

Copepod production in the southern Benguela system

L. Hutchings, H. M. Verheye, B. A. Mitchell-Innes,
W. T. Peterson, J. A. Huggett, and S. J. Painting

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Several methods have been used to indirectly estimate copepod production in the southern Benguela region, based on field sampling of copepod stages and laboratory measurements of growth and development rates under variable food and temperature regimes. Estimates of production have steadily increased from $11 \text{ gC m}^{-2} \text{ y}^{-1}$ in 1979 to $80 \text{ gC m}^{-2} \text{ y}^{-1}$ in 1987. Since 1988, extensive measurements of copepod egg production and moulting rates of *Calanus agulhensis* at sea during hydro-acoustic fisheries surveys over the south and west coasts of South Africa in November have provided more direct estimates of copepod production. Daily Mean Production: Mean Biomass (P:B) ratios varied between 0.1 and 0.3 and annual production ranged between 17 and $150 \text{ gC m}^{-2} \text{ y}^{-1}$. Copepod biomass, distribution, and demographic structure varied between cruises in different years, apparently linked to both the abundance of predators and shifts in hydrology. Production appeared to be due more to shifts in distribution of biomass and demography of *Calanus* than to variations in growth rates. Poor correlations existed between juvenile growth and female egg production, suggesting one is unable to predict population growth from egg production rates only. Weak correlations between growth rates of different stages also suggest that the only meaningful measure of copepod production requires all stages to be incubated.

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Key words: Agulhas Bank, copepods, inter-annual variation, production, upwelling.

L. Hutchings, H. M. Verheye, B. A. Mitchell-Innes, J. A. Huggett, and S. J. Painting: Sea Fisheries Research Institute, Pvt Bag X2, Roggebaai, Cape Town 8012, South Africa. W. T. Peterson: NOAA-NMFS-F/RE3, 1335 East West Highway, Silver Spring, MD 21801, USA.

Introduction

The coastal shelf off southern Africa from 30°S to 37°S is a zone of sharp contrasts (Fig. 1), with wind-driven coastal upwelling along the western margin and warmer, stratified water overlying the shelf on the southern coast (Shannon, 1985). Wind forcing is strongly pulsed over periods of 5–10 d (Nelson, 1992) and displays considerable seasonal but reduced inter-annual and decadal variation (Hutchings and Taunton-Clark, 1990).

On the Agulhas Bank on the south coast (i.e. east of Cape Point from 18 to 27°E), strongly stratified conditions occur during summer, when warm water overlies colder water on the shelf. There is evidence of upwelling from a number of sources on the Bank (Boyd and Shillington, 1994), including the shelf edge, capes inshore, the extreme eastern margin where the Agulhas Current diverges from the coast and along a broad ridge on the eastern-central region. A schematic of the flow field (Fig. 1) clearly shows the Agulhas Current on the

shelf edge off the Agulhas Bank, the shelf-edge jet off the SW Cape, the recirculation features off Lamberts Bay on the west coast and on the eastern Agulhas Bank, and a moderate alongshore flow on the western Agulhas Bank (Boyd *et al.*, 1992).

Phytoplankton responds rapidly to upwelling events on the west coast. While initial seeding by small cells occurs in newly upwelled water, they seldom reach high concentrations (Moloney, 1992; Pitcher *et al.*, 1993) and are replaced by larger cells or chain-forming diatoms which may be less vulnerable to grazing pressure from microzooplankton. Blooms develop as the water column stabilizes after upwelling and the rate of increase is dependent on wind patterns and seeding, with the bloom peak occurring within 3 to 16 d of upwelling (Brown and Hutchings, 1987; Mitchell-Innes and Walker, 1991; Pitcher *et al.*, 1992, 1993; Moloney, 1992). Phytoplankton concentrations decline equally rapidly and changes in productivity, cell size, and species composition occur (Pitcher *et al.*, 1991), with small phytoplankton cells and

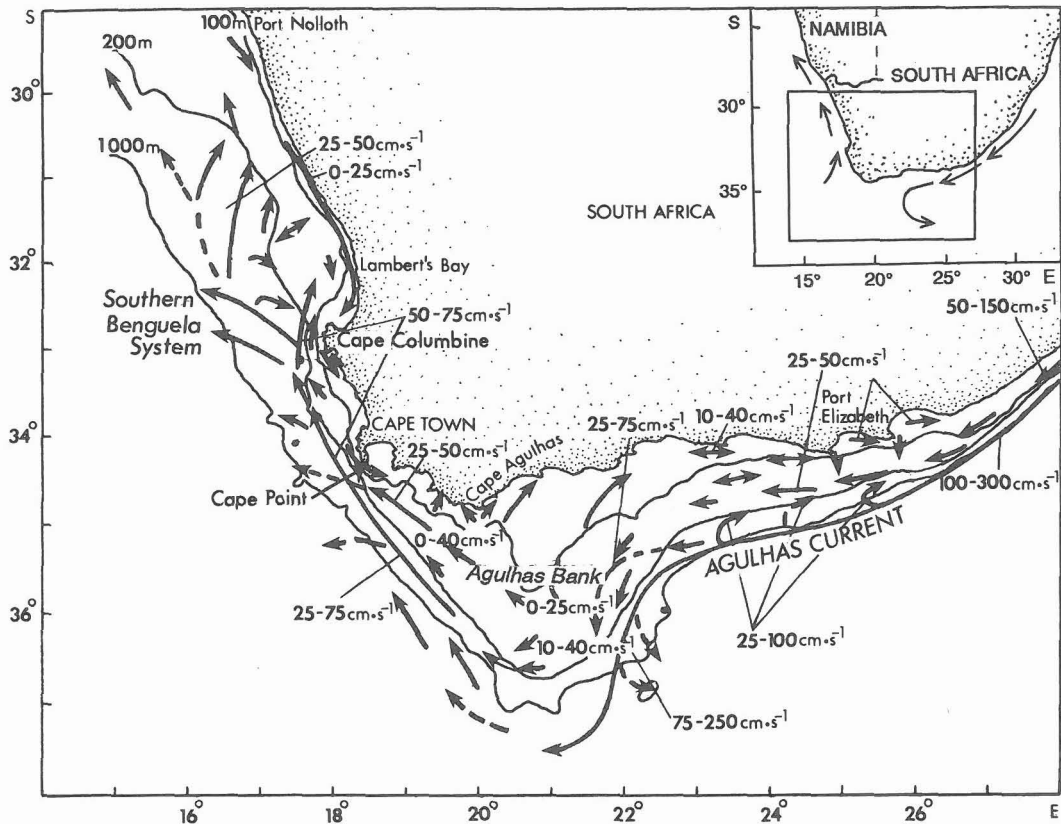


Figure 1. The southern Benguela region, with a schematic flow field of near-surface currents based on ADCP data collected between November 1989 and January 1992. From Boyd *et al.* (1992).

microheterotrophic processes dominant in aged upwelled water (Probyn, 1990, 1992; Painting *et al.*, 1993). With the strongly pulsed SE winds and three-dimensional nature of upwelling in the southern Benguela Current, phytoplankton is very patchy in space and time and poses special problems for efficient utilization by grazers (Hutchings, 1992).

On the Agulhas Bank a number of productive regions can be discerned, reviewed by Probyn *et al.* (1994). The area is dominated by subsurface maxima of Chl *a* which increase in concentration where thermoclines are shallow. On the inner shelf of the western Agulhas Bank, wind-driven upwelling dominates, with phytoplankton concentrations similar to west coast locations. Offshore, lower concentrations occur at deep thermoclines. Over the ridge of cool water on the central/eastern Agulhas Bank elevated chlorophyll concentrations occur, dominated by small cells. In the extreme east, higher, but variable, phytoplankton concentrations are found downstream from the divergence of the Agulhas Current from the coast.

Zooplankton in the southern Benguela Current is dominated by copepods, euphausiids, and thaliaceans.

Euphausiids decrease in abundance over the Agulhas Bank (Pillar, 1986), while thaliaceans increase (De Decker, 1973; Lazarus and Dowler, 1979). Copepods are abundant both on the west coast and on the Agulhas Bank (Hutchings *et al.*, 1991; Verheye *et al.*, 1994). On the west coast a low diversity of copepods occurs (De Decker, 1984), yet the biomass is dominated by a mixture of small (*Paracalanus*, *Ctenocalanus*, *Oithona*, *Clausocalanus*) medium (*Centropages*, *Metridia*), and large (*Calanoides*, *Rhincalanus*) copepods. On the Agulhas Bank only one species, the large copepod *Calanus agulhensis* (De Decker *et al.*, 1991), dominates the zooplankton biomass (Peterson *et al.*, 1992; Verheye *et al.*, 1994), with a centre of distribution over the cool ridge on the central-eastern Bank.

