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FEEDING HABITS, DAILY RATION AND VERTICAL MIGRATION OF THE CAPE HORSE MACKEREL OFF SOUTH AFRICA

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Crustaceans, principally copepods and euphausiids, were most frequently found in the stomachs of Cape horse mackerel *Trachurus trachurus capensis* collected during demersal research surveys (1992–1995) in summer on the west coast and in winter on the south coast of South Africa. Fish (mainly pelagic) were infrequent (< 10%) in the diet of fish from both coasts. The feeding periodicity, rate of gut evacuation and vertical migration of horse mackerel were investigated from midwater and bottom trawl collections taken during five diel sampling periods between 1993 and 1995 at fixed positions on the South Coast. Horse mackerel feed only during the day, mostly in late afternoon prior to their ascent into midwater at around sunset. Based on the exponential rate of decline in stomach fullness throughout the night, the rate of gut evacuation by horse mackerel was estimated to be $0.22 \cdot h^{-1}$. Using the Elliott and Persson method, the daily ration was estimated as 3.8% of wet body mass. Horse mackerel appear to migrate vertically for reasons other than feeding, and selective advantages of this behaviour are discussed.

The Cape horse mackerel *Trachurus trachurus capensis* is an important component of the Benguela ecosystem (Crawford *et al.* 1987). Two stocks are recognized, one in Namibian waters and the other extending from south of the Orange River mouth to as far east as East London (Hecht 1990, Naish 1990, Naish *et al*. 1991). The species represents an important food resource for fish, especially the Cape hakes *Merluccius capensis* and *M. paradoxus* (Konchina 1986, Payne *et al*. 1987, Roel and Macpherson 1988, Pillar and Wilkinson 1995), and also for marine mammals (David 1987, Sekiguchi *et al*. 1992), particularly off northern Namibia and the south coast of South Africa, where the current principal concentrations of horse mackerel occur (Crawford *et al* 1987, Barange *et al.* 1998).

Feeding habits of horse mackerel have been studied off Namibia (Krzeptowski 1982, Andronov 1983, 1985, Konchina 1986) and off the South African south coast (Hatanaka *et al.* 1983, Uozumi *et al.* 1984, 1985, Hecht 1990). Those studies contained useful baseline information on the types and relative quantities of prey consumed, and concluded that crustaceans, principally copepods and euphausiids, dominated the diet and that predation on fish was minimal. However, there have been relatively few attempts to investigate important aspects of feeding such as when and how much food is consumed by horse mackerel during a diel period, although the studies by Krzeptowski (1982) and Andronov (1985) are notable exceptions. Those studies revealed that horse mackerel off Namibia apparently feed only during the day and maximally in the afternoon, and have a rapid digestion time and a fast rate of consumption. The extent to which this feeding behaviour is relevant to South African horse mackerel is yet to be addressed.

Although anecdotal information suggests that Cape horse mackerel rise off the sea bed at night, behaviour that has an impact on the type of fishing gear used by commercial trawling fleets (Crawford 1989), their vertical migration is not well documented. Barange (1994) and Barange and Hampton (1994) acoustically described the vertical structure of the species in South African waters. However, the reasons for their nocturnal migrations into midwater are uncertain. In light of the increase in research emphasis on the use of acoustic methods with traditional net sampling to estimate the abundance of horse mackerel (Barange *et al.* 1998), there is a need to improve upon our current knowledge of the vertical migratory behaviour of these fish substantially.

The purpose of the present study is to describe the feeding characteristics of horse mackerel on the south and west coasts of South Africa, specifically their diel feeding periodicity, rate of gut evacuation and daily ration. The study also explores several hypotheses which could explain the vertical migratory behaviour in horse mackerel.

MATERIAL AND METHODS

Field collections

Information on the diel variability in bottom trawl catches of the Cape horse mackerel was obtained from collections taken at a fixed position 20 miles

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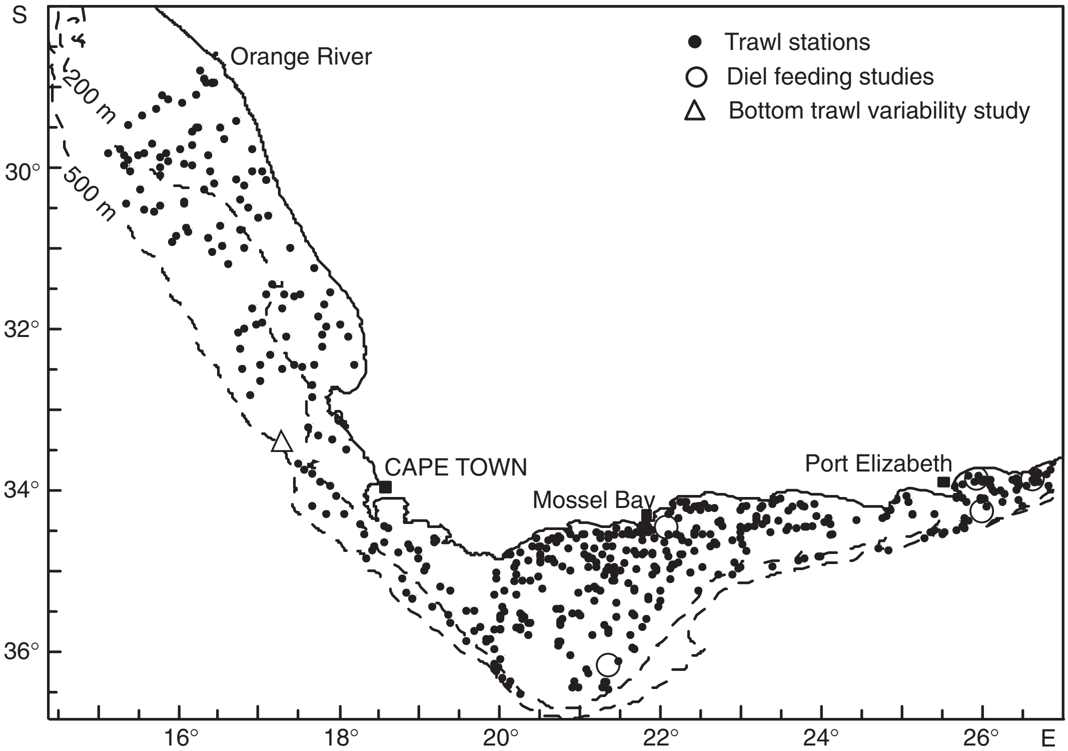

