

*Benguela Dynamics*Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci.* 19: 365–376
1998

365

THE DIURNAL VERTICAL DYNAMICS OF CAPE HAKE AND THEIR POTENTIAL PREY

I. HUSE*, H. HAMUKUAYA†, D. C. BOYER‡, P. E. MALAN‡ and T. STRØMME*

The Cape hakes *Merluccius capensis* and *M. paradoxus* are dominant predators over the Namibian shelf. They are found in a water column that includes myctophids and other mesopelagic fish, euphausiids and cephalopods. Together with their cohabitant potential prey, hake are known to undertake diurnal vertical migrations, aggregating near the bottom during daylight, but migrating off the bottom at night. An attempt to determine the underlying mechanisms of this diurnal migration by means of underwater acoustics and trawling was made at a single location on the central Namibian shelf at a depth of 350 m during four consecutive days in April 1996. Large *M. capensis*, 50–75 cm total length, dominated just over the sea bed, whereas 30–40 cm *M. paradoxus* were most abundant 5–50 m off the bottom, suggesting that the smaller *M. paradoxus* had to remain higher in the water column to avoid being eaten by the larger *M. capensis*. Large hake of both species preyed preferentially on fish, whereas the smaller hake preferred euphausiids, although there was some evidence of euphausiid consumption by most hake. There was no distinct daily feeding rhythm in either species of hake, although there was some evidence of evening predation dominating. This may indicate a feeding strategy where vision is not important.

The Benguela upwelling system is one of the most productive in the world (Waldron and Probyn 1992), providing a large biomass of plankton and planktivorous fish (Ware 1992) that in turn are preyed on by the Cape hakes *Merluccius capensis* and *M. paradoxus*, which are dominant and highly successful demersal predators in the system (Pillar and Barange 1995, Roel and Macpherson 1988, Ware 1992). Bottom waters over the Namibian shelf in particular are frequently depleted of oxygen, placing notable constraints on physical activity. It is therefore of relevance to study the behavioural ecology of Cape hake to determine what strategies they apply to tackle this demanding situation successfully. Prey availability, prey selection, feeding rhythm and vertical positioning are key parameters when such strategies are to be elucidated.

Hake are also among the most commercially important fish resources in the area (Bakun and Parrish 1981, Gordoia *et al.* 1995, Payne and Punt 1995), and it is therefore vital to apply the best forms of stock assessment to facilitate optimal management of the stocks. Among the methods used off Namibia is a combination of bottom trawl survey and hydro-acoustic abundance measurements, in which the quantity of hydroacoustically identified Cape hake off the bottom is added to the bottom trawl catches (Anon. 1995). However, pelagic hake recordings in daylight tend to be obscured by traces of mesopelagic fish and plankton. On the other hand, bottom trawl catchability of hake is higher during the day than at night

(Botha 1973, Payne 1989, Pillar and Barange 1997). The overall objective of the present investigation was therefore to describe and if possible to explain the diurnal vertical dynamics of Cape hake and their cohabitants in order to facilitate the optimization of hake survey strategies.

The general methodology of the investigation consisted of diurnal bottom and pelagic trawling plus continuous acoustic integration. As light is the modulating parameter in vertical positioning of a number of aquatic organisms (Roe 1984, Roe and Badcock 1984, Giske *et al.* 1990), underwater light extinction profiles including bioluminescence were measured, as was surface light. Stomach contents from both hake species were inspected visually and classified in order to facilitate the formulation of tentative feeding strategies.

MATERIAL AND METHODS

The investigation was carried out on board the *R.V. Dr Fridtjof Nansen* during a cruise on the Namibian shelf in April 1996. The work was carried out around the position 24°25'S, 13°40'E. One bottom trawl haul, one acoustic run, and at least one pelagic haul were made along the same track every six hours in an around-the-clock experiment which lasted four consecutive days. The acoustic echograms were anal-

* Institute of Marine Research, P.O. Box 1870, N-5024 Bergen, Norway. Email: ingvar.huse@imr.no

† National Marine Information and Research Centre, Ministry of Fisheries and Marine Resources, P.O. Box 912, Swakopmund, Namibia

‡ Sea Fisheries, Private Bag X2, Rogge Bay 8012, Cape Town, South Africa. Email: pmalan@sfri.wcape.gov.za

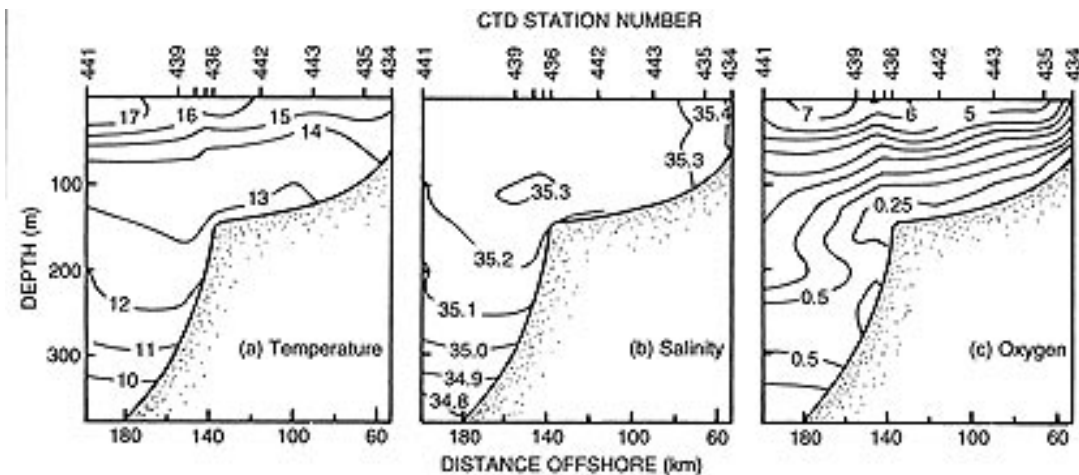


Fig. 1: Hydrographic sections westward from Walvis Bay – (a) temperature ($^{\circ}\text{C}$), (b) salinity ($\times 10^{-3}$) and (c) oxygen (mL l^{-1})

ysed by means of the Bergen Echo Integrator. In all, 12 bottom trawl hauls and 23 pelagic hauls were carried out. All trawl catches were sampled for species composition by mass and number.

