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DIFFERENTIAL FEEDING BY SARDINE *SARDINOPS SAGAX* AND ANCHOVY *ENGRAULIS CAPENSIS* RECRUITS IN MIXED SHOALS

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In a first effort to understand interactions between anchovy *Engraulis capensis* and sardine *Sardinops sagax* in the field, the size composition of the diet of these two species from a number of mixed shoals was examined. Although both species consumed similar types of food (crustacean eggs and nauplii, and copepods), sardine generally consumed significantly smaller prey (modal size-class generally 300 µm) than anchovy (modal size-class generally between 600 and 900 µm). No single explanation can be used to account for these results, and it is suggested that they are the product of differences in gill-raker morphology, feeding behaviour and within-shoal position. These results support previous single-species laboratory studies and suggest that competition between the two species in the field may be limited.

The southern Benguela ecosystem supports a large and highly productive assemblage of epipelagic fish, including anchovy *Engraulis capensis*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi*. These clupeoids support a valuable purse-seine fishery, which has been dominated over the last 20 years or so by anchovy (Crawford *et al*. 1987). However, the structure of the pelagic fish community in the southern Benguela appears to be in the process of change and there is evidence that sardine are now becoming more abundant than anchovy. Such species replacements, or "regime-shifts" (Lluch-Belda *et al.* 1989), are thought to be associated with structural changes in the ecosystem and with long-term environmental variations of basin-wide to global scales (Lluch-Belda *et al.* 1989, Scientific Committee for Oceanic Research 1994).

The abundance and position of sardine and anchovy in the foodweb makes them particularly important components of the pelagic ecosystem, where they mediate energy flow from primary producers to tertiary consumers. Although sardine and anchovy have long been considered phytophagous filter-feeders (Davies 1957, King and Macleod 1976), there is much recent evidence of feeding by both species on micro- and mesozooplankton (Koslow 1981, James 1987, James and Findlay 1989, Van der Lingen 1994, 1996). Competition between anchovy and sardine for food is not implied by their common diet, however, because their principal mode of food acquisition differs. Both species are capable of filter-feeding and particulate feeding, the former being the principal feeding mode of sardine (Van der Lingen 1994, 1995) and the latter the principal feeding mode of anchovy (James and Findlay 1989). Sardine filter-feed on phytoplankton and microzooplankton, and on mesozooplankton when at high concentrations, but they switch to particulate feeding on mesozooplankton when prey densities are low (Van der Lingen 1994). Anchovy filter-feed on microzooplankton, but switch to particulate feeding on mesozooplankton irrespective of the prey density (James and Findlay 1989). Food particle size is the prime determinant of feeding mode choice of these species, and anchovy switch from filter-feeding to particulate feeding at smaller food particle sizes than sardine.

All of the foregoing observations on the food and feeding of anchovy and sardine around South Africa are the product of single-species studies conducted in isolation. However, anchovy and sardine shoal together as juveniles in the southern Benguela, and aggregate inshore along the South African west coast from March to August (Armstrong *et al*. 1991, Roel and Armstrong 1991). Their food and feeding behaviour under those situations is unknown, although it could be expected from laboratory experiments that sardine might consume smaller particles than anchovy. This paper describes the composition and compares the size frequencies of the zooplankton component of the diet of juvenile sardine and anchovy captured from mixed shoals on South Africa's west coast.

MATERIAL AND METHODS

Sampling was conducted aboard the F. R. S. *Algoa* during June 1995 (Table I, Fig. 1). Mixed shoals of

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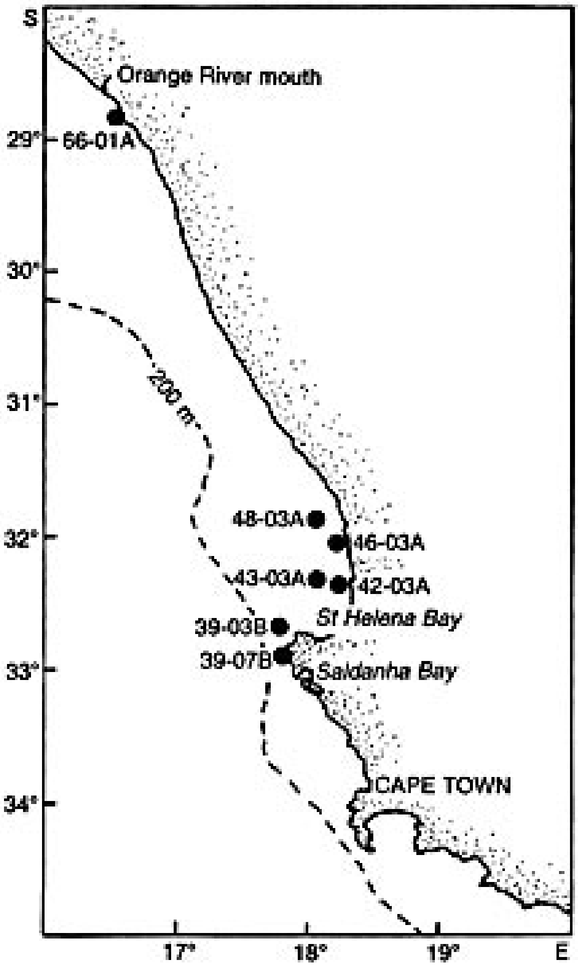

