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# THE EFFECT OF SEA TEMPERATURE AND FOOD AVAILABILITY ON THE SPAWNING SUCCESS OF CAPE ANCHOVY *ENGRAULIS CAPENSIS* IN THE SOUTHERN BENGUELA

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Data on the thermal structure, copepod biomass and production, and total number of eggs 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 off the South-Western Cape, 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 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 Bank was highest 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 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, the number of anchovy eggs was regressed against the area of 16–19°C water; a significant, positive relationship ($p < 0.001$, $r^2 = 0.56$, $n = 17$) was found. An implication of the hypothesis is that the duration of spawning may be important to recruitment.

Over the past decades, the Cape anchovy *Engraulis capensis* has supported a large purse-seine fishery in South Africa. Management of the 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 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, Bakun and Parrish 1981), whereas factors that affect spawning success may also play an important role.

Anchovy spawn on the western Agulhas Bank between September and February (Shelton 1986, Melo 1994a). During this protracted spawning season, they spawn serially, probably between 14 and 20 times in a season (Melo 1994b). Their spawning products are then transported from the western Bank, around Cape Point and northwards along the West Coast to the recruitment grounds between St Helena Bay and the Orange River Mouth (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 (S. J. Painting, Sea Fisheries [SF], unpublished data) 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.* 1991, Hutchings 1992, Melo 1994b). If anchovy do not meet their metabolic requirements, they undergo ovarian atresia (Hunter and Goldberg 1980, Melo 1994b) and may cease spawning for the remainder of the season

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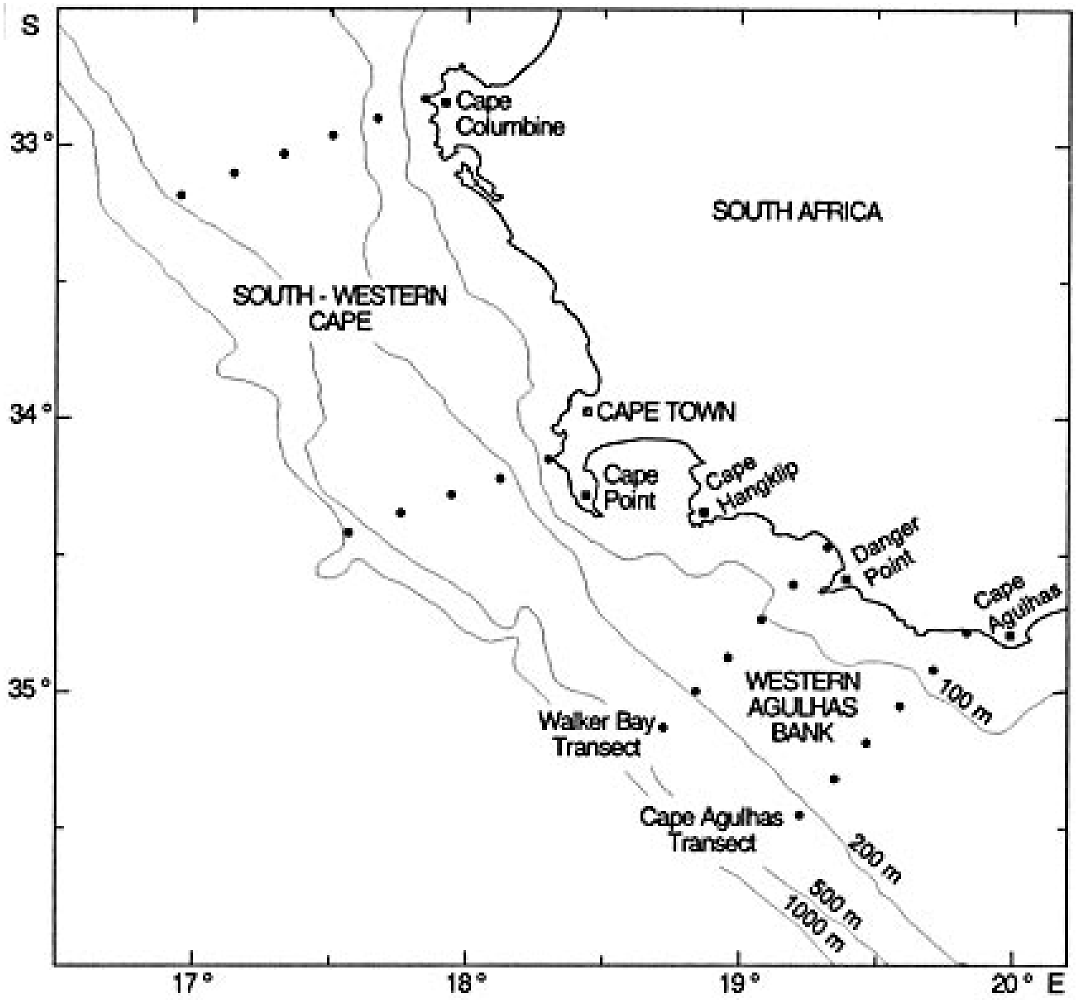


Fig. 1: The study area showing the transects and station positions off the South-Western Cape and on the western Agulhas Bank sampled during SARP seasons 1993/94 and 1994/95

(Hunter and Macewicz 1985). On the western Agulhas Bank, copepods dominate the diet of anchovy (James 1987), despite this region having a lower copepod biomass than the more productive South-Western Cape (Pillar 1986, Hutchings *et al.* 1995). Therefore, it is believed that anchovy on the western Bank are often 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 determining spawning success.

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

(i) Why do anchovy spawn in the low food environment of the western Agulhas Bank and not off the more productive South-Western Cape?
(ii) Why do anchovy prefer to spawn in 16–19°C water?
(iii) Can anchovy spawning success be explained (and predicted) in terms of environmental variables?

