**Multiple spawning events increase larval dispersal of a predatory fish in a western boundary current.**

Schilling, Everett, Smith, Stewart, Hughes, Roughan (?), Kerry, Suthers

**Target journal**: Fisheries oceanography (or go big for journal of biogeography or landscape ecology – they have some dispersal papers)

**Abstract**

Transport of larvae by ocean currents to juvenile habitats is an important mechanism for many marine species. The timing and location of spawning can greatly influence the final destinations of larvae, and identifying these aspects of spawning is valuable for species management. A previously unrecognised summer spawning event was reported for the southwest Pacific population of *Pomatomus saltatrix*, and although fishing restrictions are in place to protect the traditionally recognised spring spawning events, the importance of this new spawning event is uncertain. Here we conduct a particle tracking simulation of *P. saltatrix* spawning and resulting larval dispersal via the East Australian Current to highlight the differing contributions of the spawning events to potential settlement along the east Australian coast. By modelling the three recognised spawning events, we show that the newly recognised mid-latitude summer spawning event contributes the highest proportion of larvae to the southern portion of the distribution. This is due to reduced larval mortality (due to faster growth in the warmer water), and the seasonal strengthening of the East Australian Current driving particles further south. Spawning over broad temporal and spatial scales by *P. saltatrix* may have developed as a mechanism to ensure maximum dispersal of larvae.This finding demonstrates that species that utilise ocean currents for transport of larvae can substantially alter the final settlement locations of larvae by spawning in different locations or at different times of the year.

Keywords: particle tracking, tailor, bluefish, *Pomatomus saltatrix*, connectivity, larval transport

**Introduction**

The larval phase of many marine organisms is subject to extremely high mortality, from both predation and starvation, with large numbers of larvae spawned to overcome this (Pepin 1989). Ocean currents transport larvae away from spawning sites, with some fraction of the larvae arriving at and settling in juvenile habitats. This dispersal can result in larvae settling hundreds of kilometres away from the original spawning site (Cowen et al. 2006, Cetina-Heredia et al. 2019). Both seasonal and fine scale temporal variation in ocean currents can result is vastly different larval distributions, contributing to the highly variable recruitment of many fish species (Houde 1989b, Siegel et al. 2008). Many species spawn at specific times of the year and in specific locations, potentially utilising favourable oceanography to maximise larval survival (Cowen and Sponaugle 2009, Davies et al. 2014). Understanding the ocean transport of larvae has great value for identifying key species habitats and their connectivity.

With advances in computing power and higher resolution ocean models, biophysical models parameterised with species-specific information are increasingly being used to understand and manage connectivity in the marine environment (Gallego et al. 2007, Hinrichsen et al. 2011). By tracking particles (larvae) within a modelling framework, and quantifying their dispersal patterns relative to suitable juvenile habitats, it is possible to identify important areas for larval production (Everett et al. 2017, Munroe et al. 2018). High-resolution hydrodynamic models provide a mechanism to examine the physical factors which shape observed distributions of larvae and settled juveniles. More than 500 biophysical models have been successfully applied in many systems (Nolasco et al. 2018), including the Southern Ocean (Fraser et al. 2018), coastal boundary currents (Everett et al. 2017) and seas such as the Mediterranean Sea (Andrello et al. 2013). These models have provided insight into transport and spawning connectivity for a variety of organisms including kelp (Coleman et al. 2011, Fraser et al. 2018), invertebrates (Everett et al. 2017, Munroe et al. 2018) and fish (Paris et al. 2005, Santos et al. 2018).

Many fish species are known to have complex spawning behaviour which we are only beginning to understand (REF). These complex behaviours, in particular the timing and location of spawning, can have a significant effect on settlement location and success due to seasonally changing oceanography (REF). *Pomatomus saltatrix* for example, is a globally important recreational and commercial fish species (Juanes et al. 1996) which has recently (Schilling et al 2019) had a second, previously unknown spawning event identified in the coastal southwest Pacific Ocean. As a coastal pelagic predator with well documented spawning grounds in boundary current systems (e.g. East Australian Current, XXXXX and XXXX), *P. saltatrix* is a good candidate for the use of particle tracking models to investigate larval dispersal from the spawning regions. In the Atlantic Ocean, previous research used hydrography, wind and satellite derived temperature to investigate larval transport processes of *P. saltatrix* and found that the number of juveniles recruiting to estuaries is closely linked to oceanographic features such as……. (Hare and Cowen 1996). In the southwest Pacific Ocean, *P. saltatrix* (locally known as tailor) undertake annual migrations along the east coast of Australia approximately tracking with sea surface temperature (abundance peaks at 21.5° C) (Brodie et al. 2018). In winter, *P saltatrix* migrates north, up to 26° S (Fraser Island) where in spring the main spawning event occurs (Pollock 1984, Zeller et al. 1996), and then over summer and autumn they return south along the east coast of Australia (Brodie et al. 2018). This spawning event at Fraser Island is well documented and has resulted in a seasonal closure (August – September) of fishing to protect the species (Leigh et al. 2017). Recently it was shown that the spring spawning event extends south to 30° S, and that a previously unrecognised spawning event occurs between 28° S and 30° S during summer (Schilling et al. 2019). Given the current management of spawning habitat for this species, it is important to quantify the contribution of this temporally and spatially extended spawning to the dispersal and connectivity of P. saltatrix, above that achieved by the traditional spawning event at Fraser Island.

The goal of this study was to understand how multiple spawning events can influence the dispersal of *P. saltatrix* larvae in eastern Australia, utilising the recently recognised spawning times and locations. Specifically, this study aimed to 1. Compare potential settlement of larvae at different latitudes along eastern Australia from the different spawning events, and 2. Investigate if observed locations of juvenile *P. saltatrix* can be explained by the recently recognised spawning events.

**Methods**

*Hydrodynamic model details*

To investigate oceanographic larval dispersal from the identified spawning periods, a particle tracking simulation was run using PARCELS (Lange and van Sebille 2017, Delandmeter and van Sebille 2019). This simulation used the velocity fields from an east Australian Regional Oceanographic Model (ROMS 3.4; Kerry et al. 2016). The model domain extends from Fraser Island in the north (25.12° S) to south of the NSW/Victoria border (41.55° S) and approximately 1000 m 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 2.5-5 km cross-shore resolution and a 5 km alongshore resolution, with 30 vertical s-levels. The model simulation covers a 22-year period (1994 – 2016) and has a similar configuration to the 10-year simulation described in Kerry et al. (2016). Although the ROMS simulation is free running, as it is nested within the most recent BlueLink Reanalysis (BRAN3p5; Oke et al. 2013), its boundaries are constrained by observations. The ROMS model has been assessed with both assimilated and non-assimilated observational data and has shown high complex correlations with observed water velocities (at moorings and high-frequency radars) of between 0.8 and 1 (Kerry et al. 2016). The model has mean spatially averaged root mean squared residuals of 0.4 °C for sea surface temperature (Kerry et al. 2016).

*Particle characteristics*

PARCELS was 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 velocity fields from the ROMS model output. Each particle included a small Brownian motion walk function of 100 units which added natural variation to the movement of each particle and ensured no two particles followed the exact same path (van Sebille et al. 2018, Scutt Phillips et al. 2019).

