COMPARATIVE DIETARY ANALYSIS OF FOUR SMALL PELAGIC FISH SPECIES FROM PRESUMED MIXED SHOALS OFF SOUTH AFRICA'S EAST COAST

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MASTER OF SCIENCE

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Submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE (by coursework and dissertation) in Applied Marine Science

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ii. ABSTRACT

Stomach contents of sardine (*Sardinops sagax*), anchovy (*Engraulis encrasicolus*), west coast redeye (*Etrumeus whiteheadi*) and east coast redeye (*E. teres*) were collected from presumed mixed shoals off South Africa's east coast. The stomach contents were analysed to 1) determine the diet composition of each species in terms of dietary carbon, 2) assess whether resource partitioning by prey type and/or prey size occurs among the four species, 3) compare the results with what is known about the diet of these species on the west and south coasts of South Africa and 4) characterize diet of east coast redeye. Samples were collected via midwater trawling, and four mixed shoals (one consisting of all four small pelagic species, two consisting of three of the species and the fourth only two species) and a total of 128 stomachs were examined. Sardine sampled for stomach content analyses were relatively larger in size than all the other fish species, with anchovy being slightly larger than east coast redeye in one shoal and in another shoal, east coast redeye slightly larger than anchovy. West coast redeye was by far the smallest in all the shoals. Results showed that there were significant differences in size frequency distributions of identifiable prey items of sardine and anchovy (except in one shoal), of anchovy and the two redeye species, and of sardine and the two redeye species but there were no such differences between the diets of west coast and east coast redeye. The diet of sardine was numerically dominated by fish eggs, small calanoid copepods, and cyclopoid and poecilostomatoid copepods but dietary carbon was dominated by fish eggs and to a lesser extent small calanoid copepods. The diet of anchovy was numerically dominated by crustacean eggs, small copepods and poecilostomatoid copepods but when converted to dietary carbon was dominated by fish eggs and large calanoid copepods. The diets of both redeye species were numerically dominated by fish eggs and large crustacean zooplankton and these prey types also dominated the dietary carbon. No phytoplankton were found in stomach contents of any species. Size frequency distributions

indicate that all four species were feeding on small to medium particles (600-1000μm). The significant difference in prey size frequency distributions and in mean prey sizes between sardine and anchovy are indicative of resource partitioning. No resource partitioning was observed between east coast and west coast redeye. Compared to the west and south coasts of SA, there were lots of fish eggs and no phytoplankton on the east coast of SA.

1. INTRODUCTION

Four small pelagic fish species (anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax*, west coast redeye *Etrumeus whiteheadi* and east coast redeye *E. teres*) occur along the coast of South Africa. Of these, *E. teres* is found only off KwaZulu-Natal on the east coast (Roel and Armstrong, 1991) whereas sardine, anchovy and west coast redeye are found on the west, south and east coasts of South Africa (SA). Sardine, anchovy and west coast redeye are the mainstay of SA's pelagic fishery (Cochrane *et al.*, 1997; van der Lingen, 2002) and form the bulk of purse-seine catches (Fairweather *et al.*, 2006), accounting for about 60-90% of the total allowable catch from 1949-2005 (Sauer *et al.*, 2003; van der Lingen *et al.*, 2006).

The pelagic fishery is South Africa's largest in terms of volume of fish landed, with very variable catches (Agenbag *et al*, 2003; Sauer *et al.*, 2003). From 1950 until 1986 total catches fluctuated between 100 000 and 550 000 tons. In 1987 and 1988, the catches totalled 674 000 tons (Fig. 1), the highest catches recorded by the industry. The South African pelagic fishery is characterised by an alternating pattern of abundance between sardine and anchovy. From the late 1940s to the mid 1960s the fishery was dominated by sardine (Fig. 1) but then there was a switch from sardine to anchovy (Fig. 1; Hutchings *et al.*, 1998), and from 1966 to 1995 anchovy was the dominant species. After 1995, sardine catches have been steadily increasing (Fig. 1). Catches of sardine and anchovy have been similar for the past decade.

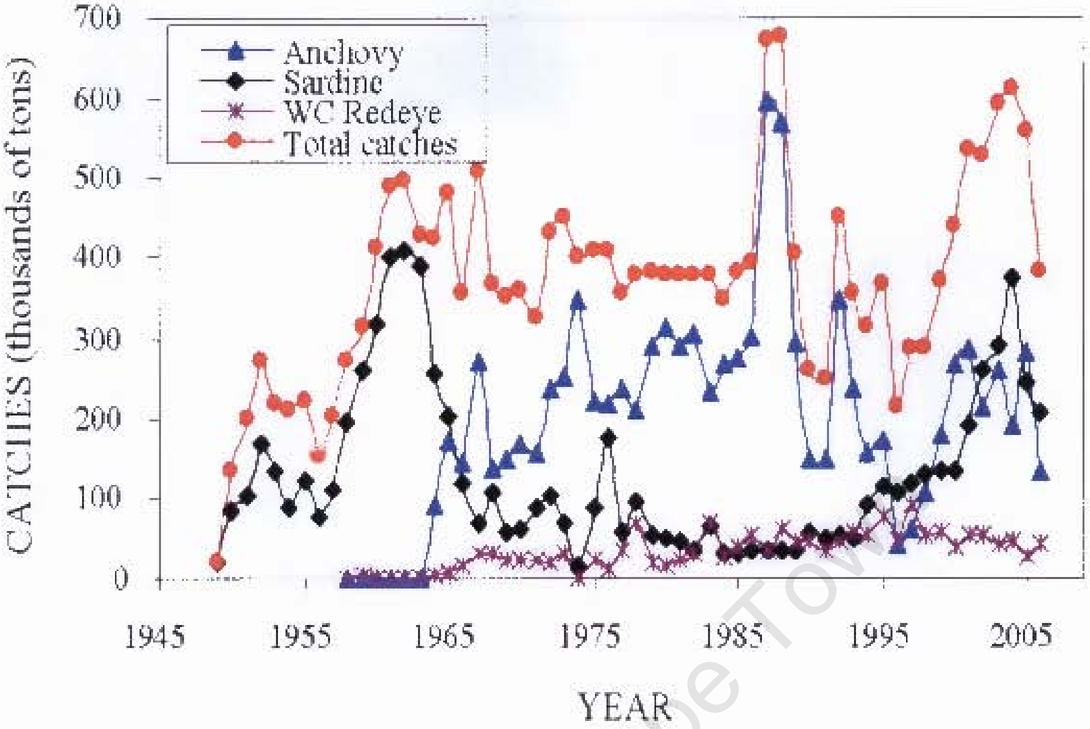

Figure 1. Annual catches of sardine, anchovy, west coast redeye, and total combined catches from 1949-2006 (Marine and Coastal Management, unpublished data)

These small pelagic fish species are not only commercially important, they are also important in the marine foodweb (van der Lingen, 1998; 2002). They play an important role in the trophic structure of the ecosystem (James, 1987; 1988; Louw *et al.*, 1998; van der Lingen 1998; 2002; Darbyson *et al.*, 2003) because they transfer energy from plankton to higher trophic levels, which include top predators such as seals, seabirds and sharks (James, 1987; van der Lingen, 1998; Cury *et al.*, 2000; Gay *et al.*, 2002; van der Lingen *et al.*, 2006). According to Cury *et al.* (2000), common characteristic of the world's upwelling systems and many other types of marine ecosystems is that the species diversity is relatively high at the bottom of the food chain and at the top but depleted at mid-trophic levels. This is called the "wasp-waist" (Cury *et al.*, 2000).

Fish productivity is related to the productivity of their environment, and food conditions also regulate growth, abundance and migration (James, 1988). Much information is available on the diet of anchovy (James, 1987; King and Macleod, 1976) and sardine (Davies, 1957; King and Macleod, 1976; van der Lingen, 1994; 1998; 1999; 2002) in the Benguela current upwelling system. Early research on the feeding habits of sardine indicated that species fed mainly on phytoplankton and to a lesser degree on zooplankton (Davies, 1957). King and Macleod (1976) noted that phytoplankton dominated the diet of sardine and anchovy adults, whereas the diet of juveniles was dominated by zooplankton.

These early studies have since been criticized for using inappropriate methods which assessed prey importance on the basis of numerical occurrence or frequency of occurrence data, instead of contribution by mass or carbon (James, 1988), and more recent work has indicated that sardine and anchovy are in fact primarily zooplanktivorous. Research done on anchovy has shown this species to be primarily a size selective, particulate feeder (James, 1987; James and Findlay, 1989), obtaining the majority of its food from medium to large particles, primarily calanoid copepods and euphausiids (James, 1987). In contrast to anchovy, sardine has been shown to be primarily a non-selective filter feeder (van der Lingen, 1994, 2002), obtaining the majority of its food from small particles (small calanoid copepods, cyclopoid copepods and fish eggs) (van der Lingen, 2002).

Research has shown that sardine and anchovy have different diets and employ different strategies of feeding. King and Macleod (1976) noted that sardine have a smaller gap between gillrakers compared to anchovy. Van der Lingen *et al.* (2006) reported that these two fish species partition their resources and are trophodynamically dissimilar. Comparative dietary analysis by Booi (2000) and Louw *et al.* (1998) further supported this trophic dissimilarity between anchovy and sardine.

Information on the food and feeding habits of west coast redeye off SA is limited to the study of Wallace-Fincham (1987), who noted that west coast redeye were zooplanktivorous and their diet was largely dominated by large copepods, followed by euphausiids and decapods, and this species was assumed by James (1988) to be a particulate feeder. Wallace-Fincham (1987) also noted that west coast redeye fed primarily during daytime and that stomachs were fuller in the afternoon than in the morning. There is no available information about the diet or feeding ecology of east coast redeye in SA waters.

Data on the feeding ecology of sardine and anchovy from mixed shoals is limited to two studies (Louw *et al.*, 1998; Booi, 2000), both of which were conducted off SA's west coast. The aim of this study was to further assess resource partitioning by small pelagic fishes in SA waters, and also to provide information on the diet and possible trophic partitioning among small pelagic species off SA's east coast, a region where dietary information for these species is particularly lacking. The overall objective of this study was to contribute towards the further understanding of marine pelagic ecosystem dynamics on the east coast of SA. In particular, four main objectives were addressed. The first was to determine the diet composition of the four small pelagic species off the east coast in terms of contribution to dietary carbon. The second objective was to assess whether trophic partitioning (by prey type and/or prey size) occurs among the four small pelagic species. Food and feeding habits of sardine and anchovy on the west and south coasts is well known. The third objective of this study was to compare results from the east coast with what is known about the diets of the species off the west and south coasts of SA. Finally, the fourth objective was to characterize diet of east coast redeye as nothing has been reported on the diet of this species before.

2. MATERIALS AND METHODS

2.1 SAMPLING

Samples of anchovy, sardine, west coast redeye and east coast redeye were collected during the Sardine Run Survey conducted by Marine and Coastal Management from 18 June to 7 July 2005. This survey was conducted off the east coast of SA, and was primarily undertaken to obtain information on the abundance and size structure of sardine involved in the sardine run, to assess the influence of oceanographic variables on the sardine run, and to collect biological data on sardine and other small pelagic fish species of the east coast (van der Lingen *et al.*, 2005). The second phase of the survey comprised an intensive survey grid that consisted of randomly-positioned transects extending perpendicular from the shore to the edge of the continental shelf in the area between Richard's Bay and Port Alfred (Fig. 2, van der Lingen *et al.*, 2005). Continuous sampling using acoustics with midwater trawls was done to identify fish targets (van der Lingen *et al.*, 2005).

In total, 22 trawl locations were selected, based on *ad hoc* decisions made when suitable schools of fish were seen on the echosounders. Midwater trawls were done using an Engels 308 midwater trawl fitted with a codend liner of anchovy mesh (James, 1987; van der Lingen, 2002). The trawl was towed at 3.4-4 knots and the duration of trawls varied between 27 and 38 minutes. The schools were caught at depths ranging from 10-40m, and the date, time, location, station number and grid number of each trawl was recorded (Table 1). Fish caught in the trawl were sorted on board and, after sorting, fish samples of approximately 50 fish per species (where possible) were immediately blast-frozen for later laboratory analysis (James, 1987; Wallace-Fincham, 1987; Louw *et al.*, 1998; van der Lingen, 2002). In the laboratory, 25 fish of each species from each shoal were thawed (James, 1987; van der Lingen, 2002), and the total and the caudal lengths of the fish were measured to the nearest millimeter and wet body mass to the nearest 0.1g (Booi, 2000; van der Lingen, 2002). The fish were cut open, their stomachs were removed and opened, and the contents were preserved in 10 % formalin in a vial for later analysis. The contents of the oesophagus and intestines were not included in the analyses in order to reduce biases caused by different rates of digestion, gut passage times and codend feeding (Hyslop, 1980; James; 1987; Louw *et al.*, 1998; van der Lingen, 2002).

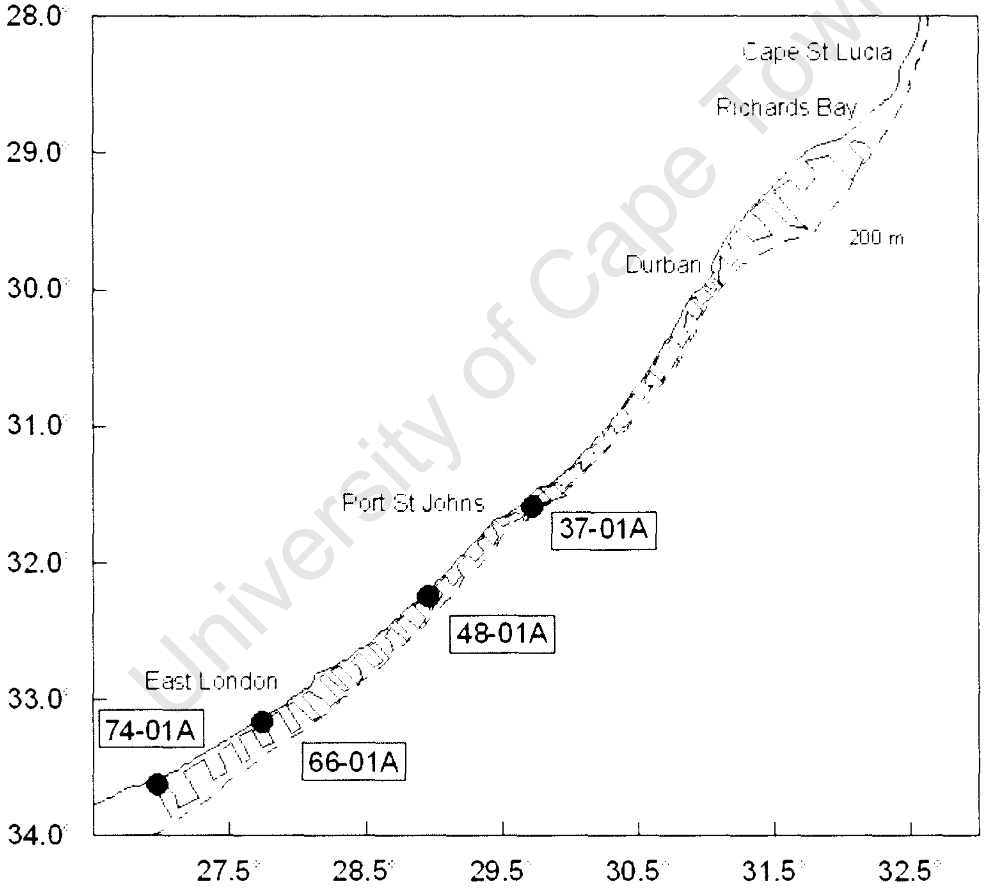

Figure 2. Location of midwater trawls during the 2005 sardine run survey from which small pelagic fish were collected for comparative dietary analysis. Black dots indicate the sample locations of the four mixed shoals.

Table 1 Summary table showing the grid number, date, time, depth range of sampled mixed shoals, species analysed and their contribution to catch mass (shown in brackets). The mean (± 1 standard deviation) length and mass are shown of the fish analysed in this study. L-W relationships of sardine, anchovy and west coast redeye were taken from Crawford (1979) and for east coast redeye from fishbase.org

Mixed shoal #	**Date**	**Time**	**Depth range**	**Species**	**Mean Length (cm)**	**Mean Wet Mass (g)**
1	26/06/2005	15:50	13-28m	Sardine (94.4%)	15.7 ± 1.3	46.5 ± 12.6
				EC Redeye (5.4%)	9.9 ± 0.7	9.8 ± 2.3
2	28/06/2005	10:30	16-31m	Sardine (50.3%)	12.9 ± 0.6	25.6 ± 3.5
				Anchovy (6.2%)	12.5 ± 0.5	12.7 ± 1.6
				EC Redeye (42.7%)	12.0 ± 0.5	17.5 ± 2.1
3	30/06/2005	13:50	10-26m	Sardine (80.6%)	15.5 ± 1.2	45.0 ± 9.9
				Anchovy (1.5%)	10.6 ± 1.5	7.8 ± 3.5
				WC Redeye (11.7%)	9.9 ± 1.9	10.8 ± 6.4
				EC Redeye (6.2%)	12.7 ± 0.6	20.8 ± 2.9
4	01/07/2005	19:36	15-29m	Sardine (6.6%)	14.1 ± 0.8	33.1 ± 5.5
				Anchovy (23.8%)	12.2 ± 0.6	11.7 ± 1.7
				WC Redeye (69.7%)	11.2 ± 0.9	14.6 ± 4.2

2.2 STOMACH CONTENT ANALYSES

Fish from four mixed shoals were used for stomach analysis (Fig. 2). In total, the contents of 128 stomachs were examined. The stomach contents from each fish were washed with 0.2 μm filtered seawater into a petri dish (van der Lingen, 2002) and were examined individually under a dissecting microscope (Leica MZ6 or Olympus S-Z PT) at 40x and 50x magnification respectively. The eyepiece was fitted with a 20mm diameter graticule with a horizontal grid of 100 divisions which enabled measurements of ingested prey items to be made. Both microscopes were calibrated for all the magnification settings (0.63 to 4) for Leica and (1 to 6) for the S-Z PT Olympus. Prey items were identified to the lowest possible taxonomic level (Boltovskoy, 1999; Gibbons, 1999), and their total length (TL, μm) (where possible), prosome length (PL, μm) and prosome width (PW, μm) were measured using the micrometer eyepiece. The copepods *Clausocalanus* spp., *Ctenocalanus* spp., *Paracalanus* spp. and *Parvocalanus* spp. could not be distinguished from each other and therefore all were classified as "small copepods" after van der Lingen (2002). The body parts of unidentifiable zooplankton (almost all copepods) were measured to avoid losing valuable data. As a consequence, it was assumed 1) that all unidentifiable zooplankton were copepods, and 2) that one body part represented one copepod.

