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Trophic ecology and habitat use of juvenile rays in intertidal sand flats

Submitted by

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Abstract

Intertidal zones around the world support diverse assemblages of mobile predators, including juvenile rays. While rays are increasingly recognised as important mesopredators and ecosystem engineers, there are substantial knowledge gaps surrounding their basic ecology, particularly during early life stages. This translates to a poor understanding of how species partition resources within productive juvenile habitats and how their diverse foraging strategies contribute to broader-scale ecosystem processes. To address these gaps, I investigated the habitat use and trophic ecology of rays in tropical intertidal sand flats of northeastern Australia.

First, I surveyed eight intertidal flats in the wet and dry tropics of North Queensland using aerial drones to identify patterns in species composition and habitat use. In total, nine species were detected across intertidal beach flats, estuary inlets, and offshore reef flats throughout the region. Species richness ranged from 5-8 per location, with the most common species including the giant shovelnose ray, *Glaucostegus typus*, Australian whipray, *Himantura australis*, cowtail stingray, *Pastinachus ater*, and mangrove whipray, *Urogymnus granulatus*. Community evenness per site (on a scale of 0-1) ranged from 0.2 (dominated by single species) to 0.77 (relatively even abundances), and differences in relative abundances suggested potential associations with specific habitat characteristics. Furthermore, a prevalence of ray foraging activity observed in the drone surveys highlighted the significance of these areas as communal feeding grounds.

Drones were then used to compare the fine-scale foraging behaviours of three sympatric ray species (cowtail stingray, *Pastinachus ater*, pink whipray, *Pateobatis fai*, and mangrove whipray, *Urogymnus granulatus*) at Pioneer Bay, Orpheus Island. The pervasiveness of foraging activity by juvenile *P. ater*, *P. fai*, and *U. granulatus* demonstrated that these species regularly obtain resources within the shallow reef flat nursery. Tidal

fluctuations had significant impacts on the foraging behaviours of *P. ater* and *U. granulatus*. Rays foraged most intensely during lower tidal height ranges, which could reflect potential changes in prey availability over the tidal gradient or that rays prioritise predator avoidance behaviours as depth increases. Unique foraging preferences provided some evidence of fine-scale resource partitioning, where species may target different prey and occupy complementary functional niches within the nursery. However, high overlap in specific aspects of foraging, such as all three species using surface feeding on smooth sand (albeit in different proportions) and feeding over similar areas suggested that all three species share some degree of functional redundancy. This chapter underscores the value of incorporating behavioural data into our interpretations of fine-scale habitat use and for understanding these processes at the species level.

Prior to conducting dietary analyses to explore resource use of juvenile ray communities, I conducted a literature review and a case study to evaluate the suitability of non-lethal gastric lavage for extracting stomach contents. The literature review showed that this technique is highly underutilised in field research on elasmobranchs, with research limited to a few taxa and life stages. In the field study, gastric lavage proved highly effective for obtaining stomach contents from four species of juvenile rays, with success rates exceeding 75%. Tag-recapture data across two study sites also provided evidence of post-release survival over extended periods (from one day to 533 days later).

I then used gastric lavage to assess dietary composition and trophic ecology of four sympatric ray species (Australian whipray, *H. australis*, giant shovelnose ray, *G. typus*, brown whipray, *Maculabatis toshi*, and cowtail stingray, *P. ater*) at Lucinda, North Queensland. Stomach content analysis (SCA) and stable isotope analysis (SIA) revealed important prey types for each species during early juvenile life stages and provided insights on their dietary overlap. *Himantura australis, M. toshi,* and *G. typus* all preferred decapod crustaceans, with a

particular importance of penaeid prawns in the diets of *G. typus* and *M. toshi*. In contrast, *P. ater* was the only species to prefer polychaetes and molluscs. High dietary overlap between early juvenile *G. typus* and *M. toshi* indicate that these species may have more limited diets due to their small body sizes and tendencies to feed along the surface, thus experiencing greater direct competition for shared prey resources. In contrast, dietary and trophic niche separation between *H. australis* and *P. ater* support previous observations of ray foraging at Lucinda, where these species feed over different spatial areas and use different foraging behaviours. Prey availability surveys I conducted using multiple methods confirmed that rays feed on abundant prey types within the intertidal zone and that key foraging areas are likely influenced by patchy prey availability over fine spatial scales.

The prevalence of foraging activity, combined with evidence of distinct feeding strategies and dietary niches, highlights the importance of unvegetated tidal flats as feeding grounds and nurseries for multi-species ray communities. Overall, this thesis advances our understanding of how species-specific behaviours drive habitat use patterns and foraging dynamics of rays, with implications for understanding their functional roles and impacts in intertidal ecosystems. Furthermore, understanding predator-prey dependencies at the species and community levels strengthens our ability to identify essential habitats and to assess the vulnerability of ray populations into the future.

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1 Chapter 1: General introduction

1.1 Intertidal zones as essential habitats

Intertidal flats surround the world's coastlines and encompass a mosaic of unique marine and estuarine habitats such as sand flats, mud flats, coral reefs, saltmarshes, seagrass, and mangrove forests (Kennish 2002, Whitfield et al. 2022). Collectively, these areas provide a variety of ecosystem services like sediment stabilisation and carbon sequestration (Beaumont et al. 2014, Chen & Lee 2022). As transitional zones between land and sea, intertidal zones are some of the most dynamic environments on earth (Desjardins et al. 2012). Their extent is shaped by the steepness of the elevation gradient and tidal amplitude, which vary considerably among geographical regions and between spring and neap tidal cycles (Leurs et al. 2023). These physical distinctions drive regular fluctuations in temperature, salinity, dissolved oxygen, and depth (Leeuwis & Gamperl 2022, Sheaves et al. 2024b). On one extreme, intertidal zones may become inundated with meters of seawater during the high tide or become completely exposed by the next low tide. To survive, marine inhabitants must either have physiological mechanisms for coping with stress or otherwise employ behavioural strategies to avoid desiccation, such as burrowing or timing their movements with tidal cycles (Horn et al. 1998, Becker et al. 2016).

Despite these challenges, intertidal ecosystems boast unique assemblages of marine species that support global fisheries and food security for humans (Walker & McComb 1992, Stibor & Sommer 2009, Nagelkerken et al. 2015). High productivity within intertidal ecosystems is largely driven by diverse macroinvertebrate communities, which act as conduits of energy between primary producers and higher trophic levels (Salgado et al. 2007, Abrantes & Sheaves 2009b, Vasconcelos et al. 2015, Kwon et al. 2020). Furthermore, most estuarine or shallow marine ecosystems represent high quality nursery grounds (Beck et al.

2001, Martinho et al. 2012) with abundant prey resources, refuge from predators, and favourable environmental conditions during critical early life stages (Beck et al. 2001, Martinho et al. 2012, Sheaves et al. 2013, Nagelkerken et al. 2015, Sheaves et al. 2015). Overall, nursery function and habitat use have become focal points of interest for conservation and management, with strong implications for supporting ecosystem-wide productivity, connectivity, and recruitment into offshore populations (Nagelkerken et al. 2015, Sheaves et al. 2015).

Although unvegetated sand and mud flats comprise over 90% of intertidal areas globally (Murray et al. 2019), they remain understudied compared to more structurally complex habitats like seagrass beds and mangroves (Sheaves et al. 2024a). These habitats are often characterised by low topographic complexity, leading to assumptions that they support lower species diversity and biomass than more structured environments (Edgar et al. 1994, Connolly 1995, Fredriksen et al. 2010). However, recent evidence challenges this perception, suggesting that while species composition may differ, unvegetated flats can support comparable levels of biodiversity and abundance to adjacent vegetated habitats (Barnes & Barnes 2012, 2014). Moreover, these areas also provide valuable ecological functions as movement corridors and feeding grounds for mobile species across tidal cycles (Nagelkerken et al. 2015, James et al. 2019).

Elasmobranchs represent a diverse subclass of cartilaginous fishes that include both sharks and rays. They are widely distributed across deep oceanic waters to shallow coastal environments (Carrier et al. 2022), in which over 200 species are associated with intertidal habitats (Leurs et al. 2023). Many species use these areas as nurseries during early life stages, where they can occur in high densities (Merson & Pratt 2001, Pierce et al. 2011). Such nursery habitats are critical for promoting growth and survival before individuals transition to deeper subtidal, reef, or offshore habitats as adults (Heupel et al. 2007, Martins et al. 2018, Heupel et al. 2019). The ecological value of nurseries is further enhanced by philopatric behaviour, where females return to the same areas across multiple years to give birth (Smale et al. 2015, Flowers et al. 2016, Laurrabaquio-A et al. 2019). Thus, the presence of multiple species and cohorts contributes to greater trophic complexity within these systems and adds to their persisting importance over time (Simpfendorfer & Milward 1993).

Rays, in particular, have evolved specialised morphological and physiological adaptations that enable them to exploit intertidal environments. The terms “ray” and “batoid” collectively refer to members of the Superorder Batoidea, for which 26 families and more than 600 species have been recognised (Last et al. 2016). Their dorsoventrally flattened morphologies permit them to move across shallow intertidal gradients, even during periods of shallow inundation (<0.5 m), while also enabling them to bury in soft sediments for predator avoidance (Semeniuk & Dill 2005, 2006). Modified pectoral fins and ventrally positioned mouths enhance their ability to extract benthic prey from loose sediments (Kolmann et al. 2015), and many species also possess broad thermal and salinity tolerances that enable them to cope with substantial environmental variability (Schlaff et al. 2014). In tropical regions, for example, studies have shown that rays can withstand seasonal temperature fluctuations of >15 °C and temperature maximums above 40°C, which they manage via behavioural thermoregulation tactics (Matern et al. 2000, Vaudo & Heithaus 2013, Higgins et al. 2024). Collectively, these adaptations allow rays to access productive feeding grounds that may be unavailable to other predators and return to these same areas to over consecutive tidal cycles (Cerutti-Pereyra et al. 2013, Martins et al. 2020b, Ruiz-García et al. 2020).

1.2 Ecological roles of rays

Rays are mesopredators, with diets largely comprised of benthic crustaceans, annelids, molluscs, and small teleosts (Flowers et al. 2021). Through both consumptive and non-consumptive effects, mesopredators also influence the behaviour, distribution, and abundance of their prey, with cascading effects on lower trophic levels (Östman et al. 2016, Byers et al. 2017, Burt et al. 2018). Simultaneously, mesopredators acting as prey also mediate the transfer of energy and nutrients through ecosystems through bottom-up pathways (Ritchie & Johnson 2009), making them essential components of ecosystem function in coastal environments (Bergström et al. 2016). As mesopredators, rays apply top-down pressure to invertebrate communities, while from the bottom-up, rays are a valuable prey resource for other elasmobranchs (e.g. hammerhead sharks (Gallagher et al. 2014, Jerome et al. 2018)), avian predators (Green et al. 1990, Ajemian et al. 2011), and marine mammals (Visser 1999). Through a shared reliance on macroinvertebrate prey, rays share potential trophic overlap with other functional mesopredators including teleosts (Muñoz & Ojeda 1997, DeFelice & Parrish 2003, Sheaves et al. 2017) and shorebirds (Thrush et al. 1994, Muñoz & Ojeda 1997, Tamaki et al. 2020). However, their unique excavation capabilities may allow them to access deeper buried prey that are inaccessible to other predators (D'Andrea et al. 2004, Takeuchi & Tamaki 2014).

Although growing research supports the various mesopredatory roles of rays, their predator-prey dynamics remain poorly investigated (Vaudo & Heithaus 2011, Flowers et al. 2021). Consequently, this can support misconceptions regarding their ecological impacts and translate into potentially harmful management decisions. For example, increased populations of cownose rays, *Rhinoptera bonasus,* along the Atlantic east coast of North America were previously attributed to collapsing commercial shellfish stocks (Peterson et al. 1989, Peterson et al. 2001, Myers et al. 2007), which prompted policies to reduce ray numbers. However, a later re-examination by Grubbs et al. (2016) found no evident relationship between increasing ray populations and bivalve stock declines. Other research has similarly focused on the impacts of rays on commercial shellfish stocks, particularly in regions where apex predators have declined (Ajemian et al. 2012, Ajemian & Powers 2013). Both studies indicated that cownose rays and spotted eagle rays, *Aetobatus narinari*, had modest impacts on the populations on hard-shelled bivalves in subtropical Bermuda and the northern Gulf of Mexico. However, with other studies reporting negative impacts of rays on invertebrate densities (Thrush et al. 1994, Tamaki et al. 2020), overall conclusions surrounding these effects may be limited by insufficient knowledge of dietary variability, community context, and modelling responses at appropriate spatial scales (Thrush 1999, Heithaus 2004).

In addition to their roles as predators, rays also act as ecosystem engineers that modify physical aspects of their environment (Samson et al. 1996, Hastings et al. 2007). Bioturbation contributes to several physical processes such as sediment turnover and reworking (Meysman et al. 2006, Grew et al. 2024), nutrient cycling (Valentine et al. 1994, Meysman et al. 2006, O'Shea et al. 2012, Takeuchi & Tamaki 2014), and creating foraging opportunities for other benthic predators (Boaden & Kingsford 2012, Kiszka et al. 2015). Feeding pits and scars created from intense feeding can also persist for several days (Hines et al. 1997, Takeuchi & Tamaki 2014, Tamaki et al. 2020) or even weeks (M. Sheaves, pers. obs.). These indentations function as small refuge pools during low tides that can be used by other benthic organisms (Thrush 1999, Cross & Curran 2000, Cross & Curran 2004) and increase the topographical complexity of the sand flat surface over time (Barnes & Cottrell 2024). As some of the largest benthic excavators in intertidal ecosystems (Heithaus et al. 2010, Sarker et al. 2021), the ability to perform ecosystem engineering at these scales may be unreproducible by other taxonomic groups.

Overall, the ways in which species contribute to ecosystem bioturbation are strongly linked to when and where they feed (Ajemian & Powers 2012). Fine-scale movement patterns shape the magnitude and spatial extent of these effects from daily tidal cycles to seasonal habitat use (Campbell et al. 2012, Cerutti-Pereyra et al. 2013, Brinton & Curran 2017). For instance, if rays regularly return to the same areas to feed over repeated tidal cycles, this results in greater localised predation pressure on benthic invertebrates, rather than distributing these effects uniformly across available habitats (Ajemian et al. 2012, Crook 2020). These impacts may be intensified in intertidal nurseries, where the more limited movements and site fidelity of juveniles concentrate their activities to more localised spatial scales (Vaudo & Lowe 2006, Davy et al. 2015, Elston et al. 2019).

1.3 Drivers of habitat use

In general, fish assemblages are structured by abiotic and biotic factors that vary across spatial and temporal scales (Whitfield 1996, Bacheler et al. 2009, King et al. 2021). Abiotic variables encompass various environmental features and water quality parameters such as temperature, salinity, and dissolved oxygen (Morin et al. 1992, McLusky & Elliott 2004). For rays that make periodic migrations across intertidal gradients (Oleksyn et al. 2020, Ruiz-García et al. 2020, Elston et al. 2022), tidal cycling is certainly an important factor, as it directly influences habitat accessibility and environmental conditions (Lam et al. 2005).

Where abiotic requirements are met, biotic factors become increasingly important for shaping fine-scale habitat use due to their direct impacts on animal behaviour (Heithaus 2004, Selleslagh & Amara 2008, Hunsicker et al. 2011). Predators generally occupy areas where there is higher potential energy intake (e.g. prey availability) to maximise individual fitness while reducing competition, particularly where resources are limited (Tregenza 1995, Le Pape & Bonhommeau 2015, Day et al. 2020). Thus, prey availability becomes a relevant predictor of predator distributions and habitat use (Heupel & Hueter 2002, Reid et al. 2004, Carroll et al. 2019). Benthic invertebrate distributions vary spatially across habitats and tidal zonation gradients (Dittmann 1995, 2000, Dittmann 2002), which creates distinct feeding landscapes for benthic predators (Barnes & Barnes 2012, Benoit-Bird et al. 2013, Sheaves et al. 2016). To add to this complexity, habitat selection also reflects the various trade-offs between foraging opportunities and predator avoidance (Hammerschlag et al. 2010, Stump et al. 2017, Lester et al. 2020).

1.4 Mechanisms of species coexistence

Understanding resource use is necessary for interpreting underlying patterns in species distributions and ecosystem function (Hairston Jr & Hairston Sr 1993, Barnes et al. 2018). An increase of trophic studies on rays in recent decades have yielded valuable insights into the dietary preferences, nutritional requirements, and foraging strategies of different species and life stages, and how these vary within populations (Flowers et al. 2021). Several studies have provided evidence of inter-specific resource partitioning within elasmobranch communities, which promotes species coexistence by minimising competition for limited resources (Papastamatiou et al. 2006a, Yick et al. 2011, Heithaus et al. 2013, Queiroz et al. 2023). Intraspecific resource partitioning also occurs among different size classes (Barbini & Lucifora 2012, Elston et al. 2020), since gape size ultimately determines the size of prey that can be consumed. The greater energetic demands associated with larger body sizes also drive transitions to higher-energy prey items and the movements of individuals into areas where these resources are accessible (Scharf et al. 2009, Sánchez-Hernández et al. 2019). However, other studies have shown high dietary overlap among ray populations (O'Shea et al. 2013, O'Shea et al. 2020), which may indicate that resources are not limited or that prey selection is more reflective of their unique competitive abilities (Weideli et al. 2023). Furthermore, individuals may also minimise direct competition through spatial or temporal partitioning mechanisms (White & Potter 2004, Ajemian & Powers 2016, Lear et al. 2021).

Despite these insights, establishing causal relationships of resource partitioning (or the lack of it) in ray communities remains challenging (Flowers et al. 2021). While competition is often invoked as the key driver of resource partitioning (Ross 1986), information on prey availability or predator carrying capacities are difficult to estimate in the field. Additionally, methodological inconsistencies across studies can lead to differing conclusions about dietary overlap among species. For example, stomach content analysis (with or without genetic prey verification) and stable isotope analysis each address different aspects of trophic ecology (Abrantes & Sheaves 2024, Baker et al. 2024), which can yield contradictory results of dietary overlap (Petta et al. 2020). Moreover, these approaches may not fully capture the spatio-temporal scales over which resource partitioning occurs (Connolly et al. 2005).

1.5 Linking habitat use, trophic ecology, and foraging behaviours

Knowledge of ray feeding ecology is generally derived from trophic studies using either stomach contents or molecular techniques (Elston et al. 2017, Elston et al. 2020, Serrano-Flores et al. 2021, Martins et al. 2022, Queiroz et al. 2023). Acoustic tracking further demonstrates when and where foraging is likely to occur based on prey availability or other external factors (Ajemian et al. 2012, Martins et al. 2020b, Elston & Murray 2024, Legernes et al. 2024). However, behavioural studies are needed to fill the gaps in “how” foraging occurs in real-time. For example, behavioural studies have provided insights into the feeding frequencies of predators (Heithaus et al. 2002, Torres et al. 2018), modes of attack (Bartashevich et al. 2024), social hunting interactions (Pollock et al. 2022), and if they themselves engage in predator-avoidance behaviours (Sansom et al. 2009).

Studying animal behaviour in marine environments presents unique challenges compared to terrestrial systems (Johnson et al. 2009). Limited accessibility to aquatic habitats, poor visibility conditions, and the often brief or sporadic nature of foraging events can make it difficult to collect comprehensive behavioural data using methods such as stationary cameras or human observers (Sims 2003, Murphy & Jenkins 2010, Dickens et al. 2011). These constraints are particularly evident for highly mobile predators that cover large distances while foraging (Heithaus et al. 2002). Thus, where direct observations are lacking altogether for a species or group, foraging behaviours may instead be inferred from other aspects of ecology, such as diets or movement (Hammerschlag 2019, Schwarz et al. 2021).

Remote sensing technologies present another tool for surveying habitat use and behavioural patterns of megafauna, which addresses some of the aforementioned limitations (Raoult et al. 2018, Schofield et al. 2019, Butcher et al. 2021). Drones enable rapid coverage of areas that may be otherwise challenging or time-consuming to survey with labour-intensive capture methods, underwater cameras, manned aerial surveys, or snorkel-based surveys (Colefax et al. 2018, Kelaher et al. 2019, Raoult et al. 2020b). Additionally, the high-resolution imagery offered by drones allows for accurate identification of species and specific behaviours with minimal disturbance to individuals (Mo & Bonatakis 2022, Bourke et al. 2023). While drone applications in marine research continue to expand, their effectiveness is primarily limited to shallow-water environments where adequate visibility can be maintained (Benavides et al. 2019). Despite this constraint, drones have proven particularly valuable for studying species that regularly use surface waters or inhabit shallow areas (Raoult et al. 2020a, Schad & Fischer 2023).

Rays are an ideal model for examining behavioural patterns due to their accessibility in shallow waters, relatively sedentary benthic lifestyle, and predictable movements into intertidal zones with the tide. Moreover, insights gained from this group could be applicable towards understanding the behavioural dynamics of other taxa where direct observation is more challenging. For rays, researchers have employed observational methods to study different aspects of behaviour. For example, anti-predation responses have been studied using snorkeler surveys (Semeniuk & Dill 2005, 2006), while stationary cameras were effective for examining habitat use within mangrove habitats (Kanno et al. 2019). More recently, drone-based studies on rays have provided novel insights into fine-scale movements (Frixione et al. 2020, Oleksyn et al. 2020) and foraging patterns (Crook et al. 2022). Only the latter study has used drones to compare foraging behaviours between two sympatric species, with results supporting species-specific patterns and functional complementarity in intertidal sand flats. However, other drone studies that mapped feeding pit densities have also revealed the significant contributions of rays to ecosystem-level bioturbation (Grew et al. 2024, Nauta et al. 2024). Overall, future drone-based behavioural studies on rays will be particularly useful for bridging the gaps between ray feeding, habitat use, and functional roles in intertidal zones.

1.6 Primary knowledge gaps and thesis overview

Although we have a general understanding of the effects of abiotic variables on marine elasmobranchs (Schlaff et al. 2014), information is more scarce on how biotic factors such as prey availability or predator avoidance influence their movements or feeding ecologies

(Heithaus 2004, Heupel et al. 2014, Roff et al. 2016). Predator-prey relationships have been largely overlooked for rays, with relatively few examples where prey availability has been used to contextualise habitat use (Tilley 2011, Vaudo & Heithaus 2013), prey selection (Pardo et al. 2015, O'Shea et al. 2018), and estimating their impacts on benthic resources (Ajemian et al. 2012). Moreover, despite growing research claiming the general importance of rays as ecosystem engineers and vital mesopredators (O'Shea et al. 2012, Heupel et al. 2014, Flowers et al. 2021), their ecological impacts also remain difficult to quantify without more knowledge on their spatio-temporal foraging behaviours.

A strong reliance on nearshore habitats, particularly during early life stages, makes coastal ray species acutely vulnerable to extinction (Pacoureau et al. 2021). Intertidal zones, in particular, face unprecedented pressures from expanding human populations and infrastructure, resulting in significant habitat loss and modification (Lotze et al. 2006, Halpern et al. 2019, Murray et al. 2019). Concurrent threats to ray populations underscore the critical importance of prioritising essential habitats to support effective species conservation, yet this remains challenging without baseline data on their habitat preferences and feeding ecology (MacKeracher et al. 2019, Birkmanis et al. 2020). These knowledge gaps are particularly evident along Australia's east coast, where there is little information on ray community structures in intertidal habitats or their resource requirements during critical early life stages. Where assumptions are made regarding resource use, this could translate to inaccurate estimates of habitat quality and poor outcomes for conservation and management (Wirsing et al. 2007, Receveur et al. 2022).

In this thesis, I explore the habitat use and trophic ecology of rays within tropical intertidal flats of northeastern Australia, using multiple methods. This work is divided into four data chapters followed by a general discussion on their implications (Figure 1.1).

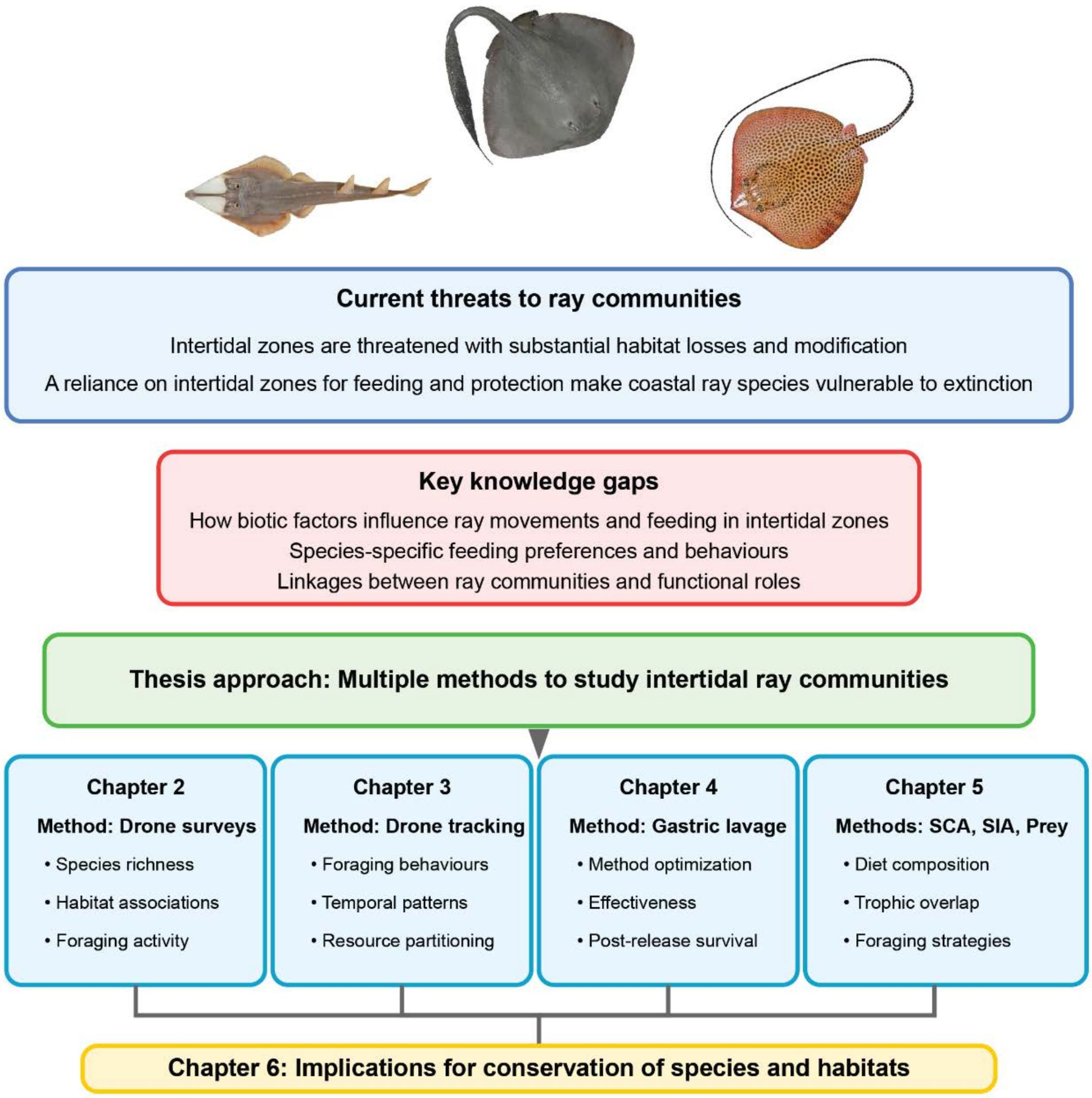


Figure 1.1. Overview of the conservation challenges and key knowledge gaps underpinning the aims of this thesis. The methods and key outputs of each chapter are summarised, which support implications for species conservation and understanding their ecological roles in intertidal zones. Ray images were provided by the Australian National Fish Collection, CSIRO.

In Chapter 2, I used aerial drones to survey ray communities across eight intertidal flats to provide baseline knowledge of species richness, species composition, and habitat associations within this region. Additionally, I used behavioural frequencies from these surveys to assess the foraging activity of main species at each site.

In Chapter 3, I used aerial drone tracking to compare the foraging behaviours of three juvenile ray species (*Urogymnus granulatus, Pateobatis fai, Pastinachus ater*) at Pioneer Bay, Orpheus Island. My aims were to assess temporal foraging patterns across the tide and if differences in behaviour supported potential resource partitioning and species-specific functional roles within the nursery.

In Chapter 4, I investigated the suitability of the non-lethal gastric lavage technique (stomach or gut flushing) I would use for dietary analysis in Chapter 5. First, I conducted a literature summary to assess which species of sharks and rays the procedure has been used on and how survival has been verified following this procedure (in the field or in captivity). Given its limited use on juvenile rays, I conducted a field study to optimise the gastric lavage procedure for neonate to juvenile-sized rays and assess post-release survival using mark-recapture methods.

In Chapter 5, I used the gastric lavage methodology developed in Chapter 4 to assess dietary composition of sympatric ray species (*H. australis, G. typus, M. toshi, P. ater*) within a primarily unvegetated sand flat environment. Stomach content analysis was combined with stable isotope analysis to assess dietary composition, foraging strategies, and dietary overlap among species. Additionally, I examined spatio-temporal prey availability to contextualise prey selection and known foraging behaviours of species within the study area.

Overall, integrating these approaches provided a more holistic view of resource use and the roles rays play in ecosystem food webs. The general discussion presented in Chapter 6 highlights how layering information on diet, foraging behaviours, and prey availability expands our knowledge on trophic ecology and ecosystem dynamics, and the need to understand these processes at the species level. Furthermore, I discuss broader implications for how these findings can be applied towards species management and conservation.

2 Chapter 2: Community structures of rays in intertidal flats of northeast Australia

2.1 Introduction

The Indo-West Pacific region contains some of the world's most diverse elasmobranch assemblages (Compagno et al. 2005, White et al. 2006). A variety of ray taxa including wedgefish (Rhinidae), guitarfish (Rhinobatidae, Glaucostegidae), sawfish (Pristidae), and stingrays (Dasyatidae) inhabit tropical and subtropical waters along the Australian east coast (Pierce et al. 2011, Taylor et al. 2011, Tobin et al. 2014, Yon et al. 2020). Many species within these families are currently threatened with extinction and are classified by the IUCN as Vulnerable, Endangered, or Critically Endangered (Pacoureau et al. 2021, Sherman et al. 2023). Although these species experience relatively high levels of protection in Australian waters, they face greater risk across their geographical ranges due to increased fishing pressure, bycatch, and habitat degradation in recent decades (Dulvy et al. 2021, Pacoureau et al. 2021). Thus, knowledge of ray distributions and abundances in more pristine habitat areas could be crucial for establishing baseline ecological data to inform broader conservation efforts.

While there is a general understanding of the geographical distributions, preferred habitats, and depth ranges of these species (Last et al. 2016), knowledge remains limited regarding factors that influence distributions and finer-scale habitat use (Cartamil et al. 2003, Vaudo & Heithaus 2012). This gap is particularly evident when teasing apart species-habitat associations in complex coastal environments, where differences in substrate composition, vegetation, hydrology, and biotic communities can cause differences at microhabitat scales (Hewitt et al. 2001, Wołowicz et al. 2007, Franca et al. 2012). Habitats that appear to have similar features may not be functionally equivalent, which consequently shapes their intrinsic habitat value for species or communities (Franca et al. 2012, Bradley et al. 2019, Reis-Filho et al. 2019). Thus, determining species-habitat associations across these different ecological contexts is vital for identifying ecologically valuable habitats and managing them at appropriate scales (Yates et al. 2015, Bradley et al. 2019, Bradley et al. 2020, DeGroot et al. 2020, Lear et al. 2024).

Intertidal zones encompass a mosaic of habitats such as sand flats, mud flats, coral reefs, seagrasses, and mangroves (Kennish 2002), of which unvegetated, soft bottom flats cover the most spatial area globally (Dhanjal-Adams et al. 2016, Murray et al. 2019). A recent review has reported that at least 45 ray species use intertidal zones during one or more life stages, predominantly as juveniles (Leurs et al. 2023). A reliance on nurseries is linked to their abundant foraging opportunities, refuge from predators, and favourable abiotic conditions (Martins et al. 2018). However, despite the apparent importance of intertidal zones for rays globally, there remains relatively little information on which species and life stages are associated with these habitats across northeastern Australia. Consequently, their value for different ray species and how ray communities participate in these ecosystems remains poorly understood.

Previous assessments of elasmobranch community composition in intertidal flats of Australia have historically depended on capture methods (e.g. gillnets) (Pierce et al. 2011, Tobin et al. 2014, Adkins et al. 2016). However, more recently some studies have adopted the use of remote sensing technologies for surveying species abundances in shallow water environments (Raoult et al. 2018, Colefax et al. 2019, Schofield et al. 2019, Raoult et al. 2020a, Yang et al. 2022). Aerial drones represent a suitable alternative for collecting data over multi-site scales, as they can cover large spatial areas with minimal effort, while obtaining high-resolution data on species occurrences and distributions (Oleksyn et al. 2021, Álvarez-González et al. 2023). Additionally, drones facilitate observations of natural behaviours with minimal disturbance, allowing researchers to interpret fine-scale patterns of habitat use, such as spatio-temporal foraging behaviours (Crook et al. 2022, Schad & Fischer 2023). While drone surveys would provide complementary perspectives to existing capture studies, currently no studies have used drone surveys to evaluate community composition of rays in tropical intertidal flats of northeast Australia.

In this study, I used aerial drones to survey ray communities at eight intertidal flat sites in tropical northeast Australia to provide baseline knowledge of species richness, species composition, and habitat associations for this region. Additionally, I used behavioural frequencies from the surveys to summarise foraging activity of ray species across these locations.

2.2 Methods

2.2.1 Study sites

Eight sites were selected north and south of Townsville, North Queensland (Figure 2.1). Site selection was based on prior knowledge that rays are present and where suitable visibility conditions were attainable across repeated visits. All sites experience semi-diurnal tidal regimes, with mean sea level ranging from 1.74-1.94 m. Differences in spring tidal height ranges were similar across sites, ranging from 2.03-2.19 m, with lesser extremes during neap tidal phases (0.58-0.78 m). Northernmost sites in the Hinchinbrook and Palm Islands regions experience the highest levels of rainfall during the wet season months from December to April (average annual rainfall 186 cm) compared to sites in the Cape Cleveland (123 cm) or Burdekin regions (110 cm). Survey areas ranged from 0.22-2.0 km^2, which was dependent on the size of the intertidal zone, as well as accessibility to launch points for the drone. All sites were fringed by mangrove forests, generally of *Avicennia* and *Rhizophora*. Sites were classified into three types: estuary inlet (Blacksoil Creek, Deluge Inlet), intertidal beach flat (Cungulla, Lucinda, and Rocky Ponds), or offshore reef flat (Pioneer Bay, Hazard Bay, Juno Bay) (Table 2.1). For all sites, sediment characteristics were assigned qualitatively based on observations made during site visits and knowledge from previous studies (Sheaves et al. 2014, Mattone & Sheaves 2017, Crook 2020, Martins et al. 2022).

Estuary inlets were characterised by steep mangrove banks and intertidal sand flats on the accreting banks, but sites differed in several aspects. Deluge Inlet receives high levels of freshwater runoff from Hinchinbrook Island, which flushes large amounts of sediments downstream and results in coarse sandy substrates within the channel (Sheaves et al. 2014). In contrast, intertidal flats in Blacksoil Creek were comprised of more homogenous fine sand flats. Surveys were conducted upstream of the estuary mouths along unvegetated sand flats and mangrove edges within the channels. At low tides, available habitat for marine life was restricted to the subtidal channels along the deeper edges, and sand flats along the accreting banks would become periodically submerged during rising tides.

Of the beach flat sites, Cungulla and Lucinda were primarily unvegetated with shallow tidal gradients. Sediment composition at Lucinda is primarily coarse sand with some patchy mixtures of fine sand and mud along the beach and mangrove forests (Crook 2020), whereas Cungulla contains mostly mud and fine sand. Rocky Ponds differed by the presence of seagrass that covered roughly 70% of the surveyed area, which was interspersed with unvegetated habitat patches.

Intertidal reef flats in the Palm Islands group consisted of sandy flat areas interspersed with coral and rocky rubble and a presence of mangroves along the upper intertidal edges. Most sampling was conducted at Pioneer Bay in front of the Orpheus Island Research Station, with additional data collected from Hazard Bay, Orpheus Island and Juno Bay, Fantome Island.

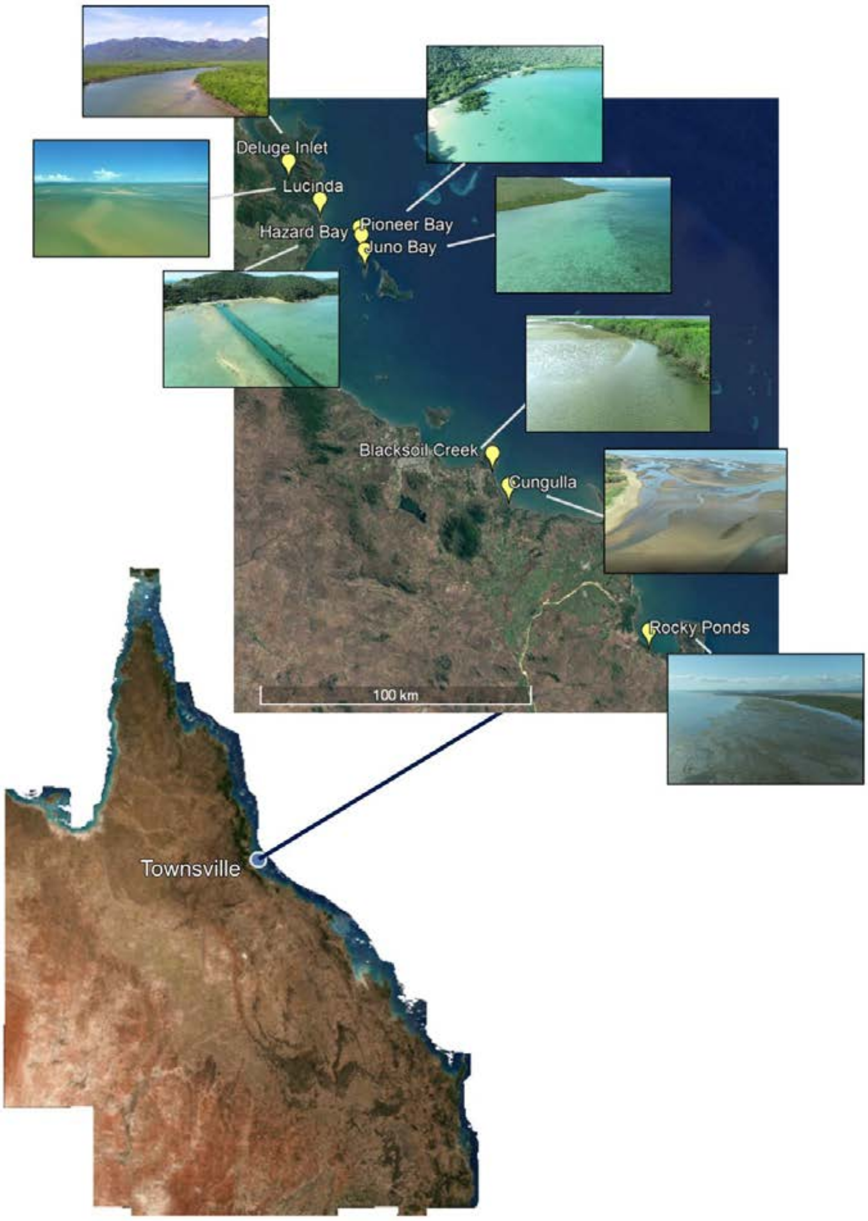


Figure 2.1. Locations of eight intertidal flats where ray communities were surveyed north and south of Townsville, North Queensland.

