CHAPTER 1 INTRODUCTION

1.1 General objectives

Following an offer from NORAD extended through FAO and UNDP, an agreement was reached in Windhoek in January 1990 between the UNDP Resident Representative and Namibian authorities for the execution of a programme of surveys of the fish resources of the Namibian shelf with R/V 'Dr. Fridtjof Nansen'.

The main objectives were agreed as follows:

- to describe the distribution, composition and abundance of the most important fish resources. Small pelagic fish, including horse mackerel, pilchard and anchovy would be investigated by the acoustic integration method combined with sampling with mid-water and bottom trawls. A swept area trawl survey programme would be used for demersal stocks. All catches would be sampled by species, weight and numbers, including biological sampling of the commercially important stocks;

- to carry out environmental studies including recording of surface temperature on a continuous basis and hydrographic sampling on a series of fixed profiles.

1.2 Objectives of survey 3/1995

The objectives of this investigation were primarily the following:

- to identify spawning regions for Cape hake off the central Namibian shelf region;

- to measure the spatial distribution of hake eggs and larvae;

- to record hydrological conditions in the area.

This study was planned as a contribution to the understanding of the basic processes of how the planktonic offspring from a fish species in an upwelling ecosystem is retained without being swept off the coast and lost for recruitment.

Emphasis would be placed on measuring vertical distribution, buoyancy and vertical velocity of the eggs in relation to low-oxygen water masses and current pattern within the upwelling region.

1.3 Participation

The scientific staff during the cruise consisted of :

From Namibia:

Chris Bartholomae, Jurgen Laudien, Michael O'Toole and Jeremias Titus.

From Norway:

Svein Floen, Terje Haugland, Ingvald Svellingen and Svein Sundby.

From South Africa:

Alan Kemp and Christian Rohleder.

1.4 Narrative

The investigation started in Walvis Bay on the evening of 27 September 1995. A "density gradient column" from Martin Instrument Company Ltd was installed and tested in the marine biology laboratory onboard the ship. This is a new and more advanced version of the instrument described by Coombs (1981) for high precision measurements of specific gravity (or buoyancy) of fish eggs. The departure from Walvis Bay was postponed to the morning of 28 September 1995, since a southerly gale was blowing and the installation of the delicate instrument needed calm conditions. The first part of the investigation consisted of mapping hydrographic conditions, horizontal egg and larval distribution, and distribution of juvenile and adult hake off the central Namibian coast, between Cape Cross to Hollam's Bird Island. The survey grid consisted of 6 lines of stations spaced every half degree of latitude with the first line commencing at 22° S and the last line at 24°30' S. Each survey line had 5 stations positioned 20 nautical miles apart with the inner most station being 20 nm from the coast. Cruise tracks are shown in Figure 1, bathymetry of the area is shown in Figure 2. The second part of the investigation consisted of a study on the vertical distribution of the hake eggs and larvae at 3 selected stations. The field measurements were terminated on 3 October 1995 (2300 hrs), when the vessel headed for Cape Town. The laboratory experiments on the hake eggs and larvae, data analysis and preparation of the preliminary cruise report continued until arrival in Cape Town.

CHAPTER 2 MATERIAL AND METHODS

2.1 Physical measurements

Hydrographic parameters were recorded with a Seabird CTD with oxygen sensor. The CTD was connected to a rosette sampler. Two water samples were collected at each station to analyse salinity and oxygen for the calibration of conductivity and oxygen sensors. Wind velocity was recorded at hydrographic stations with an Aanderaa weather recording system. Current velocity was recorded with an RD Instrument Acoustic Doppler Current Profiler (ADCP). In this report the data from the ADCP are presented as 15 min. averages in four depth strata (0-50, 50-100, 100-150, and 150-200 m depth) for each hydrographic station.

2.2 Fish plankton sampling

Eggs and larvae were sampled with a paired Bongo net, 57 cms in diameter with mesh sizes of #0.500 and #0.950 mm and a mouth area of 0.25 m^2. The net sampler was equipped with temperature and pressure sensor (U3) which had the capability of monitoring the net down to a depth of 200 m. The volume of water filtered by the net was also measured for each haul and the average flow recorded. At all stations with the exception of 06-01, 06-04, 06-06 and 06-08 (stations 786 - 789), oblique hauls were made in the 0 - 100 m layer. In the case of the latter, the net was fished to a depth of 200 m or to the bottom if shallower. The net was lowered at a rate of 1 m/sec until the required depth was reached and then retrieved at the same rate until it reached the surface. All tows were taken while the vessel maintained a speed of 2 knots. At the last three stations (790 - 792) the Bongo net was towed horisontally at 4 fixed depths, 50 m, 100 m, 150 m and 200 m.

