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ASSESSMENT OF THE FOOD AVAILABLE TO CAPE ANCHOVY DURING THEIR SPAWNING SEASON

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The Cape anchovy *Engraulis capensis* spawns serially between September and February each year on the western Agulhas Bank, South Africa. Food availability in terms of copepod biomass is important for successful spawning and subsequent recruitment. This note investigates the variability within a spawning season (1993/94 and 1994/95) of copepod biomass on the western Bank and demonstrates that the food available to the Cape anchovy cannot be adequately assessed by a single mid-season estimate, as was the previous sampling strategy. The mid-season estimate of food availability failed to reveal important fluctuations, such as the small biomass of copepods in January 1994, which contributed to the early cessation of spawning and subsequent poor recruitment in 1994. A strategy, based on monthly sampling, is recommended for future sampling programmes.

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 throughout a prolonged spawning season. The Cape anchovy *Engraulis capensis* also exhibits this reproductive strategy (Melo 1994a), spawning every 7–10 days between September and February each year (Shelton and Hutchings 1990, Melo 1994b). Energy for this intensive reproductive strategy is obtained from fat reserves and feeding during the spawning season (Hunter and Goldberg 1980). *E. capensis* spawn mainly on the western Agulhas Bank (Hampton 1992), where they feed predominantly on copepods (James 1987). Because the biomass of copepods in that region is relatively small, compared to other regions of the Agulhas Bank (Pillar 1986, Verheye *et al*. 1992, Hutchings *et al*. 1995, Richardson *et al*. in press), anchovy are sometimes food-limited (Peterson *et al*. 1992). Food limitation causes 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 number of eggs produced (Hunter and Goldberg 1980). Therefore, anchovy require continuous food throughout their spawning season for sustained serial spawning (Melo 1994a, Richardson *et al*. in press), especially when body fat reserves become depleted (Hutchings 1992).

To measure the food available to anchovy spawners, copepod biomass has been determined during the mid-season spawning peak in November (Shelton and Hutchings 1990). Food availability throughout the spawning season may provide an early forecast of recruitment, although the current time-series is too short to quantify this relationship (Cochrane and Hutchings 1995). Within-season changes of factors such as food availability, which may affect spawning success and hence recruitment of anchovy, were investigated during two seasons of the South African Sardine and Anchovy Recruitment Programme (SARP, Painting 1993). This note aims to answer the following questions:

(i) Is a mid-season estimate of food availability representative of the entire season?
(ii) Is there a significant interannual difference in food availability?
(iii) If the current sampling strategy is inadequate, how can it be improved?

MATERIAL AND METHODS

Sampling was conducted monthly between August 1993 and March 1994 (1993/94 season) and between September 1994 and March 1995 (1994/95 season) on the western Agulhas Bank aboard the South African F.R.S. *Algoa* and F.R.S. *Africana* and the Norwegian vessel, *Dr Fridtjof Nansen*. Generally, two cross-shelf transects were sampled, except in November 1993 and November 1994 when five and four were sampled respectively. Each transect consisted of six stations 10 miles apart, but occasionally seven stations were sampled on a transect. Not all stations were sampled each month as a result of adverse weather conditions, and

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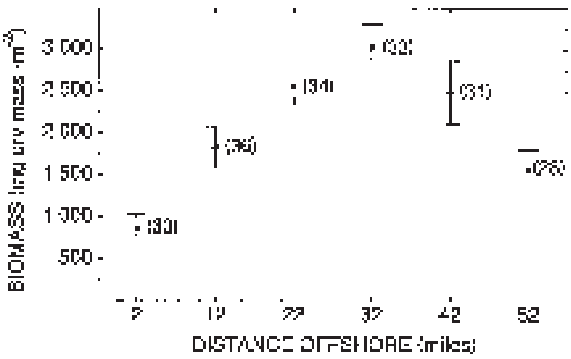

Fig. 1: Variation of copepod biomass (±*SE*) with distance offshore for the 1993/94 and 1994/95 seasons combined. Note that both transects for each month are included. The number of samples is shown in parenthesis

the September 1993 data were excluded from analysis because of the paucity of stations sampled. No sampling took place in January 1995.

