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Article type : Original Article

Multiple spawning events promote increased larval dispersal of a predatory fish in a western boundary current

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Running title: multiple spawning promotes increased dispersal

Word count: ~7300 (excluding figures, tables and references)

Keywords: particle tracking, connectivity, larval transport, pelagic larval duration, multiple spawning, tailor, bluefish, *Pomatomus saltatrix*

Abstract

Transport of larvae by ocean currents is an important dispersal mechanism for many species. The timing and location of spawning can have a large influence on settlement location. Shifts in the known spawning habitat of fish, whether due to climate or the discovery of new spawning stock, can influence the distribution of juveniles and our understanding of connectivity. The globally-distributed species; *Pomatomus saltatrix*, is one such example where a previously unrecognised summer spawning event and a more southern latitudinal extent was recently reported for the southwest Pacific population. Although restrictions are in place to protect the traditional spawning event, the importance of the newly recognised summer spawning event is uncertain. Here we investigate larval dispersal of *P. saltatrix* using particle tracking simulations to identify the contributions of the different spawning events to settlement. By modelling dispersal of larvae released in northern and mid-latitude regions over the Austral spring and summer we show that the newly recognised mid-latitude summer spawning event contributes over 50% of the larvae reaching southern latitudes. This is due to a reduced (1-2 d) pelagic larval duration (associated with temperature), resulting in reduced larval mortality, and the seasonal (summer) strengthening of the East Australian Current (EAC) transporting particles ~50km further south. These findings demonstrate that in dynamic boundary current systems such as the EAC, the final settlement location of larvae that are transported by ocean currents can vary considerably depending on the timing and location of spawning and that multiple spawning events are important for maximum dispersal.

Introduction

For many broadcast spawning species, ocean currents transport larvae away from spawning sites, with some fraction of the larvae arriving at and settling in juvenile habitats hundreds of kilometres away from the spawning location (Cetina-Heredia et al., 2019, Cowen et al., 2006). Both seasonal and fine scale temporal variation in ocean currents can result in vastly different larval distributions, contributing to highly variable spatial recruitment patterns (Houde, 1989b, Siegel et al., 2008). Many species spawn at specific times of the year and in specific locations, potentially using oceanographic conditions to maximise larval survival and recruitment (Davies et al., 2014, Cowen and Sponaugle, 2009). The influence of spatial and temporal variation in spawning on larval transport and settlement success is therefore of great importance in understanding the connectivity between spawning and settlement locations; information which is key to informing the management of exploited fish species

High-resolution hydrodynamic models, combined with a Lagrangian modelling framework parameterised with species-specific information, provide a mechanism to examine the physical factors which shape observed distributions of larvae and settled juveniles and are increasingly being used to understand and manage connectivity in the marine environment (Gallego et al., 2007, Hinrichsen et al., 2011). More than 500 hydrodynamic models coupled with larval dispersal models have been variously applied (Nolasco et al., 2018), including globally (Doblin and van Sebille, 2016), the Southern Ocean (Fraser et al., 2018), boundary current systems (Cetina-Heredia et al., 2019, Cetina-Heredia et al., 2015, Coleman et al., 2011) and regional seas (Andrello et al., 2013). These models have been used at small and large scales (Schunter et al., 2019, Hellweger et al., 2014, Roughan et al., 2011) to provide and insight into transport and connectivity for a variety of organisms such as macroalgae (Coleman et al., 2011, Fraser et al., 2018), invertebrates (Everett et al., 2017, Munroe et al., 2018, Cetina-Heredia et al., 2019) and fish (Santos et al., 2018, Paris et al., 2005) and also to examine processes such as the impacts of climate-change on dispersal (Cetina-Heredia et al., 2014, Coleman et al., 2013).

Many fish species have complex spawning behaviour, and the timing and location of spawning, in particular, can have a large influence on settlement location and success due to the spatial and seasonal variation in ocean circulation (McEvoy and McEvoy, 1992, Taylor and Able, 2006). *Pomatomus saltatrix* for example, is a globally distributed fish (Juanes et al., 1996) with recognised spawning migrations in western boundary current systems worldwide (East Australian Current, Gulf Stream, Agulhas Current and Brazil Current). These highly dynamic systems strongly influence the larval dispersal of broadcast spawners such as *P. saltatrix* (Juanes et al., 1996). In the Gulf Stream for example, the larval transport and recruitment processes of *P. saltatrix* are closely linked to warm-core ring streamer activity and that the timing of entry into nearby estuaries is determined by temperature gradients across the continental shelf and slope (Hare and Cowen, 1996).

In the southwest Pacific Ocean, *P. saltatrix* undertake annual migrations along the East Australian Current (EAC; Brodie et al., 2018). The EAC is a western boundary current which flows poleward along eastern Australia until it separates from the coast (31 – 33° S) with much of the water volume turning eastward (Cetina-Heredia et al., 2014, Oke et al., 2019). Downstream of the separation, the EAC is characterised by high eddy variability which creates a dynamic environment for larval dispersal. In winter, *P. saltatrix* migrates north along the EAC, up to 26° S (Fraser Island) where the main spawning event occurs in spring (Brodie et al., 2018). This spawning event is well documented (Pollock, 1984, Zeller et al., 1996), resulting in a seasonal closure (August – September) of fishing to protect the spawning individuals (Leigh et al., 2017). However, it was recently shown that the latitudinal range of the spring spawning event extends 400 km south to 30° S, and a previously unrecognised summer spawning event occurs between 28° S and 30° S (Schilling et al., 2019). Considering the discovery of this new spawning information it is important to quantify how these temporally and spatially extended spawning events will influence the dispersal and settlement success of *P. saltatrix*. As *P. saltatrix* does not have a “settlement” period as traditionally understood for fish species, in this paper “settlement” refers to the “transition period” when *P. saltatrix* larvae change from larvae to juveniles and actively swim into juvenile habitats. These outcomes will have broader implications for understanding how other species with multiple spawning events use variation in western boundary currents to maximise larval dispersal.

The EAC system is a major driver of connectivity for marine organisms and has previously been shown to strongly influence larval dispersal (Everett et al., 2017, Cetina-Heredia et al., 2019). Particles originating inshore of the EAC have greater coastal connectivity than those released offshore (Roughan et al., 2011) making the EAC a connectivity mechanism via the transport of larvae to appropriate juvenile habitat (Everett et al., 2017, Condie et al., 2011). The overall goal of this study was to understand how multiple (seasonal and spatial) spawning events can influence *P. saltatrix* larval dispersal in a western boundary current by quantifying the dispersal using Lagrangian methods within a high-resolution oceanographic model. Specifically, this study aimed to 1. compare potential settlement of larvae at different latitudes along southeastern Australia from the different spawning events, and 2. investigate if observed locations of juvenile *P. saltatrix* can be better explained by the addition of recently recognised spawning events.

Methods

Hydrodynamic model details

To investigate oceanographic larval dispersal from the identified spawning periods, particle tracking experiments were run using an offline Lagrangian particle tracking model, PARCELS "Probably A Really Computationally Efficient Lagrangian Simulator" (Lange and van Sebille, 2017, Delandmeter and van Sebille, 2019), described below. These simulations used the velocity fields from a Regional Oceanographic Modelling System (ROMS 3.4) configuration of the East Australian Current System (Kerry and Roughan, 2020). The model domain extends from Fraser Island in the north (25.12° S) to south of the Australian mainland (41.55° S) and approximately 1000 km offshore (162.22° E), encompassing the EAC system from where it is most coherent to where it separates from the coast and forms an energetic eddy field in the Tasman Sea (Figure 1). The model is eddy resolving, has a 2.5 – 6 km cross-shore resolution and a 5 km alongshore resolution, with 30 vertical s-levels. The vertical stretching scheme used ensures a constant-depth surface layer to better resolve the ocean surface currents (Souza et al., 2015). This model provides higher horizontal resolution on the continental shelf (2.5 km cross-shelf and 5 km along-shelf) than any other available models of the EAC system. This is important as it allows sub-mesoscale and cross-shelf processes, which may influence transport of particles along the continental shelf, to be better captured.

