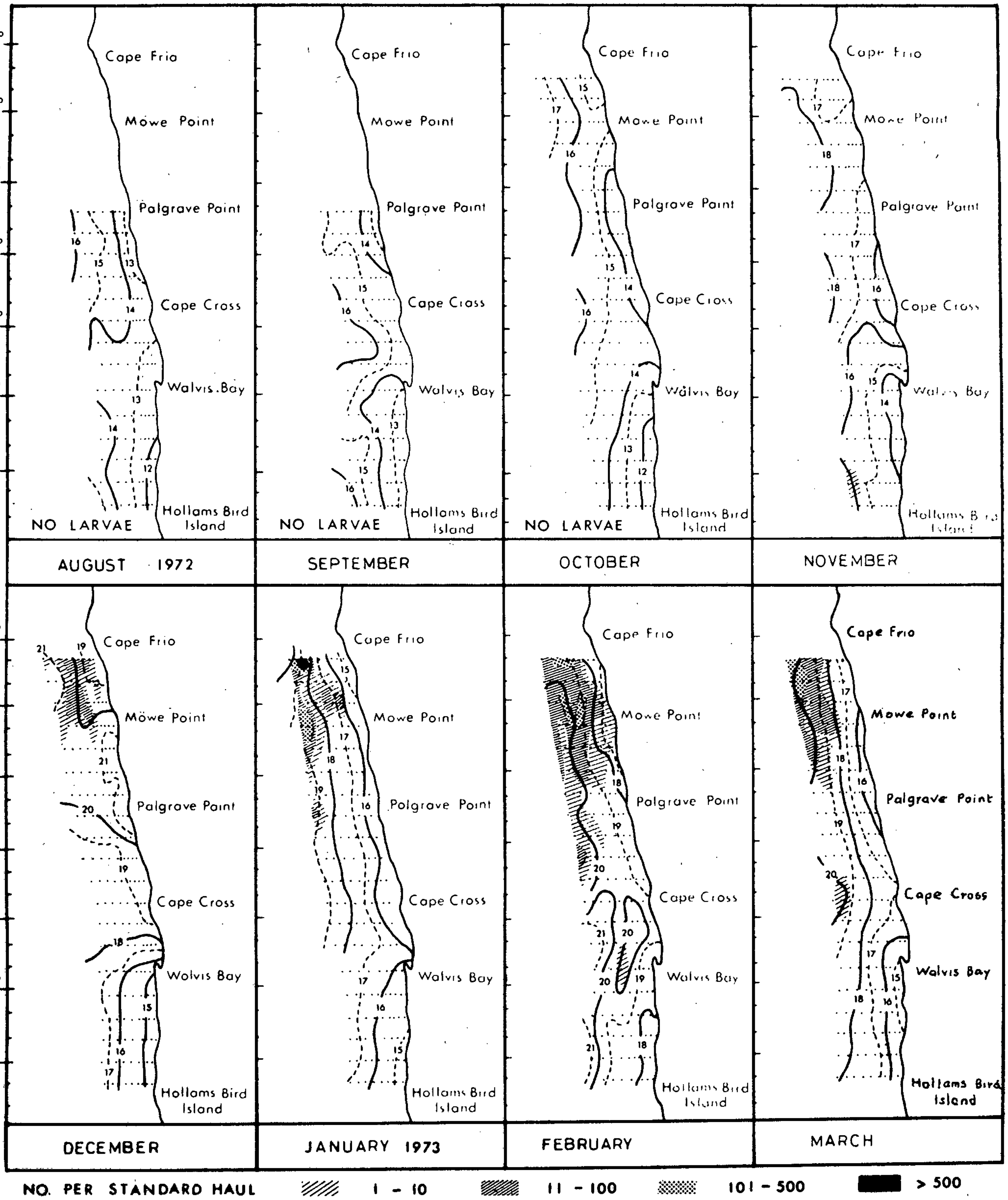


Fig. 4 Monthly distribution and abundance of anchovy larvae, August 1972 to March 1973

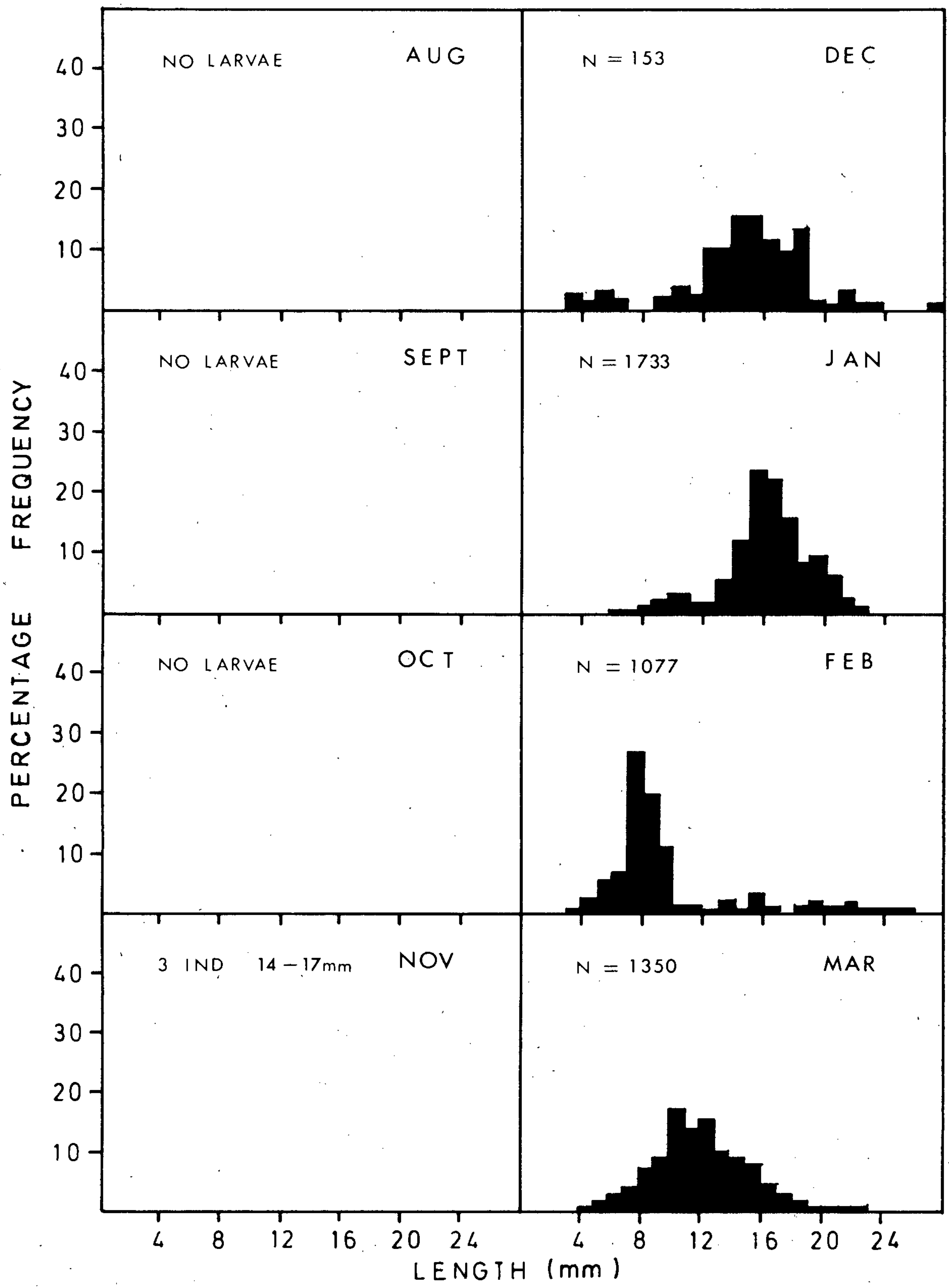


Fig. 5 Length composition of anchovy larvae collected during the survey cruises August 1972 to March 1973

SURVEY 2 (August I973 - March/April I974)

Anchovy larvae were taken in the plankton from October to March/April predominantly in the northern part of the research area. The regional distribution of larvae during summer and early autumn was similar to that of Survey 1.

The monthly distribution and abundance of larvae together with surface temperature distribution is shown on Figure 6 and the length composition of specimens collected on each cruise on Figure 7. A summary of the monthly hauls and catches is given in Table VI .

Larvae were generally scarce from spring to early summer although small isolated patches were found offshore between Cape Frio and Palgrave Point. The samples contained mainly larger size groups (I0 - 22 mm) presumably derived from sporadic spawning in September, October and November.

In January, larvae were numerous in the offshore waters north of Palgrave Point with the greatest density occurring approximately 80 km west of Mowe Point. The length composition showed that about 50 percent of the specimens were less than I0 mm long and probably hatched from eggs spawned during late December or early January. It is very likely that the more advanced stages resulted from earlier spawning.

Larvae reached peak abundance in the plankton during February and were widely distributed from Cape Frio to Cape Cross. Highest concentrations were found at stations I4-04 and I4-12 approximately 32 and 96 km south west of Cape Frio. Further south, larvae were also common 96-112 km west of Palgrave Point. Most of the specimens collected in February were recently hatched, indicating heavy spawning in early February.

Anchovy larvae were still plentiful and widespread in the offshore waters north of Palgrave Point during March/April. Maximum density (+ 500 per I0 m^2) was recorded at station 22-14 about 112 km from shore. Some isolated specimens were also found offshore in the vicinity of Cape Cross.

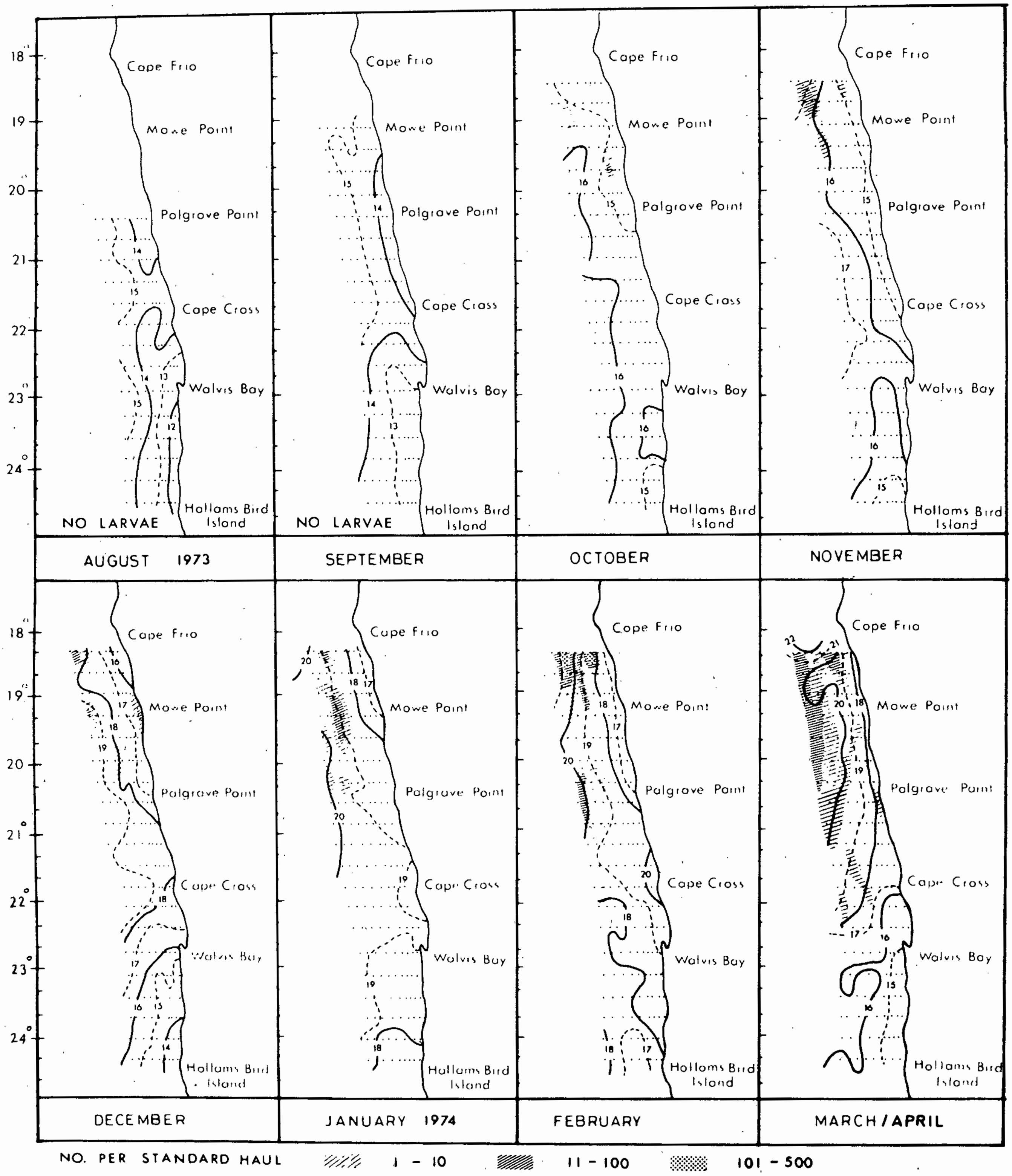


Fig. 6 Monthly distribution and abundance of anchovy larvae, August 1973 to March / April 1974

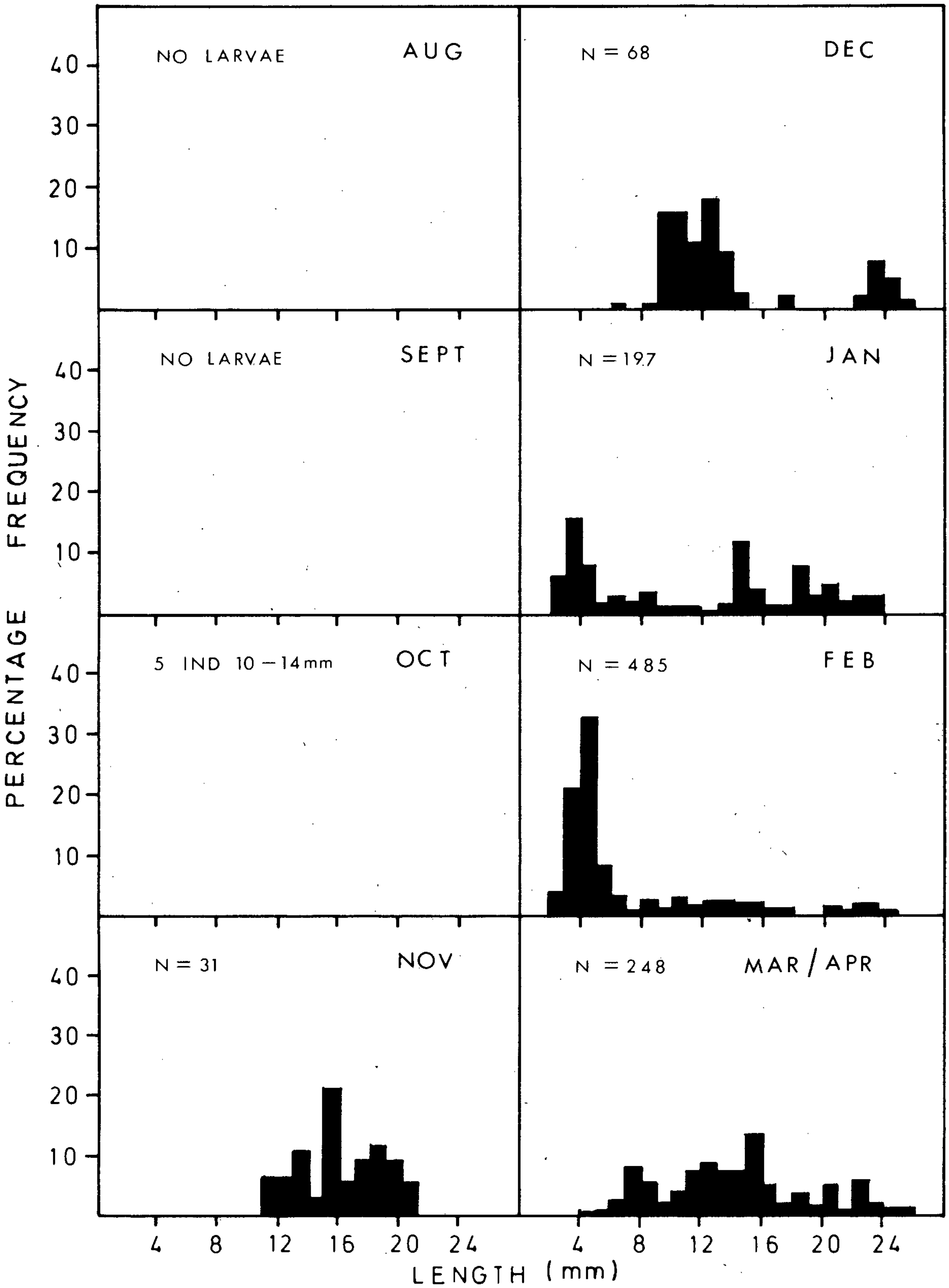


Fig. 7 Length composition of anchovy larvae collected during the survey cruises August 1973 to March / April 1974

Although the size composition of those collected during March/April ranged from 4 to 26 mm in length, 75 percent were longer than IO mm. These larger forms probably represented the same cohort of newly-hatched larvae captured during the February cruise. The small number of early stages in the plankton suggested a decline in spawning activity between February and March.

TABLE VI : A summary of the monthly hauls and abundance of anchovy larvae I973 - I974.

Month	No.of hauls taken	No.of positive hauls	No.of larvae collected	Mean no. of larvae per $10m^2$	Percentage of total collected
August	126	0	0	0	0
September	135	0	0	0	0
October	180	2	5	10,1	0,5
November	180	6	31	37,2	3,0
December	180	8	68	20,5	6,5
January	180	10	197	13,9	20,1
February	169	32	485	60,5	46,9
March/April	175	36	248	36,7	24,9

Diurnal Variation in Catches

Anchovy larvae showed marked fluctuation in abundance over a twenty four hour period. Over three times as many larvae were caught in night hauls as in day hauls. The day/night ratio of larvae of different sizes clearly indicated that the larger size groups accounted for the high numbers in the night collections. (Table VII)

Figure 8 reflects the percentage catch (at positive stations only) of three different size categories of anchovy larvae at 2-hourly intervals over a period of 24 hours. Recently hatched larvae ($<$ 5,0 mm) were most abundant during the day and least numerous at night. No larvae less than 5,0 mm in length were captured during the early hours of the morning. Peak abundance of this size category was between IOh00 and I2h00.

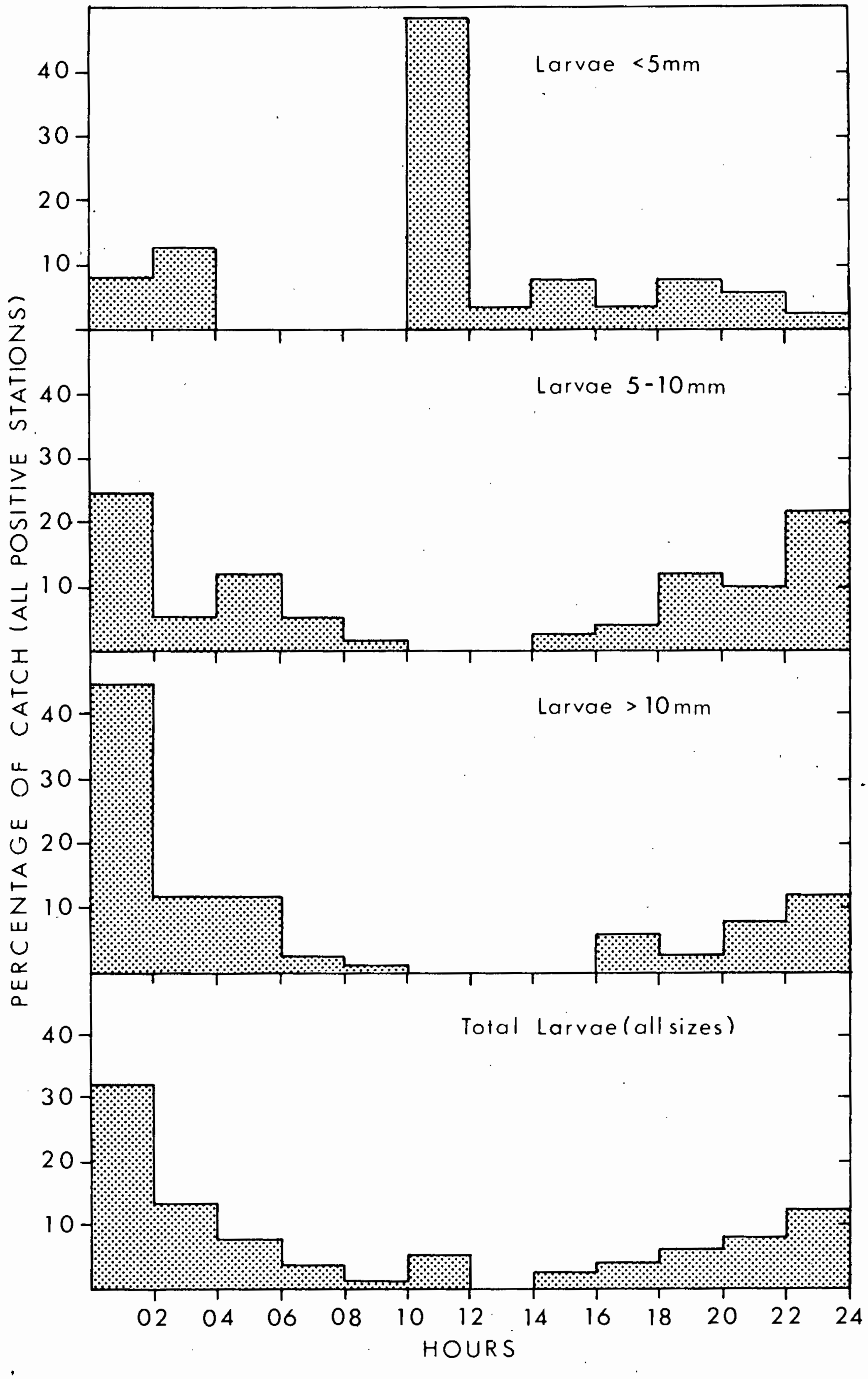


Fig. 8 Diurnal variation in catch rates of anchovy larvae according to size categories (all cruises)

TABLE VII : Size categories of anchovy larvae caught during day and night hauls.

Size group (mm)	Day Hauls No. of larvae	Percent	Night Hauls No.of larvae	Percent	D/N Ratio
< 5,0	370	72,5	142	27,5	2,6: 1
5,1 - 10,0	241	25,8	690	74,2	1: 2,9
10,1 - 15,0	363	11,4	2784	88,6	1: 7,4
>15,0	38	5,5	650	94,4	1: 17
TOTAL:	1112	26,1	4266	73,9	1: 3,8

In contrast, older larvae were rarely taken during the day and were totally absent from samples collected between IOh00 and I4h00. Towards dusk, larger larvae were taken more frequently and peak catches were recorded between midnight and 02h00. During early morning, the number of larvae in the plankton declined and collections after dawn (07h00) yielded few.

Ahlstrom (I959) also found that larvae of the northern anchovy E. mordax were almost five times as abundant in the night hauls as in the day, and it was reported that a greater proportion of larger larvae were captured in night hauls. The larvae of the Japanese anchovy E.japonicus also showed a similar diurnal trend, increasing towards dusk to reach maximum abundance at midnight, again decreasing towards dawn.(Ida I972).

Occurrence of Larvae in Relation to Temperature

Anchovy larvae were captured in regions where surface temperatures ranged from 14,8° to 22,0°C but were most abundant at temperatures between I7,0° and 21,0°C. Seventy-seven percent of the larvae caught were taken at temperatures of I8° - 21,0°C. Only 70 percent were found at surface temperatures below I8°C and 3 percent at temperatures greater than 21,0°C. The abundance of larvae in relation to surface temperature is summarised in Table VIII.

TABLE VIII : Relation between surface temperature and abundance of anchovy larvae I972 - 1974.

Surface temperature °C.	Number of standard hauls that collected:-					
	I-5 larvae	6-10 larvae	11-100 larvae	101-250 larvae	250+ larvae	Total larvae
14,1 - 15,0	0	1	0	0	0	1
15,1 - 16,0	5	1	1	0	0	7
16,1 - 17,0	4	0	3	0	0	7
17,1 - 18,0	11	4	10	1	0	26
18,1 - 19,0	26	9	21	7	1	64
19,1 - 20,0	16	10	22	2	5	55
20,1 - 21,0	9	3	25	4	1	42
21,1 - 22,0	4	0	3	0	0	7

Since the hauls were made between the surface and 50 m , larvae could have been taken at any depth or temperature within the 0 - 50 m column. Consequently, it is difficult to relate the occurrence and abundance of larvae to a particular depth or temperature. In studies on the vertical distribution of the larvae of the northern anchovy, E. mordax, off California, Ahlstrom (I959) recorded that at some stations larvae were abundant in the upper 23 m but were generally more numerous in the mixed layers between 24 and 48 metres.

Ida (I972) noted that the larvae of the japanese anchovy, E. japonicus were most abundant at depths of 20 metres. If the frequency occurrence of anchovy larvae taken during this investigation is related to temperature at a depth of 20 m, then larvae were found over a temperature range of I3,9° - 21,0°C. However, 72 percent would have been caught between I7,1 and 21,0°C, 26 percent between I5,1° and I7,0°C and less than 2 percent at temperatures below I5,0°C. The abundance of larvae in relation to temperature at a depth of 20 m is summarized in Table IX .

TABLE IX : Relation between temperature at 20m and abundance of anchovy larvae 1972 - 1974

Temperature at 20 m (°C)	Number of standard hauls that collected:-					
	1-5 larvae	6-10 larvae	11-100 larvae	101-250 larvae	250+ larvae	Total
13,1 - 14,0	0	I	0	0	0	1
14,1 - 15,0	2	0	0	0	0	2
15,1 - 16,0	6	2	1	22	1	12
16,1 - 17,0	9	6	12	4	0	31
17,1 - 18,0	17	6	21	6	1	51
18,1 - 19,0	15	3	16	6	1	41
19,1 - 20,0	3	1	6	4	4	18
20,1 - 21,0	2	1	7	1	0	11

To test whether the relationship between larval abundance and temperature classes at the surface and at 20 m was significant, the Kruskal-Wallis one way analysis of variance by rank (Siegel 1954) was applied to the individual observations on which Tables VIII and IX are based. The results yielded H° values of 20,45 and 21,38 respectively which suggested that differences were significant at the 1% level.

It is apparent, therefore, that anchovy larvae are associated mainly with high temperatures and that larvae collected within the 0-20 m layer are likely to occur at temperatures of between 17,0° and 21,0°C.

Occurrence of Larvae in Relation to Salinity.

No subsurface salinity measurements were taken and larval occurrence is related to surface salinity only. Anchovy larvae occurred at surface salinities ranging from 35,00°/oo to 35,90°/oo. The abundance of larvae in relation to surface salinity is shown in Table X .

Although the larvae demonstrated a wide tolerance to fluctuations in salinity, 70 percent of hauls containing larvae were made at surface salinities of 35,31°/oo - 35,60°/oo.

Only about 8 percent of the positive hauls were taken at surface salinity less than 35,31°/oo and 21 percent at greater than 35,60°/oo. The same analysis as used in the temperature relationship was applied to the raw data summarized in Table IX and showed that differences were significant at the I% level (H^o = 20,45 ; $P < 0,1$). Based on the observations in Table IX , most anchovy larvae are likely to occur at surface salinities of between 35,31°/oo and 35,60°/oo. Salinities of less than 35,00°/oo are apparently limiting. The upper tolerance level was difficult to determine since the regional distribution of larvae to the north and west was not encompassed. Nevertheless, larvae are probably uncommon at a surface salinity greater than 36,00°/oo.

TABLE X : Relation between surface salinity and abundance of anchovy larvae I972 - I974.

Surface salinity (°/oo)	Numbers of standard hauls that collected:-					
	I-5 larvae	6-10 larvae	11-100 larvae	IOI-250 larvae	250+ larvae	Total larvae
35,00 - 35,10	2	0	0	0	0	2
35,11 - 35,20	1	0	0	0	0	1
35,21 - 35,30	12	1	4	0	1	18
35,31 - 35,40	19	7	14	0	0	40
35,41 - 35,50	18	24	28	5	2	97
35,51 - 35,60	11	4	16	4	4	39
35,61 - 35,70	7	3	10	3	0	23
35,71 - 35,80	6	3	5	3	0	17
35,81 - 35,90	0	3	9	0	0	12

Distribution of Larvae in Relation to Hydrology

The seasonal distribution and abundance of larvae may be related to fluctuations in hydrological events. The hydrology of the area is described in detail for both years by O'Toole (I977a) but surface temperature can be examined in relation to larval distribution in Figures 4 and 6.

Survey 1 (August I972 to March I973)

Anchovy larvae were not found in the plankton between August and October when the hydrological environment was typical of upwelling conditions. In November, coastal upwelling weakened, warm water moved eastwards into the spawning grounds and only a few larvae were encountered.

Larvae first occurred in relatively large numbers in the north during December. The regional distribution of larvae was closely related to a warm influx of I9^{o} - 21^{o}C of water which invaded the area sometime between late November and early December. On the Cape Frio line, the vertical temperature section indicated a warm water intrusion about 30 m in thickness at offshore stations, becoming warmer towards the coast. Vertical mixing was evidently taking place in the upper 20 m layers especially close inshore. Further south, off Palgrave Point, the warm I9^{o} - 21^{o}C water had moved nearer to the surface and was present only as a thin layer, less than IO m in thickness. Thermal stratification was pronounced and conditions were generally stable. Anchovy larvae were noticeably more abundant on the four northerly lines (I4 - 26), where the wedge of warm water was deepest and/or thickest. Larvae were less abundant to the south where the warm water became shallower and moved offshore.

Renewed upwelling in January displaced the warmer water to the west and formed a sharp boundary between the cooler coastal and warmer oceanic water masses. The front was particularly well-developed along the Cape Frio line about 50-60 km from the coast. Further south the frontal system began to weaken and the warmer water was displaced offshore. Vertical temperature profiles showed that strong vertical mixing was associated with the front off Cape Frio and that I9 - 20^{o}C was 25-35 m thick at offshore stations. On the Palgrave Point line, mixing was not as marked and I9^{o}C water was closer to the surface and more offshore. Anchovy larvae were most abundant in the plankton in January and occurred mainly in the warm waters on the oceanic side of the front.

Larval distribution, both inshore and to the south, was closely related to the position of the frontal system. Anchovy larvae were more plentiful offshore, west of Cape Frio where vertical mixing was most marked.

In February, upwelling had weakened in the north and a widespread intrusion of warm I9°-20°C water advanced eastwards. Compared with January, the distribution of larvae was wider both inshore and to the south, apparently corresponding to the extensive distribution of warm mixed water. Although no vertical temperature sections were taken during this month, it was obvious from surface features that the frontal system was still well-developed in the north and that considerable mixing was taking place. Anchovy larvae were most abundant between the I9° and 20° surface isotherm.

Renewed upwelling in March pushed the oceanic water westward. Larvae were also found further offshore and appeared to follow the seaward displacement of the I9°-20° isotherm. The distribution of temperature with depth on the Cape Frio line showed that the wedge of I9°-20°C water was 30-35 m in thickness at the outer stations.

To the south, off Palgrave Point, the warm water mass moved offshore and closer to the surface. The upward slopes of the isotherms in the north suggested active mixing in upper layers. Anchovy larvae were more common at offshore stations where I9° and 20°C water was deepest and were also found at the outermost stations off Cape Cross (line 54) where a small intrusion of oceanic water pushed against cooler coastal water.

Survey 2 (August I973 to March/April I974)

The general hydrological features in I973/74 were similar to those of I972/73. However, the sequence of events differed somewhat during survey 2. The seasonal distribution and abundance of anchovy larvae also reflected corresponding fluctuations in response to hydrological change.

As in I972, larvae were virtually absent from the plankton during the active upwelling months (August to October) of I973. In November, larvae were not very common and occurred offshore between Cape Frio and Mowe Point in relatively warm, well-mixed I6 - 17°C water.

Warmer I8° - 19°C water advanced inshore in December and larvae were found mainly along the mixing area on the oceanic side of the front. Larva abundance increased considerably in January following an influx of I9°-20°C water towards the coast. At offshore stations north of Palgrave Point, I9°C water was present at depths of I5-20 m. Inshore and to the south, the I9°C water became shallower, seemingly limiting the distribution of larvae.

During February, highest densities of larvae were found to correspond with an intrusion of 20°-21°C water. Vertical temperature profiles along the Cape Frio and Palgrave Point line showed that I8°-20°C water was present over a greater depth than in January. South of Palgrave Point, the tongue of warm water was pushed closer to the surface and displaced offshore. Compared with January, mixing was more active in the upper layers, at offshore stations where larvae were found and specimens were more widely distributed both inshore and to the south. The centre of larval abundance occurred off Cape Frio between the I8° and 21°C isotherm.

In March/April, a very warm tongue of 21°-22°C water advanced southward and 20°C water pushed closer to the coast. Temperature distribution in the upper layers off Cape Frio showed that the warm core of I9°-20°C water was present at depths of 20-30 m but became progressively shallower towards the coast and to the south.

The distribution of anchovy larvae during March/April was closely related to both the vertical and horizontal distribution of the I9° and 20°C isotherms.

Variation in Distribution between Years.

Anchovy larvae were rarely collected during the active upwelling months (August to October) of either year.

By November, upwelling had usually weakened and warm water pushed shorewards. Although temperatures were higher and warm water intrusions more widespread in the north during November I972, anchovy larvae were more numerous in November I973 at lower temperatures. Occurrence of larvae during November I973 could have been caused by the presence of strong vertical mixing in the north associated with relatively warm I7°C water which may have stimulated anchovy to spawn earlier. In contrast, vertical mixing was not as marked during November I972 and hydrological conditions were more stable.

During summer months, the movement of warm I8°-20°C water inshore and southwards appeared to have a considerable influence on the timing and intensity of spawning. For example, incursions of I9 - 20°C water were more pronounced and larvae were more plentiful in the plankton during December I972 than in December I973.

Although, surface temperatures were generally similar in January of both years, larvae were more abundant in the plankton during Survey 1. In January I973, a well-developed oceanic front occurred in the north corresponding with the centre of larval abundance. The front was weaker and not as evident in the upper layers in January I974.

Anchovy larvae were also more numerous and widely distributed in the plankton in February I973 when warm oceanic water penetrated further south and eastwards. However, in February I974 larvae were not as abundant and the influx of warm water was weaker and less extensive.

Larvae were more abundant and widely distributed during March I973 than in March/April I974, perhaps indicating that hydrological conditions were more favourable for spawning in I973. Although water was warmer in March/April I974, vertical mixing was more evident and the core of I6°C water was IO-I5 m deeper in March I973, particularly along intermediate lines between Cape Frio and Palgrave Point.

Development and Growth

The developmental rate of South West African anchovy eggs was not determined but eggs collected off the Cape Peninsula hatch after 53 hrs at a temperature of 16,0°C and after 36 hrs at 20,0°C (D.P.F. King, Sea Fisheries Branch, personal communication). These rates of development compare favourably with those of the northern anchovy E. mordax (Zweifel and Lasker 1976), the Japanese anchovy E. japonicus (Nishikawa 1901) and the Argentine anchovy E. anchiota (de Ciechomski 1967). If anchovy eggs collected off South West Africa develop at the same rate as those from the Cape Peninsula, then eggs spawned in waters of 17,0°C would take from 1½ to 2 days to hatch. On hatching, anchovy larvae have a mean length of 2,90mm and would take from 2½ - 3 days to reach a stage where the yolk-sac is fully absorbed and the eyes are pigmented (3,75 - 3,85 mm) (D.P.F. King, Sea Fisheries Branch, personal communication). Therefore it could be assumed that the small larvae (3,5 - 4,0 mm long) collected during the SWAPELS cruises had hatched 2½ - 3 days previously.

The usual method of estimating the age of fish larval populations in the sea is to trace length cohorts of groups of larvae by sampling an area repeatedly over a short period of time. In this study, the continuous nature of spawning, which was reflected by the frequent presence of mixed size groups in the samples, made the distinguishing of cohorts between successive cruises difficult. In addition, since the time interval between each cruise averaged 30 days, a patch of newly-hatched larvae identifiable during one month was not always traceable during the following month due to mortality, net avoidance and dispersal. Nevertheless, a particular group of larvae could be distinguished on both the January and February cruises of 1974 (Fig. 6) and an estimate of the growth of anchovy larvae made.

On January 12-13, a patch of larvae consisting mainly of recently-hatched individuals (<5,0 mm long) were found in the offshore plankton west of Möwe Point. A separate group of predominantly larger larvae (20 - 25 mm) were located during the following cruise on February 8-9 but occurred west of Palgrave Point, i.e. further south. It is assumed that some of the more advanced larvae captured during the February cruise were derived from the same population as that sampled in January as hydrological evidence (O'Toole, 1977a) suggested a southward current movement during the intervening period. A comparison of the relative abundance of size classes in the two groups showed that in January, larvae measuring between 3 mm and 4 mm predominated whereas specimens of between 20 mm and 22 mm were most common in February (Table XI). This indicated a length increase of 17-19 mm in a period of 26-27 days i.e. 0,5 - 0,6 mm per day, at temperatures varying between 19°C and 20°C or that anchovy larvae of 20 mm to 22 mm in length were 28-30 days old from the time of hatching.

TABLE XI Length composition of anchovy larvae captured at two locations on January 12 - 13 and February 8 - 9 1974.

January (west of Möwe Point)		February (west of Palgrave Point)	
Size Range (mm)	Percentage	Size Range (mm)	Percentage
3,0	12,2	17,0	0
3,1-4,0	37,1	17,1-18,0	4,5
4,1-5,0	18,9	18,1-19,0	9,0
5,1-6,0	6,0	19,1-20,0	0
6,1-7,0	8,8	20,1-21,0	38,4
7,1-8,0	17,0	21,1-22,0	22,7
>8,0		22,1-23,0	20,0
		23,1-24,0	5,4
		>24,0	0

In general, the growth of E. capensis larvae was similar to that of that of the northern anchovy. Kramer and Zweifel (I970) estimated the age of a 20 mm laboratory reared E. mordax larva as 33 days from the time of hatching at a temperature of I7°C and 2I days old at 22°C.

Dispersal

The dispersal of eggs and newly hatched larvae from the breeding areas in the north will obviously be influenced by the movement of water masses in the region.

Although no in situ current measurements were taken during the surveys, certain gross features of water circulation could be detected from the distribution of temperature and salinity (see Figs. 4 and 5: O'Toole I977a). During summer, warm saline water generally moves inshore and slowly southwards over the spawning grounds. However, circulation is also variable and subject to continual fluctuation.

February and March were chosen to illustrate dispersal trends as these months are typical (Fig. 9). In February I973, anchovy larvae less than 8,0 mm long were concentrated in a large area between Cape Frio and Palgrave Point. By March, the distribution of larvae longer than I5,0 mm indicated an off-shore, westerly displacement probably as a result of renewed upwelling near the coast during the intervening period (see Fig.4).

In contrast, the dispersal of larvae over February and March/April I974 showed a different trend. Small larvae were found mainly off-shore during February but in March/April the distribution of larger specimens suggested that movement had taken place both inshore and southwards. Hydrological data over these two months (Fig.6) clearly indicated a marked southerly and inshore thrust of warm water which must have been responsible for the general direction of larval transport.

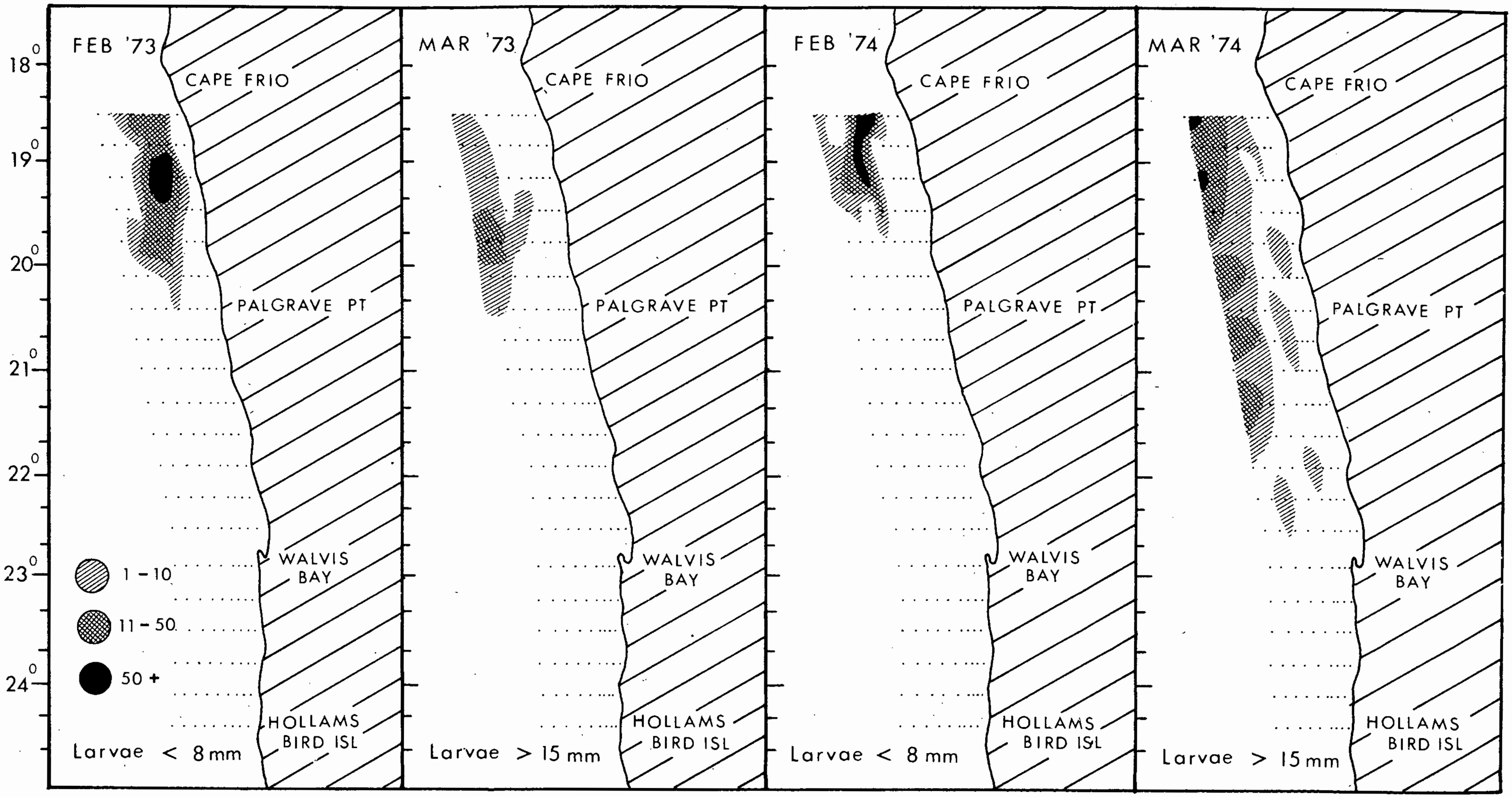


Fig. 9 Dispersal trends of developing anchovy larvae between February and March of both Surveys

DISCUSSION

The anchovy off South West Africa apparently spawn continuously from September onwards but the main breeding season during both survey years was December - March. Although sampling was not conducted from April to July in 1973 or after March/ April 1971, the scarcity of small larvae in the samples and the decrease in relative abundance suggested that the spawning season was nearing completion towards autumn. The main centre of spawning activity was between Cape Frio and Möwe Point further than 50 km from the coast. However, spawning may have been considerable to the north and west of the area sampled since larvae were often numerous on the most northerly and off= shore stations. These findings are in general agreement with Ratte (1974) who noted that gonad activity of the anchovy in South West African waters reached a peak in summer (December - February) and declined in autumn. Evidence of a protracted spawning season is suggested by King (1977 in press) who reported that anchovy eggs were most abundant off the coast from December to March.

Anchovy are known to spawn over a wide range of temperatures off South West Africa (King 1977 in press) and it is apparent from the frequency of egg and larval occurrence that warm saline water is preferred. Greatest numbers of both eggs and larvae were found where temperatures ranged from 17,0°C to 20,0°C in the upper 20 m layer and salinities averaged between 35,31‰ and 35,60‰.

Three times as many anchovy larvae were collected in night hauls than in day hauls, but differences in length composition demonstrated that the larger size groups accounted for the high numbers in the night collections. It is widely believed that the variation in the number of larvae at various stages of development collected at different times of the day and night are mainly due to the ability of the more advanced form to avoid slow-moving sampling gear during daylight. This probably explains why large anchovy larvae were more common in night hauls. Behavioural responses towards light and food may also have accounted for the increased frequency of smaller specimens in day hauls. In daylight, positive phototrophic reaction may have caused the small larvae to concentrate in patches while feeding in the upper layers whereas at night, newly hatched larvae may become more passive, disperse and slowly sink to deeper layers.

Using the distribution and seasonality of larvae as an indicative it would appear that anchovy spawning is principally confined to the warm water zone near the boundary between the southward flowing Angola Current and the colder water of the northward flowing Benguela Current. The regional distribution and the intensity of spawning seemed closely linked with the timing, distribution and the depth of warm water intrusions associated with seasonal hydrological changes in the northern part of South West Africa. For example, larvae were more numerous and wide= spread when 19 - 20°C water was deeper and extended over a large area. This was particularly evident in January 1973. Conversely, larvae tended to be less numerous with a more limited distribution when oceanic intrusions were weak and warm water was only present close to the surface. This situation occurred in January 1974. The prevalence of favourable oceanographic conditions accompanied by influxes of oceanic water during summer months may therefore influence the regional spawning area available to the adult fish. If intrusions of warm water are widespread, anchovy spawning may take place over a larger area and consequently the pelagic larvae may have a better chance of survival thus leading to good recruitment. In contrast, excessively high temperatures together with stable oceanographic conditions or an abnormal extension of cold Benguela water to the north during summer may cause anchovy spawning to be more limited and less successful.

During the planktonic phase, transportation of larval fish by water currents can play a vital role in determining the fate of a year-class. Current circulation of water in the northern part of South West Africa during the spawning season could therefore influence brood survival of the anchovy. Offshore displacement away from the mixing zone may carry developing larvae away from areas of food productions into regions where temperatures are excessively high and food of the correct type and size is scarce. On the other hand an inshore southerly drift would tend to transport the larval stages into the coastal environment where the chances of encountering more favourable conditions are greater.

REFERENCES

AHLSTROM, E.H. 1959 Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60, (161) :107-146.

ANDERS, A.S. 1965 Preliminary observations on anchovy spawning off the South African coast. S. Afr. Shipp. News Fish. Ind. Rev. 20, (11): 103-107.

ANDERS, A.S. 1975 Pilchard and anchovy spawning along the Cape east coast. S. Afr. Shipp. News Fish. Ind. Rev. 30, (9)

BAIRD, D. AND N.D. GELDENHUYS 1973 Biology and fishery of the anchovy in South Africa S. Afr. Shipp. News Fish. Ind. Rev. 28, (IO), 43-49

DZ. DE CIECHOMSKI, J. 1967 Influence of some environmental factors upon the embryonic development of the Argentine anchovy, Engraulis anchoita (Hubbs, Marini). Rep. Calif. coop. oceanic Fish. Investl. II :67-71.

FAO 1974 Catches and landings. Year book of fishery statistics, 1973, 36: Food and Agriculture Organization of the United Nations, Rome.

IDA, H. 1972 Some ecological aspects of larval fishes in waters off Central Japan. Bull. Jap. Soc. scient. Fish., 38, (9): 981-994.

KING, D.P.F. AND A.A. ROBERTSON 1973 Methods of pelagic fish eggs and larval research in South West Africa. S. Afr. Shipp. News Fish. Ind. Rev. 28, (5): 57-61.

KING, D.P.F. and P.R. MC LEOD 1976 Comparison of the food and filtering mechanism of pilchard, *Sardinops ocellata* and anchovy, *Engraulis capensis* off South West Africa 1971-72. Investl. Rep. Sea Fish. S. Afr. III

KING, D.P.F. 1977 in press The distribution and abundance of eggs of the South West African pilchard (*Sardinops ocellata*) and anchovy (*Engraulis capensis*, 1971-1972. Fish. Bull. S. Afr. 9

KRAMER, D. and J.R. ZWEIFEL 1970 Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Cal. Mar. Res. Comm., CalCOFI Rept., 14: 84-87

NISHIKAWA, T. 1901 Hisiko tyosa hokoku (A study of the anchovy). Jour. Fish. Bur., 10, (I) : 16 pp.

O'TOOLE, M.J. 1976a Incidental collections of small and juvenile fishes from egg and larval surveys off South West Africa (1972-1974). Fish. Bull. S. Afr. 8: 23-33.

O'TOOLE, M.J. 1976b A note on the presence of ripe anchovy off Cape Point. Fish. Bull. S. Afr. 8: p. 35.

O'TOOLE, M.J. 1977a Distribution of temperature and salinity off Aouth West Africa, 1972-1974. PhD. thesis, University of Cape Town, section 1, 31 pp.

O'TOOLE, M.J. 1977b Investigations into the early life history of the South West African pilchard Sardinops ocellata. PhD thesis, University of Cape Town, Section 2.53pp.

POLLOCK, D.E. 1970 Growth and mortality of the South African anchovy, Engraulis capensis (Gilchrist). MSc. thesis Univ. Stellenbosch, South Africa.

RATTE, T.W. 1973 Biology of the anchovy, E. capensis in South West African waters. Cape Cross Report. Phase III, Sea Fisheries Branch South Africa, 9pp.

ROBINSON, G.A. 1966 A preliminary report on certain aspects of the biology of the South African anchovy, Engraulis capensis. MSc. thesis, Univ. Stellenbosch, South Africa.

SIEGEL, S. 1956 Non parametric statistics for the behavioural sciences. Mc Graw-Hill. New York, 312 pp.

ZWEIFEL, J.R. AND R. LASKER 1976 Prehatch and posthatch growth of fishes - a general model. Fish. Bull. U.S., 74 (3), 609-621.

INVESTIGATIONS INTO THE EARLY LIFE HISTORY OF THE CAPE HORSE MACKEREL *TRACHURUS TRACHURUS* L. OFF SOUTH WEST AFRICA

B Y

MICHAEL J.O'TOOLE
SEA FISHERIES BRANCH
BEACH ROAD,
SEA POINT,
CAPE TOWN.

INTRODUCTION

The horse mackerel *Trachurus trachurus* Linnaeus occurs in large numbers in the waters around southern Africa. The species is particularly abundant along the west coast where depths do not exceed 400 m (Smith I970) and is of considerable economic importance. Two sub species, *T. trachurus capensis* (Cape horse mackerel/maasbanker) and *T. trachurus trecae* (Cunene horse mackerel) are now recognised and can be distinguished by the length of the secondary lateral line and the width of the scutes along the lateral line curve (Baptista I976). However, the two forms have contrasting geographic distributions. The Cape horse mackerel is found mainly from the Cunene River (I7°20'S) South West Africa to the Cape Peninsula in South Africa whereas the Cunene horse mackerel frequents the warmer subtropical waters of Angola and Zaire. Occasionally both species may be caught simultaneously, especially off the Cunene River (Wengrzyn I976) but in general the species found south of the Cunene may be regarded as *T. trachurus capensis*.

In South Africa,total landings of maasbanker declined from I00963 metric tons in I951 to 813 metric tons in I975. In contrast, however, catches of maasbanker increased off South West Africa, fluctuating between 72000 metric tons in I968 and 200000 metric tons in I973 (F.A.O. 1974). The development of the fishery off South West Africa has been relatively recent. Komarov (I964) reported that in the early I960's, extensive maasbanker resource was located by Soviet fishing vessels in the offshore waters around the Cunene River. Since then, the fish stock has been rapidly exploited by the distant water fleets of several countries, the greatest proportion of the catch being taken by vessels of the Soviet Union.

The local fishing industry at Walvis Bay is concerned mainly with the harvesting of the rich resources of pilchard and anchovy that frequently occur near the coast. Occasional catches of maasbanker are taken by local purse-seiners while fishing for pilchard, but these landings mainly consist of juvenile fish (F.H. Schulein, personal communication,Sea Fisheries Branch).

The general biology of the maasbanker has been investigated by a number of workers. The fish have a relatively long life and growth is slow (Geldenhuys I973, Kompowski and Slosarczyk I976). *Trachurus trachurus* is a serial spawner with gonads developing asynchronously (Macer I974). In South West African waters, maasbanker become sexually mature at lengths of 22-27 cm (3 - 4 years). Gonad activity is high from January to April but ripe females are sometimes found at other times of the year (Komarov I964).

According to Davies (I957) and M^c Leod (I971) juvenile maasbanker feed selectively predominantly on copepods, euphausids and small fish. Kompowski and Slosarczyk (I976) found that the adult diet was essentially similar but that myctophid lanternfish formed an important food item, especially for larger fish.

Little is known about the early life history of the maasbanker. The larval development was described by Haigh (I972) but there is no description of the egg from southern Africa. The distribution and ecology of the pelagic eggs and larvae have not been previously studied. This report is based mainly on the larval stages which were collected during the SWAPELS cruises off South West Africa between I972 and I974. Monthly surveys were conducted from August I972 to March I973 and from August I973 to March/April I974 between Cape Frio (I8°20'S) and Hollam's Bird Island (24°40'S) (Fig. I). Details of the collection methods, dates of cruises, station positions and depths are given by O'Toole (I976, I977 b). Maasbanker larvae formed 4,~~5~~2 percent of all species captured during the two-year survey and ranked fifth in order of abundance. The larvae comprised ~~3,12~~ 2,91 percent and 4,~~95~~86 percent of the total fish larvae taken on Survey 1 and Survey 2 respectively. Such aspects as seasonality, distribution, abundance diurnal variation in catches, hydrological relationships, growth and dispersal are discussed.

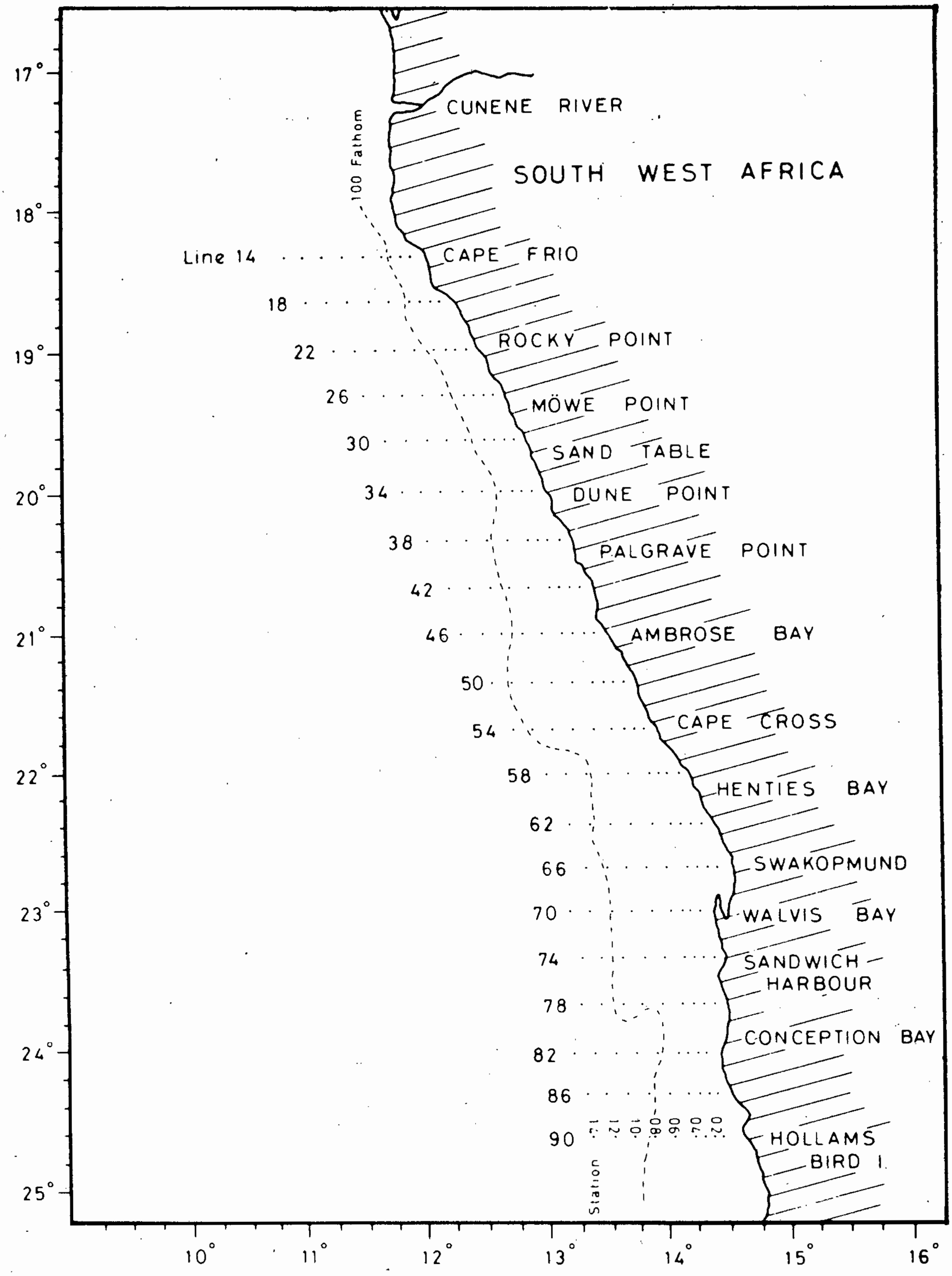


Fig. 1 Location of routine stations occupied during the SWAPELS cruises in 1972/73 and 1973/74

R E S U L T S

Description of the Egg

The egg of the maasbanker is smooth, spherical, medium in size and has a single fairly-large oil globule. The mean diameter of 300 eggs taken randomly from plankton samples was 0,910 mm (range; 0,85-0,95 mm). The oil globule is positioned at the vegetative pole and is yellowish in colour, its diameter ranging from 0,20 to 0,27 mm with a mean value of 0,22 mm. The yolk is lightly segmented and averaging 0,780 mm in diameter (range: 0,65-0,87 mm). The mean width of perivitelline space was 0,082 mm. The dimensions of the egg are given in Table I.

TABLE 1. The size range (in mm) of maasbanker eggs

No.of	Egg	Yolk	Oil globule
36	0,852 - 0,868	0,65 - 0,72	0,20 - 0,23
120	0,871 - 0,900	0,77 - 0,80	0,20 - 0,27
170	0,901 - 0,920	0,72 - 0,85	0,20 - 0,27
126	0,921 - 0,948	0,75 - 0,90	0,20 - 0,27
48	0,950	0,80 - 0,87	0,22 - 0,27

These egg dimensions agree closely with the findings of other authors. Haigh (I972) reported that maasbanker eggs from the Cape Peninsula were seldom larger than 1 mm in diameter. Eggs of T. trachurus from the northern hemisphere have a diameter of 0,7 to 1,09 mm and an oil globule of 0,19 to 0,28 mm (Ehrenbaum I909, Kiliachenkova I970).

Development of the Egg

The development of the maasbanker egg from southern Africa has not been described or illustrated.

A range of developmental stages beginning shortly after fertilization and ending just prior to hatching were present in the plankton samples and are shown in Figure 2. The early embryonic stages (Fig.2 A, B) were often milky white in appearance, a condition probably resulting from mechanical damage during collection.

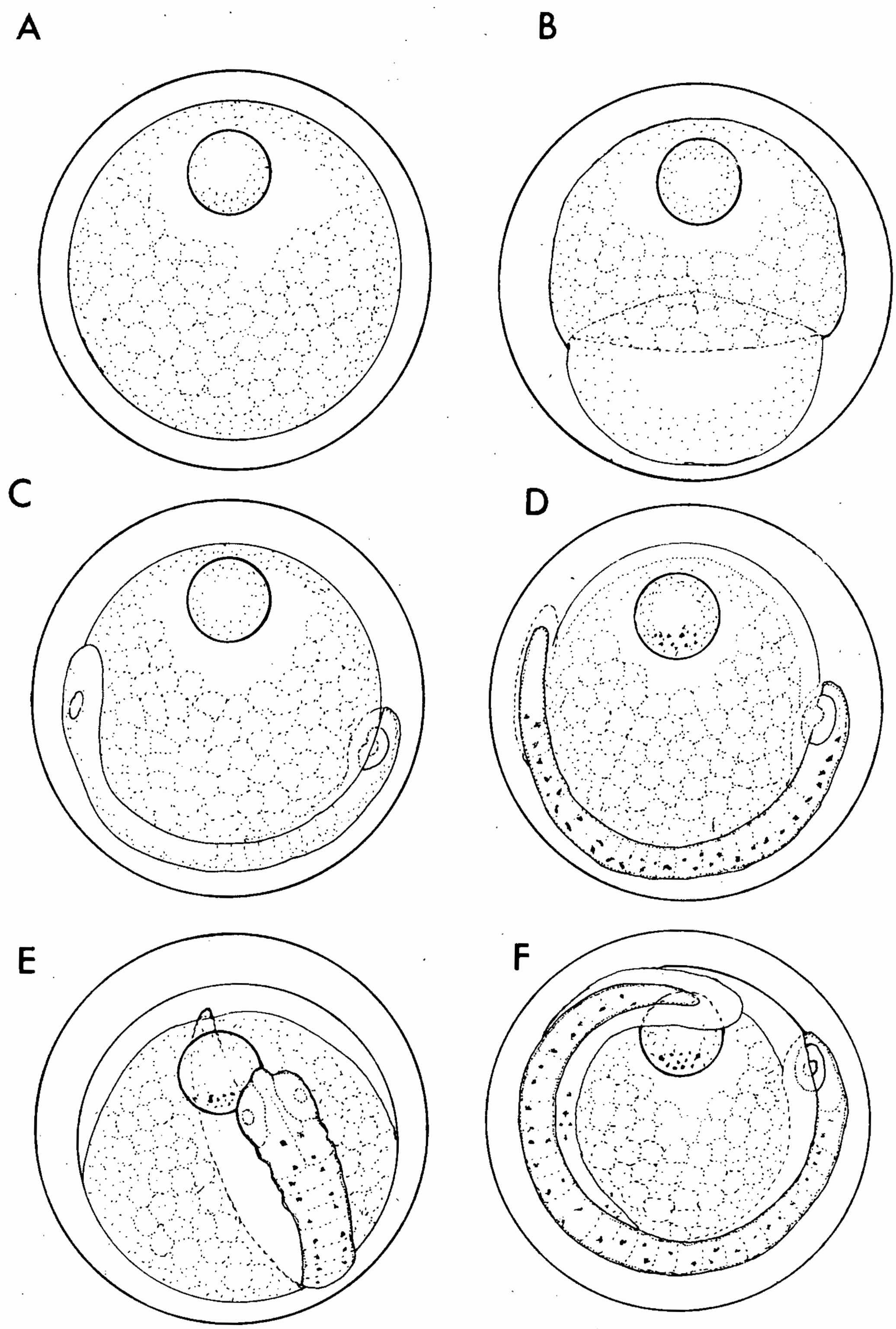


Fig. 2. Egg development of the maasbanker _Trachurus trachurus_

A: egg shortly after fertilization, B: blastodisc stage,
C: blastopore closure, D: tail separation,
E: tail flexion, F: pre-hatching.

The oil globule is roughly spherical and situated opposite the developing blastodisc. In some cases, the globule was fractured into several small droplets. During the initial development, the germ ring moves around the margin of the blastodisc until it has completely surrounded the margin of the blastoderm. At the end of this stage the embryonic axis is clearly visible and the optic vesicles are present but not completely formed.

The developing embryo lacks pigmentation and the oil globule is at the periphery of the yolk in a median position (Fig 2C). The tail bud becomes free from the yolk shortly after the blastopore closes and a number of pigment spots appear on the underside of the oil globule. Pigmentation of the embryo at this stage consists of a double row of small dendritic melanophores along the dorsal surface on each side of the notochord, some of which are migrating ventrally. The row of pigment spots extends from behind the eyes to the caudal region (Fig.2D). However, the tail itself lacks pigmentation.

As the body elongates, the tail begins to curl around the yolk and the fin folds develop. In the beginning, scattered melanophores migrate ventrally along the lateral surface of the embryo at the mid and posterior part of the body. The two rows of melanophores viewed dorsally, form a characteristic arch on the cranial region (Fig. 2 E). Prior to hatching, the embryo increases in length and encircles the yolk (Fig.2F). The fin fold deepens becoming lightly pigmented anteriorly and 15 - 18 myomeres can be counted. In fresh material, movement of the embryo is frequently observed at this stage. During late embryonic development, the oil globule moves to a foward position beneath the head.

Description of the Newly-Hatched Larva

Although Haigh (1972) gives a detailed description of the larval development, no newly-hatched larvae were described or illustrated.

Preserved yolk-sac larvae measured between 2,25 and 2,5 mm. Pigmentation consists of irregularly spaced melanophores along the dorsal and ventral margins of the body (Fig. 3). Dorsally, the line of melanophores extends posteriorly from the head to

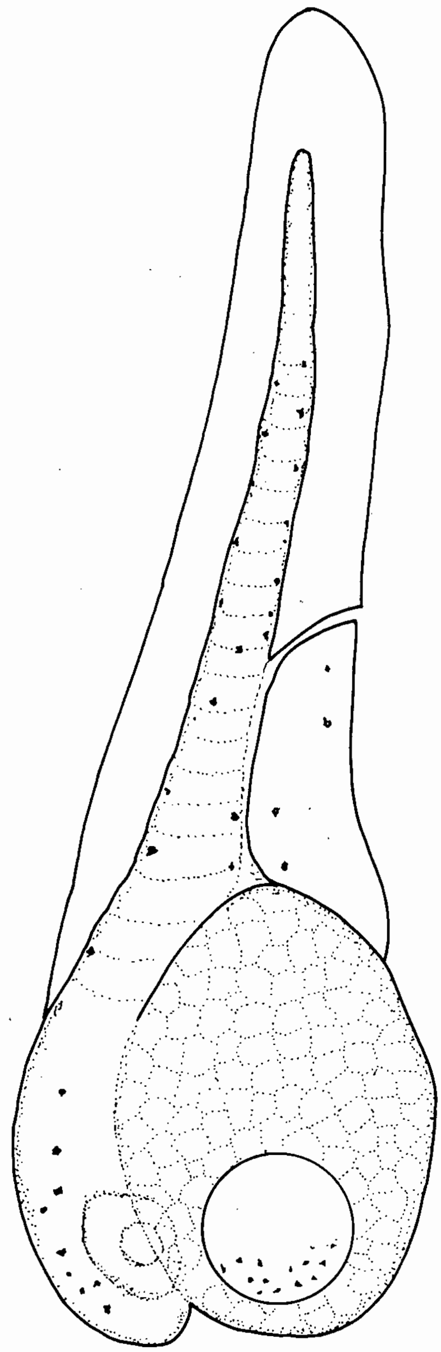


Fig. 3. Newly - hatched maasbanker larva (2,5 mm)

about 4/5 of the body length and ventrally to approximately the same position. The head region is lightly pigmented and spots form a noticeable arch behind the eyes. A few isolated pigment spots are present on the anterior part of the fin fold. In general, pigmentation of the yolk-sac larva showed little difference from that of the late embryonic form. The oil globule is characteristically situated at the anterior part of the yolk-sac beneath the head, a useful feature in the identification of <u>Trachurus</u> larvae (Ahlstrom and Ball 1954). Newly-hatched larvae lack eye pigmentation and the mouth is not yet fully formed.

When the larva is between 3,00 and 3,20 mm in length, the eyes begin to develop pigment and the pectoral fin buds appear. The melanophores on the head region now form a discrete cap and extend forward between the eyes. Pigmentation on the rest of the body remains essentially unchanged. The yolk-sac becomes much reduced and the mouth rudiments are partially formed. By the time the larva reaches approximately 4,00 mm in length the eyes are fully pigmented and the yolk-sac is entirely absorbed. The mouth and jaws are functional and a few scattered melanophores appear on the upper and lower jaw and in the region of the cleithrum.

Distribution and Abundance of Eggs

Maasbanker eggs were identified but not counted during the course of the investigation. Since many of the larvae collected during the surveys were newly-hatched ($< 5,0$ mm) and eggs often occurred together with larvae, it is assumed that egg distribution closely resembled larval distribution. Eggs were present in the plankton from October to March/April, chiefly in the northern offshore region. Greatest numbers of eggs were observed in summer months, particularly from January to March/April. The seasonal occurrence of eggs agrees with the findings of Komarov (1964) who reported that fish with ripe gonads were found in the Cunene River - Cape Frio region between the months of January and April.

Distribution and Abundance of Larvae

Maasbanker larvae were widely distributed between Cape Frio and Conception Bay but were most abundant in the northern part of the research area (Figs. 4-5). Approximately 70 percent were found north of Palgrave Point during the two years surveyed. Only about 6,5 percent of the larvae were collected south of Henties Bay (22°S). The percentage occurrence of the total number of larvae taken in the different parts of the research area during 1972/73 is summarized in Table II.

TABLE II : The percentage of larvae collected in the different parts of the research area during 1972 - 1974

Area	Station Line	1972/73	1973/74	1972/74
Cape Frio - Mowe Point	14 - 26	64,9	19,8	33,8
Mowe Point - Palgrave Point	30 - 42	19,0	46,0	37,1
Palgrave Point - Henties Bay	46 - 58	10,0	29,4	21,7
Henties Bay - Sandwich Hb	62 - 74	5,7	4,2	5,6
Sandwich Hb - Hollams Bird Is	78 - 90	1,2	0,5	1,7

Maasbanker larvae were found over the entire inshore/offshore sampling range but predominantly (over 85 percent) at distances greater than 30 km from the coast (Table III). The distribution of larvae to the north and to seaward was not delineated but the southern limit of larval occurrence was apparently in the vicinity of Conception Bay. The frequent presence of large numbers of larvae on the most northerly line at Cape Frio and at offshore stations suggested that larval distribution extended a considerable distance further north and west of the survey area. Although the distribution of maasbanker larvae was similar during both years, the centre of abundance differed. During 1972/73, maximum concentrations of larvae were found in the north between Cape Frio and Mowe Point, whereas in 1973/74, larvae were more abundant further south, between Mowe Point and Cape Cross.