The Gisund Super two-panel bottom trawl used had a headline length of 31 m, a footrope length of 47 m, a vertical opening of 4.5 m and a distance between the wings during towing of about 22 m. All trawl hauls were monitored by SCANMAR trawl sensors for vertical opening, bottom contact and distance between the doors. The length of a haul was recorded as distance trawled, measured by GPS, and checked against the lengths of the traces of the hauls on the GPS plot on the MacSea mapping system. All catches were standardized to a towing distance of 1.5 miles at the fishing depth. The different layers of the pelagic community were sampled with a pelagic trawl to identify the species composition. The pelagic trawl used was an Åkra trawl with a vertical opening of 22–24 m, equipped with a cable trawl sounder. Thyborøen 7.9 m^2 , 2 050 kg trawl doors were used with both trawls. A surface light meter (Li-Cor 1000) logged surface illumination every 15 minutes during the whole cruise. Underwater illumination and light extinction were measured with a photomultiplier-based light meter (sensitivity down to 10^{-6} lux) mounted on a FOCUS 400 towed vehicle. Bioluminescence was also measured in the same manner; it could be readily observed with the SIT video camera on the same vehicle.

Stomach contents of hake were collected from eight bottom and six deep pelagic hauls. The 14

M. capensis samples yielded a total of 281 fish and the 13 *M. paradoxus* samples a total of 341 fish, both totals including fish with empty stomachs. Fish with everted stomachs were not included in the material. The stomach contents were examined visually only, and each fish was assigned a classifier consisting of up to three of the major components ranked by apparent biomass. No attempt was made to assess the stage of digestion. The Mann-Whitney *U*-test was used to test day/night differences in trawl catches.

RESULTS

Hydrography

A hydrographic East/West CTD and oxygen transect of the shelf at the latitude of Walvis Bay, some 85 miles north of the study area, taken at the beginning of the cruise, is presented in Figure 1. It shows a moderate upwelling situation, with the lowest surface temperatures and highest salinities inshore. Bottom oxygen concentrations were $<0.5 \text{ mL l}^{-1}$ out to a seabed depth of 300 m, and $\pm 0.25 \text{ mL l}^{-1}$ to a seabed depth of 150 m.

Acoustics

The study area was characterized by good concentrations of both hake species and a substantial pelagic

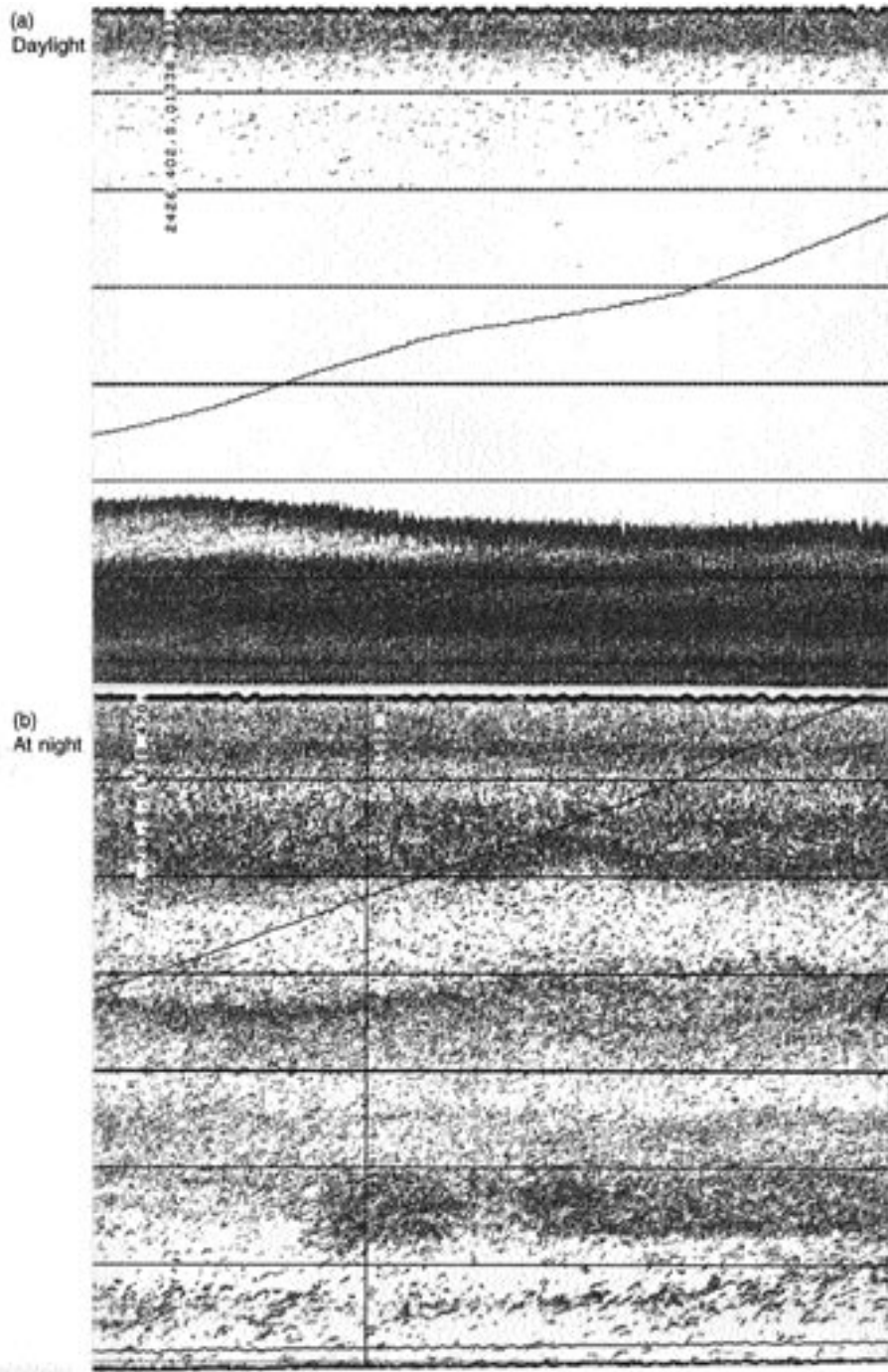


Fig. 2: Echograms of acoustic scattering layers in the study area in (a) daylight and (b) at night

