

NOTE

$\delta^{15}\text{N}$ isotope studies of life history and trophic position of *Fundulus heteroclitus* and *Menidia menidia*

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ABSTRACT: We used $\delta^{15}\text{N}$ isotopic signatures to follow the trophic position as well as the life history of 2 of the most abundant fish species of the Waquoit Bay estuarine system: common killifish *Fundulus heteroclitus* and Atlantic silverside *Menidia menidia*. Juvenile fish bore isotopic signatures specific to the estuary in which they had been growing. The fish changed in $\delta^{15}\text{N}$ as they grew and had significant, estuary-specific differences in $\delta^{15}\text{N}$ signatures. *F. heteroclitus* increased in length by 3 to 4 cm as they increased in $\delta^{15}\text{N}$ by up to 4‰. The magnitude of the shift in $\delta^{15}\text{N}$ is consistent with movement of the fish ~1 trophic step up the food web. *F. heteroclitus* remained within their native estuaries year-round, and retained the isotopic signatures of their prey in each estuary. *M. menidia* moving offshore during the winter months lose estuary-specific differences in $\delta^{15}\text{N}$, and appear to feed at a higher trophic level than fish residing in the estuaries. Evidence from gut content analysis, coupled with results of the stable isotopic measurement, closely concurs with the life history characteristics of these 2 well-known fish species, and provides additional insight into life history habits and feeding.

KEY WORDS: Stable isotopes · Food webs · Trophic level · Life history · Migration · Nitrogen loading

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Stable isotopic signatures have been used to study biogeochemical transformations, food webs, and ecosystem dynamics (Peterson & Fry 1987). More recently, isotopic signatures have also been found effective in discerning various aspects of populations dynamics, such as migrations and changes in trophic position (Hesslein et al. 1991, Hansson et al. 1997). Here we use changes in $\delta^{15}\text{N}$ measurements in 2 common near-shore fish species to examine where individuals feed, define their seasonal migrations, assess the effect of increased size as they grow, and identify their trophic position throughout the year.

The basis of the $\delta^{15}\text{N}$ isotope technique is that enzyme and diffusion processes discriminate against the heavier isotope of nitrogen (^{15}N), creating fractionation that reveals certain transformations. One transformation of interest is that as nitrogen moves up food webs, fractionation changes the isotopic ratio of the consumer compared to its food source (Hesslein et al. 1991, Deegan & Garritt 1997, McClelland et al. 1997). Isotope ratios are expressed as the difference ($\delta^{15}\text{N}$) between the isotope ratio in a sample and that of atmospheric nitrogen. Consumers average 3 to 5‰ heavier in $\delta^{15}\text{N}$ than their food (Peterson & Fry 1987). This shift can be useful in assessing trophic position of consumers.

As aquatic predators grow, they tend to select larger sized prey (Werme 1981, Ikeda et al. 1994) and in marine systems, this results in the animal moving to a higher trophic level in the food web (Wyatt 1976). Thus, fish often move up food webs as they grow, and their $\delta^{15}\text{N}$ signatures should reflect this ascent by becoming heavier.

Fundulus heteroclitus (common killifish) and *Menidia menidia* (Atlantic silversides) are 2 of the most abundant fish species found in near-shore coastal waters of New England, USA. *F. heteroclitus* live up to 4 yr, are omnivorous feeders (Werme 1981), and typically reside year-round in salt marshes and shallow estuaries (Valiela et al. 1977). *F. heteroclitus* eat a variety of foods, but assimilate animal food more efficiently than algae and detrital items (Prinslow & Valiela 1974). This species may shift to algal and detrital foods when prey becomes scarce in midsummer (Werme 1981, Wiltse et al. 1984). In localised areas, individual *F. heteroclitus* maintain a limited summer home range with little migration (Lotrich 1975). In winter months, *F. heteroclitus* move upstream (Fritz et al. 1975), or bury themselves in the mud (Bigelow & Schroeder 1953) within the estuaries.

