Modelling coastal connectivity in a Western Boundary Current: Seasonal and inter-annual variability

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Abstract

Understanding the transport and distribution of marine larvae by ocean currents is one of the key goals of population ecology. Here we investigate circulation in the East Australian Current (EAC) and its impact on the transport of larvae and coastal connectivity. A series of Lagrangian particle trajectory experiments are conducted in summer and winter from 1992–2006 which enables us to investigate seasonal and inter-annual variability. We also estimate a mean connectivity state from the average of each of the individual realisations. Connectivity patterns are related to the movement of five individual larval species (two tropical, two temperate and one invasive species) and are found to be in qualitative agreement with historical distribution patterns found along the coast of SE Australia.

We use a configuration of the Princeton Ocean Model to investigate physical processes in the ocean along the coast of SE Australia where the circulation is dominated by the EAC, a vigorous western boundary current. We assimilate hydrographic fields from a 10-km global analysis into a 3-km resolution continental shelf model to create a high-resolution hindcast of ocean state for each summer and winter from 1992–2006. Particles are released along the coast of SE Australia, and at various isobaths across the shelf (25–1000 m) over timescales ranging from 10–90 days. Upstream of the EAC separation point across-shelf release location dominates the particle trajectory length scales, whereas seasonality dominates in the southern half of the domain, downstream of the separation point.

Lagrangian probability density functions show dispersion pathways vary with release latitude, distance offshore and the timescale of dispersion. Northern (southern) release sites are typified by maximum (minimum) dispersal pathways. Offshore release distance also plays a role having the greatest impact at the mid-latitude release sites. Maximum alongshore dispersion occurs at the mid-latitude release sites such as Sydney. Seasonal variability is also greatest at mid-latitudes, associated with variations in the separation point of the EAC. Climatic variations such as El Niño and La Niña are also shown to play a role in dictating the connectivity patterns. La Niña periods have a tendency to increase summer time connectivity (particularly with offshore release sites) while El Niño periods are shown to increase winter connectivity.

The EAC acts as a barrier to the onshore movement of particles offshore, which impacts on the connectivity of offshore release sites. Consequently particles released inshore of the EAC jet exhibit a greater coastal connectivity than those released offshore of the EAC front. The separation point of the EAC also dictates connectivity with more sites being connected (with lower concentration) downstream of the separation point of the EAC. These results can provide a useful guide to the potential connectivity of marine populations, or the spread of invasive pests (via ballast water or release of propagules from established populations).

1. Introduction

The pelagic dispersal of marine larvae links populations across a wide geographic range and reduces their chance of extinction (Johannes, 1978). The supply of larvae (both numbers and timing of arrival), that can be affected by oceanographic conditions and behaviourally dependent connectivity patterns, can play a critical role in determining the distribution and abundance of many marine species. Understanding and predicting the spatial distribution of organisms is among one of the most important goals in population ecology (Siegel et al., 2003).

The importance and scale of long-distance dispersal of larvae by oceanic currents has been well documented (e.g., Booth et al., 2005).
2007), and in some cases the patterns of dispersal have been modelled (e.g., North et al., 2008; Fox et al., 2009). But in general, there is little detailed understanding of the connectivity of marine populations via oceanic currents (Largier, 2003). Such information is, however, important for a variety of purposes including designing the size and arrangement of marine protected areas (Botsford et al., 2003), managing commercial fish stocks and for understanding (and helping to manage) the spread of marine pests (Glasby and Lobb, 2008). The dispersal of marine pests has typically been quantified in relation to more easily measured vectors such as ships (hulls and ballast water), or aquaculture infrastructure (Carlton, 1987; Ruiz et al., 1997). But the potential for pests to disperse via currents is enormous as propagules of many species can remain in the water column for periods of weeks to months.

Previously estimates of dispersal have relied on either simplified advection diffusion models or passive particle models that use mean currents to define the potential for spread (Largier, 2003; Cowen et al., 2006). In recent times, progress has been made in understanding the connectivity of populations in simple flow environments using idealised models (Aiken et al., 2007; Bode et al., 2006), and in region specific estimates of larval dispersion (e.g., Xue et al., 2008; Condie and Andrewartha, 2008, inter alia). Increasingly high level circulation models are being used to simulate the dispersion of passive and active particles within and among estuaries and in the coastal ocean (Mitarai et al., 2009; Huret et al., 2007). With the improvement of physical circulation models it is now possible to run semi-realistic simulations of the coastal environment at high spatial and temporal resolution to aid an understanding of population connectivity (Gillanders et al., 2010).

In a complex western boundary current system the use of mean currents gives a simplified approximation to the likely dispersion patterns, and it does not allow for the spatial complexity of the circulation (such as coastal separation, encroachment of the jet, or the complex eddy field circulation). Nor do these methods typically account for seasonal and inter-annual variability, making it difficult to quantify the statistical (and biological) reliability of the model. Estimates of source and sink regions do not necessarily identify the pathway that larvae take between spawning and settlement. Furthermore transport pathways may affect population resilience, for example larvae caught in a rotating eddy for a month may be starved of food, more prone to predation, or subject to less than ideal temperatures.

Here we address some of the shortcomings in oceanographic modelling applied to connectivity questions in the East Australian Current (EAC). We have used the output from a state of the art model (POM) to model physical processes in the ocean along the coast of SE Australia. POM has a free surface, a curvilinear grid and vertical sigma coordinates. The velocity components; u, v and w correspond to velocities in the alongshore (x direction), offshore (y direction) and vertical (normal to the sigma surfaces) directions, respectively. The primitive equations are solved on an Arakawa-C staggered grid using finite difference methods (Blumberg and Mellor, 1987). The Smagorinsky (1963) scheme is utilised in calculating horizontal diffusion and is applied with an inverse turbulent Prandtl number (TPRNI) of 1.0 and a horizontal diffusivity coefficient (HORCON) of 0.1. Temperature and salinity are advected using three iterations of the Smolarkiewicz upstream advection scheme (Smolarkiewicz, 1984). The Craig and Banner (1994) scheme for calculating the wave-driven flux of turbulent kinetic energy at the surface has been implemented and a hydrostatic correction term for sigma-coordinate models has also been included (Chu and Fan, 2003). Coastal boundary conditions at the western boundary are: zero normal velocity, free-slip tangential velocity and zero gradient for vertical velocity, temperature and salinity.