Zooplankton in the upper 200 m was collected by means of a vertically towed Bongo net fitted with nets of 200-μm mesh. Samples were preserved in 5% buffered formalin. Copepods were identified to species and counts were converted to dry mass·m^{-2} using literature-derived values of body mass (Peterson *et al.* 1992, Verheye *et al.* 1992) and from knowledge of volume filtered and depth of tow. Data are presented by mass rather than numerically to provide a better measure of the potential food environment.

To analyse within-season changes in copepod biomass, a one-way Model I ANOVA, with month as the independent variable, was conducted for each spawning season. To identify significant differences between months, *a posteriori* multiple comparisons were computed using Tukey's HSD test. The representivity of the November estimate to the entire season was assessed by comparing the *t*-test results between November 1993 and 1994 with those of all data from each spawning season. Copepod biomass data were log-transformed to reduce heteroscedasticity and to improve normality. The assumption of homoscedasticity for the ANOVA and *t*-tests was verified using Levene's test (Milliken and Johnson 1984, in StatSoft 1996).

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-Bernal 1994). Power was determined from standard tables and is a function of the Type I error (α), average sample size (n_{av}) 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

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

where σ_m is the standard deviation of the treatment means and σ is the overall standard deviation.

When there are unequal sample sizes in each treatment, the following is applied:

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

where *k* is the number of treatments, n_i is the number of samples in each treatment *i*, m_i is the mean of each treatment *i*, *m* is the overall mean and *N* is the total number of samples.

Average sample size (n_{av}) is calculated from the equation

$$n_{av} = \frac{\sum_{i=1}^{k} n_i}{k} \quad ,$$

A power analysis is only conducted if no significant difference is found. Power analysis also provides information concerning the number of samples required (n_{av}) to obtain a desired level of power for specific values of α, *k* and *f*.

RESULTS

There was a two-fold variation in copepod biomass in both the 1993/94 (827–2 198 mg·m^{-2}) and 1994/95 (1 787–3 628 mg·m^{-2}) seasons. Despite these considerable within-season fluctuations, no significant differences in biomass were found among months in either season. This was because of the high within-month variability as a result of the comparatively low biomass at the inshore station (Fig. 1). Because the biomass at that station was significantly smaller than at any other station on the transect ($p < 0.0001$, $F = 19.28$, $n = 186$),

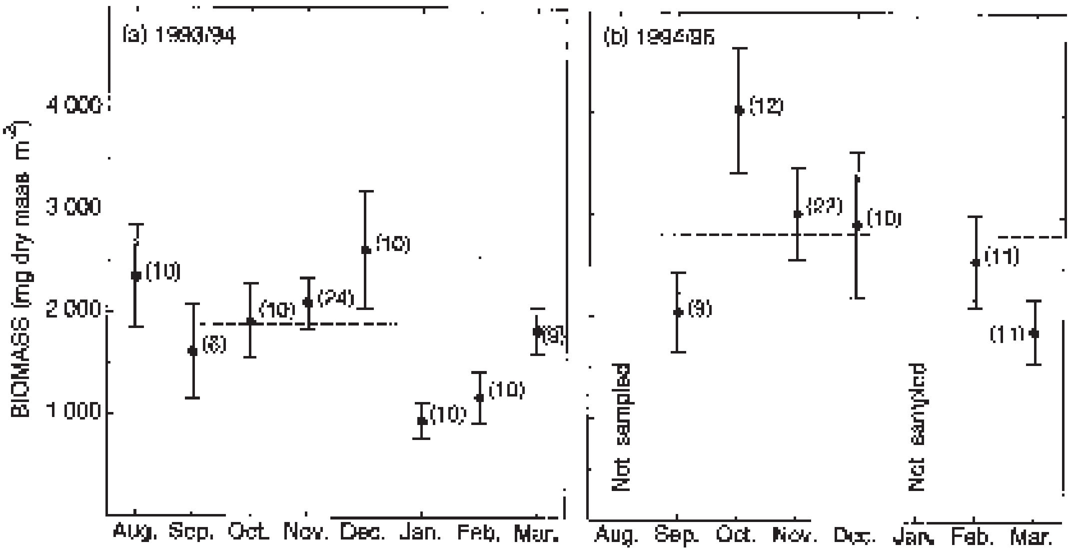

Fig. 2: Monthly variation in copepod biomass (±*SE*) for (a) 1993/94 and (b) 1994/95. The overall mean for each season is represented by a dotted line. The number of samples is shown in parenthesis

the inshore data were not included in further analyses. This is justified when relating copepod biomass to anchovy spawning success, because anchovy and their spawning products are mainly concentrated farther offshore (Anders 1965, Hampton 1992, Fowler and Boyd in press), where copepod production is higher and their biomass more consistent (Richardson *et al.* in press).

