

The Trophic Basis of Fish Assemblages in Temperate Estuarine and Coastal Ecosystems

Belinda K. Goddard (✉ belindakgoddard@gmail.com)

University of New South Wales <https://orcid.org/0000-0002-3223-5897>

Alistair Becker

Port Stephens Fisheries Institute

David Harasti

Port Stephens Fisheries Institute

James A. Smith

University of New South Wales

Iain M. Suthers

University of New South Wales

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Abstract

More than half of the fish biomass of coastal rocky reefs depends on zooplankton; however, the trophic basis of estuarine fish assemblages remains unknown. We quantified the trophic basis (i.e. basal energy sources) of fish community biomass inhabiting three habitat types (seagrass, natural reef and artificial reef) in two estuaries, and at two coastal rocky reef sites. Estuarine fish assemblages were surveyed with Baited Remote Underwater Video (BRUVs). Species abundance, richness and biomass of fish were classified into 9 functional feeding groups (3 elasmobranch and 6 teleost). Comparable metrics for coastal fish assemblages were obtained from published surveys using BRUV, remote underwater video and visual census survey methods. Using the functional feeding group biomass and the group-specific diet composition, the breakdown of energy sources was calculated using a food web analysis. Estuarine reef habitats had different species and different functional feeding group composition than seagrass habitat. The majority of fish biomass in the seagrass habitat was supported by detritus (51% at one estuary) or macrophytes (58% at the other estuary). In contrast, zooplankton supported most fish biomass (45-59%) at the coastal reef locations, and in reef habitat in one estuary (35-43%), but not the other estuary (33-34%). The trophic basis of estuarine and coastal fish assemblages reveals their potential response to urbanisation including changes to habitat, nutrient supply and current flow.

Introduction

Marine ecosystems are supported by primary production (Litchman and Klausmeier 2008; Oczkowski et al. 2016), decomposition and the detrital pathway (Moore et al. 2004). Primary producers, such as phytoplankton and macrophytes support consumers through a food web of multiple trophic levels and these higher trophic levels fertilise benthic macrophyte and detrital pathways (Wassmann 1998; Parrish et al. 2009). Phytoplankton, macrophytes and detritus are the three main sources of energy to marine ecosystems (Frisch et al. 2014), and the flow of energy from these sources is represented in the abundance of functional feeding groups of fish, such as grazers, piscivores and zooplanktivores. Recent studies have focused on using the relative biomass of functional feeding groups and the dietary composition of fish assemblages to understand the sources and basal processes supporting food webs and ecosystems (Ainsworth et al. 2010; Abrantes et al. 2015; Smith et al. 2016; Holland et al. 2020).

Kelp and other macrophytes dominate Australia's temperate rocky reefs over 8000 km of coastal habitat, collectively known as the "Great Southern Reef" (Bennett et al. 2015a). The vast macroalgal communities that characterise this system would suggest that benthic productivity is a key source supporting coastal food webs (Bennett et al. 2015b). However, there is growing recognition of the importance of plankton too as an energy source for rocky reefs (Zuercher and Galloway 2019), especially for associated fish assemblages (Truong et al. 2017), similar to what has been observed in tropical systems (Hamner et al. 1988; Morais and Bellwood 2019). Zooplanktivores often dominate the fish biomass on temperate rocky reefs in south-eastern Australian (Truong et al. 2017; Harasti et al. 2018; Holland et al. 2020), suggesting that zooplankton is a dominant energy source supporting of fish biomass. Zooplanktivores capture

Loading [MathJax]/jax/output/CommonHTML/jax.js and pass this pelagic subsidy on to piscivores and other

higher trophic levels (Young et al. 2010). Using a food web analysis encompassing 9 fish functional feeding groups, Truong et al. (2017) found that 53% of reef fish biomass off Sydney, Australia was ultimately supported by zooplankton, providing evidence that the pelagic pathway is a dominant energy source even in macroalgae-dominated temperate reef systems. This is supported by a recent analysis of a decade of visual census data by citizen scientists (Reef Life Survey; Edgar et al. 2020) over 12 degrees of latitude off eastern Australia (Holland et al. 2020).

Estuarine rocky reefs are present in many estuaries, particularly along the littoral fringes where they support valuable fisheries (Pease 1999). Research on estuarine habitat has typically focused on saltmarsh, mangroves and seagrass habitats (Hindell 2006; York et al. 2006; Nagelkerken and Faunce 2008; Connolly 2009), although estuarine rocky reefs are also known to provide important refuge and prey for benthic predators (Glasby 1999; Creese et al. 2009; Becker et al. 2010; Morton and Gladstone 2014; Davis et al. 2016). There is often high productivity and tidal-driven supply of zooplankton in estuaries (David et al. 2005; Qin et al. 2015), which may support significant fish biomass (Kennish 2019) with tidal currents transporting zooplankton past estuarine rocky reefs, as occurs on coastal reefs (Champion et al. 2015). However, it is unclear how reliant estuarine fish assemblages are on zooplankton compared to coastal reefs, and whether macrophytes or detritus are more important energy sources than for the open coast.

The goal of our study was to compare across estuarine and coastal habitats, the fish functional feeding groups and their basal energy sources. Basal energy sources supporting fish assemblages can be calculated by combining a diet matrix with the relative biomass of fish functional feeding groups (Truong et al. 2017). Our study followed this approach to conduct a fish assemblage food web analysis of three estuarine habitats (natural reef, artificial reef, seagrass) as well as (for comparison) coastal rocky reefs. This analysis incorporated fish surveys of two estuaries, existing fish surveys, and published dietary information. We compared estuarine habitats more generally based on their biomass of functional feeding groups. Two fish survey techniques were used in this study (baited remote underwater video and visual census), so survey techniques were also compared in terms of the species and functional feeding groups observed.

Methods

Estuaries and Study Design

Fish communities were surveyed in two estuaries in south-eastern Australia; Botany Bay, an ocean embayment; and Lake Macquarie, a wave-dominated estuary (Roy et al. 2001; Fig. 1). In both estuaries, three habitats types: natural reefs, artificial reefs (Reef Balls®) (Folpp et al. 2020) and seagrass beds, were investigated using stereo baited remote underwater videos (hereafter referred to as BRUVs; Cappo et al. 2004; Harvey et al. 2007). Each estuary was monitored during the cooler, winter/spring (June-November), and warmer, summer/autumn (December- May) seasons over 3 years.

BRUVs consisted of two GoPro Hero 7 cameras in SeaGIS housings mounted to a frame, and allowed for accurate length measurements of fish (Langlois et al. 2020). Three replicate BRUVs were deployed at three sites within each habitat during warm and cool seasons, resulting in 5 seasonal trips over the study period. Deployments lasted for 30 minutes, with previous research showing this is a sufficient soak time for estimates of fish diversity and relative abundance for comparative purposes in NSW (Harasti et al. 2015). BRUVs were baited with 500 g of crushed pilchards (*Sardinops sagax*) secured in a mesh bag which extended ~ 1 metre horizontally from the camera housing, attracting fish into the field of view (Watson et al. 2005).

The estuarine BRUV footage was analysed using SeaGIS 'EventMeasure' software (www.seagis.com.au), where the relative abundance (MaxN) was determined for each species (Cappo et al. 2004; Dorman et al. 2012). All individuals were identified using published references (Kuitert 1993), classified to genus, and species where possible.

Estuarine Fish Assemblage Composition

Estuarine fish assemblages were compared using MaxN and their subsequent estimated biomass within the nine functional feeding groups used by Truong et al. (2017) and Holland et al. (2020) (Supplementary Table S1). The nine functional feeding groups included three elasmobranch groups (piscivorous sharks, non-piscivorous sharks, and invertivore rays), and six teleost groups (piscivores, invertivores, soft-bottom fish, omnivores, zooplanktivores and herbivores). These teleost groups were further classified as either 'coastal' for predominantly pelagic fish, 'demersal' for species that reside on both hard and soft substrate, or 'reef' as inhabiting predominantly hard benthic substrate, as this influences their diet composition (Supplementary Table S1 and S2; Truong et al. 2017). The functional feeding group biomass were compared among habitats, estuaries and between the cooler and warmer seasons.