Anchovies, which are important predators of copepods and euphausiids, spawn on the Agulhas Bank during the summer months (September to March), peaking in November. The highest concentrations of fish occur on the western Agulhas Bank in an area which has marginal food supplies for the adult spawners but which is apparently best suited for the subsequent survival of recruits (Peterson *et al.*, 1992; Hutchings, 1992).

Several methods have been used to estimate copepod production in the southern Benguela region (Hutchings *et al.*, 1991; Verheye *et al.*, 1992). Based on monthly cross-shelf transects and crude assumptions of generation time, Hutchings (1979) estimated production to be $11 \text{ gC m}^{-2} \text{ y}^{-1}$. Later, Borchers and Hutchings (1986), by assuming that turnover time was approximately two to three times less than the generation time, raised the earlier estimates to $20\text{--}30 \text{ gC m}^{-2} \text{ y}^{-1}$.

By incorporating laboratory-based estimates of development time with excess food at controlled temperature for a single species, *Calanoides carinatus*, extrapolating to all species and assuming half the zooplankton was carnivorous and the ecological efficiency was 20%, they subsequently estimated zooplankton production to be approximately $50 \text{ gC m}^{-2} \text{ y}^{-1}$. Based on daily sampling of all stages of *Calanoides* at a fixed location on the west coast at 33°S over a 27-d period, combined with temperature data and development times, Verheye (1991) estimated production of mesozooplankton to be approximately $80 \text{ gC m}^{-2} \text{ y}^{-1}$, assuming no seasonality in growth and extrapolating from *Calanoides* to other species of herbivorous copepods.

Since 1988, extensive measurements of copepod egg production and moulting rates of *Calanus agulhensis* at sea during hydro-acoustic pelagic fish surveys over the south and west coasts of South Africa in November have provided more direct estimates of copepod production. Daily Mean Production:mean Biomass (P:B) ratios varied between 0.1 and 0.3 and annual production ranged between 17 and $150 \text{ gC m}^{-2} \text{ y}^{-1}$. Peterson *et al.* (1992), Largier *et al.* (1992), and Peterson and Hutchings (1995) reported on findings on the Agulhas Bank during 1988 and 1989 and discussed the methodology in some detail; this article reports on inter-annual variability of copepod biomass and production in relation to wind, Chl *a*, and anchovy abundance over the period 1988 to 1993 and provides limited comparisons with the west coast. Some 1100 shipboard measurements of copepod moulting rate and egg production have now been made.

Methods

Wind measurements from Cape Point lighthouse consisted of hourly estimates of speed and direction. Data for the years 1986 to 1993 have been extracted and plotted as progressive vectors showing the northward and westward displacement over the summer period from 1 October to 31 March.

Plankton sampling took place during hydro-acoustic surveys of spawning pelagic fish (anchovy and sardine) during November each year on the 78 m research vessel "Africana". These surveys consisted of 30–40 transects across the shelf which were distributed in a stratified random manner, with a greater number of transects in

zones where high densities of fish were expected. On selected transects and at alternate stations on each transect (i.e. 10 n mile spacing), plankton sampling took place (Fig. 2).

Temperature and fluorescence profiles were obtained with a thermistor and an Aquatracka fluorometer attached to a rosette sampler fitted with 18 l bottles. Water was collected at the surface and the fluorescence maximum for Chl *a* and nutrient (nitrate, silicate, and phosphate) analyses and for particle counting with a Coulter Multisizer fitted with a $140 \mu\text{m}$ aperture tube ($2.8\text{--}80.0 \mu\text{m}$ ESD). Data were collected in a logarithmic distribution by size and the statistics calculated geometrically. Copepods were collected from the upper 200 m with a vertically towed 57 cm diameter Bongo net ($200 \mu\text{m}$ mesh) equipped with flow, depth, and temperature sensors and samples were preserved in buffered 5% formalin. The abundance of copepods was estimated by counting two subsamples of 2 ml each taken with a wide-bore pipette. Copepods were identified to genus and species wherever possible. *Calanus agulhensis* were identified to stage.

Live copepods for experimental work were collected from the fluorescence maximum by drifting a 0.5 m diameter, $300 \mu\text{m}$ mesh net for 5–10 min while on station. The animals were gently transferred from the 2 l codend to a 20 l bucket containing surface water and were incubated in water from the fluorescence maximum which had been filtered through a $63 \mu\text{m}$ mesh to remove eggs. Selected stages were incubated for 24 h in darkened bins cooled with sea water pumped from a depth of 6 m, approximating the temperature of the upper mixed layer. For moulting rate experiments, 20–50 individuals of each stage were gently pipetted under dim light into small dishes and transferred, after checking for the correct identification and damage to the antennae or furcal rami, into 2 or 5 l plastic jars; two females per litre bottle were incubated with five replicates for estimates of egg production.

Usually, the most abundant stages were picked from the sample, while ensuring that all stages were selected at least once along each transect. Incubations were terminated by preserving the contents in 5% formalin, after checking that females were still alive in the egg production experiments. If one of the pair had died, results were discounted. The preserved specimens, including the empty moults, were counted in the laboratory; if there was a difference of more than 10% between the number of moults and the number of animals that had advanced a stage, the results were discounted. Moulting rates of juveniles and egg production rates of females were calculated following the equations published in Peterson *et al.* (1991). Growth rates were calculated taking into account the change in weight between stages as outlined in Peterson and Hutchings (1995): $g_i = \{\ln(W_{i+1}/W_i) \times MR_i\}$, where W_i

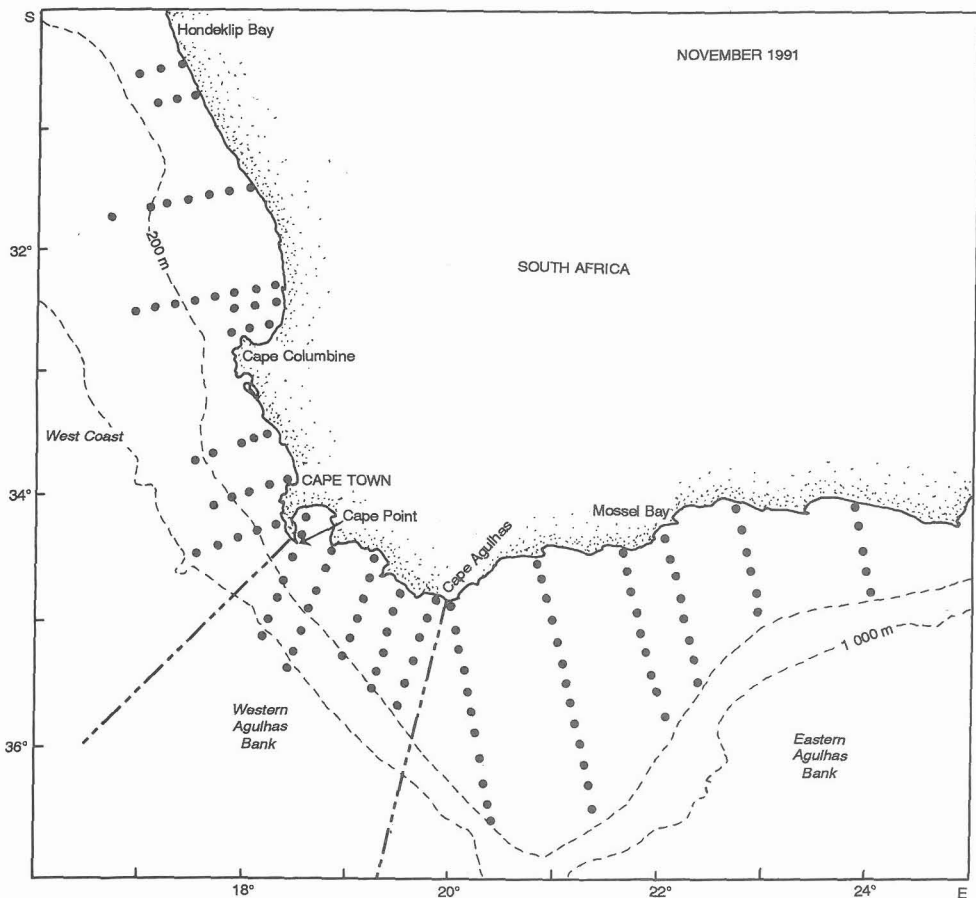


Figure 2. Plankton sampling locations on the November 1991 Pelagic Fish Spawner Survey. Approximately one-third of the total number of fish egg collection stations occupied are sampled. Similar grids were occupied in other years.

is the weight of the i th stage and MR_i is the proportion of individuals within a stage moulting per 24 h. Growth rates of females were calculated from egg production: $g_f = (N_e \cdot W_{egg}/W_{fem}) \times 24/T$, where $N_e = \text{eggs fem}^{-1} \text{d}^{-1}$, $T = \text{incubation time in hours}$, $W_{egg} = 600 \text{ ng dry wt}$ and $W_{females} = 202 \text{ } \mu\text{g dry wt}$ (Peterson and Hutchings, 1995).