2. Methods

2.1. Ocean circulation model description

Here we use a configuration of the Princeton Ocean Model (POM) to model physical processes in the ocean along the coast of SE Australia. POM has a free surface, a curvilinear grid and vertical sigma coordinates. The velocity components; u, v and w correspond to velocities in the alongshore (x direction), offshore (y direction) and vertical (normal to the sigma surfaces) directions, respectively. The primitive equations are solved on an Arakawa-C staggered grid using finite difference methods (Blumberg and Mellor, 1987). The Smagorinsky (1963) scheme is utilised in calculating horizontal diffusion and is applied with an inverse turbulent Prandtl number (TPRNI) of 1.0 and a horizontal diffusivity coefficient (HORCON) of 0.1. Temperature and salinity are advected using three iterations of the Smolarkiewicz upstream advection scheme (Smolarkiewicz, 1984). The Craig and Banner (1994) scheme for calculating the wave-driven flux of turbulent kinetic energy at the surface has been implemented and a hydrostatic correction term for sigma-coordinate models has also been included (Chu and Fan, 2003). Coastal boundary conditions at the western boundary are: zero normal velocity, free-slip tangential velocity and zero gradient for vertical velocity, temperature and salinity.

2.2. Model configuration

Over the last 10 years POM has been configured for the NSW continental shelf off the southeast coast of Australia (Marchesiello and Middleton, 2000; Oke and Middleton, 2001; Roughan et al., 2003; Baird et al., 2006a; Macdonald et al., 2009, inter alia) where the flow is dominated by the EAC. The model spans 1025 km of the NSW continental shelf between 28˚ and 37.5˚ S. At 28˚ S the grid area spans 395 km east from 153.5˚ to 157˚ E and at 37.5˚ S it spans 500 km east from 149.5˚ to 155.5˚ E. The maximum depth of the domain is 2000 m. This configuration improves on previous NSW
shelf configurations as the minimum depth is reduced from 50 m to 15 m and a better depiction of the coastline is used. This enables better representation of shallow water and near shore processes.

The SEAPOM configuration has 130 and 325 grid cells in the east–west and north–south directions, respectively (Fig. 1). The resolution ranges from 1 to 6 km in the east direction and 1.5 to 6 km in the north direction. There are 36 sigma levels with spacing ranging from 1.1% to 4.35% of the total depth. This gives more resolution on the continental shelf and in the top and bottom layers, for example, in shallow water (15 m) the first sigma level is less than 3 m thick. The model solves the external (barotropic) mode with a 1.7 s timestep and the internal (baroclinic) mode with a 60-s timestep.

2.3. Downscaling an eddy-resolving global ocean model for the continental shelf

Here we use the Bluelink ocean data assimilation system (BODAS), an ensemble optimal interpolation system to assimilate data into our high-resolution continental shelf model. BODAS, which is one of the many Bluelink products (Oke et al., 2007) recreates the ocean state once every seven days using temperature and salinity data from a combination of satellite altimetry, Argo, XBT, TAO and other sources. This is then assimilated into a global ocean general circulation model with a 10-km spatial resolution around Australia, resulting in BRAN (BlueLink ReANalysis) (Oke et al., 2007; Brassington et al., 2006).

BRAN 2p1 is a daily hindcast of ocean state from 1992–2006. The present BRAN configuration, however, does not provide sufficiently high resolution in the horizontal or the vertical to investigate shelf processes. Hence for applications such as the transport of small particles, particularly those that may come into shallow water within close proximity of the coast we downscale the coarse resolution BODAS to initialise a higher-resolution continental shelf model.

For the first time BODAS hydrographic fields have been used to force the higher resolution SEAPOM configuration of the coastal ocean off SE Australia (Baird et al., submitted for publication). In this project BODAS temperature and salinity fields are assimilated into the higher-resolution SEAPOM configuration, meaning that, what was previously an idealised numerical simulation of the EAC, is now a fairly realistic high-resolution hindcast of the ocean state off the coast of SE Australia for any one day from 1992–2006. The reader is referred to Baird et al. (submitted for publication) for full details of the circulation model, SEAPOM.

Along the eastern and southern boundaries we apply a volume constraining radiation boundary condition with relaxation that permits oblique waves to radiate outwards (Marchesiello et al., 2001) to elevation and the baroclinic horizontal velocity components. For the barotropic horizontal velocity components the Flather condition is applied (Flather, 1976). The relaxation to BODAS occurs once every seven days over a 24-hour period, at every gridbox in the horizontal and vertical. Sensitivity experiments showed that the optimum relaxation strength (i.e. when the root mean square error in sea-surface temperature (SST) is minimised over the continental shelf) is when \( \tau = 1 \text{d}^{-1} \) (Baird et al., submitted for publication). In addition to BRAN forcing, SEAPOM has been forced with daily averaged wind fields (NCEP) and radiative fluxes for each period (Kalnay et al., 1996).

The advantages of our high-resolution SEAPOM model are many. Most obviously is the resolution of the model both in space, and a higher resolution time step. We have a more advanced vertical mixing scheme, which is particularly important in shallow regions. The shelf topography is of a higher resolution (Fig. 1), which means that we are able to resolve alongshore locations more precisely. The bathymetry of the POM model is also more accurate; for example it was noted that in the BRAN2p1 configuration, Lord Howe Island lies 600 m sub-surface. We have increased vertical resolution in the important continental shelf region and sigma co-ordinates in the vertical which enables very high resolution in shallow water (see Fig. 2. Baird et al., submitted for publication). The resolution of SEAPOM should be able to better depict small scale processes, such as those on the continental shelf, or across tight fronts and eddies and enables investigations such as particle dispersion scenarios.

2.4. Model initialisation

SEAPOM initialisation occurs in two stages. Stage one is diagnostic where temperature and salinity are initially set to BODAS fields and held constant while allowing velocity to evolve. Stage two is prognostic where temperature and salinity are allowed to evolve and are relaxed to the BODAS data following assimilation (once every seven days). Forcing such as solar radiation and surface winds are also introduced during this stage (Baird et al., submitted for publication). Stage two begins 14 days (two assimilation cycles) before the tracer experiments are commenced.