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Populations of *Menidia menidia* are shortlived, with <1% of breeding adults being older than 2 yr (Conover & Ross 1982). Juvenile and adult *M. menidia* are opportunistic omnivores, and food items consumed range from zooplankton to detritus (Cadigan & Fell 1985). Small meiobenthic invertebrates (harpacticoid copepods, amphipods, and ostracods) have been found in gut contents of *M. menidia* from Waquoit Bay, Cape Cod, Massachusetts, USA (Griffin 1999). In populations from Chesapeake Bay northward, *M. menidia* are rare or absent from the shallow waters in midwinter and are thought to migrate into deeper water to overwinter for ~3 to 4 mo (Conover & Ross 1982, Conover & Murawski 1982).

Use of $\delta^{15}\text{N}$ signatures as a tool to study trophic position of fishes is facilitated by human activity in coastal areas, where nutrient input to watersheds is increased, largely due to wastewater enriched with nitrogen. Wastewater derived nitrogen characteristically has a heavier $\delta^{15}\text{N}$ signature compared to other nitrogen sources such as atmospheric deposition and fertilizer (McClelland et al. 1997). It therefore imparts a distinctive isotopic signature to the freshwater transporting nitrogen to the estuaries. For example, the different patterns of land use in the watersheds of the various estuaries of Waquoit Bay led to different stable isotopic signatures of water and producers (McClelland et al. 1997, McClelland & Valiela 1998). The greater the relative contribution of wastewater in the nitrogen input to an estuary, the heavier the $\delta^{15}\text{N}$ stable isotopic signature in water, primary producers, and consumers (McClelland et al. 1997). Consumers such as *Fundulus heteroclitus* and *Menidia menidia*, if they feed within a single estuary, should acquire isotopic signatures characteristic of the estuary, and also show the effects of changing trophic position during growth.

In this case, 2 species of fish—1 resident and 1 migratory—were studied in estuaries where food items bear distinct $\delta^{15}\text{N}$ values. We hypothesized that in the resident species (*Fundulus heteroclitus*), the $\delta^{15}\text{N}$ signatures would be estuary-specific, and would show this pattern throughout the year. In the migratory species, we hypothesized that the $\delta^{15}\text{N}$ signatures would be estuary-specific only in the fish that were born and had been growing in the estuary, and the overwintering adult *Menidia menidia* would not bear estuary-specific signals as they return.

We therefore used the $\delta^{15}\text{N}$ isotopic ratio of *F. heteroclitus* and *M. menidia* to see if the method was useful in following migratory behaviors of 2 species of fish that show contrasting natural histories, and to examine whether the signatures were also able to detect changes in trophic level as the fish grew.

Methods. Study site: Fish were sampled over a 3 yr period in 3 estuaries of Waquoit Bay: Childs River,

Quashnet River, and Sage Lot Pond (Fig. 1). The estuaries of Waquoit Bay are shallow with a maximum depth of 3 m, and salinity ranges from 0 to 32 ppt (Curley et al. 1971). The watersheds of the estuaries differ in land cover mosaics and provide a range of nitrogen loading rates: Childs River, 601 kgN ha⁻¹ yr⁻¹; Quashnet River, 350 kgN ha⁻¹ yr⁻¹; Sage Lot Pond, 14 kgN ha⁻¹ yr⁻¹ (Valiela et al. unpubl. data). This range of nitrogen loads encompasses 75% of the coastal nitrogen loads found for marine systems (Nixon et al. 1996).

Sampling of fish: We collected *Fundulus heteroclitus* and *Menidia menidia* in order to determine size distributions, seasonal patterns of abundance and to measure $\delta^{15}\text{N}$ signatures. Fish were sampled bi-monthly from 1996 to 1998 using a 5 m wide beach seine net towed for 10 m, parallel to the shore, at 5 stations within each estuary (Fig. 1). After each tow we identified the species and measured standard lengths of each fish caught (Tober et al. 2000).

From each estuary, 30 *Menidia menidia* and 30 *Fundulus heteroclitus* (10 from each size class, see below) were collected mid-month from May to November 1998. The fish were categorized into 3 different standard length size classes (class 1, 2 to 5 cm; class 2, 5 to 8 cm; and class 3, >8 cm). These size classes were arbitrarily chosen in 3 cm increments reflecting the size range most susceptible to our gear type. Ages of fish in each size class were determined by examining growth rings on scales (Bagenal & Tesch 1978) to discern between young-of-year (YOY) and adult fish. We collected fish at different sites within the estuaries, to assess possible variation in isotopic signatures of fish within each estuary. To prevent unassimilated food from affecting the measurement of $\delta^{15}\text{N}$, fish were held in tanks of filtered sea water for 36 to 48 h, allowing the guts to clear. The fish were pithed, dried at 60°C for 2 to 3 d, and ground into a homogenous powder. The 10 fish from each size class were combined to create a composite sample. Each sample was analyzed at the Boston University Stable Isotope Laboratory using a Finnigan Delta-S isotope ratio mass spectrometer.

