

Chokka squid (*Loligo vulgaris reynaudii*) abundance linked to changes in South Africa's Agulhas Bank ecosystem during spawning and the early life cycle

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Chokka squid biomass and catch are highly variable, likely owing to their links to changes in the ecosystem, which impact spawning and recruitment. A synthesis of basic ecosystem components for the domain in which chokka squid live (i.e. South Africa's west coast and Agulhas Bank), was prepared using published and new data. It included substratum, bottom temperature, bottom dissolved oxygen, chlorophyll, and copepod abundance. Alongshore gradients of these indicated that the main spawning grounds on the eastern Agulhas Bank are positioned where bottom temperature and bottom dissolved oxygen are optimal for embryonic development. This location, however, appears suboptimal for hatchlings because the copepod maximum (food for paralarvae) is typically on the central Agulhas Bank some 200 km to the west. Data on currents suggest that this constraint may be overcome by the existence of a net west-flowing shelf current on the eastern Agulhas Bank, improving survivorship of paralarvae by transporting them passively towards the copepod maximum. CTD data and a temporal analysis of AVHRR satellite imagery reveal the copepod maximum to be supported by a "cold ridge", a mesoscale upwelling filament present during summer when squid spawning peaks. *In situ* sea surface temperature (SST) data used as a proxy for cold ridge activity demonstrate considerable interannual variability of the feature, especially during *El Niño*–Southern Oscillation events. Negative linear correlations between maximum summer SST (monthly average) and squid biomass the following autumn ($r^2 = 0.94$), and annual catch ($r^2 = 0.69$), support the link between the "cold ridge–copepod maximum" and the early life cycle of chokka squid, and holds promise for prediction.

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Introduction

The marine environment around southern Africa is one of the most diverse, complex, and highly variable anywhere in the world (Figure 1; Lutjeharms *et al.*, 2001). The oceanography of South Africa's east coast and outer Agulhas Bank (south coast) is strongly influenced by the warm, fast-flowing ($\sim 2 \text{ m s}^{-1}$) Agulhas Current. This is a well-defined western boundary current with origins in the Moçambique Channel (Lutjeharms, 2001), and it transports some 70–135 Sv. At the southern tip of the Agulhas Bank, the Agulhas Current undergoes a number of configurations, which include retroflexion eastwards along the Subtropical Convergence into the South Indian Ocean, the formation of anticyclonic rings shed into the South Atlantic (Duncombe Rae, 1991), or continuous flow along the shelf edge of the western Bank (Lutjeharms and Cooper, 1996). On the outer Agulhas Bank the oceanography is dominated by associated shear boundary processes, such as meanders, eddies, and break-away filaments (Lutjeharms *et al.*, 1989). Large-scale upwelling is common east of Port Elizabeth, as a result of the divergence between the shelf edge (and Agulhas Current) and the coast (Lutjeharms *et al.*, 1999). Intense thermoclines induced by shelf-edge upwelling and insolation are characteristic of the eastern and central Bank (Largier and Swart, 1987). The inner shelf is influenced

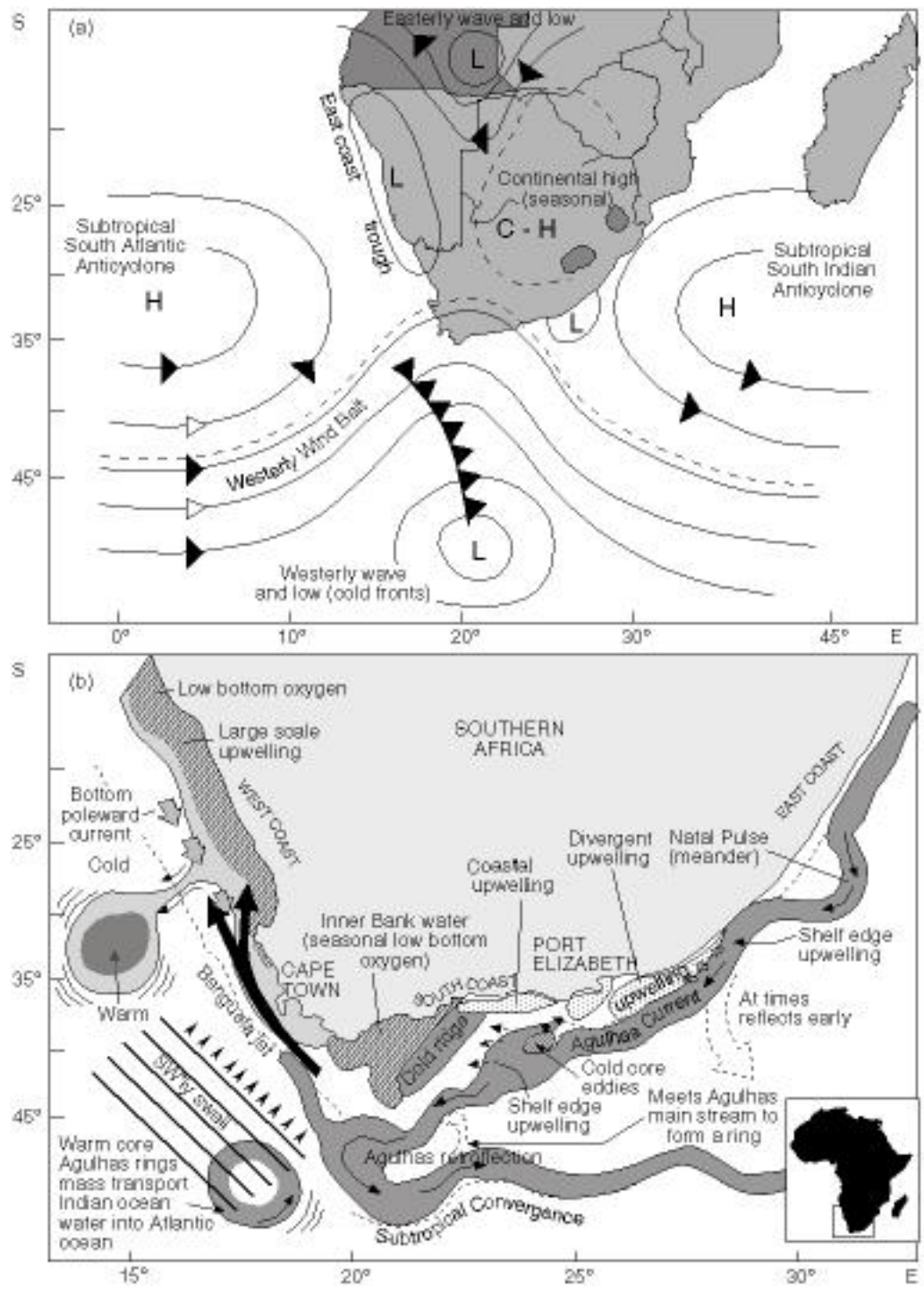


Figure 1. (a) The complexity and variability of the marine environment around southern Africa is partly due to the latitude and associated weather. In summer, the oceanic high pressure cells either side of southern Africa dominate the wind field, causing southeasterly winds on the west coast and northeasterly winds on the eastern Agulhas Bank and east coast. In winter, the westerly wind belt migrates north, moving cold fronts and strong westerly winds to southern Africa. (b) The oceanography is also dominated by the warm Agulhas and cold Benguela Currents. These drive many of the physical processes and key features on the shelf.

by wind-driven coastal upwelling, particularly during summer (Schumann *et al.*, 1982). Upward doming of the thermocline in an elongated formation is often found on the central Agulhas Bank. This feature, referred to as a “cold ridge” (Figure 1b), is commonly associated with high levels of primary and secondary production (Boyd and Shillington, 1994). Large, solitary, transient, meanders in the Agulhas Current, referred to sometimes as a “Natal Pulse”, are at times found on South Africa’s east coast (De Ruijter *et al.*, 1999). These have profound influences on the shelf oceanography there, as well as on the trajectory of the Agulhas Current (Roberts *et al.*, submitted). Ring formation has been associated with the Natal Pulse (Van Leeuwen *et al.*, 2000).

The west coast is completely different, dominated by the cold Benguela upwelling system (Shannon and Nelson, 1996), one of the largest eastern boundary upwelling systems in the world and primarily driven by the South Atlantic High Pressure (anticyclone) and associated south-easterly winds (Figure 1a). Consequently, the region has abundant primary and secondary production, frequently leading to low levels of dissolved oxygen in the bottom layer, and at times almost anoxic conditions (Chapman and Shannon, 1987). There, the outer shelf is influenced by the north-flowing, cooler, slower ($0.25\text{--}0.50\text{ m s}^{-1}$) Benguela Current (Boyd *et al.*, 1992). This eastern boundary current is less defined than the Agulhas Current, and essentially is the eastern component of the South Atlantic gyre. A narrow frontal jet, referred to as the Benguela jet, is common along the shelf edge between the Cape Peninsula and Cape Columbine (Figure 1b). Compared with the Agulhas Current, the Benguela jet is small, with maximum velocities of $\sim 0.75\text{ m s}^{-1}$ and a flow of 1–7 Sv. North of Cape Columbine the jet undergoes bifurcation, moving onto the wider shelf and into the South Atlantic towards the Walvis Ridge. The northern boundary of the Benguela is where the continental margin narrows at 16°S , and is marked by the permanent warm Angola–Benguela Front (Boyd, 1987). Agulhas rings (Duncombe-Rae *et al.*, 1992), other eddy features (Lutjeharms and Matthysen, 1995), and filaments (Nelson *et al.*, 1998) interact with the west coast shelf, causing water to be drawn offshore. A poleward undercurrent on the shelf and slope vary in strength and seasonal dependence (Nelson, 1989).

Much of the variability on the shelf around South Africa is consequently caused by the dynamics of the Agulhas Current, Benguela Current (and jet), and north–south seasonal migration of atmospheric high-pressure cells situated over the SE Atlantic and SW Indian Oceans (Figure 1a; Tyson and Preston-White, 2000). In winter, the westerly belt expands to the latitudes of southern Africa, causing strong westerly winds to dominate, with large swells. In summer, the westerly belt contracts south, and the wind field is then largely driven by the two anticyclones, causing coastal upwelling on the west coast and Agulhas Bank.

Chokka squid (*Loligo vulgaris reynaudii*) live within this diverse environment on the shelf between the Orange River and the Great Fish River (Figure 2). Seldom are squid found deeper than 200 m, and most of the biomass is over the Agulhas Bank. Egg masses recovered from fishing jigs and trawlers, as well as diver observations, indicate that spawning takes place on the narrower eastern Agulhas Bank in a distinct area between Plettenberg Bay and Port Alfred (Augustyn, 1990; Sauer *et al.*, 1992; Sauer and Smale, 1993; Sauer, 1995a, b; Roberts, 1998a). Such a discrete geographical location for spawning suggests an environmental niche there that suits either egg development or paralarva survival, or both. Should this be the case, then variability and uncharacteristic changes in this niche (ecosystem) could either weaken or strengthen the inherent biological advantages, and ultimately impact recruitment. This could explain, at least in part, the fluctuations in biomass and catch that impact the fishery (Figure 3).

To investigate this hypothesis, the approach taken was first to define the ecosystem in which chokka squid live, as quantitatively as possible. Using longshore gradients to synthesize this information, environmental advantages of the spawning grounds on the eastern Agulhas Bank were then identified. The cold ridge to the west supports the copepod maximum in the ecosystem (abundant food for squid paralarvae), and was investigated in detail to establish variability and uncharacteristic behaviour with implications for survival and recruitment of paralarvae.

Readers are referred variously to Figures 2, 4, 6, 7, 8 and 9 to identify the location of places mentioned throughout the text.

