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RESEARCH ARTICLE

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Trophic strategies of garfish, *Arrhamphus sclerolepis*, in natural coastal wetlands and artificial urban waterways

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Abstract We used carbon stable isotope and stomach content analyses to test whether snub-nosed garfish, *Arrhamphus sclerolepis* (Hemiramphidae), in the extensive artificial urban waterways of southeast Queensland, Australia, rely on autotrophic sources different to those in natural wetlands. Carbon isotope values of *A. sclerolepis* were similar to those in previous investigations, with enriched values in natural habitat (mean = −13.9‰, SE = 0.6) and depleted values (−19.1‰, 0.1) in artificial habitat. *A. sclerolepis* in natural habitat consumed large amounts of seagrass during the day and night, and at night also ingested small quantities of crustacean prey. In artificial habitat, *A. sclerolepis* consumed macroalgae during the night and switched to invertebrates (terrestrial ants) in the day. Values of δ^{15} N in all the fish were 3–8‰ more enriched than sources. Mathematical modelling of feasible source mixtures showed that in natural habitat the bulk of the dietary carbon is obtained from seagrass, but the nitrogen is obtained from animal prey. In artificial habitat, carbon is obtained from a mixture of macroalgae and animals. We could not determine the nitrogen sources in artificial habitat of *A. sclerolepis* since, even after accounting for trophic fractionation of δ^{15} N, the values were outside the range of potential sources. If the types of animals ingested vary over time, perhaps one or more types of animal important in the provision of nitrogen was not sampled during the study. This study demonstrates that not only does *A. sclerolepis* occur in both artificial and natural habitats, but it uses the same strategy of bulk herbivory with the inclusion of smaller amounts of animal prey. This understanding of how ecological processes support fisheries production in artificial habitat improves the overall understanding of the effects of urbanisation on coastal food webs.

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Introduction

Coastal wetland habitats are being fragmented or lost around the world because of urbanisation (Cohen et al. 1997). In many places, natural vegetated wetlands are being replaced by artificial urban waterways lacking macrophytes (Maxted et al. 1997). Fish in estuaries are part of food webs ultimately supported by energy (carbon) from conspicuous macrophytes in natural wetlands such as seagrass (Connolly et al. 2005) or saltmarsh (Wainright et al. 2000). In artificial urban waterways, in situ autotrophs supporting production are presumably restricted to algal sources such as [macroalgae, microphytobenthos (MPB) and phytoplankton] and possibly terrestrial plants (especially grasses). Given the mobility of organic matter in estuaries (Odum 1984), food webs in artificial waterways might conceivably also be driven by allochthonous inputs of macrophytes from adjacent natural wetlands.

An early study found that prey items in the stomachs of fish were similar in artificial canals and adjacent wetlands in Florida (Kinch 1979), however, the autotrophic sources at the base of the food webs were not examined. More recent evidence based on carbon isotope analysis has shown that at least some fishes have different trophic pathways in natural and artificial habitats. Connolly (2003) demonstrated that in southeast Queensland, an economically important species, snub-nosed garfish (*Arrhamphus sclerolepis*), had enriched carbon isotope values, consistent with seagrass, in natural habitat and depleted carbon isotope values, con-

sistent with macroalgae, in artificial habitat. Given that fish isotope values can change over time (e.g. Vizzini and Mazzola 2002), our first aim was to determine whether the differences in carbon isotope values of *A. sclerolepis* found by Connolly (2003) in 1 year in natural and artificial habitat remained evident the following year. We would take consistency in the carbon isotope values over time as evidence that food web processes are consistent from year to year for this species. Our second aim was to test which of the several plausible models explain trophic pathways for *A. sclerolepis* in natural and artificial estuarine waterways.

