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LARGE BODIED FISH COMMUNITIES AND DRIVERS OF USE IN THE SHALLOW WATERS OF A COASTAL HABITAT MOSAIC

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ABSTRACT

Shallow coastal habitats support diverse communities of larval and juvenile fishes, providing refuge from predation while facilitating growth. The function of shallow coastal habitats as nurseries has created considerable interest in managing these areas. However, shallow coastal habitats may be important for benefits that extend beyond nursery function. Contemporary research suggests large bodied fishes also occur in shallow coastal habitats, and that predation may be a more common activity within nursery habitats than previously thought. Shallow coastal habitats may be utilised frequently by large bodied fishes and provide additional ecological functions for these poorly studied fish communities.

Few studies have considered cross-shore sampling of the shallow coastal habitat mosaic, thus current knowledge on how fish communities may differentially use micro-habitats within the shallow coastal habitats is limited. For this thesis the shallow coastal habitat mosaic was delineated into three continuous micro-habitats: the littoral, intertidal and subtidal habitats. The littoral habitat occurs at the interface of the terrestrial and the marine environment and is fully exposed during low tides. Contiguous from the littoral habitat, the intertidal habitat is exposed at varying depths depending on daily tidal cycles. Extending seaward from the intertidal habitat is the subtidal habitat that is always inundated with water. Although some research has focused individually within one of these micro-habitats, no research is yet to consider them as a broader connected ecosystem.

A shallow coastal habitat mosaic in Cleveland Bay, northern Queensland, Australia, was sampled using a large (115 mm) mesh monofilament gill net over a one year period. The community of large bodied fishes (> 200 mm) was defined and their distribution across the mosaic of littoral, intertidal and subtidal habitats identified. Further, the influence of salinity, temperature, and dissolved oxygen on fish community structures was also investigated. In an attempt to determine drivers of habitat use, ecological functions including life history stage, reproductive activity and foraging activity which may potentially influence how large bodied fishes use the habitat mosaic were investigated.

A total of 1119 individuals from 26 families and 36 species were sampled, though four families accounted for 79.1% of the total sample (Latidae, Polynemidae, Ariidae, and Carcharhinidae). Fish communities sampled were diverse and significant differences in community structure were present between habitats. The littoral and subtidal communities were significantly different from each other with the intertidal community sharing some species-specific characteristics with both the littoral and subtidal. Teleosts were the dominant group in the littoral and intertidal habitats while sharks dominated the subtidal habitat. Very few habitat generalists, species that occurred in all three habitats, were sampled. Clear habitat preferences and avoidance occurred with most of the dominant species entirely absent from at least one of the habitats. A relationship between environmental factors (temperature, dissolved oxygen and salinity) and fish assemblages was identified. These patterns are likely driven by a combination of biological and ecological processes, however further research will be necessary to better understand the role of these processes in shaping the large bodied fish communities of shallow coastal waters.

Life history stage was defined for 977 individuals from 26 families and 28 species. Reproductive and foraging activity was determined for the most abundantly sampled teleost and sharks. Ontogenetic shifts in habitats use were apparent with juvenile teleosts dominant in the littoral habitat while adult teleosts were dominant in the intertidal habitat (few teleosts were caught in the subtidal habitat). In contrast to teleosts, sharks were mostly present as young-of-the-year (YOY) and juveniles, suggesting the intertidal and subtidal habitats both act as a shark nursery (only three sharks were captured in the littoral habitat). Interestingly, YOY sharks were more common in the intertidal habitat as compared with the subtidal

suggesting an ontogenetic shift in habitat use occurs for young sharks as well. Imminent spawning activity (defined by the presence of hydrated oocytes in the ovaries of females) was only observed in *E. tetradactylum* in all three habitats. Shark reproductive activity (defined by visible eggs or embryos and an enlarged/distended uterus) was observed in one shark, *Rhizoprionodon taylori*, with parturition observed in the subtidal habitat. Active foraging was evident in *L. calcarifer, E. tetradactylum* and *P. argenteus* with gut contents suggesting foraging occurred throughout the habitat mosaic. Some species specific foraging behaviours were identified with *L. calcarifer* consuming mostly teleosts in the littoral habitat, and crustaceans in the intertidal habitat. The behaviour of switching prey may allow *L. calcarifer* to exploit and dominate the littoral and intertidal habitats. Teleosts prey items were also predominant in the guts of *R. taylori* and *Carcharhinus tilstoni/limbatus* though opportunistic foraging was observed with *Arius* spp. eggs common in both shark guts. The use of the intertidal and subtidal habitats by young sharks may be encouraged by a seasonal abundance of nutrient rich food sources such as *Arius* spp. eggs.

This thesis illustrates that large bodied fish are common in the shallow coastal habitat mosaic and that the habitat mosaic provides many benefits beyond nursery function. Future research should sample both large and small fish communities simultaneously to completely understand the importance of shallow coastal waters to all fishes regardless of size or life history stage. The efficacy of future management will benefit from an understanding of all fish communities within, and ecological services provided by shallow coastal water ecosystems.

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CHAPTER 1. GENERAL INTRODUCTION

Plate 1. Cleveland Bay on an afternoon sampling trip

The shallow waters of marine coastal habitats are crucial components of tropical marine ecosystems. The increased availability of sunlight to shallow coastal habitats allows primary producers, such as algae and seagrasses to flourish (Burke et al. 2001). The primary producers are the basis for extensive and productive food webs and ecosystems (Orth et al. 2006, Eyre et al. 2011). Shallow coastal habitats are very diverse in structure and may include estuaries, mudflats, wetlands and mangrove forests. The combined high productivity and diversity in structure of shallow coastal habitats allows a diverse array of fish species to inhabit these areas (Groombridge et al. 2000).

Shallow coastal habitats are highly dynamic environments that are exposed to large fluctuations in environmental factors (i.e. depth, temperature, salinity) driven by tidal, lunar and/or seasonal cycles (Blaber et al. 1989). The tidal variation in vertical space magnifies these parameters creating a habitat that may be extreme in temperature, salinity and oxygen levels. For example, during daytime low tides, temperatures may rise causing dissolved oxygen to decrease producing a hypoxic environment in which few marine fish can survive (Horn et al. 1999). Freshwater input can also cause rapid changes in salinity within shallow coastal habitats. For example, salinity can fluctuate during monsoon seasons when freshwater floods inundate the coastal habitat (Duke & Wolanski 2001). Shallow coastal habitats are also subjected to storm events such as cyclones, tsunamis and storm surges which can alter habitat structure and function, or extreme weather events can create permanent morphological changes (Krishnamurthy 2010). In comparison to offshore waters, shallow coastal habitats are chaotic environments with little environmental stability.

Shallow coastal habitats are an important source of protein for the global community by producing 90% of marine fish catch (Sherman 1993, Hinrichsen 1998). Moreover, the fish consumption per capita has undergone a global increase from 9.9 kg in 1960 to 16.4 kg in

2005 (FAO 2008) indicating that the dependence on shallow coastal habitats for marine-based protein is increasing. In many developing countries, marine based protein can comprise up to 50% of the total protein consumption (FAO 2008). Clearly, shallow coastal habitats are very important ecosystems that contribute to the food security of the global community.

Human civilizations preferentially settle close to coastal habitats to benefit from and exploit available resources such as fertile farmland, freshwater and aquatic food sources (Kennett & Kennett 2006). Currently, 61% of the world's human population occurs along coastal margins (Agardy et al. 2005) and not surprisingly habitat degradation is an increasingly common concern (Airoldi & Beck 2007, Hanski 2011). Anthropogenic habitat degradation can create biological changes with a decline of marine organisms such as sea turtles, marine mammals, fish and marine invertebrates resulting in species extinctions and profound shifts in ecosystems (Beck et al. 2001, Wen et al. 2010, Santos et al. 2011, Verdiell-Cubedo et al. 2012a). The global human population of 2000 was estimated to increase 47% by 2050 (UN 2004), which will further exacerbate anthropogenic pressures on coastal ecosystems.

The effects of fishing on shallow coastal habitats can be detrimental (Thronson & Quigg 2008, Wen et al. 2010). Ecological shifts can occur in fish communities when the overfishing of single species extends to a point that even carefully managed rebuilding and recovery efforts may fail (Trimble et al. 2009). The consequences of extreme overfishing was observed in some Canadian fisheries where impoverished populations and large scale shifts in ecosystem structure and function was responsible for a 50% reduction in harvests over a 30 year period (Hutchings et al. 2012). While humans remain dependent on marine based protein for sustenance, it is essential to better understand those ecosystems that support protein production.

If current trends in shallow coastal habitat usage continue, effective management and conservation practices of all human activities will be crucial in maintaining healthy and productive shallow costal habitats. Shallow coastal habitats will require adaptive and effective management to meet global marine protein demands. To mitigate anthropogenic impacts practices such as habitat restoration, marine protected area declarations, fisheries management and ecosystem-based assessments (Agardy 2003) are increasingly utilised. However, management intervention can more effective when strategies are developed and designed around a robust and comprehensive knowledge of the impacted species or ecosystem.

Current knowledge suggests shallow coastal habitats are important nurseries for teleosts (Lazzari et al. 2003, Franco et al. 2006), sharks (Castro 1993, Francis 2013) and rays (Goodman et al. 2011, Dale et al. 2013). Nursery habitats offer larval and juvenile fish refuge from predators while providing increased access to food sources. For example, Able et al. (2013) identified a surf zone in New Jersey as functioning as an important nursery habitat for three species of teleost, *Pomatomus saltatric*, *Mugil curema* and *Trachinotus carolinus*, with the habitat utilised as a nursery throughout the year. The nursery function of shallow coastal habitats highlights their ecological value and contribution to marine ecosystems. Thus, shallow coastal habitats are areas of interest for fisheries management.

Contemporary research has suggesting shallow coastal habitats support large and mature fishes (Tobin et al. 2014) that use these habitats for ecological functions such as foraging (Chong et al. 1990, Krumme et al. 2008), spawning (Præbel et al. 2009, Quinn et al. 2012) and parturition (Dibattista et al. 2008). For example, Franco et al. (2006) identified shallow coastal seagrasses as critical spawning habitat for adult grass gobies, *Zosterisessor ophiocephalus* while McCallister et al. (2013) describe the importance of shallow coastal habitats in Florida for a parturition by a diverse array of tropical sharks. Identifying the additional ecological values that shallow coastal habitats support is necessary in order for management to preserve these functions.

The knowledge that shallow coastal habitats are important nursery habitats (Blaber et al. 1995, Ryer et al. 2010, Able et al. 2013) has been a focus of management for natural resource managers, however these habitats may provide additional ecosystems functions which may be excluded from current management practices. Mitigating the effects of human populations on coastal ecosystems requires a comprehensive understanding of the fish communities that utilise them and why. I aim to address this knowledge gap by identifying large bodied fish communities in a shallow coastal habitat mosaic and to determine possible drivers of habitat use within this thesis.

The shallow coastal habitat mosaic in Townsville, Australia functions as a nursery habitat for sharks (Simpfendorfer & Milward 1993, Chin et al. 2013) and supports local commercial gill net fisheries (Harry 2011, Tobin et al. 2014) that target mostly teleosts including *Lates calcarifer* (barramundi), *Platycephalus fuscus* (flathead) and *Eleutheronema tetradactylum* (blue threadfin). A purposed plan to extend the Townsville Port (POTL 2010) may alter the structure of the shallow coastal habitat mosaic and thus alter the fish communities that use them. Clearly there is a need to understand what communities of fish use the coastal habitat and why. Such knowledge is mandatory to guide management and mitigate potential development impacts on the fish communities within.

1.1 PROJECT STRUCTURE AND OUTPUTS

This study was designed to fill a critical knowledge gap that is “What large bodied fish use the habitat mosaic of shallow coastal waters, and what functions do species gain from those habitats?”

The specific project aims were to:

1. describe the large bodied fish (> 200 mm) communities that inhabit the littoral, intertidal and subtidal habitats of a tropical shallow water costal mosaic in North Eastern Australia, and
2. identify the ecological functions (reproduction, foraging and nursery) that species gain from those habitats

CHAPTER 2. LARGE TROPICAL FISHES AND THEIR USE OF THE NEARSHORE LITTORAL, INTERTIDAL AND SUBTIDAL HABITAT MOSAIC

Plate 2. Gillnet sampling in the intertidal habitat (photo credit Centre for Sustainable Tropical Fisheries and Aquaculture)

2.1 INTRODUCTION

Shallow coastal habitats are often identified as supporting important nursery function as a result of a high abundance of larval and juvenile teleosts (Blaber & Blaber 1980, Faunce & Serafy 2006, Nagelkerken 2009) as well as young-of-the-year and juvenile sharks (Simpfendorfer & Milward 1993). Nursery habitats provided refuge from predators and increased food sources to larval and juveniles fishes (Blaber et al. 1995, Baker & Sheaves 2009a, Able et al. 2013). Shallow coastal habitats are diverse and encompass a wide range of habitat types including estuaries, mangroves and wetlands. Sheaves (2009) suggested that these habitats create a coastal ecosystem mosaic that links freshwater, brackish and marine habitats. The coastal ecosystem mosaic is connected to offshore waters through the export of nutrients, fish migrations, and provides a habitat for the reproduction of many offshore species (Sheaves 2009). This connectivity means that shallow coastal habitats may be important habitats that contribute to critical life history stages of many offshore species (Nagelkerken 2009).

Effective management of the coastal ecosystem mosaic is becoming progressively more challenging because of increasing industrial activities and the continual development of coastal communities (Stallings 2009, Morley et al. 2012). Few shallow coastal habitats have been undisturbed by coastal development and modifications (Blaber et al. 2000). In addition, fishing pressure is often high in these easily accessible habitats (Jackson et al. 2001, Cooke & Cowx 2004). Such cumulative pressures have resulted in impoverished fish communities (Shahidul Islam & Tanaka 2004, Courrat et al. 2009). In order for management to successfully mitigate these impacts, we must first understand what species occur in the shallow coastal habitat mosaic and what function these areas may provide.

The continuous nature of the shallow coastal habitat mosaic means clearly defining individual habitats is often difficult. Unfortunately, few studies clearly define the micro-habitats of the shallow coastal habitat mosaic and often variant terminology is used. For example a range of definitions exist for describing intertidal and subtidal habitats (Sheaves 1992, Dorenbosch et al. 2004, Nagelkerken & van der Velde 2004), with some authors combining the two habitats into an overall near shore environment (Robertson & Duke 1987). In addition, Verdiell-Cubedo et al. (2012b) defined the littoral habitat of a coastline as having a maximum depth < 1 m while Layman (2000) sampled a shallower depth range (<0.4 m) and introduced the term "shallow-surf zone" in place of littoral habitat. Here we consider the shallow coastal habitat mosaic to be comprised of three contiguous micro-habitats – the littoral, intertidal and subtidal habitats (see Fig. 2.1). The littoral is bound on the landward margin by the highest astronomical tide (HAT) and on the seaward margin by the smallest high tide and is fully exposed during low tides. The abutting intertidal extends from the smallest high tide, to the lowest astronomical tide (LAT) and is inundated to varying extents except on the lowest astronomical tide. The subtidal habitat extends seaward beyond the LAT and is contiguous with the wider offshore environment.

No study has yet considered the littoral, intertidal and subtidal habitats concurrently to understand how fish communities may structure themselves among these available habitats. Shallow coastal habitats are dynamic environments, therefore assuming similarities among fish communities across habitats may be incorrect. For instance, Tobin et al. (2014) sampled the intertidal habitat of Cleveland Bay, Australia, describing seasonal use by 30 species of teleost and 14 species of sharks and rays. However, it is apparent from the work of Simpfendorfer and Milward (1993) in the adjoining subtidal habitat that community structure varies markedly with the subtidal dominated by sharks rather than teleosts. Of the few studies that have concurrently sampled adjacent intertidal and subtidal habitats, Castellanos-Galindo et al. (2010) concluded the fish communities within the intertidal contained a distinct subset of species from those within the subtidal.

In addition to habitat effects, fish communities may also be influenced by the environment. For example, Schaffler et al. (2013) identified juvenile fish communities within a coastal seagrass habitat were structured not only by habitat complexity but also gradients of temperature and salinity. Clearly determining fish species composition and how the fish species utilise littoral, intertidal and subtidal habitats requires concurrent sampling of fish communities and monitoring of abiotic variables.

Previous research on littoral, intertidal and subtidal habitats has identified these habitats as nurseries from the high abundances of juvenile fishes inhabiting these areas (Blaber et al. 1989, Sheridan & Hays 2003, Ooi & Chong 2011). However, contemporary research is suggesting the abundance of large bodied fishes could be greatly underestimated in the coastal shallow water mosaic due to sampling method biases (Baker & Sheaves 2006, Tobin et al. 2014). Many of the sampling methods that have been used in littoral, intertidal and subtidal habitats are selective for small, slow moving animals (Faunce & Serafy 2006) and are not amenable for large mobile ones. Therefore, this study describes the community of large bodied fish (> 200 mm) within three habitats of a shallow embayment on the north east coast of Australia. The littoral, intertidal and subtidal habitats were sampled seasonally with the use of large-mesh gillnets over a one year period. Additionally, the abiotic influences on the fish communities were investigated to provide an understanding of the importance of these factors in defining community structure.

2.2 METHODS

2.2.1 Study Site and Sampling Methodology

Cleveland Bay is an embayment on the north-eastern coast of Australia near Townsville, Queensland that is approximately 27 km wide and covers an area of 225 km^2 with fringing mangrove forest, mud and sand flats occurring on the landward edge (Fig. 2.1a). The sampled area within Cleveland Bay was located within the north-western aspect of the bay (Fig. 2.1b) and subjected to semidiurnal tides with a maximum range of 4.2 meters. The landward margin of the littoral habitat was defined by a sharp gradient (1:10) spanning approximately 50 metres followed by a gradual gradient (< 1:100) of compact sand and mud ending at the lowest point of high tide (Fig. 2.1c). The littoral habitat was exposed throughout much of the tidal cycle and was fringed by patchily distributed *Rhizophora stylosa, Ceripos tagal*, and *Avicennia marina* mangroves near the terrestrial margin. The intertidal habitat was generally > 1000 m in width, and similarly composed of compact sand and mud. Seaward from the intertidal habitat, the subtidal habitat has a similar gradient to the intertidal with compact sand giving way to softer mud. These definitions generally represent the littoral, intertidal and subtidal micro-habitats within the study site as the actual positions of the HAT and LAT were not rigorously surveyed.

Sampling occurred on a seasonal basis from September 2012 to August 2013 (Summer; Dec. – Feb., Autumn; March – May, Winter; June – Aug., Spring; Sep. – Nov.) and the littoral, intertidal and subtidal habitats were sampled at least twice each within each season. As far as was feasible, each habitat was randomly sampled across the available range of tidal states (high, low, ebb and flood tides) and thus heights (water depth). A balanced and structured sampling design was not possible due to the limiting effects of local weather conditions. Winds stronger than 15 knots generated small surf that prevented sampling in the intertidal and littoral habitats of the sampling site, and logically the littoral habitat was inaccessible on low tides. Depth was recorded at the start and end of each sample and an average depth taken to represent each sample. Salinity, temperature and dissolved oxygen were recorded with an YSI Multi-Probe (Model 85; YSI Incorporated) for each sample

Fish communities were sampled with a single monofilament gillnet (300 m x 2.5 m constructed with 18 ply, 115 mm stretched mesh monofilament). Net length was limited to 200 m while sampling in the subtidal habitat to reduce the risk of interactions with local marine mega fauna such as *Dugong dugong*. The sampling net was always deployed perpendicular to the shoreline and allowed a minimum soak time of 30 minutes. Each time the net was deployed and retrieved was considered a sample. The geographic location of each deployment was recorded using a GPS and sampling effort mapped within each habitat. Captured individuals were identified to species level where possible and measured (fork length for teleosts, stretched total length for sharks, and disc width for rays, mm). Teleost of the family Ariidae were identified to family level only. Two tropical sharks, *Carcharhinus tilstoni* and *Carcharhinus limbatus* are not distinguishable based on phenotypic characteristics alone (Harry et al. 2012) and hybridisation also occurs (Morgan et al. 2012); as such individuals were identified as *C. tilstoni – C. limbatus* complex.

2.2.2 Data Analysis

Non-parametric testing was used to describe the effect of habitat on depth, water temperature, salinity and dissolved oxygen. Box plots were used to demonstrate the relative variability in each of these factors across habitats.

