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Implications of spawning migration patterns of the giant mud crab *Scylla serrata* (Forskål, 1775) on opportunities for larval dispersal

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ABSTRACT

Connectivity is an essential driver for aquatic species distribution, genetic variability and stock structure. The giant mud crab (*Scylla serrata*) is a coastal portunid commonly associated with estuaries and mangrove systems. This species has been observed to undertake a seaward spawning migration, as the larval development is known to be more successful under the stable environmental conditions typically found in marine waters. The larvae return to the coastal areas through advection, where they are recruited and enter the estuaries after metamorphosing into the first instar. Here, we used numerical modelling to test hypotheses regarding probabilities of larval settlement of the giant mud crab and the effect of the distance offshore from which females release the eggs. Our scenarios considered the biological characteristics of larvae and oceanographic conditions for six locations for mud crabs along a complex coastline - the Queensland east coast, Australia. The models suggest that all locations tend to self-supply, and to exchange mud crab larvae with other regions, but in different magnitudes. The spawning distance offshore considerably affects larval distribution and settlement. The main drivers for larval advection in areas within the continental shelf are wind patterns and coastal currents, while offshore along the Australian continental slope, the main drivers are ocean currents. Self-recruitment is predominant, although we also observed a significant degree of connectivity between each location and the surrounding coastline. Short spawning migrations benefit self-recruitment in all scenarios, but long offshore migrations favour connectivity among different locations. This source/sink balance seems to depend on the local oceanographic features. Nevertheless, offshore spawning by the giant mud crab has the potential to provide for successful recruitment in a variety of environmental contexts. This study provides novel predictions of the probabilities of larval settlement for mud crab populations considering ocean advection that can be applied to different contexts.

1. Introduction

Connectivity among geographically discrete populations provides recruits from distinct regions (Bryan-Brown et al., 2017; Sheaves, 2009; Webster et al., 2002). The combination and diversification of stocks with different traits enhance genetic variability, which otherwise would be impossible if they remained isolated (Furlan et al., 2012; Sheaves, 2009). The movement of species between habitats, such as from feeding sites to spawning grounds, also provides energy and nutrients to oligotrophic regions, flowing from coastal to oceanic areas (Nemeth, 2012; Sheaves, 2009). Therefore, understanding population connectivity plays a crucial role in successful conservation strategies and fisheries management (Criales et al., 2019), especially if the movement is between distinct areas regulated by different policies (Engelhard et al., 2017).

Some specificities of the migratory behaviour of breeding stocks during the spawning season play a vital role in the sustainability of harvested populations (Kerr et al., 2010). Factors like spawning ground

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location and environmental triggers for spawning can strongly contribute to larval survival and growth (Storlazzi et al., 2017), whereas other variables such as oceanographic features and habitat quality might influence the success of larval recruitment, (Dias, 1996; Li et al., 2023). Ocean circulation and its drivers are key elements to larval advection (Rudorff et al., 2009), influencing connectivity between populations and their roles as sources or sinks (Figueira, 2009). Therefore, alterations in ocean circulation patterns, such as modifications in current flow caused by climate change (Li et al., 2023), can impact larval distribution and recruitment. Understanding the larval dispersal patterns of marine species and their regional particularities is necessary for elucidating uncertainties regarding recruitment and subsequent fisheries productivity and the factors affecting population dynamics.

One crustacean species whose larval dispersal and recruitment may be strongly influenced by ocean currents is the giant mud crab (*Scylla serrata*), as the ovigerous females have been observed to spawn offshore in some regions (Alberts-Hubatsch et al., 2016; Hill, 1994; Robertson and Kruger, 1994). The giant mud crab is a portunid found in tropical, subtropical, and temperate zones throughout the Indo-West Pacific region, making it the most widespread species of the genus *Scylla* (Keenan et al., 1998). Being fast-growing (Hill, 1975; Meynecke et al., 2010), the largest mud crab species (Heasman, 1980; Knuckey, 1999), and having a high market value, the giant mud crab is a valuable fishery resource (Sayeed et al., 2021) in many African and Asian countries, western Pacific Islands and Australia. Giant mud crab populations along the Australian east coast are connected to some degree (Fratini et al., 2010; Gopurenko and Hughes, 2002; Hewitt et al., 2022b) and stocks along this coast are managed across two state jurisdictions – Queensland and New South Wales – each having different management strategies and regulations (Calogeras and Buckworth, 2023).

Giant mud crabs use different habitats according to their life stage and sex. Estuaries are the residence of juveniles, subadults and adults during most of their lifespan (Alberts-Hubatsch et al., 2016; Demopoulos et al., 2008; Hill et al., 1982). However, in some regions, ovigerous females leave estuaries and migrate seawards to release eggs (Hewitt et al., 2022a; Hill, 1994). Consequently, ocean and coastal waters are short-term habitats for the earliest pre-settlement larval (zoea) (Alberts-Hubatsch et al., 2016) and post-larval (megalopa) stages before larvae metamorphose into the first instar (crablets) and enter estuaries (Webley and Connolly, 2007). Despite its potential importance for population connectivity and spatial management, the oceanic phase remains one of the least understood of the giant mud crab life history (Alberts-Hubatsch et al., 2016), mainly due to the difficulty of tracking gravid females. Hence, there are still several uncertainties about their movement offshore, the location of spawning grounds, and aspects related to the behaviour, settlement areas and recruitment during the earliest larval stages.

While not a substitute for observational data, numerical methods can be used to constrain some of the uncertainties in the giant mud crab life history when used to estimate probabilities of larval advection, spawning and consequent settlement locations that are more likely to be successful (Criales et al., 2019; Schilling et al., 2022). Biophysical numerical modelling is a computational method that aggregates ocean circulation patterns with biological features to predict or estimate the movement and trajectory of organisms considering oceanographic factors (Baptista et al., 2020; Wolanski, 2017). Numerical modelling has been used to investigate larval dispersal patterns for different purposes, including the effectiveness of marine protected areas for conservation (Engelhard et al., 2017), larval dispersal patterns and recruitment (Baptista et al., 2020; Storlazzi et al., 2017), fisheries management (Criales et al., 2019; Kerr et al., 2010), and habitat connectivity (Pullinger and Johnson, 2010; Storlazzi et al., 2017; Swearer et al., 2019; Wolanski, 2017) of many species, including crustaceans (Banas et al., 2009; Criales et al., 2019; Rudorff et al., 2009).

Using the giant mud crab populations of northeastern Australia as a case study, we applied numerical simulations of dispersal to constrain the spawning migratory behaviour of females. Genetic studies indicate that giant mud crab populations along the Australian east coast are well connected (Gopurenko and Hughes, 2002; Gopurenko et al., 1999). However, although the offshore distance of the spawning grounds to produce this high level of connectivity remains unknown, it is hypothesised that the oceanographic features greatly affect larval movement and destination for many species (Hewitt et al., 2022b; Schilling et al., 2022; Storlazzi et al., 2017).

In Australia, the oceanographic dynamics on the east coast are driven by the East Australian Current (EAC), a southward flow formed by the division of the Southern Equatorial Current (SEC) when reaching the Australian continental slope (Church, 1987). The hydrodynamic patterns of the EAC are one of the main drivers for many ecological processes, like the diffusion of nutrients along Australia's east coast, which affects primary productivity, dispersal, connectivity and distribution of a range of marine species with a pelagic larval phase (Gervais et al., 2021; Phillips et al., 2020). It includes several populations of the giant mud crab (*Scylla serrata*) (Hewitt et al., 2022b), for which larval development is usually favourable when it occurs in seawater (Baylon, 2010; Fratini et al., 2010).

Here, we use a particle tracking model to simulate giant mud crab larval dispersal to determine probable high recruitment areas, spawning areas more likely to be successful and their variation in time for six different mud crab locations on Queensland's east coast. We are aiming to investigate: 1) the difference in settlement location related to the distance offshore of release, 2) the most likely spawning areas for larvae dispersing into high-catch regions of Queensland's east coast, and 3) the distance offshore at which released larvae have the most significant probability of dispersing to viable mud crab habitats.

