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# Habitat partitioning in Moreton Bay bug species to inform fisheries management

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ABSTRACT

Habitat preferences influence partitioning in many marine taxa that can inform fisheries management. Despite this, little is known about how habitat partitioning contributes to spatial distributions in many commercially important species. This study aims to investigate habitat partitioning and influential variables affecting the distribution in Moreton Bay bug species *Thenus parindicus* and *Thenus australiensis* for the benefit of management on the east coast of Queensland, Australia. These Scyllarid lobsters spend much of their lives buried within sediment, but little research focuses on what influences the distribution of each species. In this study, a fishery-independent survey was conducted in a key commercial trawling area off the coast of Townsville to determine *Thenus* species distributions and habitat preferences. Variables used to examine the habitat preferences and distributions of both species included depth, sediment grain size, Trask sorting coefficient and calcium carbonate content. We found that all variables evaluated significantly affected species distributions. Multivariate analyses suggest that Trask sediment sorting coefficient and depth were the strongest influential variables. This contrasts with previous findings that mean grain size is the most important sediment parameter influencing *Thenus* distributions. The results indicate habitat partitioning between *T. parindicus* and *T. australiensis* but not habitat exclusion. These findings, along with the likely influential variables of species' distributions will help better understand the habitat ecology of these lobsters and inform management for the Moreton Bay bug fishery.

## 1. Introduction

Understanding distributions and habitat preferences of fished species is imperative for successfully managing fisheries. For this reason, fisheries management plans should incorporate any available habitat information (Fluharty, 2000). An awareness of differences in the ecology and population dynamics of closely related fished species is critical in predicting how these populations will respond to fishing pressure. Previous research in marine taxa has shown that habitat and population dynamics are intrinsically linked, therefore understanding how closely related species' habitats diverge may provide useful insight into long-term fishery sustainability (Hayes et al., 1996). Gathering information on where species live and their behavior is the first component of understanding spatial distributions. Moreover, determining the habitat features influencing species' distributions can provide information about how organisms relate to their surroundings.

In Australia, Moreton Bay bugs are considered a seafood delicacy in increasing demand. Harvested mainly along the east coast of Queensland, little is known about their habitat partitioning and species distribution. Moreton Bay bug, or "bay lobster," is the common name for *Thenus* spp. in Australia, which comprises both *Thenus australiensis* and *Thenus parindicus* (Burton and Davie, 2007). It should be noted that before this genus was revised in 2007, these species were referred to as *Thenus orientalis* and *Thenus indicus,* respectively. In Australia, they are found from the east coast near northern New South Wales, up through the Northern Territory and down to Shark Bay in Western Australia (George and Griffin, 1972; Holthuis, 1991). Within this distribution, Moreton Bay bugs occupy sandy substrates between coral reefs and soft inshore mud/sand flats (Jones, 2007). Both species of *Thenus* demonstrate a distribution that is aggregated and non-random. Other groups of lobsters, such as Palinurids, also display local non-random distributions (Herrnkind et al., 1975; Goñi et al., 2001; Negrete-Soto et al., 2002; Butler, 2003; Jones, 2007). This pattern has not been found to be caused by migrations or collective spawning behavior; therefore, it is likely

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driven by either the distribution of preferred habitat, trophic dynamics, or other biological components (Jones, 2007). Much like other lobster groups, *T. australiensis* displays a uniform distribution across all seasons (Lyons et al., 1981; Jones, 1988; Spanier and Lavalli, 1988).

In Queensland, the Fisheries Act of 1994 includes requirements for strict protection of fish habitat driven by the need to understand target species distributions (Lynch, 1995). *Thenus* spp. are nocturnal predators with peaks of activity around dusk and dawn. During the day, bay lobsters bury themselves in sediment (Jones, 2007). Due to this behavior, commercial fishers have had greater success landing *Thenus* spp. during their active phase at night. Little is known about the population dynamics and life histories of Moreton Bay bugs, but the limited evidence suggests these species are distinct beyond just morphology. *T. parindicus* has a faster growth rate (Courtney, 1997), and is typically smaller with a shorter life expectancy (2–4 years) thought to be approximately half that of *T. australiensis* (4–8 years) (Jones, 2007). *T. parindicus* has an estimated mean fecundity of 12,455 eggs compared to *T. australiensis* with 32,230 eggs (Jones, 2007). These differences suggest that these species will likely have different responses to fishing pressure.

In Australia, Moreton Bay bug fisheries collectively report approximately 600 tonnes annually with almost 90% of catch originating in Queensland. Valued around $25 per kilogram, Queensland fisheries annually contribute approximately 13.5 of the 15-million-dollar national catch value (Roelofs et al., 2021). Based on this contribution and increase in targeting, it is critical to understand the ecology of Moreton Bay bugs for better stock assessments of this fishery in Queensland.

Fisheries logbook records indicate that the Townsville region and the Gladstone-Fraser Island region each contribute about 40% of the total *Thenus* catch for Queensland, and approximately 35% of landings in Australia (Queensland Department of Agriculture and Fisheries (DAF), unpublished data; Roelofs et al., 2021). The area off Townsville between the coast and the Great Barrier Reef consists of extensive mud and sand flats, interspersed coral reefs and islands, and extensive reef flats, providing a large variety of habitats (Browne et al., 2010). This region is also heavily trawled, providing a long history of logbook records of *Thenus* catch as well as other benthic species (Courtney, 2002; Courtney et al., 2007). Currently, stock assessments based on these logbook data indicate that stock is stable (Roelofs et al., 2021). However, these records do not differentiate between *Thenus* species, limiting the accuracy of catch rate estimations critical for true stock assessments of each species. Without separation of species, it is possible one species' vulnerability to fishing pressure is being masked. Recent increase in targeted fishing for *Thenus* spp. has highlighted the need for greater management focus on species differentiation to accurately assess long term trends in catch rates and abundance for each species.

As tag-recapture data indicate negligible overall movement by juvenile and adult *Thenus* spp., they are unlikely to leave preferred habitats (Jones, 2007; Courtney, 1997; unpublished data). Combining information on habitat partitioning and preferences with high resolution spatial catch reporting data may provide a means to differentiate the species in logbook records based on their likely spatial distributions. This could improve the accuracy of catch rate trends used as abundance indices for each species, stock assessment and management.

Despite the recent increase in market demand, little published work explores how Moreton Bay bugs use their habitat. The few studies that have been conducted suggest that substrate grain size and water depth are the two major factors separating habitats of *T. parindicus* and *T. australiensis*. Based on aquarium experiments and field studies in northern Australia, Jones reported the smaller of the two species, *T. parindicus*, is found in shallow waters ranging from depths of 10–30 m on silt and sand flats. The larger species, *T. australiensis* inhabits inter-reef flats of coarser sand ranging in depths between 30–60 m (Jones, 1988, 1993, 2007). No evidence of overlapping ranges has been previously documented. In Jones (1988) aquarium experiments, he presented a variety of sediment sizes to each species and noted a clear preference of *T. parindicus* for sediments finer than 0.063 mm (coarse silt to clay) and a preference of *T. australiensis* for sediments of moderate to coarse size sands (>0.063 to 2 mm) (Jones, 1988). These findings, coupled with local fishing insights, identify *T. australiensis* as "reef bugs" located in sandy areas farther offshore near the Great Barrier Reef, distinct from "mud bugs" (*T. parindicus*) believed to favor shallower inshore mudflats.