After each haul, the contents of the nets were washed into buckets and the plankton concentrated through a 0.500 mm mesh filter. The live plankton was then transferred to dishes and examined under binocular microscopes. All hake eggs were identified and counted for each haul. Hake larvae were also counted and measured to the nearest millimeter.

The general contents of each plankton haul was noted and the number of jellyfish counted (Annex I A). Ichthyoplankton of other species were examined and identified and in the case of larval fish the numbers caught and size measurements were also taken. After analysis and extraction of live hake eggs for measurement of buoyancy in the density gradient column, the samples were preserved in 5% formalin and stored.

The number of hake eggs and larvae collected at each station was standardised to numbers under 10 m^2 of sea surface.

2.2.1 Identification of hake eggs

Hake eggs collected in the Bongo net hauls were identified according to descriptions given in the literature (Matthews and De Jager, 1951; Porebski, 1976; O'Toole, 1978). Identification was also assisted by the application of the surface adhesion test described by Porebski (1975) in which live hake eggs on exposure to air adhere to the surface of the water. In addition hake eggs were collected from ripe and running females and fertilised on board the vessel and the development followed through to hatching.

The hake egg is spherical, with a smooth chorion, narrow perivitelline space and homogeneous yolk. It has a diameter ranging from 0.82 to 1.08 mm and a single oil globule measuring from 0.15 to 0.26 mm in diameter. Pigmentation in the egg is absent during early embryonic development but melanophores appear later on the oil globule and yolk and along the dorsal surface of the developing larva. Drawings of the hake egg at various stages of development are given in Figures 3 and 4.

2.2.2. Identification of hake larvae

Hake larvae taken in the Bongo net hauls were easily identified by the characteristic shape of the body and pigmentation patterns given in the literature (Porebski, 1976; Olivar and Fortuno, 1991). The main feature is the relative prominence of the head especially during the earlier larval stages and the heavy pigmentation found on the lateral surface of the tail between the anus and the caudal tip. A diagram of a development series of hake larvae is given in Figure 5. Live newly hatched larvae measured between 2.22 to 2.37 mm notochordal length with a large yolk sac and oil globule (0.25-0.26 mm) positioned in the anterio ventral position (Fig. 6). The lengths were somewhat smaller than those measurements given for live newly hatched hake larvae by Porebski, (1976) and Brownell (1979) i.e. 2.5 - 3.2 mm notochord length.

2.3 Sampling of spawning hake and artificial fertilization

Five demersal trawl hauls were made to sample spawning hake and to confirm identification of hake from the acoustic recordings. At one station mature eggs from two females were successfully artificially fertilised with milt from 4 male hakes. The eggs and milt was mixed in two 10 l buckets containing surface water of salinity 35.05 p.s.u. and temperature of 13.5 °C. The fertilised egg

were transferred to clean sea water after about half an hour and allowed to stand for about 3 hours in open air on the trawl deck. The temperature in the buckets increased to about 16 °C during this period.