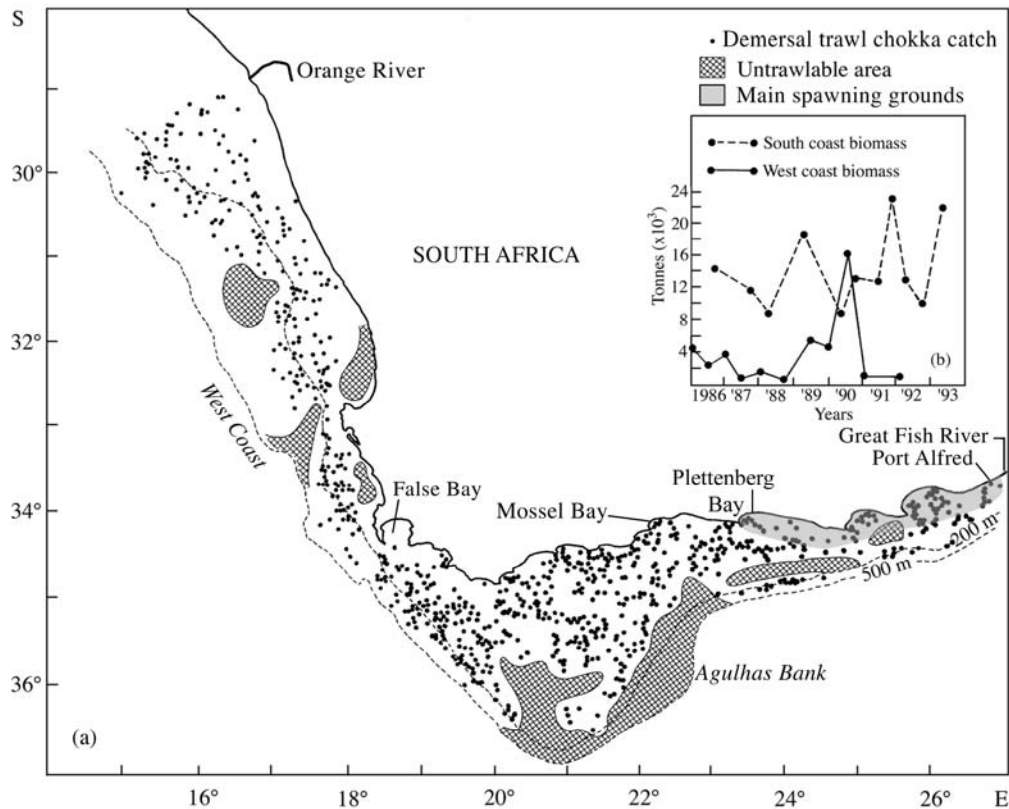


Figure 2. (a) Demersal trawl catches indicate that chokka squid (*Loligo vulgaris reynaudii*) are found on the west coast and Agulhas Bank to a depth of about 300 m. Most of the biomass is on the Agulhas Bank (insert b). The main spawning grounds are between Plettenberg Bay and Port Alfred.

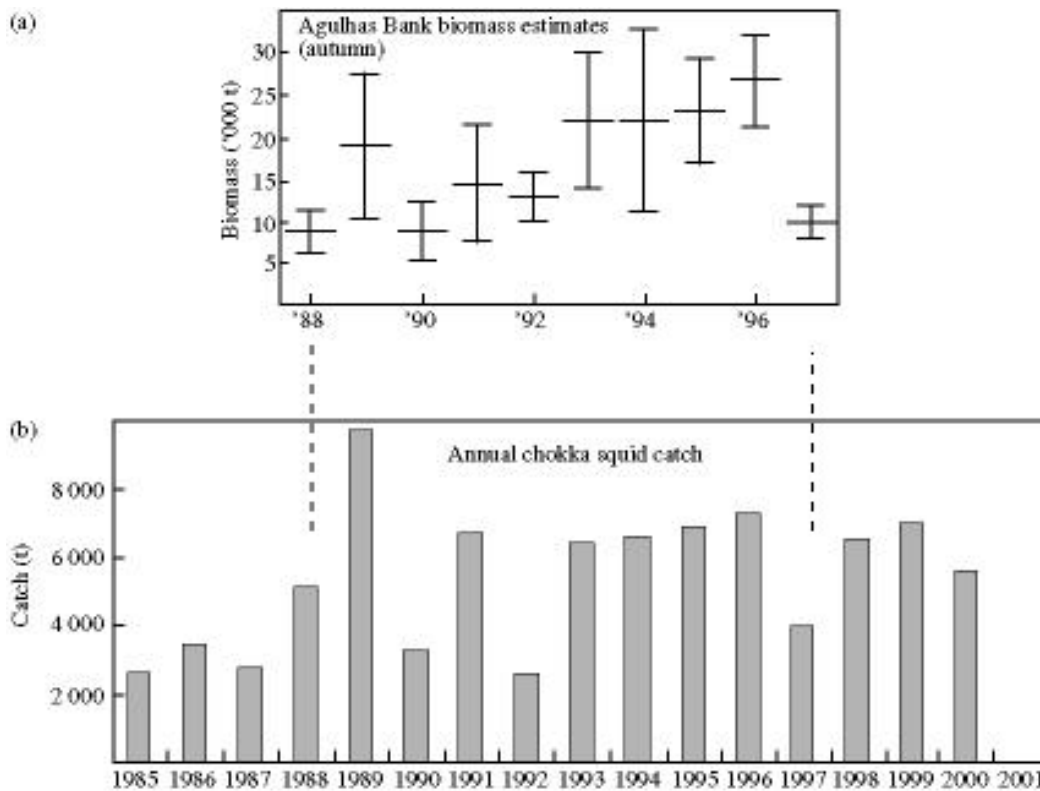


Figure 3. (a) The (autumn) chokka squid biomass on the Agulhas Bank is conservatively estimated to range between 8 000 and 28 000 t (no surveys were carried out for 1998–2000). (b) Annual catches appear to follow a similar trend to that in (a).

Data and methods

The study used both published and new data.

Squid biomass and catch

Estimates of chokka squid biomass and the jig catches of squid were taken from Roel (1998), and the Marine & Coastal Management (MCM) database respectively. Biomass estimates were calculated from demersal trawl surveys undertaken annually in the austral autumn (for survey detail, see Roel, 1998). There were no biomass surveys in 1998, 1999, or 2000. Jig catch statistics were derived from mandatory monthly catch return forms submitted by fishers (comments on the accuracy of these data are made by Roel, 1998, and Schön, 2000)).

Productivity

The mean horizontal distribution of chlorophyll was obtained from Brown and Cochrane (1991), and is augmented using composite Coastal Zone Colour Scanner (CZCS) data (see below). Copepod distribution data are limited, and are currently not available in suitable format for statistical analysis and mapping, so an impression of copepod biomass distribution was derived from a west coast (May 1991) and an Agulhas Bank (November 1989), which overlapped at Cape Agulhas. In both, copepod biomass was considered unusually high (J. A. Huggett, MCM, pers. comm.).

Oceanography

The most comprehensive published record of currents in the upper mixed layer for South Africa's west coast and Agulhas Bank are those of Boyd *et al.* (1992) and Boyd and Oberholster (1994). That work was based on ADCP (150 kHz) data collected by the FRS "Africana" and "Algoa" during May, September, and November of the years 1989–1994. The data are presented as average current vectors over 15'×15' blocks of longitude and latitude, and one specific set of data used for exemplification was collected during an anchovy (*Engraulis encrasicolus*) biomass survey in November 1992.

CTD and dissolved oxygen (DO) data for 86 surveys were extracted from the MCM oceanographic database. Since 1983, routine demersal biomass surveys have been undertaken in May and September on the Agulhas Bank (20–27°E), and in January and July on the west coast (29°S–20°E). Pelagic acoustic biomass surveys undertaken in November each year cover both coasts. Measurements were made with Neil Brown Mk 3 and 5 CTDs, with water samples taken at standard depths. DO was determined from water samples taken immediately after CTD retrieval using the Winkler titration method (Strickland and Parsons, 1972). Bottom CTD measurements were collected 3–10 m from the sea floor, depending on sea conditions, but ship size precluded stations in depths <30 m.

Data were statistically treated in 15'×15' blocks of longitude and latitude, though blocks with <3 stations were excluded from the analysis. Maps of bottom temperature and dissolved oxygen were produced depicting minima, means, and maxima.

SST data were collected at the entrance to the Knysna Lagoon. Until June 1994, they were collected daily using a bucket and mercury thermometer. Then, in April 1995, an electronic *mini Hugrun* underwater temperature recorder (UTR) was installed at the same site in a depth of 6 m. This instrument records the average hourly temperature (accuracy $\pm 0.01^\circ\text{C}$). Inter-calibration between these methods showed $<0.4^\circ\text{C}$ difference in the average data, and the same trends. Another SST data set was collected by a UTR located at Tsitsikamma, which yielded essentially the same monthly trends as at Knysna. All time-series of SST are ongoing (see www.oceanafrica.com).

Satellite imagery

The ocean colour image used here is a composite of *Nimbus-7* Coastal Zone Colour Scanner (CZCS) data collected between 1978 and 1986, sourced from

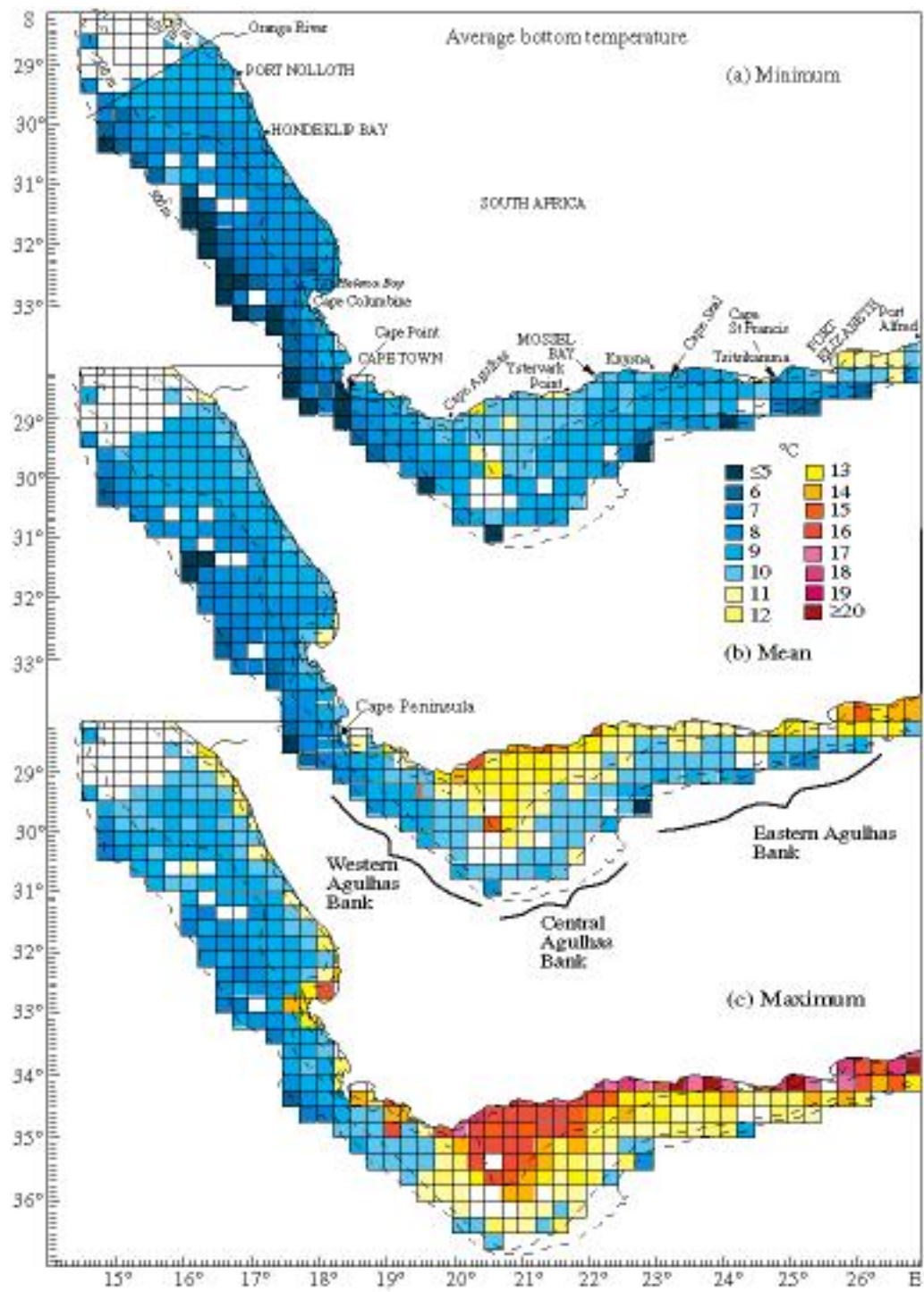


Figure 4. Bottom temperatures (°C) on the shelf between the Orange River and Port Alfred. (a) Minimum, (b) mean, and (c) maximum values are shown for each 15'×15' block.