To determine whether gut contents agreed with our stable isotope results, we examined 225 *Menidia menidia* (75 from each size class) in June, July, and August 1998. Standard lengths were measured and gut contents were sorted, identified, and recorded as present or absent. The percentage of fish examined (for each size class) having a particular food item in the gut was calculated. Gut contents of *Fundulus heteroclitus* from Waquoit Bay have been described previously (Werme 1981). In this study, gut content composition was estimated by the volume of different food items found for each size class.

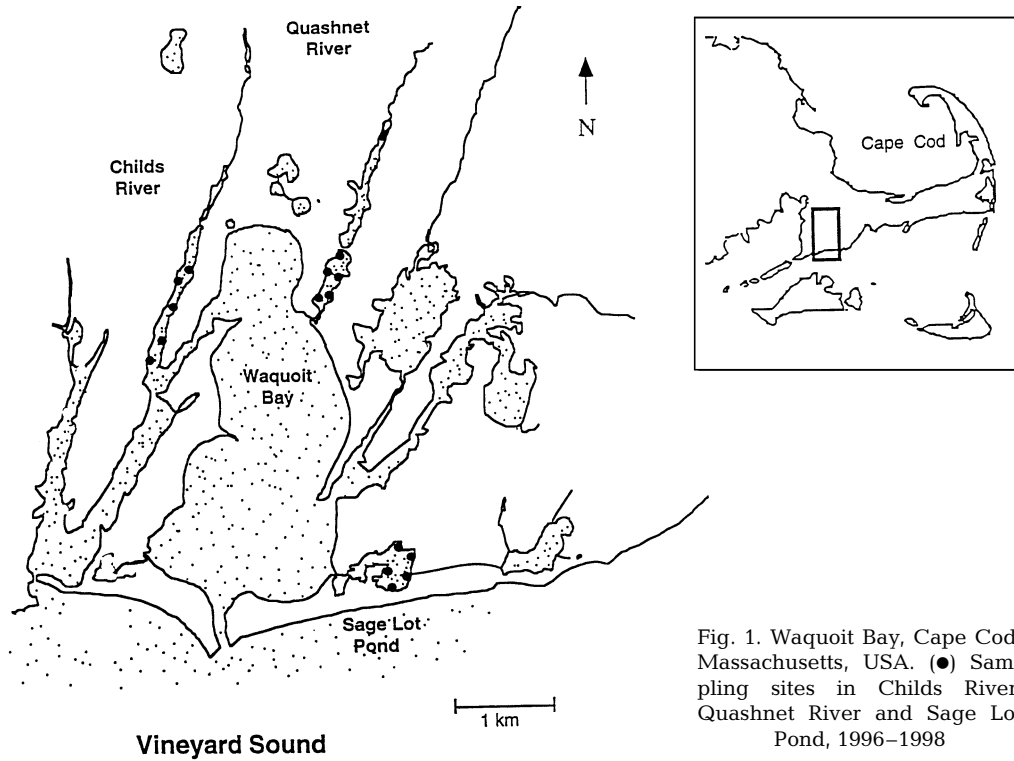


Fig. 1. Waquoit Bay, Cape Cod, Massachusetts, USA. (●) Sampling sites in Childs River, Quashnet River and Sage Lot Pond, 1996–1998

Results and discussion. Length-frequency distribution: The distribution of size and growth rates of *Fundulus heteroclitus* and *Menidia menidia* in the 3 estuaries of Waquoit Bay did not differ (Tober et al. 2000), so we pooled these data (Fig. 2). In all the estuaries (Fig. 2a), age 1 *F. heteroclitus* (i.e. fish born the previous year) were between 4 and 5 cm in length after surviving the winter, and reached 6 to 7 cm by August. Age 0 fish first appeared in our samples in July, and grew to between 3 and 5 cm by October. This distribution of sizes within the population is much like that reported elsewhere (Valiela et al. 1977, Meredith & Lotrich 1979).