After identification, prey items were grouped into categories (Table 2). Results from the stomach content analyses were used to determine prey species composition and to construct length frequency histograms of prey size. Scatterplots of prosome length against prosome width, total length against prosome width, and total length against prosome length for each genus/type of prey were drawn and regressions fitted to these data. These regressions were used to predict prosome length and total length from prosome width, which was necessary because in some instances only prosome length could be measured. The regression equation for predicting the prosome length of unidentified copepods was derived by combining measurements from all the calanoid copepods together. Prey size either measured directly or derived from these scatterplots, was converted to prey mass and carbon content using literature-derived length/mass and mass/carbon relationships (James, 1987; Richardson *et al.*, 2000; van der Lingen, 2002). The prey size on the length frequency histograms represented prosome length for all the calanoid copepods, total lengths for harpacticoid copepods, amphipods, euphausiids, mysids, tunicates and polychaeta, and diameter for fish and crustacean eggs.

Table 2 Equations used to estimate the dry mass (DM) and carbon content (CC) of identifiable zooplankton ingested by anchovy, sardine, west coast redeye and east coast redeye. Dry mass and carbon content are in µg, except where indicated otherwise.

Group	**Dry mass/carbon content**	**Source**
Calanoid copepods	$\mathrm{Ln}(DM) = 2.74*\ln(PL) - 16.41$	Chisholm and Roff (1990)
	$CC = 0.424*DM$	van der Lingen (2002)
Cyclopoid copepods	$\mathrm{Ln}(DM) = 1.96*\ln(PL) - 11.64$	Chisholm and Roff (1990)
	$CC = 0.424*DM$	van der Lingen (2002)
Poecilostomatoid copepods	$\mathrm{Ln}(DM) = 1.96*\ln(PL) - 11.64$	Chisholm and Roff (1990)
	$CC = 0.424*DM$	van der Lingen (2002)
Harpacticoid copepods	$\mathrm{Ln}(DM) = 1.96*\ln(PL) - 11.64$	Chisholm and Roff's (1990) cyclopoid equation modified after van der Lingen (2002) (*PL* to *TL*)
	$CC = 0.424*DM$	van der Lingen (2002)
Amphipods	$DM = 0.005*(TL)^{2.311}$	Espinoza and Bertrand (in press)
	$CC = 0.370*DM$	Espinoza and Bertrand (in press)
Cladocerans & ostracods	$DM = 3.946*(TLmm)^{2.436}$	James (1987)
	$CC = 0.424*DM$	van der Lingen (2002)
Euphausiids	$DM = 0.0012*(TLmm)^{3.16}$	James (1987)
	$CC = 0.424*DM$	van der Lingen (2002)
Mysids	$DM = 0.0012*(TL)^{3.16}$	James (1987)
	$CC = 0.424*DM$	van der Lingen (2002)
Fish eggs	$DM = 0.093*(Vol)+0.0012$	Hunter and Leong (1981)
	$CC = 0.457*DM$	Napier (1993)
Crustacean eggs	$\mathrm{Ln}(DM) = 0.0143*(\varnothing) - 3.381$	van der Lingen (2002)
	$CC = 0.400*DM$	Huntley and Lopez (1992)
Tunicates	$DM = 11.3*(TL)^{1.77}$	Heron *et al.* (1988)
	$CC = 0.387*DM$	Deibel (1986)
Polychaeta	$WW=0.01*(TL)^{2.136}$	Espinoza and Bertrand (in press)
	$DW=0.157*WW$	Espinoza and Bertrand (in press)
	$CC = 0.518*DM$	Espinoza and Bertrand (in press)

2.3 FEEDING INTENSITY

The possibility that some of the species consistently had more food in their stomachs than others was investigated by comparing feeding intensity (stomach content mass as a percentage of fish mass) of the fish species. Feeding intensity (FI) was calculated as:

$$FI = \frac{total\ \ carbon\ \ in\ \ diet\ \ per\ \ fish}{carbon\ \ content\ \ of\ \ fish\ \ (g)} \times 100$$

The dry mass of stomach contents was calculated by adding the mass of all identifiable prey from the stomachs of each individual fish. The average dry body mass was calculated by multiplying the average wet mass by the average ratio of dry body mass and wet body mass for large and small adult sardine (van der Lingen, 1999). Dry body mass was then converted to fish carbon using a ratio of carbon content:dry body mass (0.45), and that was applied to all fish species (van der Lingen, 1999).

2.4 STATISTICAL ANALYSES

For all statistical tests, probability values of 5% or less were used to infer statistically differences. A one–way ANOVA (Zar, 1999), using Statistica version 7, was used to compare the fish sizes (length) within the four mixed shoals, except for shoal number 1, which had only two species so a t-test (Zar, 1999) was used.

Data were pooled per species per shoal for the diet analyses but size frequency distributions were assessed individually and for the pooled sample. Diet composition was analysed by calculating the relative dietary contribution of different prey categories in terms of their numerical abundance (%N) and carbon content (%C), with both being expressed in terms of pie diagrams.

Differences in the prey size frequency distributions between species in a mixed shoal were assessed using Kolmogorov-Smirnov (K-S) tests (Zar, 1999), testing the hypotheses that there were significant differences in the size frequency distributions of ingested prey items between different species pairs. Because a series of pairwise comparisons was used, the critical values were adjusted using a sequential Bonferroni procedure (Holm 1979 in Quinn and Keough, 2002).

Previous work has shown that sardine fed on smaller particles than anchovy, which in turn fed on smaller particles than west coast redeye (James, 1987; Wallace-Fincham, 1987; Louw *et al*., 1998; Booi, 2000, van der Lingen, 2002). A one–way ANOVA (Zar, 1999), using Statistica version 7, was used to test for differences in the mean prey sizes of each species in each mixed shoal, except for shoal number 1, which had only two species so a t-test (Zar, 1999) was used.

3. RESULTS

There were four mixed shoals, each with different species mixes, and different fish sizes, except for sardine and anchovy in shoal number 2. Sardine and anchovy had low feeding intensity values compared with the two redeye species, which also showed greater variability in feeding intensity (Fig. 3).

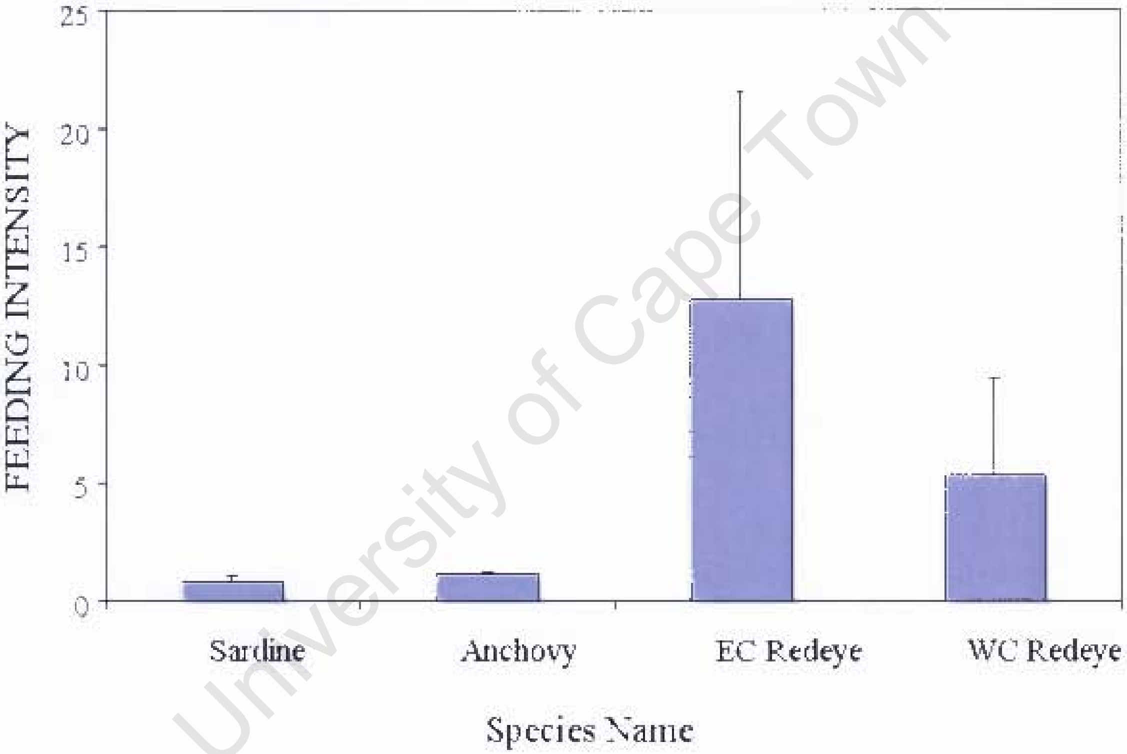

Figure 3. Differences in feeding intensity shown by the four small pelagic species. The data were pooled across the four schools sampled and across the time of day

3.1 Morphometric relationships

Scatterplots and associated morphometric relationships determined in this study of identifiable and unidentifiable zooplankton ingested by anchovy, sardine, west coast redeye and east coast redeye are given in Table 3. The correlations between PL, PW and TL were reasonably strong except for *Calanus* spp., *Euchaeta* spp., *Oithona* spp., and *Microsetella* spp.which had weak, but still statistically significant, relationships.

Table 3 Morphometric relationships calculated for different zooplankton groups (and genera) found in the diets of small pelagic fish. Length measurements are in µm. For all cases, prosome width (PW) was measured and, where individuals were in good condition, prosome length (PL) and/or total length (TL) were also measured.

Group	Genus	Morphometric relationship	n	r^2	p
Calanoid copepods	*Aetideus*	PL = 1.6981*(PW) + 330.84	44	0.65	<0.01
	Calanus	PL = 1.0905*(PW) + 1120.2	94	0.21	<0.01
	Candacia	PL = 2.2236*(PW) + 163.2	58	0.84	<0.01)
	Centropages	PL = 1.9123*(PW) + 280.58	139	0.85	<0.01
	Eucalanus	PL = 1.9223*(PW) + 805	10	0.72	<0.01
	Euchaeta	PL = 1.5514*(PW) + 890.36	102	0.38	<0.01
	Metridia	PL = 2.0408*(PW) + 169.67	58	0.53	<0.01
	Rhincalanus	PL = 2.3373*(PW) + 474.43	181	0.51	<0.01
	Scolecithrix	PL = 1.1946*(PW) + 583.56	291	0.51	<0.01
	Temora	PL = 2.0313*(PW) - 26.29	275	0.78	<0.01
	Undinula	PL = 1.988*(PW) + 361.03	86	0.54	<0.01
	Unid. copepods	PL = 2.4899*(PW) - 69.78	2412	0.82	<0.01
Cyclopoid copepods	*Oithona*	PL = 1.3197*(PW) + 163.78	199	0.28	<0.01
Poecilostomatoid copepods	*Oncaea*	PL = 1.2138*(PW) + 192.57	1149	0.59	<0.01
	Corycaeus	PL = 2.1005*(PW) + 9.2251	646	0.74	<0.01
Harpacticoid copepods	*Microsetella*	TL = 5.246*(PW) + 3.5436	107	0.48	<0.01
Amphipods	*Parathemisto*	TL = 1.4089*(PW) + 476.78	13	0.74	<0.01
Euphausiids	*Euphausia*	TL = 4.2864*(PW) - 204.79	19	0.64	<0.01

3.2 Mixed shoal #1: Sardine and East coast redeye

Stomach contents from this shoal were very fresh, indicating recent ingestion of prey before capture. Two fish species (sardine and east coast redeye) were examined. There was a significant difference in the sizes of the two fish species (Fig. 25a, t=12.3, df=186, $p<0.0001$) with sardine sampled for stomach content analyses relatively large than east coast redeye (Table 1). There were 829 prey items identified from the stomachs of sardine and 1020 from the stomachs of east coast redeye. Ten individual fish per species were examined.

Numerically, small prey items (poecilostomatoid copepods, and small copepods) dominated the stomach contents of sardine (Fig. 4). However, assessment of the diet in terms of relative carbon contribution resulted in a dramatic change in the importance of prey items. Large zooplankton contributed a small numerical proportion to the stomach contents but they dominated in terms of dietary carbon, contributing about half of the carbon ingested (Fig. 4). The stomachs of east coast redeye were numerically dominated by large crustaceans (euphausiids and calanoid copepods), and the large prey items were also dominant when converted to dietary carbon. The large particles (>1300μm) contributed about 98% of the ingested carbon (Fig. 4).

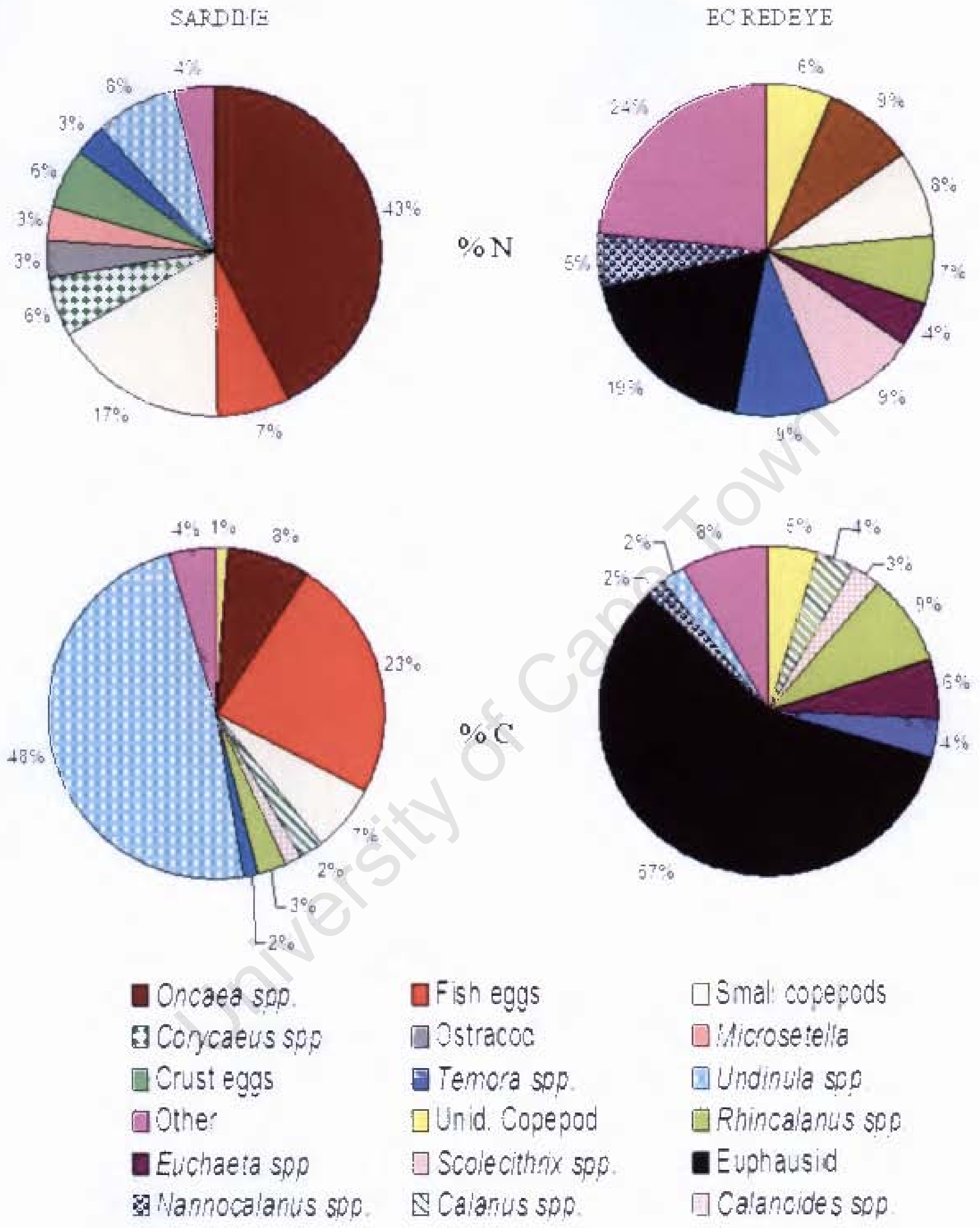

Figure 4. Relative contribution in terms of numbers (%N; top) and carbon (%C; bottom) of prey to the diet of sardine (left) and east coast redeye (right) from mixed shoal #1.

The size frequency distributions of identifiable prey items from the stomachs of individual sardine were very similar, except for fish number 5 (Fig 5), with sardine mostly feeding on prey items ranging between 400-1200μm, and a few feeding on prey items

>1200μm. Fish number 5 ate both small and medium sized prey items (400-1000μm) and also large prey items (1800-2550μm). Size frequency distributions of identifiable prey items from the stomachs of individual east coast redeye were very similar (Fig 6), with fish mostly feeding on large prey items ranging between 600-3000μm, and all fish eating some prey items >3000μm (Fig. 6).