2.4 Buoyancy measurements of hake eggs and newly hatched larvae

The fertilised eggs were then transferred to the density gradient column system. Three 80 cm high density gradient columns are placed in a plexiglass container filled with fresh water which can be temperature regulated to room temperature. Since we wanted to raise the hake eggs as close as possible to natural temperature conditions, the system was cooled down to sea surface temperature by connecting a cooling shunt in the plexiglass container to the 5 m deep sea water intake of the ship. In this way the temperature within the columns was held between 14.5 and 17 °C. The salinity gradients were calibrated by high precision density floats placed in the columns. The accuracy of the density floats were +/- 0.0002 g/cm3. The salinity in the columns increased from about 32.5- 33.0 p.s.u. at the surface to 35.0 - 35.5 p.s.u at the bottom of the columns. The levels of neutral buoyancy of the eggs were measured to the nearest mm by a digital cathetometer, and the visual observation of the eggs were made easier by a backlight of the system. In the parts of the column where individual measurements of the eggs were difficult because of high concentrations, the number of eggs was counted within 10 mm high intervals. The salinity gradient in the columns varied from 0.002 - 0.006 p.s.u./mm. The gradients were weaker at the bottom of the column due to technical problems when the gradients were filled under conditions when the ship was rolling. The density distribution of the artificially fertilised eggs was measured 5 times during the development, the first time 23 hrs after fertilisation and the last time 61.5 hrs after fertilisation which was 1.5 hrs before the first larvae started hatching. The velocities of the ascending newly hatched larvae and the descending velocities of the empty chorions were measured in order to calculate the densities (neutral buoyancy) of the hatched larvae and the mass of the chorion. Swimming behaviour of the larvae was observed. "Wild" hake eggs, sampled by the Bongo net at 150 m and 200 m depth during the second part of the survey, were placed in a separate density gradient column and the neutral buoyancy distribution was measured at a time after the eggs had reached their salinity levels of neutral buoyancy. These eggs consisted of a mixture of all stages and some of the eggs started hatching about 2 hrs after they were inserted to the column.

CHAPTER 3 RESULTS

3.1 Physical conditions

The cruise was conducted late in the spring upwelling season during a time when peak hake spawning usually occurs (Assorov and Berenbeim, 1983; Olivar et al, 1981). However, in the weeks preceding the survey, upwelling was particularly intense off the coast of Namibia and temperatures were lower than normal for this time of the year. During the survey, the wind was persistently blowing from the south varying in speed between 5 and 18 m/s (Figure 7). The wind was strongest during the first two days of the cruise and it resulted in a typical upwelling situation in the research area. According to the hydrographic pattern the current is assumed to have a generally northerly direction in the surface layers although the currents from the ADCP data for 0-50 m depth (Figure 8) shows a quite complex structure of current pattern. Technical problems with the ADCP are most probably the reason for the rather complex and confusing current pattern displayed in Figures 8-11. However, the temperature and salinity distributions (Figures 12-29) display clear and typical upwelling features with the 13 °C isotherm rising from about 150 m depth above the shelf break to the surface about 40 n.m. closer inshore. This indicates a northeastward, offshore, transport of the upper water masses and an onshore transport of the water masses below 100 m depth. The upwelling was at its strongest stage the day after the maximum wind speed. During the last days of the survey, when wind was decreasing, the upwelling water masses retreated rapid to greater depths. The oxygen minimum above the bottom close to the coast was less extended than in the two previous years, only reaching values below 1 ml/l along the southernmost section (Fig. 17).

3.2 Distribution and abundance of hake eggs and larvae

Oblique Bongo net tows were taken from the surface to a depth of 100 m at 25 stations over the central Namibian shelf region between Cape Cross and Hollam's Bird Island. A further 3 stations were sampled in the southern part of the region from the surface down to a depth of 200 m. Station data for the Bongo net hauls area given in Table 1.

The number of hake eggs and larvae collected during the survey was relatively small, but the eggs were widely distributed over the research area. A total of 11 stations or 21.4 % of the hauls contained eggs and larvae and were mostly located in the region where the bottom depth ranged from 100 to 300 m.

Eggs were most abundant at stations west of Hollam's Bird Island where densities of 0.10 per 10 square meters of sea surface were recorded. These eggs were at various stages of development from the blastocap phase to near hatching indicating recent spawning. Newly spawned hake eggs were also found at stations between 100 and 300 m isobath west of Cape Cross.

Hake larvae ranged in size from recently hatched yolk sac stage (3.5 mm notochord length) to the post-larval phase at 15.0 mm total length. The greatest numbers of larvae were newly hatched and were found at the inshore station off Hollam's Bird Island at concentrations of 0.28 per 10 m^2 of sea surface. Larger larvae occurred predominantly in the northern area between Swakopmund and Cape Cross at densities of between 0.01 and 0.02 per 10 m^2 of sea surface.

The distribution and densities of the eggs and larvae over the research area are shown in Figure 30a and b.

Table 1. Station data for Bongo net hauls taken during survey of the central Namibian shelf region, September 29th to October 2nd 1995 (R.V. Dr Fridtjof Nansen).