To estimate the biomass of the functional feeding groups, for each deployment the lengths of all individuals contributing to MaxN were measured in EventMeasure (per Langlois et al., 2021). Length data was then aggregated at the estuary level to determine the mean length of each species within each estuary. The MaxN for each species within each replicate BRUV drop was converted to biomass using $W = aL^b$, where W is the average weight of the species, L is the mean length determined above, and a and b are constants derived from Fishbase (Froese 2019) or published literature where possible (Supplementary Table S1). The average weight was then multiplied by the MaxN value to calculate the relative biomass of each species within each BRUV deployment. Functional feeding group biomass was then calculated by summing the biomass of species within each group. The overall functional feeding biomass for each variable (Estuary, Habitat, Seasons) was taken as an average from three replicate BRUV deployments.

Multidimensional scaling (MDS) plots based upon the Bray-Curtis similarity matrix (Clarke and Gorley 2006) were generated to depict patterns of functional feeding group biomass among the three habitats, two seasons and two estuaries. All estuarine data was fourth root transformed to reduce the influence of rare or highly abundant functional feeding groups (Anderson et al. 2008). Where too few unique

Loading [MathJax]/jax/output/CommonHTML/jax.js p be run, Monte Carlo random draws were applied (Anderson

and Robinson 2003). Principle coordinate ordination (PCO) was conducted on a matrix of functional feeding group biomass to determine the major groups driving dissimilarities between the three estuarine habitats. Permutational Analysis of Variance (PERMANOVA) was then run on the functional feeding group biomass similarity data comparing between Estuaries (2 levels: Botany Bay, Lake Macquarie), among Habitats (3 levels: Artificial Reef, Natural Reef, Seagrass), and between Seasons (2 levels: Cool, Warm), with all factors considered fixed and orthogonal.

Coastal Fish Assemblage Composition

Species composition and MaxN data for Port Stephens coastal rocky reefs was sourced from Harasti et al. (2018). A subset of this dataset, from Broughton (32.62°S, 152.32°E) and Fingal Islands (32.75°S, 152.19°E; Fig. 1) during 2015 and 2016, was used for both cool (July-September) and warm (February-April) seasonality. The reefs were within depths of 20–35 metres, and were analysed with the same BRUV methodology previously described for the estuarine component.

MaxN was averaged across the 8 replicate BRUV deployments at each site during each Season. PERMANOVA was conducted on the Site (2 levels: Broughton Island, Fingal Island), Season (2 levels: Cool, Warm) and Year (2 levels: 2015, 2016), with all factors considered fixed and orthogonal. This analysis allowed the examination of possible among year-effects on fish community composition. Species abundance data was converted to biomass using the same methods as used with the estuarine dataset, with species lengths measured in EventMeasure. Because Harasti et al. (2018) only measured lengths of recreationally and commercially important species, additional length data for all other species was obtained by reanalysing videos from selected deployments which were known to contain high abundances of species previously not measured. In a few cases, the Port Stephens BRUV footage was too poor to calculate reliable length data (e.g. poor visibility or complete length of fish obscured due to other fish or camera angle), so species lengths were taken from a nearby study (Truong et al. 2017).

Species from the Port Stephens dataset were allocated to functional feeding groups as per the estuarine habitats (Supplementary Table S1). The biomass of the species was summed across the functional feeding groups to calculate a group biomass. These were then converted to relative proportional biomass of each functional feeding group, per Site and Season, across the fish community, to be comparable with the estuarine data.

The mean energy source results from Truong et al. (2017) were included as an additional example of a typical nearby coastal reef location, to provide more context for the patterns observed at other locations. These results were derived from 14 sites collected by the Reef Life Survey (RLS; Edgar et al. 2020) and three additional sites surveyed using visual census and remote underwater video (RUV).

Baited versus Unbaited Methods in Coastal Habitats

As some functional feeding groups, such as herbivores, may be under-represented using BRUV, underwater visual census data was also obtained from the RLS program for the Port Stephens coastal

influenced the observed fish assemblage composition. Three

RLS survey sites closest to the BRUV survey positions around Fingal Island were used: Fingal Island North East (32.74°S, 152.20°E), Fingal Island Sanctuary (32.75°S, 152.19°E) and Fingal Sponges Fingal Island (32.74°S, 152.21°E) (Supplementary Figure S2).

Species counts from RLS surveys were averaged across the two replicate surveys conducted in each site during both warmer (November-April) and cooler (June-September) seasons, and fish lengths were converted to biomass. The underwater visual census estimates were then converted to relative functional feeding group biomass and compared to the coastal BRUV data with ANOVA with Tukey post-hoc tests used to determine the direction significant effects. Finally, the BRUV methods used by Harasti et al. (2018) at Port Stephens, the RUV methods used by Truong et al. (2017) in Sydney and the RLS data sourced from both locations were also compared using ANOVA. The Sydney data also contained diver surveys adopting a similar method to RLS at each of the RUV locations.

Food Web Analysis and Energy Sources

A diet matrix, developed by Truong et al. (2017) was used to define local food webs and identify basal energy sources supporting fish biomass (see Supplementary Table S2). The matrix identified links between predators and prey connected through fish and non-fish functional feeding groups to the basal energy sources: phytoplankton, macrophytes and detritus. For some analyses, zooplankton was used a basal food source in place of phytoplankton due to the direct links between zooplankton and higher trophic groups. Additionally, zooplankton are the main consumers of phytoplankton, meaning the basal support provided by phytoplankton to the fish assemblage would only be marginally higher than zooplankton. This single diet matrix was used to define the food web for all surveyed habitats, meaning that any difference in calculated energy sources between systems and habitats is due solely to differences in species composition. For example, if a coastal site has a greater proportion of zooplanktivorous fish than an estuarine site, zooplankton will support a greater proportion of the fish assemblage. Deriving diet matrices for each system or habitat would probably lead to more accurate basal energy source estimates, but this would require extensive high-resolution diet data which is typically not available. Estuarine visual surveys would improve the confidence in using BRUV methods for food web analysis, but all such visual methods are limited by daylight and water visibility.

Once the diet matrix was specified, the importance of the trophic pathways to the fish assemblage was measured by weighting these pathways using the observed relative biomass of the functional feeding groups (Truong et al. 2017). Firstly, the basal energy sources were estimated for each functional feeding group by summing the product of every possible unique pathway between the fish group and a basal energy source. Secondly, the group-specific estimates were multiplied by the relative biomass of each group and then summed to create an assemblage-wide estimate of support for each basal energy source. See Supplementary Figure S1 for a worked example of estimating the proportion of basal food sources supporting a functional feeding group. There are typically many pathways in a food web (hundreds of thousands), so these calculations were automated using the algorithm of Truong et al. (2017), run in R Version 4.0.3 (R Core Team 2020).

Sensitivity Analysis

Fish diets are inherently variable due to food availability, seasonality, and other ecological processes (Becker and Laurenson 2007). To explore the influence of this variability and uncertainty on basal energy source calculations, we conducted a sensitivity analysis which manipulated the proportion of prey items consumed by each functional feeding group. The dietary proportion of individual prey items were varied by $\pm 10\%$, with energy sources re-calculated each time. All of the other dietary items for the targeted functional feeding group were adjusted to balance the relative diet matrix. This was repeated 50 times per functional feeding group, with the prey item and 10% increase or decrease selected at random. This provides a mean value for each consumer group and energy source, representing the influence of variation in that consumer's diet on the estimated energy sources values. The complete output of this analysis is reported in Supplementary Table S3 for each of the eight survey sites and habitats. All analyses in this study were done using Primer v6+ (Anderson et al. 2008) or R (R Core Team 2020).

