

# Size-selective predation by three estuarine zooplanktivorous fish species

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Handling Editor: Daniel Roelke ABSTRACT

**Context.** Zooplanktivorous fish are a key link between abundant zooplankton and higher trophic levels but the foraging behaviour of zooplanktivorous fish is not fully understood. Selective feeding behaviours have been observed, with many species of planktivorous fish targeting certain species and sizes of zooplankton for prey. However, why certain size classes of zooplankton are preferred remains unclear. **Aim.** This study investigated prey selection by three zooplanktivorous fish species through the lens of optimal foraging theory. **Methods.** We assessed the size structure of zooplankton in the environment and compared this with the size distribution of zooplankton in gut contents from three zooplanktivorous fish. **Key results.** The targeted prey size of *Atypichthys strigatus* and *Scorpis lineolata* aligns with the prey size classes in the environment that contain the highest overall biomass. *Trachurus novaezelandiae* showed little evidence of targeting these size classes. **Conclusions.** These prey sizes therefore represent the most efficient prey to target because the return on foraging effort is greatest. By contrast, *T. novaezelandiae* showed only an underselection of large and small prey. **Implications.** By incorporating this information on this key trophic link between zooplankton and fish, ecosystem models could better resolve the size dependant predation, particularly in size-based models.

**Keywords:** Atypichthys strigatus, diet, estuarine ecosystem, gut contents, laser optical plankton counter, optimal foraging theory, planktivory, prey choice, Scorpis lineolata, Trachurus novaezelandiae.

## Introduction

Optimal foraging theory is a broad framework that seeks to understand foraging behaviour, including predation that transfers biomass from lower to higher trophic levels. Underlying this theory is the assumption that an animal will make foraging decisions that maximise the amount of energy ingested, while minimising the energy used during feeding (Pyke *et al.* 1977). Although sometimes criticised for being too simple and not representative of the natural environment (Pierce and Ollason 1987), this theory continues to provide a useful framework for exploring foraging behaviour and has been used recently to make and test predictions about foraging for a range of taxa, including marine mammals (Foo *et al.* 2016; Tyson *et al.* 2016), birds (Hernández-Pliego *et al.* 2017), lions (Barnardo *et al.* 2020) and fish (Thygesen *et al.* 2016).

Marine ecosystems are strongly structured by size (Sheldon *et al.* 1972; Andersen *et al.* 2016; Hatton *et al.* 2021), resulting in small prey being highly abundant compared with larger prey. Yet, small prey contain less biomass per individual and may be harder to detect than are larger prey (Hansen *et al.* 2013). This presents marine predators with a choice of whether to feed on the abundant easy to catch prey or target larger prey?

Zooplanktivorous fish are a key trophic link between abundant zooplankton and larger predators. On temperate rocky reefs, zooplankton can support over 50% of the fish community biomass, with much of this flowing through small zooplanktivorous fish (Truong *et al.* 2017; Goddard *et al.* 2022). The foraging strategy of zooplanktivorous fish presents an interesting test of optimal foraging theory. Zooplankton are highly

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abundant (often >1000 individuals m<sup>-3</sup>) and small zooplankton are often an order of magnitude more abundant than large zooplankton (Sheldon et al. 1972; Heneghan et al. 2016), meaning that the chance of a zooplanktivorous fish encountering small prev is much greater than is their chance of encountering large prey. However, a large copepod can contain up to 15 times more biomass than a small copepod (Chisholm and Roff 1990), which may make large zooplankton a preferential prey source. This creates a situation where zooplanktivorous fish could feed randomly on the basis of encounter rates of zooplankton (commonly known as filter feeding), essentially eating mostly smaller zooplankton or they could target larger zooplankton (particulate feeding) if the trade-off in terms of biomass return for energy used in searching for and capturing the larger prey is favourable. If consuming the greatest amount of biomass for the least effort is the goal of zooplanktivorous fish, then perhaps their feeding strategy is mediated not by the abundance of different prey but by the biomass of each prey type in the environment. It is plausible that they would target the prey type with the highest biomass in the environment, rather than abundance. Some species have been observed to switch between filter-feeding and particulate-feeding behaviours in response to changes in prey density (Jansen et al. 2019). A similar but alternative theory may be the targeting of calories rather as biomass as the calories are a direct measure of energy (Cumminns and Wuycheck 1971; Balogh et al. 2022). This is most likely if the different prey types have large differences in calorific content but not biomass.

Prey selectivity of zooplankton by zooplanktivorous fish has previously been explored, with a focus on mouth size and gill raker dimensions proving mixed results. Although mouth size is important for small fish (<30 mm), fish are quickly capable of feeding on almost all zooplankton and, at larger fish sizes, the limiting factor becomes handling time and capturing prey (Wanzenbock 1995). Similarly, gill raker size has been shown to not be a limiting factor on the capture of small particles, although it may reduce the efficiency of capture, leading to increased relative capture of larger particles (Langeland and Nøst 1995; Budy et al. 2005). Overall, prey selectivity in zooplanktivorous fish is not simply driven by morphology, but there is also active selection of different size prey, particularly for larger zooplanktivorous fish, which have the ability to capture all sizes of prey and can significantly alter their own behaviour while foraging (Tanaka et al. 2006).