Species of Hemiramphidae are reported to be at least partly herbivorous (Carseldine and Tibbetts 2005). Where diel analysis of stomach contents has been done on confamilial species, a tendency to switch from plant material in the day to animal prey at night has been found (Robertson and Klumpp 1983). It is unknown whether *A. sclerolepis* displays this dietary switching between day and night, or over longer periods during ontogenetic development (Tibbetts 1991). In natural habitat, there are two main potential trophic pathways for *A. sclerolepis*: (1) direct consumption of seagrass, including any epiphytic algae (enriched carbon isotope values), or (2) consumption of animal prey that, ultimately, also rely on seagrass or attached epiphytic algae (Fig. 1a). In artificial habitat, *A. sclerolepis* obtains its nutrition from either: (1) direct consumption of in situ algae (depleted carbon isotope values), (2) consumption of an animal intermediary that utilises in situ algae, or (3) consumption of an animal intermediary that utilises detrital macrophyte material transported on currents from adjacent natural habitat (Fig. 1b). In the latter scenario, macrophyte detritus supporting the animal intermediary must be from a mixture of enriched and depleted sources from adjacent natural habitat, resulting in *A. sclerolepis* having a carbon isotope value in the middle of this source range (Connolly 2003).

Methodology

Sample collection

Autotrophs and *A. sclerolepis* were collected in natural wetlands over *Zostera capricorni* meadows and artificial waterways (canal estates) in August 2003. Locations were similar to those used in the previous year by Connolly (2003) at 153°42′E 27°93′S. *A. sclerolepis* were collected from four sites in each habitat between 14:00 and 17:00, and 23:00 and 03:00, over a 10-day period. Sites and time of day to be sampled on each occasion were allocated randomly. Day and night sampling was independent through time, i.e. no sites were sampled during both day and night over a single 24-h period.

Stable isotope analysis

The dominant autotrophs were collected at all sites. In natural wetlands this included mangroves (*Avicennia marina*), seagrass (*Z. capricorni*), saltmarsh succulents (*Suaeda australis*) and saltmarsh grass (*Sporobolus virginicus*). Local macroalgae sources (*Rhizoclonium* sp., *Cladophora* sp., *Enteromorpha* sp. and *Spirogyra* sp.), pooled as Chlorophyta, were collected at all sites in both habitats. Terrestrial grass (Poaceae) was collected at artificial habitat sites. MPB was collected at all sites by centrifuging superficial sediments with colloidal silica (Connolly et al. 2005) to obtain clean samples of microalgae, predominantly diatoms.

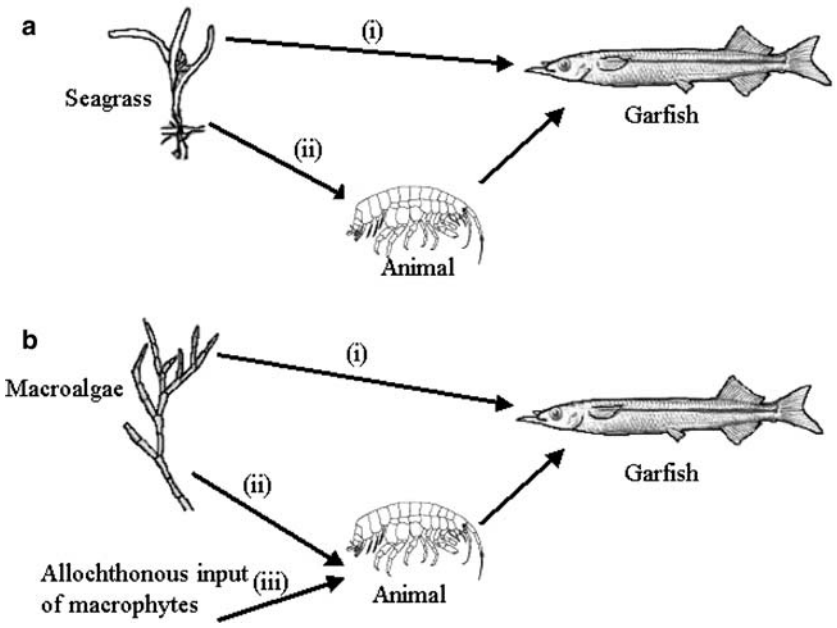

Fig. 1 Trophic models for *A. sclerolepis* in **a** natural wetlands and **b** artificial waterways. (i) Direct consumption of autotroph, (ii) direct consumption of an animal intermediary that utilises autotroph and, in artificial waterways (iii) consumption of animal intermediary that utilises detrital macrophytes (having both enriched and depleted $\delta^{13}C$ values) transported from adjacent natural wetlands

Arrhamphus sclerolepis were 13–22 cm TL. There were four sites per habitat and three fish were selected at each sampling time. Fish from day and night were pooled for isotope analysis since isotope ratios do not vary over such short periods (Peterson and Fry 1987). Fish muscle tissue and autotroph samples were dried, ground and analysed on an Isoprime Isotope Ratio Mass Spectrometer. The ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as the relative difference (‰) between the sample and recognised international standards. Analytical precision was determined from duplicate samples as being ±0.5‰.

