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A Review of Giant Mud Crab *Scylla serrata* (Family Portunidae) Spawning Migration: The Lost Link in the Species' Life History

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Abstract
Spawning migration is a behavioural trait observed in various aquatic animals. Understanding this behaviour is vital for fisheries management and the sustainability of harvested populations. Ovigerous female Giant Mud Crabs *Scylla serrata* (Forskål, 1775), a valuable portunid in the Indo-West Pacific region, have been observed to undertake spawning migrations in some regions. As this stage of the species' life history remains poorly understood, this systematic review aimed to critically analyse the literature on Giant Mud Crabs, focused on their spawning migrations. We also investigated methods applied to studying the movement ecology of other crab species to identify techniques that could be used to address the Giant Mud Crab spawning migration. Although ecological studies into this species have increased recently, the scarcity of knowledge on female Giant Mud Crab behaviour between mating and spawning remains a constraint. The direct study of wild ovigerous females remains a challenge, as they are rarely caught in estuaries where commercial and recreational crab pots are deployed. Overall, the review identified mark-recapture (25%) and acoustic telemetry (25%) were the most frequently employed methods utilised to study the movement ecology of at least 21 crab families, predominantly the family Portunidae. We highlighted five approaches, including mark-recapture, acoustic telemetry, Pop-up Satellite tags, zooplankton surveys and numerical modelling used in crab research that could be applied to track ovigerous female Giant Mud Crabs during the spawning migration and discussed their respective strengths and weaknesses. A combination of methods and possible collaboration with citizen science programs was identified as an appropriate strategy to elucidate the Giant Mud Crabs spawning migration.

Keywords Portunidae · Behavioural ecology · Large-scale movement · Decapoda · Tracking methods · Essential habitats

Introduction

Spatiotemporal spawning migration is a life strategy adopted by many aquatic organisms, which can play a crucial role in connectivity and species survival (Domeier, 2012). Especially for harvested populations, understanding this behavioural trait is fundamental for fisheries management, as migration can considerably influence recruitment (Kell et al., 2015) and, therefore, the productivity and sustainability of stocks (Abrantes et al., 2015; Biggs et al., 2021). Characteristics like the duration of the spawning season and spatial distribution in spawning areas impact reproductive efficiency and species adaptability. For example, while a spawning strategy that is spatially and temporarily linked to a particular habitat can provide greater recruitment success, it will be less resilient to environmental changes, habitat loss and overexploitation than a more general spawning strategy

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that can be successful year-round and across a wider area (Kerr et al., 2010).

Spawning migration plays a crucial role in the survivorship of many marine and estuarine species that depend on more than one habitat during their life cycle (Sheaves, 2009). Similar to many other decapod crustaceans and fishes, *Scylla serrata* (hereafter referred to as "Giant Mud Crab") is currently understood to have a triphasic life history that comprises (1) an offshore planktonic stage of eggs and larvae carried by ocean advection to settlement areas, (2) a growth stage in inshore/estuarine habitats where they stay during most of their lifespan, and (3) a spawning migration of females only (i.e., for egg extrusion) away from the growing habitats to complete their lifecycle (Alberts-Hubatsch et al., 2016; Pittman & McAlpine, 2003). In Northern Australia, Hill (1994) observed that 97.1% of the 447 individuals Giant Mud Crabs captured offshore by trawl fishing vessels were females, and 61.5% of those females were gravid at the time of capture. This behaviour has been observed in various estuarine crab species, in which females migrate from low-salinity areas towards higher-salinity waters to spawn, potentially due to the larval requirement for stable environmental conditions (Abe et al., 1999; Aguilar et al., 2005; Carr et al., 2004; Hill, 1994; Landeira et al., 2020; Potter & de Lestang, 2000; Robertson & Kruger, 1994; Sant'Anna et al., 2012). However, aspects of the Giant Mud Crab life history remain poorly understood, particularly outside the estuarine and inshore adult habitats.

The Giant Mud Crab is a portunid crab of high economic, social, and cultural importance throughout much of the Indo-West Pacific. This species inhabits estuarine and coastal inshore areas associated with mangrove forests and is generally believed to have limited movement within and among nearby estuaries during the subadult and adult phases (Alberts-Hubatsch et al., 2014; Bonine et al., 2008; Demopoulos et al., 2008; Hyland et al., 1984). While adult males have occasionally been captured offshore (Hill, 1994; Patterson et al., 2023), ovigerous females of *Scylla* spp., including *S. serrata*, have been suggested to undertake seaward migrations to release eggs in some regions, such as Australia and Thailand (Alberts-Hubatsch, 2015; Hewitt et al., 2022a; Hill, 1994; Koolkalya et al., 2006). However, little is known about the particularities of this behaviour.

Some knowledge gaps regarding the spawning migration of Giant Mud Crabs include whether regional environmental and demographic differences might influence spawning behaviour, the triggers that prompt females to initiate seaward movement, and the location of the spawning grounds. The spawning season and population parameters related to reproductive features, such as size at maturity, vary across its geographical distribution (Khaksari et al., 2023; Onyango, 2002; Prasad & Neelakantan, 1989; Robertson, 1996). For example, recent studies have hypothesised that reduced salinity during the wet season may trigger females to initiate seaward migration in Australia (Hewitt et al., 2022a), as their larvae would need more stable water conditions (i.e., temperature and salinity) for survival (Baylon, 2010; Nurdiani & Zeng, 2007). In this case, the spawning migration would occur in distinct seasons across the species' distribution, as in some regions of the Indo-West Pacific, the rainy season is during winter, while in others it occurs during summer. In addition, size at maturity might affect the distance offshore of the spawning grounds, due to the allometric relationship in decapods between body size and swimming capacity (Florko et al., 2021). Other questions regarding the best conditions for egg extrusion, migration routes and whether the spawning migration is terminal remain, partly due to the difficulties associated to track female mud crabs when they leave the estuarine waters towards the sea.

This systematic review focuses on the spawning migration of female Giant Mud Crabs and also considers literature on the migratory behaviour of other crab species. We evaluated various techniques previously applied to crab research that may be used to infer the seaward migration of ovigerous female Giant Mud Crabs. The objectives of this study were: (1) to provide an overview of previous efforts to elucidate the spawning migration of Giant Mud Crabs, and (2) to review the techniques that have been used in crab research, which could be applied to investigate the seaward spawning migration of Giant Mud Crabs.

Materials and Methods

References were sourced from three scientific databases: Scopus, Web of Science and EBSCOhost, with the search completed on the 13th of January 2025. The literature search comprised two steps: (1) the published research on Giant Mud Crabs and, more specifically, on spawning migration, and (2) what techniques have previously been used to infer the migration and movement of crabs. The first research question was specific to the species of interest. A descriptive search for the term "*Scylla serrata*" was conducted to provide background knowledge on the species, particularly regarding spawning migration. After removing duplicates, the search results were collated and analysed to determine the number of publications related to the theme and their relevance. Then, the publications related to Giant Mud Crabs' spawning migration were tabulated. Publications in which the research included multiple species (except *S. serrata*) or was about an unrelated theme or species were discarded.

The second search used the strings [*Scylla* OR Portunidae AND Spawn* AND Migrat* OR mov*] in the title, abstract and keywords, or [crab AND spawn* AND migrat* OR mov*] in the title. The documents were imported into Covidence systematic review software (Veritas Health Innovation, Melbourne, Australia; available at www.covidence.org) that uses PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses methods to systematically review the literature) (Page et al., 2021). Each article's title and abstract content were analysed to check their relevance and applicability to our research questions. The remaining publications were used in the literature review and included in a separate descriptive statistical analysis. The variables used were: taxonomic family, method applied, country where the investigation was conducted and year of publication. The publications were categorised into the following methods: mark-recapture, acoustic telemetry, Pop-up satellite tags, fishery-based surveys, observational methods in the field, video imagery analysis, dataloggers, zooplankton surveys, stable isotopes, laboratory experiments or captive animals, numerical modelling, mixed methods, comparative analysis between methods, and literature review. The publications were grouped bt decades to examine the utilisation of the methods over time.

