A Decade of Namibian Fisheries Science
Payne, A. I. L., Pillar, S. C. and R. J. M. Crawford (Eds). *S. Afr. J. mar. Sci. 23: 317–336*
2001

INTERACTION BETWEEN CAPE HAKE SPAWNING AND THE CIRCULATION IN THE NORTHERN BENGUELA UPWELLING ECOSYSTEM

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Cape hake in Namibian waters are demersal and mesopelagic spawners, spawning peaking offshore between 100 and 400 m deep, depending on local environmental conditions. The cross-shelf circulation, low-oxygen layers and mesoscale gyres are three important environmental factors influencing hake spawning behaviour and subsequent transport of the spawning products. Normally, hake spawn offshore near the bottom at depths of 150–400 m. However, during one cruise, spawning was concentrated below several subsurface mesoscale gyres, resulting in reduced dispersion of the eggs and larvae. When the low-oxygen layer above the bottom is pronounced, hake spawning has been observed close to the top of the layer at oxygen concentrations as low as 0.2–0.3 mℓ ℓ^{-1}. The relatively small size of the eggs and their high specific gravity make them ascend quite slowly from the spawning depths, 10–40 m per day. Consequently, hake eggs spawned deeper than 200 m hatch before they reach the upper mixed layer. The newly hatched larvae are relatively undeveloped, without functional eyes or mouth, and display little swimming activity during their first hours, but laboratory observations have revealed subsequent periods of downward swimming activity. Based on current field observations, on buoyancy measurements of eggs and larvae and on observed larval behaviour, it is concluded that hake eggs and larvae are transported onshore by features of the upwelling subsurface circulation that compensate for offshore movement of surface water. This may be the basic mechanism concentrating early juvenile hake nearshore. Spawning activity near the low-oxygen layer might be a behavioural adaptation to minimize egg predation, because few other species are expected to survive such low concentrations of oxygen.

Key words: buoyancy, eggs, larvae, recruitment processes, retention, vertical distribution

The spawning products of fish living in upwelling ecosystems have the potential to be lost offshore by Ekman transport. For upwelling ecosystems where offshore transport is particularly strong, Parrish *et al*. (1981) suggested that recruitment variability, particularly pelagic fish recruitment, may be more related to variability in the rate of loss of larvae offshore than to variability in food availability. However, several mechanisms to counteract offshore larval loss have been advanced, e.g. concentration of the larvae by eddy formation, frontal convergence, deep-water spawning and vertical migration of larvae. Bakun and Parrish (1990) stressed the importance of conducting proper process-orientated field studies in order to understand the recruitment dynamics in upwelling regions.

Here, the results of three process-orientated experimental field studies on shallow-water Cape hake *Merluccius capensis* in the northern Benguela upwelling ecosystem are presented. The aim of the study was to demonstrate how the spawning behaviour of hake and the physical properties of their eggs and larvae combine to counteract offshore larval loss, and that these same properties contribute to concentrating the spawning products inshore in the upwelling system.

Hake *Merluccius* spp. are typical components of the fish assemblage in upwelling ecosystems (Alheit and Pitcher 1995). Of the three hake species in the northern Benguela, the shallow-water Cape hake has the broadest distribution, covering the entire Namibian coast from nearshore out to some 400–500 m (Gordoa *et al*. 1995). The deep-water Cape hake *M. paradoxus* is distributed mainly outside the 400 m isobath, except off southern Namibia where it is also found shallower, especially south of Lüderitz, where its distribution extends into waters only 100 m deep (Gordoa *et al.* 1995, Hamukuaya 1999). The Angolan hake *Merluccius polli* is only found north of 20°S. The present study focuses on the drift and dispersion of eggs and larvae of Namibian *M. capensis*. To date, it has not proved possible to distinguish *M. capensis* from *M. paradoxus* at the egg stage. However, the

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Manuscript received November 2000; accepted August 2001

Table I: Overview of the hake recruitment cruises conducted on the R.V. *Dr Fridtjof Nansen*

Cruise number	1	2	3
Dates	27 Sep. 1995–07 Oct. 1995	12 Oct. 1997–18 Oct. 1997	25 Sep. 1998–05 Oct. 1998
Area	Central Namibia	Southern/central Namibia	Central/northern Namibia
Geographical area covered	24°30´–22°00´S	26°30´– 22°30´S	24°30´– 17°50´S
Number of CTD stations	33	42	52
Current mapping	0	ADCP	ADCP
Plankton gear	Bongo net	Hydrobios Multinet	Hydrobios Multinet
Mesh size (μ)	500 and 950	405	405
Number of plankton stations	31	40	42
Number of bottom trawl stations	5	12	17
Number of midwater trawl stations	0	2	3

complete lack of mature *M. paradoxus* in trawl catches made near where the newly spawned hake eggs used in this study were found, along with the presence of mature *M. capensis* in the same trawl catches, lends confidence to the assumption that all eggs used in this study originated from the latter species.

Based on maturation studies from trawl catches (Assorov and Berenbeim 1983), Namibian *M. capensis* spawn from late winter (September) to autumn (March), with peak spawning between October and December. Botha (1986) documented a similar spawning period for South African west coast hake, but also a secondary peak in February/March. Time-series of an extensive South African ichthyoplankton survey programme between 1972 and 1974 (O'Toole 1978, 1999) confirmed this pattern of spawning for Namibian *M. capensis*, but the secondary peak in February/March was very weak. The spring peak of spawning dominated: 92% of hake larvae were caught in the period October–December (O'Toole 1976). Olivar *et al.* (1988) recorded practically no hake spawning off Namibia during autumn (March/April) during their surveys in 1981.

Spawning locations for Namibian *M. capensis* have been reported along most of the coast from about 27 to 18°S (Olivar and Shelton 1993), apparently separate from the spawning areas of the same species in South African waters. O'Toole (1978) showed that the major spawning sites are localized off central Namibia, between 25°S (Hollams Bird Island) and 20°S (Palgrave Point), with greatest larval abundance between Cape Cross and Spencer Bay. Trawl surveys indicate a similar location of peak spawning (Assorov and Berenbeim 1983). This pattern of spawning was also found during Spanish ichthyoplankton surveys between 1979 and 1981, but with the most intense spawning region displaced slightly farther north, between Walvis Bay and Palgrave Point (Olivar *et al*. 1988). Sedletskaya (1988) found spawning hake at depths of 125–380 m and stated that spawning was most intense at depths of 150–250 m. Botha (1973) reported hake as spawning in midwater, i.e. above the seabed. O'Toole (1978) caught >95% of his hake larvae in a band from 10 to 100 km offshore, although the precise location of highest concentrations varied between surveys. Olivar *et al*. (1988) found that peak concentrations of larvae were closer inshore than peak concentrations of eggs and that larvae >8 mm long were only at stations closest inshore, clearly suggesting onshore movement in the first month of life. They also found the youngest (yolk sac) larvae farther north than older ones. The nursery areas for young hake are generally nearer shore. Chłapowski and Krzeptowski (1980) found 1-year-old hake concentrated mainly inshore of the 200 m isobath.

The vertical distributions of hake eggs and larvae in the northern Benguela were paid little attention until Sundby and O'Toole (1995), in a process-orientated pilot study on hake recruitment mechanisms, measured the buoyancy of both eggs and larvae. They made use of artificially fertilized eggs from mature fish taken in bottom trawls.

MATERIAL AND METHODS

The process studies on Namibian *M. capensis* were conducted during three cruises of the R.V. *Dr Fridtjof Nansen* (Table I). Data on hake egg buoyancy, from artificially fertilized eggs and wild-caught eggs, were collected during all three cruises. The spatial distribution of the eggs presented in this paper is limited to Survey 3, because it was the most comprehensive with respect to spatial extent and detailed mapping.

During the pilot cruise in 1995, the central Namibian coast was covered from Hollams Bird Island to Cape Cross (Sundby and O'Toole 1995). On most plankton stations the vertical resolution was limited to oblique Bongo hauls in the two depth intervals 0–100 and 0–200 m. However, at three of the stations, more precise

vertical distribution was determined by towing the Bongo net horizontally at four fixed depths, 50, 100, 150 and 200 m. The Bongo net was equipped with a closing mechanism. The second cruise, in 1997, covered the southern and central Namibian coast from Lüderitz to Walvis Bay. A Hydrobios Multinet plankton sampler with five nets was used. Oblique hauls were made between the surface and a maximum depth of 600 m, with the water column divided into five equal depth intervals. The third cruise was conducted in 1998 (Sundby *et al.* 1998). On that cruise, oblique hauls were made from the bottom to the surface in fixed 50-m depth intervals, except for the deepest haul, which was taken from the bottom to the nearest 50 m depth interval (e.g. 0–50, 50–100, 100–150, 150–200 m, 200 m – bottom). During 1998, the central and northern Namibian coast was covered from Hollams Bird Island to the mouth of the Kunene River. Otherwise, plankton sampling with the Multinet was carried out similarly to that on the 1997 cruise. All eggs and larvae were identified, staged and measured onboard the vessel using 10–50× magnification. Staging of hake eggs was according to the description of Matthews and de Jager (1951), who divided them into 15 stages. However, for the purposes of this paper, it was considered sufficient to group them into three Stages, as follows:

Stages used in the current paper	Stages of Matthews and de Jager (1951)	Age (h) of the stages at 12°C
I	1–11	0–37
II	12–14	37–73
III	15	73–98

Wind velocity was measured continuously with an Aanderaa ship weather station while the ship was underway between hydrographic stations. Temperature, salinity and oxygen were measured with a Seabird 911 CTD. Acoustic Doppler Current Profiler (ADCP) data were recorded during the second and third cruises, specifically to study the cross-shelf circulation in relation to the transport and dispersal of hake eggs and larvae. The instrument used was a 150 kHz "Broadband" ADCP, manufactured by RD Instruments. Data were recorded both underway (at <8 knots) and while stationary. Most data were earth-referenced through bottom-tracking, not GPS. Errors are estimated as between 5 and 10 cm s^{-1}. Further details of the processing of the ADCP data are found in Sundby *et al.* (1998).

Artificially fertilized hake eggs were obtained from mature male and female hake taken in bottom trawls. Fertilization was carried out partly by stripping running males and females. A general problem, however, was that very few females with running gonads were caught (an observation also made by Botha 1973). Hence, an alternative strategy was to section the gonad and to squeeze out fully hydrated, free-running eggs that were sometimes found in the centre of the gonad. These eggs were mixed with milt from mature males. The eggs were stored in plastic jars filled with water taken from the sea surface (temperature ~12 –15°C) for several hours until successfully fertilized live eggs floated on the surface film of the seawater. This peculiar hydrophobic property of the eggs is characteristic for hake and a good indication of the viability of the eggs (Porębski 1975).

