http://dx.doi.org/10.1071/MF09275

Feng, M., Slawinski, D., Beckley, L.E. and Keesing, J.K. (2010) Retention and dispersal of shelf waters influenced by interactions of ocean boundary current and coastal geography. Marine and Freshwater Research, 61 (11). pp. 1259-1267.

http://researchrepository.murdoch.edu.au/id/eprint/3478/

Retention and dispersal of shelf waters influenced by interactions of ocean boundary current and coastal geography

Ming Feng[A,C], Dirk Slawinski[A], Lynnath E. Beckley[B] and John K. Keesing[A]

[A] CSIRO Marine and Atmospheric Research, Floreat, WA 6014, Australia.

[B] School of Environmental Science, Murdoch University, 90 South Street, Murdoch, WA 6150, Australia.

Abstract

Retention and dispersal of shelf waters under the influence of ocean boundary currents is crucial to recruitment processes of many coastal species. In this study, a Lagrangian particle tracking method based on an eddy-resolving, data-assimilating, hydrodynamic model is used to study spatial variations of local retention rates and alongshore dispersal of surface waters on the continental shelf off the west coast of Australia. The circulation on the shelf off the west coast of Australia is dominated by the southward-flowing eastern boundary current, the Leeuwin Current, which is interrupted by episodic wind-driven, northward, inshore surface transport during the austral summer, and by mesoscale eddy formations during the austral winter. Low-retention shelf regions tend to experience high alongshore currents, owing to the near-shore influence of the Leeuwin Current, protruding coastal geography, or formation of mesoscale eddies, whereas high-retention regions are sheltered from the direct influence of the Leeuwin Current by coastal geographic features. Alongshore dispersal also exhibits spatial as well as seasonal heterogeneity, with predominantly southward dispersal during the austral winter, and more symmetrical dispersal during the austral summer. Shelf retention and seasonal dispersal are linked with recruitment processes of invertebrate and fish species off the west coast of Australia.

Additional keywords: Capes Current, connectivity, Lagrangian particle tracking, Leeuwin Current.

Introduction

Larval retention and dispersal are pivotal to population dynamics, genetic structure, and biogeography of many coastal species (Cowen *et al.* 2000). Larval transport in an open system has been studied by assuming a linear coastline and a Laplacian dispersal kernel that decays exponentially from a release point (e.g. Kaplan and Botsford 2005). Whereas realistic ocean circulation models have been used to simulate larval dispersal in recent years (e.g. Petersen *et al.* 2010), models based on idealised linear coastlines are still being used to test dispersal theories, such as the influence of the oceanic mesoscale circulation on marine connectivity (Siegel *et al.* 2008). It is important to understand interactions between ocean boundary currents and coastal geography that may generate spatial heterogeneity in marine connectivity, and the west coast of Australia is an ideal test bed.

The continental shelf off the west coast of Australia has an average width of 66 km between the North West Cape (Ningaloo Reef; 22°S) and the Cape Leeuwin (34°22′S). The pressure-driven, poleward-flowing Leeuwin Current dominates the ocean circulation on the open shelf (Fig. 1), and plays a significant role in marine biology off the coast. The Leeuwin Current is responsible for the existence of coral reefs as far south as the Houtman Abrolhos Islands (hereafter called the Abrolhos), 29°S (Collins *et al.* 1993), and the presence of tropical species along the west and south coasts (Maxwell and Cresswell 1981; Hutchins and Pearce 1994). There has been some indirect evidence of ecologically important alongshore connectivity off the coast (Simpson 1991; Beckley *et al.* 2009; Pearce and Hutchins 2009).

The Leeuwin Current is stronger during the late austral autumn to winter (April to August), and weaker during summer owing to prevailing northward winds (Smith *et al.* 1991; Feng *et al.* 2003). The episodic northward winds during the austral summer drive intermittent northward inshore currents and offshore Ekman transport (Pearce and Pattiaratchi 1999). The Leeuwin Current has the largest eddy kinetic energy among all mid-latitude eastern boundary current systems, which induces strong cross-shelf transport, especially in the shelf region south of the Abrolhos and north of Rottnest Island (32°S) during the austral autumn and winter (Feng *et al.* 2005, 2007). Whereas the Leeuwin

Current may enhance poleward transport of marine populations (e.g. Condie *et al*. 2005), the existence of the strong eddy field may disrupt alongshore connectivity (e.g. Griffin *et al*. 2001). The purpose of this study is to use a Lagrangian particle tracking model, based on ocean circulation outputs from an eddy-resolving, data-assimilating hydrodynamic model to assess the spatial heterogeneity of local retention and alongshore dispersal on the continental shelf off the west coast of Australia, under the influence of the seasonally varying ocean boundary current.

Methods

The hydrodynamic model output used in this study was derived from BRAN, or Bluelink ReANalysis, which was based on a global ocean model, OFAM (Ocean Forecasting Australia Model), developed as part of the Bluelink partnership between CSIRO, the Bureau of Meteorology (BoM), and the Royal Australian Navy (Schiller *et al.* 2008). BRAN was forced by the European Centre for Medium-Range Weather Forecasts (ECMWF) wind stress, and heat and freshwater flux-forcing at sea surface, and assimilated satellite and *in situ* oceanography data (Oke *et al.* 2008). BRAN was used to create a 1993–2008 archive of daily values of ocean currents, sea surface height, salinity and temperature in three dimensions, resolved at 10 km horizontally and 10 m vertically (in the upper ocean) in the Australian region. Tidal currents were not simulated in BRAN, but tidal amplitudes off the subtropical west coast of Australia are relatively small, except in shallow embayments, such as Shark Bay. Tidal currents were neglected in the study as only the statistics averaged across the shelf were used.