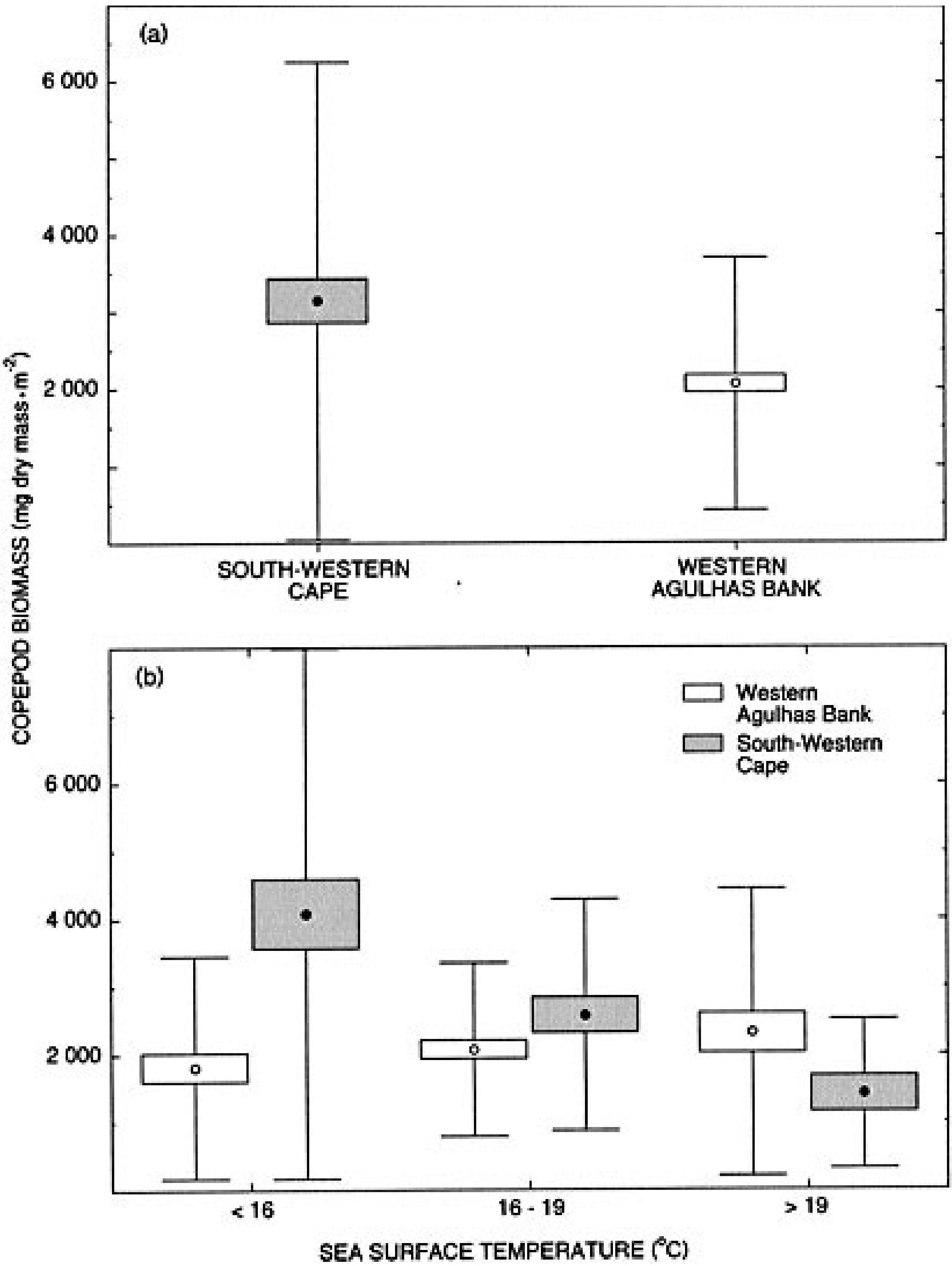


Fig. 2: Comparison of copepod biomass off the South-Western Cape and on the western Agulhas Bank for (a) all temperatures combined and (b) grouped into temperature ranges (<16°C, 16–19°C and >19°C). The box is one standard error and the whisker is one standard deviation