Catch-per-unit-effort (CPUE) was calculated for each species within each sample as number of fish caught per 100 m net hour and was used as an index of relative abundance. Initially the effect of habitat on community structure was explored at the broad taxonomic level of teleost, shark and ray. A chi squared contingency table using count data tested if each taxonomic group was similarly represented within each habitat. A three-way analysis of variance (ANOVA) tested the influence of taxonomic group, season and habitat type (littoral, intertidal and subtidal) on relative abundance. The effect of habitat on diversity was explored with species richness (N). The effect of habitat on length of fish captured was tested with ANOVA on the most abundant species sampled to meet the requirements of ANOVA analysis. Where significant differences were apparent, post hoc analyses were used to define homogenous groups.

To further explore the influence of habitat and season on community composition, non-parametric multi-dimensional scaling (nMDS) was performed using the software PRIMER (v.6.2.1). A Bray-Curtis similarity matrix was created based on log transformed count data. To nullify the effects of samples with few fish and the limited sampling from weather constraints, samples were randomly grouped within each combination of habitat and season. Log transformation buffers the influence of highly abundant species, and the removal of rare species ($n < 5$ individuals across all habitats) avoids these species driving the results. Analysis of similarity (ANOSIM) tested for difference in fish community structure between habitats and seasons. Where significant differences were detected, similarity percentage (SIMPER) analysis was used to identify species with the highest contributions to each fish community (Clarke 1993). A similarity index (ratio of similarity/standard deviation) was also calculated for each species to evaluate each species importance as a discriminating species for each fish community.

To determine if relationships occurred between the fish communities and four environmental variables (water temperature, salinity, dissolved oxygen and habitat) a canonical correspondence analysis (CCA) was used. Water temperature (°C), salinity (ppt) and dissolved oxygen (%) were treated as continuous variables while habitat was treated as a categorical variable. The CCA was produced using the vegan package (Oksanen et al. 2013) in the statistical software ‘R’ (R Development Core Team 2008). A permutation test (499 permutations) was used to determine the significance of the environmental variables on the community sampled.

2.3 RESULTS

2.3.1 Nearshore habitat sampling and characteristics

A total of 72 net shots were completed in the nearshore habitat; 11 net shots in the littoral habitat, 38 net shots in the intertidal habitat and 23 net shots in the subtidal habitat. The water depth varied significantly among all habitat comparisons with a mean depth of 0.98 m ± 0.04 s.e. for littoral habitat samples, 1.48 m ± 0.06 s.e. for the intertidal and 3.66 m ± 0.07 s.e. for the subtidal (Kruskal-Wallis, d.f. = 2, $P < 0.001$)(Fig. 2.1a) with outliers indicating sampling conducted at the deepest and shallowest points during the tidal change. Water temperature varied significantly among habitats (Kruskal-Wallis, d.f. = 2, $P < 0.001$) with a gradient of decreasing temperatures across the littoral (mean 27.60°C ± 0.55 s.e.), intertidal (mean 26.40°C ± 0.26 s.e.) and subtidal (mean 25.60°C ± 0.27 s.e.) habitats (Fig. 2.1b). Post hoc analysis demonstrated a significant difference between the littoral and subtidal habitats, and clearly temperature was most stable in the littoral habitat (Fig 2.1b). Salinity did not vary among habitats (average salinity of 34.25 ± 0.35 s.e. for the littoral, 35.08 ± 0.12 s.e. for the intertidal and 35.18 ± 0.08 s.e. for the subtidal habitat)(Kruskal-Wallis, d.f. = 2, $P = 0.26$), though salinity was clearly most stable in the subtidal habitat (Fig. 2.1c). Dissolved oxygen within the littoral (mean 89.35% of saturation ± 1.49 s.e.) and intertidal (mean 91.27% of saturation ± 0.59 s.e.) and subtidal (mean 87.11% of saturation ± 0.37 s.e.) varied significantly between habitats (Kruskal-Wallis, d.f. = 2, $P = 0.001$). Post hoc analysis demonstrated a significant difference occurred between the intertidal and the subtidal habitats (Fig. 2.1d).

2.3.2 Nearshore Community Characteristics

A total of 1119 individuals from 26 families comprising of 36 species were sampled from the inshore habitat mosaic. Three teleosts (Latidae, Polynemida, and Ariidae) and one shark (Carcharhinidae) family dominated (79.1%) the community (Table 2.1). The overall community was dominated by teleosts (69.6%) with 25 species from 19 families; fewer sharks (24.6%) with 7 species from 2 families; and a small contribution of rays (5.8%) with 5 species from 5 families. The proportion of each taxonomic group varied among the three habitats (χ^2, df = 4, $P < 0.001$) with teleosts dominant in the littoral and intertidal habitats, while sharks were dominant in the subtidal habitat (Fig. 2.3). Rays were absent from the littoral habitat and made minor contributions to the intertidal and subtidal communities. Within the littoral and intertidal habitats, teleost were 2.8 and 2.2 times more likely to occur, respectively, compared to the subtidal. In contrast, within the subtidal sharks were 10.7 and 47.3 times more likely to occur, respectively, than the intertidal and littoral (Fig. 2.3). Rays were 1.71 times more likely to occur in the intertidal than the subtidal habitat. More species were sampled in the intertidal (n = 34) than in the littoral (n = 18) and subtidal habitats (n = 19). The relative abundance of animals present was influenced by a significant interactive effect between habitat and taxonomic groups ($F_{4,71} = 17.1$; $P < 0.001$). The dominant taxonomic group in the littoral and intertidal were teleosts with sharks dominant in the subtidal, in contrast the least dominant taxonomic group or less common were sharks and rays in the littoral and rays in the intertidal and subtidal (Fig. 2.4).

Species-specific use patterns of the habitat mosaic were clear. Of the 17 most commonly sampled species (> 5 individuals) only 5 were present across all habitats with the remaining 12 absent in one of the three habitats (Table 2.1). No species was present in only one habitat. The most dominant species (*Lates calcarifer*) was not sampled in the subtidal habitat. The second and third most dominant species were teleosts *Eleutheronema* *tetradactylum* and *Arius* spp which occurred in all habitats. In contrast, the three most dominant sharks (*Rhizoprionodon taylori, Carcharhinus fitzroyensis*, and *Carcharhinus tilstoni/limbatus*) and the most dominant ray (*Anoxypristis cuspidata*) were not sampled in the littoral habitat, but occurred in the intertidal and subtidal habitats. Only one shark (*Carcharhinus amboinensis*) occurred in all three habitats, though there was a clear preference for the subtidal habitat as compared to the intertidal and more so the littoral habitat.

To determine if fish length distribution varied between habitats, the nine most abundant species were analysed; *L. calcarifer, E. tetradactylum*, *Arius* spp., *R. taylori, C. fitzroyensis*, *C. tilstoni/limbatus, A. cuspidata*, *C. amboinensis,* and *P. argenteus*. Significantly smaller *E. tetradactylum* were sampled in deeper subtidal waters than in the shallower waters of the littoral (Tukey HSD, $P < 0.05$), or the intertidal habitats (Tukey HSD, $P < 0.05$). The trend was reversed for *C. amboinensis* and *A. cuspidata* with significantly larger individuals sampled in the deeper subtidal waters as compared with the shallower intertidal waters (Tukey HSD, $P < 0.05$; $P < 0.001$, respectively). For *L. calcarifer* and *P. argenteus* fork length did not vary between the littoral and intertidal habitats (ANOVA, d.f. = 1, $P = 0.5228$; d.f. = 1, $P = 0.1346$). Additionally, *Arius* spp. fork length did not vary between the littoral, intertidal and subtidal habitats (ANOVA, d.f. = 2, $P = 0.1346$).

2.3.3 Habitat Effect on Community Structure

The fish communities structure varied significantly among habitats (ANOSIM R-statistic = 0.249, $P = 0.046$) but not seasons (ANOSIM R-statistic = 0.04, $P = 0.367$). The multiple pairwise comparison tests identified the littoral habitat community differed significantly from the subtidal community (R-statistic = 0.707, $P = 0.006$), though the intertidal community was not distinct from either the littoral (R-statistic = -0.061, $P = 0.592$)

or the subtidal (R-statistic = 0.271, $P = 0.058$). The nMDS ordination clearly showed separation of the littoral and subtidal communities with the intertidal community bridging the intermediate space (Fig. 2.6).

SIMPER analysis identified a clear shift between teleosts discriminating the communities of the littoral and intertidal habitats and sharks discriminating the subtidal habitat. Four teleost species, four teleost and one shark species, and three sharks and one teleost species were considered discriminating species for the littoral, intertidal and subtidal communities respectively (Table 2.2). The teleost, *Eleutheronema tetradactylum*, was the only species identified as being discriminant all three habitat communities. Among all three habitats, the two most discriminating species contributed a similar cumulative contribution of around 64% (Table 2.2). However, the similarity index (ratio of similarity/standard deviation) of the two most discriminating species within each habitat displayed large variations (range 0.76 – 7.02) suggesting the discriminating strength of species varied considerably among habitats (Table 2.2).

The CCA revealed a relationship occurred between the fish communities and three environmental variables; habitat, salinity and temperature (Table 2.3). The effects of salinity and temperature were largely independent as indicated by the perpendicular vectors (Fig. 2.7). The subtidal habitat was separate from the temperature, DO and salinity vectors, whereas the littoral and intertidal were parallel to the temperature vector. Further, the CCA clearly separates the subtidal and the littoral habitats with the intertidal between. Three sharks, *C. fitzroyensis*, *C. amboinensis* and *R. taylori*, occurred in greater numbers in the subtidal habitat while *C. tilstoni/limbatus* were more closely associated with the intertidal habitat and occurred near the salinity vector. Seven species of teleosts occurred between the littoral and intertidal habitats. *Eleutheronema tetradactylum* and *C. amboinensis* are located between the intertidal and subtidal. *Mugil cephalus, P. argenteus* and *S. commersonianus* showed strong association with the temperature vector. *Anoxypristis cuspidata* did not occur near any environmental vector or near the three habitats suggesting an environmental interactive effect or other environmental influences may affect their distribution.

2.4 DISCUSSION

The present study has contributed valuable knowledge about the large bodied fish communities within a nearshore shallow water mosaic and their use of the littoral, intertidal and subtidal habitats within. Prior research has generally been confined to sampling only one of these nearshore habitats (Simpfendorfer & Milward 1993, Tobin et al. 2014) and thus provides incomplete information about the diversity and dynamism of nearshore fish communities. The three habitats within the sampled shallow water mosaic had distinct community structures. Teleosts dominated the littoral habitat, sharks dominated the subtidal habitat, and the bridging intertidal habitat represented a mix of teleosts, sharks and rays. However, many of the species sampled were infrequently present with common species absent from at least one habitat. Our results demonstrate that the structure of large bodied fish communities may vary markedly between adjacent nearshore habitats. Importantly, this study demonstrated that the community of fish found in nearshore subtidal habitats cannot predict the community of fish found in the nearby littoral habitat.

While a small group of species were common generalist users of the littoral, intertidal and subtidal habitats, most of the abundant species demonstrated strong habitat preference patterns. Four teleost (*Arius* spp., *E. tetradactylum*, *P. kaakan*, and *N. soldado*) and one shark (*C. ambionensis*) species were generalist users, suggesting there were no barriers to generalist use and that each habitat served a useful purpose or ecological role. While generalist use may suggest species actively reside within each habitat for a specific purpose, alternatively habitat use could be as simple as moving between two adjacent habitats. Movement corridors have been described for leopard sharks, *Triakis semifasciata*, in Monterey Bay where adult females navigate through tidal channels to access intertidal foraging opportunities opened by flooding tides (Carlisle & Starr 2010). In the case of our study, more focused research is required to understand whether the four teleost and one shark species specifically reside within each habitat to attain a benefit, or alternatively use the intertidal habitat as a simple movement corridor. Additionally, identifying other movement corridors through adjacent habitats such as rivers and tidal channels would provide valuable information on species that were not present in one or two of the sampled micro-habitats.

Multiple ecological functions (nursery, foraging, and refuge) have been identified as being fulfilled within shallow coastal habitats for larvae and juvenile teleosts (Abrahams & Kattenfeld 1997, Blaber & Blaber 1980, Sheaves 2001), but for large bodied teleosts the ecological importance is uncertain. A common focus of historical research in shallow coastal habitats was that these habitats benefit larvae and juvenile teleosts by providing a number of ecological functions including nursery, foraging, and refuge (Lasiak 1981, Shenker & Dean 1979, Weinstein 1979). Contemporary research is starting to expand the concept of multiple ecological functions which may be provided by shallow coastal habitats by sampling larger mature fishes. However, batoid (i.e. rays and skates) communities have been described utilising shallow (1 – 3 m) coastal habitats possibly as a result of their unique dorso-ventrally flattened body suggesting batoids may play key roles in ecological structuring of coastal habitats (Vaudo & Heithaus 2012). Additionally, large teleosts and sharks have been described occurring in very shallow (<1 m) coastal waters (Tobin et al. 2014) possibly to utilise the habitats for similar ecological services which juveniles utilise these areas – increase foraging and refuge from offshore predation threats. Contemporary research is clearly demonstrating that shallow coastal habitats serve many functions beyond the protection of small and juvenile fishes (Baker and Sheaves 2009, Vaudo & Heithaus 2009, Tobin et. al. 2014).

Shallow coastal habitats may be attractive foraging grounds as the foraging success of large bodied teleosts increases (Sheaves 2001) because prey animals within shallow habitats have fewer options for evading predation. The higher abundances of teleosts in the littoral and intertidal may indicate these habitats are important for teleost foraging. Indeed Baker and Sheaves 2007 found that depth did not influence predation rates across a shallow depth gradient (0.2 to 3 m), highlighting that the shallow-water refuge paradigm may be too simplistic. The shallowest waters of our study site occurred in the littoral habitat where mangrove stands also occurred. While mangrove prop roots and pneumatophores may provide shelter for some small fishes (Laegdsgaard & Johnson 2001, Nagelkerken et al 2008), Primavera (1997) demonstrated continued foraging success (albeit at diminished rates) of L. *calcarifer* in such environments. For species such as *L. calcarifer*, *P. argenteus*, *S. commersonianus*, and *P. fuscus*, which occurred in higher abundances in the littoral and intertidal, these habitats may provide optimal foraging conditions and opportunities not present in the subtidal habitat. However future work, such as tethering experiments, is needed as the higher predator densities we have described may not mean higher foraging rates (Sheaves, 2001).

Sharks are known to utilise shallow coastal waters for parturition (Feldheim et al. 2014) and foraging (Kinney et al 2011), with many coastal bays identified as important nursery areas for young-of-the-year (YOY) and juvenile sharks (Simpfendorfer & Milward 1993). However, our study indicates depth limits may occur with few shark individuals (n = 3) present in the littoral community. While clearly some shark species commonly enter shallow littoral waters (Carlisle & Starr 2010, Chin et al. 2013a, Chin et al. 2013b), sharks where uncommon in the mangrove fringed littoral habitat sampled by this study. Three of the four most dominant sharks sampled preferred the subtidal habitat over the intertidal habitat with *R. taylori*, *C. fitzroyensis* and *C. amboinensis* abundances 10-fold, 13-fold and 2-fold higher respectively in the deeper water habitat. In contrast, frequently sampled *C. tilstoni/limbatus* and *S. lewini* were generally twice as likely to be sampled in the intertidal habitat compared with the subtidal habitat. Although the littoral habitat was not as frequently sampled as the intertidal and subtidal habitats, sampling frequency is considered sufficient to be confident in the relative abundance estimates produced. In fact, the relatively shallow nature of the littoral habitat may have increased the probability of shark capture as gill nets become less selective when set in waters shallower than the depth of the net (White et al 2013). It seems clear that in the shallow habitat mosaic sampled in this study, the littoral habitat did not offer any service of benefit to local shark populations.

Concluding that a species obtains certain ecological services from simple presence or absence within a habitat should be done with some caution (Beck et al 2001). For some species, presence within a particular habitat may occur as a trade-off between multiple needs and/or benefits. For example, the behaviours of young-of-the-year *Sphyrna lewini* in Kāne'ohe Bay Hawaii suggests that preferred refuge habitats were occupied over habitats which provided an increase in foraging opportunities but had higher predation threats (Lowe 2002). This trade-off is highly detrimental to the YOY condition as prey abundance was insufficient to increase growth and higher rates of natural mortality resulted. Clearly, confidently understanding the benefits obtained by fish species from coastal habitats requires concurrent consideration and assessment of multiple benefits and services.

Shallow coastal waters (<1 m) have been identified as supporting high abundances and diverse communities of rays (Vaudo & Heithaus 2009, Jirik & Lowe 2012). For example, Vaudo and Heithaus (2009) sampled an elasmobranch community of a shallow intertidal sand flat in Shark Bay, Australia and sampled 12 species of rays. Comparisons between adjacent subtidal habitats identified significantly higher abundances and diversity of rays in the shallow intertidal sand habitats (< 1 m) than the deeper subtidal habitats (1 – 2 m)(Vaudo & Heithaus 2009). In contrast to Shark Bay, only 5 rays were sampled in Cleveland Bay, and within this group two species *A. cuspidata* and *R. neglecta* were clearly dominant. In addition, no rays were sampled in the littoral habitat. Ray presence among the three sampled Cleveland Bay habitats contrasts current knowledge of shallow water ray communities being more diverse and with higher species abundances than deeper subtidal habitats (Matern et al. 2000, Craig et al. 2010, Jirik & Lowe 2012). Sampling method may explain these differences. For example Vaudo and Heithaus (2009) employed visual survey techniques while boating, and our study relied on sampling with static gillnets, a method that may be selective against disc shaped rays (White & Potter 2004). The commonly sampled rays, *Anoxypristis cuspidata* and *R. neglecta*, have morphological protuberances increasing the likelihood of capture by gillnet (White et al. 2013). It is possible the sampling technique of this study under-sampled the disc shaped ray fauna, particularly within the littoral habitat where feeding pits were often observed during field sampling. Unfortunately the often turbid nature of the sampled habitats precludes visual surveys though seine or fence netting may prove to be a better sampling technique for the disc-shaped rays.

For some *Pristis* species, littoral habitats have been identified as important nurseries. Simpfendorfer et al. (2010) described young but relatively large (1 – 1.5 m) juvenile *Pristis pectinata* preferring very shallow (< 50 cm deep) mud and sandy bank waters in Florida, suggesting theses habitats may provide ecological services such as foraging, refuge from predation and physiological growth advantages. However, we observed no *Anoxypristis cuspidata* in the shallow littoral waters of Cleveland Bay and possibly the absence of predation threat allows use of deeper waters in tropical Australia. We did observe a possible ontogenetic shift in habitat use, with larger *A. cuspidata* sampled in the deeper subtidal habitat with smaller animals occurring in the intertidal habitat. This is similar to the ontogenetic effects of habitat use described for *Pristis microdon* in western tropical Australia (Whitty et al. 2009).

Habitat selection by fishes is often driven by physical properties such as temperature or salinity of the water mass encountered (Harrison and Whitfield 2006, Vaudo and Heithaus 2009). For example, the exploitation of thermal gradients allows for an increased rate of feeding, digestion and thus growth for some sharks (Sims et al. 2001, Simpfendorfer et al. 2005, Vaudo and Heithaus 2009). Similarly variations in salinity have been demonstrated to affect food intake and thus growth rates in teleosts (Bœuf & Payan 2001, Harrison and Whitfield 2006). In our Cleveland Bay site, temperature was hottest and salinity most variable in the shallow littoral habitat. Temperature of the subtidal habitat was generally two degrees cooler than the littoral habitat and salinity was much more stable in the subtidal habitat. These clear patterns may have a causative relationship with the species abundance patterns we have described, however other factors such as turbidity, water turbulence and wave frequency may also play a role in shaping species distributions and community structures. Moreover, resource partitioning may influence species' habitat choices when important resources such as prey are limited (Sala and Ballesteros, 2001). The findings of Kinney et al (2011), who quantified resource partitioning in young sharks inhabiting the deeper waters of Cleveland Bay, may have some relevance in the describing the unique species patterns we have described in the adjoining shallow habitat mosaic. Future research should explore the role of resource partitioning in shaping the communities this study has described.

A review of literature clearly demonstrates that nursery function is a common declaration of an important function shallow coastal waters offer for teleosts, rays and sharks. (Blaber 1980, Beck et al. 2001, Hajisamae and Chou 2003, Tse et al. 2008). However, contemporary research is building a repertoire of additional functions that shallow coastal waters may serve including teleost spawning (Tobin et al 2014), shark and ray parturition (Farrugia et al., 2011) and predation (Sheaves 2001, Baker and Sheaves, 2009). Accordingly, successful management initiatives must consider these additional functions to ensure the conservation of the community of fishes and the functions those species attain from these habitats. Current management of the shallow water coastal habitats mosaic without the knowledge of the ecological benefits and services they provide may risk disrupting the structure of fish communities and/or alter ecosystem functions. Species that occur in fewer habitats may be less resilient to environmental change or anthropogenic pressures due to their limited habitat use (Munroe et al. 2014). The species-specific habitat preferences observed for most species suggests that the loss or modification of one habitat could severely disrupt the community structure and population persistence. Clearly, future research conducted in shallow coastal habitats should consider the wide range of possible available species and life history stages, as well as the range of ecological services that may be provided.

2.5 Tables and Figures

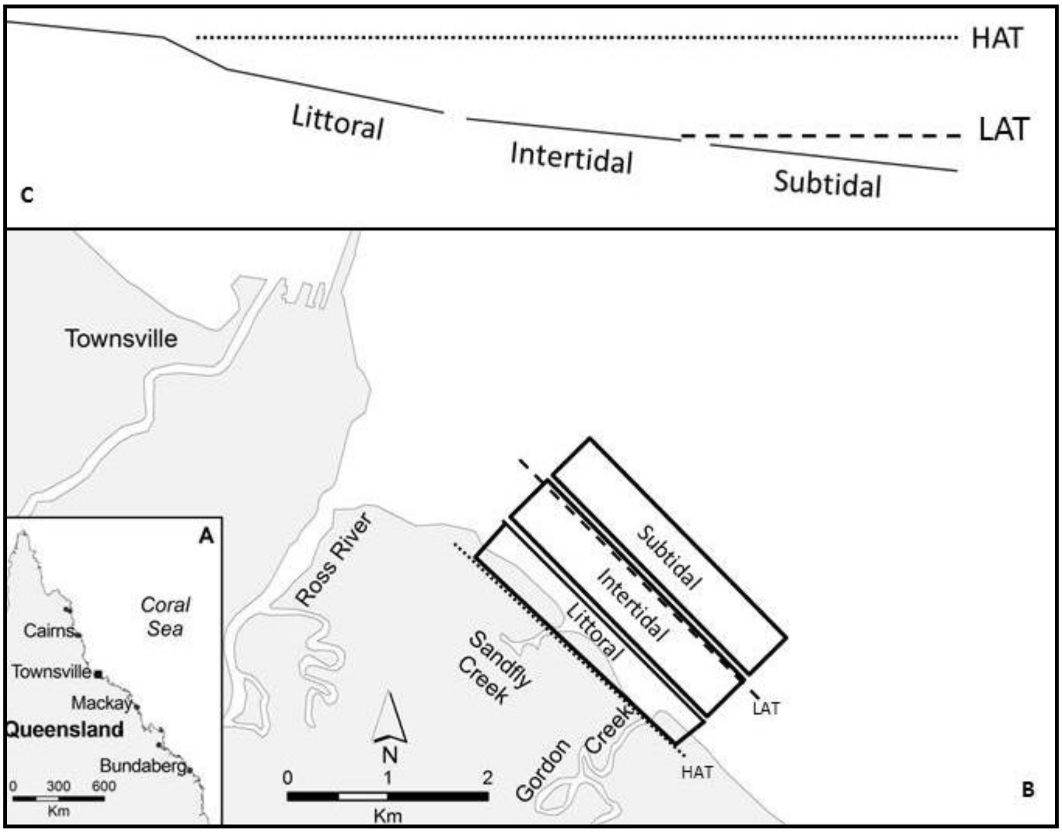

Figure 2.1 Location of study site in (a) Queensland, Australia, (b) aerial view of the littoral, intertidal and subtidal habitats in Cleveland Bay, and (c) cross section of littoral, intertidal and subtidal habitats. The dashed line marks the lowest astronomical tide (LAT) and the dotted line marks the highest astronomical tide (HAT).

Table 2.1 Summary of fish sampled in the littoral, intertidal and subtidal habitats ordered by total count. Relative abundance within each habitat is calculated as number of fish per 100 m-1 net hr -1. Mean fork length and length range is also presented.

Family	Name	Total Count	Littoral	Intertidal	Subtidal	Fork Length (mm)
Latidae	*Lates calcarifer*	330	6.02	4.48		558 (355 - 1005)
Polynemidae	*Eleutheronema tetradactylum*	180	1.26	1.63	1.94	375 (160 - 585)
Ariidae	*Arius* spp.	106	1.21	1.15	0.69	367 (250 - 800)
Carcharhinidae	*Rhizoprionodon taylori*	101		0.22	2.23	517 (350 - 620)
Carcharhinidae	*Carcharhinus fitzroyensis*	58		0.09	1.33	606 (405 - 1150)
Carcharhinidae	*Carcharhinus tilstoni/limbatus*	58		0.83	0.49	574 (395 - 1590)
Pristidae	*Anoxypristis cuspidata*	54		0.85	0.37	864 (607 - 1240)
Carcharhinidae	*Carcharhinus amboinensis*	39	0.10	0.24	0.64	653 (471 - 1060)
Haemulidae	*Pomadasys argenteus*	32	0.97	0.26		321 (225 – 380)
Mugilidae	*Mugil cephalus*	23	0.05	0.48		460 (397 - 555)
Carangidae	*Scomberoides commersonianus*	22	0.24	0.37		417 (330 - 620)
Haemulidae	*Pomadasys kaakan*	17	0.19	0.22	0.07	370 (305 - 470)
Sciaenidae	*Nibea soldado*	15	0.29	0.17	0.02	344 (245 - 390)
Sphyrnidae	*Sphyrna lewini*	15		0.24	0.10	406 (340 - 605)
Mugilidae	*Liza vaigiensis*	14	0.49	0.09		511 (400 - 680)
Polynemidae	*Polydactylus macrochir*	12	0.29	0.13		619 (450 - 750)
Rhinopteridae	*Rhinoptera neglecta*	7		0.13	0.02	-
Platycephalidae	*Platycephalus fuscus*	5	0.15	0.04		575 (530 - 610)
Megalopidae	*Megalops cyprinoides*	4	0.15	0.02		410 (365 - 470)
Synodontidae	*Synodus variegatus*	4		0.02	0.07	249 (215 - 275)
Sphyrnidae	*Sphyrna mokarran*	3			0.07	1207 (1090 - 1280)
Chirocentridae	*Chirocentrus dorab*	2			0.05	325 (325 - 325)
Leptobramidae	*Leptobrama muelleri*	2		0.04		221 (197 - 245)
Rhinidae	*Rhynchobatus australiae*	2		0.02	0.02	1182 (934 - 1430)
Scatophagidae	*Selenotoca multifasciata*	2		0.04		200 (185 - 215)
Carangidae	*Parastromateus niger*	1		0.02		210
Carangidae	*Scomberoides tala*	1		0.02		385
Carangidae	*Caranx ignobilis*	1		0.02		215
Carcharhinidae	*Negaprion acutidens*	1	0.05			479
Dasyatidae	*Himantura granulata*	1		0.02		170
Drepanidae	*Drepane punctata*	1		0.02		235
Lobotidae	*Lobotes surinamensis*	1	0.05			350
Lutjanidae	*Lutjanus argentimaculatus*	1	0.05			380
Rhinobatidae	*Glaucostegus typus*	1		0.02		390
Scombridae	*Scomberomorus queenslandicus*	1			0.02	600
Sparidae	*Acanthopagrus berda*	1		0.02		225
Triacanthidae	*Triacanthus biaculeatus*	1		0.02		230

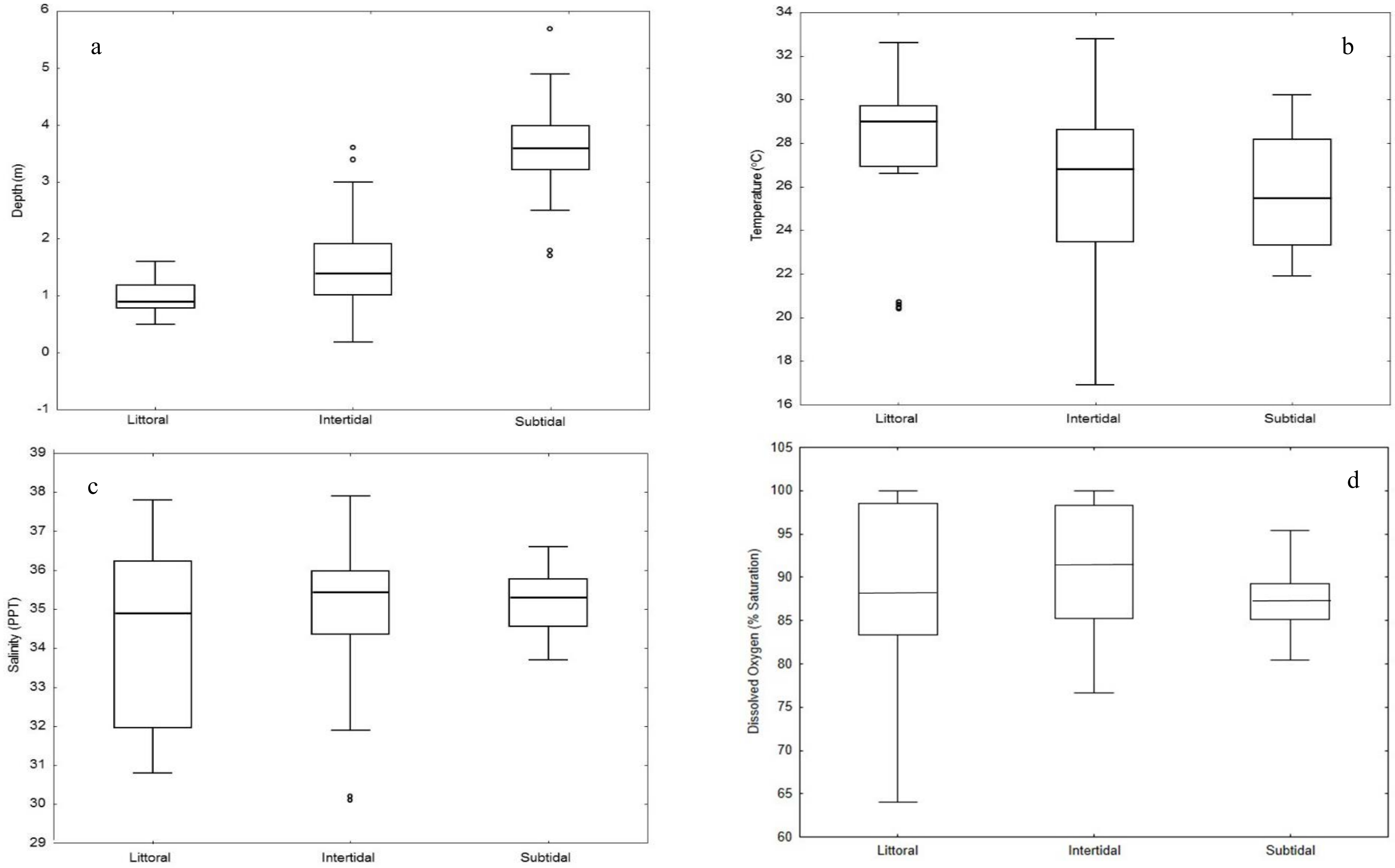

Figure 2.2 Box plots summarising the a) depth, b) temperature, c) salinity and d) dissolved oxygen characteristics recorded within the littoral, intertidal and subtidal habitats. The box represents the interquartile range and includes the median as a solid line; the whiskers represent the minimum and maximum values; and outliers are represented by circles.

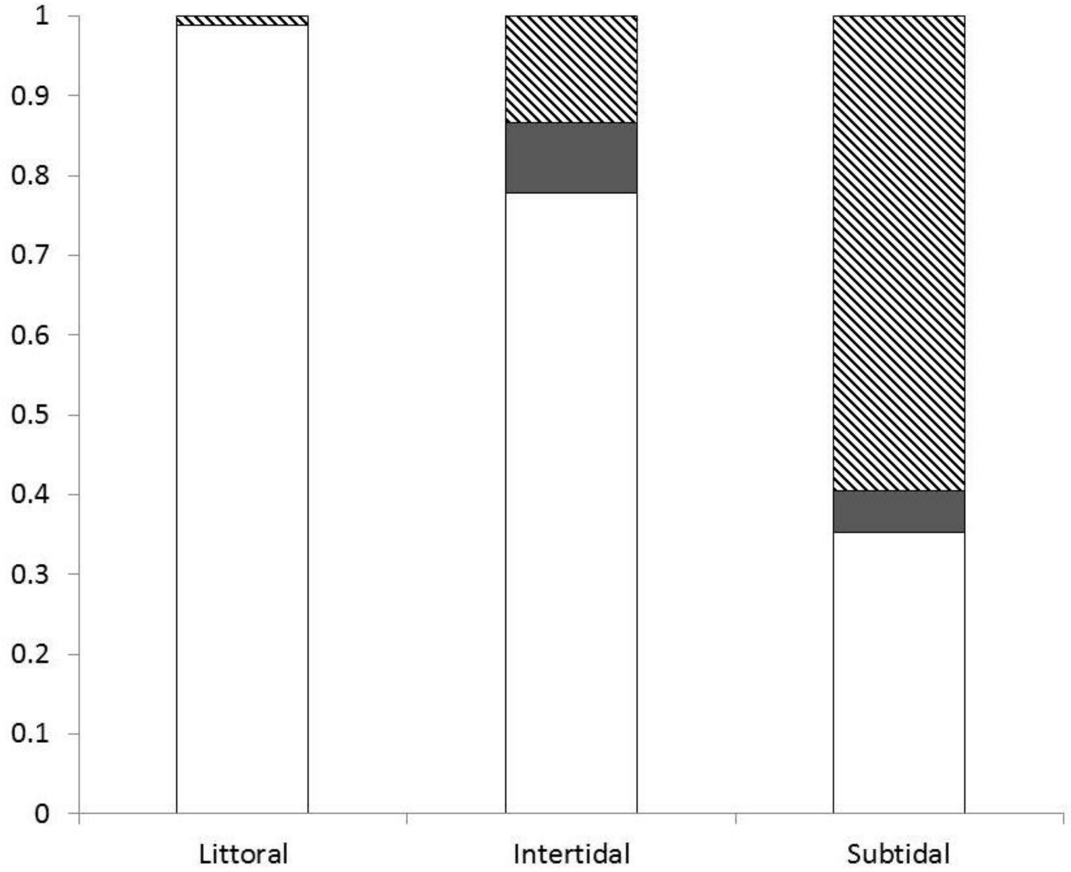

Figure 2.3 The proportion of teleosts, sharks and rays sampled from the littoral, intertidal and subtidal habitats. Note: white - teleosts, stripes - sharks, and grey- rays.

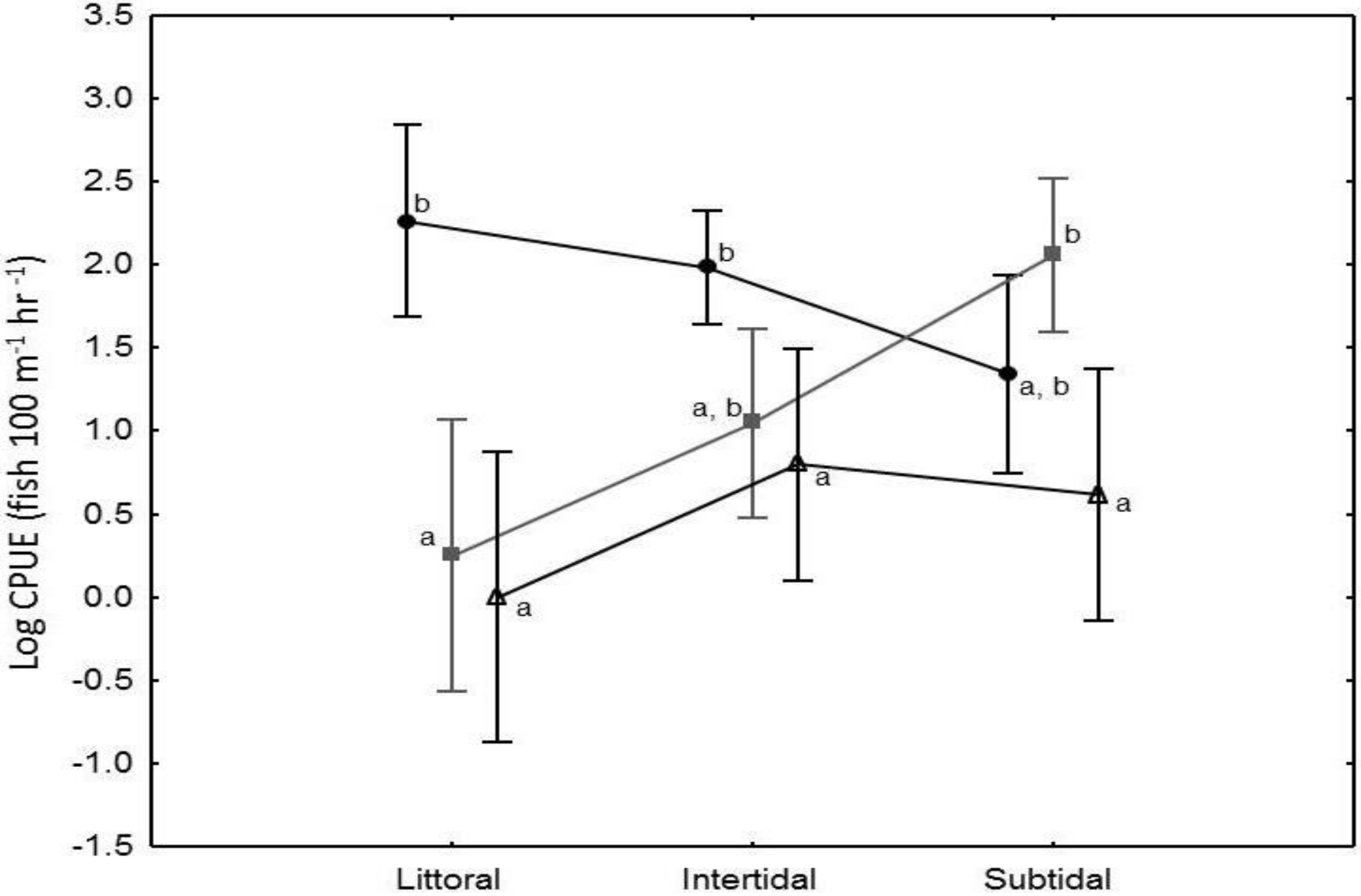

Figure 2.4 The standardized catch per unit effort (log transformed) of teleosts, sharks and rays caught with the littoral, intertidal and subtidal habitats. Error bars are 95% confidence intervals. Note: (●) Teleosts, (■) Sharks and (Δ) Rays. Homogenous groups are identified as group **a** and as group **b**.

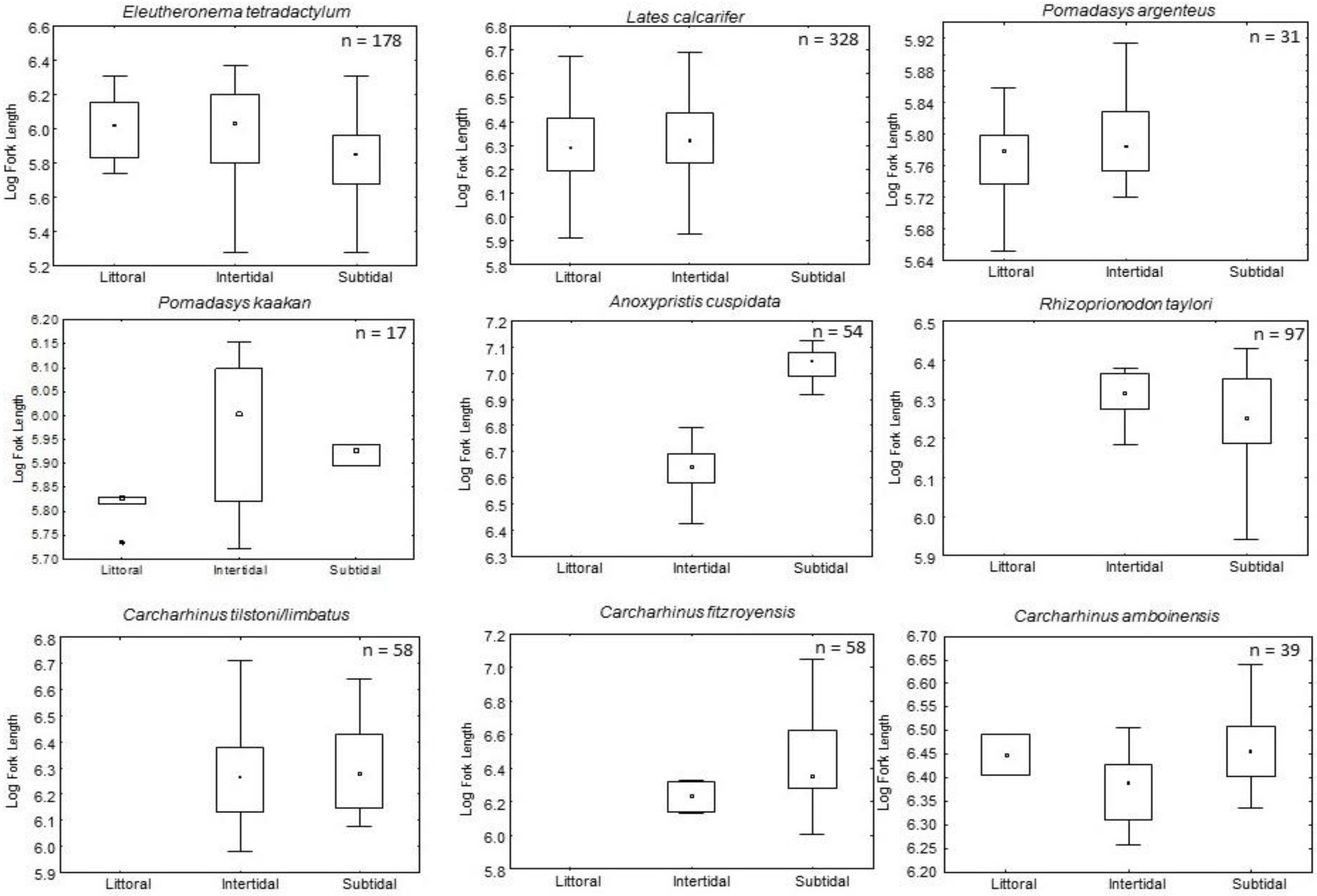

Figure 2.5 Box plots of logged transformed fork length compared among habitats for a) *Eleutheronema tetradactylum*, b) *Arius* spp., c) *Lates calcarifer*, d) *Pomadasys argenteus*, e) *Anoxypristis cuspidata*, f) *Rhizoprionodon taylori*, g) *Carcharhinus tilstoni/limbatus*, h) *C. amboinensis* and c) *C. fitzroyensis*.

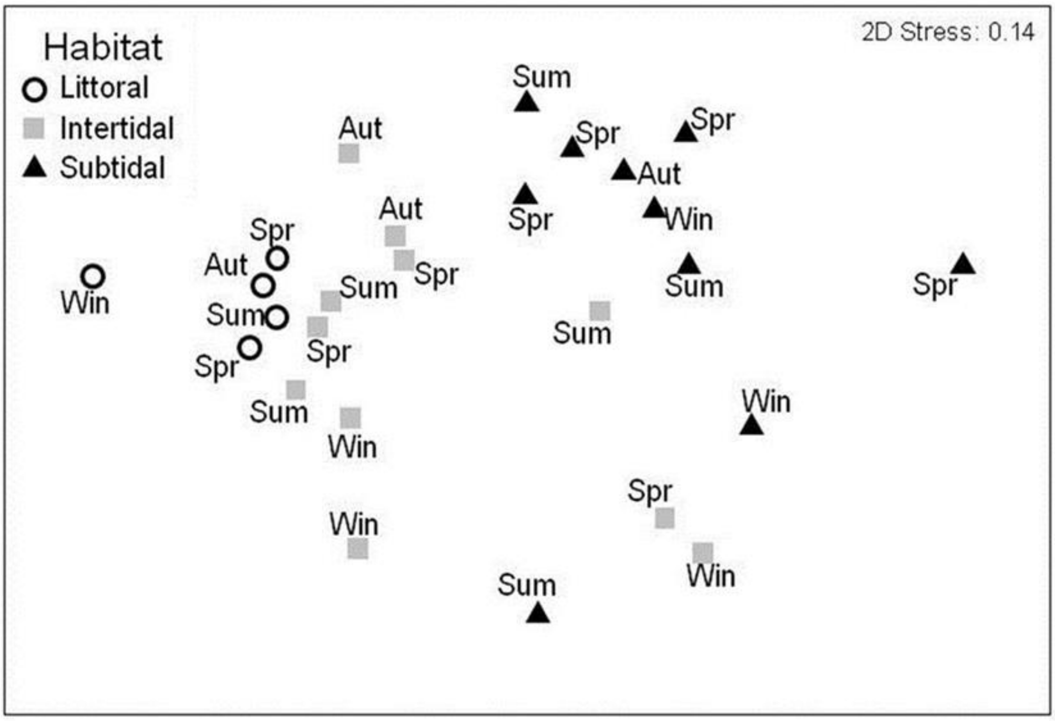

Figure 2.6 Non-metric multi-dimensional scaling ordination plot of the sampled fish communities across seasons and the littoral, intertidal and subtidal habitats during September 2012 to August 2013.

Table 2.2 SIMPER analysis results across habitats with the average similarity and species contribution for fish species contributing up to 80% of the cumulative average similarity.

Species	Average Abundance	Average Similarity	Similarity/SD	Contribution %	Cumulative Contribution %
Littoral (Av. Similarity: 55.93%)					
Lates calcarifer	3.08	24.85	7.02	44.42	44.42
Pomadasys argenteus	1.52	11.90	3.97	21.28	65.70
Arius spp.	1.52	7.60	1.14	13.59	79.28
Eleutheronema tetradactylum	1.35	5.21	1.01	9.32	88.60
Intertidal (Av. Similarity: 33.43%)					
Eleutheronema tetradactylum	1.78	14.17	1.41	42.39	42.39
Lates calcarifer	2.04	7.02	0.76	20.99	63.37
Carcharhinus tilstoni/limbatus	0.89	2.68	0.64	8.01	71.38
Arius spp.	1.04	2.41	0.52	7.22	78.61
Scomberoides commersonianus	0.6	1.14	0.39	3.41	82.02
Subtidal (Av. Similarity: 33.32%)					
Rhizoprionodon taylori	1.65	14.15	1.27	42.46	42.46
Carcharhinus fitzroyensis	1.33	7.23	0.78	21.71	64.17
Eleutheronema tetradactylum	0.99	3.65	0.64	10.94	75.11
Carcharhinus tilstoni/limbatus	0.73	3.64	0.57	10.91	86.02

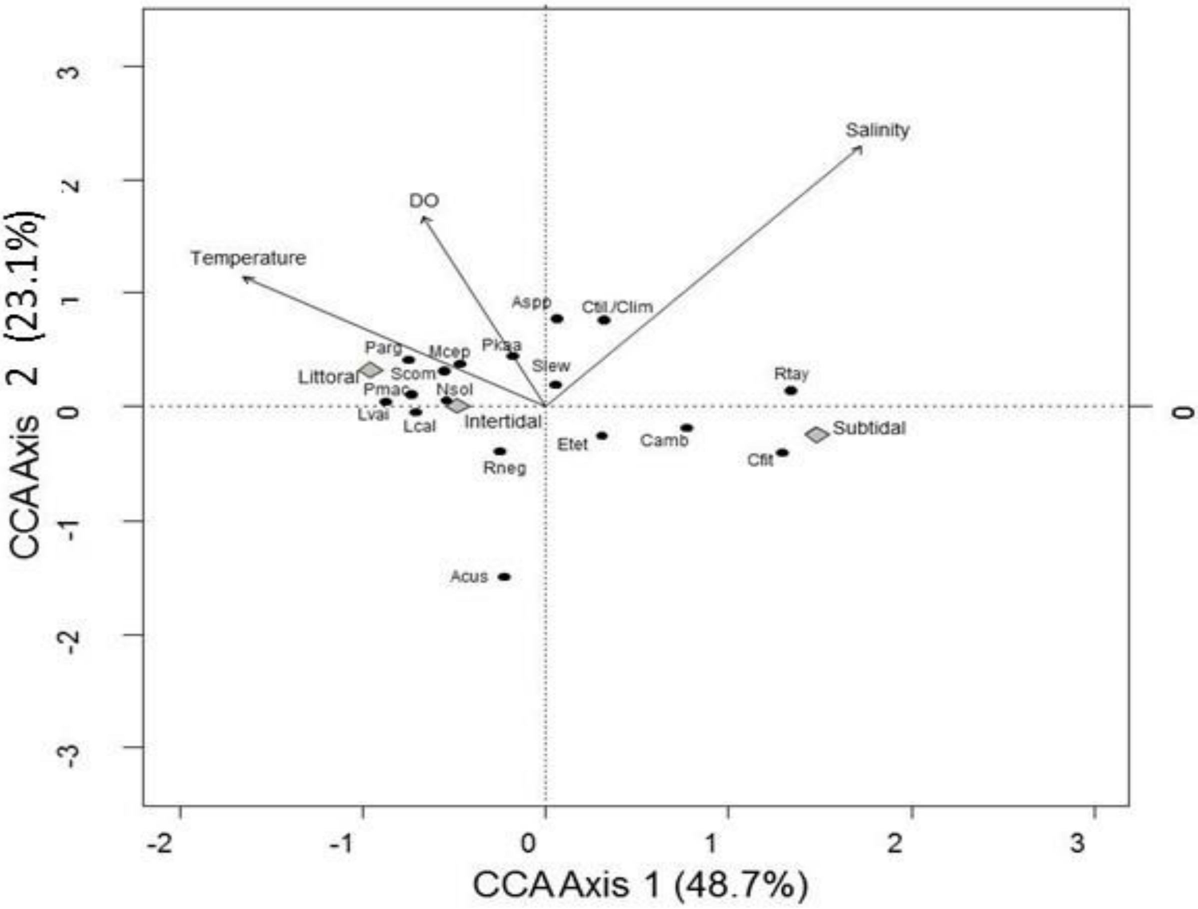

Figure 2.7 A canonical correspondence analysis biplot created from the species and environmental data. The environmental data was habitat (littoral, intertidal and subtidal), temperature (°C), dissolved oxygen (%) and salinity (ppt). The black arrays show the continuous variables with the length of the vector indicating strength of relationship while the direction corresponds to the species associated. The grey squares are the nominal variables designated as habitats. The species (solid black circles) are abbreviated as follows: Acus; *Anoxypristis cuspidata*, Rneg; *Rhinoptera neglecta*, Slew; *Sphyrna lewini*, Camb; *Carcharhinus amboinensis*, Cfit; *Carcharhinus fitzroyensis*, Rtay; *Rhizoprionodon taylori*, Ctil/Clim; *Carcharhinus tilstoni/limbatus*, Nsol; *Nibea soldado*, Etet; *Eleutheronema tetradactylum*, Mcep; *Mugil cephalus*, Parg; *Pomadasys argenteus*, Pkaa; *Pomadasys kaakan*, Scom; *Scomberoides commersonianus*, Aspp; *Arius* spp., Lvai; *Liza vaigiensis*, Pmac; *Polydactylus macrochir*, Lcal; *Lates calcarifer*.

Table 2.3 Summary of results of Canonical Correspondence Analysis (CCA) including environmental averages. Permutation test of significance for first canonical axis: F = 7.442 , P <0.001.

	Axis 1	Axis 2	Axis 3
Accumulate Constrained Eigenvalues	0.5056	0.2405	0.1752
Proportion Explained	0.4874	0.2319	0.1689
Cumulative Proportion	0.4874	0.7193	0.8882

Permutation results on Variables	df	F	P	Littoral	Average Intertidal	Subtidal
Salinity	1	3.8829	**0.0040**	34.25	35.08	35.18
Temperature	1	3.3301	**0.0140**	27.60	26.40	25.60
DO	1	2.0214	0.2001	64.79	75.16	84.88
Habitat	2	3.0169	**0.0040**	-	-	-

CHAPTER 3. ECOLOGICAL INFLUENCES ON A LARGE BODIED FISH COMMUNITY IN A SHALLOW COASTAL HABITAT MOSAIC

Plate 3. Developed shark embryos observed in *Rhizoprionodon taylori*

3.1 INTRODUCTION

It is widely acknowledged that shallow coastal waters commonly function as nursery habitats, as these areas provide both an increase in food source access (Blaber et al. 1995) and refuge from predation (Paterson & Whitfield 2000). The refuge function of nursery habitats has generally been supported by the relatively low abundance of piscivorous fishes (Shenker & Dean 1979, Robertson & Duke 1987). However, large piscivorous fishes do occur within some shallow coastal habitats (Tobin et al 2014, Chapter 2 *in press*), and have also been described in nursery habitats (Bennett 1989, Baker & Sheaves 2006). Bennett (1989) seine net sampled fish communities of a South African beach and concluded that the area functioned as a nursery habitat; however it was also noted that larger and mature fishes of different species were commonly caught by local rod and reel anglers. Although shallow coastal habitats may be commonly identified as serving important nursery function, other ecological functions may co-occur.

Studies that describe nursery function invariably use sampling gears biased towards small bodied fishes. Sampling small bodied and juvenile fishes is most efficient with small mesh seine nets, (Faunce & Serafy 2006), however seine gear is ineffective in capturing large bodied fishes (> 200 mm) that may occur in the sampled habitats (Baker & Sheaves 2006). Thus, conclusions on the functions of shallow coastal habitats may be limited to the nursery function due to biased sampling of fish communities. Large bodied fishes may co-occur and possibly be attracted to these habitats for other ecological functions. Sampling in shallow coastal habitats with a wide range of sampling gears would allow for less biased interpretation about the services these habitats offer to fish communities.

Nursery habitats (Blaber & Blaber 1980) reduce predation (Sheaves 2001), and increase foraging success for juvenile fish (Lasiak 1981, Abrahams & Kattenfeld 1997), sharks (Heupel &

Simpfendorfer 2008) and rays (Simpfendorfer et al. 2010). However, contemporary research suggests that these habitats may provide further ecological functions for larger bodied fishes, including foraging (Krumme et al. 2008), refuge (Sims et al. 2001) and reproduction (Dibattista et al. 2008, Præbel et al. 2009). For example, Baker and Sheaves (2005) described many small piscivorous fishes in shallow coastal habitats and concluded that predation/foraging within these habitats may affect the structure of shallow coastal fish communities. In another study, adult spotted halibut (*Verasper variegatus*) were identified utilising the shallow coastal habitat of Matsukawa-ura, Japan as a nursery and as an adult foraging habitat (Wada et al. 2011). Regardless of the dorso-ventrally flattened advantage of the halibut by Wada et al. (2011) and the small size of piscivorous (generally < 100 mm) identified in Baker and Sheaves (2005), additional research indicates that body shape and size may not be a limiting factor for large fish accessing shallow coastal habitats (Tobin et al. 2014).

Spawning in shallow coastal habitats has been observed for many fish species including killifish (Taylor 1990), puffers (Yamahira 1996), and Artic charr (Low et al. 2011). The benefits of spawning in shallow habitats may include elevated oxidation and incubation temperatures for eggs (Strathmann & Hess 1999) while also reducing predation (Tewksbury II & Conover 1987). However, eggs must be suitably adapted for the surviving the shallow water environment (Taylor 1999) such as adopting spherical shapes that reduce desiccation and by having high levels of carotenoids to facilitate oxygen transport (DeMartini 1999). Adult surf smelt, *Hypomesus pretiosus,* spawn in the shallow coastal habitats of Puget Sound during spring tides with preferred spawning sites characterised by low solar radiation, medium to high wave action, and north-facing aspect (Quinn et al. 2012). Atlantic silverside, *Menidia menidia,* spawn as high tides peak allowing spawning individuals to access the very upper regions of the intertidal zone (1.2 – 2.4 m above mean low water) where fertilised eggs are attached to algae mats, a tactic that increases egg survivorship due to reducing exposure to predators (Middaugh et al. 1981, Tewksbury II &

Conover 1987). Clearly, some shallow coastal habitats support spawning and knowledge about these critical habitats can ensure continued effective management.

Anthropogenic activities are increasingly threatening shallow coastal habitats. The impacts of coastal development (Thronson & Quigg 2008, Wen et al. 2010, Sundblad & Bergström 2014), dredging (Bonvicini pagliai et al. 1985, Bilkovic 2011) and agriculture (Primavera 2006, Schock et al. 2014) have been well documented. Anthropogenic activities if left unregulated may permanently modify fish communities in shallow coastal habitats (Blaber et al. 2000, Stallings 2009, Morley et al. 2012). Robust knowledge of what fishes occur in these habitats and what services these habitats offer to inhabiting fishes is required for management to be continuously effective and to ensure efficient utilisation of coastal habitats for fisheries. Further, identifying if the services that fish attain preferentially occur in the littoral, intertidal and/or subtidal habitats would provide additional information for management and may aid in determining if conservation is warranted. Chapter 2 described a distinct community of large bodied teleosts, sharks and rays utilising a shallow coastal habitat mosaic in tropical Australia. Habitat partitioning was evident among the habitat mosaic with sharks dominating the deeper subtidal water community, while teleosts dominated the shallower littoral community and a mixed community of sharks, rays and teleosts occurred in the bridging intertidal habitat. Why this partitioning of taxonomic groups occurs is the focus of this chapter and may be better understood by investigating the potential ecological functions offered.

The aim of this chapter was to identify the ecological services that may be gained by large bodied fishes (> 200 mm) using the inshore habitat mosaic of littoral, intertidal and subtidal zones. Life history stage, reproductive activity and foraging traits were explored. The information obtained provides invaluable knowledge on the ecological functions of these habitats to the large bodied fish community and increases our understanding of the functions of shallow coastal habitats to ensure effective fishery management.

3.2 METHODS

3.21Field Sampling

The shallow coastal habitat mosaic sampled is described in Chapter 2.

3.2.2 Life History Traits

Identifying if any ontogenetic shifts in habitat use, or if life history stages had a specific habitat requirement, the presence of life history stages were investigated. Most teleosts sampled were released alive requiring life history stage to be inferred from published maturity indices. Juveniles were classified as any fish smaller in length-at-50% maturity while larger fish were classified as adults. This life history classification method was validated by macroscopic investigation of gonads from a sub-sample of teleosts using criteria of West (1990). Shark and ray life history traits included the group young-of-the-year (YOY) – in addition to juveniles and adults. YOY sharks were identified during sampling by the presence of an umbilical scar indicating recently born shark. Juvenile and adult sharks, similarly to teleosts, were identified based on published maturity indices. Also, some validation of life history stage was possible by examination of clasper calcification in males by determining the level of calcification (1 – not calcified, 2 – partially and 3 – fully calcified). Not calcified claspers indicated a YOY shark, while partially represented juveniles and fully represented adults. A sub-sample of female sharks were used to determine life history stage through macroscopic examination of the uterus development (see Table 3.4).

Life history stages were initially explored at broad taxonomic level of teleosts, sharks and rays. The influence of habitat on the life history stages of teleosts and sharks was explored using Pearson’s Chi squared test. The effect of habitat on life history stage was examined at the individual species level for the more commonly sampled species. When estimating life history stage from length, individuals sampled categorized as the *C. tilstoni/limbatus* complex were assumed to be *C. tilstoni* based on Harry (2011) identifying an increased abundance of *C. tilstoni* in Cleveland Bay than *C. limbatus*.

3.2.3 Reproductive Activity

Macroscopic investigation of uteruses for female sharks was used to infer the reproductive function of the shallow coastal habitat mosaic for the shark community. Uterus condition was based on the criteria of Walker (2005)(Table 3.2). For analysis, female reproductive activity was simplified into active (stages 4-6) and inactive (stage 1-3). Reproductive activity was explored using Pearson's chi squared test to compare the proportion of active and inactive females between habitats. Male sharks were excluded as there is no inactive and active stage present mature male sharks. The effect of habitat on sex ratio was explored using a Pearson's chi squared test. Sex ratios were explored with the most abundantly sampled sharks (*R. taylori. C. fitzroyensis, C. amboinensis* and *C. tilstoni/limbatus*) and the presence of claspers indicated male sharks and the absence indicated female sharks.

3.2.4 Foraging Activity

The foraging activity was explored by examining stomach fullness indices, digestive state of stomach contents, and identifying ingested prey items. Sufficient samples were available for three teleost (*L. calcarifer, E. tetradactylum and P. argenteus*) and two sharks (*R. taylori* and *C. tilstoni/limbatus*). Stomach fullness was estimated by expressing stomach weight as a proportion of whole specimen weight as described by Mychek-Londer and Bunnell (2013):

$$\left(\frac{prey\ weight\ g}{fish\ weight\ g}\right) * 100 = Stomach\ fullness\ (S)$$

The fish weight from the predator was determined using published length-weight relationships obtained from Fishbase.org (Froese & Pauly 2014). One-way ANOVA tested the effect of habitat on stomach fullness, however if assumptions of ANOVA were violated a Kruskal-Wallis test was used.

Stomach contents were then examined and contents identified into the following taxonomic groups: teleosts, crustaceans, molluscs, annelids and echinoderms. Some contents were unable to be classified which were in advanced stages of digestion and thus were listed as unidentifiable. Stomach contents were classified according to digestive stage with 1 indicating no digestion or little digestion, whereas a value of 4 indicates an advance stage of digestion (Espinoza et al. 2013)(Fig. 3.1). The effect of habitat on digestive stage for each prey item in teleost and shark stomach contents was explored using Pearson's Chi squared test for the most abundantly sampled species.

3.2.5 Permits and Ethics

Research presented in this thesis was conducted in accordance with James Cook University animal ethics permits A1933 and A1566.

3.2 RESULTS

Life history stage was classified for 977 individuals from 16 families and 28 species (Table 3.1). Reproductive activity analysis was possible for four teleosts (*L. calcarifer, E. tetradactylum, P. argenteus* and *P. kaakan*) and four sharks (*R. taylori*, *C. fitzroyensis, C. amboinensis* and *C. tilstoni/limbatus*)(Table 3.2). Foraging activity was analysed for species with at least five samples from two or more habitats and included three teleosts (*L. calcarifer, E. tetradactylum* and *P. argenteus*) and two sharks (*R. taylori* and *C. tilstoni/limbatus*)(Table 3.2).

3.2.1 Life History Traits

The overall teleost community was dominated by adults (66%), though the proportion of adults and juveniles varied among habitats (χ^2, d.f. = 2, $P < 0.0001$). Adults dominated the intertidal and the subtidal habitats (68% and 95%, respectively). In contrast to the teleost community, the shark community was predominately immature young-of-the-year (34%) and juveniles (27%), with fewer mature specimens (39%). Habitat did influence the proportion of life history stages present (χ^2, d.f. = 4, $P < 0.0001$) with YOY dominant in the intertidal and adults dominant in the subtidal (64% and 49%, respectively). With exception of one adult specimen the ray community was entirely juvenile.

Of the four most abundant teleosts (*L. calcarifer, E. tetradactylum*, *P. argenteus* and *P. kaakan*), species specific patterns in life history stage were present (Fig. 3.2). *Lates calcarifer* was the only species for which habitat influenced life history with juveniles the dominant life history stage in the littoral habitat (56%) compared to adults in the intertidal (60%). Adult *E. tetradactylum* was the only life history stage present in the littoral habitat and adults were dominant in the intertidal and subtidal habitats (Fig. 3.2), while *P. argenteus* and *P. kaakan* were only present as adults (Fig. 3.2).

Of the four most common species, (*R. taylori, C. fitzroyensis, C. amboinensis,* and *C. tilstoni/limbatus*) the proportion of life history stages varied among habitats (χ^2, d.f. = 2, $P < 0.0001$) with YOY dominant in the intertidal and adults dominant in the subtidal. Adult *R. taylori* were dominant in the intertidal and subtidal habitat (100% and 77%, respectively)(Fig. 3.2). No YOY *R. taylori* were sampled in any habitat. In contrast, *C. fitzroyensis* occurred exclusively as YOY in the intertidal (100%) while juveniles dominated over YOY in the subtidal (78%)(Fig. 3.2). In contrast to *C. fitzroyensis,* even numbers of YOY and juvenile *C. amboinensis* occurred in the intertidal (Fig. 4) whereas in the subtidal only juveniles occurred (Fig. 3.2). Additionally, *C.*

tilstoni/limbatus had equal proportions of YOY and juveniles in the intertidal and juvenile *C. tilstoni/limbatus* were dominant in the subtidal habitat (Fig.3.2).

One ray species, *Anoxypristis cuspidata*, was numerous enough to examine the influence of habitat on life history stage. However, no habitat effect was present in either intertidal or subtidal habitats as *A. cuspidata* occurred exclusively as juveniles (Fig. 3.2). No YOY or mature specimens were sampled.

3.2.2 Reproductive Activity

Imminent spawning was only detected in one teleost, *E. tetradactylum*; however imminent spawners were present in all three habitats (Fig. 3.3). The proportion of imminent spawning *E. tetradactylum* females was universally low across all habitats, and habitat did not influence the presence of imminent spawners (χ^2, d.f. = 2, $P = 0.86$).

Although imminent spawning was not detected in *L. calcarifer*, *P. argenteus* and *P. kaakan*, multiple stages of ovarian development and spent stages were observed. Developing ovaries were observed for all four species of teleosts, however not within all habitats (Fig. 3.3). For *L. calcarifer*, developing ovaries were only observed in the intertidal. In contrast, developing ovaries were observed in all three habitats for *E. tetradactylum* and in the intertidal and subtidal for *P. argenteus* and *P. kaakan*. Spent ovaries were only observed for *E. tetradactylum, L. calcarifer*, and *P. kaakan* (Fig. 3.3). Similar to the observations for developing ovaries, spent ovaries were only observed in the intertidal for *L. calcarifer,* whereas for *E. tetradactylum* they occurred in all three habitats and in the intertidal and subtidal for *P. kaakan*.

All four teleost species showed sex specific patterns. For *E. tetradactylum* the samples were mostly females (3.4 females : 1 male), and there was no influence from habitat (χ^2, d.f. = 2, $P = 0.982$). *Lates calcarifer* occurred mostly as males (1 female : 4.4 males) and the ratio was consistent in the littoral and intertidal habitats. A total of 6 females and one male were sampled for *P. kaakan*, all in the intertidal habitat with an additional three females in the subtidal habitat. For *P. argenteus* only females were sampled.

Only one shark, *R. taylori,* was observed to be reproductively active (Fig. 3.4). Adult *R taylori* were only sampled in the intertidal habitat, with two of seven females reproductively active. However, the subtidal habitat had 19 of 30 females with reproductively active uteruses exhibiting stages 4 and 5 (Fig. 3.4). Additionally, 7 pregnant sharks and 3 sharks in the act of parturition were captured in the subtidal habitat. No additional shark species were reproductively active.

Three species of sharks were present exclusively as YOY and/or juveniles - *C. fitzroyensis*, *C. amboinensis* and *C. tilstoni/limbatus* – with similar sex ratios (1 : 1.20, 1 : 1.24 and 1 : 0.94, respectively). The sex ratio of females to males for *R. taylori* was 1 : 0.23.

3.2.3 Foraging Activity

Lates calcarifer stomach fullness did not differ between habitats (ANOVA, d.f. = 1, P = 0.09) (Fig. 7a), but digestive stage did (χ^2, d.f. = 4, $P < 0.0001$) (Fig. 3.6a). Advanced stage digestion (stage 4) and empty stomachs were common in the littoral, whereas in the intertidal stage 3 and stage 2 digested stomachs dominated samples (Fig. 3.7a). Stomachs containing one prey category comprised 38% of the stomachs sampled. Identified prey items for *L. calcarifer* included *P. kaakan*, *P. argenteus,* mullet sp. and prawns (tiger, *Penaeus esculentus* and banana prawn, *P. merguiensis*) mantis shrimps and crabs. The stomachs sampled in the littoral were dominated by teleosts (90%) with few crustaceans (7%), while in the intertidal stomachs were dominated by crustaceans (68%) and some teleosts (24%).

For *E. tetradactylum* stomach fullness did not vary among habitats (ANOVA, d.f. = 2, P = 0.173) (Fig. 7b), but digestive stage did (χ^2, d.f. = 8, $P < 0.001$) (Fig. 3.5b). There were more stage 3 and stage 4 digested stomach contents in the intertidal than in the subtidal and littoral habitats (Fig. 3.6b). Stomachs containing one prey category comprised 31% of stomachs sampled. Many of the identifiable prey items for *E. tetradactylum* were prawns (tiger and banana prawns), crabs, mantis shrimps, and few bivalves. Most fish prey items were in advanced stages of digestion preventing species identification. In contrast to *L. calcarifer, E. tetradactylum* stomach contents in the littoral, intertidal and subtidal were dominated by teleost prey. Crustaceans were only present in stomach contents in the intertidal and contributed 40% to the total prey items in the intertidal habitat. However, an additional prey item, molluscs, was found in 3% of stomachs in the intertidal habitat that was not present in *L. calcarifer* stomach contents.

In contrast to *L. calcarifer* and *E. tetradactylum*, *P. argenteus* stomach fullness index did vary between the littoral and intertidal habitats (ANOVA, d.f. = 1, $P = 0.041$) with less full stomachs occurring in the littoral (Fig. 3.5c). However, digestive stage of stomach contents did not vary between habitats (ANOVA, d.f. = 4, $P = 0.062$) (Fig. 3.6c). Stomachs containing one prey category comprised 20% of stomachs sampled. *Pomadasys argenteus* had a more varied diet compared to *L. calcarifer* and *E. tetradactylum* with bivalves, sand dollars, mantis shrimps, crabs, prawns, polychaetes, and teleosts found within its stomachs. *P. argenteus* stomach contents were dominated by molluscs (44%). Teleost prey items were present in only 9% of stomachs in the intertidal.

The stomach fullness index of *R. taylori* did not differ between habitats (ANOVA, d.f. = 1, $P = 0.97$) (Fig. 3.7a), however digestive stages of stomach contents did (χ^2, d.f. = 4, $P < 0.05$) with stage 4 digestion more common in the subtidal than in the intertidal habitat (Fig. 3.8a). Stomach contents containing one prey category comprised 44% of stomachs sampled. The prey items of *R. taylori* stomachs were dominantly comprised of teleosts in the intertidal and subtidal habitats (65% and 61%, respectively). However, crustaceans comprised a greater percentage of stomach contents in the intertidal than in the subtidal (22% and 3%, respectively). Crustacean prey items were dominantly prawns, with teleost prey items in advance stages of digestion preventing species identification. However two eggs from *Arius* spp. were identified in one stomach of *R. taylori* and no remains of a teleost were identified.

The stomach fullness index of *C. tilstoni/limbatus* did not differ between habitats (ANOVA, d.f. = 1, $P = 0.94$) (Fig. 3.7b) and the digestive stages of stomach contents did not differ between habitats (χ^2, d.f. = 3, $P = 0.73$) (Fig 3.8b). In comparison to *R. taylori*, *C. tilstoni/limbatus* stomach contents were only comprised of one prey category -teleosts. However a unique teleost prey item occurred, eggs of *Arius* spp. (with no teleost remains), in 41% of stomachs sampled for *C. tilstoni/limbatus*.

3.3 DISCUSSION

This study presents new information on how a previously undefined large bodied fish community (see Chapter 2, *in press*) use the shallow waters of coastal ecosystem mosaic that includes littoral, intertidal and subtidal habitats. Previous research has identified shallow water coastal habitats as important nurseries for teleosts, sharks and rays (Kimirei et al. 2013, McCallister et al. 2013, Cerutti-Pereyra et al. 2014) however, as this study has identified the shallow coastal habitat mosaic supports additional ecological functions and benefits. A community of mature teleosts and a co-occurring community of young-of-the-year and juvenile sharks and rays were identified within the shallow coastal habitat mosaic. Active spawning or parturition was rare, only occurring in one teleost and one shark; however the habitat mosaic clearly supports important reproductive activities for some species. In addition, foraging among the shallow coastal habitat mosaic may be an important activity for some teleosts and sharks. It is apparent that sampled shallow coastal habitats provided valuable ecological functions for the large teleosts, rays and shark communities that have not previously been described.

The teleost community was dominated by large and mature fishes. However, the distribution of juvenile teleosts suggested some components of the habitat mosaic support nursery function, as juveniles were more likely in the shallow littoral teleosts community as compared to the deeper intertidal and subtidal teleosts communities. This observed pattern further suggests an ontogenetic shift in habitat use by teleosts with offshore movement occurring with maturity. Shifts in habitat use with ontogeny are described for many species of fishes, though typically on larger spatial scales than described here (Laurel et al. 2009, Chin et al. 2013, Félix-Hackradt et al. 2014). For example, yellow snapper, *Lutjanus argentiventris*, use shallow coastal waters as juveniles before migrating to deep offshore waters with increasing size and maturity (Aburto-Oropeza et al. 2009). Species making shifts in habitat use with ontogeny often travel 10 to 100s of kilometres, whereas this study demonstrated an ontogenetic shift may occur on a much finer scale of a few hundred meters. Habitat partitioning by ontogenetic stage was evident in the most common teleost *L. calcarifer*. Juvenile *L. calcarifer* were dominant in the littoral habitat, while in the intertidal habitat *L. calcarifer* were mature and generally larger. Further replication of this study with increased spatio-temporal aspects would be beneficial to determine if ontogeny and habitat portioning is replicated in alike micro-habitats. Clearly, the littoral habitat offers advantages to juveniles when it is inundated by high tides as juvenile fishes dominate the fish community.

Many shark species utilise shallow coastal habitats as young-of-the-year and juveniles (Castro 1993, Simpfendorfer & Milward 1993, Carlson 2002) benefiting from increase access to prey, refuge from predators and warmer waters that benefit physiological processes and thus growth. The sampling in this study further supports the use of shallow coastal habitats by YOY and juvenile sharks, with very few mature specimens sampled. Further, in the Cleveland Bay study area the intertidal habitat may extend the nursery function of the adjoining subtidal habitat previously identified as a shark nursery (Simpfendorfer & Milward 1993).

Habitat partitioning may also benefit fishes through minimising competition between species for limited resources (Simpfendorfer et al. 2005, Taylor et al. 2011, Heithaus et al. 2013). Habitat partitioning was evident in the shallow coastal habitat mosaic with teleosts dominant in the shallow waters and sharks dominant in deeper waters. Habitat partitioning occurring within marine communities has been described previously (Prochazka 1998, Fairclough et al. 2008, Sheaves et al. 2014b). Sheaves et al. (2014b) demonstrated resource partitioning between two co-occurring sparid fishes, *Acanthopagrus australis* and *A. pacificus*, with the *A. pacificus* diet dominated by crustaceans while the *A. australis* diet was dominated by bivalves. The spatial partitioning of habitat use described in the shallow coastal habitat mosaic may allow sharks and teleosts to co-occur in shallow coastal waters without competing for prey.

It is generally accepted that shallow coastal waters are important shark and ray nurseries, however some large and mature sharks may also utilise these habitats (Heithaus & Dill 2002, Knip et al. 2012). For example, broadnose sevengill sharks, *Notorynchus cepedianus*, are large sharks (up to 3 m) commonly found in shallow coastal waters (Ebert 2003, Williams et al. 2011). Further, large and mature female leopard sharks, *Triakis semifasciata* , will aggregate in shallow waters throughout California for physiological advantages (Hight & Lowe 2007). However in this study, mature sharks were limited to only one small bodied species *R. taylori* (mean FL of 50 cm) and large sharks were rare. The similarity of *R. taylori* length with the lengths of other species present as YOY and juveniles, suggests that habitat use may not be partitioned by maturity but by body size.

Spawning is a critical activity for the population persistence of teleosts. Spawning sites vary among teleosts, with some sites characterised by turbulent fast moving waters to ensure fertilisation and/or transport to nursery habitats (Johannes 1978, Bakun & Parrsh 1982, Boehlert & Mundy 1988) or habitats containing suitable substrates for egg attachment (Hoshikawa et al.

2004, Polte & Asmus 2006). For example, capelins, *Mallotus villosus*, in northern Norway select intertidal habitats for spawning thus subjecting eggs to marked fluctuations in temperature and salinity (Præbel et al. 2009). However, capelin eggs have physiological and bio-mechanical adaptations (Præbel et al. 2009) to survive in the intertidal habitat and eggs benefit from less exposure to waterborne predation. During this study only one teleost, *E. tetradactylum*, was observed in imminent spawning condition. Imminent spawners of *E. tetradactylum* were present in all three habitats suggesting the shallow coastal ecosystem mosaic as an overall spawning habitat with no specific micro-habitat preferred. Interestingly Tobin et al. (2014) identified 10 species of teleosts in imminent spawning condition from the very same intertidal habitat sampled here. However a relatively dry wet season occurred during the sampling period possibly interrupting normal spawning behaviour (Scoppettone et al. 2000). The identification of developing and spent ovaries in *L. calcarifer, P. argenteus* and *P. kaakan* suggests spawning still occurred in these species, though the physical conditions of the shallow coastal habitat appeared not conducive to supporting spawning for the sampled year.

The need to forage is often a significant driver in habitat choice and use for many species within shallow coastal habitats (Savino & Stein 1989, Milinski 1993) .However, a species need to forage requires a balance against predation risk. Shallow coastal habitats are commonly referred to refuges for larval and juvenile teleosts as the relative abundance of large bodied predators is low. However the relatively high abundance of small larval and juvenile teleosts within a habitat may logically be expected to attract predators. Indeed, *L. calcarifer* was commonly sampled in littoral habitats with stomach contents dominated by small teleost prey. Body size did not limit the foraging success for *L. calcarifer* in the littoral habitats (Primavera 1997, Lundvall et al. 1999) and thus, the refuge function for larvae and juvenile teleosts may be dampened in some habitats. In contrast, stomach contents of intertidal *L. calcarifer* were dominated by crustaceans, suggesting a prey switching behaviour that allows barramundi to exploit and dominate more than one habitat.

The prey items of both *E. tetradactylum* and *P. argenteu*s were most diverse in the intertidal habitat indicating the intertidal habitat may provide a greater diversity of possible prey than either the littoral or subtidal habitat. Alternatively, *E. tetradactylum* and *P. argenteu*s may have increased foraging success in the intertidal habitat due to unknown factors that promotes more successful foraging. For example, Brenner and Krummer (2007) described variable foraging success in the four-eye fish, *Anableps anableps*, meditated by magnitude of tide as well as daylight. Successful foraging occurred mostly during daylight and on large magnitude tides increasing foraging access to intertidal algae, grapsid crabs and insects. The relative importance of the littoral, intertidal and subtidal habitats to the foraging of each species requires further investigation as stomach contents do not necessarily reflect localised abundance of all potential prey. The stomach contents observed likely reflect species-specific foraging success rather than the relative abundance of prey themselves.

Similarly to teleosts, the sharks sampled had a preference for teleost prey with a lesser contribution by crustacean prey. Different metabolic demands of different life history stages may explain the variation in foraging behaviour between shark species. *Rhizoprionodon taylori* were generally sexually mature adults whilst *C. tilstoni/limbatus* were generally YOY and juveniles. The variations in life history stages between *R. taylori* and *C. tilstoni/limbatus* may suggest an increase in energy demands for early life growth and subsequent maturation between the two species. Barry et al. (2008) determined a growth rate of 226 and 325 mm year^{-1} for 0 and +1 age classes of *C. limbatus* indicating high rates of growth which would need to be supported by frequent successful foraging and increased rates of metabolism. Opportunistic foraging was also evident with *Arius* spp. eggs commonly found in stomachs of *C. tilstoni/limbatus*. Seasonal opportunistic foraging has been observed in in other species of teleosts, specifically involving the opportunistic foraging on nutrient dense teleosts eggs. Samoilys (1997) observed a planktivorous fish, *Caesio* spp., opportunistically feeding on the eggs of coral trout, *Plectropomus leopardus,* during the coral trout's seasonal spawning period. The parturition of some coastal shark species may occur simultaneously with seasonally available resources to allow YOY and juveniles an increase in foraging opportunities. Additionally, resource partitioning may also occur between *R. taylori* and *C. tilstoni/limbatus* allowing both species to utilise the shallow coastal habitat mosaic without competing for resources. Kinney et al. (2011) determined resource partitioning within a communal shark nursery in Cleveland Bay, Australia and suggested that *R. taylori* fed on a more specialised diet to possibly avoid competition with other shark species in the habitat. However, determining drivers for foraging activity within the shallow coastal habitat mosaic on stomach content alone is limited. Stomach content analysis is highly variable due to the rate of digestion varying between species, water temperature, and identification of prey items (Baker et al. 2014). It is clear that the shallow coastal habitat mosaic can support foraging activity and that determining drivers of foraging activity requires further consideration.

As anthropogenic pressures on shallow coastal habitats are likely to continue and possibly increase as a results of the dependency of human populations on the productivity of these environments further creating pressure for management to mitigate these threats. Management is more effective when complete and accurate knowledge of the ecological values of habitats are understood and are incorporated into current management practices. This research demonstrates that shallow coastal habitats are of ecological importance to large bodied fish communities, supporting important refuge, reproduction and foraging activities. The disruption or elimination of these habitats through port expansion or land reclamation (POTL 2010) may have profound effects on the coastal ecosystem mosaic. Without a concentrated effort to fully understand the ecological importance of coastal habitats, the large bodied fish communities of the shallow coastal habitat mosaic may become permanently altered.

3.4 Tables and Figures

Table 3.1 Summary of fish, sharks and rays sampled from the littoral, intertidal and subtidal habitats that were utilised for ecological analysis according to total count sampled.

Family	Name	Total	Littoral	Intertidal	Subtidal
Latidae	*Lates calcarifer*	328	124	204	-
Polynemidae	*Eleutheronema tetradactylum*	178	25	75	78
Carcharhinidae	*Rhizoprionodon taylori*	97	-	9	88
Carcharhinidae	*Carcharhinus fitzroyensis*	58	-	4	54
Carcharhinidae	*Carcharhinus tilstoni/limbatus*	58	-	38	20
Pristidae	*Anoxypristis cuspidata*	54	-	39	15
Carcharhinidae	*Carcharhinus amboinensis*	39	2	11	26
Haemulidae	*Pomadasys argenteus*	31	19	12	-
Mugilidae	*Mugil cephalus*	23	1	22	-
Carangidae	*Scomberoides commersonianus*	22	5	17	-
Haemulidae	*Pomadasys kaakan*	17	4	10	3
Sphyrnidae	*Sphyrna lewini*	15	-	11	4
Mugilidae	*Liza vaigiensis*	14	10	4	-
Polynemidae	*Polydactylus macrochir*	12	6	6	-
Platycephalidae	*Platycephalus fuscus*	5	3	2	-
Megalopidae	*Megalops cyprinoides*	4	3	1	-
Synodontidae	*Synodus variegatus*	4	-	1	3
Sphyrnidae	*Sphyrna mokarran*	3	-	-	3
Rhinopteridae	*Rhinoptera neglecta*	3	-	3	-
Leptobramidae	*Leptobrama muelleri*	2	-	2	-
Rhinidae	*Rhynchobatus australiae*	2	-	1	1
Carangidae	*Parastromateus niger*	1	-	1	-
Carangidae	*Scomberoides tala*	1	-	1	-
Scombridae	*Scomberomorus queenslandicus*	1	-	-	1
Triacanthidae	*Triacanthus biaculeatus*	1	-	1	-
Carcharhinidae	*Negaprion acutidens*	1	1	-	-
Rhinobatidae	*Glaucostegus typus*	1	-	1	-
Dasyatidae	*Himantura granulata*	1	-	1	-

Table 3.2 Summary of the number of species and cumulative samples sizes for each taxonomic group and ecological service investigated.

	Teleosts		Sharks		Rays	
Ecological Service	Species	Samples	Species	Samples	Species	Samples
Life History	24	645	7	271	5	61
Reproductive Activity	4	84	4	70	-	-
Foraging Activity	3	151	2	55	-	-

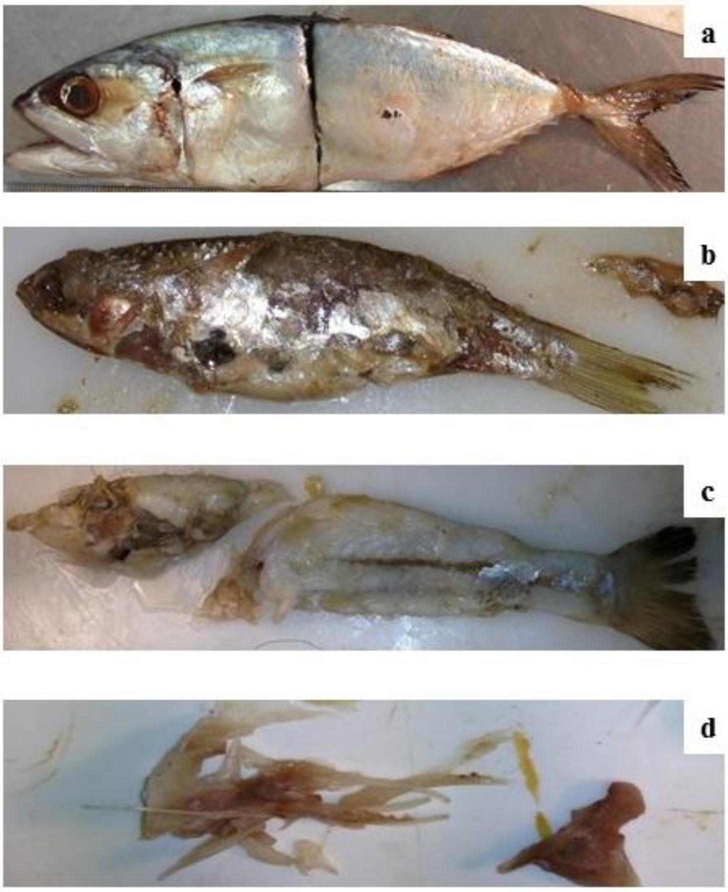

Figure 3.1 Examples of stomach content in the four stages of digestion. Note: a) stage 1, b) stage 2, c) stage 3 and d) stage 4

Table 3.3 Characteristics of the macroscopic stages for female teleosts ovaries. Adapted from West (1990) and Pember (2006).

Stage	Macroscopic Characteristics
I	Immature; ovaries are not developed and thin, no oocytes present
II/III	Developing; ovaries are no longer thin and exhibit a slight increase in size, few oocytes visible
IV	Maturing; ovaries occupy increased percentage of body cavity, large oocytes become visible
V	Spawning imminent; ovaries are fully engorged and occupy 75% of the body cavity, hydrated oocytes visible
VI	Spent; ovaries are flaccid and have a purplish/bruised appearance. Few hydrate oocytes may still be visible

Table 3.4 Characteristic of macroscopic stages for female shark uteruses. Adapted from Walker (2005).

Stage	Macroscopic Characteristics
I	Immature; uterus is uniformly thin and tubular
II	Uncertain; uterus has an enlarger portion posteriorly, but is still thin and tubular
III	Uncertain; uterus is tubular and enlarged
IV	Mature; eggs visible macroscopically in utero
V	Mature; developing embryos are macroscopically visible in utero
VI	Mature; uterus is enlarged and distended

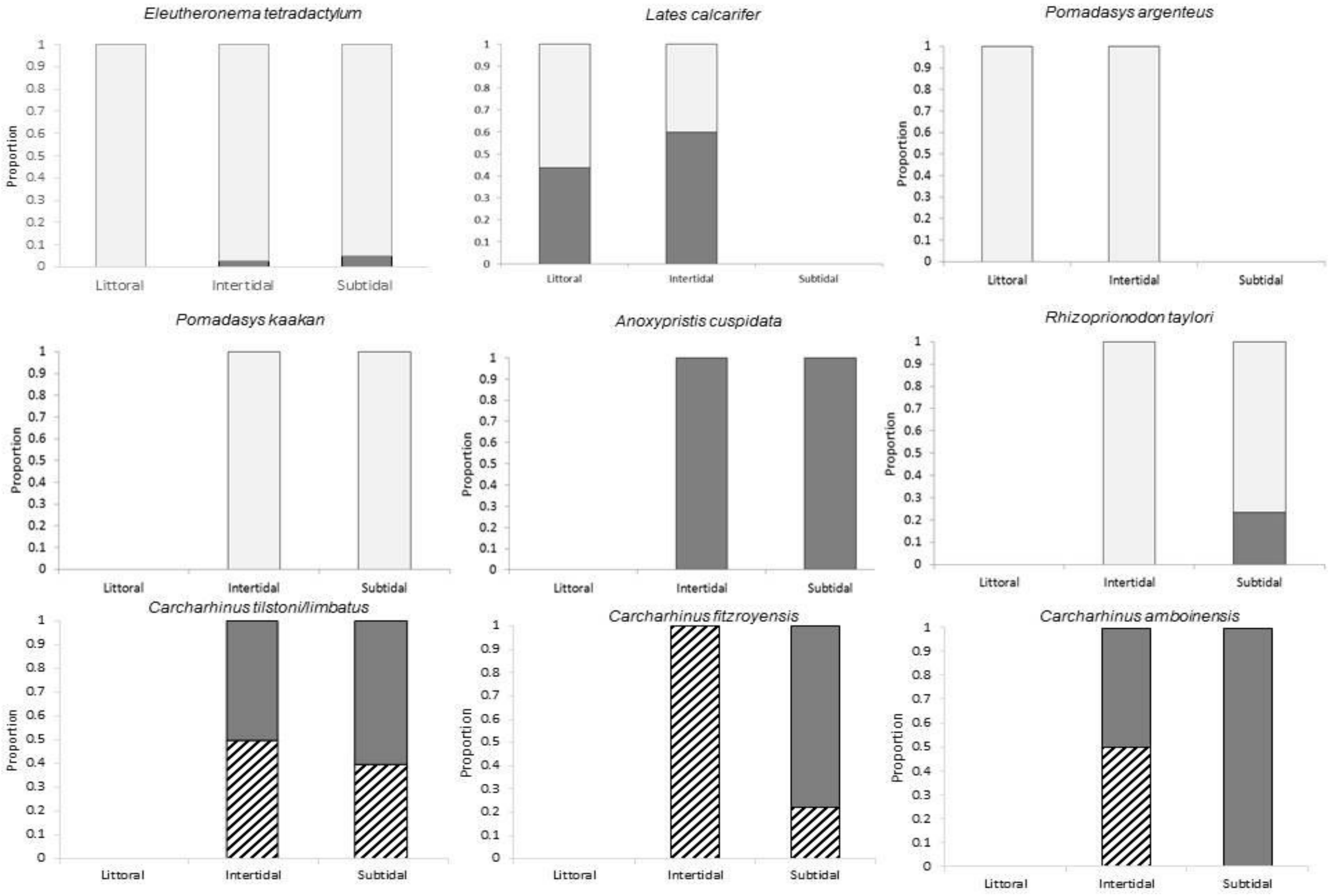

Figure 3.2 Life history stage proportions for nine most commonly sampled species across the littoral, intertidal and subtidal habitats. Note: stripes – YOY, dark grey – juveniles, and light grey – adults.

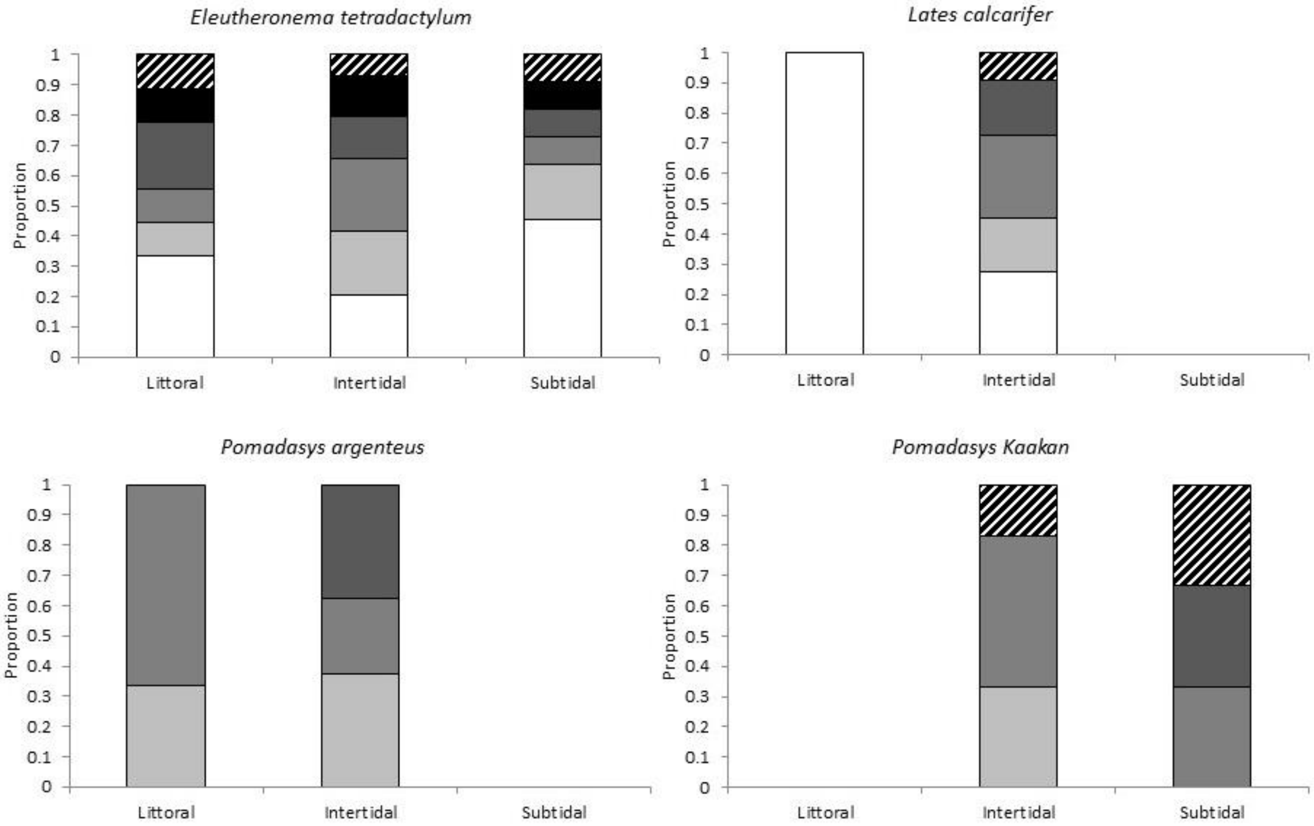

Figure 3.3 The proportions of ovary stages for *Eleutheronema tetradactylum*, *Lates calcarifer*, *Pomadasys argenteus* and *Pomadasys kaakan* among the littoral, intertidal and subtidal habitats. Note: stage 1 - white, stage 2 - light grey, 3- medium grey, stage 4 – dark grey, stage 5 – black, and stage 6 - stripes.

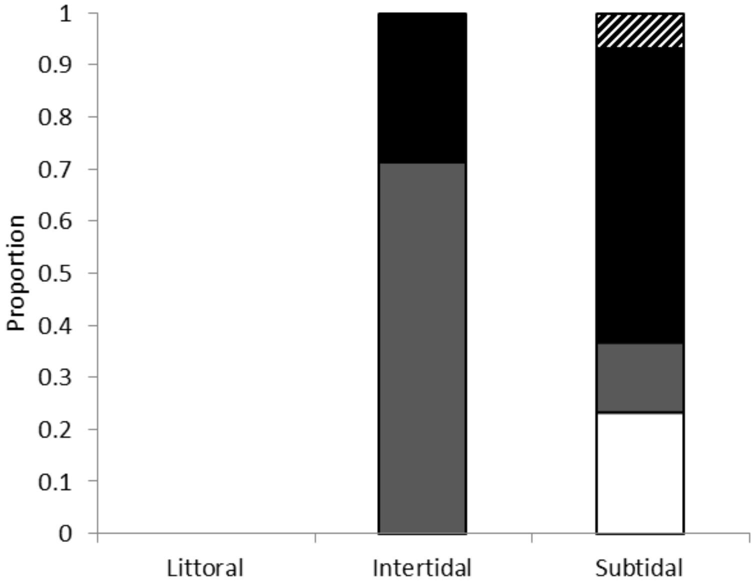

Figure 3.4 The proportion of the reproductive stages of *Rhizoprionodon taylori* uteruses in each habitat. Note: stage 1 – white, stage 2 – light grey, stage 3- dark grey, stage 4 – black and stage 6 - stripes.

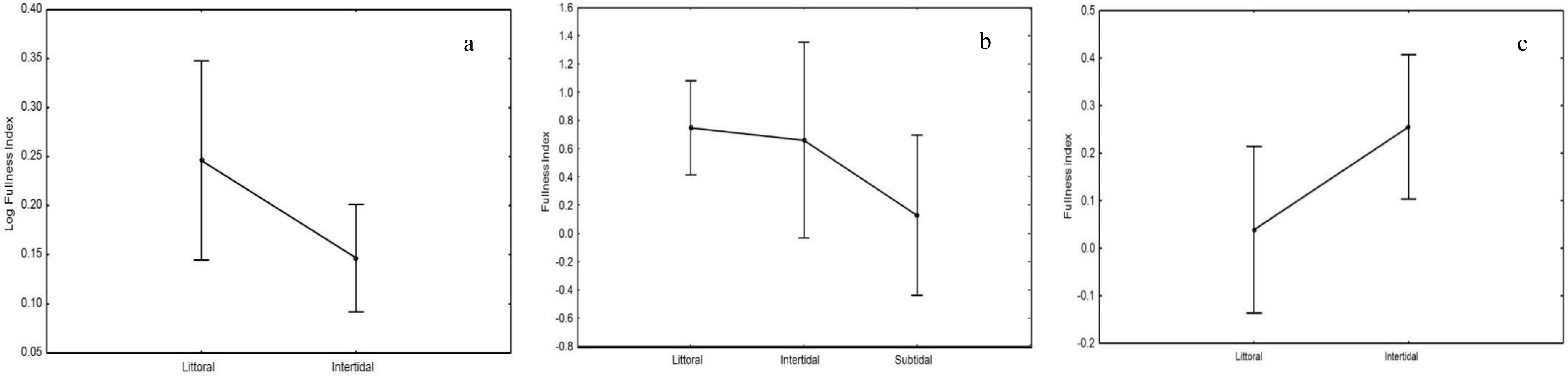

Figure 3.5 Mean (+/- SE) stomach fullness index for a) *Lates calcarifer,* b) *Eleutheronema tetradactylum* and c) *Pomadasys argenteus* across the littoral, intertidal and subtidal habitats.

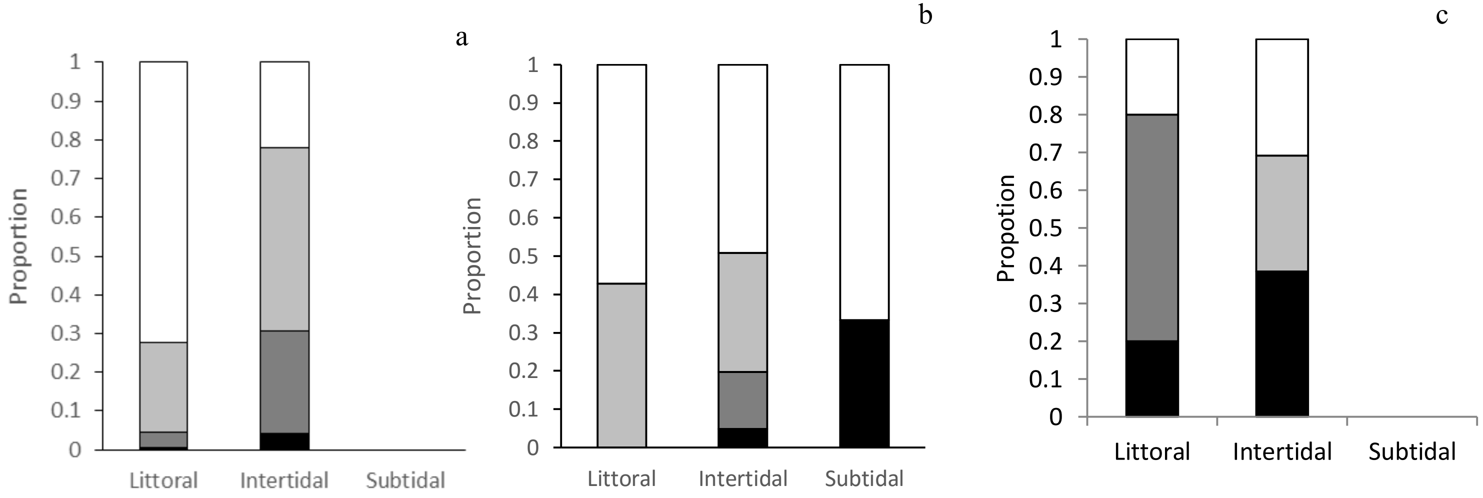

Figure 3.6 Proportion of digestive stages of stomach contents for a) *Lates calcarifer,* b) *Eleutheronema tetradactylum* and c) *Pomadasys argenteus* across the littoral, intertidal and subtidal habitats. Note: digestive stages represented by colours; black – stage 1, dark grey – stage 2, light grey – stage 3 and white – stage 4.

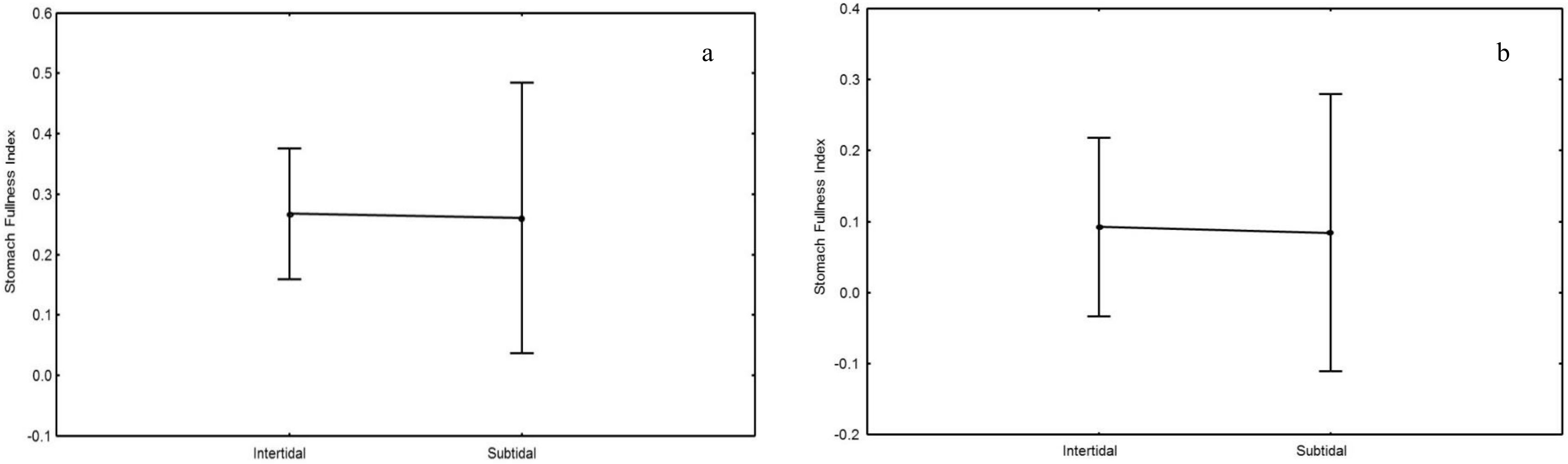

Figure 3.7 Mean (+/- SE) stomach fullness index for a) *Rhizoprionodon taylori* and b) *Carcharhinus tilstoni/limbatus* between the intertidal and subtidal habitats.

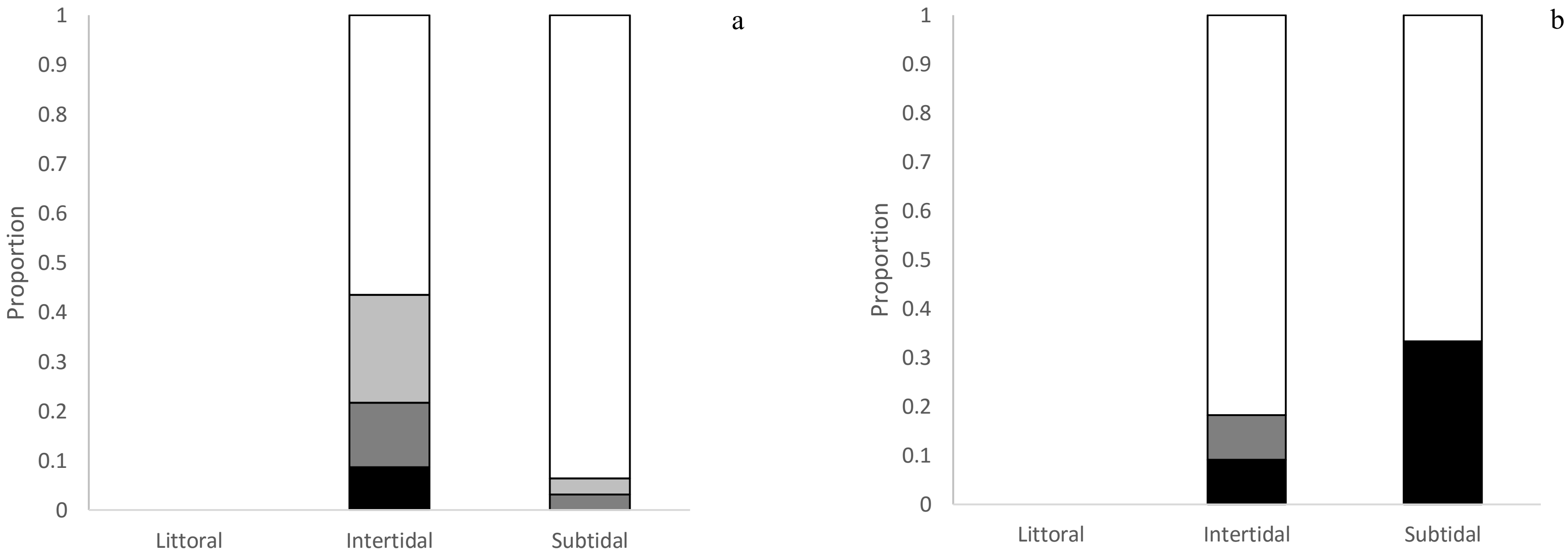

Figure 3.8 Proportion of digestive stages of stomach contents for a) *Rhizoprionodon taylori* and b) *Carcharhinus tilstoni/limbatus* between the intertidal and subtidal habitats. Note: digestive stages represented by colours; black – stage 1, dark grey – stage 2, light grey – stage 3 and white – stage 4.

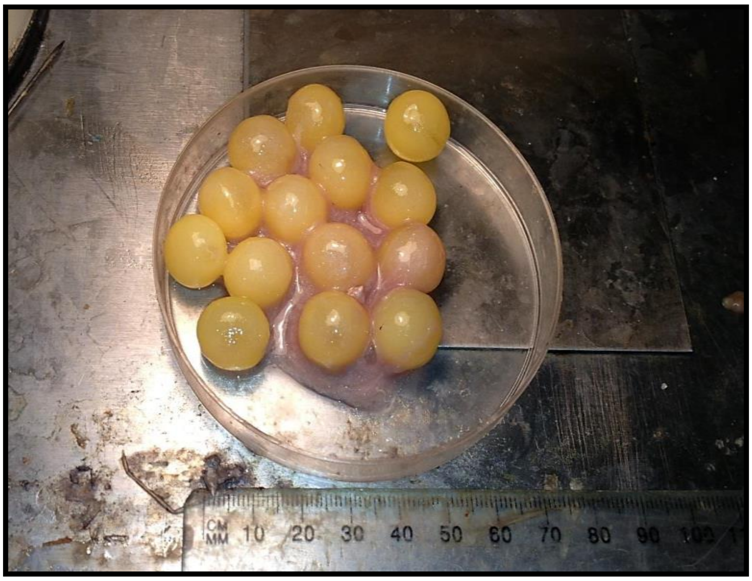

Plate 4. Catfish eggs, *Arius* spp., found in the stomach of a Australian/Common Blacktip shark, *C. tilstoni/limbatus*

Shallow coastal habitats are utilised by a diverse community of fishes, yet these environments and the communities within them are subjected to extreme variability in physical characteristics. These environments have daily cyclic tides that inundate and expose habitats causing variations in temperature, salinity and dissolved oxygen. Further, increasing threats from anthropogenic influences make these areas a priority for management practices. Until recently, shallow coastal habitats have been a focus for research as a result of their importance in supporting and nurturing larval and juvenile fishes by functioning as a nursery habitat. However, contemporary research suggests that shallow coastal habitats may be utilised by large and mature fishes (Tobin et al. 2014) for ecological functions that extend beyond the nursery function. The ecological importance of shallow coastal habitats for foraging (Baker & Sheaves 2005), spawning for teleosts (Dibattista et al. 2008, Præbel et al. 2009) and parturition for elasmobranchs (Márquez-Farías 2007) has been previously described. The findings of this thesis extends our knowledge of the importance of shallow coastal habitats by describing a previously unknown community of large bodied fishes and how these communities benefit from utilising the shallow coastal habitat.

This thesis demonstrated that many species of large bodied fishes use shallow coastal habitats and that habitat use is driven by species-specific needs. Some species use the environment for specific ecological requirements such as spawning, parturition, refuge and foraging, whereas a combination of ecological services may be utilised by other species. Clearly the nursery paradigm often associated with shallow coastal habitats needs to be redefined or extended, because considering shallow coastal habitats only as nurseries will stifle long-term management. Further, management needs to consider all the ecological functions that shallow coastal habitats provide for entire fish communities (larvae, juveniles and adults) to ensure effective resource management. This thesis suggests that future management for shallow coastal habitats should adopt a risk-based management approach to effectively manage all aspects (fishing resources, anthropogenic and natural environmental impacts, and conservation) associated with these complex systems.

Distinctly different communities of teleosts, sharks and rays were observed in the littoral, intertidal and subtidal habitats, identified in Chapter 2. Teleosts were the dominant taxonomic group in the littoral and intertidal habitats, and Chapter 3 identified that juveniles dominated the littoral habitats, while adults dominated the intertidal habitat. Juvenile teleosts occur in increased abundances in shallow habitats, likely to seek refuge from predators and to forage within these habitats (Boesch & Turner 1984, Baker & Sheaves 2009b). Thus, juvenile teleosts may use the littoral habitat for a nursery function. However, the high abundances of adult teleosts in the intertidal habitat suggest it functions as a refuge from offshore predators. Additionally, Chapter 3 identified juvenile sharks and rays utilising the intertidal and subtidal habitats as a nursery. Simpfendorfer and Milward (1993) identified that the extensive subtidal areas of Cleveland Bay function as a nursery for neonate, young-of-the-year and juvenile sharks and rays. The results of this thesis demonstrated that the nursery function of the subtidal habitat extends into the intertidal habitat suggesting that shark nurseries may be more spatially vast than currently thought.

Environmental influences, such as turbidity, salinity and temperature, are known to affect the spatial distribution of sharks (Hight & Lowe 2007, Ortega et al. 2009), teleosts (Castellanos-Galindo & Krumme 2013, Schaffler et al. 2013) and rays (Schlaff et al. 2014). The littoral habitat was characterised by a high abundance of teleosts and limited presence of sharks. However one teleost, *L. calarifer*, was the dominant teleost in the littoral habitat. There were no physical barriers preventing additional species of teleosts and sharks from utilising the littoral habitat, suggesting the dynamic nature of the habitat may influence the distribution and abundances of teleosts and sharks. For instance, barramundi, *L. calcarifer,* are a catadromous finfish and their use of the littoral habitat may correlate with their ability to withstand changes in salinity levels. Whereas many species of sharks are stenohaline, thus occupy a narrow salinity range which would limit their use of the littoral habitat. For example, juvenile pigeye sharks, *C. amboinensis*, will shift their home ranges when wet season flooding decreases salinities in shallow coastal habitats to areas with optimal salinity levels (Knip et al. 2011). The limited distribution of the shark community suggests the variability in salinity and/or the increased temperature may not be conducive for young-of-the-year and juveniles sharks to reach maturation, thus limiting their distribution to the intertidal and subtidal habitats.

Critical life events, such as teleost spawning and shark parturition, often occur in habitats that are spatially discrete and have a unique set of physical and environmental conditions. Identifying and managing these habitats is critical for conserving populations of fishes that would otherwise be exploited or impacted by anthropogenic activities. Multiple shark nursery areas are protected by marine park declarations (Chapman et al. 2009, Lynch et al. 2013) and teleost spawning sites are also protected from fishing practices (Evans et al. 2008, Teske et al. 2010), emphasising that habitats that fulfil these functions are valued for conservation. However, this thesis identified that teleost spawning and shark parturition was not common in the littoral, intertidal and subtidal habitats. Additional ecological functions, foraging, refuge and nursery, were identified within the shallow coastal habitat suggesting the value of the shallow coastal habitat mosaic for spawning or parturition may be limited, but the additional functions may warrant conservation.

The results of this thesis illustrate the global challenge in managing the impacts of coastal development and fishing on species of conservation interest (Iwasaki & Shaw 2008, Gaines et al. 2010, Davies & Baum 2012). This is observed from the abundance of narrow sawfish, *Anoxyprists cuspidata*, a species listed as globally endangered (IUCN Red List) in the intertidal and subtidal habitats. It is prohibited to take *A. cuspidata* by Queensland fisheries management regulations and in international agreements (CITES) Appendix I however, incidental capture still occurs (Tobin et al. 2014) and coastal development may impact their preferred habitats. The habitat preferences of *A. cuspidata* identified in this thesis may be useful for designing effective adaptive management should fishing or coastal development negatively impact the intertidal and subtidal populations. For example, commercial net fishing occurs throughout the shallow coastal habitat mosaic, and restricting the use of net fishing to the littoral habitat would remove the risk of *A. cuspidata* to incidental capture. Although there may be some negative consequences for restricting commercial net fishing in the shallow coastal habitat mosaic, the risk of capture and the possible impact to the populations of *A. cuspidata* would be minimised. Moreover, if the presence of *A. cuspidata* is seasonal then spatial closures may only need to occur when *A. cuspidata* are present creating an effective management approach that balances fisheries and species conservation. Clearly, this thesis has identified valuable information on the distribution of *A. cuspidata* in the shallow coastal mosaic, however further research focusing on spatial distribution of *A. cuspidata* beyond the shallow coastal mosaic is needed before implementation of management policies that would reduce access or limit fishing gear as these habitats are highly productive for many target fishery species.

Clearly, shallow coastal habitats are complex ecosystems where one function cannot define their value (Sheaves et al. 2014a). Acknowledging that shallow coastal habitats may provide value that extends beyond sustaining larvae and juveniles will allow research to fully assess the ecological functions of shallow coastal habitats and determine effective management for these complex systems.

4.1 Future research

Large bodied fishes comprise a greater proportion of the fish communities associated with shallow coastal habitats than existing knowledge suggests. Further research should include the sampling of additional shallow coastal habitats to understand if the fish communities and their distinct community structuring within Cleveland Bay is unique, or is in fact, a previously unidentified characteristic of shallow coastal habitats. In addition, determining seasonal and inter-annual effects on fish communities is required to increase our understanding of these habitats and thus effective management.

Previous studies have identified that fish communities migrate between adjacent habitats (Wright et al. 1990, Irlandi & Crawford 1997, Castellanos-Galindo et al. 2010) suggesting the fish communities identified in this thesis may migrate within the shallow coastal habitat mosaic. Incorporating telemetry research would provide detailed information on how species move between the littoral, intertidal and subtidal habitats that may not be apparent by gear sampling alone.

Sampling the disc-like ray community using gillnets was inefficient as they are less likely to entangle. Multiple types of gear (i.e. seine nets, long line, and dip nets) should be utilised to provide complete and accurate information on the ray community sampled. Multiple gear sampling would also aid in foraging analysis by identifying prey items that characterise each habitat. Additionally, utilising tethering experiments would also provide insight into foraging behaviours within the fish communities by observing active foraging. Identifying if these habitats support unique prey communities, and how those prey communities are consumed by predators would further extend our understanding of the possible foraging function these habitats may support.

REFERENCES

Able K, Wuenschel M, Grothues T, Vasslides J, Rowe P (2013) Do surf zones in New Jersey provide “nursery” habitat for southern fishes? Environmental Biology of Fishes 96:661-675

Abrahams MV, Kattenfeld MG (1997) The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioral Ecology and Sociobiology 40:169-174

Aburto-Oropeza O, Dominguez-Guerrero I, Cota-Nieto J, Plomozo-Lugo T (2009) Recruitment and ontogenetic habitat shifts of the yellow snapper (*Lutjanus argentiventris*) in the Gulf of California. Marine Biology 156:2461-2472

Agardy T (2003) An environmentalist's perspective on responsible fisheries: the need for holistic approaches. In: Sinclair M, Valdimarson G (eds) Responsible Fisheries in the Marine Ecosystem. Food and Agriculture Organization of the United Nations and CAB International, Wallingford (UK)

Agardy T, Alder N, Ash N, DeFries R, Nelson G (2005) Synthesis: condition and trends in systems and services, trade-offs for human well-being, and implactions for the furture. In: Hassan R, Scholes R, Ash N (eds) Ecosystems and human well-being: current state and trends: findings of the Condition and Trends Working Group, Washington, D.C. (USA)

Airoldi L, Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. Oceanography and Marine Biology: An Annual Review 45:345-405

Baker R, Buckland A, Sheaves M (2014) Fish gut content analysis: robust measures of diet composition. Fish and Fisheries 15:170 - 177

Baker R, Sheaves M (2005) Redefining the piscivore assemblage of shallow estuarine nursery habitats. Marine Ecology Progress Series 291:197-213

Baker R, Sheaves M (2006) Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. Marine Ecology Progress Series 323:75-82

Baker R, Sheaves M (2009a) Overlooked small and juvenile piscivores dominate shallow-water estuarine "refuges" in tropical Australia. Estuarine, Coastal and Shelf Science 85:618-626

Baker R, Sheaves M (2009b) Refugees or ravenous predators: detecting predation on new recruits to tropical estuarine nurseries. Wetlands Ecology and Management 17:317 - 330

Bakun A, Parrsh RH (1982) Turbulence, transport, and pelagic fish in the California and Peru current systems. Aquatic Sciences and Fisheries Abstracts 23:99-112

Barry KP, Condrey RE, Driggers III WB, Jones CM (2008) Feeding ecology and growth of neonate and juveniles blacktip sharks *Carcharhinus limbatus* in the Timbalier-Terrebone Bay complex, LA, U.S.A. Journal of Fish Biology 73:650-662

Beck MW, Heck Jr KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51:633-641

Bennett B (1989) The fish community of a moderately exposed beach on the southwestern Cape coast of South Africa and an assessment of this habitat as a nursery for juvenile fish. Estuarine, Coastal and Shelf Science 28:293-305

Bilkovic DM (2011) Response of tidal creek fish communities to dredging and coastal development pressures in a shallow-water estuary. Estuaries and Coasts: J ERF 34:129-147

Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17:143-162

Blaber SJM, Brewer DT, Salini JP (1989) Species composition and biomasses of fishes in different habitats of a tropical Northern Australian estuary: Their occurrence in the adjoining sea and estuarine dependence. Estuarine, Coastal and Shelf Science 29:509-531

Blaber SJM, Brewer DT, Salini JP (1995) Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the gulf of Carpentaria, Australia. Estuarine, Coastal and Shelf Science 40:177-193

Blaber SJM, Cyrus DP, Albaret JJ, Ching CV, Day JW, Elliott M, Fonseca MS, Hoss DE, Orensanz J, Potter IC, Silvert W (2000) Effects of fishing on the structure and functioning of estuarine and nearshore ecosystems. ICES Journal of Marine Science: Journal du Conseil 57:590-602

Boehlert GW, Mundy BC (1988) Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. American Fish Society Symposium 3:1-67

Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7:460-468

Bonvicini pagliai AM, Cognetti Varriale AM, Crema R, Curini Galletti M, Vandini Zunarelli R (1985) Environmental impact of extensive dredging in a coastal marine area. Marine Pollution Bulletin 16:483-488

Brenner M, Krummer U (2007) Tidal migration and patterns in feeding of the four-eyed fish *Anableps anableps* L. in north Brazilian mangrove. Journal of Fish Biology 70:406-427

Burke L, Kura Y, Kassem K, Ravenga C, Spalding M, McAllister D (2001) Pilot Assesment of Global Ecosystems: Coastal Ecosystems. World Resource Institute, Washington, D.C. (USA)

Carlson JK (2002) Shark nurseries in the northeastern Gulf of Mexico. In: McCandless C, Pratt H, Kohler N (eds) Shark nursery gounds of the Gulf of Mexico and east coast waters of the United States: an overview. NOAA Fisheries, Narragansett, RI

Castellanos-Galindo G, Krumme U, Willis T (2010) Tidal influences on fish distributions on tropical eastern Pacific rocky shores (Colombia). Marine Ecology Progress Series 416:241-254

Castellanos-Galindo GA, Krumme U (2013) Tidal, diel and seasonal effects on intertidal mangrove fish in a high-rainfall area of the Tropical Eastern Pacific. Marine Ecology Progress Series 494:249-265

Castro JI (1993) The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environmental Biology of Fishes 38:37-48

Cerutti-Pereyra F, Thums M, Austin CM, Bradshaw CJA, Stevens JD, Babcock RC, Pillans RD, Meekan MG (2014) Restricted movements of juvenile rays in the lagoon of Ningaloo Reef, Western Australia – evidence for the existence of a nursery. Environmental Biology of Fishes 97:371-383

Chapman DD, Babcock EA, Gruber SH, DiBattista JD, Franks BR, Kessel SA, Guttridge T, Pikitch EK, Feldheim KA (2009) Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. Molecular Ecology 18:3500-3507

Chin A, Heupel MR, Simpfendorfer CA, Tobin AJ (2013) Ontogentic movements of juvenile blacktip reef sharks: evidence of dispersal and connectivity between coastal habitats and coral reefs. Aquatic Conservation - Marine and Freshwater Ecosystems 23:468-474

Chong VC, Sasekumar A, Leh MUC, D'Cruz R (1990) The fish and prawn communities of a Malaysian coastal mangrove system, with comparisons to adjacent mud flats and inshore waters. Estuarine, Coastal and Shelf Science 31:703-722

Cooke SJ, Cowx IG (2004) The role of recreational fishing in global fish crises. Bioscience 54:857-859

Courrat A, Lobry J, Nicolas D, Laffargue P, Amara R, Lepage M, Girardin M, Le Pape O (2009) Anthropogenic disturbance on nursery function of estuarine areas for marine species. Estuarine, Coastal and Shelf Science 81:179-190

Dale JJ, Drazen JC, Holland KN (2013) Stingray life history trade-offs associated with nursery habitat use inferred from a bioenergetics model. Marine Biology 160:3181-3192

Davies TD, Baum JK (2012) Extinction risk and overfishing: reconciling conservation and fisheries perspectives on the status of marine fishes. Scientific Reports 2:561

DeMartini EE (1999) Intertidal spawning. In: Horn MH, Martin KLM, Chotkowski MA (eds) Intertidal fishes: Life in two worlds. Academic Press, San Diego, CA

Dibattista JD, Feldheim KA, Thibert-Plante X, Gruber SH, Hendry AP (2008) A genetic assessment of polyandry and breeding-site fidelity in lemon sharks. Molecular Ecology 17:3337-3351

Dorenbosch M, MVerweij MC, Nagelkerken I, Jiddawi N, van der Veld G (2004) Homing and daytime tidal movements of juvenile snappers (Lutjanidae) between shallow-water nursery habitats in Zanaibar, western Indain Ocean. Environmental Biology of Fishes 70:203-209

Duke NC, Wolanski E (2001) Muddy coastal waters and depleted mangrove coastlines - depleted segrass and coral reefs. In: Wolanski E (ed) Oceanographic Processes of Coral Reefs Physical and Biology Links in the Great Barrier Reef. CRC Presss, Washington, DC.