A 2-dimensional Lagrangian particle tracking model was implemented, in which particle movements were passively advected by the 0–20 m depth-averaged, daily velocity field from BRAN. A 4th-order Runga-Kutta sub-time-stepping scheme was used to update the particle locations every 6 h (by linearly interpolating velocity from daily fields). Random effects were considered by perturbing the initial particle seeding.

The continental shelf between 22° and 35°S off the west coast of Australia was divided into 26 half-degree (55 km) latitudinal segments (Fig. 1). The offshore boundary of each segment was determined by the 200-m isobath, except for the North West Cape segment where the 1000-m isobath was used as the offshore boundary owing to the unresolved narrow shelf (<10 km) by BRAN. In each segment, 5000 particles were randomly seeded daily for model years 1996 through 2000 and the particles were tracked for one month. Sensitivity tests showed that the results from this study were robust if the number of particles released at each segment was reduced by 50%.

All beached particles were first removed from the calculations. The retention rate of a segment was defined as the percentage of particles initially seeded in one segment that remain in the segment after a certain tracking period. The dispersal rate from one segment to another was defined as the percentage of particles seeded in the initial segment that subsequently have entered the other segment at the end of a certain tracking period. All the retention and dispersal values were averaged over the 5 years of 1996–2000.

Results

Local retention

Retention rates of surface waters vary spatially along the continental shelf off the west coast of Australia (Fig. 2). Based on a 5-year average, the lowest retention rate of < 3% occurs off North West Cape (Ningaloo, ~22°S) and the highest retention rate of >40% occurs at Geographe Bay, after 14 days of particle release. Shelf regions identified to have significantly higher retention rates than their standard deviations comprised: Carnarvon (24.0–25.5°S), in the broad Abrolhos region (26.5–29.5°S), between Perth and Geographe Bay (32.0–33.5°S), and south of Cape Leeuwin (34.5–35.0°S). In addition to North West Cape, low retention shelf regions were identified off Shark Bay (~26°S), near Jurien Bay (30–31°S), and off Cape Leeuwin (~34°S).

The spatial heterogeneity of shelf water retention rates is largely related to the magnitude of alongshore velocity, and to a lesser extent, the width of the continental shelf (Fig. 3). Shelf regions of low retention tend to experience stronger alongshore currents: the narrow shelves off North West

Cape and Cape Leeuwin tend to have greater influence from the Leeuwin Current, and the shelf region off Shark Bay has protruding coastal geography and is more exposed to the Leeuwin Current (Fig. 1); and the formation of mesoscale eddies near Jurien Bay caused significant cross-shelf exchanges of waters (Feng *et al.* 2005, 2007). In contrast, most shelf regions with higher retention rates are sheltered from the direct influence of the Leeuwin Current by coastal geography and have weaker alongshore currents: the region south of Abrolhos is sheltered by the island chain; the Leeuwin Current is diverted offshore upstream of Geographe Bay; and the region south of Cape Leeuwin is located in the shadow of the Cape.

Seasonal variations of local retention are also noticeable in some shelf regions, mostly associated with seasonal variations of the shelf currents (Fig. 4). Shelf regions around Perth and off Cape Leeuwin experience the lowest retention during the April–June period as the Leeuwin Current accelerates off the south-west coast. In most shelf regions, retention rates during July–September are relatively high in the annual cycle, when the influence from the Leeuwin Current starts to slacken and the wind-driven offshore Ekman transport is yet to pick up.

Alongshore dispersal

Spatial particle dispersal patterns were demonstrated using particles released from the shelf segment of southern Abrolhos (29–29.5°S). In April–June, the strong Leeuwin Current seems to act as a barrier to cross-shelf exchanges for particles released from the southern Abrolhos – most released particles moved southward while confined on the continental shelf and many of them reached Geographe Bay within three weeks (Fig. 5). In October–December when the northward winds impeded the Leeuwin Current and drove the inshore Capes Current and offshore Ekman transport, there was more northward and offshore dispersal of particles (Fig. 6). There were also some particles that crossed the shelf break and moved southward along a more offshore route, compared with the April–June period. Very few particles passed Cape Leeuwin and reached the south coast within four weeks in both seasons.

Alongshore dispersal of particles released from the southern Abrolhos reiterated the spatial dispersal patterns in different seasons (Fig. 7). In January–March, the alongshore dispersal was rather symmetrical, with most of the particles confined within ~100 km from their release sites. The alongshore dispersal in October–December was slightly more northward after two weeks. In April–June, southward alongshore dispersal became more dominant, and was similar in September–December. Overall, there were greater numbers of particles lost from the shelf during the summer months (October–March) compared with winter (April–September).

Alongshore dispersal at other shelf locations was similar to the southern Abrolhos with more symmetrical dispersal in October–December, whereas dominantly southward dispersal occurred in April–June when the Leeuwin Current was strong (Fig. 8). However, spatial heterogeneity of dispersal patterns was also evident, whereas in most high retention regions the alongshore dispersals were similar to that of the southern Abrolhos, there were more southward excursions for particles released off North West Cape, Shark Bay and Jurien Bay during April–June, and there was more northward alongshore movement of particles released from Jurien Bay during October–December.

