# Coupling of estuarine benthic and pelagic food webs to land-derived nitrogen sources in Waquoit Bay, Massachusetts, USA

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ABSTRACT: The fact that land-derived sources of nutrients promote eutrophication in the receiving coastal waters implies coupling between land and marine environments. Increasing nitrogen inputs in the estuaries are followed by major shifts in biota composition and abundances. In the present paper we used N and C isotopic ratios to analyze the coupling of benthic and pelagic components of food webs to estuaries receiving different N loads from their watersheds. We found that primary producers, benthic taxa, and fishes were coupled to the watersheds and estuaries where they were collected. In contrast, zooplankton was uncoupled. Primary consumers and predators feeding on benthic prey within the estuaries were also coupled to the watershed and estuaries, but predators feeding on zooplankton were not. We hypothesized that short water residence time in these estuaries uncoupled plankton from terrestrial influence. Stable isotopic measurements of N in producers, consumers, POM, and sediment in different estuaries of Waquoit Bay, Massachusetts, USA, demonstrate a consistent link between land-use on contributing watersheds and the isotopic ratio in all the benthic components and food webs. The remarkably consistent link suggests that the benthos was tightly coupled to land-derived inputs, and that these components, particularly macrophytes, could be good indicators for monitoring increases in land-derived N inputs. Our results showed that stable isotopes of N and C have the potential for use in basic research and applied monitoring, but need to be applied considering the features of estuaries that might couple or uncouple organisms regarding dependency on land, such as hydrodynamic exchanges.

KEY WORDS: Eutrophication · Benthic coupling · Pelagic coupling · Land–estuary coupling · Food webs · Estuaries · Waquoit Bay

## INTRODUCTION

Eutrophication is a major agent of change to coastal habitats worldwide (GESAMP 1990, National Research Council 1994). Increasing population densities along coastlines and the use of fertilizers have produced higher nutrient loading, which in turn has increased primary production, leading to major shifts in the species composition and abundances of flora and fauna living in estuaries (Valiela et al. 1997, Grall & Chau-vaud 2002), as well as eutrophication in estuaries and coastal waters (Nixon 1995, Cloern 2001). The fact that land-derived sources of nutrients create eutrophication in receiving coastal waters implies considerable coupling due to the flow of material between land and estuarine environments.

Stable isotopes have been used to detect land-derived sources of N (McClelland et al. 1997, McClelland & Valiela 1998b, Wigand et al. 2001). Wastewater, fertilizers, and atmospheric N, for example,

have different $\delta^{15}$N values, and hence the N exported from a given watershed bears stable isotopic signatures characterized by the land use on the watershed.

Stable isotopes have also been used to define food webs within estuaries (Peterson & Fry 1987). Because elements such as carbon and nitrogen fractionate in predictable ways in aquatic organisms, it is possible to construct food webs based on these data. The ratio of $^{15}$N to $^{14}$N is used to determine trophic position. Consumers become enriched in $\delta^{15}$N relative to their food by 3 to 4‰ (Michener & Schell 1994). As a result of this stepwise trophic level enrichment, nitrogen stable isotopes have become a valuable tool in food web analysis.

The estuaries of Waquoit Bay, Massachusetts, USA, offer the opportunity to examine the isotopic response of estuarine flora and fauna to increased N loads at the watershed–estuarine scale. Estuaries that enter Waquoit Bay are similar in depth and water residence time, but they differ in the degree of urbanization and land use and hence in the N load received (Valiela et al. 2000, 2004). Studies carried out in these estuaries have shown a strong correlation between the $\delta^{15}$N of estuarine biota and the relative contribution by wastewater to the land-derived N load entering the estuaries (McClelland et al. 1997, McClelland & Valiela 1998a).

Thus, land use practices on watersheds may alter N loads, and therefore the components of the food web may incorporate the $\delta^{15}$N signal of local watershed-derived N sources. Species that live in the benthos have to sustain conditions across time; pelagic species, in contrast, either move advectively with estuarine circulation, or swim. These quite different exposures to ambient conditions may determine how likely it is that organisms in the benthos or plankton are reliable indicators of land-derived nutrient inputs. In turn, the linkage of isotopic values of organisms and watershed-derived inputs might reveal a coupling between land use and estuarine food webs. In this paper, we use C and N isotope signatures of primary producers and consumers of estuaries in the Waquoit Bay system to ascertain which components of benthic and pelagic food webs are coupled to estuaries receiving different N loads from their watersheds.