Fig. 1: Position of trawls from which mixed samples of *Sardinops sagax* and *Engraulis capensis* were collected for stomach content analysis during June 1995

fish were captured with an Engels 308 midwater trawl, fitted with a cod-end liner of 12-mm mesh. Samples from each trawl were immediately blast-frozen on capture. In the laboratory, 10 randomly selected fish of each species from each shoal were thawed, measured (fork length, *FL* mm) and the stomachs removed. The contents of the cardiac stomach and the fundus of the stomach were fixed in 10% formalin and stained with Rose Bengal. In order to reduce bias and eliminate the effects of cod-end feeding, the contents of the oesophagus or intestine were excluded from the analysis (Hyslop 1980, James 1987). Several authors have reported minimal differences between the stomach contents of individual fish of any one species within a shoal (Davies 1957, Hand and Berner 1959, James 1987, Rojas de Mendiola 1989). Consequently, the stomach contents of all individuals of each species within a shoal were pooled prior to microscopic analysis.

All identifiable zooplankton material in the pooled stomach content samples was counted and measured under a stereomicroscope at ×45 magnification. Prosome length and/or width of all copepods present in the sample were measured by means of an ocular micrometer. Where necessary, prosome lengths were derived from regression equations relating prosome width to prosome length. Length frequency histograms of the copepod fraction of the diet for each species in each shoal were constructed using size-classes of 100 μm. Where samples were too large to count in their entirety, randomly selected subsamples were examined and a minimum of 100 prey items were counted and measured.

To determine whether the different species in any one shoal were eating prey of the same sizes, length frequency histograms of copepod prosome length were compared using Chi-squared contingency tables. In order to reduce bias in the analyses, all instances where the expected frequencies were less ≤5% were pooled with neighbouring size-classes (Zar 1984). The null hypothesis in all comparisons was that the fish consumed the same size-classes of prey at similar frequencies.

RESULTS

Mixed shoals of anchovy and sardine were taken from 13 trawls made during the survey, although sufficient data for stomach content analysis were obtained from only seven of the 13 shoals (Table I). Sardine were significantly ($p < 0.001$) larger than anchovy (Table I) in six of the seven shoals analysed herein, although differences in length were rarely large. There was no consistent relationship between the size of fish caught and their area of capture (Fig. 1).

Appreciable quantities of phytoplankton were only observed in the diet of anchovy and sardine at one (46-03A) and two (46-03A and 39-07B) of the seven stations respectively. Crustacean eggs and copepod nauplii, copepodites and adults constituted the zooplankton component of the diet of both fish species. Although all prey types were recorded from fish stomachs at all stations, the relative frequencies of the different prey types varied among stations and species.

Table I: Number, mean fork length (*FL*) and standard deviation (*SD*) of anchovy and sardine recruits caught in mixed shoals during June 1995. Significant differences ($p < 0.05$; Mann-Whitney two-tailed U test) in mean length between species in any one shoal are indicated. The time of capture and the proportional composition (the ratio of anchovy to sardine in %) of each shoal are also given

Species	Trawl number	*n*	Mean ± *SD* (*FL* mm)	Capture time	Proportion (% anchovy; sardine)
Anchovy	66-01A	10	78.2 ± 6.5*	12:00	12:84
Sardine		10	109.2 ± 7.1		
Anchovy	48-03A	10	86.6 ± 2.0 *NS*	21:00	88:09
Sardine		10	86.7 ± 9.8		
Anchovy	46-03A	10	88.4 ± 5.7*	07:00	71:25
Sardine		10	100.2 ± 8.1		
Anchovy	43-03A	10	76.2 ± 6.8*	20:30	68:32
Sardine		10	86.8 ± 7.6		
Anchovy	42-03A	10	88.9 ± 6.7*	04:00	80:17
Sardine		10	97.8 ± 8.0		
Anchovy	39-07B	10	83.0 ± 3.1*	07:00	88:12
Sardine		10	101.9 ± 8.6		
Anchovy	39-03B	10	85.9 ± 4.7*	00:30	54:46
Sardine		10	96.0 ± 6.6		