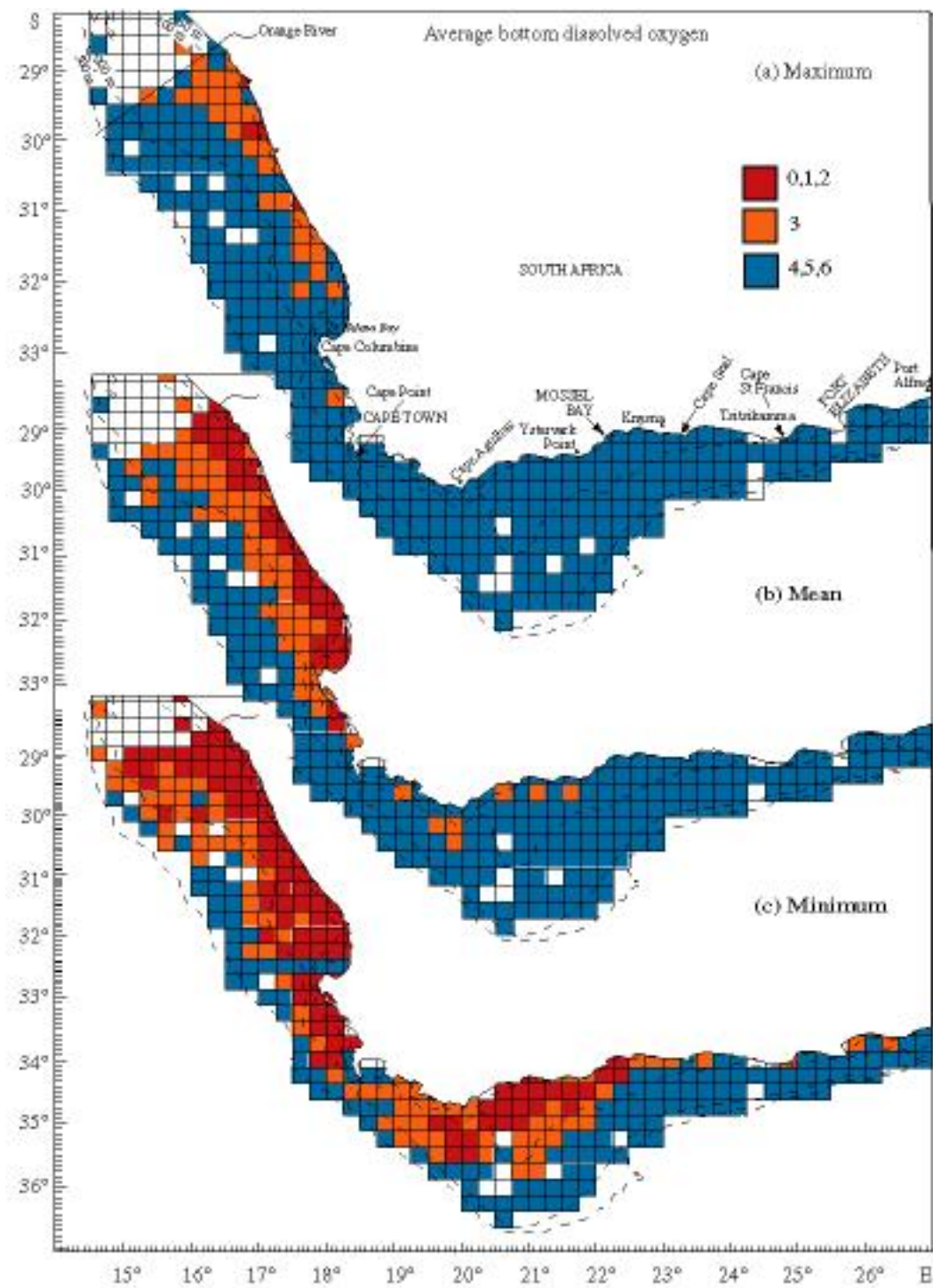


Figure 5. Bottom dissolved oxygen (ml l^{-1}) on the shelf between the Orange River and Port Alfred. (a) Maximum, (b) mean, and (c) minimum values are shown for each $15' \times 15'$ block.

www.seawifs.gsfc.nasa.gov/SEAWIFS/CSCZ_DATA. For the temporal analysis of the cold ridge, daily NOAA AVHRR images from 1985 to 1993 were used. In all, 420 cloud-free images were scanned visually for cold-water incursions onto the Agulhas Bank between 21 and 25°E.

West coast and Agulhas Bank ecosystem

Bottom temperature

The influence of temperature on egg development has been determined for a number of ommastrephid and loliginid squid species (e.g. Boletzky *et al.*, 1973; O'Dor *et al.*, 1982; Barón, 2002; Oosthuizen *et al.*, 2002). All showed that the rate of embryonic development increases at higher temperatures, until a threshold is reached and mortality occurs. Initial work on chokka squid by Augustyn *et al.* (1992) suggested egg mortality at temperatures <10°C and >24°C. More recently, however, Oosthuizen *et al.* (2002) demonstrated in laboratory trials that optimal temperatures for chokka squid egg development ranges between 12 and 17°C, and that outside of this, the proportion of embryonic abnormalities rapidly increase, resulting in mortality.

The colour maps in Figure 4 depict minimum, mean, and maximum bottom temperature (BT) for the west coast and the Agulhas Bank. The benthic environment on the west coast is dominated by low temperature. If all data between 30 and 500 m are included, then the range is 3.2–16.4°C. The average of the minimum BTs shown in Figure 4a is 7.7°C. The low temperatures reflect both quasi-permanent large-scale upwelling, and a deep shelf break at 400 m. In fact, almost half the west coast shelf is between 200 and 400 m, and BTs at such depths there range between 5 and 7°C (Figure 4a, c). At times, cold water (<7°C) can almost reach the coast (Figure 4a). Deeper than 100 m, BTs are higher, with an average around 10°C, but seldom exceed 11°C. The maximum BTs on the west coast are near Cape Columbine and St Helena Bay, between 14 and 15°C (Figure 4c).

In contrast, the Agulhas Bank benthic environment is warmer, with an overall average BT about 2.5°C higher (11.2 vs. 8.7°C). There too, the range of BTs between 30 and 500 m deep is greater, i.e. 3.3–22.1°C, a reflection of a shallower shelf break (200 m), the presence of the Agulhas Current, a wider shelf, and less intense coastal upwelling. BTs on the outer shelf are 2–3°C warmer on the Bank than over the west coast outer shelf, typically 9–10°C, and are maintained by shelf-edge upwelling induced by the dynamics of the fast flowing Agulhas Current (Lutjeharms *et al.*, 1989; Roberts *et al.*, submitted). Predictably, mean BT is highest (Figure 4b) adjacent to the coast, but also on the extensive shallow inner central Agulhas Bank, where the 100 m contour is >100 km offshore. Maximum BTs (Figure 4c) there can exceed 16°C, and data presented by Eagle and Orren (1985) show that BT is high mainly during winter, when storms and wave action erode the intense thermocline, resulting in isothermal mixing of the water column.

The distribution of BTs on the western Agulhas Bank reflect characteristics of both the west coast and the Agulhas Bank proper. The temperature range of the inner shelf is 9–16°C (Figures 4a, c), and the mean 10–11°C (Figure 4b). On the outer and mid-shelf, temperatures drop to 7°C, with maxima of about 10°C. There is a slight warming trend from west to east.

BTs at depths of 100 m are also high on the extreme eastern Agulhas Bank, east of 26°E. There, mean BT is 14°C, and the range 10–19°C. BTs are higher because of the shallower shelf (the 100 m contour moves to the shelf edge between Port Elizabeth and Port Alfred), and the influence of the warm Agulhas Current. Regions of high BT (i.e. <100 m deep) account for some 32% of the Agulhas Bank shelf, compared with just 5% of the west coast.

East of Port Alfred the shelf is narrow (<20 km) and strongly influenced by the Agulhas Current. Few oceanographic data have been collected there, but of those, Beckley and Van Ballegooyen (1992) showed that shelf BT increases in an eastward direction. There is a significant subsurface front on the inner shelf near the Mbashe River, east of which the BT ranges between 19 and 24°C. At 100 m, BTs are >18°C.

The benthic environment on the west coast, including inshore, is clearly too cold for successful development of chokka squid eggs, which require a range of 12–17°C. Such a temperature range is, however, found on the central and eastern Agulhas Bank in the extensive area shallower than 100 m. In terms of BT, the shelf between Port Alfred and the Mbashe River also appears to be suitable for

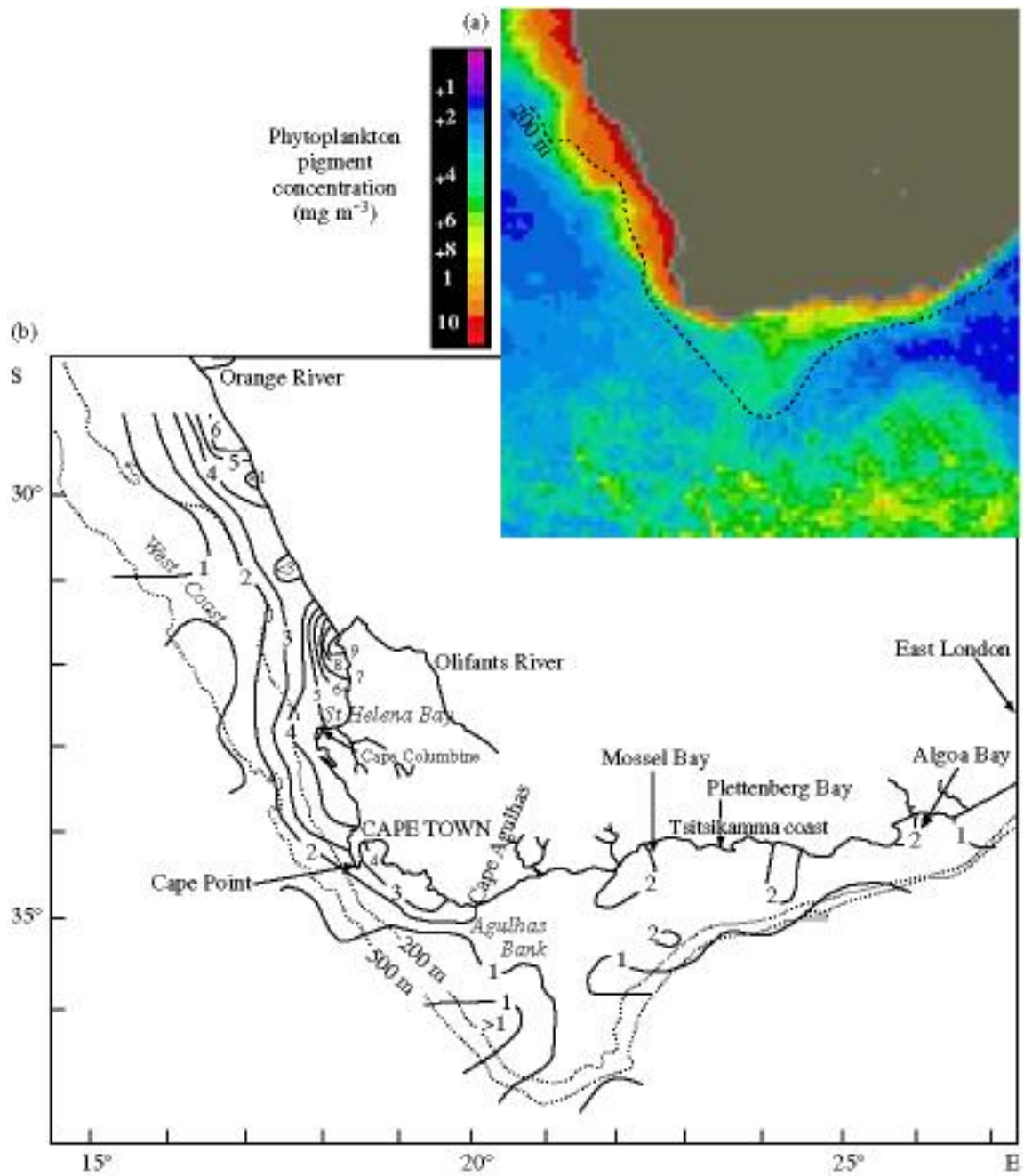


Figure 6. (a) Composite (1978–1986) of CZCS ocean colour satellite data, illustrating extensive high levels of chlorophyll on the west coast relative to those on the Agulhas Bank. (b) Mean distribution of chl-*a* in the upper 30 m, reproduced with modification from Brown and Cochrane (1991).

spawning, but temperatures approach the upper threshold for successful egg hatching. East of the Mbashe River, the BT is too high for hatching.