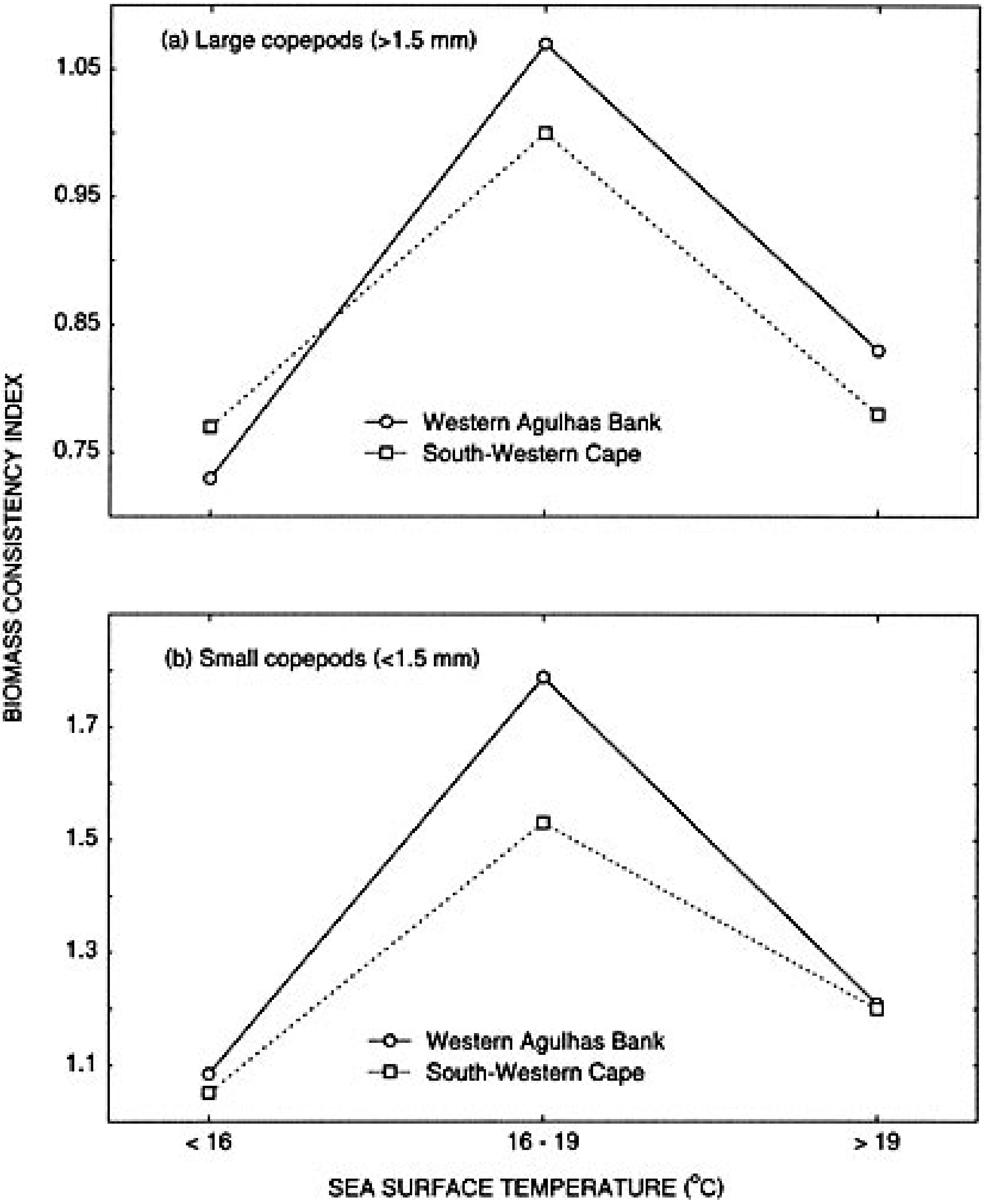


Fig. 3: Index of the consistency of copepod biomass (the ratio of the mean to the standard deviation), grouped into <16°C, 16–19°C and >19°C temperature ranges for the western Agulhas Bank and off the South-Western Cape; (a) large copepods and (b) small copepods

## MATERIAL AND METHODS

Sampling was conducted monthly between August 1993 and March 1994 and between September 1994 and March 1995 (except January 1995) aboard the Sea Fisheries vessels F. R. S. *Algoa* and F. R. S. *Africana* and the Norwegian research vessel *Dr Fridtjof Nansen*. Four transects, three of which consisted of six stations and one of five stations (10 miles apart), were sampled (Fig. 1). Data were collected from both the South-Western Cape and the western Agulhas Bank as part of the South African Sardine Anchovy Recruitment Programme (SARP, Painting 1993). At each station, a vertical temperature profile was obtained by means of an electronic bathythermograph. Hourly wind data prior to and during each cruise were collected from the Cape Point lighthouse. These data are representative of the winds on the western Agulhas Bank to at least Danger Point (L. Hutchings, SF, unpublished data), although farther east the wind has an increasingly westerly component (Jury 1988). On the western Bank, south-easterly winds are favourable for upwelling and north-westerly winds for downwelling (Boyd *et al*. 1985). In that region, a two-day time delay occurs between the onset of upwelling-favourable winds and surface upwelling (Jury 1988).

At each station, anchovy eggs in the upper 70 m of the water column were collected by means of a Calvet net and counts were standardized to numbers·m$^{-2}$ from knowledge of the volume of water filtered by the net. The total number of eggs on the western Agulhas Bank was calculated according to Fowler (1998). It was assumed that the total number of anchovy eggs in the region is an index of spawning intensity. Zooplankton in the upper 200 m were collected by means of a vertically towed Bongo net (0.255 m$^2$ mouth area) of 200-µm mesh. Samples were preserved in 5% buffered formalin. Copepods were identified to species, staged and counted, and their numbers were converted to biomass (mg dry mass·m$^{-2}$) using body mass values from Verheye (1991) and Peterson *et al*. (1992). Estimates of copepod growth rate for *Calanus agulhensis*, the dominant copepod by mass on the western Agulhas Bank (Verheye *et al*. 1994), were determined from daily rates of egg production of females and daily moulting rates of juveniles using the bottle incubation technique (Hutchings *et al*. 1995).

Three measures were used to estimate the food available to anchovy. First was copepod biomass, 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, i.e. the amount of copepod biomass that may be removed each day without depleting the ambient biomass. This value was calculated by multiplying the biomass of each copepod species by their daily growth rate, which was estimated by applying growth rates obtained for *C. agulhensis* developmental stages, assuming size-dependence. 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. Because anchovy prefer to eat large copepods (James and Findlay 1989), the index of copepod consistency and the estimate of production were separated into two size fractions: small copepods (<1.5 mm total length) and large copepods (>1.5 mm).

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 examining otoliths by 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 (StatSoft 1996). 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 Software), and was taken as the mean percentage in the upper 200 m for the two transects on the western Bank. Because the hydrographic variables had different scales of measurement, each variable ($X_j$) was stan-dardized to:

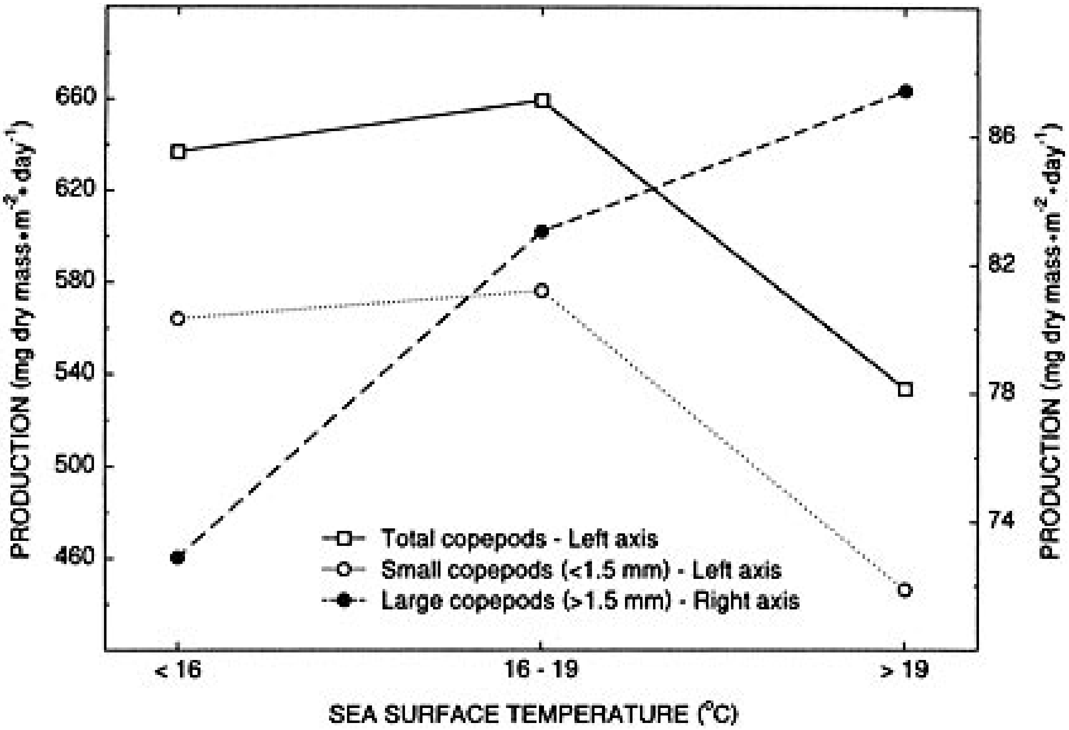


Fig. 4: Total daily copepod production in <16°C, 16–19°C and >19°C water on the western Agulhas Bank

$$\frac{X_j - \overline{X}_j}{S_j} \quad ,$$

where $\overline{X}_j$ is the mean and $S_j$ the standard deviation of variable $j$, before classification.

