

Diet overlap and resource partitioning among three forage fish species in Coorong, the largest inverse estuary in Australia

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Abstract Protracted drought in southern Australia has degraded the system function of the Coorong estuary and intensified resource competition among forage fish species. The present study investigates the gut content, prey composition and dietary overlap of three forage fishes: smallmouth hardyhead (*Atherinosoma microstoma*), Tamar River goby (*Afurcagobius tamarensis*) and sandy sprat (*Hyperlophus vittatus*) influenced by environmental variation in the Murray Estuary and Coorong. The prey species identified in fish stomachs were dominated by crustaceans (amphipods, ostracods and harpacticoids), but nematodes and acanthocephalans were also common in all forage fishes. The diet of the sandy sprat and Tamar River goby highly overlapped ($\alpha = 0.8$) in the Murray Estuary and all three forage fishes showed potential diet overlap ($\alpha \geq 0.6$) in the North Lagoon. Spatiotemporal variation of prey diversity was observed in smallmouth hardyhead while temporal variation of prey diversity was observed in sandy sprat and Tamar River goby. Overall, the prey abundance was temporally variable and predominantly regulated by salinity, pH, dissolved oxygen, water transparency and chlorophyll *a* in the Murray Estuary and

Coorong. This study adds to our knowledge on dietary overlap and resource partitioning among small-bodied forage fishes mediated by environmental factors in the Murray Estuary and Coorong.

Keywords Salinity · pH · Chlorophyll · Forage fish · Zooplankton · Gut content

Introduction

Food competition and diet sharing are fundamentally important to understand fish feeding biology and trophic interactions between species in a fish community (Costello et al. 2002). Fish diets can be overlapped between species due to partitioning of food resources and are influenced by variation of environmental variables (Platell and Potter 2001). Estuaries are highly productive and often function as a habitat for migration, breeding and feeding ground for fish and other fauna (Jendyk et al. 2014). Thus, a productive estuary supports the abundance and diversity of fish species (Whitfield 1999; Dolbeth et al. 2008). The ontogeny, survival and growth of fish are largely influenced by habitat and food availability in an estuary (Taylor et al. 2006). Typically, the estuarine productivity is spatiotemporally variable due to environmental changes (Whitfield 1999) and primary production is greatly regulated by physical and biological factors within the dynamic system (Day et al. 1989). Therefore, the food variability in estuaries can affect predator–prey interactions through prey selection (Cantanhêde et al. 2009)

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and result in potential overlapping in diet due to species competition (Eriksson et al. 2005).

Prey selection in fish depends on prey size, abundance and distribution in the environment (Cantanhêde et al. 2009). Fish dietary overlap is a consequence of prey selection owing to intraspecific and interspecific competition for food and resource (Abrantes et al. 2015). The trophic niche describes the response of an organism or population to the change of competitors and resources and how it in turn affects these biological and environmental factors. The type of trophic response to environmental variables varies from one species to another and thus the trophic niche reflects the impact of a species on the ecosystem (Woodland and Secor 2011). As a result, dietary overlap occurs in fish because of changes in habitat competition (Munday et al. 2001; Wedderburn et al. 2014), foraging behaviour (Higginson and Ruxton 2015) and developmental stages (Nunn et al. 2012). For instance, variation in prey selection and overlapping in diets of redfin perch (*Perca fluviatilis*) and golden perch (*Macquaria ambigua ambigua*) were observed during drought and flood condition in terminating lakes of the Murray–Darling Basin in Australia (Wedderburn et al. 2014). In other study, Bachiller and Irigoien (2015) reported significant dietary overlap among small pelagic fish species in the Bay of Biscay in Spain due to spatial variation in food availability. However, environmental variability may have a major effect on feeding ecology of fish through influencing spatial and seasonal variation of food availability in an ecosystem (Xie et al. 2000).

The Coorong is a terminus wetland of the largest river system (Murray–Darling River) in Australia. In the 1930s, a series of barrages were constructed to separate the Murray Estuary and Coorong from the riverine freshwater system to prevent saline water intrusion up to the Murray River and adjacent lakes (Webster 2010). As a result, the Coorong has been transformed into an inverse estuary where the amount of water evaporation exceeds the freshwater inputs and salinity in the lagoon was higher than in the ocean (Leterme et al. 2015). The Coorong is recognised as a habitat of significant importance to the native and migratory fish and bird species (Paton 2010). Naturally, the Murray Estuary and Coorong promote the proliferation of small-bodied forage fish that are used as food for piscivorous fish to support commercial and recreational fisheries (Brookes et al. 2015). Since the European settlement, the Murray Estuary and Coorong have dramatically

changed from their natural form due to river regulation, water extraction and the construction of tidal barrages that create a physical and ecological barrier between the marine and freshwater environments (Webster 2010). In the last decade, the Murray Estuary and Coorong were more severely impacted, leading to ecological degradation due to protracted drought and lack of freshwater inflow from up streams. Consequently, the water salinity became marine in the Murray Estuary, hypersaline in the North Lagoon and extremely hypersaline (>100) in the South Lagoon (Webster 2010; Leterme et al. 2015).

Salinity is the most driving factor influencing the variation in abundance and distribution of flora and fauna in the Murray Estuary and Coorong (Brookes et al. 2015). Elevation of salinity associated with drought and low freshwater flow has reduced the abundance and distribution of phytoplankton (Jendyk et al. 2014), zooplankton (Geddes et al. 2016) and benthos (Dittmann et al. 2015) in the Murray Estuary and Coorong. Hyper-salinity due to low freshwater flow has reduced fish species diversity in the Coorong (Zampatti et al. 2010). Noell et al. (2009) investigated the flow related effects on fish ecology and found a declining trend in fish species diversity along the salinity gradient in the Murray Mouth and Coorong region. Consequently, in the South Lagoon, only one euryhaline species smallmouth hardyhead persist in extreme hyper salinity (Hossain et al. 2016). Recently, Geddes et al. (2016) reported the low diversity of zooplankton community in the Murray Estuary and Coorong compared to other estuaries in south-east Australia. Low diversity and availability of food resource may affect the overall food web and feeding ecology of small-bodied forage fishes in the Murray Estuary and Coorong region.

