The Biology, Distribution and Ecology of *Lampanyctodes hectoris* and *Maurolicus muelleri* along the South-African coast

Submitted in partial fulfillment of the requirements
for the degree of Master of Science
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by
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To my mother, Margie Prosch, who made this study possible.

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Valuable technical assistance with art work and the catalogueing of egg and larval samples was received from Mr J. van der Westhuizen, Ms S. Wright, Mr E. Hoppe and Ms H. van der Pol.

The officers and crew of the RS Africana have been most helpful during the collection of samples for this study, which on occasion took place under trying circumstances.

My colleagues Mr Andrew Payne and Mr Aldo Berruti kindly allowed me to include some of their unpublished data on demersal fish predation and bird predation respectively.

This study has been made possible by grants from the Department of Environmental Affairs and Tourism and the Fisheries Development Corporation of South Africa.

My wife Diane has been a constant source of encouragement and support.

DECLARATION

The collection of commercial catch statistics, length measurements and otoliths for Lampanyctodes hectoris were made by Sea Fisheries Research Institute (SFRI) technical staff. The collection of all Maurolicus muelleri samples and non-commercial L. hectoris samples were made during various research cruises on board RS Africana by SFRI personnel. I participated in approximately 60 per cent of these cruises and analysed all of these samples in the laboratory with minimal technical assistance.

The information on demersal fish predation was made available to me by Mr Andrew Payne, head of the Demersal Fish Section at the Sea Fisheries Research Institute. This data base was compiled during routine hake research cruises and I extracted the relevant data as presented in this study.

The data presented in Chapter 3 was collected during the Cape Egg and Larvae Programme (CELP) which was conducted over a thirteen month period in 1977/78. Some 120 stations were sampled each month, and a large number of SFRI personnel contributed towards this programme. Mr Peter Shelton, Head of the Pelagic Fish Section at the SFRI was the project leader of the CELP. The sorting of eggs and larvae from the plankton samples was carried out by a very large number of technical assistants over a five year period. I contributed to the final identification of eggs and larvae into genera, and where possible to species level. Special attention was given to the correct identification of light- and lanternfish eggs and larvae.

The information on the predation of resident South African pelagic seabirds on mesopelagic fish, was collected by Mr Aldo Berruti and used with his permission.

All references have been accurately reported.

Signed by candidate

R. M. Prosch

ABSTRACT

Lampanyctodes hectoris, commonly called lanternfish, is a myctophid and was first recorded in the South African pelagic catches in 1969. The average annual landings since then have been approximately 4% of the pelagic catch, the largest being 42 560 metric tons in 1973 (10,45% of the total landing). *Maurolicus muelleri*, commonly called lightfish, is a sternoptychid, and is not taken commercially. An attempt was made to document the basic biology of these two species before possible commercial fishing pressure brings about a change in these parameters. Samples of *L.hectoris* taken from commercial catches and research cruises, and samples of *M. muelleri* obtained from research cruises were analysed to obtain the biological parameters.

L. hectoris spawning in the southern Benguela Current System occurs throughout the year, but mainly during the late winter to early spring with a peak in spring. *M. muelleri* spawning occurs throughout the year with a peak in spring/early summer and a smaller peak in winter. Maturity analysis show the same pattern, and also indicate that *M. muelleri* spawning has both a vertical and a horizontal dimension and its eggs were found in the temperature range 14 to 17°C.

The growth parameters calculated for *M. muelleri* and *L. hectoris* using daily ring enumeration were:
L_c(cm, caudal length)= $6.00(1-\exp[-1.15\{t-0.06\}])$ for lightfish and L_c(cm, caudal length)= $7.00(1-\exp[-1.66\{t-0.06\}])$ for lanternfish. Estimates of natural mortality using length frequencies and an emperical equation using the asymptotic length L_∞,the

growth constant K, and an estimate of the mean water temperature in which the fish stock in question lives, were calculated. Estimates for *L. hectoris* are 2,37 using length frequencies and 2,32 to 2,96 when using the emperical formula. The equivalent values for *M. muelleri* are 4,90 and 1,9 to 2,43.

Predation on both *L. hectoris* and *M. muelleri* by commercially important demersal fish species are recorded. The hakes *Merluccius capensis* and *M. paradoxus* , the snoek *Thyrsites atun* and the horse mackerel *Trachurus trachurus* feed on both light- and lanternfish. These prey species are important in the diet of all these predators, especially when expressed in terms of mass. Resident South African pelagic seabirds seldom feed on these species, although they may be important to non-resident pelagic seabirds.

The calorific values obtained ranged from 23,2 to 28,9 kJ for lanternfish and, 22,5 to 23,2 kJ for lightfish. The total lipid content of lanternfish expressed as a precentage of wet weight ranged from 9,3 to 31,2 and show seasonal fluctuations as well as a declining trend with an increase in size. The total lipid content for lightfish ranged from 3,0 to 19,3 and also show fluctuations associated with length and season. The protein content (percentage dry weight) of both light- and lanternfish show little variation with length or season, and values of 14,0 to 15,0 for lanternfish and values of 13,5 to 18,9 for lightfish were calculated. A relationship with a negative slope between lipid and water content in lanternfish was determined.

PREAMBLE

"During recent years an increasing proportion of conventional fish stocks have reached a state of full exploitation or even over-exploitation, and the search for new fishery resources has been intensified. At present, it seems that krill, cephalopods and mesopelagic fish are the most promising potential resources" (Gjøsaeter and Kawaguchi 1980).

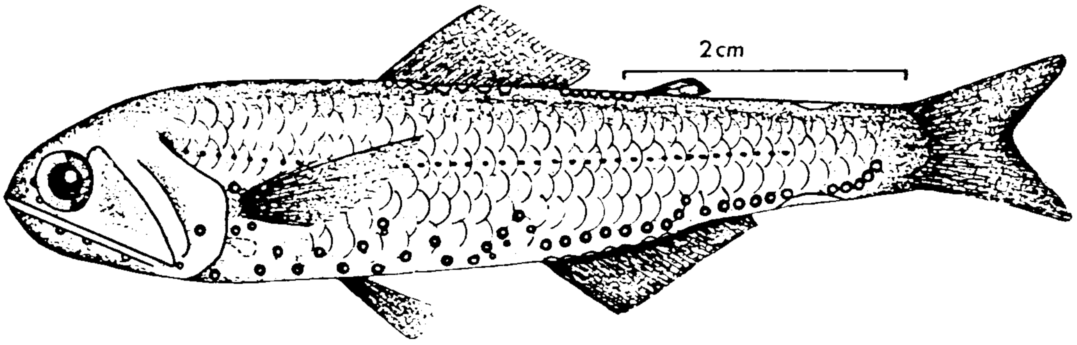
This statement is also valid in the South African context, where the mainstays of the Pelagic Fishing Industry, the pilchard (Sardinops ocellatus) and the horse mackerel (Trachurus trachurus) stocks collapsed resulting in this Industry being dependent on a recruit based anchovy (Engraulis japonicus) fishery (Shelton 1981 and Armstrong et al 1985).

The dependence of the Industry on one species, together with a shortage of fish-meal necessitated a synthesis of the current state of knowledge in the field of alternative resources. The Alternative Resources Group of the Benguela Ecology Programme identified the lanternfish Lampanyctodes hectoris (a myctophid), the lightfish Maurolicus muelleri (a sternoptychid), the round-herring Etrumeus whiteheadii (an engraulid) and three species of squid: Loligo reynaudii, Todaropsis eblanae and Todarodes sagittatus as possible alternative resources. All of these alternative resources are preyed upon by the commercially-important hake during some stage of its life-cycle (Sea Fisheries Research Institute, Cape Town, unpublished). An assessment of the system effects of commercial exploitation of mesopelagic stocks is therefore considered to be an integral part of the study carried out by this research group.

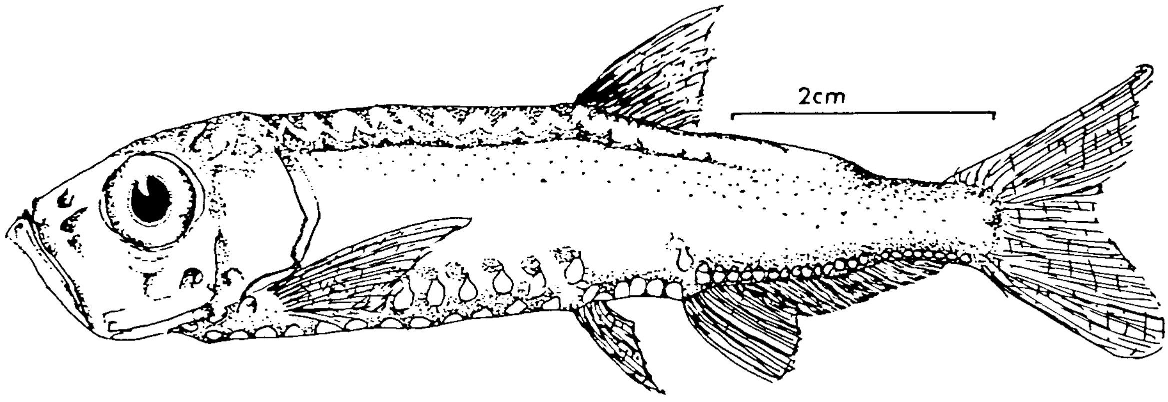
Fig. 1 illustrates the two mesopelagic species studied and gives an indication of their dimensions.

Although L. hectoris and M. muelleri are both popularly referred to as mesopelagic, they are pseudoceanic upper-slope derivatives, and appear to be confined to the upwelling region of the Benguela Current System where they exhibit a markedly patchy distribution and a seasonal variation in abundance (Hulley et al in prep.). However, in the context of the present study where the interaction between these species and demersal species such as hake and pelagic species such as anchovy and pilchard will be discussed, they can be regarded as mesopelagic. This "zone" has been defined in different ways based on depth, temperature and light regimes. Depth seems to be the best criterion and mesopelagic fish can thus be defined as species generally spending the day at depths between approximately 200 and 1 000 m. Generally they perform a diel migration, coming to the upper 200 m or even the surface during the night. Species of many fish families fall within this group, but generally the Myctophidae and Gonostomatidae are dominant. Sternoptychidae, Bathylagidae, Chiasmodontidae, Trichiuridae and Nomeidae seem to be fairly important in some areas (Gjøsaeter and Kawaguchi 1980).

The lanternfish family Myctophidae is by far the most diverse and widespread family of mid-water fishes in the world oceans. As presently recognized it contains about 30 genera and 300 species. Their larvae are important in the plankton and make up about 50 % of all fish larvae taken in open-ocean plankton tows and, in many



LANTERNFISH:
Lampanyctodes hectoris



LIGHTFISH:
Maurolicus muelleri

Fig. 1: *L. hectoris* and *M. muelleri*, showing dimensions.

areas lanternfish make up the largest fish biomass of a midwater trawl catch (Moser and Ahlstrom 1974). Myctophids undertake extensive vertical migrations. In one study they were found to range diurnally from 400 to 750 metres and nocturnally to the upper 100 metres (Paxton 1972). These migrations, during which the animals are subjected to great changes in temperature, salinity, oxygen etc. are generally believed to be feeding migrations (Nafpaktitis and Nafpaktitis 1969). According to the latter authors several myctophids are restricted in their distribution to relatively well-defined water masses although many show a much wider distribution, inhabiting adjacent water masses with weakly defined boundaries. A few appear to be distributed circumglobally, however careful studies have shown that "wide ranges" often are inhabited by two or more morphologically very similar species, each occupying only part of the original range, in addition, recent investigations have indicated that wide distributions may very well be the result of passive transport by oceanic currents (Nafpaktitis and Nafpaktitis 1969). Individuals thus carried away from their optimum water mass to an alien environment are reproductively lost to their species, since the new environmental factors prevent the normal development of the gonads or of the gametes (Nafpaktitis and Nafpaktitis 1969).

Sternoptychidae are generally oceanic, some are pseudoceanic and some are benthopelagic. Juveniles and adults occur at about 200 - 1,500 m by day. Some are diel vertical migrants, others are partial or non-migrants. The population is usually stratified by size or depth during the day, with smaller individuals dwelling shallower (Badcock 1984).

Lanternfish made their first documented appearance in the South African commercial catches in 1966 and since then a fortuitous fishery for *L. hectoris* has developed incidental to the anchovy/ pilchard fishery. The catch weight was recorded separately from anchovy for the first time in 1969 (Centurier-Harris 1974) and Table 1 shows the annual landings of lanternfish since 1969. It has contributed up to approximately 10 per cent of the total purse-seine catches and the 1985 landing was the second highest recorded.

Lightfish is not taken commercially, although specimens do occur in the catches from time to time.

The aim of this study was to research the basic biology of the two mesopelagic fishes *Lampanyctodes hectoris* and *Maurolicus muelleri* off the South African coast. Since *L. hectoris* is only marginally exploited and *M. muelleri* not at all, they provide a unique opportunity to conduct research into unexploited resources before compensatory mechanisms, such as a younger age at maturity, brought about by fishing pressure, manifest themselves.

Table 1: Species composition of South African purse-seine landings ('000 t), 1969 - 1985 (Armstrong et al 1985).

Year	Pilchard	Anchovy	Horse Mackerel	Chub Mackerel	Round Herring	Lantern Fish
1969	56,1	149,2	26,8	91,7	23,3	4,9
1970	61,8	169,3	7,9	77,9	23,7	18,2
1971	87,6	157,3	2,2	54,2	21,6	2,0
1972	104,2	235,6	1,3	56,7	20,6	15,2
1973	69,0	250,9	1,6	58,8	28,7	42,4
1974	16,0	349,8	2,5	30,7	1,3	0,3
1975	89,2	223,6	1,6	69,3	23,6	0,1
1976	176,4	218,3	0,4	0,5	11,7	0,1
1977	57,8	235,5	1,9	21,3	35,0	5,6
1978	97,0	209,5	3,6	2,4	67,0	1,0
1979	52,9	291,4	4,3	2,7	21,0	8,7
1980	50,4	315,5	0,4	0,2	14,1	0,1
1981	46,2	292,0	6,1	0,3	24,3	10,3
1982	35,2	306,1	1,1	2,7	31,2	0,7
1983	60,5	240,2	1,4	3,8	69,0	1,6
1984	26,7	272,4	2,5	0,7	29,0	13,6
1985	30,7	271,9	0,8	0,1	39,8	31,0

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CHAPTER 1

SYSTEMATICS AND WORLD-WIDE DISTRIBUTION OF THE LANTERNFISH LAMPANYCTODES HECTORIS AND THE LIGHTFISH MAUROLICUS MUELLERI, WITH PARTICULAR REFERENCE TO THE DISTRIBUTION AND SIZE COMPOSITIONS OF THE POPULATIONS IN THE BENGUELA CURRENT SYSTEM

1.1 CLASSIFICATION OF THE MYCTOPHIDAE, GONOSTOMATIDAE AND STERNOPTYCHIDAE

Maurolicus muelleri has long been regarded as an advanced member of the family Gonostomatidae (eg. Gjøsaeter and Kawaguchi 1980) however, Weitzman (1974) placed the species amongst the marine hatchetfishes, family Sternoptychidae. In his study on the Gonostomatidae, Norman (1930) examined specimens of *M. muelleri* from the Atlantic, the Mediterranean and New Zealand and was unable to find any difference of sufficient importance to warrant the recognition of more than one species. Grey (1964) compared a range of meristic features of specimens from the Mediterranean, North and South Atlantic, North and South Pacific, and Red Sea and concluded that the genus is monotypic.

The taxonomy of gonostomatid fishes is more advanced than that of myctophids (Gjøsaeter and Kawaguchi 1980). Grey (1960, 1964) established the taxonomy at the generic level which was used extensively in the literature until Weitzman (1974) proposed a new evolutionary classification (Table 1.1). This new classification was based on their osteology and resulted in considerable

Table 1.1 Comparison of the classification systems of Grey (1960, 1964) and Weitzman (1974) (after Gjøsaeter and Kawaguchi 1980)

GREY (1960, 1964)	WEITZMAN (1974)
Gonostomatidae (20 genera)	Gonostomatidae
1. *Diplophos* Gunther	(6 genera)
2. *Triplophos* Brauer	
3. *Bonapartia* Goode and Bean	
4. *Margrethia* Jespersen and Taning	
5. *Gonostoma* Rafinesque	
6. *Cyclothone* Goode and Bean	
7. *Thorophos* Bruun*	Sternoptychidae
8. *Araiophos* Grey	(10 genera including
9. *Maurolicus* Cocco	*Polyipnus* Cocco
10. *Danaphos* Bruun	*Argyropelecus* Gunther
11. *Valenciennellus* Jordan and Evermann	*Sternoptyx* Herman
12. *Argyripnus* Gibert and Cramer	
13. *Sonoda* Grey	
14. *Vinciguerria* Jordan and Evermann	Photichthyidae (7 genera)
15. *Polymetme* McCulloch	
16. *Yarrella* Goode and Bean	
17. *Pollichthys* Grey	
18. *Photichthys* Grey	
19. *Woodsia* Grey	
20. *Ichthyococcus* Bonaparte	

* Including *Neophos* Myers

changes in the arrangement of genera. He transferred seven genera from Gonostomatidae to Photichthyidae, which is newly established, and seven genera from Gonostomatidae to Sternoptychidae. In his classification, Sternoptychidae, incorporating Maurolicus muelleri, and Photichthydae are given high ranking as families with abundant micronektonic fishes together with Gonostomatidae and Myctophidae.

Lampanyctodes hectoris was first described by Günther (1876, cited by Wisner 1976). Subsequent updated descriptions were documented by Gilchrist, who erroneously described a new species Scopelus argenteus (Fraser-Brünner 1949, Wisner 1976).

Paxton (1972) recognized two subfamilies in the family Myctophidae, namely the Myctophinae and the Lampanyctinae on the basis of osteological and photophore characters of adults (Fig. 1.1).

Moser and Ahlstrom (1974) showed that lanternfish larvae fall naturally into two groups on the basis of eye shape - those with narrow elliptical eyes and those with round or nearly round eyes. The generic composition of these two groups agrees closely with that of the two subfamilies established by Paxton (1972).

The subfamily Lampanyctinae is considerably larger than the Myctophinae, containing about 19 genera and 200 - 250 species, compared with 12 genera and about 75 species in the Myctophinae (Moser and Ahlstrom 1974). Paxton (1972) divided the genera into four Tribes on the basis of a combination of osteological features and photophore characteristics. In general the larvae of the Lampanyctinae are much less diverse in larval characters and

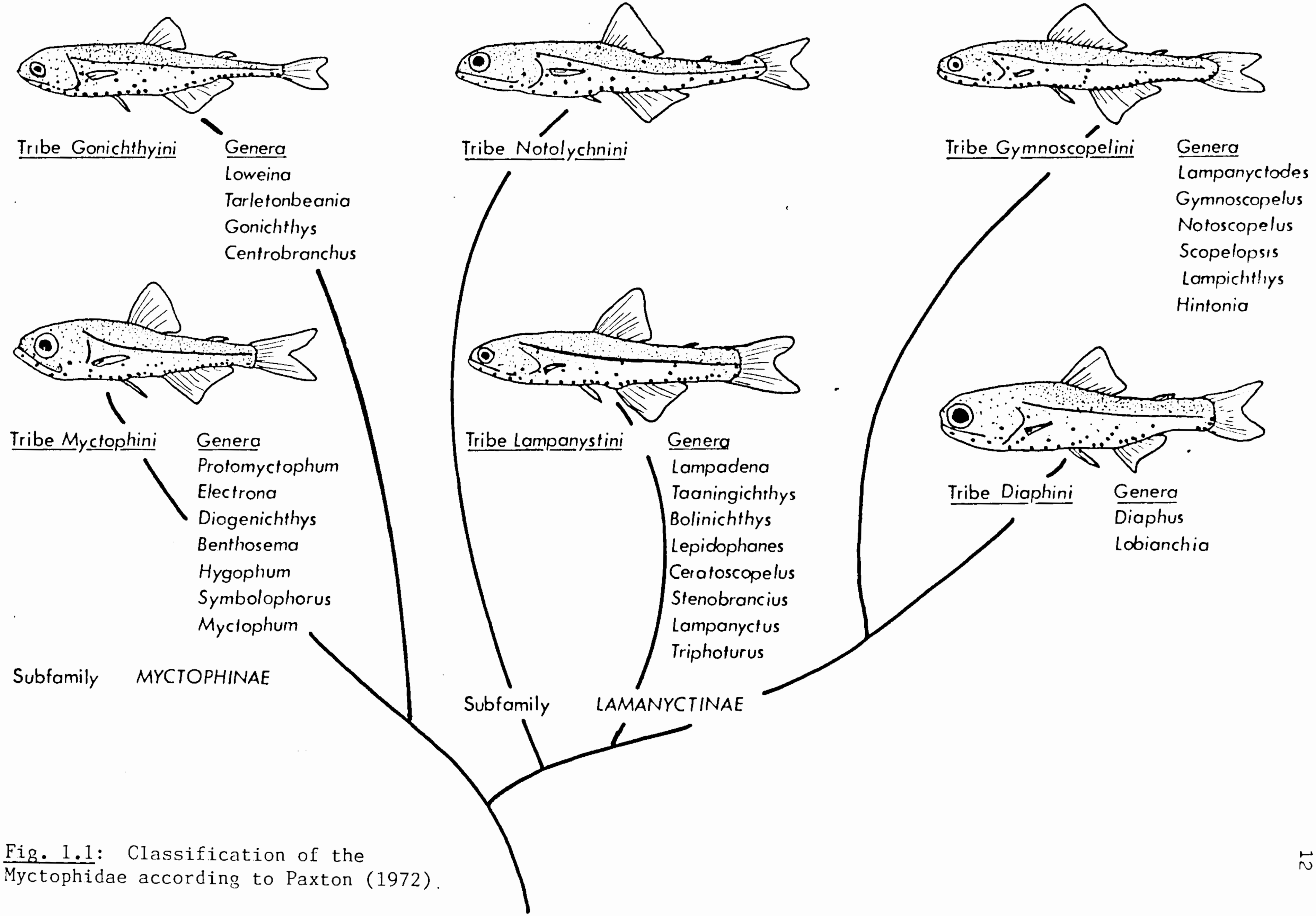

Fig. 1.1: Classification of the Myctophidae according to Paxton (1972).

specializations than are the larvae of the Myctophinae (Moser and Ahlstrom 1974). Ahlstrom et al (1976) documented the development of larvae and early juveniles of L. hectoris and concluded that although it is most closely related to genera in the Tribe Gymnoscopelini, especially Lampichthys, it is also related to genera in the Tribe Lampanyctini, notably Lampadena, Ceratoscopelus and Lepidophanes. These genera are among those placed in the Tribe Gymnoscopelini in a new classification of the Myctophidae proposed by these authors.

1.2 AREAL DISTRIBUTION

M. muelleri is a widespread member of the mesopelagic fauna and the occurrence of this species in eastern Pacific waters from 5^0 N to 34^0 S (Bussing 1965, Ahlstrom 1971), in south-western Atlantic waters from 40^0 S to 45^0 S (de Ciechomski 1971 cited by Robertson 1976), in the south-eastern Atlantic and south-west Indian Oceans (Grindley and Penrith 1965), in south-eastern Austrailian waters (Anon. 1977) and in New Zealand waters (Robertson 1976) has led Robertson (1976) to suggest that the species has a circumglobal distribution in the Southern Hemisphere, although mid-ocean records are lacking. In the Northern Hemisphere M. muelleri is also widespread, having been reported from the Mediterranean (Norman 1930, Badcock 1984), the Japan Sea (Okiyama 1971), the north-eastern Atlantic east of 35^0 W and between 35^0 and 65^0 N (Badcock 1984) and the North Atlantic, North Pacific and the Red Sea (Grey 1964).

The known distribution of L. hectoris is shown in Fig. 1.2. It is primarily distributed in the region of the Subtropical Convergence

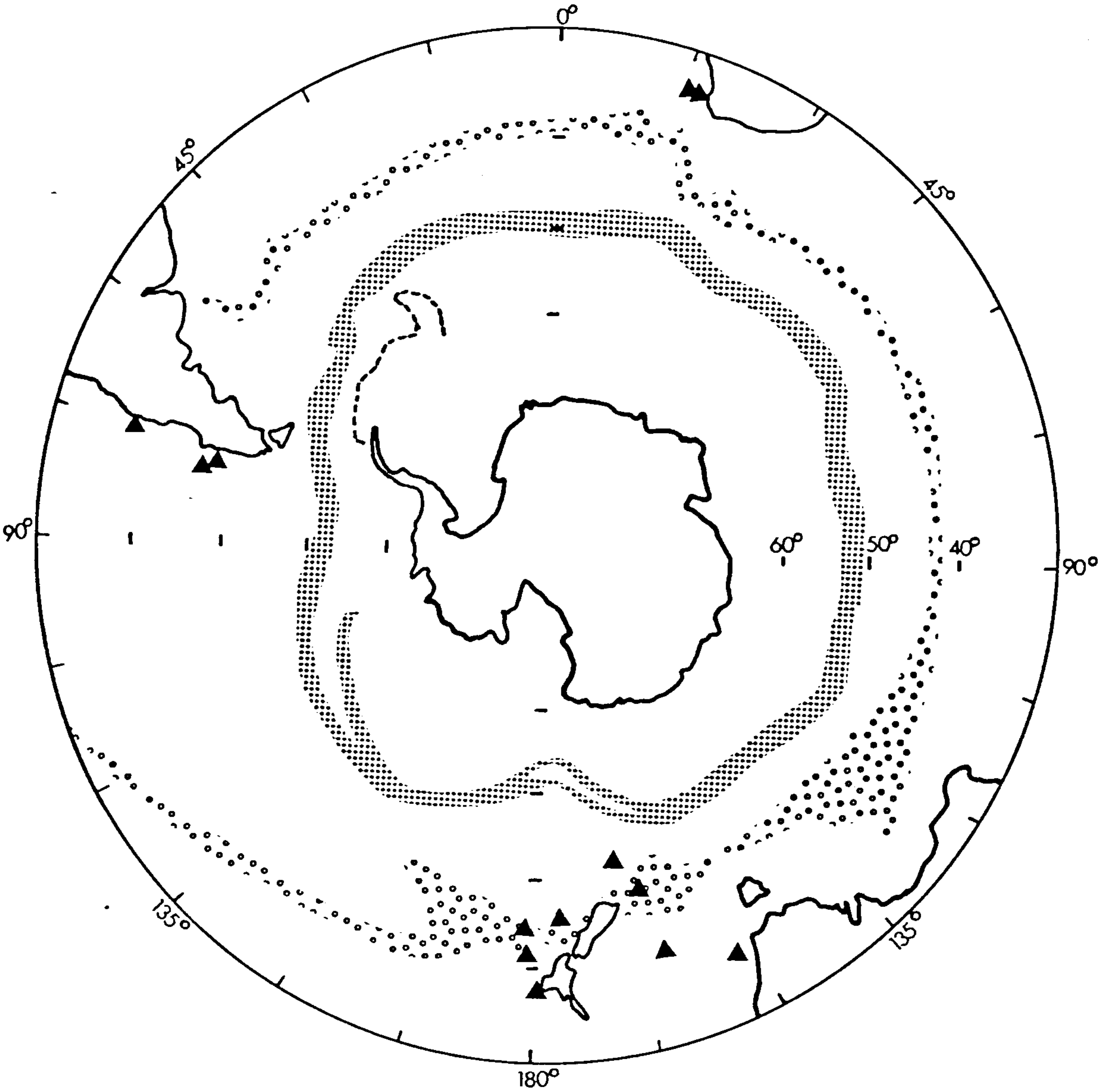

Fig. 1.2: The known distribution of *Lampanyctodes hectoris* (▲). The regions of the Polar Front (⁙) and subtropical convergence (°) are delimited (redrawn from McGinnis 1982).

off Chile, New Zealand, Australia and Southern Africa. It is apparently absent in the waters of the southwestern Atlantic. The fact that a number of L. hectoris have been collected in bottom trawls and that the species is primarily found near land masses, may indicate that it is limited to continental shelf and slope waters (Hulley 1981, McGinnis 1982). Robertson (1977) describes the species as a common near-shore lanternfish over shelf and slope waters in subtropical latitudes of the Southern Hemisphere. According to McGinnis (1982), myctophid species south of 30°S reveal patterns of distribution which correlate with hydrologically recognizable regions, thus defining several biogeographic complexes. He defines five zonal hydrological regions, namely a warm water region, the transitional region of the subtropical convergence, the subantarctic region, the region of the antarctic polar front and the Antarctic region. L. hectoris is classified as a transitional water species restricted to the transitional region of the subtropical convergence. No record of L. hectoris in the Northern Hemisphere has been documented (Hulley, South African Museum, Cape Town, personal communication).

Off South Africa L. hectoris is found from the Orange River in the North (approximately 28° 14'S 16° 30'E) to Cape Point in the South (approximately 34° 30'S 18° 30'E). Occasionally catches are made close inshore and further eastward up to Cape Agulhas (Centurier-Harris 1974).

The commercial fleet catches L. hectoris mostly in the Cape Columbine/ St Helena Bay area, usually from January to May and within 30 nautical miles off the coast (Crawford 1980) (Fig. 1.3). A fish-spotter plane hired by the Fishing Industry to locate

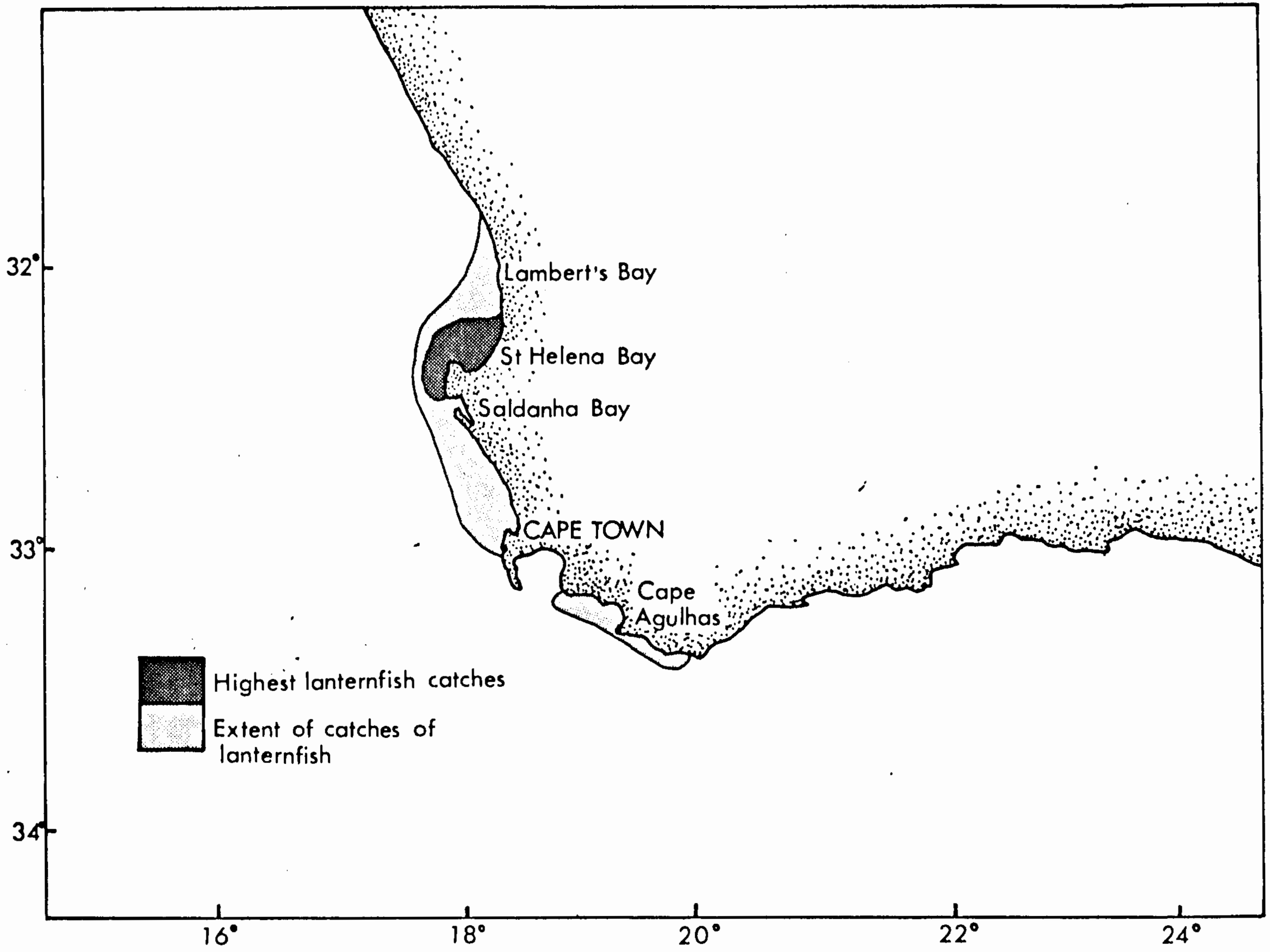

Fig. 1.3: The distribution of commercial catches of lanternfish off the West Coast.

fish-shoals confirmed this distribution (Fig. 1.4). Figs 1.5 and 1.6 show that L. hectoris was caught between January and July during the 1968-1976 period, and catches were most abundant in the St Helena Bay/Saldanha Bay area although fish were landed at all fishing grounds.

1.3 LENGTH DISTRIBUTION

The seasonal and yearly unweighted commercial catch length-frequency distributions of L. hectoris per month for the years 1968 to 1984 are shown in Figs 1.7 and 1.8 respectively. This data set was constructed from fish sampled at field stations operated by the Sea Fisheries Research Institute at Lambert' Bay, St.Helena Bay and Saldanha Bay on the South African west coast, and Hout Bay on the southwest coast. Commercial landings are sampled on a routine basis.

The range in length of fish caught was 3,0 to 7,4 cm and the mode differed from month to month. No set pattern is evident, but it is clear that the length distributions usually consists of a large number of size classes. Another interesting observation is that no fish less than 3,0 cm were landed by the commercial fleet. This is probably due to the mesh size used. However research cruise samples indicate an influx of juvenile fish in August.

The yearly length-frequency distributions (Fig. 1.8) also differ from year to year, but most fish were in the 4,0 to 6,0 cm range. However, both the monthly and yearly length-frequency distributions are probably influenced by the small sample size.

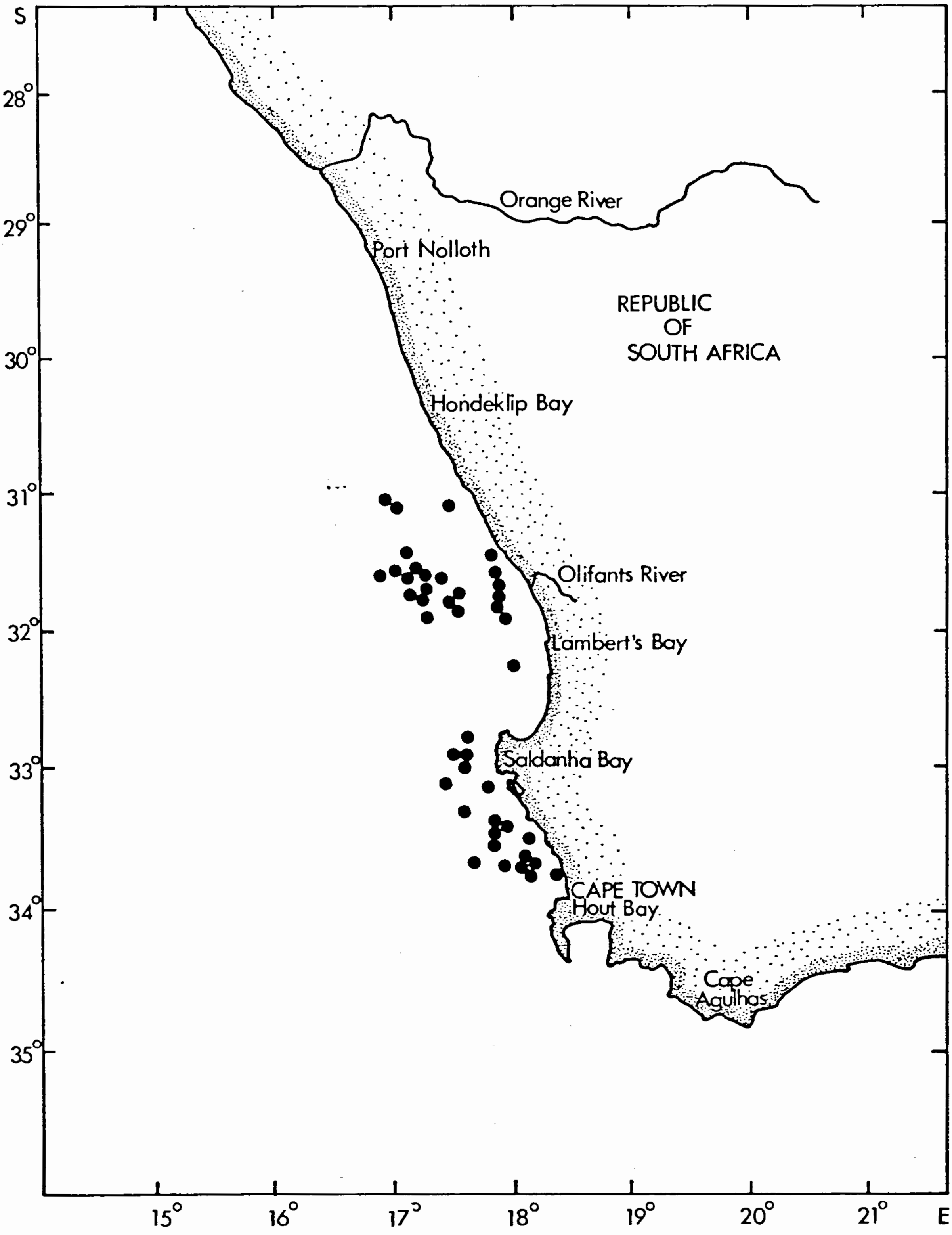

Fig. 1.4: The distribution of L. hectoris over a number of years (1974 - 1983) as observed by a spotter plane.

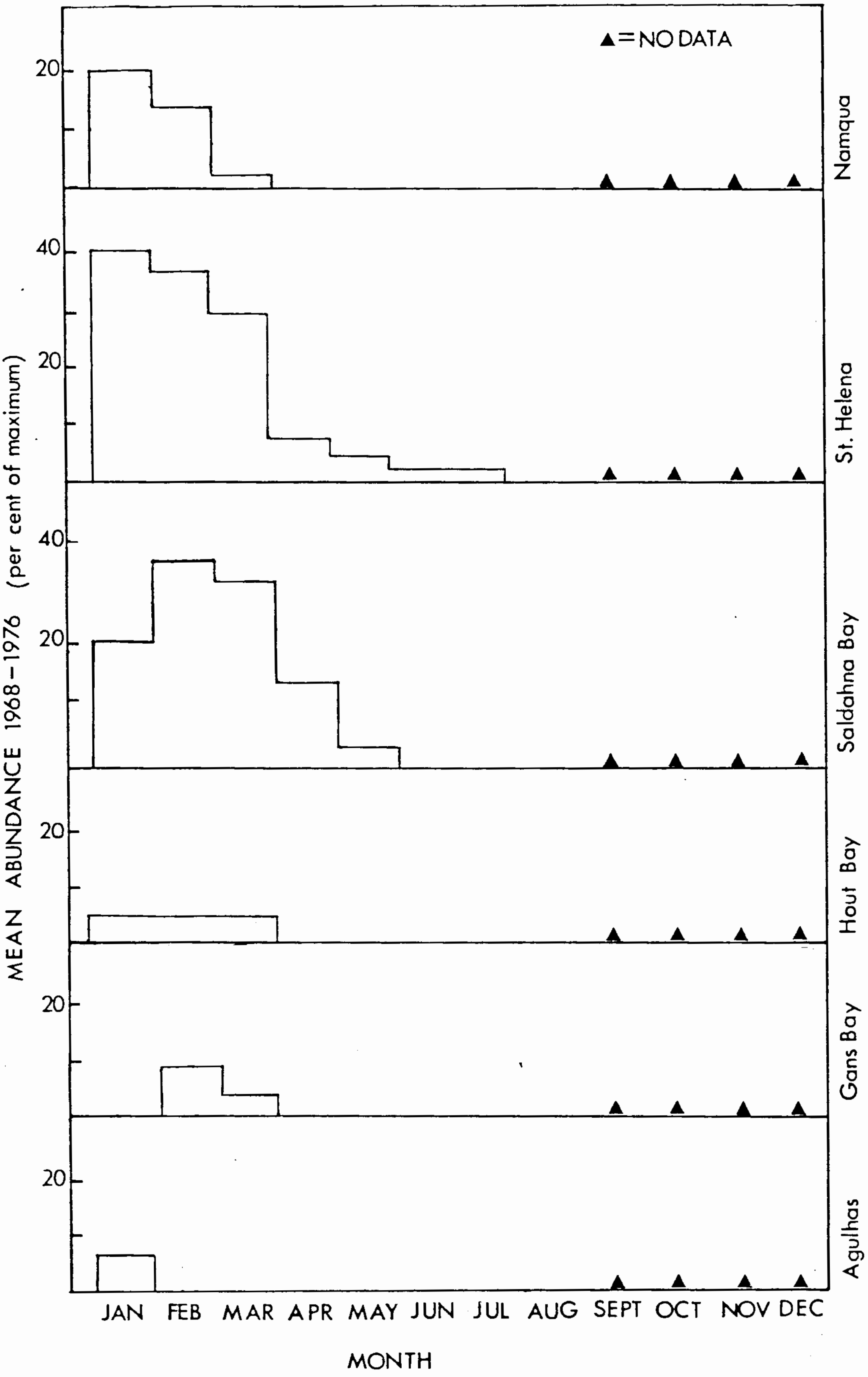

Fig. 1.5: Monthly abundance indices for L. hectoris for six fishing grounds (Crawford 1980).

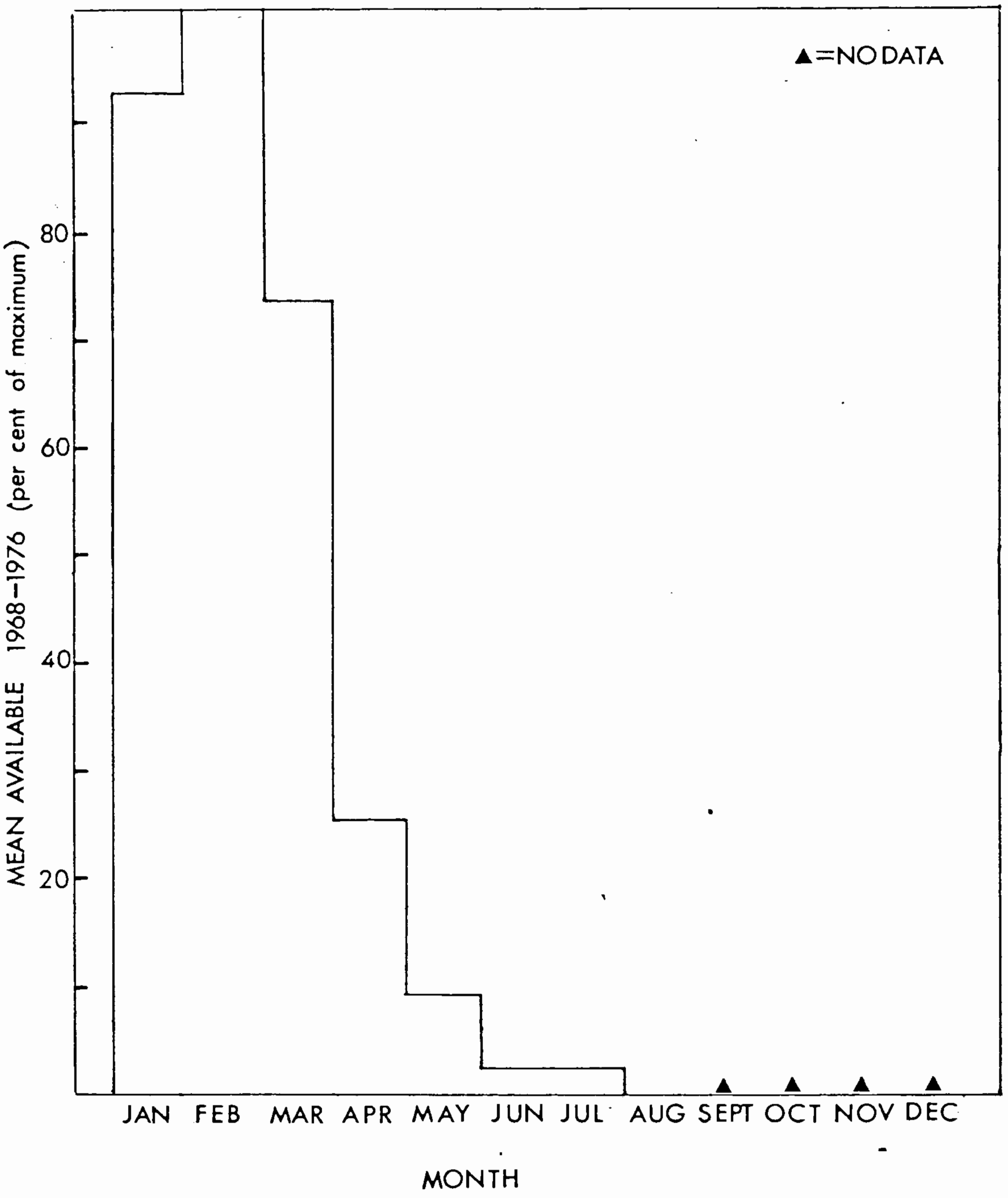

Fig. 1.6: Monthly availability indices for *L. hectoris* (Crawford 1980).

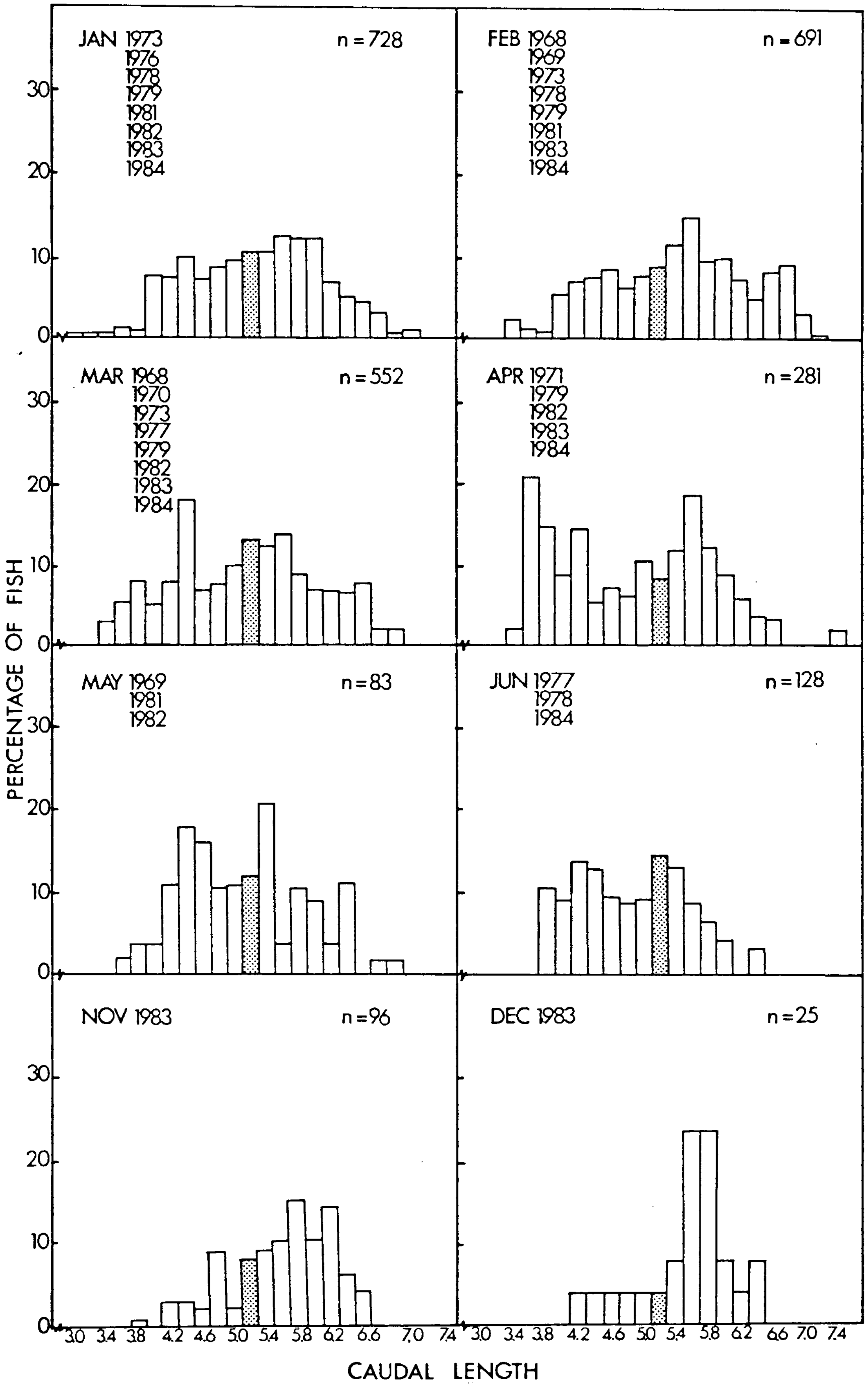

Fig. 1.7: Seasonal length frequency distributions for L. hectoris compiled from samples taken from the commercial fleet.

Note: The 5.2 cm length group has been shaded throughout to provide a constant visual reference.

