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DIET OF SARDINE *SARDINOPS SAGAX* IN THE SOUTHERN BENGUELA UPWELLING ECOSYSTEM

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The diet of sardine *Sardinops sagax* in the southern Benguela was investigated by microscopic examination of stomach contents. The relative dietary importance of prey size and prey type was assessed by calculating the carbon content of prey items. Sardine is an omnivorous clupeoid, ingesting both phytoplankton and zooplankton, with the relative importance of these two food types varying both spatially and temporally. Stomach contents were numerically dominated by small prey items, principally dinoflagellates, followed by crustacean eggs, cyclopoid copepods, calanoid copepods and diatoms. Virtually all prey items ingested by sardine were <1.2 mm maximum dimension, the particle size below which sardine only filter-feed. Despite the numerical dominance by phytoplankton, zooplankton contributed the major portion to sardine dietary carbon, small calanoid and cyclopoid copepods, anchovy eggs and crustacean eggs being the primary prey types. These results indicate that, like anchovy *Engraulis capensis*, sardine in the southern Benguela are primarily zoophagous, and contrast with earlier dietary studies on sardine in the region. However, the two species appear to partition their prey on the basis of size; sardine consume small zooplankton, whereas anchovy consume large zooplankton. This difference has been observed in other upwelling ecosystems where the two genera co-exist and is likely to contribute to the regime shifts observed between sardine and anchovy.

Key words: feeding, phytoplankton, sardine, southern Benguela, zooplankton

As is the case in most of the world's upwelling ecosystems, pelagic fish of the southern Benguela are dominated by clupeoids, namely anchovy *Engraulis capensis*, round herring *Etrumeus whiteheadi* and sardine *Sardinops sagax*. These species have supported a substantial pelagic fishery over the past 50 years, with average annual landed catches over the past 10 years of around 300 000 tons (Marine & Coastal Management, unpublished data). In addition to their commercial importance, clupeoids are an important component of the pelagic foodweb, being the major prey item for several species of fish, birds and marine mammals (Beckley and van der Lingen 1999), thereby mediating the transfer of energy from lower to upper trophic levels. Occupancy of this mid-trophic level position by a small number of species, termed wasp-waist ecosystems by Cury *et al.* (2000), is a common characteristic of upwelling systems.

The success of clupeoids in upwelling ecosystems was initially attributed to their ability to feed directly upon primary producers (Ryther 1969), and this two-level food chain hypothesis was well-supported (Longhurst 1971, Durbin 1979, Walsh 1981). However, subsequent studies have challenged this hypothesis and have suggested that clupeoids are omnivorous (Cushing 1978, James 1988a, b), deriving the bulk of their energy from zooplankton, primarily through size-selective particulate-feeding (Koslow 1981, James 1987). In their review on the biology of clupeoid fish, Blaxter and Hunter (1982) concluded that phytoplankton dominated the diets of clupeoids in regions where strong upwelling was a persistent oceanographic feature (e.g. off Peru), whereas zooplankton was the dominant food of clupeoids in regions where upwelling was weaker and less persistent (e.g. off southern California).

Previous studies on the diet of sardine in the Benguela region indicated that the species was primarily phytophagous, with a "preference" for diatoms (Davies 1957, King and Macleod 1976). Experimental studies have confirmed that sardine are able to capture considerable quantities of phytoplankton through filter-feeding (van der Lingen 1994) and can assimilate diatom carbon and nitrogen efficiently (van der Lingen 1998a). Field studies in the southern Benguela have shown that adult sardine display no feeding periodicity and appear to feed continuously through the diel cycle (van der Lingen 1998b), suggesting that filter-feeding is the dominant feeding mode used by this species in its natural environment (Durbin 1979).

The objective of this study was to assess the diet of sardine in the southern Benguela upwelling ecosystem by quantitatively determining the major contributors to dietary carbon, and to thereby verify whether phytoplankton is the primary component of the diet of sardine. This knowledge will permit a

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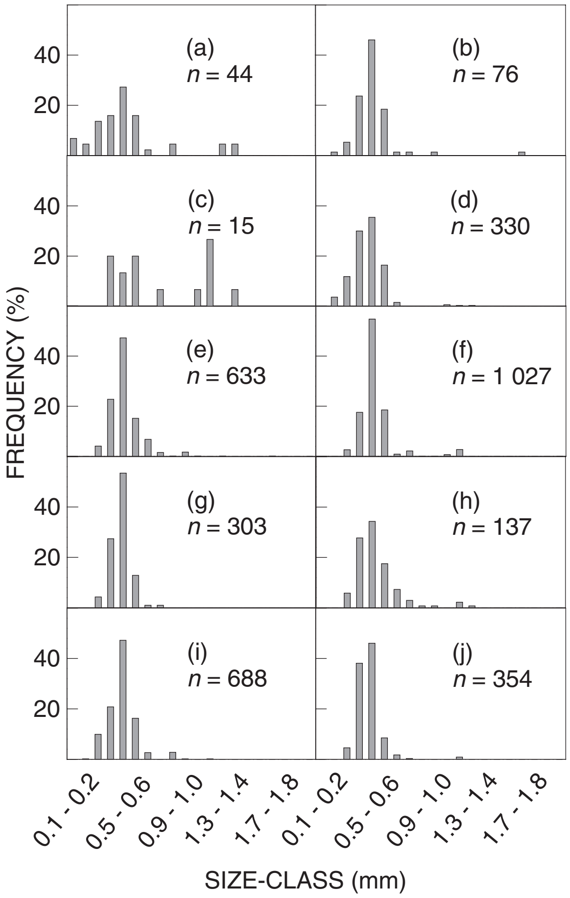

Fig. 1: Size frequency distributions of identified prey from the stomachs of ten individual sardine (a–j) collected in November 1992. The number of prey items (*n*) identified per fish is given

more accurate determination of the trophic position of sardine in the southern Benguela, and will allow a detailed comparison between their diet and that of anchovy, the trophodynamics of which have been extensively studied (James 1987, 1988a, James and Findlay 1989, James and Probyn 1989, James *et al.* 1989a, b). This comparison will allow a better understanding of trophic interactions between these two species, which will be useful for ecosystem modelling studies (e.g. Jarre-Teichmann *et al.* 1998, Shannon *et al.* in press), and may also provide insight into possible mechanisms underlying the alternating periods of dominance observed between these two species, a sequence known as regime shifts (Lluch-Belda *et al.* 1992, Schwartzlose *et al.* 1999).

MATERIAL AND METHODS

Sardine were collected during research cruises undertaken in October and November 1992, November 1993 and November 1994. Samples were taken from shoals captured using an Engels 308 midwater trawl net with a 30-m sweep length and fitted with a codend liner of 8-mm anchovy mesh. Ten fish per trawl were randomly selected and immediately blast-frozen for later laboratory analysis. In the laboratory the total length (*TL,* mm) and wet body mass (*WBM,* g) of each fish was determined, and their stomachs were removed by dissection. Stomach contents were extracted from the cardiac stomach and the fundulus of the stomach, and food boluses were gently broken up using fine dissection needles. The contents of the oesophagus, pyloric stomach and intestine were not extracted in order to avoid biases caused by differential rates of prey digestion, gut passage times or codend feeding (James 1987).

For samples collected in October and November 1992, the stomach contents of each fish were examined individually. Stomach contents were diluted to 20-mℓ using 0.2 µm-filtered seawater, and a 10-mℓ subsample was examined under the microscope. Analysis showed minimal differences between the stomach contents of individual fish from the same shoal with respect to the size frequency distributions of ingested prey, although notable differences were found in the number of identifiable prey (Fig. 1). Minimal differences between the stomach contents of individual fish from sardine shoals have also been reported elsewhere (Davies 1957, Hand and Berner 1959, Louw *et al.* 1998); consequently, the stomach contents of all ten fish from each shoal were pooled prior to analysis of samples taken during the November 1993 and 1994 surveys.