Stomach content analysis

Dietary items from the foregut of *A. sclerolepis* were sorted taxonomically and dried to constant weight in an oven. For each dietary item, frequency of occurrence (FoC %) and the total volume contribution (vol %) were calculated. The relative contribution of each prey item to the total number of prey was not considered here, given the large contribution of plant material.

An additional 66 *A. sclerolepis* collected across all sites and times of the day were measured to give length in millimetre and dry weight in milligram. The regression relationship was $W = 0.096\ L - 0.722$; $R^2 = 0.98$. An objective measure of stomach fullness was calculated by dividing the total dried weight of material in the stomach by the total dried weight of *A. sclerolepis* determined from the length–weight regression.

Data analysis

Differences in fish isotope values between and within habitats were analysed using a nested ANOVA. All data were tested for homogeneity of variances and normality prior to analysis and transformed using $\log_{10}(x)$ where necessary.

The stomach fullness index was analysed using an ANOVA with two fixed factors (habitat and time of day, each with two levels), an interaction term and a sites factor nested within the interaction. Data were arcsine transformed to satisfy the assumption of homogeneity of variances.

No seagrass was found in the stomachs of *A. sclerolepis* in artificial habitat, so ANOVA was used to test for the differences in amounts of seagrass ingested at different times of day only in natural habitat. *A. sclerolepis* in natural habitat had so little macroalgae that ANOVA was used to test only for differences between macroalgae ingested at different times of the day in the artificial habitat. Data were arcsine transformed where necessary. Animals dominated stomach contents of *A. sclerolepis* from artificial habitat, although only in the day, but were found in only small amounts in natural wetland and only at night; data did not meet the assumptions of ANOVA, but since the pattern was obvious, no test was done.

Isotope mixing model

A two-source mixing model (Phillips and Greg 2001) was used to estimate source contributions to the nutrition of *A. sclerolepis* in both habitats. In the model, sources for the mixture (*A. sclerolepis*) were the dominant food items in the stomach of fish: seagrass and amphipods in natural wetlands, and macroalgae and ants in artificial waterways. Amphipods and ants were collected from the wild, once we had determined the important dietary items for *A. sclerolepis*. Amphipods were collected at three natural wetland sites over seagrass. The dominant ant species (*Paratrechina muinutula, Pheidole megacephala, Camponotus* sp. 1, *Camponotus* sp. 2 and *Rhytidoponera metallica*) in the stomachs of fish were collected from terrestrial grasslands adjacent to artificial waterways. Invertebrate material was rinsed in 10% (vol) HCl to remove exoskeletons before carbon, but not nitrogen, isotope analysis, since acid washing can inadvertently alter $\delta^{15}N$ values (Bunn et al. 1995). Carbon and nitrogen sources for *A. sclerolepis* in natural and artificial habitats were analysed separately. To account for fractionation in the isotope model, we subtracted 3‰ from the nitrogen isotope values of *A. sclerolepis* for both natural and artificial waterways (Peterson and Fry 1987), and made no adjustment for carbon isotope fractionation.

Results

Stable isotope analysis

$\delta^{13}C$ values of autotrophs could be separated into three groups: (1) enriched sources of seagrass, saltmarsh grass and terrestrial grass; (2) sources with intermediate values, consisting of MPB and macroalgae; (3) depleted sources of saltmarsh succulents and mangroves. Terrestrial grass had the most depleted $\delta^{15}N$ (at < 3‰) and MPB in artificial habitat had the most enriched $\delta^{15}N$ value (6‰) (Fig. 2).