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 × 1.08 km. Only images with <30% cloud cover on the western Agulhas Bank were used. Images from 12 SARP cruises (except August 1993 and September 1994) and five November Spawner Biomass Surveys (1988–1992) satisfied this criterion. The percentage of the cloud-free area with water temperatures between 16 and 19°C was then calculated from each image by pixel summation.

All statistical testing using $t$-tests, $F$-tests and ANOVA were performed on log-transformed data to reduce heteroscedasticity and improve normality. Homogeneity of variance among groups was then verified using Levene's test (Millikan and Johnson 1984, as cited in StatSoft 1996).

## RESULTS

During the anchovy spawning season, the mean SST on the western Agulhas Bank was significantly higher (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, $p < 0.001$, $df = 311$). Also, the variability in temperature on the western Bank was significantly lower than off the South-Western Cape ($F$-test, $p < 0.05$). Consequently, water between 16 and 19°C was more common on the western Bank, where it occurred at 47% of the stations, compared to 35% off the South-Western Cape.

Copepod biomass over the two seasons was significantly higher off the South-Western Cape than on the western Bank (Fig. 2a, $t$-test, $p < 0.001$, $df = 311$). However, copepod biomass in 16–19°C water was not significantly different between the two regions (Fig. 2b, $t$-test, $p > 0.05$, $df = 128$). Copepod biomass increased slightly in warmer water on the western Bank, although the increase was only marginally significant (Fig. 2b, ANOVA, $p < 0.1$, $n = 197$), but

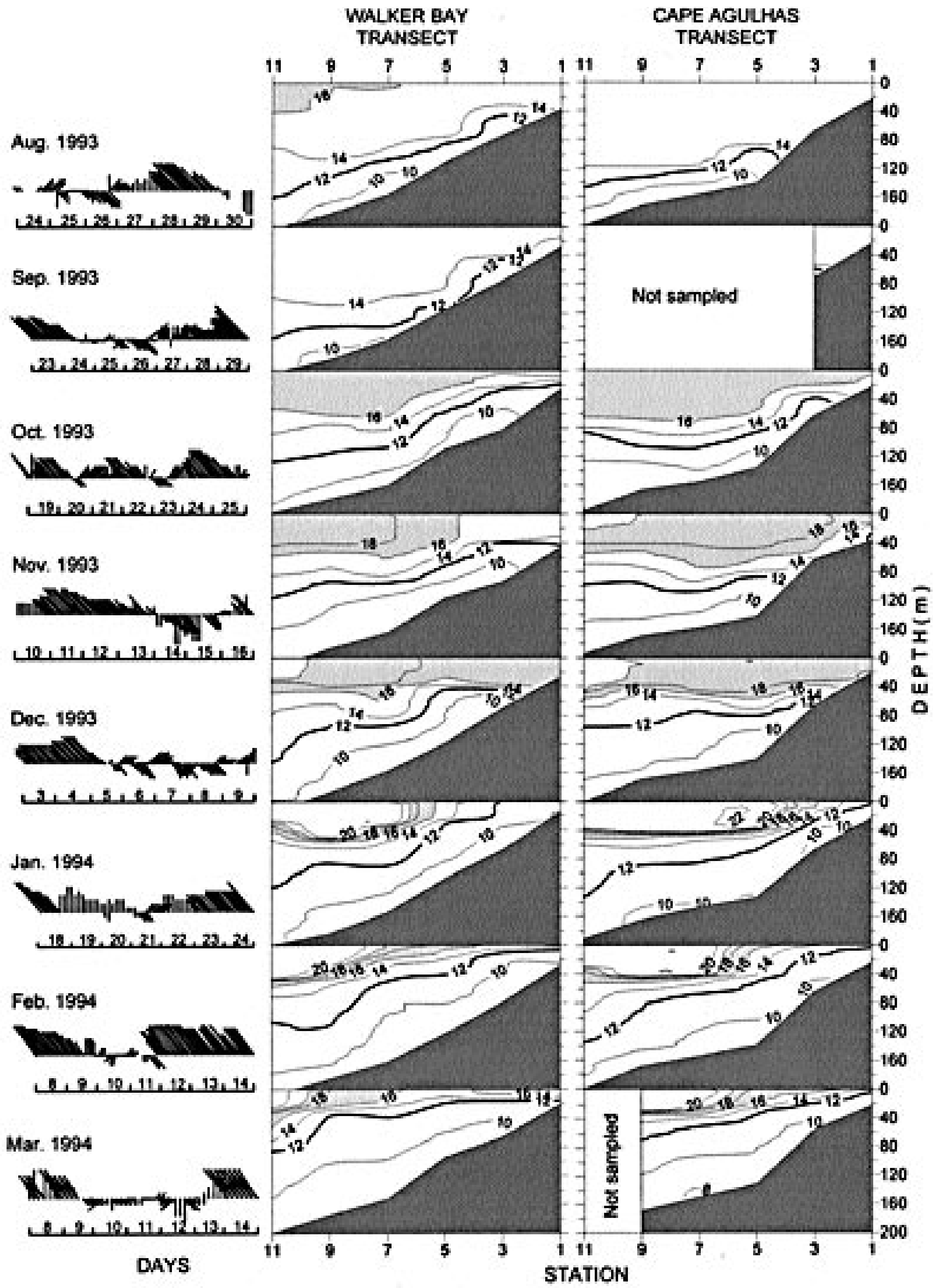


Fig. 5: Vertical sections of the thermal structure of the Walker Bay and Cape Agulhas Transects on the western Agulhas Bank between August 1993 and March 1994. The stippled area shows water between 16 and 19°C. Stick vectors depict the wind speed and direction one week prior to each survey

Table I: Mean values of hydrographic variables for the three periods defined by the cluster analysis; winter, spring and summer

| Period | Maximum SST (°C) | Minimum SST (°C) | Maximum UML depth (m) | Minimum UML depth (m) | Frontal strength (°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 |

SST = Sea surface temperature
UML = Upper mixed layer

decreased markedly off the South-Western Cape (ANOVA, $p < 0.001$, $n = 116$). In terms of the consistency of copepod biomass, 16–19°C water on the western Bank was a better food environment for anchovy than off the South-Western Cape (Fig. 3). Furthermore, the consistency of copepod biomass was maximal in 16–19°C water for both small and large copepods (Fig. 3). The biomass of small copepods was also more consistent than the large copepod biomass.

