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The Feeding Ecology of, and Carbon and Nitrogen Budgets for, Sardine *Sardinops sagax* in the Southern Benguela Upwelling Ecosystem

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by

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University of Cape Town

Thesis presented for the Degree of

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In the Department of Zoology, University of Cape Town

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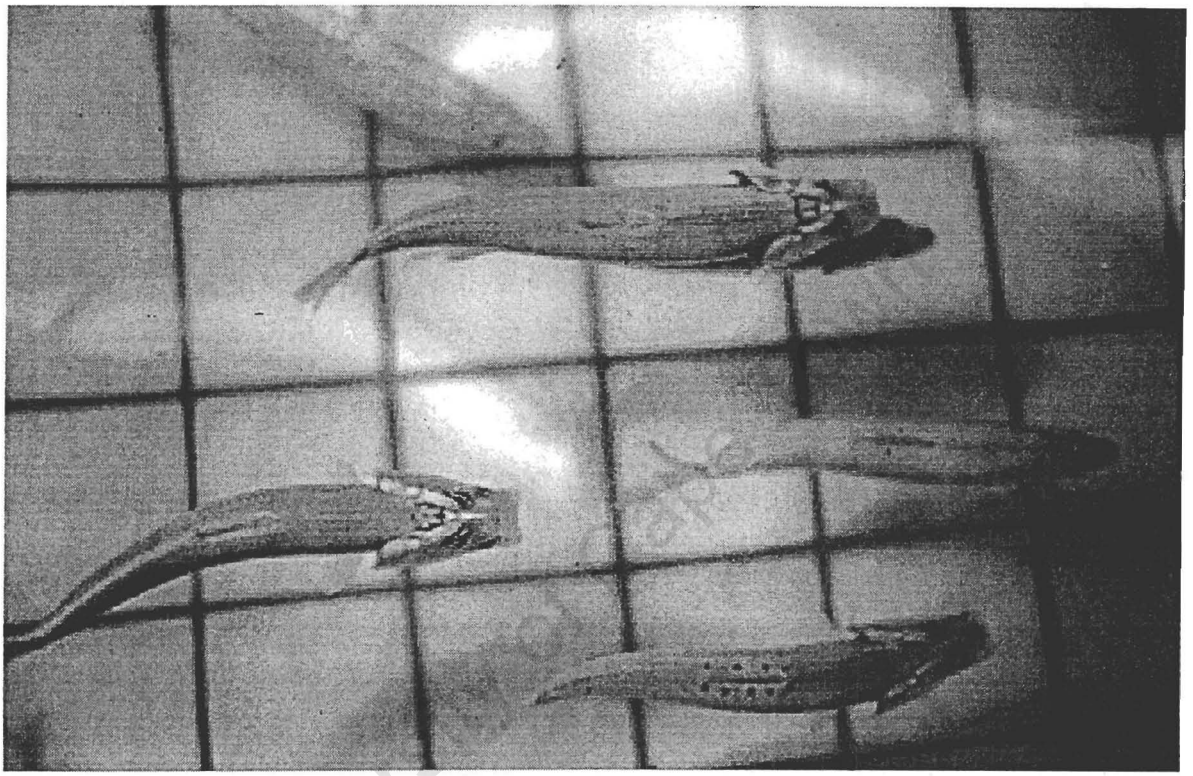

Frontispiece: *Sardinops sagax* engaged in filter-feeding

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Declaration

This dissertation is my own work, and presents the results of original research I conducted at the Chief Directorate: Marine and Coastal Management, Department of Environmental Affairs and Tourism, between 1991 and 1998. The concepts, methodology, data analysis and interpretation were developed by myself in consultation with my supervisors and after examination of the relevant literature.

All experiments described herein (Chapters 2, 3, 4 and 5) were carried out by myself with assistance from various people, and data from samples taken during experiments was collected either by myself or under my direction. Analysis of the data collected during experiments was conducted entirely by myself. Field samples were collected by myself or others operating under my direction. Data collection from field samples (Chapters 5 and 6) was done by myself and a technical team operating under my direction. Analysis of field data was conducted entirely by myself. All uncited hypotheses, discussions and conclusions contained in this dissertation are my own.

This work has not been submitted for a degree at any other university, and all the assistance I received during the execution of this research is fully acknowledged.

Signed by candidate

Carl David van der Lingen

23/9/99

Date

Acknowledgements

This work was conducted whilst I was employed by the Chief Directorate: Marine and Coastal Management (formerly Sea Fisheries Research Institute), Department of Environmental Affairs and Tourism. I would like to thank the former Directors of the Sea Fisheries Research Institute, namely Drs. L.V. Shannon and A.I.L. Payne, for their support, and the funds and facilities to conduct this research. This work forms part of the Benguela Ecology Programme.

Many people contributed in varying ways towards this thesis, most specifically:

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The Feeding Ecology of and Carbon and Nitrogen Budgets for Sardine *Sardinops Sagax* in the Southern Benguela Upwelling Ecosystem

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Abstract

Combined laboratory and field studies were employed to examine the feeding ecology of sardine *Sardinops sagax* in order to evaluate conflicting hypotheses regarding the trophic position of clupeoids in upwelling ecosystems, and to compare the trophodynamics of sardine with those of the co-occurring anchovy *Engraulis capensis*. Carbon and nitrogen budget models constructed using data from these studies were used to quantify the effect of particular food environments upon sardine growth.

Sardinops sagax is primarily a filter-feeder, with food particles <1230µm total length eliciting a filtering response while larger particles elicit particulate-feeding at low concentrations and filter-feeding at high concentrations. This species is able to retain cells as small as 13µm, feeds at near-maximum efficiency when filter-feeding, and displays size-selectivity during particulate-feeding. Significant linear relationships between respiration rate and swimming speed obtained for sardine demonstrate that filter-feeding is the most energetically cheap feeding mode. Although omnivorous, sardine absorbs carbon and nitrogen more efficiently from zooplankton than from phytoplankton. Gastric evacuation follows an exponential pattern in sardine, and is influenced by food type; phytoplankton is evacuated faster than zooplankton. Feeding periodicity in sardine is size dependent; small fish show a feeding peak at, or around, sunset whereas larger fish appear to feed continuously. Estimates of daily ration range between 0.99 to 7.58% wet body mass.d^{-1}, depending on fish size and food type. Sardine stomach contents are numerically dominated by small particles, principally dinoflagellate phytoplankton, but the majority of the sardine's dietary carbon is derived from zooplankton, principally small calanoid and cyclopoid copepods. The budget models indicate that sardine is capable of positive growth under most of the trophic conditions it is likely to encounter in the southern Benguela upwelling system.

The classical hypothesis that the high abundance of clupeoids in upwelling ecosystems results from their phytophagy is rejected; like anchovy, sardine are primarily zoophagous. However, these two species are trophodynamically distinct and show resource partitioning on the basis of prey size; sardine consume small zooplankton whilst anchovy consume large zooplankton. This difference is likely to contribute to regime shifts observed between these two species.

Chapter 1: Introduction

1.1: Clupeoids and Marine Fisheries

Members of the Order Clupeoidei, including the anchovies, herrings, sardines and menhadens, are of major significance to the world's marine fisheries. These fish are processed for food, oil or fish meal; are critically important to the worlds protein resources; and make a major contribution to the economies of fishing nations and those importing meal for livestock feeds (Blaxter and Hunter 1982). Clupeoids have supported the largest commercial fisheries in the world for decades; annual catches of over 20 million metric tonnes of these fish are common, and clupeoids have contributed between 23 and 48% to the total mass of global marine landings from 1950 to 1996 (Figure 1.1; FAO 1998). Of the 10 principal (in terms of mass) marine species landed in 1993, five were clupeoids (FAO 1995), including the Peruvian anchoveta *Engraulis ringens* (10% of the world total marine fish catch), the Japanese sardine *Sardinops sagax* (formerly *S. melanostica*; 3%), the South American sardine *S. sagax* (formerly *S. sagax sagax*; 2%), the Atlantic herring *Clupea harengus* (2%), and the European sardine *Sardina pilchardus* (1%). In 1996 clupeoids comprised 30.1% of the world's marine catch (FAO 1998), with Peruvian anchoveta and Japanese and South American sardine again being the major contributors.

Current (1996) world catches of clupeoids are of the order of 22 million metric tons per annum, having declined slightly over the last few years but increased generally since the 1950's (FAO 1998). However, the growth rate in total landings by marine fisheries has decreased from an average of 7.4% during the 1960's to 0.5% in the first three years of the 1990's, and landings have recently levelled off at approximately 70 million metric tons per annum (FAO 1995). In addition to this levelling off in total landings of marine fisheries, there have been significant changes in the composition of these landings; since 1983 increases in total catch have come primarily from four shoaling pelagic species, two of which are clupeoids (anchoveta *E.*

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ringens and Japanese sardine *S. sagax*), whilst the more valuable cods, hakes and haddocks have shown a steady decline since then (FAO 1995, 1997). Approximately 60% of the 200 major fish resources (accounting for 77% of global marine fish landings) are now considered to be in urgent need of corrective conservation and management measures, with 35% of resources considered overfished, 25% fully fished, and 40% still developing (FAO 1997).

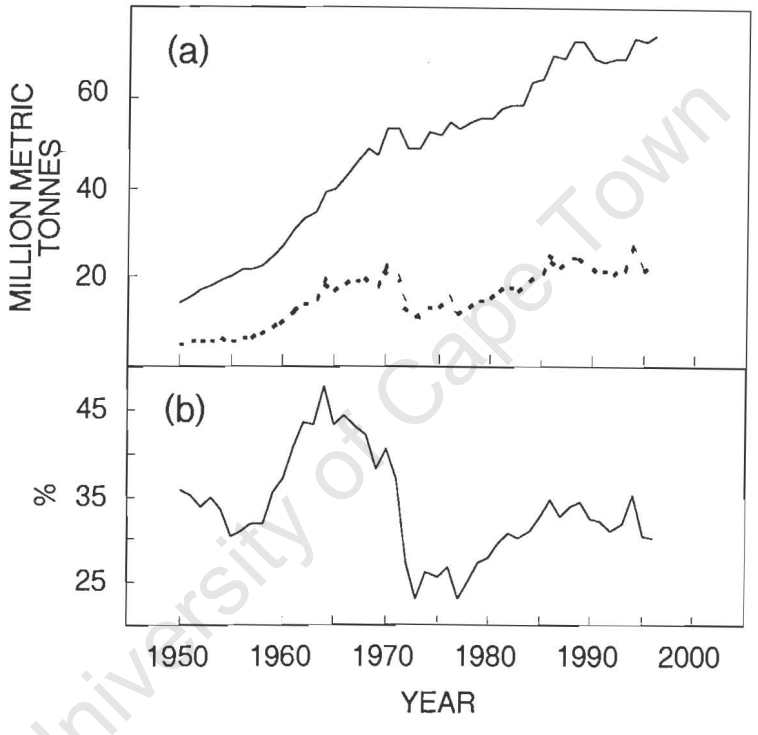

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Figure 1.1: (a) World total marine (solid line) and clupeiform (dashed line) catches, and (b) clupeiform catches as a percentage of total world marine catch from 1950-1996. Data from FAO (1998).

The projected growth in demand for fish resulting from increases in global population is likely to be met predominantly by increased aquaculture production, although optimistic projections of future marine fisheries development suggest that a further 10-20 million metric tonnes could be captured (FAO 1997). However, such increases can only be realized if degraded resources are rehabilitated; if discards and wastage are reduced; and if currently underdeveloped resources are exploited. Improvements in the conservation and management of existing capture fisheries

through stock rebuilding, more rational harvesting strategies, and the application of food technology to improve the utilization of bycatch and of small pelagic species for direct human consumption, may also increase marine fish landings (FAO 1995).

In South African waters, commercially important clupeoids include the sardine *Sardinops sagax* (formerly *S. ocellatus*) anchovy *Engraulis capensis*, and round herring *Etrumeus whiteheadi* (Crawford *et al.* 1987, Armstrong and Thomas 1989). A well-established pelagic fishery, centered off the southwest Cape, has harvested these species since the early 1940's. The pelagic fishery was initially dominated by sardine, with catches of this species peaking in excess of 410 000 metric tons in 1962 but falling rapidly thereafter to below 100 000 metric tons per annum (Figure 1.2; Crawford *et al.* 1987). Sardine catches during the 1980's were below 50 000 metric tones per annum (Shannon *et al.* 1992) but have recently increased, with approximately 120 000 metric tons per annum being landed over the last four years (Chief Director of Sea Fisheries 1994, 1995, Marine & Coastal Management unpublished data).

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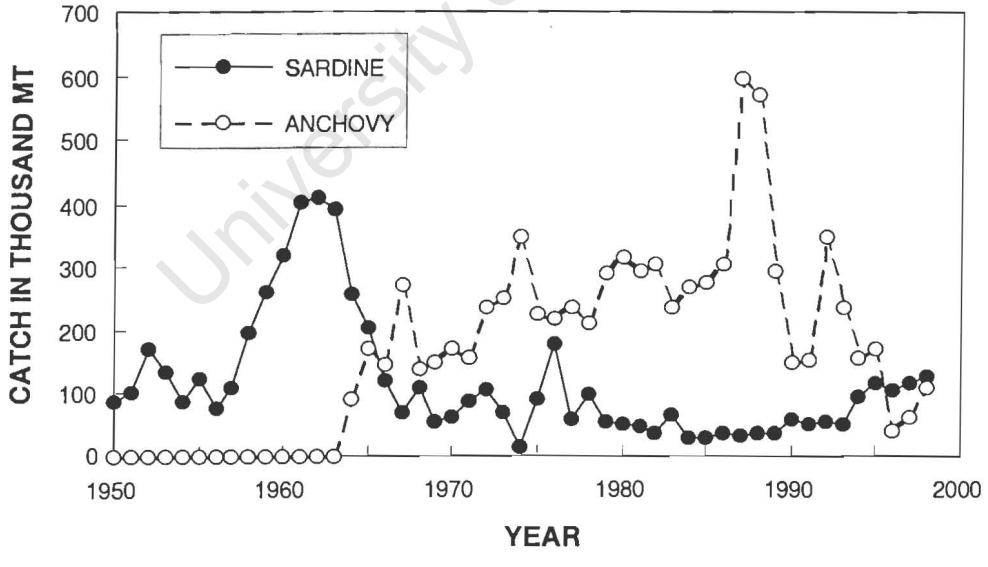

Figure 1.2: South African catches of sardine and anchovy during the period 1950-1998. Data from Crawford (1980), de Oliveira *et al.* (1998), and Marine & Coastal Management (unpublished data).

Anchovy has been the dominant component of the pelagic fishery since 1966

(Crawford *et al.* 1987), with catches ranging from 150 000 to 600 000 metric tons annually (Hutchings 1992) and seldom falling below 200 000 metric tons (Shannon *et al.* 1992). During the last three years however, sardine catches have been greater than those of anchovy (Figure 1.2; Marine & Coastal Management unpublished data). Round herring catches are approximately 50 000 metric tons annually (Chief Director of Sea Fisheries 1994, 1995).

Efficient management of clupeoid stocks worldwide has been hampered by characteristically high variability in population size (Cushing 1971, Blaxter and Hunter 1982), with rapid declines and rapid recoveries in stock size being frequently documented (Lasker and MacCall 1983, Crawford 1987, Lluch-Belda *et al.* 1989, Lluch-Belda *et al.* 1992a). These population fluctuations have been attributed to highly variable recruitment (Wooster and Bailey 1989, Armstrong and Shelton 1990, Bloomer *et al.* 1994), which, because of the short lifespan exhibited by most clupeoids, results in variable stock sizes. This natural variability is often compounded by overfishing (Blaxter and Hunter 1982, Beverton 1990). Recruitment fluctuations are believed to be primarily driven by environmental forcing (Blaxter and Hunter 1982, Bakun 1985, Rothschild *et al.* 1989, Armstrong and Shelton 1990, Shannon *et al.* 1992, Cochrane and Hutchings 1995), with density-dependent effects considered weak or non-existent (Blaxter and Hunter 1982, Wooster and Bailey 1989). The principal environmental factors thought to affect recruitment success include the transport of eggs and larvae (Shelton and Hutchings 1982, Bakun and Parrish 1982), intensity and duration of upwelling (Cury and Roy 1989, Roy *et al.* 1992), and wind-driven turbulence (Peterman and Bradford 1987, Shelton and Hutchings 1990). Attempts to predict recruitment strength of Cape anchovy *Engraulis capensis* in the Southern Benguela using models based on environmental parameters (Bloomer *et al.* 1994 and Cochrane and Hutchings 1995) are currently impeded by insufficient data and lack precision.

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1.2: Trophic Ecology of Clupeoids

Clupeoids predominate in the major upwelling regions of the world's oceans

(Blaxter and Hunter 1982), and it is in these areas that their populations attain remarkably high abundances and sustain large fisheries. Their commercial importance has led to considerable interest in clupeoids, and many workers have attempted to explain the high abundances exhibited by these fish. Ryther's (1969) estimate that areas of coastal upwelling produce 100 times the fish biomass as the entire open ocean led him to suggest that the success of clupeoids in upwelling areas was due to their ability to feed directly upon primary producers. This two-level food chain hypothesis, with clupeoids being regarded as essentially phytophagous and feeding predominantly upon large chain-forming diatoms such as *Chaetoceros* and *Fragilaria* (Yoneda and Yoshida 1955, Bensam 1964, Loukashkin 1970, King and MacLeod 1976), was initially well-supported (Longhurst 1971, Durbin 1979, Walsh 1981). Blaxter and Hunter (1982) concluded that phytoplankton dominated the diet of clupeoids in regions where strong upwelling was a persistant oceanographic feature (*e.g.* Peru and the South African west coast), whereas zooplankton was the dominant food of clupeoids in regions where upwelling was weaker and less persistant (*e.g.* the southern Californian coast). However, subsequent studies have challenged the two-level food chain hypothesis, and have suggested that clupeoids are omnivorous (Cushing 1978, James 1988a, b), deriving the bulk of their energy from zooplankton through size-selective particulate feeding (Koslow 1981, James 1987).

A few genera of clupeoids are macrophagous (such as the active fish-eating tarpon *Megalops* and ten-pounder *Elops*), but the majority are microphagous planktivores, feeding on phytoplankton, zooplankton and small crustacea (Longhurst 1971, James 1988b). Two feeding modes are employed by microphagous clupeoids, namely filter feeding and particulate feeding (Blaxter and Hunter 1982). Filter feeding fish swim with their mouths opened wide and operculae flared, and sieve food particles from the water on the gill rakers on their branchial arches. Obligate filter-feeders such as the Atlantic menhaden *Brevoortia tyrannus* (Durbin and Durbin 1975) and the anchoveta *Cetengraulis mysticetus* (Blaxter and Hunter 1982) are characterized by a very fine filtering mechanism, a large gut:body length ratio and many pyloric caecae, and feed primarily on diatoms (Blaxter and Hunter 1982).

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Particulate feeding fish capture each prey individually by aligning themselves towards specific prey items and rapidly opening their mouth, creating a suction that draws in the prey and surrounding water. In contrast to filter feeders, particulate feeding fish depend on vision to locate and capture their prey (Durbin 1979). No clupeoids have yet been shown experimentally to be obligate particulate feeders, although studies of the diet of the round herring *Etrumeus whiteheadi* suggest that this species employs particulate feeding only (Wallace-Fincham 1987, James 1988b). The gill rakers of round herring are coarse compared to those of the obligate filter feeders, and the alimentary canal is short, straight, and possesses few pyloric caecae (Wallace-Fincham 1987).

Most microphagous clupeoids are able to both filter feed and particulate feed, and can switch between feeding modes when conditions dictate, generally filter feeding on smaller and particulate feeding on larger food particles (Blaxter and Hunter 1982, Gibson and Ezzi 1985, James and Findlay 1989). These mixed, or intermediate feeders possess coarser gill rakers, and have a gut:body length ratio lower than those of the obligate filter feeders (Durbin and Durbin 1975, James 1988b). The ability to switch between feeding modes makes these intermediate feeders highly opportunistic and flexible foragers, which maximise their energy intake through employing the feeding mode most appropriate to a particular food environment. Their high abundance and success in upwelling areas therefore appears to be due to this flexibility of feeding behaviour, which enables them to efficiently utilize a wide range of particle sizes (James 1988b).

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1.3: Regime Shifts

Clupeoid assemblages found in upwelling systems are usually dominated by sardine and anchovy. This sardine/anchovy species pair is found in the four major eastern boundary current systems of the world, including the Benguela, California, Canary and Humboldt currents, and is also found in the coastal waters of Japan (Figure 1.3). As has occurred in the Benguela, these systems have been extensively

fished, and have shown large-scale fluctuations in sardine and anchovy populations, with sardine often abundant when anchovy are scarce and vice versa. This occurrence of worldwide, long-term fluctuations in co-occurring sardine and anchovy populations, termed the "regime problem" (Lluch-Belda *et al.* 1989), is currently receiving considerable attention (Lluch-Belda *et al.* 1992a; Schwartzlose *et al.* 1999). Analysis of clupeoid scale deposition patterns in the sediments of anaerobic basins (Soutar and Isaacs 1969, 1974, De Vries and Pearcy 1982, Shackleton 1987, Baumgartner *et al.* 1992) has indicated that such fluctuations occurred in the past, long before the advent of fishing, and implies that these fluctuations are attributable to causes other than fishing (Lasker 1985).

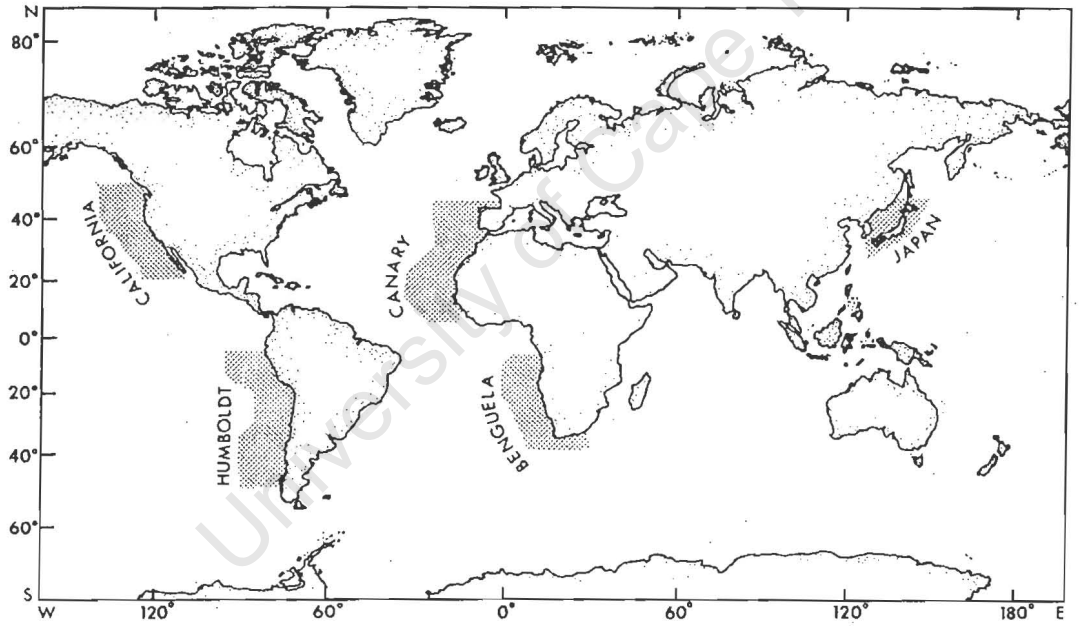

Figure 1.3: Map illustrating the five regions of the worlds oceans where the sardine/anchovy species pair is found. From Crawford (1987).

The causes of such species replacements (termed regime shifts), which occur over relatively short time periods but persist for decades, are not well understood. Interspecific competition for food and/or space was originally invoked as a causal mechanism of regime shifts (Daan 1980, Skud 1982, Lasker and MacCall 1983, Lasker 1985), whilst later studies implicated interspecific predation on eggs and early

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larvae (Alheit 1987, Valdés Szeinfeld and Cochrane 1992). In contrast, Kawasaki (1992) suggested that fluctuations in temperate pelagic fish communities were principally determined by changes in the abundance of Japanese sardine *Sardinops sagax*, which, as a phytoplanktivore, is one of the closest species to first-level production, and is therefore the most strongly influenced by climatic changes.

Other studies have suggested that the mechanisms driving species replacements may be associated with structural changes in the ecosystem, and with long-term environmental variations of basin-wide to global scales (Lluch-Belda *et al.* 1989, Scientific Committee on Oceanic Research 1994), termed "global teleconnections". For example, Lluch-Belda *et al.* (1992b) revealed a strong similarity between the abundance and distribution of sardine and long-term changes in sea-surface temperature in both the California and the Humboldt current systems. Global teleconnections notwithstanding, a major question concerning regime shifts is how to link global variability to the biological populations involved.

Most recently, Schwartzlose *et al.* (1999) have suggested that hypotheses regarding regime shifts can be divided into two categories. The first category proposes that continuous modifications in habitat may benefit one species over the other, and changes in factors such as food composition and temperature have been suggested as likely candidates. For example, if sardine are able to utilize phytoplankton to a greater extent than anchovy (King and Macleod 1976), increases in phytoplankton standing stock may promote growth of the sardine population relative to anchovy, as has been suggested by Kawasaki (1992) for the Northwestern Pacific sardine. Similarly, the ability of sardine to spawn over a wider temperature range than anchovy (Lluch-Belda *et al.* 1991) may mean that sardine are better able to take advantage of warm conditions during the spawning season. The second category of hypotheses suggests that episodic environmental events, that trigger changes in populations and/or ecosystems, may lead to altered species dominance. Events leading to the formation of particularly strong year classes could result in rapid population growth (Kondo 1980), whereas mass mortalities, such as

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that recorded for sardine off Australia in 1995 (Hyatt *et al.* 1997), could lead to a severe reduction in population size.

Whatever the mechanisms governing regime shifts, there is accumulating evidence that in all four regions where sardine are heavily fished (i.e. the Japanese, Californian, Humboldt and Benguela systems), recent changes in the relative abundance of sardine and anchovy were initiated during the 1980's (Lluch-Belda *et al.* 1992a). The near-synchronous and in-phase fluctuations of sardine stocks in three of these systems (Japanese, Californian and Humboldt) supports the view that these stocks are influenced by climate operating at a global scale, as do other studies that have examined synchronous population fluctuations in spatially-segregated stocks (e.g. Ranta *et al.* 1997, Grenfell *et al.* 1998). In the southern Benguela, hydro-acoustic surveys to estimate sardine and anchovy biomass have been conducted since 1984 (Hampton 1987, 1992, Barange *et al.* 1999). These surveys have indicated a steady increase in the biomass of sardine spawners; in contrast, the biomass of anchovy spawners has shown a substantial decline, although fluctuations of more than an order of magnitude have been observed (Figure 1.4).

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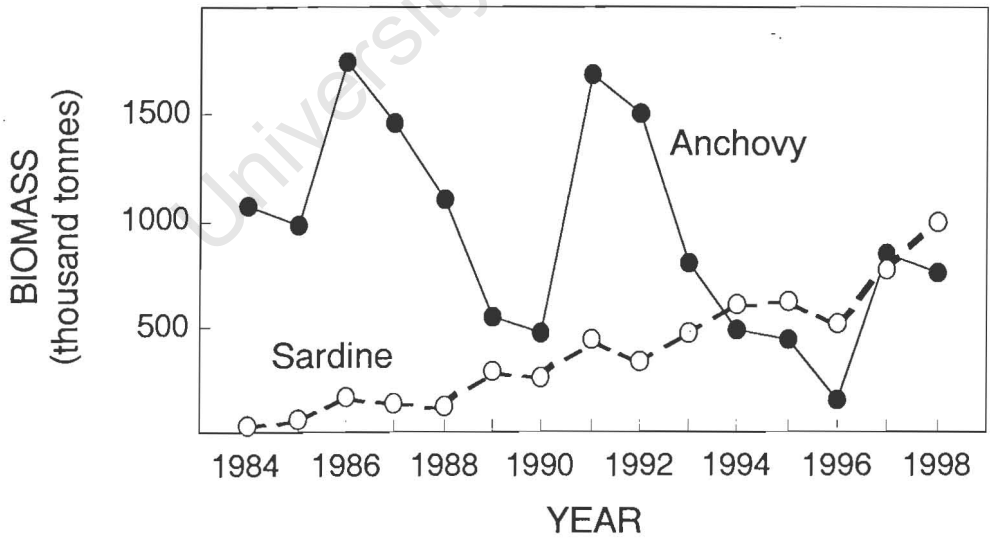

Figure 1.4: Estimated biomasses of sardine and anchovy in the southern Benguela, 1984-1998. Coefficients of variation (CVs) have not been shown; these range between 12-33% for anchovy and 21-87% for sardine. From Barange *et al.* (1999) and Marine & Coastal Management unpublished data.

This contrasting trend in relative biomasses of these two species has led to suggestions that the southern Benguela is currently undergoing a regime shift, with sardine now becoming more abundant than anchovy (Crawford 1998). Regime switches to sardine dominance occurred during the 1980s in the Northwestern (Japan) and Southeastern Pacific (Peru), although catches of sardine in these regions have declined since the late 1980s (Schwartzlose *et al.* 1999). Sardine in the northeastern Pacific (California) appear to be still increasing in both biomass and geographical range, and are now found as far north as British Columbia (Schwartzlose *et al.* 1999).

Regime shifts between sardine and anchovy have important implications for management, since these decadal-scale regimes appear to be characteristic of the four regions supporting the largest fisheries on these species. Because of these shifts, it is unrealistic to expect that fisheries on individual species can be sustained over the long-term; fisheries should rather be geared to take advantage of periods of abundance of a particular species when they occur. Similarly, management of these pelagic species should attempt to sustain regimes of abundance for as long as possible, since fishing has both the potential to decrease the extent and duration of peaks in abundance, as well as to depress and prolong troughs (Schwartzlose *et al.* 1999). Understanding the mechanisms which initiate and sustain regime shifts may therefore substantially assist in the management of these commercially important species.

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1.4: Aims and Structure of this Dissertation

The aim of this dissertation is to describe the feeding ecology of, and construct carbon and nitrogen budgets for, sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. Understanding the trophodynamics of this clupeoid species in this region will allow the evaluation of the two hypotheses regarding the trophic position of clupeoids in upwelling ecosystems in general;

(a) the "classical", two-level food chain hypothesis, that suggests that clupeoids derive most of their nutrition from feeding directly on phytoplankton (Ryther 1969); or
(b) the alternative, multi-level food chain hypothesis, that suggests that clupeoids are omnivorous and derive their nutrition primarily from feeding on zooplankton (James 1988b).

A combined laboratory and field approach was employed to fulfil the above aim, with the following studies being conducted:

(1) A laboratory investigation of the feeding behaviour of sardine, and how feeding behaviour is affected by food particle size and concentration;
(2) Laboratory measurements of respiration rates of sardine, and how temperature, voluntary swimming speed and feeding behaviour affect respiration rates;
(3) A laboratory investigation to examine nitrogen excretion and absorption efficiencies of sardine fed upon phytoplankton and zooplankton diets;
(4) A combined laboratory and field investigation of gastric evacuation rates of sardine and how these are affected by prey type and size, and field studies to assess feeding periodicity and estimate the daily ration of sardine; and
(5) A field investigation into the diet of sardine in South African waters.

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In this dissertation, each of the above studies is presented as a separate chapter. Each chapter contains a brief introduction, details the particular methodologies used, describes the results obtained, and discusses the implications of the results. In the penultimate chapter, carbon and nitrogen budget models are constructed for sardine using empirical relationships derived from the laboratory investigations listed above.

The methodology used in this dissertation, particularly that of the laboratory experiments, closely follows that used by James (1988a) in his examination of the

feeding ecology of Cape anchovy *Engraulis capensis,* and first used on Atlantic menhaden *Brevoortia tyrannus* (Durbin and Durbin 1975, 1981, 1983, and Durbin *et al.* 1981). Whereas technical improvements in some of the techniques have been made (for example using frame-by-frame analysis of video camera footage instead of 8mm movie camera film and a microfiche reader to measure fish swimming speed, and using a dissolved oxygen meter to measure changes in dissolved oxygen concentration in place of a modified Winkler technique), the methodological similarity permits a detailed comparison of the respective trophodynamics of sardine and anchovy in the southern Benguela. Such comparisons are made in the discussion section of each chapter. The final chapter summarizes the respective trophodynamics of sardine and anchovy in the southern Benguela, and assesses the hypothesis that trophodynamic differences between these two species are responsible for regime shifts.

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Chapter 2:
Effect of Particle Size and Concentration on the Feeding Behaviour of Adult Sardine

2.1: Introduction

Previous field-based research examining the feeding biology of sardine in the Benguela upwelling ecosystem indicated that they were primarily filter-feeders, showing an apparent "preference" for phytoplankton and having a mean ratio of phytoplankton to zooplankton in their stomachs of 2:1 by volume (Davies 1957). King and Macleod (1976) suggested that juvenile sardine were zooplanktophagous, feeding predominantly on calanoid copepods, but switching to phytoplanktivory at approximately 100mm standard length. Adult sardine were regarded as essentially non-selective filter-feeders; the change from a selective zooplanktivorous to a non-selective phytoplanktivorous feeding regime being attributed to a decrease in porosity of the filtering mechanism (King and Macleod 1976). James (1988b) considered sardine to be capable of both filter- and particulate-feeding, but suggested that sardine was primarily a size-selective feeder, with zooplankton accounting for 60-80% of the diet of this species.

This study was conducted to investigate the effects of particle size and concentration on the feeding behaviour, selectivity and consumption rates of adult sardine. The experimental approach reported here closely follows that of James and Findlay (1989) for Cape anchovy; i.e. feeding the fish a wide variety of food organisms of different size and monitoring their resulting feeding behaviour and clearance rates. A detailed comparison of the feeding behaviour of these two clupeoids can therefore be made, allowing an assessment of whether these co-existing species exhibit resource partitioning or direct competition for a common, and occasionally limiting (Shannon and Field 1985, Peterson *et al.* 1992) food resource. In addition, the results obtained from this study will be used in the construction of carbon and nitrogen budgets for sardine.

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2.2: Material and methods

Adult sardine (229.3 ± 10.3mm total length) were collected by dip-netting from Cape Town harbour. The fish were transported to the laboratory in 200l black plastic drums and were transferred into 3000l tanks supplied with a continuous flow of 5μm-filtered sea water at ambient temperature (17.2° ± 1.6°C). The fish were acclimated to laboratory conditions for 2 months before being used in experiments. Fish were fed once a day on a coarsely grated frozen mixture of trout pellets supplemented with a vitamin premix, ascorbic acid and cod liver oil, bound with gelatine. Fish also received frozen euphausiids (*Euphausia lucens*) once a week.

Both cultured and wild plankton were used in the experiments (see Table 1). Cultured zooplankton included brine shrimp *Artemia franciscana* (nauplii to adults), the rotifer *Brachionus plicatilis*, and the harpactacoid copepod *Tisbe* spp. The diatoms *Thalassiosira weissflogii, Chaetoceros didymus* and *Skeletonema costatum* were also cultured for use as experimental food. Natural plankton assemblages, consisting of copepod (*Calanus agulhensis, Centropages brachiatus* and *Paracalanus parvus*) and cladoceran (*Evadne spinifera*) species, the dinoflagellate *Noctiluca miliaris*, and chains of *S. costatum* were also offered to the fish. Natural zooplankton were captured using a drift-net of 200μm mesh, and were used immediately after collection. Natural phytoplankton were captured using a 37μm mesh Spanish net.

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A single type and size-class of food particle was employed for 25 experiments. However, in order to determine whether sardine selected prey on the basis of particle type or size, 6 experiments involving mixed size-classes of the same food type (e.g. *Artemia franciscana* nauplii and juveniles) or mixed size-classes of varied food types (e.g. natural zooplankton) were conducted. Two of these mixed size experiments were also "multiple experiments", in which food concentrations in the tank were regularly replenished to approximately initial levels after being depleted by the fish.

Experiments consisted of introducing a known concentration of food particles into a tank containing a school of sardine and observing the feeding response of the

fish. Experiments were conducted in a 2m diameter, 2500l capacity fibreglass tank situated under a 55% shadecloth roof. Schools of 15 sardine were used for all experiments, each school being used for 7 consecutive experiments before being replaced to avoid habituation of the fish to experimental conditions. New fish introduced into the tank were acclimated for a minimum period of 1 week before experiments were initiated. Fish were starved for 2 days prior to experimentation to standardize hunger state.

Table 2.1: Summary of experimental food types and sizes used.

Food organism	**Size (µm)**
Cultured:	
Artemia franciscana (nauplii to adults)	393-6532
Brachionus plicatilis	196-240
Tisbe spp. (nauplii)	156 ± 50
Thalassiosira weissflogii	13 ± 3
Skeletonema costatum	17 ± 5
Chaetoceros didymus	46 ± 11
Wild:	
Centropages brachiatus	873-1657
Calanus agulhensis	1670-2790
Paracalanus parvus	873 ± 232
Evadne spinifera	742 ± 119
Noctiluca miliaris	480-852
Skeletonema costatum (chains)	117 ± 39

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The experimental apparatus consisted of the tank, the floor of which was marked with a grid of lines 10cm apart, a video camera mounted above the tank, and a porous air tube which provided a continuous fine-bubble curtain around the perimeter of the tank. Prior to experimentation the volume in the tank was reduced to 1000l and the sea water supply switched off. Once the fish had resumed normal behaviour (cessation of the startle response) they were filmed for 15 minutes to determine non-feeding swimming speeds. The bubble curtain was then activated and the food added to the tank.

Preliminary experiments in the absence of fish showed that 3 minutes bubbling after the addition of food was sufficient to ensure homogeneous distribution of the particles. Food concentrations inside the tank were determined by subsampling immediately (t=0) after the bubble curtain was discontinued, and at regular intervals thereafter. Two different sampling methods were used:

(1) Zooplankton subsamples were taken by means of a clear perspex tube (45mm internal diameter for small zooplankters <1000μm total length, or 100mm internal diameter for large zooplankters >1000μm total length) which mated with mesh-bottomed (37μm for small zooplankters or 300μm for large zooplankters) cups placed randomly on the tank bottom. A constant volume integrating the entire water column was thus sampled and the food particles contained therein concentrated on the mesh. Food particles were collected from the mesh, preserved in 5% buffered formalin and stored for later examination. This technique did not reduce the water volume inside the tank, and did not disturb the fish overmuch. Preliminary experiments in the absence of fish showed that 5 subsamples were sufficient to determine the particle concentration inside the tank accurately (coefficient of variation never >30%). Food samples collected from mixed size-class or multiple experiments were size-fractionated using 900, 500 and 200μm screens and the particles in each size-class were identified and counted.

(2) Phytoplankton subsamples were taken by randomly collecting 5 200ml aliquots with a syringe from the tank. Concentrations were determined within 3 hours of collection using a Coulter multisizer (orifice size 140μm). Before enumeration, a pure sample of the phytoplankton was run through the multisizer in order to obtain a size-frequency profile and to identify the channels containing the particles. Three replicates from each aliquot were counted, giving 15 subsamples for each sampling time. Phytoplankton samples were also examined microscopically to determine average cell size and chain length.

Food concentration was measured at either 10 or 30 minute intervals after cessation of bubbling. All replicates were counted and a mean concentration with standard deviation for each sampling time was calculated. Fifty individual food particles from each experiment were measured (maximum dimension) to determine

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average particle size.

Feeding behaviour was recorded with a video camera recording at 25 frames second^{-1}. The fish were recorded for 5-minute periods between each food sampling time (always 2 or 3 minutes after food sample) to assess their feeding behaviour. Each video sequence was analysed frame-by-frame to determine swimming speed, feeding intensity (% of the school feeding) and feeding act (opening of the mouth combined with a flaring of the gills) duration. Swimming speed was determined by counting the number of frames taken by individual fish to cross completely one of the grid lines, and was expressed as body lengths per second. Thirty measurements of swimming speed were taken in each video sequence; only fish whose path did not deviate by more than approximately 20° from their original heading during the counting period were considered. Feeding intensity was determined by measuring the proportion of the school feeding in a single randomly chosen frame when all 15 fish were clearly observable, and was repeated 20 times for each video sequence. This approach assumed that fish observed with closed mouths in a single-frame measurement were non-feeding, and may therefore have overestimated true feeding intensity since fish observed with closed mouths may in fact have been in-between feeding acts, and may have either just closed, or were about to open, their mouths. Feeding act duration (FAD) was determined by counting the frames taken for a single feeding act. Five FAD subsamples of 20 observations each were taken from every video sequence.

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Multiple experiments were conducted in a manner similiar to that described above, with the difference that food concentrations were replenished every 40 minutes to approximately original levels. Newly added food was mixed in the water by reactivating the bubble tube for a 5 minute period. Each run within a multiple experiment lasted for 40 minutes, with food samples being taken at 10 minute intervals. Video sequences were taken as before.

Means and standard deviations for each of the data sets within each experiment were calculated for all time-intervals. Differences between the variables

measured during the course of an experiment were determined by ANOVA/Tukey multiple range analysis, with statistical significance being accepted at the $p < 0.05$ level.

Clearance rates were determined for each time interval between significantly different food concentrations within each experiment, using the formula of Harvey (1937 in Friedland *et al.* 1984):

$$F = \frac{V.(LnCi - LnCf)}{t \times N} \qquad (1)$$

where F = clearance rate (litres fish^{-1} minute^{-1}), V = water volume (litres), Ci and Cf = food concentrations at t=i and t=f respectively (number litre^{-1}), t = interval between t=i and t=f (minutes), and N = feeding intensity (average number of fish feeding during t).

This formula was used in preference to that originally used by Frost (1972) and other authors (Gibson and Ezzi 1985, James and Findlay 1989) because Frost's (1972) formula assumes an unchanging instantaneous feeding intensity during the entire experimental period. As sardine show a steady decline in feeding intensity after food introduction, the use of Frost's (1972) formula would lead to underestimation of the clearance rate.

The maximum theoretical clearance rate (F_{max}) was calculated from the formula:

F_{max} = mouth area x max. swimming speed when filter-feeding (2)

Therefore, F_{max} can be used to evaluate filtration efficiency, $\%F_{max}$ being the proportion of volume swept clear to volume filtered (Durbin and Durbin 1975):

$$\%F_{max} = (F/F_{max})x100 \qquad (3)$$

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Clearance rates were plotted against particle size and against mean concentration (<C>) for particles of the same size. Mean concentration was calculated from the formula of Seale and Beckvar (1980):

$$<C> = \frac{Cf-Ci}{Ln(Cf/Ci)} \qquad (4)$$

where <C> = mean concentration (number litre^{-1}).

2.3: Results

Feeding behaviour

Sardine swim by means of the "kick and glide" technique typical of clupeoid species (e.g. *Engraulis mordax* Leong and O'Connell 1969, Videler 1993). For sardine the burst consisted of 1-6 tail beats and was followed by a glide of up to 8 body lengths (BL) duration. In the absence of food sardine swam in a roughly spherical school in the midwater of the tank. Swimming speeds for non-feeding fish were 0.87 ± 0.46 BL second^{-1} (= 20.0 ± 10.6 cm s^{-1}).

When food particles were added to the tank, the initial response of the school was to break apart and for individuals to increase their swimming speed. At the same time the fish would begin to "gulp" - flaring the operculae for short periods. These gulps were physically similiar to filtering acts, but were of a very limited duration, generally less than 0.5s. After a short (less than 1 minute) period of gulping the fish would either begin to filter- or to particulate-feed. All phytoplankton and most zooplankton offered to the fish elicited a filtering response, regardless of prey concentration. Larger zooplankters elicited particulate feeding when present in low concentrations but a filtering response when present in high concentrations. These two feeding modes are described in more detail below.

Filter-feeding

Filter-feeding sardine reformed after the initial dispersion and swam in a tight

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school with their mouths opened wide and their operculae markedly flared. Each bout of filtering lasted on average 1.3 seconds, ranging from 0.2 to 4.6 seconds (Figure 2.1a). At the end of a filtering bout the mouth and operculae were closed rapidly and quickly flared again. Typically the duration of the inter-filter period was 17% of the preceding filter-bout duration. When filter-feeding, the amplitude of the tail beat during the burst phase was much increased compared to non-feeding fish, and the glide phase coincided with the end of a particular filtering act. The school generally followed the curve of the tank and did not turn or change direction sharply. Fish at the leading edge of the school were invariably the most active filterers, while those towards the rear of the school filter-fed in a less intense fashion.

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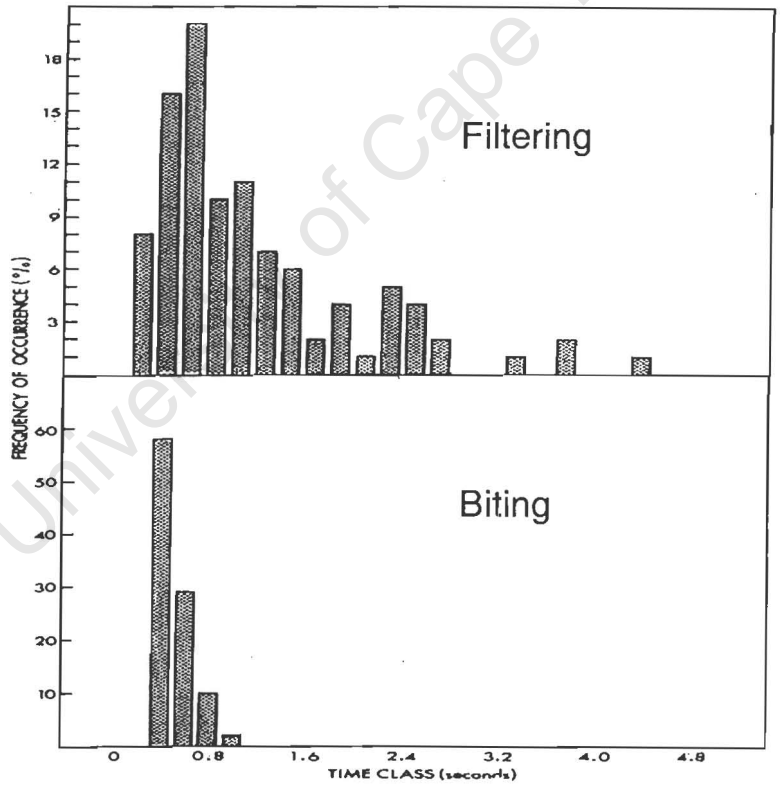

Figure 2.1: Frequency distributions of feeding-act duration for different feeding modes of sardine.

The results of two filter-feeding experiments are given in Figure 2.2. Zooplankton concentrations declined exponentially (Figure 2.2a), indicating that a constant proportion of food particles were being removed per unit time. When filter-

feeding on zooplankton, sardine initially increased their swimming speed from non-feeding levels (Figure 2.2b). During this initial period almost all of the fish in the school were filtering, with feeding intensities of over 80% being common (Figure 2.2c). As food concentrations decreased, so too did swimming speeds and the proportion of the school feeding.

