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Currents along the Tsitsikamma coast, South Africa, and potential transport of squid paralarvae and ichthyoplankton

MJ Roberts* and M van den Berg

Marine and Coastal Management, Department of Environmental Affairs and Tourism, Private Bag X2, Rogge Bay 8012, South Africa
** Corresponding author, e-mail: squid@metroweb.co.za*

In July 1998, a bottom-mounted Acoustic Doppler Current Profiler was deployed at 36m depth in the centre of the Tsitsikamma National Park on the eastern Agulhas Bank, South Africa. The purpose was to investigate transport of chokka squid *Loligo vulgaris reynaudii* paralarvae hatched on the inshore spawning grounds (<60m) and ichthyoplankton spawned within the park. Analysis of the first 12 months of data (July 1998–June 1999) shows that surface flow was mainly eastward (alongshore), with a maximum velocity (u-component) of +115cm s^{-1} and an average of +24cm s^{-1}. Generally, velocity decreased with depth, with a maximum bottom velocity (u-component) of +65cm s^{-1} and an average of +10cm s^{-1}. Data from a nearby thermistor array show that the water column was usually isothermal during winter (July–September), with bottom flow in the same direction as the surface layer. In summer (December–March), vertical stratification was most intense, and surface and bottom flows differed in velocity and direction. Potential net monthly displacements calculated for three depths (5m, 23m and 31m) indicate that passive, neutrally buoyant biological material (e.g. squid paralarvae, fish eggs and larvae) would likely be transported eastwards in the surface layer for eight of the 12 months, and would generally exceed distances of 220km $month^{-1}$. Displacement in the bottom layer was more evenly distributed between east and west, with net monthly (potential) transport typically 70–100km, but reaching a maximum of 200km. Wind-driven coastal upwelling, prevalent during the summer, causes the surface layer of the coastal counter-current to flow offshore for several days, resulting in potential displacement distances of 40km from the coast. These results suggest that squid paralarvae hatched on the inshore spawning grounds are not generally transported towards the 'cold ridge', a prominent semi-permanent oceanographic feature of cold, nutrient-rich upwelled water, where food is abundant, and that fish larvae, whether from the surface or bottom layer, are exported beyond the boundaries of the Tsitsikamma National Park.

Keywords: Agulhas Bank, currents, paralarvae, South Africa, squid spawning grounds

Introduction

In South African waters, chokka squid *Loligo vulgaris reynaudii* spawn mainly on the eastern Agulhas Bank in depths <60m between Plettenberg Bay and Cape Padrone (Augustyn *et al*. 1994). This region is east of a prominent, semi-permanent oceanographic feature, referred to as the 'cold ridge' (Figure 1, Largier and Swart 1987, Boyd and Shillington 1994, Roberts 2005). This elongated, tongue-like feature is formed when the shelf thermocline is locally lifted towards the sea surface (doming), resulting in cold, nutrient-rich, bottom-layer water entering the photic zone. Primary and secondary production is generally elevated above this layer (Probyn *et al*. 1994). Ship-borne Acoustic Doppler Current Profiler (ADCP) measurements presented by Boyd *et al*. (1992) and Boyd and Oberholster (1994) indicated a net barotropic westward flow of water over the mid-shelf region of the eastern Agulhas Bank, with more variable currents inshore. Based on these data and the distribution of sampled squid paralarvae shown in Figure 1, Roberts (2005) speculates that the eastern position of the chokka squid spawning grounds may be allied to a spawning strategy that relies on the westward transport of squid paralarvae towards the abundant food source near the 'cold ridge'. Roberts (2005) suggests that anomalies in the physical and biological processes of such a system could influence successful recruitment, and explain at least in part the observed high variability in squid biomass and catches. More specifically, he shows that the 'cold ridge' is an upwelling filament that originates in the intense coastal upwelling zone along the Tsitsikamma coast, which displays unusual behaviour during ENSO events. Anomalies in the westward current regime might also explain why paralarvae are found east of the Kei River mouth (Figure 1).

Larval transport has also been of interest in the dynamics of the Tsitsikamma National Park (TNP), a marine protected

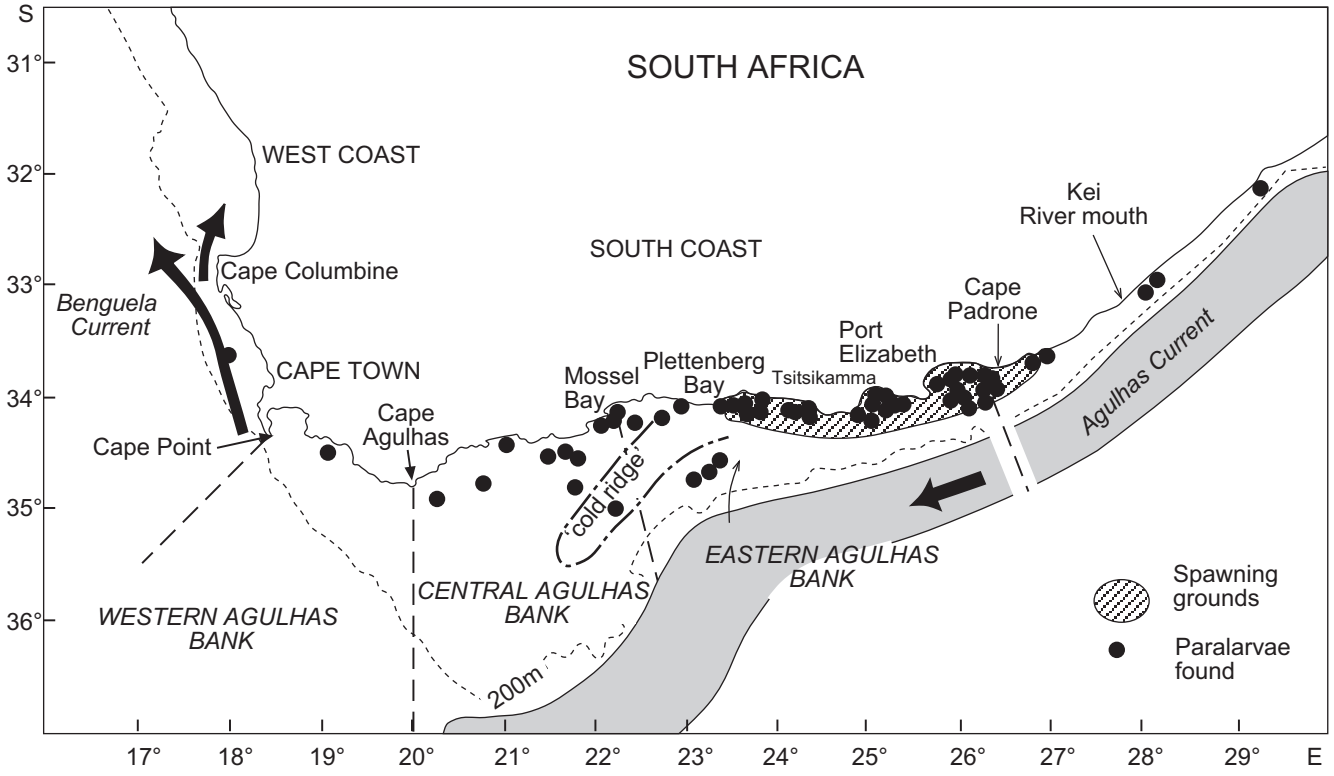


Figure 1: Map showing the main spawning grounds of chokka squid on the eastern Agulhas Bank, east of the 'cold ridge'. Positions where paralarvae have been found are indicated (data from Augustyn *et al*. 1994)

area located within the squid spawning grounds just east of Plettenberg Bay (Figure 2). Potential benefits of the TNP not only include enhancement of catch in adjacent fished areas, through the export of surplus juvenile and adult fish, but also the supply of recruits through larval transport (Attwood *et al*. 1997a, 1997b). Tilney *et al*. (1996) attempted to evaluate the export potential of sparid fish larvae from the TNP using a bottom-moored (ACM2) current meter deployed at a depth of 51m over 6 months period (Figure 2). Together with sea surface temperature (SST) satellite imagery depicting coastal upwelling events on the South Coast, Tilney *et al.* (1996) proposed that larvae are transported beyond the boundaries of the park via three mechanisms, which they referred to as 'current-closure scenarios' (see Figure 6 in Tilney *et al.* 1996): (1) coastal, barotropic, alongshore flow oscillations (east-west), mainly during winter; (2) surface layer, offshore-onshore, closure circulation associated with minor coastal upwelling during spring/summer; and (3) surface layer, offshore-onshore, closure circulation associated with major coastal upwelling, also during spring/summer. The 'closure' implies that the particle trajectory is offshore and westwards during upwelling, and returns inshore during relaxation, after the cessation of easterly wind (i.e. producing a closed trajectory).