The aim of this study is to a) assess habitat partitioning between the two Moreton Bay bug species in the Townsville trawling area, and b) determine environmental factors influencing species' distributions and any habitat partitioning. These findings may enable more accurate catch rate time series which can be used as proxies of abundance for management of the *Thenus* spp. fishery. To achieve these objectives, a fishery-independent survey was conducted in the Townsville Moreton Bay bug fishery in which biological data (species, sex, size) and habitat data (bathymetry, bottom sediment samples) were collected. Univariate and multivariate analyses of the sediment physical properties and lobster catch data were undertaken to examine habitat partitioning and species' distributions.

## 2. Methods

### 2.1. Data collection

A 14-day fishery-independent survey of the trawled fishing grounds adjacent to Townsville was performed to collect direct observations of species densities and co-located sediment properties using a stratified random sampling design. The survey area extended from Bowen to Hinchinbrook Island in the inshore areas of the Great Barrier Reef Marine Park (GBRMP) (Fig. 1). A total of 140 sites were randomly distributed among strata that were based on 30-minute logbook reporting grids. The number of sites allocated to each stratum was calculated based on the product of each stratum area and commercial logbook data catch per unit effort (CPUE) in that stratum over the preceding 20 years (since satellite vessel tracking was introduced) as a proportion of the total for the entire survey area. Larger strata with greater CPUE therefore received a greater proportion of the total pool of sites. Sites with small area and low CPUE that did not meet a threshold of minimum sampling effort were allocated three sites to avoid undersampling (representing 2% of sampling effort; Dichmont et al., 2000). The survey took place from 20 July – 4 August 2021, over the period of the full moon when bugs exhibit elevated catchability, aboard a chartered trawl vessel, the FV Murchison. Survey trawls were conducted between 5:00 pm and 7:30 am each night in accordance with commercial trawling regulations. Sites in the survey ranged from 14–59 m in depth. Due to adverse weather and gear issues, 10 of the 140 sites were unable to be sampled.

Upon arrival at each site the vessel stopped, and a sediment sample was taken using a 5 kg sediment grab. At sites with greater depths, strong winds, and currents an 8 kg sediment grab was used. The grab was lowered to the seafloor and deployed to extract up to 500 g of sediment. A subsample of up to 200 g was bagged and labelled before being preserved in a freezer onboard. Next, the vessel reorientated and undertook a one-nautical mile bottom trawl over the site. Four identical nets with 2.25-inch mesh sizes and five-fathom head rope length were deployed with otter boards, two from each outrigger boom. Nets were equipped with turtle exclusion devices and bycatch reduction devices. Upon completion of the transect, the catch was sorted on the tray and *Thenus* spp. were set aside. Species and sex were identified for each individual, and carapace length was recorded. This sequence was repeated at each of the 130 sites.

### 2.2. Sediment processing

After completion of the survey, sediments were processed in a laboratory to determine grain size and carbonate content. To measure mean grain size of a sample, we conducted a wet sieving process that most effectively disaggregates the mud fraction of the sample, and secondly

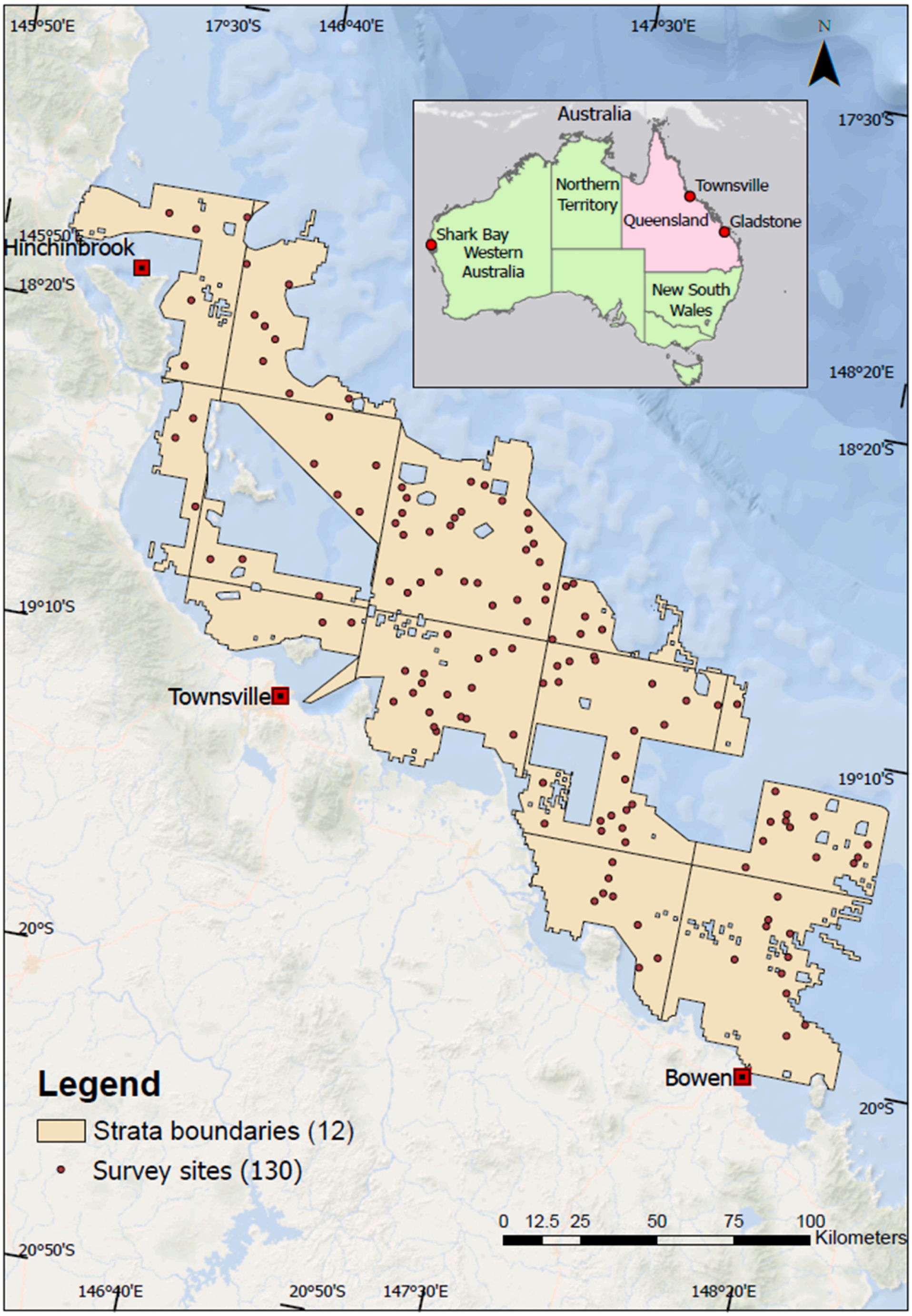


**Fig. 1.** Map of the fishery-independent survey of *Thenus* species off Townsville beginning in July 2021. The sites were randomly distributed within 12 strata with number of sites allocated based on strata area and CPUE.

