Nitrogen excretion and absorption efficiencies of sardine *Sardinops sagax* fed phytoplankton and zooplankton diets

C. D. van der Lingen*

Sea Fisheries Research Institute, Private Bag X2, Rogge Bay 8012, South Africa

ABSTRACT: Laboratory experiments to measure nitrogen excretion rates and estimate absorption efficiencies were conducted on adult sardine *Sardinops sagax* fed phytoplankton and zooplankton diets. Sardine are predominantly ammoniotelic, with an endogenous total nitrogen excretion rate of $28.11 \pm 1.90 \, \mu g \, N \, g^{-1} \, DBM$ (dry body mass) h$^{-1}$. Neither fish size nor temperature had a significant effect on endogenous excretion rates. Peak post-feeding exogenous nitrogen excretion rates were 3.5 to 10 times higher than endogenous rates, were linearly related to nitrogen ration, and occurred within 3 h of the ingestion of food. Absorption of a meal was rapid; 50% of the exogenous nitrogen was excreted by 2.2 ± 1.0 h and 90% by 7.4 ± 3.6 h. Faeces elimination was exponential and dependent on food type; phytoplankton was eliminated faster than zooplankton. Elimination of the meal was much slower than the excretion of dissolved nitrogen, requiring 13.0 ± 4.1 h for 50% elimination and 50.8 ± 8.3 h for 90% elimination. Faeces C:N ratios decreased over time for fish fed phytoplankton, but increased when zooplankton was the food. A constant portion of the ingested and absorbed nitrogen was excreted (69.8 ± 11.1 and 74.4 ± 12.1% respectively), and it is estimated that adult sardine require an absorbed daily maintenance ration of 2.64 mg N g$^{-1}$ DBM d$^{-1}$. Sardine are omnivorous, but have higher absorption efficiencies when fed zooplankton (77.6, 88.2 and 93.3% for dry mass, carbon and nitrogen respectively) than when fed phytoplankton (42.6, 62.6 and 78.7%). That *Sardinops sagax* is able to better utilize zooplankton than phytoplankton suggests that this species derives more of its nutritional requirements from carnivory than from herbivory.

KEY WORDS: *Sardinops sagax* · Planktivorous fish · Nitrogen excretion · Absorption efficiency · Phytoplankton · Zooplankton

INTRODUCTION

Sardine *Sardinops sagax* is a major component of landings by pelagic fisheries in upwelling regions of the world and, together with anchovy *Engraulis* spp., frequently dominates world fishery production (FAO 1997). The success of sardine and anchovy in upwelling regions was initially attributed to their ability to feed directly upon phytoplankton (Ryther 1969), and therefore to harness the high productivity of these systems through an efficient, 2-level food chain. However, recent studies have suggested that most clupeoids are omnivorous and derive the bulk of their energy intake from zooplankton (Koslow 1981, James 1987, James 1988).

Sardine is predominantly a filter-feeding species which is able to capture food particles down to 17 \(\mu\)m in size (van der Lingen 1994), and which maximizes its energy gain through prolonged bouts of energetically cheap filtering (van der Lingen 1995). Sardine stomachs typically contain both phytoplankton and zooplankton prey (Davies 1957, King & Macleod 1976, van der Lingen 1996), and the minimal diet variation in stomach content mass suggests that these fish filter-feed almost continuously (van der Lingen 1998).
Sardinops sagax is therefore morphologically and behaviorally well equipped to utilize both phytoplankton and zooplankton as food sources.

This paper 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 & 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 chupeoid species.

**MATERIAL AND METHODS**

Laboratory populations of sardine were collected and maintained as described by van der Lingen (1994). 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 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 1). Fish were deprived of food for 2 to 5 d 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 h over periods of 1 to 4 d 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 h, after which food was added to the tank. Water and faeces samples were then collected regularly, initially every hour for a 6 to 12 h period, and then with decreasing frequency over periods of 2 to 6 d 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 1). Natural assemblages of zooplankton used in the 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 1).

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.

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 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 filters 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
Table 1. Sardinops sagax. Summary of information for laboratory experiments on absorption efficiency of sardine. 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: experiments conducted on large adult fish; SA: experiments conducted on small adult fish. The mean carbon and nitrogen content and mean C:N ratio of 5 small adult sardine is also given.

<table>
<thead>
<tr>
<th>Expt</th>
<th>Starvation time (d)</th>
<th>Temperature range (°C)</th>
<th>Food type</th>
<th>Ration size (% DBM)</th>
<th>Feeding duration (h)</th>
<th>Carbon content (%DM)</th>
<th>Nitrogen content (%DM)</th>
<th>C:N ratio</th>
<th>Samples collected</th>
</tr>
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<td>LA 4A</td>
<td>5</td>
<td>16.6–21.0</td>
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<td>4.29</td>
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<tr>
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<td>21.47</td>
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Fish

<table>
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<td>NH₄</td>
<td>44.77 ± 10.64</td>
</tr>
<tr>
<td>urea, faeces</td>
<td>4.22 ± 0.66</td>
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</table>

Available in the food using the following expression:

\[
\text{% absorption efficiency} = \frac{\text{component}_{\text{food}} - \text{component}_{\text{faeces}} \times 100}{\text{component}_{\text{food}}} \tag{1}
\]

Experiments to determine the relative contribution of ammonia to the total nitrogen excreted by sardine were conducted in a 3 m³ glass display tank containing approximately 300 subadult sardine of 30 to 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 min 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.