Pooled samples were diluted to 250 ml using 0.2 µm-filtered seawater, and 3–9 5-mℓ subsamples (depending on the density of prey items identified) were collected using a wide-bore (3 mm) glass pipette. Subsamples were then examined separately using a Leica light microscope at 40 or 80× magnification; these magnifications permitted the detection and identification of prey items down to 25 µm in size. Zooplankton were identified to the lowest possible taxon. Owing to the difficulty in identifying *Paracalanus* spp., *Ctenocalanus* spp., *Clausocalanus* spp. and *Parvocalanus* spp., these calanoid genera were classified as "small copepods". Diatoms and dinoflagellates large enough to be seen under the magnifications used were identified. The total length (where possible) and prosome length of all identified copepods was measured to the nearest 12.5 µm using an ocular micrometer, as was the maximum dimension (*MD*) of other zooplankton (length, diameter,

Table I: Classification scheme, genera, measurements taken, morphometric relationships, and equations used to calculate the dry mass and carbon content of identifiable zooplankton ingested by sardine examined in this study. Length measurements are in µm and dry mass is in µg, except where indicated otherwise

Category	Genera	Measurements taken and morphometric relationships	Dry mass	Carbon content	Source
Calanoid copepods	*Acartia* *Calanus* *Calanoides* *Centropages* *Nanocalanus* *Metridia*	TL or PL All genera: $TL = 1.198\ (PL) + 52.4^{a}$	$\ell n(DM) = 2.74\ \ell n(PL) - 16.41^{b}$	$0.424\ DM^{c}$	[a] Determined for *Calanus* (this study, $n = 100$, $r^2 = 0.95$) and applied to all calanoids other than small copepods [b] Chisholm and Roff (1990) for calanoid copepods ($n = 175$, $r^2 = 0.88$) [c] van der Lingen (1998a)
"Small copepods"	*Clausocalanus* *Ctenocalanus* *Paracalanus* *Parvocalanus*	TL or PL All genera: $TL = 1.132\ (PL) + 120.1^{d}$	$\ell n(DM) = 2.74\ \ell n(PL) - 16.41^{b}$	$0.424\ DM^{c}$	[d] This study ($n = 100$, $r^2 = 0.83$)
Cyclopoid copepods	 *Oithona* *Oncaea* *Copilia* *Corycaeus*	TL or PL $TL = 1.684\ (PL) + 35.8^{e}$ $TL = 1.367\ (PL) + 11.3^{f}$ As for *Oncaea* spp. As for *Oncaea* spp.	$\ell n(DM) = 1.96\ \ell n(PL) - 11.64^{g}$	$0.424\ DM^{c}$	[e] This study ($n = 200$, $r^2 = 0.93$) [f] This study ($n = 100$, $r^2 = 0.87$) [g] Chisholm and Roff (1990) for cyclopoid copepods ($n = 60$, $r^2 = 0.85$)
Harpacticoid copepods	*Macrosetella* *Euterpina* *Clymnestra*	TL	$\ell n(DM) = 1.96\ \ell n(TL) - 11.64^{h}$	$0.424\ DM^{c}$	[h] Chisholm and Roff's (1990) cyclopoid equation modified (PL to TL)
Cladocerans and ostracods	*Evadne* *Penillia* *Podon*	TL	$DM = 3.946(TL\text{mm})^{2.436i}$	$0.424\ DM^{c}$	[i] James (1987)
Crustacean eggs	Copepod eggs Euphausiid eggs	Diameter (Ø)	$\ell n(DM) = 0.0143\ (\text{Ø}) - 3.381^{j}$	$0.400\ DM^{k}$	[j] Regression equation from literature-derived data (see text) [k] Huntley and Lopez (1992)
Crustacean nauplii	Copepod nauplii Cirripede nauplii	TL	$DM = 80.627\ (TL)^{4.27l}$	$0.424\ DM^{c}$	[l] James (1987)
Euphausiids	*Euphausia* *Nyctiphanes*	TL	$DM(\text{mg}) = 0.0012\ TL(\text{mm})^{3.16m}$	$0.424\ DM^{c}$	[m] James (1987)
Fish eggs	*Engraulis* eggs Other fish eggs	Major (a) and minor (b) axes of anchovy, diameter of others, $\text{Vol.} = 4/3\pi b^3 + \pi r^2(a\text{-}500)$ $\text{Vol.} = 4/3\pi r^3$	$DM = 0.0930\ (\text{Vol}) + 0.0012^{n}$	$0.457\ DM^{o}$	[n] Hunter and Leong (1981) [o] Napier (1993)
Tunicates	*Thalia* *Oikopleura*	TL	$DM = 11.3\ (TL)^{1.77p}$ Not calculated	$0.387\ DM^{p}$ $C = 0.04\ (TL\text{mm})^{3.29q}$	[p] Heron *et al.* (1988) [q] Deibel (1986)
Tintinids	*Favella*	TL, diameter Cylinder; $\text{Vol.} = \pi r^2 h$	Not calculated	$C(\text{ng}) = 0.053\ (LV) + 444.5^{r}$	[r] Verity and Langdon (1984)

TL = Total length
PL = Prosome length

etc). The maximum dimension, diameter and length (where possible) of diatoms and dinoflagellates was also measured. Phytoplankton species that were too small for identification under the stereo microscope were identified and measured under a Zeiss inverted microscope. A 1-mℓ aliquot from the pooled sample was diluted in 99 ml of 0.2 µm-filtered seawater, allowed to settle overnight, and examined at 64–128× magnification. Three strips, each constituting 0.75% of the settled sample, were examined and phytoplankton cells were identified and measured.

Maximum dimension measurements of all identifiable prey were grouped into 0.2-mm size-classes, and size frequency histograms were constructed for each shoal. After identification, prey items were grouped into the following categories: calanoid copepods (*Acartia* spp.*, Calanoides* spp.*, Calanus* spp.*, Centropages* spp.*, Metridia* spp.*, Nanocalanus* spp. and "small copepods"); cyclopoid copepods (*Oithona* spp.*, Oncaea* spp.*, Copilia* spp. and *Corycaeus* spp.); cladocerans and ostracods (*Evadne* spp.*, Penillia* spp.*, Podon* spp. and ostracods); other crustaceans (harpactacoid copepods, euphausiids, and "pycnogonid-type 1"); crustacean eggs (copepod and euphausiid eggs); cructacean nauplii (copepod, euphausiid and barnacle nauplii); fish eggs; tunicates (*Thalia* spp. and *Oikopleura* spp.); tintinids (*Favella* spp.); diatoms and dinoflagellates (Table I). The percentage frequency of occurrence of the major prey categories was then calculated for each shoal.

Sardine stomachs typically contained appreciable quantities (10–30% by volume) of unidentifiable material. Some of the unidentifiable material would have been partly digested remains of ingested zooplankton and phytoplankton prey, but it is likely that the remainder consisted of particulate detritus that was sufficiently large to be retained by the sardine's gill rakers. Only food items that could be identified were recorded; therefore, the dietary contribution made by particulate detritus was not considered in this study.