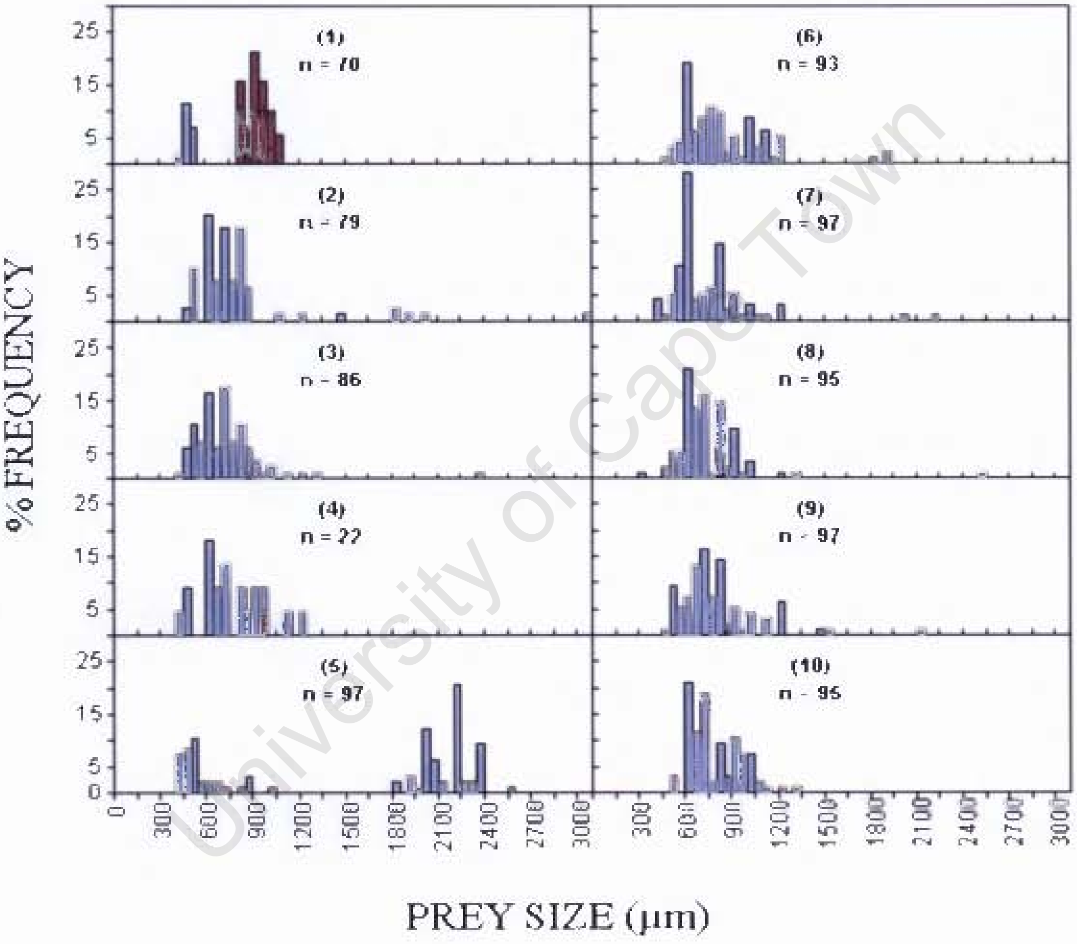

Figure 5. Size frequency distributions of identifiable prey from the stomachs of ten individual sardine (1-10) from mixed shoal #1. The number of prey items (n) identified per fish is given. Note: the red bars are the fish eggs.

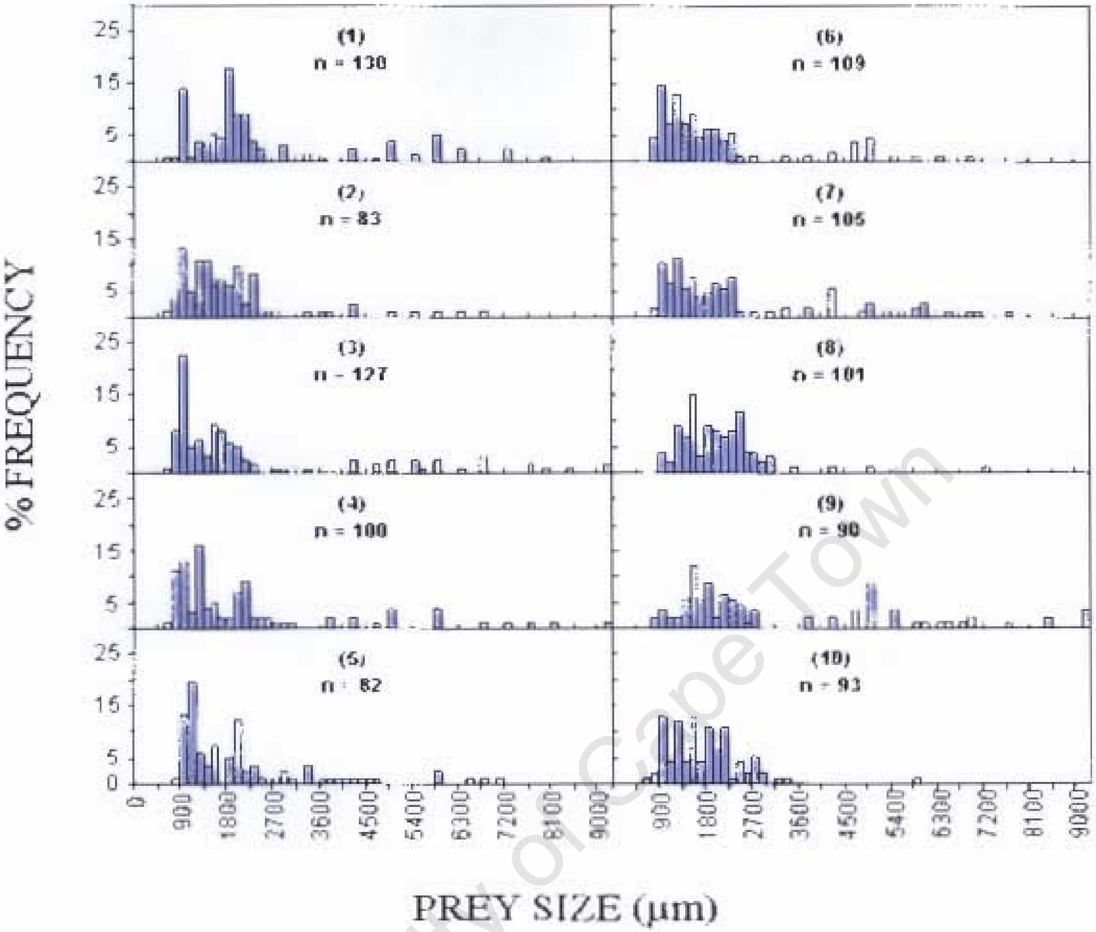

Figure 6. Size frequency distributions of identifiable prey from the stomachs of ten individual east coast redeye (1-10) from mixed shoal #1. The number of prey items (n) identified per fish is given.

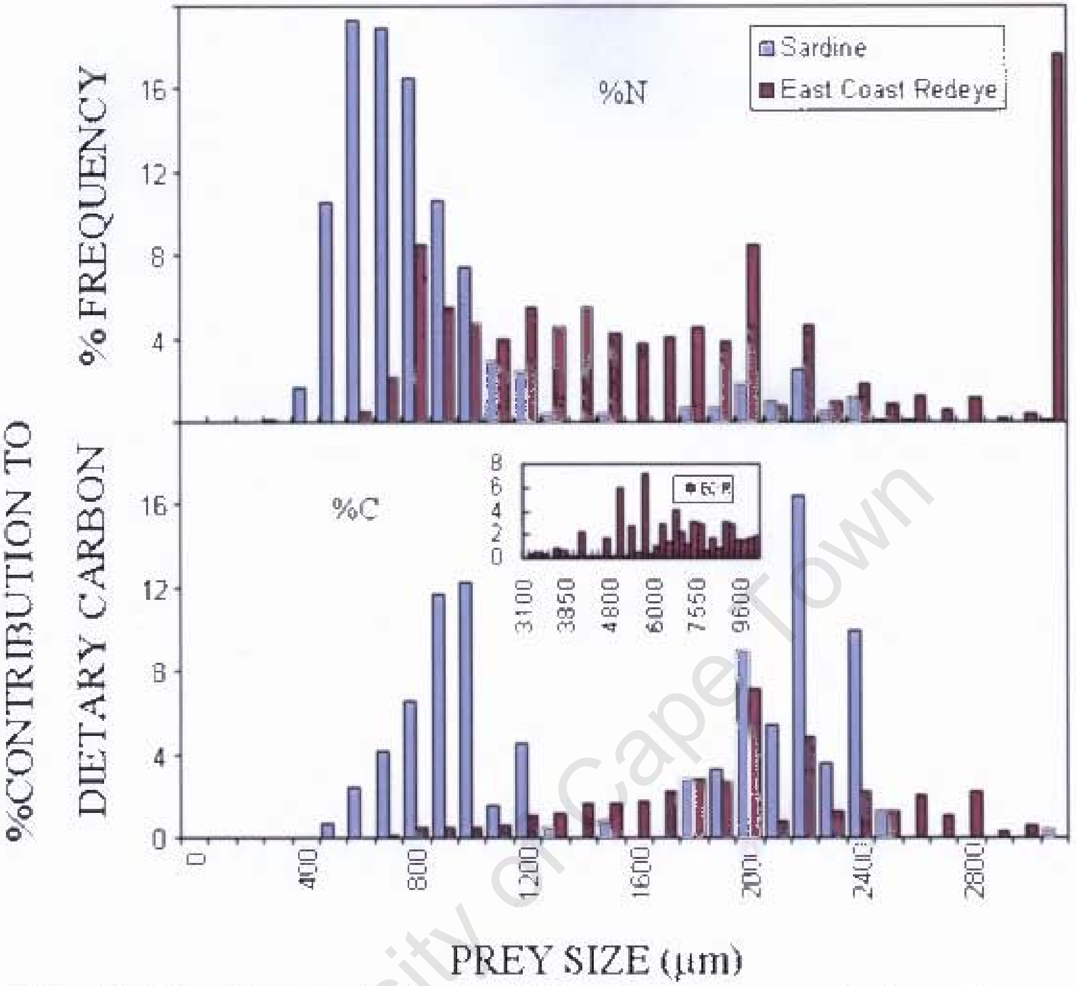

Figure 7. Combined size frequency distributions (%N) and percentage contribution to dietary carbon (%C) by size classes of identifiable prey items from the stomachs of sardine and east coast redeye from mixed shoal #1.

The size frequency distributions of prey items found in the stomachs of all sardines combined by carbon contribution (Fig. 7). showed two peaks. The first peak ranged between 500 and 1300μm and the second peak ranged from 1800-2500μm. The size frequency distributions of prey items found in the stomachs of all east coast redeye combined covered a broad range from 800 - >3000μm (Fig. 7), in addition to a number of larger (>5000μm) prey items.

There was a significant difference in the size frequency distributions of prey ingested by sardine and east coast redeye (Table 4). There were also marked differences in mean prey sizes of ingested prey items (Fig. 25b, t=22.46, df=1847, p<0.0001) with east coast redeye feeding on significantly larger prey items than sardine. In some instances the data were not normally distributed but as they were not obviously skewed the arithmetic mean was nonetheless an appropriate measure of central tendency for prey sizes (the median and mode were similar to the arithmetic mean).

Table 4 Results of the Kolmogorov-Smirnov (K-S) test showing differences in the size frequency distributions of prey ingested by sardine, anchovy, west coast redeye and east coast redeye. The value of n represents the number of size categories used in the analysis for that mixed shoal. The sequential Bonferroni procedure was used in all cases, with α_{crit} being the adjusted α values used (significance level was set at 0.05).

Mixed shoal #	Spp. interaction	n	K-S test statistic (D_i)	α_{crit}	D_{crit}	Results
1	Sardine vs EC Redeye	61	0.68695	0.05	0.17091	Sig
2	Sardine vs Anchovy	41	0.08520	0.05	0.20760	NS
	Sardine vs EC Redeye	41	0.58839	0.025	0.22804	Sig
	Anchovy vs EC Redeye	41	0.59447	0.017	0.23720	Sig
3	Sardine vs Anchovy	41	0.28837	0.025	0.22804	Sig
	Sardine vs WC Redeye	41	0.61773	0.0083	0.26002	Sig
	Sardine vs EC Redeye	41	0.54673	0.01	0.24904	Sig
	Anchovy vs WC Redeye	41	0.45581	0.0125	0.24481	Sig
	Anchovy vs EC Redeye	41	0.39818	0.017	0.23720	Sig
	WC Redeye vs EC Redeye	41	0.14090	0.05	0.20760	NS
4	Sardine vs Anchovy	51	0.23701	0.05	0.18659	Sig
	Sardine vs WC Redeye	51	0.55416	0.017	0.21321	Sig
	Anchovy vs WC Redeye	51	0.38679	0.025	0.20103	Sig

3.3 Mixed shoal #2: Sardine, anchovy and east coast redeye

Stomach contents from this shoal were also very fresh, indicating recent ingestion of prey before capture. Three fish species (sardine, anchovy and east coast redeye) were examined, all of which differed in size (Fig. 25a, F=99.9, df=2, 349, p<0.0001). Sardine sampled for stomach content analyses were relatively small compared with other shoals (Table 1) but significantly larger than anchovy and east coast redeye in this shoal with anchovy being significantly larger than east coast redeye (Fig. 25a, Tukey test, $p<0.0001$). In total, 645, 230, and 592 prey items respectively were identified in the stomachs of sardine, anchovy and east coast redeye. Ten individual fish per species were examined.

Stomach contents of sardine were numerically dominated by small copepods and poecilostomatoid copepods, but these were not dominant in terms of their contribution to dietary carbon. When prey items were converted to dietary carbon, fish eggs and large prey items (>1000μm) dominated the diet of sardine, together contributing to about 83% of the ingested carbon (Fig. 8). The stomachs of anchovy were found to contain crustacean eggs, fish eggs and zooplankton. Numerically, cyclopoid copepods and small copepods were dominant. However, when the prey items were converted into dietary carbon, fish eggs and large particles dominated in the diet of anchovy (Fig. 8). The stomachs of east coast redeye were numerically dominated by *Scolecithrix* spp., unidentified copepods and small copepods. Large particles dominated ingested carbon, contributing about 94% (Fig. 8).

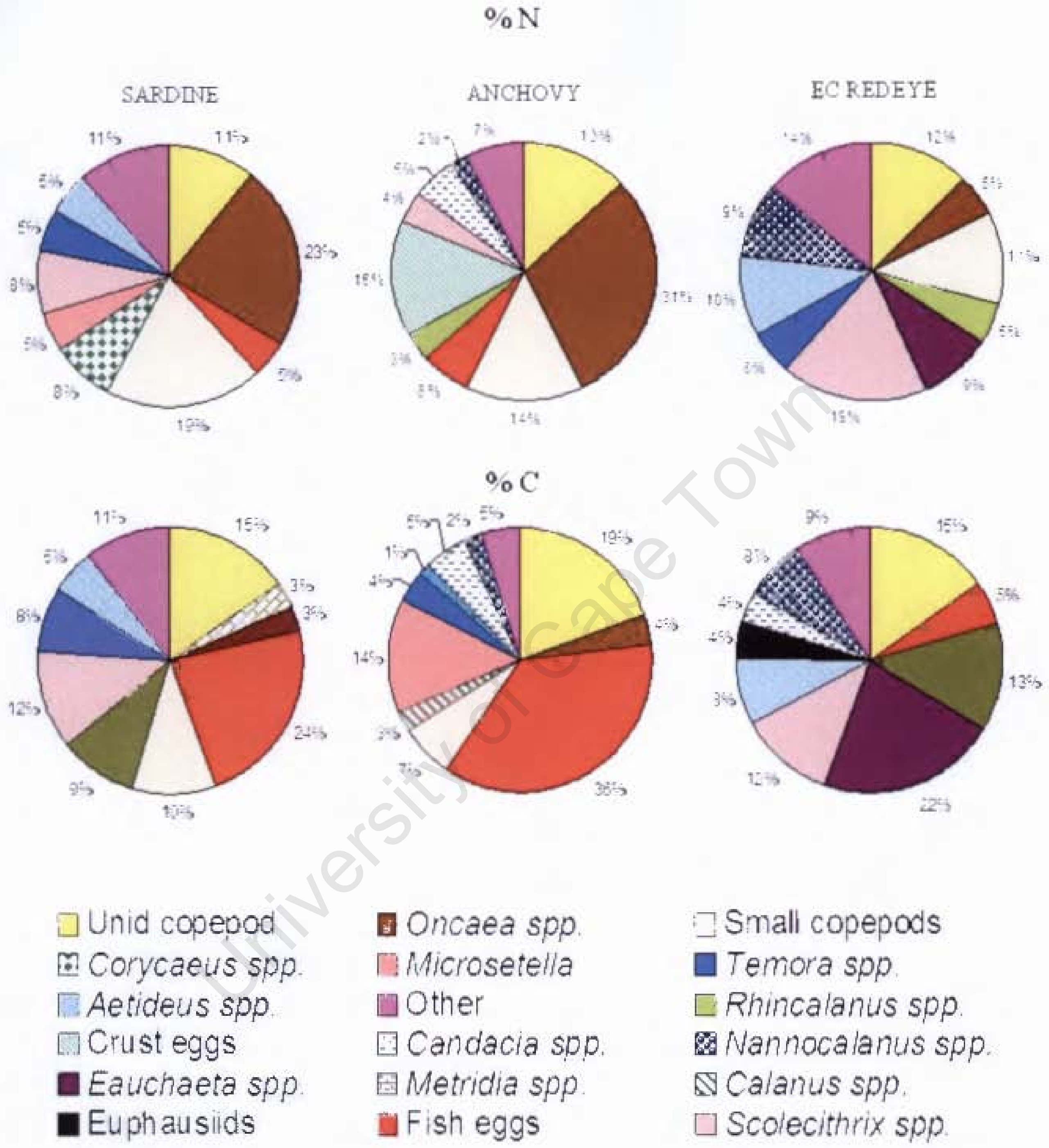

Figure 8. Relative contribution in terms of numbers (%N; top) and carbon (%C; bottom) of prey to the diet of sardine (left), anchovy (middle) and east coast redeye (right) from mixed shoal #2.

The size frequency distributions of identifiable prey items from the stomachs of individual sardine were generally very similar (Fig. 9). Sardine were feeding on a broad range of prey items ranging from 400-2100μm. The size frequency distributions of identifiable prey items of individual anchovy were similar (Fig. 10), except for fish numbers

3 and 8. Fish number 8 had the most atypical prey size frequency distribution; approximately 80% of the prey of this fish was small. Fish number 3 only ingested large prey items (>800µm) whereas other individual fish generally fed on a broad range of prey items ranging between 400µm and 1750µm. A few of the individual fish also fed on large prey items (>2000µm) (Fig. 10). The size frequency distributions of identifiable prey from the stomachs of east coast redeye were very similar (Fig. 11), with fish generally ingesting prey items ranging between 550µm and 3000µm. Fish number 9 had only five prey items in its stomach, and these five prey items were all large (>900µm).