Results

Giant Mud Crab

The first search resulted in 1801 publications. After 795 documents were removed, the remaining 1006 documents were categorised into subject areas. Over 35% of the publications were related to the best conditions for developing, growing, and the grow-out phase of Giant Mud Crabs in aquaculture facilities, which provides crucial information for understanding spawning migration (e.g., larvae tolerance to environmental conditions and early benthic stages growth). However, the number of publications in biology and ecology has increased recently and has become the most relevant theme in 2023 and 2024. Only 23 documents pertinent to the spawning migration or seaward movement of Giant Mud Crabs were retrieved (Table 1).

Although studies on the spawning migration of ovigerous female Giant Mud Crabs have increased recently, some aspects of this life stage remain unknown. After analysing the available publications, we identified knowledge gaps regarding this behaviour, from the time females supposedly leave estuarine waters to egg extrusion and the possibility of returning to estuaries. We separated the spawning migration

Table 1 Publications directly related to the spawning migration of ovigerous female giant mud crabs that were retrieved in this literature review

Authors	Area of study	Life history stage	Country/Region	Method
Charles et al. (2024)	Biology & Ecology	Larva	Australia	Numerical modelling
Khaksari et al. (2023)	Biology & Ecology	Subadult/adult	Persian Gulf	Fishery data
Patterson et al. (2023)	Biology & Ecology	Adult	Australia	Numerical modelling
Hewitt et al. (2022b)	Biology & Ecology	Larva	Australia	Numerical modelling
Pratiwi et al. (2022)	Fisheries	Adult	Indonesia	Fishery data
Hewitt et al. (2022a)	Biology & Ecology	Adult	Australia	Acoustic telemetry
Jumawan et al. (2021)	Fisheries	Adult	Philippines	Fishery data
Grubert et al. (2019)	Fisheries	Adult	Australia	Numerical modelling
Fratini et al. (2016)	Biology & Ecology	Adult	Unspecified/ Pacific Region	Genetic studies
Alberts-Hubatsch et al. (2016)	Biology & Ecology	All	Australia	Literature review
Meynecke and Richards (2014)	Biology & Ecology	All	Australia	Numerical modelling
Rezaie-Atagholipour et al. (2013)	Biology & Ecology	Subadult/adult	Persian Gulf and Gulf of Oman	Fishery data
Nirmale et al. (2012)	Socioeconomics	Adult	India	Interviews (Traditional Ecological Knowledge)
Ogawa et al. (2012)	Biology & Ecology	Adult	Japan	Fishery data
Webley and Connolly (2007)	Biology & Ecology	Post-larva	Australia	Laboratory studies
Onyango (2002)	Reproduction	Adult	Kenya	Laboratory studies
Robertson (1996)	Biology & Ecology	Adult	South Africa	Fishery data
Hill (1994)	Biology & Ecology	Adult	Australia	Fishery data
Robertson and Kruger (1994)	Biology & Ecology	Subadult/adult	South Africa	Laboratory studies
Prasad and Neelakantan (1989)	Reproduction	Subadult/adult	India	Laboratory studies
Heasman et al. (1985)	Reproduction	Adult	Australia	Fishery data
Hyland et al. (1984)	Biology & Ecology	Adult	Australia	Mark- recapture
Hill (1978)	Biology & Ecology	Adult	South Africa	Acoustic telemetry

Some of the earlier studies might have incorrectly identified Scylla serrata, as the genus Scylla was reclassified by Keenan et al., 1998) into distinct events to provide a more detailed summary of each one (Fig. 1).

Crab Spawning Migration

In the second search, 656 documents were retrieved. After removing duplicates, 509 documents remained. Then, 210 documents were screened and sought for retrieval. After the studies were assessed for eligibility, 118 publications remained. Two documents from other sources (i.e., grey literature) were manually added, resulting in 120 documents included in this analysis (Annex 1). Twenty-one crab families were represented, and the family Portunidae, which includes the genus Scylla, was predominant, with 57 publications. This total represents nearly half of all publications assessed (47.5%) (Fig. 2). Research considering more than one family was categorised as "Multiple families".

Mark-recapture (25%) and acoustic telemetry (25%) were the most prevalent techniques of all publications. Mark-recapture has been used to track crab movements since the 1960s. Acoustic telemetry and laboratory experiments have been frequently applied since the 1990s. The use of acoustic telemetry in crab movement ecology research has been increasing considerably in recent decades as the technology has improved. Moreover, numerical modelling is one of the most used techniques in the current decade. Stable isotopes and pop-up satellite tags have also been used, though less frequently, and achieved meaningful results (Fig. 3).

Most of the crab studies retrieved in the review were conducted in the USA, followed in a much lower proportion by Australia and Canada. Nevertheless, the studies were widespread around the globe, including 30 countries/regions in all continents (Annex 2). Research into the genus *Scylla* was identified in studies from Australia, South Africa, Kenya, Micronesia, Vietnam, Fiji, the Persian Gulf, the Philippines and Malaysia.

Discussion

Spawning Migration of Giant Mud Crabs

Understanding the main biological traits and behavioural characteristics of Giant Mud Crabs, from mating to the period when ovigerous females are assumed to be offshore to extrude eggs, is required to overcome the difficulties of tracking and to determine the most appropriate methods for researching the spawning migration. Although various methods have been used to address questions about this species' life history stage, many knowledge gaps remain.