The daily production of small and large copepods for different temperature ranges on the western Bank is shown in Figure 4. Production of small copepods was relatively constant at around 560 mg·m$^{-2}$·day$^{-1}$ in water <19°C, decreasing to 460 mg·m$^{-2}$·day$^{-1}$ in warmer water. Production was substantially lower for large copepods, increasing from 73 mg·m$^{-2}$·day$^{-1}$ in <16°C water to 87 mg·m$^{-2}$·day$^{-1}$ in >19°C water. Production of large copepods was highest in water >16°C and production of small copepods was highest in <19°C water. Total copepod production was slightly higher in 16–19°C water (Fig. 4).

Food conditions for anchovy, in terms of production and the consistency of copepod biomass, appear to be optimal in 16–19°C water. The temporal changes in that water mass in relation to the hydrography of the western Agulhas Bank were investigated for the 1993/94 and 1994/95 seasons and are presented in Figures 5 and 6 respectively. The temperature regimes were similar between the Cape Agulhas and Walker Bay transects. The cluster analysis of the descriptive hydrographic variables for each month identified three seasonal periods: winter (August-September), spring (October-December) and summer (January-March, Fig. 7). The mean values of the descriptor variables in each of these periods are shown in Table I. 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 (Table I, Fig. 6 – September 1994). A deep (to approximately 100 m), upper mixed layer was present and fronts were weak (Table I, Fig. 5 – August 1993, September 1993; Fig. 6 – September 1994). Cold bottom water was deep; the 10°C isotherm was below 130 m and there was a relatively low 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 I). Although there were occasional south-easterly winds in winter, the cold bottom water never reached the surface.

During spring, mid-shelf surface waters warmed to 19°C and the upper mixed layer shallowed (Table I, Fig. 5 – November 1993; Fig. 6 – 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 downwelling and quiescence were common (Fig. 5 – November 1993; Fig. 6 – November 1994). South-easterly winds caused occasional surface upwelling, with its characteristic frontal signature (Fig. 6 – December 1994 – Walker Bay Transect). An oceanic front (20°C) was often present (Fig. 6 – December 1994). In spring, 30% of the shelf water was 16–19°C, a marked increase from winter conditions (Table I).

During summer, cool water was located inshore and warm water offshore (Table I, Fig. 5 – January 1994; Fig. 6 – March 1995). South-easterly winds were more persistent in summer than in spring, upwelling cold, nutrient-rich water to the surface (Fig. 5 – January 1994, February 1994; Fig. 6 – March 1995). Cold bottom water moved up to within 35 m of the surface. The <12°C water moved farther onto the shelf and constituted >60% of the water in the upper 200 m. The surface mid-shelf water was warmer and a well-defined oceanic front varied between 15 miles (Fig. 5 – January 1994 – Cape Agulhas Transect) and 45 miles (Fig. 5 – March 1994 – Walker Bay Transect). Water of 16–19°C was situated between the upwelling and oceanic fronts. 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 (Fig. 5 – January 1994). During periods of north-westerly winds and quiescent conditions, the upwelling front submerged (Fig. 5 – March 1994 – Walker Bay Transect).