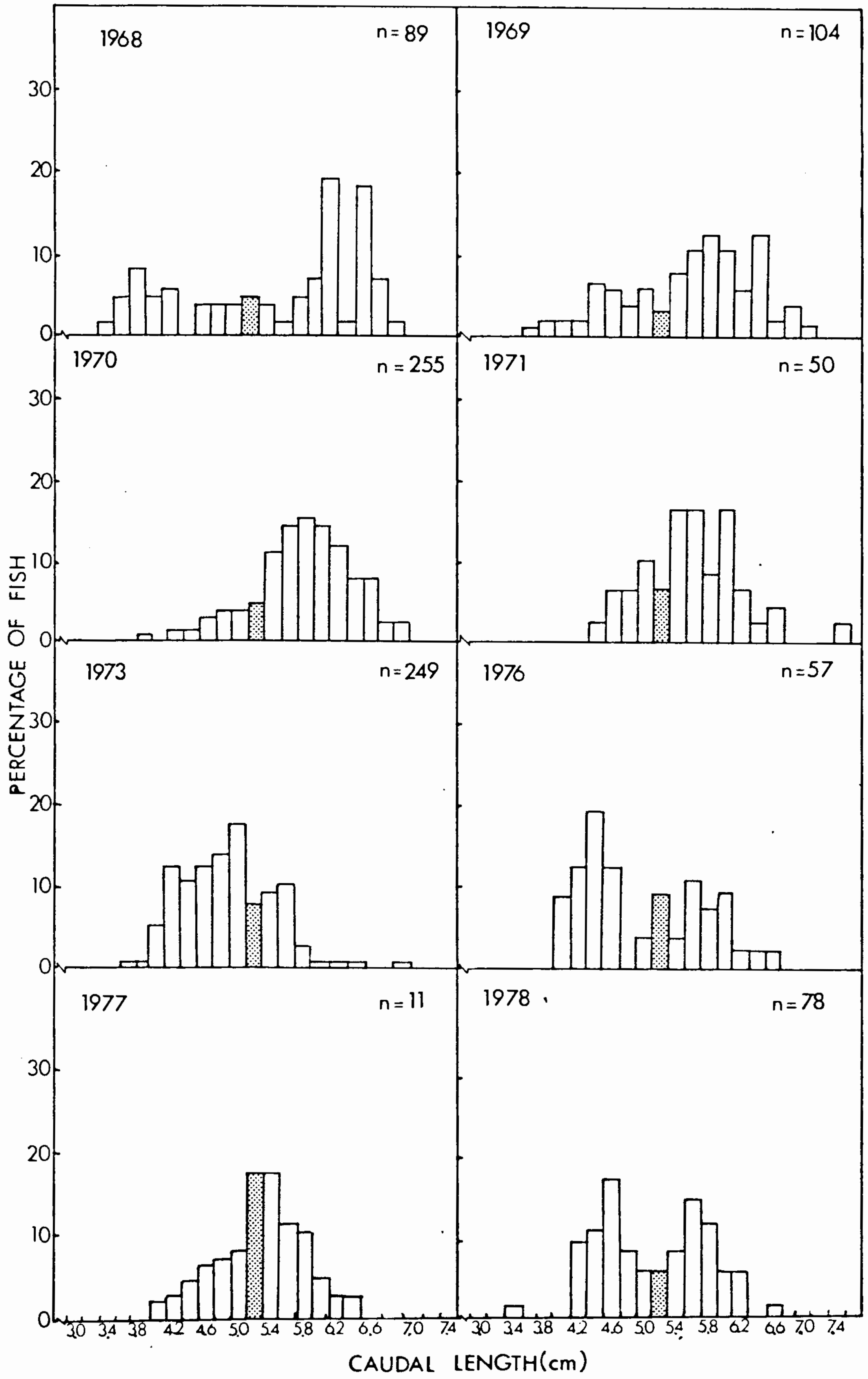

Fig. 1.8: Mean annual length frequency distributions for *L. hectoris* compiled from samples taken from the commercial fleet.

Note: The 5.2 cm length group has been shaded throughout to provide a constant visual reference.

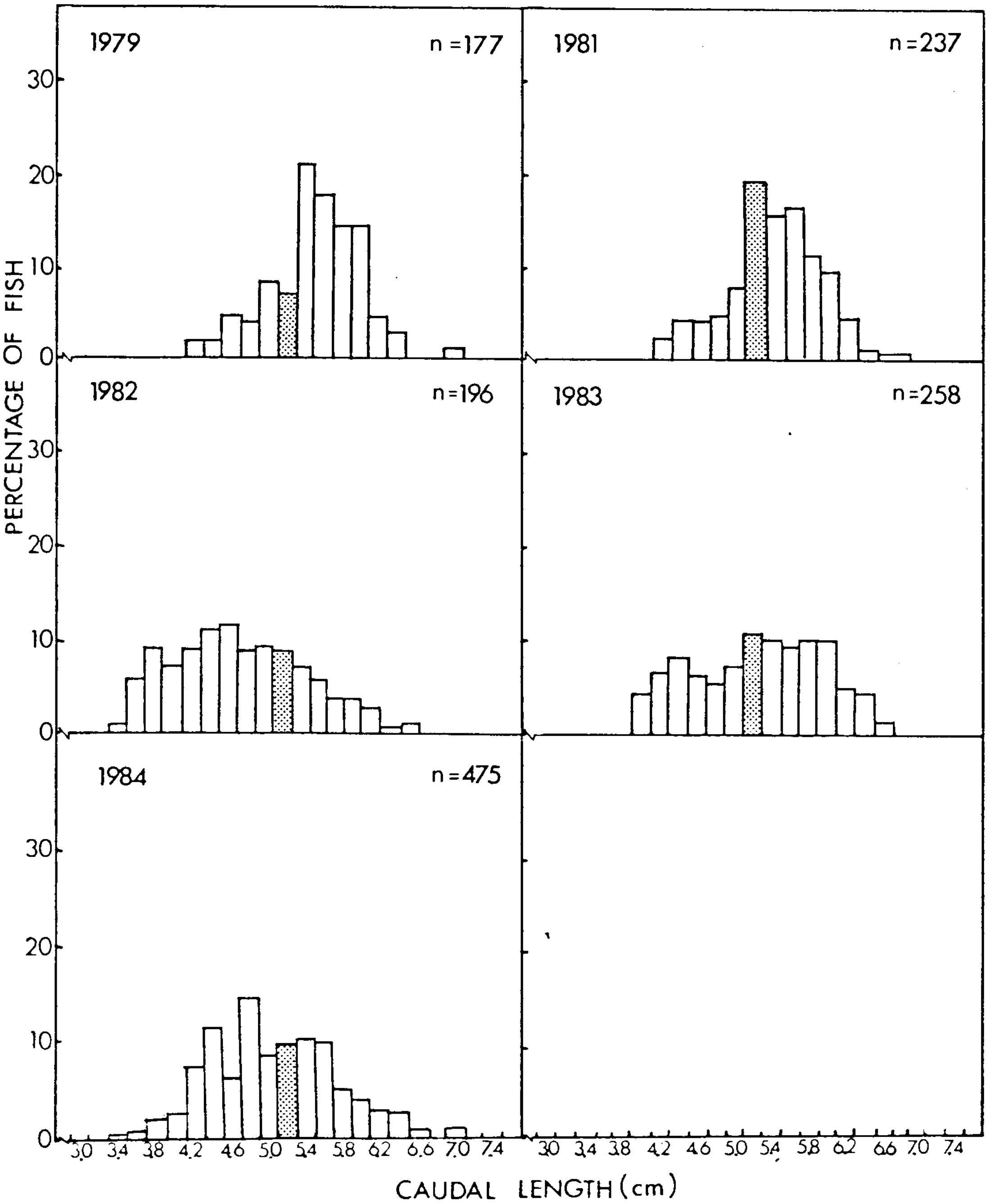

Fig. 1.8: Continued.

Therefore an in depth analysis of these distributions is not warranted. L. hectoris length frequencies were not calculated for any research cruises since the sample numbers were too small.

The unweighted monthly and yearly length-frequency distributions for M. muelleri are shown in Figs 1.9 and 1.10 respectively. These length frequencies were compiled from research cruises, since this species is not landed by the commercial fleet. The monthly length-frequency mode does change from approximately 3,4 to 3,8 cm (9 - 11 months of age, Chapter 2) in April/May to 4,2 to 4,6 (13 - 16 months of age) in November. Therefore, assuming the same growth pattern for the years sampled, the length-frequency distributions indicate that maximum spawning takes place in late winter/spring, a deduction borne out by the Cape Egg and Larval Survey (Chapter 3).

Another interesting aspect is the influx of very young fish, 1,0 to 2,8 cm in August 1982 and 1983. These fish are 2 to 5 months old (Chapter 2) indicating that spawning also takes place in autumn/winter. Smaller numbers of small fish were also caught in May 1983 and 1984 suggesting some spawning activity in summer.

The yearly length frequency distributions from research midwater trawl hauls (Fig. 1.10) have remained similar over a three year period (1982 - 1984), the only difference being a narrow length distribution in 1984 which is most likely due to the fact that only two months, April and May, were sampled in this year. The combined length frequency distribution for 3 years (Fig. 1.10) is probably a fair reflection of the population structure within 100 nautical miles of the coast in the Southern Benguela system. Any

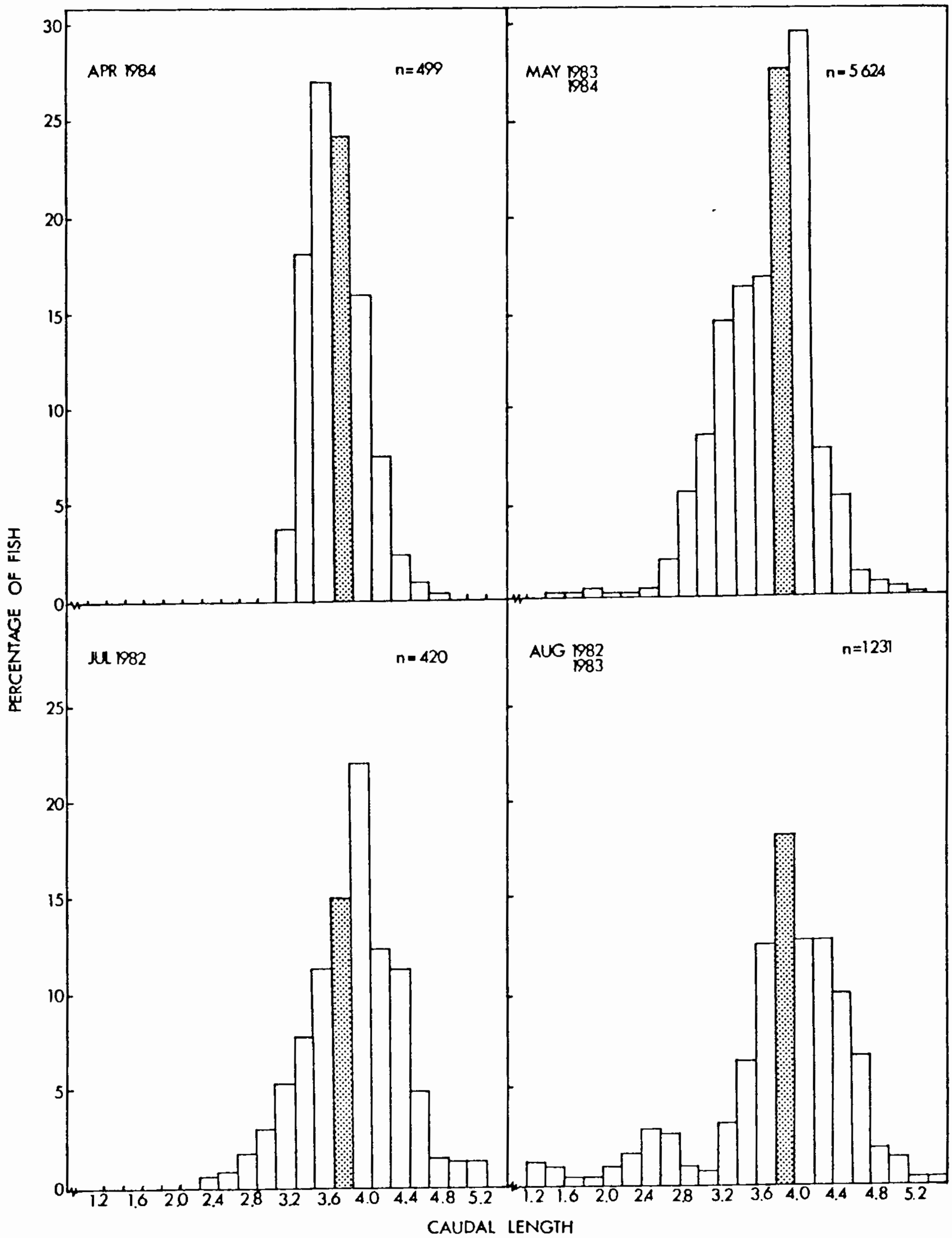

Fig. 1.9: Seasonal length frequency distributions for *M. muelleri* compiled from samples taken during research cruises.

Note: The 3.8 cm length group has been shaded throughout to provide a constant visual reference.

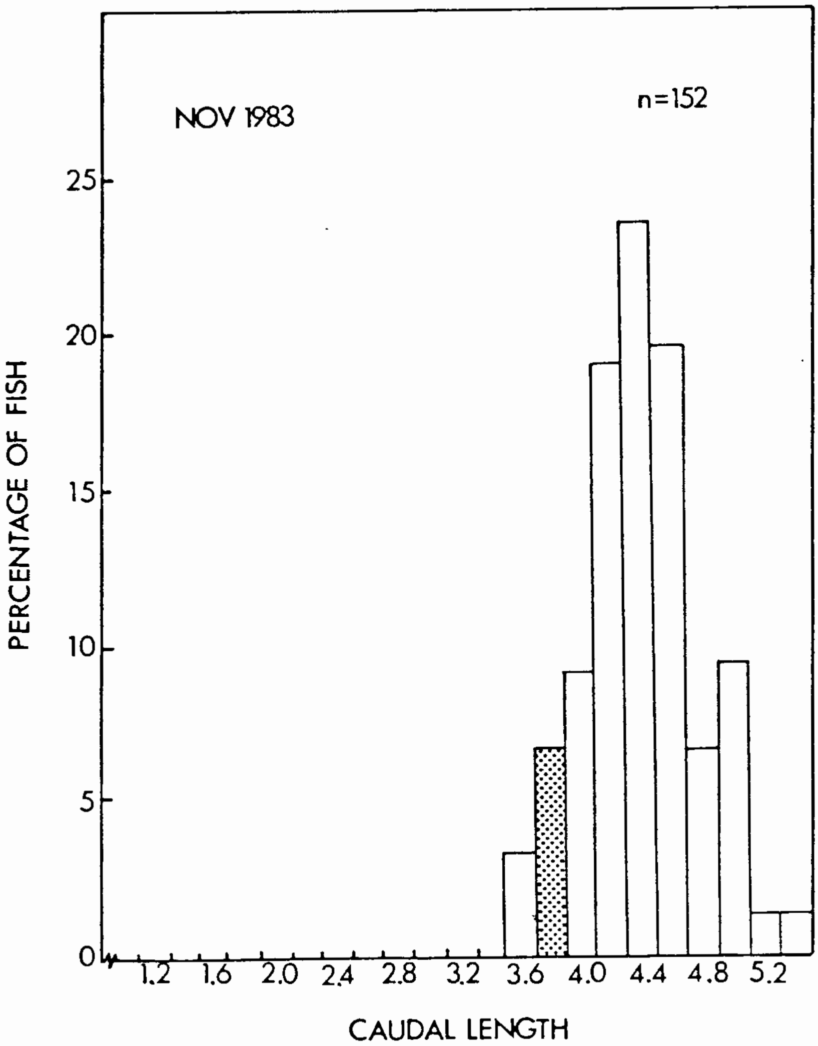

Fig. 1.9: Continued.

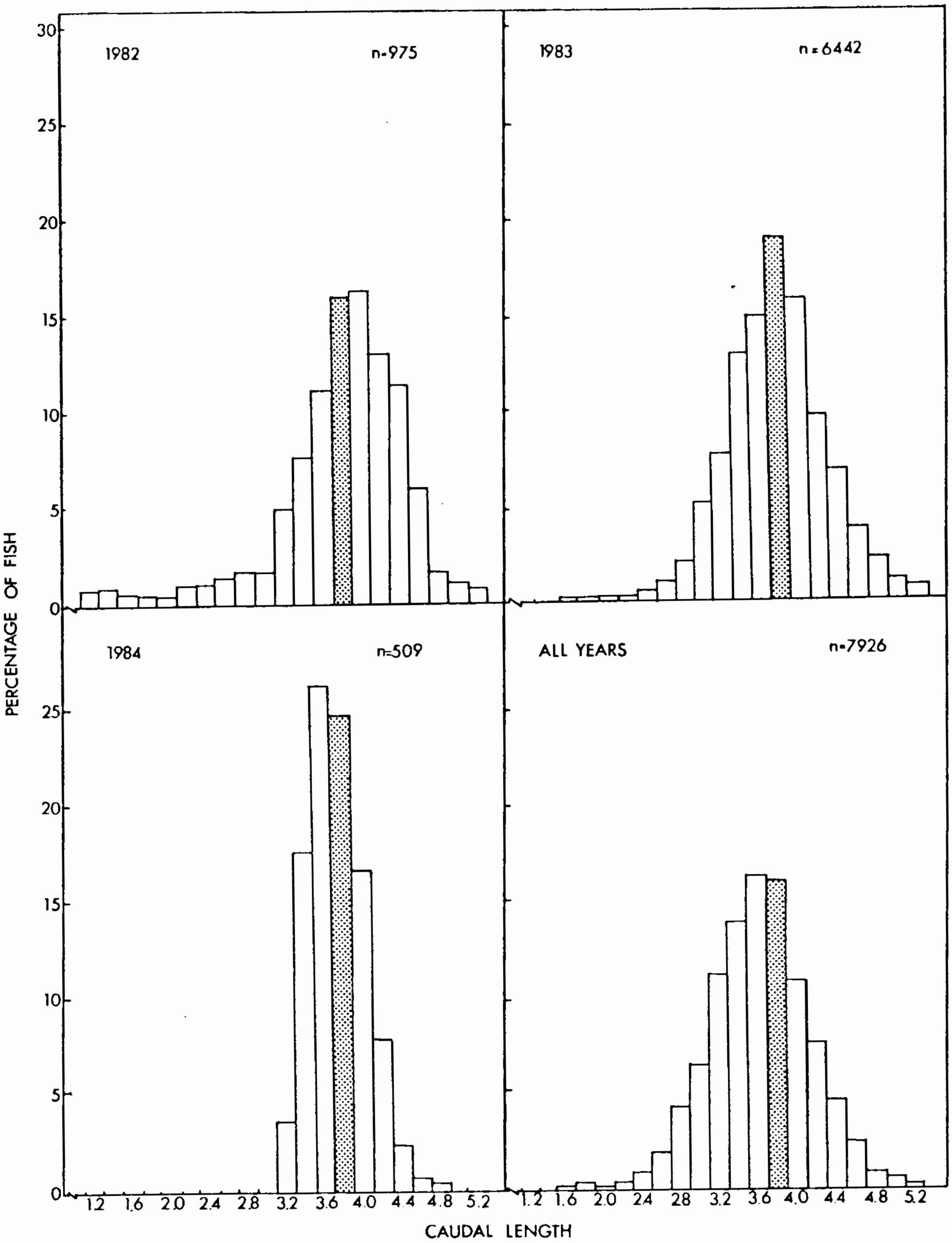

Fig. 1.10: Mean annual length frequency distributions for *M. muelleri* compiled from samples taken during research cruises.

Note: The 3.8 cm length group has been shaded throughout to provide a constant visual reference.

trends in size structure with distance offshore was not investigated.

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CHAPTER 2

GROWTH AND NATURAL MORTALITY OF THE LIGHTFISH MAUROLICUS MUELLERI AND THE LANTERNFISH LAMPANYCTODES HECTORIS

2.1 FISH LENGTH: OTOLITH LENGTH AND FISH LENGTH: OTOLITH RADIUS RELATIONSHIPS.

2.1.1 INTRODUCTION

The relationships between fish length and a hard body structure such as scales or otoliths have been calculated for a large range of fishes. A fish length: scale radius has been documented for the roach *Rutilus rutilus* (Thoressen 1979) and a fish length: scale length was calculated for the South African anchovy *Engraulis japonicus* (Pollock 1970). Otolith measurements, especially otolith radii, are more commonly used e.g. the Californian anchovy *Engraulis mordax* (Spratt 1975), the South West African pilchard *Sardinops ocellatus* (Thomas 1983 a), the South African pilchard *Sardinops ocellatus* (Baird 1970), round-herring *Etrumeus teres* and anchovy *Engraulis japonicus* (Prosch *in prep*.).

The fish length:otolith radius (FL:OR) relationship may be used to calculate fish lengths from otolith radii measurements when it is not possible to take a measurement of the fish length, as when seabird stomachs are analysed to determine prey composition. Prey items are often in a digested state and only the otoliths are salvaged. Length frequencies for each prey item can be constructed by measuring otoliths which have not been eroded by stomach acids, provided that a fish length: otolith radius or

fish length: otolith length (FL:OL) relationship is available. As it is more difficult to accurately measure the otolith radius because the centre of the otolith is not well defined, the FL:OL is more appropriate for these calculations.
Fig. 2.1 shows which otolith dimensions were measured.

In a growth study it may be necessary to interpret a hard body structure such as otoliths (Thomas 1983 a, Melo 1984, Baird 1970, Geldenhuys 1978), vertebrae (Laroche and Davis 1973) fin rays (Beamish 1981) or opercula (Fagade 1974). Scales are difficult to collect, the preservation technique is cumbersome and they are often shed when the fish is caught. Therefore the most commonly used method of ageing is the enumeration of rings on otoliths. In order to interpret annual or daily rings deposited, it is necessary to determine length at annual ring formation or the length at any number of daily rings. This data can then be used to construct a growth curve. The FL:OR relationship is used to back-calculate growth to determine the length at ring formation.

2.1.2 METHODS

One otolith was taken from each fish after the fish's length had been recorded to the nearest millimetre (caudal length). These otoliths were then washed in 0,5% potassium hydroxide, twice with distilled water, once with a small quantity of acetone and again with distilled water. They were then left to dry thoroughly. The otoliths were subsequently mounted permanently in a clear epoxy resin within shallow wells drilled into a black perspex slide, as described by Thomas (1984). Two otoliths were placed inner side down (the sulcus faced downward) in each well and were

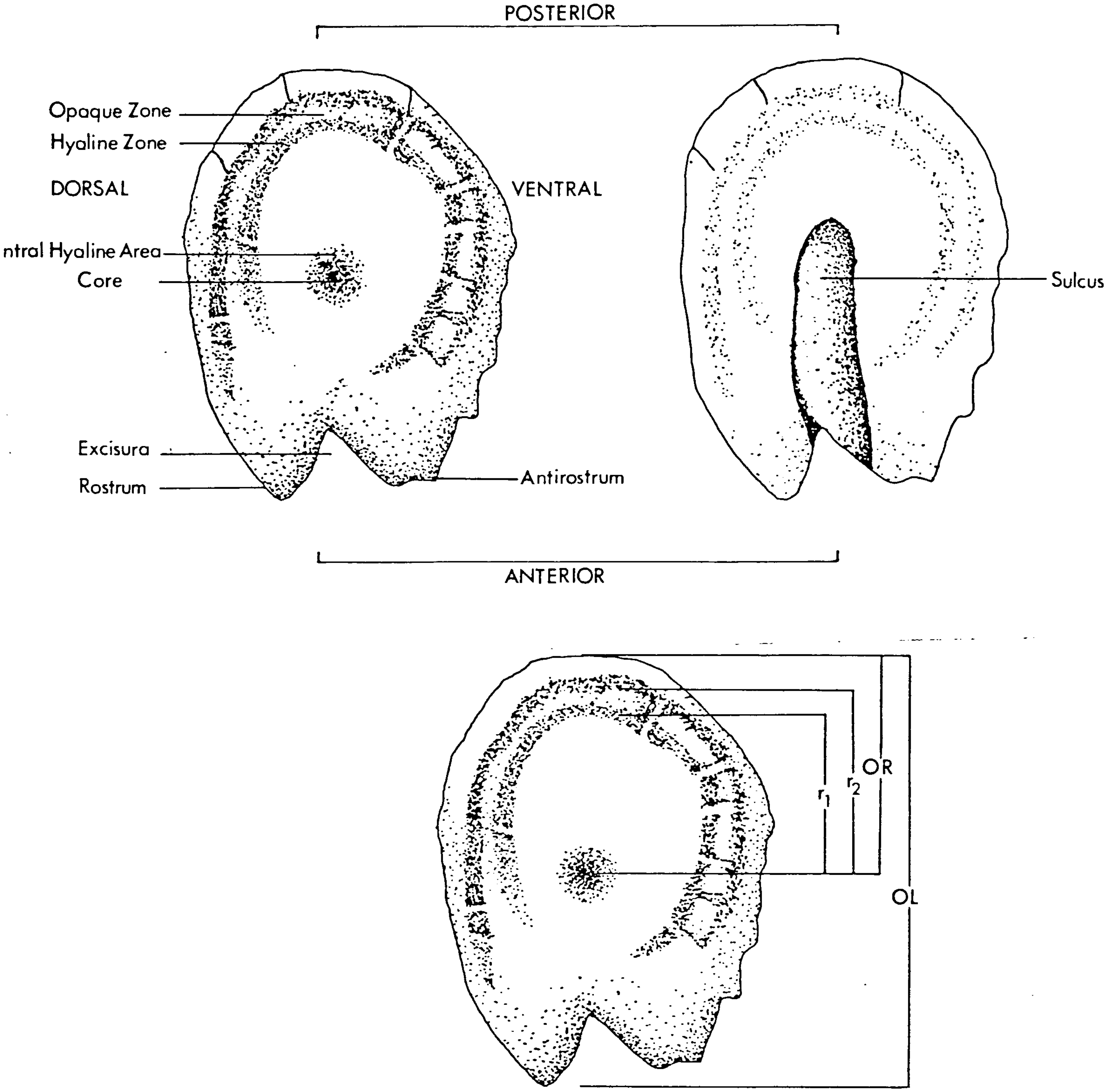


Fig. 2.1: The dimensions of the *L. hectoris* otolith and the measurements made. The same dimensions were measured for the *M. muelleri* otolith.

retained in position with a small drop of catalysed resin. When this had set, more resin was added and later, usually after a twenty four hour period, a coverslip was placed in position with a few final drops of resin. These stages are important, otherwise contraction of the resin causes the coverslip to break. Fish were grouped into 0,5 cm length classes, and samples from different months were analysed separately. The otolith length and otolith radius were measured for both lantern- and lightfish otoliths using an IBAS Interactive Image Analysis System whereby the magnified image of the otolith, under reflected light, is projected onto a video screen and measured using a magnetized tablet. A magnification correction factor was introduced and the measurements, in millimeters, were stored on disc. The months for which otoliths were collected and measured were January, February and May 1981; January, February, March, April, May and July 1982; January, February, March, April 1983 and January 1984 for lanternfish. Samples from April 1981, July and March 1982, November and May 1983 and April 1984 were used for the lightfish measurements.

2.1.3 RESULTS

Figs 2.2 a and b show the FL:OL relationships for lantern- and lightfish respectively whilst Figs 2.3 a and b indicate the FL:OR (posterior) relationships. A relationship was also found to exist for the FL:OR (anterior end) for both lantern- and lightfish. These are shown in Figs 2.3 c and d respectively.

Polynomial regressions were fitted and all the relationships show the effect of seasonal variation. Data points above the regression line indicate an increase in the otolith dimension

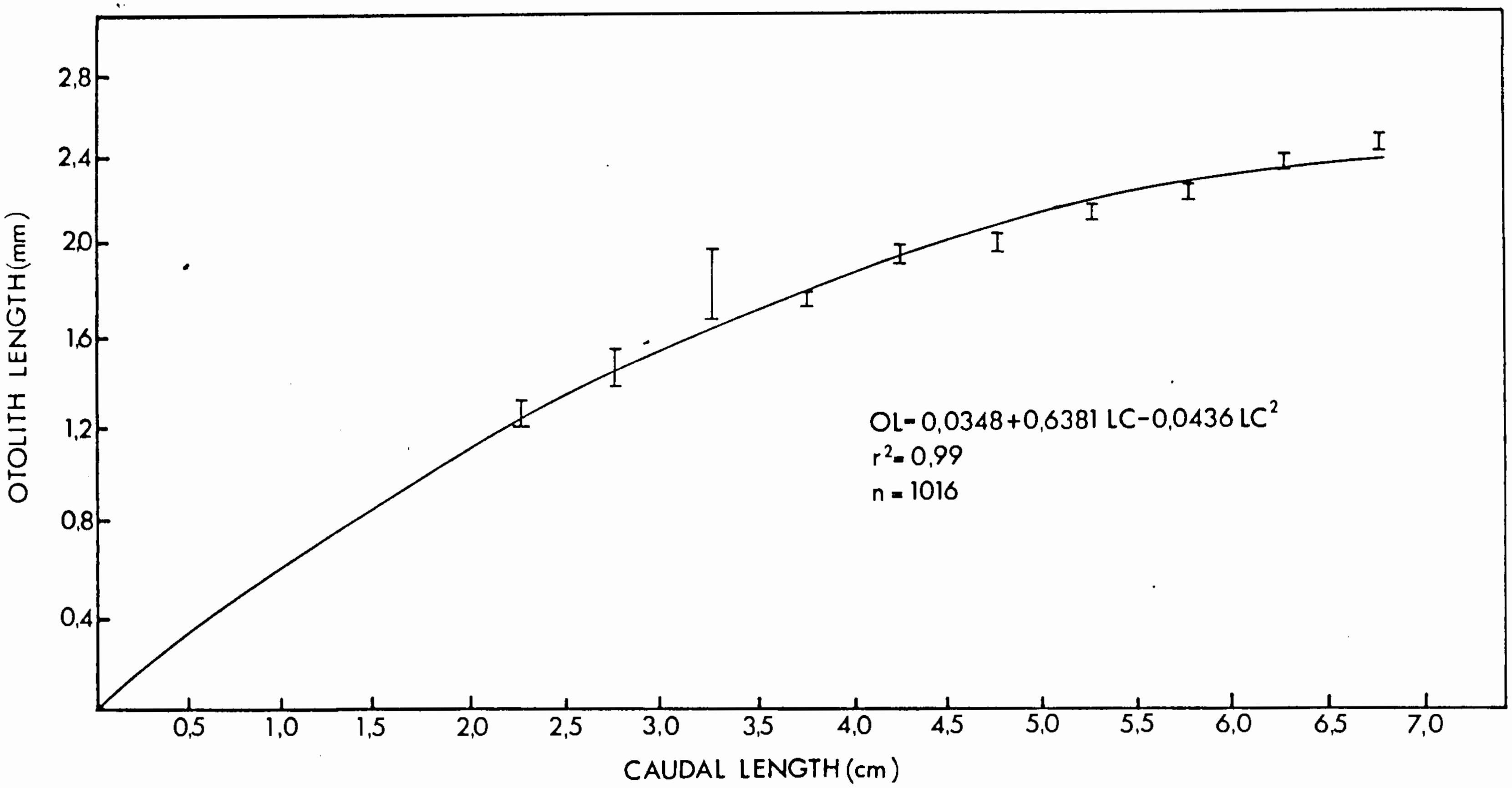


Fig. 2.2(a): The fish length : otolith length relationship for *L. hectoris*. The vertical bars indicate the 95% confidence limits.

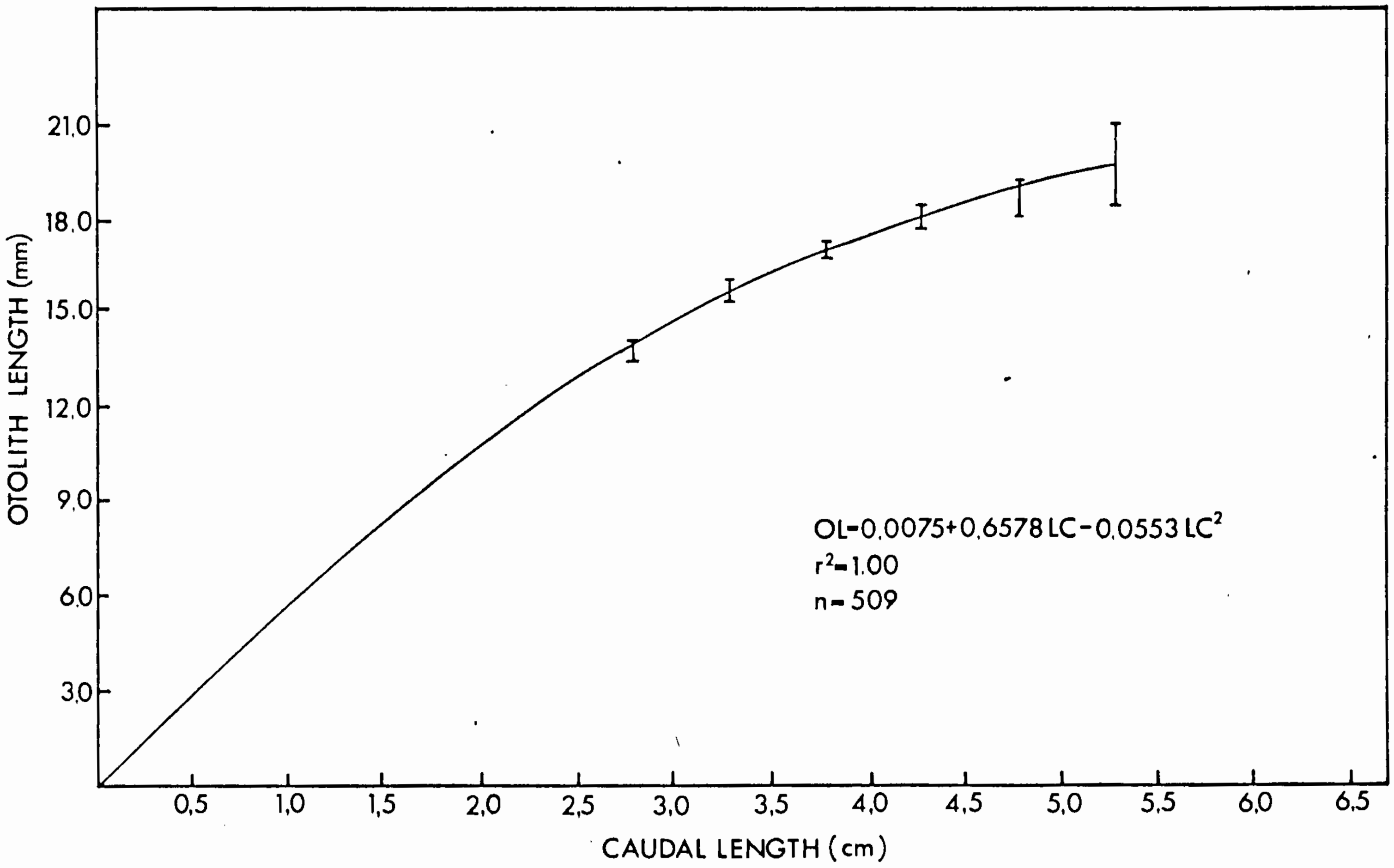


Fig. 2.2(b): The fish length : otolith length relationship for *M. muelleri*. The vertical bars indicate the 95% confidence limits.

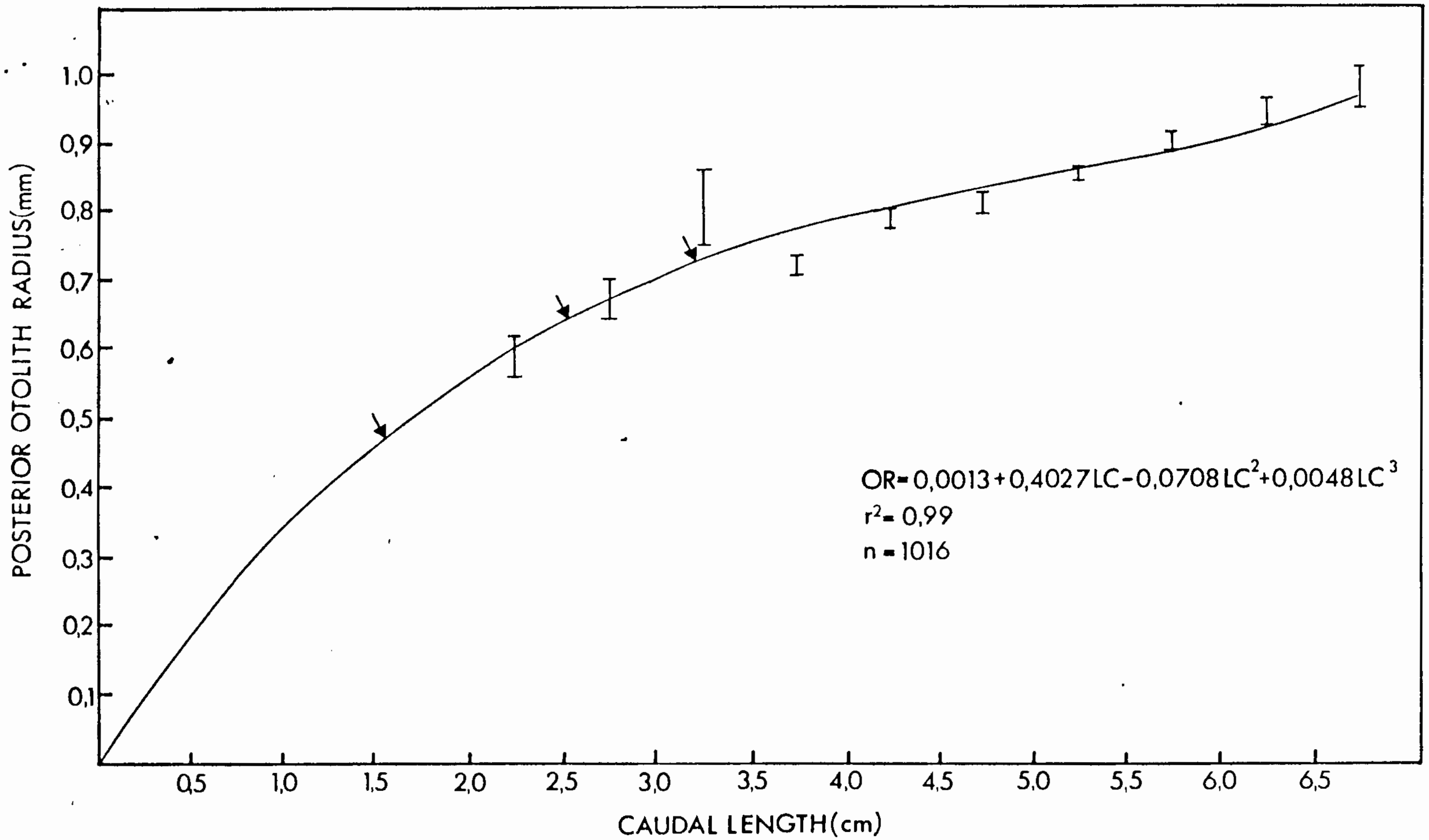


Fig. 2.3(a): The fish length : posterior otolith radius relationship for L. hectoris. The arrows indicate the lengths at ring formation as measured in Section 2.2. The vertical bars indicate the 95% confidence limits.

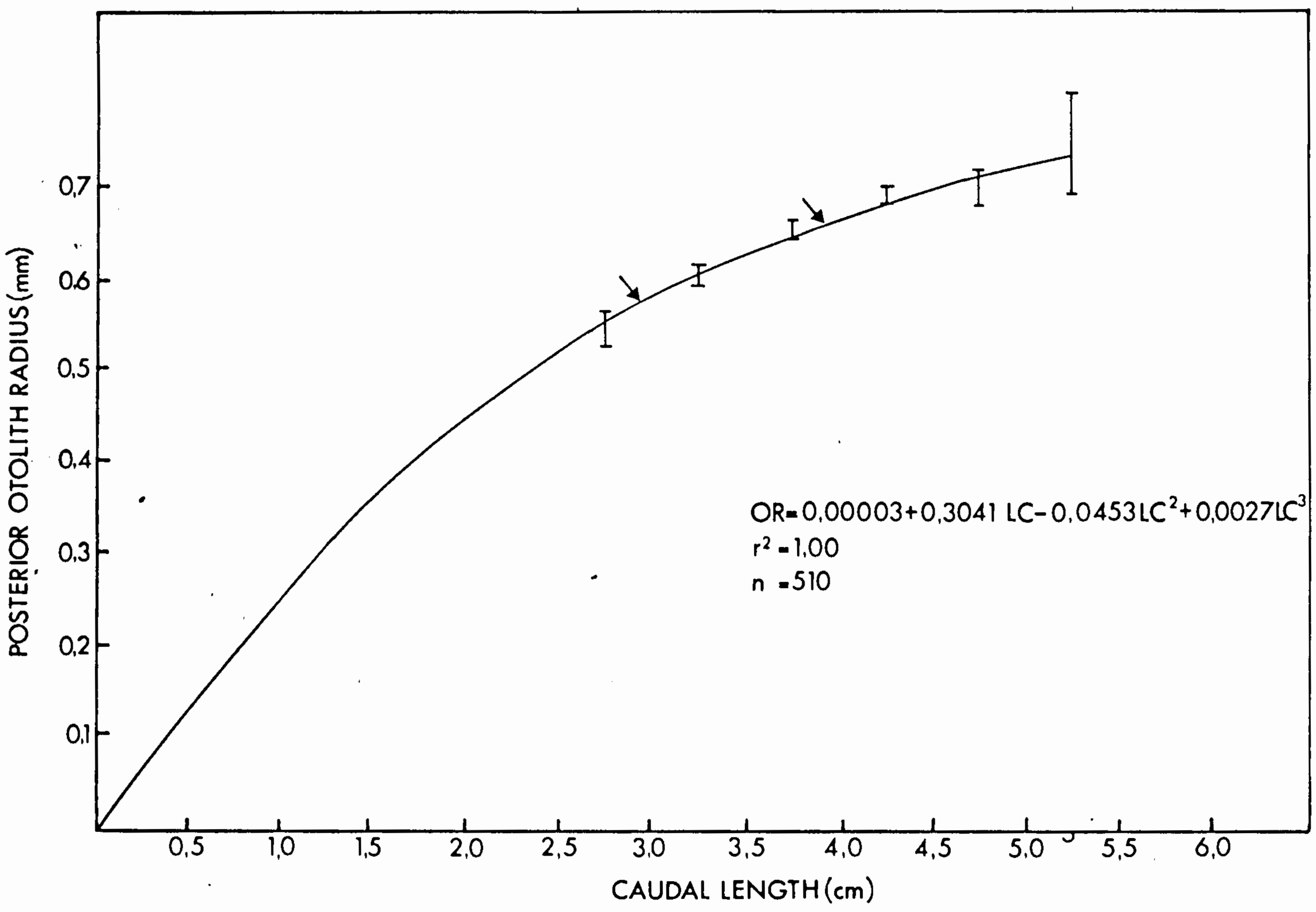


Fig. 2.3(b): The fish length : posterior otolith radius relationship for *M. muelleri*. The arrows indicate the lengths at ring formation as measured in Section 2.2. The vertical bars indicate the 95% confidence limits.

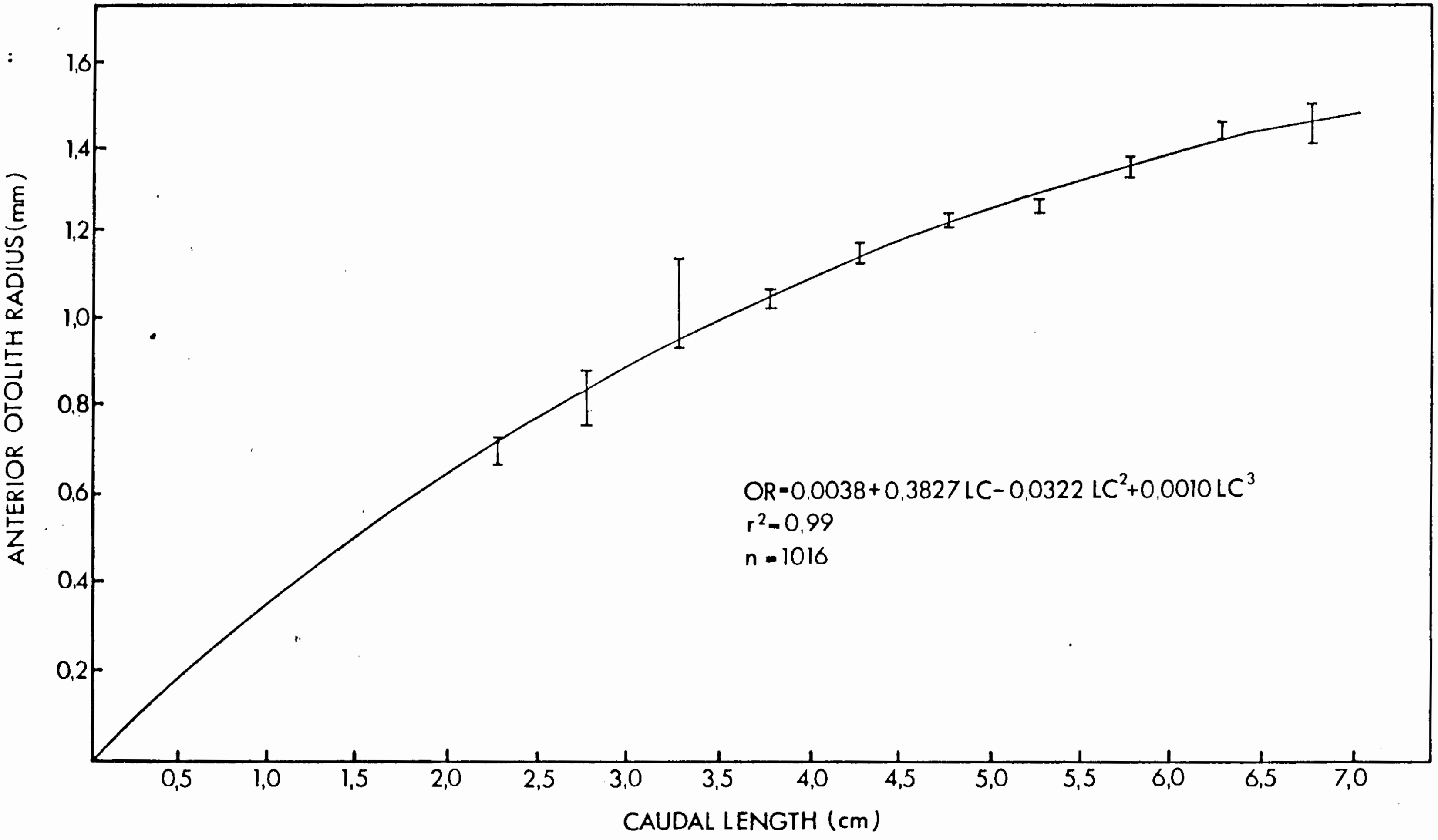
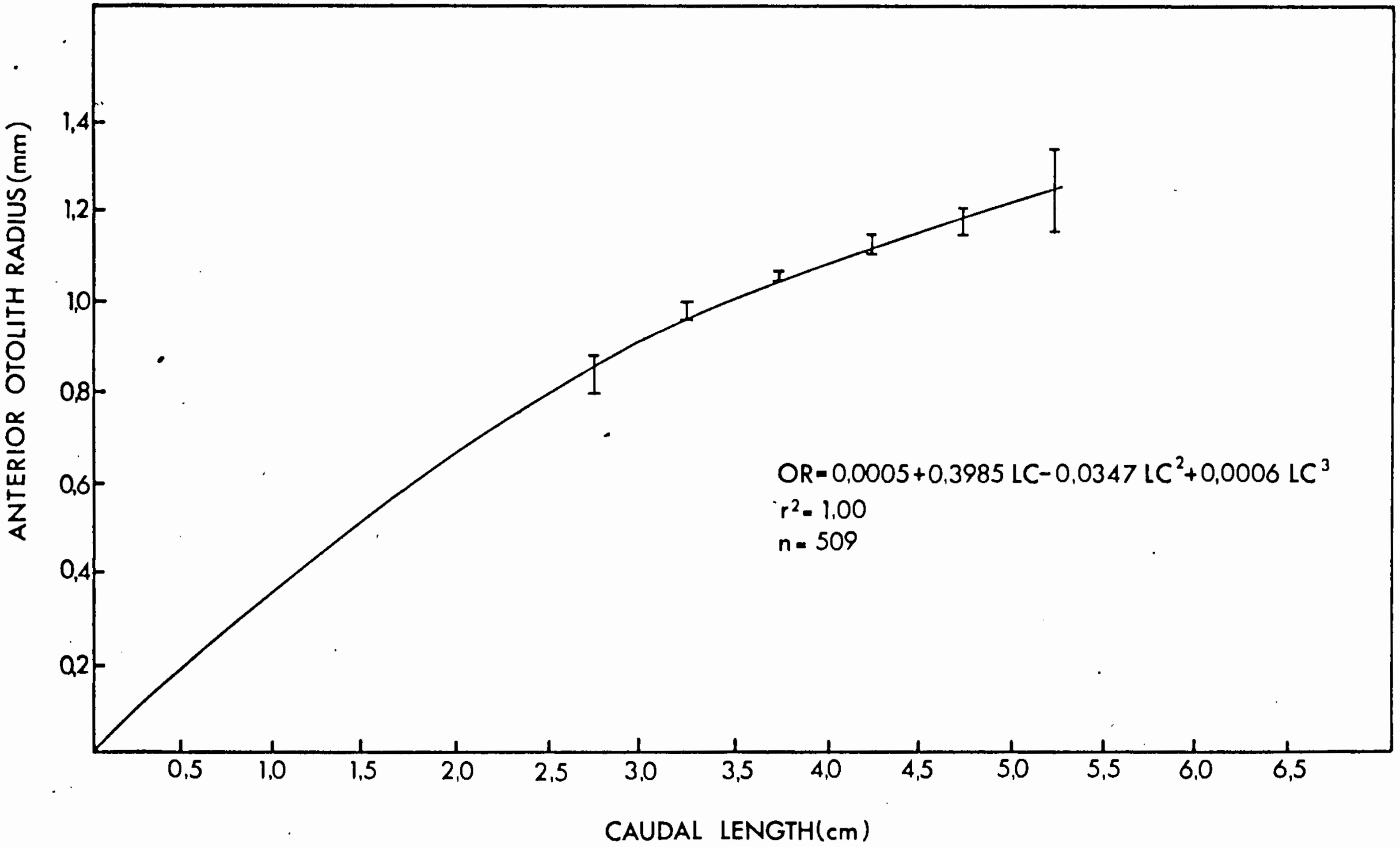


Fig. 2.3(c): The fish length : anterior otolith radius relationship for *L. hectoris*. The vertical bars indicate the 95% confidence limits.