Production rates of the population were estimated by first calculating the biomass of each stage in the water column by multiplying the abundance estimates from the vertical Bongo hauls by the individual weights of each stage (assumed constant for the whole period) and then multiplying by the growth rates, summed over all stages.

$$P = \left(\sum_{j=1}^{j=6} g_j \cdot B_j \right) + g_f \cdot B_f,$$

where $P = \text{production } (\mu\text{g dw m}^{-2} \text{d}^{-1})$, g_j is the juvenile growth rate (N6-CV), g_f is the female growth rate, and B the biomass of juveniles and adult females in

the water column. Mortality of females was ignored for purposes of the calculations.

Results

Winds

Progressive vector diagrams (cumulative displacement) for winds during summer (October to March) for Cape Point (34°S) for the years 1986 to 1994 (Fig. 3) indicated fewer south-east winds during the summers 1987/1988 and 1990/1991 to 1992/1993 inclusive, with stronger SE winds during 1988/1989 and 1993/1994. These variations are linked to the El Niño manifestations in the Pacific in 1986/1987 and 1992/1993, but statistical relationships are weak. Short-term variations in windspeed and direction, indicated by kinks in the progressive vectors, play an important role in altering the distribution of properties in the water column. Strong winds ($> 15 \text{ m s}^{-1}$), which can blow from the east or west (Jury, 1994), may disrupt thermoclines on the Agulhas Bank,

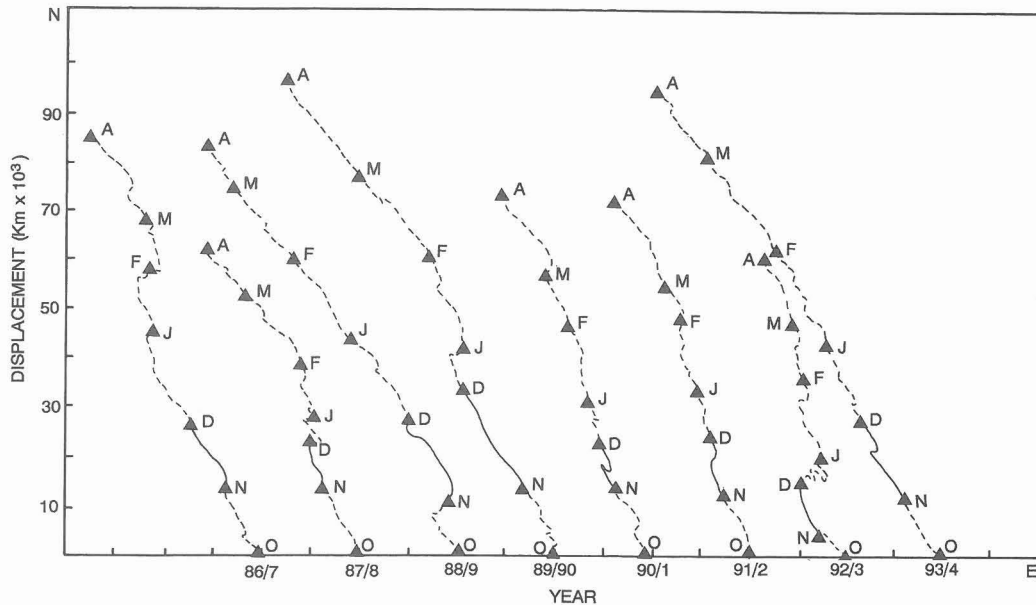


Figure 3. Progressive wind vectors for the summer months at Cape Point (34°S) for 1986–1993. Displacement to the north and west indicates SE winds. The origin of each vector is displaced to the right for clarity. The vector during November is highlighted.

dissipating strong subsurface Chl *a* maxima through the upper mixed layer in a manner similar to that described by Lasker (1978).

Temperature, phytoplankton and particle size distributions

November 1991 has been selected to illustrate the general distribution of parameters, with notable deviations in other years indicated below. While surface temperatures reflect the upwelling conditions on the west coast, they do not reveal the density structure present on the Agulhas Bank as clearly as 30 m temperatures (Fig. 4a), which show the subsurface ridge of cool water in the central and eastern parts of the Agulhas Bank. The overlying layer of warm oligotrophic water poses particular difficulties for the use of satellite imagery to detect structural and phytoplankton changes on the Agulhas Bank (Probyn *et al.*, 1994). However, the lack of strong surface gradients in temperature, combined with relatively strong winds, allows us to incubate in mixed layer water over 24 h with very little variation compared to the west coast, where surface temperature gradients may approach 10°C or more on occasion.

Chlorophyll *a* concentrations at the fluorescence maximum (Fig. 4b) are elevated in the wind-driven upwelling zone along the west coast and along the axis of the cool ridge. Total particle volume is closely correlated with total Chl *a* (uncorrected for phaeopigments) with r^2 approximately 0.7–0.8 for all cruises

except in November 1990, when r^2 decreased to 0.37. Large cells dominate in the upwelling zone and small cells over the cool ridge on the eastern Agulhas Bank. Sporadic shelf-edge upwelling along the outer margin of the Agulhas Bank (Boyd and Shillington, 1994) is linked to the occurrence of larger cells and diatom chains. Mean Chl *a* concentrations (Fig. 5) at the fluorescence maxima for different areas and years show high, variable concentrations of predominantly large cells on the west coast (WC) compared with the western Agulhas Bank (WAB) or eastern Agulhas Bank (EAB); low concentrations were generally associated with a lower proportion of large cells (Mitchell-Innes and Pitcher, 1992). Minima occurred in 1988 and 1993 on the west coast and the western Agulhas Bank, but in 1990 on the eastern Agulhas Bank.

Copepods

Total copepod biomass in November 1991 (Fig. 6) shows a minimum on the western Agulhas Bank, increasing on the west coast and on the eastern Agulhas Bank. This minimum coincides with a maximum concentration of anchovy (Roel *et al.*, 1994). This distribution of copepod biomass holds true for most years (Fig. 7), with the proportion of *Calanus* decreasing sharply on the west coast.

Calanus abundance, standing stock, and demographic structure on the Agulhas Bank are illustrated in Figure 8. While inter-annual variations are roughly half to