* $p < 0.05$
NS = Not significant ($p > 0.05$)

The diets of both anchovy and sardine were generally numerically dominated by small zooplankton particles, reflecting the small size of the crustacean eggs. Generalizations about the overall size structure of the diet of either species cannot be made from the total data-set, because of variations in the frequencies with which the different prey types (specifically copepods) were consumed. However, unimodal size frequency distributions were generally observed for sardine, whereas those of anchovy tended to be bimodal (an egg mode and a copepod mode). The unimodal size frequency distributions observed for sardine can be explained by the relatively small size of the copepods eaten. Indeed, if crustacean eggs are ignored from comparisons of the size structure of the diet, it is apparent that sardine consumed smaller copepods than anchovy (Fig. 2). These differences were significant in all cases (Table II), although the number of utilizable shoals is reduced from seven to four in the analyses. Sardine also consumed a more restricted size range of copepods than did anchovy, and few sardine ingested copepods with a prosome length >1 mm, whereas prey of that size was frequently recorded in the guts of anchovy.

Table II: Chi-square (χ^2) statistics generated by contingency table comparisons of the size frequency distributions of copepods in the guts of sardine and anchovy from the various trawls

Trawl	ν	χ^2	Significance
46-03A	12	82.4	<0.001
48-03A	6	328.4	<0.001
43-03A	7	67.4	<0.001
39-03B	9	146.9	<0.001

Although there was no consistent modal size-class of copepods eaten by anchovy, sardine tended to eat prey of 300–500 µm prosome length. The lack of good agreement between shoals in the size of prey eaten by either fish species does not reflect differences in the size of the fish and probably reflects spatial variations in the size structure of ambient prey communities. Consequently, no great significance should be attached to them.

DISCUSSION

The stomach contents of fish must reflect the size and taxonomic composition of the prey environment to some extent. When the size structure of the food is skewed towards small particles (as suggested in Fig. 2d), the diets of both anchovy and sardine appear similar. However, when the food environment is composed of a wide size range of prey (Fig 2a–c), it is clear that sardine and anchovy feed on different-sized components of the zooplankton when shoaling together: sardine ingested smaller copepods than anchovy. Although the differences in ingested copepod size observed between the two species are highly