Such mechanisms, however, complicate the 'westward transport hypothesis' for squid paralarvae that is proposed by Roberts (2005) and, given the short time of six days before starvation (Vidal *et al*. in press), appear to render the 'cold ridge' out of reach for many newly hatched paralarvae. Attwood *et al*. (2002) followed up on the work of Tilney *et al.* (1996) using surface drogues and showed the potential for larval export from the TNP. They also found that the coastal current is more westward than eastward, which does not support the 'current-closure scenarios' hypothesis.

To advance understanding of factors influencing squid and fish recruitment on the Agulhas Bank, both the 'westward transport hypothesis' and the 'current-closure scenarios' needed to be further investigated and reconciled. Part of the problem is that different data and analyses were used to derive each hypothesis. The ship-borne ADCP results presented by Boyd *et al*. (1992) and Boyd and Oberholster (1994) were based on 40 cruises, but only 10 covered the study area referred to here, and at best were made three times a year. These sparse data may not necessarily reflect the general flow regime on the mid-shelf or inshore, and certainly ignore seasonal trends. On the other hand, Tilney *et al*. (1996) measured bottom currents only, which are slower than surface flow, and therefore the potential for larval transport in the surface layer was underestimated in that study. Even including the drogue work by Attwood *et al*. (2002), there are insufficient time-series data to cover the flow dynamics and seasonal trends of currents along the Tsitsikamma coast. Moreover, none of these studies took into consideration the intense thermal stratification that occurs on the eastern Agulhas Bank (Schumann and Beekman 1984, Swart and Largier 1987, Schumann 1999), and the possibility of opposing surface and bottom flows complicating larval transport.

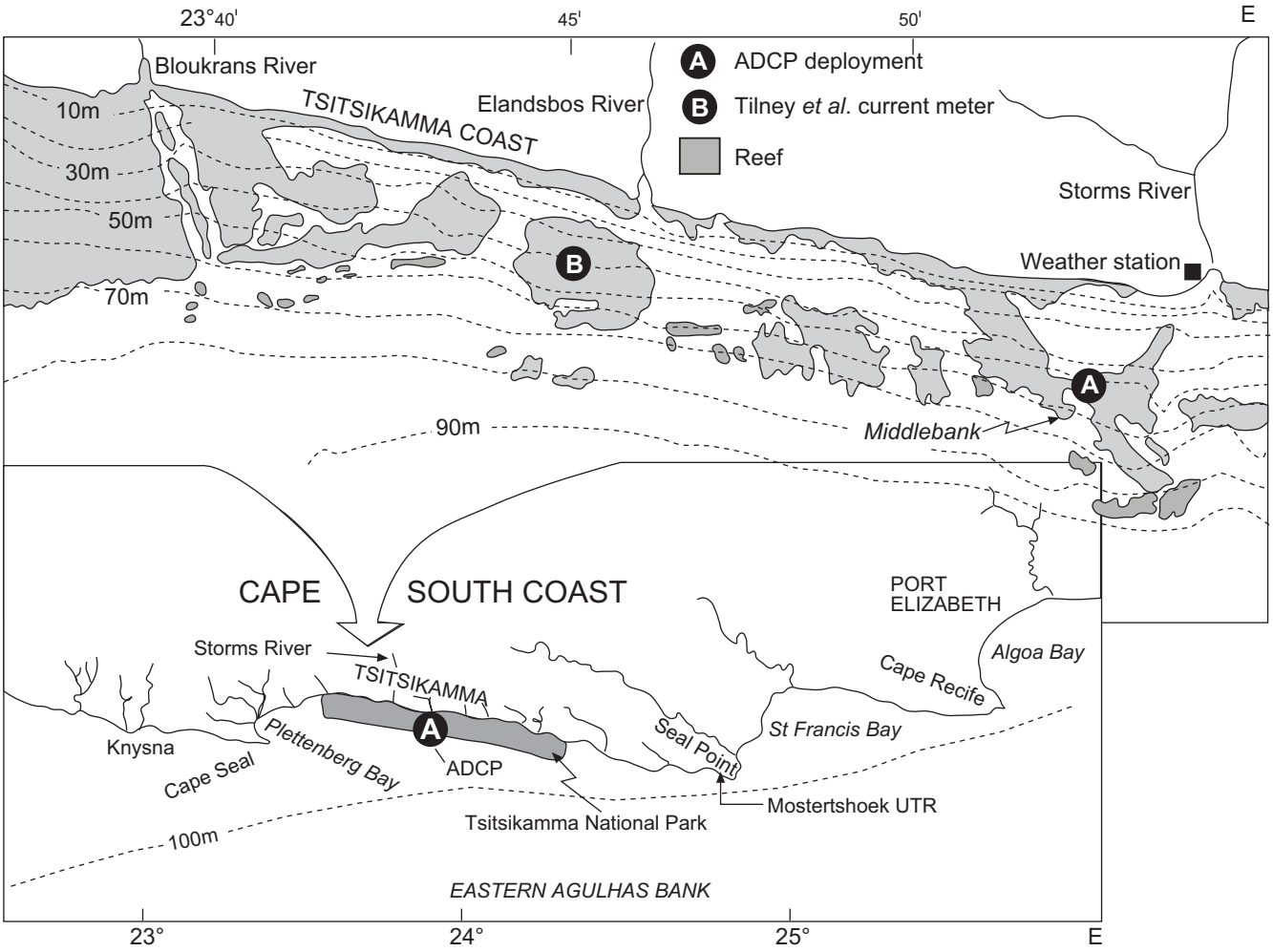


Figure 2: The locality of the Tsitsikamma coast on the South Coast, showing its bathymetry and the position of the ADCP (Ⓐ: this study) and the bottom-moored current meter (Ⓑ: Tilney *et al*. 1996)

Mindful of these shortcomings, and the fact that measurements at a single site do not necessarily present a complete understanding of the flow pattern in an area, the aim of this paper was to augment previous studies with a continuous 12-month, multi-layered description of the coastal current along the Tsitsikamma coast. These data were then used to assess the potential transport of squid paralarvae on the inshore spawning grounds, including ichthyoplankton from the TNP.

Material and Methods

The TNP extends 72km along the coast of the eastern Agulhas Bank east of Plettenberg Bay, and up to 5.5km offshore to a depth of around 100m. In July 1998, a 300kHz ADCP was deployed at the centre of the TNP (2.5km from the shore) on a prominent reef known as Middlebank at 34°02.72'S, 23°52.51'E (Figure 2). The reef has a steep offshore slope of about 45°, which rises from the seabed at 60m to the shallowest point at 23m. Inshore of this high point, the reef drops less steeply (~15°) to 45m. The ADCP was deployed on the inshore slope of the reef at a depth of 36m. This position was chosen as a compromise between minimising flow changes on account of reef topography and to remain within a safe working depth for SCUBA diving during deployment and recovery of the instruments. An array of Hugrún mini underwater temperature recorders (UTRs), positioned at depths of 12m, 19m, 27m and 31m in the water column, was deployed 20m away from the ADCP mooring. Service and data download was every four months.

The ADCP was configured to record every 30 minutes using an ensemble size of 120 pings (one ping per second). The water column was sampled using 15 bins, each of 2-m depth, between 3m and 31m. Prior to processing, the data for each bin were checked for quality on a monthly basis. For this analysis, only bins in which >75% of the readings computed to be 'good' were used (see Lee Gordon 1996 for details defining 'good' data.) This criterion eliminated the 3m bin. The first 12 months of data presented here did not require filters to remove noise, but were averaged to hourly values. It is noteworthy that a decline in the percentage of 'good' data was observed between depths 17–27m during the summer (November–March),

which may be related to stratification of the water column. Directional data were converted to true north (i.e. –25°) internally at the time of measurement.

Wind data, measured 15m above sea level, were obtained at hourly intervals from a dial-in automatic weather station located at Storms River (see Figure 2). This location is not ideal, because the coastline topography is exceptionally steep and rises to a coastal plain at an altitude of 180–220m. In addition, the small embayment at Storms River mouth introduces an inflection in the otherwise linear coastal topography (Figure 2). This may have influenced measurements made at this site, so these data were not necessarily representative of the wind field farther offshore. A New Hampshire Lanczos filter, with 71 weights and a power point of 36h was used to remove land breeze effects in the analysis.