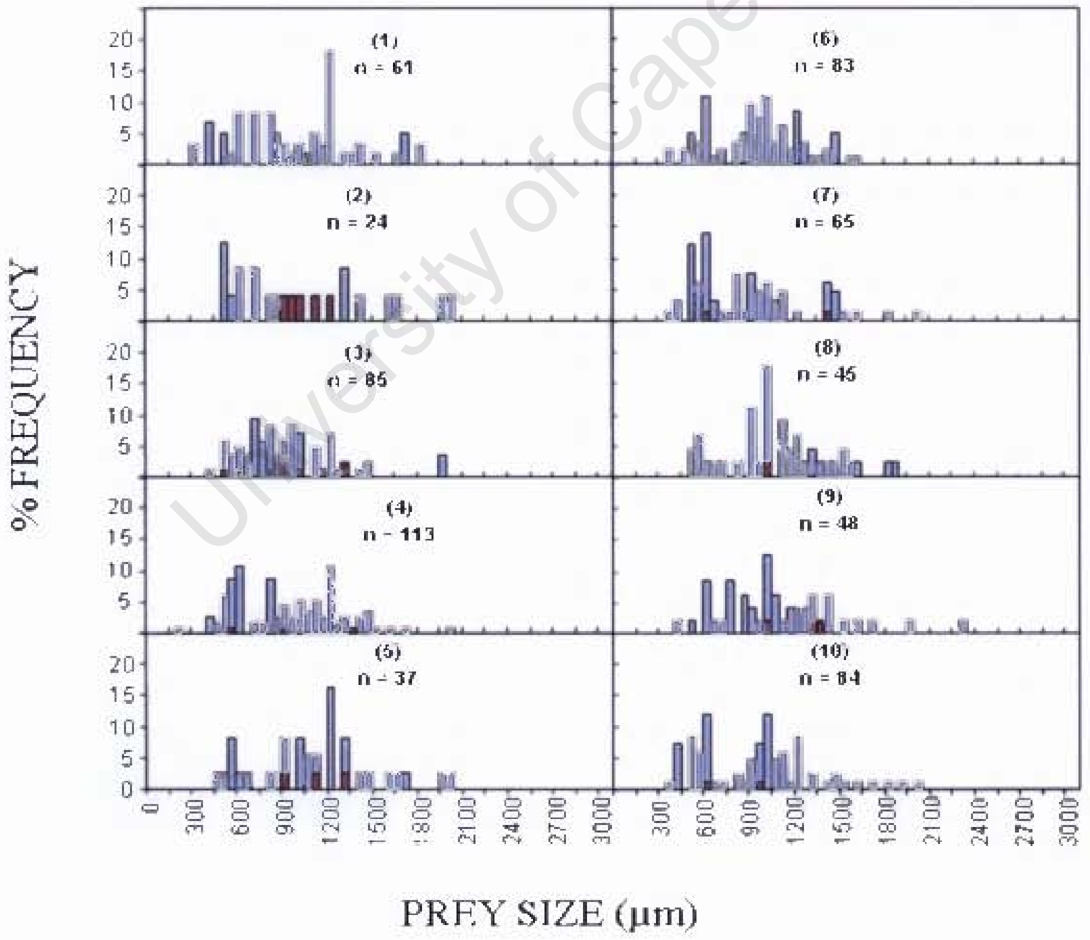

Figure 9. Size frequency distributions of identifiable prey from the stomachs of ten individual sardine (1-10) from mixed shoal #2. Note: the red bars are the fish eggs.

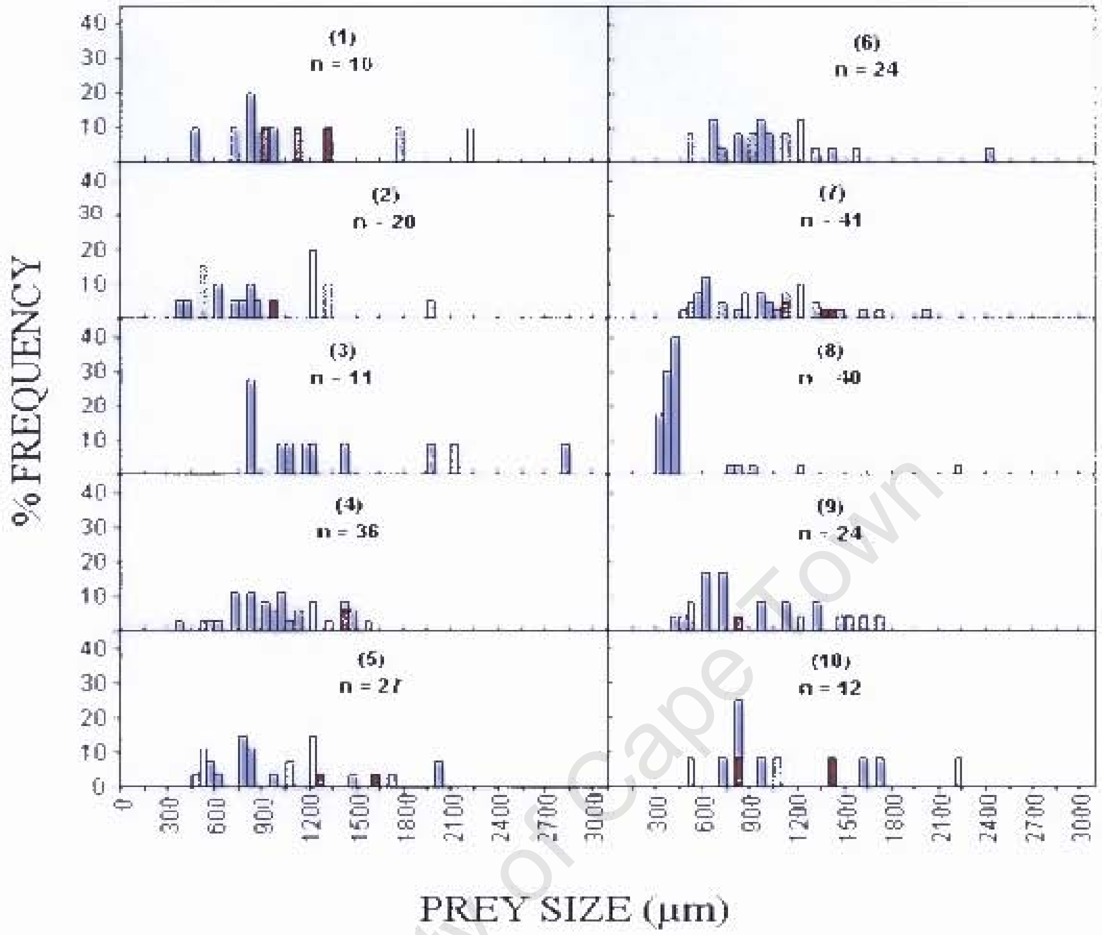

Figure 10. Size frequency distributions of identifiable prey from the stomachs of ten individual anchovy (1-10) from mixed shoal #2. Note: the red bars are the fish eggs.

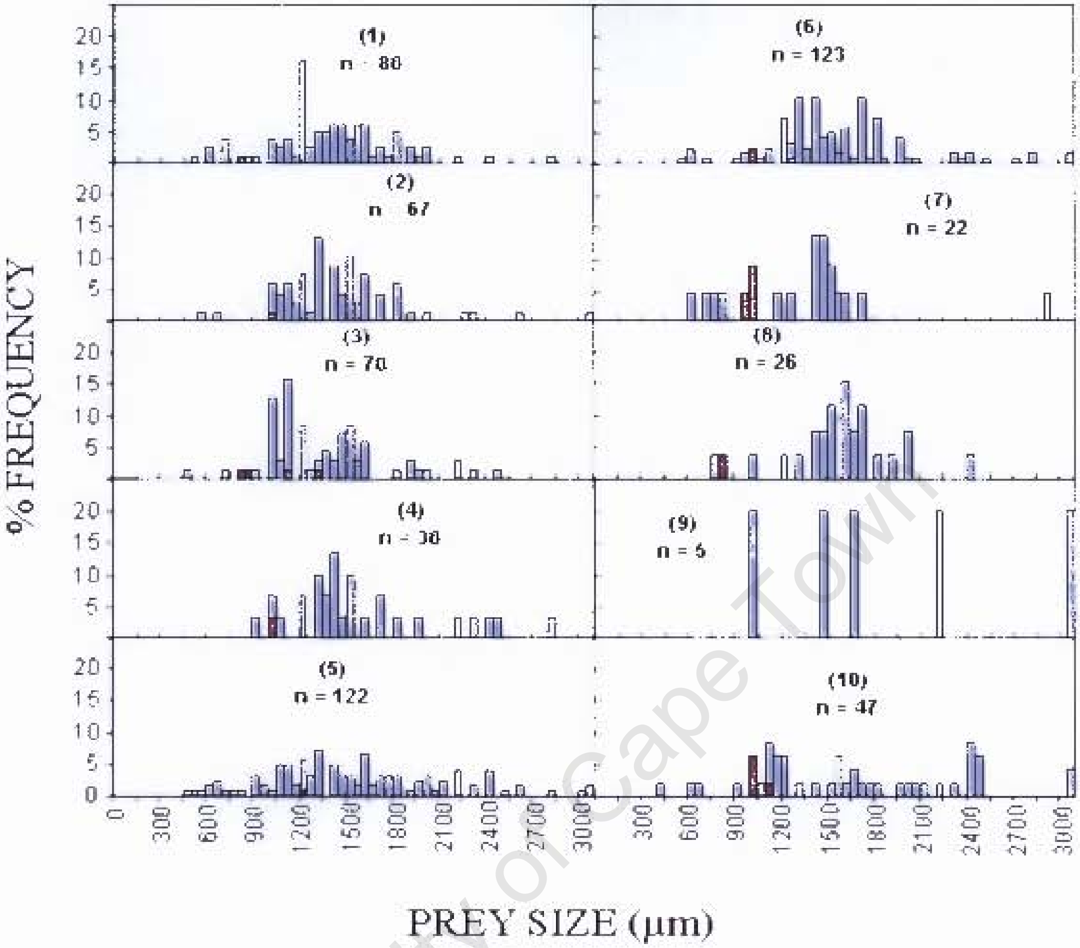

Figure 11. Size frequency distributions of identifiable prey from the stomachs of ten individual east coast redeye (1-10) from mixed shoal #2. Note: the red bars are the fish eggs.

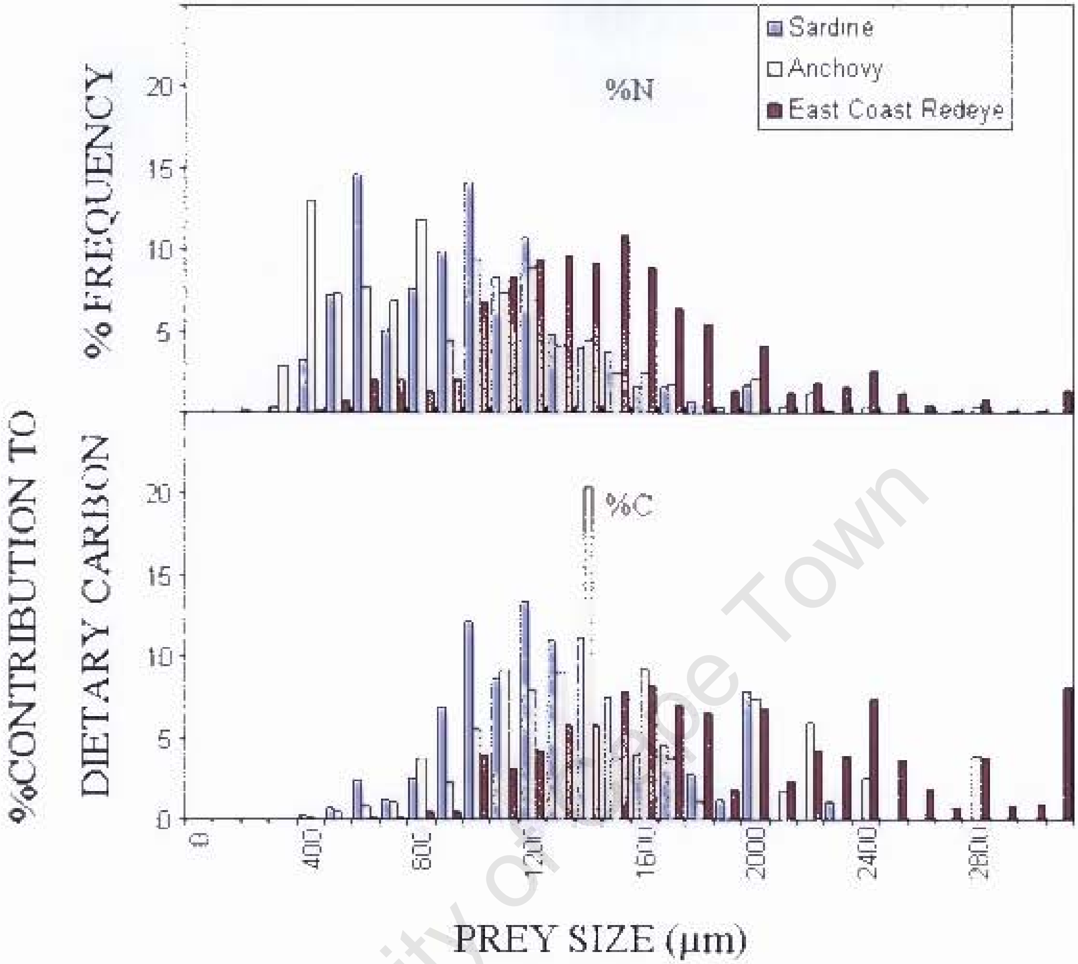

Figure 12. Combined size frequency distributions (%N) and contribution to dietary carbon (%C) of identifiable prey items from the stomachs of sardine, anchovy and east coast redeye from mixed shoal #2.

The size frequency distributions of prey items found in the stomachs of all the individual sardines combined covered a broad range (Fig. 12), but large zooplankton contributed more to dietary carbon than smaller zooplankton. There was a peak in prey between 700 and 1700µm, dominated by fish eggs and small copepods, and a second peak at 2000µm, dominated by large calanoid copepods. The size frequency distributions of prey items found in the stomachs of all individual anchovies combined covered a similar range to that of sardine (Fig. 12), but with a small shift in the peaks towards larger prey items. The size frequency distributions of prey items found in the stomachs of all the individual east coast redeye combined were shifted to the right compared with those of sardine and anchovy (Fig.

12). There was a peak between 1000 and 1900µm (dominated by *Scolecithrix* spp. and *Aetideus* spp.), and another peak between 2000 and 2500µm (dominated by *Euchaeta* spp. and *Rhincalanus* spp.). East coast redeye tended to ingest larger prey items than the other two species (Fig.12).

There was no significant difference in the size frequency distributions of prey ingested by sardine and anchovy (Table 4). There was also no significant difference in the mean prey sizes of ingested prey items between sardine and anchovy (Fig. 25b, F=236.33, df=2, 1479, p=0.6102), indicating that both species were feeding on prey items of the same size range. However, there was a significant difference in the size frequency distributions (Table 3) and in the mean prey sizes of prey ingested by sardine and east coast redeye, and by anchovy and east coast redeye (Fig. 25b, F=233.36, df=2, 1479, p<0.0001). East coast redeye ingested significantly larger prey items than the other two species.

3.4 Mixed shoal #3: Sardine, anchovy, west coast redeye and east coast redeye

Stomach contents from this shoal were also very fresh, indicating recent ingestion of prey before capture. Four fish species (sardine, anchovy, west coast redeye and east coast redeye) were examined, all of which differed in size (Fig. 25a, F=422.8, df=3, 538, p<0.0001). Sardine sampled for stomach content analyses were relatively large compared with other shoals, except for mixed shoal no 1 (Table 1), and were significantly larger than east coast redeye, anchovy and west coast redeye in this shoal (Fig 25a, Tukey test, p<0.0001). East coast redeye were also significantly larger than anchovy and west coast redeye and anchovy were significantly larger than west coast redeye (Fig. 25a, Tukey test, p<0.0001). In total, 957, 740, 475, and 1255 prey items respectively were identified in the stomachs of sardine, east coast redeye, anchovy and west coast redeye. Ten individual fish per fish species were examined for anchovy, west coast redeye and east coast redeye, and 20 individual fish for sardine.

Fish eggs, poecilostomatoid copepods, cyclopoid copepods and small copepods were numerically dominant prey items in sardine stomachs (Fig. 13) but when converted into dietary carbon, fish eggs contributed 88.6% of the ingested carbon (Fig. 14). Numerically, anchovy stomachs were dominated by poecilostomatoid copepods and crustacean eggs. (Fig. 13). Fish eggs were present in small numbers and contributed 15% in terms of carbon, but this was much less than for the other fish species (Fig. 14). Instead copepods contributed the bulk of the dietary carbon for anchovy. Numerically, the stomachs of west coast redeye were dominated by fish eggs (Fig. 13), and fish eggs and large zooplankton material (>1000μm) contributed to about 90% of the ingested carbon, with fish eggs contributing >50% (Fig. 14). Fish eggs also numerically dominated the stomachs of east coast redeye (Fig. 13) and they retained dominance when converted into dietary carbon, contributing 80% of the ingested carbon (Fig. 14).

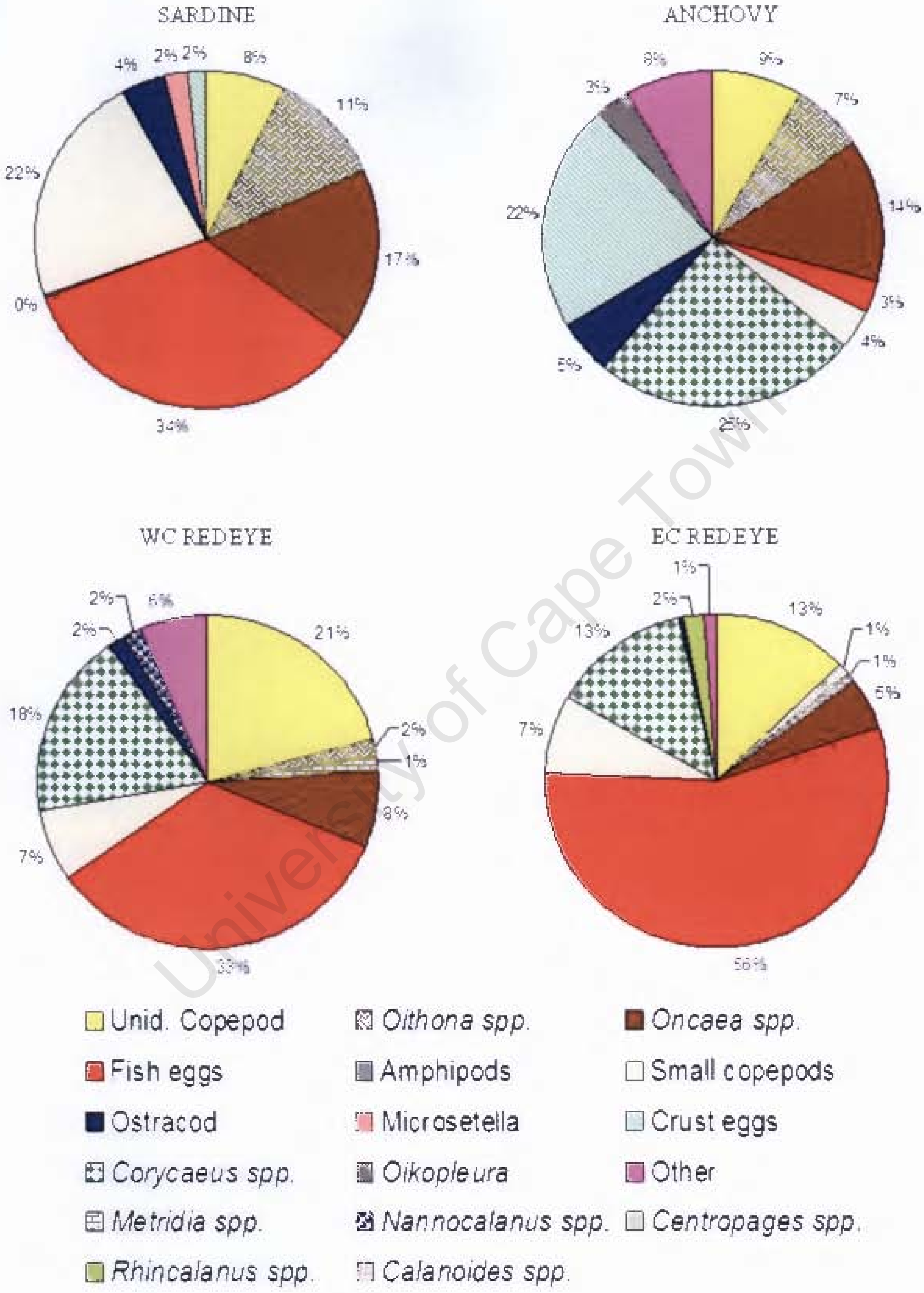

Figure 13. Relative contribution in terms of numbers (%N) of prey to the diet of sardine, anchovy, west coast redeye and east coast redeye from mixed shoal #3.

