VARIABILITY OF COPEPOD ABUNDANCE AND GROWTH IN THE SOUTHERN BENGUELA UPWELLING SYSTEM AND IMPLICATIONS FOR THE SPAWNING OF THE CAPE ANCHOVY

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Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in the Faculty of Science (Department of Zoology), University of Cape Town

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March 1998

DECLARATION

This thesis reports the results of original research I carried out at the Sea Fisheries Research Institute and the Marine Biology Research Institute between 1993 and 1997. The ideas presented in this thesis are largely my own, although data were obtained from a number of sources.

Data on anchovy egg abundance were provided by Justine Fowler. Simon Bloomer supplied the birthdate distributions for anchovy. To test some of the hypotheses developed in this thesis, historical data from the Sea Fisheries Research Institute were provided by Drs Hans Verheye and Larry Hutchings. Microzooplankton data in Chapter 3 were provided by Mr Carl van der Lingen and Dr Su Painting. Fish data were supplied by Janet Coetzee and Dr Rob Leslie. All samples for measurement of copepod biomass and growth were counted by myself and technical staff of the Sea Fisheries Research Institute.

This work has not been submitted for a degree at any other university and any assistance I received is fully acknowledged.

Signed by candidate

signature removed

Anthony James Richardson

For mum and dad

On the robustness of *Calanus*...

"... specimens often lacked caudal furcae, or the tips of their antennae, and sometimes lacked spines or even joints on some of the pleopods. They lived well in spite of these injuries and, indeed, it is surprising how much a Calanus *will endure."*

Marshall and Orr (1952)

On the study of fisheries...

"... the science of recruitment does not yet exist"

Cushing (1995)

TABLE OF CONTENTS

ABSTRACT

In the southern Benguela upwelling system, anchovy spawn serially between September and February each year. It has been suggested that this energy-intensive reproductive strategy requires continual ingestion of copepods, which dominate the diet of anchovy at this time. This thesis investigates the spatial and temporal variability of copepod abundance and growth, and their impact upon the spawning of anchovy. Sampling was conducted monthly between August-March 1993/94 and 1994/95. It is noteworthy that the primary spawning ground of anchovy, the western Agulhas Bank, had a significantly smaller biomass of copepods than the adjacent West Coast region. In terms of the growth rates of copepods, the effect of food-limitation on fecundity and somatic growth outweighed that of temperature. Growth rates were positively related to both Chl *a* concentration and phytoplankton cell size. Mean growth rates were closely related to body size, showing a 10-fold decline, from 0.545 d^{-1} (500 μm TL) to 0.056 d^{-1} (2750 μm TL). This was primarily a result of food-limited growth of large copepods. Small copepods always grew at near-maximal rates, a consequence of their ability to consume small particles which are omnipresent at a relatively constant background density. In contrast, large copepods were frequently food-limited by the availability of large cells. Thus, growth rates of the large copepodites of the dominant copepod species on the western Agulhas Bank (*Calanus agulhensis*) varied seasonally. Growth was moderate in September/October following water column stabilization after winter, slow in November/December as the upper mixed layer warmed, and fast during the upwelling period on the western Agulhas Bank (January-March). This temporal variation in growth mirrored changes in Chl *a* concentration following seasonal warming and wind patterns. The spawning of sardine, which is more phytophagous than anchovy, followed these seasonal fluctuations, with spawning peaks in September/October and January/February when optimal food conditions for adults (in terms of Chl *a*) and larvae (in terms of production of copepod eggs and nauplii) prevailed. Conversely, anchovy spawning peaked from October to December, temporally separate from sardine and coincident with optimal feeding conditions for adults in terms of their preferred food source (large copepods) within their favoured spawning habitat (16-19 °C). A simple mass-balance model of copepod biomass on the western Agulhas Bank showed that there was sufficient copepod production on the western Agulhas Bank for anchovy and other pelagic fish to satisfy their metabolic requirements. Production not consumed was exported to the West Coast and this increased throughout the anchovy spawning season. It is concluded that the high and consistent biomass of large copepods on the western Agulhas Bank is a consequence of the advection into the region of large copepods from the eastern Bank with the advective removal of both small and large individuals. Although the western Agulhas Bank has a smaller biomass of copepods than the adjacent West Coast and there is strong density-dependent competition for food, it is a more suitable spawning area for anchovy in terms of its greater thermal stability, larger area of 16-19 °C water, and more consistent food environment. The persistence of these optimal conditions prolongs the spawning season. This may compensate for the high and variable mortality of anchovy eggs and larvae in the region downstream of their spawning grounds, and thus improve the likelihood of good recruitment.

ACKNOWLEDGEMENTS

I would initially like to thank Dr Craig Johnson of the University of Queensland for encouraging me to undertake this PhD at the University of Cape Town. The financial assistance and support provided by the Benguela Ecology Programme and the University of Cape Town (UCT) through my supervisor at UCT, Prof. John Field, are gratefully appreciated. Thanks also to Dr Coleen Moloney for insightful comments along the way. I am especially indebted to Dr Hans Verheye, my supervisor at the Sea Fisheries Research Institute (SFRI), who provided intellectual stimulation, friendly advice, and innumerable rewrites throughout my research. Many a time did I receive back a draft which was almost illegible with red pen! His belief in producing quality work and his indefatigable ability to correct (and improve) drafts which I thought were satisfactory is warmly appreciated. I would also like to thank the director of SFRI, Dr Andy Payne, for making the wonderful facilities of the institute available for my research and for the participation of the institute in the SARP programme, of which my work forms a part.

As part of this multidisciplinary project, I collaborated with many people including Simon Bloomer, Janet Coetzee, Justine Fowler, Yolanda Melo, and Betty Mitchell-Innes and would like to acknowledge their help and guidance. I am deeply indebted to the technicians in the Plankton Section at SFRI, including André du Randt, Diane Gianakouras, Alan Kemp, and Carolyn Myburgh, both at sea and in the laboratory. I am especially thankful to Susan Payne, Anastasia Polito, and Elana Wright for their tireless work counting plankton samples. Without their help, I would still be counting bugs! I would also like to thank the scientists in the "Plankton Section" of the Sea Fisheries Research Institute for their discussions and assistance, including Larry Hutchings and Su Painting. I gratefully acknowledge Mark Gibbons, Jenny Huggett, Rob Leslie, and Carl van der Lingen for their interesting and useful discussions and for reading draft manuscripts. Special thanks go to Grant Pitcher for many stimulating conversations, about cricket, rugby (I'm still waiting for the wallabies to beat the boks!), and his insight into science. Betty Mitchell-Innes was very helpful and provided valuable knowledge of the functioning of the southern Benguela system. There has been a warm and friendly atmosphere at SFRI, which has made me feel like a real plankton "bum".

My special thanks also go to my parents who I have missed deeply. I apologize for the years I've spent away from home during very sad times. Without their support, encouragement, and love this thesis would not have been possible (hopefully now I can get a job!). Lastly, I would like to thank the many friends I've made in South Africa for keeping me sane and believing in me, particularly Glynnis Felaar who has always been a source of comfort, love, and support. I have had a wonderful time doing my PhD in South Africa.

GENERAL INTRODUCTION

The Benguela Current off the west coast of southern Africa is one of the world's four major eastern boundary systems (Parrish *et al.* 1982). These systems are characterized by coastal upwelling, a process whereby surface waters that are pushed away from the coast by equatorward winds are replaced by cool water from intermediate depths (Mann and Lazier 1991). Upwelled water is rich in nutrients and promotes growth of phytoplankton, which then support large standing stocks of herbivorous zooplankton.

In upwelling areas, copepods often dominate the zooplankton in terms of numbers and weight (Hutchings *et al.* 1991). As such, they are important nitrogen remineralizers (Moloney *et al.* 1991) and their faecal pellets provide an important energy source for the benthic community (McCave 1975). Moreover, copepods are a major link between primary producers and higher trophic levels. Many marine invertebrates such as chaetognaths, decapods, scyphozoans, siphonophores, ctenophores, and hydromedusae are carnivorous and are dependent upon copepods (Gibbons *et al.* 1992). In turn, these invertebrates are a source of food for animals at higher levels in the food web. Copepods are also utilized directly by most species of fish at some stage of their life cycle (Cushing 1978; Cushing 1990) and some whales (Best 1967). Egg and naupliar stages of copepods are a suitable size to be ingested by clupeoid larvae (Turner 1984), especially the first-feeding larvae that are the most vulnerable to starvation (Blaxter and Hunter 1982). In upwelling areas, several adult pelagic fish, including sardine *Sardinops sagax* (van der Lingen 1994), round herring *Etrumeus whiteheadi* (Wallace-Fincham 1987), and anchovy *Engraulis capensis* (James 1987), *Engraulis mordax* (James and Chiappa-Carrara 1990), and *Engraulis anchoita* (Ciechomski, de 1967), also feed on copepods.

Pelagic fish stocks in upwelling areas are characterized by large variations in stock size (Pauly and Tsukayama 1987; Lluch-Belda *et al.* 1992), presumably because of their short life spans and the dynamic nature of upwelling environments (Shelton 1987). Fluctuations occur on a decadal time-scale (Crawford *et al.* 1987), possibly in response to changes in their food environment (Verheye and Richardson in press; Verheye *et al.* in press), and on an annual time-scale as a result of recruitment variability (Cury *et al.* 1995). Hutchings (1992) identified several critical processes affecting the recruitment success of anchovy in the southern Benguela system. These include the energy available for the spawning of anchovy in terms of their food environment and fat reserves, changes in the behaviour of the jet current which transports eggs and larvae to the recruitment grounds, and secondary production in the nursery region of the West Coast during larval development.

To investigate the effect of these key processes on fluctuations in anchovy recruitment, a South African SARP (Sardine Anchovy Recruitment Project) was initiated in 1993 (Painting 1993), similar to the international programme of the same name (Anon 1989). This programme focuses on the intra-seasonal variation of growth and survival of early stages of pelagic fish, and the reproductive output of their adults. An important feature of SARP is the high temporal resolution of sampling within the spawning season. In the South African SARP, sampling was conducted monthly throughout the anchovy spawning season.

Anchovy was the main fish species targeted in the South African SARP because it has been the dominant pelagic fish in the system from the 1970s to the mid-1990s (Verheye *et al.* in press). Understanding recruitment variability of this species is of particular importance, considering that approximately 70% of the annual catch is from 0-year-old recruits (Cochrane and Hutchings 1995). The life-cycle of the Cape anchovy has been the focus of intense study and has been well documented (King *et al.* 1978; Shelton and Hutchings 1982; Shelton and Hutchings 1990; Hutchings 1992). Anchovy spawn predominantly on the western Agulhas Bank (Fig. 1) between September and February (Shelton 1986; Melo 1994a). Anchovy spawn serially during this protracted spawning season (Melo 1994b). The spawning products are then transported from the western Agulhas Bank, around Cape Point and northward in the jet current along the West Coast to the recruitment grounds between St Helena Bay and the Orange River Mouth (Fig. 1, Hutchings 1992, Shelton and Hutchings 1990). After three months the larvae metamorphose and recruit to the fishery at six months of age. Anchovy become sexually mature at one year of age and return to the western Agulhas Bank to spawn.

The serial spawning strategy of anchovy is energy intensive, requiring continual ingestion of food (Hunter and Goldberg 1980; Armstrong *et al.* 1991a; Hutchings 1992; Melo 1994b). If anchovy do not meet their metabolic requirements, they undergo ovarian atresia (Hunter and Macewicz 1980; Melo 1994a) and may cease spawning for the remainder of the season (Hunter and Macewicz 1985). The study of copepods was an important component of SARP because anchovy spawners on the western Agulhas Bank feed almost exclusively on copepods (James 1987). Furthermore, it is believed that anchovy on the western Agulhas Bank are sometimes food limited (Peterson *et al.* 1992; Cochrane and Hutchings 1995) because this region has a smaller copepod biomass than the more productive West Coast (Pillar 1986; Hutchings *et al.* 1995). The food environment for anchovy has been estimated during November (1988-1997), the assumed mid-season spawning peak (Shelton and Hutchings 1990). The representativeness of this single estimate of the food environment to the entire spawning season is not known. Cochrane and Hutchings (1995) concluded that food availability was

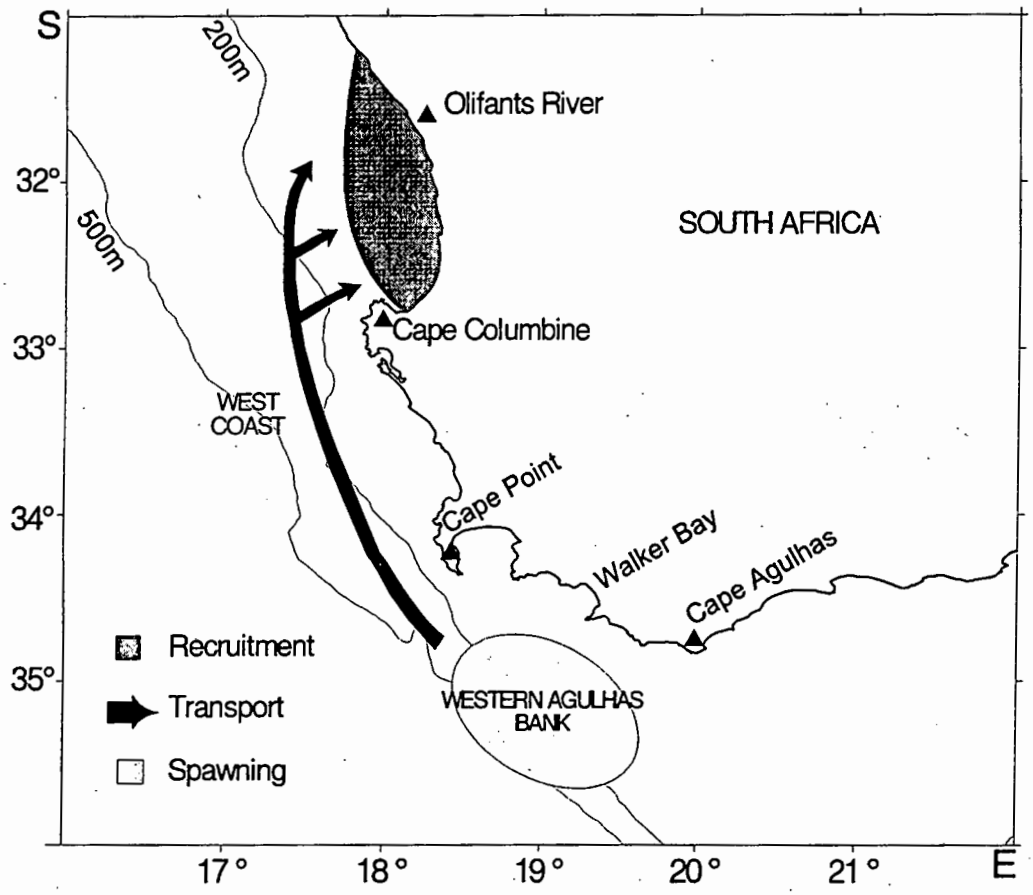


Fig. 1. The life cycle of the Cape anchovy, showing spawning and recruitment grounds in the southern Benguela upwelling system.

one of the most promising variables for forecasting anchovy recruitment.

The broad objectives of this study were to investigate the variability of copepod abundance and growth in the southern Benguela system, and to use this information to examine their impact upon the spawning of the Cape anchovy. To avoid repetition, methods common to many of these chapters are combined into Chapter 1. Other procedures specific to each chapter are discussed therein. Chapter 2 examines the biomass of copepods in the southern Benguela region and its intra-seasonal and cross-shelf variation. The shortcomings of the sampling strategy to detect intra-seasonal variation of copepod biomass are discussed, and improvements for future sampling programmes are suggested. Chapter 3 deals with factors that influence the sex ratio of copepods. Three hypotheses concerning the sex ratio of adult copepods are tested: (1) sex ratios of pelagic copepods are related to trophic mode, with a greater proportion of females in herbivores than in carnivores or omnivores; (2) sex ratios are skewed toward females because of greater mortality of males; and (3) sex ratios are influenced by changes in environmental variables such as food, temperature, or population density. The adaptive advantage of sex ratios that are skewed toward females and vary in response to food are discussed in terms of the maintenance of viable copepod populations in food-poor regions.

Growth rate is another important aspect of the population dynamics of copepods, especially considering its rapidity; Schmitt (1965) estimated 9 billion copepods were produced annually in 10 m^3 of the Baltic Sea. Chapter 4 focuses on the egg production of six common calanoid copepods and somatic growth of *Calanus agulhensis* (ex *Calanus australis*) and *Calanoides carinatus*. The fecundity estimates for *Nannocalanus minor* are the first comprehensive values reported for this species from any marine system, and the somatic growth estimates for *C. carinatus* are the first *in situ* measurements of all stages for this copepod. A multiple regression approach is used to assess the relative importance of ambient food quantity in terms of Chl *a* concentration, phytoplankton cell size, and temperature to growth. The proposition that growth rate in the field is more affected by temperature than food (Huntley and Lopez 1992) is challenged. Sources of variability in relationships between growth rate and ambient food that are a consequence of the dynamic nature of upwelling systems are discussed. In Chapter 5, growth rates of copepods ranging in size from 500 to 2750 μm are detailed. The interplay between body size and food limitation and its effect on growth rate are investigated, allowing the formulation of a probabilistic model that relates prey density and growth at the population level. The general consensus that zooplankton in upwelling areas are seldom food limited (Mann and Lazier 1991) because of the high primary production and rapid growth of phytoplankton is questioned. Chapter 6 describes the temporal and spatial variation in juvenile and female growth of the dominant large copepod, *Calanus agulhensis*, on the western

Agulhas Bank. The variation in growth rate is interpreted at the seasonal and event scales and related to the timing of both sardine and anchovy spawning.

Chapter 7 examines the paradox of why anchovy spawn on the relatively food-poor western Agulhas Bank, aiming to provide insight into the factors which control spawning success. The optimal spawning habitat for anchovy is described, and the relationship between spawning success and the area of suitable spawning habitat is quantified. Chapter 8 examines the relationship between the total egg abundance of anchovy, its gonadal atresia, and food availability in terms of copepod abundance, providing extra information on the food conditions that are optimal for the spawning of anchovy. Chapter 9 explores the changes in copepod biomass on the western Agulhas Bank with respect to advective export and anchovy predation. The consequence of competition for food and density-dependent regulation of spawning success is discussed. Lastly, a simple mass-balance model of copepod biomass on the western Agulhas Bank is developed in Chapter 10 by synthesizing concepts from previous chapters. This model enables the relative contributions of growth, advection (input and loss), and predation to fluctuations in copepod biomass to be assessed. It also provides an answer to the question about whether there is enough food on the western Agulhas Bank for pelagic fish.

CHAPTER 1
GENERAL METHODOLOGY

Sample collection

Sampling was conducted monthly between August 1993 and March 1994, and between September 1994 and March 1995 (except January 1995), aboard the Sea Fisheries research vessels F.R.S. *Algoa* and F.R.S. *Africana*, and the Norwegian research vessel *Dr. Fridtjof Nansen*. The standard survey grid for plankton sampling consisted of five transects (Fig. 1.1), although the entire grid was not always completed because of inclement weather or time constraints (Table 1.1). Expanded surveys were conducted in November 1993 (six transects) and 1994 (nine transects) as part of the annual Pelagic Spawner Biomass Hydroacoustic Survey (Verheye *et al.* 1994; Hutchings *et al.* 1995). The inshore station on each transect was two miles from the coast, and all subsequent stations were ten miles apart, with the outer station close to the 500-m isobath (Fig. 1.1). Stations were numbered from inshore to offshore, with only odd numbers being used. The transects at Cape Agulhas, Walker Bay, and Cape Columbine consisted of six stations, at Cape Point five because of the narrower shelf, and Olifants River had twelve owing to the very broad shelf in that region.

At each station, temperature and fluorescence profiles were measured using a Chelsea Instruments Aquatracka. Chl *a* data from the surface and the depth of maximum fluorescence were then used after each cruise to convert the *in situ* fluorescence values from the Aquatracka to Chl *a* concentration (Mitchell-Innes, Sea Fisheries Research Institute (SFRI), unpublished data). Nitrates, nitrites, silicates, and phosphorus were collected at the surface and analysed according to the methods of Mostert (1988). Only nitrates are presented in this thesis because it is considered to be the primary factor limiting growth of phytoplankton in upwelling regions (Andrews and Hutchings 1980; Brown and Hutchings 1987).

Chl *a* concentration

At each station, water samples were collected at the surface and fluorescence maximum with a Magnum rosette sampler with six 18-ℓ bottles. After filtration of 250 ml of seawater from each depth through Whatman GF/F filters, the filters were homogenized, extracted in 90% acetone for 24 h at -20 °C in the dark, centrifuged for 12 minutes at 1000 r.p.m., and then analysed fluorometrically using a Turner Designs Model 10-000R fluorometer. The concentration of Chl *a* was calculated according to Parsons *et al.* (1984) and adjusted for phaeopigments by reading fluorescence before and after acidification with two drops of 10% HCl.

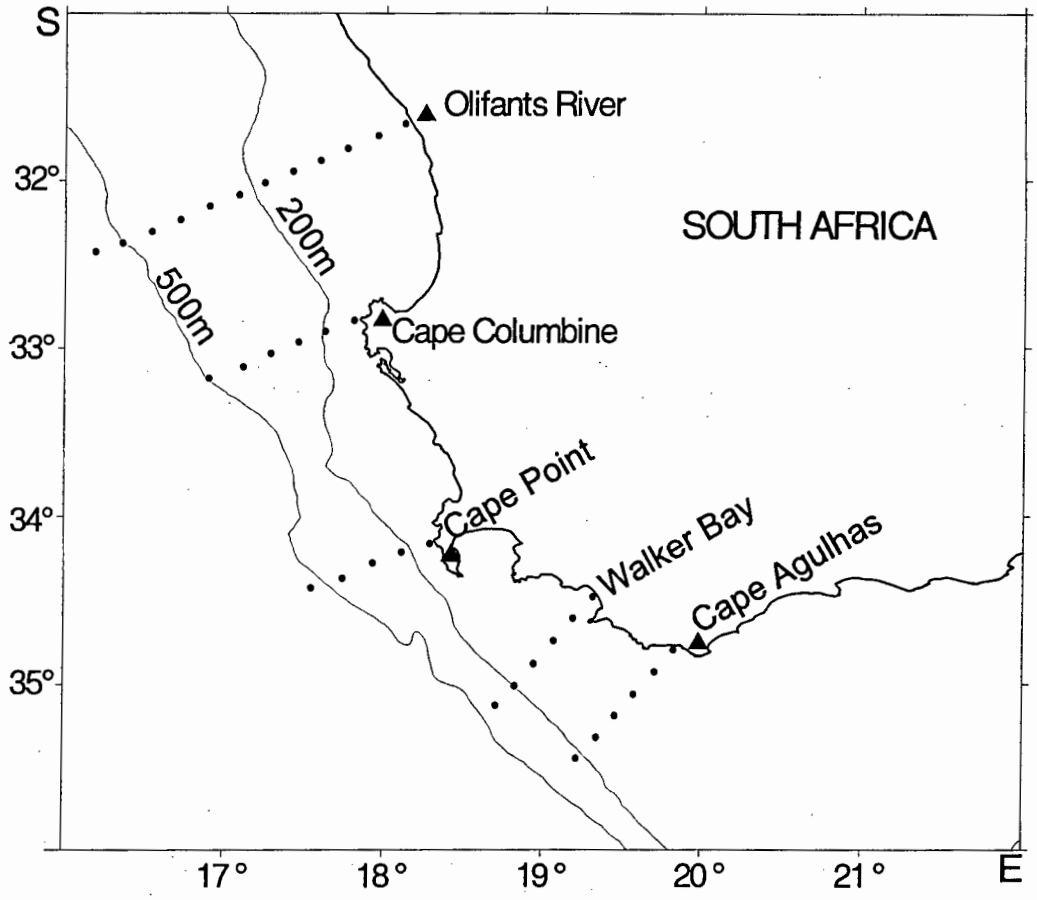


Fig. 1.1. The positions of stations in the SARP programme.

Table 1.1. General information concerning each cruise during SARP. Transects abbreviated as CA = Cape Agulhas, WB = Walker Bay, CP = Cape Point, CC = Cape Columbine, OR = Olifants River.

SARP	NAME	DATE	VOYAGE	TRANSECTS COMPLETED
I	August 1993	30/8/93 - 2/9/93	ALGOA Voy. 3	WB, CA, CP
II	September 1993	28/9/93 - 5/10/93	ALGOA Voy. 4	WB, CA, CP
III	October 1993	26/10/93 - 2/11/93	ALGOA Voy. 5	WB, CA, CP, CC, OR
IV	November 1993	9/11/93 - 3/12/93	AFRICANA Voy. 117	WB, CA, CP, CC
V	December 1993	9/12/93 - 15/12/93	ALGOA Voy. 7	WB, CA, CP, CC, OR
VI	January 1994	24/1/94 - 31/1/94	ALGOA Voy. 8	WB, CA, CP, CC
VII	February 1994	12/2/94 - 18/2/94	ALGOA Voy. 9	WB, CA, CP, CC, OR
VIII	March 1994	15/3/94 - 19/3/94	ALGOA Voy. 11	WB, CA, CP, CC
IX	September 1994	5/9/94 - 11/9/94	AFRICANA Voy. 123	WB, CA, CP, CC
X	October 1994	8/10/94 - 16/10/94	DR FRIDTJOF NANSEN Voy. 94	WB, CA, CP, CC, OR
XI	November 1994	14/11/94 - 7/12/94	AFRICANA Voy. 126	WB, CA, CP, CC, OR
XII	December 1994	9/12/94 - 15/12/94	ALGOA Voy. 16	WB, CA, CP
XIII	February 1995	8/2/95 - 16/2/95	ALGOA Voy. 17	WB, CA, CP, CC, OR
XIV	March 1995	7/3/95 - 15/3/95	ALGOA Voy. 19	WB, CA, CP, CC, OR

As this technique underestimates the concentration of Chl *a* at high fluorescence values, a phenomenon known as quenching (APHA 1995), a series of experimental trials were conducted to estimate the degree of quenching for various Chl *a* concentrations (B. Mitchell-Innes, SFRI, unpublished data). Samples with a high but unknown concentration of Chl *a* were analysed fluorometrically, and also analysed after sequential dilution until quenching ceased. From the final unquenched reading, and knowing the overall dilution factor, the initial fluorescence adjusted for quenching was calculated. From these experimental results, the equation of best fit between unquenched and quenched fluorescence values was:

$$F_{adj} = 1.122148 \times F_{init} + 0.000245 \times 10^{F_{init}}$$

$$(r^2 = 0.994, p < 0.0001)$$

where

F_{adj} = fluorescence value adjusted for quenching,

F_{init} = initial fluorescence reading (unadjusted for quenching).

As quenching was negligible (<5%) below a Chl *a* concentration of 1 $mg.m^{-3}$, this equation was only applied to fluorescence readings above this value.

Copepod abundance

Zooplankton in the upper 200 m were collected using a Bongo net with a 200-µm mesh fitted with an electronic flowmeter and depth sensor. The net was hauled vertically at 1 $m.s^{-1}$. Samples were preserved in 5% buffered formalin. In the laboratory, the samples were allowed to settle in a graduated measuring cylinder for 24 h and then diluted to 10 times the settled volume of copepods. Two 2-ml subsamples were removed and all the copepods within the subsamples were counted and assigned to a taxonomic group (Table 1.2).

The numbers per m^3 at each station were calculated as:

$$\text{Nos.m}^{-3} = \frac{\sum_{i=1}^{k} X_i}{4} \times \frac{SV}{V}$$

where

X_i = numbers of species i in both subsamples,

k = total number of species counted,

Table 1.2. Taxonomic groups counted, and their individual body masses. Juv = juvenile (C1-C5).

ORDER[1]	TAXA	STAGES COUNTED	MASSES (µg dry weight)	Sizes (TL, µm)
Calanoida	*Calanus agulhensis*	♀	202[2]	2763[5]
		♂	110[3]	2724[5]
		C5	97[2]	2309[5]
		C4	46[2]	1700[5]
		C3	22[2]	1193[3]
		C2	9[2]	939[5]
		C1	4[2]	785[5]
	Calanoides carinatus	♀	123[4]	2640[6]
		♂	73[4]	2420[6]
		C5	62[4]	2280[6]
		C4	30[4]	1850[6]
		C3	18[2]	1310[6]
		C2	7[2]	940[6]
		C1	4[2]	700[6]
	Centropages brachiatus	♀	25[2]	1756[5]
		♂	20[3]	1600-1810[7]
		Juv	9[2]	*
	Copepod nauplii	Grouped	1[3]	525[3]
	Metridia lucens	♀	108[3]	2500-2900[8]
		♂	80[3]	2000-2300[8]
		Juv	30[3]	*
	Other calanoids	Grouped	30[3]	1800[9]
	Pleuromamma spp	♀	150[3]	2000-3000[10]
		♂	110[3]	2000-3500[10]
		Juv	30[3]	*
	Rhincalanus nasutus	♀	300[3]	3900-5100[8]
		♂	270[3]	2700-3800[8]
		Juv	150[3]	+
	Small copepods (*Ctenocalanus vanus*, *Paracalanus parvus*, *Clausocalanus* spp.)	Grouped	10[3]	750-1260[7]
Cyclopoida	*Oithona* spp.	Grouped	0.5[2]	480-1500[11]
Harpacticoida	Harpacticoids	Grouped	30[3]	600-1300[12]
Poecilostomatoida	*Oncaea* spp.	Grouped	30[3]	600-1250[13]
	Corycaeus/Corycella	Grouped	30[3]	660-1400[14]

[1] Classification according to Huys and Boxshall (1991)
[2] Peterson *et al.* (1990a)
[3] Sea Fisheries Research Institute, unpublished estimate
[4] Verheye (1991)
[5] Stuart and Huggett (1992)
[6] Binet and Suisse de Sainte Claire (1975)
[7] Brodsky (1950)
[8] Rose (1933)
[9] for *Nannocalanus minor* ♀ (Rose 1933)
[10] range for *Pleuromamma gracilis* and *Pleuromamma abdominalis* adults (Rose 1933)
[11] range for *Oithona plumifera* and *Oithona nana* adults (Rose 1933)
[12] range for *Microsetella rosea*, *Clytemnestra scutellata* and *Clytemnestra rostrata* adults (Rose 1933)
[13] range for *Oncaea conifera* and *Oncaea ornata* adults (Rose 1933)
[14] range for *Corycella rostrata* and *Corycaeus limbatus* adults (Rose 1933)
* assumed the same as *Calanus agulhensis* C2
+ assumed the same as *Calanus agulhensis* C4

SV = settled volume,

V = volume of water filtered by the bongo net.

The volume of water filtered was calculated by multiplying the average flow rate for the plankton tow by its depth and the bongo mouth area (0.255 m^2). Copepod biomass per m^3 was calculated as the product of individual body mass (Table 1.2) and numbers per m^3. Estimates per m^2 were obtained by multiplying by sampling depth. A total of 356 stations was sampled.

Copepod growth rate

Davis (1987) argued that the only way to measure zooplankton production accurately is by estimation of species-specific growth rates. Female growth rate can be measured relatively easily and directly by measuring egg production (Peterson *et al.* 1991). Juvenile growth rate, however, is more difficult to estimate and for many species it is assumed to be proportional to female growth rate, as it is for the genus *Acartia* (Sekiguchi *et al.* 1980; Berggreen *et al.* 1988). For the dominant species of large copepod on the anchovy spawning grounds, *Calanus agulhensis*, female growth rate is not a function of their juvenile rate (Hutchings *et al.* 1995; Peterson and Hutchings 1995). In temperate and polar regions, which have been the focus of most research on juvenile copepods, juvenile growth has been estimated by following the progression of cohorts after spring or fall phytoplankton blooms (McLaren and Corkett 1981; Middlebrook and Roff 1986; McLaren *et al.* 1989). The measurement of juvenile growth poses greater difficulties in upwelling areas where the egg production of females is continuous (Armstrong *et al.* 1991b), precluding the use of distinct cohorts to estimate juvenile growth. In these regions the moulting ratio method can be used (Hutchings *et al.* 1995; Peterson and Hutchings 1995).

In this study, growth rates of copepods were estimated using *in situ* bottle incubation techniques. Female growth rates for several common species in the southern Benguela, *viz. Calanoides carinatus*, *Calanus agulhensis*, *Centropages brachiatus*, *Nannocalanus minor*, *Neocalanus tonsus*, and *Rhincalanus nasutus*, were measured using the egg production method (Peterson *et al.* 1991). Juvenile growth rates (N6-C5) were measured by the moulting ratio method (Peterson *et al.* 1991) for two of the species (*Calanus agulhensis* and *Calanoides carinatus*), because they are the dominant large copepods in the southern Benguela system (Peterson *et al.* 1992; Hutchings *et al.* 1995) and they are robust and amenable to experimental manipulation (Marshall and Orr 1952, Walker and Peterson 1991). Individuals for both egg production and moulting ratio experiments were collected at each station using a drift net (mouth area: 0.255 m^2) with 300 μm-mesh and fitted with a 2-ℓ plastic

bottle as a cod-end. The net was lowered manually to the depth of maximum fluorescence, determined previously from the fluorescence profile, and allowed to drift for 10 minutes. Upon retrieval, the sample was diluted in a bucket containing 20 ℓ of seawater at ambient surface temperature. Copepods were concentrated from this bucket using a sieve and washed into a Petri dish. Lively specimens were selected using a wide-mouthed dropper under a dissecting microscope with subdued light. All copepods were incubated in 63-μm filtered seawater collected at the depth of maximum fluorescence. Animals were incubated for 24 h in darkened bins cooled with seawater pumped from a depth of 6 m, approximating the temperature of the upper mixed layer (Hutchings *et al.* 1995). After 24 h the contents of the bottles were poured through a 63 μm mesh for the larger copepods (*Calanus agulhensis*, *Calanoides carinatus*, *Rhincalanus nasutus*, and *Neocalanus tonsus*) and a 20-μm mesh for the smaller copepods (*Centropages brachiatus* and *Nannocalanus minor*). Samples were then preserved with 5% buffered formalin.

Copepod egg production

Females were placed in 1-ℓ bottles and their survival at the end of the 24-h experiments was checked under a microscope. Experiments with dead or moribund females were excluded from the analysis. Although the bottles were not fitted with a screen to prevent females from ingesting their eggs, the low density of females used minimized the effects of egg cannibalism (see Laabir et al. 1995). In the laboratory, the number of eggs per bottle was counted and the egg production (E, eggs.♀$^{-1}$.d^{-1}) calculated from Peterson *et al.* (1991) as:

$$E = N_e \times \frac{24}{T}$$

where

N_e = number of eggs,

T = the duration of the incubation experiment (h).

To compare values of female egg production with those of juvenile somatic growth, egg production was converted to instantaneous weight-specific female growth (g_f, d^{-1}) by applying the following equation from Roff *et al.* (1995):

$$g_f = \ln\left(\frac{W_e \times E}{W_f} + 1\right)$$

where

W_e = average egg weight (μg dry weight),

W_f = average female body weight (μg dry weight).

Implicit in this equation is that the addition of body mass by females is negligible in comparison to the mass of eggs produced. As this study was performed as part of a routine survey and owing to the large number of females incubated, average body weights of females (Table 1.2) and eggs (Table 1.3) have been used for the calculation of female growth rate.

Egg production experiments were also conducted on *Nannocalanus minor*. As no value for the mass of *Nannocalanus minor* was available from the literature, it was estimated by converting its total length (TL) of 1800 μm (Rose 1933) to prosome length (PL) using the following equation (C. van der Lingen, SFRI, unpublished data):

$$PL = \frac{TL - 52.4}{1.198}$$

PL was then converted to mass using the equation from Chisholm and Roff (1990a) of:

$$\ln(\text{dry weight}) = 2.74\ln(PL) - 16.41$$

This yielded a mass of 35 μg dry weight.

During the first four cruises, multiple females were incubated per bottle; two per bottle for larger copepods such as *Calanus agulhensis* and *Calanoides carinatus* and three or four per bottle for smaller copepods such as *Centropages brachiatus* and *Nannocalanus minor* (Anon 1993). Although it is common to incubate between 1 and 30 females per bottle (Checkley 1980a; Peterson and Bellantoni 1987; Fransz *et al.* 1989; Armstrong *et al.* 1991b; Durbin *et al.* 1992), females were incubated singly after November 1993 for a number of reasons. Firstly, the standard error (*SE*) for egg production of females incubated singly is half that of the same number of females incubated in pairs, and one third that of females incubated in triplets, and so on

Table 1.3. Egg mass of copepods used for estimation of female growth rate.

SPECIES	EGG MASS (μg dry weight)
Calanus agulhensis	0.6[1]
Calanoides carinatus	0.5[2]
Centropages brachiatus	0.075[2]
Nannocalanus minor	0.25[3]

[1] using egg mass of *Calanus finmarchicus* (McLaren *et al.* 1989)

[2] Peterson (1989)

[3] from egg diameter (ED): ln(dry weight) = -3.578+0.01470*ED (C. van der Lingen, SFRI, unpublished data) and assuming egg size for *Nannocalanus minor* is 150 μm (excluding perivitelline space)

($SE_{\text{singly}} = \frac{\sigma}{\sqrt{n}}, SE_{pairs} = \frac{\sigma\sqrt{2}}{\sqrt{\frac{n}{2}}}, SE_{triplets} = \frac{\sigma\sqrt{3}}{\sqrt{\frac{n}{3}}}$). Thus, the estimate of mean egg production from incubating females singly is more precise, allowing increased power for the testing of hypotheses. Secondly, the percentage of usable replicates decreases as the number of individuals incubated per bottle increases (Fig. 1.2), because experiments were excluded when any of the females had died. Lastly, incubating females singly reduces the probability of egg cannibalism because of decreased female to egg density (Checkley 1980a; Peterson *et al.* 1988); it also minimizes other possible deleterious effects of over-crowding.

During the 1993/94 season, about five replicate experiments were performed at each station, as is common practice during the Pelagic Spawner Biomass Surveys (Hutchings *et al.* 1995). Southwood (1966) states that the number of replicates needed (n) for a desired level of precision (SE) is given by:

$$n = \left(\frac{\text{CV}}{\text{SE}}\right)^2$$

where

CV = coefficient of variation,

SE = predetermined standard error as a proportion of the mean.

Data from egg production experiments of *Calanus agulhensis* in 1993/94 (n = 524) showed that the CV was inversely related to the Chl *a* concentration (Fig. 1.3 inset). This implies that the number of replicates needed for a desired level of precision decreases as Chl *a* concentration increases (Fig. 1.3). Because the concentration of Chl *a* (or fluorescence) was determined at each station before egg production experiments were initiated, a greater number of replicate egg production experiments were performed under conditions of poor Chl *a* concentration during the 1994/95 season.

Moulting ratios

To estimate moulting rate, at least 15 individuals (average: 36) of a developmental stage were incubated in 2-ℓ jars. The number of individuals that had and had not moulted to the next stage were counted and the moulting ratio (MR_i) of each juvenile stage i was calculated after Peterson *et al.* (1991) as:

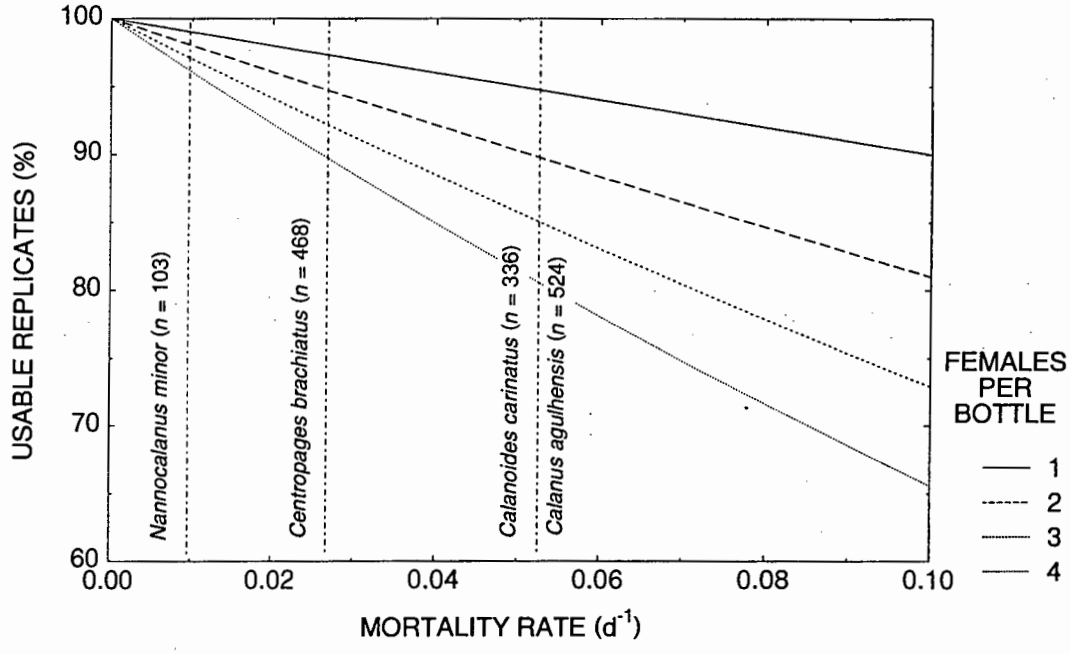


Fig. 1.2. The percentage of usable replicates as a function of the mortality rate of copepods for experiments with one, two, three, or four individuals incubated per bottle. The percentage of usable replicates is equal to $(1 - \text{mortality rate})^n$, where n = number of females per bottle. For comparison, the mortality rates (the proportion of the total number of females incubated that died) of four species of copepods during 1993/94 are shown.

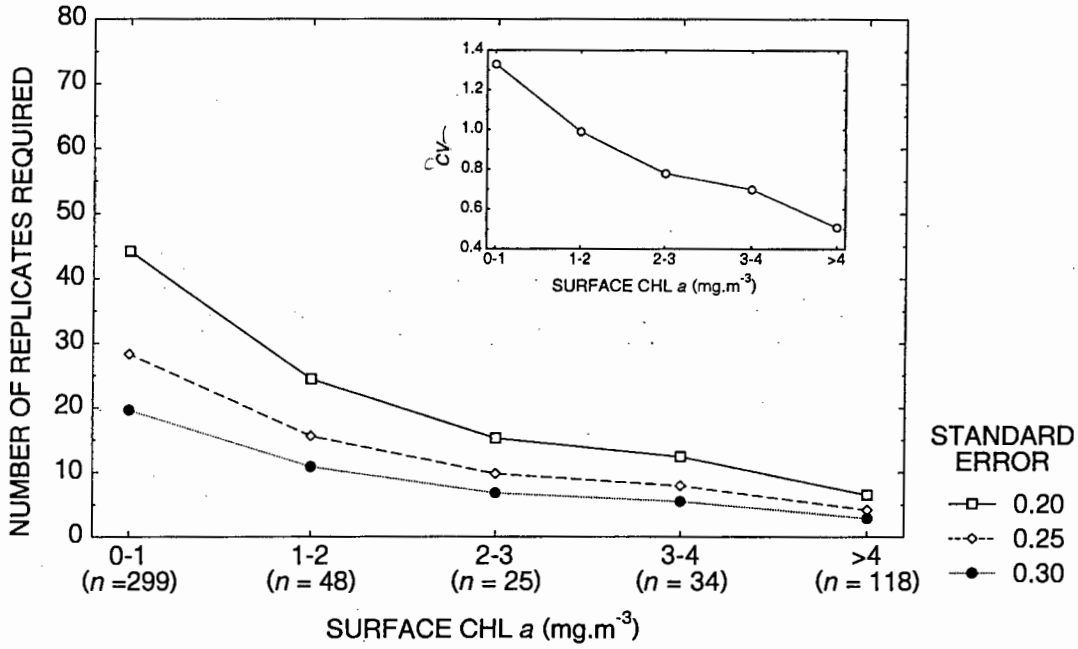


Fig. 1.3. The number of replicates required to obtain a desired level of precision for different ambient surface Chl *a* concentrations grouped on an interval scale. The number of experiments within each interval is shown below the *x*-axis. All Chl *a* concentrations >4 $mg.m^{-3}$ were grouped because the CV remained relatively constant in this range. Inset: The CV of *Calanus agulhensis* egg production against surface Chl *a* concentration.

$$MR_i = \frac{N_{i+1}}{N_i + N_{i+1}}$$

where

N_i = the number of individuals in stage i at the end of the experiment,

N_{i+1} = the number of individuals in stage $i+1$ at the end of the experiment.

The daily stage-specific growth rate (g_i, d^{-1}) was calculated from the moulting ratio using masses from Table 1.2 and applying the following formula (modified from Peterson *et al.* (1991)):

$$g_i = \ln\left(\frac{W_{i+1}}{W_i}\right) \times MR_i \times \frac{24}{T}$$

where

W_i = average body weight of copepodites stage i,

W_{i+1} = average body weight of copepodites stage $i+1$.

Although average weights of copepodites can decrease with food-limitation (Berggreen *et al.* 1988), the associated error in calculating growth rates is small because stage duration (or moulting ratio) is more sensitive to food-limitation than growth increment (Webber and Roff 1995). Exoskeletons were also counted and experiments were excluded from analyses if the difference between the moulting ratio calculated from the exoskeletons and that from the animals themselves was greater than 10%. Stage durations from each experiment were calculated as the reciprocal of the moulting ratio (Falkowski *et al.* 1984). Average duration of each stage was then estimated using a geometric mean to give each ratio (stage duration) equal weight (Zar 1984).

During the 1993/94 season, as many individuals as possible (within the limited time between stations of about 45 minutes) were incubated per experiment. By assuming that the moulting process can be modelled by the binomial distribution, the number of individuals needed for a moulting ratio for a desired level of precision can be approximated by the formula given by Southwood (1966):

$$n \geq \frac{t^2 pq}{H^2}$$

where

t = value of Student t from statistical tables (t =2 for $n > 10$ and $\alpha = 0.05$),

H = predetermined half-width of the confidence interval as a proportion,

p = moulting ratio,

$q = 1 - p$.

Although moulting does not strictly follow a binomial process because of individual variability, this formula is useful as an indication of the minimum number of individuals needed. Since H as defined here is constant and not relative to the size of p, the assumption here is that $p = 0.1 \pm 0.05$ or $p = 0.5 \pm 0.05$ is of interest. A graphical representation of the relationship between n and p is shown in Fig. 1.4, together with the moulting ratios of *Calanus agulhensis* stages from 1993/94 for comparison. It shows that the most individuals per experiment are required for $p = q = 0.5$ and the fewest when $p \rightarrow 0$ or $p \rightarrow 1$. Therefore, when possible during 1994/95, more individuals were incubated per experiment for C2s than other stages.

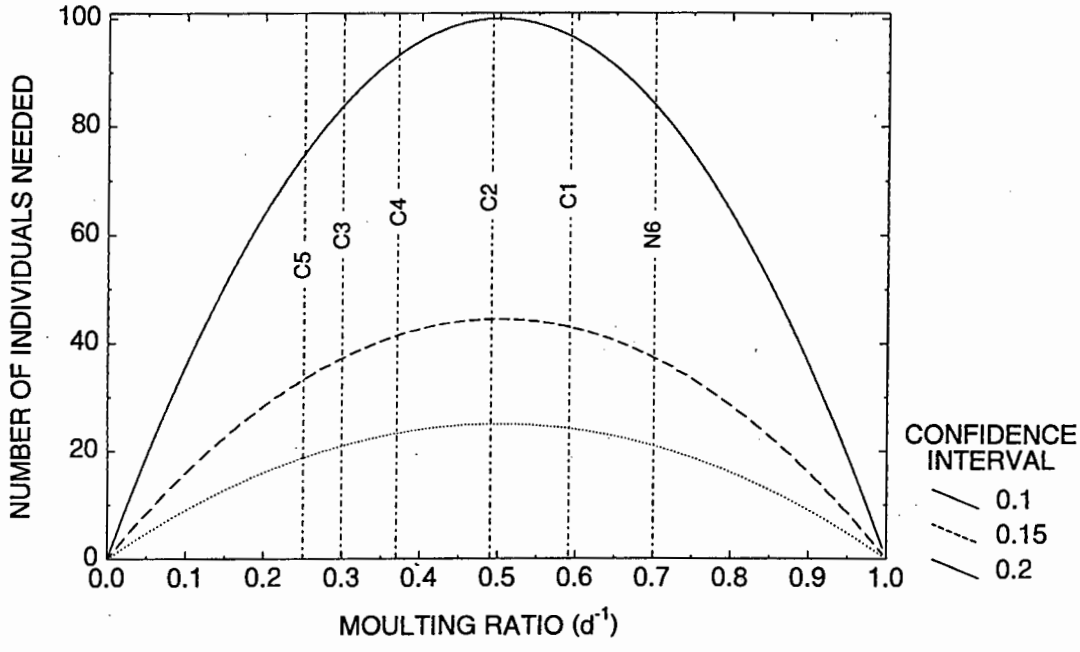


Fig. 1.4. An estimate of the minimum number of individuals per incubation for different probabilities of moulting, p, and specified half-widths of confidence intervals, D. For comparison, the moulting ratios of *Calanus agulhensis* on the western Agulhas Bank are shown.

CHAPTER 2

COPEPOD BIOMASS IN THE SOUTHERN BENGUELA SYSTEM

ABSTRACT

On the basis of 356 Bongo net (200-μm mesh) samples collected monthly between August-March 1993/94 and 1994/95 in the southern Benguela system, the temporal and spatial patterns of copepod biomass were examined. The region was divided into three areas: western Agulhas Bank, the South-Western Cape region, and St Helena Bay. Copepod biomass was significantly larger in the St Helena Bay region (4954 mg dry weight.m^{-2}) than off the South-Western Cape (3068 mg dry weight.m^{-2}), and these were both greater than on the western Agulhas Bank (2066 mg dry weight.m^{-2}). The distribution of Chl *a* varied similarly, with the greatest mean concentration in St Helena Bay (2.9 mg.m^{-3}), a smaller concentration off the South-Western Cape (2.6 mg.m^{-3}), and the lowest level on the western Agulhas Bank (2.2 mg.m^{-3}). This suggests that higher levels of Chl *a* support larger biomasses of copepods. In terms of the horizontal distribution of copepod biomass, the greatest biomass of copepods off the South-Western Cape was found inshore, concurrent with high levels of Chl *a*. It is noteworthy that the largest copepod densities on the western Agulhas Bank were found midshelf, spatially disassociated from the maximum density of Chl *a* located inshore. This suggests that copepod populations are supplemented by processes other than *in situ* growth. Historically, the food environment of anchovy in terms of copepods on the main spawning grounds, the western Agulhas Bank, has been evaluated once only during the spawning season (November). Sampling at this time during the present study failed to reveal important temporal fluctuations: copepod biomass varied two- to three-fold during the anchovy spawning season. Despite these considerable monthly variations in copepod biomass, no statistically significant differences among months were found. However, the power of the analyses (the probability of rejecting a false null hypothesis) was between 20 and 50%, well below the commonly accepted minimum of 80%, because of the insufficient number of samples collected each month. For future sampling programmes of this nature, it is recommended that more than twice the number of stations are sampled to obtain statistically significant differences.

INTRODUCTION

Information on the variability of copepod biomass could be directly applicable to understanding the recruitment of pelagic fish. Cochrane and Hutchings (1995) and Korrûbel *et al.* (in press) concluded that food availability to anchovy spawners was one of the most promising variables to forecast recruitment. This is because anchovy spawners on the western Agulhas Bank feed almost exclusively on copepods (James 1987) and are sometimes food limited (Peterson *et al.* 1992; Cochrane and

Hutchings 1995). To measure the food available to anchovy, copepod biomass has been determined during the mid-season spawning peak in November (Shelton and Hutchings 1990) from 1988 to the present (Verheye *et al.* 1994; Hutchings *et al.* 1995). However, the representativeness of this single estimate of food availability to the entire spawning season is not known. The intra-seasonal study of the variability in the abundance, distribution, and productivity of copepods was an important component of the South African Sardine and Anchovy Recruitment Programme (SARP, Painting 1993). An improved recruitment forecast may be possible if knowledge of food availability throughout the spawning season was available.

This chapter seeks answers to the following questions:

(i) Are there regional differences in the biomass of copepods within the southern Benguela system?

(ii) Does copepod biomass vary across the shelf?

(iii) Is there a significant intra-annual variation in copepod biomass?

(iv) Is a mid-season estimate of food availability representative of the entire season?

(v) If the current sampling strategy is inadequate, how can it be improved?

MATERIALS AND METHODS

Copepod biomass and Chl *a* concentration were estimated according to the procedures detailed in Chapter 1. The survey area was divided into three areas (see Chapter 1, Fig. 1.1), *viz.* the western Agulhas Bank (Cape Agulhas and Walker Bay transects), the South-Western Cape region (Cape Point and Cape Columbine lines), and St Helena Bay (Olifants River transect). The Olifants River transect was only sampled 7 out of 14 times during the SARP surveys (Chapter 1, Table 1.1), precluding the analysis of intra-seasonal and cross-shelf variations as was done for the other regions.

To analyse intra-seasonal changes in copepod biomass, a one-way Model-I ANOVA with month as the independent variable was conducted on data from the western Agulhas Bank and the South-Western Cape region for each sampling season. Copepod biomass values were log transformed to reduce heteroscedasticity and to improve normality. The assumption of homoscedasticity for ANOVA and *t*-tests was verified using Levene's test (Milliken and Johnson 1984, in StatSoft 1996). *Post hoc* comparisons were conducted using Tukey Honest Significant Difference test adjusted for unequal *n* (StatSoft 1996).

The frequency distribution of Chl *a* was skewed towards small concentrations, violating the

assumption of normality for ANOVA. Thus, the non-parametric Kruskal-Wallis test (equivalent to a one-way ANOVA) was conducted to detect differences among regions, with *post hoc* comparisons computed using the Mann-Whitney *U*-test (equivalent to a *t*-test).

The capability of the sampling programme to detect within-season differences in copepod biomass was assessed by power analysis, a useful technique when there is no significant difference among treatments (Cohen 1988). Because power is the probability of rejecting a null hypothesis that is false, high power is desirable (Cohen 1988; Peterman 1990; Searcy-Bearnal 1994). Power was determined from standard tables in Cohen (1988) and is a function of the Type I error (α), average sample size ($\overline{n}$), and the standardized effect size. The standardized effect size is the effect of the treatments (months) on the response variable (copepod biomass). The bigger the effect size (*i.e.* the greater the difference among months), the easier it is to detect a difference and the greater power to reject a false null hypothesis. The standardized effect size (f) according to Cohen (1988) is:

$$f = \frac{\sigma_m}{\sigma}$$

where

σ_m = standard deviation of the treatment means,

σ = overall standard deviation.

As there were unequal sample sizes in each treatment, the following equation from Cohen (1988) was used to calculate σ_m:

$$\sigma_m = \sqrt{\frac{\sum_{i=1}^{k} n_i (m_i - m)^2}{N}}$$

where

k = number of treatments,

n_i = number of samples in each treatment i,

m_i = mean of each treatment i,

m = overall mean,

N = total number of samples.

Average sample size ($\overline{n}$) was calculated from the equation:

$$\overline{n} = \frac{\sum_{i=1}^{k} n_i}{k}$$

Power analysis also provides information concerning the number of samples required ($\overline{n}$) to obtain a desired level of power for specific values of α, k, and f. This allows recommendations on the number of samples needed to detect significant differences to be made for future sampling programmes. For all power analyses $\alpha = 0.05$ was used.