The growth rates of larvae are temperature dependant (Houde 1989a, Green and Fisher 2004), so the duration of tracking for each particle (settlement time) was temperature dependant and estimated using degree-days (DD; thermal constant; Neuheimer and Taggart 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; Figure S1). Larval growth in *P. saltatrix* is both temperature- and size-dependant with larvae growing faster in both warmer waters and at larger sizes, resulting in exponential growth in the larval size range (Hare and Cowen 1995, 1997). Published growth and temperature data for *P. saltatrix* were combined from various sources to estimate a thermal constant for various stages of development. Larvae (2.1 mm) hatch from eggs at 39 DD (Deuel et al. 1966), growth from the yolk sack occurs at a rate of 0.039 °C d-1 until 2.9mm (59.3 DD; Deuel et al. 1966), 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 S2). This growth rate closely matches observed growth rates in larval *P. saltatrix* (Hare and Cowen 1995, Juanes et al. 1996). For a 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 S2). A settlement time of 500 DD (10.7 mm) was used as it is just before the transition from larvae to juvenile whereby swimming would become vastly more important than passive drift from ocean currents (Hare and Cowen 1994, Hare and Cowen 1996, Neira et al. 1998).

Larval mortality was incorporated into this model by releasing many particles and applying a daily mortality rate to each cohort of particles. Because mortality is a daily constant for each cohort, the number of particles dying each day is constant between cohorts until particles reach the settlement time. 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 value was selected as it is the approximate mean *M* for the temperatures observed in this region (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 larvae that spend longer in the water column (and therefore more vulnerable to predation) before settlement.

*Forward simulation of observed spawning events*

Particle release locations and months were specified to simulate the observed spawning periods, derived from Schilling et al. (2019). Three spawning events were modelled in this study, a northern spring (26 – 27.5° S release locations) event, a mid-latitude spring (28.5 – 30° S) event, and a mid-latitude summer (28.5 – 30° S) event (Figure 1). The spring spawning events spanned August – December inclusive and the summer spawning event combined February and March releases. Within these release locations particles were released every 0.5° latitude on the 100m isobath to encompass all locations *P. saltatrix* in spawning condition were observed. 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 were released from each location every day (during the spawning months) for 22 years (the duration of the ROMS model).

*Backward simulations from locations of observed juvenile P. saltatrix*

Backward simulations were run using the same particle characteristics, except mortality was not incorporated as we know the settlement locations of the particles and are only interested in the potential spawning locations that could have resulted in transport to these locations, rather than any measure of density. Locations were determined by juvenile tailor observations (Leigh et al. 2017, Schilling et al. 2018, Schilling 2019). Because the East Australian Current dominates the region, 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). A cohort of 100 particles was released per location (Table 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, with catch-per-unit-effort (CPUE) used as an indicator of recruitment. Tailor catch is most variable in the south of its distribution (> 37° S), therefore we used a CPUE index from the Victorian Fisheries Authority (Victorian Fisheries Authority 2017). The CPUE data from the Gippsland Lakes seine net fishery (Victorian Fisheries Authority 2017) was provided as the mean for each year (1978 – 2018). Because *P. saltatrix* are most commonly caught at age 2 in the southwestern Pacific Ocean (Leigh et al. 2017, Schilling 2019), the results from the particle tracking model were lagged by 2 years after summing the total number of particles thought to settle during each financial year (in order to cover the whole spawning period). We used CPUE data for years 1998 – 2018 to align with 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 particles which successfully settled (final location on the continental shelf) in 1° latitude bins. Larvae which were not on the continental shelf (≤ 200m depth) at settlement (500 DD) were considered mortalities (cite Everett 2017 again?). 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 latitudinal transport distance. 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 percentage of settled larvae.

**Results**

*Settlement time*

The number of days until larval settlement (500 DD) varied among the three spawning events (Figure 2). Using all particles which reached 500 DD, the mean settlement days 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.

*Dispersal from spawning events*

The larval dispersal simulated by the particle tracking model was almost exclusively southward except for 0.09 % of particles from the northern spring release which finished north of 26° S (Figure 3, Table 3). A high proportion of particles in each spawning period were dispersed offshore, particularly south of the separation zone where the East Australian Current separates from the Australian mainland (Figure 2, Table 2). The mid-latitude spring release had a particularly low number of larvae reach 500 DD on the shelf (0.23 %) compared to 0.75 % and 0.96 % respectively for the northern spring and mid-latitude summer spawning events.

While both the northern spring and mid-latitude summer spawning events had areas of high settlement density (near the spawning locations), the mid-latitude spring spawning event had a wider dispersal of particles with no high density areas of settlement (Figure 3). The mid-latitude summer spawning event extended the furthest south with moderate dispersal offshore (Figure 3).

When the contribution of each spawning event was investigated by settlement latitude, it showed that the three spawning events are disproportionately important for different latitudes of eastern Australia. The northern spring spawning event (which covers the originally identified 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 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 S3).

*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 5 &6). The coastal affiliation was particularly strong for the spring spawning events with the highest density areas of likely spawning locations almost exclusively found along the continental shelf (Figure 5). The exception was for juveniles from Gippsland Lakes (the most southern site) which had a higher proportion of offshore potential spawning locations (Figure 5). For the summer spawning event there was a much broader distribution of potential spawning sites, although northern coastal spawning locations still showed the highest density of potential spawning locations (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 offset predicted larval settlement was strongly correlated between approximately 2003 and 2012. Despite this, there were several years where predicted larval settlement did not match the CPUE data including pre-2004 and after 2012. In the 1997-98 financial year 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 S4 – S6).

**Discussion**

This study simulated larval dispersal from three recognised spawning events for *P. saltatrix* in a western boundary current, and highlighted the varying importance of the spawning events to settlement success. The northern spring spawning event supplied the majority of the settling larvae in the north of the distribution while the mid-latitude summer spawning event had a higher proportion of larvae reaching the southern portion of the species distribution compared to larvae from both the northern and mid-latitude spring spawning events. This research highlights how species may use multiple spawning events to exploit dynamic ocean currents for effective larval dispersal. This study also demonstrates how spawning information can be combined with particle tracking models to better understand habitat connectivity.

*Settlement times*

The use of degree days to model temperature dependant growth rates and therefore settlement times resulted in substantial differences in settlement times and mortality among the 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 were subject to increased mortality 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). Without the use of temperature dependant growth rates, the settlement day would not have varied between spawning events and therefore the daily mortality rate would not have produced any differences in survival. Excluding mortality from these simulations, as some previous connectivity studies have done, results in the mid-latitude spring spawning event being over represented in the final larval survival and settlement numbers (Figure S6). Degree days have been used successfully before in particle tracking models (Everett et al. 2017, Samsing et al. 2017) and our findings confirm that when available, temperature dependant growth should be included in particle tracking models to account for faster growth and earlier settlement, and therefore reduced mortality occurring in warmer waters (Houde 1989a, Neuheimer and Taggart 2007).

*Larval dispersal*

The forward simulations revealed that the northern spring spawning event is highly important for overall population connectivity and recruitment. 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 spawning of P. saltatrix (REF), contribute more settled larvae to the southern part of the species range (south of 34° S). The mid-latitude summer spawning event also 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 confirmed mid-latitude spawning events drive recruitment in southern Australian (south of 37° 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. This contrasts some recent research that suggests larval dispersal across the Southeast Australian Biogeographic Barrier is extremely limited for planktonic larvae (Aguilar et al. 2019). Our current study shows that particularly in late summer when the EAC is strong, larvae have the potential to be transported and settle in the ‘barrier’ region between eastern Australia and southern Australia.