Table 2.1. Characteristics of the eight sites surveyed using aerial drone transects from 2020-2022.

Region	**Site name**	**Site type**	**Substrate characteristics**	**Mangrove characteristics**	**Size of survey area (km^2)**	**Mean sea level (m)**	**Spring mean tidal range (m)**	**Neap mean tidal range (m)**
Cape Cleveland	Blacksoil Creek	estuary inlet	sand flat, steep mud banks	on steep mud banks and along landward edges of sand flats	0.42	1.75	0.65-2.84	1.44-2.05
	Cungulla	beach flat	mud flat	along flat edges	1.43			
Hinchinbrook	Deluge Inlet	estuary inlet	sand flat, steep mud banks	on steep mud banks and along landward edges of sand flats	0.98	1.94	0.85-3.04	1.65-2.23
	Lucinda	beach flat	sand flat	corner of sand flat	1.14			
Palm Islands	Pioneer Bay, Orpheus Island	reef flat	sand flat, coral rubble, dead micro atolls	on sand flat and edges	0.22	1.94	0.85-3.04	1.65-2.23
	Hazard Bay, Orpheus Island	reef flat	sand flat, coral rubble, dead micro atolls	on sand flat and edges	0.27			
	Juno Bay, Fantome Island	reef flat	sand flat, coral rubble, dead micro atolls	on sand flat and edges	0.38			
Burdekin	Rocky Ponds	beach flat	sand flat, seagrass meadow	along flat edges	2.00	1.74	0.73-2.76	1.35-2.13

2.2.2 Transect design

Drone video transects collected from 2020-2022 were completed using the DJI Phantom 4 Standard unit, with all pre-programmed settings maintained at default parameters. Depending on conditions the camera gimbal was angled at 45-90° downward while recording video to reduce glare from the water surface, and flight speeds were maintained at <3 m/s to ensure objects remained in the video frame for a sufficient time (McIvor et al. 2022).

Flights were completed during daytime hours, most often in the early morning between 6-11 AM when visibility was optimal (e.g. low wind, reduced glare). Due to opportunistic data collection and environmental factors (e.g. turbidity), sampling effort (e.g. number of site visits, total number of transects, tidal phases) varied between sites. Video lengths were subject to battery life of the drone and did not exceed twenty minutes per flight. Transects followed linear trajectories, with data extracted from the length and width of the video frame.

All drone surveys were completed within intertidal zones, apart from subtidal edges during low tides. Areas were avoided where depths exceeded 1 m or where turbidity obscured visibility to the substrate level. Where possible, sites were sampled during multiple tidal phases. Due to changes in depth over the tidal cycle, flight paths were designed to cover subtidal habitats during low tides and newly submerged intertidal areas as the tide progressed. For this reason, manual operations were more suitable than automated, repeated flights since the intertidal study areas would regularly dry out or become too deep for reliable identification. For most transects, the drone followed a haphazard pathway to fly over habitats that met the suitability criteria, with the exception of the Palm Island sites, where exact transect paths were replicated with each visit (Figure 2.2). Flights were generally continuous except for times when the pilot hovered briefly over a ray to confirm the species identity.

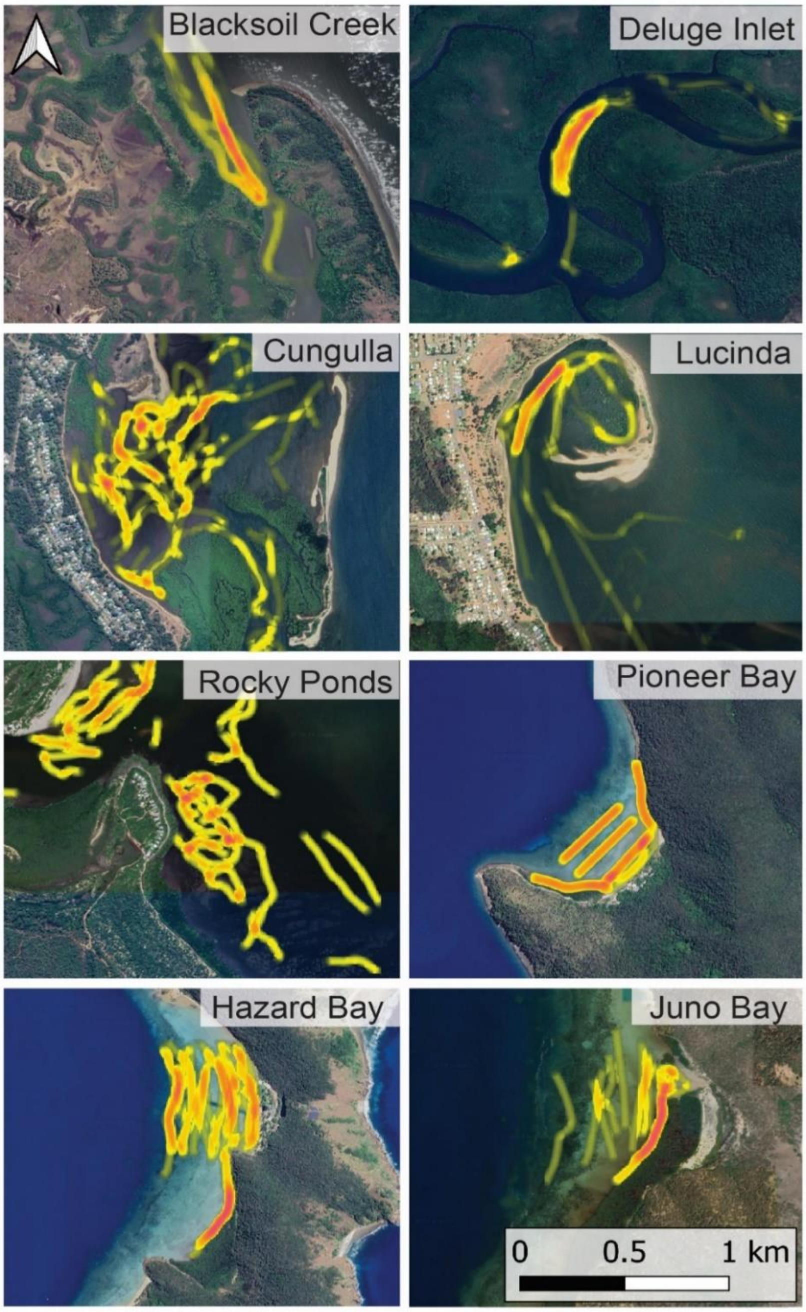


Figure 2.2 . Flight paths of all linear transects completed across intertidal flats in North Queensland. Darker line colours indicate areas that were covered more frequently, while fully transparent areas indicate areas that were not included in any flight path.

Drone heights across transects varied, since videos were collected for multiple purposes (e.g. site exploration, behavioural observation, evidence of life) and that visibility from a given height depended on daily fluctuations in cloud cover, wind, and glare. Drone heights used for analysis ranged from 5-30 m, which encompassed the minimum height at which rays were detectable without being disturbed (Bourke et al. 2023) and the maximum height where species level identification was achievable. Most flights were between 10-20 m.

Transect areas (in km^2) were calculated by multiplying transect distance by width of the field of view width (FOV), which was determined using the relationship between drone height and ground sampling distance (GSD). To account for any changes in height that may have occurred throughout a flight, median drone heights were used to calculate the FOV. For Blacksoil Creek and Deluge Inlet, transects primarily followed dry sand and mud bank edges due to limited visibility along steeper edges. As basing estimates on the entire FOV (which generally included areas that were too deep or dry on either side of the edges) would overestimate the transect area, areas were not calculated for transects at these locations.

2.2.3 Video processing

All transect videos were screened for quality in VLC media player. Video segments were excluded where 1) the coverage area was dry or water too shallow for rays to be present; 2) the drone repositioned or moved to another location between recordings; or 3) turbidity, glare, or wave action resulted in poor visibility and rays could not be properly identified. Furthermore, to minimise the likelihood of duplicate ray observations, videos were excluded within an hour of a previous flight if there was overlap in the transect path.

All rays identified from the transects were counted and identified to the species level. Where species level identification could not be certain, these observations were categorised as “unknown”. Two sympatric whiprays (Australian whipray, *Himantura australis,* and brown whipray, *Maculabatis toshi*) co-occur within sand flat habitats on the east coast of Australia (Last et al. 2016). The latter are common at Blacksoil Creek and to a lesser degree at Lucinda (see catch data in Chapters 4-5). Morphological similarities made it difficult to distinguish small *H. australis* and *M. toshi* from overhead. Therefore, both whipray species were grouped at Blacksoil Creek and Lucinda to avoid underreporting species richness or assuming the abundances of each species.

Behaviours were classified as either foraging, swimming, or resting while in the video field of view. Briefly, foraging was indicated by a ray displacing sediment with their pectoral fins, rostrum or spiracles, or appeared to be feeding along the surface. For all foraging behaviours, these were assigned to the most appropriate substrate type (e.g. unvegetated sand, seagrass, mud bank). Swimming was when a ray was moving in a fixed direction, while resting was when a ray was stationary or buried in the sediment. If swimming was immediately followed by a feeding event, this was classified as foraging. Behaviours were not recorded if an individual was not present in the video frame for >5 seconds, noticeably changed its behaviour when the drone approached (e.g. swimming away rapidly), or where visibility was obscured.

2.3 Statistical analysis

Ray communities were compared using multiple metrics. Species-site associations were visualised using non-metric multidimensional scaling (nMDS) analysis from the *vegan* package in R (v. 4.1.1) (Oksanen et al. 2016). Binary-presence absences of species across transects were used to construct the Jaccard’s dissimilarity matrix for the ordination. Rare species that contributed <5% to the species composition across all sites were excluded to reduce the disproportionate influence of rare species on the ordination. Environmental fitting (‘envfit’ function) was used to overlay species as vectors onto the nMDS ordination, where direction indicates the gradient of increasing occurrence for each species and vector length represents the strength of correlation with the ordination axes (Sheaves et al. 2007).

Species richness was calculated as the total number of species per site. Community evenness was then expressed using the Shannon Equitability Index (E), which incorporates species richness and the proportional abundance of each species (Magurran 2003). Ranging from 0 to 1, lower values indicate that abundances are skewed towards one or more dominant species, while a value of 1 signifies all species occurred in equal abundance. Overall species composition was summarised for each site by dividing the total counts of each species by the total number ray observations.

Relative abundances were then compared for all beach flat sites (Cungulla, Lucinda, Rocky Ponds), and for Pioneer Bay. Estuary inlet sites were excluded since abundances could not be reliably standardised to the transect areas, while Hazard Bay and Juno Bay were excluded due to low transect representation (n = 5 for each). This approach effectively normalised the differences in sampling effort while preserving the proportional structure of the ray abundances per transect. For all transects, species densities were calculated by standardising counts to transect areas (in km^2), which were then divided by the overall ray density to obtain the percentage contributions of each species at a site. To avoid biased percentages due to low sample sizes (e.g. a transect with one ray would give 100% for one species), percentages were only calculated for transects with five or more rays. To compare relative species abundances, the mean percentage contributions and 95% confidence intervals (CIs) of each species were estimated using 10,000 bootstrapping replicates with replacement. Differences in relative abundances were then inferred where no overlap occurred in the CIs.

2.4 Results

2.4.1 Community structure and species composition

In total, data were extracted from 155 video transects (Appendix A, Table A1). Most transects had drone heights of 10-20 m (n = 105), followed by 5-10 m (n = 36), and >20 m (n = 14). Sampling effort was greatest for Blacksoil Creek (42 transects). For all other sites, sampling effort ranged from 5-27 transects. By transect area, Pioneer Bay had the greatest aerial coverage (870.7 km^2), followed by Lucinda (723.7 km^2), Cungulla (417.8 km^2), Hazard Bay (321.8 km^2), Rocky Ponds (310.6 km^2), and Juno Bay (221.9 km^2).

Nine ray species were identified across three families: Dasyatidae, Aetobatidae, and Glaucostegidae (Figure 2.3). The most frequently encountered species were Australian whipray/brown whipray, *H. australis*/*M. toshi* (n = 1,321), broad cowtail stingray, *Pastinachus ater* (n = 548), mangrove whipray, *Urogymnus granulatus* (n = 383), giant shovelnose ray, *Glaucostegus typus* (n = 286), and pink whipray, *Pateobatis fai* (n = 82). Other less commonly encountered species (<5% of total species composition across all sites) included the blue spotted lagoon ray, *Taeniura lymma* (n = 18), whitespotted eagle ray, *Aetobatus ocellatus* (n = 13), and porcupine ray, *Urogymnus asperrimus* (n = 3). For a visual summary of all ray detections at each site, see Appendix A, Figure A1.

The nMDS ordination revealed distinct clustering of sites based on their associations with different ray species (Figure 2.4). Clustering of Blacksoil Creek and Deluge Inlet was due to associations with *H. australis*, *M. toshi*, and *U. granulatus*, while Cungulla and Lucinda both showed greater associations with *G. typus*. Rocky Ponds, along with all reef flat sites, were more positively associated with *P. ater*, *P. fai*, and *U. granulatus*.

2.4.1.1 Estuary inlets

Five species were detected at Blacksoil Creek. Assemblages of *H. australis* and *M. toshi* highly dominated species composition (90.3% of total ray observations), with rarer occurrences of *G. typus*, *P. ater*, and *U. granulatus*. This site exhibited the lowest community evenness score (E = 0.2) (Table 2.2). Deluge Inlet contained the same number of species as Blacksoil Creek (S = 5) but with a more balanced community structure (E = 0.75). Main species included *H. australis* (43.1% of total ray observations), *P. ater* (25.2%), and *U. granulatus* (23.6%), with more rare occurrences of *A. ocellatus* and *G. typus*.

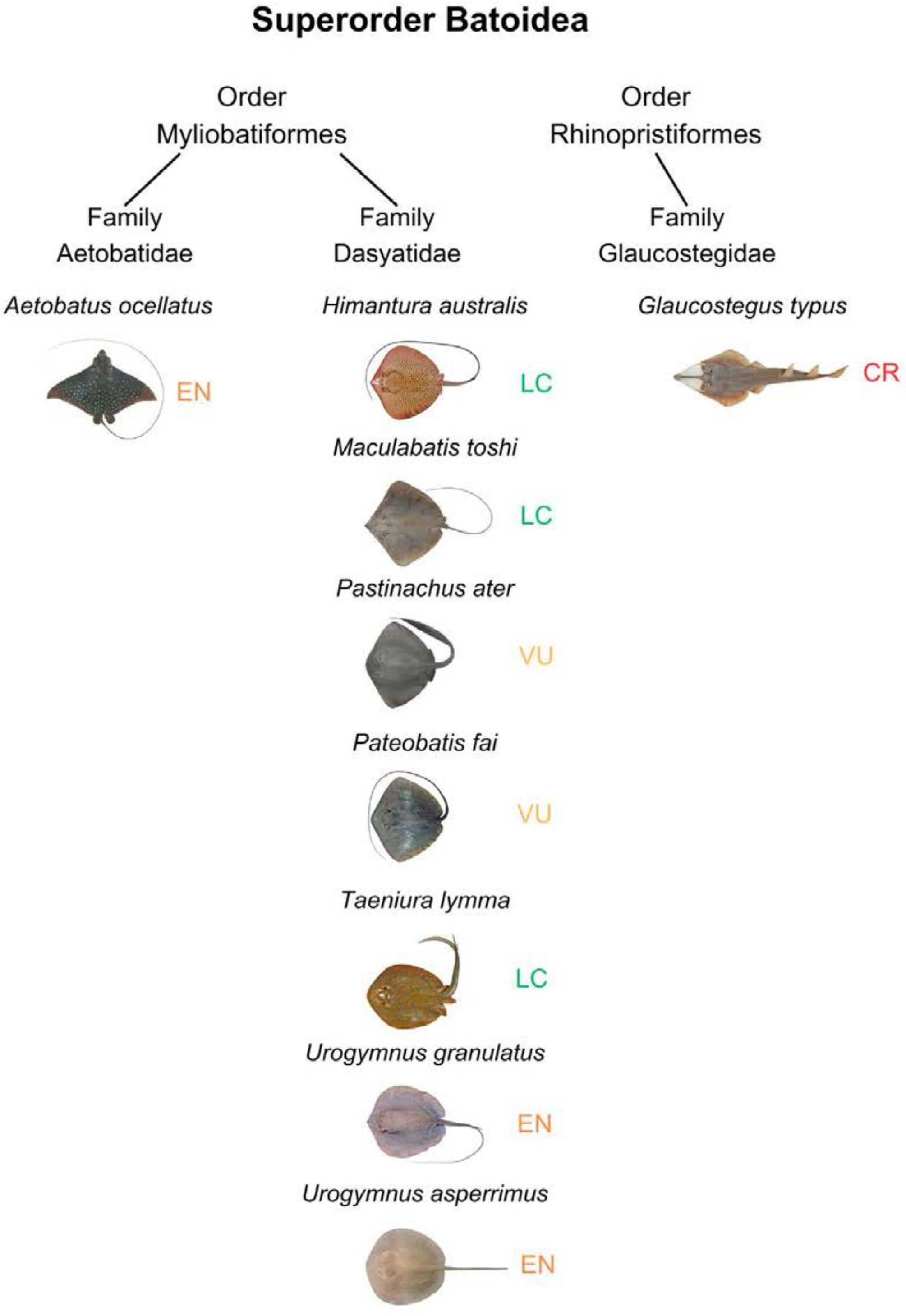
2.4.1.2 Beach flats

Five species were present at Cungulla, with a community evenness score of 0.57 (Table 2.2). Species composition was mainly comprised of *H. australis* (53.1% of total ray observations), *P. ater* (28.5%) and *G. typus* (11.2%), in which *H. australis* comprised 55.1% (42.9-66.6% CI) of the total ray density (Figure 2.5a). Other species present included *A. ocellatus*, *U. granulatus*, and *U. asperrimus*. Lucinda exhibited a more balanced community structure (S = 7; E = 0.68), with species composition more evenly distributed among *H. australis*/*M. toshi* (36.3% of total ray observations), *P. ater* (33.8%) and *G. typus* (26.5%). These species were similarly abundant, contributing 37.0% (9.6-46.6% CI), 37.4% (7.1-48.6% CI), and 23.5% (15.3-33.7% CI) of the total ray density, respectively (Figure 2.5b), and were more abundant than *A. ocellatus*, *P. fai*, and *U. granulatus*. The patchy seagrass meadows at Rocky Ponds supported the greatest species richness (S = 8) and community evenness (E = 0.77). The most common species were *P. ater* (30.8% of total ray observations), *G. typus* (26.6%), and *U. granulatus* (21.3%). Abundances of these species, and those of *H. australis*, did not differ greatly within the survey area (ranging from 8.8-

29.2% of the total ray density (Figure 2.5c), while abundances were less for *P. fai T. lymma*, and *U. asperrimus*.

2.4.1.3 **Offshore reef flats**

Species composition was similar across the three reef flats sampled in the Palm Islands group. Seven species were present overall including *P. fai*, *P. ater*, *U. granulatus*, *A. ocellatus*, *T. lymma*, *G. typus*, and *H. australis*, with species richness of 4-5 species per site (Table 2.2). Pioneer Bay, Hazard Bay, and Juno Bay exhibited similar community evenness scores, ranging from 0.64-0.77. At all sites, *U. granulatus* dominated the species composition (45.7-53.0% of total ray observations), followed by *P. ater* (22.4-31.2%) and *P. fai* (8.2-21.6%). *Glaucostegus typus* was absent from Pioneer Bay and there was only a single occurrence at Hazard Bay. However, this species was encountered more frequently at Juno Bay (8.6%). In terms of transect abundances in Pioneer Bay, *U. granulatus* and *P. ater* were similarly abundant, comprising 43.5% (30.1-57.1% CI) and 36.5% (26.7-45.7% CI) of the total ray density, respectively. These species were more abundant than *P. fai* with 14.6% (10.3-19.8% CI) (Figure 2.5d).



Graphics sourced from Australian National Fish Collection, CSIRO.

Figure 2.3. A hierarchical list of ray species identified within intertidal flats in North Queensland. Graphics were sourced from the Australian National Fish Collection, CSIRO.

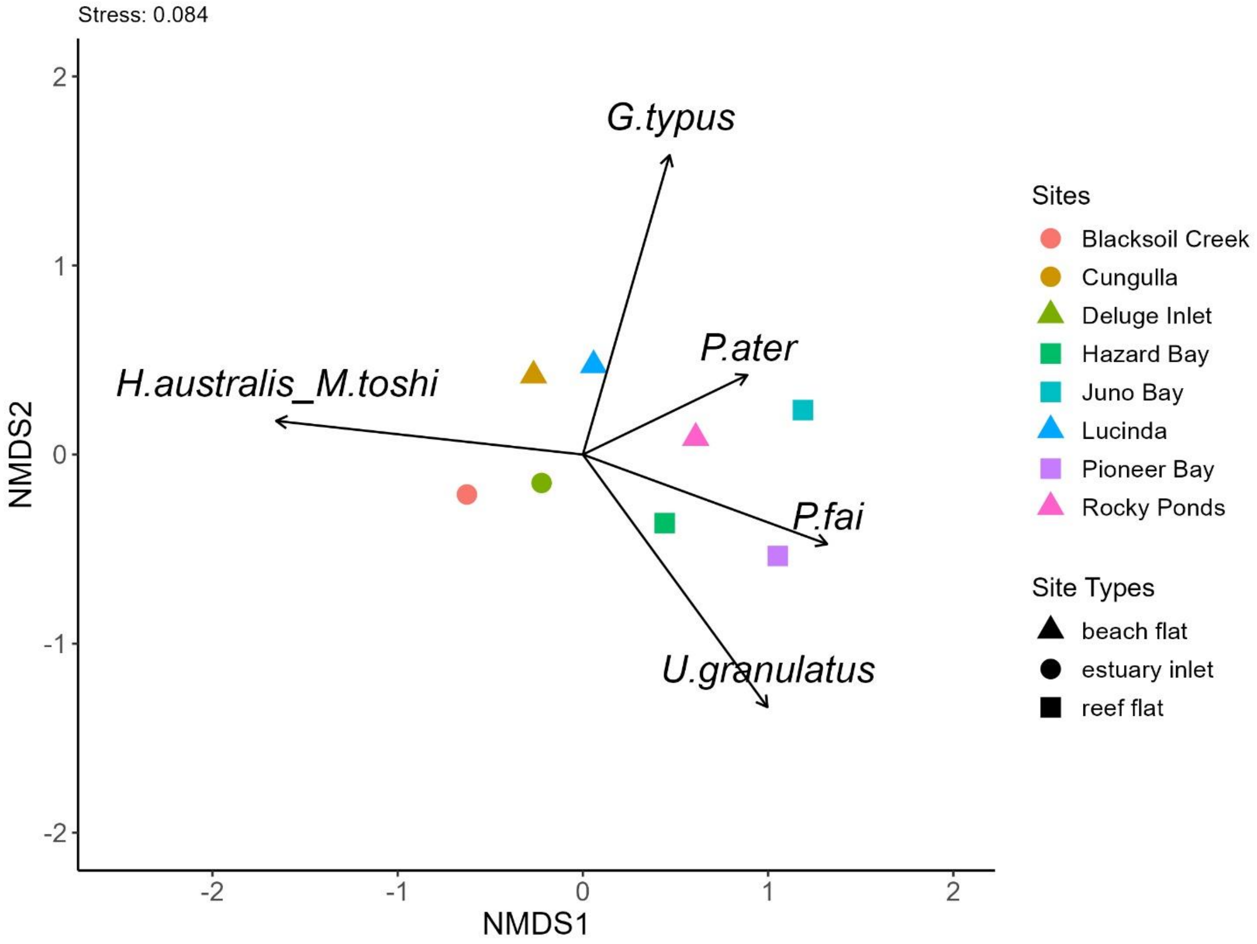


Figure 2.4. nMDS ordination plot showing site clusters based on species occurrence. Points represent the centroid of each site, and overlaid vectors represent the correlations with ray species within the ordination space.

Table 2.2. Species composition summary (% of total ray observations) per site. Species richness is denoted by S and community evenness (ranging from 0-1) by E. Main species were those that comprised >5% of the total species composition (percentage in parentheses). All other species present at the site are listed as Other.

Region	Site	Number of observations	S	E	Main species	Other
Cape Cleveland	Blacksoil Creek	1022	5	0.20	*H. australis/M. toshi (90.3)*	*G. typus (0.5), P. ater (2.2), U. granulatus (2.0), Unknown ray (5.0)*
	Cungulla	277	6	0.57	*H. australis (53.1), P. ater (28.5), G. typus (11.2)*	*A. ocellatus (0.4), U. asperrimus (0.4), U. granulatus (1.1), Unknown ray (5.4)*
Hinchinbrook	Deluge Inlet	123	5	0.75	*H. australis (43.1), P. ater (25.2), U. granulatus (23.6)*	*A. ocellatus (2.4), G. typus (1.6), Unknown ray (4.1)*
	Lucinda	479	7	0.68	*H. australis/M. toshi (36.3), P. ater (33.8), G. typus (26.5)*	*A. ocellatus (0.4), P. fai (0.4), U. granulatus (2.1), Unknown ray (0.4)*
Palm Islands	Pioneer Bay	315	5	0.65	*U. granulatus (53.0), P. ater (28.8), P. fai (13.3)*	*A. ocellatus (0.6), T. lymma (1.0), Unknown ray (3.2)*
	Hazard Bay	122	5	0.64	*U. granulatus (54.1), P. ater (31.2), P. fai (8.2)*	*H. australis (2.5), G. typus (0.8), Unknown ray (3.3)*
	Juno Bay	116	4	0.77	*U. granulatus (45.7), P. ater (22.4), P. fai (21.6), G. typus (8.6)*	*Unknown ray (1.7)*
Burdekin	Rocky Ponds	169	8	0.77	*P. ater (30.8), G. typus (26.6), U. granulatus (21.3), H. australis (9.5)*	*A. ocellatus (0.6), P. fai (4.7), T. lymma (3.6), U. asperrimus (0.6), Unknown ray (2.4)*

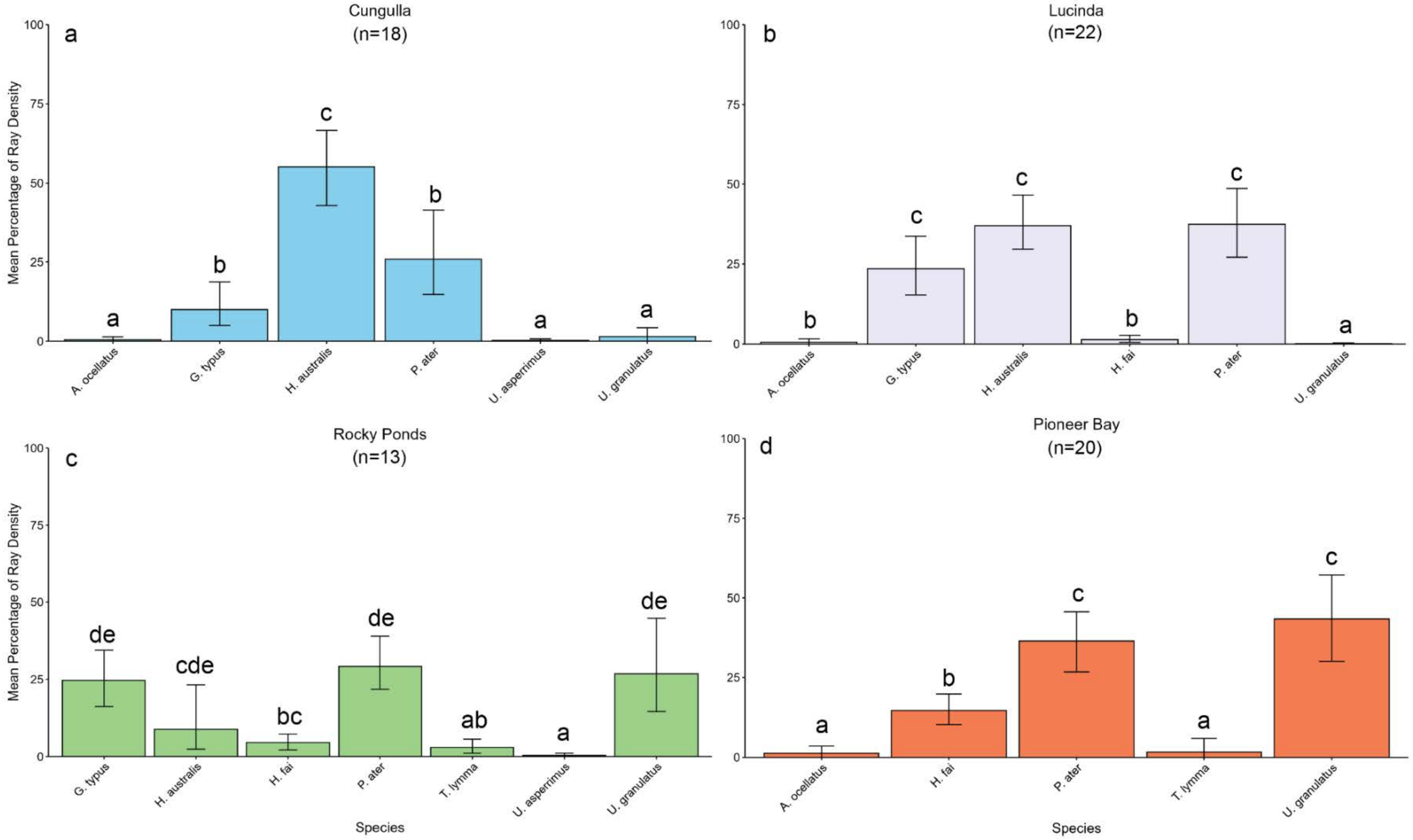
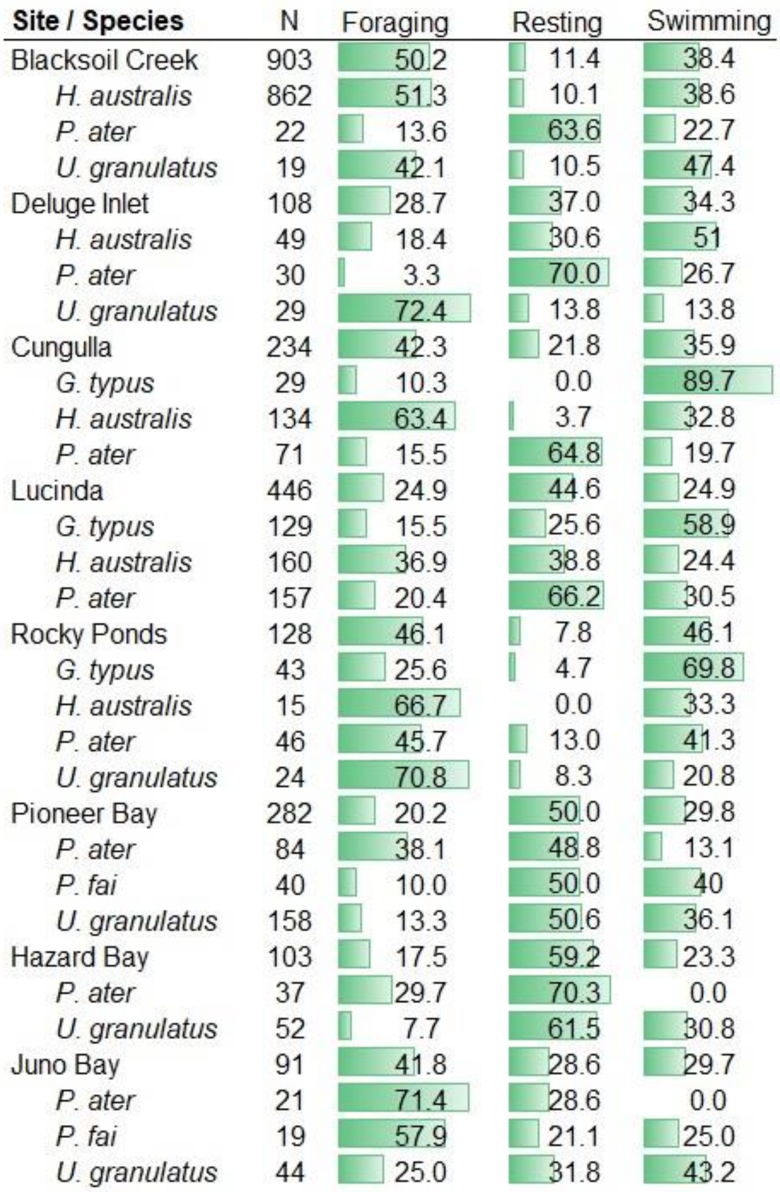


Figure 2.5. The mean contributions of each species (out of 100%) to the total ray density for beach flat and reef flat sites, shown with 95% confidence intervals. The number of transects included for each site are included in parentheses. Different letters indicate no overlap in the CIs, with "a" denoting the species with the lowest relative abundances.

2.4.2 Behaviour

Across sites, species with >10 classified behaviours included *H. australis*, *P. ater*, *G. typus*, *P. fai,* and *U. granulatus*. The total number of behaviours classified as either foraging, resting, or swimming ranged from 91-903 per site. Results were interpreted here for foraging.

Foraging was the most common behaviour of rays at Blacksoil Creek (50.2% of total observations), which was driven by high foraging activity of *H. australis/M. toshi* (Figure 2.6). At Deluge Inlet, foraging was most frequently observed by *U. granulatus* (72.4% of total observations) and less for *H. australis* (18.4%), and *P. ater* (3.3%). At Cungulla, most foraging events were documented by *H. australis* (63.4% of total observations) but was also observed for *P. ater* (15.5%) and *G. typus* (10.3%). At Lucinda, foraging was observed for *H. australis* (36.9% of total observations), followed by *P. ater* (20.4%) and *G. typus* (15.5%). At Rocky Ponds, foraging was the most common behaviour for *U. granulatus* (70.8%) and *H. australis* (66.7%). Across the three reef flats, foraging for *P. ater* ranged widely from 29.7-71.4% of total behaviours per site. Foraging for *U. granulatus* less frequent, ranging from 7.7-25.0% of the total observations, while foraging of *P. fai* ranged from 10.0-57.9% per site.



Site / Species	N	Foraging	Resting	Swimming
Blacksoil Creek	903	50.2	11.4	38.4
H. australis	862	51.3	10.1	38.6
P. ater	22	13.6	63.6	22.7
U. granulatus	19	42.1	10.5	47.4
Deluge Inlet	108	28.7	37.0	34.3
H. australis	49	18.4	30.6	51
P. ater	30	3.3	70.0	26.7
U. granulatus	29	72.4	13.8	13.8
Cungulla	234	42.3	21.8	35.9
G. typus	29	10.3	0.0	89.7
H. australis	134	63.4	3.7	32.8
P. ater	71	15.5	64.8	19.7
Lucinda	446	24.9	44.6	24.9
G. typus	129	15.5	25.6	58.9
H. australis	160	36.9	38.8	24.4
P. ater	157	20.4	66.2	30.5
Rocky Ponds	128	46.1	7.8	46.1
G. typus	43	25.6	4.7	69.8
H. australis	15	66.7	0.0	33.3
P. ater	46	45.7	13.0	41.3
U. granulatus	24	70.8	8.3	20.8
Pioneer Bay	282	20.2	50.0	29.8
P. ater	84	38.1	48.8	13.1
P. fai	40	10.0	50.0	40
U. granulatus	158	13.3	50.6	36.1
Hazard Bay	103	17.5	59.2	23.3
P. ater	37	29.7	70.3	0.0
U. granulatus	52	7.7	61.5	30.8
Juno Bay	91	41.8	28.6	29.7
P. ater	21	71.4	28.6	0.0
P. fai	19	57.9	21.1	25.0
U. granulatus	44	25.0	31.8	43.2

Figure 2.6. Number of behavioural observations (N) and the percentage of behaviours that were identified as foraging, swimming, or resting for species with >10 observations (excludes unidentified behaviours).

2.5 Discussion

2.5.1 Species composition

Drone surveys documented nine ray species from three families (Dasyatidae, Aetobatidae, and Glaucostegidae) within tropical intertidal flats of northeast Queensland (Table 2.3). This represents approximately half of the 23 ray species and nine families that have been reported in Queensland's intertidal waters (Last et al. 2016, Leurs et al. 2023). Ray communities showed some similarities due to the presence of common species including giant shovelnose ray, *G. typus*, Australian whipray, *H. australis*, cowtail stingray, *P. ater*, pink whipray, *P. fai*, and mangrove whipray, *U. granulatus*. However, differences in species richness and relative abundances among sites provided insights on species-habitat preferences. Occurrences of rare species including *A. ocellatus*, *T. lymma*, and *U. asperrimus* were noted, although low frequencies precluded any further discussions on their habitat use patterns or interactions with other species.

Body sizes were not estimated directly from the drone surveys. However, exclusive catches of juvenile rays at Blacksoil Creek and Lucinda (Chapters 4-5), combined with prior knowledge of Pioneer Bay as an elasmobranch nursery, was consistent with the concept of communal nurseries where multiple species co-occur in the absence of adults (Simpfendorfer & Milward 1993, Heupel et al. 2019).

Table 2.3. Ray species associated with intertidal zones in northeast Queensland, Australia (as described by Leurs et. al. 2023). Rays with exclusively southern distributions that do not overlap with the broader Townsville region are not listed.

Family	**Scientific name**	**Common name**	**Distribution across Queensland east coast**	**Detected in current study**
Aetobatidae	*Aetobatus ocellatus (narinari)*	Spotted eagle ray	statewide	Y
Dasyatidae	*Hemitrygon fluviorum*	Estuary stingray	statewide	N
	Himantura australis (uarnak)	Australian whipray	statewide	Y
	Maculabatis astra	Blackspotted whipray	statewide	N
	Maculabatis toshi	Brown whipray	statewide	Y
	Neotrygon kuhlii (australiae)	Kuhl's maskray	statewide	N
	Pastinachus ater (sephen)	Broad cowtail stingray	statewide	Y
	Pateobatis fai	Pink whipray	statewide	Y
	Taeniura lymma	Bluespotted fantail ray	statewide	Y
	Urogymnus asperrimus	Porcupine whipray	statewide	Y
	Urogymnus granulatus	Mangrove whipray	statewide	Y
Glaucostegidae	*Glaucostegus typus*	Giant shovelnose ray	statewide	Y
Gymnuridae	*Gymnura australis*	Australian butterfly ray	statewide	N
Myliobatidae	*Aetomylaeus vespertilio*	Ornate eagle ray	statewide	N
Pristidae	*Anoxypristis cuspidata*	Narrow sawfish	N QLD -southern extent Rockhampton	N
	Pristis clavata	Dwarf sawfish	statewide	N
	Pristis pristis	Largetooth sawfish	N QLD - southern extent Cairns	N
	Pristis zijsron	Green sawfish	statewide	N
Rhinidae	*Rhynchobatus australiae*	Bottlenose wedgefish	statewide	N
Trygonorrhinidae	*Aptychotrema rostrata*	Eastern shovelnose ray	S QLD - northern extent Townsville	N
Rhinopteridae	*Rhinoptera neglecta*	Australian cownose ray	statewide	N

Estuaries are recognised as critical nursery habitats for elasmobranchs (Simpfendorfer et al. 2005, Knip et al. 2010, Heupel et al. 2019). However, with only a handful of studies investigating habitat use and community structures of rays in estuary environments (Collins et al. 2007b, Cadwallader 2020, Elston & Murray 2024), their significance to ray species remains poorly understood (Constance et al. 2024, Elston & Murray 2024). Addressing these gaps is particularly important in tropical regions, where species distributions in estuarine channels may be limited by salinity tolerance and seasonal changes in freshwater inputs (Davis et al. 2012, Grant et al. 2019).