Ebert DA (2003) California natural history guides: sharks, rays, and chimaeras of California, Vol 71. University of California Press, Berkeley, CA, USA

Espinoza M, Clarke TM, Villalobos-Rojas F, Wehrtmann IS (2013) Diet composition and diel feeding behaviour of the banded guitarfish *Zapteryx xyster* along the Pacific coast of Costa Rica, Central America. Journal of Fish Biology 82:286-305

Evans RD, Russ GR, Kritzer JP (2008) Batch fecundity of *Lutjanus carponotatus* (Lutjanidae) and implications of no-take marine reserves on the Great Barrier Reef, Australia. Coral Reefs 27:179-189

Eyre BD, Ferguson AJP, Webb A, Maher D, Oakes JM (2011) Metabolism of different benthic habitats and their contribution to the carbon budget of a shallow oligotrophic sub-tropical coastal system (southern Moreton Bay, Australia). Biogeochemistry 102:87-110

Fairclough DV, Clarke KR, Valesini FJ, Potter IC (2008) Habitat partitioning by five congeneric and abundant Choerodon species (Labridae) in a large subtropical marine embayment. Estuarine, Coastal and Shelf Science 77:446-456

FAO (2008) The state of the world fisheries and aquaculture. In: Department FaA (ed). FAO, Rome, Italy

Faunce CH, Serafy JE (2006) Mangroves as fish habitat: 50 years of field studies. Marine Ecology Progress Series 318:1-18

Félix-Hackradt FC, Hackradt CW, Treviño-Otón J, Pérez-Ruzafa A, García-Charton JA (2014) Habitat use and ontogenetic shifts of fish life stages at rocky reefs in South-western Mediterranean Sea. Journal of Sea Research 88:67-77

Francis MP (2013) Temporal and spatial patterns of habitat use by juveniles of a small coastal shark (*Mustelus lenticulatus*) in an estuarine nursery. Public Library of Science ONE 8 (2)

Franco A, Franzoi P, Malavasi S, Riccato F, Torricelli P, Mainardi D (2006) Use of shallow water habitats by fish assemblages in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science 66:67-83

Froese R, Pauly D (2014) FishBase. World Wide Web electronic publication, www.fishbase.org, version (06/2014)

Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences of the United States of America 107:18286-18293

Goodman MA, Conn PB, Fitzpatrick E (2011) Seasonal occurrence of cownose rays (*Rhinoptera bonasus*) in North Carolina's estuarine and coastal waters. Estuaries and Coasts: J ERF 34:640-651

Groombridge B, Jenkins M, World Conservation Monitoring C (2000) Global biodiversity: earth's living resources in the 21st century. World Conservation Press, Cambridge, U.K

Hanski I (2011) Habitat loss, the dynamics of biodiversity, and a perspective on conservation. AMBIO 40:248-255

Harry AV (2011) Life histories of commerically important tropical sharks from the Great Barrier Reef World Heritage Area. Doctor of Philosophy, James Cook University, Townsville

Heithaus MR, Dill LM (2002) Food availability and tiger shark predation rish influence bottlenose dolphin habitat use. Ecology 83:480-491

Heithaus MR, Vaudo JJ, Kreicker S, Layman CA, Krutzen M, Burkholder DA, Gastrich K, Bessey C, Sarabia R, Cameron K, Wirsing A, Thomson JA, Dunphy-Daly MM (2013) Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem. Marine Ecology Progress Series 481:225-237

Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine enviornment. Aquatic Biology 1:227-289

Hight BV, Lowe CG (2007) Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoregulation? Journal of Experimental Marine Biology and Ecology 352:114-128

Hinrichsen D (1998) Coastal waters of the world: trends, threats and stratiges. Island Press, Washington, DC

Horn MH, Martin KLM, Chotkowski MA (1999) Introduction. In: Horn MH, Martin KLM, Chotkowski MA (eds) Intertidal Fishes: Life in two worlds. Acadamic Press, San Diego, California

Hoshikawa H, Kuwahara H, Tajima K-i, Kawai T, Kaneta T, Tsuda F (2004) Characteristics of a Pacific herring *Clupea pallasii* spawning bed off Minedomari, Hokkaido, Japan. Fish Sci 70:772-779

Hutchings JA, Côté IM, Dodson JJ, Fleming IA, Jennings S, Mantua NJ, Peterman RM, Riddell BE, Weaver AJ (2012) Climate change, fisheries, and aquaculture: trends and consequences for Canadian marine biodiversity 1This manuscript is a companion paper to Vander Zwaag et al. (doi:10.1139/a2012-013) and Hutchings et al. (doi:10.1139/er-2012-0049) also appearing in this issue. These three papers comprise an edited version of a February 2012 Royal Society of Canada Expert Panel Report. Environmental Reviews 20:220-311

Irlandi EA, Crawford MK (1997) Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110:222-230

Iwasaki S, Shaw R (2008) Fishery resource management in Chilika Lagoon: a study on coastal conservation in the Eastern Coast of India. Journal of Coastal Conservation 12:43-52

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Jon E, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638

Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics. Environmental Biology of Fishes 3:65-84

Kennett DJ, Kennett JP (2006) Early state formation in southern Mesopotamia: sea leves, shoreline, and climate change. Journal of Island and Coastal Archaeology 1:67-99

Kimirei IA, Nagelkerken I, Mgaya YD, Huijbers CM (2013) The mangrove nursery paradigm revisited: otolith stable isotopes support nursery-to-reef movements by Indo-Pacific Fishes. Public Library of Science ONE 8 (6)

Kinney MJ, Hussey NE, Fisk AT, Tobin AJ, Simpfendorfer CA (2011) Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. Marine Ecology Progress Series 439:263-276

Knip DM, Heupel MR, Simpfendorfer CA (2012) Habitat use and spatial segregation of adult spottail sharks *Carcharhinus sorrah* in tropical nearshore waters. Journal of Fish Biology 80:767-784

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. Marine Ecology Progress Series 425:233-246

Krishnamurthy RR (2010) Coastal morphological changes in India and its relevance to coastal managment In: Shaw R, Krishnamurthy RR (eds) Communities and Coastal Zone Management Research Publishing Services, Singapore

Krumme U, Brenner M, Saint-Paul U (2008) Spring-neap cycle as a major driver of temporal variations in feeding of intertidal fishes: evidence from the sea catfish *Sciades herzbergii* (Ariidae) of equatorial west Atlantic mangrove creeks. Journal of Experimental Marine Biology and Ecology 367:91-99

Lasiak TA (1981) Nursery grounds of juvenile teleosts: evidence from the surf zone of King's Beach, Port Elizabeth. South African Journal of Science 77:388-390

Laurel BJ, Ryer CH, Knoth B, Stoner AW (2009) Temporal and ontogenetic shifts in habitat use of juvenile Pacific cod (*Gadus macrocephalus*). Journal of Experimental Marine Biology and Ecology 377:28-35

Layman CA (2000) Fish assemblage structure of the shallow ocean surf-zone on the eastern shore of Virginia Barrier Islands. Estuarine, Coastal and Shelf Science 51:201-213

Lazzari MA, Sherman S, Kanwit JK (2003) Nursery use of shallow habitats by epibenthic fishes in Maine nearshore waters. Estuarine, Coastal and Shelf Science 56:73-84

Low JJ, Igoe F, Davenport J, Harrison SSC (2011) Littoral spawning habitats of three southern Arctic charr (*Salvelinus alpinus* L.) populations. Ecology of Freshwater Fish 20:537-547

Lundvall D, Svanback R, Persson L, Bystrom P (1999) Size-dependent predation in piscivores: Interactions between predator foraging and prey avoidance abilities. Canadian Journal of Fisheries and Aquatic Sciences 56:1285-1292

Lynch TP, Harcourt R, Edgar G, Barrett N (2013) Conservation of the critically endangered Eastern Australian population of the grey nurse shark (*Carcharias taurus*) through cross-jurisdictional management of a network of marine-protected areas. Environmental Management 52:1341-1354

Márquez-Farías JF (2007) Reproductive biology of shovelnose guitarfish *Rhinobatos productus* from the eastern Gulf of California México. Marine Biology 151:1445-1454

McCallister M, Ford R, Gelsleichter J (2013) Abundance and distribution of sharks in northeast Florida waters and identification of potential nursery habitat. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 5:200-210

Middaugh DP, Scott GI, Dean JM (1981) Reproductive behavior of the Atlantic silverside, *Menidia menidia* (Pisces, Atherinidae). Environmental Biology of Fishes 6:269-276

Milinski M (1993) Predation risk and feeding behaviour. In: Pitcher TJ (ed) Behaviour of teleost fishes. Chapman & Hall, London

Morgan JT, Harry A, Welch D, Street R, White J, Geraghty P, Macbeth W, Tobin A, Simpfendorfer C, Ovenden J (2012) Detection of interspecies hybridisation in Chondrichthyes: hybrids and hybrid offspring between Australian (*Carcharhinus tilstoni*) and common (*C. limbatus*) blacktip shark found in an Australian fishery. Conserv Genet 13:455-463

Morley SA, Toft JD, Hanson KM (2012) Ecological effects of shoreline armoring on intertidal habitats of a Puget Sound Urban Estuary. Estuaries and Coasts: J ERF 35:774-784

Mychek-Londer JG, Bunnell DB (2013) Gastric evacuation rate, index of fullness, and daily ration of Lake Michigan slimy (*Cottus cognatus*) and deepwater sculpin (*Myoxocephalus thompsonii*). Journal of Great Lakes Research 39:327-335

Nagelkerken I (2009) Evaluation of nursery function of mangroves and seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. In: Nagelkerken I (ed) Ecological Connectivity among Tropical Coastal Ecosystems. Springer Netherlands

Nagelkerken I, van der Velde G (2004) Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? Marine Ecology Progress Series 274:143-151

Ooi AL, Chong VC (2011) Larval fish assemblages in a tropical mangrove estuary and adjacent coastal waters: Offshore–inshore flux of marine and estuarine species. Continental Shelf Research 31:1599-1610

Ortega LA, Heupel MR, Beynen PV, Motta PJ (2009) Movement patterns and water quality preferences of juvenile bull sharks (*Carcharhinus leucas*) in a Florida estuary. Environmental Biology of Fishes 84:361-373

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Olyarnik S, Short FT, Waycott M, Williams SL (2006) A global crisis for seagrass ecosystems. Bioscience 56:987-996

Paterson AW, Whitfield AK (2000) Do shallow-water habitats function as refugia for juvenile fishes? Estuarine, Coastal and Shelf Science 51:359-364

Pember MB (2006) Characteristics of fish communities in coastal waters of north-western Australia, including the biology of the threadfin species *Eleutheronema tetradactylum* and *Polydactylus macrochir*. Doctor of Philosphy, Murdoch University, Western Australia

Polte P, Asmus H (2006) Intertidal seagrass beds (*Zostera noltii*) as spawning grounds for transient fishes in the Wadden Sea. Marine Ecology Progress Series 312:235-243

POTL (2010) Townsville Port Urban Waterfront Master Plan. In: Limited PoT, Consulting BLL, Design LL, Associates C, Group A, Bucknall RL, Engineers UC, Marinas DA, GHD (eds), Townsville

Præbel K, Christiansen JS, Fevolden S-E (2009) Temperature and salinity conditions in a sub-Arctic intertidal spawning habitat for capelin. Marine Biology Research 5:511-514

Primavera JH (1997) Fish predation on mangrove-associated penaeids: the role of structures and substrate. Journal of Experimental Marine Biology and Ecology 215:205-216

Primavera JH (2006) Overcoming the impacts of aquaculture on the coastal zone. Ocean & Coastal Management 49:531-545

Prochazka K (1998) Spatial and trophic partitioning in cryptic fish communities of shallow subtidal reefs in False Bay, South Africa. Environmental Biology of Fishes 51:201-220

Quinn T, Krueger K, Pierce K, Penttila D, Perry K, Hicks T, Lowry D (2012) Patterns of surf smelt, *Hypomesus pretiosus*, intertidal spawning habitat use in Puget Sound, Washington State. Estuaries and Coasts: J ERF 35:1214-1228

Robertson AI, Duke NC (1987) Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Marine Biology 96:193-205

Ryer CH, Laurel BJ, Stoner AW (2010) Testing the shallow water refuge hypothesis in flatfish nurseries. Marine Ecology Progress Series 415:275-282

Samoilys MA (1997) Periodicity of spawning aggregations of coral trout *Plectropomus leopardus* (Pisces: Serranidae) on the northern Great Barrier Reef. Marine Ecology Progress Series 160:149-159

Santos RG, Martins AS, Farias JN, Horta PA, Pinheiro HT, Torezani E, Baptistotte C, Seminoff JA, Balazs GH, Work TM (2011) Coastal habitat degradation and green sea turtle diets in Southeastern Brazil. Marine Pollution Bulletin 62:1297-1302

Savino JF, Stein RA (1989) Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. Environmental Biology of Fishes 24:287-293

Schaffler JJ, Montfrans Jv, Jones CM, Orth RJ (2013) Fish species distribution in seagrass habitats of Chesapeake Bay are structured by abiotic and biotic Factors. Marine and Coastal Fisheries 5:114-124

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish Biol Fisheries 24:1089-1103

Schock NT, Murry BA, Uzarski DG (2014) Impacts of agricultural drainage outlets on Great Lakes coastal wetlands. Wetlands 34:297-307

Scoppettone GG, Rissler PH, Buettner ME (2000) Reproductive longevity and fecundity associated with nonannual spawning in cui-cui. Transactions of the American Fisheries Society 129:658-669

Shahidul Islam M, Tanaka M (2004) Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis. Marine Pollution Bulletin 48:624-649

Sheaves M (1992) Patterns of distribution and abundance of fishes in different habitats of a mangrove-lined tropical estuary, as determined by fish trapping. Marine and Freshwater Research 43:1461-1479

Sheaves M (2001) Are there really few piscivorous fishes in shallow estuarine habitats? Marine Ecology Progress Series 222:279-290

Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. Marine Ecology Progress Series 391:107-115

Sheaves M, Baker R, Nagelkerken I, Connolly RM (2014a) True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. Estuaries and Coasts: J ERF:1-14

Sheaves M, Sheaves J, Stegemann K, Molony B (2014b) Resource partitioning and habitat-specific dietary plasticity of two estuarine sparid fishes increase food-web complexity. Marine & Freshwater Research 65:114-123

Shenker JM, Dean JM (1979) The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. Estuaries 2:154-163

Sheridan P, Hays C (2003) Are mangroves nursery habitat for transient fishes and decapods? Wetlands 23:449-458

Sherman K (1993) Large marine ecosystems as global units for marine resource management. In: Sherman K, Alexander L, Gold B (eds) Large marine ecosystems: stress, mitigation and sustainability. American Association for the Advancement of Science, Washington, DC

Simpfendorfer CA, Freitas GG, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a Southwest Florida estuary. Estuaries 28:78-85

Simpfendorfer CA, Milward NE (1993) Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environmental Biology of Fishes 37:337-345

Simpfendorfer CA, Wiley TR, Yeiser BG (2010) Improving conservation planning for an endangered sawfish using data from acoustic telemetry. Biological Conservation 143:1460-1469

Sims D, Nash J, Morritt D (2001) Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Marine Biology 139:1165-1175

Stallings CD (2009) Fishery-independent data reveal negative effect of human population density on caribbean predatory Fish communities. Public Library of Science ONE 4 (5)

Sundblad G, Bergström U (2014) Shoreline development and degradation of coastal fish reproduction habitats. AMBIO 43:1020-1028

Taylor MH (1990) Estuarine and intertidal teleost. In: Munro AD, Scott AP, Lam TJ (eds) Reproductive seasonality in teleost: Envrionmental influences. CRC Press, Inc., Boca Raton, FL

Taylor MH (1999) A suite of adaptations for intertidal spawning. American Zoologist 39:313-320

Taylor S, Sumpton W, Ham T (2011) Fine-scale spatial and seasonal partitioning among large sharks and other elasmobranchs in south-eastern Queensland, Australia. Marine and Freshwater Research 62:638-647

Teske PR, Forget FRG, Cowley PD, von der Heyden S, Beheregaray LB (2010) Connectivity between marine reserves and exploited areas in the philopatric reef fish *Chrysoblephus laticeps* (Teleostei: Sparidae). Marine Biology 157:2029-2042

Tewksbury II HT, Conover DO (1987) Adaptive significance of intertidal egg deposition in the Atlantic Silverside *Menidia menidia*. Copeia 1987:76-83

Thronson A, Quigg A (2008) Fifty-five years of fish kills in coastal Texas. Estuaries and Coasts: J ERF 31:802-813

Tobin AJ, Mapleston A, Harry AV, Espinoza M (2014) Big fish in shallow water; use of an intertidal surf-zone habitat by large-bodied teleosts and elasmobranchs in tropical northern Australia. Environmental Biology of Fishes:1-18

Trimble AC, Ruesink JL, Dumbauld BR (2009) Factors preventing the recovery of a historically overexploited shellfish species, *Ostrea lurida* Carpenter 1864. Journal of Shellfish Research 28:97-106

UN (2004) World population to 2300. Population and Development Review 30:181-187

Verdiell-Cubedo D, Torralva M, Andreau-Soler A, Oliva-Paterna FJ (2012a) Effects of shoreline urban modification on habitat structure and fish community in littoral areas of a Mediterranean Coastl Lagoon (Mar Menor, Spain). Wetlands 32:631-641

Verdiell-Cubedo D, Torralva M, Ruiz-Navarro A, Oliva-Paterna FJ (2012b) Fish assemblages in different littoral habitat types of a hypersaline coastal lagoon (Mar Menor, Mediterranean Sea). Italian Journal of Zoology 80:104-116

Wada T, Kamiyama K, Shimamura S, Matsumoto I, Mizuno T, Nemoto Y (2011) Habitat utilization, feeding, and growth of wild spotted halibut *Verasper variegatus* in a shallow brackish lagoon: Matsukawa-ura, northeastern Japan. Fish Sci 77:785-793

Walker TI (2005) Reproduction in Fisheries Science. In: Hamlett WC (ed) Reproductive biology and phylogeny of chondrichthyes : sharks, batoids and chimaeras. Science Publishers, Enfield, NH

Wen C, Pratchett M, Shao K, Kan K, Chan B (2010) Effects of habitat modification on coastal fish assemblages. Journal of Fish Biology 77:1674-1687

West G (1990) Methods of assessing ovarian development in fishes: A review. Australian Journal of Marine and Freshwater Research 41:199 - 222

Williams GD, Andrews KS, Farrer DA, Bargmann GG, Levin PS (2011) Occurrence and biological characteristics of boradnose sevengill sharks (*Notorynchus cepedianus*) in Pacific Northwest coastal estuaries. Environmental Biology of Fishes 31:379-388

Wright JM, Clayton DA, Bishop JM (1990) Tidal movements of shallow water fishes in Kuwait Bay. Journal of Fish Biology 37:959-974

Yamahira K (1996) The role of intertidal egg deposition on survival of the puffer, *Takifugu niphobles* (Jordan et Snyder), embryos. Journal of Experimental Marine Biology and Ecology:291-306