<u>Fig. 2.3</u>(d): The fish length : anterior otolith radius relationship for <u>M</u>. <u>muelleri</u>. The vertical bars indicate the 95% confidence limits.

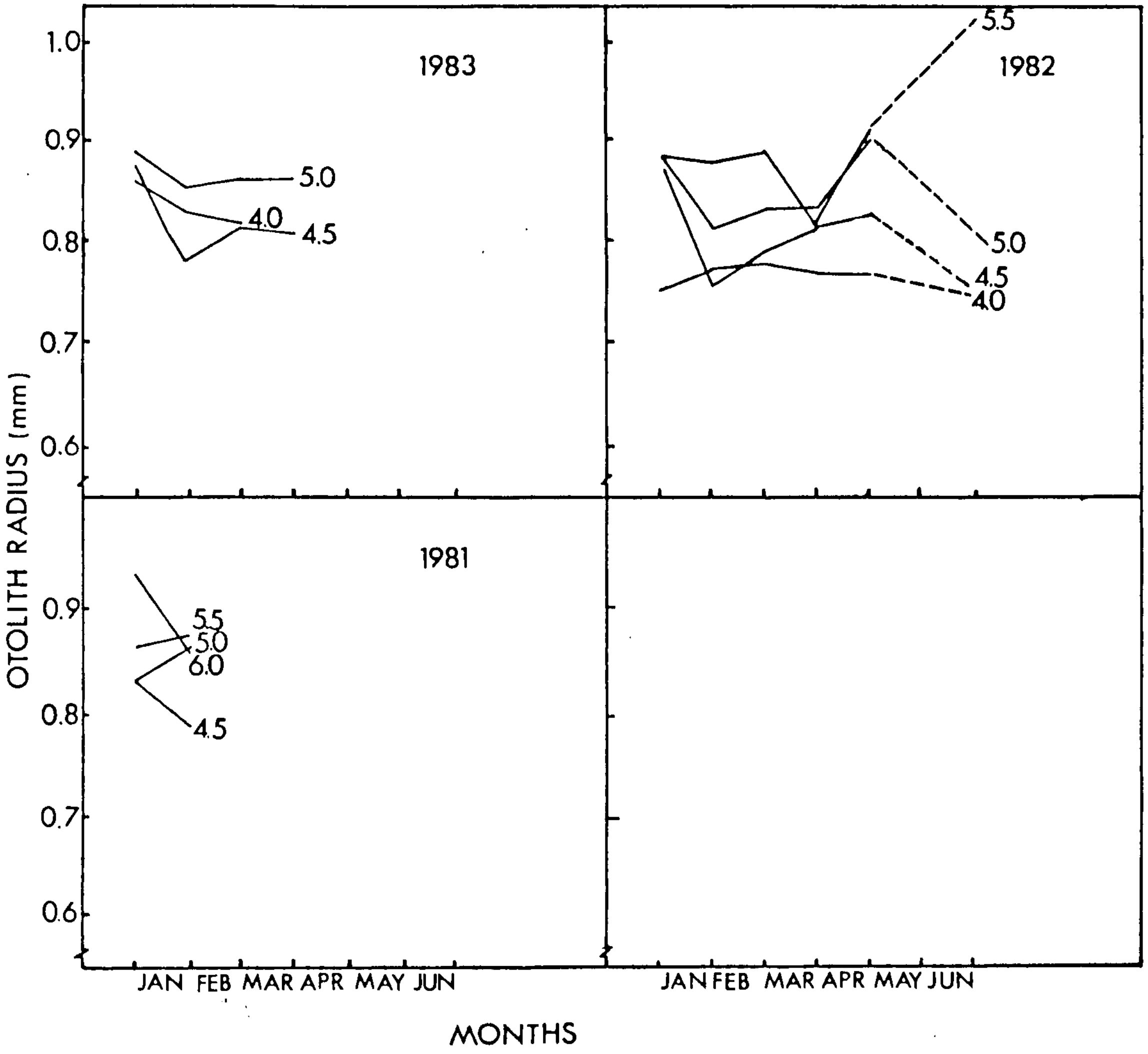


Fig. 2.4: The otolith radius per month for a number of L. hectoris length groups. The broken lines indicate no data is available.

relative to the fish length. Data points below the regression line indicate an increase in the fish length relative to the otolith dimension.

The seasonal oscillation is shown in Fig. 2.4, where the mean otolith radii at monthly intervals are plotted for three years. This could only be done for lanternfish, which were sampled over a number of consecutive months.

2.2 BACK-CALCULATION OF LENGTH AT RING FORMATION

2.2.1 INTRODUCTION

The formation of rings on hard body structures is well documented and is a universal phenomenon having been recorded for Antarctic (Townsend 1980), tropical (Reshetnikov and Claro 1976) and temperate (Spratt 1975) species. The interpretation of such rings to determine growth is a routine procedure in most fisheries.

However, in order to interpret age material correctly it is necessary to determine whether the rings seen on a body structure are deposited on an annual basis or more or less frequently. The back-calculation of the time of ring formation, as used by Reay (1972) and Thomas (1983 a) was employed. A description of the technique can be found in Thomas (1983 a). This technique, together with the daily growth study (Section 2.3), indicate at what lengths and ages rings are laid down on the otolith.

2.2.2 METHODS

Under reflected light otoliths show two types of rings, hyaline rings, which appear as dark bands and opaque ones, which appear white or grey.

The hyaline ring radii on both light- and lanternfish otoliths were measured (See Fig. 2.1) using the IBAS Image Analysis System described in Section 2.1.

Rings were measured from the otolith centre to the start of each hyaline ring. The otolith radii were adjusted to the expected radii using the FL:OR relationship for each species. The standardized ring measurements (ODst) were calculated using the formula $ODst=OD.\frac{ORst}{OR}$ where OD is the ring measurement, ORst is the standardized otolith radius, and OR is the otolith radius measured. The length of each fish at commencement of ring formation could then be calculated from the polynomial regressions (Figs 2.3 a and b). Lanternfish otoliths were grouped by sampling location to determine whether regional differences exist.

2.2.3 RESULTS

Tables 2.1 and 2.2 summarize the results. Table 2.1 indicates the lanternfish ring radii for different sampling locations and different years as well as the mean for all the measurements and Table 2.2 those for lightfish. The back-calculated fish lengths at ring formation are also shown.

The lanternfish hyaline rings for different areas were deposited

Table 2.1: Lanternfish ring radii measurements (mm) for different sampling areas and years and the mean calculated for all years and areas. The corresponding fish lengths are indicated.

Sandy Point	Mean	SD	m	Fish Length
1st Ring	0,47	0,12	496	1,6
2nd Ring	0,64	0,14	443	2,5
3rd Ring	0,75	0,15	195	3,5
Lamberts Bay				
1st Ring	0,51	0,14	379	1,7
2nd Ring	0,66	0,13	327	2,7
3rd Ring	0,75	0,14	159	3,5
Saldanha Bay				
1st Ring	0,48	0,09	36	1,6
2nd Ring	0,67	0,13	32	2,7
3rd Ring	0,76	0,12	9	3,6
1981				
1st Ring	0,44	0,13	88	1,4
2nd Ring	0,61	0,10	73	2,3
3rd Ring	0,69	0,11	20	2,9
1982				
1st Ring	0,47	0,12	442	1,6
2nd Ring	0,62	0,11	334	2,4
3rd Ring	0,72	0,11	119	3,2
1983				
1st Ring	0,50	0,12	461	1,7
2nd Ring	0,69	0,11	429	2,9

All Field Stations - All Years

	Mean	SD	n	Fish Length
1st Ring	0,48	0,12	985	1,6
2nd Ring	0,65	0,14	851	2,6
3rd Ring	0,75	0,14	378	3,5

Table 2.2: Lightfish ring radii measurements (mm) for different years and the mean for all years combined. The corresponding caudal fish lengths (cm) are indicated.

1982	Mean	SD	n	Fish Length
1st Ring	0,57	0,11	314	2,9
2nd Ring	0,64	0,12	70	3,7
1983				
1st Ring	0,59	0,08	26	3,1
2nd Ring	0,68	0,04	4	4,2
Both Years Combined				
1st Ring	0,58	0,12	340	3,0
2nd Ring	0,66	0,14	74	3,9

at approximately the same length and there was also little variation in length at ring formation between years for those years sampled. Little variation in length at ring formation was apparent between the years sampled for lightfish.

2.3 DAILY GROWTH

2.3.1 INTRODUCTION

The technique of counting daily growth rings in order to age juvenile fish and larvae and to establish the validity of annual rings is widely used e.g. the northern anchovy *Engraulis mordax* (Methot and Kramer 1977), the pilchard *Sardinops ocellatus* off the South West African coast (Thomas 1983 b), the anchovy *Engraulis japonicus* off the South West African (Melo, 1984) and South African coasts (Prosch *in prep.*). Brothers *et al* (1976) demonstrated this technique on a number of fishes and concluded that it is best suited to larvae, juveniles, fast growing fish and tropical species. Gjøsaeter (1978) and Gjøsaeter and Blindheim (1978) used this procedure to age mesopelagic fish species.

2.3.2 METHODS

Otoliths were taken from fish in the range 4.5 - 6.0 cm caudal length for lanternfish and 3.2 - 3.8cm caudal length for lightfish. The material was washed as described earlier, then left to dry thoroughly. Otoliths were then embedded in LR White Resin (London Resin Company) with the sulcus placed centrally in a rubber mould and oven dried for approximately 15 hours at 30^0 C. The resin blocks were removed from the mould and polished on a mechanical grinder in a medial-lateral plane (See Fig. 2.1) using silicon carbide paper and 7µm alumina powder. This process was monitored continually using a stereomicroscope to ensure that the otolith was being sectioned through both anterior and posterior tips. The specimens were then washed in distilled water to remove residual alumina powder and etched in 0,25% hydrochloric acid for 20 seconds. Each block was then coated with a gold/palladium alloy using a vacuum evaporator and examined at 45^0 tilt in a Cambridge S 200 Scanning Electron Microscope at 400 x and 800 x magnification. Photographs were taken from the centre to the posterior end of the otolith keeping the magnification constant. Some material was photographed at both magnifications as they showed up different detail. The series of photographs for each specimen was compiled into a montage.

Regular rings were observed spreading from the centre. These were close together at the centre, becoming widely spaced and difficult to discern towards the edge, especially in the larger fish where there was a slowing down in growth. Smaller, irregular sub-daily rings were observed, but were usually easily distinguished from the larger regular rings.

The rings were counted from the centre at 4cm intervals in the direction of maximum growth. This is not usually a straight line from the centre of the otolith, but assumes a wavy pattern. Length intervals on the photograph were scaled to the theoretical otolith radius for that fish length (Figs 2.3 a and b). Using this theoretical relationship the intervals could be reduced to fish length measurements. Hence the number of days growth at any fish length could be deduced.

Daily rings can be counted for larval otoliths using light microscopy. For small fish a slowing down in growth has not occurred and fewer rings have been laid down, making the rings easier to count. Lanternfish larval otoliths sampled during a November 1984 research cruise were cleaned as described previously. They were then mounted on microscope slides with coverslips using a clear resin (Harvey's Fibreglass, Cape Town). Daily ring were counted using a phase contrast light microscope at a magnification of 1000 x. Unfortunately no larval lightfish were obtained for this study.

2.3.2 RESULTS

The back-calculated daily growth is shown in Figs 2.5 a and b and the Von Bertalanffy growth equation coefficients were fitted to this data by the method of Gaschutz *et al* (1980). For lanternfish both readings from electron and light microscopy analyses were combined, whilst the lightfish growth parameters are based on the electron microscopy results only.

The growth parameters obtained were:

Lightfish

$L = 6.00\ (1-\exp[-1.15\{t-0.06\}])$

$L(0.5) = 2.38$ cm

$L(1.0) = 3.96$ cm

$L(2.0) = 5.36$ cm

Lanternfish

$L = 7.00\ (1-\exp[-1.66\{t-0.06\}])$

$L(0.5) = 3.63$ cm

$L(1.0) = 5.53$ cm

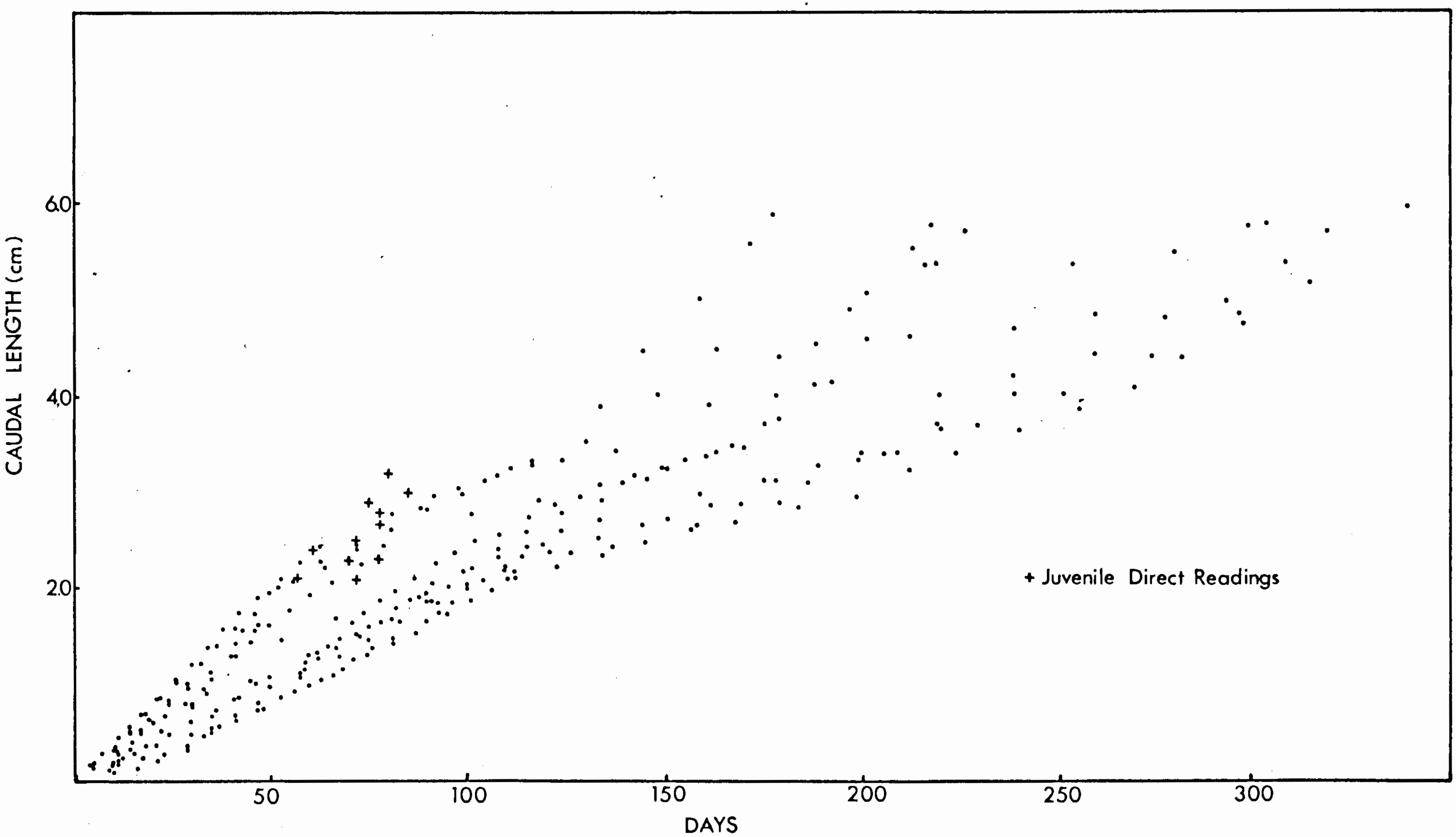


Fig. 2.5(a): L. hectoris back-calculated scanning electron microscopy daily ring counts. Juvenile direct, light microscopy ring counts are also shown.

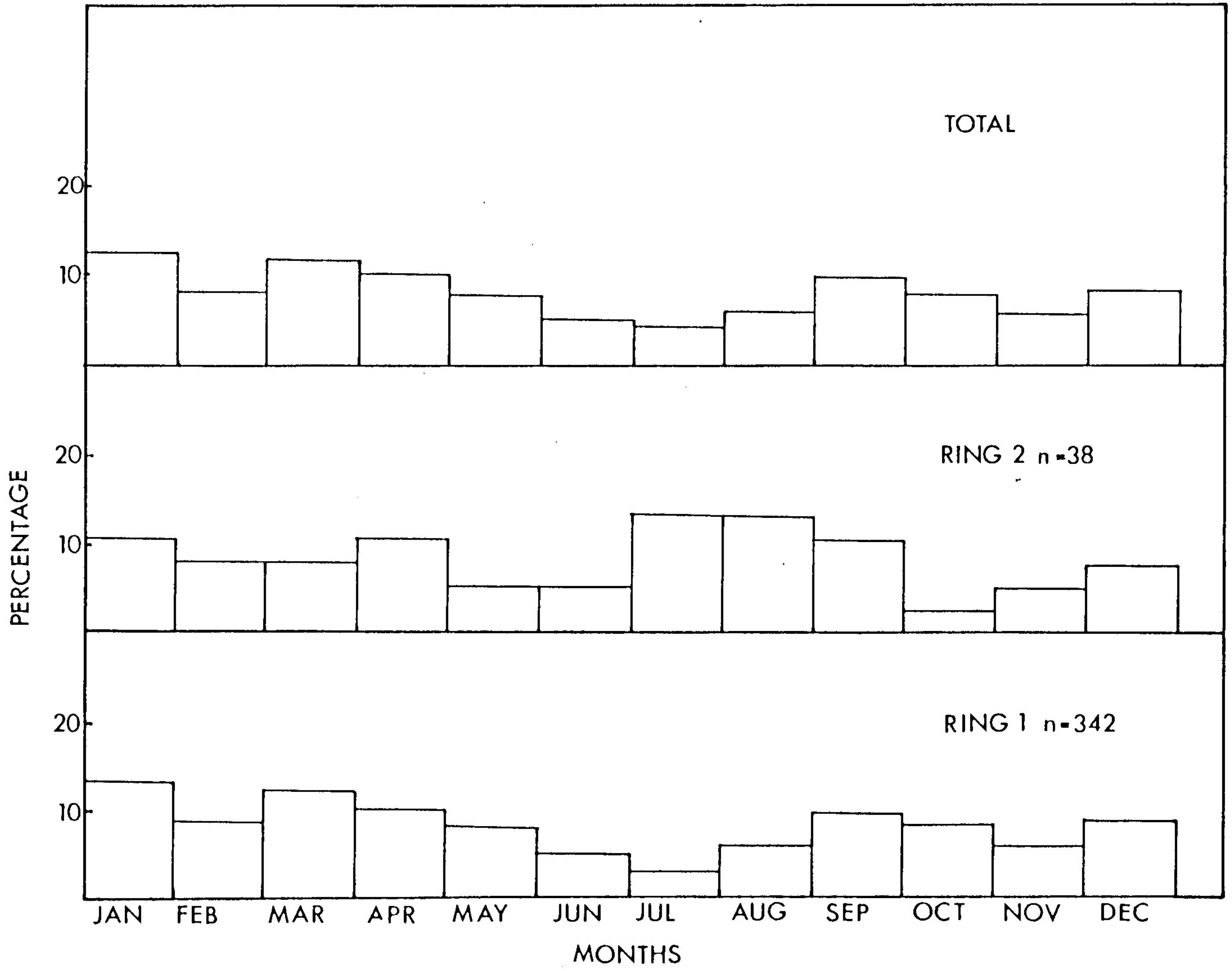
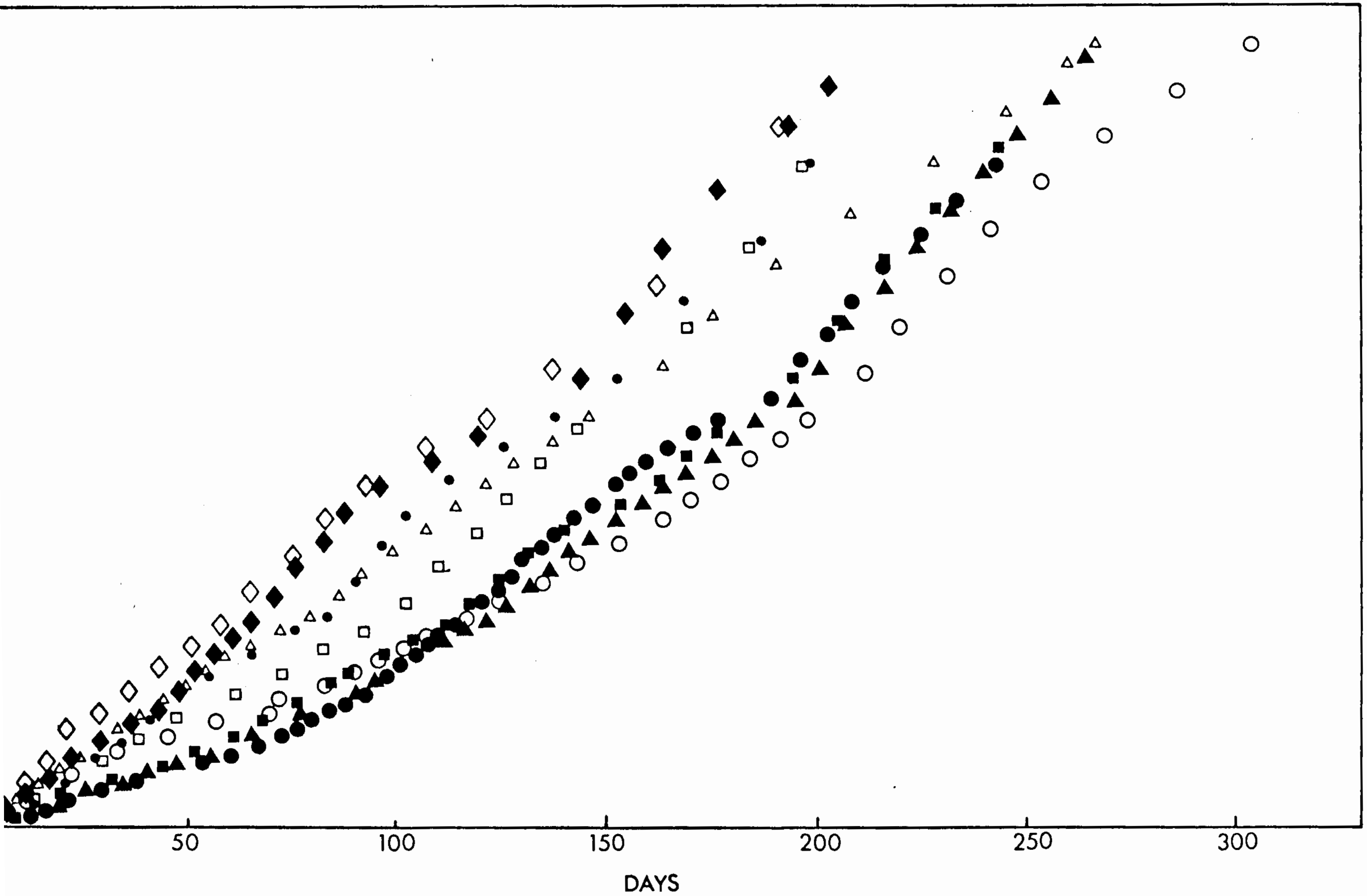


Fig. 2.6(b): The monthly percentage of back-calculated hyaline rings for *M. muelleri*.

L(2.0)= 6.72 cm



g. 2.5 (b): *M. muelleri* back-calculated scanning electron microscopy daily ring counts. The growth of ividual fish is shown by the different symbols.

of fish for each time interval (month) sampled was converted to length using Figs 2.3 a and b. These lengths were in turn converted into days using the growth parameters calculated in Section 2.3. Using the date of capture for each sample, these days were back-calculated to give an indication of the time of ring formation.

It was assumed that the date of capture was the 15th of each month as only the months at capture and not the exact dates were known. This may have introduced an error, but should even out considering the large number of readings and the fact that fishing occurs throughout the month.

It was assumed that growth was the same for all the fish sampled.

2.4.3 RESULTS

The back-calculated times of ring-formation are shown in Figs 2.6 a and b. The calculations have been summed to give an indication of the monthly frequency of each ring laid down.

Hyaline rings are laid down throughout the year for both light- and lanternfish. No significant peaks are present for any of the rings back-calculated.

2.5 NATURAL MORTALITY

2.5.1 INTRODUCTION

This is an important parameter, since most stock assessment models are sensitive to the value of M (natural mortality coefficient). It is also a parameter which is determined with the least precision, and calculations are often made using a likely range of M values rather than a single absolute value.

Natural mortality rates are often difficult to measure directly in exploited populations, but in the early stages of exploitation an idea of M can be gauged from the growth pattern of the species. Species with rapid rates of growth (a large K coefficient in the von Bertalanffy equation) are likely to have high rates of natural mortality, for example clupeoid fish such as anchovy. Those with small K's are likely to have low coefficients of natural mortality, for example gadoid fish such as hake.

Most tropical myctophids and smaller gonostomatids seem to have a one-year life cycle (Clarke 1973, 1974) and species such as Benthosema pterotum, B. fibulatum and Diaphus dumerilii all have instantaneous natural mortality rates of about M= 5,0, corresponding to an annual mortality of more than 99 %. Mesopelagic fish from colder waters have a longer life cycle, but few estimates of mortality rates have been made, examples being Benthosema glaciale, Notoscopelus kroeyerii and Maurolicus muelleri which have mortality estimates of 0,7, 0,8 and 1,8 respectively (Gjøsaeter and Kawaguchi 1980). However, the authors state that these results are only tentative due to the selectivity of gear and other sources of error.

2.5.2 METHODS

Methods of estimating natural mortality in animal populations include tagging, direct census or a plot of the total mortality rate (Z) against fishing effort. The first two methods are not feasible, whilst the third requires a fairly long annual series of good data on fishing effort. Therefore an analysis of the catch curves was done for both _L. hectoris_ and _M. muelleri_ using research samples taken over a number of years and an extensive area.

In the initial stages of exploitation, the length and age frequency distribution of the catch approximates closely that of the population in its virgin unexploited state. Hence the decline in relative abundance of successive age classes with increasing age should approximate the natural mortality rate. The assumptions made are that catchability remains constant and that the decline in numbers at length in the mean length distributions reflect mortality rather than (i) effect of within- season recruitment patterns (ages are year fractions rather than discrete years) and between season recruitment levels, (ii) emigration from sampling area as fish increase in length.

Lanternfish can be regarded as in the initial stages of exploitation. However, ideally a value of M should be obtained before exploitation commences by research sampling on a suitably large scale, and determining the age structure of the population in advance. This approach was followed with lightfish, whereby research sampling was done over a three year period over an extensive research area along the west coast of South Africa. The length frequency distributions obtained in July 1982, August 1982, May 1983, August 1983, November 1983, April 1984 and May 1984 were combined in a single length-frequency distribution.

Using the age structure proposed in this study, the von Bertalanffy growth equation with age expressed in terms of length, and the descending limb of the length frequency distribution for both L. hectoris and M. muelleri, the numbers in each length interval j were regressed against the "age" (Aj) in years corresponding to the median length (Lj) in that interval:

$$A_j = - \frac{1}{K} (L_n(1 - \frac{L_j}{L_\infty})) + t_o$$

The slope of the regression gave an estimate of total mortality (Z), which can be regarded as an approximation of M, since M. muelleri is an unexploited population whilst L. hectoris is in the initial stages of exploitation.

The method of using length frequencies to estimate mortality is subject to a certain amount of bias because successive length intervals represent increasing increments of age and hence increasing periods over which mortality occurs. The catches taken from length intervals close to the asymptote of the growth curve therefore represent a larger proportion of the average numbers alive in the sea than catches from smaller length intervals. Hence a plot of catches against age will be less steeply sloped than a plot of population numbers against age, and will tend to underestimate mortality.

Pauly (1980) proposed an equation using the asymptotic length L_∞, the growth constant K, and an estimate of the mean water temperature in which the fish stock in question lives, to calculate an estimate of natural mortality. He used one hundred and seventy five fish stocks to derive the following equation:

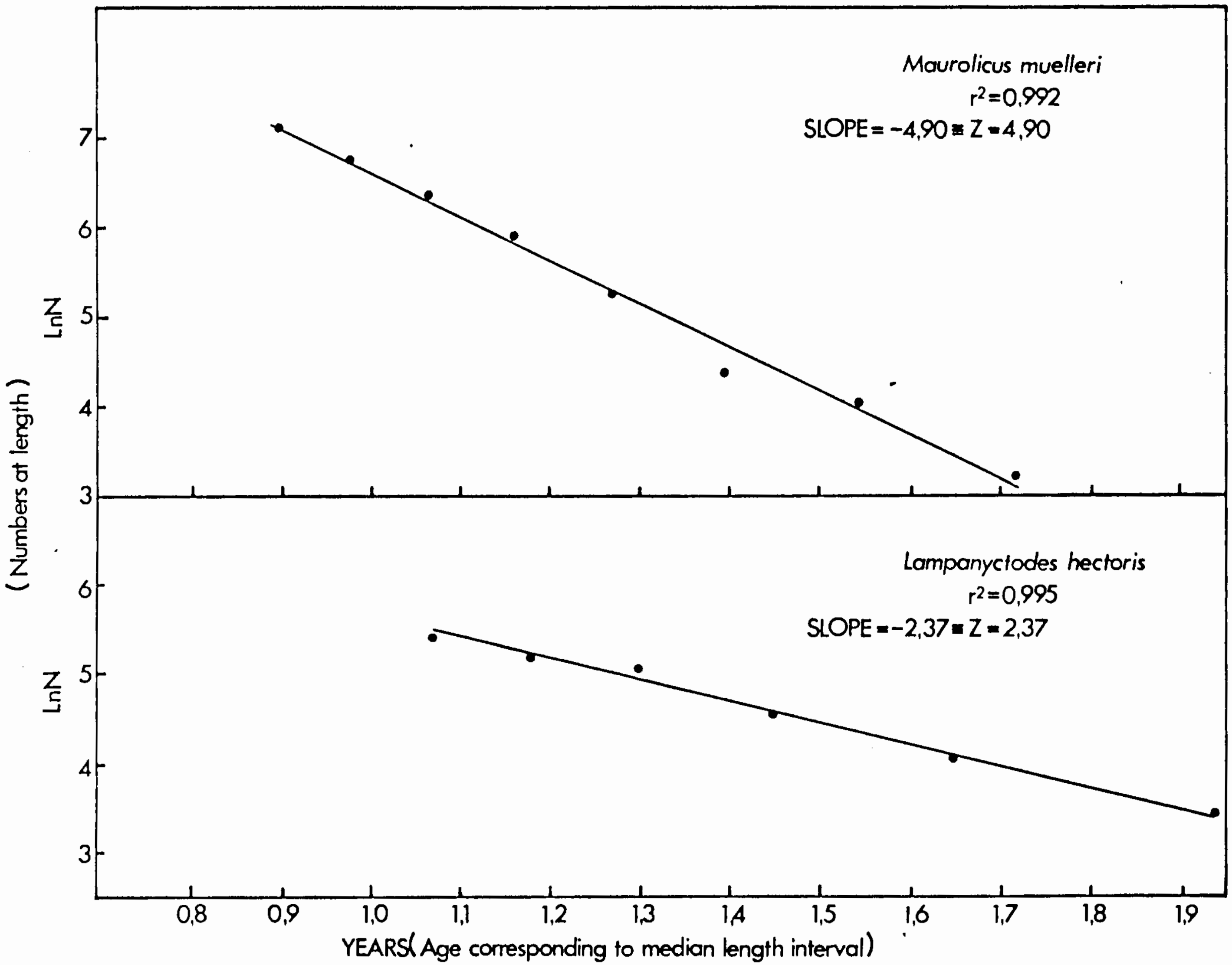


Fig. 2.7: Estimates of natural mortality for L. hectoris and M. muelleri.

$\log M = -0.0066 - 0.279 \log L_{\infty} + 0.6543 \log K + 0.4634 \log T$
This equation can be used to give another estimate of natural mortality for the lightfish and lanternfish stocks off the South African coast.

2.5.3 RESULTS

The estimates of the total mortality rate Z for both L. hectoris and M. muelleri are shown in Fig. 2.7. The high values suggest that the annual mortality is more than 90 %.

Using the asymptotic lengths and growth constants proposed in Section 2.3.2 and temperatures of 10 and 17 degrees centigrade (these values were chosen as it represents the most likely temperature range for these species), another estimate of natural mortality was derived. Values of 2,32 to 2,96, and 1,90 to 2,43 for lantern- and lightfish respectively, were derived using Pauly's equation.

2.6 DISCUSSION

Seasonal variation in growth has been recorded for a number of pelagic fishes off the southern African coast e.g. the South West African pilchard, Sardinops ocellatus, (Thomas 1984) and anchovy, Engraulis japonicus (Melo 1984) and the South African anchovy, Engraulis japonicus, (Prosch in prep).

Growth studies on mesopelagic fish indicated that generally fish from cold waters are slow growing, although growth may be rapid during the first part of life. Warm-water mesopelagic fish seem, however, to have a fast growth, and most of them probably reach maximum size in one year or less (Gjøsaeter and Kawaguchi 1980). Maurolicus muelleri was studied in the Northeast Atlantic by Gjøsaeter (1978), who estimated the parameters of the von Bertalanffy growth function to be :

$$Lt = 59\text{mm}\ (1-\exp[-0,88\{t+0,06\}])$$

M. muelleri does seem to have a fast growth until sexual maturity is reached and a very slow growth later (Gjøsaeter 1978). The growth parameters calculated for M. muelleri in this study are comparable with those already mentioned i.e.

$$Lc(\text{cm, caudal length}) = 6.00(1-\exp[-1.15\{t-0,06\}])$$

The initial growth can be observed in Fig. 2.5 b however, no levelling off of growth was detected for the size range sampled.

There is very little life history data available for Lampanyctodes hectoris. The Division of Sea Fisheries Annual Report 40 (1972) gives the following growth equation:

$$Lt(\text{cm, total length}) = 9,95(1-\exp[-0.309\{t+1,52\}])$$

Using the total length/caudal length conversion of Crawford (1980) it is possible to compare the growth rate proposed in this study ($Lt = 1.1549\ Lc + 0.4724$; 9.95 cm total length= 8.14 cm caudal length) to the one given above. The growth rate proposed here is faster (6.85cm total length compared with 5,38 after 12 months growth, 8,23cm and 6,60 respectively after 24 months' growth). Sub-samples taken from commercial catches from 1968-1984 (Chapter 1) indicate that the majority of the fish sampled were 12 months of age or less. Few fish were 24 months of age.

However, the above equation suggests that most of the fish in the samples were two to three years of age. Age readings done on L. hectoris in the 1970's at the Sea Fisheries Research Institute (unpublished data) interpreted all hyaline rings on the otolith as annual rings. This resulted in too slow an estimation of growth rate considering the daily growth study and the studies done elsewhere on mesopelagic fish. The growth equation:

$$Lc(\text{cm, caudal length}) = 7.00(1-\exp[-1,66\{t-0,06\}])$$

should thus be used.
A fast initial growth with some levelling off later was observed for L. hectoris.

The fish length:otolith length and fish length:otolith radius relationships calculated (Figs 2.2 and 2.3) indicate a seasonal variation in these relationships. According to Reay (1972) the "assumption" of a constant relationship between otolith length and body length was found to result in varying values of estimated length when such a relationship was used, depending on the season during which the samples were obtained. A knowledge of the seasonal variation in otolith-body length ratios are necessary for accurate back-calculation of mean body lengths. In order to determine the extent of seasonal influence on the FL:OR relationships for lanternfish (Figs 2.3 a and b), the mean otolith radius at monthly intervals for three years are shown in Fig. 2.4. For some months the mean otolith radius fluctuated so much that it was smaller than that for a fish 1,0cm smaller, e.g. the 6,0cm length class in February 1981 had a mean otolith radius smaller than that of a 5,0cm fish, similarly the mean otolith radius for the 5,5cm length class in April had a smaller mean otolith radius than the 5,0cm length class for the same month and was close to that of the 4,5cm length class. If the relationship in Fig. 2.3 a had been constant the graphs in Fig. 2.4 would have been straight lines.

A general downward trend is apparent for the mean otolith radii (Fig. 2.4) for the period January to February, an upward trend for February to May, and a decrease after May (4,0; 4,5 and 5,0cm length classes in 1982). The downward trends are the result of a slower growth rate which result in comparatively large otoliths, but disproportionately small radii.

Fig. 2.3 a suggests that the growth in fish length in relation to the growth in otolith radius slows down at between 3,0cm and 4,0cm caudal length. The same phenomenon can be observed in the FL:OL relationship (Fig. 2.2 a). Such slowing down periods have been correlated with the formation of hyaline rings in the pilchard S. ocellatus off South West Africa (Thomas, Sea Fisheries Research Institute, Cape Town, personal communication) and the anchovy E. japonicus off South Africa (Prosch in prep.). The same association is evident for lanternfish for the third and to a lesser extent the second hyaline ring formed. It is not known whether the same holds true for the first ring formed.

Fig. 2.3 b suggests that the growth in fish length in relation to the growth in otolith radius for lightfish slows down at between 2,5 and 4,0cm. As the hyaline rings are formed at approximately 3,0 and 3,9, this slowing down period can also be associated with the formation of hyaline rings. This phenomenon can also be observed in the FL:OL relationship (Fig. 2.2 b).

The back-calculated times of hyaline ring formation show no definite peaks (Figs 2.6 a and b). Hyaline rings are laid down throughout the year for both light- and lanternfish. Lanternfish spawn mainly in winter/spring (Chapter 3) and one would expect a peak of first hyaline ring formation followed by peaks of second and third ring formations. The reason for the even distribution in Fig. 2.6 a is not clear, especially since it would appear if rings are deposited once fish attain a specific length (Table 2.1). The reasons for this even distribution may be that the CELP survey did not cover the entire spawning area and therefore fish may be fed into the system throughout the year, obscuring possible peaks in hyaline ring formation. Moreover spawning may take place throughout the year, but survival may not necessarily be highest in the peak spawning months. Seabirds feed on juvenile anchovy Engraulis japonicus throughout the year, although peak spawning occurs in summer, indicating that peak recruitment does not necessarily occur in the month of maximum spawning (Berruti, Sea Fisheries Research Institute, Cape Town, personal communication).

Lightfish hyaline ring formation also takes place throughout the year on a nearly uniform basis (Fig. 2.6 b) and hyaline rings appear to be deposited at a specific length (Table 2.2), therefore the same explanation given above may be valid for this species.

The high mortality rates shown in Fig. 2.7 correspond to an annual mortality of more than 90 %. Although this seems very high, the majority of the fish aged were one-year of age or less, indicating that these mortality estimates may be a true reflection of the real situation. The mortality estimate of L. hectoris using the relationship proposed by Pauly (1980) is close to that obtained using length frequency distributions, i.e. 2,32 to 2,96 as opposed to 2,37. However, the M. muelleri values show a big difference, 1,90 to 2,43 using Pauly's relationship as opposed to 4,90 when length frequency distributions are used. This difference may be due to an emigration effect whereby the emigration of older individuals out of the Benguela upwelling system causes a rapid degeneration of the length frequency distribution. Evidence suggest that L. hectoris is contained within the Benguela upwelling system (Hulley, South African Museum, Cape Town, personal communication). This may account for the similar natural mortality estimates obtained for this species.

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CHAPTER 3

THE SPAWNING BEHAVIOUR OF THE LANTERNFISH LAMPANYCTODES HECTORIS AND THE LIGHTFISH MAUROLICUS MUELLERI

3.1 INTRODUCTION

Spawning seasons for myctophid and sternoptychid fishes have been deduced from the maturity stage of the ovary and the seasons in which the larvae occur.

Myctophidae in temperate and subtropical regions spawn mainly from late winter to summer (Table 3.1). Winter spawning in high latitudes seems to be an adaptation to low water temperature (Gjøsaeter and Kawaguchi 1980) and the period of principal spawning for most myctophid species appears to be timed to coincide with the seasonal peak in food production (Clarke 1973). Lampanyctodes hectoris larvae were common at seasonally occupied stations off Castlepoint off New Zealand (41^0 S), especially in the spring months, and were present from late winter to late autumn (Robertson 1977). To my knowledge this is the only documented account of L. hectoris larvae sampled.

Maurolicus muelleri spawn mainly in spring/summer (Table 3.2). In New Zealand waters, eggs of M. muelleri were taken during all months except April to July, indicating a long spawning season from late winter to early autumn. Egg densities were highest in spring and summer, and the length of the spawning season seemed to vary with locality (Robertson 1976). However, Sternoptychids

Table 3.1 Spawning season of the species of the family Myctophidae (Sp. = spring; Sum. = summer; F. = fall; W. = winter) (Gjøsaeter and Kawaguchi 1980)

Species	Main spawning season	Areas
Benthosema glaciale	W. to Sp.	Mediterranean
B. glaciale	Early Sp.	W.N.Atl. (40° - 50°N)
B. suborbitale	Sp.	Off Hawaii
Bolinichthys longipes	Sp. to Sum.	Off Hawaii
B. supralateralis	Sum. to F.	Off Hawaii
Ceratoscopelus maderensis	Sum.	Mediterranean
C. warmingi	Sp. to Sum.	Off Hawaii
Diaphus anderseni	Sp. to Sum.	Off Hawaii
D. brachycephalus	Sp. to Sum.	Off Hawaii
D. elucence (= *D. perspicillatus*)	Sum.	Off Hawaii
D. fragilis	Sum.	Off Hawaii
D. holti	Sum.	Mediterranean
D. rafinesquei	F. to W.	Mediterranean
D. rolfbolini (= *D. phillipsi*)	Sp. to Sum.	Off Hawaii
D. schmidti	Sp. to Sum.	Off Hawaii
Electrona rissoi	Sp. Sum. F. W. (?)	Mediterranean
Hygophum hygomi	F. to W.	Mediterranean
H. proximum	Sp. to early Sum.	Off Hawaii
H. reinhardti	Sp. Sum. F. W. (?)	Off Hawaii
Lampanyctodes hectoris	W. to Sp.	Off New Zealand
Lampanyctus alatus	Sp. Sum. F. W. with a peak in Sp. to Sum.	Mediterranean
L. niger	Late Sum. to W.	Off Hawaii
L. nobilis	Sp. Sum. F. W. (?)	Off Hawaii
L. steinbecki	Sp. to W.	Off Hawaii
Lampadena luminosa	Sp. to Sum.	Off Hawaii
Lobianchia dofleini	W. to Sum.	Mediterranean
L. dofleini	W. to Sp.	W.N.Atl. (32°N, 64°W)
L. gemellarii	Sp. to Sum.	Off Hawaii
L. gemellarri	W.	Mediterranean
M. benoiti (= *Hygophum benoiti*)	Sp. to F.	Mediterranean
M. humboldti (= *Symbolopholus veranyi*)	Sp. to F.	Mediterranean
M. punctatum	W. to Sum. with a peak in Sp.	Mediterranean
M. selenoides (= *M. selenops*)	Sp.	Off Hawaii
Notolychnus valdiviae	Sp. to Sum. with a peak in Sum.	Off Hawaii
Notoscopelus elongatus	W. to Sum.	Mediterranean
Stenobrachius leucopsarus	W.	Off Oregon, USA
Taaningichthys minimus	W. (?)	Off Hawaii
Triphoturus nigrescens	Sp. to Sum.	Off Hawaii

Table 3.2: Spawning seasons of some species of the family Sternoptychidae (Sp. = spring; Sum. = summer; F. = fall; W. = winter).

Species	Main spawning Period	Areas	Sources
Danaphos oculatus	Sp.Sum. F.W. (?)	Off Hawaii	Clarke, 1974
Maurolicus muelleri	Sp to F.	Off w. Norway	Wiborg, 1954
M. muelleri	Sp.	Japan Sea	Nishimura, 1959
M. Muelleri	Sp. to F.	New Zealand	Robertson, 1976
M. muelleri	Sp. to F. with a peak in Sum.	e.N.Atl. (59°N, 19°W)	Williams & Hart, 1974
M. muelleri	Sp. to Sum	Off Norway	Gjøsaeter, 1978 (cited by Gjøsaeter and Kawaguchi, 1980)
Valenciennellus tripunctulatus	Sp. Sum. F. W.	Off Hawaii	Clarke, 1974

such as Danaphos oculatus and Valenciennellus tripunctulatus showed no indication of seasonality in reproduction. According to Clarke (1974), the larvae of these species either hatch at a larger size or live at greater depths than those of the seasonal species, and the former's spawning is thus not timed to any seasonal fluctuations in food concentration or size distribution in the upper layers.

From August 1977 to August 1978 the Sea Fisheries Research Institute conducted the extensive Cape Egg and Larval Programme (CELP) between just north of the Olifants River and Cape Barracouta in the south. The samples taken from these cruises were analysed for L. hectoris and M. muelleri eggs and larvae.

3.2 METHODS

The CELP stations sampled during each cruise are shown in Fig. 3.1. A total of hundred and twenty stations were sampled each month (20 lines of 6 stations each) except in November and December 1977 which were sampled in a single cruise. Although an attempt was made to sample all the stations every month, gear, time and weather restrictions sometimes resulted in the omission of a few stations. The grid stations were approximately ten nautical miles apart whilst the sampling lines were approximately twenty nautical miles apart at their base.

A Bongo net towed at slow speeds is recommended as the best of simple gear for ichthyoplankton surveys. It provides a minimum of variation in the biases caused by uneven filtration per unit depth, avoidance of the net, and escapement or extrusion of

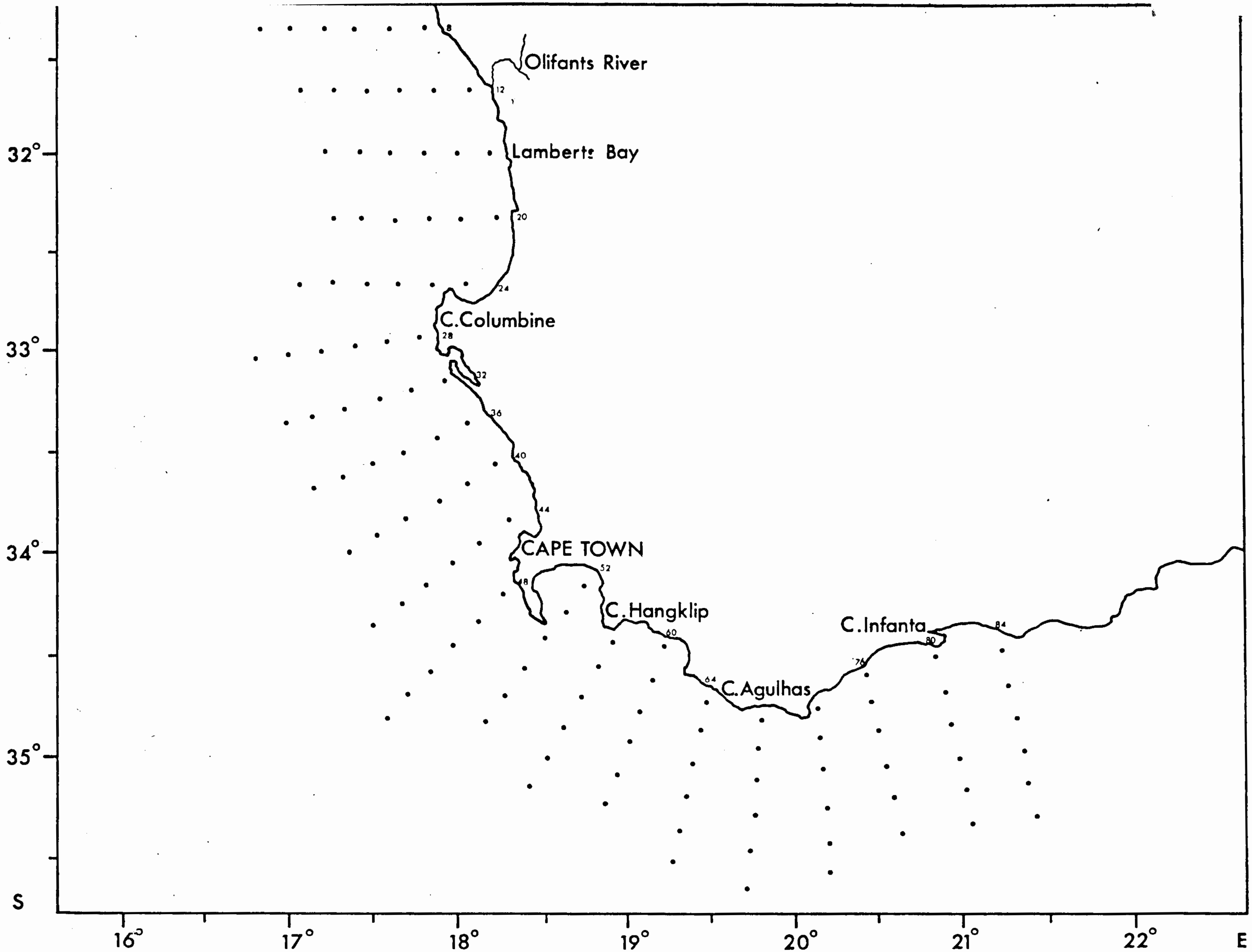


Fig. 3.1: The station grid used during the Cape Egg and Larvae Survey.

organisms through the meshes (Smith and Richardson 1977). The Bongo towing frame used was made of moulded fibreglass, and comprised two circular frames, each 57 cm in diameter, connected by a central yoke to which the towing wire, a bathythermograph and a 25 kilogram dead weight depressor were suspended. Thus, there were no bridles in front of the mouth of the net.