Such seasonality in the hydrography of the western

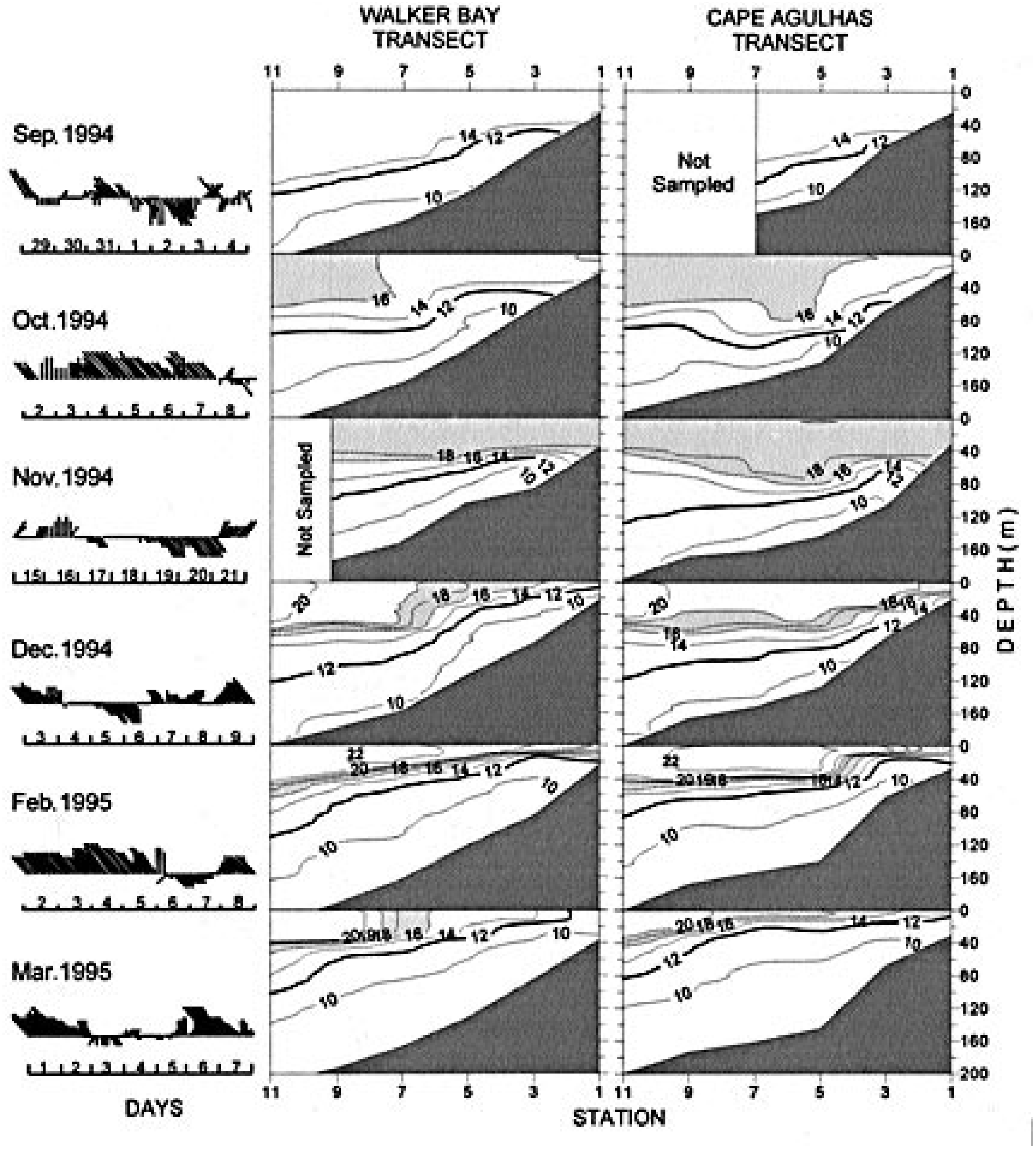


Fig. 6: Vertical sections of the thermal structure of the Walker Bay and Cape Agulhas Transects on the western Agulhas Bank between September 1994 and March 1995. The stippled area shows water between 16 and 19°C. Stick vectors depict the wind speed and direction one week prior to each survey

Agulhas Bank may have a marked affect on the spawning of anchovy. Thermal changes in the volume of 16–19°C water and the biomass of large copepods were similar, with a winter low, peaking in spring and decreasing sharply in summer (Figs 8a, b). This trend was also evident in the spawning success of anchovy (Fig. 8c) and in the birthdate distribution of the recruits the following year (Fig. 8d).

The relationship between anchovy egg numbers and the volume of 16–19°C water on the western

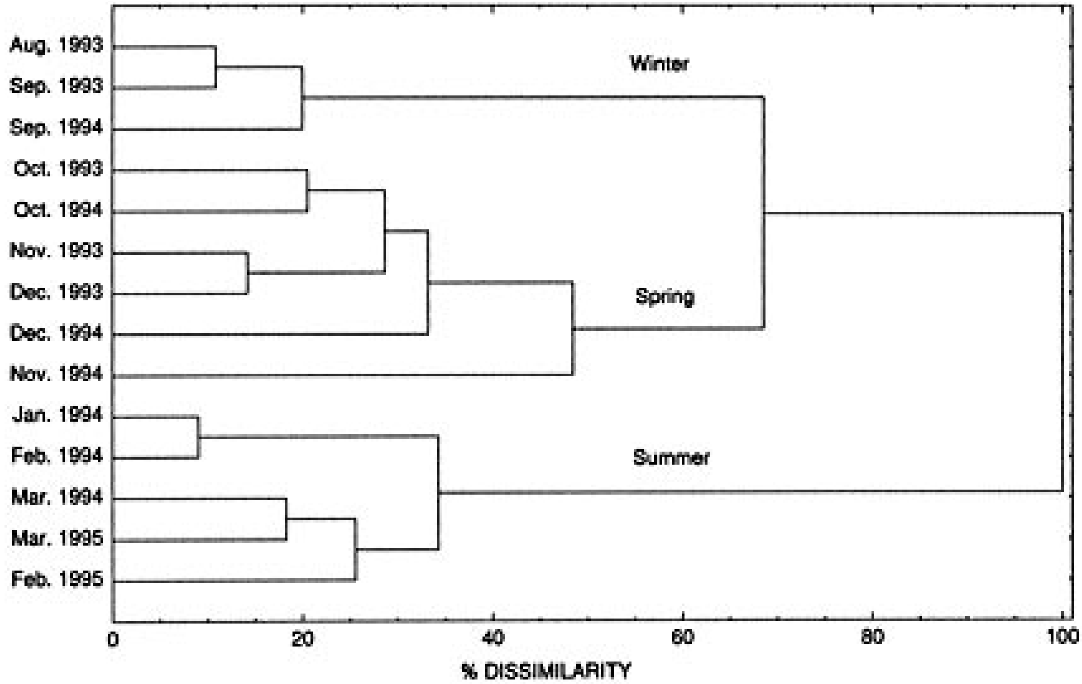


Fig. 7: A hierarchical cluster analysis showing three distinct periods (winter, spring and summer) in terms of the thermal structure of the western Agulhas Bank throughout the anchovy spawning season. The City-block (Manhattan) distance measure and the furthest neighbour amalgamation procedure were used on a suite of predictor variables (see text)

Agulhas Bank was quantified by regression analysis. A significant, positive correlation was found between the number of anchovy eggs over the entire western Bank and the volume of 16–19°C water (Fig. 9a, $p < 0.01$, $r^2 = 0.49$, $n = 12$). Anchovy egg number was only slightly less predictable for area than for volume ($p < 0.05$, $r^2 = 0.45$, $n = 12$), because of the strong correlation between the area and volume of 16–19°C water ($p < 0.001$, $r^2 = 0.93$, $n = 12$). The inclusion of other surveys (November 1988-1992 and 1995) improved the relationship (Fig. 9b, $p < 0.001$, $r^2 = 0.56$, $n = 17$). Two groups of points are apparent on Figure 9b, the winter and summer group at the lower end of the regression and the spring group at the upper end.

## DISCUSSION

The choice of a suitable 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 (Hutchings 1992). This strategy has the advantage of separating spawning products from spawners, so reducing cannibalism (Valdéz Szeinfeld and Cochrane 1992). In addition, the high stratification and thermal constancy found on the western Bank throughout the spawning season may benefit first-feeding larvae (Parrish *et al*. 1983) and reduce the likelihood of abnormalities in egg development, which can occur in <14°C water (King *et al*. 1978). This higher thermal constancy on the western Bank relative to the South-Western Cape 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 affect the choice of spawning area is the food available to spawners. Although copepod biomass was significantly higher 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 compensat-