NOAA AVHRR images were used to highlight SST on the South Coast during an upwelling event between 13 and 20 January 2000. Images on 16, 17, 18 and 20 January were chosen to best represent the evolution of the upwelling plume. Cloud cover was removed from the images using composites of data from several satellite passes.

Results

Polar histograms of the surface (5m) and bottom (31m) currents from July 1998 to June 1999 (not shown) illustrated that currents flowed predominately in an east-west direction at both depths, with the principal axis being between 78° and 259°. Interestingly, this axis was not parallel to the coastline, but aligned with a deeper bathymetry, the 100-m isobath (Figure 2), and the principal wind axis (not shown).

The characteristics of velocity for this dataset are depicted in Figures 3 and 4, which show the east-west (u-) and north-south (v-) velocity components. These components were resolved using true north-east co-ordinates, which closely match the observed principal flow axis. Positive values in the u-component plots represent eastward flow. Similarly, positive values in the v-component plots represent northward (onshore) flow. The surface (5m) u-component velocities (Figure 3a) reached maximum peak values of +115cm s^{-1} in December/January and –101cm s^{-1} in October. Velocities of this magnitude did not appear to be sustained for periods of more than three days. The average eastward and westward velocity components were +24cm s^{-1} and –21cm s^{-1} respectively (Figure 3a). Velocities above these averages generally did not persist for periods of more than five days, although in August 1998 an eastward current with above-average velocity flowed for 15 days. Periods of sustained high velocity appear to have been more common in the eastward current than in the westward current, and lacked seasonality. To validate this, however, a longer time-series is required. Slack water (i.e. u-component <5cm s^{-1}) was seldom measured, and when found did not last longer than five days.

East-west component velocities at 31m (Figure 3b) were considerably smaller than those at the surface. The maximum peak velocity in the eastward bottom current was +65cm s^{-1} and coincided with the maximum peak eastward surface current on Day 186, in December. The maximum peak westward velocity was –40cm s^{-1}, observed on three occasions in October. All three events were of short duration, lasting between 24h and 72h, and coincided with maximum westward surface velocities. The average bottom eastward and westward velocity components were +10cm s^{-1} and –11cm s^{-1} respectively (Figure 3b). Most sustained high-velocity events in the bottom layer coincided with those in the surface layer, resulting in similar overall velocity trends. However, during summer there were instances when the bottom velocity was low and the surface flow high (e.g. surface velocity on Day 168 was 63cm s^{-1}), or the surface current was slack and the bottom current was relatively fast (e.g. bottom velocity on Day 209 was 28cm s^{-1}). On some occasions, surface and bottom currents flowed in opposite directions. For example, on Day 262 surface velocity was +25cm s^{-1} for about 12h while bottom velocity was –30cm s^{-1}).

The maximum peak v-component velocities in the surface layer (Figure 4a) were +39cm s^{-1} in December and –36cm s^{-1} in June. Relative to the u-component, these velocities were short in duration, seldom lasting for more than a few hours. Average values indicate that the offshore and onshore velocity components in the surface layer were similar in magnitude, i.e. –7cm s^{-1} and +6cm s^{-1} respectively. In the bottom layer (Figure 4b), the maximum peak v-component velocities of +20cm s^{-1} and –15cm s^{-1} were about half those observed in the surface layer (averaging +3cm s^{-1} and –2cm s^{-1} respectively). Compared to the u-component, the frequency of variability in the v-component, in both the surface and bottom, was much higher. Semidiurnal tides and inertial currents could be attributed in part to this variability in velocity (Welsh 1964, Schumann and Perrins 1982, Largier 1987, Schumann 1999). Towards the end of the study, during April, May and June, there was an underlying low-frequency oscillation (of a period of a few days to weeks) in the v-component velocity. This was most pronounced in the surface layer, but also noticeable in the u-component.

The flow regime can further be examined using 12-month progressive (cumulative) u- and v-component displacement plots for the surface and bottom layers (Figure 5). In both layers, the u-component was dominant. In the surface layer, the theoretical 12-month net alongshore displacement was estimated to be 1 306km eastward. It is important to note that this displacement cannot be interpreted literally, because this distance would extend far beyond the eastern boundary of the Agulhas Bank and onto the narrow Eastern Cape shelf domain, which is dominated by the strong southwestward-flowing Agulhas Current. However, such displacement could explain the appearance of squid paralarvae far east of the main spawning grounds, at Kei River mouth (Figure 1). The alongshore displacement depicted in Figure 5a is characterised by seven periods (indicated) when substantial easterly flow was concomitant with lengthy periods of sustained high velocities (Figure 3a). For instance, the persistent easterly flow in August (Event 1) lasted four weeks. Substantial displacement events in the westerly direction, similar in magnitude to the large easterly displacements, were found in July 1998 and May 1999, also on account of lengthy periods of sustained high current velocity. But overall, westward flow in the surface layer does not appear to be a major feature of the currents off the

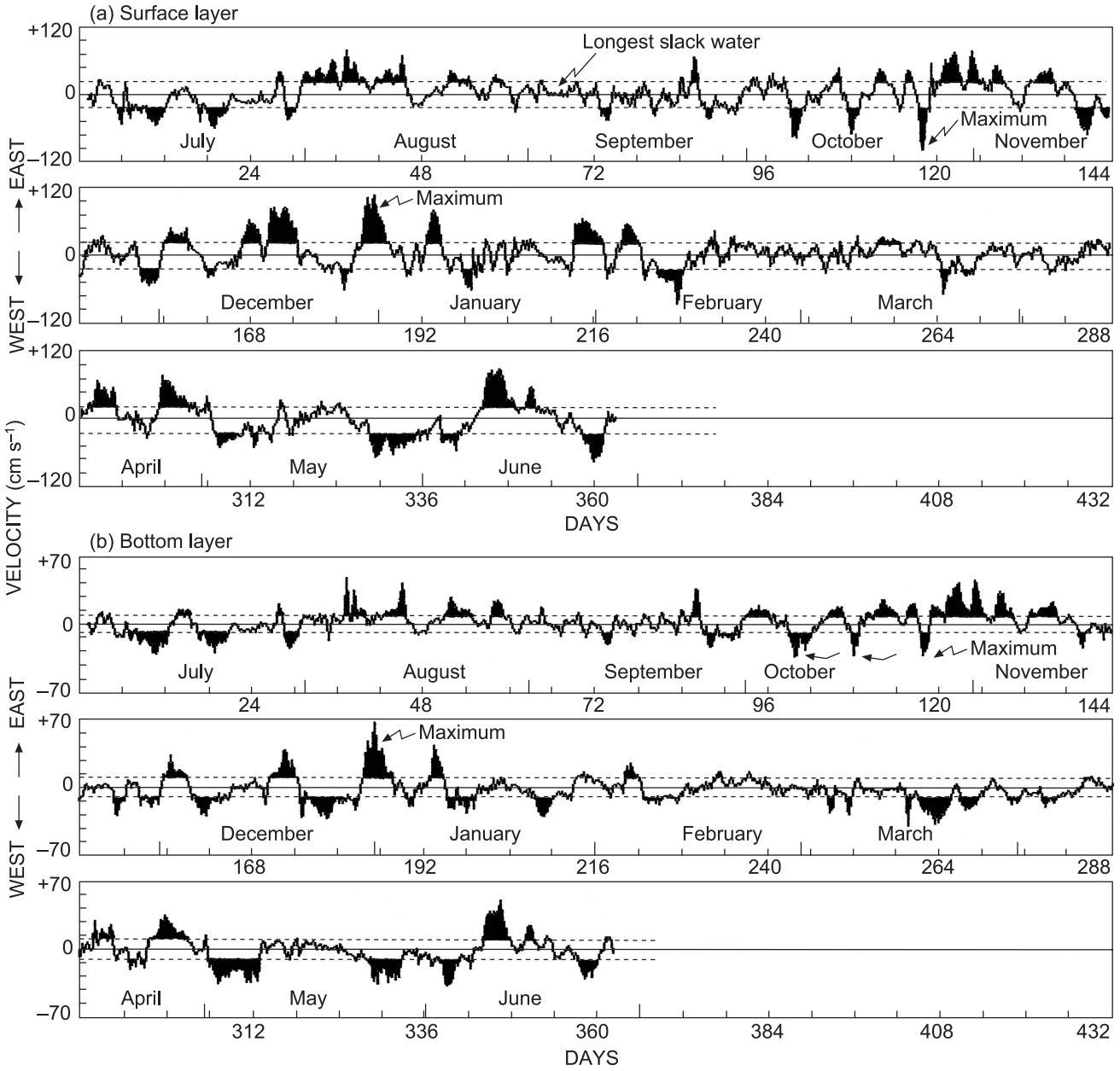


Figure 3: ADCP measurements of the 12-month (July 1998–June 1999) time-series of the east-west (u-) velocity component of the Tsitsikamma inshore current for (a) surface layer (5m) and (b) bottom layer (31m). Positive y-axis values indicate eastward flow, negative values denote westward flow. Note the different y-axis scales. Average eastward and westward velocities are represented by the dotted line and shaded regions highlight above-average velocities

Tsitsikamma coast, nor is any form of seasonal behaviour in displacement. On this scale, the relative contribution of the onshore-offshore flow (v-component) to total displacement in the surface layer is clearly seen in Figure 5a to be of minor importance. However, as shown later, it should not be ignored.