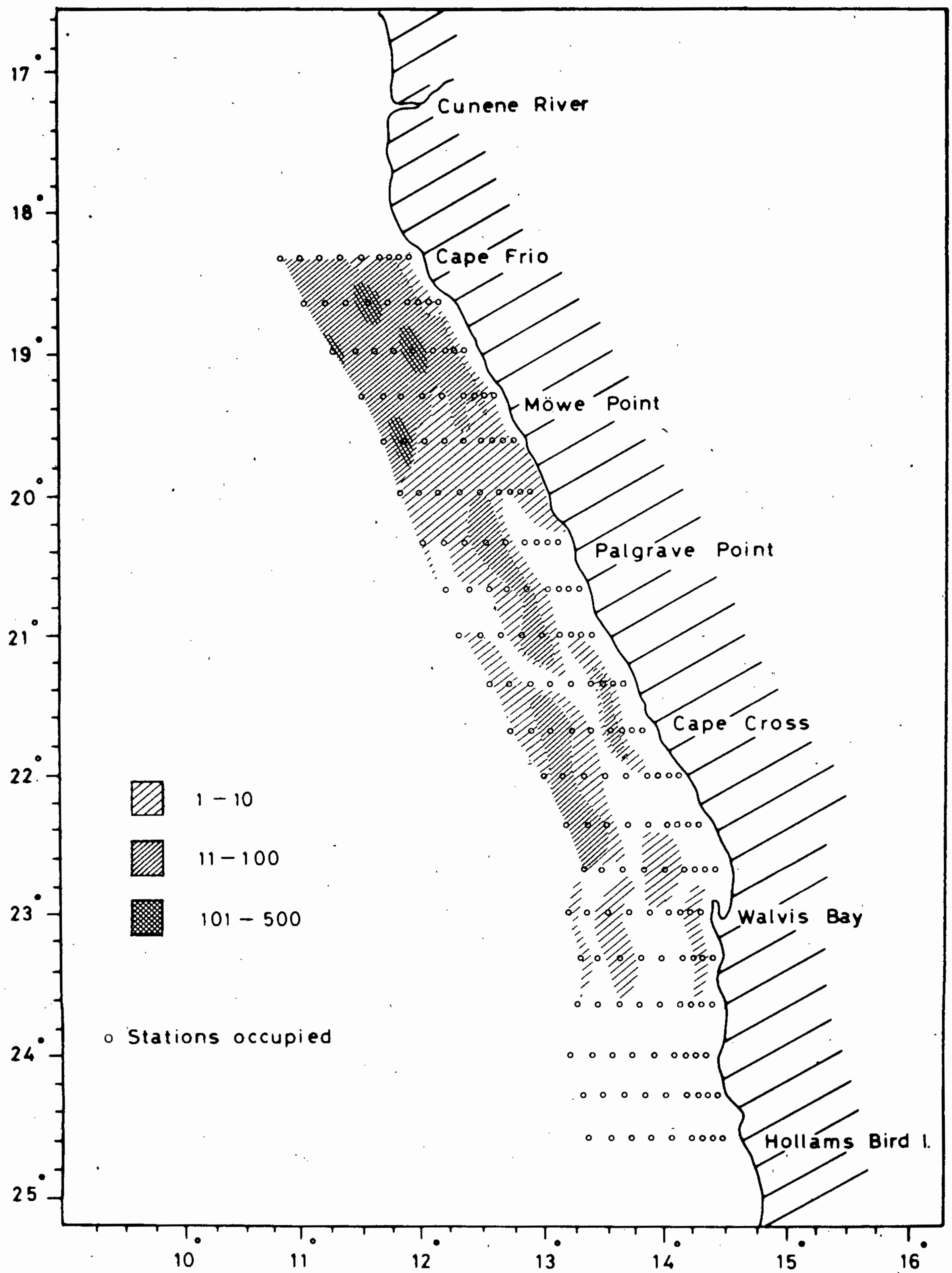


Fig. 4 Distribution and abundance of maasbanker larvae during Survey 1 (values represent cumulative standard haul totals for all cruises)

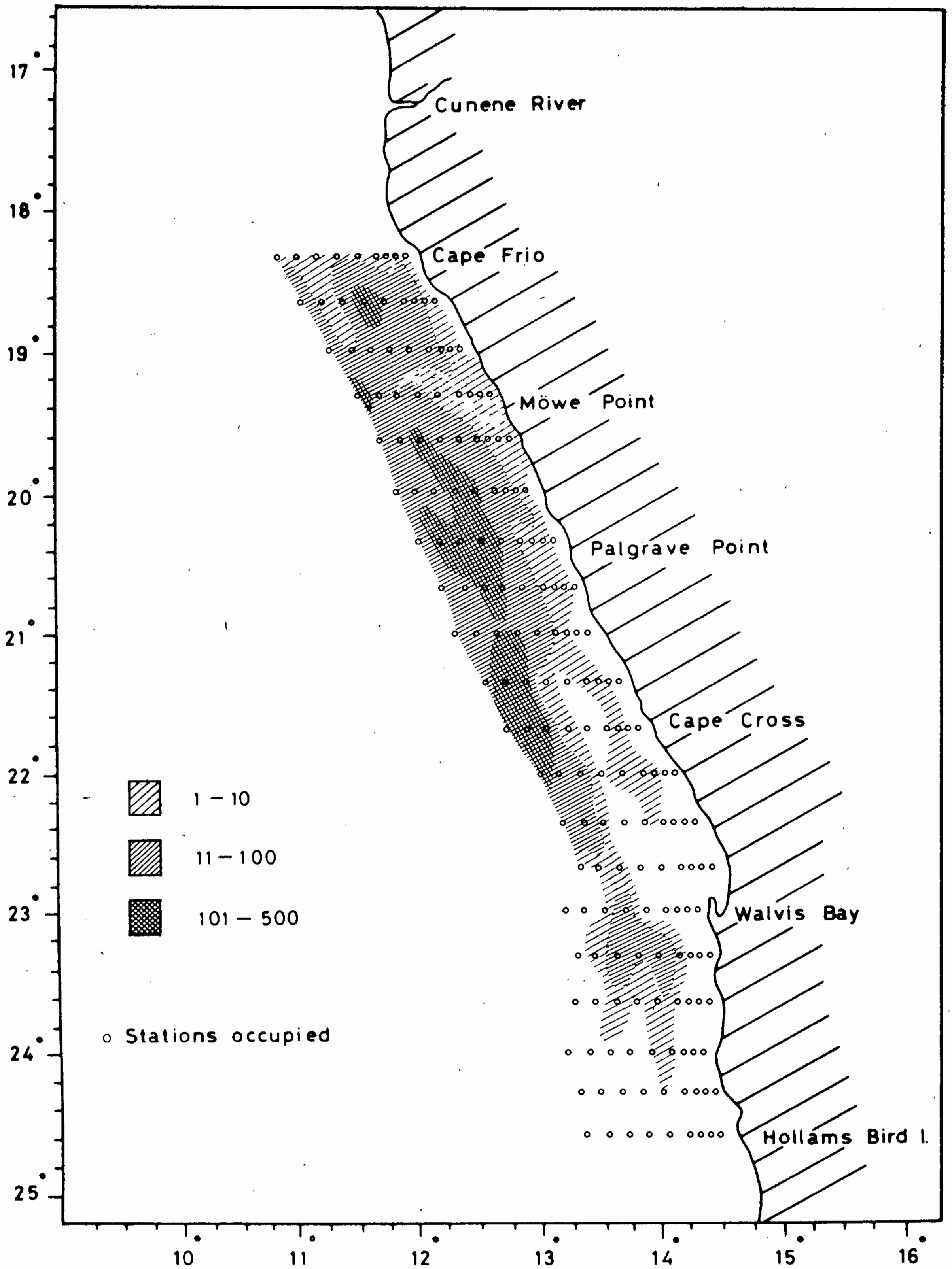


Fig. 5 Distribution and abundance of maasbanker larvae during Survey 2 (values represent cumulative standard haul totals for all cruises)

TABLE III : The percentage occurrence of maasbanker larvae in relation to distance from shore, I972 - I974

Distance from shore	I972/73	I973/74	I972/74
10 km or less	0,5	0,2	0,4
10 - 20 km	5,4	1,7	3,2
20 - 30 km	4,9	3,9	4,0
30 - 50 km	31,3	14,4	23,5
50 - 100 km	40,5	68,2	56,5
100 km or more	17,5	11,7	12,4

Survey 1. (August I972 - March I973)

During Survey 1 maasbanker larvae were found in the plankton from October to March but 88 percent of the total number were collected between January and March. Larval distribution, abundance and surface isotherms for the monthly cruises are illustrated in Figure 6. A summary of the monthly hauls and larval abundance is given in Table IV and the length frequencies of larvae during each month in Figure 7.

Larvae were first taken off Cape Cross during October, the catch consisting of mixed size groups (5 - 14 mm) probably resulting from isolated spawning during mid or late September. Maximum concentrations occurred about 30 km west of Cape Cross.

Fewer larvae were found in the plankton in November. Scattered patches of smaller larvae (3 - 10 mm) were found off the coast between Mowe Point and Conception Bay.

In December, the number of larvae increased and were particularly dense at offshore stations west and south-west of Cape Cross. The larvae measured between 5 and I5 mm but early larval stages (6 - 8 mm) were more abundant. The smaller stages probably hatched from eggs spawned in the latter half of November.

TABLE IV: A summary of the monthly hauls and abundance of maasbanker larvae, I972 - I973

Month	No.of hauls taken	No.of positive stations	No.of larvae collected	Mean no. of larvae per I0 m^2	Percentage of total collected
August	126	0	0	0	0
September	126	0	0	0	0
October	156	8	23	9,0	2,9
November	180	7	18	6,2	2,2
December	180	14	56	12,8	7,0
January	180	47	506	30,5	63,1
February	177	30	140	9,4	17,5
March	177	32	59	7,5	7,4

Dense concentrations of maasbanker larvae were found north of Palgrave Point during January accounting for over 60 percent of the total number collected during the eight month survey. The larvae were most abundant between Cape Frio and Mowe Point, especially at stations 18-08 and 30-12. Seventy five percent consisted of yolk-sac and early larval stages ranging from 3 - 8 mm in length. The high percentage of smaller larvae and the wider distribution compared with December, indicated heavy spawning in the north sometime between late December and early January.

Larvae were less abundant and were found further inshore during February. Greatest concentrations occurred 30-60 km from the coast between Cape Frio and Mowe Point. The majority of samples contained yolk-sac and early larval forms, probably derived from eggs spawned in late January or early February.

A further decrease in larval abundance was evident in March, the regional distribution being limited mainly to offshore areas north of Palgrave Point. Additional isolated patches were found offshore at Cape Cross and to the south of Walvis Bay. Most of the specimens were small (3 - 8 mm) resulting from eggs spawned in early March.

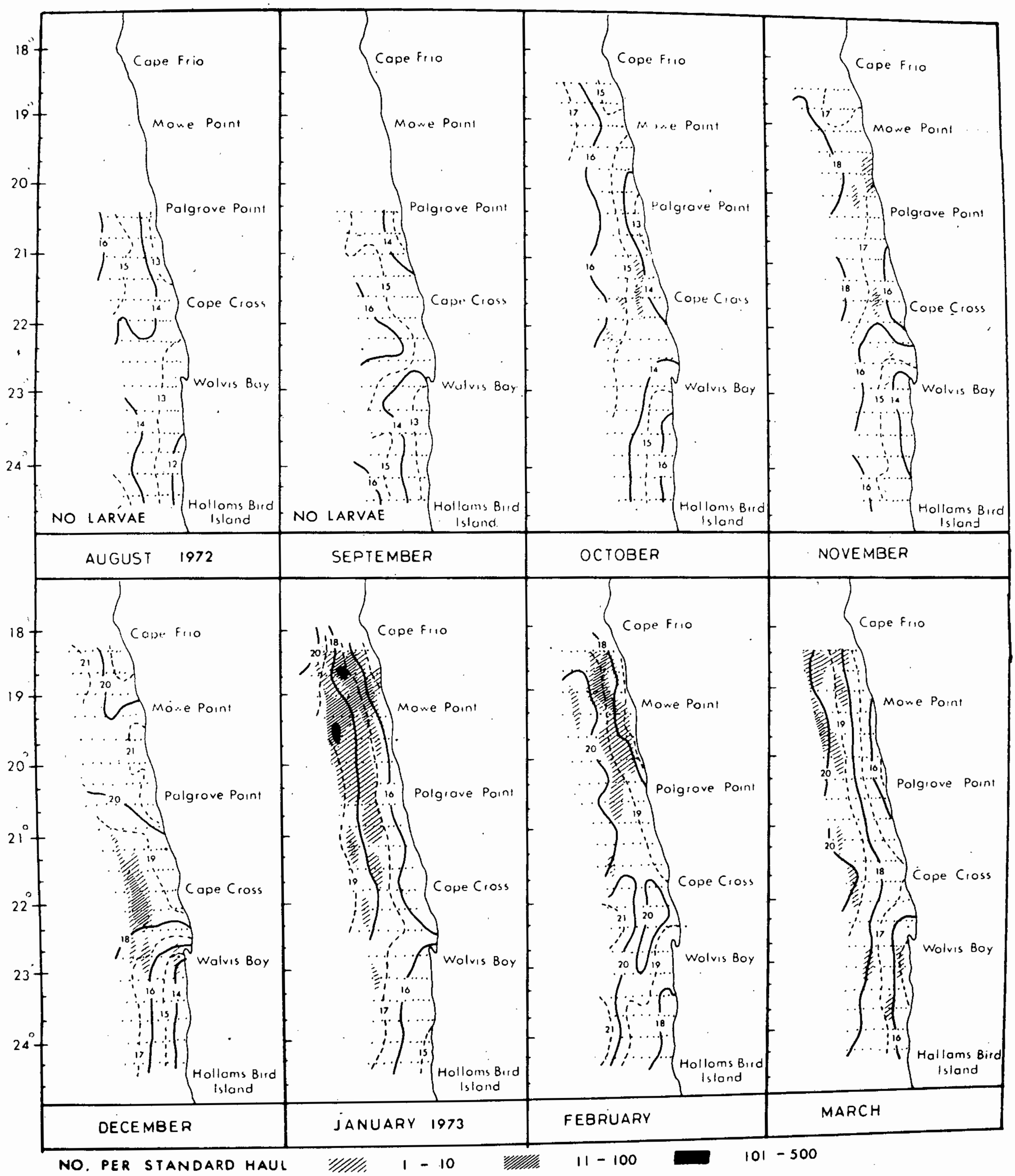


Fig. 6 Monthly distribution and abundance of maasbanker larvae, August 1972 to March 1973.

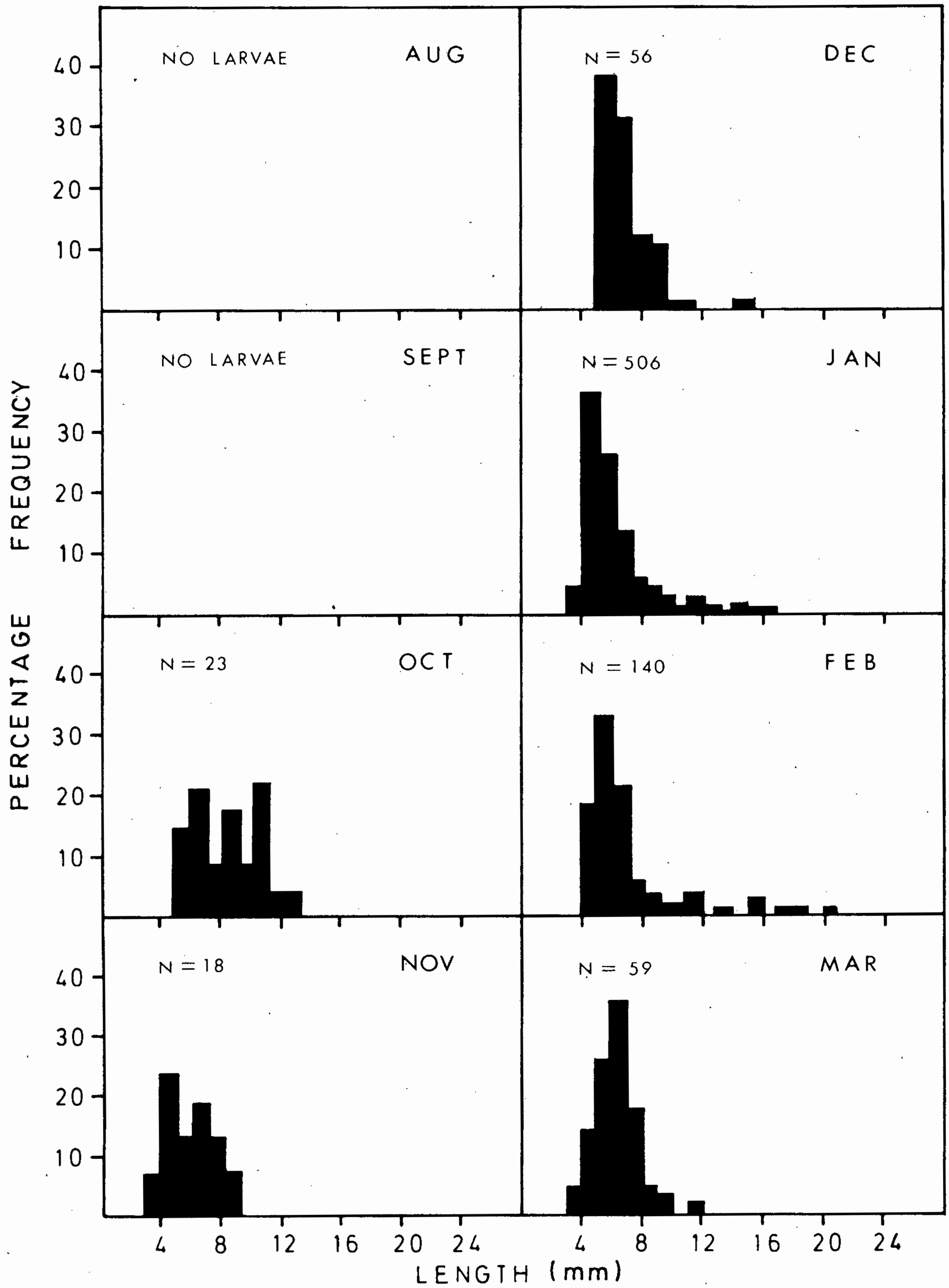


Fig. 7 Length composition of maasbanker larvae collected during the monthly survey cruises, August 1972 to March 1973

Survey 2 (August I973 to March/April I974

Larvae were taken from November to March/April but 98 percent were collected during the months of January, February and March/ April. Peak abundance occurred in March/April, two months later than in I972/73. Larval distribution, abundance and surface temperature during the eight monthly cruises of Survey 2 is shown in Figure 8 and summarized in Table V. The length composition of the larvae is illustrated in Figure 9.

In November, isolated patches of larvae occurred in the north between Palgrave Point and Cape Cross. Most of the specimens were newly-hatched (3-8 mm) and probably originated from sporadic spawning in early November.

Larvae remained scarce in the plankton during December but those collected were captured further north between Mowe Point and Palgrave. Small specimens between 3 and 8 mm predominated and were presumably derived from eggs spawned in early December.

During January, early stages were abundant and widely distributed in the offshore plankton between Cape Frio and Palgrave Point. The presence of large numbers of small larvae showed that spawning activity increased substantially between mid December and early January. Maximum catches were made at stations I4 on line 26, 112 km from the shore. Further south a small patch of larvae was located west of Cape Cross at a distance of I00 km from shore.

Maasbanker larvae were very common during February with maximum catches being made offshore between Palgrave Point and Cape Cross, 150-200 km further south than in January. Larvae were particularly dense about 80-100 km from the coast at stations I0 on line 38 and 42 and station 12 on line 50. Approximately 75 percent of the specimens collected measured from 3 - 6 mm and probably resulted from heavy spawning in late January and early February.

Larvae were taken in greatest abundance during the March/April cruise. Distribution was more widespread to the south and inshore compared with other months. Maximum catches were made at station 6 on line 30, station 8 on line 34 and station 10 on line 38 in the area between Mowe Point and Palgrave Point.

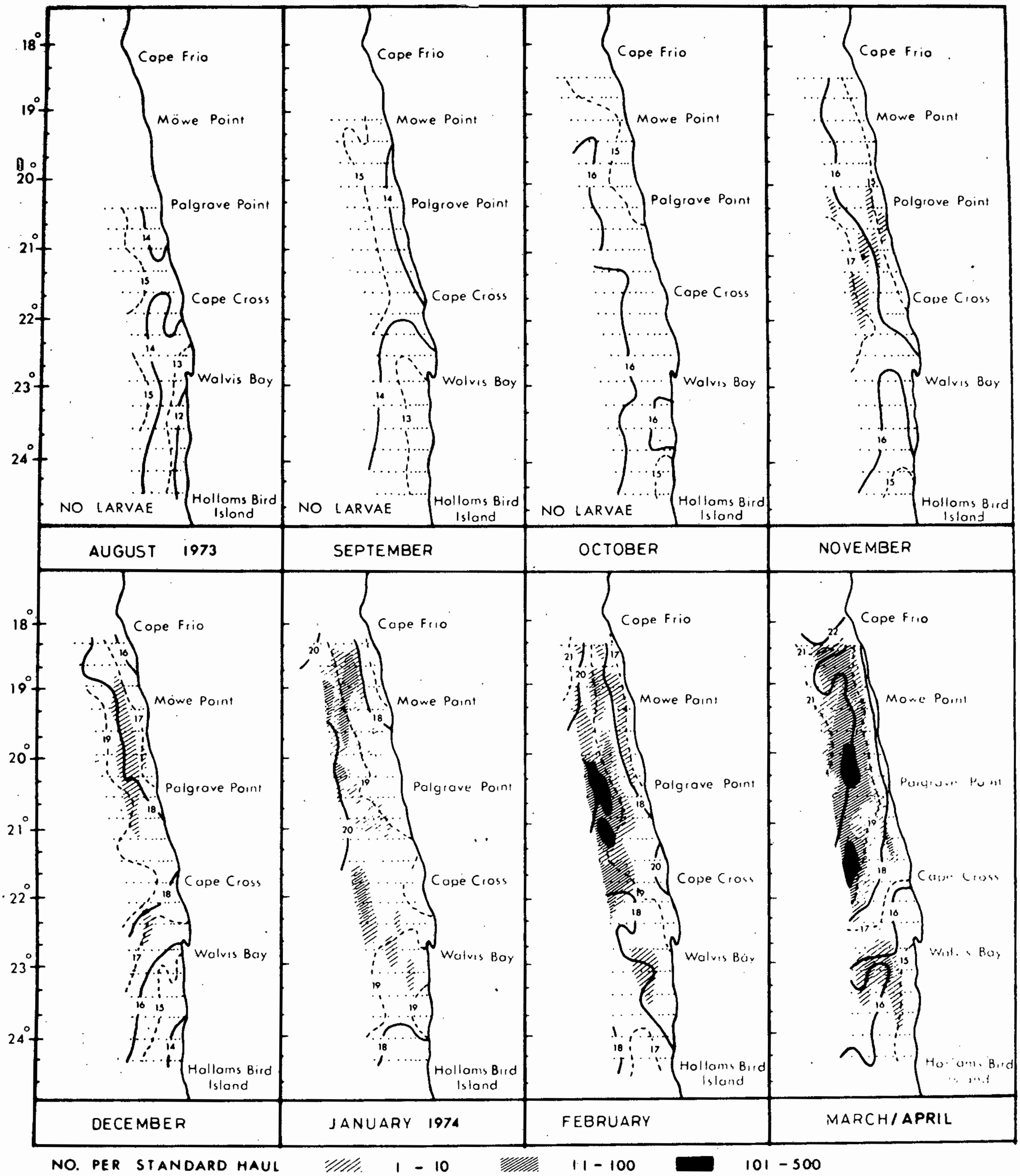


Fig. 8 Monthly distribution and abundance of maasbanker larvae, August 1973 to March / April 1974

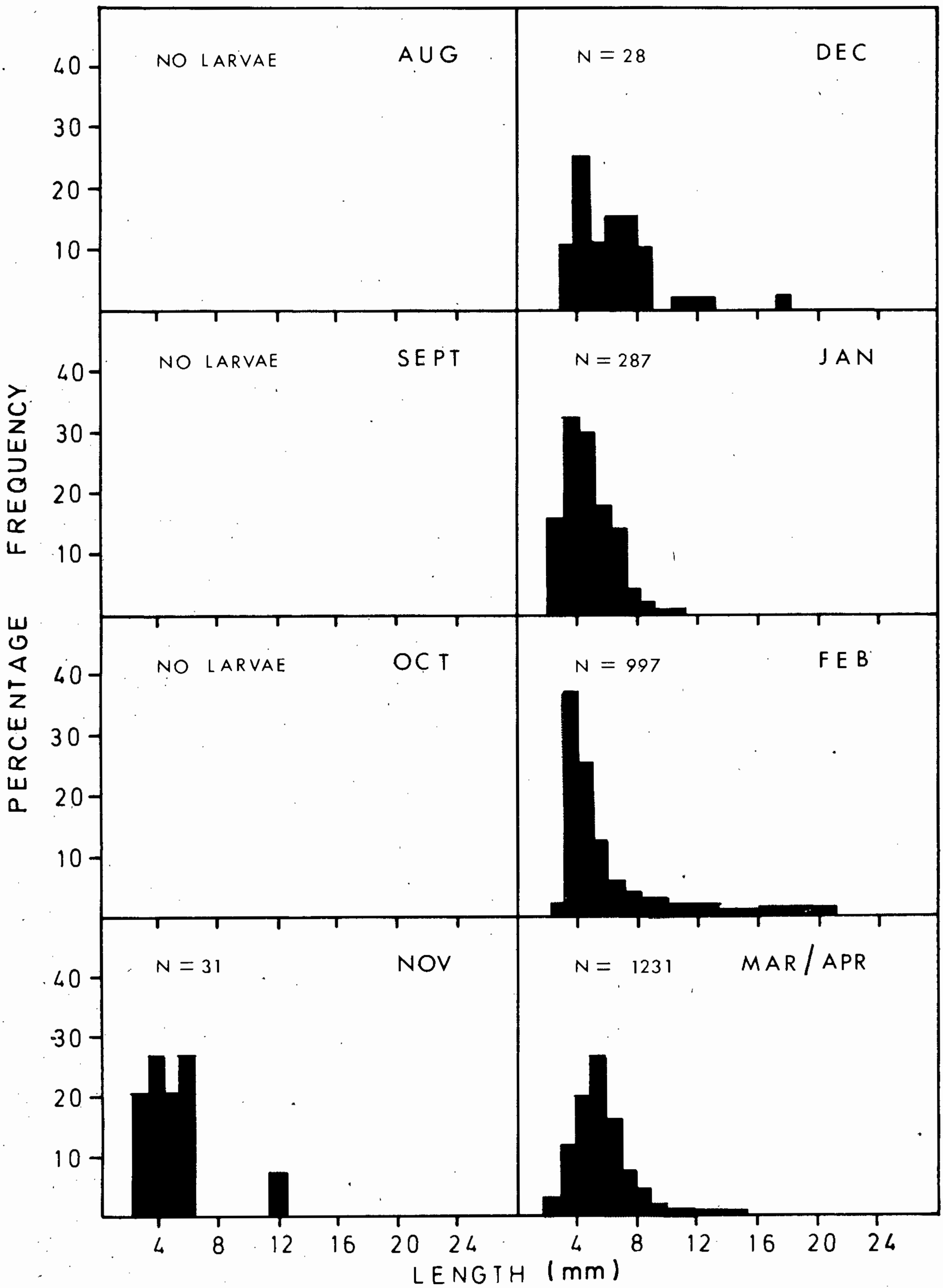


Fig. 9 Length composition of maasbanker larvae collected during the monthly survey cruises, August 1973 to March / April 1974

Considerable quantities were also captured at offshore stations west of Cape Cross. The majority of specimens comprised post yolk-sac and early larval stages, which must have resulted from intense spawning activity during late March.

TABLE V : A summary of the monthly hauls and abundance of maasbanker larvae, 1973 - 1974

Month	No.of hauls	No.of positive hauls	No.of larvae collected	Mean no. of larvae per $10m^2$	Percentage of total collected
August	126	0	0	0	0
September	135	0	0	0	0
October	180	0	0	0	0
November	180	10	31	5,2	1,2
December	180	14	28	4,7	1,0
January	180	35	287	16,5	11,1
February	169	46	997	42,8	38,7
March/April	175	77	1231	37,1	47,8

Diurnal Variation in Catches

Maasbanker larvae showed no consistant difference in abundance between day and night collections taken on the regular survey cruises. The pattern applied to all larvae irrespective of size (Table VI).

TABLE VI : Diurnal variation in the number and size composition of maasbanker larvae

Length group (mm)	Night Hauls		Day Hauls		
	No.of larvae	Percentage	No.of larvae	Percentage	N/D ratio
5,0	964	44,7	1193	55,3	1,2:1
5,1-10,0	518	48,7	546	51,3	1,1:1
10,1-15,0	136	63,3	79	36,7	1,7:1
15,0	38	27,9	98	72,1	1:2,5
All sizes	1656	46,4	1916	53,6	1,2:1

The percentage of larvae of various length classes plotted over two hourly intervals also showed no consistent diurnal rhythm (Fig.IO).

It is noteworthy that Ahlstrom (I959) and Farris (I961) have similarily demonstrated that larvae of the jackmackerel T. symmetricus exhibited no diurnal variation in catch frequency.

A possible explanation is that larvae avoided the net equally well during the day and night, or as Farris (I961) suggested " the larvae do not dodge the net despite their apparent ability to do so". Alternatively, larvae may remain close to the surface feeding during the daytime instead of descending to deeper layers which is often the case with other species of larval fish. The diurnal vertical distribution of maasbanker larvae was not studied, but Farris (I961) reported only a slight tendency for jack-mackerel larvae to migrate towards the surface during the day.

Several authors report the clustering of larval and juvenile Trachurus under jellyfish (Ehrenbaum I909) and floating debris and seaweed (Delsman I926, Ida I972). This habit is apparently common to the Carangidae.

In South West African waters, Kompowski and Slosarczyk (I976) reported maasbanker fry sheltering under the mantles of jellyfish. During this study, maasbanker larvae were frequently found in regions where jellyfish were abundant. The close relationship between larvae and drifting objects could be responsible in some ways for the apparent absence of diurnal variation in catch-rates. Larvae may associate the collecting gear with a drifting object and consequently exhibit no escape response.

Relationship between Larval Occurrence and Temperature

Maasbanker larvae were found in waters where surface temperatures ranged from 13,8^{o} to 21,5^{o}C. However, over 81 percent of larval occurrences were at surface temperatures of between 17,1^{o}C and 21,0^{o}C. Only I5 percent of the number of hauls containing larvae were found at temperatures of less than I7,1^{o}C and 4 percent at temperatures greater than 21,0^{o}C. The abundance of maasbanker larvae in relation to surface temperature is summarized in Table VII.

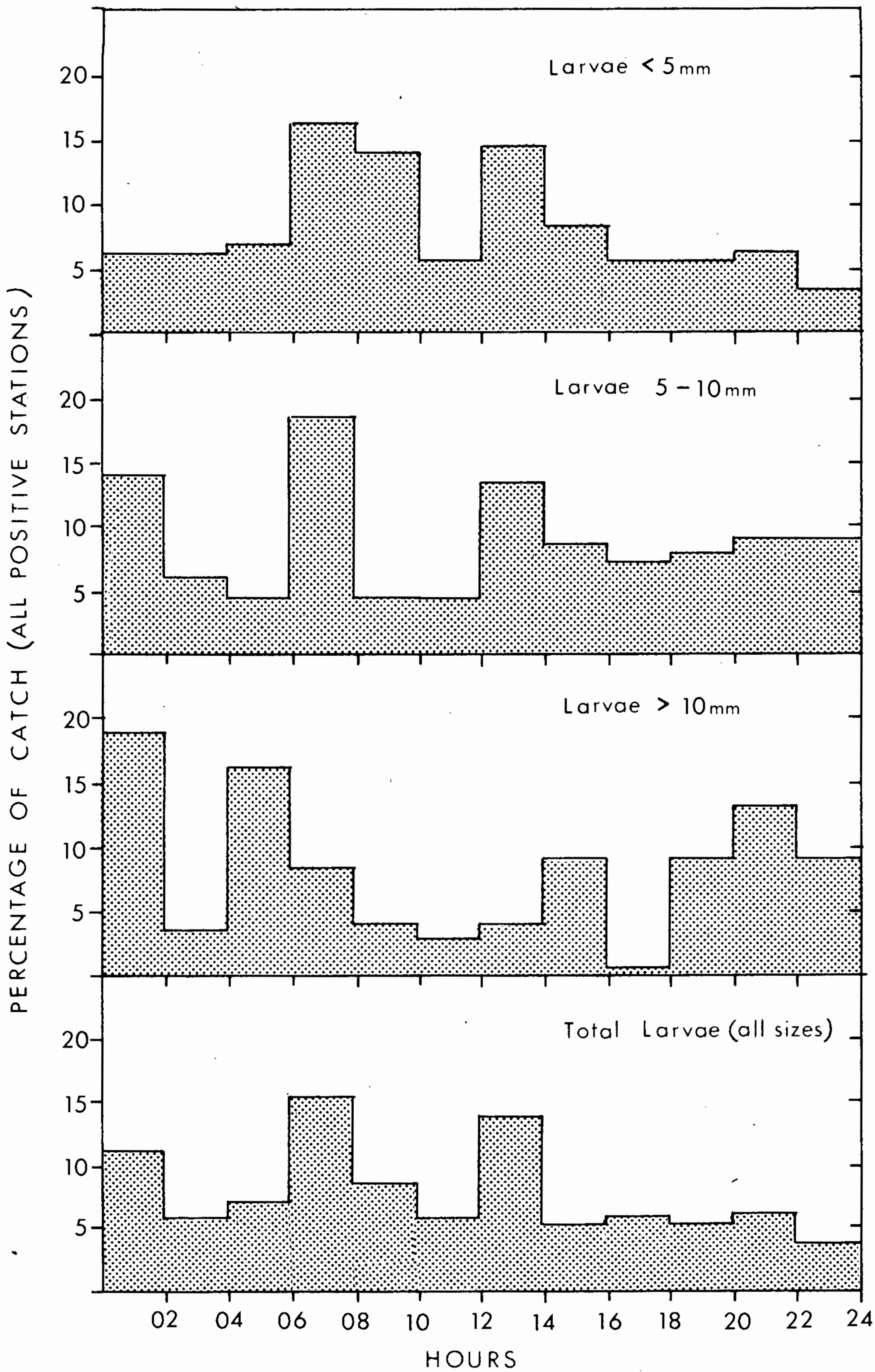


Fig. 10. Diurnal variation in catch rates of maasbanker larvae according to size categories (all cruises)

TABLE VII : Relationship between surface temperature and abundance of maasbanker larvae, 1972 - 1974

Surface temperature (°C)	Number of standard hauls that collected:-					
	1-5 larvae	6-10 larvae	11-100 larvae	101-250 larvae	250 + larvae	Total
12,1 - 13,0	0	0	0	0	0	0
13,1 - 14,0	4	0	0	0	0	4
14,1 - 15,0	7	1	3	0	0	11
15,1 - 16,0	9	2	2	0	0	13
16,1 - 17,0	10	4	1	0	0	15
17,1 - 18,0	20	8	11	3	0	42
18,1 - 19,0	25	12	35	5	2	79
19,1 - 20,0	20	11	26	4	0	61
20,1 - 21,0	14	12	17	0	0	45
21,0 - 22,0	5	0	5	1	0	11

The standard oblique hauls only provided information on the relative abundance of larvae in the 0-50 m layer. However, larvae could have occurred at a variety of temperatures within this stratum. The distribution of maasbanker larvae with depth was not determined during the routine collections but the results of a later investigation (O'Toole 1977c) indicated that maasbanker larvae were most abundant at a depth of 25 m near the thermocline.

Ahlstrom (1959) working on a related species of Trachurus (T. symmetricus) reported that about 80 percent of the larvae occurred in the upper 50 m and that the centre of abundance fluctuated between 10 and 44 m. The larvae of T. japonicus were found in greatest abundance at depths of 20 m (Ida 1972).

If temperature at 20 m is related to the occurrence of larvae collected during the regular monthly cruises, then larvae were found over a temperature range of 12,5°-21,0°C. Within this range 74 percent of the larvae were caught between temperatures of 15,1°C and 19,0°C (Table VIII). Sixteen percent of the larvae were found at temperatures of less than 15°C and less than 9 percent at temperatures greater than 19°C.

TABLE VIII : Relationship between temperature at 20 m and abundance of maasbanker larvae, 1972–1974

Temperature at 20 m (°C)	Number of standard hauls that collected:-					
	1–5 larvae	6–10 larvae	11–100 larvae	101–250 larvae	250+ larvae	Total
I2,1 - 13,0	1	0	0	0	0	1
13,1 - 14,0	11	1	0	0	0	12
14,1 - 15,0	23	4	6	0	0	33
15,1 - 16,0	27	10	12	2	0	51
16,1 - 17,0	32	6	20	3	0	61
17,1 - 18,0	13	8	34	4	2	61
18,1 - 19,0	13	4	15	3	1	36
19,1 - 20,0	7	6	6	1	0	20
20,1 - 21,0	2	1	2	0	0	5

The Kruskal-Wallis test (Siegel I956) was applied to the raw data summarized in Tables VII and VIII to determine whether there was significant differences between the abundance of larvae and the temperature classes at which they occurred. The analysis yielded H-values of greater than 20,50 for temperature ranges at the surface and at 20 m, which indicated that significant differences occurred at the 1 percent level. Although the test does not demonstrate the optimal temperature ranges it can be concluded from Tables VII and VIII that maasbanker larvae are more likely to be abundant at surface temperatures ranging from I7,1°–21,0°C and between 15,1° and I9,0°C at a depth of 20 m.

Relationship between Larval Occurrence and Salinity

Maasbanker larvae were found at surface salinities ranging from 35,00°/oo to 35,90°/oo, but approximately 70 percent were taken at salinities of between 35,20°/oo and 35,60°/oo. Only I8 percent of the hauls containing larvae were at surface salinities less than 35,20°/oo and 12 percent at salinities greater than 35,60°/oo. The greatest number of larvae taken in a single haul (427 per I0 m^2) was recorded at a surface salinity of 35,48°/oo.

The abundance of maasbanker larvae in relation to surface salinity is shown in Table IX.

TABLE IX : Relationship between surface salinity and abundance of maasbanker larvae, 1972 - 1974

Surface salinity $^{o}/oo$	Number of standard hauls that collected:-					
	1-5	6-10	11-100	101-250	250+	Total
35,00 - 35,10	11	1	4	0	0	16
35,11 - 35,20	27	7	6	0	0	40
35,21 - 35,30	28	10	19	1	0	58
35,31 - 35,40	28	7	22	2	1	60
35,41 - 35,50	19	9	19	6	2	55
35,51 - 35,60	15	8	17	2	0	42
35,61 - 35,70	6	2	8	1	0	17
35,71 - 35,80	10	1	6	1	0	18
35,81 - 35,90	1	0	1	0	0	2

The Kruskal-Wallis test was also applied to larval abundance and salinity values in the same manner as the temperature relationship. H^{o}-values of 20,48 suggested that differences were significant at the 0,1 level. Direct observations from Table IX showed that the most favourable salinity range was between 35,20 and 35,60^{o}/oo, the lower threshold being at approximately 35,00^{o}/oo and the upper limit of tolerance at approximately 35,90^{o}/oo.

The Relationship between Larval Distribution and Hydrological Parameters

Maasbanker larvae were found almost exclusively in the mixing areas between the cold Benguela Current flowing north and the warm Angola current flowing south. The seasonal occurrence of larvae in the plankton could be closely related to the timing of the intrusions of warm saline water from the north and west. Larvae rarely occurred in upwelling regions south of Walvis Bay and were also scarce in the tongues of very warm, highly saline water which periodically intruded from the north west.

The hydrology of the survey area from August I972 to March I973 and from August I973 to March/April I974 has been described and illustrated by O'Toole (I977a). The monthly distribution of maasbanker larvae in relation to surface temperature is shown for Survey 1 and Survey 2 in Figures 6 and 8 respectively. The relationship between larval distribution and surface salinity is not discussed since both these hydrological parameters are closely allied. The larvae were usually associated with the high salinities (35,3°/oo-35,6°/oo) which accompanied the seasonal influxes of warm oceanic water.

Survey 1 (August I972 to March I973)

Maasbanker larvae were uncommon in the plankton during the upwelling month of spring. Those collected during October and November were found in the mixing areas between relatively warm I6°-17°C offshore water and cooler I4°C coastal upwelled water.

In December, warmer I9°-21°C water moved inshore and occupied much of the northern area. Conditions were relatively stable north of Palgrave Point but mixing between cold and warm water was more evident further south. Larvae were found offshore between Cape Cross and Walvis Bay in the mixing zone of warmer I7°-19°C water and cooler I4° to 16° coastal water.

In January, relatively cold coastal water had upwelled along the coast in the north distrupting the well-defined thermoclines of the previous month. Vertical temperature data off Cape Frio indicated the existence of a sharp front separating the warmer I8°-20°C oceanic water from the cooler I5°-I6°C inshore water. To the south, the boundary area weakened and the warm water was pushed closer to the surface and offshore. Maasbanker larvae were taken in maximum numbers during January and were widely distributed along this mixing zone, but were less abundant in the south where conditions were more stable.

Warm water advanced further inshore in February moving the oceanic front closer to the coast. Although no vertical temperature data was taken during this month, surface features suggested that the front was not as extensive and somewhat weaker than during January. Hydrological conditions in the south appeared to be relatively more stable than in the north. Larvae were again found in the mixed waters associated with the frontal system and occurred closer inshore, corresponding to the inshore movement of the $18^{o}C$ surface isotherm. Nevertheless, they were not as common or widespread in the plankton as during January.

In March, an increased uplift of cold water was apparent along the coast between Mowe Point and Palgrave Point, resulting in the oceanic water being pushed further offshore. The oceanic front was, however, still evident offshore in the north where considerable vertical mixing took place. Maasbanker larvae were found further west, than in February, corresponding to the seaward displacement of the $18^{o}C$ surface isotherm. Vertical temperature profiles in areas where larvae occurred showed that mixing was marked in the upper layers at offshore stations. In contrast, conditions became progressively more stable further south as the warm water moved offshore. Nevertheless, isolated patches of maasbanker larvae were found in the south, each time associated with localized intrusions of warm water.

Survey 2. (August 1973 to March/April 1974)

The general pattern of hydrological events was similar to conditions noted during Survey 1, but considerable differences were observed in the timing and seasonal distribution of the warm water intrusions. These changes were reflected in the seasonal occurrence and distribution of maasbanker larvae during Survey 2. Again, as in 1972, larvae were virtually absent during the active upwelling months (August to October).

Maasbanker larvae were first taken in the plankton in November between Palgrave Point and Cape Cross where vertical mixing occurred associated with an intrusion of 16^{o}-$17^{o}C$ water.

In December, warmer $18^{o}-19^{o}C$ water pushed inshore in the north between Mowe Point and Cape Cross, forming a fairly sharp front between the cooler inshore water and the warmer offshore water. Larvae were found in the mixed waters between the 17^{o} and $19^{o}C$ surface isotherm.

Maasbanker larvae were more numerous and widespread during January. Incursions of warm $18^{o}-20^{o}C$ water were also more extensive over the whole area and pushed closer to the coast than in December. Vertical temperature profiles showed that from north to south the warm upper mixed layers became progressively shallower and eventually moved offshore, being replaced by colder, subsurface water. The distribution of larvae followed a similar pattern, becoming scarce towards the south, where mixing was not as evident and stratification more pronounced.

In February, hydrological conditions were generally similar to those of January, except that the wedge of mixed oceanic water in the north occupied a greater depth offshore. Maasbanker larvae were correspondingly more plentiful and widely distributed in February though the centre of abundance had moved further south, being closely associated with the horizontal and vertical distribution of the $19^{o}C$ isotherm. Maximum catches were made off Palgrave Point, where the warm intrusion was deepest.

During late March/early April, warmer 20^{o} to $21^{o}C$ water moved inshore and southwards over a wide area north of Cape Cross. Maasbanker larvae were caught in greatest quantities during this month and were extremely widespread in the plankton north of Cape Cross. Compared with February, vertical temperature sections off Cape Frio and Palgrave Point showed that the warm mixed water extended further inshore, and to a depth of 30 m. Southwards, towards Cape Cross, the warm layers moved nearer to the surface and offshore. The distribution of larvae closely followed the offshore displacement of the warmer water and could be correlated with the horizontal and vertical distribution of the $18^{o}C$ isotherm.

Dispersal

Certain dispersal patterns could be observed by comparing the changes in horizontal distribution of small and large larvae between cruises and relating the apparent movement to hydrological conditions.

The months of January and February were selected for comparison because the population of larvae could be more easily traced and the gross water movement within the spawning grounds were generally typical of summer conditions. The distribution of two size categories of larvae (those less than 5,0 mm and those greater than 15,0 mm) are shown for January and February of both surveys in Figure 11.

In January 1973, newly-hatched maasbanker larvae were common in the offshore plankton between Cape Frio and Palgrave Point whereas in February the older specimens were found closer to the coast. The general drift of developing larvae inshore during this period was obviously associated with the extensive easterly influx of oceanic water in the north over these two months (Fig.6). The dispersal of larvae between January and February 1974 also indicated a transportation inshore during the intervening period. This was probably associated with the advance of warm water that occurred between these months (Fig.8).

Age and Growth

The developmental rate of maasbanker eggs and the growth of newly hatched larvae in relation to temperature has been established by King <u>et al</u> (1977) from the Cape Peninsula. Eggs were found to hatch after periods ranging from 81 hrs when incubated at 12,5°C to 26 hrs at 21,7°C. Newly hatched larvae increased by about 0,6 mm per day when reared at temperatures of 17,0° to 19,0°C and showed a linear growth rate to the time of yolk-sac absorption and eye pigmentation.

Although incubation rates were not determined for maasbanker eggs collected on SWAPELS, the time required to complete development may be similar to those of the Cape.

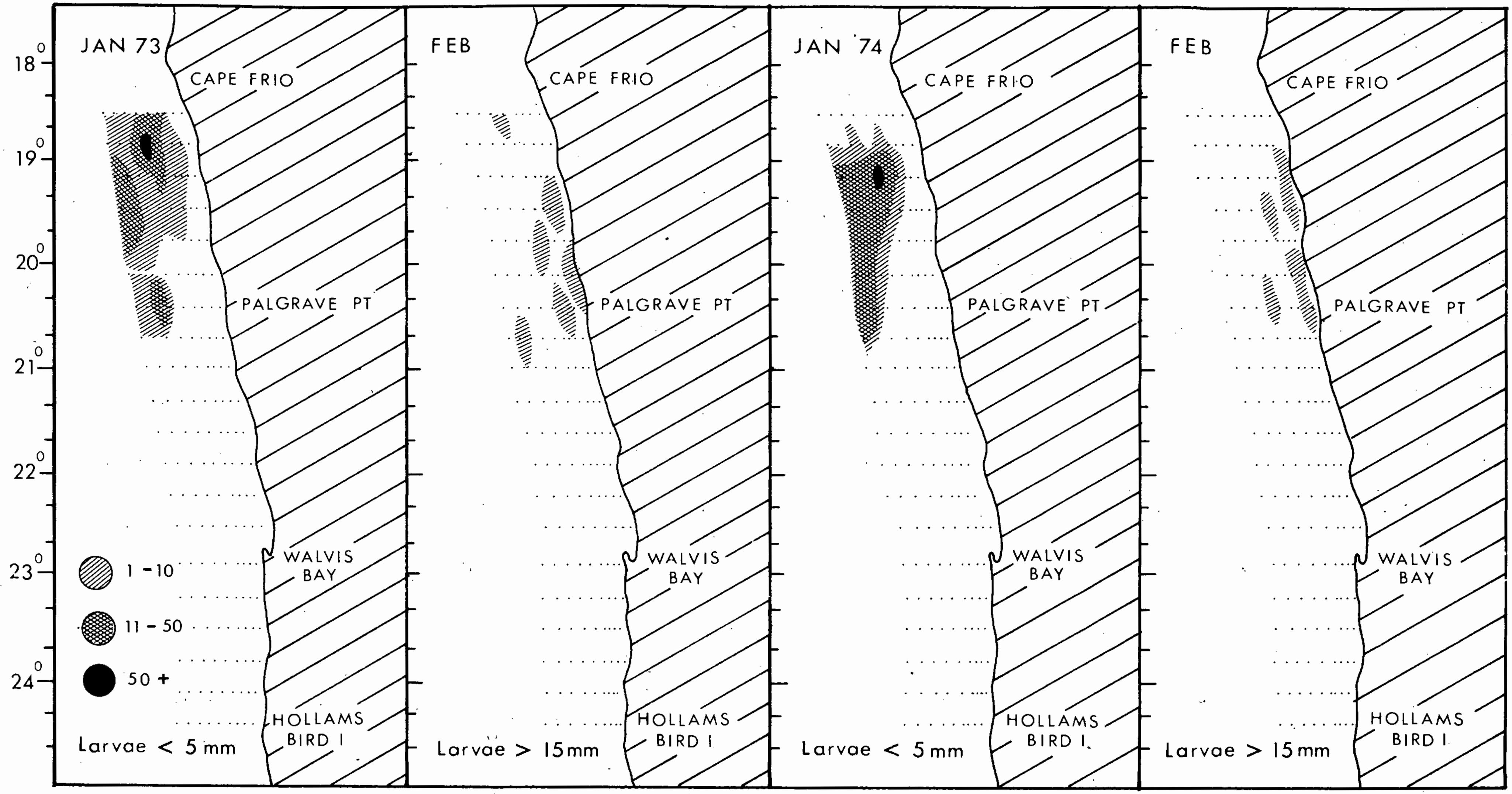


Fig. 11 Dispersal trend of developing maasbanker larvae between January and February of both surveys

Since spawning of maasbanker off South West Africa takes place mainly at temperatures of between 17,0° and 19,0°C it can be deduced from King et al (1977) that eggs would require about 26-30 hrs (1-1½ days) from the blastocap stage to hatching and that larvae of between 3,50 and 4,0 mm in length would be about 5 days to 1 week old.

The growth of larvae collected at sea can sometimes be estimated by analysis of successive length frequency diagrams but will depend on such factors as the time interval between sampling, mortality of larvae and dispersal patterns.

In this study, it was difficult to follow a group of larvae satisfactorily between cruises since the majority of specimens collected were between 3 and 8 mm in length. However, hydrological findings and dispersal patterns suggested that some of the large larvae captured inshore between Cape Frio and Palgrave Point in February 1973 may have been derived from the newly-hatched population which were abundant off-shore during the previous month (Fig. II). If this was the case, a rough calculation of growth may be made provided that the newly hatched larvae taken on January 15-16 had increased by at least 10,0 mm during the intervening period of 33 days between sampling the area. Such an increment does not seem unreasonable from growth rates of jack-mackerel T. symmetricus given by Farris (1961). The length frequency of all larvae collected between Cape Frio and Palgrave Point during January and those specimens larger than 15,0 mm taken in the same area in February is shown below:-

January (all larvae)		February (larvae greater than 15,0 mm)	
length range (mm)	percentage	length range (mm)	percentage
<4,0	8,5	15,1 - 16,0	18,7
4,1 - 5,0	46,3	16,1 - 17,0	22,9
5,1 - 6,0	25,2	17,1 - 18,0	41,3
6,1 - 7,0	12,8	18,1 - 19,0	8,7
7,1 - 8,0	6,3	19,1 - 20,0	6,8
>8,0	0,9	>20,0	1,5

Larvae of between 4 and 6 mm in length were the most common size group in January whereas specimens of I6 to I8 mm were the dominant length classes of the larger forms. This suggests that larvae increase by approximately 12,00 mm in a period of 33 days at an average rate of 0,36 mm per day. If the above growth rate therefore is used with that of the newly hatched larvae (King <u>et</u> <u>al</u> I977) the age of maasbanker larvae of lengths 16 to 18 mm would be between 40 and 47 days old from the time of hatching.

DISCUSSION

In South West Africa, the Cape horse mackerel or maasbanker spawns mainly in the northern offshore waters between Cape Frio (18°20'S) and Cape Cross (22°S). Heaviest spawning apparently takes place at distances of 50 - 100 km from the coast in the intermixing zone of warm oceanic and cool coastal water masses. The seasonality and abundance of newly-hatched larvae indicated that spawning was continuous from October to March/April. During spring, spawning was isolated and sporadic whereas in summer and early autumn it was intense and more widespread. The presence of large numbers of early larval stages at the northern and offshore limits of the grid suggested that the spawning area was insufficiently covered and could have extended a considerable distance outside the research area. Although SWAPELS was discontinued between April and July I973 and after April I974, the decline in larval abundance towards the end of Survey 1 (March I973) indicated that spawning was nearing completion towards mid-autumn. In I974, however, newly-hatched larvae were very abundant, suggesting that the breeding season may have lasted longer - perhaps into late April or even May. The conclusions interpreted from the seasonality of larvae are confirmed by Komarov (I964) who reported that the gonads of maasbanker caught off South West Africa were in a ripe condition between January and April. He also reported that spawning probably occurs outside this period as fish with active gonads were captured at other times of the year.

The increase of temperatures during summer caused by inshore and southerly movements of the oceanic front was closely linked with the timing of the main spawning season. Furthermore, the seasonal occurrence and abundance of newly hatched larvae in the plankton suggested that the duration and extent of spawning was associated with the distribution and intensity of mixing between oceanic and coastal water. For example during the summer of I972/73, the main breeding season was relatively short. Peak spawning occurred between late December and early January and was synchronous with the development of marked vertical mixing along a well-defined boundary zone of warm and cold water (Fig.6, O'Toole I977a). These conditions were apparently brought about by renewed coastal upwelling which disrupted the warm well-stratified layers that occurred in the region during December. The progression of larval abundance during the following months indicated a decrease in spawning activity towards February and a corresponding shrinkage of the spawning area northwards. In March, the spawning area withdrew further away from the coast probably as a result of the offshore displacement of warm mixed water.

The reverse appeared to be the case in I973/74. The season was longer and more intensive lasting from December to March/April and reaching its peak towards the end. Spawning was less intense during January, possibly because of less mixing and the fact that the boundary zone between warm and cold water was less apparent (Fig. 8, O'Toole I977a). However, as the season progressed, deep intrusions of warm mixed water pushed southwards and inshore increasing the size and extent of the spawning area.

Generally, the seasonal distribution of maasbanker larvae during both years was closely related to the horizontal and vertical distribution of I8°C water. Since the majority of larvae collected were between 3,5 and 8,0 mm in length (1-2 weeks old) it is possible that the eggs and spawning adults were also concentrated close to the I8°C isotherm.

Maasbanker larvae rarely occurred in the cold low salinity water (12^{o} - 15^{o}C; $34,90^{o}$/oo - $35,10^{o}$/oo) characteristic of the Benguela Current and were also scarce in areas of very warm highly saline water (21^{o}-22^{o}C ; $35,80^{o}$/oo - $35,90^{o}$/oo) which periodically intruded from the north-west. Regions of stability, where temperature gradients were well-developed i.e. near the coast during summer were also apparently unsuitable spawning areas. Larvae were most abundant where temperatures ranged from $16,0^{o}$C to $19,0^{o}$C within the upper 20 m layer and surface salinities were between $35,20^{o}$/oo and $35,60^{o}$/oo.

The horse mackerel is known to be a proportional spawner. Komarov (I964) suggested that the serial spawning nature of the maasbanker enabled the fish to reproduce whenever favourable conditions occurred. Macer (I974) also inferred that Trachurus trachurus can control the number of eggs released during the spawning season because if its flexibility of oocyte development and its ability to re-absorb gonads. He also postulated that more eggs might be released when environmental conditions were more suitable and vice versa. Thus, maasbanker may spawn over a longer period off South West Africa, if environmental factors continued to be favourable. Conversely, spawning may be restricted or reduced if conditions were unsuitable. The results of this study suggest that conditions during the I973/74 spawning season were more suitable than those of I972/73. In this instance, favourable conditions could be defined as a wider distribution of the convergent zone between the water masses associated with mixing in the upper layers. Unfavourable factors may be characterised by a more stable environment with less vertical mixing or a wider distribution of cold upwelled water. The dispersal of developing larvae from the sites of spawning would influence survival and be dependent on the circulation of water over the continental shelf and slope during summer/autumn. Gyral movements or coastal upwelling during the spawning season may transport the small planktonic larvae offshore over the continental slope into areas where high mortalities may result from excessively high temperatures and food scarcity.

However, influxes of warm water inshore and southwards appear to be generally typical in the north during summer and seem to carry developing larvae towards the coast thus preventing them from being swept offshore away from the nursery areas.

There is little information on migration of maasbanker off the South West African coast. Komarov (1964) reported that stable fish populations are found the whole year round in the region of Cape Frio and result from an uninterrupted approach of shoals of premature and mature individuals into the area. He also suggested that after spawning in the north, part of the Cape Frio stock migrate southwards to feed off the Orange River where large catches are frequently made by Soviet vessels. The results of this investigation and O'Toole (1976) suggest that developing larvae and juveniles remain mainly in the nursery area to the north of Cape Cross, although there was some evidence of transportation inshore. Wengrzyn (1976) showed that maasbanker increased in size southwards and found that the smaller fish preferred to stay in the northern waters to feed. Nevertheless, young maasbanker are known to occur over a wide area off the coast. Large catches of small maasbanker have periodically been made by purse-seiners both in the northern grounds and in the vicinity of Walvis Bay (F.H. Schulein, Sea Fisheries Branch, personal communication). Dense shoals of juveniles have often been observed by the author in the sheltered waters of Walvis Bay harbour. It is therefore probable that some juveniles migrate southwards presumably feeding in the productive upwelling areas of the Benguela Current and eventually returning to the northern waters as adults to spawn. The remainder may remain to feed and reach sexual maturity in the warmer mixed waters of the north, where, according to Komarov (1964) an abundance of food exists throughout the year.

LITERATURE CITED

AHLSTROM, E.H. I959 Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fishery Bull. Fish. Wildl.Serv. U.S. 60:(I6I) 107-146.

AHLSTROM, E.H. AND O.P. BALL. 1954 Description of eggs and larvae of jack mackerel(Trachurus symmetricus) and distribution and abundance of larvae in I950 and I951. U.S. Fish Wildl. Serv., Fish. Bull. (97), 56 : 209-245

BAPTISTA, S.R. DA F. 1976 Some notes on the Angolan pelagic fishery (ICSEAF divisions 1.1, 1.2, 1.3). Internal Report, Sea Fisheries Branch, 20 pp.

DAVIES, D.H. 1957 The South African pilchard (Sardinops ocellata) and maasbanker (Trachurus trachurus). Young fish survey. Investl Rep. Div. Sea Fish. S.Afr. 29 : 1-36.

DELSMAN, H.C. 1926 Fish eggs and larvae from the Java Sea (I) Treubia 8 : 199-239.

EHRENBAUM, E. 1909 Eier und Larven von Fischen. Tiel. Nord. Plankt. Lief. 4 : 1-216.

FAO 1974 Catches and Landings. Year book of fishery statistics, I973, 36 : Food and Agricultural Organization of the United Nations, Rome.

FARRIS, D.A. 1961 Abundance and distribution of eggs and larvae and survival of larvae of jack mackerel (Trachurus symmetricus) Fishery Bull.Fish.Wildl.Serv.U.S. 61, (I87) 247-278.

GELDENHUYS, N.D. 1973 Growth of the South African maasbanker Trachurus trachurus L. and age composition of the catches I950-1971. Investl Rep.Sea Fish.Brch.S.Afr. IOI : 24 pp.

HAIGH, E.H. 1972 Development of Trachurus trachurus (Carangidae).the South African maasbanker. Ann. S.Afr. Mus. 59 (8) 139-150.

IDA, H. 1972 Some ecological aspects of larval fishes in waters off Central Japan. Bull. Jap.Soc. scient. Fish., 38, (9) : 981-994.

KILIACHENKOVA, V.A. 1970 Development and distribution of eggs and larvae of Trachurus trachurus L. Rapp. P-v Renu. Consi perm.int. Explor. Mar. I59 : 194-198.

KING, D.P.F, M.J. O'TOOLE AND A.A. ROBERTSON. 1977 in press Early development of the South African maasbanker Trachurus trachurus at controlled temperatures. Fish. Bull.S.Afr. (9).

KOMAROV, Y.A. 1964 Some data on the reproduction of the horse mackerel Trachurus trachurus L. from the South West African coast. Translated from the Russian. Trudy AtlantNIRO, t.xi ; 87-99.

KOMPOWSKI, A. AND W. SLOSARCZYK | I976 | Some investigations on the horse mackerel (_Trachurus trachurus_ L.) in the ICSEAF area in I973. _ICSEAF, Coll. Sc. Pap. 3_ : 27-3I, Madrid.

MACER, C.T. | I974 | The reproductive biology of the horse mackerel _Trachurus trachurus_ L. in the North Sea and English Channel. _Jour. Fish. Biol._ : _6_ : (3) ,

MC LEOD, P.R. | I97I | Competition and feeding studies. _Cape Cross Report, Phase 3_ , _Sea Fisheries Branch_, Cape Town, I2 pp.

O' TOOLE, M.J. | I976 | Incidental collections of small and juvenile fishes from egg and larval surveys off South West Africa (I972-I974). _Fish. Bull. S. Afr. 8_, 23-33.

O' TOOLE, M.J. | I977a | Distribution of temperature and salinity off South West Africa, I972-I974. _PhD thesis, University of Cape Town_ , _section I_ , 3I pp.

O' TOOLE, M.J. | I977b | Investigations into the early life history of the South West African pilchard _Sardinops ocellata_ Pappe. _PhD thesis, University of Cape Town, section 2_, 53pp.

O' TOOLE, M.J. | I977c in press | A note on the relationship between the vertical distribution of maasbanker larvae (_Trachurus trachurus_ Linnaeus) and environmental parameters off South West Africa. Fish. Bull. S. Afr. _9_ .

SIEGEL, S. | I956 | Non parametric statistics for the behavioural sciences. _Mc Graw-Hill, New York_, 3I2 pp.

SMITH, J.L.B. 1970 The sea fishes of Southern Africa. 5th Ed. Central News Agency, Cape Town: 580 pp.

WENGRZYN, J. 1976 The catches and characteristics of the Southwest African horse mackerel stocks in the exploitation phase. ICSEAF Coll. Sc. Pap. 3 , 45-49.

ASPECTS OF THE EARLY LIFE HISTORY

OF THE HAKE, *MERLUCCIUS CAPENSIS*

CASTELNAU OFF SOUTH WEST AFRICA.

B Y

MICHAEL J.O'TOOLE,
SEA FISHERIES BRANCH,
BEACH ROAD,
SEA POINT,
CAPE TOWN.

INTRODUCTION

The hake, genus *Merluccius*, occurs off the south and west coasts of southern Africa at depths of 40 - I000 metres (Smith I970). Commercially, it is the most important trawled species taken in these waters.

Catches of hake off southern Africa have increased tenfold in only ten years, from I06700 metric tons in I962 to over a million tons in I972 (Draganik I974). Recent years have seen a rapid expansion in fishing effort for hake off South West Africa by the distant water fleets of several countries resulting in the landings from the ICSEAF divisions I,3 and I,4 (I5° - 22°S) increasing from 86800 metric tons in I965 to 568000 metric tons in I972 (Ikeda I975). The stocks are mainly exploited by vessels of the Soviet Union, Spain, Bulgaria, Cuba and South Africa. Soviet vessels alone account for over 75 percent of the total hake catches from these waters (FAO I974).

Two species of hake are recognised off the west coast of southern Africa, *Merluccius capensis* Castelnau and *M. paradoxus* Franca. The distinction between the two forms is based chiefly on differences in the number of vertebrae, otolith structure and gill raker pigmentation (van Eck I969, Botha I97I). Both species also differ in depth distribution, *M. capensis* tending to be found inshore, whereas *M. paradoxus* prefer the deeper water offshore (Kuderskij I973, Botha I973). Owing to the difficulty in visually distinguishing between the two species, landings and catch statistics of hake are usually referred to simply as *Merluccius sp.*

Chlapowski (I975) reported that the quantitative occurrence of the two groups of hake showed contrasting differences along the north-south line. Catches off S.W.Africa were almost exclusively *M. capensis* but the catch frequency of *M. paradoxus* increased towards the southern Cape grounds where it eventually becomes the dominant species. Both species spawn on a modest scale (Jones and van Eck I967), *M. paradoxus* at greater depths than *M. capensis* (Pschienichniy and Assorov I969, Botha I973) Spawning generally takes place from September to December but may occur at other times between November and April (Pschienichniy I972).

Hake exhibit marked diurnal vertical movement. Fishermen frequently report shoals close to the sea bed during the day while shoals rise and become more loosely structured as darkness approaches. During the spawning season, hake are more pelagic in behaviour than at other times of the year and show little diurnal movement. (Botha 1973). A similar phenomenon was reported by Dark (1975) for the pacific hake, <u>M. productus</u>. Spawning apparently takes place at intermediate depths during the pelagic phase (Botha <u>op.cit</u>).

Despite the commercial importance of the South African hake, there is little information on the distribution, seasonality or ecology of the planktonic eggs and larvae in these waters. Previous work on the early life history of the hake has mainly been concerned with descriptions of the egg and larval stages. (Matthews and de Jager 1951; Haigh 1972). Hake larvae were reported in the plankton off South West Africa by Hart and Marshall (1951). The only other reference is a general account on the occurrence of eggs and larvae between the Cunene River (17°S) and Agulhas bank (37°S) based on a two-month investigation by Porebski and Koronkiewicz (1975).

Hake eggs and larvae were common in ichthyoplankton samples taken during the S W A P E L S surveys 1972 to 1974, the larvae ranking ~~seventh~~ sixth in order of species abundance. The research area shown in Figure 1 was investigated monthly between August 1972 and March 1973 and August 1973 and March/April 1974. An account of the methods of collection, cruise dates, station positions and depth are given by O'Toole (1976, 1977b). A brief description of the egg is given and the seasonality, distribution and abundance of larvae are outlined. Hydrological relationships, dispersal and diurnal variation in catches of larvae are also discussed.

R E S U L T S

Identification of the Eggs and Larvae

Hake eggs collected during this study were identified from descriptions given by Matthews and de Jager (1951) aided by descriptive literature on the early life history of hake species from other parts of the world. (d'Ancona 1933, Ahlstrom & Counts 1955, Arbault and Boutin 1968, de Ciechomski and Weiss 1973).

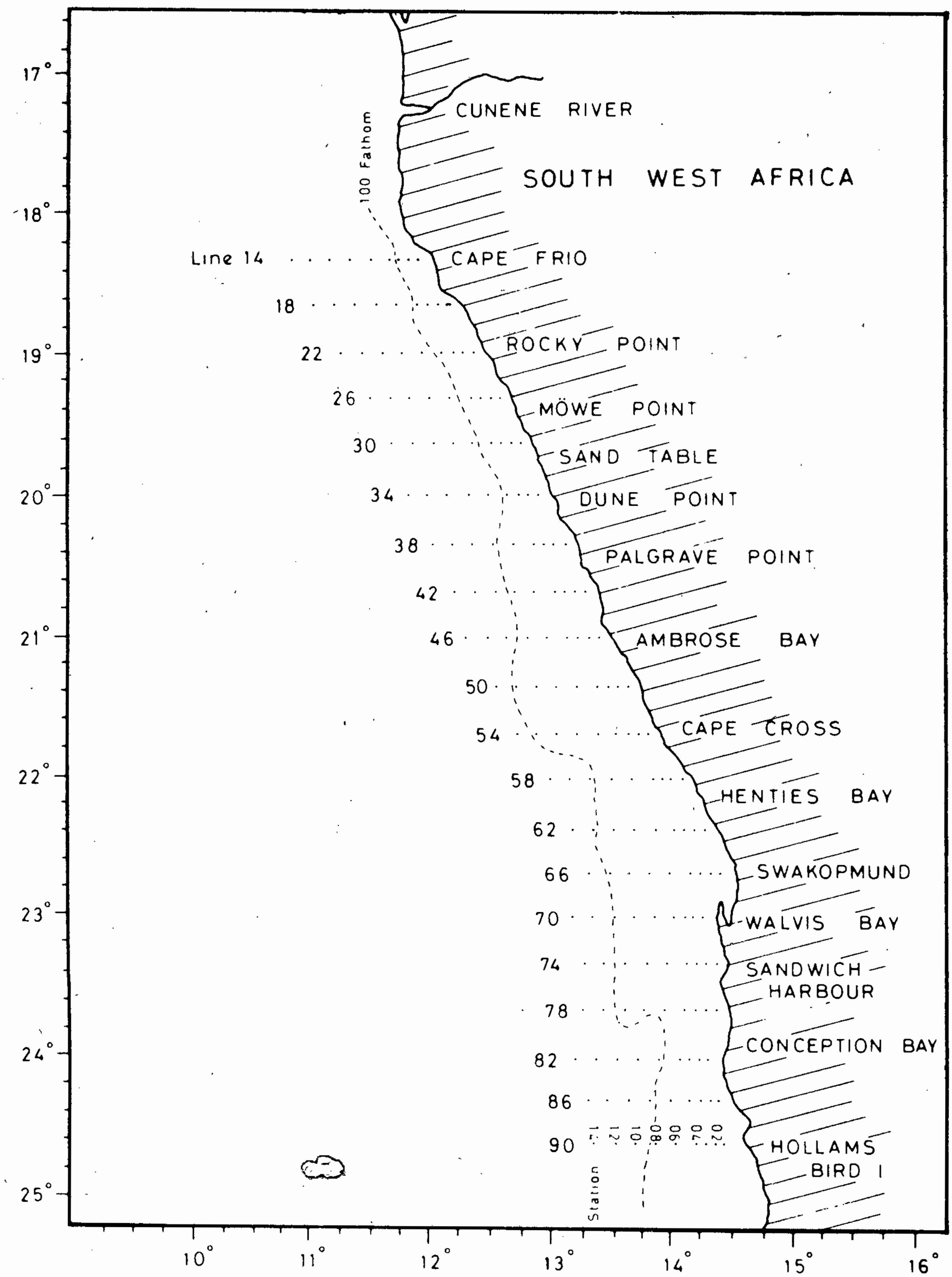


Fig. 1 Location of routine stations occupied during the SWAPELS cruises in 1972/73 and 1973/74

The larvae were easily recognised from the illustration given by Hart and Marshall (I951) and the more comprehensive description of *M. capensis* larvae by Haigh (I972).

The eggs are spherical with a smooth unsculptured membrane, a narrow perivitelline space and a single oil globule. The diameter of the eggs ranged from 0,85 to 1,06 mm (mean 0,94mm) and the oil globule from 0,15 to 0,26mm (mean 0,22mm). The size range of 200 eggs extracted from random samples is shown below. Approximately 80 percent of those measured were between 0,90 and 1,00 mm in diameter closely agreeing with the size range of eggs recorded by Matthews and de Jager (I951) and Porebski and Koronkiewicz (I975).

Size Range (mm)

Egg	0,81 - 0,90	0,91 - 0,95	0,96 - 1,00	>1,01
Oil Globule	0,15 - 0,21	0,18 - 0,24	0,17 - 0,24	0,20-0,26
No. Examined	32	84	76	8

Owing to the difficulty in separating the two adult hake species, even greater difficulty was expected in distinguishing between species at the egg and larval stages. During the routine cruises, eggs of both species may have been collected in the samples, but no attempt was made to separate them. Larval and juvenile hake were undistinguishable from those described as *M. capensis* by Haigh (I972).

Porebski and Koronkiewicz (I975) reported that hake eggs taken in the plankton north of the Orange River were slightly smaller than those found further south and certain differences were also noted in larval pigmentation though these characters were not specified. In view of the latitudinal variation in egg size and the corresponding regional distribution of the two species (Chłapowski I975), it is probable that the eggs and larvae collected in this investigation were predominantly *M. capensis*.

Distribution of the Eggs.

Hake eggs were identified in the samples but were not counted. The results of this report are therefore based entirely on the distribution and abundance of the larval stages. However, the limited observations on egg distribution showed that the southern part of the research area was the main centre of spawning. Eggs were found from October to December during Survey 1 and from September to January on Survey 2, noticeably more eggs being taken in the Walvis Bay area, particularly during November and December. Eggs and newly-hatched larvae frequently occurred in the same haul.

The general findings substantiate the results of other workers. Chlapowski (I974) found that the gonads of M. capensis in the Cunene division I,3 were immature during November but during the same month, over 60 percent of the fish in the Cape Cross division I,4 were maturing, spawning or spent. Porebski and Koronkiewicz (I975) also noted that greatest numbers of eggs and larvae occurred off Walvis Bay in November and December.

Distribution and Seasonality of the Larvae

Although hake larvae were found over the entire research area during both surveys, over 95 percent of the specimens were taken from waters south of Palgrave Point (20°20'S). Abundance declined sharply further north (4,7% in I972/73 and 4,6% in I973/74). The percentage of the total numbers collected in the different parts of the survey area is summarized in Table 1.

Table I : The percentage of hake larvae taken in the different parts of the survey area (I972 - I974)

Area	Station line	I972/73	I973/74
Cape Frio - Mowe Point	14-26	1,9	2,9
Mowe Point - Palgrave Point	30-42	2,0	2,2
Palgrave Point - Henties Bay	46-58	1,7	8,8
Henties Bay - Sandwich Hb.	62-74	67,4	70,6
Sandwich Hb. - Hollams Bird Is.	78-90	27,0	15,5

Larvae were captured over the entire inshore/offshore range of the sampling grid but were most numerous 20-100 km from the coast (Table II). The regional distribution to the north and west was adequately encompassed but larval distribution to the south was not delimited. The general distribution and the main centre of abundance was very similar for both surveys. (Figs. 2 and 3). Highest densities were found about 40-60 km north-west of Walvis Bay. Hake larvae, nevertheless, were more plentiful during I973/74 compared with I972/73.

TABLE II : The percentage occurrence of hake larvae in relation to the distance from shore (I972 - I974)

Distance from shore	I972/73	I973/74
I0 km or less	1,2	3,2
I0-20 km	12,3	5,0
20-30 km	22,3	9,0
30-50 km	22,3	9,9
50-100 km	41,5	72,2
100 km or more	0,3	0,5

Although sampling was conducted from August to March/April, larval stages were only taken between October and March. Ninety-two percent of the total number captured on both surveys were taken in October, November and December. Over 60 percent were caught during the month of December alone. Specimens found between January and March/April accounted for only 7 percent of all those collected.

Survey I : (August I972 - March I973)

The monthly distribution, abundance and length composition of hake larvae together with surface isotherms for each cruise is shown in Figures 4 and 5 respectively. A summary of the monthly hauls and abundance is given in Table III .