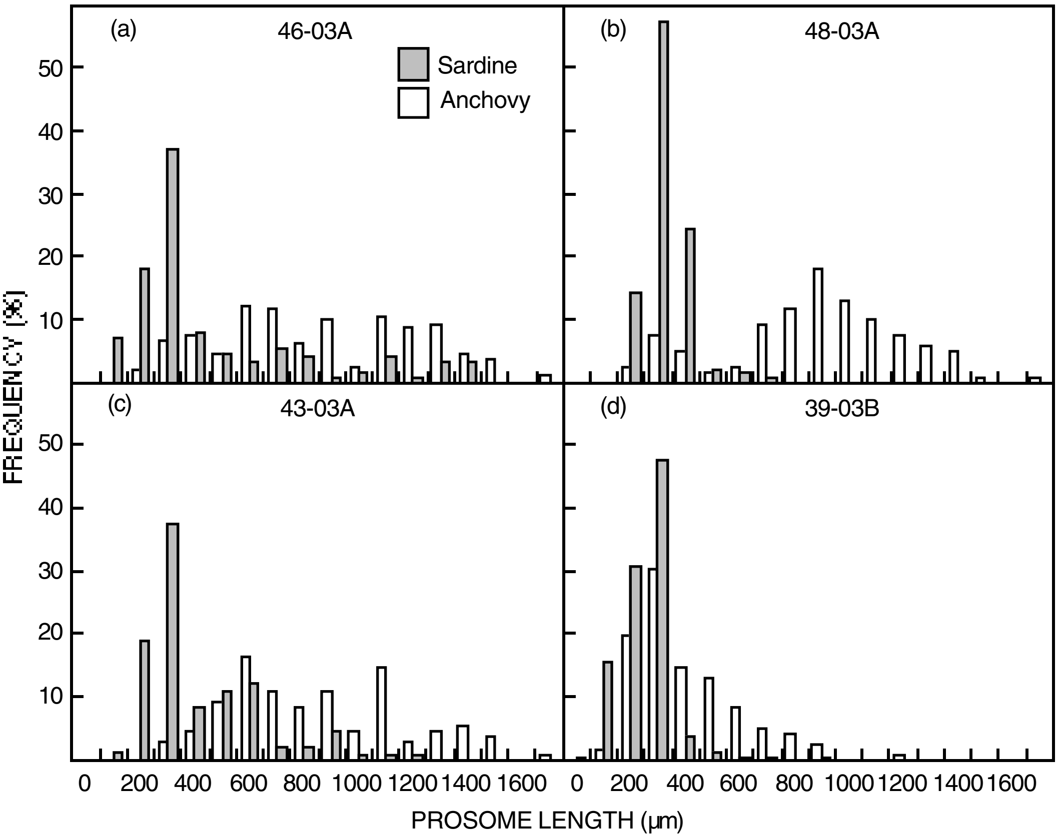

Fig. 2: Size frequency of copepod prosome length in stomach contents of *Sardinops sagax* and *Engraulis capensis* recruits from mixed shoals from trawl number (a) 46-03A, (b) 48-03A, (c)43-03A and (d) 39-03B, June 1995

significant, the absolute size of the data-set is small and conclusions should therefore be regarded as tentative. However, the data are extensive in the sense that they have been generated from a number of distinct shoals and are not the result of intensive studies of a single shoal. The present data support the findings of previous field and laboratory studies that sardine are principally filter-feeders that obtain the majority of their nutritional requirements from smaller food particles (Van der Lingen 1994, 1995, 1996), whereas anchovy are principally particulate feeders that generally consume larger food particles (James 1987, 1988, James and Findlay 1989).

The observed differences in ingested copepod size between sardine and anchovy recruits may be explained by several factors. First, these species show differences in the morphology of their feeding apparatus, sardine having a smaller gap between their gillrakers than anchovy (King and Macleod 1976). Applying the equations relating mean gillraker gap to fish size for each species, provided by King and Macleod (1976), to the mean sizes of sardine (97 mm) and anchovy (84 mm) under study, gives estimates of 0.238 and 0.313 mm for the gillraker gaps of sardine and anchovy respectively. Since food particles ingested by these fish, whether by filter- or particulate feeding, have to be retained by the gillrakers, the smaller gillraker gap of sardine may, in part, be responsible for the observed difference in ingested copepod size.

Differential feeding behaviour can also be invoked to explain the differences in the size composition of the diet of sardine and anchovy. Filter-feeding is essentially non-selective, whereas particulate-feeding fish select specific food particles, generally the largest in their visual field (Lazarro 1987). Particulate-feeding anchovy are therefore more likely to ingest larger particles than filter-feeding sardine, as shown by the results presented herein. The unimodal size distribution of small copepods found in sardine stomachs is consistent with this hypothesis, as is the bimodal size of copepods ingested by anchovy; larger sizes having being ingested through particulate feeding, whereas smaller copepods were ingested through filter-feeding, or incidentally when particulate feeding.

The third factor that could be implicated in explaining these observed differences in the size distributions of ingested copepods is that sardine and anchovy may exhibit different spatial distributions within a mixed shoal. Fish of similar size shoal together for hydrodynamic advantage (Pitcher *et al*. 1985), for food gathering (e.g. detection) and for predator avoidance (Pitcher and Parrish 1993). However, differences in spatial distribution have been observed within mixed shoals. Heterospecific aggregations of silverside *Allanetta harringtonensis*, round herring *Jenkensia lamprotaenia*, anchovy *Anchoa choerostoma* and sardine *Harengula humeralis* display a vertical stratification pattern in their aggregation at very small scales (cm), with fish sorting by species and size (Parrish 1989). Similar spatial segregation has been observed in South African laboratory studies on a small mixed shoal of sardine and anchovy adults. While both species remained loosely aggregated in a common shoal when feeding on zooplankton prey, the filter-feeding sardine maintained a position above and slightly behind the particulate-feeding anchovy (C. D. vd L, pers. obs.). Spatial segregation by sardine and anchovy recruits in mixed shoals is therefore likely, and it could result in differential encounter rates with copepod prey of different size.

Although the results of this study suggest that sardine and anchovy recruits in mixed shoals ingest copepods of different size, it is unlikely that any single explanation can account for this. Rather, the observed differences are attributable to a combination of reasons. The present data corroborate the findings of earlier studies, and provide further evidence for the hypothesis that sardine and anchovy, while both planktivorous species, are generally trophodynamically distinct. This finding is in contrast to those of de Silva (1973) and Li *et al.* (1992), who have suggested that competition between co-occurring clupeoids off Scotland and Japan respectively may be important.

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