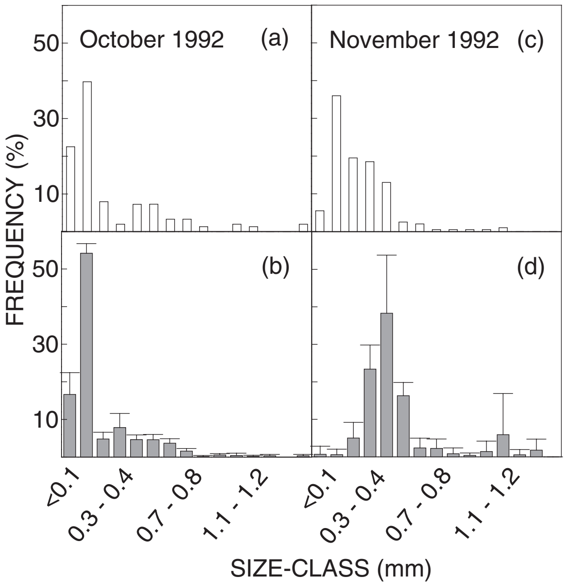

Fig. 2: Size frequency distributions of (a and c) the ambient food environment as sampled using a Magnum rosette (samples from three depths in the upper water column combined) and (b and d) of identifiable prey from sardine stomachs collected in October and November 1992. Error bars denote 1 *SD* from ten fish

For crustacean zooplankton ingested prey (excluding crustacean eggs), dry mass was calculated from length measurements using the equations given in Table I. Carbon content was estimated as 42.4% of the dry mass (the mean carbon content for zooplankton reported by van der Lingen 1998a). The dry mass of crustacean eggs was estimated from egg diameter using a linear regression from literature-derived values and those from personal communications (equation given in Table I; $n = 17$, $r^2 = 0.90$, $p < 0.01$; data from Checkley 1980, Hirche 1980, Hosie and Ritz 1983, Peterson 1986, 1989, Stuart and Nicol 1986, Pillar 1987, Verheye 1991, Huntley and Lopez 1992, Kleppel 1992, Peterson and Hutchings 1995, J. A. Huggett, Marine & Coastal Management, pers. comm.), and carbon content was estimated as 40% of egg dry mass (Huntley and Lopez 1992). Fish egg dry mass was estimated from volume, and carbon content was estimated as 45.7% dry mass (Napier 1993). The carbon content of tunicates and tintinids was estimated using either length or volume measurements (Table I). The carbon content of phytoplankton was calculated from cell volume using equations provided by Smayda (1978). For each sardine shoal sampled, the relative contribution to total ingested carbon was calculated for each of the major prey categories and for each prey size-class.

Only a single trawl was sampled for sardine stomach content analysis during the cruises in October and November 1992, whereas 10 and 17 trawls respectively were sampled during the November cruises of 1993 and 1994. Immediately after the trawls of October and November 1992, water samples were collected using a Magnum rosette from three depths covering the depth at which the sardine shoal had been captured. A 4-ℓ subsample from each depth was concentrated onto a 37-µm mesh, and retained plankton were identified and measured (maximum dimension) under the microscope. These samples allowed an assessment of the ambient food environment as sampled with the Magnum rosette.

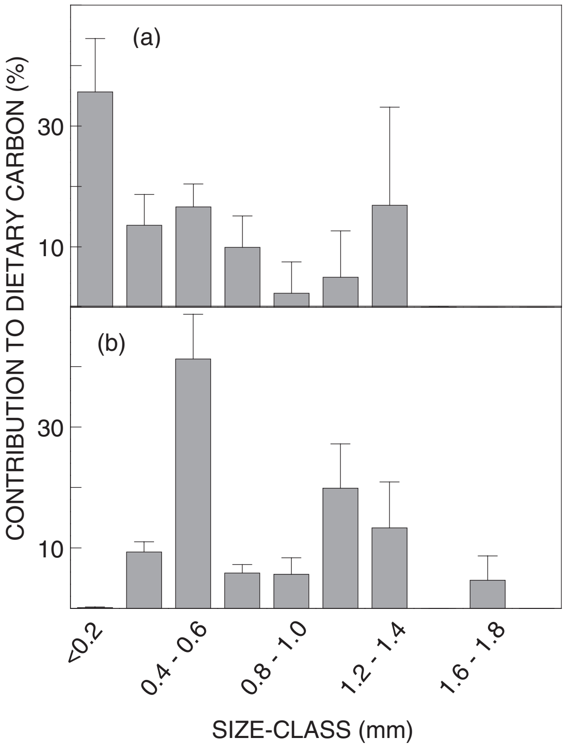

Fig. 3: Mean percentage contribution to dietary carbon by size-class of identifiable prey in the stomachs of sardine collected in (a) October 1992 and (b) November 1992. Error bars denote 1 *SD* from 10 fish

RESULTS

Sardine sampled for stomach content analyses ranged in size from 144.0 to 230.4 mm *TL* and from 20.9 to 103.2 g *WBM*. Eleven of the 29 sardine shoals examined consisted of subadult, sexually immature fish (50% sexual maturity is attained at ± 180 mm *TL*, Akkers and Melo 1996), seven of which were sampled during the 1993 survey. By contrast, all but two of the shoals sampled during the 1994 survey consisted of adult fish. All sardine sampled were captured in surface or near-surface waters; no samples were collected deeper than 50 m. More shoals were collected at night than during the day, although samples were collected from fish captured throughout the diurnal cycle. Sardine were captured off the south-western and southern coasts of South Africa in a region bounded by Cape Columbine (33°S, 18°E) and Port Elizabeth (34°S, 26°E). Samples collected during the November 1993 survey were primarily taken from midshelf waters over the central (from Cape Agulhas to Mossel Bay) and eastern (east of Mossel Bay) Agulhas Banks, whereas the majority of those from the 1994 survey were taken from inshore waters of the western Agulhas Bank (from Cape Point to Cape Agulhas) and off the south-western coast (north of Cape Point).

October and November 1992

Size frequency distributions of identifiable prey from the stomachs of fish taken from the same shoal in November 1992 showed a high degree of similarity (Fig. 1) indicating comparable feeding behaviour. Considerable variation in the number of prey in individual stomachs indicated variable feeding intensity within a shoal.

In October 1992, the size frequency distribution and the species composition of sardine stomach contents corresponded to that of the food environment as assessed using Magnum samples (Fig. 2a, b). The food environment was dominated by particles <0.2 mm, consisting primarily of the dinoflagellate *Peridinium* spp., crustacean eggs and nauplii, and the cyclopoid copepod *Oithona* spp. Whereas sardine stomachs were also numerically dominated by these prey items, crustacean eggs, cyclopoid copepods and anchovy eggs were the dominant prey in terms of dietary carbon. Because of the small size of *Peridinium* spp., its numerical dominance did not translate into an appreciable portion of the ingested carbon, whereas the opposite was found for anchovy eggs. The relative contribution to dietary carbon showed a decreasing trend with increasing prey size (Fig. 3a), the smallest size-class (<0.2 mm) accounting for approximately 36% of dietary carbon. The exception to this trend was the 1.2–1.4 mm size-class, which represented anchovy eggs and large calanoid copepods, and accounted for 17% of the carbon of ingested prey.