The northern spring spawning event had large numbers of larvae which settled north of the East Australian Current (EAC) separation zone (~32° S) before they could be advected offshore. These northern 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 separation zone where the EAC separates from the Australian coast. The results of this are seen in the concentrations of particles which ended up offshore, approximately 33 – 35° S. This could be further examined using the paths of individual particles which get advected offshore and entrained into eddies. These eddies are highly common along the east coast of Australia and particularly strong south of the EAC separation zone (Suthers et al. 2011, Everett et al. 2012). Climate change is driving change in the EAC region with the flow strengthening up to 35 % (Sun et al. 2012), and separation occurring further south (Cetina-Heredia et al. 2014), which will likely result in increased larvae being dispersed offshore This has large implications for the larval transport of many species, including *P. saltatrix*, which utilise this western boundary current for dispersal. Increased dispersal of many species is already being observed along this coast, through the transport south of tropical larvae and subsequent tropicalisation of temperate areas (Vergés et al. 2014, Miranda et al. 2019).

The backwards simulations from locations where juvenile *P. saltatrix* are found showed that the three identified spawning events have the potential to supply larvae to all locations. 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) and this is likely why the recruitment (and catch) of *P. saltatrix* to 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 sites for the backwards tracking showed very high likelihood that the larvae were spawned in the spawning region and this corresponding to the regular observed annual recruitment. All backwards tracking models were 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.

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 (Rose and Kulka 1999, Maunder et al. 2006), our model exhibited similar ‘recruitment’ patterns as observed in the CPUE data. The positive correlation between predicted larval settlement and the CPUE data from the Gippsland Lakes (38° S) provides evidence that our model is portraying real dispersal and settlement dynamics of this species. Using 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 the 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 dramatically 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 showed that the larvae did get dispersed south but ended up too far east, not on the continental shelf (Figures S4 – S6). Shoreward swimming would have greatly increased predicted settlement in these years, but further research into the swimming abilities of larval *P. saltatrix* is required for this to be modelled accurately. In 1997, there was no predicted larval settlement south of 37° S, which seems highly unlikely as there was no decline in CPUE following this. As the CPUE is based upon total harvest and effort it is influenced by multiple year classes and therefore there will be some natural variation 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 age composition of the harvested fish was known.

The differing larval dispersal from multiple spawning events for *P. saltatrix* likely reflects adaptation by this population to maximise dispersal and larval recruitment to a wide area of coastline in a highly dynamic oceanographic region. Having multiple spawning events spread over space and time, resulting in varied larval dispersal patterns, has been observed in other species of fish and invertebrates (Lambert and Ware 1984, Davies et al. 2014), suggesting that this may be a reliable way of ensuring that larvae have the opportunity to recruit to suitable habitat over a wide region when the oceanographic has large interannual variability.

*Conclusion*

This paper has shown that by spawning in different areas and times of the year, broadcast spawning species such as *P. saltatrix* can substantially alter the final settlement locations of larvae. We have demonstrated that dispersal of larval *P. saltatrix* along the east coast of Australia is dependent on the multiple spawning events which contribute varying proportions of larvae along the coast. The recently confirmed summer spawning event is particularly important for settlement in the southern portion of this species distribution. 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 marine fish.

*Acknowledgements*

This work was funded by an Australian Research Council Linkage Project (LP150100923) and the NSW Recreational Fishing Trust. This research includes computations using the computational cluster Katana supported by Research Technology Services at UNSW Sydney. Thanks to John Morrongiello and Francis Juanes who made useful comments on the thesis chapter which was the basis of this paper.

**Tables**

**Table 1** Site details for the particle tracking simulations. Both forwards and backwards simulations were done from the specified latitudes. 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)** | **Forward or Backwards Tracking** |
| Northern spawning event | 26, 26.5, 27, 27.5 | Forwards |
| Mid-latitude spawning event | 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.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **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 on 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 were calculated on the effective number of released larvae (Table 2) to be more accurate.

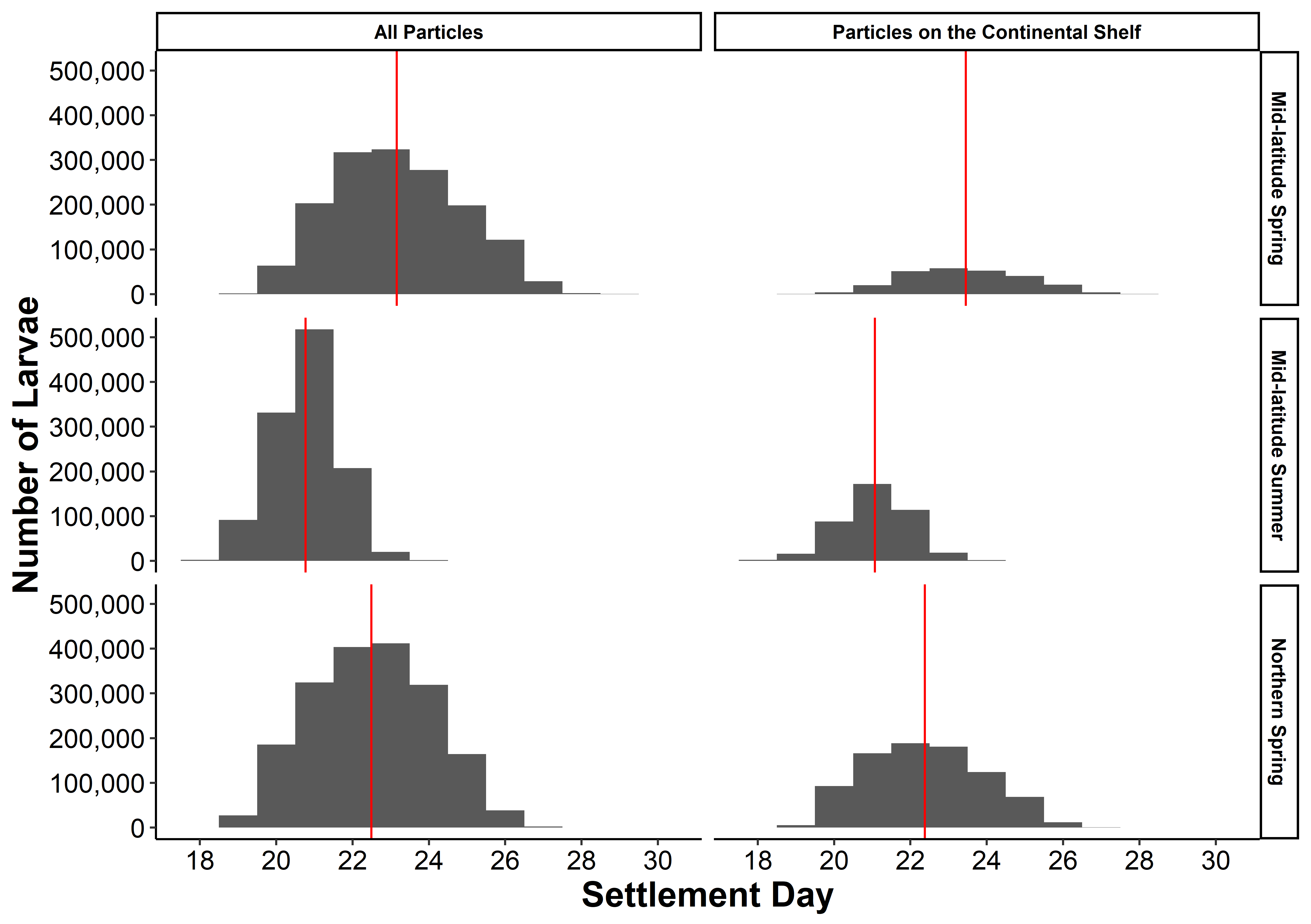
|  |  |  |  |
| --- | --- | --- | --- |
| **Settlement latitude (°S)** | **Northern spring (%)** | **Mid-latitude spring (%)** | **Mid-latitude summer (%)** |
| 25 – 26 | 0.003 | 0.000 | 0.000 |
| 26 – 27 | 0.071 | 0.000 | 0.000 |
| 27 – 28 | 0.245 | 0.000 | 0.002 |
| 28 – 29 | 0.144 | 0.014 | 0.061 |
| 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**

**A close up of a map

Description automatically generated**

**Figure 1** Map of eastern Australia covering the latitudinal rage of *Pomatomus saltatrix* (25 – 39° S). Symbols show the release location for the forwards (filled triangles) and backwards (open circles) simulations. The dashed line represents the boundaries of the regional oceanographic model (Kerry et al. 2016) which provided the velocity estimates used in the simulations.