Results

Estuarine Fish Assemblage Composition

Functional feeding group biomass differed between estuarine Habitats, with reef habitats aligning closer together than seagrass habitats. Permanova results indicated a significant difference in functional feeding group biomass with a three-way interaction between estuary, habitat and season. The PCO analysis indicated this dissimilarity was largely due to the rays observed at the Botany Bay seagrass sites (Fig. 2). Post-hoc pairwise tests of the interaction effect showed differences among estuaries was caused by different communities within only the seagrass habitat during cool seasons ($t = 4.4003$, $P(\text{MC}) = 0.0133$). For Habitats, pairwise tests indicated differences between natural reef and seagrass in the warm seasons in Lake Macquarie were significantly different ($t = 12.184$, $P(\text{MC}) = 0.0032$), as well as among natural reef and seagrass ($t = 4.3558$, $P(\text{MC}) = 0.0106$), and artificial reef and seagrass ($t = 3.2412$, $P(\text{MC}) = 0.0359$) in the cool seasons in Botany Bay. For the Seasonal factor, only seagrass replicates within Lake Macquarie were significantly different between warm and cool seasons ($t = 5.7764$, $P(\text{MC}) = 0.0024$).

Energy sources for estuarine fish assemblages

The assessments of basal energy sources supporting the fish communities revealed the majority of fish biomass within estuaries are supported by macrophytes (Fig. 3). Across all three habitats, in both estuaries, there was a significant difference in the proportion of the fish community supported by each basal energy source ($F = 5.725$, $P < 0.0001$). Post-hoc tests showed these differences were driven by variation in macrophytes and detrital input ($P = 0.043$). There was no significant difference detected among the contributions by zooplankton and detritus or macrophytes ($P > 0.05$) to supporting fish communities, with this trend consistent among estuaries and habitats (Fig. 3).

Differences Among Survey Methods

There were differences in the coastal reef fish assemblages at Port Stephens between surveys using BRUV and the RLS (Supplementary Figure S3), but no differences were ascribed to herbivorous fish biomass. The three RLS sites are more similar to one another compared to the two BRUV study sites (Supplementary Figure S3). SIMPER analysis identified 5 species each contributing between 5–18% to the dissimilarity. These included four planktivores: Australian mado (*Atypichthys strigatus*; 18.07%), onepot puller (*Chromis hypsilepis*; 14.72%), yellowtail scad (*Trachurus novaezelandiae*, 10.22%), eastern hulafish (*Trachinops taeniatus*; 9.60%) and one demersal non-piscivore, snapper (*Chrysophrys auratus*; 5.64%). Australian mado and snapper were recorded in higher abundances in BRUV surveys, and onepot puller, yellowtail scad and eastern hulafish were recorded more abundantly in RLS.

When converted to biomass, the major functional feeding groups that differed between baited camera and diver surveys at Port Stephens were invertivores, non-piscivorous sharks, piscivores, rays and zooplanktivores (Fig. 4). Overall, there was a marginally significant difference between the BRUV and visual census methods at Port Stephens (PERMANOVA: Pseudo- $F = 2.9836$, $P = 0.046$). Visual census estimated higher proportional biomass of the schooling functional feeding groups, such as zooplanktivores, whilst the BRUVs estimated a higher biomass of the typical recreationally and commercially targeted groups (piscivores, non-piscivorous sharks and rays). When assessing the combined BRUV and visual census data at Port Stephens, and the RUV at Sydney coastal sites there was no significant difference overall in the relative functional feeding group biomass (PERMANOVA, $P > 0.05$).

Estuarine versus Coastal Fish Assemblage Compositions

Multivariate visualisation shows the estuarine and coastal rocky reef functional feeding group biomass were distinctively different across both study regions, with both coastal regions also showing clear differences to all estuarine habitats (Fig. 5).

To identify general patterns between estuarine and coastal systems, the relative biomass of functional feeding groups was also subsequently averaged across the three estuarine habitats, and the corresponding BRUV and RLS coastal datasets were combined (Fig. 6). Omnivores represented higher proportion of the fish community biomass in estuaries than on coastal reefs (Fig. 6). Piscivores and herbivores contributed higher proportions of the overall biomass on coastal reefs, while no herbivores were observed in either estuarine ecosystem. The zooplanktivores had similar relative biomass in Botany Bay estuarine and both coastal fish communities, despite the BRUV deployments recording twice the diversity and functional feeding group biomass on coastal reefs than on the estuarine habitats.

Estuarine versus Coastal Energy Sources

Comparison of the basal energy sources supporting fish assemblages in each of the three estuarine habitat types and the coastal sites (Table 1) revealed a significant two-way interaction between location ($n = 11$) and basal energy source (ANOVA, $F_{30,252} = 5.251$, $P < 0.0001$). Estuarine fish assemblages were supported by higher levels of macrophytes than fish on coastal rocky reefs, but post-hoc tests also identified significant differences between both estuarine seagrass sites. The Lake Macquarie artificial Loading [MathJax]/jax/output/CommonHTML/jax.js different to Port Stephens, with seagrass also being

significantly different to Sydney ($P < 0.05$). Detritus supported relatively similar levels of biomass across habitats (Table 1), except at Botany Bay in which seagrass habitat had a significantly higher percentage of relative fish biomass supported by detritus ($P < 0.05$; see Fig. 3). Zooplankton levels were only significantly different in the Botany Bay seagrass and the Port Stephens RLS dataset ($P < 0.05$). Supplementary Tables S4a and S4b comprise a complete list of the significant results of the significant interaction of both location and basal energy source type.

Table 1

Proportion of the fish community biomass supported by different basal energy sources for each of the habitats and sites. These values use the mean fish biomasses across replicates and survey trips, and thus encompass considerable variation in assemblage composition at each site and habitat. The 'unidentified' source represents unknown dietary items in the diet matrix. Across each of the sites the percentage of basal energy can be greater than one due to functional feeding groups relying on more than one basal energy source.

Site	Zooplankton	Phytoplankton	Macrophytes	Detritus	Unidentified
PS- RLS	0.45	0.49	0.25	0.24	0.02
PS- BRUV	0.46	0.51	0.19	0.28	0.01
Port Stephens Average	0.46	0.51	0.21	0.27	0.02
Sydney- RLS	0.48	0.51	0.28	0.20	0.01
Sydney- RUV	0.53	0.54	0.31	0.14	0.01
Sydney- Transect	0.59	0.59	0.28	0.12	0.01
Sydney- Average	0.53	0.56	0.31	0.12	0.01
Botany Bay- Artificial reef	0.43	0.47	0.29	0.21	0.02
Botany Bay- Natural reef	0.35	0.42	0.31	0.28	0.01
Botany Bay- Seagrass	0.17	0.28	0.20	0.51	0.01
Botany Bay- Average	0.32	0.39	0.27	0.33	0.01
Lake Macquarie- Artificial Reef	0.33	0.38	0.39	0.20	0.02
Lake Macquarie- Natural Reef	0.34	0.39	0.37	0.22	0.03
Lake Macquarie- Seagrass	0.13	0.19	0.58	0.21	0.02
Lake Macquarie- Average	0.27	0.32	0.45	0.21	0.02

A general comparison of basal energy sources for estuarine and coastal fish assemblages (i.e. habitats and survey techniques combined) reveals broad differences (Fig. 7), with coastal reef fish having on average 1.5 times more zooplankton than estuarine fish ($P < 0.05$). The two estuaries

showed differences, with Lake Macquarie being mostly macrophyte supported, and Botany Bay being macrophyte and detritus supported (Fig. 7). Variation among habitats and surveys was strong, however, so there were no significant differences in proportions for any energy source between both estuaries or between both coastal locations.

The averaged estuarine and coastal functional feeding groups, across habitats and survey techniques, were reliant on different levels of basal energy sources, with coastal rocky reef fish relying on a higher proportion of zooplankton than estuarine fish (Fig. 7) across both estuaries and coasts ($P < 0.05$). The percentage of detrital support was only significantly different between Botany and Sydney ($P < 0.05$), while macrophytes were significantly different between Lake Macquarie and both coastal systems ($P < 0.05$). There were no significant differences between estuaries or coasts in their relative percentages of functional feeding groups being supported by the major basal energy sources. Within locations there were significant differences in the percentage of the functional feeding groups supported by each basal energy source at Lake Macquarie estuarine ($F_{2,186} = 10.4$, $P < 0.05$), Port Stephens ($F_{2,186} = 27.2$, $P < 0.05$) and Sydney coastal sites ($F_{2,186} = 27.8$, $P < 0.05$).