In November 1992, Magnum samples were dominated by crustacean nauplii and the cyclopoid copepods *Oithona* spp. and *Oncaea* spp., 95% of prey being <0.6 mm. Sardine stomach contents were numerically dominated by prey 0.4–0.5 mm (Fig. 2d), *Oithona* spp., *Oncaea* spp. and fish eggs being the dominant prey types. Although copepod nauplii dominated the food environment, they were only present at low frequencies in sardine stomachs. Whereas *Oithona* spp. and *Oncaea* spp. accounted for 84% by number of ingested prey, they only contributed 52% of the ingested carbon, whereas fish (primarily anchovy) eggs contributed 36% to ingested carbon. There were two peaks in the relative contribution by size-class to ingested carbon (Fig. 3b), from prey organisms 0.4–0.6 mm (i.e. the cyclopoid copepods) and 1.0–1.4 mm (anchovy eggs and calanoid

Table II: Numerical prey composition (%) of sardine sampled during November 1993

Trawl	Prey composition (%)										
	Cyclopoid copepods	Calanoid copepods	Cladocerans and Ostracods	Other crusta-ceans	Crusta-cean eggs	Crustacean nauplii	Fish eggs	Tunicates	Tintinids	Diatoms	Dinoflagellates
06-07A	32.8	3.1	1.3	2.7	5.2	0.7	0.2	0	0	14.4	39.6
09-05A	27.0	0.5	1.4	0.6	11.6	2.0	0	0	0	4.7	52.4
21-01A	12.9	2.5	2.9	0.7	10.3	1.2	0	0	0	12.3	56.7
21-09A	38.9	7.0	13.6	7.3	6.6	3.7	0.3	0	0	1.3	21.3
22-07A	49.3	8.4	0.9	1.0	10.2	1.9	0	2.8	0	0.9	24.7
23-15A	15.6	8.4	1.3	2.3	21.2	5.6	0.6	0.2	0	4.1	40.7
24-03A	26.6	9.5	2.9	1.0	38.9	5.1	7.0	0.3	0	2.2	6.3
25-13A	3.9	2.1	0	0.5	62.7	17.3	5.4	0	0	0.3	7.9
29-05A	6.3	74.8	2.8	0.5	1.5	0	4.7	0	0	0	9.3
33-01B	2.1	95.7	0.5	0.5	0	0.5	0.5	0	0	0	0
Mean	21.5	21.2	2.8	1.7	16.8	3.8	1.9	0.3	0	4.0	25.9
SD	15.9	34.3	3.9	2.1	19.7	5.1	2.7	0.9	0	5.2	20.4
CV(%)	74	162	139	124	117	134	142	300	–	130	79

copepods).

The close correspondence between the size frequency distributions of available and ingested prey, and between the composition of the ambient food environment and ingested prey, suggest that sardine were feeding non-selectively at both stations. The low occurrence of prey items >1.2 mm indicated that fish were filter-feeding only.

November 1993

More than 50% by number of stomach contents of sardine collected during November 1993 were <0.4 mm *MD*. The modal size of ingested prey was <0.6 mm *MD* for eight of the ten shoals examined (Fig. 4). Prey size increased eastwards, with broader size frequency histograms and modal sizes of 1.4–1.6 and 1.0–1.2 mm for fish captured in the two easternmost trawls (29–05A and 33–01B) respectively. Small particles were not only numerically dominant in sardine stomachs, but their relative occurrence was the least variable. The coefficients of variation (*CV*) associated with the mean occurrence per size-class for all shoals combined was <100% for the four smallest prey size-classes. Therefore small particles were common in all samples. The *CV*s for larger prey size-classes ranged from 103 to 225%, indicating the infrequent occurrence of these prey items in sardine stomachs.

The major prey items found in the stomachs of sardine sampled in November 1993 included dinoflagellates, cyclopoid copepods, calanoid copepods and crustacean eggs (Table II). *Ceratium* spp. and *Peridinium* spp. were the principal dinoflagellates encountered, numerically dominating four of the ten samples examined, primarily those collected in the western part of the survey area. Commonly encountered *Ceratium* species included *C. furca*, *C. lineatum*, *C. tripos* and *C. macroceros*, whereas *Peridinium* species included *P. excentricum* and *P. depressum*. Diatoms were much less common than dinoflagellates and accounted for only 4.0% of prey items ingested in 1993. The most commonly ingested diatom was *Coscinodiscus gigas*.

Cyclopoid copepods, principally *Oithona* spp., were encountered in all samples and were numerically the dominant or second dominant prey item in six of the ten samples examined. Calanoid copepods were also encountered in all samples; in samples from the western region of the survey calanoids were primarily "small copepods" and on occasion *Centropages brachiatus*. *Calanus agulhensis* was the dominant calanoid in sardine stomachs from the eastern region, numerically dominating stomachs of fish from the two easternmost trawls. Cyclopoid copepods and dinoflagellates showed the least variability in their relative mean occurrence, with *CV*s of 74 and 79% respectively, whereas the other prey categories all showed *CV*s of >100% (Table II).

Small food particles dominated the dietary carbon of sardine sampled in 1993 with 70.4% being derived from prey of <1.2 mm *MD* (Fig. 5a). The ingestion of dietary carbon was therefore primarily by filter-feeding, because sardine switch from filter-feeding to particulate-feeding at a prey size of approximately 1.2 mm (van der Lingen 1994). In general, the 0.4–0.6 mm size-class was the largest contributor to dietary carbon and was the modal size-class in terms of average carbon

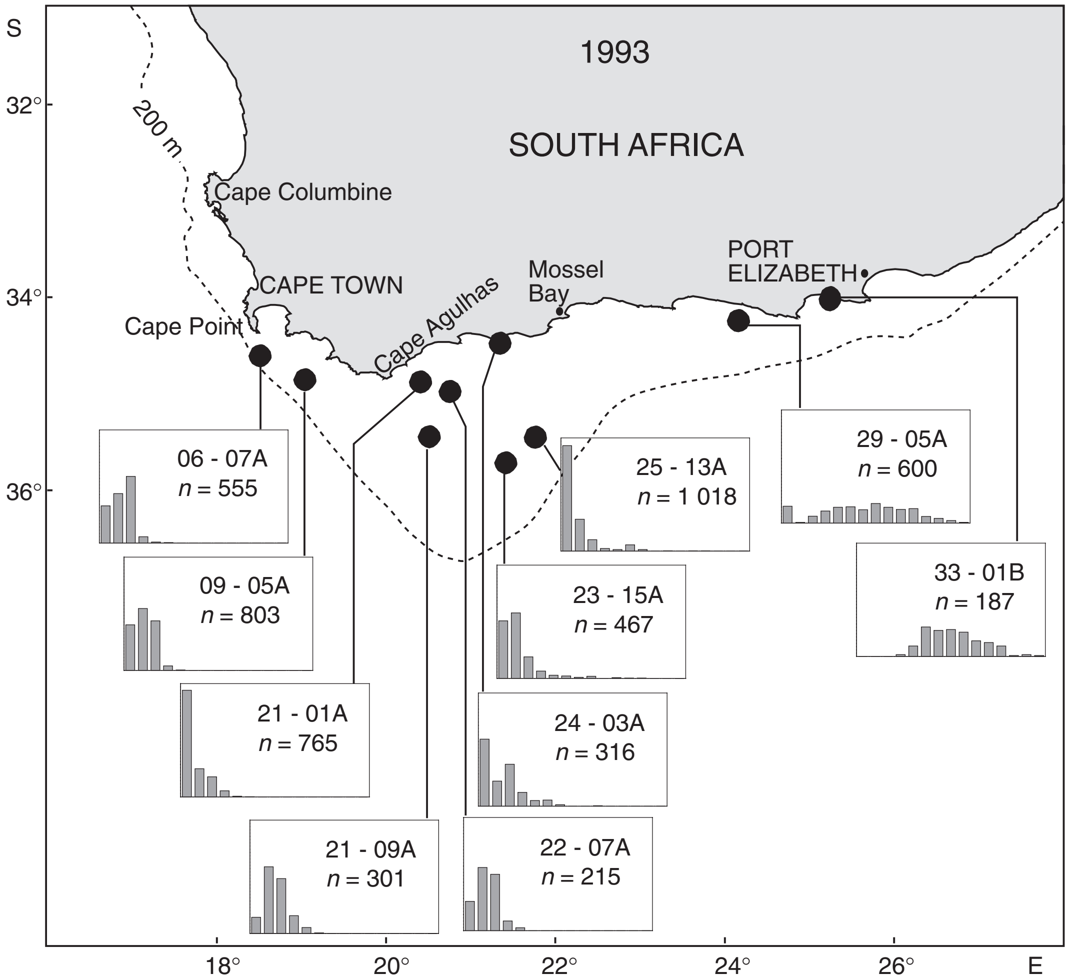

Fig. 4: Size frequency distributions of identified prey in the stomachs of sardine collected from various trawls in November 1993. The x-axes of the graphs are scaled in 0.2-mm size-classes, from 0–0.2 to 2.8–3.0 mm; the y-axes are scaled in 25% intervals, from 0 to 75%. The number of prey items (*n*) identified per sample is given

contribution. Larger size-classes were more important for fish in the eastern part of the survey area. Coefficient of variation (*CV*) values for the mean carbon contribution per size-class were low for small prey items (<100%), whereas higher *CV*s were associated with larger prey sizes, indicating that small prey were more consistent contributors to dietary carbon.

