The trophic basis of fish assemblages in temperate estuarine and coastal ecosystems

Belinda K. Goddard1 · Alistair Becker2 · David Harasti2 · James A. Smith1,3 · Roshni C. Subramaniam4 · Iain M. Suthers1,4

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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, compared with two coastal rocky reef sites. Fish assemblages were surveyed with Baited Remote Underwater Video (BRUVs) and the species abundance, richness and biomass of fish were classified into nine functional feeding groups (6 teleost and 3 elasmobranch). Comparable metrics for coastal fish assemblages were obtained from published surveys using BRUVs. 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% in Botany Bay) or macrophytes (58% in Lake Macquarie). 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%). Trophic pathways which support fish assemblages, are key in identifying mitigation measures which can help conserve these populations with growing urbanisation of estuaries and coasts.

Keywords BRUV · Functional feeding group · Trophic · Macroalgae · Seagrass · Zooplanktivore · Detritus · Herbivore · Omnivore · Piscivore · Invertivore · Atypichthys · Trachurus · Pelagic subsidy · Trophic basis · Food web

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). The flow from the main sources of energy to marine ecosystems is represented in the biomass of functional feeding groups of fish, such as grazers, piscivores and zooplanktivores (Truong et al. 2017). 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).

Australia’s temperate rocky reefs are dominated by kelp and other macrophytes, extending 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 as an energy source for rocky reef ecosystems (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 can dominate the fish biomass on temperate rocky reefs in southeastern Australia (Truong et al. 2017; Harasti et al. 2018), suggesting that zooplankton is a dominant energy source (Holland et al. 2020). Zooplanktivores capture zooplankton delivered by oceanic currents and pass this pelagic subsidy on to piscivores and other higher trophic levels (Young et al. 2010). Using a food web analysis encompassing nine fish functional feeding groups of fish, 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 was substantiated by a recent analysis of a decade of visual census data (Reef Life Survey, Edgar et al. 2020) over 12 degrees of latitude off eastern Australia (Edgar et al. 2020; Holland et al., 2020).

Estuarine environments typically include saltmarsh, mangroves and seagrass habitats (Hindell 2006; York et al. 2006; Nagelkerken and Faunce 2008; Connolly 2009). Rocky reef habitat is present in many estuaries, particularly along the littoral fringes where they support valuable fisheries (Pease 1999) and while they are less conspicuous than other habitats, a growing body of research shows they 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, which stable isotope based studies have shown to be important (Paterson and Whitfield 1997; Melville and Connolly 2003) are more significant 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 and seagrass) and compared this to coastal rocky reefs. This analysis incorporated fish surveys of two estuaries, existing coastal fish surveys, and published dietary information. We compared estuarine habitats to the coast more generally based on their biomass of functional feeding groups.

**Methods**

**Estuaries and study design**

Fish communities were surveyed in two estuaries in southeastern 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 (2018–2020). Botany Bay was sampled over three deployment dates during each cool and warm season, while Lake Macquarie was sampled over three cool and four warm deployment seasons.

Our BRUV system consisted of two GoPro Hero 7 cameras in SeaGIS housings (www.seagis.com.au) 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 6 and 7 seasonal trips in Botany Bay and Lake Macquarie, respectively. Deployments lasted for 30 min, as previous research suggests this is a sufficient soak time for comparative estimates of fish diversity and relative abundance in NSW (Harasti et al. 2015). BRUVs were baited with 500 g of crushed pilchards (Sardinops sagax) secured in a mesh bag and extended ~1 m 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, 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 (Kuiter 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 six teleost groups (piscivores, invertivores, soft-bottom carnivores, omnivores, zooplanktivores and herbivores) and three elasmobranch groups (piscivorous sharks, invertivorous sharks, and invertivorous rays). 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). Functional feeding group biomasses were compared among habitats, estuaries and between cooler and warmer seasons.