The inclusion of two estuary inlets (Blacksoil Creek and Deluge Inlet) provided baseline insights on ray community structures within a poorly studied habitat context in northeast Australia. Homogenous sand flats in Blacksoil Creek were dominated by two sympatric whiprays: *H. australis* and *M. toshi*, indicating associations between juveniles and estuarine channels before transitioning to deeper water habitats as adults (Cerutti-Pereyra et al. 2013, Last et al. 2016). Greater abundances of *P. ater*, and *U. granulatus* at Deluge Inlet also align with previous reports of these species entering estuaries (Last et al. 2016). A recent review highlighted substantial knowledge gaps surrounding age-growth relationships, reproduction, habitat use, and population structures of *H. australis* and *P. ater,* among other estuarine species (Constance et al. 2024). Although information was not included for *M. toshi* and *U. granulatus*, similar knowledge gaps undoubtedly exist, given the lack of formal study on these species from estuaries. Overall, while we can ascertain that multiple species are associated with estuaries, significant research is still needed to understand community structures, habitat use patterns, and the broader role of these environments for supporting different life history stages (Grant et al. 2019, Constance et al. 2024).

The interconnected seagrass and unvegetated habitat patches at Rocky Ponds supported high species richness (eight species) and diverse community structures. Studies from other regions have similarly reported high diversity of sharks and rays in seagrass systems, supporting their roles as productive feeding grounds and nurseries (Peterson & Grubbs 2020, Young & Carlson 2024). In Australia, the most comprehensive assessments of ray communities in seagrass systems come from Shark Bay, Western Australia (Vaudo & Heithaus 2009, Heithaus et al. 2013, Vaudo & Heithaus 2013). Using a combination of visual surveys and capture data, Vaudo and Heithaus (2009) found that rays comprised 92% of all elasmobranch encounters in nearshore sand flats. When combined with broader sampling efforts across the bay, a total of 28 shark and ray species were identified (White & Potter 2004). Several species common to Shark Bay were also abundant at Rocky Ponds, including *P. ater*, *H. australis*, *P. fai*, and *G. typus*. However, *U. granulatus* was absent from Shark Bay, as this location exceeds its southern distribution range.

Rays, in general, are strongly associated with unvegetated soft-bottom substrates, which they use for feeding and to bury themselves during periods of inactivity (Flowers et al. 2021). Species richness was the same between the unvegetated sand and mud flats at Lucinda and Cungulla (seven species). Previous capture studies from similar tidal flat environments in Cape Cleveland Bay reported six ray species were present (Tobin et al. 2014, Adkins et al. 2016). Similarly, nine ray species were recorded in the intertidal mud flats of Moreton Bay (Pillans et al. 2007, Pierce et al. 2011). Similarities in community structures between vegetated and unvegetated habitats could be linked to the ubiquitous presence of mangrove edges, since the most common species associate with mangroves, either directly or by using adjacent flat areas (Kanno et al. 2023). Connectivity between vegetated and unvegetated habitat patches may also facilitate movement between microhabitat patches and yield a greater overlap in species assemblages (Boström et al. 2017, Skilleter et al. 2017), making it meaningful to consider how various aspects of habitat heterogeneity, rather than vegetation coverage alone, shape community structures.

All offshore reef flats in the Palm Islands group contained similar ray communities, reflecting their geographic proximity to one another and their shared habitat characteristics. Species composition was dominated by *P. ater*, *U. granulatus* and *P. fai*, which are common across tropical and subtropical reef environments throughout their ranges (Chin et al. 2010, Last et al. 2016, Yon et al. 2020, Elston et al. 2021). At Pioneer Bay, the consistent presence of juvenile *U. granulatus* and *P. ater* is likely driven by high fidelity to the reef flat over consecutive tidal cycles (Davy et al. 2015, Martins et al. 2020b, Martins et al. 2020a), which is likely mirrored at Hazard Bay and Juno Bay. Moreover, lesser occurrences of *P. fai* may reflect their preferences for deeper subtidal areas, rather than being restricted to the shallow intertidal edges (Vaudo & Heithaus 2009). Reef flats were also characterised by lower abundances of *H. australis* and *G. typus*, which were more common in tidal beach flats and estuaries. Although high densities of juvenile *G. typus* have been reported in offshore reef flats at Heron Island by Gaskins et al. (2020), this study did not survey the reef flat itself. Despite both species occurring on reef flats, they primarily associate with unvegetated soft bottom habitats rather than interacting directly with the coral reef structure (O'Shea et al. 2012, Cerutti-Pereyra et al. 2013, Freeman 2019, Gaskins et al. 2020), which could explain their lower abundances.

2.5.2 Behaviour

Observations of feeding, swimming, and resting in intertidal habitats demonstrated how these areas support a variety of functions for rays. The prevalence of foraging on intertidal flats suggests that habitat use may be influenced, at least in part, by prey availability over varying habitat scales (Ajemian et al. 2012, Pardo et al. 2015, O'Shea et al. 2018). Rays primarily fed on soft bottom sand and mud substrates in open flat areas but also on patchy seagrass and near mangrove edges, where present (J. Myers, pers. obs.). Some examples of species-specific patterns in habitat use were also observed. For example, *U. granulatus* frequently foraged along mangrove-lined mud banks in estuary inlets, while *H. australis* fed exclusively on unvegetated sand flats (J. Myers, pers. obs.). While this could suggest that both species exploit different habitat niches (White & Potter 2004, Simpson et al. 2021), further investigations would be needed to tease apart species-level feeding behaviours and their broader interactions within ray communities.

Rays commonly engage in cyclical movements across intertidal gradients during rising and ebbing tides to remain in shallow water or to avoid stranding (Cartamil et al. 2003, Brinton & Curran 2017, Martins et al. 2020b). With a high representation of rising tides in the transects (72 of 155 videos), swimming may have been indicative of these intertidal migrations. However, given the brief observation periods (<5 s), it was not possible to discern whether rays were moving with fixed trajectories or making smaller-scale movements between bouts of feeding or resting. Resting alone or in small groups is believed to conserve energy while rays are not actively foraging. Moreover, rays may also rest or bury themselves in sandy patches or along intertidal edges to avoid predator detection (Vaudo & Heithaus 2013, Meese & Lowe 2019, Crook 2020, Martins et al. 2020b, Martins et al. 2020a). Overall, given that interpretations on behaviour are based on brief snapshots of activity, prolonged observations would be needed to understand how environmental and biological factors shape habitat use at these scales.

2.5.3 Considerations of drone use

Drone use is inherently coupled with limitations based on visibility and detectability (Colefax et al. 2019, Raoult et al. 2020a, Butcher et al. 2021). In this study, data collection was constrained to daylight hours and to periods of low wind, minimal glare, and suitable water clarity. Coastal areas in North Queensland also experience high levels of turbidity, particularly during the wet season months, which often compromised visibility when conditions were not ideal. The ability to detect individual rays was also influenced by water depth. Reliable observations were generally limited to depths less than 1.5 m where visibility was attainable to the substrate level, although it was still possible to overlook buried rays. Additionally, overhead surveys were less effective when passing over structural habitats, where rays could be concealed within the mangrove roots. It was also possible for more cryptic species (e.g. *M. toshi*) to go undetected due to their small body sizes and plain colouration.

Another limiting factor was that daily tidal ranges and phases (spring/neap) influenced which areas could be sampled at a given time, which required manual path planning to collect usable data. In this study, ray communities were characterised using more robust indices of species richness and relative abundances, since the opportunistic, exploratory nature of the data precluded the ability to calculate absolute densities or directly compare these across repeated transects. However, some of these limitations could be reduced in future research where more standardised sampling designs are possible.

2.6 Conclusions

This chapter contributes baseline knowledge of species richness and community structures of rays in tropical intertidal flats of northeast Australia. While structured habitats like mangroves, seagrass beds, and coral reefs are globally recognised as essential habitats for elasmobranchs (White & Potter 2004, Vaudo & Heithaus 2009, Heupel et al. 2019, Peterson & Grubbs 2020, Young & Carlson 2024), more research is still needed to understand their importance to local species. Unvegetated habitats also support diverse ray assemblages within the broader habitat mosaic and deserve greater consideration in future research (Sheaves et al. 2024a).

Formal assessments of ray populations remain rare across tropical intertidal zones of the world. Continued research at multi-site scales will be valuable for evaluating species-habitat relationships and for identifying specific predictors of habitat quality. Prolonged monitoring could also reveal patterns in seasonal abundances, which have been documented in other contexts (Vaudo & Heithaus 2009, Pierce et al. 2011, Tobin et al. 2014). Furthermore, combining drone-based surveys with other sampling approaches (e.g. capture data) could eliminate specific methodological biases to provide more robust estimates of species densities and population sizes.

With intertidal environments currently facing unprecedented modifications from climate change and anthropogenic disturbance (Murray et al. 2019), this knowledge has significant implications for conservation and management of both species and habitats, particularly for those facing elevated extinction risk. For example, the pervasiveness of *G. typus* across intertidal beach flats indicates that both vegetated and unvegetated habitats are valuable for this critically endangered species. Similarly, while endangered *U. granulatus* are almost exclusively studied in coral reefs, the value of other habitat types for supporting their populations remains largely unknown. While sites chosen for this study represented relatively pristine environments with little disturbance from anthropogenic pressures, future inclusion of intertidal habitats with varying degrees of modification could provide comparative insights into the vulnerabilities of ray populations to future environmental changes.

3 Chapter 3 – Comparing foraging behaviours of sympatric stingrays in a reef flat nursery

3.1 Introduction

Rays in intertidal zones function as both mesopredators and ecosystem engineers, significantly shaping ecosystem dynamics primarily through their feeding behaviours (Flowers et al. 2021). Ray bioturbation contributes to several physical processes such as sediment turnover and reworking (Meysman et al. 2006, Grew et al. 2024), nutrient cycling (Valentine et al. 1994, O'Shea et al. 2012, Takeuchi & Tamaki 2014), and creating foraging opportunities for other benthic predators (Boaden & Kingsford 2012, Kiszka et al. 2015). Ray feeding pits can also drastically transform the geomorphology of soft-bottom substrates over time, particularly if feeding occurs consistently over concentrated spatial areas or habitats (Cross & Curran 2000, Giaroli et al. 2024, Nauta et al. 2024). Understanding the drivers of foraging habitat selection is, therefore, essential for assessing the ecological impacts of rays within these ecosystems.

Where multiple species coexist, the contributions of rays to ecosystem processes vary based on differences in foraging behaviours among sympatric species and life stages. Unique foraging preferences, even when acting over small scales, can have differential impacts on the surrounding environment. For example, if one species habitually feeds along the top layers of sediment, they likely turn over less sediments over time than another species that relies on excavation techniques to extract deeper buried prey. Such behaviours could be indicative of dietary resource partitioning among sympatric competitors, resulting in distinct trophic niches (Yick et al. 2011, Pardo et al. 2015, Mulas et al. 2019, Elston et al. 2020). Additional partitioning mechanisms include foraging at different times (Bass et al. 2021, Hayata et al. 2021, Lear et al. 2021) or differentially selecting areas by depth, substrate, or proximity to specific habitat features (e.g. mangrove edges) (White & Potter 2004, Ajemian & Powers 2016). Such patterns reflect how species exploit different resources to reduce interspecific competition and facilitate species coexistence within marine communities (Link & Auster 2013, Lear et al. 2021).

While knowledge of ray feeding ecology is generally derived from trophic studies (Elston et al. 2020, Martins et al. 2022, Queiroz et al. 2023), behavioural observations also provide valuable insights on fine-scale habitat use. For rays in nearshore environments, behaviours have been described using multiple approaches, such as stationary underwater cameras (Kanno et al. 2019), boat or snorkel surveys (Semeniuk & Dill 2005, 2006, Vaudo & Heithaus 2012), and aerial drones (Oleksyn et al. 2021). The latter method is most appropriate for collecting information over prolonged time frames, since individuals can be tracked with minimal disturbance (Bourke et al. 2023), while providing high spatial resolution. Multiple studies have used drones to assess patterns in abundance or fine-scale movements of rays in intertidal flats (Kiszka et al. 2016, Oleksyn et al. 2020, Ruiz-García et al. 2020, McIvor et al. 2022). However, very few studies have provided detailed descriptions of ray foraging or linked these behaviours to potential resource partitioning and broader ecosystem function (however, see (Frixione et al. 2020, Oleksyn et al. 2021, Crook et al. 2022). Overall, more comparative studies are needed to bridge the gaps between foraging behaviour, diet, and fine-scale habitat selection, and to understand these processes at the species level.

The intertidal reef flat at Pioneer Bay, Orpheus Island is a year-round nursery for shark and rays (Martins 2019). Three ray species are common on the reef flat, including the broad cowtail stingray, *Pastinachus ater*, mangrove whipray, *Urogymnus granulatus*, and pink whipray, *Pateobatis fai*. Previous studies at this location have demonstrated dietary niche separation between *U. granulatus* and *P. ater* (Martins et al. 2022), with evidence that these species also differ in their fine-scale habitat use (Kanno et al. 2019). However, the behavioural mechanisms underlying these differences remain unexplored. The aim of this chapter was to compare the foraging behaviours of the three ray species at Pioneer Bay to understand temporal foraging patterns across the tide and to assess if differences in foraging behaviours support potential resource partitioning and species-specific functional roles.

3.2 Methods

3.2.1 Study site

Pioneer Bay is a 400 m wide intertidal reef flat located on the western side of Orpheus Island in the northern Great Barrier Reef (Figure 3.1). The site experiences semi-diurnal tidal cycles. The tidal flat is mostly unvegetated, except for patches of mangroves that grow along the shoreline edges and some growths of macroalgae. Substrates included a mix of smooth sand and rubbly sand on the inner flat, which transitions to coral rubble on the outer flat and extending towards the reef crest (~350 m from the beach). For more detailed information about the features of Pioneer Bay, refer to previous studies (Kanno et al. 2019, Martins et al. 2020a, Martins et al. 2020b, Higgins et al. 2024).

3.2.2 Video collection

Drone behaviour tracks were collected in November 2021 and March 2023. The 2021 data were collected in November at the start of the tropical wet season, while data were collected in March 2023 during peak summer months (late wet season). Tidal ranges were similar between years (ranging from 0.9-2.6 m in 2021 and 1.2-3.3 m in 2023 during the daytime low-high cycle), indicating similar patterns of tidal submergence. For the 2021 dataset, videos were collected during rising tides that occurred in the morning hours, while in 2023, tracks were collected in the morning and afternoon hours to represent low, rising, and high tides.

Rays were tracked with a DJI Phantom 4 drone (operated by an on-ground pilot), following methods by Crook et al. (2022). Flights were conducted during suitable visibility conditions: during daylight hours, wind speeds <25 km/hr, no rainfall, and tidal height <3.0 m. To start each behaviour track, the drone was launched and flown haphazardly at a height of 15-20 m until a ray was located. Recording began once the drone was lowered to 3–5 m altitude and positioned directly above the ray. Even at such low altitudes, ray behaviour is generally unaffected by the presence of a drone (Bourke et al. 2023). The tracked ray was centred in the field of view for the duration of the track. Other rays that passed through the field of view were not tracked. Tracks were terminated once the drone battery dropped below 20% or the target ray was lost from view. The pilot then returned the drone to the launch point before starting a new track. Effort was taken to direct the search away from the final position of the previous tracked ray to avoid repeatedly tracking the same individual.

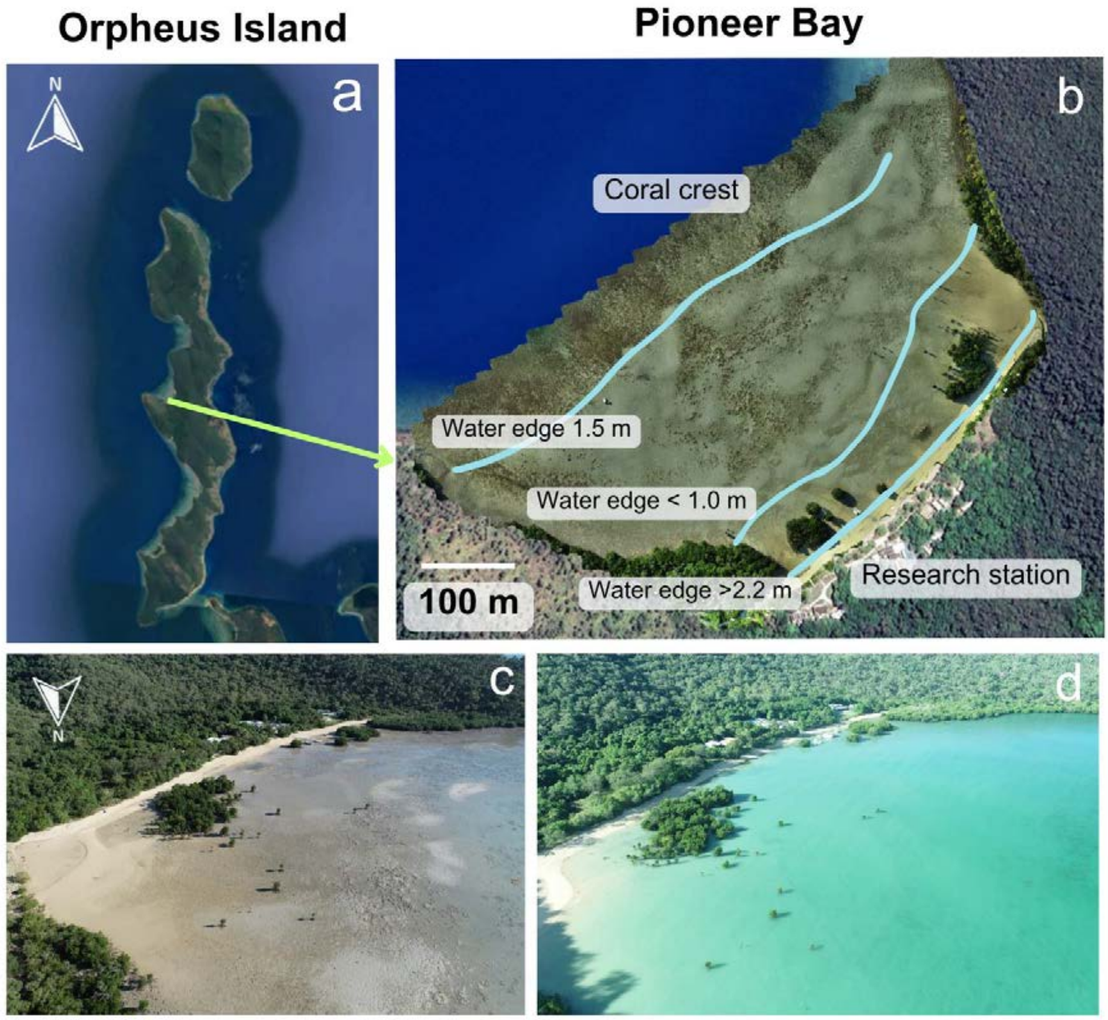


Figure 3.1. Map showing the location of Pioneer Bay on the western side of Orpheus Island, off the coast of Lucinda, QLD (a). A low tide orthomosaic of the intertidal zone was taken at 40 m altitude to show the distribution of substrates and mangrove vegetation within the bay (b). The blue lines indicate the approximate position of the waterline edges for various tidal heights. The images below show south facing overviews of the inner reef flat at tidal heights of 1.5 m and 2.5 m (c,d).

3.2.3 Video analysis

First, metadata details were recorded from each flight, including date, time of day, tidal height, and track length. Track length varied based on the drone's battery level when a ray was located and weather conditions (particularly wind) that affected battery life. Information was then extracted on all feeding events in each track. Foraging was generally initiated when a ray ceased forward swimming movement or moved backward to hover over a spot of interest before initiating one of four feeding types. Four foraging types were recognised, as defined by Crook et al. (2022). *Suction feeding* was when a ray remained stationary, flattening its disc against the substrate and ejecting sediment through the spiracles. *Water jetting* was when a ray remained stationary while emanating sediment plumes from all sides of the disc. *Excavation feeding* was when a ray fed intensely with the rostrum and pectoral fins to displace sediment from the anterior and lateral disc margins, whereas *surface feeding* was when a ray foraged along the top of the sediment and created minimal sediment disturbance. If more than one behaviour was observed, the most prominent type was recorded as the primary foraging type and the other as a secondary foraging type.

A feeding event was considered terminated once the ray moved away before foraging again or ceased foraging activities for >10 seconds. If a ray recommenced feeding less than 0.5 m from where the first feeding attempt occurred without switching foraging types or substrate, this was considered a continuation of the same feeding event. Total duration (in seconds) was calculated from the start and end time of each foraging event. If a foraging event had already commenced at the start of a track or if foraging continued after tracking concluded, duration was not recorded.

Substrates where feeding occurred were classified into three main categories (Figure 3.2). Feeding events were assigned to "smooth sand" where there was little or no coral rubble present in the video frame and “rubbly sand” if a ray foraged on sand that was heavily interspersed with coral rubble (~50% of video frame). “Coral rubble” was assigned when a ray fed directly on fragments of dead coral, either on solid coral substrate or rubbly sand. In the initial video analysis, a further classification of “mangrove” was used for all feeding events on soft or rubbly sand that occurred within 1 m of the mangrove roots. However, the “mangrove” classification was later excluded from analysis, since potential feeding events were either difficult or impossible to observe from overhead if the ray was obstructed by the mangrove roots or foliage. Where visibility could be maintained, there appeared to be little or no feeding activity.

To examine where feeding events were recorded in the reef flat, the GPS coordinates for each event were recorded using the position of the drone at the onset of foraging as a proxy. To assess how often feeding events left a visible presence on the substrate, feeding pit/scar formation was recorded for smooth sand and rubbly sand substrates. Although surface feeding did not result in true pit formation, shallow scars were occasionally left in the substrate, and these were included. If the substrate was obscured by displaced sediments or pit formation could not be confidently assumed by the intensity of the foraging event, pit formation was classified as “NA”.

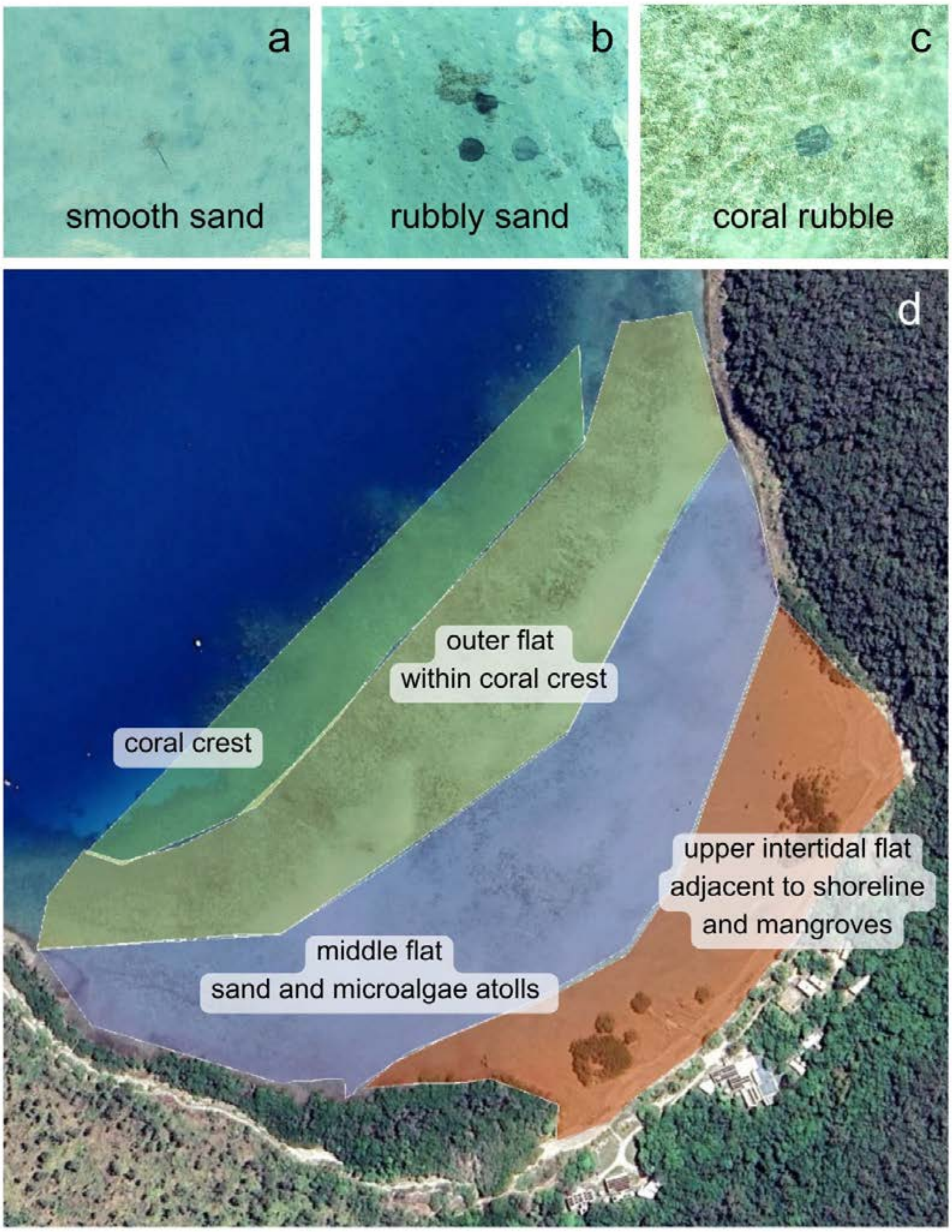


Figure 3.2. Foraging events were classified by substrate type. Smooth sand patches contained little or no coral rubble (a). Rubbly sand (b) was used to classify events that occurred on sand that was patchily interspersed with coral rubble fragments (~50% of video frame), but not directly on the coral. Coral rubble (c) was assigned when an event occurred directly on a fragment of coral, either on solid coral substrate or rubbly sand. Foraging areas were modified from Martins et al. (2020b) (d).

3.3 Statistical analysis

3.3.1 Foraging activity across the tide

Foraging activity was summarised using two metrics. The number of feeding events was summarised for each track, which were standardised to feeding events per hour. Additionally, the amount of time (in seconds) spent foraging per track was represented as a proportion of the total track length. All statistical analyses were run using R version 4.2.2 (R Core Team, 2022) with statistical significance assessed at $\alpha = 0.05$. Residual diagnostics for all models were evaluated using the *DHARMa* (Hartig 2016) and *performance* packages (Lüdecke et al. 2021). Due to variable tracking times, a linear regression was applied (Gaussian distribution) to identify the relationship between foraging rate and track length. For proportion of time foraging in track, a beta-regression model was run using the *glmmTMB* package (Brooks et al. 2017) due to the bounded nature of proportional data (values constrained between 0 and 1). Prior to analysis, a transformation of $(y * (n-1) + 0.5) / n$ was applied to values of exactly 0 or 1 (Smithson & Verkuilen 2006). For both response variables, additive models were compared against interaction models. In both cases, the additive models were selected as the most parsimonious, indicating no significant interactions between track length and species.

Foraging metrics were compared by species and tidal height categories (low, mid, and high). Year was also included to test for potential differences between the 2021 and 2023 tracks. Prior to analysis, statistical outliers for each species × tidal height combination were identified based on the interquartile ranges (values exceeding 1.5 × IQR above Q3 or below Q1). While these extreme values provide insights into individual behavioural variability, they were removed ($n = 3$ for foraging rate, $n = 2$ for proportion of time foraging in track) to more effectively generalise species-level patterns. Models were constructed for each response variable (foraging rate and proportion of time foraging) using the same family distributions as the previous models with track length, and results were interpreted based on additive models. The significance of each variable was evaluated using the 'Anova' function in the *car* package (Fox et al. 2012). The predicted marginal means were generated using the *emmeans* package, with a Bonferroni correction applied to all pairwise comparisons (Lenth 2022). For the proportion of time foraging, coefficients were back-transformed from the logit scale for interpretation. All means were reported with ± 1 SE.

3.3.2 Foraging preferences among species

Frequencies of foraging events for each substrate and foraging type were summarised across species. A chi-square test of variable independence was then used to examine if foraging type was dependent on substrate ($\alpha = 0.05$). Residuals from the chi-square test were used to identify the direction (positive or negative) and strength (distance from zero) of associations between specific foraging types and substrates. It is to note that water jetting was excluded from this analysis due to a low number of observations (<1%).

Species-specific differences among substrates, foraging types, and foraging sections were tested using multinomial logistic regression with a logit link function in the *mclogit* package (Elff et al. 2022). This model structure was chosen because it could examine the effects of each fixed factor on a categorical response variable (species identity) while accounting for the non-independence of multiple feeding events within individual tracks. Prior to analysis, data were filtered to remove incomplete observations and rare event categories that would compromise model convergence (e.g., water jetting = <1% of all observations for foraging type; coral crest = 2 observations for foraging area). The estimated marginal means were used to estimate the probability of each species selecting each level within substrate type (coral rubble, rubbly sand, smooth sand), foraging type (surface, excavation, suction), and foraging area (outer flat, middle flat, shoreline/mangrove edges). Significance values were adjusted for multiple comparisons using the Tukey method (Lenth 2022).

3.4 Results

3.4.1 Tracking summary

A total 96 tracks were collected across two site visits in 2021 (n = 44) and 2023 (n = 52) (Table 3.1), of which 89 contained at least one feeding event. Most tracks were collected during mid (n = 42) tidal heights, with 340 recorded feeding events (all from rising tide periods). There were 37 tracks in the low height category, which contained 318 feeding events (265 during low tide, 83 for rising). Track representation was lowest for the high height range (n = 17), with only 34 feeding events recorded (all from rising stage). Track length ranged from 4.4-21.4 minutes, with a mean of 13.7 ± 0.4 SE.

Total foraging events per track ranged from 0-28 (mean events = 7.0 ± 0.6 SE). By species, the number of foraging events included 312 for *P. ater*, 168 for *P. fai*, and 212 for *U. granulatus.* Location of foraging events varied within the reef flat due to tidal habitat availability (Figure 3.3). More feeding events were observed on the northeast side of the bay on the inner flat close to the beach and mangrove stand. Feeding event duration varied broadly from 2-315 s across all species (mean = 42.1 ± 4.3 s) (Figure 3.4). Longest foraging durations occurred for *P. ater*, with multiple occurrences of feeding events exceeding 100 s. For *P. fai* and *U. granulatus*, most feeding events lasted <30 s. Excavation foraging types were associated with the longest feeding times, while most feeding events using either suction or surface feeding were short (<20 s), and results were variable for water jetting. The proportion of feeding events that created a feeding pit or scar was greatest for *P. ater* (51.7%) and lower *U. granulatus* (22.8%) and *P. fai* (9.1%).

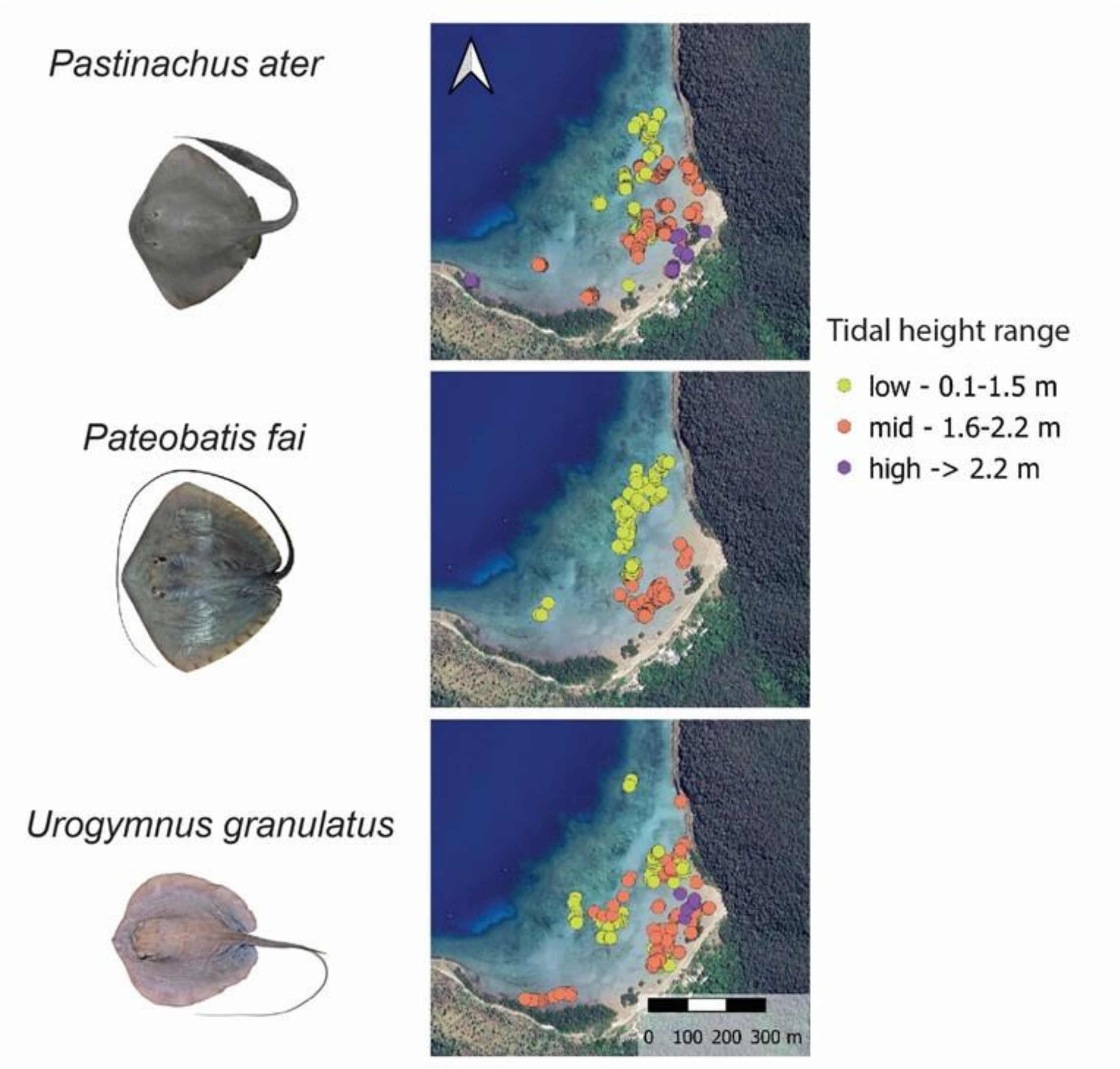


Figure 3.3. Locations of feeding events recorded for each species tracked within Pioneer Bay. Each point represents a single feeding event, and colour denotes the tidal height range.

Table 3.1. Summary of ray behaviour tracks collected in Pioneer Bay, categorised by tidal height category and tidal stage.

	Tidal height range			
	Low	Mid	High	
Species	0.1-1.5 m	1.6-2.2 m	>2.2 m	Total tracks
P. ater	14	16	10	40
P. fai	10	7	0	17
U. granulatus	13	19	7	39

	Tidal stage			
	Low	Rising	High	Total tracks
P. ater	10	29	1	40
P. fai	9	8	0	17
U. granulatus	9	29	1	39

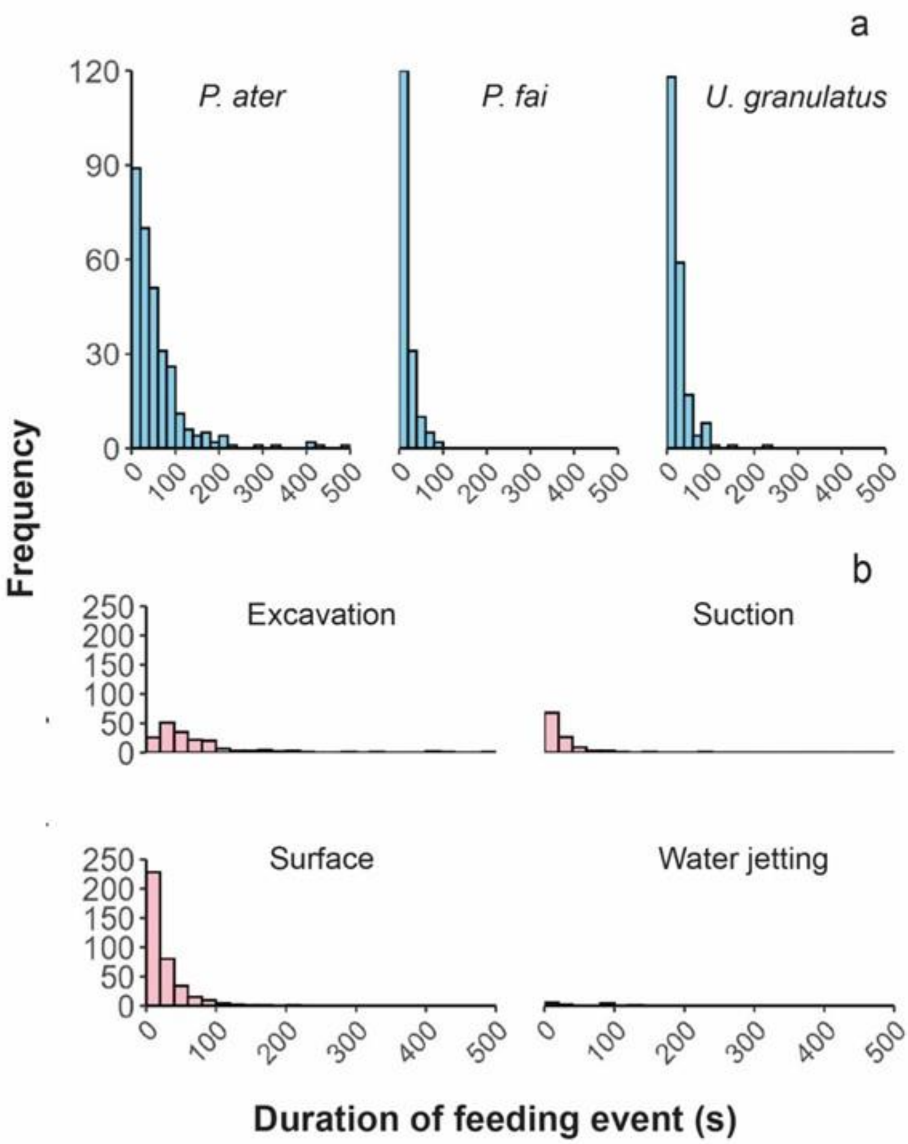


Figure 3.4. Histograms showing (a) the frequency distribution of feeding event durations (in seconds) for each of the three ray species tracked in Pioneer Bay, and (b) frequency distributions for each foraging type.

3.4.2 Foraging activity across the tide

For foraging rates, the inclusion of track length and species explained little variability (adj. $R^2 = 0.036$; F-statistic = 2.141, $DF_{3,90}$, $p = 0.101$), with no significant effects of track length ($p = 0.742$) or year ($p = 0.606$). For proportion of time foraging, these variables explained ~40% of the model variance (marginal $R^2 = 0.393$), with no significant effects of track length ($p = 0.1868$) or year ($p = 0.944$). Thus, all tracks were interpreted collectively across years and without further standardization by track length.