Small-bodied forage fishes are an important component in the marine and estuarine food webs and can transfer energy from primary producers to piscivorous fish, birds and mammals (Springer and Speckman 1997). In the last few decades, research in forage fish in marine and estuarine habitats has been globally active due to its ecological importance, commercial use for animal food and significant contribution to human food security (Alder et al. 2008). Forage fishes such as smallmouth hardyhead (*Atherinosoma microstoma*), Tamar River goby (*Afurcagobius tamarensis*) and sandy sprat (*Hyperlophus vittatus*) are the main prey species for a range of fish, birds and mammals in the Murray Estuary and Coorong (Deegan et al. 2010; Paton 2010). Smallmouth hardyhead is mostly abundant in the

southern part of the Coorong although is widely distributed throughout system (Noell et al. 2009; Hossain et al. 2016). On the other hand, Tamar River goby and sandy sprat are abundant in the Murray Estuary and North Lagoon but usually absent in the South Lagoon of the Coorong (Hossain et al. 2016; Wedderburn et al. 2016). The abundance and distribution of forage fish are greatly influenced by the changing salinity in the Murray Estuary and Coorong (Zampatti et al. 2010; Hossain et al. 2016).

In this inverse estuary, recent studies have focussed on fish trophic ecology (Geddes and Francis 2008), trophic dynamics (Deegan et al. 2010) and diets of large estuarine fish species (Giatas and Ye 2015). Geddes and Francis (2008) reported that change in prey abundance has strongly affected the overall trophic ecology and food web structure in the Coorong. Deegan et al. (2010) found that the length reduction of food chain among fish species is attributed to the decline of prey diversity along with the increasing salinity gradient in the Murray Estuary and Coorong. Very recently, Bice et al. (2016) reported that the freshwater discharge to the Murray Estuary could improve the productivity in the system. However, the complex food web in the Murray Estuary and Coorong is not well understood. Other than few empirical data, little is known on prey selection, dietary composition and resource partitioning among small-bodied forage fish species in the Murray Estuary and Coorong where a great variation of salinity prevails in the environment.

The aim of this study was to investigate prey selection and diet overlap among three key forage fish species, smallmouth hardyhead, Tamar River goby and sandy sprat in the Murray Estuary and Coorong. We hypothesise that (i) elevated salinity would lead to a shift in food resources and increase diet overlap among forage fish species and (ii) prey composition and abundance are affected by the variation of salinity and other environmental variables in the Murray Estuary and Coorong.

Materials and methods

Study region

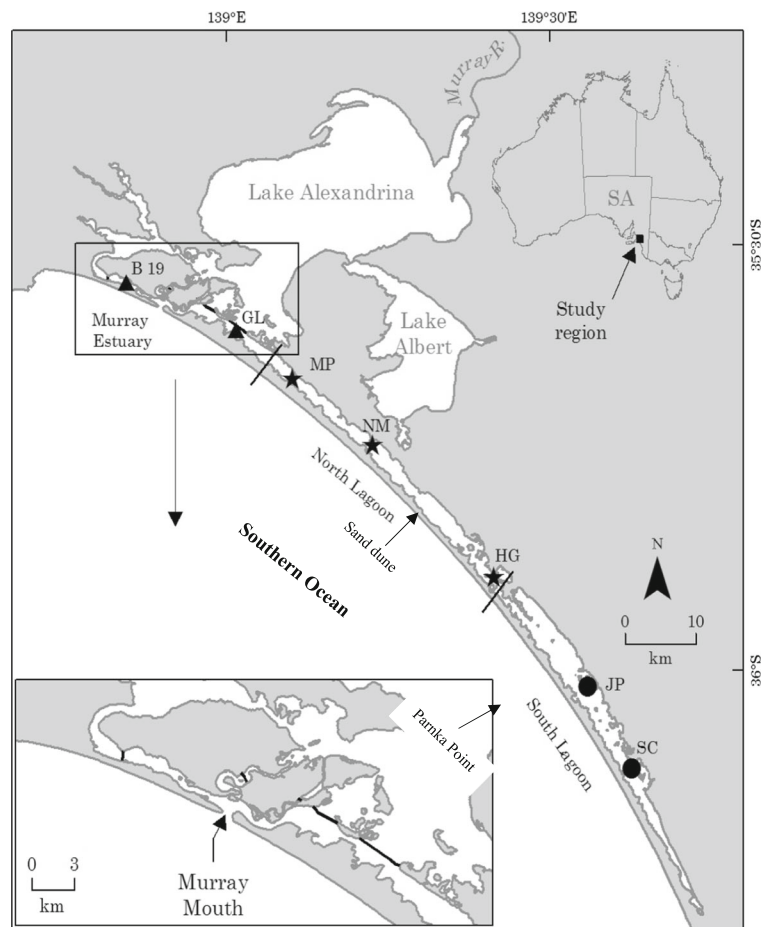
The Murray Estuary and Coorong is located 70 km south of Adelaide, South Australia. The Coorong is a long (>100 km), narrow (<4 km) and shallow (mean depth \approx 2 m) estuarine lagoon and lies at the terminus of

the largest Murray-Darling River in Australia. The Coorong is a wetland of international importance for supporting numerous species of fish, invertebrates and birds (Paton 2010). Typically, the Murray Estuary and Coorong split into three distinct regions: Murray Estuary in the vicinity of the mouth of the Murray River, North Lagoon and South Lagoon (Fig. 1). The Murray Estuary is connected to the Southern Ocean and Encounter Bay by a narrow channel at the Murray Mouth of the Murray River. The Coorong is protected from the Southern Ocean by a barrier of established fore sand-dune and is naturally divided into the North Lagoon and South Lagoon at the Parnka Point near the Hells Gate. A series of tidal barrages separate the Murray Estuary and Coorong from the Murray River and Lower Lakes (i.e., Lake Alexandrina and Lake Albert) and form distinctive environmental features in the system. As a result, the Murray Estuary is a dynamic system influenced by both tidal flushes and Murray River flows. While the Murray Estuary and the North Lagoon are more affected by freshwater releases from the Lower Lakes via the barrages, the South Lagoon also receives low inflows of South East Drainage Scheme (SEDS) from Salt Creek (Ye et al. 2012). Overall, the Murray Estuary and Coorong is characterised as a reverse estuary with strong north-south gradients of increasing salinity.