Sensitivity Analysis

The sensitivity analysis reveals the functional groups whose diets have the most influence on the energy source results (and thus how results may be influenced by diet uncertainty or variation). The analysis showed that altering the diet consumption by $\pm 10\%$ caused $< 4\%$ change in the basal energy sources supporting communities across all estuarine and coastal sites (Supplementary Table S3). The sensitivity of basal energy sources to changes in diet was consistent across estuarine and coastal habitats (Table 2). Within seagrass habitats, the modification of omnivores diets caused the most variability across all basal energy sources (0.2–1.79%), and rays in Botany Bay seagrass (0.4–1.62%). Zooplanktivores in both estuarine habitats, as well as omnivores and invertivores within Lake Macquarie, caused the most variability in reef habitats' basal food sources (0.4–3.24%). For the coastal sites, the variability of basal energy sources was most closely aligned to the variability in invertivore and zooplanktivore diets. Changes in the diets of the highest functional feeding groups, such as piscivores and sharks, had the least influence on the percentage change of functional feeding groups supported by basal energy sources ($< 1\%$). Thus, obtaining accurate diet information was generally most important for consumers that occur in high abundances and those near the base of the food web.

Table 2

Results of the sensitivity analysis presenting the percentage change in the 5 basal energy source outputs (Z = zooplankton, P = phytoplankton, M = Macrophytes, D = Detritus, Un = Unidentified) per functional feeding group. White indicates minimal change (< 0.1%); Red = increased percentage change of the energy food source with 4 shades indicating the increased variation in the energy source outputs with alterations to the food web. Darker red indicates higher level of change in basal energy source outputs with alterations to diet sources. This sensitivity analysis highlights that variation in diet sources has a greater impact on basal energy sources for highly abundant species close to the bottom of the food web that may not have high variation in their diets.

	Lake Macquarie Natural Reef					Broughton Island- BRUV				
Piscivorous Sharks	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.04	0.03	0.08
Non Piscivorous Sharks	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00
Coastal Pelagic Piscivores	0.15	0.10	0.05	0.11	0.04	0.19	0.14	0.18	0.16	0.12
Demersal Invertivores	0.16	0.19	0.33	0.32	1.33	0.06	0.08	0.45	0.21	1.30
Reef Piscivores	0.00	0.00	0.00	0.00	0.00	0.04	0.03	0.08	0.00	0.03
Cephalopoda	0.02	0.01	0.00	0.02	0.00	0.03	0.02	0.01	0.03	0.00
Rays	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.13	0.12	0.02
Reef Invertivores	0.00	0.01	0.02	0.02	0.04	0.02	0.03	0.23	0.11	0.25
Soft Bottom Fish	0.02	0.01	0.01	0.03	0.00	0.03	0.02	0.05	0.06	0.00
Demersal Omnivores	0.43	0.42	0.40	0.25	0.48	0.08	0.08	0.25	0.04	0.13
Reef Omnivores	0.05	0.11	0.33	0.39	0.00	0.00	0.01	0.08	0.04	0.00
Coastal Zooplanktivores	0.97	0.69	0.20	0.89	0.00	0.67	0.50	0.41	0.78	0.00
Reef Zooplanktivores	0.56	0.36	0.09	0.47	0.13	0.22	0.15	0.11	0.24	0.11
Reef Herbivores	0.00	0.00	0.02	0.02	0.00	0.01	0.01	0.15	0.08	0.00
Soft Bottom Decapods	0.04	0.08	0.04	0.15	0.00	0.04	0.08	0.11	0.17	0.00
Carnivorous Reef Zoobenthos	0.03	0.04	0.03	0.02	0.00	0.02	0.02	0.05	0.01	0.00
Herbivorous Reef Zoobenthos	0.19	0.34	2.27	3.57	0.00	0.09	0.17	2.85	1.92	0.00
Soft Bottom Zoobenthos	0.70	1.41	0.00	2.53	0.00	0.67	1.33	0.00	2.86	0.00
Sessile Filter Feeders	0.46	0.03	0.00	0.06	0.00	0.17	0.01	0.00	0.03	0.00
	Z	P	M	D	Un	Z	P	M	D	Un

Discussion

Compared to the dominance of zooplanktivory and pelagic subsidies observed on temperate coastal reefs (this study; Truong et al. 2017; Holland et al. 2020), fish assemblages of estuarine ecosystems were more dependent on macrophytes and occasionally detritus. The fish biomass supported by plankton in estuaries was approximately half that of coastal reefs (even when combining estuarine reefs and seagrass to create a general 'estuarine assemblage'). Herbivorous fish were not recorded in either estuary (due to the BRUV method), yet due to the large biomass of omnivorous fish which graze on macrophytes (Supplementary Table S2), macrophytes were still a dominant energy source within estuaries (Dennison et al. 1993; Chartrand et al. 2012). This underestimate may not be large, given the abundance of true herbivores in estuaries is relatively low in the region (Gray et al. 2010; Possamai et al. 2018)

The biomass of functional feeding groups varied among habitats within estuaries, with natural and artificial reefs supporting similar compositions, whereas seagrass, driven by the dominance of rays was different, particularly in Botany Bay. Rays feed on soft bottom decapods, zoobenthos and bivalves (Supplementary Table S2), that commonly burrow into sediment (Glaspie and Seitz 2017), with seagrass habitats providing increased access to prey. Reef habitats have increased habitat complexity, providing food availability and protection from predators (Folpp et al. 2013), which may have driven increased species richness.

Functional feeding group biomass at Broughton and Fingal Island did not vary annually, however there were differences among Sites and between Seasons. Biomass was strongly influenced by the increased presence of large schools of piscivores in summer, with the overall average biomass increasing 10-fold. This is consistent with previous studies that observed a higher fish biomass in the warmer seasons. For example, the abundance of piscivores such as yellowtail kingfish (*Seriola lalandi*) varies seasonally and is linked to the macro coastal processes such as the delivery of warm tropical waters by the East Australia Current (Gillanders et al. 2001a; Champion et al. 2018). This variation shows the importance of multiple surveys for estimating a site- or habitat-wide fish assemblage, and that energy flow within a fish assemblage is likely to show fine-scale variation based on that assemblage's composition.

Our understanding of fish abundances and assemblage structure is influenced by survey methods (Watson et al. 2005; Heagney et al. 2007; Colton and Swearer 2010; Watson et al. 2010; Harvey et al. 2012; Lowry et al. 2012). For example, snapper (*Chrysophrys auratus*) is a popular recreational fishing species which exhibits diver avoidance behaviour (Colton and Swearer 2010; Watson et al. 2010), and were therefore recorded in higher abundances through BRUVs, rather than underwater visual census methods. Other species may be attracted to the activity and aggregation of other fish (Watson et al. 2005), which may have contributed to a higher abundance of mado being recorded with BRUVs, rather than underwater visual census surveys. The group that was most abundant in underwater visual census surveys and contributed the greatest to the dissimilarity between survey methods were schooling zooplanktivores, including onspot puller, yellowtail scad and eastern hulafish. When fish abundance was converted to relative biomass of functional feeding groups, differences were not evident between BRUV

and RLS methods and therefore, for the purpose of estimating the basal energy sources, the BRUVs surveys were a reasonable method.

Estuarine and coastal ecosystems supported distinctly different functional feeding groups, with the relative biomass highlighting the dominance of different groups across systems. The key estuarine functional feeding group were the omnivores which dominated the estuarine habitats, representing a higher relative biomass than on coastal reefs. Lake Macquarie and Botany Bay both have urbanised shorelines and omnivores can dominate artificial habitats within these estuaries (Folpp et al. 2013) due to the increased habitat complexity (Moreau et al. 2008; Mayer-Pinto et al. 2018). The predominance of piscivore biomass on coastal rocky reefs was driven by large yellowtail kingfish (*Seriola lalandi*) which are more abundant in the coastal-pelagic environment than in estuaries (Gillanders et al. 2001b; Champion et al. 2019). The relative biomass of zooplanktivores was similar on estuarine and coastal reefs, illustrating that there can be large differences in energy sources among habitats within a location (i.e. estuarine seagrass and reef habitats).