$\delta^{13}C$ and $\delta^{15}N$ values of *A. sclerolepis* were similar to Connolly's (2003) results, within 2.5‰ for carbon and 1‰ for nitrogen. Neither $\delta^{13}C$ nor $\delta^{15}N$ values differed among sites for either habitat, but both elements differed between habitats. In natural habitat, *A. sclerolepis* had significantly more enriched $\delta^{13}C$ values (mean = −13.9‰, SE = 0.6) than in artificial habitat (−19.1‰, 0.1) [ANOVA: main factor (habitat) $F_{1,6} = 967$, $P < 0.001$, nested factor (site) $F_{6,40} = 0.08$, $P = 0.998$], whereas $\delta^{15}N$ values were significantly more enriched in artificial habitat (10.4‰, 0.3) than natural habitat (8.8‰, 0.2) [ANOVA: main factor (habitat) $F_{1,6} = 28$, $P < 0.005$, nested (sites) $F_{6,40} = 2$, $P = 0.199$]. $\delta^{15}N$ values for

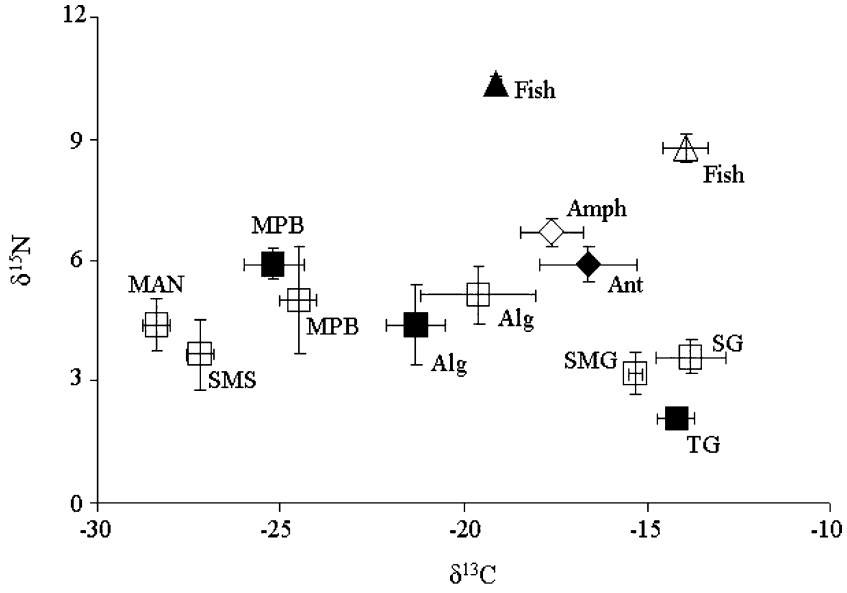

Fig. 2 $\delta^{13}C$ and $\delta^{15}N$ values for fish (*triangles*), autotrophs (*squares*) and animal sources (*diamonds*) in natural waterways (*open symbols*) and artificial waterways (*filled symbols*). All values are means (±SE), although some SE values are too small to show. *Alg* algae; *MPB* microphytobenthos; *TG* terrestrial grass; *MAN* mangroves; *SG* seagrass; *SMG* saltmarsh grass; *SMS* saltmarsh succulents; *Amph* amphipods; *Ant* terrestrial ants

A. sclerolepis in both habitats were more enriched than for all the autotrophs, typically by 3–8‰ (Fig. 2).

Amphipods had $\delta^{13}C$ values more depleted (mean = −17.6‰, SE = 0.8), but $\delta^{15}N$ values more enriched (6.7‰, 0.3) than seagrass. Ant $\delta^{13}C$ values were more depleted (−16.6‰, 1.3) and $\delta^{15}N$ values more enriched (6.0‰, 0.4) than terrestrial grass values (Fig. 2).

Stomach content analysis

The stomachs of 119 *A. sclerolepis* were examined: 63 from natural habitat (32 day, 31 night) and 56 (29 and 27) from artificial habitat. More food was found in the stomachs of *A. sclerolepis* during the day than at night regardless of habitat [ANOVA: main factor (time), $F_{1,12} = 19$, $P < 0.001$; Fig. 3]. A small number of *A. sclerolepis* had empty stomachs and were removed from all analyses (Table 1).