Date	Station	Grid	Sounding (m)	Depth of Tow (m)	Time	Volume Filtered m^3
2.10.95	C785	06-10	1753	101	06h48	110.7
2.10.95	C786	06-08	1017	200	09h11	245.6
2.10.95	C787	06-06	317	202	11h36	165.8
2.10.95	C788	06-04	295	201	13h57	169.2
2.10.95	C789	06-01	123	122	17h02	146.3
2.10.95	C784	05-10	1984	101	02h55	71.4
2.10.95	C783	05-08	1013	101	00h32	133.4
1.10.95	C782	05-06	310	102	22h18	179.9
1.10.95	C781	05-04	245	102	18h37	72.8
1.10.95	C780	05-01	165	103	16h22	107.2
1.10.95	C779	04-01	142	101	12h42	178.3
1.10.95	C778	04-04	177	102	10h01	163.0
1.10.95	C777	04-06	294	101	06h22	98.4
1.10.95	C776	04-08	645	102	01h26	130.3
1.10.95	C775	04-10	1427	102	22h53	130.0
30.9.95	C774	03-10	1223	102	10h20	141.5
30.9.95	C773	03-08	480	101	07h49	141.7
30.9.95	C772	03-06	342	100	05h25	213.3
30.9.95	C771	03-04	146	101	01h04	163.3
29.9.95	C770	03-01	123	99	22h28	184.4
29.9.95	C769	02-01	91	85	18h37	109.9
29.9.95	C768	02-04	120	102	16h10	126.0
29.9.95	C767	02-06	230	101	13h29	129.5
29.9.95	C766	02-08	289	100	09h47	319.7
29.9.95	C763	01-08	381	101	16h43	182.5
28.9.95	C762	01-06	230	101	13h44	265.3
28.9.95	C761	01-04	145	101	11h09	251.3
28.9.95	C760	01-01	96	92	08h10	271.0

3.3 Vertical distribution and abundance of hake eggs and larvae

Stratified Bongo net tows at depths of 50 m, 100 m, 150 m and 200 m were taken at 3 of the stations in the southern part of the survey area. These areas were chosen because hake eggs were obtained in tows taken at these positions earlier. The locations were station 04-06 (line 4), station 05-04 (line 5) and station 06-01 (line 6) (stations 790 - 792 in Figure 1). At each position, the net was lowered to each of the required depth stratum and towed for 10 minutes before retrieval.

Hake eggs were found at only two of these stations, station 04-06 (790) and station 05-04 (791) and occurred at depth layers of 150 m and 200 m (Table 2).

Over 99% of all eggs collected during these stratified tows were taken at station 05-04 (791) with 75% occurring at the 150 m depth layer. The remaining 25% of eggs were found at the deeper 200 m layer. Only a few hake eggs were taken in tows from station 04-06 (790) and these again occurred in the 200 m depth zone. Examination under the microscope showed that recent spawning had taken place as all development stages from the blastocap phase to near hatching were present in the samples.

Table 2. Numbers of hake eggs and larvae collected during oblique Bongo tows taken at stratified depth layers at 3 stations along the central Namibian shelf, 2nd-3rd October 1995.

STATION GRID	DEPTH m	Nos. Eggs	Nos. Eggs/10 m^2 sea surface	Nos. Larvae	Nos. Larvae/10m^2 sea surface
04-06(a)	50	0	0	0	0
04-06(b)	100	0	0	1	0.01
04-06(c)	150	0	0	0	0
04-06(d)	200	2	0.10	0	0
05-04(a)	50	0	0	0	0
05-04(b)	100	0	0	0	0
05-04(c)	150	720	4.45	0	0
05-04(d)	200	95	1.00	1	0.01
06-04(a)	50	0	0	0	0
06-04(b)	100	0	0	0	0
06-04(c)	150	0	0	0	0
06-04(d)	200	0	0	0	0

Only two hake larvae were found in the stratified tows and these occurred at station 04-06 (790) and 05-04 (791) at depths of 100 and 200 m respectively. Both larvae were newly hatched,

measuring 2.7 mm and 4.5 mm with the larger specimen having a light green gut, indicating recent feeding on phytoplankton.

Hake eggs or newly hatched larvae were not found above the 100 m layer at any stations.

It was interesting to note that hake eggs or larvae were not collected in any of the samples taken at station 06-01 (792). Instead, medusae (both red and mags) were relatively abundant throughout the water column at this station. In contrast, plankton tows made a day earlier at approximately the same location yielded several eggs and newly hatched larvae with little jellyfish taken in the hauls.