The towing frame was fitted with two cylindrical-conical nets, one of 300 micron and the other 500 micron mesh. A digital flowmeter was mounted centrally in each net opening. A diagrammatic view of the Bongo net is shown in Fig. 3.2.

The equipment was used to sample to a depth of 100 metres in a double oblique haul. However, when the thermocline, as shown by the bathythermograph, was below 100 metres the net was towed below the thermocline. The length of wire to be let out was determined by a relationship of wire out against depth. However, after the CELP cruises it was discovered that the angle of the wire was a critical factor in determining the depth of the net. A temperature/depth probe and conducter cable with deck readout are currently used.

On station the net was lowered at 0,5 m/s, allowed to stabilize for 30 seconds at the required depth to ensure a clear temperature versus depth trace by the bathythermograph - and recovered at 0,5 m/s. Throughout the operation an attempt was made to maintain the ship's speed at 2 knots.

Both samples for each trawl were preserved in formalin although due to manpower restrictions only the 300 micron samples have

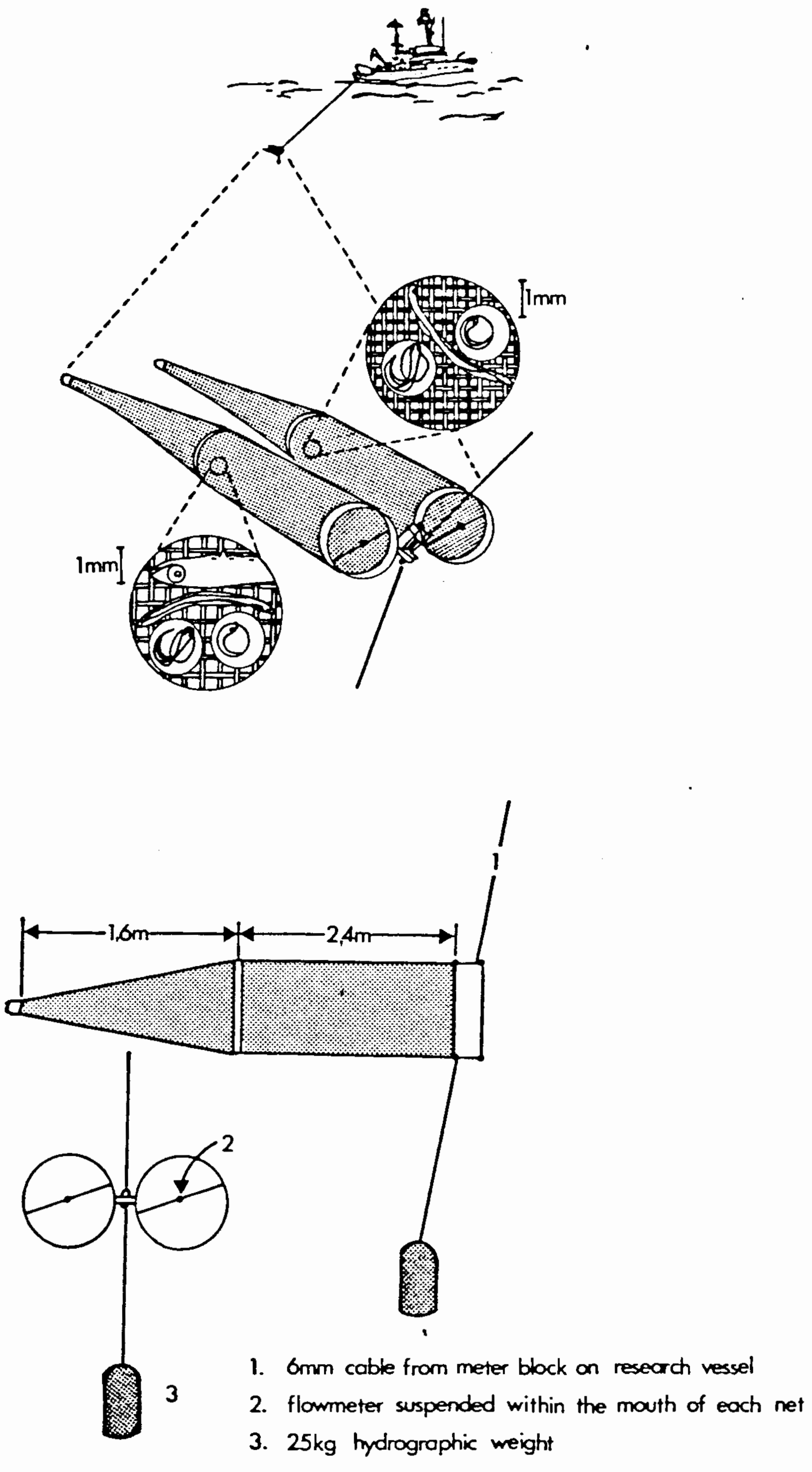


Fig. 3.2: Diagrammatic view of the Bongo net used in the CELP survey (redrawn from Smith and Richardson 1977).

been analysed to date. The samples were analysed in the laboratory and the total number of eggs and larvae of each species recorded. Various publications were consulted to ensure the proper identification of L. hectoris and M. muelleri eggs and larvae (Ahlstrom et al 1976, Paxton 1972, Robertson 1976 and 1977, Badcock 1984 and Okiyama 1971).

The egg and larval counts were standardized as the number per 10 m sea surface by multiplying the counts with a standard haul factor (SHF):

$$SHF = \frac{D \times 10}{c \times r \times a}$$

where D = depth attained by net
c = calibration factor for the flowmeter
r = flowmeter revolutions
a = mouth area of the net in square metres
(Smith and Richardson 1977)

At each station the temperature, salinity and chlorophyll were measured.

3.3 RESULTS

The total numbers of light- and lanternfish eggs and larvae sampled per month, expressed as percentages of the total annual counts are shown in Figs 3.3 and 3.4. Although the number of stations sampled each month varied, the mean egg and larvae expressed as a percentage for each month show little change from the totals shown in Figs 3.3 and 3.4.

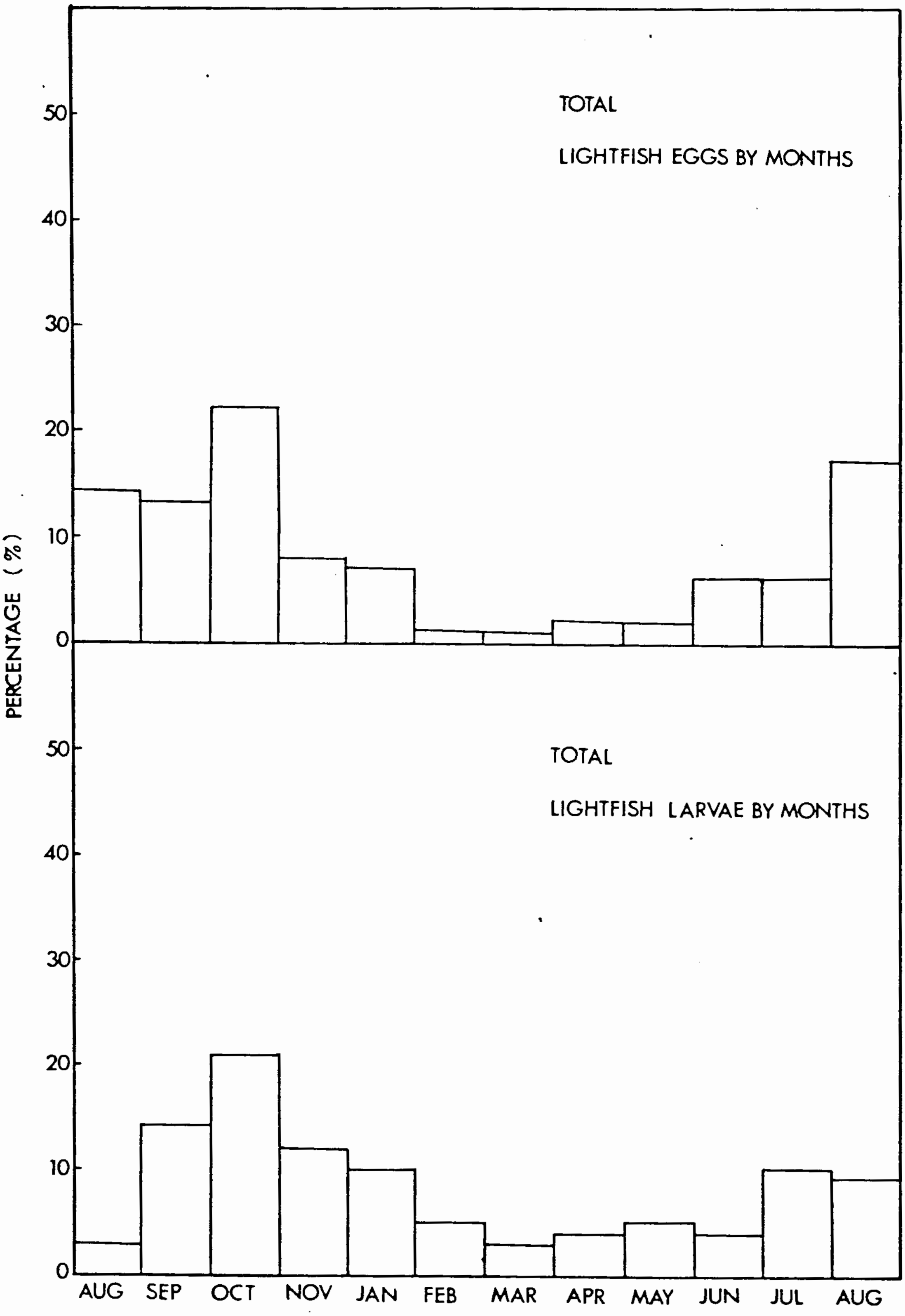


Fig. 3.3: Total M. muelleri eggs and larvae for each month during the CELP survey.

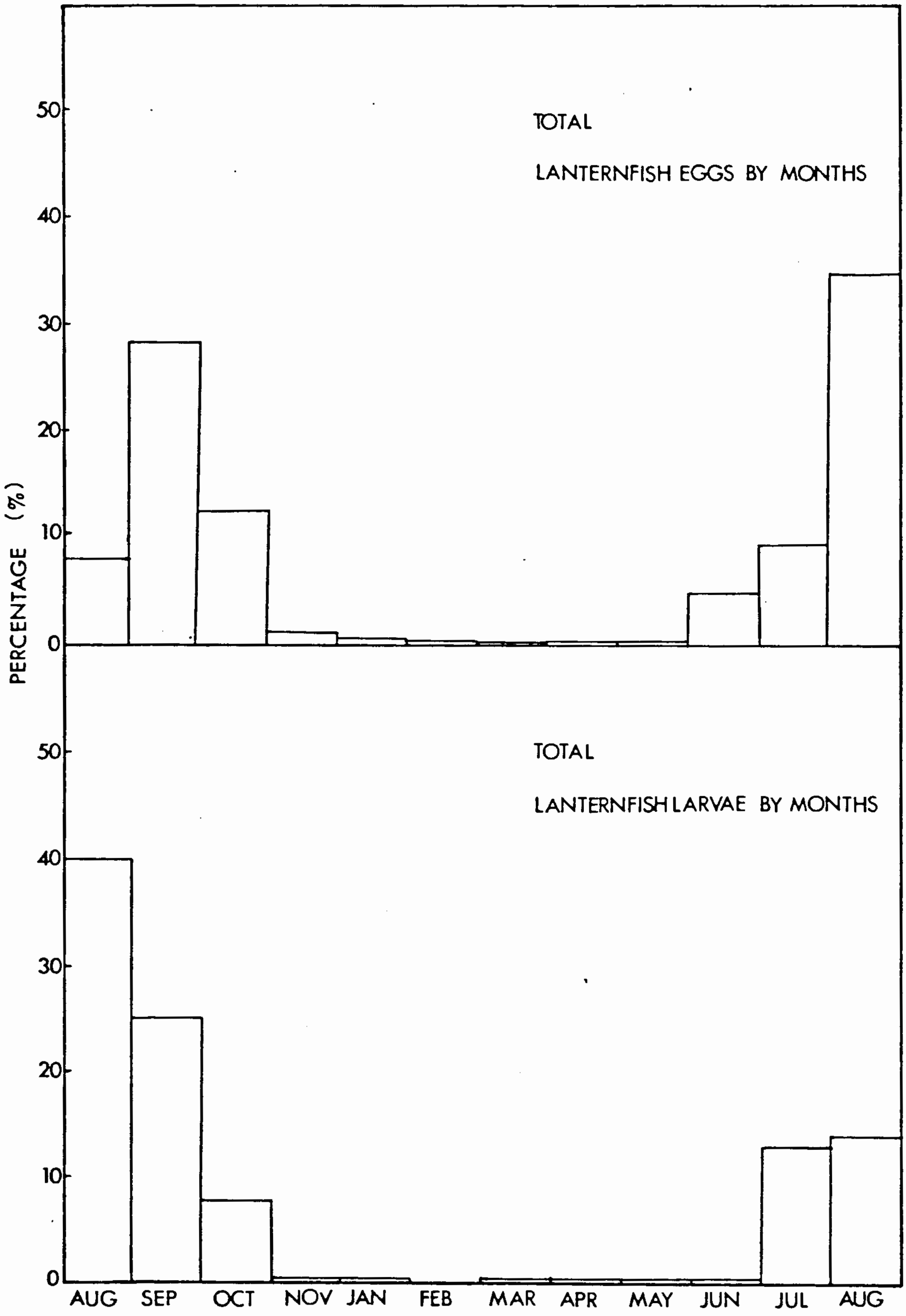


Fig. 3.4: Total *L. hectoris* eggs and larvae for each month during the CELP survey.

The horizontal distribution of *L. hectoris* eggs and larvae for successive months between August 1977 and August 1978 is shown in Figs 3.5 and 3.6. Little spawning activity was apparent from January to May and both eggs and larvae showed an offshore distribution pattern with low densities close inshore. Few eggs were found east of Cape Agulhas and the most eastern distribution extended up to Cape Infanta. The densest concentration of eggs were found off the West Coast. Although larvae had a more extensive horizontal distribution and occurred in larger numbers on the Agulhas Bank, the largest numbers were found off the West Coast. The most easterly distribution for larvae extended to Cape Infanta. It is thus apparent that the CELP grid adequately covered *L. hectoris* spawning inshore off the south coast. However, the grid did not adequately cover the spawning offshore and along the west coast north of the Olifants River. The largest concentrations of eggs and larvae generally occurred in the Cape Columbine/ Saldanha Bay area.

Figs 3.7 and 3.8 show the monthly horizontal distribution for *M. muelleri* eggs and larvae. As in the case of *L. hectoris* the CELP grid did not adequately cover the spawning offshore and along the west coast north of the Olifants River. Both eggs and larvae did not usually occur inshore and large numbers of eggs and larvae were taken throughout the year. Although larger concentrations of lightfish than lanternfish eggs were found on the Agulhas Bank, spawning was again mainly off the west coast. A few eggs and larvae were found as far east as Cape Infanta. Eggs and larvae were present throughout the year with a peak in spring and a smaller peak in winter (Fig. 3.3).

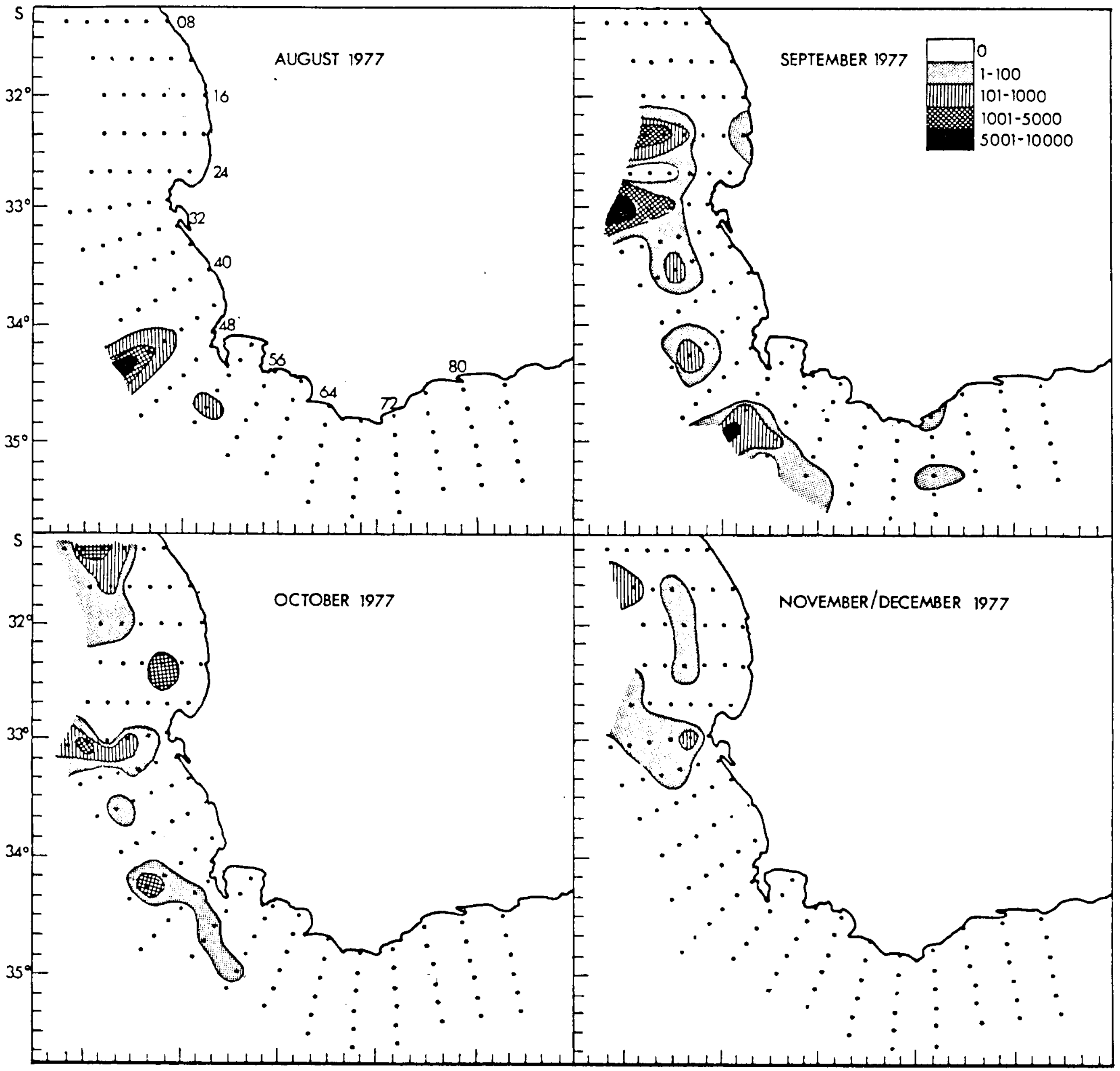


Fig. 3.5: Monthly horizontal distribution of L. hectoris eggs over the CELP grid.

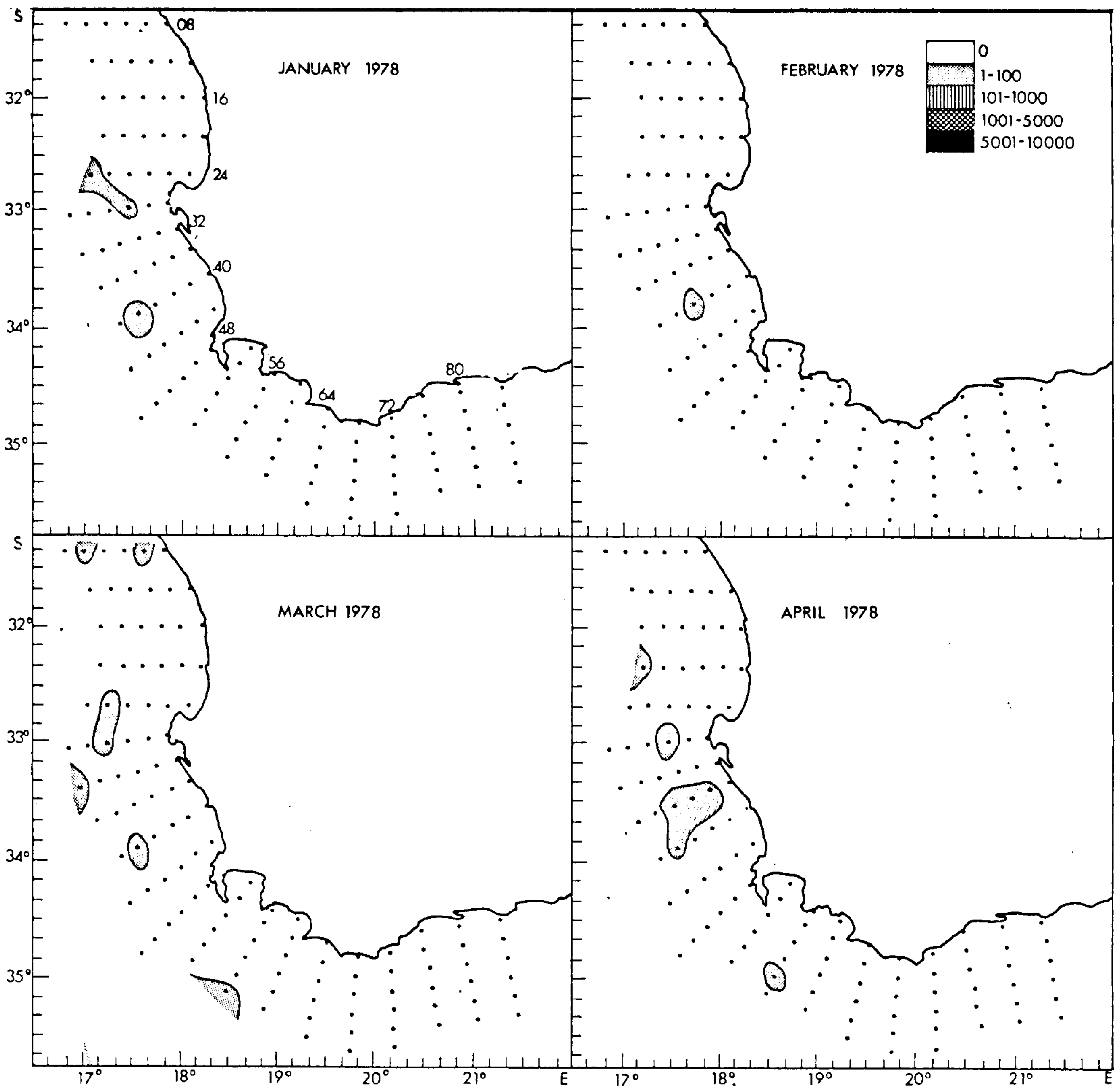
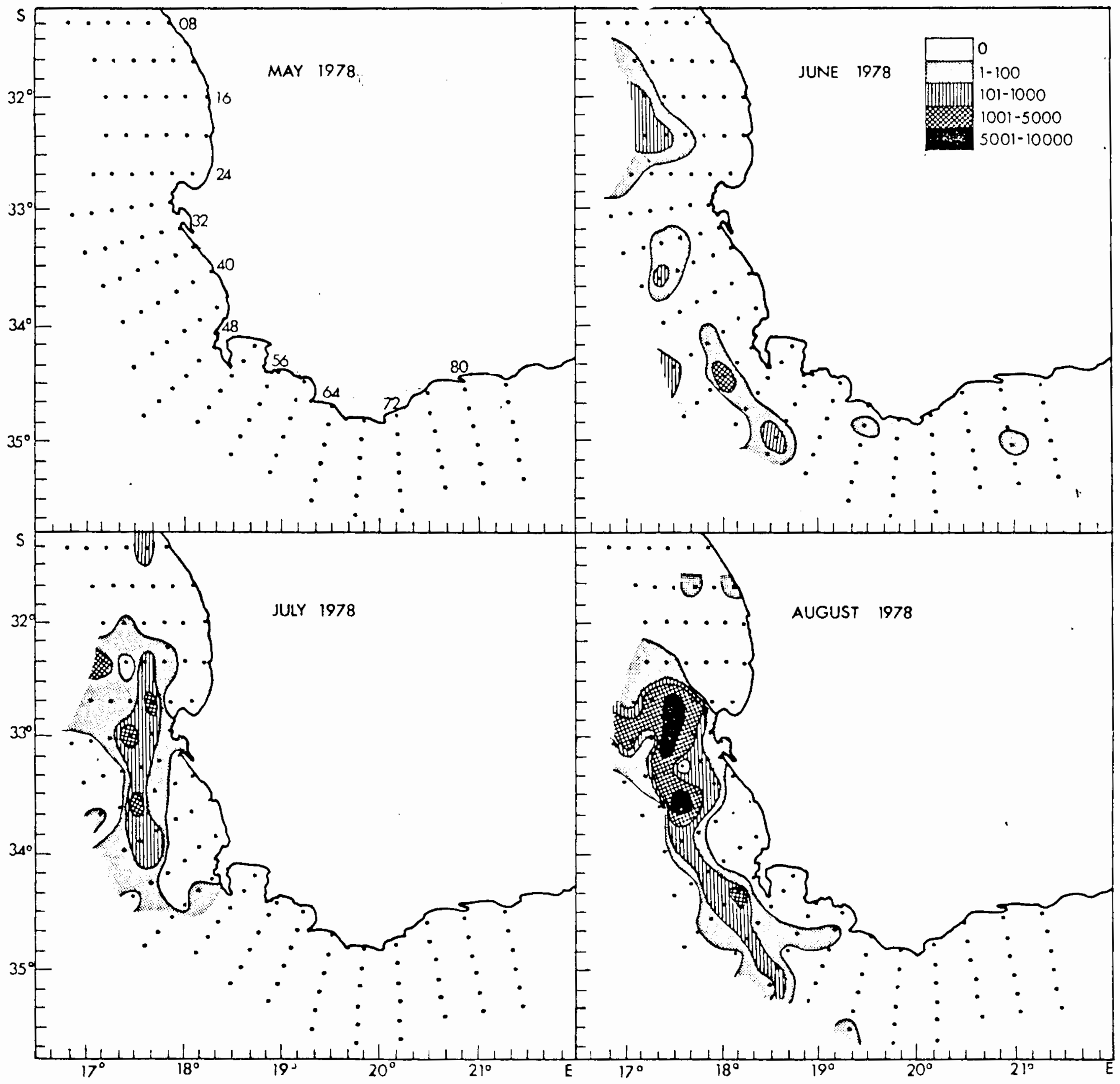


Fig. 3.5: Continued.



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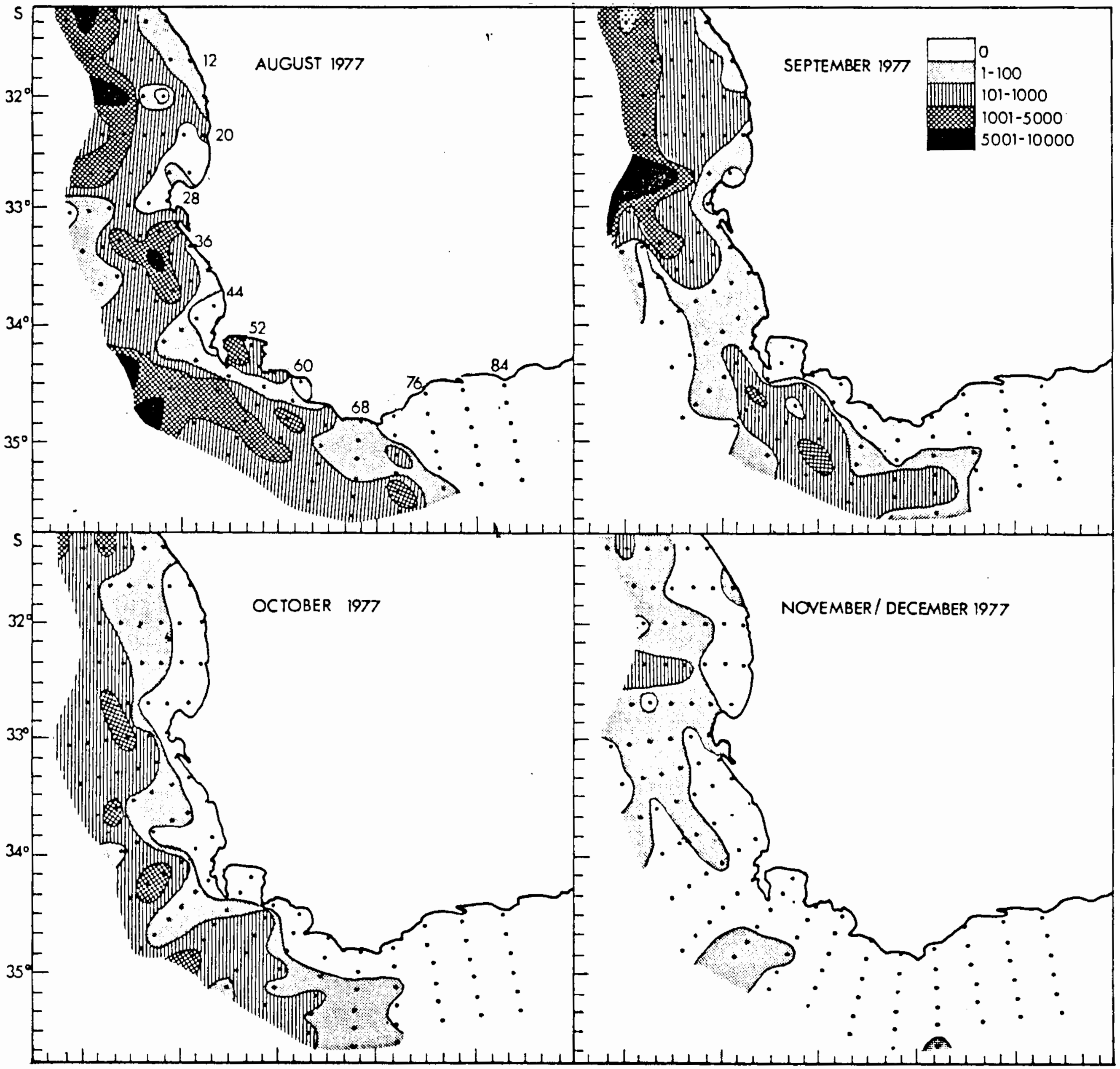


Fig. 3.6: Monthly horizontal distribution of *L. hectoris* larvae over the CELP grid.

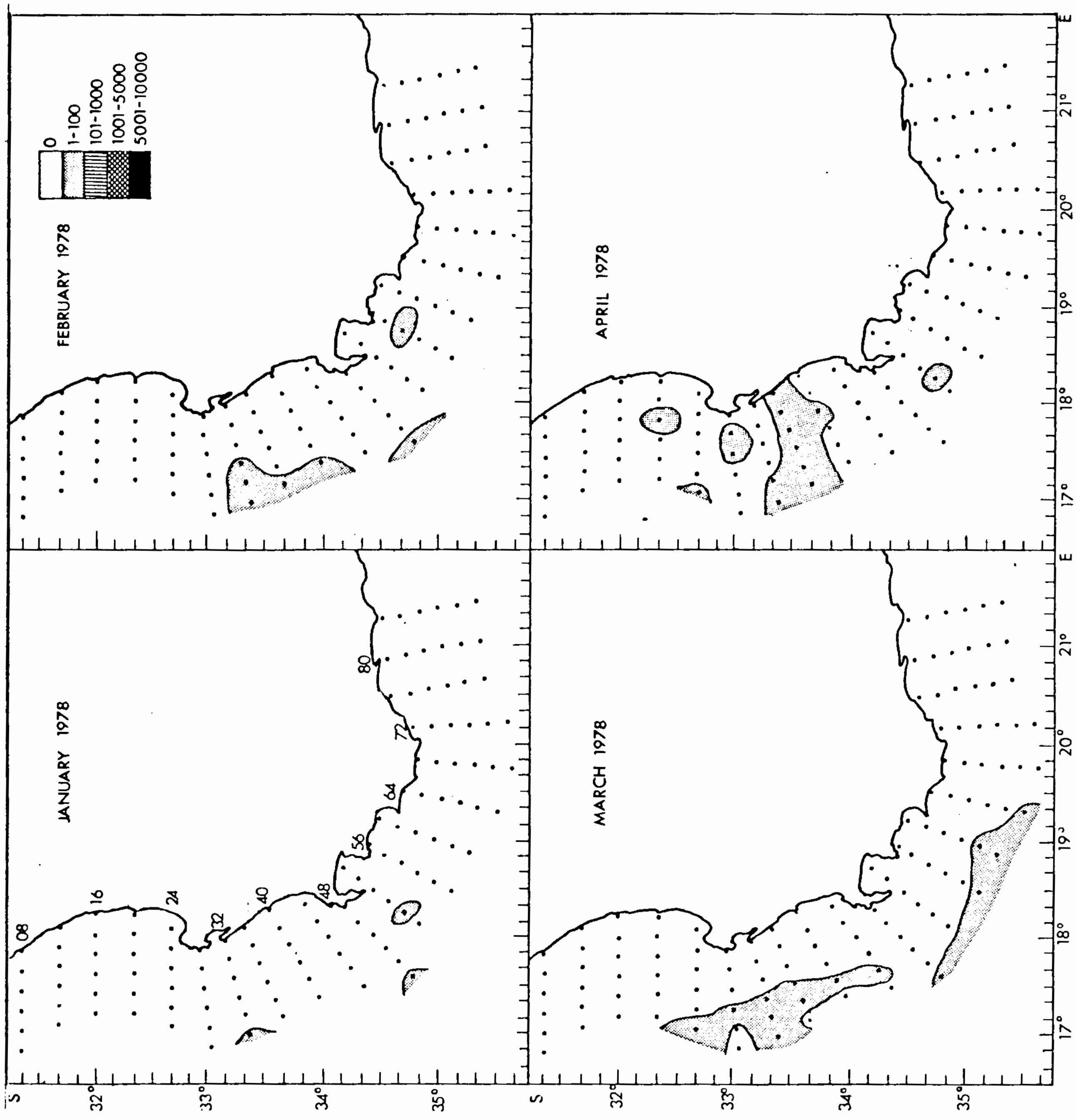


Fig. 3.6: Continued.

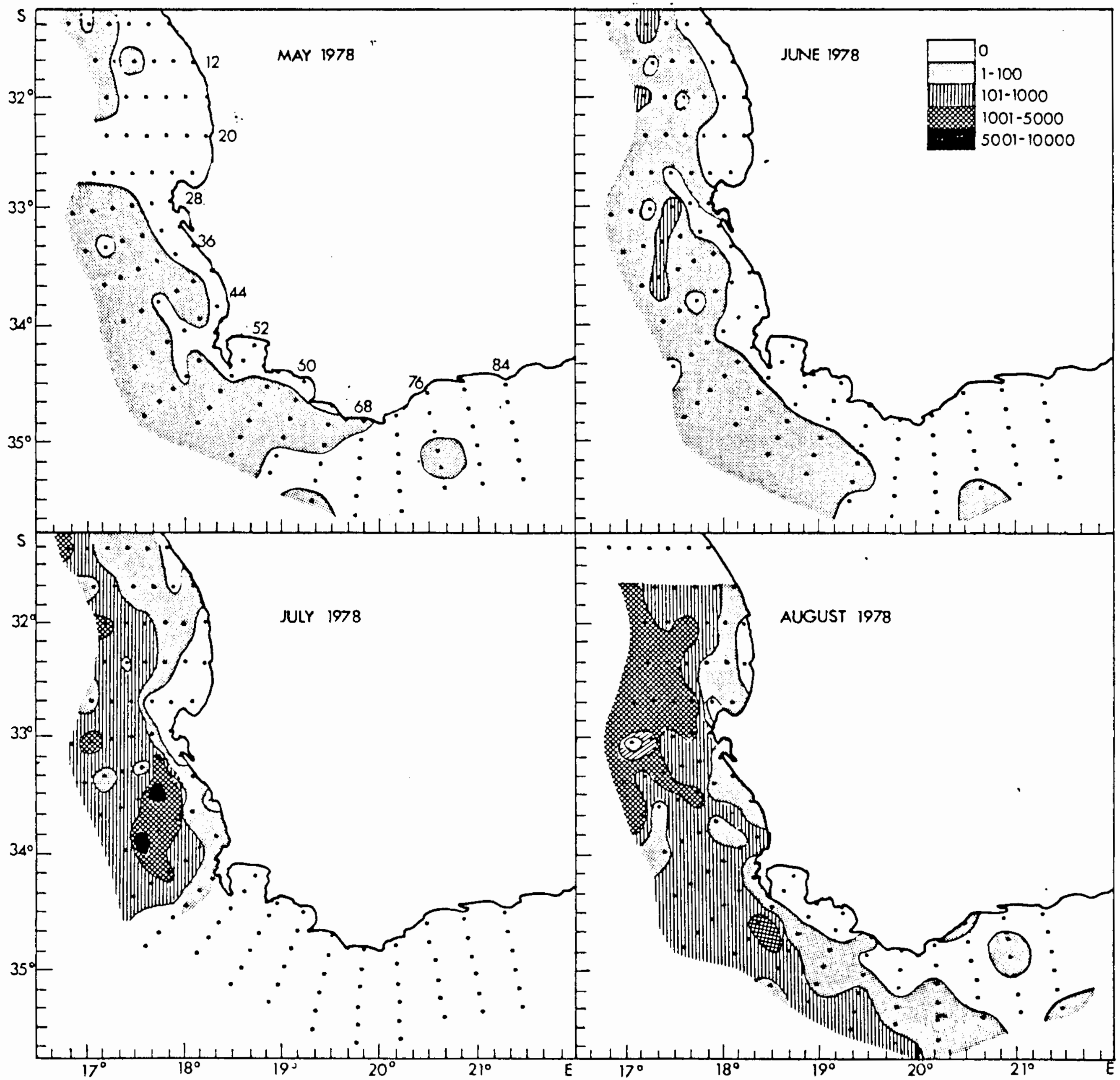


Fig. 3.6: Continued.

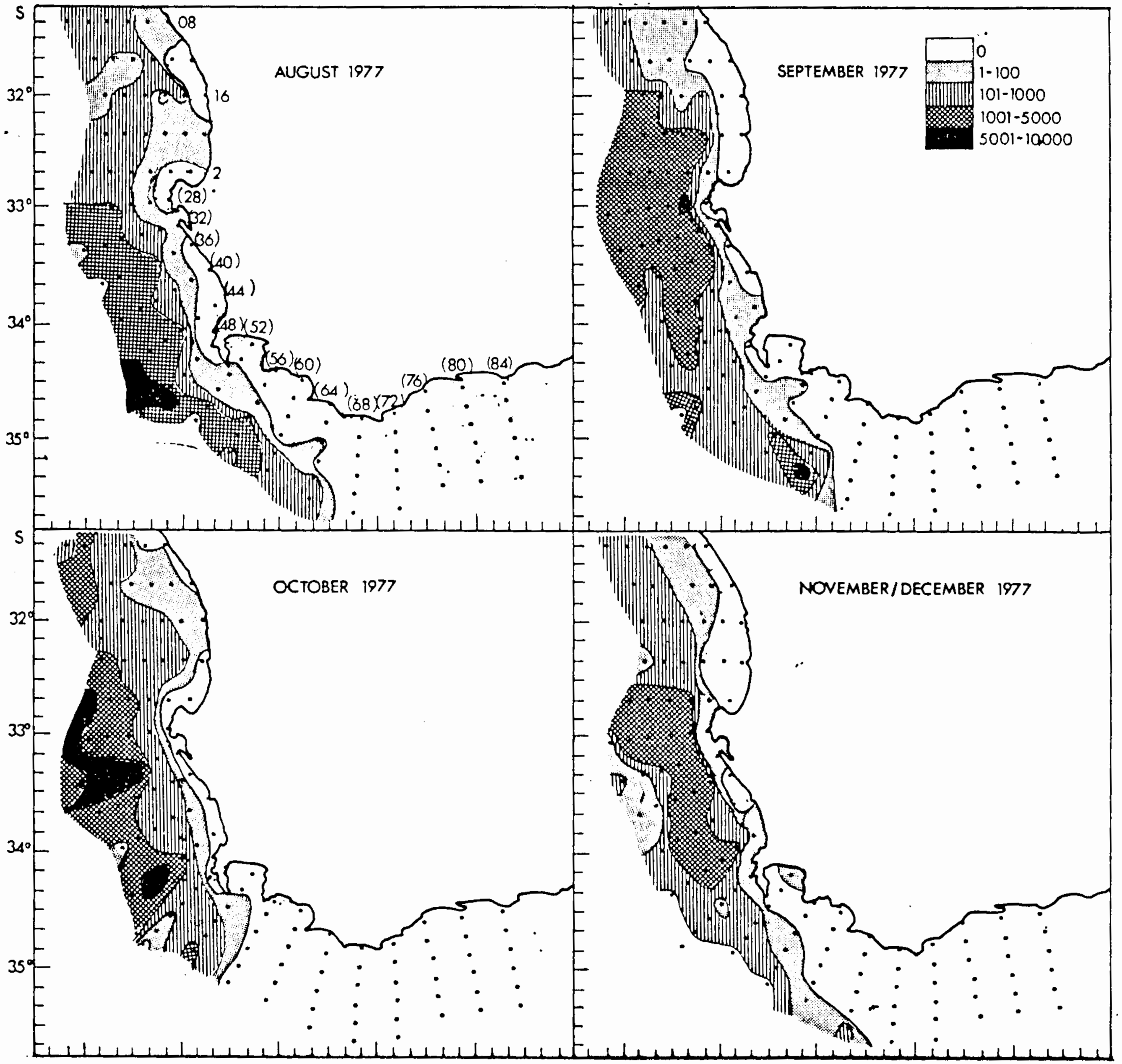


Fig. 3.7: Monthly horizontal distribution of M. muelleri eggs over the CELP grid.

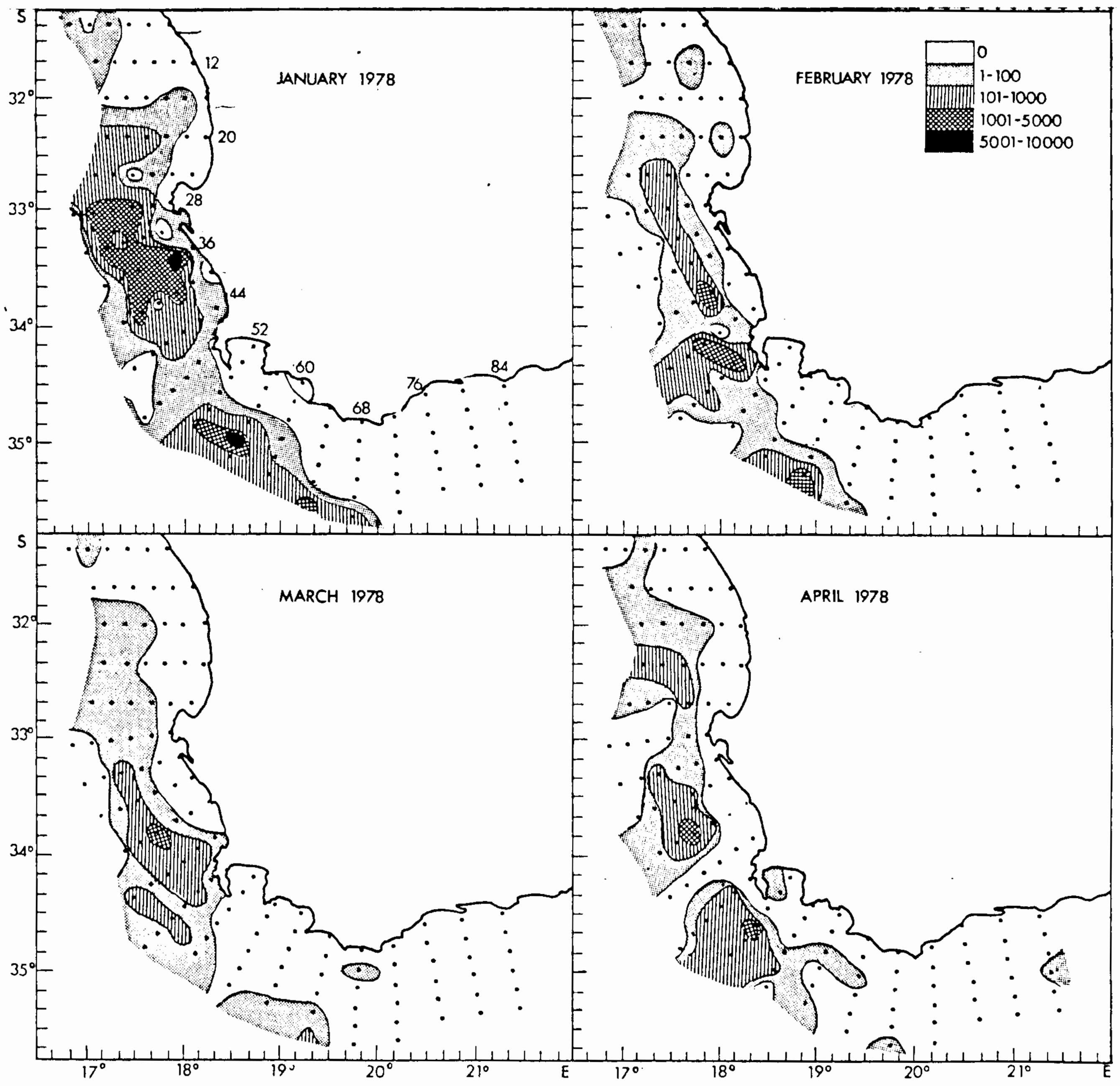
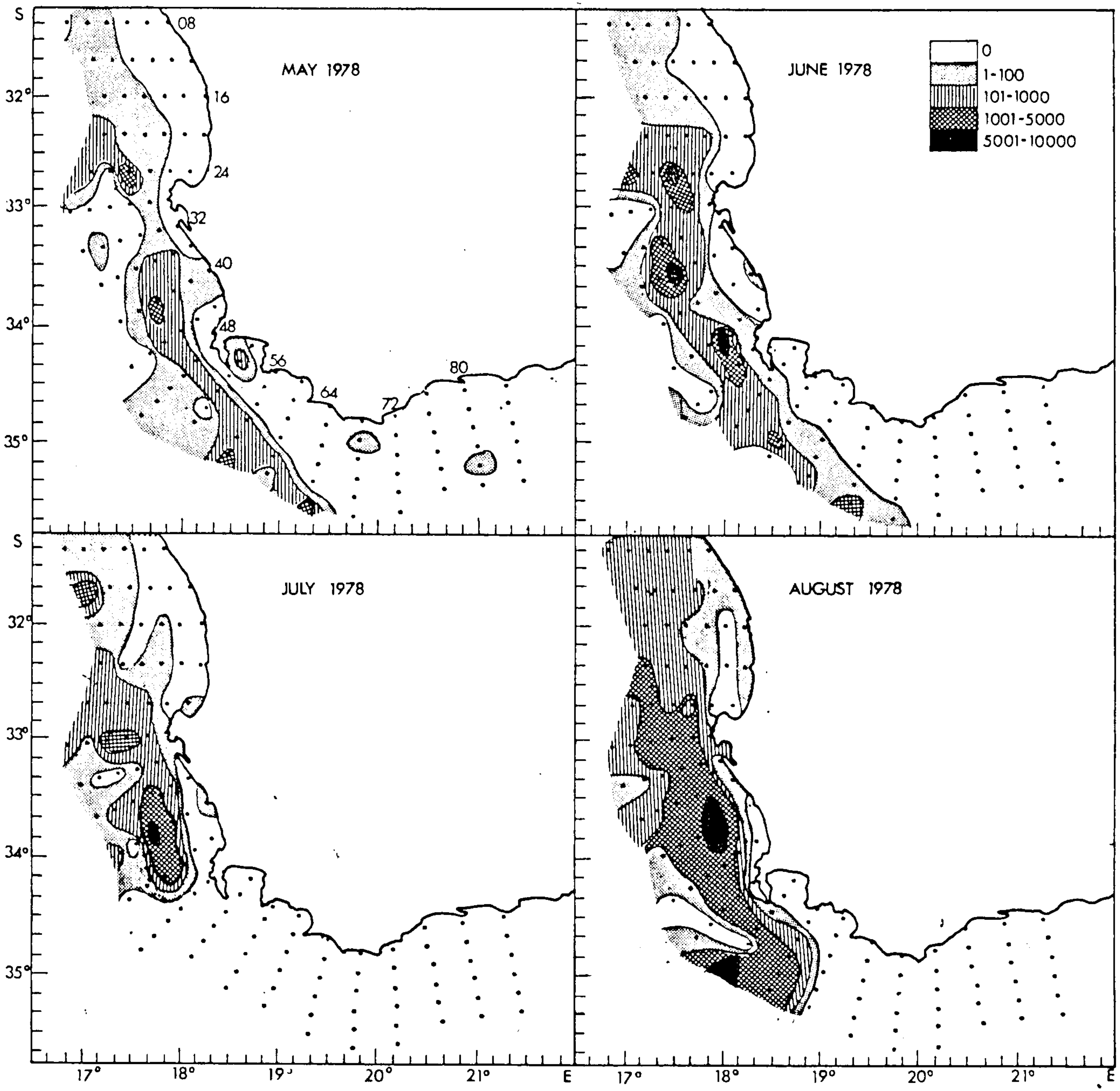


Fig. 3.7: Continued.