2. Materials and methods

2.1. Case study area

The case study encompassed mud crab habitats of the northeastern coast of Australia, adjacent to the Great Barrier Reef in Queensland, Australia (Fig. 1). Queensland's east coast contributes approximately 52% of mud crab production in Australia, including commercial, recreational and indigenous catches (Kirke et al., 2023). While mud crabs can be found in many estuaries along Queensland's expansive coastline (approximately 3000 km), in this study, we focused on six locations considered important for fisheries and larval recruitment in terms of catchability, geography, and conservation. Four locations are high-catch areas for mud crabs on Queensland's east coast: Princess Charlotte Bay, Hinchinbrook Channel, Gladstone Harbour (The Narrows) and Moreton Bay (Heaven, 2018). Mackay and Eurimbula Creek were included in this study due to their geographical and conservation characteristics, respectively. The Mackay region is centrally located between two high-catch areas for mud crabs and, therefore, is potentially a stepping stone for connectivity. Eurimbula Creek is a sanctuary for mud crabs, meaning mud crabs are fully protected from harvest and must not be retained by commercial or recreational fishers. As a result, the selection of these six locations helped interpret the population dynamics and distribution of larvae in the region and, more generally, investigate the spatial inter-dependence of giant mud crabs in Queensland.

Adult mud crab habitat is mangrove-lined, shallow muddy estuaries and sheltered coastlines. Each of the six locations corresponds to a network of such estuaries, often close to the mouth of rivers that provide organic matter and are protected from wave energy by barrier islands or peninsulas. For dispersal, we considered each location to encompass the area including the network of estuaries and the associated protected embayment, under the logic that larvae must first disperse to this area to recruit subsequently. As such, in most cases, the site is defined by a polygon. For two locations without a significant offshore embayment, the corresponding polygon corresponded to a single cell of the connectivity matrix, described below (Table 1). The differences in site area

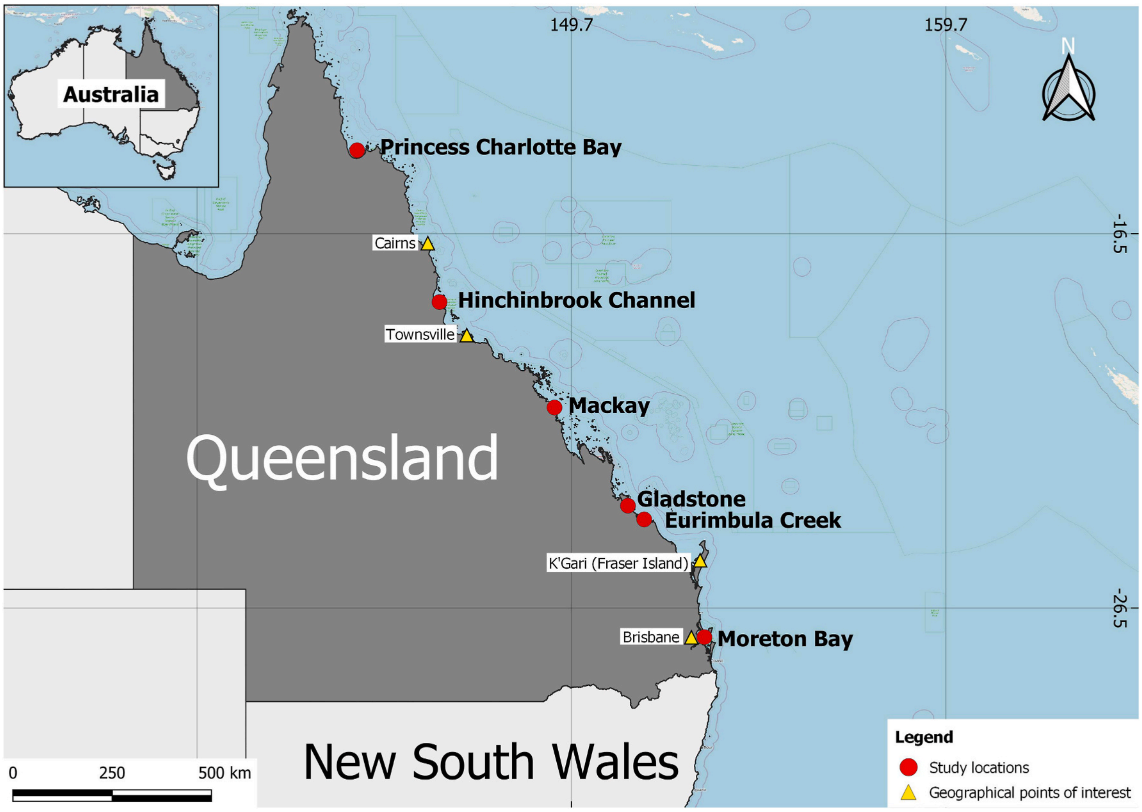

Fig. 1. Mud crab locations included in this study (red circles). Some important geographical points are also included for reference (yellow triangles). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Geographical position and the unit of spatial information used for each location included in this study.

Location	Coordinates				Unit of Spatial Information
	Latitude		Longitude		
	Northernmost limit	Southernmost limit	Westernmost limit	Easternmost limit	
Princess Charlotte Bay	14.233118° S	14.128695° S	143.707481° E	143.963492° E	Polygon
Hinchinbrook Channel	18.272071° S	18.499854° S	146.037757° E	146.264129° E	Polygon
Mackay[a]	21.150957° S		149.224212° E		Single point
Gladstone Harbour	23.554797° S	23.877651° S	151.001351° E	151.390786° E	Polygon
Eurimbula Creek	24.170930° S		151.844156° E		Single Point
Moreton Bay	27.071192° S	27.479427° S	153.059819° E	153.363127° E	Polygon

[a] Single point in Mackay region refers to the Pioneer River's mouth.

were taken into account when computing connectivity and recruitment probabilities.

2.2. Oceanographic characteristics of the study area

The regime of currents on Queensland's east coast along the continental slope is dominated by the divergence of the SEC when reaching the Queensland continental shelf, forming the northwards flowing Hiri Current (HC) and then the Gulf of Papua Current (GPC) and the southwards flowing EAC (Fig. 2) (Brinkman et al., 2002; Church, 1987; Weeks et al., 2010). Inshore of the continental slope and the Great Barrier Reef, the water is relatively shallow, and currents tend to respond to the seasonal changes in the wind (Johnson et al., 2018). Inshore waters generally flow north, but also with some periods of east/southeastward movement during the monsoon season nearshore along much of the coastline in the spring-summer period of interest here, which corresponds to the likely spawning period for female mud crabs on Queensland's east coast (Heasman et al., 1985). These characteristics are critical for understanding larval dispersal in the study area.

2.3. Numerical modelling

The relationship between offshore spawning location and alongshore connectivity was investigated using numerical simulations of larval dispersal. Larval dispersal simulations typically involve running hydrodynamic and biophysical models (Swearer et al., 2019). The former simulates the ocean currents forced by the wind, tides, and solar radiation. The latter uses the hydrodynamic model's output to simulate the ocean currents' effect on the larvae (Storlazzi et al., 2017). In a particular class of biophysical model called Individual Based Models (IBM), larvae are represented as discrete particles, liberated at a specific geographical position and depth. Then, their movement due to the current and any known swimming behaviour is calculated. Post-processing of the larval trajectories allows distinct cause-effect scenarios to be examined (Swearer et al., 2019).