The goal of our study was to explore the foraging strategy of three common zooplanktivorous fish in Sydney Harbour. To investigate selective feeding, we measured the sizestructured zooplankton abundance and biomass in the environment over the summer period, and compared this with the size-structured diet of planktivorous fish collected over the same period. The specific aims were to (1) examine the average size-structured zooplankton abundance and biomass in Sydney Harbour over a 3-month period, (2) determine the prey size and diet composition of three planktivorous estuarine fish, and (3) compare the prey size of the gut contents with the size structure of zooplankton available in the water to quantify size-selective predation.

## Materials and methods

## Zooplankton sampling

Zooplankton were sampled in the lower reach of Sydney Harbour between November 2013 and February 2014 (summer) at three sites (Site 1:  $-33.834^{\circ}$ ,  $151.278^{\circ}$ , Site 2:  $-33.839^{\circ}$ ,  $151.277^{\circ}$ , Site 3:  $-33.849^{\circ}$ ,  $151.266^{\circ}$ ), along the southern shore close to the mouth of the estuary and the dominant tidal flow. The total distance between sites was 2.1 km. All sites were sampled in the morning on 10 days, during five ebb and five flood tides (sampled 2–3 h after the predicted high or low tide). At each site, three horizontal replicate plankton tows were made with a 40-cm diameter, 100- $\mu$ m mesh net at 1-m depth. A mechanical flowmeter (Model 2030R, General Oceanics Inc., Miami, FL, USA) was attached to the net to calculate the sampling volume. A detailed description of the Sydney Harbour ecosystem is available in Johnston *et al.* (2015).

The zooplankton size distribution and biomass from all towed samples was determined using a laboratory-based laser optical plankton counter (LOPC; Herman *et al.* 2004), coupled to a pump system (Moore and Suthers 2006). When a particle passed through the beam of the LOPC, the attenuance of light was detected and recorded as the corresponding equivalent spherical diameter (ESD) of the particle. The zooplankton size was classified into a size-frequency distribution with 30-µm bins. Only particles between 300 and 3000 µm ESD were included, because particles outside this size range were unlikely to be sampled accurately by the plankton net (Moore and Suthers 2006). Zooplankton biomass was calculated from the volume of a prolate spheroid (ratio of 1:3, width:length) and the specific gravity of water (Suthers *et al.* 2006; Garcia *et al.* 2022).

Because the goal of this study was to investigate foraging behaviour of zooplanktivores rather than variation in the zooplankton community, all zooplankton samples were averaged together to provide a representative zooplankton snapshot over the whole sampling period. This aligns with the fish collection discussed below.

### Fish gut content sampling

Over the same time period as the zooplankton sampling, *Atypichthys strigatus* (Günther, n = 17), *Trachurus novaezelandiae* (Richardson, n = 24) and *Scorpis lineolata* (Kner, n = 22) were collected either by using unbaited hook-and-line or spearfishing from the study area. These methods have been used successfully in other studies to sample

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these species while avoiding contamination of gut contents with bait (Gaston and Suthers 2004; Champion et al. 2015). On the basis of previous research, these species are suspected zooplanktivores and were observed to be the most abundant around our sampling sites. It was confirmed that these species are some of the most abundant small fish in Sydney Harbour by using data from fish surveys undertaken by the Reef Life Survey (Edgar and Stuart-Smith 2014). Individual fish were immediately placed on ice and later frozen, until dietary analysis took place. Fish were collected throughout the sampling period, irrespective of tide, and although fish were not collected evenly in space, all were collected within 500 m of the zooplankton sampling sites. In all, 58 of the 63 fish (92%) were collected on the same day as the zooplankton samples, with five individuals of A. strigatus being collected opportunistically on different days.

The gut contents of each fish were weighed and prey items were identified to a coarse taxonomic resolution. The fullness and percentage (by volume) of plant matter, zooplankton and unidentifiable material were recorded for each gut. Because it was not feasible to use the LOPC for partially digested gut contents, the size distribution (ESD) of zooplankton in the gut contents was manually determined from the length and width of zooplankton, to compare with the size distribution of zooplankton in the water column (the LOPC data). From each gut, a random sample of each zooplankton taxonomic group was photographed using a Leica M80 Microscope with Leica Application Suite (ver. 4.4, Leica Microsystems GmbH, Wetzlar, Germany). ImageJ (ver. 1.48, see https://imagej.nih.gov/ij/; Schneider et al. 2012) was used to measure the length (l. mm) and width (w, mm) of each prey item in the photographs. Length and width measurements were converted into an ESD (um) by assuming the shape of an ellipsoid and using the following equation:

$$ESD = 2\sqrt[3]{\frac{l \times w^2}{8}} \times 1000$$
 (1)

To determine the size range of zooplankton having the highest incidence of consumption by estuarine planktivorous fish, the ESD measurements of identified prey within the fish guts were compiled into frequency histograms for each fish (30- $\mu$ m bins; corresponding to those of the LOPC). The prey-size distributions of all individuals from each species were then averaged to obtain an average prey-size distribution for each species.