Recruitment and growth patterns differ between *Menidia menidia* and *Fundulus heteroclitus* (Fig. 2b). A small cohort of larger overwintering *M. menidia* entered the shallow estuaries in the spring. According to published reports (Conover & Murawski 1982, Warkentine & Rachlin 1989), these larger fish spent the winter offshore. This overwintering cohort disappeared (Fig. 2b; and see Cadigan & Fell 1985), and age 0 fish appeared in samples by June. The age 0 fish grew, possibly as several cohorts, through the summer. The fish left the shallow estuaries when they reached a length of 6 to 8 cm (Fig. 2b). A substantial number of smaller fish remained in the estuaries in late fall, but they did not seem to survive the winter within the shallow estuaries (Fig. 2b; and see Schultz et al. 1998, Griffin 1999).

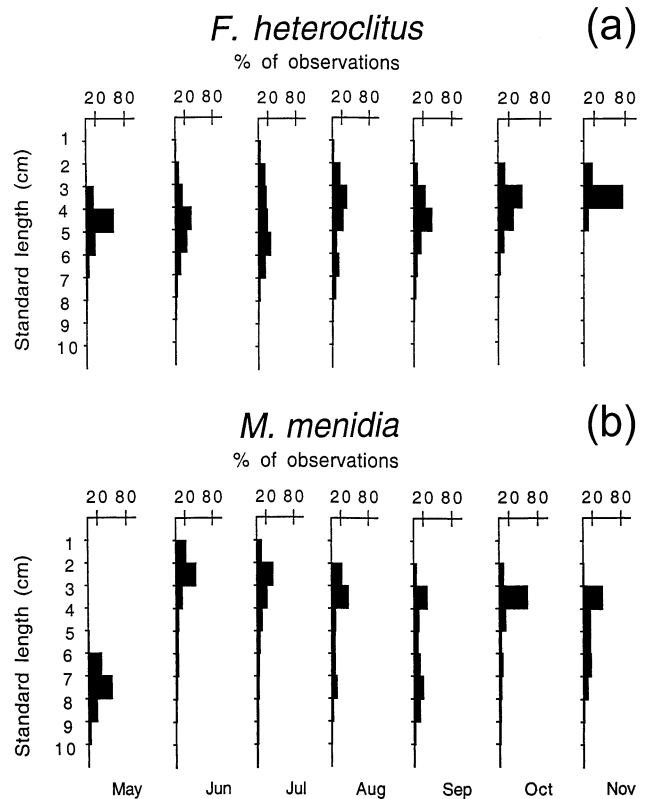


Fig. 2. (a) *Fundulus heteroclitus* and (b) *Menidia menidia*. Length/frequency distribution, May–November

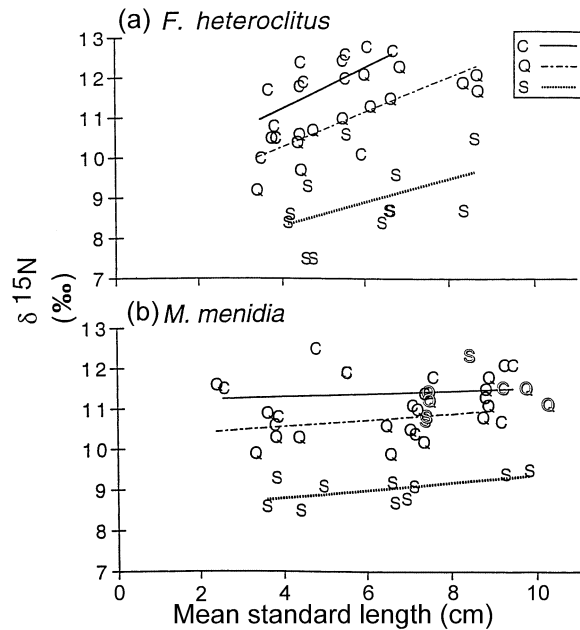


Fig. 3. (a) *Fundulus heteroclitus* and (b) *Menidia menidia*. $\delta^{15}\text{N}$ versus mean standard length in: Childs River (C), Quashnet River (Q) and Sage Lot Pond (S). Wide, non-filled letters [Childs River (C), Quashnet River (Q), and Sage Lot Pond (S)] in (b) represent fish caught in spring that migrated in from offshore waters