In contrast, the u-component of the bottom layer appears to have a seasonal trend in displacement (Figure 5b). There was similarity between the bottom and surface u-component during July–November 1998 and May–June 1999, but the effect of dissimilar flows (at times opposite) is clear between December and March, where little net displacement took place relative to the upper layer. Factors such as wind, vertical stratification, coastal-trapped waves and upwelling frontal jets could be responsible for this dissimilarity. However, the former may be more pertinent, because temperature data from a nearby thermistor array (Figure 6) showed that during the period December–March vertical stratification in the water column is most intense (i.e. difference of >4°C between surface and bottom temperature), and Schumann (1999) demonstrated that easterly winds are more prominent during that time. Compared to the surface layer (Figure 5a), northward (onshore)

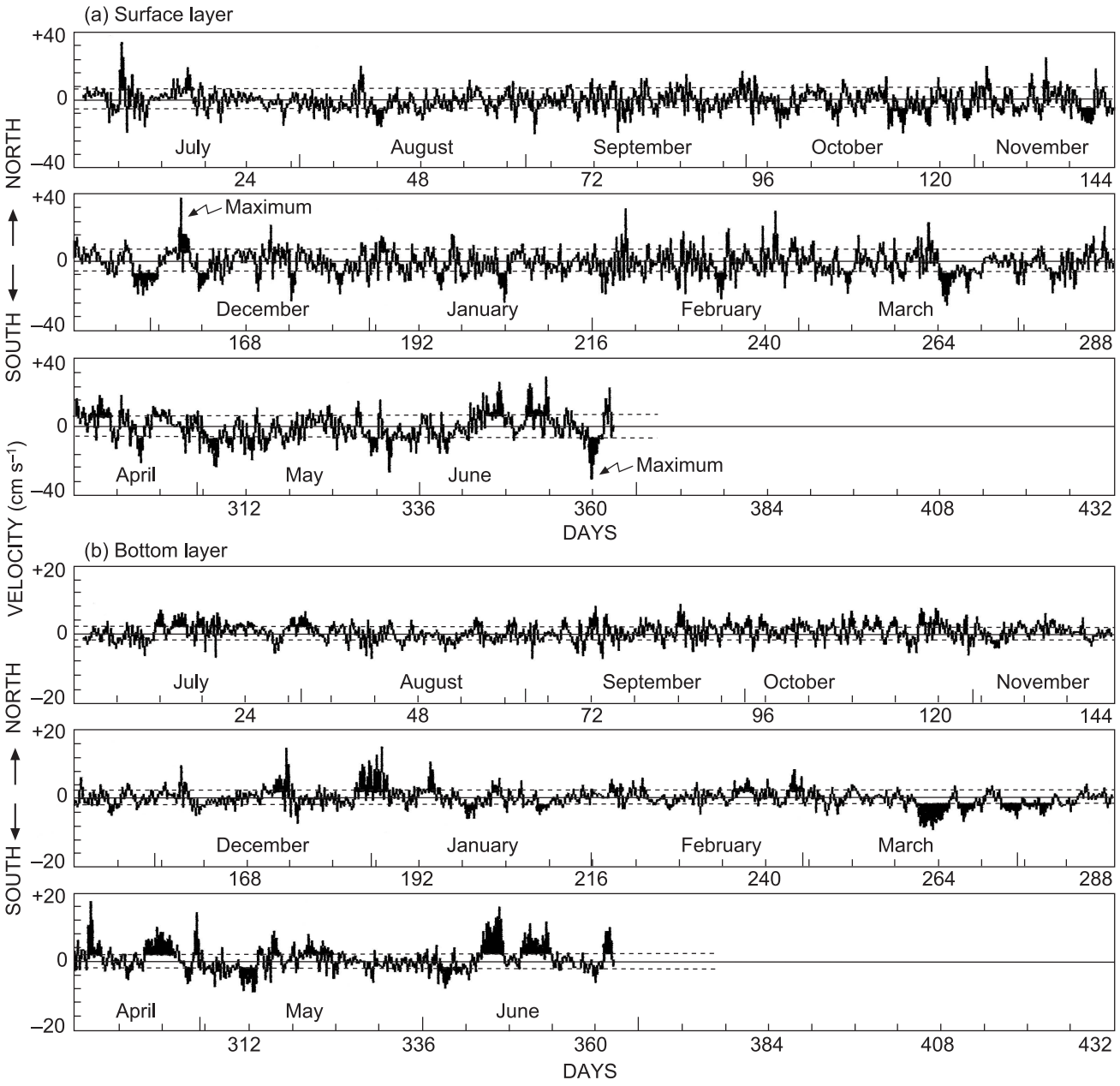


Figure 4: ADCP measurements of the 12-month time-series (July 1998–June 1999) of the north-south (v-) velocity component of the Tsitsikamma inshore current for (a) surface layer (5m) and (b) bottom layer (31m). Positive y-axis values indicate northward flow, negative values denote southward flow. Note the different y-axis scales. Average northward and southward velocities are represented by the dotted line and shaded regions highlight above-average velocities

displacement in the bottom layer is more obvious, particularly during October–February. Both layers show a change in this trend between March and May, when there was more offshore displacement. Displacements such as these could be in response to Ekman transport in the upper water column, i.e. offshore displacement in the surface layer as a result of wind-induced coastal upwelling and onshore displacement in the bottom layer (Schumann 1999).

An indication of the potential transport of non-swimming larvae (assumed here to be passive, neutrally buoyant particles) can be gained by combining the u- and v-component displacements, providing total progressive displacement. Again, it must be emphasised that displacement obtained using current measurements made at a single site is theoretical and does not consider surrounding constraints such as bathymetry, coastline, differential horizontal flows and turbulence — factors that can result in large deviations from the theoretical 'trajectories' presented here. Progressive displacement plots can highlight seasonal and depth differences. With this in mind, data for July

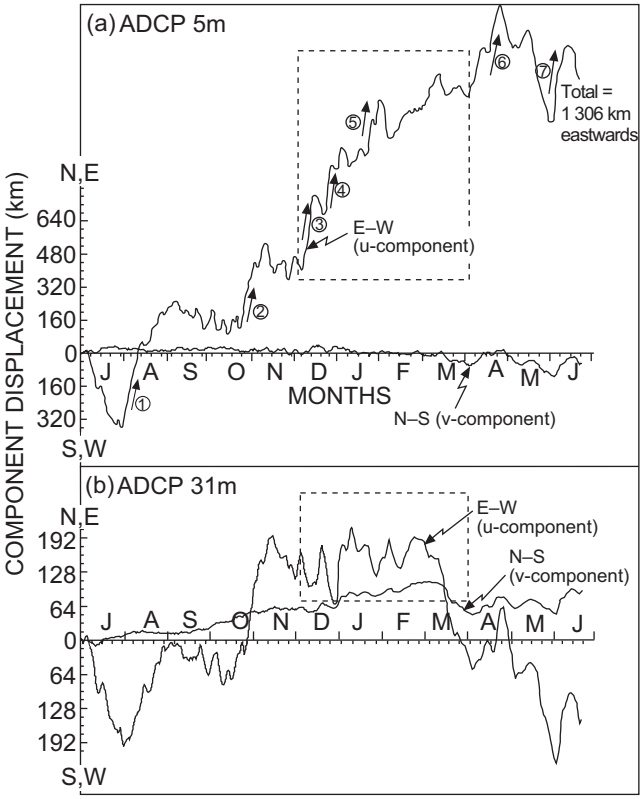


Figure 5: Twelve-month (July 1998–June 1999) component displacement (progressive vectors) in (a) the surface layer (5m) and (b) bottom layer (31m) flows off the Tsitsikamma coast. Flow in the surface layer was characterised by seven periods of sustained easterly (+u-) displacement (denoted 1–7), with no seasonal trend. Contribution of the north-south (v-) component to the surface current is small. Much of the surface trend is also seen in the bottom current (b), except during December–March (dotted box)