Bottom dissolved oxygen

De Mont and O'Dor (1984), O'Dor *et al.* (1994), and Pörtner and Zeillinski (1998) have demonstrated that the rate of metabolism of adult squid is high, perhaps 7× that of fish, demanding a good supply of

dissolved oxygen. Howell and Simpson (1994), working in Long Island Sound, showed that squid (*Loligo pealeii*) were not found where the bottom dissolved oxygen (BDO) was $<2.1 \text{ ml l}^{-1}$. Roberts and Sauer (1994) stated that adult chokka squid are not found inshore on the west coast where BDO is low, suggesting a threshold of 3 ml l^{-1} .

The results of a spatio-statistical analysis of BDO on the west coast and Agulhas Bank are given on Figure 5. As with temperature, there is a stark difference in BDO between the west coast and particularly the eastern Agulhas Bank, with the inner central and western Bank forming a transition zone of high variability. BDO on the West Coast is about 1 ml l^{-1} less than on the Agulhas Bank (3.39 vs. 4.24 ml l^{-1}).

The mean data in Figure 5b show BDO on the west coast to be commonly $<3 \text{ ml l}^{-1}$ on both the inner and mid-shelf, especially north of Cape Columbine. Maxima (Figure 5a) in many blocks do not exceed 3 ml l^{-1} at all on the inner shelf. In contrast, the bottom layer on the outer shelf is well oxygenated much of the time (Figure 5b) but, as indicated in Figure 5c, low BDO can at times almost extend to the shelf edge. Though not visible in Figure 5c, BDO can drop to almost zero on the inner and mid-shelf. In contrast, BDO in St Helena Bay ranges between 0.02 and 6 ml l^{-1} (Figure 5a, c), the largest range along the South African coastline.

Bottom water on the Agulhas Bank is well oxygenated (mean values in Figure 5b), especially on the eastern and outer central Bank, where minima are always $\geq 4 \text{ ml l}^{-1}$ (Figure 5c). This is likely due to the active shelf-edge upwelling along the inner boundary of the Agulhas Current (Chapman and Largier, 1989; Lutjeharms *et al.*, 1999; Roberts *et al.*, submitted). As a result, the bottom mixed layer on the eastern and outer central Bank contains Indian Ocean Central Water, with a BDO $\geq 4 \text{ ml l}^{-1}$.

As already mentioned, the western and inner central Bank have characteristics of both west coast and eastern Agulhas Bank. In the data set analysed here, the minimum BDO for the region east of 20°E is 1.36 ml l^{-1} , substantially higher than on the west coast. If the western Bank (Cape Point to Cape Agulhas) is included, then the lowest BDO is 0.22 ml l^{-1} . The transient (seasonal) nature of low BDO on the western and inner central Bank is evidenced by comparing minima (Figure 5c) and maxima (Figure 5a). This data set also shows that BDO on the inner central Bank is highest of all parts of the Agulhas Bank, $\geq 6 \text{ ml l}^{-1}$. Only St Francis and Algoa Bays have similar high levels. Work by Chapman and Largier (1989) and Eagle and Orren (1985) showed low BDO usually on the inner central Bank during late summer and autumn, when the thermocline is most pronounced.

These data, allied to the requirements for egg development, show why chokka squid do not use the west coast or western Bank for spawning. BDO (and BT) is optimal for chokka squid spawning over the eastern Bank throughout the year, or over the inner central Agulhas Bank in early summer before BDO drops. The latter area would then be considered fringe spawning.

Phytoplankton (chlorophyll) distribution

Chokka squid recruitment is dependent on survival of their paralarvae. Once hatched, paralarvae are at risk from starvation, predation, and advective loss, the last of these significant in the context of chokka squid because the spawning grounds are close to the fast-flowing Agulhas Current. Little is known about predation levels on squid paralarvae, but starvation may be a very important control. Chokka squid paralarvae are thought to feed mainly on copepods (Venter *et al.*, 1999), whose spatial distribution and abundance is driven by the oceanography and concomitant primary production.

Numerous studies of primary production have been undertaken on the west coast, but fewer on the Agulhas Bank (e.g. De Jager, 1957; Shannon *et al.*, 1984; Shannon and Field, 1985; Mitchell-Innes, 1988; Brown and Cochrane, 1991; Brown, 1992; McMurray *et al.*, 1993; Probyn *et al.*, 1994). Collectively, these studies demonstrate that the west coast, with its large-scale upwelling, is the most productive region around southern Africa. This fact is illustrated in the ocean colour image of chl-*a* shown in Figure 6a, a 9-year composite of *Nimbus-7* CZCS satellite imagery. The orange and red colours indicate high levels of chlorophyll ($2\text{--}10 \text{ mg m}^{-3}$) at the surface. Blue indicates very little chlorophyll ($\sim 0.15 \text{ mg m}^{-3}$). High levels of chlorophyll on the west coast extend along the entire coast and well onto the wide shelf (the shelf break is at 400 m), the highest predictably inshore, yielding a distinct cross-shelf gradient. By comparison, chlorophyll distribution on the Agulhas Bank is limited. Levels are highest on the eastern Bank adjacent to the coast between Algoa and Mossel Bays,

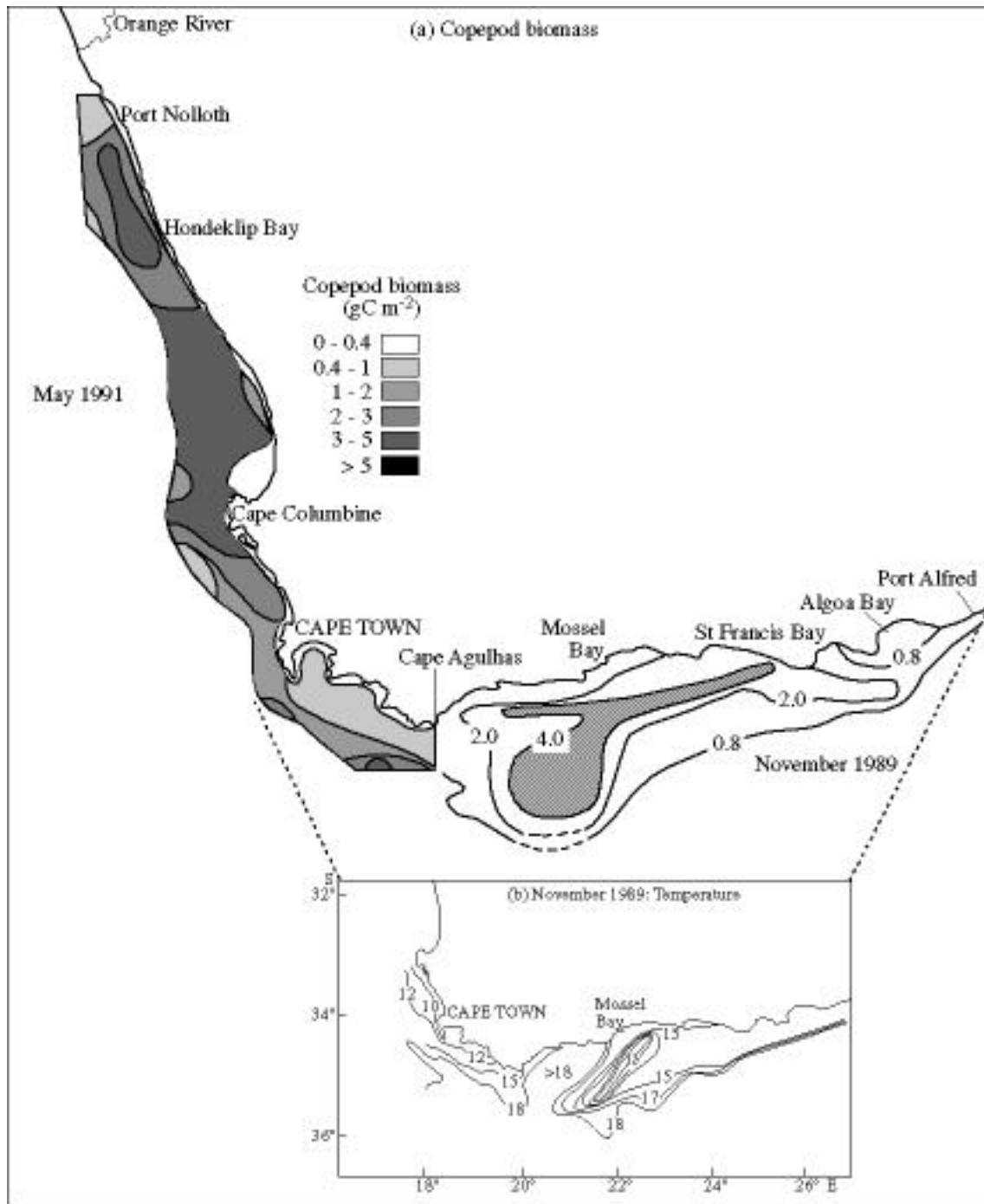


Figure 7. (a) Composite distribution of copepod biomass between the Orange River and Port Alfred during two surveys (denoted by different shading). (a) West coast (May 1991) and Agulhas Bank (November 1989). Data are joined at Cape Agulhas (20°E). (b) Subsurface temperatures at a depth of 20 m show a ridge of cold upwelled water off Mossel Bay.

noticeably low west of Mossel Bay, and at intermediate level (green, $\sim 0.5 \text{ mg m}^{-3}$) offshore over the central Bank.

The same observation was made by Brown and Cochrane (1991), who published a large-scale (Orange River–Port Alfred) perspective on mean chl-*a* in the upper 30 m (Figure 6b). They used a data set covering the years 1971–1989, including data used earlier by Shannon *et al.* (1984). The map in Figure 6b is constructed from mean concentrations of chl-*a* measured *in vitro*, either spectrophotometrically or fluorometrically, for half-degree blocks of latitude and longitude. For the west coast and western Bank, the chlorophyll distribution shown in Figure 6b is consistent with that depicted in Figure 6a, correlating with known local upwelling patterns (Shannon, 1985). The cross-shelf gradient is strong, with levels $\leq 1 \text{ mg m}^{-3}$ near the shelf edge, and $\geq 4 \text{ mg m}^{-3}$ adjacent to the coast. Chlorophyll is also high near the mouth of the Olifants River, likely influenced by agricultural run-off, which is not seen in the satellite composite. Chlorophyll concentration over the central and eastern Bank is considerably lower than on the west coast, mainly between 1 and 2 mg m^{-3} . There are a few areas $> 2 \text{ mg m}^{-3}$ inshore, notably near Mossel Bay, Tsitsikamma, and Algoa Bay, all within the coastal upwelling regions along the coast, and corresponding with the relatively high chlorophyll seen in Figure 6a. The intermediate chlorophyll levels observed in the satellite composite over the central Bank are also clear on Figure 6a, but the *in situ* mean values are 2–3 times greater. Although primary production on the Agulhas Bank is less extensive than along the West Coast, chlorophyll concentrations of 6–12 mg m^{-3} are found between Plettenberg Bay and Algoa Bay (Figures 14 and 15 of Shannon *et al.*, 1984).

Zooplankton

Chokka squid paralarvae seemingly prey mainly on copepods (Venter *et al.*, 1999), of which two species are abundant around southern Africa, *Calanoides carinatus*, which dominates the cold Benguela upwelling system of the west coast, and *Calanus agulhensis*, which inhabits the warmer and relatively more stable waters of the Agulhas Bank (Huggett and Richardson, 2000). Irrespective of species, copepod biomass is generally greatest on the west coast.

Huggett (2003) produced large-scale distribution maps of copepod biomass. For the purposes of this study, however, a more appropriate impression of copepod abundance is gained from the map shown in Figure 7, which combines two different surveys: to the west coast in May 1991, and to the Agulhas Bank in November 1989. These were selected from a number of unpublished surveys for their abundance of copepods, which highlights several characteristics. For instance, copepod biomass is extensive on the west coast, with large areas in the range 3–5 gC m^{-2} , and not just inshore, where upwelling and primary production are most intense. Similarly on the Agulhas Bank, copepod biomass is greatest over the mid- and outer shelf, though more restricted than on the west coast. This distribution is aligned with the main upwelling region high in chlorophyll on the south coast between Knysna and Tsitsikamma, as well as confirming the intermediate levels of chlorophyll over the central Bank clear in Figure 6a.

Copepod biomass on the Agulhas Bank appears to be $\sim 4 \text{ gC m}^{-2}$, almost equivalent to that on the west coast. However, biomass is low east of St Francis Bay and over the outer shelf, possibly the result of the oligotrophic Agulhas Current and an associated advective loss. Several authors (e.g. Largier *et al.*, 1992; Peterson *et al.*, 1992; Verheye *et al.*, 1992, 1994; Boyd and Shillington, 1994; Peterson and Hutchings, 1995; Hutchings *et al.*, 1995) mention that high densities of copepods on the central Bank are associated with a quasi-permanent, shallow, subsurface ridge of cold upwelled water off Mossel Bay, seen in Figure 7b. Huggett and Richardson (2000) quantitatively demonstrate this association in their Figure 2, which used data from three cruises (1988, 1989, 1990). More recent data and analyses in Huggett (2003) support this. Boyd and Shillington (1994) suggest that cyclonic circulation around the cold ridge may enhance local retention of copepods.