#### Data analysis

All analysis was conducted using R (ver. 4.0.2, R Foundation for Statistical Computing, Vienna, Austria). A split-plot ANOVA was used to test for differences in total zooplankton biomass between tides and sites, with tide and site as fixed factors and day as a random factor. It was a split-plot design because only one level of tide (ebb or flood) was sampled per day (the 'plot'). The zooplankton biomass was  $log_{10}$ -transformed to meet the assumptions of normality and homogeneity of variance.

To assess selective predation in our zooplanktivorous fish, we used a simulation approach similar approach to Chappell and Smith (2016). We generated three null models of expected prey distributions under the assumption that nonselective feeding would result in prey-size distributions reflecting the zooplankton distribution in the environment. There was one model for each species. Using the abundance (%) of each 30 µm ESD zooplankton size class in the water, we created a simulated population of known size distribution. From this population, we then drew 2000 random samples of x prey items, where x represents the average number of prey items found in each species gut. From these 2000 samples, we generated a mean size-frequency distribution with a 95% confidence interval. We then assessed size-selective predation by comparing the observed predation rates for each size class with the null predictions. If a size class occurred in the fish guts more frequently than predicted by the null simulation, this suggested that this size class was disproportionately preyed on. To estimate the magnitude of the selectivity, we again followed Chappell and Smith (2016) and present the proportional effect (PE) ratio, which is the ratio of observed predation to the expected predation. A PE < 1 signifies underselection, whereas a PE > 1 signifies overselection. Compared with traditional selectivity indices such as those of Chesson (1978), the simulation approach allows for robust analyses of low sample sizes and provides a benchmark of null selection to compare against (Chappell and Smith 2016).

#### Results

#### Zooplankton biomass

In total, 86 plankton tows were analysed using the LOPC. Four samples, each from a different site or day, contained too much gelatinous material for accurate analysis; so, they were excluded. The zooplankton biomass varied over an order of magnitude both among days and within days among sites. The smallest zooplankton biomass was recorded at Site 1 with  $106.0 \text{ mg m}^{-3}$  (25 November 2013), and the largest was  $1722.2 \text{ mg m}^{-3}$ , at Site 3 (27 February 2014). The largest range in zooplankton biomass across the three sites on a single day was  $1120.0 \text{ mg m}^{-3}$ (27 February 2014). No significant difference in zooplankton biomass was found between ebb and flood tides (ANOVA:  $F_{1,8} = 1.17$ , P = 0.31), but Site 3 contained significantly more zooplankton biomass than did Site 1 across all tides (ANOVA:  $F_{2,72} = 5.48$ , P < 0.01, Supplementary Fig. S1). No significant interaction was found between tide and site (ANOVA:  $F_{2.72} = 0.83$ , P = 0.44).

Despite this variation in total biomass among samples, when the percentage biomass and abundances in each size

class were investigated, consistent patterns were observed and we present an overall average zooplankton distribution, which shows consistent declines in abundance with size, and a peak in biomass between 495 and 705  $\mu$ m ESD (Fig. 1). Among sites, there were only minor differences in the biomass percentage size distributions, with Site 3 having a lower percentage biomass than the other sites in the small bins (<375  $\mu$ m ESD) and Site 1 having a slightly more even distribution of biomass (a lower peak between 495 and 705  $\mu$ m ESD; Supplementary Fig. S1).

#### **Fish diets**

In total, 4140 prey items were identified in the guts of 17 Atypichthys strigatus, 22 Scorpis lineolata and 24 Trachurus novazelandiae individuals. No guts were empty, although seven contained fewer than ten identifiable prey items. A. strigatus, T. novaezelandiae and S. lineolata all consumed zooplankton. In A. strigatus and T. novaezelandiae, zooplankton comprised 100% of the identifiable gut contents. In S. lineolata, zooplankton comprised 40%, with plant matter making up the other 60%. Copepods were the most abundant prey items for all species (Fig. 2a). They were found in 97% of all guts (Fig. 2b) and represented 64, 66 and 41% of all prey items by count in A. strigatus, *S. lineolata* and *T. novaezelandiae* respectively. *A. strigatus* had the greatest average number of prey items in their guts  $(145.1 \pm 21.4 \text{ s.e.})$ , followed by *S. lineolata*  $(46.9 \pm 6.8 \text{ s.e.})$ , and *T. novaezelandiae* had the fewest  $(26.8 \pm 4.4 \text{ s.e.};$  Table 1). *S. lineolata* was the only species to consume plant material, sand grains or barnacle cirri. *T. novaezelandiae* had the smallest species richness in its diet, containing eight prey types, compared with 13 and 14 prey types for *A. strigatus* and *S. lineolata* respectively.