Field sampling

Sampling was conducted at three regions: the Murray Estuary, the North Lagoon and the South Lagoon from November 2013 to March 2014. Two sites in the Murray Estuary, three sites in the North Lagoon and two sites in the South Lagoon were selected for sampling to cover the broad salinity gradient typical of that environment. At each site, forage fishes were sampled using a seine net in the Murray Estuary and Coorong lagoons. A seine net of 61-m long, 29-m wing length (22-mm mesh) and 3-m bunt length (8 mm mesh) was used in a semi-circle and swept over an area \sim 600 m² to a maximum depth of 2 m at each site to catch both juvenile and adult forage fish. Among the fish collected, 20 individuals of each species of smallmouth hardyhead, Tamar River goby and sandy sprat were transferred to an aerated holding tank and euthanised using AQUI-S™ (40 mg

Fig. 1 Map of the Murray River estuary, North Lagoon and South Lagoon showing the 7 sites; Beacon 19 (B19), Godfrey's landing (GL), Mark point (MP), Noonameena (NM), Hells Gate (HG), Jack point (JP) and Salt Creek (SC)



L^{-1}). The euthanised forage fish were preserved in 10% formalin for gut content analysis. Zooplankton samples were taken in the vicinity of fish sampling sites using a modified 35-L Schindler-Patalas plankton trap with 50- μ m mesh. Zooplankton collected in the cod-end were stored in a 250-mL plastic container and fixed in 5% formalin for identification and counting. Water samples were also collected and filtered to measure chlorophyll *a* concentration on a spectrophotometer (Turner 450 Fluorometer).

Along with forage fish and zooplankton sampling at each site, physicochemical variables including salinity, water temperature, dissolved oxygen (DO) and pH were measured at 30 cm below water surface using a water quality meter (TPS, model 90FL) around mid-day. Water transparency was also measured using a Secchi disk. Three replicates were used at each sampling site. All samples were collected on a boat in the Murray Estuary and North Lagoon, and from the shore in the South Lagoon.

Laboratory analysis

Gut content

To assess the fish gut content, a small incision was made through the abdomen of each fish and the entire gut was removed and transferred to a petri dish. The contents of the gut were then removed using a fine forceps and the prey items were identified up to the lowest taxon and counted under a dissecting microscope (Olympus SZ30). In some cases, a compound microscope (Olympus CX 40) was used for species identification.

Zooplankton identification

For identification and quantification, zooplankton samples were poured onto a gridded Greiner square petri dish (12 × 12 cm). An inverted microscope (Nikon Eclipse TS100F) was then used to identify the prey individuals to the lowest possible taxonomic level using

several identification keys and count the number (Hamond 1971; Hamond 1973; Smirnov and Timms 1983; Bayly 1992; Shiel 1995).

Data analysis

Statistical analysis

The Shannon-Weaver index (H') data of the diet of each forage fish (univariate) were used to construct a Euclidean distance resemblance matrix (Anderson et al. 2008). Relative abundance data of zooplankton were transformed into $\log(x + 1)$ to down-weight undue influence of highly abundant zooplankton and a dummy species was added in the samples without any specimen (Anderson et al. 2008). The $\log(x + 1)$ transformed data were used to construct a Bray-Curtis resemblance matrices (Anderson 2001). Environmental variables were normalised and employed to construct Euclidean distance resemblance matrices. Permutational analysis of variance (PERMANOVA; pseudo- $P > 0.05$) was run using Euclidean distance resemblance matrices of Shannon-Weaver index from the diet of each forage fish to test the diet difference among the months and regions in the Murray Estuary and Coorong (Clarke and Warwick 2001). For smallmouth hardyhead, the analysis consisted of two factors including five sampling months as random five levels and three sampling regions as fixed three levels. In the case of sandy sprat and Tamar River goby, only two sampling regions were used as fixed two levels in the analysis. PERMANOVA was also conducted using Bray-Curtis resemblance matrices to detect significant differences of zooplankton abundance, and the factors included months as random five levels and regions as fixed three levels. Pairwise post-hoc comparisons using the multivariate analog of the t -test (pseudo- t) were performed at each level to identify significant difference. Unrestricted permutation was accomplished for each factor and interaction with 999 permutations to detect differences at $\alpha = 0.05$ (Anderson 2001). A distance-based linear model (DistLM) was performed to identify the effect of environmental variables on zooplankton abundance. Normalised environmental data and $\log(x + 1)$ transformed zooplankton abundance data were used in DistLM analysis (Anderson et al. 2008). Correlations among the environmental variables were generated in the DistLM analysis. A distance based redundancy analysis (dbRDA) was then plotted during DistLM analysis

to give a visual representation of the influence of environmental variables on the variation of zooplankton abundance. All tests were performed using PRIMER v6 (Clarke and Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008).

Dietary analysis

The Shannon-Weaver index (H') was used to assess the prey diversity of the dietary contents in each forage fish species. Shannon-Weaver index (H') was calculated as

$$H' = -\sum p_i \ln p_i$$

where p is the relationship between the total number of prey of species i and total number of prey in the sample (Clarke and Warwick 2001; Clarke and Gorley 2006).

Diet data were expressed as composition in stomach of each forage fish by frequency of occurrence (% F) in the diets to determine diet composition (Hyslop 1980):

$$\text{Frequency of occurrence (\% } F_i) = (N_i / N) \times 100.$$

where F_i = percent frequency of prey type i , N_i = number of prey i in the gut, and N is total number of prey in the gut contents.

Feeding strategy of forage fish was determined using the Costello (1990) graphical method modified by Amundsen et al. (1996). In this approach, prey-specific abundance was calculated as

$$P_i = (\sum S_i / \sum S_{ii}) \times 100$$

where P_i is the prey-specific abundance of prey i ; S_i is the stomach content (by number) comprising prey i , and S_{ii} is the total stomach content only in predators with prey i in the stomach.

The prey-specific abundance was plotted against the frequency of occurrence of prey to determine diet specialization (i.e., feeding strategy) and prey importance. In the graph, prey types positioned in the upper part of the graph represent a specialist feeding strategy of the predator, and those positioned in the lower part indicate a generalist feeding strategy of the predator. Moreover, the diet specialization was also calculated by the diet evenness index (Evenness = $H' / H' \text{ max}$), ranging from a more stenophagous diet (close to zero) to a more euryphagous diet (close to one) based on the method of Oscoz et al. (2005). The evenness index was employed together with the Costello (1990) graphical

method modified by Amundsen et al. (1996) to estimate the feeding characteristics of each fish species.