RESULTS

Estimates of copepod biomass (mean ± standard error) and range for the western Agulhas Bank, the South-Western Cape region, and St Helena Bay during SARP are shown in Table 2.1. Copepod biomass was significantly different in the three regions (ANOVA, $F = 18.4$, $df = 353$, $p < 0.0001$). Copepod biomass was smallest on the western Agulhas Bank compared with the two other regions in both seasons and was significantly smaller overall (Table 2.1). Mean Chl *a* concentration also exhibited a decreasing trend from St Helena Bay in the north to the western Agulhas Bank in the south (Table 2.2, Kruskal-Wallis test, $H = 8.6$, $n = 355$, $p < 0.05$).

The cross-shelf distributions of copepod biomass on the western Agulhas Bank and off the South-Western Cape are markedly different (Fig. 2.1). Off the South-Western Cape, copepod biomass is largest inshore and declines offshore. In contrast, biomass on the western Agulhas Bank is greatest midshelf, with the smallest biomass inshore. Stations 1 and 3 on the western Agulhas Bank were significantly smaller than the same stations on the South-Western Cape coast ($p < 0.001$). There were no significant differences between all other stations ($p > 0.05$). The cross-shelf Chl *a* concentrations declined offshore for both the western Agulhas Bank and the South-Western Cape region (Fig. 2.2).

There was marked intra-seasonal variability of copepod biomass on the western Agulhas Bank and off the South-Western Cape. On the western Agulhas Bank there was almost a three-fold variation in copepod biomass in 1993/94 (Fig. 2.3, range: 827.0-2197.5 mg dry weight.m^{-2}) and a two-fold change in 1994/95 (range: 1786.6-3627.5 mg dry weight.m^{-2}). Off the South-Western Cape in 1993/94 there was a five-fold variation (Fig. 2.4, range: 1414.5-7291.4 mg dry weight.m^{-2}) and a two-fold fluctuation for 1994/95 (range: 1589.6-3499.7 mg dry weight.m^{-2}). Despite these

Table 2.1. Estimates of mean ± standard error and range of copepod biomass (mg dry weight.m^{-2}) on the western Agulhas Bank (WAB), the South-Western Cape region (SWC), and St Helena Bay (SHB) during SARP. The number of stations sampled (n) is also shown. Different superscripts indicate significant differences among multiple comparisons of overall mean copepod biomass using Turkeys HSD at $p < 0.05$.

	1993/94			1994/95			OVERALL	
AREA	MEAN ± SE	RANGE	n	MEAN ± SE	RANGE	n	MEAN ± SE	n
WAB	1681.1 ± 125.2	23.0-6616.8	108	2532.5 ± 199.9	166.9-9298.1	89	2065.8^{a} ± 117.1	197
SWC	3404.9 ± 499.7	227.4-19507.3	59	2705.4 ± 257.1	154.1-8409.9	55	3067.5^{b} ± 287.5	114
SHB	2902.3 ± 472.2	263.4-8600.7	22	6916.7 ± 824.5	562.4-16441.7	23	4954.1^{c} ± 563.3	45

Table 2.2. Estimates of mean ± standard error and range of Chl *a* concentration ($mg.m^{-3}$) on the western Agulhas Bank (WAB), the South-Western Cape region (SWC), and St Helena Bay (SHB) during SARP. The number of stations sampled (*n*) is also shown. Different superscripts indicate significant differences among multiple comparisons of overall mean Chl *a* concentration using Mann-Whitney *U*-test at $p < 0.05$.

	1993/94			1994/95			OVERALL	
AREA	MEAN ± SE	RANGE	*n*	MEAN ± SE	RANGE	*n*	MEAN ± SE	*n*
WAB	2.380 ± 0.253	0.11-22.82	206	1.969 ± 0.185	0.10-10.41	157	2.202^{a} ± 0.165	363
SWC	2.962 ± 0.268	0.23-11.31	111	2.192 ± 0.245	0.10-10.29	102	2.593^{b} ± 0.184	213
SHB	2.858 ± 0.257	0.62-7.42	49	2.863 ± 0.544	0.11-11.43	37	2.860^{bc} ± 0.278	86

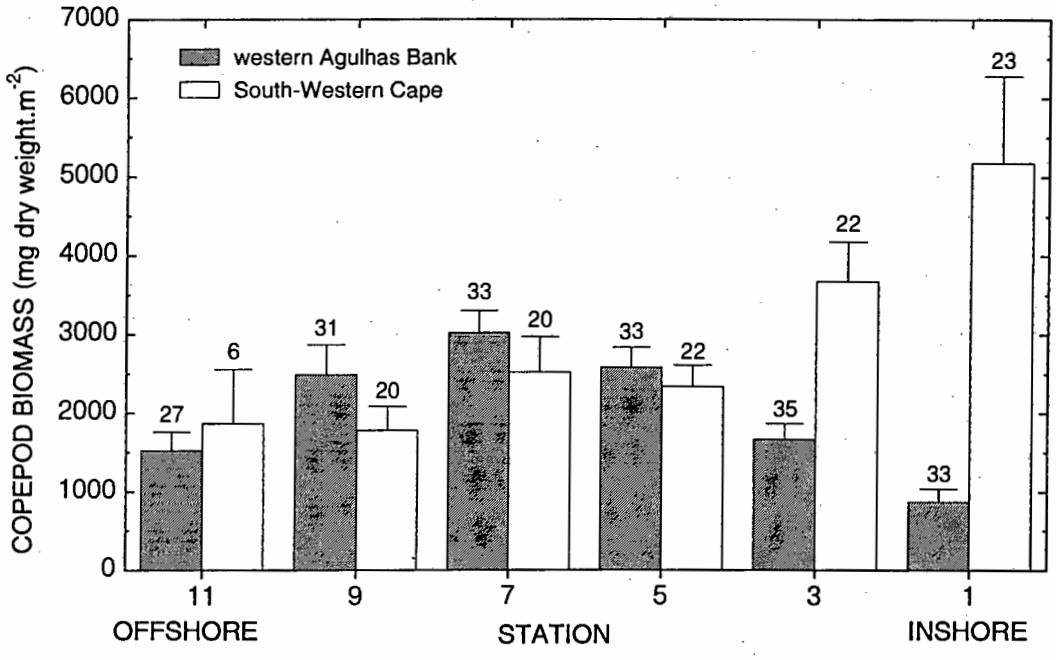


Fig. 2.1. Cross-shelf distribution of copepod biomass on the western Agulhas Bank and off the South-Western Cape coast for the two SARP seasons combined. Standard errors and number of samples are shown.

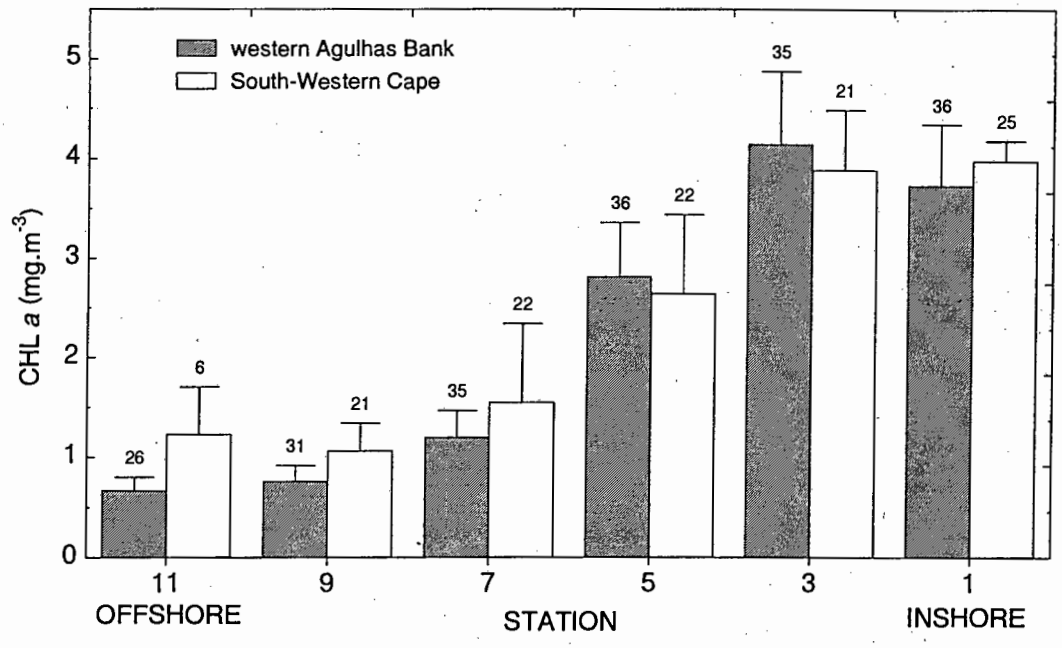


Fig. 2.2. Cross-shelf distribution of Chl *a* concentration on the western Agulhas Bank and off the South-Western Cape coast for the two SARP seasons combined. Standard errors and number of samples are shown.

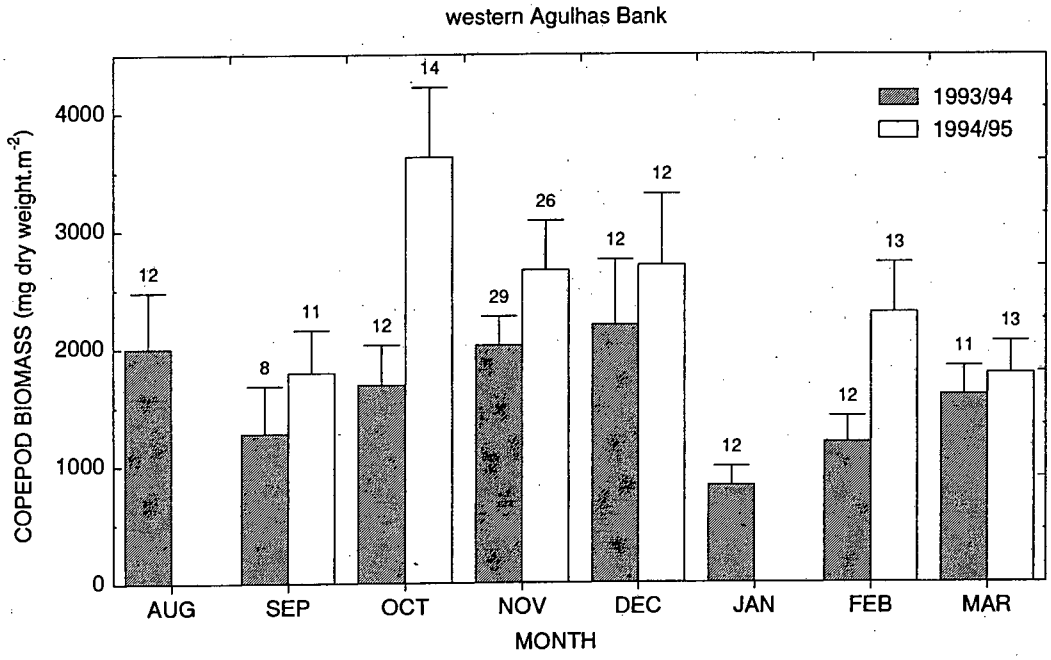


Fig. 2.3. Monthly variability of copepod biomass on the western Agulhas Bank from August 1993 to March 1994 and from September 1994 to March 1995. Standard errors and number of samples are shown.

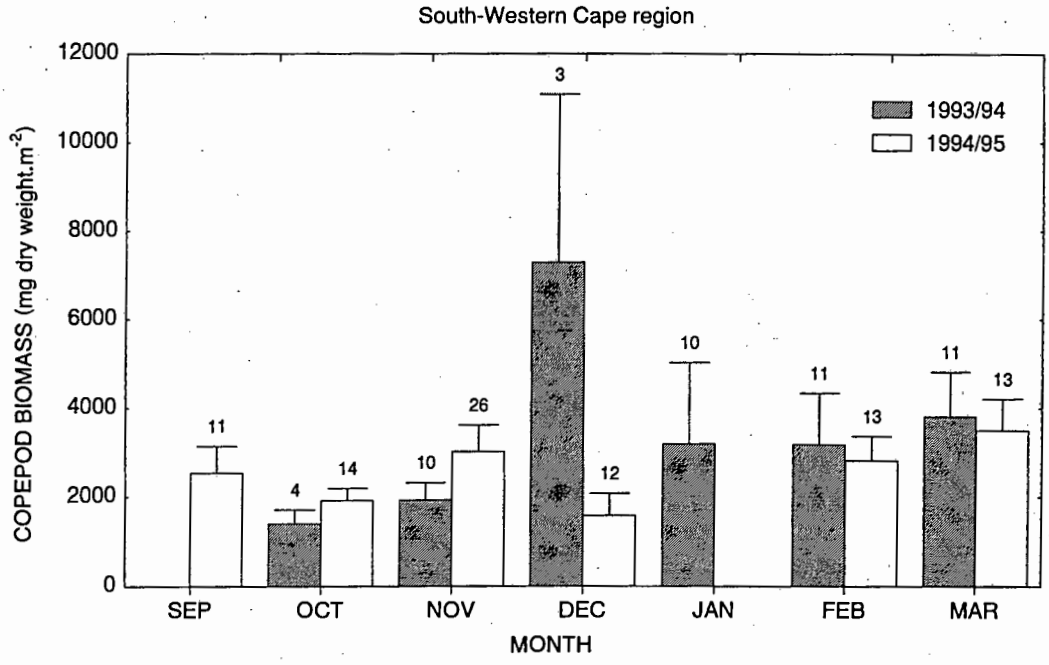


Fig. 2.4. Monthly variability of copepod biomass off the South-Western Cape from August 1993 to March 1994 and from September 1994 to March 1995. Standard errors and number of samples are shown.

considerable within-season fluctuations, no statistically significant differences in biomass were found amongst months in either season or region. The power of the ANOVA test for the western Agulhas Bank was 52% in 1993/94 ($k = 8, f$ 0.29, $\bar{n}$ = 13.5) and was 45% for the 1994/95 season ($k = 6, f =$ 0.27, $\bar{n}$ = 14.8). For the South-Western Cape region the power was 44% for 1993/94 ($k = 7, f =$ 0.35, $\bar{n}$ = 8.4) and only 18% for 1994/95 ($k = 6, f = 0.22$, $\bar{n}$ = 9.2).

DISCUSSION

Copepod biomass varied both spatially and temporally in the southern Benguela upwelling system.

Regional comparison of copepod biomass

The biomass of copepods was greater on the West Coast of South Africa than the western Agulhas Bank. This conclusion confirms findings from previous studies by Pillar (1986) and Hutchings *et al.* (1995). A summary of copepod biomass estimates obtained with a 200-μm mesh bongo net (as in the present study) for the three regions is shown in Table 2.3. The declining trend of copepod biomass from the northern to the southern area is evident, with a mean of 3638 mg dry weight.m^{-2} in St Helena Bay, 2831 mg dry weight.m^{-2} off the South-Western Cape region, and 2596 mg dry weight.m^{-2} on the western Agulhas Bank. There was a similar decrease in Chl *a* concentration from St Helena Bay in the north to the western Agulhas Bank in the south, which has been noted previously (Brown 1992; Hutchings 1992). Therefore, larger copepod biomass was associated with regions of greater Chl *a* concentration. Andrews and Hutchings (1980) and Hutchings (1981) have reported a similar relationship.

Considering that the copepod biomass on the western Agulhas Bank is smaller than off either the South-Western Cape region or in St Helena Bay, it is puzzling that anchovy expend a substantial amount of energy returning from their food-rich recruitment/nursery grounds on the West Coast to the relatively food-poor western Agulhas Bank to spawn. This paradox will be examined in detail in Chapter 7.

Inshore-offshore variation

There is a general trend of decreasing copepod biomass with distance from the coast off the South-Western Cape. A similar pattern was observed by Pillar (1986), Verheye and Hutchings (1988) and Andrews and Hutchings (1980). Copepod biomass was also found to be generally larger inshore in the northern Benguela system (Fearon *et al.* 1986). In contrast, the copepod biomass on the western Agulhas Bank peaks midshelf. This pattern was also observed by Pillar (1986). It should be noted

Table 2.3. Estimates of mean copepod biomass from various cruises in the southern Benguela system. Only samples collected in the upper 200 m of the water column with a vertical bongo fitted with a 200-μm mesh were included. WAB = western Agulhas Bank, SWC = South-Western Cape, and SHB = St Helena Bay.

AREA	DATE	COPEPOD BIOMASS (mg dry weight.m^{-2})
WAB	November 1988	884[1]
WAB	November 1989	2351[1]
WAB	June/July 1988	1483[2]
WAB	June 1989	1910[2]
WAB	November 1990	3946[3]
WAB	November 1991	1927[3]
WAB	November 1992	2020[3]
WAB	November 1995	4095[4]
WAB	November 1996	4749[4]
SWC	March 1983	4990[5]
SWC	June/July 1988	1148[2]
SWC	June 1989	2355[2]
SHB	June/July 1988	2983[2]
SHB	June 1989	4293[2]

[1] Peterson *et al.* (1992)

[2] Verheye *et al.* (1992)

[3] Hutchings *et al.* (1995)

[4] Sea Fisheries Research Institute, unpublished data

[5] Painting *et al.* (1993)

that copepod biomass on the western Agulhas Bank in September 1993 could have been underestimated because the offshore stations were not sampled.

The declining concentration of Chl *a* from inshore to offshore on both the western Agulhas Bank and off the South-Western Cape coast suggests that high levels of Chl *a* are a consequence of coastal upwelling. The upwelling front rarely migrates to beyond station 5 (Chapter 7, Fig. 7.4, Fig. 7.5), with Chl *a* concentrated inshore of this front under conditions of upwelling or downwelling, although there can be high levels over much of the shelf during quiescence (Chapter 6, Fig. 6.5). The large biomass of copepods inshore on the South-Western Cape Coast is associated with high levels of Chl *a* (*cf.* Figs 2.1 and 2.2; also see Andrews and Hutchings 1980). It is noteworthy, however, that the maximum biomass on the western Agulhas Bank was midshelf, spatially separated from the region of greatest Chl *a* concentration inshore. This may be a consequence of the advective input of copepod biomass from the adjacent eastern Agulhas Bank region (see Chapter 10). Variability in the distribution of Chl *a* at the event scale is discussed in Chapter 6.

Temporal variability

In the present study, copepod biomass on the western Agulhas Bank varied by a factor of two to three. This contrasts with the findings of Pillar (1986) who reported a steady decline in copepod biomass from September to March. Verheye *et al.* (1992) suggested that this decline was attributable to increased predation as pelagic fish migrate to the western Agulhas Bank to spawn during spring and summer. Several factors could be responsible for the substantial variation observed in the present study. Intra-seasonal changes in the advective loss from the region may play an important role and are discussed in detail in Chapter 9. Moreover, the effect of predation could vary seasonally and may influence the biomass of copepods on the western Agulhas Bank (Chapter 9).

The usual sampling strategy of estimating copepod biomass in November during the anchovy spawning season could fail to reveal important fluctuations, *e.g.* the November 1993 estimate on the western Agulhas Bank missed the very small biomass of January 1994 (Fig. 2.3), and November 1994 missed the large biomass of October 1994 (Fig. 2.3). The small biomass of copepods in January 1994 could have precipitated the high levels of gonad atresia observed for anchovy at this time (see Chapter 8). This could have shortened the spawning season and contributed to the catastrophic recruitment of the following year (Hampton and Barange 1996).

There was a two- to five-fold variation of copepod biomass off the South-Western Cape. Similarly, Andrews and Hutchings (1980) noted a two- to three-fold variation of copepod biomass off the

South-Western Cape coast region between October to March. This they attributed to the dynamic physical environment.

Recommendations for future sampling

Although no significant differences in copepod biomass were detected among months, the power of the analyses was substantially below the recommended minimum of 80% (Cohen 1988; Searcy-Bearnal 1994). Therefore, if there was a real month-to-month difference in copepod biomass of the magnitude observed in the present study, there was a 45-80% chance of incorrectly finding no difference. In the future, more stations are required to detect significant differences amongst mean monthly biomass estimates. If a power of 80% was stipulated *a priori*, 23 stations each month would have been required for 1993/94 and 30 stations for 1994/95 on the western Agulhas Bank. Off the South-Western Cape, 17 stations would be needed each month in 1993/94 and 48 stations in 1994/95. Thus, it is recommended that at least twice as many stations be sampled as the 12 stations on the western Agulhas Bank and 11 on the South-Western Cape coast region to obtain statistically significant differences in future sampling programmes. The very small power of the analyses and the large number of stations needed to detect significant differences is attributable to the large cross-shelf variability of copepod biomass on each transect.

In subsequent chapters, data on copepod biomass collected monthly are used for regression analysis, despite finding no statistically significant difference in this chapter. This is justified on the basis that it cannot be concluded there are no significant differences in biomass, given the very low power of the analysis. It is likely that there are differences in copepod biomass considering the large fluctuations observed, but the sampling programme was inadequate to detect them. The imprecise estimates of mean monthly biomass serve to make it even more difficult to elucidate relationships using regression analysis.

CHAPTER 3

SEX RATIOS OF CALANOID COPEPODS AND THE INFLUENCE OF ENVIRONMENTAL VARIABLES

ABSTRACT

Data on copepod sex ratios collected in the southern Benguela upwelling system during austral spring and summer of 1993-1995 are used to test three hypotheses: (1) sex ratios of pelagic copepods are related to trophic mode, with a greater proportion of females in copepods that are mainly herbivorous compared with those that are predominantly carnivorous or omnivorous; (2) sex ratios skewed toward females are a result of reduced longevity of males; and (3) sex ratios may be influenced by environmental variables. Sex ratios were related to trophic mode, with samples collected by a vertically-towed net showing that the predominantly herbivorous species had a smaller proportion of males (*Calanus agulhensis* 25.3% and *Calanoides carinatus* 20.7%) than species that are mainly carnivorous (*Metridia lucens* 54.4% and *Pleuromamma* spp. 56.4%) or omnivorous (*Centropages brachiatus* 59.2%). Ship-based 24-h moulting rate experiments on C5s of one species, *C. agulhensis*, were performed concurrently with the collection of the net samples. The sex ratio from these experiments was 33% male, suggesting that the sex ratio for newly-moulted individuals is already heavily skewed toward females. However, this ratio was skewed further by greater post-moult mortality of males: the proportion of male *C. agulhensis* from the experiments was significantly greater than from the net samples (33.0 *vs* 25.3%, $G = 13.7, p < 0.001$). In relation to environmental variables, moulting rate experiments showed that the sex ratio of *C. agulhensis* was unrelated to temperature or population density. However, there was a smaller proportion of males under conditions of poor (29.9%) than good food (38.3%). This may be an adaptive strategy to poor food conditions: it may be beneficial to be female during periods of poor food because females are larger, have greater longevity, and have more lipid reserves than do males, enabling a greater proportion of females than males to survive periods of starvation. Females could then continue to reproduce when food conditions improve. It is proposed that moulting rate experiments of C5s are useful for investigating factors that influence sex ratios, especially when used in conjunction with sex ratios measured from net samples.

Introduction

There are several advantages of having an equal proportion of males and females in an animal population that reproduces sexually. It ensures the greatest chance of encounters between individuals of the opposite sex, reduces intersexual competition, and increases genetic variability (Fisher 1958). However, skewed sex ratios toward females are a common feature of many animals, including

calanoid copepods (Tande and Hopkins 1981; Miller *et al.* 1984; Fleminger 1985; Uye and Sano 1995). In a study of the copepod community of the north-western Mediterranean, Kouwenberg (1993) found that sex ratios were related to the mode of nutrition, with pronounced female dominance in herbivorous species and approximately equal proportion of the sexes in omnivores and carnivores. A concomitant problem of a preponderance of females in a population is the reduced likelihood of sexual contact between members of the opposite sex. Kouwenberg (1993) proposed that many herbivorous species exhibit swarming behaviour, which facilitates the mating process by increasing the encounter rate between the sexes.

Skewed adult sex ratios can arise in two ways. First, sex ratios could be about equal at the beginning of adulthood and are then skewed by a variety of factors. The longevity of males may be shorter than females (Woodhead and Riley 1957, 1959) because of inefficient feeding structures of males (Corkett and McLaren 1978; Tande and Hopkins 1981), male death soon after mating (Chislenko 1964 in Moore 1983), or differential predation on the sexes because of sexual dimorphism.

The second way in which skewed sex ratios could arise is that they are genetically controlled or are influenced by environmental factors (Fleminger 1985), both of which are already apparent at the beginning of adulthood. It has been suggested that changes in sex ratio are related to temperature (Takeda 1950), food (Kouwenberg 1993), hydrostatic pressure (Vacquier and Belser 1965), population density (Moraitou-Apostolopoulo 1972; Kouwenberg 1993), and chemical balance (Voronov 1976 in Moore and Sander 1983). To explain these observations, it has been postulated that individuals can change their sex in response to environmental variables (Fleminger 1985).

This chapter seeks answers to the following questions:

1. Are sex ratios of pelagic copepods related to trophic mode?
2. Are sex ratios skewed toward females a consequence of greater male mortality?
3. Do sex ratios change in response to food availability, temperature, or population density?

Most studies have estimated sex ratios from net samples alone. In this study, estimates of sex ratios obtained from net samples were compared with sex ratios of recently-moulted adults from 24-h experiments of *Calanus agulhensis* and *Calanoides carinatus* C5s. Whether skewed sex ratios are evident at the beginning of adulthood or a consequence of differential mortality between the sexes, is then assessed. The effect of environmental factors on sex ratios was also evaluated from both net samples and moulting rate experiments.

MATERIALS AND METHODS

Sex ratios from net samples

Zooplankton samples collected throughout the southern Benguela system were used to estimate the percentage of males of *Calanus agulhensis*, *Calanoides carinatus*, *Centropages brachiatus*, *Metridia lucens*, and *Pleuromamma* spp. Throughout this chapter, the sex ratios are always expressed as the percentage of males in the adult population.

Relationship of sex ratios to environmental variables

The influence of food availability, temperature, and population density on the observed sex ratios of copepods collected by net was investigated. Owing to the small abundance of adults at many stations, the estimates of sex ratio from each station had a large associated variability. A better estimate of the mean sex ratio was obtained by calculating the sex ratio for data pooled into groups, rather than comparing the sex ratio at each station with the environmental variable in question. Thus, environmental variables were categorized into low and high levels.

Temperatures ≤15 °C were defined as cool and >15 °C as warm, based on the temperature where the structure of the food web in the southern Benguela system changes from being dominated by microflagellates to being dominated by diatoms or dinoflagellates (Mitchell-Innes and Pitcher 1992). These temperature categories were applied to all species. The food environment was defined in terms of the primary mode of nutrition of each species. Although all copepods are omnivorous to some degree (Turner 1984), copepods can be separated into those that are predominantly herbivorous, carnivorous, or omnivorous (Kouwenberg 1993, Mauchline 1998). For herbivorous species, poor food (Chl *a* ≤2 $mg.m^{-3}$) and good food (>2 $mg.m^{-3}$) conditions were defined, based on the Chl *a* concentration below which copepods are considered to be food limited (Hutchings 1992). For copepods that are mainly carnivorous, the density of microzooplankton was used as a measure of food availability. As no *a priori* indication of poor and good microzooplankton density was available, poor (≤median of 8.04 mg dry $weight.m^{-3}$) and good (>median) food conditions were defined. For the omnivore *Centropages brachiatus*, the sex ratio under good and poor food environments was investigated separately for Chl *a* and microzooplankton. To investigate the effect of population density on sex ratios, median densities of adults ($nos.m^{-3}$), ignoring stations where the species was absent, were calculated for *Calanus agulhensis* (4.65), *Calanoides carinatus* (5.70), *Centropages brachiatus* (9.63), *Metridia lucens* (10.87), and *Pleuromamma* spp. (2.85) and used to define small (≤median) and large (>median) densities for each species.

Sex ratios from moulting ratio experiments

The sex ratios of recently-moulted individuals of *Calanus agulhensis* and *Calanoides carinatus* were measured from moulting ratio experiments on C5s (see Chapter 1). For *C. agulhensis*, a total of 108 experiments were conducted, with 549 of the 3466 C5s incubated moulting to adults. For *C. carinatus*, 15 experiments were performed, with 37 of the 465 C5s moulting to adults. It was assumed that the sex ratios from moulting ratio experiments reflected the *in situ* sex ratios of newly-moulted individuals in the sea at that time, because the duration of the experiments (24 h) was short enough for the experimental conditions not to affect the experiments.

The relationships between the sex ratio of recently-moulted *Calanus agulhensis* individuals and environmental variables were also tested and the same critical values were used as described above for net samples. The effect of environmental variables on the sex ratio of *C. carinatus* from experiments could not be assessed because of the small number of experimental animals.

The effect of population density on the sex ratio from moulting ratio experiments for *Calanus agulhensis* was calculated not only for total density, but also for small and large densities of males and females. The median densities of males (2.61 m^{-3}) and females (3.85 m^{-3}) were used to define small (≤median) and large (>median) densities. It is valid to investigate the relationship between sex ratio from moulting ratio experiments with densities from net samples because each is independent of the other. In contrast, the relationship between sex ratios from net samples with either male or female density from net samples as has been done previously (Kouwenberg 1993) is not valid, because the sex ratio is related to male density, *i.e.* as the density of females decreases, the sex ratio increases.

Statistical analysis

Deviation of the sex ratio from a hypothesized 1:1 ratio was tested with a *G*-test (maximum likelihood χ^2) for goodness of fit. The *G*-test was also used to test null hypotheses concerning the independence between sex ratio and environmental variables (food, temperature, and density of adults). The *G*-test was adjusted for continuity using the Yates correction because there was only 1 degree of freedom (Zar 1984).

RESULTS

Sex ratios from net samples

From samples collected by net, the proportion of males of the largely herbivorous copepods was small, indicating female dominance (Table 3.1): *Calanus agulhensis* (25.3% male) and *Calanoides*

carinatus (20.7% male). Sex ratios of the predominately carnivorous copepods were skewed toward males: *Metridia lucens* (54.4%) and *Pleuromamma* spp. (56.4%). The sex ratio of the omnivore *Centropages brachiatus* was even more skewed towards males (59.2%). All sex ratios differed significantly from the 1:1 hypothesized ratio between males and females (Table 3.1).

There was a significantly greater proportion of *C. agulhensis* females under conditions of poor food (23.6%) than under good food (30.9%, Table 3.2). In contrast, for *Metridia lucens*, there was a greater proportion of females under conditions of good food (48.8%) than under poor food (60.0%). There were no significant differences in the sex ratios for *Calanoides carinatus*, *Centropages brachiatus*, or *Pleuromamma* spp. under poor and good food conditions (Table 3.2).

There was a significantly greater proportion of *Calanus agulhensis* females at warm temperatures (24.4%) than under cool conditions (35.4%, Table 3.3). There were no significant differences between the sex ratios in cool and warm waters for *Calanoides carinatus*, *Metridia lucens*, *Pleuromamma* spp., or *Centropages brachiatus* (Table 3.3).

For *Calanus agulhensis*, there was a significantly greater proportion of females at large densities (23.8%) than at small densities (35.1%, Table 3.4). Sex ratios of *Calanoides carinatus*, *Centropages brachiatus*, *Metridia lucens*, and *Pleuromamma* spp. were not significantly related to the density of their adults, although they all showed an increase in the proportion of males at large population densities (Table 3.4).

Sex ratios from moulting ratio experiments

The overall proportion of males of *Calanus agulhensis* from moulting ratio experiments was 33.0% (181 ♂ and 368 ♀). This sex ratio is significantly greater than the sex ratio of 25.3% from the net samples ($G = 13.7$, $df = 1$, $p < 0.001$) and was also significantly different from a 1:1 sex ratio ($G = 63.1$, $df = 1$, $p < 0.0001$). The sex ratio from the experiments performed on *Calanoides carinatus* was 27.0% (10 ♂ and 27 ♀). Although this sex ratio was also greater than that measured from the net samples (20.7%), as it was for *C. agulhensis*, the difference was not significant ($G = 0.99$, $df = 1$, $p > 0.05$), possibly because of the small number of individuals in these experiments. This sex ratio, however, was significantly different from equality ($G = 6.4$, $df = 1$, $p < 0.05$).

Table 3.1. Sex ratios from net samples of five calanoid copepod species in the southern Benguela system collected between August and March of 1993/94 and 1994/95 . The null hypothesis of a 1:1 sex ratio was assessed by a *G*-test, $^{**}p < 0.01$ and $^{****}p < 0.0001$.

		SEX RATIO		
SPECIES	MODE OF NUTRITION	♂	♀	% MALE
Calanus agulhensis	herbivore[1]	762	2254	25.3****
Calanoides carinatus	herbivore[2]	264	1010	20.7****
Metridia lucens	carnivore[3]	3845	3219	54.4****
Pleuromamma spp.	carnivore[4]	390	301	56.4**
Centropages brachiatus	omnivore[5]	3125	2152	59.2****

[1] the genus *Calanus* is primarily herbivorous (Turner 1984)

[2] Schnack (1982)

[3] appears to be herbivorous, based on mandibular dentition (M.J. Gibbons pers. comm.)

[4] assuming the same feeding strategy as *Pleuromamma gracilis* (Kouwenberg 1993)

[5] Peterson *et al.* (1988)

Table 3.2. Sex ratios of copepods from net samples under conditions of poor and good food for copepods that are predominantly herbivorous (Chl *a*, ≤ or >2 $mg.m^{-3}$), carnivorous (microzooplankton, ≤ or >median density of 8.04 mg dry $weight.m^{-3}$), and omnivorous (Chl *a* and microzooplankton separately). See Table 3.1 for the classification of the mode of nutrition for the copepods studied. The null hypothesis of no relationship between sex and food was assessed by a *G*-test, $^{n.s.}$ = non significant, *** $p < 0.001$, and **** $p < 0.0001$.

		POOR FOOD			GOOD FOOD			
SPECIES	FOOD TYPE	♂	♀	% MALE	♂	♀	% MALE	CHANGE
Calanus agulhensis	Chl *a*	551	1783	23.6	211	471	30.9	7.3^{***}
Calanoides carinatus	Chl *a*	141	557	20.2	123	453	21.4	$1.2^{n.s.}$
Metridia lucens	microzooplankton	2131	1418	60.0	1714	1801	48.8	-11.2^{****}
Pleuromamma spp.	microzooplankton	225	166	57.5	165	135	55.0	$-2.5^{n.s.}$
Centropages brachiatus	microzooplankton	1759	1160	60.3	1366	992	57.9	$2.4^{n.s}$
Centropages brachiatus	Chl *a*	2073	1470	58.5	1052	682	60.7	$1.8^{n.s.}$

Table 3.3. Sex ratios of copepods from net samples at cool (≤15 °C) and warm temperatures (>15 °C). The null hypothesis of no relationship between sex and temperature was assessed by a *G*-test, $^{n.s.}$ = non significant and *** $p < 0.001$.

	<15 °C			>15 °C			
SPECIES	♂	♀	% MALE	♂	♀	% MALE	CHANGE
Calanus agulhensis	86	157	35.4	676	2097	24.4	-11.0^{***}
Calanoides carinatus	138	479	22.4	126	531	19.2	$-3.2^{n.s.}$
Metridia lucens	1293	1099	54.1	341	269	55.9	$1.8^{n.s.}$
Pleuromamma spp.	49	32	60.5	2552	2120	54.6	$-5.9^{n.s.}$
Centropages brachiatus	934	636	59.5	2191	1516	59.1	$-0.4^{n.s.}$

Table 3.4. Sex ratios of copepods from net samples in areas of small and large densities of adults (see text for values). The null hypothesis of no relationship between sex and density was assessed by a *G*-test, $^{n.s.}$ = non significant and **** $p < 0.0001$.

	SMALL DENSITY			LARGE DENSITY			
SPECIES	♂	♀	% MALE	♂	♀	% MALE	CHANGE
Calanus agulhensis	140	259	35.1	622	1995	23.8	-11.3^{****}
Calanoides carinatus	26	135	16.2	238	875	21.4	$5.2^{n.s.}$
Centropages brachiatus	425	328	56.4	2720	1824	59.9	$3.5^{n.s.}$
Metridia lucens	445	412	51.9	3400	2807	54.8	$2.9^{n.s.}$
Pleuromamma spp.	71	60	55.0	319	241	57.0	$2.0^{n.s.}$

For *Calanus agulhensis*, a significantly greater proportion of individuals moulted to female under conditions of poor food (29.9%) than under good food (38.3%, Table 3.5). Both these sex ratios were about 7% greater than those estimated from the net samples under conditions of poor (23.6%) and good food (30.9%). The sex ratio of *C. agulhensis* from moulting ratio experiments was not related to temperature, total population density, or to the density of males or females (Table 3.5).

DISCUSSION

1. Are sex ratios of pelagic copepods related to trophic mode?

Sex ratios of copepods were related to their mode of nutrition, with the predominantly herbivorous species having sex ratios severely skewed toward females, and those of non-herbivores slightly skewed toward males, corroborating the hypothesis by Kouwenberg (1993). Data from other studies further support this contention. The proportion of males of predominantly herbivorous copepods is often small: *Calanus marshallae* 5.3% (Peterson 1979), *Undinula vulgaris* 25% (Webber and Roff 1995), and *Rhincalanus nasutus* 24.2% (Richardson unpublished data). In contrast, the sex ratio of the primarily carnivorous cyclopoid *Oncaea mediterranea* has a sex ratio of 57% (Moore and Sander 1983). The sex ratios of primarily omnivorous copepods such as those of the genera *Acartia* and *Centropages* (Turner 1984) are close to equality: *Acartia tranteri* 51.9% (Kimmerer and McKinnon 1987), *Acartia tumida* 50% (Mednikov 1961), *Centropages mcmurrichi* 50% (Mednikov 1961), and *Centropages typicus* 44% (Kouwenberg 1993). Thus, sex ratios appear to be related to the mode of nutrition. The pertinent question is why?

Although a 1:1 sex ratio is theoretically optimal (Fisher 1958), other ratios may be more favourable given the persistence of certain conditions such as food availability (Moore and Sander 1983). The differences in the sex ratios could be directly related to trophic mode because of the different nutritional value of phytoplankton and microzooplankton. Herbivores could be more susceptible to food stress because phytoplankton is of relatively low nutritional value and there may be only good food conditions for copepods during blooms. In contrast, carnivores and omnivores feed on a more-nutritious food source which may always provide reasonable food for copepods. The sex ratio of these copepods could then approach 1:1, because food would then not be the dominant factor controlling their sex ratios.

Limited food availability has been proposed by Mednikov (1961) to account for the preponderance of females in bathypelagic and abyssal systems. Kouwenberg (1993) suggested that herbivorous copepods have a smaller proportion of males as an adaptation to a limited food supply, ensuring females a greater share of the available food. Similarly, Moore and Sander (1983) suggested that the

Table 3.5. The sex ratio of *Calanus agulhensis* measured using the moulting ratio method under conditions of poor (≤2 $mg.m^{-3}$) and good (>2 $mg.m^{-3}$) Chl *a*, cool (≤15 °C) and warm (>15 °C) temperature, and small and large density (see text for values). The null hypotheses of no relationships between sex and food, temperature, or density were assessed by *G*-tests, $^{n.s.}$ = non significant and * $p < 0.05$.

	LOW			HIGH			
CATEGORY	♂	♀	% MALE	♂	♀	% MALE	CHANGE
Food	83	195	29.9	111	179	38.3	8.4^{*}
Temperature	53	89	37.3	141	285	33.1	$-4.2^{n.s.}$
Abundance (♀)	96	190	33.6	98	184	34.8	$1.2^{n.s.}$
Abundance (♂)	127	231	35.5	67	143	31.9	$-3.6^{n.s.}$
Abundance (total)	83	180	31.6	111	194	36.4	$4.8^{n.s.}$

plasticity of sex ratios is a selective mechanism which reduces intersexual competition for food resources which are scarce in the environment. Skewed sex ratio towards females also relaxes the pressure for a high reproductive output (and hence feeding rates). These are essentially group selection arguments describing the benefits that accrue to the species.

The mechanism that promotes skewed sex ratios in poor food environments has to operate at the level of the individual. It may be beneficial to be female when food is scarce because females are larger, have greater longevity (Parrish and Wilson 1978), and have more lipid reserves than do males, enabling a greater proportion of females than males to survive periods of starvation. Females could then continue to reproduce when food conditions improve. Thus, it is advantageous for individuals to be female if there are regularly recurring periods of starvation. Not all individuals, however, would become female as there is still a benefit for some males to remain in the population because they can deposit their spermatophores on more females. This hypothesis is only applicable to species where males feed: if males did not feed then periods of starvation would not affect them. Using gut fluorescence techniques, it has been shown that male *Calanus agulhensis* feed on Chl *a* (J. Huggett, unpublished data).

Currently, these hypotheses are speculative and require more information on the sex ratios of copepods with different trophic modes, assessment of food quality in the field, and indices of how food quality varies in marine systems.

2. Are sex ratios influenced by environmental variables?

Sex ratios of most of the species studied were not related to environmental variables. The constancy of the sex ratio of *Centropages brachiatus* to food availability was similar to that found for *Centropages typicus* for different concentrations of Chl *a* in the laboratory (Davis and Alatalo 1992). It is unknown why the sex ratio of *Metridia lucens* may be positively related to microzooplankton.

The sex ratio of *Calanus agulhensis* changed in response to environmental variables, with food availability being the most likely causative factor. A greater proportion of females were produced in food-poor waters than under conditions of good food. The change in the sex ratio of *C. agulhensis* in response to food availability may be an adaptation to the poor food environment it commonly encounters. Although *C. agulhensis* and *Calanoides carinatus* are the two dominant large copepods in the southern Benguela upwelling system, they have markedly different distributions. *C. agulhensis* is centred on the warm-water, generally poor-Chl *a* Agulhas Bank region and *Calanoides carinatus* concentrated in the cooler food-rich water inshore on the South African west coast. It is noteworthy

that *C. agulhensis* produces a greater proportion of females under conditions of poor food, a strategy which appears absent in *C. carinatus*. This may contribute to the lack of persistence of *C. carinatus* on the Agulhas Bank.

Interrelationships of environmental variables in the field make determination of changes in sex ratios difficult. The effect of temperature on the sex ratio of *Calanus agulhensis* from net samples was probably a result of the overall negative relationship between the concentration of Chl *a* and temperature in the southern Benguela system (Chapter 4, Fig. 4.5). Moreover, the density of *C. agulhensis* is related to Chl *a* concentration, with large abundance offshore at smallest Chl *a* concentrations. The lack of a significant relationship between sex ratio and temperature for moulting ratio samples was probably a result of the fewer number of adults compared with net samples. The concurrence of small population densities and sex ratios skewed toward females observed in some studies may be a response to a poor food environment. For *Temora stylifera* and *Centropages typicus*, there is a greater proportion of females during periods of smallest abundance (Kouwenberg 1993). In some species of harpacticoids, sex ratios are biased towards females as density decreases during winter (Johnson and Scheibling 1987). Uye (1995) recognized that the sex ratio of a marine cyclopoid was more skewed toward females in winter than in summer. At times of smallest abundance, there are usually adverse environmental factors culminating in a scarcity of food (Kouwenberg 1993) and a large proportion of females may favour survival.

Sex determination in animals is both genetic, by chromosomal control, and epigenetic, under the influence of environmental factors. It has been postulated that many species of copepods change their sex in response to environmental variables such as nutrition, temperature, pressure, population density, and parasitism (Fleminger 1985 and references therein). Fleminger (1985) found females of many calanoid genera, including *Calanus*, to be dimorphic in the number of aesthetascs and hypothesized that one form was a true female, and the other was the result of a genetic male maturing as a functional female during its final moult to adulthood. Nutrition is likely to influence sex determination in the genus *Calanus* (Conover 1965; Corkett and McLaren 1978; Tande and Hopkins 1981). Furthermore, Fleminger (1985) reports unpublished experiments by S. Marshall that show that the sex of *Calanus pacificus californicus* was probably influenced by the amount of food between C3 and C5. The difference in the proportion of males between good and poor food environments for *C. agulhensis* was 7.3% from net samples and 8.4% from moulting ratio experiments. This is within the range expected if individuals changed their sex (the morph that changed from male to female in the study of *Calanus pacificus californicus* by Fleminger (1985) comprised 2-12% of the population).

3. Are sex ratios skewed because of lower longevity of males?

Skewed sex ratios toward females in many copepod species is usually attributed to shorter male longevity. By comparing the results of the moulting rate experiments and the net samples, this study suggests that greater mortality of males does have an impact on the sex ratio. For instance the sex ratio declined from 33% to 25.3% for *Calanus agulhensis* and from 27.0 to 20.7% for *Calanoides carinatus*. This impact, however, may be less than was previously thought because the sex ratios of these species were already markedly skewed toward females immediately after the final moult to adulthood.

By measuring the sex ratio of recently-moulted adults, processes that operate subsequent to moulting, such as earlier male death and differential predation-related mortality of adults are removed. Moulting ratio experiments are a useful tool for estimation of post-moult sex-specific mortality of adults. In future, it is advisable to incubate more individuals in each experiment than in the present study because moulting rates of C5s are slow.

CHAPTER 4

THE RELATIVE IMPORTANCE OF FOOD AND TEMPERATURE TO RATES OF EGG PRODUCTION AND SOMATIC GROWTH

ABSTRACT

Fecundity and somatic growth rates of *Calanus agulhensis* and *Calanoides carinatus*, the dominant large calanoid copepods in the southern Benguela upwelling system, as well as fecundity of several other common copepods, were measured between September and March of 1993/94 and 1994/95. Mean egg production of most copepods was small, <30 eggs.♀$^{-1}$.d^{-1} (*C. carinatus* 23.7, *C. agulhensis* 19.0 *Neocalanus tonsus* 16.1, and *Rhincalanus nasutus* 26.1), whereas mean fecundity of *Centropages brachiatus* was significantly greater (83.6 eggs.♀$^{-1}$.d^{-1}). This study also presents the first comprehensive field estimates of the fecundity of *Nannocalanus minor* (mean: 26.1 eggs.♀$^{-1}$.d^{-1}, range: 0.0-96.2 eggs.♀$^{-1}$.d^{-1}) and of somatic growth of N6 and all copepodite stages of *C. carinatus* (decreasing from 0.58 d^{-1} for N6 to 0.04 d^{-1} for C5). Somatic growth rates of *C. agulhensis* also declined with age, from 0.57 d^{-1} for N6 to 0.09 d^{-1} for C5. Data on growth rates were used to assess the relative importance of food (as measured by total Chl *a* concentration), phytoplankton cell size (proportion of cells >10 μm), and temperature to the growth of copepods. Multiple regression results suggested that fecundity and somatic growth rates were positively related to both Chl *a* concentration and phytoplankton cell size, but not to temperature. Although it was not possible to separate the effects of Chl *a* concentration and phytoplankton cell size, data from previous laboratory experiments suggest that copepod growth is not limited by small cells *per se*, but by the low Chl *a* concentrations that are associated with these particles in the field. Despite growth not being directly related to temperature, a dome-shaped relationship was evident in some species, with slower growth rates at cool (<13 °C) and warm (>18 °C) temperatures. The shape of this relationship mirrors that of Chl *a* *versus* temperature, where poor Chl *a* concentrations are associated with cool and warm temperatures. It is concluded that the effect of food limitation on growth of copepods outweighs that of temperature in the southern Benguela region. Sources of variability in relationships between growth and Chl *a* concentration are discussed.

INTRODUCTION

Not only are copepods the most abundant metazoans on earth, but they also grow rapidly (see Humes 1994). Davis (1987) argued that the only way to measure zooplankton production accurately is by estimation of species-specific growth rates. Field-based research on growth of copepods has focused on female egg production (Durbin *et al.* 1992; Plourde 1993; Jónasdóttir *et al.* 1995; McKinnon and

Ayukai 1996; Pond *et al.* 1996), rather than juvenile growth, because of its ease of measurement using bottle incubations. Work on juvenile growth has been conducted in temperate and polar regions by following the progression of cohorts after spring or fall phytoplankton blooms (McLaren and Corkett 1981; Middlebrook and Roff 1986; McLaren *et al.* 1989). Few studies have measured juvenile and adult growth rate simultaneously in dynamic regions such as upwelling areas (Walker and Peterson 1991; Hutchings *et al.* 1995), where the use of distinct cohorts to estimate juvenile growth is difficult because female egg production is quasi-continuous.

Identifying factors that control the growth of copepods is essential to understanding nutrient and carbon fluxes in the marine environment. There has been considerable debate in the literature about the relative importance of the two main factors that control copepod growth, *viz.* food and temperature. Egg production (Durbin *et al.* 1983; Kimmerer and McKinnon 1987; Peterson *et al.* 1991; Tourangeau and Runge 1991; McKinnon and Ayukai 1996) and somatic growth (Peterson and Hutchings 1995; Webber and Roff 1995) in natural copepod populations have been found to be limited by the quantity of available food. In terms of food quality, the nutritional value of phytoplankton has also been shown to influence growth (Ambler 1985; Kleppel and Burkart 1995; Jónasdóttir *et al.* 1995; Kleppel and Burkart 1995). Another aspect of food quality, particle size, can also limit copepod growth because small particles are used inefficiently by many large species (Paffenhöfer 1984; Berggreen *et al.* 1988; Armstrong *et al.* 1991b). The influence of temperature on growth rates in the wild has been well documented, especially in temperate seas (Middlebrook and Roff 1986; Davis 1987; McLaren *et al.* 1989). In their review of field measurements of growth rate, Huntley and Lopez (1992) concluded that copepods grow at maximum rates in the field, with an exponential increase in growth rate with temperature over a wide range of habitats. They suggested that food may not be limiting in nature, and the impression that food is limiting may be a consequence of sampling at incorrect scales.

The objectives of this study are twofold. Firstly, to estimate egg production and somatic growth of a number of common copepods from direct measurements using bottle incubations in the southern Benguela upwelling system. Secondly, to assess the relative importance of food quantity (expressed as Chl *a* concentration), phytoplankton cell size, and temperature on rates of egg production and somatic growth of copepods in this system.

MATERIALS AND METHODS

Rates of egg production (eggs.$♀^{-1}$.d^{-1}) were estimated for *Calanus agulhensis*, *Calanoides carinatus*, *Centropages brachiatus*, *Nannocalanus minor*, *Neocalanus tonsus*, and *Rhincalanus nasutus*, as well

as somatic growth rates (d^{-1}) and stage durations (d) for N6-C5 of *C. agulhensis* and *C. carinatus* using the protocol detailed in Chapter 1.

Relationships between growth and environmental variables such as Chl *a* concentration, phytoplankton cell size, and temperature were only assessed for *Calanus agulhensis* N6-♀ and *Calanoides carinatus* ♀, *Centropages brachiatus* ♀, and *Nannocalanus minor* ♀ because of the paucity of data for female *Neocalanus tonsus* and *Rhincalanus nasutus* (see Table 4.1), and juvenile *Calanoides carinatus* (see Table 4.4). The functional response of fecundity and somatic growth to food availability in terms of Chl *a* concentration was described by an Ivlev curve (Ambler 1986; Hutchings *et al.* 1995) of the form:

$$g = g_a(1-e^{-k*c})$$

where

g = egg production or somatic growth,

g_a = asymptotic rate of egg production or somatic growth,

k = the rate at which g approaches this asymptote,

c = Chl *a* concentration.

To assess the effect of phytoplankton cell size on fecundity and somatic growth, a measure of the dominance of large cells was derived. At each station, the proportion of cells that were >10 μm was calculated as the ratio of Chl *a* in the >10 μm fraction to the total Chl *a*. It has been suggested that Chl *a* in cells <10 μm is used inefficiently by many copepods (Peterson and Bellantoni 1987; Berggreen *et al.* 1988; Armstrong *et al.* 1991b).

Statistical differences among growth rates were evaluated by non-parametric tests because the data were heteroscedastic, preventing the use of parametric statistics (Zar 1984). To identify significant differences in growth, one-way non-parametric ANOVA was conducted on rates of egg production and somatic growth using the Kruskal-Wallis test. *A posteriori* comparisons were then computed using the Mann-Whitney *U*-test. As a number of multiple comparisons were conducted, the Bonferroni adjustment was used, *i.e.* the type-I error was divided by the number of comparisons.

To assess the relative effect of temperature, Chl *a* concentration, and the proportion of large cells on fecundity and somatic growth, a multiple regression analysis was conducted for each species/stage.

Backward multiple regression was performed, with non-significant variables removed sequentially until only significant factors remained. Standardized partial regression coefficients were calculated to highlight the relative importance of the independent variables to growth (Zar 1984).

RESULTS

Egg production rates

Estimates of egg production rates of six copepod species are summarized in Table 4.1. The minimum egg production rate was zero for all species. Egg production rates were significantly different among species (Kruskal-Wallis ANOVA, $H = 244.4$, $n = 2144$, $p < 0.0001$). Mean egg production rate for *Calanus agulhensis*, *Calanoides carinatus*, *Nannocalanus minor*, *Neocalanus tonsus*, and *Rhincalanus nasutus* was small, below 30 eggs.♀$^{-1}$.d^{-1}, whereas that for *Centropages brachiatus* was significantly greater (83.6 eggs.♀$^{-1}$.d^{-1}).

Results of the multiple regression analysis between fecundity and temperature, Chl *a* concentration, and the proportion of large cells are shown in Table 4.2. Fecundity was unrelated to temperature for all species. In contrast, fecundity was positively related to total Chl *a* concentration or the proportion of cells >10 μm in size (or both) for all species, although only poorly so for *Centropages brachiatus*. In *Calanus agulhensis* and *Calanoides carinatus*, the standardized partial regression coefficients show that egg production was more related to total Chl *a* concentration than to the proportion of cells >10 μm in size.

To aid interpretation of the multiple regression results, scatterplots of copepod egg production against temperature, Chl *a* concentration, and the proportion of cells >10 μm in size are shown in Fig. 4.1. Although the multiple regression results suggested no relationship between egg production and temperature, this type of analysis only identifies linear relationships. A visual inspection of the plots between fecundity and temperature, however, suggests a dome-shaped relationship between these variables for some of the species. For example, egg production by *Calanus agulhensis* is ≤60 eggs.♀$^{-1}$.d^{-1} for temperatures <13 °C and >18 °C, and up to 120 eggs.♀$^{-1}$.d^{-1} between 13 and 18 °C.

Scatterplots of egg production rate against Chl *a* show saturation of egg production at high Chl *a* levels (Fig. 4.1), suggesting that the linear relationship between growth rate assumed in the multiple regression is not the most appropriate. Consequently, the functional response of fecundity to Chl *a* concentration was described by an Ivlev curve (Ambler 1986; Hutchings *et al.* 1995). The proportion of the variance explained by these curves was between 10 and 38% (Table 4.3).

Table 4.1. Egg production of copepods collected in the southern Benguela system during this study: mean ± standard error (eggs.♀$^{-1}$.d^{-1}), range (eggs.♀$^{-1}$.d^{-1}), and the number of samples (*n*). Different superscripts indicate significant differences between means using the Mann-Whitney *U*-test at $p < \frac{0.05}{{}^{6}C_{2}} = 0.0\dot{3}$ (the Bonferroni adjustment).