2.5. Model validation and assessment

To be able to simulate connectivity patterns one must have confidence in the ocean circulation model. To this end, robust model validation and assessment was undertaken by Baird et al. (submitted for publication). Comparisons between observed velocities (obtained with a shipboard ADCP) and temperature
Roughan and Middleton, 2002, 2004), SEAPOM and BRAN (Fig. 2) during February 1999 show that SEAPOM performs better in the complex shelf region off Port Stephens. SEAPOM better captures the strength of the EAC jet offshore, the location of the zero isotach as well as the northward counter current inshore of the jet (Fig. 2C, D, and E). BRAN does not capture the northward inshore flow (Fig. 2A and B), it underestimates the strength of the jet, the location of the temperature front, and underestimates the strength of the upwelling, indicated by warmer temperatures through the bottom boundary layer. A further example of the improvement in the temperature and velocity resolution of the downscaled product (SEAPOM) is shown in Fig. 3 (Baird et al., submitted for publication, their Fig. 12). While BRAN captures the gross features of the poleward flowing EAC (Fig. 3B) and its separation from the coast, SEAPOM (Fig. 3A) depicts a series of coastal eddies inshore of the separated WBC jet and a significant northward coastal flow. Such a flow field is commonly found in the Port Stephens region (e.g., Fig. 2). This has major implications for the transport of particles in a direction counter to that of the swift poleward flowing WBC.

2.6. Numerical experiments

In order to investigate seasonal and inter-annual variability 28 different simulations were conducted spanning the Austral summer (DJF) and winter (JJA) starting from December (summer) of 1992 to August (winter) of 2006. Model day 0 is taken to be at the end of the two stage initialisation, i.e. after 34 days, and is equivalent to a day close to the start of summer or winter (which varies each year as BODAS output is only every seven days).

2.7. Particle tracking

One of the applications of these high-resolution hindcasts is to investigate the trajectories and dispersion of particles under different scenarios (e.g., year, season, release latitude, release isobath). Particles are moved in the model using a formulation based on the advection–diffusion equation. We advect the particles on-line using a 3-D particle tracking scheme available as a POM add-on, which makes use of the model velocities (horizontal and vertical). At each time step we interpolate the velocities linearly at the sub-gridscale level. Dispersion is incorporated into the particle tracking routine with the inclusion of a random walk component. The 2.5 level Mellor and Yamada (1982) turbulence closure scheme is used to calculate the instantaneous turbulent kinetic energy (TKE) throughout the model domain. The effects of sub-grid scale processes are approximated by the turbulence diffusion terms, which are scaled as a random number normalised between 0 and 1 (Roughan et al., 2003; Xue et al., 2008).

A series of particle tracking simulations were conducted. Particles were released in the surface waters above various isobaths of biological significance (25, 50, 100, 200 and 1000 m) at 17 × 0.5° latitudinal intervals from 29–37°S with seven extra release sites corresponding with the mouth of major estuaries along the coast (Table 1, Fig. 1), giving a total of 120 particle release sites per simulation. Particles were released in the surface sigma layer, i.e. at a depth of 0–3 m below the surface. The offshore locations were chosen to give flexibility in the interpretation of the results. For example, wherever possible, vessels are required to discharge ballast water at least 200 nm from shore and in water at least 200 m deep to minimise chances...
of species arriving to ports or estuaries where they might settle and establish. Hence the releases above the 200- and 1000-m isobaths could be representative of such events.

Ten particles were released from each release site on model days 0, 5, 10, 15 and 20, giving a total of 6000 particles for each season (168,000 across 28 seasons). When a particle reaches a boundary (northern, eastern, southern or the western coastal boundary) it stops propagating. Settlement is considered to have occurred when a particle comes within a third of a grid box of the coast within each latitudinal band (i.e. in surface waters).

Large-scale flows will affect the displacement of the centre of mass of patch, where as small scale variability will determine the relative dispersal of the larvae (Gabric and Parslow, 1994). The EAC is an advection driven regime with along-shore velocities of up to 2 ms$^{-1}$, as such advection dominates over sub-grid scale diffusion. Additional particle tracking experiments were conducted to test the sensitivity of the results to the number of particles. Finally an additional high-density particle-tracking simulation was undertaken for July–August 2004 to undertake model-data comparisons.

### 2.8. Biological parameters

In this study we do not include biological parameters explicitly. However, we make approximations for pelagic larval duration (PLD) by investigating particle trajectories on timescales ranging from 10–90 days, i.e. covering a wide range of planktonic durations for marine propagules. We account for seasonal spawning preferences by comparing summer and winter simulations and we allow for preferences in depth by investigating release sites over various isobaths across the shelf. We do not account for the role of larval behaviour (e.g., vertical and horizontal swimming) in modifying trajectories, thus our discussion of the typical larval trajectories considers time frames prior to when the larvae are able to swim well. We acknowledge that the inclusion of diurnal vertical migration may alter the results significantly (e.g., North et al., 2008; Roughan et al., 2005), however, this work is a first step towards understanding mean connectivity along the coast of SE Australia. We only consider coastal settlement that by default accounts for habitat suitability; it also allows for an investigation into connectivity between estuaries. Applying these results to habitat suitability is the subject of ongoing work.

In Section 6.1 we relate the simulated particle paths to five specific larval species that are found along the coast of SE Australia as an example of how the results could be used. The particular species are chosen as they spawn across different latitudinal ranges (tropical or temperate), have been observed to ‘settle’ or survive along the coast of SE Australia and because they vary in their pelagic larval duration (PLD). We have chosen two tropical fish species, two temperate commercial fish species and one invasive marine pest. All species identified are broadcast spawners, hence the dispersion of particles is of particular relevance for their survival. Furthermore, larvae are typically

![Fig. 3. Comparison of SST (colourbar, °C) and velocity fields (black vectors, ms$^{-1}$) from SEAPOM (l) and BRAN (r) (Baird et al., submitted for publication, Fig. 12).](image-url)