Discussion

In this study, a Lagrangian particle tracking method based on BRAN, an eddy-resolving data-assimilating hydrodynamic model, was used to study spatial variations of local retention rates and alongshore dispersal of surface waters on the continental shelf off the west coast of Australia. Off the coast, interaction between the ocean boundary current and coastal geometry was found to be important for the spatial heterogeneity of retention and dispersal patterns. Low-retention shelf regions tend to experience high alongshore currents, owing to the nearshore influence of the Leeuwin Current (narrow shelf), protruding coastal geography, or formation of mesoscale eddies, whereas high-retention regions were sheltered by coastal geographic features from the direct influence of the Leeuwin Current. Alongshore dispersal also exhibited spatial as well as seasonal heterogeneity, with predominantly southward dispersal during winter and more symmetrical dispersal during summer, with particles released from more exposed shelf regions experiencing longer alongshore excursions.

Although the results are applicable to other ocean boundary current regions, in the following discussion, shelf retention and dispersal patterns are reviewed in the context of recruitment processes of invertebrate and fish species off the west coast of Australia. Early-stage (planktonic) invertebrate and fish larvae are usually buoyant and mixed by surface winds and waves, and have been observed to concentrate in the surface layer of the ocean (e.g. Muhling and Beckley 2007). Thus, the particle tracking by surface currents may provide insight into the retention and dispersal of the planktonic stages of larvae off the west coast of Australia.

Retention rates and invertebrate species

Shelf regions with high retention rates may enhance self-recruitment of invertebrate species, e.g. the commercially fished saucer scallop *Amusium balloti* and Roe’s abalone *Haliotis roei*, off the west coast of Australia.

The saucer scallop, *Amusium balloti*, is an Indo–Pacific species abundant in four shelf regions off the west coast, centred on Shark Bay area, the Abrolhos, the south-west near Fremantle, and Geographe Bay (Fig. 2; Caputi *et al.* 1998; Harris *et al.* 1999). Between the Abrolhos and Fremantle, *A. balloti* spawning occurs from July to March (Joll and Caputi 1995), with a pelagic larval phase of 10–14 days (Rose *et al.* 1988). Thus, with the exception of the Shark Bay fishery, which lies inside the shelter of an almost continuous island chain, the shelf areas with sufficient scallop populations to support commercial fisheries occur near regions with high particle retention rates (Fig. 2).

Roe’s abalone *Haliotis roei* occurs from Shark Bay south to Victoria (Wells and Keesing 1990). Off the west coast, *H. roei* spawns from July to September (Wells and Keesing 1989) and has a larval duration of about a week (WA Department of Fisheries 2005). Commercial catches for this species, which provide a useful proxy of abundance, are highest off Kalbarri (27.5– 28.0°S) and off Perth (31.5–32.5° S) (WA Department of Fisheries 2005; Hancock and Caputi 2006), within shelf areas of high retention rates (Fig. 2).

Caution needs to be taken in interpreting these correlations, as both invertebrate species have particular habitat preferences that may be independent of ocean currents. *A. balloti* prefers wide shelves and in the lee of islands where there are soft-sediment habitats as a result of these geomorphologic patterns, and *H. roei* is an inshore species limited to shallow waters (Wells and Keesing 1990) where the currents that determine rates of retention may be quite different from those from BRAN. Nevertheless, the consistency of spatial patterns of both invertebrates with our modelled retention rates warrants further analysis.

Retention v. dispersal, and their relations with fish larvae distribution

The model results also support measurements on distributions of larval fishes off the west coast of Australia. At 31.5°S (Two Rocks), Muhling *et al.* (2008*a*) found that larval fish assemblages had greater spatial connectivity across the shelf in the austral autumn and winter than summer, and they noted the strong influence of the Capes Current on reducing cross-shelf advection and retaining assemblages of larval fishes on the inner shelf during summer. These are consistent with the seasonal variation of retention rates derived from particle tracking results at this location (Fig. 4).

There are relatively few larval fish studies that have covered a wide latitudinal range along the west coast of Australia. Surveys of eggs and larvae of the economically important sardine, *Sardinops sagax*, show clear alongshore connectivity on the shelf during winter, with eggs more abundant in the north (Abrolhos) and larvae distributed further south towards Geographe Bay (Muhling *et al.* 2008*b*). Surveys of eggs and larvae of the tropical sardine, *Sardinella lemuru*, between Shark Bay and Dongara (near Abrolhos) suggested summer spawning on the outer shelf and northward transport owing to strong southerly winds (Gaughan and Mitchell 2000). The recruitment of tropical fishes from Abrolhos to Rottnest Island (off Fremantle), particularly of those in the family Pomacentridae, indicates the autumn arrival of juveniles with the acceleration of the Leeuwin Current (Hutchins and Pearce 1994; Pearce and Hutchins 2009). These observations corroborate the dispersal patterns derived from the particle-tracking results for the continental shelf off the west coast of Australia.

Limitations and future research

A few assumptions should be borne in mind when interpreting the particle-tracking model results for larval dispersal. The model does not take into account the availability of suitable nursery habitats or post-settlement processes that affect larval survivorship (e.g. Keesing and Halford 1992). Other assumptions include that larvae evenly occupy the top 20 m of the water column and there is no vertical migration or swimming capacity amongst the larvae, topics that have received considerable attention in recent years (Leis 2006, 2007; Leis *et al.* 2009). Despite the limitations of the model, the results tend to support measurements on distributions of invertebrate populations and larval fishes off the west coast of Australia, as discussed in above section. The results may also be applicable to other biochemical tracers on the shelf.