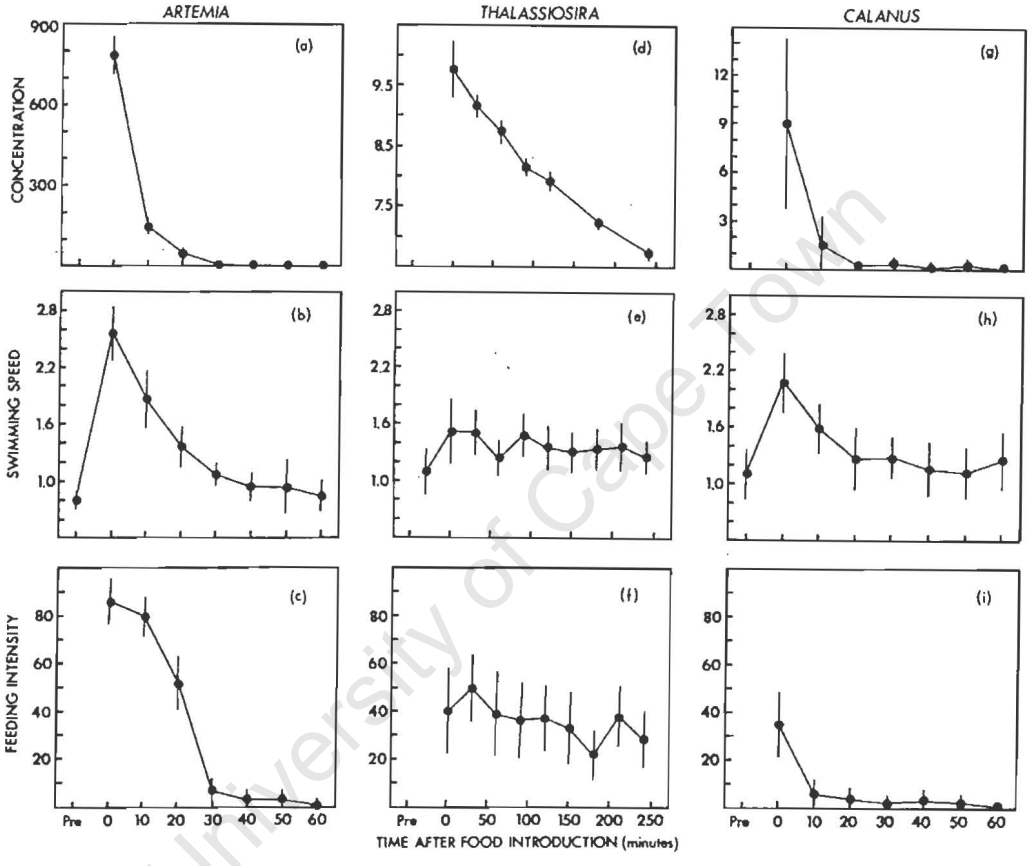

Figure 2.2: Feeding responses of sardine to various food types. (a to c) Filter-feeding on *Artemia franciscana* nauplii (487 ± 38 µm): (a) particle concentration (no.l^{-1}); (b) fish swimming speed (body lengths second^{-1}); (c) feeding intensity (% of school feeding). (d)-(f) filter-feeding on *Thalassiosira weissflogii* cells (13±3µm): (d) particle concentration (number x 10^3 millilitre^{-1}); (e) fish swimming speed (body lengths second^{-1}); (f) feeding intensity (% of school feeding). (g)-(i) particulate-feeding on *Calanus agulhensis* adults (2479±462µm): (g) particle concentration (number litre^{-1}); (h) fish swimming speed (body lengths second^{-1}); (i) feeding intensity (% of school feeding). Mean ± 2 standard deviations are shown.

The response of sardine feeding on phytoplankton presented a very different picture. Particle concentrations decreased very slowly, and were seldom significantly different from one sample to the next (Figure 2.2d). This indicated that the fish were less efficient at removing these particles. There was no significant increase in

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swimming speed after the introduction of food, as was the case for fish filter-feeding on zooplankton (Figure 2.2e). Feeding intensity was never initially as high as when filter-feeding on zooplankton, but a substantial proportion (25-40%) of the school exhibited filtering behaviour when offered diatoms (Figure 2.2f). This proportion remained fairly constant over the entire experimental period.

Particulate-feeding

Particulate-feeding was characterized by a rapid opening and closing of the mouth accompanied by a partial flaring of the operculae. The operculae were never flared as wide as during filtering. Each bite lasted on average 0.4 seconds (Figure 2.1b). When particulate feeding, the fish did not school but executed independent motions as they aligned themselves towards specific food particles. Changes in direction were thus frequent.

Figure 2.2 depicts the results from an experiment where a particulate-feeding response was elicited from the fish. Prey concentration decreased dramatically after the introduction of food (Figure 2.2g). Swimming speed increased significantly from non-feeding levels (Figure 2.2h), but rapidly returned to non-feeding levels once the food had been depleted. Feeding intensity also decreased rapidly after the reduction in food concentration (Figure 2.2i).

Feeding mode switch

The transition from filter- to particulate-feeding was gradual, increasing particle size resulting in a concomitant increase in the proportion of bites by feeding fish (Figure 2.3). There was, however, a distinct difference between the threshold particle size (above which biting became the dominant feeding mode) for cultured and wild zooplankton, being approximately 3060μm TL and 1310μm TL respectively. This marked disparity is ascribed to differences in the appearance and behaviour of the prey organisms. Copepods are able to swim rapidly and show a well-developed escape response compared with *Artemia franciscana*. Therefore, to catch the larger wild zooplankton sardine were required to align themselves visually with respect to the prey particle, i.e. to particulate-feed. The shift from filtering to biting was not only

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size- and prey type-dependent, but was also affected by particle concentration. High concentrations of large zooplankters (e.g. a swarm of mysids *Mysidopsis major*) elicited a filtering response from the fish.

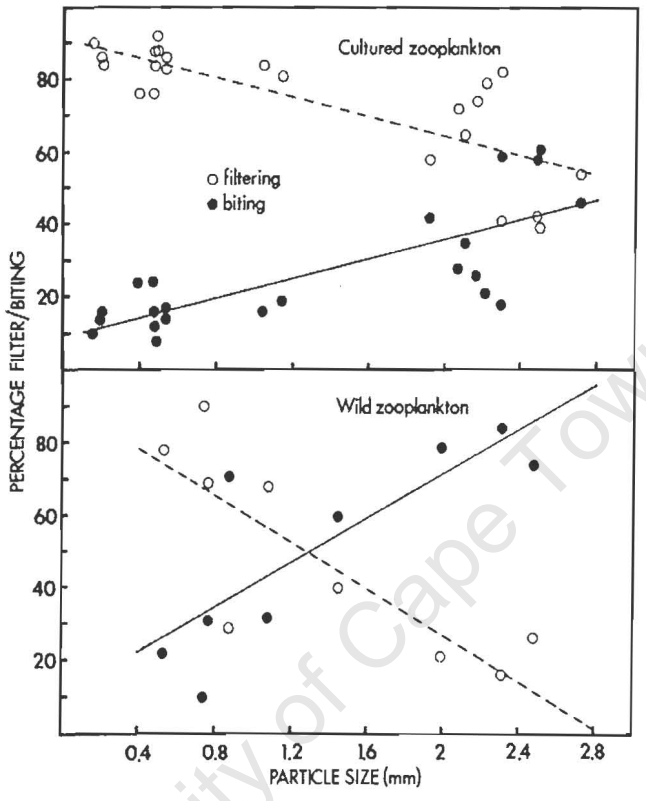

Figure 2.3: Relationship between proportion of feeding fish filtering or biting and particle size for sardine. Cultured zooplankton: % filtering = -0.014*(particle size)+91.29; % biting = 0.014*(particle size)+8.71; $r^2 = 0.60$; $p<0.01$. Wild zooplankton: % filtering = -0.031*(particle size)+90.36; % biting = 0.031*(particle size)+9.64; $r^2 = 0.66$; $p<0.01$.

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Feeding rates

Clearance rates for filter-feeding sardine were independent of particle size over the range 393-1227μm ($t = 1.77$, $n = 110$, $p>0.05$; Figure 2.4) and had a mean value of 11.78 ± 4.91 ($n = 110$) litres fish^{-1} minute^{-1}. This value is 93% of the calculated F_{max} value of 12.74 litres fish^{-1} minute^{-1}, indicating that the sardine are maximally efficient at filtering over this size range. Clearance rates were identical for fish filter-feeding on both cultured (e.g. *Artemia franciscana, Brachionus plicatilis*) and wild (e.g. *Evadne spinifera*) zooplankton particles. Clearance rate during filter-feeding was also independent of mean concentration (<C>) for particles of similar size ($t = 0.10$, $n = 21$,

p>0.05; Figure 2.5).

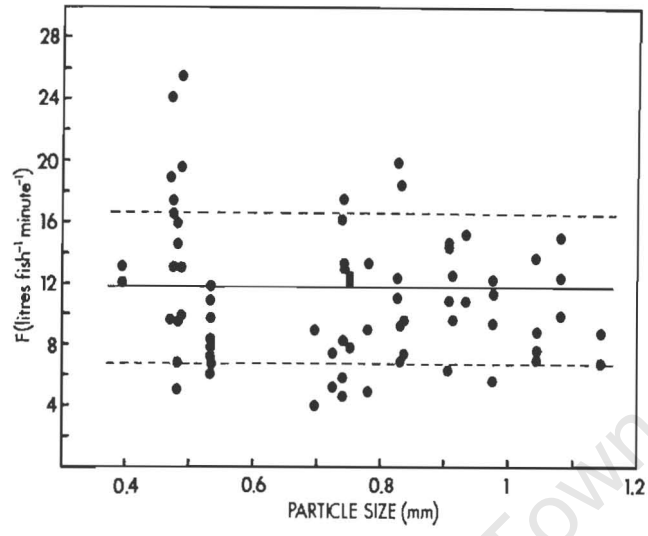

Figure 2.4: Clearance rate (F) as a function of particle size (393-1227μm) for filter-feeding sardine. Solid line indicates mean clearance rate, dashed lines indicate 2 standard deviations.

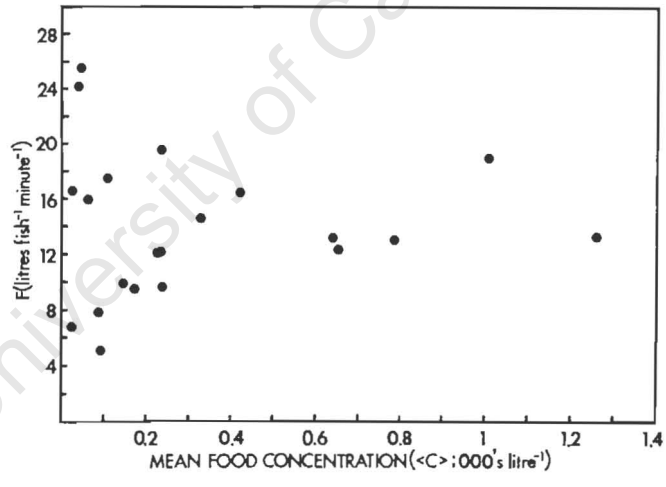

Figure 2.5: Clearance rate (F) as a function of mean particle concentration for sardine filter-feeding on *Artemia franciscana* nauplii (492±42μm).

Below particle sizes of 206μm TL, clearance rates declined as the efficiency of small particle retention decreased (Figure 2.6). Rotifers (*Brachionus plicatilis*, 204μm TL) were cleared at a rate of 6.34 ± 2.39 (n = 14) litres fish^{-1} minute^{-1}). Clearance rates on cultured diatoms (13-17μm TL) were 0.28 ± 0.09 (n = 11) litres fish^{-1} minute^{-1}, demonstrating that the fish were extremely inefficient at retaining these small particles. Sardine were more efficient at retaining the chains of wild *Skeletonema costatum* (117 ± 55μm TL), showing a clearance rate of 3.57 ± 1.20 (n = 3) litres fish^{-1}

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minute^{-1}.

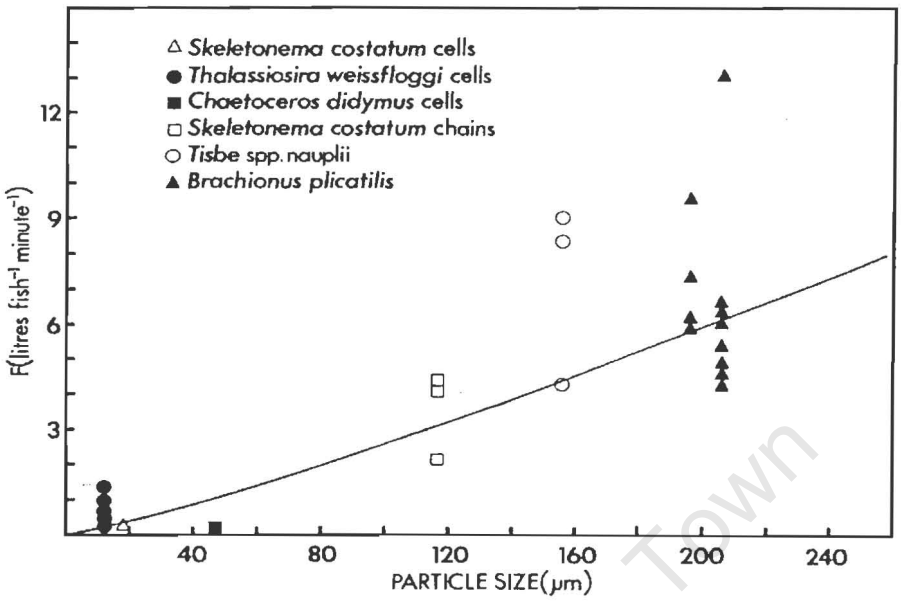

Figure 2.6: Clearance rate (F) as a function of particle size for sardine feeding on phytoplankton and microzooplankton. The fitted regression line ($F = 0.0112*(\text{particle size})^{1.19}$; $r^2=0.91$; $p<0.001$) is shown.

Clearance rates by fish particulate-feeding on particles greater than 1445μm TL ranged from 11.14 to 62.11 litres fish^{-1} minute^{-1}, larger food particles being removed at a faster rate. Combination of the results for both types of feeding response (excluding the data for particulate-feeding on large *Artemia franciscana*, which is considered invalid for the reasons discussed above) allows a predictive equation of clearance rate as a function of particle size to be constructed. A 5th order polynomial, with no discontinuity between filter- and particulate-feeding clearance rates, was found to provide a highly significant ($t = 18.738$, $n = 175$, $p<0.001$) and representative curve. Predicted clearance rate reached a saturation value of 46.53 litres fish^{-1} minute^{-1} (Figure 2.7).

Selective feeding

The results obtained from the experiments employing mixed food demonstrate that sardine can feed selectively, removing larger particles preferentially. Figure 2.8a depicts the relative proportion by number of 3 size-classes of wild zooplankton in sequential samples from a multiple mixed experiment. Significant differences in

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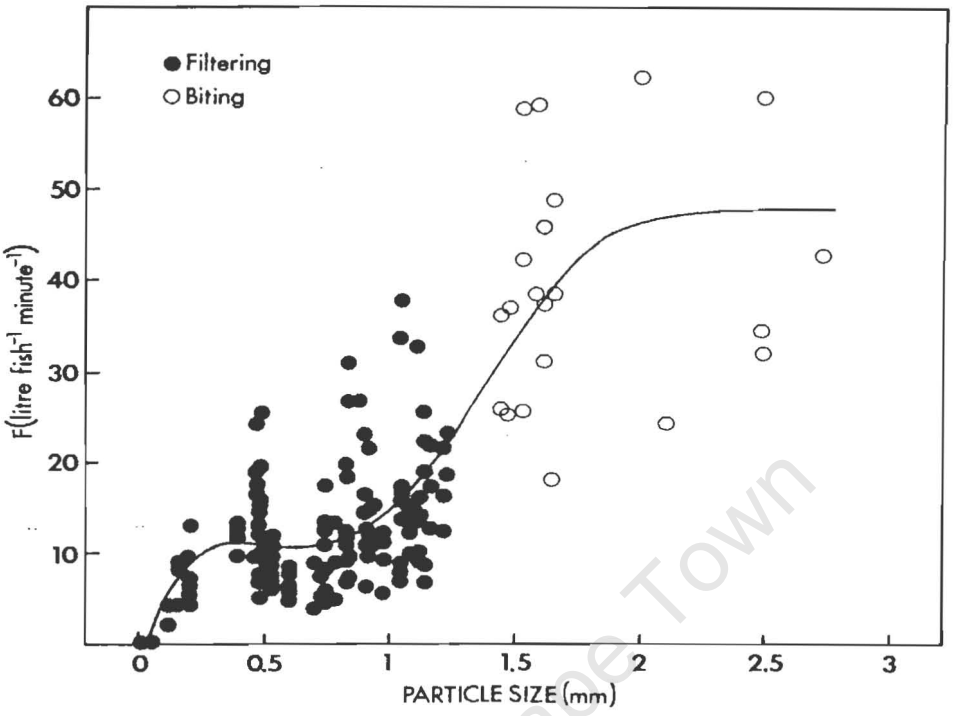

Figure 2.7: Clearance rate (F) as a function of particle size for both feeding modes of sardine. The fitted regression line ($F = -2.5421+0.0939*(\text{particle size})-0.0002*(\text{particle size})^2+2.3829X10^{-7}*(\text{particle size})^3-9.7258x10^{-11}*(\text{particle size})^4+1.3623x10^{-14}*(\text{particle size})^5$; $r^2=0.67$; $p<0.001$) is shown.

Table 2.2: Statistical parameters for changes in relative abundance of 3 size-classes of wild zooplankton used as prey in a mixed food experiment.

Time interval (min)	Size class					
	> 900 µm		> 500 µm		>200 µm	
	t	Sig.	t	Sig.	T	Sig.
0-10	5.544	p<0.001	1.925	p<0.1	4.733	p<0.001
10-20	8.324	p<0.001	2.667	p<0.01	4.470	p<0.001
20-30	2.163	p<0.05	1.783	p<0.1	1.614	p<0.2

relative proportions are apparent for all three size-classes (Table 2.2). The largest class (retained by a 900µm screen) showed a marked decline in relative proportion between all samples, the middle size-class (retained by a 500µm screen) showed a less significant decrease, while the smallest class (retained on a 200µm mesh) showed a highly significant increase in relative proportion between the first two sample pairs, but no increase thereafter. In this experiment, the >900µm and 500-

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900μm size-classes were composed of adult (1545 ± 311μm TL) and juvenile (1152 ± 252μm TL) *Centropages brachiatus* respectively, while the small size-class consisted of *Evadne spinifera* (873 ± 143μm TL). During the initial part of each run (t=0 to t=10) filtering was the dominant mode of feeding, but from t=10 onwards biting became dominant, presumably being directed at the remaining zooplankters of the middle size class (Figure 2.8b).

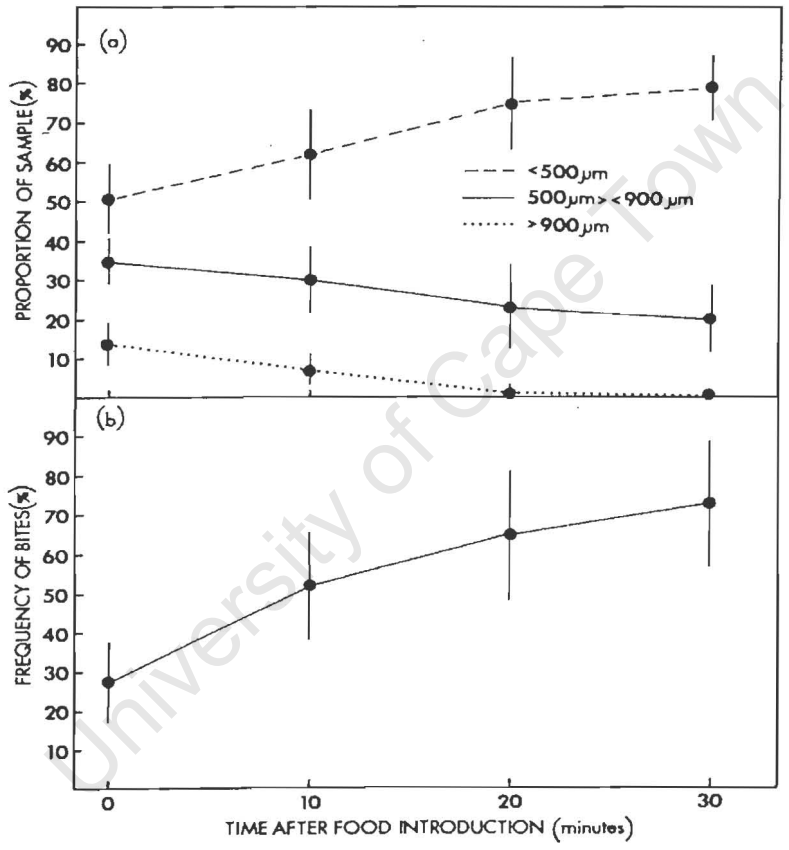

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Figure 2.8: Feeding response of sardine to mixed food assemblages. (a) proportion of sample at various times after food introduction for three size-classes of wild zooplankton; large (>900μm - adult *Centropages brachiatus* 1545±311μm), medium (500μm><900μm - juvenile *C. brachiatus* 1152±252μm) and small (<500μm - *Evadne spinifera* 873±143μm); (b) frequency of bites at various times after food introduction. Points plotted are the means from 7 runs, vertical bars indicate 2 standard deviations.

2.4: Discussion

The experiments reported here demonstrate that *Sardinops sagax* is able to capture food particles over a broad spectrum of prey sizes, from individual phytoplankton cells to large macrozooplankton, by means of either of two feeding modes. Sardine capture their food primarily through non-selective filter-feeding (tow-net filtering, *sensu* Lazzaro 1987), although they are able to feed selectively when engaged in particulate-feeding.

Several other clupeoid species exhibit both filter- and particulate-feeding modes, depending on the size and concentration of available prey. Species that exhibit this feeding flexibility include *Alosa pseudoharengus* (Janssen 1976, 1978), *Clupea harengus* (Gibson and Ezzi 1985, Batty *et al.* 1986), *Dorosoma petenense* (Holanov and Tash 1978), *Engraulis capensis* (James and Findlay 1989) and *E. mordax* (Leong and O'Connell 1969, O'Connell 1972, Hunter and Dorr 1982). These species generally filter-feed when presented with high concentrations of small particles (e.g. phytoplankton or small zooplankton) and particulate-feed on larger prey. To date only one clupeoid, *Brevoortia tyrannus*, has been shown experimentally to be an obligate filter-feeder (Durbin and Durbin 1975), while no obligate particulate-feeding species have been reported.

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Possession of two feeding modes, and the ability to rapidly switch back and forth between the two, must be highly advantageous in the patchy food environment inhabited by marine clupeoids, especially because the fish are likely to be faced with complex spatial and temporal variations in prey size range and concentration. Food intake can thus be maximized in every situation, with the feeding mode realizing the greatest return per unit effort being used in a given food environment (James and Findlay 1989, Batty *et al.* 1990). The switch from filtering to biting (or vice versa) depends on the relative profitability of each mode (Gibson and Ezzi 1992), and is influenced by particle size and concentration (Gibson and Ezzi 1990), predator to prey size ratio and the relative concentrations of large and small prey (Crowder 1985), light intensity (Batty *et al.* 1990), and the relative energetic costs associated with each

feeding mode. Hence, mode shifts to filter-feeding are more common when fish are large, prey are small and present in high concentrations, and light intensity is low. Mode shifts to particulate-feeding occur when fish are small, prey are large and present in low concentrations, and there is sufficient light for visual feeding (Crowder 1985).

Comparisons of feeding behaviour and rates between various clupeoid species are difficult to make because of the different experimental and analytical techniques used by various authors. However, there are similarities in feeding behaviour of the species examined. There appears to be a relationship between filter-bout duration of a particular species and development of the epibranchial gland, an organ considered responsible for food particle concentration in microphagous fish (Blaxter and Hunter 1982). Species lacking epibranchial glands show filter bouts of relatively short duration (e.g. *Clupea harengus* 0.2-0.7s Gibson and Ezzi 1985) whereas those possessing small epibranchial glands have filter bouts of intermediate duration (e.g. *Alosa pseudoharengus* 0.5-2s Janssen 1976, *Engraulis mordax* 0.6-4.4s Leong and O'Connell 1969, *E. capensis* 0.4-3.0s, James and Findlay 1989). Obligate filter-feeders such as *Brevoortia tyrannus* possess large epibranchial glands (Nelson 1967) and filter almost continuously (Durbin and Durbin 1975). Therefore, development of the epibranchial gland in clupeoids appears to be related to the degree of microphagy (Blaxter and Hunter 1982) and may possibly represent stages in a series progressing from facultative to obligate filterers. Sardine filter bouts range from 0.2-4.6s, implying a well developed epibranchial gland and a high degree of specialization towards microphagy.

When compared with other clupeoids sardine are highly efficient at retaining small particles. The particle size at which the clearance rate is half the predicted maximum when filtering ($F = 50\%F_{max}$) for sardine is 200μm TL ($F = 6.37$ litres fish^{-1} minute^{-1}). This is in comparison to approximately 40μm TL ($F= 2.58$ litres fish^{-1} minute^{-1}) for juvenile (Friedland *et al.* 1984) and 400μm TL ($F = 11.65$ litres fish^{-1} minute^{-1}) for adult *Brevoortia tyrannus* (Durbin and Durbin 1975), although the latter authors cautioned that their calculated F_{max} may have been an overestimate. Cape

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anchovy *Engraulis capensis* were unable to retain particles of less than 100μm maximum dimension (James and Findlay 1989). The high retention efficiency for small particles exhibited by sardine implies that this species is capable of exploiting both phytoplankton and microzooplankton as a food source.

The retention of small particles by sardine is somewhat surprising, given that King and Macleod (1976) found that the gill-raker gap in adult fish was approximately 300μm. However, these authors concluded that overlap of the gill rakers on the second, third and fourth gill arches, and interlocking of the gill rakers on the upper and lower arches, significantly reduced the effective gill-raker gap. Retention of particles smaller than the minimum gill-raker gap has been reported for other marine filter-feeding planktivores (Nelson 1979 in Lazarro 1987), and is attributed to the importance of the denticle gaps and edges in collecting the smallest particles (Nelson 1979 in Lazarro 1987). Sardine, in contrast to Cape anchovy, possess serrated denticles on their gill rakers (King and Macleod 1976).

The fact that sardine can entrap phytoplankton cells of small size, albeit with low efficiencies, means that they are capable of utilizing primary production directly, in addition to exploiting zooplankton as a food source. However, observations that some diatoms (e.g. *Thalassiosira*) are able to pass through the gastro-intestinal tract without apparent digestion (unpublished data) implies that utilization of phytoplankton may not be as efficient as supposed. The resistance of phytoplankton to fish digestion has been observed in several other fish (Lazarro 1987). In clupeoids, Velasquez (1939 in Lazarro 1987) and Smith (1963 in Lazarro 1987) found 46 genera of algae which survived passage through the gut of gizzard shad (*Dorosoma cepedianum*).

Although sardine are capable of both filter- and particulate-feeding, filter-feeding was the dominant feeding mode exhibited under experimental conditions. Particles of up to 1230μm TL were captured by filtering, regardless of concentration, at an average clearance rate of 11.78 litres $fish^{-1}$ $minute^{-1}$. Larger particles in high concentrations were also captured by filtering, but reduced concentrations of these large particles elicited a particulate feeding response. A schematic representation of

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the feeding repertoire of sardine compared to that of Cape anchovy *Engraulis capensis* is given in Figure 2.9.

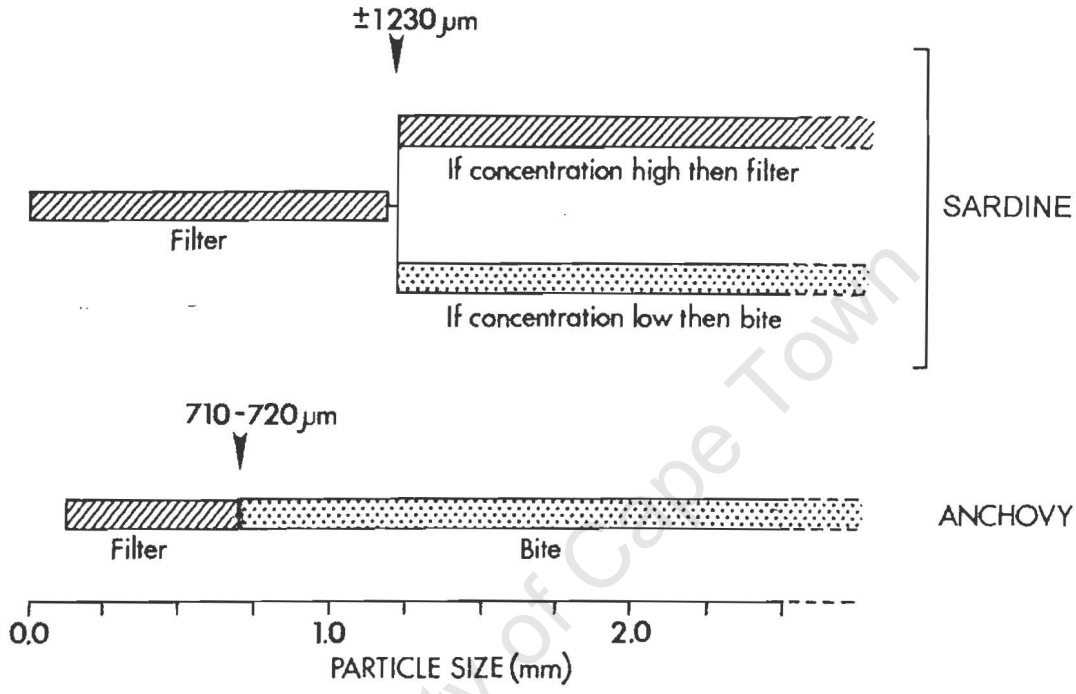

Figure 2.9: Schematic representation of feeding behaviour as related to particle size for sardine. Also shown is that for anchovy *Engraulis capensis* (from James and Findlay 1989).

Field observations on the feeding and schooling behaviour of sardine lend support to the hypothesis that filter-feeding is the dominant mode of food aquisition for this species. Schülein (pers. comm., in James 1988a) described a school of 500-700 fish, 10-30cm apart, displaying strong filtering behaviour with "...their mouths and opercula widely expanded (like wings), and each fish breaking the water surface." Davies (1957), after analysing 16 600 stomachs, concluded that sardine was primarily a filter-feeder, and considered this species to be phytophagous, having a mean stomach content ratio of 2:1 by volume of phytoplankton to zooplankton. Cushing (1978) erroneously assumed that Davies' (1957) mean ratio reflected surface area as opposed to volume; his suggestion that zooplankton were more significant in the diet than phytoplankton may therefore be false. King and Macleod (1976) also considered

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sardine to be primarily phytophagous and, finding no evidence of selective feeding behaviour, implied that the fish were filter-feeders only. This latter study was, however, limited to the inshore regions north of Walvis Bay, an area typically high in phytoplankton biomass but with low densities of zooplankton (L. Hutchings, Marine & Coastal Management, pers. comm.). The conclusions reached by King and Macleod (1976) may therefore have been biased by locality.

The formation of fish schools has been seen as a mechanism for reducing predation pressure and facilitating reproduction (Partridge 1982). It has been suggested, however, that schooling of planktivorous fish occurs at the expense of foraging efficiency (Eggers 1976, Duffy and Wissel 1988). This is due to the overlap of individual visual fields, resulting in a reduced prey-encounter rate for each fish. Therefore, particulate-feeding planktivores reduce their school density when feeding. It follows that filter-feeding (non-visual) planktivores would not have to reduce their school density to the same extent during feeding. Eggers (1976) further suggested that the costs of schooling are reduced if prey concentrations are high, if school size is small, or if distance between school members is high.

Cape anchovy *Engraulis capensis*, rise to the surface and disperse at night, and descend and become aggregated during the day (Thomas and Schülein 1988). Their feeding shows a marked synchronicity, peaking between dusk and midnight for juveniles on the west coast, and between midnight and dawn for adults on the south coast (James 1987). During these times, the anchovy are primarily engaged in particulate (i.e. visual) feeding (James 1987). Sardine, in contrast, do not undertake significant diel vertical migration but tend to form small, scattered schools by night and dense schools by day (Hampton *et al.* 1979, Thomas and Schülein 1988), generally remaining in the top 20m of the water column. Therefore sardine appear to balance the gains from schooling (protection, ease of reproduction) against the costs (reduced prey consumption) by predominantly filtering in small schools, the maximum size of which is limited by food abundance (Duffy and Wissel 1988).

Particulate-feeding by sardine is most probably restricted to fish on the

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periphery of the school, because it is doubtful that large prey items would be able to infiltrate the school without detection by these peripheral fish. The proportion of food captured by particulate-feeding is therefore likely to be negligible compared to that captured by filter-feeding, unless the fish continually change position within the school.

Consumption rates and hence time to attain daily ration for sardine may be derived from biomass estimates of southern Benguela zooplankton. Estimates of mesozooplankton biomass have been provided by several authors (e.g. Andrews and Hutchings 1980, Pillar 1984a, 1984b, Hutchings 1985, Peterson *et al.* 1990, Verheye 1991), but microzooplankton estimates are scarce. Armstrong *et al.* (1987) reported the densities of copepodites, nauplii and copepod eggs, which they found dominated the zooplankton fraction of microplankton samples from an upwelling front in the southern Benguela. Using the maximum density isopleths provided by Armstrong *et al.* (1987) for each of the three groups (30, 300 and 60 litre^{-1} respectively) and assigning dry weights of 860ng, 83ng and 56ng respectively per individual (Beers 1966 for copepodites and nauplii, J. Huggett, Marine &Coastal Management, pers. comm. for eggs) allows an estimate of maximum microzooplankton biomass to be made (54.2μg dry weight litre^{-1}). Proportions of 25%, 50% and 100% of this maximum value were combined with the average mesozooplankton biomass (54.5 ± 51.8 μg dry weight litre^{-1}; n = 29) to give estimates of the quantity of zooplankton food available to filter-feeding sardine.

Using clearance rates of 11.78 litres fish^{-1} minute^{-1} for mesozooplankton and 5.1 litres fish^{-1} minute^{-1} for microzooplankton, enables an estimation of the ingestion rates of filter-feeding sardine under these three food environments to be made. The resultant calculations indicate that sardine are able to obtain their daily requirement (2-3% dry body weight day^{-1}, equivalent to 10% wet body weight day^{-1}, Shannon and Field 1985, Armstrong *et al.* 1991a) in 6-12 hours (depending on the biomass of microzooplankton present) exclusively through filter-feeding on meso- and microzooplankton. Because of the uncertainty concerning the digestibility and hence assimilation of diatoms by sardine, estimates of phytoplankton biomass have not

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been included in the above calculations. Any energy gained by sardine through ingesting phytoplankton will have the effect of reducing the time required to attain daily ration to less than 12 hours.

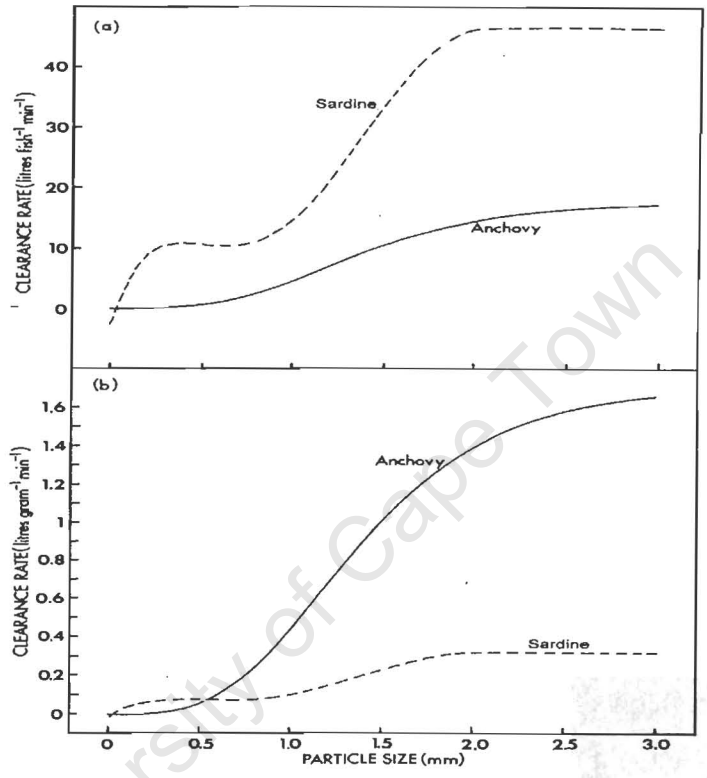

Figure 2.10: Predicted clearance rates (F) as a function of particle size for *Sardinops sagax* and *Engraulis capensis*. (a) F expressed on a per fish basis; (b) F expressed on a per gram basis i.e. weight standardized. Data for *E. capensis* from James and Findlay (1989).

Predictive equations of clearance rate as a function of particle size can be used to facilitate comparisons between sardine and Cape anchovy; species that coexist in the southern Benguela upwelling ecosystem. On a per fish basis, sardine show much higher clearance rates than anchovy (Figure 2.10a). However, when rates are standardized and expressed as a function of fish weight, sardine are only more efficient at removing particles of less than 580μm TL, anchovy having distinctly faster clearance rates on particles larger than this size (Figure 2.10b). This difference strongly implies resource partitioning between the two species, in contrast to previous suggestions of competition between coexisting species pairs of sardine and anchovy

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(Lasker and MacCall 1983, Lasker 1985). Therefore, as a result of different feeding strategies, sardine are more efficient removers of small particles, while anchovy remove large particles more effectively (Figure 2.11).

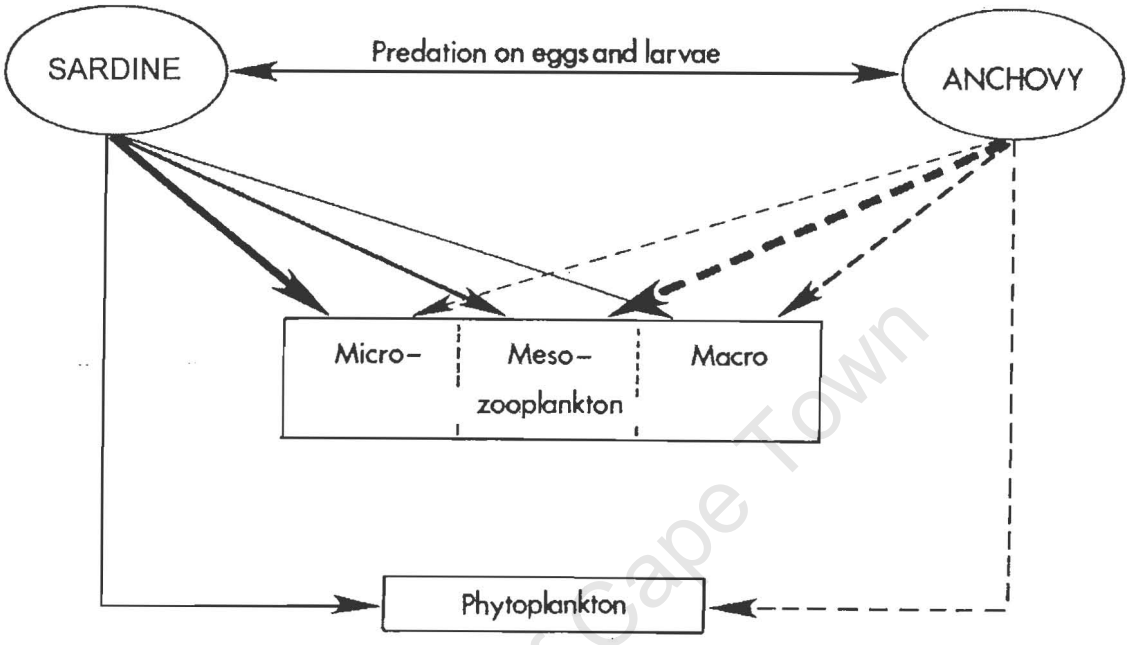

Figure 2.11: Schematic representation of resource partitioning between *Sardinops sagax* and *Engraulis capensis*. Arrow size reflects the perceived importance of specific components (e.g. mesozooplankton) in the diet of each species.

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Chapter 3: Respiration Rate of Adult Sardine in Relation to Temperature, Voluntary Swimming Speed and Feeding Behaviour

3.1: Introduction

Catches by the pelagic fishery in the Benguela ecosystem are dominated by three clupeoid species; sardine *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi* (Armstrong and Thomas 1989). Although all three species are planktivorous, each consumes different plankton fractions. Sardine feed primarily upon phytoplankton (Davies 1957, King and Macleod 1976) and microzooplankton (see Chapter 2), and are essentially non-selective filter-feeders (Chapter 2). Anchovy are predominantly particulate-feeders (James and Findlay 1989), with mesozooplankton such as calanoid copepods and euphausiids comprising their major dietary component (James 1987). Round herring feed exclusively on zooplankton (Wallace-Fincham 1987), presumably through particulate-feeding only (James 1988b).

The trophodynamics of *Engraulis capensis* are well documented (James 1987, James and Findlay 1989, James and Probyn 1989, James *et al.* 1989a), and carbon and nitrogen budgets for this species have been constructed (James *et al.* 1989b). The calculated maintenance ration derived from these budgets has been compared with yearly estimates of mesozooplankton biomass and production on fish spawning grounds during the peak spawning period in order to assess the probability of successful spawning by anchovy in a potentially food-limiting environment (Peterson *et al.* 1992). Such predictions of spawning success can provide valuable information for the management of this commercially important, recruit-based fishery. Construction of carbon and nitrogen budgets for sardine requires that similar information be collected for this species.

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The present study was undertaken to investigate the relationship between voluntary swimming speeds and oxygen consumption rates of sardine during several activity states, namely non-, filter- and particulate-feeding, and to determine whether this relationship was significantly different for each activity state. Additionally, the influence of temperature upon oxygen consumption rates was examined, and data were collected for calculation of a respiratory quotient (RQ) for this species.

The experimental approach reported here closely follows that used by James and Probyn (1989) to determine the relationship between respiration rate, swimming speed and feeding behaviour for *Engraulis capensis*. This common approach enables a detailed comparison of the metabolic costs associated with various feeding strategies employed by these co-occurring planktivorous clupeoids, and may permit a better understanding of the trophic interactions between this species pair.

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3.2: Materials and methods

Sardine used for oxygen consumption rate experiments were collected and maintained as described in Chapter 2. Nineteen experiments (Table 3.1) were conducted using a school of 10 adult fish (256.0 ± 9.8 mm total length, TL; 146.4 ± 15.3 g wet weight) maintained in a 2.0m diameter, 3000l fibreglass pool, subject to the ambient light regime. Fish were starved for periods of 1-6 days prior to experimentation in order to permit evacuation of the gastrointestinal tract and ensure that the last meal had no effect on the metabolism of the fish during experimentation. Two control experiments, without fish in the sealed respirometer, were also conducted.

Of the 19 experiments performed, 12 were conducted at ambient (14.9-18.3°C), 4 at lower, and 3 at higher temperatures (Table 3.1). The experimental temperatures used encompass the range observed in the southern Benguela, where the sea surface temperature shows seasonal variation from 10 to 22°C (Shelton and Hutchings 1990). When temperatures other than ambient were required, the experimental tank was connected to a temperature-controlled 800l reservoir via a

submersible pump and an overflow system. Temperatures were raised or lowered from ambient to the required level over a period of 2-3 days to allow for gradual thermal acclimation of the fish. Experiments at non-ambient temperatures were only initiated after the tank had been maintained at the required temperature for at least 4 days.

Prior to experimentation, the tank was thoroughly cleaned and the water volume reduced to 1000l, resulting in a water depth of 30 cm. A transparent polycarbonate lid, which rested on a flange around the inside perimeter of the tank, was then lowered onto the water surface. The lid was held in position by a 40kg circular steel bar lowered onto its periphery, which ensured that an airtight seal was formed between the tank walls, flange and lid. This effectively produced a closed-system respirometer. The polycarbonate lid was fitted with several sealable ports for positioning dissolved oxygen and temperature probes, obtaining water samples, and adding food. The fish were left undisturbed for 30 min after fitting of the polycarbonate lid, thereby allowing them sufficient time to resume normal behaviour.

Each experiment consisted of regular measurements of oxygen concentration in the water and appraisal of concomitant swimming speeds and feeding behaviour of the fish. Respiration rates for each sampling period were calculated using the following formula:

$$\text{Respiration rate (mg } O_2 \text{ g}^{-1} \text{ wet wt h}^{-1}) = \frac{(DO_i - DO_f)*V}{(t/60)*W} \qquad (1)$$

where DO_i and DO_f are dissolved oxygen concentrations at time i and time f respectively (mg O_2 litre^{-1}), V is the water volume in the tank (= 1000l), t is the interval between time i and time f (minutes), and W = total wet weight of all fish in the tank (g).

Table 3.1: Summary of experiments performed. Pu: pulsed [single or double (x2)] addition of food; Co: continuous addition of food; * samples collected for respiratory quotient (*RQ*) determination; BW: body weight; F: filter-feeding; P: particulate-feeding. Composition of wild phytoplankton: (1) 80l of collected phytoplankton concentrated to 5l on a 37 µm mesh and added for each pulse; consisted of 43, 23, 16 and 13% *Chaetoceros* spp., *Thalassiosira* spp., *Nitzschia* spp. and *Skeletonema costatum* by number respectively. (2) 160l of collected phytoplankton concentrated to 10l on a 37 µm mesh; consisted of 47 and 22% *Chaetoceros* spp. and *S. costatum* by number respectively. (3) 130l of collected phytoplankton concentrated to 15l on a 37 µm mesh; consisted of 40 and 19% *S. costatum* and *Nitzschia* spp. by number respectively. Composition of wild zooplankton: (4) Zooplankton passed through 500µm mesh and retained on a 100µm mesh; consisted of 25, 18 and 15% *Oithona* spp., copepod eggs, and copepod nauplii by number respectively. (5) Zooplankton retained on a 500µm mesh; consisted of 64, 17 and 16% *Acartia africana, Oithona* spp. and 'small calanoid copepods' (*Clausocalanus* spp., *Paracalanus* spp. and *Ctenocalanus* spp.) by number respectively. (6) Zooplankton retained on a 500µm mesh; consisted of 61, 19 and 13% *A. africana*, *Centropages brachiatus* and *Oithona* spp. by number respectively. (7) Zooplankton retained on a 950µm mesh; consisted of 61, 22 and 13% *Calanoides carinatus*, *Oithona* spp. and *C. brachiatus* by number respectively.

Expt	Initial temp. (°C)	Starvation time (d)	Food organism	Food size (mm)	Food addition	Ration (% wet BW)	Feeding response
1	16.0	6	Wild phytoplankton (1)	0.02 ± 0.02	Pu (x2)	0.55	F
2	16.7	1	Wild phytoplankton (2)	0.01 ± 0.02	Pu	1.42	F
3	14.9	1	Wild phytoplankton (3)	0.01 ± 0.02	Pu	0.19	F
4	14.9	4	Artemia nauplii	0.57 ± 0.12	Pu (x2)	2.63	F
5	16.7	2	Artemia Juveniles	3.90 ± 1.56	Pu (x2)	1.69	F
6	16.4	3	-				
7	17.4	2	-				
8*	16.3	5	Mysids (Gastrosaccus)	11.68 ± 2.83	Pu	0.65	P
9*	19.0	5	Artemia adults	5.44 ± 2.58	Pu/Co	2.02	P
10*	20.1	2	Artemia juveniles	4.76 ± 1.17	Co	2.14	P
11	11.9	4	Artemia nauplii	0.51 ± 0.07	Co	0.54	F
12*	10.0	1	-				
13	9.7	4	Artemia nauplii	0.58 ± 0.07	Co	0.62	F
14	12.6	2	-				
15	22.7	3	Artemia nauplii	0.58 ± 0.10	Co	0.49	F
16	18.3	1	Wild zooplankton (4)	0.51 ± 0.23	Co	1.63	F
17	16.0	5	Wild zooplankton (5)	0.88 ± 0.24	Pu (x2)	0.53	F
18	16.5	2	Wild zooplankton (6)	1.23 ± 0.29	Pu	0.34	F
19	16.1	2	Wild zooplankton (7)	1.75 ± 0.95	Co	1.86	P

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Dissolved oxygen concentration was measured using a calibrated Hanna HI 9143 dissolved oxygen meter (Hanna Instruments) with a resolution of 0.01 mg O_2 $litre^{-1}$. Calibration was achieved using a modified microWinkler technique (Williams and Jenkinson 1982, Oudot *et al.* 1988). The dissolved oxygen probe was mounted in one of the sealable ports of the polycarbonate lid, and projected 8 cm into the water below the level of the lid. A submersible water pump was positioned directly underneath the oxygen probe, providing sufficient water movement to ensure that the oxygen-depleted membrane surface was constantly replenished. In order not to generate water currents within the tank, the submersible pump was only activated 3 minutes prior to recording dissolved oxygen levels, and switched off immediately thereafter. Activation of the pump had no apparent effect on fish swimming behaviour. Temperature was recorded with a digital readout thermometer, the probe of which was also mounted in the polycarbonate lid.

