

## DEPTH-STRATIFIED DENSITY ESTIMATES AND DISTRIBUTION OF THE CAPE HAKE *MERLUCCIIUS CAPENSIS* AND *M. PARADOXUS* OFF NAMIBIA DEDUCED FROM SURVEY DATA, 1990–1999

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In this study demersal survey data for the period 1990–1999 are used to investigate the average distribution of the Cape hake *Merluccius capensis* and *M. paradoxus* off Namibia in terms of density and mean length. Further, biomass estimates are compared on the basis of depth and density stratification. The main distribution of *M. capensis* was north of 27°S and that of *M. paradoxus* south of 24°S. *M. paradoxus* was deeper than *M. capensis*. For both species, average length increased with depth. *M. paradoxus* expanded its range to the north through the 1990s as its population size (off South Africa and Namibia) increased. In Namibian waters, small *M. paradoxus* were found only south of 25°S. Mean length of *M. capensis* increased north of 21°S, largely as a result of decreased numbers of small fish in shallower water. Abundance estimates stratified by depth were no different from those post-stratified on similar densities.

Key words: abundance, Cape hake, density estimates, distribution, *Merluccius*, Namibia

Two hake species, deep-water Cape hake *Merluccius paradoxus* and shallow-water Cape hake *M. capensis*, are found along the Namibian shelf and slope (Inada 1981). Although *M. paradoxus* lives deeper than *M. capensis*, its distribution overlaps at intermediate depths (Botha 1980, Assorov and Berenbeim 1983, Gordoa *et al.* 1995). For both species, small individuals are found shallower than large fish (Van Eck 1969, Botha 1980, Gordoa and Duarte 1991, Huse *et al.* 1998, Burmeister 2000). *M. paradoxus* is found along the entire Namibian slope with a change in distribution at approximately 25°S; north of this latitude it is found only on the lower part of the slope (Macpherson *et al.* 1985, Burmeister 2000). *M. capensis* lives along the entire shelf and upper slope off Namibia (Gordoa *et al.* 1995). In Namibian waters *M. capensis* is more abundant than *M. paradoxus*, but the biomass of the latter has increased since 1990 (Strømme *et al.* 1999).

Norway's R.V. *Dr Fridtjof Nansen* (initially the old ship, but since 1994 the new one) completed 17 surveys of Cape hake off Namibia between 1990 and 1999. The main objectives of these surveys were to map the distribution of the Cape hake and to obtain indices of abundance for the species (Anon. 1990). The abundance estimates were calculated by post-stratification of observed densities (see Strømme *et al.* 1999). As observed densities were used to classify the strata, it was not possible to calculate the variance and *CV* of the abundance estimates (Cochran, 1977).

For the current study, survey abundance estimates

were recalculated on the basis of the depth distribution of the two species. To calculate abundance, 100-m depth strata were used, so permitting calculation of the variance and associated precision of the survey estimates. The survey data were also used to investigate the average patterns of distribution of the two species during the 1990s. This was achieved for both hake species by averaging the distributions calculated during all the surveys.

### MATERIAL AND METHODS

The first Namibian hake survey by a Norwegian ship was conducted from January to March 1990. Subsequently, the surveys were conducted bi-annually in most years between 1990 and 1997, and annually thereafter (Table I). The surveys covered the entire Namibian shelf and slope. Only the R.V. *Dr Fridtjof Nansen* was used for the surveys, until January–February 1999, when Namibia commenced using its own research vessel for the purposes.

#### Survey design

The surveys had a systematic transect design, with a semi-random distribution of stations along each transect. Transects were perpendicular to the coast and about

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Table I: Biomass estimates for Cape hake off Namibia, both depth-stratified and determined by post-stratification (Nansen biomass, after Strømme *et al.* 1999)

Survey	Nansen biomass (tons)		Depth-stratified biomass (tons)	
	<i>M. capensis</i>	<i>M. paradoxus</i>	<i>M. capensis</i>	<i>M. paradoxus</i>
Jan.–Mar. 1990	497 000	25 000	588 466	30 995
Sep.–Oct. 1990	460 000	35 000	776 504	25 589
Jan.–Mar. 1991	470 000	40 000	778 114	32 597
Oct.–Dec. 1991	533 000	100 000	910 215	90 122
Apr.–Jun. 1992	658 000	164 000	1 032 087	184 081
Oct.–Dec. 1992	892 000	150 000	1 187 247	143 898
Jan.–Mar. 1993	654 000	170 000	871 594	220 785
Apr.–May 1993	568 000	140 000	770 112	114 841
Jan.–Feb. 1994	520 000	210 000	632 933	220 507
Apr.–Jun. 1994	530 000	260 000	763 611	237 502
Oct.–Nov. 1994	350 000	145 000	418 472	148 286
Apr.–Jun. 1995	370 000	205 000	492 454	196 487
Jan.–Feb. 1996	446 000	306 000	637 986	265 317
Sep.–Oct. 1996	365 000	256 000	542 968	245 296
Jan.–Feb. 1997	307 000	218 000	458 706	213 478
Jan.–Feb. 1998	1 018 000	278 000	1 436 343	227 883
Jan.–Feb. 1999	686 000	248 000	888 753	204 072