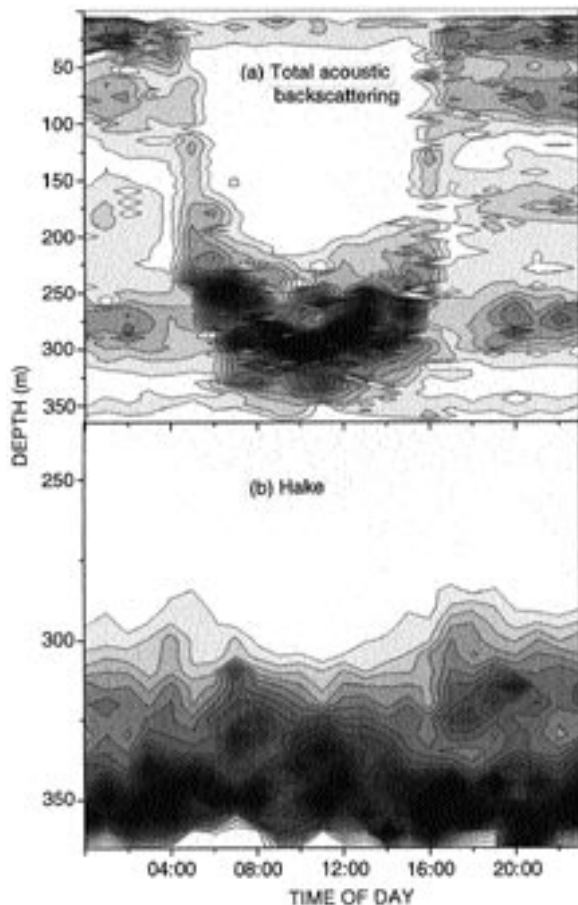


Fig. 3: Isopleths by depth and time of day of (a) total acoustic backscattering and (b) hake. Values are hourly averages of four 24-h periods

component consisting of mesopelagic fish, euphausiids and squid. The pelagic component underwent extensive diurnal vertical migration (Fig. 2). At least four layers (five with the obscured hake layer) were identified during the day (Fig. 2a), and they could be followed through diurnal vertical migration where, at night, the deepest mesopelagic layer split to form two sub-layers, giving a total of six quite stable layers at night (Fig. 2b). These were (from the surface downwards) one diurnally stable surface layer, four vertically migrating mesopelagic layers, and a hake layer deeper than 300 m. Mean hourly values of acoustic backscattering are given in Figure 3a. The Figure was compiled from post-processed acoustic data, all acoustic information scrutinized during the four diurnal

cycles the experiment lasted being combined into one diagram. The six layers can be discerned readily from the combined four-day data, illustrating the day-to-day stability of the pattern.

The species composition in the pelagic layers was identified from trawl catches. As the trawl often had to pass through one or several pelagic layers during setting and hauling, the risk of polluting the samples was high, but because the swept volume of the trawl at the sampling depth was substantially larger than during setting and hauling, the trawl catches should generally be dominated by the species composition at the sampling depth. The surface plankton layer consisted mainly of large medusae (*Chrysaora* sp.) and other plankton, and was obscured at night by the top mesopelagic layer. The four mesopelagic layers consisted of several species of mesopelagic fish, euphausiids and squid. The myctophids *Lampanyctodes hectoris* and *Symbolophorus boops* constituted more than 80% of the total mesopelagic biomass, according to pelagic trawl catches. *L. hectoris* dominated the three lower mesopelagic layers in the evening, and late at night was also abundant in the top layer. *S. boops* was found in all mesopelagic layers during the night, but decreased in abundance with depth. The mesopelagic lightfish *Maurollicus muelleri* was found in all mesopelagic layers at night, most abundantly in the lower layer, sparingly represented in the first and third layers, but more prominent in the second layer. It should, however, be noted that the smallest *M. muelleri*, which were particularly abundant in the two uppermost layers, were not caught representatively by the 22 mm mesh size of the net. Euphausiids were found in all layers, but were most abundant in the second mesopelagic layer, although this statement should be viewed with discretion because obviously an unknown and probably large proportion of the euphausiids was lost as a result of mesh selection. The small (± 10 g) squid *Lycoteuthis lorigera* was found in quantities of the order of 5% of total mesopelagic biomass. It migrated from depths of around 230 m in daylight to the two top layers at night. The larger (± 1 kg) squid *Todarodes angolensis* was less abundant, and stayed generally deeper than *L. lorigera* during daylight, but small specimens migrated to as high as the second mesopelagic layer in the evening.

The mean individual masses of *L. hectoris* and *S. boops* did not directly correlate with depth. *L. hectoris* averaged 1.75 g in the top layer, 1.52 g in the second layer, 1.98 g in the third layer and 2.07 g in the fourth mesopelagic layer. *S. boops* averaged 8.95 g in the topmost mesopelagic layer, 6.95 g in the second, 7.93 g in the third and 8.04 g in the fourth mesopelagic layer. In other words, both species were represented by larger specimens in the top layer,

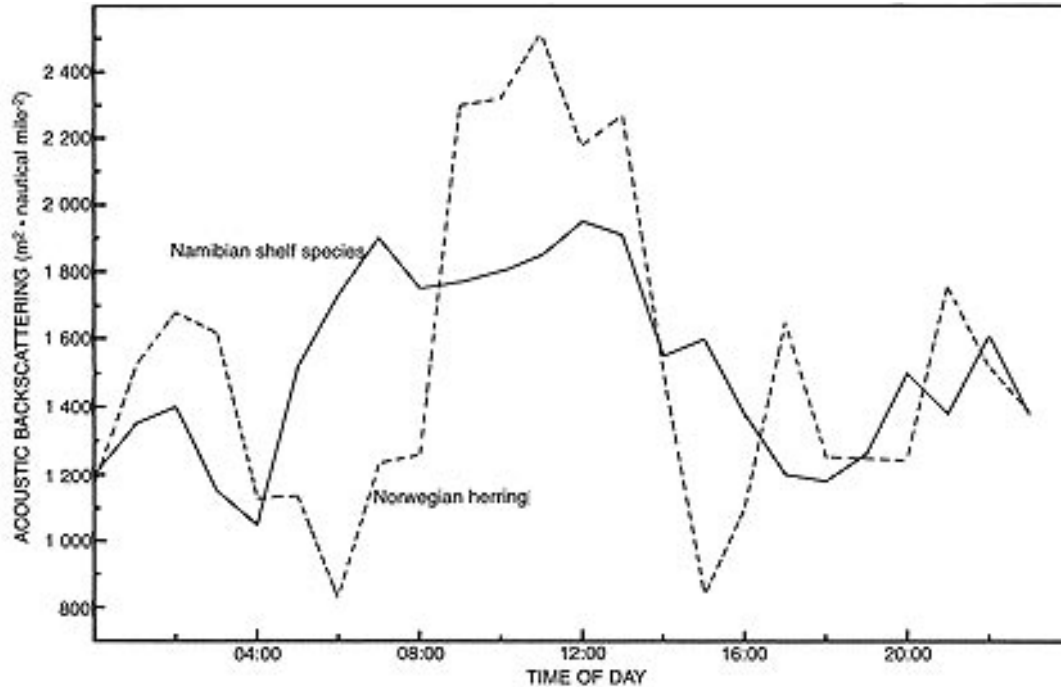


Fig. 4: Mean hourly acoustic backscattering for all species over the Namibian shelf compared with that for Norwegian herring (the herring data after Huse and Korneliussen 1995)

smaller specimens in the second mesopelagic layer, and then progressively larger fish with depth. *M. muelleri* did, however, have mean individual masses which correlated positively with depth, 0.27 g in the top layer, 0.28 g in the second layer, 0.57 g in the third layer and 0.96 g in the fourth mesopelagic layer. *T. angolensis* also had masses correlated positively with depth, but this was not the case with *L. lorigera*.