The model is a free-running simulation covering a 22-year period (1994 - 2016; Kerry and Roughan, 2020). It is a temporal extension of the 10-year free running simulation described in Kerry et al. (2016) and Rocha et al. (2019). Model output is saved as daily averages. Although the simulation is free running, as it is nested within the assimilating BlueLink Reanalysis (BRAN3p5; Oke et al., 2013) its boundaries are constrained by observations. This is important because the northernmost extent of *P. saltatrix* spawning occurs at 26° S (Fraser Island; near the northern extent of the model). At this location, the EAC has a strong coherent poleward flow along the 2000m isobath (Sloyan et al., 2016, Kerry and Roughan, 2020), and with the boundary of the model constrained by observations we are confident that the poleward flowing EAC is being accurately represented at the northern boundary of the model domain.

The model of the EAC was assessed against Sea Surface Height (SSH) and geostrophic velocity data from the Archiving, Validation and Interpretation of Satellite Oceanography Data (AVISO) product (CNES, 2015), SRS Satellite Level 3 1-day composite Sea Surface Temperature (SST) data obtained though Australia's Integrated Marine Observing System (IMOS, https:portal.aodn.org.au) and Argo profiling floats (Roemmich et al., 2009). Comparisons of volume transported by the EAC were also made with estimates from full depth moorings (Sloyan et al., 2016) and a combination of XBT, Argo and altimetry data

(Zilberman et al., 2018). The simulated hydrodynamics were found to be consistent with the observations providing confidence in the model as it provides a very good representation of the currents in the EAC separation region, and accurately represents the spatial patterns of mesoscale SSH variability driven by the dynamic mesoscale eddy field, the EAC separation and the seasonal SST cycle over the 22 year simulation period (Kerry et al., 2016, Kerry and Roughan, In Revision).

Particle characteristics

The Lagrangian particle simulations were conducted using PARCELS v2.0 which is an open source framework for simulating Lagrangian particle trajectories, designed to efficiently process large amounts of data. Lagrangian simulations were run using only surface velocities as *P. saltatrix* larvae are found almost exclusively at the surface in this region (Miskiewicz et al., 1996). The paths of each particle were interpolated using 5 min steps based upon the daily velocity fields from the ROMS model output. Each particle included a small Brownian motion walk function of 100 m^2 s^{-1} which added natural variation to the movement of each particle and ensured no two particles followed the exact same path (Scutt Phillips et al., 2019, van Sebille et al., 2018). This means on top of particle advection from modelled velocities, particles were advected with a velocity scaled by the diffusion coefficient in a random direction.

The growth rates and pelagic larval durations (PLDs) of many larvae are temperature dependent (Houde, 1989a, Green and Fisher, 2004), so the duration of tracking for each particle (pelagic larval duration) was temperature dependent and estimated using degree-days (DD; thermal constant; Neuheimer and Taggart, 2007, O'Connor et al., 2007). With this approach, each particle is assumed to settle when the cumulative sum of daily temperatures experienced by that particle reaches the thermal constant (Everett et al., 2017; Figures S1 & S2). Larval growth in *P. saltatrix* is both temperature- and size-dependent with larvae growing faster in both warmer waters and at larger sizes, resulting in exponential growth in the larval size range (Hare and Cowen, 1997, Hare and Cowen, 1995). Published growth and temperature data for *P. saltatrix* were combined to estimate a thermal constant for various stages of development (Deuel et al., 1966, Hare and Cowen, 1995, Juanes et al., 1996). Larvae (2.1 mm) hatch from eggs at 39 DD, growth from the yolk sack occurs at a rate of 0.039 mm °C d^{-1} until 2.9mm (59.3 DD), at which point the growth rate growth changes to 0.003 mm mm^{-1} $°C^{-1}$ d^{-1} which results in an exponential shaped curve with our specified settlement occurring at 500 DD (10.7 mm; Figure S3). This growth rate closely matches observed growth rates in larval *P. saltatrix* (Juanes et al., 1996, Hare and Cowen, 1995). For a constant water temp of 22 °C, this means larvae will settle after 23 days which matches the observed transition from larvae to juvenile in this species (Hare and Cowen, 1994; Figure S1). We used a settlement time of 500 DD (10.7 mm) as it is just before the transition from larvae to juvenile whereby swimming would become vastly more important than passive drift from ocean currents (Neira et al., 1998, Hare and Cowen, 1994, Hare and Cowen, 1996). The temperatures experienced by each particle along its path were obtained from the ROMS model at each timestep (daily) and were used to calculate the DD for each particle (Figure S2) over its lifespan.

Natural mortality was incorporated into this model by releasing many particles and applying a daily mortality rate to each cohort of particles. Because natural mortality is a daily constant for each cohort and the same number or particles are released each day per location, the number of particles dying each day is constant between cohorts until particles reach the settlement time and the number of particles in each cohort may begin to vary. To save computing time and reduce the number of starting particles we needed to model, we only applied mortality from day 16 onwards (prior to any particle reaching 500 DD and settlement occurring), when mortality starts to vary between cohorts. As the actual larval mortality rate of *P. saltatrix* in this region is unknown we applied an instantaneous daily mortality rate (*M*) of 0.25, which is equivalent to a 22.12 % actual daily mortality rate. This mortality value was selected as it is the approximate mean *M* for the temperatures observed along the EAC system (Houde, 1989a). While this value may vary from the actual *M*, applying a daily mortality rate in conjunction with the growth specified in degree-days allowed us to model the effect of increased cumulative mortality on larval cohorts that have a longer PLD, spending longer in the water column (and are therefore more vulnerable to predation) before settlement. Larvae which were not on the continental shelf (between the coast and the 200m isobath) at settlement (500 DD) were also considered mortalities in terms of analysis (dispersal mortality; Everett et al., 2017). To better represent percentages of settlement, the effective number of particles released was determined by calculating the number of particles which would have been released in each spawning event to be equal to the actual number of particles on day 16 (when we started to apply natural mortality) if mortality had been applied from day 1.

Forward simulation of observed spawning events

Particle release locations and months were specified to simulate the observed *P. saltatrix* spawning periods (Schilling et al., 2019). Three spawning events were modelled in this study, a northern spring spawning event (26 – 27.5° S release locations), a mid-latitude spring spawning event (28.5 – 30° S) and a mid-latitude summer spawning event (28.5 – 30° S; Figure 1, Table 1), where in each case, season refers to the southern hemisphere (Austral) seasons. The spring spawning events spanned August – December inclusive and the summer spawning event combined February and March releases. Incorporating the 'new' spawning information into particle tracking models (Schilling et al., 2019), allowed exploration of the importance of these 'new' spawning events. Within these release locations, particles were released every 0.5° latitude at the surface over the 100 m isobath. These release locations therefore encompass all locations where *P. saltatrix* in spawning condition have been observed in this region (Schilling et al., 2019). As no data is available on relative spawning biomass at different locations or times, we assumed a constant daily spawning rate at all locations. A cohort of 1000 particles was therefore released from each location every day (during the spawning months) for 22 years (the duration of the ROMS simulation).

Backward simulations from locations of observed juvenile P. saltatrix

Backward Lagrangian particle tracking simulations were run using the same particle characteristics as specified in the forward simulations, except mortality. Mortality was not incorporated as the settlement locations of the particles are already known and this model seeks to identify the potential spawning locations that could have resulted in transport to these settlement locations, rather than any measure of density. Locations were determined by juvenile tailor observations (Table 1; Leigh et al., 2017, Schilling et al., 2018, Schilling, 2019). Because the poleward flowing EAC dominates the circulation upstream of 31° S, we did not simulate any backwards tracking releases north of 31° S as the majority of the particles were estimated to leave the northern boundary of the ROMS model (which corresponds to the most northern spawning for this population). As no mortality was modelled for the backwards simulations, a smaller cohort of 100 particles were released per location (Table 1; Figure 1) every 7 days for 22-years on the 100 m isobath. These particles were subset to only include those which were predicted to have spawned during the spawning months (August – December, February or March).

Catch-per-unit-effort

We explored whether the modelled transport and settlement of *P. saltatrix* was correlated with observed recruitment, using catch-per-unit-effort (CPUE) as an indicator of recruitment. *P. saltatrix* catch is most variable at the southern end of its distribution (> 37° S), therefore we used a CPUE index from the southern latitudes (Victorian Fisheries Authority, 2017) as it is most likely to show a clear signal in larval dispersal-driven recruitment variation. The CPUE data from the estuarine Gippsland Lakes seine net fishery (Victorian Fisheries Authority, 2017) was provided as the mean for each year (1998 – 2018).