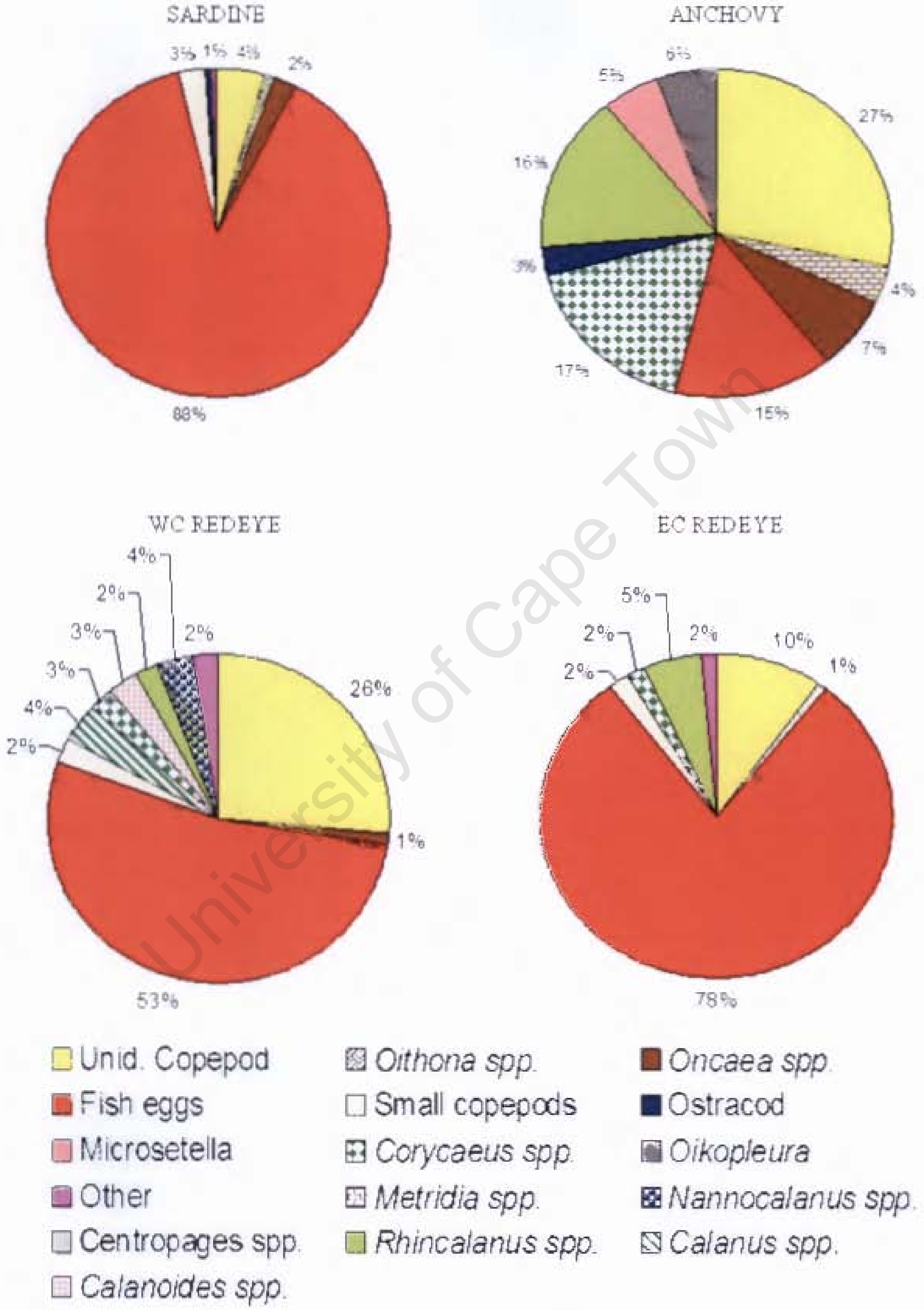

Figure 14. Relative contribution in terms of carbon (%C) of prey to the diet of sardine, anchovy, west coast redeye and east coast redeye from mixed shoal #3.

The size frequency distributions of identifiable prey items from the stomachs of individual sardine were very similar (Fig. 15), except for fish number 18 which only ingested fish eggs. Sardine were feeding on small prey items 300µm as well as larger prey items >1000µm, but prey sizes generally ranged between 300 and 950µm in size (Fig. 15). The size frequency distributions of identifiable prey items from the stomachs of individual anchovy were variable (Fig. 16). Some of the fish consumed few prey across a broad range of prey sizes (e.g. fish numbers 2, 8 and 9), whereas others consumed many prey items concentrated in a narrow size range (e.g. fish numbers 5, 6 and 10). Generally, anchovy were feeding on prey items ranging between 350-1000µm in size (Fig. 16). The size frequency distributions of identifiable prey items from the stomachs of individual west coast redeye were very variable (Fig. 17) and had two main peaks. Fish were feeding on prey items ranging between 450 and 1200µm in size (Fig. 17) and 1500 and 2000µm. The size frequency distributions of identifiable prey items from the stomachs of individual east coast redeye generally ranged between 500-1200µm in size (Fig. 18). Fish number 4 fed only on fish eggs and fish numbers 8 and 9 ate a broad size range that included prey items >1300µm (Fig. 18).

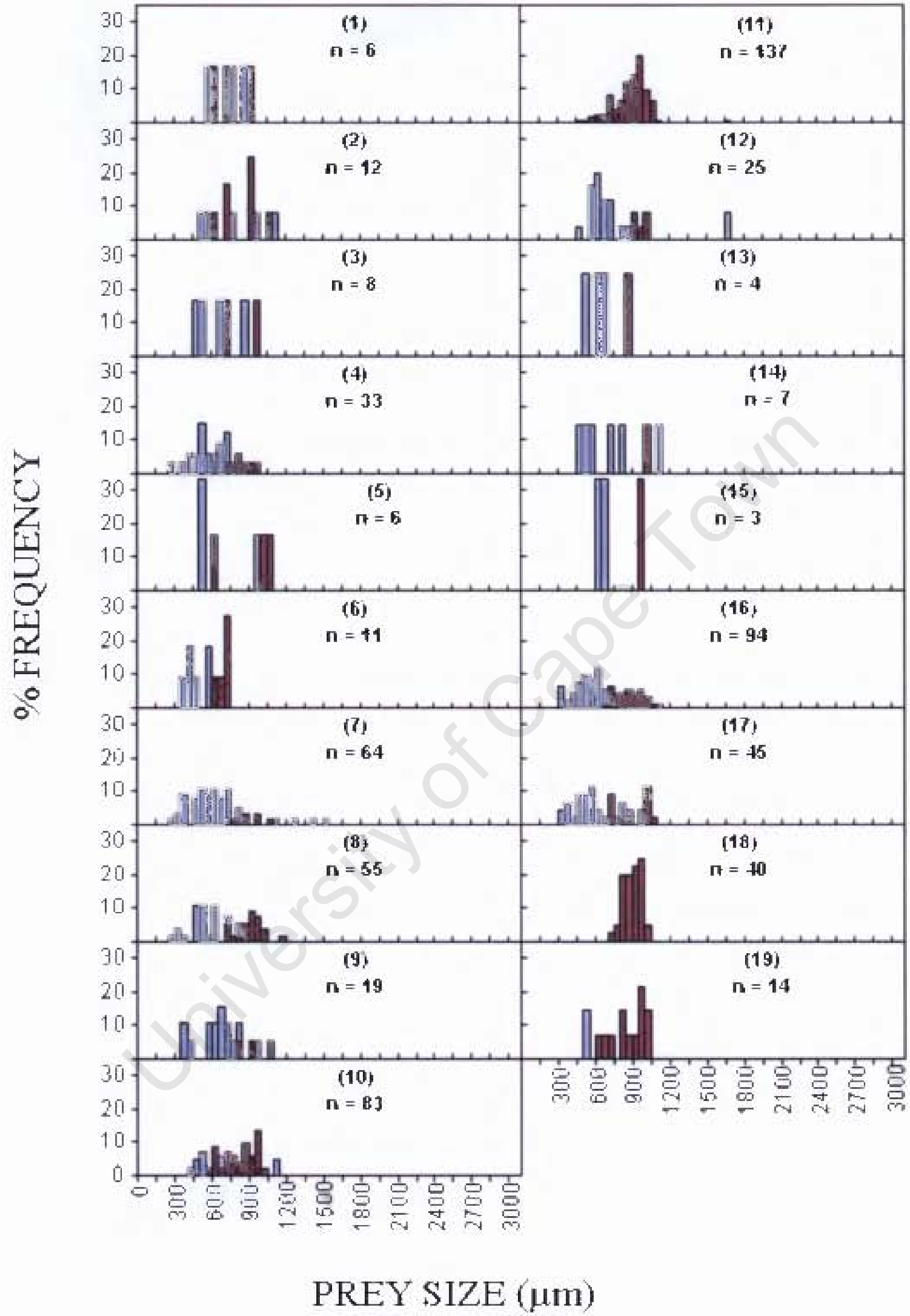

Figure 15. Size frequency distributions of identifiable prey from the stomachs of 19 sardine (1-19) from mixed shoal #3. Note: the red bars are the fish eggs.

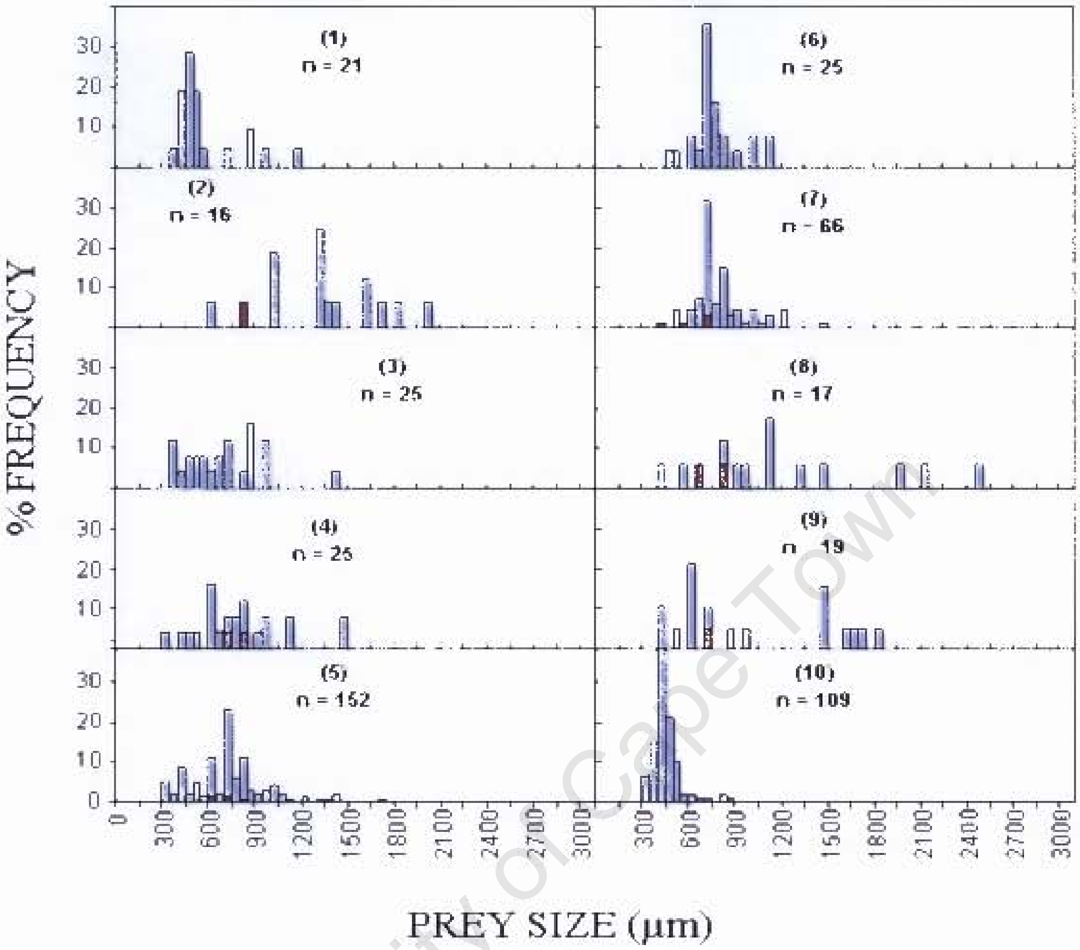

Figure 16. Size frequency distributions of identifiable prey from the stomachs of ten anchovy (1-10) from mixed shoal #3. Note: the red bars are the fish eggs.

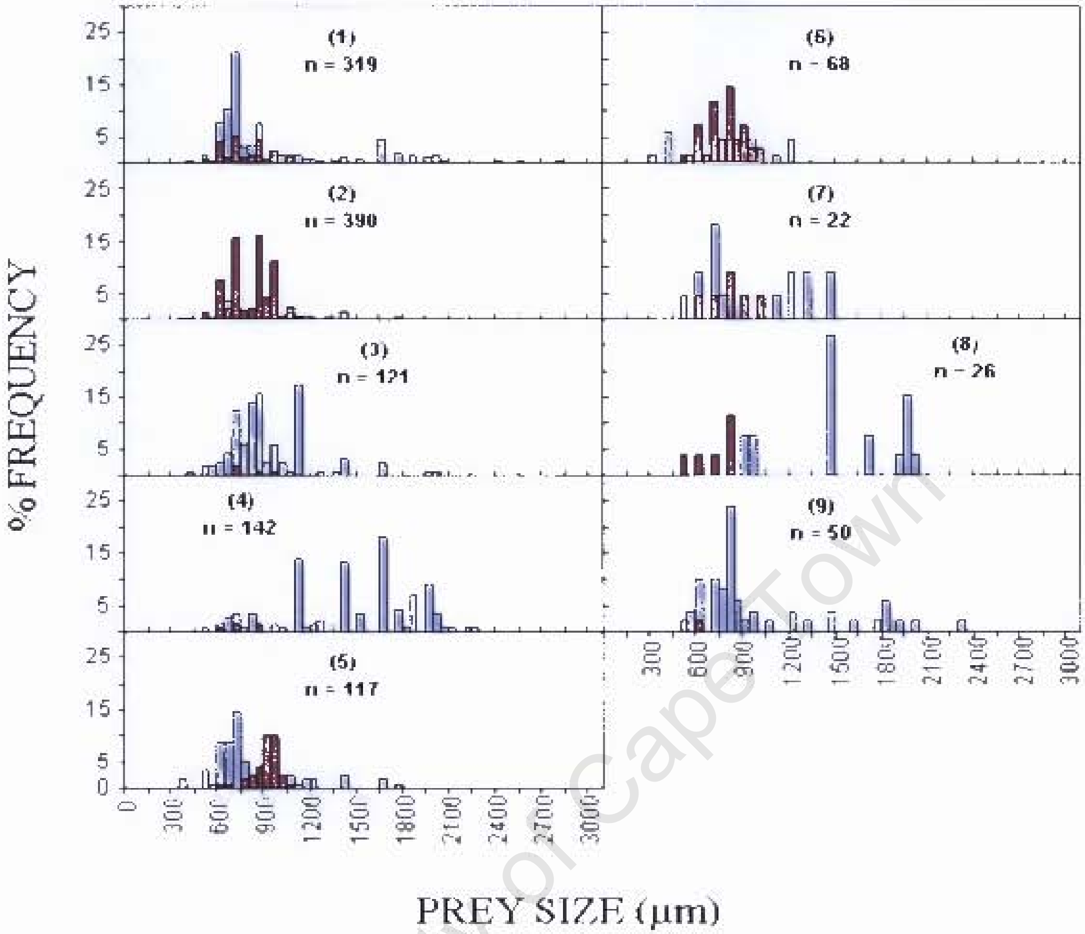

Figure 17. Size frequency distributions of identifiable prey from the stomachs of nine individual west coast redeye (1-9) from mixed shoal #3. Note: the red bars are the fish eggs.