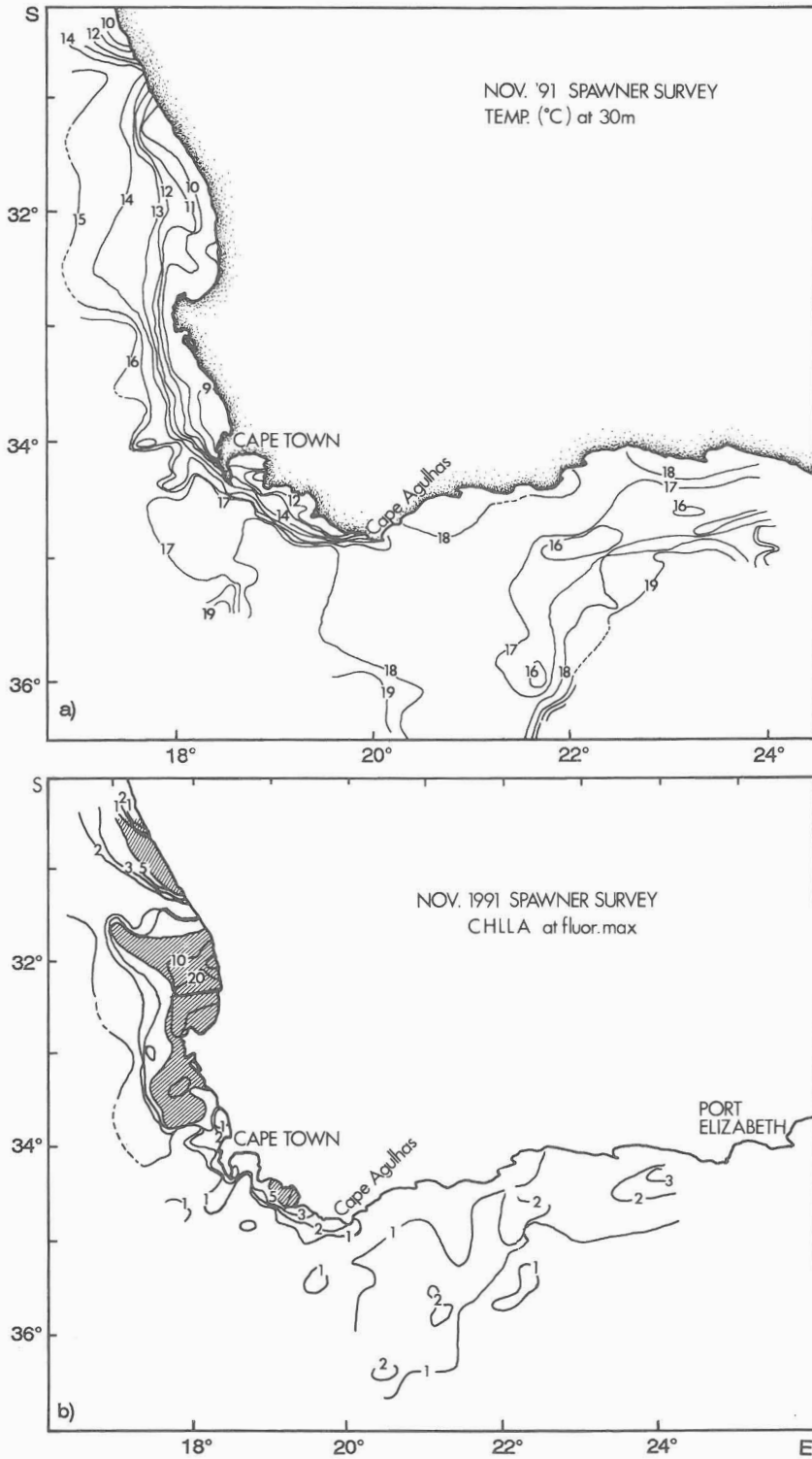


Figure 4. (a) Temperatures ($^{\circ}\text{C}$) at 30 m during November 1991, showing the upwelling west of Cape Agulhas and the cool ridge on the eastern Agulhas Bank. (b) Chlorophyll *a* concentrations (mg m^{-3}) at the fluorescence maximum, November 1991.

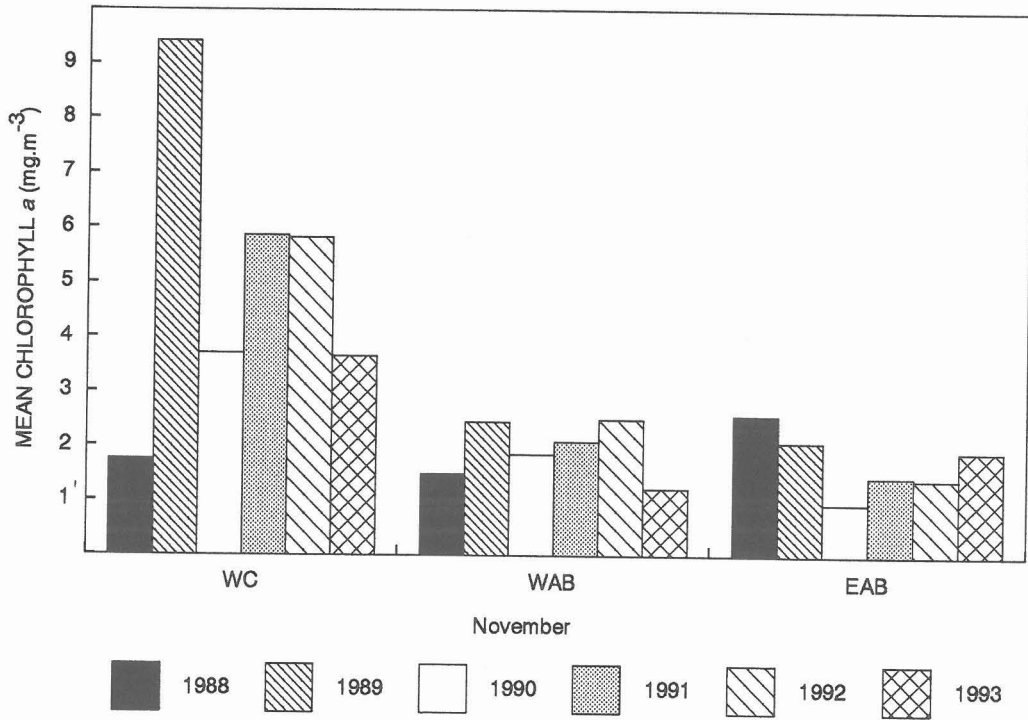


Figure 5. Mean Chl *a* concentration (mg m^{-3}) at the fluorescence maximum, by area and year, 1988-1993. WC = west coast; WAB = western Agulhas Bank; EAB = eastern Agulhas Bank.

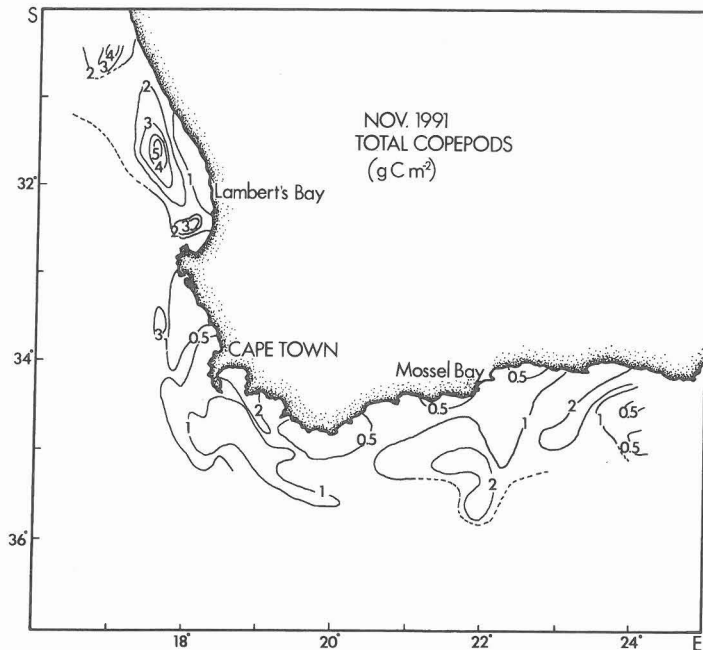


Figure 6. Distribution of copepod standing stock (gC m^{-2}) in November 1991 in the upper 20 m.

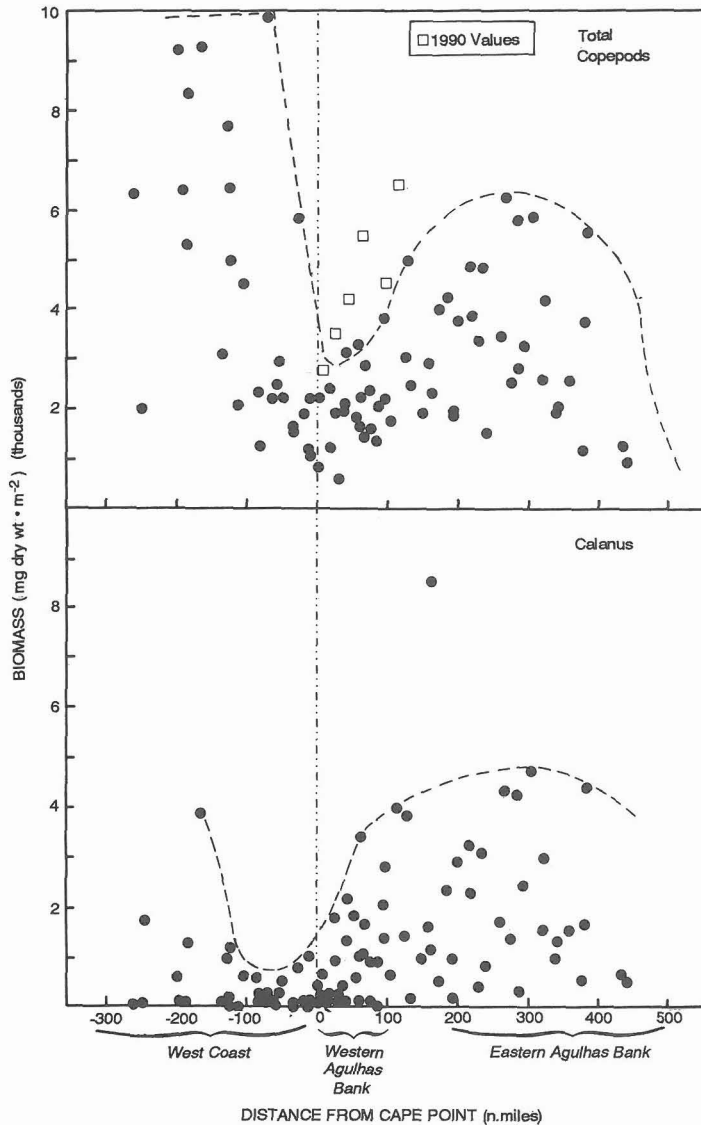


Figure 7. (a) Mean copepod and (b) *Calanus* standing stock per transect plotted against distance from Cape Point, all years combined. November 1990 values for the western Agulhas Bank (0–100 nautical miles east of Cape Point) are open squares.