Because *P. saltatrix* are most commonly caught at age 2 in the southwestern Pacific Ocean (Schilling, 2019, Leigh et al., 2017), the relative predicted number of settled larvae south of -36° S during July - June (to cover the spawning season) were lagged by 2 years. Despite *P. saltatrix* being well recognised for its migratory nature (Juanes et al., 1996, Brodie et al., 2018), in the southwest Pacific population, juveniles (< 30 cm) are not known to undertake migrations and usually remain in or near estuaries (Morton et al., 1993, Schilling et al., 2017, Schilling et al., 2018). This means despite the migratory nature of this species, it should be possible to align predicted settlement with estuarine CPUE as the fishery is largely based upon fish which would have had limited opportunity to migrate, particularly at the southern extreme of the populations' distribution. We therefore used CPUE data for years 1998 – 2018 to align with the time covered by the particle tracking model (1996 – 2016).

Data analysis

Larval distributions from each particle tracking simulation were mapped to show the positions of all particles at 500 DD. Settlement from each spawning event was quantified by finding the percentage of all settled particles (final location inshore of the 200m isobath) in 1° latitude bins. Active movement is not included in the model, so estimates of survival are conservative with actual survival likely to be higher due to shoreward swimming (Hare and Cowen, 1996). Therefore, the estimates presented are conservative lower estimates of relative settlement success, but likely fully represent potential dispersal and latitudinal transport distances. The same analysis was conducted with no mortality to assess the importance of including mortality in these models. For the CPUE analysis, the Pearson correlation coefficient was calculated to test for a statistically clear correlation between CPUE and the modelled larval settlement. Distance travelled was tested using a linear model with $\log_{10}$ transformed distance, the response and year and spawning event as fixed factors. Residual plots were inspected to check assumptions of the linear model and probability distributions were plotted for each spawning event to visualise distribution of distance travelled by particles in each spawning event. In this study we adopt the approach proposed by Dushoff et al. (2019) to describing our statistical results, using language of statistical clarity.

Results

Settlement time

The temporal length of the PLD (500 DD) varied among the three spawning events (Figure 2). Using all particles which reached 500 DD, the mean PLDs for each spawning event were: northern spring 22.5 days, mid-latitude spring 23.2 days, and mid-latitude summer 20.8 days. For larvae that settled on the continental shelf the means varied slightly: northern spring 22.4 days, mid-latitude spring 23.5 days, and mid-latitude summer 21.1 days. This is important because a longer PLD implies increased exposure to mortality and potential further transport. In our simulations we applied a 22% daily mortality which means that, for every day extra prior to settlement, 22% of the surviving larvae die. In terms of the current results, the two-day difference between spawning events is equivalent to 40 % of the particles alive at the earlier settlement day dying prior to settlement day two days later. The longer PLD was also reflected in the distance transported with the mid-latitude spring spawning event clearly having a higher mean distance travelled (332 km) compared to both the northern spring (272 km) and mid-latitude summer spawning events (271 km; $P < 0.001$).

Dispersal from spawning events

The larval settlement locations simulated by the particle tracking model were almost exclusively southward except for 0.003 % of particles from the northern spring release which settled north of 26° S (Figure 3, Table 3). When investigating the distributions of larvae arriving on continental shelf within each spawning event, the northern spring spawning event had a peak in settlement around the release locations (27 – 28° S), while the peaks in settlement for both mid-latitude spawning events were approximately 1 – 2 degrees south of the initial spawning locations (30 – 32° S). The northern spring spawning event retained more larvae than the mid-latitude spawning event. The mid-latitude spawning events also had a larger proportion of the successfully settling larvae arrive south of 30° S compared to the northern spring sample (Figure 4a). When these proportions were investigated as part of the total number of larvae arriving on the continental shelf, the northern spring spawning event supplied approximately 40 % of all larvae on the continental shelf, the majority of these north of 30° S (Figure 4b; Table 2). The mid-latitude spawning events supplied an overall lower proportion of the larvae but were increasingly important for larval supply with increasing latitude. The mid-latitude summer supplied double the larvae on the continental shelf compared to the mid-latitude spring spawning event, largely due to the higher survival (Figure 4b; Table 3).

In terms of dispersal mortality, a high proportion (55 – 84 %) of particles in each spawning period which survived to 500 DD were dispersed offshore, particularly south of the separation zone where the EAC separates from the Australian mainland (Figure 3, Table 2). The mid-latitude spring spawning event had a low number of larvae reach 500 DD on the continental shelf (0.23 % of effective number of larvae released) compared to 0.75 % and 0.96 % respectively for the northern spring and mid-latitude summer spawning events (Table 2). This is reflected in the northern spring and mid-latitude summer spawning events having areas of high settlement density along the coast (near the spawning locations), while the mid-latitude spring spawning event had a wider dispersal of particles with a more even distribution of settlement latitudes (Figures 3 & 4). The mid-latitude summer spawning event was similar to the mid-latitude spring spawning extend although it extended further south with moderate dispersal offshore (Figures 3 & 5).

When the contribution of each spawning event was investigated by settlement latitude, it showed that the three spawning events play a disproportionate role in delivering larvae (Figure 5). The northern spring spawning event (which covers the original Fraser Island spawning event) supplied all larvae settling north of 28° S but the proportion of particles settling in each 1° latitudinal bin from the northern spring spawning decreased as latitude increased. The mid-latitude spring spawning event contributed a small proportion of particles settling between 28 and 30° S (< 15 %) but contributed between about 15 and 30 % for all latitudes south of 30°S. The mid-latitude summer spawning event contributed the largest proportions (30 – 60 %) of larvae that settled south of 29° S, with this spawning event contributing over 50 % of the larvae settling south of 37° S. When mortality was excluded from these simulations, the importance of the mid-latitude spring spawning event increased while the importance of the mid-latitude summer spawning period decreased (Figure S4).

Backward tracking

The backwards simulation of all larvae released at known juvenile locations revealed that the most likely spawning sites were dispersed along the coast to the north of the release sites (Figures S5, S6). Some particles were predicted to have come from offshore but in general the EAC appears to have restricted onshore-offshore movement (Figures S5, S6). After limiting the analysis to particles which were predicted to have originated on the continental shelf (as spawning only occurs along the coast), the connectivity matrix revealed that while it was unlikely particles came from north of 33° S, it was possible that larvae in the southern latitudes (< 36° S) were potentially transported from up to 10 degrees further north (26° S;

Figure 6). While there was higher probability for larvae to be transported short distances, it was still possible that larvae from all three spawning events could be contributing larvae to all locations where juvenile *P. saltatrix* are observed (Figure 6).

Catch-per-unit-effort

A statistically clear positive correlation (r = 0.463) was found between the predicted larval settlement south of 37° S and the CPUE data from the Gippsland Lakes (t_{19} = 2.777, p = 0.034; Figure 7). The lagged predicted larval settlement was strongly correlated between approximately 2004 and 2012. Despite this, there were several years where predicted larval settlement did not match the CPUE data including pre-2004 and post-2012. In the 1997-98 catch year (July – June) there were no larvae predicted to settle south of 37° S, driven by stronger offshore currents which resulted in no larvae being transported south of 36° S. There was large variation in interannual distribution patterns with some years' larvae being transported much further south, while in other years there were large amounts of offshore transport (Figures S7 – S9).

Discussion

This study simulated larval dispersal from three recognised spawning events in the EAC, a dynamic western boundary current, revealing that the importance of different spawning events to settlement success can vary due to oceanographic processes. This research demonstrates that multiple spawning events within dynamic ocean currents with seasonal variation can greatly influence patterns of larval dispersal and settlement and that multiple spawning events can increase overall dispersal. This has relevance to all species spawning within global boundary current systems. Our analysis shows that dispersal of larval *P. saltatrix* along the southeast coast of Australia is dependent on the multiple spawning events which contribute varying proportions of larvae along the coast, and that the recently confirmed summer spawning event is particularly important for settlement in the southern portion of this species' distribution. This has relevance to all species spawning within global boundary current systems. By combining spawning information with particle tracking models, it is possible to better understand dispersal dynamics and connectivity which can lead to more effective fisheries management.