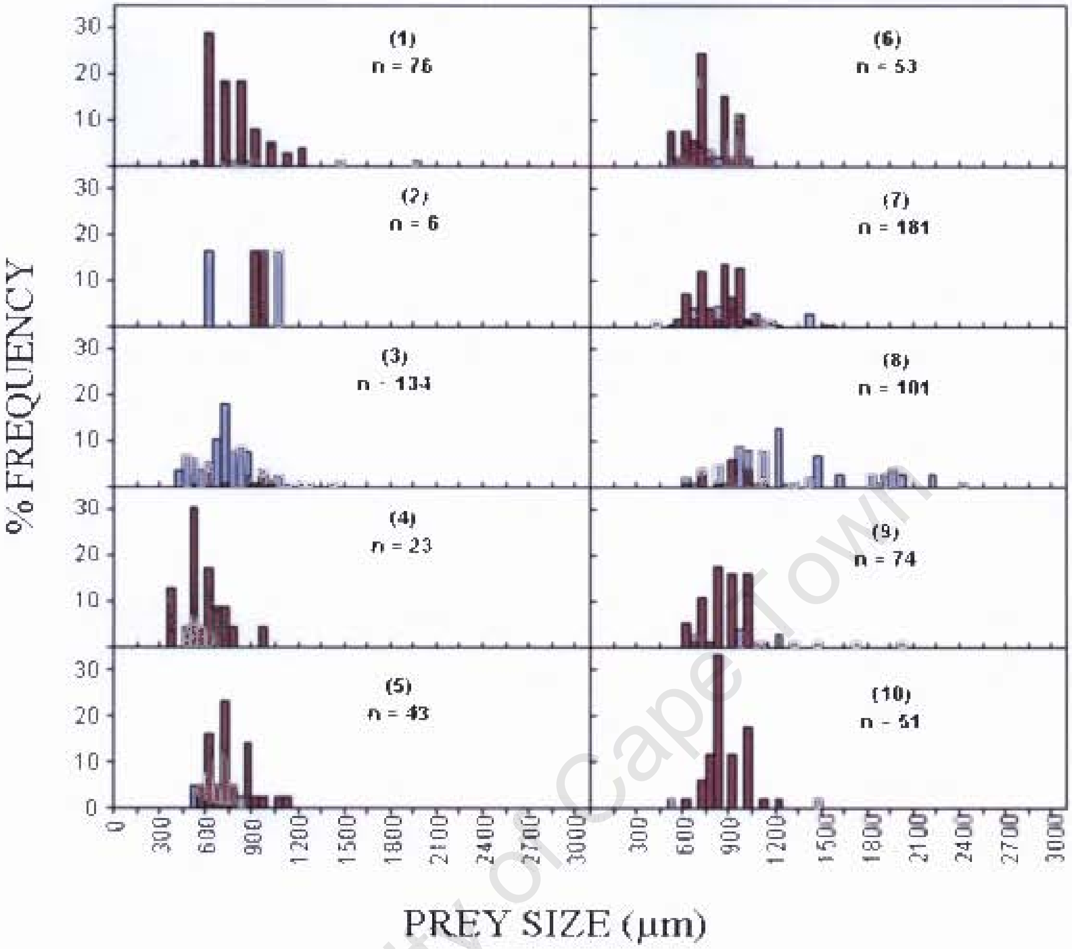

Figure 18. Size frequency distributions of identifiable prey from the stomachs of ten individual east coast redeye (1-10) from mixed shoal #3. Note: the red bars are the fish eggs.

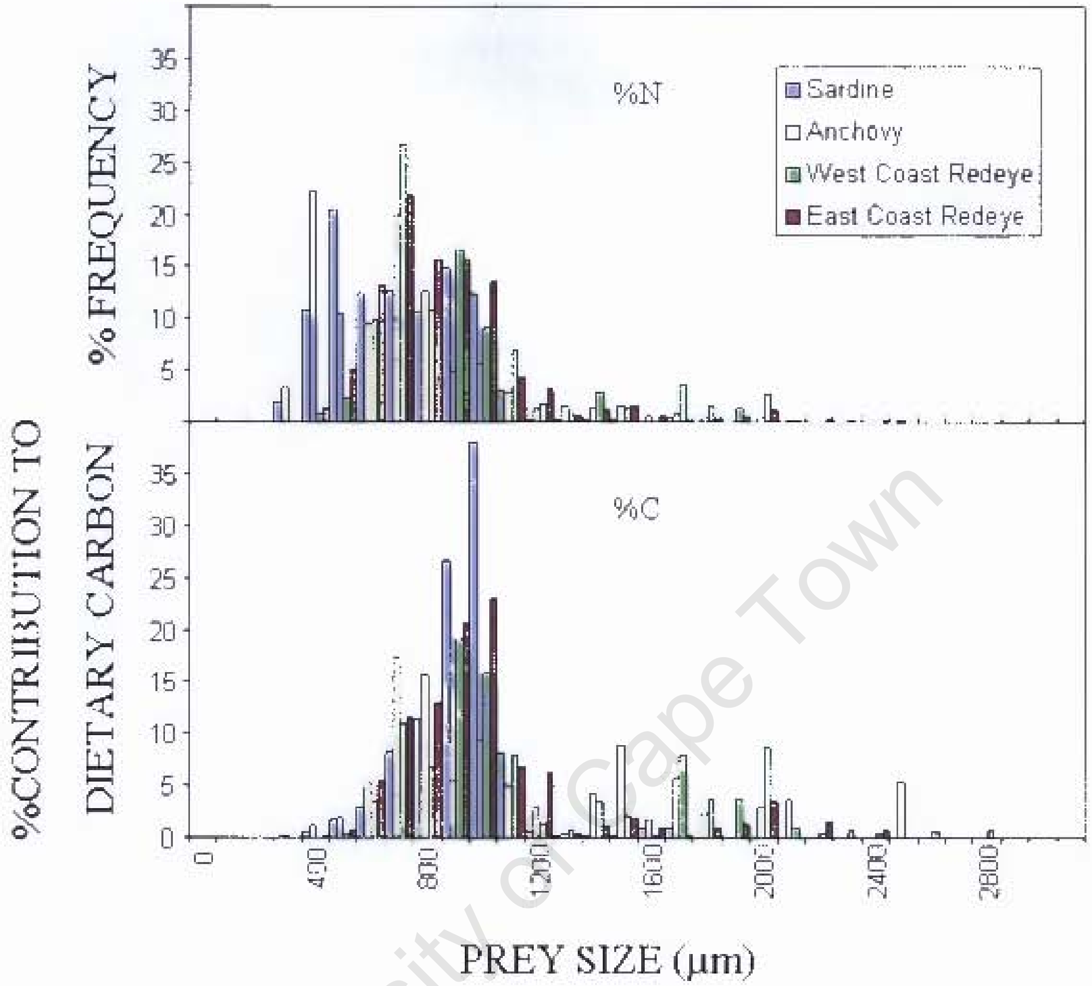

Figure 19. Combined size frequency distributions (%N) and contribution to dietary carbon (%C) of identifiable prey items from the stomachs of sardine anchovy west coast redeye and east coast redeye from mixed shoal #3.

The size frequency distributions of prey items found in the stomachs of all the individual fish combined showed one major peak over a broad range (Fig. 19), ranging between 600 and 1200µm for carbon and dominated by fish eggs. Compared to sardine and the two redeye species, the peak for anchovy was shifted slightly to the left. Anchovy and the two redeye species generally ate larger prey items than sardine (Fig. 19).

There were significant differences in the prey size frequency distributions of the fish species (Table 4, Fig. 25b, F=145.53, df=3, 3423, p<0.0001), with west coast redeye ingesting slightly larger prey than east coast redeye which in turn were ingesting larger prey than sardine and anchovy. Sardine and anchovy tended to eat similar sized prey (Fig. 25b, F=145.53, df=3, 3423, p=0.91111).

3.5 Mixed shoal # 4: Sardine, anchovy and west coast redeye

Stomach contents from this shoal were relatively well digested and hence difficult to identify. Three fish species (sardine, anchovy and west coast redeye) were examined, all of which differed in size (Fig. 25a, F=399.7, df=2, 350, p<0.0001). Sardine sampled for stomach content analyses were significantly larger than anchovy, which in turn were significantly larger than west coast redeye (Fig. 25a, Tukey test, p<0.0001). In total, 495, 122 and 122 prey items respectively were identified in sardine, anchovy and west coast redeye stomachs respectively. Ten individual fish per fish species were examined. Anchovy and west coast redeye had relatively few prey items in their stomachs.

Only crustacean eggs, fish eggs and zooplankton material were found in the stomachs of sardine from this shoal. Numerically, small copepods, poecilostomatoid copepods, and cyclopoid copepods dominated in the stomachs of sardine (Fig. 20). Large zooplankton (>1000µm) contributed a small proportion to the number of prey items ingested by sardine but, together with fish eggs, they contributed about 70% to the ingested carbon (Fig. 20). Anchovy stomachs were numerically dominated by poecilostomatoid copepods, small copepods, and to lesser extent large copepods (Fig. 20), but large particles (>1000µm) dominated the diet of anchovy in terms of contribution to dietary carbon. Numerically, the stomachs of west coast redeye were dominated by unidentified copepods (Fig. 20), and these also dominated prey carbon, together with fish eggs and other large prey items.

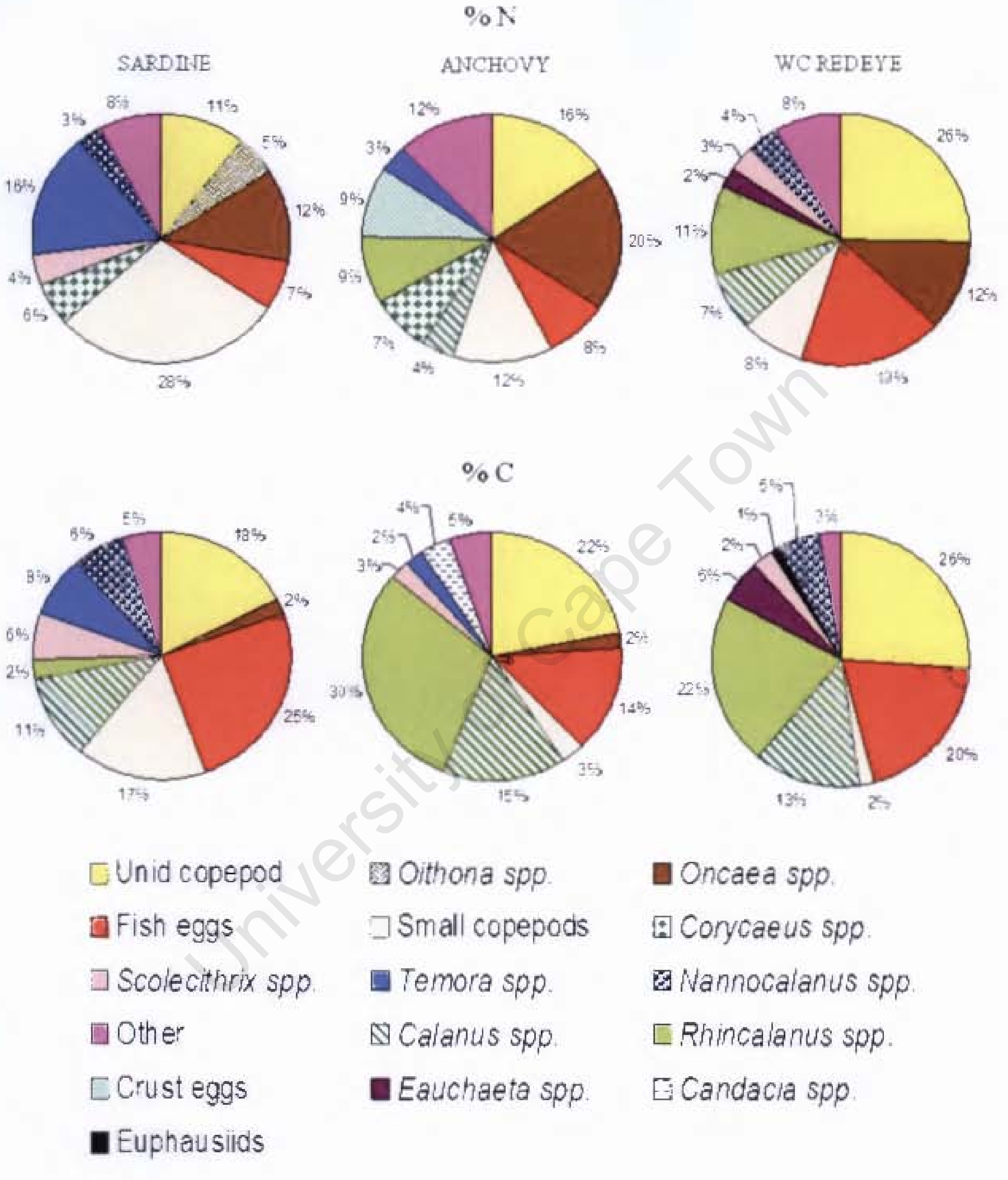

Figure 20. Relative contribution in terms of numbers (%N; top) and carbon (%C; bottom) of prey to the diet of sardine (left), anchovy (middle) and west coast redeye (right) from mixed shoal #4.

The size frequency distributions of identifiable prey items from the stomachs of individual sardine were generally very similar (Fig. 21), with sardine feeding on prey items ranging between 300μm and 2400μm. The size frequency distributions of identifiable prey items from the stomachs of individual anchovy in terms of the smallest identified prey were similar (Fig. 22), except for fish number 8 in which the smallest identified prey was 700µm. The numbers of prey items that were identified and measured were very low and it was therefore difficult to assess the diet of anchovy in this shoal. Anchovy were feeding on prey items ranging from 400µm to >3000µm (Fig. 22). The size frequency distributions of identifiable prey items from the stomachs of individual west coast redeye were also variable (Fig. 23), but the stomachs were quite empty, with few prey items, which made dietary description difficult. Generally, west coast redeye were feeding on prey items ranging between 500µm and 2400µm (Fig. 23).

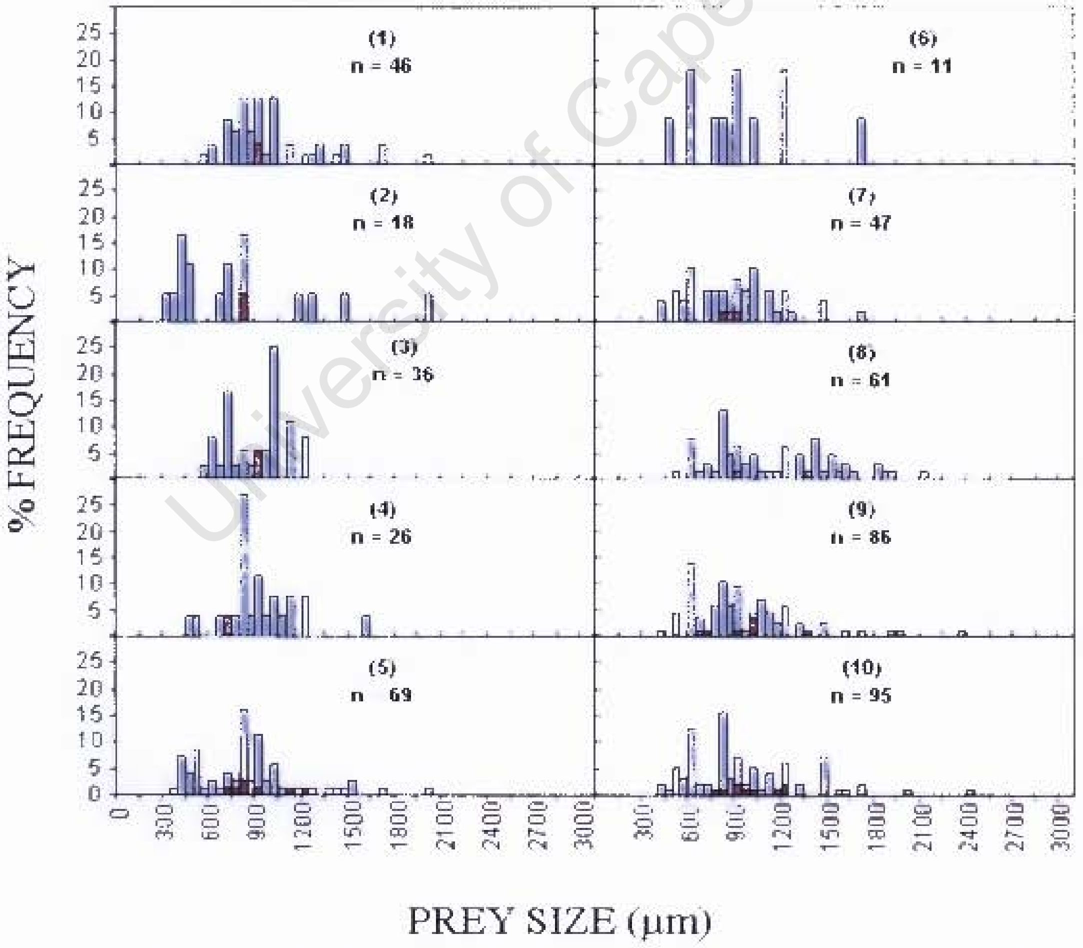

Figure 21. Size frequency distributions of identifiable prey from the stomachs of ten individual sardine (1-10) from mixed shoal #4. Note: the red bars are the fish eggs.

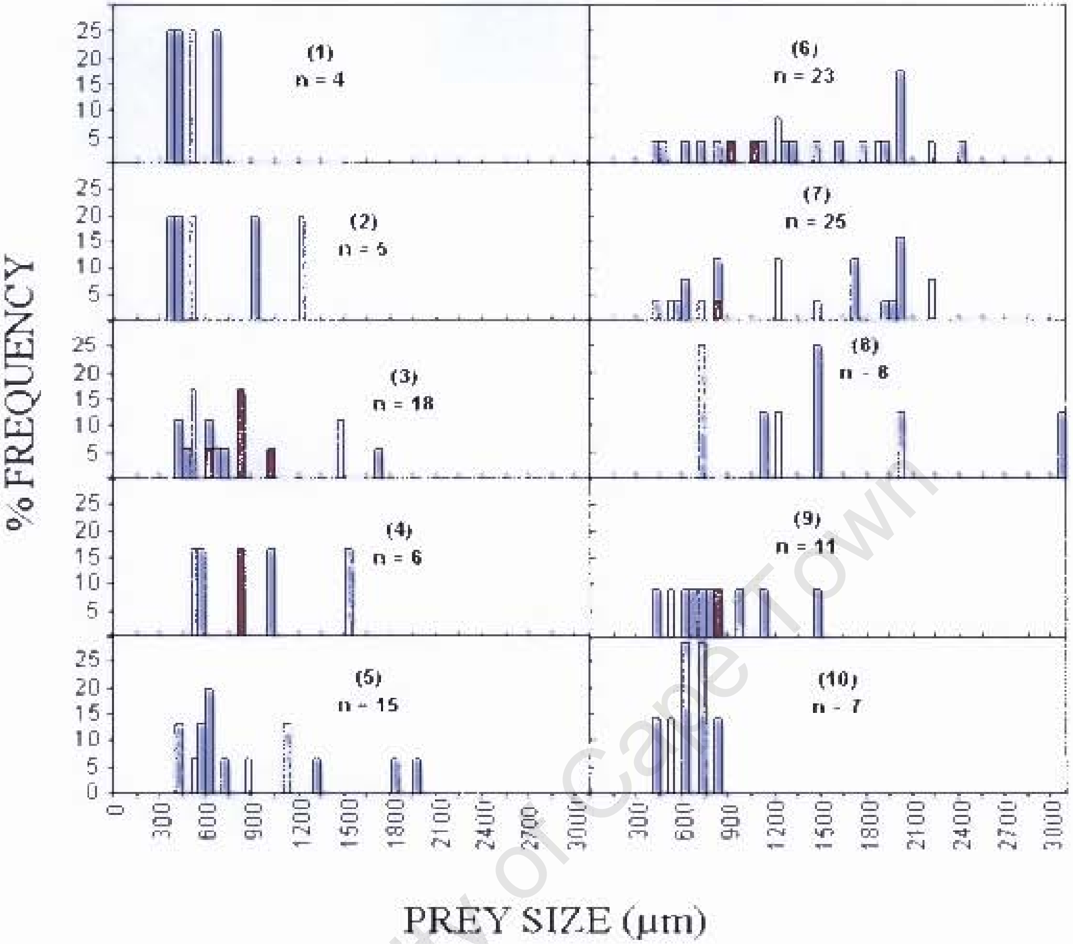

Figure 22. Size frequency distributions of identifiable prey from the stomachs of ten individual anchovy (1-10) from mixed shoal #4. Note: the red bars are the fish eggs.