### Table 1

<table>
<thead>
<tr>
<th>Site</th>
<th>Lat</th>
<th>Lat band</th>
<th>Estuary</th>
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<tr>
<td>R1</td>
<td>29'</td>
<td>29</td>
<td>–</td>
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<tr>
<td>R2</td>
<td>29</td>
<td>29.5</td>
<td>Clarence River</td>
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<tr>
<td>R3</td>
<td>30'</td>
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<tr>
<td>R4</td>
<td>30</td>
<td>30</td>
<td>Coffs Harbour</td>
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<tr>
<td>R5</td>
<td>30</td>
<td>30.5</td>
<td>Kalang River</td>
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<tr>
<td>R6</td>
<td>30</td>
<td>30.5</td>
<td>Nambucca River</td>
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<td>R7</td>
<td>30</td>
<td>31</td>
<td>Southwest Rocks</td>
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<td>R8</td>
<td>31</td>
<td>31.5</td>
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<td>31</td>
<td>32</td>
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<td>32</td>
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<td>R11</td>
<td>32</td>
<td>32.5</td>
<td>Port Stephens</td>
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<td>R12</td>
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<td>33</td>
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Major estuaries and nominal latitudinal bands are identified.
confined to the mixed layer hence the approach used here of surface release sites is appropriate. The focus species are:

- Damsel Fish (Pomacentridae): A tropical family which spawns north of 28°S and have been observed to settle as far as 37°S, with a PLD of 15–30 days (Booth et al., 2007). Typically reef associated fishes, but can occur down to depths of 40–50m.
- Butterflyfish (Chaetodontidae): Also a tropical family which spawns north of 25°17’S, and has a PLD of 40–60 days (Hoese et al., 2006) with settlement observed as far south as 37°1’S (Booth et al., 2007). Typically associated with shallow (1–20 m) coral reefs.
- Snapper (Pagrus auratus): A temperate species of commercial relevance which broadcast spawns and recruits in estuaries, with a PLD of 18–31 days (Kingsford and Atkinson, 1994). Breeding adults are associated with offshore rocky reefs extending from the near shore out to the edge of the continental shelf.
- Blue Mackeral (Scomber australasicus): Neira and Keane (2008) found greatest larval abundances 10 nm shoreward of the shelf break linked to bathymetric (100–125 m deep) and hydrographic factors (19–20°C), typically in EAC or EAC ‘mix’ water, northwards of 34.6°S. They spawn June–October (Neira and Keane, 2008) and PLD is approximately five weeks, however, they swim well after 3–4 weeks (I Suthers Pers. comm.).
- European shore crab (Carcinus maenas): Considered a marine pest in Australia and many other countries. It is an estuarine species whose larvae can be transported across the shelf (observed up to 40 km offshore) before being returned to estuaries where they settle (Queiroga, 1996). It can have a larval duration around 30–40 days in the Austral summer and 40–50 days in winter, depending on water temperature (deRivera et al., 2007).

3. Results

3.1. Particle trajectories—seasonal and inter-annual variability

The main feature defining the movement of the particles along the coast of SE Australia is the poleward flowing EAC, its separation from the coast and the mesoscale eddy field. During the study period the location of the separation point varies between 30° and 33° S and hence the region where particles are advected offshore changes between years and seasons. Upstream of the EAC separation point particle trajectories are predominantly poleward (Fig. 4) particularly at the mid-shelf and shelf break release sites (100-, 200- and 1000-m isobaths, not shown). The near coastal release sites (25-m isobath shown in Fig. 4) do exhibit minimal northward transport. Between 34° and 36° S (i.e. downstream of the EAC separation) resultant particle distributions are bi-modal. Particles tend to either remain adjacent to the coast or to be swept eastward to the open ocean depending on the proximity of the EAC to the coast and the position of the EAC separation. In this way the EAC can act as a barrier to the onshore movement (and coastal connectivity) of particles released offshore, aiding retention inshore of the jet, whereas particles captured within the EAC are driven offshore.

![Fig. 4. Particle paths after 10, 30, 60 and 90 days (l-r) for the first tracer released at the 25 m isobath. The colour of the particle path ranges from red through orange and white to blue as the latitude of particle seeding moves poleward, i.e. red (blue) for particles seeded at northern (southern) latitudes. The instantaneous model velocities (temperature) at the end each time period are overlaid in black arrows (shading). Each row shows a different year and season as indicated in the panel, i.e. winter 1993, summer 1994, winter 2003, summer 2004 (top–bottom).](image-url)
Inter-annual variability in the particle paths is evident in Fig. 4 where representative trajectories are shown for Summer 1994 and 2004 and Winter 1993 and 2003 for each release at the 25 m isobath after 10, 30, 60 and 90 days. The presence (Summer 1994, Winter 1993) or absence (Summer 2004, Winter 2003) of the EAC eddy field dictates the circulation from the separation point poleward. Recirculation and retention is a maximum when eddies are present, whereas poleward transport is a maximum when the EAC remains attached to the coast to the southern end of the domain.

Particles tend to be advected more quickly during summer (Fig. 4) than winter, indicative of the strong seasonal cycle of the EAC. Furthermore northward movement is more pronounced during the winter simulations, e.g., Winter 1993. The EAC circulation features clearly dominate the particle trajectories. The presence or absence of an EAC eddy also dictates circulation and retention on the continental shelf region. When the eddy field is far offshore, coastal transport is northward downstream of the EAC separation point. Northward coastal transport can also be great when a cyclonic eddy encroaches on the continental shelf driving velocities of up to 1 m/s northward, downstream of the separation point (e.g., off Sydney).

### 3.2. Trajectory timescales

Intuitively the length of the particle trajectories increases with time from 10–90 days. In the first 10 days the majority of the particles are constrained within close proximity of the coast, after 30 days some particles have settled at the coast and some are still within the coastal area but have not settled while others have left the coastal area. After 60 days nearly all particles have either settled or have left the coastal area and have been entrained into eddies which break away from the EAC in the southern half of the domain. By 90 days most of the particles have reached a boundary meaning that they would have left the model domain if they had not already settled (Fig. 4).

### 3.3. Trajectory length scales

The mean trajectory length scales (i.e. the distance travelled by a particle) helps to identify the variability within the particle trajectories (Fig. 5). The distance travelled is considered to be the straight line alongshore distance from the particle end point to its origin. Fig. 5 compares the mean distance travelled by particles released at three sites (R2, R15, R24, where R2 is upstream of the EAC separation point and R15, R24 are downstream), inshore (25 m) and offshore (1000 m), in summer and winter, for timescales of 10–90 days (L-R) where 0 km indicates the particle release site. The distances particles travelled are grouped into 100 km bins and positive (negative) distance indicates equatorward (poleward) transport.