$\delta^{15}\text{N}$ isotope signatures in fish tissue: We tested whether the $\delta^{15}\text{N}$ isotopic signatures differed among the estuaries, regardless of size of fish, by using a non-parametric Wilcoxon test (Sokal & Rohlf 1981). The $\delta^{15}\text{N}$ values of *Fundulus heteroclitus* (Fig. 3a) varied significantly among the 3 estuaries (Wilcoxon test, $z = -5.4$, $p < 0.05$). $\delta^{15}\text{N}$ values for Sage Lot Pond were lighter than those for Quashnet River and those from Childs River (Fig. 3).

We then performed a regression analysis of the $\delta^{15}\text{N}$ values against the size of the fish, to examine whether isotopic signatures changed as the fish grew. The regression results showed that the isotopic signature of *Fundulus heteroclitus* became heavier as the fish in-

creased in length (Fig. 3a, Table 1). Rates of increase in $\delta^{15}\text{N}$ with length did not differ among estuaries, but the intercepts were significantly different (Table 2), reflecting the difference in estuarine $\delta^{15}\text{N}$ signatures. In each estuary, *F. heteroclitus* increased in length by 3 to 4 cm as they increased in $\delta^{15}\text{N}$ up to 4‰ (Fig. 3a). The magnitude of the shift in $\delta^{15}\text{N}$ is consistent with movement of the fish ~1 trophic step up the food web. This shift occurred within the benthic food web, because the diet of *F. heteroclitus* remains a mix of benthic fauna throughout its life (Werme 1981).

As was the case for *Fundulus heteroclitus*, $\delta^{15}\text{N}$ values of *Menidia menidia* differed significantly among the estuaries (Wilcoxon test, $z = -5.9$, $p < 0.05$; Fig. 3b). In contrast to the pattern found in *F. heteroclitus*, the $\delta^{15}\text{N}$ isotopic signatures of *M. menidia* did not increase as the fish grew (Table 1). Values for fish that migrated in from offshore waters were not included in the regressions (Table 1) because the isotopic signatures of these fish were acquired outside the estuaries. These results suggested that as long as *M. menidia* stayed within the estuary in which they were born, they acquired and maintained the characteristic isotopic signal of that estuary, and these values did not change as the fish increased in size (Fig. 3b).

It is apparent that the larger *Menidia menidia* recently entering the estuaries in the spring from offshore waters (Conover & Murawski 1982) do not show differences in $\delta^{15}\text{N}$ related to the estuary in which they were caught (Fig. 3b). The fact that these large fish (size class 3) exhibit a heavy $\delta^{15}\text{N}$ signature indicates that they have been feeding 1 to 2 steps higher in trophic level than the age 0 fish residing in the estuaries.

In pristine waters, we should expect that the smaller *Menidia menidia* would bear a lighter $\delta^{15}\text{N}$ signature than the larger fish because of their smaller size. This is evident in the *M. menidia* caught in Sage Lot Pond, an estuary with relatively low nitrogen loading. In Quashnet River and Childs River, however, the smaller *M. menidia* fed on prey that bear the heavier wastewater-influenced $\delta^{15}\text{N}$ signatures, and consequently this led to $\delta^{15}\text{N}$ signatures that were heavier in the smaller fish.

There is not much information on offshore food habits for *Menidia menidia* in Massachusetts; thus we lack data on food habits for *M. menidia* recently arrived in the Waquoit Bay estuaries from offshore waters in the spring. There is a report (Warkentine & Rachlin 1989) that the dominant food item of offshore *M. menidia* off New Jersey were mysids, copepods, and barnacle larvae. These planktonic taxa are themselves consumers of prey and are larger than their food source. We can assume that the planktonic taxa found in unenriched offshore waters would exhibit lighter $\delta^{15}\text{N}$ signatures, similar to those found in Sage Lot

Table 1. Regression of $\delta^{15}\text{N}$ versus mean standard length (data in Fig. 3). *F significant at $p = 0.05$