dry sieved the course fraction of the sample into eight grain size classes based on protocols outlined by Folk (1980). To wet sieve, samples were prepared with 5% Calgon (Sodium Hexa-Metaphosphate) solution, then wet sieved through a 63-micron mesh sieve. This mud fraction was diluted, mixed, and three subsamples of 100 ml were removed and dried in an oven at 80 degrees Celsius. The dry weight was used to determine the mud weight of each sample after applying a Calgon and volume correction factor. The remaining coarse fraction was dried and sieved through 63, 125, 250, 500, 1000, 2000, 4000, and 8000-micron mesh sieves shaken for ten minutes at 60 amps on an electromechanic sieve shaker. The weight of sediment in each sieve was recorded and used to determine the proportion of sample weight that was gravel (2000–8000-micron sieves) and sand (63–1000-micron sieves). The sediment remaining in the pan under the 63-micron sieve did not separate in the wet sieving process and was added to the mud weight from the wet sieve to get total mud weight. In this study, the mean grainsize of a sample refers to the value determined by the G2Sd package in R statistical platform (v.4.1.1) (R Core Team, 2021) using the weight of each sediment grainsize class relative to the total sample weight and the sediment grainsize classes present in that sample. This mean grain-size value provides an approximation accepted as standard practice where it is impractical to measure all grains in a sample individually. These values fell into Wentworth grain size classifications of mud, sand, or gravel, and can be further classified within these.

Calcium carbonate content was determined by acid digestion. Approximately 5–10 g of each original sediment sample was removed and dried in an oven at 80 degrees Celsius. Dry weight was recorded, and the sediment was treated with ten percent hydrochloric acid solution. Then samples were rinsed with distilled water and dried again. Dry weight was recorded and subtracted from original dry weight to determine the percentage of calcium carbonate.

### 2.3. Grain size distribution analyses

The weights of each grain size class for each sediment sample were analyzed using the G2Sd package in R. The output provided arithmetic and geometric mean grain size, the distribution of grain size, standard deviations, the Trask sorting coefficient (a measure of sediment grain size sorting), sediment type descriptions, texture, and other parameters that describe each sediment sample. A principal component analysis of variance was conducted using the R package Vegan (Dixon, 2003) on each sediment sample using Wentworth classifications, arithmetic mean grain size, and Trask sorting coefficient to determine the relationship of each sample to each other and the causes of variance among the parameters. Matrix scatterplots were used to visualize linearity. Normalized data was transformed to remove scales of different variables. Other assumptions of PCA were met in that the sediment variables were continuous and presented linear relationships. For seven out of 130 sites, calcium carbonate content was not determined as these samples were collected from depths exceeding 50 m during periods of intense wave action, resulting in inadequate sediment volume to effectively undergo acid digestion. These sites were therefore omitted from multivariate analyses.

### 2.4. Assessment of habitat partitioning

Maps of species distribution by site were made in ArcGIS Pro. The lobster catch rate data at each site (X/nautical mile) were considered as an index of relative abundance. Associations between the sedimentary variables, depth and lobster relative abundance were then examined to investigate differences in species' distributions. Depth and mean grain size were assessed based on Jones (2007, 1988) report that these parameters are the primary influential variables of habitat partitioning of these species. A two-factor ANOVA and a frequency analysis were used to test differences in abundance associated with mean grain size and Trask sorting coefficient between species and depth. Assumptions of normality and homogeneity of variance were checked by Levene's tests and residual plots. The abundance data were square root transformed to better meet the assumptions of ANOVA. Frequency analyses were also used to evaluate differences between the species' distributions across mean grain size by Wentworth classifications, calcium carbonate content, and Trask sorting coefficient. Sediment sorting is how similar the grain size of particles of a sample are, or the frequency distribution of grains across size classes calculated using the Trask method. The assumptions of Pearson's chi square tests were met as the data assessed were count data for each species and the categories used for assessment were mutually exclusive.

Canonical analyses of principle coordinates (CAP, Anderson and Willis, 2003) were performed in order to evaluate dissimilarity of individual bugs of the two species across habitat factors. CAP was performed using the R package BiodiversityR (Kindt and Coe, 2005) and included distance-based redundancy analyses as designed by Legendre and Anderson (1999).

## 3. Results

### 3.1. Sedimentology of the Townsville region

A total of 1.5% of samples had a mean grain size classification of mud, 82.3% of samples were sand, and 16.2% of samples were gravel. Sediment mean grain size ranged from 53.6 + /- 151.3 μm (SD) to 2898.5 + /- 3761.6 μm across the 130 sediment samples. Most samples were dominated by coarse sand. The overall average mean grain size fell into the coarse sand fraction for approximately 69 of 130 samples (53%).

The mean Trask sorting coefficient was 2.5 ∅ units. According to the classifications set forth by Trask (1930) values $< 2.5$ are well sorted, 2.5–4.5 are normally sorted, and $> 4.5$ are poorly sorted (Friedman, 1962). Approximately half of the samples were well-sorted, ~40% normally sorted, and ~10% poorly sorted. Sediment samples from nearshore areas had an average calcium carbonate percentage of 28% (Fig. 2. A). Most of the nearshore samples tended to be poorly sorted fine sand or mud (Fig. 2. B). Offshore samples had an average calcium carbonate percentage of 45% (Fig. 2. A). Sediment samples in this region were a mix of mostly coarse sand, well to normally sorted (Fig. 2. B).

The principal component analysis illustrated a distinct separation of samples by mean grain size to Trask sorting coefficient on PC2 and by Trask sorting coefficient to depth and calcium carbonate content on PC1 (Fig. 3). PC1 and PC2 accounted for 65.22% of the total variance among samples (Fig. 3). Larger mean grain size groups of coarse and very coarse sand showed distinct banded clustering. Smaller mean grain size samples were not so strongly clustered. Trask sorting coefficient held a loading value of 0.71 for PC2 and mean grain size held a loading value of − 0.62, indicating these factors explained PC2 independent of depth and calcium carbonate content. Calcium carbonate content and depth held PC1 loading values of 0.65 and 0.69 respectively (Fig. 3).

### 3.2. Species' distributions in the Townsville region

A total of 1215 bugs were sampled during the 14-day survey period. Of these, 792 were *T. australiensis* and 423 were *T. parindicus*. *Thenus australiensis* were found exclusively at 73 of 130 sites. These sites were predominantly offshore. *Thenus parindiucus* were found exclusively at 19 sites near the coastline. Both species were co-located at 32 sites towards the center of the survey area, and neither species were found at six sites (Fig. 4).

Individuals were sampled at water depths between 14 and 59 m. *Thenus parindicus* was distributed in shallower depths compared to *T. australiensis* (Fig. 5). Almost all *T. parindicus* were found between 10–30 m with a mean depth of 23.4 m (+/- 1.50 SE). The majority of *T. australiensis* were recorded at depths between 30–55 m, with a mean depth of 39 m (+/- 1.07 SE). The interaction of depth and species abundance was found to be significant (ANOVA; F1,43 = 4.965, $p < 0.01$). In waters up to 27 m, *T. parindicus* was the more abundant species, but when depth exceeded this *T. australiensis* dominated (Fig. 5). Frequency analyses showed a significant difference in distribution among depths within and between species ($^{(\chi^{2}9}$ (N = 1215)= 708.62, $p < 0.01$).