Ivlev's (1961) electivity index was used to identify the level of prey selection of forage fish (Chesson 1978). Electivity index was calculated as

$$\text{Electivity index } E_i = \frac{r_i - p_i}{r_i + p_i}$$

where r_i is the proportion of prey in diet and p_i is proportion of prey in ambient environment. The values (E_i) range from -1 to $+1$, where -1 indicates the absence of prey in guts and therefore suggests prey avoidance. Conversely, positive values suggest active selection of a prey type. Zero indicates no or little selection (i.e., random selection).

Dietary overlap of forage fish was calculated using Schoener's overlap index (Fjøsne and Gjørseter 1996).

$$\text{Schoener's overlap index } a = 1 - 0.5 \left(\sum_{i=1}^n |P_{ij} - P_{ik}| \right)$$

The index determines overlap (α), where P_{ij} = the proportion of the i th resource (prey category) used by species j , and P_{ik} = the proportion of the i th resource used by species k . Overlap index values range from 0 (no overlap) to 1.0 (complete overlap); values of 0–0.29 indicate low dietary overlap, 0.3–0.59 moderate overlap, and ≥ 0.6 high overlap between the two fish species (Langton 1982).

Results

Forage fish diets and feeding strategy

A total of 574 fish (266 smallmouth hardyhead, 190 sandy sprat, and 118 Tamar River goby) were dissected to identify the gut contents. Sizes of the forage fishes in catch ranged 16–85 mm for smallmouth hardyhead, 15–89 mm for Tamar River goby and 18–70 mm for sandy sprat. Overall, 16 prey types, including seven crustaceans, four insects, two rotifers, one nematodes, one polychaetes and one acanthocephalan were identified in the gut contents of the three forage fishes during the study period from November 2013 to March 2014 (Table 1). The gut content of all three forage fishes was dominated by crustaceans. Gut content analysis showed different occurrences of harpacticoids (65%), ostracods (58%), amphipods (53%) and mysids (6%) in smallmouth hardyhead. Dietary analysis indicated a

high occurrence of amphipod (90%), followed by harpacticoida (31%), ostracods (28%) and mysids (18%) in Tamar River goby. Similarly, harpacticoida (73%) dominated in the sandy sprat gut followed by amphipod (59%), ostracods (37%) and mysids (5%). Occurrences of insects were greater in smallmouth hardyhead (Chironomidae 32%; Diptera 21% and Corixidae 2%) than in Tamar River goby (Diptera 2%), whereas these prey items were completely absent in sandy sprat over the study period. In addition, rotifers were identified in the gut of Tamar River goby but were absent from the guts of smallmouth hardyhead and sandy sprat. Finally, nematodes and acanthocephalan commonly occurred in the diets of all three forage fishes while polychaete worms (Nereidae) were identified in smallmouth hardyhead and Tamar River goby. The occurrence of Nereidae was high (26%) in Tamar River goby and low (4%) in smallmouth hardyhead, but completely absent in sandy sprat. The modified Costello graphic analysis on the relationship between abundance and occurrence of 11 major prey categories showed that smallmouth hardyhead was a generalist feeder and fed mainly on epibenthic crustacean such as amphipods, ostracods and harpacticoids (Fig. 2a). In Tamar River goby, the graphic analyses for 12 prey items revealed that the feeding strategy of this species was a generalist feeder as most of prey items positioned in the lower part with the exception of amphipods at the upper right corner of the graph (Fig. 2b). Similarly, graphic analysis for nine prey categories indicated the generalist feeding strategy of sandy sprat as most prey items were at the lower part of the graph (Fig. 2c). These results were confirmed by the high value of the evenness index (smallmouth hardyhead: 0.43 ± 0.01 SE; Tamar River goby: 0.40 ± 0.02 SE and sandy sprat: 0.44 ± 0.02 SE).

Dietary overlap and electivity index

The 16 prey types were also used to assess the diet overlap among the forage fish in the Murray Estuary and North lagoon (Table 1). Samples from the South Lagoon were excluded from diet overlap calculations due to the sole presence of smallmouth hardyhead. The diet was highly overlapped ($\alpha = 0.8$) between sandy sprat and Tamar River goby in the Murray Estuary (Fig. 3), where there exhibited moderate diet overlap ($\alpha = 0.53$) among the three species. In the North Lagoon, all three forage fish species showed high

Table 1 Frequency of occurrence (F %) of prey types in the gut of three forage fish species

Phyla/Class	Taxon	Smallmouth hardyhead	Tamar River goby	Sandy sprat
Crustacea	Amphipoda	53	90	59
	Ostracoda	58	28	37
	Harpacticoida	65	31	73
	Calanoida	0	1	6
	<i>Bosmina</i> sp.	0	1	4
	Mysidacea	6	18	5
	Nauplius	0	0	8
Insecta	Chironomidae	32	0	0
	Diptera	21	2	0
	Corixidae	2	0	0
	Staphylinidae	0	0	0
Rotifera	<i>Brachionus</i> sp.	0	4	0
	<i>Filinia</i> sp.	0	1	0
Nematoda	Nematoda	42	8	3
Polychaeta	Nereidae	4	26	0
Acanthocephala	Acanthocephala	10	31	9

dietary overlap ($\alpha \geq 0.6$) (Fig. 3). The prey type in water samples from the field was used to calculate food selectivity for forage fishes. Seven prey types were used to calculate the electivity index for smallmouth hardyhead, eight for sandy sprat and 10 for Tamar River goby. All three forage fish species exhibited high preference and positive selection for amphipods, harpacticoids and mysids and negative selection for nematodes (Table 2). Sandy sprat ($E_i = 0.61$) and Tamar River goby ($E_i = 0.54$) positively selected ostracods whereas smallmouth hardyhead showed negative selection ($E_i = -0.37$) for ostracods. Nereidae was negatively selected by smallmouth hardyhead ($E_i = -0.25$) and positively selected by Tamar River goby ($E_i = 0.54$, Table 2).