Here, the larval dispersal simulations were performed using the "PARCELS" (Probably A Really Computationally Efficient Lagrangian Simulator) (Delandmeter and van Sebille, 2019) IBM fed by hydrodynamic information from the eReefs product (Steven et al., 2019). The

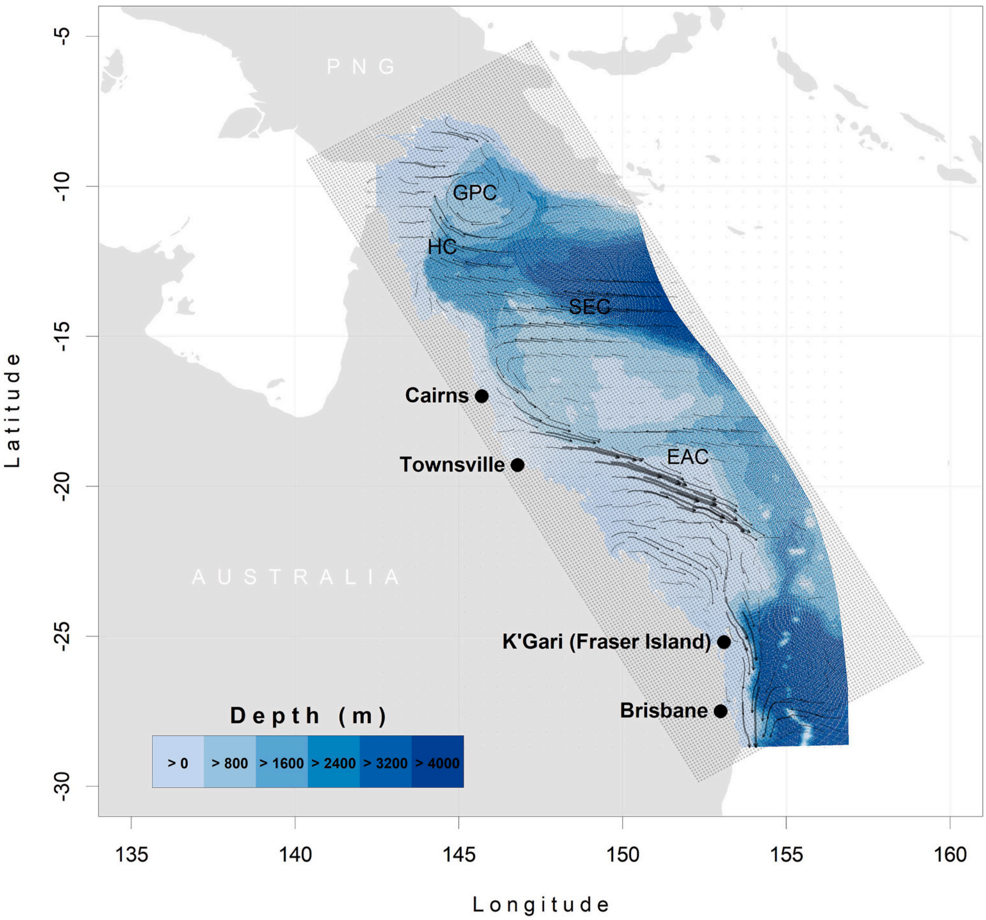

Fig. 2. Mean surface ocean velocity from the eReefs GBR4 simulation for the Queensland east coast during the spring/summer of 2016–2021. The ocean depth is shaded and indicates the extent of the GBR4 domain. PNG – Papua New Guine; GPC – Gulf of Papua Current; HC – Hiri Current; SEC – Southern Equatorial Current; EAC – East Australian Current. The grid used for calculating the connectivity matrix is drawn in grey.

eReefs project provides a comprehensive high-resolution simulation of the currents across the Great Barrier Reef region, forced by tides, local winds and the large-scale circulation at the open boundaries (Steven et al., 2019). The eReefs data is available on the GBR1 and GBR4 grids, at 1 km and 4 km resolution, respectively, the former covering the edge of the Great Barrier Reef and the latter covering most of the Coral Sea. We combined data from both domains to adequately represent the areas likely to support the oceanic spawning migration of giant mud crabs. Separate larval dispersal simulations were performed using each dataset, and the results were combined.

Particles were released daily between October and February from 2016 to 2021 to coincide with the observed austral spring/summer spawning season in southeast Queensland (Alberts-Hubatsch, 2015; Heasman et al., 1985; Hewitt et al., 2022a). The planktonic larval dispersal duration used was 28 days. This period corresponds to the maximum time observed for zoea to develop into megalopa for typical water temperatures in the study area (Richardson and Pattiaratchi, 2020), based on laboratory experiments in which associated factors like temperature and salinity correlated to the best results for larval development period and survival rates (Baylon, 2010; Hamasaki, 2003; Nurdiani and Zeng, 2007).

As we aimed to determine the impact of the (unknown) spawning location on population connectivity, particles were released throughout the domain, and an analysis was performed to identify which particles dispersed to a suitable habitat. In each simulation, one particle was released per numerical grid cell in the GBR1 and GBR4 domains. These 236,520,000 individual particle trajectories – one for each release day and grid cell - were summarised into a single connectivity matrix, which gives the probability of a particle from each starting location arriving at a destination after the 28-day dispersal period (discussed below). That is, element (i,j) of the connectivity matrix is the number of particles released from location i that arrive at location j, including all valid particles released across the entire time frame. A particle is considered invalid if it became trapped on land at any point in its trajectory – an effect known as “beaching”. The connectivity matrix was defined on a homogeneous 10 km grid, rotated to follow the coastline’s orientation better and illustrated in Fig. 2. Connectivity matrices for each eReefs simulation (GBR1 and GBR4) were combined by averaging the two. In regions without data on the GBR1 grid, connectivity probabilities were determined entirely from the GBR4 data. While it is possible that dispersal in individual years or months will have differing patterns, potentially of relevance for short-lived species, we restricted our analysis to the mean connectivity. The connectivity matrix was constructed using R (R Core Team, 2023).

Two quantities were calculated individually for each location from the resulting connectivity matrix. In our study, we defined the “catchment area” as the oceanic area where particles were released, resulting in any probability greater than zero to settle in the study locations. Firstly, the probability of successful recruitment to each of the six mud crab locations was determined as a function of release location. We referred to this zone of potential provenance for each regional population as the “spawning area”. Secondly, the destination of larvae released offshore of each of the six locations was calculated as a function of the seaward distance from that location to test different probabilities of particles released at the same latitude but different longitudes settled in distinct coastal areas. We referred to where larvae could disperse when released offshore as “dispersal” of mud crab larvae for a particular population.

2.4. Larval behaviour

Giant mud crab larvae pass through some stages prior to metamorphosing into the first crablet and entering the estuary. The first five life stages are planktonic zoea (Baylon, 2010; Nurdiani and Zeng, 2007), during which their swimming ability is unknown. For this reason, we considered that their dispersal is likely to be strongly determined by ocean current drift. The earliest larval stages of several marine species, including other portunids, show some active vertical movement through the water column (Almeida et al., 2021; Kunze et al., 2013). However, this behaviour has not yet been demonstrated for the zoea of *S. serrata* (Epifanio and Cohen, 2016). In any case, as the ocean currents adjacent to the continental shelf in the study region are relatively uniform vertically due to weak stratification and a relatively shallow shelf (Church, 1987), even if giant mud crab larvae do perform a vertical migration, it would be expected to have a minor impact on their dispersal. Hence, we treated the zoea as passive particles whose dispersal could be approximated by simulating the drift due to ocean currents (Hewitt et al., 2022b; Storlazzi et al., 2017).

Depending on the water conditions, the zoeal phases last approximately 28 days before metamorphosing into megalopa (Baylon, 2010; Hamasaki, 2003), which occurs in coastal waters near estuarine habitats. Mud crabs only move towards the estuarine habitat after the metamorphosis into the first crablet stage (Webley et al., 2009). Although the nature of the active migration of megalopa is poorly understood, it is likely to depend upon a complex set of environmental cues, mainly in response to light (Webley and Connolly, 2007). As such, passive dispersal from the spawning ground to the coastal zone adjacent to the juvenile habitat is a necessary but insufficient recruitment condition. Our approach estimates the former, noting that it is a robust and informative but incomplete estimate of the actual recruitment probability. Most importantly, it provides an upper bound on potential recruitment - a low probability of larval drift from a spawning location to a habitat guarantees a low recruitment probability.

3. Results

Results of spawning areas and dispersal for each location are presented in this section, followed by a compilation of the main results, providing a comparative analysis for all locations together. While Fig. 5a and b illustrate the connectivity among locations, Table 2 includes all the metrics presented throughout this section.