Both species had the highest frequency of occurrence at sites with mean grain sizes in the coarse sand fraction (Fig. 6). *Thenus parindicus* was distributed across sites with significantly smaller mean grain sizes compared to *T. australiensis* $^{(\chi^{2}}$7(N = 1215) = 83.298, $p < 0.01$). *Thenus parindicus* was recorded at sites with mean grain sizes ranging from 53.5 μm to 1916.1 μm; mud to very coarse sand according to Wentworth classification (Wentworth, 1922). *Thenus australiensis* was observed at sites with mean grain sizes between 275.3 μm and 2898.5 μm; medium fine sand to very fine gravel by Wentworth classification.

Individuals were observed at sites with Trask sorting coefficient values between 1.294–8.554 ⌀ units. *Thenus australiensis* displayed the highest frequencies at sites with a Trask sorting coefficient between 1–2 ⌀ units, well sorted, while *T. parindicus* was recorded in greatest frequencies at sites between 3.5–5.25 ⌀ units, normal to poorly sorted (Fig. 7. A). The difference in species distributions across Trask sorting coefficient values was significant when sorted into bins of 1.75 ⌀ units $^{(\chi^{2}}$7(N = 1215) = 279.07, $p < 0.01$). When analyzed with Trask sorting coefficient, abundance was found to be significantly different between species (ANOVA; F1123 = 32.16, $p < 0.0$). *Thenus* spp. were recorded at

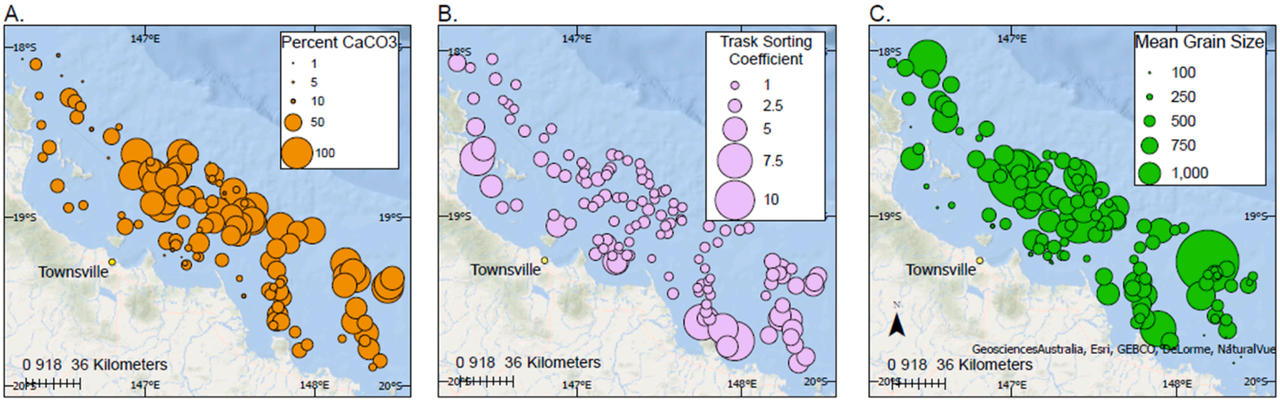


**Fig. 2.** Map of sediment parameter results by site from the survey off Townsville. A) percent calcium carbonate content, B) sediment sorting value measured in Trask units (∅), larger bubbles mean more poorly sorted, C) mean grain sizes in microns.

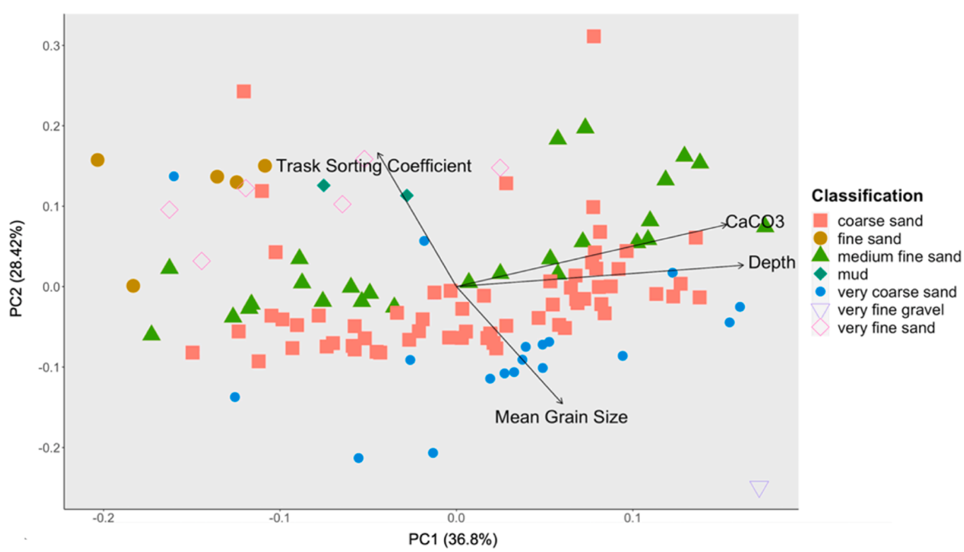


**Fig. 3.** PCA ordination plot of sediment samples taken during the 2021 Townsville survey and habitat parameters varying significantly across sites, grouped according to Wentworth grain size classifications.

sites with sediment containing between 0.95–95.0% calcium carbonate. Both species were observed throughout the same range, however, *T. parindicus* was found in higher frequencies at sites with lower calcium carbonate percentages compared to *T. australiensis* (Fig. 7. B). The difference was further confirmed to be statistically significant by Pearson's chi square when percentages were distributed in categories by 5% ($(\chi^2$18 (N=1215) = 275.9, $p < 0.01$).

The multivariate constrained CAP analysis of individual *Thenus* spp. caught in Townsville and previous variables evaluated via univariate statistics successfully classified 89.00% of all individuals. For each individual, depth and all sediment variables differed by species (Pillai* = 0.56728; $F_{9,1143}$ = 165.33; $p < 2.2e\text{-}16$). This CAP model correctly classified 89.8% of *T. parindicus* sampled and 88.5% of *T. australiensis* based on depth and sediment properties at each sampled location with instances of catch. There was visible clustering of each species, with moderate overlap (Fig. 8. A). Depth and sediment calcium carbonate content explained the greatest variance between species in the analysis of individuals. Species composition of sites (i.e., presence of only *T. parindicus*, only *T. australiensis*, or mixed species) differed based on depth and sediment variables including calcium carbonate content (Pillai* = 1.010; $F_{10,114}$ = 22.64; $p < 2.2e\text{-}16$). A CAP analysis using these same variables correctly classified species composition of sites in 96.6% of cases (Fig. 8. B). The model successfully classified 86.2% of sites with both species (mixed), 100% of sites with exclusively *T. australiensis*, and 100% of sites with exclusively *T. parindicus*. There was clear clustering of each category of species with minimal overlap. Depth and Trask sorting coefficient were most influential in predicting species composition at sites, while calcium carbonate and mean grain size had the least influence. Six sites where neither species was recorded and seven sites that did not provide enough sample volume to process for calcium carbonate content were omitted from both ordinations. The seven sites without calcium carbonate analysis removed 68 of 1215 bugs caught during the survey.