The El Niño Southern Oscillation (ENSO) has a strong influence on the strength of the Leeuwin Current through the equatorial and coastal waveguides (Meyers 1996; Feng *et al.* 2003). Very strong La Niña and El Niño events were experienced in 1996–2000 (Feng *et al.* 2008), which may have provided some extreme conditions for alongshore connectivity. Further study is necessary to understand connectivity under the influence of the ENSO cycle.

There have also been observations that there are strong warming signals on the shelf (Pearce and Feng 2007), and the shelf temperatures will continue to warm under future climate-change scenarios. Further studies are needed to quantify the changes to the marine environment in a changing climate. Under future climate-change conditions, when ocean temperatures warm up, many tropical and temperate marine species may migrate southward along the shelf to find a habitat of suitable temperature regime. The retention and connectivity among different shelf regions will require examination to evaluate their roles as a corridor for the poleward transport and migration.

Acknowledgements

This work was funded by Western Australian Marine Science Institution and CSIRO Wealth from Oceans National Research Flagship. We thank Russ Babcock, Peter Craig, Jim Gunson, and Nick

Mortimer for valuable comments on an early draft of this paper. We would like to thank the MFR Editor, Andrew Boulton, and Scott Condie, Mary Batteen, and one anonymous reviewer for providing constructive comments.

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Fig. 1. Seasonal surface (0–20 m) velocities from BRAN averaged during 1997–2006. The velocities are plotted at every third grid point. Grey boxes in the top left panel indicate particle release segments off the west coast of Australia.

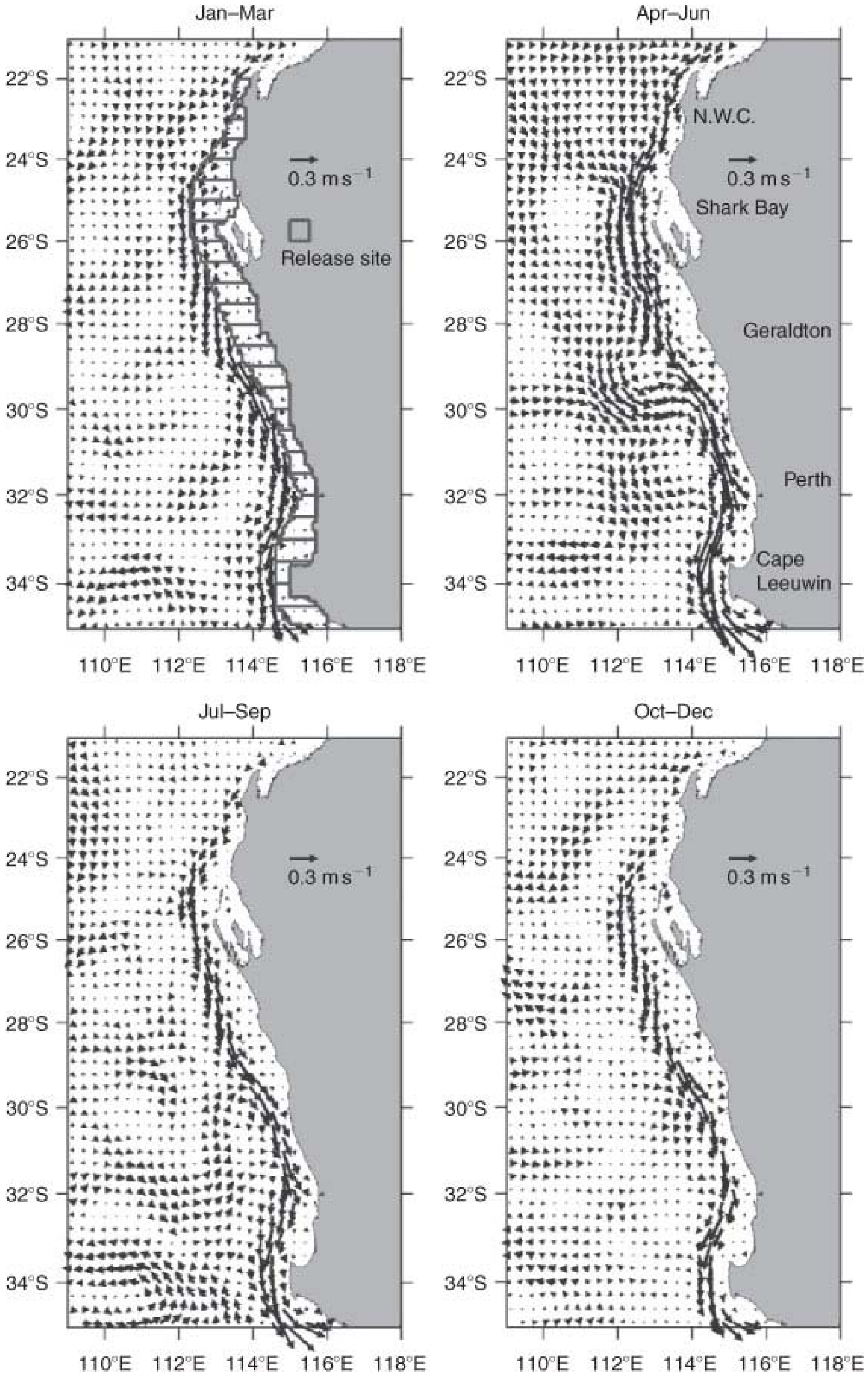

Fig. 2. Retention rates and standard deviations off the west coast of Australia after two weeks of particle tracking (a), and the boundaries of the saucer scallop fisheries in Western Australia (b) (source: Harris et al. 1999). A.I., Abrolhos Islands; N.W.C., North West Cape.