Fish swimming speed and feeding behaviour were monitored with a video camera mounted 2.5m above the tank and recording at 25 frames s^{-1}. Since swimming speed was monitored using a single camera, measurements were only valid for two dimensions. This measurement technique was considered legitimate, however, since fish movement in the 3rd dimension (vertical plane) was minimal as a result of the reduced water volume and shallow depth.The floor of the tank was marked with a reference grid of lines 10cm apart. The fish were recorded for a 10 min period midway between each dissolved oxygen sampling time. Each video sequence was analysed to determine swimming speed, and feeding intensity (% of the school feeding) when the fish were feeding. Swimming speed was determined by counting the number of frames taken by individual fish to completely cross one of the grid lines, and was expressed as body lengths (BL) per second. Thirty measurements of swimming speed were taken in each video sequence; only fish whose path did not deviate by more than approximately 20° from their original heading during the counting period were considered. Feeding intensity was determined by measuring the proportion of the school feeding in a single randomly chosen frame when all 10 fish were clearly observable, and was repeated 50 times for each video sequence. Means and

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standard deviations for swimming speed and feeding intensity (where applicable) within each experiment were calculated for all time intervals. Differences between the variables measured during the course of an experiment were determined by ANOVA/Tukey multiple range analysis, with statistical significance being accepted at the $p < 0.05$ level.

Once the polycarbonate lid was fitted and the fish had resumed normal behaviour, measurements of oxygen concentration and swimming speed were taken for 2-4 h before food was added. Dissolved oxygen and temperature readings were taken 30 minutes after placement of the lid, and every 30 minutes thereafter. Food particles were added to the tank after the non-feeding period, and measurements of oxygen concentration, swimming speed and feeding intensity were made.

Food organisms (Table 3.1) were first concentrated before being added to the tank. Food was added via a sealable port in the middle of the polycarbonate lid, connected through a flexible tube of 8 mm internal diameter to a funnel situated away from and above the level of the tank. Water containing food particles in the funnel was continually replenished, and a tap positioned immediately below the funnel regulated the rate at which the food was added to the tank. Food was added in one of 2 manners; either as a 'pulse' at a constant rate for a 10 to 15 min period once or twice during an experiment, or 'continuously' at a constant rate for a 1 to 3 h period during the experiment. Different methods of food addition were employed in order to provide a range of food concentrations within the experimental tank, resulting in the fish displaying each feeding mode over a range of swimming speeds.

From three to five subsamples were taken from the food vessel before addition of the food to the experimental tank. These replicates were preserved in 5% buffered formalin and later examined microscopically to identify, count and measure the food particles. Fifty individual food particles from each experiment were measured (maximum dimension) to determine average particle size. After enumeration, and in order to calculate experimental ration (% wet fish body weight), the samples were

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individually concentrated onto pre-weighed Whatman GFF 25mm filter papers using a vacuum filter, and their wet weights determined on a Sartorius micro-balance.

In experiments where the RQ was determined, three 125ml water samples were taken through one of the sealable ports for carbon dioxide analysis. Samples were collected at the same time as dissolved oxygen measurements were taken. Total carbon dioxide was determined using the methods described in Culberson (1981) and Jagner (1981): pH was determined on the NBS (National Bureau of Standards) scale and total alkalinity was measured using a Gran titration procedure. All calculations were also referenced to the NBS scale (P. Monteiro, formerly Marine and Coastal Management, pers. comm.). The RQ was calculated using the formula (Kutty 1968):

$$RQ = \frac{\text{volume of } CO_2 \text{ produced}}{\text{volume of } O_2 \text{ consumed}} \qquad (2)$$

Respiration rates and mean swimming speed during non-feeding were plotted against temperature, and regressions were fitted to the data. Respiration rates were also plotted against mean swimming speed for each of the three activity states (non-, filter and particulate-feeding), and regression equations were fitted to the data. In order to examine the effects on metabolism of feeding behaviour as distinct from swimming speed, respiration rates were also plotted against mean feeding intensity. The slopes of the fitted regressions were taken as indicators of the energetic cost of a particular mode, and significant ($p < 0.05$) differences in the slopes were tested for using a modified Student's t-test (Zar 1984).

3.3: Results

Control experiments showed no significant ($p>0.05$) change in dissolved oxygen concentration with time. In all other experiments, non-feeding activity was characterised by unchanging swimming speeds and low respiration rates (Figure 3.1). When offered phytoplankton, sardine showed no significant ($p>0.05$) change in

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swimming speed (Figure 3.1a). Feeding intensity was initially moderate with half of the school engaged in filter-feeding, and declined slowly as the fish removed the small food particles (Figure 3.1b). Respiration rates when filter-feeding on phytoplankton were not significantly ($p<0.05$) different to those determined during the preceding non-feeding period (Figure 3.1c).

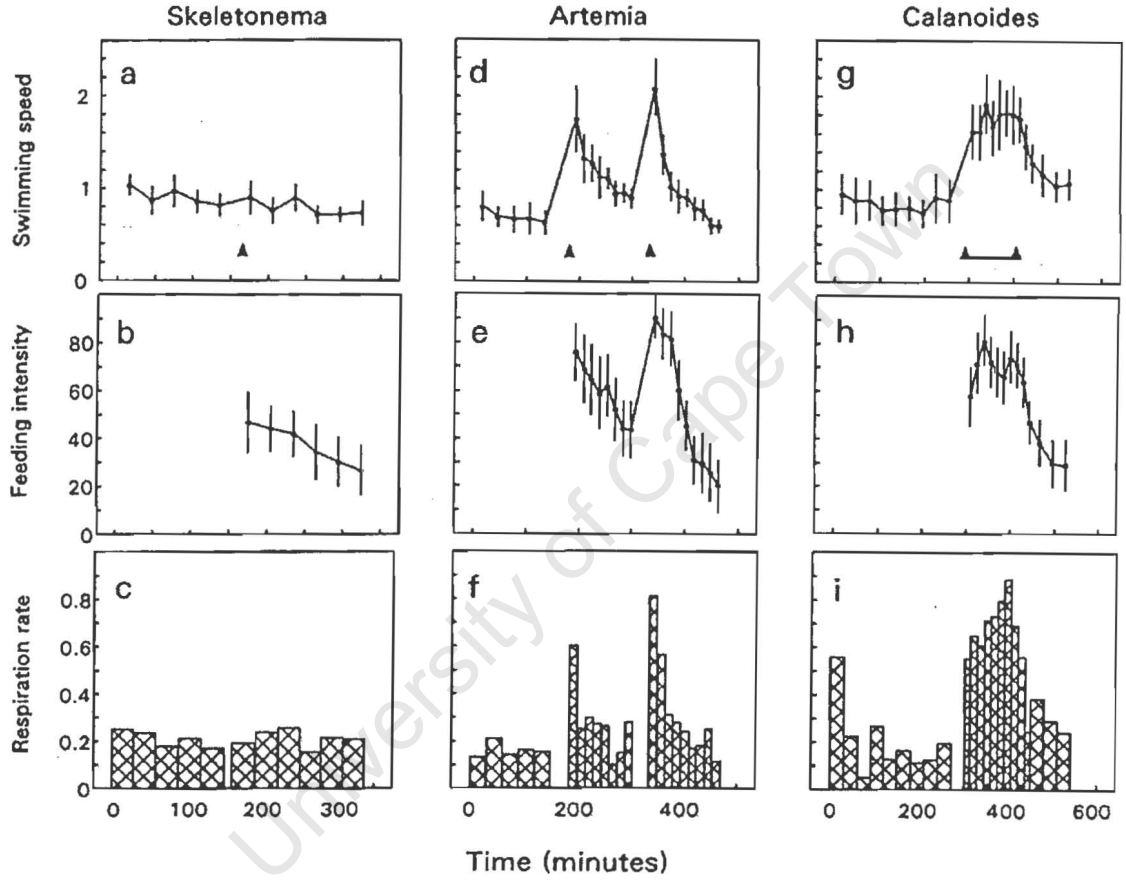

Figure 3.1: Swimming speed (BL.s-1), feeding intensity (% of school feeding) and respiration rate (mg O_2 g^{-1} wet weight h^{-1}) of sardine engaged in various activities: (a to c) filter-feeding on *Skeletonema costatum* and *Nitzcshia* spp. (14 ± 21 µm); (d to f) filter-feeding on *Artemia franciscana* nauplii (571 ± 124 µm); (g to i) particulate-feeding on *Calanoides carinatus* (2411 ± 134 µm). Means ± SD for swimming speed and feeding intensity are shown. Each graph shows the initial non-feeding response, followed by the feeding response. Time of food addition is indicated by single arrows (pulsed food addition) or arrows joined by a thick line (continuous food addition) on the swimming speed graphs.

The addition of zooplankton resulted in markedly increased swimming speeds, high feeding intensities, and an associated increase in respiration rate during both

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filter- and particulate-feeding. Swimming speed declined rapidly as food concentrations declined in the pulsed-food experiment (Figure 3.1d), but remained elevated during the continuous-food experiment (Figure 3.1g). Feeding intensity mirrored swimming speed for both pulsed- and continuous-food experiments, declining rapidly in the former (Figure 3.1e) as the fish removed food particles through filter-feeding, and remaining elevated in the latter as the fish particulate-fed (Figure 3.1h). Respiration rates increased by up to six-fold during periods of fast swimming speeds and high feeding intensities (Figure 3.1f), with the highest rates being associated with particulate-feeding (Figure 3.1i). Once food concentrations in the tank had been reduced by the fish, swimming speeds, feeding intensities and respiration rates declined gradually to pre-feeding levels.

The effect of temperature on respiration rate and swimming speed during non-feeding activity is shown in Figure 3.2. Both respiration rate and mean swimming speed increased asymptotically with temperature. An equation of the form:

$$y = a+be^{cx} \qquad (3)$$

was found to provide significant regressions in both cases. Statistical parameters for the respiration rate/temperature and swimming speed/temperature regression equations are given in Figure 3.2.

Q_{10} values for sardine were calculated from the data by applying the following formula

$$Q_{10} = (R_2/R_1)^{10/T2-T1} \qquad (4)$$

where R_i is the oxygen consumption rate at temperature T_i (Schmidt-Nielsen 1982).

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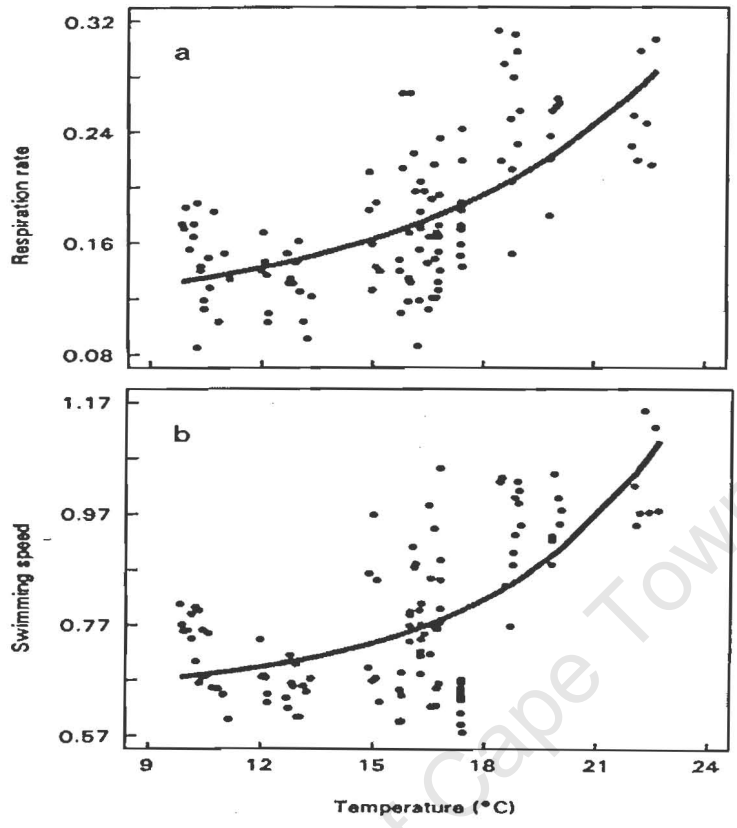

Figure 3.2: (a) Respiration rate (mg O_2 g^{-1} wet weight h^{-1}) and (b) swimming speed ($BL.s^{-1}$) as a function of temperature for non-feeding sardine. Equations and statistical parameters for the fitted curves are: (a) $y = 0.1058 + 0.0061e^{0.1492x}$, $r^2 = 0.43$, $n = 117$, $F = 766.4$, $p < 0.001$; (b) $y = 0.6425 + 0.0043e^{0.2057x}$, $r^2 = 0.45$, $n = 117$, $F = 2219.7$, $p < 0.001$.

Oxygen consumption rates were derived from the predictive asymptotic equation (Figure 3.2a) at temperatures of 10, 12, 14, 16, 18, 20 and 22°C, and the Q_{10} values for each temperature interval are given in Table 3.2. Q_{10} values increased with increasing temperature over the temperature range observed, from 1.41 over 10-12°C to 2.33 over 20-22°C, and had a mean (± standard deviation) value of 1.82 ± 0.35.

Respiratory quotients were measured when the fish were displaying both non-feeding and particulate-feeding activity, and results from the four RQ experiments are presented in Table 3.3. There was no significant (t-test; t = -0.387; p=0.72) difference between the average values derived from non-feeding and particulate-feeding activity, and the mean RQ for the combined data was 0.955 ± 0.099.

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Table 3.2: Predicted oxygen consumption rates and Q10 values for sardine exhibiting non-feeding behaviour at various temperatures.

Temperature (°C)	Respiration rate (mg O_2 g^{-1} wet weight h^{-1})	Temperature interval	Q_{10}
10	0.133		
12	0.142	10-12	1.41
14	0.155	12-14	1.53
16	0.172	14-16	1.69
18	0.195	16-18	1.87
20	0.226	18-20	2.09
22	0.267	20-22	2.33
Mean Q_{10}			1.82 ± 0.35

Table 3.3: Oxygen consumption, carbon dioxide production, and calculated RQs for sardine during various activity states.

Experiment	O_2 consumption (mg g^{-1} wet weight h^{-1})	CO_2 production (mg g^{-1} wet weight h^{-1})	RQ
8: non-feeding	0.165	0.168	1.018
8: particulate-feeding	0.354	0.386	1.090
9: non-feeding	0.255	0.267	1.047
9: particulate-feeding	0.485	0.430	0.887
10: non-feeding	0.248	0.217	0.875
10: particulate-feeding	0.540	0.507	0.939
12: non-feeding	0.179	0.148	0.827
Mean RQ			0.955 ± 0.099

The relationships between respiration rate and swimming speed for each of non-feeding, filter-feeding and particulate-feeding activity states are shown in Figure 3.3. Non-feeding activity was characterized by slow swimming speeds ranging from 0.6 to 1.2 BL s^{-1} (= 15.4 to 30.7 cm s^{-1}) and respiration rates of 0.08 to 0.32 mg O_2 g^{-1} wet weight h^{-1} (Figure 3.3a). The plot of swimming speed coefficient of variation (SSCV) versus swimming speed indicates that non-feeding is a highly variable activity, with SSCV's ranging from 8-40% of the means (Figure 3.3b). The average non-feeding respiration rate was 0.178 ± 0.055 mg O_2 g^{-1} wet weight h^{-1} at a mean swimming speed of 0.78 ± 0.14 BL s^{-1} (= 20.0 ± 3.6 cm s^{-1}).

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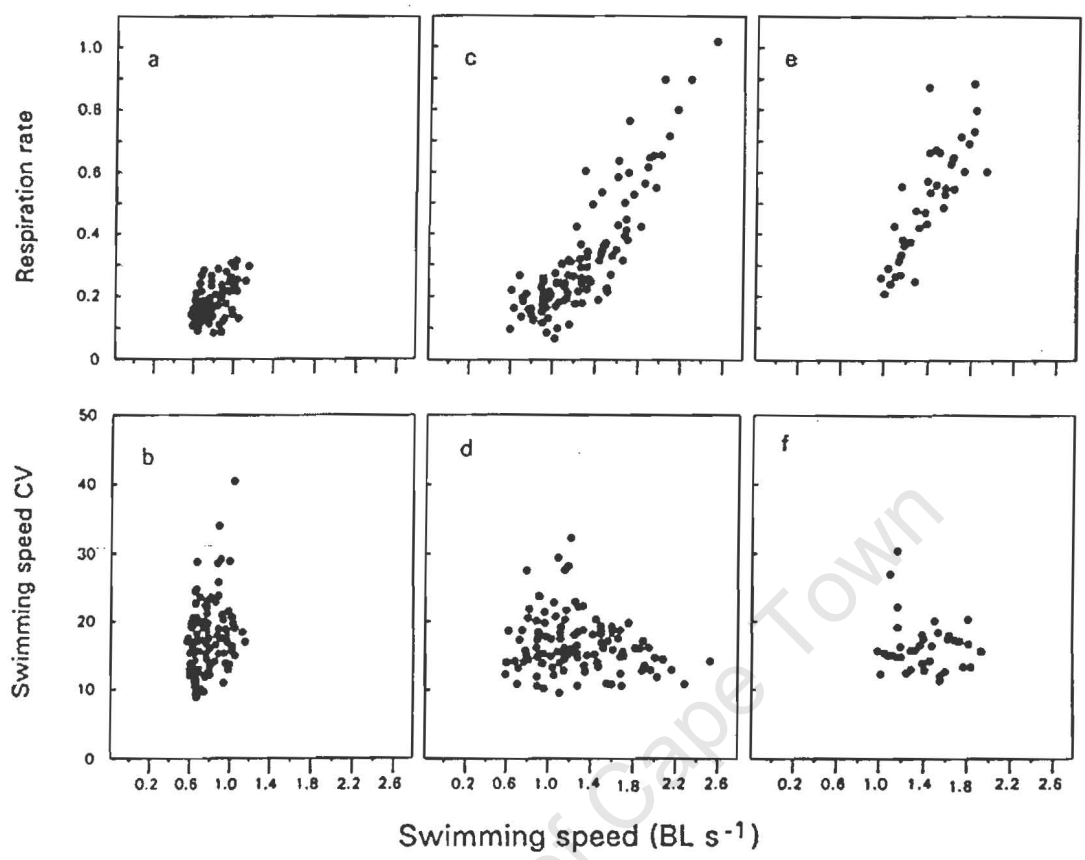

Figure 3.3: Relationship between respiration rate (mg O_2 g^{-1} wet weight h^{-1}), coefficient of variation (CV) of swimming speed (%) and swimming speed (BL.s^{-1}) for sardine engaged in (a, b) non-feeding, (c, d) filter-feeding and (e, f) particulate-feeding.

Swimming speed during filter-feeding ranged from 0.6 to 2.6 BL s^{-1} (= 15.4 to 66.6 cm s^{-1}), with respiration rates increasing proportionately with swimming speed and ranging from 0.07 to 1.03 mg O_2 g^{-1} wet weight h^{-1} (Figure 3.3c). The plot of SSCV versus swimming speed (SSCV ranging from 9 to 33%) for filter-feeding shows slightly less variability than for non-feeding activity, suggesting that filter-feeding may be a more consistent activity state (Figure 3.3d). Particulate-feeding fish exhibited swimming speeds of 1.0 to 2.0 BL s^{-1} (= 25.6 to 51.2 cm s^{-1}), and respiration rate was again proportional to swimming speed (Figure 3.3e), ranging from 0.20 to 0.90 mg O_2 g^{-1} wet weight h^{-1}. The plot of SSCV versus swimming speed (SSCV ranging from 12 to 31%) also shows less variability than for non-feeding activity (Figure 3.3f).

Linear regressions were found to provide the best fit to the respiration

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rate/swimming speed data for all 3 activity states, and predictive plots are presented in Figure 3.4. The equation and statistical parameters for each regression are given in Table 3.4.

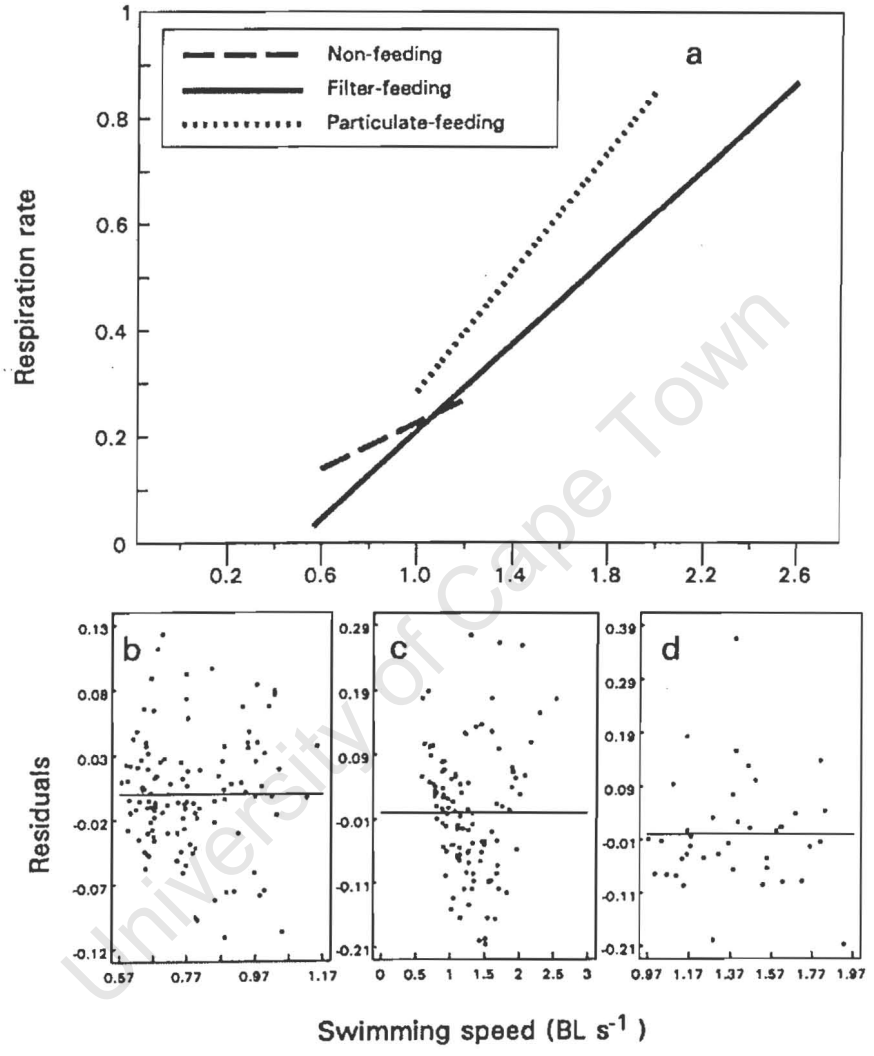

Figure 3.4: (a) Derived linear regressions of respiration rate (mg O_2 g^{-1} wet weight h^{-1}) as a function of swimming speed ($BL.s^{-1}$) for sardine engaged in various activities. Parameters for the regression equations are given in Table 3.4. (b to d) Respiration rate residuals plotted against their corresponding swimming speeds for (b) non-feeding, (c) filter-feeding and (d) particulate-feeding activity states.

The linear relationships between respiration rate and swimming speed for all 3 activity states derived in this study are inconsistent with other studies, which reported a log-linear relationship between these variables (Brett 1964, 1965, Brett and Sutherland 1965, Muir and Niimi 1972, Beamish 1981, Durbin *et al.* 1981, James and

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Probyn 1989, Beamish 1990). Log transformations, such as the ones employed by those authors, are used to correct for heteroscedasticity, to transform multiplicative effects into additive ones, or to normalize data (Zar 1984). To test for homoscedasticity, respiration rate residuals from the regressions for each activity state of sardine derived in this study were plotted as a function of their corresponding swimming speeds (Figure 3.4b-d), and their homoscedasticity assessed by inspection. Additionally, the residuals were examined for normality of distribution using the Kolmogorov-Smirnov test (Zar 1984). No heteroscedastic trends were seen in any of the three cases, and residual distribution was normal at the $p < 0.05$ level ($D_{rout.} = 0.057$, $D_{0.05,119} = 0.081$; $D_{filt.} = 0.052$, $D_{0.05,111} = 0.085$; $D_{part.} = 0.137$, $D_{0.05,39} = 0.140$). Hence regressing untransformed respiration rate against swimming speed was justified in this instance.

Table 3.4: Statistical parameters for the predictive equations of respiration rate as a function of swimming speed for sardine engaged in non-, filter- and particulate-feeding. The equation is of the form $y = mx + c$, where y is respiration rate (mg O_2 g^{-1} wet weight h^{-1}), x is swimming speed ($BL.s^{-1}$), m is the slope and c is the intercept. SE values for the slope and intercept are given, as are the regression F-ratio and significance of the derived regressions. All slopes are significantly ($p < 0.05$) different to each other.

Parameter	Non-feeding	Filter-feeding	Particulate-feeding
N	119	111	39
Slope	0.2219 ± 0.0304	0.4131 ± 0.0234	0.5711 ± 0.0660
Intercept	0.0047 ± 0.0241	-0.2035 ± 0.0312	-0.2891 ± 0.0935
r^2	0.31	0.74	0.67
F-ratio	53.3	312.8	75.0
P	< 0.001	< 0.001	< 0.001

The slope of a regression was taken as indicative of the relative energetic cost of that particular feeding mode (James and Probyn 1989). All 3 slopes were significantly ($p < 0.05$) different from each other, with non-feeding showing the lowest slope value, filter-feeding an intermediate value and the highest slope value being that derived for particulate-feeding (Table 3.4). Figure 3.4 and Table 3.4 demonstrate that particulate-feeding is the most energetically expensive activity state for sardine, and that feeding of either mode is energetically more expensive than non-

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feeding. Standard (basal) metabolic rate was estimated by extrapolation of the relationship between non-feeding swimming speed and respiration rate to 0 BL s^{-1}, which yielded a standard metabolic rate of 0.009 ± 0.024 mg O_2 g^{-1} wet weight h^{-1}.

The relationships between respiration rate and feeding intensity for both filter- and particulate-feeding are shown in Figure 3.5. During filter-feeding, high respiration rates tended to be associated with high feeding intensities (Figure 3.5a), although there was considerable scatter between these variables. The plot of feeding intensity coefficient of variation (FICV) versus feeding intensity showed a very marked decline in CVs at higher feeding intensities (Figure 3.5b), indicating that the school behaved uniformly at high filter-feeding intensities.

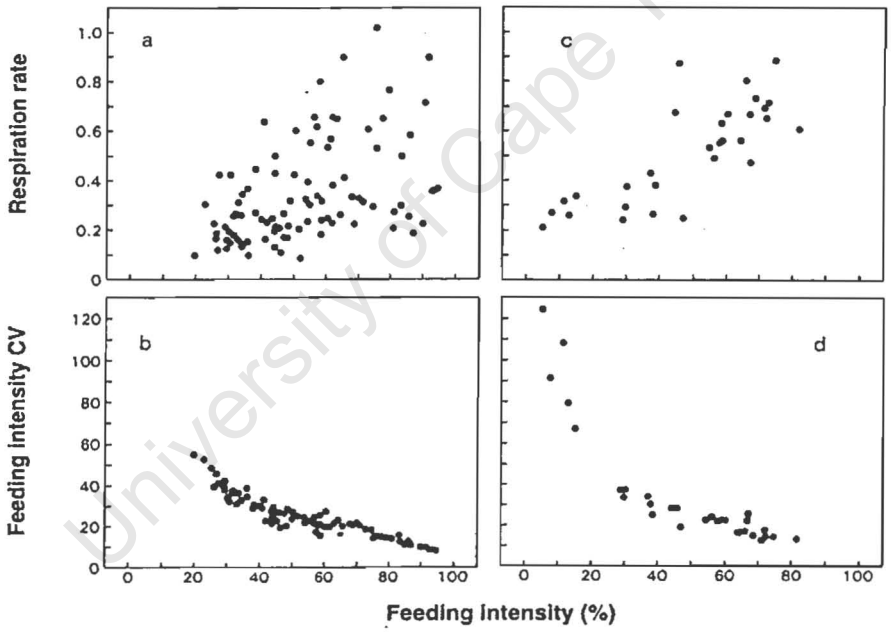

Figure 3.5: Relationship between respiration rate (mg O_2 g^{-1} wet weight h^{-1}), coefficient of variation (CV) of feeding intensity (%) and feeding intensity (%) for sardine engaged in (a, b) filter-feeding and (c, d) particulate-feeding.

High respiration rates were also associated with high feeding intensities for sardine engaged in particulate-feeding (Figure 3.5c), and there was less scatter between these variables than for filter-feeding. The plot of feeding intensity coefficient of variation (FICV) versus feeding intensity showed an exponential decline in CV with feeding intensities (Figure 3.5d).

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Significant regressions were derived for the respiration rate/feeding intensity relationships for both feeding modes, with an exponential equation best describing the relationship in each case. The predictive curves are presented in Figure 3.6, and the equation and statistical parameters for each regression are given in Table 3.5.

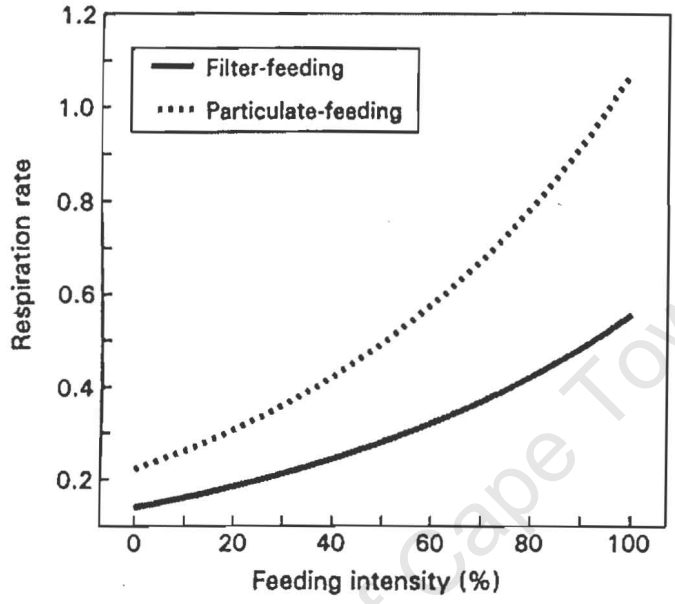

Figure 3.6: Derived regressions of respiration rate (mg O_2 g^{-1} wet weight h^{-1}), as a function of feeding intensity (%) for sardine engaged in filter-feeding and particulate-feeding. Parameters for the regression equations are given in Table 3.5.

Table 3.5: Statistical parameters for the predictive equations of respiration rate as a function of feeding intensity for sardine engaged in filter- and particulate-feeding. The equations are of the form $y = e^{c + mx}$, where y is respiration rate (mg O_2 g^{-1} wet weight h^{-1}), x is feeding intensity (%), m is the slope and c is the intercept. SE values for the slope and intercept are given, as are the regression F-ratio and significance of the derived regressions.

Parameter	Filter-feeding	Particulate-feeding
N	98	39
Slope	0.0137 ± 0.0025	0.0158 ± 0.0019
Intercept	-1.9639 ± 0.1411	-1.4973 ± 0.0990
r^2	0.24	0.64
F-ratio	30.2	66.9
P	< 0.001	< 0.001

The variance in respiration rate explained by feeding intensity was much less than that explained by swimming speed for filter-feeding (24% and 74% respectively),

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but similar for particulate-feeding (64% and 67% respectively). This suggests that swimming speed is the prime determinant of respiration rate when filter-feeding, but that feeding intensity (i.e. feeding behaviour) assumes equal importance as a determinant of respiration rate when the fish are engaged in particulate-feeding.

Feeding intensity was significantly correlated with swimming speed during both filter- and particulate-feeding, with high feeding intensities associated with elevated swimming speeds (Figure 6.7). These high correlations prevented the use of these two variables in deriving multiple regressions of respiration rate for both feeding modes. This is due to the fact that intercorrelation among independent variables generates spurious conclusions in multiple regressions (Zar 1984).

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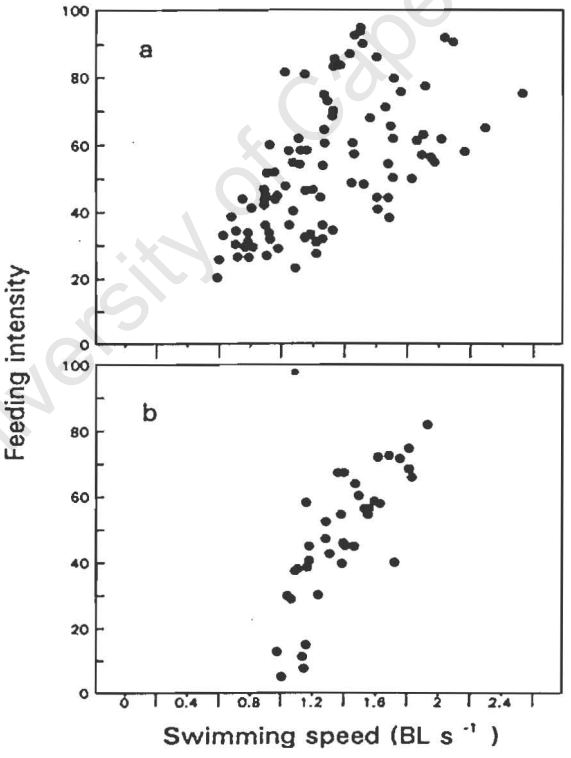

Figure 3.7: Relationship between feeding intensity (%) and swimming speed (BL.s-1) for sardine engaged in (a) filter-feeding and (b) particulate-feeding.

3.4: Discussion

This study has described the relationship between non-feeding (= routine) respiration rate and temperature, derived mean values for Q_{10} and RQ, and elucidated the effects of swimming speed and feeding behaviour on the metabolism of adult *Sardinops sagax*.

The effect of temperature on the active metabolism of fish has been reviewed by Fry (1971), but there appears to be no single pattern to describe the relationship for all species (Beamish 1990). For sardine, elevated temperatures resulted in increased respiration and swimming speed, with both variables increasing at an increasing rate with temperature. The Q_{10} for *Sardinops sagax* calculated here (1.82 over 10-22°C) is both lower than that determined for the same species elsewhere in its range, and lower than that found for other clupeoids. Villacencio *et al.* (1981 in Blaxter and Hunter 1982) calculated a Q_{10} of 3.2 for juvenile (8.5 cm) *S. sagax* between 15 and 20°C, whereas Villacencio (1981 in Blaxter and Hunter 1982) reported a Q_{10} of 2.6 for adult (12 cm) anchovetta *Engraulis ringens* between 15 and 20°C. Using the data in Hettler's (1976) Table I enables a Q_{10} of 2.1 to be calculated for young (74-81 g) Atlantic menhaden *Brevoortia tyrannus* between 10 and 25°C. Talbot and Baird (1985) reported a Q_{10} of 2.3 for estuarine round herring *Gilchristella aestuarius* between 15 and 25°C. The low Q_{10} value determined for sardine in this study may be indicative of a high degree of eurythermy. This suggestion appears credible, since sardine are common members of the pelagic fish component in several eastern boundary current systems such as the Benguela, California and Humboldt current systems (Crawford 1987). These systems are characterised by equatorward surface flow and coastal upwelling, resulting in high sea surface temperature variability (Parrish *et al.* 1983).

Respiratory quotients (RQ) indicate the type of physiological fuel involved in metabolism and, in fish, typically range from 0.7 for the catabolism of fats, through 0.9 for protein, to 1.0 for carbohydrates (Brett and Groves 1979). The mean RQ value of 0.96 for sardine suggests that metabolism is based on the breakdown of both protein

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and carbohydrates, although in general fish utilize dietary carbohydrate poorly (Brett and Groves 1979). This contrasts with the suggestion of Lasker (1970) who stated that Pacific sardine *Sardinops caerulea* (= *S. sagax* Parrish *et al.* 1989) metabolize fat as their major energy source. Lasker (1970) however gave no information on how such a conclusion was derived. James and Probyn (1989) showed *Engraulis capensis* to have an RQ of 0.915 ± 0.183, and suggested that protein was the metabolic fuel for this species. Although there is no statistical difference between the mean RQ values of these two clupeoids ($t = -0.616$; $p = 0.55$), the higher value for sardine suggests a greater carbohydrate utilization by this species. This lends support to the hypothesis (Davies 1957, Chapter 2) that phytoplankton is a more important dietary component for sardine than for anchovy, although both species consume phytoplankton (James 1988b).

The standard respiration rate of sardine estimated in this study, 0.009 mg O_2 g^{-1} wet weight h^{-1}, is an order of magnitude lower than that calculated from 34 fish species (0.089 mg O_2 g^{-1} wet weight h^{-1}) by Brett and Groves (1979). However, estimates of standard metabolic rate for pelagic fish derived by extrapolation are of limited ecological value, since such fish are never inactive but shift through a series of activity states including feeding, spawning, horizontal and vertical migrations (James and Probyn 1989). A more relevant standard metabolic rate value is 0.138 mg O_2 g^{-1} wet weight h^{-1}; the predicted respiration rate at the lowest observed non-feeding swimming speed.

The routine respiration rate determined in this study for adult *Sardinops sagax* lies within the range of routine rates estimated for other clupeoids (Table 3.6). The high value observed by Lasker (1970) was derived from experiments performed upon single sardines in a small (7.8l) respiration chamber, and is likely to be the result of laboratory artefact such as stress, attributable to confinement and isolation from the shoal (Blaxter and Hunter 1982). The low value recorded by Villavincencio (1981 in James and Probyn 1989) for this species is surprising, since respiration rates usually decrease with increasing size both within and among species (Brett and Groves

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Table 3.6: Routine respiration rates (mg O_2 g^{-1} wet weight h^{-1}), fish size, temperature (°C) and swimming speed (BL s^{-1}) of various clupeoids.

Species	Routine respiration rate	Fish size (length or wet weight)	Temperature	Swimming speed	Source
Sardinops sagax	0.178 ± 0.055	25.6 cm TL / 146 g	9.7-22.7	0.78±0.14	This study
	0.32[1]	12-25 cm SL	16.5-22	0.42	Lasker (1970)
	0.053	"Juvenile"			Villavincencio *et al.* (1981 in James & Probyn 1989)
Clupea harengus	0.20-0.25				Aneer (1979 in James & Probyn 1989)
	0.093±0.005	28.2 cm TL	9.3	0.3	Johnstone *et al.* (1993)
C. harengus membras	0.2	12-27 cm L	10-11	"Normal"	Chekunova (1979 in Johnstone *et al.* 1993)
Brevoortia tyrannus	0.263-0.314	23.3 g	23-24		Hettler (1976)
	0.100±0.009	25.8 cm FL / 302 g	20±1	0.47±0.06	Durbin *et al.* (1981)
Engraulis ringens	0.084				Villavincencio (1981 in James & Probyn 1989)
E. capensis	0.111±0.033	9.32 cm L	16.2±0.4	1.73±0.29	James & Probyn (1989)

1 Converted from ml O_2 using V=(nRT)/P where V is gas volume, n is millimoles (gas weight/32), R is the gas constant 0.08205, T is temperature (K), P is atmospheric pressure (1); P. Monteiro, formerly Marine and Coastal Management, pers. comm.

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1979). Clupeoids show large metabolic ranges compared to less active species (Durbin *et al.* 1981), with the ratio of active to routine respiration rate attaining a level as high as 10.7 for *Engraulis capensis* (James and Probyn 1989; their Table V). Whereas the maximum active respiration rate for sardine was 5.8 times greater than the average routine rate, the true active (*sensu* Brett 1965) respiration rate remains unknown, since the experiments reported here measured respiration rates during voluntary swimming only.

The slopes of the predicted respiration rate/swimming speed relationships derived in this study demonstrate that at any given swimming speed, filter-feeding by adult sardine is energetically cheaper than particulate-feeding. This result would tend to support the hypothesis that filter-feeding is the principal food acquisition mode of sardine (Davies 1957, King and Macleod 1976, Chapter 2). However, the feeding mode that realises the greatest return, in terms of energy expenditure versus energy gain, is dependent upon the size and concentration of food particles present. Sardine have been shown to exclusively filter-feed on particles less than 1230 μm total length, and to filter- or particulate-feed on particles greater than this size, depending upon concentration (Chapter 2).

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The results presented here differ from those determined for *Engraulis capensis*, a species which is also capable of both filter- and particulate-feeding (James and Findlay 1989). Filter-feeding by anchovy was shown to be energetically more expensive than particulate-feeding, leading James and Probyn (1989) to hypothesise that the change in body shape and increased resultant drag associated with flared operculae during filter-feeding was responsible for increased metabolic costs. Following James and Probyn's (1989) line of reasoning, it would intuitively be expected that this would also apply to sardine, since the act of filtering also results in marked changes in body shape.

However, viscous force, which is proportional to fish surface area (Webb 1975) and results in drag, is only one of the forces acting upon a body submerged in a fluid.

Gravitational and inertial (proportional to fish mass) forces also act upon moving bodies, although gravitational forces are insignificant when the body is well submerged (Webb 1975). The relative importance of inertial and viscous forces is expressed in the dimensionless Reynolds Number (R_e), which is a function of organism size, velocity, fluid density and kinematic viscosity (Videler 1993). The Reynolds Number increases with increasing organism size, ranging from <1 for protozoa to 10^8 for the blue whale *Balaenoptera musculus* (Webb 1975, Videler 1993). Hence viscous forces are dominant for small organisms whereas inertial forces are dominant for larger organisms.

The relative importance of viscous forces is therefore likely to be higher for anchovy, since anchovy are smaller than sardine and, at any given swimming speed, anchovy will have a lower R_e than sardine, although inertial forces will dominate for both species. Estimates of R_e, calculated using equation (12) of Webb (1975), range from 4.2×10^4 to 1.1×10^5 for sardine, and 1.7×10^4 to 4.2×10^4 for anchovy, swimming from 20 to 50 $cm.s^{-1}$ at 15°C. This difference between sardine and anchovy may be the reason for the observed differences in feeding-mode metabolic costs. Thus, turning frequently to capture prey by particulate-feeding is relatively more expensive for the heavier sardine, whereas the increased drag associated with filter-feeding is relatively more expensive for the smaller anchovy.

A comparison of the relative energetic costs of both feeding modes for these two species is given in Figure 3.8a. Although the respiration rate of particulate-feeding anchovy was similar to that of sardine for both feeding modes over the same swimming speed range, filter-feeding by anchovy was exceptionally expensive, particularly at speeds above 30 cm s^{-1} (= 3.2 BL s^{-1}). Figure 3.8b depicts the predicted respiration rate as a function of swimming speed for sardine, anchovy and the obligate filter-feeding menhaden *Brevoortia tyrannus* (Durbin and Durbin 1975) engaged in filter-feeding only. Although the data set for menhaden is small, with swimming speeds ranging from 25 to 45 cm s^{-1} (= 1 to 1.7 BL s^{-1}), the predicted respiration rate versus swimming speed equation derived by Durbin et al. (1981) does not appear to be

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significantly different from that derived for sardine, although both are distinctly lower than that for anchovy. Menhaden and sardine used to derive these equations were of a similar length (25.8 cm fork length and 25.6 cm TL respectively), and were substantially larger than the anchovy (9.3 cm TL). The similarity in absolute swimming speeds between these three species is surprising, given that larger fish have faster absolute swimming speeds than smaller fish (Videler 1993).

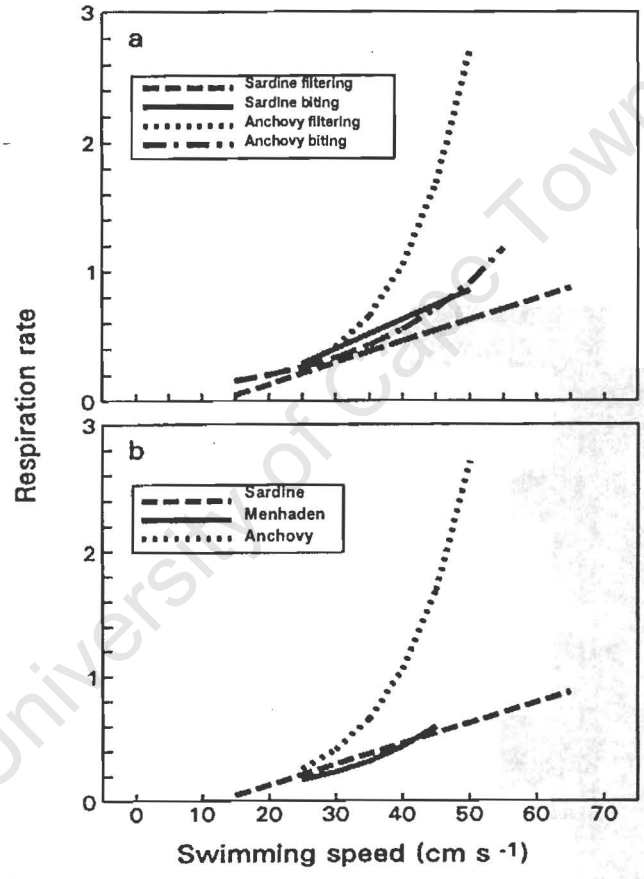

Figure 3.8: Predicted respiration rates (mg O_2 g^{-1} wet weight h^{-1}) as a function of swimming speed ($cm.s^{-1}$) for (a) sardine and anchovy engaged in both filter-feeding and particulate-feeding, and (b) sardine, anchovy and menhaden engaged in filter-feeding only. Predictive equations are from James and Probyn (1989) for anchovy (mean wet wt 7.1g, mean TL 9.3 cm) and from Durbin *et al.* (1981) for menhaden (mean wet wt 302g, mean FL 25.8 cm).

These observations suggest a general principle applicable to clupeoid fish capable of filter-feeding: that the energetic cost attributable to filtering decreases in

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relative importance with increasing fish size. This principle is supported by the data of Janssen (1976), who observed that whereas alewives (*Alosa pseudoharengus*) are capable of both filter- and particulate-feeding, different-sized individuals within the same school displayed different feeding behaviours when offered the same food. Large (17.8 to 18.0 cm TL) fish filter-fed exclusively upon *Daphnia pulex* whilst smaller (4.9 to 11.4 cm TL) fish were exclusively particulate-feeders. Similarly, gizzard shad *Dorosoma cepedianum* displays a dietary switch at a size of 2.5 cm caudal length from exclusively zooplankton to one comprising phytoplankton, zooplankton, and detritus, implying a change in feeding mode from particulate- to filter-feeding at this size (Drenner *et al.* 1982). Sardine also display a dietary switch, the proportion by volume of zooplankton decreasing from 87.3% for fish < 10 cm SL to 22.9% for fish > 10 cm SL (King and Macleod 1976). Although the change in diet and feeding mode utilisation with increasing size for sardine and gizzard shad is a function of morphological development, it is possible that hydrodynamic factors may also influence this switch.

That particulate-feeding is energetically more expensive than filter-feeding in *Sardinops sagax* may be due to the different swimming behaviour associated with each feeding mode. Particulate-feeding is a more complex activity than filtering, since it involves frequent changes in direction and abrupt accelerations and decelerations as the fish align themselves towards specific food particles (Chapter 2). In contrast, filter-feeding involves a "constant-motion" behaviour pattern, with the fish maintaining a more consistent swimming speed and displaying low amplitude changes in direction (Chapter 2). In a detailed study of fish swimming mechanics, Boisclair and Tang (1993) analysed simultaneous estimates of fish swimming behaviour and swimming cost for 10 species, and concluded that energy expenditures associated with different swimming patterns were significantly different. Boisclair and Tang (1993) demonstrated that "routine" swimming (characterized by marked changes in swimming direction and speed) was a more expensive swimming pattern than "directed" swimming (characterized by quasi-rectilinear movements executed at relatively constant swimming speed), and ascribed the increased energetic costs to increased swimming pattern complexity.

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Similar results have been obtained from other studies. Forstner and Wieser (1990) observed that a swimming pattern of high complexity was associated with higher metabolic costs than one of low complexity in roach *Rutilus rutilis*. Weatherley *et al.* (1982) and Puckett and Dill (1984) demonstrated that unsteady motions were associated with substantial increases in energetic costs compared with steady swimming at the same average speed for rainbow trout *Salmo gairdneri* and coho salmon *Oncorhynchus kisutch* respectively. Webb (1990) attributed the elevated energetic costs of routine swimming (unsteady motions of linear and centripetal acceleration) in rainbow trout compared to steady swimming (relatively constant rectilinear speeds) to additional resistance components associated with acceleration.