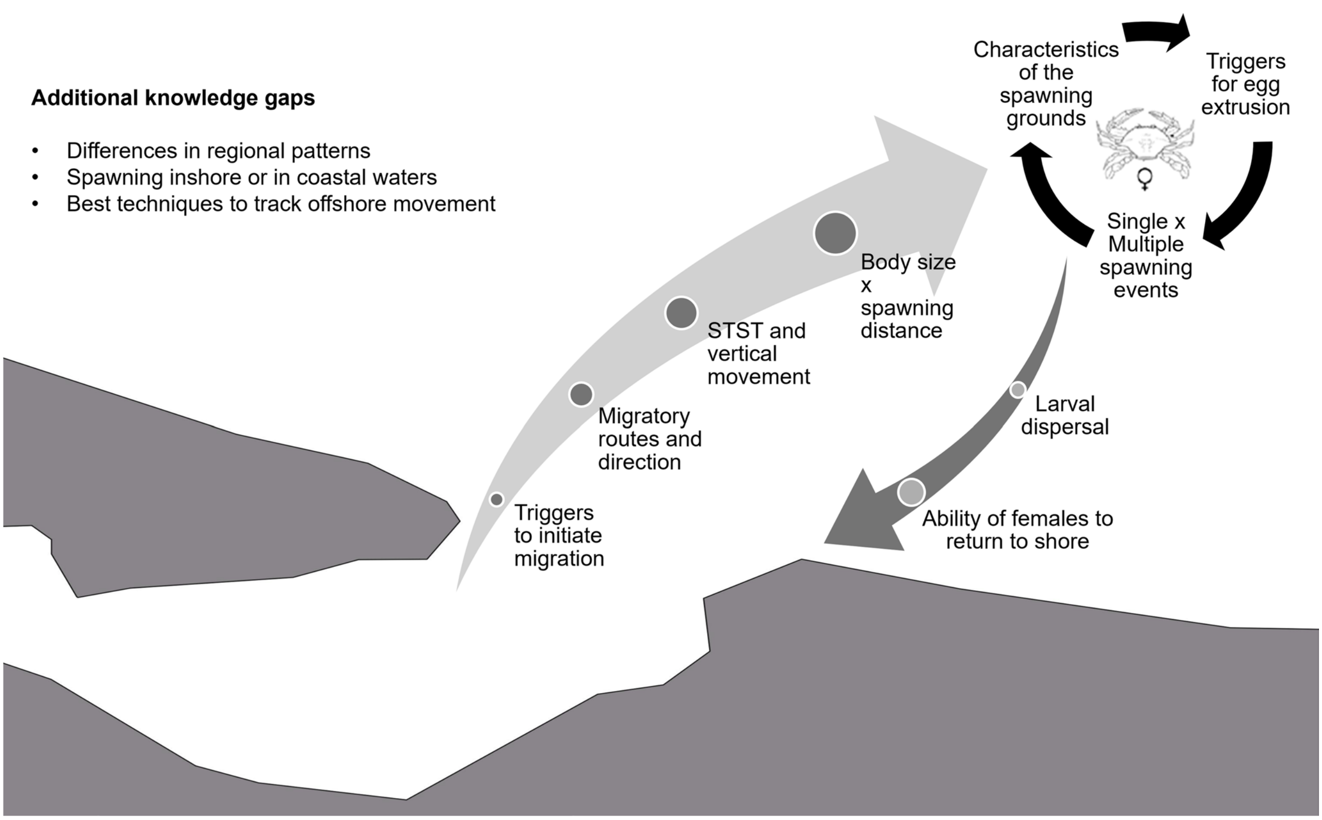


Fig. 1 Schematics illustrating the knowledge gaps on the Giant Mud Crab spawning migration

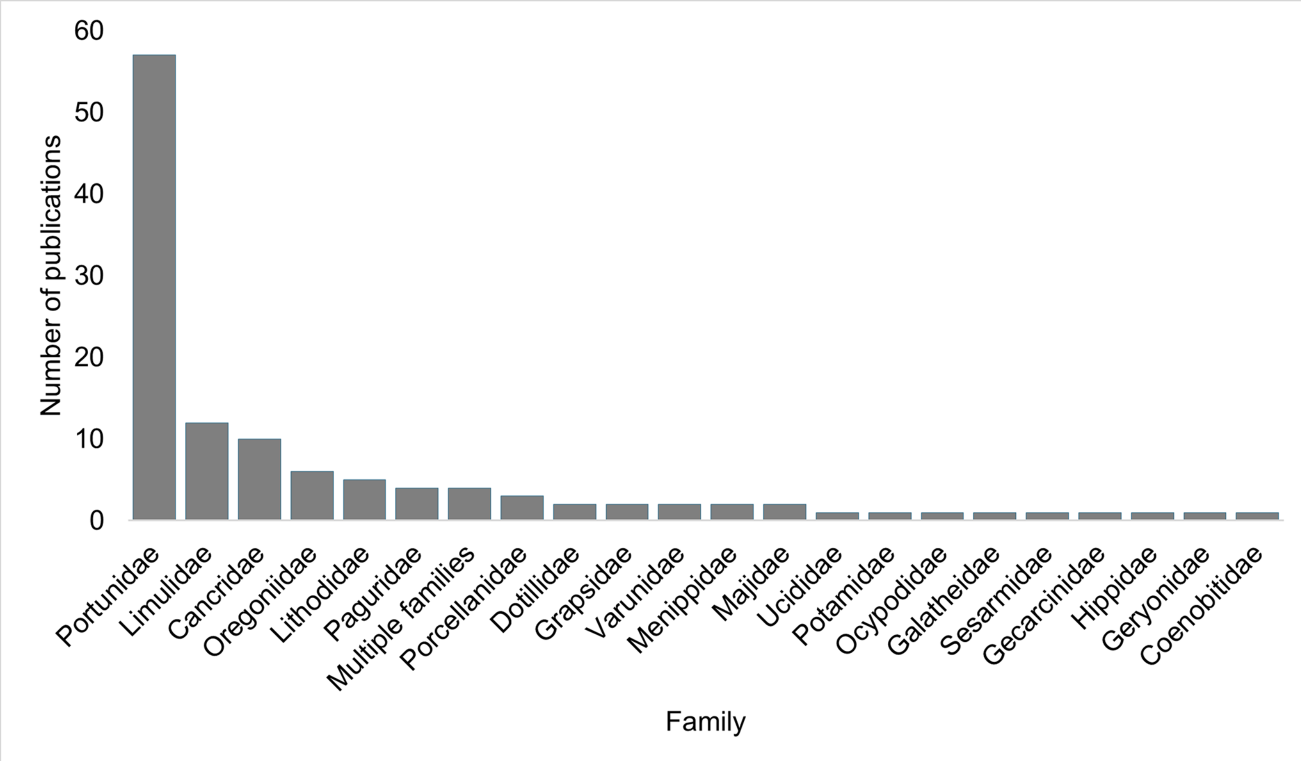
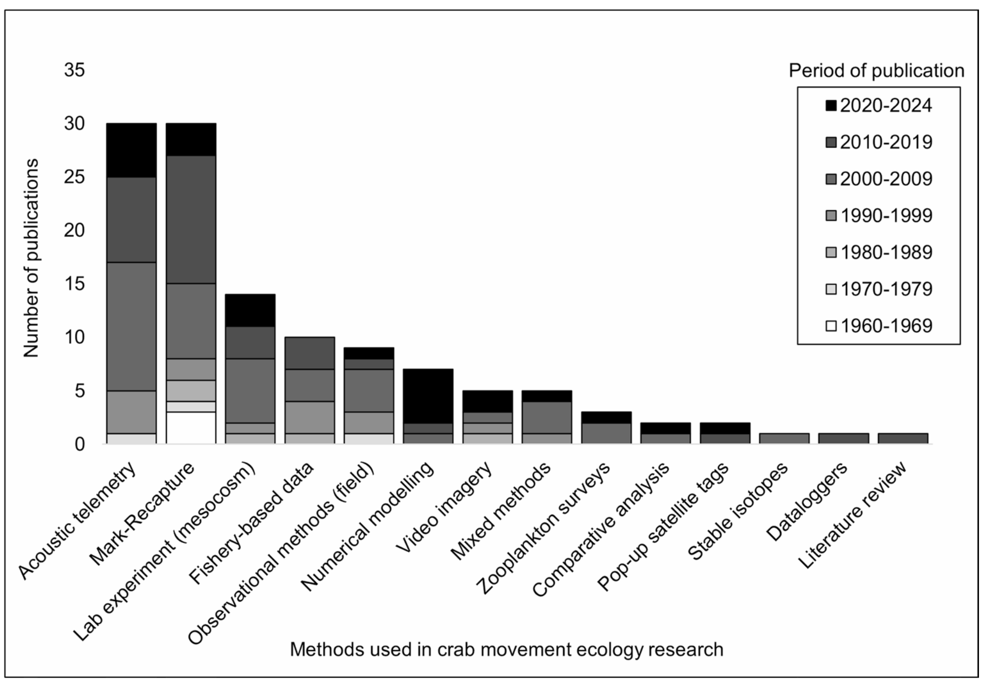


Fig. 2 Number of publications per crab taxonomic family resulting from the literature search on the methods used to study crab movement

Fig. 3 The proportion of papers using each methodology applied to crab movement ecology used in this literature review. The 'decade' from 2020 to 2029 includes papers from only five full years (2020–2024)



This literature review retrieved a relatively low number of publications ($n=23$) specifically related to the spawning migration of Giant Mud Crabs. We identified that Alberts-Hubatsch et al. (2016) provided a crucial contribution with a thorough overview of the life history, movement and habitat use of Giant Mud Crabs. Therefore, our review focuses specifically on current knowledge of spawning migration and suggests methods to address the gaps.