Alongshore environmental gradients and spawning habitat

The alongshore gradients depicted in Figure 8 offer a means by which the information presented above can be simplified and viewed coherently in relation to the spawning grounds. Factors that affect

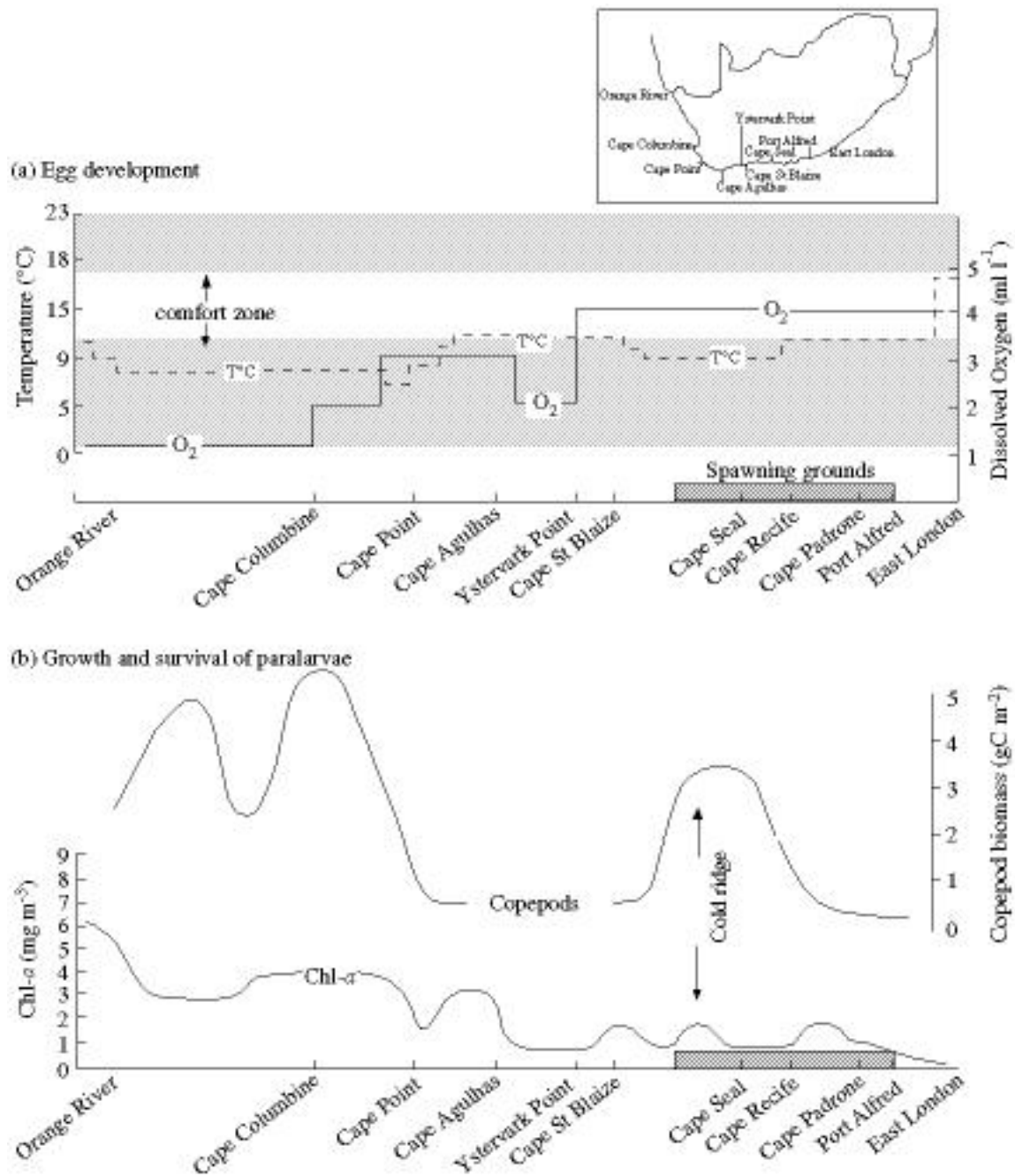


Figure 8. Alongshore gradients around the coast between the Orange River and East London in relation to the main chokka squid spawning grounds. (a) Minimum levels of bottom temperature and bottom dissolved oxygen. (b) Phytoplankton and copepod concentrations. Data taken from Figures 4a, 5c, 6b, and 7a, approximately 15 miles from the coast.

the eggs and the paralarvae have been separated. Gradients were constructed using data at a distance of ~15 nautical miles from the coast, extracted from Figures 4a, 5c, 6b, and 7a. This is the closest inshore measurement possible, given the spatial scales used, although it is acknowledged that such a distance offshore may not correctly portray some shallow inshore environments (e.g. embayments), so some misinterpretation is possible.

The alongshore gradient of BT in Figure 8a suggests that squid can hatch successfully only between Cape Point and Cape St Blaize, and between Cape Recife and just west of East London, because minimum temperatures elsewhere are outside the optimal temperature range (12–17°C) for embryonic development (the shaded zone in Figure 8a). From East London eastwards, BT increases above 19°C, too warm for successful embryonic development. This potential spawning habitat is reduced when BDO is considered; adult squid are generally not found where BDO is $\leq 3 \text{ ml l}^{-1}$. Low BDO excludes the west coast as spawning habitat, but also the region between Cape Agulhas and Ystervark Point. The strong seasonality of low BDO in the latter region could mean that it is not always unsuitable for spawning. It is questionable whether the western Bank (Cape Point–Cape Agulhas) offers suitable habitat, because the minimum BDO approaches the 3 ml l^{-1} critical threshold. Of importance in this study is the fact that the main spawning grounds between Plettenberg Bay and Port Alfred are positioned where the BDO is almost always $\geq 4 \text{ ml l}^{-1}$.

There is a declining west–east trend in chlorophyll (Figure 8b), and hence phytoplankton. To some extent, the copepod biomass gradient follows that of chlorophyll, with concentrations highest on the west coast. Such a region could be good for squid paralarvae because food is plentiful, but Forsyth (1993) showed that low temperatures retard growth of squid paralarvae and juveniles. Over the Agulhas Bank, though, most of the copepod biomass is centred off the coast between Tsitsikamma and Mossel Bay, with biomass low to either side. The main spawning grounds of chokka squid are positioned on the eastern side of this maximum, resulting in some mismatch between place of hatching and location of abundant food. This is suboptimal compared with BT and BDO, which are well matched with the sites of egg deposition. Therefore, it would appear that the position of the spawning grounds favours egg development over survival of paralarvae.

BT, BDO, and chlorophyll are based on statistical data, so the conclusions can only be seen as generalized. In the case of copepods, specific survey data were used. In a complex, dynamic, marine system such as that surrounding southern Africa, great variability will exist in these parameters on daily, seasonal, and longer time-scales. Accordingly, the gradients shown in Figure 8a could vary, and suitable spawning habitat may be found sometimes outside the main region identified here. This could explain why eggs are found occasionally in False Bay and near East London, i.e. fringe spawning. Conditions within the main spawning grounds too may occasionally be adverse and discourage spawning, perhaps also promoting fringe spawning.

Perhaps the gradients shown in Figure 8 are used by mature adults to find the spawning grounds. It is known now that some species of fish make use of natural (magnetic, physical, and chemical) fields for navigation (Dingle, 1996).

Currents and western transport

Currents can play important roles in the life cycle of some squid species, e.g. *Illex illecebrosus*, *Illex argentinus*, *Todarodes pacificus*, and *Ommastrephes bartramii* (see Roberts *et al.*, 1998). With all these ommastrephids, western boundary currents transport free-floating eggs and paralarvae from the spawning grounds in subtropical regions to feeding grounds in temperate climes several thousand kilometres away (O’Dor and Dawe, 1998). For example, *Illex illecebrosus* spawn off the Florida coast, and their translucent gel balloons about 100 cm in diameter, containing 50 000–100 000 eggs, settle to neutrally buoyant depths of typically 200–400 m in the Gulf Stream, where temperatures are optimal for embryonic development (O’Dor and Balch, 1985). By the time they hatch, the paralarvae have been transported to the food-rich Grand Banks, where they remain until maturity. In the case of loliginid squid, there are no known cases where currents play a similar role, but the life cycles of loliginids are less understood. The environmental gradient analysis in this study indicates a mismatch of a few hundred kilometres between the main spawning grounds of chokka squid and optimal feeding for paralarvae to the west. Although on a smaller scale, this is analogous to the life cycle of the

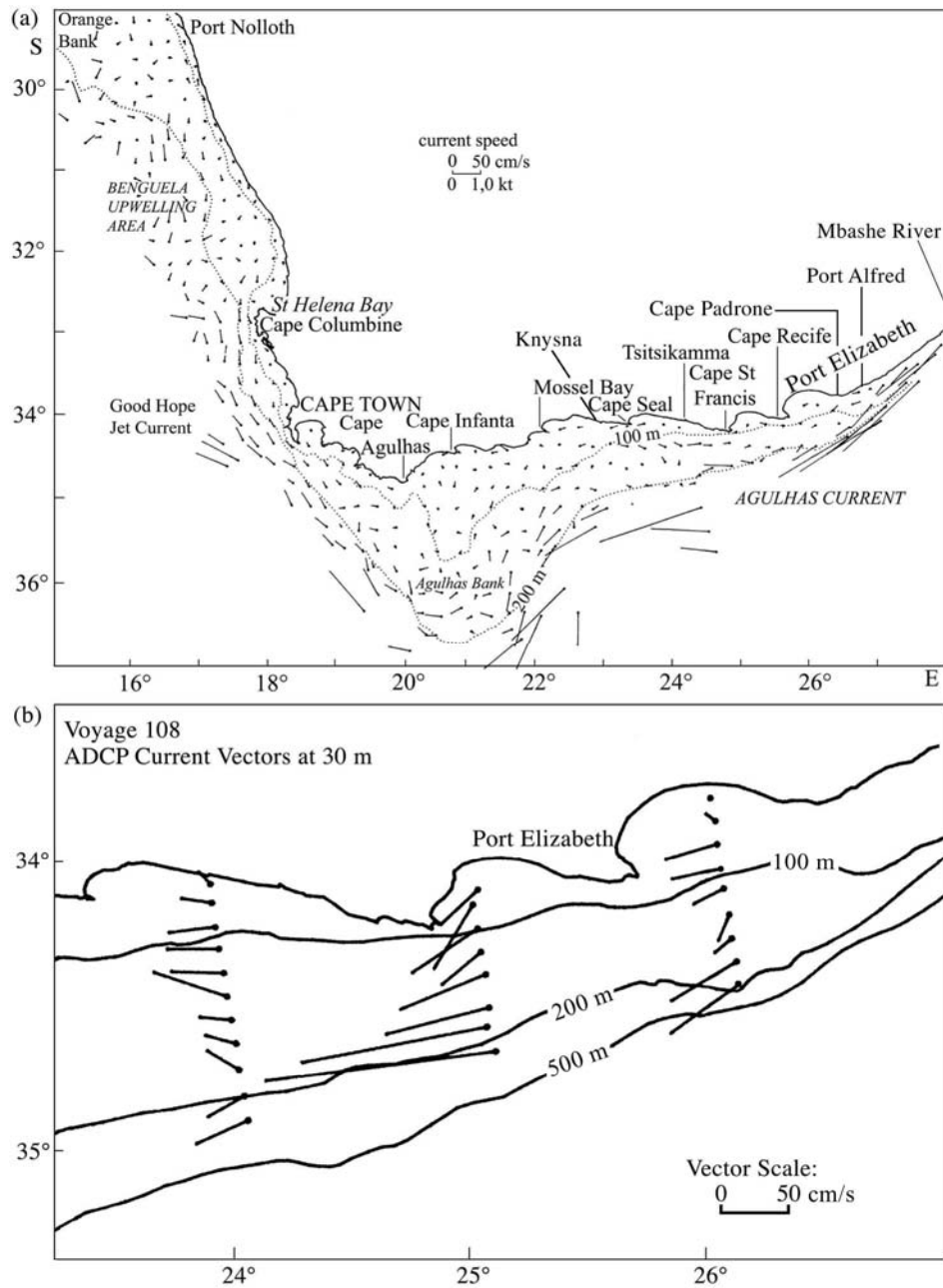


Figure 9. (a) Average currents at a depth of 30 m on the west coast and the Agulhas Bank. Data were collected between 1989 and 1994 using ship-borne ADCPs and averaged over 15'×15' blocks of longitude and latitude (reproduced from Boyd and Oberholster, 1994). The direction of current is away from the dot. (b) ADCP data collected at 30 m during cruise 108 in November 1992.

ommastrephids mentioned above, and it may suggest that currents provide a critical link in the life cycle of chokka squid.