There is, therefore, clear evidence that the energy expended by a swimming fish is not only dependent upon swimming speed, but is also strongly influenced by the complexity of the swimming pattern employed. The "routine" and "directed" swimming patterns of Boisclair and Tang (1993) are comparable to swimming patterns displayed by sardine during particulate- and filter-feeding respectively. The increased metabolic costs associated with particulate-feeding are, therefore, a result of the higher complexity of this swimming pattern.

An additional factor which may account for the relatively low cost of filter-feeding is the fact that sardine swim in a tight school when filtering (Chapter 2). When particulate-feeding however, the fish do not school *per se*, but form a loose aggregation (or shoal *sensu* Pitcher 1979) within which they execute independent motions. In addition to reducing predation pressure and facilitating reproduction (Partridge 1982), schooling has also been suggested as a mechanism which confers a hydrodynamic advantage (Weihs 1973, Breder 1976). Each individual fish leaves a vortex trail that leads the fish which is/are following into a series of vortices at a point where water flow is in the direction the fish are swimming (Breder 1976). This results in the fish which follow(s) expending less energy than it/they would in the absence of schooling. However, this advantage only occurs when nearest neighbours are in diagonal positions in the lateral plane, and the lateral distance between fish is less

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than one body length (Blaxter and Hunter 1982). In the current study, school compaction in the lateral plane by filter-feeding sardine was more conspicuous than it was in non- or particulate-feeding fish. Although no data on school structure were collected, lateral inter-fish distance during filter-feeding was certainly less than one body length. It is plausible, therefore, that formation of a compact school during filter-feeding bestows a hydrodynamic advantage upon the fish, hence reducing energy expenditure during this feeding mode. A schooling-derived hydrodynamic advantage resulting in reduced metabolic rates has also been postulated for American shad *Alosa sapidissima* (Ross *et al.* 1992)

This study has demonstrated that filter-feeding is energetically cheaper than particulate-feeding for sardine. At slow swimming speeds, filter-feeding does not appear to increase metabolic costs significantly. Previous experimental work (Chapter 2) has established that sardine filter-feed upon a wide variety of food organisms, ranging from single phytoplankton cells through to macrozooplankton. Although sardine is predominantly a filter-feeder, low concentrations of particles larger than 1230μm total length elicit a particulate-feeding response. These findings indicate that sardine maximize their net energetic gain through prolonged bouts of low-cost filter-feeding. The feeding response flexibility of this species however, allows it to utilize large, scarce food organisms through particulate-feeding.

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Chapter 4:
Nitrogen Excretion and Absorption Efficiencies of Sardine fed with Phytoplankton and Zooplankton Diets

4.1: Introduction

Sardine is predominantly a filter-feeding species which is able to capture food particles down to 17µm in size (Chapter 2), and which maximizes its energy gain through prolonged bouts of energetically cheap filtering (Chapter 3). Sardine stomachs typically contain both phytoplankton and zooplankton prey (Davies 1957, King and Macleod 1976), indicating that this species is therefore morphologically and behaviorally well equipped to utilize both phytoplankton and zooplankton as food sources.

This chapter describes the nitrogen excretion, and absorption efficiencies in terms of dry mass, carbon and nitrogen, of sardine fed phytoplankton and zooplankton diets. These data are required for the construction of carbon and nitrogen budgets for *Sardinops sagax*. The methodology employed here follows that used by Durbin and Durbin (1981) and James *et al.* (1989a) to examine the absorption efficiencies of Atlantic menhaden *Brevoortia tyrannus* and Cape anchovy *Engraulis capensis* respectively, and therefore permits detailed comparisons between these clupeoid species.

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4.2: Material and methods

Laboratory populations of sardine were collected and maintained as described in Chapter 2. Two size classes of adult sardine were used in experiments: large adults were 252.8 ± 19.0 mm total length (*TL*), 136.4 ± 30.7 g wet body mass (*WBM*), and 46.8 ± 14.5 g dry body mass (*DBM*), and small adults were 205.0 ± 11.3 mm *TL*, 64.2 ± 12.5 g *WBM*, and 17.6 ± 3.8 g *DBM* (Table 4.1). Experiments to measure endogenous excretion rates of both ammonia and urea, and experiments where fish were fed either phytoplankton or zooplankton diets, were conducted on both groups (Table 4.1). Fish were deprived of food for 2-5 days prior to use in all experiments.

Experiments were conducted in 2.0 m diameter, 2670 l capacity fibreglass tanks subject to the ambient light regime. During experiments to determine endogenous ammonia and urea excretion rates, water samples were collected every 3 hours over periods of 1 to 4 days during which the fish were not fed. Experiments during which the fish were fed began with measurements of endogenous ammonia and urea production over 3 to 24 hours, after which food was added to the tank. Water and faeces samples were then collected regularly, initially every hour for a 6 to 12 hour period, and then with decreasing frequency over periods of 2 to 6 days after the introduction of food. Three of the experiments in which phytoplankton was offered as food used natural assemblages (primarily *Chaetoceros* spp.) collected from coastal waters with a drift net of 37 µm mesh; in the fourth experiment the benthic diatom *Melosira* spp. was collected from the sand filters of the aquarium facility (Table 4.1). Natural assemblages of zooplankton used in experiments consisted primarily of copepods which were collected using a drift-net of 200 µm mesh. The species composition, ration size, and carbon and nitrogen content of food used in experiments was determined from subsamples (Table 4.1).

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Table 4.1: Summary of information for laboratory experiments on absorption efficiency of *Sardinops sagax*. The starvation time, temperature range, food type, ration size, feeding duration, carbon and nitrogen content of the food, food C:N ratio, and samples collected are listed for each experiment. LA indicates experiments conducted on large adult fish; SA indicates experiments conducted on small adult fish. The mean carbon and nitrogen content and mean C:N ratio of five small adult sardine is also given.

Experiment	Starvation time (d)	Temperature range (°C)	Food type	Ration size (% *DBM*)	Feeding duration (h)	Carbon content (%*DM*)	Nitrogen content (%*DM*)	C:N ratio	Samples collected
LA 4A	5	16.6-21.0	Zooplankton[1]	0.247	1	43.81	10.22	4.29	NH_4, urea, faeces
LA 7A	3	14.8-19.8	Zooplankton[2]	0.875	3	41.07	10.33	3.98	NH_4, urea, faeces
LA 7B	3	15.2-19.9	Zooplankton[2]	1.132	3	41.07	10.33	3.98	NH_4, urea, faeces
LA 8A	3	15.8-20.2	Not fed	-	-	-	-	-	NH_4, urea
LA 8B	3	15.4-20.0	Not fed	-	-	-	-	-	NH_4, urea
LA 9A	3	19.1-21.2	Zooplankton[3]	0.986	2.5	43.80	9.91	4.42	NH_4, urea, faeces
LA 9B	3	19.3-21.2	Zooplankton[4]	0.285	2.5	43.80	9.91	4.42	NH_4, urea, faeces
LA10A	3	17.6-21.8	Not fed	-	-	-	-	-	NH_4, urea
LA 10B	3	18.4-22.0	Not fed	-	-	-	-	-	NH_4, urea
LA 11A	3	15.1-18.9	Not fed	-	-	-	-	-	NH_4
LA 11B	3	16.0-19.0	Not fed	-	-	-	-	-	NH_4
SA 1A	3	16.7-22.0	Not fed	-	-	-	-	-	NH_4, urea
SA 1B	3	16.9-22.0	Not fed	-	-	-	-	-	NH_4, urea
SA 2A	2	15.7-22.5	Phytoplankton[5]	0.929	4	18.35	2.31	7.95	NH_4, urea, faeces
SA 2B	2	16.2-23.0	Zooplankton[6]	0.589	1	41.04	9.85	4.17	NH_4, urea, faeces
SA 3A	2	17.7-21.9	Phytoplankton[7]	0.340	3.5	16.06	3.06	5.25	NH_4, faeces
SA 3B	2	18.0-22.0	Phytoplankton[7]	0.678	3.5	16.06	3.06	5.25	NH_4, faeces
SA 4A	2	19.1-20.8	Not fed	-	-	-	-	-	NH_4
SA 4B	2	19.5-21.1	Not fed	-	-	-	-	-	NH_4
SA 5A	2	16.1-22.1	Not fed	-	-	-	-	-	NH_4
SA 5B	2	16.8-22.0	Phytoplankton[8]	1.132	3	21.47	3.71	5.8	NH_4, faeces
FISH						44.77 ± 1.86	10.64 ± 0.66	4.22	

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Table 1 (cont.)....

[1] Comprising 68% A*cartia africana* and 17% *Calanus agulhensis*.
[2] Comprising 77% small copepods (*Paracalanus* spp. and *Ctenocalanus* spp.) and 16% *Centropages brachiatus*.
[3] Comprising 29% small copepods (*Paracalanus* spp. and *Ctenocalanus* spp.), 18% *Centropages brachiatus*, 17% *Podon* spp. and 17% *Oikipleura* spp.
[4] Comprising 34% *Oikipleura* spp., 19% copepod nauplii, 18% small copepods (*Paracalanus* spp. and *Ctenocalanus* spp.), and 10% *Podon* spp.
[5] Comprising 100% *Melosira* spp.
[6] Comprising 95% A*cartia africana.*
[7] Comprising 84% *Chaetoceros didymis* and 10% *Skeletonema costatum*.
[8] Comprising 48% *Chaetoceros* spp., 33% *Asterionella* spp. and 11% *Skeletonema costatum*.

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Prior to experimentation, the tanks were thoroughly cleaned and flushed with 5 µm-filtered sea water at ambient temperature. The water volume in the tank was reduced to 1000 l in order to facilitate high food concentrations and ensure a good feeding response. The addition of food to the experimental tank elicited a strong feeding response in all experiments, with fish increasing their swimming speed and feeding by either filtering or biting, depending on food type. As food concentrations declined, both swimming speed and the proportion of the shoal feeding decreased. Feeding was considered to have stopped when less than 10% of the shoal was feeding, and at this time uneaten food which had settled onto the bottom of the tank was removed. The water volume in the tank was then increased to 2670 l using 5 µm-filtered sea water at ambient temperature. It was assumed that all food not removed from the tank at the end of the feeding period had been consumed. When phytoplankton was the food source, the amount remaining in suspension at the end of the feeding period was considered to be insignificant compared to that which was ingested or which had settled out.

Sea water was not supplied to the tanks after the termination of feeding, and this resulted in a gradual increase in water temperature over the experimental period. When necessary, the tanks were flushed in order to reduce water temperatures. The increase in temperature during experiments in which the fish were not fed permitted an assessment of the effect of temperature on endogenous excretion rates, and as this was done for both groups of experimental fish, allowed a comparison of endogenous excretion rates for fish of different size.

Water samples were collected using a 100 ml syringe, and were filtered through pre-rinsed Whatman GF/F filters into a clean beaker. All glassware was acid washed. Triplicate 5 ml subsamples for ammonia and urea analysis were stored in clean borosilicate test tubes at -20 °C until

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processed. Ammonia and urea concentrations were determined following the methods described by Koroleff (1983), scaled down to a 5 ml sample volume. All determinations were carried out in triplicate.

Faeces were collected through siphoning into a clean 20 l bucket, and the water removed from the tank was returned by back-filtration through a 63 µm mesh. Collected faeces were rinsed in distilled water, concentrated onto pre-weighed Whatman GF/F filter papers through filtration under a low vacuum, and dried for 24 h at 60 °C. Faeces dry mass was determined to the nearest 0.1 mg using a Sartorius 2462 electrobalance, and the carbon and nitrogen content of each faeces sample was determined using a Leco CHNS 932 analyser. Dry mass, carbon and nitrogen absorption efficiencies were calculated from the total amounts of each constituent in the faeces and that available in the food using the following expression:

$$\% \text{ absorption efficiency} = \frac{\text{component}_{food} - \text{component}_{faeces}}{\text{component}_{food}} * 100 \qquad (1)$$

Experiments to determine the relative contribution of ammonia to the total nitrogen excreted by sardine were conducted in a 3 m^3 glass display tank containing approximately 300 subadult sardine of 30-40 g *WBM.* One experiment was performed on unfed fish, and a second was done on fish which had been fed mysids *Mysodopsis major*. Water samples were collected every 15 minutes and were analysed for ammonia using the methods described above. Total dissolved organic nitrogen (T-DON) was determined using the method of Nydahl (1978). Because the total mass of sardine in the tank was not determined, absolute total nitrogen and ammonia excretion rates could not be calculated. The relative contribution made by ammonia to the total nitrogen excreted was estimated by regressing ammonia and T-DON concentrations against time, and dividing the T-DON slope value by the ammonia slope value.

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4.3: Results

Endogenous ammonia and urea excretion

Large-scale changes in ammonia concentrations in the experimental tanks meant that its excretion rate between subsequent samples could be accurately determined. No statistically significant relationship between endogenous ammonia excretion rate and temperature (range = 15.0 to 22.1 °C) was observed for fish in either of the experimental groups. A two-sample t-test to compare endogenous ammonia excretion rate across the temperature range for each group indicated no significant difference between groups ($t < 0.001$). The data for both groups were therefore combined, giving a mean endogenous ammonia excretion rate ± 95% CL of 19.28 ± 1.30 µg $N.g^{-1}$ *DBM*.h^{-1} at a mean temperature of 19.1 °C.

Owing to the high variability in the urea data, less confidence could be placed in the estimation of urea excretion rates. Endogenous urea excretion rate was determined by regressing urea concentration in the tank (expressed as µg urea.g^{-1} *DBM*) against time, and using the slope parameter of significant regressions to estimate excretion rate. Estimated endogenous urea excretion rates ranged from 1.06 to 3.33 and had a mean value (± 95% CL) of 2.46 ± 0.87 µg $N.g^{-1}$ *DBM*.h^{-1}.

Significant ($p < 0.05$) regressions between ammonia concentration and time, and between T-DON concentration and time were obtained from both experiments to determine the relative contribution of ammonia to total nitrogen excretion. Ammonia constituted 68.6% of the total nitrogen excreted by unfed fish, and 75.3% for fish fed mysids. The mean endogenous ammonia excretion rate of 19.28 ± 1.30 µg $N.g^{-1}$ *DBM*.h^{-1} is therefore equivalent to a total nitrogen excretion rate of 28.11 ± 1.90 µg $N.g^{-1}$ *DBM*.h^{-1}. The total nitrogen:ammonia ratio of 1.328 determined for fish which had been

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fed mysids was used to estimate the total nitrogen excretion for all experiments during which the fish were fed.

Exogenous nitrogen excretion

Exogenous nitrogen excretion was calculated by subtracting the endogenous nitrogen excretion (28.11 µg $N.g^{-1}$ *DBM*.h^{-1}) from the total nitrogen excretion (ammonia excretion multiplied by 1.328) during the period of elevated excretion following feeding. Elevated excretion was defined as the period during which excretion levels exceeded the upper 95% confidence limit of the endogenous rate.

Ammonia excretion rates followed a similar pattern in all experiments where fish were fed, increasing above endogenous levels within one hour after the introduction of food, reaching a peak level, and declining thereafter. For fish fed phytoplankton, peak ammonia excretion rates of 60 to 90 µg $N.g^{-1}$ *DBM*.h^{-1} occurred 1.5 to 5.0 (mean = 2.9 ± 1.5) hours after the initiation of feeding (Figure 4.1). Excretion rates returned to endogenous levels 4.5 to 13.0 (mean = 9.1 ± 3.5) hours after the initiation of feeding. Ammonia excretion rates for fish fed zooplankton were higher and peaked sooner after the initiation of feeding than those in experiments where phytoplankton was the food. Peak excretion rates of fish fed zooplankton were observed 0.5 to 3.0 (mean = 1.6 ± 0.9) hours after the initiation of feeding and ranged from 45 to 195 µg $N.g^{-1}$ *DBM*.h^{-1} (Figure 4.2). Excretion rates returned to endogenous levels 2.5 to 20.0 (mean = 10.9 ± 6.1) hours after the initiation of feeding.

Despite differences in the timing and levels of peak ammonia excretion rates between fish fed phytoplankton and zooplankton, food type had no effect (t-test; $p < 0.05$) on the times to 50% and 90% exogenous nitrogen excretion respectively. The time required for 50% of the exogenous nitrogen

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excretion was 2.2±1.0 hours after the mid-point of feeding, and that required for 90% of the exogenous nitrogen excretion was 7.4±3.6 hours.

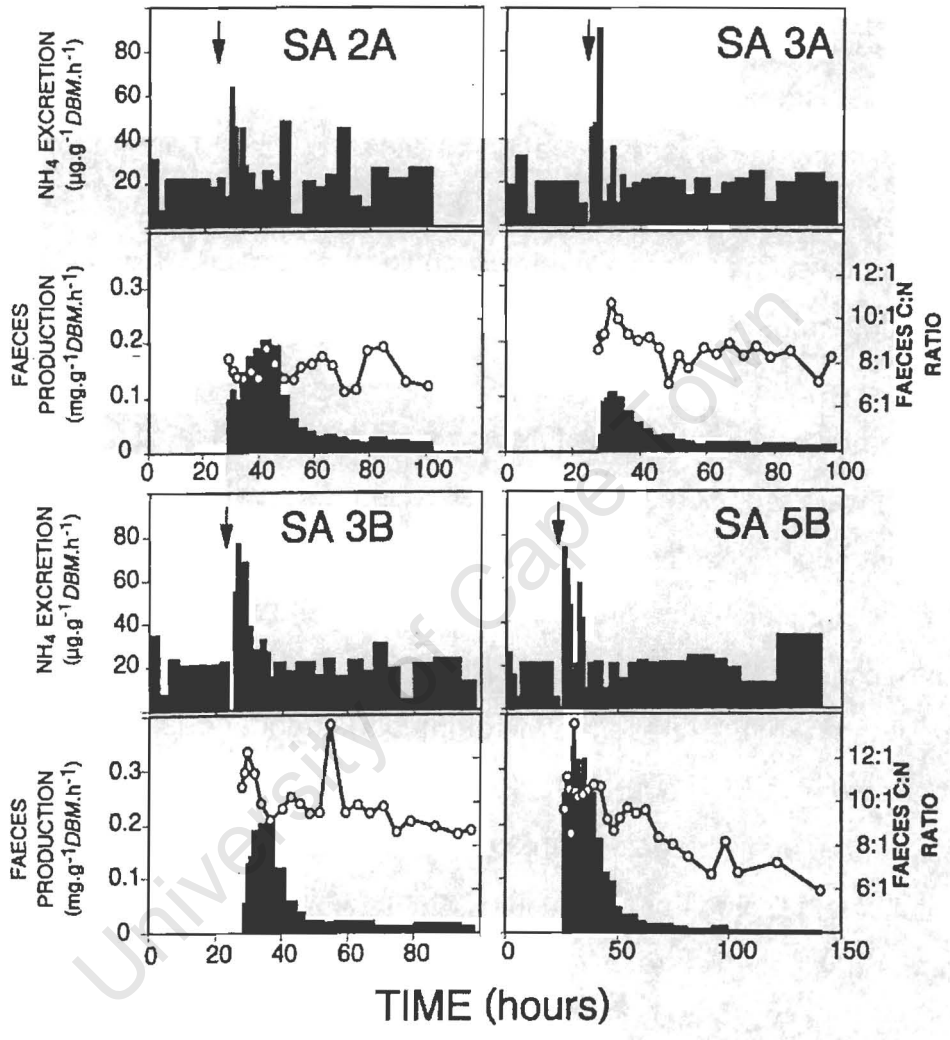

Figure 4.1: Ammonia excretion rate (histogram; µg $N.g^{-1}$ *DBM*.h^{-1}), faeces production rate (histogram; mg dry $mas.g^{-1}$ *DBM*.h^{-1}) and faeces C:N ratio (**O** and line) during experiments in which sardine were fed with phytoplankton. Arrows indicate the initiation of feeding.

A significant, linear relationship between peak ammonia excretion rate and nitrogen ration was observed (Figure 4.3), and had the form:

$$y = 0.088x + 51.3 \ (n = 10; r^2 = 0.40; p < 0.05) \qquad (2)$$

where y is peak ammonia excretion rate in µg $N.g^{-1}$ *DBM*.h^{-1} and x is ingested ration size (µg $N.g^{-1}$ *DBM*).

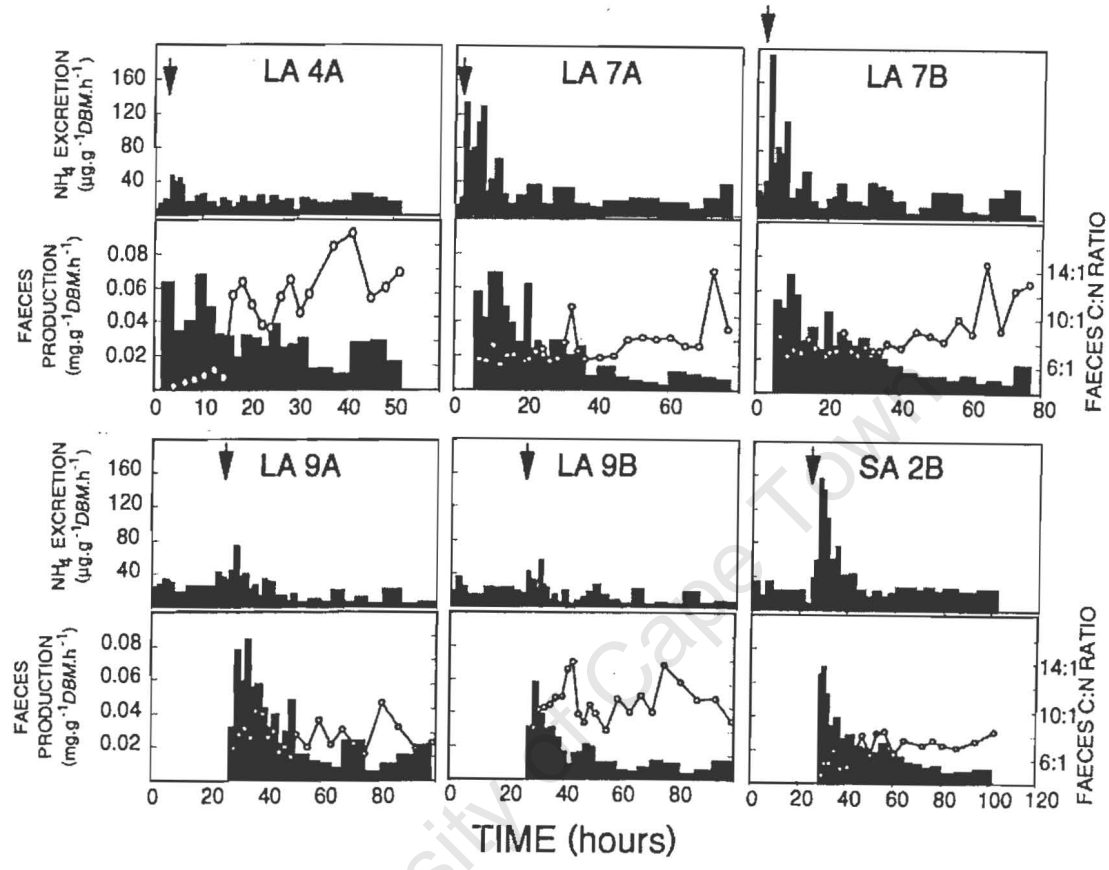

Figure 4.2: Ammonia excretion rate (histogram; µg $N.g^{-1}$ *DBM*.h^{-1}), faeces production rate (histogram; mg dry mas.g^{-1} *DBM*.h^{-1}) and faeces C:N ratio (**O** and line) during experiments in which sardine were fed with zooplankton. Arrows indicate the initiation of feeding.

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Significant relationships were also observed between the total exogenous nitrogen excretion (e_N; mg.g^{-1} *DBM*) and the total nitrogen in both the ingested (R_N; mg.g^{-1} *DBM*) and the absorbed (pR_N; mg.g^{-1} *DBM*) rations (Figure 4.4). These regressions were forced through the origin to ensure that they adhered to theoretical considerations, namely that zero ingestion results in zero exogenous excretion. The least squares linear regressions were:

$$e_N = 0.698 \pm 0.111\ R_N\ (n = 10;\ r^2 = 0.48;\ p<0.03) \quad (3)$$

$$e_N = 0.744 \pm 0.121\ pR_N\ (n = 10;\ r^2 = 0.45;\ p<0.03) \quad (4).$$

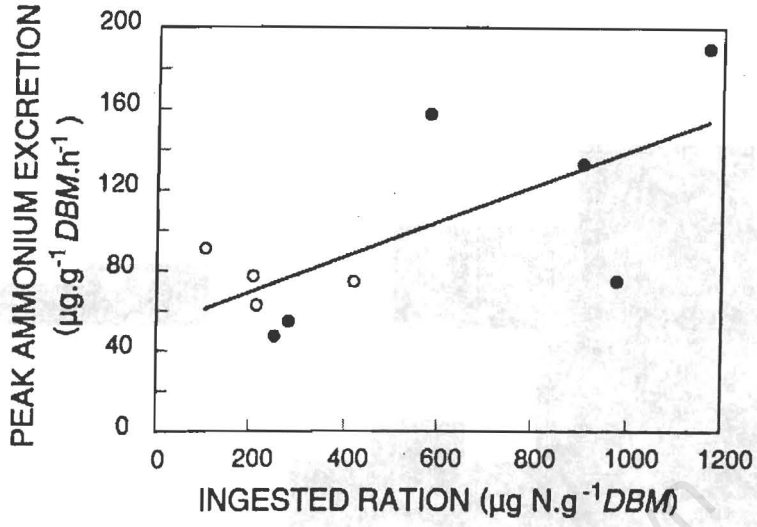

Figure 4.3: Relationship between peak ammonium excretion rate after feeding (µg N.g^{-1} *DBM*.h^{-1}) and ingested nitrogen ration (µg N.g^{-1} *DBM*) for sardine. Data from experiments in which phytoplankton was used as food are indicated by an open circle (O) and those from experiments with zooplankton are indicated by a closed circle (●). A linear regression is fitted to the data.

Regression equations (3) and (4) indicate that 69.8 ± 11.1% of the nitrogen in the ingested ration and 74.4 ± 12.1% of the nitrogen in the assimilated ration was excreted. In conjunction with the estimated daily endogenous nitrogen excretion rate (0.028 * 24 = 0.675 mg N.g^{-1} *DBM*.d^{-1}), equations (3) and (4) may be used to estimate the daily maintenance ration (i.e. zero net growth) required by sardine. Re-arranging equation (3) gives:

$$r_N = 0.302R_N \qquad (5)$$

where r_N is nitrogen retained by the fish (mg N.g^{-1} *DBM*). For zero net growth during one day, sufficient nitrogen must be ingested to supply that which is excreted endogenously, i.e.:

$$0.302R_d = 0.675 \qquad (6)$$

so:

$$R_d = (0.675/0.302) = 2.24 \text{ mg N.g}^{-1} \textit{DBM}.\text{d}^{-1} \qquad (7)$$

where R_d is the ingested daily maintenance ration. Similarly, absorbed daily maintenance ration can be estimated:

$$pR_d = (0.675/0.256) = 2.64 \text{ mg N.g}^{-1} \textit{DBM}.\text{d}^{-1} \quad (8)$$

For zero net growth, i.e. no gain or loss in nitrogen, sardine require an ingested ration of 2.24 mg N.g^{-1} *DBM*.d^{-1}, equivalent to 2.11% of their body nitrogen per day, and an absorbed ration of 2.64 mg N.g^{-1} *DBM*.d^{-1}, equivalent to 2.48% of their body nitrogen per day.

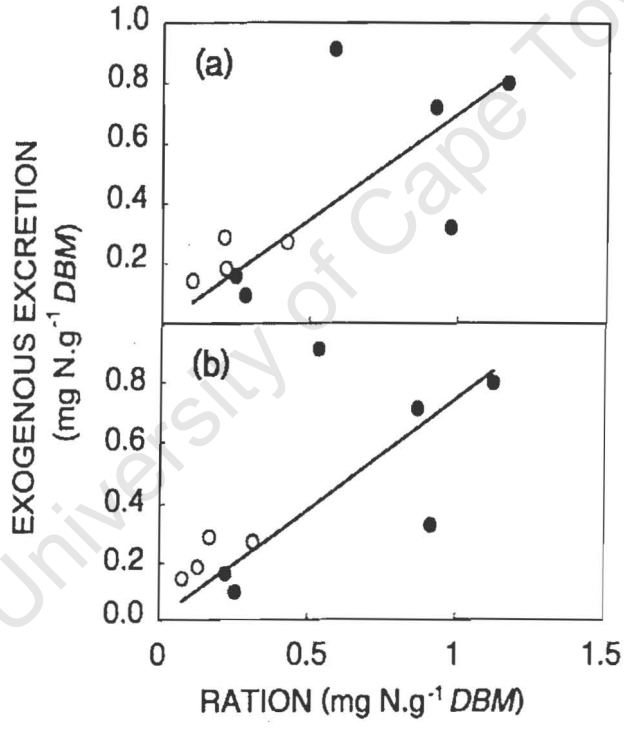

Figure 4.4: Relationships between exogenous nitrogen excretion (mg N.g^{-1} *DBM*.h^{-1}) and (a) ingested and (b) absorbed nitrogen ration (µg N.g^{-1} *DBM*) for sardine. Data from experiments in which phytoplankton was used as food are indicated by an open circle (**O**) and those from experiments with zooplankton are indicated by a closed circle (●). Linear regressions are fitted to the data.

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Faeces elimination

Sardine faeces were cohesive, robust and easy to collect. Faeces from fish fed phytoplankton were brown-green in colour, whereas those from fish fed zooplankton were red-brown. For fish fed phytoplankton, faecal elimination rates increased from an initial low rate to a peak 5.0 to 17.0 (mean = 8.9 ± 5.5) hours after the midpoint of feeding (Figure 4.1). Peak faecal elimination rates for fish fed phytoplankton ranged from 0.11 to 0.35 $mg.g^{-1}$ *DBM*.h^{-1}, and elimination rates declined exponentially from peak values for 12 to 25 hours, after which they continued at a low (0.01 to 0.02 $mg.g^{-1}$ *DBM*.h^{-1}), constant rate for the duration of the experiment (Figure 4.1). For fish fed zooplankton, faecal elimination rates were much lower, were less variable, and increased more rapidly from initial low rates to peak levels. Peak faecal elimination rates for fish fed zooplankton occurred 3.5 to 7.0 (mean = 6.2 ± 2.0) hours after the midpoint of feeding (Figure 4.2), and ranged from 0.06 to 0.08 $mg.g^{-1}$ *DBM*.h^{-1}. An exponential decline from peak rates was evident for 27.5 to 37 hours, after which faeces continued to be eliminated at a low (0.005 to 0.02 $mg.g^{-1}$ *DBM*.h^{-1}) rate for the rest of the experiment.

The coefficient of the exponential decline in faecal elimination rates was estimated by regressing the natural log of faeces elimination rate against time over the period of exponential decline. Significant ($p < 0.01$) linear regressions were obtained for all experiments. The period of exponential decline was much shorter for fish fed phytoplankton (mean = 16.5 ± 5.8 hours) than for those fed zooplankton (mean = 32.8 ± 3.6 hours), and the coefficients of the exponential decline in faecal elimination rates were higher and were more variable for fish fed phytoplankton (mean = -0.105 ± 0.043.h^{-1}) compared to those fed zooplankton (mean = -0.048 ± 0.013.h^{-1}).

Elimination of the meal was much slower than the excretion of dissolved nitrogen from the ration for fish fed either zooplankton or

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phytoplankton. Despite the difference in faecal elimination rates between fish fed different diets, food type had no effect on the time required to eliminate 50% and 90% of the faeces produced; the mean time to 50% elimination was 13.0 ± 4.1 hours, and that required for 90% elimination was 50.8 ± 8.3 hours.

Despite some variability in the faeces C:N ratio data (Figures 4.1 and 4.2), significant trends in this ratio over time were observed in seven of the 10 experiments conducted (Table 4.2). In three of the four experiments in which fish were fed phytoplankton, the faeces C:N ratio showed a similar and significant decrease over the duration of the experiment (Figure 4.1; Table 4.2), declining from a ratio of approximately 11:1 to 9:1. The single phytoplankton experiment during which the C:N ratio did not change over time was that where *Melosira* spp. was used as the food organism. This decline in C:N ratios over time indicates that either the efficiency of carbon absorption from the faeces increased, or the efficiency of nitrogen absorption decreased.

Table 4.2: Regression parameters including sample size, r^2 value, significance level and slope value ± standard error (C:N ratio.h^{-1}) for the equations relating faecal C:N ratios to time for sardine fed with phytoplankton and zooplankton diets. NS indicates not significant.

Food type	Experiment	n	r^2	p	Slope
Zooplankton	LA 4A	20	0.63	0.001	0.221 ± 0.038
Zooplankton	LA 7A	26	0.32	0.005	0.046 ± 0.013
Zooplankton	LA 7B	26	0.53	0.001	0.068± 0.013
Zooplankton	LA 9A	22	-0.05	NS	-
Zooplankton	LA 9B	22	-0.04	NS	-
Zooplankton	SA 2B	18	0.39	0.005	0.033 ± 0.009
Phytoplankton	SA 2A	20	-0.03	NS	-
Phytoplankton	SA 3A	21	0.36	0.005	-0.025 ± 0.007
Phytoplankton	SA 3B	21	0.35	0.005	-0.036 ± 0.011
Phytoplankton	SA 5B	25	0.48	0.001	-0.044 ± 0.009

In contrast, the faeces C:N ratios for fish fed zooplankton significantly increased over the duration of the experiment in four of the six experiments

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(Figure 4.2; Table 4.2). For three of these experiments the regressions were similar, increasing from 5:1 to 9:1 (Figure 4.5). In the case of experiment LA 4A, the C:N ratio increased markedly to 15:1. This increase in the C:N ratio during the experiment suggests that either the efficiency of nitrogen absorption increased, or the efficiency of carbon absorption decreased, over this time period.

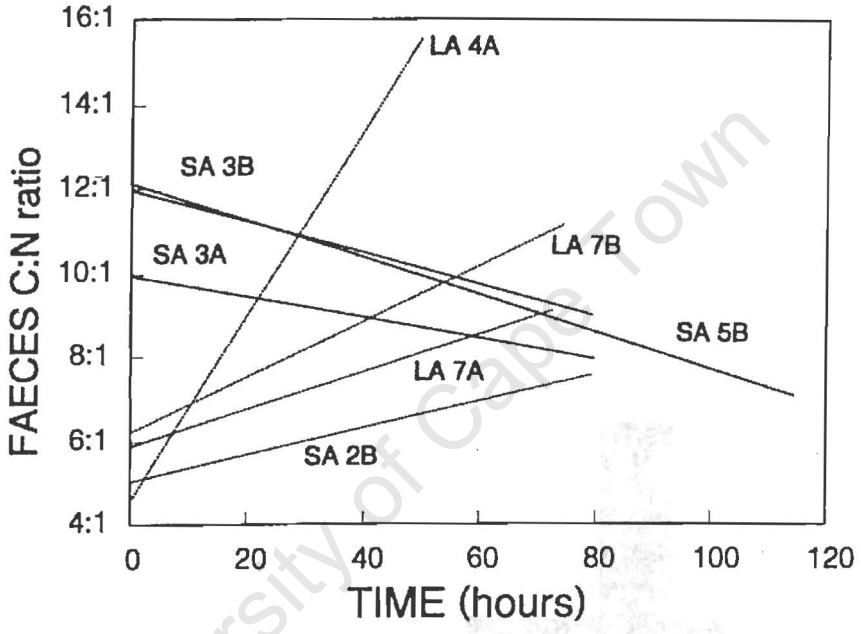

Figure 4.5: Linear regressions of faeces C:N ratio as a function of time for experiments where a significant relationship was found between these two variables (see Table 4.2). Regressions from experiments in which phytoplankton was used as food are indicated by a solid line and those from experiments with zooplankton are indicated by a dotted line.

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Absorption efficiencies

Overall dry mass, carbon and nitrogen absorption efficiencies for sardine fed phytoplankton and zooplankton were calculated using equation (1). In all experiments nitrogen absorption efficiencies exceeded those for carbon, and both were higher than the dry mass absorption efficiencies (Table 4.3). There was little variation in the dry mass and carbon absorption efficiencies for experiments during which the fish were fed phytoplankton. However, a low nitrogen absorption efficiency of 60.1% was calculated when

Melosira spp. was the food source, compared to values ranging from 75.2 to 83.2% when planktonic diatoms were used as food. Because *Melosira* spp. is a tachypelagic genus, being primarily benthic but occasionally found in the plankton (Cupp 1943), and rare in southern African waters (Taylor 1964), it is unlikely to form part of the sardine's diet in the field. Absorption efficiency data for sardine fed this diatom were therefore not included when estimating mean absorption efficiencies. Mean absorption efficiencies of fish fed pelagic diatoms were 42.6, 62.6 and 78.7% for dry mass, carbon and nitrogen respectively (Table 4.3).

Table 4.3: Dry mass, carbon and nitrogen absorption efficiencies (%) of sardine fed with zooplankton and phytoplankton diets. Mean absorption efficiencies (± one standard deviation) for phytoplankton and zooplankton are given.

Experiment	Food type	Dry mass	Carbon	Nitrogen
LA 4A	Zooplankton	76.7	90.0	92.0
LA 7A	Zooplankton	83.9	89.8	94.3
LA 7B	Zooplankton	86.3	93.0	96.6
LA 9A	Zooplankton	80.4	88.9	93.4
LA 9B	Zooplankton	60.9	79.3	90.8
SA 2B	Zooplankton	77.4	88.4	92.4
Average		77.6 ± 9.0	88.2 ± 4.7	93.3 ± 2.0
SA 3A	Phytoplankton	42.2	62.6	77.8
SA 3B	Phytoplankton	39.5	68.2	83.2
SA 5B	Phytoplankton	46.2	57.0	75.2
Average		42.6 ± 3.4	62.6 ± 5.6	78.7 ± 4.1
SA 2A	Algae	51.3	60.1	60.1

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Absorption efficiencies for sardine fed zooplankton also showed little variation, with the exception of the dry mass absorption efficiency estimated for experiment LA 9B (Table 4.3). Mean absorption efficiencies of fish fed zooplankton were 77.6, 88.2 and 93.3% for dry mass, carbon and nitrogen respectively (Table 4.3). The mean dry mass, carbon and nitrogen absorption efficiencies were significantly higher for sardine fed zooplankton than for

those fed phytoplankton ($t_{dry\ mass}$ = 8.43, $p<0.001$; t_{carbon} = 6.83, $p<0.01$; $t_{nitrogen}$ = 5.81, $p< 0.05$).

4.4: Discussion

Like other marine teleosts, *Sardinops sagax* is predominantly ammoniotelic (Handy and Poxton 1993), with ammonia constituting 68.6% of the total nitrogen excreted by unfed fish, and 75.3% for fish fed on mysids. Endogenous excretion rates determined for sardine (19.28 and 2.46 µg $N.g^{-1}$ *DBM*.h^{-1} for ammonia-N and urea-N respectively) are comparable to those of other clupeoids (McCarthy and Whitledge 1972, Durbin and Durbin 1981, James *et al.* 1989a). The endogenous ammonia excretion rate for sardine lies between those of menhaden and Cape anchovy, species for which excretion rates were determined using similar methodology to that employed in this study and between which comparisons are therefore valid. Menhaden are large (101g *DBM*), sardine are medium-sized (33g *DBM*) and Cape anchovy are small (3g *DBM*), and the decrease in endogenous ammonia excretion rates with increasing size across this group of clupeoids most probably reflects a size-specific decline in metabolic rate.

Neither temperature nor fish size affected endogenous excretion rates of sardine in this study, although small fish have faster excretion rates than large fish and excretion rates increase with temperature (Handy and Poxton 1993, Jobling 1994). It may be that the size difference between the two experimental groups of fish used here was too small to produce a notable size-related effect, but the lack of a significant increase in ammonia excretion rate over a 7°C range is surprising. This may imply a high degree of eurythermy by sardine, as has been previously indicated by the relatively low oxygen consumption Q_{10} value of 1.82 over 10-22° for this species (Chapter 3).

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The elevation of nitrogen excretion rates shortly after feeding has been reported for several fish species (Brett and Zala 1975, Savitz *et al.* 1977, Davenport and Sayer 1986, Sayer 1988, Du Preez and Cockroft 1988a, 1988b, Handy and Poxton 1993, Jobling 1994). For *Sardinops sagax*, ammonia excretion rates after feeding on phytoplankton were 3.5 times endogenous levels, whereas rates of fish fed zooplankton were almost 10 times endogenous levels. James *et al.* (1989a) reported elevated ammonia excretion rates of up to 600 µg $N.g^{-1}$ *DBM*.h^{-1} for Cape anchovy fed on zooplankton, a 25-fold increase from endogenous levels, and Durbin and Durbin (1981) reported elevated ammonia excretion rates of 120 µg $N.g^{-1}$ *DBM*.h^{-1} for Atlantic menhaden fed on phytoplankton, a 16-fold increase from endogenous levels. The significant linear relationship between peak nitrogen excretion rate and nitrogen ration observed here for sardine has previously been reported by Jobling (1981a) for young plaice *Pleuronectes platessa*, and also by Ramnarine *et al.* (1987) for juvenile Atlantic cod *Gadus morhua*. Since the physiological mechanisms governing nitrogen excretion are likely to have a maximum capability, it has been suggested that an asymptotic relationship would best describe this relationship (Jobling 1981a, Ramnarine *et al.* 1987). The linear relationship reported here for sardine would suggest that ration sizes used were too small to reach asymptotic levels in nitrogen excretion.

Sardine excreted a constant proportion of nitrogen from the ingested (69.8 ± 11.1%) and absorbed (74.4 ± 12.1%) rations. Similar relationships have been reported for other fish species (Gerking 1971, Savitz *et al.* 1977, Weisburg and Lotrich 1982), and for the other clupeoids studied (Durbin and Durbin 1981, James *et al.* 1989a). Atlantic menhaden also excreted more than half of their ingested and absorbed rations (61.6% and 65.5% respectively; Durbin and Durbin 1981), whereas Cape anchovy were more efficient at retaining nitrogen, and excreted only 41.5% of the ingested and 47.8% of the absorbed ration (James *et al.* 1989a). The absorbed daily

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maintenance ration of 2.64 mg $N.g^{-1}$ *DBM*.d^{-1} required by sardine is higher than that estimated for either Atlantic menhaden or Cape anchovy (0.70 and 2.17 mg $N.g^{-1}$ *DBM*.d^{-1} respectively), and appears to contradict the endogenous excretion data which reflected a decreasing metabolic rate with increasing size. However, this difference may be a result of the poor estimation of the slope of the regression between exogenous excretion and ration determined in this study.

Faecal elimination rates of sardine were affected by food type. Rates were higher but declined more rapidly for fish fed phytoplankton, whereas the lower elimination rates for fish fed zooplankton declined over a longer period of time. The times to 50% and 90% faeces elimination were not affected by either food type or ration size. Peak faecal elimination rates for sardine (0.06 to 0.35 $mg.g^{-1}$ *DBM*.h^{-1}) are lower than those reported for either Atlantic menhaden (0.7 to 2.0 $mg.g^{-1}$ *DBM*.h^{-1}; Durbin and Durbin 1981) or Cape anchovy (0.2 to 1.4 $mg.g^{-1}$ *DBM*.h^{-1}; James *et al.* 1989a), and are likely to be a result of small ration size.

The effect of food type on faeces C:N ratios observed here, with faeces from sardine fed phytoplankton showing a declining trend during the course of an experiment whereas those from fish fed zooplankton showed an increasing trend, has not been reported elsewhere. James *et al.* (1989a) reported that the C:N ratios of Cape anchovy faeces declined during most experiments, and did not note any food type effect. By contrast, Harris (1991) found that the C:N ratios of faeces from white steenbras *Lithognathus lithognathus* fed a formulated diet increased during the course of an experiment. Faeces C:N ratios were higher than those of the corresponding food C:N ratios for Atlantic menhaden fed on either phytoplankton or zooplankton (Durbin and Durbin 1981), although these authors gave no information concerning whether C:N ratios changed during the experiment.

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Because the ash content of faeces was not measured in the present study, changes in the absorption efficiency of carbon and nitrogen during the course of an experiment could not be measured as was done by Durbin and Durbin (1981) and James *et al.* (1989a). However, a declining C:N ratio over time indicates a decrease in the efficiency of nitrogen absorption, whereas an increasing ratio indicates an increase in the efficiency of nitrogen absorption.

Sardine have higher absorption efficiencies for nitrogen than for carbon regardless of food type, a response shared by Cape anchovy and Atlantic menhaden. Sardine also absorb both elements more efficiently from zooplankton than from phytoplankton. Food type has no effect on nitrogen or carbon absorption by menhaden, but anchovy fed phytoplankton have similar nitrogen but lower carbon absorption efficiencies than those fed zooplankton (Table 4.4).

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Table 4.4: Mean carbon and nitrogen absorption efficiencies (% ± one standard deviation) of sardine *Sardinops sagax* (this study) anchovy *Engraulis capensis* (James *et al.* 1989a) and menhaden *Brevoortia tyrannus* (Durbin and Durbin 1981) fed with phytoplankton and zooplankton diets. Values with the same superscript are not significantly different from each other, as assessed using the Kruskal-Wallace analysis of variance with ranks and with $p < 0.05$. The number of experiments used to determine the mean values is given in brackets.

Species	Zooplankton carbon	Zooplankton nitrogen	Phytoplankton carbon	Phytoplankton nitrogen
Sardine	88.2 ± 4.7^{a} (6)	93.3 ± 2.0^{b} (6)	62.6 ± 5.6^{c} (3)	78.7 ± 4.1^{e} (3)
Anchovy	77.9 ± 7.2^{a} (10)	87.4 ± 4.3^{b} (10)	50.6 ± 0.7^{c} (2)	83.2 ± 1.8^{e} (2)
Menhaden	86.7 ± 0.4^{a} (3)	91.3 ± 0.9^{b} (3)	86.4 ± 3.2^{d} (7)	92.4 ± 2.0^{f} (7)

No significant ($p < 0.05$) differences were observed between zooplankton-derived carbon and nitrogen absorption efficiencies of sardine, anchovy and menhaden (Kruskal-Wallace analysis of variance by ranks [Zar 1984]; Table 4.4), whereas significant differences were observed for

phytoplankton-derived carbon and nitrogen absorption efficiencies between species. When fed phytoplankton, menhaden had higher carbon and nitrogen absorption efficiencies than sardine or anchovy, whereas sardine and anchovy showed similar absorption efficiencies on this diet. Because of the small size of the data sets however, a rigorous statistical analysis could not be performed, and observations regarding the relative absorption efficiency of these species should be regarded as tentative.

That menhaden appear to be the most efficient species at utilizing phytoplankton seems reasonable, because this species is an obligate filter-feeder which consumes substantial quantities of phytoplankton and is able to retain particles of 13-16µm (Durbin and Durbin 1975). The absorption efficiency data presented here would imply that sardine are a primarily carnivorous species, as they have higher absorption efficiencies for both carbon and nitrogen when fed zooplankton compared to phytoplankton. Whereas crustacean zooplankton do form a significant component of the sardine's diet both locally (Davies 1957, King and Macleod 1976) and globally (Hand and Berner 1959, Alamo and Bouchon 1987), substantial quantities of phytoplankton in the stomach of this species have also been recorded by those authors. Sardine are thus clearly omnivorous, and the relative dietary importance of phytoplankton and zooplankton is likely to vary both spatially and temporally. Compared to Cape anchovy, which cannot capture food particles smaller than 200 µm (James and Findlay 1989), sardine can entrap particles of down to 17µm (Chapter 2), and are therefore better able to utilize phytoplankton blooms when they encounter them. Although both species have similar absorption efficiencies for phytoplankton, this difference in small particle capture efficiency means that phytoplankton are likely to be more significant in the diet of sardine than in that of Cape anchovy.