SPECIES	MEAN ± SE	RANGE	*n*
Calanoides carinatus ♀	$23.7^{a} \pm 1.6$	0.0 - 143.5	350
Calanus agulhensis ♀	$19.0^{a} \pm 0.6$	0.0 - 130.8	1492
Centropages brachiatus ♀	$83.6^{b} \pm 4.7$	0.0 - 278.7	158
Nannocalanus minor ♀	$26.1^{a} \pm 2.9$	0.0 - 96.2	82
Neocalanus tonsus ♀	$16.1^{a} \pm 4.3$	0.0 - 98.2	33
Rhincalanus nasutus ♀	$26.1^{a} \pm 4.2$	0.0 - 61.2	19

Table 4.2. Results of multiple regression analyses. In each multiple regression, the dependent variable is either fecundity (eggs.♀$^{-1}$.d^{-1}) or somatic growth rate (d^{-1}), and the independent variables are temperature (°C), Chl *a* concentration (mg.m^{-3}), and the proportion of large cells. The standardized partial regression coefficients and the r^2 of the models are given, together with their respective significance level: n.s. = non significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, and $^{****}p < 0.0001$.

SPECIES/STAGE	TEMPERATURE	CHL *a*	PROPORTION OF CELLS >10 μm	r^2
Calanoides carinatus ♀	n.s.	0.457^{****}	0.293^{****}	0.39^{****}
Calanus agulhensis ♀	n.s.	0.464^{****}	0.192^{****}	0.35^{****}
Centropages brachiatus ♀	n.s.	0.274^{***}	n.s.	0.07^{***}
Nannocalanus minor ♀	n.s.	n.s.	0.506^{****}	0.26^{****}
C. agulhensis N6	n.s.	0.500^{*}	n.s.	0.26^{*}
C. agulhensis C1	-0.311^{*}	0.348^{**}	n.s.	0.26^{***}
C. agulhensis C2	n.s.	n.s.	0.526^{****}	0.27^{****}
C. agulhensis C3	n.s.	0.311^{**}	0.232^{*}	0.23^{****}
C. agulhensis C4	n.s.	0.314^{**}	0.333^{**}	0.33^{****}
C. agulhensis C5	n.s.	n.s.	0.396^{****}	0.15^{****}

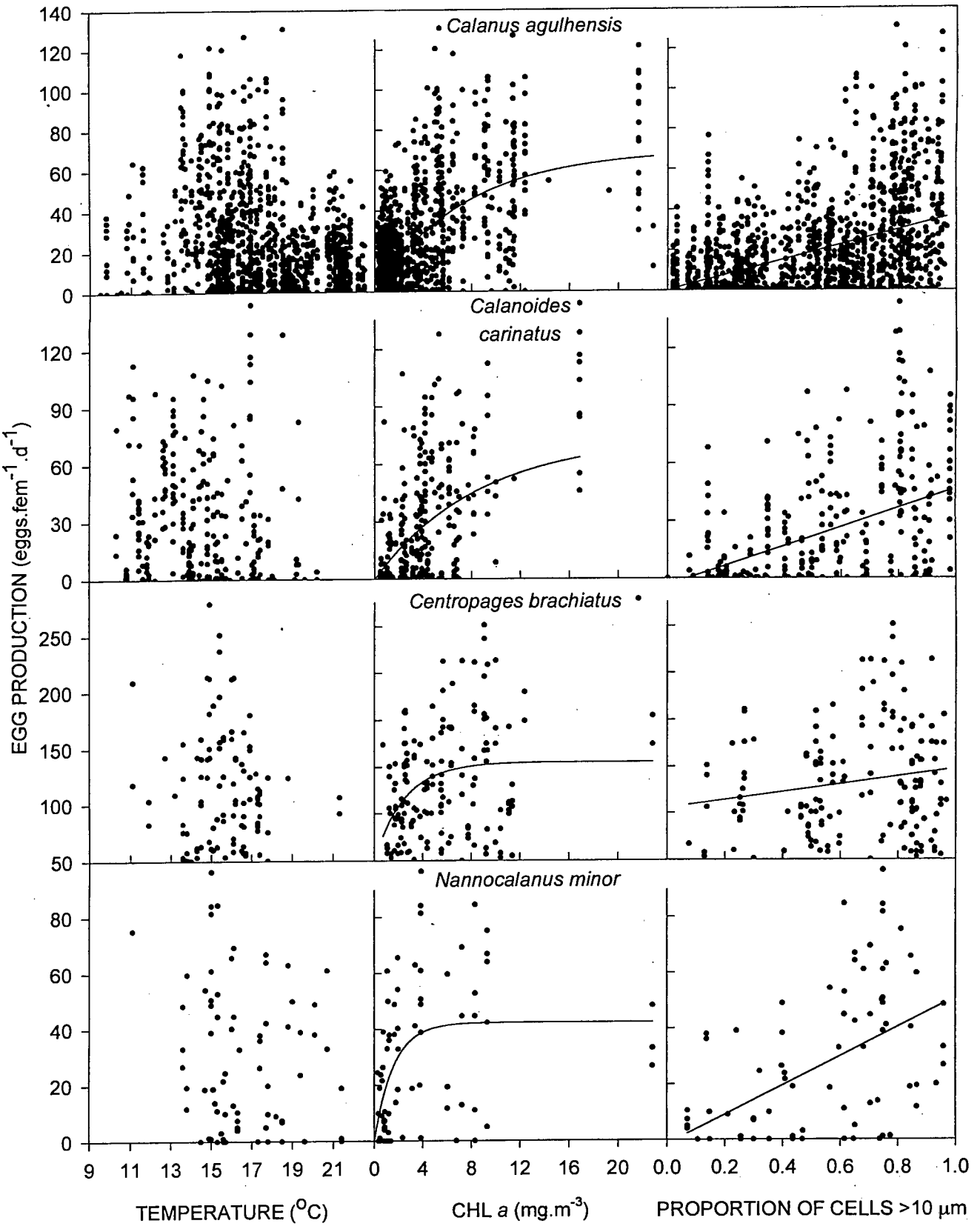


Fig. 4.1. Scatterplots of daily egg production rate of *Calanus agulhensis*, *Calanoides carinatus*, *Centropages brachiatus*, and *Nannocalanus minor* *vs* sea surface temperature (left), Chl *a* concentration (centre, with Ivlev curves fitted, see Table 4.3 for equations), and the proportion of phytoplankton cells >10 µm in size (right, with linear regressions fitted, see Table 4.3 for equations). Note the different *y*-scales.

Fecundity of each species increased linearly with the proportion of cells >10 μm in size (Fig. 4.1). Despite the multiple regression selecting either the concentration of Chl *a* or the proportion of cells >10 μm in size as the variables most related to egg production for a particular species, it can be seen that both variables are always positively related to fecundity (Table 4.3).

Somatic growth rates

Somatic growth rates of *Calanus agulhensis* and *Calanoides carinatus* are given in Table 4.4. Both species exhibit a similar trend, with older stages generally growing more slowly than their younger conspecifics. Growth rates of *C. agulhensis* stages were significantly different from one another (Kruskal-Wallis ANOVA, $H = 262.8$, $n = 465$, $p < 0.0001$). From *a posteriori* multiple comparisons using the Mann-Whitney *U*-test (Table 4.4), somatic growth rates of *C. agulhensis* N6, C1, and C2 were found to be not significantly different, but were faster than for the older stages. In addition, stages C3 and C4 also had similar growth rates, but these were significantly slower than for stages N6 to C2. The growth rate of C5 was significantly slower than that of all other stages.

Multiple regression analyses reveal that somatic growth rates (d^{-1}) were generally independent of temperature (Table 4.2), except for *Calanus agulhensis* C1 where the relationship was negative. Somatic growth for all stages was positively related to either Chl *a* concentration (N6 and C1) or the proportion of cells >10 μm in size (C2 and C5) or both (C3 and C4, Table 4.2).

Scatterplots of somatic growth against temperature, Chl *a* concentration, and the proportion of cells >10 μm in size are shown in Fig. 4.2. Interestingly, the relationship between somatic growth and temperature for the larger stages (C3-C5) appeared dome-shaped (Fig. 4.2), similar to that observed for female fecundity. For example, growth rates of *Calanus agulhensis* C5 were generally slow (<0.2 d^{-1}) for temperatures <13 °C and >18 °C, and faster (up to 0.4 d^{-1}) for temperatures between 13 and 18 °C.

As the scatterplots of growth rate against Chl *a* concentration showed saturation (Fig. 4.2), Ivlev curves were again fitted (Table 4.3). Somatic growth rates of all *Calanus agulhensis* stages accelerated with increasing concentrations of Chl *a*. The proportion of the variance explained was between 4 and 27%.

Somatic growth rates of all stages increased linearly as the proportion of cells >10 μm in size increased (Table 4.3). Despite the multiple regression selecting either the concentration of Chl *a* or

Table 4.3. Egg production and somatic growth related to Chl *a* concentration (Ivlev curve) and the proportion of cells >10 μm in size (linear equation). The parameters of the respective curves are shown, together with the proportion of the variance explained (r^2). Also shown for the linear equation is the significance level: n.s. = non significant, $^{*}p < 0.05$, $^{***}p < 0.001$, and $^{****}p < 0.0001$. Note that no significance level is possible using non-linear equations. The number of samples is the same as in Tables 4.1 and 4.4.

	GROWTH *vs* CHL a $g = g_a(1-e^{-k*c})$			GROWTH *vs* CELL SIZE $Y = a + bX$		
SPECIES/STAGE	g_a	k	r^2	a	b	r^2
Calanoides carinatus ♀	73.698	0.117	0.27	-3.378	49.929	0.21^{****}
Calanus agulhensis ♀	69.371	0.135	0.38	0.322	36.814	0.20^{****}
Centropages brachiatus ♀	105.133	0.401	0.10	55.652	41.396	0.03^{*}
Nannocalanus minor ♀	42.335	0.630	0.30	-1.308	52.015	0.26^{****}
C. agulhensis N6	0.593	4.641	0.27	0.514	0.094	$0.09^{n.s.}$
C. agulhensis C1	0.635	2.580	0.13	0.417	0.278	0.18^{***}
C. agulhensis C2	0.552	2.010	0.19	0.304	0.367	0.27^{****}
C. agulhensis C3	0.373	1.222	0.15	0.161	0.257	0.16^{***}
C. agulhensis C4	0.399	0.648	0.24	0.105	0.318	0.27^{****}
C. agulhensis C5	0.124	0.998	0.04	0.028	0.133	0.15^{****}

Table 4.4. Somatic growth rates (d^{-1}) of *Calanus agulhensis* and *Calanoides carinatus*: mean ± standard error (d^{-1}), range (d^{-1}), geometric mean of stage duration (D, d), and the number of samples (n). Different superscripts indicate significant differences at $p < \frac{0.05}{{}^{6}C_{2}} = 0.0\dot{3}$ (Mann-Whitney U-test). There were insufficient data for *C. carinatus* to test differences among mean growth rates.

	Calanus agulhensis				*Calanoides carinatus*			
STAGE	MEAN ± SE	RANGE	D	n	MEAN ± SE	RANGE	D	n
N6	$0.566^{a} \pm 0.015$	0.406 - 0.665	1.235	21	0.584	_	1.188	1
C1	$0.557^{a} \pm 0.023$	0.152 - 0.811	1.557	59	0.533	_	1.050	1
C2	$0.462^{a} \pm 0.020$	0.097 - 0.838	2.114	82	0.451 ± 0.079	0.082 - 0.802	2.519	9
C3	$0.278^{b} \pm 0.017$	0.000 - 0.709	3.101	90	0.135 ± 0.022	0.097 - 0.215	3.967	5
C4	$0.260^{b} \pm 0.016$	0.000 - 0.720	3.463	105	0.199 ± 0.024	0.091 - 0.272	3.906	8
C5	$0.089^{c} \pm 0.009$	0.000 - 0.420	7.365	108	0.044 ± 0.014	0.000 - 0.167	9.318	15

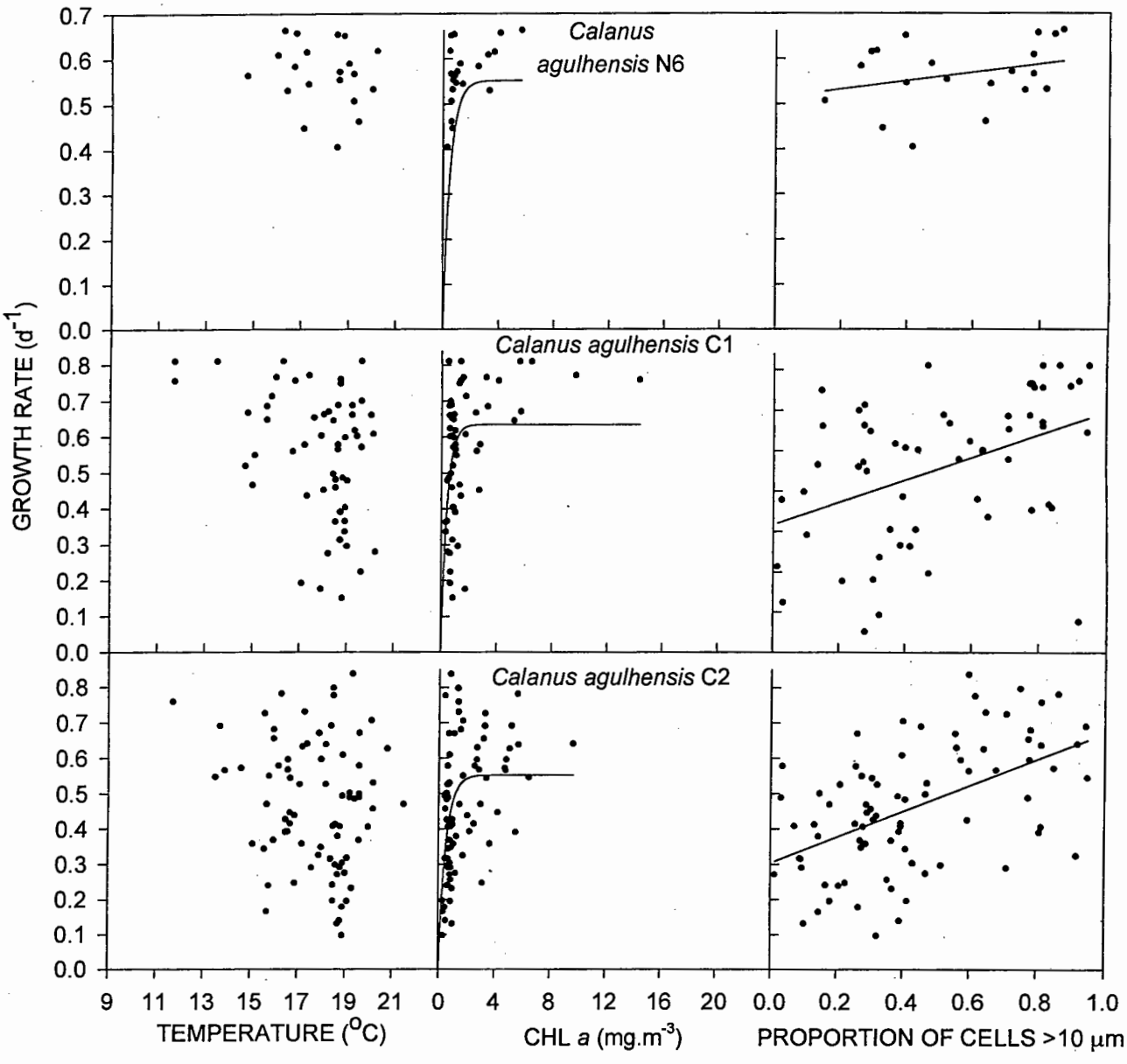


Fig. 4.2. Scatterplots of daily somatic growth rate of developmental stages N6-C2 of *Calanus agulhensis* (*C.a.*) *vs* sea surface temperature (left), Chl *a* concentration (centre, with Ivlev curves fitted, see Table 4.3 for equations), and the proportion of phytoplankton cells >10 µm in size (right, with linear regressions fitted, see Table 4.3 for equations). Note the different *y*-scales.

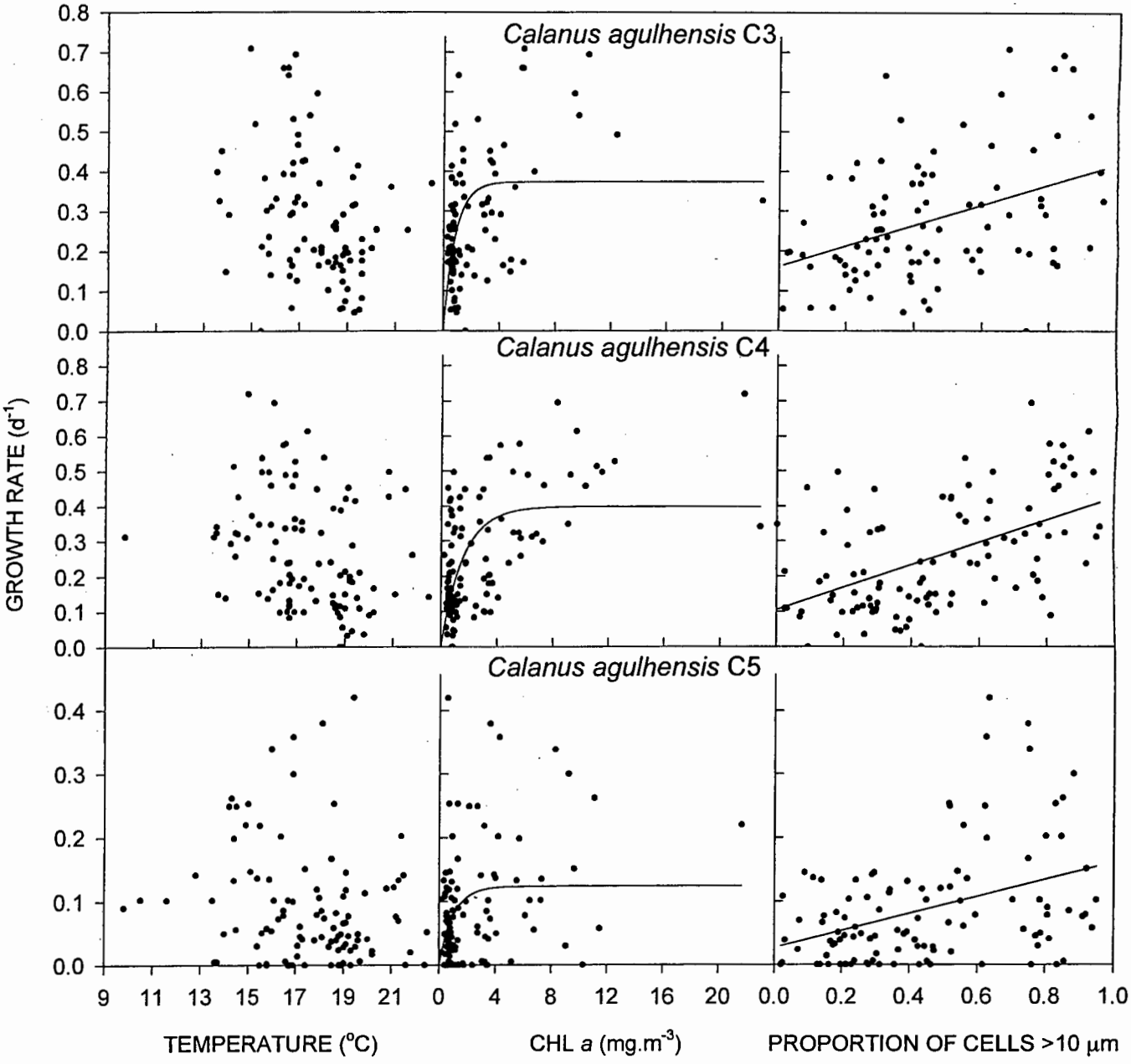


Fig. 4.2 continued. Scatterplots of daily somatic growth rate of copepodites C3-C5 of *Calanus agulhensis* (*C.a.*) *vs* sea surface temperature (left), Chl *a* concentration (centre, with Ivlev curves fitted, see Table 4.3 for equations), and the proportion of phytoplankton cells >10 µm in size (right, with linear regressions fitted, see Table 4.3 for equations). Note the different *y*-scales.

the proportion of cells >10 μm in size as the variables most related to somatic growth, it can be seen that both variables are always positively related to growth (Table 4.3). This suggests that Chl *a* concentration and the proportion of cells >10 μm in size are highly correlated, an assertion that is confirmed by Fig. 4.3.

DISCUSSION

This study provides the most comprehensive set of estimates of copepod egg production rates from any upwelling region (2134 experiments), as well as of somatic growth rates of *Calanus agulhensis* in the southern Benguela system (465 experiments). Moreover, the first extensive field estimates of somatic growth rate of N6 (0.58 d^{-1}) to C5 (0.04 d^{-1}) of *Calanoides carinatus* (39 experiments) are presented, although there are a few previous measurements from the same region, *viz. c.* 0.36 d^{-1} for C2 (n = 1), 0.20 d^{-1} for C3 (n = 3), and 0.13 d^{-1} for C4 (n = 3) estimated from Fig. 10 in Walker and Peterson (1991). Somatic growth of both *C. agulhensis* and *C. carinatus* declined sharply with age (Table 4.4), as has been noted previously (Peterson and Painting 1990; Hutchings *et al.* 1995; Peterson and Hutchings 1995). Such a decline in growth rate with body size may be a general phenomenon, and has been documented in both field (Greze 1978; Peterson *et al.* 1991) and laboratory studies in terms of stage duration (Peterson and Painting 1990) and somatic growth (Harris and Paffenhöfer 1976; Paffenhöfer 1976; Vidal 1980). This decrease may not only reflect allometry (Peters 1983; McLaren *et al.* 1989), however, but may also be a consequence of increased food-limitation of larger copepods (Webber and Roff 1995). This contention is explored further in Chapter 5.

To our knowledge, the rates of egg production for *Nannocalanus minor* presented in this study (mean: 26.1 eggs.♀$^{-1}$.d^{-1}, range: 0-96.2 eggs.♀$^{-1}$.d^{-1}; n = 82) are the first comprehensive estimates for this species from any marine system. In a preliminary study of copepod growth in the northern Benguela system, egg production rate of this species was found to be substantially smaller (mean = 2 eggs.♀$^{-1}$.d^{-1}, range: 0-8 eggs.♀$^{-1}$.d^{-1}, n = 14, Verheye *et al.* 1998) than those reported here, perhaps owing to the reduced data set in that study. *N. minor* is an important species globally, being distributed widely within tropical and temperate regions of the Atlantic, Pacific and Indian oceans and showing a preference for warm water (Unterüberbacher 1964; De Decker 1973). It is also an important food item of mesopelagic fish such as myctophids (Kinzer and Schultz 1985).

Maximum growth rates

Maximum growth rates of copepods are important because they define the upper limit of growth under given environmental conditions (Kleppel *et al.* 1996). As such, they allow the degree of

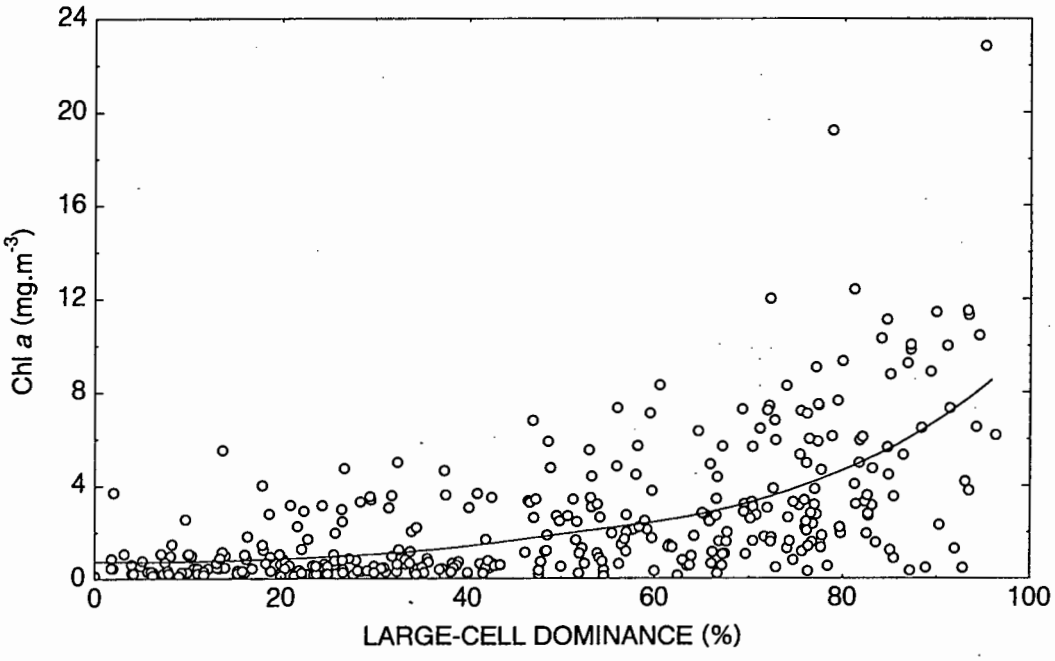


Fig. 4.3. The relationship between Chl *a* concentration and the dominance of large phytoplankton, expressed as the percentage contribution of cells greater than 10 μm to the total Chl *a* concentration. A distance-weighted least squares line was fitted (StatSoft 1996).

limitation of growth by factors such as food and temperature to be assessed. The rates of egg production and somatic growth of copepods reported here for the southern Benguela upwelling region are high, probably a consequence of the large Chl *a* concentrations and fast primary production that are encountered during bloom conditions in upwelling regions (Mitchell-Innes and Pitcher 1992)

The maximum estimate of fecundity for *Calanoides carinatus* was 143 eggs.♀$^{-1}$.d^{-1}, substantially greater than a previous estimate in the southern Benguela system of 40 eggs.♀$^{-1}$.d^{-1} (Armstrong *et al.* 1991b). This difference may be attributable to the larger number of samples collected over a wider variety of food types in the present study. Our estimate is similar to that of 150 eggs.♀$^{-1}$.d^{-1} in the laboratory under excess food conditions (Borchers and Hutchings 1986). Presumably, *C. carinatus* is sometimes not food-limited in the field.

The maximum egg production rate of 130 eggs.♀$^{-1}$.d^{-1} estimated for *Calanus agulhensis* was more than three times that measured under excess food conditions in the laboratory (Attwood and Peterson 1989). Although it is possible that the food resource (*Thalassiosira weissflogii*, 14 µm ESD) used in that study was of a sub-optimal size for growth of female *C. agulhensis*, a smaller flagellate (*Pseudoisochrysis paradoxa*, 4 µm ESD) provided in excess was a suitable food resource for *Calanoides carinatus* (Borchers and Hutchings 1986), which is similar in size to *C. agulhensis*. It is therefore more likely that *T. weissflogii* is not a nutritious food for *C. agulhensis*, or that experimental conditions were inadequate. This highlights that laboratory estimates of egg production should only be applied to natural populations with caution.

No previous estimates of maximum egg production of *Rhincalanus nasutus* (61.2 eggs.♀$^{-1}$.d^{-1}) are available in the literature. Maximum egg production by *Centropages brachiatus* was 278 eggs.♀$^{-1}$.d^{-1} substantially greater than its maximum of 95 eggs.♀$^{-1}$.d^{-1} observed in the upwelling zone off Chile (Peterson *et al.* 1988). This discrepancy may be owing to the larger number of samples collected in the present study. The estimate of maximum egg production presented here is similar to a recent estimate from the northern Benguela region of 225 eggs.♀$^{-1}$.d^{-1} (Verheye *et al.* 1998) and that of 200 eggs.♀$^{-1}$.d^{-1} for the closely-related species *Centropages typicus* in the laboratory (Dagg 1978).

The maximum egg production of *Neocalanus tonsus* was 98 eggs.♀$^{-1}$.d^{-1}. This is very similar to the 95 eggs.♀$^{-1}$.d^{-1} measured during spring in the southern Pacific Ocean when *Thalassiosira weissflogii* was added to the experimental incubations (Ohman 1987). *N. tonsus* is a sub-Antarctic species that is only found periodically in the southern Benguela system after intrusion of cold water (De Decker

1984). It is noteworthy that *N. tonsus* is fecund in the southern Benguela upwelling system because some copepods do not lay eggs outside of their typical area of distribution (Williams and Conway 1988).

Maximum somatic growth rates presented here for *Calanus agulhensis* are similar to those reported by Hutchings *et al.* (1995) for the Agulhas Bank, South Africa. However, the estimates of (N6) naupliar growth in both studies (*c.* 0.6 d^{-1}) are slower than those for calanoid nauplii (0.85 d^{-1}) in the tropical ocean (Roff *et al.* 1995). Although this difference could be attributable to the warmer water temperature in the latter study, maximum growth rates of *C. agulhensis* N6 in the present study and that by Hutchings *et al.* (1995) were probably underestimated. This is because the duration of the incubation (24 h) is the minimum stage duration that can be estimated. Stage durations in the field for calanoid nauplii can be less than a day (Webber and Roff 1995), and in some of our experiments all the nauplii had moulted within 24 h.

Relationship between growth and Chl *a*

The significant relationships between growth and both Chl *a* concentration and the proportion of cells >10 μm in size imply that growth rate is often food limited in the southern Benguela system. Thus, although maximum growth rates are sometimes fast (as discussed above), copepods only grow at these rates relatively infrequently. The predictability of egg production and somatic growth from Chl *a* concentration (most below 30%) for the species and life-history stages examined were similar to that reported in other studies in upwelling regions (Peterson *et al.* 1988; Armstrong *et al.* 1991b; Hutchings *et al.* 1995).

There are a number of possible reasons for the relatively poor correlations between growth and Chl *a* concentration in this study. Firstly, copepods have different modes of nutrition (Mullin 1966; Turner 1984; Verity and Paffenhöfer 1996; Mauchline 1998), so that Chl *a* is not always the best measure of food. Egg production is only weakly related to Chl *a* concentration for the omnivorous (Boyd *et al.* 1980) *Centropages brachiatus* (r^2 = 10% - Table 4.3; r^2 = 3% in Peterson *et al.* 1988), compared with the predominantly herbivorous species *Calanus agulhensis* (belonging to a mainly herbivorous genus (Turner 1984)) and *Calanoides carinatus* (Schnack 1982) (r^2 = 38% and 27% respectively - Table 4.3). Secondly, some species of phytoplankton are a more nutritious food source than others (Cahoon 1981; Napp *et al.* 1988; Kleppel and Burkart 1995), so that estimates of Chl *a* concentration as a bulk index of food may not adequately reflect the actual nutritive value of the food. For instance, dinoflagellates, which are common in upwelling regions, have relatively more carbon than diatoms for a given Chl *a* concentration (Chan 1980). Moreover, Kleppel and Burkart (1995) concluded that

dietary diversity, which is not reflected in a single Chl *a* value, increases copepod production. Thirdly, weak coupling between growth and food supply in upwelling areas could be attributable to wind-driven advection causing spatial mismatch between vertically migrating copepods which can maintain themselves within their preferred habitat and their food resource which remains in the upper mixed layer and is subject to surface advection (Peterson *et al.* 1988; Armstrong *et al.* 1991b).

Fourthly, the relationship between growth and ambient food concentration is likely to be poorer in dynamic upwelling regions where Chl *a* concentration is changing rapidly, because of the lag between the ingestion of food and its conversion to production. Moreover, this time lag varies for different species, with the lag ranging from 9.5 to 91 h for five species of marine copepods (Tester and Turner 1990). The effect of this time lag on the relationship between growth and Chl *a* concentration can be illustrated by a simple model (Fig. 4.4). It is assumed that growth (somatic growth or fecundity) is only a function of Chl *a* concentration, although it is lagged by a variable amount. Phytoplankton growth and decay is represented by a sine wave with a bloom development time of 8 d (Brown and Hutchings 1987). Sampling is simulated by repeatedly recording the growth and Chl *a* concentration throughout the development and decay of the phytoplankton bloom. Growth and the concentration of Chl *a* are perfectly correlated when there is no time lag between growth and Chl *a* concentration (Fig. 4.4a). With a one-day lag between ingestion and assimilation into growth, two very different rates of growth occur for the same Chl *a* concentration (Fig. 4.4b). Faster growth is observed during the decay phase of the bloom because of the prior high Chl *a*, and slower copepod growth during the earlier growth phase of the bloom. As the time needed for conversion into production increases to one quarter of the bloom development time (two days), the relationship between growth and Chl *a* concentration deteriorates so that there is no relationship (Fig. 4.4c). At a time lag of three days, the relationship becomes negative (Fig. 4.4d), and at a four-day time lag there is a perfect negative relationship (Fig. 4.4e). Thus, instantaneous growth rate is not directly related to the contemporaneous food density.

Fifthly, the lag between growth and Chl *a* concentration may not be constant within a species. The time needed for rates of egg production to recover to their maximum is related to the duration of starvation (Attwood and Peterson 1989; Calbet and Alcaraz 1996). For instance, in *Calanus agulhensis*, restoration to maximum fecundity following a one-day starvation period is about 1 d, whereas after one week of starvation recovery takes 5 d (Huggett 1996). Correlations between growth and food conditions would be expected to be weaker in physically dynamic regions such as upwelling areas than in more stable ones. This may partially account for the very poor correlations between growth rates and food availability that have been found in upwelling regions in this and other studies (Peterson *et al.* 1988; Armstrong *et al.* 1991b; Hutchings *et al.* 1995).

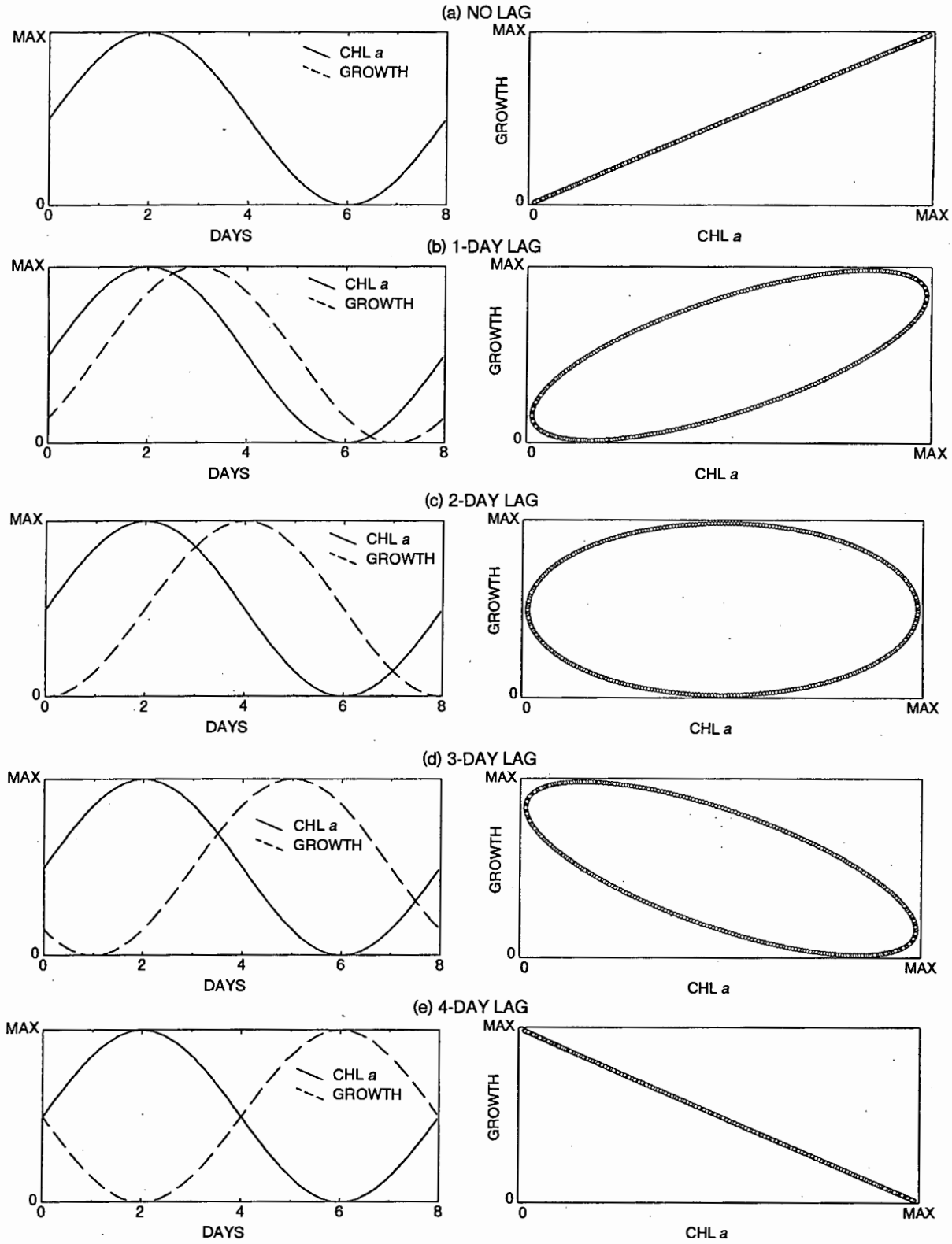


Fig. 4.4(a)-(e). The relationship between copepod growth rate and Chl *a* concentration, assuming that growth is dependent upon Chl *a* concentration which varies as a sine wave with a period of 8 d. Time lags (in days) between growth and Chl *a* concentration vary from (a) 0 to (e) 4 days. Time-series of copepod growth and Chl *a* concentration (left) and the relationship between growth and Chl *a* concentration (right) are shown.

Lastly, a large portion of the variability in relationships between growth and food is related to individual variation in growth. For example, egg production of *Calanus agulhensis* at one station with a Chl *a* concentration of 21 $mg.m^{-3}$ ranged from 30 to 120 $eggs.♀^{-1}.d^{-1}$ and that of *Calanoides carinatus* ranged from 45 to 145 $eggs.♀^{-1}.d^{-1}$ at a Chl *a* concentration of 17 $mg.m^{-3}$ (see Fig. 4.1). This individual variability may be partially attributable to the number of particles encountered by individual copepods (see Chapter 5).

The effect of cell size

Copepod growth rate was faster when there were more large than small cells present. This confirms earlier work in the southern Benguela region. For instance, during a 27-day anchor station study in the St Helena Bay region, *Calanoides carinatus* produced more eggs during a bloom of the large diatom *Coscinodiscus gigas* (250 μm diameter) than during a microflagellate bloom (<6 μm) between upwelling events (Armstrong *et al.* 1991b). Along a cross-shelf transect in the same region, Walker and Peterson (1991) found a three- to five-fold improvement in egg production of *C. carinatus*, *Calanus agulhensis*, and *Centropages brachiatus* in areas dominated by large cells in comparison with areas dominated by small cells.

Large copepods such as females feed more efficiently on large cells (Frost 1977), particularly cells >20 μm ESD (Berggreen *et al.* 1988), obtaining their maximal daily ration at relatively small carbon concentrations (Frost 1972). It is known from laboratory experiments, however, that copepods can grow rapidly on small cells at very large densities. Borchers and Hutchings (1986) found high egg production (150 $eggs.♀^{-1}.d^{-1}$) by *Calanoides carinatus* fed excess concentrations of the small flagellate *Pseudoisochrysis galbana* (4 μm ESD). Peterson *et al.* (1990b) also reported high egg production by *C. carinatus* (mean 74.5 $eggs.♀^{-1}.d^{-1}$) on a diet of the small diatom *Thalassiosira weissflogii* (12 μm ESD, Sea Fisheries Research Institute, unpublished data) at a density of 8000 $cells.ml^{-1}$, equivalent to a Chl *a* concentration of 78 $mg.m^{-3}$ (using their C:Chl *a* ratio of 23.7). It should be noted that in these laboratory experiments, cell concentrations were used that are rarely encountered in the field (Brown 1992). Small cells are normally associated with poor Chl *a* conditions, because the concentration of Chl *a* increases as phytoplankton cell size increases in the southern Benguela system (see Fig. 4.3), corroborating the findings of Mitchell-Innes and Pitcher (1992). This makes the relative importance of cell size and Chl *a* concentration to growth rate difficult to distinguish in the field. By interpreting the data from this study in terms of previous laboratory experiments, it is suggested that copepod growth in the field may not be limited by cell size when small phytoplankton cells dominate the phytoplankton assemblage, but by the typical concentrations of these cells.

Effect of temperature on growth

Many biological rates such as fecundity generally increase with temperature, within the tolerance range of an organism (Kinne 1970). For *Calanus agulhensis* and *Calanoides carinatus*, laboratory studies under conditions of excess food have shown substantially faster growth rates at warmer temperatures (Peterson and Painting 1990). In cool temperate coastal regions where much of the scientific research on copepods has focused, temperature is considered the main factor controlling growth (McLaren and Corkett 1981; Davis 1987; McLaren *et al.* 1989). When other factors such as food are limited, however, temperature does not accurately predict growth rate (Middlebrook and Roff 1986; Kleppel *et al.* 1996). The growth rates of copepods in this study were not directly related to temperature over the range examined (9-23 °C). This lack of a positive relationship has been noted previously on the Agulhas Bank (Hutchings *et al.* 1995). In the southern Benguela system, favourable food conditions are restricted spatially to the narrow upwelling belt inshore (Brown 1992), and temporally to quiescent conditions between upwelling events (see Chapter 6). Thus, growth rates estimated in the laboratory under food-saturated conditions at specific temperatures are not always representative of field values. Undoubtedly, growth rate is dependent upon temperature on a global scale, although the assertion that copepods may not be food limited in nature (Huntley and Lopez 1992) is clearly overstated (Kleppel *et al.* 1996).

Growth rate of copepods in a variety of aquatic habitats is controlled by food rather than temperature, including freshwater systems (Hart 1991; Ban 1994), tropical seas (McKinnon and Thorrold 1993; Webber and Roff 1995), and some temperate coastal regions (Peterson 1985; Peterson and Bellantoni 1987; Armstrong *et al.* 1991b; Bautista *et al.* 1994; Peterson and Hutchings 1995; Pond *et al.* 1996). The domed relationship between growth rate and temperature that was discernible in some plots (Figs 2 and 3) may be a consequence of the domed association between Chl *a* concentration and temperature (Fig. 4.5). This pattern is typical of the southern Benguela upwelling system (Mitchell-Innes and Pitcher 1992; Pitcher *et al.* 1996). The domed relationship in the present study, however, is shifted towards warmer temperatures, probably because of the inclusion of the warmer western Agulhas Bank region in this study (Fig. 4.5). Cool temperatures (<13 °C) indicate water that is newly upwelled with a poor Chl *a* concentration. As the water warms, the concentration of Chl *a* increases as diatoms dominate initially, followed by dinoflagellates. Above 18 °C, there is a change from a diatom/dinoflagellate-dominated phytoplankton community of large biomass to a microflagellate-dominated, small-biomass microbial community (Mitchell-Innes and Pitcher 1992). Impoverished food conditions, therefore, limit copepod growth at both cool and warm temperatures, so that growth cannot be assumed to be a function of temperature alone in upwelling regions, as it has been in models of other systems (Miller and Tande 1993).

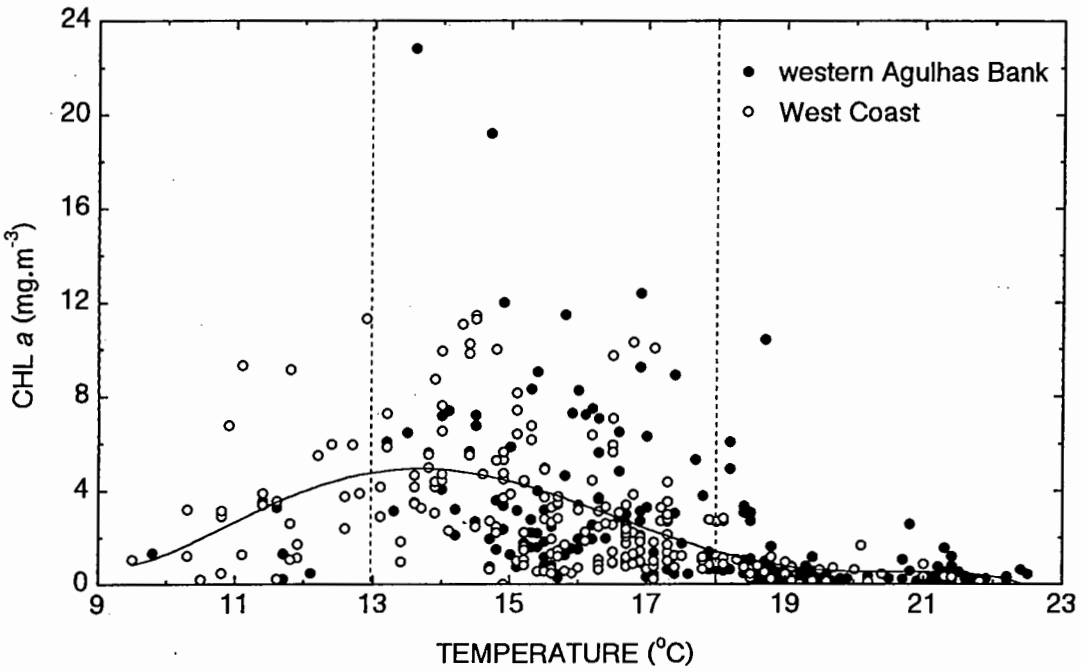


Fig. 4.5. Chl *a* concentration against sea surface temperature. A distance-weighted least squares line was fit. A dome-shaped relationship is evident.

CHAPTER 5

GROWTH RATES OF COPEPODS: THE INTERPLAY BETWEEN BODY SIZE AND FOOD

ABSTRACT

Growth rates of copepods were estimated from shipboard measurements of egg production by adult female *Calanus agulhensis, Calanoides carinatus*, *Nannocalanus minor*, and *Centropages brachiatus* and moulting rates of juvenile stages (N6-C5) of *C. agulhensis*. Data were obtained during austral spring and summer of 1989-1995 in the southern Benguela upwelling system. While maximum growth rates showed less than a three-fold decline over the body size range 525-2763 μm total length (probably owing to allometric considerations), mean growth rate decreased by an order of magnitude, suggesting limitation of growth rate by an environmental factor. Most of this decline in mean growth rate was attributable to food limitation of growth of large copepods. Frequency distributions of growth rate under low food densities were severely skewed toward slow growth rate for large copepods, whereas they were more symmetric for smaller copepods. In contrast, at high food concentrations, the frequency distributions had a high degree of symmetry for all copepods. These frequency distributions were interpreted in terms of a probabilistic model describing the encounter rate of suitably-sized food particles by copepods. The effect of food limitation on growth rate was summarized by plotting the coefficient of variation of growth rate against body size. A strong positive relationship was found ($r^2 = 0.94$, $p < 0.001$), indicating that small copepods were always growing well, whereas the growth rate of large copepods was more variable. It is suggested that this difference is a consequence of the ability of small copepods to consume small particles which are present at a relatively constant background density.

INTRODUCTION

The two main factors controlling growth of copepods are temperature and food. The influence of temperature on growth rates in the wild has been well documented, especially in temperate seas (Middlebrook and Roff 1986; Davis 1987; McLaren *et al.* 1989). Huntley and Lopez (1992) concluded that copepods grow at maximum rates in the sea, with an exponential increase in growth rate with temperature over a wide range of habitats. In contrast, growth of copepods has been found to be more related to food rather than temperature in a variety of aquatic habitats, including freshwater systems (Hart 1991; Ban 1994), tropical seas (McKinnon and Thorrold 1993; Webber and Roff 1995), some temperate coastal regions (Peterson and Bellantoni 1987; Armstrong *et al.* 1991b; Bautista *et al.* 1994; Pond *et al.* 1996), and in an upwelling system (Peterson and Hutchings 1995; see Chapter 4). In the latter system, the southern Benguela, the lack of dependence of growth on

temperature is attributable to slower growth at warm (18-22 °C) temperatures (Chapter 4, Fig. 4.1), a consequence of very low (usually <2 $mg.m^{-3}$) food concentrations at these temperatures (Mitchell-Innes and Pitcher 1992; Pitcher *et al.* 1996).

Two studies in contrasting ecosystems suggest that the degree of food limitation in copepods may be related to body size, with larger species being more food limited. The first, in the tropical ocean, shows that there is progressive food-limitation of somatic growth and egg production with increasing body size (Chisholm and Roff 1990b; Webber and Roff 1995). In the second study, in a temperate fjord, egg production by females was food limited, unlike the somatic growth of juveniles (Peterson *et al.* 1991). More recently, in a global synthesis of copepod growth rates measured in the field, Hirst and Sheader (1997) suggested that food may be limited in a body-size dependent way, with larger individual being food limited. This contention requires testing in a variety of marine systems.

In the present chapter, the hypothesis that food limits growth in a body-size dependent manner is assessed using shipboard data on copepod growth rates collected in the southern Benguela upwelling region. Growth rates of copepods over a broad size range (500-2750 μm) were measured, including somatic growth of pre-adult stages (662 moulting rate experiments) and fecundity of several species (2084 egg production experiments).

MATERIALS AND METHODS

To enable presentation of frequency histograms of growth rate for juveniles stages of *Calanus agulhensis*, data on somatic growth rates that were collected during SARP and presented in Chapter 4 were augmented with data from November 1989-1992. These experiments were performed on November Spawner Biomass Surveys between Cape Columbine and Cape Agulhas (Verheye *et al.* 1994). Data on female *Neocalanus tonsus* and *Rhincalanus nasutus* and copepodites of *Calanoides carinatus* were excluded from the analysis in this chapter because of the paucity of experiments (see Tables 4.1 and 4.5 in Chapter 4). Sizes (total length, TL) of the species included here are presented in Chapter 1 (Table 1.2).

To compare rates of female egg production with those of juvenile somatic growth, egg production was converted to growth rate (g_f, d^{-1}) as described in Chapter 1. The functional response of growth rates to Chl *a* concentration was described by an Ivlev curve (see Chapter 4). Although these graphs are similar to those presented in Chapter 4, they are given here to facilitate comparison of growth rates based on body size. Moreover, the extra data on somatic growth from the November Spawner Biomass Surveys is included and egg production is converted to growth rate. All *y*-axes have the

same scale to aid comparison among species/stages.

At each station, the concentration of Chl *a* at the depth of maximum fluorescence was used as a measure of ambient food availability to copepods. Stations were categorized into poor (≤ 2 mg.m^{-3}) and good (>2 mg.m^{-3}) total Chl *a* concentration as in Chapters 3 and 4. Stations with >50% of the Chl *a* in the <10 μm size-class were defined as small-cell dominated, and with <50% of the Chl *a* in the <10 μm class as large-cell dominated as in Chapter 4. Food available to copepods was also measured by particle volume in 5 μm size class intervals over the range 5-75 μm equivalent spherical diameter (ESD), using a Coulter Multisizer fitted with a 140 μm aperture. A total of 168 surface samples were collected over a broad spatial (the entire cruise grid) and temporal (August-March) scale.

RESULTS

Growth rates (mean ± standard deviation and range) and average stage durations are given in Table 5.1. Mean growth rates decreased by more than an order of magnitude with increasing copepod size, from 0.545 d^{-1} for *Calanus agulhensis* N6 (525 μm TL) to 0.053 d^{-1} for *C. agulhensis* females (2763 μm TL). A negative exponential function best described the relationship between mean growth rate and mean body size (Fig. 5.1, $r^2 = 0.96$, $n = 10$, $p < 0.0001$). This decrease corresponded to a marked increase in stage duration of *C. agulhensis*, from 1.27 d for N6 to 8.48 d for C5.

In contrast, maximum growth rate exhibited less than a three-fold decline over the above size-range, from 0.849 d^{-1} (*C. agulhensis* C2) to 0.328 d^{-1} (female *C. agulhensis*, Table 5.1). There was a significant linear decline of maximum growth rate with increasing size (Fig. 5.1, $r^2 = 0.79$, $n = 10$, $p < 0.001$). It should be noted that the maximum growth rates for *C. agulhensis* N6 and C1 were underestimated because all individuals had moulted in the 24-h experiments. Often large copepods did not moult or lay eggs within the 24-h incubation period, whereas the minimum growth rate of smaller copepods was always above zero (Table 5.1).

The coefficient of variation (CV), the ratio of the standard deviation to the mean, was used to compare the variability in growth rate of copepods of different size. A strong positive relationship between the CV of growth and body size was evident (Fig. 5.2, $r^2 = 0.94$, $n = 10$, $p < 0.0001$). Thus, small copepods were consistently growing rapidly (small CV), whereas the growth rate of large copepods was more variable.

Table 5.1. Growth rates (mean ± standard deviation and range) of copepods examined, and the geometric mean of stage durations (*D*) for juvenile *Calanus agulhensis*. *n* = the number of samples.

SPECIES/STAGE	MEAN ± SD	RANGE	*D*	*n*
Calanus agulhensis N6	0.545 ± 0 110	0.204 - 0.693	1.27	36
Calanus agulhensis C1	0.510 ± 0.206	0.116 - 0.811	1.59	92
Calanus agulhensis C2	0.421 ± 0.195	0.027 - 0.849	2.12	114
Calanus agulhensis C3	0.278 ± 0.164	0.000 - 0.709	2.65	126
Calanus agulhensis C4	0.240 ± 0.162	0.000 - 0.720	3.11	150
Centropages brachiatus ♀	0.214 ± 0.138	0.000 - 0.608		158
Nannocalanus minor ♀	0.159 ± 0.152	0.000 - 0.523		82
Calanus agulhensis C5	0.097 ± 0.096	0.000 - 0.468	8.48	143
Calanoides carinatus ♀	0.086 ± 0.104	0.000 - 0.460		350
Calanus agulhensis ♀	0.053 ± 0.062	0.000 - 0.328		1492

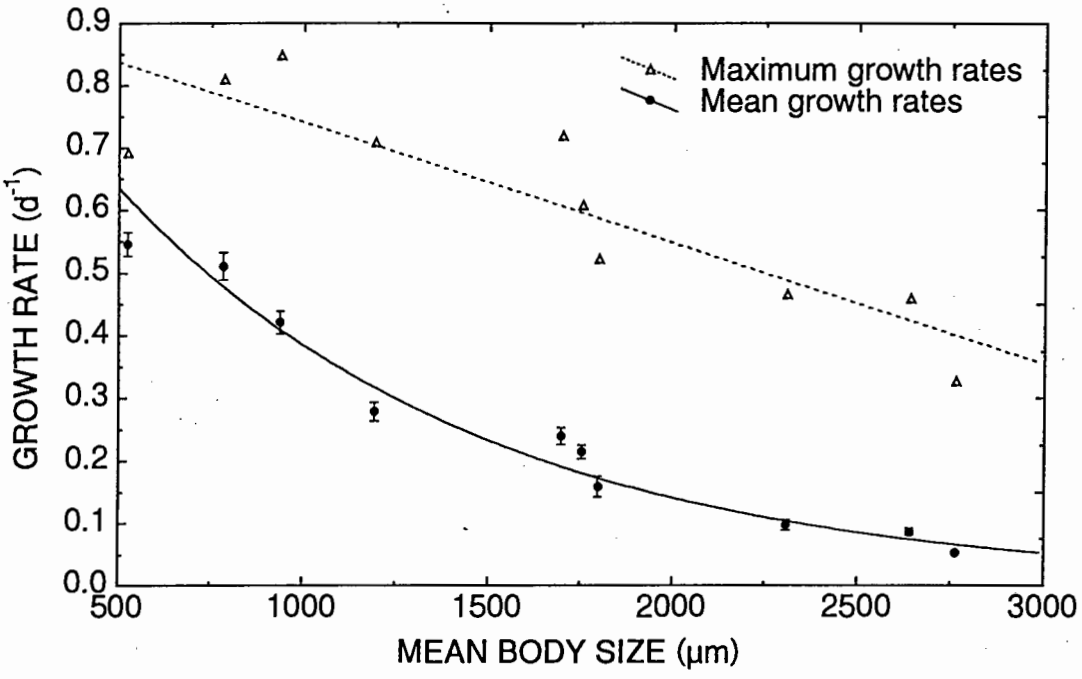


Fig. 5.1. The relationship of mean (± standard error) and maximum copepod growth rates *versus* mean body size in the southern Benguela system. The equation fitted to maximum growth rates is $y = 0.93363 - 0.00019x$, $r^2 = 0.79$, $n = 10$, $p < 0.001$. The equation fitted to mean growth rates is $y = 1.0485445e^{-0.001001x}$, $r^2 = 0.96$, $n = 10$, $p < 0.0001$. The n for each species is shown in Table 5.1.