## MATERIALS AND METHODS

**Study site.** To define the coupling between land and the benthic and pelagic food web components in estuaries we measured N and C stable isotopes in benthic invertebrates, juvenile fishes, major taxa of zooplankton, macrophytes, particulate organic matter (POM), and sediment from 3 estuaries that receive different nitrogen loads. These estuaries have similar water residence times (approximately 1 to 2 d), and range in salinity from 0 to 32 ppt. They receive relatively low (Sage Lot Pond), intermediate (Quashnet River), and high (Childs River) nitrogen loads of 14, 350, and 600 kg N ha$^{-1}$ yr$^{-1}$, respectively (Valiela et al. 1997). N loads to Waquoit Bay include atmospheric deposition, fertilizer use, and wastewater disposal. Wastewater contributes ~50% of the total N load and 75% of the anthropogenic (wastewater + fertilizer) N load to the bay (Valiela et al. 1997). The $\delta^{15}$N values of groundwater dissolved inorganic nitrogen (DIN) entering estuaries increase with the increased N load of the system (Childs River 9.5, Quashnet River ~5.8, Sage Lot Pond 0.5, McClelland & Valiela 1998b). Producers within the estuaries appear to integrate the stable N signatures from groundwater reflecting the proportion of N delivered to the estuary from wastewater inputs (McClelland & Valiela 1998b). These differences make it possible to assess the response of estuarine organisms to different degrees of loading, with different isotopic signatures. Therefore $\delta^{15}$N signatures can be used to indicate coupling of food web components to the watersheds and estuaries. We sampled organisms, POM, and sediment at 3 stations in Sage Lot Pond (SLP) and at 5 stations in Quashnet River (QR) and Childs River (CR) (Fig. 1). Sampling stations were arranged in transects along the estuaries to capture the variation across the estuaries.

**Coupling of primary producers and benthic and pelagic organisms to land-derived N sources.** To assess coupling between land and the producers of the benthic and pelagic food webs within the Waquoit Bay estuaries, we sampled POM, sediment, and macrophytes from each site. We refer to POM as a 'producer' because it is composed largely of organic matter from producers and because the $\delta^{15}$N of POM in Waquoit Bay is primarily influenced by phytoplankton (Yelenik et al. 1996, McClelland & Valiela 1998b). We collected water near the water–sediment interface and at 0.5 m below the surface at every site and filtered it through Whatman GF/C glass fiber filters (effective pore size ≈1.2 µm) to obtain the POM. Surface sediment was collected from the benthic dredge samples (see benthic collection method described below) and was treated with 1.0 N HCl to remove bicarbonate. Macrophytes were collected by hand at each site and cleaned with deionized water.

To determine the coupling between land and benthic and pelagic fauna, we sampled organisms from both the benthos and the water column. We collected benthic invertebrates by taking 3 Ekman dredges at each site from the 3 subestuaries. Contents of the dredges were rinsed through a 0.5 mm sieve; invertebrates were sorted by species. We used a 5 m seine (1 cm mesh size) to collect fish, shrimps, and crabs
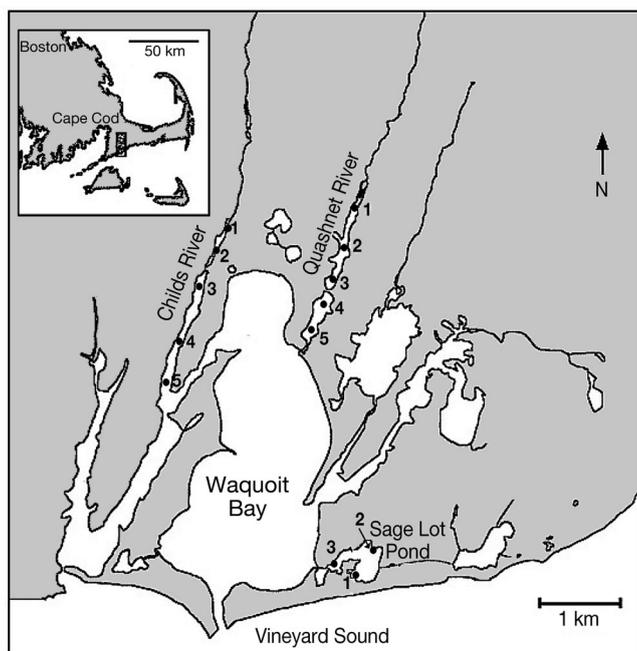
Fig. 1. Waquoit Bay map showing sampling sites at Childs River, Quashnet River, and Sage Lot Pond