The hake layer (Fig. 3b) consisted of both species of hake. Acoustic values determined during daylight were adjusted by trawl catch data and acoustic night values because the hake layer was obscured by the other layers during the day. The acoustic observations indicated some ascent from the sea bed at dawn and dusk, and also a pronounced pelagic distribution in the early evening.

Figure 4 shows the mean hourly acoustic backscattering values over the whole water column. It is dominated by mesopelagic fish, euphausiids and squid, and it shows low values at night, very low values in the morning and evening, and very high values during daylight. The other curve on Figure 4 shows the same relationship for six combined abundance estimation

surveys for herring *Clupea harengus* in Norway, shown for comparison. The picture there is the same as in the present study. The major difference probably originates from the fact that the day length is shorter in northern Norway during winter than in Namibia in April.

Trawling

The time of day and the depth of all trawl stations are shown on Figure 5. The pelagic hauls were made partly to elucidate the diurnal variation in vertical hake distribution. Therefore, many pelagic hauls were in the hake zone, as deep as 50 m from the bottom. However, the different mesopelagic layers were sampled to facilitate adequate analysis of the echograms as well as to observe vertical movements of potential hake prey. The haul which caught hake highest up in the water column was carried out at 20:00, and the fishing depth was 265–290 m, i.e. 65–90 m from the bottom. The hake catch in that haul consisted of four *M. paradoxus* (mean mass 0.35 kg). It was the only haul with hake catches shallower in the

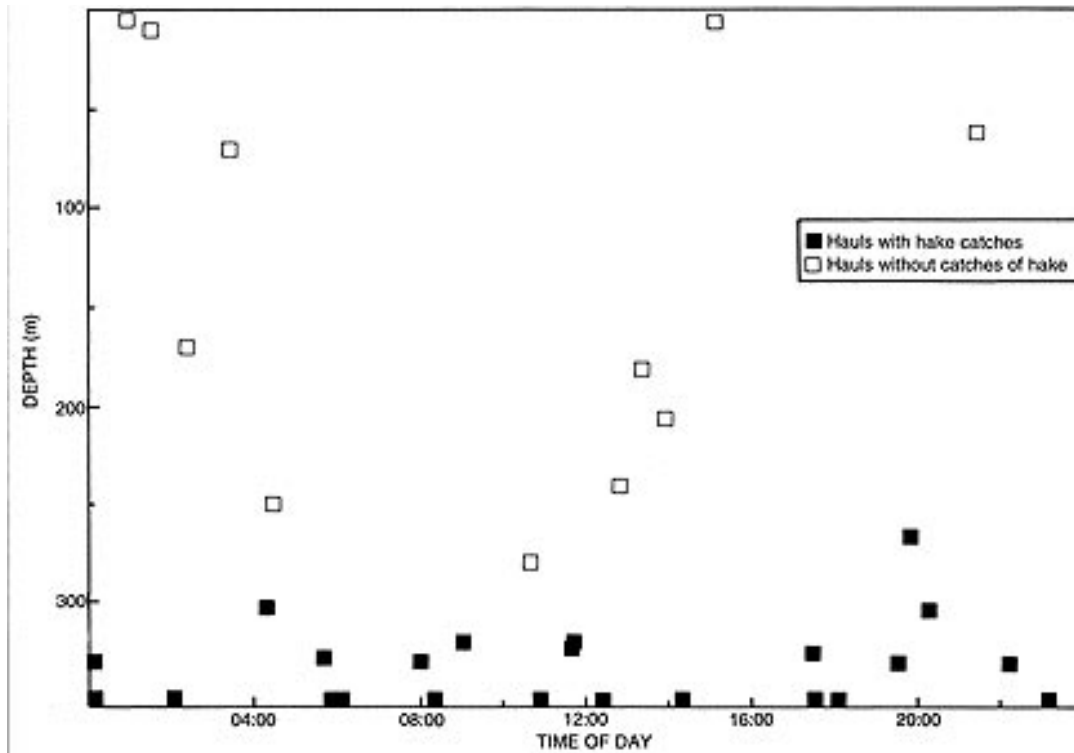


Fig. 5: Time and depth of all trawl hauls during the current survey

water column than 300 m, but deeper than 300 m, both species were found in all hauls.

The mass, number and mean mass of *M. capensis* and *M. paradoxus* in bottom trawl hauls are shown on Figure 6. Total masses of both hake species indicate that catchability was high during the day and lower at night. The total mass of each hake species in the trawls was similar, but there were always more *M. paradoxus* than *M. capensis*, showing that the *M. paradoxus* were generally smaller than *M. capensis*

in the study area. Table I also shows that the cumulative catches by day were significantly higher than catches at night for both species and for *M. capensis* alone. Times of day and night were derived from the light data given later (see Fig. 9); daylight was set to be between 06:00 and 17:00. The number and the mean mass of *M. capensis* and *M. paradoxus* in pelagic hauls are given in Figure 7. Numbers of pelagically caught *M. capensis* were diurnally stable, whereas more *M. paradoxus* were caught in daylight than at

Table I: Day-night variation in bottom trawl catches

Species	Parameter	Day (06:00–17:00)			Night			U-test
		n	Mean	SE of mean	n	Mean	SE of mean	
<i>M. capensis</i>	Total mass (kg)	6	97.2	18.2	6	52.2	5.1	$p = 0.04$
<i>M. paradoxus</i>	Total mass (kg)	6	68.3	16.4	6	40.5	7.4	Not significant
<i>M. capensis</i>	Number	6	46.5	8.9	6	30.8	6.0	Not significant
<i>M. paradoxus</i>	Number	6	133.0	27.6	6	77.7	10.1	Not significant
<i>M. capensis</i>	Mean mass (kg)	6	2.12	0.14	6	1.87	0.19	Not significant
<i>M. paradoxus</i>	Mean mass (kg)	6	0.50	0.03	6	0.52	0.05	Not significant
All hake	Total mass (kg)	6	165.5	21.5	6	92.7	10.1	$p = 0.01$