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The results reported here will be used to construct carbon and nitrogen budgets for *Sardinops sagax*, as has been done using similar methodology for Cape anchovy (James *et. al* 1989b) and Atlantic menhaden (Durbin and Durbin 1983). The development of such experimentally-derived budgets can provide valuable insights regarding the trophic position of sardine in the southern Benguela upwelling system, and will permit a quantification of how changes in the fish's trophic environment impact upon growth.

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Chapter 5:
Gastric Evacuation, Feeding Periodicity and Daily Ration of Sardine in the Southern Benguela Upwelling Ecosystem

5.1: Introduction

The epipelagial region of the Southern Benguela is dominated by three clupeoids: anchovy *Engraulis capensis*, sardine *Sardinops sagax* and round-herring *Etrumeus whiteheadi*. Together, these species form the bulk of purse-seine catches which have fluctuated between 135 000 and 676 000 metric tons during the period 1950-1993 (Roel and Armstrong 1991, Chief Director of Sea Fisheries 1995). These species are not only commercially important but, because of their low position on the food chain, they also play a significant role in energy flow to higher trophic levels (Cushing 1978, James 1988b), which include predators such as seals and seabirds (Crawford *et al.* 1992).

Information is available on the feeding ecology of anchovy (James 1987, James and Findlay 1989, James and Probyn 1989, James *et al.* 1989a), but such information is lacking for round herring and is limited for sardine. Sardine from the west coast of South Africa and the Namibian coast appear to be phytoplanktivorous filter-feeders (Davies 1957, King and Macleod 1976) and, although they are capable of particulate-feeding, they maximize their net energetic gain through prolonged bouts of low-cost filter-feeding (Chapters 2 and 3). Laboratory experiments conducted to examine absorption efficiencies of sardine fed phytoplankton and zooplankton diets suggests that whilst omnivorous, this species derives more of its nutritional requirements from carnivory than from herbivory (Chapter 4). This chapter describes the gastric evacuation and feeding periodicity of sardine, and provides estimates of the daily ration for this species in the southern Benguela.

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5.2: Material and methods

Gastric evacuation

Both laboratory and field experiments were performed to examine patterns and estimate rates of gastric evacuation in sardine. Laboratory experiments were performed on adult sardine that had been acclimatized to laboratory conditions for at least two months. Field experiments were performed in Walker Bay (34°35'E 19°04'S) aboard the *F.R.S. Africana* during a cruise on the Western Agulhas Bank in September 1994.

Laboratory experiments were performed in a 3000l fibreglass tank supplied with a continuous flow of 5µm-filtered sea water at ambient temperature (Table 5.1). Temperature was monitored hourly during each experiment. Fish were deprived of food for 3-5 days prior to use in an experiment. Six laboratory experiments were conducted using different food organisms (Table 5.1). Prior to an experiment five 1l subsamples of the food organisms were collected for identification and the determination of food particle size.

Addition of food to the tank elicited an immediate feeding response; particulate-feeding on large zooplankton and filter-feeding on diatoms and small zooplankton. Fish were allowed to feed for periods of 0.5 to 1.5h, depending upon food type and concentration. Thereafter the tank was flushed and uneaten food was siphoned out (t = 0). At t = 0 and at regular intervals thereafter, three to five fish were removed from the tank and rapidly killed by an overdose of anaesthetic (MS222 or ethylene-glycol-monophenyl-ether). Total length (*TL*, mm) and wet body mass (*W*, g) were recorded, and fish stomachs, from the anterior end of the oesophagus to the junction of the pyloric stomach and pyloric caecae, were excised and preserved in 5% buffered formalin.

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Table 5.1: Summary of information for laboratory and field gastric evacuation rate experiments on sardine, including starvation time (Starv.), mean total length (*TL*), mean wet body mass (*W*), mean water temperature during the experiment (Temp.), food organism composition and mean food particle size. One standard deviation is given with all mean values.

Expt #	# of fish	Starv. time (days)	*TL* (mm)	*W* (g)	Temp (°C)	Feeding Period (hour)	Food organism	Estimated ration (%*W*)	Particle size (µm)
Lab. A1	18	5	260.6 ± 9.0	150.4 ± 19.9	17.7 ± 0.1	1	*Mysidopsis major*	4.09	7683 ± 1329
Lab. A2	15	3	248.5 ± 12.7	126.5 ± 19.1	16.8 ± 0.1	2	Diatoms[1]	3.28	117 ± 56
Lab. B1	40	5	206.8 ± 10.4	67.1 ± 11.8	14.6 ± 0.6	1.5	Diatoms[2]	0.92	54 ± 46
Lab. B2	40	5	204.2 ± 13.8	63.0 ± 15.0	14.6 ± 0.4	0.5	Zooplankton[3]	3.42	862 ± 363
Lab. B3	31	4	203.0 ± 11.2	61.9 ± 12.0	15.0 ± 0.5	1	Zooplankton[4]	1.88	776 ± 848
Lab. B4	40	3	205.8 ± 11.6	65.2 ± 12.8	17.8 ± 0.2	1	Zooplankton[5]	7.92	1497 ± 1235
Fld. 1S	106	?	157.0 ± 7.8	28.2 ± 4.1	15.1 ± 0.4	?	Mixed plankton[6]	?	206 ± 187
Fld. 1L	39	?	199.1 ± 12.5	62.2 ± 13.1	15.1 ± 0.4	?	Mixed plankton[6]	?	206 ± 187
Fld. 2L	89	?	189.8 ± 10.5	51.6 ± 7.7	14.9 ± 0.2	?	Mixed plankton[7]	?	190 ± 183

[1] Comprising 95% *Skeletonema costatum* chains.
[2] Comprising 70% *Skeletonema costatum* chains, and *Chaetoceros* spp., *Asterionella* spp. and *Nitschia* spp.
[3] Comprising 64% *Oithonia* spp., 18% *Centrophages brachiatus* and 11% small copepods (*Paracalanus* spp., *Clausocalanus* spp. and *Ctenocalanus* spp.
[4] Comprising 86% *Oithona* spp., 4% *Calanoides carinatus* and 3% small copepods.
[5] Comprising 64% *Centrophages brachiatus*, 19% *Calanoides carinatus* and 9% small copepods.
[6] Comprising 38% *Coscinodiscus* spp., 25% *Peridinium* spp. and 13% crustacean eggs and nauplii.
[7] Comprising 50% *Coscinodiscus* spp., 18% *Peridinium* spp. and 9% crustacean eggs and nauplii.

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Field experiments were performed in a 3000l aluminium tank supplied with a continuous flow of 60l·min^{-1} of sea water. A Hugrun® Seamon underwater temperature recorder (UTR-A) placed in the tank recorded temperature every 5 minutes. Two field experiments were performed on fish collected using Engels 308 midwater trawls of short duration. A sample of 20 fish was taken from each trawl to provide stomach contents data for t = 0. Fish in the tank were observed to ensure that no feeding occurred, and dead or moribund fish were removed. At 2-hourly intervals after t = 0, 5 to 20 fish were removed and rapidly killed by blast-freezing. In the laboratory fish were thawed, and their total length and wet body mass were recorded. Their stomachs were then excised and preserved in 5% buffered formalin. Two distinct size classes (14 to 16cm and 18 to 20cm *TL*) were present amongst fish used in Experiment 1. Data for the two size classes were analysed separately (Table 5.1: Experiments Fld. 1S and Fld. 1L for small and large fish respectively).

Stomach contents were extracted from preserved stomachs and were washed into a petri dish using 0.2µm-filtered sea water. The contents were then vacuum-filtered using pre-weighed Whatman GF/F 47mm glass-fibre filter papers, and the residue was rinsed three times under vacuum using distilled water. After rinsing, the filter papers were weighed to the nearest 0.1 mg (Sartorius 2462 electrobalance), and the wet mass of the stomach contents (*S*) was determined. After weighing, the stomach contents of the fish sampled at t = 0 in each field experiment were pooled, made up to 100ml in filtered sea water, and two 5ml subsamples were taken and examined under a light microscope for identification of food organisms.

For each data set, stomach content mass was expressed as a percentage of fish wet body mass (*Sr*), and was plotted against time after the termination of feeding. Linear, square root, and exponential functions were fitted to the data (Bromley 1994);

$$Sr_t = Sr_0 - Rt \qquad (1)$$

$$Sr_t = Sr_0 - 2\sqrt{Sr_0}*Rt + (Rt)^2 \qquad (2)$$

$$Sr_t = Sr_0(e^{-Rt}) \qquad (3)$$

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(see Table 5.2 for the glossary of variables used). The suitability of the fitted curves in describing the relationship between stomach content mass and time was assessed by comparing the coefficient of determination (r^2) derived for each curve for each experiment.

Table 5.2: Glossary of variables used.

Symbol	Definition
W	Wet body mass of the fish (g)
S	Wet mass of stomach contents (g)
Sr	*S* as a % of *W*
C	Daily ration (g)
Cr	*C* as a % of *W*
R	Instantaneous rate of gastric evacuation (h^{-1})
t	Suffix for time
k	Suffix for observations

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Feeding periodicity and daily ration

Feeding periodicity was assessed by analysing stomach content mass data for fish caught using an Engels-308 midwater trawl. Two sampling approaches were employed. Firstly, sampling of sardine collected approximately every 3 hours during the diel cycle was conducted within a single area of abundant fish. Two such samplings were carried out over periods of 56h and 69h respectively in the inshore region of the western Agulhas Bank during Reproduction and Feeding of Sardine (RAFOS) cruises. The second approach used samples collected during Sardine and Anchovy Recruitment Programme (SARP) cruises conducted during the summers (August to March) of 1993/94 and 1994/95, primarily over the western Agulhas Bank.

In the laboratory the fish were measured and weighed. The stomach of each fish was then excised, blotted dry, and weighed to the nearest 0,1mg. The stomachs were cut open, the contents removed, and the empty stomach re-weighed. Stomach content mass, obtained by subtraction, was expressed as a percentage of fish wet body mass. This parameter was used as an index of fullness for evaluating feeding periodicity and estimating daily ration.

Estimates of stomach content mass obtained by the subtraction method were checked by weighing 220 stomach samples. There was a significant ($p < 0.001$) linear relationship between "estimated" and "actual" stomach content mass, and this relationship was used to correct the stomach content mass data prior to analysis. Stomach content mass (*Sr*) was plotted against fish wet body mass (*W*) to test for possible differences in stomach content mass according to fish size, and relationships between *Sr* and *W* were assessed by linear, multiplicative and exponential regressions.

Feeding periodicity was analyzed by plotting mean stomach content mass (*Sr*) against time of day for each of the three data sets (RAFOS I and II and SARP). Values of mean stomach content mass were obtained by pooling samples into 1-h intervals according to the time at which they were collected; values were only calculated for samples where $n > 5$. Geometric means were calculated for each sample for each data set (Hayward 1991, Héroux and Magnan 1996). A one-way ANOVA/Tukey multiple range analysis was used to test for differences in mean stomach content mass between samples, with statistical significance being accepted at $p < 0.05$.

Daily ration was estimated using the Eggers (1977) and Elliott and Persson (1978) models. The Eggers (1977) model has the form:

$$C = \bar{S} * R * 24 \qquad (4)$$

where $\bar{S}$ is the geometric mean stomach content mass during the 24h period.

The Elliott and Persson (1978) model sums over 24 hours the amount of food consumed during consecutive time intervals, and has the form:

$$C = \sum_{k=1}^{k=n-1} \left[(\bar{S}_{k+1} - \bar{S}_k . e^{-Rt_k}) . R . t_k \right] \qquad (5)$$

$$1 - e^{-Rt_k}$$

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where C is the daily ration (g) when $\sum_k t_k = 24$, $\bar{S}_k$ is the geometric mean stomach content mass during observation k, t_k is the time elapsed (h) between observations k and k+1, and n is the number of observations over the 24h period. Daily ration as a percentage of wet body mass is calculated using

$$Cr = (C/W) * 100 \qquad (6)$$

5.3: Results

Gastric evacuation

Stomach content mass declined significantly (ANOVA; $p < 0.05$) with time, and the exponential expression was found to best describe gastric evacuation in all laboratory experiments. In the field, gastric evacuation was best described by the square root expression in Experiments Fld 1S and Fld 1L, and by the linear expression in Experiment Fld 2L. However, with the exception of Experiment Fld 1S, the coefficients of determination for the "best fit" expressions were only marginally higher that those for the exponential expression, so the exponential expression was fitted to all the data sets (Figures 5.1 and 5.2).

Gastric evacuation rates (R) ranged from 0.06 to 0.29·h^{-1} in laboratory experiments, with fish fed diatoms showing substantially higher values than those fed zooplankton (Figure 5.1). Because of the marked difference in laboratory estimates of gastric evacuation rates resulting from food type, separate mean values were calculated for the different food types. Fish fed zooplankton had a mean gastric evacuation rate of 0.09 ± 0.03·h^{-1} whereas those fed phytoplankton had a mean gastric evacuation rate of 0.27 ± 0.03·h^{-1}. Gastric evacuation rate values from field experiments ranged from 0.05 to 0.10·h^{-1} (Figure 5.2), and had a mean value of 0.08 ± 0.02·h^{-1} which was not significantly different from the estimate derived from laboratory fish fed zooplankton.

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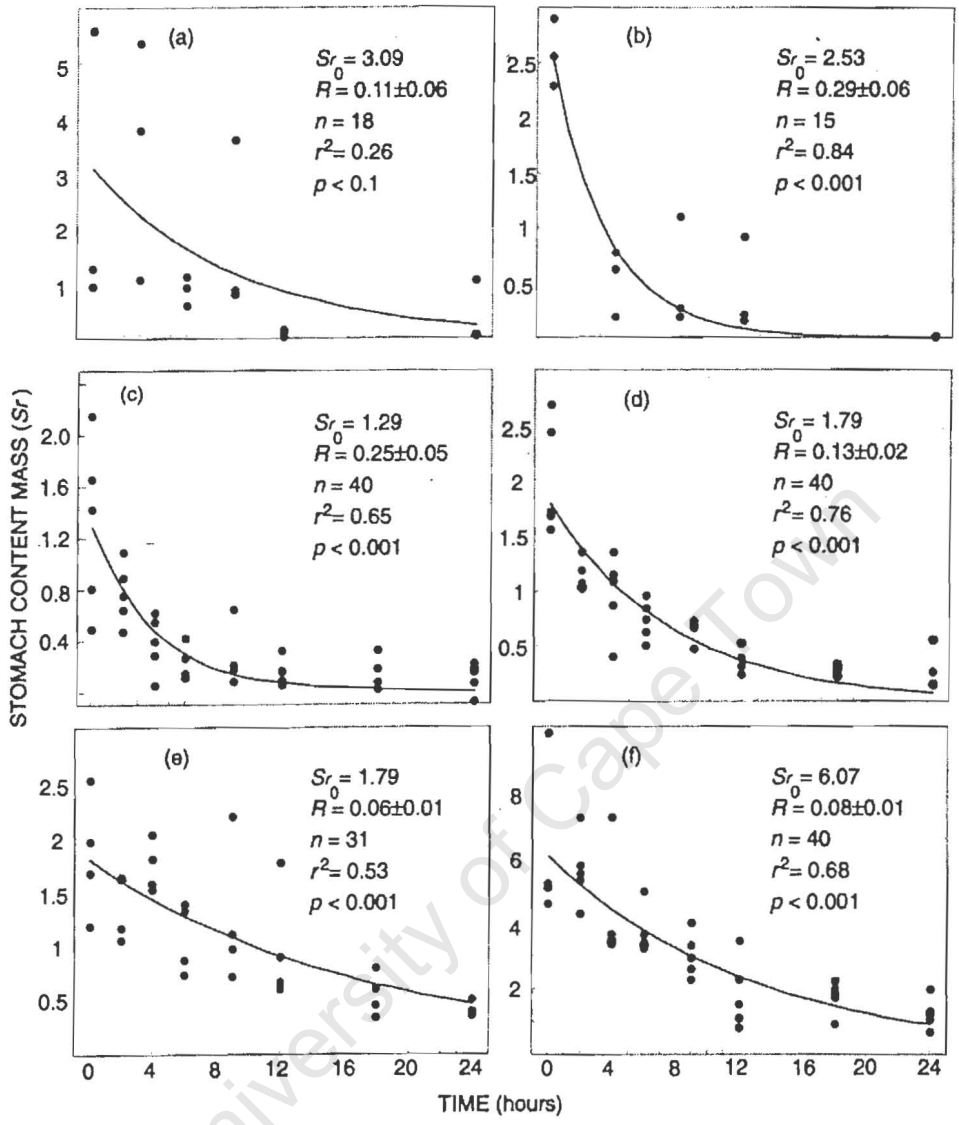

Figure 5.1: Exponential decline in stomach content mass (S_r) of sardine after cessation of feeding in laboratory experiments: (a) Experiment A1, (b) Experiment A2, (c) Experiment B1, (d) Experiment B2, (e) Experiment B3 and (f) Experiment B4. Note the different scales on the y-axes.

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Feeding periodicity

There were significant relationships between stomach content mass (*Sr*) and fish mass (*W*), and a power function provided the best fit to the data in all cases:

RAFOS I: $Sr = 5.137W^{0.467}$ ($n = 855$; $r^2 = 0.11$; $p < 0.001$);

RAFOS II: $Sr = 4.126W^{0.450}$ ($n = 993$; $r^2 = 0.44$; $p < 0.001$);

SARP: $Sr = 3.702W^{0.129}$ ($n = 3037$; $r^2 = 0.28$; $p < 0.001$).

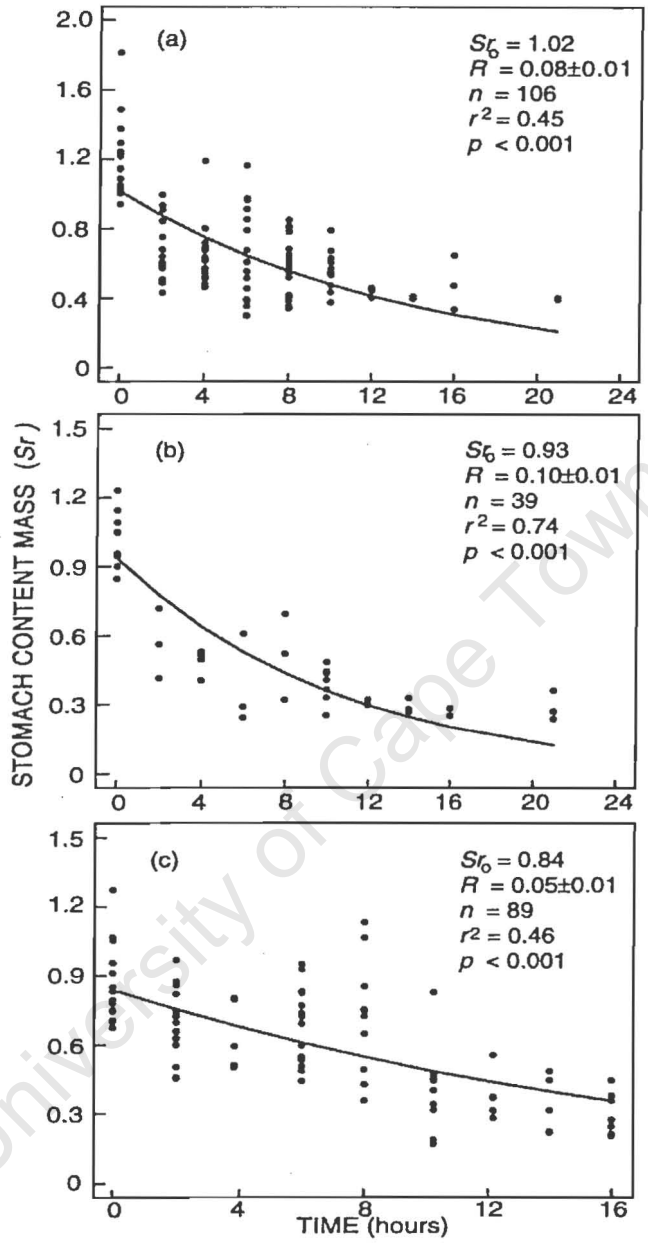

Figure 5.2: Exponential decline in stomach content mass (S_r) of sardine after cessation of feeding in field experiments: (a) Experiment 1S, (b) Experiment 1L and (c) Experiment 2L. Note the different scales on the x- and y-axes.

To remove this size effect, the datasets were divided into mass categories of W : 0 to 24.9g, 25 to 49.9g, 50 to 74.9g, 75 to 99.9g and 100+g. These categories correspond roughly to sardine of ages 0+, 1+, 2+, 3+ and 4+ years, and each was analyzed separately for assessment of feeding periodicity and daily ration. Four categories were assessed for the data from each of the RAFOS cruises (categories

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2 to 5 for RAFOS I and 1 to 4 for RAFOS II), and all 5 categories were assessed for the data from the SARP cruises.

RAFOS I:

Stomach content mass at different times of the day are shown in Figure 5.3. Although there were significant differences in stomach contents during the course of the day, no marked feeding periodicity was evident. Nevertheless stomachs of fish collected at 00:30 tended to be fuller than those collected at other times, suggesting that peak feeding occurred at night.

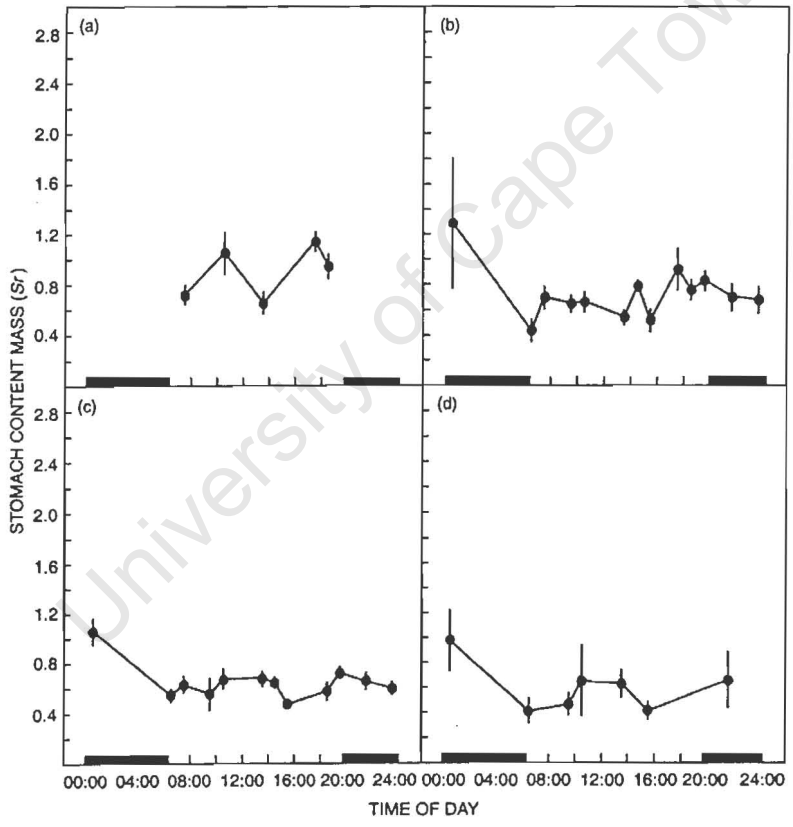

Figure 5.3: Geometric mean values (± 95% confidence limits) of stomach content mass (*Sr*) as a function of time of day for sardine from the RAFOS I cruise: (a) Category 2 (25 to 49.9 g), (b) Category 3 (50 to 74.9 g), (c) Category 4 (75 to 99.9 g), and (d) Category 5 (100+ g). Dark bars indicate night-time.

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RAFOS II:

Fish in all four categories showed a similar pattern of stomach fullness (Figure 5.4), with higher mean stomach content mass values being observed at the beginning (00:30 to 06:30) and the end (18:30 to 23:30) of the diel cycle. Therefore, feeding activity was probably higher at night than during the day, although only small differences in mean stomach content mass were observed.

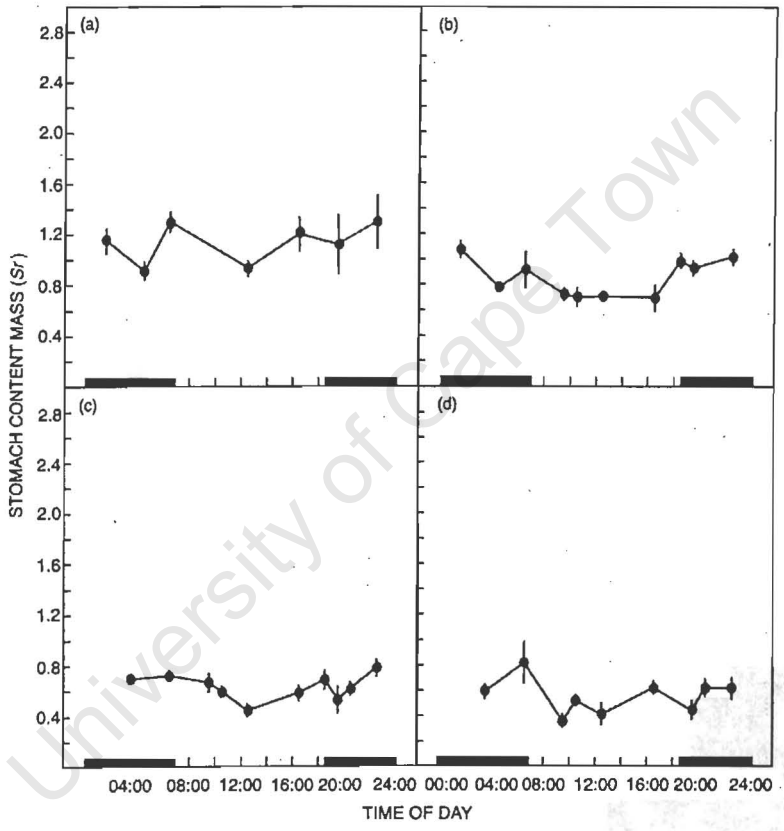

Figure 5.4: Geometric mean values (± 95% confidence limits) of stomach content mass (*Sr*) as a function of time of day for sardine from the RAFOS II cruise: (a) Category 1 (< 24.9 g), (b) Category 2 (25 to 49.9 g), (c) Category 3 (50 to 74.9 g), and (d) Category 4 (75 to 99.9 g). Dark bars indicate night-time.

SARP:

Feeding periodicity appeared to be size dependent, with smaller fish (particularly Category 1) showing an increase in mean stomach content mass in the period 16:30 to 20:30 (Figure 5.5). Mean stomach content mass of fish within Categories 3, 4 and 5 did not show any distinct pattern.

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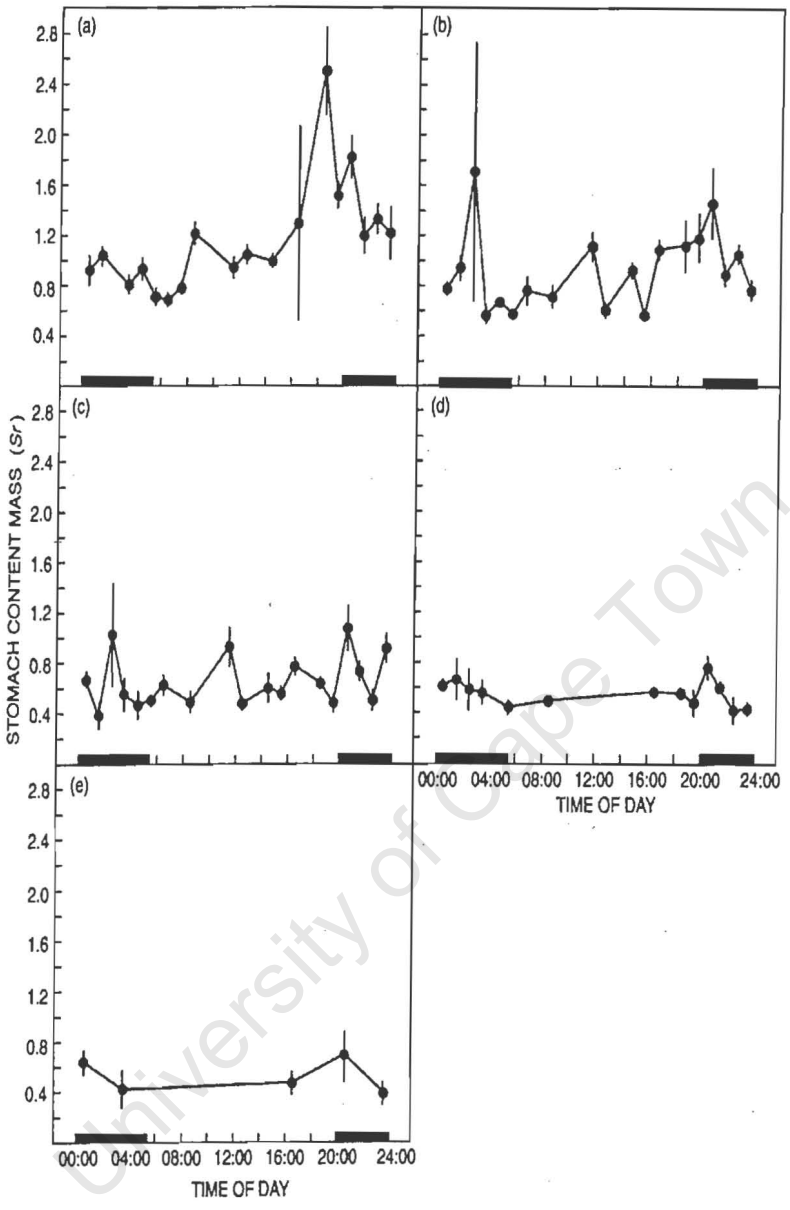

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Figure 5.5: Geometric mean values (± 95% confidence limits) of stomach content mass (*Sr*) as a function of time of day for sardine from the SARP cruises: (a) Category 1 (< 24.9 g), (b) Category 2 (25 to 49.9 g), (c) Category 3 (50 to 74.9 g), (d) Category 4 (75 to 99.9 g), and (e) Category 5 (100+ g). Dark bars indicate night-time.

Daily ration

Daily ration was calculated using the mean values of R estimated for fish fed zooplankton and phytoplankton ($0.09 \pm 0.03 \cdot h^{-1}$ and $0.27 \pm 0.03 \cdot h^{-1}$ respectively). The Eggers (1977) and the Elliott and Persson (1978) models provided similar values for each mass category both within and across data sets (Figure 5.6). Daily ration

estimates ranged from 0.99 to 2.52%*WBM*·d^{-1} for fish consuming zooplankton, and from 2.97 to 7.58%*WBM*·d^{-1} for fish consuming phytoplankton, and smaller fish had higher daily rations than did larger fish.

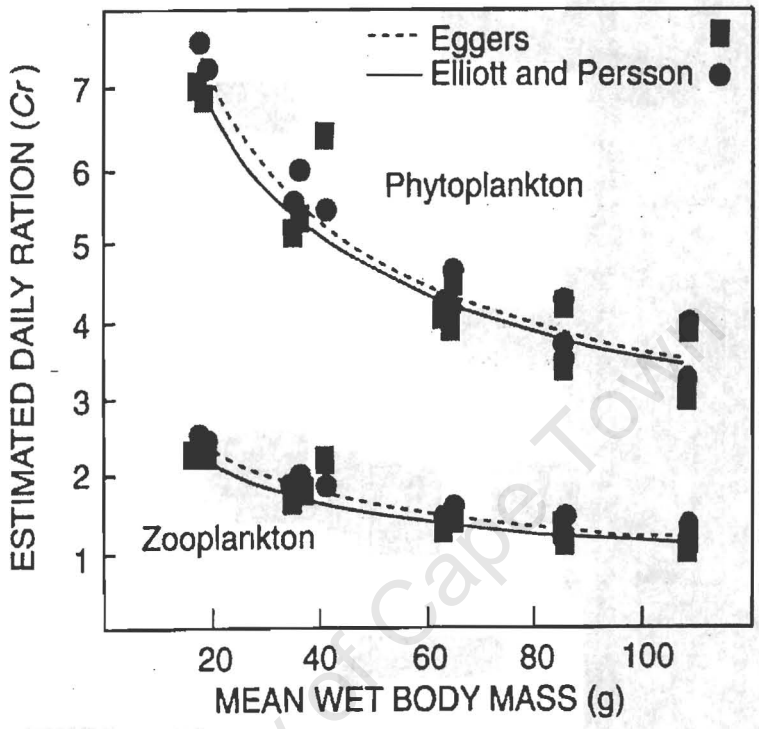

Figure 5.6: Estimated daily ration of sardine as a function of mean wet body mass for each mass category determined in this study. Power function regression equations are fitted to the data for both the Eggers (1977) and the Elliott and Persson (1978) models, using the instantaneous rates of gastric evacuation estimated for both phytoplankton (R = 0.27·h^{-1}) and zooplankton (R = 0.09·h^{-1}).

Power function regression equations relating daily ration (*Cr*) to fish wet mass (*W*) were derived using estimates of R for both phytoplankton and zooplankton, for both the Eggers (1977) and the Elliott and Persson (1978) models:

Eggers (1977):

zooplankton: $Cr = 7.5888W^{0.4138}$; r^2=0.85; $p < 0.001$.

phytoplankton: $Cr = 23.5649W^{0.4129}$; r^2=0.85; $p < 0.001$.

Elliott and Persson (1978):

zooplankton: $Cr = 8.6743W^{0.4281}$; r^2=0.93; $p < 0.001$.

phytoplankton: $Cr = 26.0594W^{0.4297}$; $r^2=0.94$; $p < 0.001$.

5.4: Discussion

Gastric evacuation

Considerable controversy exists as to an appropriate model for gastric evacuation in fish (Jobling 1981b, 1986, Persson 1986, Bromley 1994), but the form of the gastric evacuation model may depend on prey size: large prey items such as fish may be evacuated linearly, whilst smaller prey are evacuated exponentially (Jobling 1987, Bromley 1994). Sardine are primarily filter-feeders that feed almost continuously or at frequent intervals (Figures 5.3 to 5.5), and the exponential function appeared to be the most appropriate gastric evacuation model for this species (Figures 5.1 and 5.2). Food type was found to have a marked effect on evacuation rates of sardine (Figure 5.1), with diatoms being evacuated at rates 2-5 times faster than zooplankton. Neither zooplankton size nor temperature significantly affected gastric evacuation rate, although the temperature range investigated (14.6 to 17.8°C) was possibly too small for temperature effects to be discerned. Rates of gastric evacuation in the field were surprisingly low, given that the fish stomachs contained predominantly phytoplankton and small zooplankton:, these low rates of evacuation may have resulted from a slowing of digestion caused by the trauma of capture (Lockwood 1980, Köster *et al.* 1990 in Bromley 1994).

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An assumption in using experimentally-derived estimates of evacuation rate in daily ration models is that the estimates are realistic. In the laboratory experiments fish fed voluntarily on a single meal for a limited period, after being starved for a prolonged period (Table 5.1): these feeding conditions differ from the natural feeding of sardine (Figures 5.3 to 5.5). Feeding multiple meals has been found to increase evacuation rates in some fish species (Persson 1984, Rösch 1987), so it is possible that the rates of gastric evacuation presented here are underestimates. However, Ruggerone (1989) reported that an evacuation model based on single meals was adequate for estimating the evacuation of prey consumed by continuously feeding Coho salmon *Oncorhynchus kisutch*, and dos Santos and Jobling (1992) concluded

that of single-meal models could be used to obtain reasonable estimates of total daily ration.

The estimated rates of gastric evacuation for *Sardinops sagax* determined in this study are slower than those described for other clupeoids. Because of the dependence of evacuation rate on temperature and food type however, direct rate comparisons between species are likely to be meaningless.

Feeding periodicity and daily ration

Feeding periodicity in *Sardinops sagax* is size dependent; small (<25g) fish showing a peak in feeding activity at or around sunset, whereas larger fish appear to feed continuously. Continuous feeding is indicative of filter-feeding, and the feeding periodicity observed in smaller sardine possibly reflects a higher occurrence of particulate-feeding by this size class of fish. The feeding behaviour of juvenile sardine has not been examined experimentally, but field studies have demonstrated that juveniles are more zooplanktophagous than adults (Hand and Berner 1959, King and Macleod 1976), suggesting that juveniles employ particulate-feeding to a greater degree than do adult sardine.

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Studies relating to feeding periodicity of clupeoids were reviewed by James (1988b), who described the data as "scarce and conflicting". Nevertheless, James (1988b) considered most clupeoids to be nocturnal foragers, with peak feeding activity occurring at dusk and dawn. James (1987) demonstrated a pattern of dawn and dusk feeding for Cape anchovy *Engraulis capensis*, and a similar pattern was reported for *E. anchoita* by Angelescu (1982 in James 1987). Both authors suggested that feeding activity during the day was primarily by filter-feeding, the fish tending to aggregate in dense shoals at depth. Particulate-feeding was associated with peak feeding at dusk and dawn, when the fish were dispersed in the upper layers of the water column (James 1987). These findings contrast with those of Tudela and Palomera (1995), who described a marked pattern of daytime feeding in *E. encrasicolus*, with an approximately 200-fold difference between maximum and minimum stomach fullness. Bulgakova (1993) described the feeding periodicity of

this species as varied, and concluded that feeding pattern depended on the size structure of the plankton. She suggested that feeding occurred during the day when the diet comprised large zooplankters, whereas feeding on small plankton captured through filter-feeding could take place at any time of day.

Durbin (1979) suggested that, because filter-feeding fish are non-visual feeders, they should be able to feed effectively at both low and high light intensities, and hence may show longer daily feeding periods than those of particulate-feeding planktivores. Sardine of >25 g did not show marked variation in stomach content mass (Figures 5.3 to 5.5), and hence did not display marked feeding periodicity. This suggests that these fish filter-feed almost continuously, and corroborates earlier findings which indicated that filter-feeding is the dominant feeding mode of adults of this species (Chapters 2 and 3).

The types of organisms ingested by Pacific sardine *S. sagax* (formerly *S. caerulea*, Parrish *et al.* 1989) remained similar during the diel cycle (Hand and Berner 1959), indicating that feeding mode may not differ between night and day. Barange and Hampton (1997) reported that sardine schools in the southern Benguela had the same mean density at night as during the day, suggesting that sardine does not disaggregate at night. By contrast, lower night-time packing densities in anchovy may be associated with particulate-feeding behaviour. This reduction in school density is unnecessary for sardine, since filter-feeding fish do not feed visually and can feed in darkness (Holanov and Tash 1978).

Estimates of daily ration made in this study were derived through the Eggers (1977) and the Elliott and Persson (1978) models. Both of these have been widely used to estimate fish daily ration (*e.g.* Pillar and Barange 1995, Tudela and Palomera 1995), and both require information about evacuation rates and the quantities of food present in the stomachs of field-collected fish. The Eggers (1977) and the Elliott and Persson (1978) models have been assessed extensively and compared (Boisclair and Leggett 1988, Boisclair and Marchand 1993, Héroux and Magnan 1996). Whereas daily ration estimates do not usually differ significantly, the

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Eggers (1977) is considered more appropriate for estimating the daily ration of species that feed throughout the day on a wide range of prey types, exhibit occasional feeding peaks, and have no rigid feeding periodicities (Héroux and Magnan 1996).

The large differences in estimated daily ration between fish feeding on zooplankton (0.99 to 2.52%*WBM*.d^{-1}) and those feeding on phytoplankton (2.97 to 7.58%*WBM*.d^{-1}) are a result of the marked difference in rates of gastric evacuation for fish fed these prey types. The estimated daily ration for fish feeding on phytoplankton may be too high, because sardine stomachs containing exclusively phytoplankton are seldom encountered (pers. obs.). Because sardine primarily filter-feed (Chapters 2 and 3), their stomachs typically contain both phytoplankton and zooplankton prey (Davies 1957, King and Macleod 1976), and it is likely that the presence of larger zooplankton particles would retard gastric evacuation. However, an exclusively phytoplankton diet could occur in localized regions of dense phytoplankton blooms.

The Eggers (1977) and the Elliott and Persson (1978) models provided similar estimates of the daily ration of sardine (Figure 5.6). No other estimates of daily ration for *Sardinops sagax* could be located in the literature (FishBase 1996, Froese and Pauly 1996), although there are data available on stomach content mass. An average stomach content mass value of 0.8%*W* was reported for Far Eastern sardine *S. sagax* (formerly *S. melanostica*) by Kawasaki and Kumagai (1984). The seasonal average stomach content mass of adult (20 to 35 cm *TL*) Peruvian sardine *S. sagax sagax* was 1.07%*W* (calculated from Table 1 of Alamo and Bouchon 1987). Applying the Eggers (1977) model to these values, and using gastric evacuation rates of 0.09·h^{-1} and 0.27·h^{-1} determined in this study for fish fed zooplankton and phytoplankton respectively, provides daily ration estimates of 1.73 to 5.18%*W*·d^{-1} for Far Eastern sardine and 2.31 to 6.93%*W*·d^{-1} for the Peruvian sardine populations. These estimates are within the range of 0.99 to 7.58 %*W*·d^{-1} derived in this study (Figure 5.6).

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Chapter 6:
Diet of Sardine in the Southern Benguela Upwelling Ecosystem

6.1: Introduction

Previous studies on the diet of sardine in the Benguela region suggested that this species was primarily phytophagous, with an apparent preference for diatoms (Davies 1957, King and Macleod 1976). Recent experimental studies have confirmed that sardine are able to capture significant quantities of phytoplankton through filter-feeding (Chapter 2), and can assimilate diatom carbon and nitrogen efficiently (Chapter 4). The objective of this study was to assess the diet of sardine in the southern Benguela upwelling ecosystem by quantitatively determining its major dietary components. In addition to determining whether phytoplankton is indeed the sardine's primary dietary component, this study also allowed detailed comparison between the diet of sardine, and that of the co-occurring clupeoid anchovy *Engraulis capensis*.

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6.2: Material and methods

Sardine collected for stomach content analyses were collected during Marine & Coastal Management research cruises undertaken in October 1992, November 1992, November 1993 and November 1994 (Figure 6.1). Samples were taken from shoals captured using an Engels 308 midwater trawl fitted with anchovy mesh cod-end lining. Fifty fish per trawl were randomly selected and were immediately blast-frozen for later laboratory analysis, and the date, time, position and depth of each trawl was recorded.

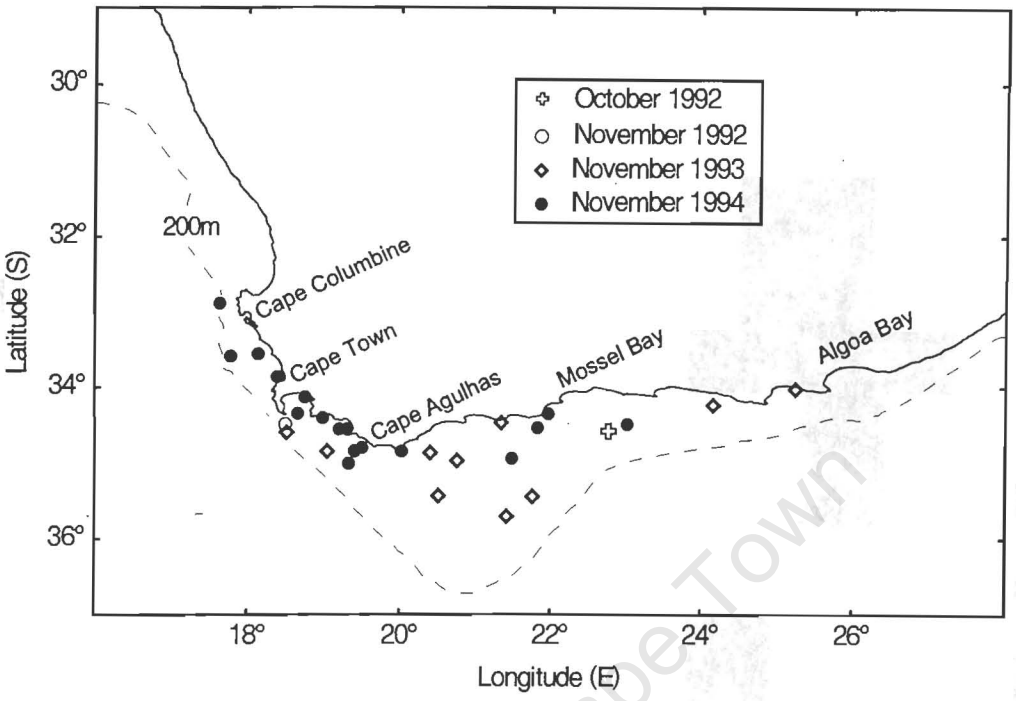

Figure 6.1: Locations of trawls from which sardine were sampled for stomach content analysis.

In the laboratory the total length (*TL*, mm) and wet body mass (*WBM*, g) of ten fish from each trawl was determined, and their stomachs were removed by dissection. Stomach contents were extracted from the cardiac stomach and the fundulus of the stomach. 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 cod-end 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 20ml using 0.2µm-filtered seawater, and a 10ml subsample was examined under the microscope. Analysis showed minimal differences between the stomach contents of individual fish from the same shoal, particularly with respect to the size frequency distributions of ingested prey (see Figure 6.2). Minimal differences between the stomach contents of individual fish from sardine shoals have also been reported elsewhere (Davies 1957,

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Hand and Berner 1959); consequently, the stomach contents of all ten fish were pooled prior to analysis for samples taken during the November 1993 and 1994 surveys. To produce the pooled samples, stomach contents from 10 individual fish were combined in a glass Petri dish, and the food boluses gently broken up using fine dissection needles. Pooled samples were then diluted to 250ml using 0.2µm-filtered seawater, and 3-9 5ml subsamples (depending on the quantity of prey items identified) were collected using a wide-bore (3mm) glass pipette. Subsamples were examined separately under the microscope.

Microscopic analysis of stomach content subsamples was done using a Leica light microscope at 40 or 80x magnification; these magnifications permitted the detection and identification of prey items down to 25µm in size. Identifiable zooplankton were listed to genus and species where possible. Due to the difficulty in identifying *Paracalanus* spp., *Ctenocalanus* spp., *Clausocalanus* spp. and *Parvocalanus* spp. copepods, these calanoid genera were listed as "small copepods". Diatoms and dinoflagellates large enough to be seen under the light microscope were identified and listed. The total length (where possible) and prosome length of all identified copepods was measured to the nearest 12.5µm using an ocular micrometer, as was the maximum dimension (*MD*) of other zooplankton (length, diameter etc). The maximum dimension, diameter and height (where possible) of diatoms and dinoflagellates was also measured.

Phytoplankton species too small for identification under the light microscope were identified and measured under an inverted microscope. A 1ml aliquot from the pooled sample was diluted in 99 ml of 0,2µm-filtered seawater, allowed to settle overnight in an inverted phytoplankton counter, and examined at 64-128x magnification. Three strips, each constituting 0.75% of the settled sample, were examined and phytoplankton cells were identified and measured as above.

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Maximum dimension measurements of all identifiable prey from sardine stomachs were grouped into 0.2mm size-classes, and size frequency histograms were constructed for each shoal. After identification, prey items were grouped into the following major categories: cyclopoid copepods (*Oithona* spp., *Oncaea* spp., *Copilia* spp. and *Corycaeus* spp.), calanoid copepods (*Acartia* spp., *Calanoides* spp., *Calanus* spp., *Centropages* spp., *Metridia* spp., *Nanocalanus* spp. and the "small copepods"), 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 *Oikipleura* spp.), tintinids (*Favella* spp.), diatoms and dinoflagellates (Table 6.1a and b). The frequency of occurrence of the major prey categories was then calculated for each shoal.

In order to provide a basis for comparing the relative contributions of various prey categories to the diet, the food type, size and shape data were used to calculate the dry mass and carbon content of ingested prey using the formulae given in Table 6.1. For crustacean zooplankton (excluding crustacean eggs), dry mass was calculated from length measurements using the equations given in Table 6.1a; carbon content was estimated as 42.4% of the dry mass (the mean carbon content for zooplankton values given in Table 4.1). The dry mass of crustacean eggs was estimated from egg diameter using a linear regression derived from values given in the literature and personal communications (equation given in Table 6.1; n = 17; $r^2 = 0.90$; $p<0.01$; data from Checkley 1980, Hirche 1980, Hosie and Ritz 1983, J. Huggett Marine & Coastal Management pers comm, Huntley and Lopez 1992, Kleppel 1992, Peterson 1986, 1989, Peterson and Hutchings 1995, Pillar 1987, Stuart and Nichol 1986, Verheye 1991). Carbon content was estimated as 40% of egg dry mass (Huntley and Lopez 1992). The dry mass of fish eggs was estimated from volume;

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Table 6.1a: 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. TL is total length and PL is prosome length.