Female Giant Mud Crabs are understood to migrate offshore to spawn, but the seaward movement might commence before eggs are fertilised during extrusion. The timing of initiating the seaward movement might be driven by physiological readiness and optimal conditions (Nathan et al., 2008). After mating, female Giant Mud Crabs can retain the sperm in their seminal receptacles for several months before fertilising the eggs (Hay, 2009). In eubrachyuran crabs, fertilisation happens internally when the eggs produced in the ovaries are transported through oviducts to the seminal receptacles, where fertilisation occurs (McLay & Becker, 2015). Hence, egg fertilisation might occur after females have left the estuary on their way to the spawning grounds, which could explain the difficulty of catching ovigerous females in estuaries. For brachyurans in general, factors like incubation period and fecundity are strongly correlated with body size (Crowley et al., 2019; Davis et al., 2004; Fratini et al., 2016). Therefore, the Giant Mud Crab has the longest incubation period (up to 30 days, depending on water temperature (Hamasaki, 2003) and produces the largest number and size of eggs and larvae among all *Scylla* species (Ates et al., 2012).

The triggers for ovigerous females to commence the spawning migration, and whether this is standard behaviour or is specific to some regions, remain uncertain, although some progress has been made since Alberts-Hubatsch et al. (2016) (e.g., see Hossain (2025). Ogawa et al. (2012) hypothesised that the offshore migration by large gravid females might even commence before the spawning season. A recent study has observed that environmental parameters, including temperature, salinity, pH, light and diet have a significant impact on moulting and reproductive success in female Giant Mud Crabs (Hossain, 2025). In the southern half of their Australian distribution (i.e., south of latitude 27°S), the spawning migration of female Giant Mud Crabs likely occurs during the rainy season, perhaps prompted by reduced temperatures and increased flow (Alberts-Hubatsch, 2015; Hewitt et al., 2022a). A reduction in salinity due to rainfall has also been hypothesised to trigger the females' spawning migration (Alberts-Hubatsch, 2015; Hewitt et al., 2022a). In other regions, such as the Philippines (Jumawan et al., 2021), the Persian Gulf and the Gulf of Oman (Rezaie-Atagholipour et al., 2013), and South Africa (Robertson & Kruger, 1994), the spawning season seems to vary throughout the year. It is unclear whether these variations are related to latitude (i.e., climate zones), increased flow and reduced salinity during the wet season, or increased water temperature during warmer months (Alberts-Hubatsch et al., 2016).

Once Giant Mud Crab eggs hatch, the planktonic zoea is assumed to drift under ocean advection (Charles et al., 2024; Hewitt et al., 2022b) while passing through five larval stages (Z1-Z5) over about 28 days, depending on environmental conditions (Baylon, 2010; Nurdiani & Zeng, 2007). As yet, there is no evidence of whether zoeae have swimming capabilities during this phase (Epifanio & Cohen, 2016), although megalopae have been observed to move vertically through the water column, stimulated by light, and use currents to reach the coast (Webley & Connolly, 2007). Megalopae are assumed to stay in coastal waters, but it is still unclear whether they metamorphose into crablets before entering the estuaries to settle (Webley et al., 2009), or the metamorphosis into the first instar occurs in estuarine waters (Alberts-Hubatsch et al., 2014). This is a general concept, but only the proportion of larvae that drift shorewards and reach inshore waters may successfully recruit (Charles et al., 2024).

During the zoeal stages, Giant Mud Crabs are stenohaline, strongly dependent upon the optimal salinity (between 25 ppt and 35 ppt) and temperature (between 26 °C and 32 °C) to survive and grow (Baylon, 2010). Since most estuaries are characterised by variable salinity and temperature, the larvae may not survive in this unstable environment (Alberts-Hubatsch et al., 2016). Even if the variability were not lethal, the larvae would expend considerable energy on osmoregulation (Baylon, 2010; Ruscoe et al., 2004), which could compromise growth and condition (Torres et al., 2011).

However, if the spawning migration of female Giant Mud Crabs is solely to seek adequate water quality conditions to release eggs and enhance larval survival, it may not always be necessary to move offshore. During the long dry season or when evaporation exceeds precipitation, the salinity and temperature conditions in some estuaries may be sufficiently stable for larval survival and development (Mattone et al., 2022; Wolanski, 1986). Hence, females could spawn in inshore or coastal waters in these situations without risking larval survivorship.

Notwithstanding the triggers for starting the seaward movement or some regional differences, the spawning migration might play a crucial role in the Giant Mud Crab's distribution, as this behavioural trait is a successful strategy for larval dispersal (Charles et al., 2024). Giant Mud Crabs are the most widespread species of the genus *Scylla* (Keenan et al., 1998), found in tropical, subtropical, and temperate regions throughout the Indo-West Pacific region. Genetic studies have hypothesised that, historically, the biogeographical spread of *S. serrata* originated in the western Pacific and rapidly expanded throughout the Indo-West Pacific during the late Pleistocene (Fratini et al., 2010; Gopurenko et al., 1999) (Fig. 4). Currently, their known natural distribution spans from latitudes 38°S to 34°N and longitudes between 23°W and 172°W, including the African east coast (Fondo & Ogutu, 2021; Rumisha et al., 2017), the Persian Gulf (Rezaie-Atagholipour et al., 2013) the Red Sea (Keenan et al., 1998), South and Southeast Asia (Hasan et al., 2021; Sayeed et al., 2021), and various Pacific nations