20–25 miles apart (Fig. 1). The transect positions were constant because the first transect of each survey started on the same position throughout the survey period. Subsequently it was assumed that the position of the first transect of the first survey was selected randomly, so ensuring that the random assumption was not violated.

Trawl stations were of 30 minutes successful bottom trawling and were selected in such a manner that each 100-m bottom depth zone had at least one station per transect. In the extreme south where the shelf is wide, stations on the shelf were located at intervals of 10 nautical miles. Catch rate ( $\text{kg h}^{-1}$ ), species and size composition, and acoustic component were recorded for each station and the data captured using the NAN-SIS database (Strømme 1992). Data from all surveys between January 1990 and February 1999 were used in the study.

## Data analysis

### DEPTH STRATIFICATION

The survey area (bottom depth 100–600 m) was subdivided into 100-m depth strata, because both species of Cape hake have a depth-related distribution and stations along each transect have depth structure. Depth is also widely used as the major stratifying variable in demersal surveys elsewhere (Smith and Gavaris 1993). For each stratum, the mean density and variance was calculated for each hake species for each survey. If stations were grouped into strata based

on a factor other than the response variable, e.g. on depth, the variance within each stratum could be calculated (Thompson 1992).

The stratified mean density ( $\bar{y}_{str}$ ) was calculated by where  $L$  is the number of strata,  $A$  the total area, and

$$\bar{y}_{str} = \frac{\sum_{i=1}^L A_i \bar{y}_i}{A},$$

$A_i$  is the area of stratum  $i$ . The stratum mean density ( $\bar{y}_i$ ) was calculated from

$$\bar{y}_i = \frac{\sum_{j=1}^{n_i} y_{ij}}{n_i},$$

where  $y_{ij}$  are the individual densities in stratum  $i$  and  $n_i$  are the number of individual densities in stratum  $i$  (Cochran 1977).

The variance of the stratified mean ( $\text{var}(\bar{y}_{str})$ ) was calculated by

$$\text{var}(\bar{y}_{str}) = \sum \frac{W_i^2 s_i^2}{n_i},$$

with

$$s_i^2 = \frac{\sum_{j=1}^n (y_{i,j} - \bar{y}_i)^2}{n_i - 1},$$

and  $W_i$  as the proportion of the stratum area ( $A_i$ ) to the total area ( $A$ ), i.e. ( $W_i = \frac{A_i}{A}$ ). The standard error ( $SE$ ) of

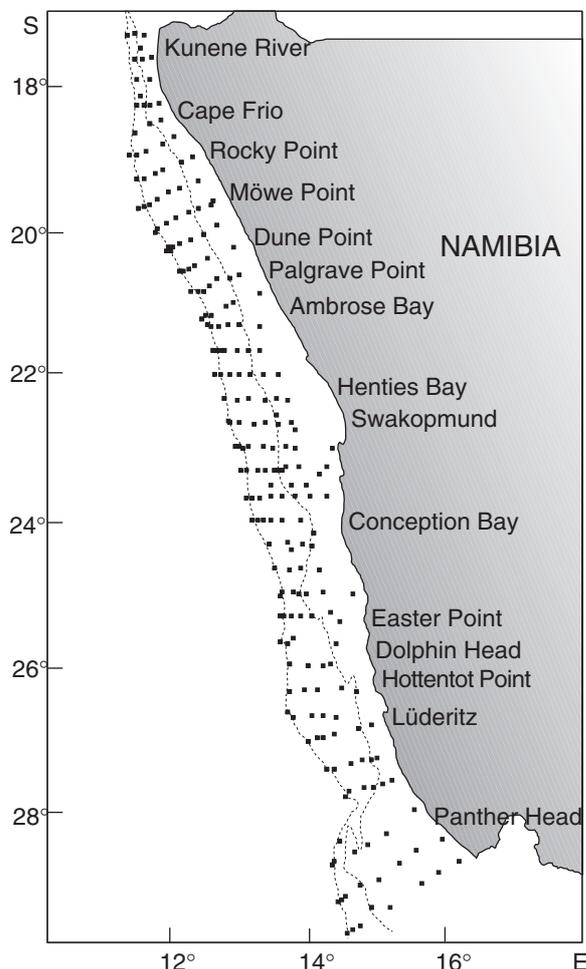


Fig. 1: Stations trawled during the 1999 hake survey off Namibia, with 200- and 500-m depth contours shown