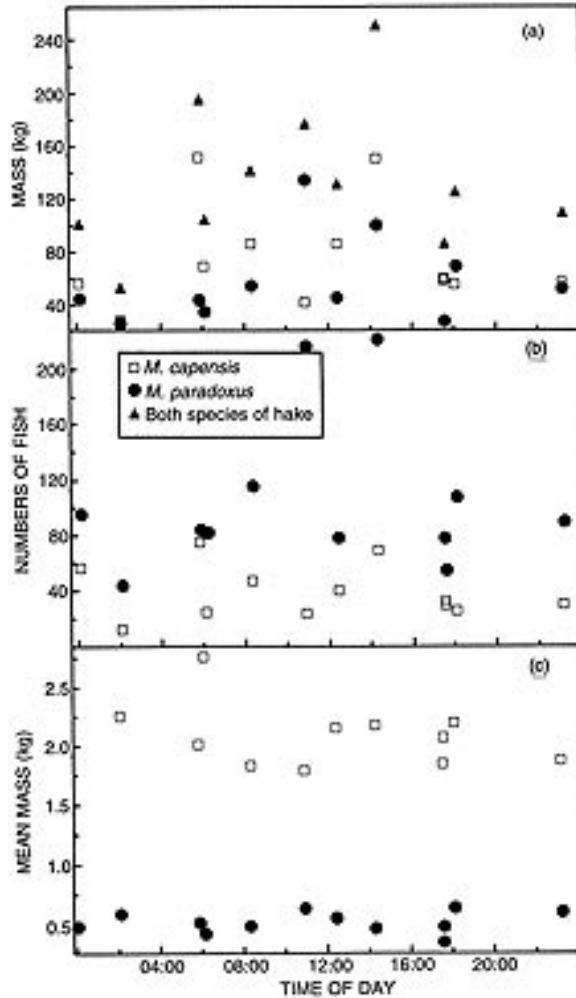


Fig. 6: (a) Mass, (b) numbers and (c) mean mass of both species of hake in bottom trawl hauls

night, as was also the case for the bottom hauls (Fig. 6). Also, as in bottom trawls, the number of *M. paradoxus* caught in pelagic trawls was consistently and substantially higher than that of *M. capensis*. The mean masses of *M. paradoxus* were diurnally stable, whereas the daylight-caught *M. capensis* were significantly smaller than at night.

Hake stomach contents

Figure 8 shows the percentage of hake with stomach

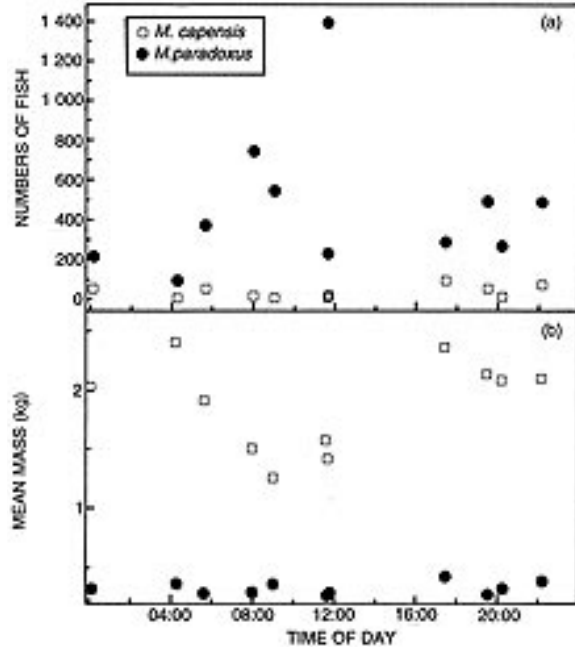


Fig. 7: (a) Numbers and (b) mean mass of both hake species in all pelagic trawl hauls

contents caught in the bottom (Fig. 8a) and pelagic trawls (Fig. 8b) respectively. There was an increase in the percentage of hake with food in their stomachs towards evening. In the bottom hauls, there was little difference in percentages of stomachs with food between species, whereas in the off-bottom hauls *M. paradoxus* had a higher frequency of stomachs with food. Table II shows the species composition of the food concerned.

Nearly all the *M. capensis* were larger than 50 cm, and nearly all the *M. paradoxus* were smaller than 50 cm. Generally, Table II shows that, in this investigation, the *M. capensis* were omnivorous whereas the *M. paradoxus* tended to eat mainly euphausiids. None of the *M. paradoxus* sampled contained horse mackerel *Trachurus* sp., jacobever *Helicolenus dactylopterus* or hake. More of the *M. capensis* caught off the bottom had eaten euphausiids than those caught at the bottom. Compared with the findings of Pillar and Barange (1997), the present data seem to resemble the summer situation identified by those authors, but with an even greater dominance by euphausiids. This finding can, however, be related to the difference in methods applied during analysis, the visual scrutiny of major components employed in the current study cumulatively overestimating such components com-

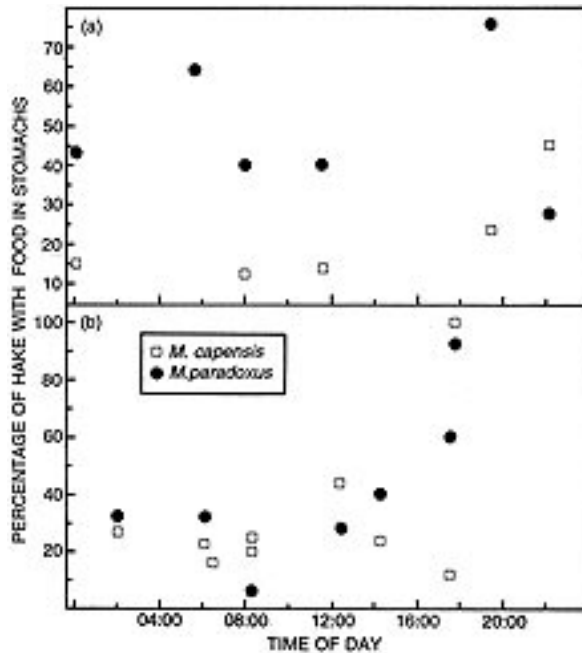


Fig. 8: Percentage of hake with food in their stomachs in (a) pelagic and (b) bottom trawl hauls

pared to components occurring as smaller fractions in the stomachs.

Light and bioluminescence

The surface light measurements for the observation period are given in Figure 9. All days were clear and sunny, with peak readings of 17–1 800 μE , cor-

responding to around 90 000 lux. The underwater readings showed substantial levels of extinction, reducing the daylight illumination level to about 1 lux at 100 m.

The underwater light meter produced sensible readings down to 10^{-6} lux, about 400 m water depth in daylight in the survey area at that time of year. It also picked up significant quantities of bioluminescence, particularly at night, oscillating between 10^{-2} and 10^{-4} lux.