CATEGORY	GENERA	MEASUREMENTS TAKEN AND MORPHOMETRIC RELATIONSHIPS	DRY MASS	CARBON CONTENT	REFERENCES
Calanoid copepods	*Acartia* *Calanus* *Calanoides* *Centropages* *Nanocalanus* *Metridia*	TL or PL All genera: TL = 1.198*(PL) + 52.4[a]	Ln(DM) = 2.74*ln(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] See Chapter 4
"Small copepods"	*Clausocalanus* *Ctenocalanus* *Paracalanus* *Parvocalanus*	TL or PL All genera: TL = 1.132*(PL) + 120.1[d]	Ln(DM) = 2.74*ln(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.	Ln(DM) = 1.96*ln(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)
Harpactacoid copepods	*Macrosetella* *Euterpina* *Clymnestra*	TL	Ln(DM) = 1.96*ln(TL) – 11.64[h]	0.424*DM[c]	[h] Chisholm and Roff's (1990) cyclopoid equation modified (PL to TL)

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Table 6.1a cont.....

Cladocerans and ostracods	*Evadne* *Penillia* *Podon*	TL	DM = 3.946(TLmm)$^{2.436i}$	0.424*DM^{c}	^{i} James (1987)
Crustacean eggs	Copepod eggs Euphausiid eggs	Diameter (∅)	Ln(DM) = 0.0143*(∅) – 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(mg) = 0.0012TL(mm)$^{3.16m}$	0.424*DM^{c}	^{m} James (1987)
Fish eggs	*Engraulis* eggs	Major (a) and minor (b) axes of anchovy, diameter of others; Vol = 4/3πb^3 + πr^2(a-500)^{o} Vol = 4/3πr^3	DM = 0.0930*(Vol)+ 0.0012^{n}	0.457*DM^{o}	^{n} Hunter and Leong (1981) ^{o} Napier (1993)
	Other fish eggs				
Tunicates	*Thalia* *Oikipleura*	TL	DM = 11.3*(TL)$^{1.77p}$ Not calculated	0.387*DM^{p} C=0.04*(TLmm)$^{3.29q}$	^{p} Heron *et al.* (1988) ^{q} Diebel (1986)
Tintinids	*Favella*	TL, diameter Cylinder; Vol = πr^2.h	Not calculated	C(ng) = 0.053*(LV)+44.5^{r}	^{r} Verity and Langdon (1984)

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Table 6.1b: Classification scheme, genera, measurements taken, geometric shape and equation used to determine cell volume, and equations used to calculate the carbon content of identifiable phytoplankton ingested by sardine examined in this study. Length and volume measurements are in µm, and carbon content is in pg. *MD* is maximum dimension. Phytoplankton shapes were taken from James (1987) and the volume to carbon equations from Smayda (1978).

CATEGORY	GENERA	MEASUREMENTS TAKEN AND GEOMETRIC SHAPE	CARBON CONTENT
Diatoms		*MD*, diameter and height	
	Asterionella	Cone; Vol = $1/3\pi r^2.h$	
	Biddulphia	Cylinder; Vol = $\pi r^2.h$	
	Chaetoceros	Cylinder; Vol = $\pi r^2.h$	Log(C) = 0.76*[log(Vol)] – 0.35
	Coscinodiscus	Cylinder; Vol = $\pi r^2.h$	
	Pleurosigma	2x cone; Vol = $2/3\pi r^2.h$	
	Rhizosolenia	Cylinder; Vol = $\pi r^2.h$	
	Skeletonema	Cylinder; Vol = $\pi r^2.h$	
	Thallassiosira	Cylinder; Vol = $\pi r^2.h$	
Dinoflagellates		*MD*, diameter and height	
	Ceratium	3x cone; Vol = $\pi r^2.h$	
	Dinophysis	Ellipsoid; Vol = $4/3\pi(d/2)^2+[\pi(d/2)^2.(h-d)]$	Log(C) = 0.94*[log(Vol)] – 0.60
	Peridinium	3x cone; Vol = $\pi r^2.h$	
	Prorocentrum	Ellipsoid; Vol = $4/3\pi(d/2)^2+[\pi(d/2)^2.(h-d)]$	

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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 6.1a). The carbon content of phytoplankton was calculated from cell volume (Table 6.1b). For each sardine shoal sampled, the relative contribution to the estimated 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 1992 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 bracketing the depth at which the sardine shoal had been captured. A four-litre 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.

6.3: Results

Sardine sampled for stomach content analyses ranged in size from 144.0 to 230.4mm TL, and from 20.9 to 103.2g WBM (Table 6.2). Eleven of the 29 sardine shoals examined consisted of subadult, sexually immature fish (50% sexual maturity is attained at ± 180rnm TL; Akkers and Melo 1996), with seven of these shoals being 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 51m (Table 6.2). More shoals were collected at night than during the day, although samples were collected from fish captured throughout the diurnal cycle (Table 6.2). Sardine were captured off the southwestern and southern coasts in a region bounded by Cape Columbine in the northwest to Algoa Bay in the east (Figure 6.1). Samples collected during the

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November 1993 survey were primarily taken from midshelf waters over the eastern Agulhas Bank, whereas the majority of those from the 1994 survey were taken from inshore waters of the western Agulhas Bank.

Table 6.2: Trawl number, time and depth of capture, and mean (± 1 standard deviation) total length and wet body mass of sardine from which samples were collected for stomach content analysis. Trawl numbers increase from west to east.

Cruise	Trawl #	Time (SAST)	Depth (m)	Total length (mm)	Wet body mass (g)
Oct. 1992	D14-04A	11:40	15-26	174.7 ± 14.2	60.2 ± 15.2
Nov. 1992	38-01A	13:18	13-25	157.7 ± 16.9	41.3 ± 14.4
Nov. 1993	06-07A	06:57	12-24	197.4 ± 10.8	62.0 ± 10.0
	09-05A	04:42	40-51	166.0 ± 12.7	33.7 ± 10.4
	21-01A	00:13	15-32	158.9 ± 12.9	29.6 ± 7.6
	21-09A	06:46	22-34	144.0 ± 6.3	20.9 ± 2.9
	22-07A	08:53	20-33	162.9 ± 13.0	31.2 ± 8.5
	23-15A	01:27	11-30	161.7 ± 9.6	33.5 ± 6.8
	24-03A	01:12	16-32	150.9 ± 7.1	24.6 ± 3.8
	25-13A	11:15	30-41	176.4 ± 11.5	47.3 ± 10.6
	29-05A	03:17	10-22	224.1 ± 8.8	93.5 ± 12.7
	33-01B	15:23	15-26	224.2 ± 9.0	101.7 ± 9.6
Nov. 1994	02-02A	03:05	12-24	230.4 ± 11.7	103.2 ± 15.7
	04-02A	03:38	10-23	216.9 ± 7.1	84.1 ± 9.0
	04-05A	08:45	10-22	221.6 ± 5.3	88.0 ± 5.2
	05-02A	01:01	9-21	210.3 ± 9.8	79.4 ± 12.5
	09-02A	04:32	13-25	208.3 ± 19.7	67.3 ± 18.7
	09-05A	01:29	20-34	213.1 ± 4.2	68.3 ± 5.4
	11-01A	00:29	22-36	178.4 ± 25.6	42.7 ± 21.6
	13-03A	19:57	30-42	218.5 ± 4.8	64.9 ± 13.0
	14-01A	23:13	18-30	228.3 ± 5.9	87.2 ± 6.2
	16-02A	22:32	18-36	212.2 ± 5.6	65.6 ± 7.0
	16-04A	01:00	15-38	207.1 ± 6.8	66.9 ± 7.6
	17-01A	16:26	13-23	219.8 ± 9.7	83.2 ± 11.6
	19-01A	14:16	20-34	153.0 ± 5.0	26.0 ± 3.3
	24-05A	05:52	30-60	210.9 ± 11.0	62.6 ± 11.2
	25-03A	22:34	20-31	199.4 ± 11.8	62.6 ± 13.2
	27-01A	01:03	10-23	196.2 ± 25.3	58.9 ± 22.1
	28-05A	23:45	30-41	215.4 ± 14.7	78.8 ± 18.9

Sardine stomachs were typically found to contain large quantities of unidentifiable material as well as the identifiable zooplankton and phytoplankton. Some of the unidentifiable material would have been partly-digested remains of

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ingested zooplankton and phytoplankton prey, but it is likely that the remainder consisted of particulate detritus, organic carbon, marine snow, and other organic and inorganic aggregates which were sufficiently large to be retained by the sardine's gill rakers. Only food items that could be identified using the methods described above were recorded; hence the dietary contribution made by the potential food categories listed above was not considered in this study.

October and November 1992:

Size frequency distributions of identifiable prey from the stomachs of individual sardine collected from the same shoal showed a high degree of similarity (Figure 6.2). However, there was considerable variation in the numbers of identifiable prey from individual stomachs. These results indicate that whereas all of the fish in any one shoal were not necessarily feeding at the same time (i.e. feeding intensity was variable), those fish that were feeding showed comparable feeding behaviour.

At stations where the food environment was assessed using the Magnum rosette, the mean size frequency distribution of sardine stomach contents closely corresponded to that compiled from Magnum samples (Figure 6.3). Similarly, the dominant plankton in Magnum samples also dominated sardine stomach contents. At station D14-04A (October 1992) Magnum samples indicated that the food environment was dominated by particles of <0.2 mm *MD*, and consisted primarily of the dinoflagellate *Peridinium* spp., crustacean eggs, crustacean nauplii, and the cyclopoid copepod *Oithona* spp. (densities of 93.0, 3.8, 11.3, and 3.3 organisms.l^{-1} respectively at 10m depth). Sardine stomachs from this trawl were dominated by *Peridinium* spp (34.7 ± 15.5% by number), crustacean eggs (32.0 ± 9.6%), crustacean nauplii (11.6 ± 5.4%) and *Oithona* spp. (10.7 ± 2.1%). This 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 the sardine were feeding non-selectively, and the low occurrence of prey items >1.2mm *MD* indicates that the fish were feeding by filtering only.

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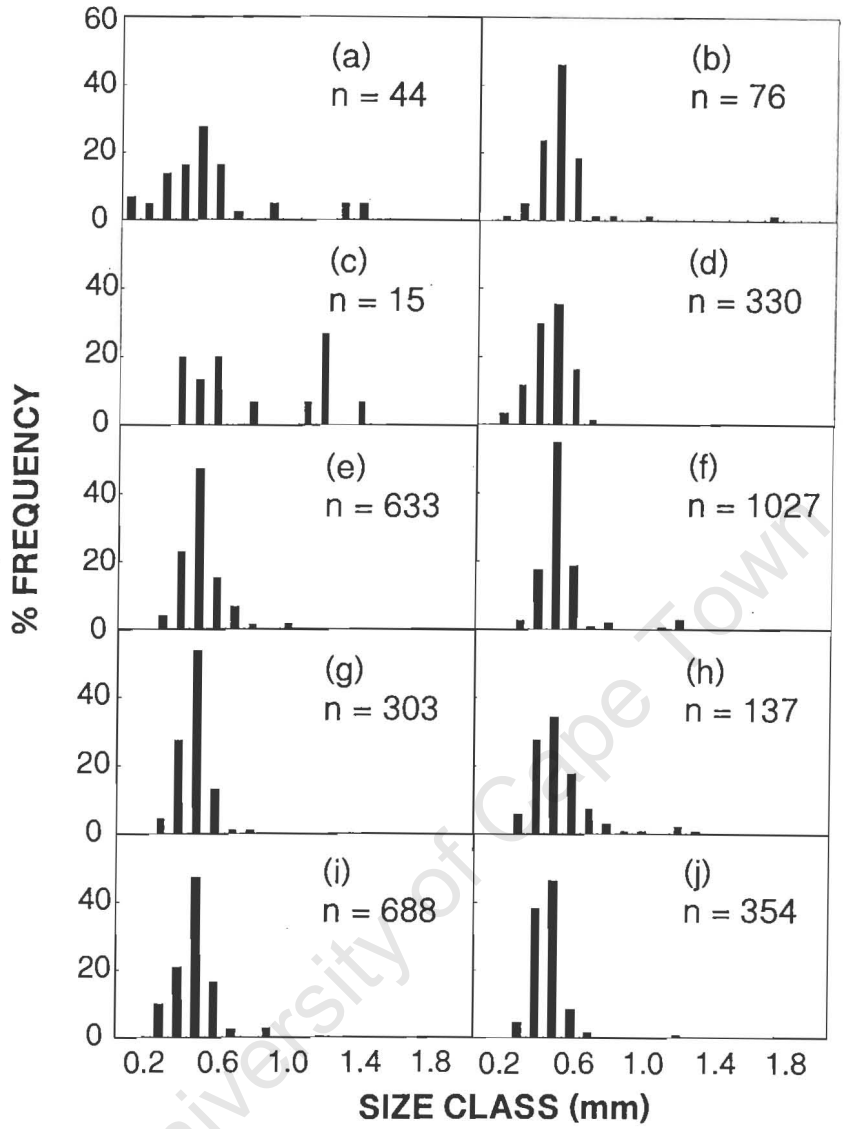

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Figure 6.2: Size frequency distributions of identifiable prey from the stomachs of ten individual sardine (a – j) collected from trawl 38-01B, November 1992. The number of prey items identified per fish is given (n).

The dominant prey items in terms of dietary carbon at station D14-04A were crustacean eggs (33.7 ± 7.4% contribution to dietary carbon), cyclopoid copepods (18.4 ± 6.0%) and anchovy eggs (16.9 ± 16.2%). Because of the small size of *Peridinium* spp., its numerical dominance did not translate into a significant portion of the ingested carbon (3.7 ± 3.3%), whereas the opposite was true of anchovy eggs. The relative contribution to dietary carbon by prey items showed a decreasing trend

with increasing prey size (Figure 6.4a), with the smallest size class (<0.2mm *MD*; comprising *Peridinium* spp., copepod eggs and nauplii) accounting for 35.6 ± 8.8% to dietary carbon.

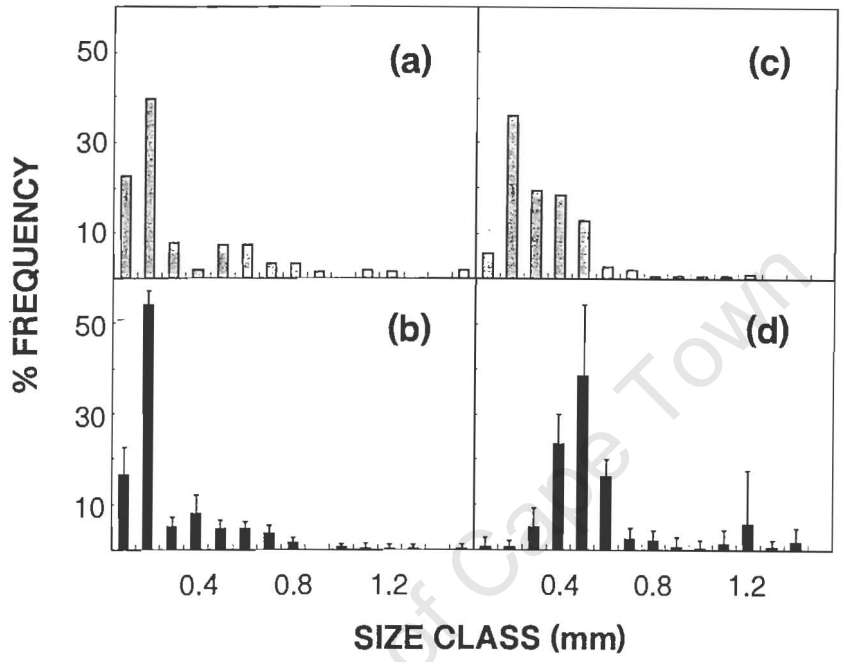

Figure 6.3: Size frequency distributions of the ambient food environment as sampled using a Magnum rosette (samples from 3 depths combined; grey bars) and of identifiable prey from sardine stomachs (mean size frequency distribution plus 1 standard deviation from 10 fish; black bars) collected at stations D14-04A (October 1992; a, b) and 38-01B (November 1992; c, d).

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The exception to this trend was the 1.2-1.4mm *MD* size class, which represented anchovy eggs and large calanoid copepods, and accounted for 16.9 ± 16.2% of the carbon of ingested prey. The significant contribution to ingested carbon by these few large prey items is a result of the rapid increase in volume, and hence carbon, with small increases in length, and emphasises the importance of large, high volume food items in the diet.

At station 38-01B (November 1992), Magnum samples were dominated by crustacean (principally copepod) nauplii and the cyclopoid copepods *Oithona* spp. and

Oncaea spp. (densities of 26.3, 18.0 and 3.3 organisms.l^{-1} respectively at 9m depth). Size frequencies of zooplankton collected by the Magnum rosette at all three depths were dominated by particles of 0.1-0.2mm maximum dimension, but the proportion of particles >0.5mm increased with depth. Sardine stomach contents were numerically dominated by prey of 0.5-0.6mm maximum dimension, with this size class accounting for close to or over 50% of the identifiable prey (Figure 6.3d). The dominant prey type encountered in sardine stomach contents was *Oithona* spp., which accounted for a mean value of 66.0 ± 26.7% of all the prey organisms identified. *Oncaea* spp. was the second most commonly encountered zooplankton prey item (18.3 ± 12.6%), with anchovy eggs also relatively important (5.9 ± 2.3%). Although copepod nauplii dominated Magnum samples, they were only present at low frequencies in sardine stomachs (1.1 ± 1.2%).

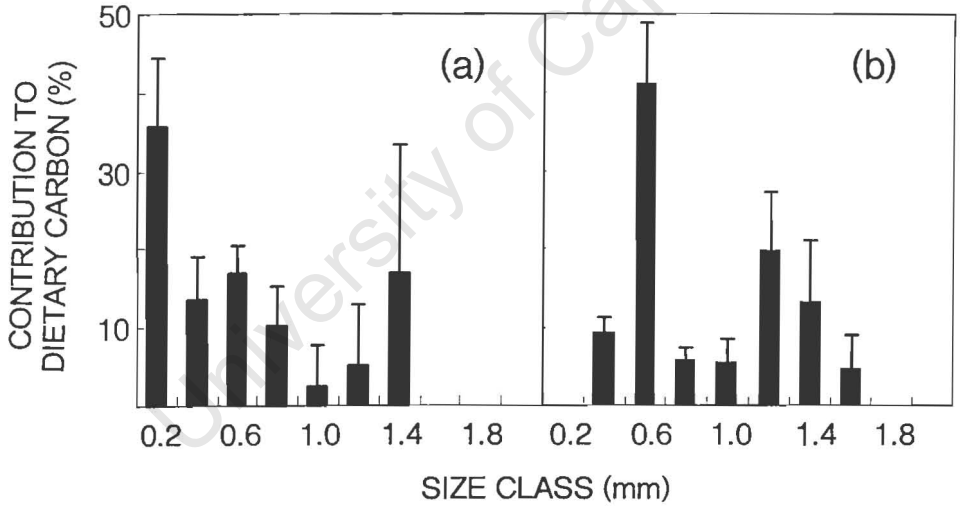

Figure 6.4: Mean (± standard deviation) percentage contribution to dietary carbon by size class (mm) for sardine collected at (a) station D14-04A (October 1992) and (b) station 38-01B (November 1992).

Whereas *Oithona* spp. and *Oncaea* spp. accounted for 84% on average of the prey organisms ingested, they only contributed 52% of the calculated ingested carbon. Fish (primarily anchovy) eggs were responsible for 35.9 ± 33.5% of the carbon of prey ingested by sardine. The mean relative contribution by size class to the total carbon

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ingested is shown in Figure 6.4b. Two peaks are evident; the first from prey organisms of 0.4-0.6 mm (i.e. the cyclopoid copepods) which contributed 41% of the total carbon, and the second of particles of 1.0-1.4 mm (anchovy eggs and calanoids) which contributed 33% to the ingested carbon.

November 1993:

Stomach contents of sardine collected during November 1993 were dominated by small prey items, with over 50% by number being <0.4mm *MD*, and the modal size of ingested prey being <0.6mm *MD* for eight out of the 10 shoals examined (Table 6.3). Prey size increased eastwards, with broader size frequency histograms and modal sizes of 1.4-1.6mm and 1.0-1.2mm respectively being observed for fish captured in the two easternmost trawls (29-05A and 33-01B). Small particles were not only numerically dominant in sardine stomachs, but also showed the least variability in their relative occurrence. The coefficients of variation (CV) associated with the mean occurrence value for all shoals combined was <100% for the four smallest prey size classes. Hence small particles were common in all samples. The CVs for larger prey size classes ranged from 103-225%, indicating the relatively infrequent occurrence of these prey items in sardine stomachs.

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The major prey items found in the stomachs of sardine sampled in November 1993 included dinoflagellates, cyclopoid copepods, calanoid copepods and crustacean eggs. *Ceratium* spp. and *Peridinium* spp. were the principal dinoflagellate phytoplankton encountered, and numerically dominated four of the ten samples examined, primarily those collected in the western part of the survey area (Table 6.4). Commonly encountered *Ceratium* species included *C. furca* (0.15-0.25mm *MD*), *C. lineatum* (0.15-0.3mm *MD*), *C. tripos* (0.2-0.5mm *MD*) and *C. macroceros* (0.3-0.75mm *MD*), whereas *Peridinium* species included *P. exicentricum* and *P. depressum* (both species 0.05-0.15mm *MD*). Diatom phytoplankton were much less common than dinoflagellates in sardine stomachs, and accounted for only

Table 6.3: Size frequency distributions of identified prey ingested by sardine collected during the November 1993 survey. The number of food items identified from pooled samples are given for each trawl (n), and the mean frequency (%), standard deviation (%) and coefficient of variation (CV; %) values are given for each size class for the sample from that trawl .

Trawl	N	Size class (mm)														
		0.0-0.2	0.2-0.4	0.4-0.6	0.6-0.8	0.8-1.0	1.0-1.2	1.2-1.4	1.4-1.6	1.6-1.8	1.8-2.0	2.0-2.2	2.2-2.4	2.4-2.6	2.6-2.8	2.8-3.0
06-07A	555	23.1	30.6	41.3	4.0	0.7	0.4	0	0	0	0	0	0	0	0	0
09-05A	803	28.1	38.2	30.6	2.7	0.3	0	0	0	0	0	0	0	0	0	0
21-01A	765	65.9	17.4	12.4	3.8	0.4	0.1	0	0	0	0	0	0	0	0	0
21-09A	301	10.0	41.2	33.9	11.0	3.7	0.3	0	0	0	0	0	0	0	0	0
22-07A	215	18.1	39.1	34.9	6.1	1.9	0	0	0	0	0	0	0	0	0	0
23-15A	467	35.6	40.5	13.3	4.5	1.9	1.5	0.6	1.3	0	0.4	0.2	0.2	0	0	0
24-03A	316	41.5	15.5	26.0	8.5	3.5	3.8	1.0	0	0	0.3	0	0	0	0	0
25-13A	1018	65.2	19.7	7.1	1.7	1.0	3.9	1.0	0	0.2	0	0.1	0.1	0	0	0
29-05A	600	10.5	0.5	4.3	7.5	9.8	10.2	8.3	12.2	9.8	8.5	9.0	4.2	3.0	1.7	0.5
33-01B	187	0	0	0	1.1	6.4	18.2	16.0	16.6	15.0	9.6	8.6	6.4	0.5	1.1	0.5
Mean		29.8	24.3	20.4	5.1	3.0	3.8	2.7	3	2.5	1.9	1.8	1.1	0.4	0.3	0.1
Std. dev.		22.5	16.0	14.6	3.2	3.1	6.0	5.3	6.1	5.4	3.8	3.7	2.3	0.9	0.6	0.2
CV (%)		76	66	72	63	103	158	196	203	216	200	206	209	225	200	200

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Table 6.4: Frequency of occurrence of the main prey categories identified in sardine stomachs from trawls sampled during the November 1993 survey. The mean frequency of occurrence, standard deviation and coefficient of variation (CV) values are given for each prey category.

Trawl	Cyclopoid copepods	Calanoid copepods	Cladocerans and Ostracods	Other crustaceans	Crustacean 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
Std. Dev.	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

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4.0% of prey items ingested in 1993. The most commonly ingested diatom was *Coscinodiscus gigas*, which ranged in size from 0.2-0.4mm *MD*.

Cyclopoid copepods, principally *Oithona* spp., were encountered in all samples and were the numerically dominant or second dominant prey item in six of the ten samples examined (Table 6.4). 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 found in sardine stomachs from the eastern region, with sardine collected from the two easternmost trawls (29-05A and 33-01B) having stomach contents numerically dominated by large *C. agulhensis*. Crustacean eggs were also frequently encountered in stomach contents, and were the dominant prey item in two of the samples examined (24-03A and 25-13A). Cyclopoid copepods and dinoflagellates showed the least variability in their relative mean occurrence, having CVs of 74 and 79% respectively, whereas the other prey categories all showed CVs of >100% (Table 6.4).

The majority of dietary carbon ingested by sardine sampled in 1993 came from small food particles, with 70.4% being derived from prey of <1.2mm *MD* (Figure 6.5a). This means that sardine obtained the majority of their dietary carbon through filter-feeding, since they switch from filter-feeding to particulate-feeding at a prey size of approximately 1.2mm (Chapter 2). In general the 0.4-0.6mm size class was the largest contributor to dietary carbon and was the modal size class in terms of average carbon contribution. Larger size classes were more important for fish collected in the eastern part of the survey area, with the most important size classes in terms of carbon for the two easternmost samples were 2.0-2.2 and 2.2-2.4mm for trawls 29-05A and 33-01B respectively. Coefficient of variation (CV) values for the mean carbon contribution per size class were low for small prey items (<100%), whereas higher CVs were associated with larger prey sizes (>100%), indicating that small prey were more consistent in terms of their contribution to dietary carbon.

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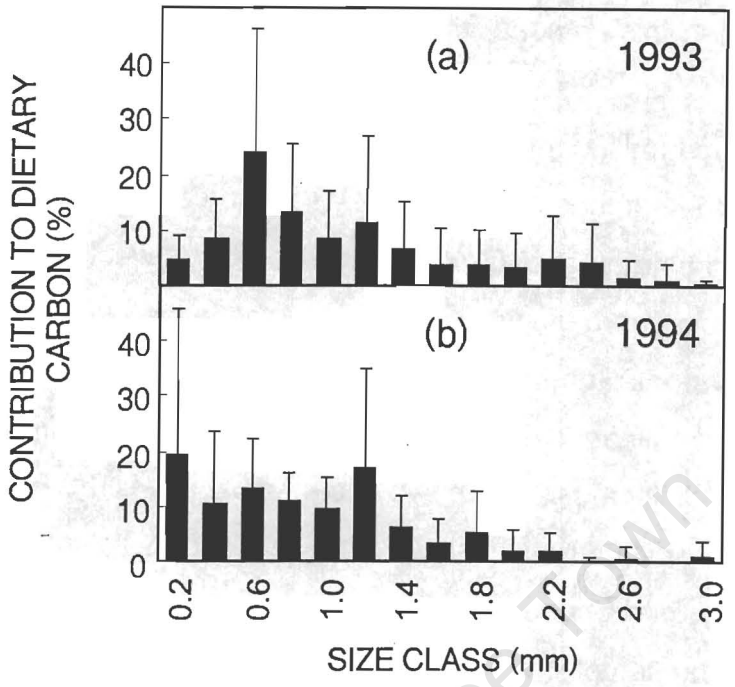

Figure 6.5: Mean (± standard deviation) percentage contribution to dietary carbon by size class for sardine sampled in (a) November 1993 and (b) November 1994.

Zooplankton contributed a far larger proportion of the dietary carbon ingested by sardine sampled in 1993 than did phytoplankton (Figure 6.6a), with 98.2% on average of estimated ingested carbon being of zooplankton origin. Phytoplankton accounted for >1% of ingested carbon at only three of the ten samples examined, with these three samples coming from the western region of the survey area. Of the zooplankton component, calanoid copepods were the dominant prey category and accounted for 40.2 ± 35.9% of the ingested carbon. Cyclopoid copepods were the second most important prey category, and provided 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.

November 1994:

Small particles dominated stomach contents of sardine collected during November 1994 to an even greater extent than was the case for fish sampled in

1993. Over 60% by number of prey items identified were <0.2mm *MD*, and the modal size of ingested prey was <0.6mm in all 17 samples examined (Table 6.5). In addition to having a higher proportion of small prey, stomach contents from sardine collected in 1994 also showed a narrower size range than those from fish collected in 1993. Over 99% of prey items were <1.2mm *MD* in 1994, whereas this value was 86% for fish sampled in 1993. Small prey items ingested by fish sampled in 1994 showed low variability in their relative occurrence; CVs for the four smallest size classes were <100% whereas the mean abundance of the larger prey items was associated with higher variability (Table 6.5).

As was seen in samples collected during 1993, dinoflagellates were again the major prey category, numerically dominating eight of the 17 samples examined (Table 6.6) 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. Sardine from one trawl (04-02A) had stomach contents that were almost entirely composed of the diatoms *Pleurosigma* spp. and *Thallassiosira subtilis*. Other diatom genera encountered included *Asterionella*, *Biddulphia*, *Chaetoceros, Coscinodiscus, Rhizosolenia* and *Skeletonema*. 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 (Table 6.6). The third and fourth numerically dominant prey items ingested by sardine sampled in 1994 were crustacean eggs (16.6%) and cyclopoid copepods (8.8%). Calanoid copepods were encountered at low to moderate numbers in most samples. The tintinid *Favella* spp. was found in sardine stomachs at six of the 17 trawls sampled, and was the dominant prey item at one of these (14-01A) where it accounted for 69.3% by number of identified prey.

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Table 6.5: Size frequency distributions of identified prey ingested by sardine collected during the November 1994 survey. The number of food items identified from pooled samples are given for each trawl (n), and the mean frequency (%), standard deviation (%) and coefficient of variation (CV; %) values are given for each size class for the sample from that trawl .

Trawl	n	Size class (mm)														
		0.0-0.2	0.2-0.4	0.4-0.6	0.6-0.8	0.8-1.0	1.0-1.2	1.2-1.4	1.4-1.6	1.6-1.8	1.8-2.0	2.0-2.2	2.2-2.4	2.4-2.6	2.6-2.8	2.8-3.0
02-02A	292	47.3	23.6	20.2	4.5	2.7	1.0	0.3	0	0.3	0	0	0	0	0	0
04-02A	7800	87.6	5.7	1.2	1.1	1.2	0.8	1.4	0.5	0.5	0.1	0	0	0	0	0
04-05A	1632	96.3	1.2	2.0	0.5	0	0.1	0	0	0	0	0	0	0	0	0
05-02A	9620	91.9	3.8	1.4	1.3	0.6	0.2	0.3	0.2	0.2	0.1	0	0	0.1	0	0
09-02A	764	92.3	3.2	3.4	0.8	0.3	0	0.1	0	0	0	0	0	0	0	0
09-05A	753	60.7	28.6	7.0	2.8	0.4	0.5	0	0	0	0	0	0	0	0	0
11-01A	1405	88.3	5.2	4.8	0.9	0.5	0.4	0	0	0	0	0	0	0	0	0
13-03A	1293	73.6	7.0	13.5	4.6	0.9	0.2	0	0.1	0	0	0	0	0	0	0
14-01A	907	23.7	72.9	2.0	1.0	0.1	0.2	0.1	0	0	0	0	0	0	0	0
16-02A	2303	85.7	7.6	3.5	2.7	0.2	0	0	0	0.1	0	0	0	0	0	0
16-04A	2453	26.2	14.7	45.4	10.2	3.2	0	0.2	0	0	0	0	0	0	0	0
17-01A	1319	60.8	10.5	20.7	6.4	0.9	0.2	0.2	0.1	0.1	0.1	0	0	0	0	0
19-01A	1207	47.5	19.2	21.1	7.8	2.5	0.5	0.5	0.3	0.3	0.3	0.1	0	0	0	0
24-05A	518	55.6	26.5	12.4	2.1	2.3	0.4	0.2	0.2	0.4	0	0	0	0	0	0
25-03A	698	41.4	35.8	13.9	6.9	1.5	0.3	0.1	0	0	0	0	0	0.2	0	0
27-01A	657	39.0	45.4	12.6	2.3	0.4	0.4	0.1	0	0	0	0	0	0	0	0
28-05A	449	20.7	23.4	31.6	10.9	7.1	3.1	1.6	0.9	0.2	0.2	0.2	0	0	0	0
Mean		61.1	19.7	12.8	3.9	1.5	0.5	0.3	0.1	0.1	0.1	0	0	0	0	0
Std. Dev.		26.1	18.7	12.2	3.4	1.8	0.7	0.5	0.2	0.2	0.1	0.1	0	0	0	0
CV (%)		43	95	95	87	120	140	167	200	200	100	0	-	-	-	-

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Table 6.6: Frequency of occurrence of the main prey categories identified in sardine stomachs from trawls sampled during the November 1994 survey. The mean frequency of occurrence, standard deviation and coefficient of variation (CV) values are given for each prey category.

Trawl	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	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
Std. Dev.	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

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Small prey items captured by filter-feeding were the largest contributors to dietary carbon ingested by sardine sampled in 1994, with 80.5% being derived from prey of <1.2mm *MD* (Figure 6.5b). Two peaks in carbon contribution by size class were evident; the first for prey of 0.0-0.2mm *MD* was primarily composed of diatoms, some dinoflagellates, and crustacean eggs and nauplii. The second peak for prey of 1.0-1.2mm *MD* corresponded to the larger calanoid copepods and some of the fish eggs. Coefficient of variation values for the mean carbon contribution by size class were again lower for small prey items than they were for the larger prey.

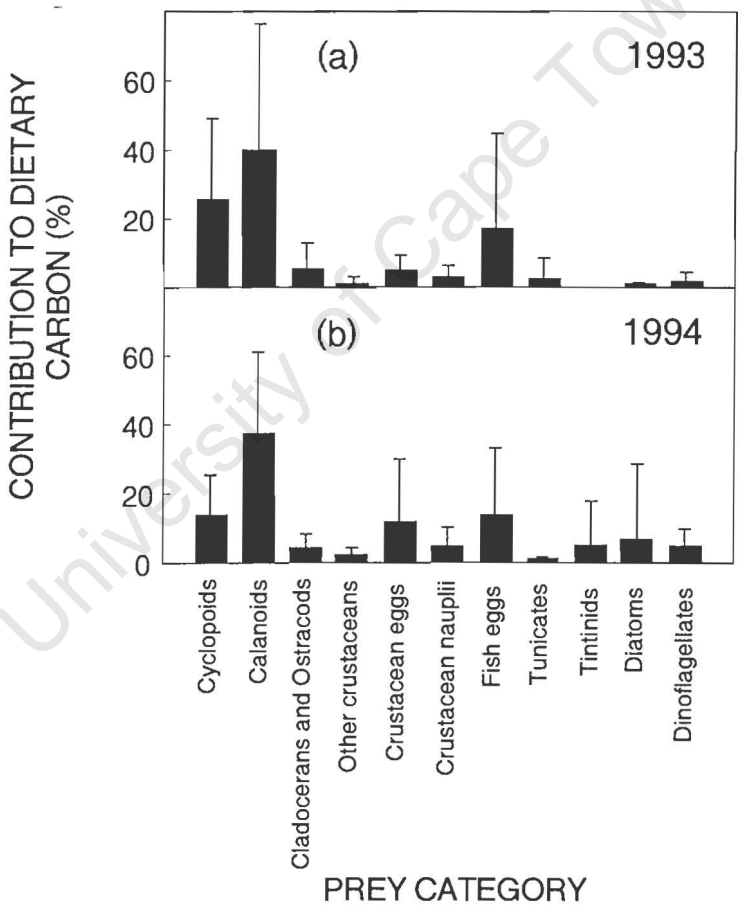

Figure 6.6: Mean (± standard deviation) percentage contribution to dietary carbon by prey category for sardine sampled in (a) November 1993 and (b) November 1994.

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Zooplankton contributed 89.9% and phytoplankton 10.1% to the dietary carbon ingested by sardine sampled in 1994 (Figure 6.6b). Of the phytoplankton-derived carbon, 4.1% on average was obtained from dinoflagellates and 6.0% from diatoms. The high mean carbon contribution from diatoms is due to the data from trawl 04-02A, where 92.9% of the ingested carbon was derived from diatoms. Calanoid copepods were the major source of zooplankton-derived carbon, providing 36.7% on average of dietary carbon for fish sampled in 1994. Fish (primarily anchovy) eggs supplied the second largest proportion of dietary carbon (13.5%), and were closely followed by cyclopoid copepods which contributed 13.1% to dietary carbon. Crustacean eggs were the fourth most important contributors to dietary carbon (11.1%).

6.4: Discussion

Sardinops sagax is an omnivorous clupeoid, ingesting both phytoplankton and zooplankton. Stomach contents of sardine collected off the southwestern and southern coasts of South Africa during the early summer of 1992, 1993 and 1994 were numerically dominated by small prey items, principally dinoflagellate phytoplankton. Cyclopoid and calanoid copepods, and crustacean eggs were the dominant zooplankton encountered in sardine stomachs. Despite the numerical dominance by phytoplankton, crustacean zooplankton and anchovy eggs contributed the major portion to dietary carbon.

For stomach content samples collected during November 1993, 86.2% of all ingested prey items were <1.2mm *MD*, the particle size at which sardine switch from filter-feeding to particulate-feeding (Chapter 2). For samples collected during 1994, this value was 99.4%. The low variance associated with the mean frequency of occurrence values for the smaller size classes indicates that these size classes are common in all stomach content samples, and hence are consistently ingested by sardine. These results corroborate previous experimental (Chapters 2 and 3) and

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field data (Davies 1957, Hand and Berner 1959, King and Macleod 1976, Alamo and Bouchon 1987, Chapter 5) that suggested 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. It must be stressed however that the Magnum rosette is not a comprehensive sampler of the food environment; whilst it is likely to provide realistic estimates of the density of small plankton species, larger zooplankton are likely to avoid this sampler. Exhaustive sampling using a variety of towed nets in conjunction with discrete samplers such as the Magnum would ideally be employed to provide representative and all-inclusive sampling of the food environment; this was not done in this study. Sampling problems notwithstanding, a close correspondence between stomach contents and the food environment has been reported in almost all publications 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), suggesting that non-selective filter-feeding seems to be the primary feeding mode employed by sardine globally. The analysis of stomach contents of individual fish showed that sardine from the same school ingested prey of similar size frequency and composition.

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Although stomach contents of fish from both years were numerically dominated by small prey items, sardine captured in 1993 showed a broader size range of prey than those collected in 1994. The higher incidence of larger, zooplankton prey in the stomach contents of fish collected in 1993 may possibly be linked to the smaller average size of fish sampled that year; fish in 1993 were 176.7 ± 28.9mm *TL* and 47.8 ± 28.8g *WM*, whereas those captured in 1994 were 208.2 ± 18.8mm *TL* and 70.0 ± 18.1g *WM*. Field studies have indicated that juvenile sardine are more zoophagous than adults (Hand and Berner 1959, Nakai 1962 in Kawasaki

and Kumagai 1984, King and Macleod 1976), suggesting that smaller fish employ particulate-feeding to a greater degree than do large fish. In addition, feeding periodicity in sardine is size-dependent, with small fish showing a peak in feeding activity at or around sunset whereas large fish appear to feed continuously (Chapter 5). That small sardine are more zoophagous and particulate-feed more frequently than large fish appears to be borne out by the results of the dietary analysis presented above.

Although numerically dominant, phytoplankton only contributed a small portion (1-10%) of the dietary carbon ingested 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 from the Benguela upwelling ecosystem, in which sardine was considered to be primarily phytophagous. 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. The relationship between the occurrence of these two food categories appeared inverse, with large quantities of phytoplankton and little zooplankton being consumed by sardine in autumn and spring, whereas more zooplankton and less phytoplankton was consumed in summer and winter. Dinoflagellates were relatively unimportant in stomach contents, and copepods were the most important zooplankton consumed (Davies 1957). King and Macleod (1976) reported that phytoplankton accounted for 10.3-15.2% of the total food volume ingested by juvenile (20-100mm SL) sardine, and for 71.9-83.3% for adult sardine (>100mm SL) sampled in the northern Benguela. The diatoms *Fragilaria karstenii, Chaetoceros* spp., *Coscinodiscus* spp., *Rhizosolenia setigera* and *Stephanopyxis turris* were the dominant phytoplankton encountered by those authors. Kruger and Cruickshank (1982) also reported that stomach contents of sardine sampled in the northern Benguela were dominated by phytoplankton, particularly the diatoms *Thalassiosira decipens, Delphineis karstenii* and

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Chaetoceros spp. It must be emphasized however, that comparisons between the diet of sardine in different systems are difficult to make because the availability of different food resources is likely to differ between systems.

The reports listed above suggest that diatom phytoplankton is the major food source for sardine in both the northern and the southern Benguela, whereas the results from this study contradict these findings and suggest that zooplankton contributes most to the dietary carbon of fish in the southern Benguela. However, the volumetric method employed by Davies (1957) and King and Macleod (1976) to assess the relative dietary importance of phytoplankton and zooplankton may overestimate the contribution made by phytoplankton. This is essentially because a diatom:copepod ratio of 2:1 by volume translates into a carbon ratio of 1:2.6 (see equations in Tables 6.1 and 6.2); therefore zooplankton are a far superior carbon source than are phytoplankton. Using volumetric measurements as indices of relative importance therefore provides an inaccurate representation of the real contribution to the diet by food type. The superiority of zooplankton as a food source relative to phytoplankton is further realized if nitrogen is used as the currency for comparison. Assuming carbon:nitrogen ratios of 4:1 and 6:1 for zooplankton and phytoplankton respectively, 1 unit volume of copepod has 7.8 times as much nitrogen as that contained within 1 unit volume of diatom phytoplankton. In terms of carbon and nitrogen contribution to the diet, diatoms are therefore a poor food source compared to zooplankton. Since diatoms have a lower carbon content per unit volume than dinoflagellates (Smayda 1978, Hitchcock 1982), a unit volume of dinoflagellates will provide a greater contribution to ingested carbon and nitrogen than that supplied by diatoms.

The use of inappropriate methodology when examining stomach contents has been identified as the cause leading to the 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 frequency of

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occurrence, which biases results in favour of small, plentiful prey items such as phytoplankton, and underestimates the importance of larger items like zooplankton. Whilst 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, as is shown above. Objective processing techniques which 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 to determine the true importance of a prey category (Konchina and Pavlov 1995).

Estimating the nutritional value of ingested prey depends on the accuracy of the relationships relating prey size to carbon content. The length-mass equations used in this study (Table 6.Ia) derived by Chisholm and Roff (1990) for copepods (which provided the majority of zooplankton-derived carbon in this study) were highly significant (r^2 values of 0.88 and 0.85 for calanoids and cyclopoids respectively and $p<0.0001$ for both), but were generated from tropical copepod species. Although James (1987) provided a length-dry weight regression for copepods from the southern Benguela, he did not differentiate between different copepod taxa. Relationships determined for the particular genera or even species from the region of study would obviously provide the most accurate estimations. Similarly, although the cell volume to carbon content relationships for diatoms and dinoflagellates have been widely used, they were not derived for local phytoplankton species. A second factor affecting the accuracy of nutritional value of various prey types is the assumption that unidentifiable prey occur at the same frequency as do identifiable prey, since the relative occurrence of prey types will be affected by differential digestion rates. Phytoplankton are evacuated faster than zooplankton by sardine (Chapters 4 and 5) and may also be digested more rapidly. If this is the case, the relative contribution by phytoplankton reported here may be an underestimate. Similarly, the dietary contribution made by crustacean eggs may be overestimated by this study, because copepod eggs appear to be resistant to digestion and have

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been shown to survive passage through clupeoid digestive tracts (Flinkman *et al.* 1994).

Although phytoplankton was a relatively unimportant contributor to the dietary carbon of sardine examined in this study, it is likely that the relative importance of phytoplankton in the diet of this species varies both spatially and temporally. In some regions and/or seasons, phytoplankton may well provide a substantial dietary contribution. It is possible that the timing and location of sardine samples collected for stomach content analysis in this study may have contributed to phytoplankton being underestimated as a dietary component. Firstly, phytoplankton biomass (as indexed by chlorophyll a) shows clear along-shore and cross-shelf gradients, with mean chlorophyll a concentrations being higher west of Cape Agulhas than those found to the east, and concentrations being lower offshore than inshore (Brown and Cochrane 1991, Brown 1992). The low phytoplankton contribution to the diet of sardine sampled in 1993 could reflect this gradient since many samples were collected over the phytoplankton-poor eastern Agulhas Bank. Most of the 1994 samples were collected from the inshore region between Cape Agulhas and Cape Columbine; the position of these samples could therefore be responsible for the increased importance of phytoplankton in the sardine's diet in 1994 compared to 1993. Secondly, phytoplankton biomass over the western Agulhas Bank shows a seasonal cycle. A modest spring (September/October) bloom over the WAB is truncated by the influx of warm, nutrient-impoverished Agulhas Current water over the shelf in November, and phytoplankton biomass levels only increase when the summer (January – March) upwelling cycle begins (Mitchell-Innes *et al.* 1999). For both 1993 and 1994, phytoplankton biomass was lowest over the WAB in November compared to other months sampled between September and March (Mitchell-Innes *et al.* 1999). Since sardine were sampled in November during both 1993 and 1994, it is likely that the dietary contribution by phytoplankton reported here probably represents a seasonal minima in this region.

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Fish (primarily anchovy) eggs contributed 16.5 and 13.5% for 1993 and 1994 respectively of dietary carbon ingested by sardine. In some instances the contribution from anchovy eggs was over 50% of ingested carbon, although samples where anchovy eggs provided a substantial input were only encountered over the eastern Agulhas Bank. The occurrence of anchovy eggs in sardine stomachs has been previously noted both in the southern Benguela (Valdés-Szeinfeld 1991) and in other regions where these two species co-exist (Santander *et al.* 1983, Alheit 1987). Valdés-Szeinfeld (1991) reported that 88% of sardine examined had anchovy eggs in their stomachs, with each fish having an average of about 130 eggs. She suggested that this intense predation by sardine accounted for up to 56% of total anchovy egg mortality. Although anchovy eggs were significant contributors to sardine dietary carbon in this study, they were not found in sardine stomachs in the large quantities found by Valdés-Szeinfeld (1991). Nevertheless, it is clear that anchovy eggs may be an important food source for sardine in localized areas. However, the fact that sardine and anchovy show some degree of spatial segregation during the summer, with sardine tending to be found inshore and anchovy offshore (Barange and Hampton 1997), would act to reduce predation on anchovy eggs by sardine.

Like sardine, anchovy *Engraulis capensis* derive the bulk of their nutritional input from crustacean zooplankton (James 1987). Mesozoopankton, principally large calanoid copepods and euphausiids of >1mm maximum dimension are the dominant zooplankton consumed by anchovy, although the small cyclopoid copepods *Oithona* spp. and *Oncaea* spp. may on occasion dominate stomach contents (Peterson *et al.* 1992). In contrast, sardine derive most of their dietary input from smaller zooplankton. These two species therefore appear to be trophically distinct, and minimise competition by partitioning their food resource on the basis of size. Sardine feed on small zooplankton captured by filter-feeding whilst anchovy feed on large zooplankton captured by particulate-feeding (James 1987). Because of the higher incidence of filter-feeding by sardine and their ability to capture smaller particles than

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those ingested by anchovy (Chapter 2), it is likely that phytoplankton is a more important dietary component for sardine than anchovy. In addition, the spatial segregation reported for these two species (Barange and Hampton 1997) is likely to be a contributing factor to the lack of dietary overlap between these species.