Settlement times

Differences in temperature can have substantial impacts on the distribution of fish populations, as temperature directly influences the pelagic larval duration (PLD; Schunter et al., 2019, O'Connor et al., 2007). In our study, using degree-days to model temperature dependent growth rates resulted in different PLDs and therefore mortality among the larvae from three spawning events. For larvae settling in a suitable location (i.e. on the continental shelf), the mid-latitude summer spawning event settled on average a day earlier than the northern spring spawning event and 2 days earlier than the mid-latitude spring spawning event. This means that both the mid-latitude and northern spring spawning events incurred up to 40 % of extra mortality of larvae compared to the shorter PLD, as they were vulnerable to predation in the pelagic environment for longer. This was reflected in the percentage survival and percentage settlement of the three spawning periods with the mid-latitude summer spawning event showing almost double the survival percentage of the mid-latitude spring spawning event (Table 2). Excluding mortality from these simulations, as some previous connectivity studies have done, would have resulted in the mid-latitude spring spawning event being over-represented in the final larval survival and settlement numbers (Figure S4).

It is well recognised that increasing temperature reduces the PLD of most taxa and changing ocean temperatures have large implications for connectivity through changes in dispersal distance and survival

(O'Connor et al., 2007, Treml et al., 2012, Cetina-Heredia et al., 2015). The waters off southeast Australia are recognised as a global warming hotspot (Hobday and Pecl, 2014). This may lead to *P. saltatrix* larvae being exposed to higher temperatures, resulting in a shorter PLD which may reduce the dispersal capacity. Additionally, the spawning periods or locations may shift as has already been identified in the Mediterranean as *P. saltatrix* migrate to more optimum water temperatures (Sabatés et al., 2012). For accurate predictions on the effects of warming waters in the southwest Pacific, more research is needed on how *P. saltatrix* will respond to warming waters, including larval tolerances to temperature and continued monitoring of spawning times and locations.

By including a temperature dependent PLD in particle tracking models, these models are better able to capture the important differences in survival and dispersal which may be driven by changes in water temperature. Degree-days (Everett et al., 2017, Samsing et al., 2017) and mortality associated with temperature thresholds (Cetina-Heredia et al., 2015) have been used successfully before in particle tracking models but it is still uncommon for models to incorporate the effects of temperature. Our findings confirm that when available, temperature dependant settlement (PLDs) should be included in particle tracking models to account for faster growth, earlier settlement, and therefore reduced mortality occurring in warmer waters (Neuheimer and Taggart, 2007, Houde, 1989a).

Larval dispersal

The forward simulations revealed that the northern spring spawning event is highly important for overall *P. saltatrix* population connectivity and recruitment in eastern Australia. Assuming a constant rate of spawning (day^{-1}), the northern spring spawning event has the largest number of larvae which settle on the continental shelf. However, both mid-latitude spawning events, which incorporate the recent information expanding the latitudinal and temporal spawning extent of *P. saltatrix* (Schilling et al., 2019), contribute more larvae to the southern part of the species range (south of 34° S). The mid-latitude summer spawning event contributed the highest proportion of settled particles south of 30° S, with the importance of this spawning event increasing with latitude. It is likely the two recently identified mid-latitude spawning events drive recruitment in southern Australian (south of 36° S), where commercial catch of *P. saltatrix* is small and often variable (Litherland et al., 2016, Victorian Fisheries Authority, 2017). The fact that the simulated larval settlement matched some of the observed patterns in CPUE from the southern region suggests that oceanography is an important driver of *P. saltatrix* recruitment.

The northern spring spawning event had large numbers of larvae which settled north of the EAC separation zone (~32° S) before they could potentially be advected offshore. These particles were often driven by onshore currents which resulted in low velocities and short distances travelled due to interactions with the land. The greater offshore dispersal evident in both mid-latitude spawning events was driven by the EAC eastern extension (Oke et al., 2019), resulting in higher concentrations of particles which are advected offshore, between approximately 33 and 35° S. This offshore dispersal pattern could be further examined using the paths of individual particles which were advected offshore and entrained into eddies. These eddies are common along the east coast of Australia and particularly strong south of the EAC separation zone (Everett et al., 2012, Suthers et al., 2011). Furthermore, climate change is driving substantial change in the EAC region with the flow strengthening by up to 35 % (Sun et al., 2012), and separation occurring further south (Cetina-Heredia et al., 2014), which will likely result in more larvae being dispersed offshore or potentially retained in eddies and returned to the shelf (Cetina-Heredia et al., 2019). This has large implications for the larval transport of many species in this region, including *P. saltatrix*, which use this western boundary current for dispersal of early life history stages to higher latitudes. Similar implications exist for broadcast spawners in other boundary current systems which are also changing (Saba et al., 2016, Sakamoto et al., 2005). Increased poleward dispersal of many species is already being observed in many boundary current systems including coastal south eastern Australia, through increased poleward transport of tropical larvae and subsequent “tropicalisation” of temperate areas (Vergés et al., 2014, Miranda et al., 2019).

The backwards simulations showed that the three identified spawning events have the potential to supply larvae to all locations where juvenile *P. saltatrix* are found. The most southern backwards release site (Gippsland Lakes, 38° S) had lowest likelihood of larvae being spawned in the identified spawning region (north of 30° S) again supporting why the recruitment (and catch) of *P. saltatrix* in this southern region is highly variable (Leigh et al., 2017, Victorian Fisheries Authority, 2017), with larvae not being consistently transported this far south. All other backwards simulation release locations showed very high likelihood that the larvae were spawned in the spawning region, corresponding to the regular observed annual recruitment. All backwards tracking models showed a high likelihood of spawning along the coast (particularly north of 33° S), which highlights the fact that the EAC is the dominant coastal current with few currents delivering water from the more easterly ocean onto the continental shelf. This is consistent with previous research showing that western boundary currents can act as connectivity barriers between onshore and offshore areas (Roughan et al., 2011).

Although CPUE data is known to be a biased metric due to many factors such as changes in fisher behaviour, catchability, and management, and caution must be taken when linking CPUE to abundance (Maunder et al., 2006, Rose and Kulka, 1999), our model exhibited overall similar patterns to that observed in the CPUE data (r = 0.463, t_{19} = 2.777, p = 0.034, Figure 7). The positive correlation between predicted larval settlement and the CPUE data from the Gippsland Lakes (38° S) provides evidence that our model is reflecting some of the dispersal and settlement dynamics of this species. Using different oceanographic models with forecasting potential, it may be possible to forecast larval settlement of *P. saltatrix* and thus predict years of high and low potential catch for this fishery. The relationship between CPUE and modelled settlement was less clear towards the end of the simulated period, however, which may have been due to changes in the fishery, with fishing effort starting to increase in 2011 after a long decline (Victorian Fisheries Authority, 2017). CPUE rose after 2016, while predicted settlement did not. If shoreward swimming was incorporated into this particle tracking model, this pattern may have been better captured (Putman and Mansfield, 2015). Annual larval settlement distributions for this period showed that the larvae did get dispersed south but ended up too far east, not on the continental shelf (Figures S4 – S6). In 1997, there was no predicted larval settlement south of 37° S, which seems highly unlikely as there was no visible decline in CPUE in 1999. As the CPUE is based upon total harvest and effort it incorporates variations from multiple year classes and therefore there will be some inherent differences between CPUE and predictions made from a single year of settlement. Because the catch of *P. saltatrix* contains multiple age classes, a more detailed analysis may be possible if the full age composition of the harvested fish was known. Another recent study which investigated lobster larvae settlement in the same region using a similar Lagrangian particle tracking methodology but with a courser resolution (10km) hydrodynamic model (OFAM BRAN 3p5) found similar disjuncts over the same time period when comparing predicted settlement to observed juvenile settlement (Cetina-Heredia et al., 2019). Neither the present study nor Cetina-Heredia et al. (2019) included particle behaviour such as swimming, yet the similarity in ability to match settlement with predicted larval transport suggests that these ocean models can capture most of the oceanographic dynamics. However there continues to be a need to understand the impacts of active swimming and other fine-scale oceanographic processes which may be contributing to observed larval settlement patterns (Fiksen et al., 2007, Munroe et al., 2018, Putman and Mansfield, 2015).