DISCUSSION

Generally, the hake encountered during this investigation did not migrate to upper water masses, but stayed within 60 m of the bottom. This result supports the finding of Pillar and Barange (1993), who stated that hake >20 cm only migrate a few metres off the bottom, whereas younger hake migrate more extensively. The acoustics showed no evidence of a dramatic diurnal migration by hake, but indicated dusk and dawn off-bottom peaks and a low (i.e. close to the bottom) around noon.

Total trawl catches of hake were highest during the day. This is in accordance with previous studies (Botha 1973, Payne 1989, Pillar and Barange 1997), and may be the result of either or both of migration or gear avoidance at night. Daytime caught *M. capensis* off the sea bed were significantly smaller than those caught at night, indicating that larger *M. capensis* stayed on the bottom during the day and rose only at night. Day/night bottom trawl catch ratios were 1.9 and 1.7 respectively for *M. capensis* and *M. paradoxus*. This is in fairly good accord with the results of Gordoa and Macpherson (1991) for the same area, but not with the extensive material collected by Pillar and Barange (1997) off South Africa. Those authors

Table II: Prey selection by each species of hake caught at the bottom and off-bottom

Predator species	Occurrence of prey species (%)									Number of hake with food
	Krill	Krill + myctophids	Myctophids	Hake	Jacopever	Squid	Mixed contents	Horse mackerel	Miscellaneous	
<i>M. capensis</i> , bottom	20.4	2.0		16.3	8.2	6.1	36.7	4.1	6.1	49
<i>M. paradoxus</i> , bottom	74.2	13.6	3.0			1.5	6.1		1.5	66
All hake, bottom	51.3	8.7	1.7	7.0	3.5	3.5	19.1	1.7	3.5	115
<i>M. capensis</i> , pelagic	38.9	5.6	11.1	22.2			11.1	5.6	5.6	18
<i>M. paradoxus</i> , pelagic	73.6	16.7	1.4			1.4	6.9			72
All hake, pelagic	66.7	14.4	3.3	4.4		1.1	7.8	1.1	1.1	90
All <i>M. capensis</i>	25.4	3.0	3.0	17.9	6.0	4.5	29.9	4.5	6.0	67
All <i>M. paradoxus</i>	73.9	15.2	2.2			1.4	6.5		0.7	138
All hake	58.0	11.2	2.4	5.9	2.0	2.4	14.1	1.5	2.4	205

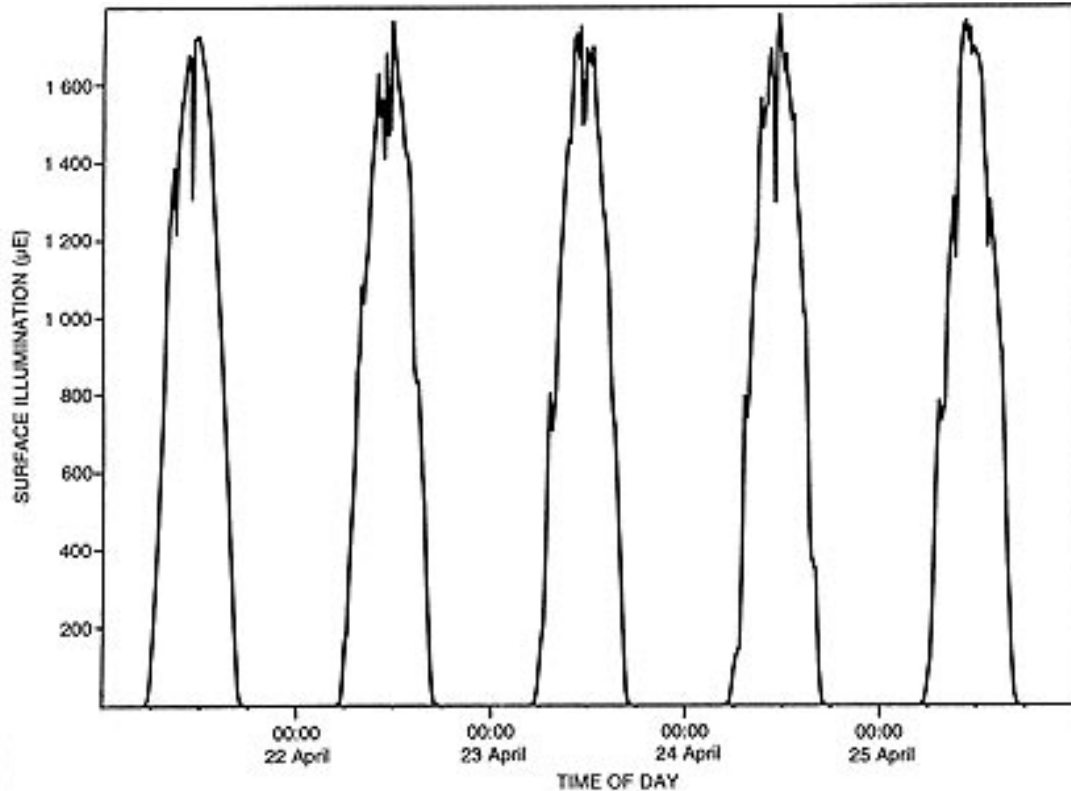


Fig. 9: Surface illumination during the experimental period

found the day/night catch ratio of *M. capensis* to be generally much larger than for *M. paradoxus*. Apart from a geographical difference, the most likely explanation is the 3 m difference in vertical opening between the trawls used. If *M. capensis* rose 2–3 m off the bottom at night they could still be caught by the 5-m opening of the trawl net on the *Dr Fridtjof Nansen*, but they would not be taken by the 2-m opening trawl used by Pillar and Barange (1997). *M. capensis* catches were larger than those of *M. paradoxus* in 10 of 12 hauls. However, there were more *M. paradoxus* than *M. capensis* in all bottom hauls, exemplifying the size difference of the two species in this area, i.e. large (>50 cm) *M. capensis* and smaller (<50 cm) *M. paradoxus*.

In 9 of the 11 pelagic hauls in which hake were caught, the *M. paradoxus* catch was greater than that of *M. capensis*, and there were more *M. paradoxus* than *M. capensis* in all hauls. This may indicate that the smaller *M. paradoxus* have to maintain a pelagic position when larger *M. capensis* occupy the bottom

zone, because smaller hake are an important food source for large *M. capensis* (Payne *et al.* 1987, Roel and Macpherson 1988, Punt *et al.* 1992, Pillar and Barange 1997). It may also relate to the fact that young *M. paradoxus* tend to feed on pelagic prey.