Dietary prey diversity in forage fish

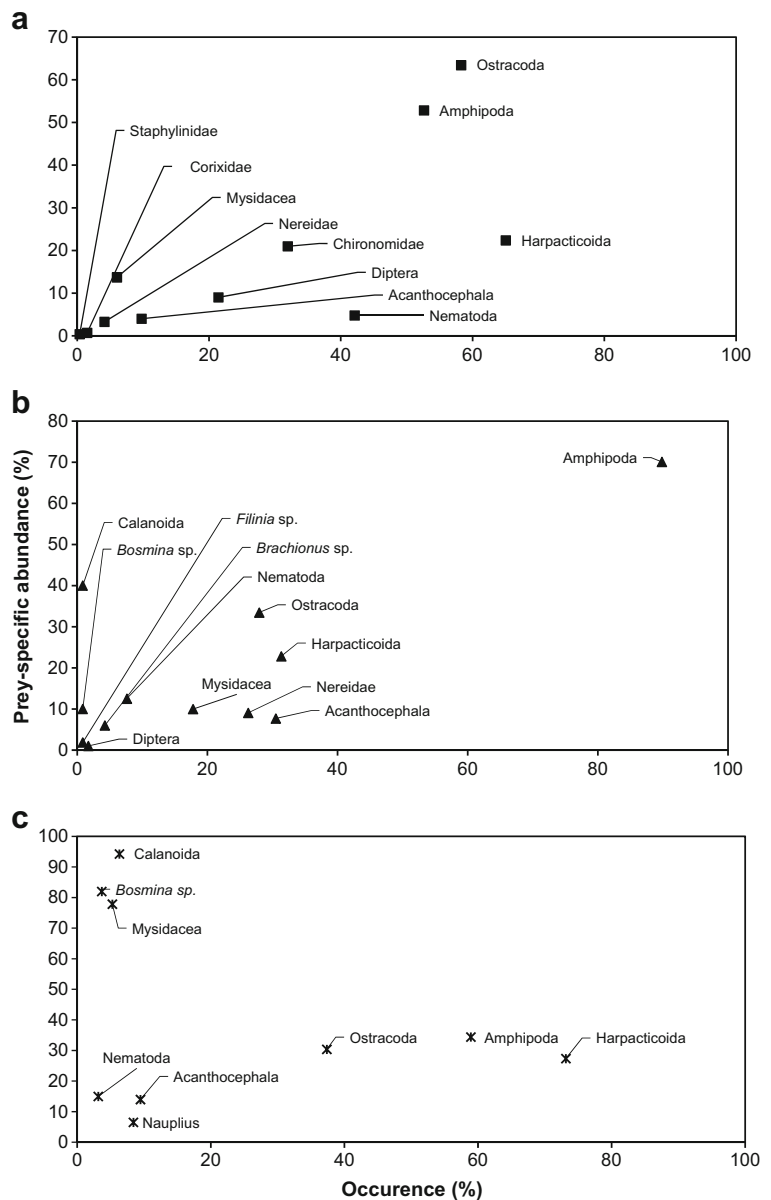
Significant spatial and temporal variation of dietary prey diversity was detected in smallmouth hardyhead among regions ($P = 0.028$) and months ($P = 0.032$) during the study period (Table 3). Dietary prey diversity in sandy sprat and Tamar River goby showed an inconsistent pattern in the Murray Estuary and the North Lagoon during the study period (Table 3). There was a significant month by region interaction of prey diversity in sandy sprat ($P = 0.001$) and Tamar River goby

($P = 0.001$) but not in smallmouth hardyhead ($P = 0.196$, Table 3). Pairwise tests detected significant differences in the diversity of dietary prey in sandy sprat between the Murray Estuary and North Lagoon except in February 2014 (Murray Estuary vs North Lagoon: pseudo- $t = 1.48$, $P = 0.137$) and March 2014 (Murray Estuary vs North Lagoon: pseudo- $t = 1.42$, $P = 0.161$). Similarly, pairwise comparison identified significant differences in the diversity of dietary prey in Tamar River goby between Murray Estuary and North Lagoon except in November 2013 (Murray Estuary vs North Lagoon: pseudo- $t = 1.09$, $P = 0.296$) and February 2014 (Murray Estuary vs North Lagoon: pseudo- $t = 1.15$, $P = 0.224$).

Temporal variation in zooplankton abundance

A significant month by region interaction ($P = 0.001$) was detected in zooplankton abundance (Table 4), suggesting that the pattern of spatial variation was not consistent between months. Pairwise test identified significant differences in zooplankton abundance among months except November 2013 vs December 2013 (pseudo- $t = 1.29$, $P = 0.184$); January 2014 vs February 2014 (pseudo- $t = 1.57$, $P = 0.09$) and February 2014 vs March 2014 (pseudo- $t = 1.43$, $P = 0.14$). Significant difference in zooplankton

Fig. 2 The modified Costello graphic analysis represents feeding strategy based on plotting the relationship between percentage of abundance and frequency of occurrence in 11 major taxonomic categories **a** for smallmouth hardyhead, in 12 prey items, **b** for Tamar River goby and in nine prey items, and **c** for sandy sprat



abundance was observed between the regions (Murray Estuary vs South Lagoon: pseudo- $t = 4.08$, $P = 0.003$ and North Lagoon vs the South Lagoon: pseudo- $t = 2.82$, $P = 0.004$) in November 2013. Similarly, zooplankton abundance was significantly variable between the regions (Murray Estuary vs South Lagoon: pseudo- $t = 5.67$, $P = 0.003$ and North Lagoon vs South Lagoon: pseudo- $t = 4.42$, $P = 0.005$) in December 2013. Zooplankton abundance showed significant difference between the Murray Estuary and the South Lagoon in January 2014 (pseudo- $t = 2.32$, $P = 0.029$) and in

February (pseudo- $t = 2.56$, $P = 0.003$). Similarly, zooplankton abundance was significantly variable between the Murray Estuary and the North lagoon (pseudo- $t = 2.84$, $P = 0.022$) and between the Murray Estuary and the South Lagoon (pseudo- $t = 6.31$, $P = 0.003$) in March 2014.