along the shoreline. Ascidians were collected by hand. All organisms were washed with deionized water. In the case of fishes and holothuroids, the digestive tract was removed, and the remaining muscle washed with deionized water. The crabs were maintained 24 h in filtered seawater for gastric evacuation. Zooplankton were collected at each site by towing a zooplankton net (12 cm diameter, 45 cm length, mesh size = 60 μm) against the current for 20 min. The major taxa were sorted by developmental stage, rinsed with deionized water, and collected on Whatman filters. *Acartia tonsa* was the dominant copepod found in all 3 estuaries. We measured $\delta^{15}N$ and $\delta^{13}C$ of adult, copepodid, and nauplius stages of this species. We also measured the $\delta^{15}N$ and $\delta^{13}C$ of polychaete larvae found in the estuaries. The zooplankton samples for isotope analysis were composites of 20 to 200 individuals. Specimens of the ctenophore *Mnemiopsis leidyi* were collected by hand and rinsed with deionized water before analysis.

Producer and consumer samples were dried at 55°C, ground to fine powder, weighed, and loaded into tin capsules. Seston and zooplankton samples were kept in pre-weighed filters, weighed, and then loaded into tin capsules. Isotope analyses were performed by mass spectrometer in the 'Stable Isotope Facility' of the University of California at Davis (USA). Results are reported as comparisons with atmospheric nitrogen (for N) and Vienna Pee Dee Belemnite (for C) as standards and calculated as:

$$\delta^{13}C \text{ or } \delta^{15}N \text{ (‰)} = [(R_{sample} - R_{standard})/R_{standard}] \times 10^3$$

where $R$ is ($^{15}N/^{14}N$) or ($^{13}C/^{12}C$). Duplicate determinations on the same sample usually differed by <0.2‰.

To determine if the isotopic signature of various taxonomic groups of benthic and pelagic organisms was correlated to the N load and percentage of wastewater contribution from the subwatersheds emptying into the estuary in which the taxa were collected, we pooled species into broad taxonomic groups. The relationship of $\delta^{15}N$ signatures of primary producers and organisms vs. N load was described by linear regression analysis (Type I regression, Neter et al. 1985). The $\delta^{15}N$ signatures of primary producers were also regressed to wastewater percentage in each estuary. To examine whether the different taxonomic groups differed in their relationships to nitrogen load, we compared slopes using Student's *t*-tests (Devore 2000). To have a more comprehensive data set in this paper, we included isotopic data collected for this study as well as data from previous studies done in these estuaries (Hauxwell et al. 1998, McClelland & Valiela 1998a, Griffin & Valiela 2001, Shriver et al. 2002, Carmichael 2003).

**Nutrient sources and trophic level effects on $\delta^{15}N$ signature.** The isotopic signature of any species may depend, not only on the N source, but also on the trophic position of the species. To distinguish the relative importance of nitrogen source and trophic level on the $\delta^{15}N$ isotope values of the organisms, we grouped the species as grazers, filter feeders, deposit feeders, scavengers, and predators. The assignation of feeding habit was based on a review of literature (Appendix 1). The $\delta^{15}N$ signatures of each taxon assigned to each feeding type were then averaged for each estuary. To assess the coupling of the mean isotopic signature and the nitrogen load entering estuaries, we regressed (Type I regression, Neter et al. 1985) these variables. To examine whether the different trophic groups differed in their relationships to the nitrogen load, we compared slopes using *t*-tests (Devore 2000); where differences between slopes were not found, the intercepts were compared using analysis of covariance (ANCOVA) (Sokal & Rohlf 2003) to determine the enrichment in $^{15}N$ from food types to consumers.

## RESULTS AND DISCUSSION

In this section we first analyze the relationships of the N load and wastewater percentage to the isotopic signatures of taxa and trophic groups. Then we examine the relationships between producers and consumers in each estuary and define differences in $\delta^{15}N$

Table 1. $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± SE) for macrophytes, sediment, particulate organic matter (POM), and benthic and pelagic consumers for Sage Lot Pond, Quashnet River, and Childs River. Values are from this study and/or other sources (1: present study; 2: McClelland & Valiela 1998; 3: Shriver et al. 2002; 4: Carmichael 2003; 5: Griffin & Valiela 2001). Blank spaces: no data