Hake larvae first occurred in the plankton during October near Walvis Bay when ten specimens ranging from 6-I4 mm in length were captured. The time taken to complete larval development is unknown but is probably at least a month, depending upon the temperature of the water (Ahlstrom and

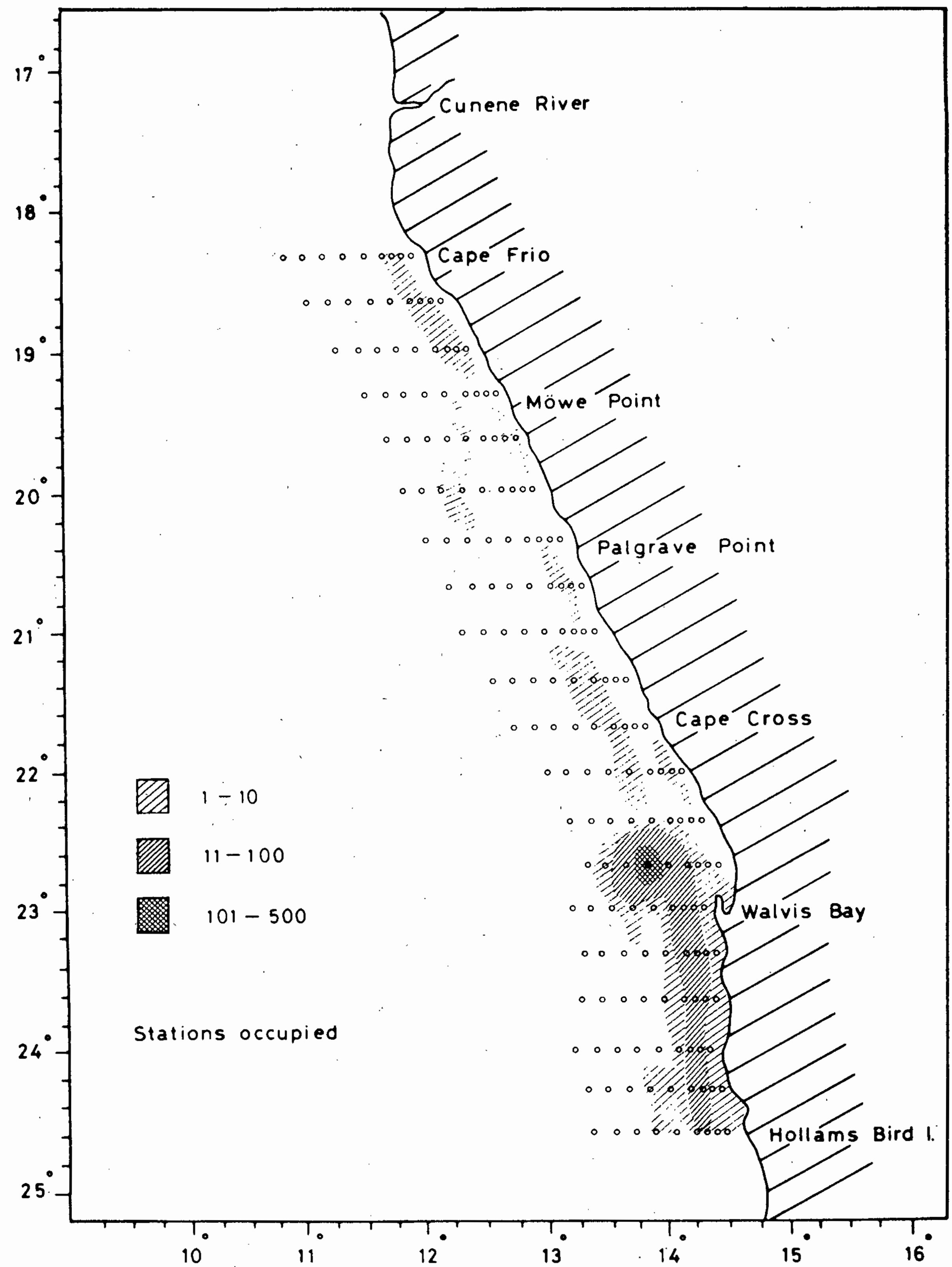


Fig. 2 Distribution and abundance of hake larvae during Survey 1 (values represent cumulative standard haul totals for all cruises)

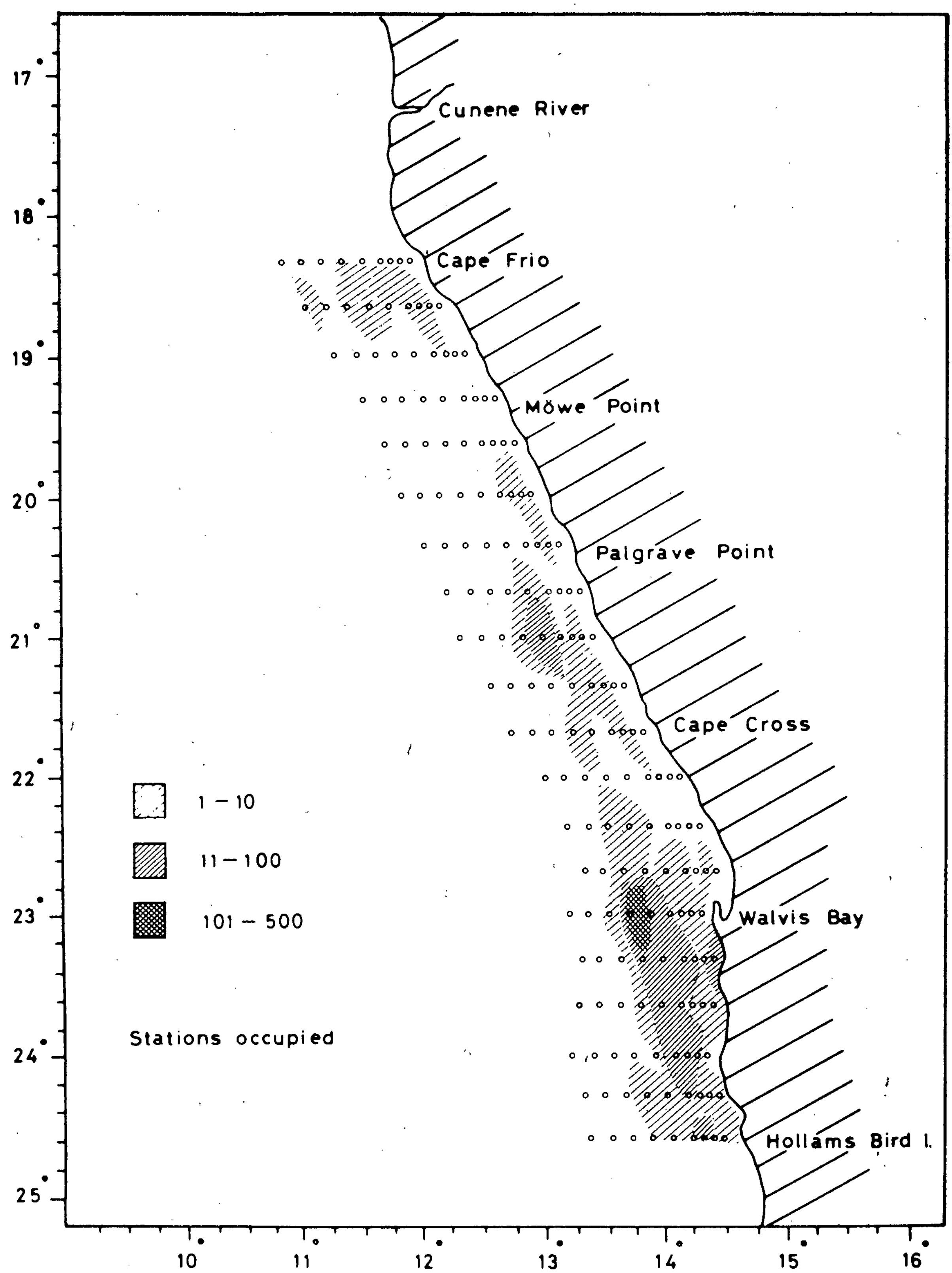


Fig. 3 Distribution and abundance of hake larvae during Survey 2 (values represent cumulative standard haul totals for all cruises)

Counts I955). It is, therefore, probable that larvae taken during October resulted from eggs spawned sometime in September.

More larvae were caught in November, mainly inshore south of Cape Cross. The centre of abundance was 20-30 km west of Walvis Bay but a few isolated specimens were found offshore north of Cape Cross. Most of the larvae (80%) consisted of yolk-sac and early stages, which hatched from eggs spawned between October and early November.

Highest concentrations were taken during the month of December, predominantly south of Cape Cross, 8-100 km from the coast. Hake larvae were particularly common about 80-100 km north-west of Walvis Bay. Over 75 percent of the specimens captured in December were longer than I2,0 mm and probably originated from heavy spawning in November. It is also possible that some of the November larval population were represented in the catches.

A sharp drop in abundance was noticeable in January. The distribution consisted of a few isolated specimens captured at scattered localities between Mowe Point and Walvis Bay. Larvae measured from 5-12 mm which suggested that some localized spawning took place in December.

No larvae were taken in February. Only nine specimens were found in March, 20-50 km from the coast south of Walvis Bay. These larvae were 5-8 mm in length and were presumably derived from eggs spawned between late February and early March.

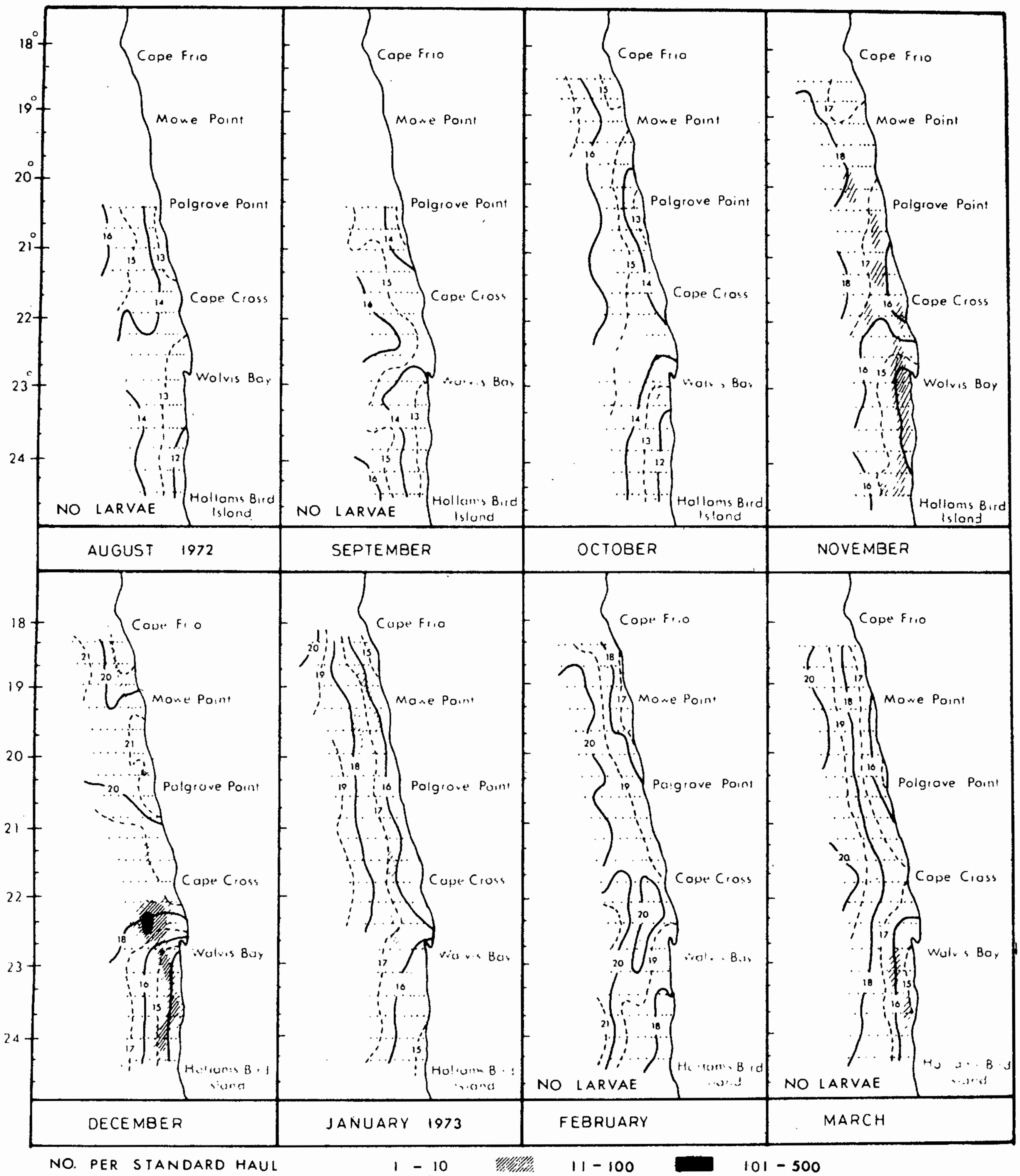


Fig. 4 Monthly distribution and abundance of hake larvae, August 1972 to March 1973

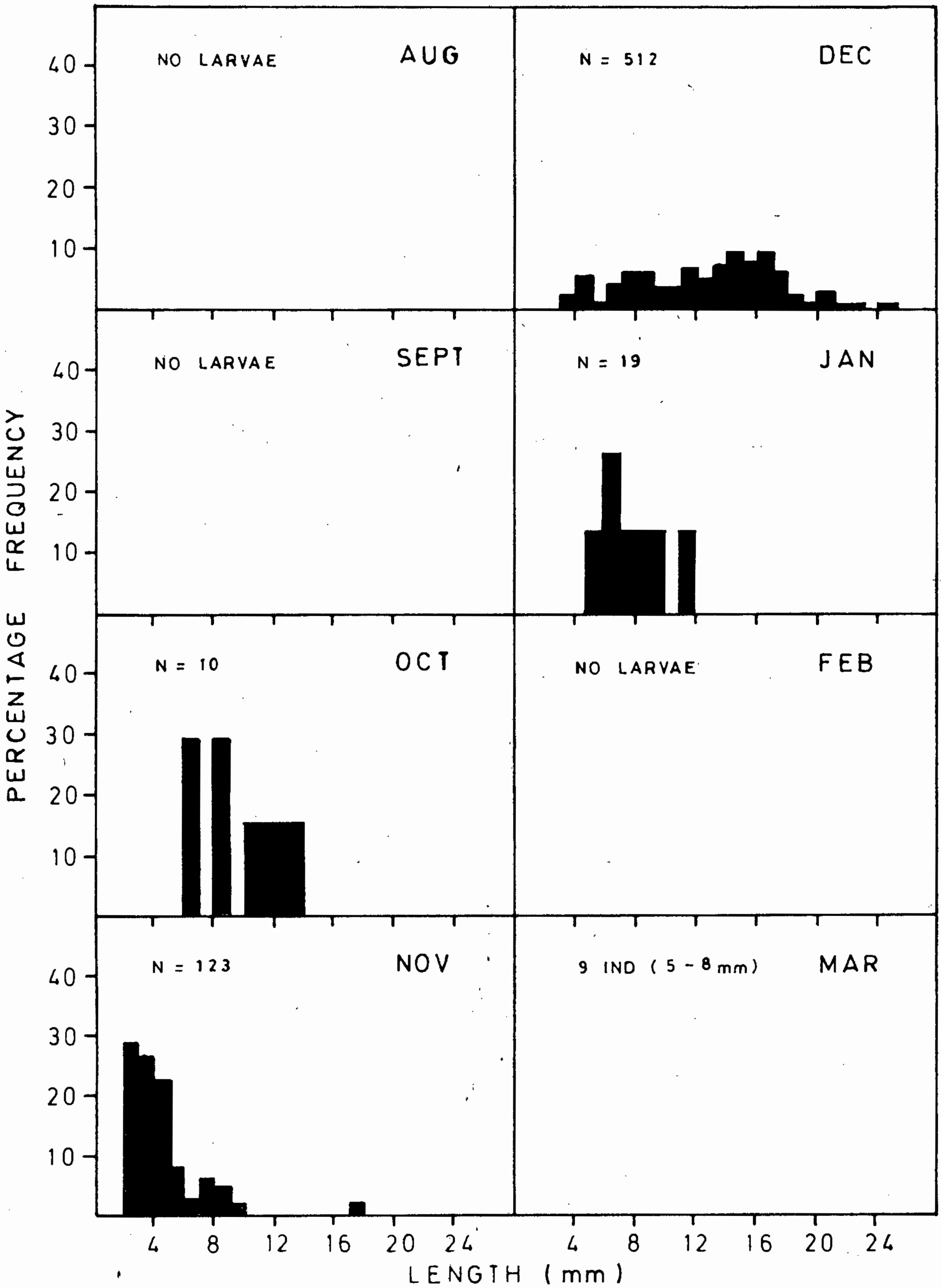


Fig. 5 Length composition of hake larvae collected during the survey cruises August 1972 to March 1973

TABLE III : A summary of the monthly hauls and abundance of hake larvae during Survey I

Month	No.of hauls	No.of positive hauls	No.of larvae collected	Mean no.of larvae per IO m^2	Percentage of total collected
August	123	0	0	0	0
September	126	0	0	0	0
October	156	2	10	5,5	1,5
November	180	21	123	6,3	18,3
December	180	20	512	25,5	76,1
January	180	6	19	3,3	2,8
February	177	0	0	0	0
March	177	0	9	4,5	1,3

SURVEY 2 : (August I973 - March/April I974)

The monthly distribution and abundance of hake larvae with temperature distribution is illustrated in Figure 6 and summarized in Table IV. The length frequencies are given for each month in Figure 7. Larvae were initially collected in the plankton in October at isolated localities between Mowe Point and Conception Bay mainly inshore south of Walvis Bay. The specimens caught were 4-15 mm in length but mostly less than 8 mm.

The distribution in November was similar to that of October but the numbers increased considerably. Largest catches were made in the south, about 30 to 60 km offshore between Walvis Bay and Conception Bay. Larvae were also common further south at inshore stations near Hollams Bird Island. The length composition showed that over 80 percent of those captured were composed of newly-hatched stages. An intensification of spawning must therefore have occurred between late October and early November. The remainder of the larvae were between I4 and 25 mm in length and probably represented the same population sampled during October.

The December cruise produced the largest catch of hake larvae during the entire survey. Concentrations were found south-west of Palgrave Point and in the vicinity of Walvis Bay. The centre of greatest abundance was 40 - 64 km west of Walvis Bay at a similar location to that of the November cruise. Over 90 percent of the specimens were newly-hatched (3 - 8 mm in length), indicating heavy spawning between late November and early December.

By January, larvae had become scarce in the plankton. A few patches of isolated specimens with lengths ranging between 4 and 20 mm were found offshore north-west of Walvis Bay.

In February the numbers of larvae declined even further. A few newly-hatched specimens were found south-west of Cape Frio, west of Palgrave Point and south-west of Walvis Bay.

Hake larvae were slightly more common during March/April and the regional distribution was similar to that of February. Many of the specimens were newly-hatched which suggested that sporadic spawning still occurred at isolated localities in March.

TABLE IV : A summary of the monthly hauls and abundance of hake larvae during Survey 2

Month	No.of hauls	No.of positive stations	No.of larvae collected	Mean no. of larvae per $10m^2$	Percentage of total collected
August	126	0	0	0	0
September	135	0	0	0	0
October	180	13	75	5,6	9,2
November	180	17	247	14,2	27,1
December	180	14	490	34,8	53,8
January	180	5	26	5,1	2,9
February	169	4	20	5,1	2,2
March/April	175	10	53	5,3	5,8

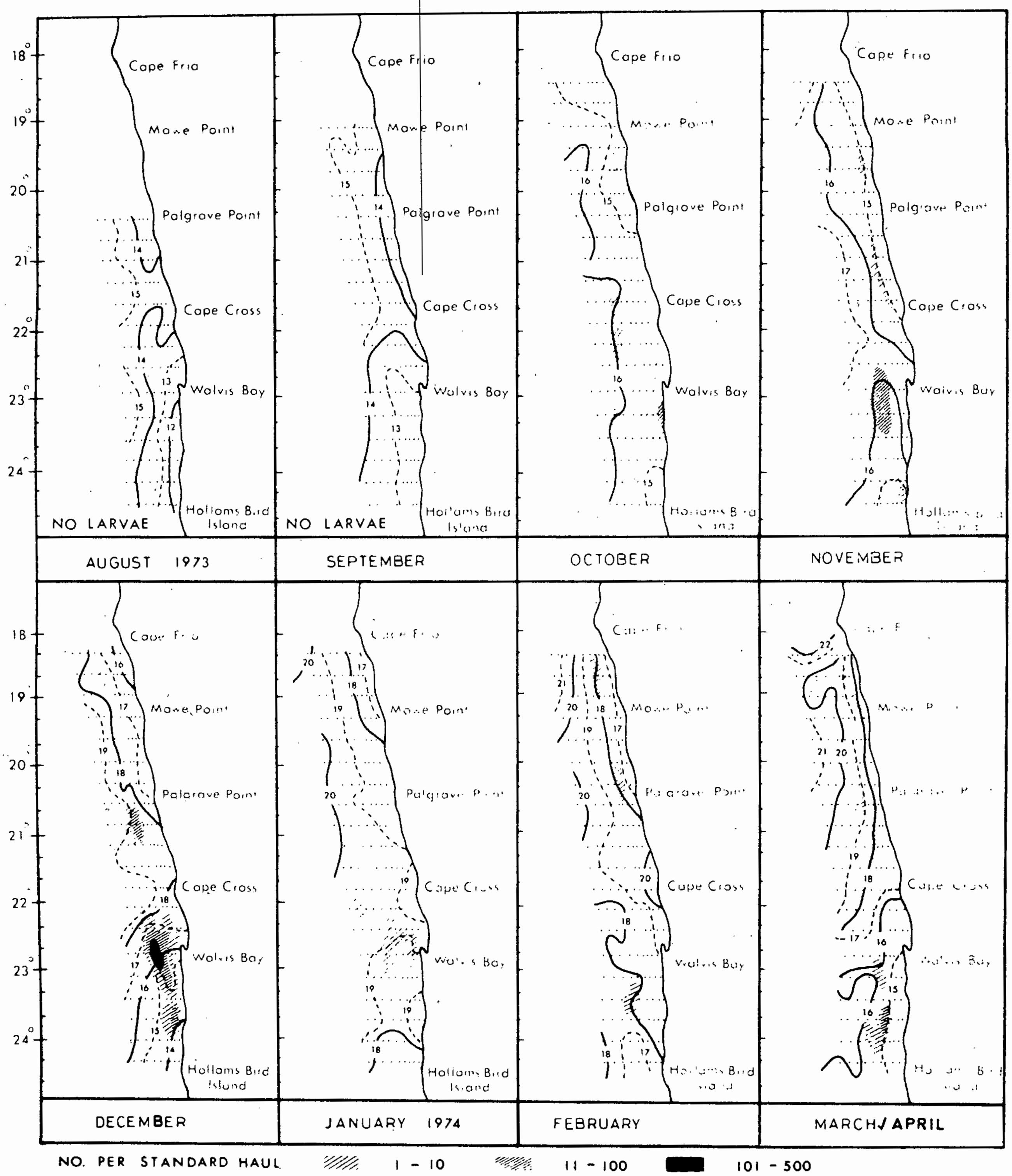


Fig. 6 Monthly distribution and abundance of hake larvae, August 1973 to March / April 1974

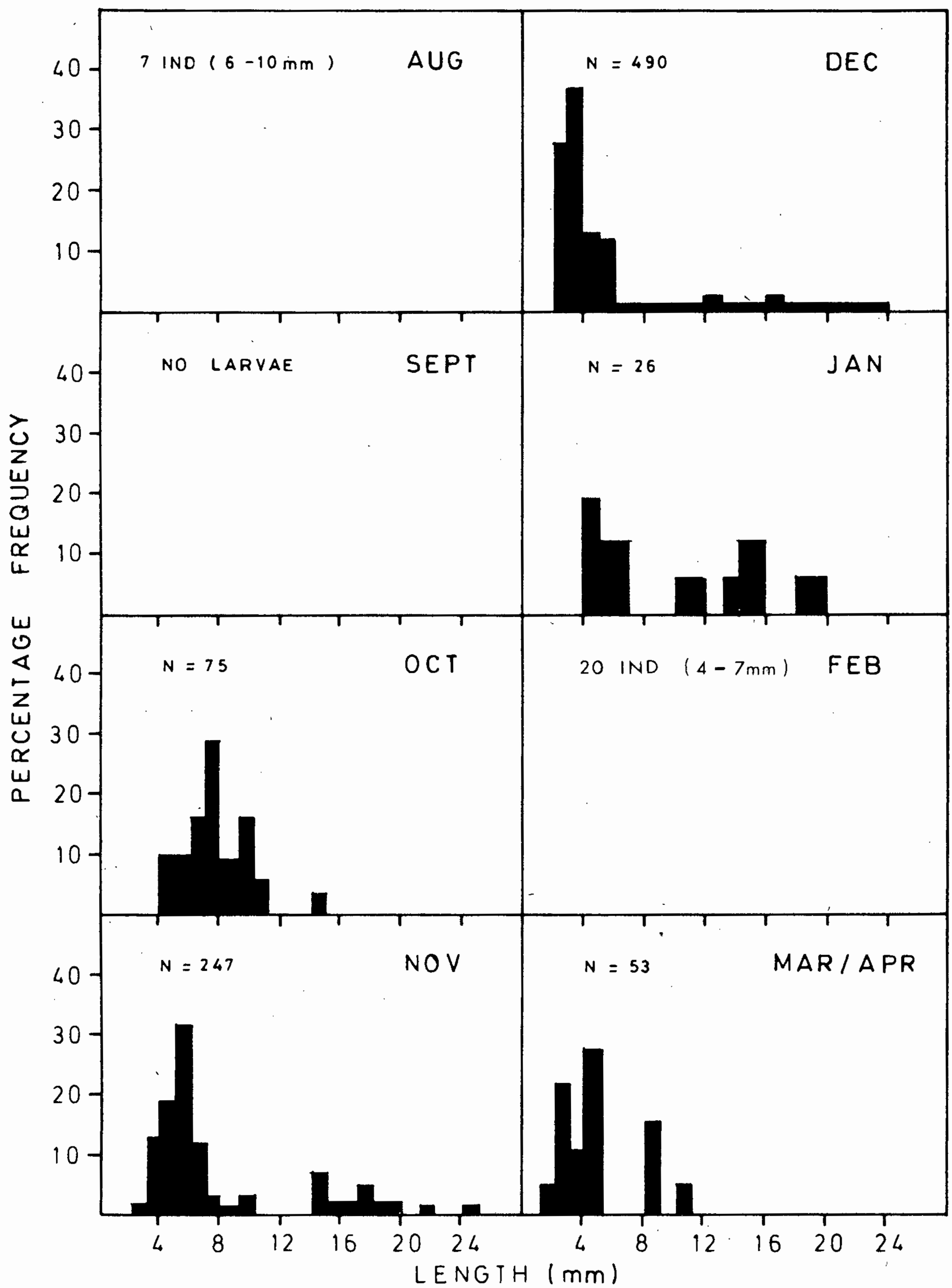


Fig. 7 Length composition of hake larvae collected during the survey cruises August 1973 to March/April 1974

Diurnal Variation in Catches

A comparison of the total number of hake larvae taken at different times showed that hauls were equally productive during the day and night (Table V). Nevertheless, differences existed when larval size was considered (Fig 8).

Newly-hatched larvae (those less than 5,00 mm in length) were caught mainly during the day and early morning hours. Maximum catches were made in hauls taken between I2h00 and I4h00.

In contrast, the older larvae (those greater than IO,0 mm in length) were practically absent from daytime collections, but the percentage occurrences increased markedly after dusk and reached a peak between midnight and 02h00. Towards early morning, numbers dropped sharply and few were caught after 08h00. Larvae of intermediate sizes (5-10 mm) were common in both day and night hauls but were about twice as abundant in collections made at night.

TABLE V: Day and night catches of different size hake larvae

Size group	Day hauls (58)		Night hauls (64)		D/N Ratio
	No.of larvae	Percent	No.of larvae	Percent	
5,0	328	76,2	110	23,7	3 : 1
5,1 - 10,0	55	35,4	100	64,6	1 : 2
10,1 - 15,0	7	7,6	87	92,3	1 : 12
I5,0	19	17,7	84	82,2	1 : 5
TOTAL	409	51,7	381	48,3	1 : 1

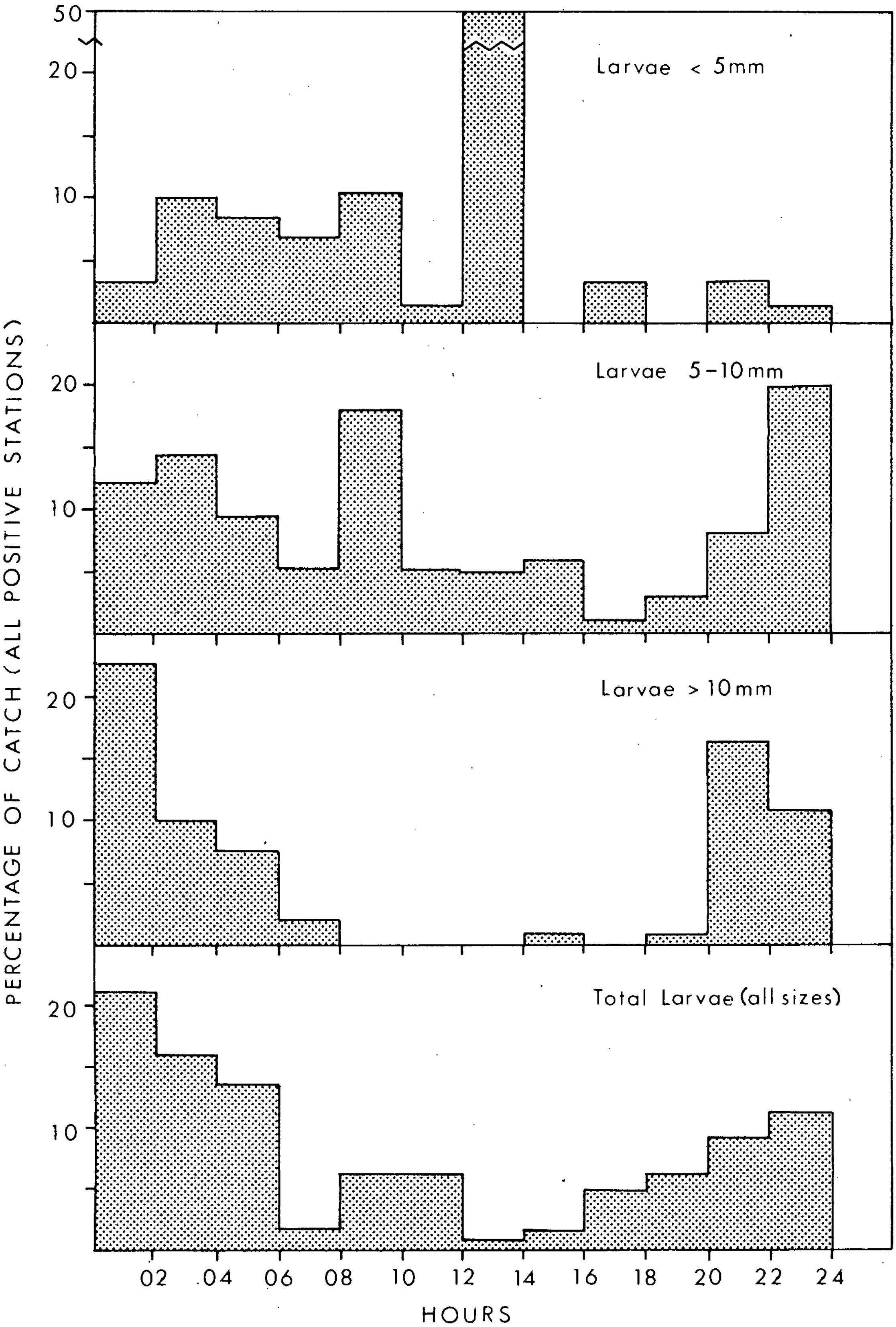


Fig. 8 Diurnal variation in the catch rate of hake larvae according to size categories (all cruises)

The Relationship between Larval Abundance and Temperature

The relationship between abundance of larvae and surface temperature is summarized in Table VI. Hake larvae were found in waters where the surface temperatures ranged between I2,6° and 20,4°C. Over 60 percent of all positive hauls were made at temperatures of I4,8° to I6,5°C. Approximately I5 percent were taken at surface temperatures greater than I8°C and 20 percent at temperatures less than I5,0°C. The temperature range is similar to the findings of Porebski and Koronkiewicz (I975) who reported that hake larvae collected between Cape Frio and the Orange River occurred at mean surface temperatures of between I5,2° and 15,9°C.

Variations in the depth distribution of larvae were not studied; consequently, an exact temperature-catch relationship could not be determined, except in vertically isothermal conditions. The vertical distribution of other species of larval hake has previously been studied. Ahlstrom and Count (I955) and Ahlstrom (I959) found that larvae of the Pacific hake, *Merluccius productus* were most abundant near or within the thermocline.

TABLE VI : Relationship between surface temperature and abundance of hake larvae I972-I974

Surface temperature (°C)	No. of standard hauls that collected: I-5 larvae	6-10 larvae	11-100 larvae	101-250 larvae	250 + larvae	Total
12,1 - 13,0	1	2	0	0	0	3
I3,1 - 14,0	7	7	3	0	0	17
14,1 - 15,0	11	3	8	0	0	22
15,1 - 16,0	7	5	7	0	0	19
16,1 - 17,0	16	5	1	1	1	24
17,1 - 18,0	7	3	3	0	0	13
18,1 - 19,0	9	1	0	0	0	10
19,1 - 20,0	3	2	0	0	0	5

Fahey (I974) also reported that the larvae of the silver hake, *M. bilinearis* apparently concentrate near the thermocline during summer months.

The depth of the thermocline in regions where hake larvae were found during this investigation varied from I5 to 30 metres. If 20 metres is taken to represent the average depth of the thermocline and larval abundance is related to temperature at this depth, then over 75 percent of the hauls containing larvae occurred at temperatures of I3°-15°C. Approximately I5 percent were found at temperatures greater than I5°C and 5 percent at temperatures less than I3°C. The relationship between abundance and temperature at 20 metres is given in Table VII.

TABLE VII : Relationship between water temperature at 20 metres depth and abundance of hake larvae I972 - I974

Temperature at 20 metres (°C)	Number of standard hauls that collected					
	I-5 larvae	6-10 larvae	II-100 larvae	101-250 larvae	250 + larvae	Total
10,1 - 11,0	1	1	0	0	0	2
11,1 - 12,0	2	0	3	0	0	5
12,1 - 13,0	11	6	1	0	0	18
13,1 - 14,0	15	10	8	0	0	33
14,1 - 15,0	13	5	5	1	1	25
15,1 - 16,0	9	3	4	0	0	16
16,1 - 17,0	6	0	1	0	0	7
17,1 - 18,0	5	0	0	0	0	5
18,1 - 19,0	1	0	0	0	0	2

In order to test whether there was a significant relationship between larval abundance and temperature, the Kruskal-Wallis one way analysis of variance by rank (Siegel I956) was applied to the original data summarized in Tables VI and VII.

H^{o} values of 18,58 and 21,38 were obtained for temperature ranges at the surface and at 20 metres respectively which indicated significant differences at the 1 percent level. A possible indication that hake larvae were mainly at approximately 20 m could be inferred from H-values since there was a better temperature-dependence at 20 m than at the surface.

Occurrence of Larvae in Relation to Salinity

Larval occurrence is only related to surface salinity as no subsurface salinity measurements were taken during the routine surveys. Hake larvae occurred over a salinity range of 34,89°/oo to 35,70°/oo. Approximately 85 percent were found at relatively low salinities ranging from 34,90°/oo to 35,15°/oo. The frequency of occurrence of more than 6 larvae per positive hauls is related to surface salinity in Table VIII .

TABLE VIII : The relation between surface salinity and the frequency of occurrence of hake larvae at levels of abundance 6

Salinity Range (°/oo)	34,81-34,90	34,91-35,00	35,01-35,10	35,11-35,20	>35,20
No. of positive hauls	2	5	39	4	2
Percentage frequency	3,8	9,5	76,0	7,7	3,3

The Relationship between Larval Distribution and Hydrology

An account of the seasonal hydrological features off South West Africa during both surveys is given by O'Toole (1977a). The present discussion is confined to a general outline relating the seasonality and distribution of hake larvae to hydrological changes in the spawning grounds south of Cape Cross.

The gross movements of water masses can be followed by examining the horizontal distribution of surface temperature outlined on the larval distribution charts (Figs. 4 and 6).

SURVEY 1 (August 1972 to March 1973)

Hake larvae were not found in the plankton during the strong upwelling months of August and September. The vertical distribution of temperature along the Walvis Bay and Hollams Bird Island line showed conditions typical of late winter/early spring with cold water (11°-14°C) widespread and temperature isothermal in the upper 50 metres. Larvae first occurred in small numbers off Walvis Bay in October following a slight increase in temperature associated with a movement of 14 - 15°C water closer to the coast.

In November, upwelling slackened considerably and 16°C water advanced inshore. Weak thermoclines formed in the deeper layers but the upward slopes of the isotherms indicated that vertical exchanges were still evident, especially at depths of 0-20 m. Hake larvae were more plentiful in the plankton during November when upwelling decreased and incursions of warmer water took place. Larval concentrations were mainly in the relatively cold 14°-15°C mixed water inshore off Walvis Bay. Peak abundance occurred in December when temperature increased due to substantial intrusions of warm water in the north. The more stratified warmer waters north of Walvis Bay, formed a well-defined boundary zone with the cooler coastal waters further south. Highest densities of larvae were found offshore north-west of Walvis Bay in the region of mixing between 16° and 18°C water.

The number of hake larvae declined sharply in January and remained relatively scarce during late summer and early autumn (February - March). Hydrological conditions indicated that, during this period, high temperatures associated with increased stability prevailed in the spawning grounds.

Survey 2 (August 1973 to March/April 1974)

During 1973, no hake larvae were caught during the months of August and September. Upwelling was strong over the whole area and conditions were almost identical to those found during the same months of 1972.

By October, however, upwelling had weakened considerably, resulting in a marked intrusion of warm 16°C water into the spawning grounds.

Thermoclines were well developed, particularly inshore in the upper 25 m . Further offshore, mixing was taking place between the warmer I6°C water pushing eastwards, and the cooler I4°C water moving offshore. Hake larvae were common during October inshore south of Walvis Bay, predominantly between the I5° and I6°C surface isotherms.

By November, I6°C water had advanced further inshore and southwards over the spawning grounds. Larvae increased in abundance but was found further offshore in the mixing zone between the warmer I6°C ocean water and the cooler I4°C subsurface water.

In December, temperatures had increased north of Walvis Bay due to an influx of I7° and I8°C water. The intrusion formed a well-defined frontal zone with the colder upwelled water in the south. Hake larvae were taken in greatest quantities during this month. Highest densities occurred west of Walvis Bay in the region of strong vertical mixing associated with the two water masses.

Larval abundance declined sharply in January, coinciding with higher temperatures and marked thermal stratification in the upper IO metres. Hydrological conditions in February were similar to those of January and larvae were noticeably scarce. Larvae reappeared during March/April, following a decrease in temperatures and an increase in mixing.

Dispersal

The drift of newly hatched hake larvae would depend directly upon the prevailing oceanographic conditions and the movement of currents during the spawning season. An examination of Figures 4 and 6 showed that the peak spawning months of both years (November and December) generally coincided with a period when warm water pushed southwards and inshore over the spawning grounds against cold northward flowing Benguela water. The regional distribution of hake larvae during these months indicated little change, suggesting that developing larvae remained in the vicinity of Walvis Bay possibly being confined there by the interaction of the two water masses.

It was not possible to illustrate dispersal within the gross spawning area from the monthly differences in size class distribution because both large and small larvae were frequently taken together in individual samples. However, larvae captured in November 1972 were mostly recently hatched and occurred close to the coast at Walvis Bay (Figs. 4 and 5). In December, specimens taken in the samples were considerably larger and were concentrated more offshore north west of Walvis Bay. Thus a slight offshore movement of larvae between these months is suggested. Although a comparison of surface temperature patterns showed an influx of relatively warm water between November and December, vertical temperature profiles off Walvis Bay (O'Toole 1977a) indicated a weak offshore displacement of subsurface water at depths of 20-30m which may have carried the developing larvae northwestwards. During the same period in 1973, there was no evidence of larval dispersal within the main spawning area (Fig.6).

Catches of larger larvae were occasionally made in the south near Hollam's Bird Island, especially in November, suggesting that these advanced stages may have been carried northwards from spawning centres located south of the research area.

Rate Development of Eggs

There is no information on the developmental rate of hake eggs at different temperatures off South West Africa. However, Matthews and de Jager (1951) successfully incubated artifically fertilized eggs of M. capensis off the Cape Peninsula and found that hatching occurred 60 hrs after fertilization. Although egg development was not related to temperature in this report, an examination of station records (Annual Report, Sea Fisheries Branch, 1949) and consultation with Mr.J.P. Matthews, Sea Fisheries Branch, confirmed that incubation took place at a temperature of 13,7°C. The time taken for eggs of M.capensis to hatch at this temperature is almost identical to that of the pilchard S. ocellata (King 1975). Since various stages of pilchard and hake eggs were frequently collected together in samples during the SWAPELS cruises it is possible that rates of development are similar.

Age of Larvae

A basis for determining roughly the larval growth rate at sea and consequently estimating the age of a larva of a given size can sometimes be made by tracing the movement and progressive increase in size of specimens captured in a given area over a relatively short period of time. In the case of hake, it was possible only to trace a cohort of developing larvae between November and December I972 when a slight drift offshore was apparent. The length frequency curve for larvae collected at positive stations within the main spawning area i.e. lines 66, 70 and 74 (Fig. 1) for both months is shown in Figure 9.

In November, one major cohort consisting of recently hatched larvae between 3 mm and 6 mm in length (mean 4,0 m) and a smaller group of larger specimens between 7 mm and IO mm in length (mean 8,0 mm) were identified. During the December cruise, catches of larger larvae made in the same area, but more offshore, also showed two size frequency peaks, a large cohort of specimens between 14 mm and 18 mm in length (mean 16,0 mm) and a less dominant group of 19-22 mm in length (mean 20,0 mm). If some of the recently hatched group of larvae collected near Walvis Bay in November (Fig 4) were represented by the more advanced specimens taken offshore in December, as hydrological interpretations suggest, then it is possible to roughly estimate the growth rate. The mean length of larvae in the two cohorts increased from 4 mm to 16 mm and from 8 mm to 20 mm during the intervening period, representing an increase of 12,0 mm in 26 days or a growth rate of about 0,45 mm per day.

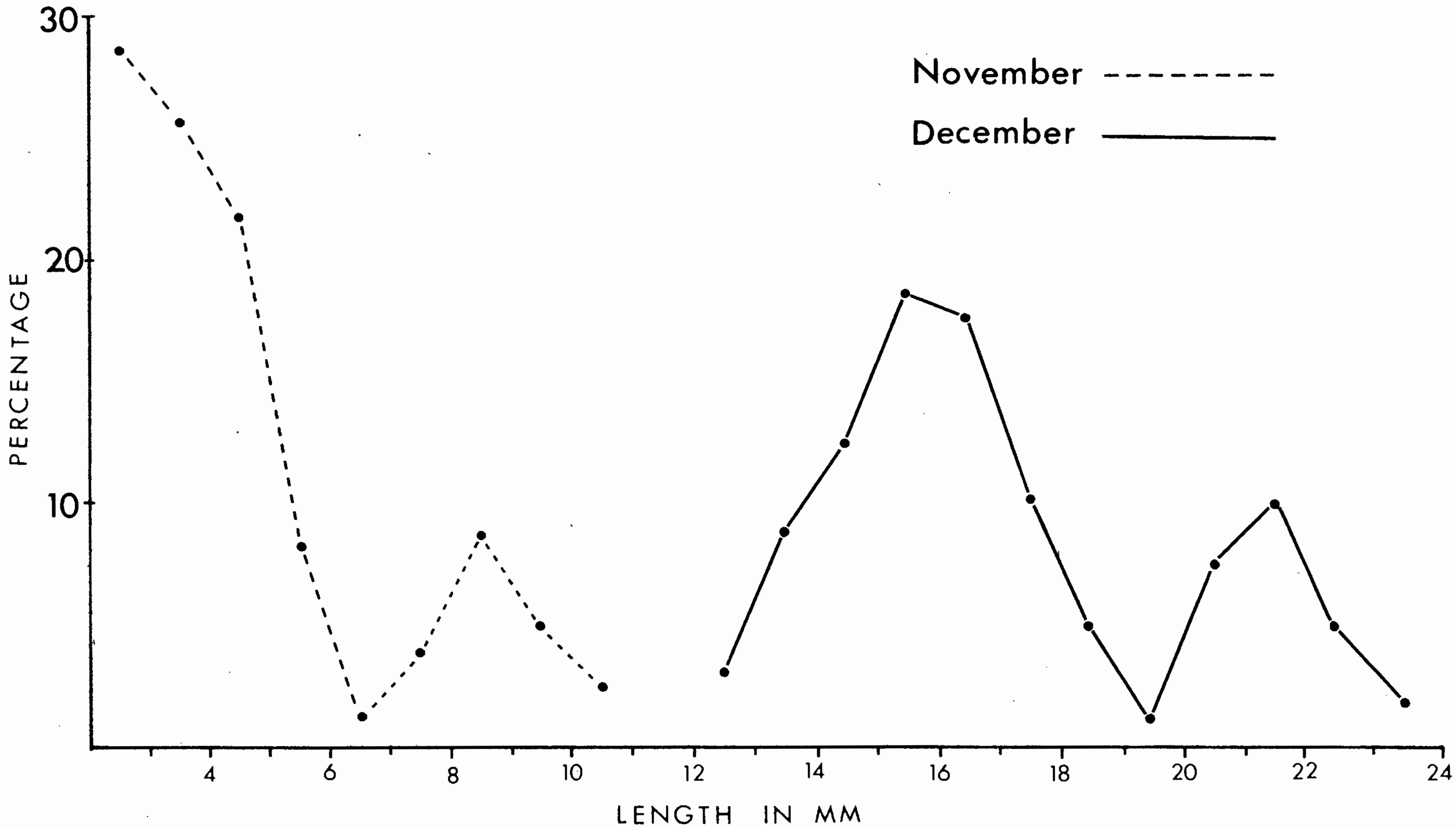


Fig. 9 Length frequency curves for larvae collected off Walvis Bay in November and December 1972

D I S C U S S I O N

The area between Henties Bay (22^oS) and Hollam's Bird Island ($24^o40'S$) is an important spawning ground of the hake. The seasonality and distribution of newly hatched larvae suggests that spawning occurred continuously from September to April. However, the majority of fish apparently spawned between October and December (midspring - early summer)during the two years studied. Newly hatched larvae predominated off Walvis Bay at distances of 50 - 100 km from the coast. The northward and seaward limits of the spawning grounds were adequately encompassed but spawning may also have occurred further south since small larvae were sometimes abundant on the most southerly line of stations. These interpretations are supported by evidence on the distribution of sexually mature hake (Chlapowski I975) and on egg occurrence and seasonality (Porebski and Koronkiewicz I975).

In January of both years, there was a sharp decline in hake larval abundance, indicating that the spawning season may be relatively short and almost complete by that time of the year. However, the occasional occurrence of newly hatched larvae in the plankton during summer, especially in the north, indicates that some fish spawn later.

Newly hatched hake larvae were more abundant in full daylight and early morning collections, while larger specimens were mainly taken at night. Fahey (I974) reported similar findings for larvae of the silver hake M. bilinearis. The most generally accepted explanation for the high incidence of large larvae in night hauls is that the more-advanced stages can avoid slow-moving collecting gear more effectively during daytime in response to visual warning. Diurnal vertical migration, although not studied during this investigation, may have been the source of the disparity between day and night catches. However, Ahlstrom (I959) reported that Pacific hake larvae M. productus had a similar depth range in both day and night hauls and Fahey (I974) noted that the larger silver hake larvae displayed only limited diurnal vertical migration in the upper 33 m of water. It is, therefore, probable that differences are mainly due to avoidance.

The fact that newly hatched larvae were consistently more abundant during daylight could be due to behavioural responses to food and light.

Monthly fluctuations in the abundance of small larvae suggested that the intensity and timing of hake spawning differed between years. For example, the main spawning season commenced a month earlier during Survey 2 than during Survey 1. Hake larvae first appeared in the plankton during October when upwelling was usually weakening and temperatures higher. In October 1972, however, the water temperature in the spawning grounds remained relatively low due to persistent coastal upwelling. Newly hatched larvae were noticeably scarce during this month suggesting little spawning activity. In contrast, upwelling was much reduced in October 1973 which resulted in higher temperatures and the establishment of thermoclines in the shallow layers near the coast (O'Toole 1977 a). Early larval stages were correspondingly more abundant, which suggested that heavy spawning was induced earlier, possibly by favourable biotic or abiotic conditions being reached more rapidly. During November and December, catches of hake larvae reached a peak at a time when intrusions of warm water pushed southwards and inshore in the vicinity of Walvis Bay. The sharp boundary zone between these intrusions and the cooler coastal water off Walvis Bay appeared to be the focus of heavy spawning. The end of the main breeding season was marked by increasingly high temperatures and the formation of strong temperature gradients inshore. However, some isolated spawning continued to take place during late summer/early autumn where the environment was temporarily suitable e.g. south of Walvis Bay March/April 1974 (Fig.6) following a drop in temperature associated with an intensification of mixing.

Continuous spawning from October to December made it difficult to trace the dispersal of developing hake larvae. Hydrological evidence suggested that there was little or no transportation northwards and only a slight movement offshore. The months of heaviest spawning generally coincided with the period when the north-flowing Benguela Current weakened and movements of warm offshore water southwards and towards the coast took place. The interaction of these two water masses off Walvis Bay appeared to contain developing larvae within the main spawning area, thereby allowing them to remain in the productive coastal environment.

The time taken for larvae to complete development will depend directly upon temperature and food availability. Larval stages of M. capensis develop juvenile features and possess a full complement of fin rays at lengths of about 25 mm. A rough estimate of the pelagic phase of development would be 1½ to 2 months. Juveniles then presumably descend to deeper layers and adopt a demersal habitat. Although juvenile hake measuring between 25 and 35 mm were collected at night on several occasions (O'Toole I976), the location of capture (South of Walvis Bay) also indicated that there was little movement of juveniles outside the general breeding area.

There was no evidence from this study of a horizontal spawning migration of hake off South West Africa. The facts that on SWAPELS international vessels exploiting hake were observed in the traditional fishing grounds (i.e. Cunene River to Palgrave Point and Walvis Bay to Conception Bay) during most of the year and that no mention of fleet movement has been made by ICSEAF (I975, I976) lend support to this argument. Furthermore, the sudden appearance of larvae in the vicinity of Walvis Bay during October and November and the fact that distributional patterns of recently hatched larvae suggest no noticeable seasonal movement of spawning fish imply that hake simply spawn wherever the are concentrated provided environmental conditions are suitable.

The hake stocks fished in the northern waters of South West Africa appear to be a separate population. According to Draganik (I976), the total hake landings from ICSEAF Division 1,3 (15°-20°S) are practically equal to those of the southern stock, ICSEAF Division I,4 (20°-25°S). However, little evidence of spawning activity was found in the north. During summer/early autumn, the northern offshore waters are important spawning areas for other fish species (O'Toole I977b, I977c, I977d) and seem to be particularly favourable as a nursery area for the larval stages.

The presence of some recently hatched hake larvae in this region during summer/autumn, although small in relation to those derived from the earlier spawning in the south, does indicate that the northern stock may be predominantly summer/autumn spawners. An explanation of this lack of spawning activity in the north may be either that hake breed outside the limits of the survey area or that many of the eggs and larvae occur at depths below 50 m and are consequently out of reach of the sampling gear. Another possibility is that the northern population may spawn mainly between March/April and August (mid autumn to winter) a period not surveyed during this investigation.

LITERATURE CITED

AHLSTROM, E.H. 1959 Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl.Serv., Fish. Bull. 60 , (I6I) : I07-I46

AHLSTROM, E.H. AND R.C. COUNTS 1955 Eggs and larvae of the Pacific hake Merluccius productus U.S.Fish.Wildl. Serv., Fish. Bull. (99), 56 : 295-329

ARBAULT, S. AND N. BOUTIN 1968 Ichthyoplancton oeufs et larves de poissons teleosteens dans le Golfe de Gascogne en I964. Rev. Trav. Inst. Pech. Marit. 32/4 pp. 413-476

BOTHA, L. 1971 Growth and otolith morphology of the Cape hakes. Merluccius capensis (Cast.) and M.paradoxus (Franca). Investl Rep. Sea. Fish. Brch. S.Afr. 97 : 32 pp.

BOTHA, L. 1973 Migration and spawning behaviour of the Cape hakes. S.Afr. Shipp. News Fish. Ind. Rev.28 (4) : 62-67

CHLAPOWSKI, K. 1974 Length composition and maturity of hakes Merluccius capensis and M paradoxus caught in the ICSEAF area during the period from November I972 to January I973. ICSEAF, Coll. Sc. Pap. I pp. I82-I92.

CHLAPOWSKI, K. 1975 Hake Merluccius capensis and Merluccius paradoxus in Polish catches in South West African area. ICSEAF. Coll.Sc.Pap. 2 ; 39 - 42

D'ANCONA, E. 1933 Gadidae in uova, larve e stadi giovanili di Teleostei. Fauna e Flora del Golfo di Napoli, Monogr. 38: I78-255.

DARK, T.A. 1975 Age and growth of Pacific hake Merluccius productus Fish. Bull. U.S. 73, (2) : 336-355.

DRAGANIK, B. 1974 Hake stocks exploited in the ICSEAF Convention Area ; ICSEAF,W.G./74 Inf. Doc./I Rev.

DRAGANIK, B. 1976 Fishing mortality of hake stocks exploited in Subarea I of the ICSEAF convention area. ICSEAF Coll. Sc. Pap. 3 , 59 - 83

DZ de CIECHOMSKI AND Y.G. WEISS 1973 Nota sobre la presencia de huevos y larvas de merluza Merluccius merluccius hubbsi en el Mar Argentino. PHYSIS, Sec. A.V. 32. n.84 : I55-160.

FAHAY, M.P. 1974 Occurrence of silver hake, Merluccius bilinearis, eggs and larvae along the middle Atlantic continental shelf during I966 Fish. Bull. U.S. 72, (3) : 813-834.

FAO 1974 Catches and Landings. Year book of fishery statistics, I973, 36 : Food and Agriculture Organization of the United Nations, Rome.

HAIGH, E.H. 1972 Larval development of three species of economically important South African fish. Ann. S.Afr. Mus. 59 (3) 47-70.

HART, T.J. AND N. B. MARSHALL. 1951 Breeding ground of pilchard off the coast of South West Africa. Nature, Lond. I68 : p 272.

ICSEAF 1975 Collection of scientific papers. International commission for the south-east Atlantic fisheries.(ICSEAF), 2 , I86 pp. Madrid.

ICSEAF 1976 Collections of scientific papers. International commission for the south-east Atlantic fisheries (ICSEAF), 3, 208 pp. Madrid.

IKEDA, I. 1975 On the stocks of Cape hakes in Divs. I-3 and I-4, Cunene and Cape Cross. ICSEAF Coll. Sc. Pap. 2 : 54-58.

JONES, B.W. AND T.H. VAN ECK 1967 The Cape hakes : Its biology and fishery. S. Afr. Shipp. News. Fish. Ind. Rev. 22 (II) : 90-97.

KUDERSKIJ, S.K. 1973 Niekotoryje osobiennosti razpriedielienia mierluz Juzoj Afriki W zawisimosti ot gidrologiczjeskich uslowii. AtlantNIRO, Trudy , Wyp LIII.

MATTHEWS, J.P. AND B.V.D. DE JAGER 1951 The development of the Cape stockfish (Merluccius capensis). Union of South Africa, Dept. of Commerce and Industry, Fish. and Mar. Biol. Survey Div. Investl.Rep. I3 : IO pp.

O'TOOLE, M.J. 1976 Incidental collections of small and juvenile fishes from egg and larval surveys off South West Africa (I972-I974). Fish. Bull. S. Afr. 8 : 23-33.

O'TOOLE, M.J. I977a Distribution of temperature and salinity off South West Africa, I972-I974. PhD thesis, University of Cape Town, Section I, 31 pp.

O'TOOLE, M.J. 1977b Investigations into the early life history of the South West African pilchard Sardinops ocellata Pappe. PhD thesis, University of Cape Town, Section 2, 53 pp.

O'TOOLE, M.J. 1977c Investigations into the early life history of the South West African anchovy Engraulis capensis Gilchrist. PhD thesis, University of Cape Town, Section 3, 37pp.

O'TOOLE, M.J. I977d Investigations into the early life history of the Cape horse mackerel Trachurus Trachurus off South West Africa. PhD thesis, University of Cape Town. Section 4,

POREBSKI, J. AND A. KORONKIEWICZ I975 Distribution of eggs and larvae of Merluccius spp. in south west African waters according to the materials collected by r.v."Professor Siedlecki" in November-December I972 and January-February I973. ICSEAF. Coll.Sc. Pap.2, 92-101.

PSCHIENICHNIY B.P. 1972 Niekotoryje dannye o charakterie ikromietania i plodovitosti mierluzy banki Agulias . Ryb. Chozy. (9) : p.24.

PSCHIENICHNIY, B.P. AND W.W. ASSOROV. 1969 Niekotoryje czyerty biologii merluzy (Merluccius)atlanticheskova okieana i pobieriezhia yugo-zapadnoy Afriki. Wop.Ichtiol. Tom.9, Wyp.3, (56) : 423-430.

SIEGEL, S. 1956 Non parametric statistics for the behavioural sciences. McGraw-Hill, New York, 312 pp.

SMITH, J.L.B. 1970 The sea fishes of southern Africa, 5th ed. Cape Town ; Central News Agency : 580 pp.

VAN ECK, T.H. 1969 The South African hake; Merluccius apensis or Merluccius paradoxus ? S.Afr. Shipp. News Fish. Ind.Rev. 24 (5) 95-97

THE DEVELOPMENT AND DISTRIBUTIONAL ECOLOGY OF THE LARVAE OF THE WEST COAST SOLE <u>AUSTROGLOSSUS</u> <u>MICROLEPIS</u> (BLEEKER) FROM THE SOUTH EAST ATLANTIC.

B Y

MICHAEL J.O'TOOLE,
SEA FISHERIES BRANCH,
BEACH ROAD,
SEA POINT,
CAPE TOWN.

INTRODUCTION.

Austroglossus microlepis (Bleeker), commonly known as the West Coast sole, constitutes a small but important demersal fishery on the Atlantic coast of Southern Africa. The commercial fishery for this species is particularly well-developed in South West Africa where landings have fluctuated between I50 metric tons in I960 and I895 tons in I973 (Statistics collected by the S.W. A. Administration and the Sea Fisheries Branch).

The West Coast sole is strictly an Atlantic form and can readily be distinguished from other species found in the area by its general body shape, relatively large size, and differences in fin ray counts (Smith I970). Despite the existence of a commercial fishery, nothing is known about the spawning or early life history of the species. The larval stages have not been described or identified.

In August I972, the Sea Fisheries Branch commenced an extensive egg and larval research programme (S W A P E L S) off South West Africa to study the spawning of the pilchard Sardinops ocellata Pappe and the anchovy Engraulis capensis Gilchrist. Data collection cruises were undertaken from August I972 to March I973 and from August I973 to April I974. During the course of the investigation, larvae of A.microlepis were identified and found to be relatively common in the inshore plankton. Results of the first survey showed that larvae of the family Soleidae formed 3 percent of all fish larvae collected (O'Toole I973). Larvae of the West Coast sole themselves comprised approximately 42 percent of the sole larvae and ranked sixth in order of species abundance. During the second survey, A. microlepis constituted approximately one percent of all fish larvae captured and was the seventh most abundant species in the plankton.

This report describes and illustrates the larval development from yolk-sac stage to the juvenile. Information is also given on such aspects as larval seasonality, distribution, abundance, hydrological relationships and dispersal.

MATERIAL AND METHODS

The research area, together with the location of routine stations, is shown on Figure 1. Ichthyoplankton collections were made in the 0-50 m layer using a 57 cm diameter Bongo net, with meshes of 0,940 and 0,500 mm. Further details of the methods, sampling procedure and net performance is given by King and Robertson (1973) and O'Toole (1977). Station positions and depths are listed by O'Toole (1976). The number of larvae captured by the nets at each station was standardized to the total number under 10m^2 of sea surface (see Kramer et al 1972; Ahlstrom 1973). Larval distribution charts were drawn assuming linear larval density gradients between stations in space and time. Abundance is expressed as the number per 10 m^2 of sea surface.

The larvae of A. microlepis were first identified by diagnosing the adult characteristics in some juvenile specimens. A developmental series was then built-up by tracing these distinguishing meristic data and pigmentation patterns back to the yolk-sac stage. In advanced specimens, meristic counts were determined by clearing and staining using the trypsin alizarin technique of Taylor (1967). Although eggs of the West Coast sole were possibly present in the collections, they were not identified and thus are not mentioned in this report.

Larvae were examined through a binocular microscope and measured to the nearest hundredth of a millimetre with an ocular micrometer. The length of large specimens were taken against a finely graduated glass slide. All observations were made from the right-side. The lengths of yolk-sac and early larval stages were measured from the anterior border of the head to the tip of the notochord and after caudal fin ray formation, from the tip of the snout to the base of the median caudal rays (Standard length, SL). Head length was measured from the tip of the snout to the cleithrum and body depth from the anal opening to the base of the dorsal fin.

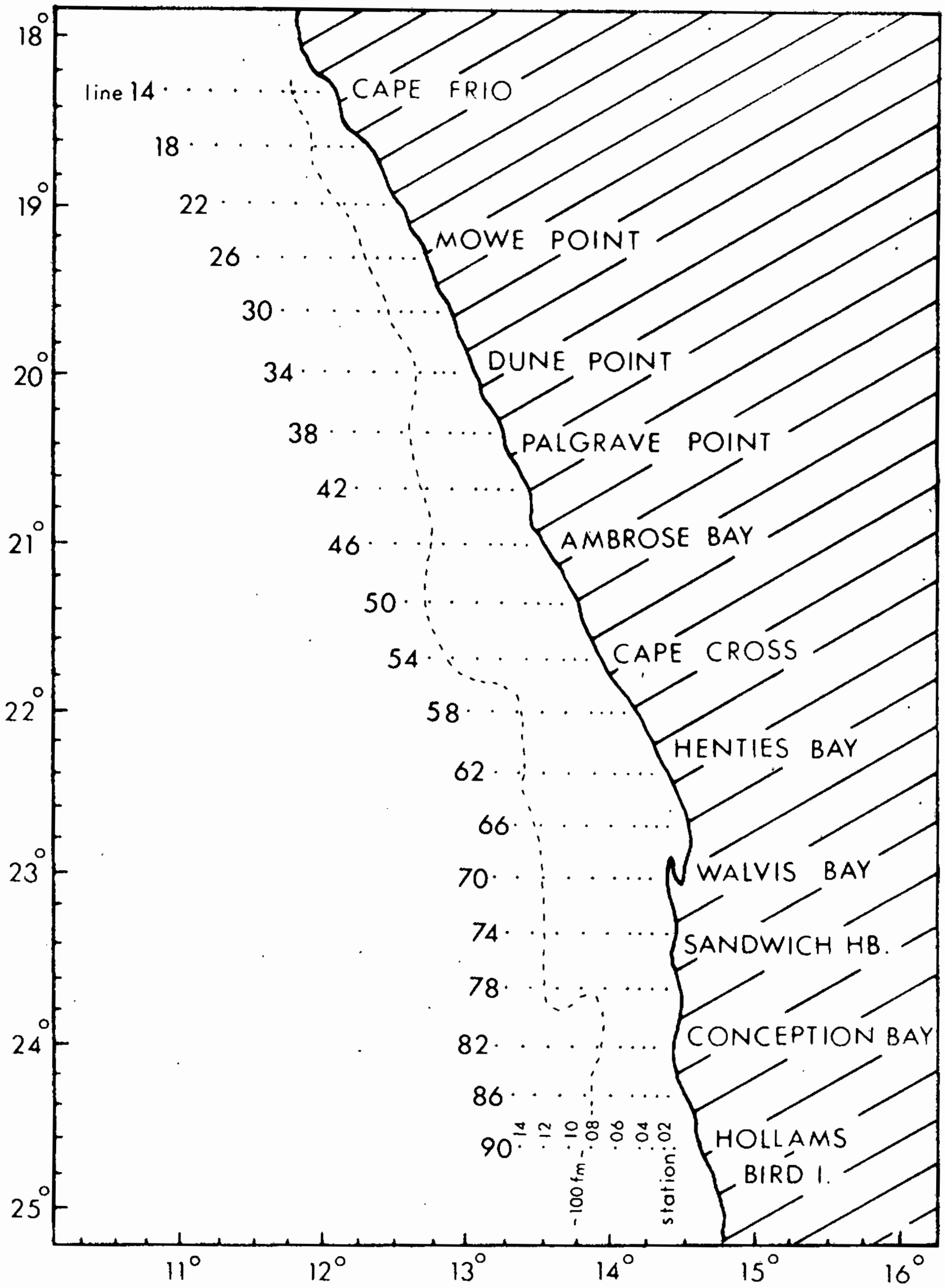


Fig. 1 Location of routine stations occupied during the SWAPELS cruises in 1972/73 and 1973/74

Since the larvae examined during this study were preserved in 10% buffered formalin, the lengths of the specimens, especially the early stages, were probably less than those of live fresh material. The yolk-sac larva of the sole Heteromycteris capensis Kaup. was found to shrink as much as 20% when fixed in preservative (C. Brownell, University of Cape Town, personal communication). The shrinkage of larvae was not taken into account when describing the development or establishing the length distribution, but, since the larvae were preserved and measured in the same way throughout the investigation, the length distribution was assumed to be comparable from year to year.

RESULTS

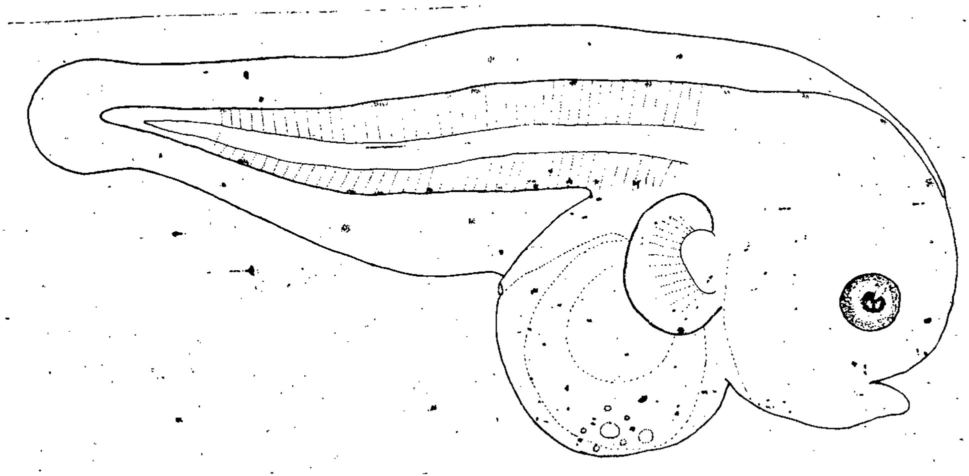
Larval development of the West Coast sole.

A total of 541 specimens ranging in size from 2,85 to 28,00 mm SL were collected during the ichthyoplankton surveys. A series of larvae considered to be representative of most developmental stages were selected from the samples for description and are illustrated in Figures 2 and 3. Morphometric measurements and meristic counts were made on I55 specimens in I6 length classes. The results are given in Table I.

Yolk-sac Larva.

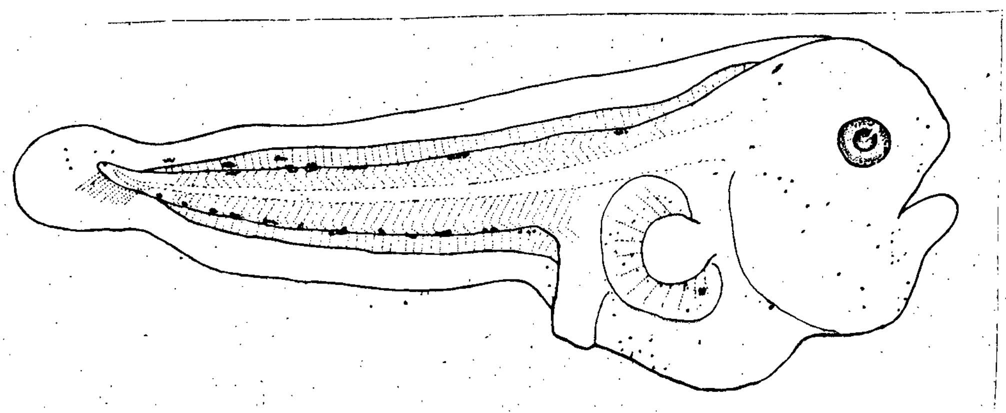
The smallest larva had a notochord length of 2,85 mm. The eyes were fully pigmented and the mouth was functional (Fig.2A). Pectoral buds were well-developed and the dorsal, ventral and caudal region of the body was surrounded by a large fin fold. The gut was fully formed and typically S-shaped.

Pigmentation consisted of a series of 8-10 widely-spaced melanophores situated along the dorsal and ventral surface of the body at the base of the fin fold. A few prominent melanophores were present on the fin fold itself. Small contracted pigment spots were scattered on the yolk-sac, lower jaw, pectoral fin and on the head region behind the eye.



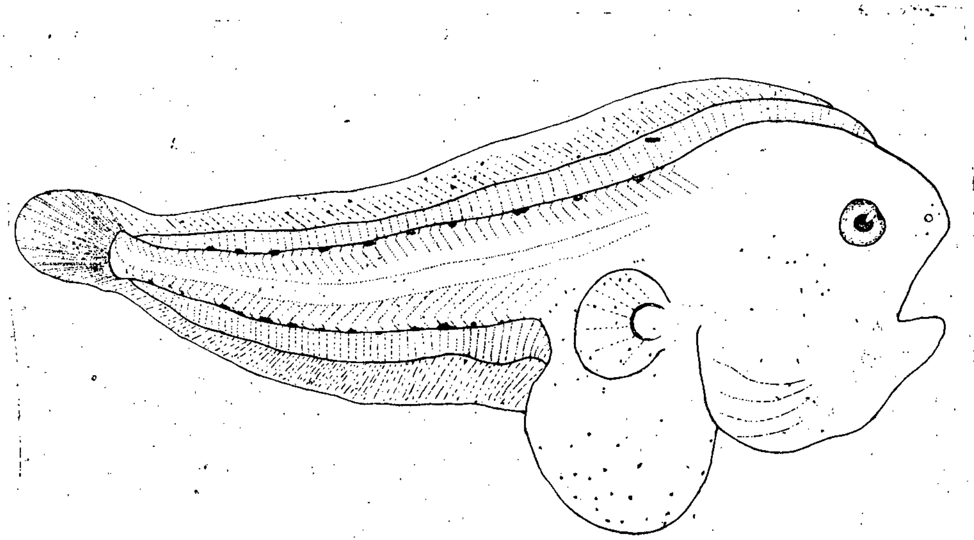
A

Yolk-sac larva (2,85 mm)



B

Larva undergoing flexion (5,50 mm)



C

Post flexion larva (6,60 mm)

Fig. 2 Larval development of the West Coast sole *Austroglossus microlepis*

Myomeres were not very distinct but at least 45 could be counted. The length of the larva on hatching is unknown. The smallest larva collected had little yolk and was relatively well developed suggesting that the yolk-sac phase was nearing completion. In some specimens, several small oil globules were discernible in the abdominal sac, approximately midway along the ventral surface.

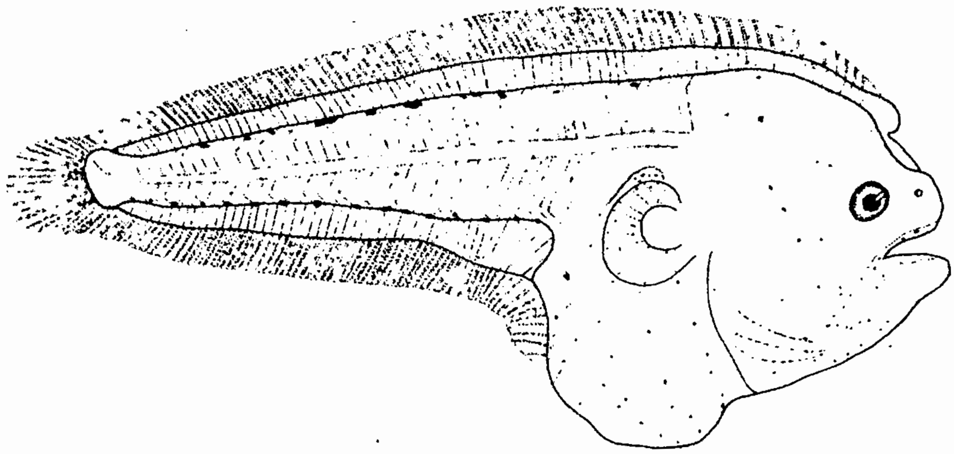
Larva.

The larval stage of development in teleosts is often defined as that period between the absorption of the yolk-sac and the acquisition of the full complement of adult fin rays. In the West Coast sole, this phase occurs between lengths of approximately 3 and 8 mm.

During larval development, pigmentation is basically similar to that of the yolk-sac stage. However, the dorsal and ventral melanophores,along the body margin increase in number and become somewhat embedded. The large melanophores on the fin fold disappear at a length of approximately 3 mm and the region becomes speckled with small pigment spots. Pigmentation increases gradually on the head and gut. Tail flexion commences in larvae of between 5,20 and 5,50 mm length. A larva undergoing flexion is illustrated in Figure 2 B. During this process, the pterygiophores are formed and the dorsal, anal and caudal fin rays commence development. The urostyle is fully flexed at a length of 6,60 mm and the caudal fin rays are almost complete (Fig. 2C). The nares are visible as a single small tubercle on the snout anterior to the eye. The full complement of dorsal and anal fin rays is attained at a length of 7,50 mm and the fins themselves are lightly speckled with small pigment spots. Myomeres number between 56 and 58.

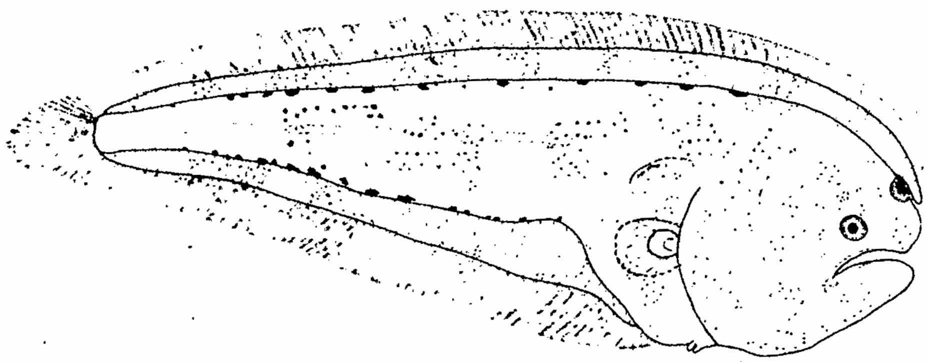
Metamorphosis

Metamorphosis commences at lengths of between 8,25 and 8,50 mm when the anterior part of the dorsal fin separates from the head to form the characteristic rostral hook.



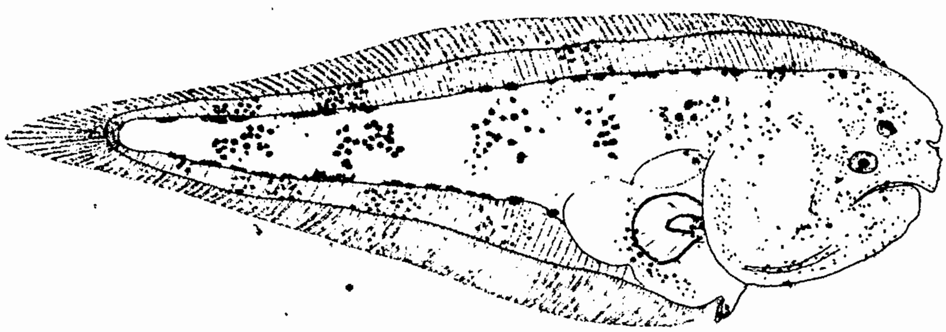
A

Larva (9,60 mm)



B

Larva undergoing metamorphosis (15,50 mm)



C

Juvenile after metamorphosis (23,40 mm)

Fig. 3 Larval development of the West Coast sole
<u>Austroglossus microlepis</u>

TABLE 1: Morphometric measurements and meristic counts for larvae of the West Coast Sole, *A. microlepis*.