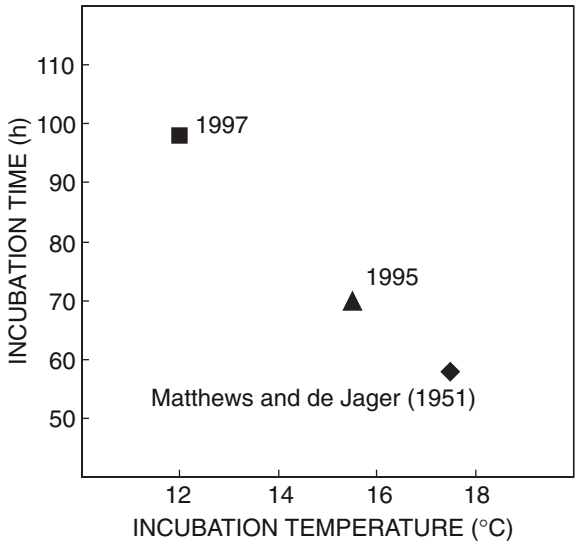

Fig. 1: Observed incubation time of Cape hake *Merluccius capensis* eggs as a function of temperature, based on experiments on board the R.V. *Dr Fridtjof Nansen* in 1995 and 1997 and by Matthews and de Jager (1951)

During all three cruises, a seawater density-gradient three-column system (see Coombs [1981] for its principle description) manufactured by Martin Instruments Co Ltd was used aboard ship to measure the specific gravity of the eggs. During the pilot cruise, the density-gradient column system was cooled by ambient seawater from 3 m depth. Consequently, the temperature varied between 14.4 and 16.7°C, depending upon the distance offshore of the ship at the time. During the other two cruises, the system was temperature-controlled by means of a cooling unit. During the

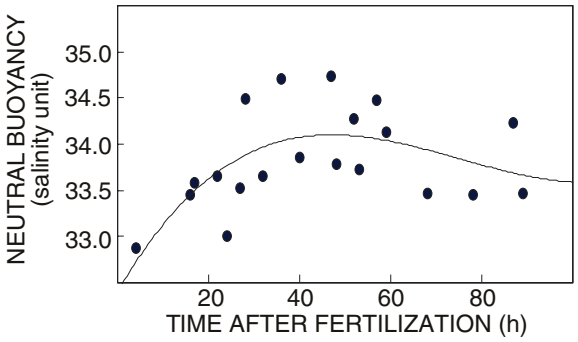

Fig. 2: Development of neutral buoyancy of Cape hake *Merluccius capensis* eggs from fertilization to just prior to hatching. Incubation time is normalized to 12°C

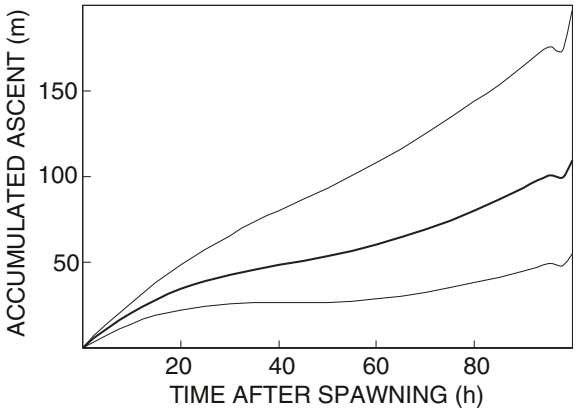

Fig. 3: Modelled accumulated ascent of Cape hake *Merluccius capensis* eggs in Namibian waters from spawning to hatching (including the hatching process). The thick line represents eggs with mean specific gravity and mean egg diameter, the thin lower line, eggs with maximum specific gravity and minimum egg diameter, and the thin upper line, eggs with minimum specific gravity and maximum egg diameter

1997 cruise the temperature was kept within the range 11.8–12.1°C. During the 1998 cruise the temperature was kept constant at 11.0°C. The salinity gradients within the columns were calibrated with glass floats, and the accuracy in the density of these floats was ±0.0002 g cm^{-3}.

Eggs used for buoyancy measurements were both wild-caught and artificially fertilized. The latter were normally inserted into the density-gradient columns 4–24 h after fertilization when those eggs seen to be successfully fertilized and alive had risen to the surface of the incubation jars. Specific gravity of the eggs in the density-gradient columns was measured about four times per day until hatching. The buoyancy of newly hatched larvae was also measured during their first hours after hatching, because the mobility of hake larvae is very limited then. However, after about half a day, the increasing activity of the larvae precluded reliable measurement of the level of neutral buoyancy.

Based on the buoyancy measurements of the eggs and on the egg diameter, the ascending velocities, w, of the hake eggs were calculated according to the equations of Sundby (1983). This means that the Stokes equation

$$w = 1/18\ g\ d^2\ \Delta\rho\ \nu^{-1}$$

was used when the Reynolds number $Re = wd/\nu$ was <0.5, and the modified equation,

$$w = 19\ (d - 0.4D)\ \Delta\rho^{2/3}\ \nu^{-1/3}$$

was used when the Reynolds number was >0.5. The gravity acceleration is here expressed as g, d is the egg diameter, $\Delta\rho$ the difference in specific gravity between the surrounding seawater and the egg, ν the molecular viscosity and D is a diameter that is the uppermost limit of size to which the Stokes equation applies.

RESULTS

Egg buoyancy and stage development

The results of the experiments on artificially fertilized hake eggs from the three cruises were combined to generate a description of the hatching times of the eggs and on the changes of specific gravity through development. Hatching of a specific batch of eggs normally took place over a period of 6–10 h even though they were incubated at equal temperature. In 1995, when the average incubation temperature was 15.5°C, most eggs hatched 68–74 h after fertilization. The latest-hatching eggs emerged 80 h after fertilization, but on average the incubation time was about 70 h. During the 1997 cruise the average incubation temperature was 12.0°C, and most eggs hatched some 95–100 h after fertilization. Matthews and de Jager (1951) reported an incubation time of 58 h but did not give the incubation temperature. Calibration experiments during the 1997 cruise indicate that the experiments of Matthews and de Jager were conducted at 17–18°C. Figure 1 shows incubation time as a function of temperature, based on the experiments of

Matthews and de Jager (1951) and the current ones for 1995 and 1997. During the 1998 cruise, when the temperature was kept at 11.0°C, experiments had to be terminated 21 h after fertilization because the cruise ended. It was therefore not possible to estimate the incubation time at 11.0°C.

The calculated regression equation for incubation time, T, as a function of temperature, t, is

$$T\,(\mathrm{h}) = 362.6 - 106.5\ \ell\mathrm{n}\ t\,(^{\circ}\mathrm{C}) \quad .$$

Figure 2 shows the neutral buoyancy of hake eggs taken from all experiments as a function of time after fertilization. The times are normalized to development at 12.0°C (based on the temperature relationship in Fig. 1), because this is the most representative ambient temperature for hake eggs in Namibian waters. At that temperature, eggs hatch on average 98 h after fertilization, similar to the results for Pacific hake *M. productus* (Zweifel and Lasker 1976), but shorter than those for European hake *M. merluccius*, which at 12.0°C hatch after 127 h (Coombs and Mitchell 1982). At fertilization the neutral buoyancy of *M. capensis* eggs is at a salinity of ~32.5. The specific gravity of the eggs then increases and peaks 40–50 h after fertilization. This corresponds to Developmental Stage 11 (the "embryonic shield") of Matthews and de Jager (1951) and is just prior to the stage when the embryo can be seen clearly. The heaviest eggs then have neutral buoyancy near that of ambient seawater, 34.9–35.0, which means that the buoyancy force exerted on the eggs is near zero, giving them very little hydraulic lift in the water column. From 50 h post-fertilization until the time of hatching, the specific gravity decreases slightly, giving the eggs more lift again.

During all experiments, the specific gravity of hake eggs increased substantially a few hours prior to hatching. The eggs then became heavier than ambient seawater, corresponding to a neutral buoyancy expressed in salinity of >36. The cause of this change is unclear, but it is obviously connected to the hatching process. As hatching is terminated, the larva rids itself of the chorion, the heavy fraction of the egg, and it becomes substantially lighter. Neutral buoyancy of the larvae was measured during the first hours after hatching when they were relatively passive. On average, the neutral buoyancy expressed in salinity was 31.1, based on the egg batch, which had a neutral buoyancy of 33.45 before hatching. Independent calculations of a larval neutral buoyancy can be made from data collected during the 1995 cruise. The average excess specific gravity attibutable to the chorion mass was calculated as 0.00122 g cm^{-3} by measuring the sinking speed of the empty eggshells after hatching in the density-gradient columns. Subtracting this mass from the egg would give the larvae a neutral buoyancy expressed in salinity of 31.9.

Simulated ascent rate of eggs

Based on the shipboard experimental measurements of hake eggs and larvae and on hydrographic measurements in the field, simulations of the ascent rate of eggs and larvae in the field can be made. In a population of fish eggs, many combinations of egg size and buoyancy normally exist (Solemdal and Sundby 1981), although small eggs tend to be heavier (Kjesbu *et al.* 1992). Figure 3 shows the modelled ascent rates of hake eggs off Namibia from the spawning depth to the time just after hatching. The thick line represents the ascent of the eggs with mean neutral buoyancy and mean egg diameter. The upper line shows the fastest possible ascent of an egg, represented by an egg with the lightest fraction and the biggest size (1.08 mm according to Olivar and Fortuño 1991). The lower line describes the slowest possible ascent of an egg, represented by a combination of the heaviest fraction and the smallest size (0.82 mm according to Olivar and Fortuño 1991). The small dip in the ascent by the end of the egg stage shows how ascent is influenced by an increase in specific gravity during the hatching process. However, owing to the shortness of the time that eggs are in this situation (about 2 h, as described above), it hardly influences the vertical distribution.

At hatching, the simulation shows that an average egg would have ascended about 100 m. The lightest and biggest eggs, however, would have ascended about 175 m above the spawning depth. The heaviest, smallest eggs would have ascended only 50 m at hatching. For the heaviest eggs the accumulated rise from about 20 to 60 h after spawning is very small, because of their high specific gravity (near that of ambient water masses) in this period. The simulation shows that eggs would reach the surface layer before hatching only if the spawning depth was shallower than 175 m. However, the spawning depth needs to be shallower than 120 m if a major fraction of the eggs were to reach the surface layer. The abrupt rise after hatching shows the effect of the larvae losing their heavy chorion. However, the simulation after this stage cannot be continued because quantitative data on swimming behaviour of the larvae are unavailable at present. Observations of the early larval stages in the density-gradient columns, however, do show that, after hatching, the larvae swim downwards for several seconds between passive intervals each of about 1–2 minutes, when they ascend passively. In this way, larvae may be able to maintain their vertical position or even descend.