Significant interactions between basal energy source and location were driven by the increased detrital support of fish communities in the seagrass estuarine sites. Rays, for example, dominated the functional feeding group relative biomass in seagrass habitats, particularly in Botany Bay, and the trophic links between soft bottom decapods and zoobenthos drove the percentage basal support. They are often keystone predators in their ecosystems and exert top-down controls on the other groups present (Libralato et al. 2006), suggesting the influence of detritus is important in this estuarine habitat (Akin and Winemiller 2006). On the other hand, the dominance of planktivory on coastal rocky reefs of Port Stephens is consistent with other studies of nearby coastal regions (Champion et al. 2015; Truong et al. 2017; Holland et al. 2020).

Fish diets vary spatially and temporally, with some of this variation possible between coastal and estuarine ecosystems. Diets also vary within a functional feeding group based on different species and their morphology (Motta 1988; Bellwood and Choat 1990), and across habitats and due to food availability (Akin and Winemiller 2006). The sensitivity analysis in this study revealed that variation in diets of lower trophic groups (e.g. zooplanktivores), and those with a higher biomass (e.g. omnivores and invertivores) had a higher influence on the proportion of the functional feeding group biomass and their basal energy sources. Uncertainty in the diet compositions in some of the higher trophic groups (e.g. invertivores) can drive this increased variation, which could be improved through stable isotope analysis of gut contents (Abrantes and Sheaves 2009). Additionally, lower trophic groups, such as zooplanktivores, have a large influence on basal energy sources due to their homogenous diets, and as they are prey for piscivores. Developing specific diet matrices for the estuaries, habitat type and seasonality would reduce some of the uncertainty in the functional feeding groups diets. For example, our BRUV and RLS surveys were done at different times and fish assemblage composition may differ due to factors other than survey method, but our comparison was useful to reveal broad biases such the detection of herbivorous fish among methods.

Conclusion And Limitations

Temperate rocky reef ecosystems support a high diversity of fishes which vary from coastal to estuarine ecosystems. The fishes of estuarine ecosystems were more omnivorous and thus supported more by macrophytes, whereas coastal reefs are dominated by zooplanktivorous fish and supported predominantly by plankton. Besides considerable variation, on average ~ 20% of the fish biomass in seagrass is supported by plankton, compared to ~ 30% on estuarine reefs and ~ 50% on coastal reefs (Fig. 3, Fig. 7). However, fish in estuarine seagrass habitats can also be supported by detritus, as was observed in Botany Bay. Other estuary types such as coastal lagoons (ICOLLs or TOCs) may support different fish functional feeding groups, such as those dominated by detritivores (e.g. mullet). Our analysis could be improved with better methods for herbivorous fishes in estuaries (i.e. un-baited surveys) and a better understanding of seasonal and ontogenetic variation in diet.

Our results indicate that all coastal and estuarine processes will affect fish assemblages, but those processes that influence macrophytes (e.g. eutrophication, habitat loss) will be more influential in estuaries, whereas those that influence plankton supply (e.g. upwelling, current flow) will be more influential in coastal systems. The strong variation among surveys and sites, highlights the need to further investigate the variation in diets and functional feeding group composition within estuarine habitats such as mangroves, to better understand the potential impacts of climate change, rainfall, seagrass loss and urbanisation on basal energy sources and fish food webs.

Declarations

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Consent to participate- Not applicable.

Consent for publication- All authors consent to the publication of this manuscript.

Availability of data and material- Data and materials available at <https://github.com/belindagoddard/Trophic-Basis-Fish-Assemblage>

Code availability- Code available at <https://github.com/belindagoddard/Trophic-Basis-Fish-Assemblage>

Authors contributions- The analysis and initial draft was completed by Belinda K. Goddard. Iain M. Suthers and Alistair Becker conceived the study. James A. Smith updated and improved the numerical scripts. All authors contributed to the analysis and writing of the paper.

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Figures

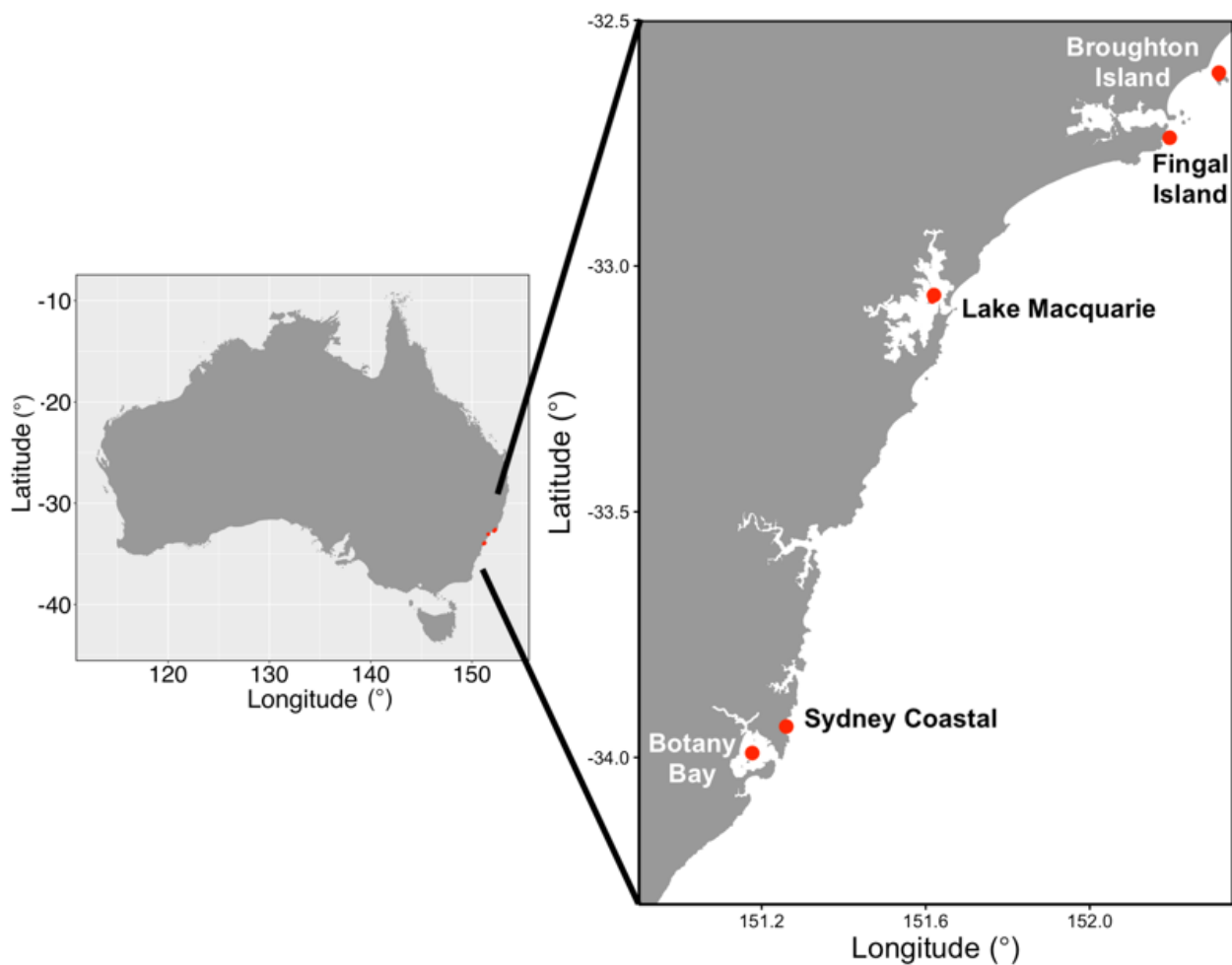


Figure 1

Site map of the two estuarine (Botany Bay and Lake Macquarie) and two coastal (Sydney and Port Stephens) study locations. Rocky reefs at the two islands (Broughton and Fingal Island) are classified within the Port Stephens coastal rocky reefs.