Foraging rates, represented as the number of feeding events h^{-1}, exhibited high variability across tracks (Figure 3.5). Across all tracks, foraging rates were similar for all three species during low tidal heights. At mid tidal heights, mean foraging rates of *U. granulatus* were 1.8 times lower than *P. ater,* and 1.9 times lower than *P. fai*. Moreover, foraging rates of *U. granulatus* were 3.7 times lower than *P. ater* during high tidal ranges. The proportion of time foraging per track also showed high variability, particularly for *P. ater*, which foraged more than *P. fai* and *U. granulatus* across all tidal height ranges (Figure 3.5).

Collectively, the variables tidal height and species explained 21.6% of the variance in foraging rates. Tidal height range had a significant negative impact on foraging rates ($\chi^2 = 22.918$, df = 2, $p < 0.001$), while no differences were detected among species ($\chi^2 = 5.601$, df = 2, $p = 0.061$). Foraging rates were highest at low tidal heights (mean = 37.48 ± 3.37 feeding events h^{-1}), followed by mid (mean = 34.35 ± 3.21 feeding events h^{-1}), and high (mean = 9.08 ± 5.31 feeding events h^{-1}). The largest difference in foraging rates occurred between low and high (t-value = -4.571, $p < 0.0001$), representing a 76% decrease in feeding events h^{-1}. Similar differences were identified when comparing mid and high tides (t-value = 4.261, $p < 0.001$), with a decrease of 74% in feeding events h^{-1}. No significant differences were identified between low and mid tidal heights (t-value = -0.682, $p = 0.495$).

The proportion of time rays foraged per track differed by tidal height ($\chi^2 = 29.192$, df = 2, p = < 0.001) and species ($\chi^2 = 22.449$, df = 2, p < 0.001), which explained 33.1% of the model variance. Rays foraged the most at low tidal heights (mean = 0.44 ± 0.04 of tracking time), followed by mid (mean = 0.28 ± 0.04 of tracking time) and high (mean = 0.11 ± 0.03 of tracking time). The largest differences occurred between low and high tidal heights (t-value = 5.394, p < 0.001), with a 75% decrease in the proportion of time foraging per track. A 36% decrease occurred between low and mid (t-value = -2.722, p = 0.001) and a 61% decrease between mid and high (t-value = 3.575, p = 0.001). By species, *P. ater* (mean = 0.40 ± 0.04 of tracking time) foraged significantly more than *P. fai* (mean = 0.19 ± 0.05 of tracking time; t-value = 3.129, p = 0.005) and *U. granulatus* (0.19 ± 0.03 of tracking time; t-value = 4.378, p < 0.001), whereas no differences were apparent between *P. fai* and *U. granulatus* (t-value = 0.106, p = 1.000).

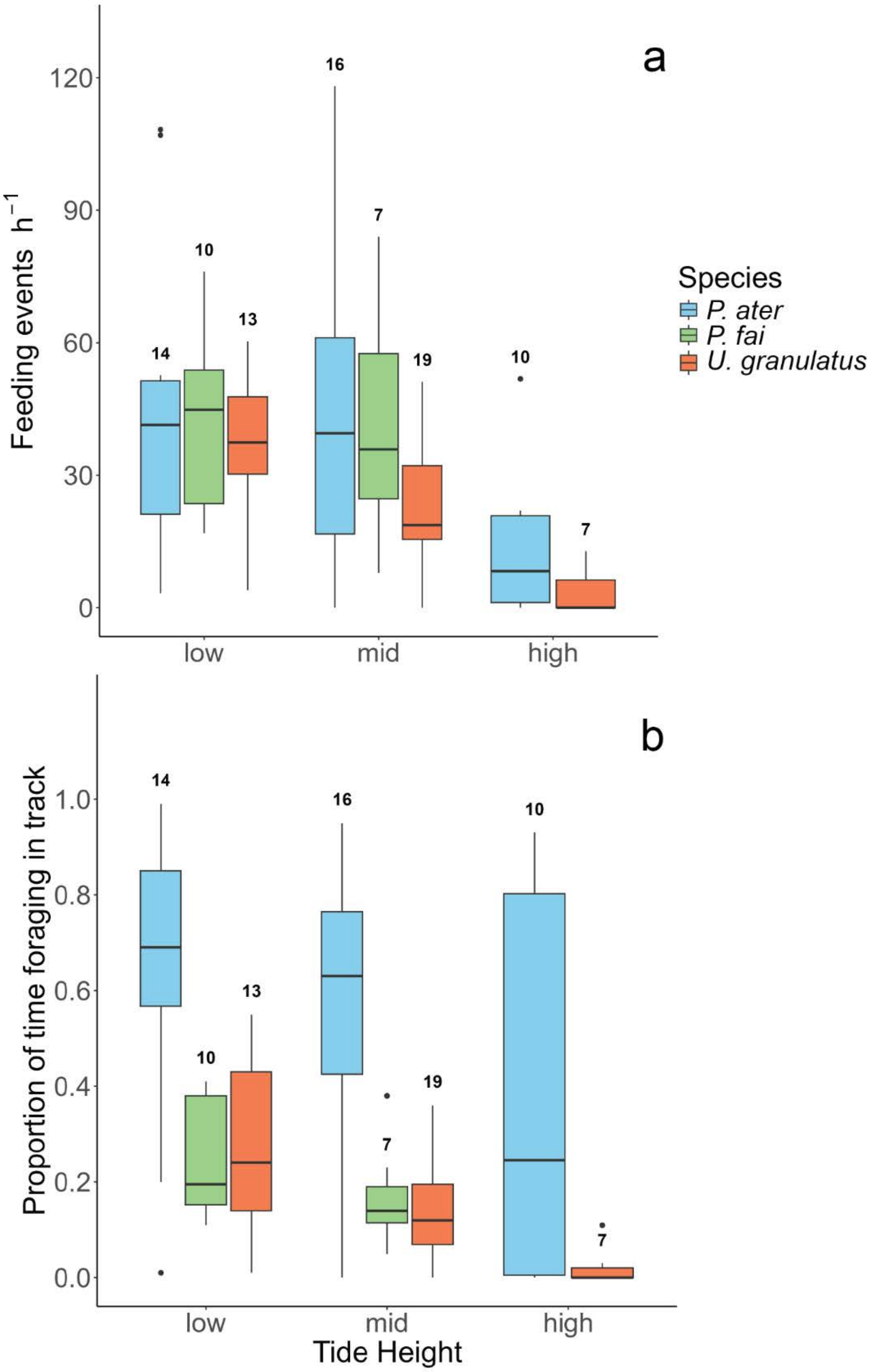


Figure 3.5. Boxplots showing the number of feeding events h^{-1} (a) and the proportion of time foraging per track (seconds of foraging divided by total tracking time) (b) across three tidal height categories (low = 0.1-1.5 m, mid = 1.6-2.2 m, high = >2.2 m).. Numbers above the bars denote the number of tracks.

3.4.3 Foraging preferences among species

Significant relationships were identified between foraging types and substrates ($\chi^2 = 71.471$, $p < 0.001$) (Table 3.2). Specifically, rays used excavation more frequently on smooth sand (73.4% of feeding events) and the least on coral rubble (10.1% of feeding events). Rays used suction feeding more frequently on coral rubble (42.1% of feeding events) compared to rubbly sand (21.1%) and smooth sand (36.8%). Surface feeding was most often used on smooth sand (73.9% of feeding events), followed by rubbly sand (11.7%) and coral rubble (14.4%) (Table 3.2).

Substrate, foraging type, and reef flat section explained 79.7% of the total deviance in species' foraging behaviours. By substrate, *P. ater* showed the highest probability of feeding on smooth sand (52.8 ± 8.5%) over rubbly sand (29.1 ± 11.2%) and coral rubble (11.5 ± 10.1%) (Figure 3.6a; Table 3.3). In contrast, *U. granulatus* showed the highest probability of selecting coral rubble (75.4 ± 12.8%), followed by rubbly sand (51.1 ± 11.8%) and smooth sand (23.9 ± 7.3%).

By foraging type, *P. ater* was most likely to select excavation (51.7 ± 11.2%) over surface (34.7 ± 9.3%) and suction (7.0 ± 7.1) (Figure 3.6b; Table 3.3). For *P. fai*, probabilities were similar for surface (22.8 ± 8.7%) and suction (27.2 ± 10.8%), and they rarely used excavation (6.1 ± 5.3%). *U. granulatus* had the highest probability of using suction (65.8 ± 10.8%), followed by surface (42.5 ± 8.2%) and excavation (42.4 ± 10.5%).

By foraging area, *P. ater* showed similar probabilities for feeding on the middle flat (32.5 ± 8.7%) and outer flat (37.3 ± 13.7%) and was less likely to feed along the shoreline/mangrove edges (23.6 ± 7.5%) (Figure 3.6c; Table 3.3). *Pateobatis fai* showed the highest probability of feeding on the outer flat (40.5 ± 16.5%) when compared to the middle flat (7.8 ± 4.8%) and shoreline/mangrove edges (7.9 ± 4.8%). In contrast, *U. granulatus* was most likely to select areas to feed along the shoreline/mangrove edges (68.5 ± 8.8%) and middle flat (59.7 ± 9.7%) when compared to the outer flat (22.2 ± 14.9%).

Table 3.2. Residuals of the chi-square analysis output showing the associations between combinations of foraging types and substrates ($\chi^2 = 71.471$, $p < 0.001$). Observed frequencies (N) represent the number of feeding events recorded for each foraging combination, and the standardised residual values (Res.) indicate the strength (distance from zero) and direction (positive or negative) of associations.

	coral rubble		rubbly sand		smooth sand	
Foraging type	N	Res.	N	Res.	N	Res.
excavation	19	3.26	31	0.86	138	2.02
Suction	48	7.42	24	2.14	42	7.68
Surface	54	2.64	44	2.39	278	3.96

Table 3.3. Pairwise comparisons of predicted marginal means for substrate type, foraging type, and reef flat section use by ray species in Pioneer Bay. Differences in probabilities are shown as percentages, and SE denotes ± 1 standard error. Statistically significant differences ($p < 0.05$) are denoted in bold.

	Contrast	Species	Difference (%)	SE	z-ratio	p-value
substrate	coral rubble - rubbly sand	*P. ater*	-17.6	13.3	-1.33	0.38
	coral rubble - smooth sand	*P. ater*	-41.3	12.8	-3.23	**0.00**
	rubbly sand - smooth sand	*P. ater*	-23.7	12.9	-1.84	0.16
	coral rubble - rubbly sand	*P. fai*	-6.6	11.8	-0.56	0.84
	coral rubble - smooth sand	*P. fai*	-10.1	11.6	-0.88	0.66
	rubbly sand - smooth sand	*P. fai*	-3.5	10.1	-0.34	0.94
	coral rubble - rubbly sand	*U. granulatus*	24.2	15.0	1.62	0.24
	coral rubble - smooth sand	*U. granulatus*	51.4	14.6	3.52	**0.00**
	rubbly sand - smooth sand	*U. granulatus*	27.2	12.9	2.10	0.09
foraging type	excavation - suction	*P. ater*	44.7	12.8	3.48	**0.00**
	excavation - surface	*P. ater*	17.1	10.4	1.65	0.23
	suction - surface	*P. ater*	-27.6	11.0	-2.52	**0.03**
	excavation - suction	*P. fai*	-21.1	11.0	-1.93	0.13
	excavation - surface	*P. fai*	-16.8	7.7	-2.18	0.08
	suction - surface	*P. fai*	4.3	11.2	0.39	0.92
	excavation - suction	*U. granulatus*	-23.6	13.7	-1.72	0.20
	excavation - surface	*U. granulatus*	-0.3	9.9	-0.03	1.00
	suction - surface	*U. granulatus*	23.3	11.6	2.01	0.11
reef flat section	middle flat - outer flat	*P. ater*	-4.8	15.1	-0.32	0.95
	middle flat – shoreline/mangroves	*P. ater*	8.9	10.4	0.86	0.67
	outer flat – shoreline/mangroves	*P. ater*	13.7	14.8	0.93	0.62
	middle flat - outer flat	*P. fai*	-32.7	16.5	-1.98	0.12
	middle flat – shoreline/mangroves	*P. fai*	-0.1	6.2	-0.01	1.00
	outer flat – shoreline/mangroves	*P. fai*	32.6	16.8	1.94	0.13
	middle flat - outer flat	*U. granulatus*	37.5	17.2	2.17	0.08
	middle flat – shoreline/mangroves	*U. granulatus*	-8.8	11.9	-0.74	0.74
	outer flat – shoreline/mangroves	*U. granulatus*	-46.3	16.7	-2.77	**0.02**

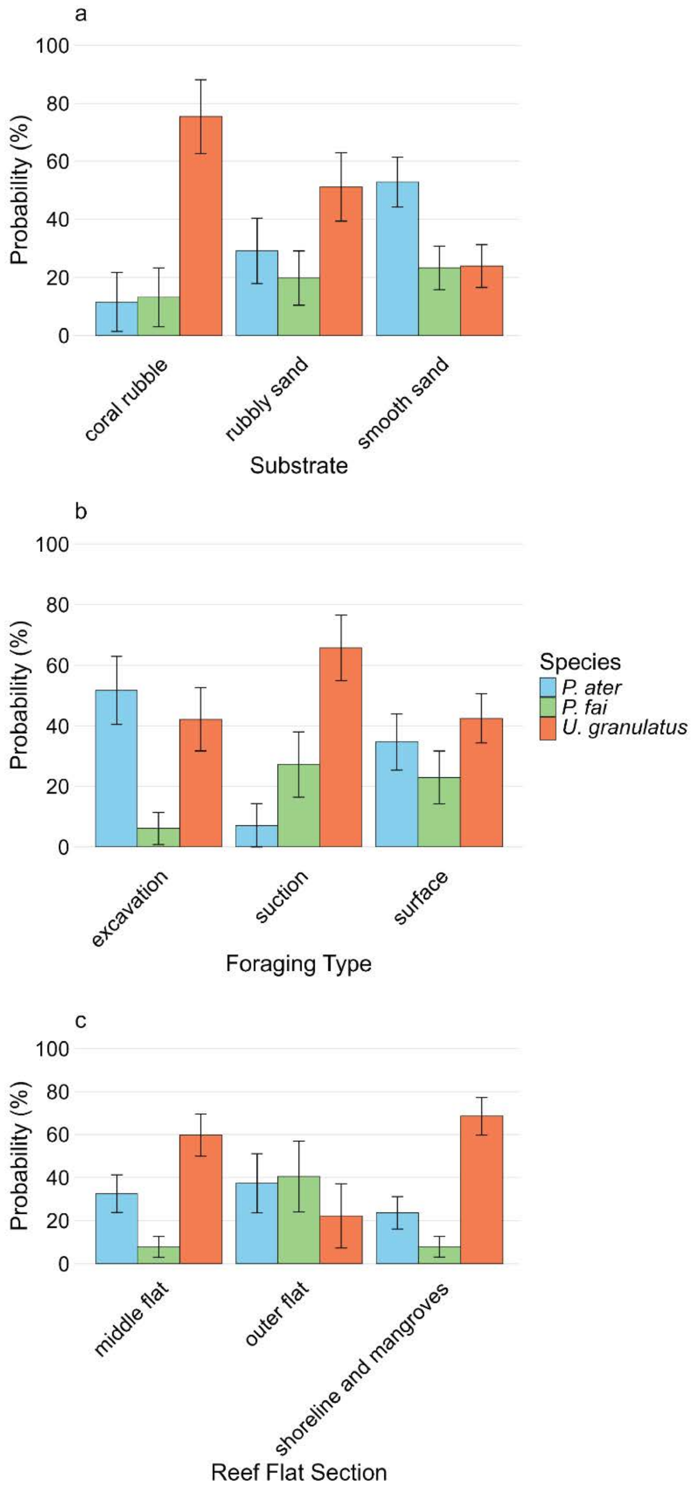


Figure 3.6. Predicted probability percentages (± 1 SE) of feeding events by substrate (a), foraging type (b) and reef flat section (c). Bars are coloured by species.

3.5 Discussion

Intertidal flats are characterised by the movements of transient fish species, which enter upper intertidal zones during flooding tides and subsequently leave during ebb tides to avoid stranding (Gibson 2003, Krumme 2009). Rays also make periodic migrations across intertidal gradients (Oleksyn et al. 2020, Ruiz-García et al. 2020, Elston et al. 2022), which inherently determines where foraging can occur at a given time. For species that physically modify their habitats with their behaviours, this can significantly influence their functional roles (Hastings et al. 2007). In these dynamic environments, foraging patterns were expected to follow one of two different strategies: 1) rays feed continuously as they exploit available habitats across the tidal cycle or 2) rays time foraging efforts to align with when preferred foraging patches become available (MacArthur & Pianka 1966, Burrows 1994). With the former strategy, impacts of ray foraging would be distributed over broader spatial areas, while for the latter, bioturbation and predation pressures may be concentrated within smaller habitat patches (Crook et al. 2022, Grew et al. 2024).

At lower tidal heights in Pioneer Bay, rays fed along the subtidal edges near the reef crest, which then extended to newly submerged habitats closer to the beach and mangrove edges as these became accessible. In this case, foraging appeared to be opportunistic, with rays taking advantage of available foraging opportunities across different microhabitats as they migrate with the tidal cycle. However, rays did not feed equally across the tidal progression, and this showed species-specific patterns. For example, *P. ater* foraged most intensely during low tidal heights, with lower foraging rates observed as the flat became submerged in deeper water. This pattern matches previous observations of this species, in which *P. ater* commonly rest along the mangrove edges or on open sand flat patches during high tides (Martins et al. 2020b). No differences in foraging behaviours were identified for *P.*

fai, although the absence of data during high tidal ranges provided a more limited overview of tidal variability.

Temporal foraging patterns were most pronounced for *U. granulatus*. As with *P. ater,* rays fed most actively during lower heights and less actively later in the tide. Notably, in five of the seven tracks during upper height ranges, the tracked ray spent most of the tracking time resting or buried near the mangrove edges, where little or no feeding was observed. This pattern likely reflects preferences for this species to move into the mangrove stands during rising and high tides, where they generally remain as long as water levels permit (Davy et al. 2015, Martins et al. 2020a). Given visibility was obstructed by the root structures, aerial surveys could not reliably assess feeding activity in the mangroves. However, ground-level observations I conducted of *U. granulatus* during high tides generally showed individuals to be resting alone or in small groups. Another study using stationary video cameras reported some occurrences of feeding by *U. granulatus* within these habitats (Kanno et al. 2019), indicating mangroves may also be used for feeding, although this could be opportunistic while using these areas for refuge.

Changes in foraging activity over the tide could also be driven by external factors, such as the need to make trade-offs between prey availability and predator avoidance with depth (Vaudo & Heithaus 2013, Davy et al. 2015, Sherman et al. 2020). Several predatory shark species are common within the Pioneer Bay reef flat including blacktip reef sharks, *Carcharinus melanopterus*, sharptooth lemon sharks, *Negaprion acutidens,* and great hammerheads, *Sphyrna mokarran* (Schlaff et al. 2017, Martins et al. 2022, Lubitz et al. 2023), and direct predation events have been observed (A. Martins & J. Myers, pers. obs.). Thus, rays may invest more time in predator avoidance behaviours such as burying or using structural refuges while predators have greater access to upper intertidal flat areas (Semeniuk & Dill 2005, 2006, Bond et al. 2019).

Species-specific foraging preferences provided some evidence of fine-scale resource partitioning within the reef flat. However, high overlap in specific aspects of foraging, such as all three species using surface feeding on smooth sand (albeit in different proportions) and feeding over similar areas suggested that all three species share some degree of functional redundancy. While resource partitioning enables species coexistence by minimising interspecific competition (Schoener 1974, Walter 1991, Saulnier et al. 2020), differences in foraging patterns across microhabitats and sediment depths may be shaped by species-specific morphological and behavioural adaptations rather than as a direct response to competition (Motta & Huber 2004, Wetherbee et al. 2004). Associations between substrate choice and foraging type demonstrated that foraging type is dependent on the substrate, or conversely, that substrates are selected which are most compatible with preferred foraging types. Both *P. ater* and *P. fai* predominantly used surface feeding on smooth sand, suggesting that these species may target similar prey resources from the surface layers of substrate. However, *P. ater* also used excavation feeding more than all other species, which was associated with greater sediment disturbance, which may enable this species to access deeply buried prey (Crook et al. 2022). Together, the ability to alternate between these different foraging types may allow *P. ater* to exploit a broader range of prey across the sediment gradient.

Foraging of *U. granulatus* was the most distinct from other species due to greater preferences for feeding among coral rubble. In more rare cases, individuals manipulated or fully rotated coral rubble fragments with their rostra (a behaviour that was unique to this species). Two foraging events were also documented along the rocky edge bordering the northern end of the bay, which further demonstrated their preferences for topographically diverse habitats. Coral rubble was most associated with suction and surface feeding, and both types were used interchangeably. In this case, rays may use surface feeding if a target prey is located along the surface of the coral, while proactively forcing water into the buccal cavity for suction feeding would be more effective for drawing out concealed prey from crevices (Wilga & Motta 1998, Shibuya et al. 2012).

Trophic studies on sympatric *P. ater* and *U. granulatus* have shown *U. granulatus* specialises on decapod crustaceans, while *P. ater* is characterised by a more generalist diet of bivalves, crustaceans, and annelids, demonstrating that these species occupy distinct trophic niches (Crook 2020, Elston et al. 2020, Martins et al. 2022). Combining knowledge on species diets and foraging behaviours provides some indication as to which prey types may be associated with specific behaviours. For example, higher frequencies of excavation feeding (used almost exclusively by *P. ater*) may be associated with polychaetes or other infaunal prey, which may have little importance in the diets of other species. Additionally, dietary niches of *U. granulatus* may be characterised by decapod prey types associated with structural habitats (e.g. mangroves, coral). Given trophic niches have only been investigated for *P. ater* and *U. granulatus* in Pioneer Bay, it remains unclear how much dietary overlap exists with *P. fai*. However, previous studies on *P. fai* and related whipray species (genus *Himantura*) have similarly reported distinct dietary niches from *P. ater* (Vaudo & Heithaus 2011, O'Shea et al. 2013).

Comparing foraging behaviours among three ray species illustrated the diversity of functional roles that ray communities perform over localised scales, as well as their unique ecological impacts. While all ray species modified the environment through feeding pits or scars, they differed by their use of disruptive (excavation, suction, water jetting) versus non-disruptive (surface) feeding types. Across all four behaviours, excavation appeared to be associated with greater levels of sediment disturbance and feeding pit formation. As this feeding type was used more exclusively by *P. ater*, they may contribute more substantially to bioturbation of soft sediments than sympatric species that habitually feed along the surface or among coral rubble. Foraging across different substrates also showed how species likely influence macroinvertebrate communities through different trophic pathways. Unvegetated sand flats typically support burrowing infauna such as polychaetes, bivalves, and small crustaceans (Pacheco et al. 2011), while reef substrates harbor more epibenthic taxa including decapod crustaceans, amphipods, and molluscs adapted to structural complexity (Stella et al. 2010, Plaisance et al. 2011). Areas of rubbly sand, therefore, likely contain invertebrate assemblages that complement both habitat types and contribute to a heterogeneous prey landscape across the reef flat. Overall, by feeding heavily on coral rubble, *U. granulatus* may play a more pivotal role in regulating populations of coral-associated prey taxa than sympatric species. Conversely, abundances of *P. ater* and *P.fai* would apply more predation pressures on invertebrate communities associated with soft-bottom habitats.

3.6 Conclusions

This chapter underscores the value of incorporating behavioural data into our interpretations of fine-scale habitat use and for understanding these processes at the species level. The pervasiveness of foraging activity by juvenile *P. ater*, *P. fai*, and *U. granulatus* demonstrates that these species regularly obtain resources within the shallow reef flat nursery. Moreover, species use diverse tactics to feed in response to tidal habitat availability and exploit different microhabitat niches within the intertidal zone. This study also provides the first descriptions of foraging behaviours for *P. fai* at this location, establishing preliminary knowledge on their functional roles and potential interactions with sympatric species.

Some limitations were apparent from this study, such that behaviours of individual rays were analysed over relatively short periods (7-18 min tracks, mean = 13.5 min). While drone tracking provided a high-resolution “snapshot” of foraging, these data may potentially exclude rare feeding events or yield little information if feeding frequency of the predator is low. Where greater temporal coverage is required, future studies could consider extending the tracking duration using overlapping drone deployments (Crook et al. 2022) or by combining drones with complementary observational techniques (e.g. stationary cameras). Moreover, with data collection restricted to two site visits, further research is needed to understand the full extent of temporal variability in Pioneer Bay. For example, variations in water depth between spring and neap tides significantly affect both habitat availability and predator access to the upper intertidal zones (Leurs et al. 2023, Sheaves et al. 2024a). Additionally, the substantial temperature fluctuations between summer and winter months in Pioneer Bay may influence trade-offs between optimal foraging and thermal tolerance limits (Higgins et al. 2024). Collectively, such efforts would advance our understanding of the complex interplay between resource acquisition, predator avoidance, and physiological constraints on ray behavioural ecology.

Continued exploration of ray foraging behaviours will provide critical insights into which areas support high levels of feeding activity in productive nursery environments. Furthermore, these efforts will demonstrate the various strategies that develop across multi-species communities to minimise competition and enhance ecosystem stability through functionally diverse pathways (Duffy 2002, Hooper et al. 2005, Leduc et al. 2015). Pairing behavioural studies with complementary research methods will be particularly valuable for verifying these patterns. Specifically, integrating benthic prey surveys across various microhabitats and sediment depths would provide more definitive linkages between foraging behaviours, substrate choice, and prey selection. Moreover, as the specific contributions of rays to processes such as bioturbation and nutrient dynamics can be difficult to quantify in the field (Flowers et al. 2021), future *in situ* experiments could be particularly useful for bridging the gaps between specific behaviours and functional outputs and for understanding the scales over which these processes occur.

4 Chapter 4. Summarising 40 years of gastric lavage studies to evaluate efficiency and survival in sharks and rays

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4.1 Introduction

Stomach content analysis (SCA) is a fundamental technique for studying the feeding ecology of fish (Hyslop 1980, Amundsen & Sánchez-Hernández 2019). It is traditionally performed by euthanising an animal to dissect its stomach and represents a snapshot of the overall diet (Baker et al. 2024). Historically, lethal SCA has been the primary method for describing the diets of sharks and rays, with sample sizes ranging from hundreds (Lowe et al. 1996, Wetherbee et al. 1997, Dale et al. 2011, O'Shea et al. 2013) to over one thousand individuals (Barnett et al. 2013) for a single study. To maximise information collected from euthanised animals, biological and life history parameters have also been obtained, such as reproduction or age-growth relationships (Awruch et al. 2009, Lucifora et al. 2009).

Nowadays, researchers are less inclined to kill large numbers of sharks and rays to collect biological or dietary data, despite the useful knowledge that may be gained from it (Heupel & Simpfendorfer 2010). In addition to the welfare of individual animals, conservation concerns have also put lethal sampling into question, particularly where more vulnerable populations might be negatively impacted if individuals are removed. With many elasmobranchs now vulnerable to extinction, it is harder to justify “killing for conservation” (Hammerschlag & Sulikowski 2011). Nonetheless, studying the diet has several implications for conservation and fisheries management, such as providing knowledge of predation pressure on fisheries species or identifying essential feeding habitats that support survival and recruitment (Barnett & Semmens 2012, Barnett et al. 2017, Galván-Magaña et al. 2019).

Where these studies are necessary, we cannot simply reduce the numbers of animals used without compromising data quality, since large sample sizes are often required to accurately describe diets over time (Kamler & Pope 2001), particularly for species with broad dietary niches, such as the broadnose sevengill shark, *Notorynchus cepedianus* (Ebert 2002, Barnett et al. 2010a) or tiger shark, *Galeocerdo cuvier* (Lowe et al. 1996, Dicken et al. 2017). Obtaining entire stomachs for dietary analysis is still a valid option for species targeted by fisheries, as large numbers of samples can be collected over prolonged time frames (Simpfendorfer et al. 2001a, Huveneers et al. 2007, Gonzalez-Pestana et al. 2021). However, for the vast majority of species that are not targeted for human consumption, it is imperative to consider ways of replacing lethal sampling altogether (Hammerschlag & Sulikowski 2011).

Stable isotope analysis (SIA) has been used to study trophic ecology of marine vertebrates since the late 1980s (Estep & Vigg 1985, Harrigan et al. 1989). Since then, non-lethal biochemical approaches including SIA have increased in elasmobranch trophic studies (Petta et al. 2020, Bornatowski et al. 2023). However, it is important to acknowledge that both methods answer different ecological questions and are not interchangeable (Hussey et al. 2012, Petta et al. 2020). With SCA, specific prey species or types can be identified either visually or with the aid of genetic verification (da Silveira et al. 2020). On the other hand, SIA generally provides dietary information at lower taxonomic resolution and can lead to erroneous conclusions on relative prey importance if stable isotope compositions of prey overlap (Abrantes & Sheaves 2024). Therefore, pairing SIA with SCA can overcome the limitations associated with each method individually, especially where little or no prior knowledge exists on the diet (Abrantes & Sheaves 2024, Baker et al. 2024).

Given the feeding ecology of many shark and ray species remains poorly studied, incomplete, or unknown, there is a continual need for SCA in ecological research. Gastric lavage presents a non-lethal alternative to stomach dissection, which involves flushing the stomachs of live animals to assess prey consumption. It is generally performed using some type of pulsed water flow device to induce regurgitation or stomach inversion. The first records of this technique being applied to elasmobranchs was by Medved (1985) and Nelson and Ross (1992). Despite being successful in early studies, gastric lavage has not been widely used in subsequent decades. This is somewhat surprising since the procedure is relatively simple to perform, does not require specialist equipment, and animals can be released afterward. Gastric lavage also remains more cost-effective than other emerging techniques, such as identifying prey items from cloacal swabs with DNA metabarcoding (Clark et al. 2023, Olin et al. 2023). However, it is still considered highly invasive compared to these other approaches, which requires careful consideration in its use.

Currently, information pertaining to the effectiveness of gastric lavage and survival of individuals is touched on across studies but has not been consolidated. Therefore, in this chapter, I summarised studies that have used gastric lavage on sharks and rays to identify which species/groups it has been effective for, the difficulties encountered, and if post-release survival has been assessed. Secondly, a field study is presented to demonstrate 1) how gastric lavage was performed on neonate to juvenile-sized rays, 2) its effectiveness at obtaining stomach contents, and 3) post release survival over time using mark-recapture methods.

4.2 Methods

4.2.1 Literature summary

Published studies were searched in Web of Science and Google Scholar databases from Jun-Jul 2024 using combinations of search terms including gastric lavage, gastric evacuation, nonlethal sampling, and stomach flush, which was paired with shark, ray, or elasmobranch. Studies were retained if the full text was available, and it mentioned gastric lavage in the title, abstract, or methods. The following details were then extracted: year published, field setting or captivity, purpose of study, species, shark or ray, life stages (neonate/young-of-year, juvenile/subadult, or adult), sample size, gastric lavage efficiency, and how post-release survival was assessed. Note, to truly evaluate efficiency, animals would need to be dissected (unless stomach was inverted) to confirm without doubt that all contents were removed or if empty stomachs were actually empty. Thus, for the purpose of this study, efficiency represents the percentage of shark or rays sampled where stomach contents were collected.

4.2.2 Field study

Data collection took place at two intertidal sand flats in North Queensland, Australia. At both sites, there are considerable changes in water depth across the tidal cycle, in which rays regularly migrate onto the upper intertidal zones during rising and high tides. Lucinda (-18.5327° S, 146.3347° E) is an extensive intertidal flat on the border of the wet and dry tropics (full description of site provided by Crook et al. (2022). Aside from the mangroves at the northern end, the study area is primarily unvegetated with a mixture of coarse and fine sediments. The most commonly encountered ray species are the Australian whipray, *Himantura australis,* broad cowtail stingray, *Pastinachus ater*, and giant shovelnose ray, *Glaucostegus typus*, while brown whipray, *Maculabatis toshi,* and mangrove whipray, *Urogymnus granulatus,* are also present in smaller numbers (Crook 2020). Rays were caught over 48 days from Nov 2022 to Apr 2024, and the number of days passed between consecutive site visits ranged from 1-107.

Blacksoil Creek (-19.299407° S, 147.042662° E) is an estuary inlet located at Cape Cleveland, approximately 112 km southeast of Lucinda (see Chapter 2 for more details). The inlet is surrounded by saltpans, with little urban development or farmland in its immediate catchment (Mattone & Sheaves 2017). The study area encompasses 0.5 km^2 near the estuary mouth. During low tides, exposed sand flats cover most of the creek area, which are surrounded by narrow subtidal channels along the deeper mangrove edges. The most common species are *H. australis* and *M. toshi*. Although *G. typus* and *P. ater* are occasionally present, these were not targeted, due to low occurrence. Rays were caught on 16 dates from Feb 2022 to Jun 2024, and the number of days passed between visits ranged from 1-293.

All rays were caught under general fisheries permit 259152, with ethical approvals from James Cook University (Animal ethics approval 2838). Individuals caught at Lucinda were also used for diet and trophic analyses in Chapter 5. Juvenile rays were captured in shallow water (<1 m) by encircling them in a beach seine net. Individual rays were then transferred to handheld dip nets and placed in a holding tray lined with 1 mm mesh netting. Gastric lavage procedures were adapted from Elston et al. (2020) and are demonstrated in (Figure 4.1). A 500 GPH capacity bilge pump was connected to a 12V marine battery. The apparatus was fitted with an 8 mm diameter flexible plastic tube with a bevelled end, which was inserted into the mouth. A valve was fitted to the tube to adjust water pressure to the lowest amount needed to generate a firm, steady flow. Size of tube and flow rates were dependent on ray size, as an oversized tube blocked materials from exiting the stomach and a tube that was too narrow would not generate sufficient water pressure. For all stingray species, an 8 mm tube was used on all individuals >50 cm DW, with an approximate flow rate of ~ 6.4 L/min. A smaller 6 mm tube was used on rays ranging 30-50 cm DW (flow rate = 4.4 L/min.), and a 4 mm tube for rays <30 cm DW (flow rate = ~2.4 L/min.). For *G. typus,* the 4 mm tube was used if total length was <80 cm.

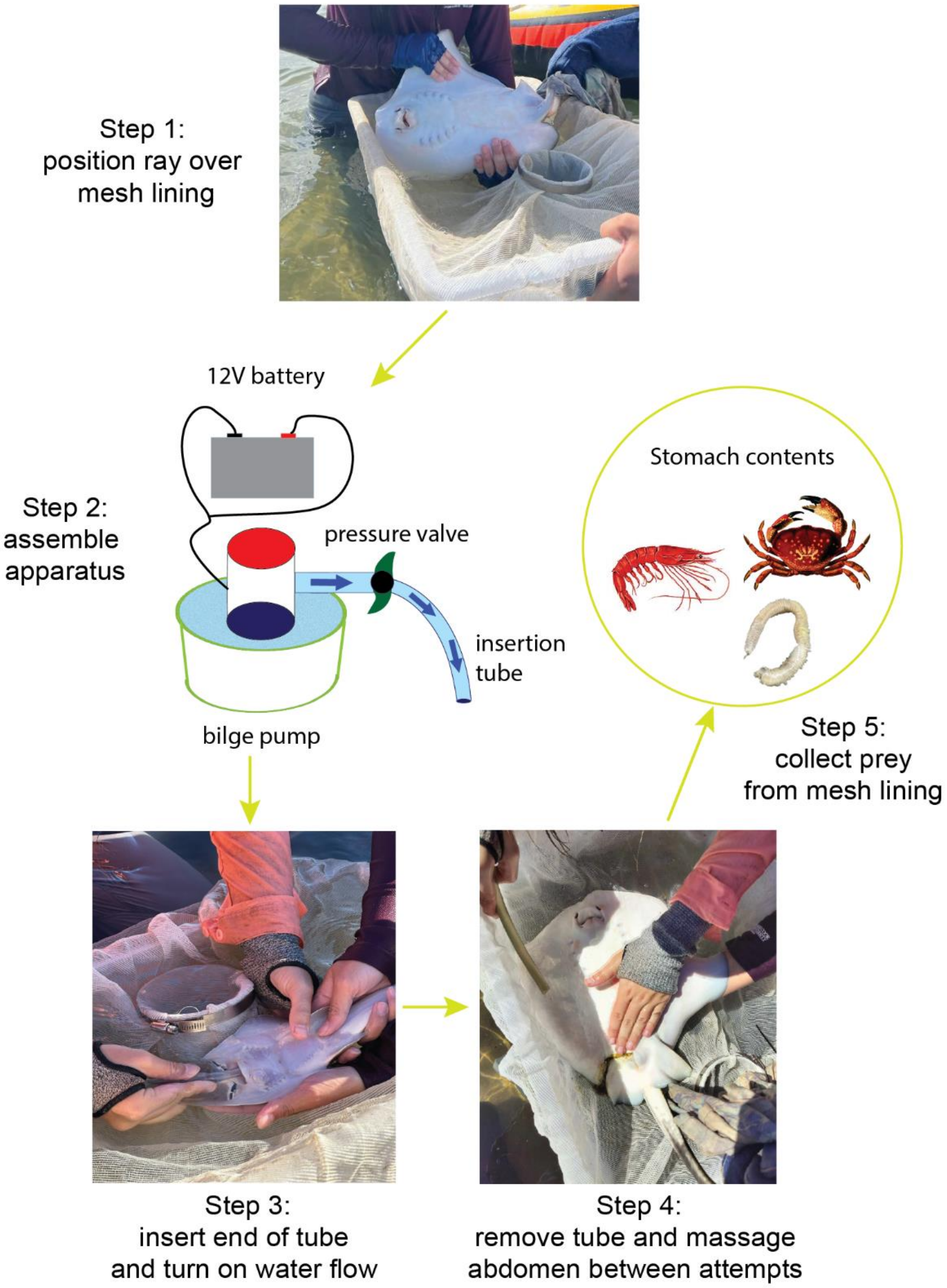

Figure 4.1. Diagram illustrating gastric lavage procedure on small rays (juvenile G. *typus* in Step 3 and *P. ater* in Step 4).

Gastric lavage was performed by two handlers. One person would grip the base of the ray's tail with a gloved hand and invert the ray, supporting the dorsal side by placing a hand underneath the disc. The other handler would insert the bevelled end of the tube into the mouth by applying gentle pressure to bypass the oesophagus. The ray was then tilted with its head pointed downward to aid with flushing the regurgitated material onto a mesh lining. Once water flow was initiated, flushing lasted between 10-15 seconds per attempt, with 2-3 attempts per individual. Once there was visual extension of the abdominal area, the tube was removed, and the abdomen was lightly massaged forward towards the mouth. Prey items were expelled from either the mouth, gills, or spiracles. Commonly during the procedure, faeces or digested materials from the lower gut were also pushed through the cloaca. Any expansion of the stomach and gut ceased once excess water was massaged out of the stomach. If no material was regurgitated after the third attempt, the ray's stomach was assumed to be empty.