| Species | Sage Lot Pond | | | | Quashnet River | | | | Childs River | | | | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\delta^{13}C$ | n | $\delta^{15}N$ | n | $\delta^{13}C$ | n | $\delta^{15}N$ | n | $\delta^{13}C$ | n | $\delta^{15}N$ | n | |
| **Macrophytes** | | | | | | | | | | | | | |
| *Cladophora vagabunda* | −15.30 | 1 | 3.40 | 1 | −14.76 ± 0.62 | 2 | 4.34 ± 0.49 | 2 | −14.73 ± 0.81 | 2 | 6.52 ± 1.59 | 2 | 1, 2 |
| *Codium fragile* | −12.28 | 1 | 5.85 | 1 | −13.03 | 1 | 6.10 | 1 | −13.23 | 1 | 8.19 | 1 | 1 |
| *Enteromorpha* sp. | −19.10 ± 0.21 | 2 | 4.90 ± 0.10 | 2 | −17.70 ± 0.60 | 2 | 6.40 ± 0.30 | 2 | −18.70 ± 0.20 | 2 | 8.40 ± 0.20 | 2 | 2 |
| *Fucus vesiculosus* | −14.60 | 1 | 4.59 | 1 | −14.48 | 1 | 5.86 | 1 | −12.91 | 1 | 7.90 | 1 | 1 |
| *Gracilaria tikvahiae* | −19.50 | 1 | 5.10 | 1 | −16.87 ± 0.15 | 3 | 6.16 ± 0.17 | 3 | −15.94 ± 0.62 | 3 | 8.03 ± 0.28 | 3 | 1, 2 |
| *Ulva lactuca* | −11.25 ± 0.14 | 4 | 3.82 ± 0.31 | 4 | −6.54 | 1 | 7.91 | 1 | −6.46 ± 1.15 | 2 | 9.28 ± 0.7 | 2 | 1 |
| *Spartina alterniflora* | −13.26 ± 0.06 | 2 | 3.28 ± 0.49 | 2 | −12.70 ± 0.22 | 3 | 7.79 ± 0.81 | 3 | −13.35 ± 0.06 | 2 | 8.15 ± 0.21 | 2 | 1 |
| *Zostera marina* | −10.26 | 1 | 1.99 | 1 | | | | | | | | | 1 |
| **Sediment** | −14.94 ± 0.33 | 6 | 2.19 ± 0.36 | 6 | −21.45 ± 1.75 | 6 | 4.27 ± 0.33 | 6 | −19.36 ± 0.74 | 9 | 4.94 ± 0.12 | 9 | 1 |
| **POM** | | | | | | | | | | | | | |
| Surface | −20.24 ± 1.24 | 6 | 3.70 ± 1.32 | 6 | −20.69 ± 0.70 | 5 | 5.20 ± 0.52 | 5 | −20.06 ± 1.00 | 5 | 6.27 ± 1.10 | 5 | 1 |
| Bottom | −17.48 ± 0.64 | 2 | 5.17 ± 1.08 | 2 | −19.33 ± 1.35 | 3 | 5.29 ± 1.20 | 3 | −19.91 ± 0.28 | 3 | 5.29 ± 1.36 | 3 | 1 |
| **Amphipoda** | | | | | | | | | | | | | |
| *Cymadusa compta* | −14.40 ± 0.30 | 2 | 4.10 ± 0.20 | 2 | | | | | −16.00 ± 0.40 | 2 | 7.60 ± 0.20 | 2 | 2 |
| *Gammarus mucronatus* | −13.63 ± 0.81 | 2 | 6.69 ± 0.97 | 2 | | | | | −14.80 ± 0.40 | 2 | 7.80 ± 0.30 | 2 | 2 |
| *Gammarus oceanicus* | | | | | −15.49 | 1 | 5.39 | 1 | | | | | 1 |
| *Microdeutopus gryllotalpa* | −13.40 ± 0.10 | 2 | 3.80 ± 0.10 | 2 | | | | | −14.80 ± 0.40 | 2 | 6.60 ± 0.10 | 2 | 2 |
| **Ascidiacea** | | | | | | | | | | | | | |
| *Molgula manhattensis* | | | | | −16.70 | 1 | 7.24 | 1 | −18.19 ± 1.04 | 2 | 7.16 ± 1.34 | 2 | 1 |
| **Bivalvia** | | | | | | | | | | | | | |
| *Argopecten irradians* | | | 6.68 ± 0.38 | 2 | | | 6.81 | 1 | | | 8.18 ± 0.11 | 2 | 3 |
| *Geukensia demissa* | −19.00 | 1 | 5.76 ± 0.60 | 4 | | | 7.50 ± 0.19 | 3 | −18.50 | 1 | 8.18 ± 0.38 | 4 | 2 |