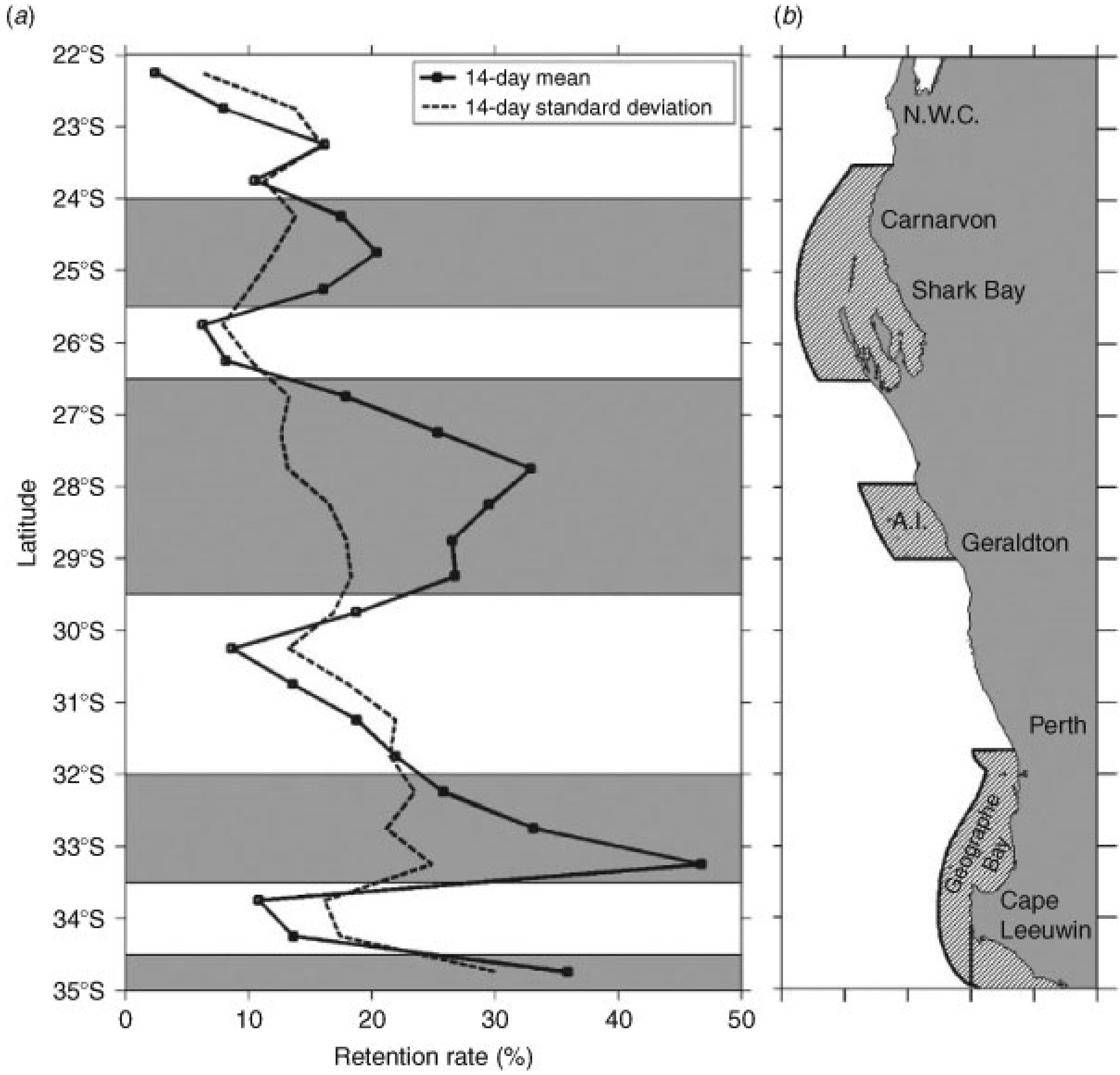

Fig. 3. Relationships between shelf retention rates after two weeks of particle tracking with (a) shelf widths and (b) alongshore velocities in different shelf segments.