the stratified mean and the 95% confidence intervals were calculated by  $SE = \sqrt{\text{var}(\bar{y}_{str})}$  (Cochran 1977). The precision for the estimates (CV) was calculated from

$$CV = \frac{SE}{\bar{y}_{str}}$$

(Zar 1996). The abundance estimates were calculated from  $B = \bar{y}_{str}A$  and the associated variances from  $\text{var}(B) = \text{var}(\bar{y}_{str})A^2$ .

Sampling proportions ( $P_i$ ), the number of stations in a stratum of given size, were calculated from

$$P_i = \frac{n_i}{A_i} ,$$

where  $n_i$  is the number of stations in stratum of area  $A_i$  (Cochran 1977).

POST-STRATIFICATION

The abundance estimates obtained from the hake surveys were calculated by contouring around similar densities (e.g. Strømme *et al.* 1999). These contoured areas were then classified into density strata and used for the overall abundance estimation. It is, however, not possible to calculate a variance and CV for these abundance estimates, because the stratification was based on the density levels used in the abundance calculations (Thompson 1992).

Analyses of hake distribution

Mean densities by 100-m depth and 1° latitude were calculated for all the surveys pooled. Each survey was given the same weight, so survey densities were not weighted according to biomass. These means were used in the investigation of average distribution, 1990–1999.

Mean lengths were used for length comparisons between the depth and latitude zones. Length frequency distributions could not be compared statistically, e.g. with Kolmogorov-Smirnov tests, because the assumption of random collection was invalid. Samples were collected in clusters (trawl hauls), and similarity within clusters was great – fish of similar size tended to be caught together – violating the assumption that individual samples were independent (Pennington and Vølstad 1994). Gordo and Duarte (1991) also found that, although hake is not a schooling species, hake of similar size tend to be found in aggregations. Furthermore, the effective sample sizes were low and indicate uncertainty around the overall length frequency distribution (Burmeister 2000, Folmer and Pennington 2000, Pennington *et al.* in press).

If the mean lengths of two distributions are different, then it may be assumed that the overall distributions also are different. Conversely, if mean lengths are not different, and no additional information is available, there is no reason to assume that the distributions are different. Mean lengths for different depth zones and latitudes were calculated from

$$\bar{L} = \frac{\sum_{i=1}^n \sum_{L=m}^k L f_{i,L}}{\sum_{i=1}^n \sum_{L=m}^k f_{i,L}} ,$$

where  $\bar{L}$  is the mean length for the particular stratum or area,  $L$  the length,  $m$  and  $k$  the smallest and largest lengths encountered in a particular sample, and  $n$  is