3.1. Spawning areas for each recruitment location

3.1.1. Spawning area for Princess Charlotte Bay

The spawning area for Princess Charlotte Bay was approximately 330,200 km^2, the most extensive compared to the other locations assessed in this study. The probability of settling in Princess Charlotte Bay ranged from 52‰ to 140‰. Overall, even if a female mud crab released the eggs approximately 600 km offshore from Princess Charlotte Bay, the larvae would still have a probability (although small) of returning to the same location by passive dispersal. The simulation also showed that particles released about 800 km south of Princess Charlotte Bay and 250 km to the north may still plausibly settle in Princess Charlotte Bay, albeit at low probability (Fig. 3a).

3.1.2. Spawning area for Hinchinbrook Channel

Simulations for the Hinchinbrook Channel resulted in probabilities of larvae settling in the Hinchinbrook Channel between 30‰ and 82‰. Overall, the catchment for Hinchinbrook Channel included an area of approximately 112,300 km^2. The modelling showed a tendency for south-to-north movement near shore, meaning that eggs released immediately south of Hinchinbrook Channel had the highest probability of settling within Hinchinbrook Channel. However, larvae released up to 300 km to the north or south still had some probability of dispersing into the Hinchinbrook Channel (Fig. 3b).

3.1.3. Spawning area for Mackay

The probabilities of larvae settling in the Mackay region (i.e., Pioneer River) ranged from 2.9‰ to 7.9‰, and the catchment for this location was spread within an area of 79,300 km^2. The entire area extended approximately 280 km to the north (south of Townsville), 230 km to the south and 220 km offshore. The simulation showed a high chance of a northward movement; therefore, larvae released south/southeast of Mackay were prone to settle in Mackay. However, larvae could also reach the Mackay region from other directions, albeit with far lower probabilities (Fig. 3c). The probabilities of arrival to Pioneer River in Mackay were lower than for different locations, in part due to the smaller entrance area of its estuarine zone.

3.1.4. Spawning area for Gladstone

The spawning area simulation for Gladstone Harbour resulted in probabilities between 36‰ and 98‰. Overall, the catchment included an area of 103,400 km^2, which expanded approximately 480 km to the north, 210 km to the east and 240 km to the south, limited by K’gari (Fraser Island). The modelling showed a tendency for particles released nearshore to drift northwest. Hence, larvae released in the southeast of Gladstone were more likely to reach the Gladstone region than those released in the north. However, the catchment area extended further to the north than to the south (Fig. 3d).

Table 2
Compilation of the main results of spawning areas and dispersal as a function of the distance offshore for each study location.

			Princess Charlotte Bay	Hinchinbrook Channel	Mackay	Gladstone	Eurimbula Creek	Moreton Bay
Spawning area	**Spawning Area (km^2)**		330,200	112,300	79,300	103,400	47,900	286,400
	Maximum distance (km)	**North**	250	300	280	480	270	1000
		South	800	300	230	240	170	100
		East	600	300	220	210	120	400
Dispersal vs distance offshore	**Offshore maximum distance (km)**	**Self-recruitment**	180 (800)[a]	200	200	380	150	400
		Recruitment north	750	750	180	210	310	350
		Recruitment south	800	400	400	580	510	430

[a] As explained in subsection 3.2.1, our simulations show that larvae released up to 180 km offshore can potentially return to Princess Charlotte Bay. Larvae released from 180 km to 500 km from the coast tend to drift northwards. However, due to the regional oceanographic features, larvae released between 500 km and 800 km from the coast might also return to Princess Charlotte Bay.

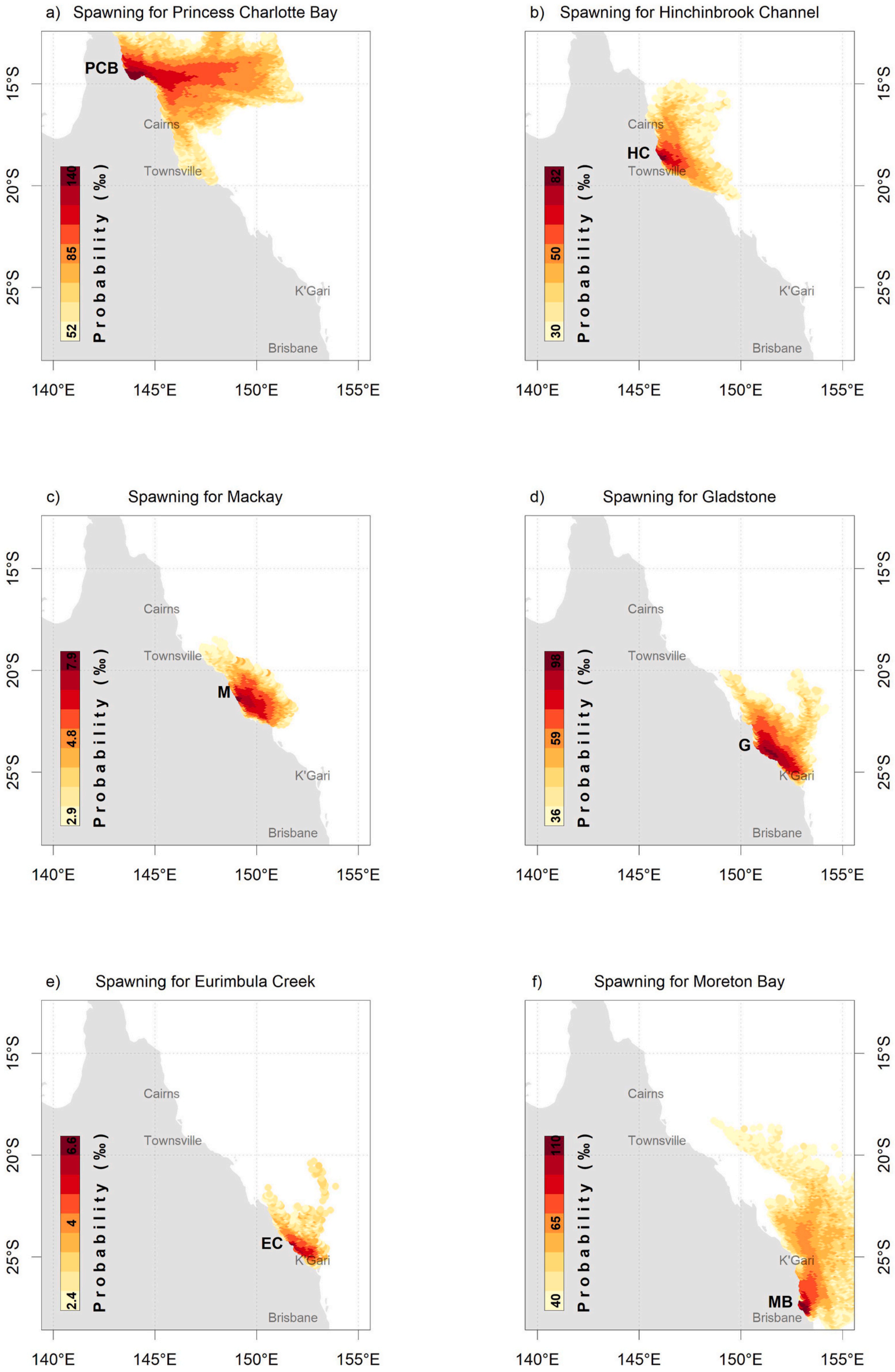

Fig. 3. Spawning areas with settlement probabilities for six mud crab locations on Queensland's east coast. a) Princess Charlotte Bay (PCB); b) Hinchinbrook Channel (HC); c) Mackay (M); d) Gladstone (G); e) Eurimbula Creek (EC); f) Moreton Bay (MB). Scale bar ranges from light yellow for the lowest probability to dark red for the highest probability. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.1.5. Spawning area for Eurimbula Creek

The spawning area simulation for Eurimbula Creek had probabilities ranging from 2.4‰ to 6.6‰. The catchment comprised an area of approximately 47,900 km^2 and reached nearly 270 km northwards, 120 km offshore, and 170 km southwards (limited by K'gari). The modelling presented similarities between Gladstone and Eurimbula Creek, as they are in the same region and have analogous oceanographic characteristics. The model for Eurimbula Creek exhibited a high probability of particles moving northwestwards, meaning there is a higher probability of larvae settling in Eurimbula Creek when released in the southeastern areas than in the north (Fig. 3e).