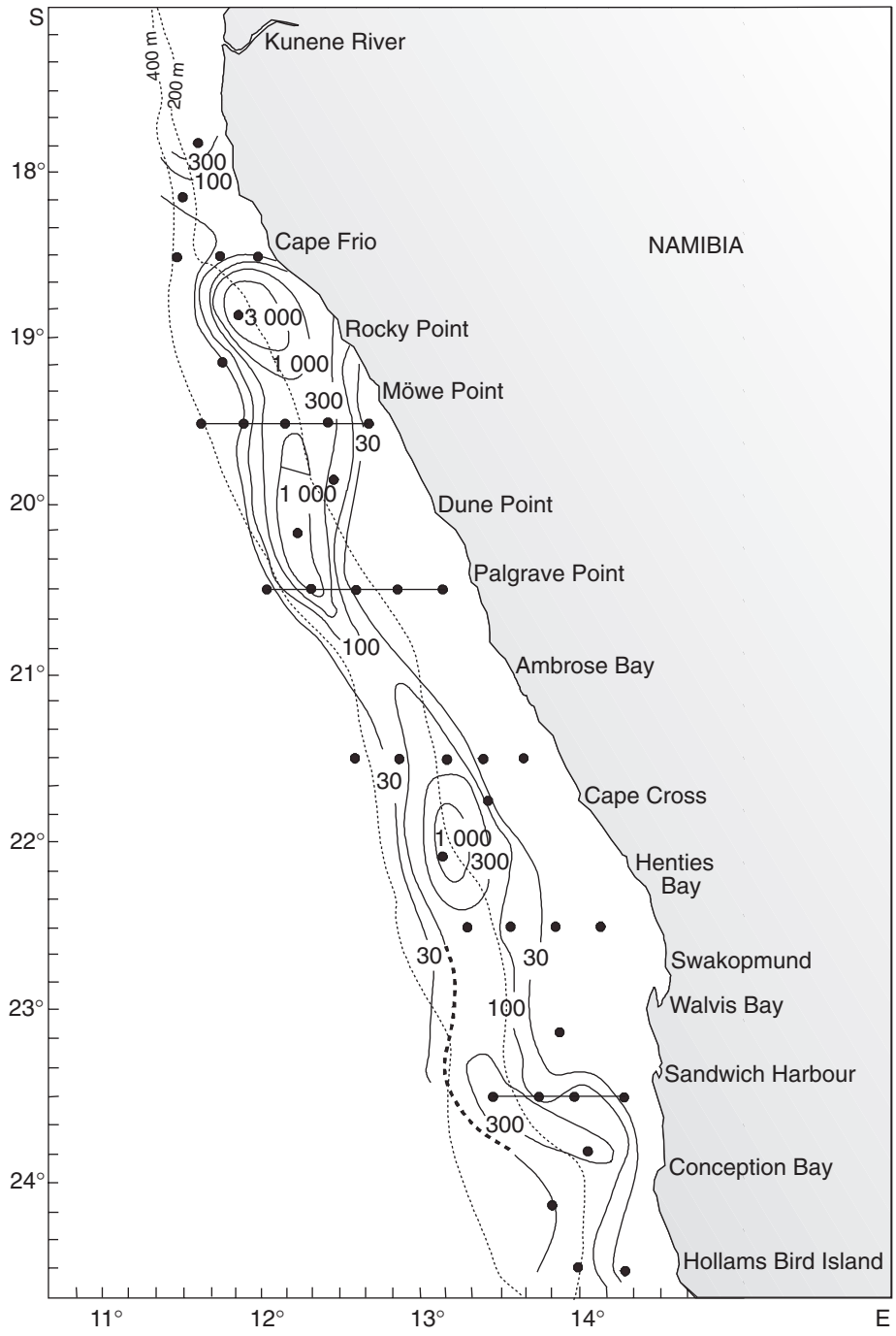

Fig. 4: Distribution of all stages of hake *Merluccius* spp. eggs (number per 10 m^2) during Cruise 3 (September/October 1998). The three lines indicate the vertical sections off Sandwich Harbour (Fig. 9), Palgrave Point (Fig. 10) and Möwe Point (Fig. 11)

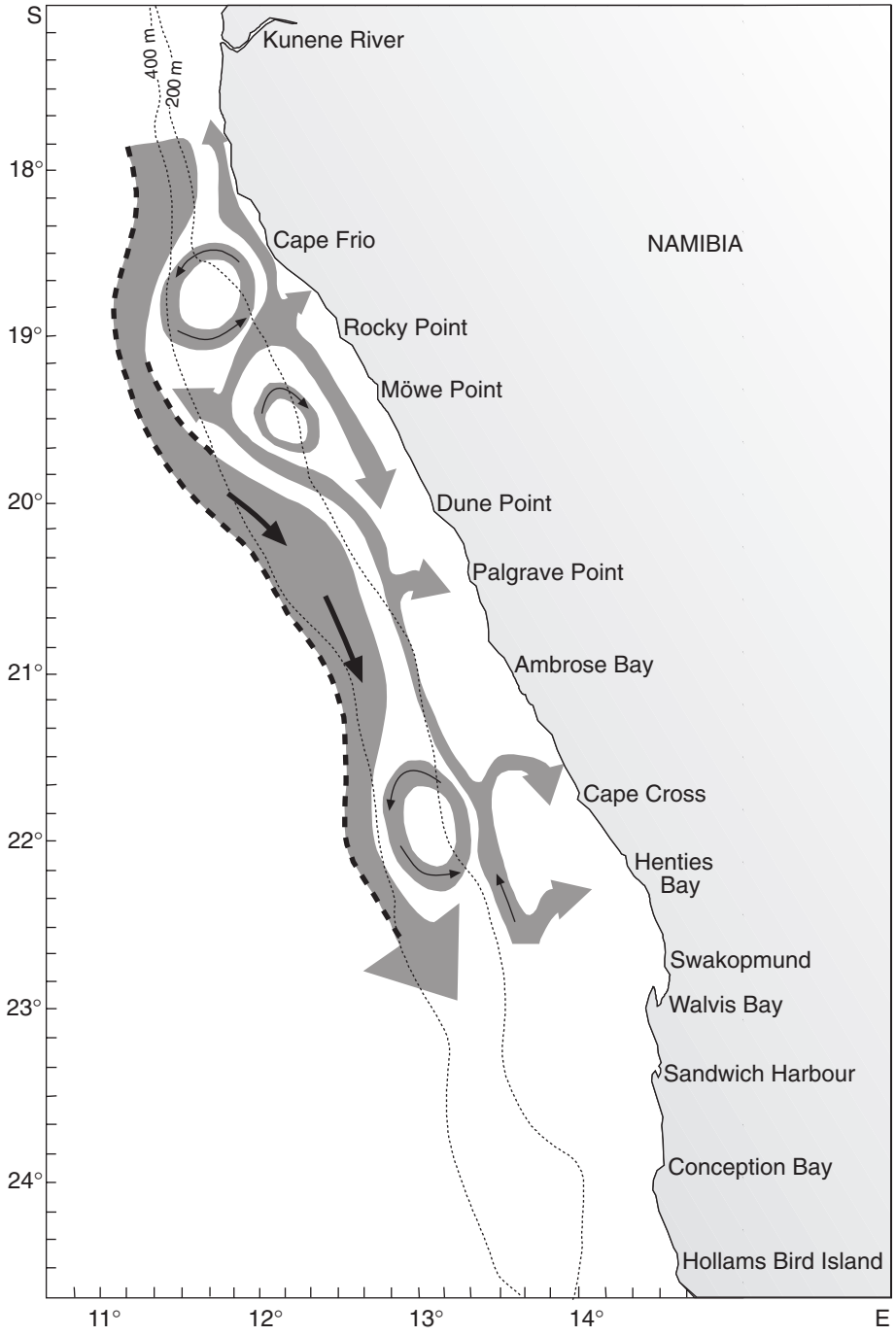

Fig. 5: Subsurface circulation (35–50 m deep) mapped by hydrography and ADCP during Cruise 3 (September/October 1998; after Sundby *et al.* 1998)

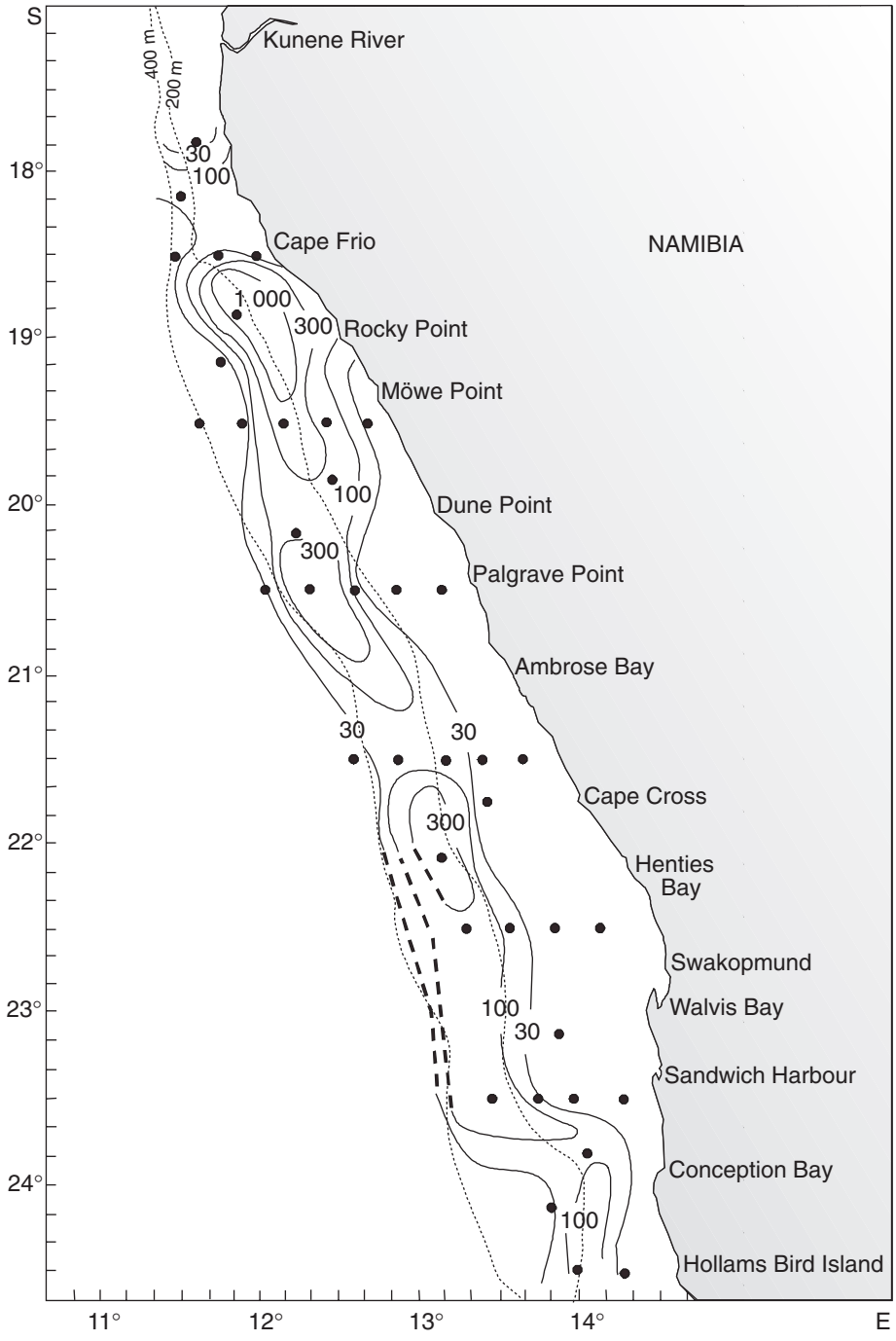

Fig. 6: Distribution of Stage I hake *Merluccius* spp. eggs (number per 10 m^2) during September/October 1998 (Stage I = Stages 1–11 of Matthews and de Jager 1951)