## 4. Discussion

This study found significant evidence of habitat partitioning by species, but not habitat exclusion in the *Thenus* populations in coastal waters adjacent to the Townsville region. In a location-based analysis of each site, depth and Trask sediment sorting coefficient were the most influential variables on species distributions observed in this study. However, multivariate analysis of each individual bug caught showed depth and sediment calcium carbonate content as influential variables. We found *T. parindicus* inhabiting shallower habitats with poorly sorted sediment compared to *T. australiensis* which inhabits deeper habitats with more well sorted sediments containing greater calcium carbonate

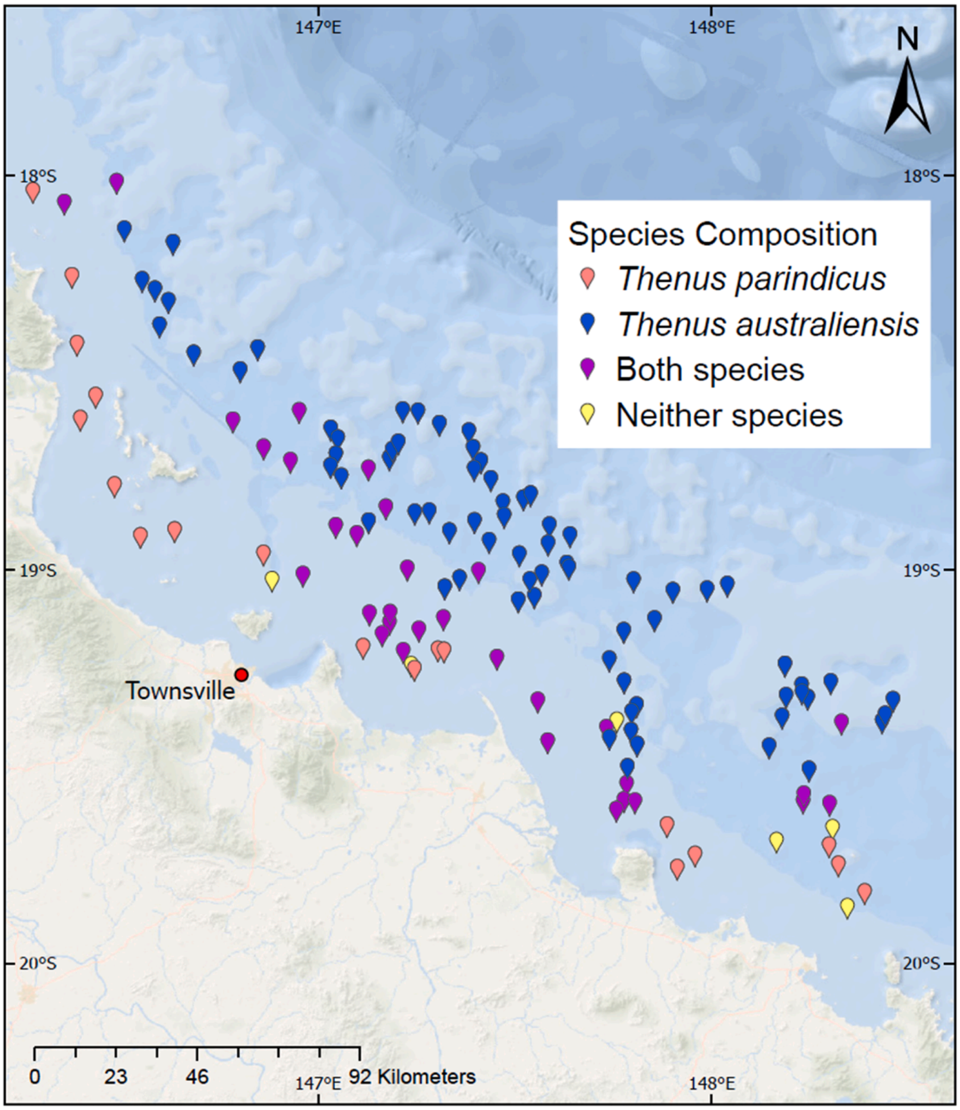


**Fig. 4.** Distribution of Moreton Bay bugs (*Thenus* spp.) across sites near the Townsville trawling region, QLD, Australia. Colours indicate species presence / absence.

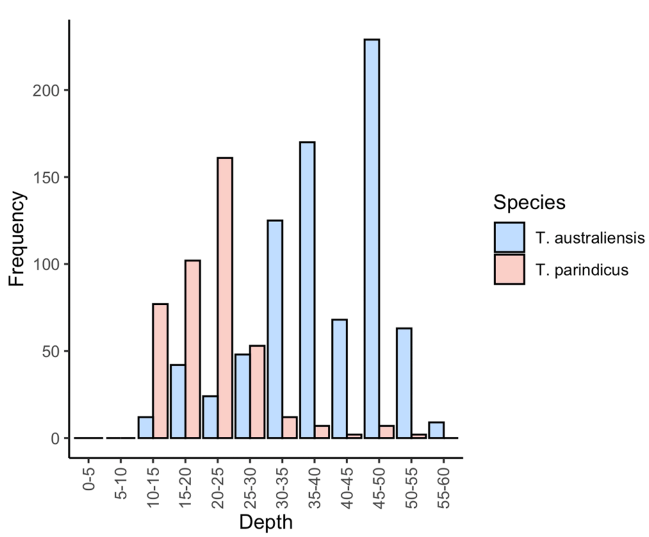


**Fig. 5.** Frequency distribution of Moreton Bay bug species across the Townsville trawling region depth range by increments of five meters.

percentages. Our results provide further insight into the relationship between *Thenus* spp. and their habitat. The information gained in this study can be used to conduct improved stock assessments of these species, therefore providing a more comprehensive foundation from which management decisions can be made for the fishery. The results can be used to construct predictive models to retro-actively estimate species-specific catch rates based on logbook records and location. Similar approaches were successful for separating tiger prawn species in the Northern Prawn Fishery logbooks and provide an opportunity to enhance our ability to utilize decades of existing data for assessment insight (Venables and Dichmont, 2004).