Salinity (DistLM, $P = 0.001$) and pH (DistLM, $P = 0.001$) were the most significant variables to predict the temporal variations in zooplankton abundance and composition in the Murray Estuary and Coorong (Table 5). With these two variable combined, they

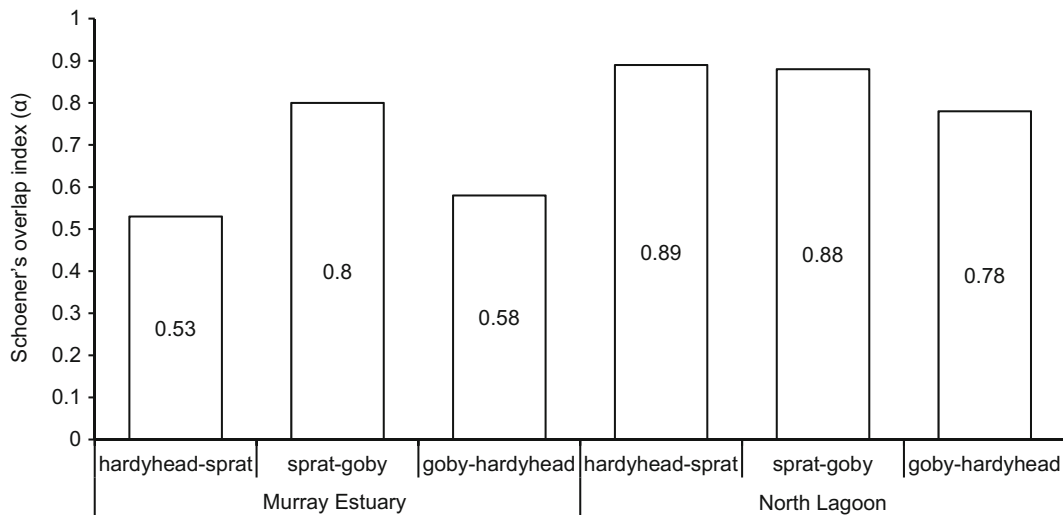


Fig. 3 Dietary overlap for forage fishes at the Murray Estuary and the North lagoon. The South Lagoon was excluded from the calculation due to sole presence of smallmouth hardyhead. Values

range from 0 (no overlap) to 1.0 (complete overlap). Values 0–0.29 indicate low; 0.3–0.59 moderate; and ≥ 0.6 high dietary overlap

together contributed 39% (proportion: 0.39) to the variation in zooplankton assemblage. Water transparency in this study ranged 25–200 cm in the Murray Estuary, 12–50 cm in the North Lagoon and 20–80 cm in the South Lagoon. The DO, water transparency and chlorophyll *a* also significantly contributed to the model (DistLM, $P = 0.001$), but these factors together explained only ~15% (proportion: 0.148) variation (Table 5). Similarly, in the dbRDA analysis, the first two axes (i.e. dbRDA1

and dbRDA2) explained 94% of the variability in zooplankton assemblage while pH and salinity were the key factors of the variability (Fig. 4).

Discussion

The current study addresses food selection and dietary overlap among the three forage fish species in the

Table 2 Electivity index (Ei) of each prey item of three forage fish species from three regions in the Murray Estuary and Coorong over the study period. Zooplankton collected from different sites of each region in the Murray Estuary and Coorong was used to calculate electivity index

Taxa	Smallmouth hardyhead	Sandy sprat	Tamar River goby
Amphipoda	0.75	0.83	0.88
Ostracoda	-0.37	0.61	0.54
Harpacticoida	0.54	0.86	0.30
Calanoida	0	-0.78	-0.99
<i>Bosmina</i> sp.	0	0.05	0
Mysidacea	0.07	0.04	1.00
Nauplius	0	-0.97	0
Chironomidae	0.54	0	0
Diptera	0	0	0
Corixidae	0	0	0
Staphylinidae	0	0	0
<i>Brachionus</i> sp.	0	0	0.33
<i>Filinia</i> sp.	0	0	-1.00
Nematoda	-0.72	-0.45	-0.55
Nereidae	-0.25	0	0.54
Acanthocephala	0	0	0

Table 3 PERMANOVA results of Shannon-Weaver index of dietary prey of each forage fish at three regions in the Murray Estuary and Coorong during the study period. This

PERMANOVA table includes fixed factors contributing to the changes of prey diversity during this study

Forage fish	Source	df	SS	MS	Pseudo-F	<i>P</i> (perm)
smallmouth hardyhead	Month	4	1.45	0.36	2.55	0.032
	Region	2	2.63	1.32	7.00	0.028
	Month × Region	5	1.00	0.20	1.40	0.196
	Residuals	254	36.18	0.14		
sandy sprat	Month	4	3.16	0.79	7.58	0.001
	Region	1	1.11	1.11	1.05	0.344
	Month × Region	4	4.38	1.09	10.50	0.001
	Residuals	170	17.72	0.10		
Tamar River goby	Month	4	1.89	0.47	3.42	0.009
	Region	1	0.04	0.04	0.03	0.935
	Month × Region	3	3.65	1.22	8.81	0.001
	Residuals	109	15.07	0.14		

*Significant difference was set at $P < 0.05$

Murray Estuary and Coorong. This study shows that three forage fishes feed on a wide range of prey including crustaceans, insects, nematodes, polychaetes and rotifers. Here, the diets of forage fishes were dominated by crustacean followed by insects, nematodes and polychaetes. Greater occurrence of insect was detected in the diet of smallmouth hardyhead and Tamar River goby while this prey was not consumed by sandy sprat. Importantly, freshwater and estuarine rotifers also contributed to the diet of Tamar River goby. In the current study, dietary analysis explores the dynamic prey selection and food sharing of all three forage fish in the Murray Estuary and Coorong. Geddes et al. (2016) reported that the diversity, abundance and distribution of estuarine and marine zooplankton community are significantly affected by hypersalinity associated with low river flow in the Coorong. In the current study, the variation in

occurrence and prey selection of the forage fish is more likely due to the variability in abundance and shifting of prey distribution regulated by elevated salinity in the Murray Estuary and Coorong.

Previous studies in the Coorong (Geddes and Francis 2008; Deegan et al. 2010) reported a predominance of crustacean and polychaetes in the diet of smallmouth hardyhead. Typically, atherinids are reported to prey on planktonic and epi-benthic preys in estuaries (Prince et al. 1982; Humphries and Potter 1993). The diet composition of small-bodied forage fish in the Murray Estuary and Coorong and other Australian estuaries (Humphries and Potter 1993; Becker and Laurenson 2008) suggests that this species feeds on plankton and invertebrates in the water column and at the sediment-water interface. In the present study, the occurrence of high proportion of aquatic insects (chironomids, Dipterae, Corixidae and Staphylinidae) in the diet

Table 4 PERMANOVA results of zooplankton abundance at three regions in the Murray Estuary and Coorong during the study period. This PERMANOVA table includes fixed factors contributing to the changes of zooplankton abundance during this study