Model limitations

This study aimed to model the potential latitudinal dispersal of *P. saltatrix* larvae in order to understand the importance of the recently described extensions in spawning latitude and timing (Schilling et al., 2019). The model used in this study was a free running ocean model which does not replicate oceanic conditions such as individual eddies exactly but it does reproduce broad spatial, seasonal and interannual patterns which allow us to investigate patterns of interannual and seasonal transport, as has been shown in many other studies in other regions. Passive transport and temperature dependent growth and mortality are not the sole factors influencing the final distribution of larvae and it is well known that active horizontal swimming can be important in determining the final destinations of fish larvae (Putman and Mansfield, 2015, Fiksen et al., 2007). Despite not modelling this component of transport, this model was able to capture the much of the interannual variation seen in the CPUE data from the southern end of the distribution. For horizontal swimming to be incorporated into this particle tracking model, further research into the swimming abilities of larval *P. saltatrix* is required. It is likely that swimming would occur in a westward direction, towards the Australian coastline (and suitable juvenile habitat) but the magnitude of the swimming ability for larval *P. saltatrix* is currently unknown. The resultant larval distributions presented in this study suggest that *P. saltatrix* larvae could be transported far offshore, including near Lord Howe Island (31.556° S, 159.082° E), but *P. saltatrix* are never observed there as juveniles or adults (Van Horn et al., 2018). We believe that if active westward swimming was incorporated into this model, the resultant distributions would be more concentrated towards the Australian coast. This would also have helped improve the relationship between some of the lagged settlement estimations and the CPUE data in the years our model performed less well, i.e. when it predicted southward transport but too far east of the continental shelf.

The hydrodynamic model used in our simulations is the highest resolution available for this region, particularly on the continental shelf, and is shown to perform well, however it still may not accurately capture some of the local hydrodynamics which may influence delivery of larvae to suitable habitat (Pineda et al., 2007, Kerry and Roughan, In Revision). As an example, the winds incorporated into the ROMS model are coarse and therefore is unlikely to accurately capture the local onshore winds (the 'sea-breeze') close to the coast. It is likely that incorporating high-resolution winds into the ROMS model would increase shoreward transport on the continental shelf but to a lesser degree than active swimming. The Brownian motion defined in our simulation to account for sub-grid scale phenomena and ensure unique particle paths was relatively high (100 $m^2 s^{-1}$). This may have resulted in overestimated dispersal of particles. If this parameter was reduced, it is likely that the offshore dispersal of larvae would be reduced with a lower proportion of larvae randomly moving out of the strong flow of the EAC. As our hydrodynamic model was high resolution and the goal of our study was to study the latitudinal transport of larvae, regardless of the limitations in longitudinal transport, we are confident that the latitudinal transport of *P. saltatrix* is well represented by this study and that our conclusions regarding the importance of multiple spawning promoting increased dispersal within boundary current systems are supported.

Conclusion

This paper has shown that spatial and temporal variability in spawning (i.e. different latitudes and seasons) can substantially alter the final settlement locations of larvae, and that multiple spawning events may ensure maximum dispersal. This has important implications globally for all broadcast spawning species. If the timing or location of spawning changes (as is anticipated with climate change), it is possible that the resultant larval dispersal may vary greatly. Future work may further consider the changes that are occurring to ocean currents with climate change and how this may alter the larval transport of fish and the impact on fisheries recruitment.

Data Availability

All code used in this analysis is available in on GitHub at: https://github.com/jaseeverett/TailorParticleTracking. The output files from PARCELS are available on request from the authors. The ROMS model output is available at https://doi.org/10.26190/5e683944e1369 (Kerry and Roughan, 2020).

Acknowledgements

This research includes computations using the computational cluster Katana supported by Research Technology Services at UNSW Sydney. Thanks to Erik van Sebille and Phillippe Delandmeter for their assistance in setting up the PARCELS model. John Morrongiello and Francis Juanes made useful comments on an earlier draft of this paper. Thanks to Justin Bell from the Victorian Fisheries Authority for providing the CPUE data. This is contribution no. 254 of the Sydney Institute of Marine Science.

Author Contributions

HTS, JDE, JAS, IMS, JMH & JS conceived and designed the study, HTS, JDE, CK, MR conducted the simulations and did the analysis. HTS wrote the first draft and all co-authors critically revised and contributed to the final manuscript. All authors agreed for the work to be published.

Funding

This work was funded by an Australian Research Council (ARC) Linkage Project (LP150100923) and the NSW Recreational Fishing Trust. In addition to this: CK was partially funded by an ARC Linkage Project LP160100162. JDE was funded by ARC Discovery Project DP150102656. JDE and HTS were partially funded by a University of NSW (UNSW) Research Infrastructure Scheme Network Lab awarded to IMS and MR. HTS was also partially funded by a UNSW Faculty of Science Writing Scholarship and a NSW Government Research Attraction and Acceleration Program grant awarded to the Sydney Institute of Marine Science.

Conflict of Interest Statement

The authors of this paper have no conflicts of interest.

Ethics Statement

Ethics approval was not required for this work.

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Tables

Table 1 Site details for the particle tracking simulations. Forward tracking locations were based upon documented spawning events (Schilling et al., 2019). Backwards tracking locations were based on estuaries were juvenile *P. saltatrix* have been observed. All simulations were started on the 100 m isobath.

Location	**Latitude (°S)**	**Tracking Direction**
Northern spawning	26, 26.5, 27, 27.5	Forwards
Mid-latitude spawning	28.5, 29, 29.5, 30	Forwards
Hastings River	31.4	Backwards
Wallis Lake	32	Backwards
Sydney Harbour	33.8	Backwards
Jervis Bay	35.1	Backwards
Wagonga Inlet	36.2	Backwards
Twofold Bay	37	Backwards
Gippsland Lakes	38	Backwards

Table 2

Details of the forward tracking particles. As mortality was only modelled from the day prior to any settlement occurring (day 16), the effective number of released larvae is the number of released larvae which would be equivalent to applying mortality the whole time period and having the actual number of released larvae when mortality started to apply. The percentages were calculated using the effective number of larvae. DD is degree-day.

Spawning event	Larvae released in model	Effective number of released larvae	Larvae surviving to 500 DD	Percent survival to 500 DD (%)	Larvae settled on shelf	Percent settlement on shelf (%)
Northern spring	3,366,000	111,466,577	1,876,658	1.684	839,376	0.753
Mid-latitude spring	3,366,000	111,466,577	1,538,584	1.380	253,234	0.227
Mid-latitude summer	1,298,000	42,983,844	1,172,266	2.727	412,769	0.960

Table 3 Percentage of particles settling over the continental shelf in each degree of latitude from three spawning events. Spring spawning events include August – December and the summer spawning period includes February and March. Spawning locations are shown in Figure 1. The percentages (3 dp) were calculated on the effective number of released larvae (Table 2).

Settlement latitude (°S)	**Northern spring (%)**	**Mid-latitude spring (%)**	**Mid-latitude summer (%)**
25 – 26	0.003	0.000	0.000
26 – 27	0.071	0.000	0.000
27 – 28	0.245	0.000	0.002
28 – 29	0.144	0.014	0.061
29 – 30	0.077	0.029	0.192
30 – 31	0.065	0.042	0.226
31 – 32	0.052	0.040	0.180
32 – 33	0.044	0.035	0.118
33 – 34	0.031	0.032	0.080
34 – 35	0.013	0.017	0.048
35 – 36	0.005	0.009	0.024
36 – 37	0.002	0.005	0.014
37 – 38	0.001	0.004	0.015
38 – 39	0.000	0.000	0.001
Successful Settlement	0.753	0.227	0.960