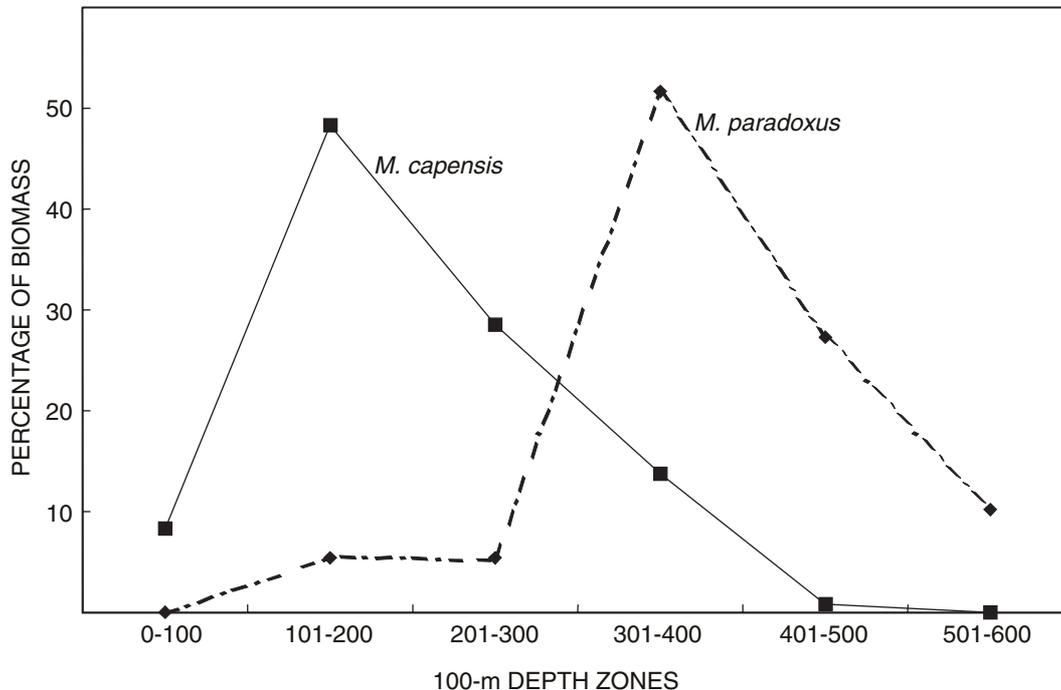


Fig. 2: Relative abundance of Cape hake in different depth zones estimated from survey data, 1990–1999

the number of stations within a stratum. The number of individuals of length class  $L$  caught at the  $i$ th station,  $f_{i,L}$ , was calculated from

$$f_{i,L} = F_{i,L} W_i \quad ,$$

where  $W_i = \frac{W_{i,Total}}{w_i}$ ,  $F_{i,L}$  is the frequency of individuals of length class  $L$  measured at the  $i$ th station,  $W_i$  the weighting factor for the species concerned at the  $i$ th station,  $W_{i,Total}$  the total weight of the species concerned caught at the  $i$ th station and  $w_i$  is the sample weight of the species at station  $i$ . After the raising was done, the length frequencies of the individual stations within a survey could be added to obtain a combined length frequency for the required strata.

## RESULTS AND DISCUSSION

### Distribution

The estimated percentage of the overall abundance (by weight) per depth stratum for each species of hake is

given in Figure 2. More than 75% of the *M. capensis* resource was in water shallower than 300 m and this species did not occur deeper than 500 m. In contrast, more than 75% of the *M. paradoxus* resource was deeper than 300 m.

There was a clear tendency for the mean size of both species to increase with depth (Fig. 3). Further, *M. capensis* was larger than *M. paradoxus* wherever the two species occurred concurrently. An increase in mean length with depth is well documented for the Cape hake off Namibia and South Africa (Botha 1980, Gordoa and Duarte 1991, Payne and Punt 1995) and for other demersal species (Macpherson and Duarte 1991). The finding that *M. capensis* was larger than *M. paradoxus* in the overlap zones was expected, because the former has a more inshore distribution and attains larger size (Inada 1990).

The highest average biomass of *M. capensis* was north of 27°S, biomass being much lower south of this latitude (Fig. 4). Density minima were observed between 19 and 21°S and south of 25°S, coincident with the main upwelling cells off the Namibian coast (Nelson and Hutchings 1983, Anon. 2000), perhaps indicating that *M. capensis* avoids cold, upwelled water. Support for this hypothesis comes from reports that *M. capensis*