Zooplankton contributed on average 98.2% of the dietary carbon ingested by the sardine sampled in November 1993 (Fig. 5b). Phytoplankton accounted for >1% of ingested carbon at only three of the ten samples, all of which originated from the western region of the survey area. Of the zooplankton component, calanoid copepods were the dominant prey category, accounting for 40.2 ± 35.9% of the ingested carbon. Cyclopoid copepods were the secondmost important prey category, accounting for 24.8 ± 24.3% of the ingested carbon. Despite their relatively low occurrence, fish (primarily anchovy) eggs were the third largest contributor to ingested carbon (16.5 ± 27.7%). None of the other major zooplankton prey categories accounted for more than 6% of ingested carbon.

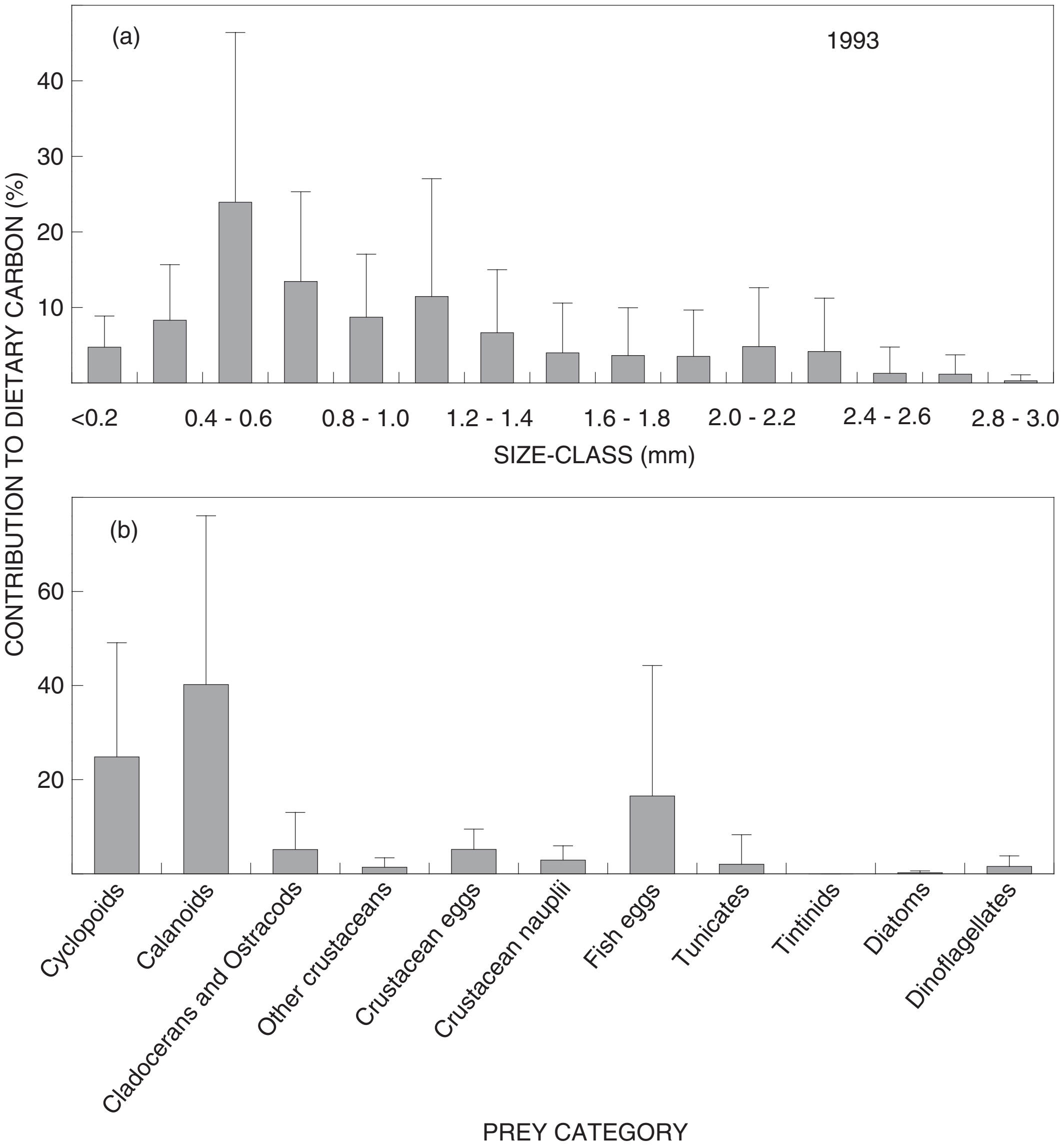

Fig. 5: Percentage contribution to dietary carbon by (a) size-class and (b) prey category in the stomachs of sardine collected in November 1993. Error bars denote 1 *SD*

November 1994

Small particles dominated stomach contents of sardine collected during November 1994, to an even greater extent than in 1993. More than 60% by number of prey items identified were <0.2 mm, and the modal size of ingested prey was <0.6 mm in all 17 samples examined (Fig. 6). In addition to the higher proportion of small prey, the stomach contents of sardine collected in 1994 also showed a narrower size range than in the 1993 collections. More than 99% of prey items were <1.2 mm in 1994, compared to 86% for fish sampled in 1993. Small prey items ingested by fish sampled in 1994 showed low variability in their relative oc-