Figures

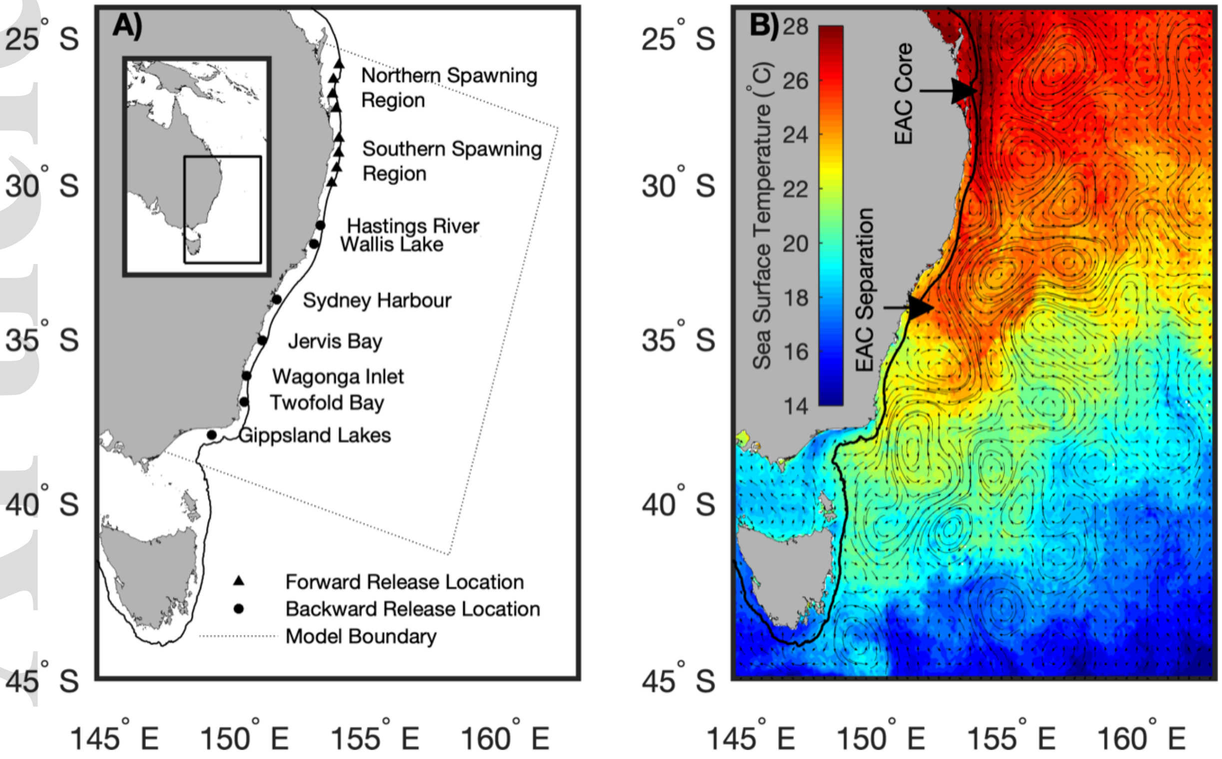

Figure 1

a) Map of eastern Australia covering the latitudinal range of *Pomatomus saltatrix* (25 – 39° S). Symbols show the release location for the forwards (triangles) and backwards (circles) simulations. The dotted line represents the boundaries of the regional oceanographic model which provided the velocity estimates used in the simulations (Kerry et al., 2016) and the solid black line shows the 200m isobath, b) a visualisation of the observed January 2016 (summer) ocean currents (black arrows) and sea surface temperature (colour) of the region. The SST observations are taken from MODIS-Aqua using NASA's OceanColor Web. Current velocity was derived from altimetry from NASA/CNES (Jason-1 and 2) and ESA (ENVISAT) satellites and were extracted from the Integrated Marine Observing System (IMOS) Data Portal (http://imos.aodn.org.au/imos/). Warm temperatures indicate the poleward flowing East Australian Current and associated eddy field. The core of the EAC and separation from the coast are marked with black arrows.

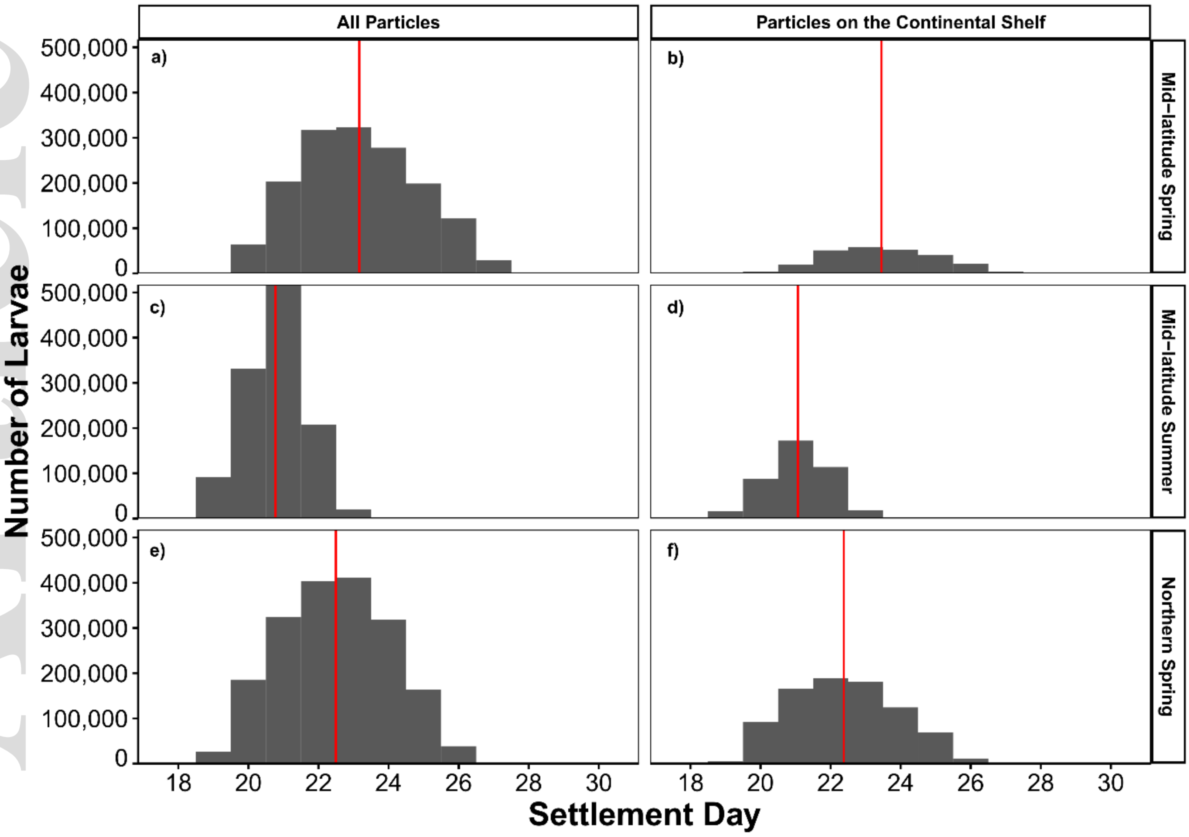

Figure 2 Histograms showing the larval settlement times (pelagic larval duration) from the three spawning events, separated into all particles which reached 500 degree-days (DD) left, and particles which were over the continental shelf at 500 DD right. The red vertical line represents the mean settlement day for each group of particles.