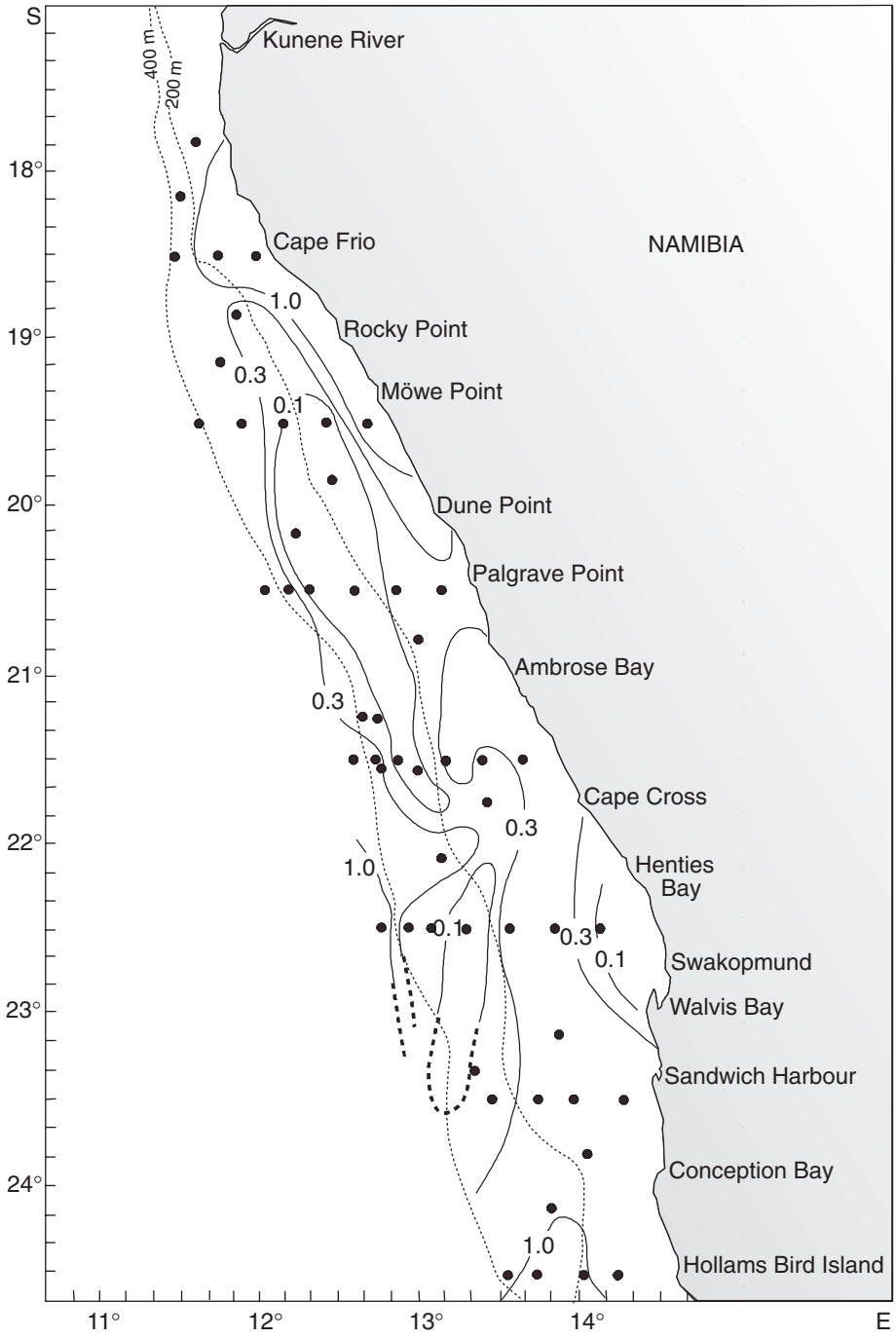

Fig. 7: Bottom oxygen concentration (mℓ ℓ^{-1}), September/October 1998

Spatial distribution of eggs and larvae

The presentation herein of the spatial distribution of eggs, larvae, water mass characteristics (temperature, salinity, oxygen concentration) and circulation features are based on the survey in 1998, which had the most comprehensive field mapping.

During the 1998 cruise, hake spawned throughout the area of investigation, from Hollams Bird Island to Cape Frio. Figure 4 shows the horizontal distribution of all stages of hake eggs. Four regions with elevated concentrations of eggs were identified. The three northernmost regions coincide with the presence of mesoscale gyres observed by the ADCP. Figure 5 synthesizes the circulation in the layer 35–50 m deep, based on the ADCP measurements (Sundby *et al.* 1998). The fourth and southernmost region of high concentration of eggs, off Sandwich Harbour (see Fig. 4), was unfortunately not covered in sufficient detail by the ADCP. Similarly, there were four patches of newly spawned eggs, or Stage I eggs (Fig. 6), similar to Stages 1–11 on the Matthews and de Jager (1951) scale, representing eggs up to 37 h old at 12°C. These eggs were distributed slightly south of the epicentres of all egg stages combined. The four patches, indicating areas of intense spawning activity, were between Cape Frio and Rocky Point, off Palgrave Point, between Cape Cross and Sandwich Harbour, and to a lesser extent off Hollams Bird Island. The oxygen concentrations at the bottom (Fig. 7), and 50 m above the bottom (Fig. 8) show variable and low values. At the bottom there was <0.1 mℓ ℓ^{-1} of oxygen over large parts of the area. Even 50 m above the bottom, the concentration was <0.1 mℓ ℓ^{-1} in the central region, Henties Bay to Möwe Point.

Low oxygen concentrations influence spawning of hake and subsequently the transport and dispersal of developing eggs. On the other hand, the presence of the mesoscale gyres also influences dispersal of eggs. Figure 9 shows the section off Sandwich Harbour with the vertical distributions of temperature, salinity and oxygen concentration (Figs 9a–c) in addition to the distributions of Egg Stages I, II and III (Figs 9d–f) and larvae (Fig. 9g). Oxygen concentrations were relatively high in the south, only slightly <0.3 mℓ ℓ^{-1} at the seabed of the outermost station (Fig. 9c). The distribution of Stage I eggs is evidence of spawning right down to the seabed at the outermost station, about 100 km offshore (Fig. 9d). The temperature there was 11–12°C, so this stage should represent eggs at an age of 0–37 h. These stages were practically absent <70 km offshore. The distribution of Stage II eggs (37–73 h; Fig. 9e) was about 100 m shallower and closer inshore. The Stage III eggs (73–98 h; Fig. 9f) were even closer inshore but rather deeper in the water column than Stage II eggs. Finally, larval (here defined as newly hatched, 2.5 mm standard length *SL*, to >10 mm *SL*) concentration was greatest inshore and still peaking subsurface (Fig. 9g). Finally, all older eggs and the larvae were at ambient temperatures of 11–12°C.

In the section off Palgrave Point (Fig. 10), a thick layer of low-oxygen water of concentration <0.3 mℓ ℓ^{-1} extended 100 m above the bottom (Fig. 10c). The distribution of the youngest eggs (Fig. 10d) shows that the hake there spawned mesopelagically, but very close to the layer of low oxygen. Because they were spawned shallower, the young eggs were here found at a wider temperature range, from about 10.5 to 14°C. Just like the distribution off Sandwich Harbour, the Stage II eggs (Fig. 10e) were higher up in the water column. In this section, the eggs were not distributed closer to shore, but were retained within the anticlockwise mesoscale gyre centred north of the Palgrave Point section (Fig. 5). Similarly, the Stage III eggs (Fig. 10f) were retained by the gyre and were distributed vertically from the surface to about 200 m. However, the larvae (Fig. 10g), which had been subjected to a longer period of transport, had slipped out of the gyre and been advected inshore.

Off Möwe Point (Fig. 11), the low-oxygen layer was less extensive than off Palgrave Point (Fig. 11c), and the distribution of the newly spawned eggs (Stage I; Fig. 11d) was closer to the bottom and still very close to oxygen concentrations <0.3 mℓ ℓ^{-1}. However, here also, most eggs were higher in the water column, with highest concentrations between 50 and 100 m deep. The ambient temperatures of the newly spawned eggs ranged from 11.5 to 15°C. Stage II eggs (Fig. 11e) also showed the effects of retention by a mesoscale gyre, which off Möwe Point was rotating clockwise and located closer inshore. No Stage III eggs were found on this section, and few larvae were found either (Fig. 11g), and then only subsurface and inshore.