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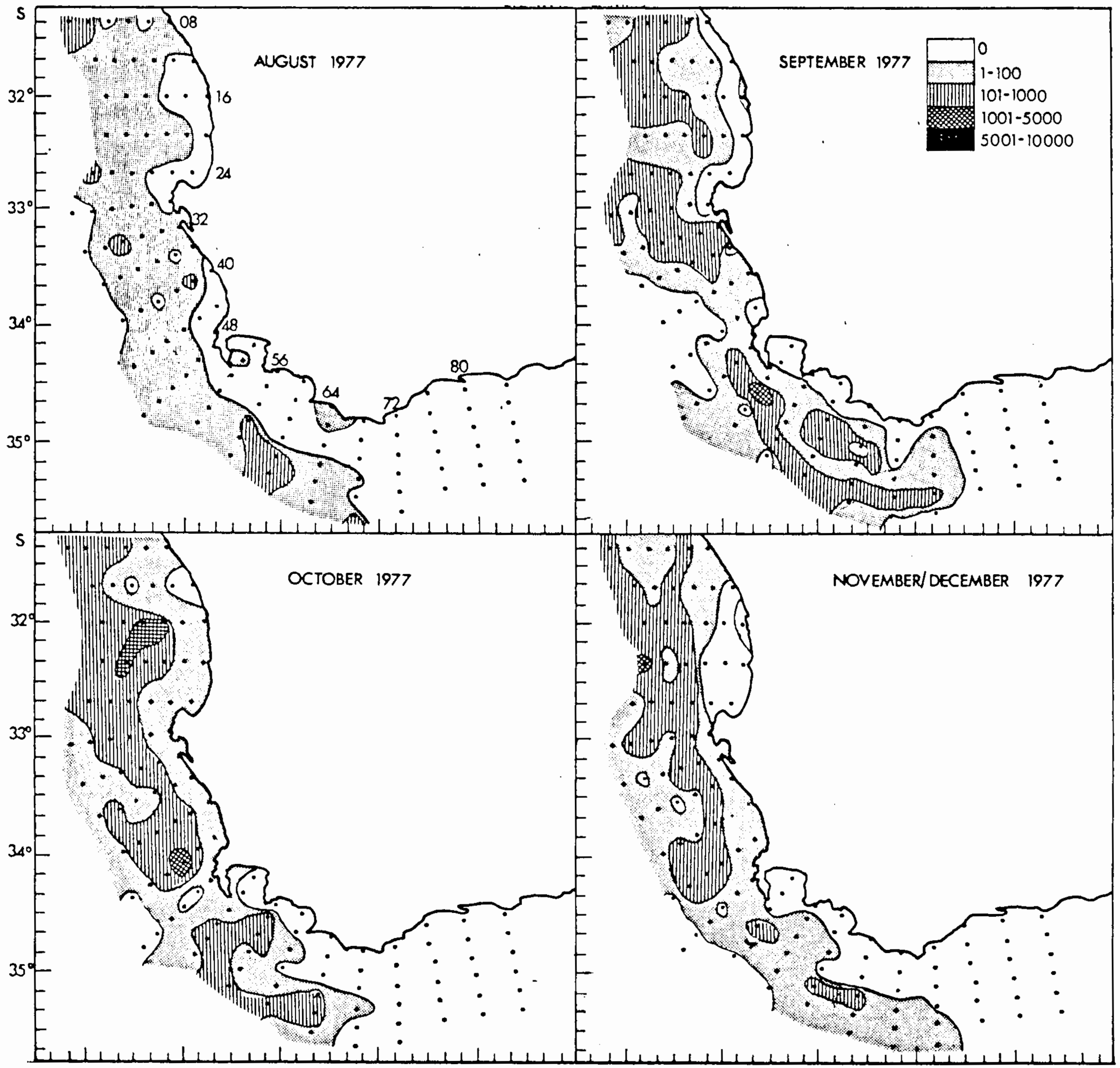
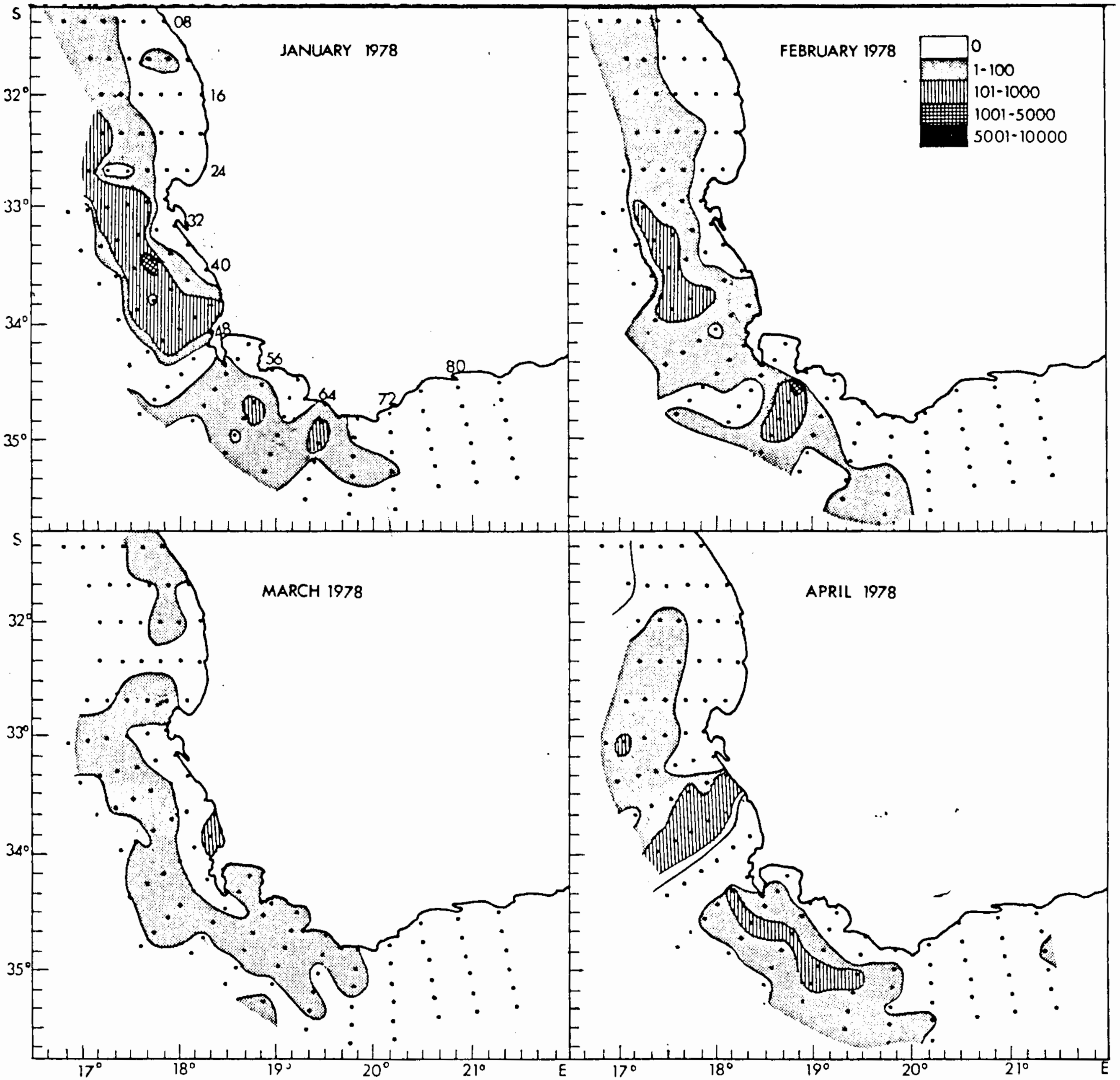


Fig. 3.8: Monthly horizontal distribution of *M. muelleri* larvae over the CELP grid.



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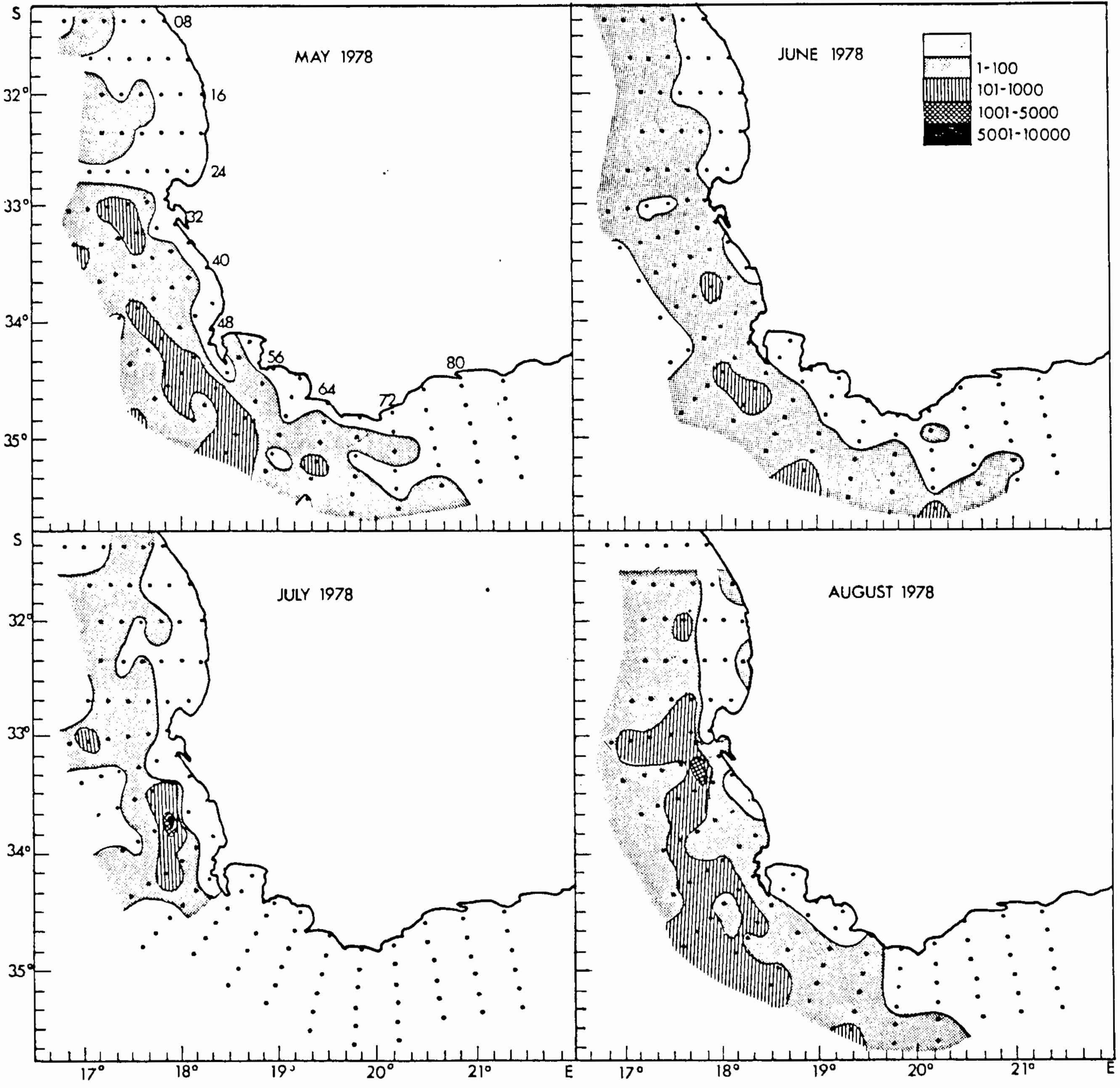

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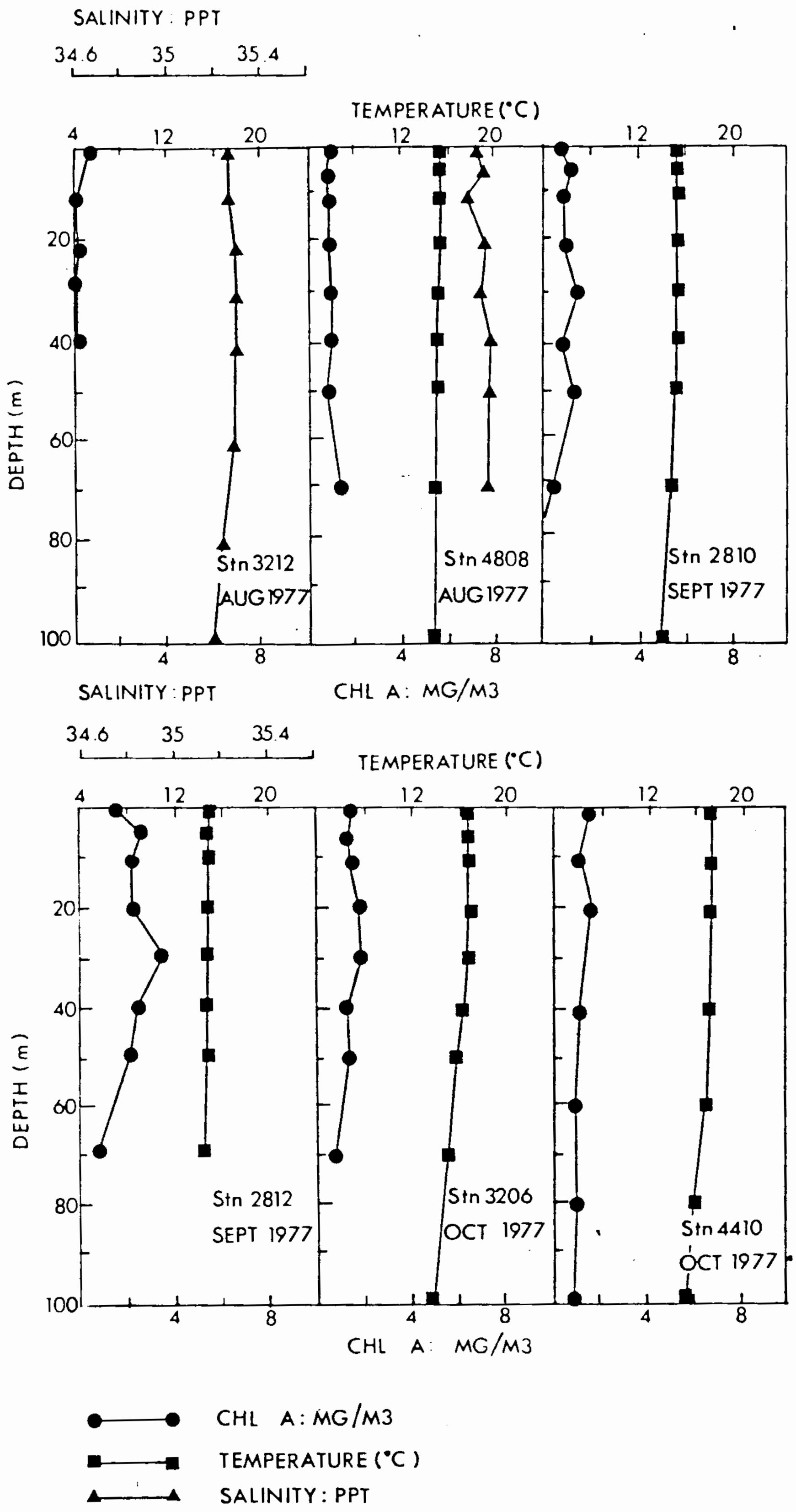

Fig. 3.9: Temperature, salinity and chlorophyll. A measurements at CELP stations where high concentrations of *M. muelleri* eggs were present.

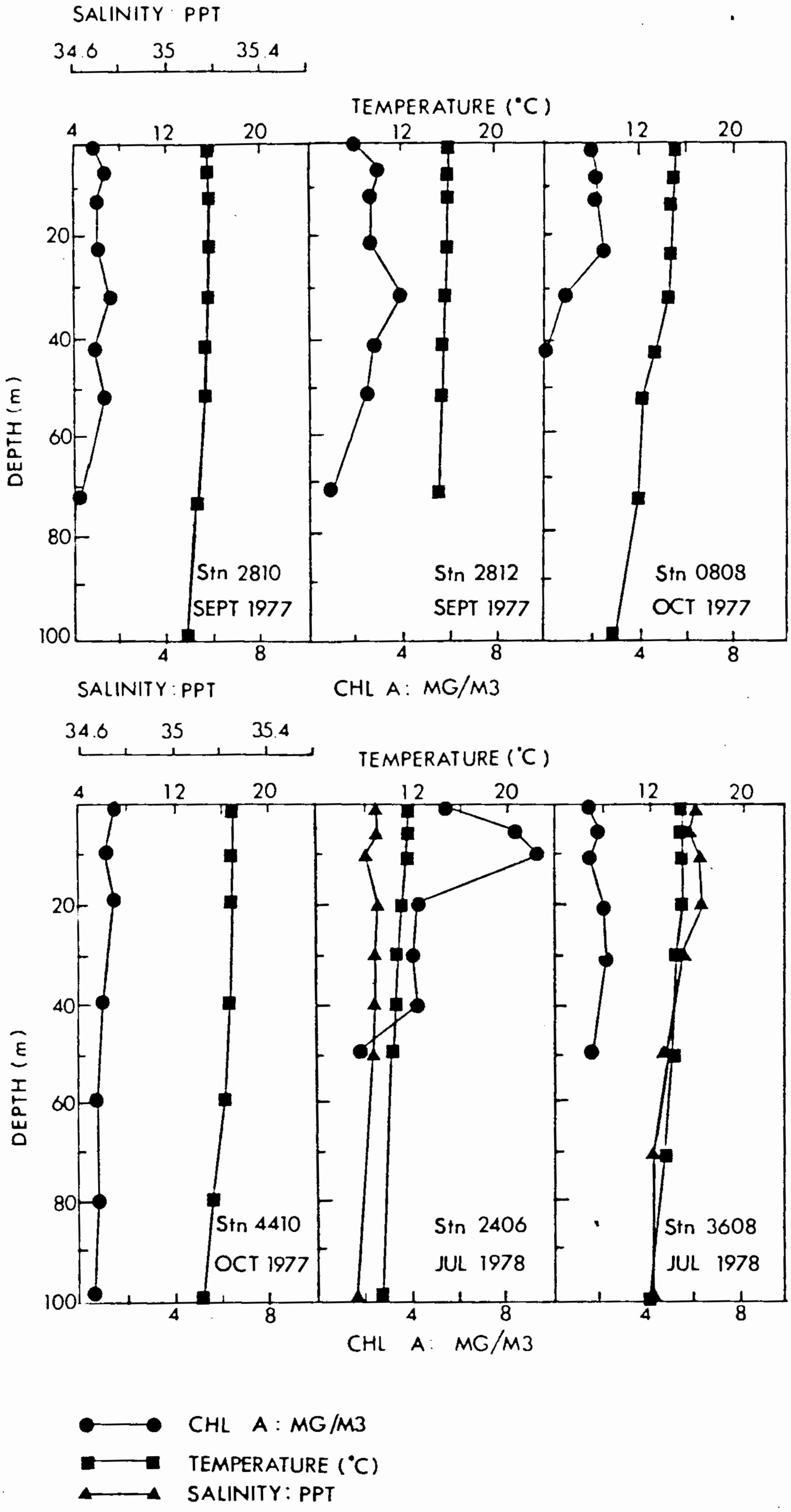

Fig. 3.10: Temperature, salinity and chlorophyll. A measurements where high concentrations of *L. hectoris* eggs were present.

M. muelleri eggs and larvae were the most and fifth most abundant respectively out of 103 species identified in the CELP samples, and *L. hectoris* eggs and larvae were fourth and second most abundant respectively (Shelton, Sea Fisheries Research Institute, Cape Town, personal communication). In an attempt to determine the environmental conditions in which light- and lanternfish eggs occur, the temperature, chlorophyll A and salinity were plotted for the stations with the highest egg count during the spawning months. This data is presented in Figs 3.9 and 3.10.

Large concentrations of lightfish eggs occurred in well-mixed oceanic water with a temperature range of 14,0 to 17,0 ^{0}C and a salinity range of 35,3 to 35,4 parts per thousand (Fig. 3.9). Chlorophyll A values ranged from 0 to 4 mg/m which can be classified as moderate values for the Benguela region (Hutchings, Sea Fisheries Research Institute, personal communication).

Large concentrations of lanternfish eggs also occurred at three stations where large concentrations of lightfish were found. All the stations shown in Fig. 3.10 suggests that large concentrations of lanternfish eggs were also found in well-mixed oceanic water. The temperature range was 9 to 17 ^{0}C, whilst salinity ranged from 34,8 to 35,2 parts per thousand. The chlorophyll A range was larger than that for lightfish and ranged from 0 to 9 mg/m. The largest chlorophyll values were encountered in the top 20 m (Fig. 3.10).

3.4 DISCUSSION

Recent Sea Fisheries Research Institute cruises have revealed that the CELP grid did not cover the total spawning area of the South African anchovy (Engraulis japonicus) (Hampton et al, 1985 and Armstrong et al, 1985). Figs 3.5, 3.6, 3.7 and 3.8 also indicate that for certain months spawning of light- and lanternfish extended beyond the grid. However, the results obtained do give an accurate description of the months during which lightfish and lanternfish spawning occurred and the horizontal distribution of the eggs and larvae within 50 nautical miles of the coast.

L. hectoris spawning off South Africa is consistent with observations made for Myctophidae in temperate and subtropical regions. Spawning occurs throughout the year, but mainly during the late winter to early summer with a peak in spring (Fig. 3.4). As previously mentioned, Robertson (1977) also documented peak spawning in spring for L. hectoris in New Zealand waters. The only month to be repeated during the survey, August, illustrates that differences in spawning intensity do occur eg. the L. hectoris egg count in August 1977 was approximately 8 % of the annual total whereas in August 1978 this had increased to 35 %. The reasons for this are not clear, but may be due to earlier spawning in 1978 or more extensive spawning offshore in 1977 in areas not covered by the grid. Alternatively the actual intensity of the spawning effort may have been lower.

The total larval count for each month as shown in Table 3.3 indicate that the number of larvae were higher than the eggs for nine out of twelve months. Although inefficient sampling of the eggs may be responsible for some of the difference it is unlikely to account for the larger differences eg. in August 1977 there were fifteen times more larvae than eggs in the samples. A probable

Table 3.3: Total number of *L. hectoris* eggs and larvae sampled for each month during the CELP survey. The egg and larval counts were standardized as discussed in the text.

Months	Eggs	Larvae
August 1977	9 306	137 207
September	34 578	87 621
October	15 150	28 104
November/December	1 275	1 356
January 1978	39	18
February	3	140
March	50	231
April	264	184
May	219	553
June	6 892	2 300
July	11 428	42 809
August	42 027	45 417
Total	121 231	345 940

Table 3.4: Total number of *M. muelleri* eggs and larvae sampled for each month during the CELP survey. The egg and larvae counts were standardized as discussed in the text.

Months	Eggs	Larvae
August 1977	85 208	3 051
September	83 099	13 004
October	135 830	19 458
November/December	49 894	10 978
January 1978	45 795	8 795
February	8 319	4 589
March	4 821	2 698
April	11 122	3 795
May	12 828	4 675
June	40 304	3 319
July	36 019	8 842
August	108 407	8 250
Total	621 646	91 455

explanation is that spawning occurs offshore and prevailing currents disperse the eggs resulting in larvae being pushed closer inshore. The more widespread distribution of the larvae supports this view. However, since it is known that eggs are in the plankton for only a few days while larvae are in the plankton for a longer period (Shelton, Sea Fisheries Research Institute, Cape Town, personal communication) the difference in numbers between eggs and larvae may be a normal occurrence.

M. muelleri spawning is more evenly distributed throughout the year, with a peak in spring/early summer (Fig. 3.3). This spawning pattern is in agreement with that found off Norway and New Zealand and in the Japan Sea (Table 3.2). In New Zealand waters, eggs of *M. muelleri* were taken during all months except April to July, indicating a long spawning season from late winter to early autumn. Egg densities were highest in spring and summer. Spawning in that population was found to be centred around 1200 hrs in the depth interval of 250 - 500 m and in water temperature of 9,0 ^{0}C (Robertson 1976). *M. muelleri* eggs off South Africa were found to occur almost entirely below the thermocline at depths greater than 40 m and hatching of lightfish larvae only occurred above 8,5 ^{0}C and, development was particularly sensitive to temperatures between 12 ^{0}C and 15 ^{0}C. Above 16,9 ^{0}C all larvae that hatched were deformed (Shelton 1979).

M. muelleri is a typical midwater migrant, in the Japan Sea the shoals are found at depths of 150 to 250 m during the day rising to 50 m less at night (Okiyama 1971). This diurnal vertical migration was also observed off the South African coast (Sea Fisheries Research Institute, Cape Town, unpublished). If spawning does occur during day time the eggs would be fertilized at the lower level of this vertical range and would take many hours to rise to the surface, as the uneven surface of the chorion would increase the surface drag, resulting in a decrease in the rate of ascent. Robertson (1981) measured the sinking rates of preserved eggs to observed the effects of sculpturing on movement through water. M. muelleri with its extensive sculpturing sank at 41 % of the rate expected of a smooth egg of the same density and diameter. One can thus infer that living sculptured eggs may ascend at a lower rate than smooth eggs of the same density, if the densities of smooth and sculptured eggs are similar. As pointed out by Robertson (1981) there is a trend for deeper water species to produce larger eggs which may reflect a need for eggs to ascend more rapidly to cover the much greater distance to the warmer, highly productive surface waters, than that experienced by shallow spawning species. Furthermore, if it is advantageous for M. muelleri eggs to ascend slowly (assuming that is the reason why the eggs are sculptured), then why has this species not persisted with small eggs as have myctophids, such as L. hectoris, living in similar habitats?

Unfortunately, the conditions under which lanternfishes reproduce are not yet known, although the larvae of this family are very numerous and more abundant than those of other bathypelagic fishes. Myctophid eggs sampled in the Scotia Sea (in between the Falklands and South Orkney Islands, approximately between 50^0 and 60^0 S) occurred exclusively between 200 and 500 m. The temperature range at 200 m was 0,28 to 1,81 ^{0}C and at 500 m was 1,42 to 2,44 ^{0}C (Yefremenko 1977). However, these temperature parameters cannot be applied to all species.

It is not possible to properly compare the temperature, salinity and chlorophyll values in the present study with those found elsewhere since the few studies done were at greater depths and/or different latitudes. Lightfish eggs sampled off New-Zealand occurred at 100 - 500 metres, with most of the eggs at the depth interval 100 - 250 m, where a temperature of 9,5 - 9,0 ^{0}C and salinity of 34,6 to 34,5 parts per thousand was measured (Robertson 1976). The temperatures measured in this study (14 to 17 ^{0}C) are consistent with that found by Shelton (1979), who concluded that lightfish larval development was particularly sensitive to temperatures between 12 ^{0}C and 15 ^{0}C. Hatching only took place above 8,5 ^{0}C, and above 16,9 ^{0}C hatched larvae were deformed. Since the upper range of the temperature measured in this study was 17 ^{0}C it may be concluded that temperature does not seriously influence the development of lightfish larvae off the South African coast.

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CHAPTER 4

THE MATURITY AND FECUNDITY OF THE LANTERNFISH LAMPANYCTODES HECTORIS AND THE LIGHTFISH MAUROLICUS MUELLERI

4.1 INTRODUCTION

Few mesopelagic fishes have been studied to estimate age at maturity and fecundity, indeed our knowledge in this field is mainly confined to a few species of Myctophidae and Sternoptychidae.

4.1.1 AGE AND SIZE AT MATURITY

In subtropical and tropical waters the small myctophid fishes *Notolychnus valdiviae*, *Benthosema suborbitale*, *Diaphus schmidti*, *D. anderseni* and *Lobianchia dofleini* attain sexual maturity about one year after hatching at 25 to 40 mm caudal length, and the medium-sized myctophids *Benthosema pteroteum*, *B. fibulatum* and *Diaphus suborbitalis* at 50 to 70 mm caudal length. The spawning behaviour of many other medium-sized species in the subtropical and tropical waters remains to be determined. On the basis of growth rates, they probably become sexually mature one year after hatching in highly productive areas, but in areas of low productivity may take more than two years (Clarke 1973, Karnella and Gibbs 1977, Gjøsaeter and Kawaguchi 1980). It is not clear from the literature whether in areas of low productivity growth is slower so that it takes two years to reach size at maturity, or whether it is a compensatory mechanism affecting age at maturity, such that the species maximizes its reproductive output when more food becomes available, that is "niche size" increases and the species responds to accelerate its rate of colonization.

The larger myctophid fishes, such as *Lampadena luminosa*, *Bolinichthys superlateralis* and *Notoscopelus caudispinosus*, appear to take more than two years to reach sexual maturity at 70 to 100 mm caudal length (Clarke 1973). In temperate or subarctic waters both larger species such as, *Stenobrachius leucopsarus* and medium-sized ones, for example *Benthosema glaciale*, take two to four years after hatching to attain sexual maturity (Halliday 1970; Smoker and Pearcy 1970 and Gjøsaeter and Kawaguchi 1980).

Hulley (1981) recorded the size at maturity for about 120 Myctophid species caught during the research cruises of FRV "Walther Herwig" in the Atlantic Ocean. A number of these were caught in the Benguela Current System, eg. *Lobianchia dofleini* attains a length of about 50 mm and may be sexually mature from about 31 mm, and *Diaphus meadi* attains a length of about 47mm and may be sexually mature from about 36 mm.

In the family Sternoptychidae, the smaller species, such as *Valenciennellus tripunctulatus* and *Danaphos oculatus*, mature within one year at 25 and 30 mm respectively (Clarke 1974). *M. muelleri* attains the same length as these species.

4.1.2 FECUNDITY

Pertseva-Ostroumova (1973) investigated the reproduction of a number of Myctophidae. The myctophids Symbolophorous evermanni, Myctophum nitidulum, Triphoturus mexicanus and Hygophum sp. have four size groups of eggs in mature ovaries, (i) small oocytes less than 0,05 mm in diameter, (ii) yolkless oocytes of 0,05 - 0,2 mm, (iii) eggs 0,25 - 0,45 mm in diameter and (iv) mature eggs between 0,54 and 0,6 mm in diameter. He concluded that spawning is intermittent in these species.

Gjøsaeter and Kawaguchi (1980) summarised the total fecundity counts of some fishes of the families Myctophidae and Sternoptychidae (Table 4.1). Although these values give an indication of fecundity they should be treated with caution as some of the myctophid counts relate solely to the quantity of mature or large maturing eggs and do not therefore accurately reflect the total fecundity (Pertseva-Ostroumova 1973). A log-log regression of mean fecundity on mean length for the myctophid species listed in Table 4.1 was developed by Gjøsaeter and Kawaguchi (1980). The equation is $\ln \bar{F} = -5{,}11 + 3{,}16 \ln \bar{L}$, where $\bar{L}$ is mean total length in millimetres and $\bar{F}$ is mean fecundity in numbers. This relationship is shown in Fig. 4.1.

The fecundity of M. muelleri sampled in other ecosystems is shown in Table 4.1. The first count shown (109 - 331) originate from fish sampled in the Japan Sea by Okiyama (1971) who estimated that each individual spawns at least twice in a lifetime and that the number of eggs per single spawning seems to be less than about 300. Badcock (1984) notes that 200 - 5000 eggs per ovary

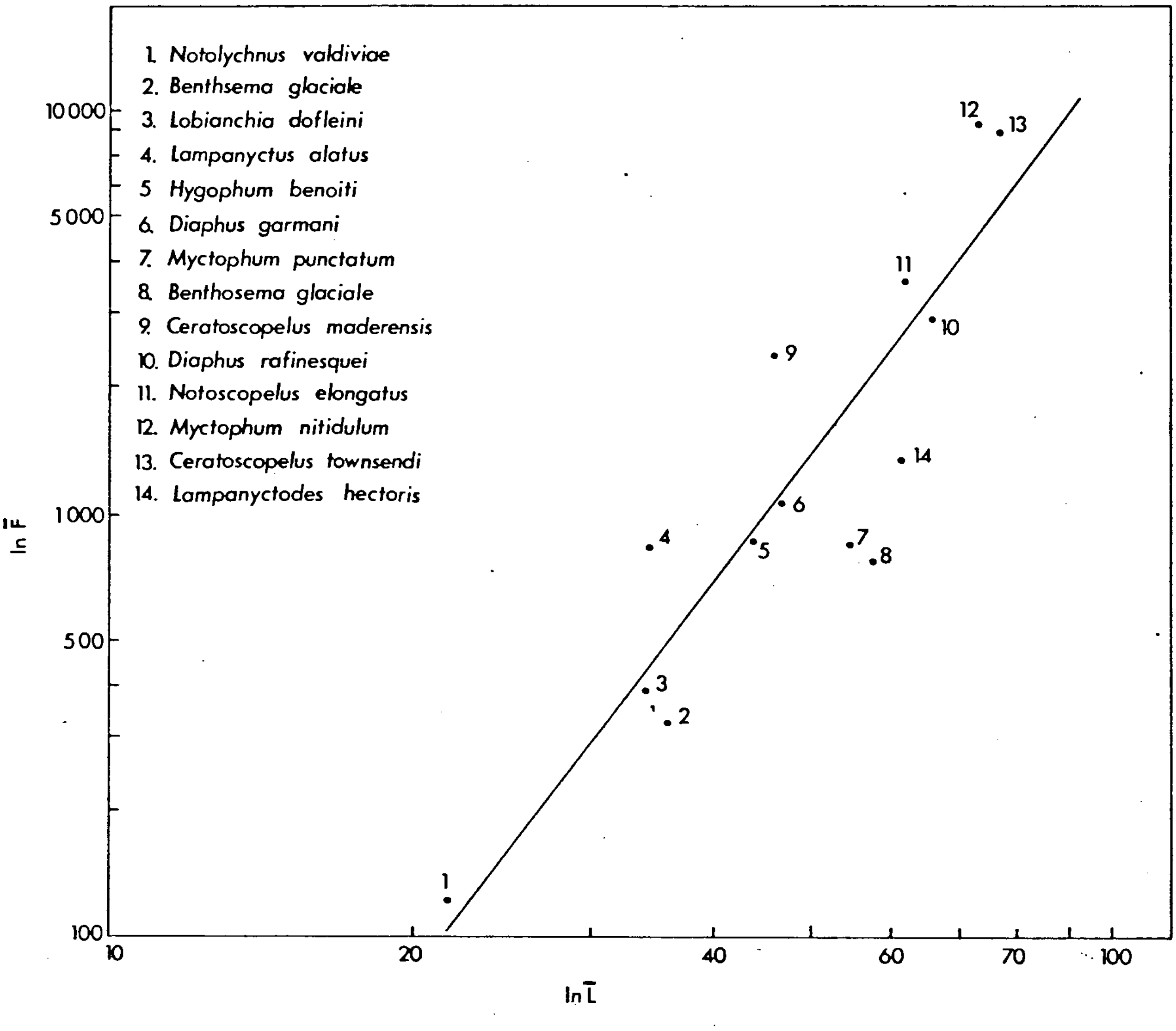


Fig. 4.1: Log-log regression of mean fecundity on mean length for the myctophid species listed in Table 4.1. The result for *L. hectoris* is also indicated.

Table 4.1: Total fecundity of some fishes of the families Myctophidae and Sternoptychidae (adapted from Gjøsaeter and Kawaguchi 1980).

Species	Number of fish	Length (range) (mm)	$\bar{F}$(range) (in numbers)
MYCTOPHIDAE			
Benthosema glaciale	6	36,0(32-40)	323(191-467)
B. glaciale	28	57,7(45-75)	781(162-1964)
Ceratoscopelus maderensis	1	46	2387
C. townsendi	2	77,2(72,3-82,0)	8000(5150-10850)
Diaphus garmani	20	46,3(41-55)	1085(350-1900)
Diaphus rafinesquei	1	66	2950
Lampanyctus alatus	2	34,5(30-39)	837(718-955)
Lobianchia dofleini	4	34,0(31-40)	388(330-484)
Hygophum benoiti	4	43,8(42-45)	882(849-1273)
Myctophum nitidulum	5	73 (72-78)	ca.8500(8000-9000
M. punctatum	3	54,7(51-61)	852(792-929)
Notolychnus valdiviae	1	22	100
N. valdiviae	1	22	120
Notoscopelus elongatus	1	62	ca.3600
STERNOPTYCHIDAE			
Maurolicus muelleri	7	(42,0-47,8)	(109-331)
M. muelleri	15	50,8(47-55)	312(200-500)
Valenciennellus tripunctulatus	?	? (25,5-30)	? (200-350)

pair are present in M. muelleri.

An attempt was made to estimate the length (and age) at maturity, and the fecundity of L. hectoris and M. muelleri. These were then compared with the values for other species discussed above.

4.2 METHODS

4.2.1 SIZE AT MATURITY

Fish sampled from both research and commercial catches were measured, sexed, and staged according to the gonad condition.

Samples of Lampanyctodes hectoris were taken from research cruises conducted in July and August 1982, May, August and November 1983, and April and May 1984. Samples from commercial fleet catches were taken in December 1983, January, February and March 1984. Since the commercial fleet does not land M. muelleri, all samples obtained were taken from the research vessel Africana. The months sampled were July and August 1982, May, August and November 1983 and April and May 1984.

The caudal length (measured from the tip of the nose to the end of the caudal peduncle) of all fish were recorded in two-millimetre length intervals and the gonad developmental stage of each fish was noted. The gonad stages used were those described by Davies (1956) for the South African pilchard and routinely used by the Sea Fisheries Research Institute for all commercially important pelagic fish species. Although ten gonad stages are used for the commercial species it was found that because of the small size of

L. hectoris and M. muelleri only five stages could be identified.

The following is a brief definition of the stage of gonad activity recognized:

Stage 1: Inactive - ovaries either immature or inactive, less than half the length of the body cavity, cylindrical but thin, pale pink or transparent. Testis flat and leaf-like, pink or transparent.

Stage 2: Inactive/Active - ovaries inactive generally, but with the beginning of enlargement taking place. Slight elongation, thickening and darker colouration; mainly translucent, pinkish yellow. Testis beginning to thicken and become elongated with slight white colouration.

Stage 3: Active - ovaries elongated and filling over half the body cavity. Colour opaque yellow with discrete pigmented ova present. Testis elongated, thickened and filling over half the body cavity. Colour opaque white with crenellated edges.

Stage 4: Active/Ripe - ovaries elongated, distended, filling approximately two thirds of the body cavity. Colour bright yellow, gonads vascular, ova discrete and becoming transparent at posterior end. Testis further enlarged, filling approximately two thirds of the body cavity. Colour opaque white; milkiness apparent at posterior end.

Stage 5: Ripe - ovaries almost filling the body cavity. Colour darker yellow, no longer opaque but semi-transparent due to even dispersal of ripe ova throughout the gonad. Testis almost filling the body cavity,opaque white; posterior half of gonad milky.

Although some of the gonads sampled could possibly have been allocated to intermediate categories, especially ripe/running, it is very difficult to identify spent fish even in much larger specimens and the preserved state of the material made a distinction between ripe and ripe/running difficult.

Resting ovaries cannot easily be distinguished from juvenile ovaries. It is, therefore, necessary to obtain data on length at first maturity only at the peak of the spawning season, when it is assured that most adult fish would have active gonads (Le Clus 1977). Therefore scatter diagrams were constructed using only the months of maximum spawning.

4.2.2 FECUNDITY

Active L. hectoris and M. muelleri were used in a fecundity study to determine the number and size range of eggs present. The ovaries were slit open and preserved in Gilson's fluid which breaks down connective tissue, thus releasing oocytes from the ovary (Le CLus 1977). The eggs were then counted and measured to the nearest 0,1 mm using a light microscope fitted with a micrometer eyepiece. The fish weight, before the removal of the ovaries, was also recorded. Eggs from plankton samples for both L. hectoris and M. muelleri were also measured and compared with those taken from the ovaries.

4.3 RESULTS

4.3.1 SEASONAL PATTERNS IN MATURATION

Figs 4.2 and 4.3 show the numbers of fish in each maturity stage for lantern- and lightfish taken during research cruises, respectively. Males and females are shown separately. Most lanternfish are mature in July/August with some gonad activity in May and November/December. No gonad activity is apparent at the beginning of the year. Lightfish gonad activity is apparent throughout the year with a peak in July/August.

4.3.2 MATURITY OGIVES

Scatter diagrams rather than ogives are shown as not enough data in each length group for each sex was available (Figs 4.4 and 4.5). An approximation of length at 50% maturity (fitted by eye), is shown. Figs 4.6 and 4.7 show the percentage of mature fish for each month sampled. The same patterns as observed in Figs 4.2 and 4.3 are apparent. In addition, the difference in spawning activity between the same sampling period in different years can be observed, for example in August 1982 and 1983 for lightfish (Fig. 4.6) and in August 1982 and 1983, and May 1983 and 1984 for lanternfish (Fig. 4.7). However, this difference may be due to the geographic extent of the sampling.

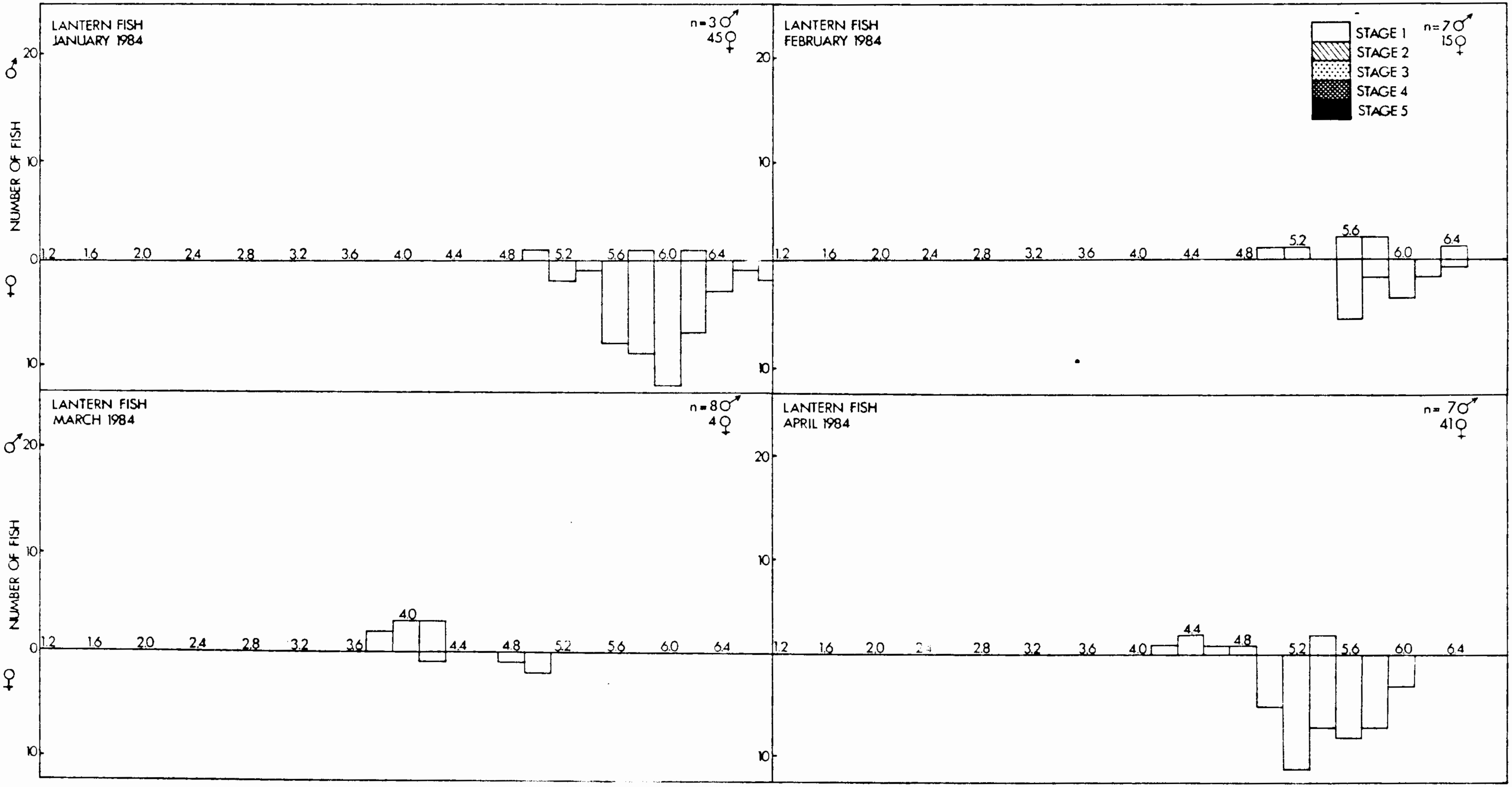


Fig. 4.2: The number of *L. hectoris* in each maturity stage, shown for a number of months. Males and females are shown separately.

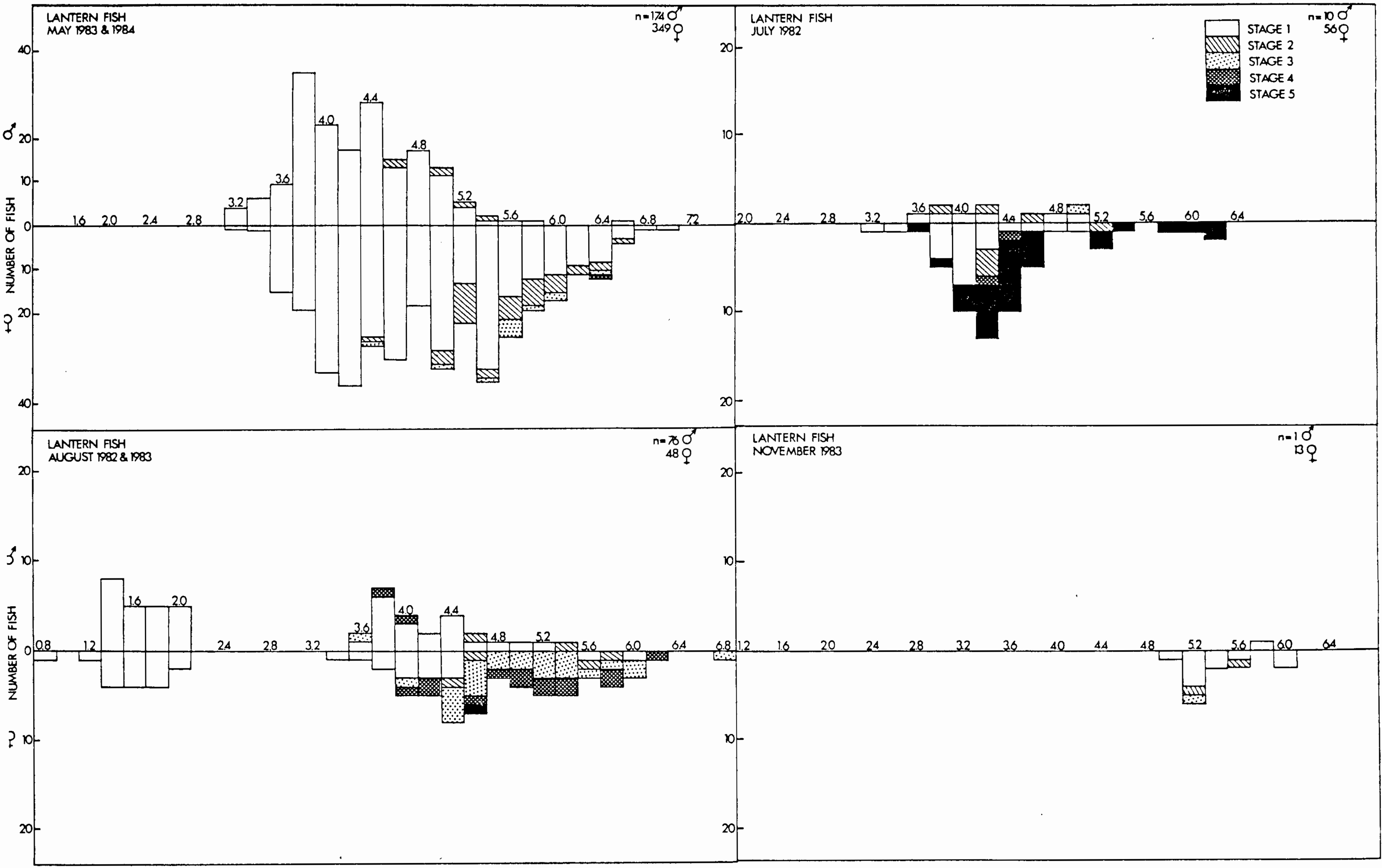
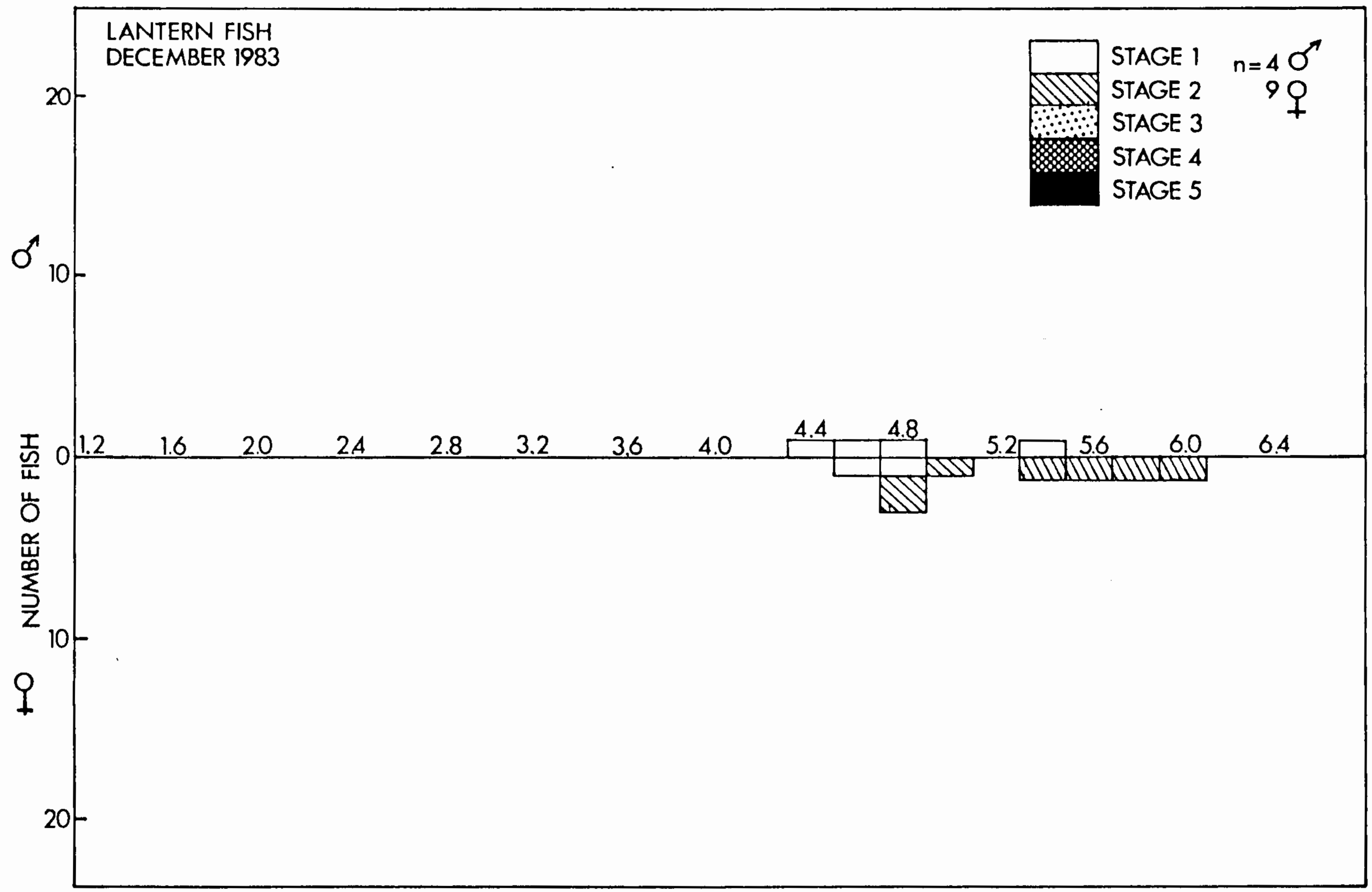


Fig. 4.2: Continued.