Source	df	SS	MS	Pseudo-F	<i>P</i> (perm)
Month	4	11,016	2754	4.37	0.001
Region	2	10,202	51,019	1.44	0.254
Month × Region	8	28,324	3540	5.62	0.001
Residuals	90	56,719	630		
Total	104	105,820			

*Significant difference was set at $P < 0.05$

Table 5 DistLM sequential results of environmental variables on zooplankton abundance at three regions in the Murray Estuary and Coorong over the study period (SS = Sum of Square; Prop = Proportion of the variation; Cumul = Cumulative variation)

Variable	SS	Pseudo-F	DistLM <i>P</i>	Prop.	Cumul.
Salinity	11,717	12.83	0.001	0.111	0.111
pH	29,583	46.77	0.001	0.280	0.390
Temperature	1229	1.96	0.104	0.012	0.402
DO	8325	15.15	0.001	0.079	0.481
Water transparency	4146	8.08	0.001	0.039	0.520
Chlorophyll <i>a</i>	3198	6.58	0.001	0.030	0.550

suggests that the subsidised food resource from terrestrial to estuarine ecosystems is possible, especially in the diets of surface feeders such as smallmouth hardyhead (Brookes et al. 2009). However, high occurrences of crustacean and insects in the diet of smallmouth hardyhead are likely due to their food selection and feeding behaviour.

Likewise, dietary composition of the Tamar River goby is supported by previous studies in the Murray Estuary and Coorong (Geddes and Francis 2008; Deegan et al. 2010) with highly abundant amphipods and low abundance of polychaetes found in previous studies. Similarly, the diets of other gobiids (*Afurcagobius suppositus*) also include copepods and polychaetes in an Australian temperate estuary (Gaughan and Potter 1997). Ordinarily, gobiids are

reported to consume benthic organisms in estuaries (Humphries and Potter 1993). In the present study, the dominance of amphipods in the diet suggests that Tamar River goby is an epibenthic feeder. However, the occurrences of *Brachionus* sp. and *Filinia* sp. in the diet of Tamar River goby are likely due to common distribution of rotifers regulated by freshwater barrage and river inflow to the Murray Estuary and the North Lagoon in the Coorong.

In contrast, small-bodied marine clupeoids are commonly distributed near shore and migrate to estuaries and wetlands for growth and development during early life history (Gaughan et al. 1996; Rogers and Ward 2007). Of these clupeoids, sandy sprat is abundant around inshore of the gulf and inside the Murray Estuary and Coorong of South Australia (Rogers and

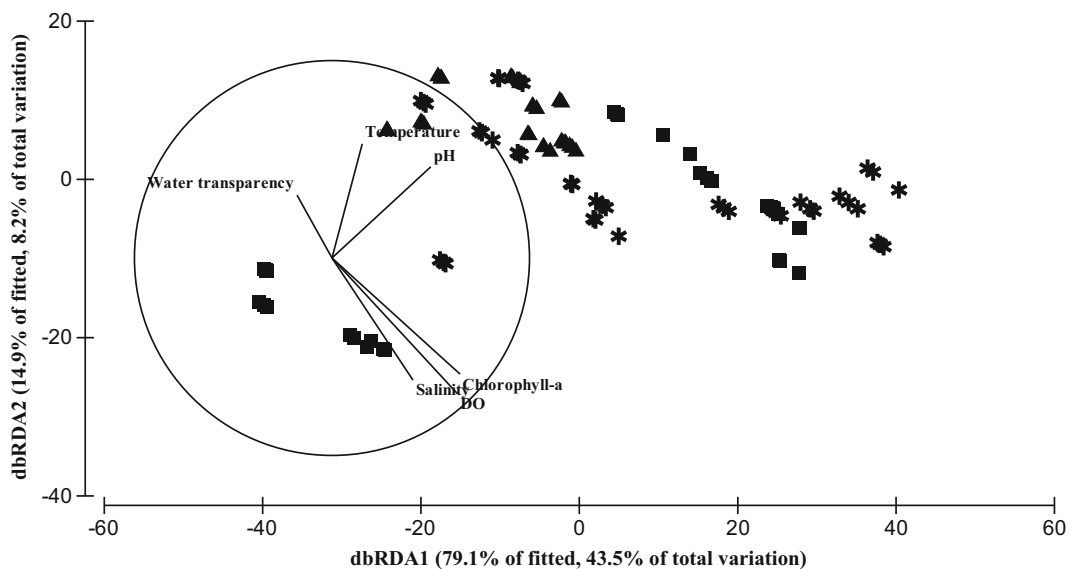


Fig. 4 Distance-based redundancy analysis (dbRDA) ordination of zooplankton abundance in three regions (Murray Estuary ▲, North Lagoon *, and South Lagoon ■) associated with predictor

variables of pH, salinity, water temperature, water transparency, DO and chlorophyll *a*

Ward 2007). Typically, sandy sprat is a pelagic opportunist feeder and fed on planktons as reported in other clupeoids (Gaughan et al. 1996). Bice et al. (2016) reported the dominance of crustaceans including the harpacticoid copepods (~73% of all prey items) in sandy sprat diet from the Murray Estuary. In the current study, crustacean contributed to the major diet of sandy sprat. The high proportion of crustacean and low proportion of polychaetes in the stomach of sandy sprat are possibly due to the opportunistic feeding habit that allows this species to prey on relatively abundant planktons and benthos in the Murray Estuary and Coorong.

Food competition and dietary overlap between fish species are often observed in estuarine systems because of low and variable abundance of invertebrate prey species (Moyle and Cech 2004). The ecological degradation due to protracted drought and low freshwater flows has severely impacted prey diversity in the Murray Estuary and Coorong (Geddes et al. 2016). Consequently, dietary overlap and food competition can be intensified due to low diversity of food resources in the Murray Estuary and Coorong. Dietary overlap of forage fish in the present study differed between regions in the Murray Estuary and Coorong. The low overlap between the diets of smallmouth hardyhead and other two species is likely due to the absence of preferred prey items for this species in the Murray Estuary except amphipods. In contrast, high diet overlap among forage fish species in the North Lagoon suggests high abundance of preferred prey and food sharing among forage fish species. Dietary overlap among forage fish species is patchy in the Murray Estuary and comparatively intensive in the North Lagoon while absent in the South Lagoon. The abundance and distribution of forage fish and prey individuals are strongly affected by salinity gradients regulated by freshwater inflow to the Murray Estuary and Coorong (Geddes et al. 2016; Hossain et al. 2016). This may reflect diet sharing among the forage fish in the North Lagoon where both forage fish and their prey are exposed to the optimal salinity environment.