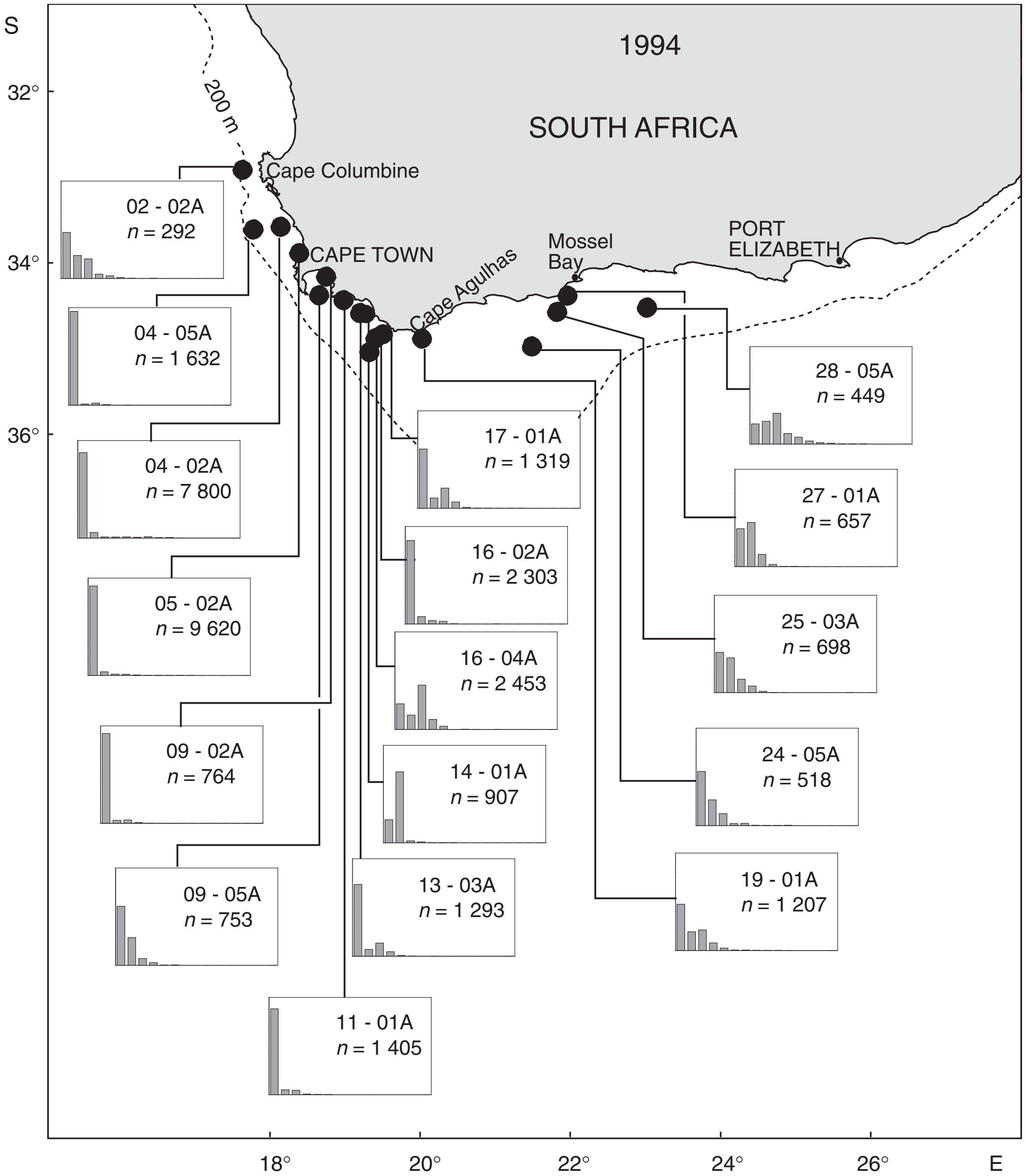

Fig. 6: Size frequency distributions of identified prey in the stomachs of sardine collected from various trawls in November 1994. The x-axes of the graphs are scaled in 0.2 mm size-classes, from 0–0.2 to 2.8–3.0 mm; the y-axes are scaled in 25% intervals, from 0 to 100%. The number of prey items (*n*) identified per sample is given

Table III: Numerical prey composition (%) of sardine sampled during November 1994

Trawl	Prey composition (%)										
	Cyclopoid copepods	Calanoid copepods	Cladocerans and Ostracods	Other crustaceans	Crustacean eggs	Crustacean nauplii	Fish eggs	Tunicates	Tintinids	Diatoms	Dinoflagellates
02-02A	32.2	6.2	0.7	3.1	25.0	6.9	0.3	0.3	0	0	25.0
04-02A	0	0	0	0	0	0	0	0	0	99.9	0.1
04-05A	0.8	0	0.6	0.1	74.2	0.5	0.1	0	0	11.6	12.3
05-02A	0.6	3.4	0	0	18.3	1.4 0	0	0	0	6.2	70.0
09-02A	3.3	1.1	2.1	0.1	26.3	2.0	0	0	0	10.0	55.0
09-05A	4.3	3.1	1.3	0.3	14.7	1.7	0.1	0	22.3	10.6	41.4
11-01A	3.4	1.7	1.4	0.1	13.8	2.9	0.3	0	0	32.4	44.1
13-03A	14.3	1.6	0.6	0.1	10.8	0.5	0	0	0.1	37.7	34.2
14-01A	1.4	1.7	2.5	0	7.4	9	0	0	69.3	2.4	6.0
16-02A	0.7	0.4	0.6	0.2	8.1	0.6	0.1	0.1	0.1	52.8	36.4
16-04A	6.2	1.1	0.4	0.3	6.4	0.3	0.1	0	0	3.9	81.4
17-01A	6.2	2.4	1.2	0.7	10.5	6.5	0.1	0.2	1.4	8.6	62.1
19-01A	23.9	9.5	6.5	1.0	4.6	2.7	0.5	0.1	7.4	26.2	17.7
24-05A	20.3	3.9	1.2	0	35.5	2.3	0.4	0.4	0	5.8	30.1
25-03A	0.4	0.1	0.6	0.2	1.1	0.1	0.4	0	0	2.3	94.8
27-01A	1.7	0.4	1.8	0	5.7	0.3	0.4	0.2	0	4.0	85.6
28-05A	29.0	24.5	0.2	0	18.9	20.0	0.7	0	0	0	6.7
Mean	8.8	3.6	1.3	0.4	16.6	3.4	0.2	0.1	5.9	18.5	41.4
SD	10.9	5.9	1.5	0.8	17.6	5.0	0.2	0.1	17.3	25.8	29.5
CV(%)	124	164	115	200	106	147	100	100	293	140	71

currence; *CV*s for the four smallest size-classes were <100%, whereas the mean abundance of the larger prey items was associated with higher variability.

As in 1993, dinoflagellates were the major prey category, numerically dominating eight of the 17 samples examined (Table III), and accounting for an average of 41.4% by number of all identified prey. *Ceratium* and *Peridinium* were again the dominant dinoflagellate genera encountered. Diatoms were, on average, the second most frequently ingested prey item (18.5%), but were the dominant prey of fish from four of the trawls examined. The stomach contents of sardine from one of the trawls (04–02A) consisted almost entirely of the diatoms *Pleurosigma* spp. and *Thallassiosira subtilis*. Other diatoms in the diet included *Asterionella* spp., *Biddulphia* spp., *Chaetoceros* spp., *Coscinodiscus* spp., *Rhizosolenia* spp. and *Skeletonema* spp. Whereas dinoflagellates occurred in high numbers in almost all samples, diatoms were encountered more frequently in samples from the western part of the survey area than from the east.

Small prey items captured by filter-feeding were the largest contributors to ingested carbon by sardine in 1994, 81% being derived from prey <1.2 mm (Fig. 7a). There were two peaks in carbon contribution by size-class, for prey <0.2 mm, consisting primarily of diatoms, some dinoflagellates, and crustacean eggs and nauplii, and for prey 1.0–1.2 mm, consisting of large calanoid copepods and fish eggs. *CV* values for the mean carbon contribution by size-class were again lower for small prey items than for large ones.

Zooplankton contributed 89.9% and phytoplankton 10.1% of the ingested carbon for sardine sampled in 1994 (Fig. 7b). Of the phytoplankton-derived carbon, 4.1% on average was obtained from dinoflagellates and 6.0% from diatoms. This high mean carbon contribution from diatoms was a consequence of a single trawl sample (04–02A), where 92.9% of the ingested carbon was derived from diatoms. Calanoid copepods were the major source of zooplankton-derived carbon, providing an average of 36.7% of dietary carbon for fish sampled in 1994. Fish (primarily anchovy) eggs accounted for the second largest proportion of dietary carbon (13.5%), followed by cyclopoid copepods (13.1%) and crustacean eggs (11.1%).