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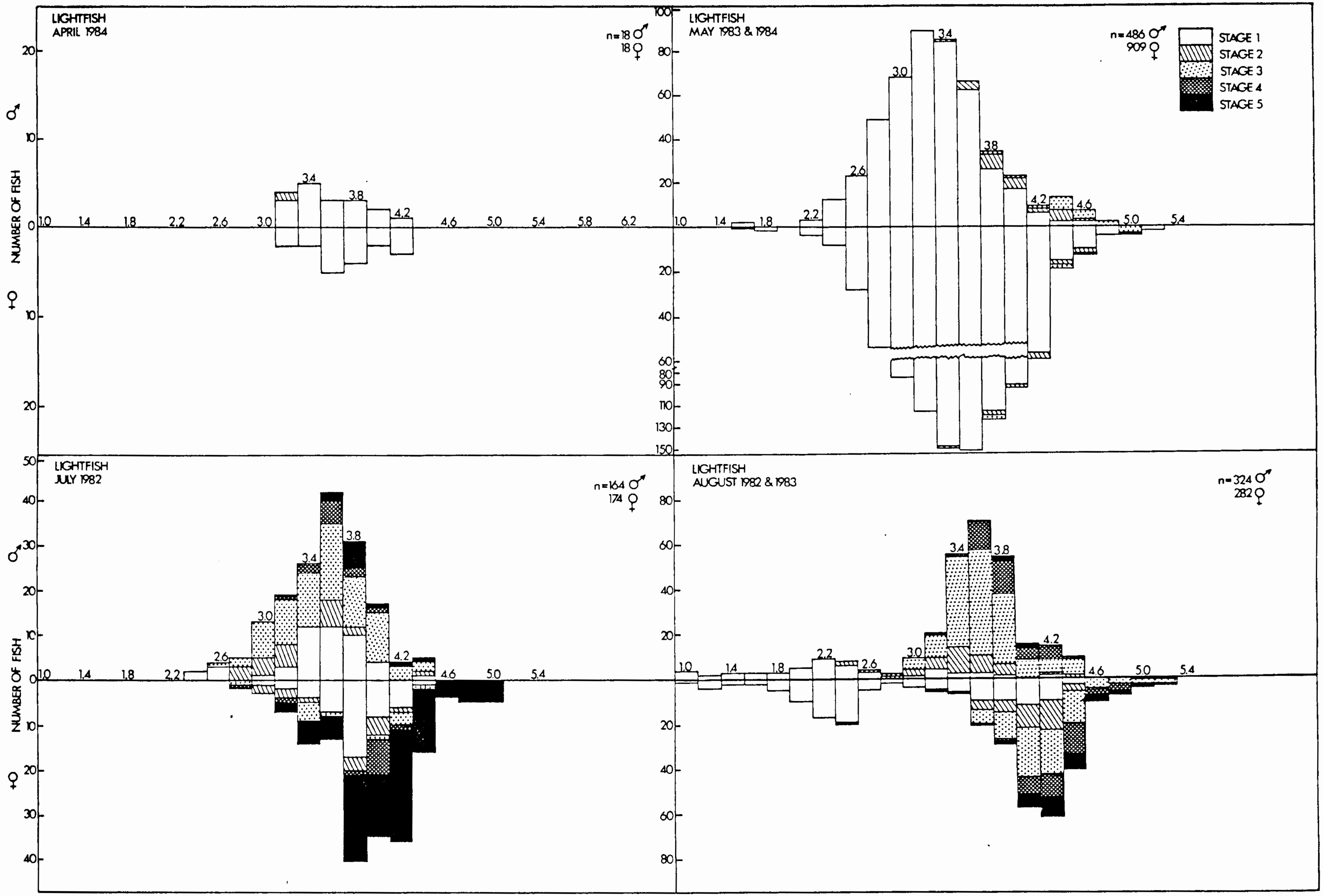


Fig. 4.3: The numbers of M. muelleri in each maturity stage, shown for a number of months. Males and females are shown separately.

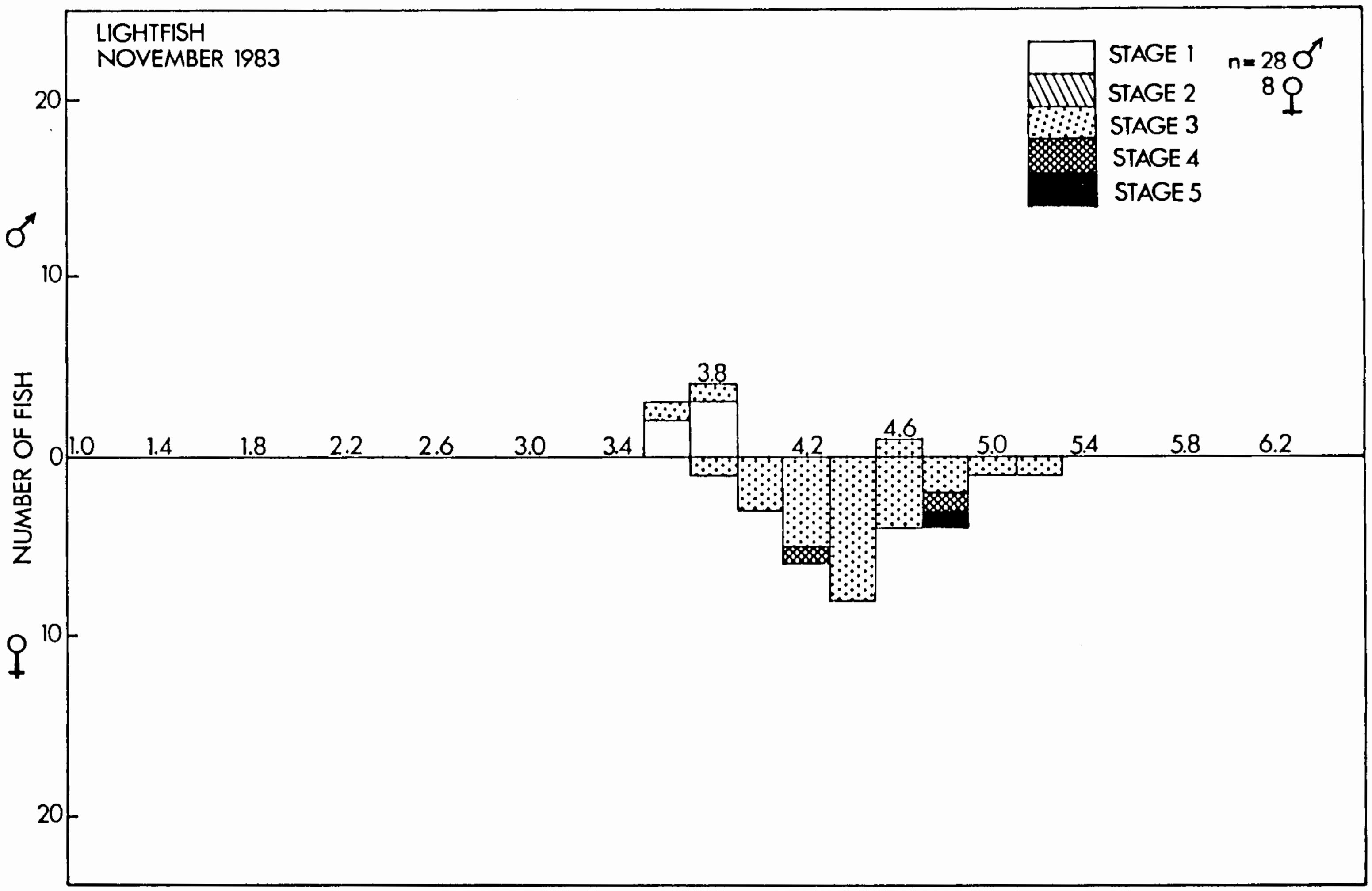


Fig. 4.3: Continued.

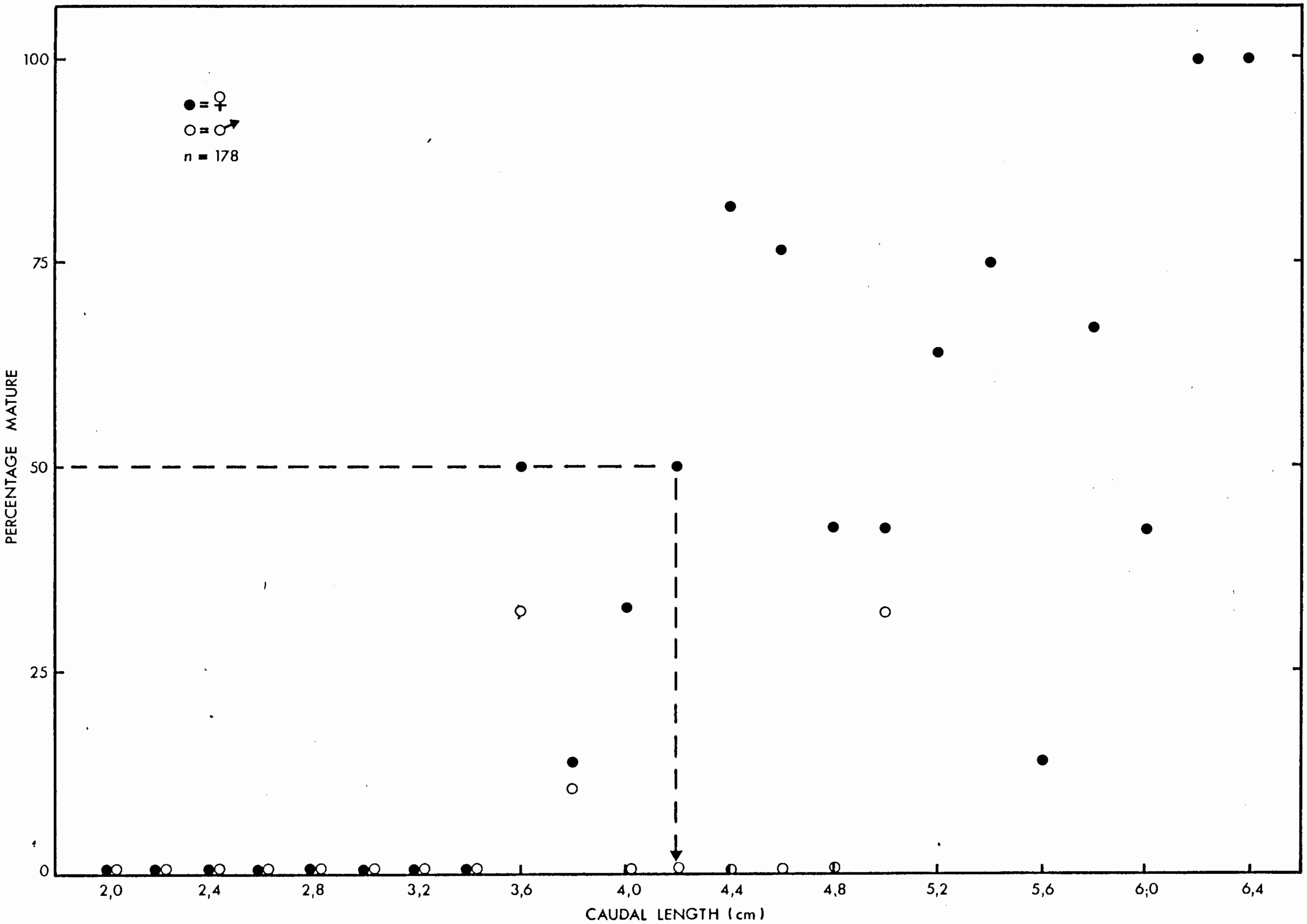


Fig. 4.4: L. hectoris maturity scatter-diagram. The dotted line indicates the approximate length at 50% maturity for females.

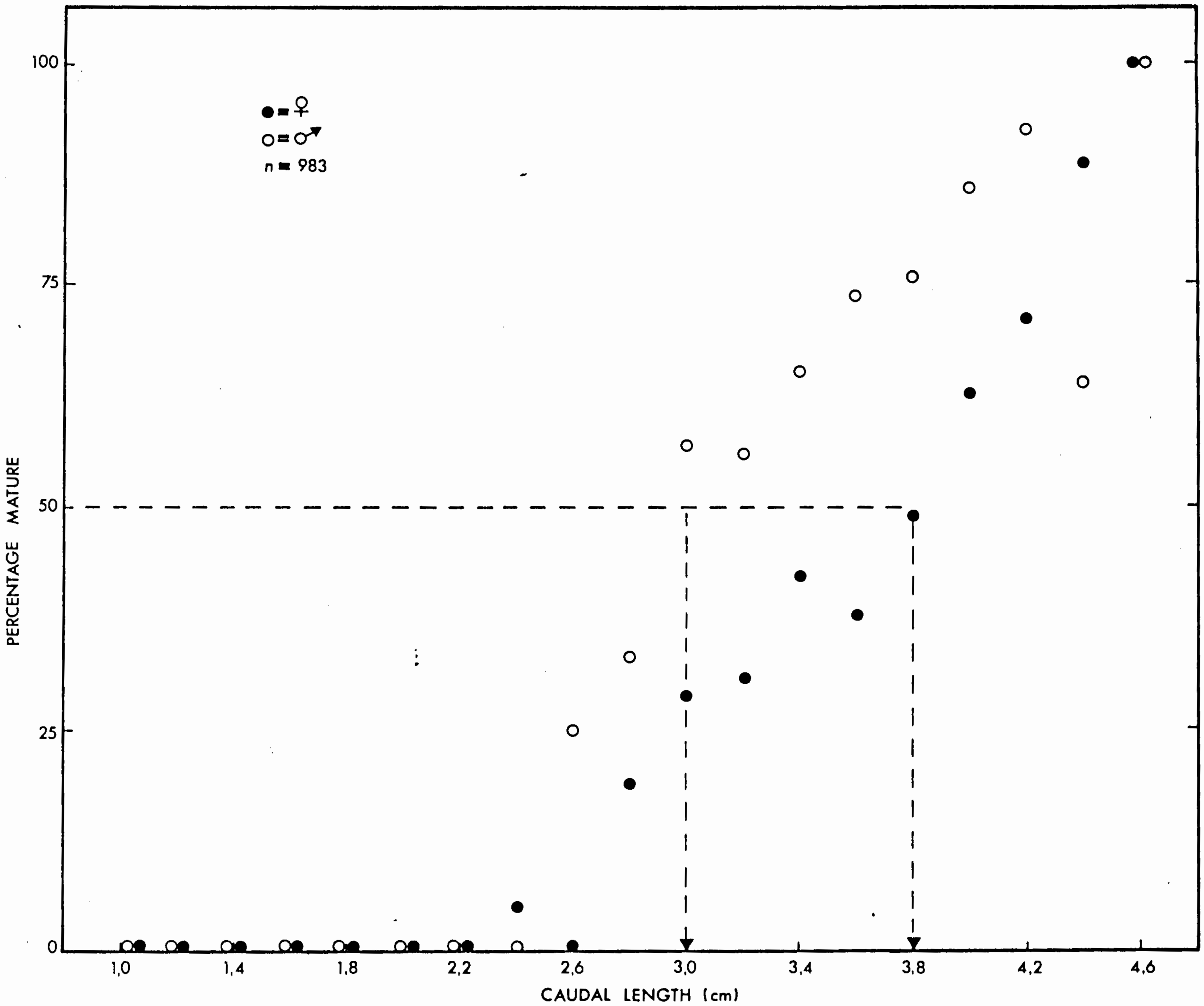


Fig. 4.5: *M. muelleri* maturity scatter diagram. The dotted lines indicate the approximate length at 50% maturity for both males and females.

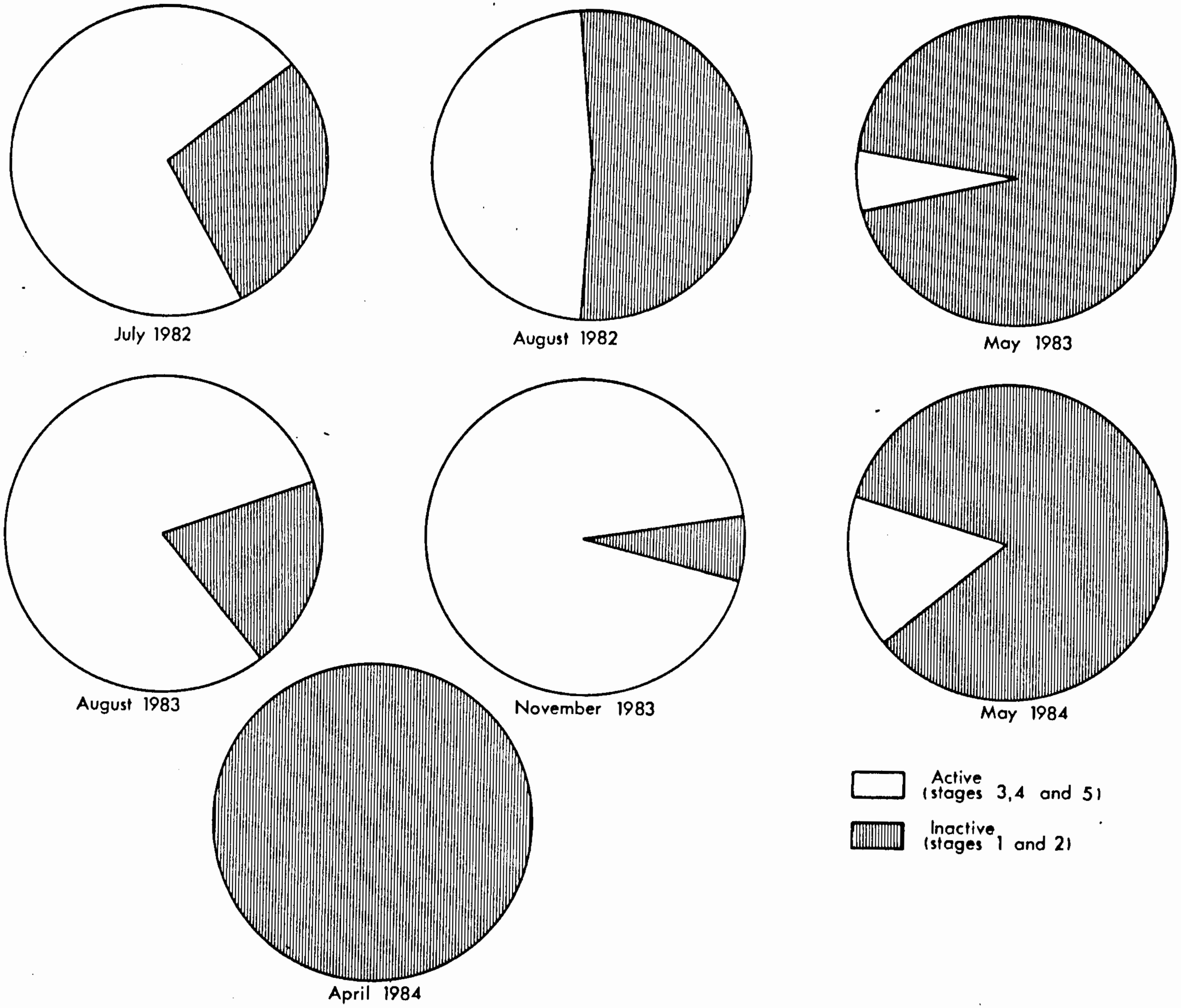
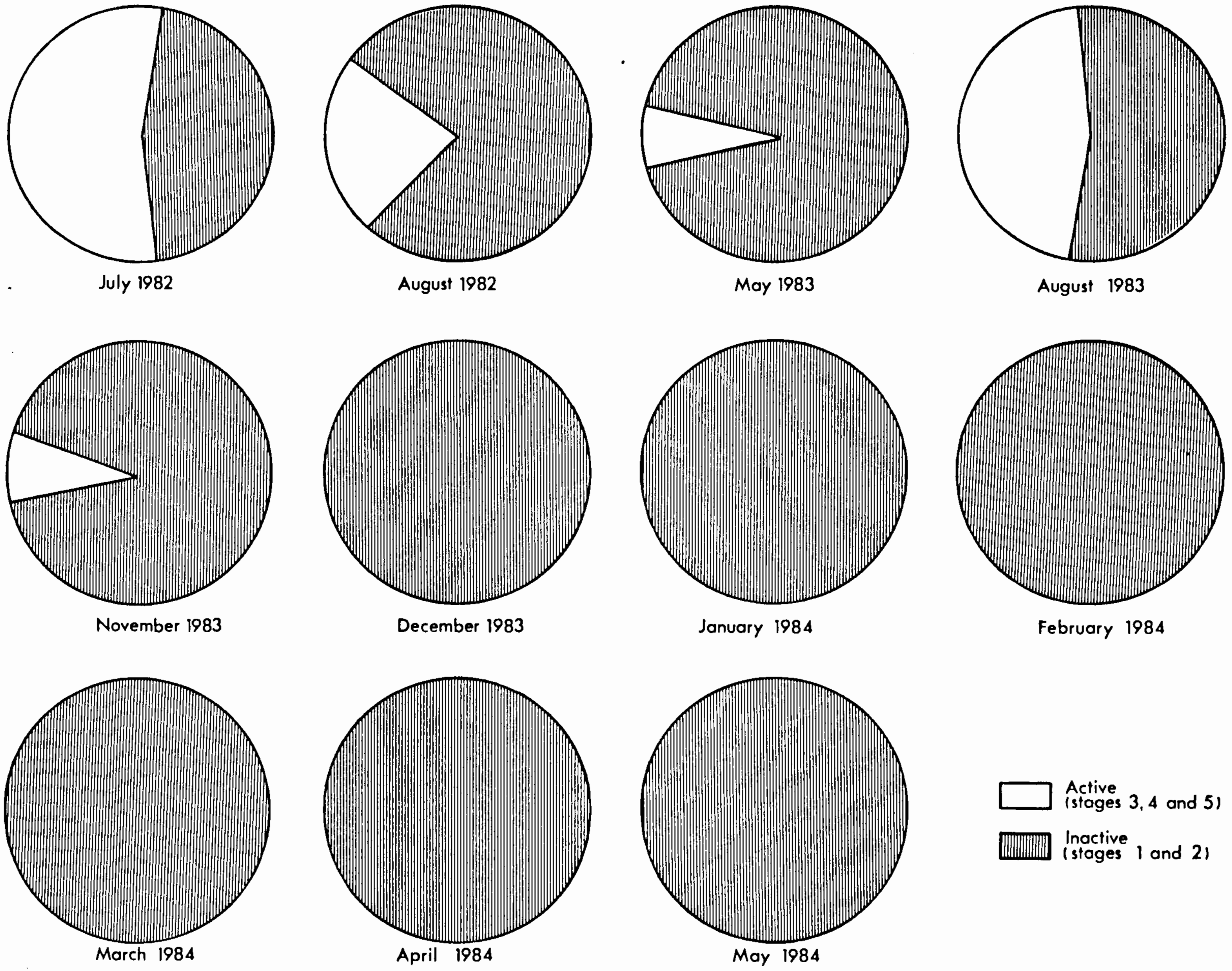


Fig. 4.6: The percentage mature M. muelleri for each month sampled.



<u>Fig. 4.7</u>: The percentage of mature <u>L</u>. <u>hectoris</u> for each month sampled.

4.3.3 COMPARISON BETWEEN MALE AND FEMALE MATURATION AND SEX RATIOS IN THE SAMPLES

Although the sample sizes for certain months are small it can be seen that female lanternfish tend to reach a greater length than males (Fig. 4.2) but the length at first maturity is the same (Fig. 4.4). Lightfish females also attain a larger length than males (Fig. 4.3) but lag behind males in maturing sexually (Fig. 4.5). The male : female ratio by number for all the months sampled was 1:2,4 for lanternfish and 1:1,5 for lightfish.

4.3.4 SIZE DISTRIBUTION OF OVA

The size distributions of planktonic and ovarian M. muelleri eggs are shown in Figs 4.8 and 4.9. Some of the fish sampled had a bi-modal ovarian egg distribution, at approximately 0,15-0,50 mm and at 0,65-1,33. However, the other fish sampled had only one mode situated at approximately 0,80-1,30 mm. The lightfish planktonic eggs sampled are larger and vary between 1,13-2,10 mm. The size distributions of planktonic and ovarian L. hectoris measured are shown in Figs 4.10 and 4.11. The planktonic eggs measured had a very narrow size distribution with a mode at 0,64-0,70 for all months. The lanternfish ovarian eggs measured were smaller and had a wider size distribution.

4.3.5 SPATIAL DISTRIBUTION OF MATURE AND IMMATURE FISH

Fig. 4.12 illustrates the gonad maturity stages sampled at various locations during a research cruise in July 1982. Although spawning occurred over the whole sampling area, maximum spawning was

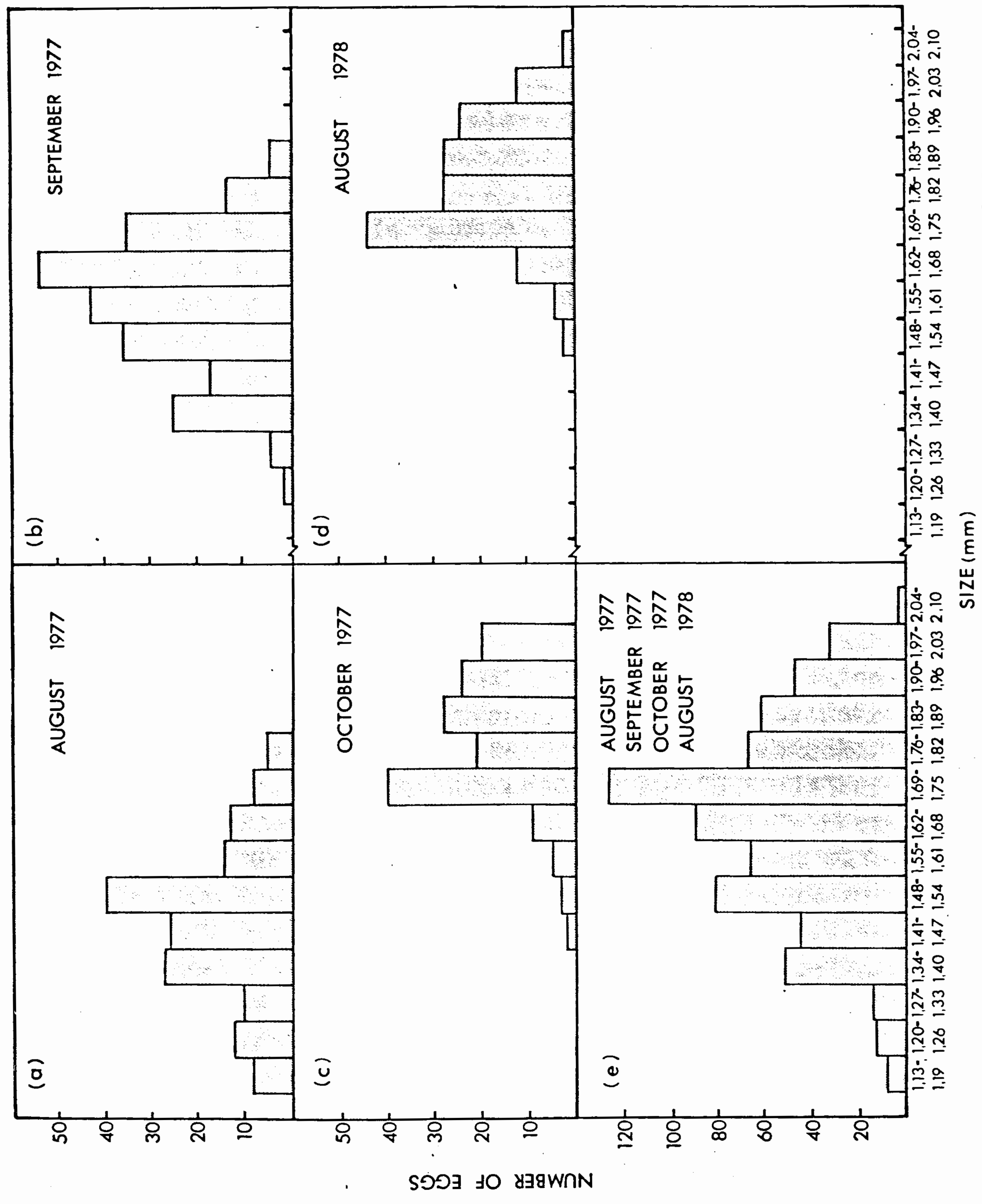


Fig. 4.8: The size distribution of planktonic M. muelleri eggs taken during the CELP cruises.

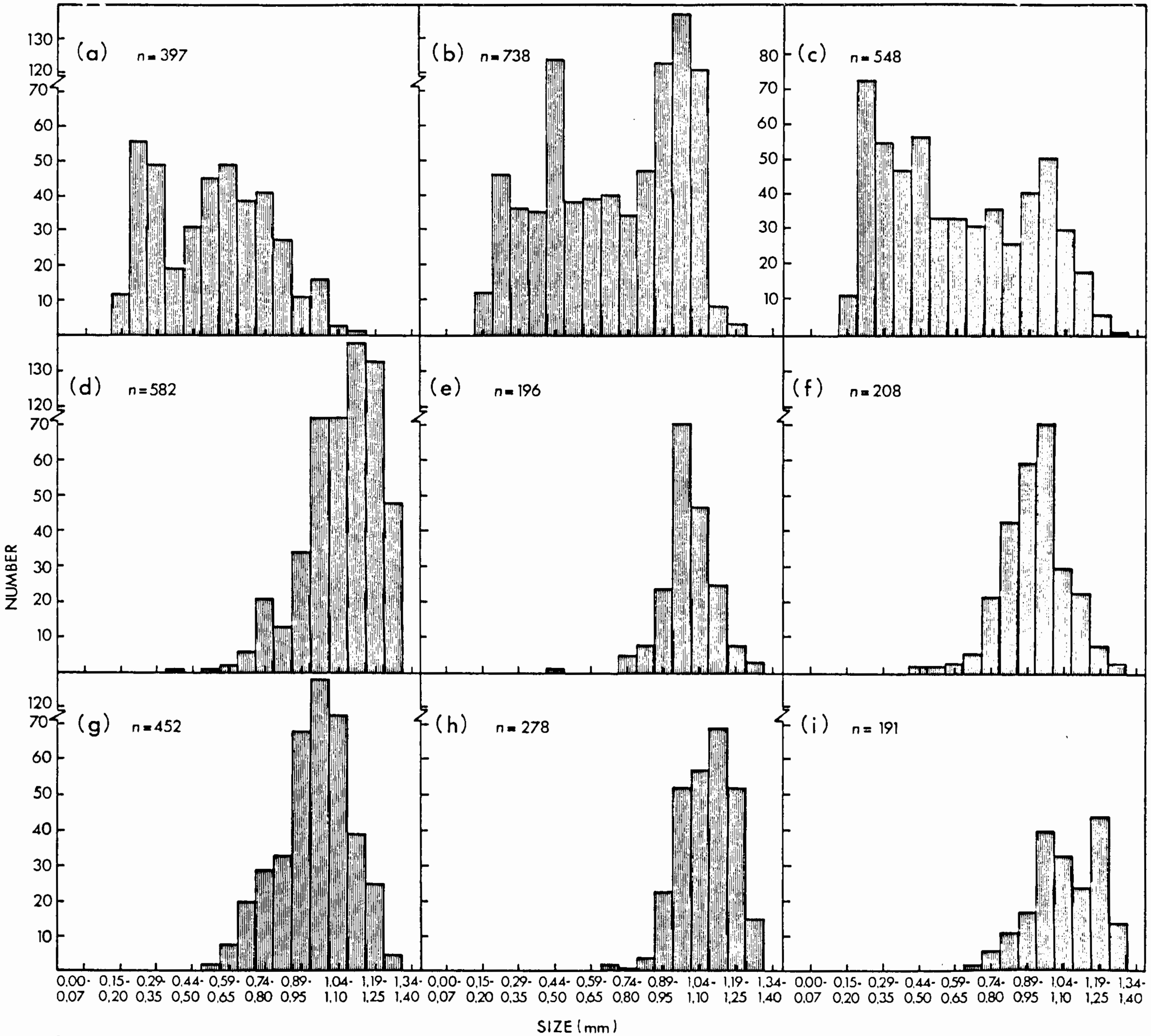


Fig. 4.9: The ovarian egg size distribution and fecundity count for a number of *M. meulleri*.

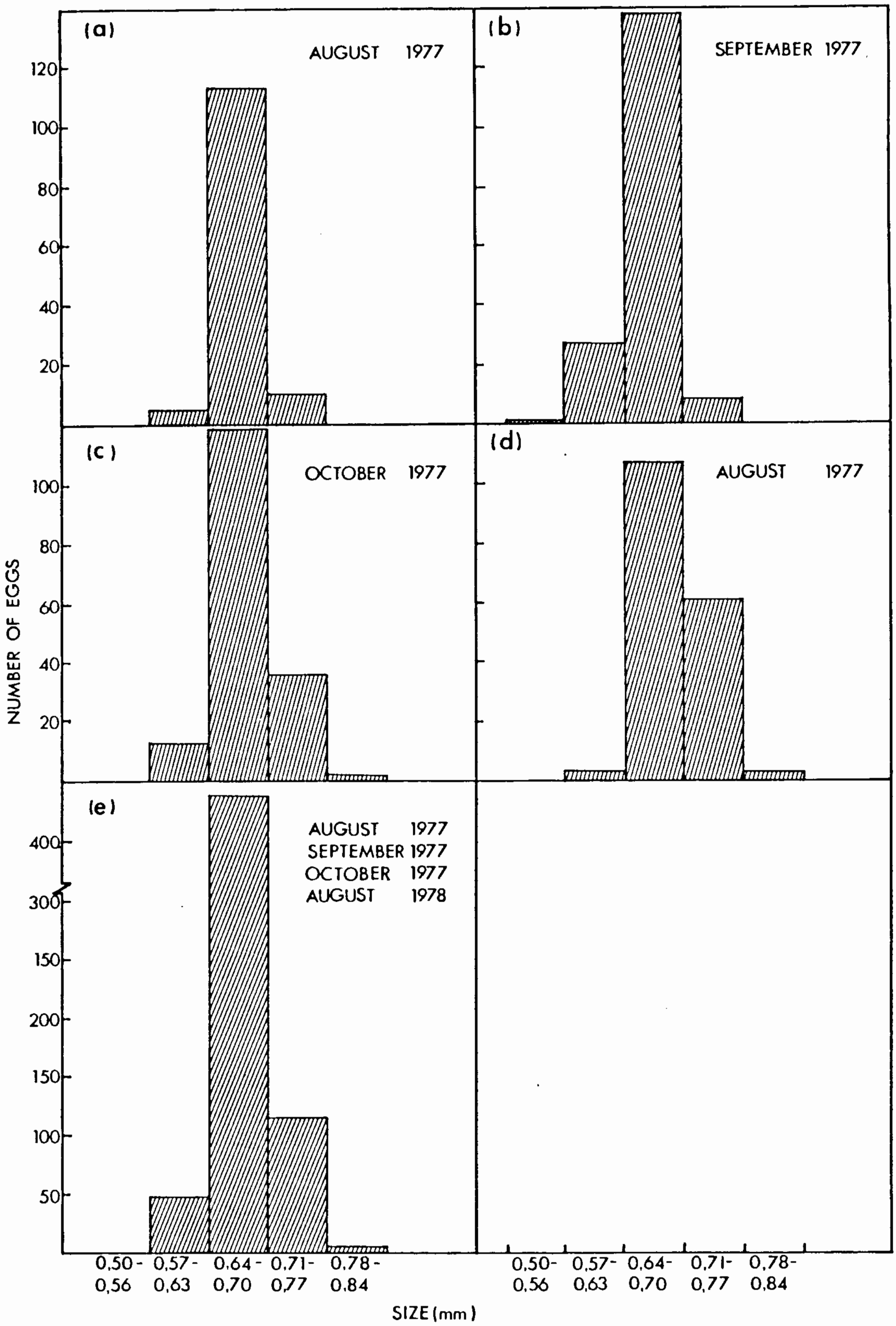


Fig. 4.10: The size distribution of planktonic *L. hectoris* eggs taken during the CELP cruises.

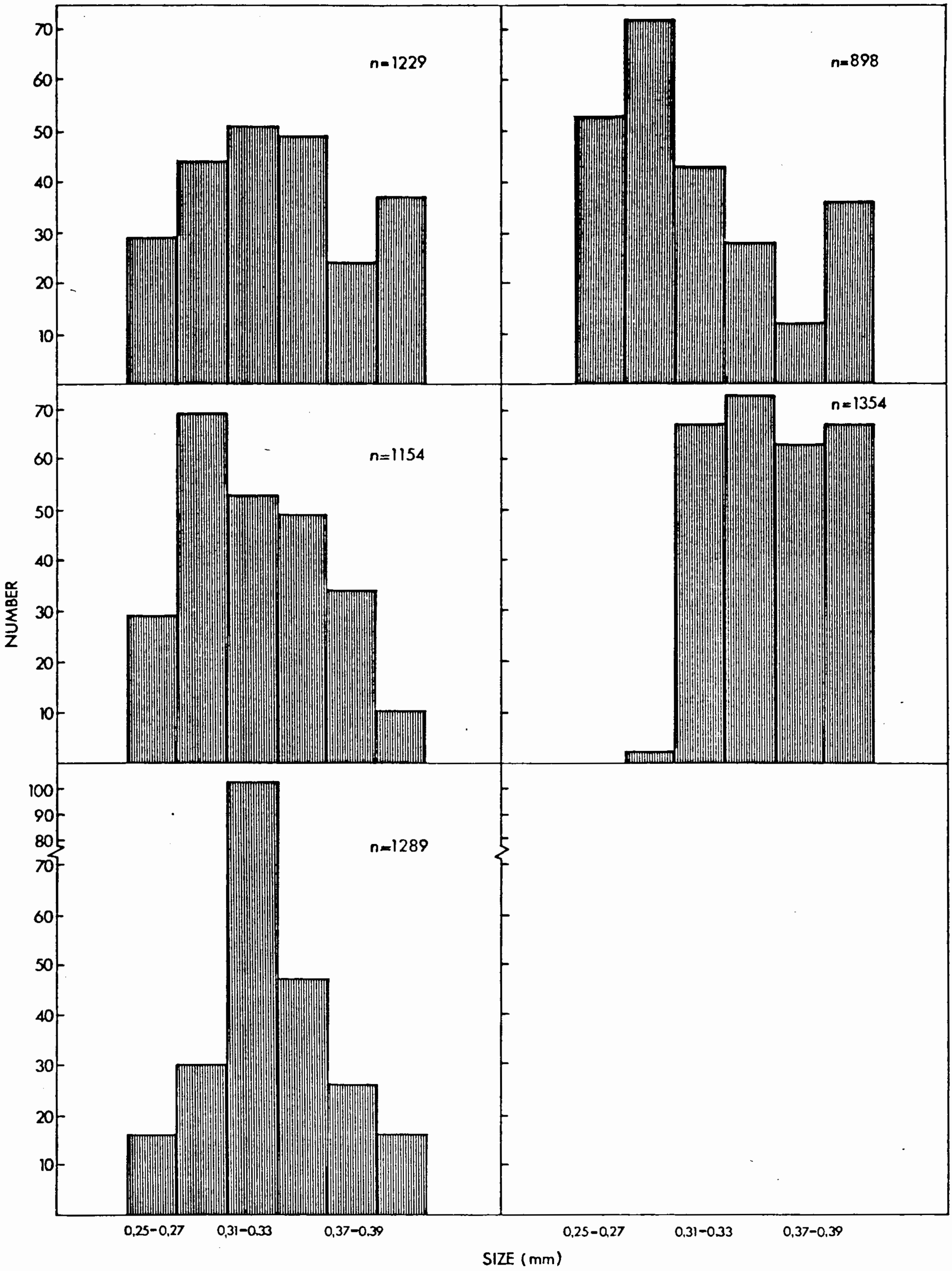


Fig. 4.11: The size distribution (long axis) and fecundity count for a number of *L. hectoris* ovarian eggs.

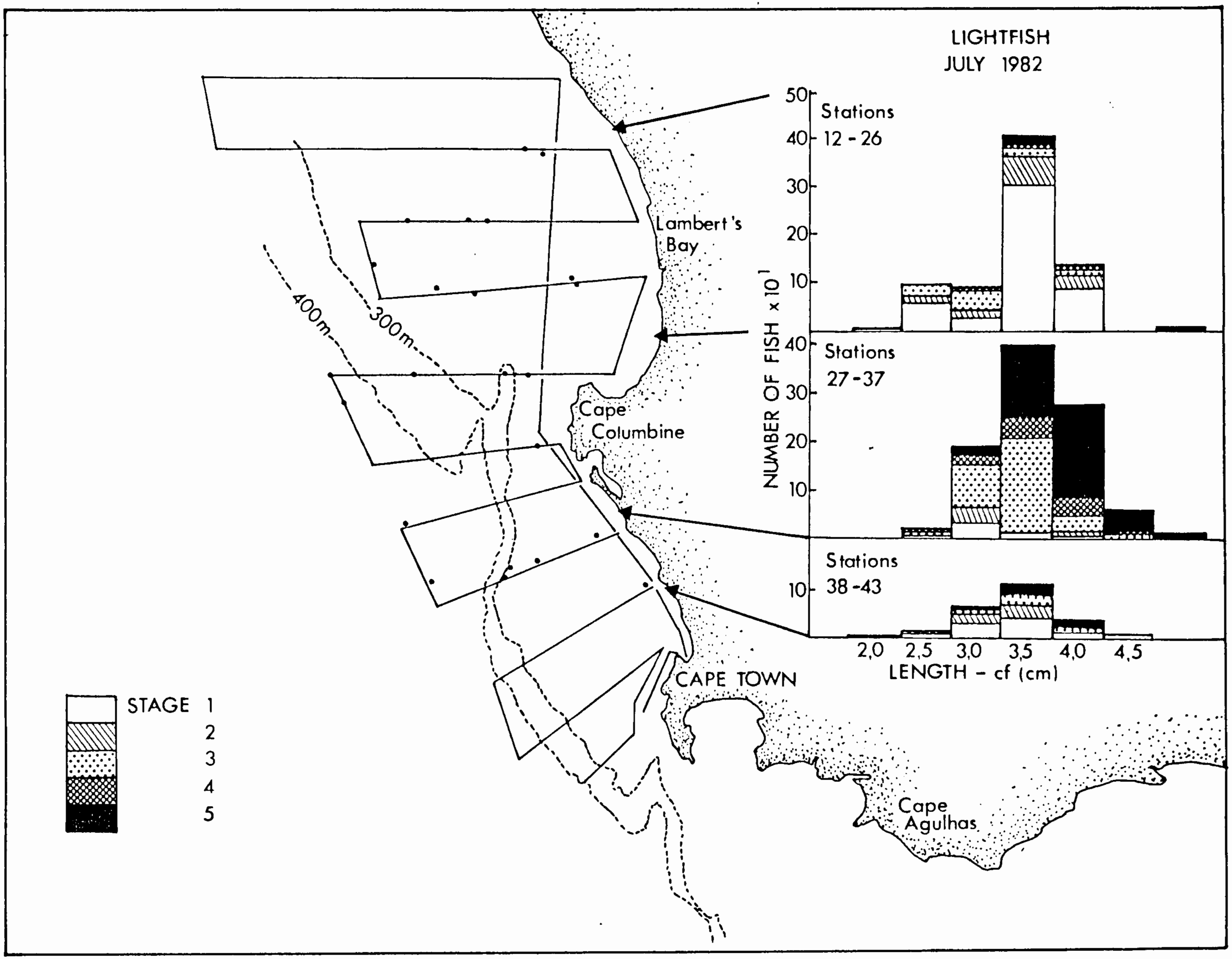


Fig. 4.12: The horizontal distribution of fish with different stages of sexual maturity during a cruise in July 1982. the area sampled was divided into three areas. The track chart and stations sampled are shown.

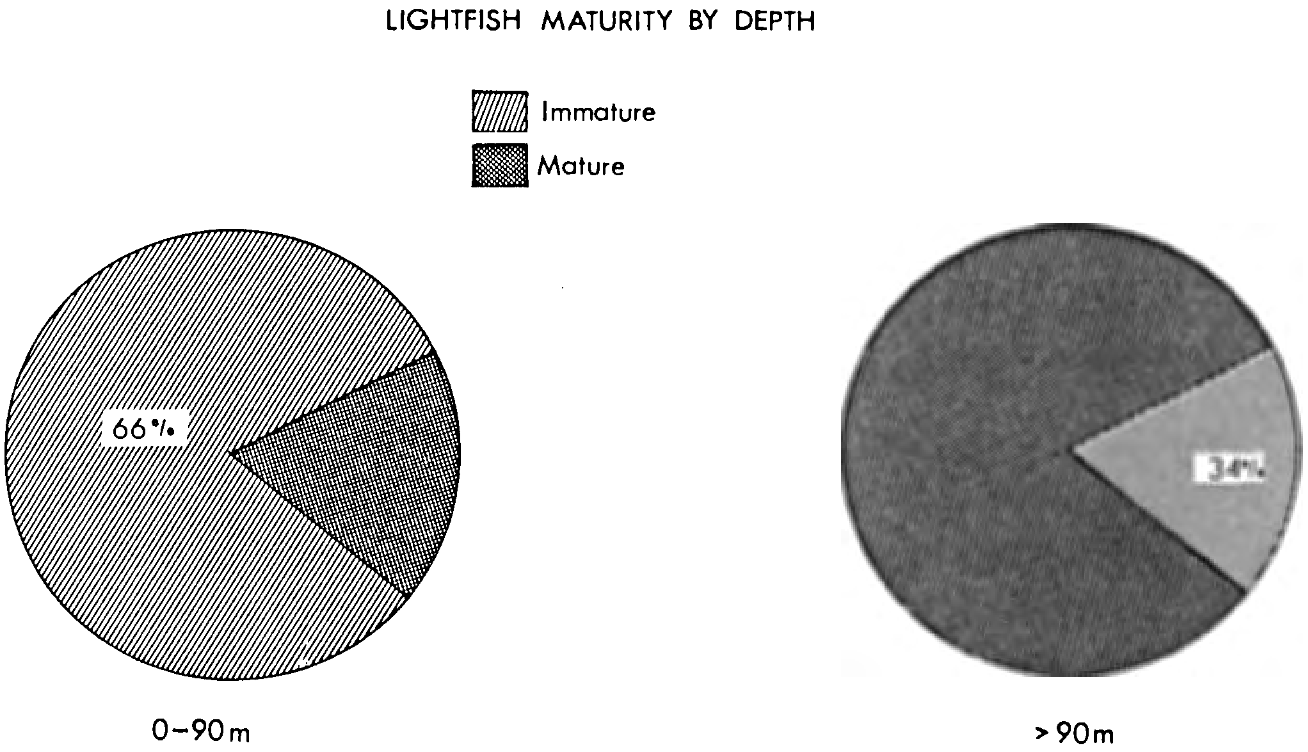


Fig. 4.13: The vertical distribution of fish with different maturity stages sampled during the cruise depicted in Fig. 4.12.

concentrated in the Cape Columbine/Saldanha Bay area.

Fig. 4.13 suggests that lightfish spawning also has a vertical dimension in that the majority of sexually active fish occur at depths greater than 90 metres.

4.4 DISCUSSION

The analyses of maturity stages confirm a late winter/spring spawning for both light- and lanternfish (Figs 4.2, 4.3, 4.6 and 4.7). Although the length at first maturity for male and female lightfish are very similar (using maturity stages three, four and five), 2,6 and 2,4 cm caudal length respectively (Fig. 4.5), female maturity lags behind male maturity. For example 50 % maturity in males is attained at approximately 3,0 cm whilst the figure in females is 3,8 cm. These lengths convert to approximately 8 and 11 months respectively using the growth rate proposed in the present study (Chapter 2). The age at first maturity is between 6 and 7 months and 100 % maturity is attained at 15 months for both sexes. Therefore fish spawned in late winter/spring can contribute to spawning the following year.