Biomasses for functional feeding groups in each deployment were estimated by measuring the lengths of all individuals contributing to MaxN in EventMeasure (per Langlois et al. 2020). Length data were then aggregated at the estuary level to determine the mean length of each species within each estuary. Due to visibility, not all individuals could accurately be measured in EventMeasure with the desired precision level of under 10 mm and residual mean square (RMS) error under 20 mm (Goetze et al. 2019). For individuals that could not be accurately measured, the average length for that species within the estuary was used. 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 either Fishbase (Froese 2019) or published literature where possible (Supplementary Table S1, Truong et al., 2017). 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 were fourth root transformed to reduce the influence of rare or highly abundant functional feeding groups (Anderson et al. 2008). Where too few unique permutations existed for a reasonable test to 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

![Site map of the two estuarine (Botany Bay and Lake Macquarie) and two coastal (Broughton Island and Fingal Island) study locations. Sydney coastal is identified on this map to indicate the location of the reference study site.](image)
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) seasons. The reefs were within depths of 20–35 m and were analysed with the same BRUV methodology previously described for the estuarine component.

MaxN was averaged across the eight replicate BRUV deployments at each site during each Season. PERMANOVA was used to compare among Sites (2 levels: Broughton Island, Fingal Island), Season (2 levels: Cool, Warm) and Years (2 levels: 2015, 2016), with all factors considered fixed and orthogonal. Species abundance data were converted to biomass using the same methods as for the estuarine dataset, with species lengths measured in EventMeasure. Because Harasti et al. (2018) only measured lengths of species that have recreational and commercial importance, additional length data for all other species were obtained by reanalysing some of the videos from that study. In a few cases, 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 coastal 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 compare with the estuarine data.

**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 following basal energy sources: phytoplankton, macrophytes and detritus. For some analyses, zooplankton was used as a basal food source in place of phytoplankton due to the direct links between zooplankton and higher trophic groups. Within our diet matrix, no fish groups fed directly on phytoplankton, while the zooplankton fed mostly on phytoplankton (Supplementary table S2, Fig. 7). Since zooplankton are the main consumers of phytoplankton, 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 had a greater proportion of zooplanktivorous fish than an estuarine site, zooplankton supported 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.

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). First, 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. Second, 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).

Robust estimates of energy sources rely on an accurate estimate of a mean fish assemblage, which in turn relies on multiple surveys of fish biomass. Our main result is thus the energy sources estimated from mean fish biomass calculated from all surveys. However, to explore how energy sources vary based on day-to-day variation in fish biomass, we also present boxplots of energy source values calculated at the level of sampling day, and test these data for differences in energy source proportions among estuarine site/habitat combinations (six levels) and between locations (coastal, estuarine) using single factor ANOVA. Food web diagrams were also generated for estuarine and coastal regions to visualise and compare trophic pathways between predators and prey. Each food web was constructed using the diet proportions of each the of functional feeding groups down to the basal energy sources, and the average relative biomass of each functional feeding group across replicates in each region (estuary or coast).
**Sensitivity analysis**

Fish diets are inherently variable due to food availability, seasonality, and other ecological processes (Becker and Laurenson 2007). Similarly, observed fish biomass will vary among surveys, especially for highly mobile and uncommon functional groups. To explore the influence of this variability and uncertainty on basal energy source calculations, we conducted two sensitivity analyses which manipulated (1) the proportion of prey items consumed by each functional feeding group (as in Truong et al. 2017), and (2) the relative fish biomass. For the diet sensitivity analysis, the dietary proportion of individual prey items were varied by ± 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. For the fish biomass sensitivity analysis, the relative biomass of each fish functional feeding group was varied ± one standard error, with the error estimated as that observed among sampling days at each site-habitat. This approach thus represents the sensitivity of the energy source results to our study’s estimate of the mean fish biomass, and by using standard error we assume that more sampling effort provides a better estimate of each group’s mean biomass. The output of each sensitivity analysis is a mean value for each energy source and each functional group, representing the influence of variation in that functional group’s diet or relative biomass 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 among estuarine Habitats, with both reef habitats aligning closer together than seagrass habitats. PERMANOVA results (Supplementary table S4) indicated a significant difference in functional feeding group biomass with a three-way interaction between estuary, habitat and season (Pseudo-$F = 6.2923$, $P = 0.0005$). 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 ($t = 4.4003$, $P(MC) = 0.0133$). For Habitats, pairwise tests indicated differences between natural reef and seagrass in the warm seasons in Lake Macquarie ($t = 12.184$, $P(MC) = 0.0032$), as well as among natural reef and seagrass ($t = 4.3558$, $P(MC) = 0.0106$), and artificial reef and seagrass ($t = 3.2412$, $P(MC) = 0.0359$) 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 ($t = 5.7764$, $P(MC) = 0.0024$).