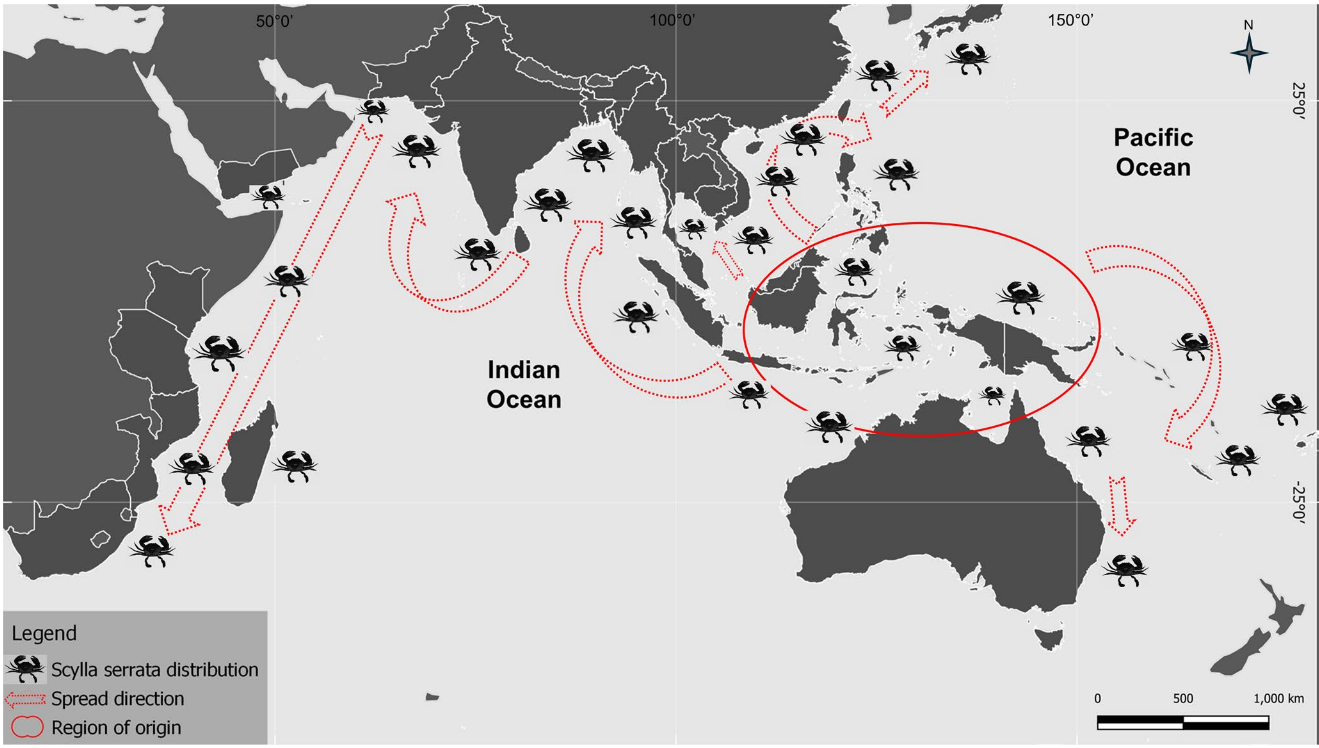


Fig. 4 Distribution of the Giant Mud Crab *Scylla serrata* throughout the Indo-Pacific region (compiled by the authors from published accounts) highlighting the species region of origin (solid red ellipse) and direction of the biogeographical spread (pointed arrows). This representation is based on the results of genetic studies carried out by Gopurenko et al. (1999) and Fratini et al. (2010)

(Dumas et al., 2012; Ewel, 2008). In Australia, Giant Mud Crabs occur from the northwestern coast of Western Australia through the Northern Territory, Queensland and the eastern coast of New South Wales (Flint et al., 2021; Kirke et al., 2023; Pillans et al., 2005; Robins et al., 2020). A particular subpopulation is more efficient in colonising distant areas if they move offshore to spawn rather than staying in inshore waters (Criales et al., 2019). As estuaries are enclosed areas with limited access to the sea, the offshore spawning migration would potentially enhance the chances of recruitment success, increase genetic diversity and widen the species range (Criales et al., 2019; Hill, 1994; Rudorff et al., 2009). The species ability to colonise is somewhat hinted at by its occurrence outside of its known distribution, either intentionally for aquaculture purposes (Hurley et al., 2021) or unintentionally as an invasive species (Lemaitre et al., 2013; Tavares & Mendonca, 2011).

Overall, the extensive species range, in addition to low genetic variability among most Indo-Pacific populations, suggests that the Giant Mud Crab has efficiently colonised different regions in a relatively short period (Fratini et al., 2010; Gopurenko et al., 1999). Due to the allometric relationship between body size and swimming capacity, larger females with more energy reserves could travel more efficiently (Florko et al., 2021). The distance travelled by females from their original estuary to the spawning sites might influence the extent of the larvae settlement areas, and their larval dispersal could be extended from a local to a regional scale, enhancing connectivity among populations (Charles et al., 2024; Criales et al., 2019; Hewitt et al., 2022b). However, migration efficiency and the maximum distance offshore would be limited by females' swimming ability and larvae's capacity to successfully return to shore, which otherwise might lead to in recruitment failure (Charles et al., 2024).

The distribution throughout tropical, subtropical and temperate zones also indicates a high level of plasticity to adapt to a wide range of environmental conditions (Gopurenko et al., 1999). Subtle genetic differences among distinct stocks are probably related to abiotic and biotic factors, but might also result from variations in exploitation intensity (Fratini et al., 2010). Other species of the genus *Scylla* do not appear to have the same level of adaptive plasticity, as none of them has successfully expanded their population to the same degree as *S. serrata* (Gopurenko et al., 1999; Keenan et al., 1998). This resilience and some of the biological characteristics of the species, such as fast growth (Hill, 1975; Jumawan et al., 2021) and high fertility (Paran et al., 2022), combined with adequate management strategies (Grubert et al., 2019), would be essential to recover intensively harvested or overexploited Giant Mud Crab stocks, mainly in developing countries (Bonine et al., 2008; Ewel, 2008;

Fratini et al., 2010; Jayamanna & Jinadasa, 1993; Rumisha et al., 2018).

However, the spawning migration of female Giant Mud Crabs may have some disadvantages, such as high energetic requirements to undertake the offshore movement (Cooke et al., 2006), the possibility of not returning to the original habitats (Bloor et al., 2013; Cooke et al., 2006), and greater vulnerability to predation (Boulêtreau et al., 2020; Hansen et al., 2020). Moreover, spawners may become predisposed to incidental capture (i.e., bycatch) if their spawning areas overlap sectors where fisheries targeting other species are operating (Biggs et al., 2021; Hill, 1994). The incidental capture of spawners can be detrimental both to recruitment and fisheries stock assessments, as bycatch data are often underreported and, therefore, rarely considered when estimating spawning stock biomass and mortality rates (Charles et al., 2020; Cook, 2019).

Knowledge Gaps on the Giant Mud Crab Spawning Migration

Ovigerous female Giant Mud Crabs have been assumed to actively use the prevalent ocean currents in their spawning migration strategy (Hewitt et al., 2022a; Patterson, 2020), similar to some marine invertebrates, including other crabs (Bloor et al., 2013; Carr et al., 2004; Forward & Cohen, 2004). This behaviour, known as selective tidal stream transport (STST), would conserve energy during the spawning migration (Forward & Tankersley, 2001) or could assist in orientation. The occasional use of STST to move short distances among adjacent areas for feeding in estuarine waters has been observed for Giant Mud Crabs (Alberts-Hubatsch, 2015; Heasman, 1980; Hewitt et al., 2023). However, the nature of the movement offshore (e.g., whether they mostly move by swimming or crawling on the seabed) and direction (i.e., if they strictly follow the current direction or use the current force but slightly change the direction using their swimming capabilities) are currently unknown.

Other uncertainties include the migration duration and distance travelled offshore before releasing eggs, the location of spawning grounds, and whether the females form aggregations to migrate and spawn (Davis et al., 2004), and whether specific environmental cues trigger spawning. Hill (1994) observed from trawl fisheries data that ovigerous females were recorded as bycatch up to 95 km from the coast, and the offshore distance varied among areas. However, as the dataset was obtained from incidental capture, female Giant Mud Crabs were found only in the sectors and seasons which the trawler fleet operated. Data from other areas and periods and specific information about the location of spawning grounds are still scarce.

Methods Applied to Track Ovigerous Female Giant Mud Crabs

Methods that have been applied to attempt to track the seaward movement of ovigerous female Giant Mud Crabs include mark-recapture (Hyland et al., 1984), acoustic telemetry (Alberts-Hubatsch, 2015; Hewitt et al., 2022a) and fishery data (Hill, 1994; Jumawan et al., 2021; Khaksari et al., 2023; Rezaie-Atagholipour et al., 2013). All rely on catching ovigerous females. However, Giant Mud Crabs are most often captured using baited traps, and ovigerous females are rarely caught by this method, which has been speculated to be because they cease feeding activity (Heasman et al., 1985; Heasman, 1980) either to maintain energy for ovarian development or to start a seaward spawning migration (Hewitt et al., 2022a). Similarly, ovigerous females of other crab species are rarely captured by baited fishing gears, which may be related to behavioural differences and reduced feeding activity compared to non-ovigerous females (e.g., Dungeness crabs, *Cancer magister* (Schultz et al., 1996; Swiney et al., 2003), Edible crabs, *Cancer pagurus* (Howard, 1982), Green crabs, *Carcinus maenas* (Young & Elliott, 2020) and Spanner crabs, *Ranina ranina* (Kennelly & Watkins, 1994). The usual behaviour of the female crabs might be so altered during late-stage ovary development that typical routine activities (e.g., foraging and feeding) might cease during the spawning migration to avoid predation, due to the higher exposure on the feeding grounds when searching for food, or save energy (Lima et al., 2021; Pittman & McAlpine, 2003). Hence, capturing gravid females for tagging is challenging (Ali et al., 2020).