Fig. 1: Survey area, showing locations of the demersal trawl stations at which horse mackerel were caught and the positions of the fixed diel study sites

south-west of Cape Columbine on the west coast of South Africa (Fig. 1). Of a total of 13 around-the-clock experiments conducted in winter and summer between 1984 and 1990, primarily to assess the diel catch variability of the Cape hakes (Pillar and Barange 1997), trawl collections from five experiments contained fish in sufficient quantities to allow description of day/night variability in the catches of horse mackerel (Table I). Details on gear used and sampling methods are given in Pillar and Barange (1997).

To evaluate diet composition, samples were collected during routine demersal fish biomass surveys aboard F.R.S. *Africana* during January (summer) on the West Coast and April–July (winter) and Septem-

Table I: Mean and standard deviation (*SD*) of day and night catches by mass of horse mackerel caught in bottom trawls during five diel variability studies

Sampling date	Day			Night			Night catch as a percentage of day catch
	Number of tows	Mass of catch (kg)		Number of tows	Mass of catch (kg)		
		Mean catch	*SD*		Mean catch	*SD*	
16–18 January 1987	5	156.8	138.4	5	7.2	6.9	4.6
22–23 June 1987	4	12.0	5.3	6	1.0	1.1	8.3
7–9 February 1988	5	333.8	170.4	5	15.0	13.0	4.5
8–9 August 1988	3	252.0	34.5	7	16.3	14.6	6.5
6–7 January 1989	5	54.2	22.1	3	6.3	5.5	11.6

Table II: Stomach sample collection information of horse mackerel caught in bottom trawls during the South and West Coast demersal biomass surveys, 1993–1995

Sampling dates	Region	Number of stomachs		Fish length (cm)	Mean fish length (cm)	Mean fish mass (g)	Mean stomach fullness (% body mass)
		Examined	% Empty				
2–28 September 1993	South Coast	772	55	15–50	31.4	320	0.82
5–31 January 1994	West Coast	527	58	10–47	30.6	279	0.58
8 June–2 July 1994	South Coast	662	66	13–54	32.9	365	0.73
22 September–27 October 1994	South Coast	387	50	14–49	28.5	258	0.36
8–31 January 1995	West Coast	484	38	12–44	30.6	281	0.95
23 April–15 May 1995	South Coast	569	56	15–52	31.9	338	0.78
Total/Mean		3 401	53.8		31.0	306.8	0.70

ber/October (spring) on the South Coast between 1993 and 1995 (Table II). Fish were collected during daylight using a 180-ft German bottom trawl with a cod-end liner of 35-mm mesh. Whenever possible, 30-minute tows were taken at each sampling site on a semi-random, depth-stratified basis to a maximum depth of some 500 m. Payne *et al.* (1987) and Badenhorst and Smale (1991) provide additional details of the survey areas and procedures.

A subsample of horse mackerel (usually 10 fish) was taken from each positive trawl (Fig. 1). These fish were either processed on board or blast-frozen for later processing ashore. On board, each fish selected was measured for total length *TL* (to the nearest millimetre) before removing the stomach, which was preserved in 4% formalin. The few fish that were suspected of stomach regurgitation and cod-end feeding were excluded from the analysis. Fish mass was determined using length/mass regressions derived from *TL* and masses of fish (± 0.01g) determined in the laboratory.

To investigate feeding periodicity, horse mackerel were collected during five diel studies carried out between October 1992 and May 1995 (Table III). Each study was conducted within a limited area at different locations over the shelf on the South Coast (Fig.1). Fish collections were made with a 180-ft German bottom trawl during the day and at night with an Engels 308 midwater trawl, fished at various depths throughout the water column. Trawling depths were selected on the basis of fish distribution, as observed with a Simrad EK400 echo-sounder operating at 38 kHz.

Generally, all horse mackerel from the midwater trawls were measured, but owing to the large numbers of fish caught in the bottom trawls, subsamples of horse mackerel were taken from those trawls. For stomach analysis, a subsample of horse mackerel was retained from each trawl (usually 10 fish per 1-cm length-class) and immediately blast-frozen.