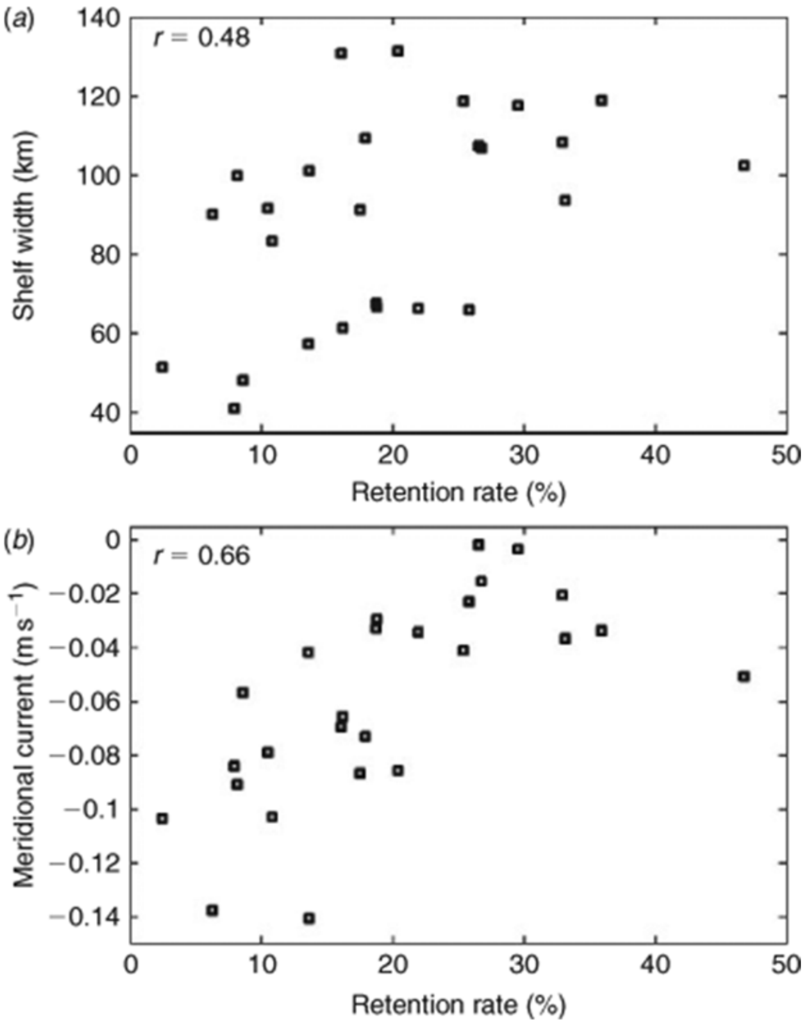

Fig. 4. Seasonal variations of shelf retention rates off the west coast of Australia after two weeks of particle tracking.

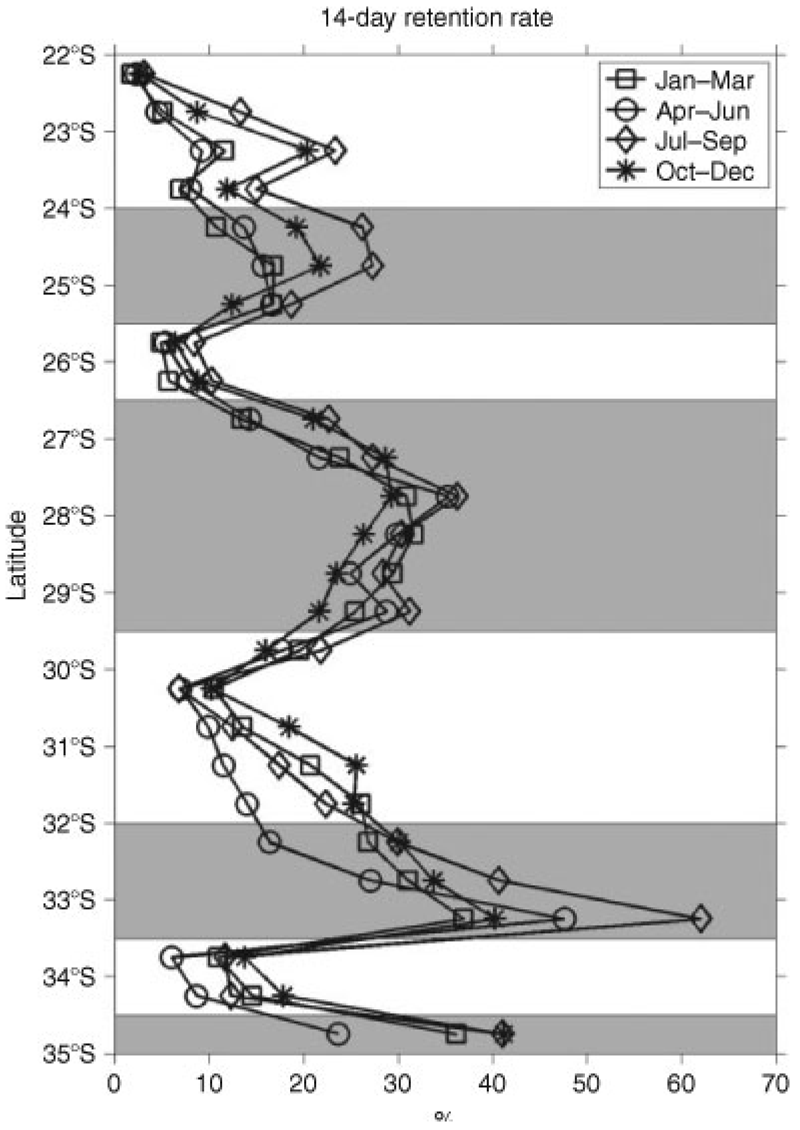

Fig. 5. Spatial dispersal patterns for particles released in the southern Abrolhos segment in April–June, after 1, 2, 3 and 4 weeks of particle tracking. Only areas with particle densities > 0.1% of original releases are plotted.