The percentage volume of seagrass consumed by *A. sclerolepis* in natural habitat varied significantly between day and night, though the difference was not consistent among sites [ANOVA: interaction (time×site), $F_{3,\ 55} = 5$, $P < 0.005$). At some sites, *A. sclerolepis* consumed seagrass during the day and night, while other sites switched at least partly at night from seagrass to animal material, predominately crustaceans. A very small amount of algae was also found during the day and night (Fig. 4).

The consumption of macroalgae by *A. sclerolepis* in artificial habitat varied significantly between day and night, though this difference was not consistent among sites [ANOVA: interaction (time×site), $F_{3,49} = 3$, $P < 0.050$]. *A. sclerolepis* clearly switched their diet to animal material (Hymenoptera: terrestrial ants) during the day, though a small quantity of macroalgae was still present in the stomachs of fish during the day (Fig. 4).

Dietary contribution of major prey types

Seagrass provides the bulk (mean = 93%, SE = 22) of the dietary carbon for *A. sclerolepis* in natural wetlands, with amphipods providing the remaining carbon (7%, 22). For nitrogen, seagrass contributed very little (3%, 19), with most nitrogen provided by amphipods (97%, 19). In artificial waterways, a mixture of macroalgae and ants contributes to the dietary carbon (53%, 18 and 47%, 18 respectively). However, no combination of macroalgae or ants could explain the $\delta^{15}N$ values of *A. sclerolepis* since, even after correcting for fractionation, *A. sclerolepis* values lay outside the range for potential sources.

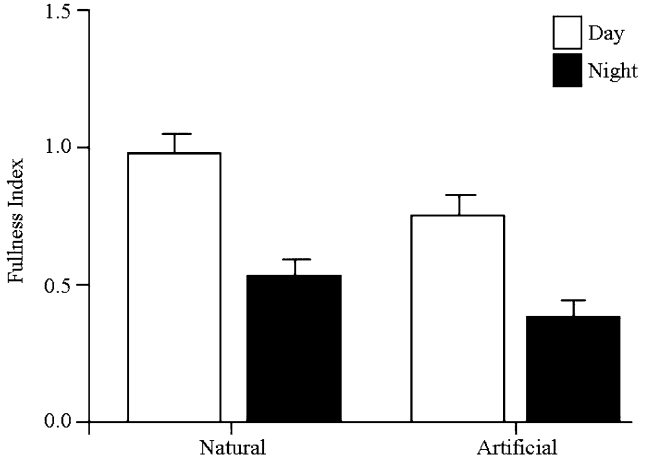

Fig. 3 Mean (±SE) stomach fullness index for *A. sclerolepis* in natural and artificial habitats during day and night. Fish with empty stomachs are not included in the analysis

Table 1 Frequency of occurrence (FoC %) and mass volume percentage (Vol %) for food types in the stomach of *A. sclerolepis* in natural and artificial habitats during the day and night

Food type	Natural				Artificial			
	Day (32, 1)		Night (31, 3)		Day (29, 3)		Night (27, 5)	
	FoC (%)	Vol (%)	FoC (%)	Vol (%)	FoC (%)	Vol (%)	FoC (%)	Vol (%)
Plant								
Chlorophyta	10	+	13	5	22	11	68	74
Halophila ovalis	19	4	4	+	–	–	–	–
Zostera capricorni	100	95	100	91	–	–	–	–
Unidentified	–	–	–	–	37	10	21	17
Animal								
Crustacea								
Amphipoda	–	–	17	+	–	–	9	+
Copepoda	–	–	4	+	–	–	–	–
Gastropoda	–	–	–	–	4	+	–	–
Unidentified	3	+	9	2	–	–	–	–
Insecta								
Coleoptera	7	+	8	+	18	2	11	1
Hymenoptera	–	–	–	–	87	76	16	7

Numbers in parentheses indicate the total number of fish caught and the number with empty stomachs respectively for day and night in both habitats + present, but less than 1% volume; – not present

Discussion

Fish isotope values

Carbon isotope values of *A. sclerolepis* were similar to those reported by Connolly (2003) from the same waterways a year earlier. More attention has previously been given to spatial (Schlacher and Wooldridge 1996; Jennings et al. 1997; Melville and Connolly 2003) than temporal variation in isotope values, but carbon isotope values of fish are known to vary in response to dietary shifts and varying environmental conditions (Gaston et al. 2004). The similarity in carbon isotope values of *A. sclerolepis* in the same season from year to year is surprising, and points to a remarkably consistent food web processes. As well as reflecting different autotrophic sources, the consistent difference in carbon isotope values also demonstrates a low level of mixing of fish between habitats, over a period of weeks to months (Hesslein et al. 1993).