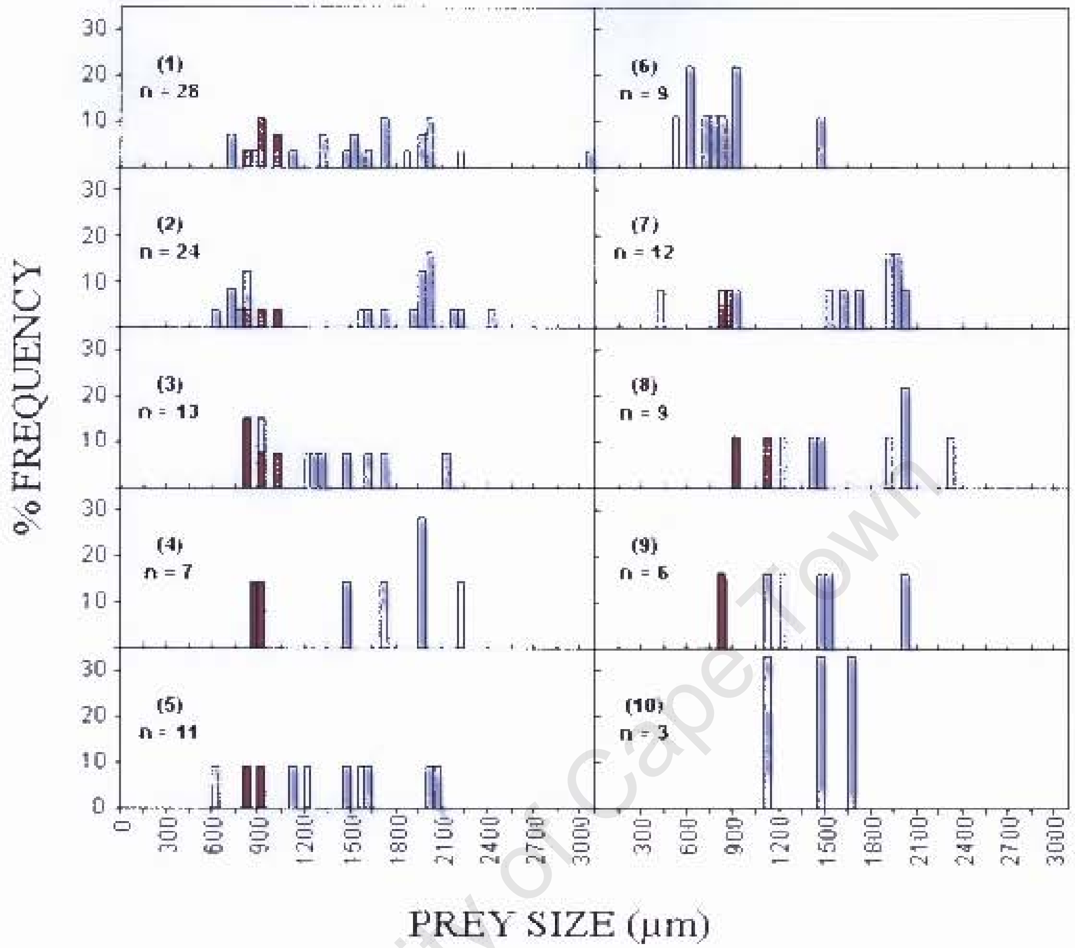

Figure 23. Size frequency distributions of identifiable prey from the stomachs of ten individual west coast redeye (1-10) from mixed shoal #4. Note: the red bars are the fish eggs.

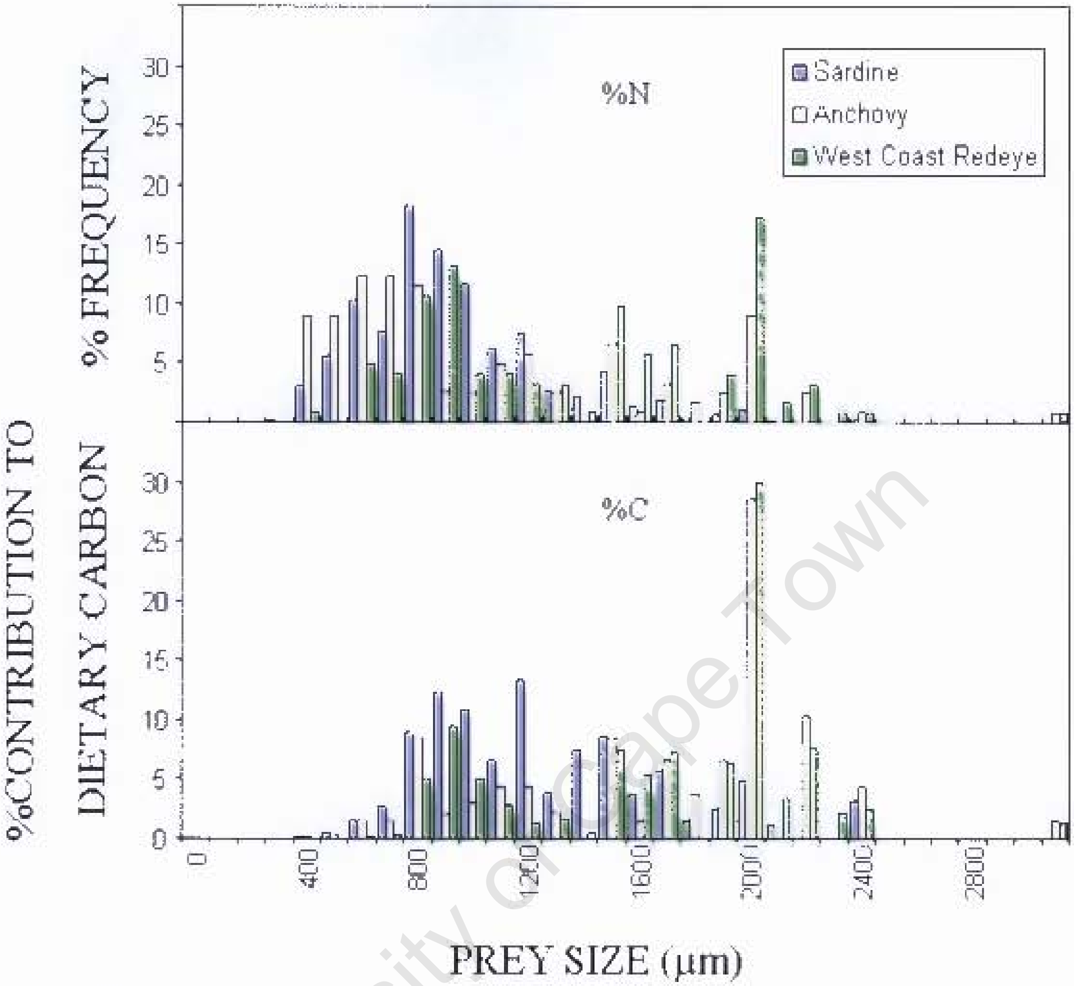

Figure 24. Combined size frequency distributions (%N) and contribution to dietary carbon (%C) of identifiable prey items from the stomachs of sardine anchovy and west coast redeye from mixed shoal #4.

The size frequency distributions of prey items found in the stomachs of all the individual fish combined covered a broad range (Fig. 24). Sardine tended to rely on smaller prey items than anchovy and west coast redeye for carbon. Anchovy and west coast redeye had large dietary carbon contributions from prey (>2000µm).

There were significant differences in the prey size frequency distributions of the prey items ingested by all three species from this mixed shoal (Table 4). There were significant differences in the mean prey sizes of ingested prey by all the fish species (Fig. 25b). F=53.78, df=2, 736, $p<0.0001$). West coast redeye ingested larger prey items than anchovy, which in turn ingested larger prey items than sardine.

4. DISCUSSION

4.1 METHODS

An assumption was made that fish caught in the same trawl were from mixed schools. This assumption seemed realistic and was based on the fact that the schools of fish were close to one another and they could have mixed.

Two assumptions were made for including body parts of unidentifiable zooplankton in the analyses namely, that 1) all unidentifiable zooplankton were copepods, and 2) one body part represented one copepod. The second assumption is realistic because most of the body parts represented cephalothorax, of which copepods have only one. There was a relatively large proportion of unidentifiable zooplankton in all of the mixed shoals, with this category contributing 4%, 12%, 14%, and 14% for shoals 1, 2, 3 and 4 by number respectively. In terms of contribution to dietary carbon, unidentified zooplankton contributed approximately 4%, 16%, 16% and 21% for shoals 1, 2, 3 and 4 respectively.

The total lengths and prosome lengths of some prey items were predicted from prosome lengths and prosome width respectively, using linear regression equations. Relationships for *Calanus* spp., *Euchaeta* spp., *Oithona* spp., and *Microsetella* spp. were based on data that had much scatter, but we assume that our estimates for prey sizes are reasonable.

As this study was conducted on the east coast of South Africa, it would be appropriate to use equations from the east coast to relate zooplankton length to dry weight and carbon. Unfortunately, no data are available for such calculations, and the relationships derived from measurements made in other systems may have introduced errors. The equations were consistently applied across the species but biases in individual weights could potentially change the relative importance of different prey categories for each fish species, and might influences comparisons among species.

4.2 DIET COMPOSITION

In this study, sardine were feeding mainly on fish eggs and zooplankton. No phytoplankton were found in any of their stomachs. Size frequency distributions of identifiable prey items from sardine stomachs was similar in most shoals, with sardine mainly ingesting small to medium (300-1500µm) prey items but also fairly large particles on occasion (>2000µm) (Fig. 26a). Sardine are known to exhibit two modes of feeding, filter feeding and particulate feeding, depending on the size and concentration of prey available to them (van der Lingen, 1994). Because they were ingesting small to medium particles, this indicates that they were using both forms of feeding. The prey size at which sardine switch from filtering to biting is approximately 1230µm (van der Lingen, 1994); in mixed shoal 3 most prey were probably captured by filtering, but mixed feeding modes were used at the remaining sites.

Anchovy were also feeding mainly on fish eggs and zooplankton and no phytoplankton were found in any of their stomachs. Prey frequency size distributions for anchovy were similar in most shoals, with mixed shoal 3 having few large prey items (Fig. 26b). Anchovy were generally feeding across a broad size range and they ate larger particles (>2000µm) than sardine. The size at which anchovy are known to switch from filtering to biting is approximately 710µm (James and Findlay, 1987), so it appears that most of the dietary carbon was obtained by particulate feeding.

The stomachs of west coast redeye were found to contain only zooplankton and fish eggs. Prey frequency size distributions of west coast redeye showed two peaks (Fig. 26c), and they appear to obtain most of their dietary carbon from two main size ranges (500-1200µm and 1300-2400µm). West coast redeye generally ingested a similar size range of particles to anchovy and sardine (350 - >2000µm) (Fig. 26c), but tended to eat larger particles than sardine when feeding in the same area. These findings are consistent with Wallace-Fincham (1987), who noted that west coast redeye were zooplanktivorous and their diet was largely dominated by large calanoid copepods, followed by euphausiids and decapods.

The stomachs of east coast redeye were also found to contain only fish eggs and zooplankton. Prey size frequency distributions of east coast redeye extended over a broad prey size range (Fig. 26d). There was a cluster of small prey consumed (500-1200µm) at mixed shoal 3, but this was similar to the other three species, and represented the large numbers of fish eggs consumed. Eat coast redeye were generally ingesting medium to large particles (350 - >3000µm), and tended to have the biggest prey size range.

In most shoals, the size frequency distributions and mean prey sizes of ingested prey items for the different fish species were significantly different. The two redeye species ate similar-sized prey and had larger mean prey sizes than anchovy, which in turn had larger mean prey sizes than sardine. The differences between the mean prey sizes were statistically significant. This could indicate that these species were feeding on different prey ranges in this environment. There were also differences in dietary composition of fish species in the different shoals, in terms of contributions by carbon. In some shoals, diets were dominated by fish eggs, whereas others were dominated by large crustaceans (euphausiids and calanoid copepods).

There were no phytoplankton found in any of the stomachs of the fish. This study was carried out on the east coast of South Africa, a region which is known to be less productive than the west coast, and which has smaller phytoplankton cells. The results obtained here are consistent with those of Blaxter and Hunter (1982), who reported that zooplankton dominated the diets of small pelagics in less productive areas. The findings of this study are also consistent with the size frequency plots in van der Lingen (2002), who also showed few particles and broad prey size frequency distributions for fish to the east (i.e., little or no phytoplankton). These findings are also consistent with what Wallace-Fincham (1987) reported on the diet of west coast redeye off the west and south coasts of South Africa.

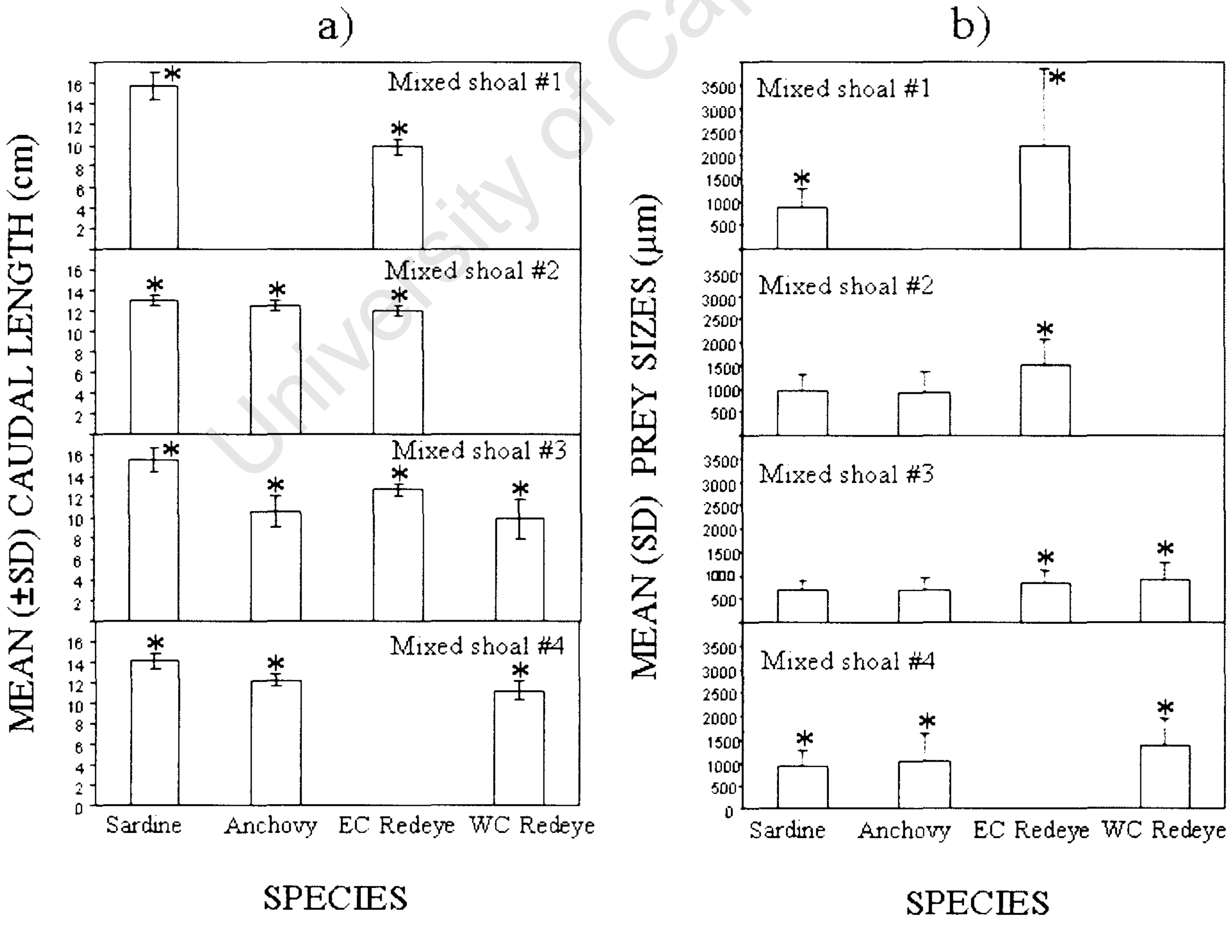

Figure 25. Summary of mean fish lengths and prey sizes for the four small pelagic species in all the mixed shoals. a) Mean (±SD) fish length. b) Mean (+SD) prey sizes of the ingested prey items. (* indicates significant differences).

In comparison to other parts of the world, there seems to be no difference in the way the small pelagics from South Africa feed. In coastal waters of Japan, Tanaka *et al.* (2006) reported that *Etrumeus. teres* and Japanese anchovy (*Engraulis. japonicus*) feed mainly on crustacean zooplankton such as copepods, and Zhang *et al.* (2004) found that sardine (*Sardinops. melanostictus*) feed primarily on zooplankton (small crustaceans) and phytoplankton (diatoms). Off the west coast of South America, it was reported that the diet of anchovy (*E. ringens*) was mainly dominated by phytoplankton (Rojas de Mendiola, 1976; Gay *et al.*, 2002; Sandweiss *et al.*, 2004) and to a lesser extent zooplankton (Alheit and Niquen, 2004), and sardine (*S. sagax*) were reported to feed mainly on copepods and phytoplankton (Alheit and Niquen, 2004; Sandweiss *et al.*, 2004). However, recent studies by Espinoza and Bertrand (in press.) have shown that phytoplankton dominated the food of anchovy in terms of numbers, but in terms of dietary carbon euphausiids and copepods were the dominant prey items. Off the west coast of North America, Koslow (1981) reported that anchovy (*E. mordax*) fed mainly on zooplankton, whereas Radovich (1952) concluded that crustaceans, particularly copepods, dominated the diet of sardine (*S. caerulea*), and the diet of herring (*Clupea harengus*) was dominated by large copepods (Darbyson *et al.*, 2003). In Europe, the diet and feeding habits of anchovy (*E. encrasicolus*) have been well documented (see Tudela and Palomera, 1995, 1997; Bulgakova, 1996; Conway *et al.*, 1998; Tirelli *et al.*, 2006). These authors concluded that anchovy primarily fed on copepods and other small particles. Dalpadado *et al.* (2000) and Prokopchuk and Sentyabov (2006) studied the diet and feeding habits of herring (*Clupea harengus*) in the Norwegian Sea. They concluded that *C. harengus* showed size-selective feeding on *Calanus finmarchicus* and *C. hyperboreus* and also on larger prey, such as krill and amphipods. In his studies off the west coast of Scotland, De Silva (1973) reported that the diet of herring (*C. harengus*) was dominated by crustaceans, particularly copepods.