The mesopelagic layers dominated the acoustic backscattering energy in the system, and probably also the biomass. There was no clearcut species separation in the mesopelagic layers, despite the distinct separation of the layering. It is possible that the lack of species separation could at times be attributable to by-catch from other layers than the one sampled, particularly in the deeper hauls, but such an explanation could not hold in all instances. Giske *et al.* (1990) found that different size groups of *Maurollicus muelleri* also form different layers. This they explained as differential risk evaluation in the juvenile and mature part of the population, the juveniles being willing to trade-off the increased risk of predation in the upper water masses with their brighter illumination against the increased potential

reproductive fitness gained through increased feeding and growth. The converse would be true for adults, however, because they would have already invested in maturation and would therefore not be willing to increase the predation risk, and so stayed deeper. Similar trade-off situations related to vertical migration have also been described by, for example, Clark and Levy (1988).

In the current investigation, different size-classes of *M. muelleri* were found in different layers, in much the same way as described by Giske *et al.* (1990). The statement applies to the squid *T. angolensis*, but not to the myctophids *L. hectoris* and *S. boops* or the squid *L. lorigera*. It was notable that the small lanternfish *L. hectoris*, which showed no vertical segregation by size, did not show up in the top layers until midnight, so avoiding the enhanced predation risk related to brighter illumination. The larger lanternfish *S. boops*, however, was earlier at the surface, and the earliest arrivals were large specimens, as were the first arrivals of *L. hectoris*. The observations on the vertical dynamics of the mesopelagic community made during this study pose more questions than they answer, and it would require a substantial research effort to fully elucidate the real situation. Nevertheless, as mesopelagics are the major macrobiological component of the ecosystem off Namibia, such an analysis should be carried out.

The variation in acoustic backscattering with time of day shown both for mesopelagic fish in Namibia and for herring in Norway is an interesting feature. Reynisson *et al.* (1995) showed the same characteristics for the redfish *Sebastes mentella* in the Irminger Sea between Iceland and Greenland, and Fréon *et al.* (1993) showed the same for sardines in the Mediterranean Sea. With so many examples in such varied species and locations, it seems logical to conclude that it is a general mechanism in pelagic fish, probably generated by diurnal variation in behaviour. The curve can be looked on as a representation of the diurnal variation in acoustic target strength of the species involved which, among other parameters, is modulated by the tilt angle of the fish (Nakken and Olsen 1977). The low values at dusk and dawn can therefore be interpreted as an increase in tilt angle related to vertical migration. The generally low values at night for herring are also caused by tilt-angle variations related to an energy-saving behaviour pattern (Huse and Ona 1996). What the cause might be for the low values at night in the present situation is not known, but it may possibly have its source in a more or less continuous vertical movement of fish throughout the night, resulting in an average aspect of less than dorsal reference to the transducer. It is also of note that, in daylight when the backscattering is strongest,

the scattering organisms are at their deepest, and consequently, gas-filled swimbladders will be most compressed, a situation which should rather minimize reflection. This shows the importance of behaviour in general and tilt-angle distribution in particular to acoustic reflection and estimation of abundance.

The present rather simplistic analysis of stomach contents does not show a clear diurnal feeding periodicity, similar to the findings of Payne *et al.* (1987), Roel and Macpherson (1988) and Pillar and Barange (1997). There were, however, indications of high values for both species in the early evening, partly supporting the results of Gordoa and Macpherson (1991) for *M. capensis* in the same area. A more detailed study would be necessary to fully elucidate the feeding strategy of hakes. On the basis of the present data on hake and their environment, it can still be suggested that hake of the sizes investigated here generally seem to wait for prey to pass by. They do, however, undertake vertical migrations, albeit small, at night. Such activity coincides with the rise of the layers of euphausiids and mesopelagic fish. For *M. paradoxus*, the vertical migration may be to retain contact with the euphausiid layer as well as to avoid predation by the larger *M. capensis* near the bottom. The latter would rise only slightly to maintain contact with both the *M. paradoxus* and such demersal prey as jacobever.

The higher frequency of stomachs with food towards evening may indicate a combination of greater prey availability with the daylight compression towards the bottom of all species involved and the associated visual feeding opportunities for hake at greater illumination. A full consequence of this would, however, be a much more pronounced diurnal feeding pattern, with higher daylight values and lower values at night. As it is, the advantage of visual feeding does not seem to be fully exploited by hake. One explanation can be that the limited oxygen availability off Namibia has favoured the development of an evolutionary stable feeding strategy under which prey are primarily procured at very close proximity. This can be in daylight when predators and prey are compressed onto the bottom, or at night when the visual detection range is at its minimum.

The diet of *M. capensis* was varied, but it contained mainly fish. Small hake and jacobever constituted the main prey items, but euphausiids were also found frequently. Quite large horse mackerel were also found, as were both small and large cephalopods. This finding agrees with the more thorough analyses of Pillar and Wilkinson (1995) and Pillar and Barange (1997). *M. paradoxus* seemed to prefer euphausiids, but also consumed myctophids frequently, and also small squid, concomitant with both predator size and

semipelagic distribution. It also coincides with the findings of Pillar and Barange (1993) for *M. capensis* of the same size, perhaps indicating that the ontogenetic stage more than the species is decisive in prey selection. Generally, the results also agree with the summer situation described by Pillar and Barange (1997), given the differences in methodology.

The mesopelagic fish in the system seemed to be underutilized by the predators present, appearing only sparingly in the diets of both hake species considering their large biomass and apparent availability through spatial and temporal overlap. The reason could be that mesopelagic fish, through cohabitation with hake, have adapted predator-avoidance strategies which take advantage of shortcomings in the feeding strategies of hake, e.g. the possible need for a short distance between predator and prey. It could also be related to a confusion effect induced by swarming prey (Milinski 1984), assisted by the emission of intermittent bioluminescence.

Bioluminescence is believed to be used as both antipredator and signalling mechanisms among some mesopelagic fish and invertebrates. The levels of bioluminescence illumination measured here were well above the visual threshold of most fish, and it may be argued that bioluminescence could provide predators with the opportunity to feed by sight. It is, however, uncertain whether such intermittent illumination can be utilized for vision at all. It is also likely that the light-meter vehicle going through the layers of bioluminescent organisms triggered a large part of the measured illumination. However, even moreso it is possible that herding of fish by the trawl gear may occasionally be enhanced by bioluminescence induced by the gear passing through the water. This may explain partly why herding by trawls is often seen to be similar by day and night (Engås and Ona 1991, Huse et al. 1994).

CONCLUSIONS

The vertical dynamics of the different biological components of the ecosystem studied seemed to be quite stable between days and were characterized by segmentation into distinct layers. The mesopelagic component exhibited a diurnal variation in acoustic backscattering properties. Hake generally did not migrate more than 60 m from the bottom. They were masked by mesopelagic fish during the day, but were available for acoustic detection at night when the mesopelagic layers lifted. The availability of hake to the bottom trawl used was higher by day than by night. Alone, bottom or pelagic trawl hauls could not

reflect the species or size composition of hake in the area by night or day.