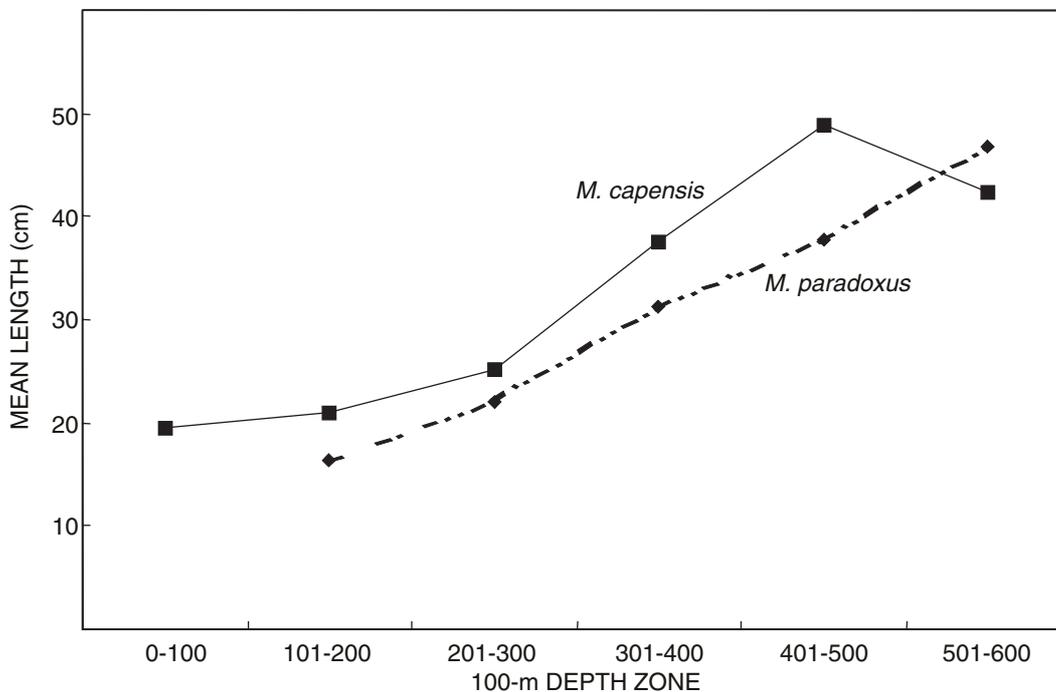


Fig. 3: Mean length of Cape hake per 100-m depth zone off Namibia, 1990–1999

has a lower tolerance for cold water than *M. paradoxus* (Inada 1990). The reason for the observed decrease in mean biomass around 24°S was unclear. North of 18°S the average biomass decreased; the density in this area was high but, because the area represented was small (narrow shelf), the biomass was low.

The mean biomass of *M. paradoxus* was generally low (compared to that of *M. capensis*), the highest values being recorded between 24 and 29°S (Fig. 4). Shannon (1985) proposed that the Lüderitz upwelling cell acts as a barrier separating fish stocks north and south of 27°S. Although this seemed to be the case for *M. capensis*, it did not appear to apply to *M. paradoxus*. The difference in the effect of the environmental barrier on the two species could be explained by their habitats. *M. capensis* is more abundant in shallower, inshore waters (Botha 1980, Assorov and Berenbeim 1983, Gordoa *et al.* 1995), a habitat more influenced by coastal upwelling. In contrast, *M. paradoxus* is more tolerant of cold water (Inada 1990) and lives in deeper water that is likely less influenced by upwelling.

The mean size of *M. capensis* increased northwards from 21°S (Fig. 5). Mean lengths were lower along the central part of the Namibian coast, where most recruit-

ment of young fish takes place (O'Toole 1976, Gordoa *et al.* 1995), and possibly also in the upwelling areas. The mean length of *M. paradoxus* increased from 28°S northwards (Fig. 5), because small fish are more abundant off the south of Namibia, the area where young fish recruit to the Namibian stock (Gordoa *et al.* 1995, Strømme *et al.* 1999, Burmeister 2000). The overall mean lengths of *M. capensis* were smaller than those of *M. paradoxus* (Fig. 5), even though *M. capensis* as a species seemingly attains larger sizes than *M. paradoxus* (Inada 1990). This was merely a consequence of the large number of small *M. capensis* found over the entire Namibian shelf (O'Toole 1976) during the surveys. In contrast, comparatively few young *M. paradoxus* were present off southern Namibia only (Burmeister 2000), so the overall mean length of that species was larger.

The biomass of *M. paradoxus* increased after 1990 (Strømme *et al.* 1999). Coincident with this increase, there has been an expansion northwards and offshore (to greater depth) in the range of this species (Fig. 6). It is believed that this expansion is a result of the increase in abundance of the *M. paradoxus* population as a whole, i.e. South African and Namibian waters (Burmeister 2000).