double, the abundance on the eastern Agulhas Bank (EAB) is roughly five times that on the western Bank (WAB). However, the greater proportion of juveniles on the EAB results in the biomass (dry wt) only being twice as high on the EAB as on the WAB. There has been an apparent increase in the proportions of young stages in the population, particularly on the western Bank, in the period 1991–1993. Biomass on the EAB declined from 1988 to 1992 and increased again in 1993. On the western Bank, biomass peaked in 1990, largely as a result of an increase in older stages. The changes in circulation on the Bank that occurred in November 1990 (Boyd and Shillington, 1994), resulted

in quite an altered distribution of *Calanus* biomass on the Agulhas Bank (Fig. 9), with a shift to the west relative to other years.

Mean production:mean biomass (P:B) ratios for juveniles and adult female *Calanus* (Fig. 10) showed that trends in female egg production did not mirror changes in juvenile growth rates on the Agulhas Bank. Juvenile growth rates in 1988 and 1989 were somewhat lower than those in 1990–1993. Even between stages, there was little predictability of moulting rate from one stage to the next (Fig. 11), even though all slopes were significant. Egg production by copepods on the west coast (18–40% of the maximum obtained from

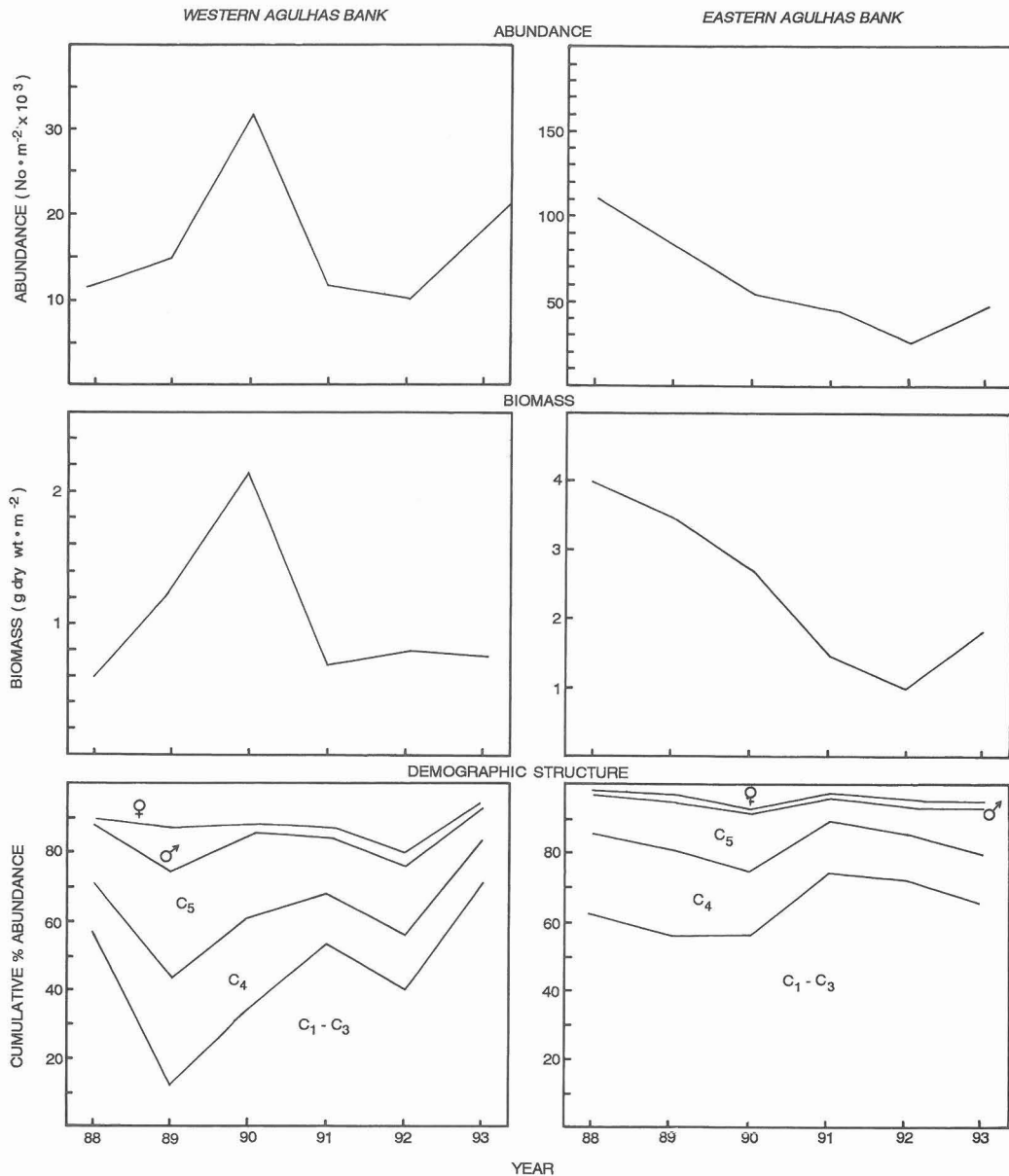


Figure 8. *Calanus* abundance (No. m⁻²), standing stock (g dry wt m⁻²) and demographic structure on the eastern and western Agulhas Bank from 1988 to 1993.

laboratory experiments with excess food) was always considerably higher than egg production by *Calanus* on the Agulhas Bank (2% of maximum), in keeping with the higher Chl *a* concentrations and larger cells present downstream from the upwelling centres on the west coast (Fig. 4). Water temperatures in the mixed layer are generally cooler on the west coast than on the Agulhas Bank, so it would appear that food has a greater influence than temperature on egg production. Figure 12 shows that the average growth rate decreases almost linearly with the logarithm of the body size for the

western and eastern Agulhas Bank. Significantly higher growth rates of N6-C3 were observed on the eastern Bank compared with the western Bank, despite there being slightly higher Chl *a* concentrations and larger cells on the western Bank. However, these values include concentrations along the inshore edge of the western Bank where *Calanus* is seldom very abundant (Fig. 9). The average for all six years indicates that P:B ratios predicted from body size alone may be good approximations of turnover time, with a change in slope between C3 and C4.

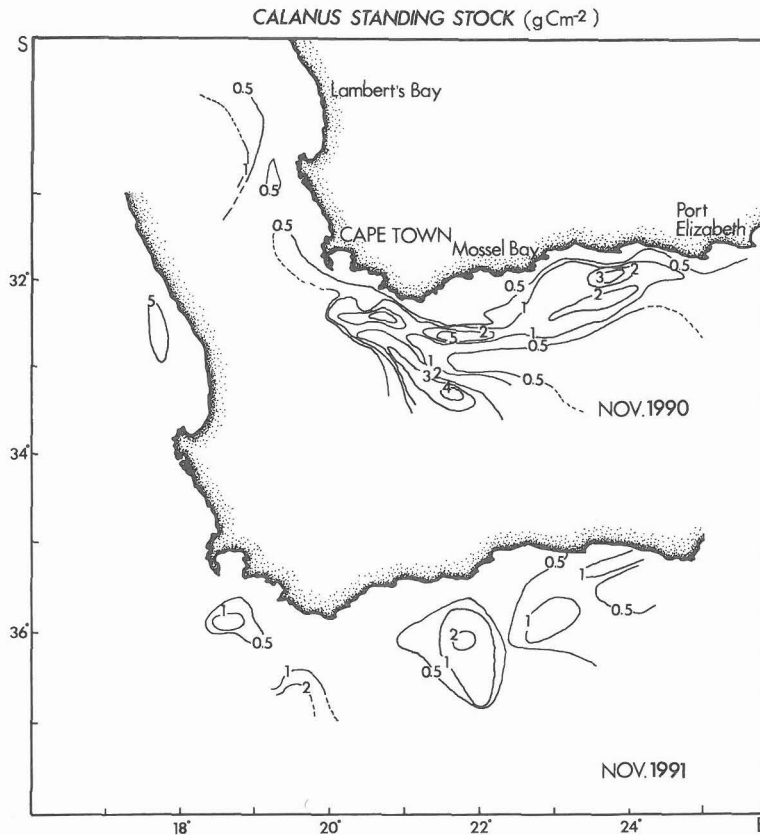


Figure 9. Distribution of *Calanus* standing stock (g dry wt m^{-2}) in November 1990 and 1991, showing the displacement of high biomass to the west in 1990. Latitude and longitude apply to lower figure.