Laboratory procedures

Total length of horse mackerel (to the nearest millimetre) and wet mass (to the nearest 0.1g) were recorded before removing the stomach. A fullness code between 0 (empty) and 4 (full) was assigned to each stomach, and the state of digestion of the food was classified between 1 (fresh material) and 4 (unidentifiable digested matter). Food items were sorted into major taxonomic groups. The most common prey in the stomachs were crustaceans, mainly copepods and euphausiids, and, where possible, these prey items were weighed separately (to the nearest 0.001 g). However, in cases of digested material, all crustacean prey were weighed together.

Data analysis

For analysis of diet composition, the percentage frequency of occurrence of each prey category was estimated. As interest was in investigating the dietary spectrum of horse mackerel, it was felt that this method was more informative than the percentage by mass of the prey. Diets were analysed by area (West and South coasts) and by season (winter and spring) on the South Coast.

Feeding periodicity was investigated with three types of data: first, the frequency of empty stomachs; second, the number of stomachs containing intact or slightly digested prey (Stages 1 and 2), expressed as a percentage of the total number of stomachs containing food (these stages were combined because of low numbers in both stages); third, the stomach fullness, which is the wet mass of stomach contents expressed as the percentage of total wet body mass of fish. Differences in feeding activity during the day were examined from material collected during the demersal biomass surveys (Table II). Collections taken during the five diel studies (Table III)

Table III: Stomach sample collection information, the number of stomachs examined and the percentage of stomachs that contained food of horse mackerel caught by bottom and midwater trawls in all diel feeding studies

Sampling dates	Sounding (m)	Trawl type	Number of tows		Study duration (h)	Fish length range (cm)	Number of stomachs examined		% containing food	
			Day	Night			Day	Night	Day	Night
13–15 October 1992	105	Bottom Midwater	7 0	0 8	33	20–48	203	200	68.5	29.5
27–28 June 1994	55	Bottom Midwater	8 0	0 9	23	23–44	155	177	54.2	8.6
14–15 October 1994	70	Bottom Midwater	2 0	0 2	9	33–46	20	20	80.0	40.0
10–11 May 1995	180	Bottom Midwater	4 0	1 1	26	25–35	100	20	76.7	50.0
13–14 May 1995	98	Bottom Midwater	4 0	1 2	28	22–32	86	39	93.1	56.4
Mean									74.5	36.9
Total			25	24			564	456		

were used to investigate diel feeding periodicity.

The estimation of daily ration followed the Elliott and Persson (1978) model, which is based on the sequential evaluation of the quantity of food consumed between each sampling period (C_t), defined as:

$$C_t = \frac{(S_{t+\Delta t} - S_t\, e^{-Rt})\, Rt}{1 - e^{-R\Delta t}} \quad ,$$

where S_t and $S_{t+\Delta t}$ are the mean quantities of food in the stomach at time t and $t_{+\Delta t}$ respectively and R is the rate of gut evacuation per hour. Two different methods were used to estimate the rate of gut evacuation. The first was based on individual stomach fullness data, normalized to the percentage of the highest starting value for each of the diel studies. The evacuation rate was ascertained using the equation

$$S_t = S_0\, e^{-Rt} \quad .$$

The second method was based on a simplified evacuation model using the computer programme MAXIM (Jarre *et al.* 1991). The model assumes an exponential evacuation rate and that feeding is constant over a discrete feeding period. The input was the mean stomach fullness (stomach mass as percentage of body mass) from pooled data from the diel studies averaged per 2-h interval. Empty stomachs were omitted from the analyses, because they would bias estimations of evacuation rates (Olson and Mullen 1986).

The daily ration was calculated using stomach fullness data from the broader-based demersal surveys. This broad temporal and spatial coverage reduces the effect of day-to-day and regional variations in rates of food intake, which would arise should the more restricted diel feeding studies be used for estimating daily ration. Data were analysed by geographical area (West or South Coast) and season (spring or winter) on the South Coast.

RESULTS

Vertical migration

Horse mackerel perform a nocturnal vertical migration into midwater. At night most of the population move off the bottom and are unavailable to bottom trawls (Table I). Examination of the echosounder record (Fig. 2a) shows that horse mackerel migrate as a population, moving towards the surface