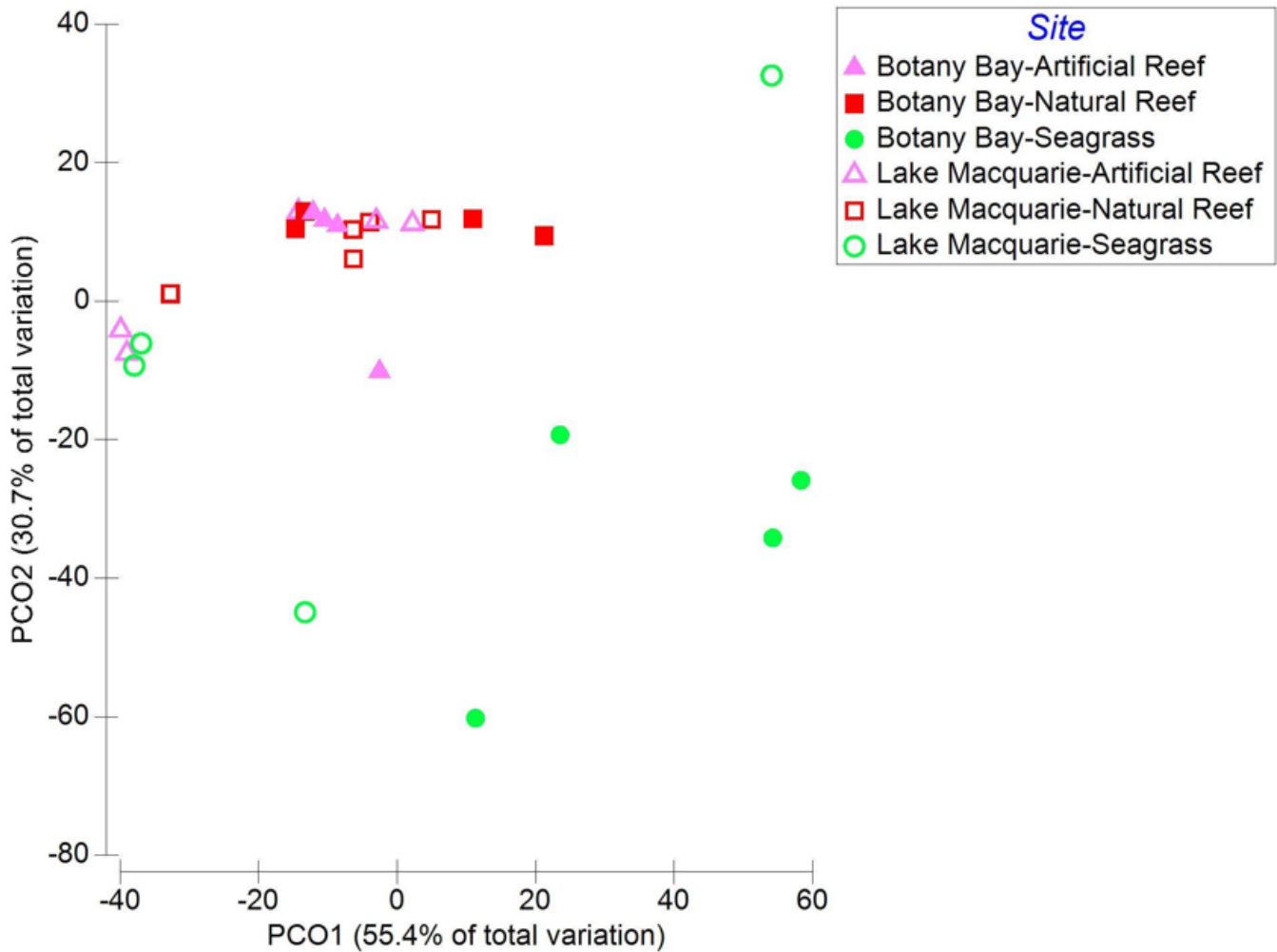


Figure 2

Principle Coordination Ordination (PCO) of the relationship of the estuarine functional feeding group biomass across the three habitats in the Botany Bay and Lake Macquarie estuaries (triangles artificial reef; squares natural reef; circles seagrass). Solid symbols represent habitats Botany Bay, and hollow symbols represent habitats in Lake Macquarie.

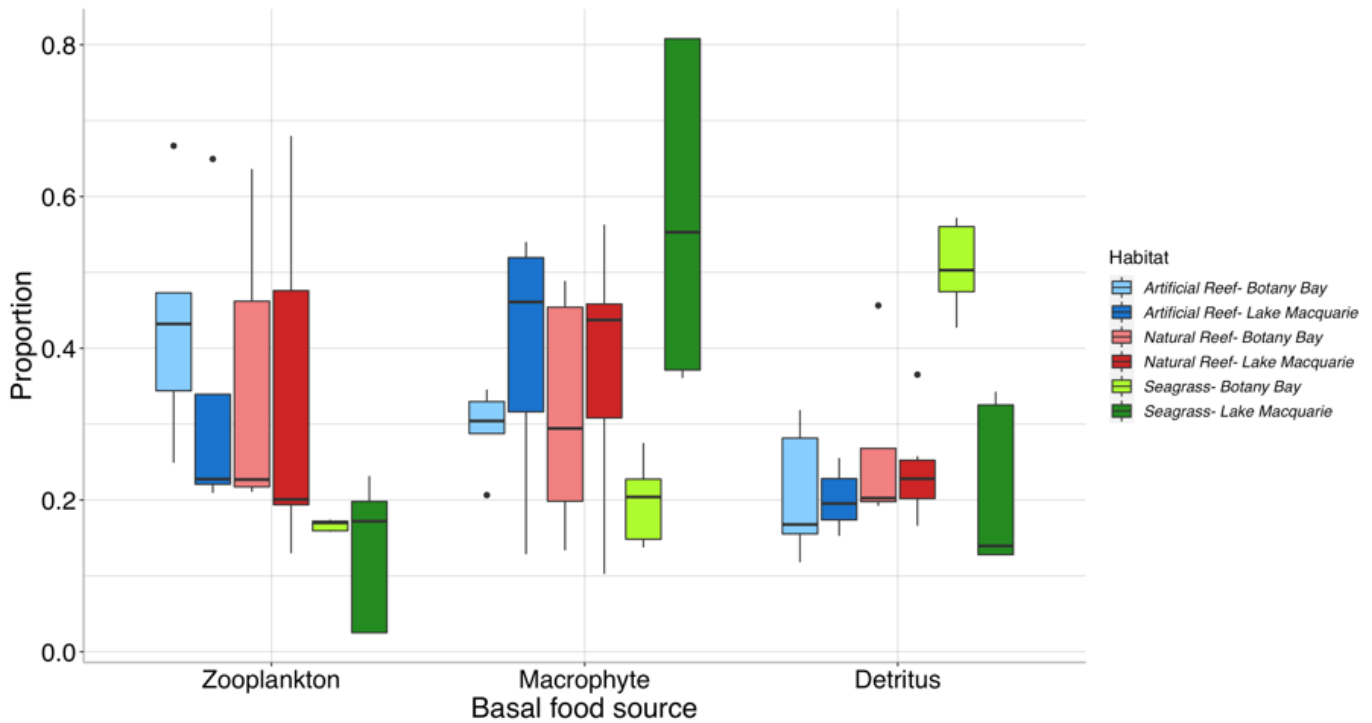


Figure 3

Boxplot showing percentage of basal energy sources supporting the biomass of three functional feeding groups in the three estuarine habitats of Botany Bay and Lake Macquarie. The planktonic subsidy is based on zooplankton; the values based on phytoplankton are marginally larger. The lighter shade of the paired colours represents Botany Bay, while the darker shade represents Lake Macquarie. The values in each boxplot represent sampling trips in each habitat, with fish biomasses taken as the mean of the replicates within each sampling trip. Thus, the spread in these boxplots represents variation in the relative biomass of the observed fish assemblage among different sampling days. The middle dark line represents the median, while the box surrounds the 25-75% quantile of variation in basal energy sources. The whiskers cover ± 1.5 times the interquartile range (IQR).