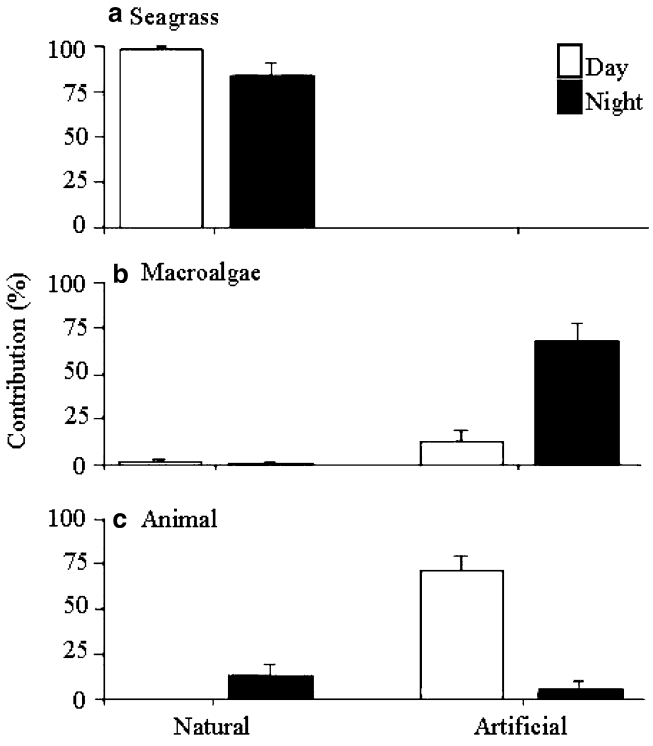

Fig. 4 Mean percentage contribution (±SE) by weight of (**a**) seagrass, (**b**) algae and (**c**) animal material in *A. sclerolepis* for natural and artificial habitats during day and night. Results do not total 100% in some cases because unidentified plant material was not included

Diet in natural wetlands

Arrhamphus sclerolepis had enriched $\delta^{13}C$ values in natural wetlands because it consumes large amounts of seagrass material during the day and night, as previously noted from natural habitats elsewhere in southeast Queensland (Blaber and Blaber 1980). *A. sclerolepis* lacks a gut microbial flora capable of digesting seagrass, relying instead on mechanical maceration and mucus-facilitated uptake to extract cell nutrients (Tibbetts 1997). At night, *A. sclerolepis* continued feeding on seagrass but also ingested crustacean prey. Although the amount of food ingested at night is lower, this diel shift has important nutritional ramifications. Seagrass provides the bulk of the dietary carbon, and animals provide the bulk of the nutrient requirements. Even though only some *A. sclerolepis* had animal material in their stomach, all fish showed a similar enrichment in $\delta^{15}N$ of about 6‰ from seagrass. This enrichment presumably results from trophic fractionation of $\delta^{15}N$ over two

trophic levels. A likely explanation is that, although on any one night an individual fish may or may not have ingested animals, over a period of weeks all *A. sclerolepis* would have ingested animals, as reflected in the consistently enriched δ^{15} N values. The potential importance of algae epiphytic on seagrass, which often has a carbon signature more similar to seagrass than other algae (Winning et al. 1999; Guest et al. 2004), requires further investigation.