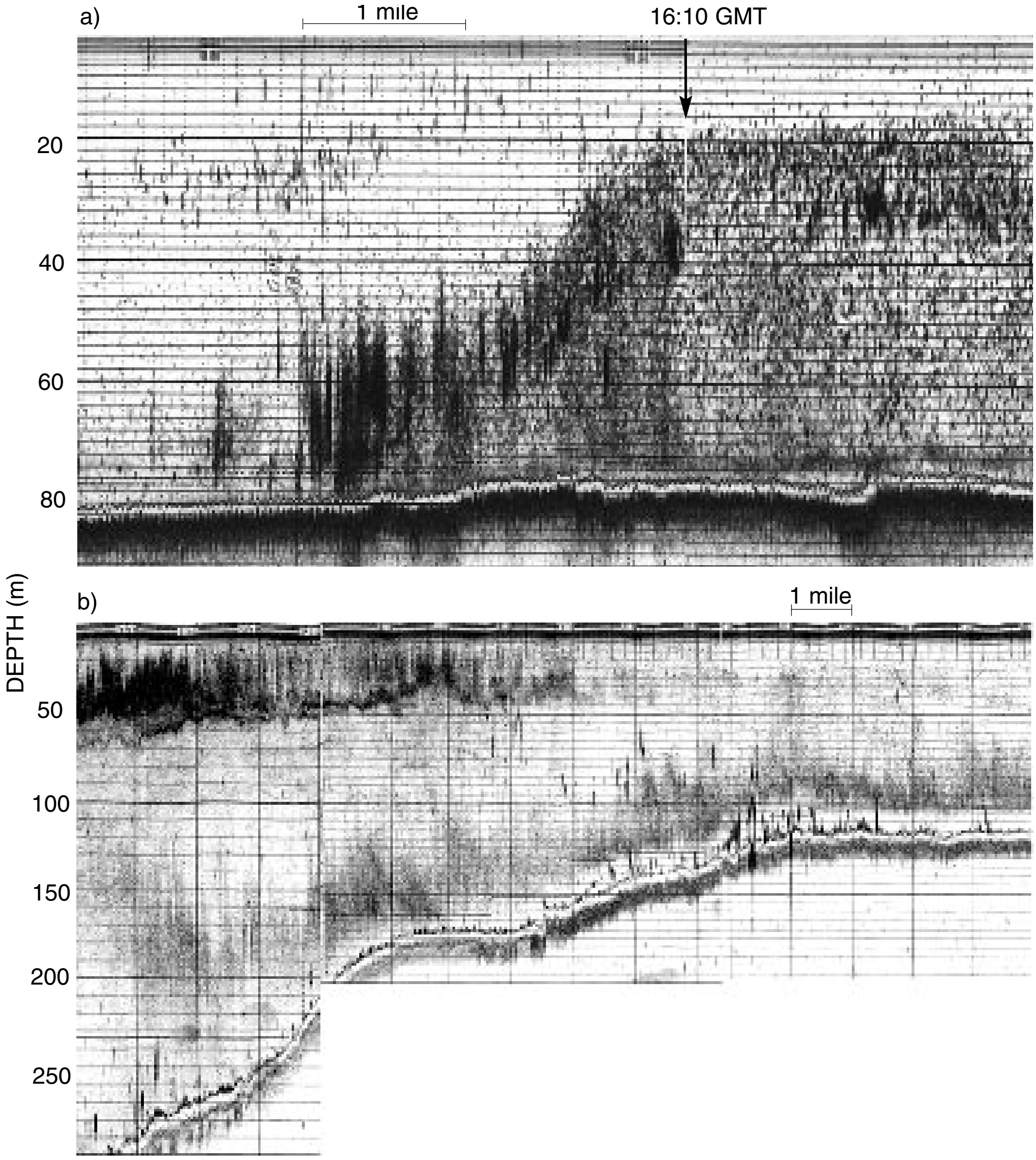

Fig. 2: Acoustic echochart showing (a) dense shoals of horse mackerel ascending in the water column towards the surface around sunset and (b) dense aggregations of horse mackerel extending 5–30 m off the bottom during the day. The more diffuse scattering layer in the water column (30 m off the bottom) in (b) is believed to be zooplankton, on which the horse mackerel may be feeding

as dense shoals just after sunset and dispersing into widespread scattering layers throughout the night. Occasionally, shoaling is maintained at night, as shown by Barange and Hampton (1994) and Barange *et al*. (1998). At daybreak the fish merge into dense layers and migrate back towards the sea bed. During the day, horse mackerel generally remain close to the sea bed, visible on echo-charts as "spikes" of fish

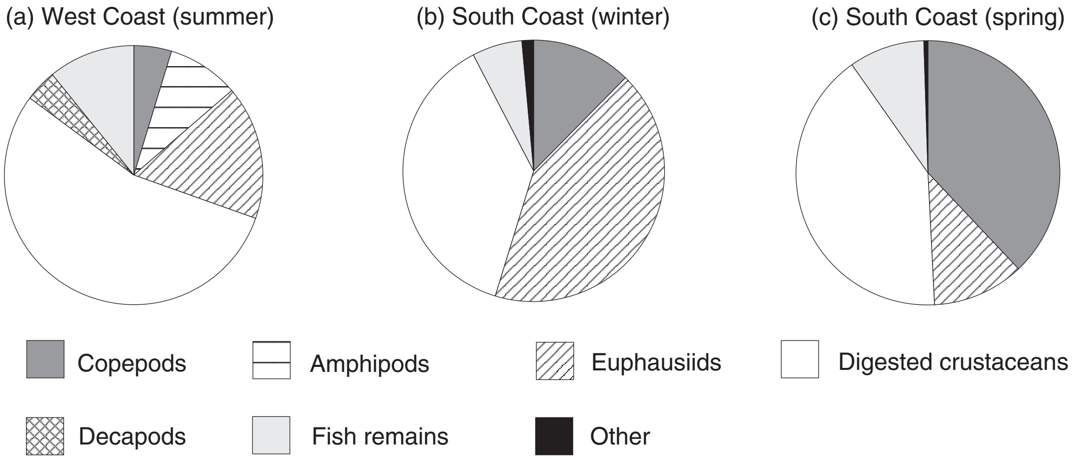

Fig. 3: Relative abundance of different prey categories, expressed as percentage frequency of occurrence of all prey in the stomachs, of horse mackerel collected during the (a) West Coast (summer), (b) South Coast (winter) and (c) South Coast (spring) demersal trawl surveys

aggregations extending off the bottom. Sometimes, however, the aggregations are positioned in midwater, and are clearly off the bottom (Fig. 2b).