P:B ratios for each stage showed considerable variation when regressed against Chl *a* with Ivlev curves (Fig. 13). Maximum values were well defined but considerable scatter existed in the plots, particularly in the region between 1 and 4 $\text{mg Chl } a \text{ m}^{-3}$, where the relationship would be most useful for modelling purposes. Similar plots using a variety of cell size categories from particle counter data did not materially improve the data fit between food availability and growth rate. Maximum P:B ratios agree well with the maxima calculated from laboratory experiments (Peterson and Hutchings, 1995), and indicate that production rates at sea are, on average, considerably lower than maximal rates determined under laboratory conditions with excess food. While incubation temperatures were centred around 17 to 19°C, they ranged from 16 to 21°C, and removal of the temperature effect on growth may improve the fit with food availability. Size fractionation of phytoplankton was attempted, but the use of a 15 μm screen for the period 1988–1992 limited the usefulness of the data.

As most of these efforts have been aimed at determining the food environment of spawning anchovy,

efforts have been made to match the production by copepods to estimated consumption by anchovy on the Agulhas Bank (Peterson *et al.*, 1992, and Fig. 14). The proportion of stations where anchovy cannot obtain their maintenance ration provides an estimate of the area within each zone which is suitable for fish feeding during the survey period. These values have been used in conjunction with fat content, gonad atresia, and advective parameters to determine the likelihood of subsequent recruitment success (Cochrane and Hutchings, in press; Peterson *et al.*, 1992). These results indicate that, apart from 1988, copepod production has always exceeded anchovy consumption on the western Agulhas Bank. However, gonad atresia in anchovy does fluctuate in sympathy with the percentage of starvation stations on the western Agulhas Bank (Fig. 14), indicating some response to food availability.

Discussion

While there are tremendous advantages to collecting a wide suite of dynamic hydrological and plankton

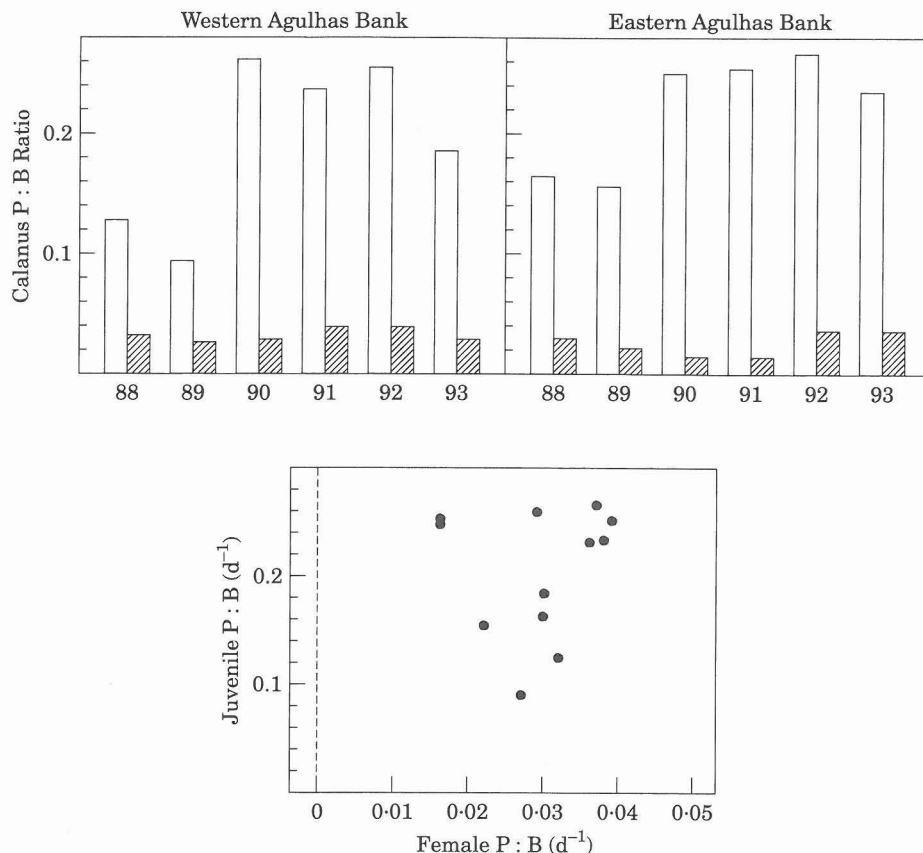


Figure 10. Daily P : B ratios for copepodites and adult female *Calanus* on the eastern and western Agulhas Bank, November 1988–1993, indicating the poor relationship between female egg production and juvenile growth. □ = C_1-C_5 ; ▨ = female.

parameters in conjunction with quantitative acoustics and fisheries biology data, the need for rapid surveying, minimal station time, and manpower constraints restrict the range and quality of plankton data that can be collected routinely.

Short-term changes in hydrology can rapidly alter the conditions observed during these surveys, particularly on the west coast (Mitchell-Innes and Walker, 1991; Pitcher *et al.*, 1991). Nevertheless, copepods usually respond rapidly to changes in conditions (Borchers and Hutchings, 1986; Armstrong *et al.*, 1991; Attwood and Peterson, 1991) and the ability to collect plankton and fish data concurrently over an extensive area of the shelf spawning habitat minimizes the effects of small-scale patchy distributions. There are a number of reasons why P : B ratios vary so widely: (a) conditions 1–5 days prior to sampling may have been different, in that animals may have experienced starvation or better feeding conditions; (b) animals ostensibly collected at the subsurface Chl *a* maximum may have been collected during retrieval of the net

from the near-surface layer; (c) vertically migrating animals, which would normally spend part of the time in deeper, darker, and cooler waters, were restrained in warm upper mixed layer temperatures under dim light for the duration of the incubation; (d) light shock may have occurred when animals that were collected from the subsurface Chl *a* maximum (1–4% light level) were exposed briefly to higher levels on the deck or under the microscope; (e) animals feeding on microzooplankton may have high production rates, unrelated to Chl *a* concentrations (Gifford and Dagg, 1989). In particular, it may be more appropriate to relate primary productivity rather than simply phytoplankton biomass to secondary productivity (Walker and Peterson, 1991). During these monitoring cruises we have had to ignore the vertical migratory and feeding behaviour of *Calanus*, although efforts are currently being made to rectify this omission.

It would appear that, despite the macroscale changes in winds during the past six years (Fig. 2), neither the hydrological structure nor the phytoplankton concen-