3.4 Occurrence of other zooplankton organisms

The dominant zooplankton organisms taken in plankton samples were copepods and euphausiids which comprised the bulk of the biomass. Other components of the plankton were made up of decapod larvae, amphipod cumaceans, polychaetes, salps and fish eggs and larvae (Annex I A and Annex I B). Large red medusae (*Chrysosara* spp) and smaller transparent magnifying medusae (*Aequorea* sp) were frequently abundant in hauls especially at stations closer to the coast.

The larvae of the lanternfish, *Lampanyctodes hectoris* and *Diaphus* spp together with those of the lightfish, *Maurolicus muelleri* were the most abundant of the ichthyoplanktonic organisms and occurred predominantly at stations located between the 300 m and 1000 m isobath. The adults of both of these fish species make up an important component of the diet of the hake stocks inhabiting the central Namibian shelf.

Larvae of the pelagic goby, *Sufflogobius bibarbatus* were also relatively common in hauls taken at shallower coastal stations.

Fish eggs were also common in some samples, the most common being those of the lightfish. Others could not be identified.

3.5 Distribution of spawning hake

Five demersal trawl stations were taken during the cruise (Fig. 1). The main portion of the catch at all stations consisted largely of 3 species: hake, horse mackerel and large red jelly fish (Annex II). Hake was the most common fish species in all hauls. The westernmost trawl haul was dominated by large hake, while the smaller ones were most abundant at the inshore stations. The near bottom oxygen values close to the coast were relatively high (1.0 - 2.0 ml/l) in contrast to

findings during hake biomass surveys off central Namibia in 1993 and 1994 when deoxygenated water of between 0.25 and 0.5 ml/l was widespread over the shelf. The highest abundance of hake was found in the southern part of the survey area (Fig. 31). This coincided largely with the distribution of the hake egg (Fig. 30a).

3.6 Artificial fertilisation of hake eggs

The hake from the trawl catches were staged with respect to maturity, and those having mature eggs were tried fertilised artificially by stripping running males. However, none of the females had visibly running mature eggs. Therefore, the gonads had to be opened and those eggs which seemed to be mature were gently washed out in a bucket filled with surface sea water and mixed with milt. This procedure gave successful fertilisation from the first trawl haul (30 September 1995, 15h30), where eggs from two females were fertilised with eggs from 4 male hake. After about half an hour eggs were floating on the surface of the bucket due to the strong surface tension between the sea water and the egg. This phenomenon was described by Porebski (1975) as an indication of live eggs. Artificial fertilisation of hake eggs from the subsequent 4 trawl catches was not successful even though a female from one of these catches had a large number of apparently mature eggs. Only a very small portion (approximately 1 %) of the mature female hakes taken in the catch were in a condition where clear ovulated eggs were present in the gonad, and as mentioned above, only eggs from two of the females in this small portion were successfully fertilised.

3.7 Buoyancy of hake eggs and larvae

Three hours after fertilisation some of the live hake eggs were gently skimmed off the surface water in the two buckets with a teaspoon and transferred to the density gradient column with 3 calibration floats. In the column, the eggs initially floated on the surface, and had to be dipped or mixed under the surface before they started sinking down through the density gradient column to their levels of neutral buoyancy. In all, about 300-350 eggs were transferred to the column. After about an hour all eggs which had been successfully mixed had reached the equilibrium level. Still more of the eggs floating on the surface of the column were mixed down over subsequent hours. The first measurement of the buoyancy distribution was made on the next day 23 hrs after fertilisation (Fig. 32a). Then the neutral buoyancy distribution of the eggs was measured 41, 46.5, 52.25, and 61.5 hrs after fertilisation (Figs. 32b-e). The eggs were distributed over a very narrow salinity range during the first 23 hrs (Fig. 32a). Then after about 26 hrs the eggs quite suddenly became heavier over a period of 2-3 hours. They also became more widely distributed. This coincided with the stage of development when the embryo first appeared in the egg, i.e. between stage 11 and 12 in Figure 4. After 41 hrs the eggs were significantly heavier (Fig. 32b and Fig.