DISCUSSION

S. sagax is an omnivorous clupeoid, ingesting both phytoplankton and zooplankton. Stomach contents of sardine collected off the south-western and southern coasts of South Africa during the early summer of 1992, 1993 and 1994 were numerically dominated by small prey items, principally dinoflagellates. Cyclopoid and calanoid copepods and crustacean eggs were the dominant zooplankton in the sardine stomachs exam-

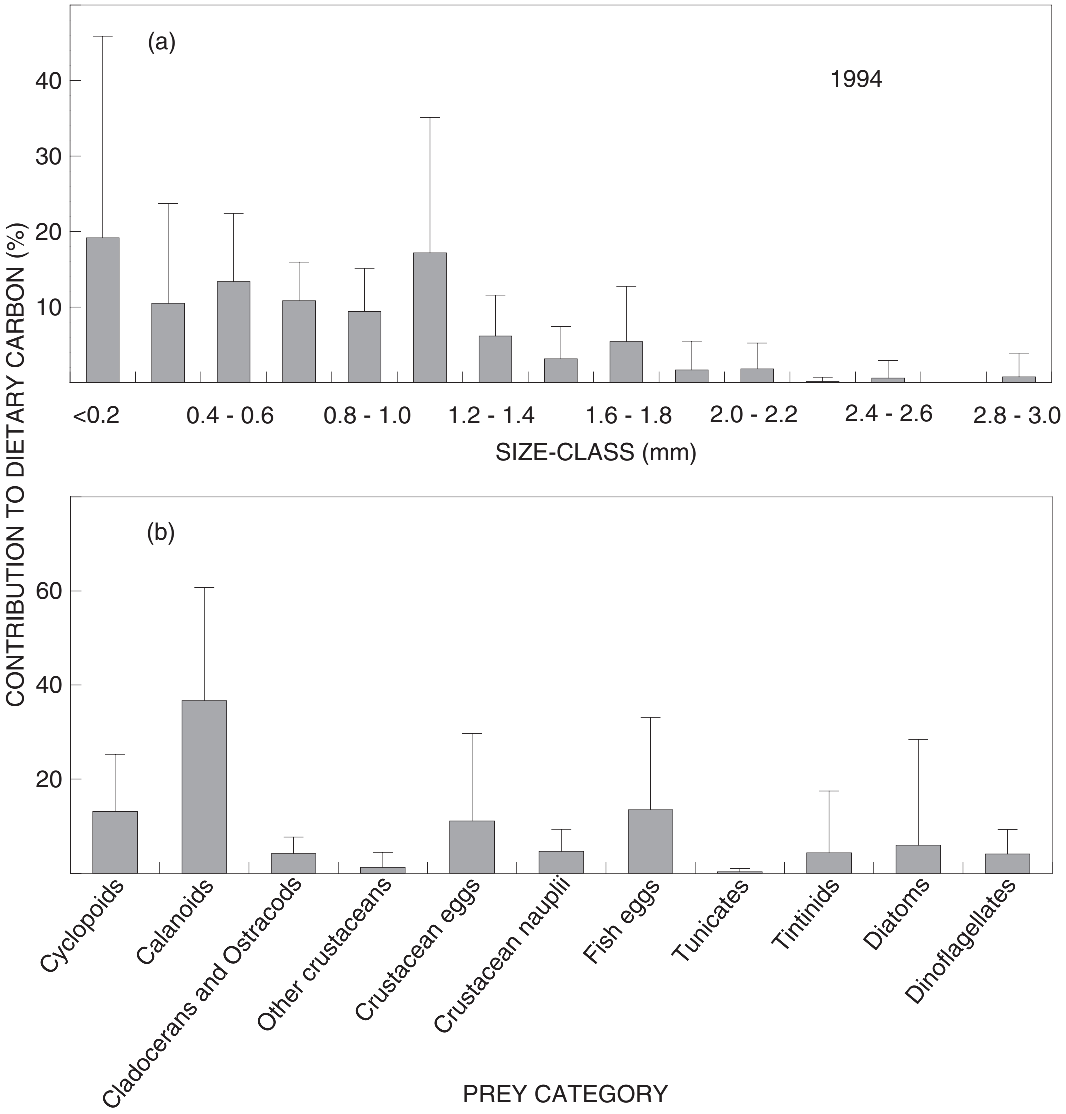

Fig. 7: Percentage contribution to dietary carbon by (a) size-class and (b) prey category in the stomachs of sardine collected from trawls in November 1994. Error bars denote 1 *SD*

ined. Despite the numerical dominance of phytoplankton in the diet, crustacean zooplankton and anchovy eggs contributed the major portion to dietary carbon. A similar finding has been reported for the Pacific sardine *S. sagax* off the Oregon and Washington coasts. Despite the volumetric importance (>60%) of phytoplankton to the diet of sardine in that region, zooplankton, including euphausiid eggs and calanoid copepods (*Pseudocalanus* spp., *Acartia* spp. and *Centropages* spp.), provided most of their ingested carbon (Miller *et al.* 2000).

During November 1993, 86.2% of all ingested prey items were <1.2 mm, the particle size at which sardine switch from filter-feeding to particulate-feeding (van der Lingen 1994). During November 1994, this value was 99.4%. The low variance associated with the mean frequency of occurrence values for the small size-classes indicated that such prey were common in all stomach content samples, and therefore were consistently ingested by sardine. These results corroborate previous experimental (van der Lingen 1994, 1995) and field studies (Davies 1957, Hand and Berner 1959, King and Macleod 1976, Alamo and Bouchon 1987, van der Lingen 1998b), which suggest that sardine are predominantly filter-feeders.

Sardine stomach contents appear to reflect both the size frequency distribution and the prey composition of the ambient plankton community as sampled by the Magnum rosette, although the Magnum rosette is not a comprehensive sampler of the food environment. However, the close correspondence between stomach contents and the food environment reported in most studies on the diet of sardine, from a variety of locations (Anon. 1952, Yoneda and Yoshida 1955, Davies 1957, Yamashita 1957, Hand and Berner 1959, King and Macleod 1976, Kawasaki and Kumagai 1984), indicate that non-selective filter-feeding seems to be the primary feeding mode employed by sardine globally.

Although stomach contents of fish from both years were numerically dominated by small prey items, sardine captured in 1993 had a broader size range of prey than those collected in 1994. The higher incidence of larger, zooplankton prey in the stomachs of fish collected in 1993 than in 1994 may be linked to the smaller average size of fish sampled that year; fish in 1993 averaged 176.7 ± 28.9 mm *TL* and 47.8 ± 28.8 g *WM*, whereas those captured in 1994 averaged 208.2 ± 18.8 mm *TL* and 70.0 ± 18.1 g *WM*. Field studies have indicated that juvenile sardine are more zoophagous than adults (Hand and Berner 1959, King and Macleod 1976, Nakai 1962 cited in Kawasaki and Kumagai 1984), suggesting that smaller fish employ particulate-feeding to a greater degree than do large fish. In addition, feeding periodicity in sardine is size-dependent, small fish showing a peak in feeding activity at or around sunset and large fish appearing to feed continuously (van der Lingen 1998b). That small sardine are more zoophagous and particulate-feed more frequently than large fish appears to be borne out by the present study.

Although numerically dominant, phytoplankton only contributed a small portion (1–10%) of the ingested carbon by sardine. Crustacean zooplankton (principally calanoid and cyclopoid copepods), anchovy eggs, and to a lesser extent crustacean eggs, were the primary contributors to ingested carbon. These results are in contrast to previous sardine dietary studies, in which sardine were considered primarily phytophagous in the Benguela upwelling system. Davies (1957) reported that stomach contents of sardine from the southern Benguela were dominated by phytoplankton, (predominantly diatoms), and reported a mean annual ratio of 2:1 by volume of phytoplankton to zooplankton. Dinoflagellates were relatively unimportant and copepods were the most important zooplankton prey items. King and Macleod (1976) reported that phytoplankton accounted for 10.3–15.2% of the total volume of food ingested by juvenile (20–100 mm standard length, *SL*) sardine, and for 71.9–83.3% for adult sardine (>100 mm *SL*) from the northern Benguela. Diatoms *Fragilaria karstenii, Chaetoceros* spp., *Coscinodiscus* spp., *Rhizosolenia setigera* and *Stephanopyxis turris* were the dominant phytoplankton encountered. Kruger and Cruickshank (1982) also reported that stomach contents of sardine from the northern Benguela were dominated by phytoplankton, particularly diatoms *Thalassiosira decipens, Delphineis karstenii* and *Chaetoceros* spp.