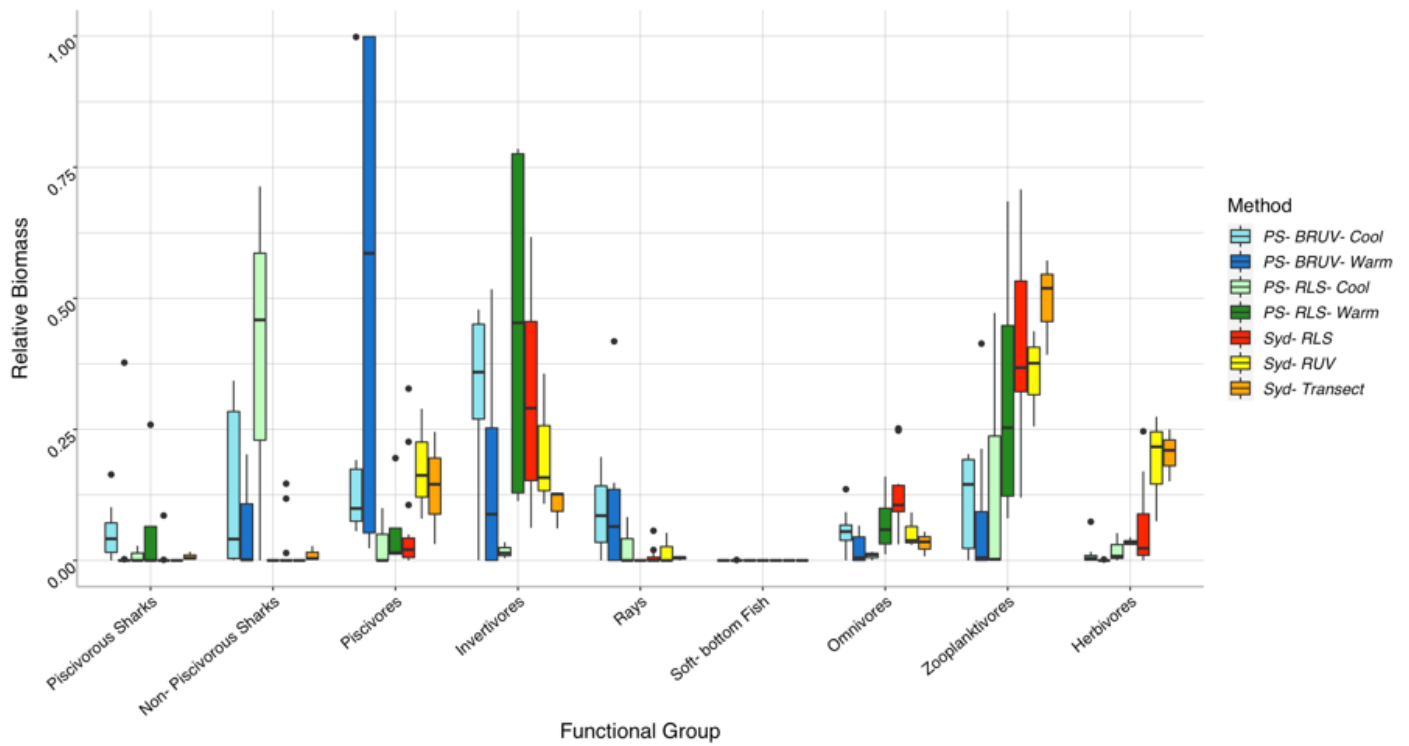


Figure 4

The average relative biomass recorded through different survey methods at the two coastal sites. The solid line in the middle of the bar is the median; the bar represents middle 50% of values; the lines indicate ± 1.5 times the interquartile range (IQR) and outliers are shown by a dot. The coastal Port Stephens data contains seasonal estimates, whilst the coastal Sydney data only contains data recorded in the warmer water months. (PS: Port Stephens coastal which is the average of both Broughton and Fingal Island; Syd: Sydney coastal; BRUV: Baited Remote Underwater Video; RLS: Reef Life Survey; RUV: Remote Underwater Video).

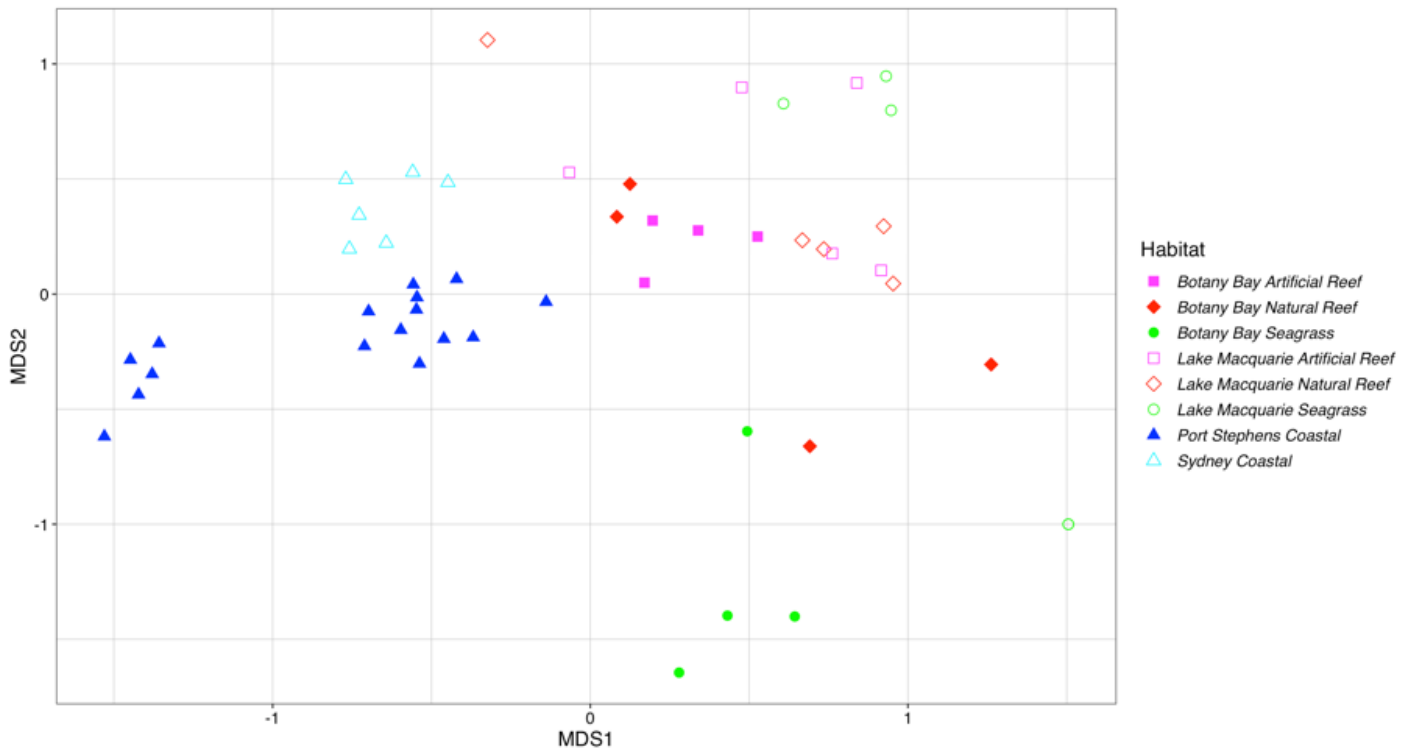


Figure 5

MDS ordination among samples of functional feeding group biomass across the averaged replicates for coastal and rocky reefs. The data is averaged across seasons. Habitats within the estuarine sites are displayed separately, with colours corresponding to the habitat type. Hollow symbols for the estuarine points reflect the Lake Macquarie data and solid symbols reflect Botany Bay. The coastal sites of Port Stephens are the average of both Broughton and Fingal Island from Harasti et al., 2018, and the Sydney sites are the average for the transect and unbaited RUV and visual census data from Truong et al. (2017).