**Energy sources for estuarine fish assemblages**

Mean energy sources are summarised in Table 1. Across all habitats within estuaries, the majority (45%) of fish biomass within Lake Macquarie is supported by macrophytes, while phytoplankton supports the majority in Botany Bay (39%). The increased percentage of fish supported by macrophytes within Lake Macquarie was driven by the seagrass habitats, while the dominance of plankton in Botany Bay was driven by the reef habitats. The often-large variation in the observed estuarine fish assemblage among sampling days created considerable variation in energy sources (Fig. 3). However, even at the level of sampling day, there were still statistically significant differences in energy sources among site-habitat combinations (Zooplankton: $F_{5,24} = 2.56$, $P = 0.05$; Macrophyte: $F_{5,24} = 3.52$, $P = 0.016$; Detritus: $F_{5,24} = 9.54$, $P < 0.001$). These differences were driven mostly by the seagrass habitats (Fig. 3).
Estuarine versus coastal fish assemblage compositions

Multidimensional scaling plots show that estuarine and coastal rocky reef functional feeding group biomasses were distinctively different across both study regions. Both coastal regions showed clear differences compared to all estuarine habitats (Fig. 4), and PERMANOVA results indicated that these differences were significant (Pseudo-$F = 4.1235$, $P = 0.001$).

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 (Fig. 5). Omnivores represented, on average, a higher proportion of the fish community biomass in estuaries (38%) than on coastal reefs (6%) (Fig. 5). Piscivores and

### Table 1 Proportion of the fish community biomass supported by different basal energy sources for each of the habitats and sites

| Site                   | Zooplankton | Phytoplankton | Macrophytes | Detritus | Unident |
|------------------------|-------------|---------------|-------------|----------|---------|
| Broughton Island       | 0.45        | 0.48          | 0.17        | 0.22     | 0.02    |
| Fingal Island          | 0.43        | 0.49          | 0.19        | 0.31     | 0.01    |
| Coastal- Average       | **0.44**    | **0.48**      | **0.18**    | **0.26** | **0.02**|
| 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**|

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.
herbivores contributed higher proportions of the overall biomass on coastal reefs, while no herbivores were observed in either estuarine ecosystem. The coastal sites (triangles) are Broughton and Fingal Island, which are averaged across years and seasons.

**Estuarine versus coastal energy sources**

Comparison of the basal energy sources supporting fish assemblages in each of the three estuarine habitat types and the two coastal sites (Table 1) revealed that overall, estuarine fish assemblages were supported by higher levels of macrophytes (27–45%) than fish on coastal rocky reefs (18%). Fish in both the Lake Macquarie and Botany Bay seagrass habitats were supported by considerably lower levels of zooplankton (13–17%) than fish in the coastal sites (35–43%). Detritus supported relatively similar levels of biomass across locations and habitats (20–31%), except for Botany Bay seagrass habitat (51%).

Again, the often large variation in the observed coastal and estuarine fish assemblages among sampling days created considerable variation in energy sources (Fig. 6). However, the surveyed fish assemblages were still different enough to detect a significant difference in energy sources (except detritus) at the day level among coastal and estuarine sites (Zooplankton: $F_{1,44} = 9.75, P = 0.003$;...
Phytoplankton: $F_{1,44} = 10.75, P = 0.002$; Macrophyte: $F_{1,44} = 12.65, P < 0.001$; Detritus: $F_{1,44} = 0.07, P = 0.794$.