![Fig. 5. Larval trajectory lengths, i.e. the mean distance travelled by particles released at three sites (R2 (1-4), R15 (5-8), R24 (9-12)), inshore (25 m) and offshore (1000 m), in summer and winter, for timescales of 10–90 days (L-R) where 0 km indicates the particle release site. The distances particles travelled are grouped into 100 km bins and positive (negative) distance indicates equatorward (poleward) transport.](image-url)
leave the vicinity of the release point. It is here (Fig. 5, Column a) that length scale variability is greatest. By 60–90 (Fig. 5, Column c and d) days the importance of timescales gives way to coastal proximity and seasonality as most particles are eventually entrained into the EAC or advected out of the domain.

Proximity of the release site to the coast can also dictate distance travelled. The inshore release sites (Fig. 5, Rows 1, 2, 5, 6, 9, and 10) exhibit high variability particularly during summer, whereas the offshore release sites exhibit less variability particularly during winter and especially upstream of the separation point of the EAC (Fig. 5, Rows 1–4). Typically the offshore release sites are in the core of the EAC (especially upstream of the separation point) and are advected poleward swiftly with less variability in the lengthscales. Seasonality dominates the trajectory length scales at the southern release sites (Fig. 5, Rows 9–12). This is consistent with the seasonality of the EAC (stronger and penetrating further southward in summer than in winter).

Northward transport is a maximum in winter, particularly at the downstream release sites (after 10 days, R2 < 100 km, R24 > 400 km northward, after 90 days R24 > 800 km northward), which is significant when investigating the dispersal pathways of species that spawn in winter. At the southern release sites the northward transport is significantly greater than any of the more northern release sites. Poleward transport is least at the southern release sites; however, this is most likely an artefact of the proximity to the southern boundary of the model domain. Interestingly our results support the analysis of Coleman et al. (in preparation) who investigated the genetic variability in seaweed along the NSW coastline. They showed that genetic similarities between coastal kelp communities separated by distance could be attributed to the less uniform nature of the velocity fields when compared with other regions with a predominantly unidirectional current.

4. Lagrangian probability density functions

The Lagrangian probability density functions (PDF, Figs. 6–8) represent the probability that a particle will pass a location at some point in the given time frame expressed as a percentage of total number of particles released. For example a high value indicates that a greater percentage of particles have entered the grid box (divided by the area of the grid cell to account for variations in grid size) by the end of the specified timeframe. The PDFs are calculated at all release sites from all the simulations. Hence we can statistically quantify the spatial probability of particle dispersion that theoretically captures the temporal variability in the dispersal process (Cowen and Sponaugle, 2009).

Maximum alongshore dispersion occurs at the mid-latitude release sites, e.g., represented by Sydney (R15, 33.49° Fig. 7). This is particularly evident inshore of the shelf break (25, 50, 100-m release sites) indicating the strength of the EAC and its proximity to the coast. Alongshore dispersion is less at the northern release sites (e.g., Clarence River, R2, 29 25° Fig. 6); however, at the sites upstream of the EAC separation point a greater number of transport pathways exist, particularly with release distance offshore and as transport timescales increase (Fig. 6 panels N, O, R, S, and T). This occurs as particles are advected southward on the EAC and eastward into the Tasman eddy field.

At the southern end of the domain dispersion is mainly restricted to within the coastal zone, however, both northward and southward transport pathways exist, with an increase in

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Fig. 6. Lagrangian probability density functions for the Clarence River Summer release site (R2). Each column represents a different release isobath (25, 50, 100, 200, 1000 m L-R). Each row represents a different trajectory timescale (10, 30, 60 and 90 days T-B). The colour scale represents the probability that a particle will pass a location at some point in the given time frame expressed as a percentage of total number of particles released divided by the area of the grid cell to account for variations in grid size.
northward transport moving south through the domain. Release sites across the shelf exhibit similar patterns with some advection into the Tasman Sea for the longer timescales (60, 90 days) and at the offshore release sites (200, 1000 m, Fig. 8, panels N, O, S, and T). Offshore release distance also plays a role having the greatest impact at the mid-latitude release sites where acrossshore (alongshore) dispersion is a minimum (maximum) for the coastal release sites and a maximum (minimum) for the offshore release sites. Seasonal variability (Fig. 7) is greatest in the middle of the domain, associated with variations in the separation point of the EAC. The winter time PDFs show much greater number of dispersion pathways.

Fig. 7. Lagrangian probability density functions for the Sydney release site (R15): Summer (L) and Winter (R). See Fig. 6 for further explanation.

Fig. 8. Summer Lagrangian probability density functions for the 36°S site (R22). See Fig. 6 for further explanation.
4.1. Sensitivity to number of particles

To investigate the effects of diffusion, additional particle tracking experiments were conducted over a 30-day period with varying numbers of particles. Ten particles were released every 30 min over a 30-day period (giving a total of 208,000 particles per site) and were advected for 30 days. Two other scenarios were investigated where 10 particles were released every 60 and 120 min resulting in \( \sim 104,000 \) and \( \sim 52,000 \) particles per site. Results of the high density particle tracking experiments show that an increased number of particles creates a somewhat smoother PDF; however, the differences are not significant when estimating circulation pathways (Fig. 9). In general PDF patterns are very similar, exhibiting southward flow which tends eastward near 31°S. The greatest difference occurs at the EAC separation point, which is to be expected as this is a highly dynamic region (Fig. 9). However, this result does not affect the general conclusions of this paper. Releasing more than 52,000 particles makes virtually no difference to the results. These results are in agreement with Griffa et al. (2004) who investigated the impact of smoothing of Eulerian velocity fields on the predictability of Lagrangian particles. The results show that the smoothing has a strong effect on the centre of mass behaviour, while the scatter around it is only partially affected. Furthermore the impact on connectivity results is minimal. We see a small increase in the number of connected estuaries where releasing more particles allows for a slightly greater range in connectivity. There is also an increase in connectivity to the north of some of the southern release sites suggesting that the experiments performed do not fully capture the variable nature of the northward flow. However, these two results do not impact on the general conclusions of this paper, in fact they serve to support the results.