#### Selective predation

In total, 1997 prey items from gut contents were measured and converted to an equivalent spherical diameter to be comparable with the zooplankton measurements from the LOPC. The three species of fish showed a similar pattern of prey sizes in their guts, although *T. novaezelandiae* contained smaller prey (Figs 3, 4). The smallest size class of prey was 240–270  $\mu$ m ESD, with only 0.06% (±0.02 s.d.) of prey in *A. strigatus* and this size class was not observed in the other two species. This smallest size class was smaller than that resolved by the LOPC, so was not included in comparisons with zooplankton in the environment. The largest size class containing prey was 2940–2970  $\mu$ m ESD, containing only a single prey item, observed in the gut of a



Fig. I. Mean zooplankton size structure in the lower Sydney Harbour during our study. Error bars show I s.e.



**Fig. 2.** (a) Average number of identifiable individuals for each prey type per gut (+s.e.). Note the  $\log_{10}$  scale on the y-axis. (b) Frequency occurrence (%) of each prey type, which shows the percentage of fish guts that contained at least one identifiable individual of the prey type.

<b>Table 1.</b> Summary of gut contents and fish total length	Table	Ι.	Summary	of	gut	contents	and	fish	total	length
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Species	n	Fish total length range (cm)	Gut contents wet weight (g)	Gut fullness (%)	ldentifiable prey (number gut <sup>-1</sup> )
Atypichtys strigatus	17	7.8–13.5	0.12 (0.02)	63.5 (5.4)	145.1 (21.4)
Scorpis lineolata	22	8.5–25.9	0.36 (0.03)	65.2 (3.5)	46.9 (6.8)
Trachurus novaezelandiae	24	19.3–24.2	0.12 (0.01)	28.8 (4.2)	26.8 (4.4)
Average			0.22 (0.02)	50.9 (3.3)	65.7 (8.9)

The total length (cm) size range of sampled fish is shown. The means (s.e.) for gut content wet weight, gut fullness (%) and identifiable individual prey (number  $gut^{-1}$ ) are shown. The last row shows the average across individuals of all species. Identifiable refers only to prey items that were both recognisable and whole enough to be measured confidently. The majority of the other material was obviously crustaceous zooplankton in nature.

*T. novaezelandiae.* The median prey size classes of each species were as follows: *A. strigatus*, 540–570 μm ESD; *S. lineolata*, 540–570 μm ESD; and *T. novaezelandiae*, 480–510 μm ESD.

Strong evidence of size-selective predation was found for *A. strigatus* and *S. lineolata*. When compared with the null model of expected diet proportions based on the assumption of random feeding and the observed size structure in the



Fig. 3. Comparison of observed zooplanktivorous fish prey-size (solid line) and the expected prey-size distribution (dashed line) on the basis of abundance of different zooplankton size classes in the environment for (a) Atypichthys strigatus, (b) Scorpis lineolata, and (c) Trachurus novaezelandiae. Error bars show 95% confidence intervals around the mean. Size classes greater than 1200  $\mu$ m ESD are not displayed because they contained few prey items (less than 0.02% total).

environment, all species showed an underselection of prey in both small (<480  $\mu$ m ESD for *A. strigatus*, <450  $\mu$ m ESD for *S. lineolata* and <420  $\mu$ m ESD for *T. novaezelandiae*) and large (>870  $\mu$ m ESD for *A. strigatus*, >690  $\mu$ m ESD for *S. lineolata* and >630  $\mu$ m ESD for *T. novaezelandiae*) size classes (Fig. 3, Supplementary Table S1). This corresponded to strong evidence of an overselection of medium size particles in *A. strigatus* (480–840  $\mu$ m ESD) and *S. lineolata* (480–690  $\mu$ m ESD). By contrast, only weak evidence of selectivity was evident in *T. novaezelandiae*, where the small and large prey underselected, whereas the moderatesize prey showed only weak evidence of selectivity, although this could be due to the low average number of prey items within their guts creating large 95% confidence intervals (Fig. 3, Supplementary Table S1).

When compared with the null model of expected diet proportions calculated using the biomass of each size class in the environment rather than the abundance, the evidence for size-selective feeding was reduced and our observed prey sizes aligned more closely with expectation for *A. strigatus* and *S. lineolata* (Fig. 4). Whereas there continued to be some evidence of underselection at small and large prey

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sizes, there was vastly reduced evidence of positive selectivity occurring in any size class (Supplementary Table S1). The peak in observed prey size corresponded to the peak in size classes that contained the most biomass in the environment, suggesting that *A. strigatus* and *S. lineolata* were likely to be targeting available biomass. By contrast, *T. novaezelandiae* showed slightly more evidence of selectivity in the biomass model than did the abundance model, with the peak in size classes consumed being smaller than would be expected on the basis of available biomass, suggesting that *T. novaezelandiae* was likely to be feeding on the basis of abundance, not biomass.