Diet in artificial waterways

Before this study, the depleted δ^{13}C values of *A. sclerolepis* in an artificial habitat had been interpreted as an evidence that the ultimate autotrophic source was either in situ algae or allochthonous inputs of a mixture of enriched and depleted macrophyte material from adjacent natural habitat (Connolly 2003). The combination of isotope and stomach content analyses used here demonstrates that *A. sclerolepis* obtains its energy primarily from in situ algae. We could detect no trophic role for detrital macrophyte material from adjacent natural wetlands. This is an important finding since it implies that the extensive network of canals in southeast Queensland, with over 150 km linear extent in the Nerang River estuary alone (Gold Coast City Council, unpublished data), produces enough algae to support this fisheries species. Macroalgae appeared more prominently than MPB in fish stomachs, although this finding must be treated cautiously given the difficulty in identifying single-celled algae in fish stomachs. Carbon isotope values of fish did not match algae exactly, and the two-source mixing model results indicate that some carbon is obtained from a more enriched source, probably animals.

As in natural habitat, *A. sclerolepis* in artificial habitat showed a diel shift in diet to include animals. In artificial habitat, however, the animals were terrestrial ants, and they were consumed during the day rather than the night. The inclusion of animal material could not explain nitrogen sources, since under typical adjustments for fractionation of δ^{15} N per trophic level, no combination of algae and/or ants could explain the δ^{15} N values of fish. Another possibility is that an unusually large fractionation shift from ants to fish in excess of 5‰ occurs. While such large fractionation rates have been recorded, they are rare (McCutchan et al. 2003). We suspect that, as in the natural habitat, animal prey is important, but the types of animals ingested, and therefore probably the δ^{15} N values, vary over time. In support of this is the fact that the ants found in the stomachs of *A. sclerolepis* were winged and are therefore breeding ants. Although different species of ants breed at different times of year at this latitude (Shattuck 1999), few, if any, breed during winter, and at this time *A. sclerolepis* would switch to different prey types. The variability in the type of animal ingested could have seasonal predictability or be merely a reflection of ever-changing local animal sources. We expect that, at times, crustaceans such as amphipods would be eaten in artificial habitat. Only further stomach content analysis at different times of the year could confirm this. Any further study in artificial habitat should also determine whether the ingestion of animals always occurs during the day, because this is a different pattern to that observed in natural wetlands and in the confamilial *Hyporhamphus melanochir* (Robertson and Klumpp 1983).

Dietary carbon and nitrogen sources

Diet switching is sometimes described as a behaviour to augment the diet during seasonal changes in prey availability (Rose and Polis 1998; Szepanski et al. 1999). In some situations, however, diet switching can be a response to dietary requirements not provided by a single food source. For example, the regent honeyeater (*Xanthomyza phrygia*) has a diet of plant nectar, but supplements part of its diet with insect material to obtain dietary protein not provided by the nectar alone (Oliver 1998). This phenomenon is also suspected in fishes. Several littoral fishes in the Mediterranean formerly considered to be herbivorous had higher δ^{15} N values than expected for a purely herbivorous diet, indicating a dietary supplement of high-protein animal material (Pinnegar and Polunin 2000). Diet switching has also been found in other species in the family Hemiramphidae (Robertson and Klumpp 1983; Carseldine and Tibbetts 2005). For example, seagrass provides the bulk of the energy for *Hyporhamphus melanochir* but, given the low N:C ratio of seagrass, small quantities of crustaceans are consumed at night to obtain the necessary dietary protein (Klumpp and Nichols 1983). The inclusion of a small amount of animal material in the diet of *A. sclerolepis* in both natural and artificial habitats would seem to indicate that this specialised feeding strategy is retained in the newly created urban habitat.

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References

Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. J Fish Biol 17:143–162

Bunn SE, Loneragan NR, Kempster MA (1995) Effects of acid washing samples on stable isotope ratios of C and N in penaeid shrimp and seagrass: implications for food web studies using multiple stable isotopes. Limnol Oceanogr 40:622–625

Carseldine L, Tibbetts IR (2005) Dietary analysis of the herbivorous hemiramphid *Hyporhamphorus regularis ardelio*: an isotopic approach. J Fish Biol 66:1589–1600