The surface waters of the Benguela system off Namibia generally move northwestwards (alongshore and offshore), owing to the action of the prevailing equatorward winds. This movement is best shown in the trajectories of surface drogues, as reported by Gründlingh (1999). The subsurface circulation pattern revealed by the ADCP measurements in 1998 (Fig. 5) shows, in addition to the mesoscale gyres, a general onshore and southward current component. Northward flow appears restricted to a narrow band over the midshelf. Similar patterns were measured in July 1999 (Mouton *et al.* 2001), with the exception of inshore, where currents were weak. The horizontal distribution of all hake larvae (Fig. 12) shows that they were more southerly distributed than eggs (Fig. 4). Moreover, Figure 13 shows that the largest (and oldest)

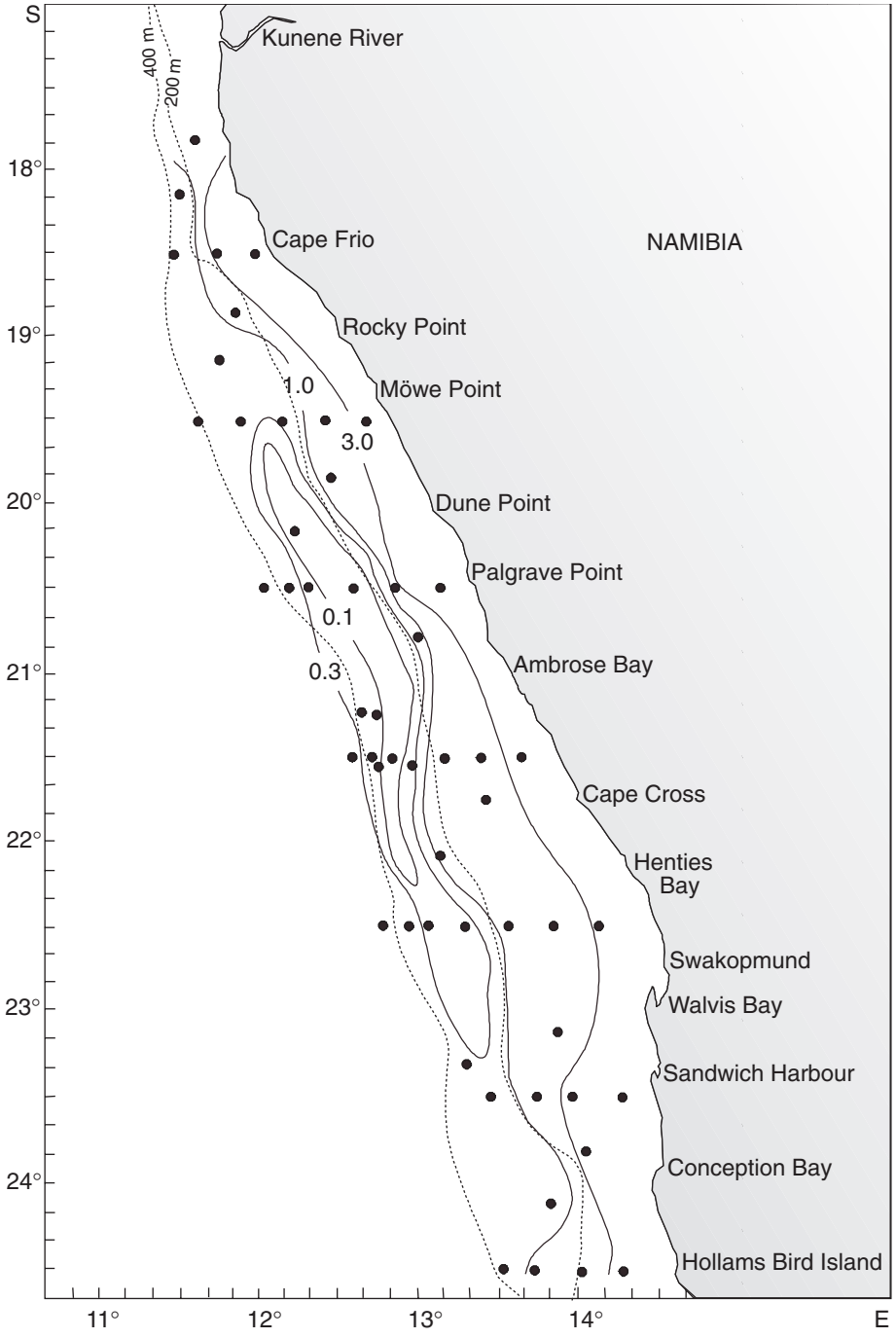

Fig. 8: Oxygen concentration 50 m above the bottom (mℓ ℓ^{-1}), September/October 1998

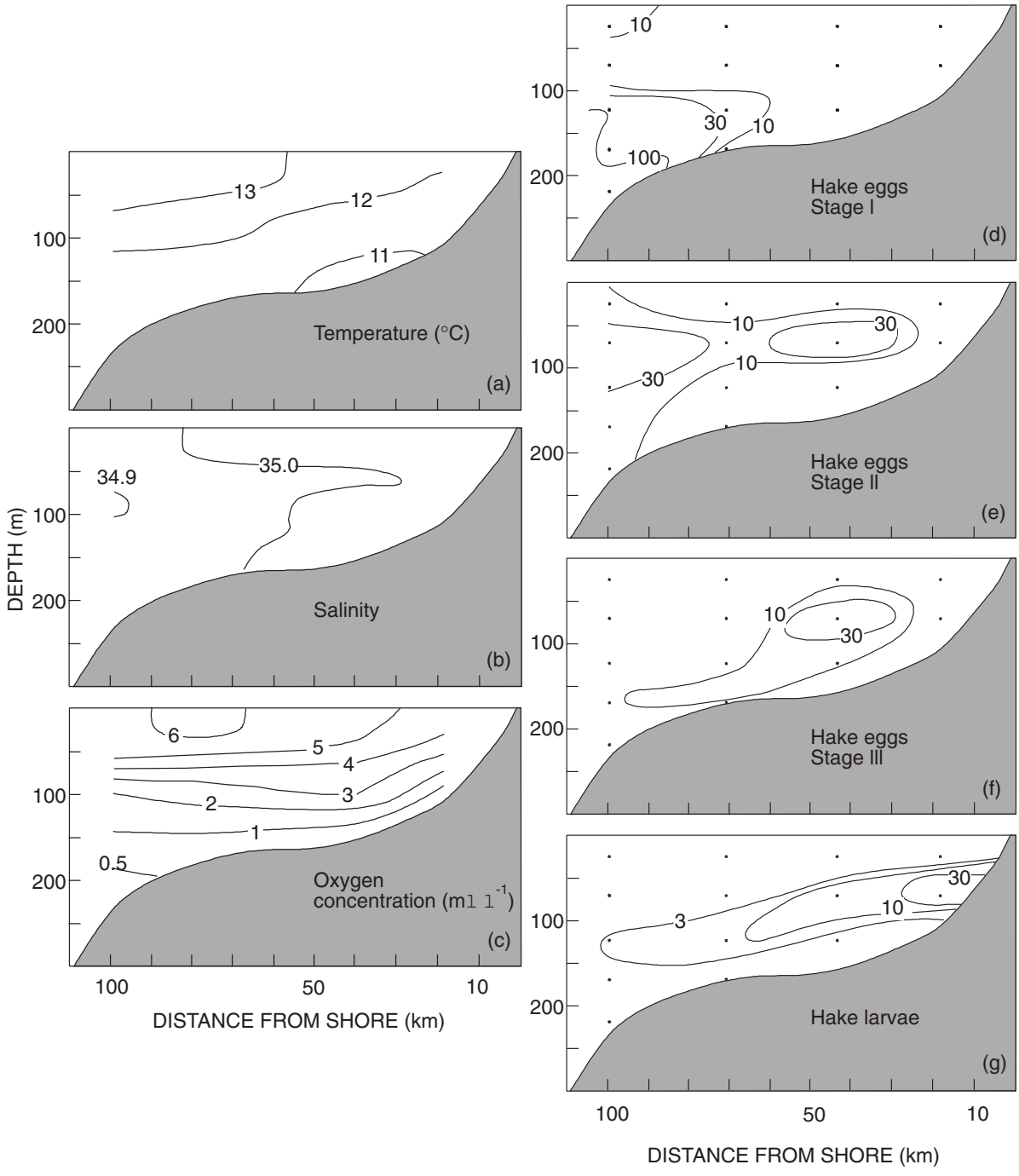

Fig. 9: Sandwich Harbour vertical section — (a) temperature, (b) salinity, (c) oxygen concentration, (d) Stage I hake eggs (= Stages 1–11 of Matthews and de Jager 1951), (e) Stage II hake eggs (= Stages 12–14), (f) Stage III hake eggs (= Stage 15), and (g) hake larvae. (d) – (g) values represent numbers per 10 m^2 per 50 m depth interval, i.e. numbers per 500 m^3