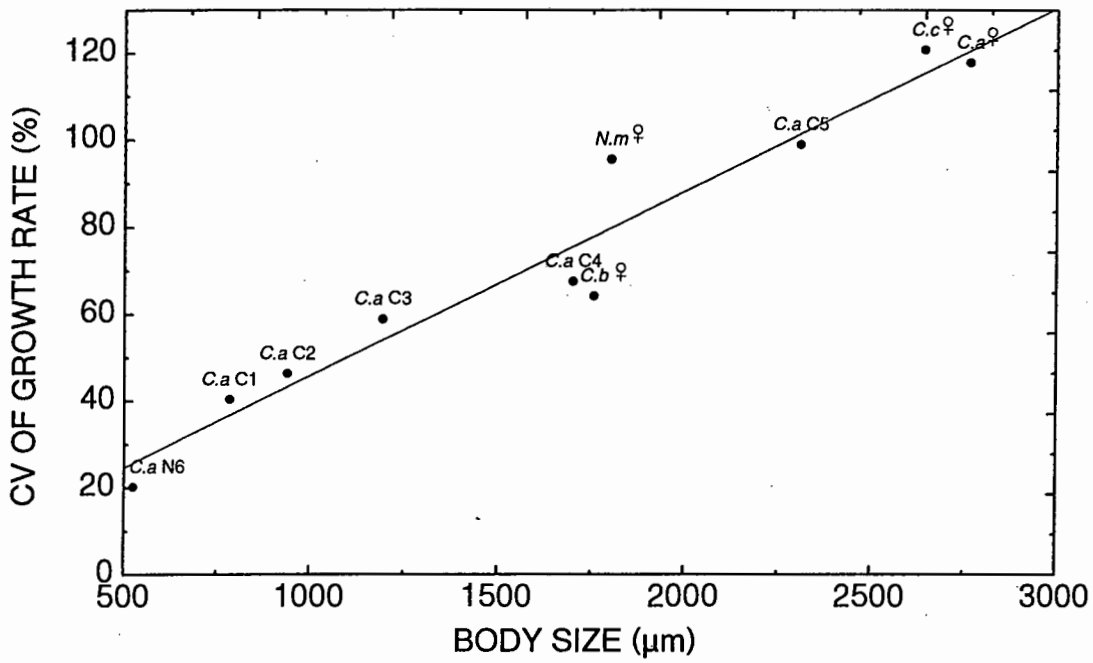


Fig. 5.2. The coefficient of variation (CV) of growth rate *versus* copepod body size. The fitted equation is: $y = 3.612 + 0.042x$, $r^2 = 0.94$, $p < 0.0001$, $n = 10$. *C.a* = *Calanus agulhensis*, *C.b* = *Centropages brachiatus*, *N.m* = *Nannocalanus minor*, and *C.c* = *Calanoides carinatus*.

Growth rates were positively related to total Chl *a* concentration (Fig. 5.3). Parameters for each Ivlev curve, the r^2, and the concentration of Chl *a* at which 90% of the maximum asymptotic growth rate was achieved are given in Table 5.2. Although less than 40% of the variability in the growth rate of each species was explained by total Chl *a*, several general patterns are evident from the Ivlev parameters. Firstly, the asymptotic growth rate, g_a, decreased significantly with increasing body size ($r^2 = 0.86$, $n = 10$, $p < 0.0001$). This suggests that food-saturated growth rate decreased with increasing body size. Secondly, the rate at which growth approaches the asymptotic rate (k), generally decreased with increasing body size ($r^2 = 0.59$, $n = 10$, $p < 0.01$). Thus, maximum growth rate was attained at lower Chl *a* concentrations for smaller copepods, as was evident from the lower Chl *a* concentration at which 90% of the maximum growth rate was achieved (Table 5.2). Lastly, the r^2 generally increased with body size, although this relationship was not significant when all copepods were included ($p > 0.05$). The small r^2 for two copepods, *viz. C. agulhensis* C5 and female *Centropages brachiatus*, did not fit this trend. This lack of dependence of growth rate on Chl *a* may be because *C. brachiatus* is omnivorous (compared with the other copepod genera which are predominantly herbivorous- see Boyd *et al.* (1980) and Turner (1984)) and C5 copepodites often store lipids in preparation for their moult to adulthood (Borchers and Hutchings 1986). After removing these two copepods from the analysis, the relationship between the r^2 and copepod size was significant ($r^2 = 0.74$, $n = 8$, $p < 0.01$). Collectively, the trends described above imply a greater dependence of growth rate of large copepods on chlorophyllous phytoplankton.

The growth rate of copepods under conditions of low (<2 $mg.m^{-3}$) and high (>2 $mg.m^{-3}$) Chl *a* for the different species is shown in Fig. 5.4a. Growth rate increased substantially under high Chl *a* concentrations relative to low Chl *a*. This proportional increase in growth rate from low to high Chl *a* was positively related to body size (Fig. 5.4b, $r^2 = 0.78$, $n = 10$, $p < 0.001$). This indicates that the degree of food limitation, as measured by Chl *a* concentration, was greater for larger copepods. A further implication may be that smaller copepods utilize non-chlorophyllous food sources.

Marked differences in the frequency distributions of growth rate under low and high Chl *a* were apparent for species of different size (Fig. 5.5). Under low Chl *a*, the frequency distributions of small copepods (*e.g. C. agulhensis* N6, C1, and C2) were more symmetric than those of large copepods (*e.g.* C5 and female *C. agulhensis*, and female *Calanoides carinatus*) which were heavily skewed toward slow growth rates. Further, the frequency distributions showed a progressive increase in skewness toward slower growth rate as body size increased. This suggests that most small copepods were growing rapidly, even under low Chl *a*, and that proportionately more individuals were growing poorly as body size increased. It is noteworthy that the change in the shape of the distributions from

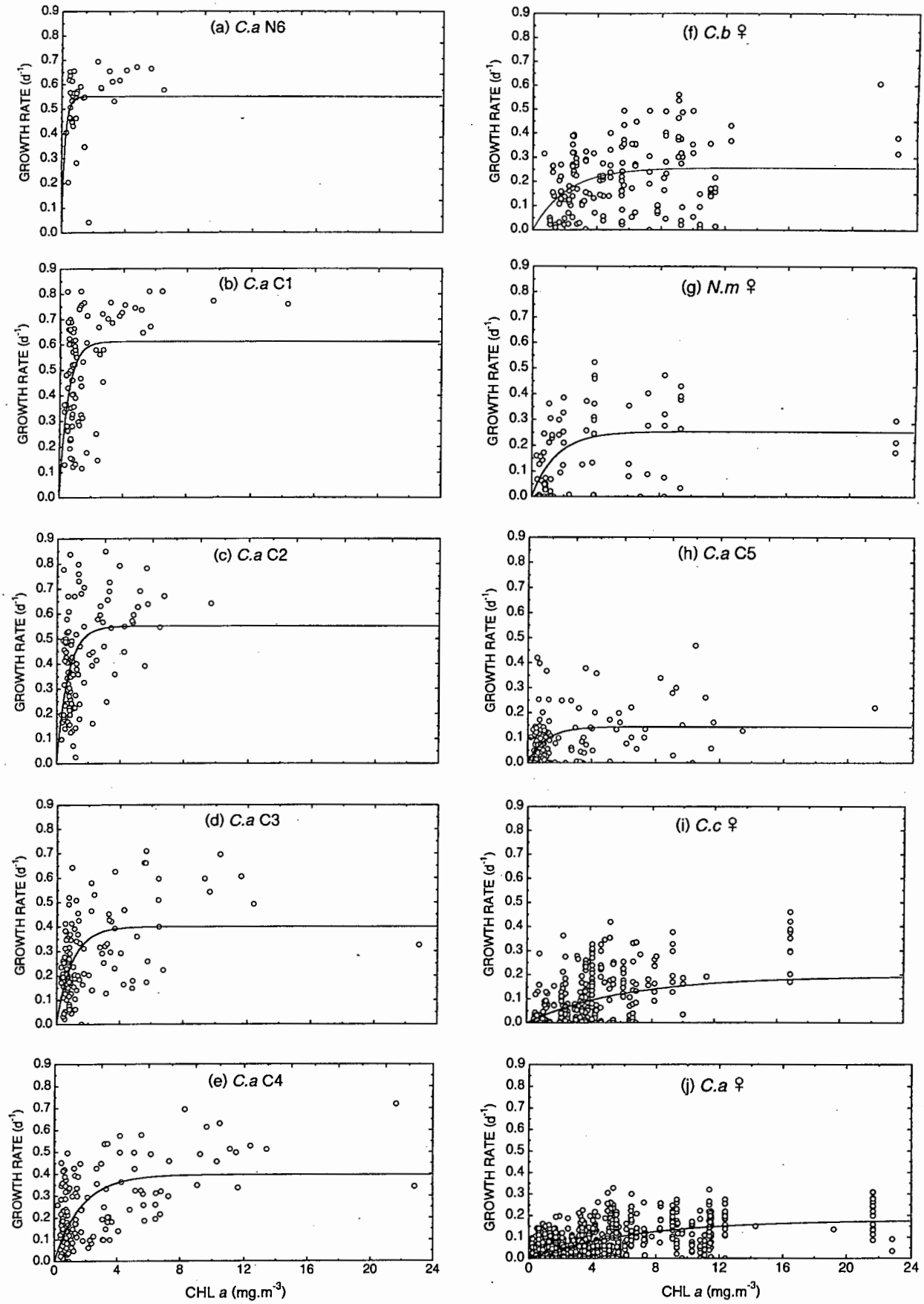


Fig. 5.3. Growth rates against Chl *a*, for (a) the smallest to (j) the largest copepod examined. Ivlev curves were fitted (see Table 5.2 for details of equations). *C.a* = *Calanus agulhensis*, *C.b* = *Centropages brachiatus*, *N.m* = *Nannocalanus minor*, and *C.c* = *Calanoides carinatus*.

Table 5.2. Asymptotic growth rate (g_a) and the rate at which growth approaches this asymptote (k) for Ivlev curves [$g = g_a(1-e^{-k*c})$] fitted to copepod growth rate (g) *vs* Chl *a* (c). The proportion of variance explained (r^2) and the Chl *a* at which 90% of maximum growth rate is obtained ($c_{0.9g_a}$) are also shown. The number of samples is the same as in Table 5.1.

SPECIES/STAGE	g_a	k	r^2	$c_{0.9g_a}$
Calanus agulhensis N6	0.550	4.827	0.05	0.5
Calanus agulhensis C1	0.612	1.970	0.11	1.2
Calanus agulhensis C2	0.551	1.435	0.17	1.6
Calanus agulhensis C3	0.400	1.035	0.22	2.2
Calanus agulhensis C4	0.396	0.591	0.26	3.9
Centropages brachiatus ♀	0.257	0.475	0.09	4.8
Nannocalanus minor ♀	0.253	0.662	0.31	3.5
Calanus agulhensis C5	0.144	0.895	0.06	2.6
Calanoides carinatus ♀	0.194	0.160	0.24	14.4
Calanus agulhensis ♀	0.180	0.150	0.38	15.4

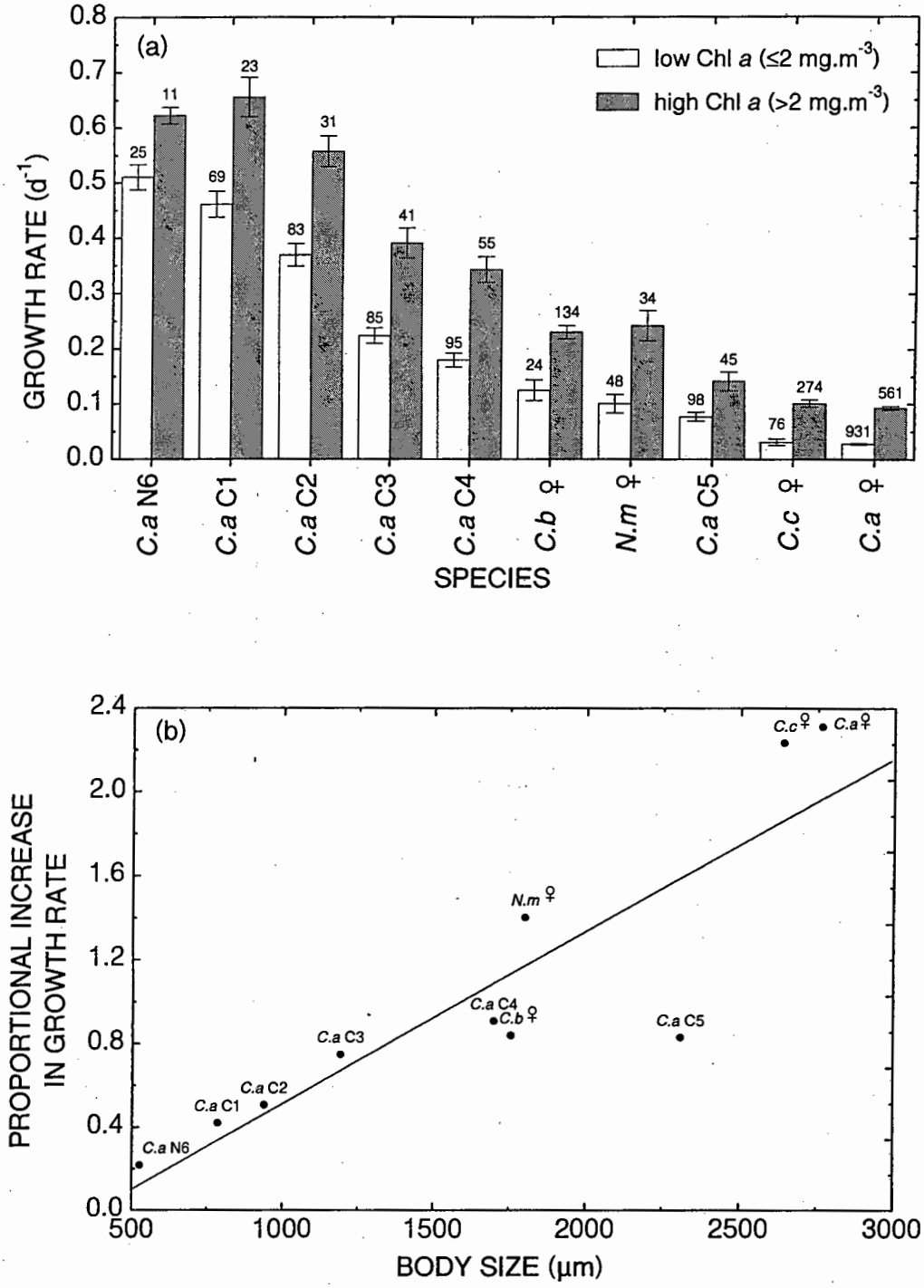


Fig. 5.4. (a) Growth rate of copepods under conditions of low and high Chl *a*. Standard errors and the number of samples are shown. (b) The proportional increase in growth rate of each species from low to high food conditions against body size. *C.a* = *Calanus agulhensis*, *C.b* = *Centropages brachiatus*, *N.m* = *Nannocalanus minor*, and *C.c* = *Calanoides carinatus*.

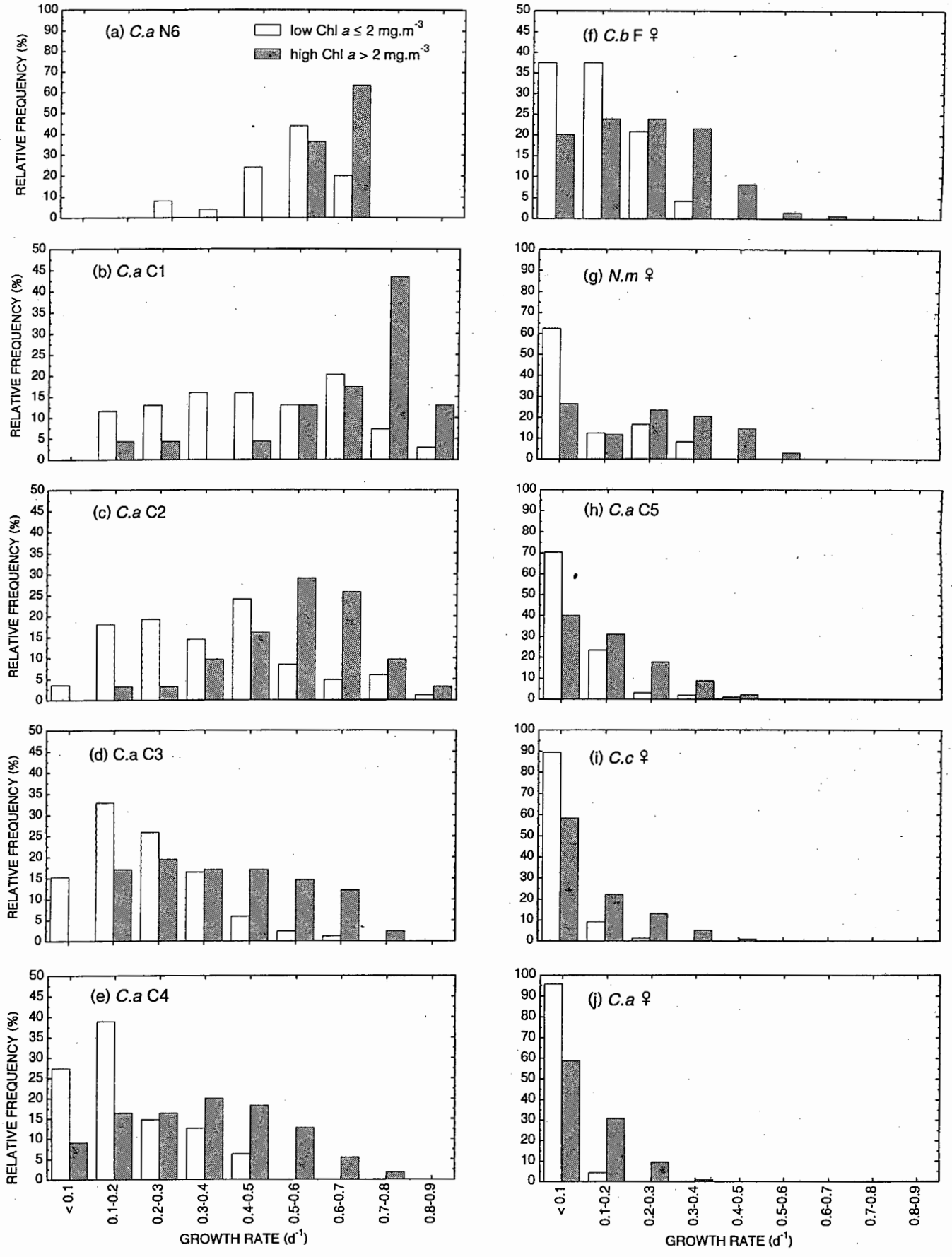


Fig. 5.5. Frequency distributions of growth rate under conditions of low and high Chl *a*, for (a) the smallest to (j) the largest copepod. Note the different *y*-scales. *C.a* = *Calanus agulhensis*, *C.b* = *Centropages brachiatus*, *N.m* = *Nannocalanus minor*, and *C.c* = *Calanoides carinatus*. The number of samples are the same as Fig. 5.4.

low to high Chl *a* was related to body size. For large copepods, the distributions under low and high Chl *a* were skewed toward slower growth rate, with greater bias at low Chl *a*. For small copepods, the distributions under low and high Chl *a* had greater symmetry than large copepods, although the mode of the distribution did shift toward faster growth rates under high Chl *a*. (Note that the frequency distribution for *C. agulhensis* N6 was truncated at a growth rate of 0.6-0.7, and for *C. agulhensis* C1 at 0.8-0.9, because all individuals had moulted within 24 h). For copepods intermediate in size there were striking changes in shape, from being skewed toward slow growth rate at low Chl *a* to greater symmetry at high Chl *a*. These changes can be summarized by plotting the skewness of each distribution against body size (Fig. 5.6). Skewness is zero for a symmetrical distribution and is positive when it is biased toward small values (slow growth rates). It can be seen that the degree of skewness increased as copepod body size increased under both low ($r^2 = 0.76$, $n = 10$, $p < 0.001$) and high ($r^2 = 0.62$, $n = 10$, $p < 0.01$) Chl *a*. Furthermore, the distributions were more skewed under low than high Chl *a*. (It should be noted that the negative skewness, *i.e.* bias towards fast growth rates, for *C. agulhensis* N6 and C1 may be because their frequency distributions of growth rate are truncated at fast growth rates).

The more extensive data set for the two largest copepods, female *C. agulhensis* and *C. carinatus*, enabled the effect of increasing Chl *a* on the frequency distributions of growth rate for large copepods to be explored in more detail (Fig. 5.7). The frequency distributions for both species were markedly skewed toward slow growth rate for Chl *a* <2 $mg.m^{-3}$ (Fig. 5.7a, f). As Chl *a* increased to 6 $mg.m^{-3}$, the distributions became progressively less skewed for both species (Fig. 5.7b, c, g, h). For Chl *a* concentrations of 6-8 $mg.m^{-3}$, the distribution changed shape (Fig. 5.7d, i), with more individuals producing more eggs, especially in the case of *C. agulhensis*. Above Chl *a* of 8 $mg.m^{-3}$, the shape of the distributions for both species tended toward symmetry (Fig. 5.7j). The skewness of the distributions did decrease significantly with increasing Chl *a* for both *C. agulhensis* ($r^2 = 0.86$, $n = 5$, $p < 0.05$) and *C. carinatus* ($r^2 = 0.92$, $n = 5$, $p < 0.01$). These findings are compatible with the concept of food limitation of large copepods at low Chl *a*.

Analysis of particle spectra reveals that the study area is dominated by particles <25 μm ESD (Fig. 5.8a), with those <15 μm ESD occurring at a consistent background density, as indicated by a lower CV of particle volume than for particles >15 μm ESD (Fig. 5.8b).

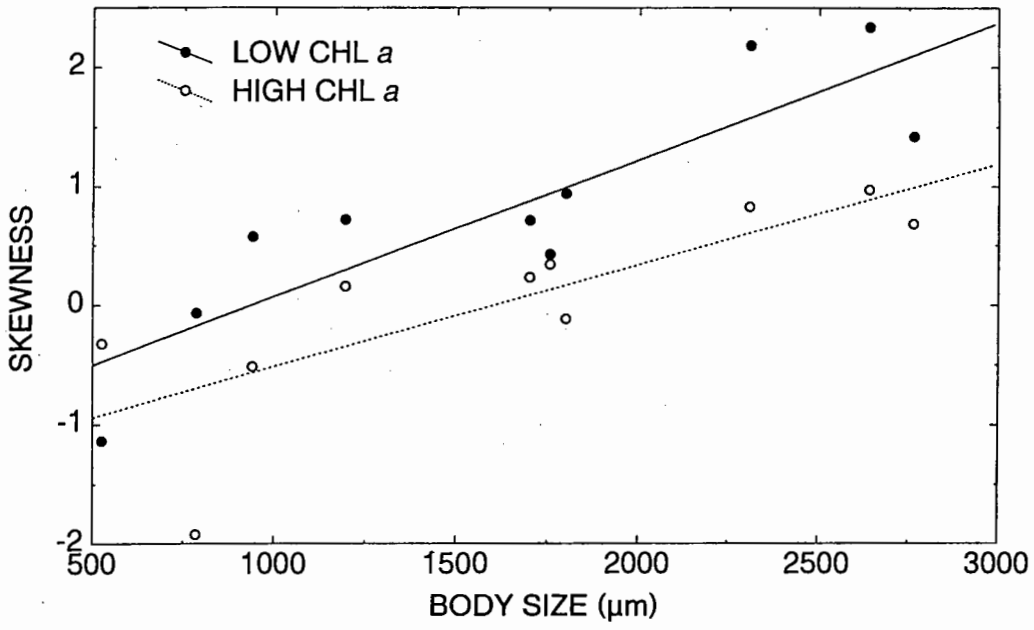


Fig. 5.6. The positive relationships between the degree of skewness of frequency distributions of growth rate and body size for different species/stages under low and high Chl *a*.

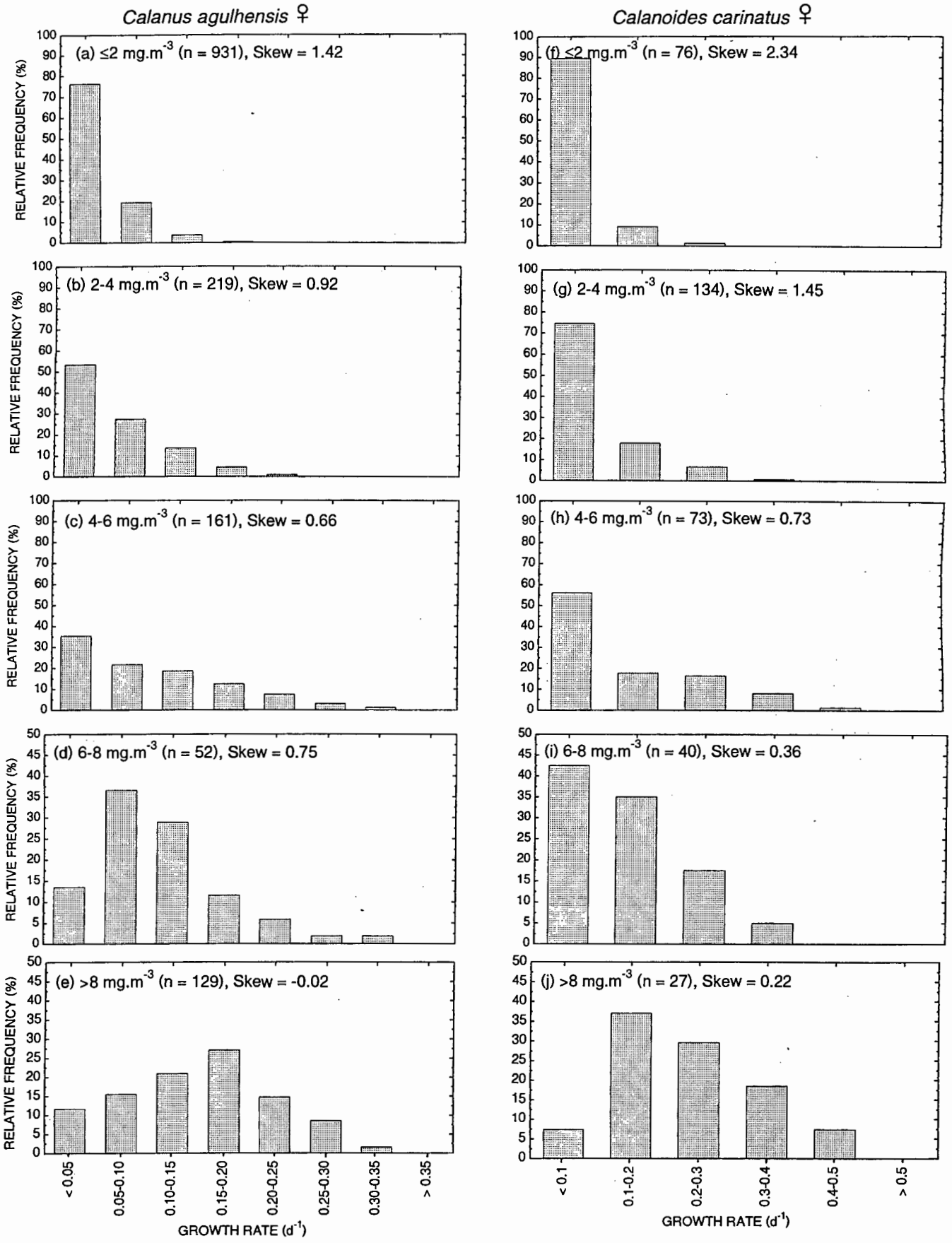
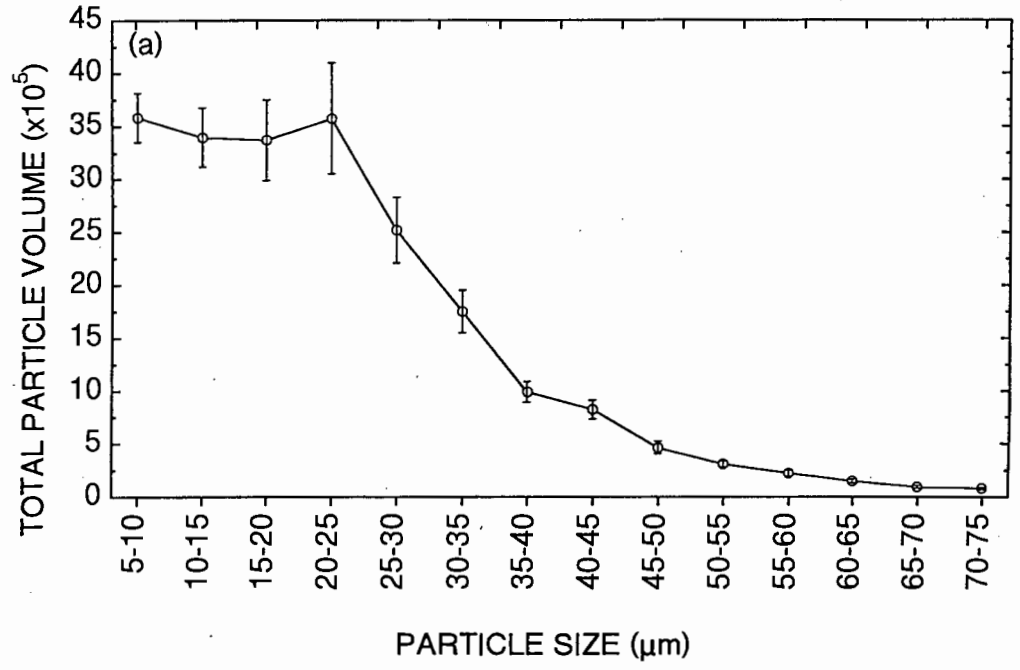


Fig. 5.7. Frequency distributions of growth rate of *Calanus agulhensis* (a)-(e) and *Calanoides carinatus* (f)-(j) for increasing concentrations of Chl *a*. The number of samples are in brackets. Note two *y*-scales are used and the *x*-scales are different for the two species because more samples were available for *Calanus agulhensis*, allowing greater resolution.



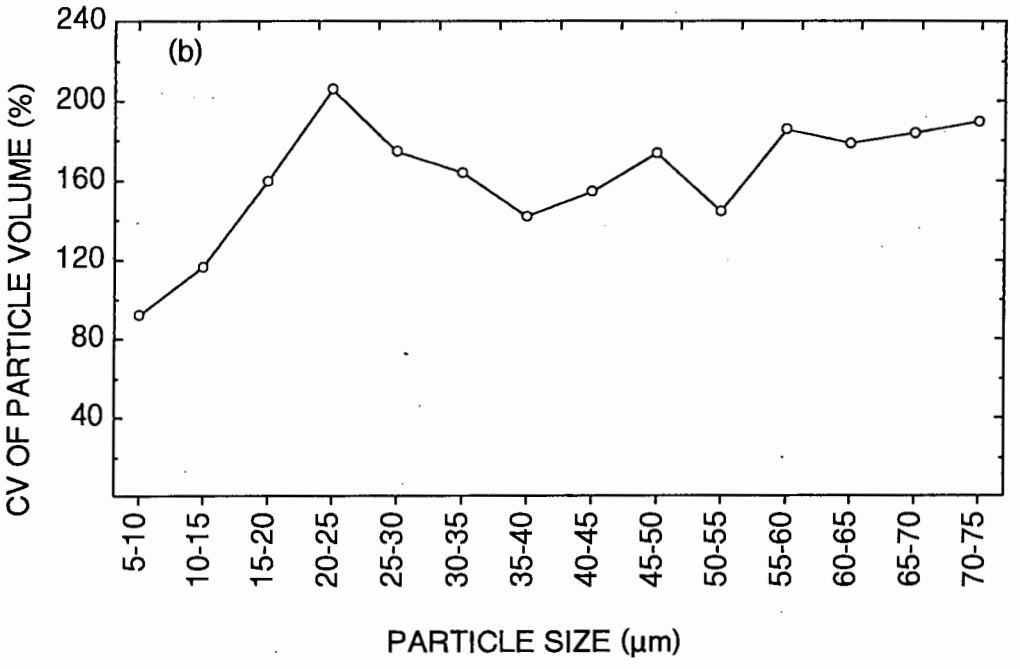


Fig. 5.8. (a) Mean (± standard error) of total particle volume (μm^3) against particle size in 5 μm intervals and (b) the coefficient of variation (CV) of particle volume against particle size. Standard errors are shown in (a). The number of samples for each interval is 168.

DISCUSSION

Body size

Growth rates of copepods in the southern Benguela upwelling system decreased with increasing body size. This decline may be a general phenomenon and has been documented in both field (Greze 1978; Peterson *et al.* 1991; Verheye *et al.* 1994; Hutchings *et al.* 1995) and laboratory studies in terms of stage duration (Peterson and Painting 1990), somatic growth (Harris and Paffenhöfer 1976; Paffenhöfer 1976; Vidal 1980), and egg production (Ambler 1985; Peterson *et al.* 1988). Allometric relationships, which describe many biological rate processes such as size-specific growth rate (Banse and Mosher 1980; Peters 1983; McLaren *et al.* 1989; Hirst and Sheader 1997), may account for the less than three-fold difference in maximum growth rates identified in this study (Table 5.1). Mean growth rate, however, was an order of magnitude slower for the largest copepod (female *Calanus agulhensis*) compared with the smallest (*C. agulhensis* N6) examined. This implies that an environmental factor may limit growth rate.

Food limitation

It is suggested that the primary factor responsible for the decrease in mean growth rate with size in the southern Benguela upwelling region is food limitation, the degree of which increases with body size. Progressive food limitation has been observed in the tropical ocean by Webber and Roff (1995), with larger copepod species food limited above copepodite C1 and smaller species above C2, and is very similar to the findings in the present study. A recent global synthesis of growth rate data showed that weight-specific fecundity of female copepods declines with increasing body weight (Kiørboe and Sabatini 1995). In addition, laboratory experiments have shown that an inadequate food supply only slightly retards the growth of young stages, whereas older stages are seriously affected (Vidal 1980). The growth rate in the field of another common large copepod in the southern Benguela region, *Calanoides carinatus*, also declines with body size (Walker and Peterson 1991; see Chapter 4, Table 4.4). These strong declines in growth rate with size contrast Vidal's conclusion from laboratory experiments that "extrapolation of growth rates from one species to another on the basis of similarity in body size is not justified" (Vidal 1980, p. 111). Because food limitation appears similar for species of the same size in the southern Benguela system, it is postulated that growth rates of calanoid copepods in this system may be estimated from body size.

The phenomenon of increased food limitation with copepod body size supports the assertion of Verheye *et al.* (1994) that there is intraspecific size-based food partitioning in *C. agulhensis*, and extends it to include interspecific food partitioning based on size. A consequence of increased food limitation of *C. agulhensis* with increasing body size is that juvenile growth rate is unrelated to

female growth rate in the southern Benguela system (see also Hutchings *et al.* 1995). Thus, female growth rate cannot be extrapolated to juveniles, although there may be less variability in growth rate of small copepods than previously thought.

Growth rates of *C. agulhensis* N6 were fast, consistent (small CV), and independent of Chl *a*. This is despite the maximum growth rate of *C. agulhensis* N6 in this study being underestimated. Stage durations in the field for calanoid nauplii can be less than a day (Webber and Roff 1995), and in some of our experiments all the nauplii had moulted within 24 h. Nauplii of freshwater and coastal marine copepods are known to have fast and consistent growth rates (Hart 1990). This is a consequence of their slow metabolic rates (Paffenhöfer 1976) and their ability to ingest picoplankton (Roff *et al.* 1995). The importance of the microbial community to supporting fast growth rates of copepods has been recognized in oligotrophic seas (Webber and Roff 1995), where the numbers of bacteria and picoplankton are less variable than larger-sized nano- and netplankton (Hopcroft and Roff 1990).

Growth rates of other small copepods (particularly *C. agulhensis* C1 and C2) were also consistent and largely independent of Chl *a* even at very low Chl *a*, implying little food limitation. This may be owing to their preference for smaller food particles. The optimal size of food particles for copepods has been estimated to be 2-5% of their prosome length (Berggreen *et al.* 1988). This translates into an optimal food size range of 8-20 μm, 12-31, and 15-37 for *C. agulhensis* N6, C1, and C2 respectively. Thus, the range of optimal food particle sizes for these small copepods includes microflagellates, which are ubiquitous and abundant throughout the southern Benguela region (Fig. 5.8; Painting *et al.* 1992; Painting *et al.* 1993). The concept that eutrophic upwelling areas are dominated by large diatoms (Cushing 1989) needs to be broadened to include the microheterotrophic pathways (Hutchings 1992). Fast growth rates of copepods can therefore be achieved by being small and feeding on small phyto- and zooplankton (Webber and Roff 1995). Moreover, the perception that young stages are more susceptible to starvation than older ones (Paffenhöfer 1976; Borchers and Hutchings 1986; Hutchings 1992) may not be valid in upwelling areas such as the southern Benguela system. The growth rate of small copepods in other aquatic systems that have a consistent microheterotrophic food web may also be relatively constant.

Although large copepods can also ingest small cells (Borchers and Hutchings 1986; Peterson *et al.* 1990b), the concentrations of small cells in the southern Benguela region is usually not adequate to support fast growth rates of large copepods (Chapter 4, Fig. 4.3). Their growth rates are frequently food limited because they preferentially ingest particles greater than 20 μm in size (Berggreen *et al.* 1988). They feed more efficiently on these large cells (Frost 1977), obtaining their maximal daily

ration at relatively low carbon concentrations (Frost 1972). In the southern Benguela system, the concentration of Chl *a* is positively related to the proportion of large cells (Mitchell-Innes and Pitcher 1992). Thus, there is a sufficient quantity of large cells to ensure fast growth rates by large copepods only when there is high Chl *a* present.

Encounter rate model

The degree of food limitation is related to the availability of appropriately-sized food particles for a copepod of a particular size. The effect of food limitation on individual copepods in the southern Benguela region was reflected in the shape of the frequency distributions of growth rate (Figs 5.5 and 5.7). The changes in shape of these distributions may be a result of the total amount of food ingested. A conceptual model is developed here to explain the different frequency distributions of growth rate for copepods of varying size. The total number of particles ingested is related to the density and size of particles available and can be described by the Poisson distribution:

$$f(x) = \frac{\lambda^x e^{-\lambda}}{x!}$$ (Evans *et al.* 1993),

where

$f(x)$ is the probability function,

λ is the expected value of x,

$x!$ is $x \times (x-1) \times (x-2) \times .. \times 1$.

In this probabilistic model, λ can be interpreted as the average encounter rate by a copepod with particles of an appropriate size for it to feed on, and x as the number of particles that are actually encountered by a copepod. For small copepods, their food source (small cells) is always abundant (Fig. 5.8b) and thus they always have a high encounter rate, independent of the total concentration of Chl *a*. Therefore, the total number of particles ingested by a population is symmetric and approximates normality (Fig. 5.9: $\lambda = 5$). The shape of this distribution is similar to the frequency distribution describing growth rate for small copepods (Fig. 5.5b, c), because growth rate is a function of the total number of particles ingested.

At low Chl *a*, phytoplankton is generally dominated by microflagellates with few large cells present (Mitchell-Innes and Pitcher 1992). Large copepods therefore encounter low numbers of large particles and the distribution of total particles encountered is severely skewed toward low numbers (Fig. 5.9: $\lambda = 1$). Because copepods must obtain a minimum amount of energy to initiate egg

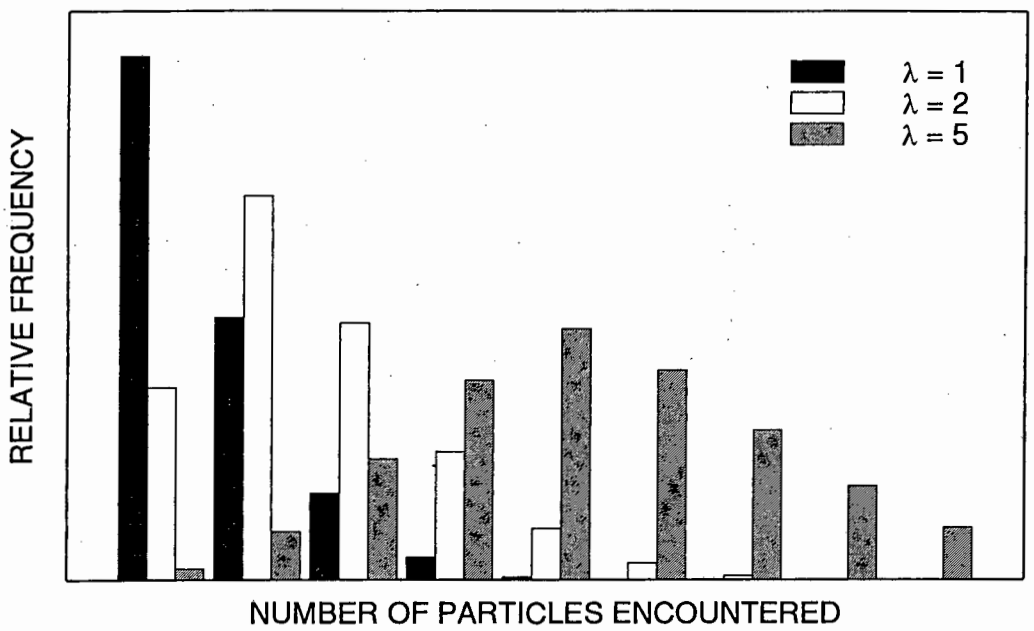


Fig. 5.9. Probability distributions of a Poisson variable for encounter rates (λ) of 1, 2, and 5. The x-axis represents the number of particles encountered per unit time.

production (Hutchings 1992) or to moult, the distribution is skewed toward slow growth at low encounter rates (Fig. 5.7a, f). At elevated Chl *a*, the greater proportion of large cells increases the probability of large copepods encountering particles of a suitable size. A sufficient food ration can now be obtained by most individuals for initiation of egg production or ecdysis, and the distribution is less skewed (*cf.* Fig. 5.9: $\lambda = 2$ with Fig. 5.7d, j). As the Chl *a* and hence encounter rate increase further, there is sufficient food for all individuals to grow (*cf.* Fig. 5.9: $\lambda = 5$ with Fig. 5.7e). The distribution is symmetric, and at high encounter rates it approximates the normal distribution (Evans *et al.* 1993). A similar frequency distribution was reported by Peterson (1988) for *Calanus marshallae* fed excess amounts in the laboratory. Therefore, calanoid copepod growth rates in the southern Benguela region appear to be controlled by the interplay between body size, food size, and food density.

The utility of the relationship between growth rate and body size was tested by incorporating supplementary data. Data on growth of species for which there was only limited data from Chapter 4, were combined with data collected from the northern Benguela system by Verheye *et al.* (1998) using egg and body weights from Table 5.3. A strong decline in growth rate with body size is still evident (Fig. 5.10).

The consistency of the relationships between copepod growth rate and body size identified in this study using two independent field techniques, the broad size range of the copepods examined (525-2763 μm), and the wide spatial and temporal scales over which the data were collected, suggest that the increase in food limitation of growth rate with increasing body size may apply to the entire community of calanoid copepods in the Benguela system. Moreover, this phenomenon may also occur in other aquatic systems with a significant microbial component.

Table 5.3. Total size and egg and body weights of copepods used to convert egg production and moulting ratios into growth rates from copepods collected in the northern Benguela upwelling system.

SPECIES/STAGE	BODY SIZE (TL, μm)	BODY WEIGHT (μdry weight)	EGG WEIGHT (μdry weight)
Calanoides carinatus C3	1310[1]	18.0[6]	_
Centropages brachiatus ♀	1756[2]	25.0[6]	0.075[9]
Nannocalanus minor ♀	1962[3]	33.7[7]	0.253[10]
Calanoides carinatus C4	1850[1]	30.0[6]	_
Scolecithrix spp. ♀	2115[3]	48.6[7]	0.200[11]
Calanoides carinatus C5	2280[1]	62.0[4]	_
Undinula vulgaris ♀	2605[3]	74.2[7]	0.263[11]
Calanoides carinatus ♀	2640[1]	123.0[4]	0.500[9]
Metridia lucens ♀	2667[5]	105.1[7]	0.329[11]
Euchaeta spp. ♀	3333[3]	101.9[7]	1.591[10]
Eucalanus spp. ♀	3373[3]	236.0[7]	0.951[10]
Rhincalanus nasutus ♀	4311[3]	300.0[8]	0.761[11]
Pontellidae ♀	4932[3]	568.5[7]	0.988[11]

[1] Binet and Suisse de Sainte Claire (1975)

[2] Stuart and Huggett (1992)

[3] measured from preserved specimens (Verheye *et al.* 1998)

[4] Verheye (1991)

[5] Mean of estimates from Rose (1933) and Unterüberbacher (1964)

[6] Peterson *et al.* (1990a)

[7] using the equation ln(dry weight) = 2.74ln(PL) −16.41 from Chisholm and Roff (1990a)

[8] Sea Fisheries Research Institute (SFRI), unpublished data

[9] Peterson (1989)

[10] from egg diameter (ED): ln(dry weight) = -3.578+0.01470*ED (C. van der Lingen, SFRI, unpublished data)

[11] from $DW_{egg} = 0.016 DW_{fem}^{0.65}$, where DW = dry weight (Kiørboe and Sabatini 1994)

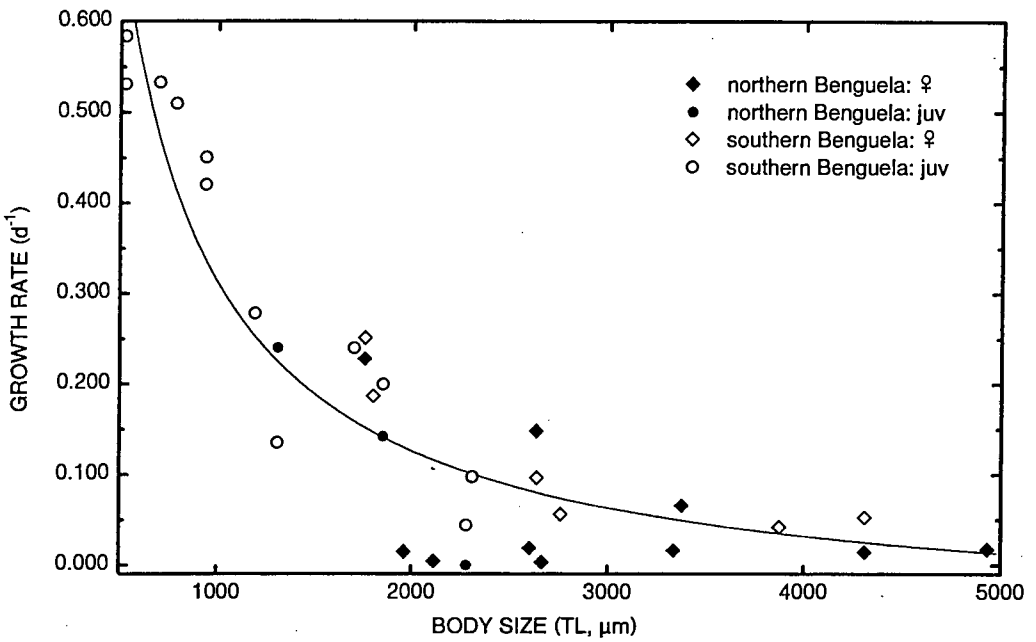


Fig. 5.10. The relationship between copepod growth rate and body size, including data from both the northern and southern Benguela regions. All estimates of somatic growth from this study are used (open symbols) and data from Verheye *et al.* (1998) from the northern Benguela system (solid symbols). The fitted equation is $y = -0.0618 + \frac{375.4748}{x}$, $r^2 = 0.86$, $n = 31$.

CHAPTER 6

SEASONAL AND EVENT-SCALE VARIATION IN GROWTH RATE OF A DOMINANT COPEPOD AND IMPLICATIONS FOR THE SPAWNING OF PELAGIC FISH

ABSTRACT

During austral summer, the western Agulhas Bank is a major spawning ground for the planktivorous Cape anchovy *Engraulis capensis* and the South African sardine *Sardinops sagax*. To explore the dynamics of their copepod prey, growth rates of developmental stages (naupliar stage N6 to adult female) of *Calanus agulhensis*, the dominant copepod by mass in this upwelling region, were measured monthly between September and March of 1993/94 and 1994/95. Growth rates of small stages (N6-C2) remained fast and relatively constant, both seasonally and across the shelf, probably a consequence of their ability to ingest small particles that are omnipresent and abundant. In contrast, there was a strong cross-shelf decline in growth rate of large copepodites (C3-female). Temporally, growth rates of large copepodites were moderate (0.046-0.343 d^{-1}) in September/October following water column stabilization after winter, slow (0.026-0.181 d^{-1}) in November/December as the upper mixed layer warmed, and fast (0.079-0.409 d^{-1}) during the upwelling season (January-March). This variation in growth rates of larger stages mirrored changes in Chl *a* that were a consequence of seasonal warming and wind patterns. The spawning of sardine follows these changes in growth rate with a spawning peak in September/October and another in January/February when the production of eggs and nauplii, which are food for pelagic larvae, is maximal. In contrast, anchovy spawn predominately from October to December, when the biomass of its food resource, predominantly large copepods, is greatest. Superimposed on these large-scale changes in copepod growth rates were event-scale fluctuations in response to winds, particularly from January to March. At the onset of upwelling, mean female copepod growth rate across the shelf was slowest (0.035 d^{-1}). During sustained upwelling, female growth rate increased to 0.079 d^{-1}, with a peak associated with the enhanced concentration of Chl *a* in the upwelling front, and slower rates inshore in newly upwelled water and offshore in oligotrophic water. Mean female growth was fastest (0.141 d^{-1}) during prolonged quiescence when high Chl *a* levels extended over most of the shelf. During downwelling, mean female growth rates decreased to 0.046 d^{-1}, with fastest rates inshore.

INTRODUCTION

Calanus agulhensis is the dominant copepod on the western Agulhas Bank region of the southern Benguela upwelling system, constituting up to 85% of the biomass of copepods (Verheye *et al.* 1994). Copepodites of this species, especially the larger C4-C6, are a favoured food source for the

Cape anchovy *Engraulis capensis* (James and Findlay 1989) during their annual spawning season between September and March (Melo 1994b) on the western Agulhas Bank.

The hydrography of this region is highly dynamic (Largier *et al.* 1992). During winter, northerly and westerly winds predominate (Shannon 1985), mixing the water column to below 100 m (Boyd *et al.* 1985). Thereafter, south-easterly winds increase, favouring upwelling (Jury 1988). The hydrographic conditions are most variable during late summer (Boyd *et al.* 1985; Largier *et al.* 1992), particularly January to March when event-scale variation in response to periodic wind events is greatest (Jury 1988). This hydrographic variability has been categorized into four phases of upwelling (Mitchell-Innes *et al.* in press). The first phase is the onset of upwelling, when cold water upwells inshore and an upwelling front emerges in response to south-easterly winds. The second phase, sustained upwelling, occurs after prolonged south-easterly winds and is characterized by the offshore movement of the upwelling and oceanic fronts, warming of the upwelled water, and stabilization of the water column. The third phase, quiescence, follows weak and variable winds and is distinguished by the absence of an upwelling front, further warming and stratification of the water column, and the location of the oceanic front at the shelf edge. The last phase, downwelling, follows north-westerly winds that cause onshore flow and relaxation of the oceanic front shorewards.

This chapter investigates the changes in growth of *Calanus agulhensis* throughout the spawning season of anchovy. On a broad scale, these are interpreted in terms of seasonal hydrographic variability. At the event scale, characteristic cross-shelf patterns of growth rate were identified between January and March for the four phases of upwelling described above. The implications of these cross-shelf, seasonal, and event-scale variations in copepod growth rate to the feeding of larval and adult pelagic fish, particularly the Cape anchovy and South African sardine, are discussed.

MATERIALS AND METHODS

Hourly wind speed and direction during the study period were obtained from the Cape Point lighthouse. Winds at Cape Point are representative of winds on the western Agulhas Bank east to at least Danger Point (L. Hutchings, SFRI, pers. comm.). Thus, only the hydrography on the Walker Bay transect is directly related to winds in this study. Moreover, only winds prior to two days before each transect are shown, because there is a two-day delay between winds and the hydrographic response on the western Agulhas Bank (Jury 1988).

Surface sea temperature, nitrate, and Chl *a* concentration, and growth rates of *Calanus agulhensis* copepodites on the two western Agulhas Bank transects (Cape Agulhas and Walker Bay, Chapter 1,

Fig. 1.1) were measured according to the procedures described in Chapter 1. The concentration of Chl *a* was used as a measure of ambient food availability for *Calanus agulhensis* because this genus is largely herbivorous (Turner 1984). Fluorescence and temperature profiles were determined using a Chelsea Instruments Aquatracka.

Surface sea temperature, surface Chl *a* concentration, and growth rates were each combined for the two transects sampled and contoured using SURFER (Golden 1995) by the method of kriging. Only growth rates of females were contoured because there were insufficient data for juvenile stages (Table 6.1). The hydrographic conditions between January and March on the Cape Agulhas and Walker Bay transects were categorized into the four upwelling phases defined by Mitchell-Innes *et al.* (in press). This enabled characteristic cross-shelf patterns of female growth rate to be determined for each phase of the upwelling cycle.

RESULTS

In August/September of 1993/94 and 1994/95, surface water was isothermal (15 °C, Figs 6.1a and 6.2a, also see Appendix 1). Water temperature increased between October and December (16-19 °C), but was still relatively constant across the shelf (Appendix 1). Thereafter, cross-shelf temperatures were more variable. Cold (<13 °C) water prevailed on the inner shelf during upwelling in January 1994, February 1994, and March 1995, with relatively warmer water (15-18 °C) inshore in March 1994 and February 1995 (Appendix 1). Offshore there was very warm water (>21 °C). Nitrate concentrations were negatively related to water temperature (Fig. 6.1b, Fig. 6.2b). Elevated Chl *a* concentrations generally corresponded with nitrate-rich water inshore (Fig. 6.1c, Fig. 6.2c) and very small concentrations coincided with oligotrophic offshore water greater than 18 °C. Seasonally, Chl *a* concentrations were moderate (2-6 $mg.m^{-3}$) in September/October, small (<2 $mg.m^{-3}$) over most of the shelf in November/December, and large (>6 $mg.m^{-3}$) over a broad area between January and March, especially in 1993/94 (Fig. 6.1c, Fig. 6.2c). During strong upwelling such as in January and February 1994, Chl *a* concentration peaked midshelf, offshore of the cold nitrate-rich, newly-upwelled water (Fig. 6.1c, 6.2c).

