GASTRIC EVACUATION, FEEDING PERIODICITY AND DAILY RATION OF SARDINE *SARDINOPS SAGAX* IN THE SOUTHERN BENGUELA UPWELLING ECOSYSTEM

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Laboratory and field experiments were conducted to determine gastric evacuation rates of sardine *Sardinops sagax*, and stomach content analyses were undertaken to assess feeding periodicity and estimate the daily ration of this species in the southern Benguela. Gastric evacuation followed an exponential pattern and was influenced by food type; phytoplankton was evacuated at a much faster rate than zooplankton. Estimated gastric evacuation rates ranged between 0.05 and $0.29 \cdot h^{-1}$, with mean values of 0.09 and $0.27 \cdot h^{-1}$ for fish fed zooplankton and phytoplankton respectively. Despite this large range, no significant relationships were found between gastric evacuation rate and fish size, temperature, food particle size or meal size. Feeding periodicity was size-dependent; small fish had a peak in feeding activity at or around sunset, whereas larger fish appeared to feed continuously. This suggests that fish of different size exhibit different foraging behaviours, possibly reflecting differences in their diets. Estimates of daily ration ranged from 0.99 to 2.52% wet body $mass \cdot day^{-1}$ for fish consuming zooplankton and from 2.97 to 7.58% wet body $mass \cdot day^{-1}$ for fish consuming phytoplankton. Small fish consumed a bigger daily ration than large fish.

The epipelagic 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 fluctuated between 135 000 and 676 000 tons during the period 1950–1993 (Roel and Armstrong 1991, Chief Director of Sea Fisheries 1995). The three 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 1988), 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.* 1989), 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 phyto-planktivorous filter-feeders (Davies 1957, King and Macleod 1976) and, although they are capable of particulate-feeding, they maximize their net energy gain through prolonged bouts of low-cost filter-feeding (Van der Lingen 1994, 1995). Small zooplankton, principally the cyclopoid copepods *Oithona* spp. and *Oncaea* spp., dominate the zooplankton fraction of the diet of sardine from the western Agulhas Bank (Van der Lingen 1996).

In this paper, the gastric evacuation and feeding periodicity of sardine are described, and estimates of the species' daily ration in the southern Benguela are provided.

MATERIAL AND METHODS

Gastric evacuation

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 3 000-ℓ fibreglass tank supplied with a continuous flow of 5-µm-filtered seawater at ambient temperature (Table I). 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 I). Prior to an experiment, five 1-ℓ 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

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

Experiment number	Number of fish	Starvation time (days)	*TL* (mm)	*W* (g)	Temp. (°C)	Feeding period (h)	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	7 683±1 329
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	1 497±1 235
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] Constituting 95% *Skeletonema costatum* chains
[2] Constituting 70% *Skeletonema costatum* chains, and *Chaetoceros* spp., *Asterionella* spp. and *Nitschia* spp.
[3] Constituting 64% *Oithona* spp., 18% *Centropages brachiatus* and 11% small copepods (*Paracalanus* spp., *Clausocalanus* spp. and *Ctenocalanus* spp.)
[4] Constituting 86% *Oithona* spp., 4% *Calanoides carinatus* and 3% small copepods
[5] Constituting 64% *Centropages brachiatus*, 19% *Calanoides carinatus* and 9% small copepods
[6] Constituting 38% *Coscinodiscus* spp., 25% *Peridinium* spp. and 13% crustacean eggs and nauplii
[7] Constituting 50% *Coscinodiscus* spp., 18% *Peridinium* spp. and 9% crustacean eggs and nauplii

zooplankton. Fish were allowed to feed for periods of 0.5–1.5 h, 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, 3–5 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.

Field experiments were performed in a 3 000-ℓ aluminium tank supplied with a continuous flow of 60 $\ell \cdot min^{-1}$ of seawater. 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 data on stomach contents at *t* = 0. Fish in the tank were observed to ensure that there was no feeding, and dead or moribund fish were removed. At 2-h intervals after *t* = 0, 5–20 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 (14–16 and 18–20 cm *TL*) were present in the sample used in Experiment 1. Data for the two size-classes were analysed separately (Table I: Experiments Fld 1S and Fld 1L for small and large fish

respectively).