After removing the inshore station from the analysis, the effect of month was significant during 1993/94 ($p < 0.01$, $F = 3.74$, $df = 76$, Fig. 2a). The multiple comparisons showed that the only significant differences among months ($p < 0.05$) were that the biomass in January 1994 (946.74 mg·m^{-2}) was lower than in August 1993 (2 357.37 mg·m^{-2}), November 1993 (2 098.42 mg·m^{-2}) and December 1993 (2 623.35 mg·m^{-2}). In the 1994/95 season there was no significant difference in copepod biomass among months ($p > 0.05$, $F = 1.90$, $df = 69$, Fig. 2b).

Because there was no significant difference among months in 1994/95, the power of the analysis was determined (Equation 1). The power value was 62% ($\alpha = 0.05$, $k = 6$, $f = 0.357$, $n_{av} = 12.5$), which is below the commonly accepted minimum of 80% (Cohen 1988, Searcy-Bearnal 1994). Therefore, if a real difference in the magnitude observed existed between months in 1994/95, there was nearly a 40% chance of incorrectly finding no difference. If a power of 80% was stipulated *a priori*, 15 stations each month would be required to detect differences in copepod biomass of the magnitude observed in 1994/95.

Over the entire season, the mean copepod biomass was significantly lower ($p < 0.001$) in 1993/94 (1 893.61 mg·m^{-2}, $SE = 139.46$ mg·m^{-2}, $n = 83$) than in 1994/95 (2 816.15 mg·m^{-2}, $SE = 220.06$ mg·m^{-2}, $n = 75$). In contrast, there was no significant difference in copepod biomass between November 1993 (2 098.42 mg·m^{-2}, $n = 24$) and November 1994 (3 024.62 mg·m^{-2}, $n = 22$).

DISCUSSION

A benefit of knowledge of within-season food availability is that critical periods can be identified. For example, poor food availability in January 1994 caused a sharp increase in gonad atresia in anchovy, a decrease in spawning and a shortening of their spawning season (Richardson in prep.). Such conditions may have been exacerbated by the late onset of spawning as a result of the recruits from the previous year being considerably smaller than normal (Hampton and Barange 1996). The level of copepod biomass in January 1994 was similar to that of November 1988, which was reported to be responsible for the recruitment failure of 1989 (Peterson *et al.* 1992, Melo 1994a, Cochrane and Hutchings 1995).

Given that within-season estimates provide a better indication of food availability and spawning success than one mid-season estimate, improved forecast of anchovy recruitment is possible. The shortened duration of spawning also increases recruitment variability, because prolonged serial spawning dampens the effect of unpredictable early-stage survival (Shelton 1987).

Within-season information of the food environment also allows additional insight into the underlying mechanisms controlling anchovy spawning success. For example, spawning success of anchovy has been related to the area of 16-19°C water throughout its spawning season, a consequence of the associated high food production and consistency of the food resource (Richardson *et al*. in press). This type of relationship necessitates monitoring over the correct spatial scales and can be elucidated by investigating within-season variability.

Given that food availability is important to the spawning and recruitment success of anchovy, a sampling strategy is recommended here for future investigations of the within-season variation in copepod biomass. First, sampling should not be done close inshore, because it inhibits the detection of differences between months and is not necessary for assessing the food environment of anchovy. Second, based on the power analysis for the 1994/95 season, a minimum of 15 stations should be sampled each month to obtain a power of 80%. This necessitates the inclusion of another five-station transect to the current sampling programme, if the inshore station is excluded.

The results have shown that a single estimate of copepod biomass is an inadequate measure of food available during the entire spawning season of anchovy. A sampling interval of one month may provide a reasonable estimate of fluctuations of copepod biomass; this period is similar to the developmental period from egg to adult for *Calanus agulhensis* (Peterson and Painting 1990), the dominant copepod of the Agulhas Bank region. Further, it has been suggested that copepod biomass is maintained on the western Agulhas Bank by slow diffusive (Peterson *et al*. 1992) and advective (Largier *et al*. 1992) input from the eastern Agulhas Bank, which may operate over a time-scale of one month.

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