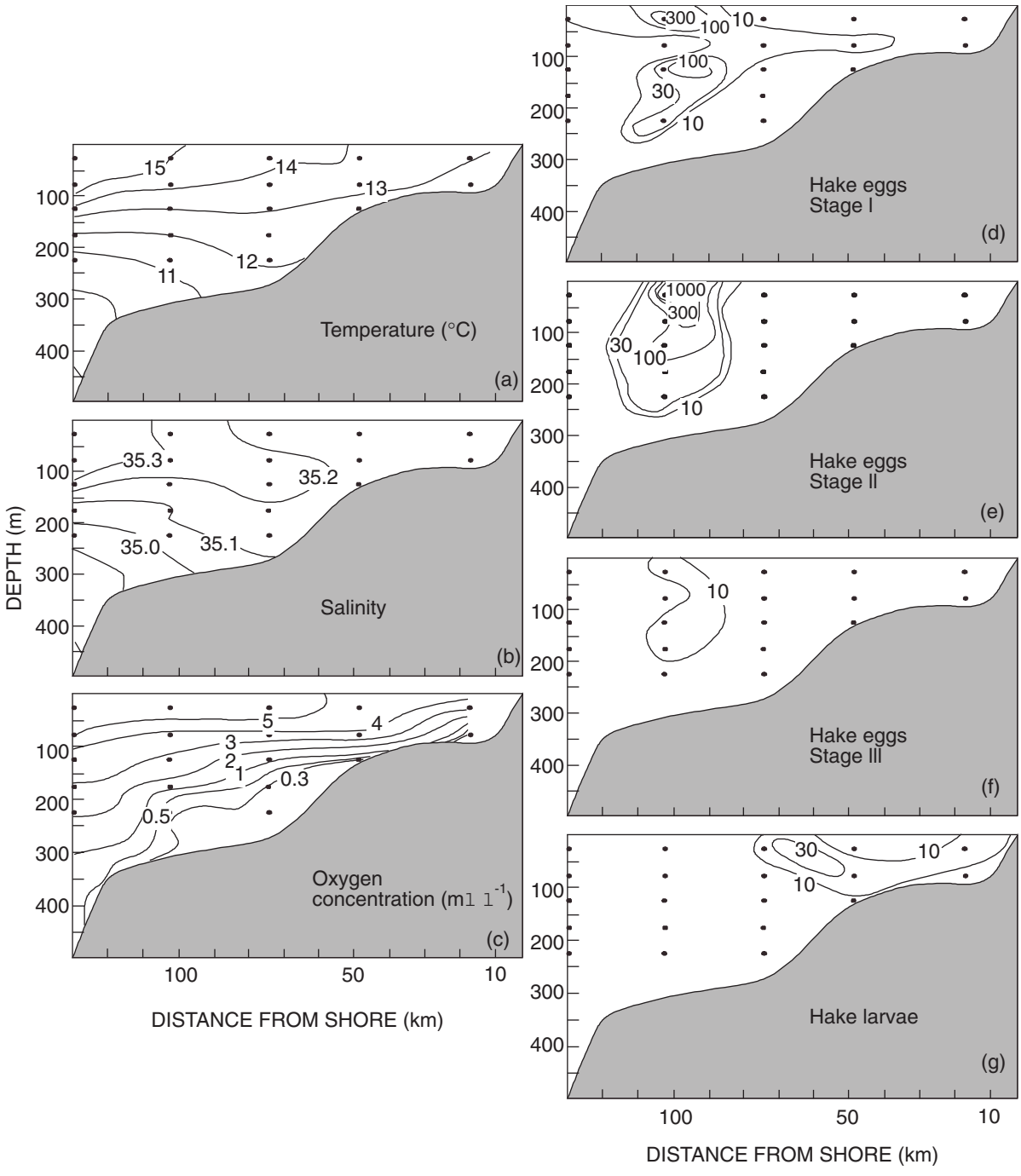

Fig. 10: Palgrave Point vertical section — (a) temperature, (b) salinity, (c) oxygen concentration, (d) Stage I hake eggs (= Stages 1–11 of Matthews and de Jager 1951), (e) Stage II hake eggs (= Stages 12–14), (f) Stage III hake eggs (= Stage 15), and (g) hake larvae. (d) – (g) values represent numbers per 10 m^2 per 50 m depth interval, i.e. numbers per 500 m^3

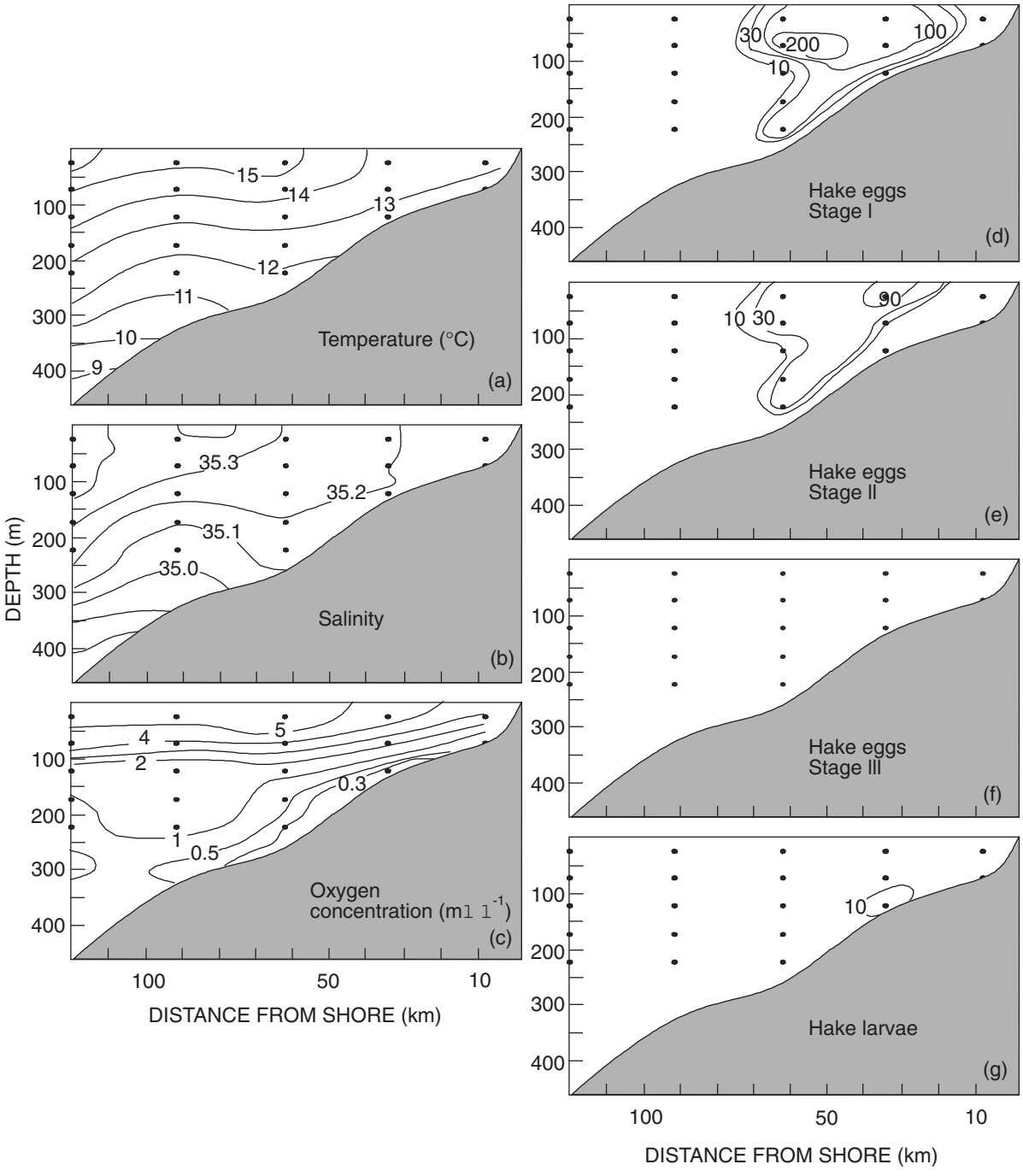

Fig. 11: Möwe Point vertical section — (a) temperature, (b) salinity, (c) oxygen concentration, (d) Stage I hake eggs (= Stages 1–11 of Matthews and de Jager 1951), (e) Stage II hake eggs (= Stages 12–14), (f) Stage III hake eggs (= Stage 15), and (g) hake larvae. (d) – (g) values represent numbers per 10 m^2 per 50 m depth interval, i.e. numbers per 500 m^3

larvae were more abundant inshore along the central parts of the Namibian coast from Conception Bay to Palgrave Point.

DISCUSSION

The buoyancy of a fish egg is the difference in specific gravity between the egg and the ambient seawater. The specific gravity of the egg is determined by the chorion mass, the composition of proteins and fat of the embryo and by the salinity of the water it contains (Kjesbu *et al.* 1992). A fish egg can control the salinity of the water within its embryo by osmoregulation, but the temperature within the egg is, of course, equal to that of the ambient seawater. Therefore, of the ambient physical parameters, only salinity influences the buoyancy of a fish egg. The vertical salinity distribution in upwelling regions such as the Benguela is quite different from other coastal waters. In most coastal regions, freshwater runoff from land is larger than evaporation and, consequently, salinity increases with depth. More specifically, it results in an upper mixed layer of low salinity, a halocline where the salinity increases abruptly, and a deep layer of more homogeneous high-saline water. During such conditions, fish eggs in a vertical steady-state distribution might be pelagically distributed in the upper layer, bathypelagically distributed and floating within the halocline, or distributed near the bottom, depending on their buoyancy (Sundby 1991). However, in upwelling areas such as the Benguela, the salinity gradient is inverse of that documented above, salinity decreasing with depth. Under such conditions, fish eggs cannot have a bathypelagic steady-state distribution. They must either rise or descend continuously, their buoyancy and size determining the speed of the rise or fall.

Eggs of *M. capensis* off Namibia are adapted to the particular physical setting of the upwelling ecosystem in a remarkable way. If the eggs had negative buoyancy, they would descend into the bottom layer, where they would be subjected to mass mortality as a result of the generally anoxic conditions there. Although hake are well adapted to extremely low oxygen concentrations, their eggs cannot survive such conditions. In contrast, if the eggs were too highly positively buoyant, they would soon reach the surface layer and be swept offshore and lost for coastal recruitment. *M. capensis* eggs are, however, just slightly positively buoyant and, compared to other species, e.g. Atlantic cod *Gadus morhua* (Solemdal and Sundby 1981, Kjesbu *et al*. 1992, Anderson and deYoung 1994), mackerel *Scomber scombrus* (Sundby 1983) and blue whiting *Micromesistius poutassou* (Ådlandsvik *et al*. 2001), the range of variation in their buoyancy is very low. Combined with the relatively small size of the eggs, which range in diameter from 0.82 to 1.08 mm, they have evolved to rise very slowly through the water column at speeds ranging from <1 to 3 m h^{-1} (Fig. 3). As the eggs remain well below the upper mixed layer, wind-induced turbulence will not influence their vertical movement significantly (Sundby 1991). The present simulations show that, if spawning occurs 200 m or more deep, even the lightest and fastest ascending eggs would hatch before they reached the offshore-moving surface layer. The heaviest eggs would ascend only some 50 m before hatching.

Even though the buoyancy of an *M. capensis* egg is extremely finely tuned to its surroundings, it does change slightly through development, as shown in Figure 2. The same phenomenon has been shown for other species in which buoyancy has been measured through its developmental stages, e.g. Atlantic cod (Mangor-Jensen 1987, Anderson and deYoung 1994, Nissling and Vallin 1995) and blue whiting (Ådlandsvik *et al.* 2001). Buoyancy variation through development has been suggested by Mangor-Jensen (1987) to be caused by variations in osmoregulation. Accordingly, an increase in specific gravity during the early stages (Fig. 2) is attributable to a limited loss of water. As the egg develops it would be able to osmoregulate more actively. The water loss is reversed and, consequently, the specific gravity decreases. For hake eggs incubated at 12°C, this situation occurs when the egg is 40–50 h old and has reached Stages 11–12 (on the scale of Matthews and de Jager 1951), in other words when the embryo becomes clearly visible. The maximum specific gravity at around 40–50 h of egg age influences the rate of ascent of eggs, particularly the heaviest fraction, which are almost neutrally buoyant then.