Stomach contents were extracted from preserved stomachs and washed into a petri dish using 0.2-μm-filtered seawater. The contents were then vacuum-filtered through pre-weighed Whatman GF/F 47 mm 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, 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 100 mℓ in filtered seawater, and two 5 mℓ 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);

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

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

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

(see Table II for the glossary of the 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 II: 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 ($\cdot$h^{-1})
t	Time
k	Suffix for observations

Feeding periodicity and daily ration

Feeding periodicity was assessed by analysing stomach content mass of fish collected in an Engels 308 midwater trawl. Two sampling approaches were employed. First, sampling of sardine collected approximately every 3 h during the diel cycle was conducted within a single area of abundant fish. Two such samplings were carried out over periods of 56 and 69 h 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–March) of 1993/94 and 1994/95, primarily over the western 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 0.1 mg. 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 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 analysed 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 ac- cording 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 Mag- nan 1996). A one-way ANOVA/Tukey multiple range analysis was used to test for differences in mean stomach 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

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

where $\bar{S}$ is the geometric mean stomach content mass during the 24 h period. The Elliott and Persson (1978) model sums over 24 h the quantity of food consumed during consecutive time intervals, and has the form

$$C = \sum^{k=n-1} \left[\frac{(\bar{S}_{k+1} - \bar{S}_k \, e^{-Rt_k})Rt_k}{} \right] \qquad , \qquad (5)$$

where C is 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 24 h period. Daily ration as a percentage of wet body mass is calculated from

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

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 coeffi- cients of determination for the "best fit" expressions were only marginally higher than those for the expo- nential expression. Therefore, the exponential expression was fitted to all the data sets (Figs 1, 2).

Rates of gastric evacuation ranged from 0.06 to 0.29$\cdot$h^{-1} in laboratory experiments, with fish fed diatoms having substantially higher values than those fed zooplankton (Fig. 1). Because of the marked
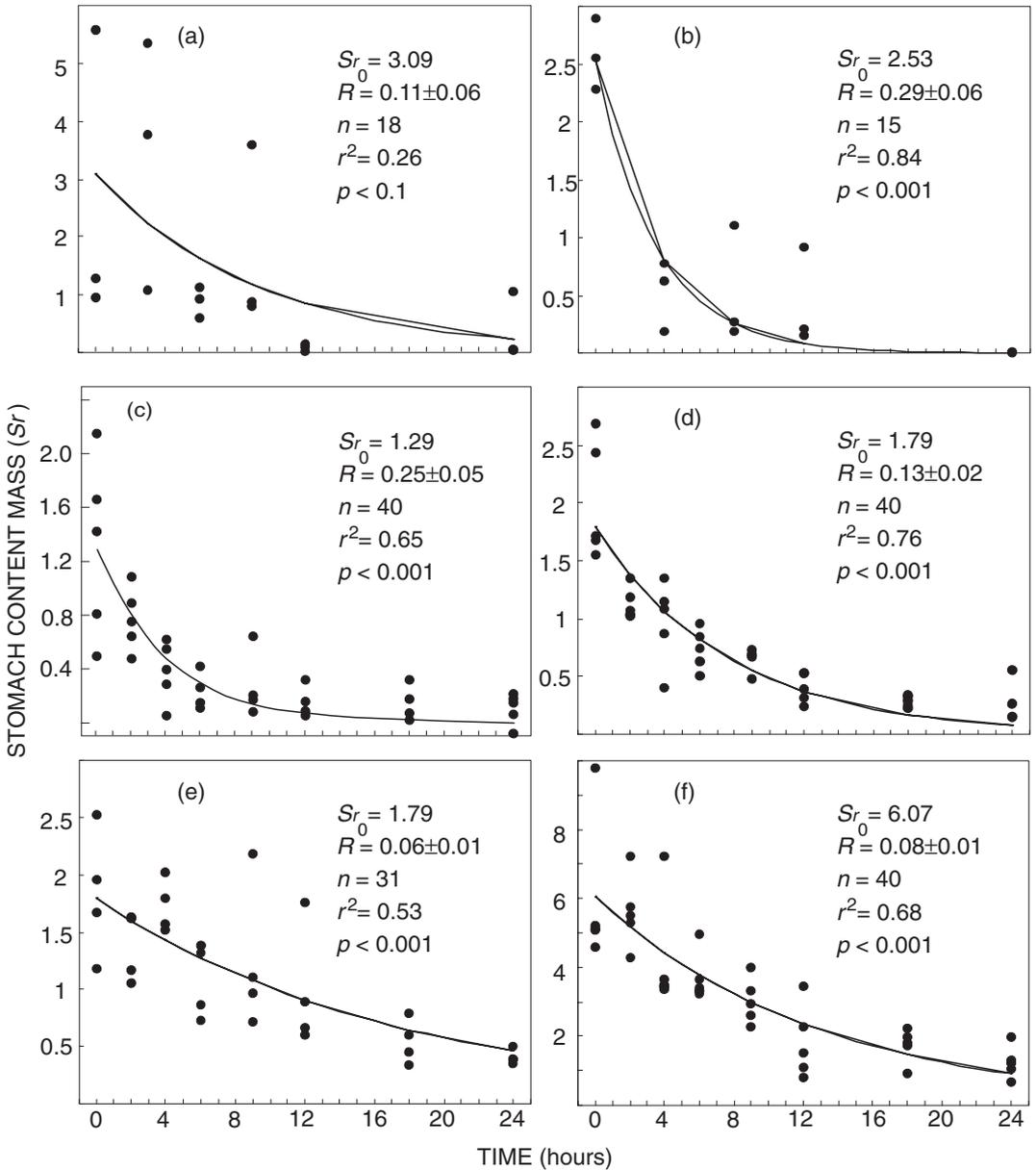
STOMACH CONTENT MASS (Sr)