Fig. 4.7 illustrates very clearly that no <u>L</u>. <u>hectoris</u> gonad activity takes place during the first five months of the year. The maturity ogive for lanternfish (Fig. 4.4) presents a more confusing picture, partly because the total sample size is small but also because few males were caught. Length at first maturity for both sexes is 3,6 cm caudal length whilst 50 and 100 % maturity for females occurred at 4,2 and 6,2 cm respectively. These lengths are equal to 5 to 6 months, 7,5 months and 16

Shelton (1979) who found lightfish eggs abundant offshore of the 200 m isobath off South Africa. As a result of the generally small number of lanternfish in samples, no quantification of the horizontal and vertical aspects of the maturity stages was possible.

M. muelleri total fecundity off South Africa (Range 24 - 738, expressed in numbers of total ova) is of the same order as that found by Okiyama (1971) in the Japan Sea (Range 109-331) and Gjosaeter (1978, cited by Gjøsaeter and Kawaguchi 1980) in the North Atlantic (Range 200 - 500) although the upper limit of the range is higher than that found by these researchers (Tables 4.1 and 4.2). Expressing fecundity in terms of body weight, *M. muelleri* off South Africa has 222 eggs/gram of wet body weight (a mean value using all counts).

Although the fecundity of a number of myctophids is known (Table 4.1), no record of *L. hectoris* fecundity is available. The fecundity of this species as presented in this study (Table 4.2) (Range 834 - 1 354) is indicated on Fig. 4.1. The high egg count found for some of the species eg. *Myctophum nitidulum* and *Ceratoscopelus townsendi* may be due to the much bigger size of these fish.

According to Robertson (1976) the yolk and oil droplet size of *M. muelleri* eggs from various parts of the world, taken from plankton samples, are relatively constant. However, the overall diameter of the egg varies, with the southern specimens having a greater diameter (Table 4.3). However, the egg diameter of eggs taken from plankton samples off the South African coast does not

Table 4.2: Total fecundity counts of individual light- and lantern fish.

M. muelleri	F	Fish Weight (g)
	397	1,84
	548	1,77
	738	1,75
	582	1,68
	196	1,64
	280	1,55
	191	1,52
	278	1,47
	24	1,36
L. hectoris	F	Fish Weight (g)
	1 229	1,48
	1 289	2,12
	834	1,48
	1 354	2.04
	1 154	1,99
	898	1,02

Table 4.3: Comparison of *Maurolicus muelleri* egg diameters from various parts of the world after Robertson (1976). The results from this study are also indicated.

Area		Total egg diameter (mm)	
Mediterranean (Straits of Messina)		1,32 - 1,58	
Mediterranean (off Algiers)		1,30 - 1,40	
Bay of Biscay		1,32 - 1,52	
South-west Atlantic		1,88 - 2,02	
Japan Sea		1,29 - 1,82	
New Zealand		1,55 - 2,05	
South Africa	(fish)	0,15 - 1,33}	Present
South Africa	(plankton)	1,13 - 2,10}	Study

support this view in that the eggs have the biggest range compared with the measurements made by Robertson (1976) (Table 4.3 and Fig. 4.8).

The bi-modal ovarian egg distribution for some lightfish suggest that this species may be a serial or batch spawner. However, not all fish sampled had one mode, suggesting that spawning has taken place already and that another spawning is imminent. Lightfish eggs found in the stomach of a specimen of the same species had a similar size distribution as those from mature adults (Fig. 4.14). This indicates that the eggs measuring 0,51 - 1,25 mm are about to be spawned. However, according to Hunter and Leong (1981) multiple spawning fishes such as pilchard, anchovy and mackerel are often believed to produce one to three and possibly more spawning batches per year. These conclusions are based on the fact that frequently two modes of yolked and sometimes three are observed in frequency distributions of ovarian egg sizes. However, in a study of postovulatory follicles in northern anchovy Engraulis mordax (Hunter and Leong 1981), it was discovered that this species spawn about 20 times per year, therefore estimates of one to three spawnings for E. mordax may be in error by a factor of about 10.

The difference in diameter of M. muelleri eggs in the ovary and in plankton samples may be explained by the fact that the lattice structure of the chorion in the ovarian eggs has not expanded yet, giving the egg a smooth appearance. Therefore the eggs have not yet become hydrated, a process which takes place only hours before spawning.

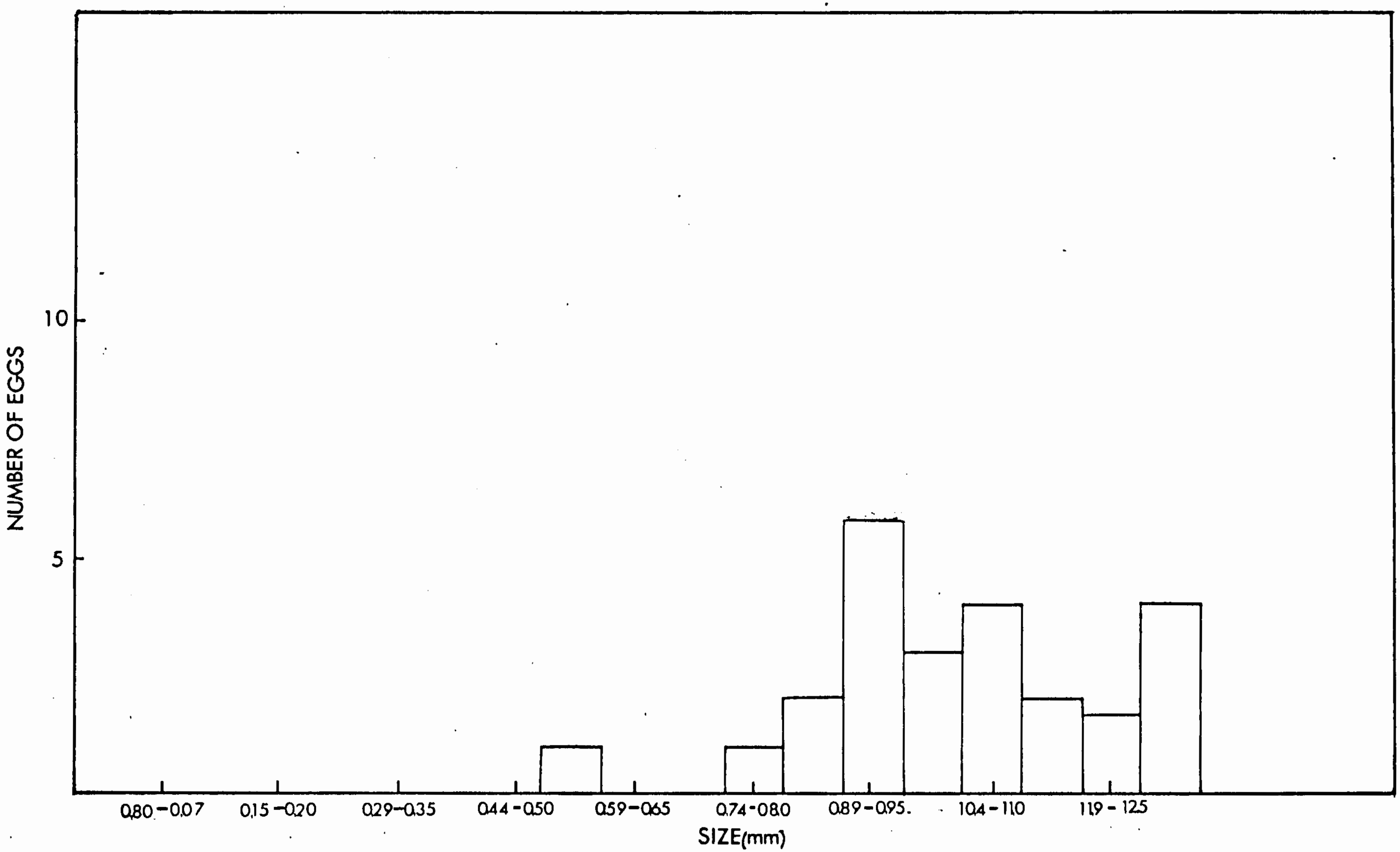


Fig. 4.14: The size distribution of *M. muelleri* eggs taken form the stomach of an immature fish of the same species.

The eggs of L. hectoris are slightly oval, therefore two sets of measurements are applicable. The long and short axes measurements for eggs taken from plankton samples were 0,74 - 0,83 and 0,65 - 0,72 mm respectively. Both sets of samples were taken off New Zealand (Robertson 1977). The egg diameter (long-axis) distributions of ovarian L. hectoris eggs off South Africa are shown in Fig. 4.11. It would appear that most fish have a single mode in their egg diameter distributions, indicating that each individual only spawns once in a season. The sizes of the eggs measured correspond with the previously mentioned category (iii) - immature eggs 0,25 - 0,45 mm in diameter - of Pertseva-Ostroumova (1973). Therefore the eggs contained in the gonad are expected to all mature at the same time. However, the possible error associated with the interpretation of frequency distributions of ovarian eggs, mentioned above, should be kept in mind.

The egg diameter distributions of planktonic L. hectoris eggs for different months as shown in Fig. 4.10 indicates that the mode, as expected, is the same for the various months and the range of the eggs, measured along the long axis (0,50 - 0,84 mm), is very similar to that found by Robertson (1977).

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CHAPTER 5

THE FEEDING OF AND THE PREDATION ON THE LIGHTFISH MAUROLICUS MUELLERI AND THE LANTERNFISH LAMPANYCTODES HECTORIS

5.1 PREDATION ON M.MUELLERI AND L. HECTORIS

5.1.1 INTRODUCTION

Although mesopelagic fish constitute a major part of the oceanic biomass, their position in the food web is poorly understood. Many predators consume mesopelagic fish, but their importance in the diet is not clear. The distribution of most commercial fish does not overlap with those of mesopelagic fishes, but where an overlap occurs, predation mortality is often heavy. Pereyra et al. (1969) reported heavy predation on the myctophid Stenobrachius leucopsarus by the commercially-exploited shelf rockfish Sebastodes flavidus in the Astoria Canyon off the Columbia river in Washington. The distribution ranges of these species did not usually overlap, but a south flowing surface current transported the myctophids to a shallow area at night. Because the depth of the shelf would be shallower than the usual daytime residence depth of the vertically migrating mycthophids, they would be concentrated at or near the bottom where they might be more available to S. flavidus.

Three trophic complexes can be distinguished within the oceanic pelagic zone, namely epipelagic, mesopelagic and bathypelagic. According to Borodulina (1972) the best known is the epipelagic complex, which includes fish such as tuna, marlin, salmon, anchovy and pilchard. The food web of the mesopelagic complex have been little investigated; and the bathypelagic not at all. Borodulina (1972) distinguishes three different types of predatory fish in the mesopelagic zone, namely plankton- feeders, actively hunting predators and passive predators, which lie in wait for and attract their prey. He investigated the feeding of the last group because they migrate with, and are caught with typical sound scatterers and are therefore important from the point of view of food interrelationships. Fish caught in the Pacific, Indian and Atlantic Oceans were studied and it was concluded that 93,2% of all food items found in the stomachs of these passive fish predators are fish, among which myctophids are the most frequent.

There are many other observations of various species of fish and other marine animals feeding on mesopelagic fish for example off California by jack mackerel (*Trachurus symmetricus*) and rockfish (*Sebastodes sp.*) (Fitch 1951) and in offshore Washington waters by salmon (*Oncorhynchus tshawytscha*).

The squid *Todarodes pacificus* in the Japan Sea (Okiyama 1965) feed on *Maurolicus muelleri*. A number of cetaceans have been found to eat mesopelagic fish: off California the pygmy sperm whale (*Kogia simus*) take *Diaphus sp.*, *Lampandena sp.* and *Symbolophorous sp.*; the Pacific spotted dolphin *Stenella graffmari* and the spinner dolphin *Stenella longirostris*, feed on a number of myctophids. The species *Benthosema panamense*, *Diogenichthys laternatus* and *Lampanyctus parvicauda* were the most important for *S. longirostris*, and *B. panamense* the most important for *S. graffmani* (Fitch 1968). The photichthyid, *Vinciguerra lucetia* formed an important part of the diet of S. longirostris. The common dolphin Delphinus delphis and the northern right whale dolphin Lissodelphis borealis also take mesopelagic fish (Fitch 1968).

Off the South African coast a number of predators have been recorded feeding on mesopelagic fish. Four species of tuna, Bluefin (Thunnus thynnus orientalis), Longfin (Thunnus alalunga), Yellowfin (Thunnus albacares) and Bigeye (Thunnus obesus) were sampled by de Jager et al (1963) and Nepgen (1970). Fish was the most important food item by weight for all species. Lanternfish, identified by de Jager et al (1963) as Myctophum cocco and Myctophum humboldti were found in all species and recorded as among the most important fish in the diet. These two species are now known as Gonichthys cocco and Symbolophorus barnardi respectively. Both occur at the surface at night (Hulley, South African Museum, Cape Town, personal communication).

Mesopelagic fish (Diaphus elucens = Diaphus perspicillatus, Lampanyctodes hectoris, Myctophum humboldti = Symbolophorus barnardi and Maurolicus muelleri) were regarded as important in the diet of trawled snoek (Thyrsites atun) although less so in handline-snoek (Nepgen 1979).

L. hectoris constituted 22,6 per cent of the diet of medium sized and 44,4 per cent of large mackerel's (Scomber japonicus) diet, making it the most important species in the diet. The only other mesopelagic fish species encountered was Protomyctophum spp. which constituted 0,7 per cent of the diet of large fish (Nepgen 1979).

Botha (1980) found that myctophids formed an important part of the South African hake diet, particularly in the deepwater hake, *Merluccius paradoxus*. Myctophids, were the second most important food category when expressed as percentage mass (22,25%) and the most important as percentage frequency (37,23%) for small (<500mm) *M. paradoxus*. It was less important for large (>500mm) *M. paradoxus*, ranking fourth when expressed as percentage mass (3,78%) and third in terms of percentage frequency (20,41%). *Merluccius capensis*, the inshore hake species, is less dependent upon myctophids. Large *M. capensis* do take myctophids in small numbers while small fish (<400mm) are more dependent upon myctophids. They rank fourth in the diet as percentage mass (7,03%) and ranked third as percentage frequency (16,22%) for small *M. capensis*. According to Assorov and Kalinina (1979) young *M. paradoxus* off South Africa feed mainly on Myctophidae and Gonostomatidae. *Maurolicus muelleri* and myctophids were the major food organisms ingested in February and June. Chlapowski (1977) states that the main food for *M. capensis* and *M. paradoxus* are Euphausiacea, Decapoda and Myctophidae.

Resident South African pelagic seabirds do not feed on mesopelagic fish. The diets of the Cape Gannet (*Morus capensis*), the Cape Cormorant (*Phalacrocorax capensis*) and the Cape (Jackass) Penguin (*Spheniscus demersus*) were investigated by Davies (1955, 1956) and Matthews (1961) and that of the Jackass Penguin (*Sphenisus demersus*) by Wilson (1985). However, there is evidence of other resident pelagic seabirds preying on myctophids eg. the Blue Petrel (*Halobaena caerulea*) at South Georgia (Croxall and Prince 1980).

The most numerous non-resident pelagic seabirds off South Africa, the Sooty Shearwater (*Puffinus griseus*) and the Whitechinned Petrel (*Procellaria aequinoctialis*) feed on mesopelagic fish, especially *L. hectoris* and *M. muelleri* (Jackson, Percy Fitzpatrick Institute of African Ornithology, University of Cape Town, personal communication). Sooty Shearwaters use underwater pursuit of prey to a depth of several metres whilst the Whitechinned Petrel seize its prey at the sea surface (Berruti, Sea Fisheries Research Institute, Cape Town, personal communication). This difference in behaviour may account for the fact that the Sooty Shearwater prey more heavily on light- and lanternfish (based on the mean number of prey items in stomachs sampled). Black-browed albatross (*Diomedea melanophris*) and prions (*Pachyptila spp.*) are also known to take lanternfish (Jackson, Percy Fitzpatrick Institute of African Ornithology, University of Cape Town, personal communication).

In the present study an attempt was made firstly to quantify the importance of *L. hectoris* and *M. muelleri* in the diets of four commercially important fish species in the southern Benguela System, namely hake (*M. capensis* and *M. paradoxus*), snoek (*Thyrsites atun*) and maasbanker (*Trachurus trachurus*). These fish were chosen firstly because of the large number of samples available and because hake is the most important South African trawled fish species. Furthermore, before any commercial exploitation of mesopelagic fish is undertaken, the effect on these important commercial species need to be investigated. Secondly the resident Cape Gannet's (*Morus capensis*) diet is also monitored on a routine basis by the Sea Fisheries Research Institute. This data is presented here in order to validate the results obtained by Davies (1955, 1956) and Matthews (1961).

5.1.2 METHODS

Six hake surveys, routinely conducted at the beginning of the year, mid-year and end of the year, yielded information which was used to obtain an indication of the diets of commercially important demersal species (Payne, Sea Fisheries Research Institute, Cape Town, unpublished). The cruises from which material was obtained were December 1982, January and June 1983, January and July 1984 and January 1985 for M. capensis and M. paradoxus; December 1982, June 1983, January and July 1984 for T. atun; June 1983, January and July 1984 for T. trachurus. The West Coast and South Coast area, stretching from the Orange River to a point South of Quoin Point (at 20 ^{0}E) were divided into different depth strata, i.e. 0-100m, 100-200m, 200-300m, 300-400m and 400-500m. These strata were then divided using degrees of latitude. The various depth/degree strata were further subdivided into 5 minute by 5 minute trawling stations. For each cruise a random number of trawlable stations were selected, usually 70 to a 120. At each station a trawl of approximately half an hour duration was done. For each species of hake and, depending on the time available, other commercially important fish species, a subsample was taken for biological analysis which included an analysis of stomach contents. The frequency of occurrence for both L. hectoris and M. muelleri and the average number and weight of these prey items in each stomach were calculated for each 5cm length group (total length) for M. capensis, M. paradoxus, T. atun and T. trachurus. The frequency of occurrence used in this study was calculated by dividing the number of predator stomachs containing a specific prey item by the number of predator stomachs containing food. Empty or everted stomachs were disregarded.

Unfortunately due to time and gear constraints on board ship, stomach contents which yielded a mixture of prey items eg. lightfish and copepods, were not analysed properly since the weight of each portion was not recorded. The result was that all the stomachs with a mixed content taken from hake, snoek and horse mackerel could not be used in the stomach weight and the mean number of prey items per stomach analyses. The frequency of occurrence analysis was not affected. However, most stomachs contained only lightfish, lanternfish or prey items excluding these two species. Therefore the error introduced for any size class in any month is small and does not affect the trends shown.

In addition all the trawls analysed for the above cruises were plotted on the cruise grid to give an indication of where fishing took place. For each trawl the number of fish of each species (eg. hake) which had _L. hectoris_ and/or _M. muelleri_ in its stomach was expressed as a percentage of the total fish of that species caught. Using this technique it is possible to determine in which areas the commercially important demersal fish take _L. hectoris_ and _M. muelleri_ and in what proportions.

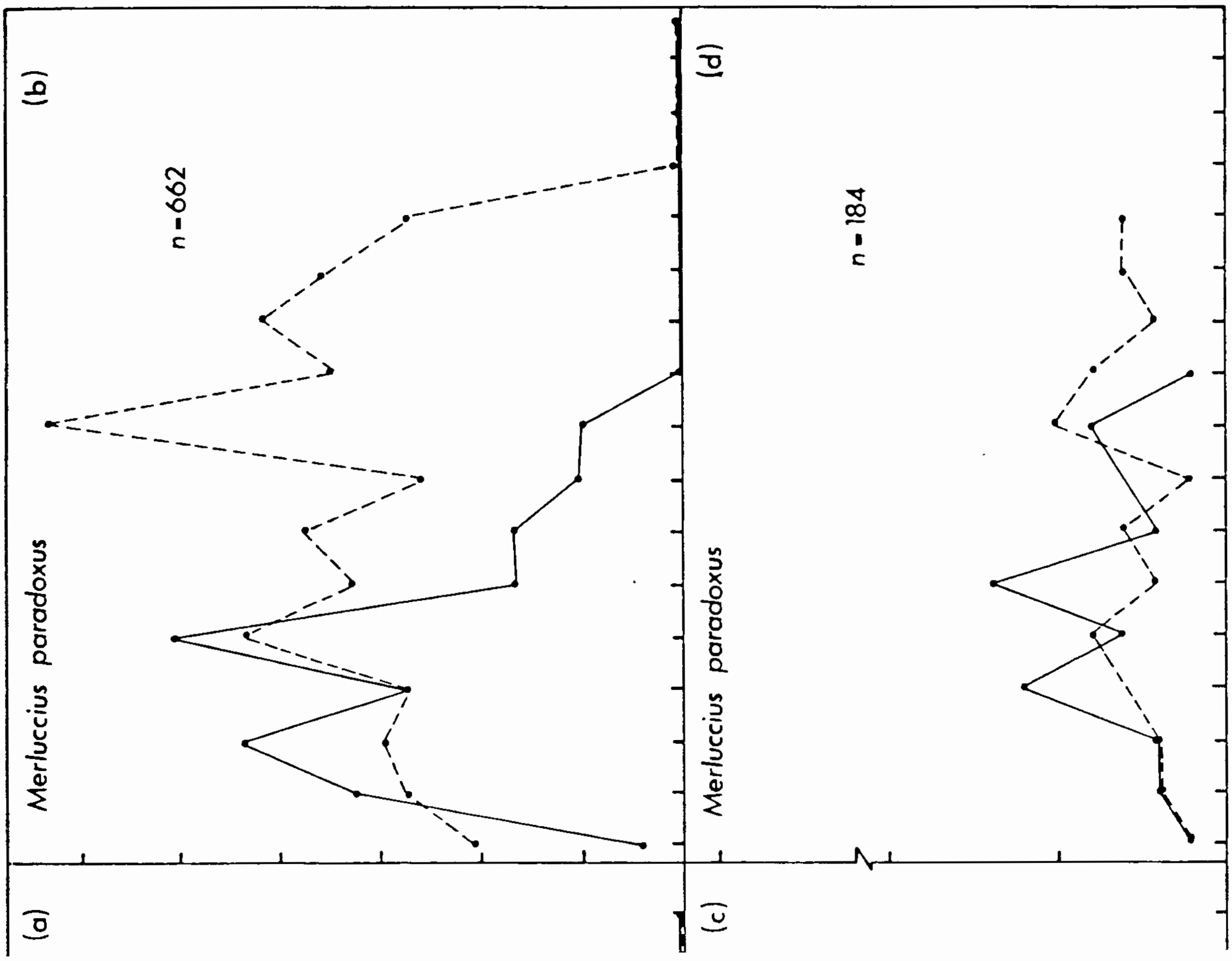
The percentage of _L. hectoris_ and _M. muelleri_ in terms of numbers, weight and frequency of occurrence, taken by the Cape Gannet (_M. capensis_) were calculated from data collected by Berruti (Sea Fisheries Research Institute, Cape Town, unpublished).

5.1.3 RESULTS

No seasonal differences in diet were observed for any of the fish predators, therefore the results for all the months sampled were combined and presented in Figs 5.1, 5.2 and 5.3. The months combined for M. capensis and M. paradoxus were December 1982, January 1983, 1984 and 1985, June 1983 and July 1984. The months for T. atun were December 1982, June 1983, January 1984 and July 1984. The months combined for T. trachurus were June 1983, Jan 1984 and July 1984.

The importance of L. hectoris and M. muelleri in the diet of M. capensis is shown in Fig. 5.1. Although only small to medium sized hake fed on these two species and the actual numbers taken were small, the frequency of occurrence have been as high as 73% for lightfish (December 1982, 35-39 cm) and 46% for lanternfish (June 1983, 25-29 cm). Lanternfish was the more consistent food item, lightfish being absent or represented in very low numbers during certain months eg. June 1983 and January 1984. The importance of these species in the diet of M. capensis can also be judged from Fig. 5.3 a, which indicates that between 15-19 and 40-44 cm, lightfish and lanternfish combined contributed more than 50% by mass of the diet of M. capensis in spite of the low numbers taken (Fig. 5.1 c).

Both lantern- and lightfish occurred in the diet of M. paradoxus during all months of sampling and the frequency of occurrence was higher over most of the size classes sampled than that observed for M. capensis (Fig. 5.1 b). The contribution of light- and lanternfish by mass to the diet of M. paradoxus are most important



ctoris and M. muelleri in the diet of (a) M. capensis and
per stomach for (c) M. capensis and (d) M. paradoxus.

months respectively. Few males were present in the sample, hence no length at 50 or 100 % maturity is available.

An interesting aspect is that L. hectoris becomes mature at 5 to 6 months, whilst the equivalent for M. muelleri is 6 to 7 months. Although this difference is small one would have expected it to have been reversed, since L. hectoris attains a greater size.

The reason for the few males caught for both light- and lantern fish, the male : female ratio being 1:1,15 and 1:2,4 respectively (based on the total for all months sampled), is not clear. In lanternfish this ratio appear to be linked to the spawning cycle (Fig. 4.2). The highest male: female ratios were sampled in the nonspawning months, eg. 1:13 (November 1983), 1:15 (January 1984), 1:5,9 (April 1984) and 1:7 (May 1984). In the spawning months more males were caught and the male : female ratios were

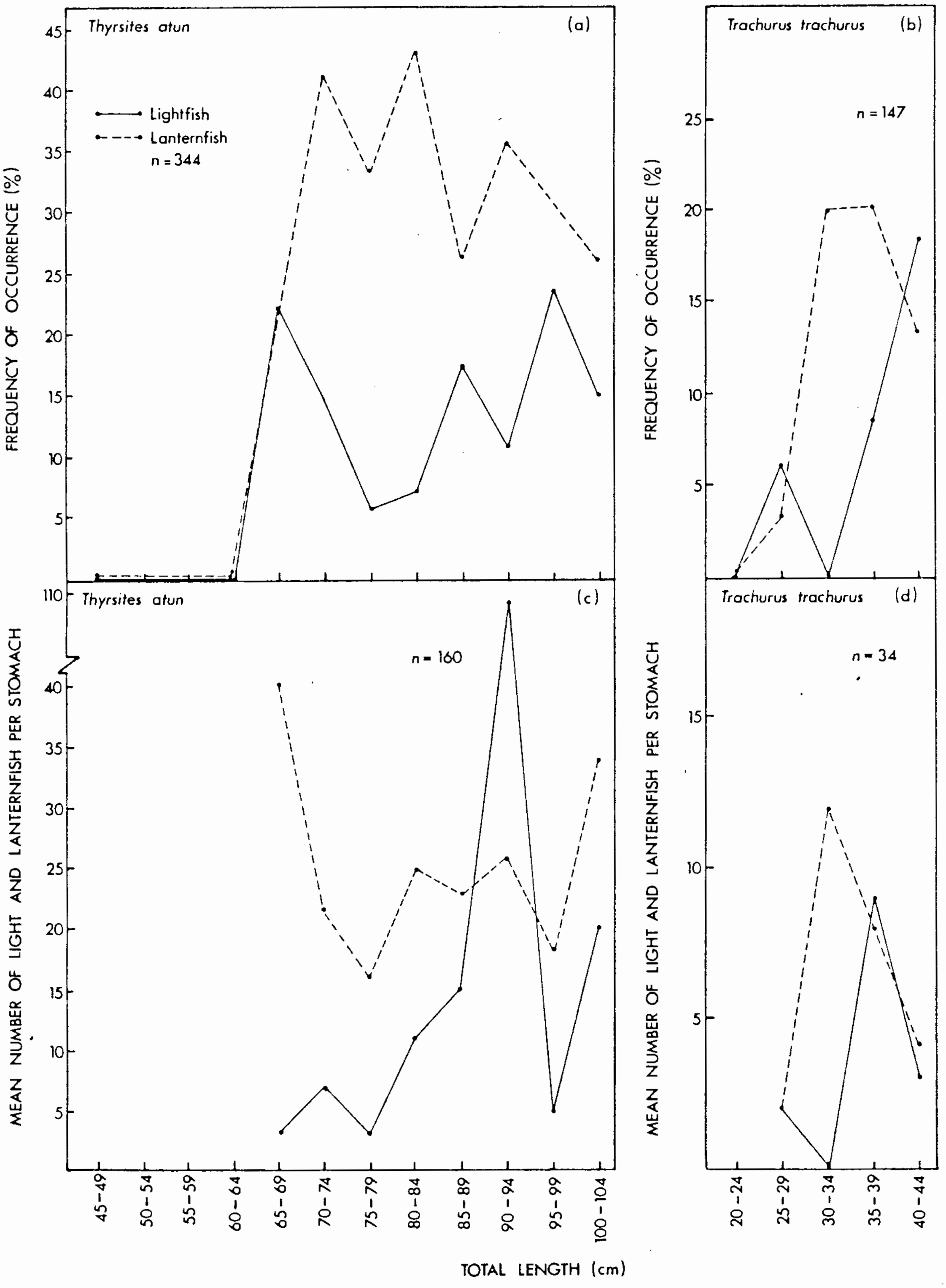


Fig. 5.2: The frequency of occurrence of L. hectoris and M. muelleri in the diet of (a) T. atun and (b) T. trachurus, and the mean number of prey items per stomach for (c) T. atun and (d) T. trachurus.

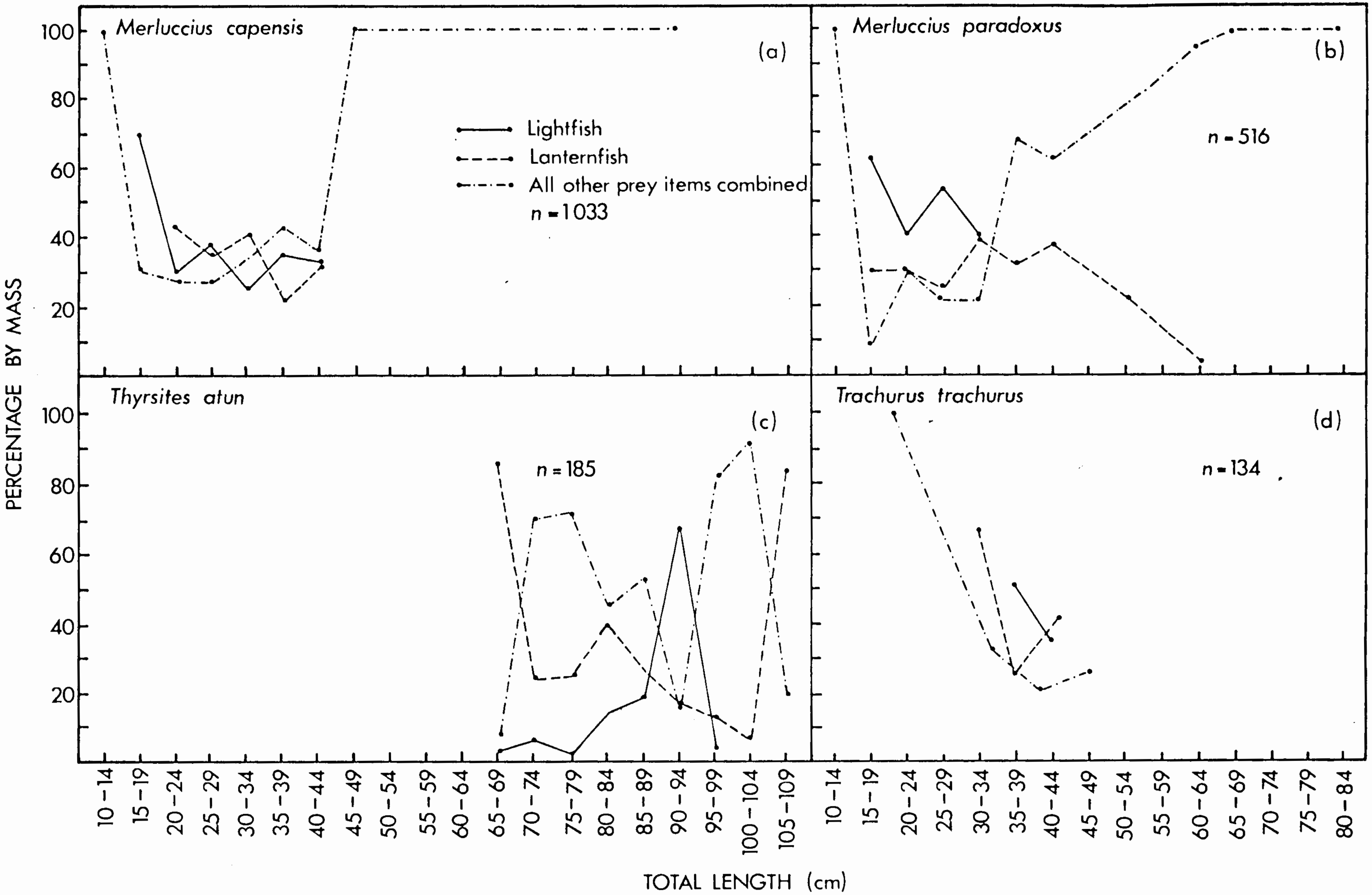


Fig. 5.3: The contribution of *L. hectoris*, *M. meulleri* and all other prey items combined, in terms of percentage mass, to the diets of (a) *M. capensis*, (b) *M. paradoxus*, (c) *T. atun* and (d) *T. trachurus* respectively.

over the size ranges 15-19 and 30-34, contributing more than 70% of the diet (Fig. 5.3 b). Although the frequency of occurrence was high the numbers taken were low (Fig. 5.1 d).

Snoek, sampled only during June 1983, January and July 1984, preyed heavily on lantern- and lightfish (Figs 5.2 and 5.3). Lanternfish were taken in greater numbers and were also more important in terms of mass than lightfish. Up to 250 lanternfish and 107 lightfish were found in individual stomachs. Fig. 5.3 c indicates that the importance of light- and lanternfish in snoek diet in terms of weight fluctuates, and were important to certain size classes eg. lightfish to the 90-94 size class and lanternfish to the 65-69 and 105-109 size classes. These fluctuations were more severe than that observed for both species of hake. The frequency of occurrence of lanternfish in the diet of T. atun is also higher than observed in the hake diets (Fig. 5.2 a). Unfortunately no small snoek were sampled.

Although only a few maasbanker (Trachurus trachurus) stomachs were sampled during the June 1983, January and July 1984 cruises, it was evident that both light- and lanternfish can be important in the diet over the length range sampled (Figs 5.2 b and d, and 5.3 d). There were no apparent seasonal differences in diet.

Fig. 5.4 was constructed to determine whether the predators discussed above always encountered light- and lanternfish in the same areas over the two-year period December 1982 to January 1985. In addition it would also give an indication of the horizontal distributions of the prey species. The biggest drawback of Fig. 5.4 is that the areal distribution of trawls

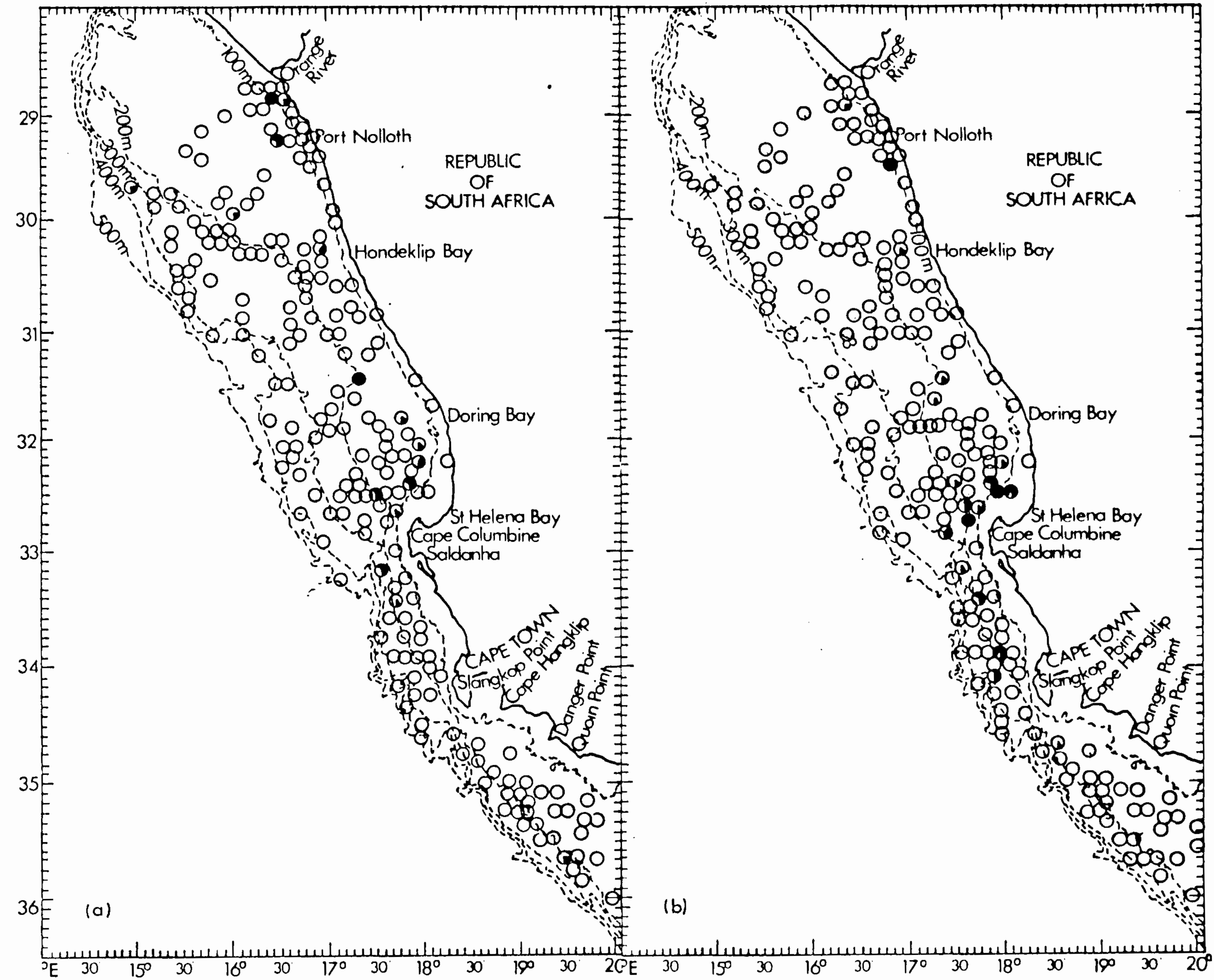


Fig. 5.4: Predation of the hake M. capensis on (a) M. muelleri and (b) L. hectoris. The circles indicate the position where the samples were taken. A dark circle indicates that all the hake in the sample had preyed on the prey species. A clear circle would indicate no predation.

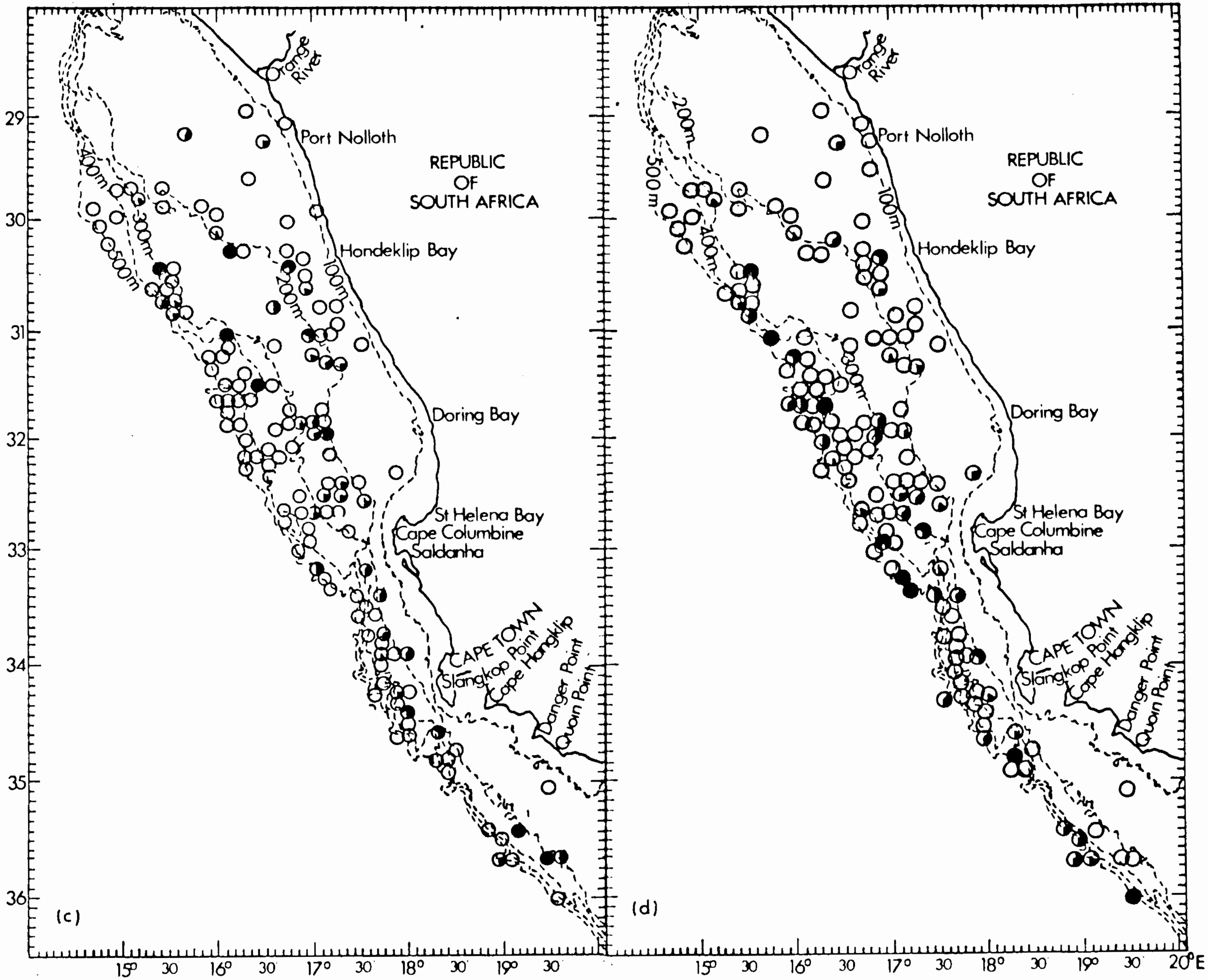


Fig. 5.4 (continued): Predation of the hake *M. paradoxus* on (c) *M. muelleri* and (d) *L. hectoris*.

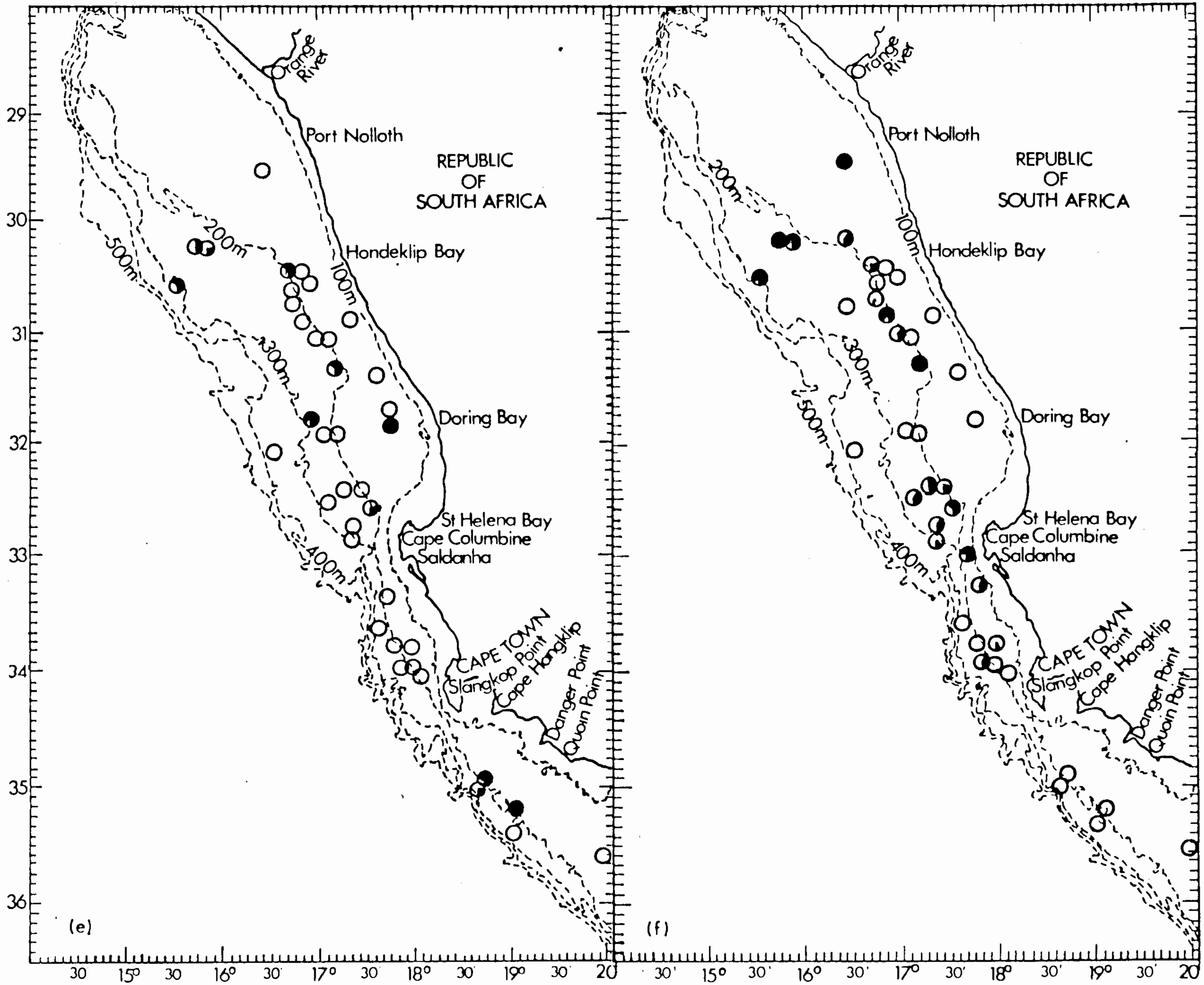


Fig. 5.4 (continued): Predation of the snoek T. atun on (e) M. muelleri and (f) L. hectoris.

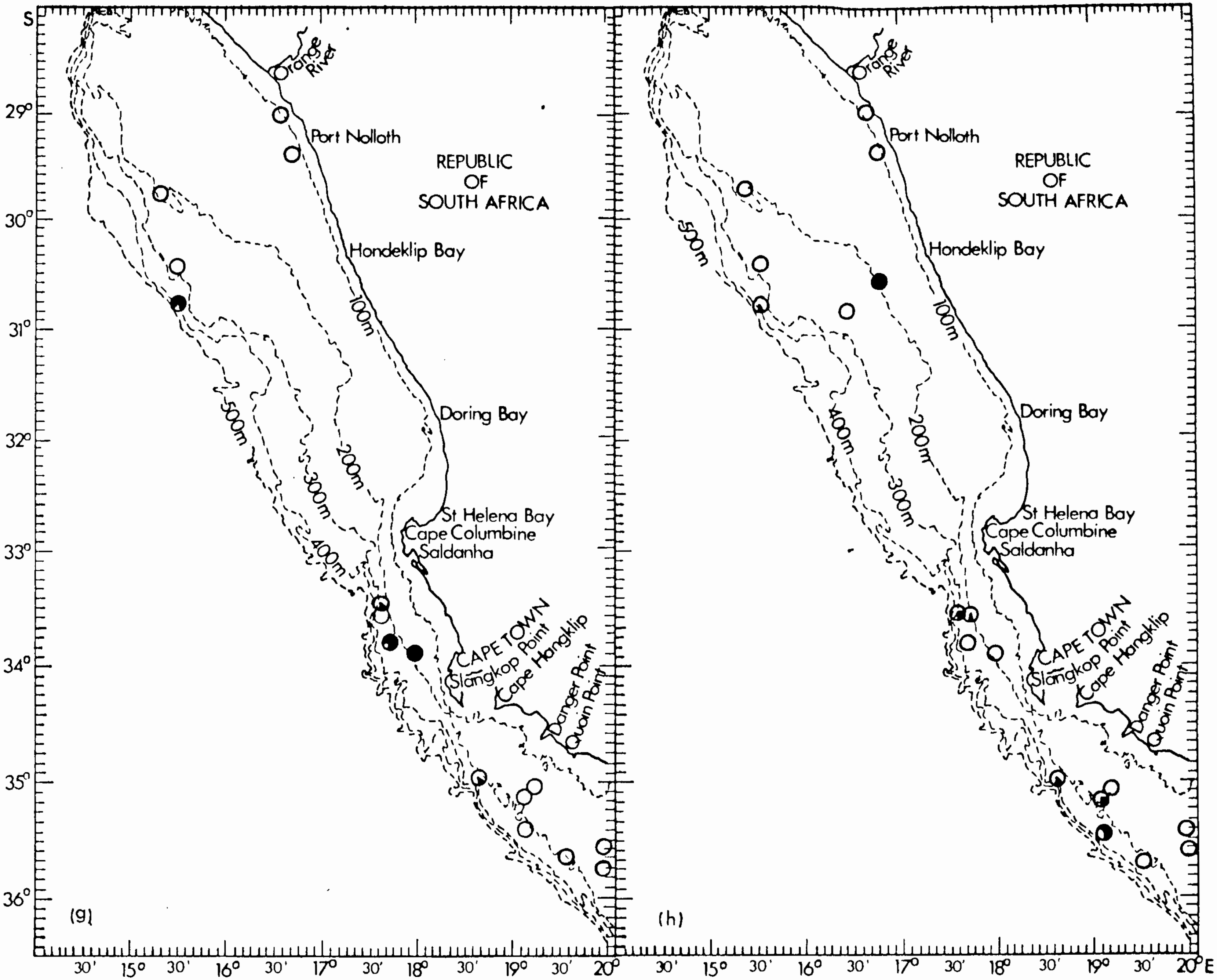


Fig. 5.4 (continued): Predation of the horse mackerel on (g) *M. muelleri* and (h) *L. hectoris*.

differed for each cruise. However, it is still possible to determine whether there is a difference in prey species distribution over time. In addition, all the cruise data were pooled for each predator/prey combination to show where "encounters" have taken place.

