




Seagrass macroinvertebrate bycatches support mosquito net trawl fishery in Madagascar

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Abstract – The use of mosquito nets, primarily for targeting small and/or juvenile fish, has rapidly increased in Western Indian Ocean shallow seagrass beds and coral reefs over the last 20 years. However, to date, invertebrate by-catch by locally-made fishing gear has not been reported. We studied the mosquito net trawl fishery in seagrass areas in the Bay of Toliara, Southwest Madagascar through the GPS tracking of fishers from August 2018 to February 2019. Catches were monitored through monthly landing surveys to characterize spatial temporal patterns in the abundance and diversity of macroinvertebrates in the seagrass beds. Fishing was carried out at low tide, mostly at night, by fishers pulling a hand-made trawl net of varying dimensions. Overall, 43 macroinvertebrate taxa were identified out of 217,080 individuals collected from 109 catch samples. Catches were generally composed of crustaceans (mainly Portunidae, Processidae, Penaeidae, and Alpheidae). The crab *Thalamita mitsiensis* largely dominated the abundance and biomass of the macroinvertebrate assemblage (from 6% to 100% and from 5 to 100% of the overall density and biomass, respectively). Macroinvertebrates composed 1.5% to 100% of the total catch per trip (i.e., 4–55 kg trip⁻¹). They were sold for human consumption or animal feed, which provided additional income to fishers (USD 1–24 trip⁻¹ and 1–72% of catch income per trip). This study revealed that macroinvertebrate resources provide valuable by-catch to small-scale fishers in Southwest Madagascar. This bycatch generates income that further encourages the use of mosquito net trawls and exacerbates their negative effects on coastal seagrass ecosystems and fisheries.

Keywords: Ecosystem approach / household income / reef fishery / socioeconomic study

1 Introduction

Many tropical fish and invertebrate species use coastal seagrass beds for feeding, protection from predators, and/or as nursery areas at the juvenile stage (Bell et al., 2001; Saenger et al., 2013). These shallow habitats influence the survival, recruitment, and, more generally, the population dynamics of such species (Saenger et al., 2013; Sambrook et al., 2019). Seagrass beds, however, are increasingly threatened worldwide and have been reduced at a rate of ~100 km² per year over the past 30 years (Waycott et al., 2009). This loss directly and indirectly results from natural events such as soil erosion in watersheds, siltation, and/or environmental disturbances, as well as from major human impacts such as dredging, nutrient

pollution, and fishing (Adite, 2003; Grech et al., 2012; Preen et al., 1995). These degradations impact the ecosystem services provided by seagrass beds, and the associated fish and invertebrate communities, to human coastal populations.

In many developing countries, local coastal communities rely on seagrass beds as fishing grounds of benthic macroinvertebrates, such as mollusks (cephalopods, bivalves, and gastropods), crustaceans (crabs, shrimps), and sea cucumbers (Cadier and Frouws, 2019). Women and children preferentially target these resources in shallow water habitats, such as reef flats and seagrass beds, contributing to household food security and cash income in many countries (de Boer and Prins, 2002; Fröcklin et al., 2014). Most macroinvertebrate species are indeed valuable and specifically targeted for direct human consumption, or for sale as food, animal feed, or shell curio trade.

However, to date, studies on tropical seagrass-associated fisheries have mainly focused on fish (Jones and Unsworth,

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2020) and main targeted macroinvertebrate taxa, including commercial sea cucumber species (e.g., Baron, 1992; Léopold et al., 2013; Purcell et al., 2012). Heavy commercial, subsistence, and/or recreational exploitation of multiple macroinvertebrate species has been reported in seagrass beds closely located to densely populated areas (Jimenez et al., 2011). Additionally, trampling exerted by invertebrate harvesters walking on seagrass beds was found to negatively affect the abundance and biomass of the target species and overall species composition (Newton et al., 1993; Nordlund et al., 2010). Overall the negative ecological effects of fishing on seagrass beds and benthic macroinvertebrate resources directly and indirectly affect fishery sustainability and, consequently, the livelihoods of small-scale fishing communities (Locke et al., 2017).

In developing countries, the impact of fishing gear use on seagrass-associated fisheries has attracted increasing research attention for the support of resource management (e.g., Costa and Netto, 2014), including benthic macroinvertebrates. Specifically, in the Indian Ocean, small-scale fishers increasingly use mosquito nets in seagrass beds, which provide appropriate, easily accessible areas for this gear type (e.g., Bush et al., 2017; Jones et al., 2018). The availability of insecticide-treated nets, initially provided for free or low-cost malaria control, has created an additional, strong incentive for the development of these practices in recent years (Short et al., 2018). Whether and how that fishing gear may affect the seagrass benthic macroinvertebrate community has, however, been poorly documented to date.

This study aimed to characterize the seagrass-associated fishery and macroinvertebrate resources in Southwest Madagascar, one of the poorest countries in the world. Mosquito net fishing in coral reef fisheries has rapidly developed over the past decade in the region, which has led to intense exploitation of seagrass resources, particularly juvenile reef fishes (Raharinaivo et al., 2020). The associated macroinvertebrate catch has not yet been investigated, while the benthic invertebrate communities in the region have not been surveyed for the last 30 years (see Bigot, 1992; Derijard, 1965; Ledoyer, 1976). To address this knowledge gap, we characterized the abundance and diversity of seagrass macroinvertebrates by monitoring the spatial temporal patterns of benthic macroinvertebrate catches in seagrass beds. From fishery data, the effects of spatial and temporal factors on the distribution and socio-economic contribution of macroinvertebrate taxa in the small-scale fishery were studied and discussed to support an ecosystem-based approach to the management of the fishery.

2 Materials and methods

2.1 Study area

The study was conducted in the northern part of the Bay of Toliara (Fig. 1), Madagascar's second largest reef and lagoon complex (157 km²) located in the most densely populated coastal area in the southwestern region (approximately 330,000 inhabitants). The small-scale commercial fishery in the Bay of Toliara is operated by approximately 900 traditional pirogues that mostly target coral reef and pelagic fish (Behvoke et al., 2021). Shallow seagrass beds (15 km²)

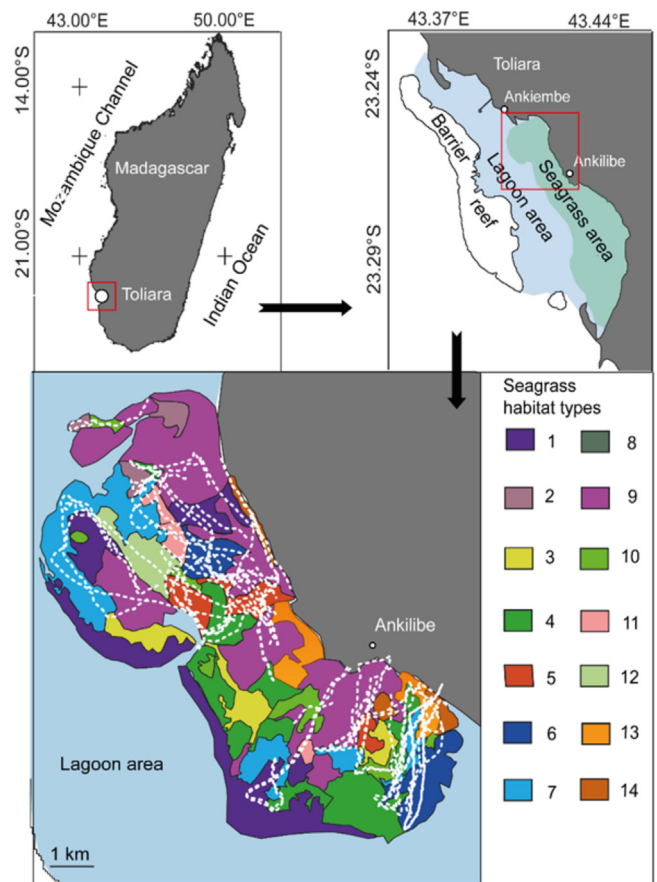


Fig. 1. Distribution of the 14 seagrass habitat types and mosquito net trawl hauls sampled in the study area in the Bay of Toliara, Southwest Madagascar. 1: mixed seagrass beds (three species) dominated by *Cymodocea serrulata*; 2: mixed beds (three species) dominated by *Syringodium isoetifolium*; 3: mixed beds (three species) dominated by *Thalassia hemprichii*. 4: mixed meadows (*Thalassia hemprichii* and *Halodula uninervis*) dominated by *Thalassia hemprichii*; 5: mixed meadows composed by *Halodula uninervis* and *Thalassodendron ciliatum*; 6: mixed meadows composed by *Syringodium isoetifolium* and *Thalassodendron ciliatum*; 7: mixed meadows with *Thalassia hemprichii* and *Cymodocea serrulata*; 8: monospecific meadows of *Cymodocea serrulata*, 9: monospecific meadows of *Halodula uninervis*, 10: monospecific meadows of *Syringodium isoetifolium*, 11: monospecific meadows of *Thalassia hemprichii*, 12: monospecific meadows of *Thalassodendron ciliatum*; 13: bare sand, and 14: bare mud. Dotted white line: trajectory of the pirogues sampled.

are heavily exploited by approximately 300 fishers (148 pirogues, with approximately half of them out per day) using locally-made mosquito net trawls and operating mostly from two coastal villages (Fig. 1).

Since the macroinvertebrate distribution is strongly influenced by substrate type (Palmer et al., 1997), habitats were preliminary described through satellite imagery and in situ observations. Landsat images were photo-interpreted to outline habitat types (polygons) in a geographic information system (GIS). Field check-up was conducted at low tide in January 2019 at 81 stations distributed throughout the study



Fig. 2. Characteristics and use of mosquito net trawls in the study area. The following components were measured: wings, codend, sweeps, headline, vertical opening, and horizontal opening. Trawl length was estimated as the headline length plus twice the wing length.

area at a depth of 0.1 to 1.5 m. At each station, sediment type (sand, mud, muddy sand), phanerogam species, rate (%) of epiphytic algae on seagrass leaves, and phanerogam height (cm) and density (%) were visually assessed over a 3-m² area.

2.2 Fishery-dependent data collection

2.2.1 Sampling gear and effort

Trawl nets in the study area consisted of an assemblage of nets: wings (6–7 cm mesh size), top panel (3–5 cm mesh size), bottom panel (<3 cm mesh size), and codend (1 mm mesh size mosquito net) with a 1 to 4-m vertical opening (Fig. 2). Headline, wings, and sweeps length ranged from 0.7 to 27.9 m, from 5 to 35 m, and from 2 to 21 m, respectively. Total trawl net length (i.e., headline length plus twice the wing length) ranged from 14.3 to 72.5 m. Shells were used on the footrope to maintain seafloor contact. Nets were towed by two fishers (male and/or female) while walking in such a way as to ensure the greatest horizontal opening as a conventional bottom trawl. Given these practices and characteristics, a mosquito net trawl was assumed to harvest all vagile benthic invertebrate taxa larger than 1 mm (Bush et al., 2017; Unsworth et al., 2008).

Fish and invertebrate catch and associated fishing effort were monitored in 2018 and 2019 to characterize the small-scale fishery in the Bay of Toliara using the same participatory method as that developed by Behivoke et al. (2021) in the area. Participation was expected to ensure high sampling rate and spatial coverage of catch data while improving fishers' awareness of the survey results (Brenier et al., 2013). The unit of observation was the fishing trip.

The fishers' mosquito net trawl was chosen as the sampling gear type due to its similarity with the experimental push net, which is widely used in ecological study of shallow vagile benthic invertebrate communities. Each of the 148 trawl nets of the fishery were characterized to account for the heterogeneity of that hand-made fishing equipment within the study area. A total of 40 volunteer fishers were sampled for a total of 109 fishing trips. Each month, 12 fishers were selected and monitored for 28 to 31 consecutive days over the austral cool season (August–October 2018) and warm season (November 2018–February 2019).

Fishing effort (i.e., sampling effort) was measured as the area swept (in m²) on each trip, that varied according to trawl net length and trip duration. Consequently, the area swept

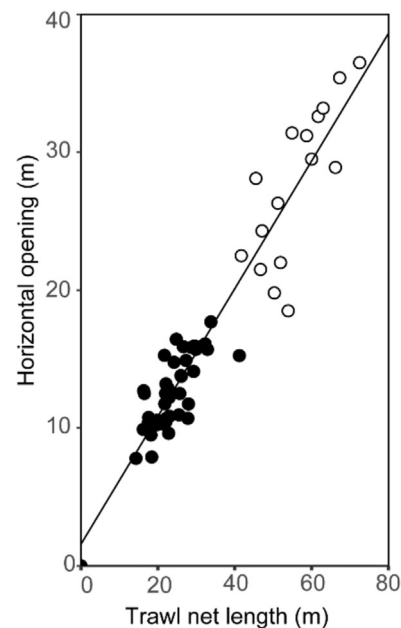


Fig. 3. Relationship between the horizontal opening and length of mosquito net trawls ($n = 57$) in the study area. The linear relationship is shown by the dotted line ($y = 0.502x$, $R^2 = 0.904$). Black and white spots represent the villages of Ankilibe and Ankiembe, respectively (see Fig. 1 for village location).

during one trip was estimated by multiplying the total distance towed during the successive hauls of that trip by the mean horizontal opening of the trawl net. The distance towed was measured by recording boat movements. Each pirogue was equipped with a GPS tracker (CatLog2) that recorded positions at 30-second time intervals. Position data were then processed in a GIS (using QGIS v 3.18) to determine the location of fishing hauls based on boat trajectory patterns following the method of Behivoke et al. (2021). That study characterized gear-specific spatial patterns of boat GPS tracks in the Bay of Toliara to identify fishing and non-fishing activities conducted during fishing trips, including those using mosquito net trawl. Each haul was represented by a polyline. The distance trawled per trip was then calculated by the cumulative length of all polylines of that trip. The horizontal opening of 58 trawl nets was measured in situ during fishing trips. Horizontal trawl

opening was estimated as 50.2% of trawl net length through linear regression (Fig. 3). The horizontal opening of trawl nets of all participant fishers was therefore extrapolated from their respective measured length using the proportional relationship, although we observed that the horizontal opening was slightly affected by environmental conditions (current, depth, sea bottom) and fishers' fatigue.

2.2.2 Characterization of benthic macroinvertebrate catches

The 109 fishing trips sampled recorded the weight of their total catch on each trip using a scale (precision 0.25 kg) as part of the participatory monitoring survey. The price of the different commercial categories of fish and invertebrates was also recorded. In order to determine the monthly composition of macroinvertebrate catches, the catches of five to twelve fishers were subsampled each month at spring and neap tide periods (i.e., two sampling times per month). The number of fishers sampled varied according to the fishers' activity and logistical survey constraints. Only nocturnal fishing trips were sampled to ensure a similar, high catchability of macroinvertebrates that are usually more active at night than at day (Pescinelli et al., 2020). This decision was supported by the fact that we observed that trawl net fishing was mostly nocturnal in the survey area. Fishers stored the whole content of the codend after each fishing haul in a fiber basket and did not carry out any pre-sorting of the catch on board. At the fishers' place of residence, a subsample of approximately 1 kg was randomly taken from the total catch of each fisher sampled using a plastic kitchen container, before the catch was sorted. The subsamples were cooled with ice, placed in sealed plastic bags, and transported to the university laboratory for weighing, sorting, and analysis of the overall catch composition.

The subsamples were processed in three steps. First, macroinvertebrates were separated from other components of the catch (e.g., fish, debris, phanerogams, and algae). Second, they were sorted out by taxon, weighed (wet weight), and photographed following the standard protocol of Andriamanirina et al. (2020). A 10-cm graduated ruler was used as a scale on each picture. Individuals of each taxon in each subsample were then counted and measured from the digital images using ImageJ software and the FIJI package (Schindelin et al., 2012). A scale-based method was used (Asadi et al., 2017). Third, one to four of the specimens of each morphotaxon were fixed with 90% alcohol for identification at the species level using a binocular and available taxonomic guides (Crosnier, 1978; Ledoyer, 1967; Thomassin, 1969). In some cases, identification was achieved at the family or genus level only due to limitations of taxonomic keys (Ferraro and Cole, 1994). In such cases, a code was assigned to each distinct morphotaxon (e.g., sp1, sp2, sp3) to differentiate them for macrofauna community structure analysis.

2.3 Data analysis

2.3.1 Macroinvertebrate richness and abundance

Monthly macroinvertebrate richness was estimated by counting the taxa (i.e., species if possible and otherwise morphotaxa) in the catch. The occurrence frequency of taxa was determined by the total number of subsamples containing

the taxa of interest divided by the total number of subsamples. The richness distribution of the main taxa was mapped by habitat type in a GIS.

Abundance and catch weight per taxon per fishing trip were estimated respectively by multiplying the number and cumulated weight of individuals of that taxon in each subsample by the ratio of the sample weight (i.e., total catch weight of the fishing trip) to the subsample weight: $A_{i,t} = A_i \cdot W_t / W_s$ and $W_{i,t} = W_i \cdot W_t / W_s$, where, A is abundance, W is mass, i is taxon, t is trip, and s is subsample. Mean density (number per ha) and biomass (kg per ha) of each taxon per fisher trip were then calculated respectively by dividing the estimated abundance and weight of that taxon by the area swept during the fishing trip. The abundance of each taxon was summed across taxa at the family level for estimating mean density (number per ha) and biomass (kg per ha) of each family per fisher trip. Temporal effects (tide (spring/neap), months, and interaction terms) on the mean density and biomass of taxa were investigated through a generalized linear model (GLM) using the function `lm` (with a Poisson distribution) of the R software v.3.6.3 (R Core Team, 2018). The residuals were plotted to examine the GLM statistical assumption. Only 65 of the 109 samples contained trajectory data that could be used to calculate density and biomass.

The spatial distribution of taxa density and biomass was mapped and analyzed according to habitat type (Fig. 1). The density and biomass in each habitat type were estimated as the average density and biomass across the samples from tows passing through that habitat type. Trawl hauls corresponding to each sample often crossed several habitat types, while catch composition was described at the sample level (i.e., one fishing trip). As an approximation, the same density or biomass value was therefore assigned to all habitat types that were crossed over a distance equal to or greater than 20% of the total distance towed during the fishing trip (e.g., Léopold et al., 2017). Habitat types that were crossed over a shorter distance were not considered in this analysis.

2.3.2 Socio-economic value of macroinvertebrate catches

The socio-economic use of the macroinvertebrate and fish catches was studied. The taxonomic composition of the commercial categories defined by fishers was characterized, and the mean monthly catch per trip of each commercial category was estimated. The mean income from the whole catch per trip and each commercial category was estimated for each month by multiplying the price per kg by the weight of the corresponding catch. The average proportion of income provided by invertebrate and fish catches per trip was also estimated and compared.

The data and related documentations that support the findings of this study are openly available in DataSuds repository (IRD, France) at <https://doi.org/10.23708/8XPDJE>. Data reuse is granted under CC-BY license.

3 Results

3.1 Diversity of seagrass beds

The characteristics and spatial distribution of seagrass habitats types showed habitat heterogeneity and fragmentation

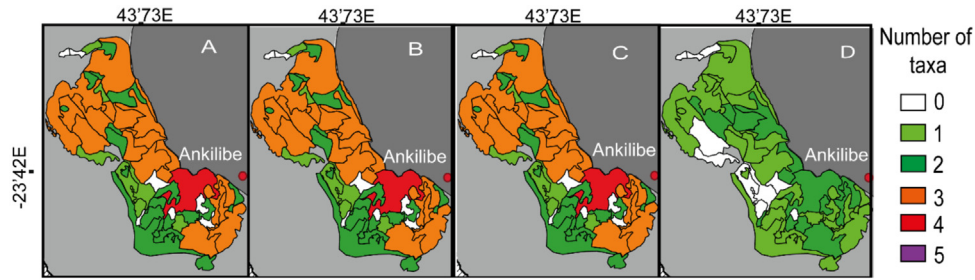


Fig. 4. Distribution of taxonomic richness (in number of taxa at family or genus levels) of the four dominant families of benthic macroinvertebrates by habitat type in the northern sub-area of the study area: A: Portunidae, B: Processidae, C: Penaeidae, and D: Alpheidae.

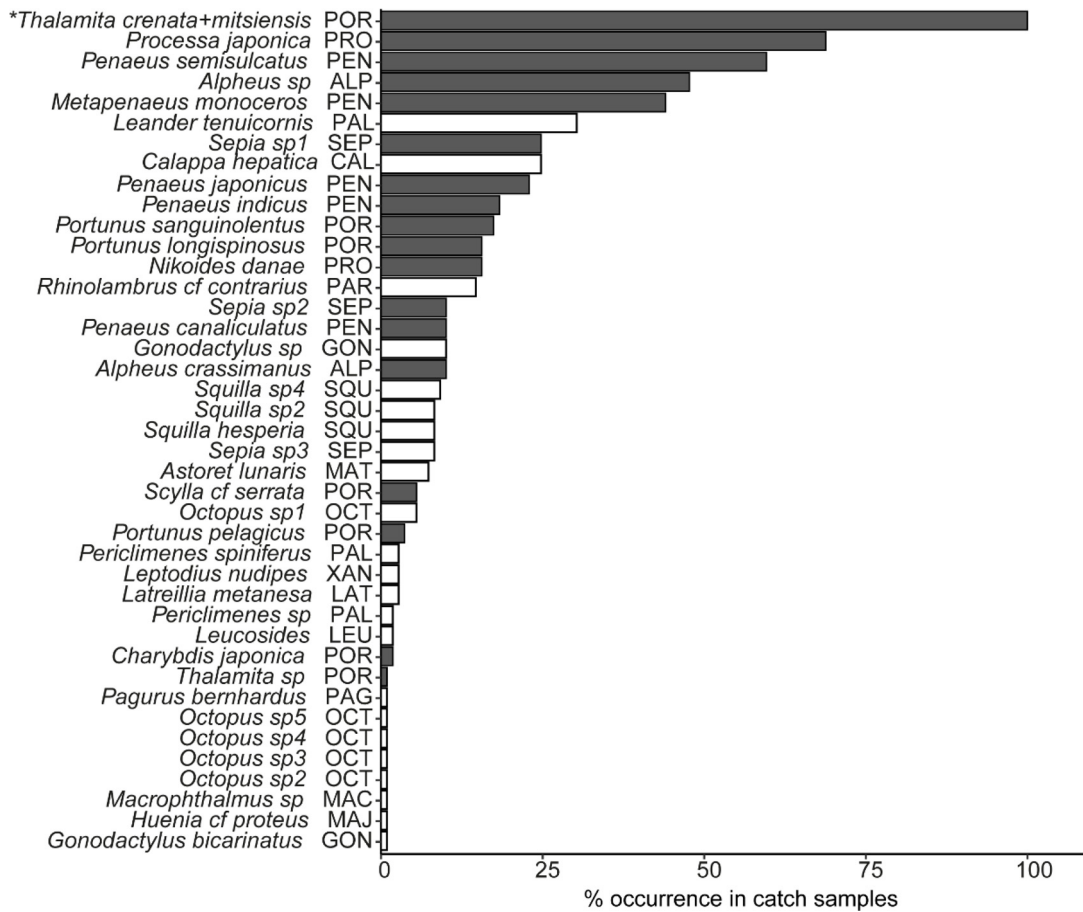


Fig. 5. Frequency of occurrence of the 43 macroinvertebrate taxa in the catch samples ($n = 109$), including the dominant families (POR: Portunidae, PRO: Processidae, PEN: Penaeidae, and ALP: Alpheidae; black bars) and other families: CAL: Callapidae, Parthenopidae, MAJ: Majoidae, Latreilliidae, MAC: Macrophthalminae, XAN: Xanthidae, LEU: Leucosiidae, GON: Gonodactylidae, SQU: Squillidae, PAL: Palaemonidae, HIP: Hippolytidae, SEP: Sepiidae, OCT: Octopodidae, and PAG: Paguridae (white bars) * Two species of the genus *Thalamita* were very similar (*Thalamita mitsiensis* and *Thalamita crenata*) leading to identification errors; therefore, both taxa were grouped for data analysis.

(Fig. 1). The study area was considerably fragmented (14 habitat types) and showed high overall phanerogam diversity (seven species in total), although the meadows were dominated by one or two species and had a very low cover of the genus *Syringodium*. The richness of the four dominant taxa in that area varied across habitat types, including between neighboring habitats and within each habitat type, without clear spatial patterns (Fig. 4).

3.2 Macroinvertebrate taxonomic richness and abundance

A total of 217,080 individuals were recorded in the subsamples. Overall, 43 invertebrate taxa from 19 families were identified. Crustaceans and mollusks were observed at the highest occurrence (90% and 10% occurrence in the subsamples, respectively) (Fig. 5). Only four families

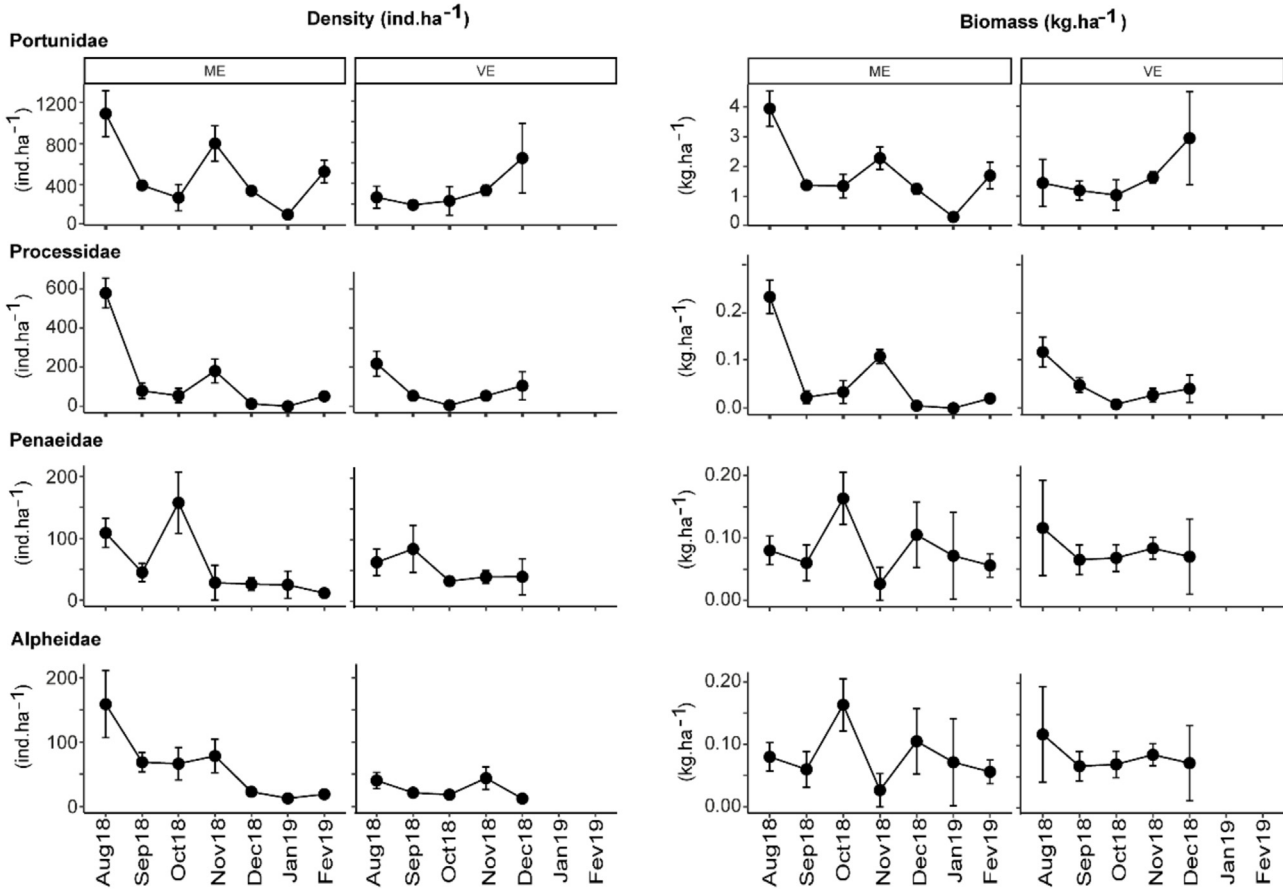


Fig. 6. Density and biomass distribution of the dominant families in the catches according to months and spring and neap tides in the northern sub-area of the study area. Lines represent mean, points represent each month, and bars represent maximum and minimum values. A different y-scale was used for each family.

(hereafter the dominant families, in terms of occurrence) were found in more than half of the subsamples: Portunidae (100%), Processidae (70%), Penaeidae (60%), and Alpheidae (50%) (Fig. 5). Most other taxa (63%) were thus rare or uncommon. The richness of Portunidae and Penaeidae ranked the highest (seven and four taxa, respectively), while the other families were represented by one to three taxa. The species *Thalamita mitsiensis/crenata* (Portunidae) was the only taxon present in all samples. The results of the taxonomic composition are provided in Appendix A.

Overall, the benthic macroinvertebrate assemblage (from 141 to 3595 ind ha⁻¹) was dominated by the family Portunidae (from 72 to 2325 ind ha⁻¹ across taxa) and, to a lesser extent, by the families Processidae (from 0 to 833 ind ha⁻¹ across taxa), Alpheidae (from 0 to 427 ind ha⁻¹ across taxa), and Penaeidae (from 0 to 368 ind ha⁻¹ across taxa) during the survey period (Fig. 6). The results of the GLM model showed that all variables considered in the model (month, tide, and the interaction between month and tide) were statistically significant (ANOVA tests, *p* value < 0.005). Total density was slightly higher at tide than at spring tide, significantly (ANOVA, *p* < 0.05) (Fig. 6). However, there was a significant

difference in the density of the four dominant families among months, except between August and January for the Processidae (ANOVA, *p* < 0.05). Mean density peaked in August for Portunidae (562 ind ha⁻¹), Processidae (312 ind ha⁻¹), and Alpheidae (80 ind ha⁻¹), and in October for Penaeidae (59 ind ha⁻¹). Minimum density values were observed in January except for the family Penaeidae in February.

The total biomass of the dominant taxa varied from 0.10 to 6.34 kg ha⁻¹ across the survey periods and followed the same temporal trend as that of density (Fig. 6). Significant monthly variation was observed (ANOVA, *p* < 0.05) except between August and November for the family Portunidae. The mean biomass of Portunidae, Processidae, Alpheidae, and Penaeidae ranged between 0.55 and 2.06 kg ha⁻¹, 0.01 and 0.16 kg ha⁻¹, 0.05 and 0.15 kg ha⁻¹, and 0.01 and 0.08 kg ha⁻¹ across months, respectively. Due to the high overall abundance and large individual size of Portunidae, its biomass highly dominated the macroinvertebrate assemblage, ranging between 0.1 and 7.5 kg ha⁻¹ (mean: 1.05 kg ha⁻¹), while the biomass of other taxa was lower than 0.3 kg ha⁻¹. The spatial distribution of macroinvertebrates showed that density and biomass of the four dominant taxa varied by approximately

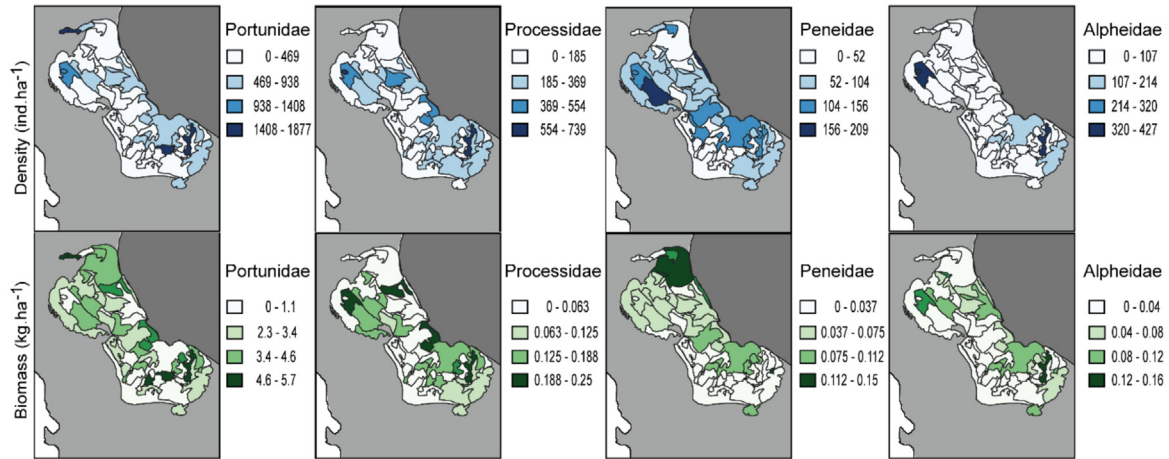


Fig. 7. Distribution of average density (ind ha^{-1} , in blue) and biomass (kg ha^{-1} , in green) of benthic macroinvertebrates by habitat type for the four dominant families.

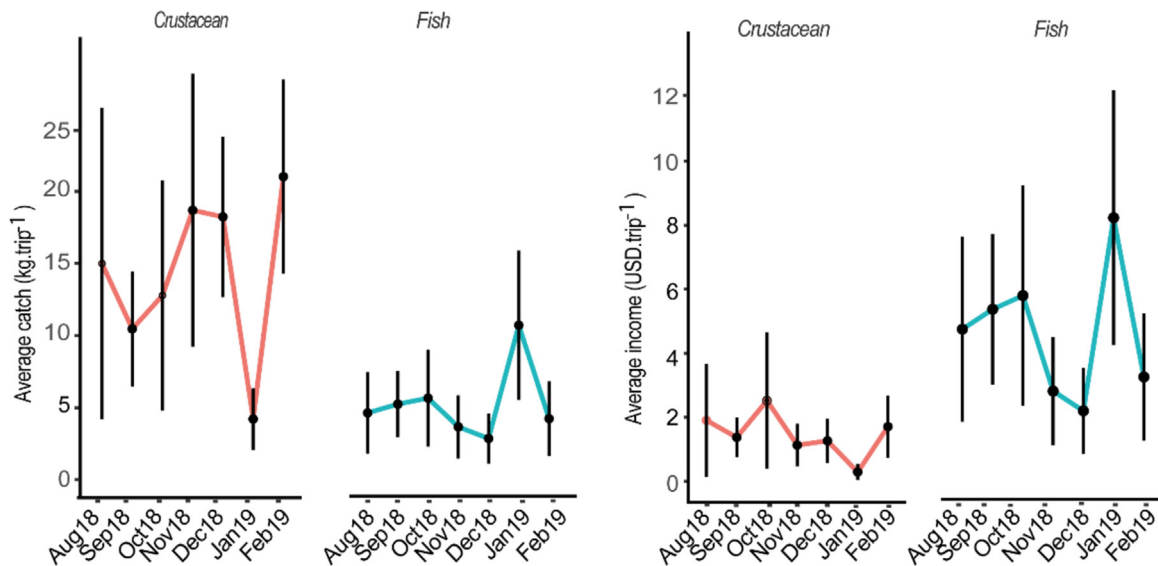


Fig. 8. Average monthly catch (left) and income (right) per trip of mosquito net trawl fishers attributable to crustaceans (i.e., the eight high-value macroinvertebrate taxa; red line) and reef fish (blue line) during the study period.

10-fold among habitat types (0 to $1,880 \text{ ind ha}^{-1}$ and 0 to 5.7 kg ha^{-1} , respectively; Fig. 7).

3.3 Socio-economic use of macroinvertebrates

Macroinvertebrates accounted for the largest component (73%) of trawl net catch throughout the monitoring period (mean: 16.0 , standard deviation (SD) 8.4 kg trip^{-1}), except in January 2019 (mean: 4.1 , SD 2.2 kg trip^{-1}). In economic terms, the income from macroinvertebrate catches averaged USD 1.5 , SD 1.3 trip^{-1} (Fig. 8), which was three times lower than that from reef fish (USD 4.3 , SD 3.2 trip^{-1}), because the price of reef fish (USD 0.9 kg^{-1} to 1.1 kg^{-1}) was usually higher than that of macroinvertebrates (Fig. 8). The total income generated by both fish and invertebrate catches of mosquito net trawl fishing ranged from USD 1 to 24 trip^{-1}

(mean: USD 5.8 , SD 3.8 trip^{-1}). Macroinvertebrate catches provided between 1% and 72% (mean: 25%) of the monthly income of trawl net fishers (Fig. 8).

Macroinvertebrate catch level greatly varied among months and fishing trips each month (Fig. 9), partly due to a change in resource abundance, as described above, and a change in the area swept (mean: $46,660 \text{ m}^2$, SD $16,400 \text{ m}^2$). Due to the price differences among taxa, fishers grouped macroinvertebrates into two categories of commercial value (low or high). We observed that eight high-value crustacean species included in the genera *Portunus* (USD $0.2\text{--}0.6 \text{ kg}^{-1}$), *Scylla* (USD $0.2\text{--}0.6 \text{ kg}^{-1}$), and *Penaeus* (USD $0.5\text{--}1.0 \text{ kg}^{-1}$) were used for human consumption. These three genera provided 97% of the income generated by macroinvertebrate catches per trip (*Thalamita*: 41%, *Portunus*: 16%, and *Penaeus*: 40%) although they represented a minor component

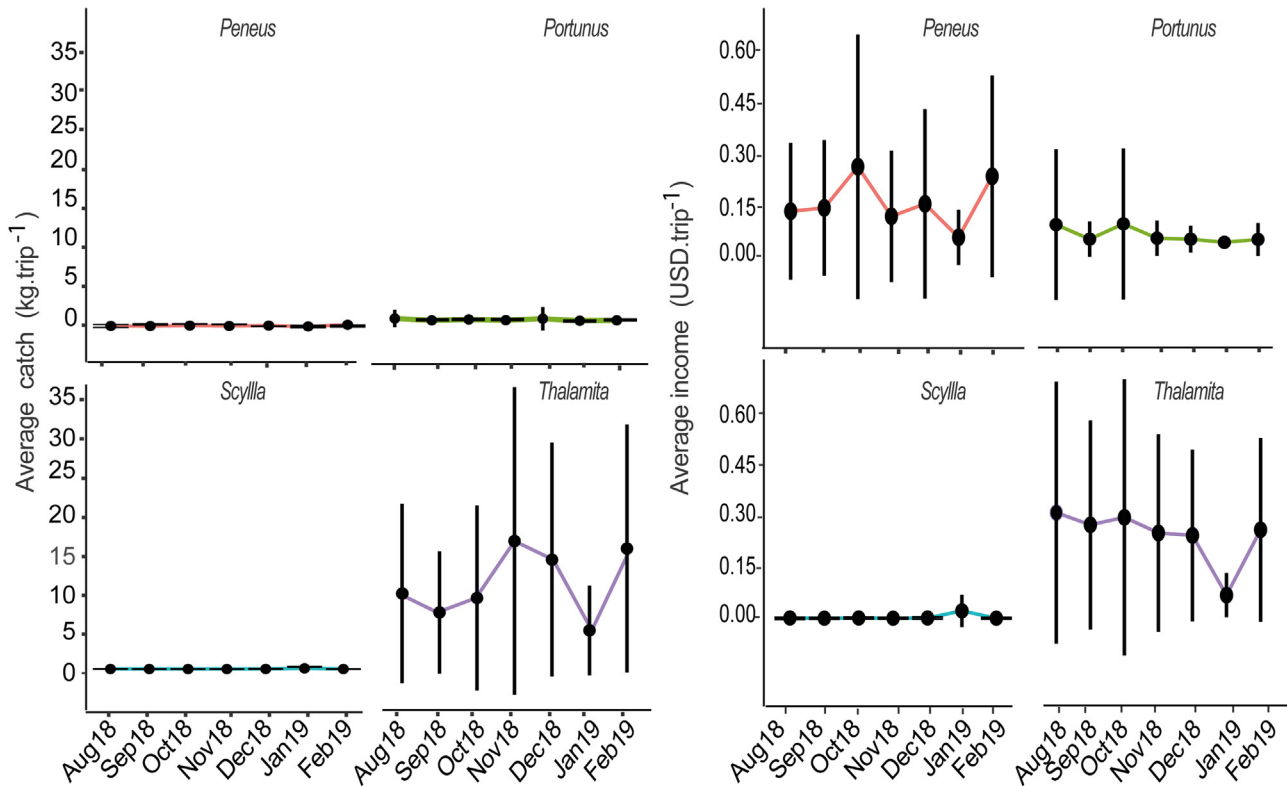


Fig. 9. Distribution of mean catch (kg ha^{-1}) and income (USD trip^{-1}) of the main commercial benthic macroinvertebrate taxa in the study area.

of the total catch weight per trip (6.1% and 3.3% in the cool and warm seasons, respectively). They were mostly sold as fresh products at Toliara markets, and occasionally self-consumed. The remaining 35 macroinvertebrate taxa were sun-dried and sold as animal feed at a 10 to 20 times lower price ($\text{USD } 0.07\text{-}0.14 \text{ kg}^{-1}$). On average, the genus *Thalamita* composed 75% and 82% of the dried catches per trip in the cool and warm seasons, respectively (Fig. 9).

4 Discussion

4.1 Characteristics of seagrass fishing ground and macroinvertebrate assemblage

We surveyed and mapped the seagrass habitats in the coastal fishing area, characterized the abundance and diversity of macroinvertebrates in one of the largest nearshore seagrass beds in Southwest Madagascar by sampling the catches of mosquito net trawl fishers, and estimated the economic importance of macroinvertebrate bycatch to these fishers. The fishery-dependent sampling method enabled the collection of relevant data on macroinvertebrate distribution over a medium-scale area (approximately 20 km^2) and period (8 months), and among varying habitat types. The wide size range and diversity of macroinvertebrates captured suggest that mosquito net trawl is an effective sampling gear of seagrass vagile macroinvertebrate fauna. However, some spatial limitations occurred because catches were heterogeneously distributed among the hauls of each individual fishing trip (approximately 1000 s m^2). Fine-scale habitat-related factors likely influenced the spatial distribution of the macroinverte-

brate species as suggested by previous studies (Ansari et al., 1991; Heck and Wetstone, 1977; Stoner, 1980) and, consequently, the results of this study. Such spatial heterogeneity is common within seagrass beds because seagrass structure, complexity, and cover rate are dynamic factors that structure the diversity and/or abundance of the macroinvertebrate community (Fredriksen et al., 2010; Frost et al., 1999), as shown by the habitat-related effects on the richness and abundance of the four dominant taxa in this study. Of note, the highest diversity of phanerogams and seagrass habitats was observed in the highly targeted fishing areas, which further suggests that the distribution of macroinvertebrate and fish target taxa interact with seagrass characteristics. Monitoring the catches of mosquito net trawl fishing at a finer spatial scale, for example at the scale of a single haul (instead of a fishing trip) through an experimental or fishery-dependent survey would therefore be preferable in subsequent ecological investigations of seagrass community spatial patterns.

We found that most of the 43 taxa identified in this study occurred at a low density, while assemblages were dominated by a small number of crustacean species from the genera *Thalamita* (Portunidae), *Processa* (Processidae), *Penaeus* (Penaeidae), and *Alpheus* (Alpheidae). Consistent patterns of tropical seagrass vagile macroinvertebrate richness and dominance have been previously reported in tropical regions. For instance, Barrilli et al. (2021) recorded 41 species of arthropods in a seagrass area in Brazil using a bottom trawling boat with a 20-mm mesh size in the collecting codend, at higher speed (two knots) than that of the present study. In our study area, the genus *Thalamita* (Portunidae) constituted the bulk of the biomass and density of the macroinvertebrate

seagrass assemblage throughout the study period, as observed by Hamid et al. (2020) in Indonesia and by Kunsook and Dumrongrojwathana (2017) in seagrass beds at Kung Krabaen Bay, Thailand.

Our results suggest that the macroinvertebrate assemblage has likely changed over the last 30 years, although empirical evidence is limited in the literature. In an unpublished study using nocturnal push-net sampling on 3-m² stations (i.e., 15,000 times smaller than the mean swept areas in our study) in a neighboring seagrass area, Bigot (1992) found a similar richness of vagile macroinvertebrates and dominance by crustaceans, but a marked difference in taxonomic composition. For instance, some very common taxa reported in this previous study (e.g., *Hyppolyte kraussiana* [Hyppolitidae], *Periclemenes seychellensis* [Palaemonidae], *Latreutes pygmaeus* [Latreutidae], mollusks, and amphipod species; Appendix B) were not observed in our study despite a considerably larger survey spatial coverage. Conversely, the previous assemblage was not dominated by the same crustacean taxon (i.e., *Thalamita*), a very mobile macroinvertebrate that may not have been caught by the sampling technique conducted by Bigot (1992).

The present study suggests that the mosquito net trawl fishing has been one of the drivers of seagrass invertebrate community dynamics in the Bay of Toliara, although difference in sampling techniques and sampling effort may partly explain the above differences in the macroinvertebrate assemblage composition over time. Indeed the use of mosquito trawl nets has steadily increased since the 2010s, while it was unreported in the fishery in the 1990's (Laroche and Ramanarivo, 1995). According to our results, this trend has generated a strong, direct pressure on vagile crustaceans in seagrass beds over the years, which has likely modified the benthic macroinvertebrate assemblage.

Environmental causes of assemblage change may also be hypothesized. Changes in seasonal water, sediment discharge, and coastal sedimentation, and/or the lack of waste water treatment in the developing city of Toliara, among other environmental factors, may have induced significant disturbance of the nearshore marine environment of the Bay of Toliara over the last three decades (Bruggemann et al., 2012), with expected effects on seagrass characteristics and macrobenthic species composition. Macroinvertebrate communities are indeed particularly vulnerable to physicochemical changes in the environment (Floury et al., 2013; Murphy et al., 2011).

4.2 Seagrass macroinvertebrates are valuable by-catch resources

To our best knowledge, this is the first study to assess the contribution of macroinvertebrates to the catches and income of mosquito net trawl fishers in tropical seagrass beds. Although trawl net fishers primarily target fish, we found that macroinvertebrate catches were valued by-catch providing significant economic surplus and, to a smaller extent, supporting food security (Unsworth et al., 2014b). The taxa used for animal feed clearly dominated the catch weight, but yielded a lower income than more valuable crabs and shrimps marketed fresh for human consumption. Based on our results, the estimated annual income per fisher would reach

approximately USD 1000 year⁻¹, assuming 0.5 trips per day all year long (Behivoque et al., 2021). In the context of rural household poverty that characterizes Southwest Madagascar, the use of mosquito net trawls is an adaptive response to declining reef fish catch and limited range of alternative economic activities, as observed in other countries in the Indian Ocean (Badjeck et al., 2010). The national ban on such nets in Madagascar in 2015 (Fishing Code Chapter 4 Article 17 of Law #2015-053) threatens the livelihoods of hundreds of poor households and has consequently been poorly enforced despite the support of environmental organizations. It is predictable that the use of mosquito net trawls will further expand as a way to diversify target resources and maintain fishing household income, which would exacerbate the above-mentioned negative effects of this gear on seagrass and coral reef ecosystems, and fisheries, including target seagrass fish resources. Mosquito net trawl is expected to raise similar issues of overexploitation of fish resources as those of beach seine equipped with mosquito net codend, due to high shares of juvenile fishes in catches (Tietze et al., 2011). Small-scale fishing in Madagascar is very important nutritionally and economically which makes sustainable management difficult, and there are few opportunities for livelihood diversification, making fishers very dependent on fishing. Village-based aquaculture, specifically algae production, has however become popular in the country as a possible alternative or supplementary activity in a number of coastal fishing communities (Chaboud, 2006), as observed in the Caribbean (Litzler, 2010).