Researchers have tried to overcome the difficulty of capturing ovigerous females and externally identifying if the eggs were fertilised by targeting mature and soft-shell females to tag (Alberts-Hubatsch, 2015; Hewitt et al., 2022a). However, soft-shell females do not necessarily move seaward immediately after mating. Instead, they may remain in the estuary whilst passing through the moult cycle stages (i.e., moving from a soft shell to a hardened carapace with no flexibility). During this period, females need to increase their food intake to develop their gonads (if it is the pubertal moult), obtain energy and fill their internal cavities with muscles while the new exoskeleton solidifies (McLay, 2015). Moreover, although sperm can usually be found in the seminal receptacle of most post-pubertal moult female Giant Mud Crabs, indicating successful insemination (Robertson & Kruger, 1994), female crabs can store sperm for many months before eggs are fertilised (Knuckey, 1999). So, tagging mature and soft-shell females might increase the likelihood of tracking inseminated females, but it is uncertain when they would commence the seaward migration. In addition, sometimes female mud crabs (*Scylla* spp.) may produce unviable eggs, mainly in the first maturity instar, and be unable to spawn (Robertson & Kruger, 1994). Hill (1994) found mostly ovigerous female Giant Mud Crabs offshore, but the author also reported some males and a substantial number of non-ovigerous females. Hill (1994) did not analyse the ovarian maturation stage to verify if the females caught offshore had fully mature or spent ovaries (Quinitio et al., 2007).

Suggested Methods to Investigate Giant Mud Crab Spawning Migration

Various techniques have been applied to address crab movements, depending on the species' biological and ecological traits (i.e., moult cycles, behaviour and geographic range). We observed that most methods used to study migration or movements, related or not to spawning, were applied to terrestrial or estuarine crab species that remain within a limited or well-defined territory. Data collection on the movement of these species is simpler than for migratory species, as the animals are more accessible for capture, handling, and observation. However, the oceanic stage of the Giant Mud Crab's life history constrains the use of some of those methods.

Hereafter, we discuss the techniques with the greatest potential to elucidate the outstanding questions regarding the spawning migration of Giant Mud Crabs. The techniques were categorised into direct and indirect methods. Direct methods rely on capturing females and using devices such as tags to track their movements. Indirect methods do not require the capture or contact with the breeding stock but are inferential rather than empirical. The selection of techniques considered the offshore movement of ovigerous female Giant Mud Crabs, oceanographic features and larvae behaviour (Table 2).

Direct Methods

Mark-Recapture Mark-recapture is a relatively inexpensive method to study the movement ecology of aquatic animals (Darnell & Kemberling, 2018; Engelbrecht et al., 2020; Simpson et al., 2020). The technique relies on identifying animals with a unique tag (e.g., numbered or colour-coded) and later recapturing the tagged individuals to estimate their movement patterns (Fazhan et al., 2022; Johnson & Eggleston, 2010). The low cost and simple application mean a large number of animals can potentially be tagged, making this one of the oldest and most widely utilised methods in ecological and fisheries research, including crabs (Medici et al., 2006). Besides movement ecology, mark-recapture can provide valuable data regarding other ecological aspects and fisheries, like population size, abundance and recruitment (Fazhan et al., 2022; Johnson & Eggleston, 2010; Semmler et al., 2021).

The disadvantages include the relatively low recapture rate of the tagged animals (Hill, 1975), accuracy is typically dependent on the capture and tagging of a reasonable proportion of the population, and the necessity for researchers to be frequently in the field to recapture the animals (Lee et al., 2014; Potter et al., 1991) unless the fishing community is highly engaged in reporting recaptures. These factors are particularly important for studies into commercially or recreationally harvested species, as information from fishers can increase the reporting rates (Semmler et al., 2021). As there is no direct fishing pressure offshore for mud crabs, mark-recapture would probably be more efficient for tracking the movement of gravid female Giant Mud Crabs that spawn in estuaries, semi-enclosed bays or near coastal waters, as there would be a greater likelihood of females to be recaptured either by fishing gears targeting mud crabs or as bycatch in coastal habitats than in offshore environments. For example, in a study conducted by Darnell and Kemberling (2018) in North Carolina, USA, the recapture rate of recently mated female blue crabs (*Callinectes sapidus*) was relatively high (17.5%-39.7%), compared with previous studies. However, two factors might have contributed to this outcome: (1) great fishing pressure in the study area combined with the high reporting rate from fishers, and (2) although female blue crabs also perform a seaward movement, their spawning grounds are near the estuary mouth or coastal areas.

To minimise the uncertainties of recapture and reduce the efforts, a combination of methods would be appropriate, including the application of citizen science and Traditional Ecological Knowledge (TEK) (Berkes, 2012). TEK comprises the long-standing knowledge and practices based on experiences that Indigenous groups and traditional communities have developed over generations (Berkes, 2012). Therefore, this important resource could even be used independently to elucidate aspects of Giant Mud Crabs spawning migration, as traditional knowledge can generally provide valuable information about the biology and ecology of many species (Charles, 2022; Nirmale et al., 2012).

In this context, Indigenous groups, artisanal and commercial fishers, either targeting the tagged species or catching them as bycatch, can play an important role (Darnell & Kemberling, 2018). Hill (1994) obtained data from prawn trawlers to study the spawning migration of Giant Mud Crabs in the Northern Territory, Australia. Although the author applied questionnaires to interview skippers instead of mark-recapture, this example illustrates the importance of cooperation of commercial fishers for data collection in remote areas. Otherwise, successful mark-recapture

Table 2 Summary of the current knowledge gaps on the Giant Mud Crab spawning migration, explaining the rationale behind the process of selection of techniques that might be applied, based on each particular phase during a spawning event

Knowledge gap	Phase	Technique	Selection rationale	Drawbacks
Triggers to initiate migration	Seaward movement	Acoustic telemetry	Enclosed waters in estuaries and the use of data-loggers for environmental parameters	-
Migratory routes and direction	Offshore movement	Acoustic telemetry	Possible tracking with an array of receivers offshore	Expensive infrastructure. Need a large array of gates offshore. Otherwise, tagged animals may remain undetected
		Pop-up satellite tags	Fine-scale tracking (if tag recovered) or estimate tracking (if tag not recovered) and environmental parameters	-
STST[1] and vertical movement	Offshore movement	Pop-up satellite tags	Fine-scale tracking (if tag recovered) and comparison with ocean current direction and velocity. Pressure sensor provides depth variation	-
Body size x Spawning distance	Offshore movement	Acoustic telemetry	Possible tracking with an array of receivers setting boundaries offshore	Expensive infrastructure. Need a large array of gates offshore. Otherwise, tagged animals may remain undetected
		Mark-recapture	Analysis of gonadal maturation, body size and relationship with distance offshore	Relies upon the interaction of crabs with offshore fisheries and support of stakeholders for the collection of individuals
Characteristics of the spawning grounds	Spawning (i.e., egg extrusion)	Acoustic telemetry; Mark-recapture	Once the spawning grounds are defined, characteristics like bathymetry, water parameters, and other conditions may be determined	Determination of the precise timing of the spawning event is unlikely.
Triggers for egg extrusion	Spawning (i.e., egg extrusion)	Mesocosm experiments	As determining the exact moment of egg extrusion is difficult, experiments in a controlled environment would be more appropriate	Capture of ovigerous females using standard methods is not common
Multiple vs. single spawning events				Crab health deteriorates after a few months in captivity
Difference in regional patterns and spatio-temporal variation in spawning behaviour	All phases	Comparison of studies across the species distribution	Meta-analysis of spatial and temporal variation	Standardisation among studies across the species distribution may be difficult
Spawning inshore or in coastal waters	Spawning (i.e., egg extrusion)	Zooplankton surveys	High abundance of zoeal stages in estuaries and coastal waters may indicate recent localised spawning activity	May need to be combined with genetic analysis for accurate identification of *Scylla serrata* zoea
		Acoustic telemetry	Multiple detections over a predicted period in coastal areas after leaving the estuary	Determination of the precise timing of the spawning event is unlikely.

programs using citizen science to help track crustaceans typically rely on a range of incentives to the public and have a considerable amount of investments that allow the programs to be continuous over the years, such as the Florida Horseshoe Crab Watch program, in the United States (Heres et al., 2021).