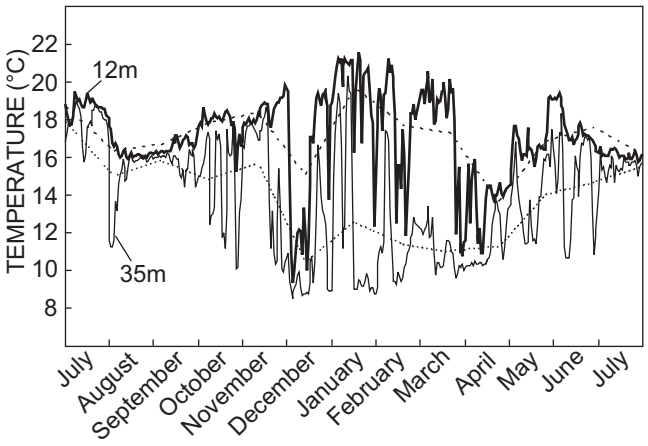


Figure 6: Daily (solid lines) and monthly (dashed lines) averaged temperatures for 12m and 35m depths on Middlebank (July 1998–July 1999). Thermal stratification is most intense during summer

and August 1998 (winter) and December, January, February 1999 (summer) were plotted (Figure 7). During winter, displacement in the surface and bottom layers was similar in direction, but differences in velocity caused disparate net transport distances (Figure 7a). In this case, surface and bottom particles released simultaneously from the origin would be hypothetically separated by 340km in the alongshore direction after 62 days, with net surface and bottom displacement of the individual particles being 200km east and 140km west of the origin respectively.

During summer (Figure 7b), when stratification occurs and on occasion surface and bottom flows differ greatly, the net alongshore displacement in the surface layer after 89 days would potentially be 705km east of the origin. In marked contrast, a passive particle released from the origin in the bottom layer would oscillate between eastward and westward displacement, with a net displacement of only 45km east of the origin.

In both examples, the contribution of the v-component to the net total displacement on these time and distance scales is relatively small (see Figure 5a). On smaller scales, however, the v-component cannot be ignored, particularly in the surface layer (see three similar events marked by asterisks in Figure 7), and given the width of the shelf, can have a potentially significant role in larval dispersion. It is important to note that the north-south axis scale has been enlarged in the figure to 2km per tick to highlight the onshore/offshore transport. This alters the true trajectory direction of these events. The onshore event in Figure 7a was caused by a slackening of the westward, alongshore surface current for about four days in mid-July (see Figure 3a). During that time, the northward velocity component (Figure 4a) increased to 20cm s^{-1}, implying a potential displacement of 22km. Of course, given that the coast is only 2.5km to the north of the ADCP site, a literal displacement of this magnitude is impossible, so there must have been either downwelling or alongshore flow closer to the coast to maintain the continuity of flow (mass transport). The two offshore events in the net eastward flow shown in Figure 7b indicate potential displacement of about 30km.

The cause of such events can be explored by considering data collected in January 2000 (Figure 8). Here, an offshore event interrupted eastward flow along the Tsitsikamma coast between 13 and 19 January. Offshore potential displacement was 40km. The event coincided with a strong easterly wind (>6m s^{-1}), which began in the early hours of 13 January (Figure 9b). Data collected (not shown) by a UTR located near Mostertshoek at a depth of 5m, 100km east of Middlebank (see Figure 2b for location), indicate a drop in temperature a few hours later, i.e. coastal upwelling began soon after the wind changed from west to east. The thermistor array on Middlebank (Figure 9c) also shows the surface-layer cooling, but it took 48h for the water column to become well mixed at 9°C. The progressive vector plot shown in Figure 8a indicates that, concomitant with this cooling, the surface layer had turned to offshore flow, which continued steadily until 19 January. Note that the axis scales differ in Figure 8a and the true direction of offshore advection relative to the coast is shown in the insert. Of interest is that this direction matches well the orientation of the 'cold ridge'

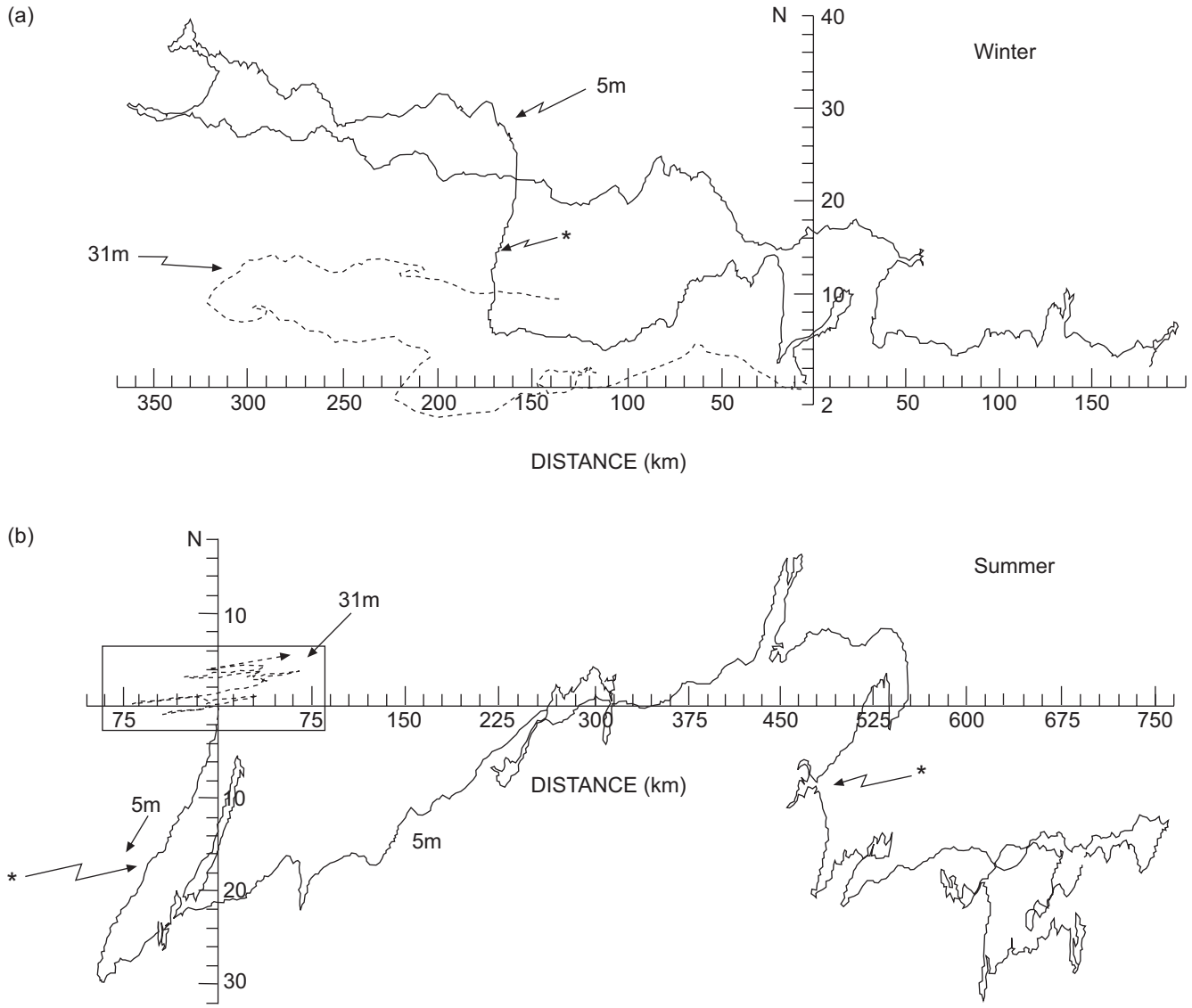


Figure 7: Potential transport (trajectories) of passive, neutrally buoyant biological material during (a) winter (July, August 1998) and (b) summer (December, January, February 1999) are presented by combining u-component and v-component displacements. The asterisks mark significant onshore and offshore displacement. Note the y-axis scale has been expanded for clarity; this distorts true direction (see Figure 8)

(see Figure 1) and supports the belief that this feature is an upwelling filament with origins in the coastal upwelling zone (Roberts 2005).