5. Connectivity

Connectivity matrices are a useful tool for describing the source-to-destination relationships for larval dispersal over a given larval development timeframe (Mitarai et al., 2008). They have been used in recent times to diagnose the timespace dynamics of larval settlement (Cowen et al., 2006; Bode et al., 2006; Xue et al., 2008; Mitarai et al., 2009). Cowen and Sponaugle (2009) define a connectivity matrix as the probability of exchange of individuals between patches. Here we column normalise the matrix, hence the matrix elements \( r_{ij} \) gives the probability that an individual released from population \( i \) will go to population \( j \). Hence in Figs. 10–12 the \( x \)-axis represents the source over the given isobath and the \( y \)-axis represents the sink latitude at the coast.

5.1. Mean connectivity and seasonal variability

Larval connectivity is inherently an intermittent and heterogeneous process on annual timescales (Siegel et al., 2008). The stochastic nature results primarily from the dependence of larvae on coastal currents for advection. This creates an unavoidable uncertainty when trying to estimate the connectivity of populations (Siegel et al., 2008). The advantage of a high-resolution hindcast such as that used here, is that it can build a reliable view of mean connectivity. Not only can we describe the connectivity within any single ‘realisation’ from year to year (1992–2006) and from season to season, (as per Section 5.2, following) where connectivity can vary significantly between realisations. More importantly, we can now begin to quantify the variability in the system using our hindcast model. Figs. 10–11 show the seasonal variability. The standard deviations of the connectivity matrices are also calculated for each scenario (not shown).

As identified in the particle trajectories and the Lagrangian probability density functions (Figs. 4–8) typically upstream of the EAC separation point particles tend to be advected poleward by the EAC. This affects the connectivity to the point that each region tends to be connected to areas downstream of it (Figs. 10–11).

Also affecting the connectivity is the proximity of the release site to the coast. Particles released inshore of the EAC jet (typically 25, 50 m) exhibit greater coastal connectivity than those released offshore of the EAC front (Figs. 10–11, Rows 1, 2, and 3). The core of the EAC generally flows above the 200-m isobath, but extends out towards the 2000-m isobath, and is typically less than 100 km wide. The separation point of the EAC (black line in matrices) also dictates connectivity with more sites being connected (with lower concentration) downstream of the separation point of the EAC.

Particles released at the offshore sites (100–1000 m isobaths (Figs. 10–11, Rows 4 and 5) become quickly entrained in the EAC jet. This combined with the greater distance from the shore means that of the particles released offshore, fewer reach the coast. This is exemplified by the lower number of connectivities. The particles that do reach the shore tend to have travelled greater distances (hence arrive further south) than particles released adjacent to the coast (e.g., Fig. 10, Panel Q, R).

Maximum number of sites that are connected (Table 2) occurred for particles released at the 50-m isobath during summer (Fig. 10, Row 2, 32%). Whereas during winter, the maximum number of sites were connected originated at the 100-m isobath (Table 2, 39%),
The total number of particles settled is a maximum for the coastal release sites (25-m isobath) during summer and winter (Figs. 10–11, Row 1) across all trajectory durations, although dispersion is lower, indicated by the number of sites that are connected. Trajectory timescales do play a role with the maximum increase in the number of connectivities associated with the offshore release sites (Summer, 100, 200-m isobaths, 10%; winter 200, 1000-m isobaths, 21%). This indicates that it takes longer for particles released at the offshore sites to return to shore. However, the actual number of particles settled decreases by an order of magnitude from the coastal release site to the shelf break release site. The pertinent result is that the majority of the opportunities for connectivity occur in the first 30 days and that the EAC acts as a barrier between onshore and offshore populations. The standard deviations are calculated for Figs. 10–11 (not shown) revealing that the variability is inversely proportional to the connectivity.

5.2. Climatic controls on connectivity

The advantage of the downscaling method used is that it allows us to investigate the connectivity patterns for specific months or years. We can then begin to understand the impact of the EAC and climatic controls on the connectivity of populations (Fig. 12). The 1997–1998 El Niño was classified as strong to very strong in the Australasian region, with very high SST anomalies and a strong southern oscillation index (SOI). The SST anomalies along the east coast of Australia were as high as +2–3°C, and the EAC jet was located well offshore. The location of the EAC jet obviously affects the transport pathways and hence the connectivity of populations (Fig. 12, Left panels). In contrast to this period, December 1999 was a typical summer-time La Niña period.

On average during December 1999 (La Niña) the total number of connectivities was more than double that during the December...
1997 El Niño period, but the number of connectivities did not increase after 30 days, i.e. trajectory duration past 30 days played no role. This is indicative of the poleward flow adjacent to the coast. However, for the December 1997 case (El Niño), while on average the total number of connectivities was 50% less than during the La Niña period, a small number of new connectivities occurred after 60 days. During the La Niña period a greater number of coastal sites received particles and a number of particles released at the 200-m isobath were returned to shore (La Niña (31 connected sites), El Niño (six connected sites)). In both years very few particles released at the 1000-m isobath returned to shore, however, there were a greater number of connected sites during the La Niña (7) than the El Niño (3).

To investigate the general nature of these results, correlations were calculated between the SOI and coastal connectivities over each of the summer and winter periods studied. It was found that on average during El Niño summers (where the EAC jet was typically stronger and further offshore) connectivities were low (negative correlation with SOI), where as during La Niña summers more particles were returned to the coast, particularly from offshore sites (positive correlation with SOI). During Winter periods, however, the converse scenario occurred with more coastal connectivities during El Niño (negative SOI) periods. This perhaps indicates that the EAC jet was stronger and penetrated further southward than during a typical winter. This could also have implications for range extension of species (discussed further below).

While connectivity appears to be more significant during La Niña summer periods, it is possible that these differences are less related to climatic variability and more a result of the domination of the coastal circulation by the EAC eddy field. The relationship between climatic variability and the EAC eddy field is an area for further investigation.