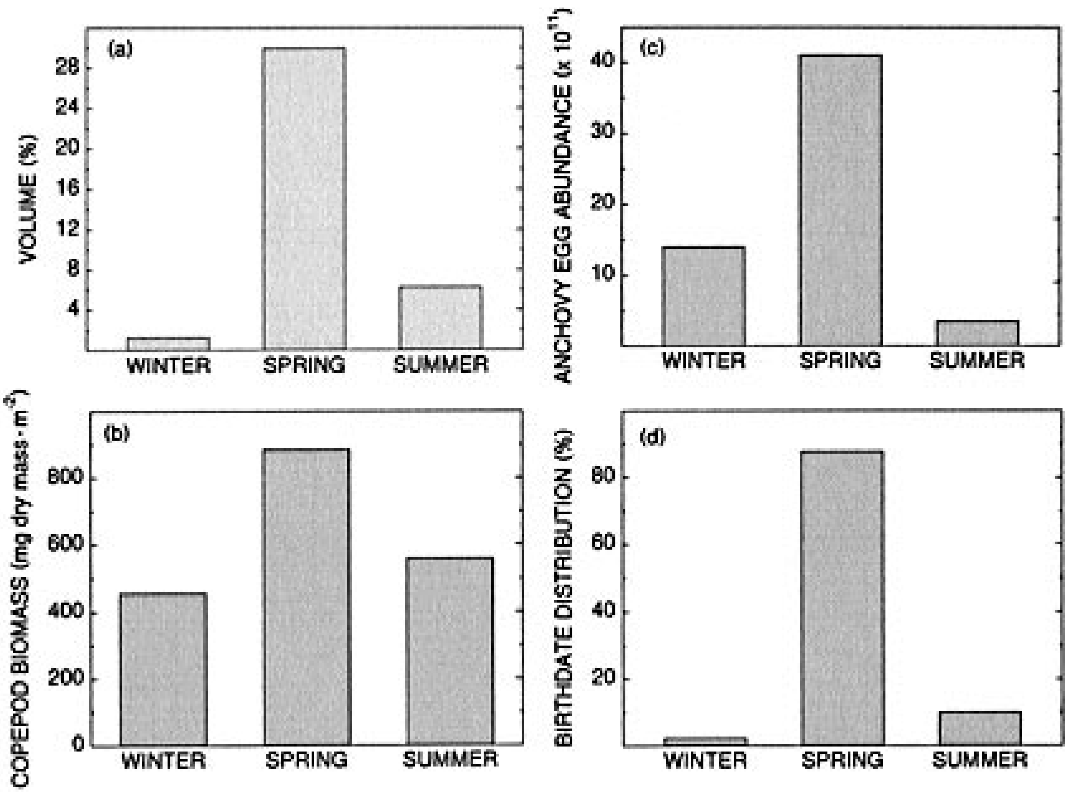


Fig. 8: Seasonal changes on the western Agulhas Bank of (a) the volume of 16–19°C water, (b) the biomass of large copepods, (c) anchovy egg numbers and (d) anchovy birthdates from recruits of 1994 and 1995

ing for the additional impact of predation by anchovy on the western Bank. A positive relationship was identified between the biomass of large copepods in 16–19°C water and anchovy spawning success on the western Bank (Richardson *et al.* 1996). Furthermore, that region had a more consistent food environment than off the South-Western Cape. A consistent food resource may prolong spawning in anchovy, especially in years when spawners have low fat reserves at the start of the 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 high energy intake at a relatively low energetic cost, so 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 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 high, total copepod production was low. Again, 16–19°C water was the optimal food environment, because it provided high production at a relatively low energetic cost. An added benefit of the high 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. Previous studies have found that the inner margin of the jet current, where most spawning products arelocated, is highly productive (Armstrong *et al.* 1987, Hutchings 1992).

Spawning success in anchovy appears to be dependent on the extent of a suitable spawning habitat, both spatially (16–19°C water) and temporally (spring). Underpinning this hypothesis is the positive relation-