Acoustic Telemetry Acoustic telemetry is a powerful tool for tracking movements, including larger migrations of marine animals in coastal and continental shelf ecosystems (Barnett et al., 2024; Matley et al., 2022). It is the most frequently used telemetry tool for investigating crustacean movements to date (Florko et al., 2021). Animals fitted with acoustic transmitters can be tracked actively or passively (Barnett et al., 2010; Crossin et al., 2017; Heupel et al., 2006). For the active method, a mobile receiver is installed on a boat to follow the animal's movement. The active method is typically labour-intensive and time-consuming; therefore, it is mostly used for short-period tracking, for known migration paths that need to be confirmed or for planning a passive receiver array design. Hence, we considered the active method unsuitable for tracking ovigerous female mud crabs at sea. For the passive method, the ability to detect tagged individuals is dependent on the detection range of receivers (typically between ~60 and 950 m), which is affected by environmental and physical variables and by the design of the receiver array, e.g. number, location and configuration of receivers deployed (Barnett et al., 2024; Hoenner et al., 2018). This technology has been utilised to study the spawning migration of several portunid species (Carr et al., 2004; Eggleston et al., 2015; Florko et al., 2021), including Giant Mud Crabs (Alberts-Hubatsch, 2015; Hewitt et al., 2022a).

Some elements need to be taken into account when applying this technique in crab research. As a general guideline for animal research using tagging methods, the tag weight should be considered according to the body weight to minimise the impact on the animal's behaviour (known as "tag burden") (Smircich & Kelly, 2014). However, tag burden may vary between species, and more research is still needed, particularly for decapod crustaceans (Florko et al., 2021). Tag loss due to ecdysis is an unavoidable limitation, as the acoustic tags are usually attached to the external carapace. Moreover, the detection of migrating female Giant Mud Crabs in the open ocean is challenging. Given the difficulty in the continuous tracking of tagged individuals in the open ocean (Freire & González-Gurriarán, 1998), a study aiming to understand the offshore migration would require an extensive offshore receiver coverage to ensure a reasonable probability of obtaining meaningful results (Ledee et al., 2021). An example of a large acoustic receiver array is the one permanently installed along the Australian coast and managed by Australia's Integrated Marine Observing System Animal Tracking Facility (IMOS ATF - https://animaltracking.aodn.org.au) in partnership with several stakeholders (Hoenner et al., 2018). Hence, if tagged ovigerous female Giant Mud Crabs passed within the detection range of any IMOS receiver, they would be detected. However, although the array has improved in recent years (a 57% increase with 327 receivers in Queensland), the area with receiver coverage is still small in relation to the area to be covered (spanning 2,100 km from the border with New South Wales to the Far North Queensland) (Barnett et al., 2024). Therefore, the probability of a tagged migrating female being detected offshore is relatively low, given the vast area of Australia's waters that migrating crabs might move within.

Nevertheless, the method can provide useful information for conservation and stocks management (Crossin et al., 2017). Of 89 female Giant Mud Crabs tagged in two estuaries in northern New South Wales, 47 were detected at the mouth of the estuary, and 14 were detected in oceanic waters (Hewitt et al., 2022a). Once female Giant Mud Crabs left the estuary, they were detected at distances between 23 and 69 km north of the estuaries, suggesting a northward migration (Hewitt et al., 2022a). The results provided by Hewitt et al. (2022a) give some important but still limited insight into their offshore spawning migration. Also highlights that with enough resources and an appropriately designed receiver array to target possible offshore migration routes, acoustic tracking has the potential to help better understand mud crab migrations and find essential spawning habitats.

Pop-up Satellite Archival Tags (PSAT) Pop-up satellite archival tags (PSATs) have recently been applied to study the movement ecology of crustaceans. Depending on the studied species, PSATs are externally attached to the animal's body using a tether and different anchoring methods. The tether releases after a pre-programmed time, allowing the positively buoyant tag to reach the surface and transmit locational and environmental data via satellite (Musyl et al., 2011; Renshaw et al., 2023; Whitford & Klimley, 2019).

Several inherent limitations will likely prevent the migration from being clearly answered. Tag and data transmission failure and premature tag release have been reported as common issues (Musyl et al., 2011; Renshaw et al., 2023). When tags are not physically recovered and, consequently, the raw data is not obtained, position accuracy is dependent on factors like the satellite location accuracy and the interval between the tag reaching the surface and the satellite receiving the data transmission. If the conditions are not ideal (e.g., inconstant animal surfacing and rough weather or oceanic conditions), the position provided by PSATs can have errors exceeding 1.5 km (Green et al., 2021). Furthermore, the reconstruction of the animal track might have a substantial error radius, as light-based geolocation is used to estimate the track. Hence, although this technique may provide crucial information (e.g., movement direction, temperature and depth data; Davidson and Hussey (2019); Renshaw et al. (2023), the relatively low position accuracy might be detrimental for pinpointing precise locations, especially if the animal does not perform large-scale movements (Hussey et al., 2018).

The literature review found two published studies that utilised this technique to analyse crab movements (Davidson & Hussey, 2019; Green et al., 2021). Davidson and Hussey (2019) successfully monitored the movement behaviour of porcupine crabs (*Neolithodes grimaldii*) in deep waters of the Eastern Canadian Arctic between five and 89 days using a combination of mark report pop-up archival tags (mrPATs) and miniPATs. Green et al. (2021) obtained crucial movement data of giant spider crabs (*Leptomithrax gaimardii*) in Victoria, Australia, tracking the crabs from one to 77 days using mrPATs. In both studies, a harness method was applied to attach the tags. Both studies experienced some technical difficulties. Green et al. (2021) reported that eight of 15 tags were released at the programmed time, four tags were released prematurely, and data of three tags were unavailable, while in Davidson and Hussey (2019) study, six of 18 tags were released at the programmed time, 11 released prematurely and data of one tag was unavailable. The average drift error was 4.6 km (including vertical and horizontal drift). The prematurely released tags successfully obtained data in both studies, but this factor might have led to misinterpretation of the animal's behaviour (Davidson & Hussey, 2019). The authors suggested that tag failure, moulting, issues related to the attachment method, and the modified crab pot might be the main causes of premature release of tags (Davidson & Hussey, 2019).

PSATs may allow researchers to address some questions regarding the Giant Mud Crab spawning migrations. For example, it might be possible to determine the movement direction and the location of spawning grounds of tagged ovigerous females. Depth (pressure) and temperature logging by PSATs may help to elucidate behaviour during migration, such as whether ovigerous female crabs use STST to move towards the spawning location or when in offshore waters or if there is vertical movement through the water column that is related to light. However, data is binned, and fine-scale data is only available if the tag can be retrieved. Anecdotal reports of crabs swimming at the surface in oceanic waters might indicate that other satellite tag models could be used, but more research is needed to confirm viability.