Growth rates of female *Calanus agulhensis* tracked the distribution of surface Chl *a*, mirroring the November/December and cross-shelf declines (Fig. 6.1d, Fig. 6.2d). Differences in the distribution of female growth between the two sampling periods, such as an earlier initial peak in 1994/95 and a broader area of fast growth rate from January to March 1994, reflected differences in the pattern of Chl *a* in each sampling period. It is noteworthy that growth rates were slow in warm (>18 °C) water.

Table 6.1. The number of growth rate experiments for stages N6-female of *Calanus agulhensis* during each cruise.

	NUMBER OF EXPERIMENTS						
CRUISE	N6	C1	C2	C3	C4	C5	♀
August 1993	0	0	0	0	0	0	18
September 1993	0	1	1	2	0	1	53
October 1993	1	2	2	3	5	4	80
November 1993	1	9	15	13	8	8	39
December 1993	0	2	4	3	4	3	34
January 1994	0	0	0	0	1	4	92
February 1994	0	0	0	2	3	3	121
March 1994	0	2	2	2	5	3	76
September 1994	0	2	0	3	6	6	38
October 1994	1	0	5	5	3	4	53
November 1994	7	15	14	14	12	12	97
December 1994	2	2	1	2	3	4	43
February 1995	1	3	4	5	4	4	71
March 1995	1	3	3	4	6	6	61
TOTAL	14	41	51	58	60	62	876

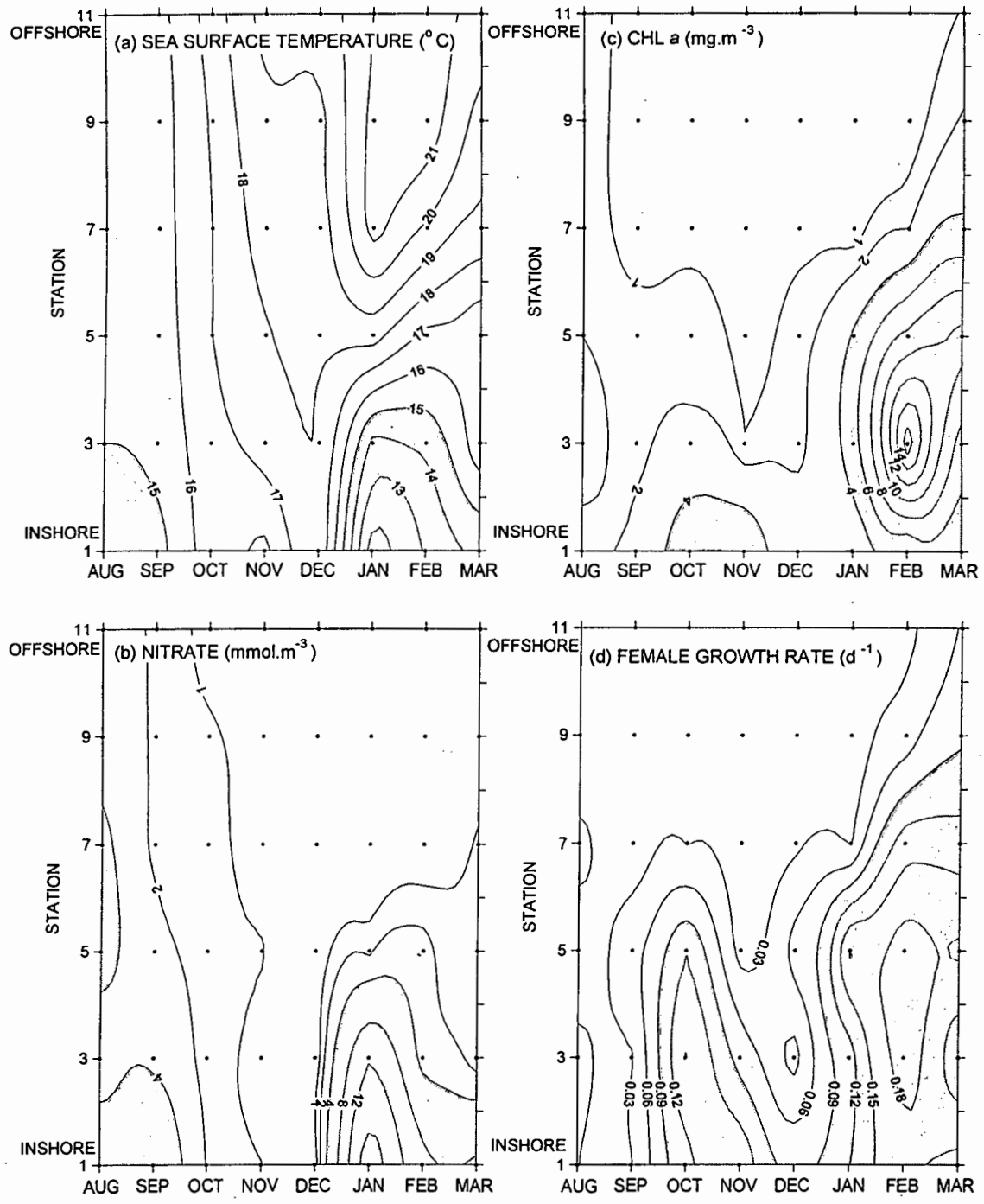


Fig. 6.1. Monthly and cross-shelf variation of (a) sea surface temperature (<15 °C shaded), (b) surface nitrate (>4 mmol.m^{-3} shaded), (c) surface Chl *a* (>4 mg.m^{-3} shaded), and (d) growth rate of female *Calanus agulhensis* (>0.09 d^{-1} shaded), between August 1993 and March 1994. Note the data from the Cape Agulhas and Walker Bay transects were combined. Dots represent stations where data were collected and are numbered from inshore to offshore.

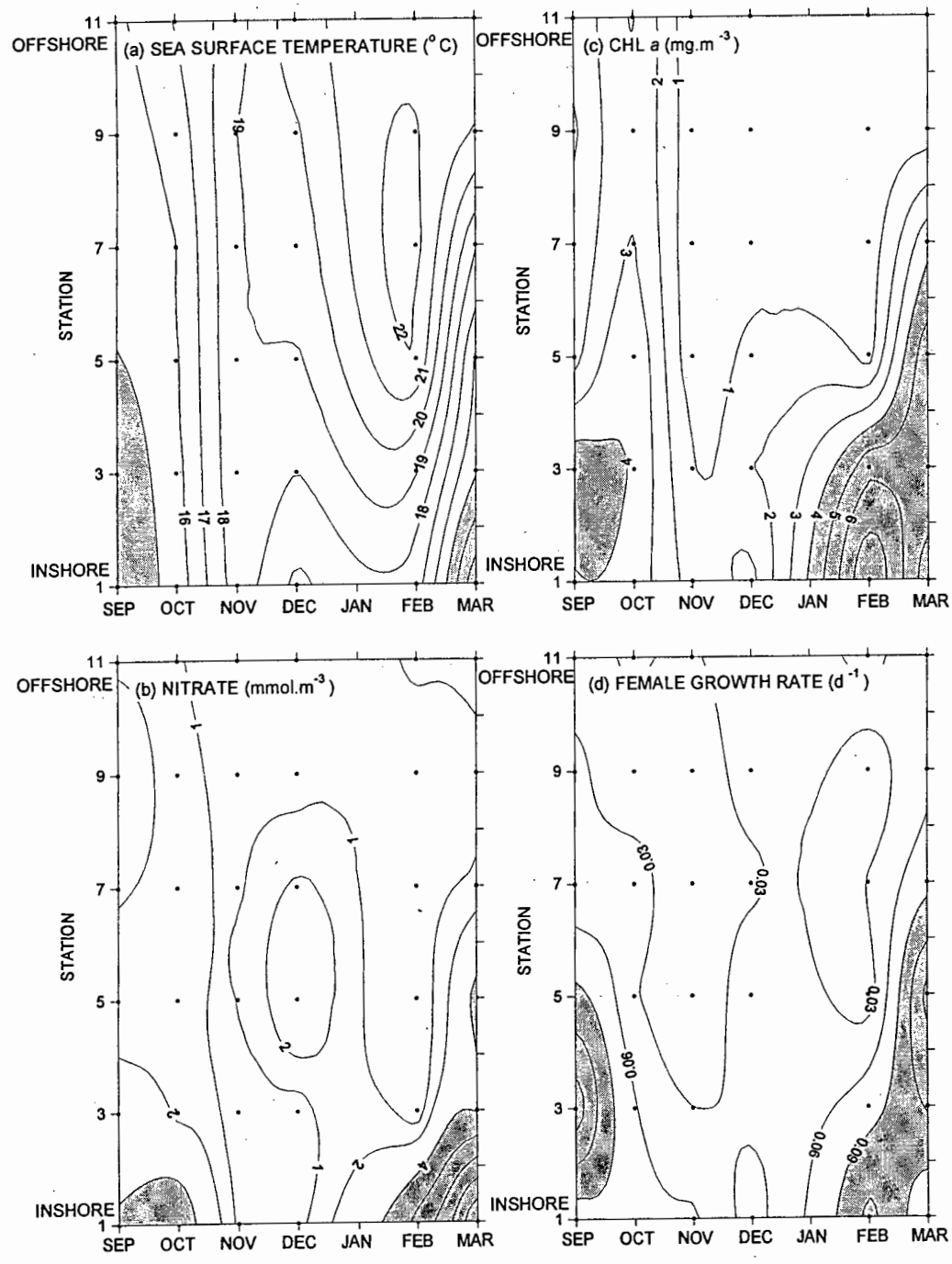


Fig. 6.2. As in Fig. 6.1, but for the period September 1994 to March 1995.

A strong cross-shelf decline in growth rates was also observed for large copepodites (C3-C5) in both 1993/94 and 1994/95 (Fig. 6.3). In contrast, growth rates of the smaller stages (N6-C2) were generally consistent, with less variation across the shelf (Fig. 6.3). It is interesting that the growth rates of C5s and females inshore were higher in 1993/94 than 1994/95, presumably because of the greater Chl *a* concentrations (*cf.* Figs 6.1c and 6.2c).

Seasonally, large copepodites (C3-C5) showed a similar growth pattern to females, with moderate to fast rates in September/October, slow in November/December, and fast in January to March during periodic upwelling (Fig. 6.4, Table 6.2). This seasonal pattern was less distinct in 1994/95, especially for C5s in December, although this estimate had poor precision. No pattern in the growth rate of the smaller stages (N6-C2) was evident for either sampling period (Fig. 6.4, Table 6.2).

The large data set for female *Calanus agulhensis* enabled a more detailed investigation of event-scale changes in growth rate (Table 6.3, Figs 6.5-6.8). Growth rates of *C. agulhensis* females were more variable from January onwards when hydrographic changes at the event scale were greatest. It was slow at the onset of upwelling (0.035 d^{-1}), increased during sustained upwelling (0.079 d^{-1}), was fastest during quiescence (0.141 d^{-1}), and decreased during downwelling (0.046 d^{-1}, Table 6.3).

The cross-shelf pattern of female growth was dependent upon the phase of the upwelling cycle (Fig. 6.5), which in turn was influenced by prior wind events. At the onset of upwelling, growth rate was greater inshore than offshore (Fig. 6.5a), although there were insufficient data to draw conclusions. During sustained upwelling, there was a mid-shelf peak in growth rate (Fig. 6.5b). The hydrography of the January 1994 Walker Bay transect, which was preceded by two days of strong southerly and south-easterly wind, was typical of this phase (Fig. 6.6, also see Appendix 1). Inshore of the upwelling front, growth rate was slow in chlorophyll-poor, newly upwelled water. Both Chl *a* concentration and female growth rates were enhanced in the frontal region around station 5. Female growth rates decreased beyond the front where phytoplankton biomass was reduced and subsurface.

Under quiescent conditions, growth of females was elevated over most of the shelf (Fig. 6.5c). The hydrography of the Walker Bay transect in March 1994 was typical of this phase (Fig. 6.7, see Appendix 1). Weak and variable winds preceded the cruise allowing the water column to stratify, promoting growth of phytoplankton in the upper mixed layer. The offshore subsurface peak in the concentration of Chl *a*, which was apparent during sustained upwelling, was absent. Female growth rate was fast over most of the shelf and only decreased in the very warm, chlorophyll-poor water at station 11 (Fig. 6.7b, c).

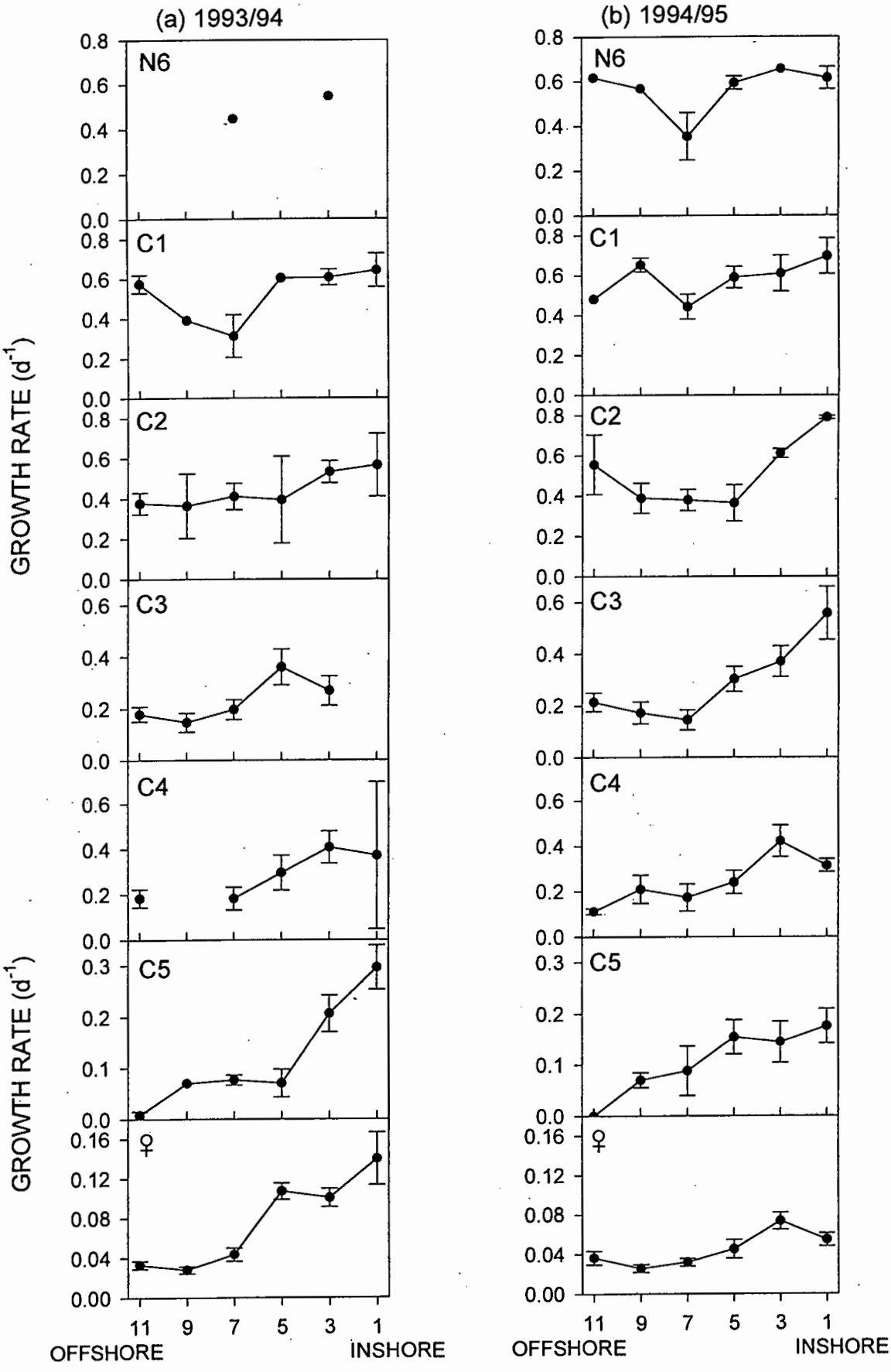


Fig. 6.3. The cross-shelf distribution of mean growth rates ± standard error (d^{-1}) of *Calanus agulhensis* N6-females for (a) August 1993 to March 1994 and (b) September 1994 to March 1995. Note the different *y*-scales.

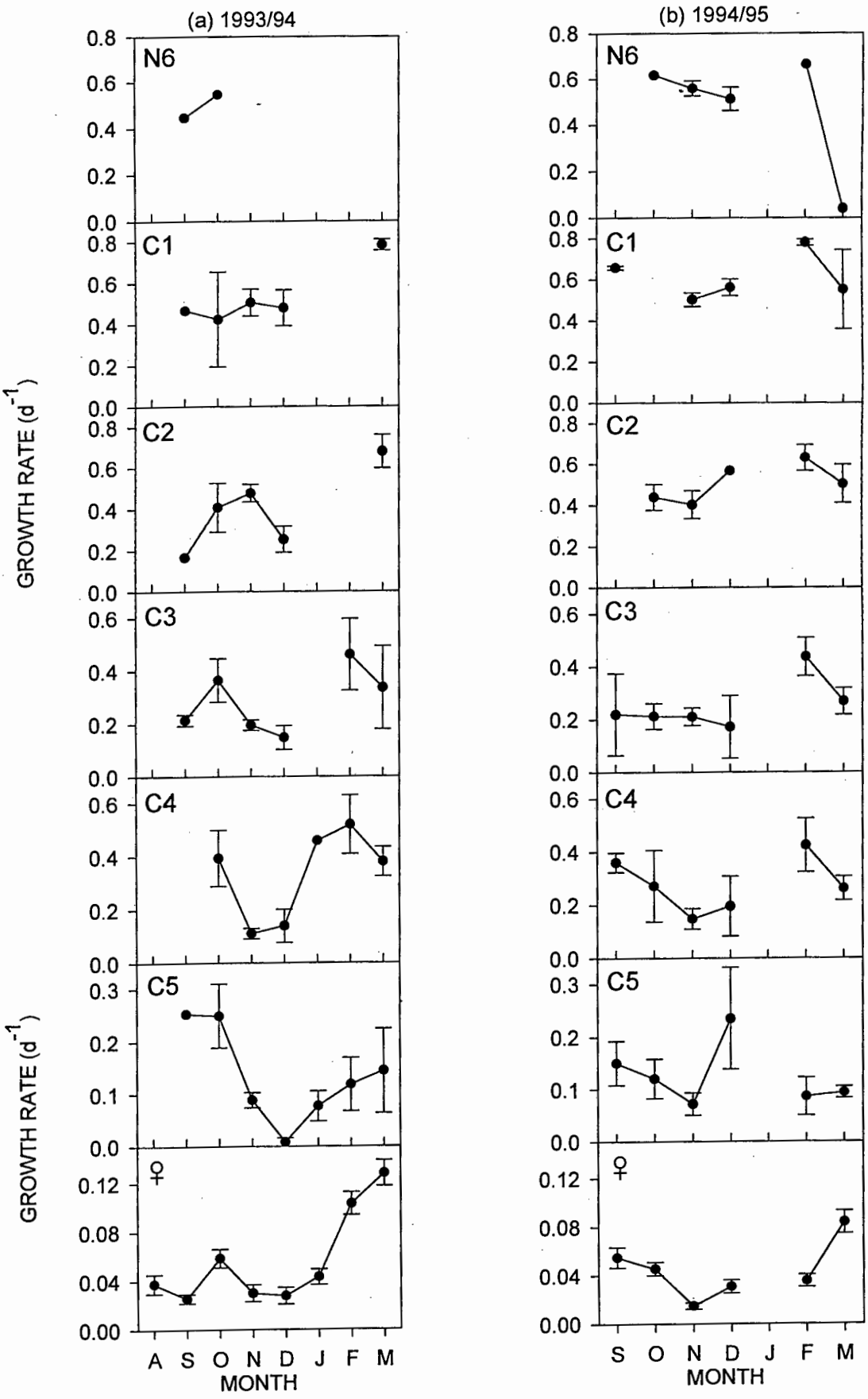


Fig. 6.4. Mean monthly growth rates ± standard error (d^{-1}) for *Calanus agulhensis* N6-females for (a) August 1993 to March 1994 and (b) September 1994 to March 1995. Note the different *y*-scales.

Table 6.2. Mean growth rates ± standard error of *Calanus agulhensis* stages for September/October, November/December, and January-March of 1993/94 and 1994/95. The number of months from which each mean was calculated is shown in brackets.

	GROWTH RATE (d^{-1})						
PERIOD	N6	C1	C2	C3	C4	C5	♀
Sep/Oct	0.536 ± 0.049 (3)	0.516 ± 0.072 (3)	0.338 ± 0.086 (3)	0.253 ± 0.037 (4)	0.343 ± 0.036 (3)	0.193 ± 0.034 (4)	0.046 ± 0.007 (4)
Nov/Dec	0.536 ± 0.023 (2)	0.512 ± 0.018 (5)	0.425 ± 0.066 (5)	0.181 ± 0.014 (5)	0.148 ± 0.018 (5)	0.056 ± 0.024 (4)[a]	0.026 ± 0.004 (5)
Jan-Mar	0.353 ± 0.312 (2)	0.706 ± 0.077 (3)	0.604 ± 0.052 (3)	0.375 ± 0.045 (4)	0.409 ± 0.043 (5)	0.104 ± 0.012 (5)	0.079 ± 0.018 (5)

[a] The estimate of C5 growth rate for December 1994 was excluded because of its poor precision. With its inclusion, the mean is 0.101 ± 0.048 d^{-1}.

Table 6.3. Mean growth rates ± standard error and the range for female *Calanus agulhensis* during the four phases of the upwelling cycle. The number of stations from which each mean was calculated is shown in brackets.

UPWELLING PHASE	FEMALE GROWTH (d^{-1})	RANGE (d^{-1})
Onset	0.035 ± 0.025 (3)	0.001-0.083
Sustained	0.079 ± 0.013 (22)	0.013-0.241
Quiescence	0.141 ± 0.022 (11)	0.015-0.234
Downwelling	0.046 ± 0.014 (11)	0.004-0.162

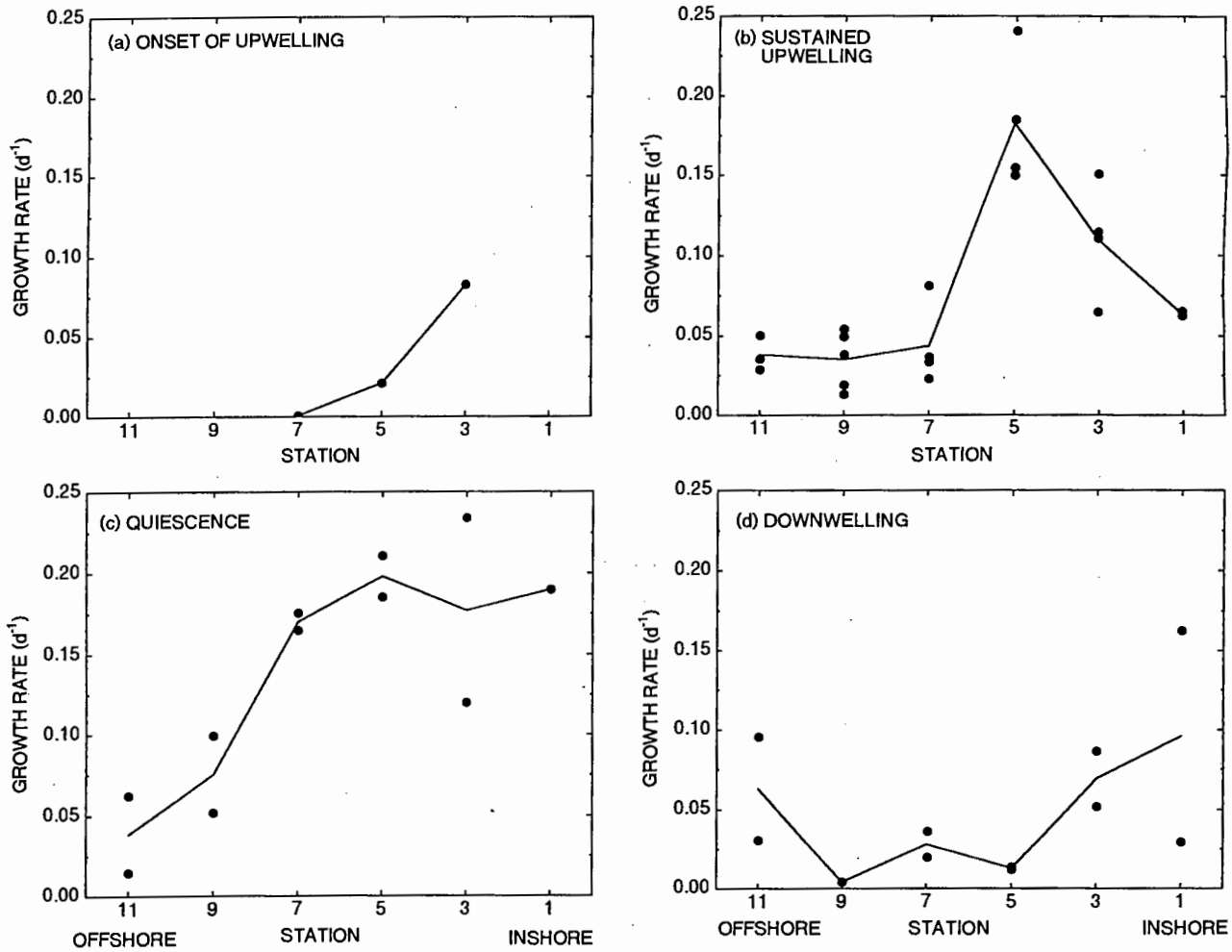


Fig. 6.5. Cross-shelf distribution of growth rates of female *Calanus agulhensis* from the Cape Agulhas and Walker Bay transects between January and March, categorized into four phases of the upwelling cycle: (a) the onset of upwelling, (b) sustained upwelling, (c) quiescence, and (d) downwelling. Dots represent the mean growth rate at a station on a transect, with the solid line depicting their mean.

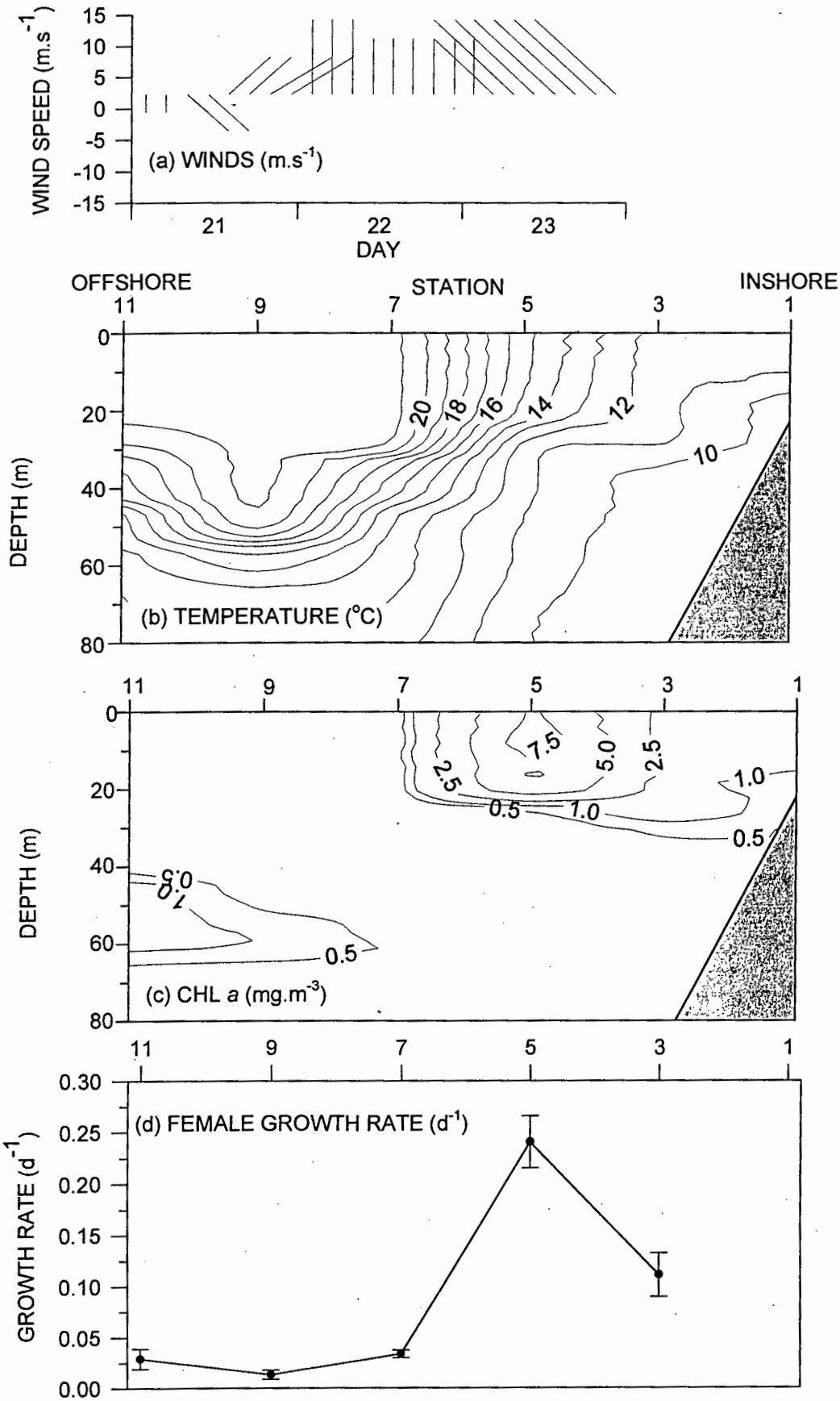


Fig. 6.6. The Walker Bay transect in January 1994 during sustained upwelling showing (a) wind strength and direction prior to sampling, (b) vertical sections of temperature and (c) vertical sections of Chl *a* concentration, and (d) mean growth rates ± standard error of female *Calanus agulhensis*.

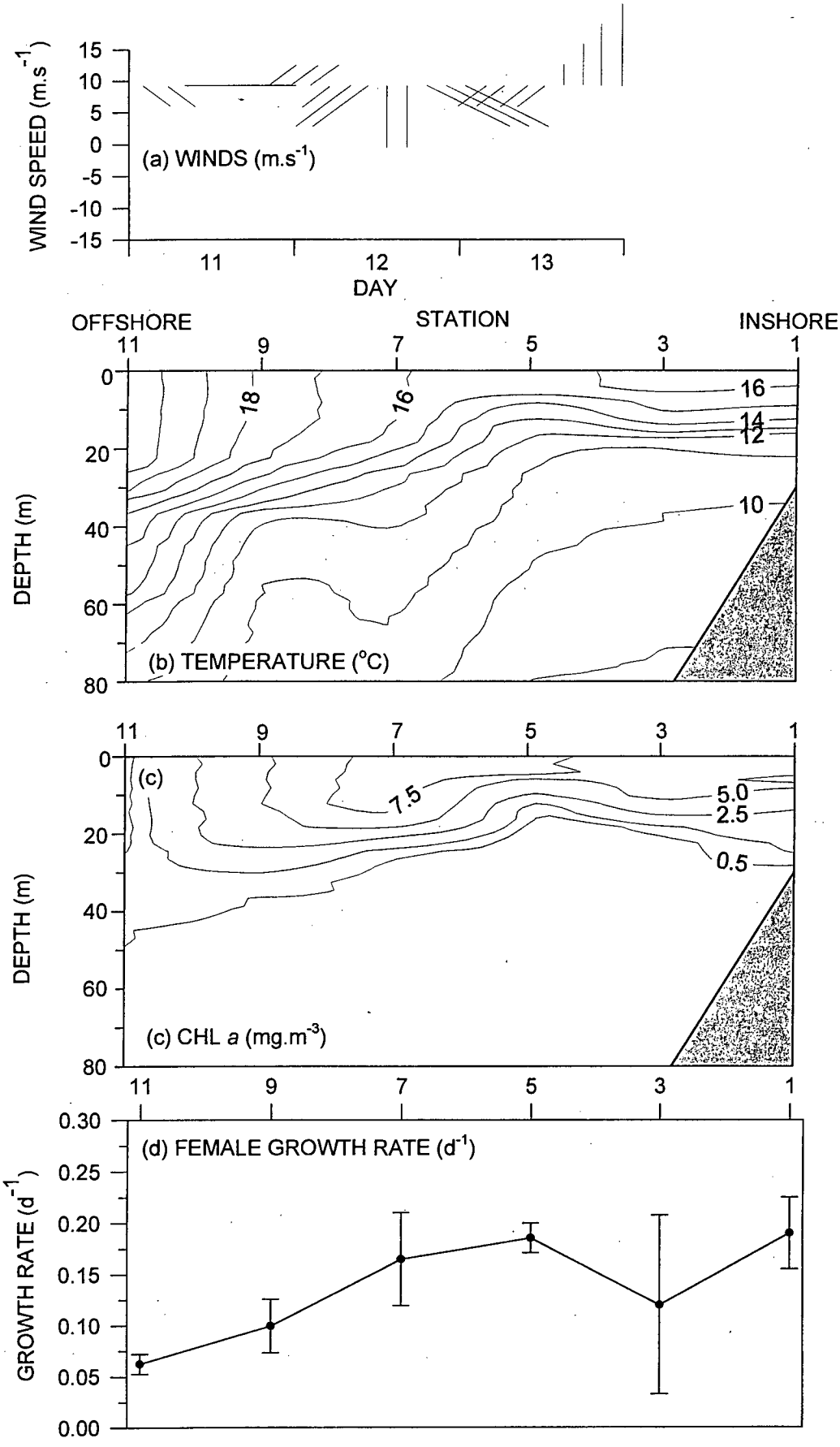


Fig. 6.7. The Walker Bay transect in March 1994 during quiescence, (a)-(d) as in Fig. 6.6.

During downwelling, female growth rates were generally slow (Fig. 6.5d). The Walker Bay transect in February 1995, after a day of north-westerly winds prior to the cruise, was representative of this phase with doming of the isotherms near the coast (Fig. 6.8, see Appendix 1). The inshore region had enhanced Chl *a* concentrations and elevated copepod growth rates. Farther offshore, growth rates were depressed as Chl *a* concentrations decreased and became subsurface.

DISCUSSION

The effect of body size

Growth rates of the larger stages of *Calanus agulhensis* varied seasonally, cross-shelf, and at the event scale, reflecting changes in their food environment in response to physical processes. The dependence of growth rates of copepods on Chl *a* in the southern Benguela system increases with body size between 500 and 2750 μm, and is similar for different species of the same size (Chapter 5). Other large species of copepods in the region may therefore exhibit patterns of growth similar to those of the larger stages of *C. agulhensis* in this study. Furthermore, daily growth rates of copepods in the southern Benguela region are size-dependent (Chapter 5), so the absolute values for growth rates of *C. agulhensis* reported are applicable to other species of similar size in the region.

The lack of correspondence between the growth rate of the younger stages of *C. agulhensis* and Chl *a* could be because small copepods use nano- and picoplankton more efficiently than larger copepods (Berggreen *et al.* 1988; Webber and Roff 1995). These cells are at a relatively constant background density in the southern Benguela system (Chapter 5, Painting *et al.* 1993) and in other areas such as tropical seas (Hopcroft and Roff 1990; Rath *et al.* 1993). Relatively constant growth rates of young juvenile stages may be a general phenomenon in aquatic systems: freshwater and marine nauplii grow relatively consistently (Hart 1990; Roff *et al.* 1995), as do small copepodites in the tropical sea (Webber and Roff 1995) and in the southern Benguela upwelling region (Chapter 5).

Food appears to be more important in determining growth rates of female *C. agulhensis* than temperature, because poor Chl *a* is associated with warm waters (Chapter 4, Fig. 4.8, Mitchell-Innes and Pitcher 1992). Control of growth by food rather than temperature has also been found in other systems such as freshwater lakes (Ban 1994), tropical seas (McKinnon and Thorrold 1993; Webber and Roff 1995), and temperate coastal regions (Peterson and Bellantoni 1987; Pond *et al.* 1996).

Cross-shelf variation

The growth rates of large copepodites declined across the shelf as Chl *a* concentrations decreased. A reduction in Chl *a* concentration from relatively nutrient-rich waters inshore to oligotrophic oceanic

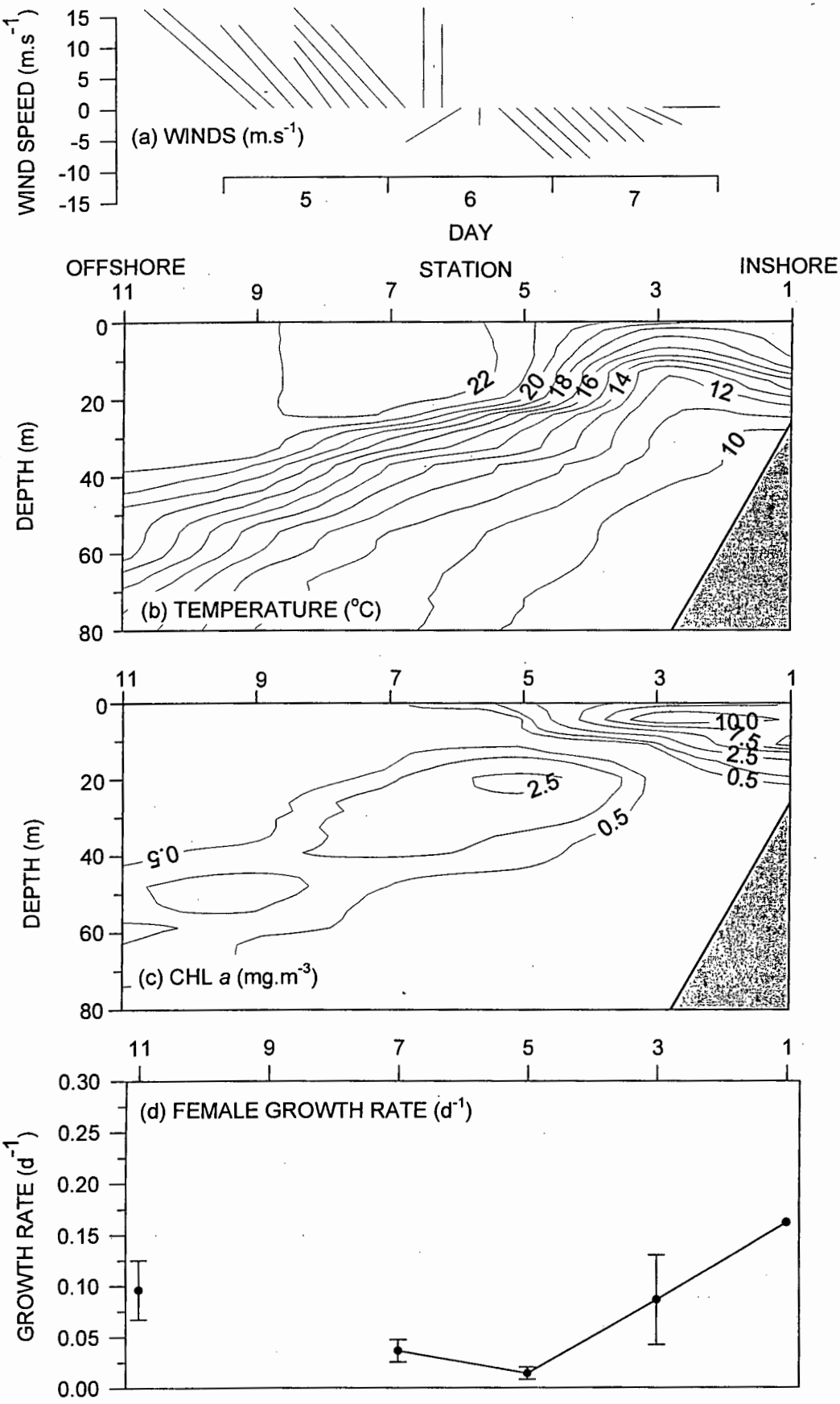


Fig. 6.8. The Walker Bay transect in February 1995 during downwelling, (a)-(d) as in Fig. 6.6.

waters farther offshore is typical of many systems, including the southern Benguela upwelling region (Pitcher *et al.* 1992). Slower growth rates in response to declining food concentrations offshore has also been observed in female *Paracalanus parvus* in southern California (Checkley 1980b) and for larger copepodites of a tropical copepod community (Webber and Roff 1995).

Seasonality

Growth of large copepodites varied in response to seasonal changes in phytoplankton biomass. In September/October, conditions were favourable for moderate Chl *a* to develop as the water column stabilized after winter (Mitchell-Innes *et al.* in press) following increased insolation, and abatement of westerly winds (Boyd *et al.* 1985). A second, larger bloom occurred from January to March during periodic surface upwelling. Although upwelling-favourable winds are common from September to March (Shannon 1985), it is not until later, January in the present study, that the cold water at depth is sufficiently shallow to permit surface upwelling of water from below the pycnocline on the western Bank (Chapter 7). This delayed movement of bottom water onto the shelf is a consequence of the broad shelf of the western Bank and the slow transport of bottom water to the region (Chapman and Largier 1989).

Event-scale variation

During late summer, rapid cycles of upwelling and relaxation are superimposed on seasonal hydrographic changes (Pitcher *et al.* 1992). Variation in female growth rate across the shelf during different phases of upwelling mirrored changes in depth-integrated Chl *a* concentration, *viz.* Chl *a* increased from the onset of upwelling to reach a maximum under quiescent conditions and then declined during downwelling (Mitchell-Innes *et al.* in press). This is a consequence of phytoplankton bloom development and subsequent successional changes in the assemblage as the upwelled water matures (Brown and Field 1986; Pitcher *et al.* 1991). At the onset of upwelling, growth rate is slow inshore because phytoplankton is virtually absent from newly upwelled water (Brown and Field 1986; Pitcher 1990). During sustained upwelling, diatoms dominate maturing upwelled water inshore of the frontal region (Pitcher *et al.* 1992), and dinoflagellates dominate within the front (Pitcher *et al.* 1996). These taxa enhance Chl *a* concentrations, providing a good food environment for copepods (Armstrong *et al.* 1991b; Mitchell-Innes and Pitcher 1992). Offshore of the upwelling front, the reduced phytoplankton biomass is dominated by pico- and nanoplankton such as small flagellates in the surface waters (Armstrong *et al.* 1987) and by dinoflagellates at the subsurface Chl *a* maximum (Pitcher *et al.* in press). These small cells provide a suitable food environment for small copepods, but not for their larger conspecifics (Berggreen *et al.* 1988). During quiescent periods, the broad band of good Chl *a* over most of the shelf, which is characteristic of aged-upwelled water (Shannon 1985), supports fast growth rates. Maximum growth rates of a closely-related species, *Calanus chilensis*, in the Humboldt upwelling

region were observed during relaxation events (Peterson *et al.* 1988). Therefore, not only is the duration of upwelling wind events important for enhancing Chl *a* concentrations (and hence elevating female growth rate) by injecting nutrients into the upper mixed layer, but so is the duration of relaxation (Pitcher *et al.* 1992).

Implications for pelagic fish

Starvation of fish larvae is an important factor affecting recruitment (Miller *et al.* 1988; Pedersen *et al.* 1990). In the southern Benguela, a subsurface jet current transports pelagic eggs and larvae from the spawning to the recruitment grounds (Shelton and Hutchings 1982; Shelton and Hutchings 1990). This jet and its associated surface front have large concentrations of copepod eggs and nauplii (Armstrong *et al.* 1987). These provide a suitably-sized food source for clupeoid larvae (Turner 1984), especially first-feeding larvae which are the most vulnerable to starvation (Blaxter and Hunter 1982). The suggestion by Armstrong *et al.* (1987) that these large densities of copepod eggs and nauplii are a consequence of the rapid female growth rate in these zones is supported by the present study. Moreover, the fast female growth of *Calanus agulhensis* in frontal regions implies that other copepods of similar size are also growing rapidly (Chapter 5). This would provide pelagic fish such as anchovy and sardine, which congregate in frontal zones (Castillo *et al.* 1996) and utilize large copepods (James 1987; van der Lingen 1994), with a productive food resource. Thus, frontal zones could not only reduce starvation-related mortality of fish larvae, but also provide optimal spawning sites for adult fish to spawn. These regions also remove spawning products from the vicinity of spawning aggregations, reducing cannibalism.

In temperate regions, fish such as herring, plaice, and cod spawn during spring or autumn blooms (Cushing 1967; Cushing 1990). At these times, female copepods are growing rapidly, providing abundant eggs and nauplii that are ingested by fish larvae. The South African sardine appears to follow this spawning strategy, with two spawning peaks, the first in September, and a larger peak in January (Crawford 1981; Fowler *et al.* 1996). These months not only supply larvae with favourable feeding conditions, but provide adult sardine, which are more efficient at retaining phytoplankton and copepod eggs and nauplii than are anchovy (van der Lingen 1994), with a good food environment.

In contrast, the period of peak spawning by Cape anchovy, October to December (Shelton and Hutchings 1990), is not concurrent with the time of fastest copepod growth (January-March), but with the period of maximum copepod biomass on the western Agulhas Bank (Chapter 7). Therefore, the spawning time of anchovy may reflect their evolutionary selection of a suitable spawning habitat in terms of sufficient copepod biomass for adults, rather than optimal feeding conditions for larvae. This postulate will be explored further in Chapter 7.

CHAPTER 7

THE EFFECT OF SEA TEMPERATURE AND FOOD AVAILABILITY ON THE SPAWNING SUCCESS OF THE CAPE ANCHOVY

ABSTRACT

Data on the thermal structure, copepod biomass and production, and total egg abundance of the Cape anchovy *Engraulis capensis* were obtained from monthly surveys during the periods August 1993-March 1994 and September 1994-March 1995 on the western Agulhas Bank and the South-Western Cape coast, South Africa. Previous work suggested that anchovy spawn on the western Agulhas Bank in temperatures between 16 and 19 °C, where they feed predominantly on copepods. This study shows that the western Agulhas Bank is a more suitable spawning area for anchovy, having greater thermal stability, a larger area of 16-19 °C water, and a more consistent food environment than off the South-Western Cape. Also, copepod production on the western Agulhas Bank was fastest in 16-19 °C water. To identify factors controlling the area of this water mass, a cluster analysis was used on a suite of hydrographic variables. Three periods were identified: winter (August-September), spring (October-December) and summer (January-March), reflecting changes in the extent of the 16-19 °C water and anchovy spawning, both of which peaked during spring. Spring was further characterized by infrequent surface upwelling. During summer, upwelling water (<13 °C) frequently reached the surface and the upwelling front migrated offshore, constricting the area of 16-19 °C water. It is hypothesized that spawning success in anchovy is dependent upon the extent of suitable spawning habitat, both spatially (16-19 °C water) and temporally (spring). To put this concept into a predictive framework, anchovy egg abundance was regressed against the area of 16-19 °C water; a significant, positive relationship ($r^2 = 0.56$, $n = 17$, $p < 0.001$) was found. An implication of the hypothesis is that the duration of spawning may be important to anchovy recruitment.

INTRODUCTION

Over the last two decades, the Cape anchovy *Engraulis capensis* has supported a large purse-seine fishery in South Africa. Management of this fishery is complicated by large interannual variations in recruitment, a phenomenon common to many pelagic fish species (Lluch-Belda *et al.* 1989). Understanding this variability is of particular importance to the Cape anchovy fishery because 70% of the catch are 0-year-old recruits (Cochrane and Hutchings 1995). Hypotheses to explain recruitment variability in marine fish have focused on post-spawning processes (Cushing 1975; Sinclair 1988; Bakun 1996), whereas factors that affect spawning success may also play an important role (Nikolsky 1963; Arkhipov 1989).

Cape anchovy spawn on the western Agulhas Bank between September and February (Shelton 1986; Melo 1994b). During this protracted spawning season, anchovy spawn serially, probably between 14 and 20 times in a season (Melo 1994a). The spawning products are then transported from the western Agulhas Bank, around Cape Point and northward along the West Coast to the recruitment grounds between St Helena Bay and the Orange River Mouth (see Fig. 1 in Introduction; Hutchings 1992).

Temperature is considered to be important in regulating spawning of anchovy. Unfavourable temperatures are thought to be responsible for spawners resorbing their eggs, a condition known as ovarian atresia (Hunter and Leong 1981). Previous work has suggested that anchovy prefer to spawn in temperatures between 16 and 19 °C (Shelton 1986), because both spawning fish (Painting *et al.* submitted) and their eggs (Anders 1965) are most commonly found within that temperature range. Therefore, temperature may directly affect the duration of spawning in anchovy.

Food availability is also important because serial spawning is an energy-intensive reproductive strategy requiring continual ingestion of food (Hunter and Goldberg 1980; Armstrong *et al.* 1991a; Hutchings 1992; Melo 1994a). If anchovy do not meet their metabolic requirements, they undergo ovarian atresia (Hunter and Goldberg 1980; Melo 1994a) and may cease spawning for the remainder of the season (Hunter and Macewicz 1985). On the western Agulhas Bank, copepods dominate the diet of anchovy (James 1987), despite this region having a smaller copepod biomass than the more productive South-Western Cape region (Pillar 1986; Hutchings *et al.* 1995). Therefore, it is believed that anchovy on the western Agulhas Bank are sometimes food limited (Peterson *et al.* 1992; Cochrane and Hutchings 1995). An explanation of this apparently anomalous choice of spawning ground may provide insight into the factors influencing spawning success.

This chapter investigates relationships between temperature and food availability, and the spawning success of the Cape anchovy during the 1993/94 and 1994/95 spawning seasons. The questions addressed in this chapter are:

1. Why do anchovy spawn in the poor food environment of the western Agulhas Bank and not off the more productive South-Western Cape region?
2. Why do anchovy prefer to spawn in 16-19 °C water?
3. Can anchovy spawning success be explained (and predicted) in terms of environmental variables?

MATERIALS AND METHODS

Data are presented from both the South-Western Cape region (Cape Point and Cape Columbine transects) and the western Agulhas Bank (Cape Agulhas and Walker Bay lines, see Chapter 1, Fig. 1.1). Hourly wind data prior to and during each cruise were collected from the Cape Point lighthouse, as described in Chapter 6, and are related to the hydrography on the western Agulhas Bank. In this region, there is a two-day time delay between the onset of upwelling-favourable winds and surface upwelling (Jury 1988).

Copepod biomass was measured according to the procedure described in Chapter 1. To estimate daily production of the copepod community, the biomass of each copepod species was multiplied by their daily growth rate. Growth rates of all copepods were assumed to be the same as similarly-sized stages of *Calanus agulhensis* (Chapter 5). Copepod sizes given in Chapter 1 (Table 1.2) were used to assign copepods to *Calanus* size classes (Table 7.1).

Three measures were used to estimate the food available to anchovy. First, copepod biomass was used. Second, was an index of the consistency of copepod biomass using the ratio of the mean to the standard deviation of the biomass. The presumption is that a relatively abundant and constant prey resource would be more beneficial to anchovy than a rapidly fluctuating resource of the same mean abundance. The third measure was total daily copepod production: this amount of copepod biomass may be removed each day without depleting the ambient biomass. To integrate the food environment over spatial scales that may be relevant to anchovy, each of these measures of food availability was determined for three temperature ranges: <16 °C, 16-19 °C (anchovy-favourable) and >19 °C (Painting *et al.* submitted).

Because anchovy prefer large copepods (James and Findlay 1989), the index of copepod consistency and the estimate of production were separated into two size fractions, *viz.* small copepods (<1.5 mm total length) and large copepods (>1.5 mm).

At each station, anchovy egg density in the upper 70 m was measured using a CALVET net. The total number of eggs on the western Agulhas Bank collected each month during 1993/94 and 1994/95 was calculated by Fowler (1998). It was assumed that the total number of anchovy eggs in the region is an index of the spawning intensity of this species.

The birthdate distributions of the 1994 and 1995 anchovy recruits were obtained by determining the ages of fish sampled during the May/June 1994 and 1995 recruit biomass surveys, by examination of

Table 7.1. Species that were assigned into the equivalently-sized stage of *Calanus agulhensis*.

EQUIVALENT *CALANUS* STAGE	SPECIES
C1	*Calanoides carinatus* C1
C2	*C. carinatus* C2, *Centropages brachiatus* juveniles, *Corycaeus/Corycella* spp., *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus* spp., *Metridia lucens* juveniles, *Oithona* spp., *Oncaea* spp., *Pleuromamma* juvenile, Harpacticoids
C3	*C. carinatus* C3
C4	*C. carinatus* C4, *C. brachiatus* ♀, *Rhincalanus nasutus* juvenile
C5	*C. carinatus* C5, *M. lucens* ♀, *Pleuromamma* ♀
♀	*C. carinatus* C6, *R. nasutus* ♀

otoliths using image analysis techniques. An age-length key was then constructed and converted to numbers-at-age using the weighted population length frequency calculated during those surveys (Waldron *et al.* 1992).

To identify seasonal patterns in hydrographic conditions on the western Agulhas Bank, a hierarchical cluster analysis, using the City-block (Manhattan) distance measure and the furthest neighbour amalgamation procedure, was performed on a suite of predictor variables. Variables were chosen to summarize hydrographic conditions spatially for each month, facilitating temporal comparisons. These variables included the minimum and maximum depth of the upper mixed layer (indicative of water column stability), the minimum and maximum sea surface temperature (indicative of temperature variation for a given month), the volume of water below 12 °C in the upper 200 m and the depth of the 10 °C isotherm (indicative of the ease in which upwelling can occur), and the volume of 16-19 °C water (a measure of the suitable spawning habitat for anchovy). The volume of water <12 °C and 16-19 °C was calculated from temperature sections in Surfer (Golden 1995), and was calculated as the mean percentage in the upper 200 m for the two transects on the western Agulhas Bank. Because the hydrographic variables had different scales of measurement, each variable (X_j) was standardized to $\frac{X_j - \overline{X}_j}{s_j}$, where $\overline{X}_j$ is the mean and s_j the standard deviation of variable X_j.

The surface area of 16-19 °C water within the 200 m isobath on the western Agulhas Bank (between Cape Point and Cape Agulhas) was calculated during each cruise from NOAA AVHRR satellite images with a resolution of 1.09 x 1.08 km obtained from the Satellite Acquisitions Centre. The area that was clouded (white areas in the images) was computed, and only images with less than 30% cloud on the western Agulhas Bank were used. Images from 12 SARP cruises (except August 1993 and September 1994) and November 1988-1994 satisfied this criterion. The percentage of the cloud-free area with water temperatures between 16 and 19 °C water was calculated from each image by pixel summation.

Regression analysis was used to extract relationships between total anchovy egg abundance and both the volume and area of 16-19 °C water. Regression rather than correlation analysis was used because there is a directionality associated with the relationships investigated (Zar 1984). Although this technique has been criticized because significant relationships can always be found if a sufficient number of independent variables are tested, this problem was minimized in two ways: first, only variables that could justifiably have an effect on the dependent variable were included, and second,

the relationship had to be repeatable. The relationship was considered repeatable if it remained significant when data from annual surveys in November (1988-1992) were included. Data from post-SARP November cruises were not included because the total egg abundance for anchovy has not been calculated (Fowler 1998).

Because the independent variables for the regressions were subject to measurement error (as opposed to setting the independent variables in an experiment which are assumed to be measured without error), functional regression was used rather than the usual approach of predictive regression (Laws and Archie 1981). Regression parameters for the functional regressions were determined from the predictive regression equation ($Y = a + bX$) using the formulae of Ricker (1973):

$$b' = \frac{b}{r}$$

$$a' = \overline{Y} - b'\overline{X}$$

where

b' = slope of functional regression,

b = slope of predictive regression,

r = correlation coefficient,

a' = intercept of functional regression,

$\overline{X}, \overline{Y}$ = mean of X and Y respectively.