The circles indicating the position of the trawls also give an indication of the percentage of fish in each trawl which had L. hectoris or M. muelleri in their stomachs. A clear circle indicate that no fish caught in that particular trawl had preyed on L. hectoris or M. muelleri. A totally black circle in turn indicates that all fish in the trawl had eaten either L. hectoris or M. muelleri.

Fig. 5.4 a indicates that lightfish was taken by M. capensis mostly between 100 and 200m on the West Coast between Saldanha Bay and the Orange River, and lanternfish was preyed upon primarily in the St. Helena Bay to Saldanha Bay areas between 100 and 300m (Fig. 5.4 b).

M. paradoxus preyed on lightfish over a wider area (Fig. 5.4 c) than M. capensis and as one would expect (because M. paradoxus is a deep-water species) fed on this prey mainly between 200 and 400m.

Lanternfish was more available to M. paradoxus than M. capensis (Figs 5.4 a and d) and was preyed upon by the former mainly between 200 and 500m over an area that stretch from Quoin Point in the south to Port Nolloth on the West Coast.

Table 5.1 (a) The number of lightfish samples obtained from gannet stomachs at Malgas Island. The total number of stomachs sampled are given in brackets (Berruti unpublished data).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978									0(50)	0(50)	0(42)	0(49)
1979	0(46)	0(44)	0(40)	0(31)	0(30)	0(40)	0(26)	5(25)	0(21)	1(51)	0(50)	0(50)
1980	0(48)	0(46)	0(46)	0(38)	0(13)	0(0)	0(30)	0(12)	0(48)	0(48)	0(35)	0(284)
1981	0(301)	0(180)	0(21)				0(48)	0(28)	16(30)	0(49)	0(21)	0(113)
1982	0(251)	0(10)	0(34)	0(16)	0(20)	0(39)	0(30)	0(30)	0(28)	3(95)	0(65)	0(60)
1983	0(79)	0(24)	0(30)	0(32)	0(24)	0(30)	0(30)	2(16)	0(30)	0(16)	0(125)	0(50)
1984	0(80)	0(30)	0(30)	0(20)	0(22)	1(30)	0(30)	0(47)	1(115)	0(34)	0(26)	0(30)
1985	0(50)	0(55)	0(28)	0(28)								

(b) The number of lanternfish samples obtained from gannet stomachs at Malgas Island. The total number of stomachs sampled are given in brackets (Berruti unpublished data).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978									0(50)	1(50)	7(42)	0(49)
1979	0(46)	0(44)	0(40)	0(31)	0(30)	0(40)	0(26)	1(25)	0(21)	0(51)	0(50)	9(50)
1980	0(48)	0(46)	0(46)	0(38)	0(13)	0(0)	0(30)	0(12)	0(48)	0(48)	0(35)	0(284)
1981	0(301)	0(180)	0(21)				0(48)	0(28)	3(30)	0(49)	0(21)	3(113)
1982	0(251)	0(10)	0(34)	0(16)	0(20)	0(39)	0(30)	0(30)	0(28)	0(95)	0(65)	0(60)
1983	0(79)	0(24)	0(30)	0(32)	0(24)	0(30)	0(30)	0(16)	1(30)	0(16)	1(125)	0(50)
1984	0(80)	0(30)	0(30)	0(20)	0(22)	0(30)	4(30)	1(47)	4(115)	0(34)	0(26)	0(30)
1985	0(50)	0(55)	0(45)	0(28)								

Table 5.1 (c) The number of lightfish samples obtained from gannet stomachs at Lamberts Bay. The total number of stomachs sampled are given in brackets (Berruti unpublished data).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978	0(30)	0(51)	0(42)	0(5)	0(3)	0(29)	0(7)	0(50)	0(19)	0(49)	0(50)	0(45)
1979	0(49)	0(50)	0(50)	0(50)	0(50)	0(17)	0(9)	0(39)	0(36)	0(50)	0(50)	0(50)
1980	0(46)	0(48)	0(51)	0(14)	0(10)	0(30)	0(30)	0(50)	0(49)	0(47)	0(54)	0(48)
1981	0(50)	0(39)	0(1)	0(50)	0(41)	0(49)	0(0)	0(10)	0(13)	0(50)	0(30)	0(13)
1982	0(50)	0(30)	0(51)	0(25)	0(20)	0(10)	0(10)	0(18)	0(15)	0(15)	0(21)	0(15)
1983	0(18)	0(13)	0(15)	0(16)	0(17)	0(18)	0(13)	0(12)	0(15)	0(15)	0(128)	0(17)
1984	0(15)	0(15)	0(30)	0(20)	0(15)	1(15)	0(30)	0(16)	1(15)	0(92)	0(100)	0(40)
1985	0(39)	0(50)	0(35)	0(30)								

(d) The number of lanternfish samples obtained from gannet stomachs at Lamberts Bay. The total number of stomachs sampled are given in brackets (Berruti unpublished data).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978	0(30)	0(51)	0(42)	0(5)	0(3)	0(29)	0(7)	0(50)	0(19)	0(49)	0(50)	0(45)
1979	0(49)	0(50)	0(50)	0(50)	0(50)	0(17)	0(9)	0(39)	0(35)	0(50)	0(50)	0(50)
1980	0(46)	0(49)	0(48)	0(51)	0(14)	0(10)	0(30)	0(50)	0(49)	0(47)	0(54)	0(48)
1981	0(50)	0(39)	0(1)	0(50)	0(41)	0(49)	0(0)	0(10)	0(13)	0(50)	0(30)	0(13)
1982	0(50)	0(50)	0(51)	0(25)	0(20)	0(10)	0(10)	1(18)	0(15)	0(15)	0(21)	0(15)
1983	0(18)	0(13)	0(15)	0(16)	0(17)	0(18)	0(13)	0(12)	0(15)	0(15)	0(128)	0(17)
1984	0(15)	0(15)	0(30)	0(20)	0(15)	1(15)	0(30)	0(16)	1(15)	0(92)	0(100)	0(40)
1985	0(39)	0(50)	0(35)	0(30)								

Table 5.2 (a) The presence of lightfish in the gannet diet at Malgas Island, expressed as numbers, by weight and frequency of occurrence. The total sample size is given in brackets and the time of sampling is indicated (Berruti unpublished data).

	% Number	% Weight	% Frequency	Coverage
1978	0(2 407)	0(34 615)	0(191)	September - December
1979	6,1(4 809)	0,4(74 461)	1,3(454)	January - December
1980	0(6 874)	0(118 539)	0(648)	January - December except June
1981	12,8(9 464)	1,2(153 167)	1,9(831)	January; February; March; July - December
1982	0,4(7 427)	0,1(125 230)	0,4(678)	January - December
1983	0,5(4 053)	0,1(79 307)	0,4(486)	January - December
1984	0,9(3 708)	0,1(75 696)	0,4(494)	January - December
1985	0(1 669)	0(36 445)	0(188)	January - April

(b) The presence of lanternfish in the gannet diet at Malgas Island, expressed as numbers, by weight and frequency of occurrence. The total sample size is given in brackets and the time of sampling is indicated.

	% Number	% Weight	% Frequency	Coverage
1978	19,2(2 407)	3,7(34 615)	4,2(191)	September - December
1979	5,0(4 809)	0,8(74 461)	2,2(454)	January - December
1980	0(6 874)	0(118 539)	0(648)	January - December except June
1981	1,4(9 464)	0,2(153 167)	0,7(831)	January; February; March; July - December
1982	0,4(7 427)	0,04(125 230)	0,3(678)	January - December
1983	0,8(4 053)	0,3(79 307)	0,2(486)	January - December
1984	3,6(3 708)	1,1(75 696)	1,8(494)	January - December
1985	12,8(1 669)	1,8(36 445)	2,1(188)	January - April

Table 5.2 (c) The presence of lightfish in the gannet diet at Lamberts Bay, expressed as numbers, by weight and frequency of occurrence. The total sample size is given in brackets and the time of sampling is indicated (Berruti unpublished data).

	% Number	% Weight	% Frequency	Coverage
1978	0(4 746)	0(61 346)	0(380)	January - December
1979	0(6 893)	0(74 297)	0(499)	January - December
1980	0(6 491)	0(71 508)	0(496)	January - December
1981	0(5 903)	0(43 735)	0(346)	January - December except July
1982	0(5 519)	0(40 224)	0(300)	January - December
1983	0(4 895)	0(38 253)	0(297)	January - December
1984	0,1(6 301)	0,1(55 188)	0,3(403)	January - December
1985	0(1 737)	0(23 671)	0(154)	January - April

(d) The presence of lanternfish in the gannet diet at Lamberts Bay, expressed as numbers, by weight and frequency of occurrence. The total sample size is given in brackets and the time of sampling is indicated.

	% Number	% Weight	% Frequency	Coverage
1978	0(4 746)	0(61 346)	0(380)	January - December
1979	0(6 893)	0(74 297)	0(499)	January - December
1980	0(6 491)	0(71 508)	0(496)	January - December
1981	0(5 903)	0(43 735)	0(346)	January - December except July
1982	0,02(5 519)	0,02(40 224)	0,3(300)	January - December
1983	0(4 895)	0(38 253)	0(297)	January - December
1984	0,2(6 301)	0,1(55 188)	0,3(403)	January - December

Snoek and maasbanker preyed on lightfish over a large area, mostly between 100 to 300m (Figs 5.4 e and g). No lanternfish were taken by snoek on the South Coast and predation was mostly confined to the area between 200 to 300m isobaths on the West Coast (Fig. 5.4 e).

The lanternfish taken by maasbanker were scattered over a wide area stretching from Cape Hangklip to Hondeklip Bay on the West Coast (Fig. 5.4 h).

Tables 5.1 a-d give an indication of the number of Cape Gannet stomach samples taken at Malgas Island and Lamberts Bay from 1978 to 1985 (only January to April available). Few lantern- or lightfish were taken by Cape Gannet, practically no light- or lanternfish were taken at Lamberts Bay and the fish taken at Malagas Island were usually taken during the spring/summer period. Tables 5.2 a-d indicate that these prey items constituted a small part of the Gannet's diet whether it is expressed as percentage number, weight or frequency.

In conclusion it is clear that both light- and lanternfish are important in the diets of the commercially important fish species investigated in the present study. Resident pelagic seabirds do not prey on these prey species, but non-resident pelagic seabirds are known to take light- and lanternfish.

5.2 THE FEEDING OF L. HECTORIS AND M.MUELLERI

The feeding of a number of mesopelagic fish has been investigated. Merrett and Roe (1974) investigated the patterns and selectivity in the feeding of mesopelagic fishes in the eastern North Atlantic. Feeding periodicity was demonstrated for six species, of which three were found to be feeding selectively : *Valenciennellus tripunctulatus* (Sternoptychidae) on calanoid copepods, *Argyropelecus aculeatus* (Sternoptychidae) on ostracods, and *Lampanyctus cuprarius* (Myctophidae) on amphipods and possibly euphausiids. Copepods, especially *Pleuromamma* spp. were the most abundant food item for four of the six species sampled. The other two fed mainly on ostracods and amphipods.

Kinzer (1982) found that four myctophid fish species off Northwest Africa, *Benthosema glaciale*, *Diaphus holti*, *Myctophum punctatum*, and *Ceratoscopelus maderensis*, were opportunistic predators and grazed heavily at night in the upper 200 m, predominantly on copepods, euphausiids and ostracods. The stomach contents closely reflected prey availability.

Gorelova (1977) investigated the contents of the stomachs and intestines of the young of two ecologically different groups of Myctophidae. The nictoepipelagic species regularly rise to the surface in the nighttime, and mesopelagic species have vertical migrations but do not venture beyond the limits of the mesopelagic region. The principal food of young nictoepipelagic myctophids were copepods, amphipods, euphausiids, mysids and decapods. The food composition of young mesopelagic myctophids was more homogeneous with Euphausiacea comprising up to 94 % of total weight.

Another study examined 988 individuals of four myctophid species, *Myctophum spinosum*, *M. nitidulum*, *M. brachygnathum* and *M. aurolaternatum* (Gorelova 1974). Most of these species inhabit the epipelagic zone (0 to 200 m). The food spectrum was very broad and included about 1000 taxa of planktonic organisms, mostly copepods, amphipods, euphausiids, mysids and some Appendicularia and Chaetognatha.

The common myctophids *Stenobrachius leucopsarus*, *Diaphus theta* and *Tarletonbeania crenularis* caught off Oregon have been observed to have been feeding primarily on the euphausiid *Euphausia pacifica*, the copepods *Metridia lucens* and *Calanus* spp., and the amphipod *Parathemisto pacifica* (Tyler and Pearcy 1975). The diets were diverse and overlapped broadly, suggesting that they are generalist feeders.

Sternoptychidae feed on zooplankton and *Maurolicus muelleri* is a selective cyclic feeder on copepods and euphausiids, copepods being the dominant food item of the young (Badcock 1984). The diet of *M. muelleri* off the coast of northwest Africa was represented by Euphiasiacea, larvae of Decapoda and Copepoda, *Calanoides carinatus* and *Candacia* sp. prevailing among the copepods (Samyshev and Schetinkin 1971). In both the food components and feeding intensity there were no significant differences between females and males, regardless of the maturity stage.

The diet of *M. muelleri* off the South African coast is not known, but considering that the food items for Myctophidae, Gonostomatidae and Sternoptychidae are basically the same (Hopkins and Baird 1977) one can expect the species documented in Fig. 5.5 to be dominant in its diet.

Centurier-Harris (Sea Fisheries Research Institute, Cape Town,

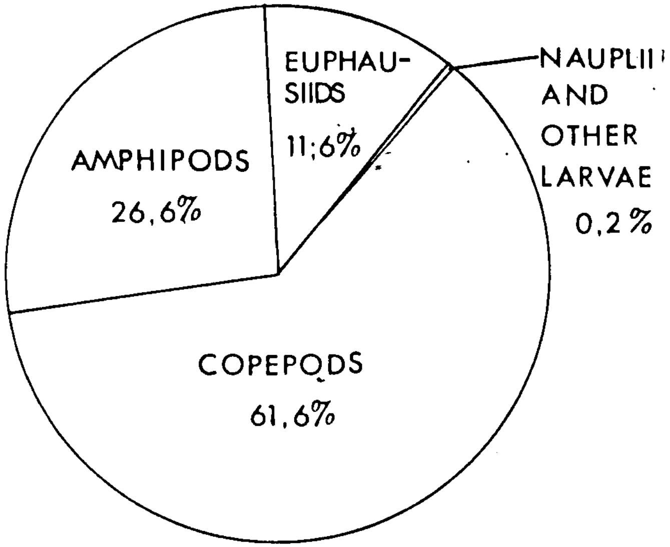


Fig. 5.5: The food of L. hectoris sampled from the South African commercial fleet (Centurier-Harris, Sea Fisheries Research Institute, Cape Town, unpublished).

COPEPODS:	*Centropages brachiatus* (cold water, neritic spp. max. abundance above thermocline)
	Calanoides carinatus (cold water, neritic spp. occurs throughout the watercolumn)
	Rhincalanus nasutus (cold water i.e <13°C common, but never abundant)
	Nannocalanus minor (more offshore)
	Clytemnestra rostrata (not very common rare in surface samples
	Pleuromamma sp (more common offshore, occurs below thermocline – a vertical migrator)
AMPHIPODS:	*Hyperia gaudichandi* (preference for colder upwelled water, neritic, diurndl migrator) .
	Paramoera capensis (common and very abundant in cool, neritic waters)
EUPHAUSIIDS:	*Euphausia lucens* (offshore oceanic neritic)
	Nyctophanes capensis (inshore neritic cold water sp.)

unpublished data) documented the gut contents of Lampanyctodes hectoris caught by the commercial fleet off the west coast of South Africa. This analysis indicated that copepods, amphipods and euphausiids were the main food items (Fig. 5.5). The fish sampled were caught close inshore by the commercial fleet, but the stomachs contained species of copepods such as Nannocalanus minor, Rhincalanus nasutus and Pleuromamma spp. which occur mostly offshore (Pillar, Sea Fisheries Research Institute, Cape Town, personal communication). Therefore, it seems likely that horizontal migration of lanternfish does take place.

Hopkins and Baird (1977), reviewed diet studies on Myctophidae, Gonostomatidae and Sternoptychidae. Although there is considerable phyletic diversity in their diet, crustaceans appear to be the principal forage, copepods, euphausiids, ostracods, amphipods and small decapods being the most important elements.

5.3 DISCUSSION

The results for hake indicate that myctophids are more important in the diet of small M. capensis in terms of weight than recorded by Botha (1980), although the results for large M. capensis are consistent with his observations. Myctophids (L. hectoris) are also more important in the diet of small M. paradoxus than the observations of Botha (1980) indicate. The results for large M. paradoxus are again consistent with his observations.

As indicated above the contribution of light- and lanternfish in the snoek diet in terms of weight fluctuate. This fluctuation may be linked to the feeding behaviour of snoek. According to

Nepgen (1979) snoek gorge themselves and then stop feeding till the stomachs are empty again. Although they feed on a variety of animals, this feeding behaviour usually results in one species being the principal food item in a stomach. The large numbers of prey taken (Fig. 5.2 c) also bear testimony to this behaviour. Both snoek and hake can be classified as opportunistic feeders (Nepgen 1979, Leslie, Sea Fisheries Researech Institute, Cape Town, personal communication) and will prey on light- and/or lanternfish when they encounter these prey items. Since this is true for all their prey items, the commercial exploitation of light- and lanternfish may have a severe impact on hake stocks as the number of "chance meetings" between hake and possible prey items will be reduced. The impact will be more severe for the smaller size classes of *M. capensis* and *M. paradoxus*, but it is not possible to say whether hake will be able to change its feeding strategy in response to this change in prey availability since no data on the results of prey deprivation on hake dynamics is available.

It is interesting to note that *M. capensis* preys on lanternfish in the St. Helena Bay area during June/July, a time when this species is thought to be unavailable to the commercial fleet. During the same period lanternfish were available to *M. paradoxus* much further south than in summer, indicating a possible change in its distribution pattern. No seasonal pattern in the availability of light- and lanternfish to *M. capensis* and lightfish to *M. paradoxus* was apparent. There was also no seasonal difference in the availability of lightfish to the snoek, *T. atun* and the horse mackerel, *T. trachurus*. This may indicate a more widespread distribution of lightfish throughout the year, making it available to both inshore and offshore predators without any seasonal constraints. Research cruises conducted by the Sea Fisheries Research Institute indicate that lightfish is widespread on the west coast throughout the year (Sea Fisheries Research Institute, Cape Town, unpublished). The reason for the seasonal constraint in lanternfish availability to snoek, horse mackerel and offshore hake may be due to an inshore migration. However no data is available to test this theory.

It can be concluded that light- and lanternfish are both important prey species for the fish predators discussed and appear to form a significant percentage of their diets throughout the year over a large area. Furthermore, both prey species appear to be present within reach of commercial trawlers throughout the year and are possibly available to exploitation for longer periods than previously thought. However, future exploitation should take cognisance of the fact that these operations may jeopardize future catches of hake, snoek and maasbanker.

The few light- and lanternfish taken by Cape Gannet support the evidence of Davies (1955 and 1956) and Matthews (1961), suggesting that this predator's diet with respect to these species has not changed.

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CHAPTER 6

A BIOCHEMICAL ANALYSIS OF THE LIGHTFISH MAUROLICUS MUELLERI AND THE LANTERNFISH LAMPANYCTODES HECTORIS

6.1 INTRODUCTION

Physiological studies on mesopelagic fish are few. Childress (1977) reviewed various aspects of the physiology of mesopelagic organisms and concluded that their chemistry is probably more variable than that of inhabitants of any other environment (eg. midwater crustaceans and fishes may be as much as 95% water or as little as 63% water). With this variation, measurements such as wet weight, volume or even dry weight are poor indicators of relative biomass.

The lipid content of midwater animals is perhaps the most studied aspect of their composition, with a focus on the chemistry of the lipids, especially wax esters, and their roles both in the individual organisms and in food chains.

Specific gravity measurements indicate that those fishes with high lipid content (_Stenobrachius leucopsarus_, _Diaphus theta_, _Stenobrachius nannochir_ and _Lampanyctus ritteri_) approach neutral buoyancy. In general, body lipid content was high in fishes that lacked gas-filled swimbladders. Lipid as a percentage of wet weight ranged from 16.0 to 22.1% (Butler and Pearcy 1972). Those myctophids in which the swimbladder is absent, or does not contain gas, and which rely on low density lipid for static lift, do not suffer the same limitations that are imposed by gas, since the compressibility of the lipid probably differs little from that of sea water. Therefore, myctophids with fat-invested swimbladders may undertake more extensive vertical migrations than fish with gas-filled swimbladders (Bone 1973).

Nevenzel et al (1969) investigated the lipids of several myctophids. A large range of total lipid values from 1,2 to 18,5% of wet weight were obtained. Two categories were apparent - the first with low total lipids: 2,1 - 4,3 per cent of wet weight, and the second with high total lipid: 14,2 - 15,8 per cent wet weight. They contend it is probable that different species may be grouped according to their lipid content using these two categories. No significant correlation between location, season or fish size and lipid content was detected.

There is a strong trend for deeper living fish species to have higher water contents. This results in an increase in lipid and a decrease in protein (Childress and Nygaard 1973). This decline in protein with depth is apparently associated with the reduction of muscle tissue (Blaxter et al 1971) and tissue density, in deeper living species (Childress and Nygaard 1974). Fishes with well-developed gas-filled swimbladders have protein contents ranging from 8 to 14.8 per cent of wet weight. Fishes without gas bladders have protein contents ranging from 3 to 11.6% of wet weight (Childress and Nygaard 1973).

The lowest calorific values have been found in deeper-living species while the highest contents have been found in vertically migrating fishes. Values ranged from about 167,4 kJ/100g to 836,8 kJ/100g.

In the present study protein, lipid, water content and calorific values were determined for light- and lanternfish. These values were then compared with those found elsewhere. From the rationale discussed above, the values obtained can also give an indication of the behaviour eg. vertical migration, of these species.

6.2 METHODS

6.2.1 CALORIFIC VALUE

Four samples of frozen lightfish and six samples of frozen lanternfish were oven dried until no reduction in body weight could be detected - usually approximately seven days. These whole fish samples were then homogenised using a Kinematica grinding machine. Great care was exercised to remove all traces of the previous sample before the next was processed and great difficulty was experienced in homogenising the samples due to the very high oil content.

Material from each sample was used to make compressed "pills" weighing approximately one gram. These compressed samples were accurately weighed using a chemical balance and the calorific value was measured using a Parr 1680 Adiabatic Oxygen Bomb Calorimeter. Each sample was processed in triplicate to determine whether the variation within the technique is of the same order as possible variations between samples.

6.2.2 PROTEIN

The Kjeldahl method of protein determination was used (Bradstreet 1965).

A five gram sample of wet fish, using the whole fish with the viscera intact, was digested with the following mixture in a 800ml Kjeldahl flask:

25ml conc. H_2SO_4
15g anhydrous K_2SO_4
0,7g HgO

500 watt electrical heaters, controlled by simmerstats, were employed for the digestion which was continued until the contents of the flask became clear and then for a further two hours.

After cooling, the digested material, approximately 200ml tap water and 2 pellets analytical reagent Zinc were added, followed by 200ml of 40% commercial NaOH solution containing 3,5% sodium thiosulphate.

Immediately after the addition of the NaOH solution, the contents of the Kjeldahl flask were heated strongly and distilled using a distillation unit. The distillate was absorbed by 100ml standard N/5 H_2SO_4 contained in a 1-litre Erlenmeyer flask and the distillation was continued until at least 200ml had distilled over.

The residual standard H_2SO_4 was titrated against standard N/5 NaOH using screened methyl red indicator; a blank titration of the reagents employed was also determined.

$$\% \text{ crude protein} = \frac{(B-S) \times N \times 14,008 \times 6,25 \times 100}{\text{weight of sample} \times 100}$$

where B = ml N/5 NaOH back titration in blank

S = ml N/5 NaOH back titration in sample

N = normality of NaOH

The principle of the method is as follows: Part of H_2SO_4 is reduced to sulphur dioxide. This sulpher dioxide reduces the organic nitrogen compounds to NH_3 (The C and H of the organic material is oxidised to CO_2 and H_2O). The NH_3 combines with the remaining H_2SO_4 to form ammonium sulphate, which has a very high boiling point. K_2SO_4 raises the boiling point of the mixture and hence hastens digestion. HgO acts as a catalyst.

6.2.3 TOTAL LIPID

The method used was an adaption of the Reflux method (Heydenrych, Fishing Industry Research Institute, University of Cape Town, personal communication) which in turn was an adaption of the Bligh and Dyer (1959) method of total lipid extraction and purification.

A five gram sample of wet, minced fish, using the whole fish with the viscera intact, was weighed into a centrifuge bottle; 12ml of distilled water, 40ml methanol and 20ml of chloroform were added. This mixture was blended for 3 minutes with a Silverson laboratory mixer/emulsifier. Another 20 ml of chloroform was added and the mixture was blended for 1 minute; 20ml distilled water was added and blended for a further 1 minute. The blender head was then washed with a minimum amount of distilled water into the flask.

The mixture was centrifuged at 2 500 to 3 000 rpm for 10 minutes; 20ml of the chloroform layer at the bottom was then removed and placed in a previously weighed 100ml beaker. This sample was evaporated to dryness, placed in an oven at 105 ^{0}C for 30 minutes, left to cool and was then weighed.

The calculation used to obtain total lipid was:

$$\text{Percentage Total lipid} = \frac{\text{weight of oil} \times 100}{\text{wet weight of sample}} \times \frac{40}{20}$$

6.2.4 WATER CONTENT

Individual fish were weighed and then transferred to an oven. Drying took place at 110 ^{0}C for approximately 12 hours after which the individual fish were again weighed. The calculation used to obtain water content was:

Percentage Water Content =

$$\frac{(\text{weight of fresh sample} - \text{weight of dried sample})}{\text{weight of fresh sample}} \times 100$$

6.3 RESULTS

The calorific values per gram of dry weight for light- and lanternfish are shown in Table 6.1. Although the calorific values of <u>L. hectoris</u> and <u>M. muelleri</u> are of the same order of magnitude, <u>L. hectoris</u> appear to have a slightly higher value. However, the two sets of data were taken in different months and the small sample size precludes definite conclusions. The values obtained

Table 6.1 The calorific values (in kilojoules) per gram of dry weight of light- and lanternfish as determined by a bomb-calorimeter. The values given are the mean of triplicate samples taken from the same fish.

Date Sampled	Lanternfish (kJ/g)
January	25,4
February	26,3
February	27,9
February	25,7
February	23,2
February	28,1
February	27,2
February	24,7
February	28,0
February	27,1
April	29,8
April	28,4
April	27,6

Date Sampled	Lightfish (kJ/g)
November	22,5
November	22,8
November	23,2
November	22,6

Table 6.2 The Lipid and Protein Content as a percentage of wet weight for *M. muelleri*. The date of capture and caudal length are indicated.

Date of Capture	Caudal Length	Lipid Content	Protein Content
3rd November 1983	3,2	4,0	18,6
3rd November 1983	3,4	3,2	18,7
3rd November 1983	3,6	4,1	17,8
3rd November 1983	3,8	3,4	18,9
3rd November 1983	4,0	3,0	17,9
10th April 1984	3,4	13,6	16,4
10th April 1984	3,6	16,8	17,3
12th April 1984	3,4	18,0	14,6
12th April 1984	3,6	19,3	14,0
12th April 1984	3,8	18,8	14,5
12th April 1984	3,0	15,5	17,1
12th April 1984	3,2	13,9	15,5
12th April 1984	3,4	14,4	16,2
12th April 1984	3,6	17,4	14,6
12th April 1984	3,8	17,5	13,5
12th April 1984	4,0	17,1	15,2

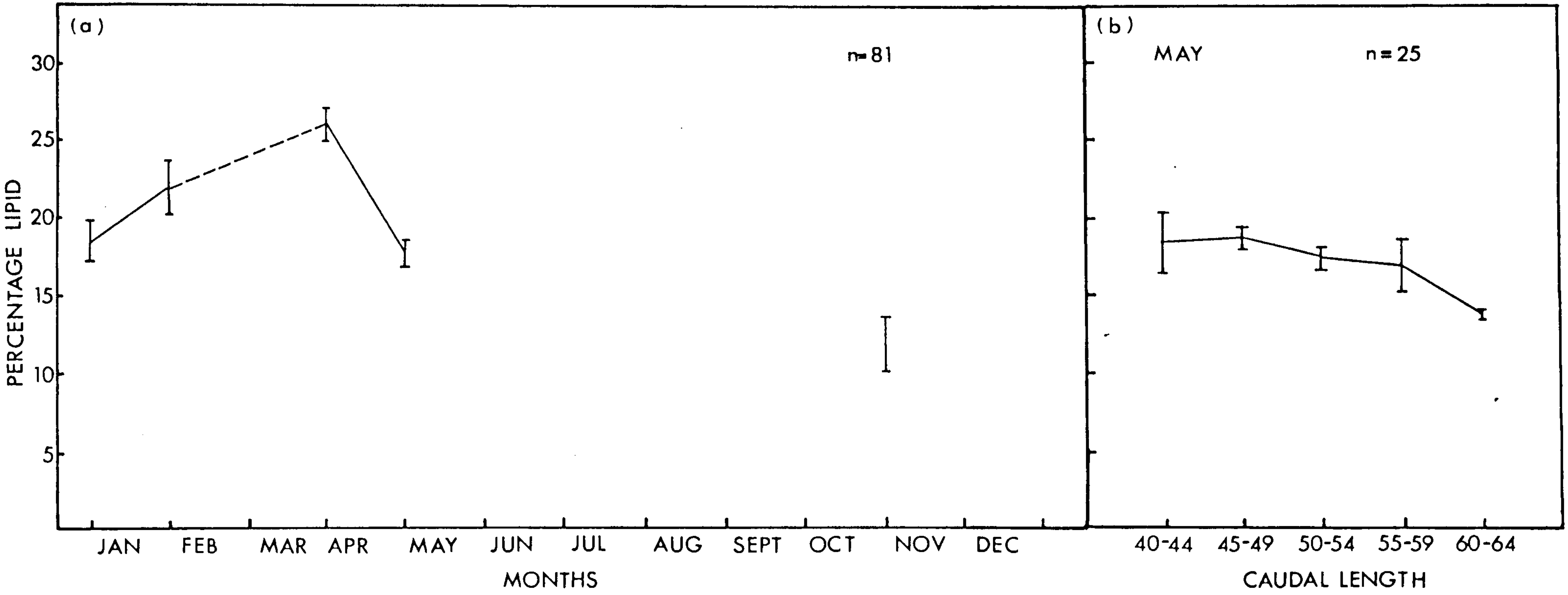

Fig. 6.1: The total lipid content for (a) all size classes of *L. hectoris* combined and (b) the total lipid content for size classes sampled in May only.

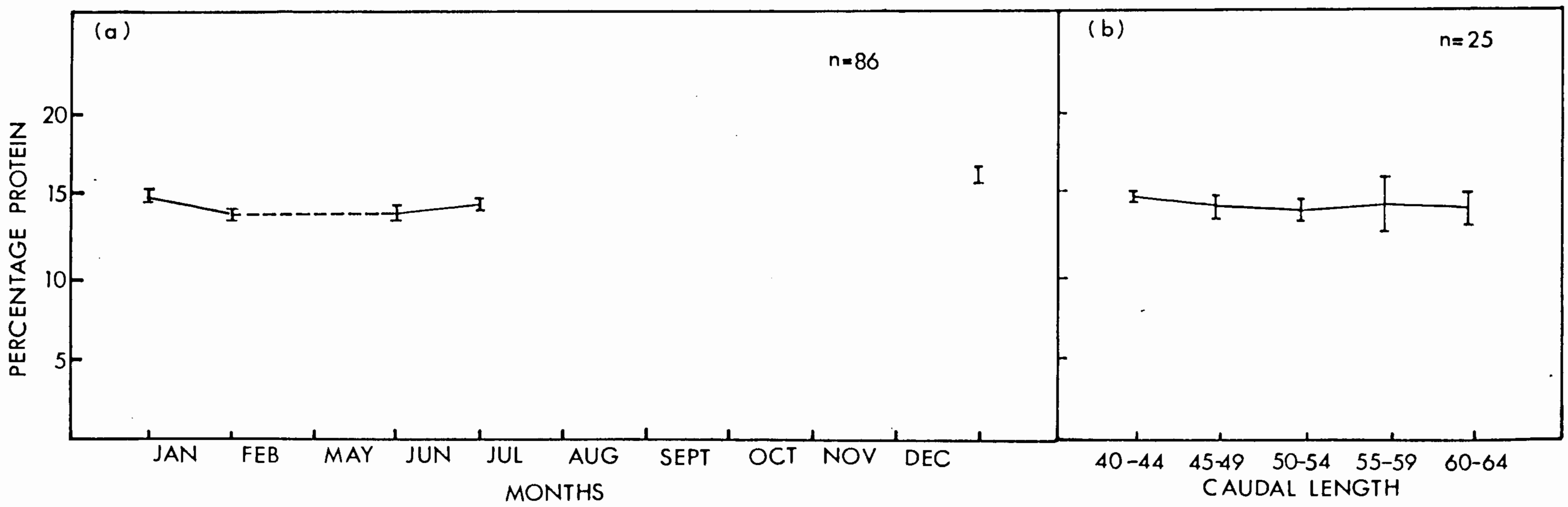

Fig. 6.2: The protein content for (a) all size classes of *L. hectoris* combined and (b) the protein content for size classes sampled in May only.

for L. hectoris showed little variation from February 1984 to February 1985 and again between February and April 1984. Since no lanternfish were sampled at the end of the year and all the lightfish were sampled in November the lower values for lightfish may by due to the time of sampling.

The lipid content for a number of months for L. hectoris is shown in Fig. 6.1 a. Monthly fluctuations in lipid content (as a percentage of wet weight) do occur and the lipid content of individual fish expressed as a percentage of wet weight ranged from 9,3 to 31,2. In addition a declining trend in lipid content with an increase in size is apparent (Fig. 6.1 b).

Although samples of M. muelleri were available only for two months (November 1983 and April 1984) a sharp increase in lipid content is apparent from November to April (Table 6.2). The lipid content also fluctuates over different size classes eg. in April the mean values are 16.2 per cent for 3,4cm, 18,4 per cent for 3,6cm and 18,2 per cent for 3,8cm fish. However, due to the small sample sizes the lightfish values for the different size classes do not differ significantly.

Figs 6.2 a and b illustrate the change in percentage protein (dry weight) for lanternfish for different months and size classes. Little variation is apparent between months and between length classes.

Due to the small number of lightfish samples analysed, no data was plotted. The protein content determined for M. muelleri also shows little variation between months or length classes (Table 6.2).

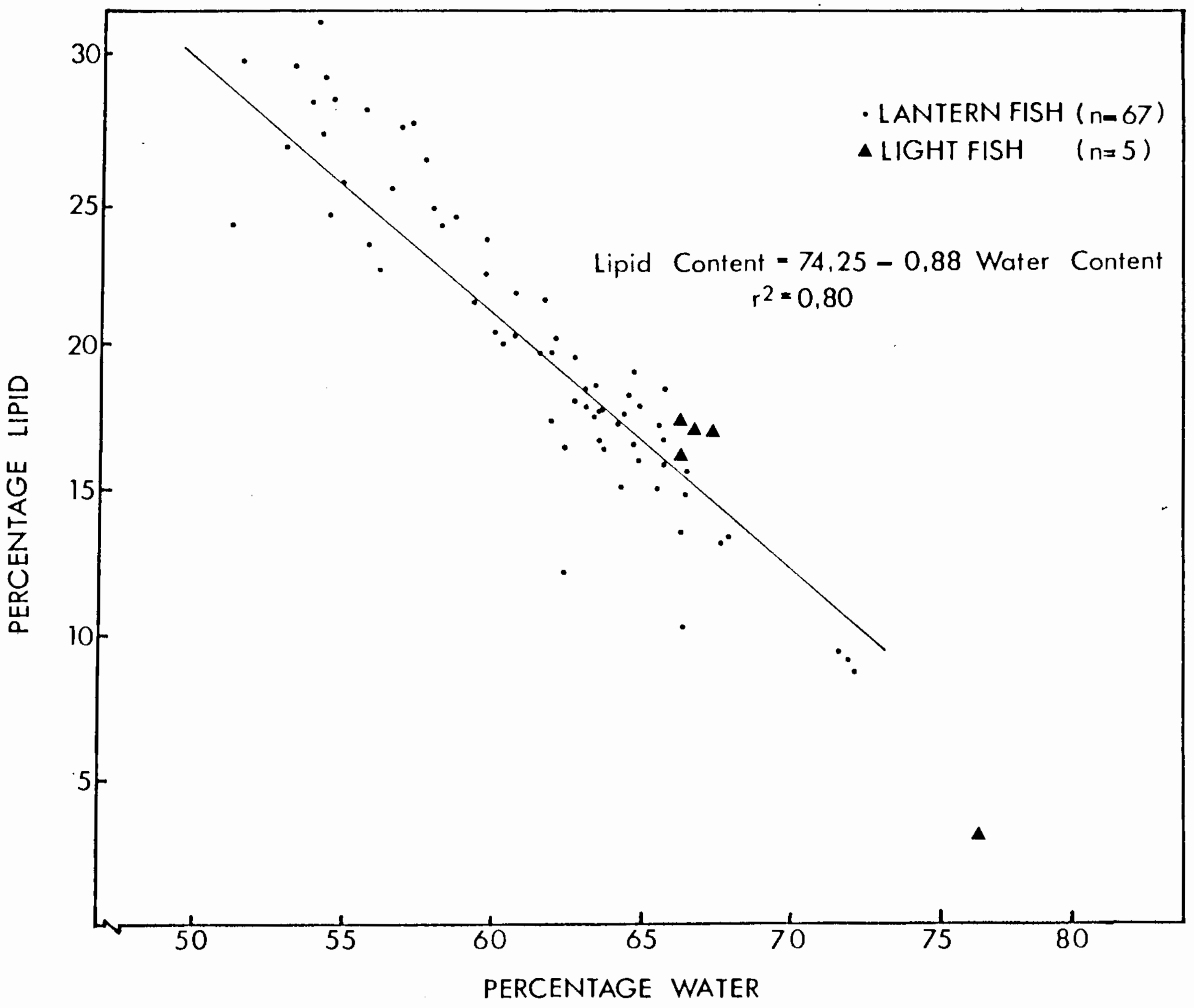

Fig. 6.3: The relationship between lipid and water content in *L. hectoris* and *M. muelleri* tissue.

A relationship with a negative slope between lipid and water content in light- and lanternfish was found (Fig. 6.3). Only a few lightfish data points are available and are also shown in Fig. 6.3. The water:lipid ratio was the same for light- and lanternfish.

6.4 DISCUSSION

The lipid values of L. hectoris (range 9.3-31.2 % wet weight) off South Africa are higher than that obtained by Butler and Pearcy (1972), Nevenzel et al (1969), Melnikova (1973) and Kayama and Ikeda (1975, cited by Gjosaeter and Kawaguchi, 1980) for a range of Myctophidae. The low values obtained in November are also higher than the minima calculated by these authors. Nevenzel et al (1969) found two distinct categories of Myctophids based on total lipid content. The first with low total lipids, 2,1 - 4,3 per cent and the second with high total lipid, 14,2 - 15,8 per cent. Using this classification L. hectoris may occupy a third class. However, this type of classification is open to error as fluctuations associated with season and/or length may influence the lipid content. Fig. 6.1 a clearly shows that monthly fluctuations in lipid content (as a percentage of wet weight) do occur in L. hectoris. Although a declining trend in lipid content with an increase in size is apparent (Fig. 6.1 b), Nevenzel et al (1969) found no evidence of seasonal or size related fluctuations in lipid content.

Childress and Nygaard (1973) found a strong negative correlation between protein and lipid for a number of mesopelagic fish species when both are expressed as percentage of ash-free dry weight. They concluded that this indicates that protein and lipid are the two major components of the ash-free dry weight. Therefore a substantial change in one can be achieved only with an inverse proportional change in the other. However, Figs. 6.1 a and 6.2 a reflect only a weak negative correlation. Therefore the substantial drop in lipid content in November was not followed by a proportional increase in the protein content.

The lipid values obtained for M. muelleri in November are of the same order as those obtained for a number of Gonostomatidae and Sternoptychidae (Kyama and Ikeda 1975, cited by Gjøsaeter and Kawaguchi 1980). The values obtained for M. muelleri were 3,0 to 4,1 per cent lipid in fresh body weight. These low values may be a function of the time of sampling. However, the high lipid values obtained for M. muelleri in April are higher than any of the values obtained for other mesopelagic fish, excluding the values determined for L. hectoris in the present study. Since the protein content shows little variation between months or length classes, the substantial drop in lipid from April to November is not compensated for by a proportional increase in the protein content. However, based on the negative correlation between lipid and water content, lipid is almost exactly replaced by water (Fig. 6.3).

The drop in lipid content for both L. hectoris and M. muelleri during the latter part of the year may be a function of spawning. Lipids are probably stored in anticipation of the major spawning in winter/spring, after which the lipid content would decrease dramatically. Protein would not be affected in this process as the fish is not expected to metabolise body muscle in the process of spawning. The decrease in lipid with increasing length is probably due to a larger percentage of larger fish being sexually mature and participating in spawning.

It is possible to estimate the calorific content of an animal directly by using a calorimeter or indirectly by calculation from the composition. The two methods show reasonable agreement for midwater animals (Childress and Nygaard 1974, Tyler 1973). All estimations of calorific content of mesopelagic fish species done by Childress and Nygaard (1973) were estimated indirectly and expressed as kJ/100g wet weight. This makes direct comparison difficult, but using the conversion:

$$\text{kJ/100g} = 4{,}2\{([\text{Carbohydrate} + \text{protein}] \times 3{,}6) + (\text{lipid} \times 9)\};$$

the calorific content per wet weight was determined (carbohydrate was ignored as it is negligible, Heydenrych, Fishing Industry Research Institute, University of Cape Town, personal communication). The calorific content per wet weight for both *L. hectoris* and *M. muelleri* were on average higher than that of 26 species including Myctophidae, Gonostomatidae, Sternoptychidae, Bathylagidae and Engraulidae, tested by Childress and Nygaard (1973). The values were closest to those obtained for the myctophids, *Diaphus theta*, *Lampanyctus ritteri*, *Stenobrachius leucopsaurus* and *Triphoturus mexicanus*.

The calorific content of both *L. hectoris* and *M. muelleri* are also higher than those of other commercially important pelagic fish. These values are, pilchard (*Sardinops ocellatus*) 21,9 kJ/g (n=131), anchovy (*Engraulis japonicus*) 21,4 kJ/g (n=121) and round-herring (*Etrumeus micropus*) 21,4 kJ/g (n=65). Maasbanker (*Trachurus trachurus*) has a value of 24,1 kJ/g (n=7) which is higher than that of lightfish, but lower than the value obtained for lanternfish. (Sea Fisheries Research Institute, Cape Town, unpublished).

The high oil content of *L. hectoris* does cause processing problems and its meal has to be mixed with that of round-herring to ensure a standard acceptable to animal-feed manufacturers. One would expect that possible future exploitation of *M. muelleri* would encounter the same problem.

Both *L. hectoris* and *M. muelleri* possess well developed gas-filled swimbladders (Ahlstrom *et al* 1976 and Badcock 1984) and a high lipid content as shown in the present study. As previously mentioned, fishes with well developed gas-filled swimbladders had a low body lipid content (Butler and Pearcy 1972) and a high protein content (Childress and Nygaard 1973) while the highest calorific values were observed in vertically migrating fish.
Both the fish species investigated in this study have been noted for their extensive diurnal vertical migrations in the Benguela upwelling region (Sea Fisheries Research Institute, Cape Town, unpublished). The high calorific and protein values found in these fish species may therefore be associated with the presence of a well developed gas-filled swimbladder together with the vertical migration undertaken, but the reason for the high lipid content is not clear. The seasonal variation in lipid content may be explained by spawning strategy, but the high overall values may be a function of their vertical migration patterns. As mentioned, fish species which rely on lipid instead

of a swimbladder do not suffer the same limitations that are imposed by gas, since the compressibility probably differs little from that of sea water (Bone 1973). These fish species may use a combination of lipid and their swimbladders to give them an ability for increased vertical migration. It may also be easier to maintain a position in the water column.

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CHAPTER 7

CONCLUSIONS AND RECOMMENDATIONS

7.1 CONCLUSIONS

The main conclusions of this study are set out below (the respective chapters are given in brackets).

1) The length frequency distributions for both *L. hectoris* and *M. muelleri* do show a seasonal variation and support the spawning pattern determined during the Cape Egg and Larvae Programme (CELP). *L. hectoris* spawning in the southern Benguela Current System occurs throughout the year, but mainly during the late winter to early spring with a peak in spring. *M. muelleri* spawning occurs throughout the year, with a peak in spring/early summer and a smaller peak in winter (Chapters 1 and 3).

2) The enumeration of daily otolith growth rings indicates that the bulk of the *L. hectoris* and *M. muelleri* populations off the South African coast do not reach an age greater than twelve months. The estimates of natural mortality suggest that more than 90% of these populations die from natural causes each year (Chapter 2).

3) The relation of otolith length and radius to body length may show large seasonal variations. The variation complicates the calculation both of ring formation dates and the growth of juveniles from otoliths (Chapter 2).

4) Most L. hectoris are mature in July/August with some gonad activity in May and November/December whilst M. muelleri gonad activity is apparent throughout the year with a peak in July/August. These observations support the length-frequency distributions and the CELP results (Chapters 1, 3 and 4).

5) Although female L. hectoris tend to reach a greater length than males, the length at first maturity is the same (3,6 cm caudal length, 5 to 6 months of age). However, M. muelleri females which also attain a greater length than males, lag behind males in maturing sexually. Length at first maturity is similar (2,6 and 2,4cm for males and females respectively, 6 to 7 months of age), but length at 50% maturity shows this lag (3,0 and 3,8cm for males and females respectively, 8 and 11 months of age) (Chapter 4).

6) M. muelleri spawning has both a vertical and a horizontal dimension. The majority of sexually active fish occur at depths greater than 90 metres and appear to be concentrated horizontally (Chapter 4).

7) Both L. hectoris and M. muelleri were important in the diets of the fish predators investigated. Both species of hake, snoek and horse-mackerel in the southern Benguela Current system preyed on lantern- and lightfish throughout the year. Before future commercial exploitation of these mesopelagic fish stocks commence, this aspect must be carefully considered (Chapter 5).

8) The total lipid content determined for both M. muelleri and L. hectoris in this study was higher than measurements made for other mesopelagic fish elsewhere. Seasonal changes in lipid content for both light- and lanternfish and a decline in lipid content with an increase in size for lanternfish was observed. A negative linear correlation between total lipid content and water content was calculated for lanternfish and it appears as if a similar relationship exists for the lightfish (Chapter 6).

9) The calorific values obtained for both L. hectoris and M. muelleri show no seasonal variation and are higher than values calculated for mesopelagic fish elsewhere and commercially important fish off the South African coast (Chapter 6).

7.2 RECOMMENDATIONS

Data collected and presented in this study have been mostly of an incidental nature in the form of spin-offs from research cruises and was collected over a number of years. The fluctuating nature of annual commercial catches of L. hectoris by purse-seiners and no commercial exploitation of M. muelleri have resulted in a severe shortage of relevant information to continue the study into these potentially important resources. The Cape Egg and Larvae Programme in 1977/78 has indicated that large populations of both these species may exist in the southern Benguela Current System. Subsequent research cruises have borne out this assessment.

Further information is necessary to alleviate this paucity in knowledge. Therefore a scientific sampling cruise, geared to nets of commercial standard, must be undertaken in order to provide a start in elucidating variability in distribution and biomass at the oceanic/neritic interface zone. The data collected from such a survey will be meshed with the results from acoustic and targeted investigations of mesopelagic fish in the upper water column. A sixteen day cruise is envisaged, preferred months being December or April although any time of the year will produce invaluable information and research material.

Two areas need to be surveyed, the first is the Columbine canyon off Cape Columbine in order to sample the benthic and epibenthic fish and the second area is close inshore and should stretch from Lambert's Bay in the north to Saldanha Bay in the south. The latter area will include the area where L. hectoris is most available to the commercial fleet. Samples will be taken from a depth range of 200-1000 m over the canyon using an Engels Mid-Water Trawl and a 180 Bottom Trawl. Closer inshore, sampling will be done using Rectangular Midwater Trawls over a depth range of 0-400 m and these will be compared with those obtained over the canyon.

In addition to obtaining material to continue studies such as ageing and biochemical analysis, a number of key questions need to be addressed. Some of these questions were formulated by a working group of the Alternative Resources Group of the Benguela Ecology Programme whilst others were highlighted in the present study;

1) What species of fishes comprise the benthic and epibenthic faunas of the lower shelf and upper slope regions in the southern Benguela Current System, and what is the relationship between

species diversity and/or depth parameters?

2) At what depths is the biomass at a maximum, and how does the mean weight of individuals vary with increasing depth?

3) What is the relationship between the epibenthic fauna and the benthic fauna in terms of shared species and biomass estimates and does this relationship vary on a diurnal cycle?

4) Are commercially available mesopelagic fish being transported from beyond the shelf break closer inshore via the Columbine canyon?

5) Is a constant source of mesopelagic fish available to the fleet?

6) Do maturity- length- and weight parameters change with increasing or decreasing depth and what environmental factors relate to these changes?

7) Are the high natural mortality estimates estimated in this study due to factors such as emigration and/or inefficient sampling of the population?

8) What is the age structure of the relevant populations?

9) Are the spawning strategies of mesopelagic fish similar to those of pelagic fish?

The importance of an escalation in research on alternative resources, especially for alternative fish resources, cannot be emphasized too strongly, especially if viewed against the background of the present problems encountered with existing stocks.

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