As evident by the rise in surface temperature at Middlebank (Figure 9c), the upwelling process had ceased by 20 January. There was an immediate return of the eastward surface current, albeit initially with an onshore component that possibly compensated the lower sea surface height adjacent to the shore. The response of the bottom layer (31m) during this event was not immediate and differed in flow direction. The change from eastward flow (Figure 8b) lagged the upper layer by several hours, with the reversal only lasting until (mid) 18 January. Offshore flow was near absent in the bottom layer, unlike the surface (i.e. current reversal occurred). This, however, could be on account of obstruction by the shallower offshore reef topography adjacent to the ADCP mooring (see Material and Methods).

It is significant that the easterly wind (driving force) stopped on 16 January and was followed by a south-westerly wind on 17 January (Figure 9b), and that upwelling was still active as evident in the SST satellite imagery shown in Figure 9a. The upwelling plume off the Tsitsikamma coast continued to expand offshore between 17 and 18 January. Wind on 18 and 19 January was light and variable. The SST image for 20 January shows relaxation in the intensity of upwelling, with little evidence of cool water in the region by 23 January. The area influenced by this upwelling event on 20 January extended some 75km from

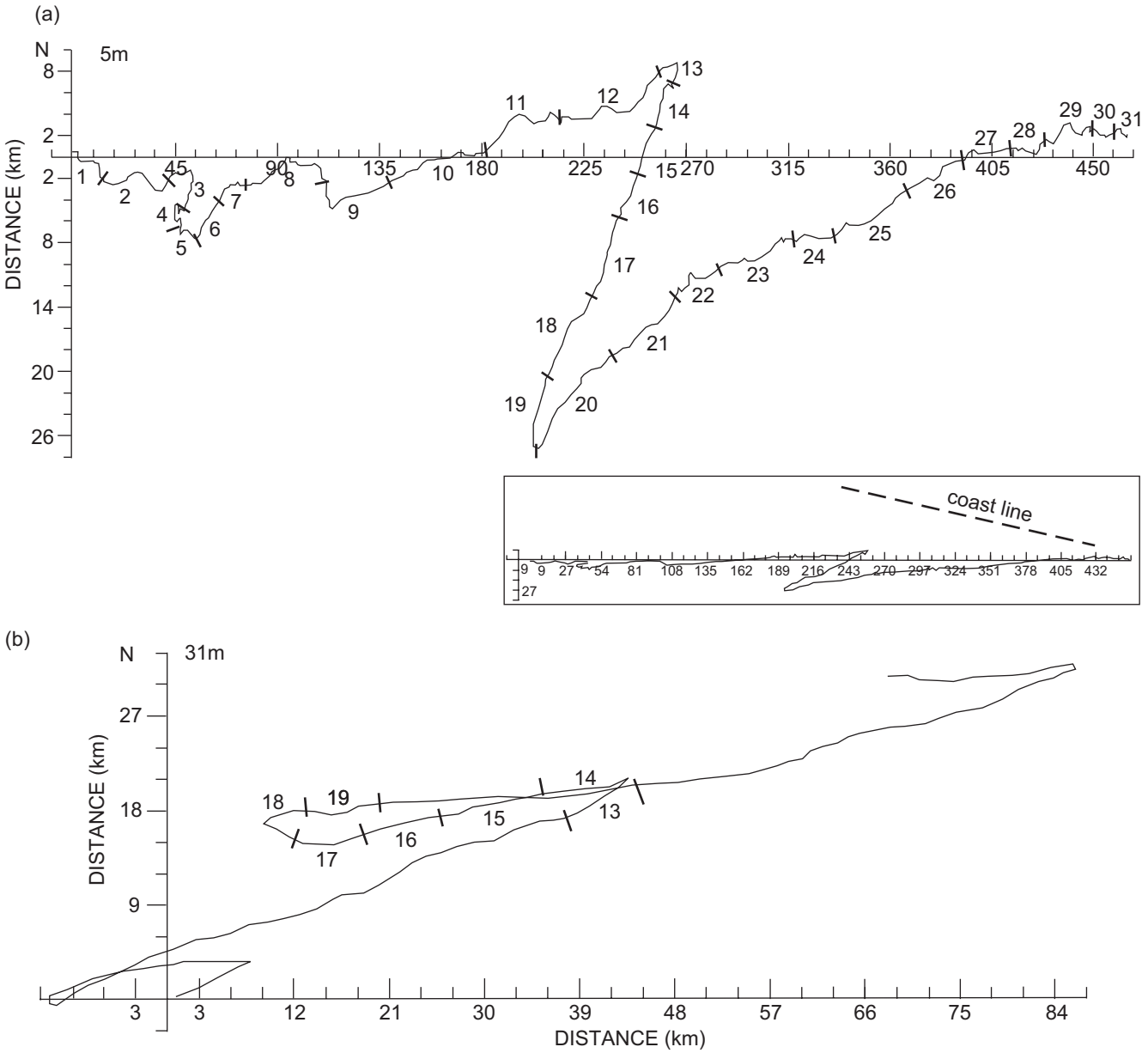
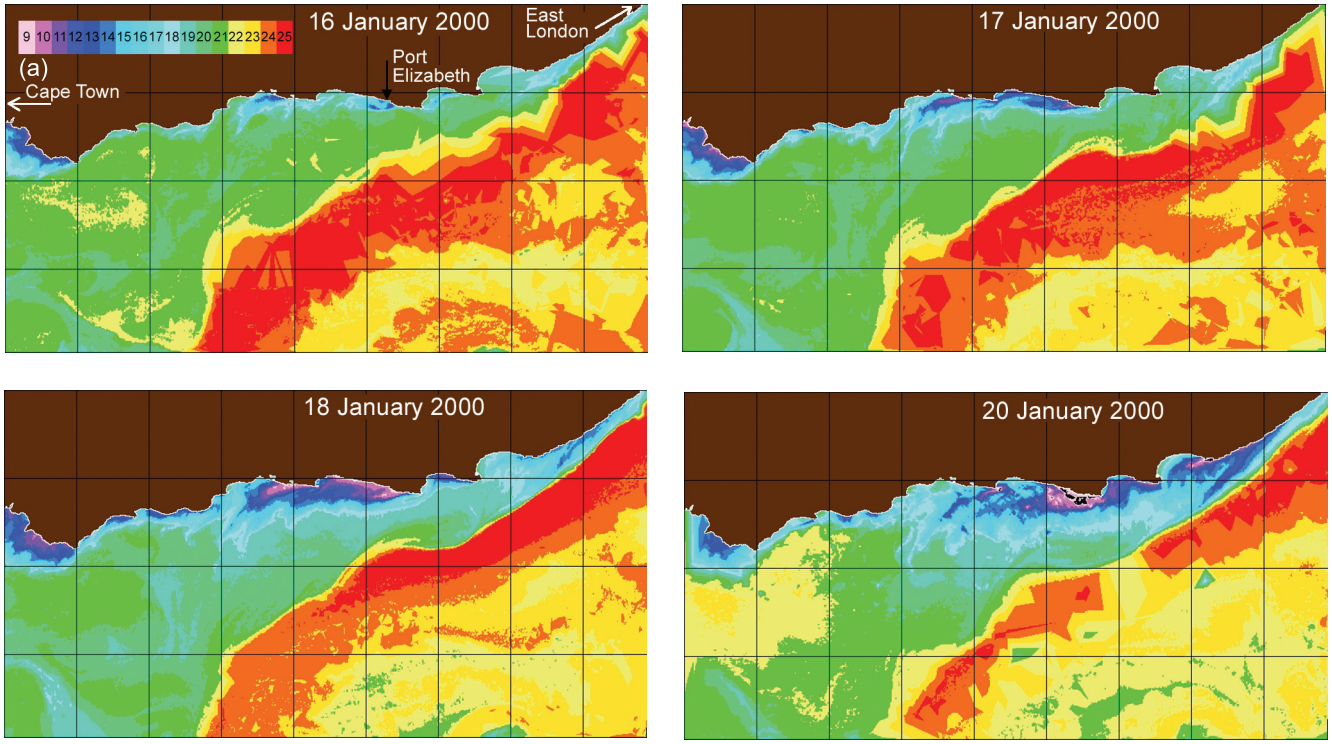
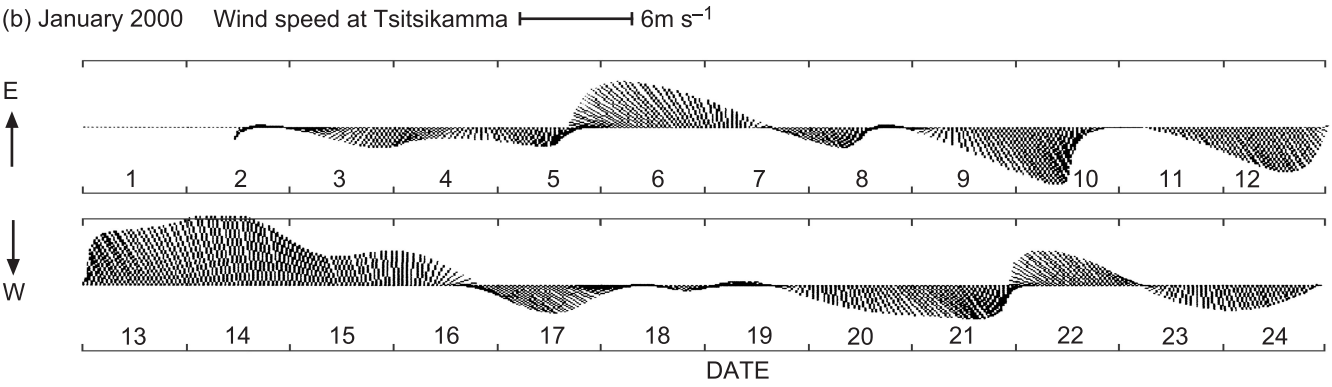