The coefficient of determination (r^2) remains unchanged for functional regression. The 95% confidence interval for the slope of the functional regression (b') was calculated according to the equation by Jolicoeur and Mosimann (1968):

$$b' \times \left(t_{\frac{\alpha}{2}} \times \sqrt{\frac{1-r^2}{1+r^2}} \pm \sqrt{\frac{1-r^2}{n-2} + 1}\right)$$

where

$t_{\frac{\alpha}{2}}$ = critical two-tailed t-value at $\alpha = 0.05$,

n = number of samples.

As both the volume and area of 16-19 °C water are presented as percentages and thus have an underlying binomial distribution (Zar 1984), the data were transformed as $p' = \arcsin\sqrt{p}$ (where p = the area or volume of water, as a proportion) to approximate normality for the functional regression analysis.

All statistical tests using *t*-tests, *F*-tests and ANOVA were performed on log-transformed data, and the assumption of homogeneity of variance among groups was verified using Levene's test (Millikan and Johnson 1984 as cited in StatSoft 1996).

RESULTS

During the anchovy spawning season, the mean SST at stations on the western Agulhas Bank was significantly warmer (17.4 °C) than off the South-Western Cape (15.8 °C, *t*-test using separate variance estimates - Blalock 1972 as cited in StatSoft 1996, $t = 5.45$, $df = 311$, $p < 0.0001$). Also, the variability in temperature on the western Agulhas Bank was significantly less than off the South-Western Cape (*F*-test, $F = 1.53$, $p < 0.05$). Consequently, water between 16 and 19 °C was more common on the western Agulhas Bank, where it occurred at 47% of the stations, compared with 35% off the South-Western Cape.

Copepod biomass over the two seasons was significantly larger off the South-Western Cape than on the western Agulhas Bank (Fig. 7.1a). However, copepod biomass in 16-19 °C water was not significantly different between the two regions (Fig. 7.1b, *t*-test, $t = 1.89$, $df = 128$, $p > 0.05$). Copepod biomass increased slightly in warmer water on the western Agulhas Bank, although it was only marginally significant (Fig. 7.1b, one-way ANOVA, $F = 2.40$, $n = 197$, $p < 0.1$), but decreased markedly off the South-Western Cape (one-way ANOVA, $F = 7.50$, $n = 116$, $p < 0.001$). In terms of the consistency of copepod biomass, 16-19 °C water on the western Agulhas Bank was a better food environment for anchovy than off the South-Western Cape (Fig. 7.2). Furthermore, the consistency of copepod biomass was maximal in 16-19 °C water for both small and large copepods (Fig. 7.2). The biomass of small copepods was also more consistent than the large copepod biomass.

Daily production of small and large copepods for different temperature ranges on the western Agulhas Bank is shown in Fig. 7.3. Production of small copepods was relatively constant at around 560 $mg.m^{-2}.d^{-1}$ in water <19 °C, decreasing to 460 $mg.m^{-2}.d^{-1}$ in warmer water. Production by large copepods was substantially smaller, increasing from 73 $mg.m^{-2}.d^{-1}$ in <16 °C water to 87 $mg.m^{-2}.d^{-1}$ in >19 °C water. Production of large copepods was largest in water >16 °C and production of small

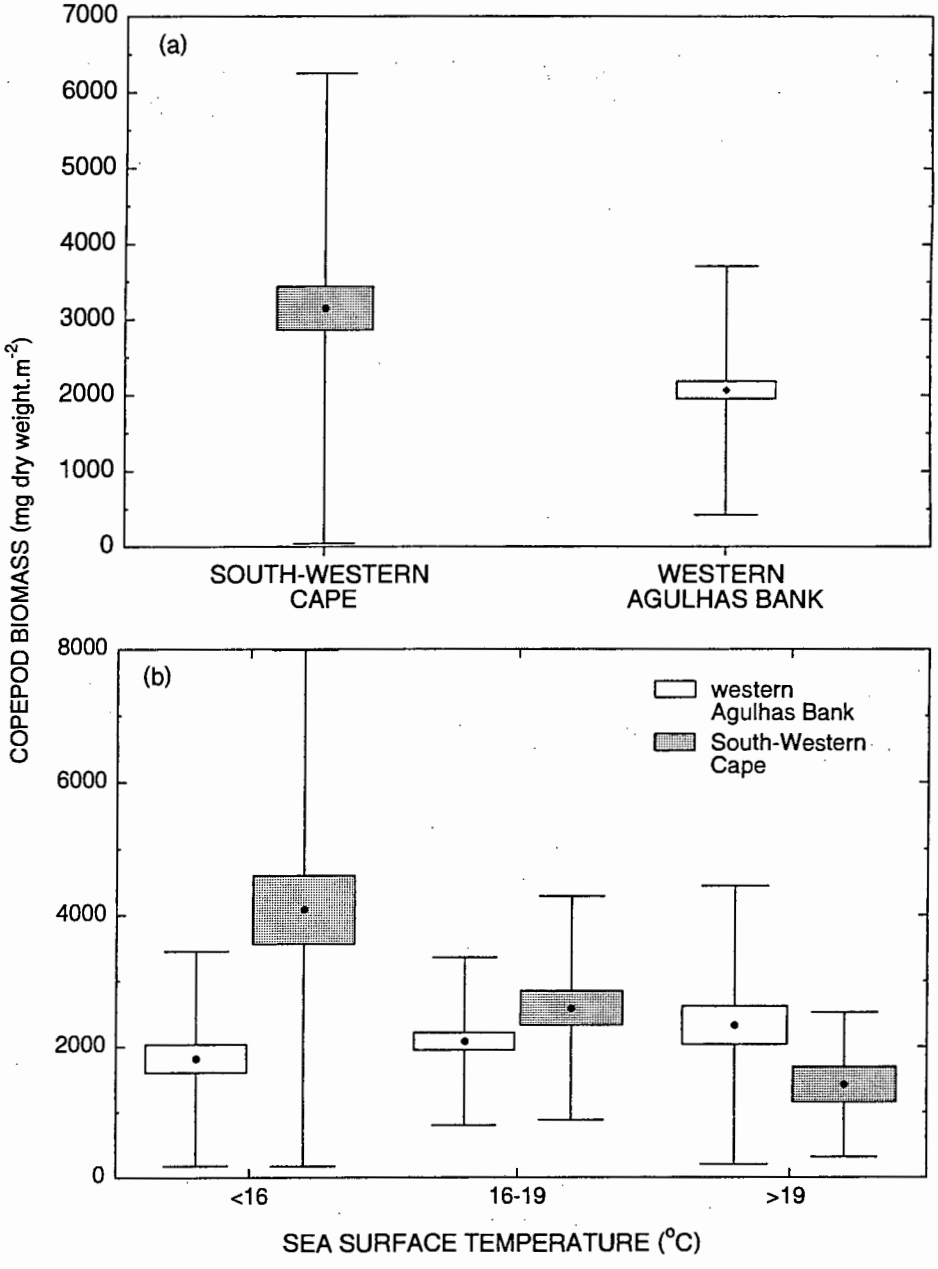


Fig. 7.1. Comparison of copepod biomass off the South-Western Cape and on the western Agulhas Bank for (a) all temperatures combined and (b) grouped into temperature ranges (<16 °C, 16-19 °C and >19 °C). The box is one standard error and the whisker is one standard deviation.

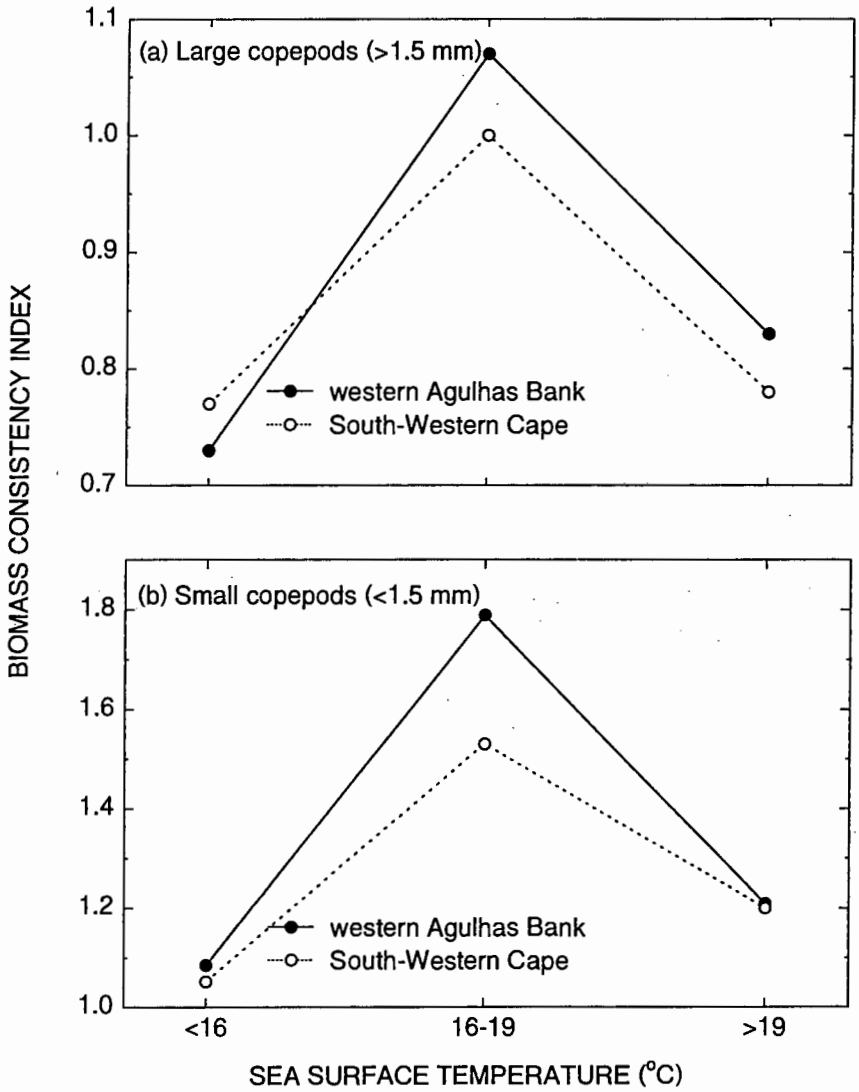


Fig. 7.2. An index of the consistency of copepod biomass (the ratio of the mean to the standard deviation), grouped into <16 °C, 16-19 °C and >19 °C temperature ranges for the western Agulhas Bank and off the South-Western Cape; (a) large copepods and (b) small copepods.

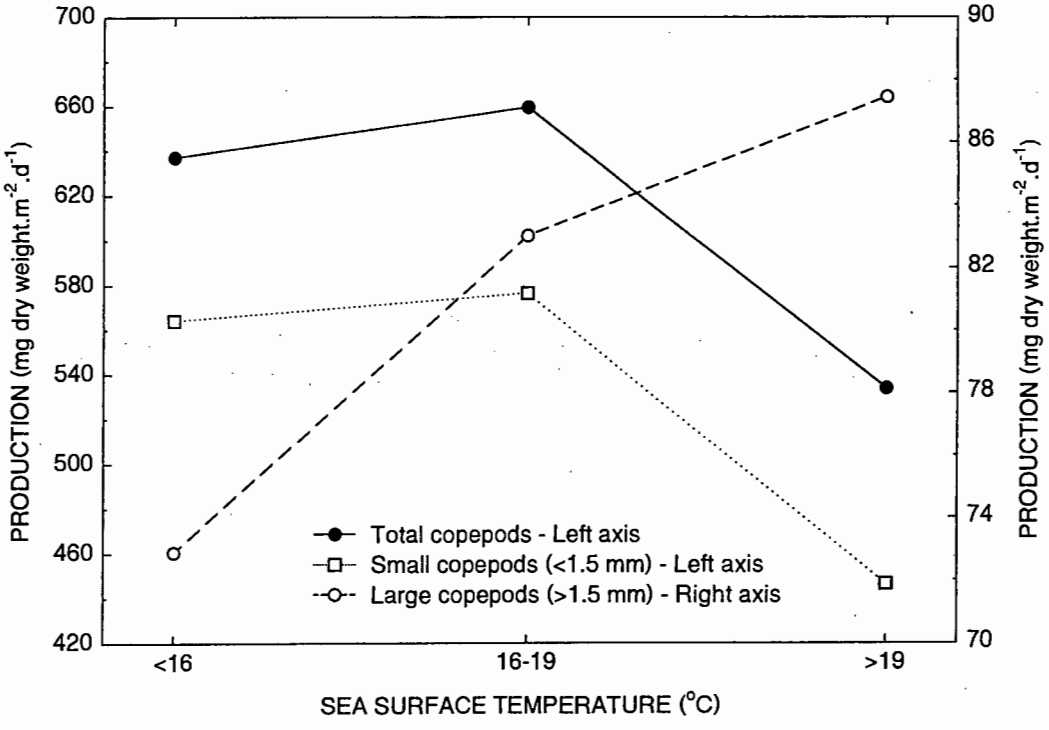


Fig. 7.3. Total daily copepod production in <16 °C, 16-19 °C and >19 °C water on the western Agulhas Bank.

copepods was greatest in <19 °C water. Total copepod production was slightly larger in 16-19 °C water (Fig. 7.3).

Food conditions for anchovy, in terms of production and the consistency of copepod biomass, appear to be optimal in 16-19 °C water. To understand the dynamics of this water mass, temporal changes in the hydrography of the western Agulhas Bank were investigated. Thermal images of sea surface temperature for each SARP cruise during 1993/94 and 1994/95 are shown in Appendix 1. Monthly temperature sections and the wind runs for the week prior to each cruise for the Cape Agulhas and Walker Bay transects (Chapter 1, Fig. 1.1), for the 1993/94 and 1994/95 seasons, are presented in Figs 7.4 and 7.5 respectively. The temperature regimes were similar between the two transects. The cluster analysis of the descriptive hydrographic variables for each month identified three seasonal periods (Fig. 7.6): winter (August-September), spring (October-December) and summer (January-March). The mean values of the descriptor variables in each of these periods are shown in Table 7.2. In winter, thermal conditions were uniform, with little difference between maximum and minimum temperatures, and 15 °C water covered most of the western Agulhas Bank (Appendix 1; Table 7.2; Fig. 7.5 - September 1994). A deep (to approximately 100 m), upper mixed layer was present and fronts were weak (Table 7.2, Fig. 7.4 - August 1993, September 1993; Fig. 7.5 - September 1994). Cold water was deep; the 10 °C isotherm was below 130 m and there was a relatively small volume of <12 °C water in the upper 200 m. The volume of 16-19 °C water represented only 1% of the shelf water (Table 7.2). Although occasional south-easterly winds occurred in winter, the cold water never reached the surface.

During spring, mid-shelf surface waters warmed to 18-19 °C (see Appendix 1) and the upper mixed layer shallowed (Table 7.2; Fig 7.4 - November 1993; Fig. 7.5 - December 1994). The depth of the 10 °C isotherm was shallower (80 m) than in winter and 38% of the shelf water was <12 °C. Periods of quiescence were common (Fig. 7.4 - November 1993; Fig. 7.5 - November 1994). South-easterly winds caused occasional surface upwelling, with its characteristic frontal signature (Fig. 7.5 - December 1994 - Walker Bay transect). An oceanic front (20 °C) was often present (Fig. 7.5 - December 1994). In spring, 30% of the shelf water was 16-19 °C, a marked increase from winter conditions (Table 7.2).

During summer, cool water was located inshore and warm water offshore (Appendix 1; Table 7.2; Fig. 7.4 - January 1994; Fig 7.5 - March 1995). South-easterly winds were more persistent in summer than in spring, upwelling cold, nutrient-rich water to the surface (Appendix 1; Fig. 7.4 - January 1994, February 1994; Fig. 7.5 - March 1995). Cold water moved up to within 35 m of the

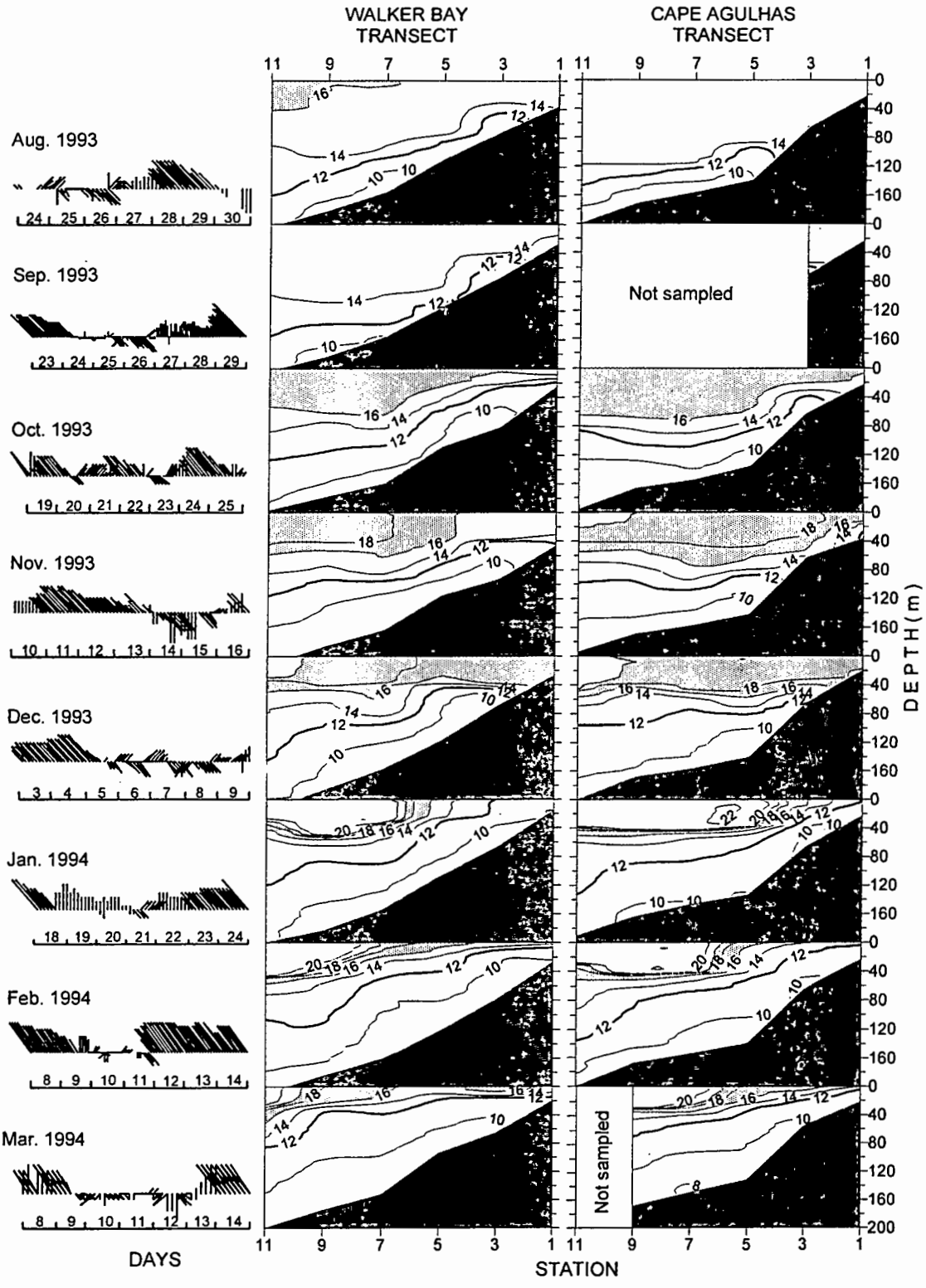


Fig. 7.4. Vertical sections of the thermal structure of the Walker Bay and Cape Agulhas transects on the western Agulhas Bank between August 1993 and March 1994. The stippled area shows water between 16 and 19 °C. Stick vectors depict the wind speed and direction one week prior to each survey.

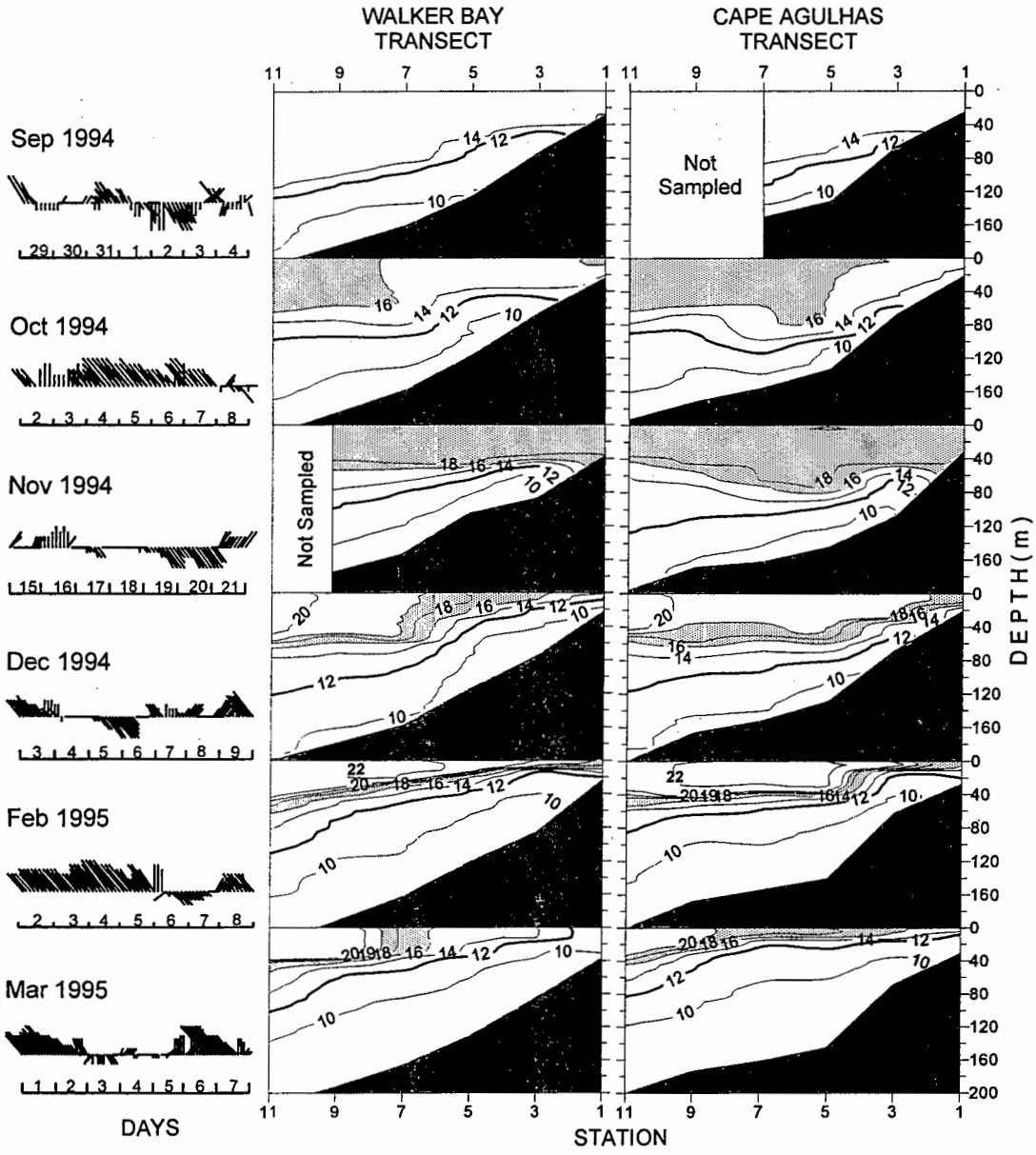


Fig. 7.5. Vertical sections of the thermal structure of the Walker Bay and Cape Agulhas transects on the western Agulhas Bank between September 1994 and March 1995. The stippled area shows water between 16 and 19 °C. Stick vectors depict the wind speed and direction one week prior to each survey.

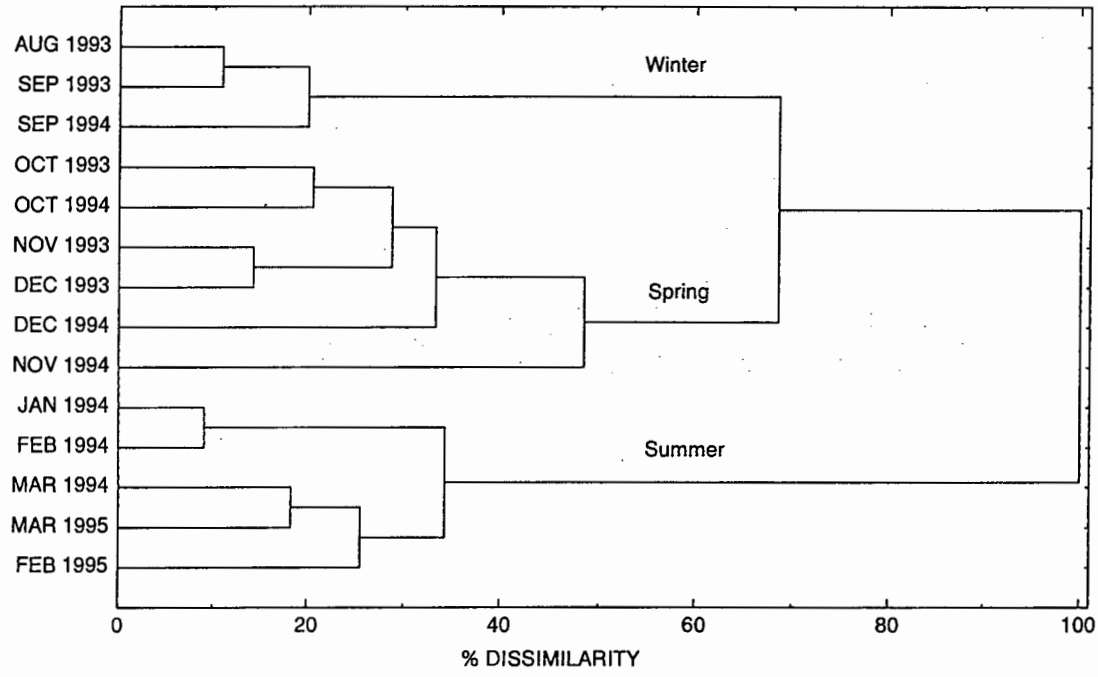


Fig. 7.6. A hierarchical cluster analysis showing three distinct periods (winter, spring and summer) in terms of the thermal structure of the western Agulhas Bank throughout the anchovy spawning season. The City-block (Manhatten) distance measure and the furthest neighbour amalgamation procedure were used on a suite of predictor variables (see text).

Table 7.2. Mean values of hydrographic variables for the three periods defined by the cluster analysis; winter, spring and summer. SST = Sea surface temperature, UML = Upper mixed layer.

PERIOD	Maximum SST (°C)	Minimum SST (°C)	Maximum UML depth (m)	Minimum UML depth (m)	Frontal strength ($^{\circ}C.mile^{-1}$)	Depth of 10 °C isotherm (m)	Volume of <12 °C water (%)	Volume of 16-19 °C water (%)
Winter	15.93	14.40	98.3	22.0	0.14	133.7	23	1
Spring	18.97	15.98	63.5	14.2	0.26	81.2	38	30
Summer	21.76	12.26	41.8	6.0	1.12	33.6	61	6

surface. The <12 °C water moved farther onto the shelf and comprised >60% of the water in the upper 200 m. The mid-shelf water at the surface was warmer and a well-defined oceanic front varied between 15 miles (Fig. 7.4 - January 1994) and 45 miles (Fig. 7.4 - March 1994 - Walker Bay transect). Water of 16-19 °C was situated between the upwelling and oceanic fronts (see Appendix 1). During periods of strong south-easterly wind, the upwelling front moved offshore and occasionally coalesced with the oceanic front, forming an intense front, especially when the oceanic front was close inshore (Appendix 1, Fig. 7.4 - January 1994). During periods of north-westerly winds and quiescent conditions, the isotherms deepened (Fig. 7.4 - March 1994 - Walker Bay transect).

Such seasonality in the hydrography of the western Agulhas Bank may have a marked affect on the spawning of anchovy. Seasonal changes in the volume of 16-19 °C water and the biomass of large copepods were similar, being smallest in winter, peaking in spring and decreasing sharply in summer (Figs 7.7a, b). This trend was also evident in the spawning success of anchovy (Fig. 7.7c) and in the birthdate distribution of the recruits the following year (Fig. 7.7d).

The relationship between anchovy egg abundance and the volume of 16-19 °C water on the western Agulhas Bank was quantified by functional regression analysis. A significant, positive relationship was found between total anchovy egg number and the volume of 16-19 °C water (Fig. 7.8a, Table 7.3). The area of 16-19 °C water estimated from the satellite images was closely related to the volume of this water mass ($r^2 = 0.74$, $n = 12$, $p < 0.001$). Anchovy egg abundance was even more-strongly related to area of 16-19 °C water than volume (Fig. 7.8b, Table 7.3). The relationship was more significant with the inclusion of data from other surveys (November 1988-1992, $r^2 = 0.56$, $n = 17$, $p < 0.001$, Fig. 7.8b, Table 7.3). Two groups of points are apparent in Fig. 7.8b, the winter and summer group at the lower end of the regression and the spring group at the upper end.

DISCUSSION

The suitability of a spawning area for fish is dependent upon a suite of factors. It has been suggested that anchovy spawn on the western Agulhas Bank, upstream of their recruitment area on the West Coast, to maximize transport of their spawning products to the productive nursery grounds (Cochrane and Hutchings 1995). This strategy has the advantage of separating spawning products from spawners, and thus reducing cannibalism (Valdés Szeinfeld and Cochrane 1992). In addition, the stratified and relatively thermally constant water column on the western Agulhas Bank throughout the spawning season could benefit first-feeding larvae (Parrish *et al.* 1982) and reduce the likelihood of abnormalities in egg development which can occur in <14 °C water (King *et al.* 1978). This greater

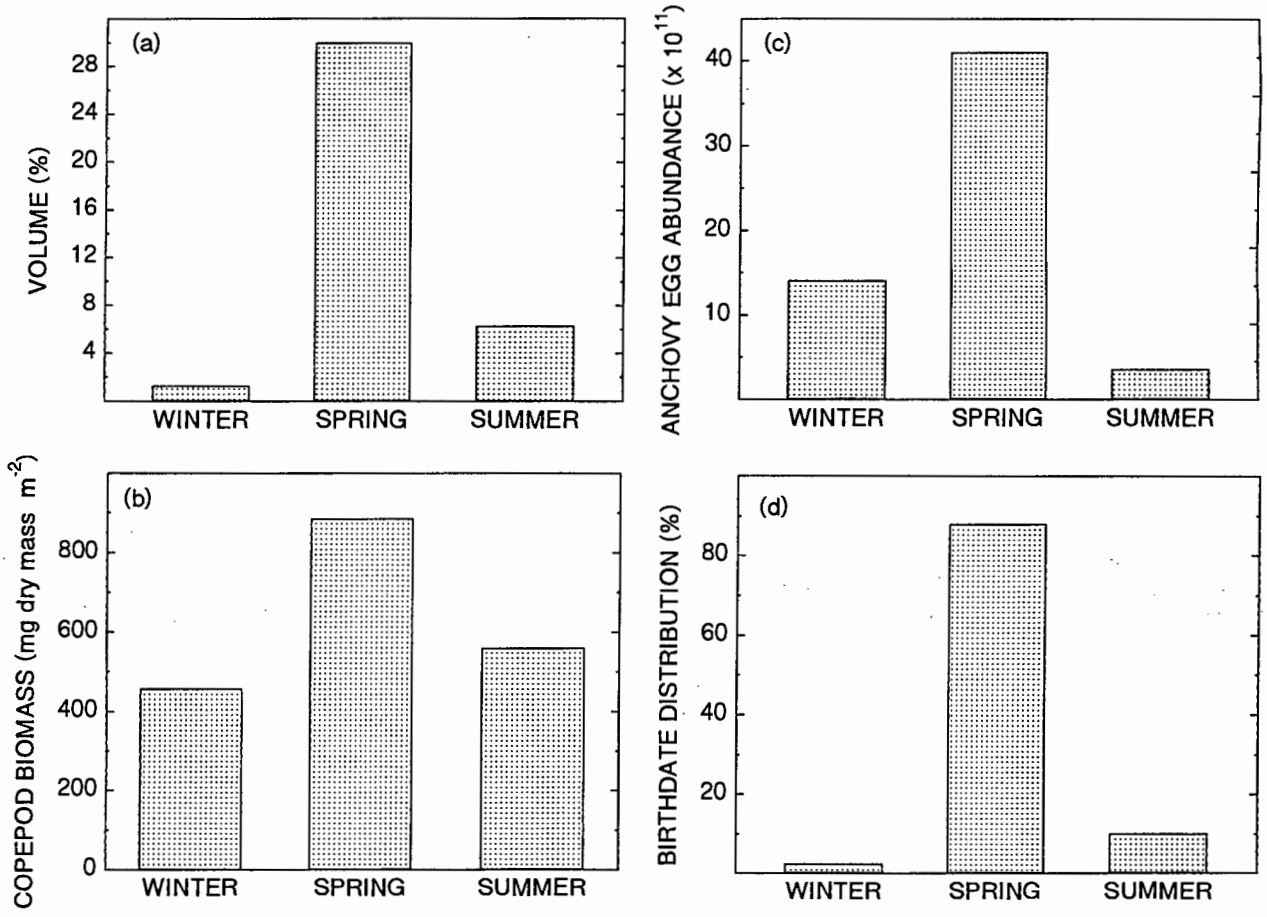


Fig. 7.7. Seasonal changes on the western Agulhas Bank of (a) the volume of 16-19 °C water, (b) the biomass of large copepods, (c) total anchovy egg abundance, and (d) anchovy birthdates from recruits of 1994 and 1995.

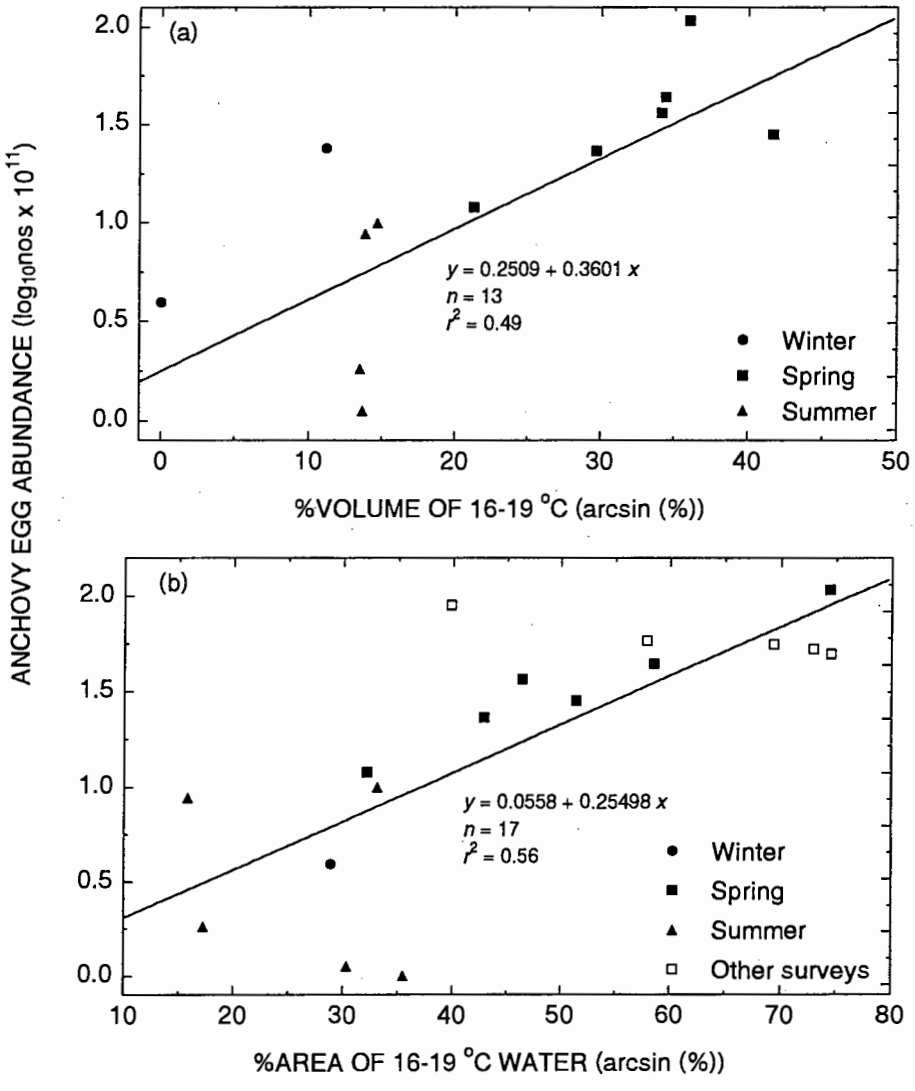


Fig. 7.8. Relationships between the total anchovy egg abundance on the western Agulhas Bank and (a) the volume of 16-19 °C water and (b) the area of 16-19 °C water, with data from other surveys included.

Table 7.3. Functional regression analyses between total anchovy egg abundance (log nos x 10^{11}) and the volume and area of 16-19 °C water for data from SARP only, and SARP and November Spawner Biomass Surveys together. The equation, 95% confidence interval (CI) for the regression slope (b'), proportion of the variance explained (r^2), and number of data points (n) are given. Significance levels are $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$.

INDEPENDENT VARIABLES	DATA	EQUATION	95% CI FOR b'	r^2	n
Volume of 16-19 °C water ($\arcsin(\sqrt{\text{volume}(\%)/100})$)	SARP	$y = 0.2473 + 0.1075x$	(0.1278,0.3801)	0.34^{*}	14
Area of 16-19 °C water ($\arcsin(\sqrt{\text{area}(\%)/100})$)	SARP	$y = -1.1875 + 0.0897x$	(0.0506, 0.1325)	0.58^{**}	12
	SARP + NOVEMBER DATA	$y = -0.7676 + 0.0782x$	(0.0509, 0.1078)	0.56^{***}	17

thermal constancy on the western Agulhas Bank relative to the South-Western Cape region is a consequence of the broader shelf area, less frequent upwelling (Jury 1988; Lutjeharms and Stockton 1991) and the stronger stratification in summer (Boyd *et al.* 1985; Largier *et al.* 1992).

An additional factor that may influence the selection of a spawning area is the food available to spawners. Although copepod biomass was significantly larger off the South-Western Cape than on the western Agulhas Bank, there was no significant difference in copepod biomass in 16-19 °C water, even without compensating for the additional impact of predation by anchovy on the western Agulhas Bank. A positive relationship has been found between anchovy spawning success on the western Agulhas Bank and the biomass of large copepods in 16-19 °C water (see Chapter 8). Furthermore, the western Agulhas Bank had a more consistent food environment than off the South-Western Cape. The consistency of the food resource may be important to prolonged spawning in anchovy, especially in years when spawners have poor fat reserves at the start of their spawning season. It is noteworthy that the small copepod size fraction was more consistent than large copepods. Anchovy are known to switch from filter feeding to the more energetically-efficient mode of biting for prey >0.72 mm (James and Findlay 1989; James and Probyn 1989). When large copepods are abundant, anchovy may feed by biting and obtain a large energy intake at a relatively small energetic cost, thus reserving more energy for spawning. When large copepods are unavailable, feeding on small copepods could sustain the normal metabolic activities of anchovy and reduce the likelihood of atresia.

In terms of copepod production on the western Agulhas Bank, small copepods, which are energetically expensive for anchovy to capture, dominated <16 °C water. In >19 °C water, even though the production of large copepods was large, total copepod production was small. Again, 16-19 °C water was the optimal food environment, because it provided good production at a relatively small energetic cost. An added benefit of the large copepod productivity in water in which anchovy spawn is that it may provide a readily available food source for larvae that are swept into and transported in the jet current along the South-Western Cape coast. Previous studies have found that the inner margin of the jet current, where most spawning products are located, is highly productive (Armstrong *et al.* 1987; Hutchings 1992).

Spawning success in anchovy appears to be dependent upon the extent of a suitable spawning habitat, both spatially (16-19 °C water) and temporally (spring). Underpinning this hypothesis is the positive relationship between anchovy egg abundance and the area of 16-19 °C water (Fig. 7.8b). Enhanced spawning of the anchovy *Engraulis anchoita* has also been noted at times of larger spawning habitat, as defined by temperature (Matsuura and Kitahara 1995). It has been suggested that the effect of

temperature noted in the field may be an artefact of the association between food and temperature (Bagenal 1973).

The extent of the spawning habitat is dynamic, both spatially and temporally, and is related to the increasing frequency of upwelling from winter to summer (Fig. 7.9). During the study period, a very small area of 16-19 °C water occurred in winter, when the sea surface temperature was cool and conditions were well-mixed as a result of the dominant westerly winds (Boyd *et al.* 1985). In winter, upwelling of cold bottom water was rare, because the occasional occurrence of south-easterly winds upwelled water from above the deep pycnocline.

During spring, the quiescent phase was dominant (Fig. 7.9). A large area of 16-19 °C water was present as a result of a strongly-stratified water column, the cold water being deep, and relatively infrequent south-easterly winds (Jury 1988; Largier *et al.* 1992).

In summer, the upwelling phase was dominant. The stratified water mid-shelf was bounded inshore by colder, newly-upwelled water and offshore by the oceanic front, which marked the transition from shelf waters to warmer oceanic waters. The cold water occupied the inner-shelf region and the persistent south-easterly winds upwelled water from below the pycnocline. The region was dynamic and varied in size, depending on the phase of the upwelling cycle, the intensity and duration of upwelling winds, and the position of the oceanic front, which is remotely controlled by the Agulhas Current (Largier *et al.* 1992). This episodic, surface upwelling, coupled with frequent inshore movement of warm (>20 °C) oceanic water, reduced the frequency of stratified 16-19 °C water favourable for anchovy spawning.

It is perhaps counter-intuitive that the optimal spawning conditions on the western Agulhas Bank, in terms of temperature and food, were in spring (Fig. 7.7), when upwelling frequency and Chl *a* concentrations were less than in summer (Chapter 6, Figs 6.1 and 6.2). Off the South-Western Cape, where the shelf is narrow and upwelling is strong, copepods are concentrated inshore (Fig. 7.1, Chapter 2, Fig. 2.1, Andrews and Hutchings 1980, Hutchings 1981) where their food (Chl *a*) is most abundant (Chapter 2, Fig. 2.2, Brown 1992). In contrast, copepod biomass decreases inshore on the western Agulhas Bank (Fig. 7.1, Chapter 2, Fig. 2.1), suggesting that growth may not be the major controlling process. Advective losses from the western Agulhas Bank may influence the biomass of copepods (Chapter 9, Chapter 10), and at times may be greater than the advective input of copepods from the eastern Agulhas Bank (Largier *et al.* 1992; Peterson *et al.* 1992). Advective flow and resulting loss of copepods from the mid-shelf region may be greater at times during summer (Chapter

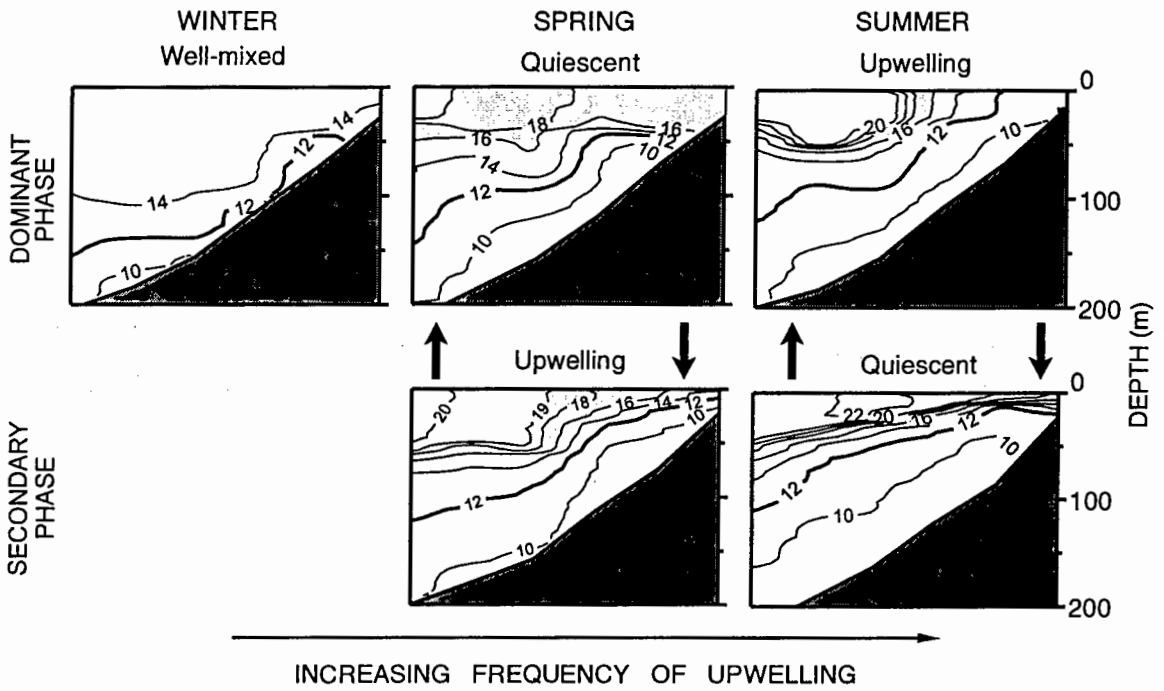


Fig. 7.9. The different phases of upwelling in winter, spring, and summer in the southern Benguela system. In winter, only the well-mixed phase occurs. In spring, a quiescent and an upwelling phase is present, with the quiescent phase dominant. In summer, the upwelling phase dominates the quiescent phase (modified from Mitchell-Innes *et al.* (in press)). The stippled area is water between 16 and 19 °C.

9), when there is often a strong frontal jet associated with upwelling inshore (Mann and Lazier 1991; Largier *et al.* 1992). Conversely, during spring when quiescence is more frequent, advective losses are probably reduced and copepod biomass may increase. Therefore, the seasonal change in the relative magnitude of advective input and output of copepods on the western Agulhas Bank may explain why the biomass of large copepods peaks in spring and is out of phase with the production cycle of phytoplankton.

Advective loss of copepods from the western Agulhas Bank could account for the relationship shown here between the area of 16-19 °C water and anchovy spawning success: the occurrence of a strong front and small copepod biomass is concomitant with a reduction in area of 16-19 °C water. Also, density-dependent predation on copepods by anchovy may increase when the area of 16-19 °C water is reduced. This may result in a food shortage as a result of the removal of female copepods, which, because of their large size would be preferentially ingested by anchovy (James and Findlay 1989), causing slow replenishment of copepod populations.

An implication of the spawning habitat hypothesis is that the duration of spawning may affect recruitment. The large fecundity and protracted spawning season of anchovy not only increases the carrying capacity of the western Agulhas Bank by spreading the predatory impact of anchovy on copepods over a longer period (Hutchings 1992) and reducing cannibalism, but also compensates for the high and variable mortality of their eggs and larvae in the strongly pulsed southern Benguela upwelling system (Nelson and Hutchings 1983). In this context, reduction in the duration of the spawning season would make below-average recruitment more likely: the risk-spreading advantage of serial spawning would be reduced (Lambert and Ware 1984). The duration of the spawning season varies: *e.g.* during 1965-1968 spawning extended from October to January (Crawford 1981); in 1977-1978 a broader spawning peak between October and February was reported by Shannon *et al.* (1984). Also, spawning by anchovy in November 1988 ceased early, possibly as a result of poor food conditions (Peterson *et al.* 1992), which resulted in high atresia (Cochrane and Hutchings 1995) and a poor recruitment in 1989 (Hutchings 1992). Because conditions favourable for spawning in anchovy occur predominantly during spring, years in which spring conditions persist would increase the likelihood of good recruitment. Ultimately, the duration of the spring period may be controlled by the position of the South Atlantic high pressure cell, which influences the onset and duration of the south-easterly upwelling winds on the western Agulhas Bank (Nelson and Hutchings 1983; Shannon 1985).

It is concluded that the spring period and associated large area of 16-19 °C water, high and consistent copepod biomass and good production rates are crucial to the spawning success of Cape anchovy. The veracity of this hypothesis could be tested by comparing a time-series of the area of 16-19 °C water derived from satellite imagery and the data from the new SARP programme, which monitors anchovy eggs and larvae off Cape Point. The assertion that the duration of the optimal spawning period may control recruitment could also be tested by applying the regression relationship between temperature and spawning to satellite-derived estimates of the area of 16-19 °C water throughout several spawning seasons. This estimate of spawning success could then be compared to estimates of recruitment strength.

CHAPTER 8

THE SPAWNING OF ANCHOVY IN RELATION TO ITS FOOD ENVIRONMENT

ABSTRACT

This chapter explores the relationship between the spawning of the Cape anchovy *Engraulis capensis* and the abundance of its food in terms of copepod biomass. Total anchovy egg abundance and gonadal atresia, and copepod biomass were collected monthly between August-March 1993/94 and 1994/95 on the western Agulhas Bank, South Africa, the major spawning ground of anchovy. During the 1993/94 spawning season, anchovy ceased egg production in January 1994, owing to a high proportion of females in an atretic condition in response to the limited food availability. During the 1994/1995 season, food appeared to be non-limiting, although the paucity of data provided an equivocal picture. To identify separate relationships between total egg abundance and atresia or food availability, functional regression was used on the data from both seasons. A significant inverse relationship was found between the total abundance of anchovy eggs and the proportion of the population in an atretic condition. Egg abundance was positively related to food availability when information concerning size selectivity (large copepods) and temperature preference (16-19 °C) of anchovy was incorporated into the estimate of the food environment. These findings support the contention that food is important to the spawning of the Cape anchovy and a consistent food resource throughout the season reduces atresia and prolongs spawning.

INTRODUCTION

Pelagic fish, such as sardine (Bensam 1964; Blaxter and Hunter 1982), anchovy (Hunter and Goldberg 1980; Hunter and Macewicz 1980), horse mackerel and mackerel (Hunter and Leong 1981) spawn serially for several months. The Cape anchovy *Engraulis capensis* exhibits this reproductive strategy (Melo 1994b), spawning every 7-10 days between September and February each year (Shelton and Hutchings 1990; Melo 1994a). The energy required for this intensive and sustained reproductive process is derived from fat reserves and the ingestion of food during spawning (Hunter and Goldberg 1980).

Anchovy spawn mainly on the western Agulhas Bank (Hampton 1992), where they feed predominantly on copepods (James 1987). Because the biomass of copepods in this region is relatively small compared to other regions off the South African west coast (Chapter 2; Pillar 1986; Verheye *et al.* 1992; Hutchings *et al.* 1995), anchovy are sometimes food limited (Peterson *et al.* 1992). Food limitation can cause resorption of developing oocytes, a condition known as ovarian atresia (Hunter and Leong 1981; Melo 1994a), and results in a decrease in spawning frequency and in

the batch fecundity (Hunter and Goldberg 1980). It has been suggested that anchovy require continuous food throughout their spawning season for sustained serial spawning (Melo 1994a), especially when body fat reserves become depleted (Hutchings 1992).

This chapter presents data on the total egg abundance of the Cape anchovy, the atretic condition of the population, and its food environment in terms of copepod biomass from the western Agulhas Bank. These data are used to derive relationships between the number of anchovy eggs and both gonadal atresia and their food environment.

MATERIALS AND METHODS

Copepod biomass on the western Agulhas Bank was measured monthly, between August-March of 1993/94 and 1994/95 as described in Chapter 1. As anchovy are size-selective predators preferring large copepods (James and Findlay 1989), the biomass of copepods was catergorized into two size fractions, *viz.* small copepods (<1.5 mm total length, TL) and large copepods (>1.5 mm TL). The large size fraction includes all copepods larger than or equal to a *Calanus agulhensis* C4 (Chapter 1, Table 1.2).

Total anchovy egg abundance on the western Agulhas Bank was used as a measure of spawning success (Fowler 1998, also see Chapter 7). For histological examination of ovarian atresia, anchovy were collected from *ad hoc* mid-water trawls during the SARP cruises. Ovaries were preserved and prepared using standard methods (Hunter and Goldberg 1980; Hunter 1985). Atretic condition was determined according to the classification of Hunter and Macewicz (1985). Data on atresia are presented as the percentage of the total number of females sampled that had atresia.

To summarize these data and facilitate identification of relationships between total anchovy egg abundance and predictor variables, functional regression analysis was used (see Chapter 7). Only justifiable relationships were investigated and they were considered repeatable if they remained significant when data from annual surveys in November (1988-1992) were included. Copepods could not be separated according to size for the November 1988 Spawner Biomass Survey because a different counting procedure was used. Thus, only total egg abundance and gonadal atresia data are presented for that year. The estimate of copepod biomass in September 1993 was negatively biased because the offshore region where greatest biomass is found (Chapter 2, Fig. 2.1) was not sampled due to bad weather. Thus, data from September 1993 were excluded from the regression analyses.

RESULTS

Intra-seasonal variability of anchovy egg abundance, gonad atresia, and copepod biomass during the 1993/94 season is shown in Fig. 8.1. Total egg abundance was greatest between October and December (Fig 8.1a). The very large density of eggs in October 1993 is the result of one station with eggs more than an order of magnitude more abundant than at any other station sampled during SARP (Fowler 1998). Gonad atresia showed an increase toward the end of the season with 100% atresia by March (Fig. 8.1b). There was more than a two-fold variation in copepod biomass in the 1993/94 season, ranging from 827.0 $mg.m^{-2}$ in January 1994 to 2197.5 $mg.m^{-2}$ in December 1993 (Fig. 8.1c). A noteworthy feature was that the copepod biomass in January 1994 was considerably smaller than in other months. Accompanying the small biomass of copepods in January 1994 was a sharp increase in the proportion of fish that were in an atretic condition, rising from about 10% prior to January 1994 to >50% thereafter. This increase in atresia in January 1994 was associated with a sharp decline in the total number of anchovy eggs. Despite amelioration of the food environment in February and March, anchovy did not resume spawning.

It was difficult to interpret the results during the 1994/95 season because no data were collected during August 1994 and January 1995 (Fig. 8.2). In addition, owing to the very small recruitment of anchovy in 1994 (Hampton and Barange 1996), no samples were collected for histological analysis from trawls in December 1994, February 1995, and March 1995. However, some trends are still apparent. Greatest anchovy egg abundance was again found from October to December, but was smaller than in 1993/94 (Fig. 8.2a). There was also variability in the biomass of copepods throughout the season, with a two-fold variation ranging from 1786.6 $mg.m^{-2}$ in September 1994 to 3627.5 $mg.m^{-2}$ in October 1994 (Fig. 8.2c).

Total anchovy egg abundance was inversely related to atresia, with large total egg numbers at times of lowest levels of atresia (Fig. 8.3). The significance of this relationship improved and maintained its predictability with the inclusion of data from November Spawner Biomass Surveys (Fig. 8.3, Table 8.1).

The number of anchovy eggs was not directly related to copepod biomass (Fig. 8.4a). However, by including information on the preferential food size (large copepods) and optimal spawning habitat (16-19 $^{\circ}C$ water), there was a significant positive relationship between total anchovy egg abundance and food availability (Fig. 8.4b, Table 8.1). This relationship improved when data from November Spawner Biomass surveys were included (Fig. 8.4b, Table 8.1). March 1994 and March 1995 are included in the figures but were excluded from the analysis because spawning had already ceased and had therefore been decoupled from food availability (Figs 8.1, 8.2).