There are, however, some practical barriers to the use of PSATs for biological studies on Giant Mud Crabs. Firstly, the best time-until-release to program into the tag is difficult to determine because the tags return a single location after release. The egg incubation period of approximately 15 days (Hamasaki, 2003) provides an estimate of the likely migration duration, meaning that pop-off could occur before or after the spawning, even if a known gravid female Giant Mud Crab is tagged. As a result, it may take a considerable number of tags to develop an accurate picture of the migration, which may be limited by the relatively high expense and non-reusability of PSATs (Musyl et al., 2011) unless they can be recovered. Secondly, it is unknown whether the tag could interfere with the normal behaviour of the tagged crab, such as a change in the swimming ability (Fisher et al., 2017). Recent improvements in technology, which reduced the PSAT's size and weight, are promising for the utilisation in smaller-bodied animals like mud crabs, as the application of this technology must always consider minimising the tag burden. The paucity of ovigerous females caught in estuaries, and their recorded interaction with other fisheries as bycatch (Hill, 1994), and the possibility for entanglement in their mangrove-lined habitat means the ovigerous females to be tagged should ideally be caught and released near the estuary mouth.

Indirect Methods

Particle Tracking Simulation Particle tracking simulations have been used to estimate connectivity via larval dispersal for several crustaceans and to infer the potential movement of ovigerous female portunids towards their spawning grounds (Charles et al., 2024; Criales et al., 2019; Hewitt et al., 2022b; Patterson, 2020; Rudorff et al., 2009). Our review identified seven publications that used this technique to respond to research questions regarding the spawning migration of crab species. Most studies were related to larval supply, recruitment, dispersal and connectivity, with the major limitation being that the results are model estimates, allowing inferences that could be strengthened by empirical validation of some form.

This technique is relatively inexpensive and versatile, as it can be applied to investigate various ecological questions, including, for example, the probability of Giant Mud Crab larval settlement as a function of the offshore spawning distance and its associated value for self-recruitment or connectivity among different populations (Charles et al., 2024). However, as some parts of the Giant Mud Crab life history are still poorly understood, one limitation of simulations is the difficulty of precisely incorporating the species behaviour into the model due to the limited information available. Previous studies used particle tracking simulations to investigate the Giant Mud Crab spawning migrations or offshore movement (Hewitt et al., 2022b; Meynecke & Richards, 2014; Patterson, 2020; Patterson et al., 2023). These studies assumed that ovigerous female Giant Mud Crabs strictly follow the direction of flow, either passively (Hewitt et al., 2022b; Patterson, 2020) or actively (Patterson, 2020). New investigations could add different scenarios in which females use STST (Carr et al., 2004; Forward & Cohen, 2004) together with some change in the vector direction caused by active swimming (Forward & Tankersley, 2001) or wind during the periods when females reach the surface, therefore potentially expanding the distribution areas.

In addition, research into the larval distribution along the coast, larvae supply, and larval behaviour would be advantageous in validating the simulations. For example, a time series of larval distribution would be important to assess where larvae successfully recruited to and from mud crab habitats. This information could be used to populate the model and to compare with the catch rates for a given year, allowing researchers to determine whether the below or above catch rates of mud crabs would be from larval drift or habitat quality linked to the estuarine conditions post-metamorphosis into crablets.

Zooplankton Surveys Given the challenges of tracking the adult egg-carrying females, an alternative would be to attempt to track the Giant Mud Crab larvae after spawning. In this way, zooplankton surveys are another possible technique to gather data about the spawning migration of Giant Mud Crabs. The understanding is that areas where females had recently spawned would have a higher abundance of the first stage of zoea larva (Z1) than the surroundings (Eaton et al., 2003). This abundance would decrease in samples collected further from these sectors towards the shoreline, and, at some point, the samples would contain only subsequent zoeal phases (i.e., Z2, Z3, Z4, Z5) (Eaton et al., 2003; Paran et al., 2022). Nevertheless, two main issues would need to be solved. Firstly, the wide study area due to the potential larvae drift from the spawning grounds would be a considerable limitation. Secondly, there are difficulties in accurately distinguishing the early-stage Giant Mud Crab larvae from other decapods, although morphological differences have been specifically observed in zoea (Z1) among distinct *Scylla* species (Ates et al., 2012). Advances in molecular analysis provide one potential solution to rapidly identify individual species in zooplankton samples, though not to stage the larvae (Machida et al., 2009).

The very low concentrations of the larval stages mean that surveys to detect them would necessarily be sizeable unless the surveys are conducted in enclosed bodies of water or relatively well-known spawning grounds. However, such surveys exist. For example, regular plankton surveys are undertaken in some countries [e.g., the Australian Plankton Survey – Integrated Marine Observing System (IMOS) - https://imos.org.au/facilities/shipsofopportunity/auscontinuousplanktonrecorder], covering large stretches of the coastal ocean. They may potentially uncover concentrations of Giant Mud Crab larvae serendipitously. A significant challenge is the vast oceanic area in which Giant Mud Crab larvae might be located (Charles et al., 2024). If it was possible to refine the possible spawning grounds and timing through other methods, then more focused plankton surveys could prove effective at finding Giant Mud Crab larvae stages. If the larvae could be located at sea and their stage of development accurately determined, then particle tracking simulations could be used to backtrack to the likely site of egg release (Charles et al., 2024). While applying this method might seem unfeasible in ocean waters, it could be effective in near coastal waters or in investigating spawning events in bays and estuaries.

Conclusions

The oceanic life-history stage of the Giant Mud Crab remains the most elusive part of its life. The difficulty of tracking ovigerous females during the spawning migration is a significant constraint to understanding this behavioural trait and the subsequent chain of events. There are two setbacks to overcome: (1) the difficulty in obtaining ovigerous female Giant Mud Crabs, and (2) the selection of the most appropriate tracking method to be applied. Indirect approaches like numerical modelling and zooplankton surveys might help provide multiple lines of evidence on several questions regarding the spawning migration of Giant Mud Crabs. However, they also have limitations, such as the unknown behaviour of larvae during the planktonic phase (zoea).

We reviewed the spectrum of approaches that can be used to monitor the seaward spawning migration of Giant Mud Crabs, a problem that has evaded resolution to date. Each method has strengths and weaknesses. Hence, deciding which method to apply depends on the specific research objectives and logistical constraints, including budget. The continuous advancement of animal tracking technology has widened the possibilities. Smaller electronic tags (e.g., PSATs and acoustic transmitters) allow the application of these devices in smaller-sized animals, and the large networks of acoustic receivers increase the detection range for animals tagged with acoustic transmitters. Adding more acoustic receivers in strategic migratory corridors could fill some gaps in the coverage area. Under certain conditions, combining methods through multiple lines of evidence is likely the most appropriate option and may lead to more consistent outcomes. For example, electronic transmitter (PSAT and/or acoustic tags) deployment on females in combination with numerical modelling of larval dispersal might be used to estimate the most likely spawning areas, and systematic zooplankton surveys could then be conducted in these areas to confirm their viability as spawning grounds.

As the deployment of baited crab pots targeting Giant Mud Crabs in estuaries seems to be ineffective for capturing ovigerous females, other alternatives might be attempted, like placing the crab pots in different habitats, identifying mature females that are not yet ovigerous but are likely to be soon, using other fishing gears to capture the female crabs on the way out of the estuary, or finding stakeholders who can potentially catch them at sea (e.g., commercial prawn trawlers or net fishers). Then, the ovigerous females could be tagged and released immediately to continue their journey towards the spawning grounds, removing some of the uncertainty associated with tag deployment.

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Declarations

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