33c), and they had reached stage 13 in Figure 4, which was according the developmental time (42 hrs) given by Matthews and de Jager (1951). After this stage the average density of the eggs became slightly lower again (Fig.33c), but they continued to spread out over a wider density range (Figs 32 c,d). The last measurement of neutral buoyancy distribution was made 61.5 hrs after fertilisation (Fig. 32e), 2.5 hrs before the first larva hatched. Four hours later, 68 hrs after fertilisation, about 30 larvae were hatched. After 74 hrs most of the larvae were hatched; 15 live eggs were still unhatched in the column. After 80 hrs only 9 eggs were left in the column. The hatching time was therefore somewhat longer than the hatching time of 58 hrs. given by Matthews and de Jager (1951). Newly hatched larvae were relatively underdeveloped in comparison to those of some of the pelagic fish species and had no functional mouth or eyes. Bailey (1982) reported a similar condition for the Pacific hake larvae and found that development had to proceed for a further few days before the mouth and eyes were fully formed and first feeding took place.

At hatching the larvae started ascending through the column due to loss of the chorion which is the heavy part of the egg (Kjesbu et al. 1992). The ascending speed varied between 0.23 and 0.4 mm/s but was fairly constant at 0.3 mm/s when they past through salinity of about 33.4 p.s.u. They always ascended with head up, probably because of the low density of the oil globule in the yolk sac. Some strikes of the tail occurred without influencing the upward speed during ascent. After a couple of hours at the surface the larvae increased their activity and started to swim down through the column. The empty chorions descended with quite constant speed of 0.5 mm/s.

Figure 33a shows the temperature in the density gradient column. Because of the upwelling, it varied slightly between 17 and 14.5 °C as the ship cruised in and out of the cooler inshore surface water. The mortality of the eggs through development was nearly linear (Fig. 33b).

Figure 32f shows the neutral buoyancy distribution of "wild" hake eggs sampled by the Bongo net towed at 150-200 m depth. There was a mixture of all stages of eggs and the first larvae started to hatch about 2-3 hours after transfer to the column. The neutral buoyancy distribution of these eggs was spread over a wider range of salinity than the artificially fertilised eggs, but the average neutral buoyancy was only slightly different.

CHAPTER 4. DISCUSSION AND CONCLUSION

The standard depths for the Bongo net samples during the cruise was 0-100 m. Very few hake eggs were caught at these depths as it appears from Figure 30a. However, the last Bongo net samples were taken from 0 to 200 m depth. Here, substantially larger numbers of hake egg were found. Subsequent stations on horizontal Bongo net samples at 50, 100, 150 and 200 m depth (Table 2) confirmed that the eggs were found below 100 m depth. Measurements of neutral buoyancy of these eggs showed average values of 34.2 p.s.u. This corresponds remarkably well with independent measurements of neutral buoyancy of the artificially fertilized hake eggs. This is a rather low positive buoyancy (Sundby 1991). Calculations of ascending velocities of the eggs based on these measurements show that the eggs will rise on the average less than 60 m between spawning and hatching. The acoustic measurements showed that hake was generally vertically distributed within 20 m above the bottom. The main distribution of the hake was found at the shelf with bottom depths between 200 and 300 m. This implies that hake eggs should rarely be found above 150 m depth. Again, these independent considerations correspond well with the Bongo measurements.

As can be seen from the hydrographic sections (Figs. 12 -17) the depth layers, where the hake eggs are abundant, will be subjected to a strong onshore transport and subsequently be brought up to the surface in the near-shore regions. Hence, the larvae should be found inshore at the first-feeding stage. The field measurements by the Bongo net stations also confirm that first-feeding larvae are found inshore (Fig. 30b). Consequently, the spawning depth of the adult hake and the buoyancy of the hake eggs seems to be an ecological adaptation to retain the eggs and early larvae within the productive near shore upwelling area. First feeding hake larvae have large mouths which enable them to feed on a wide size range of planktonic animals

Although the hake eggs only have a small positive buoyancy, also the heavy fraction of the eggs seems to have a slight positive buoyancy. Compared to pelagic eggs like Arcto-Norwegian cod, North Sea mackerel and plaice eggs (Sundby 1983) the Namibian Cape hake eggs show a very narrow buoyancy distribution. Therefore, the hake eggs will largely be prevented from sinking and being exposed to low-oxygen or anoxic water as may occur frequently in this region. The very narrow buoyancy distribution might therefore also be an ecological adaptation to reduce killing by anoxic water.