Estuary	n	F	r ²
<i>Fundulus heteroclitus</i>			
Childs River	13	4.6*	0.29
Quashnet River	14	28.3*	0.70
Sage Lot Pond	12	2.8	0.21
<i>Menidia menidia</i>			
Childs River	13	0.2	0.02
Quashnet River	14	1.2	0.09
Sage Lot Pond	10	4.4	0.35

Table 2. ANCOVA tests for size of fish versus $\delta^{15}\text{N}$. **F* significant at $p = 0.05$

Test	Source of variation	df	SS	<i>F</i>
<i>Fundulus heteroclitus</i>				
Difference in slopes	Estuaries	2	0.5	0.4
	Within	33	20.3	–
Homogeneity of γ -intercepts	Adjusted means (within estuaries)	2	55.1	46.4*
	Error	35	20.8	–
<i>Menidia menidia</i>				
Difference in slopes	Estuaries	2	0.1	0.2
	Within	31	10.2	–
Homogeneity of γ -intercepts	Adjusted means (within estuaries)	2	32.7	52.4*
	Error	33	10.3	–

Pond (McClelland et al. 1997). Thus *M. menidia* feeding on these predatory taxa in pristine waters would have $\delta^{15}\text{N}$ values around 3‰ heavier than the prey. This is consistent with our measurements of $\delta^{15}\text{N}$ of *M. menidia* entering the Waquoit Bay estuaries in the spring (Fig. 3b).

Part of the explanation for larger *Menidia menidia* exhibiting heavier $\delta^{15}\text{N}$ values may be the differences in prey eaten by fish of a different sizes. Gut contents

of *M. menidia* collected in the estuaries of Waquoit Bay (Fig. 4) show that the smaller fish fed largely on smaller planktonic items, such as gastropod larvae and copepods. The larger fish, of comparable size to the returning adults, fed mostly on larger benthic fauna (Fig. 4).

Table 3. *Menidia menidia*. Two-way ANOVA for % fish examined eating food item. Main factors were estuary and food item. **F* significant at $p = 0.05$

Size class (cm)	Factors	df	SS	<i>F</i>
2–5	Estuary	2	2652	2.9
	Food Item	1	5930	12.8*
	Error	14	6514	–
5–8	Estuary	2	135	0.4
	Food Item	1	440	2.5
	Error	14	2450	–
>8	Estuary	2	485	1.6
	Food Item	1	3201	21.2*
	Error	14	2112	–

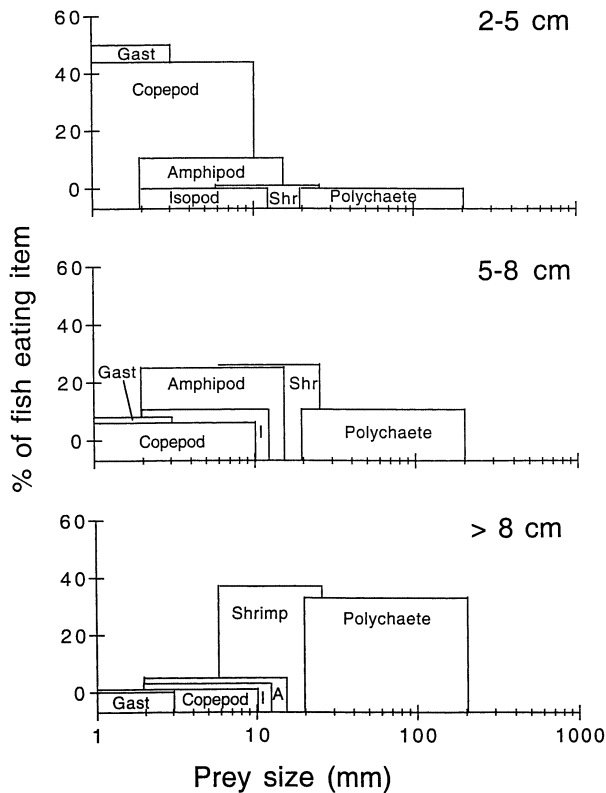


Fig. 4. *Menidia menidia*. Size ranges of prey items in guts for fish in 3 different size classes. Data for the 3 estuaries were pooled because there were no inter-estuary differences (Table 3). Gast = Gastropod larvae, Shr = Shrimp, I = Isopod, A = Amphipod. Note: x-axis log scale. Sizes of prey items from Smith (1964)