Total handling time ranged from ~5-15 minutes, which also included taking a 5 mm diameter muscle tissue sample from the posterior end of the disc for SIA in Chapter 5 and a clip from the pelvic fin for future genetics assessments. A marker tag (numbered for identification) was inserted on the spiracles of *H. australis*, *M. toshi*, and *P. ater*, whereas marker tags were attached to the dorsal fin of *G. typus* (Crook 2020, Martins et al. 2020b). Only the two largest *M. toshi* were given a marker tag, since all others were too small for attachment via the spiracle. Rays were released as close as possible to the capture location and were visually inspected for two minutes (unless they swam off) to ensure recovery. Generally, a ray either buried itself in the sediment or swam off immediately. No signs of injury or predation attempts were witnessed during the immediate recovery period. During repeated site visits, recaptured rays were identified by their marker tags. Gastric lavage was repeated if at least three days had passed from previous capture and the ray appeared in good condition (exhibiting normal behaviour, no remaining stress colouration, no deterioration in body condition).

Gastric lavage efficiency was represented by the frequency of occurrence (% of stomachs that contained prey) and was calculated by dividing the total number of non-empty stomachs by the total flushed stomachs × 100. This metric was calculated collectively for each species (pooling sites) and for species at each site. However, we note that measuring true gastric lavage success assumes that all stomachs were fully emptied with each flush and that an absence of stomach content was due to an empty stomach rather than poor technique or other external factors. The frequencies of successes (sample obtained) and failures (empty stomachs) were summarised by species (sites pooled) and by location for *H. australis* and *M. toshi* (Appendix B, Table B1), which were then compared using Fisher's exact tests. Where a significant result was obtained ($p < 0.05$), pairwise comparisons were run between specific pairs. For *G. typus*, frequencies and resulting gastric lavage efficiency were only calculated for rays caught in 2023, since *G. typus* caught in 2024 were used for multiple research objectives, and it was not consistently reported if an absence of stomach contents meant that gastric lavage was not performed or that an individual had an empty stomach. However, recaptured *G. typus* from 2024, for which contents were recorded ($n = 11$), were still included to assess post-release survival. Moreover, frequency of occurrence and counts of specific prey types were recorded for future trophic analyses.

To assess post-release recovery and survival of recaptured rays after gastric lavage, the total number of days between the first capture (when gastric lavage was performed) and last known recapture were recorded. This metric was omitted for individuals that shed their marker tag between the first and second captures, as this made the initial capture date uncertain. Recapture data were summarised for each species to obtain the maximum length of time over which survival could be verified, the mean number of days between captures, and to calculate recapture rates (%). Given that only three rays were recaptured from Blacksoil Creek (of which only two *H. australis* retained their marker tags), these recaptures were pooled with *H. australis* from Lucinda.

4.3 Results

4.3.1 Literature summary

Excluding our field study, 23 studies were published between 1985-2023 that used gastric lavage on either sharks or rays (Table 4.1). Only four studies were conducted before 2010, with the majority from 2010-2019 (Figure 4.2a). Studies mostly included later-stage juveniles, subadults, and adults, with only three studies featuring neonate or young-of year age classes (Figure 4.2b). Ten studies were conducted on rays and thirteen on sharks, with fifteen and eleven different species represented, respectively. The purposes of field studies (n = 15) were primarily to describe the diet of one or more species and to test gastric lavage efficiency, while captivity studies (n = 7) were designed to assess factors related to gastric evacuation times. Where sample sizes were reported, these ranged broadly from 15-336 individuals (Table 4.1). Size ranges indicated that most studies were conducted on small-bodied shark species <200 cm total length, and the largest ray species included was the spotted eagle ray, *Aetobatus narinari* (reaching 187 cm DW). Gastric lavage efficiency ranged broadly from 29-100% for sharks and from 60-95% for rays.

Although multiple studies confirmed short-term recovery by visual inspection after release, only one study assessed longer-term survival. Therefore, evidence of survival was mostly derived from captivity settings. Survival was verified for days or weeks after gastric lavage for shark species including *Squalus acanthias* and *Sphyrna lewini*, as well as two species of skates: *Leucoraja eglanteria* and *Raja erinacea*. Where individuals were not killed immediately afterward to verify gastric evacuation rates, authors reported using the same individuals for other experiments or releasing them. No studies reported mortality or ill effects during or directly after gastric lavage.

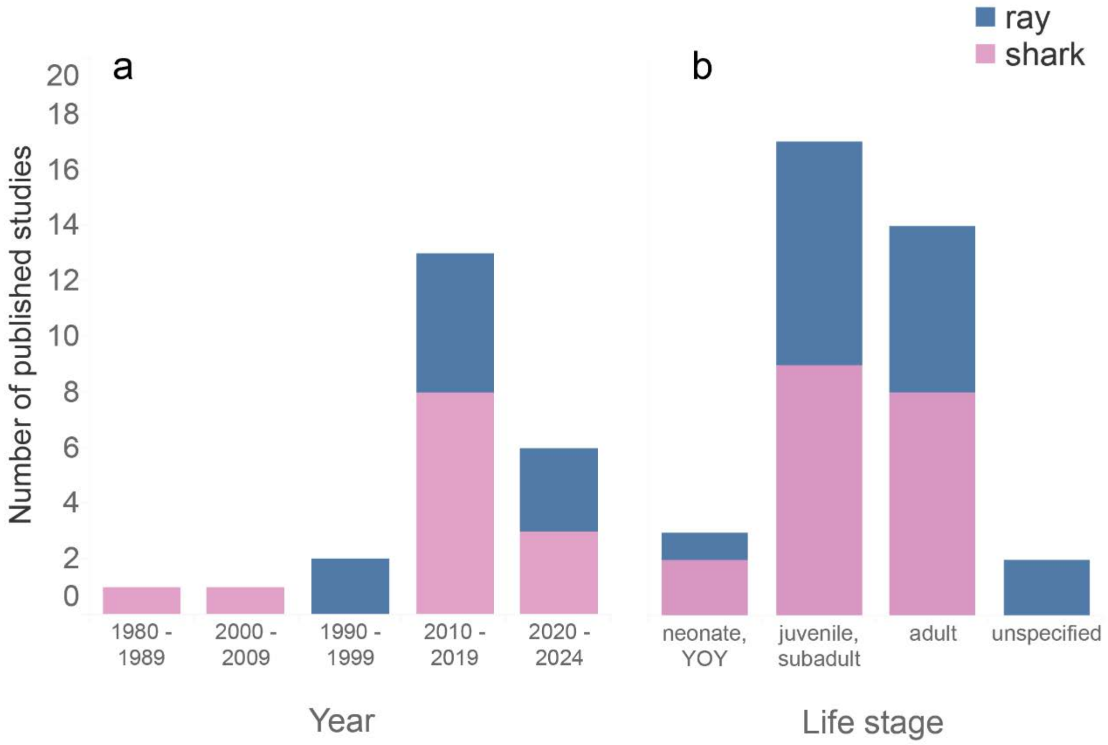

Figure 4.2. Histograms depicting number of published studies across decades (a) and number of studies where each life stage was included (b). If multiple life stages were included, these studies were included for all applicable categories. Bar colour designates the number of studies for sharks and rays.

Table 4.1. Summary of all studies that have reported using gastric lavage on sharks or rays. For studies with multiple species, sample sizes, size ranges, and % non-empty stomachs are reported for each species in the order listed. Details were pooled for all studies that included data from multiple sites. For sharks, sizes are given in centimetres as total length unless otherwise specified (PCL = precaudal length, LPC = length to caudal peduncle). For all rays except *Glaucostegus typus*, disc width is reported. Any characteristic that was unspecified within a study is denoted with UNSP.

Shark or ray	Study type	Study purpose	Species included	Life stages	Sample size by species	Size ranges or mean size (cm)	Gastric lavage efficiency (%)	Tube size (mm)	Main prey types recovered from field study or prey fed in captivity	How was recovery or survival assessed?	Reference
shark	captive	gastric evacuation	*Carcharhinus plumbeus*	juvenile	18	43-71	UNSP	UNSP	crab, menhaden	killed afterward	Medved, R. 1985
ray	captive	gastric evacuation	*Raja erinacea*	UNSP	UNSP	33-51	UNSP	3	polychaetes, crustaceans, sand lance, bivalves	not assessed	Nelson & Ross, 1992
ray	captive	gastric evacuation	*Raja erinacea*	UNSP	UNSP	33-51	UNSP	3	polychaetes, krill, sand lance, bivalves	monitored in captivity	Nelson & Ross, 1995
shark	captive	gastric evacuation	*Sphyrna lewini*	juvenile	64	50-60	UNSP	UNSP	herring	monitored in captivity	Bush & Holland, 2002
shark	field	diet	*Notorynchus cepedianus*	subadult, adult	336	150–290	54	30	sharks, teleosts, rays, and mammals	not assessed	Barnett et al. 2010a

shark	field	diet with DNA verification, efficiency	*Notorynchus cepedianus*	subadult, adult	100	150–290	50	30	sharks, teleosts, rays, and mammals	tag-recapture, acoustic tracking	Barnett et al. 2010b
ray	field	diet	*Glaucostegus typus, Himantura fai, Himantura uarnak, Pastinachus atrus, Himantura astra / toshi*	juvenile, adult	74, 46, 20, 10, 8	UNSP	69,80,69, 60,75	20	crustaceans, polychaetes for *P. atrus* only	not assessed	Vaudo & Heithaus, 2011
ray	field	diet	*Aetobatus narinari*	juvenile, adult	18	99-170	78	UNSP	bivalves	not assessed	Ajemian et al. 2012
shark	field	diet	*Squalus acanthias, Mustelus antarcticus*	juvenile, subadult, adult	139, 136	25-73, 60-140	55, 92	UNSP	teleosts, cephalopods, crustaceans	not assessed	Yick et al. 2012
shark	field	efficiency	*Squalus acanthias*	juvenile, adult	45	84	89	20-37	mixed invertebrates, teleosts	killed afterward	Bangley et al. 2013
shark	captive	gastric evacuation	*Squalus acanthias*	adult	15	98	UNSP	37	menhaden	monitored in captivity	Bangley et al. 2014
ray	field	efficiency	*Urogymnus asperrimus*	juvenile	55	43-81	95	14.4	annelids, crustaceans	visual inspection after release	Elston et al. 2015
ray	captive	gastric evacuation	*Leucoraja eglanteria*	subadult, adult	77	57-73	UNSP	no tube used	sand lance	not assessed	Stehlik et al. 2015

shark	field	diet	*Carcharhinus amblyrhynchos, Carcharhinus melanopterus, Triaenodon obesus*	adult	31, 45, 31	68-158	32, 58, 29	20	teleosts	not assessed	Frisch et al. 2016
ray	field	diet	*Urobatis jamaicensis*	juvenile, adult	117	18	77	10	polychaetes, prawns	visual inspection after release	O'Shea et al. 2018
shark	field	diet	*Galeocerdo cuvier*	YOY	UNSP	UNSP	UNSP	UNSP	birds, other contents not reported	not assessed	Drymon et al. 2019
shark	field	diet	*Carcharhinus melanopterus*	neonate, juvenile	274	29-47 LPC	62	25-38	UNSP	not assessed	Weideli et al. 2019
ray	field	diet	*Pastinachus ater, Urogymnus granulatus*	juvenile	50, 39	28-140	71, 78	14.4	bivalves, crustaceans	visual inspection after release	Elston et al. 2020
ray	field	diet	*Styracura schmardae, Hypanus americanus*	juvenile, adult	74	68, 67	64	10	crustaceans, annelids	not assessed	O'Shea et al. 2020
shark	captive	gastric evacuation	*Squalus acanthias*	adult	15	81-93	UNSP	50	sand lance	monitored in captivity	Stehlik et al. 2021
shark	field	diet	*Triakis semifasciata*	juvenile, adult	30	40-139	100	no tube used	annelids, mixed invertebrates, plant matter	not assessed	Cooper, A. 2022
ray	field	diet with DNA verification	*Aetobatus narinari*	YOY, juvenile, adult	61	59-187	82	9.5-15.8	bivalves	not assessed	Cahill et al. 2023

shark	field	diet	*Negaprion acutiden, Carcharhinus melanopterus*	juvenile	115, 188	55, 48 PCL	46, 79	25-38	teleosts	not assessed	Weideli et al. 2023
ray	field	diet, efficiency	*Glaucostegus typus, Himantura australis, Maculabatis toshi, Pastinachus ater*	neonate, YOY, juvenile	83, 47, 34, 63	30-115, 26-76, 18-35, 30-68	81, 80, 94, 71	4-8	crustaceans, polychaetes and molluscs for *P. ater only*	tag-recapture	current study

4.3.2 Field study

A total of 209 rays were sampled using gastric lavage, which included 43 from Blacksoil Creek and 166 from Lucinda (Table 4.2). Including recaptured rays, gastric lavage was used 243 times. Observed size ranges confirmed all rays to be juveniles. A broader size range of *H. australis* were caught at Blacksoil Creek (30-76 cm disc DW) than Lucinda (26-51 cm DW), while sizes of *M. toshi* were similar across sites, ranging from 18-35 cm DW overall. Gastric lavage efficiency was 83.3% for *H. australis* and 100% for *M. toshi* at Blacksoil Creek. For Lucinda, percentages were 71.4% for *P. ater*, 78.1% for *H. australis*, 81.8% for *M. toshi*, and 80.7% for *G. typus* (Table 4.2). Gastric lavage efficiency showed marginal variation due to species (Fisher's exact test, p = 0.051), while no differences were observed between sites (p = 0.1343). Across both sites, 31 samples were obtained from recaptured rays, including nine *H. australis,* one *M. toshi*, five *P. ater,* and sixteen *G. typus*. Notably, there were two *H. australis* individuals for which three samples were obtained over time. The first, which was captured at Blacksoil Creek, was recaptured twice within twelve weeks (~four weeks between attempts). The other was caught three times at Lucinda, where ~30 days passed between attempts.

Seven recaptured rays (six *G. typus,* one *M. toshi*) shed their marker tags over the study period, which was evident by scar tissues on the spiracle or dorsal fin where the tag was fitted. Days between recaptures were not calculated for these individuals. Recapture rates were unknown for *M. toshi*, since most individuals were too small to be tagged. Only one recapture at Blacksoil Creek was recorded with uncertainty, based on scar tissue on its disc from tissue sampling. Excluding these individuals, recaptures of *G. typus*, *H. australis*, and *P. ater* provided evidence of short and longer-term survival after handling. Recapture rates for each species at Lucinda were 33.8, 19.2, and 23.4%, respectively, although only 9.5% of *H.*

australis were recaptured at Blacksoil Creek (Table 4.2). It was also common for individuals to be recaptured more than once (seven *G. typus* and one *H. australis* at Lucinda, one *H. australis* at Blacksoil Creek).

Although 23 *G. typus* were recaptured at Lucinda, the number of days between captures was only calculated for 17 rays due to tag loss (Figure 4.3). Recaptures ranged from 1-67 days following gastric lavage, with a mean of 29.1 ± 23.3 SD. For *P. ater* (n = 15), recaptures occurred from 1-71 days (mean = 23.1 ± 16.2 SD). Across both sites, recaptures were less frequent for *H. australis* (n = 7) and spanned a highly variable range of 22-533 days (mean = 157 ± 176.5 SD). Visual assessments did not reveal any rays with notable decreases in body condition, extended abdominal cavity, bruising, or abnormal colourations or markings. The exception to this was that some rays recaptured within 1-2 days had lingering pink colouration on the underside of the disc, which could be an indicator of stress.

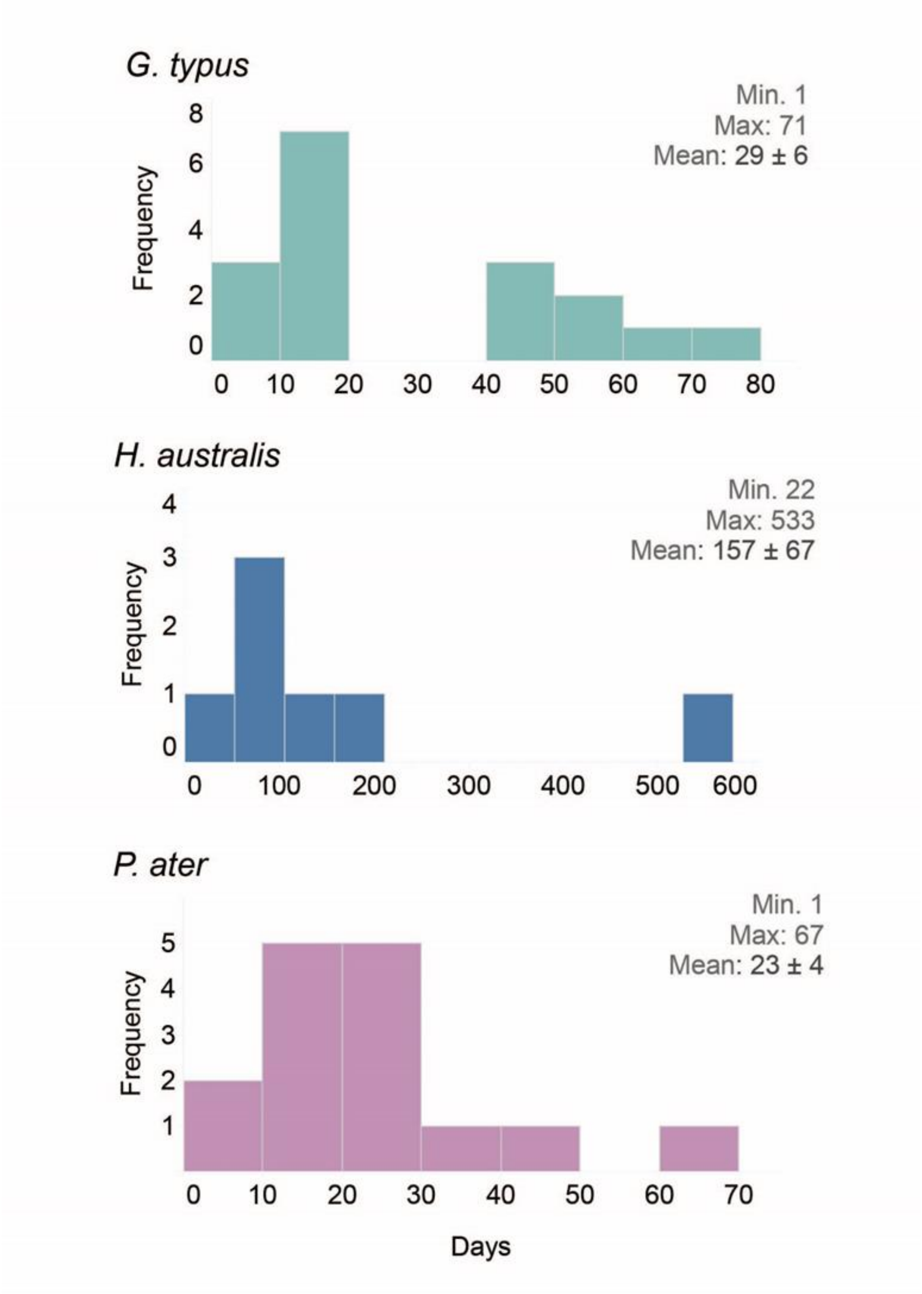

Figure 4.3. Histogram illustrating the number of days that passed between first and last recaptures of *G. typus*, *H. australis*, and *P. ater*.

Table 4.2. Gastric lavage summary for *Himantura australis, Maculabatis. toshi, Pastinachus ater,* and *Glaucostegus typus* caught at Blacksoil Creek and Lucinda. From the 2024 dataset, it was known that at least 26 *G. typus* were sampled since stomach content samples were obtained. The "-" denotes that this the number of flushes resulting in empty stomachs was unknown and gastric lavage efficiency was not calculated. Recapture rate refers to the percent of the total that were recaptured over the study. This measure was omitted from *M. toshi*, since most individuals were too small to be given a spiracle marker tag.

Site	Species	No. rays sampled by gastric lavage (excluding recaptures)	No. rays sampled by gastric lavage (including recaptures)	No. non-empty stomachs (including recaptures)	Gastric lavage efficiency (%)	No. recaptured rays	No. samples obtained from recaptured rays	Recapture rate (%)	Mean size ± SE (cm)	Size range (cm)
Blacksoil Creek	*H. australis*	21	24	20	83.3	2	3	9.5	49.8 ± 3.6	30-76
	M. toshi	22	23	23	100.0	1	1	-	24.8 ± 0.7	20-35
Lucinda	*H. australis*	26	32	25	78.1	5	6	19.2	37.9 ± 1.3	26-51
	M. toshi	11	11	9	81.8	0	0	-	25.7 ± 1.3	18-34
	P. ater	64	70	50	71.4	15	5	23.4	39.5 ± 0.6	30-68
	G. typus (2022-2023)	48	57	46	80.7	23	16	33.8	45.9 ± 1.0	30-115
	G. typus (2024)	17	26	-	-					

4.4 Discussion

4.4.1 Trends in gastric lavage use

Gastric lavage (stomach flushing) has long been established as an alternative to lethal stomach dissection for collecting stomach contents of marine vertebrates including fish (Kamler & Pope 2001), sea turtles (Forbes & Limpus 1993), and marine mammals (Antonelis Jr et al. 1987). Notably, only 23 published studies have used this technique on elasmobranchs, and its use has only modestly increased since 1985, despite growing demands for non-lethal SCA. However, some trends emerge when summarising its use across studies. Gastric lavage has been predominantly used on smaller-bodied sharks or rays, which may be because it is challenging or impossible to perform on animals that cannot be boarded onto a vessel or manually lifted and positioned over a collection tray. Notably, *N. cepedianus* is the largest species for which gastric lavage has been used (maximum 296 cm TL), which were brought onto a vessel for sampling (Barnett et al. 2010a, Barnett et al. 2010b). No studies have reported flushing larger animals while in the water and restrained to the side of a vessel.

Although not explicitly mentioned, there may also be concerns about stomach flushing causing internal damage (particularly for developing individuals), which may result in low numbers of studies on neonates and young-of-year life stages. However, elasmobranchs have robust stomachs that can even be inverted and pushed through their mouths (Cortés & Gruber 1990, Brunnschweiler et al. 2005). Anecdotal reports have also revealed dissected sharks with several stingray barbs puncturing their stomachs, which further suggests their resilience to internal damage (M. Braccini, personal communication, A. Barnett, communication with several fisherman). Although shark and ray morphology appears well suited for gastric lavage, species physiology and behaviour must also be considered when assessing its use. For example, it may not be suitable for species that are highly vulnerable to capture and handling stress, such as hammerhead sharks (Sphyrnidae) (Gallagher et al. 2014, Jerome et al. 2018).

4.4.2 Factors influencing gastric lavage efficiency

Gastric lavage seems to be an effective method of extracting stomach contents of sharks and rays, with success rates often exceeding 50% (Table 4.1). However, sample sizes varied considerably, which may affect our ability to generalise findings across studies. One notable pattern was that gastric lavage was more successful at extracting stomach contents from rays than sharks. Results of our field study coincided with this result, in which efficiency was high for all four ray species. Rates were comparable to studies that used similar methodologies on juvenile *U. asperrimus* (95%), *P. ater* (71%), and *U. granulatus* (78%) (Elston et al. 2015, Elston et al. 2020). One reason for higher success in rays may be related to feeding frequency. Stingrays are known to be continuous feeders (Gilliam & Sullivan 1993, Jacobsen & Bennett 2013), which may be because their prey are easier to acquire, being predominantly benthic and slow-moving. In contrast, larger sharks that target faster-moving pelagic prey may feed less frequently due to lower encounter and catchability (Wetherbee et al. 2004). Another factor is that sharks, particularly species like sevengill sharks and tiger sharks, have been observed to regurgitate or 'evert' their stomachs when hooked, which could result in empty stomachs (Simpfendorfer et al. 2001b, Barnett et al. 2010b). However, this limitation is not limited to non-lethal methods, since high rates of empty stomachs are also common in stomach dissections (Bethea et al. 2004, Bethea et al. 2006).

Variable success was likely driven by several other factors that are unique to the context of each study. For instance, the likelihood of obtaining stomach contents may depend on differences in stomach morphologies (Waters et al. 2004) or animal size (Cailteux et al.

1990, Bangley et al. 2013, Weideli et al. 2019). Additionally, for animals with broad diets, prey types with specific morphologies may be more easily dislodged from the stomach than others. For example, Cahill et al. (2023) admitted there was a higher dominance of gastropods in the stomachs of *A. narinari* caught by commercial fisheries (Serrano-Flores et al. 2019) than those sampled by gastric lavage, likely because these items were not as easily extracted during flushing. Success may also depend on if sampling corresponds to times when feeding is most likely to occur. For example, many reef sharks exhibit crepuscular hunting behaviours, so sampling during the day could result in over-digested prey or empty stomachs (Hammerschlag et al. 2017). In our study, we observed that rays collected early during the rising tides had more freshly consumed prey in their stomachs, since this was when individuals moved into the upper intertidal flats to feed.

Studies also varied by equipment (e.g. flexible tubing vs. PVC pipe) and flushing techniques. When optimising protocols for our field study, a major consideration was selecting appropriately sized tubes relative to the size of the animal. Bangley et al. (2013) found that differences between mouth width and tube diameter had the greatest impact on gastric lavage efficiency and recommended that the tube should be no more than 10–20 mm smaller than the mouth diameter. Methods by Elston et al. (2015) described extracting stomach contents from *U. asperrimus* (43-81 cm DW) with a 14.4 mm tube. A study by Vaudo and Heithaus (2011) also performed gastric lavage on *G. typus*, *H. australis* (prev. known as *H. uarnak*), *M. toshi, P. ater*, with a 20 mm diameter tube. As most individuals included here were smaller than in previous studies, both tube sizes would have been unsuitably large, particularly for young-of-year *M. toshi* (generally <25 cm DW) and *G. typus* (TL <50 cm TL). Therefore, we trialled a range of tube diameters (4, 6, and 8 mm) and established guidelines for which sizes were most appropriate for different size classes. This optimisation procedure also done by Cahill et al. (2023) on *A. narinari* and by Weideli et al. (2019) on early developmental stages of *C. melanopterus*.

Relationships between tube size and lavage efficiency were not tested experimentally in the field study, but early attempts seemed to indicate higher success was achieved with narrower tubes, which may prevent the oesophagus from being completely obstructed during flushing. Water pressure also had to be adjusted to avoid overexpanding the stomach. Flow rates varied based on tube size, so these were manually adjusted before each gastric lavage attempt. Although it was normal for the abdomen to expand during flushing, expansion would subside once the tube was removed or after excess water and trapped air were massaged from the abdomen towards the cloaca. There were no visual indicators of internal damage, although this could have only been verified by dissecting individuals directly following lavage (Bangley et al. 2013).

Gastric lavage can be effective for obtaining stomach contents, although some additional limitations exist that likely inhibit wider adoption by researchers. A well-voiced concern is that not all items may be evacuated from the gut, leading to underestimations of the total prey consumed or erred estimates of nutritional contributions. Some studies addressed this concern by dissecting a subsample of individuals after flushing (Ajemian et al. 2012, Stehlik et al. 2015, Frisch et al. 2016, Cooper 2022). As each of these confirmed that stomachs were effectively emptied, results would not be expected to vary between gastric lavage and stomach dissection. Although skipping this step means we cannot fully eliminate these assumptions, killing a subset of individuals in every study may not be desirable or practical. Although gastric lavage has been performed on relatively few species overall, these data can still be compared to stomach dissection studies to validate its efficiency. For instance, Barnett et al. (2010a) found that gastric lavage was similarly effective as stomach dissection for *N. cepedianus*. Furthermore, results of our field study were comparable to the successes obtained using stomach dissections on similar species (O'Shea et al. 2013). Another limitation for any method of SCA is that overly digested stomach contents can influence accurate identification and counts of individual prey items, and potentially unemptied stomachs and unidentifiable materials create uncertainty for common dietary metrics based on prey abundance, volume, or weight. However, since there are several issues when basing dietary habits on volume or weight (Baker et al. 2014, Amundsen & Sánchez-Hernández 2019), more robust metrics like frequency of occurrence are now being advocated to generalise diets (Baker et al. 2024). For species such as benthic rays that consume various hard-shelled and soft-bodied prey, items that are digested more quickly could be more poorly represented in the diets.

4.4.3 Survival

Verifying survival after invasive sampling procedures is important for developing best practice protocols and justifying methods are truly non-lethal. Captivity studies provided the most information on animal wellbeing and survival after handling, since behaviours and body condition of animals can be visually monitored for prolonged periods. No ill effects from gastric lavage were reported on captive animals, and in some cases, animals were re-used or released following a recovery period of days or weeks (Nelson & Ross 1995, Bangley & Rulifson 2014). Verifying survival in the field is challenging, since most animals can only be visually observed for a short window of time. Subsequently, field studies have either not reported any information on recovery or survival or have only done so immediately after release (Ajemian et al. 2012, Elston et al. 2015, Elston et al. 2020, O'Shea et al. 2020). To our knowledge, only one field study has assessed longer-term survival following gastric lavage by implementing a combination of tag-recapture and acoustic tracking methods (Barnett et al.

2010b). In this study, *N. cepedianus* were recaptured over a span of 11-715 days, and all 20 sharks fitted with acoustic tags were detected within the array up to 18 months later, which were both strong indicators of high survival.

Tag-recaptures from our field study also provided evidence of survival for juvenile rays across various time frames post-release. Most recaptures occurred within days or weeks of the first capture, except for one *H. australis* that was recaptured 533 days later. There was one case where a tagged juvenile *G. typus* was reported dead six weeks after capture, but with the amount of time that passed, there was no conclusive evidence that this event was linked to handling. No other mortality events are known to have occurred. Shark recaptures are often <20% (Dudgeon et al. 2015), or even as low as %5 (Kohler & Turner 2001). However, similar recapture rates have been reported for ray species such as the blue-spotted lagoon ray, *Taeniura lymma* (McIvor et al. 2024) which match our results for *H. australis*. Furthermore, other studies report similar results as our recapture rates for *G. typus* (33.8%) and *P. ater* (23.4%). For example, Schwanck et al. (2020) reported 31% of southern stingray, *Hypanus americanus,* were recaptured in sand flats, cays, and creeks, and O'Shea et al. (2021) reported 51% for juvenile Caribbean whiptail stingrays, *Styracura schmardae,* within tidal creek nurseries. Thus, relatively high recapture success in this field study may be attributed to the predictable movements of juvenile rays across intertidal flats over repeated tidal cycles (Crook 2020, Martins et al. 2020a), which increased the probability of encountering tagged individuals within the study area.

The main limitation of tag-recapture data is assuming the survival of recaptured animals is representative of animals that are never recaptured throughout a study. Additionally, there may be issues with tag retention (Pine et al. 2012). Tag loss was more common for *G. typus* than other species, since external tags were more easily shed from the dorsal fin than from the spiracles. Although recaptured individuals could still be identified by scar tissue on the dorsal fin, it was impossible to estimate how many days had passed since initial capture, which reduced our ability to quantify survival over longer time frames.

4.5 Conclusions

Understanding a predator's dietary composition is fundamental for evaluating its influence on food web dynamics and ecosystem function and strengthens our ability to identify and protect essential habitats based on resource availability (Barnett et al. 2013, Heupel et al. 2014, Barnett et al. 2017). Gastric lavage is an effective approach for extracting stomach contents from a variety of shark and ray species but remains underutilised in field research, and several methodological refinements warrant further investigation. The current study demonstrates several adaptable features that make this technique particularly effective for juvenile rays, including the use of smaller diameter tubes (4-8 mm) and a valve to control water pressure based on animal size, which was critical for successfully sampling neonate rays while minimising stress and potential injury. These methodological refinements provide a framework for expanding gastric lavage across different size classes and species, although additional research is still needed to adapt the necessary protocols (e.g. tube size, water pressure, handling techniques) for larger sharks, where specimen handling presents unique challenges.

Despite gastric lavage being acclaimed as non-lethal, there is little evidence of recovery and survival for wild-caught animals, aside from verifying the condition of individuals at the time of release. A paucity of data from field-based studies results in survival being almost exclusively based on captive studies. Where possible, future studies should consider methods that integrate survival data into their research objectives. Monitoring animals over time using active tracking, acoustic arrays, or satellite positioning tags are all appropriate methods for verifying post-release survival but may not be practical due to cost, time constraints, or the size of the target species. Although general recapture rates of elasmobranchs are generally low, tag-recapture represents a practical method and may be particularly suitable for specific contexts, such as juvenile animals within defined nursery grounds (as in the field study) or species with predictable movement or aggregation patterns. Future studies could also reduce tag loss by using internal tags (e.g. Passive Integrated Transponder (PIT) tags, which would allow for more precise tracking of individuals over extended periods. Furthermore, tag-recapture can be supplemented by other methods such as electronic tracking, photo ID, or genetics (Dudgeon et al. 2012, McIvor et al. 2024). For smaller species, studies also consider including a survival component in captivity. Validating survival following gastric lavage (or any non-lethal handling procedure) will ensure that protocols comply with ethical standards and ensure the best outcomes for research and conservation.

5 Chapter 5 – Dietary habits of rays in intertidal sand flats: an assessment of trophic ecology, foraging strategies, and prey availability

5.1 Introduction

Juvenile sharks and rays are among the larger mesopredatory taxa that occupy intertidal zones, where they benefit from a combination of abundant feeding opportunities, refuge from predators, and favourable abiotic conditions (Martins et al. 2018, Heupel et al. 2019, Whitfield 2020, Leurs et al. 2023). Rays, in particular, are well adapted to feeding on the soft sediments of tidal sand and mud flats (Ebert & Cowley 2003). A reliance on intertidal areas as feeding grounds and nurseries (Leurs et al. 2023) makes it important to understand which prey resources and trophic pathways support populations and overall habitat quality (Martins et al. 2018).

Although most benthic rays consume a variety of invertebrates such as crustaceans, gastropods, bivalves, and annelids (Flowers et al. 2021), the relative importance of different prey types within the diet can vary considerably across species (Vaudo & Heithaus 2011, Yick et al. 2011, Pardo et al. 2015, de Sousa Rangel et al. 2019). Dietary resource partitioning occurs through numerous pathways, which ultimately promotes species coexistence by reducing overlap among competitors (Schoener 1974, Ross 1986, Kinney et al. 2011). For example, when comparing diets among four species of skates, two species consumed greater proportions of benthic prey, indicating that they may be able to forage more efficiently across deeper sediment gradients than species that feed on epibenthic prey (Platell et al. 1998). Differences in jaw morphologies also confer different competitive advantages when foraging, with some species being more adept at crushing hard-shelled prey (Pardo et al. 2015). Dietary niche separation is also common between size classes, in which increases in body size are generally associated with transitions to larger, higher-energy prey and ontogenetic habitat shifts (Barbini & Lucifora 2012, Elston et al. 2020, Yogi et al. 2023). In contrast, other studies have found high degrees of dietary and trophic overlap within ray communities (Vaudo & Heithaus 2011, O'Shea et al. 2013). In these contexts, prey selection may be minimally influenced by limited resources (Croxall et al. 1999) or individuals use alternative tactics to reduce competition, such as spatial or temporal habitat partitioning (White & Potter 2004, Ajemian & Powers 2016, Lear et al. 2021).

Adding further complexity to these patterns, prey selection can also vary in response to prey availability. While rays are often generalist predators that feed opportunistically on highly available prey types (Dale et al. 2011, Flores-Ortega 2011, Lim et al. 2019), other species exhibit specialist feeding strategies by selectively targeting specific prey taxa regardless of their relative abundances (Gray et al. 1997, Serrano-Flores et al. 2019). In some cases, species also shift their diets between generalist and specialist strategies due to seasonal fluctuations in prey availability, among other environmental factors (Ajemian & Powers 2012). Notably, while prey availability has been used to interpret spatio-temporal habitat use of rays (Tilley 2011, Vaudo & Heithaus 2013) or to estimate their impacts on benthic taxa (Ajemian et al. 2012, Ajemian & Powers 2013), few studies have included prey availability when assessing dietary composition (Pardo et al. 2015, Elston et al. 2017, O'Shea et al. 2018).

Examining predator-prey relationships for mobile marine predators can be challenging, particularly if the spatial extent of core foraging areas is uncertain or if they have highly generalist diets (Braccini et al. 2005, Barnett et al. 2017). However, juvenile rays present an ideal group for investigating these relationships due to their benthic feeding habits and their relatively limited movements in intertidal zones (Cartamil et al. 2003, Vaudo & Heithaus 2012). Limited knowledge of species' diets, particularly during early life stages, translates to a poor understanding of which prey resources support their abundances in essential habitats (Grubbs 2010, Navia et al. 2016). Moreover, studying predator-prey dynamics is vital for elucidating the various mechanisms that facilitate species coexistence in these areas.

In this chapter, I used stomach content analysis (SCA) and stable isotope analysis (SIA) to describe the trophic ecology of four juvenile ray species: Australian whipray, *Himantura australis*, giant shovelnose ray, *Glaucostegus typus*, brown whipray, *Maculabatis toshi*, and cowtail stingray, *Pastinachus ater*. Specific aims were to compare the dietary composition, feeding strategies, and trophic overlap among species. Furthermore, I used spatio-temporal prey availability to contextualise prey selection and fine-scale foraging behaviours of rays within the study area.

5.2 Methods

5.2.1 Study site

Lucinda Beach, N QLD (-18.5327° S, 146.3347° E) is an extensive intertidal flat (expanding >1 km seaward during lowest astronomical tide) located on the border of the wet and dry tropic regions (Figure 5.1). A full description of the site is provided by Crook (2020), which has been adapted here. The tidal regime follows a mixed semi-diurnal cycle with a maximum amplitude of 4 m. Large swaths of the sand flat are exposed at low tides, although some shallow channels between sandbars remain submerged (<1 m depth). During rising tides, middle flat areas extending to the beach are inundated first, followed by the semi-enclosed embayment on the north end of the flat that becomes fully inundated at high tides.

Within the 1 km^2 study area, sediment composition is primarily coarse sand, but there are also finer sand and muddy substrates associated with the mangrove forest in the upper intertidal bay. Aside from the mangroves, the sand flat is primarily unvegetated, except for sparse clumps of seagrass and filamentous macroalgae. Ray feeding pits are present in high densities at the northern end and are more patchily distributed else ware within the sand flat boundary. The most common ray species at the site are *H. australis, P. ater*, and *G. typus*, with lesser abundances of *M. toshi,* and mangrove whipray, *U. granulatus*.