Specimen length (mm)			Mean percentage of specimen length				Fin counts (range)		
Range	Mean	No. of larvae	Head length	Body depth	Eye diameter	Pre anal length	Dorsal	Caudal	Anal
2,85–2,98	2,90	10	28,97	29,66	9,31	53,45	-	-	
3,10–3,85	3,60	10	23,61	24,17	7,50	43,89			
4,00–4,87	4,52	20	20,80	27,21	6,64	39,16			
5,32–5,76	5,50	16	27,27	33,82	5,45	41,45			
6,15–6,79	6,45	14	30,70	36,28	5,27	44,96	18–20	10–12	12–13
7,20–7,92	7,57	12	26,02	34,21	4,40	35,01	86–89	18–19	69–74
8,32–8,76	8,55	13	27,37	35,09	4,21	43,24	90–92	18–19	72–73
9,00–9,60	9,30	10	30,00	34,95	4,19	40,32	92–95	18–19	72–73
10,29–10,60	10,43	11	28,19	38,73	4,12	38,06	93,94	18–19	72–73
11,15–11,80	11,48	6	25,17	31,10	3,48	31,10	94–95	18–19	73–74
12,32–12,87	12,56	6	26,43	33,12	3,18	28,82	93–95	19	73–74
13,30–13,85	13,65	8	26,37	32,23	3,00	26,37	93–95	19	73–74
14,21–14,97	14,45	7	25,76	32,18	3,11	25,26	93–95	19	74–75
15,00–15,60	15,47	7	23,85	31,35	2,91	25,53	94–95	19	74–75
16,20–16,89	16,60	8	23,49	29,82	2,71	29,82	92–94	18–19	75
18,60	18,60	1	25,81	27,42	2,55	30,65	95	18–19	75
23,40	23,40	1	24,83	30,13	2,82	26,92	94	19	74

The left eye begins to migrate slowly to the right side. A larva at the early stage of metamorphosis is shown in Figure 3A.

Juvenile pigmentation appears in specimens of lengths I3,00 - 13,50 mm. The row of dorsal and ventral melanophores along the body surface begins to intensify and expand. Pigment spots along the base of the dorsal and anal fins aggregate into discreet groups and stellate melanophores form in broad patches along the body mid-line. Pigmentation on the head increases.

The pectoral fin becomes reduced and the pelvic fin appears as a small bud anterior to the stomach in specimens of I3,20 mm in length. At lengths of I5,00-I5,50 mm the left eye has migrated over to the right side beneath the rostral hook(Fig.3B). Metamorphosis into the juvenile form is complete at a length of 24 mm (Fig.3C). Pigmentation on the body consists of five broad bands of large stellate melanophores running longtitudinally across the body from the dorsal to the anal fin rays. The pectoral fins is well developed and the general body shape is typically adult-like.

DISTRIBUTION AND ABUNDANCE OF LARVAE

The geographic distribution and abundance of West Coast sole larvae for both survey periods are shown in Figures 4 and 5. Larvae were collected predominantly from inshore waters between Cape Cross and Hollam's Bird Island no further than I6 km from the coast. The percentage occurrence in the different parts of the research area is summarized in Table II .

The northern limit of occurrence was in the region of Palgrave Point with only a few specimens being caught further than 30 km from the coast.

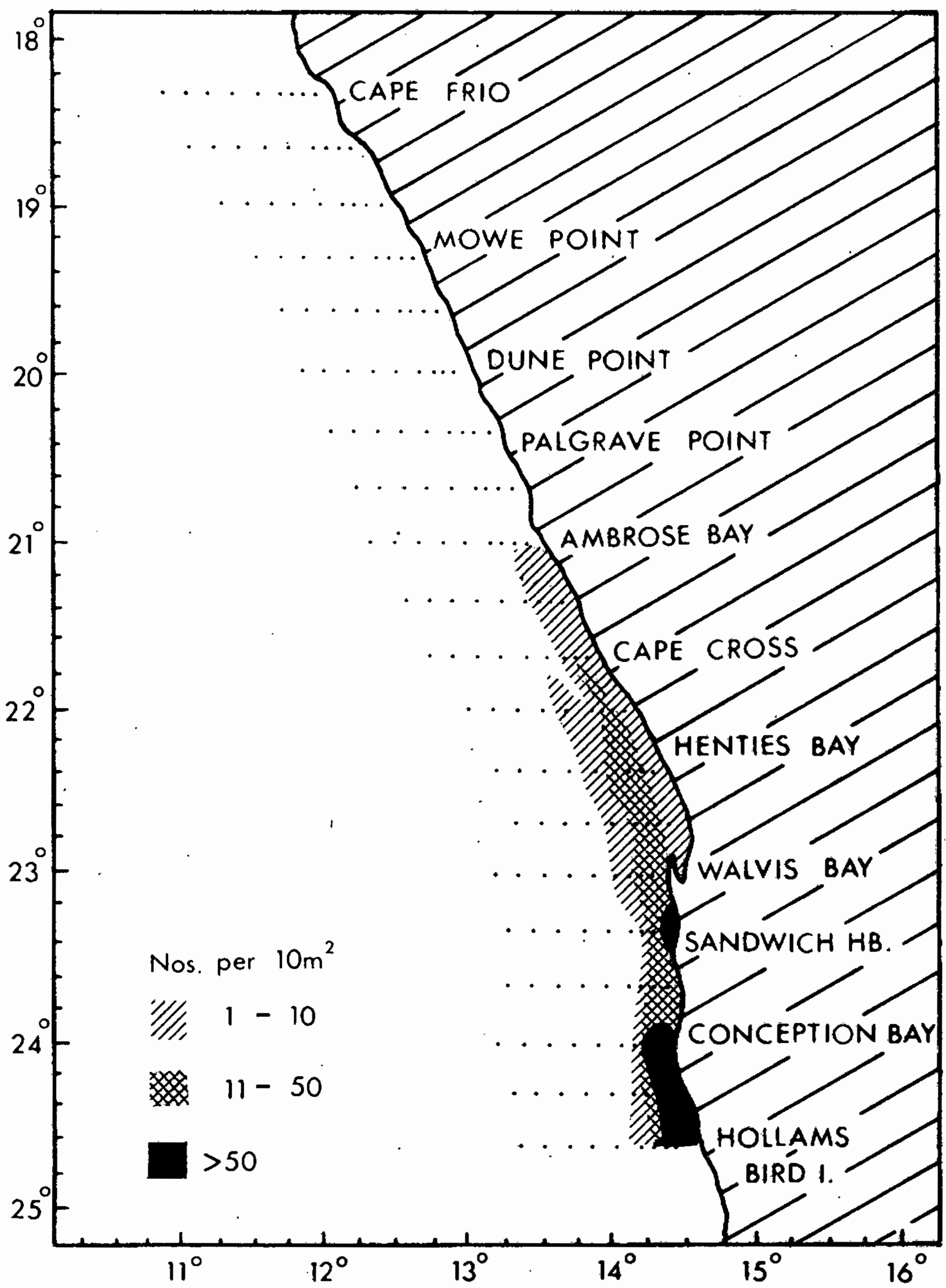


Fig. 4 Distribution and abundance of West Coast sole larvae during Survey 1 (values represent cumulative haul totals for all cruises)

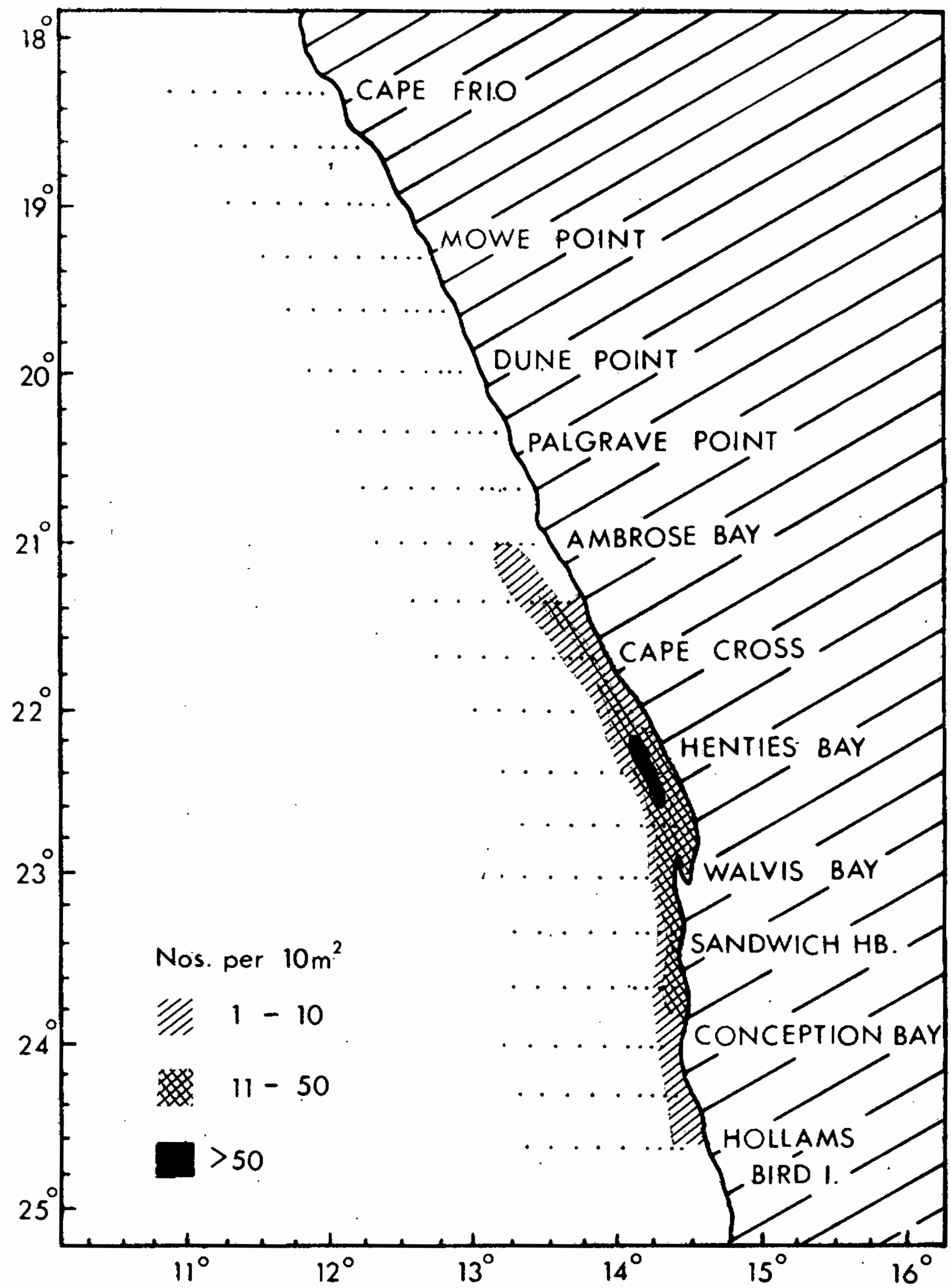


Fig. 5 Distribution and abundance of West Coast sole larvae during Survey 2 (values represent cumulative haul totals for all cruises)

TABLE II: The percentage of larvae collected in the different parts of the research area I972 to I974.

Area	Station line	I972/73	I973/74	I972/74
Cape Frio - Mowe Point.	I4-26	0	0	0
Mowe Point - Palgrave Point.	30-42	0	0	0
Palgrave Point - Henties Bay.	46-58	8,45	38,80	16,75
Henties Bay - Sandwich Hb.	62-74	25,00	42,87	39,22
Sandwich Hb - Hollam's Bird Island.	78-90	66,55	I8,33	44,I3

Larvae of the West Coast sole were collected mainly during spring (September to November). Approximately 95 percent and 73 percent of the total number captured during Survey 1 and 2 were collected between September and November.

SURVEY 1 (August I972 - March I973)

The monthly distribution and abundance of West Coast sole larvae collected during Survey 1 are shown in Figure 6. The distribution of surface temperature is also shown and is discussed later. Data on the monthly hauls and larval abundance are summarized in Table III and the size composition of the catches in Table IV.

Larvae first appeared in the plankton during September in the coastal waters between Cape Cross and Hollam's Bird Island, the specimens being all recently hatched and ranging in size from 2,85 mm to 8,00 mm. Although age could not be determined, it is very likely that these specimens were between 3 and I4 days old and hatched from eggs spawned between late August and early September. Larvae were particularly abundant off Conception Bay and Hollam's Bird Island.

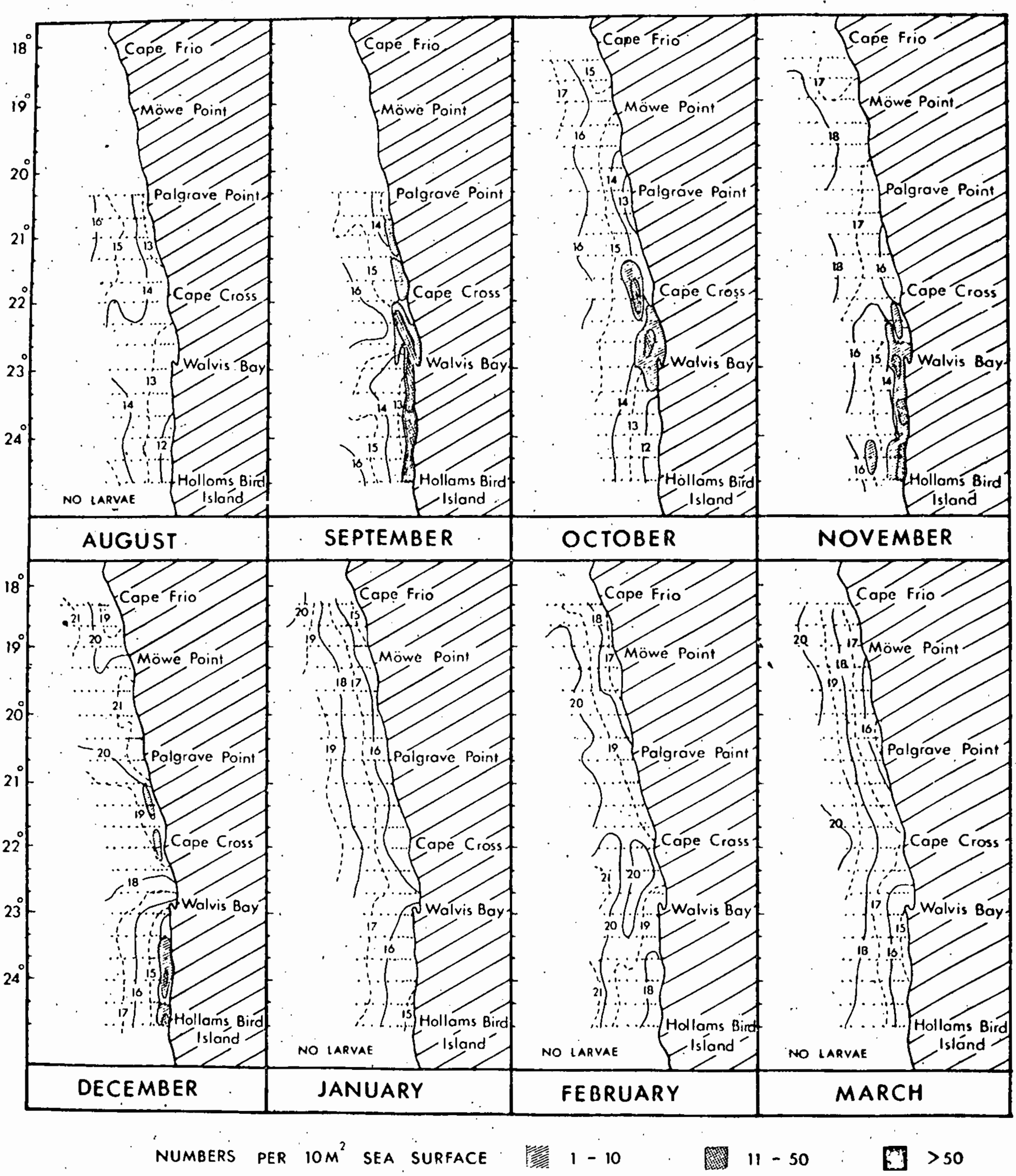


Fig. 6 Monthly distribution and abundance of West Coast sole larvae, August 1972 to March 1973.

In October, West Coast sole larvae ~~were scarce~~ in the collections and only occurred in the coastal region between Cape Cross and Walvis Bay. These larvae were generally larger than those taken in September and ranged between 5,00 mm and 12,80 mm in length, suggesting that some of the specimens may have represented the same cohort that had been sampled in September.

Larvae were more widespread and numerous in the plankton during November. The regional distribution was similar to that of September but peak abundance occurred inshore near Hollam's Bird Island. Approximately 85 percent of the specimens were recently hatched and measured between 2,85 and 8,00 mm in length, thus, suggesting that renewed spawning took place in the coastal waters south of Walvis Bay in early November.

December marked a sharp drop in the numbers of larvae captured. Isolated specimens, consisting mainly of mixed size classes (4,00-12,00 mm), were found scattered between Sandwich Harbour and Hollam's Bird Island.

In January, only four specimens were caught, all south of Walvis Bay, ranging between 4,00 and 12,00 mm in length. No West Coast sole larvae were found during February and March.

TABLE III : Summary of the monthly hauls and abundance of West Coast sole larvae 1972-1973.

Cruise Dates	No.of hauls	No.of positive hauls	No.of larvae collected.	Mean no.of larvae per $10\ m^2$ sea. surface.	% of total collected.
August 22-31	126	0	0	0	0
September 15-20	126	17	195	18,59	54,5
October 15-22	156	8	27	6,18	7,5
November 11-19	180	14	122	15,30	34,1
December 5-14	180	6	14	5,95	3,9
January 13-21	180	0	0	2,92	0
February 14-24	177	0	0	0	0
March 11-19	177	0	0	0	0

TABLE IV : Size composition of West Coast sole larvae collected during the 1972/73 cruises.

Length (mm)	SEPT. Nos.	% comp	OCT. Nos.	% comp	NOV. Nos.	% comp	DEC. Nos.	% comp	ALL MONTHS. Nos.	% comp
2,1-3,0	43	22,1			28	23,0			71	19,8
3,1-4,0	68	34,9			25	20,5			93	25,9
4,1-5,0	46	23,6			16	13,1	1	7,1	63	17,6
5,1-6,0	19	9,7	3	11,1	21	17,2	1	7,1	44	12,3
6,1-7,0	13	6,6	6	22,2	14	11,5	2	14,2	35	9,8
7,1-8,0	4	2,1	2	7,4	5	4,1			11	3,1
8,1-9,0	1	0,5	9	37,0	4	3,3	4	28,6	18	5,1
9,1-10,0			3	11,1	3	2,5	3	21,4	9	2,5
10,1-11,0			2	7,4	2	1,6	2	14,4	6	1,7
11,1-12,0							1	7,1	1	0,3
12,1-13,0			2	3,7	1	0,8			3	0,8
13,1-14,0					2	1,6			2	0,6
14,1-15,0									0	
15,1-16,0					1	0,8			2	0,6

SURVEY 2 (August I973 to March/April I974)

West Coast sole larvae were less abundant in the plankton during Survey 2. However, the geographic distribution was similar to that of Survey 1. Larvae were found from August to January.

Monthly distribution and abundance of larvae for the I973/74 Survey cruises together with temperature distribution are illustrated in Figure 7. The relative abundance and the number caught per haul are summarized in Table V and the length composition of the larvae by month in Table VI.

Only two specimens measuring 4,50 mm and 9,35 mm were captured during August. These isolated specimens were found at approximately 24 km west of Henties Bay and IO km west of Conception Bay respectively. In September, larvae were still relatively scarce with only small patches occurring inshore off Walvis Bay and Cape Cross. Specimens measured from 4,35 mm to I4,75 mm and were probably derived predominantly from eggs spawned in late August/September.

West Coast sole larvae were taken in greatest numbers during the October cruise and were distributed along the coast between Cape Cross and Conception Bay. The greatest concentration of larvae was found about I6 km west of Henties Bay, most specimens being early larval stages, suggesting an increase in spawning activity in early October.

During November, December and January few larvae were encountered. Isolated individuals were collected inshore between Palgrave Point and Hollam's Bird Island, the length range varying between 4,10 and 23,00 mm, the mean length showing a gradual increase from month to month. No larvae were taken in the plankton during February and March/April.

TABLE VI: SIZE COMPOSITION OF WEST COAST SOLE LARVAE IN 1973/74

Length group (mm)	August		September		October		November		December		January		All months	
	Number	Per= centage	Number	Per= centage	Number	Per= centage	Number	Per= centage	Num= ber	Per= centage	Number	Per= centage	Number	Per= centage
2,1 - 3,0					25	23,6							25	13,8
3,1 - 4,0					37	34,9							37	20,6
4,1 - 5,0	1	50,0	3	21,4	12	11,3	1	5,3					17	9,4
5,1 - 6,0			2	14,3	14	13,2	1	5,3			1	5,6	18	10,0
6,1 - 7,0			4	28,6	10	9,4	3	15,8	1	4,8			18	10,0
7,1 - 8,0			1	7,2	4	3,7	6	31,6	2	9,5			13	7,2
8,1 - 9,0					4	3,7	5	26,2	3	14,3	1	5,6	13	7,2
9,1 -10,0	1	50,0					2	10,6	6	28,6	2	11,1	11	6,1
10,1 -11,0							1	5,3	4	19,0	2	11,1	7	3,9
11,1 -12,0			2	14,3					2	9,5	3	16,7	7	3,9
12,1 -13,0			1	7,2					1	4,8	2	11,1	4	2,2
13,1 -14,0											4	22,2	4	2,2
14,1 -15,0			1	7,2							3	16,7	4	2,2
17,1 -18,0									1	4,8			1	0,6
22,1 -23,0									1	4,8			1	0,6

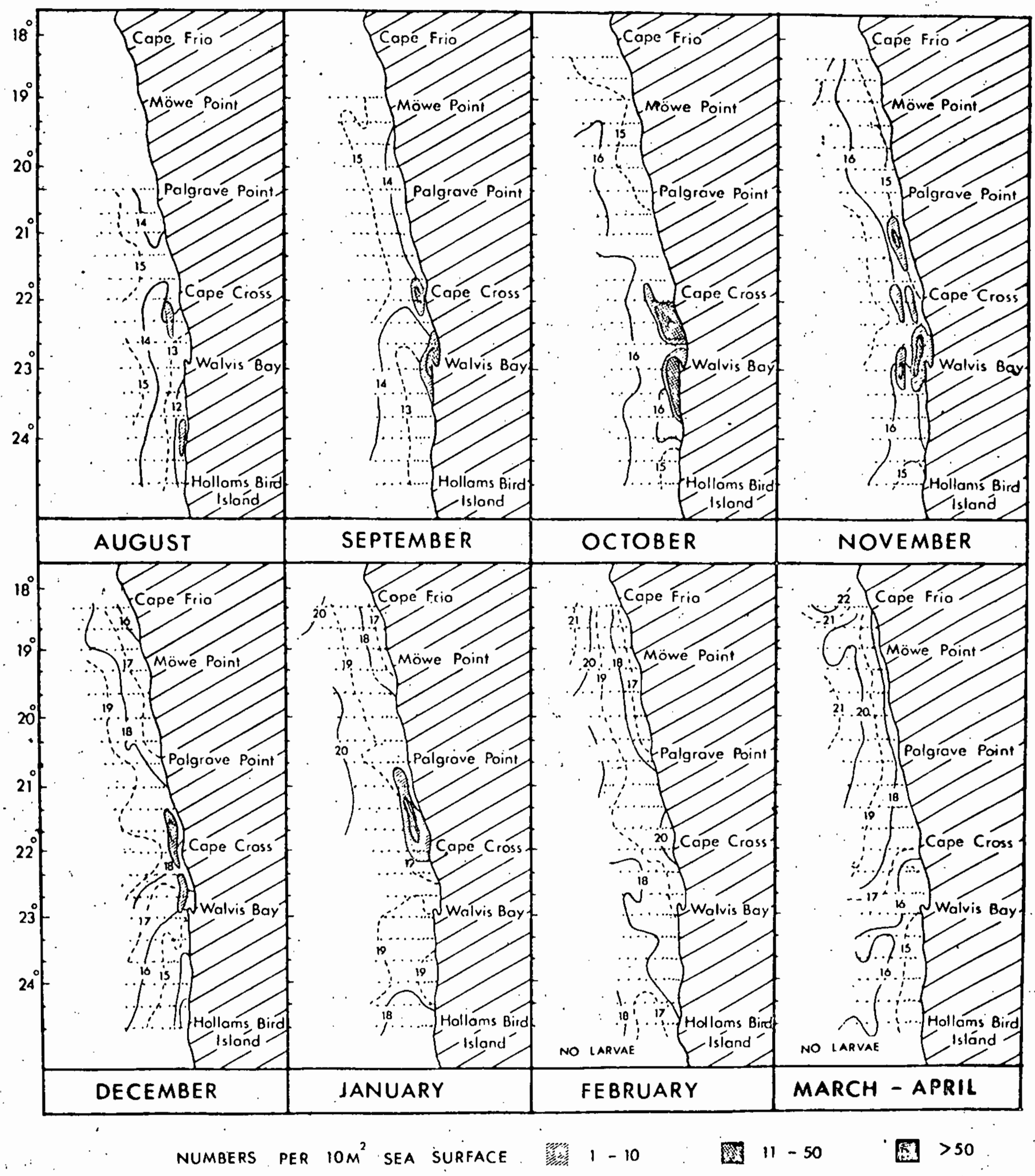


Fig. 7 Monthly distribution and abunance of West Coast sole larvae, August 1973 to March / April 1974

TABLE V Summary of the monthly hauls and abundance of West Coast sole larvae 1973/74.

Cruise Dates	No.of hauls	No.of positive hauls.	No.of larvae collected.	Mean no.of larvae per IO m^2	% of total collected
August I4-19	126	2	2	5,00	1,1
September 9-15	135	3	14	17,00	7,3
October 17-23	180	21	106	11,00	59,9
November 10-18	180	12	19	8,25	10,7
December 10-18	180	5	19	20,26	10,7
January 12-20	180	7	18	9,98	10,2
February 6-14	169	0	0	0	0
March 27/ April 4	175	0	0	0	0

THE SEASONAL OCCURRENCE OF LARVAE IN RELATION TO HYDROLOGICAL FEATURES.

The seasonal hydrological features for both survey periods have been described by O'Toole (I977). For the purpose of this report, the general sequence of events can be readily distinguished from the monthly distribution of surface isotherms, shown on the larval distribution charts in Figures 6 and 7. It is apparent that larvae of A. microlepis occurred mainly in the zone of active upwelling between Cape Cross and Hollam's Bird Island and particularly when upwelling was most intense (i.e. late winter and spring). Hydrological conditions, during the spawning season, showed that cold, low salinity water, was widespread along the coast. Temperature and salinity were generally uniform with depth, indicating a well-mixed water layer. Towards summer, upwelling decreased gradually and warm saline water advanced inshore, leading to more stable conditions and a corresponding decrease in the number of larvae.

Larvae of the West Coast sole were found at surface temperatures ranging from 11,4° to 19,8°C. Nevertheless, approximately 74 percent of all hauls containing larvae occurred at temperatures between 12,1° and 16,0°C. Of the remaining positive hauls, 23 percent were taken at temperatures greater than 16,0°C and 3 percent at temperatures lower than 12,0°C. The abundance of larvae in relation to surface temperature is summarized in Table VII.

Planktonic fish larvae generally inhabit the upper 50 metres of water (Ahlstrom 1959) but may become stratified at certain depth levels depending on biological and physical factors. The depth distribution of *A. microlepis* larvae was not investigated during this study and consequently the larvae may have occurred at a variety of temperatures within the 0-50 m layer. However, depth profiles showed that temperature was usually uniform to 50 metres, especially during the upwelling months, when larvae were most abundant. It is therefore likely that the optimum surface temperature range reflects to within one degree the thermal conditions in the water column.

TABLE VII : Relationship between surface temperature and number of hauls containing West Coast sole larvae, 1972-1974

Surface temp. (°C)	Number of hauls 1 - 10 larvae	11 - 50 larvae	More than 50 larvae	Total
11,1-12,0	1	2	0	3
12,1-13,0	6	5	0	11
13,1-14,0	11	11	5	27
14,1-15,0	9	5	2	16
15,1-16,0	9	4	2	15
16,1-17,0	5	3	1	9
17,1-18,0	3	1	0	4
18,1-19,0	1	3	0	4
19,1-20,0	3	1	0	4

Larvae of the West Coast sole were found over a narrow surface salinity range of between 34,91 and 35,30°/oo. Approximately 84 percent of all occurrences were taken at salinities of 35,01°/oo-35,20°/oo. Only 9,5 percent of hauls containing larvae were made at surface salinities less than 35,00°/oo, and 6,5 percent at salinities greater than 35,20°/oo. The ten largest hauls of larvae were taken at salinities of 34,91°/oo to 35,20°/oo (Table VIII) with eight of the hauls occurring in the 35,01°/oo-35,20°/oo range.

TABLE VIII : Relationship between surface salinity and number of hauls containing larvae of the West Coast sole 1972-1974.

Surface Salinity (°/oo)	Number of hauls 1 - 10 larvae	11 - 50 larvae	More than 50 larvae	Total
34,91-35,00	5	2	2	9
35,01-35,10	15	19	5	39
35,11-35,20	23	13	3	39
35,21-35,30	5	1	0	6

DISCUSSION

The coastal waters between Cape Cross and Hollam's Bird Island is an important spawning location of the West Coast sole *A. microlepis*. The abundance and length composition of the larvae indicate a relatively short spawning season from early spring until early summer, rapidly decreasing thereafter. Spawning was generally confined to upwelling areas within 30 km from shore and is apparently heaviest in the vicinity of Conception Bay and Hollam's Bird Island and between Cape Cross and Walvis Bay.

The northern limit of larval distribution suggested that little spawning took place north of Palgrave Point. This does not totally agree with the distribution of commercial catches over the past few years. Since I970, when demersal research commenced in S.W.A., the sole catches have predominantly come from the area between Rocky Point (I9^{o}S) and Palgrave Point (20^{o}30'S). This was particularly evident during the peak sole years I971 to I974, during which period this larval research was conducted(A.Payne, Sea Fisheries Branch, personal communication). Only a small portion of the sole landings resulted from fishing in the more extensive grounds south of Walvis Bay, presumably because the sole population was more scattered in the offshore grounds where fishing was allowed. As sexually active fish were recorded from the northern grounds (A. Payne, Sea Fisheries Branch, personal communication), the result of spawning north of Palgrave Point should have been noted in the collections of larvae. The complete absence of any West Coast sole larvae in the north,during the months of the survey, indicates that further research is necessary to finalise the whole mechanism of egg and larval dispersal of this species. The southern extension of spawning was not delineated, which implied that some spawning took place to the south of Hollam's Bird Island. Since no collections were taken from April to July I973 (mid autumn to mid winter) or after April I974, the duration of the spawning season could not be strictly determined. The fact, however, that larvae suddenly appeared in the plankton in early spring and disappeared in early summer, suggested that spawning was probably insignificant at other times of the year.

Recently hatched larvae were more numerous and widespread during the I972/73 survey, suggesting that spawning was more intense and took place over a greater area during that season than in I973/74. During the first survey, peak spawning occurred in early September and early November. In contrast, the breeding area was geographically more restricted during the second survey, with peak spawning in early October. An earlier decline in upwelling during the I973/74 spawning season could have resulted in a shorter breeding season (compare October and November of both years, Figs.6 & 7).

However, since the number of West Coast sole larvae captured during the ~~surveys were~~ relatively small compared with other pelagic fish larvae (O'Toole 1977), patchiness in distribution, diurnal migration, or gear inadequacies, may have caused the apparent variation in larval abundance between years.

The pelagic eggs and developing larvae of the West Coast sole should drift northwards along the coast from the southern spawning grounds. Although the direction of water movement was not monitored during the routine ichthyoplankton surveys, the seasonal distribution of temperature and salinity confirms the general trends outlined by Hart and Currie (1960). The flow is usually northerly in winter and spring, when the prevailing south and south-west winds are strong and upwelling intense. Isotherms are characteristically orientated parallel to the coast, especially in the south where upwelling is strongest. In summer, when the prevailing winds weaken, upwelling is reduced and warm oceanic water tends to move southwards and inshore. A typically northward transportation is shown by comparing the distribution of two size categories of larvae between the September and October cruises of 1972 (Figs. 8 & 9). This period was selected because the cohorts could be easily traced between these months. During September, recently hatched larvae (those less than 4,00 mm) were abundant in the inshore waters between Walvis Bay and Hollam's Bird Island (Fig. 8). Maximum numbers occurred off Conception Bay. In October, larger larvae (those greater than 8,00 mm) although less numerous, were found between Cape Cross and Walvis Bay, peak concentrations being off Cape Cross (Fig. 9). Assuming, that the more advanced stages collected in October represented some of the recently hatched larvae taken in September, then the population was transported northwards some 160-180 km in a period of about 30 days and showed a growth of between 5,00 and 6,00 mm. The percentage frequency of large larvae taken in the catches decreases rapidly during metamorphosis (Table IV and VI). During this time, the developing juveniles presumably descend to deeper layers, eventually becoming benthic. Laboratory reared Heteromycteris capensis larvae were found to change behaviour and become markedly benthic after a period of 38 days (Brownell, University of Cape Town, personal communication). This period roughly coincides with the time when metamorphosing larvae become scarce in the plankton.

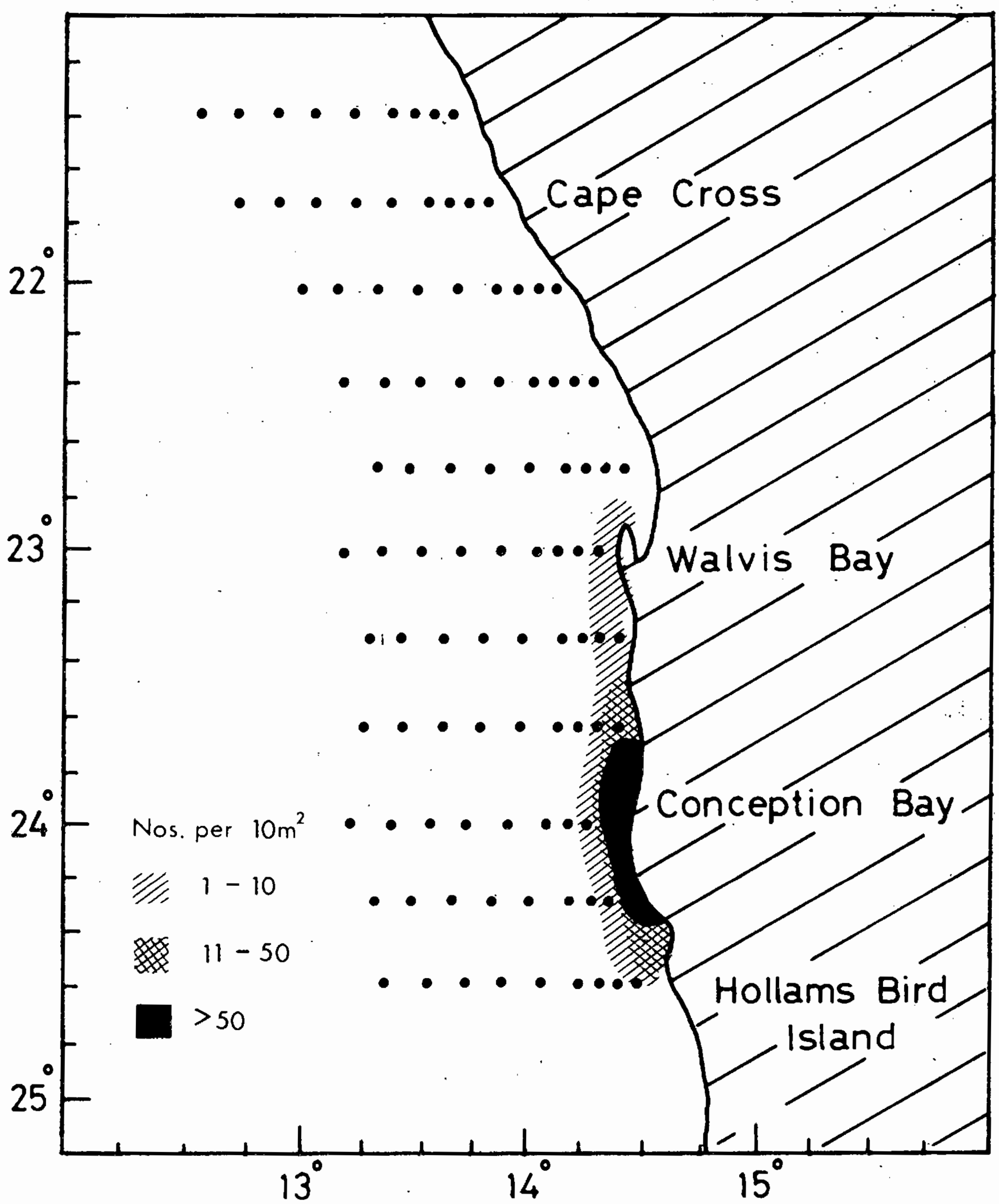


Fig. 8 Distribution and abundance of West Coast sole larvae less than 4mm in length during September 1972

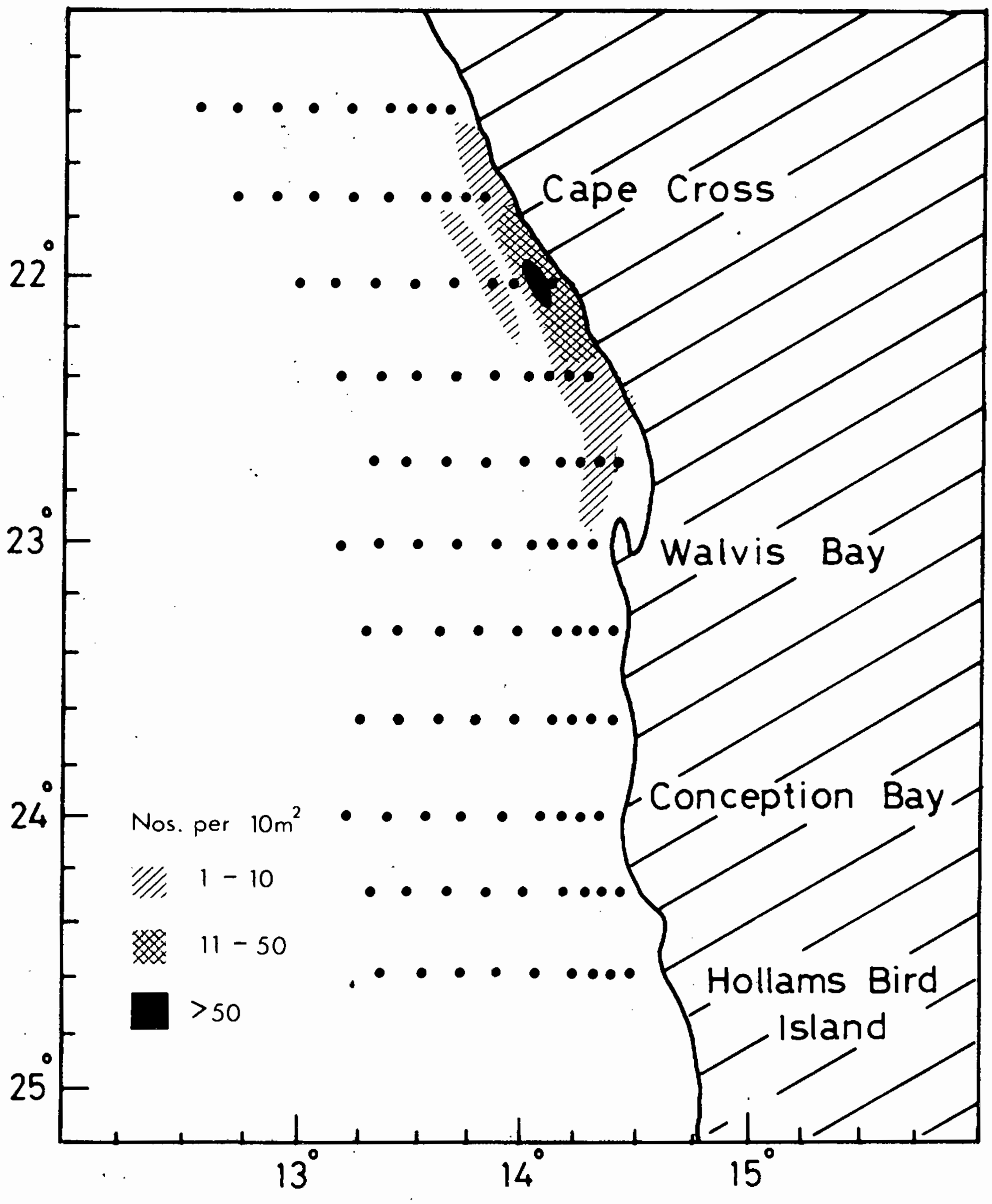


Fig. 9 Distribution and abundance of West Coast sole larvae greater than 8 mm in length during October 1972

LITERATURE CITED

AHLSTROM, E.H. 1959 Vertical distribution of pelagic fish eggs and larvae off California and Baja California U.S. Fish Wildl. Serv., Fish. Bull (161), 60 ; 107-146

AHLSTROM, E.H. 1973 Fish egg and larval surveys - handling the collections ashore. Contribution to a manual edited by H.G. Hemple. F.A.O. Fish. Tech. Paper (122) : pt 4, 27-32

HART, T.J. AND R.I. CURRIE. 1960 The Benguela Current. "Discovery Rep.," 31 : 123-298

KING, D.P.F. AND A.A. ROBERTSON 1973 Methods of pelagic fish egg and larval research in South West Africa. S.Afr. Shipp. News Fish. Ind. Rev. 28, (5) : 57-61.

KRAMER, D. M.J. KALIN, E.G. STEVENS, J.R. THRAILKILL AND J.R. ZWEIFEL. 1972 Collecting and processing data on fish eggs and larvae in the California Current Region. NOAA Tech. Rep.CIRC - 370 38 pp.

O'TOOLE, M.J. 1973 Fish larval investigations off South West Africa - a summary of results. S. Afr. Shipp. News Fish. Ind. Rev. 29, (11) : 53-59.

O'TOOLE, M.J. 1976 Incidental collections of small and juvenile fishes from egg and larval surveys off South West Africa (1972-1974). Fish. Bull. S. Afr. 8: 23-33.

O'TOOLE, M.J. 1977 Investigations into some important fish larvae in the S.E.Atlantic in relation to the hydrological environment. Phd. thesis, University of Cape Town.

SMITH, J.L.B. 1970 The Sea Fishes of Southern Africa, 5th Ed. Cape Town; Central News Agency : 580 pp.

TAYLOR, W.R. 1967 An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natn. Mus. I22 , (3596); I7 pp.

DESCRIPTION OF THE LARVAE AND EARLY JUVENILES OF THE BEARDED GOBY, <u>SUFFLOGOBIUS</u> <u>BIBARBATUS</u> (VON BONDE), WITH NOTES ON ITS DISTRIBUTION, ABUNDANCE AND ECOLOGY IN THE SOUTH EAST ATLANTIC.

B Y

Michael J. O'Toole,
Sea Fisheries Branch,
Cape Town,
Rep. South Africa.

ABSTRACT

Large numbers of larvae and juveniles of the bearded goby Sufflogobius bibarbatus (von Bonde) were taken in the neritic waters of South West Africa, during a two-year egg and larval survey. Larval and juvenile stages are described and illustrated. The geographic distribution, seasonality and relation of larvae to temperature and salinity are given. Diurnal migration, diet and possible explanations for the species abundance are discussed.

I. INTRODUCTION.

The bearded goby, Sufflogobius bibarbatus was first reported in the coastal waters off South West Africa by Barber and Haedrich (1969) when three juvenile specimens were taken in the plankton associated with a scattering layer near Hollam's Bird Island ($24^{o}40'$S). They suggested that the species was responsible for some of the strong sonic recordings in the layer and that it may be very abundant in the neritio waters of the region. More recent work on this phenomenon by d'Arcangues (1974) showed that S. bibarbatus indeed formed an important component of the scattering layer.

The Sea Fisheries Branch conducted an extensive fish egg and larval survey off the South West African coast during the years 1972 to 1974. The surveys were undertaken to study the seasonality, distribution and abundance of eggs and larvae of the commercially important pelagic species in the region. Larvae of the bearded goby were more abundant and widely distributed than any other species taken in the ichthyoplankton collections. Sufflogobius constituted 66,6% of all larvae collected in 1972/73 (O'Toole, 1974a) and 60% of all larvae taken in 1973/74. Adults and juveniles also formed 53% of all small fishes incidentally collected during the surveys. (O'Toole 1976). Little is known about its biology and the eggs, larvae and juveniles have not been described. As no goby eggs were collected during the surveys, it is presumed therefore that the bearded goby spawns on the bottom like other gobioid fish.

The extent of its local distribution has been documented as St.Helena Bay to San Sebastian Bay at depths of 28-50 fathoms (Smith 1969; von Bonde 1923). However, recent findings (Barber & Haedrich, 1969; O'Toole, 1973, 1976 and d'Arcangues, 1974) indicate that the species is more abundant and widespread than at first believed. The taxonomy of the adult, formerly Gobius bibarbatus von Bonde, was revised by Smith (1956) and assigned to a new genus, Sufflogobius because of its ability to self-inflate and the presence of two skin flaps beneath the chin.

II. SURVEY AREA.

The region between Cape Frio (18°20'S) and Hollam's Bird Island was surveyed monthly from August 1972 to March 1973 and from August 1973 to April 1974. These periods were selected to coincide with the known spawning months of the commercial species.

The sampling grid consisted of 180 stations on twenty lines, each containing nine stations (Fig.1). The lines were spaced 32 km apart. The inshore station on each line was approximately 8 km from the coast and the outer station approximately 112 km offshore. The grid was sampled from north to south on a continuous 24 hour basis. During certain months some stations were not sampled due to poor weather conditions or technical difficulties. Station positions, omissions,depths and dates of the cruises have been given by O'Toole (1976).

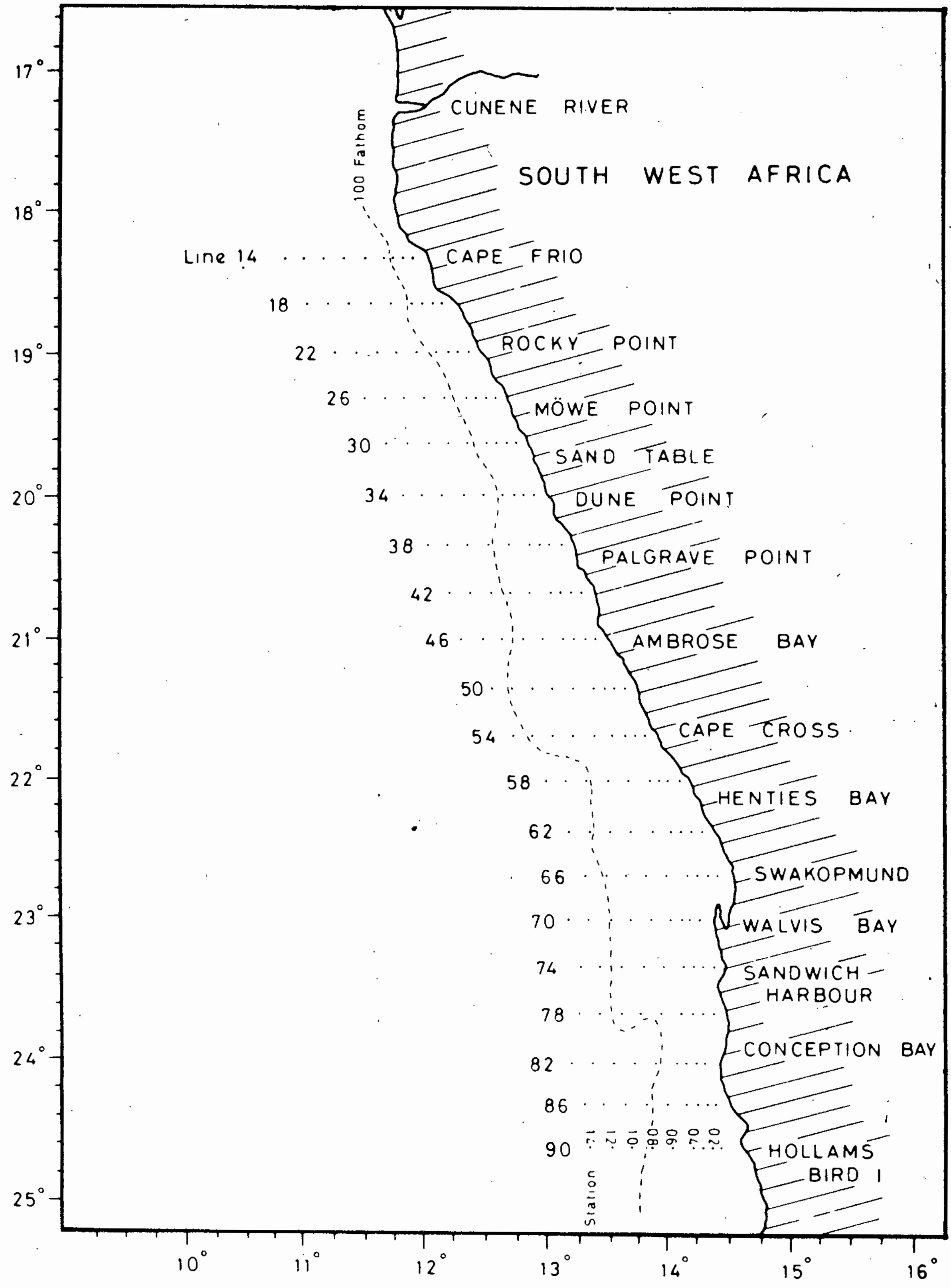


Fig. 1 Location of routine stations occupied during the SWAPELS cruises in 1972/73 and 1973/74

III. MATERIAL AND METHODS.

Ichthyoplankton collections were made using a 57 cm mouth diameter bongo net similar to that of Posgay et al (1968). Paired nets of 0,94 mm mesh size were used on the first survey. A mesh size of 0,94 mm was used on the left unit and 0,50 mm on the right unit during the second survey. Oblique hauls were made at a speed of 2 knots, between the surface and a depth of 50 m or within a few metres of the bottom in shallow coastal waters. Surface salinity and temperatures to the full depth of the haul were recorded at each station. A more detailed account of sampling methods is given by King & Robertson (1973).

The larvae of S.bibarbatus were extracted from the samples, counted and standardized to the number under 10 m^2(Kramer et al 1972). Since large numbers were present in the samples, specimens were not measured individually. However, as larvae were generally found to consist of uniform length classes within each sample, approximate percentages of these length groups were estimated.

A developmental series from yolk-sac larvae to juveniles was selected and the individuals measured by means of an ocular micrometer under a stereoscopic microscope. This series was also used when describing larval morphology and melanophore formation. Some individuals of the series were cleared (Taylor, 1967) and stained with Alizarin Red-S to obtain fin ray counts. Terms used in morphometric measurements are similar to those defined by Moser (1972).

Although many juveniles and adults ranging from 30 mm to 90 mm were taken during the surveys (O'Toole, 1976), this report is concerned mainly with larvae and early juveniles up to 30 mm in length.

IV. RESULTS.

GENERAL MORPHOLOGY.

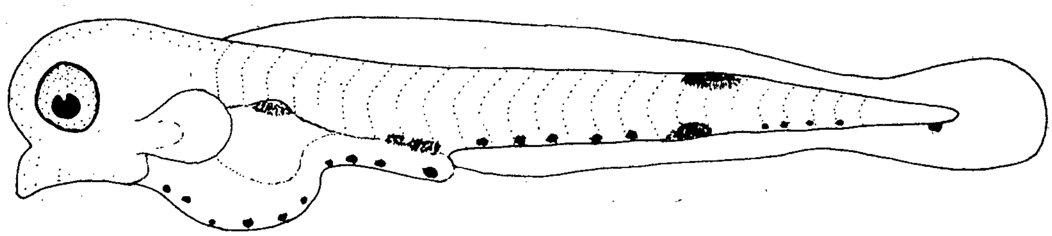
The smallest larva caught was 2,25 mm in length. In larvae of length 2,25 - 2,50 mm, the yolk-sac is still present and the mouth and pectoral buds are formed (Fig.2A). The notochord begins to flex in larvae of approximately 5,0 - 5,2 mm (Fig.2B) and is usually completed before attaining a length of 7,0 mm (Fig.2C). Juvenile pigmentation begins to develop when the larva reaches approximately 20 mm. The larvae of Sufflogobius develop smoothly and gradually. Preanal length increases from 42% of the standard length (SL) at 2,8 mm to 55% at IO mm. The gut tends to shorten at larval lengths of I4-16mm and levels off at approximately I8 mm when it is 50-52% of the SL (Fig.4A). Head length averages I7-23% of the SL in larvae of of 2,8 to IO,0 mm long (Fig.4B). The head lengthens considerably in larvae of I2 to I9 mm averaging 30-32% of the standard length in juvenile specimens. Body depth, measured at the pectoral fin, increases gradually during larval development (Fig.4C) from I4% of the SL in 2,8 mm length larvae to I7% of the SL in larvae of IO,5mm length. Subsequent body deepening shows a slow increase from I7% of the SL in I2 mm larvae to 22% of the SL in 30 mm juveniles.

A similar increase in body depth occurs at the origin of the second dorsal fin (Fig.4D). However, depth changes more rapidly in early larval development averaging 9,5% of the SL at 2,8 mm to I8% of the SL at IO,5 mm. A slight increase in body depth to 20% of the standard length occurs by the time juveniles reach 26 mm in length . Body depth continues to increase at both points in juveniles of 30 mm.

FIN DEVELOPMENT.

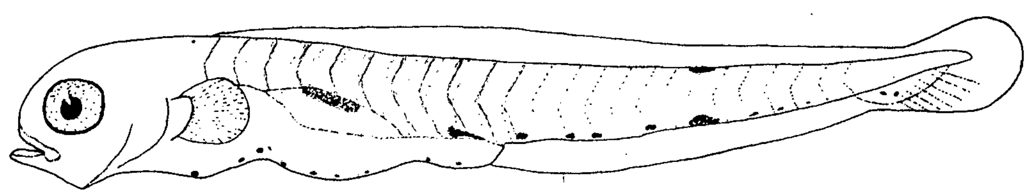
Yolk-sac larvae possess a well-developed fin fold surrounding the dorsal,anal and caudal regions. No fin rays are visible although the pectoral fin buds are clearly seen even on the smallest larvae. The appearance of fin rays occurs in the following sequence: Pectoral, caudal, dorsal, anal and pelvic.

A



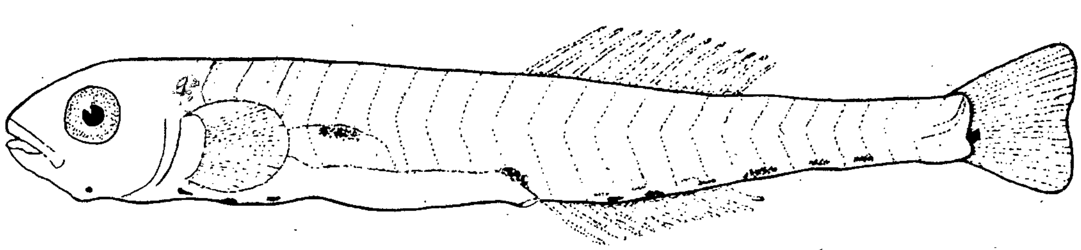
Yolk - sac larva (2.3 mm)

B



Larva undergoing flexion (5.2 mm)

C



Post - flexion larva (7.6 mm)

Fig. 2 Larval development of the bearded goby, <u>Sufflogobius</u> <u>bibarbatus</u>

TABLE I. Meristics from cleared and stained larvae and juveniles of <u>Sufflogobius bibarbatus</u>

Length (mm)	Nos. measured	Dorsal D_1 D_2	Anal	Pectoral	Pelvic fin	Caudal Principal Rays	Caudal Procurrent Rays	Nos. of vertebrae
4,5	2	-	-	-	-	4+4	-	-
5,4	4	1+7	1+6-7	5-8	-	7+7	-	-
8,1	3	1+12	1+12	15-18	-	7+7	-	26
9,2	4	1+12	1+12	15-18	-	7+7	-	26
10,1	5	1+12	1+12	17-18	-	8+7	-	26
10,6	3	1+12	1+12	18-19	-	8+7	-	26
12,0	5	1+12	1+13	20	-	8+7	2+2	26
13,3	4	3+1+12	1+13	21	1+5	8+7	3+4	26
13,8	5	3+1+12	1+12	21	1+5	8+7	4+5	26
14,3	5	3+1+13	1+12	22	1+5	8+7	6+7	26
15,2	5	3+1+13	1+12	22	1+5	8+7	8+8	26
15,6	3	6+1+13	1+13	22	1+5	9+8	9+8	26
16,4	4	6+1+13	1+13	23	1+5	9+8	9+9	26
17,8	5	6+1+13	1+13	22	1+5	9+8	10+11	26
18,7	5	6+1+13	1+13	21	1+5	9+8	11+11	26
19,9	5	6+1+13	1+13	22	1+5	9+8	11+11	26
20,0	5	6+1+13	1+13	22	1+5	9+8	11+11	26
22,6	3	6+1+13	1+13	22	1+5	9+8	11+11	26
24,0	4	6+1+13	1+13	22	1+5	9+8	11+11	26
25,7	3	6+1+13	1+13	23	1+5	9+8	11+11	26
26,5	3	6+1+13	1+13	23	1+5	9+8	11+11	26
28,0	5	6+1+13	1+13	22	1+5	9+8	11+11	26

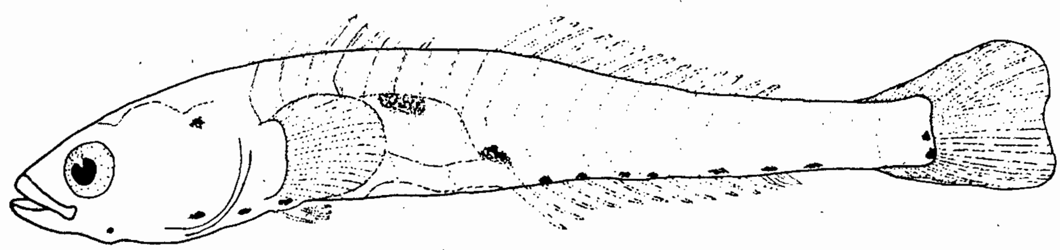
Rays begin to develop in the pectoral fin when larvae reach approximately 5 mm. Most of the rays are formed before the larvae reach 7 mm and the adult complement of 22 rays is attained by I3-I4 mm (Table I). The caudal fin starts to develop at the base of the notochord slightly anterior to the tip. The full number of 9 principal rays in the superior lobe and 8 in the inferior lobe is reached by approximately I5 mm. The dorsal and anal fins develop immediately after notochord flexion. Before a length of 7 mm is reached, one dorsal and one anal spine, together with about 8-10 rays are present on both fins. The spines initially appear on the first dorsal at approximately I2 mm and the last spine forms at about I6 mm. The pelvic fins develop last (12,5 mm) and the full complement of 5 rays and 1 spine are reached by I3,0-I3,5 mm.

PIGMENTATION.

The melanophore pattern of yolk-sac larvae consists of an arrangement of small pigment spots characteristically placed along the mid-ventral line (Fig. 2A). A series of 6 - 10 small melanophores are located between the thorax and anus. In the gut region, a cluster of internal pigmentation is present in the dorsal area of the gas cavity and on the dorsal surface of the gut anterior to the vent. These melanophores remain throughout the entire larval development. Posterior to the anus, a series of 8-10 pigment spots extend along the mid-ventral line almost to the tip of the notochord. Two or more melanophores fuse to give rise to a large stellate melanophore which is situated about midway in the series. On the dorsal surface, another conspicuous stellate melanophore is present above but slightly posterior to the corresponding ventral one. A small pigment spot is seen on the base of the notochord tip and remains throughout larval development.

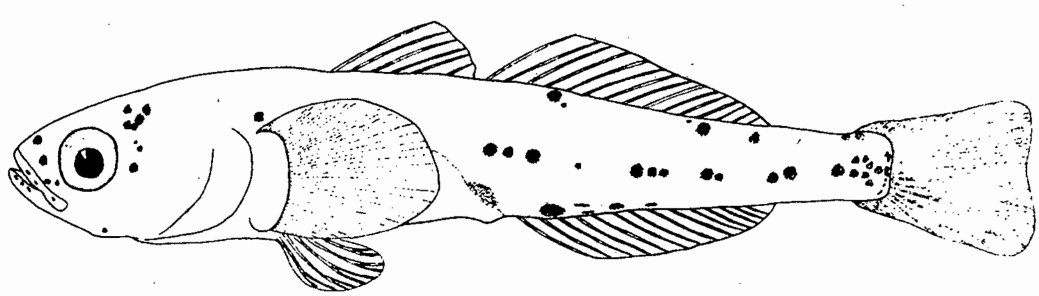
Pigmentation remains unchanged until the larva undergoes flexion, during which the melanophore on the dorsal surface begins to disappear and the first 4-5 spots posterior to the anus become embedded (Fig. 2B). Towards the end of notochord flexion (6,5 - 7,0 mm), the pigmentation on the mid-ventral line between the thorax and anus changes.

A



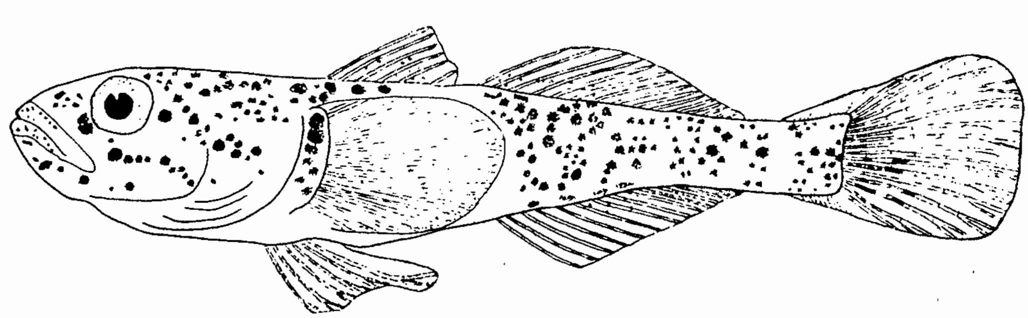
Larva (16.0 mm)

B



Larva undergoing metamorphosis (22.0 mm)

C



Juvenile (30.0 mm)

Fig. 3 Larval development of the bearded goby *Sufflogobius bibarbatus*

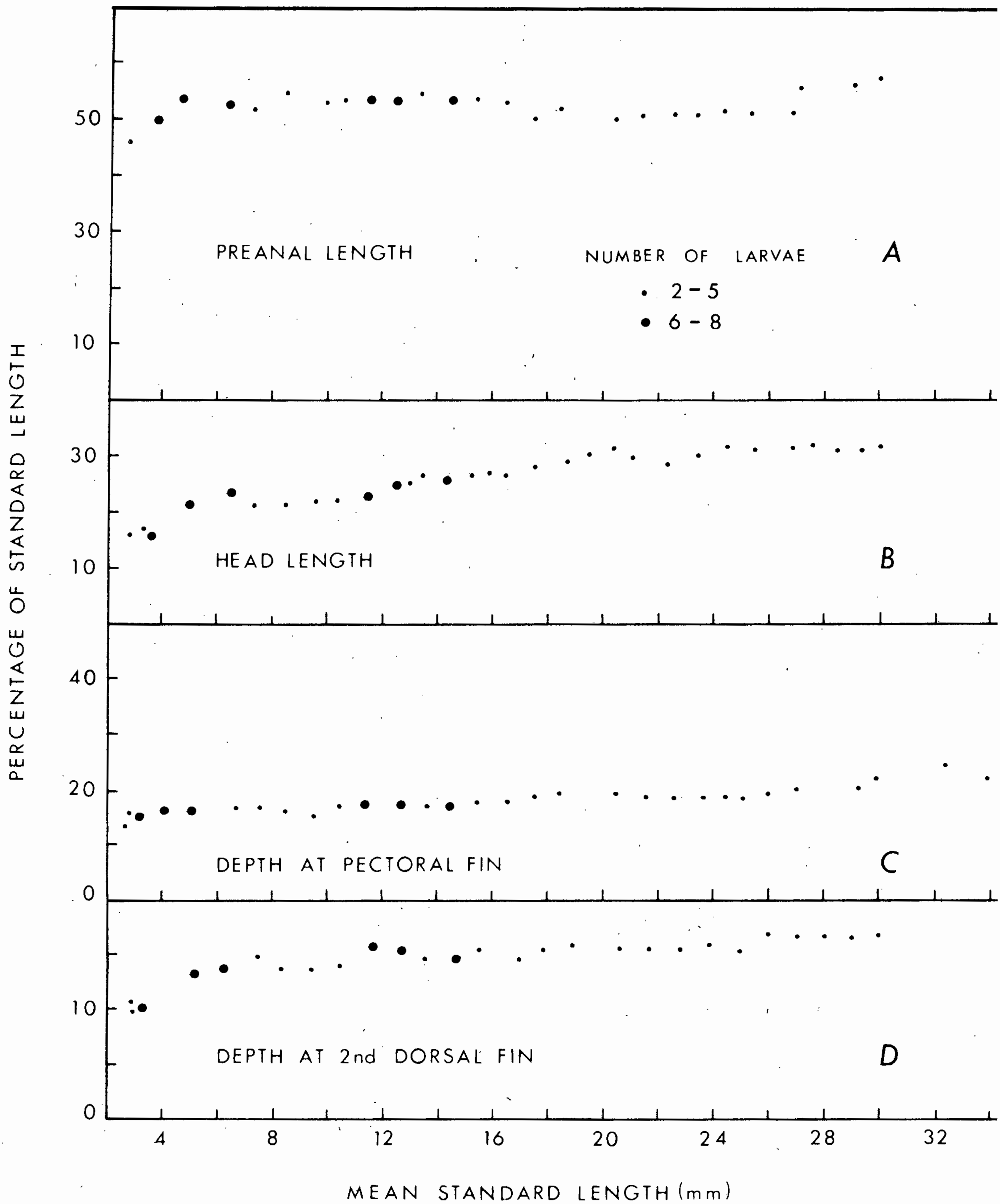


Fig. 4 Relationship between preanal length, head length, depth at pectoral fin and depth at 2nd dorsal fin to body length in Sufflogobius

The first three spots becoming enlarged, elongated and embedded, while the others disappear (Fig. 2C). At a length of approximately 7,5 mm, a characteristic pigment spot forms on the base of the lower jaw and persists through the entire larval period. The spots along the mid-ventral line posterior to the anus re-group to form three embedded oval shaped melanophores on each side of the body followed by three larger internal pigment spots. The caudal melanophore enlarges and the fin rays become melanistic on the ventral base. Pigmentation remains basically unchanged until juvenile metamorphosis, except for the appearance, at about 10 mm in length, of some internal melanophores in the hind lobe of the brain. Figure 3A shows a larva of I6 mm with characteristic late larval pigmentation.

Juvenile pigmentation commences at approximately 20,0 mm when several spots appear on the upper and lower jaws (Fig.3B). A group of stellate melanophores form on the snout and the cranial region. The pigmentation at the base of the caudal fin becomes more pronounced and large stellate melanophores form along the lateral line. Before a length of 25 mm is attained, the number of melanophores increase on the jaws, snout, cranial region and operculum. Pigmentation appears on the dorsal surface and at the base of the dorsal fin. When the juvenile reaches approximately 30 mm, the body is heavily pigmented. (Fig. 3C). The dorsal and caudal fin rays are speckled with pigment. In juveniles of 40 - 50 mm in length, the melanophores along the lateral surface and on the fins, group into irregular bands characteristic of the adult form.

DISTRIBUTION AND SEASONALITY OF THE LARVAE.

The larvae of the bearded goby were abundant and widely distributed in the neritic waters of South West Africa. The cumulative distribution and relative abundance for all positive stations during both surveys periods is shown in Figure 5 and 6. Highest densities were found in the south of the research area, between Walvis Bay (23^{o}S) and Hollam's Bird Island (24^{o}40'S). Approximately 80% of all larvae caught in Survey 1 and 60% of those caught in Survey 2 were taken in this region (Table II).

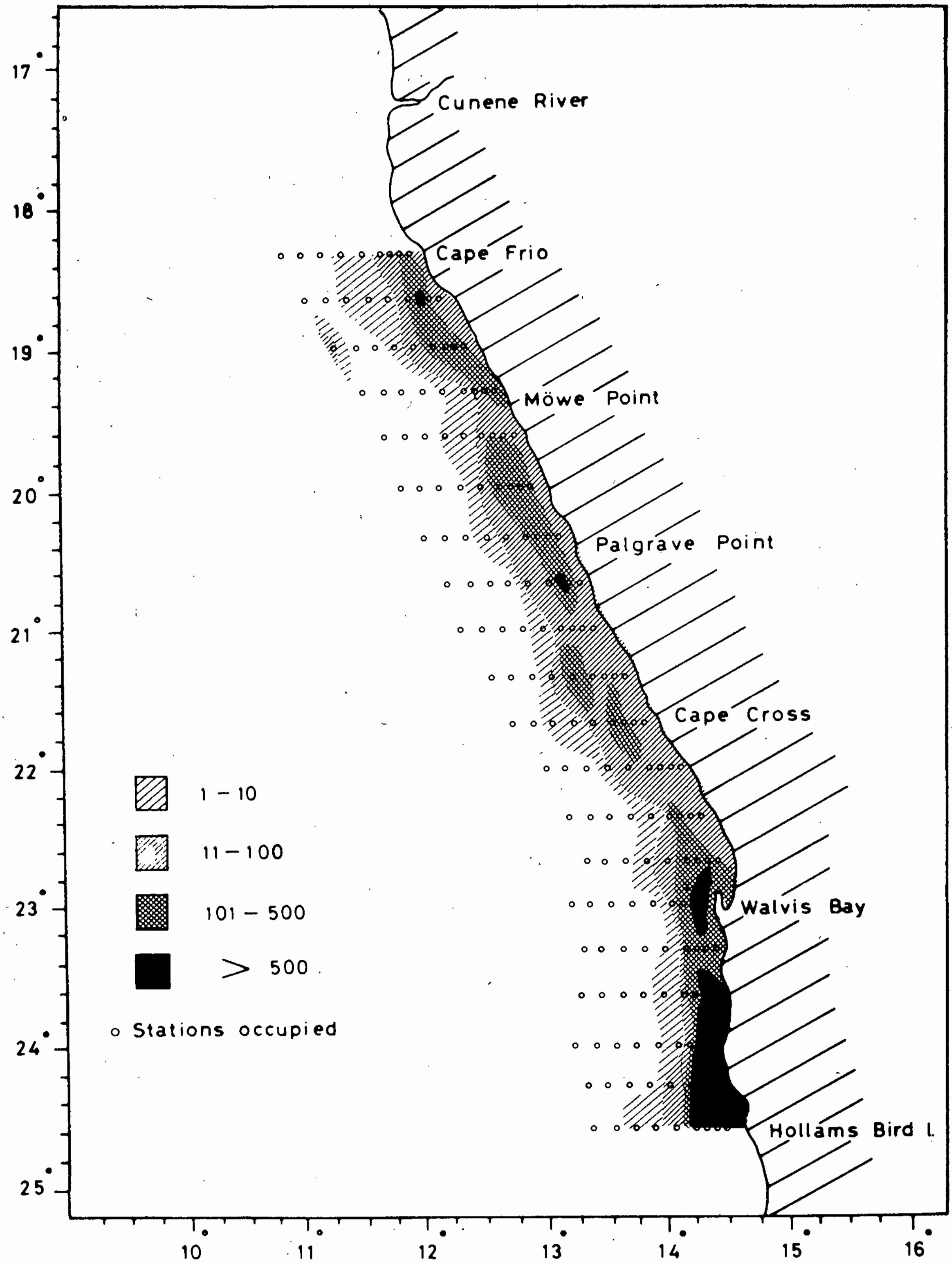


Fig. 5. Distribution and abundance of bearded goby larvae during Survey 1 (values represent cumulative haul totals for all cruises)

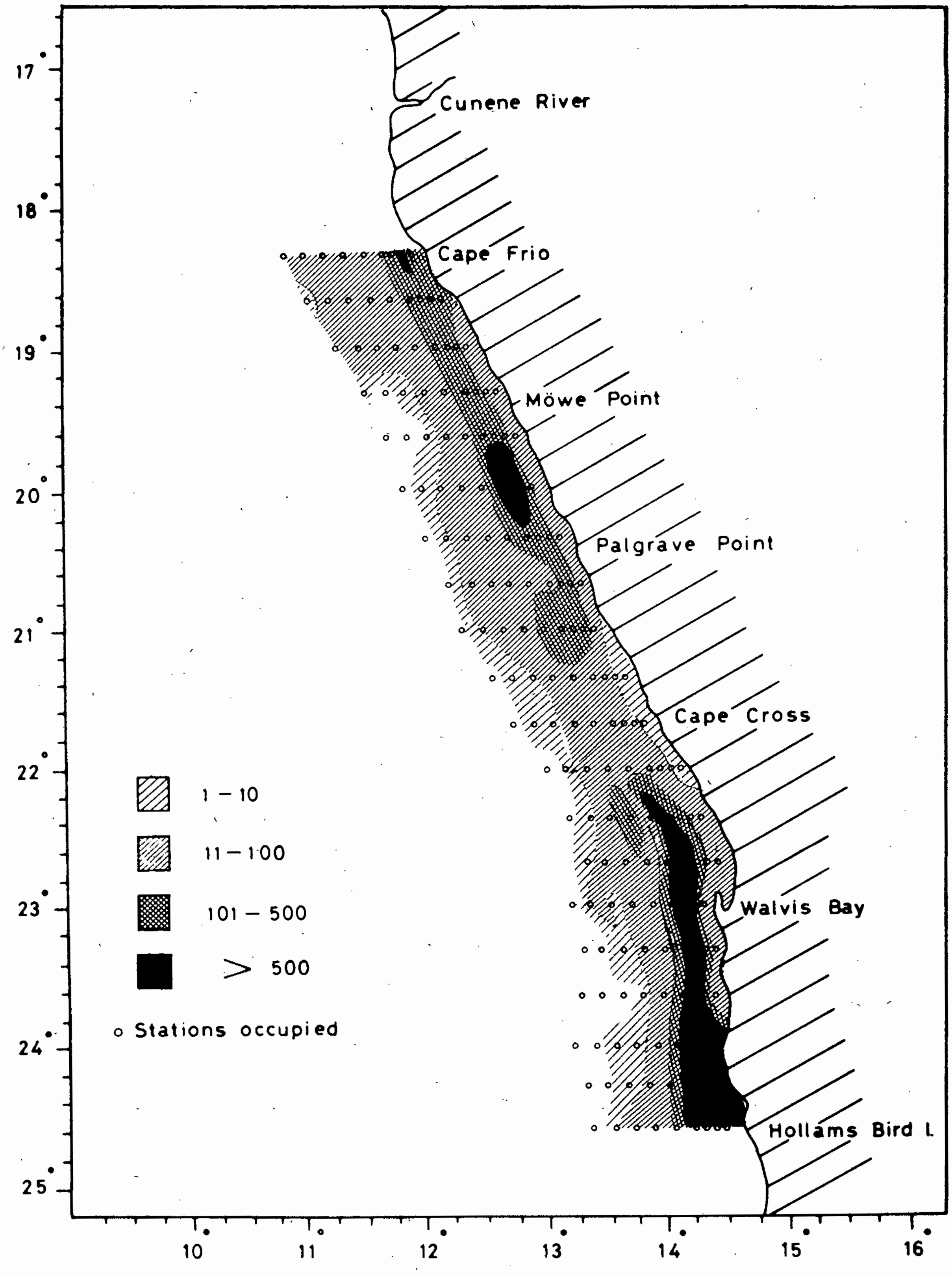


Fig. 6. Distribution and abundance of bearded goby larvae during Survey 2 (values represent cumulative haul totals for all cruises)

TABLE II. The percentage of bearded goby larvae taken in the different parts of the research area.