## Discussion

This study showed evidence of size-selective predation occurring in three estuarine zooplanktivorous fish, with two species (*A. strigatus* and *S. lineolata*) showing strong evidence, whereas *T. novaezelandiae* showed only weak evidence of size-selective predation. By comparing the observed prey-size compositions with expected prey-size



compositions on the basis of feeding relative to environmental abundance and biomass in each size class, we propose that size-selective predation is driven by the increased amount of biomass available in the environment for preferred size classes relative to the other size classes. Our finding supports the theory of optimal foraging theory. Because the goal of foraging is to consume the greatest biomass for the least effort, the size classes with the greatest biomass in them represent the most 'profitable' food sources. Understanding the foraging decisions made by planktivorous fish is vital because they often link zooplankton as an abundant resource with the fisheries typically comprising higher trophic levels (Pikitch *et al.* 2014).

#### **Fish planktivory**

Previous studies have defined *T. novaezelandiae* as a planktivore (Kingsford 1989; Bulman *et al.* 2001; Dawson *et al.* 2020), whereas *A. strigatus* and *S. lineolata* have previously been defined as piscivores (Bulman *et al.* 2001) or planktivores (Kingsford 1989; Glasby and Kingsford 1994; Champion *et al.* 2015). However, this study found only **Fig. 4.** Comparison of observed zooplanktivorous fish prey-size (solid line) and the expected prey-size distribution (dashed line) on the basis of total biomass of different zooplankton size classes in the environment for (a) Atypichthys strigatus, (b) *Scorpis lineolata*, and (c) *Trachurus novaezelandiae*. Error bars show 95% confidence intervals around the mean. Size classes greater than 1200 µm ESD are not displayed because they contained few prey items (less than 0.02% total).

evidence of planktivory with some benthic foraging only for *A. strigatus* and omnivorory for *S. lineolata*. It is likely that *A. strigatus* and *S. lineolata* may have a flexible diet that can vary with ontogeny and in both time and space, particularly in offshore locations such as those in Bulman *et al.* (2001). The classification of *T. novaezelandiae* is consistent with other members of the *Trachurus* genus (Tanaka *et al.* 2006).

There is strong evidence for prey-size selection occurring in all three species. Prey smaller than 465  $\mu$ m ESD and larger than 900  $\mu$ m ESD were found in the gut contents significantly less often than would be expected on the basis of their environmental abundance. This was matched with significantly more prey of a moderate size (480–~780  $\mu$ m ESD) being observed in the gut contents of both *A. strigatus* and *S. lineolata* than expected on the basis of abundance. Owing to low numbers of prey in *T. novaezelandiae* gut contents, there was insufficient power to detect any positive prey selection and, instead, the contents matched the expected consumption of moderatesized prey. There was variation among species, with *A. strigatus* showing the strongest evidence of prey selectivity while also consuming a higher proportion of larger prey (>705  $\mu$ m ESD) than do the other species. Whereas there are no comparable studies of prey-size selection for *T. novaezelandiae* and *S. lineolata*, it has previously been observed that, in coastal environments, *A. strigatus* had a preference for slightly larger zooplankton (Champion *et al.* 2015). This may be because in the offshore location, the available zooplankton were also larger than they were in the estuarine samples in the current study (Champion *et al.* 2015).

When compared with biomass available in each size class of zooplankton prey (rather than raw abundance), the observed prey-size distributions were a much closer match to the expected distributions. There continued to be an underselection of small and large particles, but the peak in prey size consumed closely matched the size classes of zooplankton in the environment containing the most zooplankton. Avoidance of small prey as an active choice was demonstrated previously in a mesocosm experiment, which demonstrated that turbidity was not an influence on selection by planktivorous bluegill sunfish (Gardner 1981). The present study suggests that the reason for this avoidance may be that the energetic costs of capturing the small prey are not as efficient as when targeting the size classes with the most biomass. In the future, it would be useful to investigate whether prey selectivity changes with the ontogenv of the predator because this has been observed in larval and juvenile yellow perch that switch from a high captureefficiency technique to a lower capture but higher biomassreturn strategy as they mature (Graeb et al. 2004).

As our prey-size measurements for the environmental zooplankton and gut contents were obtained using different methodologies (LOPC vs manual sizing), it is possible that there could be a methodological bias between the measurements. The LOPC has been rigorously validated and used in many studies and has been shown to provide accurate measurements across the size range observed in our study (Herman et al. 2004; Herman and Harvey 2006). By contrast, manual measurements are variable in method and may be subject to bias, particularly because zooplankton in gut contents are not in pristine condition. Previous manual measurements of copepods have shown to be highly accurate (within 1% accuracy), giving us confidence in our method (Araoz 1991). Our measurement method followed that of Skjoldal et al. (2013) and because the majority of zooplankton prey observed in this study were typical copepods with an elliptical shape (Araoz 1991), our method of calculating their volume is valid for most prey items, although it does ignore appendages, which had often fallen off. This may result in a small underestimation of size; however, because the appendages contain very small amounts of total volume and, therefore, biomass (<5%), it is reasonable to assume that our measurements and prey size estimate would be within 5% accuracy and any variation around this would not change the interpretations of the patterns observed in this study.