5.3. Particle source locations

Additional high-resolution simulations were run to correspond with September of 2004. With a large number of particles released, the source of particles to a particular location can be

![Fig. 11. Mean winter connectivity matrices. Description as per Fig. 10. Note the greater number of coloured boxes below the dashed line (indicating greater northward transport) compared to the summer connectivity matrices (Fig. 10).](image-url)
investigated. This serves as an opportunity to aid in the interpretation of ship board larval fish surveys that were undertaken at the Tasman Front during September 2004 (Mullaney et al., submitted for publication; Baird et al., 2008). Particle tracking simulations (Fig. 14) show the source location of the 232 particles (from a total of 121,500 released on the shelf) that are found near the Tasman Front sampling site on 5 September 2004. Two sink regions are specified as purple and grey, north and south of the 18°C isotherm. Particles from mid-north coast took 2–7 days for direct transport to the northern sector of the Tasman Front. An earlier wave of particles from the mid-north coast was advected south when the poleward extension of the EAC was strong, and find themselves back at the Front 15–32 days after release having travelled a long way to the south (Fig. 14, top histogram). Despite travelling below 36°S, they are found to the north of the 18°C isotherm. There is an interesting gap in particles between the grey and purple plumes. This water must not have been near the coast in the last 32 days. Further south, particles have arrived from the south coast (purple) about 15–32 days (Fig. 14, bottom histogram). The particles at the Tasman Front originate from coastal releases at a variety of times and from much of the NSW coast. Interestingly, no particles came from the Stockton Bight region (33°S,152°55'E), an important nursery ground for larval fish.

Table 2
The connectivities of all sites (%) and the number of particles settled (%) during summer and winter for timescales of 10, 30, 60 and 90 days (columns) at each isobath release (rows).

<table>
<thead>
<tr>
<th></th>
<th>Summer</th>
<th></th>
<th>Winter</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10</td>
<td>30</td>
<td>60</td>
<td>90</td>
</tr>
<tr>
<td>Estuaries connected at 25 m</td>
<td>17</td>
<td>19</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Particles settled at 25 m</td>
<td>74</td>
<td>76</td>
<td>76</td>
<td>76</td>
</tr>
<tr>
<td>Estuaries connected at 50 m</td>
<td>25</td>
<td>30</td>
<td>32</td>
<td>32</td>
</tr>
<tr>
<td>Particles settled at 50 m</td>
<td>57</td>
<td>59</td>
<td>60</td>
<td>60</td>
</tr>
<tr>
<td>Estuaries connected at 100 m</td>
<td>21</td>
<td>28</td>
<td>30</td>
<td>31</td>
</tr>
<tr>
<td>Particles settled at 100 m</td>
<td>24</td>
<td>27</td>
<td>28</td>
<td>28</td>
</tr>
<tr>
<td>Estuaries connected at 200 m</td>
<td>11</td>
<td>18</td>
<td>20</td>
<td>21</td>
</tr>
<tr>
<td>Particles settled at 200 m</td>
<td>4.5</td>
<td>7.1</td>
<td>7.5</td>
<td>7.6</td>
</tr>
<tr>
<td>Estuaries connected at 1000 m</td>
<td>2</td>
<td>6</td>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td>Particles settled at 1000 m</td>
<td>0.7</td>
<td>2.0</td>
<td>2.3</td>
<td>2.5</td>
</tr>
</tbody>
</table>

Incr. represents the increase in number of connected sites (as a % of the total allowable number of connections) from 10 days to 90 days, indicating the relative importance of trajectory duration.

Fig. 12. Summer connectivity matrices for December 1997 (L) and December 1999 (R): showing the relationship between particle sources and particle sinks along the coast of SE Australia given as a percentage of total particles released from any given source. Particles were released in the surface waters at the 20, 50, 100, 200 and 1000 m isobaths (top to bottom) and connectivities were calculated after 10, 30, 60 and 90 days (left to right).
6. Discussion

Here we have implemented a new high resolution model of the coastal ocean of SE Australia with fairly realistic temperature and salinity fields, producing a high resolution hindcast of the ocean state (Baird et al., submitted for publication). This has the benefits of high resolution adjacent to the coast, and across small scale features, such as the Tasman Front. It is also advantageous in that we can include online particle tracking algorithms at high temporal resolution which is not possible from the BRAN output alone. The disadvantage of this method is that it is computationally intensive. We can use these simulations to investigate species specific dispersal pathways and as a baseline for future change scenarios.

6.1. Species-specific dispersal pathways

With the high-resolution hindcast model that we use in this study, we now have the ability to construct species specific and spatially explicit models to describe connectivity. Neira and Keane (2008) highlight the importance of linking high resolution oceanographic data with the spatio-temporal characteristics of ichthyoplankton spawning. Hence one of the aims of this study is to investigate how dispersal pathways (particle trajectories) differ seasonally, inter-annually, with latitude and distance offshore. These variables go part of the way towards distinguishing the dispersal pathways of different larval species. We make use of the particle trajectories calculated for four specific durations, 10, 30, 60 and 90 days, which will provide indicative information for a wide range of marine species.

In this section we relate the simulated particle paths to the five larval species that were introduced in Section 2.8. All the species are known to spawn in the Austral summer along this coastline, (except blue mackerel which spawns in winter and C. maenas which spawns in both seasons) so the seasonal connectivity matrices are appropriate. The various scenarios identified here are summarised in Table 3.

6.1.1. Damselfish

For the tropical species we consider release sites from the 100-m isobath offshore. While they spawn in shallow reef environments, if they are advected out of the Great Barrier Reef region southward into our domain we assume that they have travelled southward in the core of EAC which typically lies over the shelf break. The connectivity results show that the 100 m release depth with a PLD of 30 days is very successful (Fig. 10), with 21–28% of the sites connected, whereas offshore at the 1000-m release depth only 2–6% of the sites are connected.

6.1.2. Butterflyfish

The results relevant to the butterflyfish exhibit similar patterns to the damselfish, however, the extended PLD increases the probability of connectivity. It also increases the likelihood that northern sites are connected with sites to the far south. Booth et al. (2007) have observed occurrences of butterflyfish along the NSW coastline as far south as 37°S (R24), however, the more southern recruitment events tended to be much more episodic than those at Sydney (33.8°S, R15). Our mean matrices shows that on average recruitment from releases at the most northern sites is...
possible at R15 (Sydney), but does not occur within 30 days at R24 (Eden, 37°S). By 60 days, however (butterflyfish) particles from the most northern sites have reached as far as 36°S (R21) (Fig. 10 K).