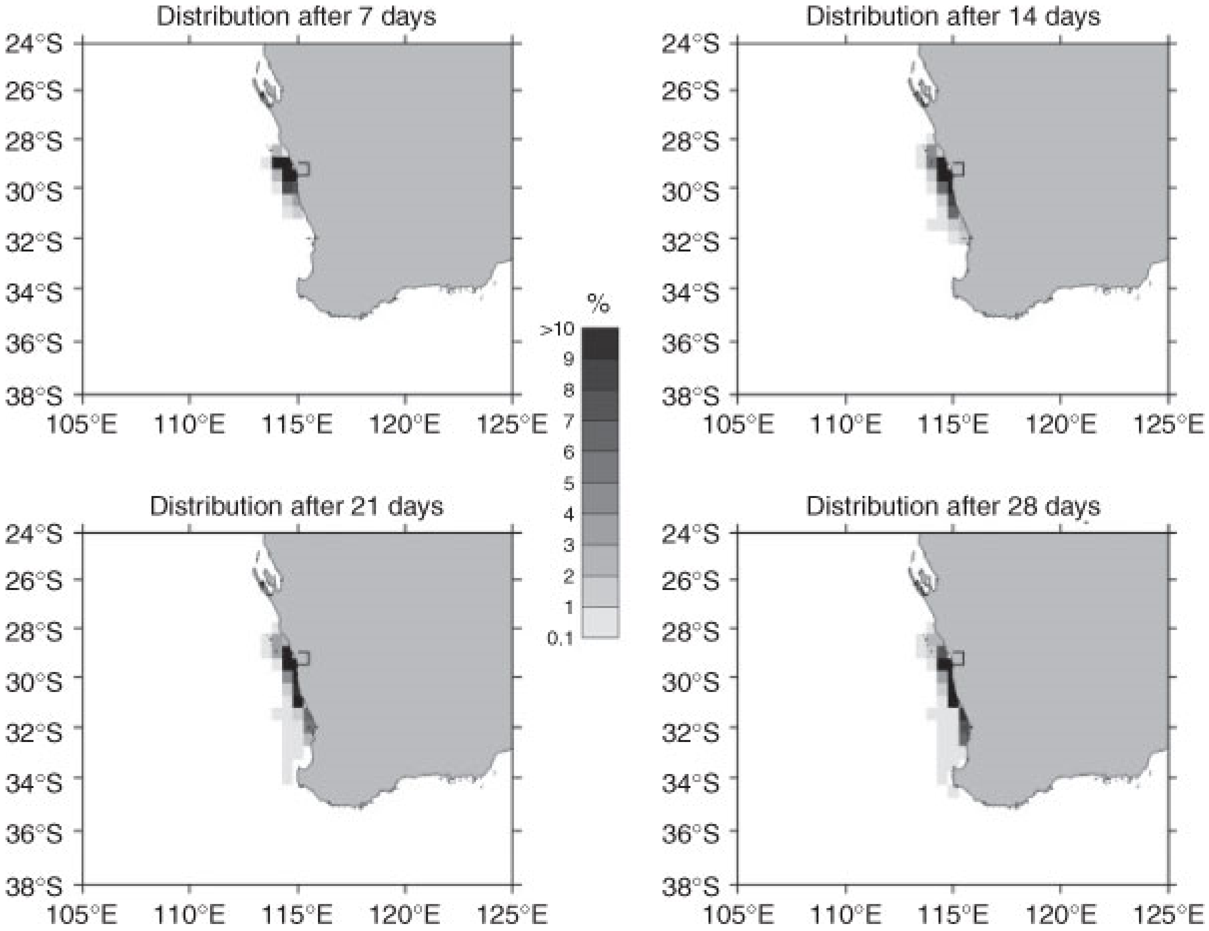

Fig. 6. Spatial dispersal patterns for particles released in the southern Abrolhos segment in September–December, after 1, 2, 3 and 4 weeks of particle tracking. Only areas with particle densities > 0.1% of original releases are plotted.