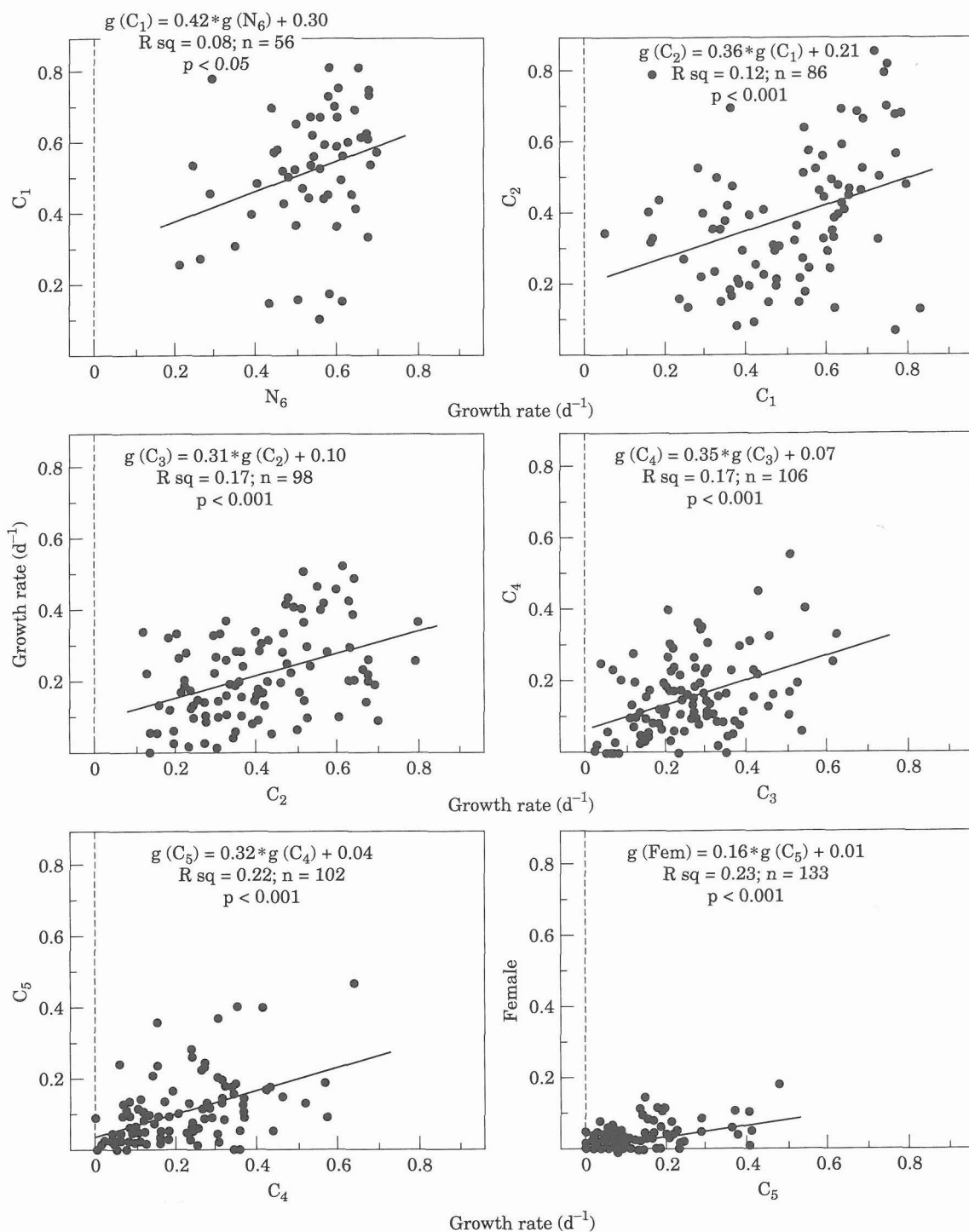


Figure 11. Relationships between growth rates of different stages. r^2 increase with stage, but are generally low.

trations altered substantially over the November survey periods, apart from circulation patterns in November 1990. The increase in the measured rates of growth of copepods in 1990 to 1993 compared with the 1988/1989

measurements does not appear to be related to changes in Chl *a* concentration or cell size (Fig. 5). Different handling techniques, as suggested by Peterson and Hutchings (1995), may have been partially responsible.

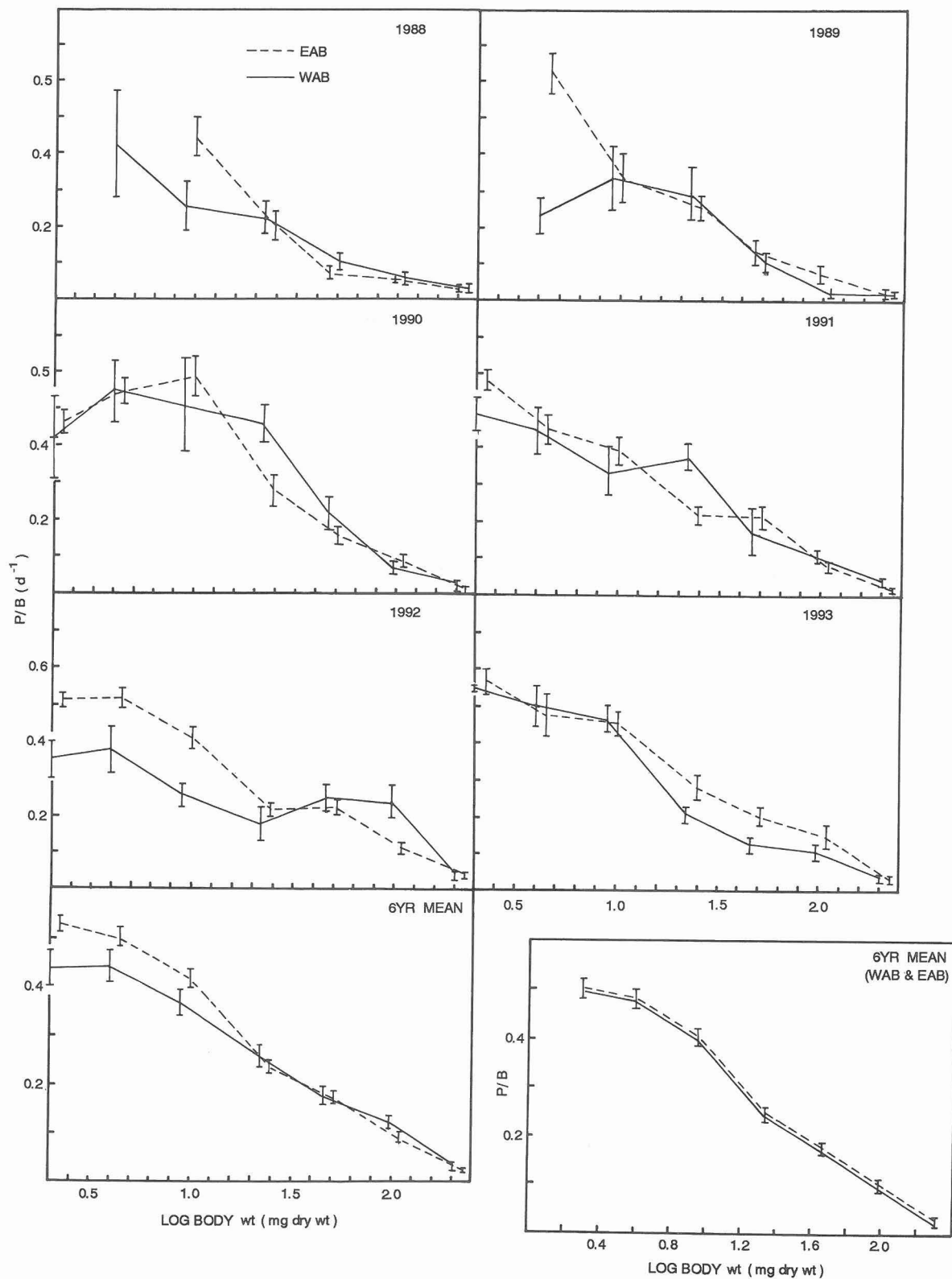


Figure 12. P:B ratios per stage and year for the western (WAB) and eastern (EAB) Agulhas Bank. Lowest two panels = mean values. Vertical bars are std. errors.