3.1.6. Spawning area for Moreton Bay

The probabilities for recruitment into Moreton Bay varied from 40‰

to 110‰. The total catchment area measured 286,400 km^2 and reached approximately 1000 km to the north, 400 km to the east and 100 km to the south. The simulation showed a tendency for movement from north to south, and particles were likely to drift to Moreton Bay if released in the Moreton Bay region or even in the further north. However, there was still a substantial chance (about 65‰) of particles released offshore around latitude 23°S (north of K'Gari) ended up in Moreton Bay if released far from the coast. The large catchment area for Moreton Bay meant that mud crab larvae released offshore Queensland's east coast, outside the GBR, even north of latitude 20°S could potentially be recruited in Moreton Bay (Fig. 3f).

3.2. *Dispersal of mud crab larvae as a function of distance offshore*

Overall, the simulation results revealed a clear relationship between the distance offshore that spawning occurred and the destination of larvae. In Fig. 4, self-recruitment can be gleaned from the probabilities along the horizontal line corresponding to the given location.

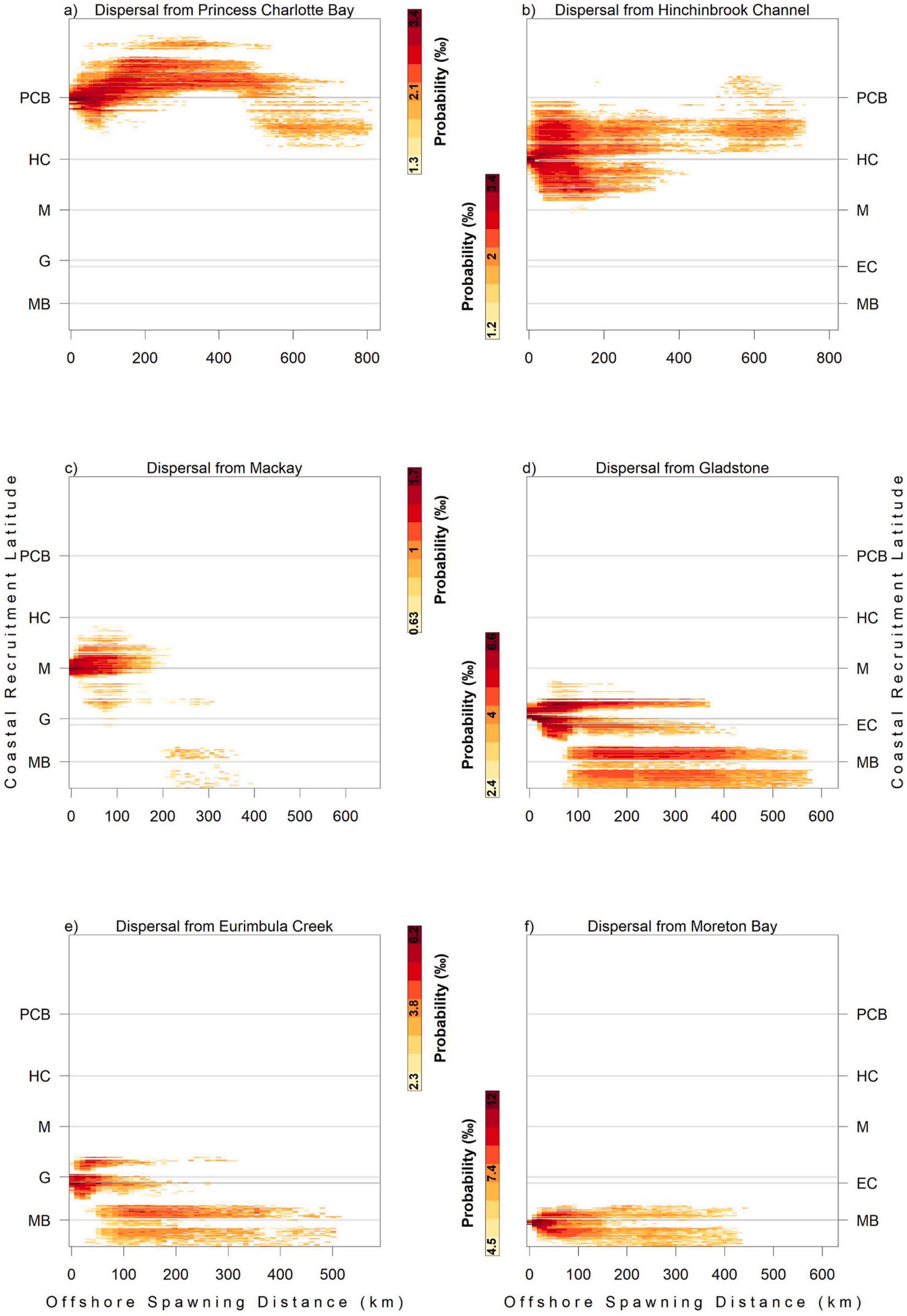

Fig. 4. Dispersal of mud crab larvae as a function of distance offshore for six mud crab locations on Queensland's east coast. a) Princess Charlotte Bay (PCB); b) Hinchinbrook Channel (HC); c) Mackay (M); d) Gladstone (G); e) Eurimbula Creek (EC); f) Moreton Bay (MB). Scale bar ranges from light yellow for the lowest probability to dark red for the highest probability. Note: y-axes correspond to the position of each location as a function of their respective latitudes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

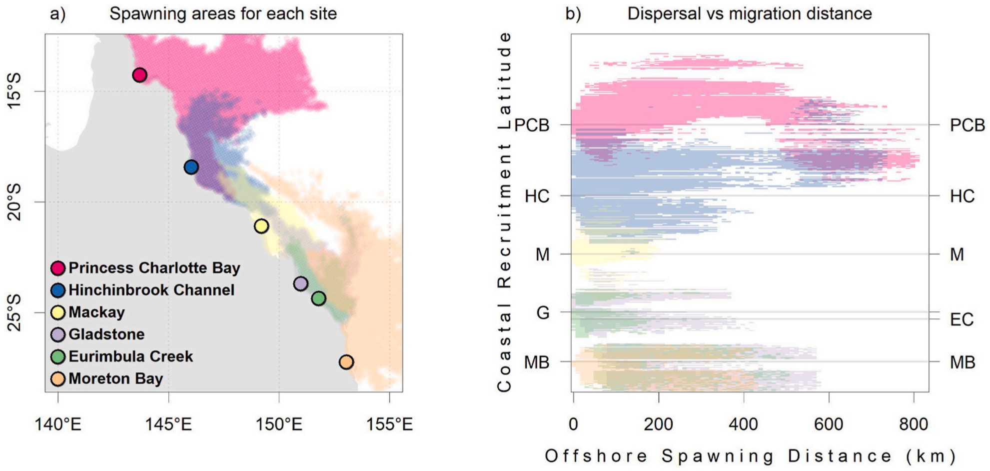

Fig. 5. a) Combined results of spawning areas for each of the six study locations. b) Combined results of larvae dispersal as a function of the seaward distance at the same latitude of the six study locations. i) Princess Charlotte Bay (PCB); ii) Hinchinbrook Channel (HC); iii) Mackay (M); iv) Gladstone (G); v) Eurimbula Creek (EC); vi) Moreton Bay (MB). Note: Fig. 5 b) y-axis corresponds to the position of each location as a function of their respective latitudes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2.1. Dispersal of mud crab larvae from Princess Charlotte Bay

Strong self-recruitment of larvae in Princess Charlotte Bay occurred for migrations within the first 200 km from shore, after which the particles tended to drift and settle northwards. However, for spawning distances beyond 500 km offshore, weak self-recruitment and recruitment further south is possible. Remarkably, even larvae spawned 850 km offshore from Princess Charlotte Bay could potentially drift back to the coast. Our results suggest that, depending on the offshore migration distance, Princess Charlotte Bay could subsidise mud crab larvae to other regions, including areas as far north as Papua New Guinea and to the south near Cairns, which represented approximately 760 km of coastline (Fig. 4a).