(a) $Sr_0 = 3.09$
$R = 0.11 \pm 0.06$
$n = 18$
$r^2 = 0.26$
$p < 0.1$

(b) $Sr_0 = 2.53$
$R = 0.29 \pm 0.06$
$n = 15$
$r^2 = 0.84$
$p < 0.001$

(c) $Sr_0 = 1.29$
$R = 0.25 \pm 0.05$
$n = 40$
$r^2 = 0.65$
$p < 0.001$

(d) $Sr_0 = 1.79$
$R = 0.13 \pm 0.02$
$n = 40$
$r^2 = 0.76$
$p < 0.001$

(e) $Sr_0 = 1.79$
$R = 0.06 \pm 0.01$
$n = 31$
$r^2 = 0.53$
$p < 0.001$

(f) $Sr_0 = 6.07$
$R = 0.08 \pm 0.01$
$n = 40$
$r^2 = 0.68$
$p < 0.001$

TIME (hours)

Fig. 1: Exponential decline in stomach content mass (Sr) of *Sardinops sagax* 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

difference in laboratory estimates of rates of gastric evacuation resulting from food type, separate mean values were calculated for the different food types. Fish fed zooplankton had a mean rate of gastric evacuation of $0.09 \pm 0.03 \cdot h^{-1}$, whereas those fed phytoplankton had a mean rate of gastric evacuation of $0.27 \pm 0.03 \cdot h^{-1}$. Rates of gastric evacuation from field experiments ranged from 0.05 to $0.10 \cdot h^{-1}$, not significantly different from the estimates derived from laboratory fish fed on zooplankton.
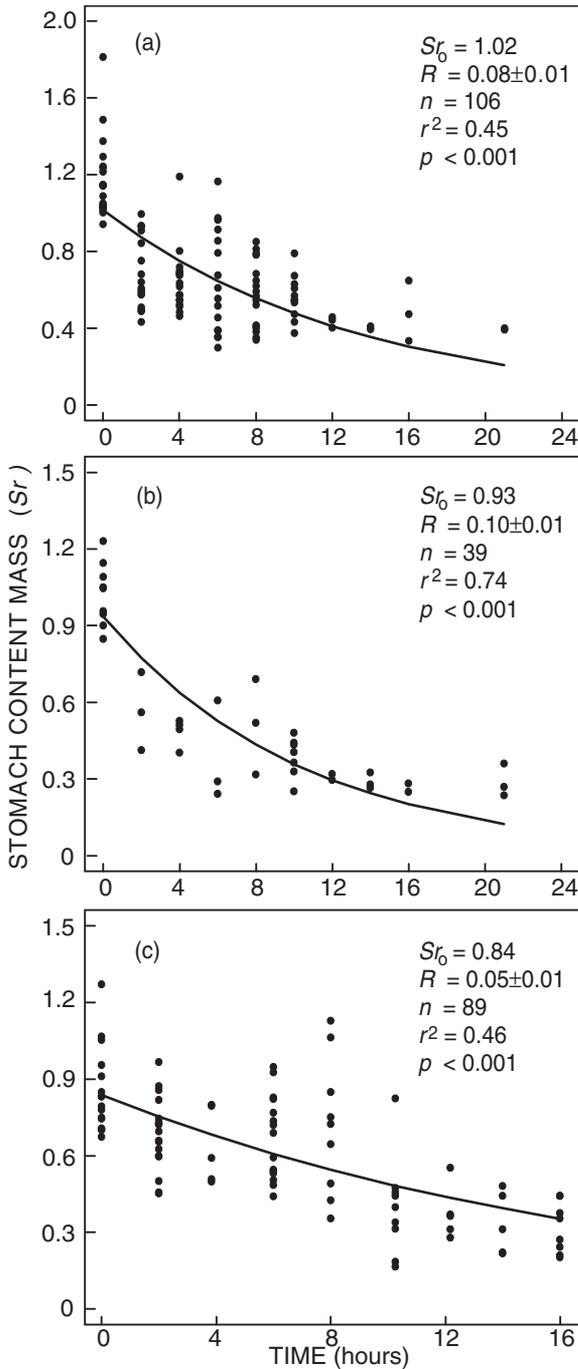
Fig. 2: Exponential decline in stomach content mass (Sr) of *Sardinops sagax* after cessation of feeding in field experiments: (a) Experiment 1S, (b)Experiment 1L and (c) Experiment 2L. Note the different scales on the x- and y-axes

Feeding periodicity

There were significant relationships between Sr and W, and a power function provided the best fit to the data in all cases:

(i)   RAFOS I: $Sr = 5.137W^{-0.467}$ ($n = 855$, $r^2 = 0.11$, $p < 0.001$);
(ii)   RAFOS II: $Sr = 4.126W^{-0.450}$ ($n = 993$, $r^2 = 0.44$, $p < 0.001$);
(iii) SARP: $Sr = 3.702W^{-0.429}$ ($n = 3037$, $r^2 = 0.28$, p < 0,001).

To remove this size effect, the datasets were divided into mass categories of W: 0–24.9, 25–49.9, 50–74.9, 75–99.9 and 100+ g. These categories correspond roughly to sardine of ages 0+, 1+, 2+, 3+ and 4+ years, and each was analysed separately for assessment of feeding periodicity and daily ration. Four categories were assessed for the data from each of the RAFOS cruises (Categories 2–5 for RAFOS I and 1–4 for RAFOS II), and all five 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 3. Although there were significant differences in stomach mass 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 was at night.

RAFOS II

Fish in all four categories showed a similar pattern of stomach fullness (Fig. 4), with higher mean values of stomach content mass observed at the beginning (00:30–06:30) and the end (18:30–23:30) 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.