Diet composition

Horse mackerel fed largely on copepods and euphausiids (Fig. 3), although other crustaceans such as decapods and amphipods were identified from stomachs of fish from the West Coast. Fish (mainly pelagic fish) were infrequent (<10%) in the diet. There was some indication of seasonality in the diet, most notably the higher incidence of euphausiids during winter in the diet of horse mackerel from the South Coast.

Feeding periodicity

Of the 1 020 stomachs examined during the five diel studies (Table II), 36.9% of the night-time samples contained food, the majority of which was digested. Of the fish taken during the day, 74.5% contained food which was recently ingested. To examine the variation in the frequency of empty stomachs, stomach fullness and in the occurrence of fresh prey in the stomachs of horse mackerel, the data from three diel studies (13–15 October 1992, 10–11 and 13–14 May 1995), which had sufficient continuity to assess diel changes, were combined (Fig. 4). All three feeding indices indicate that horse mackerel fed only during the day. Feeding appeared to commence in the late morning, leading to a maximum around mid-afternoon. Feeding declined during the late afternoon, and reached low levels after sunset. This feeding pattern is shown more clearly in Figure 5, which presents the combined stomach fullness values for the three diel studies grouped into 2-h intervals. Stomach fullness peaked a few hours before sunset, at around 15:00, and declined thereafter, with digestion continuing throughout the night.

The daylight pattern of feeding activity was further investigated using data pooled from the demersal trawl surveys, and grouped into 1-h intervals (Fig. 6). On the West Coast in summer, stomach fullness increased throughout the day, leading to a maximum in the afternoon. Correspondingly, the percentage of fish with stomachs containing fresh prey was lower in the morning than in the afternoon. A similar pattern was found on the South Coast in spring. However, on the South Coast in winter, stomach fullness values were higher and stomach contents were fresher in the early morning than in the middle of the day. It is noteworthy that the percentage of empty stomachs was high on both coasts, ranging between 38 and 66% (Table III).

Gut evacuation and daily ration

Based upon the rate of decline in the percentage of stomach fullness (*%BM*), normalized to the percentages of the maximum fullness for individual values of the three diel studies, the rate of gut evacuation (*R*) was estimated to be $0.22 \cdot h^{-1}$, following the equation:

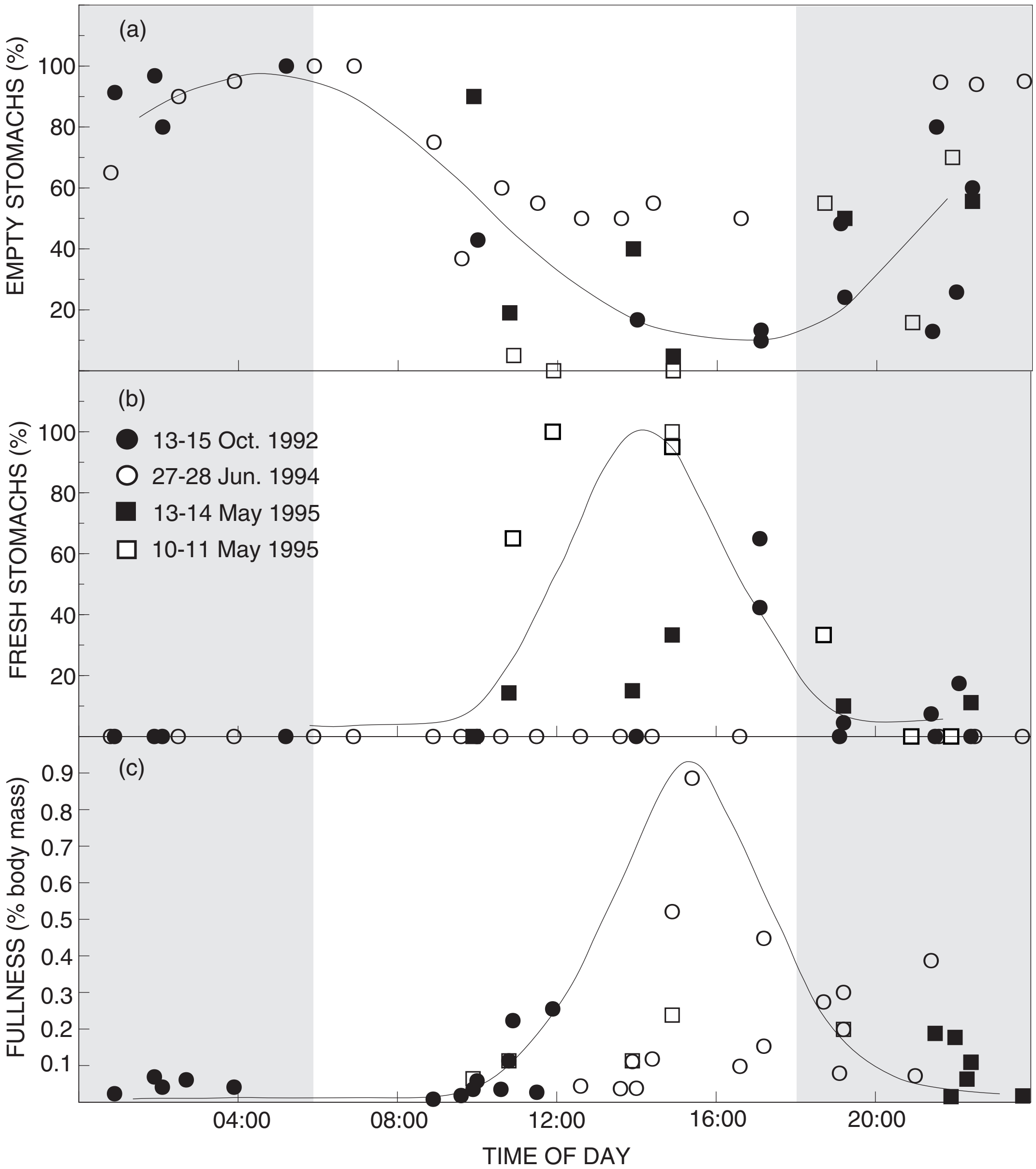

Fig. 4: Relationship between time and (a) empty stomachs, expressed as the percentage of the number of stomachs examined, (b) prey freshness, expressed as the percentage of fresh stomach contents (Stages 1 and 2) and (c) stomach fullness, expressed as the percentage of body mass of horse mackerel caught by bottom and midwater trawls during three diel studies. Shading denotes night-time periods

$$\%BM = 23.34e^{-0.22t} \quad ,$$

where t is the time (in h) after ingestion. The same evacuation rate of $0.22 \cdot h^{-1}$ was computed using the MAXIM programme, operating with mean stomach fullness data (Fig. 5) rather than individual values. Applying that evacuation rate and using the data pooled from all the demersal trawl surveys, the daily ration was estimated at 3.8% *BM*·day^{-1}.

DISCUSSION

Cape horse mackerel undergo diel vertical migrations. They ascend as a population from the bottom into midwater around sunset, remain there throughout the night, and return to the sea bed around dawn. This movement appears to be for reasons other than feeding; stomach fullness and prey freshness decreased markedly after sunset and there was no feeding during the night in all five of the diel studies reported here. This study showed that feeding takes place during the day when horse mackerel are close to the bottom. There they exploit the near-bottom daytime aggregations of copepods and euphausiids, their principal prey off South Africa (Hatanaka *et al*. 1983, Uozumi *et al*.1984, 1985, Hecht 1990) and Namibia (Krzeptowski 1982, Andronov 1983, 1985, Konchina 1986). Similarly, horse mackerel off Namibia are reported to be strong vertical migrators, and appear to stop feeding prior to their ascent into midwater at dusk and only start feeding after their population descent at around dawn (Andronov 1985).

Well-defined feeding periodicities have been reported for various species of *Trachurus* elsewhere, and most studies conclude that they are generally daytime feeders (e.g. Shuntov 1969, Webb 1977, Dahl and Kirkegaard 1987). However, their foraging behaviours may differ. For example, in the coastal waters of southern Australia and New Zealand, *Trachurus declivis* frequently feed near the surface during daylight (Shuntov 1969, Webb 1976), although this behaviour varies seasonally and is strongly influenced by the distribution and abundance of euphausiids, their principal prey (Williams and Pullen 1993). Scattering layers of horse mackerel are occasionally observed in midwater during the day off the south and west coasts of South Africa, which may be attributable to feeding aggregations. Neilson and Perry (1990) point out that teleosts are opportunistic feeders, and that this could override their endogenous rhythms as determinants of vertical migration.

Daytime feeding is consistent with the general pattern of visual predators (Wootton 1990). However, by foraging during the day, horse mackerel become vulnerable to predation. On the south coast of South Africa, horse mackerel constitute up to 60% of the daytime diet of large hake (Pillar and Wilkinson 1995). However, based on the occurrence of demersal fish in the night-time diet of hake, Pillar and Barange (1997) showed evidence to suggest that large hake move lesser distances into midwater in search of food than do small hake. Based on bottom and midwater trawling and acoustic observations on hake from the South African west coast (Barange *et al*. 1994, Pillar and Barange 1995) and off Namibia (Huse *et al*. 1998), it appears that larger hake do not migrate extensively off the bottom at night. Therefore, it would be adaptive for horse mackerel to move towards the surface at night to avoid large hake. This behaviour may minimize the risk from demersal predators such as hake, but would increase the threat from pelagic predators, such as snoek *Thyrsites atun*, cetaceans and the Cape fur seal *Arctocephalus pusillus pusillus*, all of which are identified as predators of horse mackerel, particularly on the South African south coast (Nepgen 1979, David 1987, Sekiguchi *et al*. 1992). Although predator avoidance has been judged as an attractive hypothesis to account for vertical migration in marine fish (e.g. Levy 1990), it is questionable whether it provides the only selective advantage for diel vertical migration in horse mackerel.