The simulations in Figure 3 are terminated just after hatching because appropriate information on the larval behaviour of hake is unavailable. When the larvae hatch and lose the chorion, they rid themselves of the heaviest fraction of the egg. The specific gravity of chorion material in fish eggs has been estimated to be 1.2 g cm^{-3} (Kjesbu *et al.* 1992). During the very first hours after hatching, *M. capensis* larvae were almost immobile in the density-gradient columns, with the yolk and the oil globule floating up. Therefore, it may be anticipated that larvae in the wild would also continue to ascend passively at that age, and considerably faster than before hatching. After some hours, larval activity increases and they start to swim downwards at intervals, interspersed with passive periods of slow ascent. Larvae were thus able to maintain their vertical position in the density-gradient column. If this behaviour is representative of conditions in the wild, larvae would be able to control their vertical

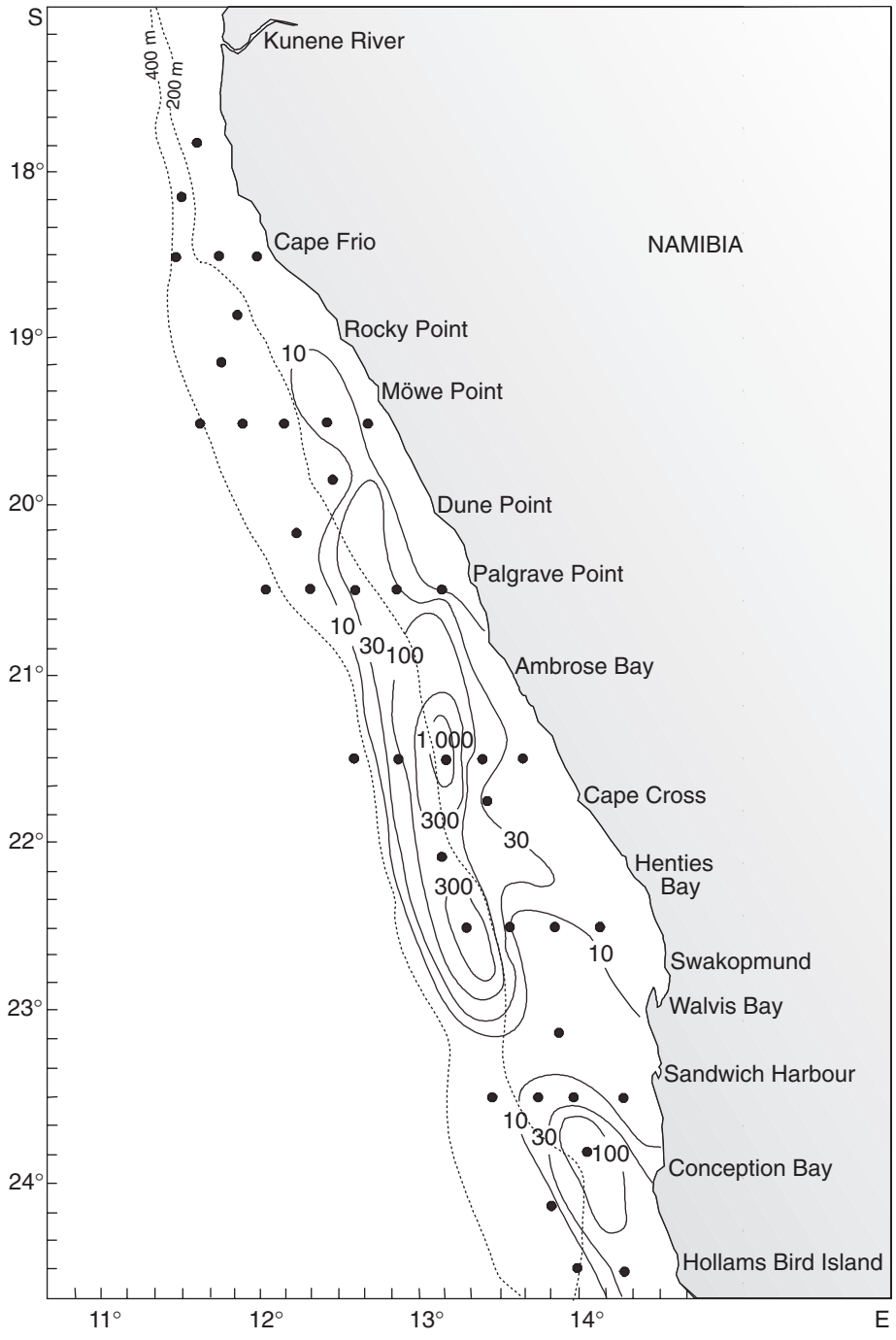

Fig. 12: Distribution of hake larvae (number per 10 m^2), all stages combined, September/October 1998

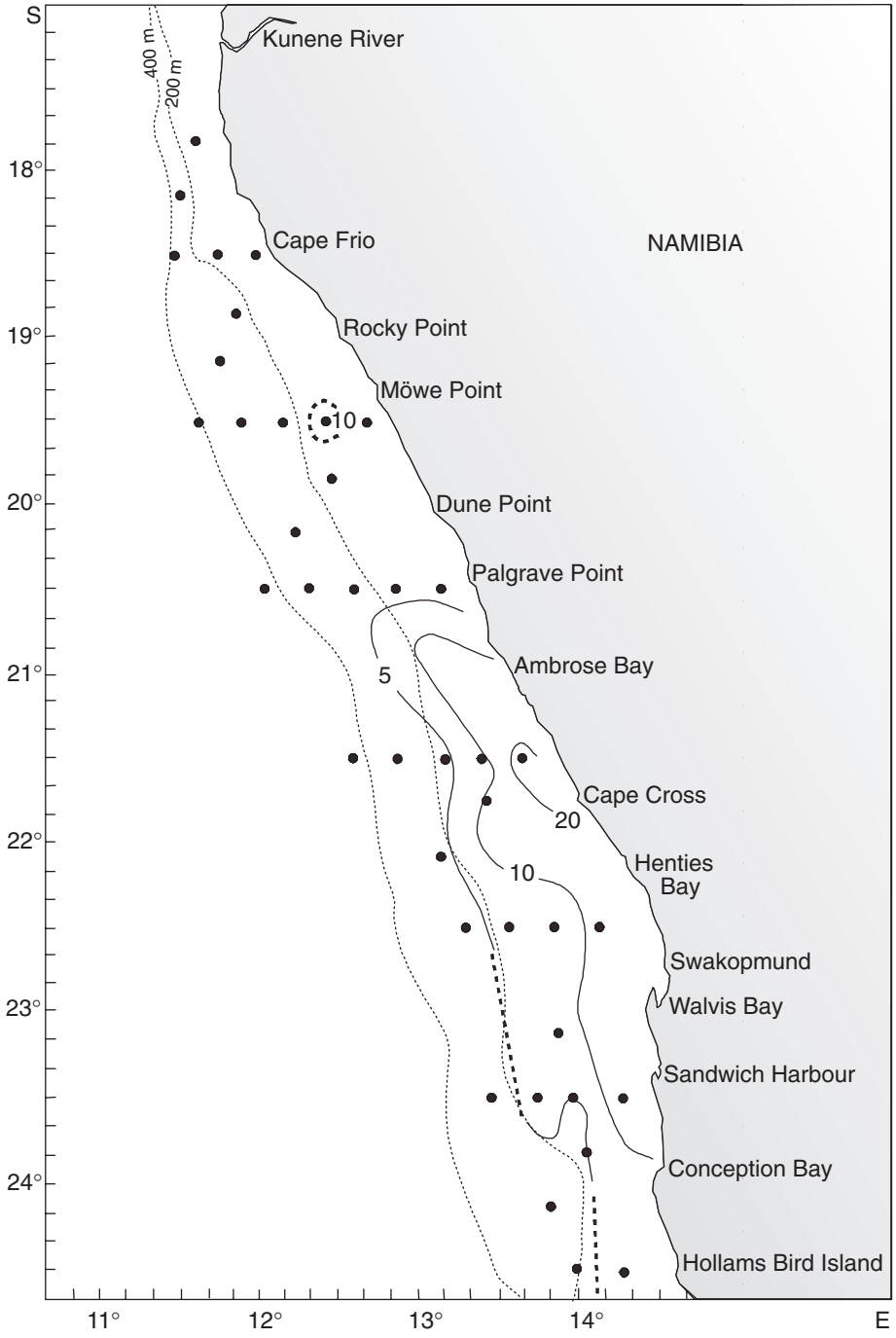

Fig. 13: Mean length (mm) of hake larvae in the area of investigation, September/October 1998

position in the water column or even migrate deeper.

Figure 9 (the Sandwich Harbour section) shows the physical conditions associated with hake eggs and larvae when spawning takes place more than 100 km offshore and near the bottom, at depths of about 250 m. Figures 9d–f display the slow ascent of the eggs through the water column from Stage I to Stage III, on average more than 100 m of vertical movement upwards. Peak concentrations of Stage III eggs were 50–100 m deep. Consequently, the total rise during egg development is not very different from the simulation. What the field data indicate additionally is that the eggs are advected onshore by features of the current system below the offshore-moving Ekman layer. The epicentre of Stage I eggs is about 50 km west of that of Stage III eggs, and larvae are most highly concentrated at the station closest to the coast. Hence, all eggs and larvae are within the subsurface layer, where movement is onshore. Although no ADCP measurements were available to confirm an onshore moving undercurrent during the actual measurements during October 1998, evidence for such an undercurrent was found during the second survey in 1997 and also through circulation modelling (Sundby *et al.* 1999).

Farther north, where the thick low-oxygen layer of <0.3 mℓ ℓ^{-1} lies just above the seabed, spawning hake behave differently. This appears on the sections off Palgrave Point (Fig. 10) and Möwe Point (Fig. 11). There, spawning took place higher in the water column, well above the low-oxygen layer. However, Stage I eggs were found in oxygen concentrations even <0.3 mℓ ℓ^{-1} (Figs 10c, d, 11c, d), indicating that the hake must have spawned close to the limit of offspring survival in terms of oxygen concentration. Because hake spawn shallower in the two northern sections, older egg stages were found higher in the water column and partly into the upper Ekman layer. However, because of the existence of the mesoscale gyres there, the older eggs were retained within the gyres. The persistence of these gyres is unclear. Based on other ADCP surveys, they seem to be non-stationary and to appear at intervals and at different locations. This interpretation is also supported by the larval distributions along the two sections, larvae being most abundant subsurface and nearshore. On a longer time-scale, there is likely still an onshore-dominating component in the transport of the spawning products.

The combination of deep offshore spawning and the slightly positive buoyancy of their eggs giving them a slow ascent rate through the water column contributes to carrying the spawning products of hake inshore by means of the onshore-moving subsurface current in the upwelling ecosystem. This concentrates the early juvenile hake inshore. In addition, there is a southward component of the subsurface current, which seems to concentrate the spawning products between Palgrave Point and Walvis Bay.