6.1.4. Blue mackerel

The blue mackerel (100, 200-m sites) spawn in winter (Fig. 11J, N) at the shelf break. Interestingly, during winter the 100-m release depth is the most successful of all the across-shelf sites, with 30% of sites being connected in the first 30 days. The 200-m site is less successful and the total number of particles settling is also lower (only 9.7%).

6.1.5. European shore crab

The first records of the European shore crab in NSW were from the southern end of our domain (Eden–Narooma) in the late 1970s (Zeidler, 1978). Since this time it has been recorded from a total of 20 estuaries or coastal lakes, many to the north (Ahyong, 2005, Glasby unpubl. data). The invasion routes for most estuaries are unknown, but it is thought that *C. maenas* was often transported within NSW together with commercially grown oysters. Nevertheless, *C. maenas* has been found in numerous estuaries where there is no commercial oyster farming. Given the long pelagic larval duration of *C. maenas*, it is quite likely that currents may have played a role in the advection and subsequent invasion of this species.
To investigate the dispersion of *C. maenas* we consider the coastal release sites, inshore of the 100-m isobath during both summer and winter, for PLDs of 30–60 days (Figs. 10, 11B, C, F, G, J, K). The connectivity matrices in Fig. 13 indicate that estuaries in the vicinity of R20–R24 are well connected, particularly during winter and so it is quite likely that there could have been transport of *C. maenas* larvae from south to north over distances of up to 200 km. The standard deviations in winter are relatively small at the southern end of the domain, suggesting that these patterns of connectivity are precise. Of the sink sites that we modelled, R20–R24 have all had reports of *C. maenas* occurring; however, oyster farms are not present. The results presented here indicate that northward advection by oceanic circulation is very possible. It is, however, unlikely that northward advection could explain the historical records of *C. maenas* as far north as Sydney (R15).

The offshore release scenarios (200–1000 m) clearly show that less than a handful of particles arrive at the coast. The few particles that do tend to reach the coast, do so after 30 days (summer) and 60 days (winter). These connectivities tend to occur in coastal areas to the south of where the EAC has separated from the coast. This has implications for the release of ballast water and the potential spread of pests. The global practice of discharging ballast water from international vessels should be considered in relation to the potential onshore transport of propagules contained in the ballast water.

These results indicate exchange of ballast offshore in water at least 200 m deep will indeed help minimise the chances of larvae arriving on the coast of SE Australia. But those larvae that could arrive on the coast would likely do so a long distance from the release point. Of the particles released at the 1000 m isobath, less than 2.5% are returned to the coast during summer and 6.3% during winter (Table 2). Furthermore, only 10% (24%) of the sites are considered particle sinks after 90 days during summer (winter). This is in contrast to the 25-m release site where up to 81% of particles are returned to the coast during winter. The results suggest that only those coastal species with long PLDs (>60 days) would have a chance of being introduced via this vector. These results therefore can help target surveys for new marine pests that might arrive in ballast water.

To investigate the possibility that dispersal is reduced by eddy fields, we consider the coastal regions to the south of the EAC separation point. Of the particles released at the 1000 m isobath, less than 2.5% are returned to the coast during summer and 6.3% during winter (Table 2). Furthermore, only 10% (24%) of the sites are considered particle sinks after 90 days during summer (winter). This is in contrast to the 25-m release site where up to 81% of particles are returned to the coast during winter. The results suggest that only those coastal species with long PLDs (>60 days) would have a chance of being introduced via this vector. These results therefore can help target surveys for new marine pests that might arrive in ballast water that is being discharged offshore.

### 6.2. Range shifting and climate change

The work presented here gives a baseline from which we can now assess the impacts of future changes in the East Australian Current and the relevance for the dispersion and transport of particles. It is anticipated that the EAC will strengthen and penetrate further to the south as the current becomes warmer, and evidence of this has already been seen (Hill et al., 2008). This will presumably transport species endemic to lower latitudes to higher latitudes, resulting in a range shift as has been observed in the urchin *Centrostephanus rodgersii* (Johnson et al., 2005).

Changes in the velocity fields will result in potentially significantly different dispersion patterns particularly over seasonal and inter-annual timescales. While the mesoscale eddy field controls the dispersion patterns downstream of the EAC separation point, how this eddy field will change remains unclear.

### 6.3. Limitations

When considering a question such as the transport of particles from a coastal region such as an estuary, (e.g., for the European shore crab) very specific parameters need to be included in order for the simulation to be realistic. Clearly this study is just a starting point. There are various limitations to the study, and the results must be interpreted with that in mind. The dominant driving force along the coast of SE Australia is the EAC and its eddy field, which makes numerical simulations fairly straightforward. However, factors which influence coastal circulation are more complex and more numbered. For example, tidal circulation and local wind forcing are two key forcing mechanisms which have not been included in this study. Condie et al. (2006) showed that in strong tidal regime, tidal currents moved larvae back and forth across the shelf, however, it was the lower frequency currents that were responsible for alongshore advection and net transport. In the EAC region tidal currents are typically an order of magnitude smaller than lower frequency currents so it is anticipated that their influence will be small. However, at the entrance to an estuary, tidal pumping may result in entrainment of particles for many tidal cycles, combined with the effects of local wind forcing, or topographic steering, particles may actually never be able to leave the estuary and reach the open ocean. Observations have shown that it is possible for certain species to travel long distances along the NSW coastline and in fact enter estuaries a long way to the south of their release point (e.g., Booth et al., 2007), which gives validity to our results. Moreover, it has been well documented that the larvae of species such as the European shore crab readily exit and re-enter estuaries (Queiroga, 1996).

The results of this study are derived from oceanographic circulation studies alone. Larval behaviour has not been included explicitly, nor have we considered mortality or fecundity. Including these processes could improve (or complicate) the results further. Cowen et al. (2006) show the importance of the early onset of active larval movement in mediating the dispersal potential. Although this was not included explicitly in our model simulations, this is perhaps an important mechanism where by larval dispersion is reduced. The low level of connectivity after 30 days suggests that early onset of motility might be important for increasing coastal connectivity.

Studies which include small-scale high-resolution estuarine models nested inside larger scale-shelf circulation models are on going at this time, with the next phase to implement full individual-based models that include specific larval characteristics and behaviour. However, the issue raises many complex and challenging problems that have not yet been resolved by the international modelling community.

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