Copepods were the most abundant prey item in the gut contents of all three species, followed by cladocerans for *A. strigatus* and *T. novaezelandiae* and large dinoflagellates for *S. lineolata* (along with plant material), with other prey types being almost an order of magnitude less abundant. Copepods and cladocerans have very similar calorific contents (Cumminns and Wuycheck 1971), suggesting that the selection in this case was most likely driven by the available biomass and search time trade-off (which will correlate with available calories).

The overlapping prey-size range also provides insight into the niche partitioning occurring in Sydney Harbour; although all three of our studied species consume zooplankton of the same size, they occur in different habitats and are consuming the zooplankton in different parts of the estuary. *A. strigatus* is an extremely reef-associated zooplanktivore, *S. lineolata* is also reef associated but also eats plants, and *T. novaezelandiae* is a zooplanktivore but is less associated with reefs, particularly within estuarine environments.

#### Zooplankton variability

Although not consistent, there was, on average, higher zooplankton biomass at Site 3 (inner site) than at Site 1 (outer site). This suggests that zooplankton may accumulate inside the estuary and not all is discharged on the ebb tide. This accumulation may be due to either estuarine production or retention within the estuary (Avila *et al.* 2012) or active use of tidal currents by zooplankton (Simons *et al.* 2006), and further research looking at estuarine gradients in zooplankton biomass and productivity would provide valuable insight in how estuarine and coastal zooplankton support higher trophic levels. The idea of retention is supported by previous research showing that 50% of the water in this lower-estuary region of Sydney Harbour is retained and not exchanged with the ocean for up to 80 days, increasing up to 90% in the inner estuary (Das *et al.* 2000).

Regardless of the large variation observed in zooplankton biomass and abundance in the environment, once this was standardised to percentage composition of size classes, there was a consistent trend in the proportions of each size class present. This showed that although there are fluctuations in the overall zooplankton abundance, the size structure of the zooplankton community is stable. This stable size structure of the zooplankton community potentially enables the zooplanktivorous fish to match their prey-size preference to the greatest available biomass that occurs in specific size classes.

## Conclusions

Increased understanding of lower trophic level predation dynamics will enable ecosystem modellers to better capture predator–prey dynamics within their models. It is now well recognised that modelling zooplankton specifically in ecosystem models is important (Heneghan *et al.* 2016), and that size-based modelling approaches may offer significant advantages over traditional food-web models (Blanchard *et al.* 2017), particularly when predators have diverse prey. By empirically matching predator–prey dynamics to specific size classes of zooplankton with a mechanism (biomass availability), our findings should enable more confidence in the modelling of zooplanktivorous fish predation.

This study has both demonstrated size-selective zooplankton predation by estuarine fish and shown that the targeted size range is likely to be preferred because it contains the largest amount of total biomass, although the extent of the selectivity varies by species. This results in the targeted size classes being the most efficient prey source in terms of return and effort during foraging. This has important considerations for zooplanktivorous fish trophic ecology because it highlights how these species do not feed randomly on zooplankton in the water. The information highlighted in this paper will enable the creation of more accurate lower trophic level and size-based ecosystem models.

## Supplementary material

Supplementary material is available online.

#### References

- Andersen KH, Berge T, Gonçalves RJ, Hartvig M, Heuschele J, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer AB, Olsson K, Palacz A, Prowe AEF, Sainmont J, Traving SJ, Visser AW, Wadhwa N, Kiørboe T (2016) Characteristic sizes of life in the oceans, from bacteria to whales. *Annual Review of Marine Science* **8**, 217–241. doi:10.1146/annurev-marine-122414-034144
- Araoz N (1991) Individual biomass, based on body measures, of copepod species considered as main forage items for fishes of the Argentine shelf. *Oceanologica Acta* 14, 575–580.
- Avila TR, Machado AA S, Bianchini A (2012) Estimation of zooplankton secondary production in estuarine waters: comparison between the enzymatic (chitobiase) method and mathematical models using crustaceans. Journal of Experimental Marine Biology and Ecology 416–417, 144–152. doi:10.1016/j.jembe.2012.02.015
- Balogh C, Serfőző Z, Kobak J (2022) Factors determining selective predation of the common carp on quagga versus zebra mussels. *Freshwater Biology* **67**(4), 619–629. doi:10.1111/fwb.13867
- Barnardo T, Tambling CJ, Davies AB, Klein-Snakenborg S, Asner GP, le Roux E, Cromsigt JPGM, Druce DJ, Kerley GIH (2020) Opportunistic feeding by lions: non-preferred prey comprise an important part of lion diets in a habitat where preferred prey are abundant. *Mammal Research* **65**, 235–243. doi:10.1007/s13364-020-00481-3
- Blanchard JL, Heneghan RF, Everett JD, Trebilco R, Richardson AJ (2017) From bacteria to whales: using functional size spectra to model marine ecosystems. *Trends in Ecology & Evolution* 32, 174–186. doi:10.1016/j.tree.2016.12.003
- Budy P, Haddix T, Schneidervin R (2005) Zooplankton size selection relative to gill raker spacing in rainbow trout. *Transactions of the American Fisheries Society* **134**, 1228–1235. doi:10.1577/T04-159.1
- Bulman C, Althaus F, He X, Bax NJ, Williams A (2001) Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. *Marine* and Freshwater Research 52, 537–548. doi:10.1071/mf99152
- Champion C, Suthers IM, Smith JA (2015) Zooplanktivory is a key process for fish production on a coastal artificial reef. *Marine Ecology Progress Series* 541, 1–14. doi:10.3354/meps11529