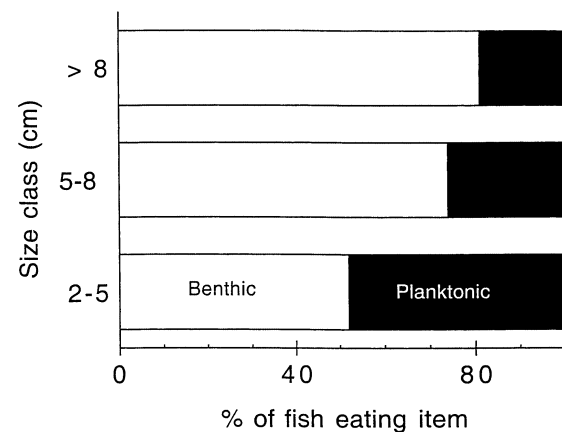


Fig. 5. *Menidia menidia*. Percentage of each size class eating benthic or pelagic prey items in estuary. Benthic organisms include harpacticoid copepods, amphipods, isopods, shrimp, and polychaetes. Planktonic organisms include gastropod larvae and copepods

We conducted an ANOVA to determine if, within each size class of fish, there were any differences in the percentage of fish examined eating a particular food item. This shift in size of prey items with size of fish (Fig. 4) was significant for size class 1 and size class 3 ($p < 0.05$; Table 3). Furthermore, the tendency for larger *M. menidia* to feed on benthic prey is evident in Fig. 5, where we re-structured the data from Fig. 4 into benthic and planktonic categories. These results suggest that *M. menidia* eat larger prey as they grow bigger, but as long as they reside in the shallow estuaries, benthic prey bearing the land-derived estuarine isotopic signature (McClelland et al. 1997), are the preferred food items. The isotope data (Fig. 3b) suggest that the change in preferred prey size occurred within the same trophic level.

Conclusion. Stable isotope data offer a detailed view of fish population dynamics and of the tight coupling of fish populations to land-derived nitrogen sources. In the case of *Fundulus heteroclitus*, the $\delta^{15}\text{N}$ data suggest that the populations feed and reside within the small estuaries in which they were born. This concurs with earlier studies, which conclude that the home ranges of *F. heteroclitus* are limited (Lotrich 1975). The isotope data also indicate that *F. heteroclitus* move up ~1 step within the benthic trophic web during a single growing season, as might be expected with an increase in length.

The $\delta^{15}\text{N}$ data tell a slightly different story in the case of *Menidia menidia*. The isotopic signatures show that even though Atlantic silversides are a rather active and free swimming species, *M. menidia* born in the shallow estuaries remain within that estuary during their initial growing season. While in the shallow estuaries, *M. menidia* appear to find food of sufficient size and abundance within the same trophic level, and hence do not move up trophic levels as they grow within the estuaries. After larger *M. menidia* move to deeper water in winter, the fish may feed on a diet of planktonic, and some benthic prey (Warkentine & Rachlin 1989). Based on our $\delta^{15}\text{N}$ results, they fed at least 1 trophic level higher when offshore than they did within the inshore estuaries. The fish in the wastewater-enriched estuaries retained the heavy signal only because wastewater, heavy in nitrogen, influenced $\delta^{15}\text{N}$ ratio in their food sources. In Sage Lot Pond, the age 0 fish exhibited lighter isotopic signatures because they are smaller, and because they are in an estuary with a less wastewater-influenced $\delta^{15}\text{N}$ ratio in their food sources. The overwintering fish that survived the winter returned to the shallow estuaries in the spring, and their offspring acquired the $\delta^{15}\text{N}$ isotopic signature characteristic of the estuarine prey, largely benthic organisms, found in the shallow estuaries.

Thus the isotopic nitrogen signatures not only provided evidence of where *Menidia menidia* reside and feed, but also revealed information about migratory behavior during their life history, and about their trophic position as they grew. We applied the isotopic method to 2 species of fish that were well studied, and so provided the opportunity to critically appraise the results of the isotope data. The isotope results correspond closely with present knowledge, and provide additional information on the life histories of these 2 fish species.

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