The multivariate CAP analyses in this study provide insight into nuances affecting *Thenus* spp. distributions in the Townsville trawling region. The analyses provide evidence that depth is likely the most important habitat factor influencing the distributions observed in *Thenus* spp. in this region. In the Townsville trawling area, we found that many *T. australiensis* occupy sandy flats in the Great Barrier Reef lagoon that contain a relatively high percentage of calcium carbonate. This may be a result of proximity to the Great Barrier Reef and associated deposition of calcium carbonate into the lagoon transported by prevailing currents pushing through the reef (Benthuysen et al., 2022). Importantly, the other main population of *T. australiensis*, located near Hervey Bay, occurs in an area with low calcium carbonate content that is distant from

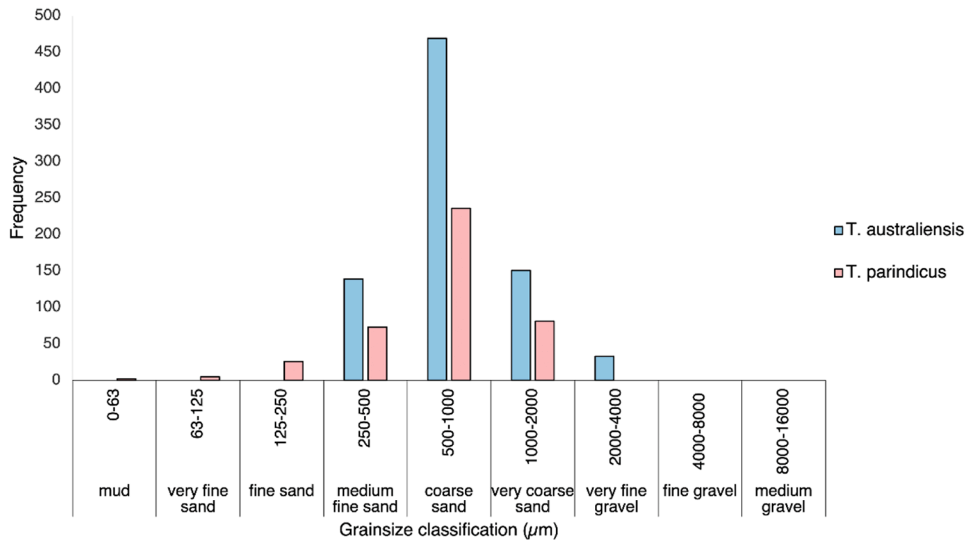


**Fig. 6.** Frequency distributions of Moreton Bay bugs (*Thenus* spp.) across sediment mean grain size per sample site organized by Wentworth grain size classification.

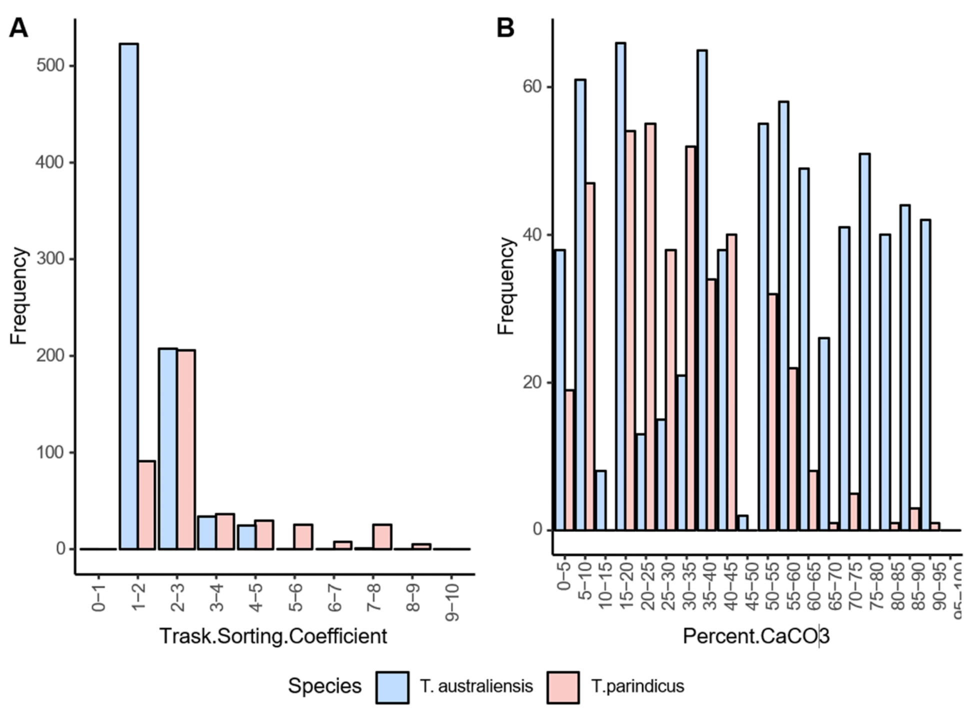


**Fig. 7.** Frequency distribution of Moreton Bay bugs (*Thenus* spp.) from the Townsville trawling region across sediment A) sediment sorting (Trask sorting coefficient) in increments of 1 ⌀unit, B) calcium carbonate content by increments of 5%.

the Great Barrier Reef suggesting that sediment calcium carbonate content is likely not an important driver of this species habitat preferences (McMillan et al., 2023). The influence of calcium carbonate content on *Thenus* spp. distributions is therefore likely a localized effect and should be considered with caution. For these reasons, we believe that depth likely has the greatest influence on *Thenus* spp. distributions, followed by sediment Trask sorting coefficient. Individuals were correctly assigned species level in 89.00% of cases (Fig. 8. A), while the species composition of sites was correctly classified in 96.6% of cases based primarily on the influences of depth and sediment sorting (Fig. 8. B). Since the latter CAP was based on assignment of species composition at locations, it may be more useful for insights about species distributions for fisheries management.

Our findings corroborate reports by Courtney (1997) that *T. australiensis* is the more abundant of the two species, comprising 65% of records in this survey. Our findings partially support Jones' previous reports that depth and mean grain size are significantly different in the habitats of *T. australiensis* and *T. parindicus* (Jones, 2007). However, there was no evidence of complete exclusion of either species across habitats. Species' distributions differed, but there was a considerable spatial overlap. In the Townsville survey, the numerically dominant species present shifts from *T. parindicus* to *T. australiensis* once depths exceed 27 m. Both species were found in the greatest frequencies in coarse sand which also contradicted previous reports that *T. parindicus* primarily exploit mud dominant sediments (Jones, 1988). Jones reported that depth and grain size were the key factors driving differences in species distributions, however this study found sediment sorting was also particularly important. Sediment sorting is determined by