**RESULTS**

**Endogenous ammonia and urea excretion**

Large-scale changes in ammonia concentrations in the experimental tanks meant that its excretion rate
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 1 h 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) h after the initiation of feeding (Fig. 1). Excretion rates returned to endogenous levels 4.5 to 13.0 (mean = 9.1 ± 3.5) h 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) h after the initiation of feeding and ranged from 45 to 195 µg N g⁻¹ DBM h⁻¹ (Fig 2). Excretion rates returned to endogenous levels 2.5 to 20.0 (mean = 10.9 ± 6.1) h 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 required for 50 and 90% exogenous nitrogen excretion respectively. The time required for 50% of the exogenous nitrogen excretion was \( 2.2 \pm 1.0 \) h after the mid-point of feeding, and that required for 90% of the exogenous nitrogen excretion was \( 7.4 \pm 3.6 \) h. A significant, linear relationship between peak ammonia excretion rate and nitrogen ration was observed (Fig. 3), and had the form:

\[
y = 0.088x + 51.3 \quad (n = 10; \ r^2 = 0.40; \ p < 0.05)
\]

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

Significant relationships were also observed between the total exogenous nitrogen excretion (\( e_N; \ \mu g \ N \ g^{-1} \ DBM \)) and the total nitrogen in both the ingested (\( R_N; \ \mu g \ N \ g^{-1} \ DBM \)) and the absorbed (\( pR_N; \ \mu g \ N \ g^{-1} \ DBM \)) rations (Fig. 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:

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

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

**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) h after the midpoint of feeding (Fig. 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 h, 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 (Fig. 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) h after the midpoint of feeding (Fig. 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 h, 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 h) than for those fed zooplankton (mean = 32.8 ± 3.6 h), and the coefficients of the exponential decline in faecal elimination

![Graph](image.png)

**Fig. 4.** Relationships between exogenous nitrogen excretion (mg N g⁻¹ DBM) and (a) ingested and (b) absorbed nitrogen ration (mg N g⁻¹ DBM) for *Sardinops sagax* fed on phytoplankton and zooplankton diets. 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.

These regressions 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), and assuming that nitrogen not excreted is retained such that:

\[ r_N = R_N - e_N \]  

(5)

where \( r_N \) is retained nitrogen (mg N g⁻¹ DBM), Eqs. (3) & (4) may be used to estimate the daily maintenance ration (i.e. zero net growth) required by sardine. Rearranging Eq. (3) gives:

\[ r_N = 0.302R_d \]  

(6)

where \( r_N \) is nitrogen retained by the fish (mg N g⁻¹ DBM). For zero net growth during 1 d, sufficient nitrogen must be ingested to supply that which is excreted endogenously, i.e.

\[ 0.302R_d = 0.675 \]  

(7)

so:

\[ R_d = (0.675/0.302) = 2.24 \text{ mg N g}^{-1} \text{ DBM } d^{-1} \]  

(8)

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

\[ pR_d = (0.675/0.256) = 2.64 \text{ mg N g}^{-1} \text{ DBM } d^{-1} \]  

(9)

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.

**Table 2.** *Sardinops sagax*. Regression parameters including sample size, \( r^2 \) value, significance level and slope value ± 1 standard error (C:N ratio h⁻¹) for the equations relating faecal C:N ratios to time for sardine fed phytoplankton and zooplankton diets. NS indicates not significant.
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 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 h, and that required for 90% elimination was 50.8 ± 8.3 h.

Despite some variability in the faeces C:N ratio data (Figs. 1 & 2), significant trends in this ratio over time were observed in 7 of the 10 experiments conducted (Table 2). In 3 of the 4 experiments in which fish were fed phytoplankton, the faeces C:N ratio showed a similar and significant decrease over the duration of the experiment (Fig. 1, Table 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. In contrast, the faeces C:N ratios for fish fed zooplankton significantly increased over the duration of the experiment in 4 of the 6 experiments (Fig. 2, Table 2). For 3 of these experiments the regressions were similar, increasing from 5:1 to 15:1 (Fig. 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.

Absorption efficiencies

Overall dry mass, carbon and nitrogen absorption efficiencies for sardine fed phytoplankton and zooplankton were calculated using Eq. (1). In all experiments nitrogen absorption efficiencies exceeded those for carbon, and both were higher than the dry mass absorption efficiencies (Table 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 3).

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 3). Mean absorption efficiencies of fish fed zooplankton were 77.6, 88.2 and 93.3% for dry mass, carbon and nitrogen respectively (Table 3). The mean dry mass, carbon and nitrogen absorption efficiencies were significantly higher for sardine fed zooplankton than for those fed phytoplankton (tdry_mass = 8.43, p < 0.001; t_carbon = 6.83, p < 0.01; t_nitrogen = 5.81, p < 0.05).