Whereas comparisons between the diet of sardine in different systems are difficult to make because the availability of different food resources is likely to vary between systems, the contrasting results between those of the aforementioned studies and here can be partially attributable to differences in analyses. The volumetric method used by Davies (1957) and King and Macleod (1976) may have overestimated the dietary contribution of phytoplankton. This is because a diatom:copepod ratio of 2:1 by volume is equivalent to a carbon ratio of 1:2.6; therefore, zooplankton is a superior carbon source compared to phytoplankton. Using volumetric measurements as indices of relative importance therefore provides an inaccurate representation of the real contribution to the diet by food type. Also, assuming carbon:nitrogen ratios of 4:1 and 6:1 for zooplankton and phytoplankton respectively, copepods have 7.8 times more nitrogen than equivalent volumes of diatoms (Smayda 1978, Hitchcock 1982).

Inappropriate methods in quantifying stomach contents have led to the erroneous assumption of obligatory phytophagy by clupeoid fish in upwelling ecosystems (Hyslop 1980, James 1988b, Konchina 1991). Initial studies tended to assess the relative importance of prey by their numerical composition, which biases results in favour of small, plentiful prey items such as phytoplankton. Although measurements of prey volume provide more accurate estimates of the relative importance of different prey categories (Cushing 1978), this method is still not sufficiently accurate. Objective processing techniques that assess dietary contribution per food category by nutritional value (i.e. dry mass or carbon content), and not by number or volume, should be used (Konchina and Pavlov 1995). However, the validity of these techniques depends on the accuracy of the relationships relating prey size to carbon content, and also on the assumption that unidentifiable and identifiable prey occur at the same frequency, because the relative occurrence of prey types will be affected by differential digestion rates. Phytoplankton is evacuated faster than zooplankton by sardine (van der Lingen 1998a, b) and may also be digested more rapidly. Therefore, the relative contribution by phytoplankton reported here may be an underestimate. Similarly, the dietary contribution of crustacean eggs may also be overestimated, because of the likelihood that copepod eggs are resistant to digestion and survive passage through clupeoid digestive tracts (Flinkman *et al*. 1994).

Although phytoplankton was a relatively unimportant contributor to the dietary carbon of the sardine under study, it is likely that its dietary importance varies both spatially and temporally for sardine. In some regions and/or seasons, phytoplankton could provide a substantial dietary contribution, and it is possible that the timing and location of the sardine examined affected the relative dietary importance of phytoplankton. Phytoplankton biomass (chlorophyll *a*) is lower offshore than inshore and higher west than east of Cape Agulhas (Brown and Cochrane 1991, Brown 1992). The low phytoplankton dietary contribution in sardine sampled in 1993 could therefore reflect the phytoplankton-poor conditions on the eastern Agulhas Bank. Conversely, in 1994 sardine were collected inshore between Cape Agulhas and Cape Columbine, where phytoplankton is relatively abundant, which could explain the higher dietary contribution of phytoplankton in 1994 relative to 1993. Also, phytoplankton biomass over the western Agulhas Bank has a seasonal cycle, being lower in November than in other summer months (Mitchell-Innes *et al.* 1999). Because sardine were sampled in November of both 1993 and 1994, it is likely that the dietary contribution by phytoplankton reported here probably represents a seasonal minima in this region.

Fish (primarily anchovy) eggs contributed 16.5 and 13.5% of ingested carbon for sardine sampled in 1993 and 1994 respectively. In some instances the contribution from anchovy eggs was >50% of ingested carbon, although samples in which anchovy eggs were of marked dietary importance were only found over the eastern Agulhas Bank. Anchovy eggs in sardine stomachs have been previously noted in the southern Benguela (Valdés-Szeinfeld 1991) and in other regions where these two genera co-exist (Santander *et al.* 1983, Alheit 1987). Valdés-Szeinfeld (1991) reported that 88% of sardine examined had anchovy eggs in their stomachs, averaging around 130 eggs per stomach. She suggested that intense predation by sardine accounted for up to 56% of total anchovy egg mortality. Although anchovy eggs were important contributors to sardine dietary carbon in this study, they were not found in the large quantities reported by Valdés-Szeinfeld (1991). Nevertheless, anchovy eggs appear to be an important food source for sardine in localized areas. However, their spatial segregation during the summer, sardines tending to be inshore of anchovy (Barange and Hampton 1997), would reduce predation on anchovy eggs by sardine.

Like sardine, anchovy derive the bulk of their nutritional input in the southern Benguela from crustacean zooplankton (James 1987). For anchovy, however, mesozoopankton, principally large calanoid copepods and euphausiids (1-20 mm) are the dominant zooplankton consumed, although the small cyclopoid copepods *Oithona* spp. and *Oncaea* spp. may on occasion dominate stomach contents (Peterson *et al.* 1992). In contrast to anchovy, sardine derive most of their dietary input from smaller zooplankton. These two species therefore appear to be trophically distinct, and minimize competition by partitioning their food resource on the basis of size. Sardine feed on small zooplankton by filter-feeding, whereas anchovy feed on large zooplankton by particulate-feeding (James 1987). Because of the higher incidence of filter-feeding by sardine and their ability to capture smaller particles than those ingested by anchovy (van der Lingen 1994), it is likely that phytoplankton is a more important dietary component for sardine. Corroborative evidence for this is shown in experimental studies that have indicated that the respiratory quotient of sardine is lower than that of anchovy (van der Lingen 1995), suggesting higher carbohydrate (i.e. phytoplankton) utilization by sardine. In addition, the spatial segregation exhibited by anchovy and sardine (Barange and Hampton 1997) is a likely factor contributing to the lack of dietary overlap between the two species.

Trophic differences between sardine and anchovy have previously been observed in the southern Benguela, as well as in other upwelling systems. Sardine and anchovy recruits from presumably mixed shoals (i.e. caught in the same trawl) sampled off the west coast of South Africa consumed zooplankton prey of different sizes, sardine ingesting significantly smaller copepods than did anchovy (Louw *et al.* 1998). Off Peru, Konchina (1991) reported that *S. sagax* consumed primarily small herbivorous copepods and tunicates, whereas anchovy *Engraulis ringens* consumed large copepods and euphausiids. The size of food ingested by anchovy was 2.5 times larger than that by sardine, and phytoplankton was more important in the diet of sardine than anchovy. Similarly, phytoplankton contributed more to the diet of *S. sagax* off Japan (65 ± 20% by mass) than for anchovy *E. japonica* (39 ± 18%), and sardine consistently ingested smaller copepods than did anchovy (Li *et al.* 1992).

The size and taxon-specific differences in diet between sardine and anchovy therefore appear to be globally consistent, sardine feeding on smaller organisms closer to the base of the foodweb. These dietary differences may be partially responsible for the long-term changes observed in the relative abundance of sardine and anchovy in the world's eastern boundary upwelling systems (Lluch-Belda *et al.* 1989, 1992). Modifications in the size structure and/or species composition of the food environment have been suggested as one mechanism whereby regime shifts may be initiated and sustained (Schwartzlose *et al.* 1999). Recent ecosystem modelling supports this hypothesis, and has shown that shifts between anchovy and sardine regimes in the southern Benguela may indeed be caused by changes in the availability of mesozooplankton prey (Shannon *et al.* in press).

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