3.2.2. Dispersal of mud crab larvae from Hinchinbrook Channel

Larvae released from different distances offshore, at the same latitude as the Hinchinbrook Channel, settled in a stretch of approximately 1050 km of coastline, potentially supplied with larvae spawned by female mud crabs. The results for dispersal as a function of distance offshore from the Hinchinbrook Channel revealed a strong tendency for larvae released within approximately 10 km offshore to settle in the Hinchinbrook Channel, with a lower probability of settling in the surrounding northern coastal areas. Beyond that distance, a more scattered distribution was found for both directions, north and south, and the probability of self-recruitment in the Hinchinbrook Channel constantly decreased until approximately 200 km offshore. Between 200 and 400 km offshore, particles had roughly the same likelihood of reaching northern and southern coastal areas. Beyond 400 km from shore, larvae likely settled north of Hinchinbrook Channel (Fig. 4b).

3.2.3. Dispersal of mud crab larvae from Mackay

Overall, Mackay could supply mud crab larvae to populations located in the north and south, which comprised approximately 950 km of coastline, depending on the offshore spawning distance. Larvae spawned by females up to approximately 100 km offshore at the same latitude as Mackay had a greater chance of successful recruitment in Mackay and in areas approximately 320 km to the north and approximately 480 to the south. From 100 km to 200 km offshore, the probabilities and the range of settlement areas constantly decreased, although there was still a trend of particles potentially reaching locations to the north, south, and Mackay. Beyond an offshore distance of 200 km, the particles could only return to shore in areas near Moreton Bay (Fig. 4c).

3.2.4. Dispersal of mud crab larvae from Gladstone

Mud crab larvae released offshore at the same latitude as Gladstone reached northern and southern areas, equating to approximately 690 km of coastline. The particle tracking simulation showed that larvae released up to 100 km offshore from Gladstone tended towards self-recruitment. Beyond 100 km offshore, larvae were still most likely to return to Gladstone, but the dispersal was more widespread, while probabilities were substantially reduced. There was an increasing tendency for larvae to drift southwards when released beyond 100 km offshore, reaching areas in Moreton Bay and the Gold Coast. A northward drift was also possible but with very low probability and only when spawning occurred between 50 km and 100 km (Fig. 4d).

3.2.5. Dispersal of mud crab larvae from Eurimbula Creek

Particles released in a straight line offshore from Eurimbula Creek reached approximately 600 km of coastline. At approximately 80 km from the coast, larvae could either return to the same estuary or move northwards and southwards (near K'gari). Beyond about 50 km from the coast, some particles remarkably tended to drift southwards. This tendency increased and became more consistent beyond 100 km offshore. After 150 km offshore, most particles moved south, reaching areas near Moreton Bay (Fig. 4e).

3.2.6. Dispersal of mud crab larvae from Moreton Bay

The particles released offshore at the same latitude as Moreton Bay had a significant probability of returning to the same region. The range of areas on Queensland's east coast where the particles would settle when released offshore of Moreton Bay was restricted to approximately 230 km of coastline. This means the larvae were not prone to drifting to areas other than Moreton Bay and their immediate surroundings (noting that our model was restricted to Queensland waters). Moreover, the greatest likelihood was for larvae to return to Moreton Bay, from up to 100 km offshore. At greater distances offshore, the larval dispersal became evenly distributed to either returning to Moreton Bay or drifting to the northern and southern areas. Nevertheless, the modelling indicated that even if female mud crabs spawned over 400 km offshore, it was still possible for larvae to self-recruit to Moreton Bay (Fig. 4f).

3.3. Synthesis of the main results

The data presented individually for each location in sections 3.1 and 3.2 are summarised in a single map to allow a qualitative comparison among different areas. It illustrates the spawning areas (Fig. 5a) and the dispersal of mud crab larvae as a function of distance offshore (Fig. 5b) for all six study locations together. The overlap of polygons representing the spawning areas for each location supports the hypothesis of connectivity among different mud crab locations. The polygons combined allow the observation of connectivity between Princess Charlotte Bay, Hinchinbrook Channel and Mackay in the northern area. In the central region, Mackay is connected to Princess Charlotte Bay, Hinchinbrook Channel, Gladstone and Eurimbula Creek, whilst in the southern region, Moreton Bay is connected to Eurimbula Creek, Gladstone and even the Hinchinbrook Channel (Fig. 5a). Therefore, each of the six locations may be regarded as providers and recipients of mud crab larvae, although to different magnitudes based on their respective probabilities.

The size of spawning areas and distances from each study location is summarised in Table 2. This synopsis of model results assists with the interpretation of the overall results while allowing for comparisons of the probabilities of giant mud crab larvae settling in one of the six mud crab habitats included in this study and dispersal of mud crab larvae as a function of the distance offshore for each of the study locations. For example, Princess Charlotte Bay had the largest spawning area and the furthest distance offshore, where particles were released and returned to the coast. In contrast, Eurimbula Creek had the smallest spawning area and the shortest distance offshore. Though Princess Charlotte Bay had the furthest distance offshore in which the larvae would self-recruit, this distance was not uniform due to the oceanographic characteristics of the region, as explained in subsection 3.2.1. Furthermore, the distance offshore for self-recruitment was similar for Gladstone and Moreton Bay.

4. Discussion

4.1. Spawning migration behaviour

Our simulation and analysis of larval drift patterns provided valuable new insights into the offshore migration of female giant mud crabs along a complex coastline. Overall, our results imply that, although a minimum offshore migration distance is needed, no single offshore migration distance could produce both the observed high local recruitment and long-distance connectivity. The results also suggested that the distance from the coast where spawning occurs and local oceanographic features may be the main factors affecting the probability of larval settlement. The likelihood of a larva settling in each study location was inversely proportional to the release distance. Therefore, particles released in areas near each mud crab region had a higher probability of drifting back to that location, and the probability decreased as the particles were released at greater distances offshore or along the coast. Indeed, at each of the mud crab regions we considered, the distance offshore tended to reduce the likelihood of a successful return, as expected. However, the decrease was not always linear, smooth, or even monotonic. Remarkably, we found that even offshore migrations of more than 400 km could result in a passive dispersal of mud crab larvae to the Queensland east coast, especially for larvae settling in Princess Charlotte Bay, where settlement was possible even from 800 km offshore. However, it is unlikely to be feasible for a female mud crab to travel such distances within the egg incubation period (Hamasaki, 2003; Patterson et al., 2023), given the average water temperature in the study region (Richardson and Pattiaratchi, 2020).

The dependence of the recruitment site on the distance offshore that spawning occurred is driven by the dramatic changes in prevailing offshore currents, with broad, weak northwards flow on the shelf inshore of the swift, narrow EAC that runs over the continental slope. Seasonal wind patterns and nearshore local currents might generally be the main drivers for larval dispersal within the Great Barrier Reef lagoon, whilst the predominant ocean current direction and intensity (Schilling et al., 2022) naturally exert a significant influence on particle movement along the Australian continental slope (Rudorff et al., 2009; Storlazzi et al., 2017). As such, there was an overall tendency for nearshore spawning to favour self-recruitment or subsidisation of populations to the north and for offshore spawning to result in southward dispersal. Whereas nearshore spawning grounds strengthened the maintenance of local populations, offshore spawning grounds benefited connectivity and genetic flow (Figueira, 2009) and, consequently, the population's overall resilience (Swearer et al., 2019).

There are, however, some exceptions to this rule. Specific dispersal patterns were observed for each region, regardless of the distance from the coastline. Dispersal offshore from Gladstone, Eurimbula Creek and Moreton Bay sites each exhibited a division in the recruitment destination from approximately 100 km offshore, resulting in only a fraction of larvae becoming entrained in the EAC. Moreover, larvae released far from the coast (up to 800 km in some regions) might still return to the same area due to the action of eddies (Azis Ismail et al., 2017; Weeks et al., 2010) and other local oceanographic factors (Brinkman et al., 2002; Church, 1987).