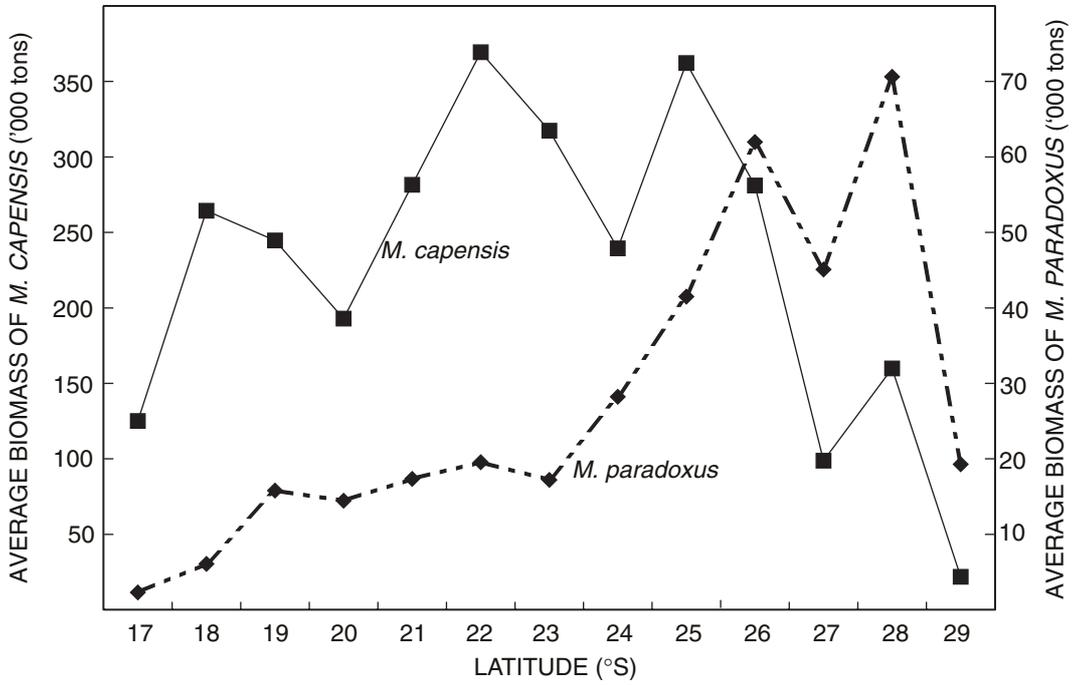


Fig. 4: Average biomass of Cape hake at different latitudes off Namibia

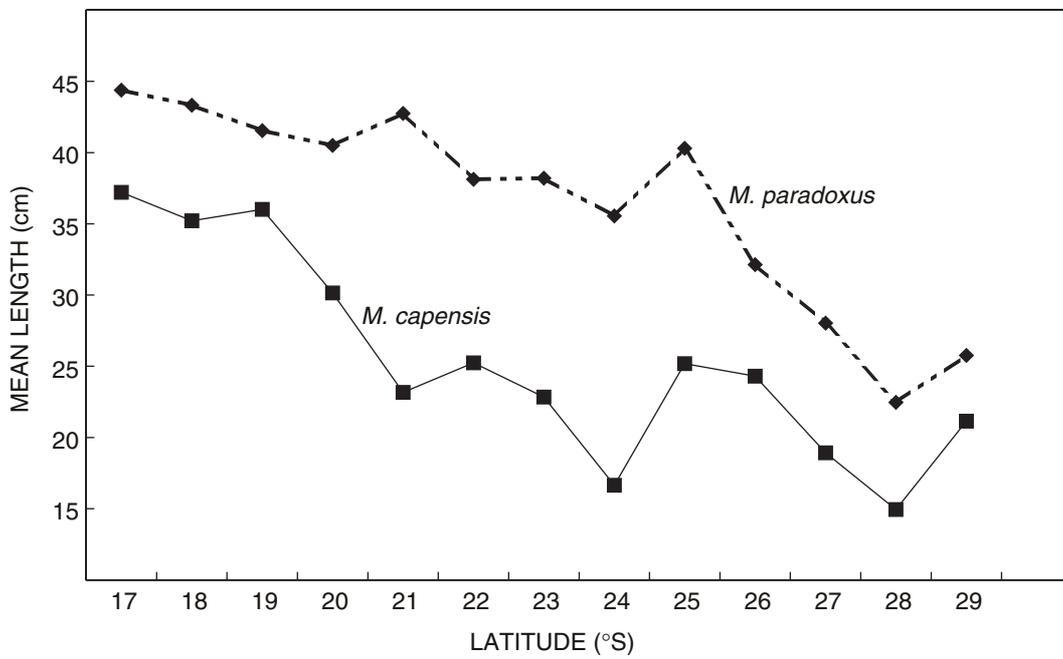


Fig. 5: Mean length of Cape hake by latitude during surveys conducted off Namibia, 1990-1999