- Chappell BF, Smith KG (2016) Patterns of predation of native reef fish by invasive Indo-Pacific lionfish in the western Atlantic: evidence of selectivity by a generalist predator. *Global Ecology and Conservation* **8**, 18–23. doi:10.1016/j.gecco.2016.08.002
- Chesson J (1978) Measuring preference in selective predation. *Ecology* **59**, 211–215. doi:10.2307/1936364
- Chisholm LA, Roff JC (1990) Size–weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. *Marine Biology* 106, 71–77. doi:10.1007/BF02114676
- Cumminns KW, Wuycheck JC (1971) Caloric equivalents for investigations in ecological energetics. SIL Communications, 1953-1996 18, 1–158. doi:10.1080/05384680.1971.11903918
- Das P, Marchesiello P, Middleton JH (2000) Numerical modelling of tide-induced residual circulation in Sydney Harbour. Marine and Freshwater Research 51, 97–112. doi:10.1071/MF97177
- Dawson G, Suthers IM, Brodie S, Smith JA (2020) The bioenergetics of a coastal forage fish: importance of empirical values for ecosystem models. Deep-sea Research – II. Topical Studies in Oceanography 175, 104700. doi:10.1016/j.dsr2.2019.104700
- Edgar GJ, Stuart-Smith RD (2014) Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data* 1, 140007. doi:10.1038/sdata.2014.7
- Foo D, Semmens JM, Arnould JPY, Dorville N, Hoskins AJ, Abernathy K, Marshall GJ, Hindell MA (2016) Testing optimal foraging theory models on benthic divers. *Animal Behaviour* 112, 127–138. doi:10.1016/j.anbehav.2015.11.028
- Garcia V, Schilling HT, Cruz D, Hawes SM, Everett JD, Roughan M, Miskiewicz AG, Pakhomov EA, Jeffs A, Suthers IM (2022) Entrainment and development of larval fish assemblages in two contrasting cold core eddies of the East Australian Current system. *Marine Ecology Progress Series* **685**, 1–18. doi:10.3354/meps13982
- Gardner MB (1981) Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. *Ecology* **62**, 571–578. doi:10.2307/1937723
- Gaston TF, Suthers IM (2004) Spatial variation in  $\delta^{13}$ C and  $\delta^{15}$ N of liver, muscle and bone in a rocky reef planktivorous fish: the relative contribution of sewage. *Journal of Experimental Marine Biology and Ecology* **304**, 17–33. doi:10.1016/j.jembe.2003.11.022
- Glasby TM, Kingsford MJ (1994) *Atypichthys strigatus* (Pisces: Scorpididae): an opportunistic planktivore that responds to benthic disturbances and cleans other fishes. *Australian Journal of Ecology* **19**, 385–394. doi:10.1111/j.1442-9993.1994.tb00504.x
- Goddard BK, Becker A, Harasti D, Smith JA, Subramaniam RC, Suthers IM (2022) The trophic basis of fish assemblages in temperate estuarine and coastal ecosystems. *Marine Biology* 169, 19. doi:10.1007/ s00227-021-04001-y
- Graeb BDS, Dettmers JM, Wahl DH, Cáceres CE (2004) Fish size and prey availability affect growth, survival, prey selection, and foraging behavior of larval yellow perch. *Transactions of the American Fisheries Society* **133**, 504–514. doi:10.1577/T03-050.1
- Hansen AG, Beauchamp DA, Schoen ER (2013) Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size. *Transactions of the American Fisheries Society* **142**, 854–867. doi:10.1080/00028487.2013.785978
- Hatton IA, Heneghan RF, Bar-On YM, Galbraith ED (2021) The global ocean size spectrum from bacteria to whales. *Science Advances* 7, eabh3732. doi:10.1126/sciadv.abh3732.
- Heneghan RF, Everett JD, Blanchard JL, Richardson AJ (2016) Zooplankton are not fish: improving zooplankton realism in sizespectrum models mediates energy transfer in food webs. *Frontiers in Marine Science* **3**, 201. doi:10.3389/fmars.2016.00201
- Herman AW, Harvey M (2006) Application of normalized biomass size spectra to laser optical plankton counter net intercomparisons of zooplankton distributions. *Journal of Geophysical Research: Oceans* 111, C05S05. doi:10.1029/2005JC002948
- Herman AW, Beanlands B, Phillips EF (2004) The next generation of optical plankton counter: the laser-OPC. *Journal of Plankton Research* 26, 1135–1145. doi:10.1093/plankt/fbh095
- Hernández-Pliego J, Rodríguez C, Dell'Omo G, Bustamante J (2017) Combined use of tri-axial accelerometers and GPS reveals the flexible foraging strategy of a bird in relation to weather conditions. *PLoS One* **12**, e0177892. doi:10.1371/journal.pone.0177892
- Jansen T, Post S, Olafsdottir AH, Reynisson P, Óskarsson GJ, Arendt KE (2019) Diel vertical feeding behaviour of Atlantic mackerel