The observation that successful larval recruitment was possible even when spawning occurred far from the coastline means that we cannot provide a meaningful outer limit on the possible offshore migration distance based on connectivity grounds alone. Even a spawning migration to areas unlikely to be reached by ovigerous female mud crabs due to the relationship between the distance (Patterson et al., 2023) and incubation period (Hamasaki, 2003) would potentially still result in recruit supply and population connectivity among regions. Also, it is noteworthy that what may be considered the optimal offshore spawning distance to maximise connectivity varies greatly between sites. For example, while long migrations from Princess Charlotte Bay could achieve wide-ranging dispersal back to coastal habitats, the same distance migration from Mackay would result in complete failure of larval recruitment. Environmental triggers, such as the temperature gradient upon traversing the EAC, could control the spawning site (Baylon, 2010; Davis et al., 2004).

Such behaviour would be highly site-specific, given that most giant mud crab habitats across thir global distribution are not adjacent to western boundary currents like the EAC. Moreover, our results show that females with the trait of spawning only once they have detected the EAC would provide no self-recruitment, meaning that the trait would soon be lost from the source population. The observation that the simulated spawning distance and recruit destination differed substantially between sites suggests that a large variability in spawning distance, unrelated to environmental triggers, could benefit the species most. Shorter spawning migrations are needed to ensure self-recruitment, potentially providing recruits better suited to the local environment. In contrast, longer dispersal distances are required to ensure a level of population connectivity consistent with the observed genetic homogeneity (Gopurenko and Hughes, 2002). Variations in the spawning migration distance would benefit the spread and maintenance of the species across a range of oceanographic contexts and increase the population's overall resilience.

4.2. Regional oceanographic features influencing the dynamics of larval dispersal on Queensland's east coast

Overall, our results indicated that all six study locations included in this investigation can, given sufficient variability in spawning migration distance, supply larvae to and obtain larvae from the adjacent areas, suggesting a high level of connectivity among them. Importantly, there is no single spawning migration distance that can explain the genetic homogeneity of the giant mud crab populations along the Australian east coast (Fratini et al., 2010; Gopurenko and Hughes, 2002; Gopurenko et al., 1999). We can conclude that offshore spawning very likely occurs and is driving connectivity. Furthermore, connectivity along the southern half of Queensland's east coast and New South Wales is strongly reliant on the southward-flowing EAC (Church, 1987; Hewitt et al., 2022b; Schilling et al., 2022; Wolanski, 2017).

All four high-catch areas for mud crabs along Queensland's east coast (Heaven, 2018) had high probabilities for recruiting mud crab larvae but with different characteristics. According to our models, most of the mud crab larvae in the study area settle either in Princess Charlotte Bay or Moreton Bay. However, although Hinchinbrook Channel and Gladstone receive a lower quantity of mud crab larvae in comparison to the other abovementioned locations, they are still considered pivotal areas for mud crab fisheries in Queensland (Heaven, 2018), probably reflecting the importance of habitat quality for larval recruitment (Dias, 1996; Kerr et al., 2010). Furthermore, Gladstone likely benefits from relative proximity to Eurimbula Creek, which, as a mud crab sanctuary (DAFF, 2012), has the potential to consistently generate larvae and be a stable supplier of giant mud crab larvae to nearby regions.

Some particular oceanographic characteristics in the Great Barrier Reef lagoon and along the Australian continental slope are crucial to understanding the larval dispersal patterns on Queensland's east coast. Prevailing southeasterly trade winds predominantly rule the oceanographic dynamics within the Great Barrier Reef lagoon, potentially leading the nearshore currents to the north/northwest most of the year (Burrage et al., 1996). However, the current direction may change southwards during the monsoon season (summer months) due to the influence of north/northeasterly winds (Steinberg, 2007). Our model covered a period that includes both phenomena, likely affecting our results. Moreover, specific features caused by the complex topography in the Great Barrier Reef generate particular local oceanographic conditions that also affect advection (King and Wolanski, 1996).

Each location along Queensland's east coast presented differing larval dispersal characteristics. Princess Charlotte Bay exhibited a self-supply of larvae and retention, had the largest catchment area and the furthest distances offshore (up to 800 km) from which particles could be released and still returned to the same location. This Far North Queensland (FNQ) region is characterised by a prevailing northward current, becoming an eddy further north when it reaches the GPC (Brinkman et al., 2002; Church, 1987). This current potentially drove the larvae to return to the shore. The widespread larval dispersal for the Hinchinbrook Channel was likely to occur due to the influence of the westward SEC bifurcation when it encountered the Australian continental shelf (Brinkman et al., 2002). The division of the coastal current southwards and northwards might lead to the spread of mud crab larvae in both directions (north and south) if they are released near the Hinchinbrook Channel.

The model identified similar patterns for study locations in central Queensland. Within the Great Barrier Reef lagoon, there was a strong tendency for northward drift and higher probabilities of larvae either self-recruiting or settling nearby when released at the same latitudes as the study areas. Moreover, either the partial obstruction on the EAC western portion around 25°S created by K'gari (Burrage et al., 1996; Schilling et al., 2022) or the cyclonic eddy that is seasonally formed off the east coast near K'gari (Azis Ismail et al., 2017) appeared to increase the rate of larval retention northwest of the island (Schilling et al., 2022). This natural barrier, in addition to the peculiar oceanographic conditions in this region, is beneficial for primary productivity (Brieva et al., 2015), creating suitable habitats for recruitment and settlement of mud crab larvae due to entrainment in nearshore areas (Schilling et al., 2022). Larvae released further offshore (over 100 km from the central Queensland coast) reached the EAC and were carried southwards, settling in Moreton Bay or further south, beyond the boundary of the model domain.

The possibility that K'gari represents a barrier for northward larval transport appears to be at odds with the lack of observed genetic breaks across this feature (Gopurenko and Hughes, 2002). Two explanations are possible. Firstly, southward gene flow occurs, which may maintain genetic homogeneity if the southern populations are subsidised by spawning offshore from Queensland (Schilling et al., 2022). The fact that the gene flow continues to be strongly south for much of the mud crab habitat on the Australian east coast would support this hypothesis. Secondly, northward gene flow may be achieved inshore of K'gari by adult crab migrations (Hewitt et al., 2022a). Gene flow could also occur along the New South Wales coast, aided by the northward nearshore current that runs counter to EAC.

The model revealed a strong trend for Moreton Bay to be the greatest recipient of larvae from most of the central Queensland coast (if mud crabs spawn at least 100 km from the shore) and from south Queensland due to the influence of the EAC on passive dispersal (Hewitt et al., 2022b). Moreover, larvae released offshore at the same latitude as Moreton Bay had a considerable probability of moving southwards, potentially crossing into New South Wales waters, which is a different fishery management jurisdiction (Calogeras and Buckworth, 2023; Hewitt et al., 2022b). However, our study could not prove this theory, as our simulations utilised models for Queensland waters.

4.3. *Implications of dispersal patterns on giant mud crab populations*

.Our results demonstrated that a seaward spawning migration of the giant mud crab, believed to occur but for which limited observational evidence currently exists, is necessary to explain the genetic homogeneity of the species in northeastern Australia. Without offshore migration, connectivity between the distanced giant mud crab habitats would likely be weak, at odds with the genetic evidence. While the connectivity patterns are specific to the northeastern coast of Australia, the inferred natural variability in the spawning behaviour of gravid females is relevant for giant mud crab ecology and management globally. No single unimodal offshore spawning migration strategy can sustain population connectivity in our case study, arguing that variability in migration is likely to be fundamental to giant mud crab population dynamics, not just in northeastern Australia, but in other key locations globally. In our study, offshore migration produced a large increase in connectivity across a range of differing oceanographic contexts, albeit always at the cost of self-recruitment and rates of larval loss.