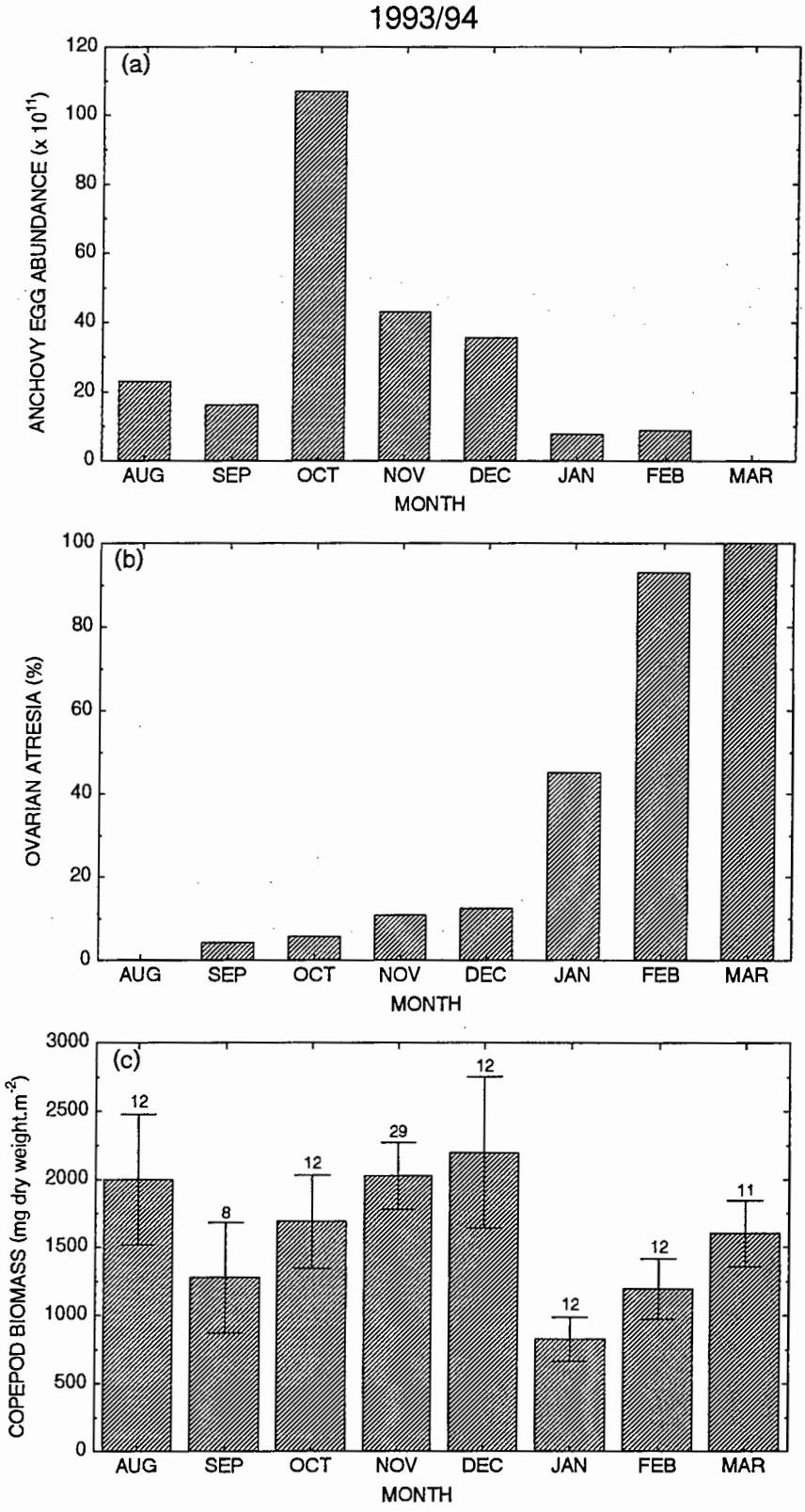


Fig. 8.1. The 1993/94 anchovy spawning season showing intra-seasonal variability in (a) total anchovy egg abundance (eggs x 10^{11}), (b) levels of anchovy atresia (%), and (c) copepod biomass (mean ± standard error, mg dry weight.m^{-2}) on the western Agulhas Bank. The number of stations sampled each month are shown. September 1993 had an artificially small biomass (see text).

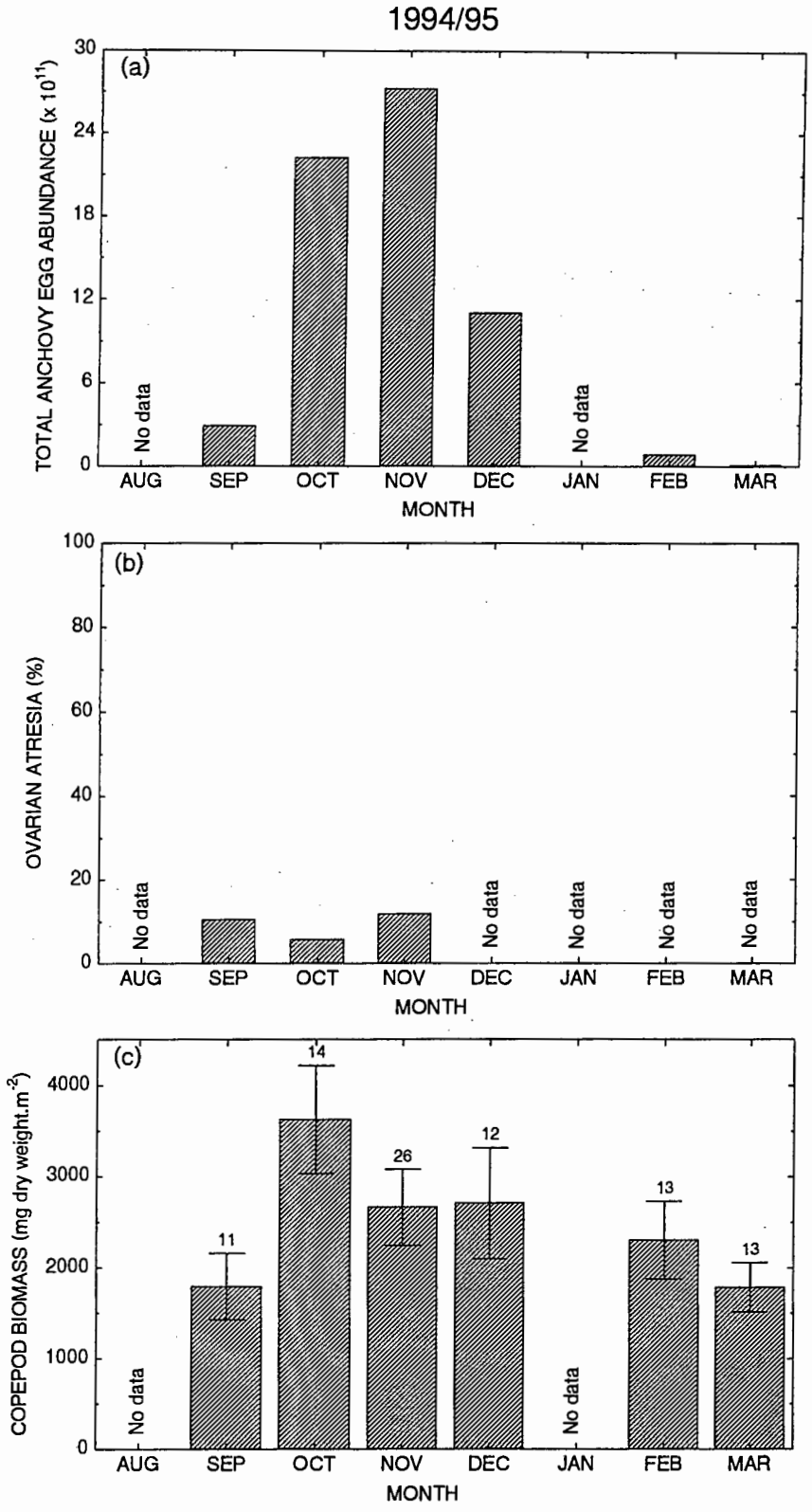


Fig. 8.2. The 1994/95 anchovy spawning season showing intra-seasonal variability in (a) total anchovy egg abundance (log eggs x 10^{11}), (b) anchovy atresia (%), and (c) copepod biomass (mean ± standard error, mg dry weight.m^{-2}). The number of stations sampled each month are shown.

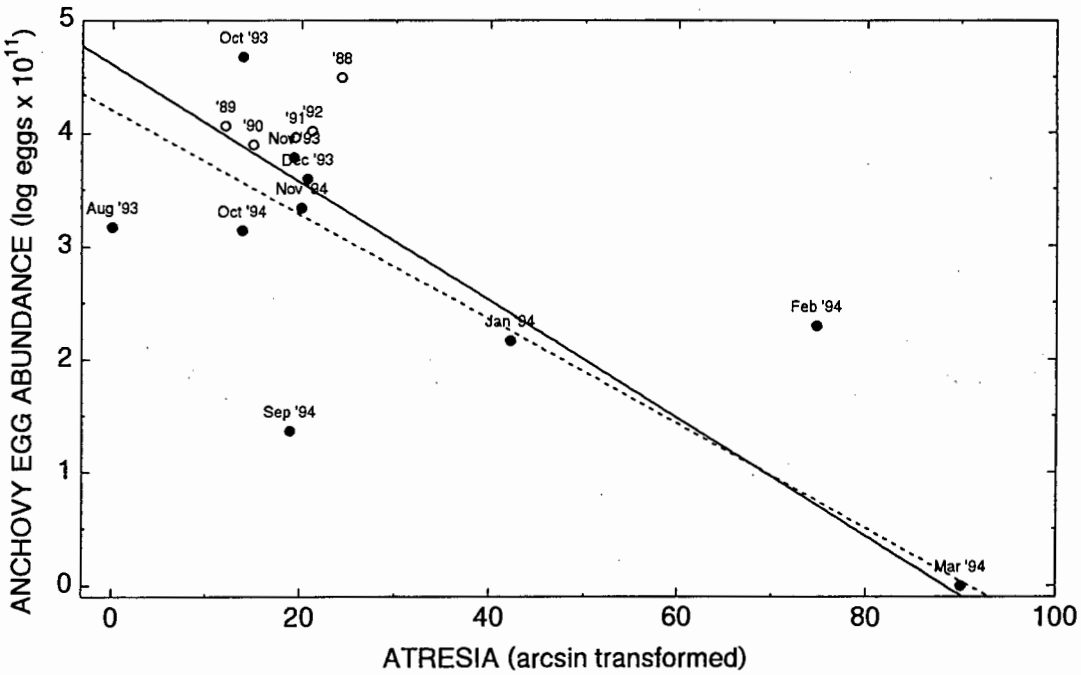


Fig. 8.3. The relationship between anchovy egg abundance (log eggs x 10^{11}) and ovarian atresia (transformed as in Table 8.1). A strong negative relationship was found for the SARP data (closed circles, dotted line), which increased in significance when estimates from November Spawner Biomass Surveys were included (open circles, solid line). Details of equations in Table 8.1.

Table 8.1. Functional regression analyses between total anchovy egg abundance (log eggs x 10^{11}) and anchovy atresia and large copepod biomass in 16-19 °C water for data from SARP only, and SARP and November Spawner Biomass Surveys together. The equation, 95% confidence interval (CI) for the regression slope (b'), proportion of the variance explained (r^2), and number of data points (n) are given. Significance levels are $^{*}p < 0.05$ and $^{**}p < 0.01$.

INDEPENDENT VARIABLES	DATA	EQUATION	95% CI FOR b'	r^2	n
Anchovy atresia ($\arcsin\sqrt{\text{atresia}(\%)/100}$)	SARP	$y = 4.208 - 0.046x$	(-0.021, -0.074)	0.52^{*}	10
	SARP + NOVEMBER DATA	$y = 4.611 - 0.052x$	(-0.031, -0.075)	0.51^{**}	15
Large copepod biomass in 16-19 °C water (log mg dry weight.m^{-2})	SARP	$y = -6.845 + 3.373x$	(1.439, 5.547)	0.35^{*}	11
	SARP + NOVEMBER DATA	$y = -6.751+3.360x$	(1.889, 4.983)	0.41^{*}	15

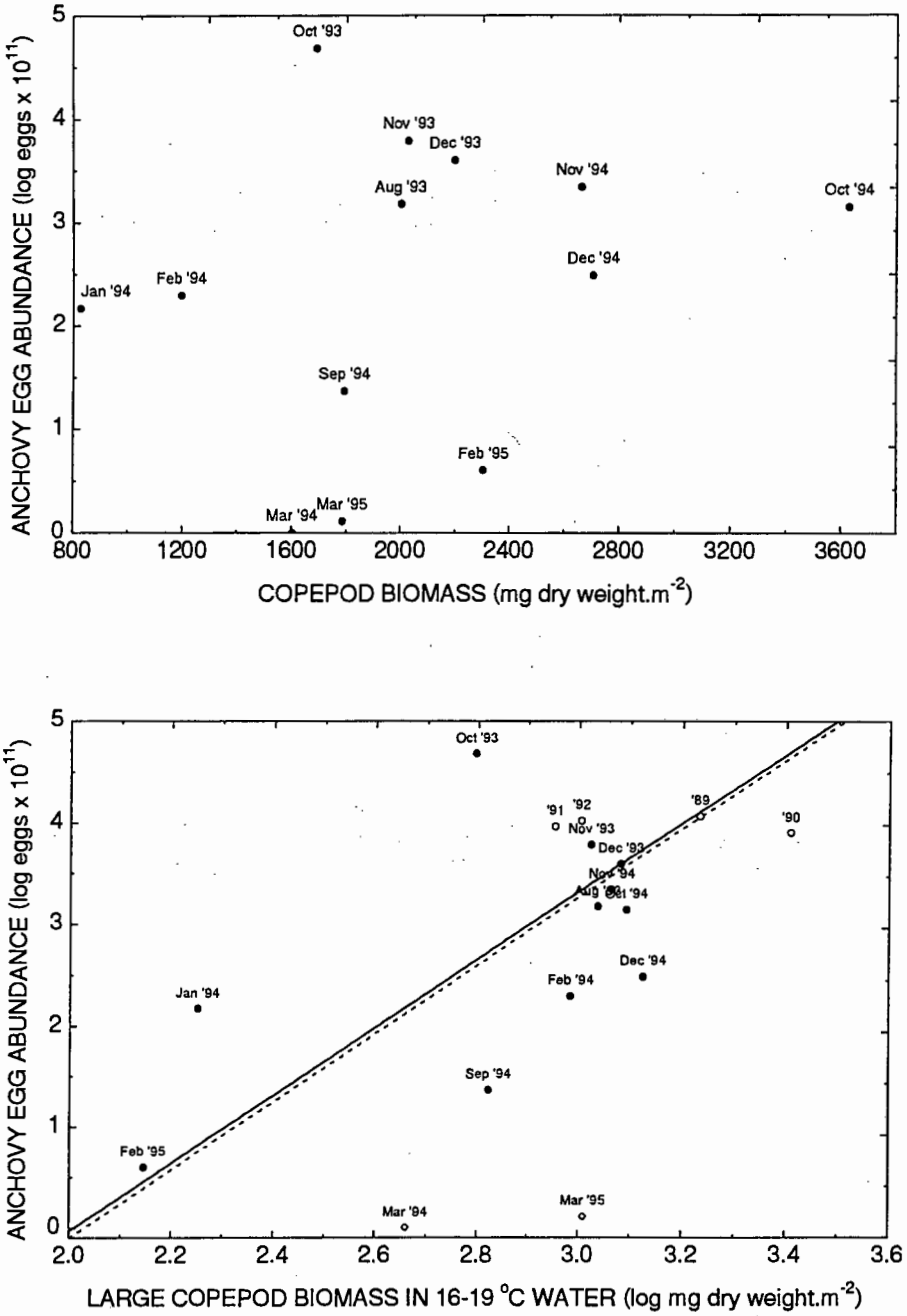


Fig. 8.4. The relationships between total anchovy egg abundance and (a) total copepod biomass and (b) biomass of large copepods in 16-19 °C water. The regressions are using the SARP data alone (solid circles, dotted line) and with the inclusion of November Spawner Biomass Surveys (open circles, solid line). March 1994 and 1995 are excluded from the regressions because anchovy had finished spawning. Details of equations in Table 8.1.

DISCUSSION

This study suggests that the spawning of anchovy is related to the availability of food of a preferred size (large copepods) within their optimal spawning temperature range (16-19 °C water). A number of studies have found increased fecundity at times of increased food ration. For example, fecundity of trout is negatively affected by a poor diet through its effect on atresia (Scott 1962; Bagenal 1969). In clupeoids fecundity may be significantly influenced by ration, including the bay anchovy (Peebles *et al.* 1996), the Japanese anchovy (Tsuruta and Hirose 1989), and herring (Bailey and Almatar 1989). A further consequence of poor food availability for anchovy could be increased egg cannibalism (Valdés Szeinfeld and Cochrane 1992). Therefore, the variable food environment during spawning and its subsequent effect on fecundity could contribute to variation in the stock-recruitment relationship (Bagenal 1973; Rothschild 1986).

Estimates of food availability throughout the anchovy spawning season allow critical periods to be identified. For example, the poor food environment for anchovy in January 1994 was the probable cause of the sharp increase in gonad atresia, a decline in their spawning activity, and a shortening of their spawning season. The level of copepod biomass in January 1994 was similar to the small biomass observed on the western Agulhas Bank in November 1988, which contributed to the subsequent recruitment failure of anchovy in 1989 (Peterson *et al.* 1992, Melo 1994a, Cochrane and Hutchings 1995). Food is especially important to the spawning of anchovy later in the season when their fat reserves become depleted (Hutchings 1992, Hunter and Leong 1981). Therefore, the meagre biomass in January 1994 could have contributed to the recruitment failure of 1994. For the spawning of the Cape anchovy during the 1993/94 season, the extent of the spawning season could have been further reduced by the late onset of spawning of many individuals as a result of the recruits from the previous year being considerably smaller than normal (Hampton and Barange 1996).

Enhanced spawning at larger food densities, in terms of either increased batch fecundity or frequency of spawning, suggests that the duration of maximum spawning would be longer if good food conditions persist. Thus, it is postulated that there is better spawning in terms of the total number of eggs in years when there is a protracted favourable food environment. A shortened duration of spawning could increase recruitment variability, because prolonged serial spawning dampens the effect of unpredictable early-stage survival (Shelton 1987). The factors that cause fluctuations in copepod biomass on the western Agulhas Bank include growth, advective input, advective loss, and predation. These are discussed in detail in Chapters 9 and 10.

It is noteworthy that the total abundance of anchovy eggs is positively related to both the area of 16-

19 °C water (Chapter 7) and the density of large copepods within that area. This implies that there is a reduced density of large copepods in 16-19 °C water when there is a small area of this water, suggesting that a density-dependent mechanism may operate. This point will be discussed in detail in the next chapter which focuses on factors controlling the biomass of copepods on the western Agulhas Bank.

Finally, a caveat is necessary. The data presented here are highly seasonal and as such, significant spurious correlations can sometimes be found. This problem was minimized by only considering justifiable relationships and requiring that the relationships be repeatable. It must also be noted that the relationships presented in this chapter are sensitive to only a few data points, especially at the extremes. To validate these relationships, more data needs to be collected, particularly at the beginning and end of the spawning seasons when few cruises were conducted.

CHAPTER 9

EFFECTS OF ADVECTIVE LOSS AND ANCHOVY PREDATION ON THE VARIABILITY OF COPEPOD BIOMASS ON THE WESTERN AGULHAS BANK

ABSTRACT

Food in terms of copepod biomass on the western Agulhas Bank is important to the spawning of the Cape anchovy. This chapter assesses the effect of advective loss and predation by anchovy on the variability of copepod biomass in this region. The effect of predation by anchovy varied inter-annually, with a strong inverse relationship between the biomass of copepods and that of anchovy. This implies density-dependent competition for food on the western Agulhas Bank. Moreover, there was evidence of density-dependent predation by anchovy within the 1993/94 and 1994/95 spawning seasons: the biomass of large copepods, which are a favoured food item of anchovy, declined when the optimal habitat for anchovy spawning (16-19 °C water) contracted, whereas small copepods were unaffected. In contrast, advective loss, inferred from an index of current strength, negatively affected the biomass of both small and large copepods. Therefore, copepod biomass is smallest during intense upwelling when there is a strong front and a small area of 16-19 °C water. Maximum anchovy spawning coincides with the time of greatest biomass of copepods before the onset of active upwelling on the western Agulhas Bank.

INTRODUCTION

Spawning success of anchovy is related to the food available in terms of copepod biomass (see Chapter 8). As the acquisition of copepod biomass data is expensive and time-consuming to acquire, the underlying mechanisms responsible for its variability (in time and space) need to be understood if such data are to be used in a predictive manner. Four processes that could influence the biomass of copepods are growth, advective input, predation, and advective loss. Predation by anchovy and advective loss are the focus of the current chapter.

Predation could have a large impact upon the biomass of copepods. Anchovy spawners congregate in large numbers on the western Agulhas Bank (Hampton 1992) and may exert a heavy predatory pressure on the copepod populations (Peterson *et al.* 1992). Furthermore, the density of anchovy changes as the area of their optimal spawning habitat varies, with anchovy and copepods being more densely crowded when the area of 16-19 °C water is squeezed (Painting *et al.* submitted) between the cool (12 °C) upwelled water that migrates offshore during active upwelling and the warm water further offshore. Strong density-dependent predation could occur at these times.

Advective loss may also influence the biomass of copepods. Organisms that are transported in the jet current (Shelton 1984; Shelton and Hutchings 1990) from the western Agulhas Bank to the West Coast include pelagic eggs and larvae (Shelton and Hutchings 1982; Nelson and Hutchings 1987; Huggett *et al.* in press) and dinoflagellates (Pitcher and Boyd 1996). Advective loss of copepods to the South-Western Cape would be expected to be greatest during times of strong upwelling (Chapter 6, Fig. 6.6), when strong north-west currents are associated with the upwelling front (Largier *et al.* 1992). Conversely, during quiescent conditions the upwelling front submerges (Chapter 6, Fig. 6.7) and currents are weak and variable (Largier *et al.* 1992). This chapter assesses the veracity of advective loss and predation as processes controlling the biomass of copepods on the western Agulhas Bank.

MATERIALS AND METHODS

Copepod biomass on the western Agulhas Bank was measured monthly between August-March of 1993/94 and 1994/95 using the protocol detailed in Chapter 1. These data were supplemented by information from November Pelagic Spawner Biomass Surveys between 1988 and 1996. Biomass was calculated for two size classes, *viz.* small (<1.5 mm, total length, TL) and large copepods (>1.5 mm TL, see Chapter 1, Table 1.2 for sizes). Although there was an estimate of copepod biomass from November 1988, no estimate of size-fractionated biomass was available from this survey. Data from September 1993 were excluded from the analysis because many offshore stations, where copepod biomass is largest (Chapter 10, Fig. 10.1), were not sampled.

To investigate relationships between copepod biomass and independent variables, linear relationships were identified by functional regression (see Chapter 7). Only relationships that had a justifiable reason were tested. Relationships were considered repeatable if they remained significant when data from Pelagic Spawner Biomass Surveys were included.

The area of 16-19 °C water, estimated from satellite images as described in Chapter 7, was used as a measure of the extent of the optimal spawning habitat of anchovy. Potential advective loss was examined by regressing copepod density against frontal strength. Frontal strength, inferred from temperature gradient, was used as an index of advective flow. This was calculated from shipboard measurements of temperature every 2 miles along the survey grid during each cruise. The maximum frontal gradient ($^{\circ}C.mile^{-1}$) from the Walker Bay and Cape Agulhas transects was used as the estimate of north-westerly current strength (Chapter 7, Fig. 7.4, Fig. 7.5).

Anchovy biomass was measured acoustically during the Pelagic Spawner Biomass Surveys in

November for the years 1988-1996, with targets identified from *ad hoc* trawls (Painting *et al.* submitted). The potential effects of predation by anchovy on the population age structure of *Calanus agulhensis* were investigated in water of different temperatures, because anchovy exhibit a temperature preference. In 16-19 °C water, anchovy are common, whereas anchovy are present but less prevalent in water <16 °C. Conversely, anchovy are seldom found in water >19 °C (Painting *et al.* submitted).

RESULTS

The total biomass of copepods on the western Agulhas Bank was inversely related to the biomass of anchovy, with lowest copepod biomass at largest anchovy densities (Fig. 9.1a, Table 9.1). Moreover, the relationship was dependent upon copepod size. There was a poor, non-significant relationship between the biomass of small copepods and anchovy density (Fig. 9.1b), whereas there was a strong negative relation for large copepods (Fig. 9.1c).

The population age structure of *C. agulhensis* during SARP was related to water temperature. In water <16 °C, the size structure of *C. agulhensis* was slightly skewed towards smaller individuals, with 44% of the population being C4 or larger in size (Fig. 9.2a). In 16-19 °C water, the population size structure was more-severely skewed towards smaller individuals, with only 34% of the population being C4 or larger (Fig. 9.2b). In contrast, in water >19 °C where anchovy are seldom found, the age structure was skewed towards larger individuals, with more than 60% of the population being C4 or larger in size (Fig. 9.2c).

No relationship was evident between the biomass of small copepods in 16-19 °C water and the area of this water mass (Fig. 9.3a). For large copepods, there was a smaller biomass at times when there was a reduced area of 16-19 °C water (Fig. 9.3b). The data did not appear to fit a linear model, so the non-linear asymptotic Ivlev curve was fitted (Table 9.1). The predictability of this relationship remained high when data from November surveys were included (Table 9.1). Small copepod biomass is found when there is a small area of 16-19 °C water: this occurs later in the anchovy spawning season (January-March 1994 and 1995 in Appendix 1).

There was a strong inverse relationship between the total biomass of copepods and frontal gradient (Fig. 9.4a, Table 9.1). This association remained significant when data from the Pelagic Spawner Biomass Surveys in November were included (Fig. 9.4, Table 9.1). Both small (Fig. 9.4b) and large (Fig. 9.4c) copepods in 16-19 °C water were negatively related to temperature gradient (Table 9.1). Points at high frontal gradients and small copepod biomass are between January and March.

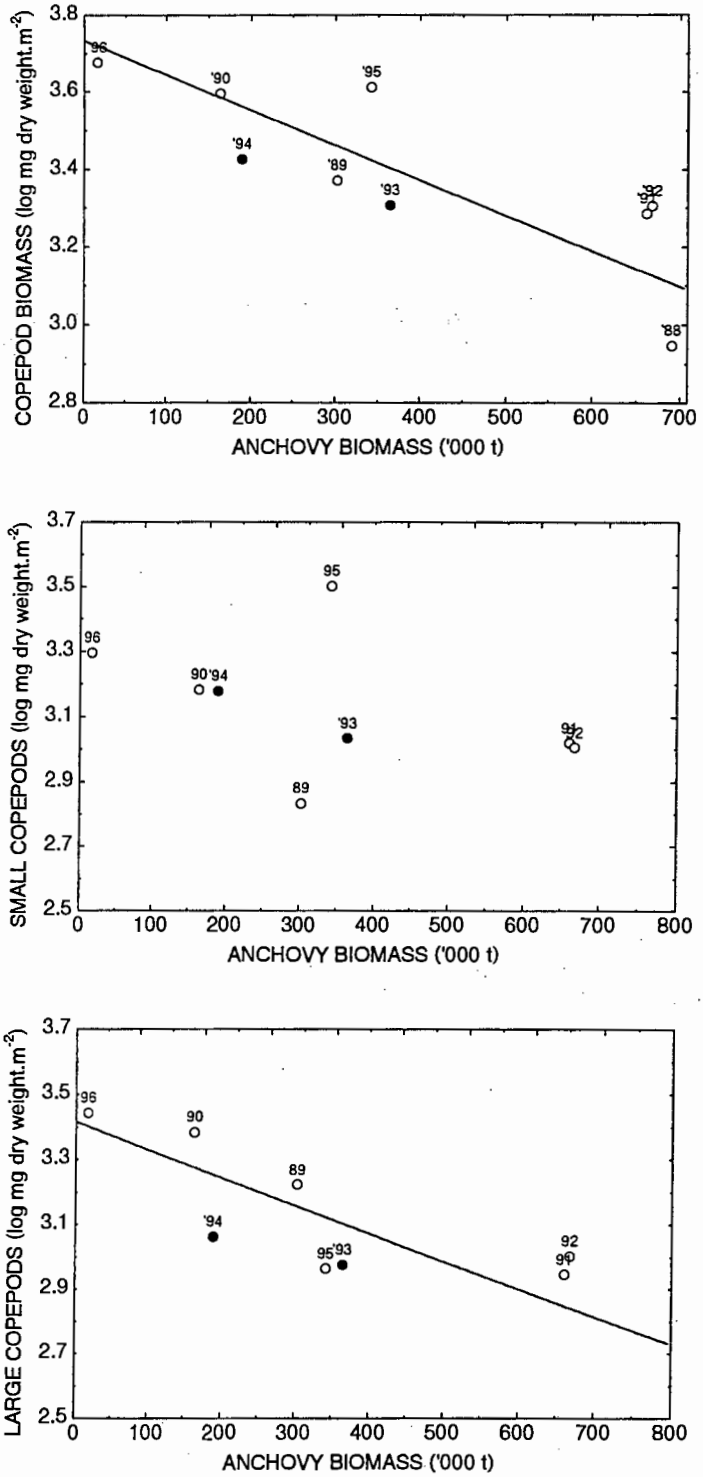


Fig. 9.1. The relationships between the biomass of anchovy and that of (a) total copepod biomass, (b) biomass of small copepods, and (c) biomass of large copepods on the western Agulhas Bank. Data are from SARP (solid circles) and other surveys (open circles). See Table 9.1 for details of the equations.

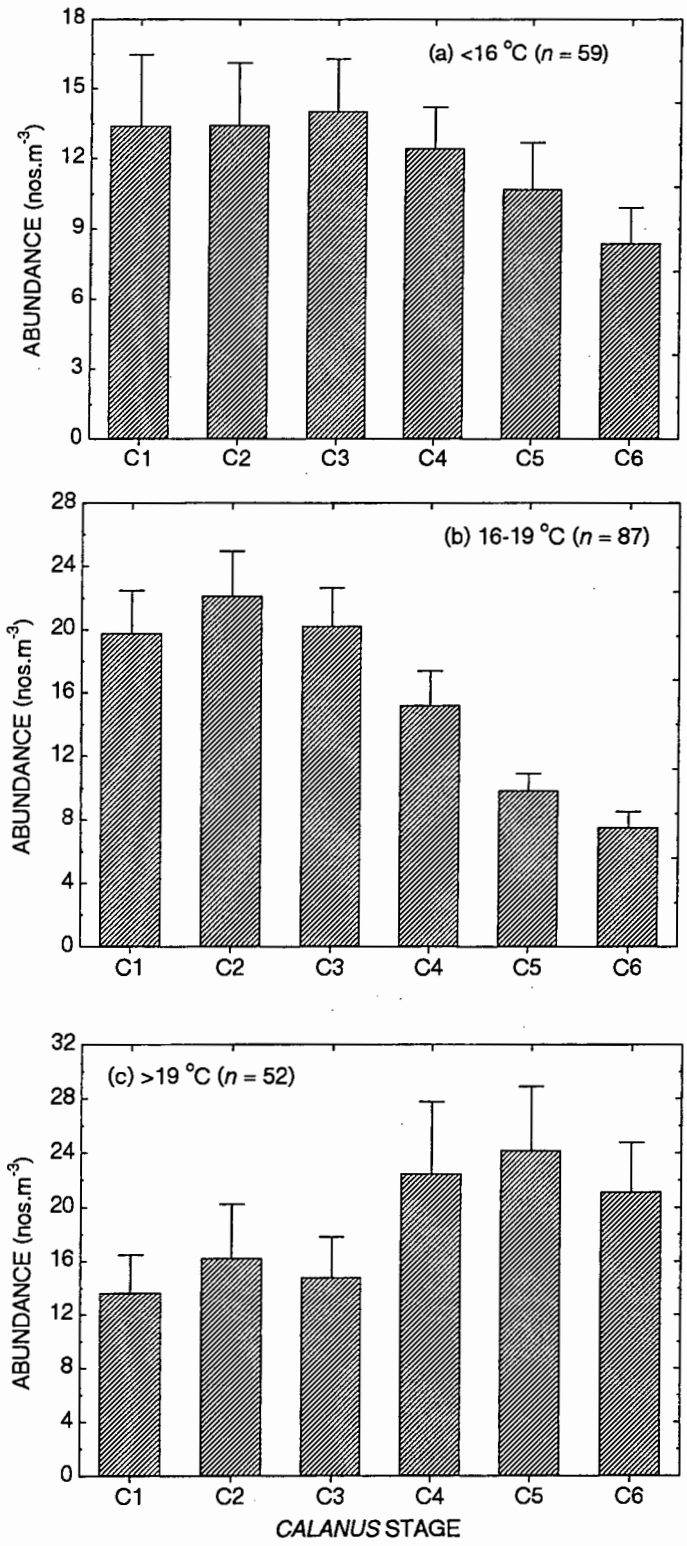


Fig. 9.2. The size distribution of *Calanus agulhensis* stages on the western Agulhas Bank, presented as mean density (nos.m^{-3}) ± standard error, in waters of (a) <16 °C (anchovy present), (b), 16-19 °C (anchovy common), and (c) >19 °C (anchovy rare). The number of samples is shown in brackets.

Table 9.1. Regression analysis of components of the copepod biomass against various independent variables: equations, 95% confidence interval (CI) for the regression slope (b'), proportion of the variance explained (r^2), and number of data points (n). $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, $^{n.s.}$ not significant. Functional regressions were used for the linear relationships.

DEPENDENT VARIABLE	INDEPENDENT VARIABLE	DATA	EQUATION	95% CI FOR b'	r^2	n
Copepod biomass (log mg dry weight.m^{-2})	Anchovy biomass ('000 t)	SARP + November Surveys	$y = 3.73473 - 0.000909x$	(-0.000451, -0.00141)	0.65^{**}	9
Biomass of small copepods (log mg dry weight.m^{-2})		SARP + November Surveys	___	___	$0.17^{n.s}$	8
Biomass of large copepods (log mg dry weight.m^{-2})		SARP + November Surveys	$y = 3.417148 - 0.00086x$	(-0.00033,-0.00145)	0.58^{*}	8
Biomass of small copepods in 16-19 °C water (log mg dry weight.m^{-2})	Area of 16-19 °C water (%)	SARP only	___	___	$0.02^{n.s.}$	13
		SARP + November Surveys	___	___	$0.02^{n.s.}$	19
Biomass of large copepods in 16-19 °C water (log mg dry weight.m^{-2})	Area of 16-19 °C water (%)	SARP only	$y = 3.070695(1-e^{-0.084571x})$	___	0.74	12
		SARP + November Surveys	$y = 3.147767(1-e^{-0.079547x})$	___	0.67	17
Copepod biomass (log mg dry weight.m^{-2})	Frontal strength (°C.mile^{-1})	SARP only	$y = 3.452489 - 0.29506x$	(-0.402580, -0.195026)	0.72^{***}	13
		SARP + November Surveys	$y = 3.114198 - 0.426624x$	(-0.588982, -0.277085)	0.46^{**}	20
Biomass of small copepods in 16-19 °C water (log mg dry weight.m^{-2})	Frontal strength (°C.mile^{-1})	SARP only	$y = 3.288769 - 0.32836x$	(-0.472800, -0.195861)	0.60^{**}	13
		SARP + November Surveys	$y = 3.286026 - 0.38100x$	(-0.554090, -0.223820)	0.28^{*}	19
Biomass of large copepods in 16-19 °C water (log mg dry weight.m^{-2})	Frontal strength (°C.mile^{-1})	SARP only	$y = 3.189727 - 0.58256x$	(-0.915850, -0.284107)	0.33^{*}	13
		SARP + November Surveys	$y = 3.26915 - 0.6795x$	(-0.968010, -0.415945)	0.37^{**}	19

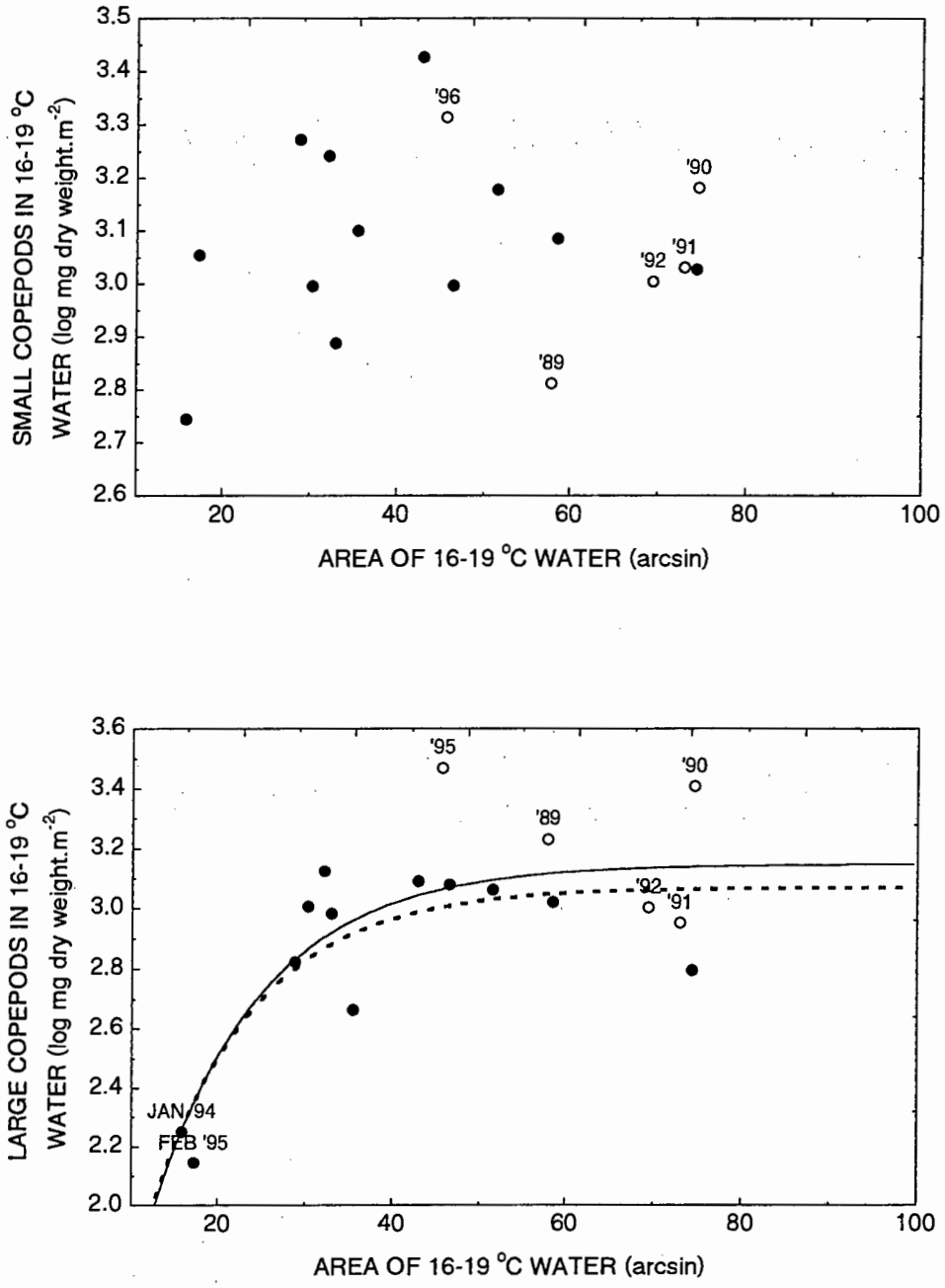


Fig. 9.3. The biomass of copepods (mg dry weight.m^{-2}) in relation to the total area of 16-19 °C on the western Agulhas Bank water for (a) small and (b) large copepods. See Table 9.1 for details of the equations.

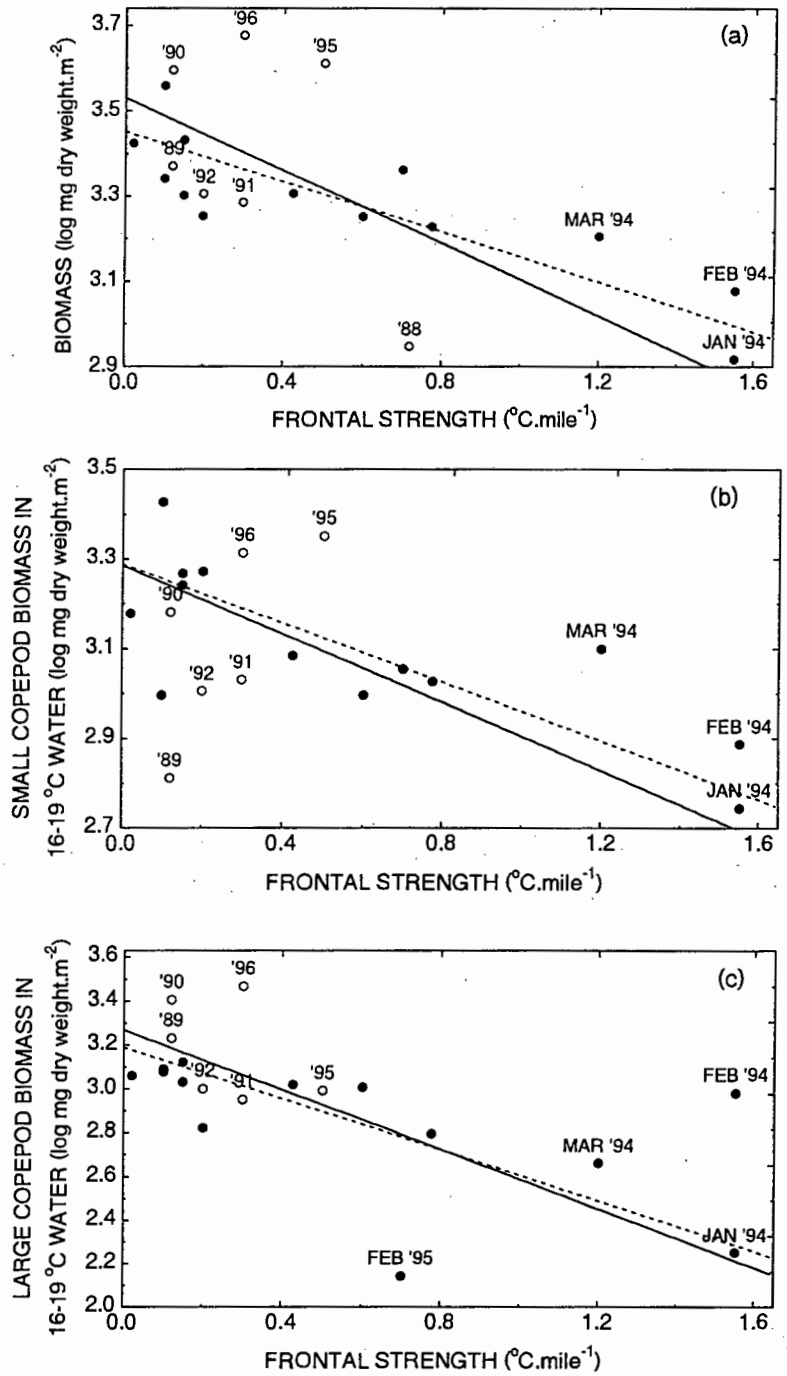


Fig. 9.4. The relationships between copepod biomass and temperature gradient for (a) all copepods, (b) small copepods in 16-19 °C water, and (c) large copepods in 16-19 °C with water. Data are from SARP (full circles, solid line) and Pelagic Spawner Biomass Surveys (open circles, dotted line). See Table 9.1 for details of the equations.

DISCUSSION

This study strongly suggests that a classic predator-prey relationship exists between anchovy and their major prey item (large copepods). Stock-recruitment models commonly assume density dependence, where recruitment is positively related to spawner biomass at small biomass levels, is independent of biomass at intermediate levels, and declines above the carrying capacity (Rothschild 1986). The present study shows that density-dependent mechanisms in terms of food supply are likely to operate on the anchovy spawning grounds. This relationship was hinted at by Cochrane and Hutchings (1995) who suggested that density-dependent competition for factors such as food or cannibalism could operate on the spawning grounds because of the (weak) inverse relationship between anchovy recruitment and the spawner biomass of the previous year. At small anchovy densities the larger food ration for each spawner would enhance spawning. Conversely, at large anchovy densities, there is poorer food available for each spawner which would retard spawning.

The effect of density-dependent predation may be intensified by the area of 16-19 °C water. When this area is small, anchovy and copepods are concentrated in this region, allowing anchovy to feed more efficiently on the dense food concentrations (James and Findlay 1989). Anchovy would then selectively ingest the larger food items in preference to the smaller particles. This may account for both the decline in the density of large copepods and the lack of a relationship between small copepods and the area of this water. The non-linear form of this equation implies that there may be a critical area of 16-19 °C water below which copepod biomass is heavily exploited. Furthermore, copepod populations would be slow to recover owing to the preferential removal of adults. Also, if anchovy are crowded when there is a small area of 16-19 °C water, there would be greater cannibalism on their eggs and larvae.

There also appears to be top-down control of the age structure of *C. agulhensis*. In water <19 °C where anchovy are present, the age structure is skewed towards younger stages, presumably because of predation-related mortality. In water >19 °C, however, the large *C. agulhensis* stages appear to be unexploited by anchovy. Although there is good production in this region (Chapter 7, Fig. 7.3), owing to its large copepod biomass (Chapter 7, Fig. 7.1), large copepods are growing slowly (Chapter 6, Fig. 6.3). Thus, the large population of copepods in this region is probably unsustainable by *in situ* egg production. The relative dominance of large individuals in this warm water is noteworthy: subadult copepods usually outnumber their adults by orders of magnitude in marine waters (Turner 1984). It is suggested that the large individuals in this warm water are advected into the region. This is discussed further in Chapter 10.

From an annual investigation of copepod biomass on the western Agulhas Bank, Pillar (1986) noted smaller biomass during summer than winter. This is counter-intuitive because upwelling and hence primary production is generally greater during summer (Probyn *et al.* 1994). Verheye *et al.* (1994) attributed the decrease during summer to increased anchovy predation. The findings of the present study support this contention. The greater mean copepod biomass in the 1994/95 season than for 1993/94 (t = 3.71, df = 195, $p < 0.001$) could be a result of the reduced predation pressure by spawning anchovy because of the poor anchovy recruitment in 1994 and the subsequent small spawning stock.

An additional explanation for the decline in copepod biomass during summer is advective loss. This transport to the adjacent South-Western Cape region away from the western Agulhas Bank would increase during summer because upwelling winds are maximal (Jury 1988) and the upper mixed layer is shallowest (Chapter 7, Figs 7.4, 7.5). It is noteworthy that advective loss on the western Agulhas Bank appeared to act on both small and large copepods, because both were negatively related to an index of advective current loss, whereas the effect of predation on large copepods impacted mainly on large copepods. It is unknown to what extent the vertical migratory behaviour of copepods (Verheye *et al.* 1992) influences advection of small and large individuals.

It is postulated that during persistent upwelling events, the upwelling front and its associated jet current intensifies, increasing the advective loss of copepods and reducing the biomass of copepods in the region. Concurrently, the front migrates offshore, reducing the area of 16-19 °C water, and more large copepods are removed by anchovy predation. These conditions are more-frequent in summer, although reasonably frequent periods of downwelling may reduce advective loss at these times. In contrast, there is a large area of 16-19 °C water and weak fronts during the spring period, both favouring enhanced biomass of copepods (Chapter 7, Fig. 7b). These mechanisms are plausible explanations for the relationship between 16-19 °C water and good spawning by anchovy. Thus, thermal imagery could be a useful tool for monitoring both the area of 16-19 °C water and frontal strength, to provide insight into the time scales of variability of the food resource for spawning anchovy.

CHAPTER 10

THE RELATIVE EFFECTS OF COPEPOD GROWTH, ADVECTION, AND PREDATION ON COPEPOD POPULATIONS OF THE WESTERN AGULHAS BANK

ABSTRACT

The Cape anchovy *Engraulis capensis* spawns serially between September and February each year, predominantly on the western Agulhas Bank. This energetically intensive reproductive strategy requires sufficient food in the form of copepods. Copepod biomass on the anchovy spawning grounds is variable, both inter-annually and within a spawning season. Four processes could account for this variability: predation, growth, advective export, and import. To evaluate the relative importance of these processes during the 1993/94 and 1994/95 anchovy spawning seasons, a mass-balance model of copepod biomass using information on their growth rates and predation by fish and invertebrates was constructed. Three periods were included in the model because copepod growth rates varied intra-annually, *viz.* September/October, November/December, and January/February. The model calculated the amount of "excess" production needed to balance growth, consumption, and the increase or decrease of biomass from one time period to the next. The output from this model shows that the *in situ* production by copepods (biomass × growth rate) usually provided sufficient food for pelagic predators (fish and invertebrates). Total copepod production did not vary substantially within the two anchovy spawning seasons (522.9 mg dry weight.m^{-2}.d^{-1} in September/October, 460.1 mg dry weight.m^{-2}.d^{-1} in November/December, and 483.7 mg dry weight.m^{-2}.d^{-1} in January/February), because growth rates were generally slow at times when large copepods dominated and *vice versa*. Average consumption by predators during 1993/94 and 1994/95 generally decreased through the spawning season from 336.1 mg dry weight.m^{-2}.d^{-1} in September/October to 185.7 mg dry weight.m^{-2}.d^{-1} in January/February. The model calculated the unaccounted for production, which is the extra production in the region which has not been ingested by predators or accounted for by the fluctuation in biomass. This quantity varied intra-seasonally, being small in September/October (183.6 mg dry weight.m^{-2}.d^{-1}), larger in November/December (251.9 mg dry weight.m^{-2}.d^{-1}), and greatest in January/February (293.7 mg dry weight.m^{-2}.d^{-1}). Most of the "excess" production was probably removed by advection, because production was still in "excess" of predatory losses even at consumption rates of twice the daily ration for all the pelagic fish predators. It is postulated that the western Agulhas Bank has a consistently high biomass of large copepods that promotes successful spawning of anchovy, because both small and large copepods are removed by advection from the region and these are replaced mainly by large individuals advected across from the eastern Agulhas Bank.

INTRODUCTION

Copepods are an important source of food for pelagic fish. In particular, the biomass of copepods appears to be critical to the successful spawning of anchovy (Chapter 7, Chapter 8, Peterson *et al.* 1992, Cochrane and Hutchings 1995), with low food availability causing ovarian atresia (Chapter 8, Melo 1994a, Peterson *et al.* 1992). Understanding the factors that control the dynamics of copepod populations on the western Agulhas Bank should provide insight into the spawning success of anchovy. The copepod biomass on the western Agulhas Bank fluctuates substantially (Chapter 2), in response to a number of processes that positively or negatively impact populations. Firstly, growth rates of copepods which are important to the maintenance of copepod populations, vary depending on body size and environmental factors. Secondly, predation by anchovy appears to reduce the biomass of copepods in the region and could vary within a season considerably (Chapter 9). Thirdly, advective export of copepods from the area could reduce local populations to varying degrees throughout the anchovy spawning season (Chapter 9). Lastly, local copepod populations could be maintained by input from the large copepod densities on the adjacent eastern Agulhas Bank (Largier *et al.* 1992; Hutchings *et al.* 1995), which could also vary intra-seasonally. This input could be through diffusive transport from the greater copepod biomass on the eastern Agulhas Bank (Peterson *et al.* 1992), or through advective transport *via* inshore currents, shelf-edge currents, or movement of thermocline water from east to west (Largier *et al.* 1992; Boyd *et al.* 1994).

This chapter explores the relative magnitudes of these four processes and their effect on the copepod populations of the western Agulhas Bank. Although many of the processes that govern the biomass of copepods are physically driven, the hydrography of the Agulhas Bank is complex because of its location between the cold, eastern boundary Benguela Current to the west and the warm, western boundary Agulhas Current to the east. As it is not readily amenable to physical modelling, a simple mass-balance approach using information on copepod growth and predation by fish and invertebrates was adopted. The model calculates the amount of "excess" production needed to balance growth, consumption, and the increase or decrease of biomass from one period to the next. The results from the model are discussed in terms of suitable spawning conditions for anchovy.

MATERIALS AND METHODS

Background

The region of interest is the western Agulhas Bank, from Cape Agulhas to Cape Point and extending to the 200 m isobath. The western Agulhas Bank is treated as a single box with variables averaged over all stations. The units of the mass-balance model are mg dry weight.m^{-2}.d^{-1}. The model calculates the "excess" production (E) from the following equation:

$$B_{t+1} = B_t + P_{60} - C_{60} + E$$

where

B_t = copepod biomass at time t,

B_{t+1} = copepod biomass at time $t + 1$,

P_{60} = copepod production between time periods, *i.e.* 60 x daily production,

C_{60} = consumption of copepods by predators between time periods, *i.e.* 60 x daily consumption.

The model spans the period from September to February of 1993/94 and 1994/95. As growth rates of large copepods in the region exhibit a bimodal pattern (see Chapter 6), three periods were used in the model, *viz.* September/October, November/December, and January/February.

Copepod biomass

Copepod biomass was measured by the procedures described in Chapter 1. Copepod species were separated into size categories, equivalent to the sizes of *Calanus agulhensis* developmental stages (Chapter 7, Table 7.1). The biomass of copepods in each of these size-classes (Chapter 6) was averaged within each of the three periods (Table 10.1). The non-calanoid copepods (*Corycaeus* spp., *Corycella* spp., harpacticoids, *Oithona* spp., and *Oncaea* spp.) were placed in a separate compartment because growth rates of these genera are slower than the similarly-sized *C. agulhensis* stage (see below). Males were not included in the model because they do not contribute to growth and they constituted only 8% of the total copepod biomass.

Copepod growth

The growth rates of *Calanus agulhensis* stages were estimated using bottle incubation techniques, as described in Chapter 1. Growth rates of these stages were applied to other species of similar size, because the growth rates of calanoid copepods in the southern Benguela system are not only related to body size, but also vary similarly in response to Chl *a* concentration for copepods of the same size (Chapter 5, Chapter 6). The estimates of growth rate for different calanoid size categories averaged for each of the three periods are shown in Table 10.2. Several species of cyclopoids and poecilostomatoids contribute substantially to the copepod biomass (Table 10.1) and thus need to be included in estimates of production. However, there are very few estimates of growth rate for these groups in the literature. If it is assumed that the ratio of the growth rates of female *Oithona* spp. and *Calanus* spp. are the same as the ratio of their population P/Bs from the study by McLaren *et al.*

Table 10.1. Biomass (mg dry weight.m^{-2}) used in the model for the different size groups (equivalent to developmental stages of *Calanus agulhensis*) during the three periods. NON-CAL = non-calanoid copepods (*Corycaeus* spp., *Corycella* spp., harpacticoids, *Oithona* spp., and *Oncaea* spp.).