SARP

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

Daily ration

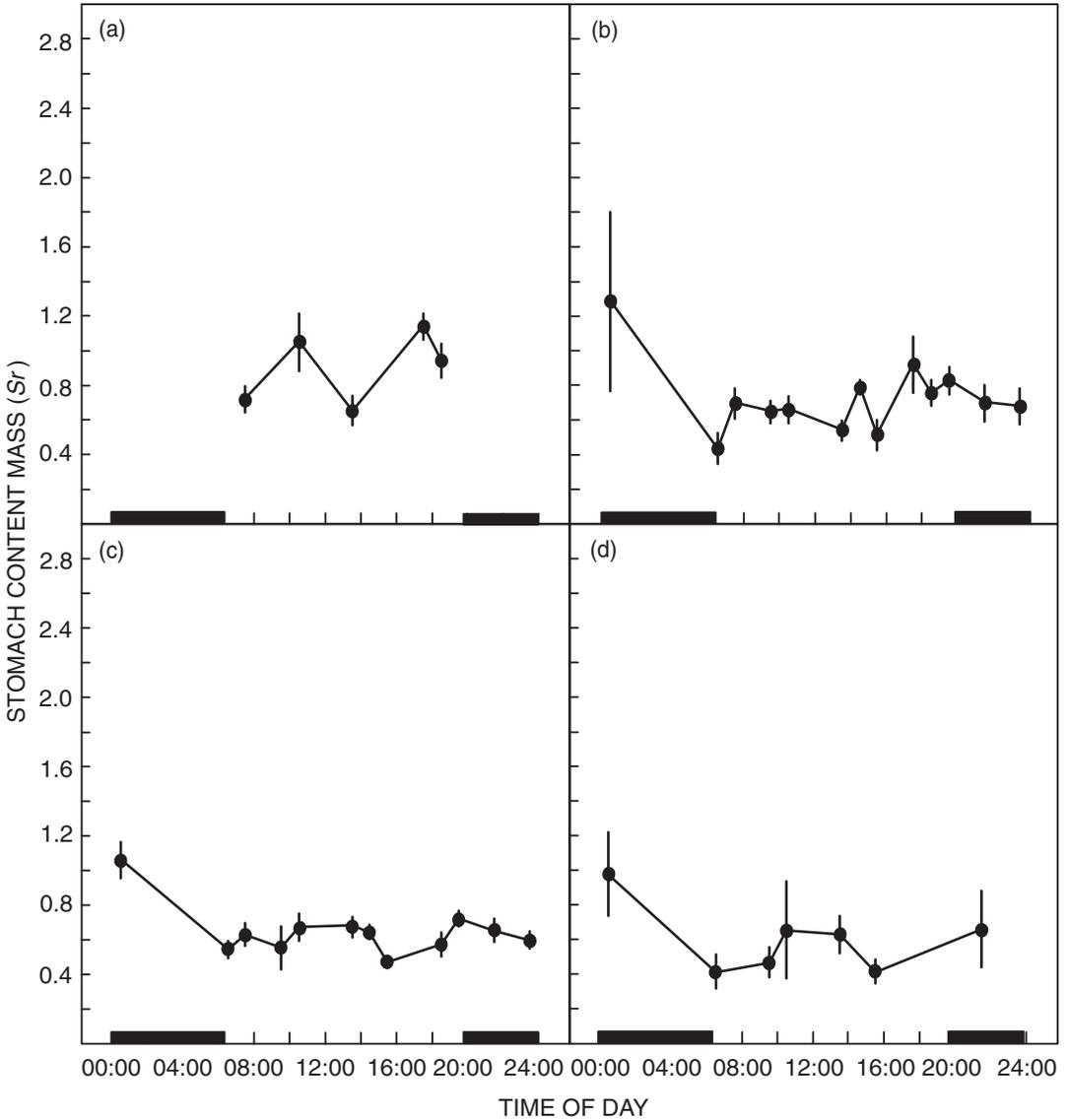Daily ration was calculated using the mean values of

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

R estimated for fish fed on 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 fish mass category, both within and across datasets (Fig. 6). Estimates of daily ration ranged from