Figure 8: Progressive vector diagrams for January 2000 using ADCP data collected at Middlebank for (a) the surface layer (5m) and (b) the bottom layer (31m). Days of the month are indicated. The eastward current was interrupted by an upwelling event between 13 and 19 January, causing an offshore flow. Note the y-axis scale in (a) has been expanded for clarity; this distorts true direction as seen in the insert

the coast. Also, the surface layer on the mid-shelf over this period was westwards, as evident by the advection of the cold-water plumes.

To assess larval transport along the Tsitsikamma coast, the net potential east-west displacement was calculated for each month between July 1998 and June 1999, using progressive vectors for depths 5m, 23m and 31m (Figure 10). This method was deemed appropriate to view potential displacement on a comparative spatial and temporal scale. The mid-depth was chosen as a compromise between work by Schumann (1999), who calculated the average depth of the upper mixed layer to be 6.9m (based on six CTD sections between January and May), and data from Figure 6, which show the mixed layer reached 35m. Figure 10 shows that net egg and (para)larval transport in the surface layer was overwhelmingly eastwards, with the greatest distance of 550km in August. The average monthly transport in the surface layer was about 200km. Net displacement was westwards in only three of the months (July, September and May). There was a general decline in net displacement with depth, with exceptions in October in midwater (23m) where displacement was greater than in the surface layer (possibly retarded by wind), and in March when displacement at 23m and 31m was opposite. Overall,





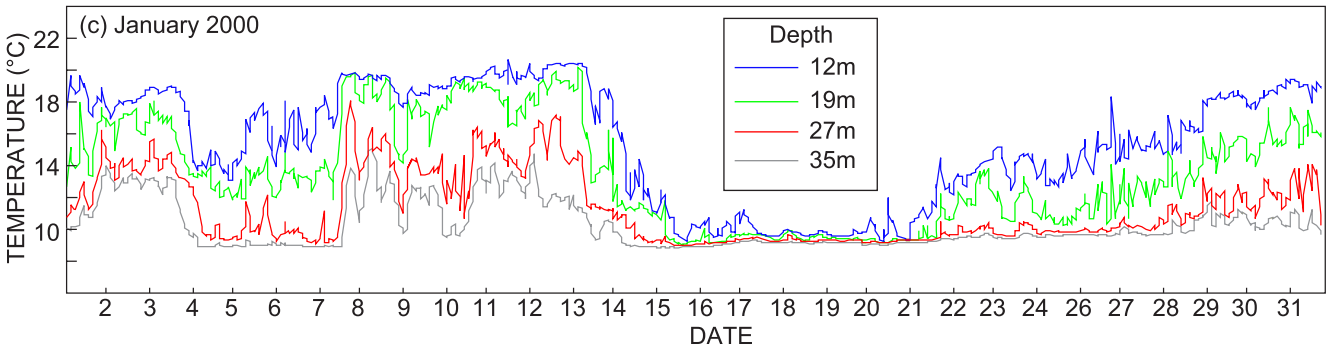


Figure 9: The upwelling event in mid-January 2000: (a) SST images depicting the evolution of the upwelling plume along the Tsitsikamma coast; (b) filtered winds measured at Storms River; (c) temperature data collected by a thermistor array on Middlebank

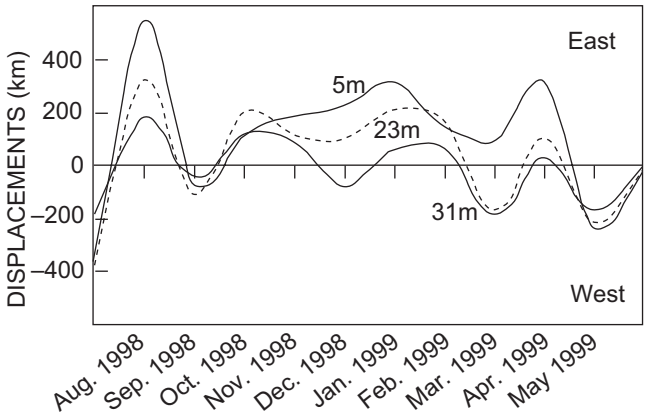


Figure 10: Potential monthly east-west (alongshore) transport of passive, neutrally buoyant biological material at 5m, 23m and 31m off the Tsitsikamma coast. Monthly displacements are based on ADCP data collected for the period July 1998–June 1999. The midwater displacement (23m) is approximately at the depth of the thermocline during the summer months

net displacement in the bottom layer lacked the dominant eastward trend found near the surface, with maximum distances of 220km.

Discussion

Coastal currents off Tsitsikamma

ADCP data collected during research ship surveys show a net westward flow at a depth of 30m over most of the eastern Agulhas Bank (Boyd *et al*. 1992, Boyd and Oberholster 1994). Exceptions to this current pattern were found on the outer- and inner-shelf regions (i.e. <15km from the coast), where averaged vectors indicate a distinct lack of net spatial and temporal trends. In the vicinity of Storms River, the limited data presented by Boyd *et al*. (1992) and as suggested by AJ Boyd (Marine and Coastal Management, unpublished data) show a mix of flow directions (including onshore). Eastward coastal flow seems to oppose the greater westward shelf flow at times, suggesting the existence of a narrow coastal counter-current off the Tsitsikamma coast.

The 6-month bottom dataset collected by Tilney *et al*. (1996), using a moored ACM2 acoustic phase-shift current meter, shows that eastward flow is common near the seabed (51m) off the Tsitsikamma coast. Those data also indicate a strong onshore component in this flow and that transient peaks (current reversals over a day) are integrated into the ambient flow. Spectral analysis indicates that these are caused by coastal trapped waves generated by synoptic weather patterns (Schumann 1983, Schumann and Brink 1990).

The drogue study by Attwood *et al*. (2002) demonstrated that the surface current off Storms River is mainly alongshore. In contrast to Tilney *et al*. (1996), Attwood *et al*. (2002) found that the current was more westwards than eastwards and showed minor onshore and offshore components, thought to be indicative of Ekman drift. The scale of the drogue tracks, however, was too small to test the coastal upwelling-related 'current-closure scenarios'. Averaged velocities for individual drogues ranged between 2cm s^{-1} and 58cm s^{-1} with a modal average of 23 cm s^{-1}. Surface current and wind were poorly correlated, often in opposite directions, suggesting that wind is not a primary driving force of the current along the Tsitsikamma coast. Attwood *et al.* (2002) found that most drogue tracks remained parallel to one another. Successive drogue releases demonstrated that the direction of the surface current can remain consistent for periods of at least four days. Between 1.5km and 4.5km from the coast (distribution of drogues), the surface current commonly exhibited a horizontal velocity gradient, with either a reduction in velocity towards the shore (as might be expected on account of coastal interference) or the opposite, where the inshore surface current was faster.

The 12-month hourly time-series of vertical current profiles collected in this study overcomes some of the limitations of previous work. The most important findings are (1) the quantification of the eastward surface flow (5m), which dominated over westward flow by 68% vs 32%; (2) there are differences between surface and bottom flow (e.g. eastward flow in the bottom layer was less dominant); and (3) seasonal trends in the flow pattern. Moreover, there is good agreement between the bottom-layer data collected by the ADCP and that of Tilney *et al*. (1996), despite the difference in depth between the two deployments (i.e. 51m vs 36m respectively). For instance, there are similar periods of sustained eastward flow (~4 weeks), which result in net eastward displacement, and the westward flow exhibited in both studies is of shorter duration than eastward flow. Transient current reversal peaks (caused by coastal trapped waves) are evident in both datasets, as is northward displacement.