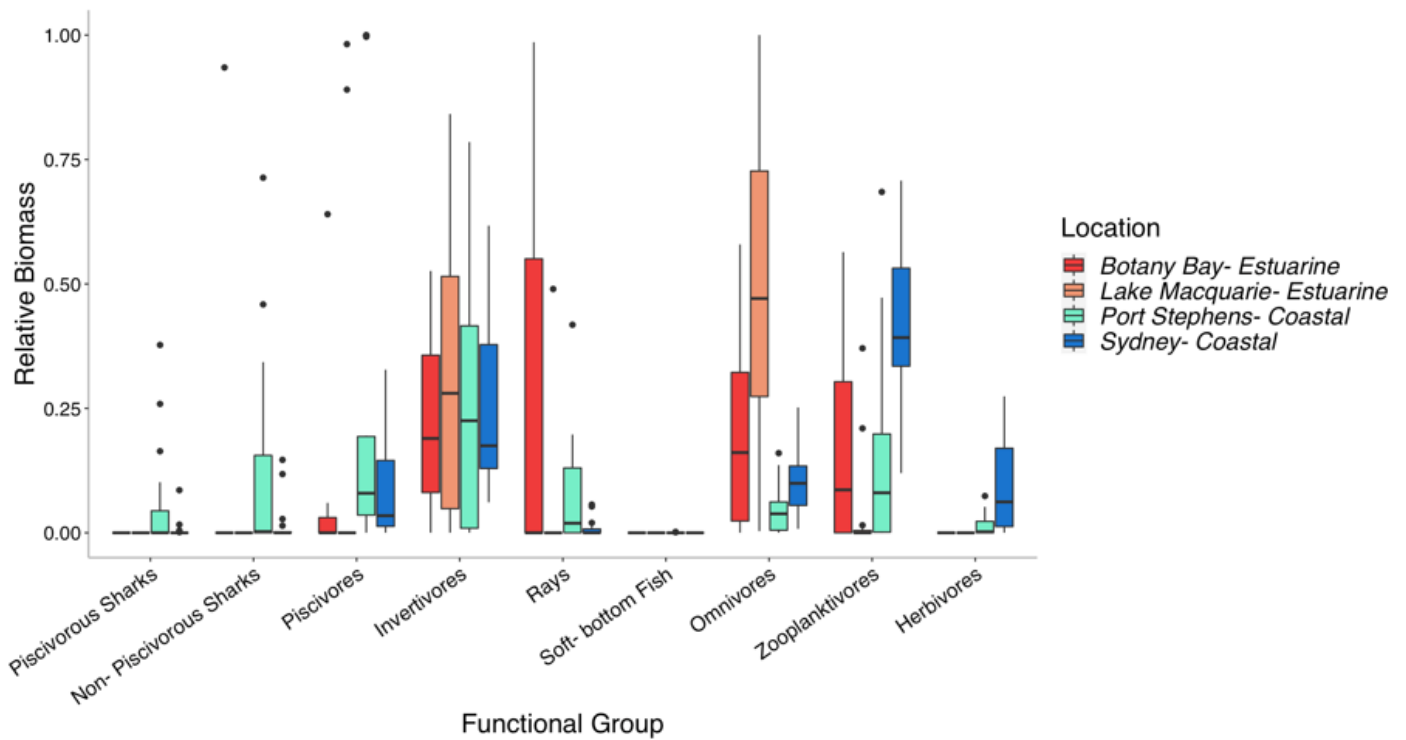


Figure 6

Boxplot reflecting the relative functional feeding group biomass on estuarine and coastal reefs. Data was drawn for all the averaged survey days (2-8 replicates), with seasonal data clustered together. The estuarine data is also the average across all three habitats. The middle dark line represents the median, while the box surrounds the 25-75% quantile of variation in basal energy sources. The whiskers cover ± 1.5 times the interquartile range (IQR).

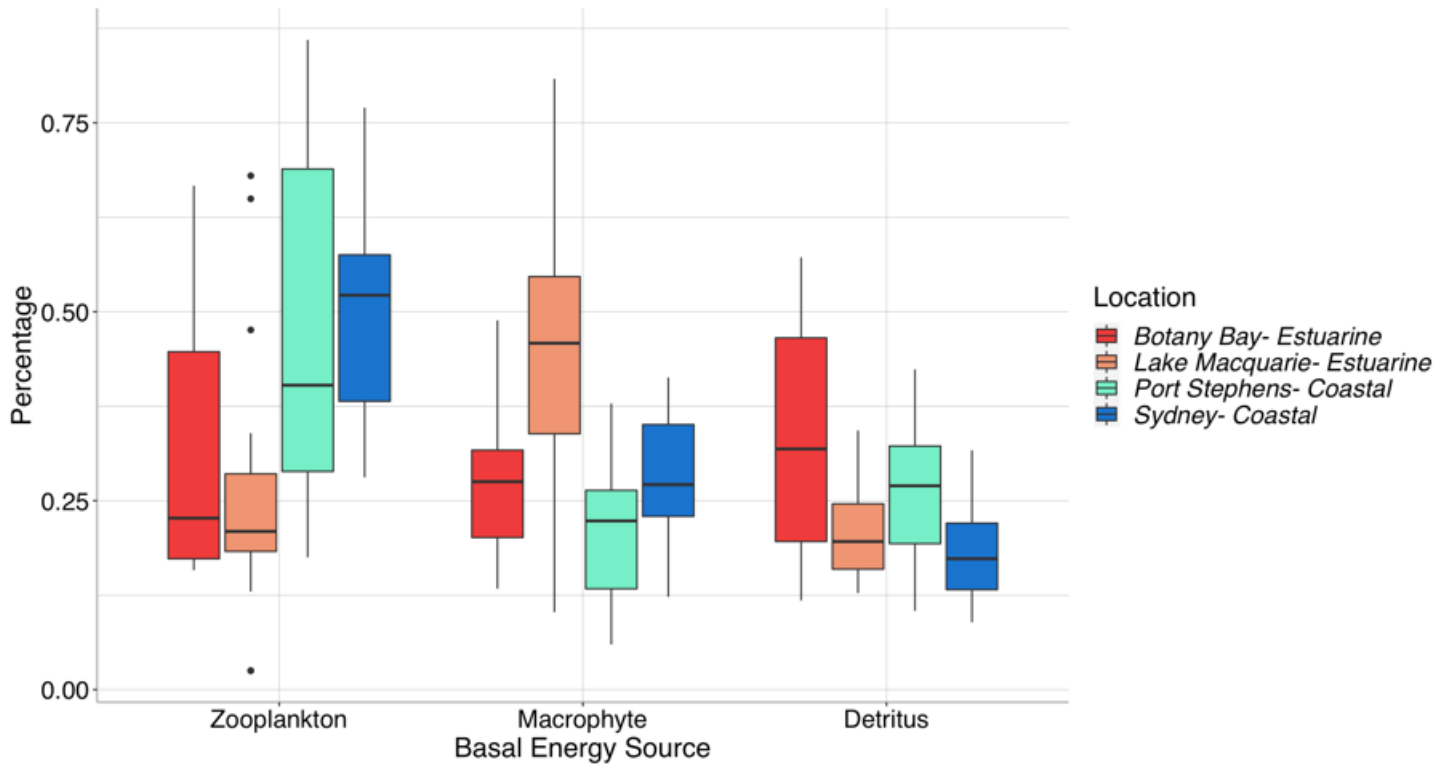


Figure 7

Proportion of the fish community on coastal rocky reefs and estuarine habitats reliant on different basal energy sources. Botany Bay and Lake Macquarie are a combination of natural and artificial reefs and seagrass, whilst the Sydney and Port Stephens coastal data is only recorded on rocky reefs. The values in each boxplot represent sampling trips within each habitat or coastal site, with fish biomasses taken as the mean of the replicates within each sampling trip. Thus, the spread in these boxplots represents variation in the relative biomass of the observed fish assemblage among different sampling days, habitats and sites. The middle dark line represents the median, while the box surrounds the 25-75% quantile of variation in basal energy sources. The whiskers cover ± 1.5 times the interquartile range (IQR).

Supplementary Files

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- [SupplementaryMaterial.docx](#)