AREA	STATION LINE	1972/73	1973/74
Cape Frio to Mowe Point	14 - 26	2,7	6,7
Mowe Point to Palgrave Point	30 - 42	3,2	12,8
Palgrave Point to Henties Bay	46 - 58	4,6	9,5
Henties Bay to Sandwich Hb.	62 - 74	14,5	22,4
Sandwich Hb to Hollam's Bird Island.	78 - 90	76,8	52,5

The southern limit of larval distribution was not established and probably extended a considerable distance to the south of the survey area. The numbers per haul showed a gradual decrease northwards from Walvis Bay with only 13,3% and 22,4% occurring north of Palgrave Point (20°25'S) in 1972/73 and 1973/74 respectively. Larvae were found over the whole inshore/offshore range (Table III). Nevertheless, about 65% of occurrences were at distances of 8 - 30 km from the coast and the seaward limit of larval distribution rarely exceeded 50 km from the coast.

TABLE III. The percentage occurrence of the total number of bearded goby larvae in relation to distance from the shore.

DISTANCE FROM SHORE	1972/73	1973/74	1972/74
10 km or less	11,9	8,4	9,8
10 - 20 km	23,5	25,5	24,7
20 - 30 km	48,1	22,2	32,8
30 - 50 km	15,7	38,7	29,2
50 - 100 km	0,6	4,9	3,2
100 km or more	0,1	0,2	0,2

Although larvae of Sufflogobius were collected during all months of both surveys, approximately 65% of the total were taken during November and December. Only approximately 13% of the larvae were found from January to March 1973, and 15% from January to March/April, 1974. Larvae were more abundant and widespread in the plankton during 1973/74 than in 1972/73.

SURVEY I. (August 1972 - March 1973)

The monthly distribution and abundance of larvae and early juvenile stages is shown in Figure 7. The length composition of the catches for each cruise is illustrated in Figure 8[a] and are expressed as the percentage of individuals in 5 mm length intervals. A summary of the monthly hauls and abundance is given in Table IV . During August and September, larvae were taken mainly in the coastal waters south of Walvis Bay. The majority of specimens measured less than 10 mm and were recently hatched from late winter spawning. In October, larval abundance decreased and were distributed further to the north. Highest densities of larvae occurred in the plankton in November and were concentrated in the inshore waters south of Walvis Bay. Many of the specimens (about 70%) were larger than 10 mm and were presumably derived from the earlier spring spawning. Some newly hatched individuals were also collected, which indicated that some recent spawning had taken place.

The distribution of larvae was more widespread in summer months and extended as far north as Cape Frio. The offshore distribution range was also more extensive, particularly in January. Larval abundance decreased gradually from December to March with the more advanced stages predominating in the samples. The presence of some newly hatched larvae north of Palgrave Point and south of Walvis Bay indicated that periodic spawning had taken place in these regions between December and February.

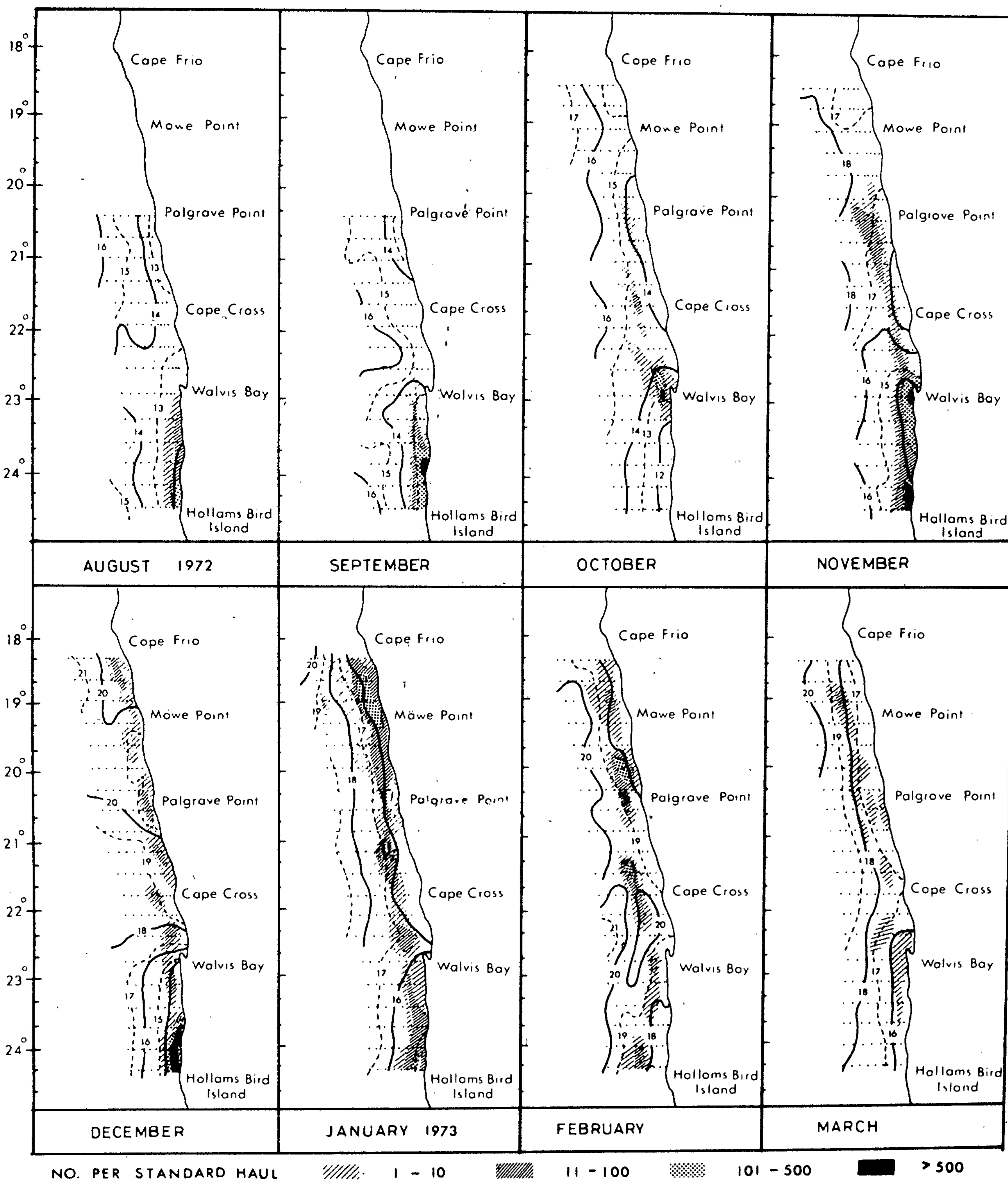


Fig. 7. Monthly distribution and abundance of bearded goby larvae, August 1972 to March 1973

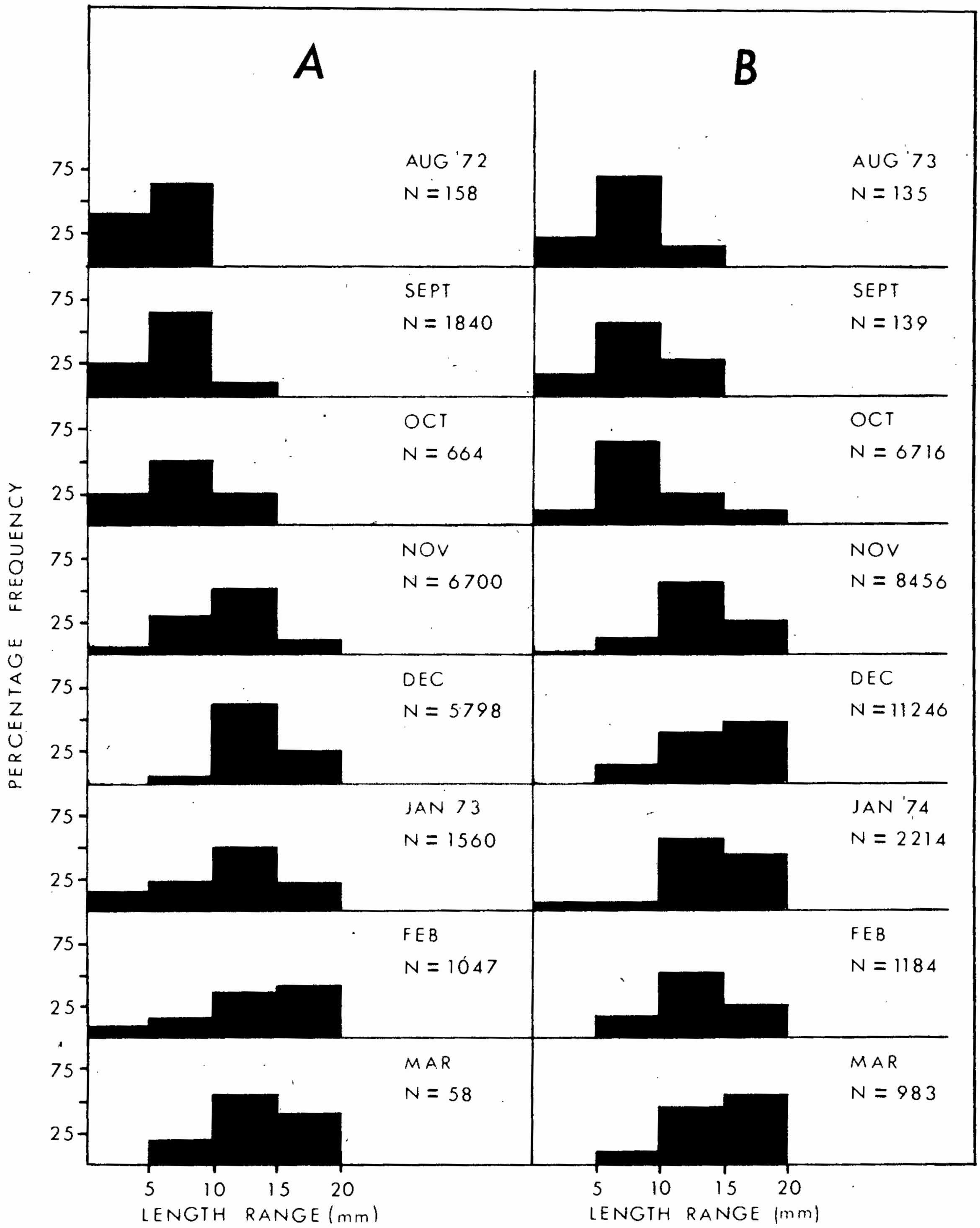


Fig. 8. Length composition of bearded goby larvae, collected during both surveys (larvae are grouped in 5 mm length intervals)

TABLE IV. A summary of the monthly hauls and abundance of bearded goby larvae I972 - 1973.

Month	No.of hauls	No. of positive hauls	No.of larvae collected	Mean no. of larvae per $10m^2$	% of total collected.
August	126	12	158	25,6	0,9
September	126	16	1840	124,5	10,3
October	156	23	664	57,1	3,7
November	180	38	6700	260,7	37,6
December	180	40	5798	426,7	32,53
January	180	73	1560	59,2	8,8
February	177	50	1047	36,6	5,9
March	177	18	58	9,5	0,3

SURVEY 2. (August I973 to March/April I974)

The distribution and abundance of the larvae and early juvenile stages of Sufflogobius for each month is illustrated in Figure 9 and the length frequency of specimens for each cruise is shown in Figure 8 b. A summary of the monthly hauls and abundance is given in Table V.

Larvae were generally scarce in the plankton during August and September and were scattered in isolated patches along the coast from Mowe Point to Hollam's Bird Island. Specimens collected during these months consisted of mixed size groups, probably resulting from spawning between July and August. In October and November, larval abundance increased greatly in the coastal waters from Cape Frio to Hollam's Bird Island. Maximum concentrations were found approximately 50 km north west of Walvis Bay in October and in the neritic waters south of Walvis Bay in November. The majority of specimens measured between 5 and I5 mm and must have derived from intense spawning between early and mid spring.

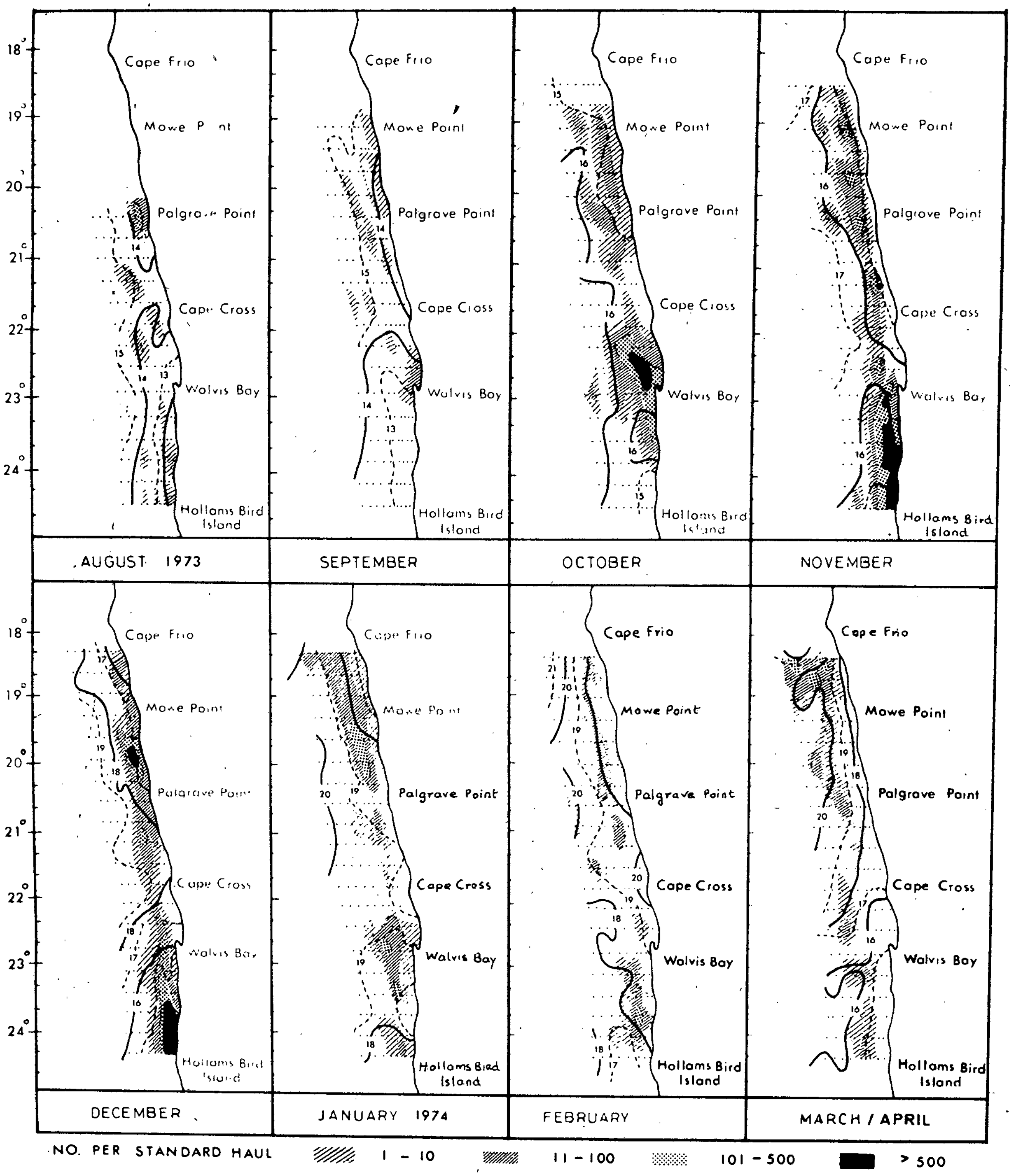


Fig. 9. Monthly distribution and abundance of bearded goby larvae, August 1973 to March / April 1974

Larvae reached peak abundance during the month of December and were found over a wide coastal belt from Cape Frio to Hollam's Bird Island. Centres of abundance occurred between Mowe Point and Palgrave Point and to the south of Walvis Bay near Hollam's Bird Island. Over 80% of the larvae were greater than IO mm in length and presumably resulted from heavy spawning in late October and November. The numbers of larvae declined sharply from December to March/April and consisted mainly of advanced larval stages and juveniles. Distribution was widespread between Cape Frio and Hollam's Bird Island but larvae were more common north of Palgrave Point and off Walvis Bay. The occurrence of some recently hatched larvae in the summer collections indicated periodic spawning in the north and south.

TABLE V. A summary of the monthly hauls and abundance of bearded goby larvae 1973 - 1974.

Month	No.of hauls	No.of positive hauls	No.of larvae collected	Mean no. of larvae per IO m^2	% of total collected.
August	126	15	135	36,6	0,4
September	135	22	139	15,4	0,5
October	180	68	6716	151,6	21,6
November	180	73	8456	271,2	27,2
December	180	70	11,346	201,8	36,2
January	180	70	2214	50,4	7,1
February	169	51	1184	28,0	3,8
March/April	175	50	983	33,2	3,2

In general, the bearded goby spawned continuously from July to February in the inshore waters over the entire area. The main spawning season for both years took place from late winter to the end of spring in the coastal waters south of Walvis Bay. During summer, spawning decreased in intensity but extended over a much wider area to the north.

The drop in larval abundance and the presence of larger size groups in the collections after mid summer indicated that the spawning season was nearing completion by early autumn. The distribution pattern was very similar for both years, but larvae were much more numerous during 1973/74 which suggested that spawning was more intense.

DIURNAL VARIATION IN CATCHES AND DIET.

Larvae and early juvenile stages were collected in greatest abundance during the hours of darkness. Newly hatched larvae were however more abundant in day hauls. Larger larvae generally increased in numbers after sunset, reaching peak abundance at midnight and particularly between 04h00 and 06h00 (Fig.10). A gradual decline in numbers occurred during daylight hauls.

The digestive tracts of 85 larvae (6 - 15 mm), 50 juveniles (21 - 42 mm), and 75 adults (65 - 85 mm), from three coastal localities, Palgrave Point, Walvis Bay and Conception Bay were examined for the presence of food organisms. Only 10 percent of the larvae, 52 percent of the juveniles and 50% of the adults contained food material in the gut. The diet consisted of a variety of phytoplankton and zooplankton. The chain forming diatom Fragilaria karsteni was the most common species in the stomach of all stages. Unidentified copepod remains, euphausids, bivalve larvae and sand particles were present in the stomachs of juveniles and adults. The stomachs of the larvae were generally empty. Six specimens measuring 12,4 - 14,8 mm contained Fragilaria karsteni , Chaetoceros sp. and small well digested copepods.

ABUNDANCE OF LARVAE IN RELATION TO TEMPERATURE.

Larvae and juveniles of Sufflogobius were found in areas where surface temperatures ranged from 11,0° to 22,0°C. Nevertheless,over 80% of all the specimens were collected over a narrower temperature range of 13,0° to 17,9°C.

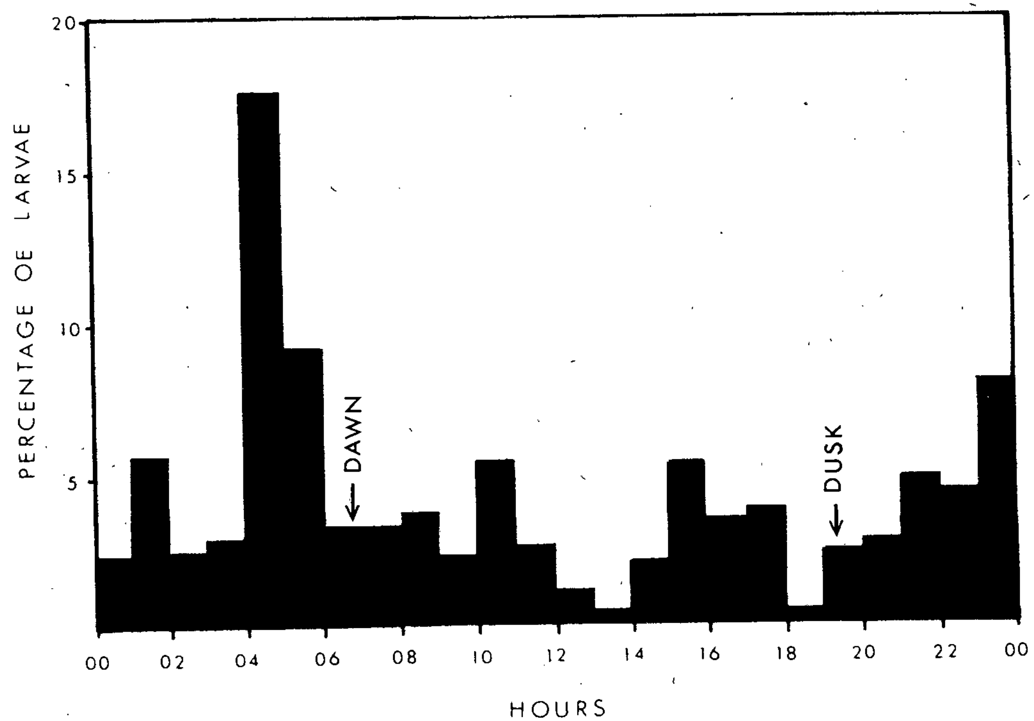


Fig. 10 Relationship between the abundance of *Sufflogobius* larvae and the time of capture (all positive hauls)

Approximately 3% of occurrences were at surface temperatures lower than 13,0°C and about I7% at temperatures greater than I8,0°C. The distribution of larvae in relation to surface temperature is shown for both surveys in Figures 7 and 9 and the larval abundance is related to surface temperature in Table VI.

TABLE VI. Relation between surface temperature and abundance of bearded goby larvae, I972 - 1974.

Surface temperature (°C)	Number of standard hauls that collected:-				
	I - 10 larvae	II - 100 larvae	IOI - 250 larvae	250+ larv.	Total
11,0 - 12,0	1	1	0	1	3
12,1 - 13,0	4	9	2	3	18
13,1 - 14,0	17	18	8	17	60
14,1 - 15,0	39	30	16	16	101
15,1 - 16,0	41	53	15	17	126
16,1 - 17,0	45	42	9	10	106
17,1 - 18,0	52	46	6	9	113
18,1 - 19,0	47	38	6	4	95
19,1 - 20,0	27	20	1	-	48
20,1 - 21,0	16	5	-	I	22
21,1 - 22,0	7	2	-	-	9

The vertical distribution of larvae was not determined during this investigation and consequently it is difficult to relate larval abundance to a particular temperature/depth range within the water column. The routine hauls only demonstrate that larvae occurred somewhere in the 0-50 m layer. A later study revealed however that larvae and juveniles occurred over a depth range of 6 - 90 m but that highest concentrations were at depths of IO - 25 m (C. d'Arcangues, University of Paris, pers. comm).

If a depth of 20 m is chosen to ~~represent~~ the zone of greatest concentration of bearded goby larvae and temperature at this level is related to larval abundance, then about 75% of all occurrences were found at temperatures between II,0° and I5,0°C (Table VII). This denotes a decrease of approximately 2 degrees compared with the surface temperature relationships. Approximately 87% of the hauls containing greater than 250 larvae per IO m^2 were taken at temperatures ranging from 11,1° to I4,0°C.

TABLE VII. Relation between water temperature at 20 metres and abundance of bearded goby larvae I972 - 1974.

Temperature at 20 m (°C)	Number of standard hauls that collected:-				
	1 - 10 larvae	11-100 larvae	101-250 larvae	250+ larvae	Total
11,1 - 12,0	20	23	23	16	82
12,1 - 13,0	54	49	37	18	158
13,1 - 14,0	42	40	27	16	125
14,1 - 15,0	30	52	12	3	97
15,1 - 16,0	29	28	2	2	61
16,1 - 17,0	22	16	1	1	40
17,1 - 18,0	14	10	1	0	25
18,1 - 19,0	12	4	0	0	I6
19,1 - 20,0	4	2	0	0	6

To test whether there are significant differences in larval abundance between temperature classes, the Kruskal-Wallis one way analysis of variance by rank (Siegel I956) was applied to the original data summarized in Tables VI and VII. Values of H^o for temperature at the surface and at 20 m were 23,54 and 22,35 respectively, both being significant at the I% level. Although the above test does not indicate which of the temperature ranges significant differences occur at, it is apparent from Tables VI and VII that the optimum thermal levels for the larvae of the bearded goby was between II,I° and I5,0°C. The lower temperature threshold is probably around IO,0°C and the upper tolerance level in the region of I8,0° to 22,0°C.

ABUNDANCE OF LARVAE IN RELATION TO SALINITY.

Larvae of the bearded goby occurred over a wide range of surface salinities from 34,85°/oo to 35,80°/oo, but approximately 80% of all the specimens were found in the low salinity coastal waters in the South over a narrow range of between 34,9I°/oo and 35,20°/oo. The relationship between larval abundance and surface salinity is shown in Table VIII.

TABLE VIII. Relation between surface salinity and abundance of bearded goby larvae I972 - I974.

Surface salinity (°/oo)	Number of standard hauls that collected:- 1 - 10 larvae	11 - 100 larvae	101 - 250 larvae	250 + larvae	Total
34,8I - 34,90	1	2	4	3	I0
34,91 - 35,00	56	54	42	I7	I69
35,01 - 35,I0	82	59	54	29	214
35,11 - 35,20	54	32	35	21	142
35,21 - 35,30	22	14	10	4	53
35,31 - 35,40	17	12	8	2	41
35,41 - 35,50	13	6	5	2	26
35,50	17	15	2	1	35

As in the case of temperature, the Kruskal-Wallis test was applied to the numbers of larvae taken per haul at the various salinity values and was found to be significantly different (H^o = 21,47; p 0,01). In general, the larvae of Sufflogobius collected in the south in spring were characteristic of poorly saline water associated with Benguela Current upwelling, whereas, those occurring in the north during summer were found at higher salinity values.

DISCUSSION.

The neritic waters off South West Africa, between latitudes I9°S and 24°S apparently supports a large population of the bearded goby, Sufflogobius bibarbatus. The seasonal distribution and size composition of the larvae suggested that spawning occurred continuously along the entire coast from July to March. Spawning was heaviest in spring months in areas of coastal upwelling south of Walvis Bay where surface temperatures and salinities varied from II,0° - 16,0°C and 34,9°/oo - 35,2°/oo. In summer, spawning decreased but occurred over a wider area, particularly north of Palgrave Point. Larvae were found mainly in regions of mixing between warm oceanic fronts and cooler coastal water. Surface temperatures and salinities in the northern area ranged from I5°-20°C and 35,2°/oo - 35,5°/oo.

It is considered unlikely that the adult population migrate 200 - 400 km northward after spring spawning to spawn again in summer. The short and limited nature of the summer spawning season, together with the environmental differences between the two breeding grounds, suggested that two populations exist within the survey area. The larger group was confined mainly to the cold low salinity coastal waters south of Cape Cross. The small summer spawning group inhabited the warmer waters further north and probably represented the northern limit of the species distribution.

The extent of the spawning grounds to the south is unknown, since the regional distribution of larvae was not completely encompassed. Nevertheless, the large numbers of recently hatched larvae frequently taken on the most southerly line of stations, implied that the spawning area extended south of Hollam's Bird Island.

Gobies are generally bottom dwellers and deposit their eggs on shells, stones and gravel. It is presumed that Sufflogobius also spawn on the bottom as no eggs were collected in the plankton hauls.

The eggs would therefore require a considerable time to hatch, since the temperature of the bottom waters in the coastal areas off South West Africa is usually low during most of the year (Stander, 1964). Complete larval development could take from 2 - 3 months depending on the temperature of the water. Juveniles apparently remain in the plankton for some time before seeking deeper layers and becoming epibenthonic. Advanced juveniles and adults captured sometimes in the nets, during spring months (O'Toole, 1976) may have resulted from eggs spawned during the previous years breeding season. The increase in spawning intensity during spring of 1973/74 suggested that conditions were more favourable than in 1972/73. However, oceanographic and biological conditions, other than temperature, may have been directly or indirectly responsible.

Caution should be exercised when explaining the large numbers of larvae and juveniles collected in the plankton. Behavioural studies on juvenile gobies in aquaria on board ship revealed that Sufflogobius is a feeble swimmer. Poor swimming ability and consequently low avoidance could result in the high capture ratio compared with juveniles of other species e.g. pilchard Sardinops ocellata, anchovy Engraulis capensis, maasbanker Trachurus trachurus and hake Merluccius capensis (O'Toole, 1974 b). The prolonged pelagic phase of late larval and juvenile stages may also result in an over-estimation of species abundance due to resampling of the population on successive cruises. Nevertheless, such an explanation would not account for the large number of smaller larvae taken in the plankton during certain months. Furthermore, the few newly hatched larvae taken in the samples indicates a possible under-estimation of abundance of young forms due to escapement through the meshes of the sampling gear. Unfortunately, an absence of earlier year's data precludes a comparison of larvae and juveniles with former years. As no previous references have been made to Sufflogobius in earlier plankton investigations off South West Africa (Hart & Currie, 1960; Matthews, 1963) it is presumed that the species has only recently become an abundant constituent of the plankton.

Since 1972, evidence of an increase in population can be substantiated by reports of occasional catches of juveniles and adults at night by purse-seine vessels fishing for pilchard. (F. Schulein, Sea Fisheries Branch, personal communication). Previous records of goby catches by pelagic fishing vessels from Walvis Bay are unknown.

It is possible that a decrease in predation may have been one of the more significant factors responsible for the apparent increase in numbers. Gobies have been known to play an important role as a source of nutrition to the higher predators in the food chain and to form a considerable proportion of the benthic biomass of bays and estuaries (Petersen,1919; Duncker, 1928; Takagi, 1960; Bhowmick, 1964; Green, 1968). Hake are also known to prey heavily on gobies in the coastal waters of South West Africa (Golovan, 1974). Between 1965 and 1972, the total annual catch of hake rose sharply from 86,000 to 568,000 metric tons in the ICSEAF divisions Cunene 1.3 and Cape Cross 1.4 (Ikeda 1975). The removal of hake in such quantities over a period of several years may have resulted in an ecological imbalance in the predator/prey relationship in favour of the bearded goby.

It is difficult to explain the large numbers of juveniles and adults frequently taken in the plankton at night-time. Barber and Haedrich (1969) suggested that juveniles were forced to the upper layers because of the low oxygen content of the bottom water off Hollam's Bird Island at the time of capture. Anaerobic conditions can often occur off the coast of South West Africa, particularly during summer months, when conditions are relatively calm and little vertical mixing takes place (Stander, 1964). Lack of oxygen, together with toxins from dinoflagellate blooms have been responsible for periodic fish mortalities in the region (Copenhagen, 1963; Pieterse and van der Post, 1967). Low oxygen values off the coast have also been associated with a temporary displacement of hake from a benthic to a mid-water habit (Cram & Schulein, 1974). In the case of <u>Sufflogobius</u>, the occurrence of juveniles and adults in the upper 50 metres, during all months, and the extensive coastal distribution (O'Toole, 1976) seems to preclude the acceptance of this theory.

Little is known, however, about the effects of low oxygen levels on the behaviour of gobioid fishes. Todd and Ebeling (1966) discovered that the large air bladder of the goby *Gillichthys mirabilis* was rich in oxygen and suggested that it could provide the fish with a source of oxygen in oligoxic waters. The fact that *Sufflogobius* can inflate its air bladder suggests that it may also be used for a similar purpose. Thus, the species could not only tolerate periodic anaerobic conditions, but would also have the added advantage of a means of avoiding predation during time spent on the bottom.

Its occurrence in the scattering layer, the marked diurnal variation in catches and the presence of certain food organisms in the stomachs suggests that *Sufflogobius* is a semipelagic neritic form with an active diurnal feed rhythm. Self inflation of the gas bladder in this instance would serve as a useful mechanism to aid ascent off the bottom in search of food in the upper layers.

Further investigations are now necessary to elucidate the ecological significance of the species in the coastal upwelling system and to test the validity of the foregoing speculations.

REFERENCES

BARBER, R.T. & HAEDRICH, R.L. (I969). Gobies associated with a scattering layer off South West Africa. Deep Sea Res. I6 (I), I05-I06.

BHOWMICK, R.M. (I966). Studies on some aspects of the biology of *Glossogobius giurus* (Hamilton) with notes on its fishery in the Hooghly estuary. Proc. Indo-Pacif. Fish. Comm II, I964, 99-I07

COPENHAGEN, W.J. (I953). The periodic mortality of fish in the Walvis region. A phenomenon within the Benguela Current. Investl Rep.Fish.mar. biol. Surv. Div. Un.S.Afr. I4, I-35.

CRAM, D.L. & SCHULEIN, F.H. (I974). Observations on surface-shoaling Cape hake off South West Africa. J. Cons. int. Explor. Mer. 35, 272-275.

d'ARCANGUES, C. (I974). Preliminary investigation into the sound scattering layer off South West Africa (February and May I974). Internal Rep. Sea Fish. Brch. S.Afr.

DUNCKER, G. (I928). Teleostei physoclisti 9. Gobiiformes. Tierwelt. N-u. Oster I2 h, I2I-I48.

GREEN, J.((I968) The biology of estuarine animals. London: Sidgwick & Jackson.

GOLOVAN, G.A. (I974). The commercial and biological characteristics of the hake (*Merluccius merluccius*) of the South East Atlantic between October I969 and January I970. Jour. of Ichthyology, I4, (4), 526-532.

HART, T.J. & R.I. CURRIE (I960). The Benguela Current. "Discovery Rep", 31 : I23-298.

IKEDA, I. (1975). On the stock of Cape hakes in division I.3 and I.4, Cunene and Cape Cross, ICSEAF Collection of Scientific Papers. 2, 54-58.

KING, D.P.F. & ROBERTSON, A.A. (1973). Methods of pelagic fish eggs and larval research in South West Africa. S.Afr. Shipp. News Fish.Ind.Rev.28 (5), 57-61.

KRAMER, D., M.J. KALIN, E.G. STEVENS, J.R. THRAILKILL & J.R. ZWEIFEL, (1972). Collecting and processing data on fish eggs and larvae in the California Current Region. NOAA Tech. Rep.CIRC 370, 38 pp.

MATTHEWS, J.P. (1963). The pilchard of South West Africa (Sardinops ocellata.) Sexual development, condition factor and reproduction. Investl Rep.mar.Res Lab. S.W.Afr. 10 : 96 pp.

MOSER, H.G. (1972). Development and geographic distribution of the rockfish, Sebastes macdonaldi (Eigenmann and Beeson, 1893), family Scorpaenidae, off Southern California and Baja California. Fishery Bulletin. U.S. NOAA National Marine Fisheries Center. 70 (3), 941-958.

O'TOOLE, M.J. (1973). Fish larvae of the Benguela Current System. Abstract. S.Afr.Nat. Oceanogr. Symp. Sea Fish. Brch.S. Afr. page 19.

O'TOOLE, M.J. (1974a). Fish larval investigations off South West Africa - summary of results. S.Afr.Shipp. News Fish. Ind. Rev. 29 (11) 53-59.

O'TOOLE, M.J. (I974b). The seasonal distribution and abundance of pilchard, anchovy, maasbanker and hake larvae off South West Africa, August I972 to March I973. Internal Rep. Sea. Fish. Brch S. Afr. I9 pages.

O'TOOLE, M.J. (I976). Incidental collections of small and juvenile fishes from egg and larval surveys off South West Africa (I972-I974). Fish. Bull. S.Afr. 8, 23-33.

PETERSEN, C.G. (I9I9). Our gobies (Gobiidae) from the egg to the adult stage. Rep.Dan. biol. Stn. 26, 47-66.

PIETERSE, F. & VAN DER POST, D.C.(I967). Oceanographical conditions associated with red-tides and fish mortalities in the Walvis Bay region. Investl Rep.mar Res. Lab. S.W.Afr. I4, I-124.

POSGAY, J.A, MARAK, R.R. & HENNEMUTH, R.C. (I968). Development and test of new zooplankton samplers. Annual Meeting Int. Comm. North west Atl. Fish. Res. (85)

SIEGEL, S. (1956). Non parametric statistics for behavioural sciences. Mc Graw - Hill, New York, 312 pp.

SMITH, J.L.B. (I956). Self inflation in gobioid fish. Nature, I77, page 714.

SMITH, J.L.B. (I969). The Sea Fishes of Southern Africa. Fifth edition. Central News Agency, South Africa.

STANDER, G.H. (I964). The Benguela Current off South West Africa. Investl Rep.mar. Res.Lab. S.W.Afr. I2, I-43.

TAKAGI, K. (I966). Distribution and ecology of the gobioid fishes in Japanese waters. J.Tokyo Univ. Fish. 52 (2) 83-127.

TAYLOR, W.R. (I967). An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natn. Mus. I22 (3596), 1-17.

TODD, E.S. & EBELING, A.W. (I966). Aerial respiration in the long jaw mudsucker *Gillichthys mirabilis* (Teleostei: Gobiidae) Biol. Bull. mar. biol. Lab., Woods Hole. I30, (2), 265-288.

VON BONDE, C. (I923). Shallow water fishes procured by the S.S. Pickle. Rep.Fish. mar. biol. Surv. Un.S.Afr.3, (I), I-40.

ECOLOGICAL INTER-RELATIONSHIPS BETWEEN THE LARVAL POPULATIONS AND WITH HYDROLOGY

INTRODUCTION

The hydrological affinities were discussed briefly for each species but the seasonal patterns observed and their influence on aspects of spawning and larval distribution and upon the inter-relationships between the species themselves was not covered.

This section thus serves to bridge the gap and in bringing in certain other theories and facts leads to a closer understanding of the ecology of the area as a whole.

Spawning Area and Seasonality

The area between Cape Frio and Hollam's Bird Island covers approximately 600 km of coastline. Within this region the commercial fish species were found to spawn in two well-defined zones which can conviently be divided into a northern sector bounded by lines I4 and 50 (Cape Frio to Cape Cross) and into a southern sector bounded by lines 52 and 90 (Cape Cross to Hollam's Bird Island). Spawning occurred in the south predominantly from spring to early summer during or shortly after periods of strong upwelling, when relatively cold low salinity Benguela Current water was widespread. In the northern sector, spawning was mostly confined to summer and autumn when tongues of warm saline oceanic or Angola Current water advanced towards the coast and mixed with the cooler coastal water. Some species spawned only in one of the two sectors while others spawned in both.

In the south, spawning was centred closer to the coast than in the northern area which tended to be more offshore. The pilchard, for example spawned continuously from late winter to mid autumn but showed two major spawning peaks. During late winter and spring, heavy egg production was noticeable inshore in the south where temperatures and salinities ranged from I4°C to I6°C and 35,10°/oo to 35,30°/oo respectively. In contrast, summer/autumn spawning was more extensive and took place in the northern off-shore waters at temperatures and salinities of I6°C to 21°C and 35,20°/oo to 35,60°/oo respectively.

Anchovy and maasbanker spawned in the northern sector from October to March/April but the main season was from summer to mid autumn. In the case of anchovy, spawning mostly occurred in a tongue of very warm, highly saline water (18°-22°C ; 35,50°/oo - 35,80°/oo)which periodically intruded from the north-west and was apparently of subtropical or Angola Current origin. However, spawning also took place, but to a lesser extent, in mixed oceanic/coastal water at intermediate temperatures and salinities (17°-21°C ; 35,31°/oo - 35,60°/oo).

In general, maasbanker spawned in the same area and under similar environmental conditions as the summer breeding pilchard population, favouring the relatively warm mixed water masses.

The hake spawning season was somewhat shorter than that of other species and occurred mainly in the southern area from October to December (mid spring to early summer). Spawning activity was centred to the west and south of Walvis Bay, the eggs and larvae being found in relatively cold low salinity water ranging from 13,0°C to 16,5°C and 34,90°/oo to 35,20°/oo. There was some evidence of hake spawning in isolated localities during summer months, especially in the north, but the number of newly hatched larvae in the plankton suggested that this was not pronounced.

The spawning location of the West Coast sole was generally confined to the south especially between Walvis Bay and Hollam's Bird Island. The period of spawning and the environment generally coincided with those of the hake. The seasonal distribution and the size composition of bearded goby larvae suggested that this species spawned continuously along the entire coast from July to March. However, the main spawning ground was centred in the south in areas of coastal upwelling, taking place during spring in waters with temperatures between 11,0°C and 16,0°C and salinities of 34,90°/oo to 35,20°/oo. The bearded goby also spawned over a wide area in the north during summer months but there was a marked decline in spawning intensity. Surface temperatures and salinities in the northern spawning area ranged from 15,0°C to 20,0°C and 35,20°/oo to 35,50°/oo respectively.

In general, the main spawning grounds of the pilchard and hake were satisfactorily encompassed during the surveys but the distribution of other larval species suggested that considerable spawning may have taken place outside the boundaries of the research area. For example, anchovy and maasbanker larvae were frequently abundant in hauls taken at the most offshore, and at the most northerly line of stations.

Similarly, West Coast sole and bearded goby larvae were abundant in the most southerly line of stations. Therefore if the spawning area of these species is to be adequately covered, sampling should be extended by at least 100 km to the north, south and off shore.

Because the survey cruises were not conducted between April and July I973 or after April I974, it is possible that some species continued to spawn into late autumn or even winter. Le Clus (I976) has shown that the South West African pilchard is a serial spawner and develops ovaries containing different size modes of yolked eggs. Spawning could therefore be extended and more batches of eggs matured and released if conditions continued to be favourable. The Pacific sardine S. caerulea is also known to mature several batches of eggs during the year and can release ova at anytime that suitable conditions arise (Mac Gregor I957). Similarly anchovy and horse mackerel species can reproduce a number of times during the year (Ratte I973, Baxter I967, Komarov, I964, Macer I974). During February/March I973 there was a general decline in the number of small pilchard and maasbanker larvae in the plankton collections, possibly indicating that the spawning season was nearing completion towards autumn. Recently hatched anchovy larvae, however, showed an increase in number suggesting that this species may have continued to spawn into autumn. In contrast, during the same period in I974, newly hatched pilchard and maasbanker larvae increased considerably both in number and distribution which indicated a possible extension of the spawning season. There is little information on fish spawning off the coast during winter months. Matthews (I963) reported that pilchard egg production in the Walvis Bay area was negligible in May and June but that spawning intensity increases gradually from July onwards to reach a peak in September and October. The seasonal occurrence and abundance of pilchard eggs (King 1975, 1977 in press) and of fish larvae during this study also suggested a gradual increase in spawning activity in the southern area from late winter. Furthermore, hydrological conditions during winter may not be altogether suitable for widespread spawning since there is usually a sharp drop in temperature associated with the intensification of upwelling.

The period August to April therefore probably covers the main breeding seasons of fish species off the South West African coast. However, it is possible that some species could spawn at any time during the year if environmental conditions were temporarily favourable.

Timing and Variation in Spawning Intensity.

The seasonal occurrence and distribution of larvae varied between years and was closely related to the onset of certain hydrological conditions. Hake spawning usually commenced with the reduction of upwelling and a gradual increase in temperature. This sequence of events differed between the two years and was reflected in the spawning patterns. In October 1972, persistent upwelling in the south caused temperatures to remain relatively low and the scarcity of newly hatched larvae in the plankton showed that little spawning took place before October. In contrast, upwelling had declined markedly between September and October 1973 resulting in higher temperatures in the spawning grounds due to influxes of warm water. Recently hatched larvae were abundant during October reflecting the earlier, more favourable conditions in 1973. Peak spawning of the hake occurred in December of both years when southward intrusions of warm (17^{o}-$18^{o}C$) water mixed with cold (14^{o}-$15^{o}C$) northward-flowing water off Walvis Bay. The main spawning season ended abruptly after December with the onset of more stable conditions and higher temperatures characteristic of summer.

The timing and intensity of anchovy,spawning was apparently influenced by intrusions of warm (18^{o}-$20^{o}C$) water into the northwest sector of the research area during summer. For example, the main spawning season commenced earlier and was more intense in 1972/73 when incursions of 18^{o} to $20^{o}C$ water were more pronounced. The earlier, heavier spawning was reflected by the greater abundance of larvae in the plankton during December 1972 compared with December 1973.

Anchovy spawning was also heavier from December I972 to February I973 when the boundary between the warm oceanic and cooler coastal water was better developed. The wider distribution of anchovy larvae both inshore and in the south during February I973 was associated with a greater south-eastward penetration of oceanic water. This suggested that a more extensive influx of I8^{o}-20^{o}C water might have increased the spawning area available to the anchovy. In addition to the horizontal distribution of warm water, the depth of the core along the oceanic side of the front seemed to influence both spawning and distribution of the larvae. Anchovy larvae were more abundant in the plankton when intrusions of I9^{o}-20^{o}C water were deeper and when greater mixing occurred in the upper 30 metres.

The main breeding season of the maasbanker coincided with the increased temperatures during summer caused by the advancement of warm water towards the coast. Spawning intensity, as evident from the abundance of larvae, was closely related to the degree of interaction between the warm and the cold water masses. During the summer of I972/73, heavy spawning in the north in December and January was synchronized with marked, vertical mixing along the well-defined boundary zone between oceanic and coastal water. Spawning was not as intense during the same period in I973/74 when mixing was less evident and the front was weaker. Maasbanker spawning was noticeably heavier and widespread during February and March/April I974 following an extensive penetration of mixed water further inshore and southward. During February and March I973, spawning was restricted more to the north when intrusions of warm water were not as pronounced.

The pilchard spawned over a longer period and within a wider range of environmental conditions than other commercial species. Spawning in late winter/spring was heavier in the south in I972 than in I973.

The variation in spawning intensity between years could not be explained from the hydrology because thermal patterns during August and September were similar for both years but other factors for instance adverse biotic conditions, could have affected the southern spawning in I973. During October and November I973, pilchard larvae were found further north than in the same months of I972 which suggested that a shift in the spawning population may have occurred, possibly caused by the wider distribution of cold coastal water to the north during the second survey period. The main spawning season of the pilchard stock in the southern sector is during a time characterised by low temperature, moderate to strong upwelling and an abundance of plankton. The fact that spawning occurred over a narrow temperature range of I4^{o} to I6^{o}C possibly indicates that temperature is the decisive parameter. Increased plankton production generated by strong upwelling may also play an important role in stimulating adult fish to spawn.

Pilchard spawning in the northern area in summer coincided with a rapid increase in temperature associated with influxes of oceanic water. During the summer and early autumn of I974 spawning was heavier than in I973 and was especially noticeable in March/April I974 when the spawning area extended further south following a southerly movement of the mixing zone.

The larvae of the bearded goby occurred over such a wide area and were collected in such considerable number during all months of the investigation that it was difficult to relate the timing and duration of spawning to any particular hydrological event.. During the second survey, larvae were almost twice as numerous in the plankton than in survey 1, indicating that spawning was more intense. There was some evidence to suggest that the earlier reduction of upwelling in the south during spring I973 may have created more favourable conditions for larval survival.

Dispersal of Larvae

The dispersal of developing fish larvae from their spawning centres was influenced to a large extent by seasonal variations in hydrological conditions and by the actual area of spawning. Water circulation of South West Africa is generally variable ans subject to considerable seasonal change depending upon the strength of the prevailing winds and upwelling. Over much of the coast, but especially in the south, upwelling is usually at its maximum in winter and spring. The flow of the Benguela Current is strongest at this time, usually moving in a northerly direction parallel to the coast. Therefore, one would expect that larvae hatched from eggs spawned in the south during late winter/spring would be carried northwards by the current. The ability to follow successive cohorts of larvae at sea is often difficult due to the time interval between sampling, continuous spawning and mortality. However, it was possible to demonstrate a northward dispersal of pilchard and West Coast sole larvae between the upwelling months of September and October 1972. The size distribution of bearded goby larvae was not analyzed between months but it is presumed that developing larvae were carried northwards since considerable spawning took place during upwelling months.

Towards the end of spring, wind strength usually decreases, upwelling weakens and oceanic water pushes southwards causing the Benguela Current to become sluggish. The main hake spawning season occurs around this period (November and December). Hake larvae showed little evidence of a northerly drift but instead were contained within the general spawning area off Walvis Bay, perhaps by eddies associated with the interaction of warm water pushing south and cold water moving north.

Upwelling generally reaches a minimum during summer and water circulation off the coast becomes variable. Intrusions of warm oceanic water inshore and southwards are evident, especially in the north. However, more complex local flow patterns may result from eddies generated at the mixing zones.

Anchovy, maasbanker and pilchard spawn in the northern region at this time, congregating further off shore to breed than the southern late winter/spring spawning species. The general trend is for developing larvae to be carried inshore and to a lesser extent southward by the invading oceanic water. For example, an inshore drift of maasbanker larvae was evident between January and February during both years. Pilchard larvae were also carried towards the coast between January and February 1974 and anchovy larvae were transported in a south-easterly direction between February and March/April 1974. Although the main direction of dispersal appeared to be inshore, developing larvae were also carried away from the coast by currents. An increase in coastal upwelling in the spawning grounds between February and March 1973 resulted in a westerly transportation of anchovy larvae and also caused spawning maasbanker to move off shore.

One would expect a westerly drift to carry developing larvae away from the productive inshore areas into increasingly warm oceanic waters where stable hydrological conditions and food scarcity could cause heavy mortalities. In contrast, inshore transportation would bring larvae into closer contact with coastal areas where more favourable biotic and abiotic conditions would be found. Nevertheless, the timing of spawning appears to be generally advantageous for larval survival since incursions of water tend to be typical hydrological features of the area during summer/autumn. Since eggs and larvae at various stages of development were frequently collected together in the same haul, spawning and larval development may take place within a broad body of water of similar characteristics. Thus, the gross movement of water masses may not only influence the dispersal of eggs and larvae but also govern the extent of the spawning area available to adult fish.

Spawning and Plankton Production Cycles

The spawning of some marine teleosts and the appearance of their larvae have frequently been reported to coincide with the period when food organisms are most plentiful in the areas in which they live. Cushing (1967) found that the herring populations in the different areas around the British Isles spawn in phase with the plankton production cycles and suggested that many of the natural changes in the abundance and distribution of fish stocks in the region were influenced by changes in plankton cycles (Cushing 1966). Bainbridge and Cooper (1973) have shown that the sudden appearance of newly hatched larvae of the blue whiting *Micromesistius poutassou* off the west of Ireland and north-west of Scotland was synchronous with the abrupt development of copepods in these areas. A similar pattern was observed by Bainbridge *et al* (1974) in which mackerel larval production was closely associated with the timing of spring plankton blooms.

Although the relative abundance and seasonality of planktonic organisms,other than fish eggs and larvae, were not studied on this occasion, it is probable that both spawning and the appearance of fish larvae off South West Africa were also linked with the timing of seasonal plankton production cycles. Since fish larvae are members of the zooplankton community, their distribution and seasonality should reflect a similar trend with the plankton in general. It may be assumed from geographic differences in distribution and timing of fish larval occurrence that there are two separate areas of high plankton production off the coast. During midwinter and spring, the coastal upwelling regions south of Cape Cross are a zone of high plankton productivity, whereas the offshore waters in the northern part of the territory are apparently rich in plankton during summer and autumn. Supporting evidence of two main areas of high plankton productivity is given by Yelizarov (1967) and Hobson (1971) who reported that greatest productivity was invariably recorded in the vicinity of Cape Frio (18°20'S) and in the south near Walvis Bay (23°S).

Temperature profiles may be used to document the mixing of warm and cold water masses and the strengthening and weakening of upwelling off the coast. Where upwelling has occurred, primary and secondary production then follows. During this process, surface water low in nutrients is transported off shore and replaced at the coast by deeper colder water rich in nutrients. After a variable period, this new surface water gradually warms up as it is displaced off shore. At some point along this progression, conditions become suitable for phytoplankton and zooplankton production which results in a high number of small plankton particles being available for newly hatched fish larvae to feed on. Since upwelling is seasonal and is most pronounced in the southern region of South West Africa in late winter/spring, one would expect that phyto and zooplankton production to be high in this area at this time. Investigations conducted within the SWAPELS area between May and November I971 confirmed that during these months plankton standing crop was greatest near the coast in the south (I. Kruger, Sea Fisheries Branch, **personal** communication). Phytoplankton and zooplankton peaks were also found to alternate between months and greatest blooms of phytoplankton occurred during July and September when upwelling was most intense. At the same time, plankton densities in the north were low but standing crop did increase significantly during November. Unteruberbacher (I964) and Kollmer (I962,1963) also reported on plankton seasonality off Walvis Bay and demonstrated that neritic plankton biomass increased considerably between winter and spring. It would therefore appear that such a time would be particularly favourable for fish to spawn in view of the increased abundance of food organisms available for feeding larvae. King and M^{c}Leod (I976) have shown that the dominant food organism of the South West African pilchard is the copepod Calanus carinatus. It is interesting to note that pilchard spawning in the south is accompanied by a significant increase in the abundance of this copepod in the plankton. (Unteruberbacher I964).

In the northern part of South West Africa, marked intrusions of oceanic and Angola Current water push inshore and southwards against the cooler coastal Benguela water during summer. This process creates a mixing or boundary zone between the water masses which can be expected to lead to an increase in primary and secondary plankton production at this time. Mixing areas between warm and cold currents are generally noted for their high biological productivity. Oceanic fronts are known to aggregate plankton and flotsam and create conditions especially favourable for growth of a higher standing crop (Knauss I957, Uda and Ishino I958, Hela and Laevastu I962). High concentrations of plankton have been reported from the boundary zone between the warm saline Oyashio current and the cold low salinity Kuroshio current (Siomina I958, Beklemishev and Burkov I958). In some cases, the standing crop of chlorophyll a and zooplankton is often higher at the zone of intermingling between two different water masses than in each separately (Siomina I958, Griffiths I963). Areas of mixing, in addition to being favourable for plankton production are also noted as centres of high pelagic fish abundance, Uda (I953, 1961) and Uda and Ishino (I958) reported that pelagic fish abundance off Japan is often closely related to the frontal system formed by the Oyashio and Kuroshio Currents. Kurc (I969) found that shoals of the sardine Sardina pilchardus were most densely aggregated at the boundary zones between warm and cold water off the Bay of Biscay. Other species such as long fin tuna and sprat also seemed to follow the same rule.

Off South West Africa, Komarov (I964) has shown that the mixing zone between the Benguela and Angola Currents support sizeable pelagic fish stocks and this study clearly demonstrates the importance of the region as a breeding area of maasbanker, anchovy and pilchard. Unfortunately there is little information on the distribution and abundance of plankton in the northern water of South West Africa especially during summer and autumn when interaction between the water masses is pronounced and widespread.

However, one would expect from the rather sudden and widespread appearance of fish larvae during this time that there was a corresponding increase in plankton biomass and abundance of food organisms in the region. The fact that patches of fish larvae were frequently aggregated along the boundary zone between water masses could suggest that food organisms were especially plentiful or suitable in these areas.

The hypothesis is put forward that the spawning in the northern and southern regions of South West Africa coincide with what is on average a period of increased plankton production in these areas. In the south, the main breeding season of fish takes place in spring/early summer at relatively cold temperatures during or shortly after periods of coastal upwelling, when the spring plankton bloom is at its peak. In contrast, fish spawning in the north occurs predominantly during summer/autumn at higher temperatures when,presumably, increased plankton biomass offshore results from the mixing of different water masses.

The influence of seasonal hydrological change on the timing of plankton production cycles in these two areas could have played an important role in the formation and separation of spawning grounds. Seasonal and regional spawning preferences by various species possibly relate to different adaptive mechanisms by the larvae to predation, starvation, food characteristics and densities. For example, higher temperatures in the northern spawning grounds probably allows the newly hatched larvae to pass more rapidly through the "critical phase" than those hatched in the colder water of the south. However, this could be due to a shorter duration, life cycle, or lower density of suitable food organisms in the plankton for the larvae to prey upon. In contrast, plankton production and density is likely to be higher and more consistent in the cooler upwelling zones and rapid growth rates through the early stages may not be as critical a factor. Some species can continue to spawn at various localities outside the main breeding period.

Such isolated spawning may be triggered by the formation of suitable hydrological conditions temporarily favourable for plankton production.

Influence of Hydrology on Spawning Area.

Changes in the quality of water masses accompanied by changes in the plankton community are known to affect adult and larval fish populations. Bainbridge and Forsyth (I972) demonstrated a relationship between a northerly shift in the spring herring population of the north western North Sea and a marked northerly distribution of the Calanus population. Hart (I974) has correlated a high larval abundance of the sand eel Ammodytes marinus in the North Sea with a greater penet penetration of Atlantic water and suggested that good environmental conditions brought about by the presence of Atlantic water and its associated plankton community could result in higher larval survival.

In this study, the seasonal distribution of some fish larvae species suggested that the gross area available to spawning adults may be linked with the horizontal and vertical distribution of certain water masses. A greater penetration of water with mixed oceanic and coastal properties in the north during summer / autumn favoured an expansion of the breeding area of pilchard and maasbanker. Conversely, a shorter more restricted spawning season seemed to result if the mixing zone was pushed further north and offshore by the the occurrence of upwelling at the coast. Anchovy spawning was mainly confined to waters with Angola Current properties. However, deeper and more widespread intrusions of this water mass could result in an expansion of its spawning area. In the south, the duration of the spawning season and extent of the spawning area of species such as hake, bearded goby and pilchard might be affected by the duration and intensity of upwelling. Substantial changes in spawning behaviour could be caused by anomalous intrusions of warm water during periods normally characterised by upwelling.

Such anomalous conditions were recorded in I963 causing dramatic changes in plankton distribution, abundance and composition (Stander and de Decker I969). During the same period, a sharp decline in pilchard spawning activity was noted together with a retardation in gonad development and a reduction in oil yields from the commercial catches.

The area over which spawning takes place can be considered as one of the more important conditions which influences the survival of a year-class (Ahlstrom I965). One could therefore argue that pilchard and maasbanker recruitment was greater from the summer/autumn spawning of I974 than I973 since there was a considerable expansion of the spawning area off the coast. Bearded goby larvae were also more widely distributed and abundant during Survey 2 which suggested that larval survival was higher compared with that of Survey I.

In the final analysis, the spawning area, success of larval survival and recruitment of fish stocks off South West Africa probably stems from the degree of seasonal hydrological changes between water masses and the resulting production and distribut= ion of plankton associated with these interactions.

Ecological Inter-Relationships between Species

Numerous factors have been attributed to disrupting the ecolog= ical balance between populations of fish species inhabiting the same environment. The rapid decline of the abundance of one species could be caused by consistently high mortalities through over-exploitation, an increase in interspecific competition, predation or a succession of poor year classes resulting from unfavourable abiotic and biotic conditions during early life. When combined, these factors would have a dramatic effect on the population as a whole. In contrast, a corresponding increase in biomass of another species may indicate a mere shift of fishing effort to that species. Alternatively, the reduction of interspecific competion, an expansion of the spawning area together with good larval survival caused by favourable hydrobiological conditions might explain the phenomenon.

Following the near collapse of the South West African pilchard fishery in I969, fear was expressed by the management that the anchovy population might increase at the expense of the pilchard. Such a species inversion has already been documented off Calif= ornia (Murphy I966) and Japan (Nakai I960) and because both pilchard and anchovy adult populations generally share the same ecological niche, it appears that the apprehension was well founded. However, the results of this study suggested that spawning pilchard and anchovy do not inhabit the same environ= ment although they probably intermingle at other times of the year. This assumption is based on the fact that the breeding areas were to a large extent geographically separate and that the larvae of both species were rarely taken together in the samples. Peak spawning also occurred over different temperature ranges and in water masses of different characteristics. It would therefore appear that competition between anchovy and pilchard is not a significant factor during the vulnerable larval period but it is possible that this increases considerably when juveniles and adult shoals later intermingle. Furthermore, since the pilchard spawn over such a wide area and temperature range it may be con= cluded that the species has an added advantage over the anchovy in the environment.

The inter-relationship between the pilchard and other species, however, may be more complicated. In the northern part of South West Africa, the spawning season and area of pilchard and maasbanker was identical with the larvae of both species occurring together in considerable numbers. Arthur (1976) showed that the diet of recently hatched larvae of jackmackerel _T. symmetricus_ and sardine _S. caerulea_ differed with the former feeding predominately on copepod adults and the latter on copepod eggs and nauplii. However as the length of the larvae increased, the size range of the food particles ingested were comparable. This is thought to be due to the fact that small jack mackerel larvae have a larger mouth which enables it to feed on particles of a greater size. Feeding incidence of jack mackerel larvae was also found to be higher with increased growth which may indicate a more voracious feeding habit than sardine larvae. The diet of pilchard and maasbanker larvae have not been compared off South West Africa but their frequent co-occurrence in hauls does suggest that competition may be intense at least during certain stages of larval development.

Juvenile and adult maasbanker are known to prey on a variety of organisms including small fish and larvae and juvenile stages of pilchard have been recorded from the stomachs of large maasbanker from South West Africa (P.McLeod, Sea Fisheries Branch, unpublished data). It is therefore possible that in addition to competition during the larval phase, developing pilchard larvae may be also subject to heavy predation by maasbanker shoals congregated in the spawning area.

In the southern area, the main spawning season of pilchard and bearded goby takes place in spring with the larvae frequently occurring together in the same hauls. However, larvae of the bearded goby were exceedingly numerous and in some cases outnumbered those of the pilchard by over 300 to 1. Possible reasons for the apparent numerical dominance of this species could be due to a lower avoidance reaction to the sampling gear. This may be the case with larger sized specimens but it would not explain the high proportion of newly hatched bearded goby in relation to pilchard larvae. An underestimation of newly hatched pilchard larvae could be caused by extrusion but this would also presumably affect recently hatched bearded goby larvae. The fact that larvae of the bearded goby were more numerous that other species in the plankton is difficult to concieve, especially when taking into account the large biomass and relatively high fecundity of pilchard and hake. Whether the larval population was always as abundant is not known in the absence of comparable data. It is possible that the species was a prolific in former years but it is strange that no mention has been made of its occurence in the region by other plankton investigators e.g. Hart and Currie (1960), Hart and Marshall (1951) and

Matthews (1963). Some evidence to suggest an increase in biomass is provided by reports on the recent appearance of the species for the first time in the commercial purse-seine catches off Walvis Bay. If there has been a change in population abundance in the last few years it could be related to the pilchard and hake fishery. The stocks of both species have been intensively exploited by local and international fishing fleets over the past ten years and the populations now appear to be declining. Golovan (1974) has shown that gobies are an important diet of the hake in the coastal waters of South West Africa. In the larval stage, pilchard may also be regarded as potential competitions with those of the bearded goby. Theoretically, therefore, it could be argued that the heavy mortalities among these stocks had an impact on the ecosystem which might have allowed the expansion of the bearded goby population through the removal of large quantities of predators and competitors.

LITERATURE CITED

AHLSTROM, E.H. 1965 A review of the effects of the environment on the Pacific sardine. ICNAF, Spec. Publ. (6), 53-74.

ARTHUR, D.K. 1976 Food and feeding of larvae of three fishes occurring in the California Current, Sardinops sagax, Engraulis mordax and Trachurus symmetricus. Fish. Bull. U.S. 74, (3), 517-530

BAINBRIDGE, V. AND COOPER, G.A. 1973 The distribution and abundance of the larvae of the blue whiting Micromesistius poutassou (Risso) in the northeast Atlantic, I948-1970. Bull Mar. Ecol. 8, (2) : 99 - 114.

BAINBRIDGE, V. AND D.C.T. FORSYTH 1972 An ecological survey of a Scottish herring fishery Part V: The plankton of the northwestern North Sea in relation to the physical environment and the distribution of herring. Bull. Mar. Ecol., 8 , 21 - 52.

BAINBRIDGE, V., G.A. COOPER AND P.J.B. HART. 1974 Seasonal fluctuations in abundance of the larvae of mackerel and herring in the northeastern Atlantic and North Sea. Reprint from "The early life history of fish" (Ed.J.H.S.Blaxter), Springer-Verlag, Berlin.

BAXTER, J.L. 1967 Summary of biological information on the northern anchovy Engraulis mordax Girard. Rep. Calif. co-op oceanic Fish. Invest. II : 110 - 116.

BEKLEMISHEV, K.V. AND V.A. BURKOV. 1958 Relationship between plankton and water masses in the frontal region in the Northwest Pacific. Akademiia Nauk SSSR, Trudy Instituta Okeanologii Tom 27, 55-65

CUSHING, D.H. 1966 Biological and hydrographic changes in British seas during the last thirty years. Biol. Rev., 41, 221 - 258.

CUSHING, D.H. 1967 The grouping of herring populations, J. mar. biol. Ass. U.K. 47 : 193-208.

GOLOVAN, G.A. 1974 The commercial and biological characteristics of the hake (Merluccius merluccius) of the South East Atlantic between October I969 and January I970. Jour. of Ichthyology, 14 , (4) 526-532.

GRIFFITHS, R.C. 1963 Studies of oceanic fronts in the mouth of the Gulf of California, an area of tuna migration. FAO Fish. Rep. 6 , (3) : 1583-1609.

HART, P.J.B. 1974 The distribution and long term changes in abundance of larval Ammodytes marinus (Raitt) in the North Sea. Reprint from "The early life history of fish" (Ed.J.H.S.Blaxter), Springer-Verlag, Berlin.

HART, J.J. AND R.I. CURRIE	1960	The Benguela Current. "Discovery" Rep. 31 : I23 - 298.
HART, T.J. AND MARSHALL N.B.	1951	Breeding ground of pilchards off the coast of South West Africa. Nature, Lond. I68 : p.272
HELA, I AND A. LAEVASTU	1962	Fisheries Hydrology. Fishing News (Books) Ltd., London 137 p.
HOBSON, L.A.	1971	Relationships between particulate organic carbon and micro-organisms in upwelled areas off South West Africa. Investigacion pesq. 35,(1):195-208.
KING, D.P.F.	1975	Influence of salinity,temperature and dissolved oxygen on embryonic development of the South West African pilchard, Sardinops ocellata. Msc thesis, Univ. of Stellenbosch, South Africa.
KING, D.P.F.	1977 in press	The distribution and abundance of eggs of the South West African pilchard (Sardinops ocellata)and anchovy (Engraulis capensis), I971-1972. Fish. Bull. S. Afr. 9.
KING, D.P.F. AND P.R. Mc LEOD	1976	Comparison of the food and filtering mechanism of pilchard, Sardinops ocellata and anchovy, Engraulis capensis off South West Africa I971-72. Investl. Rep. Sea Fish. S.Afr. III , 29 pp.

KOLLMER, W.E. 1962 The pilchard of South West Africa (_Sardinops ocellata Pappe_) The annual cycle of phytoplankton in the waters off Walvis Bay, 1958. _Investl. Rep. Mar. Res. Lab.S.W. Afr._ 4 : I - 44.

KOLLMER, W.E. 1963 The pilchard of South West Africa (_Sardinops ocellata_ Pappe). Notes on zooplankton and phytoplankton collections made off Walvis Bay. _Investl Rep. Mar. Res. Lab. S.W. Afr._ 8 : I-78.

KOMAROV, Y.A. 1964 Some data on the reproduction of the horse mackerel _Trachurus trachurus_ L. from the South West African coast. Translated from the Russian. _Trudy AtlantNIRO, t.xi_ ; 87 - 99.

KNAUSS, J.A. 1957 An observation of an oceanic front. _Tellus_, 9, (2) : 234 - 237.

KURC, G. 1969 La biologie et la peche des sardines en relation avec l'hydrologie. _Science et Peche, Bull. Inst. Peches marit._, (I78), 1-14.

LE CLUS, F. 1976 Fecundity of the South West African pilchard, _Sardinops ocellata_. _Msc. thesis, Univ. of Stellenbosch_, South Africa.

MACER, C.T. 1974 The reproductive biology of the horse mackerel _Trachurus trachurus_ L. in the North Sea and English Channel. _Jour. Fish. Biol._ 6,(3), 415-438.

MAC GREGOR, J.S. 1957 Fecundity of the Pacific sardine (Sardinops caerulea). Fish. Bull. U.S. (121), 427 - 449

MATTHEWS, J.P. 1963 The pilchard of South West Africa Sexual development, condition factor and reproduction. Investl. Rep. mar. Res. Lab. S.W. Afr. 10: 96pp

MURPHY, G.I. 1966 Population biology of the Pacific sardine (Sardinops caerulea) Proc. Calif. Acad. Sci. 34, (1); 84 pp.

NAKAI, Z. 1960 Changes in the population and catch of the Far East sardine area. Proceedings of the world scientific meeting on the biology of sardines and related species, Food and Agricultural Organization of the United Nations, Rome, 3: 807 - 853.

RATTE, T.W. 1973 Biology of the anchovy, E. capensis in South West African waters. Cape Cross Report, phase III, Sea Fisheries, South Africa 9pp

SIOMINA, G.I. 1958 Relation between phytogeographic zones in the pelagial northwestern part of the Pacific Ocean with the distribution of water masses in the region. Akademiia Nauk SSSR Trudy Instituta Okeanologii, tom 27, 66 - 76.

STANDER, G.H. AND A.H.B. DE DECKER. 1969 Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963. Investl. Rep. Div. Sea.Fish. S.Afr. 81 : 1-46.

UDA, M. 1953 On convergence and divergence in the N W Pacific in relation to fishing grounds and productivity. Bull. Jap.Soc. Sci. Fish. 19 , (4) : 435 - 438.

UDA, M. 1961 Fisheries oceanography in Japan, especially on the principals of fish distribution, concentration, dispersal and fluctuation. Rep. Calif. Coop. oceanic Fish. Invest. 8 25 - 31.

UDA, M. AND M. ISHINO. 1958 Enrichment patterns resulting from eddy systems in relation to fishing grounds. Journal of the Tokyo University of Fisheries, 44 , (1-2) :105-129.

YELIZAROV, A.A. 1967 Some results of oceanic research in fisheries areas off Southwest Africa. Oceanology, 7 (3) : 344 - 347.

VOLUME 72 PART 7 JANUARY 1977 ISSN 0303-2515

ANNALS OF THE SOUTH AFRICAN MUSEUM

SEMPER ALIQUID NOVI AFRICA AFFERT

CAPE TOWN

INSTRUCTIONS TO AUTHORS

1. MATERIAL should be original and not published elsewhere, in whole or in part. When accepted, copyright becomes the property of the Trustees of the South African Museum.

2. LAYOUT should be as follows:

(a) *Centred masthead to consist of*
Title: informative but concise, without abbreviations and not including the names of new genera or species
Author's(s') name(s)
Address(es) of author(s) (institution where work was carried out)
Number of illustrations (figures, enumerated maps and tables, in this order)
(b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
(c) *Table of contents* giving hierarchy of headings and subheadings
(d) *Introduction*
(e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
(f) *Summary*, if paper is lengthy
(g) *Acknowledgements*
(h) *References*
(i) *Abbreviations*, where these are numerous

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

4. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including legend); the reduction or enlargement required should be indicated; originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the legend; if the latter, then the final reduction or enlargement should be taken into consideration.

All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

The number of the figure should be lightly marked in pencil on the back of each illustration.

5. REFERENCES cited in text and synonymies should all be included in the list at the end of the paper, using the Harvard System (*ibid.*, *idem*, *loc. cit.*, *op. cit.* are not acceptable):

(a) Author's name and year of publication given in text, e.g.:

'Smith (1969) describes . . .'
'Smith (1969: 36, fig. 16) describes . . .'
'As described (Smith 1969*a*, 1969*b*; Jones 1971)'
'As described (Haughton & Broom 1927) . . .'
'As described (Haughton *et al.* 1927) . . .'