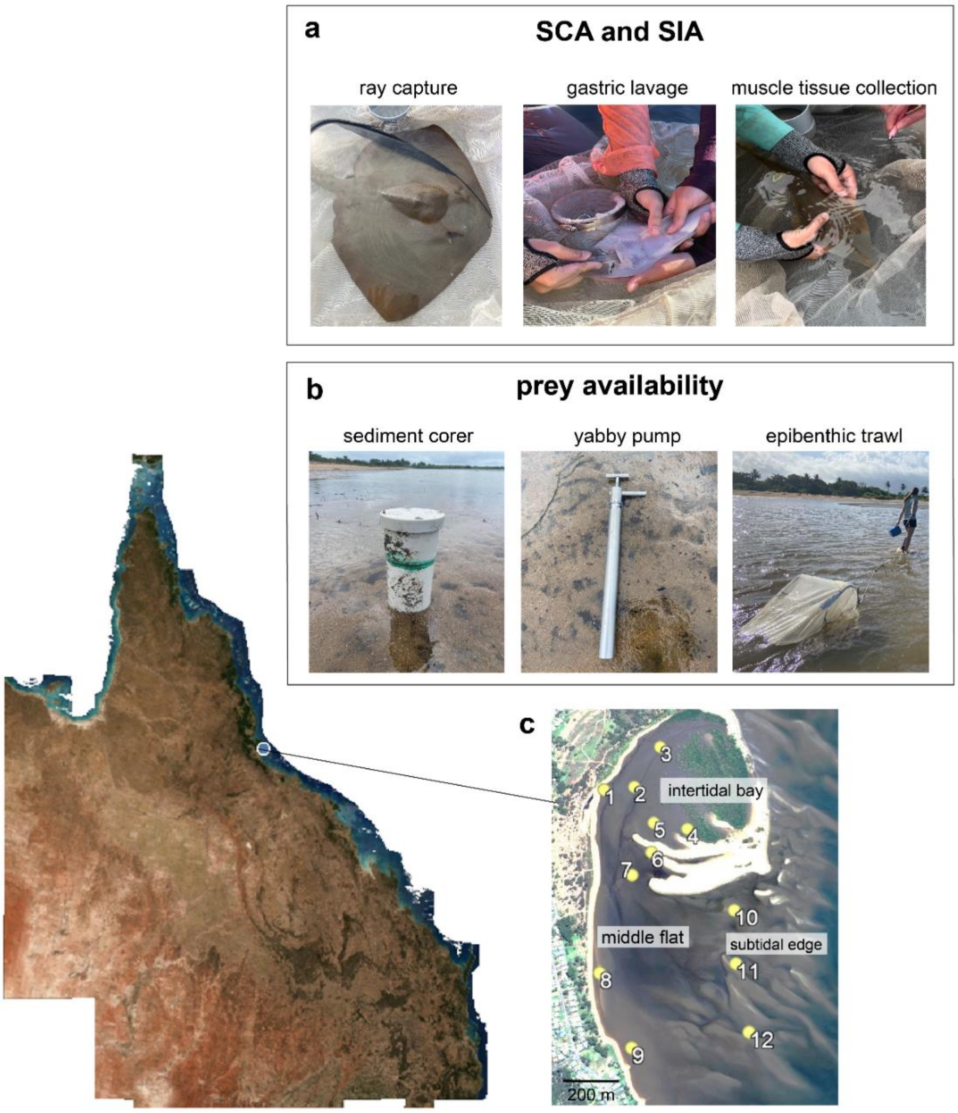

Figure 5.1. Data collection took place at Lucinda, North Queensland. Rays were captured for stomach content analysis (SCA) and stable isotope analysis (SIA) (a). Benthic prey availability was also sampled using three methods (b). The satellite overview map shows the study area at low tide, with numbered points indicating the geographic locations of the twelve sites where prey availability was surveyed (c).

5.2.2 Data collection

5.2.2.1 Gastric lavage and tissue collection

Juvenile rays were captured at Lucinda from Nov 2022 to Apr 2024, and gastric lavage was used to obtain stomach contents following previously protocols (see Chapter 4 Section 4.2.2 for full description) (Figure 5.1a). For stable isotope analysis, a 5 mm diameter biopsy of muscle tissue was collected from the bottom half of the pectoral fin of each captured ray and frozen until processing in the laboratory. All rays were released with a spiracle marker tag, and all recaptures over the course of the study were recorded. Gastric lavage was repeated on recaptured rays if at least three days had passed since initial capture, and these samples were included for SCA.

5.2.2.2 Prey availability

Benthic communities were sampled three times during the dry season (Sept to Nov 2023) and twice during the following wet season (Mar to Apr 2024). Twelve sampling sites were selected across the tidal gradient that represented different microhabitat features (Figure 5.1c, Table 5.1). Most sites were concentrated within or around the upper intertidal bay, since these were known to overlap with core foraging areas of rays (Crook et al. 2022). Other sites were chosen on the lower intertidal flat areas on the middle flat and along the subtidal edges during standard low tides (~1 m above lowest astronomical tide). Environmental characteristics were recorded for each site, including sediment type (coarse sand or fine sand/mud), tidal inundation section (subtidal edge, middle flat, or inside the upper intertidal bay), distance from nearest shoreline (m), and distance from nearest mangrove patch (m).

Rays feed along the surface on the benthos to sediment depths of 15-20 cm (D'Andrea et al. 2004, Tamaki et al. 2020). Consequently, three gear types were used to target benthic macrofauna across different depth ranges (Figure 5.1b). Two methods were used to sample infaunal prey, including a sediment corer (dimensions of 20 cm deep × 10 cm diameter) and bait (yabby) pump (60 cm deep × 5 cm diameter). At each site, five replicates were collected within a 5 × 5 m, which were pooled to represent one sample. Samples were collected from the sediment corer by pushing the device into the ground to 20 cm and removing the sediments. The bait pump was operated by pushing the device into the ground and using suction from the handle to remove sediments. Due to differences in sediment compactness, 2-3 attempts were generally required to reach 60 cm in depth. For the sediment core, the total amount of filtered sediment was calculated from the volume of a cylinder multiplied by five cores, yielding a total volume of 7.85 m^3. Sediment volumes were not calculated for the bait pump since sediment collapse between successive pumps created inconsistencies in the exact sediment volume across replicates.

An epibenthic beam trawl was also used to target surface-associated and free-swimming macrofauna while the flat was shallowly inundated. For the trawl, sites were sampled using two 20 m parallel tows, which were completed during rising tides in depths up to 0.5 m. As the trawl was pulled, it stirred up the top layers of sediment with a weighted chain and pushed sediments into a 1 mm mesh-lined funnel. Sampling effort was quantified by the drag distance (40 m) multiplied by trawl width (0.65 m), resulting in a swept area of 26 m^2 per tow.

Sediments collected from all methods were filtered through 1 mm mesh screen, which matched the mesh size for collecting stomach contents of rays for dietary analysis. All specimens were retained for later identification in the laboratory.

Table 5.1. Physical and geographic characteristics of the twelve sites where benthic prey were sampled at Lucinda.

Site	Tidal section	Primary substrate	Distance from nearest mangrove stand (m)	Distance from shore (m)	Latitude	Longitude
1	upper intertidal bay	coarse sand	230	0	-18.530831	146.336556
2	upper intertidal bay	fine sand	130	105	-18.529328	146.373019
3	upper intertidal bay	fine sand	0	75	-18.530906	146.337667
4	upper intertidal bay	fine sand	0	30	-18.531931	146.340211
5	upper intertidal bay	coarse sand	105	45	-18.531831	146.338633
6	middle flat	coarse sand	150	5	-18.533103	146.338917
7	middle flat	coarse sand	245	90	-18.540164	146.339164
8	middle flat	fine sand	635	10	-18.537261	146.337247
9	middle flat	coarse sand	790	40	-18.539094	146.338056
10	subtidal edge	coarse sand	272	100	-18.534794	146.342094
11	subtidal edge	coarse sand	425	240	-18.536281	146.341442
12	subtidal edge	coarse sand	790	575	-18.538972	146.343881

5.2.3 Identification of stomach contents

To describe the full range of prey types found across diet samples, all prey items were viewed under a dissecting microscope and assigned to taxonomic categories. For SCA, heavily digested items that could not be identified were discarded. Due to high occurrences of crustacean prey across samples of all species, all crustacean taxa were identified to the lowest taxonomic resolution achievable. Most decapod crustaceans were identified to the family level, although some genus and species level delineations were possible, depending on intactness of the specimen and level of digestion. Amphipods and isopods were recorded at the ordinal level, while non-crustacean prey taxa in Class Polychaeta, Bivalvia, and Gastropoda were retained at Class resolution, since polychaetes could not be reliably identified based on their mouth parts or natural colouration, and molluscs were generally crushed or removed from their shells.

5.2.4 Processing of stable isotope samples

For stable isotope analysis (δ^{13}C and δ^{15}N), muscle tissue samples were used from rays caught in Oct-Dec 2022 and Apr-Oct 2023. No samples were collected between these periods, since heavy rains made visibility conditions unsuitable for ray capture. For *H. australis* and *P. ater*, samples were collected across both periods, while samples for *G. typus* and *M. toshi* were only available in the 2023 period. Muscle samples were dried in an oven at 60°C for 48 h and homogenized using a mortar and pestle. Lipid extraction was not conducted as it is generally not required for rays due to their muscle tissue having a low lipid content (Carlisle et al. 2017, Crook et al. 2019). After homogenising the tissue with a mortar and pestle, approximately 1.0 µg ± 0.1 of the tissue was weighed using a microbalance and encapsulated into tin capsules. Samples were analysed at the Davis UC Davis Stable Isotope Facility (USA) with a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ

Europa 20–20 isotope ratio mass spectrometer. Results are expressed as per mil (‰) deviations from standards with a precision of ± 0.1‰ (± SD) for both $\delta^{13}C$ and $\delta^{15}N$.

5.3 Statistical analysis

5.3.1 Cumulative prey curves and dietary composition

Cumulative prey curves were constructed for *H. australis*, *P. ater*, and *G. typus* to determine whether enough samples were collected to describe species diets (Oksanen et al. 2016). The curve describes the relationship between the number of stomachs sampled and the likelihood of encountering a new prey item. As the number of samples increases, a point is eventually reached where no new prey items would be expected with a bigger sample size (the asymptote). For the cumulative prey curves and for subsequent analyses, any classifications lower than family level were pooled to ensure consistent resolution and to facilitate comparisons with other dietary studies (White et al. 2004, Pardo et al. 2015, Elston et al. 2020).

Cumulative prey curves were run using the ‘specaccum’ function within the *vegan* package in R (Oksanen et al. 2016), and the order that samples were analysed was randomised 100 times (Elston et al. 2020). Two curves were constructed for each species that included 1) all prey categories (family level or higher) and 2) only frequently consumed prey categories (excluding prey with only one occurrence across the dataset). Due to low sample size of *M. toshi* (n = 9), it was assumed these data will not adequately describe the full diet, so this analysis was not conducted for this species. To quantitatively determine if the slope of each line reached an asymptote, the slope of the mean cumulative number of prey taxa in the final four stomach content samples was compared to a slope of zero using a Student’s t-test (Ebert & Cowley 2003, Bizzarro et al. 2007, Elston et al. 2020).

Frequency of occurrence (%F) was calculated for each species as the number of stomachs containing a particular prey category divided by the total stomachs containing prey. Numerical contributions were expressed using the prey-specific abundance (%Pi) for all prey categories that were present in >1 sample. Prey-specific abundance commonly represents the number of prey items of a given prey category per total number of prey items, but only in those rays with the given prey category in their stomachs (Amundsen & Sánchez-Hernández 2019). Although %Pi can provide unrepresentative data where digestion or mastication makes numerical abundances uncertain (Baker et al. 2024), this metric was considered appropriate for this study since most prey items were wholly intact or could be pieced together into whole animals. However, counts for polychaetes likely contained some margin of error, as the presence of multiple fragments may have resulted in some degree of overestimation. Thus, %Pi for polychaetes was reported while being mindful of this limitation. Although common in dietary analyses, measurements using mass or volume were omitted, as these are less robust metrics that can lead to false assumptions about the diet (Baker et al. 2014, Amundsen & Sánchez-Hernández 2019).

Feeding strategy plots were constructed using %F and %Pi (Amundsen et al. 1996, Amundsen & Sánchez-Hernández 2019). The position of each prey category along the x-axis indicates whether it was consumed by only a few individuals (farthest left) or by the whole predator population (farthest right). Additionally, positions along the y-axis indicate whether an item was consumed following a generalist (bottom quadrant) or specialist strategy (top quadrant).

5.3.2 Multi-variate analyses

PERMANOVA was used to test for dietary variability due to species, size (using disc width (DW) for all rays except for *G. typus*, which used total length (TL), and season (Jun-

Nov = dry, Dec-May = wet). For more details on sampling effort by month, see Appendix C, Figure C1). Prey occurrence data were used to construct a dissimilarity matrix, which are less sensitive to the various assumptions associated with numerical count data (Buckland et al. 2017). Only frequently consumed prey categories (>1 occurrence for any species) were included for analysis to reduce the effects of excess zeros in the model. If the PERMANOVA found a variable to be significant, pair-wise comparisons were made and p-values adjusted using Tukey's method. Non-metric multidimensional scaling (nMDS) was used to visualise dietary overlap among species. Environmental fitting ('*envfit'* function in the *vegan* package) was applied to correlate each prey category with the nMDS axes, with the direction of each vector indicating the association of each prey category with each species and length reflecting the strength of this relationship (Oksanen et al. 2016).

5.3.3 Stable isotope analysis

The trophic niche breadth of each species was summarised by calculating the Bayesian Standard Ellipse Area (SEA_B) and small-size corrected Standard Ellipse Area (SEAc) using the SIBER package (Jackson et al. 2011). From the posterior distributions of SEAs (SEA_B), the number of occurrences that the SEA for one species was larger than that of another was summarised and represented as a percentage. Niche size was considered significantly different if 95% of values were greater for one of the species. Additionally, the SEA overlap (proxy for trophic niche overlap) was also computed as the percentage of the total overlap between two SEA ellipses divided by the sum of the non-overlapping areas. Overlap values ranged from 0-100%, with higher values indicating greater overlap in trophic niche between two species. For *H. australis* and *P. ater*, niche size and overlap were also compared between Oct-Dec 2022 and Apr-Oct 2023 samples to assess potential seasonal variability.

5.3.4 *Prey availability*

Frequency of occurrence and abundance counts were calculated for each faunal category. Notably, trawl replicates often contained high abundances of teleosts, such as benthic fish (Gobiidae) and assortments of larval fish. Teleosts were excluded from all analyses since preliminary dietary analysis revealed they were not a frequently consumed prey category for any ray species and the variability introduced by their inclusion could mask differences for other invertebrates in the trawl surveys.

To standardise taxonomic resolution, invertebrates identified to genus or species resolution were assessed at the family level for further analysis, and broader taxonomic classifications (Class or Order) were retained where family level was not obtained. Site variability was compared by nMDS based on the summarised occurrences for each site (pooled across five sampling rounds and gear types). Presence-absences were used because volumetric densities from sediment cores were not directly comparable to swept areas from the trawl, and this also reduced variability introduced by spatio-temporal patchiness in invertebrate distributions. PERMANOVA was then used to identify the effects of site-associated environmental variables on invertebrate communities (Table 5.1). Models were run separately for each sampling method to account for differences in prey selectivity.

To examine spatial distributions of key prey species across sites, invertebrate densities were calculated for the sediment core by prey dividing abundances by sediment volume (individuals per m^3). For the trawl, densities were expressed in terms of the total swept area (individuals per m^2). Mean densities across sampling rounds were compared among sites for all items with %F >30 for any species. For ease of interpretation, densities were scaled by a factor of 100.

5.4 Results

5.4.1 Stomach content analysis

In total, 166 individual rays were sampled using gastric lavage (Table 5.2). There was little size variability between *H. australis* and *P. ater*, with mean DW sizes of 37.9 ± 1.3 cm and 39.5 ± 0.6 cm (± SD), respectively. All *M. toshi* were similar in size, with a mean DW of 25.7 ± 1.3 cm. Except for two *G. typus* individuals >1 m TL, most were <1 m with a mean TL of 45.9 ± 1.0 cm. In the cumulative prey curve calculations, no statistical asymptote was reached for *H. australis* ($p = 0.080$), *P. ater* ($p = 0.220$), or *G. typus* ($p = 0.220$) when all possible prey types were included, indicating that the number of samples may not be adequate to adequately describe their full diets (Figure 5.2). However, when excluding prey taxa with only single occurrences, all three species reached a statistical asymptote ($p < 0.001$ for all). Therefore, interpreting diets based on the frequently consumed prey categories was considered appropriate for the purposes of this study.

In total, 30 unique prey taxa were identified from the SCA (Appendix C, Figure C1). Diets of *H. australis* were characterised by decapod crustaceans in families Penaeidae (%F = 60%), Ogyrididae (48.0%), Portunidae (44.0%), and Ocypodidae (32.0%), and infrequent consumption of all other taxa; Figure 5.3a). These families were largely represented by single species, including the bay prawn, *Metapenaeus bennettae*, long-eyed shrimp, *Ogyrides delli*, juvenile blue swimmer crab, *Portunus armatus*, and ghost crab, *Ocypode cordimana* (Appendix C, Figure C1). The clustering of prey in the bottom half of the feeding strategy plot indicated that. *H. australis* acts as a generalist predator of crustacean prey.

For *M. toshi*, Penaeidae was the only category that occurred more than once in the diet (%F = 88.9), which consisted of *M. bennettae* and a few occurrences of endeavour prawn, *Metapenaeus endeavouri* (Figure 5.3b). Similarly, diets of *G. typus* were highly dominated by *M. bennettae* (%F = 89.2%), with high degrees of specialisation at the population level (%Pi = 79.2%) (Figure 5.3c). Other decapod crustaceans were also present in low abundance. Diets of *P. ater* were characterised by a greater consumption of non-crustacean prey (Figure 5.3d). Polychaetes were the dominant prey in terms of occurrence (%F = 85.7) and abundance (%Pi = 57.0%). Other common prey types were bivalves (%F = 32.7%), gastropods (32.7%), and penaeid prawns (30.6%).

PERMANOVA revealed significant differences in diet due to species, explaining 44% of the variability, but no significant patterns were detected by ray size (p = 0.796) or capture season (p = 0.224) (Table 5.3). Post-hoc analysis revealed dietary distinctions between all species pairs (p = 0.006) except for *G. typus* and *M. toshi* (p = 0.996). Congruently, species occupied distinct niches within the nMDS ordination space (Figure 5.4). Prey taxa that exerted the strongest influences on dietary separation included bivalves, gastropods, and polychaetes, as well as crustaceans across families Mictyridae, Ogyrididae, Penaeidae, and Portunidae

(Appendix C, Table C2). The wide spread of *P. ater* and *H. australis* samples reflected broader dietary niches than *M. toshi* and *G. typus*.

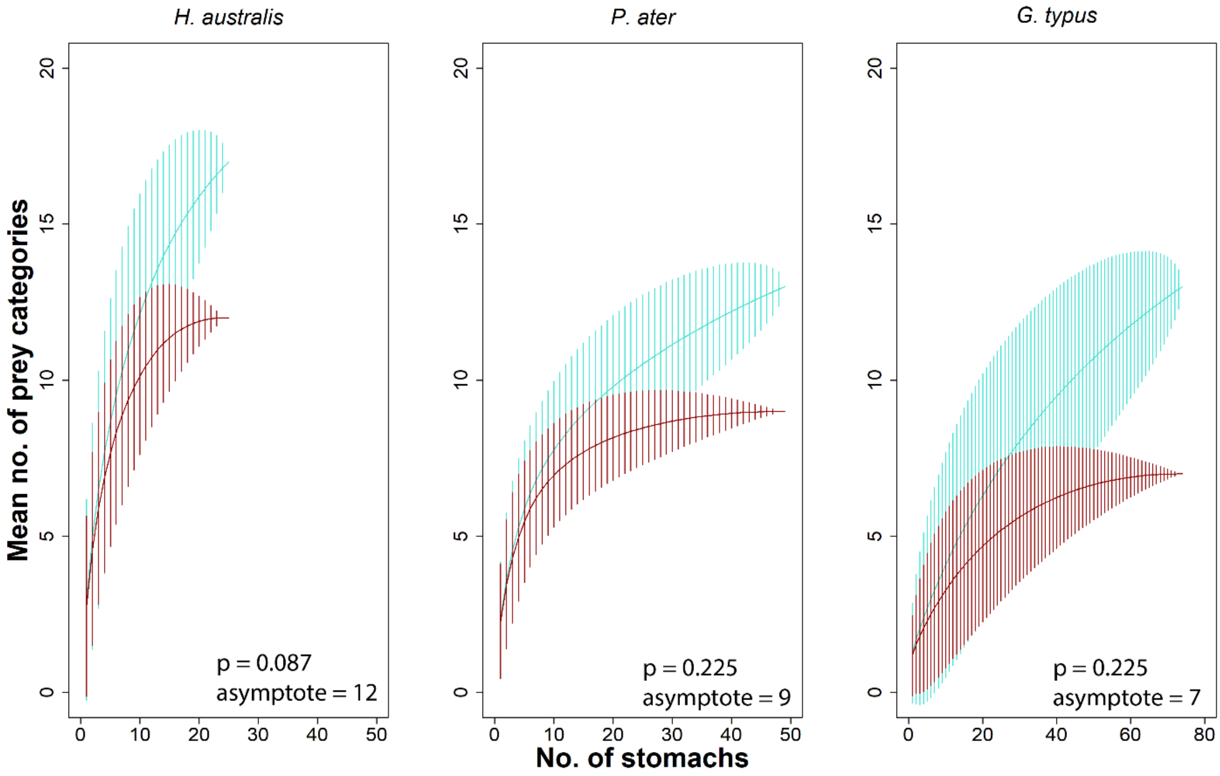

Figure 5.2. Cumulative prey curves for *Himantura australis*, *Pastinachus ater*, and *Glaucostegus typus*, showing the number of stomachs analysed against the mean number of prey categories. Each line represents a different resolution: turquoise = all prey taxa (included at family level or higher), red = frequently consumed resources (only prey taxa that occurred more than once). Error bars denote standard deviation surrounding the mean number of cumulative prey categories analysed after 100 randomisations. Asymptotes and p-values are given for the red prey curves.

Table 5.2. Summary of rays caught at Lucinda for stomach content analysis from 2022-2024. Mean sizes are accompanied by the standard error.

Species	No. rays sampled by gastric lavage	Total samples used for SCA	No. samples from recaptured rays	% non-empty stomachs	Mean size ± SE (cm)	Size range (cm)
H. australis	26	25	6	78.1	37.9 ± 1.3	26-51
M. toshi	11	9	0	81.8	25.7 ± 1.3	18-34
P. ater	64	50	5	71.4	39.5 ± 0.6	30-68
G. typus	65	74	16	80.7	45.9 ± 1.0	30-115

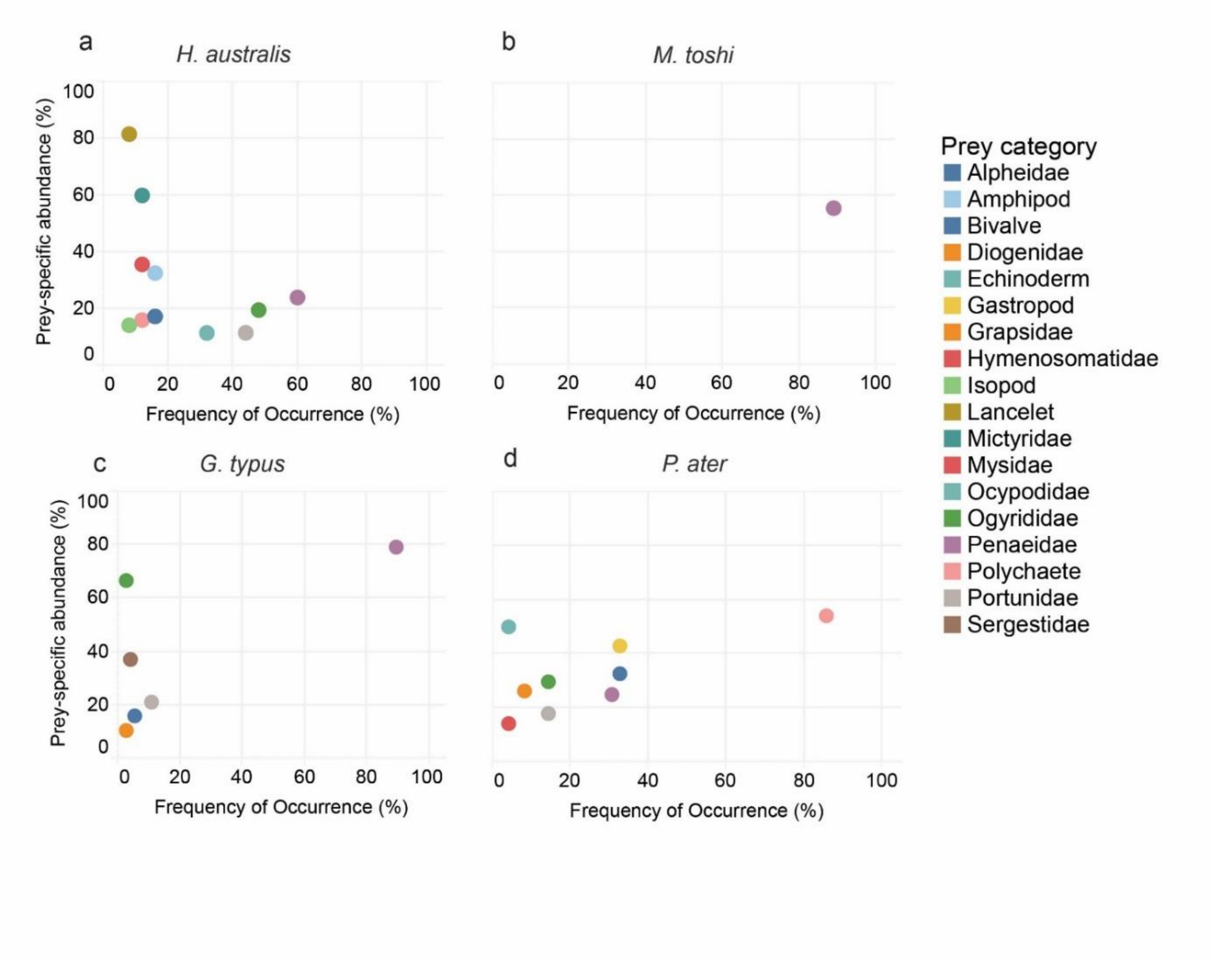

Figure 5.3. Feeding strategy plots for the four species of rays sampled at Lucinda (a-d). Frequency of occurrence (%F) was plotted against prey-specific abundance (%Pi) for all frequently consumed prey taxa (>1 occurrence for any species). All decapod crustaceans are depicted at the Family level, while all other taxa are shown at either Class or Order resolution.

Table 5.3. Results of the PERMANOVA model examining sources of variability in dietary composition from the stomach content analysis. Due to the significance of species in the model, post-hoc comparisons were made across all species pairs, with significance values corrected for multiple comparisons (denoted in bold).

Variable	F statistic	R^2	p-value
Species	27.67	0.36	**0.001**
Ray size	0.99	0.00	0.429
Season	1.27	0.01	0.228

Species pairs	F statistic	R^2	p-value (adj.)
G. typus vs H. australis	26.86	0.24	**0.006**
G. typus vs M. toshi	1.49	0.02	0.966
G. typus vs P. ater	80.90	0.42	**0.006**
H. australis vs M. toshi	4.71	0.14	**0.006**
H. australis vs P. ater	16.24	0.19	**0.006**
M. toshi vs P. ater	12.22	0.18	**0.006**

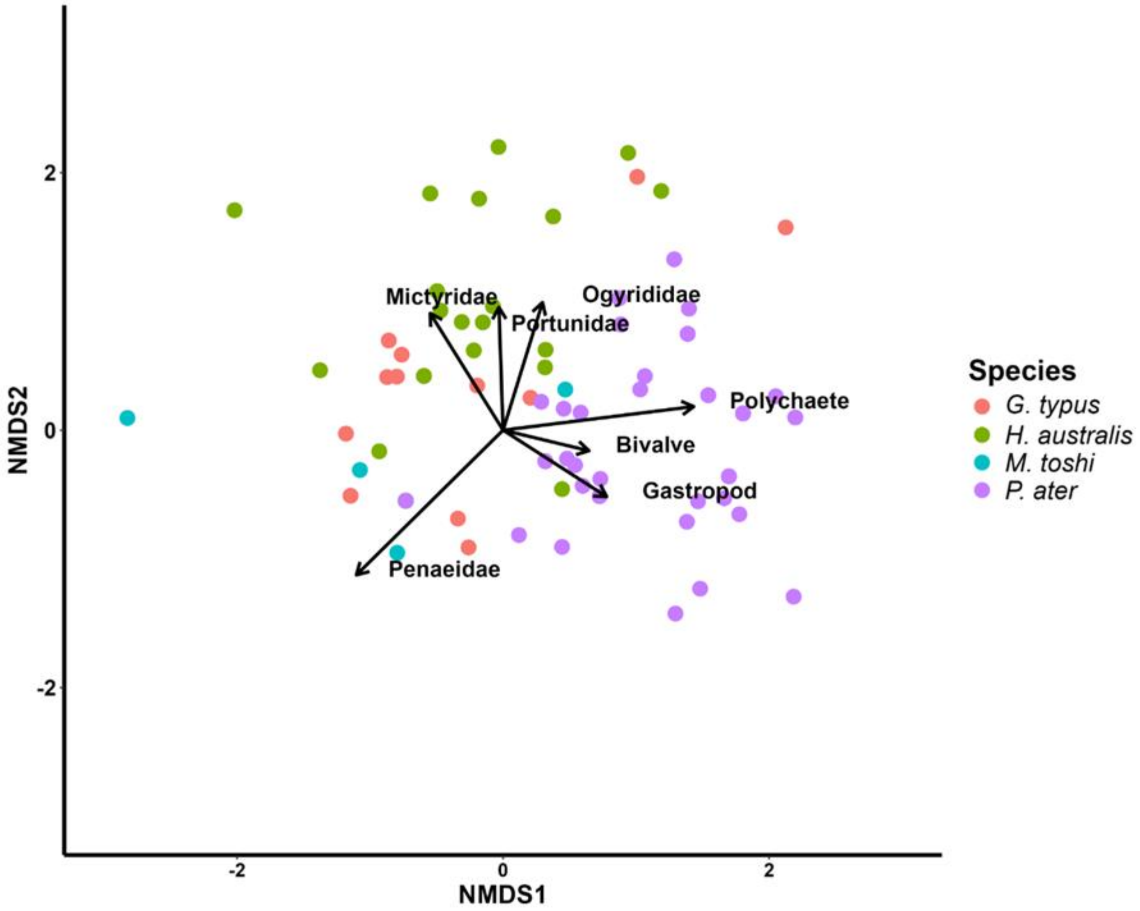

Figure 5.4. Non-metric multidimensional scaling (nMDS) ordination plot comparing diets of four ray species (stress = 0.0845). Vectors are shown for prey taxa that had the greatest influence on the construction of the ordination axes ($R^2 > 0.1$). Directions of vectors indicate associations of ray species with each prey category within the two-dimensional space, while vector lengths (Euclidean norm) represent the overall importance of each prey category for distinguishing the diets.

5.4.2 Stable isotope analysis

Values of $\delta^{13}C$ ranged from -14.1 to -12.8‰ across all four species and $\delta^{15}N$ ranged from 9.1-10.1‰ (Figure 5.5; Table 5.4). Differing degrees of overlap in the 95% credible intervals of SEA sizes were suggestive of trophic niche distinctions among species (Table 5.4). Overall, *P. ater* had the largest SEA niche size of any species, which was significantly larger than *M. toshi* and *G. typus* (Figure 5.6a). Niche size of *H. australis* was significantly larger than *M. toshi* and *G. typus*, which both exhibited similarly narrow niche sizes. Trophic niche overlap was greatest between *P. ater* and *H. australis* (56.1%), but all other species pairs shared lower degree of overlap, ranging from 16.7% to 26.1% (Figure 5.6b; Table 5.5).

For *H. australis*, SEA niche size was significantly greater for samples collected in the 2022 sampling period, and there was 7.5% overlap in the SEAs (Figure 5.6cd; Table 5.5). For *P. ater*, there was no significant difference in niche size between years, and SEAs shared a higher degree of overlap (34.6%).

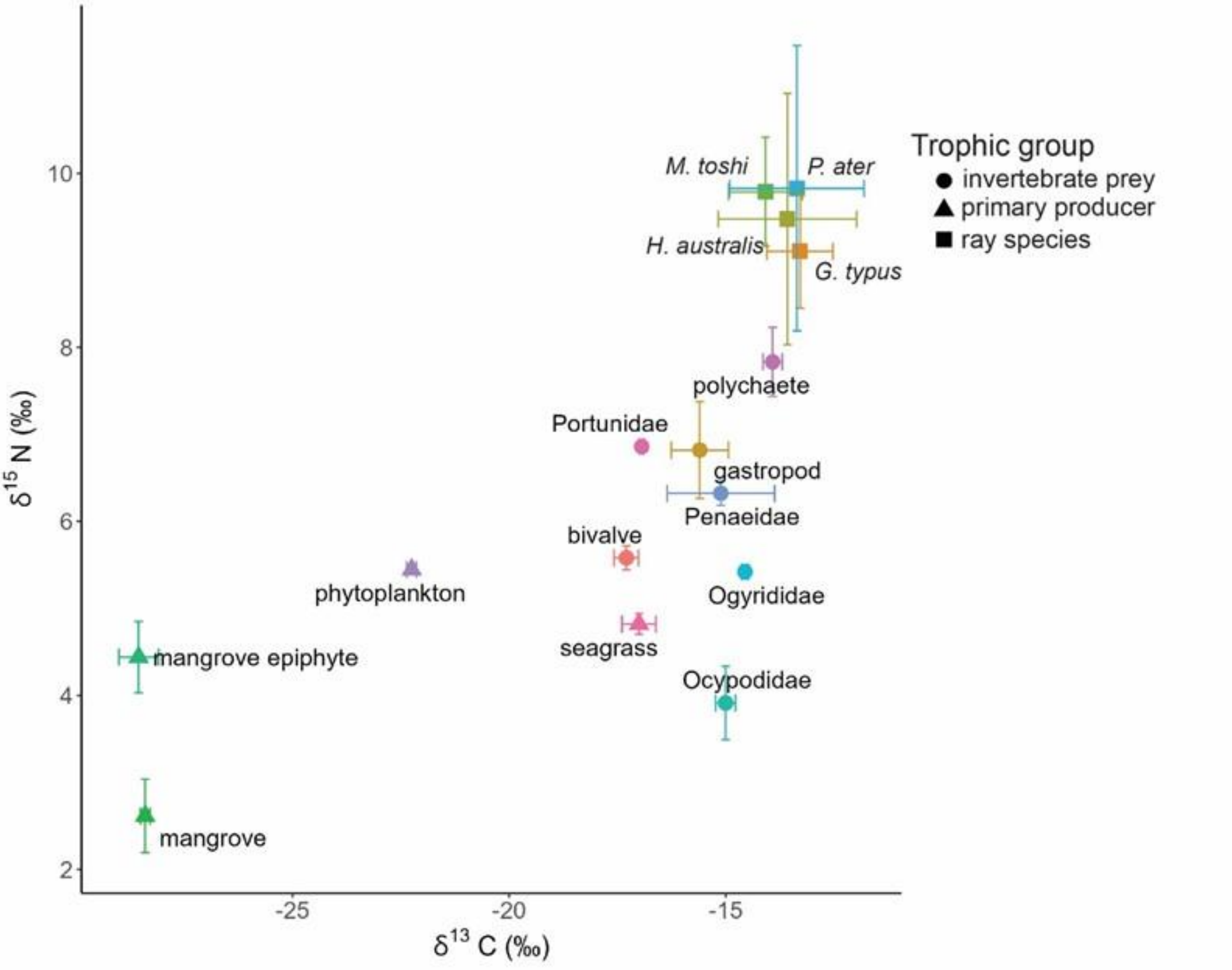

Figure 5.5. Isotopic biplot showing mean δ^{13}C and δ^{15}N values (‰; ± SE) for all ray species. For reference, values were displayed for selected invertebrate prey taxa, and primary producers that were collected and analysed at the site.

Table 5.4. Details of rays included for stable isotope analysis. The SEAc represents the small size-corrected standard ellipse area (‰^{2}). For SEA (standard ellipse area), means of SEA$_B$ are reported with the 95% credibility intervals (in parentheses).

Species	Group	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N	SEAc	SEA
H. australis	all	20	-13.6 ± 1.6	9.5 ± 1.4	3.2 ± 0.2	5.9	5.6 (3.5-8.8)
H. australis	2022	9	-13.4 ± 1.6	9.8 ± 1.9	3.3 ± 0.2	9.6	8.6 (4.7-17.9)
H. australis	2023	11	-13.7 ± 1.7	9.2 ± 0.9	3.2 ± 0.1	1.3	1.1 (0.5-2.1)
P. ater	all	22	-13.4 ± 1.6	9.8 ± 1.6	3.3 ± 0.2	8.4	8.0 (5.0-11.9)
P. ater	2022	11	-12.8 ± 1.6	9.5 ± 1.6	3.4 ± 0.3	8.5	7.7 (3.9-14.0)
P. ater	2023	11	-13.9 ± 1.4	10.1 ± 1.7	3.2 ± 0.3	8	7.2 (3.4-13.1)
M. toshi	all	10	-14.1 ± 0.3	9.8 ± 0.2	3.4 ± 0.2	1.6	1.4 (0.7-2.7)
G. typus	all	11	-13.3 ± 0.8	9.1 ± 0.7	3.2 ± 0.2	1.4	1.3 (0.7-2.4)

Table 5.5. Comparisons of trophic niche size and overlap between species pairs. For *H. australis* and *P. ater*, comparisons are shown between seasonal sampling seasons in 2022 and 2023. Differences in niche size were considered significant with probability >95% (denoted in bold).

Comparison	Probability of greater niche size for group 1 (%)	% overlap of SEA
P. ater / H. australis	84.5	56.1
P. ater / M. toshi	**100.0**	18.2
P. ater / G. typus	**100.0**	16.7
H. australis / M. toshi	**99.9**	26.1
H. australis / G. typus	**100.0**	23.7
M. toshi / G. typus	57.0	20.9
P. ater 2022 / 2023	56.0	34.6
H. australis 2022 / 2023	**100.0**	7.5

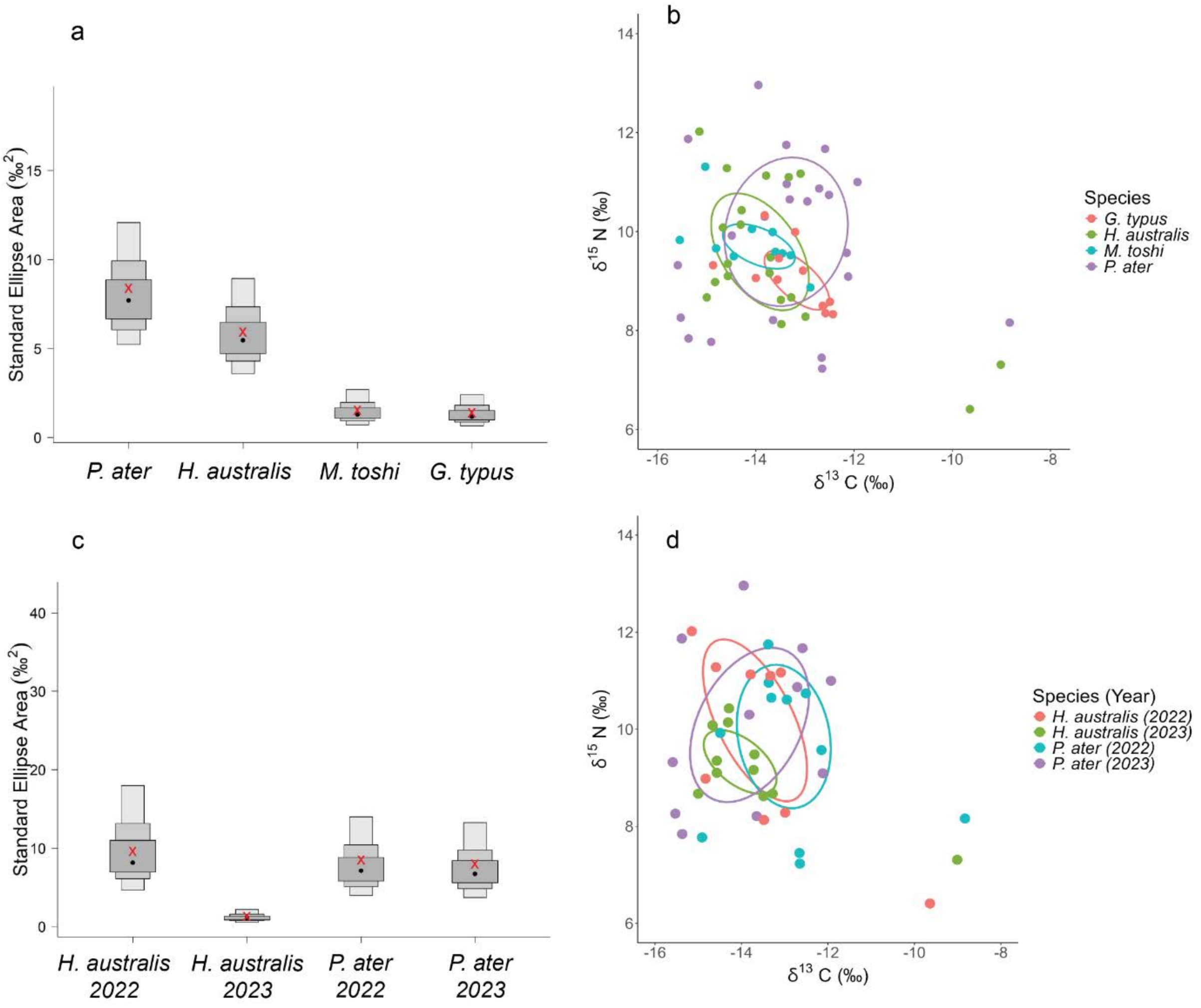

Figure 5.6. Density plots show the standard ellipse size (SEA) of each species (a) and by sampling year for *H. australis* and *P. ater* (c). On both plots, the red 'x' marks the position of the corrected standard ellipse area (SEAc). To visualize trophic overlap, the SEA ellipses for each group are also shown for each group (b,d).