However, there are important differences between the deeper (ACM2) current mooring used by Tilney *et al.* (1996) and shallower (ADCP) deployment in this study. The north-south displacement at the deeper site dominated over the east-west component, whereas the ADCP data show the opposite to be the case. More specifically, the deeper mooring showed a net northward displacement of 187km in 198 days, compared with a displacement of 80km for the same time period using ADCP data. The dominance of onshore flow over alongshore at the deep mooring is an unexpected result, but it may be caused by a channel or nearby high profile reef. Another difference is that greater maximum peak velocities were recorded by the ADCP compared with the ACM2 mooring, i.e. 65cm s^{-1} vs 17cm s^{-1}. A number of factors could be responsible for this difference, including bottom topography, tidal and inertial currents, as well as long-term shifts in the oceanographic regime on the Agulhas Bank. It is therefore likely that transport rates higher in the water column were underestimated by Tilney *et al*. (1996).

In the absence of data on surface currents, Tilney *et al*. (1996) used results from drift card studies undertaken on the South and South-West coasts to assess surface transport of ichthyoplankton (Duncan and Nell 1969, Shelton and

Kriel 1980). These studies indicated (track-averaged) maximum surface speeds of about 30cm s^{-1}. The drogue study by Attwood *et al*. (2002) showed a track-averaged maximum velocity of 58cm s^{-1}. The present ADCP surface data (5m) indicate a near-instantaneous maximum velocity of 115cm s^{-1}, suggesting that previous studies underestimated maximum surface currents along the Tsitsikamma coast by a factor of between two and four. Apart from being near instantaneous, the higher velocity obtained using the ADCP is likely a result of the greater number of observations over the year, through all conditions, and the small vertical bin size of 2m compared with 8m for the drogues. However, when averaged, the ADCP surface-layer data agree well with the other studies (i.e. 23cm s^{-1} vs +24/–21cm s^{-1} respectively). The ADCP data also show that currents can persist for periods in excess of four days, as observed by Attwood *et al*. (2002).

The present data clearly show the effect of an easterly wind on the eastward flow, and the resultant change in direction to offshore flow in the surface layer concomitant with coastal upwelling (Figure 9). The data indicate a potential offshore displacement of 40km. Given that the shelf is 80–100km wide in the study region, pelagic material in the surface layer would likely be transported to the mid-shelf. However, as noted in the satellite imagery (Figure 9), upwelling plumes indicated a westward mid-shelf flow, which would transport particles in that direction. Moreover, in theory, there should be a westward-flowing jet current along the upwelling front. The ADCP data show a return of the eastward current after cessation of upwelling, with a clear onshore component. It is therefore possible for a particle on the mid-shelf to be transported back to the coast, which supports the 'current-closure hypothesis'.

The dynamics and extent of the coastal counter-current are not known. As demonstrated in this study, wind can influence the flow throughout the water column, at least to depths of 40m, but it appears not to be the main driving force, as suggested by Attwood *et al*. (2002).

Larval transport and reconciliation of hypotheses

Little is known about the behaviour of chokka squid paralarvae. The few hatchlings that have been collected (depicted in Figure 1) were found near the surface (M Lipiński, Marine and Coastal Management, pers. comm.), suggesting that they migrate vertically despite being negatively buoyant (Vidal *et al*. in press). In the absence of information on time of spawning and hatching, egg density and swimming speeds, it was assumed, for the purposes of this study, that squid paralarvae and ichthyoplankton are influenced by advection (i.e. passive drifters) for one month, and remain at similar depths in the water column during that period. This time-span could be an oversimplification, but it is a convenient time-scale for analysis and provides an interim means to quantitatively assess their potential transport. For parasquid larvae, a one-month pelagic period could be realistic, but according to Leis (2003), this may not be the case for fish, which likely have a shorter preflexion period. However, Brouwer *et al*. (2003) found this time-span to be realistic for temperate sparid fish.

Given the dominant alongshore flow in the Tsistikamma coastal system, this simplistic approach is considered adequate for a first attempt to calculate net potential east-west displacement for each month of the study, instead of more elaborate sequential displacements for daily releases throughout the year. The results show that the net potential egg and (para)larval transport in the surface layer was overwhelmingly eastward, with theoretical distances of up to 550km. However, the diminishing dominance of the eastward current with depth would result in decreased displacement towards the bottom, with distances up to 220km being achieved. Taking vertical migration into account, the dispersion pattern becomes complex, especially if bottom and surface layers flow in opposite directions. Also, displacement would depend on the time spent by larvae at different depths.

The ADCP data collected in this study demonstrate that the inshore current along the Tsitsikamma coast flows westwards at times, which supports the westward transport hypothesis proposed by Roberts (2005). However, this pattern is not as common as the eastward flow, which would transport larvae away from the 'cold ridge' and the enhanced food source there. This hypothesis, in its simple state, is therefore relevant only under certain conditions.

Coastal upwelling can cause displacement in the surface layer, particularly during eastward flow along the coast. Neutrally buoyant larvae (and eggs) being transported eastwards would move offshore onto the mid-shelf and simultaneously westwards, and return to the coast downstream in the Tsitsikamma coastal current. Such trajectories would retard net eastward displacement, supporting the 'current-closure scenarios' suggested by Tilney *et al*. (1996). Westward advection on the mid-shelf, although commonly observed in SST and ship-borne ADCP data, still needs to be investigated to determine its prevalence and implications for larval transport. Only moored current-meter measurements can establish this. If westward flow is common, eggs and larvae could be carried into the area of the 'cold ridge' and benefit from the enhanced food supply there. In this respect, westward flow on the mid-shelf would seem to benefit larvae hatched on the deep chokka squid spawning grounds.

Coastal upwelling occurs mainly during summer, which is the main spawning period for chokka squid. Upwelling, and its apparent retentive nature, could therefore be advantageous when the eastward current flows, by limiting eastward displacement of paralarvae and the possible detrimental effects of moving into a poorer food environment. The fate of larvae in the eastward coastal current remains unknown, but loss from the Agulhas Bank is a possibility. Such displacement offers an explanation for the presence of squid paralarvae east of the Kei River mouth (Figure 1).

The method used in this study to assess larval displacement is somewhat simplistic, and upwelling and the associated 'closure' mechanisms have not been taken into account. Nonetheless, the results demonstrate the potential for larval transport in the Tsitsikamma coast region and, in the absence of knowledge on vertical migration behaviour, that both squid paralarvae and ichthyoplankton are likely to be transported beyond the boundaries of the TNP.

Conclusion

The results presented indicate the presence of an alongshore current on the Tsitsikamma coast, which is predominantly eastwards. The current can flow in the same direction for periods of four weeks, and attain high surface velocities of 115m s^{-1} (average 23cm s^{-1}). Velocity generally decreases with depth, attaining up to 65m s^{-1} near the bottom (average 11cm s^{-1}). Although not a common phenomenon, bottom and surface layers can flow in opposite directions when the water column is thermally stratified. Potential displacement trajectories indicate an average monthly transport distance from Middlebank of up to 550km to the east in the surface layer. Near-bottom transport appears to be less dominated by eastward flow, attaining a maximum distance of 200km. During periods of easterly winds and eastward coastal currents, the surface flow veered offshore, highlighting Ekman transport and concomitantly coastal upwelling. Potential displacement of at least 40km from the coast was attained during upwelling events during the study.

The present findings strengthen the belief of Tilney *et al*. (1996) and Attwood *et al.* (2002) that pelagic fish eggs and larvae in both the surface and bottom layers are exported beyond the boundaries of the TNP, thereby enhancing recruitment in adjacent fished areas. The onshore-offshore displacement observed here in the surface layer, especially during eastward flow, along the Tsitsikamma coast supports the cyclonic advection ('current-closure scenarios') and larval dispersion proposed by these authors.

The existence of a dominant eastward surface flow, however, requires modification to the 'westward transport hypothesis' proposed by Roberts (2005). Whereas it is probable that squid paralarvae on the mid-shelf are transported westward (as indicated by the ship-borne ADCP data), the present data indicate that squid paralarvae on the inshore spawning grounds, between Cape Seal and Seal Point (Figure 2b), are mainly transported eastwards in the surface layer and away from the 'cold ridge'. The onshore-offshore cyclonic advection would imply that some inshore paralarvae are advected offshore into the westward mid-shelf current, and possibly swept towards the 'cold ridge'. Alternatively, the paralarvae could be returned inshore, thereby retarding eastward displacement and maintaining them at the base of the 'cold ridge'. The fate of the paralarvae transported eastward remains unknown.

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