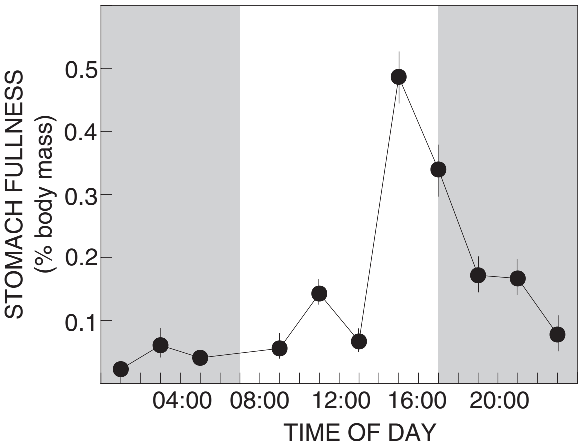

Fig. 5: Relationship between time, grouped into successive 2-h intervals, and mean stomach fullness (± *SE*), expressed as the percentage of wet body mass of horse mackerel caught by bottom and midwater trawls during three diel studies. Shading denotes night-time

In this study, horse mackerel appeared to feed more frequently in the late afternoon prior to their vertical migration into midwater at night when feeding ceased. Given their apparent rapid rate of gut evacuation, it is tempting to speculate that energetic benefits may be realized from migrating out of the cooler bottom water into the warm surface water at night. Nocturnal association with higher temperatures would serve to stimulate and increase digestion rates, whereby consumption during the next feeding period (during the day) would not be limited by the quantity of undigested food remaining in the stomach, thereby increasing feeding and growth rates (Wurtsbaugh and Neverman 1988). Following this hypothesis, the nocturnal depth of horse mackerel in the water column

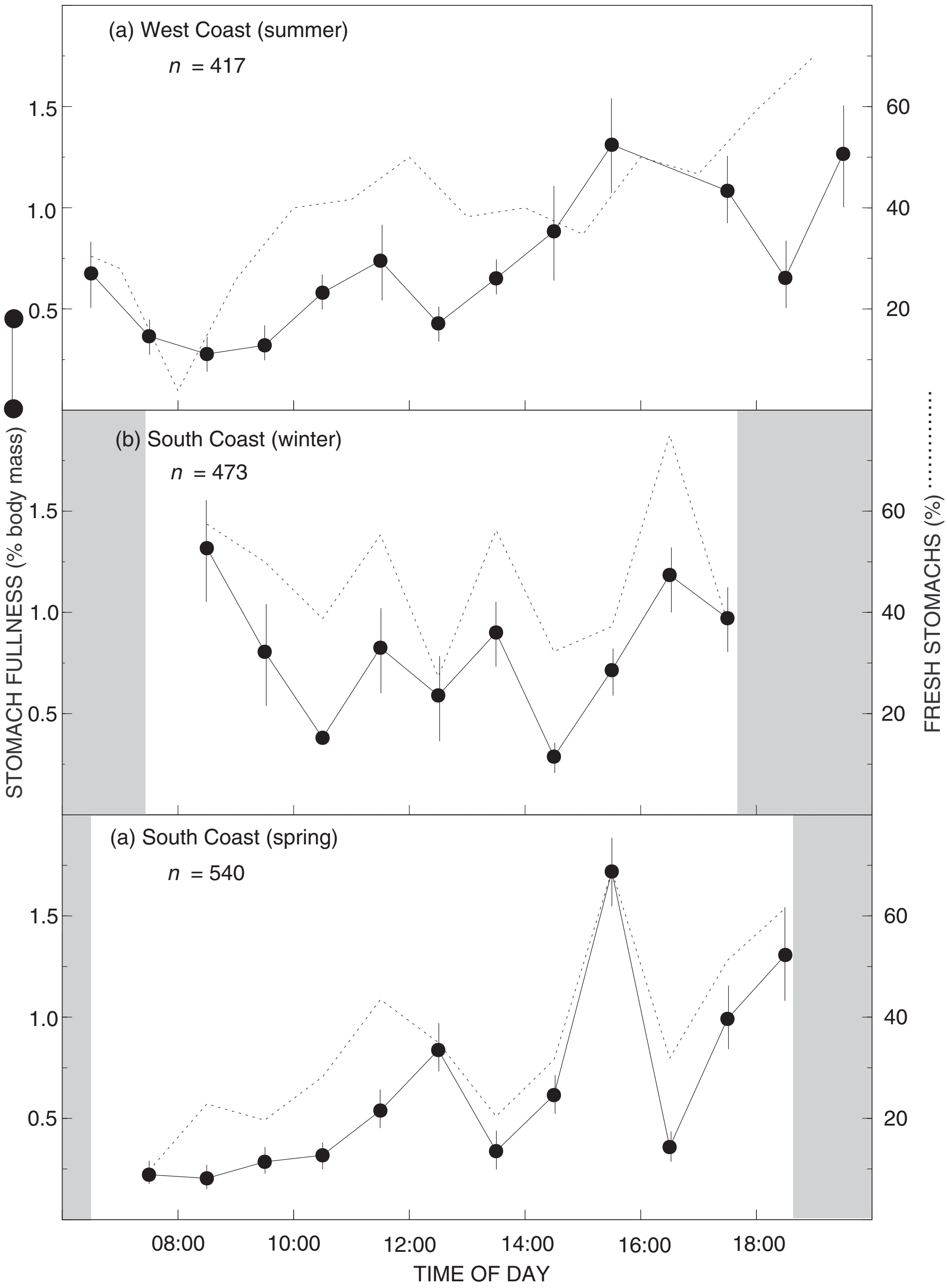

Fig. 6: Relationship between time, grouped into successive 1-h intervals, and mean stomach fullness (± *SE*), expressed as a percentage of body mass, and the mean hourly stomach freshness (± *SE*), expressed as a percentage of fresh stomachs (Stages 1 and 2) of horse mackerel collected during the (a) West Coast (summer), (b) South Coast (winter) and (c) South Coast (spring) demersal trawl surveys