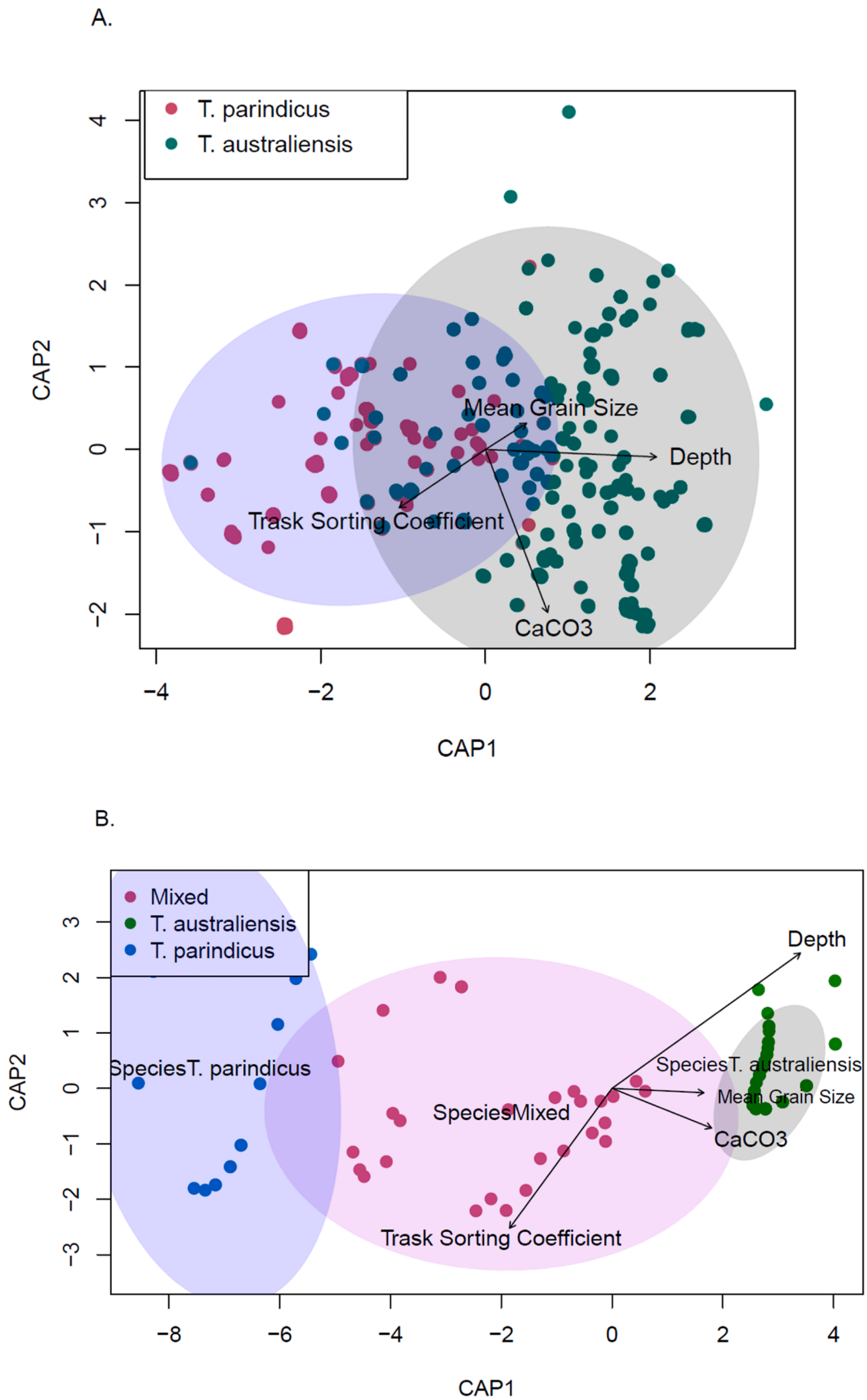


**Fig. 8.** CAP ordination plot of A) each *Thenus* individual recorded in a survey of the Townsville trawling region with colors indicating species and B) each site of the Townsville survey with composition of *Thenus* spp. and habitat variables, classified by species. Colors indicated species present at the site. Ellipses show standard deviation of each group.

environmental factors, primarily energy. Poorly sorted sediments indicate areas subject to irregular flow conditions or disturbance events. This study found *T. parindicus* preferred poorly sorted sediments (values > 4.5 ⌀ units) situated closer to the coast in shallower waters. In these waters, benthic substrate may be more heavily impacted by intermittent coastal storms and wave action, compared to deeper, offshore sediments where ancient processes likely influenced the well sorted sediments observed (between 1–3.5 ⌀ units). Sediment Trask sorting value has been linked to distribution patterns in other crustaceans. A study on juvenile horseshoe crabs, *Tachypleus tridentatus*, found that distribution increased with sediment Trask sorting coefficient. For Chinese horseshoe crabs, larger individuals were found more frequently in poorly sorted sediments farther offshore compared to smaller individuals (Chen et al., 2015).

Our findings on *Thenus* species habitat preferences will be used to inform modelling at broader spatial scales to inform stock assessment in Queensland. For this purpose, it is critical to know which habitats are suitable for each species based on environmental variables like those discussed herein (i.e., depth and sediment properties). Based on these variables, it may be possible to model the distributions of the two *Thenus* species over large areas (i.e., the entire east coast of Queensland) and thus differentiate the species in the logbook catch records based on catch locations. When supplemented with further studies and exploration of additional habitat factors, this will be valuable for assessing long term trends in catch rates of both species. Additional surveys aimed at *Thenus* spp. assessments should be conducted along more of the Queensland coast to get additional data on how *Thenus* spp. distributions change based on habitat availability. This will provide more information about potentially influential habitat factors and ecology, the population dynamics of each species, and allow for improved predictive modelling of the fishery. *Thenus* spp. surveys of mud-dominated basins farther north on the Queensland coast, and gravel-dominated regions will provide a full scope of how grain size relates to the distributions of both *Thenus* spp.. This insight can give a basis for conclusions of the species' habitat preferences. Additionally, a survey of *Thenus* populations and associated sediment in marine protected areas (MPA) could provide information on the effects of fishing closures on *Thenus* populations. Pitcher et al. (2007) reported that around half of the biomass of each species may be in MPAs inside the GBRMP. It is possible that the distributions across sediment types observed in this survey are significantly influenced by trawling activity, and density patterns are also influenced by variations in fishing effort. Species distribution could present differently in areas impervious to frequent habitat disturbance caused by trawling. In these future studies, deeper analysis of sediment composition should be explored to understand these animals' relationship with their habitat more fully. Evaluating organic content and other compositional factors could show trends in distribution related to food availability, trophic dynamics, and other factors we were unable to investigate in this study.

## CRediT authorship contribution statement

**McMillan Matthew N.:** Writing – review & editing, Supervision, Project administration, Methodology, Data curation, Conceptualization. **Daniell James:** Writing – review & editing, Supervision. **Gardiner Naomi M.:** Writing – review & editing, Supervision, Methodology. **Roberts Eric M.:** Writing – review & editing, Supervision, Methodology, Data curation. **Louw Nora:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation.

## 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.

## Data availability

Data will be made available on request.


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## References


Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525. https://doi.org/10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2.

Benthuysen, J.A., Emslie, M.J., Currey-Randall, L.M., Cheal, A.J., Heupel, M.R., 2022. Oceanographic influences on reef fish assemblages along the Great Barrier Reef. Prog. Oceanogr. 208, 102901 https://doi.org/10.1016/j.pocean.2022.102901.

Browne, N.K., Smithers, S.G., Perry, C.T., 2010. Geomorphology and community structure of Middle Reef, central Great Barrier Reef, Australia: an inner-shelf turbid zone reef subject to episodic mortality events. Coral Reefs 29, 683–689. https://doi.org/10.1007/s00338-010-0640-3.

Burton, T.E., Davie, P.J.F., 2007. A revision of the shovel-nosed lobsters of the genus Thenus (Crustacea: Decapoda: Scyllaridae), with descriptions of three new species. Zootaxa 1429, 1–38. https://doi.org/10.11646/zootaxa.1429.1.1.

Butler IV, M.J., 2003. Incorporating ecological process and environmental change into spiny lobster population models using a spatially-explicit, individual-based approach. Fish. Res. 65 (1-3), 63–79. https://doi.org/10.1016/j.fishres.2003.09.007.