From the analyses here of the distribution of newly spawned *M. capensis* eggs, it is clear that hake spawning takes place near the seabed (Fig. 9d) unless the oxygen concentration is too low for the eggs to survive. Under such conditions, hake spawn mesopelagically above the low-oxygen layer (Figs 10d, 11d). However, the resultant eggs were still very close to the low-oxygen layer and at values slightly less than 0.3 mℓ ℓ^{-1}. This is a remarkably low concentration, and few species of fish would be expected to survive it. Juvenile hake show high tolerance to low oxygen and seem to migrate away from such waters when the oxygen concentration falls below 0.5 mℓ ℓ^{-1} (Hamukuaya *et al.* 1998). As already stated, the average hake egg is slightly positively buoyant, allowing it to ascend very slowly. In addition, *M. capensis* eggs have a very narrow buoyancy distribution in comparison to many other pelagic eggs. If the buoyancy distribution had been wider, a significant fraction of the eggs would have been negatively buoyant and sunk into the anoxic water masses. Also, if the mature hake had been spawning close to the bottom but more offshore and outside the low-oxygen layer instead of mesopelagically and above the low oxygen layer, the eggs would probably have been carried laterally into the anoxic water masses because of the slow ascent rate of the eggs. It is likely that these mechanisms keep the eggs close to the low-oxygen layer but without drifting into it, minimizing predation by organisms that have less tolerance to low oxygen concentration.

The onshore movement of hake larvae from the offshore spawning areas presented here has also been reported recently for European hake *M. merluccius* spawning in the Bay of Biscay (Alvarez *et al.* 2001). That species also has eggs and larvae distributed subsurface (Coombs and Mitchell 1982). Moreover, the distribution of Pacific hake *M. productus* eggs and larvae in the California Current and the Puget Sound is subsurface (Bailey 1982). It is therefore concluded that the spawning behaviour and the physical properties of eggs of *M. capensis* have developed as an ecological adaptation to transport of the spawning products inshore in the northern Benguela. It may well provide a generic mechanism for concentrating and retaining fish eggs and larvae in upwelling regions. This is evidently a robust mechanism that limits the negative consequences of offshore loss of hake larvae from upwelling ecosystems. The extent to which larvae are transported onshore would depend on the structure of the upwelling cell. The mechanism might even contribute to increased concentration of hake larvae inshore rather than increased offshore loss when inshore upwelling is particularly strong.

ACKNOWLEDGEMENTS

We thank the crew of the R.V. *Dr Fridtjof Nansen* for assistance during sampling, Dr L. Motos, of the Fundación AZTI (Food and Fisheries Technology Institute), Portualde, Pasaia, Spain, and an anonymous reviewer for their constructive reviews of the draft manuscript, and Ms K. Gjertsen (Institute of Marine Research, Bergen, Norway) for the artwork.

LITERATURE CITED

ÅDLANDSVIK, B., COOMBS, S., SUNDBY, S. and G. TEMPLE 2001 — Observations and modelling of the vertical distribution of eggs and larvae of blue whiting (*Micromesistius poutassou*). *Fish. Res*. **50** (1–2): 59–72.

ALHEIT, J. and T. J. PITCHER (Eds) 1995 — *Hake: Biology, Fisheries and Markets*. London; Chapman & Hall: 478 pp.

ALVAREZ, P., MOTOS, L., URIARTE, A. and J. EGAÑA 2001 — Spatial and temporal distribution of European hake, *Merluccius merluccius* (L.), eggs and larvae in relation to hydrographical conditions in the Bay of Biscay. *Fish. Res*. **50**(1–2): 111–128.

ANDERSON, J. T. and B. deYOUNG 1994 — Stage-dependent density of cod eggs and larvae (*Gadus morhua* L.) in Newfoundland waters. *ICES mar. Sci. Symp*. **198**: 654–665.

ASSOROV, V. V. and D. Y. BERENBEIM 1983 — Spawning grounds and cycles of Cape hakes in the Southeast Atlantic. *Colln scient. Pap. int. Commn SE. Atl. Fish.* **10**(1): 27–30.

BAILEY, K. M. 1982 — The early life history of the Pacific hake, *Merluccius productus*. *Fishery Bull., Wash*. **80**(3): 589–598.

BAKUN, A. and R. H. PARRISH 1990 — Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*). *J. Cons. int. Explor. Mer* **46**: 269–283.

BOTHA, L. 1973 — Migrations and spawning behaviour of the Cape hakes. *S. Afr. Shipp. News Fishg Ind. Rev*. **28**(4): 62, 63, 65, 67.

BOTHA, L. 1986 — Reproduction, sex ratio and rate of natural mortality of Cape hakes *Merluccius capensis* Cast. and *M. paradoxus* Franca in the Cape of Good Hope area. *S. Afr. J. mar. Sci*. **4**: 23–35.

CHŁAPOWSKI, K. and M. KRZEPTOWSKI 1980 — Abundance and distribution of young hake (*Merluccius capensis*) off Southwest Africa March–April 1979. *Colln scient. Pap. int. Commn SE. Atl. Fish*. **7**: 133–150.

COOMBS, S. H. 1981 — A density-gradient column for determining the specific gravity of fish eggs, with particular reference to eggs of the mackerel *Scomber scombrus*. *Mar. Biol.* **63**: 101–106.

COOMBS, S. H. and C. E. MITCHELL 1982 — The development rate of eggs and larvae of the hake, *Merluccius merluccius* (L.) and their distribution to the west of the British Isles. *J. Cons. int. Explor. Mer* **40**: 119–126.

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.

GRÜNDLINGH, M. L. 1999 — Surface currents derived from satellite-tracked buoys off Namibia. *Deep-Sea Res*. II **46**: 453–473.

HAMUKUAYA, H. 1999 — The structure of demersal fish communities off Namibia with reference to the influence of abiotic factors. Ph.D. thesis, University of Port Elizabeth: 267 pp.

HAMUKUAYA, H., O'TOOLE, M. J. and P. M. J. WOODHEAD 1998 — Observations of severe hypoxia and offshore displacement of Cape hake over the Namibian shelf in 1994. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci*. **19**: 57–59.

KJESBU, O. S., KRYVI, H., SUNDBY, S. and P. SOLEMDAL 1992 — Buoyancy variations in eggs of Atlantic cod (*Gadus morhua* L.) in relation to chorion thickness and egg size: theory and observations. *J. Fish Biol*. **41**: 581–599.

MANGOR-JENSEN, A. 1987 — Water balance in developing eggs of the cod *Gadus morhua* L. *Fish Physiol. Biochem*. **3**(1): 17–24.

MATTHEWS, J. P. and B. van D. DE JAGER 1951 — The development of the Cape stockfish (*Merluccius capensis*). *Investl Rep. Fish. mar. biol. Surv. Div. Un. S. Afr.* **13**: 10 pp.

MOUTON, D. P., BOYD, A. J. and C. H. BARTHOLOMAE 2001 — Near-surface currents and hydrology off the northern Benguela in July 1999. *S. Afr. J. Sci*. **97**: 209–212.

NISSLING, A. and L. VALLIN 1995 — The ability of Baltic cod eggs to maintain neutral buoyancy and the opportunity for survival in fluctuating conditions in the Baltic Sea. *J. Fish Biol.* **48**: 217–227.

OLIVAR, M-P. and J-M. FORTUÑO 1991 — Guide to ichthyoplankton of the Southeast Atlantic (Benguela Current region). *Scientia marina* **55**(1): 383 pp.

OLIVAR, M-P., RUBIÉS, P. and J. SALAT 1988 — Early life history and spawning of *Merluccius capensis* Castelnau in the northern Benguela Current. *S. Afr. J. mar. Sci*. **6**: 245–254.

OLIVAR, M-P. and P. A. SHELTON 1993 — Larval fish assemblages of the Benguela Current. *Bull. mar. Sci*. **53**: 450–474.

O'TOOLE, M. J. 1976 — Distribution and abundance of larvae of the hake *Merluccius* spp. off South West Africa, 1972–1974. *Colln scient. Pap. int. Commn SE. Atl. Fish*. **3**: 151–158.

O'TOOLE, M. J. 1978 — Aspects of the early life history of the hake *Merluccius capensis* Castenau off South West Africa. *Fish. Bull. S. Afr.* **10**: 20–36.

O'TOOLE, M. J. 1999 — Ichthyoplankton research and monitoring in the central and northern Benguela Current ecosystem during the early 1970's – a historical perspective. In *International Workshop on Zoo-Ichthyoplankton Monitoring in the Benguela Current Ecosystem off Namibia, Swakopmund, February 1999*. Alheit, J. and M. J. O'Toole (Conveners): 7 pp. + 29 Figures (mimeo).

PARRISH, R. H., NELSON, C. S. and A. BAKUN 1981 — Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.* **1**(2):175–203.

POREBSKI, J. 1975 — Application of the surface adhesion test to identify the eggs of the hake *Merluccius* spp. *Colln scient Pap. int. Commn SE. Atl. Fish*. **2**: 102–106.

SEDLETSKAYA, V. A. 1988 — Reproduction of Cape hake (*Merluccius m. capensis*) and Cape horse mackerel (*Trachurus t. capensis*) in Namibia. *Colln scient. Pap. int. Commn SE. Atl. Fish*. **15**(2): 215–222.

SOLEMDAL, P. and S. SUNDBY 1981 — Vertical distribution of pelagic fish eggs in relation to species, spawning behaviour and wind conditions. *ICES Coun. Meet. Doc*. **1981 G: 77**: 26 pp. (mimeo).

SUNDBY, S. 1983 — A one-dimensional model for the vertical distribution of pelagic fish eggs in the mixed layer. *Deep-Sea Res*. **30**(6A): 645–661.

SUNDBY, S. 1991 — Factors affecting the vertical distribution of eggs. *ICES mar. Sci. Symp*. **192**: 33–38.

SUNDBY, S. and M. J. O'TOOLE 1995 — Investigation on spawning

hake and their eggs and larvae, 27 September – 7 October 1995. Cruise Reports of *Dr Fridtjof Nansen*. Surveys of the fish resources of Namibia. Preliminary Report Cruise No. 3/95. Bergen; Institute of Marine Research: 13 pp. + 33 Figures (mimeo).

SUNDBY, S., BOYD, A. J., THORSEN, A., THORISSON, K., KJESBU, O. S., KAINGE, P. and R. OSBORNE 1998 — Investigation on spawning hake and their eggs and larvae, 23 September–6 October 1998. BENEFIT Surveys. Cruise Report 3/98. Bergen; Institute of Marine Research: 28 pp. + 70 Figures (mimeo).

SUNDBY, S., SKOGEN, M. and O. S. KJESBU 1999 — Lysing i namibiske farvann – en økologisk tilpasning til et opp-strømningssystem (Hake in Namibian waters – ecological adaptation to an upwelling system). I: Havets miljø 1999. *Fisken Hav. Særnummer* **2**: 68–75 (in Norwegian with English abstract).

ZWEIFEL, J. R. and R. LASKER 1976 — Prehatch and posthatch growth of fishes – a general model. *Fishery Bull., Wash*. **74**(3): 609–621.