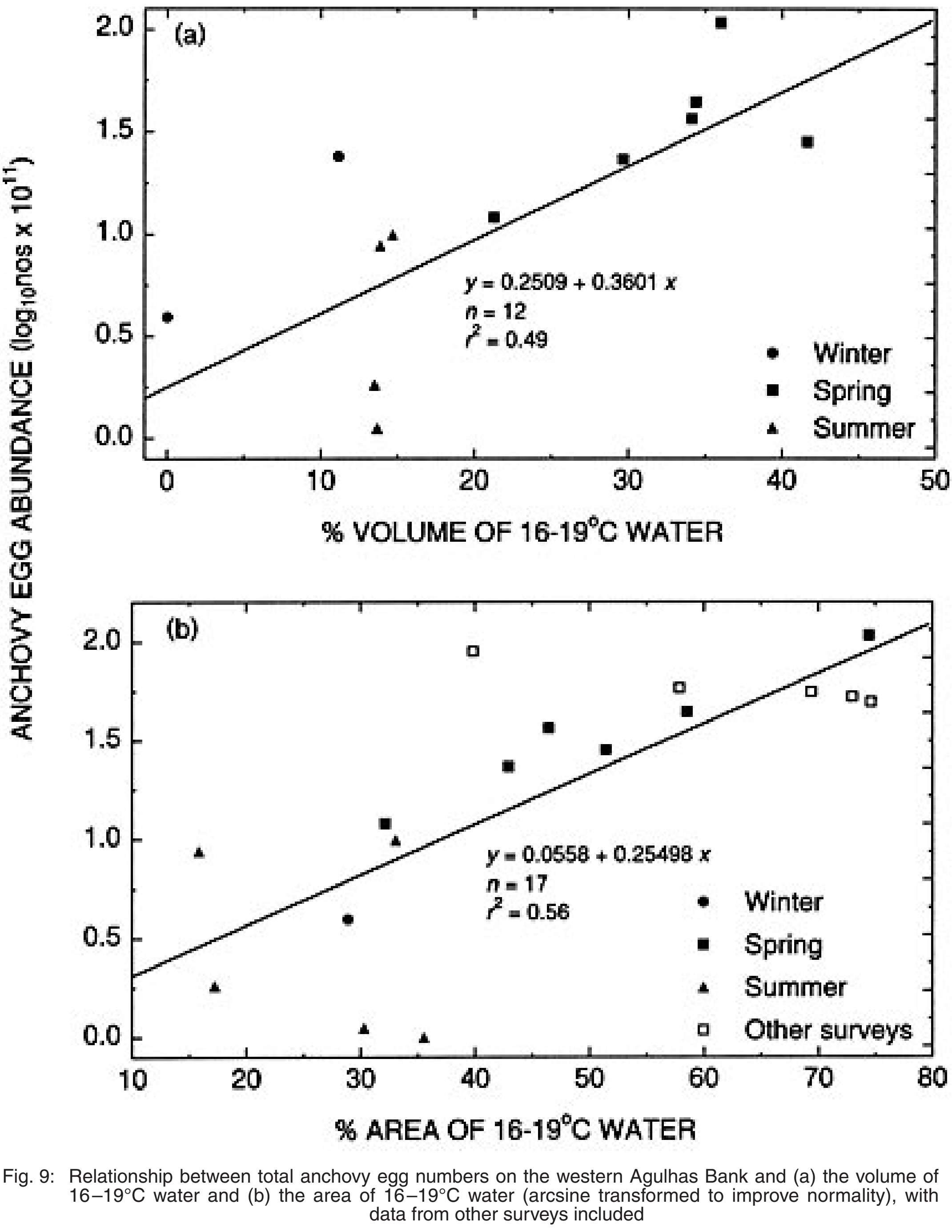


Fig. 9: Relationship between total anchovy egg numbers on the western Agulhas Bank and (a) the volume of 16–19°C water and (b) the area of 16–19°C water (arcsine transformed to improve normality), with data from other surveys included

ship between anchovy egg abundance and the area of 16–19°C water (Fig. 9b). This regression meets two important prerequisites for it to be considered realistic. First, the relationship was repeatable (within the limited set of other surveys that were available) and second, it was justifiable, based on the good food environment associated with 16–19°C water.

The extent of the spawning habitat is dynamic,

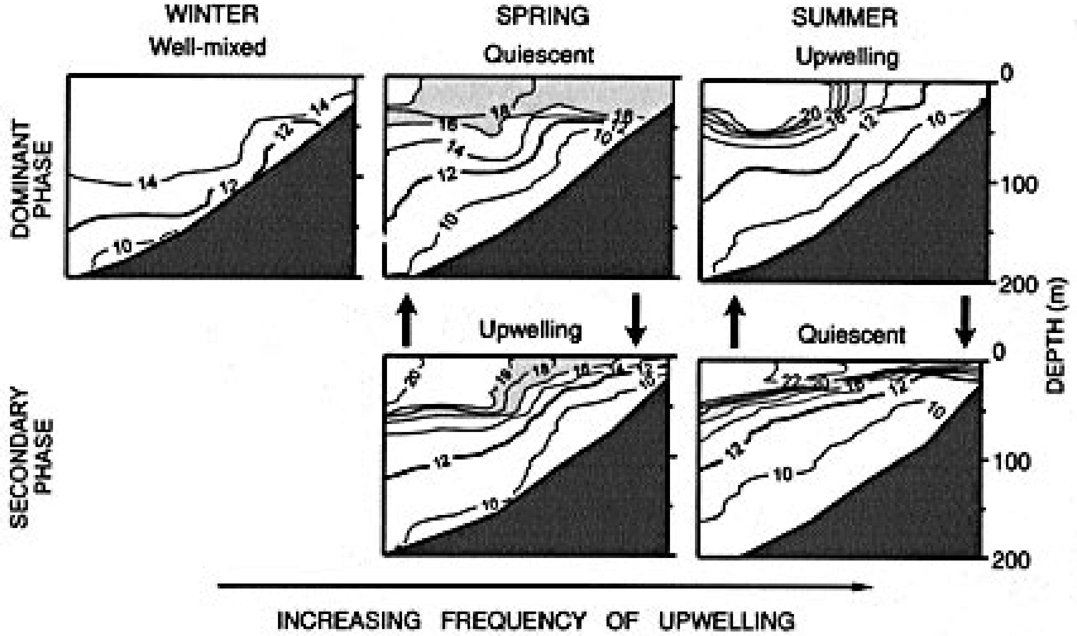


Fig. 10: The different phases of upwelling in winter, spring and summer in the southern Benguela. In winter, only the well-mixed phase occurs. In spring, there is a quiescent and an upwelling phase, with the quiescent phase dominant. In summer, the upwelling phase dominates the quiescent phase (modified from Mitchell-Innes, SF, unpublished data). The stippled area is 16–19°C water

both spatially and temporally, and is related to the increasing frequency of upwelling from winter to summer (Fig. 10). There is a very small area of 16–19°C water in winter, when the sea surface temperature is cool and conditions are well-mixed as a result of strong westerly winds (Chapman and Shannon 1987). In winter, upwelling of cold bottom water is infrequent, because south-easterly winds rarely upwell water from above the deep pycnocline (Mann and Lazier 1991).

During spring, the quiescent phase is dominant (Fig. 10). A large area of 16–19°C water is present as a result of a strongly-stratified water column, deep cold bottom water and relatively infrequent south-easterly winds (Jury 1988, Largier *et al.* 1992). This stratified water is bounded inshore by colder, newly-upwelled water and offshore by the oceanic front, which marks the transition from shelf waters to warmer oceanic waters. The region is dynamic and varies 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).

In summer, the upwelling phase is dominant. The bottom water occupies the inner-shelf region and the persistent south-easterly winds upwell water from below the pycnocline. This episodic, surface upwelling, coupled with frequent inshore movement of warm (>20°C) oceanic water, reduces the frequency of 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, are in spring (Fig. 8), when upwelling frequency and chlorophyll *a* concentrations are lower than in summer (Richardson 1998). Off the South-Western Cape, where the shelf is narrow and upwelling is strong, copepods are more concentrated inshore (Fig. 2, Andrews and Hutchings 1980, Hutchings 1981), where their food (chlorophyll *a*) is most abundant (Brown 1992). In contrast, copepod biomass decreases inshore on the western Bank (Fig. 2), suggesting that production may not be the major controlling process. Advective losses off the western Bank may influence the biomass of copepods (Richardson 1998), and at times may be greater than the advective input of copepods from the eastern Bank (Largier *et al.* 1992, Peterson *et al.* 1992). Advective flow and resulting loss of copepods from the mid-shelf may be greater during summer, 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 reduced and copepod biomass may increase. Therefore, the seasonal change in the relative magnitude of advective input and output of copepods on the western 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 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 lower copepod biomass being 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 high fecundity and protracted spawning season of anchovy not only increases the carrying capacity of the western Bank by spreading the predatory impact of anchovy on copepods over a longer period (Hutchings 1992) and reducing cannibalism, but it 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 is variable: e.g. during the years 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 1988/1989 ceased early in the season (November), 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 high production rates are important for successful spawning of 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 current 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.

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