0.99 to $2.52\%W \cdot day^{-1}$ for fish consuming zooplankton and from 2.97 to $7.58\%W \cdot day^{-1}$ for fish consuming phytoplankton, and small fish had larger daily rations than large fish. Power function regression equations relating *Cr* to *W* were derived using estimates of *R* for phytoplankton and zooplankton from both models:
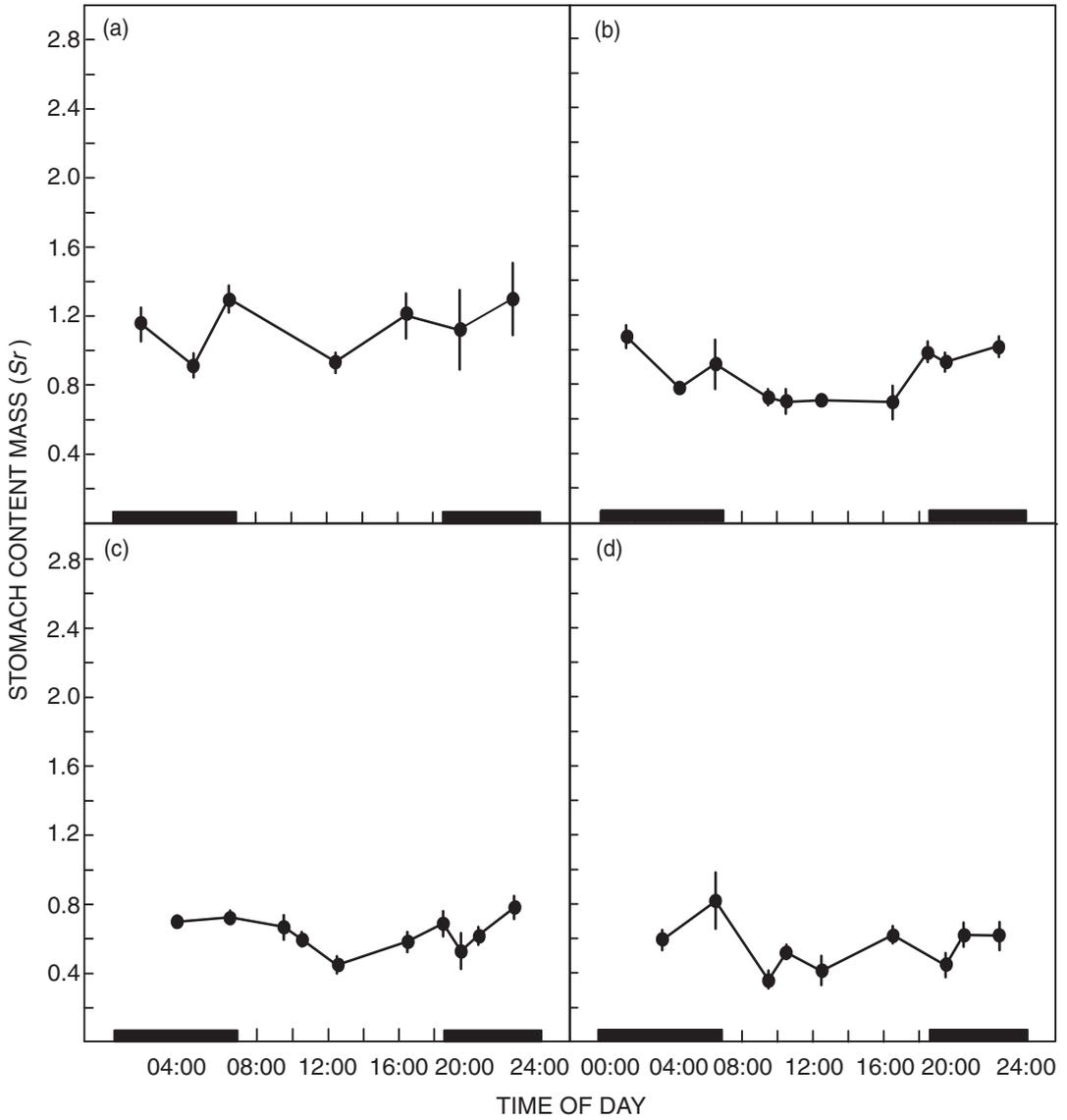
Fig. 4: Geometric mean values (±95% confidence limits) of stomach content mass (Sr) as a function of time of day for *Sardinops sagax* from the RAFOS II cruise: (a) Category 1 (<24.9 g), (b) Category 2 (25–49.9 g), (c) Category 3 (50–74.9 g) and (d) Category 4 (75–99.9 g). Dark bars indicate night-time