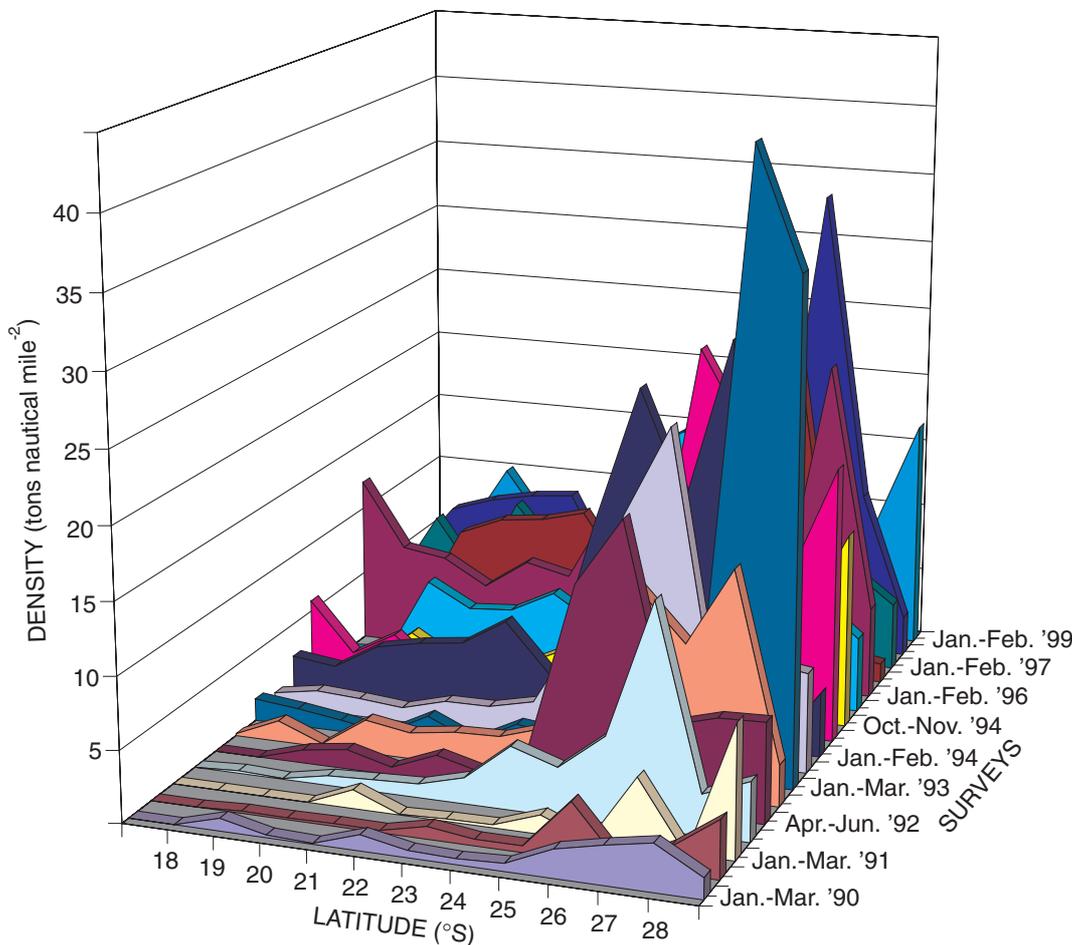


Fig. 6: Density of *Merluccius paradoxus* per degree of latitude obtained during hake surveys off Namibia, 1990–1999

The cannibalistic nature of hake (e.g. Chłapowski 1977, Macpherson 1980, Inada 1981, Payne *et al.* 1987, Roel and Macpherson 1988, Traut 1996) and the differences in fish size in the area of distribution overlap of the two species (Fig. 3) leads to *M. capensis* preying on *M. paradoxus* (Macpherson and Gordo 1994). Feeding studies on the Cape hake off both Namibia (Macpherson 1980, Roel and Macpherson 1988, Traut 1996) and South Africa (Payne *et al.* 1987, Punt *et al.* 1992, Pillar and Wilkinson 1995, Pillar and Barange 1997) clearly show a large proportion of *M. paradoxus* in the diet of *M. capensis*. However, the degree of spatial separation for the two hake species in Namibian waters, suggested by Figures 2 and 4, shows that *M. capensis* tends to be in greatest abundance inshore and north of the main

concentrations of *M. paradoxus*. This could indicate relatively less predation by *M. capensis* on *M. paradoxus* off Namibia than off South Africa, considering

Table II: Average variance, coefficients of variation (CV) and confidence interval (CI) for the depth-stratified abundance estimates of Cape hake off Namibia, 1990–1999

Parameter	Value	
	<i>M. paradoxus</i>	<i>M. capensis</i>
Average variance	0.67	6.23
CI of average variance	1.66	12.91
Average CV (%)	20.71	13.62
CI of average CV (%)	15.06	4.82