5.4.3 Prey availability

A total of 31 unique taxa were identified within the study area across six phyla: Arthropoda, Annelida, Mollusca, Brachiopoda, Echinodermata, and Chordata (Appendix C, Table C3). Crustaceans were taxonomically diverse, containing members of eight orders/suborders, including Brachyura, Anomura, Caridea, Dendrobranchiata, Stomatopoda, Axiidea, Amphipoda, and Isopoda. The sediment core contained high frequencies of polychaetes, which were present in 46.7% of all samples. Other frequently encountered taxa included bivalves (%F = 48.3%), and gastropods (%F = 36.7). Burrowing soldier crabs (*Mictyris longicarpus*) and ocypodid crabs (primarily of genus *Ocypode*) were also well represented (%F = 26.7 and 23.3%, respectively). Results were largely similar for the bait pump, with the highest %F values for polychaetes (68.3%), gastropods (41.7%) and bivalves (30.0%). In contrast, penaeid prawns (primarily *M. bennettae*) were most common in the trawl surveys (%F = 65.0%), followed by Sergestid shrimp, *Acetes sp.* (%F = 35.0%). Only two prey categories identified in the SCA (*Ogyrides delli*, and family Crangonidae) were absent from the prey availability surveys.

The influence of site-specific environmental variables on invertebrate composition varied by sampling method (Table 5.6). Invertebrate composition in the sediment core samples differed significantly between fine sand and coarse sand sites ($p = 0.004$) and by proximity to mangroves ($p = 0.032$). For the bait pump, invertebrate composition was only influenced by primary substrate ($p = 0.001$). None of the tested variables influenced invertebrate composition from the trawl surveys (all $p > 0.05$). Other variables including season, distance from beach, and tidal section were not significant for any method.

Dissimilarities in site features and invertebrate composition resulted in distinct site clusters (Figure 5.7). Invertebrate taxa that had the greatest influence on site variability included gastropods (Neritidae), bivalves (Mytillidae), swimmer crabs (Portunidae), burrowing shrimp (Callianassidae), and sand dollars (Clypeasteroida) (Appendix C, Table C4). Sites characterised by coarse sand and closer proximity to a beach (sites 1, 6, and 8) were positively correlated with the crustacean families Callianassidae, Mictyridae, and Ocypodidae. Sites with fine sand substrates closest to the mangrove forest (sites 2-4) showed positive correlations with bivalves (Mytillidae), isopods, and mangrove-associated crabs (Grapsidae and Macropthalmidae). Coarse sand sites around the opening to the intertidal bay (sites 5 and 7) were positively correlated with bivalves (Cyrenidae), gastropods (Neritidae), and crusatceans in families Alpheidae, Diogenidae, and Portunidae. Site 9 showed the strongest correlations with echinoderms (Clypeasteroida) and brachiopods. Subtidal edge sites (10-12) were distinctly separate from other sites within the ordination space, showing positive correlations with Sergestidae and weak or negative correlations with all other taxa.

Spatial distributions of main infaunal prey types from the SCA (bivalves, gastropods, polychaetes, gastropods, ocypodid crabs) were compared from the sediment core surveys, while epibenthic prey types (penaeid prawns, portunid crabs) were only assessed from the trawl (Figure 5.8). Bivalves were present at eleven sites. Highest densities (mean ± SE) were concentrated at sites 2 and 3 in the upper intertidal bay (74 ± 35 and 76 ± 32 individuals.100 m^{-3}, respectively). Densities were lower across all other sites, ranging from 0-18 individuals.100 m^{-3}), particularly along the subtidal edge (0-3 individuals.100 m^{-3}). Gastropods were also present at eleven sites, with densities ranging from 0-28 individuals.100 m^{-3}. Polychaetes were encountered at all sampling sites, with peak densities at site 7 on the middle flat (23 ± 9 individuals.100 m^{-3}). Mean densities were also relatively high across sites within and adjacent to the bay (ranging from 10-18 individuals.100 m^{-3}), while all other sites ranged from 3-18 individuals.100 m^{-3}). Ocypodid crabs were present at nine sites. Peak densities occurred at site 3 adjacent to the mangroves (31 ± 10 individuals.100 m^{-3}) and ranged from 0-23 individuals.100 m^{-3} across all other sites.

From the trawl surveys, portunid crabs were present at nine sites and occurred in consistently low densities (0-3 individuals.100 m^{-2}), whereas penaeid prawns exhibited greater abundances but with variable distributions (Figure 5.8). Peak densities of 22 ± 10 individuals.100 m^{-2} occurred within and surrounding the upper intertidal bay, with a maximum 30 individuals.100 m^{-2} and lowest densities along subtidal edge sites, with a minimum of 2 ± 1 individuals.100 m^{-2}.

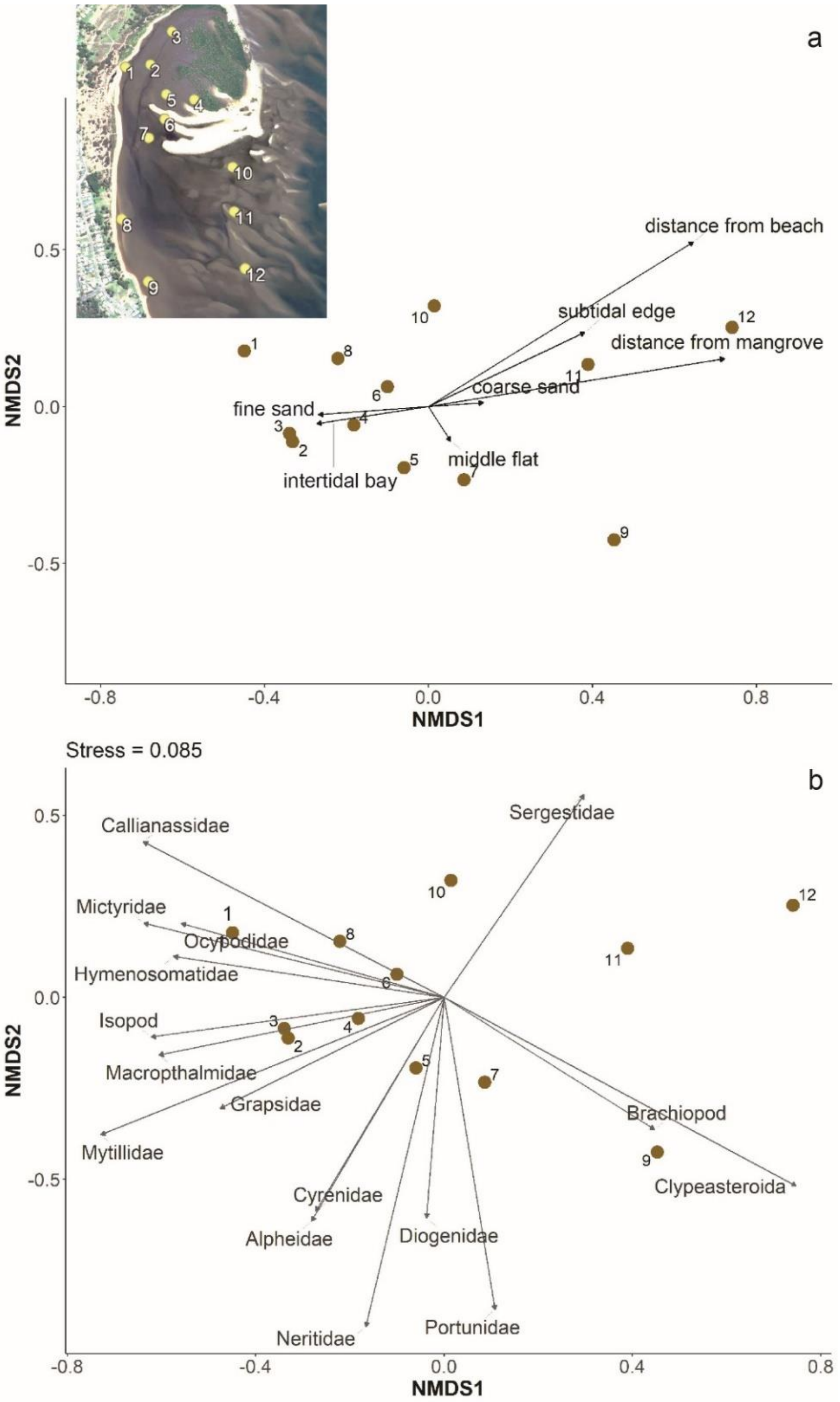

Figure 5.7. nMDS ordination plots showing the positions the twelve sampling sites and how sites were correlated with site-specific environmental variables (a) and invertebrate categories (b). For the second plot, invertebrate taxa were plotted that had greater influence on the construction of the ordination axes ($R^2 > 0.3$).

Table 5.6. Results of PERMANOVA models testing the effects of site environmental variables on invertebrate occurrences for each sampling method. Bolded p-values indicates variables that were statistically significant in the specified model.

	R^2	F statistic	p-value
Core			
Season	0.03	1.54	0.106
Primary substrate	0.05	2.72	**0.004**
Distance from mangrove	0.03	1.87	**0.032**
Distance from beach	0.03	1.56	0.086
Tidal section	0.04	1.29	0.15
Bait pump			
Season	0.02	1.01	0.397
Primary substrate	0.06	3.61	**0.001**
Distance from mangrove	0.02	1.15	0.316
Distance from beach	0.03	1.86	0.052
Tidal section	0.04	1.34	0.157
Trawl			
Season	0.03	1.79	0.104
Primary substrate	0.02	0.89	0.499
Distance from mangrove	0.02	1.13	0.330
Distance from beach	0.02	0.96	0.441
Tidal section	0.03	0.74	0.718

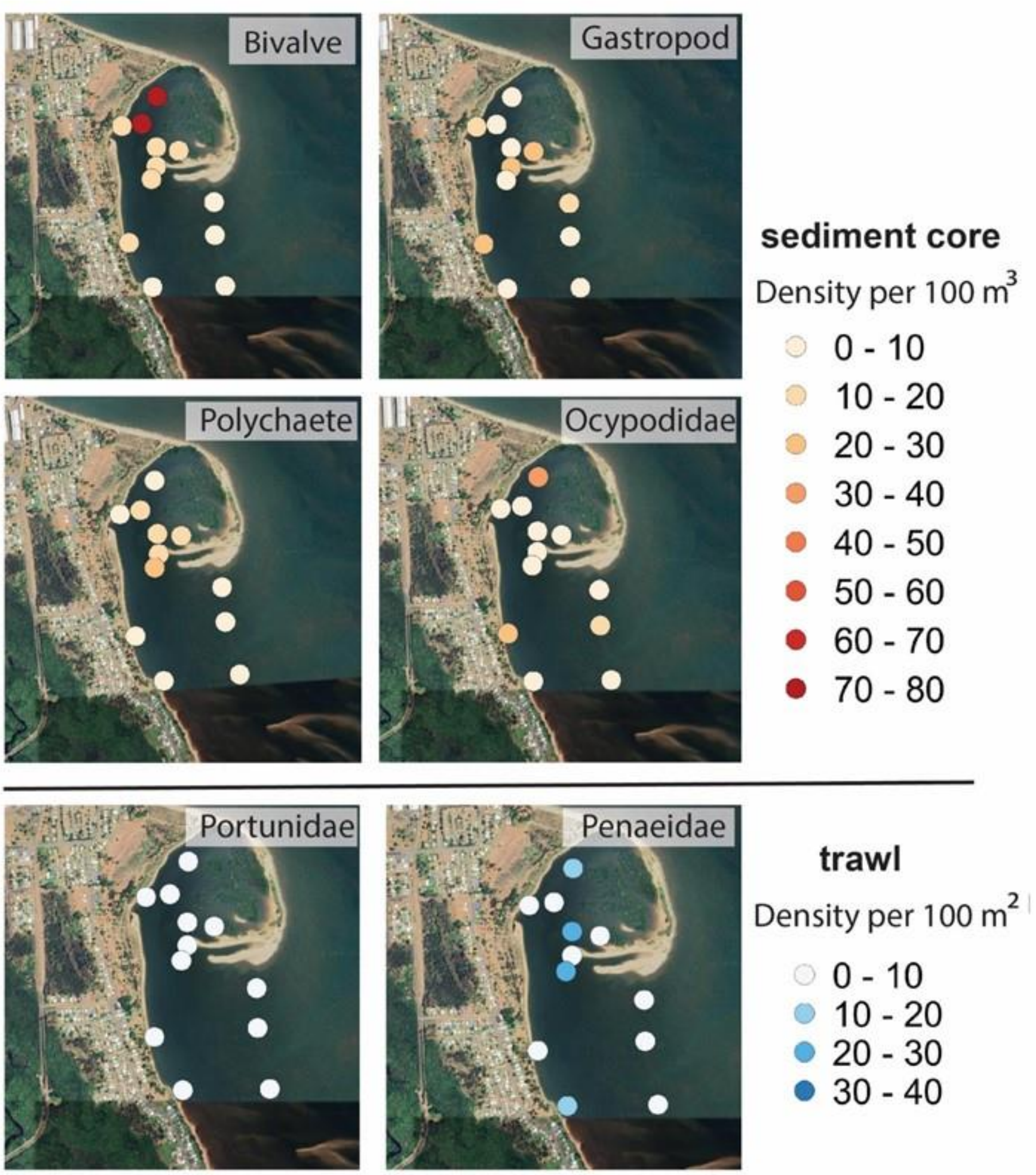

Figure 5.8. Mean prey densities across the twelve sampling sites are displayed for a subset of important prey categories from the SCA. Infaunal taxa obtained by the sediment core surveys are expressed in terms of sediment volume (individuals. 100 m^{-3}), while epibenthic taxa from the trawl are expressed in terms of swept area (individuals.100 m^{-2}).

5.5 Discussion

5.5.1 Dietary niche and overlap

Many species of elasmobranchs rely on coastal nursery areas to acquire sufficient resources to support individual fitness, growth, and survival (Heupel et al. 2007, Leurs et al. 2023). Although traditionally assumed to be resource-abundant with low competitive pressures (Branstetter 1990, Simpfendorfer & Milward 1993), evidence of high mortality rates and slow growth in elasmobranch nurseries requires closer examination of resource use (Heupel & Simpfendorfer 2002, Duncan & Holland 2006, Kinney et al. 2011). In this study, the small and narrow size ranges for each species indicated that most individuals were either neonate or young-of-year, based on established age-growth estimates (O'Shea et al. 2013, Last et al. 2016, Gaskins et al. 2020). Moreover, the year-round presence of young juveniles (Crook 2020, Crook et al. 2022), frequent recaptures (Chapter 4), and the general absence of adult rays at Lucinda meet the criteria of a communal nursery (Martins et al. 2018). Thus, these findings provided valuable information on the resource requirements of four sympatric species during critical early life stages and their trophic interactions.

The broad, complementary niches and minimal dietary overlap between *H. australis* and *P. ater* suggested some level of resource partitioning, which has also been documented from other sites in Australia (Vaudo & Heithaus 2011, O'Shea et al. 2013). *Pastinachus ater* was the only species that preferred non-crustacean prey taxa, including polychaetes, bivalves, and gastropods, which further aligns with previous dietary assessments on this species (Vaudo & Heithaus 2011, O'Shea et al. 2013, Elston et al. 2020). Although diets of *H. australis* are more limited to decapod crustaceans (Vaudo & Heithaus 2011, O'Shea et al. 2013), they consumed various crustacean taxa in a generalist manner. Interestingly, high prey-specific abundance and low frequency of occurrence of soldier crabs (Mictyridae) crabs and lancelets

(Amphioxis) indicated individual specialisation. Although lancelets were consumed infrequently, they were consumed in exceedingly high quantities (up to 49 individuals per stomach). Their highly patchy distribution in tidal flats (Webb 1975, Vargas & Dean 2010) suggests individuals may opportunistically consume several during a single feeding event rather than specialising on them directly.

Incorporating SIA also allowed for temporal comparisons in trophic niche sizes for *H. australis* and *P. ater*. While significant changes in trophic niche size for *H. australis* could indicate seasonal shifts in resource use or foraging locations (Every et al. 2019), no changes in invertebrate compositions were identified between the wet and dry season to support this as a driver of dietary variability. Thus, differences may reflect a seasonality in stable isotope composition of primary producers, which propagates through the food web to consumer tissues (Abrantes et al. 2015, Espinoza et al. 2015, Abrantes & Sheaves 2024). On the other hand, consistent trophic niches for *P. ater* indicates they rely on resources from trophic pathways that were unaffected by seasonal baseline changes.

Himantura australis demonstrated some dietary overlap with *G. typus* and *M. toshi*, although their wider dietary preferences may buffer potential competition. However, narrow dietary niches of *G. typus* and *M. toshi* and specialist feeding on penaeid prawns suggests direct competition between these species, particularly if they use similar foraging tactics. Previously, penaeid prawns have been identified as a key resource for *G. typus* and for related species of shovelnose rays (*Aptychotrema*) (Kyne & Bennett 2002, Vaudo & Heithaus 2011, Yogi et al. 2023), as well as *M. toshi* (Vaudo & Heithaus 2011, Wagiyo et al. 2023), although studies are biased towards larger individuals than those examined here. Only Yogi et al. (2023) focused on neonate-sized *G. typus*, while dietary data for *M. toshi* only exists for larger size classes (44-76 cm DW versus 18-34 cm DW used in this study).

Despite high overlap in the SCA, SIA revealed relatively low trophic overlap between *G. typus* and *M. toshi*. This disparity may emerge from these species selecting different species of penaeid prawns (e.g. *M. bennettae, M. endeavouri, Penaeus merguiensis*) or other crustacean prey, whose use of different microhabitats may alter their stable isotope composition (Fry et al. 1999, Abrantes & Sheaves 2009a, Sheaves et al. 2012b). However, with a low sample size for *M. toshi* (n = 9), the SCA likely did not encompass their full dietary breadth and potentially overestimated their dietary overlap with *G. typus*. Furthermore, as SCA and SIA operate over different time frames (SCA representing the last meal and SIA representing longer term trends), caution must be exercised when comparing them directly.

Dietary distinctions among species are driven in part by differences in morphology and foraging capabilities (Motta & Wilga 2001, Motta & Huber 2004). For example, mouth shape and size results in some species being more adept at extracting specific prey. Species that possess flattened, well developed tooth plates on the upper and lower jaws, such Myliobatidae (eagle rays) and Rhinopteridae (cownose rays), specialise on hard-shelled prey (Gray et al. 1997, Collins et al. 2007a). Similarly, the hexagonal, rough-plated tooth dentition of *P. ater* may allow them to more easily crush molluscs than other species (Elston et al. 2020). This was supported by stomach contents of *P. ater* containing fragmented or crushed from gastropods and bivalves, while prey from other species were generally intact. In contrast, whiprays (genus *Himantura*) are characterised by angular rostra and small, sub-equal teeth with a prominent horizontal groove (Last et al. 2008, Manjaji-Matsumoto & Last 2008), which may be better suited for handling benthic crustaceans. For *G. typus*, differences in body morphology likely have greater influence than mouth morphology, since an inability to oscillate their pectoral fins while foraging could prevent deep excavation (Compagno & Last

1999). This aligns foraging behaviours that have been documented for this species, where they generally feed along the surface while swimming (Crook 2020).

Changes in body size over ontogeny are also drivers of resource partitioning among size classes (Grubbs 2010, Nakazawa 2015, Yogi et al. 2023). In combination with mouth and dentition structures, larger body sizes are also associated with greater mechanical power for excavating and masticating prey (Kolmann et al. 2015, Kolmann et al. 2023). Therefore, narrow dietary scopes and a reliance on surface-associated prawns by *G. typus* and *M. toshi* may be related to their smaller body and gape sizes compared to *H. australis* and *P. ater*. For example, one study has shown that for *G. typus* <150 cm TL, penaeid prawns and brachyuran crabs were equally preferred, but brachyurans became the preferred prey for rays >150 cm (Vaudo & Heithaus 2011). Thus, penaeid prawns may be particularly valuable resources for neonate and young juvenile rays, with expected expansions in dietary niches during later life stages (Sommerville et al. 2011).

5.5.2 Prey availability and habitat use

Integrating spatial prey availability allowed me to contextualise how foraging habits of rays are influenced by the benthic prey landscape. In general, sites with fine sand/muddy substrates at the northern end of the sand flat supported different infaunal invertebrate assemblages than surrounding unvegetated habitats with coarser sand (Meijer et al. 2021, Pan et al. 2021, Mattone & Sheaves 2024). In contrast, epibenthic prey were more evenly distributed across the study area, likely facilitated by their increased ability to disperse with the tides (Hill et al. 1982, Silva et al. 2014). Thus, species that consume both infaunal and surface-associated prey (e.g. *H. australis* and *P. ater*) may adaptively select localised habitat patches with higher densities of burrowing prey, while feeding more opportunistically on epibenthic resources over more expansive areas. For example, portunid crabs, which were a main prey resource of *H. australis* (and occasionally by *G. typus* and *P. ater*), were not constrained to localised habitat patches. However, higher density patches of penaeid prawns and ocypodid crabs within and near the bay entrance indicates these areas could present more abundant foraging opportunities.

These sites shared partial overlap with core foraging areas previously described for *H. australis* at Lucinda (Crook et al. 2022). As *H. australis* was associated with excavation-style foraging techniques, authors proposed soldier crabs (Mictyridae) and ghost shrimp (Callianassidae) as potential prey, although in the current study, these prey types had minimal contributions to their diets. Low representation of deeper burrowing crustaceans could be because individuals of *H. australis* included in this study were smaller (mean 38 cm DW) than those assessed previously (mean DW 54 cm) Crook et al. (2022) and were, therefore, more limited to feeding on surface-associated prey (Takeuchi & Tamaki 2014). Crook et al. (2022) also reported that *P. ater* used a combination of surface and excavation foraging techniques, which allows them to extract molluscs, polychaetes, and crustaceans across varying sediment depths. The ubiquitous presence these prey types across the intertidal flat, albeit with some patchiness, further supports the larger foraging ranges used by this species.

While the core usage areas described for *H. australis* and *P. ater* are informative, we must exercise caution when drawing linkages between historic foraging ranges and prey availability from the present study. Habitat changes since 2017-2019 could have altered the habitat characteristics of the site, with potential effects on the core foraging areas of each species. I also note that with prey sampling limited to five site visits over a single dry to wet season period, sampling across greater temporal scales may also reveal greater variation in spatio-temporal prey availability.

Although core foraging areas of *G. typus* and *M. toshi* have not been described previously, a strong reliance on penaeid prawns suggests that foraging habitat selection could show closer spatial overlap with their preferred prey. Concentrated densities of *M. bennettae* in the low intertidal zone suggests that these areas contain greater foraging opportunities as rays move in with flooding tides. However, predator avoidance, rather than prey availability, is likely to be another significant factor driving movements into shallowly submerged habitats (Davy et al. 2015, Martins et al. 2020a, Oleksyn et al. 2020). This is particularly relevant at Lucinda, where roving predators such as hammerhead sharks are frequently present on the subtidal edges (Lubitz et al. 2023). This is further supported by acoustic tracking of rays at the site, in which rays use intertidal areas farther away from the beach as movement corridors instead of foraging grounds (Crook 2020), despite foraging opportunities being present.

5.5.3 Methodological considerations

The use of gastric lavage for SCA was an effective non-lethal alternative to stomach dissection for dietary analysis of juvenile rays. However, one key assumption of gastric lavage was that all stomach contents are successfully evacuated during flushing, and that empty stomachs truly indicated an absence of prey rather than incomplete extraction. Although no rays were sacrificed in this study to verify the complete evacuation of stomach contents, previous studies have confirmed this using post-mortem dissection (Ajemian et al. 2012, Bangley et al. 2013).

SCA also faces inherent limitations related to differential prey digestion rates and gastric evacuation times (Amundsen & Sánchez-Hernández 2019, Baker et al. 2024). In this case, soft-shelled prey such including polychaetes, as well as gastropods and bivalves that were removed from their shells, could have lingered for less time in the digestive tract (Buckland et al. 2017), potentially underestimating their consumption by all species.

However, as benthic rays are generally considered to be continuous feeders (Gilliam & Sullivan 1993, Jacobsen & Bennett 2013), rays were believed to feed during each tidal cycle while prey-rich habitats are accessible. The intactness of most prey items indicated that most recovered prey items were recently consumed, with a low number of stomachs containing prey that were unidentifiable to any degree. Thus, it was unlikely that differences in prey digestion rates would have significantly biased these results, unlike for other fish taxa where degraded prey materials make up a greater proportion of the stomach contents (Baker et al. 2014). Lastly, the snapshot nature of SCA also means that large sample sizes are typically required to capture the full dietary breadth, particularly for species with generalist habits (Baker et al. 2024). Therefore, with relatively small sample sizes obtained for *H. australis* and *M. toshi*, more individuals would be needed to fully encompass dietary variability. For all species, greater sample sizes could also reveal consumption patterns for rarer prey items and allow for stronger dietary comparisons across additional demographics, such as size class or season.

SIA provided complementary support to SCA when comparing dietary overlap among species. All ray species fed on benthic invertebrates within the intertidal flat, which yielded high levels of trophic niche overlap. This observation may reflect the limitations of SIA for distinguishing individual prey types, as prey occupying similar microhabitats or relying on the same basal carbon sources would typically yield similar isotopic signatures (Abrantes & Sheaves 2024). However, differences in niche size among some species pairs illustrated the more nuanced distinctions in resource use and dietary breadth, which may better represent longer-term trophic interactions due to the slow turnover rates of elasmobranch muscle tissues (Hussey et al. 2012). While an initial objective of this study was to estimate prey contributions using Bayesian mixing models, the substantial overlap in $\delta^{13}C$ values among prey sources, coupled with high variability in $\delta^{15}N$, created poor source geometry that precluded the effective use of this approach (Phillips et al. 2014). Thus, further sampling of primary producers and lower trophic levels could help quantify the relative importance of different nutrient sources (e.g., microphytobenthos, plankton, seagrass) for supporting ray populations in intertidal nurseries (Abrantes & Sheaves 2009b, Abrantes et al. 2015). Furthermore, greater temporal coverage in the SIA could provide greater insights for how resource pathways may change over seasons and years.

The prey availability analysis at Lucinda was one of the most comprehensive to date within the context of a ray dietary study, particularly through the use of multiple gear types. While the bait pump had the greatest sampling depth (up to 60 cm depth), similar invertebrate taxa were represented using the sediment core (20 cm depth). This similarity could suggest that more invertebrates were concentrated in upper sediment layers, their vertical distributions were consistent across this depth range (Peterson 1991, Santos et al. 2020), or that suction from the bait pump could have drawn out more organisms from lateral burrows in the upper sediment layers. Consequently, while both methods yielded information on infaunal prey composition, the sediment core provided a more standardised measure of prey availability across depths within the excavation limits of ray species. Although other prey availability assessments have primarily used sediment cores to sample infaunal prey (Tilley 2011, Ajemian et al. 2012, Pardo et al. 2015, O'Shea et al. 2018), this method was predicted to be ineffective for epibenthic taxa. A notable example of this was that penaeid prawns were abundant in the trawl surveys but absent from other methods. Thus, excluding the trawl surveys could have erroneously supported conclusions that rays highly specialise on a rare prey type or these are obtained from outside the study area (Pardo et al. 2015).

While this sampling regime provided broad spatial coverage of prey availability along the tidal gradient, this design would not have captured spatial variability at microhabitat scales (m^2). However, this could be achieved by targeting sampling to specifically overlap with core feeding areas, which could potentially be identified using a combination of acoustic tracking, drone surveys, or evidence of feeding activity (greater pit densities). Moreover, expanding sampling to include adjacent areas outside the study area could also more provide more profound insights on how prey availability influences habitat selection and potential nursery quality. Although these data provided a snapshot of prey availability, greater temporal coverage is still needed to fully characterise seasonal or annual trends in the prey landscape and effects on foraging interactions over time.

5.6 Conclusions

In this chapter, I provided foundational knowledge on the diets of four ray species during early life stages. While results supported high dietary overlap among species, there was also evidence of resource partitioning, particularly between *P. ater* and other species. Differences in trophic niches provided further insights into the potential competitive interactions among species, as well as how species-specific morphologies and foraging behaviours influence dietary composition. Future works quantifying the degree of resource limitation within these systems would strengthen knowledge on how competitive interactions among ray species or other mesopredator groups (e.g. teleosts, seabirds) influence population structures and broader community dynamics. From a conservation perspective, this is also important for understanding the impacts of limited resources on species abundances within nurseries.

Lastly, knowledge on predator-prey dependencies has valuable implications for understanding the vulnerabilities of various species to anthropogenic or climatic pressures in a changing world. In this case, generalist feeders like *P. ater* and *H. australis* may possess a greater ability to adapt their diets to accommodate shifts in prey availability. However, specialist feeders like *G. typus* may be more spatially constrained to areas where their preferred prey are abundant, leaving them more vulnerable to decline or localised extinction if these prey became unavailable. Thus, identifying and protecting essential juvenile habitats based on their underlying resources could be a strong approach to improve targeted conservation strategies for at-risk species.

6 General discussion

6.1 Synthesis of main findings

Despite the recognised importance of intertidal zones as essential habitats for marine species, substantial knowledge gaps persist regarding their value for rays (Leurs et al. 2023). Basic aspects of habitat and resource use remain poorly investigated for most species, particularly during early life stages. Furthermore, while rays are increasingly recognised as ecosystem engineers and vital mesopredators, a scarcity of information on their trophic ecology and foraging behaviours makes it difficult to estimate their broader impacts on ecosystem processes (Flowers et al. 2021). To address these gaps, I investigated habitat use and trophic ecology of rays in intertidal sand flats of tropical eastern Australia using multiple integrative approaches.

Drone surveys in Chapter 2 provided a scoping overview of species richness and composition across various habitat types and highlighted the relative importance of intertidal flats as communal feeding grounds. Drone tracking in Chapter 3 also provided novel insights into the behavioural mechanisms of foraging and how these translate to species-specific habitat use, functional roles, and potential trophic interactions. After validating non-lethal gastric lavage as an effective method for dietary sampling in Chapter 4, the use of SCA and SIA in Chapter 5 revealed key prey items of four different species during early life stages. Findings supported both high dietary overlap among some species pairs and low overlap among others, which may be driven by different morphologies and foraging strategies. Integrating prey availability also showed which invertebrate taxa are accessible within the intertidal flat boundary and provided novel linkages between dietary habits, fine-scale habitat selection over the tide, and foraging behaviour.

In the following sections, I discuss how these findings can be applied towards understanding the functional roles of rays in intertidal zones and for the conservation of species and habitats.

6.2 Ecological roles of rays

Aquatic predators perform diverse functional roles that are intrinsically linked to their population structures and spatial distributions (Hammerschlag 2019). As benthic mesopredators, feeding activities of rays exert both trophic and physical impacts on their environments (O'Shea et al. 2012, Takeuchi & Tamaki 2014, Nauta et al. 2024). These impacts may be intensified in intertidal nurseries, where the more limited movements and site fidelity of juveniles concentrate their activities to more localised spatial scales (Vaudo & Lowe 2006, Davy et al. 2015, Elston et al. 2019). Mark-recapture data from Lucinda and Blacksoil Creek in Chapter 4 supported short term (of one or more days) and longer term (e.g. monthly, seasonal) usage over time.

Although rays can be highly abundant in intertidal zones, their impacts are not uniformly distributed across all available habitats; rather, certain patches play disproportionate roles in supporting one or more functions (e.g. as movement corridors, predator refuges, or feeding grounds) (MacArthur & Pianka 1966, Vaudo & Heithaus 2012, Vaudo & Heithaus 2013). Thus, repeated usage of small core foraging areas can have substantial influence on bioturbation over localised scales (Crook et al. 2022), in which effects extend beyond the immediate feeding areas to influence the broader ecosystem mosaic (Sheaves et al. 2024b). Although rays are generally solitary foragers, drone surveys in Chapter 2 revealed some occurrences of intense clustered feeding. For example, at Blacksoil Creek, feeding aggregations of *H. australis* frequently occurred along intertidal sand flat edges, particularly during rising tides when new habitats became available, which often resulted in persistent canyon-like formations rather than single feeding pits (Figure 6.1). Over time, sediment turnover at this scale may significantly impact sand bank geomorphology, with subsequent impacts on tidal direction and flow through the channel. Similarly, feeding clusters of *U. granulatus* that formed along mangrove edges in Deluge Inlet may contribute to bank erosion and biogenic dispersal of nutrients entrenched in the muddy sediments into the

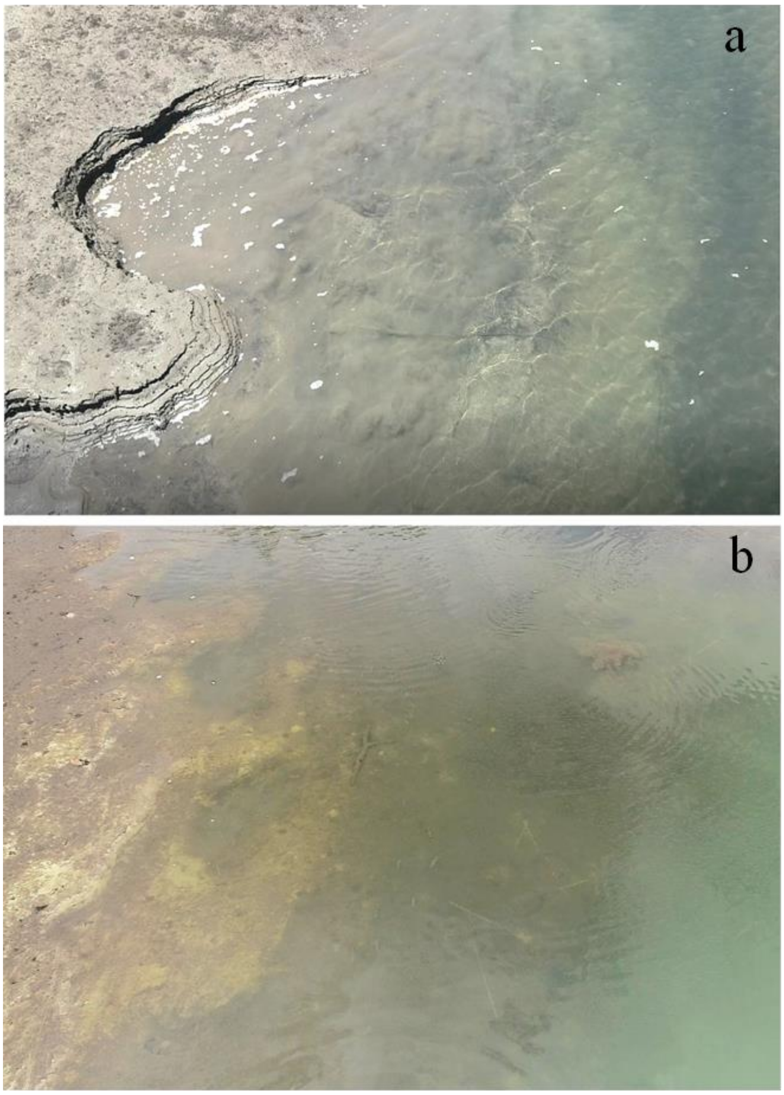

Figure 6.1. Persistent canyon-like formation formed by clusters of *Himantura australis* (a) and *U. granulatus* (b) along intertidal bank edges.

water column. Given rays are some of the largest benthic excavators in intertidal ecosystems (Heithaus et al. 2010, Sarker et al. 2021), the ability to conduct ecosystem engineering at these scales may be unreproducible by other taxonomic groups.

Translating ecological roles into ecological importance requires an understanding of both community-level processes and species-specific contributions. While current research often examines either single species in isolation (Nauta et al. 2024) or the impacts of multiple species collectively (O'Shea et al. 2012, Grew et al. 2024), this thesis demonstrates how individual species contribute to ecosystem functions in unique ways. Such distinctions are particularly interesting among co-occurring species, which co-inhabit the same environments but exploit resources and microhabitats differently (Pianka 1981). Complex marine environments like coral reefs provide compelling examples for how multi-species communities promote greater functional diversity. Caribbean parrotfish assemblages demonstrate this effectively, in which some species target filamentous algae while others focus on macroalgae, and they further partition their feeding across different reef zones and substrate types (Adam et al. 2015). Similarly, sympatric species of reef sharks will also occupy different positions as pelagic and benthic mesopredators to minimise trophic and functional redundancy with each other and predatory teleosts (Frisch et al. 2016). Unique feeding ecologies also occur in less complex environments, such as sand and mud flats (White et al. 2004, Chaudhuri et al. 2014), indicating that functional diversity similarly plays a role in structuring their macrofauna communities.

The unique foraging strategies of rays described at Lucinda (Crook et al. 2022) and Pioneer Bay (Chapter 3) suggested that despite using overlapping habitats, sympatric species promote some level of functional complementarity in different environment types (unvegetated flat and reef flat). Due to species-specific morphological adaptations and feeding strategies, these observed behaviours and their interactions with other species are likely conserved (Last et al. 2008, Kolmann et al. 2023). However, as these are the only studies that directly compare foraging behaviours of rays, further investigations, particularly those that incorporate behaviours and prey availability, would be needed to extrapolate these patterns to other species and habitat contexts.