Food web diagrams generated using relative biomasses (Fig. 5) and proportional diets for each functional feeding group (Supplementary Table S2) visualise the differences in energy flow between estuarine and coastal habitats (Fig. 7). Our food webs highlight the dominance of zooplanktivory in coastal habitats (Fig. 7a) compared to the increased relative biomass of omnivores in estuarine habitats that is supported by macrophytes (Fig. 7b).

Sensitivity analyses

The diet sensitivity analysis reveals the functional feeding 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 ± 10% caused < 4% change in the basal energy sources supporting communities across all estuarine and coastal sites (Table 2, Supplementary Table S3). The sensitivity of basal energy sources to changes in diet was consistent across estuarine and coastal habitats. 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 basal food sources within reef habitats (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.

The fish biomass sensitivity analysis reveals the fish groups whose relative biomass had the most impact on energy source results (Table 2, Supplementary Table S3). These were fish groups with large biomass but also large variation in their biomass (schooling or patchy groups) and were often higher trophic levels. This was contrary to the diet sensitivity analysis, in which it was predominantly lower trophic levels with the most influence. Uncertainty in the biomass of coastal piscivores and zooplanktivores generally had the most impact on the plankton energy source results, demersal omnivores had the most influence on macroalgae results, and demersal invertivores, demersal omnivores, and rays had the most influence on detritus results. Thus, obtaining multiple surveys of a fish assemblage which observe schooling, or abundant but patchy fish groups, will contribute greatly to robust estimates of energy flow.


**Discussion**

**General comments**

Compared to the dominance of zooplanktivity 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, 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).

The dominance of zooplanktivity on Broughton and Fingal Island aligns with the findings of Truong et al., (2017) of Sydney coastal reefs. The dominant energy source on the Sydney coastal reefs was zooplankton, with an average 53% of the fish biomass being supported by this energy source across their 17 study sites. This is similar to the 45% and 43% of fish biomass at Broughton and Fingal Island coastal reefs, respectively being supported by zooplankton and highlights the importance of plankton as an energy source for fish on coastal temperate reef systems.

**Variation in functional feeding groups**

The biomass of functional feeding groups varied among habitats within estuaries, with natural and artificial reefs supporting similar compositions, whereas seagrass, driven by
Table 2  Results of the sensitivity analysis presenting the percentage change in the 5 basal energy source outputs \((Z=\text{zooplankton}, P=\text{phytoplankton}, M=\text{Macrophytes}, D=\text{Detritus}, Un=\text{Unidentified})\) per functional feeding group

| Botany Bay Artificial Reef- diet | - biomass |
|---------------------------------|----------|
| Piscivorous Sharks              | 0.00 0.00 0.00 0.00 0.00 | 0.00 0.00 0.00 0.00 0.00 |
| Non Piscivorous Sharks          | 0.00 0.00 0.00 0.00 0.00 | 0.00 0.00 0.00 0.00 0.00 |
| Coastal Pelagic Piscivores      | 0.00 0.00 0.00 0.01 0.00 | 0.24 0.2 0.22 0.00 0.27 |
| Demersal Invertivores           | 0.06 0.08 0.22 0.23 0.86 | 7.01 5.04 0.84 10.7 17.2 |
| Reef Piscivores                 | 0.01 0.01 0.01 0.00 0.01 | 1.92 1.49 1.26 0.84 1.39 |
| Cephalopoda                     | 0.00 0.00 0.00 0.00 0.00 | 0.00 0.00 0.00 0.00 0.00 |
| Rays                            | 0.01 0.01 0.02 0.05 0.01 | 0.65 0.36 0.69 2.18 1.03 |
| Reef Invertivores               | 0.01 0.02 0.06 0.08 0.17 | 0.98 0.68 0.16 1.77 0.19 |
| Soft Bottom Fish                | 0.01 0.00 0.01 0.01 0.00 | 0.2 0.02 0.44 0.91 0.6 |
| Demersal Omnivores              | 0.40 0.44 0.82 0.35 0.54 | 4.5 3.86 8.98 6.99 6.32 |
| Reef Omnivores                  | 0.00 0.00 0.01 0.01 0.00 | 0.07 0.06 0.1 0.03 0.07 |
| Coastal Zooplanktivores         | 2.09 1.61 0.80 3.24 0.00 | 10.7 8.29 7.25 4.33 7.54 |
| Reef Zooplanktivores            | 0.08 0.05 0.02 0.11 0.04 | 2.78 2.18 1.93 1.1 1.9 |
| Reef Herbivores                 | 0.00 0.00 0.00 0.00 0.00 | 2.22 2.22 4.06 2.2 2.22 |
| Soft Bottom Decapods            | 0.05 0.11 0.06 0.29 0.00 | Z P M D Un |
| Carnivorous Reef Zoobenthos     | 0.01 0.02 0.03 0.02 0.00 | |
| Herbivorous Reef Zoobenthos     | 0.10 0.21 2.18 3.20 0.00 | |
| Soft Bottom Zoobenthos          | 0.30 0.65 0.00 1.82 0.00 | |
| Sessile Filter Feeders          | 0.36 0.02 0.00 0.07 0.00 | |