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; $Cr = 8.6743W^{-0.4281}$; $r^2 = 0.93$, $p < 0.001$;
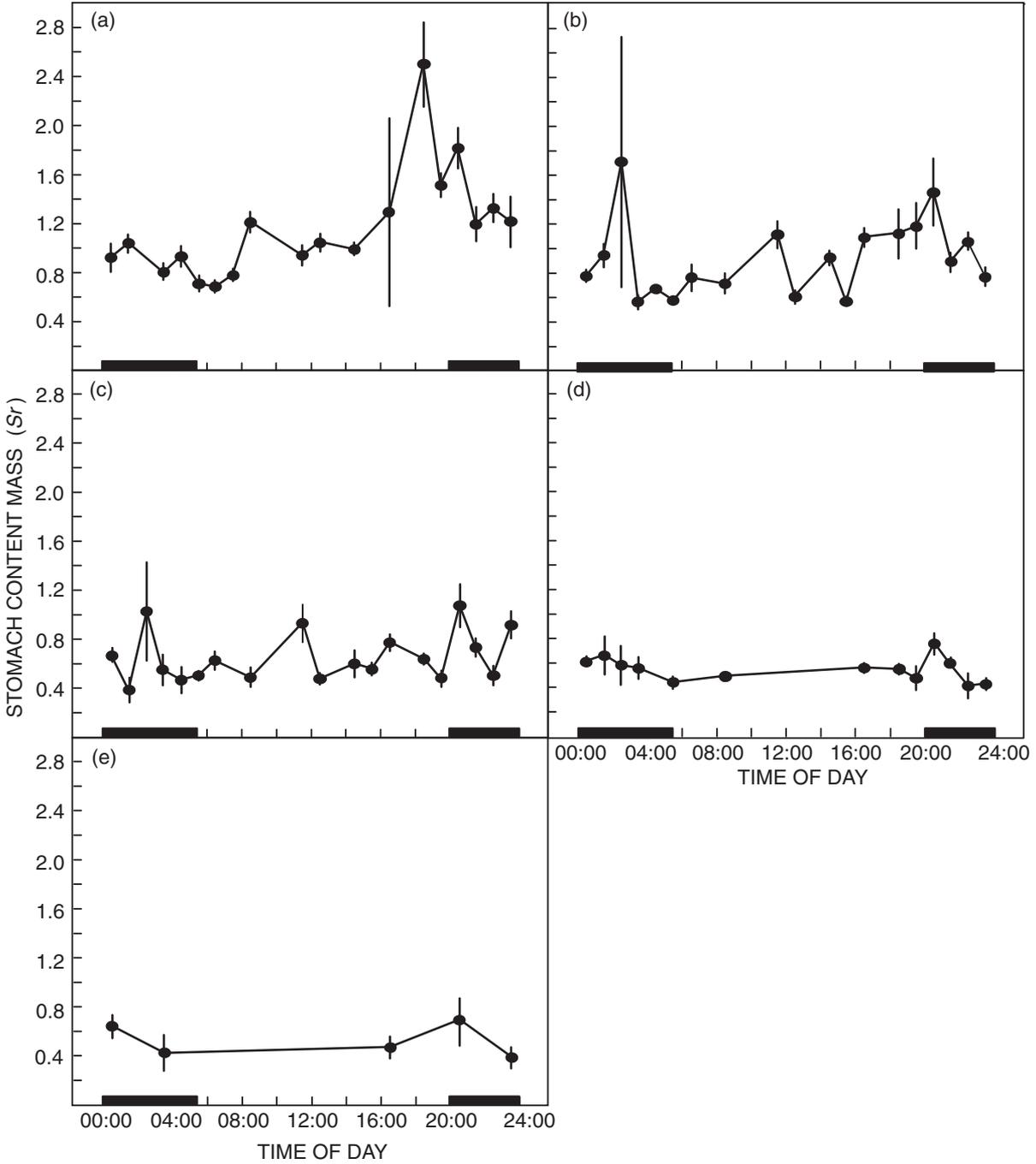 Phytoplankton; $Cr = 26.0594W^{-0.4297}$; $r^2 = 0.94$, $p < 0.001$.

Fig. 5: Geometric mean values (±95% confidence limits) of stomach content mass (*Sr*) as a function of time of day for *Sardinops sagax* from the SARP cruises: (a) Category 1 (<24.9 g), (b) Category 2 (25–49.9 g), (c) Category 3 (50–74.9 g), (d) Category 4 (75–99.9 g) and (e) Category 5 (100+ g). Dark bars indicate night-time