ACKNOWLEDGEMENTS

The assistance of Messrs F. Dausab, M. Shimanda and Ms S. L. Davis (all of the Ministry of Fisheries and Marine Resources, Namibia) and Messrs I. Svellingen, S. Floen J. Vågenes and J. Tore Øvredal (all of the Institute of Marine Research, Norway) is gratefully acknowledged, as is the patience and skill of the Captain and crew of the R. V. *Dr Fridtjof Nansen*. The Nansen Programme is also thanked for making fish time and equipment available.

LITERATURE CITED

- ANON. 1995 — Studies of survey methodology for hake. Preliminary Report of Cruise No 1/95. NORAD-FAO/ UNDP GLO 82/001: 52 pp. + Annexes.
- BAKUN, A. and R. H. PARRISH 1981 — Environmental inputs to fishery population models for eastern boundary current regions. In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, April/May 1980*. Sharp, G.D. (Conv. Ed.). Paris; Unesco: 67–104 (*I.O.C. Workshop Rep. 28*).
- BOTHA, L. 1973 — Migrations and spawning behaviour of the Cape hakes. *S. Afr. Shipp. News Fishg Ind. Rev.* **28**(4): 62, 63, 65, 67.
- CLARK, C. W. and D. A. LEVY 1988 — Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Naturalist* **131**(2): 271–290.
- ENGÅS, A. and E. ONA 1991 — Day and night fish distribution pattern in the net mouth area of the Norwegian bottom-sampling trawl. *Rapp. P-v. R un. Cons. perm. int. Explor. Mer* **189**: 123–127.
- FR EON, P., SORIA, M., MULLON, C. and F. GERLOTTO 1993 — Diurnal variation in fish density estimate during acoustic surveys in relation to spatial distribution and avoidance reaction. *Aquat. Living Resour.* **6**(3): 221–234.
- GISKE, J., AKSNES, D. L., BALINO, B. M., KAARTVEDT, S., LIE, U., NORDEIDE, J. T., VEA SALVANES, A. G., WAKILI, S. M. and A. AADNESEN 1990 — Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. *Sarsia* **75**(1): 65–81.
- GORDOA, A. and E. MACPHERSON 1991 — Diurnal variation in the feeding activity and catch rate of Cape hake (*Merluccius capensis* and *M. paradoxus*) off Namibia. *Fish. Res.* **12**(4): 299–305.
- GORDOA, A., MACPHERSON, E. and M-P. OLIVAR 1995 — Biology and fisheries of Namibian hakes (*M. paradoxus* and *M. capensis*). In *Hake: Biology, Fisheries and Markets*. Alheit, J. and T. J. Pitcher (Eds). London; Chapman & Hall: 49–88.
- HUSE, I. and R. KORNELIUSSEN 1995 — Diurnal variations in acoustic density measurements of wintering Norwegian spring spawning herring *ICES Doc. C.M. 1995/B:12, Ref. H*: 17 pp. (mimeo).
- HUSE, I. and E. ONA 1996 — Tilt angle distribution and swim-

- ming speed of overwintering Norwegian spring spawning herring. *ICES J. mar. Sci.* **53**(5): 863–873.
- HUSE, I., WEST, C. W., AGLÉN, A., ENGÅS, A. and O. R. GODØ 1994 — Day/night variation in fish directivity in the trawl opening. *ICES Doc. C.M.* **1994/B**:18: 8 pp. (mimeo).
- MILINSKI, M. 1984 — A predator's cost of overcoming the confusion-effect of swarming prey. *Anim. Behav.* **32**: 1157–1162.
- NAKKEN, O. and K. OLSEN 1977 — Target strength measurements of fish. *Rapp. P-v. Réun. Cons. perm. int. Explor. Mer* **170**: 52–69.
- PAYNE, A. I. L. 1989 — Cape hakes. In *Oceans of Life off Southern Africa*. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 136–147.
- PAYNE, A. I. L. and A. E. PUNT 1995 — Biology and fisheries of South African Cape hakes (*M. capensis* and *M. paradoxus*). In *Hake: Biology, Fisheries and Markets*. Alheit, J. and T. J. Pitcher (Eds). London; Chapman & Hall: 15–47.
- PAYNE, A. I. L., ROSE, B. and R. W. LESLIE 1987 — Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 471–501.
- PILLAR, S. C. and M. BARANGE 1993 — Feeding selectivity of juvenile Cape hake *Merluccius capensis* in the southern Benguela. *S. Afr. J. mar. Sci.* **13**: 255–268.
- PILLAR, S. C. and M. BARANGE 1995 — Diel feeding periodicity, daily ration and vertical migration of juvenile Cape hake off the west coast of South Africa. *J. Fish Biol.* **47**(5): 753–768.
- PILLAR, S. C. and M. BARANGE 1997 — Diel variability in bottom trawl catches and feeding activity of the Cape hakes off the west coast of South Africa. *ICES J. mar. Sci.* **54**: 485–499.
- PILLAR, S. C. and I. S. WILKINSON 1995 — The diet of Cape hake *Merluccius capensis* on the south coast of South Africa. *S. Afr. J. mar. Sci.* **15**: 225–239.
- PUNT, A. E., LESLIE, R. W. and S. E. DU PLESSIS 1992 — Estimation of the annual consumption of food by Cape hake *Merluccius capensis* and *M. paradoxus* off the South African west coast. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 611–634.
- REYNISSON, P., SIGURDSSON, T., MAGNÚSSON, J. and J. V. MAGNÚSSON 1995 — Diurnal variations of the echo intensity and some biological observations on redfish in the Irminger Sea (preliminary results). *ICES Doc. C.M.* **1995/G:41**: 12 pp. (mimeo).
- ROE, H. S. J. 1984 — The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 2. Vertical migrations and feeding of mysids and decapod Crustacea. *Prog. Oceanogr.* **13**: 269–318.
- ROE, H. S. J. and J. BADCOCK 1984 — The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 5. Vertical migrations and feeding of fish. *Prog. Oceanogr.* **13**: 389–424.
- ROEL, B. A. and E. MACPHERSON 1988 — Feeding of *Merluccius capensis* and *M. paradoxus* off Namibia. *S. Afr. J. mar. Sci.* **6**: 227–243.
- WALDRON, H. N. and T. A. PROBYN 1992 — Nitrate supply and potential production in the Benguela upwelling system. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 29–39.
- WARE, D. M. 1992 — Production characteristics of upwelling systems and the trophodynamic role of hake. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 501–513.