Fish gut analysis in the current study focused on the major prey types of zooplankton and other invertebrates as these forage fish species are planktivorous in a natural environment (Geddes et al. 2016). Benthic prey species were dominated by harpacticoid copepods, amphipods, nematodes and polychaetes with only few insects in the diet. In the present study, the graphic analysis on the relationship between abundance and occurrence of prey

reveals that these three forage fish in the Coorong were a generalist feeder. The generalist feeding strategy of smallmouth hardyhead is possibly due to its epibenthic and planktonic feeding habit in estuaries (Prince et al. 1982; Humphries and Potter 1993). In comparison, the generalist feeding strategy in sandy sprat is likely associated with its opportunistic feeding behaviour like other clupeoids that feed a variety of benthic and planktonic prey items (Gaughan et al. 1996). Nevertheless, like most other goby species (D'Aguillo et al. 2014; Dinh et al. 2016), Tamar River goby is considered a generalist feeder as various food types (12 type of preys) were found in the stomach. The variability and abundance of prey items can influence the conspecific or interspecific competition in the environment (Ward et al. 2006). Thus, the low prey diversity associated with environmental stress can sway food selection of forage fish species in the Coorong (Geddes et al. 2016). However, most forage fish may feed on whatever is readily available in a large quantity rather than selecting specific prey items (Becker and Laurenson 2008). Despite the general feeding habit of three forage fish species in the present study, the variability and abundance of prey items in the environment also limit prey selection and preference of forage fish in the Coorong.

In estuaries the diversity and abundance of prey organisms such as plankton, benthos and other invertebrates are regulated by environmental variability and seasonal succession (Jendyk et al. 2014; Leterme et al. 2015). The diversity of prey organisms in this study is comparable to a recent report (Dittmann et al. 2015) and the status over three decades ago in the Coorong (De and Geddes 1980). Generally, the variability of prey diversity of forage fish is directly impacted by the temporal variation of zooplankton abundance and seasonal succession of phytoplankton in the Coorong (Dittmann et al. 2012). On the other hand, movement of euryhaline fish that have strong salinity tolerance, such as smallmouth hardyhead, allows its access to diverse prey items in the Coorong, therefore showing an indirect effect on prey diversity (Lui 1969; Molsher et al. 1994). The spatial variation of dietary prey diversity in sandy sprat and Tamar River goby is probably due to the limited salinity tolerance of some prey species in the Murray Estuary and the North Lagoon.

The variation of zooplankton abundance and distribution can impact the function of predators at higher trophic levels in the food web. In the current study, temporal variation of zooplankton abundance was

mainly influenced by pH and salinity, and, to a lesser extent by other environmental variables. The pH in estuaries is regulated by dissolved ions such as carbonate and bicarbonate through freshwater inputs (Gillanders et al. 2011). Their variation is related to salinity, photosynthesis and DO levels (Ringwood and Keppler 2002). The variation in pH in this study was positively correlated ($r = 0.21$) to the salinity changes in the Coorong. The change of pH can impact zooplankton growth, development and reproduction (Keller et al. 2002; Vehmaa et al. 2012). In the current study, the water pH was ~ 8 in the Murray Estuary, 7–8 in the North Lagoon and 6–8 in the South Lagoon, which is in the similar range with other Australian salt lakes (pH 8–9) (Williams 1981; Khan 2003). Although we identified pH as a significant factor affecting zooplankton, the mechanism was unclear as pH in the estuarine system usually co-varies with salinity and other factors (Williams 1998; Gillanders et al. 2011).

Salinity is the key variable attributing to a physiological barrier limiting zooplankton distribution, species richness (Paturej and Gutkowska 2015) and diversity in estuarine systems (Williams 1998; Boeuf and Payan 2001). Salinity in the Murray Estuary and Coorong controls the abundance and distribution of vertebrates and invertebrates (Geddes 2005; Noell et al. 2009; Webster 2010). In the current study, salinity ranged 2–30 in the Murray Estuary, 11–75 in the North Lagoon and 40–85 in the South Lagoon. Salinity can influence the variability of phytoplankton dynamics (Jendyk et al. 2014), picophytoplankton communities (Schapira et al. 2010) and microbenthic communities (Dittmann et al. 2015) in the Coorong. The abundance and distribution of zooplankton are impacted by the variability of salinity in the Coorong (Geddes et al. 2016) and in other estuaries (Marques et al. 2007). The seasonal variation of zooplankton in the current study is probably prevailed due to the variability of salinity in the Coorong.

Water transparency is related to the abundance of suspended materials and affect light penetration and primary productivity through photosynthesis (Herman and Heip 1999). The depth of water transparency corresponds well with the chlorophyll *a* concentrations in the Murray Estuary ($1.22 \pm 0.53 \mu\text{gL}^{-1}$), North Lagoon ($2.81 \pm 0.90 \mu\text{gL}^{-1}$) and South Lagoon ($2.96 \pm 0.60 \mu\text{gL}^{-1}$) and reflects the variation of phytoplankton abundance. The high chlorophyll *a* in the North Lagoon and South Lagoon might be due to high abundance of diatoms and picophytoplankton (Leterme et al. 2013). The

variability of phytoplankton production regulated by salinity and nutrients is likely to influence the temporal variation in zooplankton abundance and distribution in the Murray Estuary and Coorong (Leterme et al. 2015).

In conclusion, environmental factors affected the trophic interaction through food competition and partitioning among forage fish and predators in the Coorong. Crustaceans were actively selected by all three forage fish but smallmouth hardyhead also selected insects as prey in the Coorong. The nematodes and acanthocephalans were commonly observed in the gut of forage fish. The diet overlap among forage fishes in the North Lagoon was more than in the Murray Estuary. The temporal variation of zooplankton abundance is predominantly driven by the variability of pH, salinity, DO, water transparency and chlorophyll *a*. The variation in prey abundance significantly affected the predator-prey interaction through trophic dynamics along the salinity gradient in the Coorong. This study enhances our understanding of diet selection and dietary overlap among the forage fish species in an estuarine-hypersaline lagoonal system. The variation of environmental factors may mediate the outcome of diet selection and food sharing among fish in this inverse Australian estuary. This study provides basal information for further study of food web and trophic ecology in this and other similar estuarine systems.

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