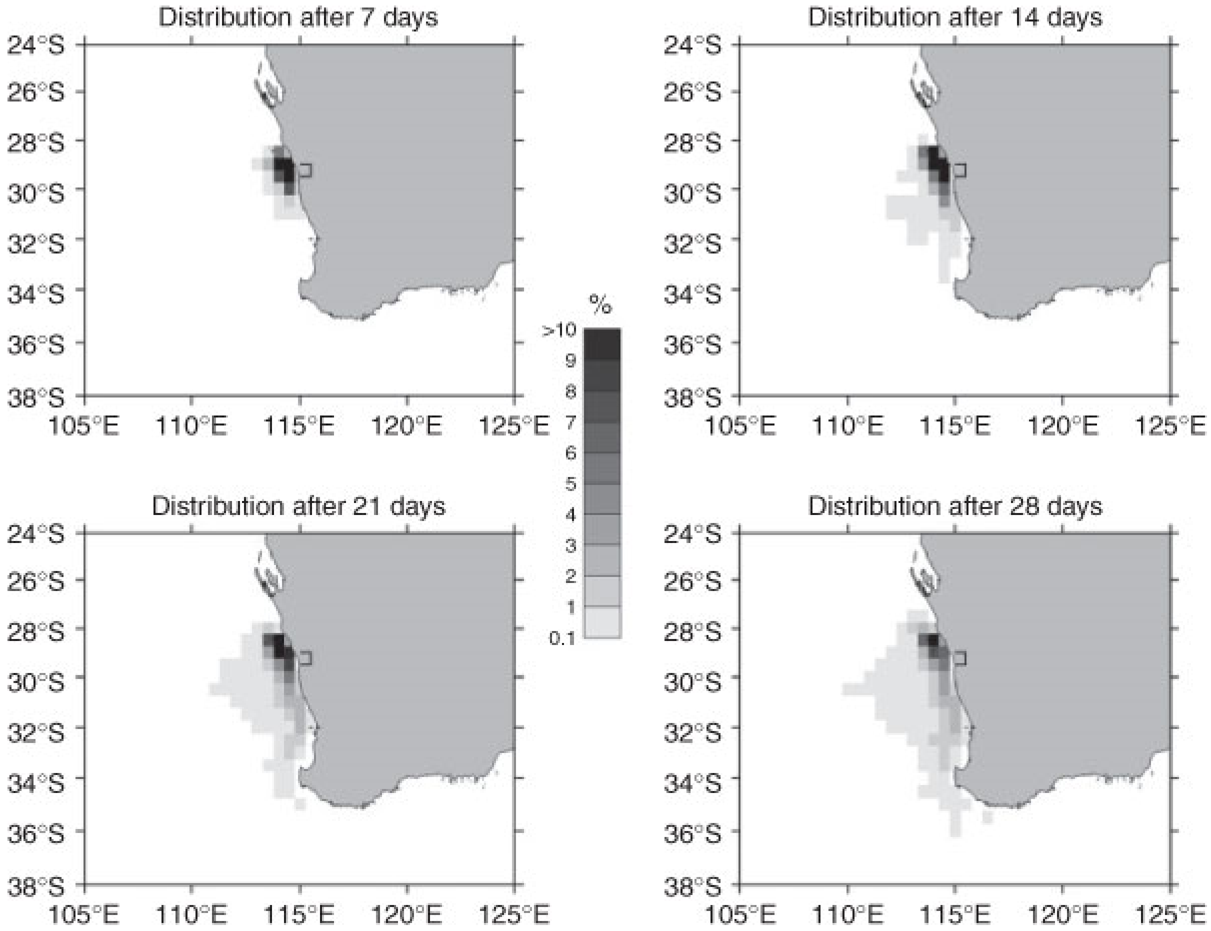

Fig. 7. Alongshore dispersal of particles released from the southern Abrolhos segment averaged for the four different seasons.

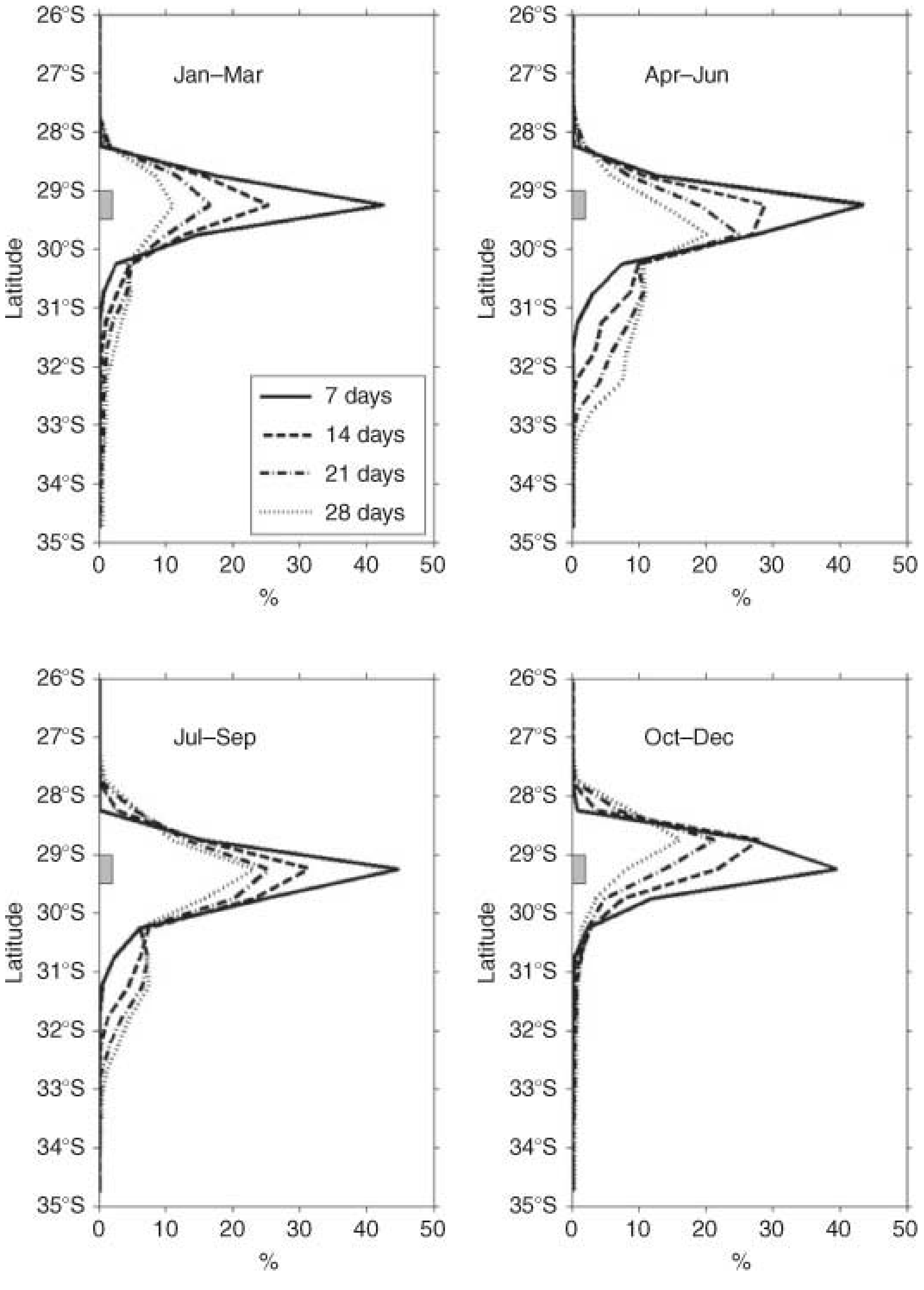

Fig. 8. Alongshore connectivity matrix along the west coast of Australia after four weeks of particle tracking in April–June and September–December. Only values with particle densities > 0.1% of original releases are plotted.