Note: no comma separating name and year
pagination indicated by colon, not p.
names of joint authors connected by ampersand
et al. in text for more than two joint authors, but names of all authors given in list of references.

(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year, e.g. Smith (1969*a*, 1969*b*) and not Smith (1969, 1969*a*).

For books give title in italics, edition, volume number, place of publication, publisher.
For journal article give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals*. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination (first and last pages of article).

Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

ANNALS OF THE SOUTH AFRICAN MUSEUM

ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume **72** Band
January **1977** Januarie
Part **7** Deel

LARVAL DEVELOPMENT OF *SARDINOPS OCELLATA* (PISCES : CLUPEIDAE)

By

ELIZABETH LOUW

&

M. J. O'TOOLE

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad

OUT OF PRINT/UIT DRUK

1, 2(1, 3, 5–8), 3(1–2, 4–5, 8, t.–p.i.), 5(1–3, 5, 7–9),
6(1, t.–p.i.), 7(1–4), 8, 9(1–2), 10(1),
11(1–2, 5, 7, t.–p.i.), 15(4, 5), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R2,50

ISBN 0 949940 99 2

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

LARVAL DEVELOPMENT OF *SARDINOPS OCELLATA* (PISCES: CLUPEIDAE)

By

ELIZABETH LOUW

South African Museum, Cape Town

&

M. J. O'TOOLE

*Sea Fisheries Branch, Walvis Bay**

(With 11 figures and 3 tables)

[*MS. accepted 23 August 1976*]

ABSTRACT

The development of yolk-sac, larval and metamorphic stages of *Sardinops ocellata* (Pappe) are described, together with notes on the transition to juveniles. Emphasis is placed on changes in body proportions, pigmentation, fin development and fin position relative to myotomes during development.

CONTENTS

INTRODUCTION

The pilchard or sardine, *Sardinops ocellata* (Pappe), has for about 30 years been of considerable importance to the commercial fisheries off the western Cape and South West African coasts. Research on the biology of this species has continued since its initiation by D. H. Davies in the 1950s. This research has been intensified since September 1970 with the commencement of the Cape

*Present address: Sea Fisheries Branch, Cape Town.

Ann. S. Afr. Mus. 72 (7), 1976: 125–145, 11 figs, 3 tables.

Cross Programme (Cram & Visser 1972) which was instigated by the decline of the South West African pelagic fishing industry in 1968. The South West African Pelagic Egg and Larval Survey (SWAPELS), forming part of the Cape Cross Programme, was started in September 1972. The purpose of this SWAPELS programme was that of stock assessment of the pilchard and anchovy by means of an intensive quantitative egg and larva survey off the South West African coast. A prerequisite of this type of work is accurate identification of the larvae concerned, based on adequate descriptions of the larvae at all stages of their development so that pilchard and anchovy larvae can be readily distinguished from one another, and also from any other clupeid-type larvae which may occur in the area. It has thus been decided to present detailed descriptions of the development of the pilchard, *Sardinops ocellata*, and the anchovy, *Engraulis capensis*, as and when sufficient larval material of the two species becomes available. In addition, in western Cape waters, the larvae of the red-eye sardine, *Etrumeus teres*, are found in considerable numbers, and their similarity to the larvae of *Sardinops ocellata* and *Engraulis capensis* necessitates a detailed description of the larvae of *Etrumeus teres*. At present, however, the available material lacks certain stages of *Engraulis capensis* and *Etrumeus teres*. Consequently the present paper deals only with the development of *Sardinops ocellata*.

Some confusion exists in the taxonomy of *Sardinops* Hubbs, which is generally accepted as comprising five species, viz. *S. caerulea* (California), *S. sagax* (South America), *S. neopilchardus* (New Zealand and Australia), *S. melanosticta* (Japan) and *S. ocellata* (southern Africa). This distinction is followed for the purposes of this paper, although the authors are aware of Svetovidov's (1952: 193) classification which places all these as sub-species of *Sardinops sagax*.

Because of their importance in the commercial fisheries of the world, considerable interest has been shown in the biology of these species, including studies of their egg and larval development. Scofield (1934), Ahlstrom (1943) and Miller (1952) have considered the development of *S. caerulea*; Uchida (1958) described the eggs, larvae and juvenile stages of *S. melanosticta*; Baker (1972) included the eggs and larval stages in his study of the biology of *S. neopilchardus*; Hart & Marshall (1951) recorded larvae of *S. ocellata* off the South West African coast and Davies (1954) described the eggs and larvae of this species from Cape waters.

Davies (1954) obtained the early larval stages of *S. ocellata* by hatching fertilized eggs collected in plankton nets, and later stages directly from plankton samples. He pointed out that the most important diagnostic feature of the larvae is the characteristic pigmentation and described briefly the yolk-sac, larval and juvenile stages mainly in respect of their pigment pattern and the development of the fins. As has already been pointed out, it was found necessary to describe the development in greater detail to ensure reliable identification and separation from the larvae of *Engraulis capensis* and *Etrumeus teres*.

MATERIAL AND METHODS

Figure 1 shows the area off the South West African coast where pilchard larvae were collected between August and December 1972, at the start of the SWAPELS programme. Material was obtained by the R.S. *Sardinops* of the Sea Fisheries Branch, in monthly plankton samples at fixed stations between Cape Frio and Hollam's Bird Island. A detailed description of SWAPELS methods is given by King & Robertson (1973). Bongo nets of 57 cm and 18 cm diameters, with mesh sizes of 0,940 mm and 0,300 mm respectively, were fished in oblique tows from the surface to a depth of 50 metres at each station. Pilchard larvae sorted from the plankton were preserved in 5 per cent formalin. Yolk-sac larvae were not obtained in the plankton hauls, but information regarding these early stages was obtained by hatching, in the laboratory, fertilized pilchard eggs taken at sea and identified from the descriptions of *Sardinops* eggs (Davies 1954; Baker 1972). The larvae reared in the laboratory did not survive beyond the yolk-sac stage.

A total of 164 larval and juvenile specimens from the study area were examined in detail for pigmentation, fin development, fin position relative to myotomes (and relative to vertebrae in metamorphosing and early juvenile specimens) and changes in body proportions during development. Juvenile material was supplemented by specimens from Cape waters in order to document the development of scale cover.

In each specimen fin rays were counted and, in addition, the total number of myotomes, the number of myotomes from cleithrum to pelvic fin, cleithrum to dorsal fin, cleithrum to anal fin and end of dorsal fin to the origin of the anal fin were determined. Myotome counts were made from the first complete myotome behind the cleithrum to the myotome immediately preceding the fin concerned, this being taken at the extreme dorsal portion of the myotome in the case of the dorsal fin and the extreme ventral portion in the case of the anal and pelvic fins. However, since most earlier studies on clupeid larvae (e.g. Ford 1930) cleared larval specimens and stained bones using alizarin in order to relate fin position to vertebrae, 24 specimens between 18,8 mm s.l. and 38,58 mm s.l. were cleared and stained (Hollister 1934) so that fin movements at metamorphosis in *S. ocellata* could be compared with the changes described for other species during this stage of development.

Measurements of head length, eye diameter, snout length, body depth (at the base of the pectoral fin) and lengths to dorsal, anal and pelvic fins were related to standard length. In considering metamorphosis of the larvae it was found that measurements from snout to dorsal and anal fins (as used by Lebour 1921 and Baker 1972) did not reflect clearly the changes in fin position evident in myotome (and vertebral) counts. This was found to be attributable to the increased rate of head growth and therefore measurements between the cleithrum and dorsal fin and cleithrum and anal fin were used instead. The measurements in the figures refer to standard length.

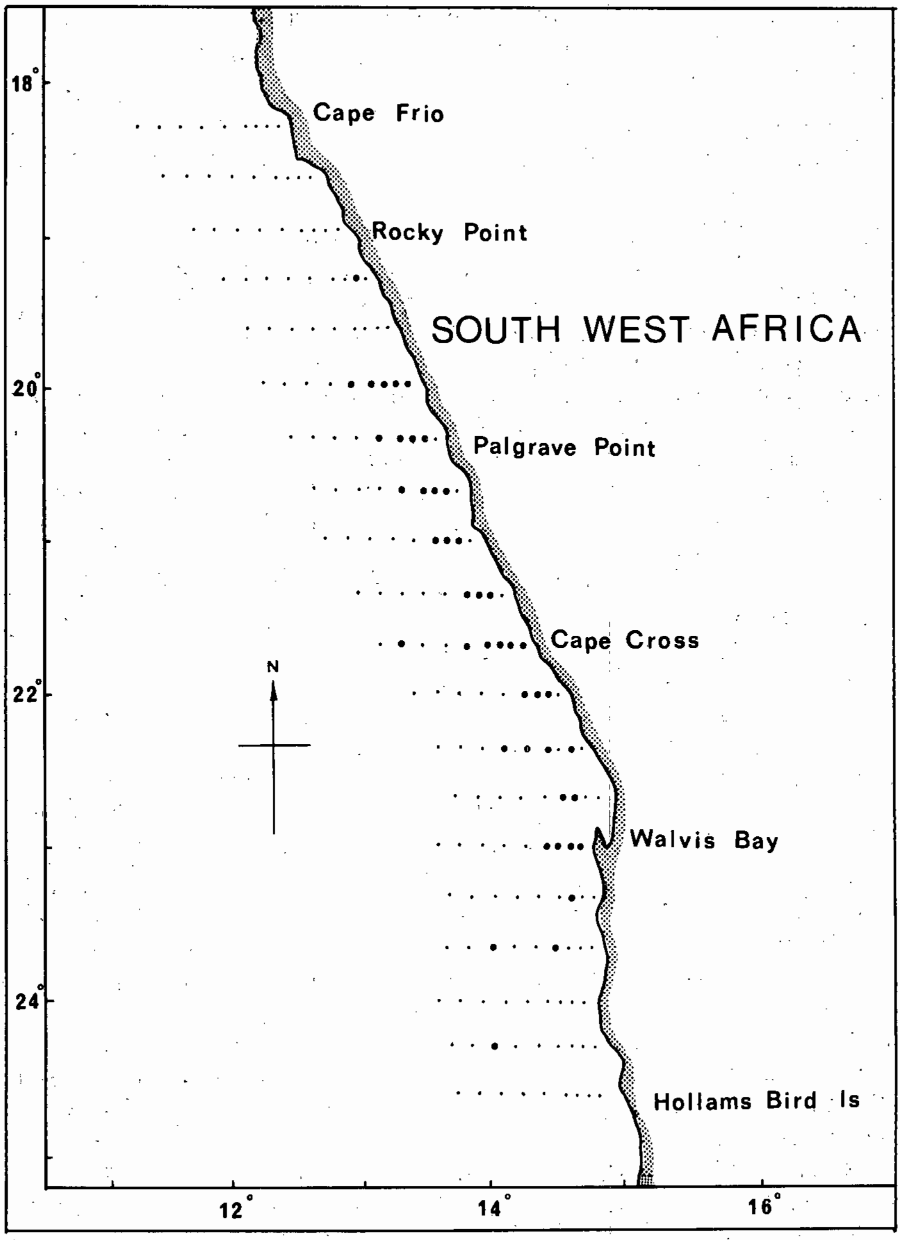


Fig. 1. Map of South West African coast, showing the grid (small dots) of the SWAPELS programme. Large dots indicate stations at which *Sardinops ocellata* larvae were obtained.

GENERAL DESCRIPTION

Sardinops ocellata larvae pass through three stages of development after hatching and before attaining the juvenile stage. These stages are the yolk-sac stage which may be regarded as a continuation of embryonic development subsequent to hatching; the larval stage; and the metamorphic stage when the larvae undergo changes and begin to acquire characteristics of the adult. The juvenile stage is that in which the fish possess all the basic adult characteristics.

YOLK-SAC STAGE LARVAE (Figs 2–3)

The newly hatched larvae of *S. ocellata* are 2,75–2,95 mm in length. The head, with unpigmented eyes and undeveloped mouth, is flexed downward over the prominent yolk-sac. This yolk-sac is segmented and has a single spherical oil globule which is posterior in position. Both yolk-sac and oil globule are devoid of pigmentation. The yolk-sac measures 0,8 × 0,6 mm in the newly hatched stages but diminishes in size with utilization of the yolk material. The dorsal, caudal and anal fin folds are broad and continuous at this stage, and the anus is situated closer to the posterior end of the body than to the head. The distance from snout to anus is 82–87 per cent of notochordal length in newly hatched larvae.

Even in newly hatched larvae most myotomes (44–47) are clearly defined and only the most posterior ones are not very distinct. The end of the vertebral column is straight. Pigmentation in newly hatched *S. ocellata* is typical of *Sardinops*, and indeed of most clupeid larvae (Lebour 1921; Miller 1952; Orton 1953; Baker 1972) in that it consists of a few scattered melanophores on the dorsal surface of the head and a row of expanded, finely branched melanophores on either side of the dorsal fin fold (Fig. 2A). During the period of utilization of the yolk-sac this dorsal pigmentation migrates ventrally as illustrated in Figure 2B. The melanophores in the posterior part of the body are the first to complete the ventral migration (Fig. 3A), and this trend continues anteriorly until all the melanophores, except those on the head, have attained the ventral position (Fig. 3B).

Soon after the end of pigment migration the arrangement of the melanophores is as follows:

(i) a few scattered melanophores on the dorsal surface of the head;
(ii) a single large melanophore at the base of the pectoral fin;
(iii) two (or occasionally three) elongated melanophores mid-ventrally, anterior to the pectoral fin;
(iv) six to seven pairs of slightly elongated melanophores along the dorsal edge of the anterior half of the gut, i.e. along the ventral edges of the myotomes, on either side of the body;
(v) a double row of four to five alternating pairs of elongate melanophores along the ventral surface of the gut, extending from the position of the swim-bladder posteriorly, to the anus.

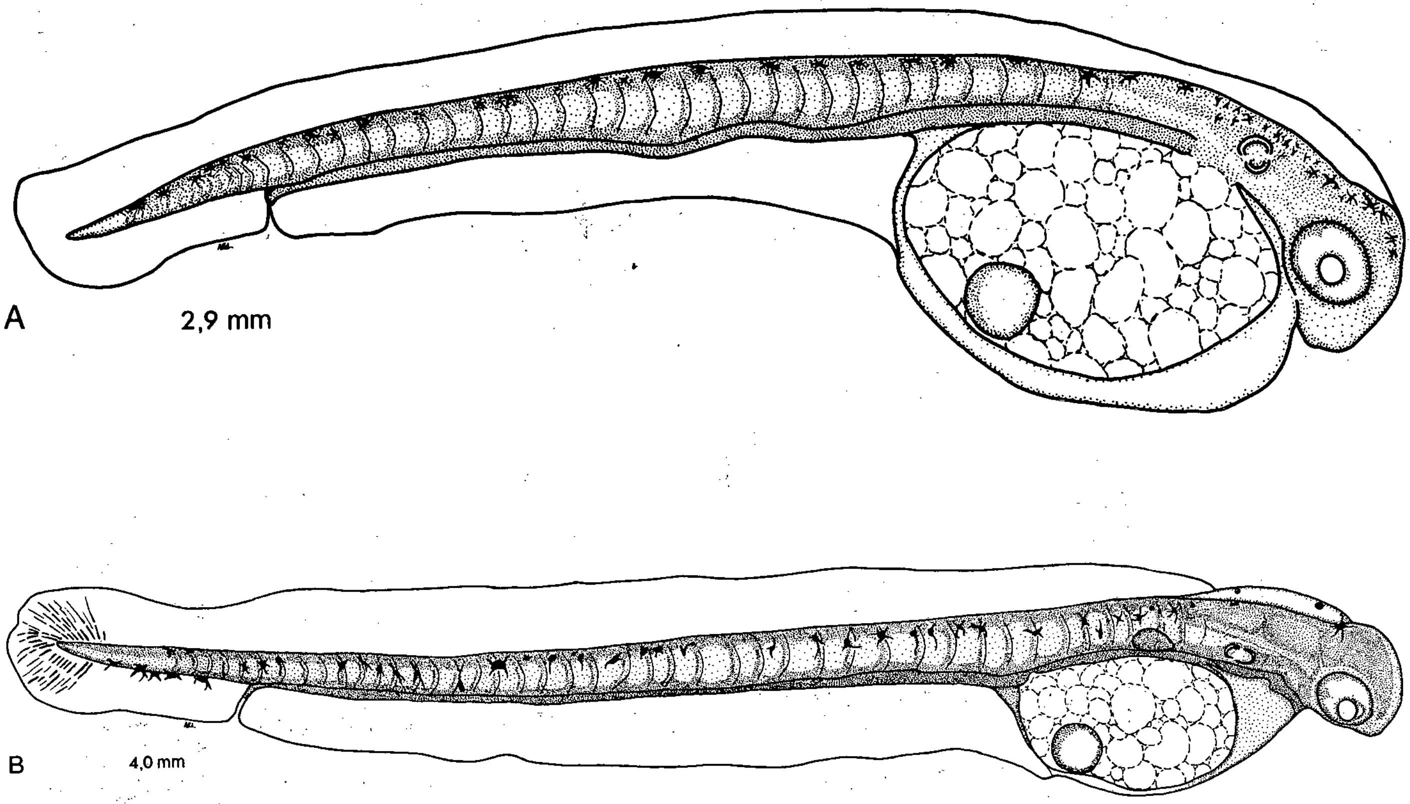


Fig. 2. Yolk-sac stage larvae. A. Newly hatched yolk-sac stage showing dorsal pigmentation. B. More advanced yolk-sac stage (2–3 days old) with pigment migrating ventrally.

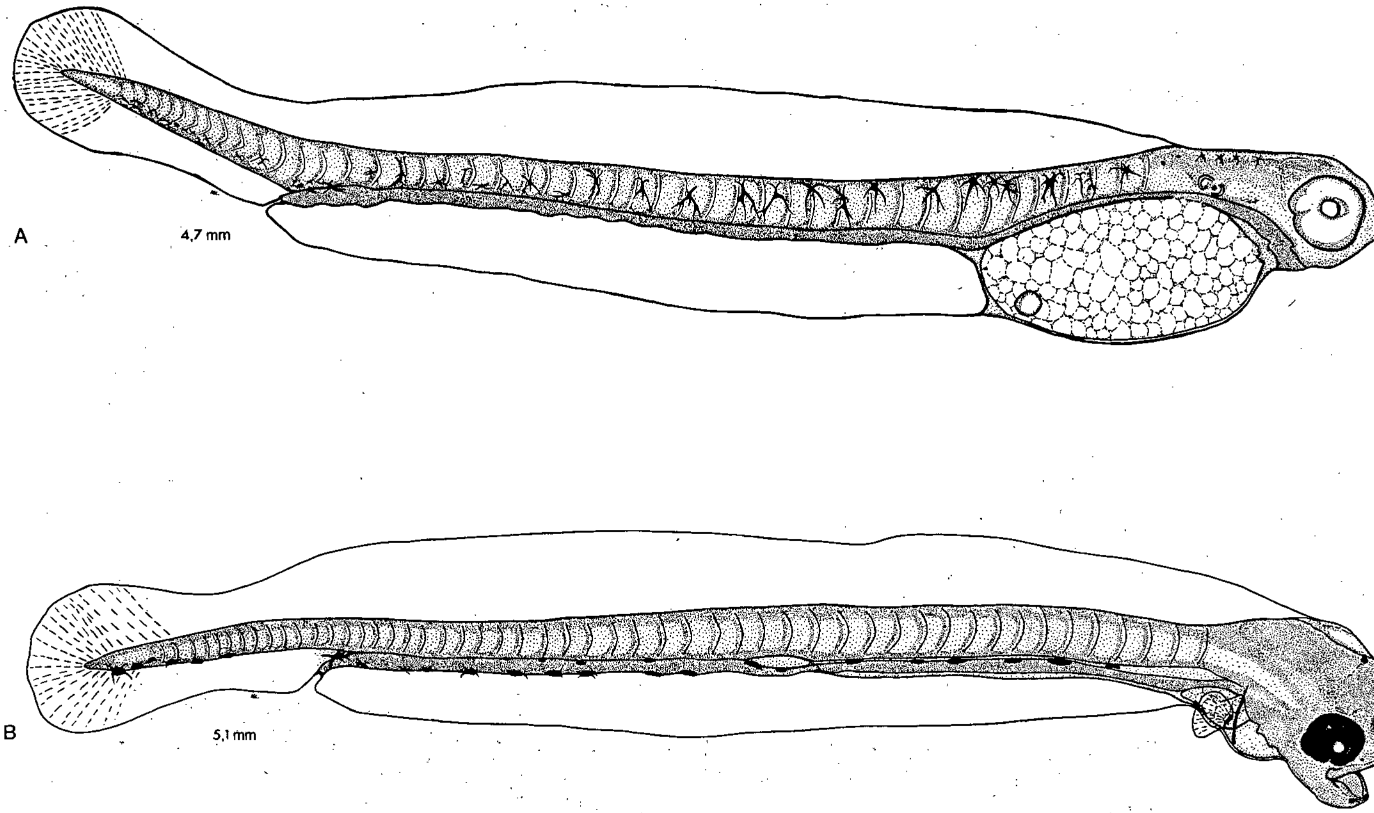


Fig. 3. Yolk-sac stage larvae. A. Stage with pigment migration well advanced (3–4 days). B. End of yolk-sac stage (5–6 days) with pigment migration complete and eye pigmented.

(vi) a few (4–5) small melanophores along the ventral edge of the myotomes, above the posterior part of the gut (these melanophores are not superficial, but visible through the muscle tissue of the myotomes);

(vii) a single very prominent melanophore on the dorsal part of the gut, in the position where the gut curves ventrally to the anus; and

(viii) two groups of melanophores situated mid-ventrally along the tail region of the body, 4–5 lying just dorsal to the base of the anal fin (once this is developed) and 5–7 close to the tip of the tail and associated with the caudal lepidotrichia once these are formed.

A small pectoral bud develops in larvae of about three days and length 4,0 mm and the first pigmentation of the eye commences a little later, at 5,0 mm notochordal length (n.l.). By the time of completion of pigment migration (6-day-old larvae, 5,1 mm n.l.) the yolk-sac is almost entirely used up and the head is no longer flexed. Up to this stage the gut is simple, comprising a long narrow tube which, towards the end of the yolk-sac stage, becomes slightly wider over its posterior half. Mid-way along the gut and in the position of the 17th–18th myotomes a small inconspicuous swim-bladder is formed.

The pectoral fins also show a slight further development by the end of the yolk-sac stage in that they are no longer only minute buds but have well-formed blades. The dorsal, caudal and ventral fin folds are still fairly broad and continuous at this stage, with a slight constriction just before the caudal region, especially in the dorsal fin fold. The caudal fin fold is the only region to have developed lepidotrichia at this stage. At the end of the yolk-sac stage all myotomes are visible and number between 48 and 50, with 38 to 40 myotomes preceding the anus.

LARVAE (Fig. 4)

The end of yolk-sac utilization marks the beginning of a period of larval development (5,5 mm n.l.–22 mm s.l.) during which the major changes taking place are in body shape and gradual fin formation. The body becomes elongated, the larvae having a characteristic very slender appearance. The continuous fin fold which was broad during the yolk-sac stage diminishes progressively and has marked constrictions before the caudal region. The ventral fin fold, anterior to the anus, becomes obliterated with the increased development of the gut, presumably coincidental with the commencement of feeding in the larvae.

The gut is narrow and straight in the anterior region, curving slightly ventrally for a short distance in the mid-body region, below the swim-bladder. Posterior to the swim-bladder the gut is wider in diameter and the wall is thicker than in the anterior part. Some authors (e.g. Baker 1972) have described this posterior region of the gut as a convoluted tube. Examination and dissection of the gut in this region have shown, however, that in *S. ocellata* the gut is in fact a straight tube with the wall slightly constricted at close and regular intervals. Corresponding to these constrictions are thickened areas of the wall which protrude into the lumen of the gut. These projections presumably form what

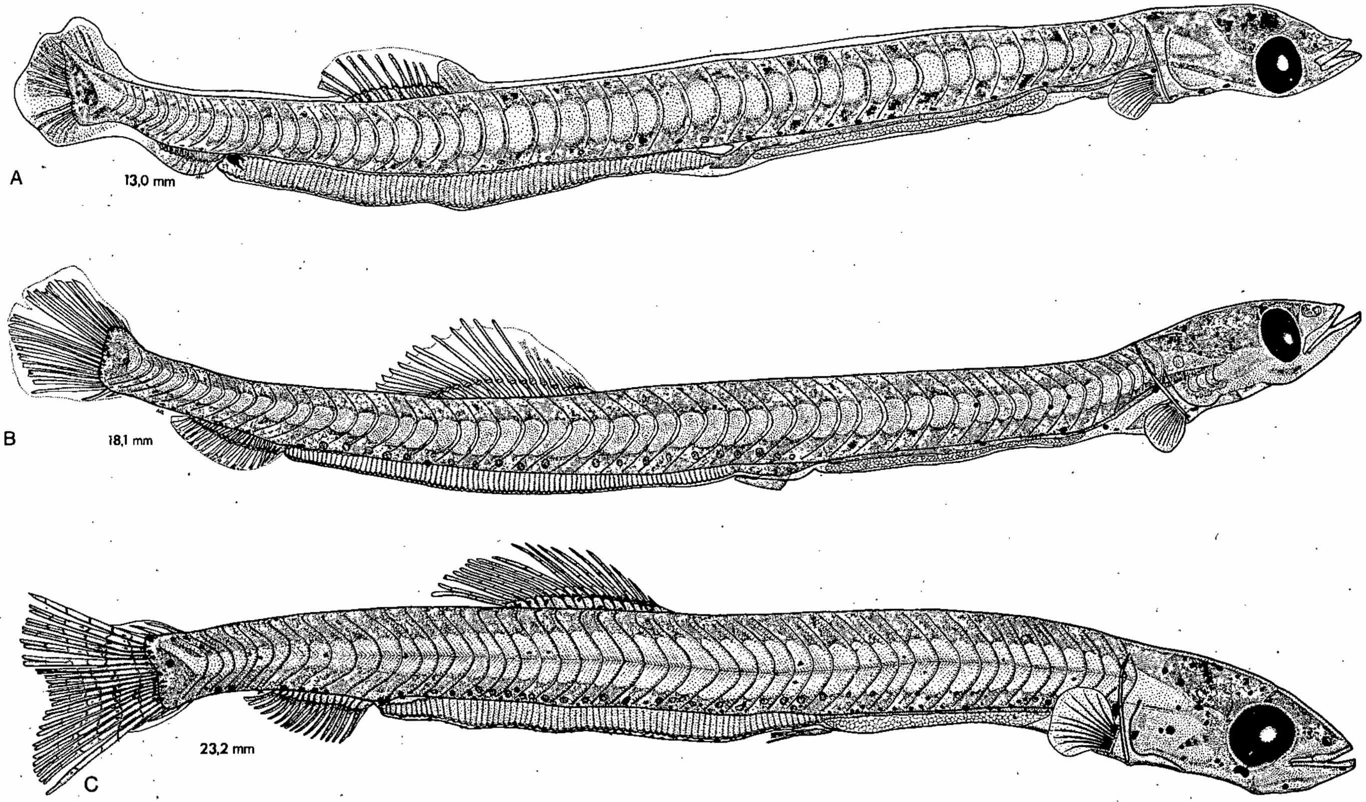


Fig. 4. Larval stages. A. Early phases of fin development. B. Fin development well advanced and bud of pelvic fin present. C. Fin development almost complete (except for pectoral fin rays); also increased amount of pigment present on head and body and myotomes extending slightly ventrally over the gut.

D'Ancona (1931) referred to as the spiral valve of the posterior intestine of larval clupeids. These thickened areas give the gut a striated appearance which we believe has led some authors to regard the gut as convoluted.

In larvae of *S. ocellata* the head is slightly elongated and the snout pointed. This snout is 3,5–4,6 per cent standard length (s.l.) and slightly longer than the diameter of the eye. The post-orbital distance (posterior edge of the eye to the cleithrum) is greater than the snout length. The bones of the head (not described here in any detail) are thin and the lobes of the brain are clearly visible through them. The jaws are well formed from an early stage (5–6 mm n.l.) and in larvae from about 15 mm s.l. the maxilla reaches to the anterior third of the eye. A pair of nostrils, with a complex internal structure, is clearly visible in larval stages and becomes increasingly developed through to the juvenile stage.

Flexion of the notochord occurs between 7,4 mm n.l. and 11,3 mm s.l. Fin development progresses fairly rapidly in the larvae from about 9,0 mm s.l., when the first rays appear in the dorsal fin fold followed by the first caudal rays at 10,5 mm s.l. and the first anal rays at 11,5 mm s.l. Prior to this only lepidotrichia were present in the unpaired fins and in the pectorals. The latter, however, do not advance beyond this condition, apart from an increase in size, until late in larval life. Subsequent development of the dorsal and anal fins proceeds apace until 16–17 rays are present in each fin prior to the commencement of metamorphosis of the larvae at 22 mm s.l. Additional rays ossify in the anterior regions of these fins during metamorphosis so that the full complement of dorsal rays (18–20) is reached by 26 mm s.l. and the anal is complete with 18–20 rays by 29 mm s.l. The last dorsal and anal rays are double from about 19 mm s.l., and, in addition, the second last anal ray is very deeply branched (almost from its base). The last two anal rays are slightly elongated and form a 'finlet' which is characteristic of *Sardinops* (Svetovidov 1952: 189). Ossification of the caudal rays which commenced at 10,5 mm s.l. progresses rapidly so that by 13,0 mm s.l. 13–15 rays are visible, although not completely developed. At this stage the ventral part of the caudal fin is more advanced than the dorsal part. By 18,1 mm s.l. (Fig. 4B) all 19 primary caudal rays are formed, and some of them are slightly branched. Some secondary rays are also present. By 20,0 mm s.l. the branching of the 17 inner primary caudal rays is appreciable and from 23,0 mm s.l. the caudal fin rapidly assumes its deeply forked shape (Fig. 5A). The pelvic fin appears as a small bud at 18,0 mm s.l. and its first rays start to develop at 22–23 mm s.l. The pelvic fin with its full complement of 8 rays, of which all except the anterior ones are branched, is fully formed by 26,0 mm s.l. The pectoral fin, in which lepidotrichia formed at a very early stage, is the last of the fins to complete development. The fin rays form only from 23,0 mm s.l., although these are then laid down rapidly so that 15–16 are present by 29 mm s.l. and the full complement of 18 rays is reached by 33 mm s.l. Details of fin ray development in the paired and unpaired fins are given in Table 1.

As is evident from Figure 4A–C little change occurs in the general appearance of the larvae after the end of the yolk-sac stage until 20–22 mm s.l., apart

TABLE 1

Development of fin rays in *S. ocellata* larvae between 8 mm and 33 mm standard length

Size range (mm)	*Mean* (mm)	*No.*	*Dorsal rays*	*Anal rays*	*Caudal rays*	*Pectoral rays*	*Pelvic rays*
8,0– 8,9	8,90	1	5–6	†	†	†	—
9,0– 9,9	9,55	2	9	†	†	†	—
10,0–10,9	10,40	4	9–12	0– 4	†	†	—
11,0–11,9	11,65	6	10–14	5– 8	5– 9	†	—
12,0–12,9	12,53	7	10–14	7– 9	12–15	†	—
13,0–13,9	13,45	22	11–16	8–10	13–15	†	—
14,0–14,9	14,41	12	12–16	10–13	15–17	†	—
15,0–15,9	15,61	9	13–16	13–15	16–18	†	—
16,0–16,9	16,18	1	15	13	18	†	—
17,0–17,9	17,50	2	15	14–16	18–19	†	—
18,0–18,9	18,51	9	15–16	15–17	½+ 19 +½	†	bud
19,0–19,9	19,53	15	15–17	15–17	1+ 19 +½	†	bud
20,0–20,9	20,27	8	16–17	15–17	2+ 19 +1	†	bud
21,0–21,9	21,60	3	16–17	15–17	2+ 19 +1	†	bud
22,0–22,9	—	0	—	—	—	—	—
23,0–23,9	23,41	3	17–18	17	3+ 19 +2	3–5	4–5
24,0–24,9	24,70	3	18	17	5+ 19 +4	6–8	6–7
25,0–25,9	25,06	1	18	17	5+ 19 +4	7	7
26,0–26,9	26,29	2	18–20	17–18	6+ 19 +5	10–12	8
27,0–27,9	27,27	1	19	17	6+ 19 +5	11	8
28,0–28,9	28,58	1	20	17	7+ 19 +5	15	8
29,0–29,9	29,59	3	19–20	18–20	8+ 19 +7	15–16	8
30,0–30,9	30,97	1	20	18	8+ 19 +7	17	8
31,0–31,9	31,33	2	19–20	19–20	8+ 19 +7	17	8
32,0–32,9	—	0	—	—	—	—	—
33,0–33,9	33,67	2	18–19	19–20	8+ 19 +7	18	8

† indicates lepidotrichia present, but no rays.
Caudal fin counts, from 18 mm s.l. are preceded and followed by additional counts; these indicate the number of secondary caudal rays on the dorsal and ventral parts of the caudal fin respectively.

from the fin development described above. The dorsal and anal fins are situated far posteriorly on the long slender larvae. The origin of the dorsal fin occurs above the 29th myotome when thickening first appears in the dorsal fin fold, but lies over myotomes 23–26 once the dorsal fin nears completion, since the anterior rays are the last to develop. The anal fin origin lies below 39–41 in very young larvae and below myotomes 36–38 in older larvae. The end of the dorsal fin and origin of the anal fin are separated by 6–8 myotomes. At the time when the pelvic fin first forms it occupies a position corresponding to the 15th, 16th or 17th myotome, and is situated well in front of the origin of the dorsal fin. The pelvic fin and the origin of the dorsal fin are separated by 8–10 myotomes prior to metamorphosis.

The pattern of pigmentation of the larvae shows little change during larval development and remains basically that attained at the end of the yolk-sac stage. However, there is an increase in the number of melanophores contributing to this pattern. The 6–7 pairs of elongate melanophores along the ventral edge of the myotomes, adjacent to the anterior half of the gut increase to 9–11 pairs at 11 mm s.l. and become even more numerous, but less elongate, at the end of the larval stage (Fig. 4C). There is a similar increase in the number of mid-ventral melanophores on the posterior half of the gut and the number of embedded melanophores above the posterior half of the gut increases to 10 pairs at 11 mm s.l. and there are as many as 17 pairs of these melanophores at 23 mm s.l. with additional smaller melanophores scattered in between them. Moreover, at the end of the larval stage, there is some pigmentation of the caudal fin. This comprises melanophores formed along the edges of the rays and arranged to form transverse rows, parallel to the outline of the caudal fin (Fig. 4C). A few melanophores also develop on the proximal radials of the dorsal fin base. From 17–18 mm s.l. a few isolated melanophores appear mid-laterally along the body and these gradually become more numerous. From the time the pelvic rays commence development there is usually a single large melanophore just anterior to the base of the pelvic fin.

METAMORPHIC STAGE LARVAE (Fig. 5A)

From 22 mm s.l. the larvae of *S. ocellata* undergo marked changes in body proportions and pigmentation, which result in larvae of 22–32 mm s.l. being termed metamorphic stage larvae. The various body proportions which were studied for the complete developmental series are illustrated in Figures 6–10. These graphs show that the body proportions all remain constant relative to standard length until the larvae attain the size of 22 mm s.l., at which stage changes in body depth, head length and in the position of the dorsal, anal and pelvic fins commence. Some of these characters show further changes at 33–36 mm s.l., thus indicating the final transition to the juvenile condition.

The onset of metamorphosis is indicated by changes in head growth and body depth and in the commencement of the ventral growth of the myotomes. During the larval stage the head length increases constantly in relation to the standard length. At the start of metamorphosis, however, the rate of increase of the head length accelerates (Fig. 6). The increase in body depth (measured as depth at the pectoral base) follows the pattern of change in head growth but to a more marked degree (Fig. 7). In addition to this overall increase in body depth in larvae of more than 22 mm s.l., it may be seen from Figure 4C that the myotomes at this stage start to grow ventrally so that they begin to cover the gut. At 23 mm s.l. the myotomes merely obscure the dorsal edge of the gut, but their expansion becomes more marked, first over the anterior half of the gut and later extending also over the posterior half of the gut, so that by 29,5 mm s.l. the gut is almost entirely covered by myotome tissue, except for a small area close to the anus. At this stage, however, they have not yet fused ventrally. In larvae of 30–31 mm s.l. most myotomes anterior to the pelvic fins are fused mid-ventrally and the first two or three scutes have developed in the most anterior mid-ventral region.

In common with the development of other clupeids, one of the most marked features of metamorphosis in *S. ocellata* is the alteration in the position

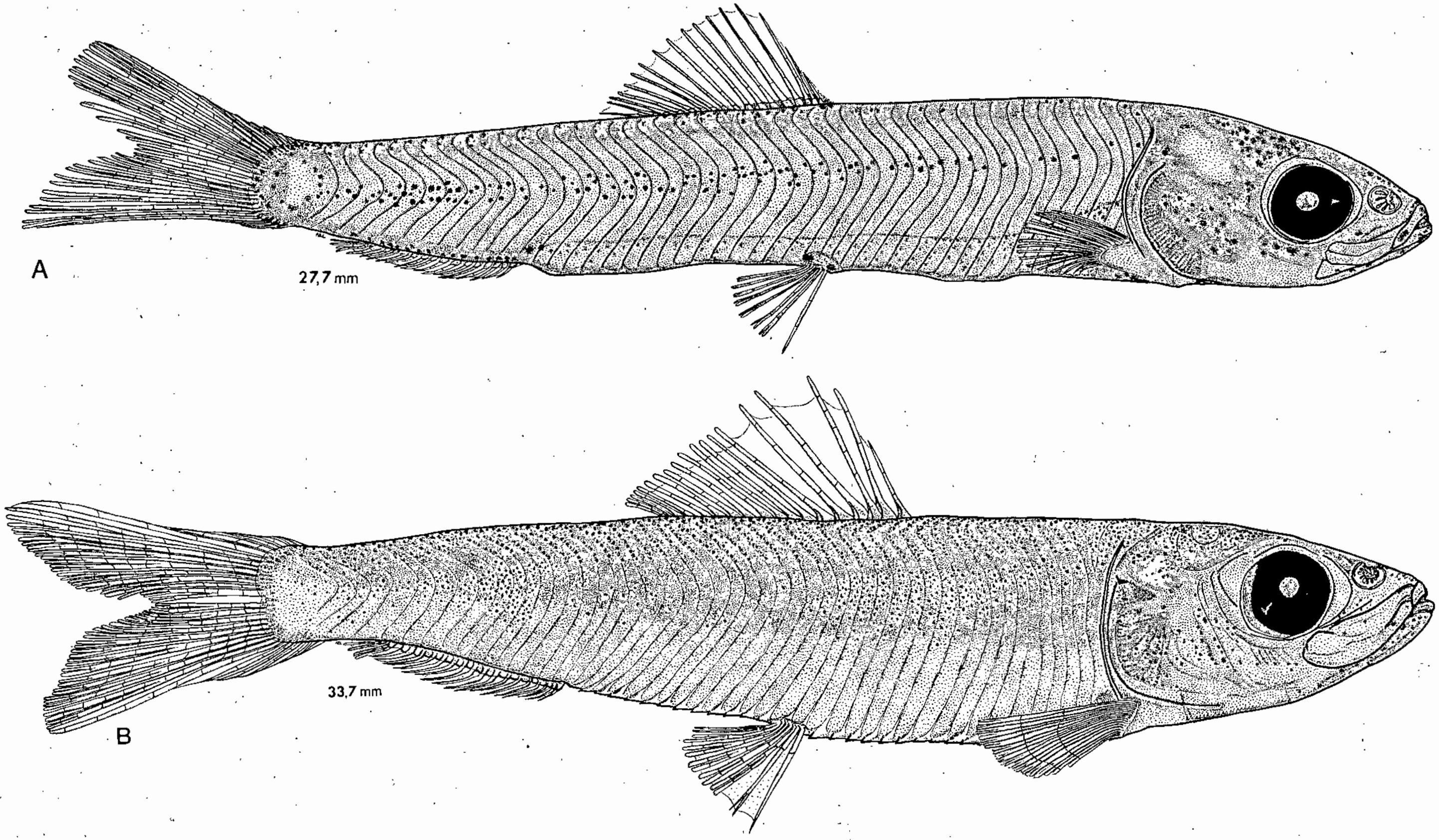


Fig. 5. A. Metamorphic stage larva showing alteration in fin positions. B. Early juvenile stage with fin migration complete and a considerable amount of dorsal pigmentation.

of the dorsal and anal fins which occurs during this stage. Instead of the steady rate of increase shown in the distances from cleithrum to dorsal fin and cleithrum to anal fin (Figs 8–9) during the larval stage, metamorphic stage larvae show a slight decrease in cleithrum to dorsal fin distance and only a very slight continued increase in cleithrum to anal fin distance. These changes in the pattern of growth occur in larvae of 24–33 mm s.l. They can be attributed to the anterior migration of the dorsal and anal fins, relative to myotomes and vertebrae. Most authors (Lebour 1921; Ford 1930; Ahlstrom 1943, 1968) documented fin migration relative to vertebrae, but others (Schnakenbeck 1929; Baker 1972) used myotomes. Attempts to stain vertebrae in specimens 18–20 mm s.l. were not satisfactory as the most anterior vertebrae did not take up the alizarin dye, although older stages stained satisfactorily. This precluded the determination of fin position relative to vertebrae in pre-metamorphic larvae. For this reason fin position relative to myotomes was used as this could be determined through-

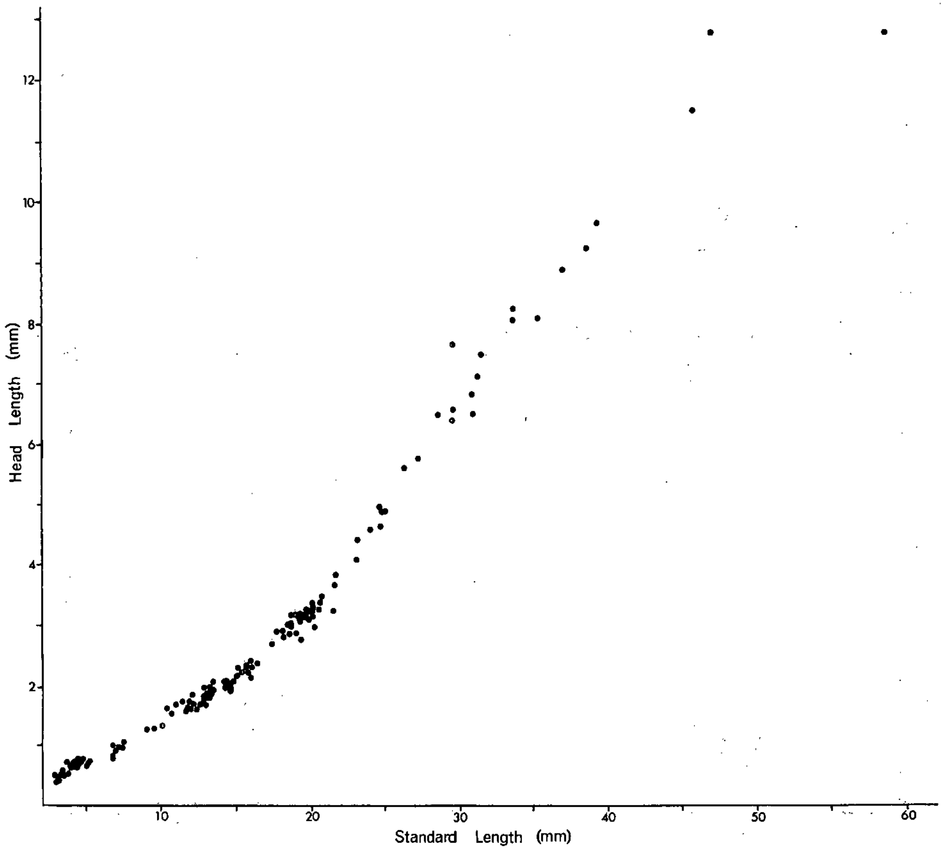


Fig. 6. Graph of increase in head length with increase in standard length. Note acceleration of head growth from 22 mm s.l.

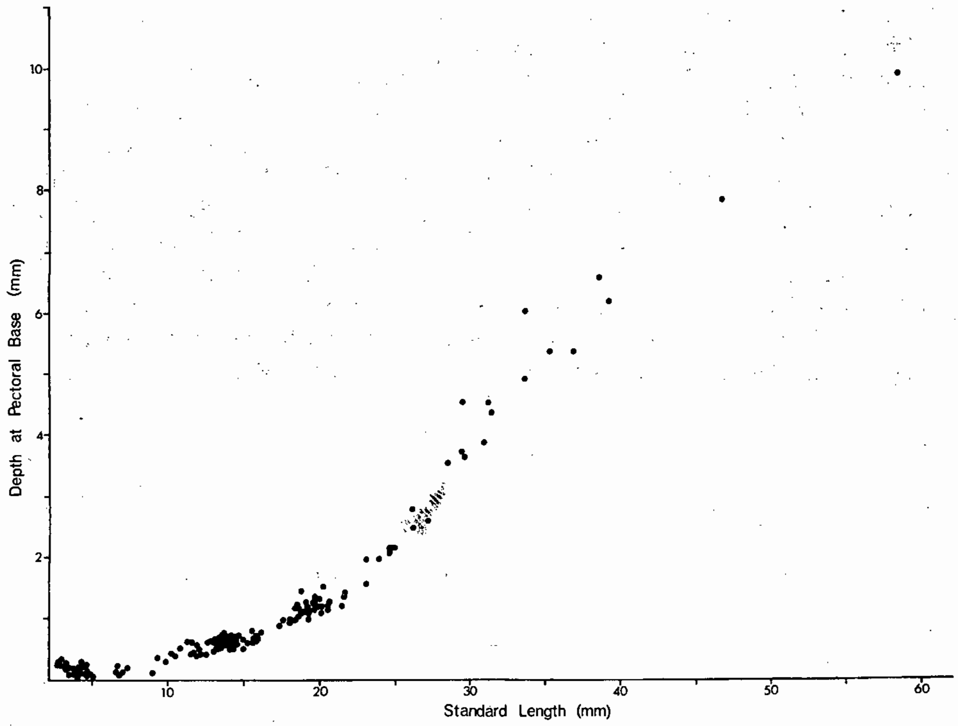


Fig. 7. Graph of body depth (as depth at pectoral base) versus standard length. Initial decrease (2–5 mm s.l.) is due to yolk-sac utilization. Note increased rate of deepening of body from 23 mm s.l.

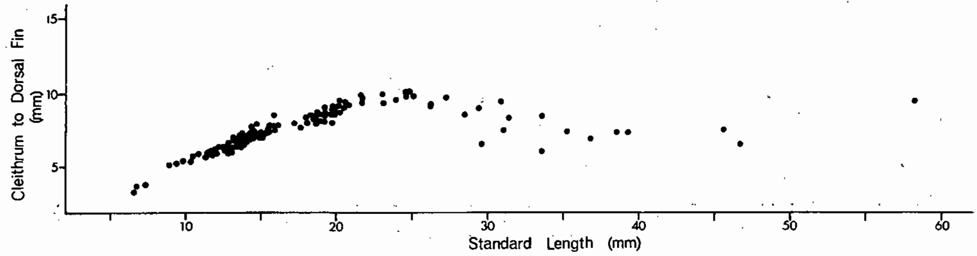


Fig. 8. Graph of distance from cleithrum to dorsal fin versus standard length, showing a decrease during the phase of anterior migration of the dorsal fin.

out development. However, to permit comparison of fin migration in *S. ocellata* with that which occurs in other species of *Sardinops*, fin positions relative to vertebrae in late larval and metamorphic stages are given in Table 2. Some differences in counts (usually of 1–3) are evident between the two methods and these differences can be attributed to two factors. Firstly, only complete myotomes posterior to the cleithrum were counted and this omits 1–2 incomplete myotomes at the anterior region of the body. Secondly, vertebral counts were taken at positions vertically below or above the fins concerned, but myotome counts at dorsal and ventral edges adjacent to the fin origins. The <-shape of the myotomes makes a further difference of 1–2 in the counts as the anterior region of the myotome corresponds to a vertebral centrum 1–2 centra anterior to the one below the posterior part of the myotome. (This difference is slightly greater in older specimens, e.g. 38,58 mm juvenile.) However, as the two methods reflect similar changes during metamorphosis, myotome counts can be accepted as a reliable method of documenting fin migration.

TABLE 2

Fin position relative to myotome (M) and vertebral (V) counts in late larval and metamorphic stages of *S. ocellata*.

Standard Length (mm)	*Dorsal Fin* M	V	*Anal Fin* M	V	*Pelvic Fin* M	V
18,80	25	—	38	—	—	—
19,00	24	—	37	—	—	—
19,22	25	—	38	—	17	—
19,63	24	26	37	39	16	18
19,71	24	—	37	—	15	—
19,87	25	26	37	39	15	17
19,96	24	—	36	—	15	—
20,54	24	—	38	—	16	—
20,70	23	—	38	—	15	—
21,68	22	24	36	38	15	17
23,16	23	25	36	38	16	18
24,64	22	24	36	38	16	17
24,64	22	24	36	38	15	17
24,81	23	26	36	39	16	18
25,06	21	25	35	38	15	17
26,29	21	24	35	37	16	17
26,29	21	23	35	37	16	17
28,58	19	22	34	36	16	18
29,56	19	22	33	36	17	18
29,56	13	15	33	36	16	18
29,64	19	22	33	36	17	18
30,97	17	19	33	36	15	17
31,20	14	17	31	34	16	19
38,58	13	17	31	36	16	20

As is evident from Figure 11 the number of myotomes preceding the dorsal fin (open triangles) is 22–25 in larvae of 20–23 mm s.l., but from 24 mm s.l. the number decreases sharply due to the forward migration of the fin. This continues until the fin reaches the position of myotomes 10–13 at 33–35 mm s.l. Migration of the dorsal fin ceases at this size, having covered the extent of 10–12 myotomes. Migration of the anal fin (Fig. 11—closed triangles) is not as extensive as that of the dorsal fin, but nevertheless is quite considerable. The origin of the anal fin shifts from the position of myotomes 36–38 at 20–25 mm s.l., to reach myotome 31 at 31–33 mm s.l.—thus involving a shift over 5–7 myotomes. At the end of migration the end of the dorsal fin and the origin of the anal fin are separated by five myotomes. Once the larvae attain the size of 33–35 mm s.l. the increases in the distances from cleithrum to dorsal fin and cleithrum to anal fin resume their pre-metamorphic rates (Figs 8–9). This can be regarded as an indication of the end of the metamorphic stage and the attainment of the juvenile stage.

During metamorphosis the rate of increase in distance from cleithrum to pelvic fin diminishes for a short growth interval (23–26 mm s.l.) (Fig. 10). This cannot be explained by any forward shift in pelvic fin position relative to myotomes as the fin retains its position at myotomes 15–17 (or vertebrae 17–18) as in the late larval stages when the pelvic bud first appeared. However, later in development the pelvic fin shifts posteriorly relative to vertebrae (but not relative to myotomes) and comes to lie vertically below vertebrae 19–20. With the migrations of the dorsal and pelvic fins, their positions relative to one

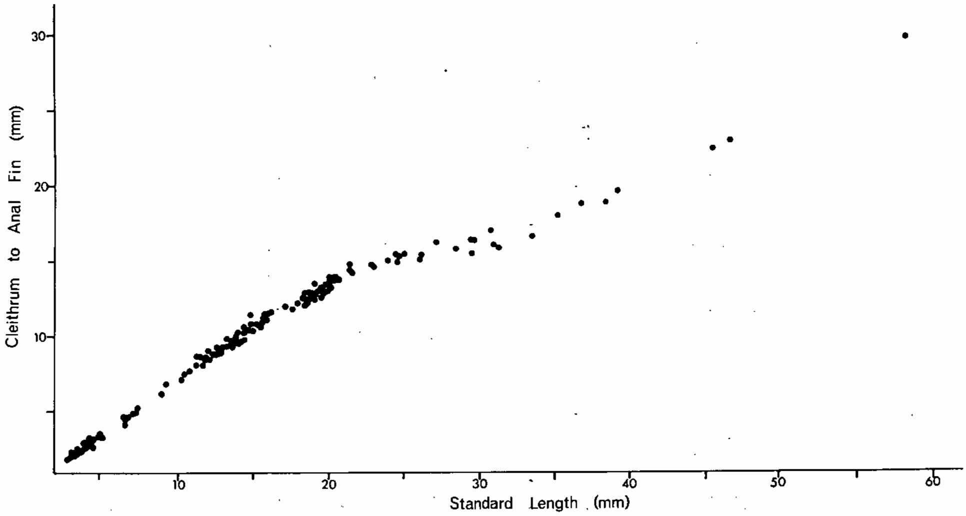


Fig. 9. Graph of distance from cleithrum to anal fin versus standard length, showing reduction in rate of increase whilst anal fin undergoes anterior migration between 23 mm and 33 mm s.l.

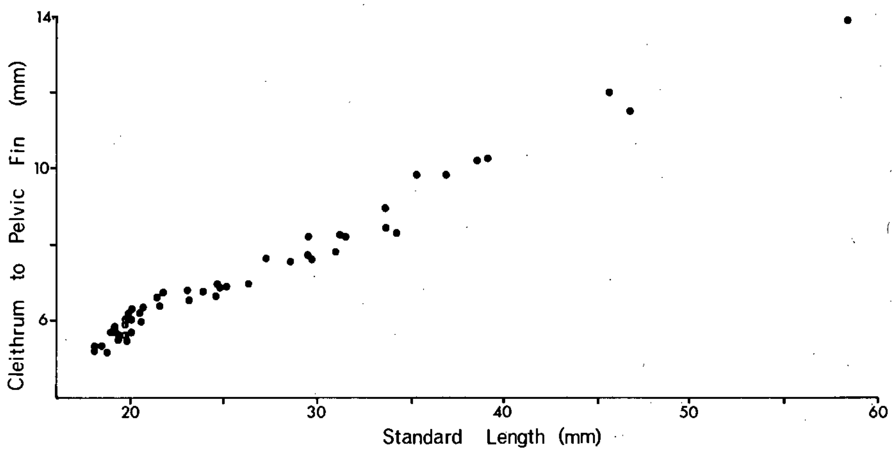


Fig. 10. Graph of distance from cleithrum to pelvic fin versus standard length.

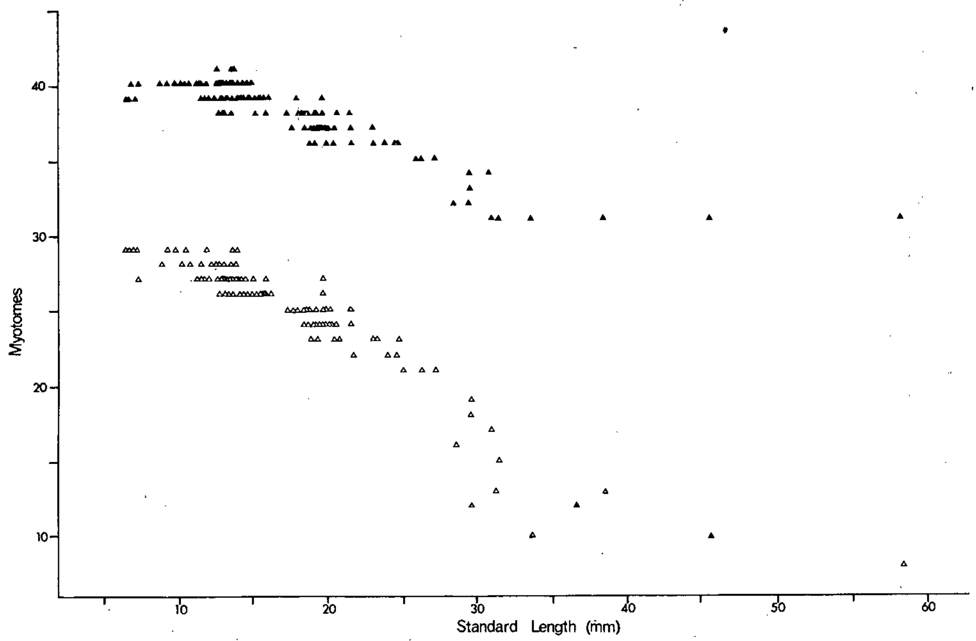


Fig. 11. Graph of the number of myotomes from cleithrum to anal fin (closed triangles) and cleithrum to dorsal fin (open triangles) indicating the anterior migration of the fins from 23 mm s.l. The gradual decrease in number of myotomes to 23 mm s.l. is due to development of additional fin rays.

another alter and instead of the pelvic fin lying anterior to the dorsal origin, it lies vertically below the dorsal origin at 27–29 mm s.l. and by 32–33 mm s.l. the pelvic origin corresponds to a position below the middle of the base of the dorsal fin as is the case in adults of the species.

Throughout the larval stage both pectoral and pelvic fins lack ossified rays. Ossification of rays in the paired fins commences in larvae over 22 mm s.l., i.e. at the onset of the metamorphic stage. By the time the juvenile stage is reached fin ray development is complete in paired and unpaired fins (Table 1).

Pigmentation also changes quite markedly during the metamorphic stage. With the ventral growth of the myotomes, much of the larval pigment pattern near the gut is obliterated or lost. It is replaced by pigment spots which form beneath the myotomes, along the dorsal surface of the gut (? on the peritoneum) and which are partially visible through the myotomes. The melanophores which first appeared in larvae of 17–18 mm s.l. along the mid-lateral sides of the body, become far more numerous, especially from 25–26 mm s.l., so that the larvae develop a fairly dark mid-lateral band of pigment (Fig. 5A). Furthermore, a large number of melanophores appears along the dorsal surface of the body. These are stellate melanophores and are arranged in lines which follow closely the edges of the myotomes, with a few melanophores scattered in between. In spite of the appearance of this quite considerable amount of pigment on the dorsal surface of the body, which might be considered an approach towards the adult coloration, larvae of 30–32 mm s.l. are still predominantly pale, as were the earlier larvae. Pigmentation on the head also increases, particularly on the dorsal surface of the head, in the region of the parietals, and there are scattered melanophores on the opercular and circumorbital bones.

Scale development commences towards the end of the metamorphic stage. Since few specimens of 30–45 mm s.l. were available from the main study area, the material was supplemented with specimens of that size range used in the study by Davies (1954) and the 1950–67 egg and larval survey in Cape waters (Haigh 1972: 49, 66, fig. 9). Scales are first formed at 30 mm s.l. These develop on the caudal peduncle and are arranged in an anteriorly pointing 'V' pattern. The scale-covered area enlarges rapidly so that it reaches the area above the anal fin by 31,5 mm s.l. and by 33 mm s.l. all of the body posterior to the mid-region of the dorsal fin base is covered. By 36 mm s.l. scale cover reaches anteriorly to the cleithrum, but anterior to the dorsal fin the scales do not overlap. Scale development is completed early in the juvenile stage.

JUVENILE STAGE (Fig. 5B)

The juvenile stage is that in which the metamorphic changes are complete and the young fish resembles the adult. As can be seen from Figure 5B the juvenile fish resembles the adult in shape; in addition to the pigment which appeared during metamorphosis, the dorsal part of the body is covered with small closely arranged melanophores, which give the fish the dark dorsal and light ventral appearance of the adult; the head is extensively pigmented, and on the opercular bones the radial ridges are clearly visible; the entire body is covered with scales and ventral scutes are present anterior to and behind the pelvic fins; the last two anal rays are distinctly longer than the more anterior rays, and the pelvic and pectoral fins are well developed.

As juvenile development proceeds pigmentation on the dorsal area of the body increases further, and silvery pigment develops on the lateral and ventral parts of the body from about 37 mm s.l. and the row of dark pigment spots which is characteristic of adult pigmentation forms from 45 mm s.l.

DISCUSSION

In yolk-sac and larval stages of development *Sardinops ocellata* follows closely the pattern of development described for *S. caerulea* (Miller 1952), *S. neopilchardus* (Baker 1972) and *S. melanosticta* (Uchida 1958). However, it is evident that some differences do occur in the development of these species, during the later phases of larval life. These differences are in the number of myotomes or vertebrae over which the fins migrate and also the relative sizes at which the changes occur. These differences are summarized in Table 3.

TABLE 3

Comparison of late stages of development in species of *Sardinops*

	ocellata	*caerulea* (Ahlstrom 1968)	*neopilchardus* (Baker 1972)	*melanosticta* (Uchida 1958*)
Posterior migration of pelvic fins	2 vertebrae	3 vertebrae	5 myotomes	?
Final position of pelvic fins	18–20th vertebrae	22nd vertebra	22nd myotome	?
Anterior migration of dorsal fin	10–12 myotomes	10 vertebrae	10–12 myotomes	?
Final position of dorsal fin	10–13th myotomes	18th vertebra	14–16th myotomes	?
Metamorphic stage	22–32 mm s.l.	25–40 mm s.l.	25–35 mm s.l.	? 30–40 mm s.l.
Juvenile	33 mm s.l.	40 mm s.l.	35 mm s.l.	? 42 mm s.l.

* Text in Japanese, information from figures and legends only.

ACKNOWLEDGEMENTS

The authors would like to express their thanks to the Sea Fisheries Branch, Walvis Bay (E.L.) and the South African Museum (M.J.O'T.) for the co-operation of these institutions during visits in the course of this study. Thanks also to Dr N. A. H. Millard and Miss M. A. Roeleveld for their helpful criticisms of the manuscript.

REFERENCES

AHLSTROM, E. H. 1943. Studies on the Pacific sardine or pilchard (*Sardinops caerulea*). 4. Influence of temperature on the rate of development of pilchard eggs in nature.—*Fish. Bull. U.S. Spec. Sci. Rep.* **23**: 1–26.

AHLSTROM, E. H. 1968. Review—Development of fishes of the Chesapeake Bay region, An atlas of eggs, larval and juvenile stages, Part 1.—*Copeia* **1968** (3): 648–651.

BAKER, A. N. 1972. Reproduction, early life history and age-growth relationships of the New Zealand pilchard, *Sardinops neopilchardus* (Steindachner).—*Fish. Res. Bull. N.Z.* **5**: 1–64.

CRAM, D. L. & VISSER, G. A. 1972. Cape Cross research programme—Phase II—A summary of results.—*S. Afr. Shipp. News Fish. Ind. Rev.* **27**: 40–43.

D'ANCONA, U. 1931. *Uova, larve e stadi giovanili di Teleostei . . .* Famiglia 1: Clupeidae. —*Fauna e Flora del Golfo di Napoli* **38** (1): 1–16.

DAVIES, D. H. 1954. The South African pilchard (*Sardinops ocellata*). Development, occurrence and distribution of eggs and larvae, 1950–51.—*Investl. Rep. Div. Sea Fish. Un. S. Afr.* **15**: 1–28.

FORD, E. 1930. Herring investigations at Plymouth. VIII. The transition from larva to adolescent.—*J. mar. biol. Ass. U.K.* **16**: 723–752.

HAIGH, E. H. 1972. Larval development of three species of economically important South African fishes.—*Ann. S. Afr. Mus.* **59**: 47–70.

HART, T. J. & MARSHALL, N. B. 1951. Breeding ground of pilchards off the coast of South-West Africa.—*Nature, Lond.* **168**: 272–273.

HOLLISTER, G. 1934. Clearing and dyeing fish for bone study.—*Zoologica, N.Y.* **12**: 89–101.

KING, D. P. & ROBERTSON, A. A. 1973. Methods of pelagic fish egg and larval research in South West Africa.—*S. Afr. Shipp. News Fish. Ind. Rev.* **28**: 57–61.

LEBOUR, M. V. 1921. The larval and post-larval stages of pilchard, sprat and herring from Plymouth district.—*J. mar. biol. Ass. U.K.* **12**: 427–457.

MILLER, D. J. 1952. Development through the prolarval stage of artificially fertilized eggs of the Pacific sardine (*Sardinops caerulea*).—*Calif. Fish Game* **38**: 587–595.

ORTON, G. L. 1953. Development and migration of pigment cells in some teleost fishes. —*J. Morph.* **93**: 69–99.

SCHNAKENBECK, W. 1929. Entwicklungsgeschichtliche und morphologische Untersuchungen am Hering.—*Ber. dt. wiss. Kommn Meeresforsch.* (N.F.) **5**: 19–77.

SCOFIELD, E. C. 1934. Early life history of the California sardine (*Sardina caerulea*) with special reference to the distribution of eggs and larvae.—*Fish. Bull Calif.* **41**: 1–48.

SVETOVIDOV, A. N. 1952. Fauna of U.S.S.R. Fishes. Vol. II No. 1: Clupeidae.—*Opred. Faune S.S.S.R.* (n.s.) **48** (2, no. 1): 1–331. (Translated from Russian.)

UCHIDA, K. 1958. Eggs, larvae and juvenile of *Sardinops melanosticta* (Temminck & Schlegel) (Clupeidae). *In:* UCHIDA, K. *et al. Studies on the eggs, larvae and juvenile of Japanese fishes.* Series I. Fukuoka: Second Laboratory of Fisheries Biology, Fisheries Department, Kyushu University.

6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidatâ Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

ELIZABETH LOUW & M. J. O'TOOLE

LARVAL DEVELOPMENT OF *SARDINOPS OCELLATA* (PISCES : CLUPEIDAE)

DEVELOPMENT AND DISTRIBUTION OF LARVAE AND EARLY JUVENILES OF THE COMMERCIAL LANTERNFISH, *LAMPANYCTODES HECTORIS* (GÜNTHER), OFF THE WEST COAST OF SOUTHERN AFRICA WITH A DISCUSSION OF PHYLOGENETIC RELATIONSHIPS OF THE GENUS

ELBERT H. AHLSTROM, H. GEOFFREY MOSER, AND MICHAEL J. O'TOOLE

Reprinted from BULLETIN OF THE SOUTHERN CALIFORNIA ACADEMY OF SCIENCES
Vol. 75, No. 2, August 1976
pp. 138–152
Made in the United States of America

DEVELOPMENT AND DISTRIBUTION OF LARVAE AND EARLY JUVENILES OF THE COMMERCIAL LANTERNFISH, *LAMPANYCTODES HECTORIS* (GÜNTHER), OFF THE WEST COAST OF SOUTHERN AFRICA WITH A DISCUSSION OF PHYLOGENETIC RELATIONSHIPS OF THE GENUS

ELBERT H. AHLSTROM[1], H. GEOFFREY MOSER[1], AND MICHAEL J. O'TOOLE[2]

ABSTRACT: *Lampanyctodes hectoris* is a species of lanternfish which is becoming an important part of the pelagic fishery off South Africa. The Southwest Africa Pelagic Egg and Larval Survey has provided an abundance of larval specimens of this species. The larvae, transitional and early juvenile stages are described and illustrated for the first time and information on their distribution and relative abundance is provided. Larval characters are used in combination with selected adult characters to elucidate the phylogenetic affinities of this genus.

Lanternfishes of the family Myctophidae are the most ubiquitous and speciose (approximately 250 species in 30 genera) of all fishes in the oceanic mid-waters. Although their total biomass is unknown, the fact that lanternfishes, on the average, make up approximately one-half of all fish larvae taken in any oceanic plankton tow gives some impression of its immensity. Although they are small fishes, usually less than 100 mm in length, they may have the greatest biomass of any vertebrate family. Knowledge of their ecological role in the world ocean is poor, but initial studies suggest that these fishes are a major element in the oceanic food web. Among the commercially important organisms known to prey on lanternfishes are salmon (Shimada, 1948; Manzer, 1968), tunas (Alverson, 1963; Pinkas et al., 1971), rockfish (Pereyra et al., 1969), fur seals (Mead and Taylor, 1953) and cetaceans (Fitch and Brownell, 1968). Recent studies (Paxton, 1967; Holton, 1969; Legand and Rivaton, 1969; Collard, 1970; Baird et al., 1975) indicate that lanternfishes are important grazers on herbivorous zooplankton.

Historically, lanternfishes have not been commercially exploited because of their small size and relatively diffuse distribution in the water column. A growing body of observations indicates that some species of lanternfishes aggregate in large numbers at certain times during their life cycles and, at such times, may be available to a fishery. There have been several well-documented observations of lanternfish swarming at the surface in dense "balls." *Benthosema panamense* exhibits this behavior during daylight in the eastern Pacific and tuna boat skippers report that yellowfin and skipjack tuna feed exclusively on these swarms when they are observed (Alverson, 1961). Similar swarms of *Diaphus garmani* were reported at night in the central Pacific (Nakamura, 1970). Lanternfishes also aggregate in extensive shoals. Observations from submarines indicate that some species of lanternfishes, such as *Ceratoscopelus maderensis* (Backus et al., 1968) and *Benthosema panamense* (Barham, 1971), form extensive aggregations in slope waters. G. Krefft (Institut für Seefischerei, Hamburg, pers. comm.) has achieved catch rates of 1¼ metric tons/hour of *Diaphus dumerili* with a commercial herring trawl off Buenos Aires. It is well known that myctophids are often a major element in deep scattering layers of the ocean (Barham, 1966; Pearcy and Mesecar, 1971). Additional knowledge of these phenomena may lead to the commercial harvesting of lanternfishes.

Recently a fortuitous fishery for the lanternfish *Lampanyctodes hectoris* has developed incidental to the anchovy/pilchard fishery off the western coast of South Africa (Centurier-Harris, 1974). Annual landings of lanternfishes (mostly *L. hectoris*) were 1,134 metric tons or 0.3 percent of the pelagic fishery catch in this region in 1969 and increased to 42,560 metric tons or 10.45 percent of the catch in 1973. The location of the fishery is shown in figure 1. This species is particularly desirable because of its high content (20 percent by weight) of fine quality oil.

---

[1] National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038.

[2] Sea Fisheries Branch, Beach Road, Sea Point, Cape Town, South Africa.

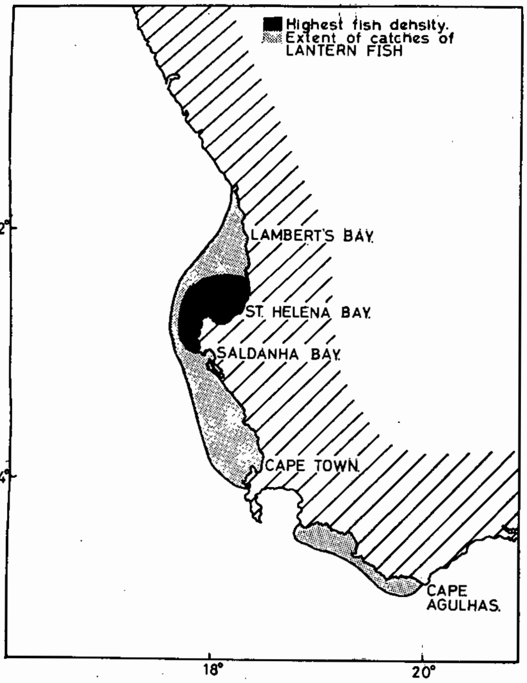


Figure 1. Region of the fishery for *Lampanyctodes hectoris* off South Africa (from Centurier-Harris, 1974).

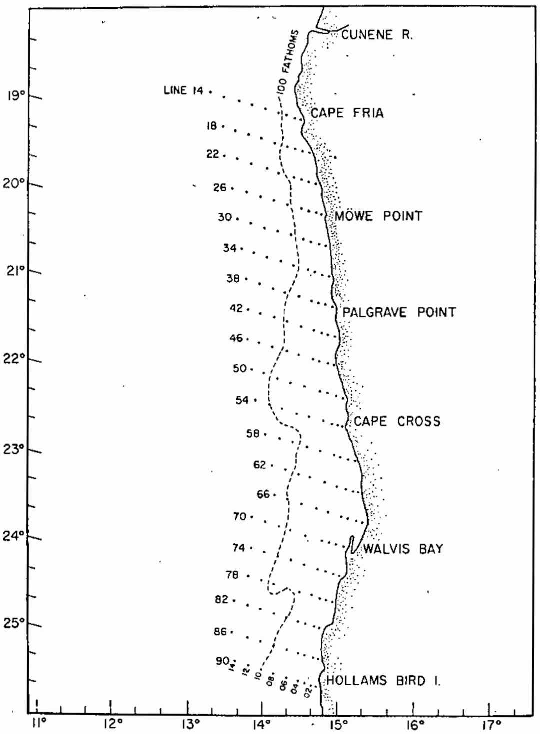


Figure 2. Station plan for Southwest African Pelagic Egg and Larval Survey (SWAPELS).

Little is known about the life history of this important species of lanternfish. However, an extensive plankton survey, the Southwest African Pelagic Egg and Larval Survey (SWAPELS), was initiated by the Sea Fisheries Branch in 1972 (O'Toole, 1974). Although the data from this survey are not completely analyzed, some information on the distribution and relative abundance of *L. hectoris* larvae will be presented in this paper, the principal purpose of which is to describe the larval, transitional, and early juvenile stages of *L. hectoris*. Previously, Moser and Ahlstrom (1972) illustrated a 9.2 mm larva of *L. hectoris* and gave a partial description of the sequence of photophore formation based on the few specimens available. Examination of the abundant larval specimens from SWAPELS has shown that Moser and Ahlstrom (1972) were in error and that their 9.2 mm larva was *Lampadena* sp. The larvae of *Lampanyctodes hectoris* have a unique generic morph, a concept discussed extensively by Moser and Ahlstrom (1970, 1972, 1974). A number of larval characters give insight into the relationships of this genus with other myctophid genera and these will be treated in the discussion section of this paper.

METHODS

Specimens for the developmental part of this study were obtained from two plankton surveys of SWAPELS (Fig. 2). Survey 1 was carried out from August 1972 to March 1973 and Survey 2 from August 1973 to April 1974. The net used on both surveys was a 57 cm bongo net; 0.940 mm and 0.940 mm mesh were paired on Survey 1 and 0.940 mm was used on the left unit and 0.500 mm on the right on Survey 2. Oblique tows were made to a depth of 50 m at all stations except where the bottom was shallower than 50 m.