****

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

A close up of a map

Description automatically generated

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

A close up of a logo

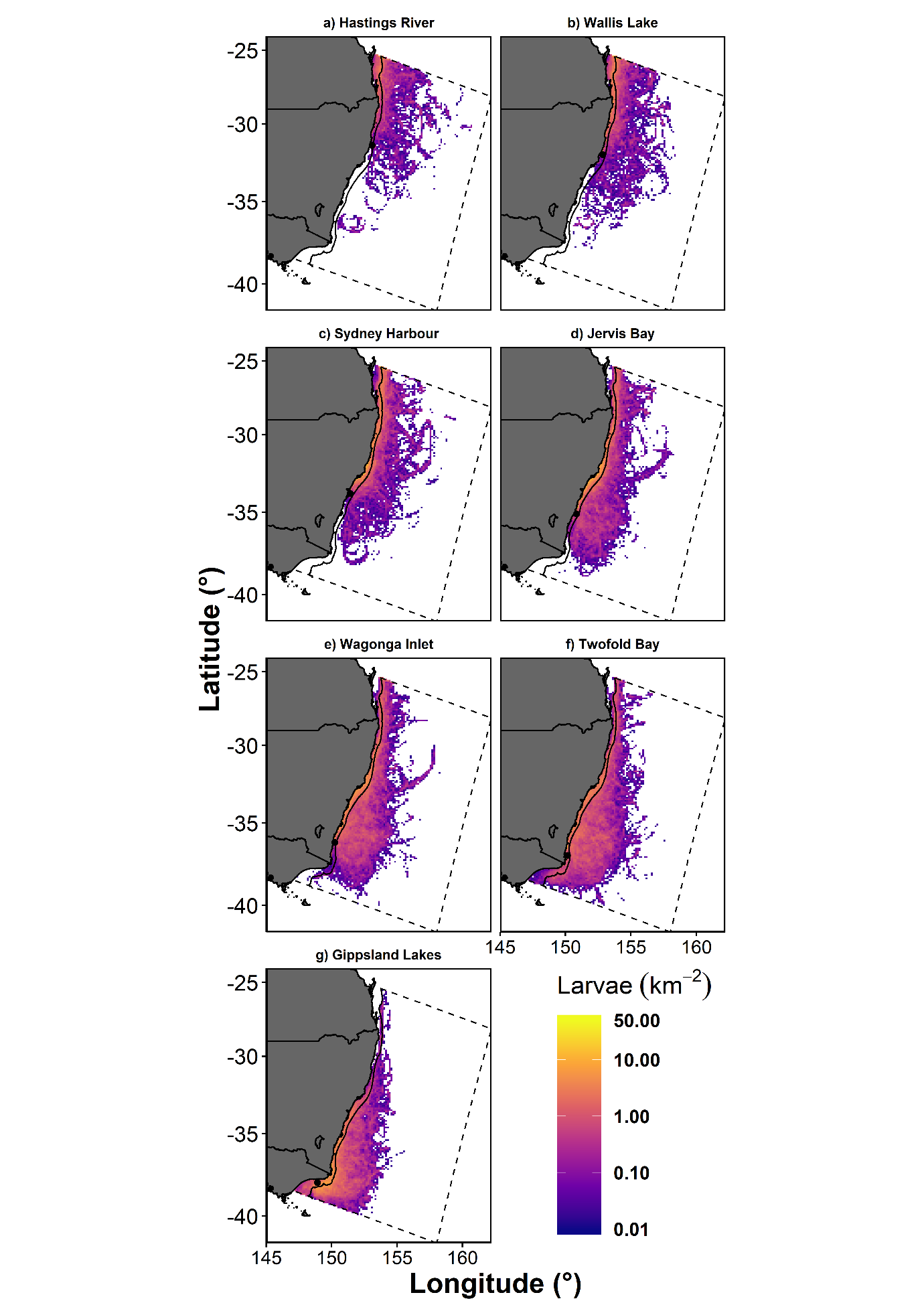
Description automatically generated

**Figure 4** Proportion of settled larvae (on the continental shelf) at 500 degree-days originating from each of the modelled spawning events, using 1° latitude bins.

A close up of a map

Description automatically generated

**Figure 5** Backwards tracking of larvae spawned during spring showing the likely spawning locations (500 degree-days previously). Colour represents the relative density of larvae as the number of released particles was arbitrary. The dashed line box represents the boundary of the regional oceanographic model which provided the velocity fields (Kerry et al. 2016). The black dots represent the release locations for the particles in each model. Note the log10 scale on the colour scale.

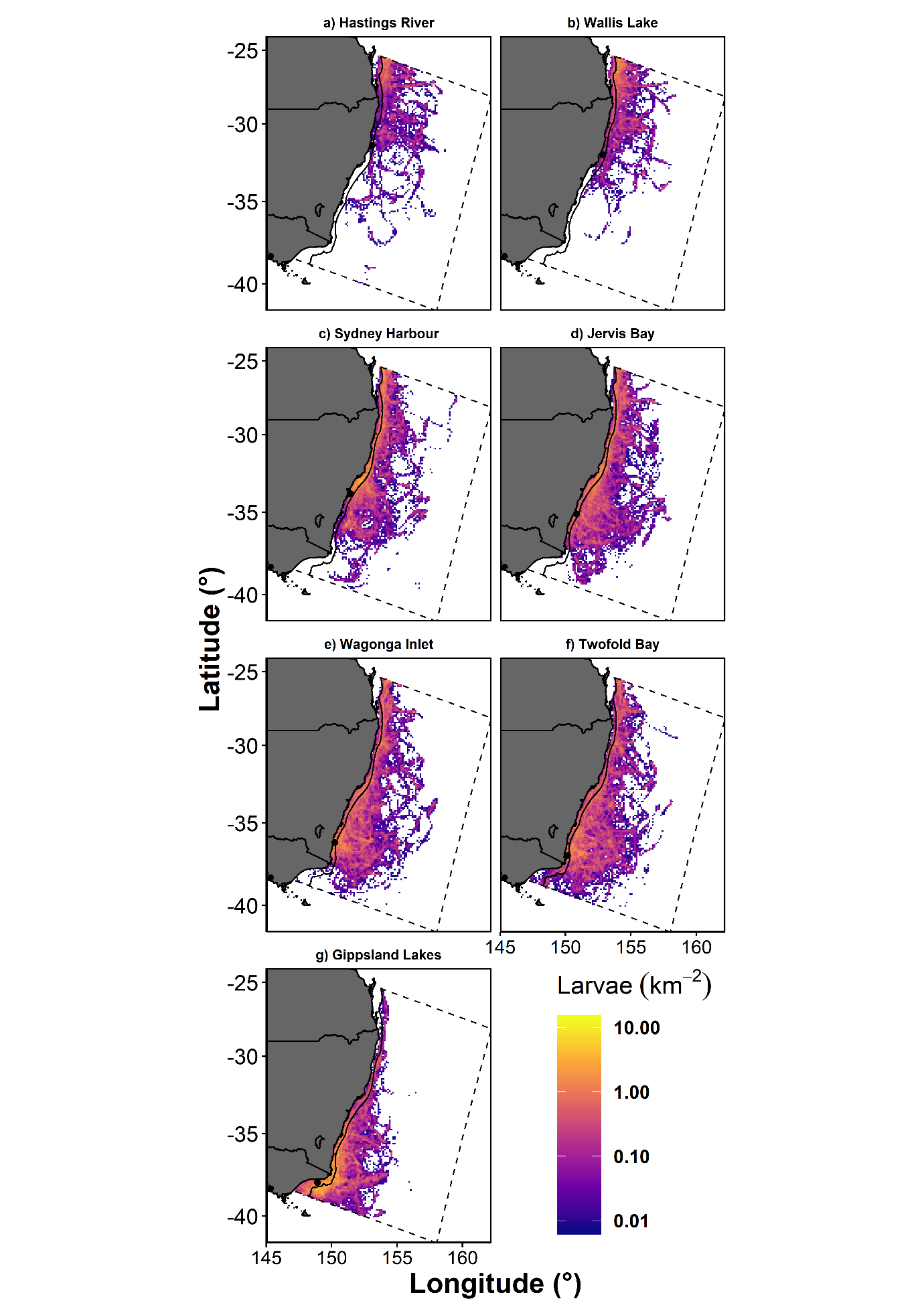


Alternate Figure 5 (portrait for A4)

A close up of a map

Description automatically generated

**Figure 6** Backwards tracking of larvae spawned during summer (February & March) showing the likely spawning locations (500 degree days previously). Colour represents the relative density of larvae as the number of released particles was arbitrary. The dashed line box represents the boundary of the regional oceanographic model which provided the velocity fields (Kerry et al. 2016). The black dots represent the release locations for the particles in each model.



Alternate Figure 6 (Portrait for A4)

A close up of a map

Description automatically generated

**Figure 7** Catch-per-unit-effort from the Gippsland Lakes in Victoria for tailor caught in seine nets (kg shot-1, black solid line) and the 2-year offset relative predicted settlement of *P. saltatrix* larvaesouth of 37° S (red dashed line). The predicted larval settlement is offset by 1 year to align the modal age of captured *P. saltatrix*. The Pearson correlation coefficient of these two datasets is *r* = 0.463 (*P* = 0.034). Note the predicted larval settlement is on a log10 scale.

**References**

Aguilar, L. A., S. A. Matthews, D. J. Ayre, and T. E. Minchinton. 2019. Modelling the differences between El Niño and La Niña years and planktonic larval duration on dispersal across the southeast Australian biogeographic barrier. Geo: Geography and Environment **6**:e00074.

Andrello, M., D. Mouillot, J. Beuvier, C. Albouy, W. Thuiller, and S. Manel. 2013. Low Connectivity between Mediterranean Marine Protected Areas: A Biophysical Modeling Approach for the Dusky Grouper *Epinephelus marginatus*. PLOS ONE **8**:e68564.

Brodie, S., L. Litherland, J. Stewart, H. T. Schilling, J. G. Pepperell, and I. M. Suthers. 2018. Citizen science records describe the distribution and migratory behaviour of a piscivorous predator, *Pomatomus saltatrix*. ICES Journal of Marine Science **75**:1573-1582.

Cetina-Heredia, P., M. Roughan, G. Liggins, M. A. Coleman, and A. Jeffs. 2019. Mesoscale circulation determines broad spatio-temporal settlement patterns of lobster. PLOS ONE **14**:e0211722.

Cetina-Heredia, P., M. Roughan, E. van Sebille, and M. A. Coleman. 2014. Long-term trends in the East Australian Current separation latitude and eddy driven transport. Journal of Geophysical Research. C. Oceans **119**:4351-4366.

Coleman, M. A., M. Roughan, H. S. Macdonald, S. D. Connell, B. M. Gillanders, B. P. Kelaher, and P. D. Steinberg. 2011. Variation in the strength of continental boundary currents determines continent-wide connectivity in kelp. Journal of Ecology **99**:1026-1032.

Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of Connectivity in Marine Populations. Science **311**:522.

Cowen, R. K., and S. Sponaugle. 2009. Larval Dispersal and Marine Population Connectivity. Annual Review of Marine Science **1**:443-466.

Davies, K. T. A., W. C. Gentleman, C. DiBacco, and C. L. Johnson. 2014. Semi-annual spawning in marine scallops strengthens larval recruitment and connectivity on Georges Bank: a model study. Marine Ecology Progress Series **516**:209-227.

Delandmeter, P., and E. van Sebille. 2019. The Parcels v2.0 Lagrangian framework: new field interpolation schemes. Geosci. Model Dev. Discuss. **2019**:1-24.

Deuel, D. G., J. R. Clark, and A. J. Mansueti. 1966. Description of embryonic and early larval stages of bluefish, *Pomatomus saltatrix*. Transactions of the American Fisheries Society **95**:264-271.

Everett, J. D., M. E. Baird, P. R. Oke, and I. M. Suthers. 2012. An avenue of eddies: Quantifying the biophysical properties of mesoscale eddies in the Tasman Sea. Geophysical Research Letters **39**:n/a-n/a.

Everett, J. D., E. Sebille, M. D. Taylor, I. M. Suthers, C. Setio, P. Cetina-Heredia, and J. A. Smith. 2017. Dispersal of Eastern King Prawn larvae in a western boundary current: New insights from particle tracking. Fisheries Oceanography **26**:513-525.

Fraser, C. I., A. K. Morrison, A. M. Hogg, E. C. Macaya, E. van Sebille, P. G. Ryan, A. Padovan, C. Jack, N. Valdivia, and J. M. Waters. 2018. Antarctica’s ecological isolation will be broken by storm-driven dispersal and warming. Nature Climate Change **8**:704-708.

Gallego, A., E. W. North, and P. Petitgas. 2007. Introduction: status and future of modelling physical-biological interactions during the early life of fishes. Marine Ecology Progress Series **347**:121-126.

Green, B. S., and R. Fisher. 2004. Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. Journal of Experimental Marine Biology and Ecology **299**:115-132.

Hare, J. A., and R. K. Cowen. 1994. Ontogeny and otolith microstructure of bluefish *Pomatomus saltatrix* (Pisces: Pomatomidae). Marine Biology **118**:541-550.

Hare, J. A., and R. K. Cowen. 1995. Effect of age, growth rate, and ontogeny on the otolith size – fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. Canadian Journal of Fisheries and Aquatic Sciences **52**:1909-1922.

Hare, J. A., and R. K. Cowen. 1996. Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. Limnology and Oceanography **41**:1264-1280.

Hare, J. A., and R. K. Cowen. 1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology **78**:2415-2431.

Hinrichsen, H.-H., M. Dickey-Collas, M. Huret, M. A. Peck, and F. B. Vikebø. 2011. Evaluating the suitability of coupled biophysical models for fishery management. ICES Journal of Marine Science **68**:1478-1487.

Houde, E. D. 1989a. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fishery Bulletin **87**:471-495.

Houde, E. D. 1989b. Subtleties and episodes in the early life of fishes. Journal of Fish Biology **35**:29-38.

Juanes, F., J. A. Hare, and A. G. Miskiewicz. 1996. Comparing early life history strategies of *Pomatomus saltatrix*: a global approach. Marine & Freshwater Research **47**:365-379.

Kerry, C., B. Powell, M. Roughan, and P. Oke. 2016. Development and evaluation of a high-resolution reanalysis of the East Australian Current region using the Regional Ocean Modelling System (ROMS 3.4) and Incremental Strong-Constraint 4-Dimensional Variational (IS4D-Var) data assimilation. Geoscientific Model Development **9**:3779-3801.

Lambert, T. C., and D. M. Ware. 1984. Reproductive strategies of demersal and pelagic spawning fish. Canadian Journal of Fisheries and Aquatic Sciences **41**:1565-1569.

Lange, M., and E. van Sebille. 2017. Parcels v0.9: prototyping a Lagrangian ocean analysis framework for the petascale age. Geoscientific Model Development **10**:4175-4186.

Leigh, G. M., M. F. O'Neill, and J. Stewart. 2017. Stock assessment of the Australian east coast tailor (*Pomatomus saltatrix*) fishery. Queensland Department of Agriculture and Fisheries, Brisbane.

Litherland, L., J. Andrews, J. Stewart, and P. Lewis. 2016. Tailor *Pomatomus saltatrix*.*in* C. Stewardson, J. Andrews, C. Ashby, M. Haddon, K. Hartmann, P. Hone, P. Horvat, S. Mayfield, A. Roelofs, K. Sainsbury, T. Saunders, J. Stewart, I. Stobutzki, and B. Wise, editors. Status of Australian fish stocks reports 2016. Fisheries Research and Development Corporation, Canberra.

Maunder, M. N., J. R. Sibert, A. Fonteneau, J. Hampton, P. Kleiber, and S. J. Harley. 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. ICES Journal of Marine Science **63**:1373-1385.

Miranda, T., J. A. Smith, I. M. Suthers, D. Mazumder, D. O. Cruz, H. T. Schilling, K. Searle, and A. Vergés. 2019. Convictfish on the move: variation in growth and trophic niche space along a latitudinal gradient. ICES Journal of Marine Science.

Miskiewicz, A. G., B. D. Bruce, and P. Dixon. 1996. Distribution of tailor (*Pomatomus saltatrix*) larvae along the coast of New South Wales, Australia. Marine and Freshwater Research **47**:331-336.

Munroe, D. M., D. Haidvogel, J. C. Caracappa, J. M. Klinck, E. N. Powell, E. E. Hofmann, B. V. Shank, and D. R. Hart. 2018. Modeling larval dispersal and connectivity for Atlantic sea scallop (*Placopecten magellanicus*) in the Middle Atlantic Bight. Fisheries Research **208**:7-15.

Neira, F. J., A. G. Miskiewicz, and T. Trnski. 1998. Larvae of temperate Australian fishes: laboratory guide for larval fish identification. UWA Publishing.

Neuheimer, A. B., and C. T. Taggart. 2007. The growing degree-day and fish size-at-age: the overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences **64**:375-385.

Nolasco, R., I. Gomes, L. Peteiro, R. Albuquerque, T. Luna, J. Dubert, S. E. Swearer, and H. Queiroga. 2018. Independent estimates of marine population connectivity are more concordant when accounting for uncertainties in larval origins. Scientific Reports **8**:2641.

Oke, P. R., P. Sakov, M. L. Cahill, J. R. Dunn, R. Fiedler, D. A. Griffin, J. V. Mansbridge, K. R. Ridgway, and A. Schiller. 2013. Towards a dynamically balanced eddy-resolving ocean reanalysis: BRAN3. Ocean Modelling **67**:52-70.

Paris, C. B., R. K. Cowen, R. Claro, and K. C. Lindeman. 2005. Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. Marine Ecology Progress Series **296**:93-106.

Pepin, P. 1989. Predation and Starvation of Larval Fish: A Numerical Experiment of Size- and Growth-Dependent Survival. Biological Oceanography **6**:23-44.

Pollock, B. R. 1984. The tailor (*Pomatomus saltatrix*) fishery at Fraser Island and its relation to the life-history of the fish. Proceedings of the Royal Society of Queensland **95**:23 - 28.

Putman, Nathan F., and Katherine L. Mansfield. 2015. Direct Evidence of Swimming Demonstrates Active Dispersal in the Sea Turtle “Lost Years”. Current Biology **25**:1221-1227.

Rose, G. A., and D. W. Kulka. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Canadian Journal of Fisheries and Aquatic Sciences **56**:118-127.

Samsing, F., I. Johnsen, T. Dempster, F. Oppedal, and E. A. Treml. 2017. Network analysis reveals strong seasonality in the dispersal of a marine parasite and identifies areas for coordinated management. Landscape Ecology **32**:1953-1967.

Santos, A. M. P., A. E. Nieblas, P. Verley, A. Teles-Machado, S. Bonhommeau, C. Lett, S. Garrido, and A. Peliz. 2018. Sardine (*Sardina pilchardus*) larval dispersal in the Iberian upwelling system, using coupled biophysical techniques. Progress in Oceanography **162**:83-97.

Schilling, H. T. 2019. Ecology of tailor, *Pomatomus saltatrix*, in eastern Australia. PhD Thesis. University of New South Wales, Sydney, Australia.

Schilling, H. T., P. Reis-Santos, J. M. Hughes, J. A. Smith, J. D. Everett, J. Stewart, B. M. Gillanders, and I. M. Suthers. 2018. Evaluating estuarine nursery use and life history patterns of *Pomatomus saltatrix* in eastern Australia. Marine Ecology Progress Series **598**:187-199.

Schilling, H. T., J. A. Smith, J. Stewart, J. D. Everett, J. M. Hughes, and I. M. Suthers. 2019. Reduced exploitation is associated with an altered sex ratio and larger length at maturity in southwest Pacific (east Australian) *Pomatomus saltatrix*. Marine Environmental Research **147**:72-79.

Scutt Phillips, J., L. Escalle, G. Pilling, A. Sen Gupta, and E. van Sebille. 2019. Regional connectivity and spatial densities of drifting fish aggregating devices, simulated from fishing events in the Western and Central Pacific Ocean. Environmental Research Communications **1**:055001.

Siegel, D. A., S. Mitarai, C. J. Costello, S. D. Gaines, B. E. Kendall, R. R. Warner, and K. B. Winters. 2008. The stochastic nature of larval connectivity among nearshore marine populations. Proceedings of the National Academy of Sciences **105**:8974-8979.

Sun, C., M. Feng, R. J. Matear, M. A. Chamberlain, P. Craig, K. R. Ridgway, and A. Schiller. 2012. Marine Downscaling of a Future Climate Scenario for Australian Boundary Currents. Journal of Climate **25**:2947-2962.

Suthers, I. M., J. W. Young, M. E. Baird, M. Roughan, J. D. Everett, G. B. Brassington, M. Byrne, S. A. Condie, J. R. Hartog, C. S. Hassler, A. J. Hobday, N. J. Holbrook, H. A. Malcolm, P. R. Oke, P. A. Thompson, and K. Ridgway. 2011. The strengthening East Australian Current, its eddies and biological effects — an introduction and overview. Deep Sea Research Part II: Topical Studies in Oceanography **58**:538-546.

van Sebille, E., S. M. Griffies, R. Abernathey, T. P. Adams, P. Berloff, A. Biastoch, B. Blanke, E. P. Chassignet, Y. Cheng, C. J. Cotter, E. Deleersnijder, K. Döös, H. F. Drake, S. Drijfhout, S. F. Gary, A. W. Heemink, J. Kjellsson, I. M. Koszalka, M. Lange, C. Lique, G. A. MacGilchrist, R. Marsh, C. G. Mayorga Adame, R. McAdam, F. Nencioli, C. B. Paris, M. D. Piggott, J. A. Polton, S. Rühs, S. H. A. M. Shah, M. D. Thomas, J. Wang, P. J. Wolfram, L. Zanna, and J. D. Zika. 2018. Lagrangian ocean analysis: Fundamentals and practices. Ocean Modelling **121**:49-75.

Vergés, A., P. D. Steinberg, M. E. Hay, A. G. B. Poore, A. H. Campbell, E. Ballesteros, K. L. Heck, D. J. Booth, M. A. Coleman, D. A. Feary, W. Figueira, T. Langlois, E. M. Marzinelli, T. Mizerek, P. J. Mumby, Y. Nakamura, M. Roughan, E. van Sebille, A. S. Gupta, D. A. Smale, F. Tomas, T. Wernberg, and S. K. Wilson. 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proceedings of the Royal Society B: Biological Sciences **281**.

Victorian Fisheries Authority. 2017. Review of key Victorian fish stocks — 2017. Melbourne, Victoria.

Zeller, B. M., B. R. Pollock, and L. E. Williams. 1996. Aspects of the life history and management of tailor (*Pomatomus saltatrix*) in Queensland. Marine & Freshwater Research **47**:323-329.

**Supplementary Material**

A screenshot of a cell phone

Description automatically generated

**Figure S1** Example of cumulative degree days at 3 different water temperatures.

A screenshot of a cell phone

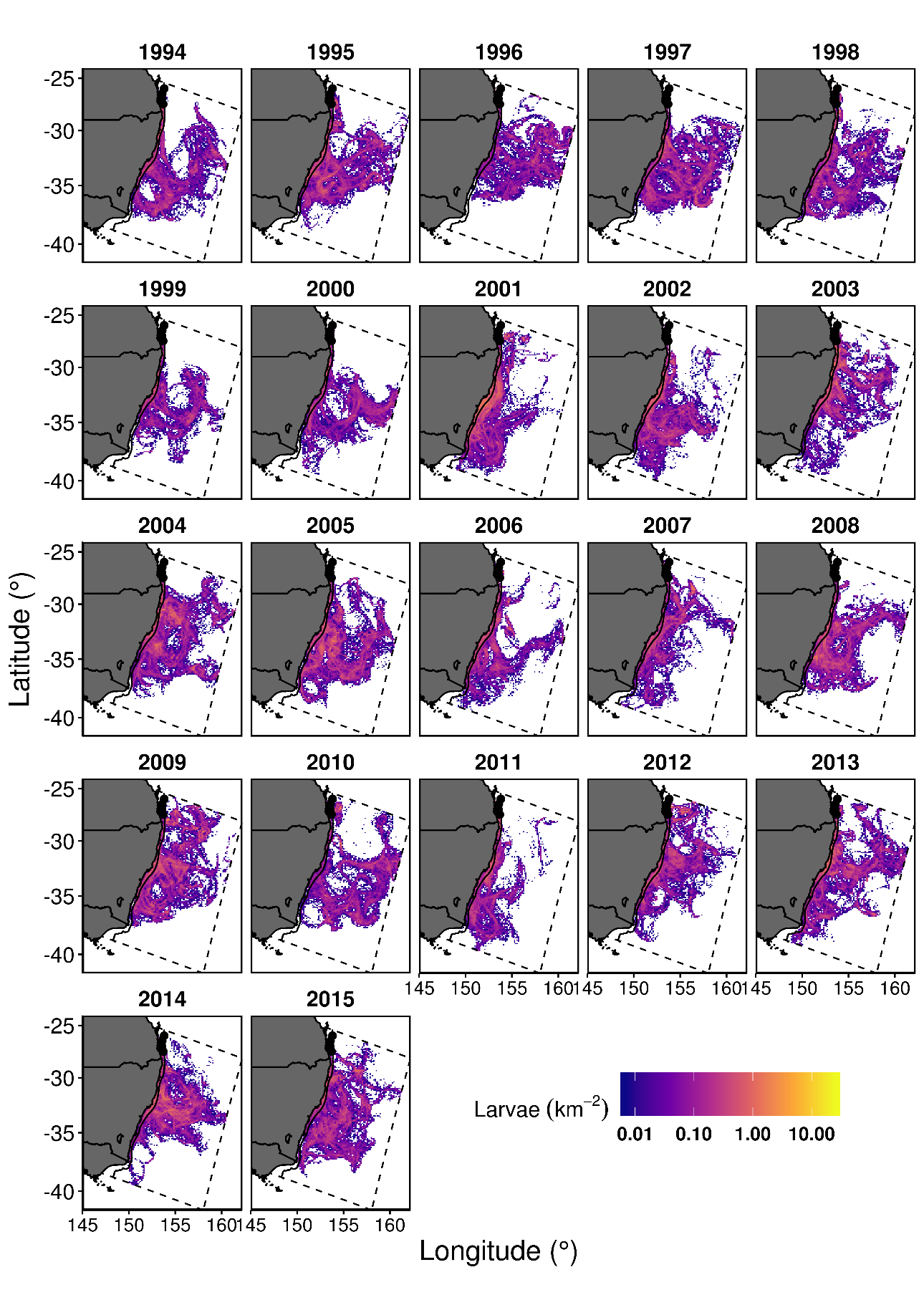
Description automatically generated

**Figure S2** Relationship between *Pomatomus saltatrix* length and degree days.

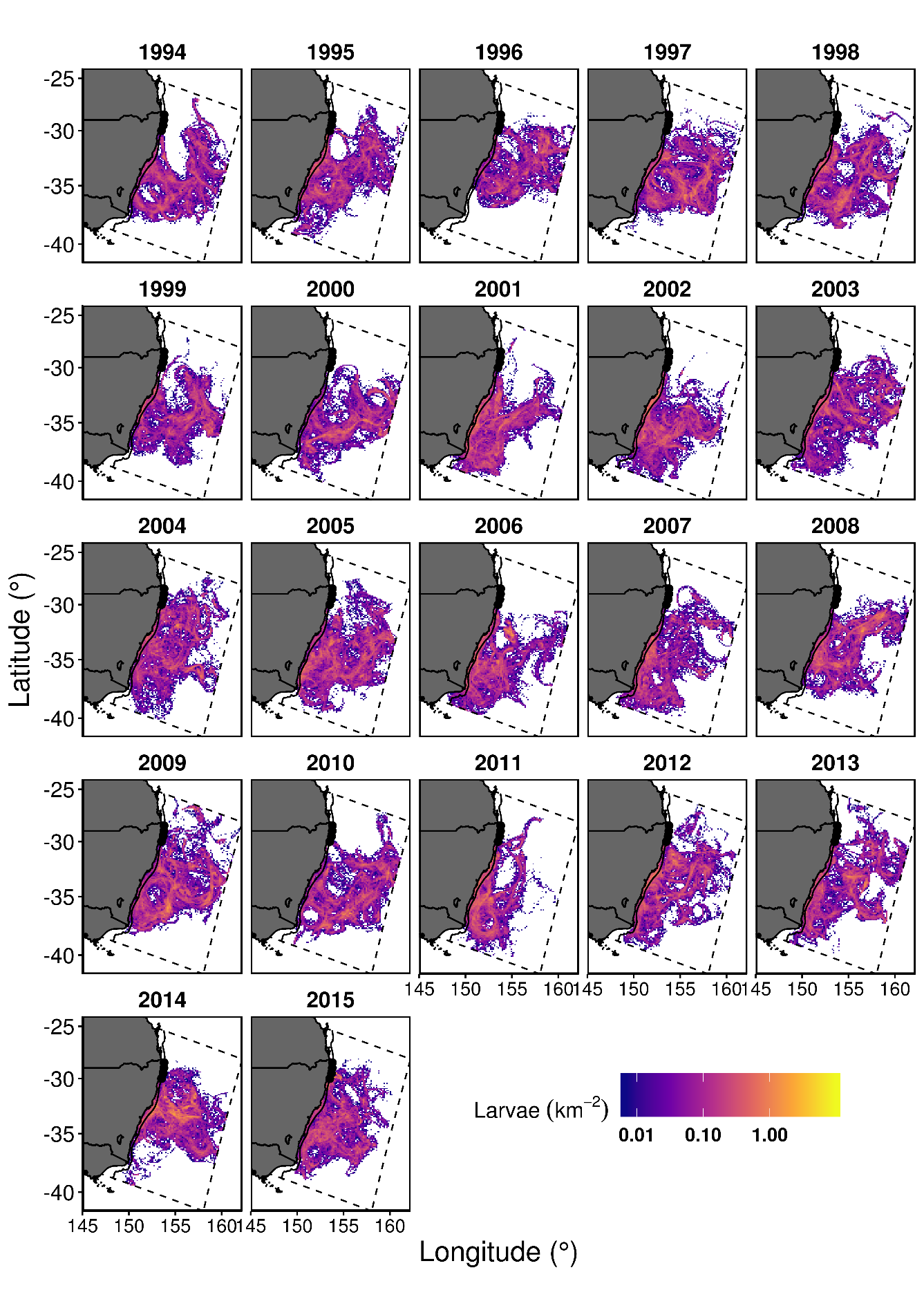
A screenshot of a cell phone

Description automatically generated

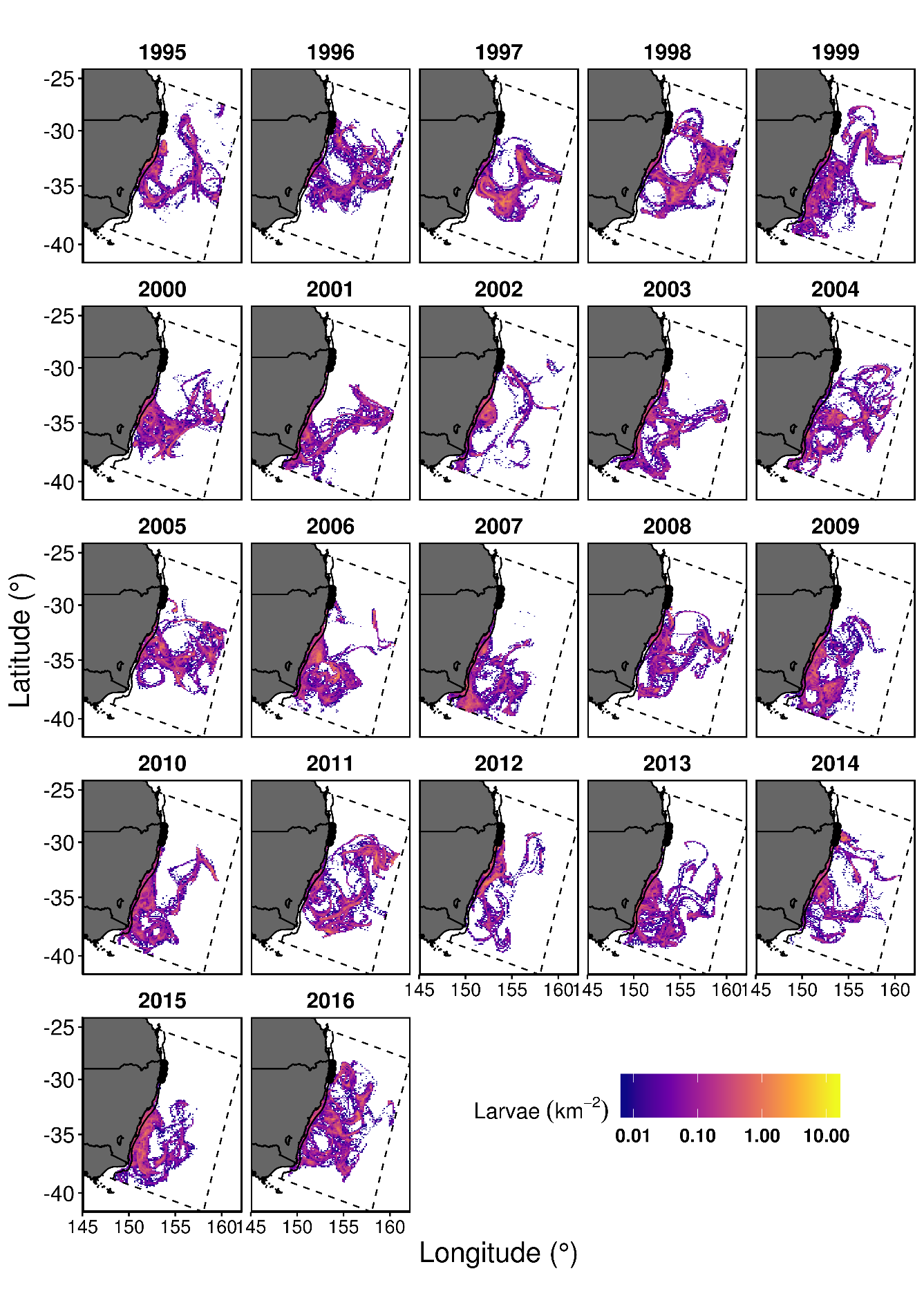
**Figure S3** Proportion of settled larvae (on the continental shelf) at 500 degree days originating from each of the modelled spawning events with no mortality applied, using 1° latitude bins.



**Figure S4** Annual variation in density of larvae at settlement time (500 degree days) for the northern spring spawning event. The black circles show the release location of the particles for each spawning event. The continental shelf (200 m depth) is shown as a solid black line within the model boundaries. The density colour scale is consistent between subplots but note the non-linear colour scale.



**Figure S5** Annual variation in density of larvae at settlement time (500 degree days) for the mid-latitude spring spawning event. The black circles show the release location of the particles for each spawning event. The continental shelf (200 m depth) is shown as a solid black line within the model boundaries. The density colour scale is consistent between subplots but note the non-linear colour scale.



**Figure S6** Annual variation in density of larvae at settlement time (500 degree days) for the mid-latitude summer spawning event. The black circles show the release location of the particles for each spawning event. The continental shelf (200 m depth) is shown as a solid black line within the model boundaries. The density colour scale is consistent between subplots but note the non-linear colour scale.