Although several trophic studies compare the dietary habits of rays (Vaudo & Heithaus 2011, O'Shea et al. 2013, Pardo et al. 2015, Elston et al. 2020), few efforts have been made to link foraging ecology with functional outputs (Heithaus et al. 2010). For rays, this can be achieved by considering both horizontal habitat partitioning and vertical distributions of target prey in the sediment column, along with how foraging capabilities differ among species (White & Potter 2004, Ajemian & Powers 2016, Munsch et al. 2016). Using Lucinda as a model (Figure 6.2), findings from Chapter 5 showed that juvenile *G. typus* and *M. toshi* primarily targeted surface-associated prey, and they likely exert minimal pressure on infaunal communities. Moreover, these species may even perform similar predatory functions as other opportunistic benthic teleosts on open sand flats (e.g. whiting) (Giaroli et al. 2023). In contrast, *H. australis* and *P. ater* exploit a wider range of epibenthic and infaunal prey in intertidal flats (Vaudo & Heithaus 2011, O'Shea et al. 2013), and would have greater influence on prey taxa across varying sediment depths. A greater diversity of species and size classes increases the scope of trophic and functional niches fulfilled by resident ray communities, although the absence of larger size classes in intertidal zones may preclude predation pressures on prey items that exceed the gape widths of young juveniles (e.g. adult swimmer crabs (Portunidae)).

In terms of bioturbation, species that predominantly surface-feed would be predicted to rework less sediment over time than those that habitually use disruptive foraging behaviours (Kristensen et al. 2012), such was the case with *P. ater* versus *U. granulatus* and *P. fai* in Pioneer Bay (Chapter 3). In summary, more efforts are greatly needed to quantify the magnitude of these functional outputs and to model variability across different ecological contexts, species assemblages, and life history stages.

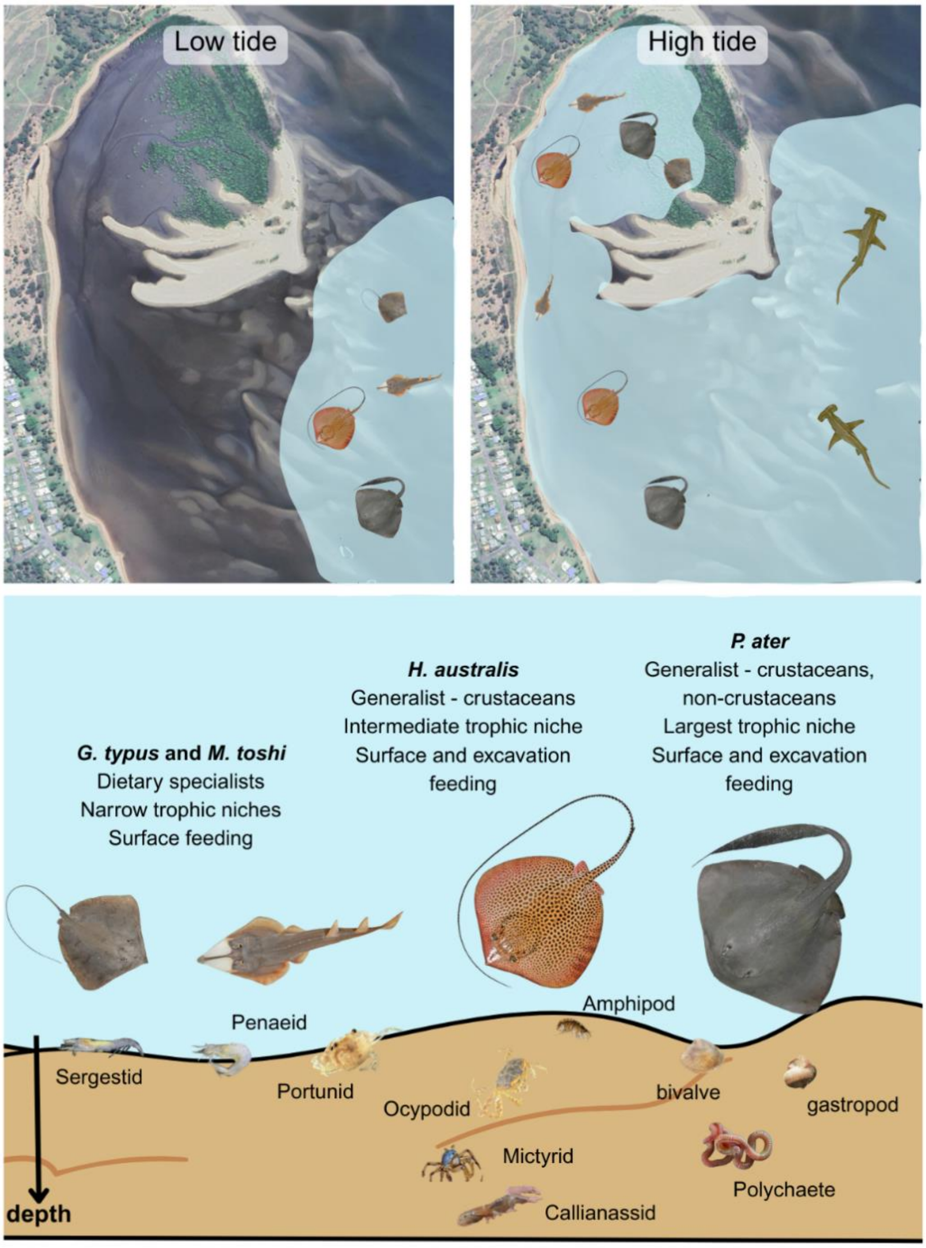

Figure 6.2. Juvenile rays at Lucinda Beach make cyclical migrations onto the upper intertidal flat with the tide to feed. Although species exhibit some degree of dietary and trophic overlap, distinctions also provided evidence of species-specific habitat use and functional roles.

6.3 Conservation and management implications

6.3.1 Conservation of essential juvenile habitats

Effective conservation of mobile marine species requires protecting critical habitats across their life history, understanding resource requirements within these habitats, and maintaining connectivity between them (Grubbs 2010, Munsch et al. 2016, Henderson et al. 2018, Sánchez-Hernández et al. 2019). Nearly 2,600 ray observations collated from multi-site drone surveys (Chapter 2) affirmed that intertidal habitats in Northeast Queensland, Australia were used by nine ray species. Additionally, exclusive captures of juveniles from Lucinda and Blacksoil Creek in Chapters 4-5 and prior knowledge of intertidal zones as essential juvenile habitats (Leurs et al. 2023) aligns with the theoretical frameworks of habitat partitioning. In this context juveniles prefer shallower environments with abundant, appropriately-sized prey resources while adults are able to exploit broader spatial ranges to access larger prey (Grol et al. 2014, Ajemian & Powers 2016, Loureiro et al. 2016). Thus, we can assume that areas containing the necessary habitats and resources for growth and survival for one species or life stage may be inadequate for others, which must be accounted for in conservation planning (Kinney & Simpfendorfer 2009, Ward-Paige et al. 2015, Oh et al. 2017). Where gaps exist in the basic ecology, this could lead to ineffective or costly management outcomes (Henderson et al. 2018). For example, increased protection of riverine and estuarine areas may have positive impacts on juveniles of highly threatened sawfish (Pristidae) but negligible impacts on adults, and consequently, current efforts are likely insufficient for preventing localised extinctions (Dulvy et al. 2016).

The scope of available information narrows further for specific habitat types, which greatly limits our ability to quantify their relative importance, either independently or collectively, within the seascape mosaic. Unvegetated sand and mud flats (which were the primary focus in this work) have received disproportionately little research attention compared to more structured habitats such as mangroves, seagrass beds, or coral reefs, despite their use by a variety of marine and estuarine fish species (Sheaves et al. 2024a). Notably, some of the ray species encountered in these systems face elevated threats of extinction, such as the critically endangered *G. typus*, and endangered *U. granulatus*. Estuaries are also recognised as nurseries for many elasmobranch species (Heupel et al. 2019), yet there is scarce knowledge on population structures, movement patterns, or habitat use requirements within these systems (Constance et al. 2024). For species that show varying degrees of association with estuarine habitats in Chapter 2, such as *H. australis*, *M. toshi*, *P. ater*, and *U. granulatus*, their roles for supporting populations remains poorly documented and likely underestimated.

Although intertidal zones are widely recognised as highly productive environments, seasonal or year-round resource limitations may still persist (Kober & Bairlein 2009, Jung et al. 2017) (Kneib 1993, Moksnes 2004). The prevalence of resource partitioning within elasmobranch communities suggests this mechanism is often necessary for species coexistence, with resource limitation driving dietary niche separation and habitat partitioning among different species and life stages (Kinney et al. 2011, Heithaus et al. 2013, Mulas et al. 2019). At Lucinda, high dietary overlap did not suggest stringent resource partitioning among species, and prey availability surveys revealed benthic macroinvertebrates to be abundant within the intertidal sand flat boundary (Chapter 5). However, it remains uncertain whether resources are limited here or at other sites where prey availability has been assessed (Pardo et al. 2015, Elston et al. 2017, O'Shea et al. 2018). Furthermore, there remains little empirical evidence demonstrating how resource availability influences key population parameters such as growth, survival, or population densities (Bethea et al. 2004, Heupel et al. 2007, Weideli et al. 2023), warranting future research in these areas.

Quantifying predator-prey dynamics and their influence on habitat selection can present significant challenges for mobile predators, particularly when these relationships must be interpreted across appropriate spatial and temporal scales (Barnett et al. 2017). Findings from Chapter 5 demonstrated the value of incorporating both SCA and SIA, which has become standard practice for many trophic ecology studies on elasmobranchs (Espinoza et al. 2015, Hernández-Aguilar et al. 2016, O'Shea et al. 2020, Galindo et al. 2021, Gül & Demirel 2022). The interpretations from SCA can be strengthened further where genetic verification of prey is possible (Barnett et al. 2010b, da Silveira et al. 2020), while the inclusion of sulfur in SIA may improve our capacity to detect differences in trophic niche and overlap among sympatric predators (Raoult et al. 2024). I argue that the inclusion of prey availability is essential for effectively linking prey selection and spatio-temporal habitat use to tease apart the context and species-specific natures of dietary variability (Figure 6.3). Continued efforts in this area will have strong implications for understanding the functional relevance of resource availability when assessing habitat quality for juvenile rays. Future research would also benefit from integrating other methodological approaches, such as combining catch or tracking data with prey availability surveys (Heithaus et al. 2002, Barnett et al. 2010a) to further explore how prey availability influences habitat use and diets in intertidal ecosystems. Additionally, parallel investigations of ray predators (e.g., hammerhead sharks) (Lubitz et al. 2023) would provide meaningful insights on the complex trade-offs between prey availability and predation risk as rays move across tidal gradients (Vaudo & Heithaus 2013, Lester et al. 2020).

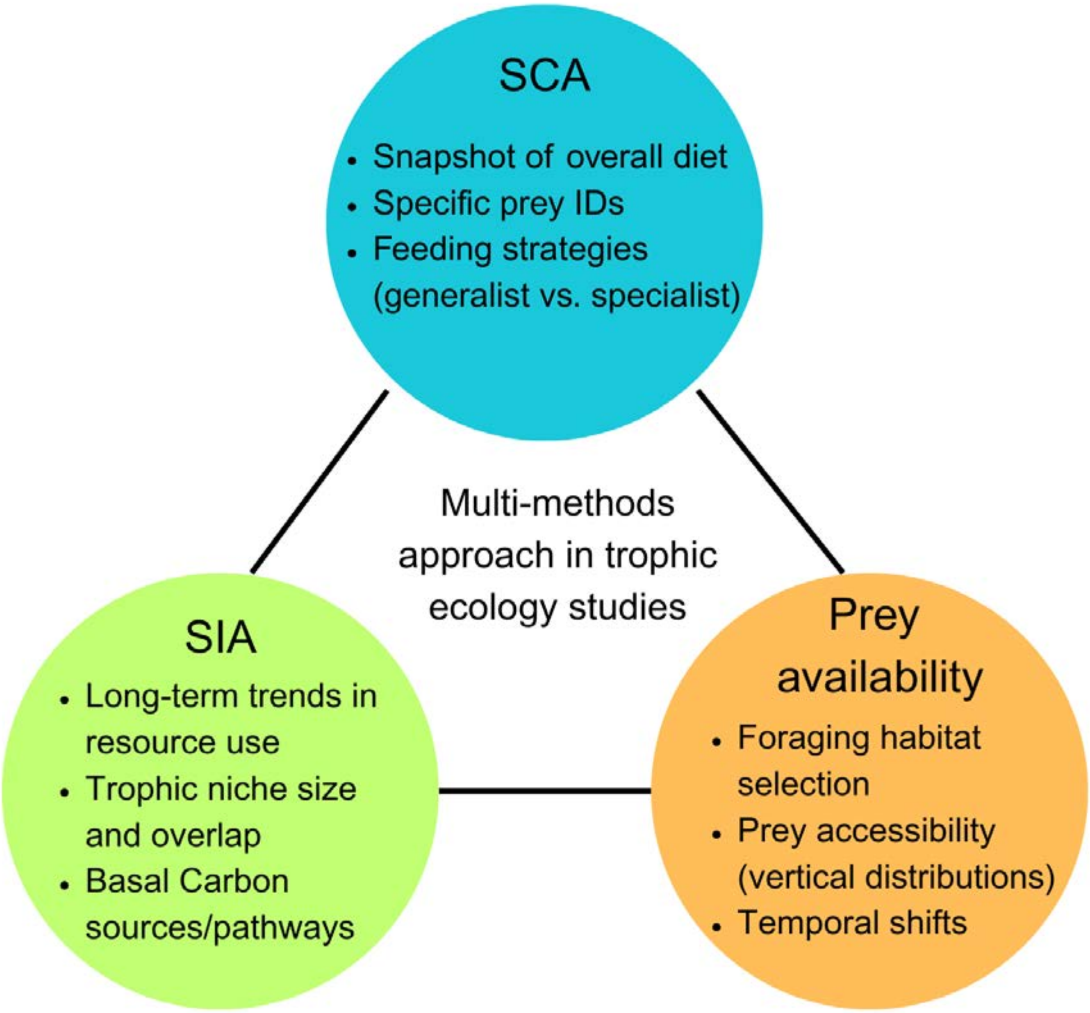

Figure 6.3. Graphic displaying the benefits of incorporating stomach content analysis (SCA), stable isotope analysis (SIA), and prey availability surveys in trophic ecology studies.

6.3.2 Assessing vulnerability of ray populations

The IUCN currently estimates that at least a third of ray species are at risk of extinction due to overfishing, bycatch, and habitat loss (Dulvy et al. 2021, Pacoureau et al. 2021), while several others remain data deficient (Sherman et al. 2023). With tidal flats across the world currently facing unprecedented modifications from climate change and anthropogenic disturbance (Murray et al. 2019), it is critical to understand which species and habitats are most vulnerable to future changes. In Australia, many of the species in this study occur within protected areas such as the Great Barrier Reef Marine Park in Northeast Queensland or Ningaloo Reef in Western Australia (Last et al. 2016), although incidental fisheries captures still present a significant threat to sharks and rays in the Indo-Australasian region (White & Kyne 2010). Furthermore, their international conservation statuses vary considerably across their geographical ranges due to overfishing (Dulvy et al. 2021, Pacoureau et al. 2021, Sherman et al. 2023). Importantly, intertidal habitats across the world face multiple anthropogenic threats including coastal development, agricultural runoff, and degraded water quality, despite being within protected areas (Murray et al. 2019, Murray et al. 2022). Threats associated with climate change impacts including rising sea levels and increasing water temperatures may be more pronounced in intertidal zones, where organisms already experience conditions that challenge their physiological limits (Mieszkowska et al. 2021, Rullens et al. 2022, Rogers et al. 2023). Combined, these factors will likely alter the spatial distribution and quality of ray habitats in upcoming decades (Flowers et al. 2021, Osgood et al. 2021, Niella et al. 2022, Rummer et al. 2022).

From a community dynamics standpoint, the presence of multiple species performing different but complementary roles provides functional redundancy that helps maintain ecosystem stability over time while also reducing dependencies on shared resource pools (Micheli & Halpern 2005, Mori et al. 2013, Leduc et al. 2015). Pristine habitats are generally associated with more diverse community structures, while areas that are depleted or degraded are often skewed towards a fewer number of dominant species (Lotze et al. 2006). Thus, habitats that support diverse ray communities may be more resilient compared to systems that are dominated by fewer species, since the loss or decline of one species may be partially or wholly compensated by others with similar roles (Duffy 2002, Griffin et al. 2008).

Knowledge of trophic ecology and predator-prey dependencies is also particularly relevant for assessing vulnerability of populations. The loss or degradation of habitats could negatively impact benthic prey communities (Munroe et al. 2015, Chevillot et al. 2019), with disproportionate effects on species with different trophic ecologies. For example, consuming a broader range of resources makes generalists more robust to environmental instability (Sánchez-Hernández et al. 2021), while species with narrow dietary niches have less dietary adaptability (Ward et al. 2006, Munroe et al. 2014). In the context of this work, generalist species like *P. ater* (Vaudo & Heithaus 2011, Elston et al. 2020) may be able to use a wider variety of habitats while adjusting their diets to accommodate available prey types. On the other hand, specialist feeders like critically endangered *G. typus* (Kyne et al. 2020) may experience greater intra- and interspecific competition for the same resources, making them more vulnerable if their target prey decreases. Moreover, competitive exclusion could have greater influence on their distributions within intertidal feeding grounds (Papastamatiou et al. 2006b, Kinney et al. 2011, Weideli et al. 2023). Thus, shifting our focus to identifying and protecting essential juvenile habitats based on their underlying resources has the potential to improve targeted conservation strategies for at-risk species.

The regular presence of rays in intertidal zones, combined with their ecological relevance, makes it worth considering whether rays could be ecological indicators for intertidal habitats. By definition, ecological indicators are organisms whose presence, abundance, or condition reflect broader patterns of biodiversity, habitat quality, or ecosystem health (Whitfield & Elliott 2002, Smale et al. 2011, Sheaves et al. 2012a). In recent years, sharks and rays have been proposed as potential indicators due to their key roles as intermediate and apex predators and their sensitivity to environmental changes (Pennino et al. 2013, Gilby et al. 2017, Osgood et al. 2020, Costa et al. 2024). Additionally, larger body sizes make them easier to detect and monitor over time in shallow environments using remote sensing technologies such as drones (Kiszka et al. 2016, Butcher et al. 2021). The use of ecological indicators has gained prominence in conservation and management as they enable cost-effective monitoring and provide quantifiable conservation targets (Niemi & McDonald 2004, Kalinkat et al. 2017). Knowing how site-specific factors directly or indirectly influence distributions of indicator species would allow policymakers to select more meaningful protection areas that preserve greater ecosystem biodiversity and function (Whitfield & Elliott 2002, Sheaves et al. 2012a).

At the species level, those with strong associations with specific habitat features could be suitable candidates as ecological indicators, although current research in this area remains limited for rays. One of the only verified examples of a ray as an ecological indicator is the estuary stingray, *Himantura fluviorum*, in which its presence in southeast Queensland has been correlated with elevated species richness, better water quality, and greater coverage of mangroves and remnant vegetation (Gilby et al. 2017). Likewise, endangered *U. granulatus* also exhibit strong preferences for intact mangrove fringe habitats during juvenile life stages (Kanno et al. 2023). Thus, monitoring this species could be particularly useful for assessing the status of these habitats where they occur in the Indo-Pacific. However, with substantial knowledge gaps regarding their population structures outside of coral reefs (Manjaji et al. 2016), further research would be needed to identify specific habitat features and environmental parameters that support their populations of *U. granulatus* and of other overlapping species.

As our current knowledge of ray community structures, habitat associations, and foraging patterns is largely derived from relatively pristine environments (e.g., in this thesis, coastal waters of the Great Barrier Reef Marine Park), future studies at locations experiencing varying degrees of habitat modification and fishing pressure would provide valuable comparative insights for management and conservation. Species losses could have negative consequences for ecosystem function, such as reduced bioturbation roles and nutrient cycling (Heithaus et al. 2010, Earl & Zollner 2017, Flowers et al. 2021), while further triggering trophic imbalances that affect higher order predators and other dependent species (Heithaus et al. 2008, Ajemian et al. 2012, Heupel et al. 2014). Therefore, integrating both species-specific indicators and community-level metrics would establish more robust frameworks for protecting vulnerable species populations in a changing world.

Appendices

Appendix A: Supporting materials for Chapter 2

Table A1. Summary of drone video transects collected across the six intertidal study sites from 2020-2022. Number of video transects and cumulative transect area coverage were used as approximations for sampling effort. Mean values are given in parentheses following the minimum-maximum ranges, whereas error estimates refer to the standard deviation of the mean.

	Site							
	Blacksoil Creek	**Deluge Inlet**	**Cungulla**	**Lucinda**	**Rocky Ponds**	**Pioneer Bay**	**Hazard Bay**	**Juno Bay**
Coordinates	19.300097, 147.043050	18.414908, 146.218600	19.398894, 147.115306	18.533064, 146.338019	19.819842, 147.669717	18.612375, 146.488919	18.634556, 146.498022	18.683697, 146.516008
No. video transects	42	14	27	26	15	21	5	5
No. dates sampled	13	6	8	5	4	11	1	1
No. transects with rays present	41	13	24	26	15	20	5	5
Season								
wet	14	2	25	0	15	13	0	0
dry	28	12	2	26	0	8	5	5
Tidal phase								
Low	13	5	0	0	5	5	1	1
Rising	16	7	18	14	5	9	1	2
High	8	2	0	10	1	3	1	1
Ebb	5	0	9	2	4	5	2	1
Drone height range								
Low (5-10 m)	10	6	14	6	0	0	0	0

Mid (11-20 m)	26	5	10	20	13	21	5	5
High (21-30 m)	6	3	3	0	2	0	0	0
Flight distance (m)	190-2240 (702)	285-2859 (929)	138-1653 (770)	320-3337 (1248)	239-911 (1955)	1642-5565 (3272)	1761-2414 (503)	1156-1724 (423.8)
Transect area (km^2)	.	.	2.9-51.2 (15.5 ± 11.3)	3.9-92.8 (26.8 ± 19.0)	4.5-44.6 (20.7 ± 10.7)	24.0-58.0 (43.5 ± 8.8)	53.3-75.3 (15.3 ± 4.4)	33.1-50.1 (12.3 ± 3.7)
Total sampling effort (sum of area across all transects (km^2)	.	.	417.8	723.7	310.6	870.7	321.8	221.9
Number of rays per transect	0-53 (12.8 ± 11.0)	0-11 (4.3 ± 3.1)	0-33 (9.6 ± 8.1)	1-65 (17.2 ± 15.0)	1-24 (11.3 ± 6.6)	3-38 (15.8 ± 9.2)	10-33 (24.4 ± 9.4)	7-57 (23.2 ± 19.6)
Transect ray density	.	.	0.0-3.5 (0.9 ± 0.9)	0.1-3.1 (0.8 ± 0.6)	0.1-1.7 (0.6 ± 0.2)	0.1-1.6 (0.3 ± 0.1)	0.2-0.51 (0.4 ± 0.1)	0.54-1.36 (0.6 ± 0.5)

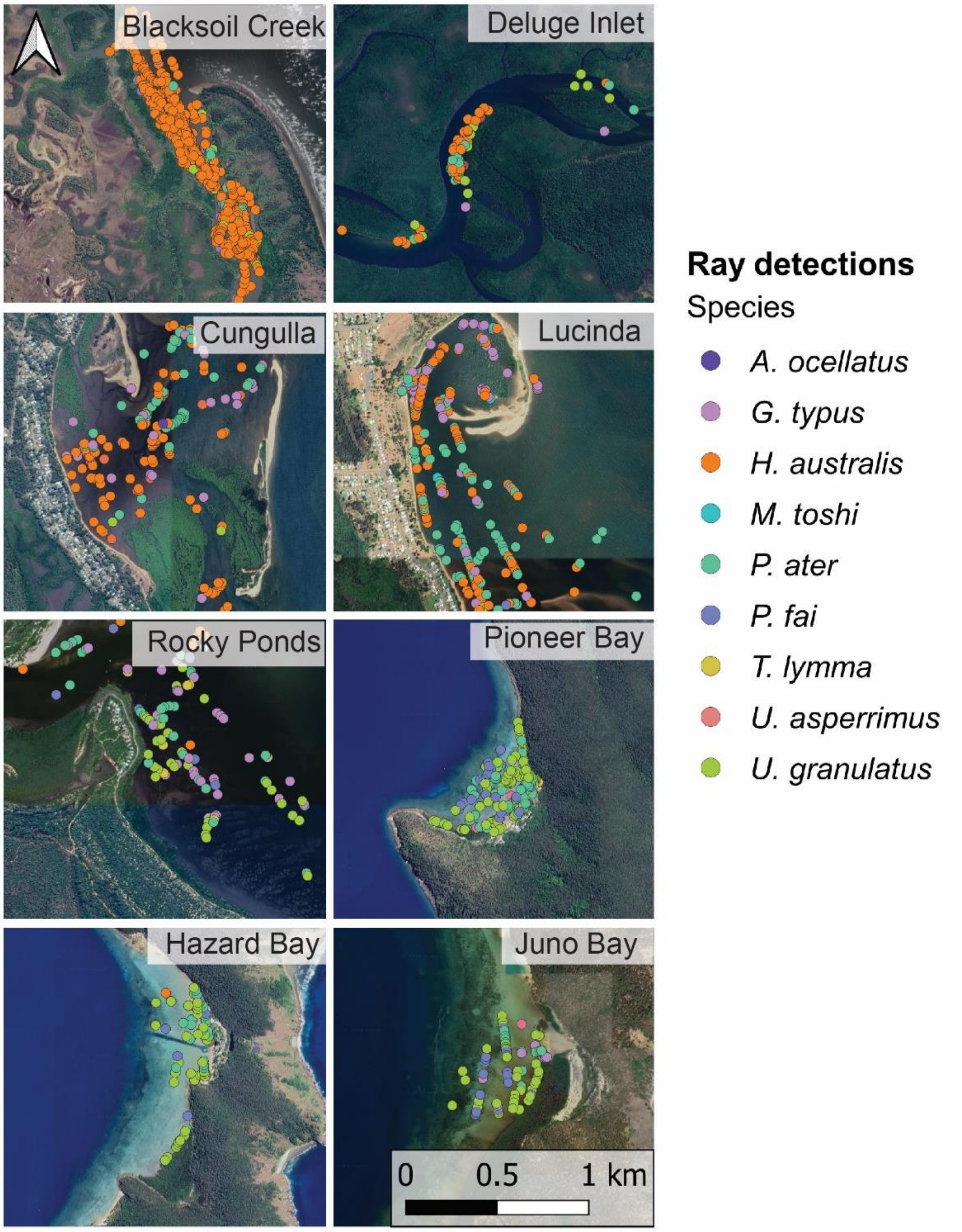

Figure A1. Locations of ray detections at eight intertidal flats in North Queensland. Points are coloured by species.

Appendix B: Supporting material for Chapter 4

Table B1. Contingency table showing the frequencies of successful (non-empty stomachs) versus unsuccessful (empty stomachs) gastric lavage outcomes by species (sites pooled for *Himantura australis* and *Maculabatis toshi*) and by location.

Site and species	No. containing stomach contents	No. empty stomachs
Both sites		
G. typus	46	11
H. australis	45	11
M. toshi	32	2
P. ater	50	20
Blacksoil Creek		
H. australis and M. toshi	43	4
Lucinda		
H. australis and M. toshi	34	9

Appendix C: Supporting information for Chapter 5

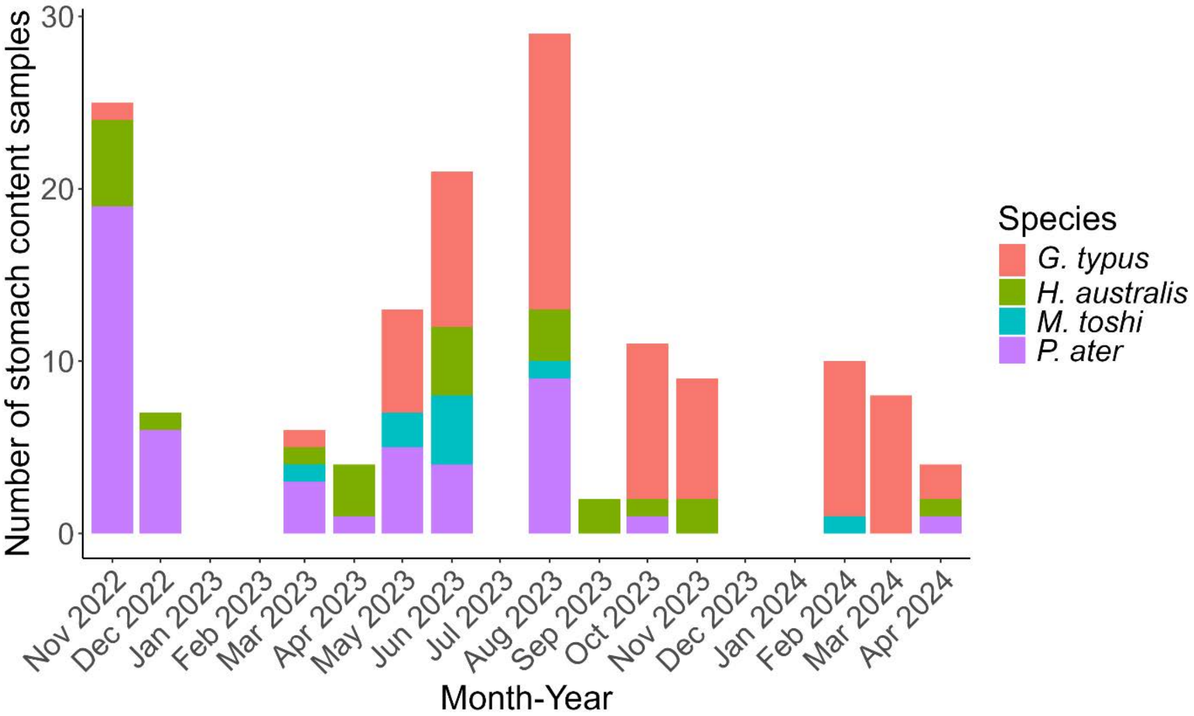

Figure C1. Histogram showing the number of stomach content samples that were collected for each species between November 2022 and April 2024.

Table C1. Frequency of occurrence (%F) of all prey taxa identified from the stomach content analysis of juvenile rays at Lucinda.

Prey category	*H. australis (n = 25)*	*M. toshi (n = 9)*	*P. ater (n = 49)*	*G. typus (n = 74)*
All crab	88.0	22.2	26.5	17.6
Infraorder Brachyura				
Grapsidae	0.0	11.1	0.0	2.7
Hymenosomatidae	12.0	11.1	0.0	1.4
Mictyridae - *Mictyris longicarpus*	12.0	0.0	0.0	0.0
Matutidae - *Ashtoret lunaris*	4.0	0.0	0.0	0.0
Ocypodidae	32.0	0.0	2.0	1.4
Ocypode cordimana	12.0	0.0	0.0	0.0
Unknown Ocypodidae	12.0	0.0	2.0	1.4
Macrophthalmidae - Macrophthalmus sp.	8.0	0.0	0.0	0.0
Portunidae	44.0	0.0	14.3	10.8
Charybdis sp.	0.0	0.0	2.0	0.0
Portunus armatus	16.0	0.0	0.0	5.4
Scylla serrata	0.0	0.0	0.0	1.4
Unknown Portunidae	32.0	0.0	12.2	6.8
Unknown brachyuran	24.0	0.0	2.0	2.7
Infraorder Anomura				
Diogenidae	4.0	0.0	8.2	1.4
All shrimp/prawn	96.0	100.0	53.1	98.6
Infraorder Caridea				
Alpheidae - *Alpheus* sp.	16.0	0.0	0.0	5.4
Crangonidae	4.0	0.0	0.0	1.4
Ogyrididae - *Ogyrides delli*	48.0	11.1	14.3	2.7
Suborder Dendrobranchiata				
Penaeidae	60.0	88.9	30.6	89.2
Metapenaeus bennettae	20.0	33.3	4.1	35.1
Metapenaeus endeavouri	0.0	33.3	0.0	0.0
Penaeus merguiensis	0.0	0.0	0.0	1.4
Unknown Penaeidae	44.0	55.6	26.5	56.8
Sergestidae - *Acetes sibogae*	0.0	11.1	0.0	4.1
Infraorder Axiidea				
Callianassidae	4.0	0.0	2.0	0.0
Trypaea australiensis	4.0	0.0	0.0	0.0
Other Callianassidae	0.0	0.0	2.0	0.0
Order Mysida - Mysidae	0.0	11.1	4.1	2.7
Order Stomatopoda - Lysiosquillidae	8.0	0.0	0.0	0.0
Unknown shrimp or prawn	16.0	0.0	10.2	29.7

Small crustaceans	24.0	0.0	2.0	1.4
Order Amphipoda	16.0	0.0	2.0	1.4
Order Isopoda	8.0	0.0	0.0	0.0
Non-crustacean prey				
Annelida - Polychaeta	12.0	11.1	85.7	1.4
Bivalve	0.0	0.0	32.7	0.0
Echinoderm - Ophiuroidea	0.0	0.0	4.1	0.0
Gastropods	0.0	0.0	32.7	0.0
Littorinidae	0.0	0.0	18.4	0.0
Unknown gastropod	0.0	0.0	20.4	0.0
Lancelet (Amphioxis)	8.0	0.0	0.0	0.0
Teleost - Gobiidae	4.0	0.0	2.0	0.0

Table C2. Results of environmental fitting analysis showing vector properties (length and direction) and correlation strengths (R^2) between prey categories and ray dietary composition in the nMDS ordination space. Significant relationships ($p < 0.05$) are shown in bold.

Prey category	Vector length	NMDS1	NMDS2	R²	p-value
Alpheidae	0.223	-0.166	0.234	0.082	**0.008**
Amphipod	0.333	0.091	0.259	0.076	**0.015**
Bivalve	0.467	0.362	-0.035	0.132	**0.001**
Diogenidae	0.232	0.158	-0.158	0.050	**0.03**
Echinoderm	0.723	0.211	0.076	0.050	**0.03**
Gastropod	0.273	0.361	-0.274	0.206	**0.001**
Grapsidae	0.140	-0.158	-0.048	0.027	0.099
Hymenosomatidae	0.477	-0.081	0.000	0.007	0.62
Isopod	0.107	0.052	0.127	0.019	0.158
Lancelet	0.231	-0.006	0.231	0.054	**0.022**
Mictyridae	0.530	-0.315	0.386	0.249	**0.001**
Mysidae	0.234	0.136	0.026	0.019	0.206
Ocypodidae	0.112	-0.103	0.192	0.047	**0.043**
Ogyrididae	0.139	0.128	0.500	0.266	**0.001**
Penaeidae	0.174	-0.502	-0.613	0.629	**0.001**
Polychaete	0.787	0.686	0.126	0.487	**0.001**
Portunidae	0.517	-0.011	0.495	0.245	**0.001**
Sergestidae	0.283	-0.103	0.168	0.039	0.061
Stomatopoda	0.223	-0.006	0.231	0.054	**0.022**

Table C3. Frequency of occurrence (%) of all benthic macrofauna represented by each method in the prey availability surveys at Lucinda.

Taxon	bait pump	core	trawl
crabs			
Infraorder Brachyura			
Grapsidae	0.0	5.0	8.3
Metapograpsus frontalis	0.0	1.7	1.7
Grapsus sp.	0.0	1.7	5.0
Unknown Grapsidae	0.0	1.7	3.3
Hymenosomatidae	6.7	8.3	20.0
Matutidae - *Ashtoret lunaris*	0.0	0.0	3.3
Mictyridae - *Mictyris longicarpus*	28.3	26.7	0.0
Macrophthalmidae - *Macrophthalmus* sp.	0.0	8.3	0.0
Majidae	0.0	0.0	1.7
Ocypodidae	20.0	23.3	8.3
Ocypode cordimana	15.0	18.3	5.0
Uca sp.	5.0	5.0	0.0
Unknown Ocypodidae	1.7	0.0	5.0
Portunidae	13.3	0.0	13.3
Portunus armatus	0.0	0.0	10.0
Unknown Portunidae	0.0	0.0	3.3
Infraorder Anomura			
Diogenidae	1.7	10.0	6.7
shrimp/prawns			
Infraorder Caridea			
Alpheidae - *Alpheus* sp.	0.0	3.3	5.0
Suborder Dendrobranchiata			
Penaeidae	3.3	3.3	65.0
Metapenaeus bennettae	1.7	0.0	51.7
Penaeus merguiensis	0.0	0.0	5.0
Unknown Penaeidae	1.7	3.3	8.3
Sergestidae - *Acetes sibogae*	0.0	0.0	35.0
Infraorder Axiidea			
Callianassidae - *Trypaea australiensis*	20.0	13.3	0.0
Order Stomatopoda - Lysiosquillidae	3.3	0.0	0.0
Small crustaceans			
Order Amphipoda	0.0	1.7	8.3
Order Isopoda	0	0	20

Annelids			
Polychaeta	68.3	46.7	6.7
Other annelid	3.3	3.3	1.7
Molluscs			
Bivalve	30.0	48.3	1.7
Mytillidae	30.0	41.7	0.0
Cyrenidae	3.3	15.0	0.0
Unknown bivalve	3.3	1.7	1.7
Gastropod	41.7	36.7	13.3
Unknown gastropod	1.7	0.0	3.3
Neritidae	28.3	18.3	6.7
Littorinidae	13.3	13.3	5.0
Turritellidae	6.7	11.7	1.7
Nassariidae	6.7	8.3	0.0
Brachiopod - *Lingula sp.*	15.0	13.3	0.0
Echinoderms	3.3	13.3	0.0
Order Clypeasteroida	1.7	10.0	0.0
Order Ophiurida	1.7	3.3	0.0
Miscellaneous			
Lancelet (Amphioxus)	0	1.7	0
Teleost	0.0	3.3	85.0

Table C4. Results of environmental fitting analysis showing vector properties (length and direction) and correlation strengths (R^2) of invertebrate taxa to site variability within the nMDS ordination space. Significant relationships ($p < 0.05$) are shown in bold.

Taxon	NMDS1	NMDS2	R^2	p-value
Amphipoda	-0.0377	0.2855	0.08	0.702
Isopoda	-0.6221	-0.1088	0.40	0.095
Neritidae	-0.1663	-0.9054	0.85	**0.002**
Littorinidae	-0.1693	-0.1704	0.06	0.767
Turritellidae	-0.4873	-0.223	0.29	0.227
Nassariidae	0.1782	-0.27	0.10	0.617
Mytillidae	-0.7293	-0.3777	0.67	**0.006**
Cyrenidae	-0.2725	-0.5876	0.42	0.080
Brachiopod	0.4469	-0.3628	0.33	0.163
Matutidae	0.2767	-0.1624	0.10	0.637
Portunidae	0.1081	-0.8583	0.75	**0.005**
Ocypodidae	-0.5579	0.2035	0.35	0.151
Macropthalmidae	-0.6055	-0.1585	0.39	0.100
Hymenosomatidae	-0.5744	0.1131	0.34	0.155
Mictyridae	-0.6375	0.2044	0.45	0.067
Grapsidae	-0.4756	-0.3051	0.32	0.177
Diogenidae	-0.0372	-0.6063	0.37	0.140
Penaeidae	-0.1288	-0.2351	0.07	0.719
Alpheidae	-0.2811	-0.615	0.46	0.069
Sergestidae	0.2979	0.5572	0.40	0.102
Callianassidae	-0.6386	0.4278	0.59	**0.016**
Stomatopod	0.433	0.1004	0.20	0.343
Other annelid	0.4286	0.2106	0.23	0.270
Polychaete	-0.0614	-0.4069	0.17	0.433
Clypeasteroida	0.748	-0.5183	0.83	**0.004**
Ophiurida	-0.0083	-0.4094	0.17	0.383

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