Techniques used for describing the development of *L. hectoris* are outlined in Moser and Ahlstrom (1970).

Lampanyctodes hectoris (Günther)
Figures 3 and 4

Literature.—The illustration of the 9.2 mm larva of *Lampanyctodes hectoris* and the remarks on photophore formation in that species in Moser and Ahlstrom (1972) are in error and refer to a larva of *Lampadena* sp. There are no illustrations or descriptions of *L. hectoris* larvae in the literature.

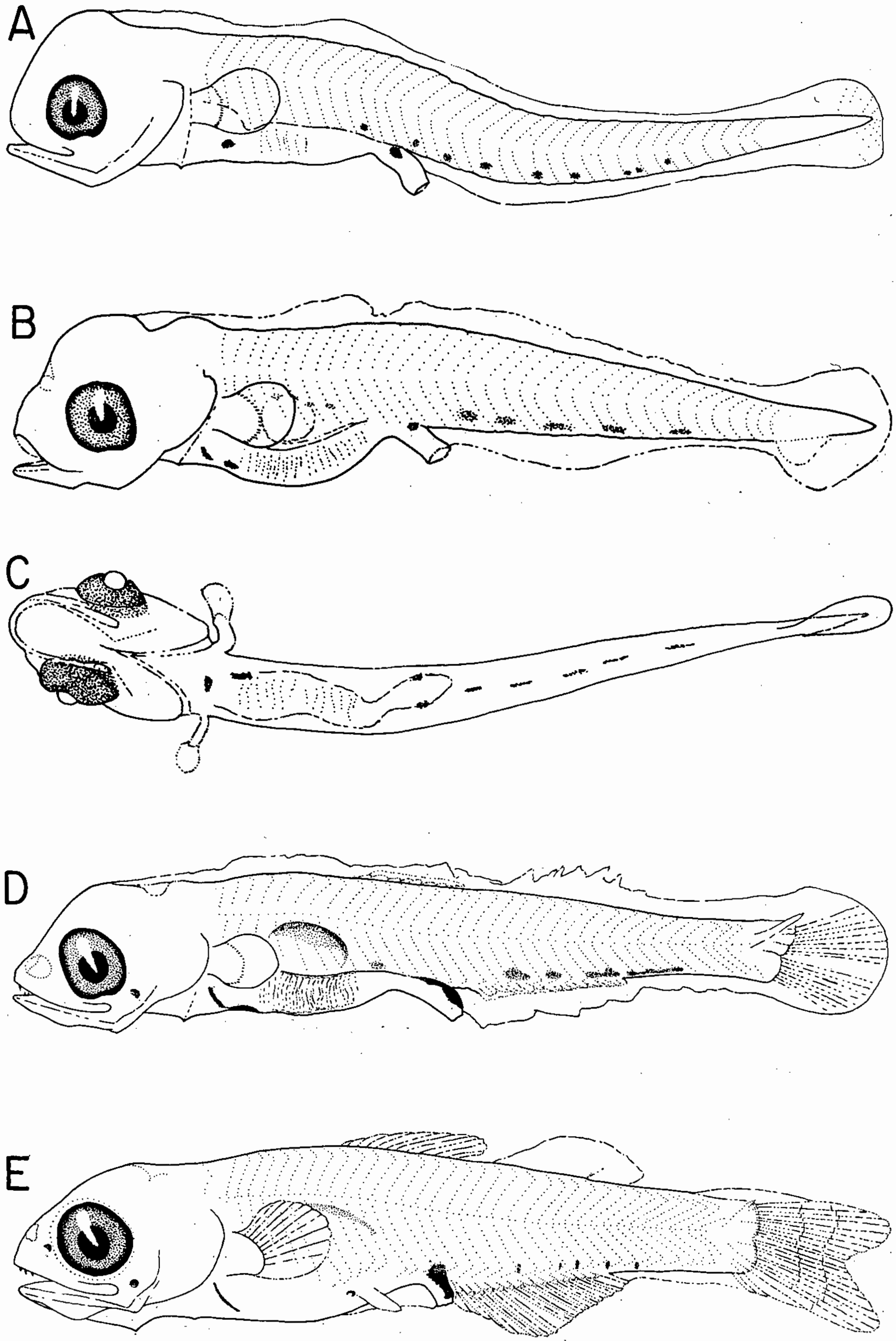


Figure 3. Larvae of *Lampanyctodes hectoris.* A. 3.8 mm; B. 5.0 mm; C. 5.0 mm, ventral view; D. 6.8 mm; E. 8.7 mm.

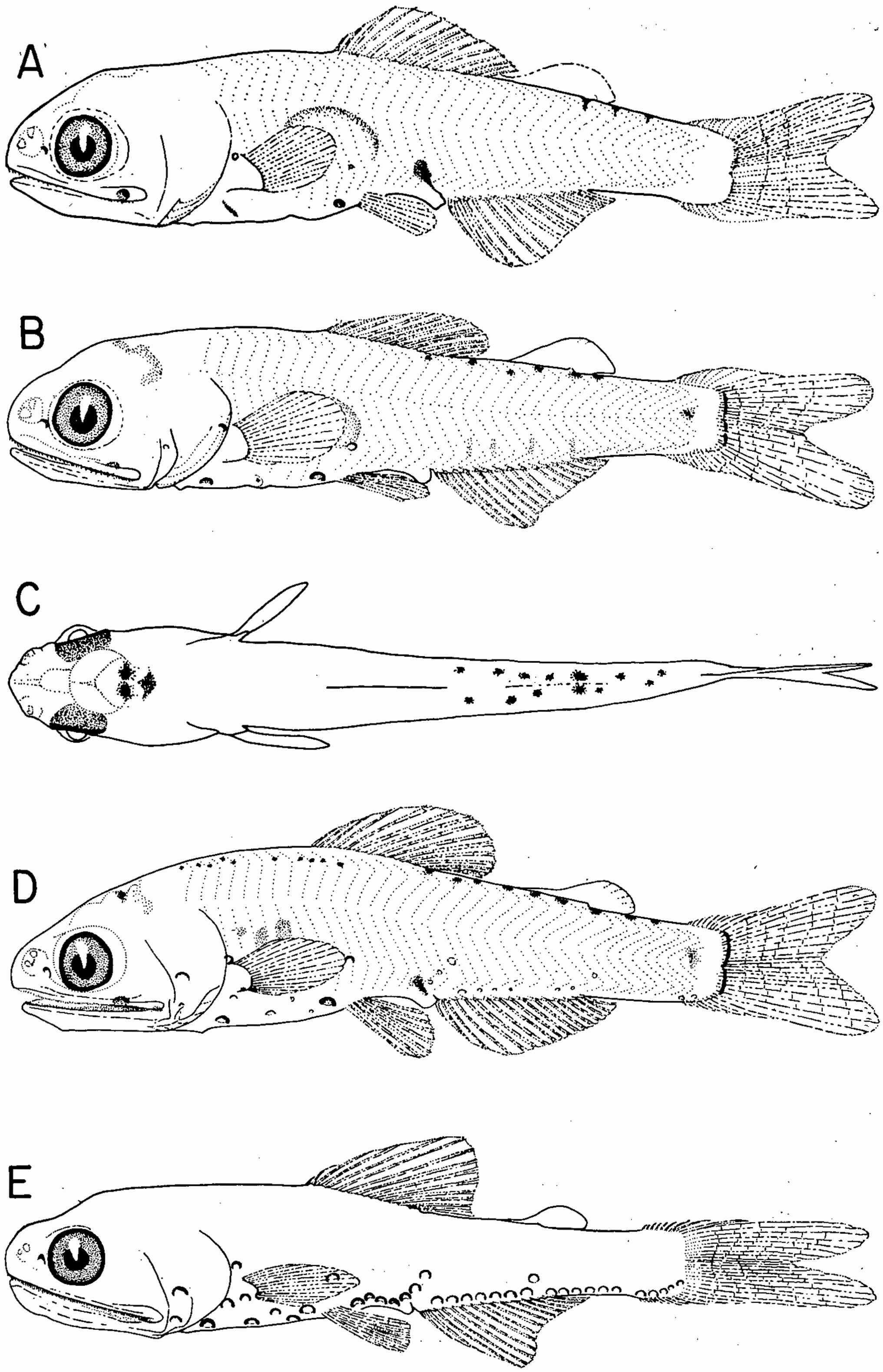


Figure 4. Developmental stages of *Lampanyctodes hectoris.* A. 11.7 mm larva; B. 13.0 mm larva; C. 13.0 mm larva, dorsal view; D. 14.9 mm transforming specimen; E. 14.2 mm juvenile.

TABLE 1. Measurements (mm) of larvae of *Lampanyctodes hectoris*. (Specimens between dashed lines are undergoing notochord flexion).

Body length	Snout to anus	Head length	Head width	Snout length	Eye width	Eye length	Length of ventral eye tissue	Body depth	Pectoral fin length	Snout to origin of pelvic fin	Snout to origin of anal fin	Snout to origin of dorsal fin
3.8	1.8	0.75	0.50	0.15	0.23	0.29	–	0.49	0.20	–	–	–
4.0	1.8	0.72	0.43	0.12	0.20	0.27	–	0.43	0.19	–	–	–
4.3	2.0	0.85	0.52	0.16	0.24	0.30	–	0.45	0.25	–	–	–
4.5	2.3	0.96	0.53	0.20	0.27	0.31	–	0.63	–	–	–	–
4.8	2.5	1.0	0.70	0.26	0.29	0.37	–	0.68	0.29	–	–	–
5.0	2.6	1.2	0.75	0.25	0.38	0.43	0.02	0.85	0.20	–	–	–
5.2	2.7	1.1	0.70	0.27	0.31	0.39	–	0.73	0.35	–	–	–
5.6	2.8	1.2	0.77	0.35	0.34	0.42	0.01	0.82	0.25	–	–	–
5.8	3.1	1.4	0.78	0.32	0.38	0.46	0.01	0.86	0.36	–	–	–
6.0	3.1	1.2	0.80	0.32	0.41	0.48	0.02	0.88	0.26	–	–	–
6.2	3.2	1.4	0.83	0.33	0.43	0.48	0.04	1.0	0.33	2.4	–	–
6.4	3.7	1.4	0.90	0.34	0.49	0.55	0.03	1.1	0.27	2.8	–	–
6.6	3.8	1.7	1.0	0.45	0.53	0.62	0.04	1.2	0.32	2.8	3.9	3.0
6.8	4.0	1.7	1.0	0.36	0.57	0.55	0.01	1.2	0.28	3.0	4.2	2.8
7.0	4.0	1.7	1.1	0.40	0.52	0.63	0.02	1.2	0.56	3.1	4.2	3.2
7.2	4.2	1.9	1.0	0.40	0.57	0.68	–	1.4	0.46	3.1	4.3	3.2
7.5	4.2	1.8	1.0	0.43	0.52	0.62	0.03	1.3	0.57	3.2	4.3	3.3
7.7	4.6	1.9	1.0	0.40	0.64	0.71	0.04	1.3	0.52	3.3	4.6	3.2
8.0	4.6	2.0	1.2	0.45	0.61	0.71	–	1.5	0.60	3.3	4.7	3.3
8.2	4.9	2.2	1.2	0.49	0.68	0.75	0.02	1.6	0.65	3.8	4.9	3.6
8.7	5.0	2.3	1.3	0.50	0.77	0.87	0.02	1.8	0.87	3.8	5.0	3.8
9.2	5.2	2.2	1.2	0.60	0.73	0.84	–	1.8	1.0	4.2	5.3	4.1
9.7	5.7	2.5	1.3	0.68	0.73	0.86	–	2.0	1.0	4.2	5.7	4.2
10.1	6.2	2.9	1.4	0.71	0.87	0.91	–	2.2	1.2	4.6	6.2	4.5
10.5	6.5	2.9	1.6	0.73	0.88	1.0	–	2.3	1.2	4.8	6.5	4.8
10.8	6.7	3.0	1.7	0.78	0.83	0.95	–	2.4	1.4	5.1	6.7	4.8
11.0	6.8	3.0	1.6	0.74	0.79	0.95	–	2.3	1.3	5.0	6.9	4.8
11.7	7.1	3.3	1.7	0.93	0.87	1.0	–	2.6	1.5	5.4	7.1	5.2
12.0	7.5	3.3	1.8	0.83	1.0	1.1	–	2.8	1.5	5.7	7.5	5.3

TABLE 1. (*Continued*)

Body length	Snout to anus	Head length	Head width	Snout length	Eye width	Eye length	Length of ventral eye tissue	Body depth	Pectoral fin length	Snout to origin of pelvic fin	Snout to origin of anal fin	Snout to origin of dorsal fin
12.3	7.4	3.4	1.8	0.80	1.0	1.0	–	2.9	1.4	5.5	7.4	5.4
13.0	7.8	3.6	2.2	0.90	1.0	1.2	–	2.9	1.7	5.8	7.8	5.8
13.8	8.3	3.7	2.0	0.96	0.98	1.0	–	3.2	1.8	6.2	8.4	6.2
14.0	8.9	4.1	1.9	0.93	1.1	1.2	–	3.2	1.6	7.0	9.1	6.1
14.9*	8.8	4.0	2.2	0.95	1.1	1.2	–	3.7	2.1	6.6	8.8	6.4
14.2**	8.6	4.6	2.0	1.0	1.2	1.2	–	3.2	1.9	6.8	8.8	6.7
16.0**	9.8	5.0	2.8	0.94	1.3	1.3	–	3.5	2.5	7.2	9.9	7.1
21.2**	13.0	6.6	3.2	1.0	2.0	2.0	–	4.9	4.0	9.8	13.0	9.5

* Transforming specimen.
** Juvenile.

TABLE 2. Meristics from cleared and stained larvae of *Lampanyctodes hectoris*.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb			left	right	
7.5	7	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7.7	10	9	0	1	3	3	5	5	–	–	–	–	5	–	–	–	–
8.3	10	9	–	–	3	3	4	5	–	–	–	–	7	–	–	–	–
8.7	10	9	2	3	4	4	7	7	1	3	–	–	11	7	–	–	–
9.2	10	9	3	4	5	5	9	9	2	3	–	–	13	9	4	4	–
9.6	10	9	4	5	6	6	10	9	4	3	–	–	14	12	5	5	–
10.1	10	9	5	6	7	7	12	12	4	3	–	–	15	12	7	7	–
10.5	10	9	6	7	7	7	11	11	4	3	–	–	16	13	7	7	–
11.1	10	9	7	8	8	8	11	12	4	3	–	–	16	13	7	7	26
11.8	10	9	7	8	8	8	13	13	4	3	0	12	16	14	8	8	37
12.3	10	9	–	9	7	8	–	12	4	3	5	14	15	14	8	8	37
12.7	10	9	9	11	9	9	13	13	4	3	8	17	16	14	8	8	37
13.2	10	9	9	10	9	9	12	12	4	3	4	13	16	14	8	8	37
14.4	10	9	8	9	10	10	13	12	4	3	10	17	16	14	8	8	37
15.9	10	9	10	10	9	9	13	13	4	3	10	20	16	14	8	8	37

Diagnostic features.—As for other species of lanternfishes, the pelagic eggs of *L. hectoris* are not known. The smallest larvae in our collection were 3.8 mm. Larvae obtain a moderate size in comparison with those of related genera. The largest larva in our collection is 14.4 mm and the smallest juvenile is 14.2 mm SL. A 14.9 mm specimen is undergoing transformation. Larvae of *L. hectoris* have a unique sequence of photophore development, beginning with the Br_2 in 6 mm larvae and followed by the Vn in 7 mm larvae, the PO_5 in 8 mm larvae, and the PLO and PO_1 in 11 mm larvae. Although several other genera develop this same complement of early-forming photophores, as explained in detail in a later section, none develops them in this sequence. Small larvae which have not developed photophores may be identified by their pattern of melanophores, the most characteristic of which are a persistent series of four to eight ventral tail melanophores, two melanophores in the foregut region, a bilateral pair at the divergence of the terminal region of the gut, a series of embedded spots above the mid-gut, and a melanistic shield above the developing gas bladder. In mid- and late-stage larvae, a bilateral series of melanophores develops on the posterior dorsum.

Morphology.—Larvae of *L. hectoris* have no striking morphological features. Body depth increases from a mean of 14 percent of the body length in preflexion larvae, to 18 percent in larvae undergoing flexion, to 22 percent in postflexion larvae and 23 percent in newly transformed juveniles (Table 1). Snout-anus length averages 50 percent of the body length in preflexion larvae, 58 percent during flexion and 60 percent in later developmental stages. Head size is moderate; relative head length increases gradually from a mean of 21 percent of body length in preflexion larvae to 25 percent during flexion, 27 percent in postflexion larvae and 31 percent in early juveniles. Relative head width decreases gradually during development; it averages 62, 58, and 54 percent of the head length for the three major larval stages and 49 percent in early juveniles. Snout length is moderate, averaging 24 percent of the head length over the entire larval period and shortens to 19 percent in early juveniles. The eye is moderately large; eye length averages 36 percent of the head length in larvae up to the completion of notochord flexion, is reduced to a mean of 33 percent in postflexion larvae and further to 27 percent in early juveniles. The eye is slightly elliptical in preflexion larvae; eye width averages 82 percent of eye length, but this increases to a mean of 89 percent in later larval stages and the eyes of early juveniles are round. There is a sliver of ventral choroid tissue that appears in larvae between 5.0 and 9.0 mm. It reaches a maximum relative depth of 8 percent of the eye length and is only slightly paler in color than the eye itself.

Ossification of some important larval features is as follows. Vertebrae begin to ossify at about 11.1 mm length and the full complement of 36 to 37 is ossifying in larvae 12.3 mm and larger. Branchiostegal rays begin to ossify in 7 mm larvae, but, the full complement of 11 as listed by Paxton (1972) is not achieved in larvae nor in the earliest juveniles.

The maxillary is ossifying in larvae as small as 3.9 mm but develops no teeth. The dentary is ossifying and bearing teeth by 5.9 mm, as is the premaxillary. Teeth are uniserial on the premaxillary with the anterior five or six teeth larger than the remainder; as many as 20 conical, usually straight teeth form on late-stage larvae. On the posterior two-thirds of each dentary bone a series of six to eight conspicuous hooked teeth form early in the larval period. The hooked part of each tooth projects anteriad at almost right angles to the base of the tooth. They persist to transformation. The dentary teeth anterior to these, and later between and posterior to the hooked teeth, are conical, straight and uniserial anteriorly. Late-stage larvae have more than 30 such dentary teeth. The hooked and uniserial teeth present on the jaws of larvae are shed or resorbed and replaced by the wide bands of numerous small teeth at transformation.

Fin formation.—A pectoral fin with differentiated base and blade is present in our smallest larvae (3.8 mm). The base remains small and inconspicuous throughout the larval period as does the blade, which has a rounded posterior margin. At transformation the pectorals extend posteriad to the origin of the pelvics. Rays begin to ossify in 7 mm larvae in a dorsal to ventral sequence and the full complement of 13 to 14 is present in larvae as small as 11.8 mm (Table 2).

The anlage of the caudal fin is present in larvae as small as 5.0 mm. The principal caudal rays begin to ossify in 7 mm larvae and the full complement of 10+9 rays is ossifying in a 7.7 mm specimen. Procurrent caudal rays also begin to ossify in 7 mm larvae and the full complement of 8 to 10 superior and 9 to 11 inferior rays is ossifying in 12 mm larvae. The hypural elements begin to ossify in 8 mm larvae and the full complement of four superior and three inferior elements is ossifying in 9 mm larvae. Flexion of the notochord begins when the larvae are about 6.5 mm long and is completed at about 8.0 mm length.

The anal and dorsal fin bases begin to form during notochord flexion. Anal fin rays are beginning to ossify in a 7.7 mm larva and dorsal rays are ossifying in an 8.7 mm larva. The full complements of 16 to 17 anal and 13 to 14 dorsal rays are ossifying in larvae 10.5 mm and larger. In both the anal and dorsal fins, the rays ossify posteriad and anteriad from the more central rays. In both fins the last ray to form is the short anteriormost ray.

Pelvic fin buds appear at about 6.2 mm length, but, the rays do not begin to ossify until the larvae reach about 9 mm. The full complement of 8 pelvic rays is ossifying in larvae 11.8 mm and larger.

Pigmentation.—Preflexion larvae (3.8 to ca. 6.0 mm) have two pairs of pigment dashes developed on the gut. The anterior pair is on the foregut posterior to the cleithra, while the posterior pair is on the free terminal section of the gut. The most conspicuous pigment in preflexion larvae is the series of four to eight melanistic spots or dashes on the ventral midline of the tail. By the end of the preflexion stage, melanistic pigment is developing over the gas bladder. Also the anterior foregut spots have coalesced and moved forward and dorsad to form a pigment shield over the anterior part of the liver.

Flexion larvae (6.2 to ca. 7.5 mm) have essentially the same pigment as in preflexion larvae. The ventral tail spots range from three to seven (mean of 4.4 for 27 specimens). The median ventral foregut pigment spot or patch is continuously present as are the paired patches or streaks of pigment on the free terminal section of the gut. Pigment above the gas bladder increases in amount, with sometimes a pair of internal pigment spots located between the gas bladder and the termination of the gut.

A single pigment spot develops over the hind brain in some specimens; of the 27 specimens between 6.2 to 7.5 mm, only four had this head pigment spot. Two specimens in this size range, 6.5 and 7.2 mm respectively, had a double row of small dorsal pigment spots (seven to eight spots per side) extending for most of the length of the tail portion of the body.

In postflexion larvae (7.7 to 13.9 mm) the pigment areas already described either persist or are more consistently present, and additional pigment develops on the head, back, and in the caudal region. The pigment over the gas bladder increases in extent and begins to spread laterally. Melanistic pigment is present on the cleithral margin forward of the pectoral base on most larvae 9.2 mm and larger. The ventral midline of pigment spots becomes imbedded and sometimes faint, but was absent on only four specimens. The number of pigment spots ranges between two and five (mean of 3.6 spots on 43 specimens). The imbedded pigment spot on the hind brain occurs on about ⅓ of the larvae between 7.7 and 8.7 mm, but thereafter is consistently present. By about 10 mm, two spots form over the cerebellum and are usually present on larvae larger than this. The double row of dorsal tail pigment spots is only sporadically present on larvae under 10.5 mm, but consistently present on larger larvae. The rows extend from about the termination of the dorsal fin, almost to the procurrent caudal rays; the usual count is seven or eight spots per side, but the range is from two to thirteen spots. Internal pigment forms over the hypurals, usually adjacent to the ural centrum; this pigment, first observed on a 7.7 mm specimen, is infrequently present on larvae under 10.5 mm. Pigment also forms at the hypural edge of the caudal fin. It was first observed on a 7.2 mm larva and was sporadically present until 10.5 mm. On older specimens this pigment becomes almost continuous along the hypural edge. The 14.9 mm transforming specimen added a line of dorsal pigment spots to the nape and trunk; however, a 14.2 mm juvenile had pigment over the entire body and the peritoneum was conspicuously black.

Photophore development.—A number of photophores form on larvae of *Lampanyctodes* prior to transformation. As is usual in myctophids, the Br_2 pair is the first to form; it was consistently present on specimens 6.6 mm and larger. The Vn, the second pair to form, was first observed on a 7.5 mm specimen and was consistently present by 7.8 mm. The third pair, PO_5, was present by 8.7 mm. A specimen 11.2 mm had two additional pairs, the PLO and PO_1; however, specimens 11.7 and 11.8 mm had added only the PLO pair, indicative that it forms somewhat sooner than the PO_1. Specimens 12.0 mm and larger consistently had both these pairs. A 12.7 mm specimen had three additional pairs faintly formed, the VLO, OP_2, and PO_2; however, none of these was present on a 13.7 mm specimen, and only the VLO pair was present on a 13.8 mm and a 14.4 mm specimen. A transforming specimen 14.9 mm long had the majority of photophores formed. The initial five pairs to form, the Br_2, Vn, PO_5, PLO and PO_1 became conspicuous photophores soon after their formation. This was not the case for the three other pairs

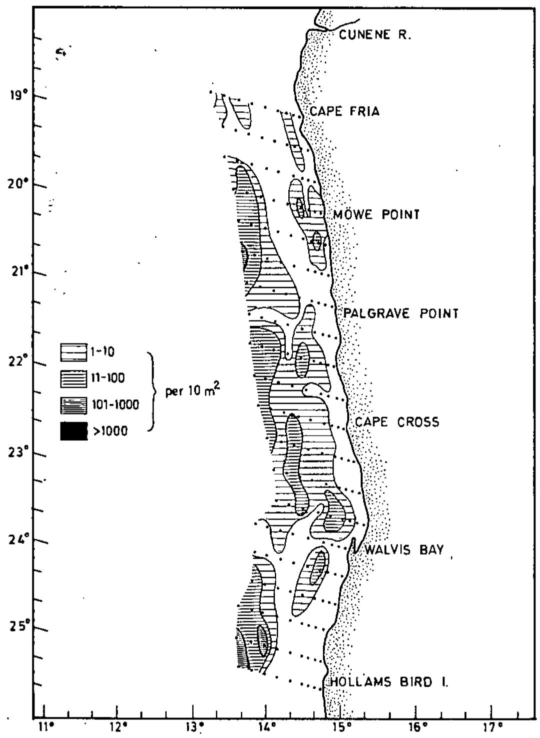


Figure 5. Distribution and abundance of larvae of *Lampanyctodes hectoris* on SWAPELS Survey 1 (August 1972 to March 1973). Numbers represent cumulative standard haul totals.

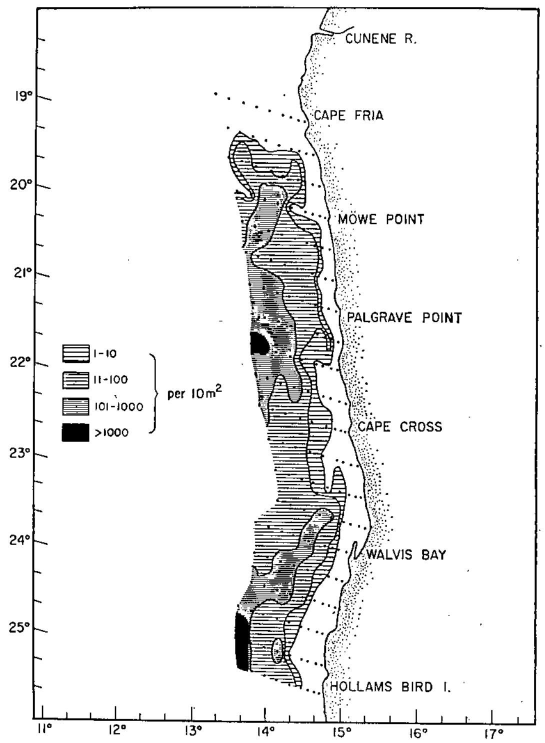


Figure 6. Distribution and abundance of larvae of *Lampanyctodes hectoris* on SWAPELS Survey 2 (August 1973 to April 1974).

mentioned above which, at best, were but faintly developed on late-stage larvae prior to transformation.

DISTRIBUTION

Lampanyctodes hectoris is a neritic species associated with land masses in the vicinity of the subtropical convergence. It is known from South Africa, New Zealand, Southern Australia, and Chile, but apparently does not occur in the western Atlantic off Argentina (McGinnis, 1974). Where it occurs, it is highly abundant, as demonstrated by the fishery off South Africa. It may occur in commercial abundance in other southern ocean areas.

There are no available data on the distribution and abundance of the larvae in the area of the fishery off South Africa, but SWAPELS provides larval data from an area just to the north of the fishery. Results from the two year survey show that larvae of the family Myctophidae formed 9.75 percent of all the fish larvae taken and larvae of *L. hectoris* comprised over 85 percent of all myctophid larvae. This species was widely distributed between latitudes 19° and 25° S (Figs. 5 and 6). Larvae were found at distances of 8 to 112 km from the coast but were most abundant in offshore waters especially between Möwe Point (20°20′ S) and Cape Cross (22° S) and between Walvis Bay (23° S) and Hollams Bird Island (25° S). Approximately 93 percent of all larvae were taken during the months of August, September, October, and November of both years. Early larval stages (those less than 5.0 mm in length) were common from August to October, but were most abundant in the plankton in August particularly in the region west of Hollams Bird Island. Over 62 percent of all early larval stages were taken during this month. The larvae of *L. hectoris* were found at surface temperatures ranging from 13.9° to 21.5° C. However, over 60 percent of all larvae occurred at mean surface temperatures of 14.0° to 15.5° C.

SYSTEMATIC RELATIONSHIPS

Although the photophores of *L. hectoris* were not mentioned in the original description of the species

(Günther, 1876), Fraser-Brunner (1949) was well aware of the unique arrangement of the light organs and, accordingly, created the genus *Lampanyctodes* for this species. He noted the marked ventral placement of the two longitudinal series of photophores, a feature which he thought was more characteristic of the "primitive" myctophine lanternfishes than of the lampanyctine genera to which it was obviously allied on the basis of morphological characters. He mentioned particularly the horizontal positioning of the two PVO photophores, an arrangement found only in the myctophine genera *Protomyctophum*, *Diogenichthys*, and *Benthosema*. His view of *Lampanyctodes* as a primitive lampanyctine genus is demonstrated by the statement, "this genus is clearly indicative of the form from which *Lampanyctus*, *Gymnoscopelus* and their allies have been derived." He did not elaborate on the relationships of *Lampanyctodes* with other lampanyctine genera nor did he construct a higher classification for lanternfishes.

It remained for Paxton (1972) to formally recognize the two subfamilies Myctophinae and Lampanyctinae and to construct a higher classification that included six tribes, two in the Myctophinae and four in the Lampanyctinae. In the latter subfamily he recognized the monotypic tribe Notolychnini, the tribe Lampanyctini consisting of eight genera, Diaphini with two genera, and Gymnoscopelini with eight genera. *Lampanyctodes* was important in his tribal arrangement as shown by his statement "the Diaphini and Gymnoscopelini are closely related, for the most primitive genus of each group, *Lobianchia* of the Diaphini and *Lampanyctodes* of the Gymnoscopelini, share a number of characters. Each form has widely ossified pubic plates, a relatively low number of ventral procurrent rays, well-developed caudal glands, one or two elevated PO photophores, and an arched or elevated series of VO photophores . . . ." He viewed *Lampanyctodes* as an essentially intermediate form that branched from the main line of gymnoscopeline evolution soon after the divergence of this tribe from the Diaphini.

Using the combination of larval and adult characters, Moser and Ahlstrom (1972) proposed a phylogenetic scheme for the subfamily Lampanyctinae that recognized the four tribes of Paxton (1972) but differed in the placement of certain genera in the Lampanyctini and Gymnoscopelini. We believe that the triad of genera, *Bolinichthys*, *Ceratoscopelus* and *Lepidophanes* belong in the Gymnoscopelini whereas Paxton placed them in the Lampanyctini. Also, we would include two other of Paxton's lampanyctine genera, *Lampadena* and *Taaningichthys*, in the Gymnoscopelini. These form a triad with the recently described *Dorsadena*. Our conception of tribal and generic relationships in the subfamily Lampanyctinae based on a combination of larval and adult characters is shown in the dendrogram (Fig. 7). Essentially the tribe Gymnoscopelini consists of the two above mentioned triads, the triad of *Lampichthys*, *Notoscopelus* and *Scopelopsis*, the well differentiated genus *Gymnoscopelus* and two monotypic isolated genera, *Hintonia* and *Lampanyctodes*. Based on Paxton's adult characters, and the larval characters given below and in Moser and Ahlstrom (1972), the genus *Gymnoscopelus* is closest to the Diaphini and in a direct line from the original tribal split. We have not yet identified the larvae of *Hintonia* and accept the view of Paxton that the genus has no distinct relationship to any member of the tribe and that this form split off early from the ancestral stock.

The genus *Lampanyctodes* is the most problematic and, phylogenetically, the most intriguing genus in the tribe. Its photophore arrangement is so unusual that it warrants a brief review. All photophores are relatively low on the body, including the PLO, VLO, 3rd SAO, POL and terminal Prc, all of which are well below the lateral line. Both a Dn and Vn pair of eye photophores are formed, although the Dn develops quite late. This feature is shared with *Lampichthys*, *Scopelopsis*, *Notoscopelus*, *Hintonia*, *Diaphus* (usually) and *Gymnoscopelus* among the Lampanyctinae and with most genera of Myctophinae.

Of particular interest is the horizontal arrangement of the two PVO photophores, an arrangement not found in any other genus of the Lampanyctinae, but present in three myctophine genera, as previously noted.

Although *Lampanyctodes* has the usual number of PO photophores, five, it is unique in having the PO_3 elevated rather than the PO_4. *Lampanyctodes* also has the usual number of VO photophores for Lampanyctinae, five, but has the series evenly arched, an unusual arrangement also found in some *Lampanyctus*. None of the AO series is elevated, the usual arrangement in most kinds of lanternfishes. The presence of a single POL is shared with all genera of *Myctophinae* except *Hygophum*, and with a half dozen genera of Lampanyctinae (*Diaphus*, *Lobianchia*, *Taaningichthys*, *Lampadena*, *Gymnoscopelus* and *Steno-*

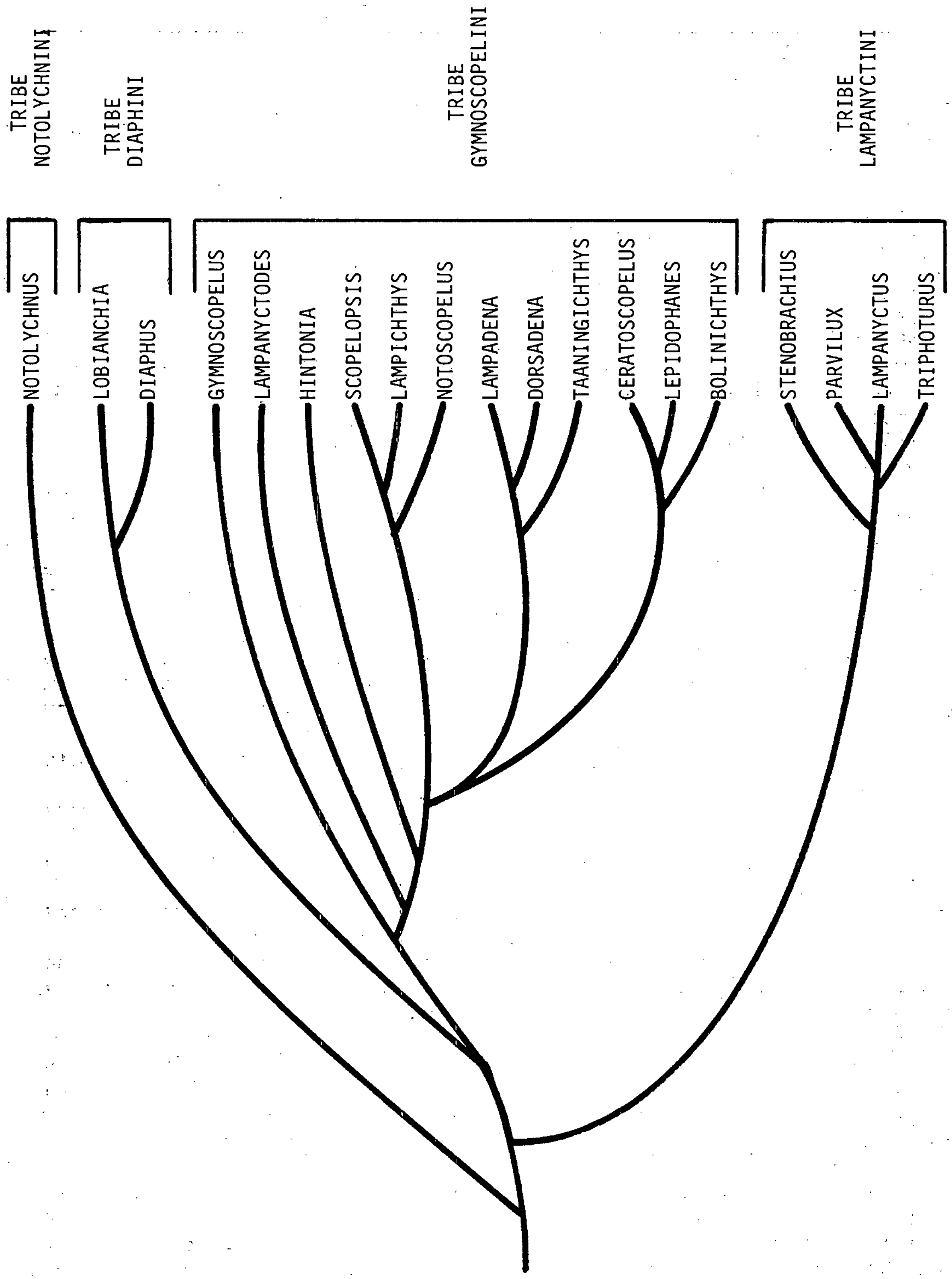


Figure 7. Dendrogram showing the generic relationships and tribal division of the subfamily Lampanyctinae based on a combination of larval and adult characters.

TABLE 3. Size at formation and sequence of early forming photophores for 10 genera of *Lampanyctinae*.

	Size at transformation (mm)	Br_2	Vn	PO_5	PLO	PO_1
Lampanyctodes hectoris	14–15	6.6 (1)	7.8 (2)	8.7 (3)	11.7 (4)	Ca 12.0 (5)
Ceratoscopelus townsendi	16.5–18	7.0 (1)	7.8 (2)	9.0 (4)	8.7 (3)	–
Lepidophanes guentheri	–	< 9.5	< 9.5	< 9.5	< 9.5	–
Notoscopelus resplendens	19–21	4.2 (1)	9.2 (3)	6.2 (2)	Ca 15.0 (4)	–
Lampichthys rectangularis	19–21	< 7.0 (1)	9.8 (3)	8.4 (2)	Ca 16.0 (4)	16.4 (5)
Lampadena urophaos	17–21	6.2 (1)	13.4 (4–5)	9.8 (3)	7.3 (2)	13.4 (4–5)
Scopelopsis multipunctatus	16.5–17.5	5.4 (1)	11.3 (3)	10.8 (2)	–	–
Gymnoscopelus aphya	Ca 30	< 23.5 (1)	–	< 23.5 (2–3)	–	< 23.5 (2–3)
Diaphus theta	10–11	6.0 (1)	–	6.2 (2)	–	7.6 (3)
Lobianchia gemellari	–	5.5 (1)	–	7.0 (3)	–	6.2 (2)

brachius). The possession of five Prc's is unusual, as is their arrangement in an ascending line that terminates well below the lateral line.

Lampanyctodes is among the genera that develops accessory patches of luminous tissue on the body, a character shared with most members of the tribe *Gymnoscopelini*, as we interpret it, and with *Diaphus* (most species) and *Lampanyctus* (some species). None of the myctophine genera develops accessory luminous tissue other than the supra and infracaudal glands. In *Lampanyctodes* the luminous tissue develops at the bases of the dorsal, anal, pectoral and pelvic fins, before and behind the dorsal fin, and on the dorsal surface of head; this pattern is suggestive of that developed on *Ceratoscopelus* and *Bolinichthys*. No secondary photophores are developed.

The fact that, in its arrangement of light organs, *Lampanyctodes* shares so many characters with so many other genera of Lampanytinae, and even shares a fundamental character (the horizontal PVO's) with some genera of the Myctophinae has produced an understandable confusion as to the position of this genus. We would agree with Fraser-Brunner (1949) and Paxton (1972) that the genus has had a long and independent evolution but do not consider it a primitive genus. We believe it is a highly specialized form and that the ventral and basically linear placement of photophores is related to its mode of life in shallow neritic waters. Our thesis that the arrangement of ventrally placed, well developed linear series of photophores, such as is found in most Myctophinae, is an adaptation for countershading in shallow-living lanternfishes has been stated in detail in previous papers (Moser and Ahlstrom, 1972, 1974).

The relationships of *Lampanyctodes* to other genera of Gymnoscopelini is seen more clearly from an examination of larval characters. It develops the dorsal series of pigment spots found in so many members of this tribe and, more importantly, forms several of the same photophores during the larval period (Table 3).

In an attempt to analyze the position of *Lampanyctodes* in the subfamily Lampanyctinae we selected 10 larval characters and 10 adult characters of this genus and compared them with all other genera in the subfamily. *Dorsadena* and *Hintonia* were excluded since their larvae are unknown. Two groups of larval characters were selected, those related to early forming photophores, and those related to pigment patterns. Adult characters were based mostly on photophore arrangements, presence or absence of luminous caudal glands, accessory luminous tissue, secondary photophores, sexual dimorphism, keel or ridge on fifth circumorbital bone, and a supra-

TABLE 4. Larval and adult characters of *Lampanyctodes hectoris* compared with other genera of the subfamily *Lampanyctinae*.

	Lampanyctodes	*Lampichthys*	*Scopelopsis*	*Notoscopelus*	*Ceratoscopelus*	*Lepidophanes*	*Bolinichthys*	*Lampadena*	*Taaningichthys*	*Gymnoscopelus*	*Diaphus*	*Lobianchia*	*Lampanyctus*	*Triphoturus*	*Stenobrachius*	*Parvilux*	*Notolychnus*
Larval characters																	
Early forming photophores																	
Br_2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−
Vn	+	+	+	+	+	+	−	+	−	−	−	−	−	−	−	−	−
PO_5	+	+	+	+	+	+	−	+	−	+	+	+	−	−	−	−	−
PLO	+	+	−	+	+	+	−	+	−	−	−	−	−	−	−	−	−
PO_1	+	+	−	−	−	−	−	+	−	+	+	+	−	−	−	−	−
Pigment characters																	
Series of ventral pigment spots (preflexion)	+	+	+	−	+	+	+	−	−	+	+	−	− +	+	+	?	+
Ventral series retained (postflexion)	+	+	+	−	−	−	−	−	−	+	+ −	−	−	−	−	−	−
Pigment back of head	+	+	+	+	+ −	+	+	+	+	+	− +	−	+ −	−	+ late	+	−
Dorsal body pigment	+	+	+	+	+ −	+	+ −	+	+	+	−	−	− +	+	+ late	+	−
Caudal pigment	+	+	+	+	−	−	−	−	+	+	+ −	+ −	−	−	−	−	+
Adult characters																	
Supramaxillary present	+	+	+	+	−	−	−	−	−	+	−	−	−	−	−	−	−
Circumorbital 5 keel or ridge	+	+	+	+	−	−	−	−	−	+	+ −	+	−	−	−	−	?
One or more VO's elevated	+	−	−	−	+	+	+	−	−	−	+	+	+ −	+	−	−	+
Single POL	+	−	−	−	−	−	−	+	+	−	+	+	−	−	+	−	−
Dn and Vn development	+	+	+	+	−	−	−	−	−	+	+ −	−	−	−	−	−	−
Supracaudal glands developed	+	+	+	+ −	+	+	+	+	+	−	−	+	+	+	+	+	+
Infracaudal glands developed	+	+	−	−	+	+	+	+	+	−	−	+	+	+	+	+	−
Accessory luminous tissue	+	+	+	+	+	+	+	−	−	+	+ −	−	+ −	−	−	−	−
Sexual dimorphism lacking	+	+	−	−	−	?	−	+	−	−	−	−	+	+	+	+	−
Secondary photophores lacking	+	−	−	+	+	−	−	+	+	+	+	+	+ −	+	+	+	+

maxillary. Presence of a character was rated as a "plus" and absence as a "dash". Because of variability occurring among species in some genera, some characters had to be rated both "plus" and "dash" (Table 4). In making a summation, characters rated as both "plus" and "dash" were weighted ½.

We do not assume that these 20 characters are of equal phylogenetic importance, even though none is trivial. We selected characters that are present or absent, hence had to ignore equally relevant characters that can not be so rated. Among the adult characters chosen, luminous glands on the caudal peduncle (supra and infra) probably are the most problematical, in that their presence or absence may not be as important phylogenetically as are the structural and functional differences in these glands among genera. These differences cannot be simply rated by this technique.

As noted earlier, the initial five pairs of photophores to develop on *Lampanyctodes* during the larval period are Br_2, Vn, PO_5, PLO, and PO_1. As indicated in table 4, all five pairs are also developed on *Lampichthys* and *Lampadena*, although not in the same sequence as in *Lampanyctodes*. Four of the above pairs are early forming on *Notoscopelus*, *Ceratoscopelus*, and *Lepidophanes*, three of the above pairs in *Scopelopsis*, *Gymnoscopelus*, *Diaphus* and *Lobianchia* and the remaining seven genera lack early forming photophores other than the Br_2 pair. We consider the striking similarity of these early forming pairs among genera as evidence of close relationship.

The other characters selected for larvae involve pigment patterns, including the presence or absence of a row of ventral midline pigment spots on the tail of preflexion and late-stage larvae, and the development of pigment on the back of the head, along the dorsal margin of the body, or at the base of the caudal fin of postflexion larvae.

Certain relationships emerge when the characters in the table are summed. *Lampanyctodes* is found to be most closely related to *Lampichthys* (17 points), then to *Scopelopsis* (13), *Gymnoscopelus* (13), *Notoscopelus* (12½), *Lampadena* (12), *Ceratoscopelus* (11), and *Lepidophanes* (11). These genera are among those we place in the tribe Gymnoscopelini. Although it is true that larval characters strongly influence this rating, so do several of the adult characters, such as the presence of a supramaxillary, Dn and Vn photophores, and accessory luminous tissue. *Lampanyctodes* is close to three genera that Paxton (1972) and Moser and Ahlstrom (1972) have previously shown to be closely allied (*Lampichthys*, *Scopelopsis*, and *Notoscopelus*), but also to *Gymnoscopelus*, and must have split off from the ancestral line of the triad soon after it diverged from the *Gymnoscopelus* line.

ACKNOWLEDGMENTS

We would like to thank Barbara Sumida and Elaine Sandknop of the Southwest Fisheries Center, La Jolla, California, for their help in staining the larvae, and Henry Orr for drafting figures 4 and 5. We thank R. McGinnis (Pacific Lutheran University), B. Nafpaktitis (Univ. Southern California), and J. Paxton (Australian Museum) for reviewing the manuscript and offering valuable suggestions.

LITERATURE CITED

Alverson, F. G. 1961. Daylight surface occurrence of myctophid fishes off the coast of central America. Pac. Sci., 15:483.

———. 1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. Bull. Inter-Amer. Trop. Tuna Comm., 7:295–396.

Backus, R. H., J. E. Craddock, R. L. Haedrich, D. L. Shores, J. M. Teal, A. S. Wing, G. W. Mead, and W. D. Clarke. 1968. *Ceratoscopelus maderensis*: Peculiar sound-scattering layer identified with this myctophid fish. Science, 160(3831): 991–993.

Baird, R. C., T. L. Hopkins, and D. F. Wilson. 1975. Diet and feeding chronology of *Diaphus taaningi* (Myctophidae) in the Cariaco Trench. Copeia, 1975(2):356–365.

Barham, E. G. 1966. Deep scattering layer migration and composition: Observations from a diving saucer. Science, 151(3716):1399–1403.

———. 1971. Deep-sea fishes: Lethargy and vertical orientation. *In* Proceedings of an International Symposium on Biological Sound Scattering in the Ocean, G. B. Farquhar (ed.), Washington Maury Center for Ocean Science, 629 pp.

Centurier-Harris, O. M. 1974. The appearance of lanternfish in commercial catches. S. Afr. Shipp. News Fish. Ind. Rev., 29(1):45.

Collard, S. B. 1970. Forage of some eastern Pacific midwater fishes. Copeia, 1970(2):348–354.

Fitch, J. E., and R. L. Brownell, Jr. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Bd. Canada, 25:2561–2574.

Günther, A. C. L. G. 1876. Remarks on fishes, with descriptions of new species in the British Museum, chiefly from southern seas. Ann. Mag. Nat. Hist., (Ser. 4) 17(43):389–402.

Holton, A. A. 1969. Feeding behavior of a vertically migrating lanternfish. Pac. Sci., 23:325–333.

Legand, M., and J. Rivaton. 1969. Cycles biologiques des poissons mésopélagiques de l'est de l'Ocean Indien. Troisième note: Action prédatrice des poisson micronectoniques. Cah. O.R.S. T.O.M. Sér. Océanog., 7:29–45.

McGinnis, R. 1974. Biogeography of lanternfishes (Family Myctophidae) south of 30° south. Unpubl. Ph.D. Dissertation, Univ. of Southern California, 366 p.

Manzer, J. I. 1968. Food of Pacific salmon and steelhead trout in the northeast Pacific Ocean. J. Fish. Res. Bd. Canada, 25(5):1085–1089.

Mead, G. W., and F. H. C. Taylor. 1953. A collection of oceanic fishes from off northeastern Japan. J. Fish. Res. Bd. Canada, 10(8):560–582.

Moser, H. G., and E. H. Ahlstrom. 1970. Development of lanternfishes (Family Myctophidae) in the California Current. Part I. (Species with narrow-eyed larvae). Bull. Los Angeles Co. Mus. Nat. Hist., Sci., 7, 145 pp.

———. 1972. Development of the lanternfish, *Scopelopsis multipunctatus* Brauer 1906, with a discussion of its phylogenetic position in the family Myctophidae and its role in a proposed mechanism for the evolution of photophore patterns in lanternfishes. Fish. Bull., U.S., 70: 541–564.

———. 1974. Role of larval stages in systematic investigations of marine teleosts; The Myctophidae, a case study. Fish. Bull., U.S., 72:391–413.

Nakamura, E. I. 1970. Observations on the biology of the myctophid, *Diaphus garmani.* Copeia, 1970(2):374–377.

O'Toole, M. J. 1974. Fish larval investigations off South West Africa. S. Afr. Shipp. News Fish. Ind. Rev., 29(11):53–59.

Paxton, J. R. 1967. Biological notes on southern California lanternfishes. California Fish Game, 53(3):214–217.

———. 1972. Osteology and relationships of the lanternfishes (family Myctophidae). Bull. Los Angeles Co. Mus. Nat. Hist., Sci., 13, 81 pp.

Pearcy, W. G., and R. S. Mesecar. 1971. Scattering layers and vertical distribution of oceanic animals off Oregon. *In* Proceedings of an International Symposium on Biological Sound Scattering in the Ocean, G. B. Farquhar (ed.), Washington Maury Center for Ocean Science, 629 pp.

Pereyra, W. T., W. G. Pearcy, and F. E. Carvey, Jr. 1969. *Sebastodes flavidus,* a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Bd. Canada, 26(8):2211–2215.

Pinkas, L., M. S. Oliphant, and J. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. California Fish Game, Fish. Bull., 152, 105 pp.

Shimada, B. M. 1948. Records of lanternfish in Puget Sound. Copeia, 1948(3):227.

Accepted for publication May 1, 1976.

Vie Milieu, 1974, Vol. XXIV, fasc. 3, sér. A, pp. 443-452.

EARLY DEVELOPMENT OF THE ROUND HERRING *ETRUMEUS TERES* (DE KAY) FROM THE SOUTH EAST ATLANTIC

by Michael J. O'Toole and David P. F. King
Sea Fisheries Branch, Cape Town, South Africa

ABSTRACT

The eggs and early larval stages of the round herring (*Etrumeus teres*) are described from the Cape Peninsula. Eggs measured from 1,32 mm to 1,47 mm in diameter. Newly hatched larvae measured between 3,85 mm and 4,50 mm. Eggs were incubated through a series of temperatures ranging from 11,0° to 20,5 °C. Hatching occurred after 135 hours at 11,0 °C and 36 hours at temperatures of 20,5 °C.

INTRODUCTION

While investigating the early life history of the pilchard *Sardinops ocellata* off the Cape Peninsula in December 1973, large numbers of unidentified clupeoid eggs at various stages of development were collected in the plankton. On hatching, they were found to be those of the round herring *Etrumeus teres* (De Kay).

The round herring, known locally in the Cape as the red-eye sardine is widely distributed throughout the world and is found along the Atlantic and Pacific coasts of America, eastern and south-western coasts of South Africa, south coast of Australia, coasts of Japan, Galapagos Islands, eastern Mediterranean and Red Sea (Whitehead, 1963).

The genus *Etrumeus* has recently been revised (Whitehead, 1963) and is now thought to consist of one species.

The total catch of red-eye sardine in South Africa rose from 5 000 metric tons in 1966 to approximately 26 000 tons in 1973. Consequently, the species has become one of the more important fish in Cape waters during recent years. The eggs and larvae of *E. teres* (= *E. micropus*) have been described from Japanese waters by MITO (1961), UCHIDA (1958) and from the Gulf of Mexico by HOUDE and FORE (1973). The early stages of the species from South African waters have not been described and rates of development, a common criterion required for abundance estimates of a spawning population, are unknown.

MATERIALS AND METHODS

Eggs were collected from the Sea Fisheries Branch research vessel *Benguela,* about 15 km due west of Duiker Point at 1735 hours on December 10th (Fig. 1). A plankton net of 1 metre diameter and 0,940 mm mesh size was towed at the surface. Water temperature at the time of collection was 16.5 °C.

The sample was sorted and the eggs removed by pipette and transferred to a large beaker of fresh sea water. The eggs were then separated according to their stages of development and two of each stage were placed into a series of incubator tubes containing 100 ml of sea water.

The incubator was constructed of an aluminium gradient block in which ten different temperatures ranging from 11,0° to 20,5 °C (± 0,1 °C) were maintained simultaneously. The system was based on the design of THOMAS *et al* (1963). Observation on egg development were made every 30 minutes during the early stages but thereafter were conducted at longer intervals.

MS-222 at concentrations of 1 : 20,000 was used to anaesthetize larvae for observation and measurement. Selected individuals were preserved at regular intervals to provide a series of developmental stages of eggs through to hatching.

RESULTS

DESCRIPTION OF THE EGG.

The egg is smooth, spherical, has a large lightly segmented yolk, a narrow perivitelline space (0,125 - 0,165 mm) and no oil globule. Egg diameter ranged from 1,32 to 1,47 mm with a mean of 1,37 mm for 160 eggs measured.

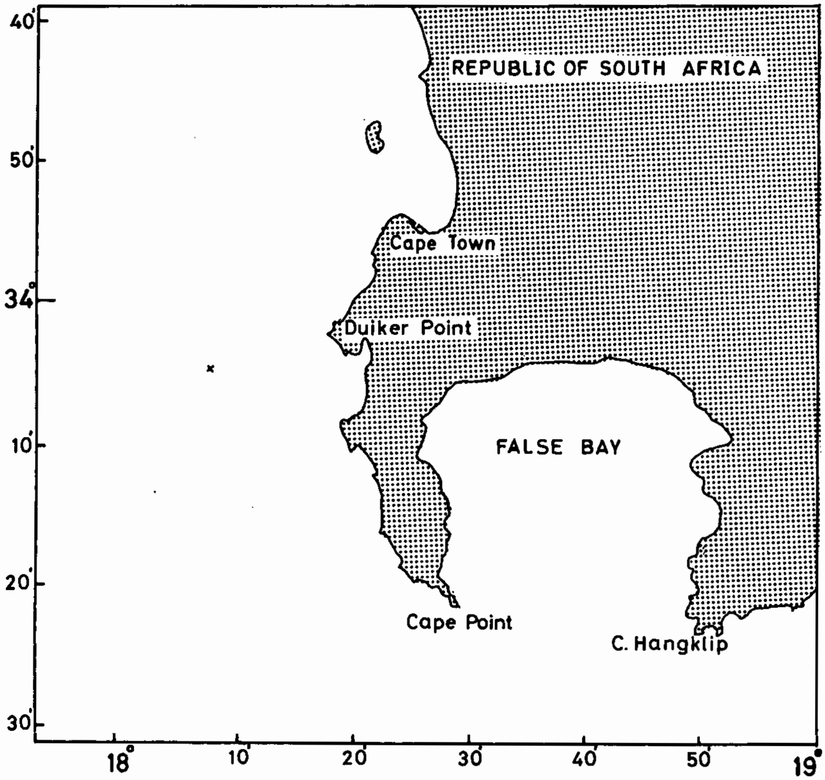


Fig. 1. — Map of the Cape Peninsula showing location where eggs were collected (x).

Development of the egg.

The blastodermal cap stage was the earliest developing egg collected in the plankton (fig. 2 A). Other stages including those of blastula formation (fig. 2 B), blastopore closure and tail separation were also present in the collection. Miller (1952) working on a related clupeid *Sardinops caerulea* observed that the time from fertilization to early blastodisc formation took 5½ hours at 16,8 °C. Assuming that blastodermal cap stage eggs were 4-6 hours old, spawning would have occurred about midday.

Prior to blastopore closure (fig. 2 C), light dendritic melanophores develop on the forehead, between the optic cups and on the hind brain region. Melanophores are also present along the dorsal

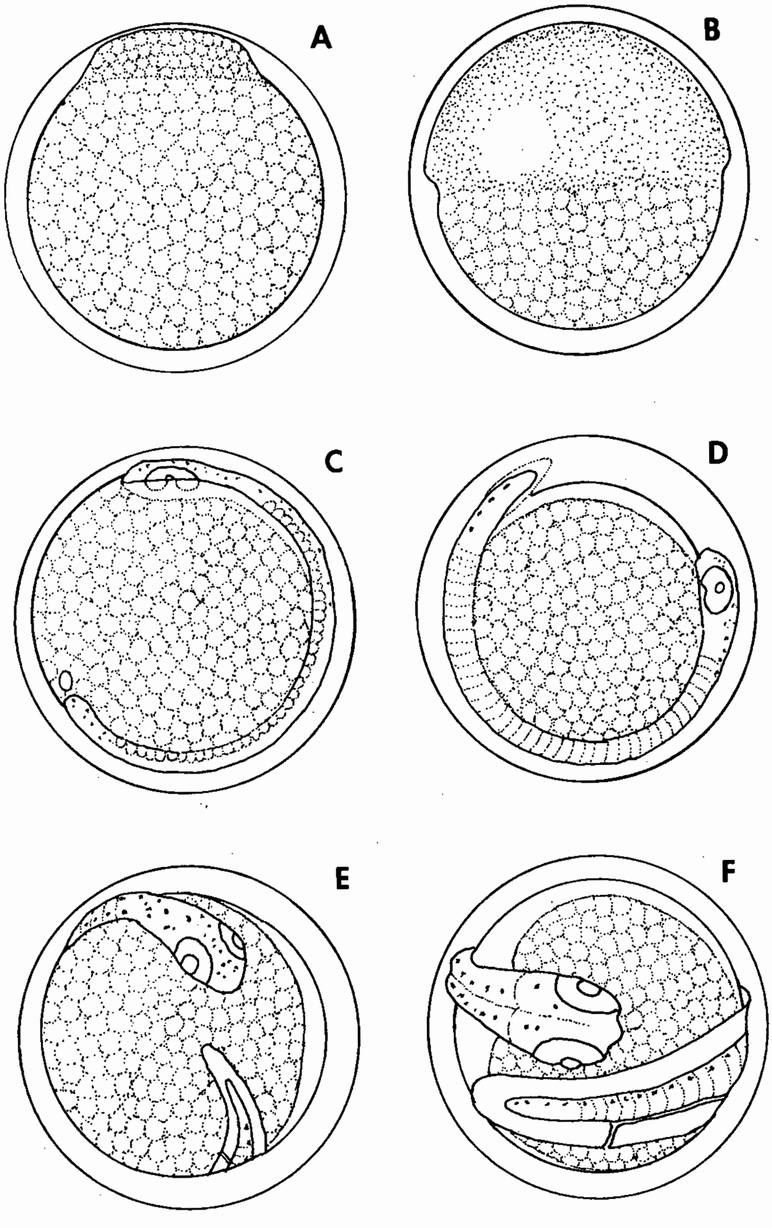


FIG. 2. — Stages in the development of round herring *Etrumeus teres* eggs. A. Blastodermal cap ; B. Blastula formation ; C. Blastopore stage ; D. Tail separation ; E. Advanced embryo ; F. Final stages of development.

surface of the embryo on each side of the notochord and extend from the hind brain to about one-third of the body length. The tail is lightly speckled with pigment spots. After the blastopore has closed the embryo lengthens and thickens. At tail separation the fin folds develop and the body somites extend to the caudal region. Melanophores on the tail are more pronounced and about 40 body myotomes can be counted (fig. 2 D). The dorsal pigmentation by this time extends almost the length of the body. As the embryo grows, the tail elongates and begins to flex around the yolk. The anus is visible as a small depression on the posterior part of the ventral fin hold (fig. 2 E). The dendritic melanophores on the dorsal surface begin to migrate ventrally in the anterior half of the body. Eggs were observed to sink to the bottom of the tubes during late development, indicating a change in specific gravity. The advanced embryo eventually ruptures the egg case by a series of rapid flexing movements and escapes head first.

Development of the larva.

Live newly hatched larvae measured between 3,85 mm and 4,50 mm body length, while preserved specimens measured between 3,75 mm and 4,00 mm body length. The larvae display typical clupeoid characteristics, with a slender sparsely pigmented body and a posteriorly placed anus. The head is noticeably flexed over the yolk and the fin folds are smooth in outline (fig. 3). Pigmentation of the newly hatched larva is similar to that of the later embryonic phase and consists of a small group of melanophores on the forehead and on the interorbital and cranial regions. The line of migrating melanophores positioned along the dorsal and lateral sides of the body extends from the hind brain to about seven-eights of the body length. The eyes are unpigmented and the mouth has not yet formed. By the time the larva is 5,00 mm long (fig. 4), half of the melanophores have migrated to the ventral surface in the anterior region and are positioned dorsal to the intestine. The mouth has formed and the jaws have become functional, but the eyes remain unpigmented. The pectoral fins have started developing and 48 to 50 body myotomes can be counted. Caudal lepidotrichia are visible on the tip of the tail. When the larvae measure between 6,00 mm and 6,50 mm b.l. (fig. 6), migration of the melanophores to the ventral surface is almost complete except for a few pigment spots between the 30th and 35th myotome. The yolk-sac is almost completely absorbed and pigmentation of the eyes commences. A conspicuous band of pigmentation appears on the lower jaws and some isolated melanophores are visible on the

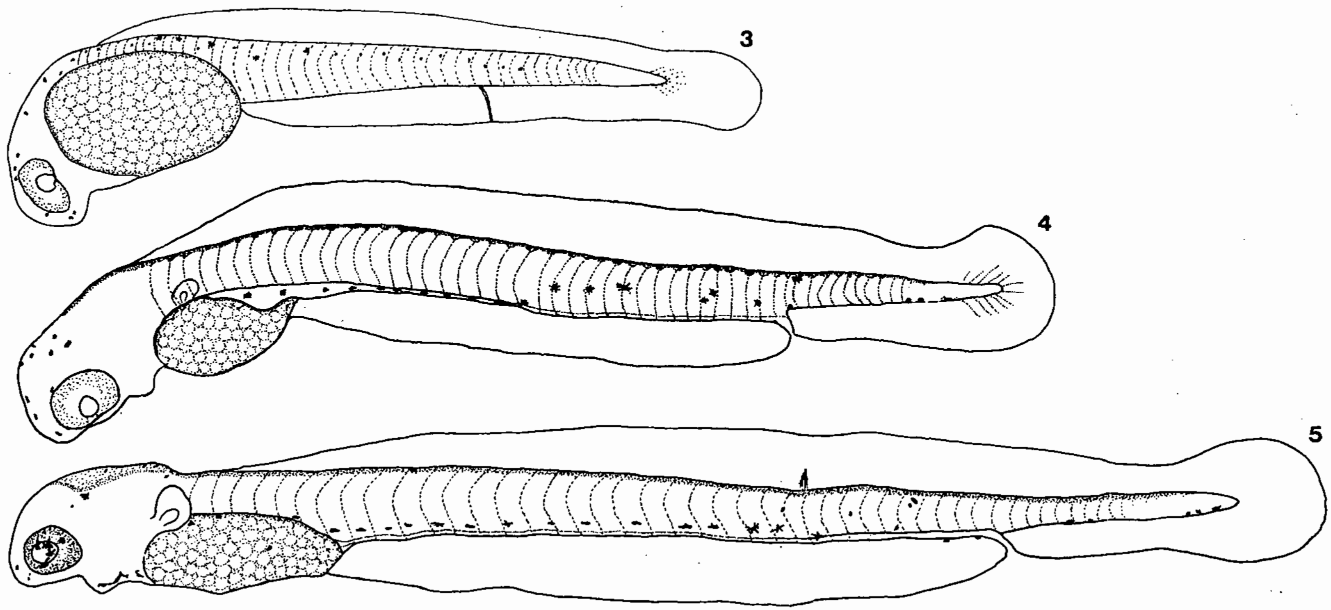


FIG. 3, 4, 5. — Yolk-sac larvae measuring 3,80 mm, 5,00 mm and 6,00 mm respectively.

yolk-sac and on the ventral fin fold between the 30th and 35th myotomes.

RATE OF DEVELOPMENT.

The duration from development to hatching decreases with increasing temperature from approximately 135 hours at 11,0°C to 36 hours at 20,5°C.

The mathematical relationship between incubation time (D) and temperature (T) is described by the regression equation $D = aT^b$ which for this experiment yields the formula $D = 21018T^{-21051}$. The curve derived from the formula is shown in figure 6.

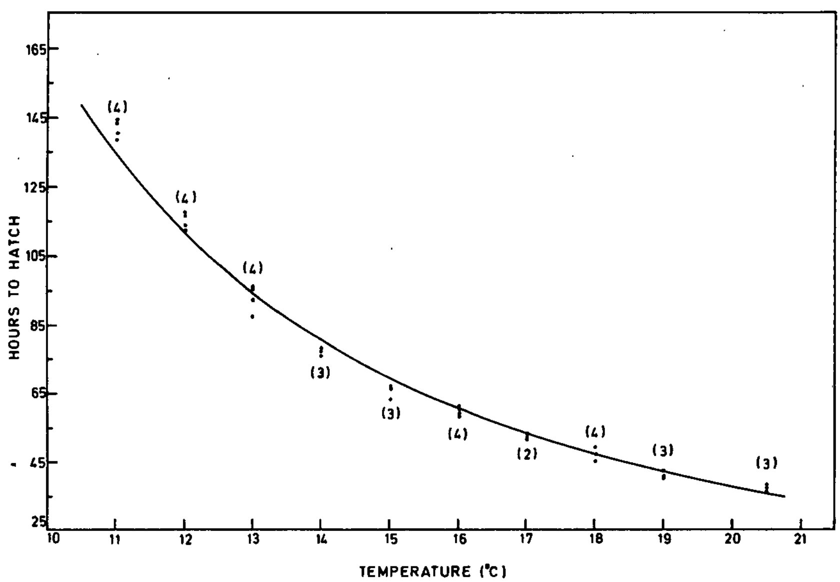


FIG. 6. — Regression curve showing influence of temperature on time of development from the blastodermal cap stage to hatching. Bracketed numerals represent the number of observations made at each temperature.

DISCUSSION

The egg and yolk-sac larva are similar to those described from Japan and the Gulf of Mexico. Pigmentation of the embryo and newly hatched larva are practically identical. However the egg of the South African form appears to be somewhat larger than its counterparts.

The size, combined with characters such as a segmented yolk, a small perivitelline space and absence of an oil globule, serves to distinguish the eggs of *E. teres* from those of other clupeid eggs in South African waters. The eggs of the pilchard, *Sardinops ocellata,* also have a segmented yolk but their size (1,48 - 1,91 mm), the large perivitelline space and the presence of an oil globule are notable differences.

Eggs of the anchovy, *Engraulis capensis* can easily be separated by their characteristic oval shape.

The early larval stages of the round herring, however, are sometimes confused with those of pilchard and anchovy. A detailed description of the larvae of these species is necessary to elucidate their distinguishing features.

ACKNOWLEDGEMENT

The authors wish to thank the Director of Sea Fisheries, for his kind permission to publish this work. The following persons are also thanked for their assistance in obtaining samples and their help in recording observations; W.R.H. Andrews, D.L. Cram, D.A. Horstman and A.A. Robertson. Mr T. Allen was responsible for construction of the incubator.

RÉSUMÉ

Des œufs typiques de clupeoïdes ont été collectés dans le plancton au large de la péninsule du Cap. L'éclosion a montré qu'il s'agissait du hareng *Etrumeus teres* (De Kay). Le développement de l'œuf du stade blastoderme à l'éclosion, à différentes températures, est décrit.

ZUSAMMENFASSUNG

Typische Clupeoiden-Eier in Planktonproben aus der Nähe der Kap-Halbinsel wurden gesammelt. Sie konnten nach dem Schlüpfen

als Eier von *Etrumeus teres* (De Kay) bestimmt werden. Das Ei und die frühen Larvenstadien sowie deren Entwicklung unter verschiedenen Temperaturen werden beschrieben.

BIBLIOGRAPHY

HOUDE, E.D. and P.L. FORE, 1973. Guide to identity of eggs and larvae of some Gulf of Mexico fishes. Leafl. Ser. *4, Fla. Dep. nat. Resources mar. Res. Lab.* Part I (23) : 14 p.

MILLER, D.J., 1952. Development through the prolarval stage of artificially fertilized eggs of the Pacific sardine (*Sardinops caerulea*). *Calif. Fish Game,* **38** (4) : 587-595.

MITO, S., 1961. Pelagic fish eggs from Japanese waters. — 1. Clupeina, Chanina, Stomiatina, Myctophida, Aguillidae, Belonida and Syngnathidae. *Sci. Bull. Fac. Agric. Kyushu,* **18** (3) : 285-310.

THOMAS, W.H., H.L. SCOTTEN and J.S. BRADSHAW, 1973. Thermal gradient incubators for small aquatic organisms. *Limmol. Oceanogr.,* **8** (3) : 357-360.

UCHIDA, K., 1958. Eggs, larvae and juveniles of *Etrumeus micropus* (Temminck et Schlegel) (Dussumieriidae). *In : Studies on the eggs, larvae and juveniles of Japanese fishes.* Series 1. Uchida, K. *et al.* Fukuoka : Second Laboratory of Fisheries Biology, Fisheries Department, Kuyshu University.

WHITEHEAD, P.J.D., 1963. A revision of recent round herrings (Pisces : Dussumieriidae). *Bull. Br. Mus. nat. Hist.,* **10** (6) : 307-380.

Reçu le 16 septembre 1974.

Fish. Bull. S. Afr. 8:23–33
1976

INCIDENTAL COLLECTIONS OF SMALL AND JUVENILE FISHES FROM EGG AND LARVAL SURVEYS OFF SOUTH WEST AFRICA (1972 – 1974)

M. J. O'TOOLE

The South West African Pelagic Egg and Larval Survey (SWAPELS) was commenced by the Sea Fisheries Branch in 1972 as part of the Cape Cross Research Programme (Cram and Visser 1972). The collections were made primarily to study the seasonal distribution and relative abundance of eggs and larvae of commercial pelagic species in the upper 50m layer between latitudes 18°20′S (Cape Frio) and 24°40′S (Hollams Bird Island).

A dense sampling grid, consisting of twenty lines with nine stations on each line (Fig. 1) was sampled monthly from August 1972 to March 1973 and from August 1973 to April 1974. The periods August to April were specifically selected to coincide with the known main spawning months of the commercially important pelagic species. The inshore station of each line was approximately 8 km from the coast whereas the outer station was 112 km off shore. Lines were spaced 32 km apart and the grid was sampled from north to south on a continuous 24-hour basis. The position and depth of each station are given in Tables I and II respectively.

During the course of the investigation some interesting mesopelagic fish and juveniles of demersal and epipelagic species were captured in the plankton nets.

The net used on both surveys was a Bongo net 57 cm in diameter; paired nets of 0,94 mm mesh size were used on the first survey but on the second survey the left-side net had a mesh size of 0,94 mm and the right 0,50 mm. Oblique hauls were made at a speed of two knots from 50 m to the surface where the depth was sufficient, or from within a few metres of the bottom in shallow coastal waters (King and Robertson 1973). Survey number, cruise dates and station omissions are presented in Table III.

CATCH COMPOSITION

A total of approximately 1 300 fish were caught during the two surveys. Seven orders were represented, consisting of juveniles and adults of the families Clupeidae, Engraulidae, Gonostomatidae, Stomiatidae, Myctophidae, Scomberesocidae, Gadidae, Merlucciidae, Syngnathidae, Carangidae, Trichiuridae, Gobiidae, Blenniidae and Soleidae.