Cohen JE, Small C, Mellinger A, Gallup J, Sachs J (1997) Estimates of coastal populations. Science 278:1211–1212
Connolly RM (2003) Differences in trophodynamics of commercially important fish between artificial waterways and natural coastal wetlands. Estuar Coast Shelf Sci 58:929–936
Connolly RM, Hindell JS, Gorman D (2005) Seagrass and epiphytic algae support the nutrition of a fisheries species, *Sillago schomburgkii*, in adjacent intertidal habitats. Mar Ecol Prog Ser 286:69–79
Gaston TF, Kostoglidis A, Suthers IM (2004) The ^{13}C, ^{15}N and ^{34}S signatures of a rocky reef planktivorous fish indicate different coastal discharges of sewage. Mar Freshw Res 55:689–699
Guest MA, Connolly RM, Loneragan NR (2004) Within and among-site variability in $\delta^{13}C$ and $\delta^{15}N$ for three estuarine producers, *Sporobolus virginicus*, *Zostera capricorni*, and epiphytes of *Z. capricorni*. Aquat Bot 79:87–94
Hesslein RH, Hallard KA, Ramlal P (1993) Replacement of sulfur, carbon and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$. Can J Fish Aquat Sci 50:2071–2076
Jennings S, Reñones O, Morales-Nin B, Polunin NVC, Moranta J, Coll J (1997) Spatial variation in the ^{15}N and ^{13}C stable isotope composition of plants, invertebrates and fishes on Mediterranean reefs: implications for the study of trophic pathways. Mar Ecol Prog Ser 146:109–116
Kinch JC (1979) Trophic habits of the juvenile fishes within artificial waterways—Marco Island, Florida. Contrib Mar Sci 22:77–90
Klumpp DW, Nichols PD (1983) Nutrition of the southern sea garfish *Hyporhamphus melanochir*: gut passage rate and daily consumption of two food types and assimilation of seagrass components. Mar Ecol Prog Ser 12:207–216
McCutchan J, Lewis W, Kendall C, McGrath C (2003) Variation in trophic shift for stable isotope ratios in carbon, nitrogen and sulphur. Oikos 102:378–390
Maxted JR, Eskin RA, Weisberg SB, Chaillou JC, Kutz FW (1997) The ecological condition of dead-end canals of the Delaware and Maryland coastal bays. Estuaries 20:319–327
Melville AJ, Connolly RM (2003) Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. Oecologia 136:499–507
Odum EP (1984) The status of three ecosystem level hypotheses regarding salt marsh estuaries: tidal subsidy, outwelling and detritus based food chains. In: Kennedy VS (ed) Estuarine perspectives. Academic, New York, pp 485–495
Oliver DL (1998) The importance of insects and lerp in the diet of juvenile regent honeyeaters, *Xanthomyza phrygia*: implications for the conservation of an endangered woodland bird. Wild Res 29:409–417
Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320
Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. Oecologia 127:171–179
Pinnegar JK, Polunin NVC (2000) Contributions of stable isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia 122:399–409
Robertson AI, Klumpp DW (1983) Feeding habits of the southern Australian garfish *Hyporhamphus melanochir*: a diurnal herbivore and nocturnal carnivore. Mar Ecol Prog Ser 10:197–201
Rose MD, Polis GA (1998) The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998–1007
Schlacher TA, Wooldridge TH (1996) Origin and trophic importance of detritus: evidence from stable isotopes in benthos of a small temperate estuary. Oecologia 106:382–388
Shattuck S (1999) Australian ants: their biology and identification. CSIRO Publishing, Australia
Szepanski MM, Ben-David M, Van Ballengerghe V (1999) Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. Oecologia 120:327–335
Tibbetts IR (1991) The trophic ecology, functional morphology and phylogeny of the Hemiramphidae (Beloniformes). PhD Thesis, University of Queensland
Tibbetts IR (1997) The distribution and function of mucous cells and their secretions in the alimentary tract of *Arrhamphus sclerolepis krefftii*. J Fish Biol 50:809–820
Vizzini S, Mazzola A (2002) Stable carbon and nitrogen ratios in the sand smelt from a Mediterranean coastal area: feeding habits and effect of season and size. J Fish Biol 60:1498–1510
Wainright SC, Weinstein MP, Able KW, Currin CA (2000) Relative importance of benthic microalgae, phytoplankton and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish-marsh food webs. Mar Ecol Prog Ser 200:77–91
Winning MA, Connolly RM, Loneragan NR, Bunn SE (1999) ^{15}N enrichment as a method of separating the isotopic signatures of seagrass and its epiphytes for food web analysis. Mar Ecol Prog Ser 189:289–294