	1993/94									1994/95								
PERIOD	N6	C1	C2	NON-CAL	C3	C4	C5	C6	TOTAL	N6	C1	C2	NON-CAL	C3	C4	C5	C6	TOTAL
Sep/Oct	3.6	4.0	633.4	281.9	20.1	135.0	227.5	52.9	1358.3	7.9	5.6	1089.5	792.5	41.8	105.1	333.1	34.9	2410.4
Nov/Dec	13.1	19.5	714.2	220.0	87.6	258.9	321.6	258	1689.9	6.4	9.4	851.8	471.9	86.9	248.2	433.1	53.6	2161.4
Jan/Feb	3.3	2.5	563.8	113.6	29.2	66.4	125.2	45.7	949.5	4.1	4.7	779.3	229.2	37.6	101.2	323.4	75.7	155.2

Table 10.2. Copepod growth rates (d^{-1}) used in the model for the different size groups (equivalent to *Calanus agulhensis* developmental stages) during the three periods. NON-CAL = non-calanoid copepods (*Corycaeus* spp., *Corycella* spp., harpacticoids, *Oithona* spp., and *Oncaea* spp.).

	1993/94								1994/95							
PERIOD	N6	C1	C2	NON-CAL	C3	C4	C5	C6	N6	C1	C2	NON-CAL	C3	C4	C5	C6
Sep/Oct	0.566	0.445	0.287	0.126	0.289	0.394	0.251	0.042	0.566	0.659	0.439	0.150	0.216	0.317	0.135	0.050
Nov/Dec	0.566	0.492	0.365	0.086	0.171	0.125	0.048	0.029	0.566	0.532	0.485	0.068	0.191	0.172	0.072	0.023
Jan/Feb	0.566	0.784	0.678	0.274	0.398	0.453	0.113	0.091	0.566	0.667	0.567	0.179	0.352	0.344	0.090	0.060

(1989), the growth rate of non-calanoid copepods (mainly *Oithona* and *Oncaea* adults) is three times faster than *Calanus agulhensis* females. The genera *Corycaeus* and *Oncaea* are of a similar size to *Oithona* in terms of total length and until recently all were classified in the order cyclopoida (Raymont 1983). On this basis, and until estimates of their growth rate become available in the literature, *Corycaeus* spp., *Corycella* spp., and *Oncaea* spp. were assumed to grow at rates equivalent to *Oithona* spp. (Table 10.2). In the absence of data on growth rates of harpacticoids, they were also assumed to grow at rates equivalent to *Oithona* spp.

Predation

Predation was assumed to be the only source of mortality, as female copepods can live for several months when predators are absent (Borchers and Hutchings 1986; Hirche 1990).

Invertebrates - A number of invertebrate predators in the southern Benguela system are almost exclusively carnivorous, feeding mainly on copepods. These include chaetognaths, decapods, scyphozoans, siphonophores, ctenophores, and hydromedusae (Gibbons *et al.* 1992). Generally, these taxa are present at low densities on the western Agulhas Bank (Gibbons *et al.* 1992), implying small predatory impact on copepod populations. Their combined effect on copepods in the standard model was assumed to be 5% of the standing stock of copepods per day (M. J. Gibbons, University of the Western Cape, pers. comm.).

Fish - Pelagic fish predators of copepods included in the model were anchovy *Engraulis capensis*, sardine *Sardinops sagax*, round herring *Etrumeus whiteheadi*, and horse mackerel *Trachurus trachurus capensis*. Pelagic fish densities on the western Agulhas Bank during the 1993/94 and 1994/95 SARP seasons are shown in Table 10.3 (SFRI, unpublished data). The densities of anchovy, sardine, and round herring were measured acoustically during each SARP cruise, with target validation by *ad hoc* trawling. Estimates of horse mackerel density were obtained from routine demersal fish stock assessment surveys aboard F.R.S. *Africana* during January 1994 and 1995. As there is no information on intra-annual changes in horse mackerel density, the January estimate was also used for the other periods. These data on fish densities, obtained in units of g wet weight.m^{-2}, were converted to dry weight.m^{-2} assuming a dry:wet weight ratio of 0.3 (James and Findlay 1989).

To estimate the consumption of copepods by pelagic fish, the daily ration of each species and the proportion of copepods in their diet are required. Estimates of daily ration were obtained from the literature (Table 10.4) and were converted to units of percentage dry food ingested per dry body mass using a ratio of dry to wet weight of copepods of 0.15 (Beers 1966). Each fish species considered has

Table 10.3. Densities (mg dry weight.m^{-2}) of anchovy, sardine, round herring, and horse mackerel on the western Agulhas Bank for the three periods of interest. The density of horse mackerel was kept constant (see text).

	1993/94					1994/95				
PERIOD	ANCHOVY	SARDINE	ROUND HERRING	HORSE MACKEREL	TOTAL	ANCHOVY	SARDINE	ROUND HERRING	HORSE MACKEREL	TOTAL
Sep/Oct	6226	5352	8998	525	21101	3323	25814	808	175	30120
Nov/Dec	4866	3579	1313	525	10282	3121	4308	2608	175	10212
Jan/Feb	5378	5404	525	525	11832	1214	10691	801	175	12881

a different proportion of copepods in their diet; the values assumed for the standard model are shown in Table 10.4. Predation by juvenile hake on copepods was assumed to be negligible because young hake feed preferentially on euphausiids and amphipods, with copepods constituting only a very small proportion of their diet (Pillar and Barange 1993).

Sensitivity analysis

A sensitivity analysis was conducted on the parameters in the model. The daily ration of pelagic fish predators and the consumption rate of invertebrate predators were halved and doubled one at a time (Platt *et al.* 1981), and the effect on the output was observed. The proportion of copepods in the diet for each species was varied between 0.5 and 1.

RESULTS

Variation of copepod production from September to February is shown in Table 10.5. There was substantially greater production in 1994/95 than 1993/94. Production was relatively constant throughout both the 1993/94 season (340.7-380.9 mg dry weight.m^{-2}.d^{-1}) and the 1994/95 season (553.0-705.0 mg dry weight.m^{-2}.d^{-1}). Production by *Calanus agulhensis* constituted 11-25% of the total copepod production. Small calanoid copepods (including *Clausocalanus* spp., *Paracalanus* spp., *Ctenocalanus* spp., and *Centropages brachiatus*, see Peterson *et al.* 1992) constituted 39-66% of the production. Most of the copepod production was in the smaller size classes (Fig. 10.1), with 55-79% of the production derived from animals in the *C. agulhensis* C2 size-class (about 1000 μm). The C4-C6 size fraction constituted only 14-34% of the total production.

There was considerable intra-seasonal variability in the consumption of copepods by pelagic and invertebrate predators (Fig. 10.2). Predation generally decreased from September to February, from 300.4 to 176.2 mg dry weight.m^{-2}.d^{-1} in 1993/94 and from 371.8 to 195.1 mg dry weight.m^{-2}.d^{-1}. This was a consequence of a smaller biomass of fish later in the season, coupled with the smaller copepod biomass in January/February, so that invertebrates consumed less (because their consumption was assumed to be a constant fraction of the copepod biomass). Anchovy consumed 73.2 mg dry weight.m^{-2}.d^{-1} of copepods in November/ December 1993 and only 46.9 mg dry weight.m^{-2}.d^{-1} in November/December 1994 (Fig. 10.2), a consequence of the relatively small density of anchovy (Table 10.3). In contrast, consumption by sardine was greater in 1994/95 than in 1993/94, because of its larger density. The effect of predation by round herring on copepods is small, except for September/October 1993, whereas consumption by horse mackerel was insignificant. Invertebrates, however, were important predators, at times consuming as much copepod production as all the pelagic fish combined (Fig. 10.2).

Table 10.4. Daily ration and the proportion of the diet that consists of copepods for the four pelagic fish included in the model. Daily ration requirements are presented in terms of the percentage of dry food weight as a percentage of dry fish weight, assuming a ratio of dry to wet fish weight of 0.3 (James *et al.* 1989) and a dry to wet weight ratio for copepods of 0.15 (Beers 1966).

	ANCHOVY	SARDINE	ROUND HERRING	HORSE MACKEREL
DAILY RATION	0.0188[1]	0.01[2]	0.014[3]	0.019[4]
PROPORTION OF COPEPODS IN THE DIET	0.8[5]	0.7[6]	0.75[7]	0.54[8]

[1] James (1987)

[2] van der Lingen (in press)

[3] C.D. van der Lingen, SFRI, pers. comm.

[4] Pillar and Barange (in press)

[5] estimated from James (1987) for spawning anchovy

[6] sardine are more phytoplanktivorous than anchovy (van der Lingen 1994)

[7] round herring are predominantly zooplanktivorous (Wallace-Fincham 1987)

[8] from Pillar and Barange (in press), assuming that copepods were present in the unidentifiable crustacean fragments as they were in the gut contents

Table 10.5. Copepod production (mg dry weight.m^{-2}.d^{-1}) estimated in the present study (1993/94 and 1994/95) and by Peterson *et al.* (1992) in November of 1988 and 1989. Small calanoid copepods include *Clausocalanus* spp., *Paracalanus* spp., *Ctenocalanus* spp., and *Centropages brachiatus* (see Peterson *et al.* 1992). The "Other copepods" category includes *Calanoides carinatus*, *Corycaeus* spp., *Corycella* spp., *Oithona* spp., *Oncaea* spp., *Pleuromamma* spp., *Metridia lucens*, and *Rhincalanus nasutus*.

	1993/94				1994/95				1988			1989		
PERIOD	*Calanus*	Small calanoids	Other copepods	Total	*Calanus*	Small calanoids	Other copepods	Total	*Calanus*	Small calanoids	Total	*Calanus*	Small calanoids	Total
Sep/Oct	83.8	127.8	129.1	340.7	76.4	371.4	257.2	705.0	_	_	_	_	_	_
Nov/Dec	89.7	179.5	97.9	367.2	110.9	326.2	115.9	553.0	47.3	80.3	127.6	49.3	137.2	186.5
Jan/Feb	52.8	235.9	92.2	380.9	92.8	345.2	148.4	586.4	_	_	_	_	_	_

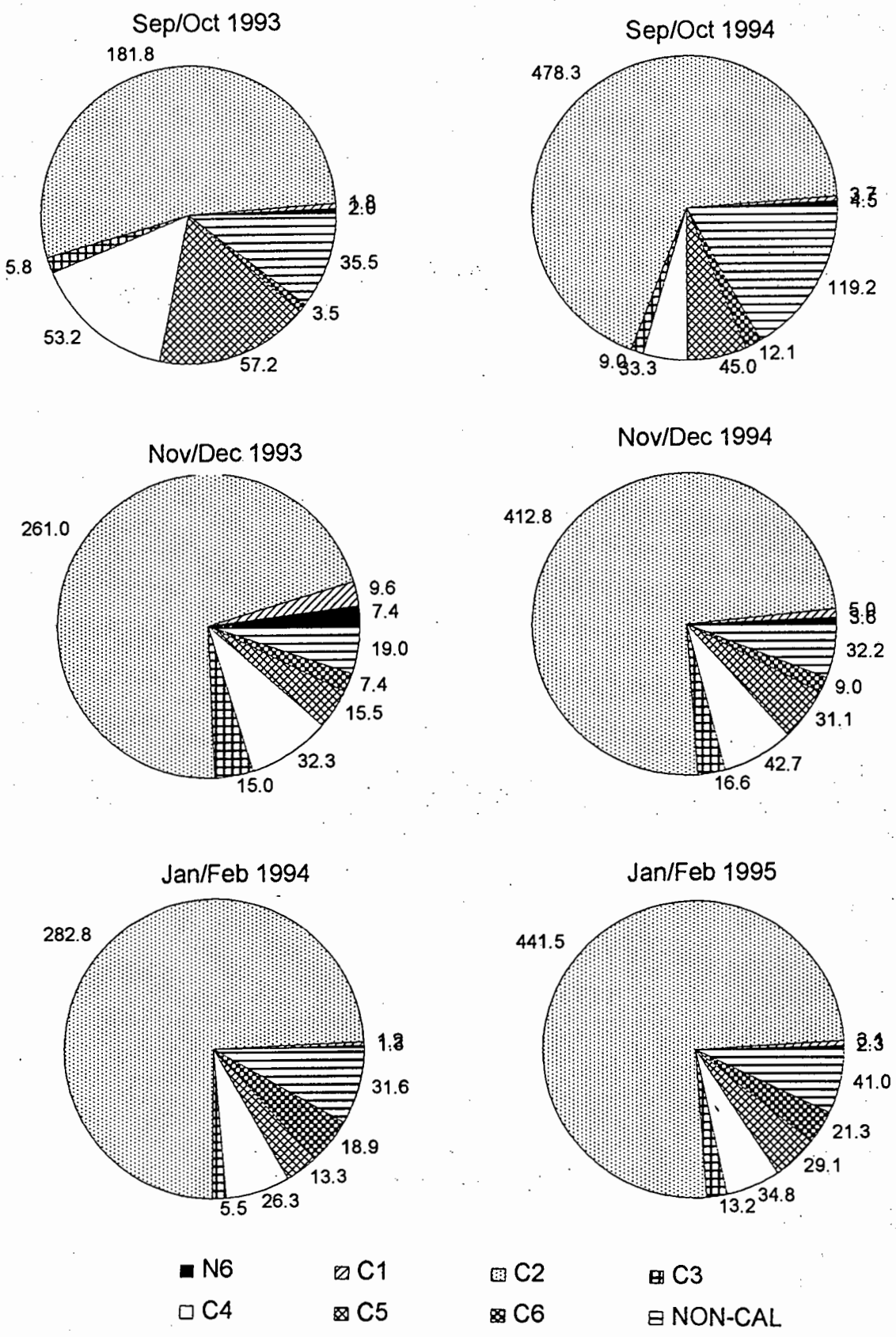


Fig. 10.1. Copepod production rates (mg dry weight.m^{-2}.d^{-1}) of the equivalent *Calanus agulhensis* size categories for the three periods in 1993/94 (left) and 1994/95 (right). NON-CAL = non-calanoid copepods.

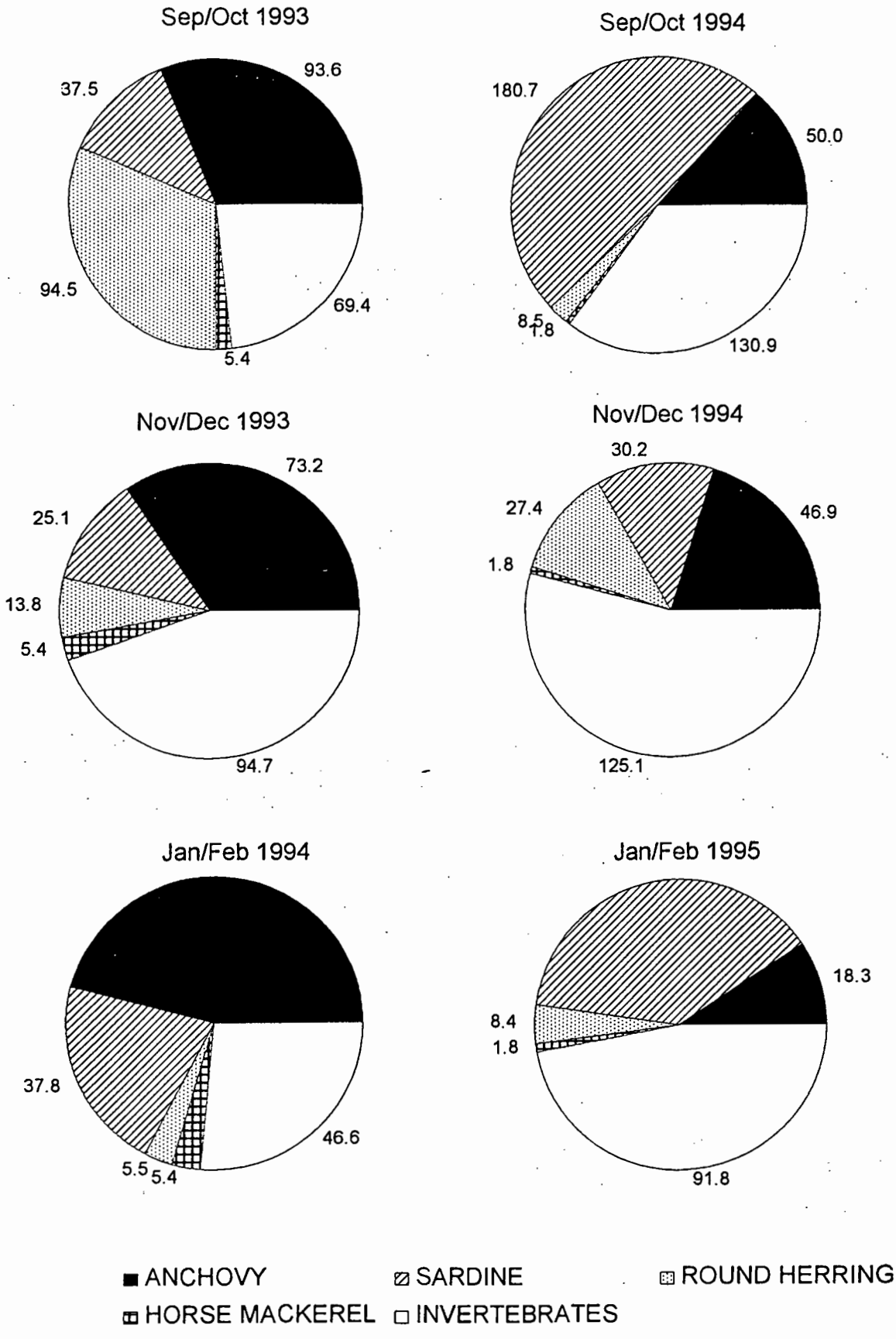


Fig. 10.2. Consumption rates (mg dry weight.m^{-2}.d^{-1}) of copepods by predators for the three periods within 1993/94 (left) and 1994/95 (right).

Consumption, production, and the amount of "excess" production for each of the periods using the standard parameter values are shown in Table 10.6. Production always exceeded predation. The "excess" production, averaged for 1993/94 and 1994/95, varied intra-seasonally: it was smallest in September/October (183.6 mg dry weight.m^{-2}.d^{-1}), increased in November/December (251.9 mg dry weight.m^{-2}.d^{-1}), and was largest in January/February (293.7 mg dry weight.m^{-2}.d^{-1}).

Although varying the maintenance ration of pelagic fish sequentially by a factor of 0.5 and 2 changed the magnitude of the "excess" production, the same seasonal trend, with greater "excess" production toward the end of the anchovy spawning season, was evident for both 1993/94 (Table 10.7) and 1994/95 (Table 10.8). Negative values of "excess" production imply that there was insufficient production to account for the effect of predation and changes in copepod biomass. Thus, only in September/October 1993 was there a possibility of copepod production not fulfilling the requirements of pelagic predators (Table 10.7). The model was particularly sensitive to anchovy biomass in 1993/94 and sardine biomass in 1994/95. Invertebrate predation had a substantial influence on the amount of "excess" production (Table 10.9). At high levels of invertebrate predation in September/October 1993, there could be insufficient production to fulfil both consumption and the changes in copepod biomass. However, the same general pattern of an increase in "excess" production from September/October to January/February is found.

DISCUSSION

The mass-balance model suggests that copepod production is in "excess" of consumption on the western Agulhas Bank, and that the magnitude of this difference varies intra-seasonally. There is generally an increase in the magnitude of "excess" copepod production, even with widely varying parameter values. It is postulated that this "excess" production is lost from the region through advection. Many planktonic organisms are advected from the western Agulhas Bank, including pelagic eggs and larvae (Shelton and Hutchings 1982; Nelson and Hutchings 1987; Huggett *et al.* in press), dinoflagellates (Pitcher and Boyd 1996), and copepods (Chapter 9).

It is concluded that the production of copepods is usually adequate to satisfy the energetic demands of anchovy throughout their spawning season. This finding is similar to that of Hutchings *et al.* (1995) who found that there was sufficient food for anchovy in November of 1990-1992. The only time that anchovy appeared to be severely food limited during November was in 1988, when Peterson *et al.* (1992) suggested that the *in situ* production of copepods in the region was insufficient to offset anchovy predation.

Table 10.6. Results from the standard model showing the copepod production, total predation by pelagic fish and invertebrates combined, and the "excess" production (mg dry weight.m^{-2}.d^{-1}) in each period for 1993/94 and 1994/95.

	1993/94			1994/95		
PERIOD	PRODUCTION	PREDATION	"EXCESS"	PRODUCTION	PREDATION	"EXCESS"
Sep/Oct	340.7	300.4	32.0	705.0	371.8	335.1
Nov/Dec	367.2	212.0	171.1	553.0	231.4	332.7
Jan/Feb	380.9	176.2	186.4	586.4	195.1	401.0

Table 10.7. The "excess" production for 1993/94 from the sensitivity analysis of the maintenance ration for pelagic fish (twice parameter value, half parameter value) and the percentage of the diet consisting of copepods (100, 50%). ALL indicates all parameters changed simultaneously. Note that negative values of "excess" production imply that there was insufficient production to account for the effect of predation and changes in copepod biomass. See Table 10.4 for the parameter values of the standard model.

	MAINTENANCE RATION					% OF COPEPODS IN DIET			
PERIOD	ANCHOVY	SARDINE	ROUND HERRING	HORSE MACKEREL	ALL	ANCHOVY	SARDINE	ROUND HERRING	HORSE MACKEREL
Sep/Oct	-61.7, 78.8	-5.5, 50.7	-62.5, 79.2	26.6, 34.7	-199.0, 147.5	8.6, 67.1	15.9, 42.7	0.5, 63.5	27.4, 32.4
Nov/Dec	98.0, 207.7	146.1, 183.7	157.4, 178.0	165.8, 173.8	53.7, 229.8	152.8, 198.6	160.4, 178.3	166.5, 175.7	166.6, 171.5
Jan/Feb	105.5, 226.9	148.6, 205.3	180.9, 189.2	181.0, 189.1	56.8, 251.2	166.2, 216.7	170.2, 197.2	184.6, 188.2	181.8, 186.8

Table 10.8. The "excess" production for 1994/95 from the sensitivity analysis of the maintenance ration for pelagic fish (twice parameter value, half parameter value) and the percentage of the diet consisting of copepods (100, 50%). ALL indicates all parameters changed simultaneously. See Table 10.4 for the parameter values of the standard model.

	MAINTENANCE RATION					% OF COPEPODS IN DIET			
PERIOD	ANCHOVY	SARDINE	ROUND HERRING	HORSE MACKEREL	ALL	ANCHOVY	SARDINE	ROUND HERRING	HORSE MACKEREL
Sep/Oct	285.2, 360.1	154.5, 425.5	326.6, 339.4	333.3, 336.0	94.2, 455.6	322.6, 353.9	257.7, 386.8	332.3, 338.0	333.6, 335.3
Nov/Dec	285.8, 356.2	302.6, 347.8	305.3, 346.4	330.9, 333.6	226.5, 385.9	321.0, 350.3	319.8, 341.3	323.6, 341.9	331.2, 332.9
Jan/Feb	382.7, 410.1	326.1, 438.4	392.5, 405.2	399.2, 401.8	297.7, 452.6	396.4, 407.8	368.9, 422.3	398.1, 403.8	399.4, 401.1

Table 10.9. The amount of "excess" production (mg dry weight.$m^{-2}.d^{-1}$) during the three periods in 1993/94 and 1994/95 after halving (2.5%) and doubling (10%) the amount of invertebrate predation. Note that negative values of "excess" production imply that there was insufficient production to account for the effect of predation and changes in copepod biomass.

	1993/94		1994/95	
PERIOD	2.5%	10%	2.5%	10%
Sep/Oct	66.7	-37.4	400.6	204.3
Nov/Dec	218.4	76.5	395.3	207.6
Jan/Feb	209.7	139.8	446.9	309.1

The substantially larger production in 1994/95 than in 1993/94 is a consequence of the presence of a greater copepod biomass during that spawning season. At elevated biomass values, pelagic fish could ingest more than their daily requirements, although the ingested ration was independent of food availability in the model. However, production was in "excess" of consumption even when the daily rations of all fish was doubled (Table 10.6). Thus, the conclusion remains that there was sufficient copepod production for pelagic fish to satisfy their daily requirements during both 1993/94 and 1994/95.

Although the results from the model suggest that there is net advective loss of copepod biomass from the region, there could still be advective input into the western Agulhas Bank. Two observations support this. Firstly, the largest copepod biomass on the western Agulhas Bank was midshelf (Chapter 2), spatially dissociated from the maximum concentration of Chl *a* inshore. Conversely, the greatest biomass of copepods off the South-Western Cape was located inshore, concurrent with high levels of Chl *a* (Chapter 2, Figs 2.1 and 2.2). Both these areas are active upwelling regions (Shannon 1985), where the largest copepod biomass is usually found in regions of greater Chl *a* concentrations when averaged over broad spatial and temporal scales. Therefore, the high mid-shelf biomass of large copepods midshelf on the western Agulhas Bank could be a consequence of advection of copepods from the eastern Agulhas Bank. Secondly, the population age structure and distribution of *C. agulhensis* suggests that large stages are advected into the region. In water >19 °C, where anchovy are seldom found (Painting *et al.* submitted), the age structure was skewed towards larger individuals, with more than 60% of the population being C4 or larger in size (Chapter 9, Fig. 9.2c). This skewness of the age distribution is unusual in a closed population of continuously spawning copepods such as *C. agulhensis*, and implies advective input of large individuals into the region. Largier *et al.* (1992) noted that distributions of *C. agulhensis* were centred on the eastern Agulhas Bank and that the distributions for older copepodite stages were closer to the western Agulhas Bank. They interpreted these findings as advection of *C. agulhensis* from the eastern to the western Agulhas Bank. The dearth of new individuals spawned *en route* is probably owing to the poor Chl *a* concentrations in the central bank region (Hutchings *et al.* 1995). In contrast, advective loss from the western Agulhas Bank removes both small and large copepods to the South-Western Cape region (Chapter 9, Fig. 9.4). Therefore, the western Agulhas Bank is a region of consistently high biomass of large copepods (Chapter 7, Fig. 7.2), because the small and large copepods that are removed by advection from the region are replaced by large individuals advected from the eastern Agulhas Bank. Peterson *et al.* (1992) calculated that copepod populations on the western Agulhas Bank during November were replenished by advective and diffusive transport, each at a rate of about 100 mg dry weight.m^{-2}.d^{-1}. Given the "excess" production observed of 170-330 mg dry weight.m^{-2}.d^{-1} calculated

here for November/December and input from the eastern Agulhas Bank of about 200 mg dry weight.$m^{-2}.d^{-1}$, this implies that the gross advective transport from the region could be about 370-530 mg dry weight.$m^{-2}.d^{-1}$ at this time.

Copepod production rates ranged from 340.7-705.0 mg dry weight.$m^{-2}.d^{-1}$ from September to February. Production rates by copepods (see Table 10.5) for November/December 1993 (367.2 mg dry weight.$m^{-2}.d^{-1}$) and 1994/95 (553.0 mg dry weight.$m^{-2}.d^{-1}$) were faster than those estimated by Peterson *et al.* (1992) for 1988 (127.6 mg dry weight.$m^{-2}.d^{-1}$) and 1989 (186.5 mg dry weight.$m^{-2}.d^{-1}$). There are two reasons for the faster rates in the present study. First, production rates are particularly sensitive to the growth rates of *Calanus agulhensis* C2s because this growth rate is applied to many species of this size (see Chapter 7, Table 7.1). *Calanus agulhensis* C2s grew 30% faster in November 1993 and 73% faster in November 1994 than those during November 1988 and 1989. This suggests that inter-annual variability in growth rate may be important to determining whether there is enough food for pelagic fish. Secondly, the large calanoid copepods *Calanoides carinatus*, *Metridia lucens*, *Pleuromamma* spp., and *Rhincalanus nasutus* and the non-calanoid copepods *Corycaeus* spp., *Corycella* spp., harpacticoids, *Oithona* spp., and *Oncaea* spp. were included in the estimates of production in the present study but not in Peterson *et al.* (1992). Together, these species represented 26-43% of the biomass (Table 10.10) and 19-36% of the production (Table 10.8). Production rates for the non-calanoid copepods were probably not over-estimated because the estimates used for *Oncaea* spp. and *Oithona* spp. were conservative: their growth rates were usually less than a third of those for similarly-sized calanoid copepods. These species are particularly important to pelagic fish, whose stomach contents are often dominated by *Oithona* spp. and *Oncaea* spp. (Peterson *et al.* 1992, C.D. van der Lingen, SFRI, pers. comm.). In fact, the estimates of copepod production derived here are underestimates because *Oithona* spp. and *Oncaea* spp. are too small to be retained quantitatively by a 200-μm mesh (especially their juveniles). A recent study in the northern Benguela region indicates that such species, when sampled with a 100-μm mesh, may contribute as much to the total copepod biomass as does the fraction caught with a 200-μm mesh (H.M. Verheye, SFRI, pers. comm.). The rates estimated in the current study were similar to but slightly slower than those measured by Hutchings *et al.* (1995) of 380-820 mg dry weight.$m^{-2}.d^{-1}$ for November 1990-1992. The rates in the present study may be slower because the non-calanoid copepods were assumed to grow slower than the calanoid copepods.

The current study is the first to investigate the intra-seasonal variation in copepod production in the southern Benguela upwelling system. Total copepod production varied by less than 12% during the

Table 10.10. Comparison of the biomass (mg dry weight.m^{-2}) of *Calanus*, small calanoids, and other copepods (excluding males) estimated in this study with those from Peterson *et al.* (1992) in November 1988 and 1989.

	1993/94				1994/95				1988			1989		
PERIOD	*Calanus*	Small calanoids	Other copepods	Total	*Calanus*	Small calanoids	Other copepods	Total	*Calanus*	Small calanoids	Total	*Calanus*	Small calanoids	Total
Sep/Oct	349.3	441.7	596.7	1387.8	537.1	851.9	1228.0	2617.0	_	_	_	_	_	_
Nov/Dec	835.4	500.8	556.1	1892.2	1087.9	687.6	727.2	2502.7	567.7	287.7	854.7	1057.5	490.0	1547.5
Jan/Feb	337.4	349.4	245.6	932.5	712.7	612.9	511.1	1836.7	_	_	_	_	_	_

1993/94 spawning season and 28% during 1994/95 (see Table 10.5). This is because the fastest growth rates occurred with the smallest biomasses (see Tables 10.1 and 10.2).

Copepods the size of a *C. agulhensis* C3 (1200 μm TL) and smaller account for 66-86% of the production, so that large copepods contribute a relatively small fraction to total production. Particulate feeding by biting on large prey items is more efficient for anchovy than is filter feeding on small prey (James and Findlay 1989; James and Probyn 1989). Thus, anchovy can feed on the high biomass and fast production of small copepods to sustain their normal metabolic activities and to reduce the likelihood of atresia when large copepods are unavailable. When large copepods are abundant, anchovy can switch to a biting mode of feeding. This provides a large energy intake at a relatively small energetic cost, allowing anchovy to reserve more energy for spawning.

The consumption of copepods by anchovy was considerably smaller in the current study (<75 mg dry weight.m^{-2}.d^{-1}) than that estimated by Peterson *et al.* (1992) of 300 mg dry weight.m^{-2}.d^{-1} in November 1988 and 112.5 mg dry weight.m^{-2}.d^{-1} in 1989. This may primarily be because anchovy stocks have declined since that period (Verheye and Richardson in press) and that it was assumed in the current model that 80% of the diet of anchovy was derived from copepods in comparison with 100% by Peterson *et al.* (1992). Anchovy biomass was 0.8-5.7 times larger than the biomass of copepods. Similar predator-prey ratios (1.5-6.9) were measured in the southern California Bight in the years 1961-1966 (Smith and Eppley 1982). Considering the density of all pelagic fish, the biomass was 4.7-15.5 times greater than that of their prey in the present study, close to the 2.3-15.0 times observed by Peterson *et al.* (1992). Therefore, large densities of pelagic fish can be supported by the biomass of copepods on the western Agulhas Bank.

Results from the model suggest that round herring was not an important competitor of anchovy, owing to their small densities in the region. This is in contrast to the suggestion that competition for food between round herring and anchovy may be important on the western Agulhas Bank (Roel and Armstrong 1991), although competition would be greater at the shelf-edge, where round herring are most common. The model results are most sensitive to variation in the amount of invertebrate predation. Estimates of invertebrate predator abundance in the region are scant (Gibbons *et al.* 1992). More work is needed to quantify the impact of invertebrate predators on copepod populations on the western Agulhas Bank. To improve our understanding of the biological processes in the region, more work is needed on the physical oceanography to quantify the connections between the western Agulhas Bank and both the eastern Agulhas Bank and the South-Western Cape Coast.

CHAPTER 11

SYNTHESIS

Copepods in the southern Benguela upwelling system exhibit spatial and temporal variability in their abundance, sex ratios, and growth rates. In terms of abundance, copepod biomass decreases from St Helena Bay in the north (4954 mg dry weight.m^{-2}) to the western Agulhas Bank in the south (2066 mg dry weight.m^{-2}) of the area of investigation. The concentration of Chl *a* shows similar variation, suggesting that high levels of Chl *a* support a large biomass of copepods.

Sex ratios of copepods are related to their trophic mode, with the predominantly herbivorous species having a smaller proportion of males (20-25%) than the omnivorous and carnivorous species (55-60%). This may be related to the poorer nutritional quality of phytoplankton compared to microzooplankton, ensuring females of herbivorous species have a greater share of a poor food resource. A comparison of the sex ratios observed in net samples with those obtained from recently moulted individuals from incubation experiments show that sex ratios were skewed towards males in herbivores at the onset of adulthood. Only a relatively small amount of the skewness is attributable to earlier male mortality which has been thought to be the most important factor skewing sex ratios previously. The sex ratio of the two dominant large copepods in the southern Benguela system, *Calanus agulhensis* and *Calanoides carinatus*, respond differently to changes in food concentration. *C. agulhensis* has a greater proportion of females under poor food conditions (29.9% male), compared to good food conditions (38.3% male). This may be an adaptive strategy to poor food conditions: it may be beneficial to be female during periods of poor food because females are larger, have greater longevity, and have more lipid reserves than do males, enabling a greater proportion of females than males to survive periods of starvation. Females could then continue to reproduce when food conditions improve. This strategy also allows females a greater proportion of the limited food supply in a food-poor region such as the Agulhas Bank. In contrast, the sex ratio of *C. carinatus*, usually found on the relatively food-rich West Coast, does not vary in response to food conditions. It is proposed that experiments in which C5s are incubated until adulthood are useful for comparing sex ratios of newly moulted individuals with sex ratios measured simultaneously from net samples to ascertain whether skewed sex ratios are a consequence of differential survivorship between the sexes.

To my knowledge, this study presents the most comprehensive data set of *in situ* copepod growth rates estimated in an upwelling system, including the first extensive field estimates of fecundity for *Nannocalanus minor* (mean: 26.1 eggs.♀$^{-1}$.d^{-1}, range: 0.0-96.2) and of somatic growth of all *C. carinatus* copepodites (from 0.58 d^{-1} for N6 down to 0.04 d^{-1} for C5). Mean egg production rate of

most copepods is generally small, below 30 eggs.♀$^{-1}$.d^{-1} (*C. carinatus* 23.7, *C. agulhensis* 19.9, *N. minor*, *Neocalanus tonsus* 16.1, and *Rhincalanus nasutus* 26.1), whereas fecundity of *Centropages brachiatus* is significantly greater (83.6 eggs.♀$^{-1}$.d^{-1}). Somatic growth rates of *C. agulhensis* and *C. carinatus* generally decline with age. It is noteworthy that neither fecundity nor somatic growth are directly related to temperature, considering that temperature has been reported to be the main factor controlling copepod growth rates (Huntley and Lopez 1992). In the present study, a dome-shaped relationship between growth and temperature is discernible in some species, with optimum growth within a window of 13 to 18 °C. The shape of this relationship mirrors that of Chl *a versus* temperature. Mean growth rates were positively related to food in terms of Chl *a* concentration, with the degree of food limitation increasing with body size. It is concluded that the effect of food-limitation on growth of copepods outweighs that of temperature in the southern Benguela upwelling region.

There is less than a three-fold decline in maximum growth rates of copepods from *Calanus agulhensis* females (2750 μm) to *C. agulhensis* N6 (500 μm), probably attributable to allometric considerations. However, there is an order of magnitude decline in mean growth rate which is a consequence of food limitation. For large copepods, frequency distributions of growth rate under poor food densities (<2 mg.m^{-3}) are severely skewed toward slow growth rates, whereas the distributions are more symmetric for smaller copepods. In contrast, at good food concentrations (>2 mg.m^{-3}), the frequency distributions have a high degree of symmetry for all copepods. These frequency distributions can be interpreted in terms of the encounter rate of individual copepods with suitably-sized food particles. This study provides strong evidence for food limitation in nature and is in direct contrast with the suggestion by Huntley and Lopez (1992) that food is not limiting in the wild.

Small copepods in the southern Benguela system are always growing well, whereas the growth rate of large copepods is more variable. This difference is probably a consequence of the ability of small copepods to consume small particles which are always present at a relatively constant background density. This may also apply to the growth rate of small copepods in other aquatic systems where there is an abundant and omnipresent microbial component, and could explain the consistent growth rates of copepod nauplii observed in many freshwater and marine systems. Greater food-limited growth of large copepods, as in the present study, has also been noted for copepods in a tropical bay (Webber and Roff 1995). In a recent global synthesis, Hirst and Sheader (1997) suggested that large copepods are more food limited than smaller species. Therefore, there is a growing body of literature

suggesting that small copepods are rarely food limited. This has important implications for energy flow through aquatic food webs.

A consequence of the increased food limitation of large copepods is that growth rates decrease exponentially with increasing body size in the southern Benguela system. Growth rates of copepods from the northern Benguela upwelling system also exhibit a similar decline. Thus, this relationship can be used to estimate growth rates, and hence production, of calanoid copepods in a broad size range (525-5000 μm) throughout the Benguela upwelling ecosystem, given knowledge of the community size structure.

The interplay between body size and food limitation on copepod growth rates explains the spatial and temporal variation of copepod growth on the western Agulhas Bank, the main spawning ground of anchovy. Growth rates of small stages (N6-C2) remain relatively constant, both seasonally and across the shelf. In contrast, there is a strong cross-shelf decline in growth rate of large copepodites (C3-female). Temporally, growth rates of large copepodites are moderate (0.046-0.343 d^{-1}) in September/October following water column stabilization after winter, slow (0.026-0.181 d^{-1}) in November/December as the upper mixed layer warmed, and fast (0.079-0.409 d^{-1}) during the upwelling season (January-March). This within-season variation in growth rates of larger stages mirrors changes in Chl *a* concentration that are a consequence of seasonal warming and wind patterns. The spawning of sardine follows these changes in copepod growth rate, with a spawning peak in September/October and another in January/February, when the production of copepod eggs and nauplii, which form the main food source for pelagic larvae, is maximal. Superimposed on these large-scale changes in copepod growth rate are event-scale fluctuations in response to winds, particularly from January to March. At the onset of upwelling, mean female copepod growth rate across the shelf is slow. During sustained upwelling, female growth rate increases, with a peak associated with enhanced concentration of Chl *a* in the upwelling front, and slower rates inshore in newly upwelled water and offshore in oligotrophic water. Mean female growth is fastest during prolonged quiescence when high Chl *a* levels extend over most of the shelf. During downwelling, mean female growth rates are slow, although faster rates can occur inshore.

Anchovy do not time their spawning to these peaks in growth rate. Anchovy spawn when copepod growth rates on the western Agulhas Bank are slowest, although there is little seasonal variation in copepod production. It seems paradoxical that anchovy spawn on the western Agulhas Bank where the copepod biomass is smaller than in other regions of the southern Benguela system, there is considerable density dependent predation, and greater turbulent mixing than is optimal (Shin 1995).

However, the western Agulhas Bank appears to be a more suitable spawning area for anchovy than off the South-Western Cape, because of its greater thermal stability, a larger area of 16-19 °C water and a more consistent food environment.

The area of the optimal spawning habitat for anchovy (16-19 °C water) is dynamic throughout their spawning season. The variability of this water mass can be categorized into three periods: winter (August-September), spring (October-December) and summer (January-March). There was a small area of 16-19 °C water in winter, with poor anchovy spawning. Spring is characterized by infrequent surface upwelling, a large area of 16-19 °C water, and peak spawning of anchovy. In contrast, there is frequent surface upwelling (<13 °C) in summer and very warm water offshore (>21 °C), a small area of 16-19 °C water, and poor anchovy spawning. The biomass of large copepods in the region also follows these trends, with a maximum during spring. The area of this water mass can be estimated from thermal imagery and could be used in a predictive manner: there is a strong positive relationship between anchovy egg abundance and the area of 16-19 °C water ($r^2 = 0.56$, $n = 17$, $p < 0.001$). It is hypothesized that spawning success in anchovy is dependent upon the extent of a suitable spawning habitat, both spatially (16-19 °C water) and temporally (the duration of the spring period). An implication of this hypothesis is that post-spawning processes may not be all important in determining recruitment, and that the persistence of good conditions in terms of 16-19 °C water (with its more consistent food supply), and hence spawning, may be important.

On the western Agulhas Bank, the biomass of copepods, the major component of the diet of anchovy, varies substantially throughout the anchovy spawning season. Historically, the food environment for anchovy has been assessed in November, with the aim of making predictions about anchovy recruitment. This single estimate, however, fails to reveal important fluctuations in biomass. Egg abundance was positively related to the food available to anchovy in terms of their preferred prey item (large copepods) and temperature preference (16-19 °C). These findings support the contention that food is important to the spawning of the Cape anchovy and that a consistent food resource throughout the spawning season prolongs spawning. Furthermore, the variability of factors that are important to spawning implies that within-season estimates of parameters such as food availability could be important for forecasting recruitment.

Intra-seasonal variation of copepod biomass on the western Agulhas Bank appears to be influenced by both physical and biotic factors. There is a strong inverse relationship between the biomass of copepods in the region and that of anchovy for the years 1988-1996. This implies density-dependent competition for food on the western Agulhas Bank. Moreover, this process probably varies intra-

seasonally, because the biomass of large copepods, which are a favoured food item of anchovy, declines when the optimal habitat for anchovy spawning (16-19 °C water) contracts, whereas small copepods were unaffected. Advective loss, inferred from an index of current strength, also negatively impacts the biomass of copepods, with both small and large individuals being affected. Maximum anchovy spawning during spring coincides with the time of greatest biomass of copepods. In contrast, copepod biomass is smallest during the active upwelling phase within the summer period, when there is a strong front and a small area of 16-19 °C water. Thus, the positive relationship between anchovy egg density and the area of 16-19 °C water may be a consequence of the favourable food environment in this water at times of smaller advective loss.

A simple mass-balance model of the western Agulhas Bank was used to investigate the magnitude of consumption of copepods by predators relative to copepod production. The model calculates the amount of "excess" production needed to balance growth, consumption, and the increase or decrease of biomass for three 2-month periods, between September and February. Production did not vary substantially within the two anchovy spawning seasons (522.9 mg dry weight.m^{-2}.d^{-1} in September/October, 460.1 mg dry weight.m^{-2}.d^{-1} in November/December, and 483.7 mg dry weight.m^{-2}.d^{-1} in January/February), because growth rates are generally slow at times of large copepod biomass and *vice versa*. Despite the generally low copepod biomass on the western Agulhas Bank in comparison to other regions within the southern Benguela system, it was concluded that *in situ* copepod production was usually adequate to not only sustain anchovy, but also that of the large populations of sardine, round herring, and horse mackerel. "Excess" production varies intra-seasonally, being small in September/October (183.6 mg dry weight.m^{-2}.d^{-1}), moderately large in November/December (251.9 mg dry weight.m^{-2}.d^{-1}), and greatest in January/February (293.7 mg dry weight.m^{-2}.d^{-1}). It is hypothesized that the "excess" production is lost from the region by advection.

Although the results of the model suggest that there was sufficient production to offset consumption by these predators, it cannot be concluded that there is no advective input into the region from the eastern Agulhas Bank. On the contrary, several observations suggest that there is considerable advection from the eastern Agulhas Bank. Firstly, the greatest biomass of copepods off the South-Western Cape is located inshore, concurrent with good Chl *a* densities. Conversely, on the western Agulhas Bank, the largest copepod biomass is found midshelf, spatially dissociated from the maximum concentration of Chl *a* inshore. This may be a consequence of advection of copepods into the region. Secondly, the population age structure of *Calanus agulhensis* in water above 19 °C is highly skewed towards larger individuals: the large copepod biomass cannot be maintained by *in situ* growth alone. Therefore, the consistently high biomass of large copepods on the western Agulhas

Bank, beneficial for the successful spawning of anchovy, may be maintained by large copepods being advected from the eastern Agulhas Bank into the region which compensates for their advective removal. This concept supports previous findings of the distribution of large *Calanus* stages and explains the high and consistent biomass of large copepods on the western Agulhas Bank. To further elucidate the population dynamics of copepods in this region, a physical model is needed because of the importance of hydrography to the maintenance and depletion of copepod populations.

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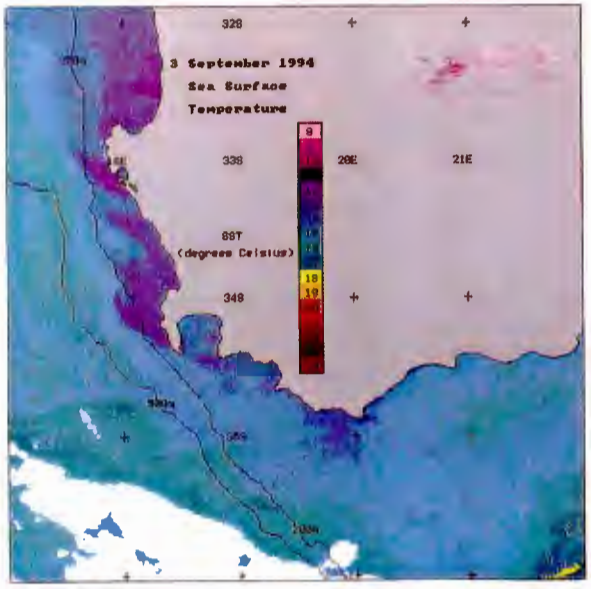
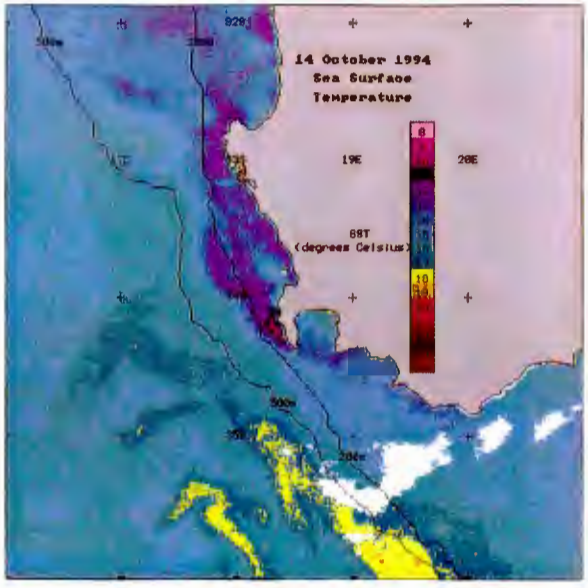
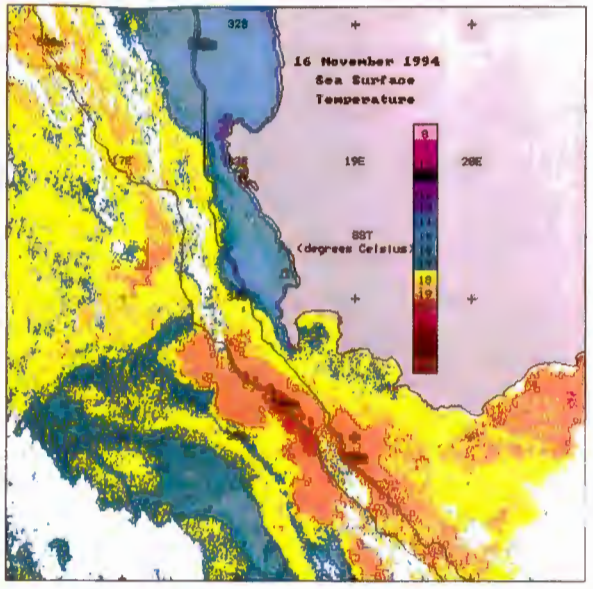
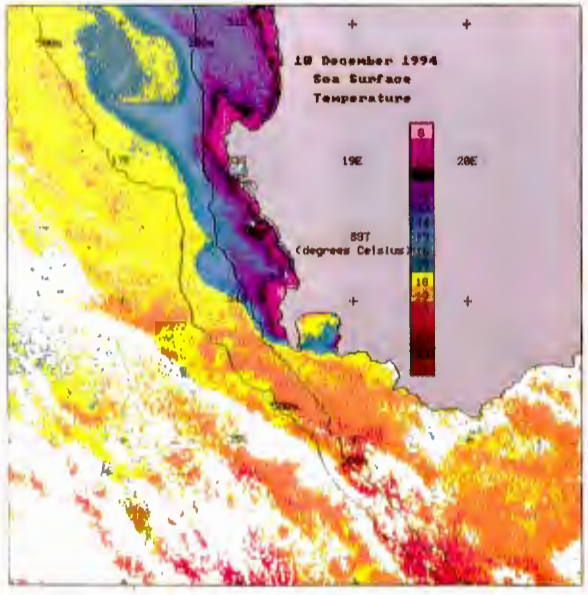
APPENDIX 1

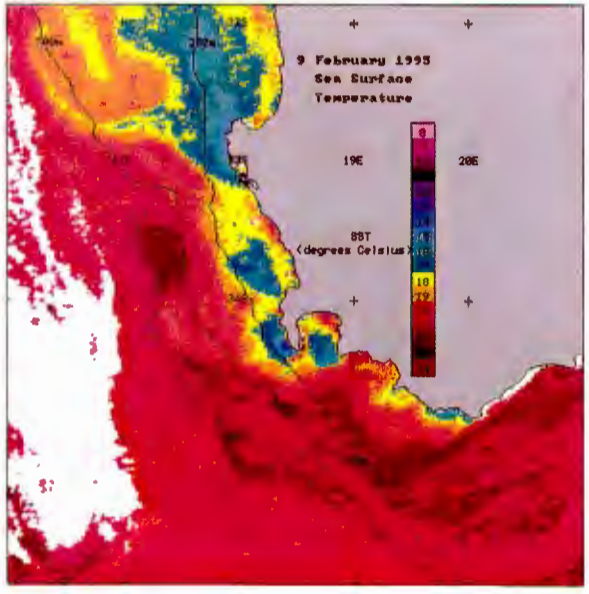
Satellite images of sea surface temperature corresponding to cruises during the 1993/94 and 1994/95 SARP seasons.

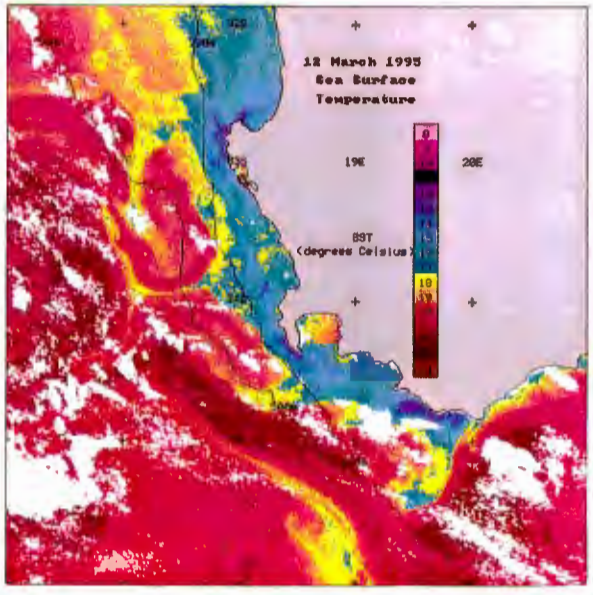




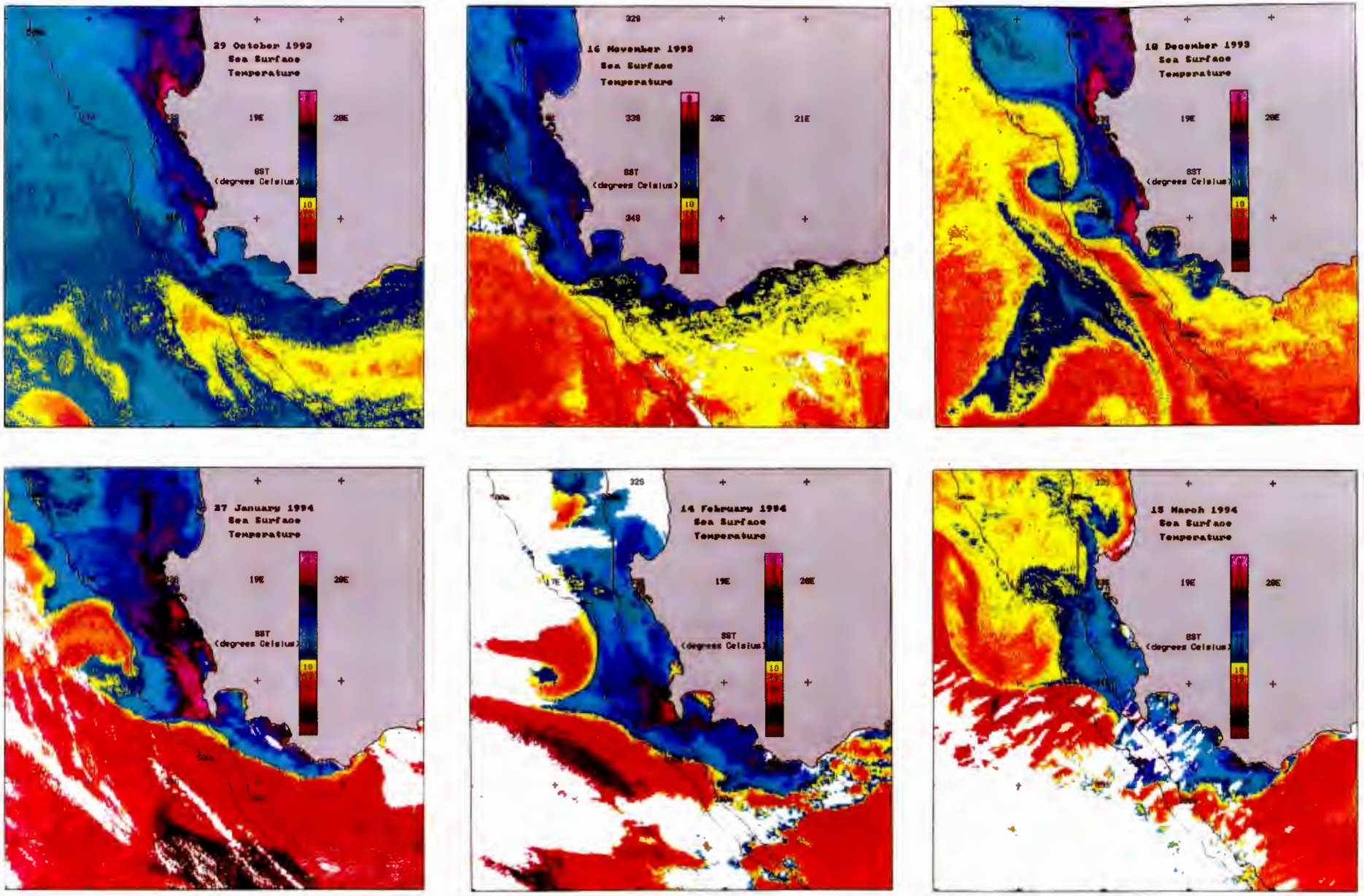








1994/95 anchovy spawning season



1993/94 anchovy spawning season