Fifty-three per cent of the total number of fish caught belonged to the species *Sufflogobius bibarbatus* (Percomorphi: Gobiidae), the order Percomorphi accounting for 61 per cent of the total

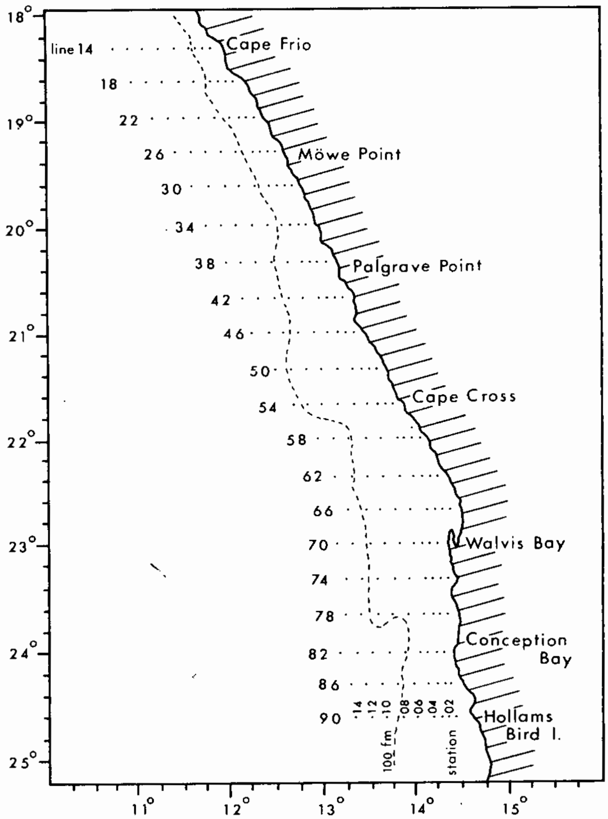


FIG. 1: LOCATION OF ROUTINE STATIONS OCCUPIED DURING THE SWAPELS CRUISES IN 1972/73 AND 1973/74

TABLE I: GEOGRAPHICAL POSITION OF EACH STATION

Line	Latitude	Station longitude								
		01	02	03	04	06	08	10	12	14
14	18°20′S	11°50′E	11°45′E	11°40′E	11°35′E	11°25′E	11°15′E	11°05′E	10°55′E	10°45′E
18	18°40′S	12°09′E	12°04′E	11°59′E	11°53′E	11°43′E	11°33′E	11°23′E	11°13′E	11°03′E
22	19°00′S	12°25′E	12°20′E	12°15′E	12°10′E	12°00′E	11°50′E	11°40′E	11°30′E	11°20′E
26	19°20′S	12°35′E	12°30′E	12°25′E	12°20′E	12°10′E	12°00′E	11°50′E	11°40′E	11°30′E
30	19°40′S	12°50′E	12°45′E	12°40′E	12°35′E	12°25′E	12°15′E	12°05′E	11°55′E	11°45′E
34	20°00′S	13°00′E	12°55′E	12°50′E	12°45′E	12°35′E	12°25′E	12°15′E	12°05′E	11°55′E
38	20°20′S	13°10′E	13°05′E	13°00′E	12°55′E	12°45′E	12°35′E	12°25′E	12°15′E	12°05′E
42	20°40′S	13°20′E	13°15′E	13°10′E	13°05′E	12°55′E	12°45′E	12°35′E	12°25′E	12°15′E
46	21°00′S	13°25′E	13°20′E	13°15′E	13°10′E	13°00′E	12°50′E	12°40′E	12°30′E	12°20′E
50	21°20′S	13°40′E	13°35′E	13°30′E	13°25′E	13°15′E	13°05′E	12°55′E	12°45′E	12°35′E
54	21°40′S	13°50′E	13°45′E	13°40′E	13°35′E	13°25′E	13°15′E	13°05′E	12°55′E	12°45′E
58	22°00′S	14°05′E	14°00′E	13°55′E	13°50′E	13°40′E	13°30′E	13°20′E	13°10′E	13°00′E
62	22°20′S	14°17′E	14°12′E	14°07′E	14°02′E	13°52′E	13°42′E	13°32′E	13°22′E	13°12′E
66	22°40′S	14°25′E	14°20′E	14°15′E	14°10′E	14°00′E	13°50′E	13°40′E	13°30′E	13°20′E
70	23°00′S	14°15′E	14°10′E	14°05′E	14°00′E	13°50′E	13°40′E	13°30′E	13°20′E	13°10′E
74	23°20′S	14°20′E	14°15′E	14°10′E	14°05′E	13°55′E	13°45′E	13°35′E	13°25′E	13°15′E
78	23°40′S	14°20′E	14°15′E	14°10′E	14°05′E	13°55′E	13°45′E	13°35′E	13°25′E	13°15′E
82	24°00′S	14°17′E	14°12′E	14°07′E	14°02′E	13°52′E	13°42′E	13°32′E	13°22′E	13°12′E
86	24°20′S	14°23′E	14°18′E	14°13′E	14°08′E	13°58′E	13°48′E	13°38′E	13°28′E	13°18′E
90	24°40′S	14°27′E	14°22′E	14°17′E	14°12′E	14°02′E	13°52′E	13°42′E	13°32′E	13°22′E

catch. Next in numerical abundance came the order Iniomi represented only by the family Myctophidae, with 27 per cent of the total. The greatest diversity was found in the family Myctophidae, represented by eleven species, three of which belonged to the genus *Diaphus*. The species *Lampanyctodes hectoris* constituted 60 per cent of all the myctophids collected and ranked second in overall species abundance (16 per cent of the total). Four species, namely *Notolychnus valdiviae* (Myctophidae), *Lampanyctus australis* (Myctophidae), *Diplophos taenia* (Gonostomatidae) and *Gaidropsarus capensis* (Gadidae) were each represented by a single specimen.

Sufflogobius bibarbatus (Gobiidae) was cap-

TABLE II: DEPTH (M) AT EACH STATION

Line	Station								
	01	02	03	04	06	08	10	12	14
14	34	104	140	200	570	1 400	2 000	2 500	3 000
18	36	40	92	134	212	240	460	960	1 370
22	45	90	102	120	210	270	294	330	660
26	42	72	104	126	180	260	310	340	510
30	45	84	102	116	144	226	306	360	435
34	40	80	105	120	150	220	272	334	410
38	46	92	114	120	140	260	290	306	424
42	40	85	108	122	152	270	310	322	490
46	32	80	110	118	170	300	362	430	600
50	21	75	93	106	130	164	310	358	530
54	33	64	90	106	128	150	240	300	355
58	26	44	72	93	115	140	175	220	310
62	22	43	66	85	110	125	146	210	236
66	26	50	78	94	120	129	134	218	282
70	62	102	114	126	140	148	208	345	325
74	42	80	112	125	154	162	176	268	270
78	34	76	110	140	172	190	226	260	330
82	64	102	128	154	232	258	275	290	470
86	28	80	108	128	154	284	324	334	668
90	38	58	70	98	148	155	320	420	655

TABLE III: SURVEY NUMBER, CRUISE DATES AND STATION OMISSIONS

Survey 1	Cruise	Omissions	Survey 2	Cruise	Omissions
1972: Aug. 22–31	1	Lines 14–34	1973: Aug. 14–19	1	Lines 14–34
Sep. 15–20	2	Lines 14–34	Sep. 9–15	2	Lines 14–18
Oct. 15–22	3	Stations 10,12,14 of Lines 30–50	Oct. 17–23	3	—
Nov. 11–19	4	—	Nov. 10–18	4	—
Dec. 5–14	5	—	Dec. 10–18	5	—
1973: Jan. 13–21	6	—	1974: Jan. 12–20	6	—
Feb. 14–24	7	—	Feb. 6–14	7	—
Mar. 11–19	8	—	Mar. 27–Apr. 4	8	—

tured at 50 stations, but species belonging to the family Myctophidae were collected at more stations (70) than any other family. *Lampanyctodes hectoris* was itself taken at 48 stations – more localities than any other myctophid.

The 71 juveniles of *Trachurus trachurus* taken at station 46-04 during November 1972 represented the largest number of individuals of a single species caught in a tow.

The distribution of some of the more significant species has been charted (Figs. 2 - 11).

ANNOTATED LIST OF SPECIES

A taxonomically arranged list of the fish species taken is given below. In the case of the more common species, the general distribution, length range, time of capture and temperature range are indicated. Records of the less common forms are listed under the species in the following abbreviated form: station of capture, survey and cruise number, number of specimens taken, standard length or length range of the specimen(s), time of day captured, sea surface temperature.

ISOSPONDYLI

Clupeidae

Sardinops ocellata Pappe

Juvenile pilchard were taken on only two occasions, approximately 25 km north-west of both Palgrave Point and Cape Cross (Fig. 2).

50-02, 1/4, (1), 62 mm, 03h48, 15,8°C
34-02, 2/5, (1), 56 mm, 01h30, 17,7°C

Engraulidae

Engraulis capensis Gilchrist

Anchovy juveniles were caught only twice –

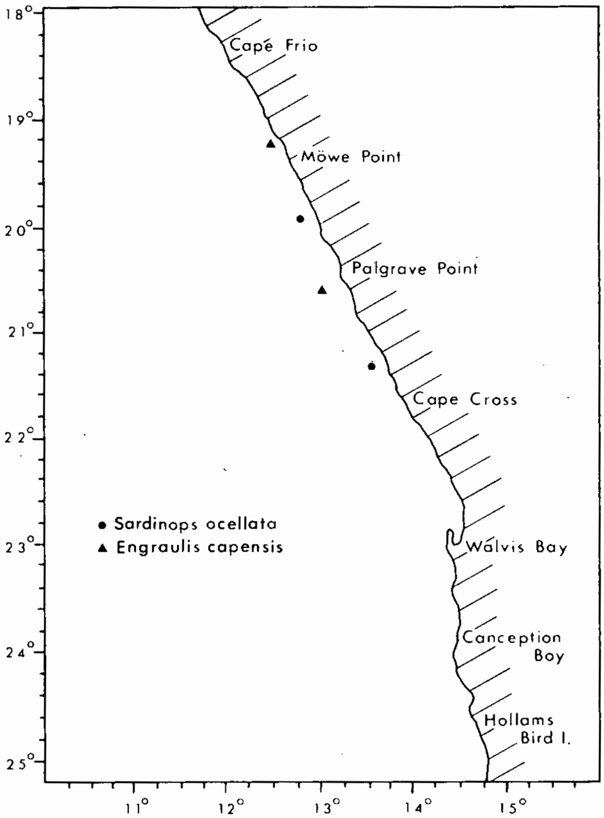


FIG. 2: LOCATION OF CAPTURE – *Sardinops ocellata* (CLUPEIDAE) AND *Engraulis capensis* (ENGRAULIDAE)

at approximately 25 km north-west of Möwe Point and 35 km south-west of Palgrave Point (Fig. 2).

26-02, 1/8, (6), 35-42 mm, 06h30, 16,1°C
42-04, 2/8, (4), 42-46 mm, 22h30, 18,1°C

Gonostomatidae

Maurolicus muelleri (Gmelin)
Juveniles of this species of lightfish were found 40 – 112 km off shore south of Walvis Bay (Fig. 3).

66-14, 1/4, (1), 33 mm, 17h08, 15,5°C
90-14, 1/4, (2), 19-28 mm, 05h50, 15,0°C
86-08, 1/7, (7), 22-35 mm, 20h18, 18,9°C
74-12, 1/8, (1), 27 mm, 21h50, 18,5°C
66-14, 2/5, (4), 23-26 mm, 23h56, 17,4°C

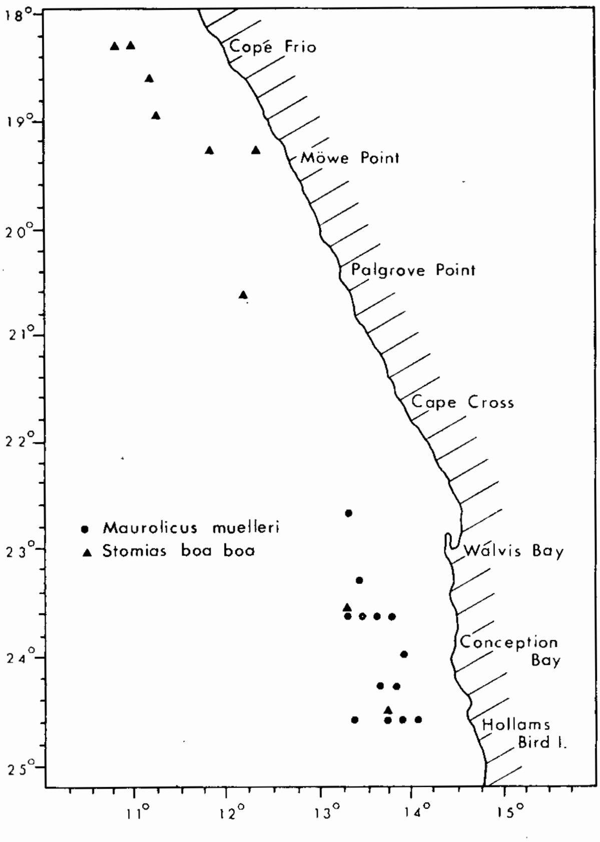


FIG. 3: LOCATION OF CAPTURE – *Maurolicus muelleri* (GONOSTOMATIDAE) AND *Stomias boa boa* (STOMIATIDAE)

82-06, 2/5, (1), 16 mm, 19h55, 15,0°C
86-08, 2/5, (2), 27 mm, 04h25, 14,0°C
86-10, 2/5, (2), 29-31 mm, 05h29, 14,5°C
78-08, 2/6, (1), 34 mm, 23h50, 17,6°C
78-10, 2/6, (4), 25-28 mm, 00h50, 18,2°C
78-12, 2/6, (2), 22-26 mm, 01h57, 18,6°C
78-14, 2/6, (2), 23 mm, 02h58, 18,6°C
90-08, 2/6, (15), 20-35 mm, 02h05, 17,1°C
90-10, 2/6, (1), 23 mm, 01h03, 17,5°C
90-06, 2/6, (5), 23-30 mm, 03h09, 17,0°C

Diplophos taenia Günther
A single juvenile was taken on one occasion approximately 85 km off shore in the northern part of the survey area.

22-10, 2/4, (1), 42 mm, 22h05, 18,5°C

Vinciguerria sp.
A single damaged specimen of this genus was captured at the outer station of the line on two occasions, but their state precluded identification to species.

42-14, 1/2, (1), 42 mm, 20h28, 14,8°C
14-14, 1/6, (1), 38 mm, 01h13, 18,6°C

Stomiatidae

Stomias boa boa (Risso)
Adults and juveniles of this predominantly deep-water species were caught mainly in the northern part of the research area (Fig. 3).

18-12, 1/3, (1), 112 mm, 05h40, 17,5°C
22-10, 1/4, (1), 42 mm, 04h30, 18,5°C
42-14, 1/5, (1), 89 mm, 21h30, 20,0°C
26-04, 1/7, (1), 113 mm, 08h20, 17,8°C
14-12, 1/8, (1), 33 mm, 03h25, 18,9°C
14-14, 1/8, (1), 66 mm, 04h26, 20,4°C
22-14, 2/3, (1), 92 mm, 20h01, 14,0°C
78-14, 2/6, (4), 105-130 mm, 02h58, 18,6°C
90-10, 2/6, (1), 58 mm, 01h03, 17,5°C

INIOMI

Myctophidae

Electrona paucirastra Bolin
Three juveniles of this species of lantern fish were captured on one occasion approximately 112 km west of Hollams Bird Island.

90-14, 1/4, (3), 31-42 mm, 02h10, 14,5°C

Hygophum macrochir (Günther)

Juveniles of this species were encountered only once, in the extreme north of the survey area.

14-12, 2/6, (3), 48-56 mm, 22h00, 21,3°C

Symbolophorus boops (Richardson)

Two species of *Symbolophorus, S. boops* and *S. veranyi* (Moreau), have been recorded from the South Atlantic. However, some confusion exists as to the validity of *S. veranyi* as a separate species (P. Hulley, S. Afr. Museum, personal communication). Differences in the pigmentation of the larvae of *Symbolophorus* collected during the surveys suggest two types, one associated with the Angola Current in the north and the other with the Benguela Current in the south. For the purposes of this report, however, all adults and juveniles caught are referred to as *S. boops*. *Symbolophorus* was widely distributed over the survey area and was the second myctophid in order of numerical abundance (Fig. 4).

66-14, 1/2, (1), 42 mm, 02h00, 14,5°C
82-04, 1/2, (2), 42-48 mm, 21h10, 14,8°C
18-14, 1/3, (1), 70 mm, 00h20, 17,8°C
26-06, 1/3, (3), 55-62 mm, 23h09, 15,9°C
22-08, 1/4, (2), 27-35 mm, 21h30, 18,0°C
30-12, 1/4, (2), 53-64 mm, 22h00, 18,2°C
82-12, 1/4, (1), 51 mm, 06h20, 15,9°C
82-10, 1/4, (1), 43 mm, 07h40, 15,8°C
90-12, 1/4, (1), 49 mm, 01h30, 15,7°C
22-08, 1/5, (1), 46 mm, 00h00, 21,0°C
30-10, 1/5, (1), 75 mm, 21h30, 20,4°C
34-14, 1/5, (1), 56 mm, 01h30, 20,2°C
42-10, 1/5, (1), 54 mm, 00h20, 20,1°C
42-14, 1/5, (1), 40 mm, 22h10, 19,8°C
50-14, 1/5, (1), 48 mm, 18h55, 18,6°C
14-14, 1/8, (1), 40 mm, 22h23, 20,9°C
14-12, 2/3, (2), 35-54 mm, 02h33, 16,0°C
26-10, 2/5, (1), 58 mm, 00h28, 19,2°C
34-08, 2/5, (1), 49 mm, 21h45, 18,7°C
34-12, 2/5, (1), 54 mm, 19h27, 19,3°C
22-12, 2/6, (5), 42-54 mm, 20h49, 19,4°C
46-10, 2/6, (1), 68 mm, 00h40, 20,0°C
58-14, 2/6, (1), 64 mm, 23h38, 18,8°C
78-14, 2/6, (1), 47 mm, 02h58, 18,6°C

Notolychus valdiviae (Brauer)

Juveniles were encountered twice in off-shore waters in the northern part of the research area.

22-14, 1/6, (1), 32 mm, 01h43, 18,3°C
14-12, 2/6, (2), 20-30 mm, 01h10, 20,4°C

Lampanyctus alatus (Goode and Bean)

Adults and juveniles were caught 80 - 112 km off shore in the north (Fig. 5).

14-14, 1/3, (1), 35 mm, 01h28, 17,5°C
14-12, 1/4, (4), 32-35 mm, 02h00, 17,4°C
14-08, 1/6, (1), 30 mm, 00h46, 18,0°C
50-14, 1/7, (1), 38 mm, 03h40, 20,7°C
34-14, 2/2, (1), 48 mm, 23h10, 15,5°C
50-14, 2/3, (1), 42 mm, 06h00, 15,5°C
14-08, 2/6, (2), 32-38 mm, 22h15, 18,1°C
18-14, 2/6, (1), 35 mm, 04h10, 18,0°C
26-14, 2/8, (1), 58 mm, 03h24, 20,6°C

Lampanyctus australis Täning

Only one juvenile specimen was taken 112 km west of Cape Frio (Fig. 5).

14-14, 1/3, (1), 24 mm, 04h20, 17,4°C

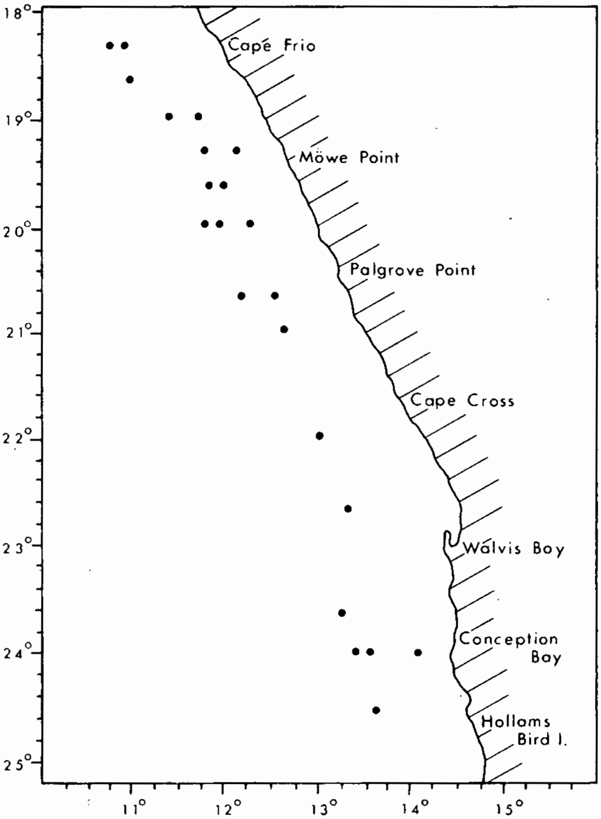


FIG. 4: LOCATION OF CAPTURE – *Symbolophorus boops* (MYCTOPHIDAE)

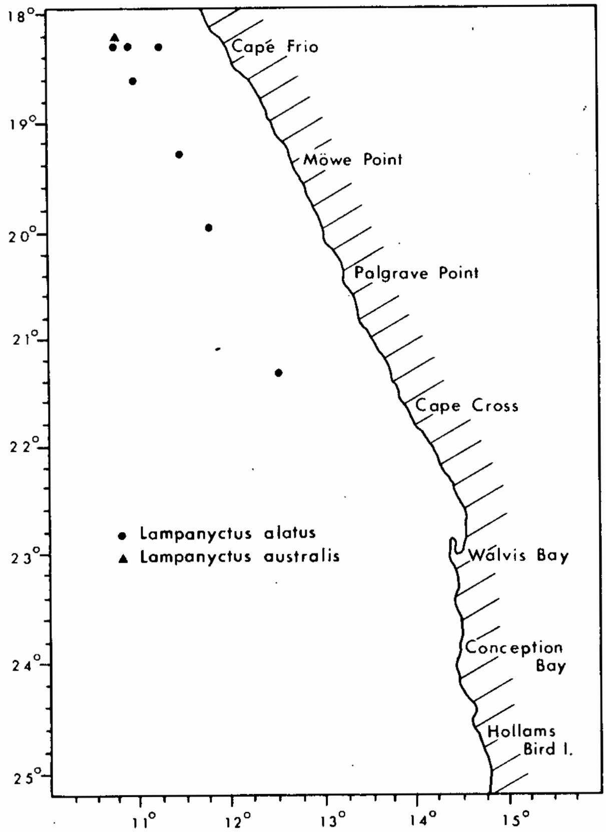


FIG. 5: LOCATION OF CAPTURE – *Lampanyctus alatus* AND *L. australis* (MYCTOPHIDAE)

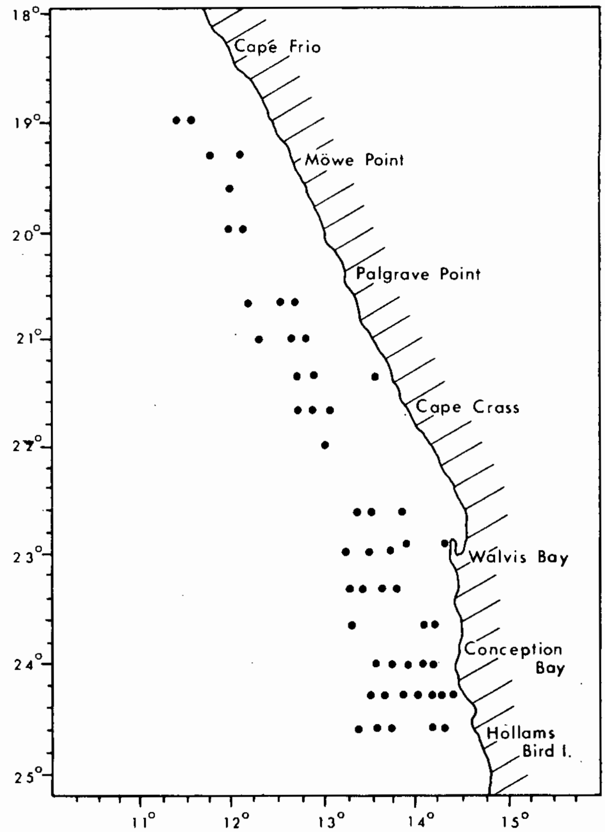


FIG. 6: LOCATION OF CAPTURE – *Lampanyctus hectoris* (MYCTOPHIDAE)

Lampanyctodes hectoris (Günther)

This species of lantern fish was the most commonly encountered myctophid and ranked second in overall species abundance. It was also the most common myctophid larva in the SWAPELS collections of ichthyoplankton (Ahlstrom *et al.* in press). Adult *L. hectoris* have been widely reported in the Cape from Lambert's Bay to Cape Agulhas and have been caught in commercial quantities in South Africa since 1969 (Centurier-Harris 1974).

A total of over 200 juveniles and adults ranging in size from 15 – 80 mm were caught. Although a few specimens were taken during every month, the species was most frequently encountered in August and September. The distribution extended from 19°00'S to 24°40'S but the majority were found 30 – 112 km off shore south of Walvis Bay (Fig. 6). Almost all the specimens were captured during the hours of darkness, with the greatest numbers taken immediately after dusk and between 01h00 and 03h00. *L. hectoris* occurred at temperatures of 12,0 – 17,5°C but were more numerous between 13,0°C and 14,0°C.

Diaphus cf. *theta* Eigenmann and Eigenmann

Juveniles were caught at the extreme off-shore station on three occasions.

14-14, 1/6, (1),	20 mm, 04h20, 20,8°C
42-14, 1/6, (1),	16 mm, 21h00, 19,2°C
18-14, 1/8, (2),	23-27 mm, 01h20, 20,0°C

Diaphus taaningi Norman

This species of lantern fish was caught regularly 60 – 112 km off shore between Cape Frio and Conception Bay and was the third most abundant myctophid in the collection (Fig. 7).

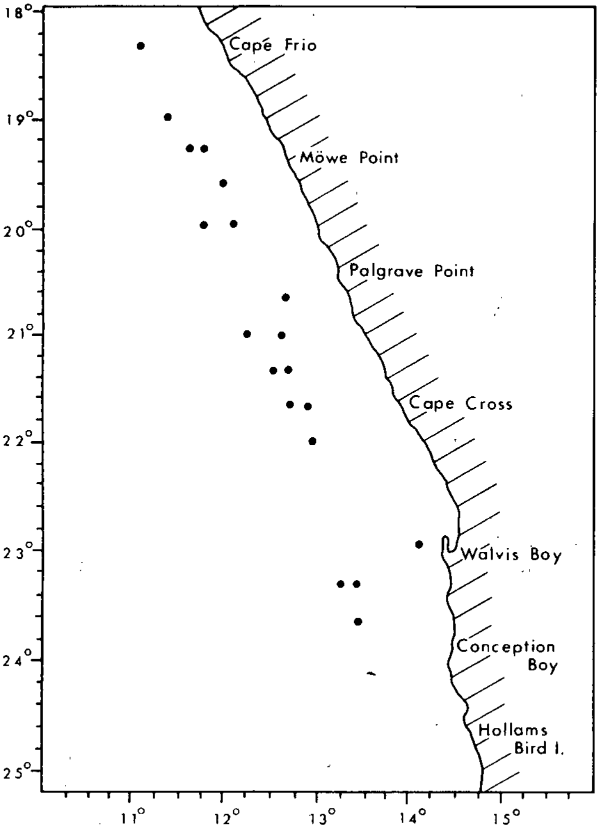


FIG. 7: LOCATION OF CAPTURE – *Diaphus taaningi* (MYCTOPHIDAE)

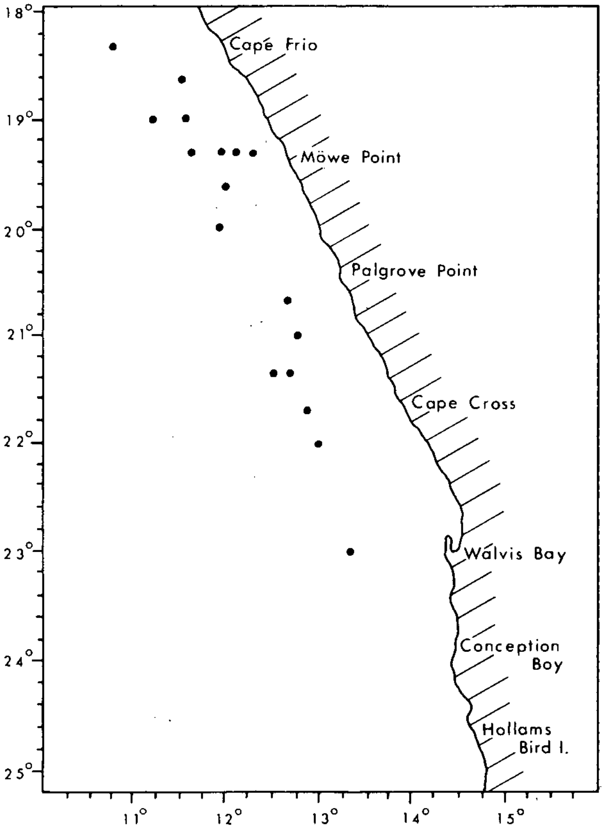


FIG. 8: LOCATION OF CAPTURE – *Diaphus dumerili* (MYCTOPHIDAE)

The specimens were mainly juveniles, ranged in size from 34 – 58 mm and were captured at night between 21h30 and 05h20. Most specimens were taken during the months of January, February and March when the water temperature lay within the range 18,5 – 20,7°C.

Diaphus dumerili(Bleeker)

This species was most frequently caught during February and March, 30 – 112 km off shore between Cape Frio and Walvis Bay (Fig. 8). The specimens were predominantly juveniles.

26-06, 1/3, (1), 32 mm, 03h55, 15,2°C
22-10, 1/4, (1), 43 mm, 23h13, 17,7°C
30-10, 1/4, (3), 22-43 mm, 21h05, 18,3°C
42-08, 1/4, (3), 18-32 mm, 23h30, 17,4°C
22-14, 1/6, (1), 19 mm, 04h20, 18,9°C
26-04, 1/7, (1), 21 mm, 08h48, 18,0°C
26-08, 1/7, (1), 35 mm, 06h25, 18,7°C
34-12, 1/7, (1), 42 mm, 00h15, 20,0°C
50-12, 1/7, (2), 37-42 mm, 03h40, 20,6°C
50-14, 1/7, (3), 25-46 mm, 02h35, 20,7°C
70-12, 1/7, (3), 32-54 mm, 00h30, 20,6°C
14-14, 1/8, (3), 16-18 mm, 22h23, 20,9°C
18-08, 1/8, (2), 29-35 mm, 05h03, 18,7°C
26-08, 1/8, (2), 52-59 mm, 02h16, 18,0°C
26-12, 1/8, (1), 18 mm, 23h52, 19,2°C
46-08, 1/8, (1), 42 mm, 02h30, 18,4°C
54-12, 1/8, (1), 51 mm, 00h45, 19,4°C
58-14, 1/8, (1), 67 mm, 23h40, 19,5°C

Myctophum sp.

Only eight specimens belonging to the genus *Myctophum* were caught during the two surveys, scattered widely over the grid.

74-12, 1/2, (1), 42 mm, 02h11, 14,0°C

86-14, 1/4, (1), 38 mm, 02h05, 16,0°C
14-08, 1/5, (1), 32 mm, 01h10, 18,6°C
14-14, 1/5, (2), 25-32 mm, 04h26, 20,4°C
18-14, 1/5, (1), 47 mm, 07h20, 19,0°C
46-14, 1/5, (2), 33 mm, 23h50, 20,9°C

SYNENTOGNATHI

Scomberesocidae

Scomberesox saurus (Walbaum)
Seven juvenile sauries were captured between 30 km and 70 km off shore between 19°S and 20°S (Fig. 9).

34-04, 1/8, (3), 42-45 mm, 00h20, 16,9°C
26-08, 2/2, (3) 43-44 mm, 06h00, 15,5°C
34-08, 2/2, (1), 62 mm, 02h48, 14,7°C

ANACANTHINI

Gadidae

Gaidropsarus capensis (Kaup)
One juvenile rockling was caught inshore in the south.

86-03, 1/3, (1), 25 mm, 13h50, 12,3°C

Merlucciidae

Merluccius capensis Castelnau
Juvenile hake were taken only during December, south of Walvis Bay (Fig. 9).

86-02, 1/5, (8), 25-32 mm, 00h10, 13,9°C
86-04, 1/5, (3), 28-30 mm, 05h10, 14,3°C
82-03, 2/5, (5), 28-35 mm, 20h50, 15,0°C
70-03, 2/5, (3), 27-28 mm, 10h28, 16,0°C
78-06, 2/5, (1), 23 mm, 08h18, 15,0°C
86-03, 2/5, (4), 28-32 mm, 01h40, 14,0°C

LOPHOBRANCHII

Syngnathidae

Syngnathus sp.
Three juvenile specimens of an unidentified species of pipefish were captured inshore between Möwe Point and Palgrave Point.

34-01, 1/5, (1), 110 mm, 02h00, 16,5°C
38-01, 2/5, (1), 123 mm, 04h20, 17,2°C

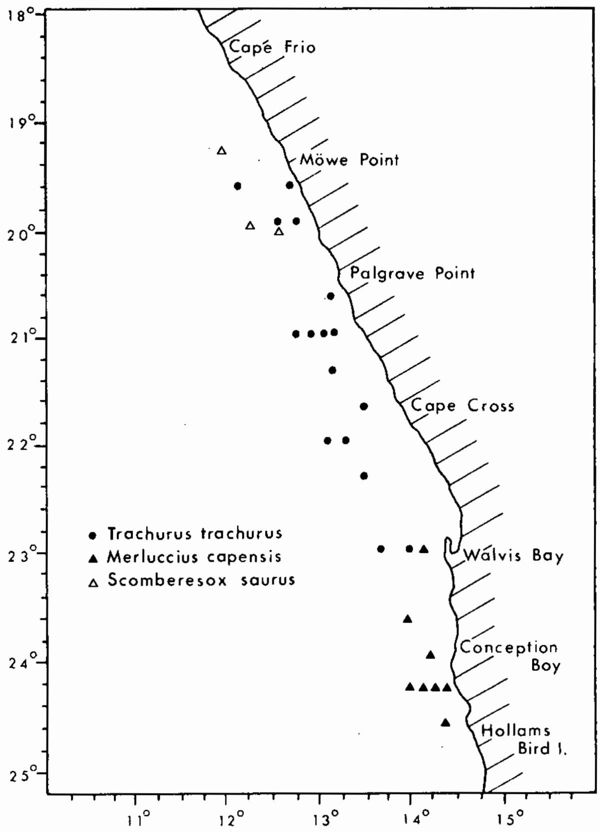


FIG. 9: LOCATION OF CAPTURE – *Trachurus trachurus* (CARANGIDAE), *Merluccius capensis* (MERLUCCIIDAE) AND *Scomberesox saurus* (SCOMBERESOCIDAE)

30-01, 2/7, (1), 100 mm, 01h20, 18,6°C

PERCOMORPHI

Carangidae

Trachurus trachurus Linnaeus
Juvenile maasbanker were caught on numerous occasions 8 – 80 km off shore between Möwe Point and Walvis Bay (Fig. 9). Greatest numbers were taken during November, February and March. Specimens ranged in length from 23 mm to 43 mm and were taken during day and night collections. However, most specimens were caught during daylight between 11h35 and 13h00. *T. trachurus* were found at temperatures ranging between 14,4°C and 20,0°C.

Trichiuridae

Lepidopus caudatus (Euphrasen)
Two juvenile frostfish were caught in the extreme north of the sampling area.

18-10, 2/7, (2), 22-25 mm, 23h35, 19,0°C

Gobiidae

Sufflogobius bibarbatus (Smith)
The bearded goby, *S. bibarbatus*, was previously only recorded from the southern coast of South Africa (Smith 1970). The species was first reported in South West African waters by Barber and Haedrich (1969), when they noted three juveniles off Hollams Bird Island. This record represents a 540-mile extension of the northerly limit of the species. Adults and juveniles were captured in large numbers during all months and ranged in length from 30 mm to 98 mm. The larvae of this species were also the most abundant in the ichthyoplankton collections during the two-year survey (O'Toole, unpublished data).

The northern limit of their distribution was at 19°20'S (Möwe Point) and specimens were found 8 – 85 km off shore (Fig. 10). The majority were, however, taken south of Walvis Bay between 8 km and 32 km off the coast. *S. bibarbatus* was found at temperatures ranging between 14,5°C and 17,5°C. The goby was taken mainly between 19h00 and 06h00, with peaks occurring at 19h00-21h00, 01h00-03h00 and 04h00-06h00.

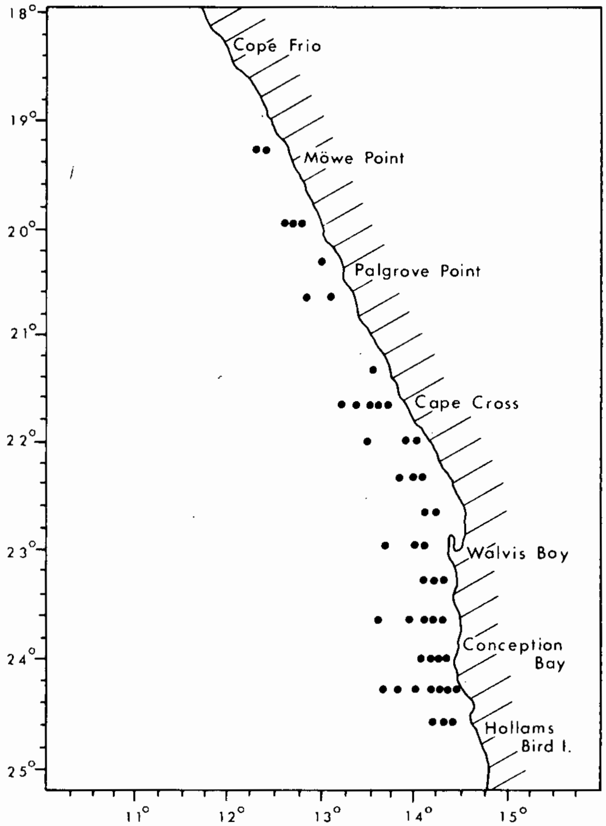


FIG. 10: LOCATION OF CAPTURE – *Sufflogobius bibarbatus* (GOBIIDAE)

Blenniidae

Chalaroderma capito (Cuvier)
This small specimen can only be tentatively identified at the present time (M. J. Penrith, State Museum Windhoek, personal communication). Larvae of this fish also were taken regularly.

18-12, 1/5, (1), 25 mm, 12h23, 21,5°C

HETEROSTOMATA

Soleidae

Austroglossus microlepis (Bleeker)
Four juveniles of the West Coast sole were captured in November and December, 8 - 40 km off shore in the Walvis Bay region (Fig. 11).

70-02, 1/4, (2), 25-26 mm, 04h05, 13,8°C
78-01, 1/5, (1), 28 mm, 06h45, 13,5°C
66-06, 2/5, (1), 24 mm, 04h20, 16,5°C

Dicologlossa cuneata (Moreau)
Juvenile Senegal sole were found only twice, inshore in the north (Fig. 11).

18-02, 1/6, (2), 26-27 mm, 15h00, 16,1°C
38-02, 1/6, (1), 31 mm, 12h15, 16,2°C

DISCUSSION

This report provides an indication of the presence and distribution of some fish species in the Benguela Current system between latitudes

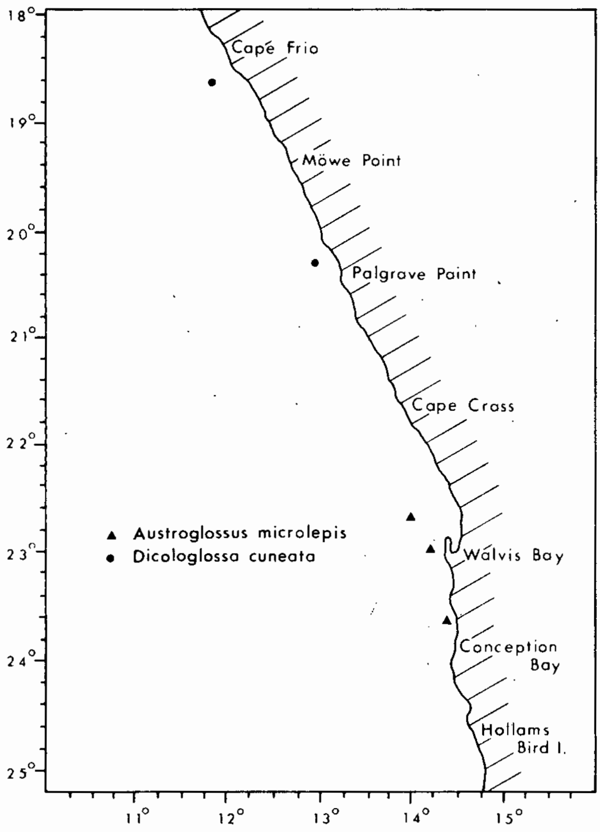


FIG. 11: LOCATION OF CAPTURE – *Austroglossus microlepis* AND *Dicologlossa cuneata* (SOLEIDAE)

18°20′S and 24°40′S. The bearded goby, *Sufflogobius bibarbatus*, has emerged as an important component of the neritic ecosystem, a fact which prior to these surveys had not been fully realized. Little is known about the biology or the behaviour of this species, although it has been shown to be a significant component of the scattering layer off South West Africa (Barber and Haedrich 1969; C. d'Arcangues, University of Paris, personal communication). Further study is needed on the biology of the species in order to establish its relationship with other species and with its immediate environment.

Net avoidance and diurnal migration appear to play an important role in determining the frequency of capture of some species. For example, juveniles of the pilchard and anchovy were rarely taken in the samples, probably owing to their ability to avoid slow-moving collecting gear. Those few that were captured were caught at night. On the other hand, juveniles of the maasbanker were taken frequently in the collections and did not exhibit any diurnal variation in catch-rate. This species would appear either to have a slow avoidance reaction or to be much more abundant than pilchard or anchovy in the upper 50 m layer during the day.

Adult gobies showed marked diurnal variation in catch frequency. Those examined in aquaria on board ship were observed to have feeble swimming ability. This fact, together with their apparent movement to the upper layers at night would explain their frequent appearance in the collections during the hours of darkness and their general absence from the upper 50 m layer during the day.

The lantern fish *Lampanyctodes hectoris* was captured at night and found to be the dominant myctophid in the survey region. Because of the existence of a new fishery for this species along the west coast of South Africa (Centurier-Harris 1974), a more detailed investigation could reveal its potential commercial significance off South West Africa.

Of the 25 species identified, 9 occurred only in the first survey, 3 only in the second survey and 13 were present during both surveys.

The geographic and seasonal patterns which emerged from these data will be examined more closely in a later report for their possible correlation with environmental and other biological parameters.

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Dr P. Hulley of the South African Museum and Dr H. G. Moser of the South West Fisheries Center, La Jolla, California, for their help in the identification of some of the myctophid specimens. Thanks are also due to Mr A. I. L. Payne of the Sea Fisheries Branch for critically reading the manuscript and for offering valuable suggestions for its improvement. The officers and crew of the R.S. *Benguela* and R.S. *Sardinops* are thanked for their willing cooperation at all times during the collection of the samples. Finally I acknowledge gratefully the technical assistance of Mr C. J. Giddey and Mrs S. M. Payne in the sorting of the net collections.

LITERATURE CITED

AHLSTROM, E. H., MOSER, H. G. and M. J. O'TOOLE – Larval development and distribution of the myctophid fish, *Lampanyctodes hectoris* (Günther) in South African waters. *Proc. Sth. Calif. Acad. Sci.* (In press).

BARBER, R. J. and R. L. HAEDRICH 1969 – Gobies associated with a scattering layer off South West Africa. *Deep Sea Res.* **16** (1): 105–106.

CENTURIER-HARRIS, O. M. 1974 – The appearance of lantern fish in commercial catches. *S. Afr. Shipp. News Fish. Ind. Rev.* **29** (1): p. 45.

CRAM, D. L. and G. A. VISSER 1972 – Cape Cross Research Programme, Phase II: A Summary of Results. *S. Afr. Shipp. News Fish. Ind. Rev.* **27** (2): 40–43.

KING, D. P. F. and A. A. ROBERTSON 1973 – Methods of pelagic fish egg and larval research in South West Africa. *S. Afr. Shipp. News Fish. Ind. Rev.* **28** (5): 57–61.

SMITH, J. L. B. 1970 – *The Sea Fishes of Southern Africa, 5th Ed.* Cape Town; Central News Agency: 580 pp.

1974 Reprint S. Afr. Shipp. News. Fish. Ind. Rev. 29, 11, 53–59

Fish larval investigations off South West Africa

Summary of results by M. J. O'Toole

Introduction

THE EARLY life histories of many South West African fish are as yet poorly understood. As part of studies by the Sea Fisheries Branch on the pelagic fish resources of this region (Cram and Visser 1972) an extensive fish egg and larva survey (SWAPELS) was started in August 1972. The basic objectives of this survey were to establish the time of spawning and geographic limits of the commercially exploited species (pilchard *Sardinops ocellata*, anchovy *Engraulis capensis*, and maasbanker *Trachurus trachurus*) and to use the data collected as a method for stock assessment.

In addition to data gathered on the above mentioned species, the survey provided valuable information on the distribution, abundance and ecology of the early stages of a wide range of other fish. Larval stages of several such species have been subsequently identified from the plankton.

The survey area extended from Cape Frio (18°20'S) to Hollams Bird Island (24°50'). See Fig. 1. Twenty lines comprising a total of 180 stations were systematically sampled monthly bewteen August 1972 and April 1973. The sampling techniques employed and the gear used have been fully described by King and Robertson (1973). Briefly, however, two types of Bongo net were used, namely a 57 cm diameter frame with 0,940 mm mesh aperture (B57) and an 18 cm diameter frame with 0,300 mm mesh aperture (B18). The B57 net was used at every station whereas the B18 net was towed only at selected inshore stations. Oblique hauls were taken to a depth of 50 m at all stations except those in very shallow water.

The catches of larvae per standard tow were used as a measure of relative abundance. When both nets were towed simultaneously, catches were combined. Environmental parameters such as temperature and salinity were also monitored. In the laboratory, all fish larvae were sorted, counted and identified as far as possible. Target species, such as pilchard, anchovy, maasbanker, hake *Merluccius capansis* and soles *Austroglossus microlepis* and *Dicologlossa cuneata* were measured to the nearest millimetre.

The results are briefly summarized here. A detailed analysis of the findings will be published in the near future.

Fish larva composition

The larvae of the bearded goby, *Sufflogobius bibarbatus*, completely dominated the ichthyoplankton during the survey period and formed 66,63 per cent of all fish larvae taken (Table 1).

Anchovy larvae were the second-most abundant group, accounting for 16,38 per cent. The larvae of mesopelagic fish (myctophid lanternfish and gonostomatids) comprised 4,56 per cent of the total fish larvae collected. The young stages of pilchard, maasbanker, soles and hake formed 3,75, 3,12, 3,00 and 1,28 per cent of the total numbers respectively.

Unidentified species belonging to the families *Callionymidae* (dragonets), *Syngnathidae* (pipefish), *Albulidae* (bonefish), *Ophidiidae* (kingklip), *Coryphaenoididae* (rattails), *Scomberescidae* (garfish), *Sciaenidae* (kablejou), *Gempylidae* (snoek), *Lophiidae* (anglerfish), *Blenniidae* (blennies), *Scorpaenidae* (scorpion fish) and *Triglidae* (gurnards) were also taken in the plankton but formed an insignificant proportion (1,05 per cent) of the total larvae composition.

Seasonal distribution and abundance

Pilchard: *Sardinops ocellata* Pappe

Pilchard larvae were widely distributed over the research area, but were mostly taken at inshore stations between Palgrave Point and Sandwich Harbour from September to November and between Cape Frio and Palgrave Point from December to February (Fig. 1.1).

The distribution of pilchard larvae in the two geographic areas corresponds with a similar pattern observed by King (1973) for egg distribution. One spawning took place during late winter and early spring in the south. A second spawning occurred in the summer and early autumn in the north. It is not yet known whether the eggs were spawned by two separate populations, although the presence of distinct areas of egg and larval abundance at different times would suggest separate spawning populations.

Larvae were found within a temperature range of 13,0° to 21,0°C, but were most abundant at surface temperatures of 14,0° to 14,9°C in early spring and 16,6° to 18,9°C in summer.

Salinity readings throughout the survey area were relatively constant (35,1°/oo to 35,4°/oo) and there is no evidence that salinity had any effect on the distribution of the larvae.

Anchovy: *Engraulis capensis* Gilchrist

Anchovy larvae were mainly confined to the northern sector of the research area, between latitude 18°20'S (Cape Frio) and 20°30'S (Palgrave Point. Larvae were particularly dense west of Cape Frio (Fig. 1.2). Their southern distribution rarely extended south of Palgrave Point. From the presence of anchovy eggs (King, *op. cit.*) and the distribution of yolk-sac larvae, it appears

TABLE I: Monthly catches of some fish larvae taken on the SWAPELS cruises, September 1972 to March 1973.

SEE TABLE II IN INTRODUCTION TO THESIS. pg 10 that spawning took place continually from October to April in this region. As the geographical and seasonal limits of anchovy spawning were not determined, it is assumed that considerable reproduction occurred further north and west of Cape Frio.

The larvae were most numerous at surface temperatures between 19,5°C and 20,5°C and had a narrow overall temperature range of 18,0° to 21,5°C.

Maasbanker: *Trachurus trachurus* Linnaeus

The larvae of maasbanker were distributed fairly uniformly between Cape Frio and Cape Cross, but rarely extended south of Walvis Bay (Fig. 1.3). The finding of yolk-sac larvae suggests two spawning populations. An early spawning took place between Palgrave Point and Walvis Bay in September and October. A later spawning of greater intensity occurred from January to March between Cape Frio and Palgrave Point. It is interesting to note that anchovy larvae appeared in the plankton at the same time as maasbanker larvae. Both species were frequently taken together during sampling. This fact would suggest that the early stages of maasbanker and anchovy not only share the same environment but possibly compete for available food in the Cape Frio nursery area.

The larvae were found within the narrow temperature range of 18,0° to 21,5°C, but were most abundant at mean surface temperatures of 19,8°C.

Hake *Merluccius capensis* Castelnau

Although two species of hake, *M. capensis* and *M. paradoxus* Franca exist in South West African waters (van Eck 1969), it would be extremely difficult to identify the adult species from examination of the larval characteristics alone. It was decided, therefore, to arbitrarily refer the hake larvae taken in this region as belonging to the species *M. capensis*, until such time as a distinction can be made between the early stages of the two species.

The larvae, although not very numerous, were collected from October 1972 to March 1973 and were widely distributed between Cape Frio and Hollams Bird Island (Fig. 1.4). The majority of larvae were caught during November and December in the coastal waters between Henties Bay (22°20'S) and Conception Bay. From the distribution of newly hatched larvae, it appears that spawning takes place inshore between latitudes 22° and 24°S.

Ninety-eight per cent of the larvae were taken between temperature of 12,5° and 18,0°C. However, sixty per cent were found between 13,5° and 15,5°C.

Sole: *Austroglossus microlepis* (Bleeker)

This species of sole is commonly known as the "West Coast sole" and is of significant commercial value to the demersal fishery of South West Africa (Lucks *et al* 1973).

The larval stages display a typically southern distribution, extending from Cape Cross to Hollams Bird Island (Fig. 1.5). The extent of their southern distribution has not been determined. It is evident from the distribution of yolk-sac larvae that this species spawns inshore between Conception Bay and Hollams Bird Island. Spawning takes place between the months of August and November.

Larvae were found at surface temperatures ranging from 11,7° to 15,5°C, but yolk-sac stages were most abundant at temperatures of 13,3° to 14,0°C.

Sole: *Dicologlossa cuneata* (Moreau)

This sole is an Atlantic species rarely appearing south of Walvis Bay (Smith 1970).

The larvae were found only in the northern part of the research area between Cape Frio and Palgrave Point (Fig. 1.6). The northern extent of its spawning has not been determined. They were mainly caught inshore along the narrow continental shelf which characterizes this region. Newly hatched stages were present in the plankton from December to February. Spawning probably took place during this period in the vicinity of Cape Frio.

Larvae were taken at surface temperatures of 18,0° to 22,0°C.

Goby: *Sufflogobius bibarbatus* (Smith)

Smith (1956) revised the taxonomy of this species, formerly *Gobius bibarbatus* Von Bonde, and delegated it to a new genus, *Sufflogobius*, based on its peculiar ability to self-inflate and the presence of two skin flaps beneath the chin. Very little information is available on this gobioid fish which is very abundant off the coast of South West Africa, so much so that purse seiners have sometimes taken considerable catches in their nets while fishing for pilchard and anchovy.

Adult gobies were frequently taken in the plankton nets during the course of the survey and it is possible that these fish actively migrate to the upper waters at night to feed.

The larvae of *Sufflogobius* completely dominated the ichthyoplanktonic fauna, forming over 66 per cent of the total fish larvae collected. Consequently, it is probably of considerable importance in the food web of the South West African coastal environment. The larval stages were very common and widely distributed along the inshore stations between Cape Frio and Hollams Bird Island (Fig. 1.7). The northern and southern ranges of their distribution have not yet been determined.

The occurrence of newly hatched larvae points to considerable spawning activity along the entire coast between August and December. However, two main spawning periods were observed. The first took place in the cold inshore waters (11,7° to 13,3°C) near Hollams Bird Island in August and September. A second spawning of lesser intensity occurred in the warmer waters (14,5° to 17,5°C) between Cape Frio and Mowe Point in October and November.

The larvae were adaptable to wide fluctuations in temperature (11,3° to 21,3°C) and displayed a comparatively long planktonic phase. Transitional stages between larvae and juveniles were frequently caught in large numbers. When goby larvae were particularly abundant in samples, other fish larvae were noticeably absent.

Mesopelagic larvae

Many of the specimens have not yet been identified to generic level. However, early stages belonging to the genera *Symbolophorus*, *Diaphus* and *Lampanyctus* were often present in the plankton. The gonostomatid *Maurolicus mulleri* was also quite abundant.

The larvae were found throughout the survey area but chiefly at offshore stations along the edge of the continental shelf (Fig. 1.8). Highest numbers were recorded off Palgrave Point, west of Cape Cross, off Walvis Bay and west of Conception Bay and Hollams Bird Island.

Larvae were found at surface temperatures ranging from 12,8° to 20,0°C.

Day and night variation in catches

Analyses of the day and night hauls revealed interesting catch difference for the various species.

Pilchard larvae were three times more plentiful at night. Maximum catches were taken during the first two hours of darkness (19.00 to 21.00 hrs). In the case of anchovy, over five times as many larvae appeared in night hauls as opposed to daylight hauls. Peak abun-

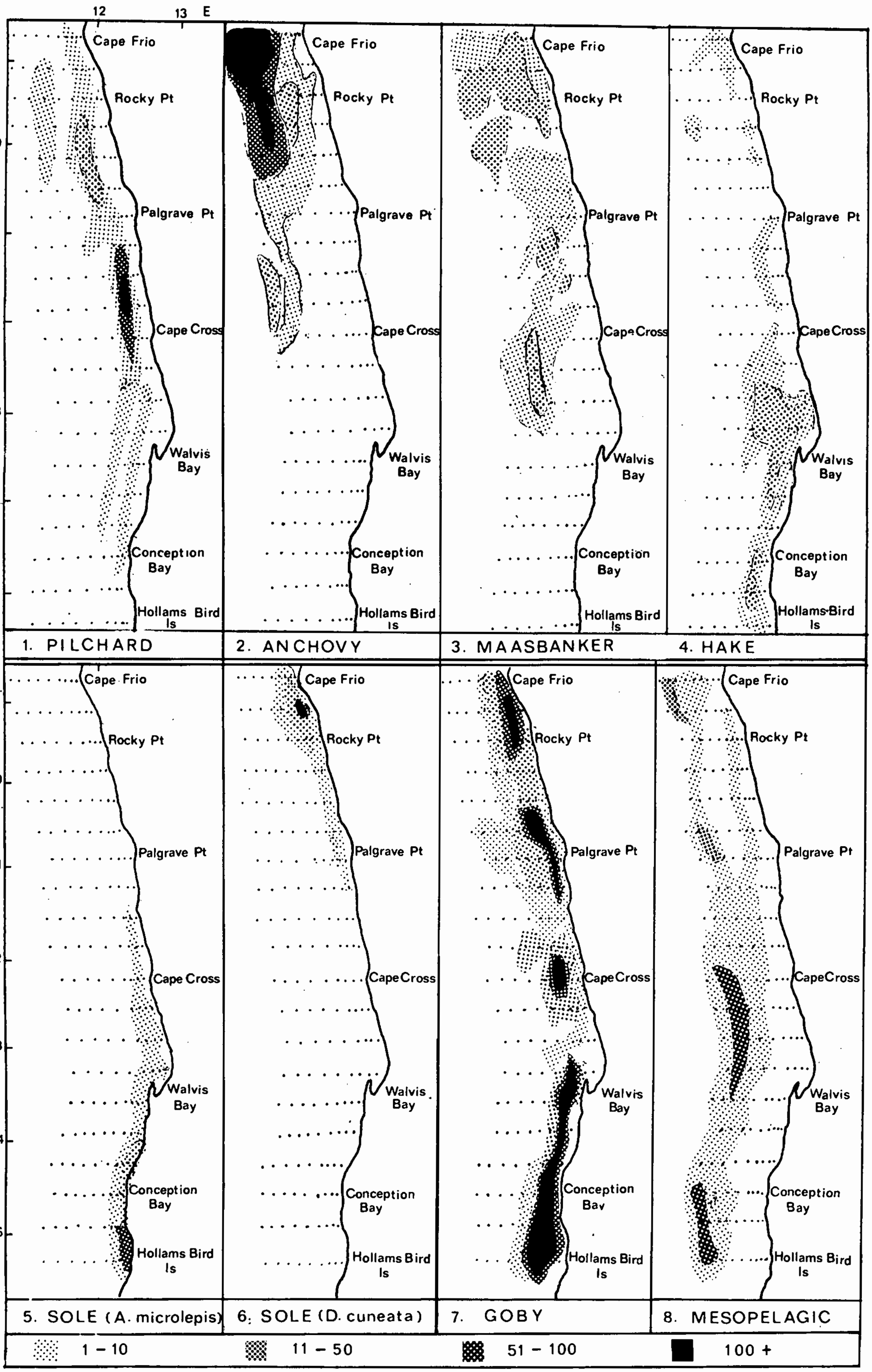


Fig. 1: The distribution and abundance of some fish larvae off South West Africa, numbers per haul, August 1972 to April, 1973.

dance was from midnight to 02.00 hrs. The larvae of hake also exhibited marked diurnal variation in catches, with three times as many being caught in night hauls. Peak catch periods were at dusk (19.30 hrs), midnight and dawn (05.00 to 05.30 hrs).

No diurnal variation was displayed by maasbanker larvae or by either species of sole larvae. The majority of goby larvae were captured between 04.00 and 11.00 hrs. They were particularly numerous in the plankton between 04.00 and 06.00 hrs. Larvae of mesopelagic fish were noticeably more abundant in night hauls. Advanced larvae and juveniles of all species were taken more frequently during the hours of darkness.

Dispersal of larvae

Although there is at present no direct oceanographic evidence to relate larva movement to the known current patterns off South West Africa, it has been possible to establish general trends from monthly size distribution of larvae.

Larvae resulting from eggs spawned in the south are carried rapidly in a northerly direction by the Benguela Current. As the larvae develop and progress northwards, the patches become scattered and eventually disperse. However, those larvae resulting from eggs spawned in the north appear to be carried in a southerly direction. Newly hatched larvae were found in the far north while the more advanced stages occurred further south.

An inshore off-shore drift was also apparent between Cape Frio and Rocky Point, but the situation was sometimes confused by the appearance of mixed size groups in the samples.

Suggestions for future work

Ecological aspects such as depth distribution, vertical migration and behaviour of larvae in relation to sampling gear will have to be studied in the near future to provide a sound basis for stock assessment.

Furthermore, in order to gain a better understanding of the ichthyoplankton environment as a whole, it is important that physical and biological parameters such as upwelling, primary production, current movement, predation and species-interaction should be investigated in greater detail.

Acknowledgments

The author wishes to thank the Director of Sea Fisheries, Dr. B. van D. de Jager, for his kind support and Mr. D. L. Cram for his encouragement. Thanks are also due to the captain and the crew of R.S. *Sardinops* and to Mr. J. Giddey and Mrs. S. Payne who devoted much time to sorting plankton samples.

References

CRAM, D. L. and G. A. VISSER, 1972 – Cape Cross Research Programme, Phase II, A summary of results. *S. Afr. Shipp. News Fish. Ind. Rev.* **27** (2) : 40 – 43.

KING, D. P. F., 1973 – Cape Cross Report (Phase III) Sea Fisheries Branch: Internal Report.

KING, D. P. F. and A. A. ROBERTSON, 1973 – Methods of pelagic fish egg and larval research in South West Africa. *S. Afr. Shipp. News Fish. Ind. Rev.* **28** (5) : 57 – 61.

LUCKS, D. K., A. I. L. PAYNE and S. MAREE, 1973 – The trawl fishery of South West Africa. *S. Afr. Shipp. News Fish. Ind. Rev.* **28** (9) : 65 – 71.

SMITH, J. L. B., 1956 – Self inflation in a gobioid fish. *Nature* **177**: p. 714.

SMITH, J. L. B., 1970 – The Sea Fishes of Southern Africa. Fifth Edition, Central News Agency, South Africa.

VAN ECK, T. H., 1969 – The South African hake: "*Merluccius capensis*" or "*Merluccius paradoxus?*" *S. Afr. Shipp. News Fish. Ind. Rev.* **24** (5) : 95 – 97.

A NOTE ON THE RELATIONSHIP BETWEEN THE VERTICAL DISTRIBUTION OF MAASBANKER LARVAE (TRACHURUS TRACHURUS L.) AND ENVIRONMENTAL PARA= METERS OFF SOUTH WEST AFRICA

M. J. O'TOOLE

The maasbanker or horse mackerel Trachurus trachurus forms an important pelagic fish resource in the south east Atlantic. The fishery, although relatively recent, is becoming increasingly valuable. Stocks are mainly being exploited by vessels of the Soviet Union and South Africa. Landings, excluding those of Angola, have fluctuated between approximately 70 000 metric tons in 1969 and 210 000 metric tons in 1973.

The Sea Fisheries Branch has been engaged in quantitative egg and larva surveys as one method of stock assessment since the ini= tiation of the Cape Cross Programme in 1971 (Cram and Visser 1972). Variation in the vertical distribution of fish larvae makes it diffi= cult to estimate species abundance reliably from extensive ichthyo= plankton collections. Such estimates would demand as a prerequisite a knowledge of the vertical distribution of the species during its larval phase. Furthermore, knowledge of the effects of biotic and abiotic factors on the depth distribution of the larvae would be useful in larval survival and recruitment studies.

Larvae of the maasbanker were found to be both abundant and wide= spread in plankton samples taken during a two-year egg and larva survey off South West Africa (O'Toole 1974). Little is known about the depth distribution of maasbanker larvae in relation to environ= mental conditions in the region. The only known observation was by d'Arcangues (University of Paris, personal communication) during an investigation of the scattering layer off the coast in February 1974.

Several larvae were taken at depths ranging from 14 m to 70 m at temperatures of 14 - 16°C.

At 12h00 on 2 January 1975, during a routine ichthyoplankton cruise by the R.S. Benguela, large numbers of maasbanker larvae were located approximately 40 km west of Palgrave Point (Fig. 1). The surface temperature ranged from $20,0^{\circ}$C to $20,3^{\circ}$C. Samples were collected simultaneously at a series of depths, using nine samplers similar to those described by Miller (1961). The samplers consisted of a 14,0 cm diameter PVC tube with a 0.50 mm conical collecting net and were spaced at 10 metre intervals along the towing cable. Bathykymographs were positioned at 30 m and 60 m to provide depth profiles of the tow. A Vee-fin depressor (57 kg) was used to submerge and stabilize the samplers during the haul. The nets were towed at approximately two knots for a period of one hour in a westerly direction.

Larvae were extracted from the samples, counted and measured to the nearest tenth of a millimetre. The mean depth fished by each net was established by interpolation of the bathykymograph traces. Temperature, salinity, oxygen and chlorophyll measurements were taken at selected depth intervals in the water column at the beginning and end of the tow.

No larvae were taken in the upper 12 metres of water. One hundred and thirty larvae, ranging in size from 2,5 mm to 7,8 mm were captured within the depth range 18-75 m. Correlation of hydrological observations and larval abundance with depth is given in Table I. Approximately 40 per cent of all the larvae were found near the thermocline at a depth of 25 m and a temperature of $18,2^{\circ}$C. Numbers fell off below the thermocline. Larvae occurred over the following range

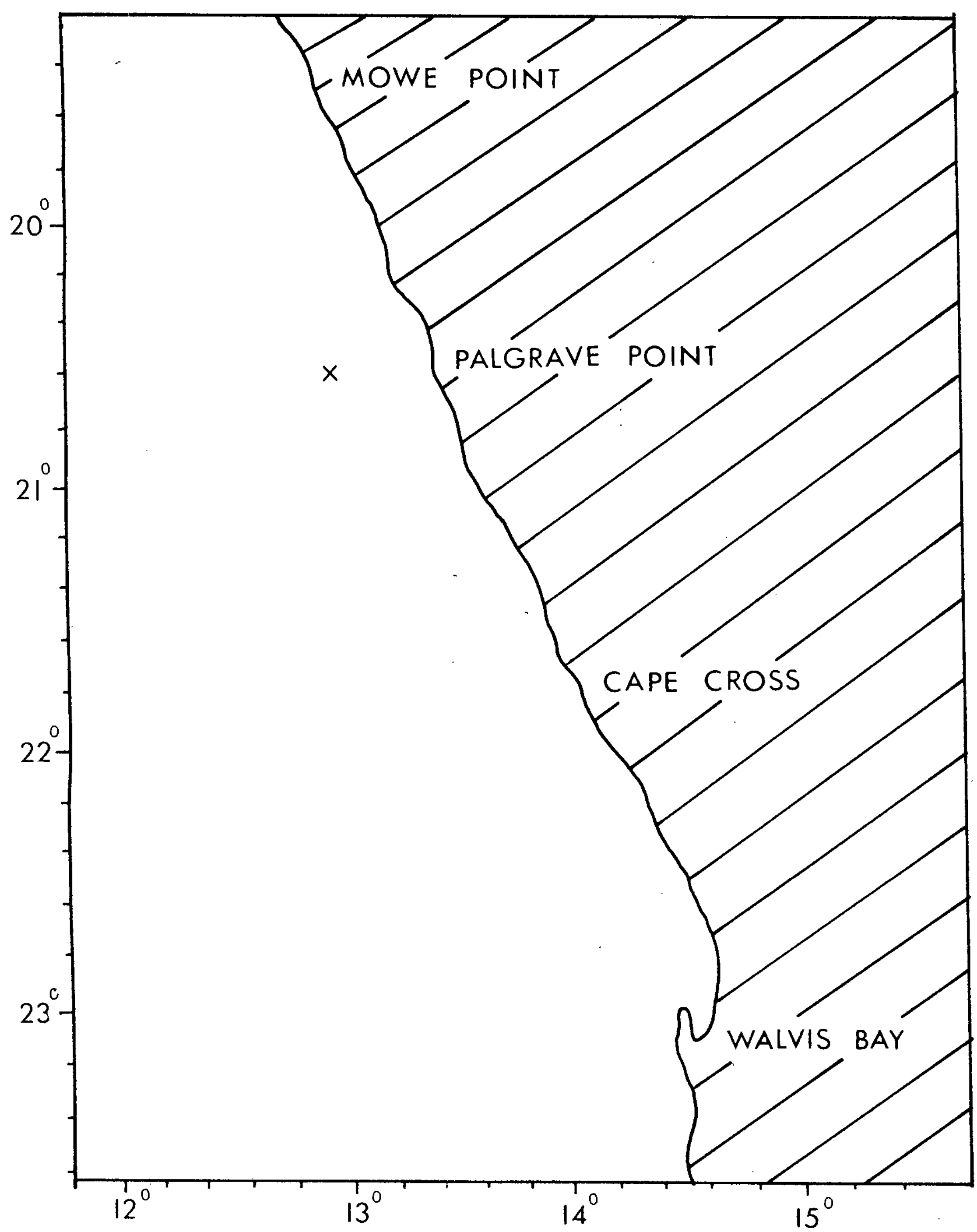


Fig. 1 Location of capture of maasbanker larvae

of environmental parameters. Temperature; 13,5 - 19,1^{0}C; Salinity, 35,20 - 35,45^{0}/oo; Oxygen 4,6 - 5,0 ml/l. However, since the entire depth distribution of the larvae was not covered, these ranges of environmental parameters should not be regarded as limiting for maasbanker larvae.

The observed vertical distribution of larvae compares favourably with similar work on related species of Trachurus. Ahlstrom (1959) noted that about 80 per cent of *T. symmetricus* larvae occurred in the upper 50 metres, but the centre of abundance fluctuated between 10 m and 44 m. The optimum depth of larvae of *T. japonicus* was found to be 20 m (Ida 1972).

During this investigation, no differences in the distribution of larval length classes with depth were found. However, more than 60 per cent of recently hatched specimens (2,5 - 4,0 mm) occurred in the vicinity of the chlorophyll maximum layer. Although the results are based on only one observation, it is possible that these early larval stages were actively feeding in this layer at the time of capture. If this assumption is correct, then the vertical dis= placement or destruction of the chlorophyll maximum layer may strongly influence the depth distribution and survival of newly hatched larvae.

ACKNOWLEDGEMENTS

I wish to thank Mr. D.P.F. King and Mr. C. J. Giddey for their assistance during sampling operations.

TABLE I: DEPTH DISTRIBUTION, ABUNDANCE AND SIZE OF *TRACHURUS TRACHURUS* LARVAE IN RELATION TO HYDROLOGICAL PARAMETERS

Hydrology					Larvae			
Mean depth(m)	Temp. (^{o}C)	Salinity ($^{o}/oo$)	Oxygen (ml/l)	Chlorophyll (ml/m^{3})	No. of larvae	Length range (mm)	% less than 4.0 mm	% more than 4.0 mm
0	20,3	35,52	5,3	2,5	-	-	-	-
8	20,0	35,50	5,2	2,8	-	-	-	-
2	19,9	35,48	5,1	3,2	-	-	-	-
8	19,1	35,45	5,0	4,6	18	3,5-7,8	22,2	77,8
5	18,2	35,32	4,9	5,8	64	2,5-6,9	40,6	59,4
4	16,3	35,25	4,6	5,0	24	3,9-5,8	25,0	75,0
3	15,2	35,25	no data	3,1	16	3,2-7,4	11,0	89,0
2	14,0	35,20	no data	2,1	4	5,0-6,5	-	100,0
5	13,5	no data	no data	2,3	4	4,0-5,2	-	100,0

LITERATURE CITED

AHLSTROM, E.H. 1959 - Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fishery Bull. Fish Wildl. Serv. U.S. 60 (161); 107 - 146.

CRAM, D.L. and G. A. VISSER, 1972 - Cape Cross Research Programme, Phase II: A summary of Results. S. Afr. Shipp. News Fish. Ind. Rev. 27 (2): 40 - 43.

IDA, H. 1972 - Some ecological aspects of larval fishes in waters off Central Japan. Bull. Jap. Soc. scient. Fish. 38 (9): 981 - 994.

MILLER, D. 1961 - A modification of the small Hardy plankton sampler for simultaneous high-speed plankton hauls. Bull. mar. Ecol. 5(45): 165-172.

O'TOOLE, M.J. 1974 - The seasonal distribution and abundance of pilchard, anchovy, maasbanker and hake larvae off South West Africa, August 1972 to March 1973, Internal Rep. Sea Fish. Brch. S. Afr., 19pp.

FIGURE LEGEND

Fig. 1: Location of capture of maasbanker larvae

Fish. Bull. S. Afr. 8: p. 35
1976

A NOTE ON THE PRESENCE OF RIPE ANCHOVY OFF CAPE POINT

M. J. O'TOOLE

On 11 November 1975, large shoals of albacore (long-fin tuna) *Thunnus alalunga* were observed feeding at the surface between 24 km and 28 km south-west of Cape Point (Cape of Good Hope). Twelve specimens with a length (Lt) of 70–90 cm were caught by trolling from 09h00 to 10h30. The weights of the tuna varied from 12 kg to 21 kg and the surface temperature in the vicinity was 18°C.

Several freshly eaten anchovy *Engraulis capensis* were disgorged by some of the fish on landing and examination of one stomach revealed that the tuna had been feeding almost exclusively on this species. Five of the disgorged specimens were still in excellent condition and were examined for gonad activity. On slitting open the body cavity, the gonads of two (males) were in a white fluid condition and those of the other three (females) were both distended and fluid. All could be assigned to the ripe (stage 5) condition. The length (Lt) of the anchovies varied between 9 cm and 11 cm.

Spawning anchovy have never been recorded in commercial purse-seine catches in the Cape since 1963, the most advanced stage previously recorded being the active/ripe (stage 4) condition (Robinson 1966). The main spawning season of anchovy in Cape waters is during spring and summer. In recent years, most spawning has occurred east of Cape Point (Baird and Geldenhuys 1973).

Using data from surface tows only, Anders (1965) was able to determine the horizontal distribution and relative abundance of anchovy eggs off the Cape in the early years of commercial exploitation (1964/65). Ahlstrom (1959) noted that eggs and larvae of the northern anchovy *E. mordax* were to be found near the surface. Alverson (1961) stated that albacore occur mainly above the thermocline but his finding was modified by Kawai (1969) who stated that it is mainly the young specimens that are found in surface waters where the thermocline is shallow. Mr B. B. S. Tromp (Sea Fisheries Branch, personal communication) noted that the thermocline in the vicinity of these tuna shoals lay at 60 – 70 m when sampled routinely on October 27 and on November 13.

It appears probable, therefore, that the anchovies were not driven to the surface layers by the predatory tuna, but had, in fact, congregated, possibly for the purpose of spawning. The presence of both males and females in a ripe condition at the surface adds further weight to this hypothesis and it thus seems that both spawning and egg development take place close to the surface.

LITERATURE CITED

AHLSTROM, E. H. 1959 – Vertical distribution of pelagic fish eggs and larvae off California and Baja California. *Fishery Bull. Fish Wildl. Serv. U.S. 161*, **60**: 107–146.

ALVERSON, D. L. 1961 – Ocean temperatures and their relation to albacore tuna *(Thunnus germo)* distribution in waters off the coast of Oregon, Washington and British Columbia. *J. Fish. Res. Bd Canada* **18** (6): 1145–1152.

ANDERS, A. S. 1965 – Preliminary observations on anchovy spawning off the South African coast. *S. Afr. Shipp. News Fish. Ind. Rev.* **20** (11): 103–107.

BAIRD, D. and N. D. GELDENHUYS 1973 – Biology and the fishery of the anchovy in South Africa. *S. Afr. Shipp. News Fish. Ind. Rev.* **28** (10): 43–49.

KAWAI, H. 1969 – On the relationship between thermal structure and distribution of long-line fishing grounds of tunas in the Intertropical Atlantic. I. Analysis based on isotherms on level surfaces, topographies of thermocline, etc. *Bull. Far Seas Res. Lab.* **2**: 275–303.

ROBINSON, G. A. 1966 – A preliminary report on certain aspects of the biology of the South African anchovy, *Engraulis capensis* (Gilchrist). M.Sc. thesis, University of Stellenbosch.