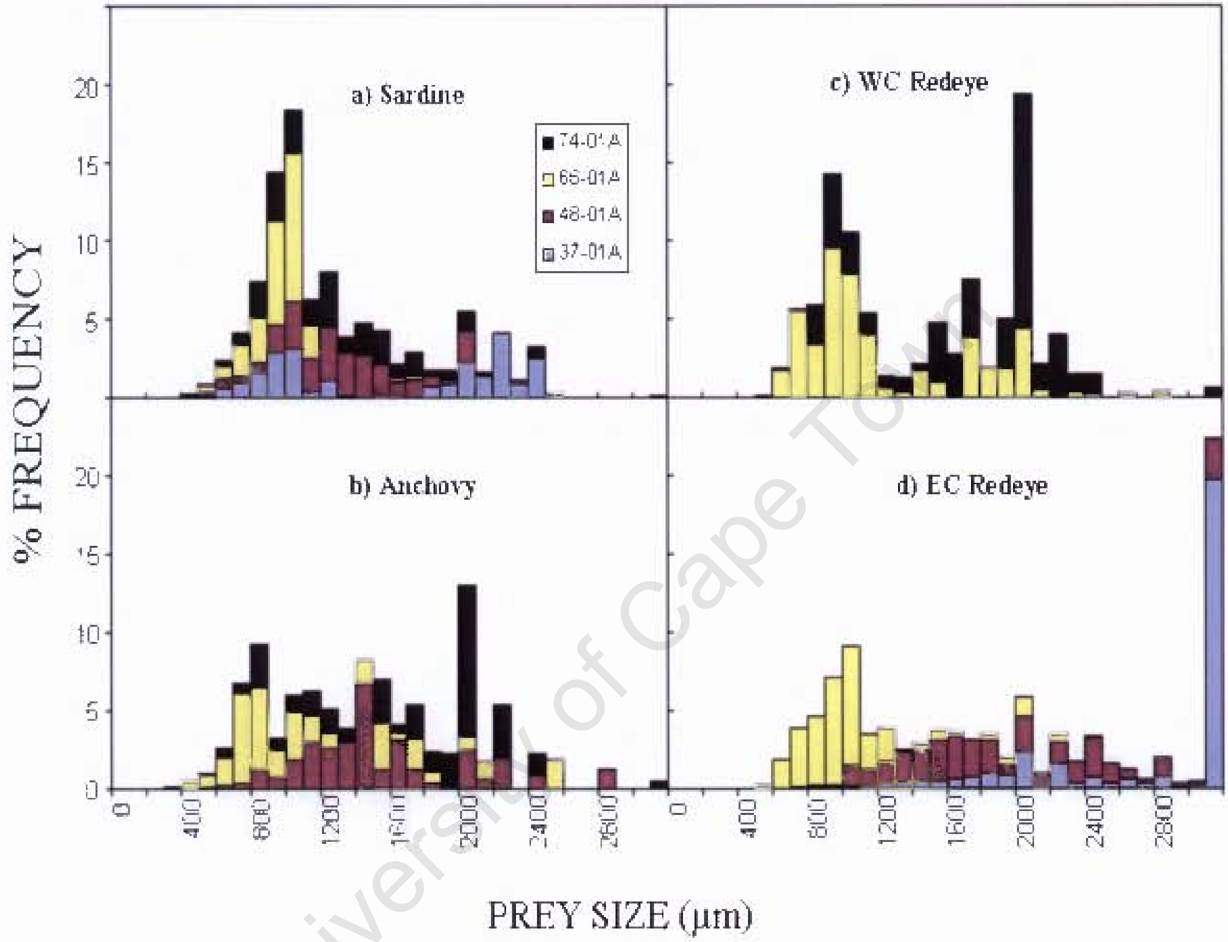

Figure 26. Contribution to dietary carbon by prey size for all the fish combined for a) sardine, b) anchovy, c) west coast redeye, d) east coast redeye.

4.3 FEEDING INTENSITY

One of the characteristics of filter feeding animals is that they tend to feed continuously, i.e., they have high metabolic rates. The low feeding intensity of sardine is expected (Fig. 3), as they are known to be primarily filter feeders, feeding continuously on small particles (van der Lingen, 2002) but it is also possible in this study that sardine were feeding through both filtering and biting, although the sizes of prey ingested indicate that biting was not dominant. Sardine do not show any feeding periodicity on the south coast (van der Lingen, 1998) and therefore it is unlikely that they would show feeding periodicity on the east coast so that the time of day of sampling should not influence the results. Anchovy also showed low feeding intensity (Fig. 3) and would be expected to show variability in stomach fullness because anchovy are primarily particulate feeders (James, 1987). As expected, the two redeye species showed high feeding intensity (Fig. 3), which is typical of animals that are known to be particulate feeders (Wallace-Fincham, 1987). East coast redeye were particularly feeding on large euphausiids, resulting in large values of feeding intensity.

4.4 GILL ARCH MORPHOLOGY

There were significant differences in the size frequency distributions and mean prey sizes of prey items ingested by the four species, with the diets of sardine and anchovy generally dominated by fish eggs, small copepods and cyclopoid copepods whereas those of west coast and east coast redeye were generally dominated by large particles. The differences observed in the size frequency distributions and diet composition of these species may at least be partially explained by gill arch morphology. Fish that generally feed on small prey items have many more gill-rakers than fish feeding on large prey items (Amundsen *et al*., 2004). Tanaka *et al*. (2006) reported that Pacific round herring (*E. teres*) had fewer gill-rakers compared to anchovy (*Engraulis japonicus*). King and Macleod (1976) investigated the gill-arch morphology of sardine and anchovy, and reported that anchovy have a larger gill-raker gap than sardine of the same size. Wallace-Fincham (1987) investigated the gill-arch morphology of west coast redeye and noted that the gill-raker gap increased with increasing fish size. We have no data on gill raker morphology for local populations of *E. teres*, but Tanaka *et al.* (2006) worked on the same species off Japan. Scatterplots of numbers of gill rakers on the first gill arch against fish length, and mean gill raker gap against fish length, are shown for anchovy, sardine and west coast redeye in Figure 27. Sardine have a relatively smaller gill-raker gap (Fig. 27b) and more numerous gill-rakers (Fig. 27a) than the other species, although all three species are similar for smallest fish (<50mm). Sardine should ingest smaller particles than both anchovy and the two redeye species, and this general tendency has been shown here. Anchovy have a similar gill-raker gap to *E. whiteheadi* but slightly more gill-rakers, suggesting that they might be more efficient at ingesting smaller particles than the two redeye species as observed here. There were no significant differences in the size frequency distributions of prey items ingested by west coast redeye and east coast redeye suggesting that these two species have a similar gill raker morphology. However, this should be checked by investigating and comparing the gill-arch morphology of west and east coast redeye using the same methods employed by King and Macleod (1976) for sardine and anchovy and Wallace-Fincham (1987) for west coast redeye.

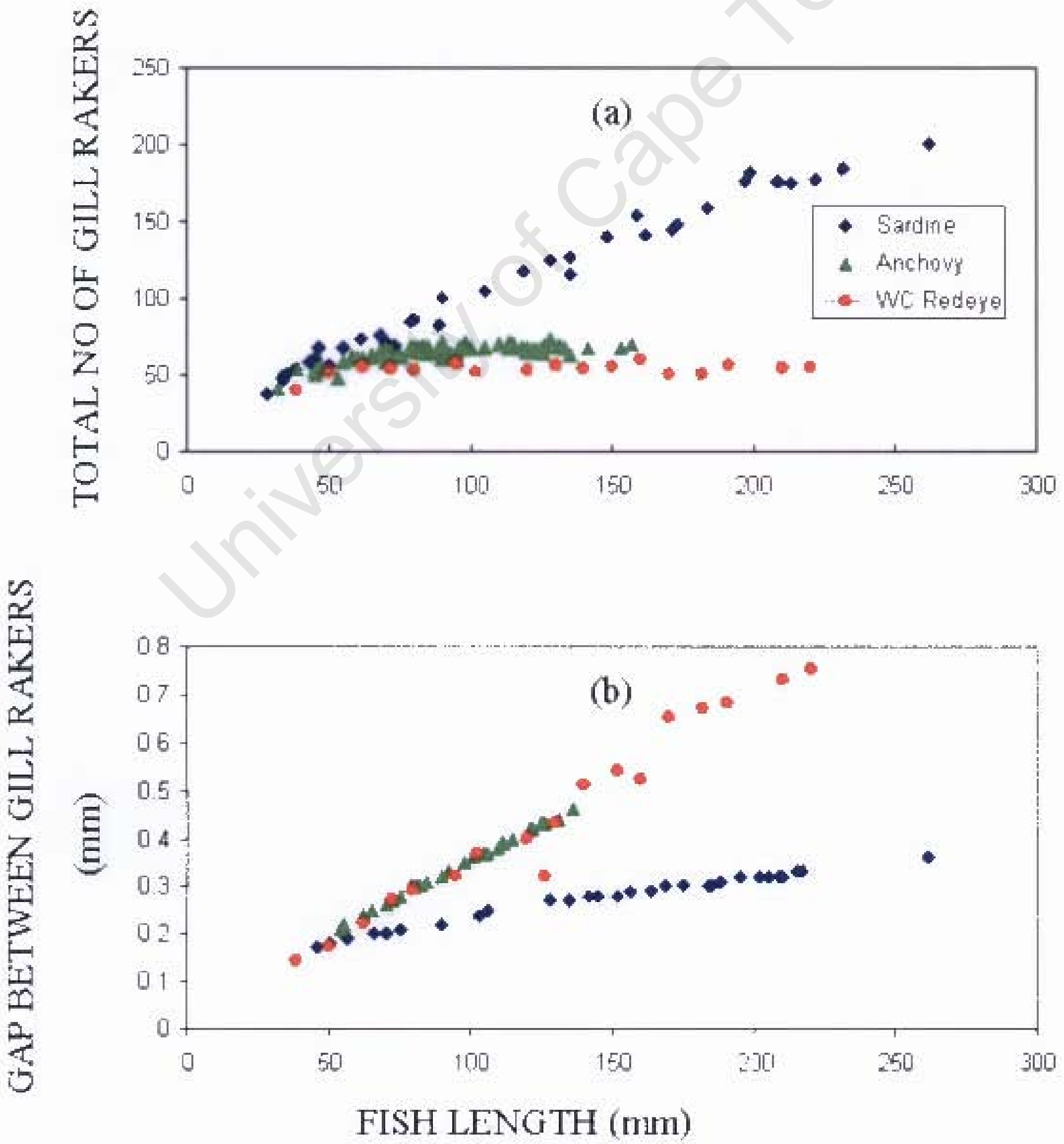

Figure 27. Relationship between fish length and total number of gill rakers (a) and between fish length and gap between gill rakers. Data for sardine and anchovy was taken from King and Macleod (1976) and for west coast redeye from Wallace-Fincham (1987).

4.5 RESOURCE PARTITIONING

During their early life history, sardine, anchovy and herring often school together (Blaxter and Hunter, 1982), as has been found in South African waters (Armstrong and Thomas, 1989). Blaxter and Hunter (1982) suggested that different species of clupeoids living in the same habitat would tend to show considerable dietary overlap. Such overlap is an indication of potential competition and this may result in resource partitioning (Garrison and Link, 2000). According to Ross (1986) and Schoener (1986), resource partitioning reflects how species differ in their use of available resources. Because of competition, some species can be excluded from the contested habitat. In contrast, others can respond to competition by changing the way they use the resources, thereby reducing competition (Page *et al.*, 2005). With these four species feeding in similar environments, probably mostly on plankton of various sorts, the question arises as to how they are partitioning the available prey among themselves. It would be expected that sharing of habitat, time of activity and food resources among them might occur at least some of the time (Garrison and Link, 2000; Gay *et al.*, 2002; Tanaka *et al.*, 2006). Population sizes, community interactions, resource availability and the resources in the ecosystem are affected by the use of resources by organisms (Ross, 1986). Resource partitioning studies are important in describing interspecific competition and the stresses it places on species occurring together (Ross, 1986; Schoener, 1974).

There is considerable dietary overlap between sardine and anchovy (Blaxter and Hunter, 1982; Booi, 2000; Louw *et al*, 1998). Van der Lingen *et al.* (2006) found sardine and anchovy to be trophically distinct, and to show resource partitioning. This was mainly based on zooplankton size, with anchovy ingesting larger zooplankton than sardine. This study has also shown that these species and the two redeye species show resource partitioning based on zooplankton size. As was expected, the diet of sardine was made up of smaller zooplankton than that of anchovy and hence there was a partitioning of resources between them. No resource partitioning was observed between east coast and west coast redeye, which can be explained by the fact that there is very little overlap in distribution between them. However, the sample size for east coast redeye was very small in this study. It is likely that east coast redeye is a particulate feeder that displays feeding periodicity, but to fully evaluate its trophic role requires a comprehensive study of its diet over a large area and throughout the year.

4.6 DIET: WEST AND SOUTH COASTS VS EAST COAST

The findings of this study (done on the east coast of SA) appear to support the conclusions of van der Lingen (2002), James (1987) and Wallace-Fincham (1987) regarding the diets respectively of sardine, anchovy and west coast redeye off the west and south coasts of South Africa. Van der Lingen (2002) reported that sardine were primarily zooplanktivorous. James (1987) also reported that anchovy were primarily zooplanktivorous, and Wallace-Fincham (1987) reported that west coast redeye were feeding on large zooplankton. Results obtained here have shown that sardine were generally feeding on small zooplankton (poecilostomatoid copepods and small copepods) and fish eggs, anchovy were feeding only on zooplankton and fish eggs, and west coast redeye were feeding only on zooplankton and fish eggs. No phytoplankton were found in any of the stomachs of sardine, anchovy and west coast redeye. Large phytoplankton cells in high concentrations are not common on the east coast. However, they are common on the west and south coasts of SA. Also, the south coast is known to be a spawning area for a wide variety of fish species (Hutchings *et al.* 2002), possibly explaining the importance of fish eggs in the diets of the small pelagic fish species in this study.

5. CONCLUSION

Sardine, anchovy, west coast redeye and east coast redeye examined in this study from presumed mixed shoals off South Africa's east coast fed only on zooplankton crustaceans and fish eggs. No phytoplankton were found in any of the stomachs of the fishes. The diet of sardine on the east coast was dominated by fish eggs followed by medium-sized copepods and to a lesser extent small copepods and poecilostomatoid copepods (Table 5). The diet of anchovy was dominated by fish eggs, medium-sized copepods and large copepods (Table 5). The diets of west coast redeye and east coast redeye were dominated by large copepods and fish eggs, contributing >95% of the total ingested carbon. Fish eggs were important in the diets of all four species, possibly indicating that predation mortality on fish eggs off South Africa's east coast is high, and suggesting an interesting avenue for future research.

Table 5 Summary table showing dominant dietary components in the order of importance. Size ranges are given.

Species	Dominant dietary component (%C)
Sardine	Fish eggs (600-1300μm), small calanoid copepods (350-600μm), medium sized copepods (650-1000μm), and poecilostomatoid copepods (400-1200μm).
Anchovy	Fish eggs (600-1400μm), medium sized calanoid copepods (500-1100), and large calanoid copepods (1500-3000μm).
West Coast Redeye	Large calanoid copepods (1500-3500μm), and fish eggs (600-1200μm).
East Coast Redeye	Euphausiids (3000-10000μm), fish eggs (600-1300μm), and large calanoid copepods (1600-3600μm).

Table 6 Summary table showing differences in fish sizes (length) and in prey size frequency distributions. ECR stands for east coast redeye and WCR west coast redeye. Sig and NS stand for significant and not significant respectively.

Mixed shoal #	Fish sizes	Prey sizes
1	Sardine >> EC Redeye (Sig)	Sardine << EC Redeye (Sig)
2	Sardine > Anchovy (Sig) Sardine > EC Redeye (Sig) Anchovy > EC Redeye (Sig)	Sardine = Anchovy (NS) Sardine < EC Redeye (Sig) Anchovy < EC Redeye (Sig)
3	Sardine >> Anchovy (Sig) Sardine >> WC Redeye (Sig) Sardine >> EC Redeye (Sig) Anchovy > WC Redeye (Sig) Anchovy < EC Redeye (Sig) WC Redeye < EC Redeye (Sig)	Sardine < Anchovy (Sig) Sardine < WC Redeye (Sig) Sardine < EC Redeye (Sig) Anchovy < WC Redeye (Sig) Anchovy < EC Redeye (Sig) WC Redeye = EC Redeye (NS)
4	Sardine > Anchovy (Sig) Sardine > WC Redeye (Sig) Anchovy > WC Redeye (Sig)	Sardine < Anchovy (Sig) Sardine < WC Redeye (Sig) Anchovy < WC Redeye (Sig)

There were significant differences in fish sizes and in the size frequency distributions of prey ingested by the four species in all the shoals, except for shoals 2 and 3 (Table 6). There were significant differences in the size frequency distributions of prey ingested by the four species in all the shoals, except for shoals 2 and 3 (Table 6). There were also significant differences in mean prey sizes of prey items ingested. In most cases sardine ingested significantly smaller prey than the other three species, and anchovy ingested significantly smaller prey than the two redeye species. West coast redeye ingested slightly larger prey items than east coast redeye fed on prey items of similar sizes. The differences in mean prey sizes, diet composition and prey size frequency distributions between sardine and anchovy is an indication that these species show resource partitioning. There was no significant difference in prey size frequency distributions between west coast and east coast redeye but there was a significant difference in mean prey sizes; in this study, the two redeye species did not show resource partitioning.

The diet described here for east coast redeye was based on only few samples, and the results should be treated as preliminary. I would recommend that further diet studies should be done on both redeye species, and that stomach contents should be related to the availability of prey items in the water column.

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