Light blue indicates minimal change (<0.1% for diet, <1% for relative biomass); 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 or relative biomass. Tables on the left are the variations in basal energy source due to diet sources being altered by ±10% and the right is relative biomass being altered by the standard error. Darker red indicates higher level of change in basal energy source outputs with alterations to diet sources or relative biomass. 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. It also highlights that variations in functional feeding group relative biomass has a higher impact on the basal energy sources output. Complete results of sensitivity analysis from all estuarine and coastal locations are in the supplementary material.
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 tenfold. 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 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 incorporating temporal sampling 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 species composition.

Estuarine and coastal ecosystems supported different functional feeding groups. Relative biomasses highlighted omnivores as a key estuarine functional feeding group, which dominated the estuarine habitats. 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).

**Basal energy sources**

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 largely influenced 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 their role as prey for piscivores. Developing specific diet matrices for the estuaries, habitat type and seasonality would reduce some of the uncertainty in the diets of functional feeding groups.

Fish abundance, richness and diversity varies diurnally, temporally, spatially and in response to environmental change (e.g. salinity and temperature) (Irigoyen et al. 2013; Morton and Gladstone 2011; Malcolm et al. 2007). These variations in fish abundance, alongside observation error, can influence the estimates of basal energy sources supporting fish communities. Our sensitivity analysis highlighted that the groups with high but patchy abundance had the most influence on basal energy source estimates. Replication of surveys is thus essential for creating robust estimates of mean energy sources, as are survey durations and techniques that can observe these functional groups. The considerable spread in energy sources given variation in the fish assemblage at the daily level (Figs. 3, 6), shows how fish assemblages over one day may not represent the mean assemblage.

**Conclusion and limitations**

Temperate rocky reef ecosystems support a high diversity of fishes, which varies from coastal to estuarine ecosystems. The fishes of estuarine ecosystems were more omnivorous and thus fed more on 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 (Figs. 3, 7). However, fish in estuarine seagrass habitats can also be supported by detritus, as seen 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 sampling herbivorous fishes in estuaries (i.e. un-baited surveys) such as Girella tricuspidata, which may have been limited by the use of BRUVs in this study, as they are not known to be attracted to the bait and more likely to be caught using gillnet or seine net methods (Gray et al. 2010, 2012). Additionally, a better understanding of seasonal and ontogenetic variation in the diets would help improve the estimates presented in this study.

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.

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Author contributions The analysis and initial draft was completed by BKG. IMS and AB conceived the study, JAS updated and improved the numerical scripts. RCS provided the food web script. All authors contributed to the analysis and writing of the paper.

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Code availability Code available at https://github.com/belin DAGoddard/Trophic-Basis-Fish-Assemblage.

Declarations

Conflict of interest We have no conflicts of interest to declare.

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