The results of this empirical study in Southwest Madagascar suggest that an ecosystem-based approach is required to manage seagrass fisheries in a way that meets the socioeconomic needs of vulnerable fishers while limiting negative ecological disturbances and negative feedback on those fishers using alternative gear types. Addressing such a complex management question, e.g., by controlling trawl net length and numbers in coastal villages, would involve building strong institutional and local social capacity as well as cross-sector collaboration between human health, environment, and fishery organizations (Trisos et al., 2019). Creating an enabling governance context would also be part of that strategy.

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Appendix AList and abundance of macroinvertebrate taxa observed in mosquito trawl net in the Bay of Toliara, Southwest Madagascar, from August 2018 to February 2019 ($n=217,080$)

Family	Taxa	Total abundance in samples (number of individuals)	Total weight (kg)
	<i>Thalamita mitsiensis</i>	138,837	511.9
	<i>Portunus longispinosus</i>	670	6.2
	<i>Portunus sanguinolentus</i>	1060	17
	<i>Scylla cf serrata</i>	101	0.9
Portunidae	<i>Potopthalmus nacreus</i>	82	0.7
	<i>Thalamita crenata</i>	26	0.3
	<i>Portunus pelagicus</i>	91	4.8
	<i>Charybdis japonica</i>	78	0.4
	<i>Thalamita sp</i>	29	0.1
Processidae	<i>Processa japonica</i>	32,292	13.7
	<i>Nikoides danae</i>	5609	1.3
	<i>Penaeus semisulcatus</i>	13,526	13.6
Penaeidae	<i>Metapeneus monoceros</i>	2305	5.2
	<i>Penaeus Japonicus</i>	2403	6.5
	<i>Penaeus caniculatus</i>	3695	0.4
Alpheidae	<i>Alpheus sp</i>	5479	5.9
	<i>Alpheus crassimanus</i>	3407	2.6
	<i>Leander tenuicoris</i>	3138	3.7
Palaemonidae	<i>Periclimenes spiniferus</i>	256	0.8
	<i>Periclemenes sp</i>	142	0.1
Hippolytidae	<i>Saron marmoratus</i>	934	1.1
	<i>Sepia sp1</i>	763	5
Sepiidae	<i>Sepia sp3</i>	250	0.1
	<i>Sepia sp2</i>	235	1.5
Callapidae	<i>Callapa hepatica</i>	361	6.3
	<i>Squilla indet. 2</i>	218	0.2
	<i>Squilla indet. 4</i>	166	4.5
Gonodactylidae	<i>Gonodactylus sp</i>	135	0.4
	<i>Gonodactylus bicarinatus</i>	8	0.1
Parthenopidae	<i>Rhinolambrus(cf contrarius /pelagicus)</i>	182	0.5
Matutidae	<i>Astoret picta</i>	106	2.8
	<i>Octopus 1</i>	76	2.1
	<i>Octopus 2</i>	1	0.1
Octopodidae	<i>Octopus 4</i>	11	0.1
	<i>Octopus 5</i>	1	0.1
	<i>Octopus 3</i>	26	8.9
Latreilliidae	<i>Latrellia cf metanessa</i>	46	0.32
Xanthidae	<i>Leptodius cf nudipes</i>	55	0.4
Leucosiidae	<i>Leucosiidae indet.</i>	17	0.2
Paguridae	<i>Paguridae indet.</i>	11	0.6

Appendix B

Comparison of the species recorded by Bigot (1992) and Herinirina et al. (this study)

Family	Taxa	in 1992	in 2019
Molluscs	<i>Aplysia sp</i>	*	
	<i>Bulla sp</i>	*	
	<i>Calliostoma sp</i>	*	
	<i>Cerithium sp</i>	*	
	<i>Columbella sp</i>	*	
	<i>Cyprae annilus</i>	*	
	<i>Cyprae lamarokii</i>	*	
	<i>Dolabella variegata</i>	*	
	<i>Nassarius coronatus</i>	*	
	<i>Phasianella variegata</i>	*	
	<i>Smaragdia sp</i>	*	
Anomoures	Paguridae	*	*
Caridae	<i>Aplheus crassimanus</i>	*	*
	<i>Alpheus sp</i>	*	*
	<i>Ampelisca tenuicornis</i>	*	
	<i>Amphithoides mahafalensis</i>	*	
	<i>Catharidus suarezensis</i>	*	
	<i>Dexaminella aegyptiaca</i>	*	
	<i>Eriopisella sechellensis</i>	*	
	<i>Hippolyte kraussiana</i>	*	*
	<i>Ichyocerorithium rostratum</i>	*	
	<i>Latreutes pygmaeus</i>	*	*
	<i>Leander tenuicornis</i>	*	*
	<i>Lembos teleporus</i>	*	
	<i>Maxillipius rectitelson</i>	*	
	<i>Nassarius coronatus</i>	*	
	<i>Nickoides danae</i>	*	*
	<i>Periclemenes seychellensis</i>	*	*
	<i>Periclemens sp</i>	*	*
	<i>Periclemenes spiniferus</i>	*	*
	<i>Polycheria atolli</i>	*	
	<i>Pontophilus pilosus</i>	*	
<i>Peneidae</i>	*	*	
<i>Saron marmoratus</i>	*	*	
<i>Smaragdia souwerbiana</i>	*		
<i>Tethygenia pacifica</i>	*		
Brachioures		*	
Annelids		*	
Arthropods	<i>Astoret picta</i>		*
	<i>Callapa hepatica</i>		*
	<i>Charybdis japonica</i>		*
	<i>Gonodactylus bicarinatus</i>		*
	<i>Lattrellia cf metanessa</i>		*
	<i>Leptodius cf nudipes</i>		*
	<i>Leucosidae</i>		*
	<i>Portunus longispinosus</i>		*
	<i>Portunus pelagicus</i>		*
	<i>Portunus sanguinolentus</i>		*
	<i>Potophtalmus nacreus</i>		*
	<i>Rhinolambrus cf contrarius /pelagicus</i>		*
	<i>Scylla cf serrata</i>		*
	<i>Thalamita crenata</i>		*
	<i>Thalamita mitsiensis</i>		*
<i>Thalamita sp</i>		*	