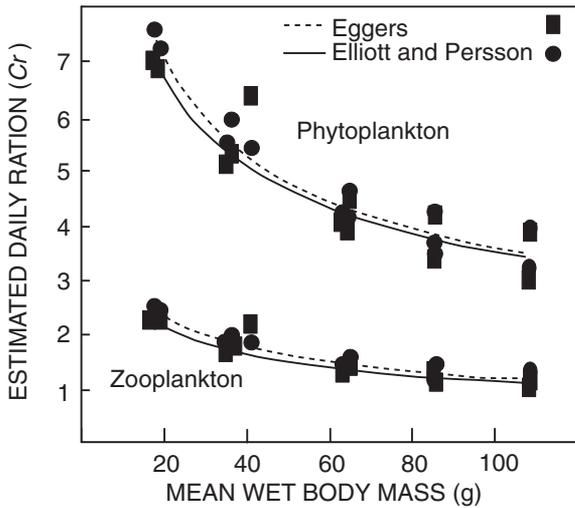
Fig. 6: Estimated daily ration of *Sardinops sagax* as a function of mean wet body mass for each mass category determined in this study. Power function regression equations are fitted to the data for both the Eggers (1977) and the Elliott and Persson (1978) models, using the instantaneous rates of gastric evacuation estimated for both phytoplankton ($R = 0.27 \cdot h^{-1}$) and zooplankton ($R = 0.09 \cdot h^{-1}$)