Shelf currents are usually less defined and more difficult to understand than western boundary currents. Until 1990 knowledge of the current patterns on the eastern Agulhas Bank was limited to inferences from bathythermograph plots (Bang, 1970), a synthesis of ship-drift measurements collected between 1959 and 1964 by Harris (1978), a study of drift cards by Lutjeharms *et al.* (1986), several unpublished shallow current-meter records in Algoa Bay, and the results of a cruise analysed by Goschen and Schumann (1988). Data acquisition was greatly improved when Acoustic Doppler Current Profilers (ADCPs) were installed on South Africa's research ships "Africana" and "Algoa" in 1989. The technique gave wide data coverage, but lacked temporal resolution, with only three surveys made annually. A substantial part of this data set was analysed and presented by Boyd *et al.* (1992), Boyd and Oberholster (1994), and Boyd and Shillington (1994), and it remains spatially the most comprehensive work published to date.

For this study, average (15'×15' blocks) current vectors at a depth of 30 m, presented in Boyd and Oberholster (1994), are reproduced in Figure 9a. Deeper currents at 50 m showed a similar pattern, indicating barotropic conditions. A number of flow domains can be observed. The fast-flowing Agulhas Current ($>100 \text{ cm s}^{-1}$) clearly dominates the offshore oceanography over the Agulhas Bank ($>200 \text{ m}$). Actual velocities can range between 150 and 350 cm s^{-1} (Boyd and Shillington, 1994). East of Port Alfred, the current strongly influences the narrow shelf environment, but this influence decreases as the shelf widens onto the eastern Bank (Goschen and Schumann, 1988).

On the eastern Bank, velocities reduce considerably, with average currents typically $20\text{--}30 \text{ cm s}^{-1}$. The net flow pattern is complex, particularly towards the central Bank. Average vectors on the mid-shelf indicate net westward flow in the upper layer, at times clear in ADCP survey data, e.g. cruise AA 108 depicted in Figure 9b. The average vectors show net westward flow on the mid-shelf moving also southwards near 23°E (Cape Seal), and around the inner central Bank to continue northwestwards along the narrower western Bank. Boyd and Shillington (1994; Figure 8a) showed the same. In Figure 9b, westward flow dominates the entire eastern Bank, but the incoherent and zero average vectors near the eastern Bank, shown in Figure 9a, indicate great variability in flow direction. The same is found on the inner central Bank, i.e. $<100 \text{ m}$ between Cape Agulhas and Cape Seal. Weak circulation is expected there, because BDO is low during summer (see above). Between Mossel Bay and Cape Seal, there is a narrow coastal eastward flow, shown by average vectors.

Western transport hypothesis

In light of these data on currents and the environmental gradients, it may well be that the spawning grounds for chokka squid are positioned not only to exploit optimal bottom temperatures, but also to use the net westward current on the eastern Bank to link hatching site with food maxima located to the west, off the Knysna–Tsitsikamma coast. Such a strategy would optimize the chances of survival during early life. Passive transport of hatchlings in this net flow would be at average speeds of $18\text{--}25 \text{ km d}^{-1}$. Actual currents on Figure 9b indicate transport speeds of $35\text{--}43 \text{ km d}^{-1}$. This implies that paralarvae as far away as Algoa Bay would take an average of 4–7 days to reach the site of favoured food, or 3–5 days in the case of Figure 9b. Such time-spans match the results of Vidal *et al.* (2002), who reported that *Loligo opalescens* hatchlings initially undergo a "no net growth phase", while dependence on the internal yolk diminishes and prey capture success increases. This they state to be a critical period in the early life history. *In vitro* prey-starved hatchlings lived between 4 and 6 days utilizing internal yolk, depending on ambient water temperature. This implies, assuming similar behaviour, that chokka squid hatchlings can survive while in transport to the richer feeding grounds.

On the western side of the copepod maximum, any fringe spawning between Mossel Bay and Cape Seal would benefit from the narrow eastward coastal current shown in Figure 9a. Currents may also define the eastern boundary of the chokka squid spawning grounds near Port Alfred. This limit may not necessarily be due to higher BTs, as stated earlier, but perhaps a consequence of the strong influence of the Agulhas Current there, as well as the potential removal of hatchlings from the eastern Agulhas Bank ecosystem (Lutjeharms *et al.*, 1986).

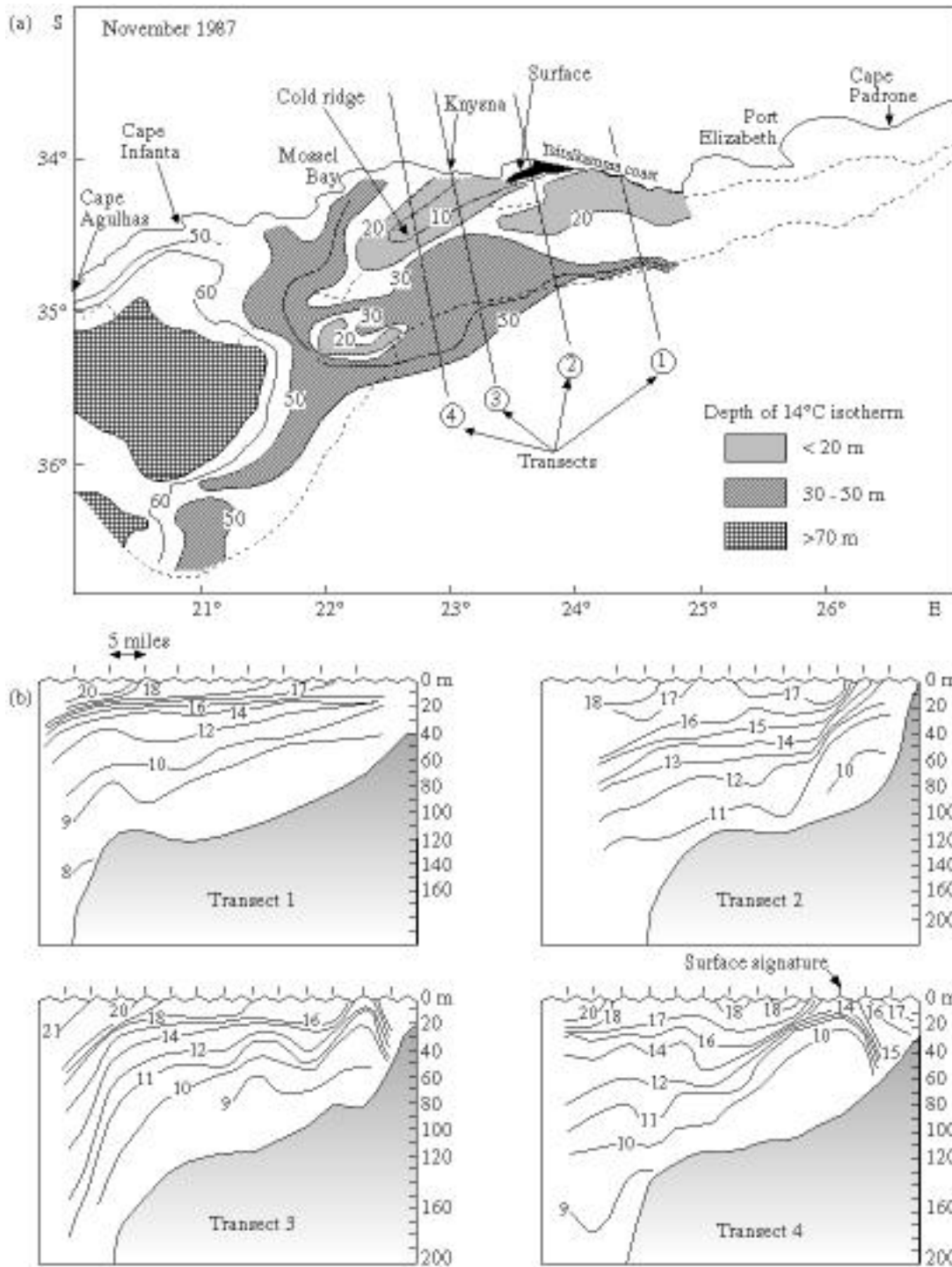


Figure 10. (a) Depth (m) of the 14°C isotherm on the central and eastern Agulhas Bank highlights upward doming of the thermocline off Knysna in November 1987, a feature commonly referred to as a cold ridge. (b) Transect 2 shows upwelling at the coast. Transects 3 and 4 show a doming in the temperature structure through the cold ridge. Transect 1 is through an upwelling plume farther east.

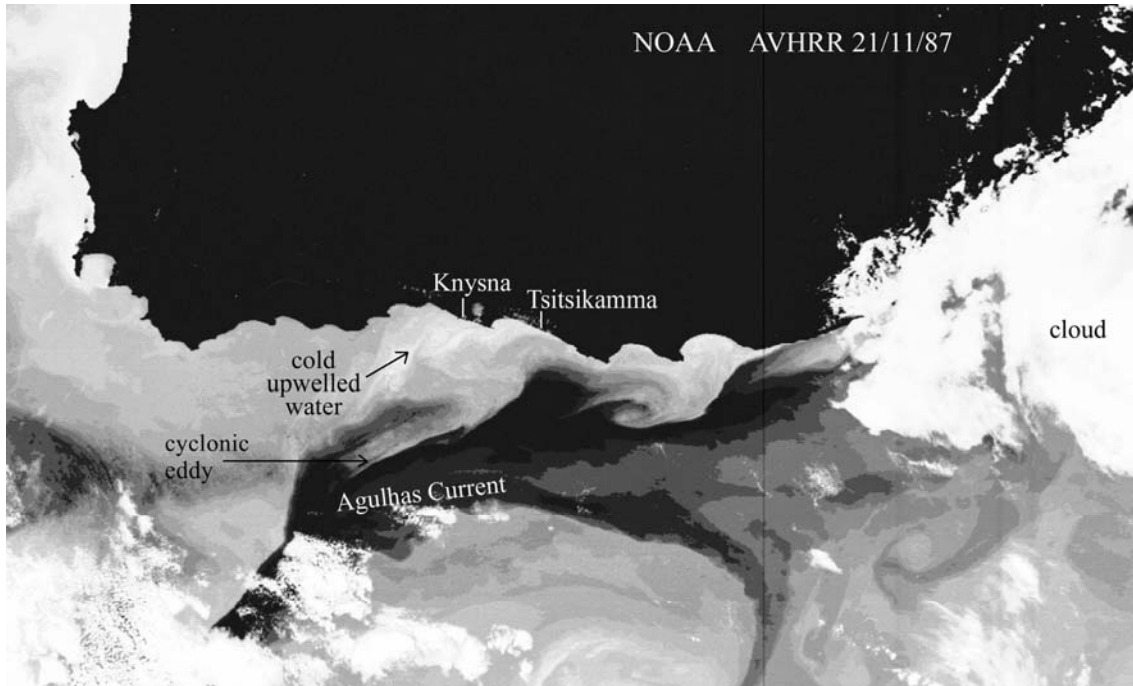


Figure 11. The cold ridge depicted in Figure 10 has a surface signature seen in this SST satellite image. Light grey indicates cold water, dark grey/black warm Agulhas Current water. Note the coincident existence of a cold core cyclonic eddy south of the cold ridge.

The cold ridge and ecosystem changes

The copepod maximum on the Agulhas Bank shown in Figure 7a is commonly associated with a subsurface ridge of colder water (Figure 7b), i.e. an upward doming of the thermocline. This is believed to underpin the enhanced secondary production found there (Largier *et al.*, 1992; Probyn *et al.*, 1994; Verheye *et al.*, 1994), and was first observed and noted by Largier and Swart (1987), and subsequently by Boyd and Shillington (1994), and Carter *et al.* (1987). No description of this feature is conclusive, but the doming implies movement of nutrient-rich bottom layers towards the surface, undoubtedly stimulating primary production.