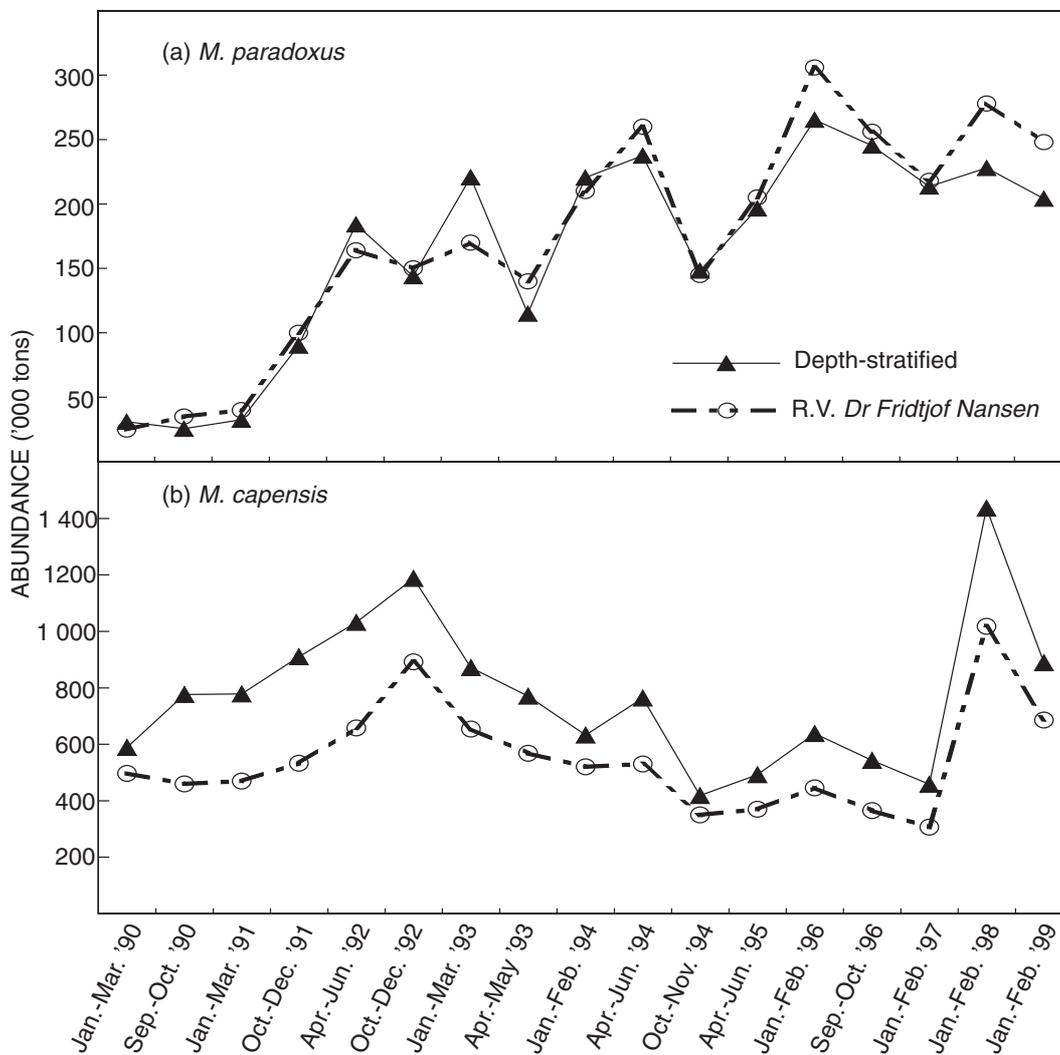


Fig. 7: Estimated abundance of (a) *Merluccius paradoxus* and (b) *M. capensis* during surveys conducted off Namibia, 1990–1999

the opportunistic feeding behaviour of the Cape hake (Payne *et al.* 1987, Punt *et al.* 1992).

#### Density estimates

Abundance of *M. paradoxus* increased throughout the survey period. For *M. capensis*, however, abundance increased up to 1992, decreased until 1997 (Fig. 7), then increased again thereafter until the end of the survey period analysed here.

Depth-stratified abundance estimates of both *M. paradoxus* and *M. capensis* showed the same general trend as the Nansen estimates (Figs 7a, b). The precision of the estimates obtained was relatively high, with mean CVs of 21 and 14% for *M. paradoxus* and *M. capensis* respectively (Table II). However, disproportionate sampling in the shallower depth strata (Table III), the area where *M. capensis* is most abundant (Macpherson *et al.* 1985, Gordoa *et al.* 1995), could have had an influence on the precision of the population estimates of that species.

Table III: Average sampling proportion (number of stations per stratum area, the latter in square nautical miles) of the strata used in the depth-stratification of Cape hake density, 1990–1999

Depth zone (m)	Sampling proportion
101–200	0.0019
201–300	0.0040
301–400	0.0048
401–500	0.0072
501–600	0.0065

The advantage of using depth stratification is that, as a method, it is replicable and transparent. In contrast, post-stratification on densities is subjective and therefore difficult to replicate. Further, sampling precision can be estimated with the depth-stratification method, whereas it is not possible with post-stratification. Clearly, if the method of depth stratification is to be used in future, attention should be given to station allocation within the different depth zones.

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