DISCUSSION

Gastric evacuation

Considerable controversy exists as to an appropriate model for gastric evacuation in fish (Jobling 1981, 1986, Persson 1986, Bromley 1994), but the form of the model of gastric evacuation may depend on prey size: large prey items such as fish may be evacuated linearly, whereas smaller prey are evacuated exponentially (Jobling 1987, Bromley 1994). Sardine are primarily filter-feeders that feed almost continuously or at frequent intervals (Figs 3–5), and the exponential function appeared to be the most appropriate model of gastric evacuation for this species (Figs 1, 2). Food type was found to have a marked effect on evacuation rates of sardine (Fig. 1), with diatoms being evacuated at rates 2–5 times faster than zooplankton. Neither zooplankton size nor temperature significantly affected rate of gastric evacuation, although the temperature range investigated (14.6–17.8°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).

An assumption in the use of experimentally derived estimates of evacuation rate in daily ration models is that the estimates are realistic. In laboratory experiments, fish were fed a single meal over a limited period, after being starved for a prolonged period (Table 1); these feeding conditions differ from the natural feeding of sardine (Figs 3–5). 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 single-meal models could be used to obtain reasonable estimates of total daily ration.

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

Feeding periodicity and daily ration

Feeding periodicity in *S. sagax* is size-dependent, small (<25 g) fish showing a peak in feeding activity at or around sunset, whereas large 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 zooplankto-phagous than adults (Hand and Berner 1959, King and Macleod 1976), suggesting that juveniles employ particulate-feeding to a greater degree than do adult sardine.

Studies relating to feeding periodicity of clupeoids were reviewed by James (1988), who described the data as "scarce and conflicting". Nevertheless, James considered most clupeoids to be nocturnal foragers, with peak feeding activity at dusk and dawn. James (1987) demonstrated a pattern of dawn and dusk feeding for anchovy *E. 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 consisted of 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 feed for longer periods than those of particulate-feeding planktivores. Sardine of >25 g did not show marked variation in stomach content mass (Figs 3–5), 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 (Van der Lingen 1994, 1995, 1996).

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 they do 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, because 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 models have been used widely 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. Both 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 Eggers (1977) model 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 ($0.99–2.52\%W \cdot$day^{-1}) and those feeding on phytoplankton ($2.97–7.58\%W \cdot$day^{-1}) are a result of the marked difference in rates of gastric evacuation for fish fed on 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 (Van der Lingen 1994, 1995), their stomachs typically contain both phytoplankton and zooplankton prey (Davies 1957, King and Macleod 1976, Van der Lingen unpublished data), 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 (Fig. 6). No other estimates of daily ration for *S. sagax* could be located in the literature (FishBase 1996, Froese and Pauly 1996), although data are 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*, Parrish *et al*. 1989) by Kawasaki and Kumagai (1984). The seasonal average stomach content mass of adult (20–35 cm *TL*) Peruvian sardine *S. sagax* was $1.07\%W$ (calculated from Table 1 of Alamo and Bouchon 1987). Applying the Eggers (1977) model to these values, and using the rates of gastric evacuation of 0.09 and $0.27 \cdot$h^{-1} determined in this study for fish fed zooplankton and phytoplankton respectively, provides daily ration estimates of $1.73–5.18\%W \cdot$day^{-1} for Far Eastern sardine and $2.31–6.93\%W \cdot$day^{-1} for the Peruvian sardine populations. These estimates are within the range of $0.99–7.58\%W \cdot$day^{-1} derived in this study (Fig. 6).

LITERATURE CITED

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