Table 3. *Sardinops sagax*. Dry mass, carbon and nitrogen absorption efficiencies (%) of sardine fed zooplankton and phytoplankton diets. Mean absorption efficiencies (±1 standard deviation) for phytoplankton and zooplankton are given.

<table>
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<tr>
<th>Expt</th>
<th>Food type</th>
<th>Dry mass</th>
<th>Carbon</th>
<th>Nitrogen</th>
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<td>LA 4A</td>
<td>Zooplankton</td>
<td>76.7</td>
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<td>89.8</td>
<td>94.3</td>
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<td>93.0</td>
<td>96.6</td>
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<td>LA 9A</td>
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<td>88.9</td>
<td>93.4</td>
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<td>79.3</td>
<td>90.8</td>
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<tr>
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<td>88.4</td>
<td>92.4</td>
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<tr>
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<td></td>
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<td>93.3 ± 2.0</td>
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<tr>
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<td>77.8</td>
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<tr>
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<tr>
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<td>Algae</td>
<td>51.3</td>
<td>60.1</td>
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DISCUSSION

Like other marine teleosts, Sardinops sagax is predominantly ammonotelic (Handy & 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 (19.26 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 & Whitledge 1972, Durbin & 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 (291 g DBM), sardine are medium-sized (33 g DBM) and Cape anchovy are small (3 g 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 Sardinops sagax in this study, although small fish have faster excretion rates than large fish and excretion rates increase with temperature (Handy & Poxton 1993, Jobling 1994). It may be that the size difference between the 2 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 Qₒ value of 1.82 over 10 to 22°C for this species (van der Lingen 1995).

The elevation of nitrogen excretion rates shortly after feeding has been reported for several fish species (Brett & Zaal 1975, Savitz et al. 1977, Davenport & Sayer 1986, Sayer 1988, Du Preez & Cockroft 1988a, b, Handy & 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 & 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 (1981) 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 1981, 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, Weisberg & Lotrich 1982), and for the other clupeoids studied (Durbin & 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 & 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 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 & 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 faecal elimination results reported here corroborate previous work which indicated that phytoplankton is evacuated by sardine much faster than zooplankton (van der Lingen 1998).

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 & Durbin 1981), although these authors gave no information concerning whether C:N ratios changed during the experiment. 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 & 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). No significant (p < 0.05) differences were observed between zooplankton-derived carbon and nitrogen absorption efficiencies of sardine, anchovy and menhaden (Kruskal-Wallis analysis of variance by ranks [Zar 1984]; Table 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 to 16 μm (Durbin & 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 & Macleod 1976, van der Lingen 1996) and globally (Hand & Berner 1959, Alamo & 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 & Findlay 1989), sardine can entrap particles of down to 17 μm (van der Lingen 1994), 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.

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 & 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.

Acknowledgements. I thank the Director of the Sea Fisheries Research Institute, Dr A. J. L. Payne, for funds and facilities for this research. Anastasia Polito and Envor Malan are warmly thanked for their extensive assistance during experiments, as is Dr Trevor Probyn for his advice concerning the biochemical analyses. I am extremely grateful to Dr Pat Garratt and Simon Chater of the Two Oceans Aquarium for allowing me to use their display fish as experimental subjects. Drs Larry Hutchings and Coleen Moloney, and 4 anonymous referees are thanked for their comments on the manuscript.

Table 4. Mean carbon and nitrogen absorption efficiencies (% ± 1 standard deviation) of sardine Sardinops sagax (this study) anchovy Engraulis capensis (James et al. 1989a) and menhaden Brevoortia tyrannus (Durbin & Durbin 1981) fed phytoplankton and zooplankton diets. Values with the same superscript are not significantly different from each other, as assessed using the Kruskal-Wallis analysis of variance with ranks and with p < 0.05. The number of experiments used to determine the mean values is given in brackets.

<table>
<thead>
<tr>
<th>Species</th>
<th>Zooplankton carbon</th>
<th>Zooplankton nitrogen</th>
<th>Phytoplankton carbon</th>
<th>Phytoplankton nitrogen</th>
</tr>
</thead>
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<tr>
<td>Sardine</td>
<td>88.2 ± 4.7a (6)</td>
<td>93.3 ± 2.0a (6)</td>
<td>62.6 ± 5.6a (3)</td>
<td>78.7 ± 4.1a (3)</td>
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<tr>
<td>Anchovy</td>
<td>77.9 ± 7.2a (10)</td>
<td>87.4 ± 4.3b (10)</td>
<td>50.6 ± 0.7a (2)</td>
<td>83.2 ± 1.8b (2)</td>
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<td>Menhaden</td>
<td>86.7 ± 0.4a (3)</td>
<td>91.3 ± 0.9b (3)</td>
<td>86.4 ± 3.2a (7)</td>
<td>92.4 ± 2.0a (7)</td>
</tr>
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</table>
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Submitted: April 21, 1998, Accepted: September 9, 1998
Proofs received from authors: December 11, 1998

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany