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Dispersal of Eastern King Prawn larvae in a western boundary current: New insights from particle tracking

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Abstract

Patterns in larval transport of coastal species have important implications for species connectivity, conservation, and fisheries, especially in the vicinity of a strengthening boundary current. An Ocean General Circulation Model for the Earth Simulator particle tracking model was used to assess the potential dispersal of Eastern King Prawn (EKP) larvae *Melicertus (Penaeus) plebejus*, an important commercial and recreational species in Eastern Australia. Particles were exposed to a constant natural mortality rate, and temperature-dependent growth (degree-days) was used to determine the time of settlement. Forward and backward simulations were used to identify the extent of larval dispersal from key source locations, and to determine the putative spawning regions for four settlement sites. The mean dispersal distance for larvae was extensive (~750–1,000 km before settlement), yet the northern spawning locations were unlikely to contribute larvae to the most southern extent of the EKP range. There was generally great offshore dispersal of larvae, with only 2%–5% of larvae on the continental shelf at the time of settlement. Our particle tracking results were combined with existing site-specific reproductive potentials to identify the relative contributions of larvae from key source locations. Although mid-latitude sites had only moderate reproductive potential, they delivered the most particles to the southern coast and are probably the most important sources of larval EKP for the two southern estuaries. Our modelling suggests that mesoscale oceanography is a strong determinant of recruitment success of the EKP, and highlights the importance of both larval dispersal and reproductive potential for understanding connectivity across a species' range.

KEYWORDS
dispersal, Eastern King Prawn, mortality, ocean general circulation model for the earth simulator, particle tracking, reproductive success

1 | INTRODUCTION

Many marine organisms have a dispersive larval stage, ranging over 10,000–100,000 of kilometres (Boehlert, 1996; Booth, Figueira, Gregson, Brown, & Beretta, 2007). Understanding the persistence of marine populations requires knowledge of larval connectivity and how it contributes to a metapopulation structure (Kritzer & Sale, 2004). This knowledge helps identify where appropriate actions should be targeted when managing populations for either fisheries or conservation purposes. For example, temporal or spatial closures may be useful in preserving spawning populations or protecting juveniles during their nursery phase, but effective implementation requires knowledge of the particular times and locations to apply these measures (Armstrong et al., 2013; van Overzee & Rijnsdorp, 2015).

Successful recruitment relies on a combination of suitable physico-chemical conditions, reproductive behaviour, and appropriate larval retention or larval transport to suitable nursery habitats (Hutchings et al., 2002). Oceanographic conditions can decouple this sequence of events (Lipcius, Stockhausen, Eggleston, Marshall, & Hickey, 1997), through the absence of spawning cues, lack of food, suboptimal larval temperatures, or advection away from nursery habitats. This is particularly true for organisms that have an extended and passive phase, and drift in oceanic currents while they develop to settlement stage. Prevailing ocean conditions, such as temperature, currents and food availability, play a large part in determining recruitment success and ultimately future fisheries catch. Consequently, remotely sensed oceanographic data might well provide a useful insight into potential landings in a future year class, or years where recruitment to nursery areas may be limited.

Large penaeid prawn species often have life cycles that include an offshore dispersive larval phase, an inshore or estuarine nursery phase, and an offshore adult phase (Dall & Sharples, 1990). Eastern King Prawn (*Penaeus* [*Melicertus*] *plebejus*, abbreviated to EKP) is one such important commercial and recreational species (approximately AUD$ 70 million per year) off eastern Australia (Ives & Scandol, 2007; Ochwada-Doyle, Gray, Loneragan, & Taylor, 2010), with a range that extends throughout 20 degrees of latitude from the lower Great Barrier Reef, Queensland (21°S) to George Bay, Tasmania (41°S) (Montgomery, 1990). Previous work has shown that the majority of spawning activity occurs at lower latitudes (Equatorward of 28°S), although smaller numbers of females capable of spawning are detected as far south as Port Stephens (32.7°S; Montgomery et al., 2007). Larvae develop in ocean waters, and post-larvae are thought to use selective tidal stream transport to migrate into estuarine nursery habitats (Church & Fandry, 1995). After the nursery phase, adolescent prawns begin northward migrations of up to 1,200 km (Montgomery, 1990) to return to the main spawning areas. In the warmer low-latitudes (Equatorward of 28°S), spawning is thought to occur all year round, but in the cooler high-latitude areas, spawning is generally limited to autumn (Montgomery et al., 2007). Much of the harvested stock, especially in New South Wales, is supplied from estuarine nurseries in the southern part of the range, but anecdotal information suggests recruitment to these estuaries is variable.

Hatchery releases of EKP post-larvae are currently used to enhance recreational harvest in areas where recruitment is limited (Ochwada-Doyle, Gray, Loneragan, Suthers, & Taylor, 2012; Taylor, 2017). The ability to understand expected recruitment to the southern part of the range and connectivity with spawning in the north may improve enhancement strategies of when and where to release larvae (Loneragan, Jenkins, & Taylor, 2013), and also assist the management of effort in the northern part of the range where adults are targeted by offshore trawling.

Advances in particle tracking and ocean models have improved modelling of connectivity in oceanic systems (Cetina-Heredia, Roughan, van Sebille, Feng, & Coleman, 2015; Holliday et al., 2012; Myksvoll, Jung, Albretsen, & Sundby, 2014) and has the potential to improve our understanding of connectivity between spawning grounds and nurseries, and whether oceanographic variability contributes to recruitment variability. Following the work of Cetina-Heredia, Roughan, van Sebille, and Coleman (2014) and Doblin and van Sebille (2016), we apply the “Ocean General Circulation Model (OGCM) For the Earth Simulator” (OFES; Masumoto, Sasaki, Kagimoto, & Komori,2004) to model the physical processes driving the dispersal of EKP larvae, alongside important ecological processes occurring in the plankton (mortality and temperature-dependent growth) and spatial variation in reproductive potential. Specifically, we developed a coupled physical–biological model to address three aims:

1. Model the potential dispersal of EKP larvae along eastern Australia, to quantify the connectivity between their northern spawning locations and southern habitats on annual and seasonal timescales;
2. Assess the likely origin of EKP recruited to representative southern estuarine nurseries; and,
3. Understand how oceanographic conditions might influence adult catch rates through recruitment potential to estuarine nurseries.

2 | METHODS

2.1 | Study region and Lagrangian particle tracking

The study region extends from Fraser Island in the north (25°S) to Bass Strait in the south (40°S), approximating the core distribution of EKP (Figure 1). Both forward and backward simulations were used to assess the dispersion of prawns from the main locations where females of spawning sizes were known to occur (Montgomery et al., 2007), and the origin of prawns at known habitat and recruitment areas (e.g., Montgomery & Winstanley, 1982; Racek, 1959; Reid & Montgomery, 2005), respectively. By tracking the dispersion of EKPs from their spawning and settlement regions, we bracket the range of likely dispersal pathways and diminish potential errors (Putman & Naro-Maciel, 2013). Particles were advected within the OGCM for the Earth Simulator (OFES) using the Connectivity Modeling System (Paris, Helgers, van Sebille, & Srinivasan, 2013) employing a fourth order Runge–Kutta scheme. OFES is a global high-resolution ocean-only model (Masumoto et al., 2004) configured on a 1/10th horizontal resolution grid with 54 vertical levels. In these simulations, however, we only used the surface 10-m velocity field. The surface model bin is representative of the currents through the water column (<200 m) and the pattern of dispersion would not have changed significantly if a different depth bin was chosen (Figs S1 and S2). The model has been initialized from World Ocean Atlas temperature and salinity fields, and then forced with the wind from the National Centers for Environmental Prediction. The OFES simulation has been validated to observational data and used in Lagrangian particle tracking experiments around Australia (Cetina-Heredia et al., 2015; van Sebille, England, Zika, & Sloyan, 2012).

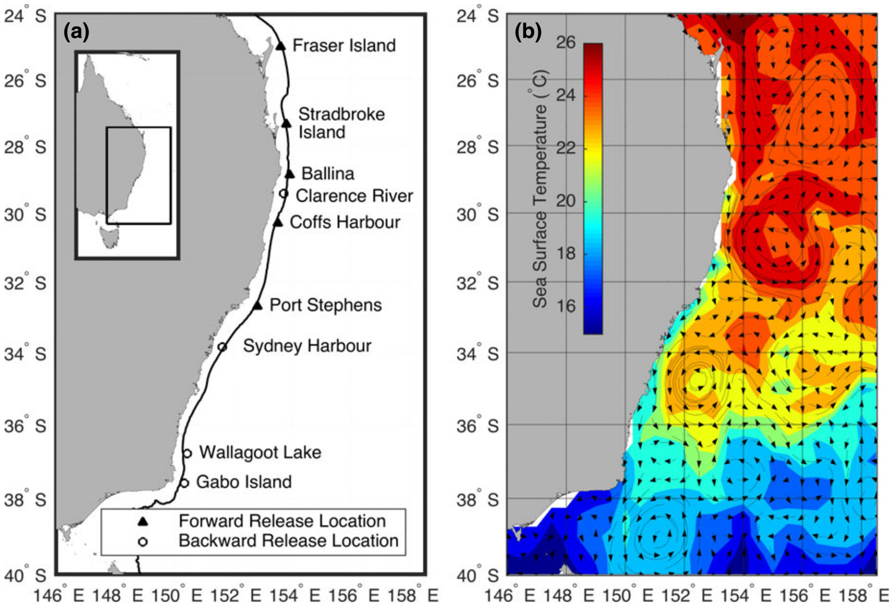

FIGURE 1 Map of eastern Australia covering the approximate latitudinal extent of the Eastern King Prawn (EKP) range (north of Fraser Island to Gippsland Lakes in Victoria). (a) The start locations used in the forward (triangles) and backward (circles) particle tracking simulations are shown. (b) The Sea Surface Temperature (°C) is shown in colour, and the arrows indicate surface velocities from OFES (1st January 1980). [Colour figure can be viewed at wileyonlinelibrary.com]

For forward simulations, EKPs were released near the edge of the continental shelf (defined as <200 m water depth), where they are thought to spawn (Ruello, 1975), at five spawning locations between Fraser Island and Port Stephens (Table 1; Montgomery et al., 2007). In the backward simulations, prawns were tracked backwards, to determine the source location of recruiting larvae, from four representative estuaries along the coast where juveniles are known to recruit. One hundred prawns were released at 6-hourly intervals between 1 January 1980 and 17 November 2010 and their location was recorded each day for 60 days. The diffusivity coefficient was zero, and the model surface water temperature was recorded for the calculation of degree-days (see below).

2.2 | Larval development and settlement

Preston (1985) observed temperature- and salinity-dependant growth of larval EKP within the hatchery environment, with the optimal growth at the first protozoeae stage occurring at salinities of 32–37 and temperatures of 21–29°C. Settlement time of EKP in this model was temperature-dependent and estimated using degree-days (DD), sometimes referred to as the thermal constant (Neuheimer & Taggart, 2007). This uses the sum of the daily temperatures needed to reach a specific settlement life stage, as larval growth is highly temperature dependent. Using the experimental data from Preston (1985), DD was calculated by multiplying an experimental temperature by the total duration of larval development to post-larva 1 (the life stage at which settlement can occur) at that temperature and estimated 427.4 (±10.4 *SE*) for EKP. The water temperature for each EKP particle in the model was recorded daily, and when the cumulative sum reached 427 DD, the EKP was considered to be at settlement stage. For a typical water temperature of 22°C, this means that larvae settle after 20 days. Incorporating temperature-dependent growth into the particle tracking model allowed us to incorporate plasticity in larval duration owing to temperature, giving more realistic estimates for settlement time and dispersal distance. Larvae which were not on the continental shelf (0–200 m water depth) at settlement age were considered mortalities in our analysis.

TABLE 1 Site details for particle tracking simulations. Both forward and backward simulations were done, and particles were released (or tracked) from the specified latitudes

	Release site	Latitude	Simulation
1.	Fraser Island	25.0°S	Forward
2.	Stradbroke Island	27.4°S	Forward
3.	Ballina	28.9°S	Forward
4.	Coffs Harbour	30.3°S	Forward
5.	Port Stephens	32.7°S	Forward
1.	Clarence River	29.4°S	Backward
2.	Sydney Harbour	33.8°S	Backward
3.	Wallagoot Lake	36.8°S	Backward
4.	Gabo Island	37.6°S	Backward

2.3 | Dispersal

The total dispersal distance (km) of each particle from release, up to and including their settlement (DD = 427), was measured by summing the daily straight-line dispersal distance. The straight-line distance from release to settlement (km) was also calculated. The mean daily dispersal speed (km/day) was estimated as the average distance travelled per day up to the time of settlement. Note that, because distances were calculated using the average straight-line distance between daily locations, the dispersal distance and speed recorded here are lower bounds. The offshore distance was calculated as the closest distance from the settlement location to the coastline. One-way analysis of variance (ANOVA) was used to test differences among locations in (i) days to the settlement, (ii) dispersal distance, and (iii) offshore distance at settlement. Only one particle release per month per location ($n = 376$) was used in the ANOVA to remove any temporal auto-correlation. Locations showing significant differences were identified using pairwise comparisons according to Tukey's least significant difference procedure.

2.4 | Survival

Given that duration until a settlement could vary between particles, it was necessary to "thin" particles to account for varying survival rates (Natural Mortality). Survival was considered constant per-unit-time, so the probability of survival (s) was specified as a function of the number of days (n) a particle spends in the plankton:

$$P(s) = e^{-Z \times n} \tag{1}$$

where Z (day^{-1}) is the instantaneous mortality rate. A value of $Z = 0.0576$ was used (approximating a survival rate of 10% after 40 days) based on data for larval *Penaeus* spp. (Kanazawa, Teshima, & Sakamoto, 1985). This value was within the broad range observed for larval fish (Houde, 1989), but remains highly uncertain. The main rationale underlying inclusion of this probability in the model was to account for relative differences in particle density that might arise through differential survival associated with planktonic duration.

2.5 | Relative contribution of larvae

In addition to estimating the relative abundance of particles arriving at a settlement location via particle tracking, we also considered the larval supply as a result of the "reproductive potential" of the adults (Montgomery et al., 2007). Combining these data provided an estimate of the relative contribution of larvae from source locations to specific settlement sites. Larval supply data was sourced from Montgomery et al. (2007), which reported a "reproductive potential" index for EKP. This index was derived by combining site-specific, size-frequency information with size-based spawning and fecundity relationships (Montgomery et al., 2007), and represents the relative abundance of larvae produced at each source location. Annual averages of the reproductive potential index from six source locations were used in this analysis.

Most of the sites described in Montgomery et al. (2007) were identical to those used in this study. However, some were altered to match the sites used here. Moreton Bay had no raw data available, but Montgomery et al. (2007) showed that Moreton Bay and Ballina had a similar reproductive potential, so these sites were made equivalent in this study. Moreton Bay was renamed Stradbroke Island (same latitude), and the reproductive potential for Fraser Island (this study) was computed as the average of the surrounding sites (Mooloolaba and Lady Elliot Island) from Montgomery et al. (2007). The Clarence River was also included as a source site following Montgomery (Montgomery et al., 2007) but the Swain Reefs site was outside our study area, so was not used.

To undertake a paired assessment of both the source and sink of EKP larvae, we extracted, from the output of the backward simulations, the number of particles which originated from the forward release sites to the backward release sites (Table 1). The particles were considered to have originated from a forward release site if they originated from within a 0.5° box at each release location. The boxes were centred at a specific latitude and continued offshore from the 5-m isobath. The relative contribution (C_{rel}) of larvae from source location i to a given settlement site was calculated as the product of the relative number of particles (N_{rel}) sourced from location i and the reproductive potential (R_{pot}) at location i, standardised to a scale of 0–1, given j source locations:

$$C_{\mathrm{rel}_i} = \frac{N_{\mathrm{rel}_i} \times R_{\mathrm{pot}_i}}{max(N_{\mathrm{rel}_i} \times R_{\mathrm{pot}_i} : i = 1, \ldots, j)} \tag{2}$$

This relative contribution of larvae (C_{rel}) accounts for the strength of the connection between sources and settlement sites (N_{rel}), but also for the difference in the number of larvae likely to be released at each source (R_{pot}). This is because the relative importance of source locations for a given settlement site will depend on how well they are connected by dispersal, but also on how many larvae are released at each source location. The C_{rel} metric is scaled from 0 to 1 for simplicity.

2.6 | Relationship between prawn landings data and particle dispersal

To investigate how larval dispersal may influence recruitment and the abundance of EKP adults, simulated prawn densities were compared with annual EKP landings (t/year, from 1985) from NSW Ocean Trawl (OT) Fishery (NSW Department of Primary Industries – Fisheries Catch Statistics Database), and prawn trawling catch-per-unit-effort (CPUE; total annual EKP catch divided by the days fished; kg/day). As a result in the change in the recording of fisheries effort, reliable CPUE was only available from 1997 onwards. Settled larval EKP densities were calculated as the number of EKP on the continental shelf (0–200 m water depth) between 24 and 37.5°S at the time of settlement. Settlement occurred if a particle was on the shelf at the first time-step where DD $\geq$ 427; (the range of DD at the time of settlement in the model was 427–454). These criteria exclude particles that may return to the shelf a day or two after this cut-off. To assess the effect of this, we tested the net change in particles on the shelf if they were allowed an additional 24 hr for settlement. This resulted in a net change of particle number of only 7%. Additionally, an increase of 24 hr, at an average temperature of 20°C, results in an increase of DD (by 20) that is greater than the standard error around our estimate of DD (10.4).

The simulated settlement of larval EKP (i.e., larvae considered "settled" if on the shelf) was to compensate for the lack of behaviour in the model, and is based on the assumption that EKP present on the continental shelf at the time of settlement have a good chance of recruiting to an estuary or coastal area due to active behaviour (Church & Fandry, 1995). Depending on latitude, prawns do not enter the offshore fishery until after 6 months of age (Racek, 1959), so the fisheries data were offset by a calendar year in order to compare the larval transport of prawns in a given year with the catch when the prawns have entered the offshore fishery the following year. Linear modelling was used to investigate the relationship between the proportion of simulated particles settled and the adult CPUE in the following year (CPUE data available from 1996 to 2010). A first-order autoregressive process (AR1) was incorporated using generalized least squares regression to account for correlation in CPUE between consecutive years, and examination of the autocorrelation in normalised residuals showed the AR1 process was sufficient. The generalized least squares regression was done using the “nlme” package (Pinheiro et al., 2016) in R (R Core Team, 2015).

3 | RESULTS

3.1 | Patterns of EKP larval dispersal

The movement of simulated prawn larvae within the study region was generally consistent with the southward flow of the East Australian Current (EAC). The mean dispersal distance for all released larvae was significantly lower for EKPs spawned at the two southern-most sites compared to the three northerly sites (Table 2; $F_{4,1875} = 44.86$, $p \ll .001$). At Fraser Island (25°S and the site furthest north), the larvae were dispersed an average of 1,025 km (*SD*: ±366) before the settlement, whereas at the most southern site (Port Stephens 32°S) the larvae dispersed an average of 747 km (±365; Table 2). Straight-line dispersal distances show similar patterns with EKP released from Fraser Island dispersing an average of 750 km (±276; Table 2) and EKP released from Port Stephens dispersing an average of 351 km (±180; Table 2). Dispersal from Fraser Island occurred primarily along the shelf, whereas the other sites showed more diffuse dispersal, including into the Tasman Sea (Figure 2). The speed of dispersal significantly decreased ($F_{4,\ 1,875} = 64.01$, $p \ll .001$) from 53 km/day (±20 *SD)* at Fraser Island to 35 km/day (±18 *SD*) at Port Stephens where the influence of the EAC was reduced (Table 2).

The distance offshore of larvae at the time of settlement was significantly different between some release locations ($F_{4,\ 1,875} = 15.81$, $p \ll .001$). EKPs (mean ± *SD*) released from the mid-latitude sites (Stradbroke Island, Ballina, Coffs Harbour) moved the furthest offshore (317 ± 214, 357 ± 210, 321 ± 202, respectively), whereas those at Fraser Island and Port Stephens were nearer the coast (250 ± 188 and 276 ± 207 km, respectively). At all sites, the offshore distribution of prawns was bimodal with a distinct split between those closest to the coast and those further offshore (Figure 3). This was also apparent in the spatial analysis (Figure 2). Distance offshore at the time of settlement was strongly correlated with mean dispersal speed (Figure 4a) and dispersal distance (Figure 4b).

3.2 | Settlement and survival

As a result of the decreasing water temperature with increasing latitude, the average time to settlement significantly increased ($F_{4,\ 1,875} = 92.47$, $p \ll .001$) from 20.5 to 22.7 days as the release location moved south (Figure 5), with all sites being significantly different from each other. This is in contrast to the dispersal speed, which was significantly lower at the two southern-most sites (Coffs Harbour and Port Stephens). Larval EKP released from Port Stephens spent an extra 2.5 days in the water column, which equated to an extra 87.5 km of dispersal (35 km/day), but this was less than the faster dispersal speeds encountered from Fraser Island (18 km/day faster than Port Stephens) which equated to 369 km throughout the average larval duration (Table 2). The increased time-to-settlement at the southern release sites also resulted in decreased survival before settlement (Table 3; Natural Mortality) with 31% of the EKPs released from Fraser Island reaching settlement compared to 27% at Port Stephens. EKPs originating from the mid-latitude sites also had higher Dispersal Mortality (Table 3) owing to their greater offshore movement (Table 2).

By combining the relative abundance (N_{rel}) of particles arriving at settlement sites from specific source locations (particle tracking; Figure 6), with the reproductive potential of adults at the source locations (R_{pot}; Montgomery et al., 2007), we show that the mid-latitude spawning locations (such as Ballina) are the most important for supplying the two most southern settlement sites, particularly Gabo Island (C_{rel}; black bars, Figure 7). This represents the mean relative

TABLE 2 Mean (±*SD*) dispersal statistics for the forward simulations. Particles were released 30 km offshore from the coast at each location

Release Location	Dispersal distance (km)			Straight-line dispersal distance (km)			Offshore distance (km)			Dispersal speed (km/day)		
	Mean (±*SD*)	Min	Max	Mean (±*SD*)	Min	Max	Mean (±*SD*)	Min	Max	Mean (±*SD*)	Min	Max
Fraser Island	1025 (±366)^a	152	1788	750 (±276)^a	43	1293	250 (±188)^a	1	710	53 (±20)^a	7	105
Stradbroke Is.	1025 (±370)^a	108	1843	618 (±242)^b	43	1161	317 (±214)^b	4	1121	52 (±20)^a	5	106
Ballina	1018 (±354)^a	151	2129	561 (±209)^c	24	1090	357 (±210)^b	1	875	51 (±19)^a	8	103
Coffs Harbour	881 (±333)^b	94	2174	483 (±194)^d	19	931	321 (±202)^b	1	906	43 (±17)^b	5	121
Port Stephens	747 (±365)^c	91	2044	351 (±180)^e	10	877	276 (±207)^a	5	912	35 (±18)^c	4	108

The superscript lettering represents statistical differences (one-way ANOVA) for each mean dispersal metric (locations not sharing a letter are significantly different at $\alpha = 0.05$).

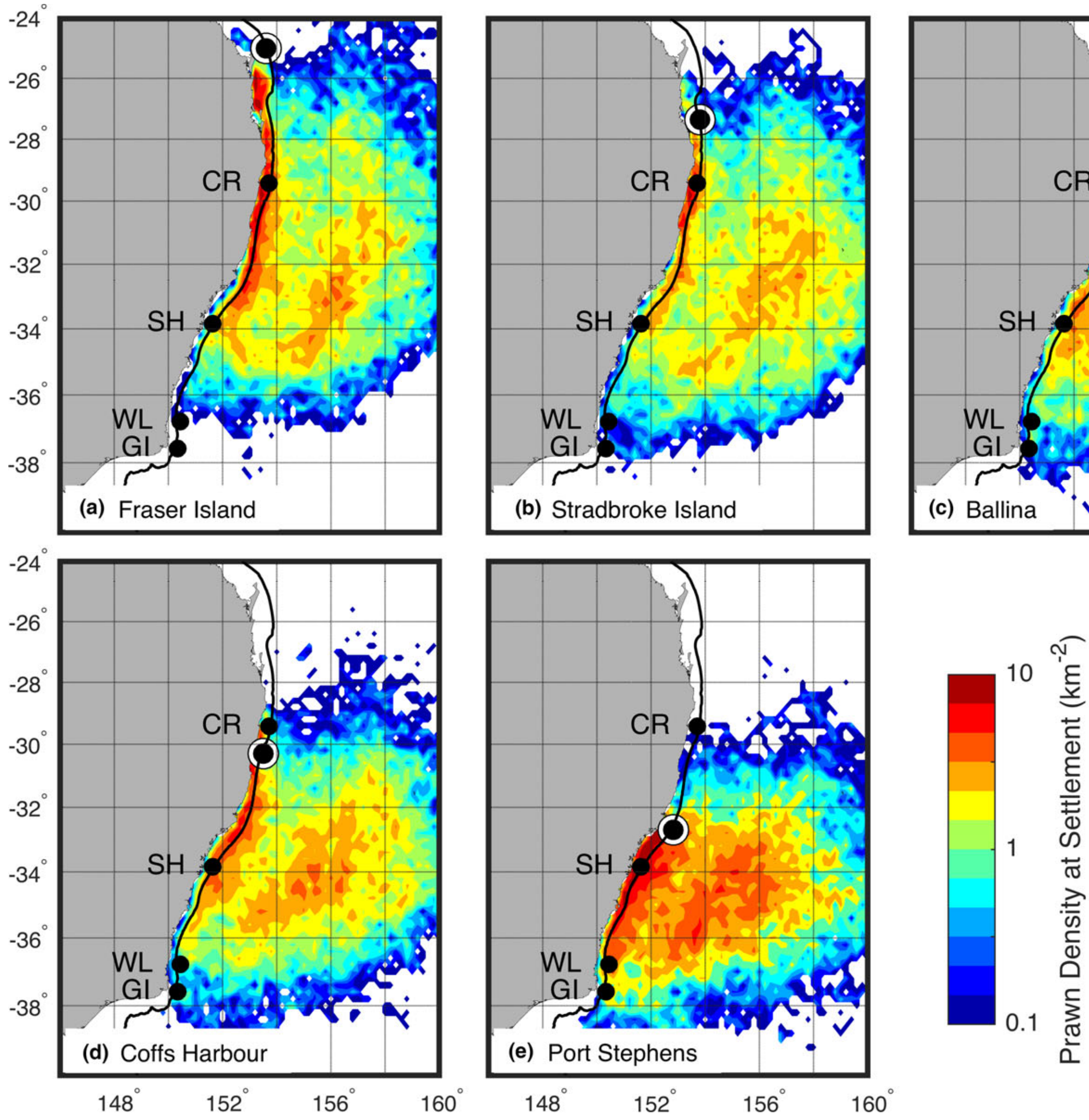

FIGURE 2 The spatial distribution of particles using the forward simulations of the particle tracking model, incorporating mortality and temperature-dependent growth. Shown is the relative density of larvae at time of settlement (i.e., when the specified "degree days" has been reached). The values of prawn density are dependent on the arbitrary number of particles released in the model, so should be interpreted as a relative metric. Each panel shows the data from a single release location (marked as a large black/white circle) and the four settlement locations investigated in this study are marked with a black dot (CR, Clarence River; SH, Sydney Harbour; WL, Wallagoot Lake; GI, Gabo Island). The 200-m continental shelf isobath is marked with a black line. [Colour figure can be viewed at wileyonlinelibrary.com]

importance of the source locations, and the connectivity between source and settlement sites is likely to vary somewhat between years (Fig. S1).

3.3 | Inter-annual variation in larval settlement

There was large inter-annual variability in the modelled shelf-settlement of EKP (Figure 8). The proportion of all simulated EKP larvae released each year that settled on the shelf ranged from 0.051 (1991) to 0.193 (2008). Fraser Island contributed the highest number of settled larvae in the majority of years, with Ballina typically contributing the lowest (Figure 8). The generalised least squares analysis showed no relationship between the 14 years of adult CPUE and the total proportion of simulated larvae settled in the previous year ($p = .81$).

4 | DISCUSSION

This study explores the patterns of larval dispersal for the commercially important Eastern King Prawn, within the EAC region, an area of rapid ocean warming (Wu et al., 2012). This study shows that it is possible for EKP to recruit into all estuaries along the south-east coast of Australia when released from known spawning locations.

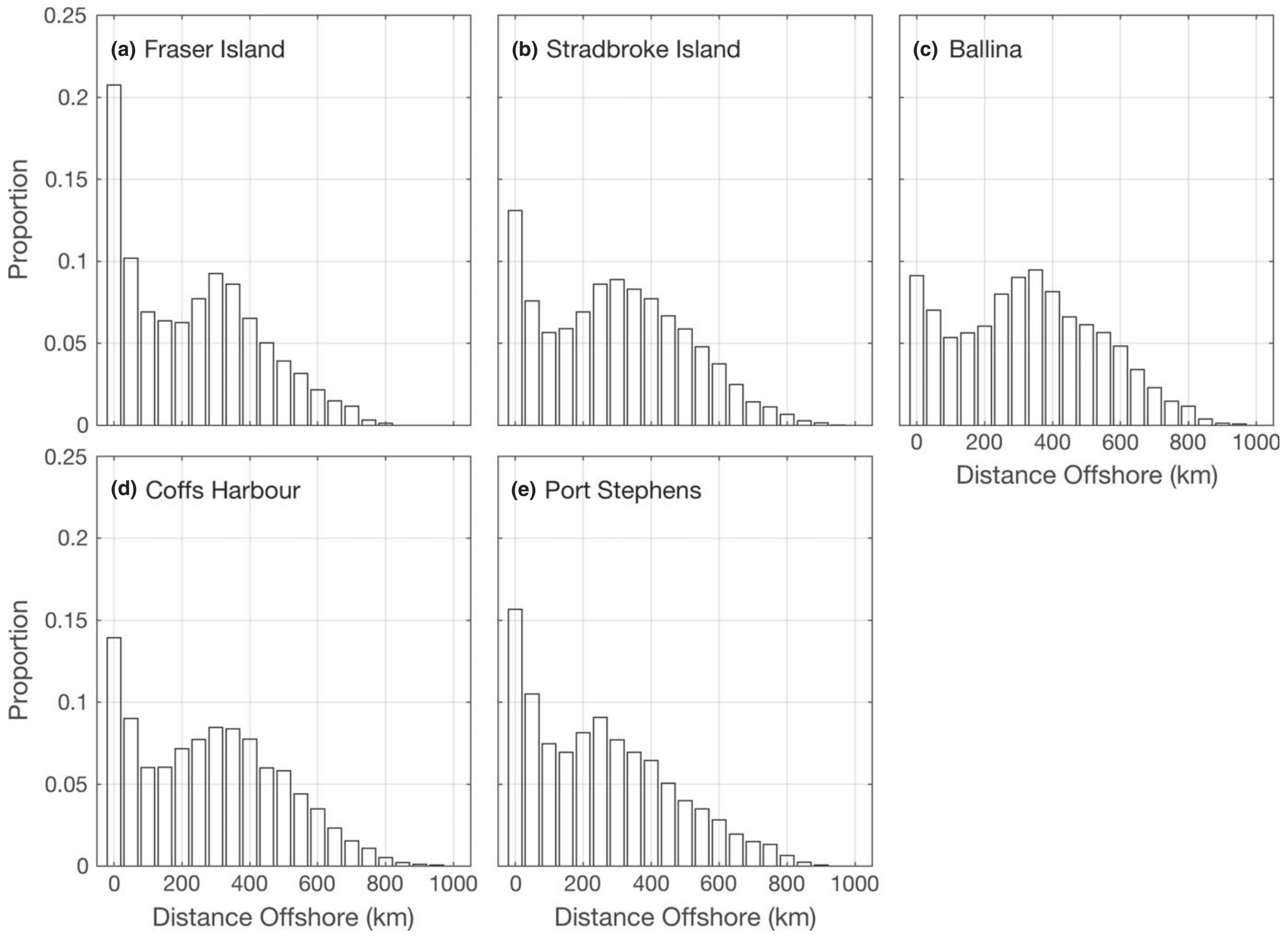

FIGURE 3 The distances (km) of larvae offshore at time of settlement (i.e., when they reached the specified "degree days"), according to their source location. Larvae not on the continental shelf at time of settlement were considered mortalities in our analysis

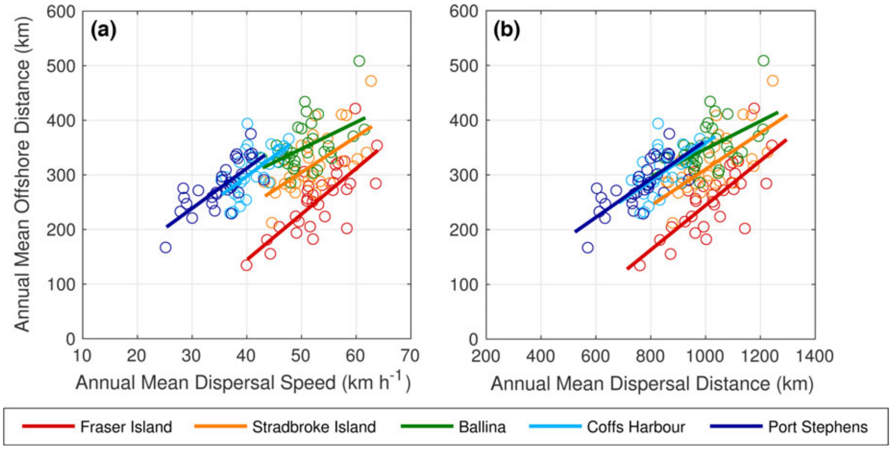

FIGURE 4 Linear regression of annual means (n = 30 years) of Offshore Distance against (a) the Mean Dispersal Speed (km/hr) and (b) the Mean Dispersal Distance at each source location. All regressions were statistically significant ($p < .05$). [Colour figure can be viewed at wileyonlinelibrary.com]

However, the large offshore dispersal of larvae reveals the risk involved in a broadcast spawning strategy for species reliant on coastal nursery habitat, because many larvae are advected far offshore (and thus unlikely able to return to the coast to settle). What is more, years with greater mean dispersal speed and distance also correlated with reduced settlement of simulated larvae. Our modelling showed that it is unlikely that larval dispersal in a given year is sufficient to ensure connectivity of EKP along the extent of its north-south range. Rather than northern EKPs reaching the southern estuaries in a single spawning event, it is more likely they "step" down the coast, settling in a mid-coast estuary before (as adults) their larvae are dispersed further south in the following years.

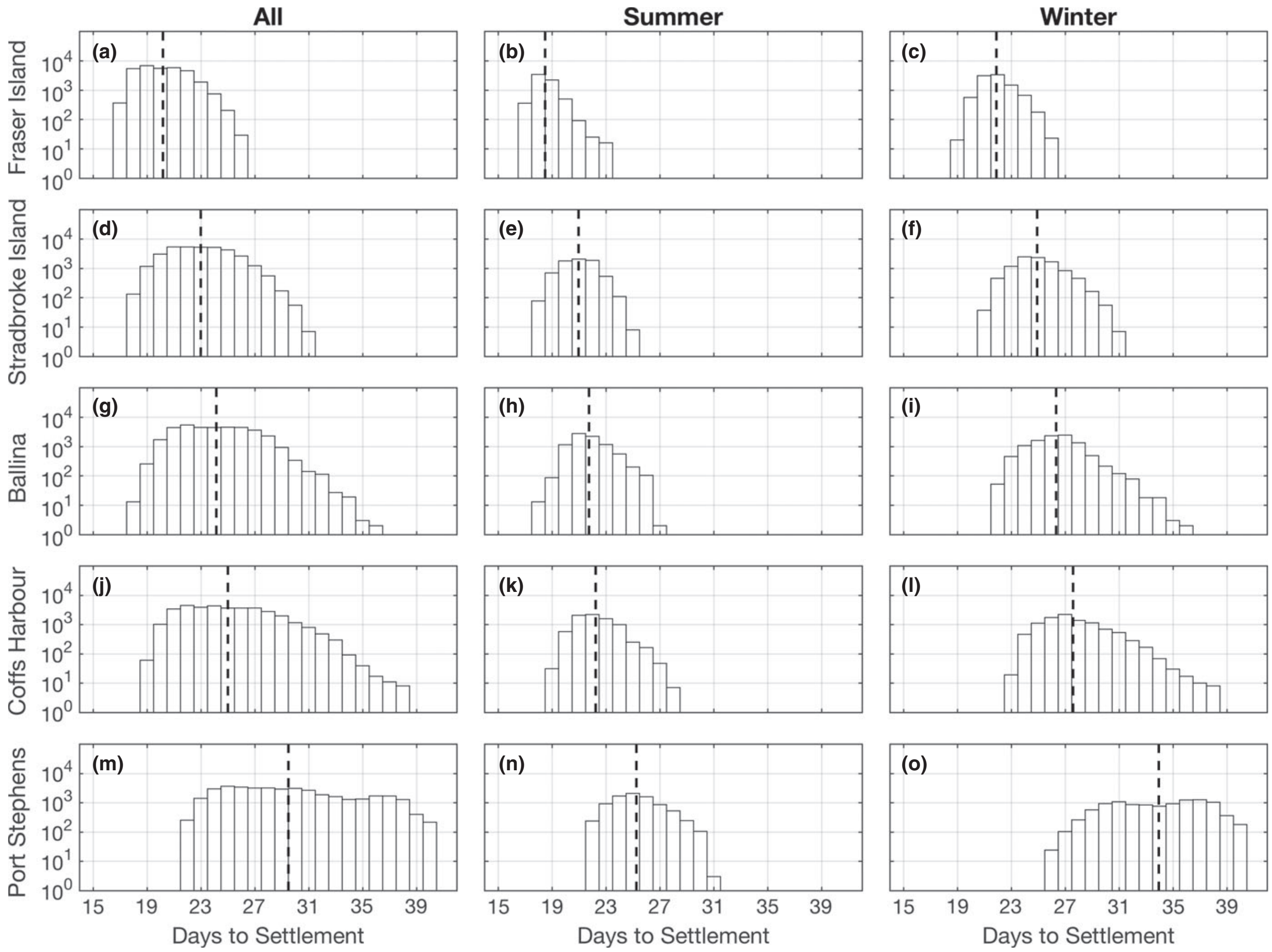

FIGURE 5 The distribution of particles according to their time to settlement (days after spawning) and source location. The particles are also split into those released in winter and those in summer. The vertical dashed line represents the mean. Prawns originating farther south spend longer in the plankton, due to the colder temperatures they are exposed to (i.e., a longer time to reach the specified number of degree-days)

This shows that oceanography (and not simply spawning stock size), is a key factor to identifying important spawning locations for a species dispersed long distances.

4.1 | Patterns of EKP larval dispersal

While many of the spawning locations of EKP are known (Montgomery et al., 2007) the connectivity between adult (spawning) and juvenile populations is less clear. Genetic analysis suggests there is a single genetic stock along the coast (Chan, 2014), but it is likely that the northern spawning sites and southern recruitment sites are not well connected every year. Rather, there is a significant degree of mixing in the mid-latitudes owing to the southern dispersal of larvae and the northern movement of adults on an annual basis (Montgomery, 1990). For example, few EKP larvae released from Fraser Island are transported past Sydney, and none reach Gabo Island (Figures 2a and 7), despite the minimal genetic distance between these locations (Chan, 2014).

The EAC can be both a mechanism for connectivity and dispersal (Roughan, Macdonald, Baird, & Glasby, 2011; this study) and also a potential barrier by dispersing organisms offshore into eddies (Everett et al., 2015) or the Tasman Front (Mullaney, Gillanders, Heagney, & Suthers, 2014). There is a bimodal offshore distribution of larval EKP from all source locations in this study (Figure 3) suggesting that some larvae are retained on the continental shelf, whereas others are swept offshore. In years with increased distance of larval dispersal, either because of longer settlement periods or increased dispersal speeds, larvae are more likely to end up further offshore (Figure 4), decreasing their chance of survival and settlement success (which probably affects the adult stock). This may have great relevance to the future settlement success of long-distance broadcast spawners such as the EKP, given that the EAC is predicted to strengthen (Cai, Shi, Cowan, Bi, & Ribbe, 2005).

Additionally, an increased settlement time (Figure 5) owing to a decrease in water temperature encountered by the larvae will also decrease survival, due to increased exposure to predators or

TABLE 3 Mortality rates of particles; i.e., the proportion of Eastern King Prawn (EKP) larvae that die from natural mortality during dispersal (Equation 1) or because they are too far offshore at time of settlement (Dispersal Mortality). The numbers of particles released is an arbitrary number, but corresponds to 100 particles released every 6 hr for 28 years

Source location	Total particles released	Natural mortality[a]	Dispersal mortality[b]	Particles settled	Total mortality
Fraser Island	4,502,400	69% (n = 3,115,575)	26% (n = 1,168,310)	218,715	95%
Stradbroke Is.	4,502,400	70% (n = 3,141,694)	28% (n = 1,238,676)	122,430	97%
Ballina	4,502,400	70% (n = 3,169,627)	28% (n = 1,253,495)	79,678	98%
Coffs Harbour	4,502,400	71% (n = 3,214,091)	26% (n = 1,171,844)	116,865	97%
Port Stephens	4,502,400	73% (n = 3,270,869)	24% (n = 1,100,275)	131,256	97%

[a] Includes mortality of all particles prior to settlement.

[b] Particles located off the continental shelf at time of settlement are assumed to have died ("Dispersal Mortality").

potential offshore movement. Settlement periods are negatively correlated with the water temperatures that EKP encounter and the increased dispersal speeds are a direct result of higher EAC velocities. This creates a negative interaction where the physical conditions that create the greatest potential for southward transport (i.e., higher velocities) are correlated with accelerated larval development (through increased water temperatures) and thus shorten the window during which larvae can be transported in the plankton. The impact of water temperature and southward transport are likely to be intensified as the climate changes. The core of the EAC and the EAC extension are expected to strengthen by 12% and 35%, respectively, by 2060 (Sun et al., 2012) and, in conjunction with increased rates of warming of the EAC (Wu et al., 2012), will have implications for dispersal and connectivity of marine organisms (Coleman, Feng, Roughan, Cetina-Heredia, & Connell, 2013).

4.2 | Oceanographic factors influencing recruitment

The recruitment of EKP to estuaries is intermittent and dependent on mesoscale oceanographic conditions and stock characteristics such as the number of larvae. Consequently, it is no surprise that recruitment of EKP to estuaries in south-eastern Australia furthest from known spawning locations, is intermittent, and the species is rarely observed in Victorian estuaries west of the Gippsland Lakes (Montgomery & Winstanley, 1982). In addition to the oceanographic variables described here, estuarine characteristics such as entrance condition (whether permanently or intermittently open) offer additional barriers to recruitment that are not considered here (Taylor, 2017).

It is clear that inter-annual variation in oceanography can influence dispersal and likely recruitment of EKP. However, we found no relationship between the proportions of settled simulated larvae in this study with adult CPUE in the NSW catch the following year. Although we believe that oceanography does influence adult CPUE, there are likely to be numerous other factors (such as fishery dynamics, estuary condition, and ecosystem effects) that contribute to the survival, growth, migration, and ultimately harvest of EKP. It is likely that these processes vary annually and by location along the coast. Eddies, for example, dominate in the south (Everett, Baird, Oke, & Suthers, 2012) and the EAC is stronger and more coherent in the north (Cetina-Heredia et al., 2014; Ridgway & Dunn, 2003). Revealing a relationship between larval dispersal and adult CPUE may require a more finely-resolved model of spawning that builds on our five representative source locations.

4.3 | Recruitment origins

Information on the connectivity of EKP through spawning has been relatively sparse. The presence of EKP larvae offshore and in deep water suggested high dispersal potential that connected the entire EKP range (Courtney, Cosgrove, Mayer, & Vance, 2002). This study used particle tracking to elucidate this issue of connectivity between source and settlement sites, and also observed strong dispersal potential, but with a more resolved appreciation of the southern spawning areas such as Ballina and Coffs Harbour. Backward simulations from estuaries known to host settled EKP show that much of the Clarence River larvae (Figure 6a) probably originated from north of Fraser Island. In contrast, larvae arriving at the three southernmost settlement locations (Figure 6b–d) are shown to originate predominantly from south of Coffs Harbour (30°S).

Our analysis, combining the delivery of particles (i.e., the relative abundance of simulated larvae arriving at a settlement site) with the likely number of particles released (i.e., the reproductive potential at spawning sites; Montgomery et al., 2007), provides further evidence that there is little direct connectivity between the northern and southern extremities of the EKP range. We also see that Ballina, and to a lesser extent Coffs Harbour, are important spawning locations for delivering recruits to estuaries along south-eastern Australia. Although Ballina has moderate reproductive potential (Table 4), it delivers more particles to the southern coast of eastern Australia and is probably the most important source location for larval EKP for the two southern-most sites. This has relevance for management of the EKP stock and highlights the importance of both connectivity and reproductive potential for assessing the importance of source or spawning locations.

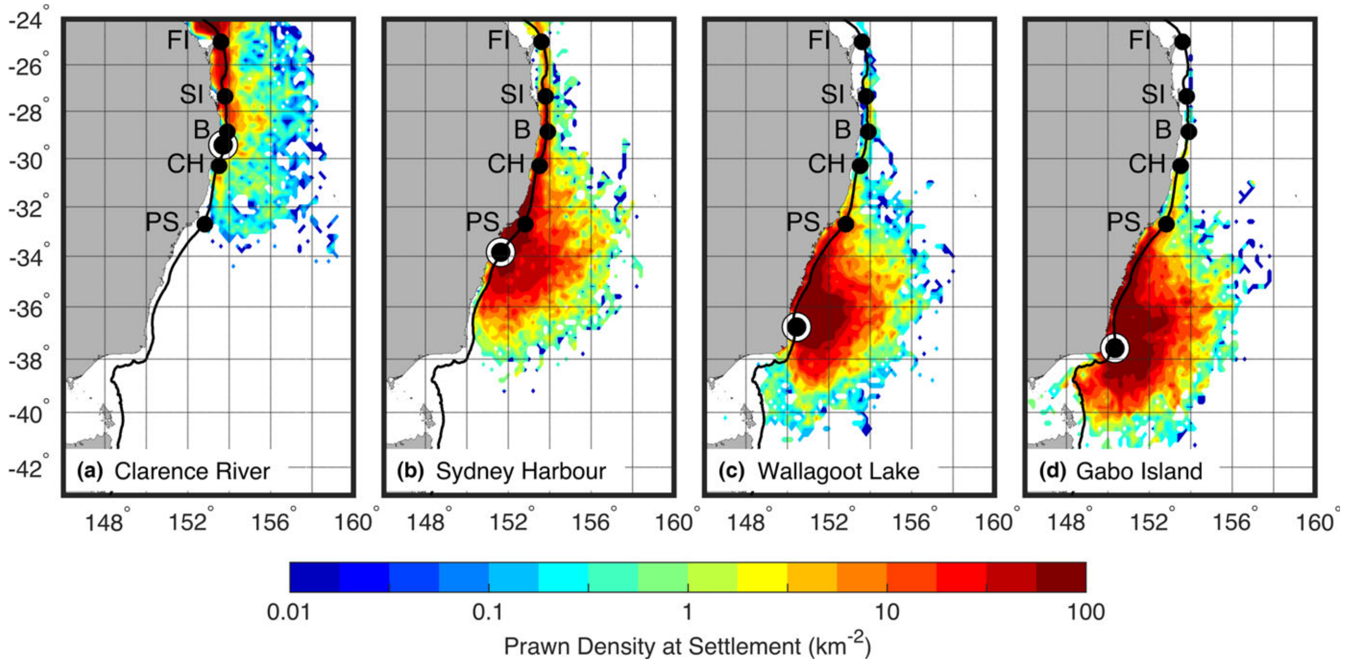

FIGURE 6 The spatial distribution of particles using the backward simulations of the particle tracking model, incorporating mortality and temperature-dependent growth. Shown is the relative density of larvae at time of release (i.e., when the specified "degree days" has been reached). The values of prawn density are dependent on the arbitrary number of particles released in the model, so should be interpreted as a relative metric. Each panel shows the data from a single settlement location (marked as a large black/white circle) and the source locations investigated in this study are marked with black dots (FI, Fraser Island; SI, Stradbroke Island; B, Ballina; CH, Coffs Harbour; PS, Port Stephens). The 200-m continental shelf isobath is marked with a black line. [Colour figure can be viewed at wileyonlinelibrary.com]

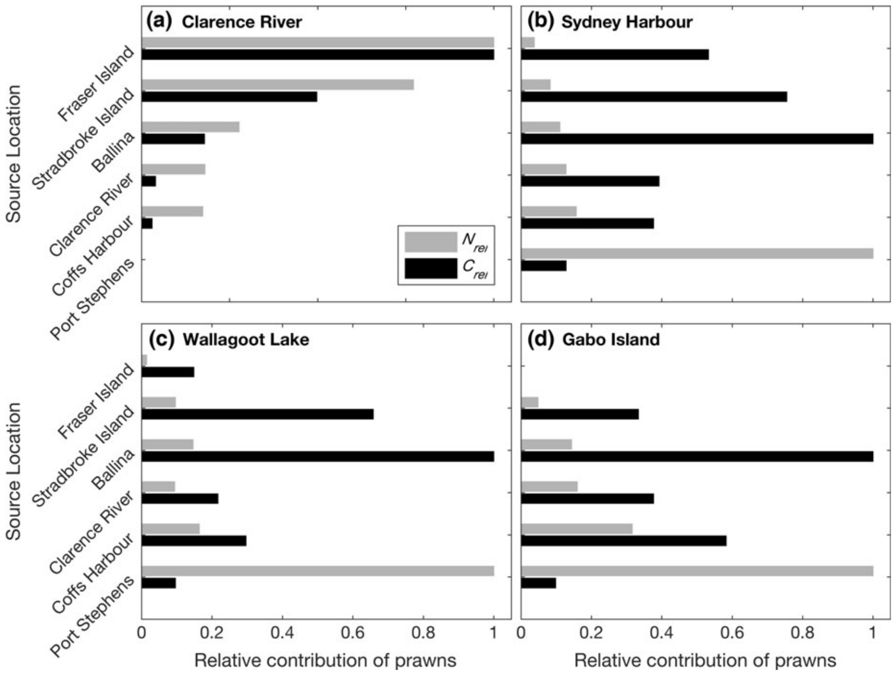

FIGURE 7 The relative contribution of larvae (black bars; C_{rel} Equation 2) from six possible spawning locations (sources) to four settlement sites (a–d). C_{rel} incorporates the relative number of particles arriving from each source location (grey bars; N_{rel} Equation 2; from particle tracking model), and the relative number of particles (i.e., larvae) released at each source location ("reproductive potential", Montgomery et al., 2007)

4.4 | Model limitations and future development

The dispersal model presented here does not account for diel-vertical migration or the role of tides, and how they can influence prawn behaviour around settlement time, however, the large-scale dispersal patterns show that the mesoscale oceanography can contribute a great deal to recruitment variability in EKP. Swimming speed has previously been used to add a behavioural component to similar dispersal models (Rothlisberg, Craig, & Andrewartha, 1996; Sponaugle, Paris, Walter, Kourafalou, & D'Alessandro, 2012), however, given the strength of the EAC, we do not expect that this would substantially alter the overall patterns in this study (Putman, Verley, Shay, &

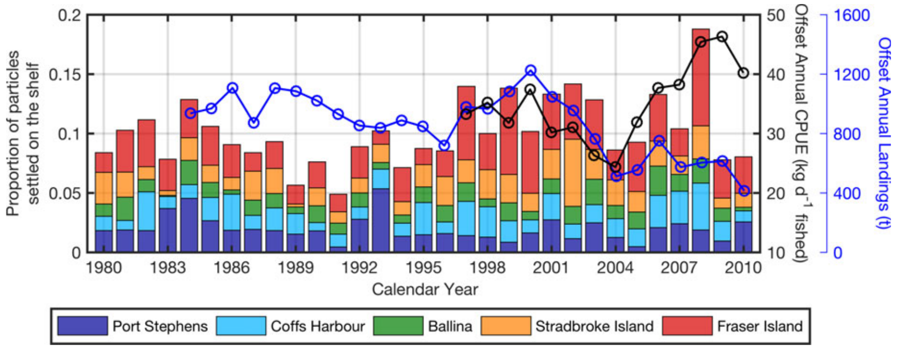

FIGURE 8 Proportion of all simulated Eastern King Prawn (EKP) larvae released per year that are retained on the continental shelf from the five source locations (coloured bars), compared to the EKP Offset Landings (blue line/circle) and EKP catch-per-unit-effort (CPUE; black line/circle) for the NSW Ocean Trawl Fishery. Catches were offset to compare a given year's catch with the previous year's larval dispersal. The colours represent the north (red) to south (blue) temperature gradient of the release locations. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Relative abundance of particles (N_{rel}) at four settlement locations sourced from six source locations, and the average "reproductive potential" (R_{pot}, Equation 2) of EKP at these six sources (Montgomery et al., 2007). R_{pot} is an index derived by combining size-frequency information with size-based spawning and fecundity. Combining particle tracking and larval supply information allowed us to estimate the relative contribution of larvae from the source locations to settlement sites (Equation 2; Figure 6)

		Settlement location			
Source location	R_{pot}	Clarence (N_{rel})	Sydney (N_{rel})	Wallagoot (N_{rel})	Gabo Isl. (N_{rel})
Fraser Island	27,247,773	225,593	35,255	1,823	0
Stradbroke Island	17,571,926	174,094	77,493	12,574	1,953
Ballina	17,571,926	62,433	102,625	19,119	5,855
Clarence River	5,925,753	40,635	119,343	12,269	6,530
Coffs Harbour	4,644,616	39,191	146,253	21,438	12,911
Port Stephens	247,014	0	934,214	130,730	40,917

Lohmann, 2012). It may, however, help to resolve the fine-scale near-shore processes (e.g., near-shore accumulation and tidal-vertical migration) that this study does not model (Church & Fandry, 1995). Increasing the model resolution may also help to resolve these near-shore processes. Previous studies have shown that the finer the spatial and temporal resolution of the model, the greater retention over the continental shelf (Putman & He, 2013).

The model used here does not provide forecasts, so the ability to predict good and bad recruitment years is not yet robust, but further advancements in particle tracking, fine-scale oceanographic modelling, and improved understanding of post-larval behaviour may allow this in future. Although we did not find a significant relationship between the settlement of simulated larvae and EKP CPUE, we feel there is great value using larval dispersal to understand variation in adult abundance and harvest rates. Doing this successfully will require a better understanding of fine-scale oceanographic processes, and the amalgamation of larval behaviour, estuary condition/capacity, and information on adult growth and migration (Lloyd-Jones et al., 2012).

4.5 | Concluding remarks

Understanding the movement and connectivity of marine organisms is important for ecology, conservation, and managing exploitation. For animals that have planktonic life stages, ocean currents can play a major role in an organism's distribution and connectivity (Roughan et al., 2011). In this study, we show that the southern half of the EKP spawning range, even although it has much less spawning potential, may be crucial for the supply of recruits the southern part of this species' range. The mesoscale oceanography is probably a strong determinant of recruitment success, and particle tracking models that follow the larval dispersal could be useful for determining the settlement success of EKP larvae to their estuarine nursery habitats and thereby contribute to a greater understanding of the factors that influence fisheries catch. Future analyses exploring the relationship between mesoscale oceanography and larval settlement of the EKP or similar species may benefit from also modelling near-shore larval behaviour and estuary characteristics.

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