The trophic disparity between sardine and anchovy described above has previously been observed both in the southern Benguela and in other upwelling ecosystems. Sardine and anchovy recruits from presumably mixed shoals (*i.e.* caught in the same trawl) sampled off the South African west Coast consumed zooplankton prey of different sizes, with sardine ingesting significantly smaller copepods than anchovy (Louw *et al.* 1998). Although statistically significant, this study was limited by a small sample size, and the trophic ecologies of sardine and anchovy recruits requires further examination. Off Peru, Konchina (1991) reported that whilst sardine *Sardinops sagax* and anchovy *Engraulis ringens* both preferentially ingested zooplankton, sardine consumed primarily small herbivorous copepods and tunicates whereas anchovy consumed large copepods and euphausiids. The size of food items consumed by anchovy was 2.5 times larger than those consumed by sardine, and phytoplankton was more important in the diet of sardine than anchovy (Konchina 1991). Similarly, phytoplankton contributed more to the diet of Far Eastern sardine off Japan (65 ± 20% by mass) than it did to that of anchovy *E. japonica* (39 ± 18%), and sardines consistently ingested smaller copepods than did anchovy (Li *et al.* 1992).

This trophic disparity between sardine and anchovy therefore appears to be globally consistent, with results indicating that sardine feed on smaller organisms, and closer to the base of the food chain, than does anchovy. Such trophic differences may be responsible, in part, 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, 1992a), since modifications in the size structure and/or species composition of the food environment have been suggested

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as one mechanism whereby regime shifts may be initiated and sustained (Schwatrzlose *et al.* 1999). This hypothesis is further explored in Chapter 8.

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Chapter 7: Laboratory-Derived Carbon and Nitrogen Budgets for Adult Sardine

7.1: Introduction

The experiments described in Chapters 2, 3 and 4 provide data on the behavioural and physiological responses of sardine to a variety of food environments. In addition to elucidating some aspects of the trophic ecology of this species, these data may also be used to construct carbon and nitrogen budgets. Such models permit a quantification of the effects of particular food environments upon growth, and can be used to examine the suitability of particular food environments as sardine habitat. Carbon and nitrogen were used as budget currencies since they are key elements required for growth and provide an easy reference standard for the utilization of field data. The models were derived to examine the effect of prey type, concentration and size on the energetics of sardine under the foraging regime and plankton densities observed in the southern Benguela upwelling ecosystem.

7.2: Materials and methods

The carbon and nitrogen budgets derived below are based on data collected from laboratory experiments performed on adult sardine of mean length 236 mm TL, mean wet and dry masses of 146.5 and 42.2g respectively, and at an average temperature of 16.5 ± 2.1°C.

Carbon budget

The carbon budget is based on the equation (Durbin and Durbin 1983, James *et al.* 1989b):

$$G_C = R_C - T_C - E_C - Q_C \quad (1)$$

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where G_C = growth, R_C = ingested ration and T_C, E_C, and Q_C are losses through respiration, excretion and defaecation, respectively.

(a) Ingested ration (R_C)

The amount of food ingested by sardine is a function of the volume searched (v, l.fish^{-1}.h^{-1}), the efficiency with which sardine remove food from that volume (A, dimensionless), the food concentration (C, mg C.l^{-1}) and the time spent foraging (h, h.day^{-1}):

$$R_C = v \times A \times C \times h \text{ mg C.fish}^{-1}\text{.day}^{-1}. \quad (2)$$

However, v and A are difficult to quantify (Durbin and Durbin 1975, James 1988a) and can be replaced by the observed clearance rate (F, l.fish^{-1}.min^{-1}) which is the product of these two variables:

$$F = v \times A \text{ l.fish}^{-1}\text{.min}^{-1}. \quad (3)$$

Clearance rate (F) is multiplied by 60 to convert it to an hourly rate and is incorporated into equation (2):

$$R_C = (60F)Ch \text{ mg C.fish}^{-1}\text{.day}^{-1}. \quad (4)$$

Clearance rate (F) is dependent on prey size (P, µm; Chapter 2):

$$F = -2.5421 + 0.0939(P) - 0.0002(P)^2 + (2.3829\text{x}10^{-7})(P)^3 - (9.7258\text{x}10^{-11})(P)^4 + (1.3623\text{X}10^{-14})(P)^5 \text{ l.fish}^{-1}\text{.min}^{-1} \quad (5)$$

Equation (5) will hereafter be referred to as $f(P)$.

Combining equations 4 and 5 allows carbon gain to be expressed in terms of P, C and h:

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$$R_C = 60 * f(P) * C * h \text{ mg C.fish}^{-1}.\text{day}^{-1} \quad (6)$$

The mean dry mass of sardine used in experiments was 42.2g:

$$R_C = 1.4218 * f(P) * C * h \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1} \quad (7)$$

(b) Absorbed ration (pR_C)

Subtracting faecal losses (Q_C) from the ingested ration (R_C) gives a measure of the absorbed ration (pR_C, where p is the absorption efficiency of sardine fed on a particular diet), which enables equation 1 to be rewritten as:

$$G_C = pR_C - T_C - E_C \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1}. \quad (8)$$

For sardine fed phytoplankton the observed carbon absorption efficiency was 0.626 (Chapter 4), giving:

$$pR_C = 0.8901 * f(P) * C * h \text{ mg C.fish}^{-1}.\text{day}^{-1}. \quad (9)$$

For sardine fed zooplankton, p was 0.882:

$$pR_C = 1.2540 * f(P) * C * h \text{ mg C.fish}^{-1}.\text{day}^{-1}. \quad (10)$$

(c) Daily carbon losses

Respiration (T_C):

Respiration represents the major portion of carbon expenditure during both non-feeding (routine) and feeding activity.

(i) Daily cost of routine respiration (T_{rC}):

The mean measured routine respiration rate (T_r) of sardine was 0.178 mg $O_2.g^{-1}$ wet mass.h^{-1} (Chapter 3), which converts to 0.618 mg $O_2.g^{-1}$ dry mass.h^{-1}. This respiration rate may be converted to carbon currency using the relationship given by

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Parsons *et al.* (1984): mg C utilised = mg O_2 consumed x 12/32 x *RQ*. The mean respiratory quotient (*RQ*) of sardine was 0.955 (Chapter 3), therefore:

$$T_r = 0.2213 \text{ mg C.g}^{-1} \text{ dry mass.h}^{-1}, \quad (11)$$

and the daily cost of routine respiration is:

$$T_{rC} = 0.2213(24\text{-h}) \text{ mg C.g}^{-1} \text{ dry mass.d}^{-1}. \quad (12)$$

(ii) Daily cost of respiration during feeding (T_{fC} and T_{pC}):

Swimming speed was the primary determinant of respiration rate when sardine were feeding, accounting for 74 and 67% of the variability in respiration rate for filter- and particulate-feeding respectively (Chapter 3). Since feeding mode is dependent upon prey size (and to a lesser extent, concentration), carbon losses through respiration during feeding will also be size-dependent. Sardine switched from filter- to particulate feeding at a prey size of ≈1230µm, although larger particles present at sufficiently high concentrations elicited a filter-feeding response. The relationship between swimming speed (s, BL.s^{-1}) and respiration rate (T) for fish engaged in filter-feeding can thus be used to determine the carbon losses of fish feeding on prey of <1230µm:

$$T_f = 0.4131s - 0.2035 \text{ mg } O_2\text{.g}^{-1} \text{ wet mass.h}^{-1}. \quad (13)$$

For sardine particulate-feeding on prey <1230µm:

$$T_p = 0.5711s - 0.2891 \text{ mg } O_2\text{.g}^{-1} \text{ wet mass.h}^{-1}. \quad (14)$$

Converting equations (13) and (14) to dry mass, and expressing respiration costs in terms of carbon gives:

$$T_f = 0.5137s - 0.2531 \text{ mg C.g}^{-1} \text{ dry mass.h}^{-1}, \quad (15)$$

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$$T_p = 0.7101s - 0.3595 \text{ mg C.g}^{-1} \text{ dry mass.h}^{-1}. \quad (16)$$

The total cost of respiration during feeding per day is calculated by multiplying by *h*:

$$T_f = h(0.5137s - 0.2531) \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1}, \quad (17)$$

and

$$T_p = h(0.7101s - 0.3595) \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1}. \quad (18)$$

The speeds at which feeding sardine swim depends upon prey type and concentration, but does not appear to be affected by prey size. Data obtained during the experiments described in Chapters 2 and 3 show that swimming speeds of sardine filter-feeding on phytoplankton ranged from 0.70 - 1.64 BL.s^{-1}; Figure 7.1a) and had a mean value of 1.03 ± 0.23 BL.s^{-1}. No statistically significant relationship was observed between swimming speed and phytoplankton concentration (expressed as mg C.l^{-1}), although concentrations of >0.4mg C.l^{-1} elicited slightly higher swimming speeds (Figure 7.1c). Swimming speed appeared to be inversely correlated to phytoplankton size: larger cells eliciting lower swimming speeds (Figure 7.1e). However, this relationship was only weakly significant ($r^2 = 0.12$; $p = 0.014$), and was deemed to be an experimental artifact.

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For the purposes of this model, sardine filter-feeding on phytoplankton were assumed to do so at a constant swimming speed (1.03 BL.s^{-1}) unaffected by prey concentration or size. The total cost of respiration during filter-feeding on phytoplankton is therefore only dependent on foraging time, and can be expressed as:

$$T_f = h(0.2760) \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1}. \quad (19)$$

Sardine feeding on crustacean zooplankton showed a wide range of swimming speeds ranging from 0.86-2.66 BL.s^{-1} (Figure 7.1b), and appeared to

regulate their swimming speed according to prey carbon concentration (Figure 7.1d), but not prey size (Figure 7.1f).

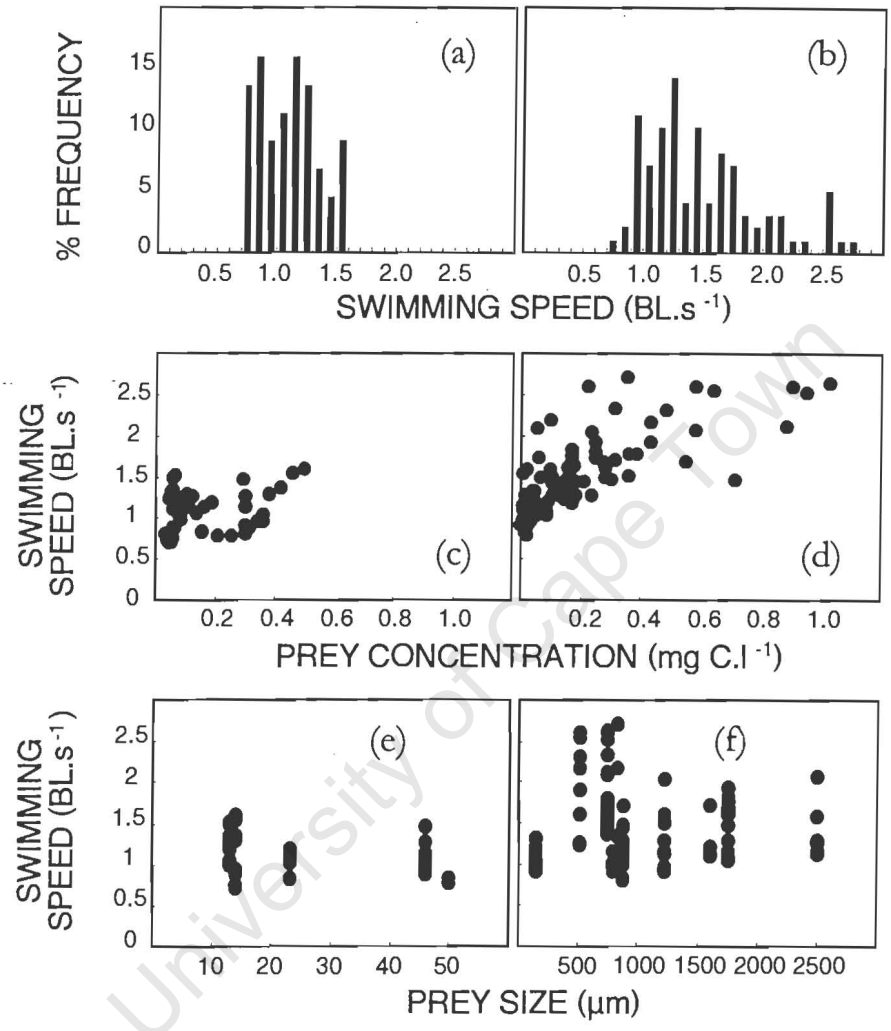

Figure 7.1: Effect of prey type, concentration and size on the swimming speeds of sardine feeding on phytoplankton and crustacean zooplankton (natural assemblages only). Swimming speed distributions of sardine (a) filter-feeding on phytoplankton and (b) filter- and particulate-feeding on zooplankton; scatterplots of swimming speed and prey concentration for sardine (c) filter-feeding on phytoplankton and (d) filter- and particulate-feeding on zooplankton; and scatterplots of swimming speed and prey size for sardine (e) filter-feeding on phytoplankton and (f) filter- and particulate-feeding on zooplankton are shown. See text for details.

A hyperbolic relationship between mean swimming during feeding on crustacean zooplankton and prey concentration for fish engaged in both filter- and particulate-feeding is evident; this relationship is best described by a linear

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regression relating ln-transformed swimming speed to ln-transformed carbon concentration (n = 98; $r^2 = 0.59$; $p < 0.001$):

$$\text{Ln}(s; \text{BL.s}^{-1}) = 0.1702[\text{Ln}(C; \text{mg.l}^{-1})] + 0.7575 \quad (20)$$

For sardine feeding on crustacean zooplankton, equation 20 may be substituted into equations 17 and 18 to express the costs of respiration during feeding in terms of prey concentration. For sardine filter-feeding on zooplankton:

$$T_f = h(1.0946C^{0.1702} - 0.2528) \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1}, \quad (21)$$

and particulate-feeding on zooplankton:

$$T_p = h(1.5133C^{0.1702} - 0.3592) \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1}. \quad (22)$$

Total daily carbon losses through respiration (T_C) are calculated by combining the routine (equation 12) and feeding (equations 19, 21 and 22) respiration costs.

For sardine filter-feeding on phytoplankton:

$$T_{fpC} = 0.0547h + 5.3112 \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1}. \quad (23)$$

For sardine filter-feeding on zooplankton:

$$T_{fzC} = h(1.0946C^{0.1702} - 0.4741) + 5.3112 \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1}. \quad (24)$$

For sardine particulate-feeding on zooplankton:

$$T_{pzC} = h(1.5133C^{0.1702} - 0.5805) + 5.3112 \text{ mg C.g}^{-1} \text{ dry mass.day}^{-1}. \quad (25)$$

Carbon losses through respiration have been expressed in terms of C and h.

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(iii) Total daily excretion (E_C):

Ammonia constituted 75.3% of the total nitrogen excreted by fed sardine (Chapter 4), the remainder (24.7%) being in the form of dissolved organic nitrogen (DON). Although the composition of DON excreted by sardine was not determined, sardine excreted urea at a mean endogenous rate of 2.46 µg $N.g^{-1}$ dry $mass.h^{-1}$ compared to a mean endogenous ammonia excretion rate of 19.25 µg $N.g^{-1}$ dry $mass.h^{-1}$ (Chapter 4). Assuming that this ammonia:urea ratio of 7.84:1 remains constant during exogenous excretion, urea will therefore account for 9.6% (75.3/7.84) of the excreted DON. For the purposes of the carbon budget, the remainder of the DON was assumed to comprise equal portions (7.6%) of creatine and trimethylamine, the other organic nitrogen compounds excreted by teleosts (Durbin and Durbin 1983, Handy and Poxton 1993).

The C:N ratio of urea [CON_2H_4] is 0.5:1, therefore for every 1g of urea nitrogen excreted, 0.4286g (12/14 x 0.5) of carbon will be lost. If urea is 9.6% of the total nitrogen excreted, then 0.0412g (0.096 x 0.4286) of carbon will be lost in urea for every 1g of nitrogen excreted. The C:N ratio of creatine [$C_4H_9N_3O_2$] is 4:3, therefore for every 1g of creatine nitrogen excreted 1.1429g (12/14 x 1.3333) of carbon will be lost. If creatine is 7.6% of the total nitrogen excreted, then 0.0869g (0.076 x 1.1429) of carbon will be lost in creatine for every 1g of nitrogen excreted. The C:N ratio of trimethylamine [C_3H_9N] is 3:1, therefore for every 1g of trimethylamine nitrogen excreted 0.2857g (12/14 x 0.3333) of carbon will be lost. If trimethylamine is 7.6% of the total nitrogen excreted, then 0.0217g (0.076 x 0.2857) of carbon will be lost in trimathylamine for every 1g of nitrogen excreted. Summing these carbon losses gives a value of 0.1498g of carbon lost for every 1g of N excreted.

Total daily losses through nitrogen excretion (E_N) are the sum of endogenous (routine or basal) and exogenous (due to feeding) excretion. Endogenous excretion by sardine was estimated at 0.675 mg $N.g^{-1}$ dry $mass.d^{-1}$, and exogenous excretion (e_N) was linearly related to ingested ration (R_N; Chapter 4):

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$$e_N = 0.698R_N \quad (26)$$

So total daily losses through nitrogen excretion are:

$$E_N = 0.698R_N + 0.675 \text{ mg N.g}^{-1} \text{ dry mass.d}^{-1}. \quad (27)$$

Converting this to carbon (x 0.1498) gives:

$$E_C = 0.1046R_N + 0.1011 \text{ mg C.g}^{-1} \text{ dry mass.d}^{-1}. \quad (28)$$

Using the mean value of C:N ratios of phytoplankton and zooplankton given in Chapter 4:

$$\text{phytoplankton C:N} = 5.525:1 \quad (29)$$

$$\text{zooplankton C:N} = 4.215:1 \quad (30)$$

and substituting the appropriate values into equation (28) allows carbon losses through excretion to be entirely expressed in terms of carbon. For phytoplankton:

$$E_C = 0.0189R_C + 0.1011 \text{ mg C.g}^{-1} \text{ dry mass.d}^{-1}. \quad (31)$$

For zooplankton:

$$E_C = 0.0248R_C + 0.1011 \text{ mg C.g}^{-1} \text{ dry mass.d}^{-1}. \quad (32)$$

Substituting equation (7) into equations (31) and (32) allows carbon losses through excretion to be expressed in terms of *P*, *C* and *h*. For phytoplankton:

$$E_C = 0.0269(FCh) + 0.1011 \text{ mg C.g}^{-1} \text{ dry mass.d}^{-1}. \quad (33)$$

For zooplankton:

$$E_C = 0.0353(FCh) + 0.1011 \text{ mg C.g}^{-1} \text{ dry mass.d}^{-1}. \quad (34)$$

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(d) Growth

The equations summarised in Table 7.1 may be substituted into equation (8) to provide estimates of daily growth of sardine as a function of *P*, *C* and *h*.

The gross and net growth efficiencies (K_{1C} and K_{2C} respectively) are calculated from the following expressions (Durbin and Durbin 1983, James *et al.* 1989b):

$$K_{1C} = G_C/R_C, \quad (35)$$

and

$$K_{2C} = G_C/pR_C. \quad (36)$$

Table 7.1: Summary of equations used in the carbon budget (mg C.g^{-1} dry mass.d^{-1}) for adult sardine.

Entity	Phytoplankton	Microzooplankton	Mesozooplankton
Ingested ration (R_C)		$1.4218*f(P)*C*h$	
Absorbed ration (pR_C)	$0.8901*f(P)*C*h$		$1.2540*f(P)*C*h$
Respiration (T_C)	$0.0547*h + 5.3112$	$(1.0946C^{0.1702})*h + 5.3112$	$(1.5133C^{0.1702})*h + 5.3112$
Excretion (E_C)	$0.0189*R_C + 0.1011$		$0.0248*R_C + 0.1011$
Growth (G_C)		$PR_C - T_C - E_C$	
Gross growth efficiency (K_{1C})		G_C/R_C	
Net growth efficiency (K_{2C})		G_C/pR_C	

Nitrogen budget

The nitrogen budget is based on the general equation (Durbin and Durbin 1983, James *et al.* 1989b):

$$G_N = R_N - E_N - Q_N \quad (37)$$

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(d) Growth

The equations summarised in Table 7.1 may be substituted into equation (8) to provide estimates of daily growth of sardine as a function of *P*, *C* and *h*.

The gross and net growth efficiencies (K_{1C} and K_{2C} respectively) are calculated from the following expressions (Durbin and Durbin 1983, James *et al.* 1989b):

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Absorbed ration (pR_C)	$0.8901*f(P)*C*h$	$1.2540*f(P)*C*h$	
Respiration (T_C)	$0.0547*h + 5.3112$	$(1.0946C^{0.1702})*h + 5.3112$	$(1.5133C^{0.1702})*h + 5.3112$
Excretion (E_C)	$0.0189*R_C + 0.1011$	$0.0248*R_C + 0.1011$	
Growth (G_C)		$PR_C - T_C - E_C$	
Gross growth efficiency (K_{1C})		G_C/R_C	
Net growth efficiency (K_{2C})		G_C/pR_C	

Nitrogen budget

The nitrogen budget is based on the general equation (Durbin and Durbin 1983, James *et al.* 1989b):

$$G_N = R_N - E_N - Q_N \quad (37)$$

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where G_N = growth, R_N = ingested ration and E_N and Q_N are losses through excretion and defaecation. This can be simplified to:

$$G_N = pR_N - E_N \text{ mg N.g}^{-1} \text{ dry mass.day}^{-1}. \quad (38)$$

The nitrogen budget may be expressed in the same three variables as the carbon budgets, namely prey size (P, µm), plankton concentration (C, mg C.l^{-1} or N, mg N.l^{-1}) and foraging time (h, h.day^{-1}).

(a) Ingested and absorbed ration (R_N and pR_N)

Equation (7) may be re-expressed in terms of nitrogen:

$$R_N = 1.4218 * f(P) * N * h \text{ mg N.g}^{-1} \text{ dry mass.day}^{-1}, \quad (39)$$

and the absorbed ration calculated using nitrogen absorption efficiencies determined in Chapter 4. For phytoplankton, $p = 0.787$ and:

$$pR_N = 1.1190 * f(P) * N * h \text{ mg N.g}^{-1} \text{ dry mass.day}^{-1}. \quad (40)$$

For zooplankton, $p = 0.933$ and:

$$pR_N = 1.3265 * f(P) * N * h \text{ mg N.g}^{-1} \text{ dry mass.day}^{-1}. \quad (41)$$

(b) Daily nitrogen losses (E_N)

The relationship between total daily nitrogen excretion and the ingested ration is given by equation (27). By substituting equation (39) into equation (27), E_N is expressed in terms of P, N and h:

$$E_N = 0.9924 * f(P) * N * h + 0.675 \text{ mg N.g}^{-1} \text{ dry mass.day}^{-1}. \quad (42)$$

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(c) Growth (G_N)

In order to standardize the input currency for both the carbon and nitrogen budgets, the nitrogen budget may be expressed in terms of the carbon content of the plankton by using the C:N ratios given above for phytoplankton and zooplankton {equations (29) and (30)}. Daily growth of *Sardinops sagax* in nitrogen as a function of *P*, *C* and *h* may then be estimated by substituting the various equations given in Table 7.2 into equation (38). The gross and net nitrogen growth efficiencies of sardine are calculated from the following expressions:

$$K_{1N} = G_N/R_N, \quad (43)$$

and

$$K_{2N} = G_N/pR_N. \quad (44)$$

Table 7.2: Summary of equations used in the nitrogen budget (in mg $N.g^{-1}$ dry $mass.d^{-1}$) for adult sardine.

Entity	Phytoplankton	Microzooplankton	Mesozooplankton
		A. Nitrogen as input currency	
Ingested ration (R_N)		$1.4218*f(P)*N*h$	
Absorbed ration (pR_N)	$1.1190*f(P)*N*h$		$1.3265*f(P)*N*h$
Excretion (E_N)		$0.9924*f(P)*N*h + 0.675$	
		B. Carbon as input currency	
Ingested ration (R_N)	$0.2573*f(P)*C*h$		$0.3373*f(P)*C*h$
Absorbed ration (pR_N)	$0.2025*f(P)*C*h$		$0.3147*f(P)*C*h$
Excretion (E_N)	$0.1796*f(P)*C*h + 0.675$		$0.2354*f(P)*C*h + 0.675$
Growth (G_N)		$pR_N - E_N$	
Gross growth efficiency (K_{1N})		G_N/R_N	
Net growth efficiency (K_{2N})		G_N/pR_N	

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Input parameters

The carbon and nitrogen budget models were constructed to describe the effects of prey size (*P*; µm), plankton concentration (*C*; mg C.l^{-1}) and foraging time (*h*; h.day^{-1}) on the potential intake, expenditure, growth and growth efficiencies of sardine. Three feeding behaviour-food type scenarios were examined; sardine filter-feeding on phytoplankton, filter-feeding on microzooplankton, and particulate-feeding on mesozooplankton. The input parameters (*P*, *C* and *h*) were allocated different range values depending on food type, and reflecting the trophic conditions of the southern Benguela (Table 7.3). To illustrate the models and assess the effect of each variable on sardine growth, two of the three input parameters were held at fixed values while the third varied over the ranges given for each of the scenarios.

Table 7.3: Variable range and fixed values for the input parameters used in the carbon and nitrogen models.

Variable	Phytoplankton		Microzooplankton		Mesozooplankton	
	Range	Fixed	Range	Fixed	Range	Fixed
Prey size (*P*, µm)	0-500	250	50-1230	700	1230-3000	2000
Plankton concentration (*C*, mg C.g^{-1}.l^{-1})	0.0-1.0	0.5	0.0-1.0	0.2	0.0-0.1	0.05
Foraging time (*h*, h.d^{-1})	0-24	12	0-24	12	0-24	12

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Phytoplankton

Phytoplankton size for the carbon and nitrogen budget models ranged from 0-500µm, encompassing large solitary diatoms such as *Coscinodiscus,* smaller chain-forming diatoms such as *Chaetoceros*, and the size range of dinoflagellates observed in sardine stomach contents (Chapter 6). A fixed value of 250µm was used.

The range of phytoplankton concentrations (0-1.0 mg C.l^{-1}) used in the carbon and nitrogen budgets reflects values observed in the southern Benguela upwelling system (Shannon and Pillar 1986, Brown and Hutchings 1987, Pitcher 1988, Brown

1992, Pitcher *et al.* 1992, McMurray *et al.* 1993, Pitcher *et al.* 1998, Mitchell-Innes *et al.* 1999). Phytoplankton biomass values given in terms of chlorophyll *a* were converted to carbon using a carbon:chlorophyll *a* ratio of 40:1 (Pitcher 1988). Depth-integrated mean phytoplankton biomass values typically range from 1-5 mg Chl *a*.m^{-3} (Brown 1992; ≈ 0.04-0.20 mg C.l^{-1}). However, vertical profiles of phytoplankton biomass generally show fluorescence maxima which may attain extremely high concentrations for both diatoms (*e.g.* 0.5 mg C.l^{-1}; Pitcher 1988) and dinoflagellates (*e.g.* 139 mg Chl *a*.m^{-3} ≈ 3.5 mg C.l^{-1}; Walker and Pitcher 1991; 50 mg Chl *a*.m^{-3} ≈ 2.0 mg C.l^{-1}; Pitcher *et al.* 1998). Therefore, the depth-integrated mean values given by Brown (1992) are underestimates of phytoplankton concentrations that would actually be encountered by sardine. A phytoplankton concentration of 0.5 mg C.l^{-1}, which approximates the density of developing phytoplankton blooms (Brown and Hutchings 1987, Pitcher 1988) was used as the fixed value for this variable. Foraging time was varied between 0-24 h.day^{-1} with a fixed value of 12 h.day^{-1}.

Microzooplankton

For the purposes of this study, microzooplankton have been defined as all zooplankton that would elicit a filter-feeding response from sardine; *i.e.* any zooplankter of <1230µm (Chapter 2). Therefore *P* ranged from 50-1230µm, and was given a fixed value of 700µm, approximating the maximum dimension of small copepods (cyclopoids and calanoids) in the Benguela system.

Estimates of the volumetric density of zooplankton in the southern Benguela are rare, since most published data are given per unit area (m^2) over the upper 200m of the water column (Peterson *et al.* 1992, Verheye *et al.* 1992, 1994, Hutchings *et al.* 1995, Richardson *et al.* 1998). Areal estimates of zooplankton (primarily copepod) biomass in the southern Benguela range from 0.5-4.0 gC.m^{-2} (Verheye *et al.* 1992, Hutchings *et al.* 1995), equivalent to 0.0025-0.02 mgC.l^{-1}. As is the case for phytoplankton, these depth-integrated estimates of zooplankton biomass are likely to significantly underestimate actual volumetric density, since they assume homogeneity in vertical distribution. Depth-stratified sampling has shown that this is seldom the case (*e.g.* Verheye and Hutchings 1988, Verheye *et al.* 1994).

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Most of the data on zooplankton abundance in the Benguela system has been derived from nets with a mesh size of 200µm or greater (Verheye *et al.* 1992). These nets have been shown to substantially underestimate the biomass of small zooplankton (Painting *et al.* 1993a), with total zooplankton retention occurring only for copepods that have a body width considerably larger than that of the mesh width (Pillar 1984a). In Northern temperate seas, copepods that pass through 200µm mesh nets have become recognized as comprising a significant portion of mesozooplankton biomass (Nakamura and Turner 1997), with the cyclopoid copepods *Oithona* spp. and *Oncaea* spp. now considered to be the most abundant metazoa in the world's oceans (Paffenhöfer 1993). Recent studies have shown that in some regions the biomass of cyclopoids often dominates over that of calanoid copepods (Sabatini and Kiørboe 1994, Nielsen and Sabatini 1996).

For the reasons described above, published estimates of zooplankton density in the southern Benguela are considered underestimates (L. Hutchings, Marine & Coastal Management, pers. comm.). A microzooplankton concentration range of 0.0-1.0 mg $C.l^{-1}$, with a fixed value of 0.2 mg $C.l^{-1}$ was considered appropriate, and was used for the carbon and nitrogen models. Foraging time was varied between 0-24 $h.day^{-1}$, and was fixed at a value of 12 $h.day^{-1}$.

Mesozooplankton

For the purposes of this study, mesozooplankton have been defined as all zooplankton that would elicit a particulate-feeding response from sardine; *i.e.* any zooplankter of >1230µm (Chapter 2). Therefore *P* ranged from 1230-3000µm, and was given a fixed value of 2000µm, approximating the maximum dimension of large copepods (*Calanus*, *Calanoides* etc.) in the Benguela system and being the prey size at which clearance rate (*F*) reaches its maximum value (Chapter 2).

Mesozooplankton concentration ranged from 0.0-0.1 mg $C.l^{-1}$, with a fixed value of 0.05 mg $C.l^{-1}$. This range was estimated from mesozooplankton biomass data reported by Verheye and Hutchings (1988). Foraging time was varied between 0-24 $h.day^{-1}$ with a fixed value of 12 $h.day^{-1}$.

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7.3: Results

Figures 7.2-7.7 illustrate the carbon and nitrogen models. Intake (A1-C1), expenditure (A2-C2), growth (A3-C3), and gross and net growth efficiencies (A4-C4) for sardine filter-feeding on phytoplankton (A), filter-feeding on microzooplankton (B) and particulate-feeding on mesozooplankton (C) over a range of prey sizes (*P*), plankton concentrations (*C*) and foraging times (*h*) are shown. In each figure the shaded area indicates the scope for growth under the various scenarios. The relationships between the model outputs (intake, expenditure, growth and growth efficiency) and *P* were curvilinear for both the carbon and nitrogen models (Figures 7.2 and 7.3), reflecting the fifth-order polynomial power function used to describe the effect of prey size on clearance rate (*F*; see Chapter 2). Model outputs varied linearly with varying input values of *C* and *h* (Figures 7.4-7.7). The effects of varying each input parameter are described in more detail below.

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Prey size (*P*)

Varying *P* whilst *C* and *h* were held at fixed values did not have a marked effect on scope for growth or net growth efficiencies between food type (phytoplankton, microzooplankton and mesozooplankton) in the carbon budget (Figure 7.2).

For sardine feeding on phytoplankton, scope for growth and growth efficiency increased hyperbolically with increasing prey size, reaching maximum levels of 50.5 mg $C.g^{-1}DM.d^{-1}$ and 0.87 respectively at a prey size of 400µm. The hyperbolic shape of these curves reflects the reduced retention efficiency and hence clearance rate of smaller particles (Chapter 2). The scopes for growth of sardine feeding on either micro- or mesozooplankton were lower than that of fish feeding on phytoplankton over much of the prey size ranges used, although scope for growth increased for microzooplankton >1000µm to a maximum value of 55.4 mg $C.g^{-1}DM.d^{-1}$ at a prey size of 1230µm. Maximum net growth efficiencies of 0.83 and 0.71 were reached for fish filter-feeding on microzooplankton and particulate-feeding on mesozooplanton respectively.

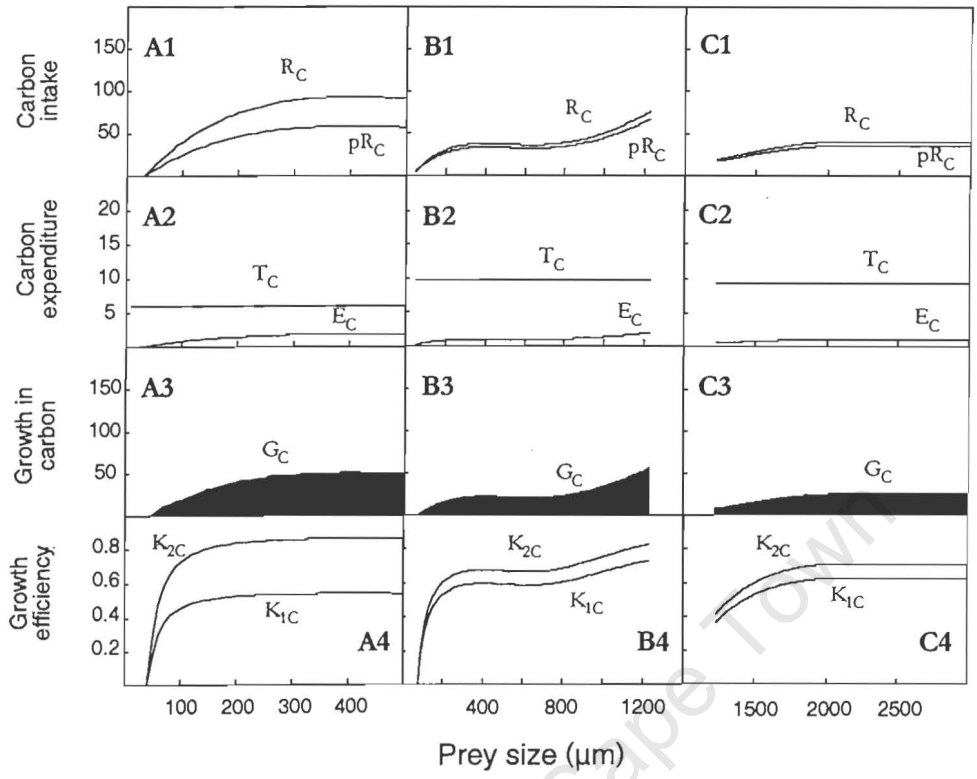

Figure 7.2: Effect of prey size (µm) upon (1) carbon intake, (2) expenditure, (3) scope for growth and (4) gross and net growth efficiencies of sardine feeding on (A) phytoplankton, (B) microzooplankton and (C) mesozooplankton. Carbon data are in mg $C.g^{-1}DM.d^{-1}$.

Varying *P* in the nitrogen budget had a more marked effect on growth and growth efficiencies between food type than was the case in the carbon budget (Figure 7.3). Sardine feeding on phytoplankton achieved a maximum growth rate of 0.83 $mgN.g^{-1}DM.d^{-1}$, and a maximum net growth efficiency of 0.062, substantially lower than maximum values attained for fish feeding on zooplankton. Maximum growth and net growth efficiencies in nitrogen were higher for sardine feeding on microzooplankton than on mesozooplankton, with values of 3.56 $mgN.g^{-1}DM.d^{-1}$ and 0.212 for the former and 1.54 $mgN.g^{-1}DM.d^{-1}$ and 0.175 for the latter.

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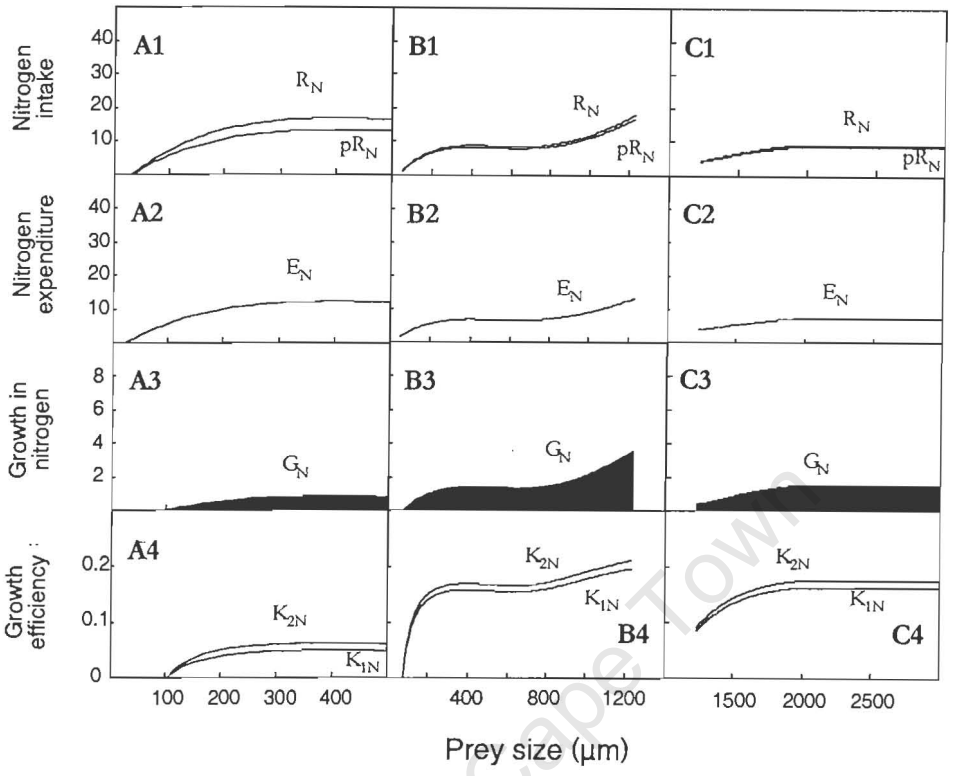

Figure 7.3: Effect of prey size (µm) upon (1) nitrogen intake, (2) expenditure, (3) scope for growth and (4) gross and net growth efficiencies of sardine feeding on (A) phytoplankton, (B) microzooplankton and (C) mesozooplankton. Nitrogen data are in mg $N.g^{-1}DM.d^{-1}$.

Plankton concentration (*C*)

Of the three input variables used, plankton concentration had the largest effect on the outputs of both the carbon and nitrogen budget models (Figure 7.4).

Ingested carbon ration was similar over the concentration ranges used for both phytoplankton and microplankton (both ranged from 0-1 mg $C.l^{-1}$), but the lower assimilation efficiency for phytoplankton carbon reduced absorbed ration significantly. Despite the substantially lower concentration range used for mesozooplankton (0-0.1 mg $C.l^{-1}$) compared to the other food types, the higher clearance rate of sardine feeding on this food resulted in carbon intake being approximately half of that for fish feeding on either phytoplankton or microzooplankton.

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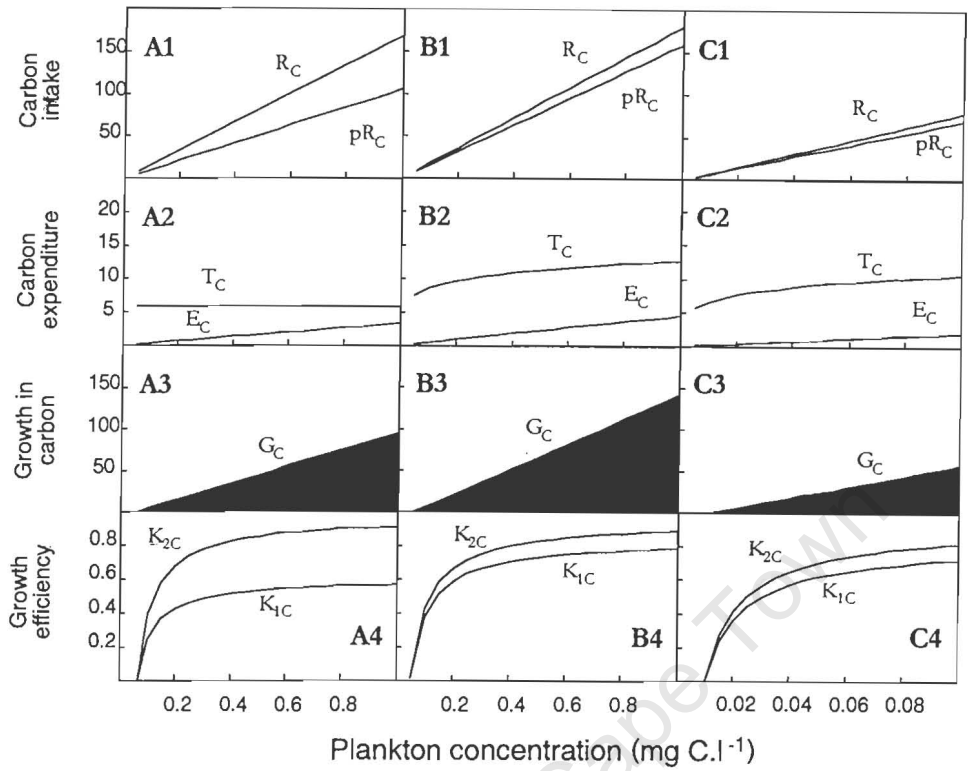

Figure 7.4: Effect of prey concentration (mg C.l^{-1}) upon (1) carbon intake, (2) expenditure, (3) scope for growth and (4) gross and net growth efficiencies of sardine feeding on (A) phytoplankton, (B) microzooplankton and (C) mesozooplankton. Carbon data are in mg C.g^{-1}DM.d^{-1}.

Because phytoplankton concentration had no effect on sardine swimming speeds, respiration costs were not affected by concentration, whereas these increased hyperbolically for fish feeding on zooplankton. Carbon lost through excretion was proportional to the ingested ration.

Sardine feeding on microzooplankton showed the highest scope for growth at the maximum concentration used, and attained a maximum growth rate of 141.4 mg C.g^{-1}DM.d^{-1}. Fish feeding on phytoplankton also attained a high carbon growth rate (95.8 mg C.g^{-1}DM.d^{-1}), whereas those feeding on mesozooplankton only reached a maximum growth of 57.1 mg C.g^{-1}DM.d^{-1}. Maximum net carbon growth efficiencies were highest for sardine feeding on phytoplankton (0.912), followed by fish feeding on microzooplankton (0.890), and microzooplankton (0.818).

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The effect of plankton concentration upon growth and growth efficiency in the nitrogen budget was substantial, and, as was the case for the carbon budget, showed a marked difference between food type (Figure 7.5). Scope for growth across the concentration ranges used was highest for sardine feeding on microzooplankton, and reached a maximum of 9.36 mg $N.g^{-1}DM.d^{-1}$ at a plankton concentration of 1.0 $mgC.l^{-1}$. Fish feeding on mesozooplankton or phytoplankton had lower growth maxima (3.74 and 2.03 mg $N.g^{-1}DM.d^{-1}$ respectively). Maximum net growth efficiencies were similar for sardine feeding on micro- and mesozooplankton (0.235 and 0.213 respectively), although the efficiency curve for microzooplankton reached its maximum sooner than was the case for mesozooplankton. Net growth efficiency was substantially lower for fish feeding on phytoplankton, reaching a maximum value of 0.085.

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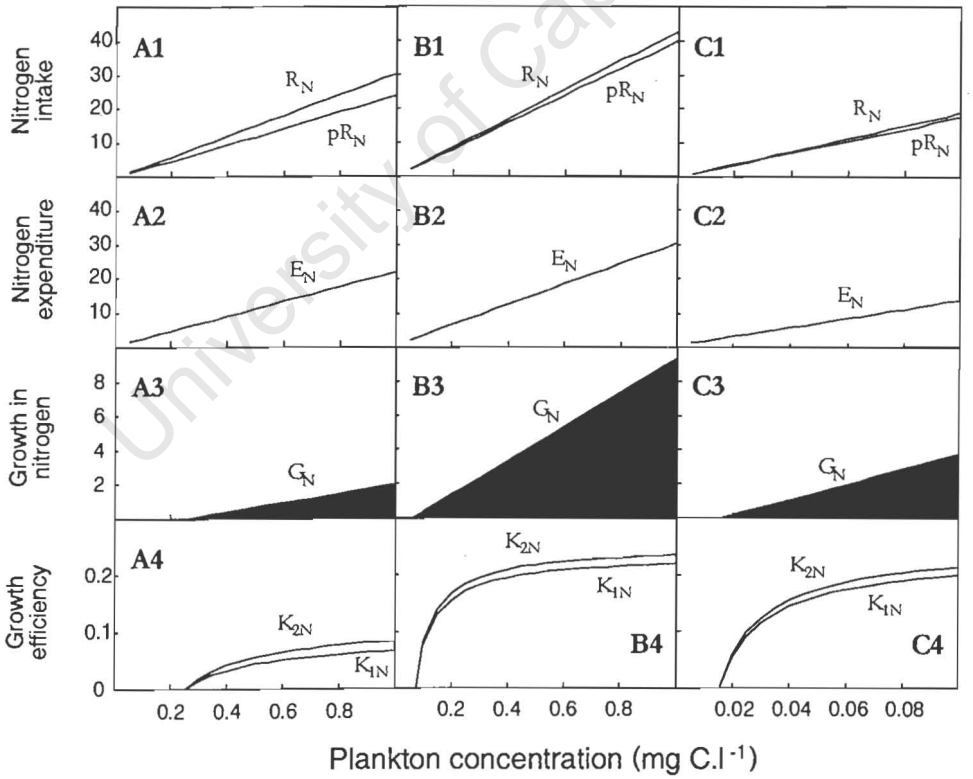

Figure 7.5: Effect of prey concentration (mg $C.l^{-1}$) upon (1) nitrogen intake, (2) expenditure, (3) scope for growth and (4) gross and net growth efficiencies of sardine feeding on (A) phytoplankton, (B) microzooplankton and (C) mesozooplankton. Nitrogen data are in mg $C.g^{-1}DM.d^{-1}$.

Foraging time (*h*)

Increased foraging time in the carbon budget model resulted in greater increases in carbon intake, scope for growth and net growth efficiency for sardine feeding on phytoplankton than for those feeding on either type of zooplankton (Figure 7.6). The lower scope for growth for fish feeding on zooplankton (maximum values of 47.7 and 54.5 mg $C.g^{-1}DM.d^{-1}$ for micro- and mesozooplankton respectively compared to a maximum of 95.2 mg $C.g^{-1}DM.d^{-1}$ for fish feeding on phytoplankton) was due to higher respiration costs as well as a lowered carbon intake. Net carbon growth efficiencies reached maximum levels after ≈ 8h in all food type scenarios, but were higher for fish feeding on phytoplankton (0.906) than for those feeding on either microzooplankton (0.751) or mesozooplankton (0.781).