may be modulated by the thermal conditions of their environment. On the eastern Agulhas Bank, where the thermocline is consistently strong and shallow (Largier and Swart 1987, Swart and Largier 1987), horse mackerel are fished commercially at night when they are more readily available to midwater fishing gear (Tilney 1997). Conversely, on the western Agulhas Bank, where the thermocline is deep and isothermal conditions are common, especially during winter months (Eagle and Orren 1985), fish are traditionally caught by daytime bottom trawling (Tilney 1997). During research cruises on the western Agulhas Bank, horse mackerel sometimes are perceived not to perform nocturnal migrations, a behaviour considered to be a problem for the acoustic assessment of horse mackerel in that region (Barange *et al*. 1998). However, during one of the present diel studies (27–28 June 1994), horse mackerel migrated vertically at night under near isothermal conditions when temperature-related bioenergetic benefits would be negligible. Furthermore, at that site horse mackerel did not appear to feed throughout the day or prior to their ascent into midwater at night. Therefore, it is unlikely that the phenomenon of post-feeding thermotaxis can adequately explain the vertical migratory patterns in some of the horse mackerel communities under study.

The present rate of gut evacuation of $0.22 \cdot h^{-1}$ for Cape horse mackerel is based on the assumption that feeding ceased after dark. This assumption was supported by the presence of increasingly digested material in the stomachs after sunset. Dahl and Kirkegaard (1987) estimated a rate of $0.26 \cdot h^{-1}$ for the North Sea horse mackerel *Trachurus trachurus* using a similar assumption (daytime feeding only) and methodology as applied in this study. The present estimate is, however, one-third of the rate reported by Andronov (1985) for horse mackerel off Namibia. However, the methodology employed in that study was generally restricted to indirect approximations of stomach evacuation, and is therefore likely to be less accurate than the present study. A number of factors, both biological and physical, influence the evacuation rate in fish, but temperature, food type and predator size appear to have the greatest impact (Bromley 1994). Therefore, direct comparisons with values reported in the literature are hindered. The short gut-residence time and rapid rate of evacuation estimated for the Cape horse mackerel appears to be in keeping with the general pattern noted for relatively active fish feeding on zooplankton, such as mackerel *Scomber scomber* ($0.1 \cdot h^{-1}$; Mehl and Westgaard 1983 cited by Dahl and Kirkegaard 1987) and small gadoids, e.g. haddock *Melanogrammus aeglefinus* and Norway pout *Trisopterus esmarki* ($0.27 \cdot h^{-1}$ for both species; Albert 1995). The high energetic demands of continuous activity must be met by high food consumption (Paul *et al*. 1990), which appears to be an important determinant of the rate of gastric evacuation (Ruggerone 1989).

The present daily ration estimate of 3.8% *BM* is smaller than the estimates of up to 12.5% obtained by Andronov (1985) for horse mackerel off Namibia. However, Andronov's study used faster rates of evacuation than used here and sampling was localized, so probably reflecting the daily ration of fish in relatively small areas, possibly where prey were abundant. Daily rations of between 2 and 5% have been estimated for zooplanktivorous fish that are, like horse mackerel, relatively strong swimmers and capable of sustained activity, e.g. Norway pout and haddock (Albert 1995), whiting *Merlangius merlangus* (Patterson 1985) and saithe *Pollachius virens* (Du Buit 1991). Although these estimates are not comparable because of the differences in methodology, it would appear that the daily ration obtained for the Cape horse mackerel in this study falls within the range of estimates for other vertical migratory fish with similar prey preferences. The present estimate is derived from data integrated over large geographical areas and varying rates of food intake. Therefore, it can be regarded as a more realistic estimate of the horse mackerel daily ration than has been assumed previously from narrower-based studies.

In conclusion, this study substantiates previous findings that Cape horse mackerel are mainly zooplanktivorous. During the day they feed on near-bottom aggregations of copepods and euphausiids, mostly in the late afternoon prior to their ascent into midwater around sunset. The study has demonstrated that these vertical migrations are for reasons other than feeding and that the importance of foraging benefits from vertical migration is minimal in the Cape horse mackerel. It is suggested here that this behaviour may be a tactic to avoid predators and/or that energetic benefits may be an important driving factor: when one factor (e.g. avoidance of predators) is of key importance, energetic considerations may still influence the vertical migration that is exhibited. Because of the variety of factors involved, vertical migration may vary geographically in South African waters (Barange *et al*. 1998). It is unreasonable to expect that any one factor can adequately explain the vertical migratory behaviour of the Cape horse mackerel and a multifactor approach is necessary in future studies towards understanding this complex phenomenon.

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