Several mechanisms have been proposed for the forcing of this prominent, central, oceanographic feature. Swart and Largier (1987) suggested that either up-slope veering of the bottom boundary layer along the shelf edge of the eastern Bank (owing to side-wall friction) could cause mid-shelf upwelling, or perhaps that cross-current Ekman transport attributable to sustained wind stress by westerly winds on a laterally sheared flow could be the driving force. Such mechanisms would be time-dependent, and related to the position of the inner margin of the Agulhas Current. Boyd and Shillington (1994) also suggested, on the assumption that the outer shelf is dominated by the Agulhas Current and the inner shelf flow by wind-forcing, that the widening of the shelf between Port Elizabeth and Knysna may be responsible for the cold ridge. The divergent nature of the resulting flow could cause upwelling of the thermocline in the shelf interior, resulting in cyclonic circulation. Boyd and Shillington (1994) analysed November cruise data between 1987 and 1991, found that the cold ridge was not always present, and suggested a connection between its development and coastal upwelling. To date, however, all mechanisms remain speculative.

Given the significance of the cold ridge in the Agulhas Bank ecosystem, and in particular the potential role it plays in chokka squid spawning, it is important that its driving forces and dynamics are better understood. From new evidence given below, it may be that the cold ridge is just an intermittent upwelling filament that originates at the coast as a consequence of wind-driven coastal upwelling. The typical configuration observed in Figure 7b may be formed by the advection of a cold-water plume in a southwest direction by the shoreward edge of the prevailing westward shelf current described in Figure 9.

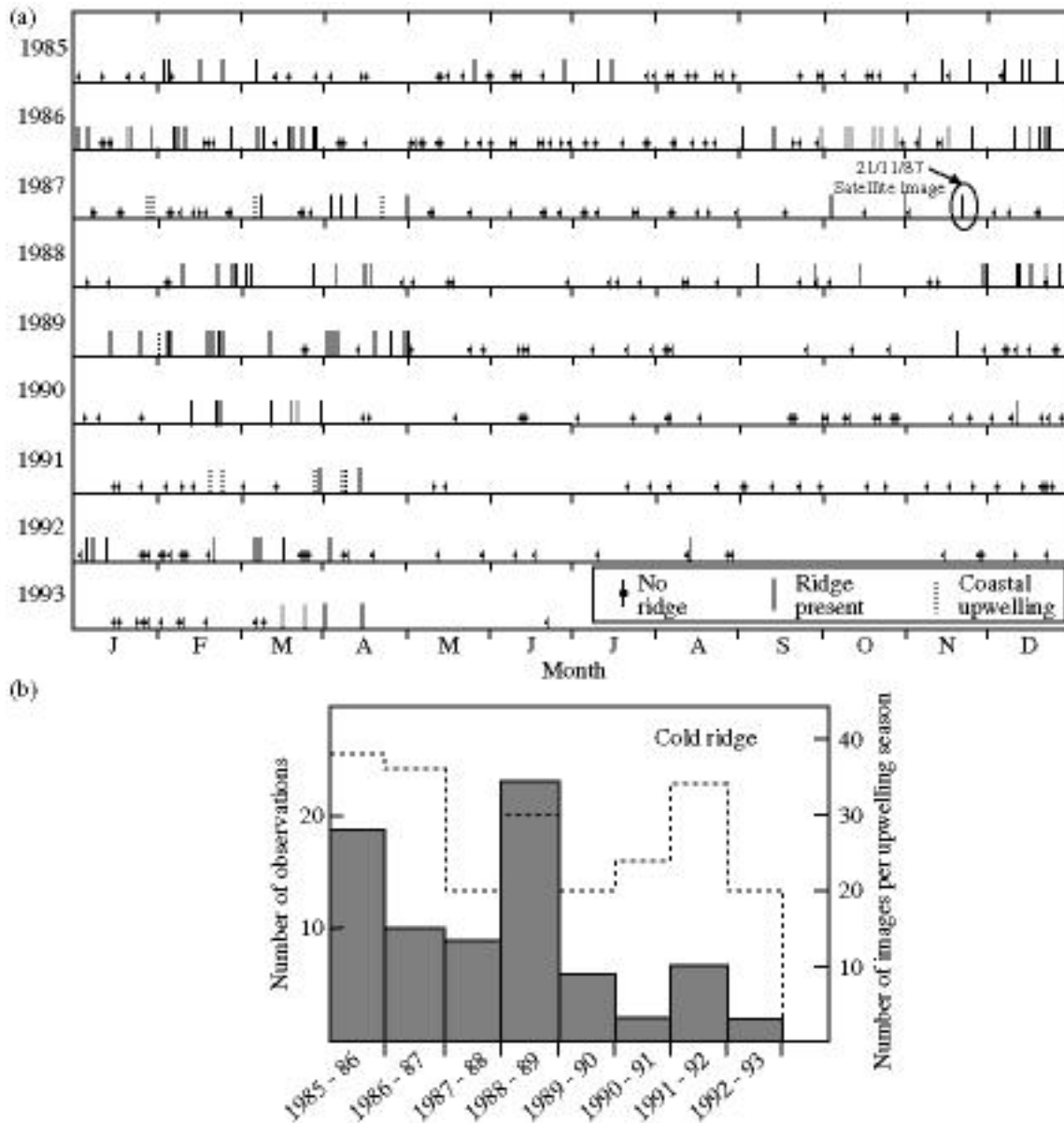


Figure 12. (a) Analysis of 420 cloud-free NOAA SST satellite images (AVHRR) between January 1985 and April 1993 indicates that the cold ridge is mainly found during summer (November–April). (b) Number of observations of the cold ridge per summer. With the exception of 1988–1989, there appears to be a declining trend over the period.

Such a situation is depicted by the depth plot of the 14°C isotherm (November 1987) in Figure 10a. This isotherm was chosen because it reflects the middle of the thermocline (see transects). The cold ridge is seen as a prominent, sloping, tongue-like, thermal structure that surfaces at the Tsitsikamma coast. A vertical temperature section (Transect 2; Figure 10b) taken across the cold coastal core (i.e. the upwelling plume) confirmed upwelling against the coast. The vertical sections for Transects 3 and 4 show a dome effect in the thermal structure, denoting cold coastal water moving offshore onto the shelf. Subsidence of the 14°C isotherm to a depth of about 10 m implies some warming in the filament’s surface layer, probably through a combination of insolation, sinking of dense cold water, and turbulent mixing with adjacent surface waters. Nonetheless, the surface water of the filament remained colder than the surrounding water.

The colder surface water of the filament conveniently provides a signature that is seen in thermal satellite imagery. For the above case, this is shown in Figure 11, which depicts a substantial filament (light grey) extending well onto the shelf. Bearing in mind that a ship's survey is not synoptic, the configuration of this filament is well matched with the subsurface thermal structure shown in Figure 10. Interestingly, the outer reaches of the cold ridge filament extend to, and possibly interact with a large Agulhas Current cyclonic eddy (dark grey), clearly visible in Figure 11. These eddies have a cold core (Lutjeharms *et al.*, 1989), seen in the thermal structure in Figure 10a as an isolated thermocline rise immediately south of the cold ridge.

The sea surface temperature in Figure 11 depicts the filament emanating from the coastal upwelling zone. Coastal upwelling on the Agulhas Bank is common during summer, and is driven by seasonal easterly winds (Schumann *et al.*, 1982). Upwelling is initiated on the western side of the prominent capes of Cape Padrone (just west of Port Alfred), Cape Recife, and Cape St Francis, and along the coastline between Tsitsikamma and Knysna (Figure 9), because the orientation is such that the easterly wind has an offshore component, which combined with Ekman transport and the steep and prominent bathymetry, readily draws cold bottom water to the surface within the inertial period of 21 h (for this latitude). Minor upwelling also occurs at the smaller capes between Mossel Bay and Cape Agulhas. Satellite imagery and *in situ* measurements show that coastal upwelling is most extensive and intensive, however, between Tsitsikamma and Knysna, commonly with plumes of cold surface water that extend 10–40 km offshore, with surface temperatures of 11–15°C (see Schumann *et al.*, 1982; Largier and Swart, 1987; Schumann, 1999).

The dependence of the cold ridge on wind-driven coastal upwelling is further demonstrated in Figure 12, in which an analysis of 8.5 years of cloud-free AVHRR satellite imagery is displayed. This encompasses the event surveyed in Figure 11 (indicated). Figure 12a shows the cold ridge mainly during summer upwelling, between November and April. However, the cold ridge, or filament, is not always formed, despite intensive coastal upwelling (e.g. see October 1986). This indicates that offshore advective forces are necessary for the formation of the classical cold ridge feature.

As already stated, net surface flow on the eastern Bank is westwards, then offshore (to the southwest) near Knysna. The flow continues onto the outer central Bank. This pattern is possibly caused by the dissimilar flow of water on the inner central Bank (shown in Figure 9a). Under such circumstances, an upwelling plume off the Tsitsikamma–Knysna coast would similarly be advected on the inshore edge of this westward flow, giving rise to the typical cold ridge configuration seen in Figures 10 and 11. The plume, more adequately described then as a filament, would exist on the boundary between the westward flow and the inner central Bank, typically overlying the 100 m contour. The physics at this interface may act to sustain the doming in the thermal structure, and maintain the cold ridge. Also, the possible impact of the small eastward coastal flow off Mossel Bay, which causes a deepening of the thermocline inside the cold ridge, needs to be borne in mind. If the interface between the westward flow and the inner central Bank did not exist on the 100 m contour, then a cold-water plume would remain closer to the coast, and have a thermal structure similar to the upwelling plume observed to the east in Figure 10a, i.e. Transects 1 and 2, in which no doming of the thermocline is seen.

Given the gaps in satellite imagery, it is not possible to comment with certainty on the temporal variability of the cold ridge. However, it does appear that the feature lasts for periods of several days to weeks. In some summers, it appears to be a semi-permanent feature, e.g. 1988–1989, but as seen in Figure 12b, that case is anomalous. Besides this anomaly, there is also an interesting declining trend in the number of observations of the cold ridge over the years 1985–1993. This, demonstrated by the dashed line in Figure 12b, is not altogether due to a decline in the number of cloud-free images, but could be caused by decade-scale changes in either the upper layer flow regime on the eastern Bank, or coastal upwelling intensity (and wind field).

Another means of observing temporal variability in the cold ridge is found in the monthly average times-series of sea surface temperature (1975–2001), shown in Figure 13. These ongoing *in situ* measurements were made at Knysna, within the upwelling region that feeds the cold ridge filament (see Figures 10, 11). However, as already stated, coastal upwelling does not necessarily imply formation of the cold ridge, so some caution needs to be exercised when using this method.

The data in Figure 13 show clear cyclical warming of coastal waters during summer, and cooling during winter. However, there were conspicuous anomalies in the summers of 1988–1989, 1993–

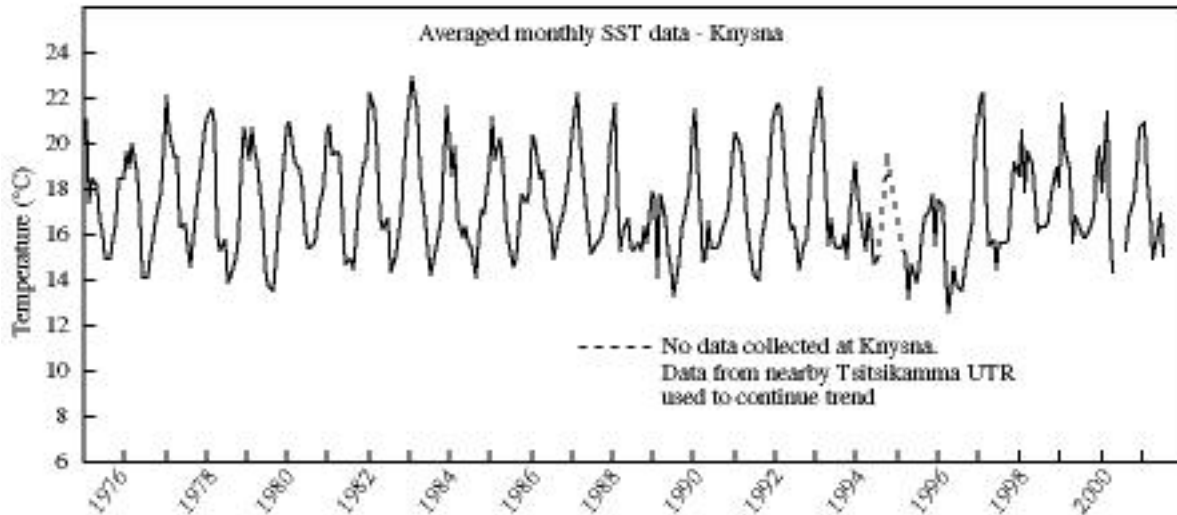


Figure 13. Average monthly SST data measured at Knysna (depth of sensor is 6 m). Note the strong seasonal heating and cooling, and the anomalous summers of 1988–1989, 1993–1994, 1994–1995, and 1995–1996.