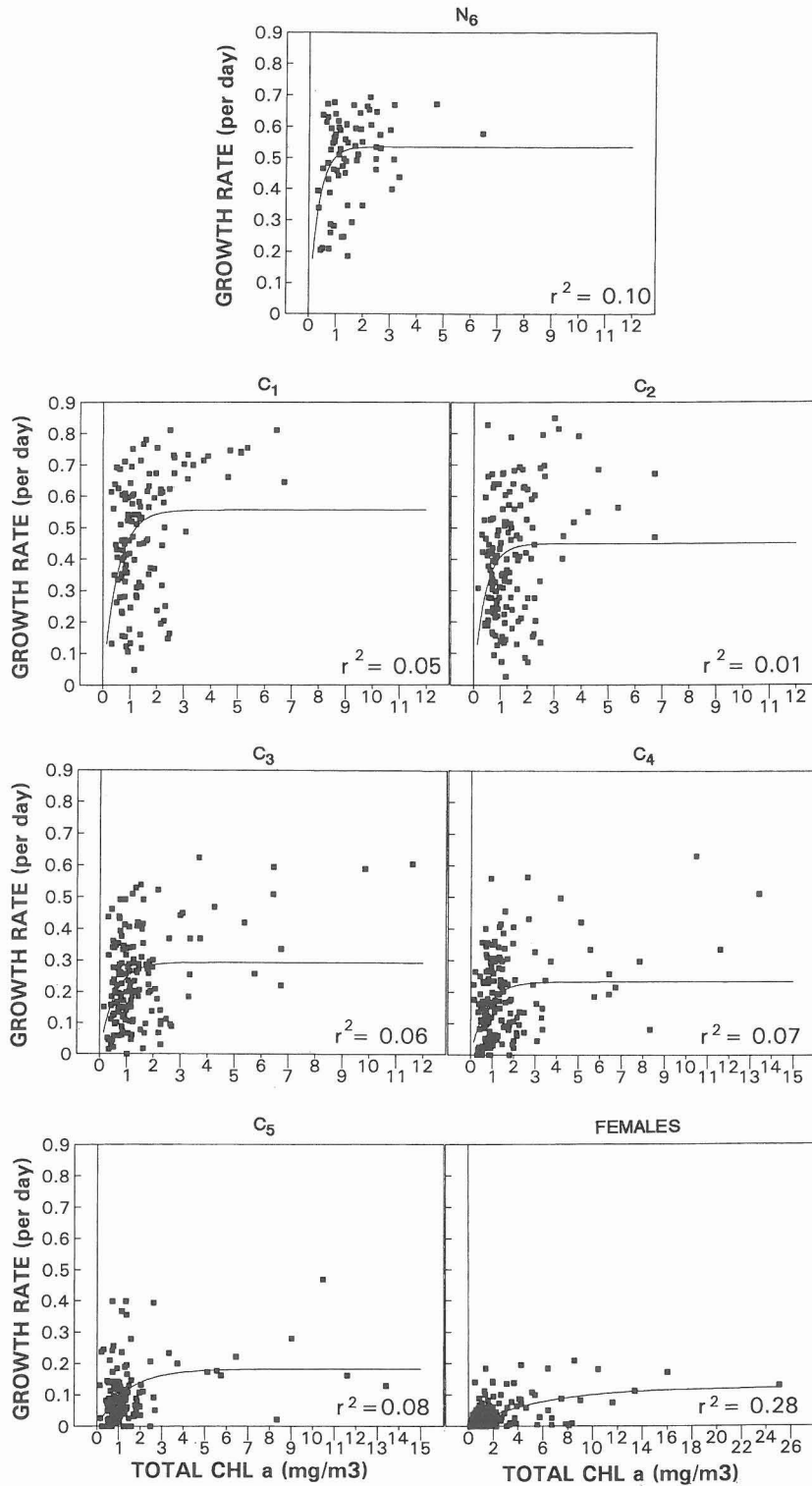


Figure 13. P : B ratios (d^{-1}) vs total Chl *a* ($mg\ m^{-3}$) for each stage. Ivlev curves fitted to each series indicate a significant correlation but poor predictability, and maximum rates are underestimated by the regression line.

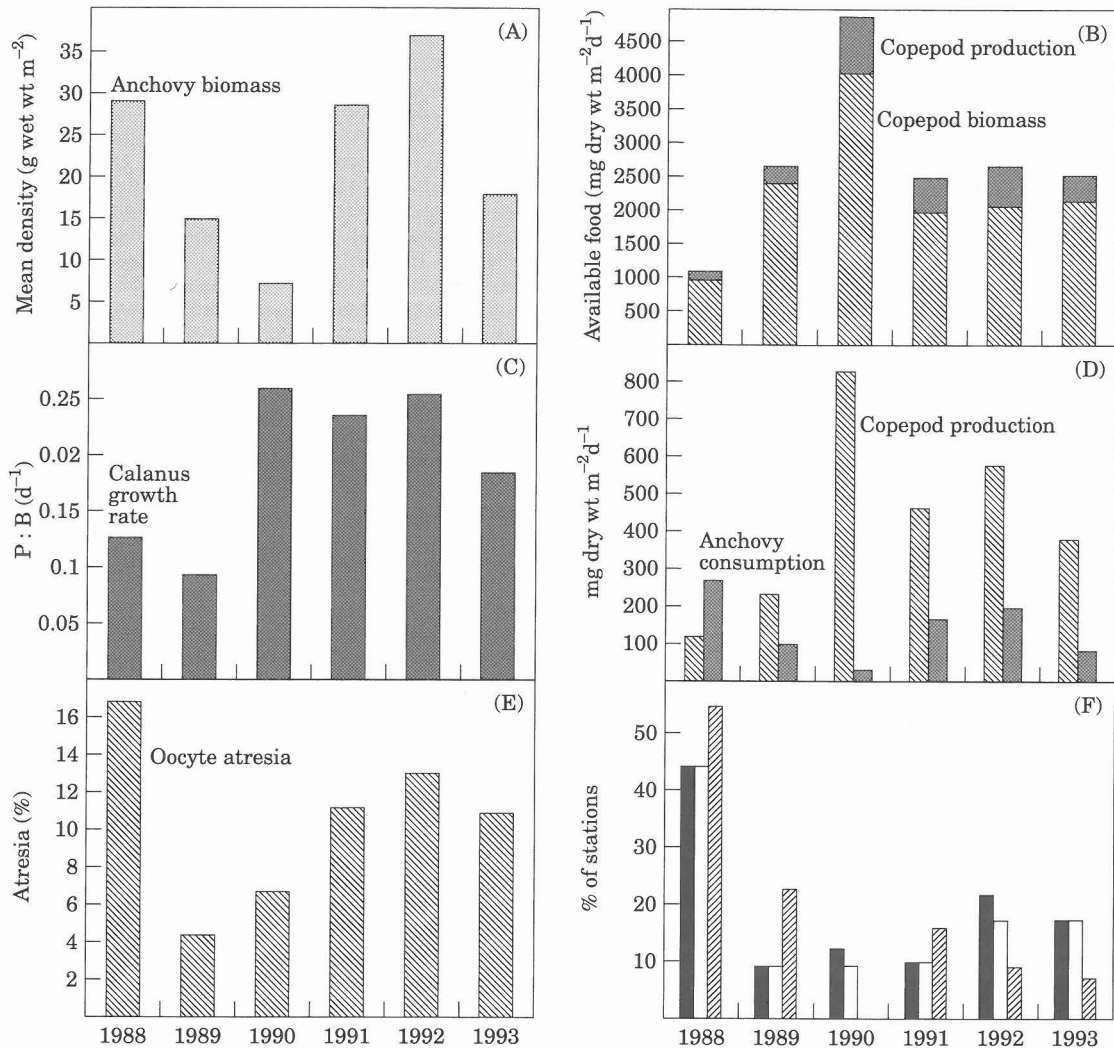


Figure 14. Composite of anchovy and plankton information for the western Agulhas Bank to assess the suitability of the area for sustained spawning. The starvation index is calculated in two ways: (a) when copepod biomass (+ production) is less than a minimum of 780 mg dry wt m⁻², or (b) when fish consumption, calculated as the daily minimum maintenance ration of 2% dry weight of fish biomass, is greater than zooplankton production estimates. The stations where the fish are unable to obtain a maintenance ration are classified as starvation stations. When oocyte atresia is high it is unlikely that the anchovy will be able to sustain further serial spawning. Starvation index: ■ = $B < 780 \text{ mg m}^{-2}$; □ = $B+P < 780 \text{ mg m}^{-2}$; ▨ = $\text{CONS.} > \text{PROD.}$

The changes in circulation in 1990 and lack of anchovy predators in 1989 and 1990 (Fig. 14) were accompanied by large variations in the biomass and size structure of the copepods on the Agulhas Bank in 1990 (Figs. 8 and 9), which resulted in very good feeding conditions for a depleted spawning anchovy population on the western Bank, with high concentrations of late-stage copepods. Subsequent recruitment of anchovy in 1991 was the best on record (Cochrane and Hutchings, 1995). Deeper thermoclines in November 1990 resulted in lower Chl *a* concentrations and smaller cells but apparently better survivorship of anchovy recruits, contrary to the views

that fish production depends on large cells and new production (Cushing, 1989).

From this large data set of direct measurements of copepod production, it is clear that the main variable controlling production is not growth rate, which can be derived from body size (Fig. 12, but see Huntley and Lopez, 1992), but the variations in biomass and demographic structure. These have apparent inverse relationships with fish density on the spawning grounds but are also associated with changes in circulation patterns. At high fish densities, e.g. November 1988, there is a critical balance between fish consumption and

copepod production, making it necessary to monitor the dynamics of the copepod population routinely. However, the high variance observed in relationships between food or temperature and copepod production, or trying to use production measurements of one stage to predict results for another stage, makes it difficult to find alternatives that are less labour-intensive than direct growth measurements of all stages. Technological improvements to assess the standing stock of copepods with acoustics or optics and to derive growth rates would do much to make monitoring of the complex interactions between spawning pelagic fish and their copepod prey easier. Integrating microscale events important to copepods over scales appropriate to the spawning area of pelagic fish remains a challenge for the GLOBEC initiative in the future.

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