(Scomber scombrus) in the Irminger current. Fisheries Research 214, 25–34. doi:10.1016/j.fishres.2019.01.020

- Johnston EL, Mayer-Pinto M, Hutchings PA, Marzinelli EM, Ahyong ST, Birch G, Booth DJ, Creese RG, Doblin MA, Figueira W, Gribben PE, Pritchard T, Roughan M, Steinberg PD, Hedge LH (2015) Sydney Harbour: what we do and do not know about a highly diverse estuary. *Marine and Freshwater Research* **66**, 1073–1087. doi:10.1071/MF15159
- Kingsford MJ (1989) Distribution patters of planktivorous reef fish along the coast of northeastern New Zealand. Marine Ecology Progress Series 54, 13–24. doi:10.3354/meps048103
- Langeland A, Nøst T (1995) Gill raker structure and selective predation on zooplankton by particulate feeding fish. *Journal of Fish Biology* **47**, 719–732. doi:10.1111/j.1095-8649.1995.tb01937.x
- Moore SK, Suthers IM (2006) Evaluation and correction of subresolved particles by the optical plankton counter in three Australian estuaries with pristine to highly modified catchments. *Journal of Geophysical Research: Oceans* **111**, 1–14. doi:10.1029/2005jc002920
- Pierce GJ, Ollason JG (1987) Eight reasons why optimal foraging theory is a complete waste of time. *Oikos* **49**, 111–118. doi:10.2307/3565560
- Pikitch EK, Rountos KJ, Essington TE, Santora C, Pauly D, Watson R, Sumaila UR, Boersma PD, Boyd IL, Conover DO, Cury P, Heppell SS, Houde ED, Mangel M, Plagányi É, Sainsbury K, Steneck RS, Geers TM, Gownaris N, Munch SB (2014) The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* 15, 43–64. doi:10.1111/faf.12004
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* **52**, 137–154. doi:10.1086/409852
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* **9**, 671–675. doi:10.1038/ nmeth.2089

- Sheldon RW, Prakash A, Sutcliffe WH (1972) The size distribution of particles in the ocean. *Limnology and Oceanography* **17**, 327–340. doi:10.4319/lo.1972.17.3.0327
- Simons RD, Monismith SG, Johnson LE, Winkler G, Saucier FJ (2006) Zooplankton retention in the estuarine transition zone of the St Lawrence Estuary. *Limnology and Oceanography* **51**, 2621–2631. doi:10.4319/lo.2006.51.6.2621
- Skjoldal HR, Wiebe PH, Postel L, Knutsen T, Kaartvedt S, Sameoto DD (2013) Intercomparison of zooplankton (net) sampling systems: results from the ICES/GLOBEC sea-going workshop. *Progress in Oceanography* 108, 1–42. doi:10.1016/j.pocean.2012.10.006
  Suthers IM, Taggart CT, Rissik D, Baird ME (2006) Day and night
- Suthers IM, Taggart CT, Rissik D, Baird ME (2006) Day and night ichthyoplankton assemblages and zooplankton biomass size spectrum in a deep ocean island wake. *Marine Ecology Progress Series* **322**, 225–238. doi:10.3354/meps322225
- Tanaka H, Aoki I, Ohshimo S (2006) Feeding habits and gill raker morphology of three planktivorous pelagic fish species off the coast of northern and western Kyushu in summer. *Journal of Fish Biology* 68, 1041–1061. doi:10.1111/j.0022-1112.2006.00988.x
- Thygesen UH, Sommer L, Evans K, Patterson TA (2016) Dynamic optimal foraging theory explains vertical migrations of Bigeye tuna. *Ecology* **97**, 1852–1861. doi:10.1890/15-1130.1
- Truong I, Suthers IM, Cruz DO, Smith JA (2017) Plankton supports the majority of fish biomass on temperate rocky reefs. *Marine Biology* **164**, 73. doi:10.1007/s00227-017-3101-5
- Tyson RB, Friedlaender AS, Nowacek DP (2016) Does optimal foraging theory predict the foraging performance of a large air-breathing marine predator? *Animal Behaviour* **116**, 223–235. doi:10.1016/j. anbehav.2016.03.034
- Wanzenbock J (1995) Changing handling times during feeding and consequences for prey size selection of O+ zooplanktivorous fish. *Oecologia* 104, 372–378. doi:10.1007/bf00328373

Data availability. All code and data are available at https://github.com/HaydenSchilling/Estuarine-Size-Selective-Predation.

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