1994, 1994–1995, and 1995–1996, implying intense upwelling seasons. The first of these “anomalous” summers corresponded with a substantial *La Niña* event in the Pacific Ocean. The others were in a period beginning with weak *El Niño* conditions, becoming weak *La Niña* conditions. Warming and cooling of eastern Bank coastal waters have been described by Schumann *et al.* (1995), and Roberts (1998b). The correspondingly high number of satellite observations of the cold ridge during the anomalous summer of 1988–1989 (Figure 12b) suggest that the Knysna surface temperature measurements can be used to infer cold ridge activity, i.e. that summer peaks in monthly average surface temperature (Figure 13) signify less cold ridge activity, and depressed summer peaks signify greater activity. Such activity could be linked to primary and secondary production.

A comparison of the structure and behaviour of the cold ridge with upwelling filaments studied in the southern Benguela and on the Californian shelf shows similarities. For example, Taunton-Clark (1985) described the formation, growth, and decay of wind-induced upwelling tongues that extend 50–80 km offshore during summer at three sites on the west coast of South Africa (Cape Peninsula, Cape Columbine, and Hondeklip Bay). Local bathymetry, orographic, and meteorological effects were implicated in the intense upwelling at those sites, and the elongated tongue-like configuration of surface isotherms originating at the coast were like those of the cold ridge. Off California, Flament *et al.* (1985) showed an upwelling filament similar in configuration to the cold ridge associated with an offshore meander (300 km) in the narrow alongshore frontal (equatorward) current on the shelf edge, which had entrained cold coastal surface water in an offshore direction. Ships’ data indicated that temperature and salinity fronts defining the filament at the surface extended to the bottom of the mixed layer. Upward doming of the thermohaline structure in the filament, also seen in the Agulhas Bank cold ridge, was observed. Good illustrations of such doming can be seen in other studies of filaments in that region (e.g. Dewey and Moun, 1990; Kosro *et al.*, 1991; Mackas *et al.*, 1991; Strub *et al.*, 1991), although the depths of the filament fronts were often deeper (100–150 m). Of importance in all these studies is that the filaments extend beyond the shelf into depths of 2 000 m, unlike South Africa’s cold ridge, which remains on the shelf in depths of 100–150 m. Lifespans of the filaments off California were often between 30 and 60 days, similar to the cold ridge. Subsidence of cold surface water in filaments was also observed (e.g. Brink *et al.*, 1991; Washburn *et al.*, 1991).

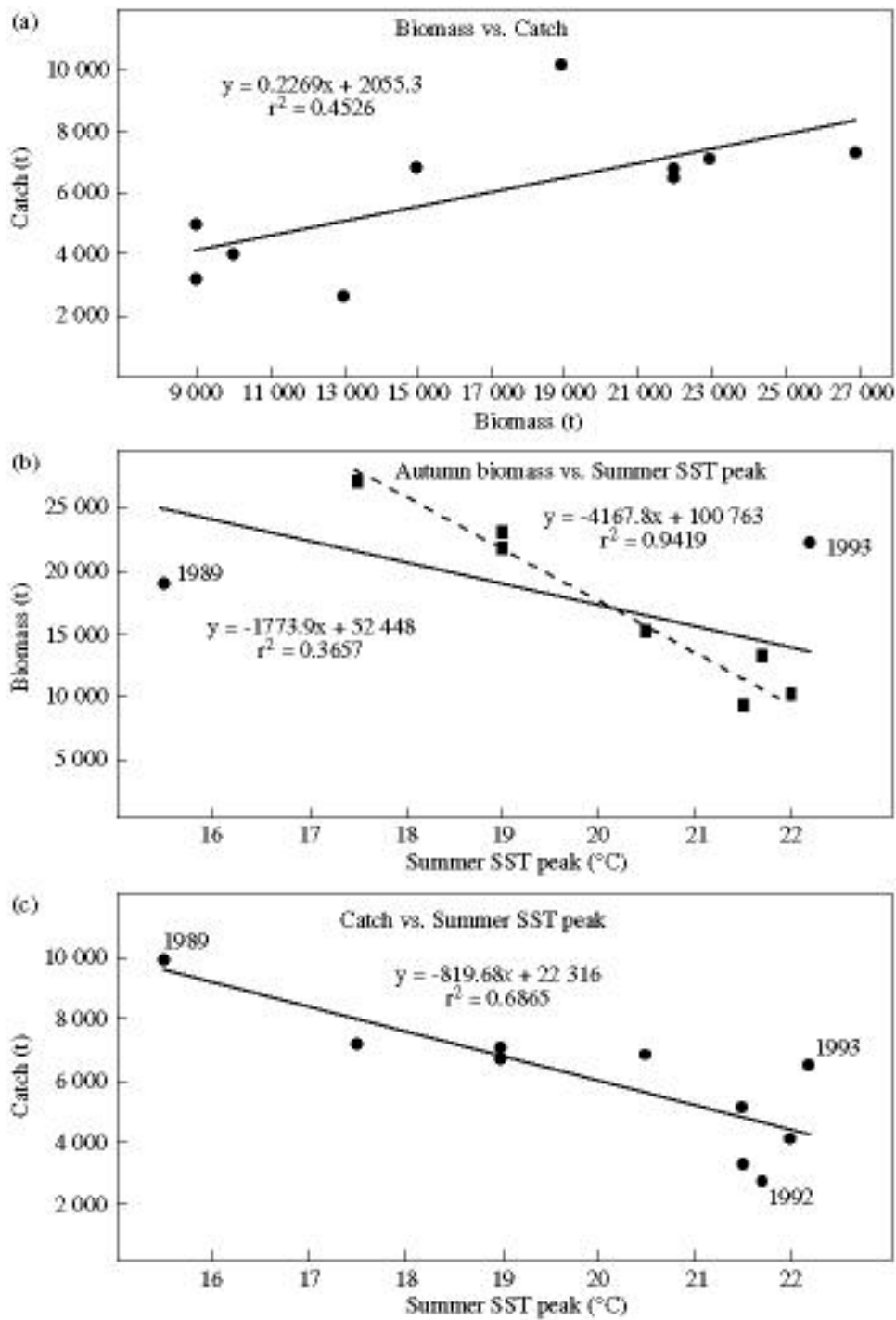


Figure 14. (a) Estimated chokka squid biomass vs. total annual jig catch, 1988–1997. The trend is seemingly linear. (b) Biomass vs. maximum monthly average SST (from Figure 13; solid line). The linear fit is improved if the anomalous years 1989 and 1993 are excluded (dashed line). (c) Total annual jig catch vs. maximum monthly average SST, with a linear trend line.

Cold ridge links to chokka squid biomass and catches

A similarity in the fluctuating trends of peak monthly average sea surface temperature for each summer in Figure 13 (referred to as the summer SST peak hereafter) and the following autumn squid biomass shown in Figure 3a, suggests some cause and effect. This is better seen in Figure 14b, in which linear regression has been superimposed on the data for the years 1988–1997. Two outliers (1989, 1993) deteriorate an otherwise good linear relation (dotted trend line), which has a fit of (r^2) of 0.9419. While a number of factors can influence biomass, it is plausible, as identified in this paper, that a western transport hypothesis, coupled with cold ridge activity (copepod abundance), can equally control paralarval survival and hence be responsible for the correlation. The relationship is appealing for biomass prediction, because the summer SST peak is obtained at the beginning of each year.

The inclusion of the outliers into this regression reduces the trend line fit to an r^2 of 0.3657 (solid line in Figure 14b), which limits its use. Several factors could be responsible for the outliers. The first is the reliability of the biomass estimates (see Roel, 1998), which unlike the temperature data, are not calibrated. In the case of 1989, the anomalously high catches shown in Figure 3b, and the corresponding relatively low biomass in Figure 3a, certainly raise questions about the estimate. Other factors could be environmental. In 1989, squid biomass in autumn was far below the anticipated level, given the intense upwelling in the previous (1988–1989) summer. Such intense upwelling may be self-limiting, as described by Cury and Roy (1989), who suggest an optimal environmental window in upwelling regimes, leading to good recruitment. Too much or too little upwelling either side of this window would lead to poor recruitment. Moreover, the lack of upwelling in summer 1992–1993, plus the high biomass in autumn 1993 (if correct), suggests that coastal upwelling and the cold ridge are not the only mechanisms to enhance paralarval food abundance and survival. Changes in the current regime on the eastern Bank could also potentially influence recruitment. The latter could lead to loss of paralarvae from the Agulhas Bank or, alternatively, boost entrainment of paralarvae in some manner. The summers of 1988–1989 and 1992–1993 were extreme in terms of sea surface temperature, and both correspond to *El Niño*–Southern Oscillation (ENSO) events. Ecosystem changes during such times could also adjust paralarval predation levels, which would influence recruitment. Finally, aside from these possibilities, the biology is not always in synchrony with the physics, and cannot always respond to physical changes, especially exceptional ones. Hence, anomalies should be expected. Ideally, these need to be anticipated to assist fisheries management.

Also of importance is the apparent positive correlation between squid autumn biomass and the corresponding annual jig catch. This has been dealt with in some detail by Roel (1998), using a GLM in anticipation of catch prediction. In that study, a linear relationship best described the data (Figure 14a), albeit with an r^2 of 0.4526. Accordingly, a (linear) correlation was found between the summer SST peak and the annual catch, with an r^2 of 0.6865 (Figure 14c). The latter plot uses all annual data points between 1988 and 1997. When utilized to predict catches for 1998, 1999, and 2000, the regression yielded values less than those actually reported i.e. 91.3, 67.0, and 89.5% of reported values, respectively. If the regression is repeated including the actual reported data for the years 1998–2000, then the fit is reduced to an r^2 of 0.5893. In either case, use of the summer SST peak appears to be a better predictor of forthcoming catch than biomass, and may therefore hold promise for squid fishery management.

Conclusions

This work has demonstrated that, within the complex oceanography surrounding southern Africa, chokka squid have found, or evolved to use, a niche on the eastern Agulhas Bank that optimizes spawning and their early life stages. Nowhere else on the shelf are both bottom temperature and bottom dissolved oxygen simultaneously at optimal levels for egg development. However, the spawning grounds are displaced from the typical copepod maximum by some 200 km, which is near a cold ridge that is optimal for feeding of paralarvae (on copepods), and hence for survival. ADCP data indicate that this spatial shortcoming is offset by the existence of a barotropic net westward current capable of transporting paralarvae to the cold ridge before starvation.

This exploitation of currents to optimize the use of separate environments during spawning and early life has been referred to in this paper as a westward transport hypothesis. Although on a smaller scale, such a strategy is analogous to that used by the ommastrephids *Illex illecebrosus*, *Todarodes pacificus*, and *Illex argentinus*, which use fast-flowing, large-scale, western boundary currents to connect spawning grounds with feeding grounds. Such a life cycle strategy, however, has three obvious weaknesses that can impact recruitment. These involve uncharacteristic behaviour of (1) bottom environmental conditions on the spawning grounds, (2) the net westward current, and (3) the cold ridge that supports the copepod maximum.

The latter was pursued in this paper, and the cold ridge was described as a coastal upwelling filament frequently found off the Knysna coast during summer. Its formation appears to be controlled by a combination of easterly winds and westward flow on the eastern Agulhas Bank. *In situ* sea surface temperature data indicate occasionally intense summer upwelling along the coast, which leads to greater cold ridge stability (i.e. it becomes quasi-permanent). This is expected to yield prolonged periods of copepod abundance beneficial for paralarva survival. However, the cold ridge can be absent much of the time during summer, especially during ENSO events.

A negative linear regression ($r^2 = 0.94$) between the maximum summer monthly sea surface temperature (an index of cold ridge activity) and the following autumn chokka squid biomass (and catches; $r^2 = 0.69$) supports the spawning and early life strategy outlined above, and is potentially useful for prediction, because the maximum monthly SST is available at the beginning of the year.

Future research should focus on environmental conditions on chokka squid spawning grounds, the flow regime on the eastern Agulhas Bank, paralarva swimming capability and transport, and cold ridge–primary production–copepod maximum coupling.

Acknowledgements

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Running headings

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Chokka squid spawning and life cycle and the Agulhas ecosystem