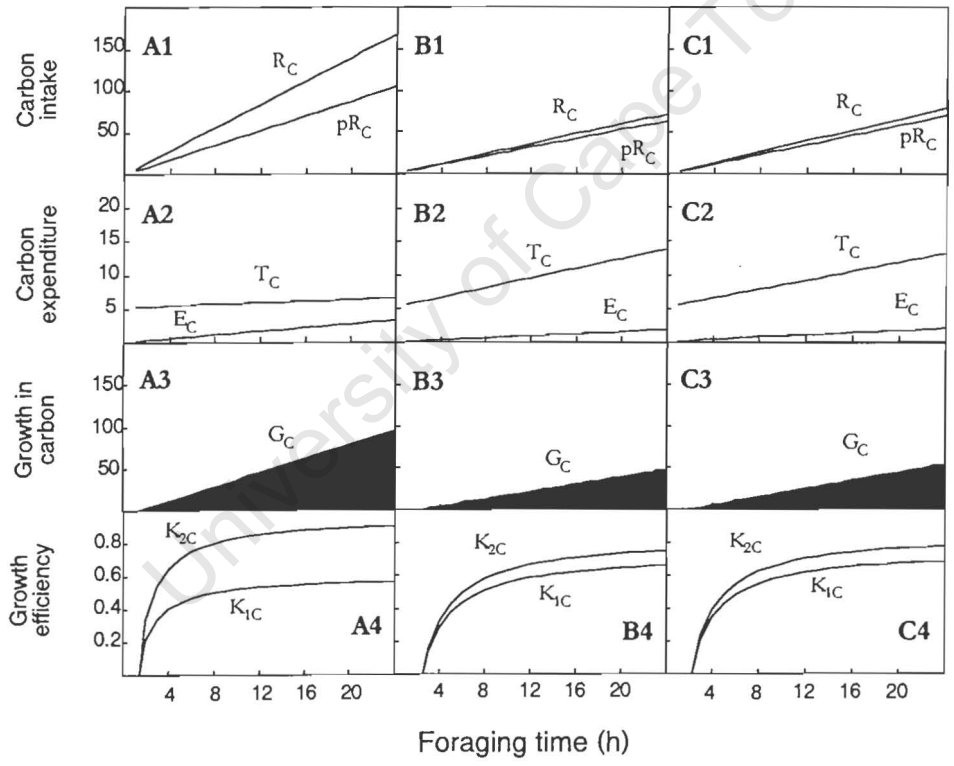

Figure 7.6: Effect of foraging time ($h.d^{-1}$) upon (1) carbon intake, (2) expenditure, (3) scope for growth and (4) gross and net growth efficiencies of sardine feeding on (A) phytoplankton, (B) microzooplankton and (C) mesozooplankton. Carbon data are in mg $C.g^{-1}DM.d^{-1}$.

Increased foraging time in the nitrogen budget model resulted in a higher nitrogen intake for fish feeding on phytoplankton than for those feeding on either type

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of zooplankton. Because nitrogen excretion is proportional to ingested ration for all food types, the reduced absorption efficiency of fish for phytoplankton nitrogen resulted in a slightly lower scope for growth, and markedly lower growth efficiencies, than fish feeding on zooplankton (Figure 7.7). Intake, expenditure, scope for growth and growth efficiencies were similar for sardine feeding on either type of zooplankton. Scope for growth maxima were 2.03, 3.34 and 3.74 mg $N.g^{-1}DM.d^{-1}$, and maximum net growth efficiencies were 0.085, 0.210 and 0.213 for sardine feeding on phyto-, micro- and mesozooplankton respectively.

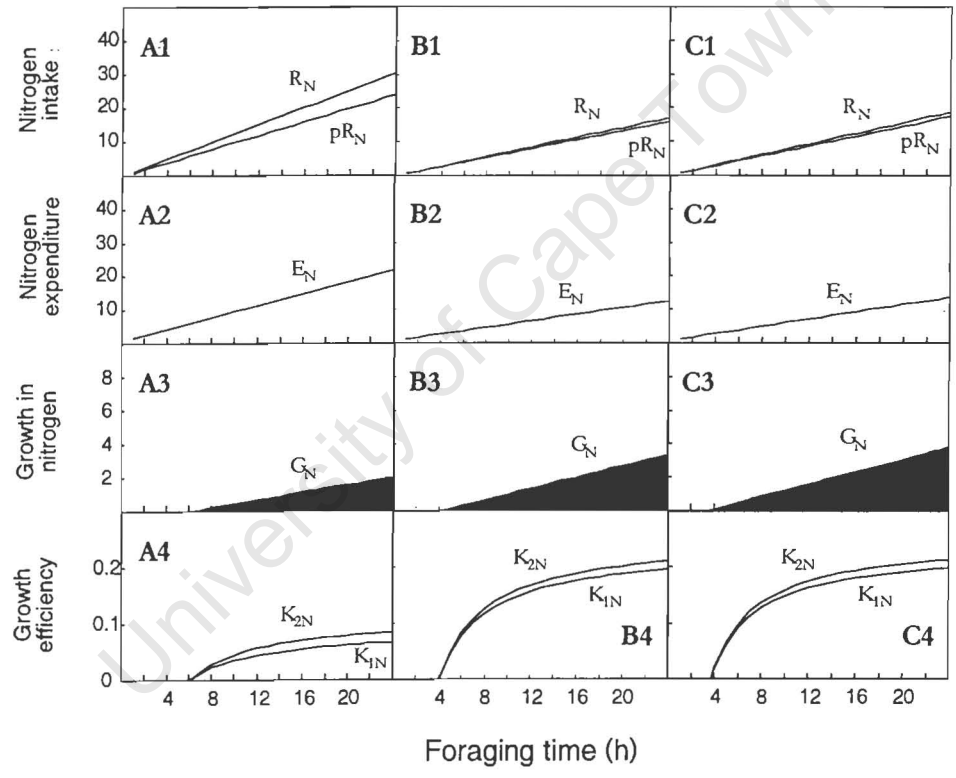

Figure 7.7: Effect of foraging time ($h.d^{-1}$) upon (1) nitrogen intake, (2) expenditure, (3) scope for growth and (4) gross and net growth efficiencies of sardine feeding on (A) phytoplankton, (B) microzooplankton and (C) mesozooplankton. Nitrogen data are in mg $C.g^{-1}DM.d^{-1}$.

The carbon and nitrogen budgets allow the estimation of minimum input values that must be met before sardine can attain their maintenance ration or show positive growth. Since prey size, plankton concentration and foraging time are independent and unrelated to each other, the minimum values for all three

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parameters must be exceeded before sardine can attain positive growth. In both the carbon and nitrogen budget models, sardine showed positive growth over most of the input ranges used, achieving their maintenance ration (i.e. > zero growth) at relatively low input values (Table 7.4). Lower values of *P*, *C* and *h* were required to fulfill the maintenance ration in terms of carbon than was the case for nitrogen, except for sardine feeding on microzooplankton and mesozooplankton, where the minimum prey size was the same for both budget models. Additionally, growth efficiencies were higher in the carbon budget than in the nitrogen budget. These results indicate that growth in carbon could occur under conditions where growth in nitrogen would be unattainable, and suggests that nitrogen, rather than carbon, limits sardine growth in the field.

Table 7.4: Minimum values of *P*, *C* and *h* derived from the budgets required for positive growth by sardine.

Variable	Food type		
	Phytoplankton	Microzooplankton	Mesozooplankton
(A) Carbon budget			
P (µm)	50	80	<1230
C (mg C.l^{-1})	0.06	0.05	0.01
h (h.d^{-1})	2	3	3
(B) Nitrogen budget			
P (µm)	110	80	<1230
C (mg C.l^{-1})	0.25	0.07	0.016
h (h.d^{-1})	6	5	4

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7.4: Discussion

The carbon and nitrogen budgets derived here for sardine were developed in the same manner, and using the same basic equations, as were the models derived by James *et al.* (1989b) for Cape anchovy *Engraulis capensis*. Budget models for both species used prey size, plankton concentration and foraging time as the input parameters, and in both cases experimental data was used to parameterize the models. Using empirically-derived relationships between, for example, prey size and clearance rate, or swimming speed and respiration rate during either filter- or

particulate-feeding, should permit more realistic modelling than was possible in cases where theoretically-defined parameters were used (e.g. Ware 1978, Durbin and Durbin 1983). This consistency in model development for sardine and anchovy therefore permits a detailed comparison of the respective trophodynamics of these co-occurring species in the southern Benguela upwelling system.

The model outputs suggest that sardine are able to survive and grow under most of the trophic environments encountered in the southern Benguela upwelling system. In each of the three feeding behaviour-food type scenarios examined, sardine showed positive growth over most of the input ranges used. In terms of carbon, small prey sizes, low plankton concentrations and very short foraging times of the order of 2-3 h would be sufficient for growth, whereas growth in nitrogen would require only slight increases in the three input parameters (Table 7.4). The ability to grow under most trophic conditions likely to be encountered, and the fact that differences in scope for growth between the three feeding behaviour-food type scenarios are small for this species, indicates that sardine is a broad-spectrum planktivore, well adapted and highly efficient at integrating its food environment. That the maximum scope for growth in both budget models was encountered for sardine filter-feeding on microzooplankton (141.4 $C.g^{-1}$ $DM.d^{-1}$ and 9.4 mg $N.g^{-1}$ $DM.d^{-1}$ at a concentration of 1 mg $C.l^{-1}$ in the carbon and nitrogen budgets respectively) suggests that this species, whilst omnivorous, has specialized in feeding on the smaller spectrum of available zooplankton prey.

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Whereas model outputs (intake, expenditure, growth and growth efficiency) were linearly related to prey concentration (C) and foraging time (h), they were curvilinearly related prey size (P), reflecting the fifth-order polynomial power function used to describe the effect of P on clearance rate (F; see Chapter 2). This power function is essentially the sum of the two curves, one describing the relationship between F and P for filter-feeding fish and the other for particulate-feeding fish. The polynomial was chosen because it provided a function across the prey size spectrum with no discontinuity between filter- and particulate-feeding, was perceived to accurately reflect the mechanisms governing particle retention and capture rate, and

was highly significant. Whereas a simple power curve ($y = ax^b$) could have been fitted to the data with high significance, such a model would imply that *F* increases proportionally with *P*, and so would not show the plateau in *F* observed for food particles of 400-1230µm. Hence the polynomial function provided a more representative fit to the data, and was therefore used in the budgets.

The carbon and nitrogen budget models developed for sardine provide contrasting results to those derived from such models for Cape anchovy *Engraulis capensis*. Whereas sardine showed positive growth over most of the input ranges in all scenarios, James *et al.* (1989b) reported that anchovy could only maintain itself in the southern Benguela by particulate-feeding on meso- and macrozooplankton. Maximum growth rates of 110 mg $C.g^{-1}$ $DM.d^{-1}$ and 14 mg $N.g^{-1}$ $DM.d^{-1}$ in the carbon and nitrogen budgets respectively could be attained by anchovy particulate-feeding on mesozooplankton (James *et al.* 1989b). Filter-feeding on dense aggregations of phytoplankton and microzooplankton did enable positive growth in anchovy, provided that the concentrations were sufficiently high. However, the minimum phytoplankton concentration required to support growth in nitrogen in anchovy (0.68 mg $C.l^{-1}$) approximates that found in phytoplankton blooms; even then, anchovy growth is limited. Similarly, James *et al.* (1989b) considered filter-feeding by anchovy on microzooplankton to be of secondary importance to particulate-feeding on meso- and macrozooplankton. However, James *et al.* (1989) used a microzooplankton concentration range of 0-0.5 and a fixed value of 0.1mg $C.l^{-1}$; for the reasons given above this is considered too low, hence those authors may have underestimated of the relative importance of microzooplankton in the diet of anchovy.

Sardine regulate their feeding behaviour primarily on the basis of prey size; small prey elicit a filter-feeding response whilst larger (> 1230 µm) prey elicit a particulate-feeding response at low concentrations, and filter-feeding if present at high concentrations (Chapter 2). Anchovy also filter-feed on small prey and particulate-feed on large prey, although the size at which this switch occurs is smaller than that for sardine (≈ 700 µm; James and Findlay 1989). However, these two species differ in their responses to plankton concentrations; when feeding on

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natural assemblages of crustacean zooplankton, sardine increase their swimming speeds with increasing prey concentration (Figure 7.2), whereas plankton concentration did not affect the swimming speed of feeding anchovy (James and Findlay 1989). Instead, anchovy regulate their swimming speeds during feeding according to prey size, with large prey eliciting faster swimming speeds (James *et al.* 1989b). Although different to that observed for anchovy, the sardine's response to plankton concentration is similar to that observed for other species. Durbin and Durbin (1975) reported a hyperbolic relationship between swimming speed and plankton concentration for Atlantic menhaden *Brevoortia tyrannus*, and Muir and Newcombe (1974 in Ware 1978) found that Atlantic mackerel *Scomber scombrus* tailored their foraging speed to food supply when filter-feeding, swimming faster with increasing plankton concentration. This behavioural response to the food environment was considered to have evolved as a strategy to maximise growth rather than growth efficiency (Ware 1974, Durbin and Durbin 1983). The hyperbolic shape of the net growth efficiency curves for sardine in the various feeding behaviour-food type scenarios observed in this study, compared to the linearly-increasing growth with increasing input value, suggests that sardine have also evolved foraging strategies which maximise growth rather than growth efficiency.

The results of this study indicate that sardine will show positive growth under most trophic conditions, and imply that sardine adults may not be food limited in the southern Benguela upwelling system, contrary to suggestions made by Shannon and Field (1985). If adult biomass is indeed not limited by food, then predation could well be a significant factor regulating population size. Predation has recently been suggested as being as important as resource limitation in structuring marine pelagic systems (Verity 1998), and certainly sardine are a major prey item for many species in the southern Benguela, including piscivorous fish, birds and mammals (Crawford *et al.* 1992, Best *et al.* 1997). However, the relative importance of predation and food in limiting sardine population growth, and temporal and spatial shifts in the comparative importance of these factors, requires further attention.

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It must be emphasized that the models developed here were derived from data collected on adult sardine; therefore, they may not accurately reflect the trophodynamics of juvenile sardine. Juvenile sardine differ from adults with respect to their feeding behaviour; they are more zooplanktivorous than adults (Hand and Berner 1959, King and Macleod 1976), and show a clear feeding periodicity peak whereas adults feed continuously (Chapter 5). Both of these findings suggest that juvenile sardine employ particulate-feeding to a greater degree than do sardine adults. Particulate-feeding by juvenile sardine may well be energetically cheaper than filter-feeding (see Chapter 3 for a discussion of feeding mode costs and fish size), hence the empirical relationships derived for adult sardine cannot be applied to juveniles.

The carbon and nitrogen models described above were developed using data collected from adult sardine maintained in the laboratory; the realism of these models is dependent on how well such laboratory-derived data can be extrapolated to field conditions. For example, sardine in the field are likely to have additional energy costs that fish in the laboratory are not subject to. Expenditures due to predator avoidance or migration were not considered in the model; such activities would increase respiratory expenditure and therefore reduce the amount of surplus energy available for growth. On the other hand, the models were run under three food environment scenarios which were restricted to a particular food type (phytoplankton, microzooplankton and mesozooplankton). These simplified food environments are probably not an accurate reflection of those encountered by sardine in the field, since the fish are likely to be faced with a mixture of food types and particle sizes. Hence running the models under such simplified food environments may have resulted in underestimates of the amount of energy available for growth.

Whereas potential food sources such as detritus or particulate aggregates could provide a supplementary food source for sardine (provided that sardine are able to assimilate some portion of the carbon and nitrogen in these potential food types), these were not considered in the models. Although the importance of detritus

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in the sardine's diet has not been assessed, it is likely to be of some significance. As a consequence of their ability to capture small particles, direct ingestion of detritus by sardine is likely, as has been reported for Atlantic menhaden (Durbin and Durbin 1975). Detritus may also impart indirect benefits, since the presence of detritus at concentrations usually encountered in nature was shown to enhance filtering efficiency and reduce the minimum size threshold at which phytoplankton were retained by juvenile Atlantic menhaden (Friedland *et al.* 1984).

In addition to elucidating the trophodynamics of sardine in the southern Benguela upwelling system and enabling a detailed comparison with anchovy, the results presented above may be of use in size-based models such as that developed for the southern Benguela by Moloney *et al.* (1991), or more generalized trophic flow models such as ECOPATH (Jarre-Teichmann *et al.* 1998). Providing accurate input information to these models will permit a better understanding of ecosystem functioning.

The sardine's ability to grow under most trophic conditions results from three factors: high ingestion rates, low energetic costs when feeding (especially filter-feeding), and prolonged foraging times. Compared to other clupeoids, sardine are highly efficient at retaining small particles (Chapter 2). This high efficiency, coupled with the fact that filter-feeding at low swimming speeds does not appear to increase metabolic costs significantly (Chapter 3), means that sardine are able to show positive growth when filter-feeding on small prey items such as phytoplankton and microzooplankton. The higher assimilation efficiency of sardine for zooplankton compared to phytoplankton, especially in terms of nitrogen, means that sardine are likely to obtain more of their nutritional requirements from carnivory than herbivory (Chapter 4). Adult sardine collected from the field showed minimal difference in stomach content mass over the diel cycle, suggesting that they feed continuously (Chapter 5). Stomach contents from fish collected primarily over the Agulhas Bank were found to be dominated by small prey items, with >85% of ingested prey being <1200 µm and therefore captured by filter-feeding (Chapter 6). Microzooplankton, primarily small calanoid and cyclopoid copepods, provided the bulk of dietary carbon

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(Chapter 6). The results from the experimentally-derived budget models therefore corroborate field studies on the diet and feeding behaviour of sardine in the southern Benguela upwelling system.

Results from the experimental and field studies described in this dissertation, together with the carbon and nitrogen budgets derived from these data, allow an evaluation of the two hypotheses regarding the trophic position of clupeoids in upwelling ecosystems with specific reference to *Sardinops sagax* in the southern Benguela. The "classical" hypothesis of Ryther (1969), who suggested a two-level food chain in which clupeoids derived the majority of their nutrition directly from phytoplankton, is rejected. Although sardine are capable of ingesting, assimilating and growing on phytoplankton, the results presented above indicate that phytoplankton is not the major dietary component of this species, although it is undoubtedly important in localized regions or at specific times of the year.

Sardine are more efficient assimilators of carbon and nitrogen from zooplankton compared to phytoplankton, derive most of their carbon from small calanoid and cyclopoid zooplankton, and show maximum growth rates under conditions of high microzooplankton density. These findings all support the alternative, multi-level food chain hypothesis of James (1988b); namely, that sardine are omnivorous, but derive their nutrition primarily from zooplankton.

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Chapter 8: Comparative Trophodynamics of Sardine and Anchovy in the Southern Benguela Upwelling Ecosystem: Are Regime Shifts Food-Linked ?

8.1: Introduction

This dissertation has provided detailed information on the feeding ecology of sardine *Sardinops sagax* in the Southern Benguela upwelling ecosystem. These data, together with similar information for Cape anchovy *Engraulis capensis* provided by James (1988a), enable the respective trophodynamics of these two species to be comprehensively compared. Although sardine and anchovy occur in all of the world's eastern boundary current systems, where they make substantial contributions to the marine catches of those areas (see Chapter 1), in no system other than the southern Benguela does sufficient information concerning the trophodynamics of these two species exist. Hence, conclusions and inferences drawn from the results of such a comparative study are likely to be of profound interest to ecologists working in other eastern boundary current systems. This detailed comparison may also permit an assessment of whether regime shifts between these two species are linked to differences in their trophodynamics.

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8.2: Interspecific comparisons

(a) Feeding behaviour and ingestion rates

Both sardine and anchovy possess two feeding modes, namely filter- and particulate-feeding. Both species filter-feed on small particles and particulate-feed on large particles, with particle size being the prime determinant of feeding mode choice. However, sardine and anchovy have different threshold sizes at which they change

from filter- to particulate-feeding, and differ in the relative dominance of their feeding modes.

Filter-feeding is the principal feeding mode of sardine. Food particles of less than 1.2 mm elicit a filtering response, whilst larger particles elicit particulate-feeding at low concentrations but filter-feeding at high concentrations (Chapter 2). The clearance rate during filtering is independent of particle size over the size range 0.4 to 1.2 mm *MD*, with a mean value (11.78 ± 4.91 litres.fish^{-1}.minute^{-1}) that is 93% of the calculated maximum, implying that sardine are highly efficient at filter-feeding over this size range. Sardine are less efficient at retaining particles of smaller size, but are able to entrap particles down to 0.01 mm in size. They are therefore able to directly feed on net-phytoplankton. Clearance rates during particulate-feeding are greater than those during filtering, and increase with increasing particle size to a predicted maximum value of 46.5 litres.fish^{-1}.minute^{-1}. Sardine display size-selectivity, preferentially removing larger prey items during particulate-feeding.

In contrast to sardine, particulate-feeding is the primary feeding mode for anchovy, which switch from filter- to particulate-feeding at a threshold prey size of 0.7 mm (James and Findlay 1989). The minimum particle size that can be entrapped by anchovy during filtering is 0.20 to 0.25 mm, hence a large portion of the phytoplankton is unavailable to anchovy. Clearance rates during particulate-feeding are greater than those during filtering, and reach a maximum value of 17.0 litres.fish^{-1}.minute^{-1}. Anchovy are highly size-selective, selecting for the largest particle available.

A comparison of predictive equations of clearance rate as a function of particle size for both species demonstrates that sardine show substantially higher clearance rates than anchovy, across the entire prey size spectrum (Figure 2.10a). However, when clearance rates are standardized and expressed as a function of fish weight (i.e. litres.g^{-1}.minute^{-1}), sardine are only more efficient at removing particles of less than 580 µm in size (Figure 2.10b), anchovy having distinctly faster clearance rates on particles larger than this size. Sardine therefore are more efficient removers of small particles,

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whilst anchovy remove large particles more effectively.

(b) Feeding costs and metabolism

Energetic costs of feeding for both sardine and anchovy were determined through the measurement of respiration rates during non-feeding, filter-feeding and particulate-feeding. For both species, respiration rate increased with swimming speed for all activity states, although the shape of the functional relationship differed between species, being linear for sardine (Chapter 3) but log-linear for anchovy (James and Probyn 1989). The relative energetic costs of each feeding mode were determined from the slope of the respiration rate/swimming speed regression derived for both species displaying each feeding mode, with higher slope values indicating higher relative energetic cost.

At any given swimming speed, filter-feeding by adult sardine is energetically cheaper than particulate-feeding (Chapter 3). This is in contrast to anchovy, where particulate-feeding is the energetically cheapest feeding mode (James and Probyn 1989). James and Probyn (1989) argued that the change in body shape and increased drag associated with flared operculae during filter-feeding was responsible for the increased metabolic costs of filter-feeding anchovy. Whilst opercular flaring by sardine must increase drag and therefore energetic costs, the formation of a compact shoal by fish during filter-feeding would confer a hydrodynamic advantage and hence reduce energy expenditure. Additionally, the increased complexity of swimming behaviour when particulate-feeding compared to filter-feeding is likely to be responsible for increased costs. Thus capturing prey by particulate-feeding is relatively more expensive for the heavier pilchard, whereas the increased drag associated with filter-feeding is relatively more expensive for the smaller anchovy.

The experimental procedures used in determining the energetic costs of feeding also allowed estimation of the respiratory quotient (RQ) for each species. Respiratory quotients indicate the type of physiological fuel involved in metabolism, and ranges from 0.7 for the catabolism of fats, through 0.9 for protein, to 1.0 for

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carbohydrates (Brett & Groves 1979). A mean RQ value of 0.96 was determined for sardine (Chapter 3), suggesting that metabolism is based on the breakdown of both protein and carbohydrates. James and Probyn (1989) estimated an RQ of 0.92 for anchovy, and suggested that protein was the metabolic fuel for this species. The higher RQ value for sardine suggests a greater carbohydrate utilization by this species compared to anchovy, and a higher capacity to utilize carbohydrates is characteristic of herbivorous species (Brett & Groves 1979). This implies that phytoplankton is a more important dietary component for sardine than anchovy.

(c) Nitrogen excretion and assimilation efficiencies

Both sardine and anchovy excrete the majority of their nitrogen in the form of ammonia, and both have comparable rates of endogenous excretion: 28.1 ± 1.9 µg $N.g^{-1}.DBM.h^{-1}$ for sardine (Chapter 4) and 34.9 ± 6.2 9 µg $N.g^{-1}.DBM.h^{-1}$ for anchovy (James *et al.* 1989a). However, these two species differ substantially in their exogenous excretion; maximum exogenous excretion by sardine was 10 times the endogenous rate, whereas maximum exogenous excretion by anchovy was 25 times its endogenous rate. This difference may be partly attributable to size-specific metabolic rates (the small anchovy are likely to have a faster metabolic rate than the large sardine), but it is likely that the much larger ration sizes used for anchovy (1 to 11%) compared to those used for sardine (0.3 to 1.1%) affected exogenous excretion rates. Sardine and anchovy both show greater absorption efficiencies for nitrogen than for carbon, and both species absorb these elements more efficiently from zooplankton than from phytoplankton. Where these two species differ however, is in their retention of nitrogen; sardine excrete more than half of their ingested and absorbed nitrogen rations (62 and 66 % respectively; Chapter 4) whereas anchovy excrete less than half of their ingested and absorbed nitrogen rations (42 and 48 % respectively; James *et al.* 1989a). Hence anchovy appear to be more efficient retainers of nitrogen than are sardine.

(d) Diet and feeding ecology

Sardine and anchovy are both omnivorous clupeoids, capable of ingesting

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phytoplankton and zooplankton. In the southern Benguela upwelling ecosystem however, zooplankton contributes a far greater amount to the dietary carbon than does phytoplankton for both of these clupeoid species, although phytoplankton can be an important dietary contributor in localized regions or at particular times of the year (Chapter 6, James 1987). Whilst zooplankton is the dominant food source for both species, sardine and anchovy consume different fractions of the zooplankton, and therefore appear to partition this resource on the basis of size. Carbon from zooplankton ingested by sardine is primarily derived from small (< 1.2 mm) calanoid and cyclopoid copepods, anchovy eggs, and crustacean eggs and nauplii. The relative paucity of food particles > 1.2 mm in sardine stomachs is indicative of a low occurrence of particulate-feeding. In contrast to sardine, anchovy derive the bulk of their carbon from larger (> 1.0 mm) zooplankton, typically calanoid copepods and euphausiids. These larger particles are captured primarily through size-selective particulate-feeding.

In addition to partitioning the zooplankton resource on the basis of size, sardine and anchovy also appear to employ different foraging strategies. Whilst anchovy are considered to be nocturnal foragers (James 1988b), they show a marked feeding periodicity in the southern Benguela with peak feeding occurring at dusk and dawn (James 1987). Feeding periodicity in anchovy appears to be associated with vertical migration, with high feeding activity at night coinciding with shoal dispersal in the surface waters, whereas low feeding activity during the day coincides with shoal aggregation and descent into deeper water (James 1987). Similarly, anchovy in the northern Benguela also show highly significant day/night differences in shoal depth (Thomas and Schülein 1988). In contrast to anchovy, sardine >25 g wet mass appear to feed continuously and show no peaks in feeding activity throughout the diel cycle, although fish less than 25 g do show a peak in feeding activity at or around sunset (Chapter 5). In the southern Benguela, vertical migration by sardine appears to be highly variable, with fish being observed throughout the water column during the day (in many cases being on or near the bottom) but forming a scattering layer close to the surface at night (Coetzee 1997). Sardine in the northern Benguela show no significant

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difference in shoal depth between night and day, but tend to form small, scattered schools by night and dense schools by day, whilst generally remaining in the top 20m of the water column (Hampton *et al.* 1979; Kruger and Cruikshank 1982; Thomas and Schülein 1988).

Large-scale studies using acoustic echo-integration techniques during spawner stock assessment surveys have examined the schooling characteristics of sardine and anchovy in the southern Benguela (Barange and Hampton 1997). These have revealed significant diel changes in school density of anchovy, with schools having a substantially greater packing density on average during the day than during the night. No such difference in average packing density was observed by Barange and Hampton (1997) for sardine, although Coetzee (1997) did find diel differences in sardine density during mesoscale studies. Barange and Hampton's (1997) study further corroborate the hypothesis that anchovy are predominantly particulate-feeders, whereas sardine primarily filter-feed, since a reduction in school density by particulate-feeding anchovy at night reduces the overlap of individual visual fields (Eggers 1976) and hence reduces intraspecific competition. This reduction in school density is unnecessary for the filter-feeding sardine.

(e) Carbon and nitrogen budgets

Carbon and nitrogen budget models developed for sardine and anchovy differ significantly in two respects. Firstly, the two species regulate their swimming speed during feeding (and hence their energetic output) according to different properties of the food environment; when feeding on zooplankton, sardine regulate their swimming speed according to prey concentration and swim faster at higher concentrations (Figure 7.1d), whilst anchovy regulate their swimming speed according to prey size, with larger zooplankton eliciting faster swimming speeds (James *et al.* 1989b).

The second major difference in the budget models derived for sardine and anchovy pertains to the effect of the food environment upon potential growth.

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Sardine showed positive growth over most of the input (particle size, prey concentration and foraging time) ranges in each of the three food type-feeding behaviour scenarios (filter-feeding on phytoplankton, filter-feeding on microzooplankton, and particulate-feeding on mesozooplankton; Chapter 7), with the maximum scope for growth occurring for sardine filter-feeding on dense concentrations of microzooplankton. Anchovy, on the other hand, only showed positive growth over a limited portion of the input range when filter-feeding on either phytoplankton or microzooplankton, although this species showed positive growth over most of the input ranges when particulate-feeding on mesoplankton (James et al. 1989b). Maximum scope for growth for anchovy occurred when particulate-feeding on mesozooplankton.

The results from the carbon and nitrogen budget models, together with the experimental and field data collected for each species, provide convincing evidence that sardine and anchovy in the southern Benguela upwelling ecosystem should be considered trophically distinct. Sardine can be regarded as a broad-spectrum or generalist planktivore, capable of ingesting a wide size range of prey items from small phytoplankton to large macrozooplankton, and able to maintain itself under most food environments. Sardine employ filter-feeding as their primary feeding behaviour, and the correspondence between the size frequency distributions of stomach contents of the this species and the ambient food environment suggests that feeding is primarily non-selective. In contrast, anchovy should be regarded as a specialist planktivore, being somewhat restricted in the size range of prey items it can capture (phytoplankton is not an important dietary component), and only able to maintain itself under specific food environments. Anchovy are primarily particulate feeders, and are strongly size selective. Because both sardine and anchovy are largely zooplanktivorous, dietary overlap between these two species is likely to occur, although this may be minimized by spatial segregation observed for adults of these two species. A summary of the various aspects described above is given in Table 8.1.

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Table 8.1: A comparison of various aspects of the trophodynamics of sardine and anchovy in the southern Benguela upwelling ecosystem. *F* is clearance rate (mass standardized) and *P* is particle size.

ASPECT	SARDINE	ANCHOVY
Dominant feeding mode	Filter-feeding	Particulate-feeding
Switch at prey size of	ca. 1230 µm	ca. 710 µm
F ($l.g^{-1}.min^{-1}$) @ *P* = 100µm	0.033	0.001
500µm	0.073	0.053
1000µm	0.101	0.441
1500µm	0.228	1.008
Cheapest feeding mode	Filter-feeding	Particulate-feeding
Respiratory Quotient	0.96 (metabolic fuel is protein and carbohydrates)	0.92 (metabolic fuel is protein)
Nitrogen assimilation	Most efficient from zooplankton	Most efficient from zooplankton
	Excretes > ½ of ingested N	Excretes < ½ of ingested N
Diet and feeding ecology	Phytoplankton ocassionally important	Phytoplankton unimportant
	Dietary carbon from small calanoid and cyclopoid copepods < 1.2 mm	Dietary carbon from large calanoid copepods and euphausiids > 1.0 mm
	Non-selective	Size-selective
	Minimal feeding periodicity	Marked feeding periodicity
	Facultative vertical migrators	Obligate vertical migrators
	No diel difference in school density	Diel difference in school density
Budget models	Regulates swimming speed according to prey conc.	Regulates swimming speed according to prey size
	Positive growth when feeding on phytoplankton microzooplankton and mesozooplankton	Positive growth at high phytoplankton or microzooplankton concentrations, most mesozooplankton conc.
	Scope for growth maximized on microzooplankton	Scope for growth maximized on mesozooplankton

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8.3: Comparative trophodynamics and regime shifts

The results summarized above provide convincing evidence that sardine and anchovy in the southern Benguela upwelling ecosystem, whilst both primarily zooplanktivorous, are trophically distinct. Sardine is a generalist planktivore, and although capable of ingesting a wide range of prey sizes, appears to have evolved its feeding ecology in order to utilize smaller zooplankton, such as cyclopoid and small calanoid copepods. Anchovy, on the other hand, have evolved a feeding ecology which utilizes larger zooplankton, principally large calanoid copepods and euphausiids. Sardine and anchovy therefore appear to minimize competition by partitioning their food resource according to prey size. It must be emphasized, however, that the above hypothesis regarding resource partitioning between these two clupeoids only applies to the adults, and may not necessarily apply during all life history stages; competition for food between larvae or juveniles may well be more important than is the case for adults. Sardine and anchovy shoal together as juveniles in the southern Benguela ecosystem, and aggregate inshore along the South African west coast from March to August (Armstrong *et al.* 1991b, Roel and Armstrong 1991). Hence interspecific competition could occur during this phase of their life history. However, preliminary studies on the size composition of the diet of juvenile sardine and anchovy from presumably mixed shoals found that sardine ingested significantly smaller prey than did anchovy (Louw *et al.* 1998), suggesting that competition between them was minimized. The study of Louw *et al.* (1998) was unfortunately limited by a small sample size, and should therefore be regarded with caution.

It has been hypothesized that cyclopoids contribute to stability of the planktonic communities in the ocean (Paffenhöfer 1993), primarily as a result of their ability to feed on small particles (protozooplankton such as ciliates and heterotrophic dinoflagellates) that are inefficiently grazed by calanoid copepods (Nakamura and Turner 1997), and their association with the microbial foodweb (Nielsen and Sabatini 1996). Compared to other upwelling ecosystems, the southern Benguela appears to be dominated by small phytoplankton of <10 µm (Probyn 1992), and simulation

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studies of trophic flows and nitrogen cycles in this region have suggested that the majority of primary production is due to these small phytoplankton cells (Figure 8.1, Moloney 1992, Painting *et al.* 1993a). These studies have led to a reassessment of the importance of the microbial food web in the southern Benguela ecosystem, with the significance of microheterotrophs in the pelagic foodweb, particularly as regenerators of nitrogen, now being recognised (Moloney 1992, Painting *et al.* 1992, 1993a, 1993b). However, the proportion of primary production transferred to fish through the microbial foodweb is currently unknown, and requires quantification (Figure 8.1).

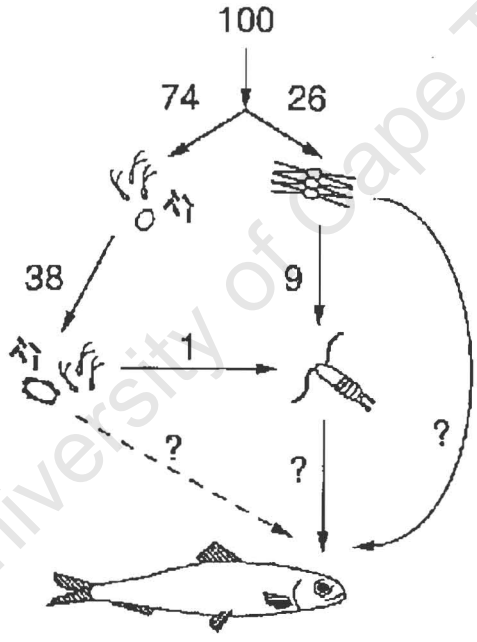

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Figure 8.1: Revised foodweb model of the southern Benguela upwelling ecosystem including the microbial foodweb. The values refer to the percentage of carbon that is passed on to the following trophic level. From Moloney (1992).

The ability of cyclopoid copepods to feed on small particles (both small phytoplankton and microheterotrophs) means that they can act as 'retrievers' (Nakamura and Turner 1997) of primary production, which will then be accessible to fish species that can efficiently capture them, such as sardine. In contrast to cyclopoids, most calanoid copepods feed primarily on large phytoplankton cells that

occur in blooms of relatively short duration. The strong pulsing of upwelling is therefore likely to cause considerable spatial and temporal mismatch between calanoids and their food supply (Hutchings 1992). Hence calanoids are likely to show a large degree of population variability.

Given that sardine derive most of their dietary input from small (cyclopoid and calanoid) copepods, and assuming that these show relatively little population variability, then sardine could be considered to have evolved a 'steady-state' trophic strategy, feeding on that fraction of the zooplankton that is ever-present. Their relatively slow metabolic rate and inefficient nitrogen retention compared to anchovy, suggests that the transfer of primary production into sardine tissue will occur at a moderate rate. In contrast, because anchovy have evolved a trophic ecology primarily directed at large, calanoid copepods that show large population variability, anchovy could be considered as operating under a 'feast or famine' scenario. When conditions are suitable for anchovy (i.e. a food environment where large zooplankton are present), they would show rapid growth as a result of their fast metabolic rate and efficient retention of ingested nitrogen; in poor conditions however, growth is likely to be minimal or even negative.

Sardine and anchovy are trophically distinct. The question that must now be asked is whether this difference can be linked to regime shifts. The difference in weight-standardised clearance rates of sardine and anchovy feeding on different-sized food particles, coupled with the difference in relative energetic costs of their predominant feeding modes, implies that the size spectrum of the planktonic food environment will have important ramifications for the feeding success of each species. Food environments dominated by small particles will favour sardine over anchovy, since sardine are more efficient removers of small particles, and can collect such food particles through employing relatively cheap filter-feeding. Hence sardine should have a greater net energetic gain in small particle-dominated environments than anchovy, as was shown by the respective carbon and nitrogen budget models constructed for these species.

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In contrast to sardine, anchovy are inefficient removers of small particles, and filter-feeding is the energetically most expensive feeding mode for this species. Food environments comprising mainly large particles will favour anchovy over sardine, due to the anchovy's greater efficiency at removing large particles through relatively cheap particulate-feeding. Sardine, in addition to being less efficient removers of large particles than anchovy, have to acquire such food through expensive particulate-feeding, unless such particles are present in sufficiently dense concentrations to elicit filter-feeding. Anchovy should therefore show a greater net energetic gain in large particle-dominated environments than sardine.

Complex spatial and temporal variations in prey size-range and concentration typify pelagic food environments. In the southern Benguela upwelling ecosystem, the size structure and biomass of phytoplankton populations are closely related to physico-chemical conditions resulting from physical forcing mechanisms (Mitchell-Innes and Pitcher 1992). Under intermittent mixing conditions such as those which occur during upwelling, water temperatures vary between 12 and 15°C, and sporadic nutrient enrichment of the euphotic zone occurs. This promotes the development of phytoplankton populations of high biomass, dominated by large, chain-forming diatoms. Conversely, under very stable conditions, warm temperatures (>15°C) and nutrient depletion of the upper layers limit diatom growth, enabling small nanoflagellate populations to predominate (Mitchell-Innes and Pitcher 1992). In turn, zooplankton community structure has been shown to be affected by phytoplankton community and size structure. Large copepods such as *Calanoides* and *Calanus* exhibit considerably higher rates of ingestion of large (>15 µm) phytoplankton compared to small cells (Peterson 1989 in Verheye *et al.* 1992), and display enhanced growth rates under diatom-dominated conditions as opposed to flagellate-dominated conditions (Walker and Peterson 1991). These large, herbivorous copepods may in fact become food-limited during the quiescent phase of the upwelling cycle, when the phytoplankton community becomes dominated by small cells (Painting *et al.* 1993a). In contrast, smaller copepod species (e.g. *Oithona*) appear to be favoured when small cells predominate (Verheye *et al.* 1993).

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Therefore, different physical scenarios can lead to food environments being dominated by either small or large particles, which would tend to favour sardine and anchovy respectively (Figure 8.2, Verheye *et al.* 1993).

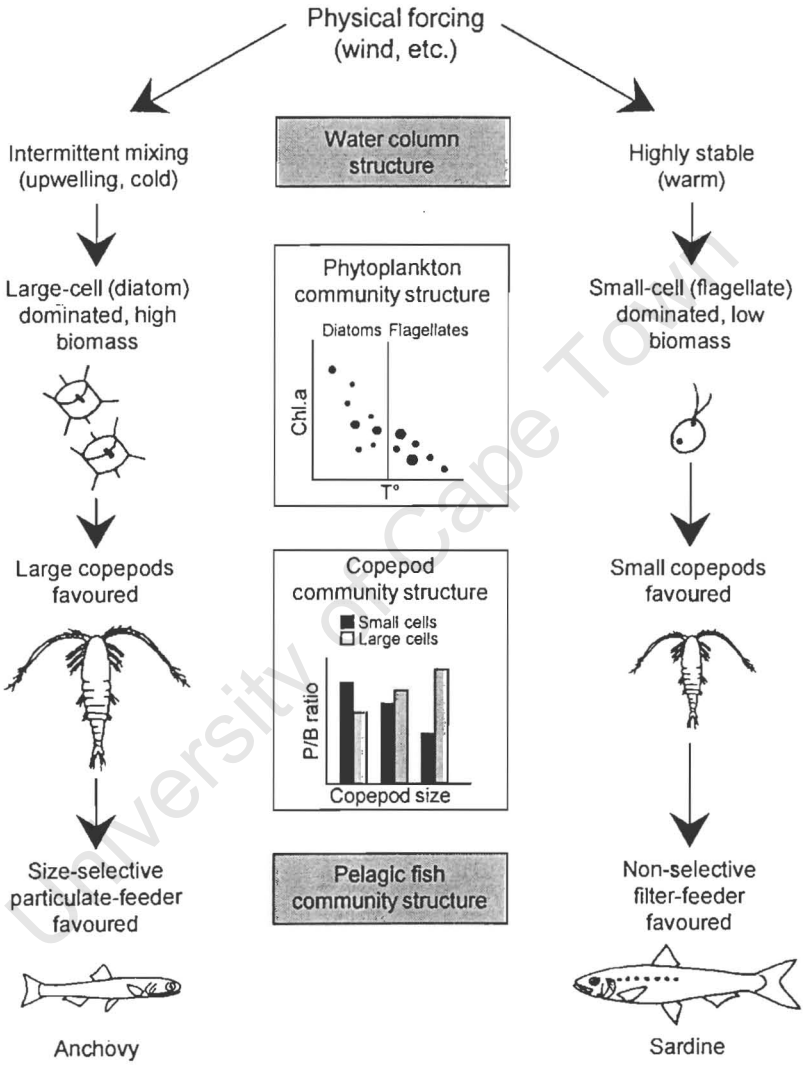

Figure 8.2: Conceptual schematic of how physical forcing may lead to environments that favour either sardine or anchovy.

Whilst different physical scenarios can therefore lead to food environments being dominated by either small or large particles, there may be more subtle differences in the food environment that favour sardine over anchovy, or *vice versa*. For example, the degree of mixing of the upper water column could lead to differences

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in the ambient food environment, even when the prey size spectra remains relatively unchanged. The reduced intensity of mixing events during stable conditions could lead to a greater degree of concentration of phytoplankton and small zooplankton in layers at, or near to, the thermocline. Conversely, when mixing events are more frequent, food particles are likely to be more homogenously distributed throughout the upper water column. When mixing is low, the concentration of small food particles in layers is likely to favour sardine over anchovy, since both species would capture these food particles by filter-feeding. In environments where food particles are not concentrated however, anchovy would tend to be favoured compared to sardine.

Provided that particular food environments (either large or small cell dominated or with or without concentration of small particles in layers) persist either spatially and/or temporally (for example in years during which upwelling is decreased) it appears credible that regime shifts may be linked to trophodynamic differences between sardine and anchovy. For this to be the case, however, changes in the ambient plankton size structure should be observed concurrently with regime shifts. Some evidence for this has been reported by Verheye *et al.* (1998), who conducted a retrospective analysis of zooplankton samples collected in the St Helena Bay area off the South African west coast between 1951 and 1996, a period encompassing times of both sardine dominance (1951-1967) and anchovy dominance (1988-1996). Verheye *et al.* (1998) found that whilst total zooplankton abundance increased by two orders of magnitude from 1951 to 1996, size-based differential rates of increase in population levels resulted in a significant shift through time in the crustacean zooplankton community structure. During the period when sardine was dominant, cyclopoid copepods <900 µm total length constituted between 24 and 60% of the crustacean zooplankton, with a mean value 41.4%; this proportion was significantly less than during the years when anchovy was dominant (55.7%; Figure 8.3).

In contrast to the pattern exhibited by cyclopoid copepods, the mean proportions of medium (1000-2000 µm *TL*), and large copepods (2000-5000 µm *TL*) and macrocrustaceans (>5000 µm *TL*) were significantly reduced from the sardine-

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to the anchovy-dominated period. The relative abundance of small calanoids and cladocerans (900-1000 µm *TL*) remained unchanged during the time-series. The results presented by Verheye *et al.* (1998) provide convincing evidence of a long-term change in the potential food environment of pelagic planktivorous fish, with the observed changes in crustacean community (and therefore size) structure coinciding with a regime shift in the southern Benguela from sardine to anchovy dominance.

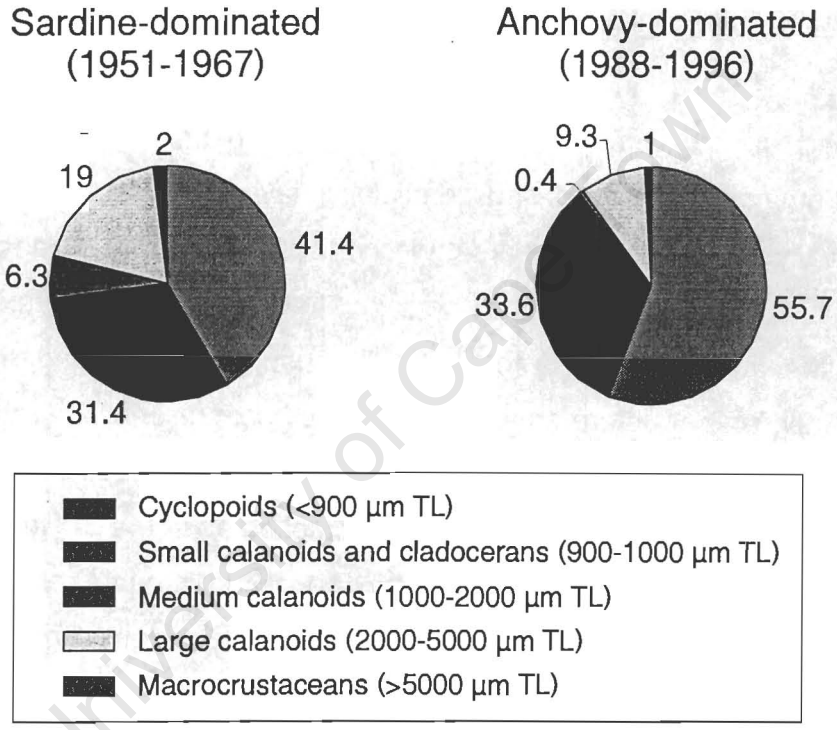

Figure 8.3: Mean size structure (percentage) of the crustacean zooplankton community from St Helena Bay (west coast) during periods of sardine and anchovy dominance. Drawn using data from Verheye *et al.* (1998).

The evidence presented above therefore supports the hypothesis that regime shifts between sardine and anchovy are associated with structural changes in the ecosystem, leading to environments that favour one species over the other. A similar hypothesis was proposed by Kawasaki and Omori (1988, 1995), who suggested that increased phytoplankton stocks resulting from increased solar radiation would lead to an increase in sardine populations. This dissertation has suggested that it is not

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primarily the level of phytoplankton biomass that favours sardine over anchovy, but is more likely to be the size structure, species composition and spatial patterning (i.e. concentration in layers) of the zooplankton community instead.

Trophodynamics will play an important role in determining the relative success of sardine and anchovy under particular environmental conditions, although trophodynamic differences alone are unlikely to account for regime shifts. Rather, trophodynamics should be considered in conjunction with spawning success or year class formation, since recovery of the subdominant genus whilst the other is still abundant appears to be triggered by the formation of one or a few powerful year classes (Schwatrzlose *et al.* 1999). Body condition at spawning of adult Far Eastern sardine *Sardinops sagax* has been found to have a marked effect on both the quantity and quality of eggs produced (Morimoto 1996 in Schwartzlose *et al.* 1999). Since body condition is essentially the integration of a sardine's trophic environment over time, a trophically-favourable environment for sardine will result in good-condition fish that produce many eggs of high quality, which are likely to have a higher probability of survival. Trophodynamically-mediated successful spawning, both in terms of egg numbers and egg quality, could therefore assist in the formation of strong year classes, and hence initiate regime shifts.

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