This long-range larval advection would allow giant mud crabs to maintain their range. The swimming capacity required for females to spawn offshore (Hill, 1994), in addition to the regional oceanographic features, would enhance larval dispersal, improve gene flow and, consequently, the species distribution. Those factors might be the drivers that make this species extensively widespread in the Indo-West Pacific region (Gopurenko et al., 1999; Keenan et al., 1998). Moreover, the previously reported low genetic variability indicates that: 1) the populations are connected within the distribution range, and 2) the species has a high level of plasticity, as it can adapt to diverse environmental conditions (Fratini et al., 2010; Gopurenko and Hughes, 2002; Gopurenko et al., 1999; Rumisha et al., 2018). These findings are consistent for regions with different characteristics, such as the Australian and African East Coasts. Even though some genetic differentiation still occurs, this can be attributed to environmental factors affecting the larval movement or survival of larvae, juveniles and adults (Fratini et al., 2010).

The oceanic larval phase plays a vital role in giant mud crab populations' survival, resilience and sustainability. Firstly, the giant mud crab larva needs optimal environmental conditions to survive and grow, particularly in terms of water temperature and salinity (Baylon, 2010; Ruscoe et al., 2004). As most estuaries are prone to cyclical changes in water parameters (Costa et al., 2018), oceanic waters potentially provide a stable environment for larval survival and development. Secondly, populations facing decline due to external factors such as fishing mortality or changes in environmental conditions (Flint et al., 2021; Robins et al., 2020), including variations caused by global warming (Gillanders et al., 2011), would be more likely to persist if they receive recruits from other regions through larval advection (Dias, 1996). Finally, large-scale connectivity among different regions is more likely to occur in the ocean than in enclosed environments (e.g., estuaries), providing more extensive interchangeability among populations with distinct biological traits (Sheaves, 2009) and, therefore, improving genetic diversity and strengthening plasticity.

The consequences for giant mud crab population dynamics will, however, depend on the source-sink balance, as it influences the maintenance of local populations and the supply of larvae to adjacent areas. The results of possible scenarios for the spawning locations of ovigerous females demonstrated that the six mud crab locations included in this investigation might all potentially contribute as sources and sinks of mud crab larvae to other populations for at least some offshore migration distances. The actual source-sink process that occur in the metapopulation may be affected by several factors other than oceanic dispersal, such as demographic parameters and habitat quality, which might determine the role of each area (Dias, 1996). Accurate identification of areas as sources or sinks is complex, as the characteristics of habitats might change year to year due to regional environmental factors (Dias, 1996; Figueira, 2009). Extreme events like modifications in ocean circulation due to climate change (Li et al., 2023; Steinberg, 2007) can be particularly detrimental for sink populations, as it might negatively affect larval supply (Dias, 1996; Schilling et al., 2022). Moreover, the impact of these changes may alter both species distribution and habitat suitability (Brierley and Kingsford, 2009). The impact of increasing ocean temperatures on the distribution of marine species has been well documented (Brierley and Kingsford, 2009), but increased temperature variability is also driving shifts in habitat suitability. For example, increased upwelling-induced cooling in the Agulhas Current - the western boundary current of the southern Indian Ocean - has resulted in multi-species mortality events (Lubitz et al., 2024).

Understanding larval dispersal dynamics is critical for the sustainable management of mud crab stocks. As the swimming capabilities of earlier larval stages of the giant mud crab are not yet known (Epifanio and Cohen, 2016), the passive dispersal (or weak swimming behaviour) during the zoeal phase is believed to be a major constraint on the success of recruitment, making release (spawning) location a key factor in dispersal (Rudorff et al., 2009; Storlazzi et al., 2017). To successfully recruit, larvae must arrive within a certain distance of suitable habitat by the time they have metamorphosed into megalopae capable of moving into nearby habitats (Webley and Connolly, 2007; Webley et al., 2009). From then on, factors other than oceanic advection (e.g., food availability and habitat quality) will determine recruitment (Alberts-Hubatsch et al., 2014; Mirera, 2017; Webley et al., 2009). Hence, elucidating the details of giant mud crab life history, including spawning ground locations, the distance offshore, or triggers for female mud crabs to release the eggs, could be extremely beneficial for mud crab stocks' conservation.

4.4. *Limitations of the study*

Our study aimed to test different probabilities of spawning areas and larval dispersal as a function of the distance offshore for six mud crab regions on Queensland's east coast, but not to determine the relative importance of each location to recruitment or population dynamics. We understand that presenting the definition of a habitat as a source or sink is much more complex and requires the investigation and inclusion of various demographic and ecological parameters. Hence, our objective was to hypothetically present how each region would perform as providers or recipients of mud crab larvae, only considering probabilities of larval dispersal and habitat designation.

Our simulations considered some biological characteristics of the giant mud crab, and our results were consistent with several behavioural traits. However, we could only test the probabilities for larval advection in relation to oceanographic features. We did not test, for instance, the distance offshore where females might feasibly swim to spawn or the consequent duration for larvae to reach the nearshore settlement areas from those offshore spawning sites. Instead, we considered where females might hypothetically go offshore, and the larvae would still return to the same or different regions along Queensland's east coast. We considered that, during the zoeal phase, the giant mud crab larva drifts passively, as there is currently no solid evidence of their swimming capabilities, even though this behaviour has been recorded for other portunid crabs (Almeida et al., 2021; Epifanio and Cohen, 2016). We also understand that our simulations were solely based on constant larval duration (i.e., 28 days). According to Baylon (2010), larval duration (zoea + megalopa) could range from 21 to 32 days at a salinity of 35 and temperature of 26 °C, which would be the overall conditions in the study area between October and February (Richardson and Pattiaratchi, 2020), noting that specific events, floods, or eddies might change the water parameters. Nevertheless, we found that differences in water conditions (i.e., salinity and temperature) would not greatly affect larval advection, even though the duration of mud crab larval development is directly related to those parameters. However, we assume that it might impact recruitment in some regions.

Although we considered the spawning period between October and February in the study region (Heasman et al., 1985), the spawning migration of mud crabs differs in relation to regional differences in the period and duration of the season. Moreover, ocean circulation might be affected year-to-year by differences in meteorological (e.g., cyclones, El Niño-Southern Oscillation) and oceanographic events (e.g., eddies), and also change over time due to climate change (Li et al., 2023; Steinberg, 2007).

Finally, our study was limited to Queensland's east coast and did not test the trans-jurisdictional movement of giant mud crab larvae due to the boundary of the model used. We, therefore, did not assess the probability of larvae moving south of Moreton Bay into New South Wales or north/northeast of Princess Charlotte Bay towards Papua New Guinea. Nevertheless, our results suggested those areas might potentially play a key role in exchanging giant mud crab larvae with Queensland.

5. Conclusions

Based on numerical simulations of larval dispersal, we estimate the impact of offshore spawning distance on the connectivity between the six major giant mud crab habitats of northeastern Australia. Nearshore spawning favours self-recruitment in all cases, but there is significant variation in the offshore spawning distance that provides connectivity between populations. These variations are related to the oceanographic context of each site – primarily, but not entirely, the distance to the core of the EAC. Given that the genetic connectivity of these populations has been well established (Gopurenko and Hughes, 2002), the results suggest that mud crabs are unlikely to have a tightly defined spawning migration distance in Australia and elsewhere. Indeed, the fact that the species thrives throughout the tropical regions of the Indo-West Pacific under very different oceanographic contexts implies that the spawning strategy must contain significant variability.

Notwithstanding the dependence on the unknown details of the offshore spawning migration behaviour, the connectivity between these sites is surprisingly complex and asymmetrical, and it is not a simple function of linear distance. Some populations act as strong sources and sinks, whereas others may have very low self-recruitment. Mud crab habitats inferred to have low self-recruitment will be sensitive to changes in larval supply. Hence, identifying these regions across all areas of the giant mud crab's range should be a key finding, enabling stocks to be managed precautionarily. If these populations' persistence depends on subsidisation, overfishing or changes in environmental conditions elsewhere may impact local populations.

CRediT authorship contribution statement

William Dantas Charles: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christopher Aiken:** Writing – review & editing, Visualization, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Julie Robins:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Adam Barnett:** Writing – review & editing, Supervision. **Nicole Flint:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.109008.

Data availability

Data will be made available on request.

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