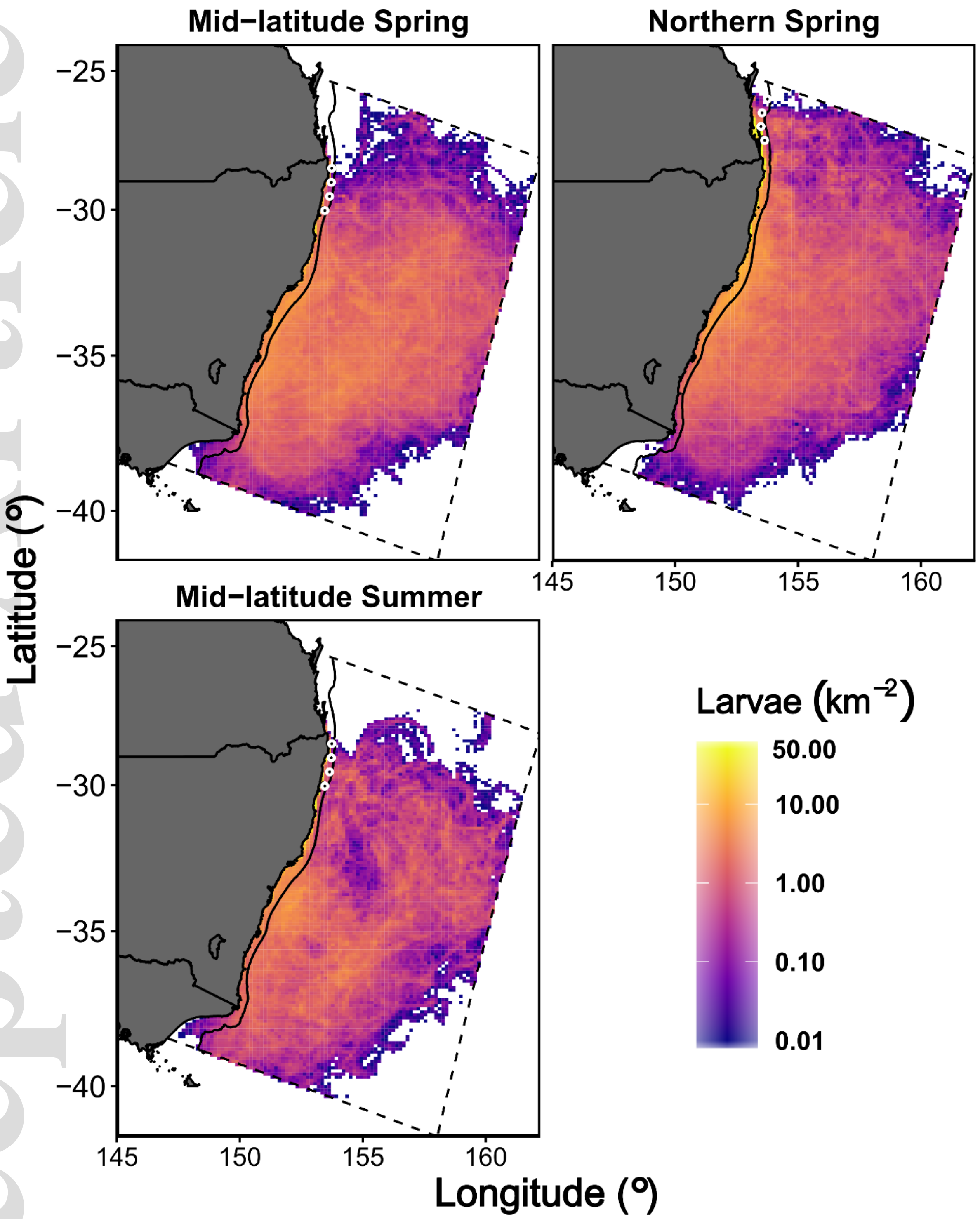

Figure 3 Relative density of larvae at settlement time (500 degree-days). The black circles with white outlines show the release location of the particles for each spawning event. The 200m isobath indicating the edge of the continental shelf is shown as a solid black line within the model boundaries (dashed line). The density colour scale is consistent between subplots but note the non-linear colour scale.

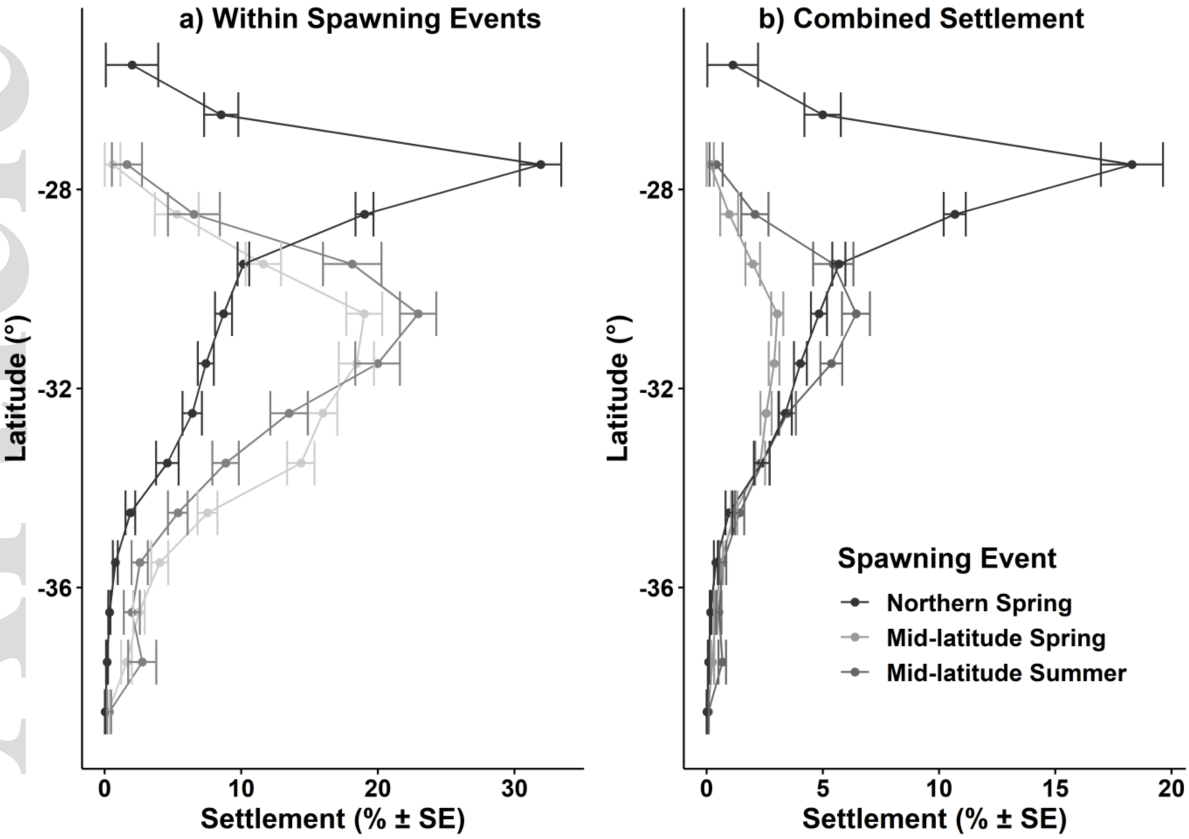

Figure 4 Settlement contributions of different spawning periods for a) percentage of particles on the continental shelf within each spawning event and, b) As a percentage of all particles settled on the continental shelf (combined spawning events). All error bars show standard error.