Chen, C.-P., Yang, M.-C., Fan, L.-F., Qiu, G., Liao, Y.-Y., Hsieh, H.-L., 2015. Co-occurrence of juvenile horseshoe crabs Tachypleus tridentatus and Carcinoscorpius rotundicauda in an estuarine bay, southwestern China. Aquat. Biol. 24, 117–126. https://doi.org/10.3354/ab00641.

Courtney, A., 1997. A study of the biological parameters associated with yield optimisation of Moreton Bay bugs,Thenus spp. Fisheries Research and Development Corporation. Department of Primary Industries Queensland. 〈https://www.frdc.com.au/project/1992–102〉.

Courtney, A.J., 2002. The status of Queensland's Moreton Bay bug (Thenus spp.) and Balmain bug (Ibacus spp.) stocks. Department of Primary Industries. 〈http://era.daf.qld.gov.au/id/eprint/3700/1/ThestatusofQLDMoretonbayandBalmainbugstocks.pdf〉.

Courtney, A.J., Haddy, J.A., Campbell, M.J., Roy, D.P., Tonks, M.L., Gaddes, S.W.,. & Taylor, J. 2007. Bycatch weight, composition and preliminary estimates of the impact of bycatch reduction devices in Queensland's trawl fishery. 〈https://www.daf.qld.gov.au/data/assets/pdf_file/0007/75769/BycatchFinalReport2007-FullReport.pdf〉.

Dichmont, C.M., Butterworth, D.S., Cochrane, K.L., 2000. Towards adaptive approaches to management of the South African abalone Haliotis midae fishery. Afr. J. Mar. Sci. 22, 1814–2338 (eISSN). 〈https://www.ajol.info/index.php/ajms/article/view/67602〉.

Dixon, P., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14, 927–930. https://doi.org/10.1111/j.1654-1103.2003.tb02228.x.

Fluharty, D., 2000. Habitat protection, ecological issues, and implementation of the sustainable fisheries act. Ecol. Appl. 10, 325–337. https://doi.org/10.1890/1051-0761(2000)010[0325:HPEIAI]2.0.CO;2.

Folk, R.L., 1980. Petrology of sedimentary rocks. Hemphill publishing company. 〈https://www.academia.edu/8538477/Petrology_of_Sedimentary_Rocks_Robert_L_Folk_〉.

Friedman, G.M., 1962. On sorting, sorting coefficients, and the lognormality of the grain-size distribution of sandstones. J. Geol. 70, 737–753. https://doi.org/10.1086/jg.70.6.30066373.

George, R.W., Griffin, D.J.G., 1972. The shovel nosed lobsters of Australia. Aust. Nat. Hist. 17, 227–232. 〈https://media.australian.museum/media/dd/Uploads/Documents/35783/ams370_vXVII_07_lowres.901fd8e.pdf#page=19〉.

Goñi, R., Reñones, O., Quetglas, A., 2001. Dynamics of a protected Western Mediterranean population of the European spiny lobster Palinurus elephas (Fabricius, 1787) assessed by trap surveys. Mar. Freshw. Res. 52, 1577–1587. https://doi.org/10.1071/MF01208.

Hayes, D.B., Ferreri, C.P., Taylor, W.W., 1996. Linking fish habitat to their population dynamics. Can. J. Fish. Aquat. Sci. 53, 383–390. https://doi.org/10.1139/f95-273.

Herrnkind, W.F., Vanderwalker, J.A., and Barr, L., 1975. Population dynamics, ecology and behavior of spiny lobsters, Panurilus argus, of St. John, US Virgin Islands. (IV) Habitation, patterns of movement and general behavior. Natural History Museum Los Angeles County Science Bulletin 20: 31–46.

Holthuis L.B. (1991) Marine lobsters of the world. FAO fisheries synopsis, 13(125), I,III. 〈https://www.proquest.com/scholarly-journals/marine-lobsters-world/docview/1024829961/se-2〉.

Jones, C.M. 1988. The biology and behaviour of bay lobsters,Thenus spp. (Decapoda: Scyllaridae), in northern Queensland, Australia. 〈https://espace.library.uq.edu.au/view/UQ:388535〉.

Jones, C.M., 1993. Population structure of Thenus orientalis and T. indicus (Decapoda: Scyllaridae). Mar. Ecol. Prog. Ser. 97, 143–155. https://doi.org/10.3354/meps097143.

Jones, C.M., 2007. Biology and fishery of the bay lobster,Thenus spp. In: The biology and fisheries of the slipper lobster. CRC Press, pp. 339–372.

Kindt, R., Coe, R., 2005. Tree diversity analysis: A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre.

Legendre, P., Anderson, M.J., 1999. Distance- based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1–24. https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2.

Lynch, A., 1995. Legislating for ecologically sustainable development: the fisheries Act 1994 (Qld). ames Cook. Univ. Law Rev. 2, 82–108. 〈https://search.informit.org/doi/10.3316/ielapa.061085547588534〉.

Lyons, W.G., 1981. The spiny lobster, Panulirus argus, in the middle and upper Florida Keys: population structure, seasonal dynamics, and reproduction. Florida marine research publications (USA). ISSN: 0095–0157 〈http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCALZOOLINEINRA8110457272〉.

McMillan, M.N., Leahy, S.M., Daniell, J., Louw, N., Roberts, E., Wickens, M., Hillcoat, K., O'Neill, M.F., 2023. Determining the spatial distribution and abundance indices for Moreton Bay Bugs, Thenus parindicus and Thenus australiensis in Queensland to improve stock assessment and management. Final Report. FRDC Project No. 2020/020. In press.

Negrete-Soto, F., Lozano-Alvarez, E., Briones-Fourzan, P., 2002. Population dynamics of the spiny lobster Panulirus guttatus (Latreille) in a coral reef on the Mexican Caribbean. J. Shellfish Res. 21, 279–288. 〈https://www.biodiversitylibrary.org/item/29727#page/285/mode/1up〉.

Pitcher, R., Doherty, P., Arnold, P., Hooper, J., Gribble, N., Chalmers, S., Coles, R., Ehrke, B., Good, N., Kistle, S., 2007. Seabed biodiversity on the continental shelf of the Great Barrier Reef World Heritage Area. Project Report. CRC-REEF Task Number: C1.1.2. FRDC Project Number: 2003/021. NOO Contract Number: 2004/015. Department of Primary Industries, Queensland.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL 〈https://www.R-project.org/〉.

Roelofs, A., Larcombe, J., Kangas, M., Zeller, B., 2021. Status of Australian Fish Stocks Report Moreton Bay Bugs (2020). Fisheries research and development corporation, 22 September 2022. 〈https://fish.gov.au/report/274-MORETON-BAY-BUGS-2020〉.

Spanier, E., Lavalli, K.L., 1998. Natural history of Scyllarides latus (Crustacea: Decapoda): a review of the contemporary biological knowledge of the Mediterranean slipper lobster. J. Nat. Hist. 32 (10-11), 1769–1786. https://doi.org/10.1080/00222939800771281.

Venables, W.N., Dichmont, C.M., 2004. A generalised linear model for catch allocation: an example from Australia's Northern Prawn Fishery. Fish. Res. 70 (2-3), 409–426. https://doi.org/10.1016/j.fishres.2004.08.017.

Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. J. Geol. 30, 377–392. https://doi.org/10.1086/622910.