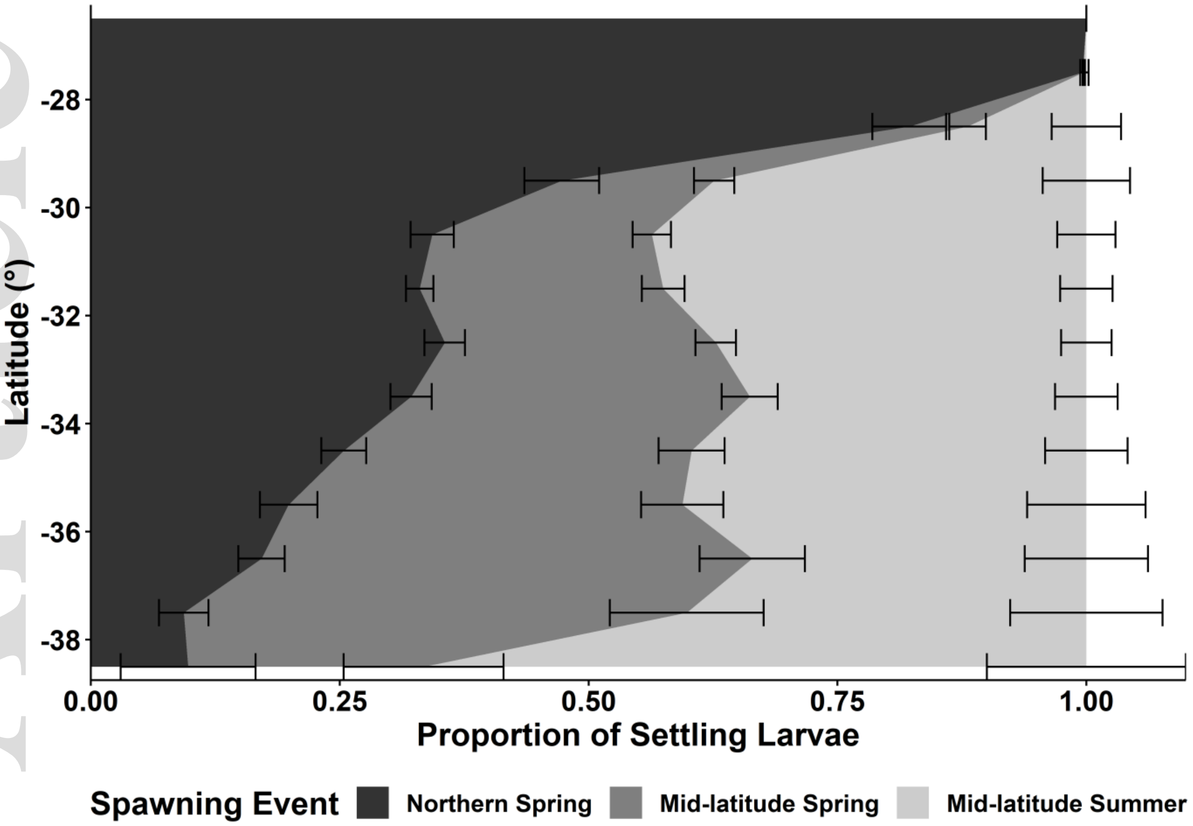

Figure 5 Mean proportion of settled larvae (on the continental shelf) at 500 degree-days originating from each of the modelled spawning events each year, using 1° latitude settlement bins and the 22 year simulation. Error bars show ±1 standard error on the mean proportions.

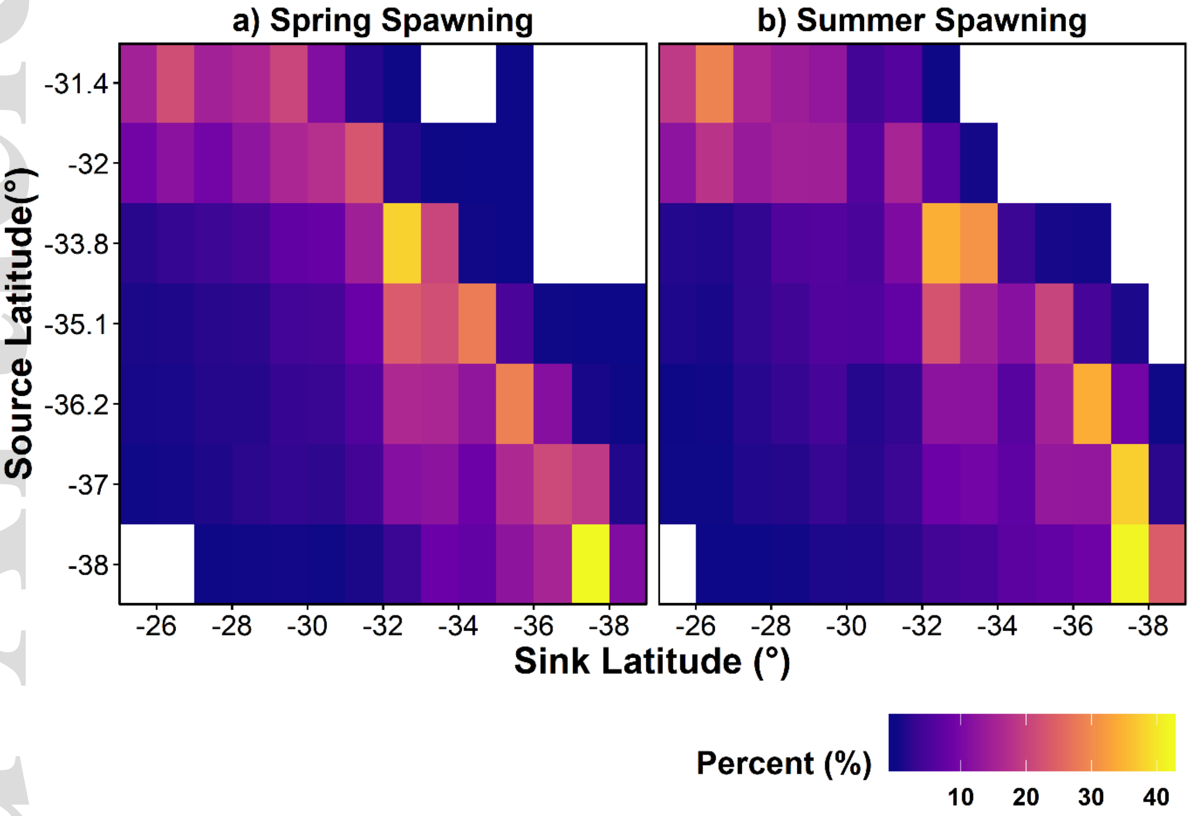

Figure 6 Connectivity matrix for the backwards simulations for all particles which reached 500 DD on the continental shelf. The y-axis (source) represents the particle release latitudes detailed in Table 1 and Figure 1. The x-axis represents the 1° settlement latitude band.

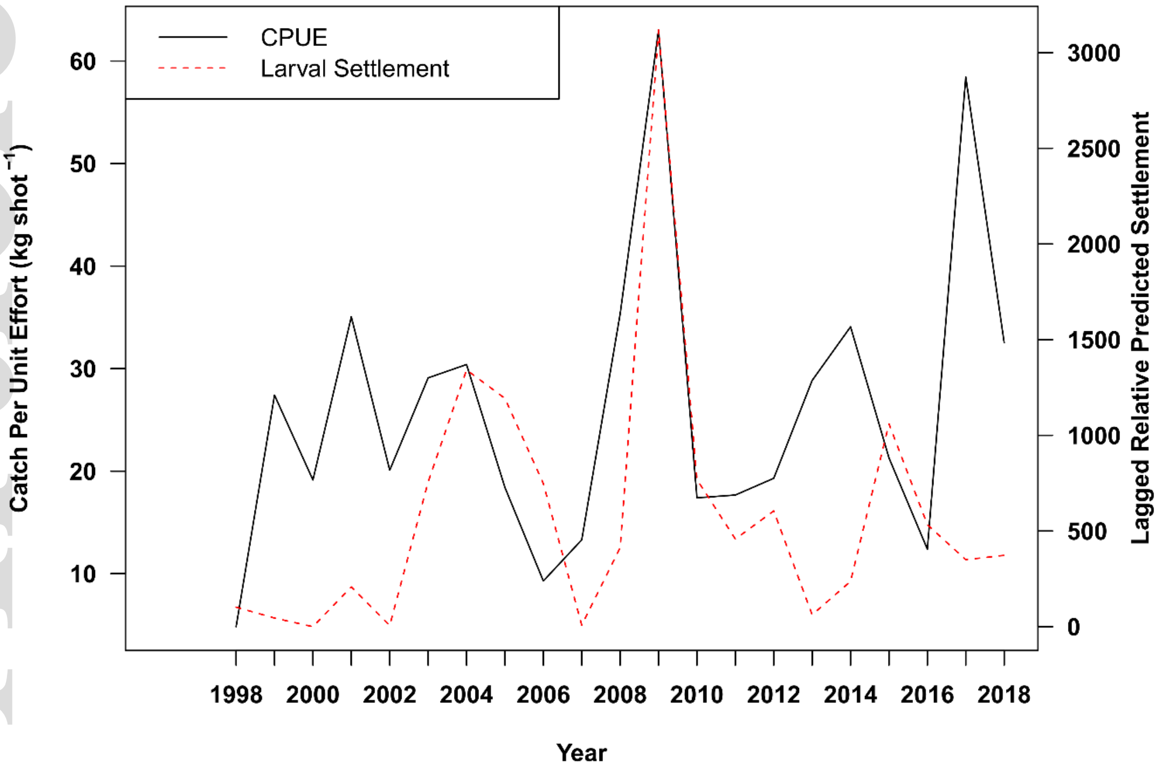

Figure 7 Catch-per-unit-effort (CPUE) from the Gippsland Lakes in Victoria for *P. saltatrix* caught in seine nets (kg shot^{-1}, black solid line) and the 2-year lagged relative predicted settlement of *P. saltatrix* larvae south of 37° S (red dashed line). The Pearson correlation coefficient of these two datasets is $r = 0.463$ ($P = 0.034$).