| *Mercenaria mercenaria* | −16.40 ± 0.30 | | 6.70 ± 0.02 | | −17.90 | 1 | 8.20 | 1 | −15.90 ± 0.20 | | 9.50 ± 0.06 | | 4 |
| *Mya arenaria* | −16.50 ± 0.10 | | 6.80 ± 0.04 | | −17.50 | 1 | 8.01 | 1 | −16.90 ± 0.20 | | 10.10 ± 0.07 | | 4 |
| **Decapoda** | | | | | | | | | | | | | |
| *Callinectes sapidus* | | | | | −11.60 ± 0.64 | 3 | 7.99 ± 0.72 | 3 | −14.18 ± 0.56 | 3 | 9.98 ± 0.07 | 3 | 1 |
| *Carcinus maenas* | −12.72 ± 0.86 | 2 | 6.92 ± 0.63 | 2 | −12.76 ± 0.09 | 2 | 10.00 ± 0.38 | 2 | | | | | 1 |
| *Crangon septemspinosa* | −13.36 | 1 | 6.82 | 1 | −12.64 ± 0.15 | 2 | 9.01 | 2 | −14.08 ± 0.84 | 3 | 9.27 ± 1.21 | 3 | 1 |
| *Hypolite zostericola* | | | 6.69 ± 0.31 | 2 | | | | | | | | | 1 |
| *Libinia dubia* | −13.29 | 1 | 7.60 | 1 | | | | | | | | | 1 |
| *Neopanopeus sayi* | −12.18 ± 0.30 | 2 | 6.04 ± 0.59 | 2 | −1058 | 1 | 6.65 | 1 | | | | | 1 |
| *Pagurus longicarpus* | | | | | | | | | −10.67 | 1 | 8.18 | 1 | 1 |
| *Palaemonetes pugio* | −13.56 ± 0.36 | 2 | 7.17 ± 0.49 | 2 | −13.27 ± 0.18 | 3 | 9.28 ± 0.08 | 3 | −14.75 ± 0.23 | 4 | 10.50 ± 0.24 | 4 | 1 |
| *Palaemonetes vulgaris* | −11.24 | 1 | 8.82 | 1 | −12.83 | 1 | 9.73 | 1 | −14.90 | 1 | 10.74 | 1 | 1, 2 |
| *Rhitripanopeus harssi* | −12.36 | 1 | 6.02 | 1 | −11.83 ± 0.29 | 2 | 7.69 ± 1.33 | 2 | | | | | 1 |
| **Gastropoda** | | | | | | | | | | | | | |
| *Crepidula fornicata* | −17.63 | 1 | 7.42 | 1 | | | | | | | | | 1 |
| *Haminoea solitaria* | | | | | −12.07 | 1 | 6.16 | 1 | −12.74 ± 0.28 | 2 | 7.82 ± 0.67 | 2 | 1 |
| *Nassarius obsoletus* | −12.64 | 1 | 6.09 | 1 | −11.42 | 1 | 6.46 | 1 | −13.65 ± 0.55 | 3 | 9.54 ± 0.19 | 3 | 1 |
| **Holothuroidea** | | | | | | | | | | | | | |
| *Leptosynapta tenuis* | −12.99 ± 0.49 | 2 | 7.89 ± 1.81 | 2 | −13.77 ± 0.52 | 2 | 8.80 ± 0.64 | 2 | | | | | 1 |
| *Sclerodactyla briareus* | | | 7.41 | 1 | −13.18 ± 0.18 | 2 | 9.78 ± 1.20 | 2 | −14.70 ± 1.18 | 3 | 11.47 ± 1.01 | 3 | 1 |
| **Isopoda** | | | | | | | | | | | | | |
| *Erichsonella filiformis* | −13.60 ± 1.80 | 2 | 4.30 ± 1.00 | 2 | | | | | −14.50 ± 0.60 | 2 | 7.70 ± 0.80 | 2 | 2 |
| *Cyathura polita* | −12.79 | 1 | 6.08 | 1 | −12.96 ± 0.93 | 2 | 10.96 ± 0.43 | 2 | −12.74 ± 0.85 | 2 | 11.61 ± 0.38 | 2 | 1 |
| **Polychaeta** | | | | | | | | | | | | | |
| *Aglaophamus circinata* | | | | | −22.37 | 1 | 10.74 | 1 | | | | | 1 |
| *Arabella iridicolor* | −14.71 ± 0.13 | 2 | 8.72 ± 1.63 | 2 | | | | | | | | | 1 |
| *Cyrratulus grandis* | −14.82 | 1 | 4.67 | 1 | | | | | | | | | 1 |
| *Clymenella torquata* | | | | | | | | | −15.85 | 1 | 6.89 | 1 | 1 |
| *Etone lactea* | | | | | −12.63 | 1 | 9.17 | 1 | | | | | 1 |
| *Glycera americana* | −13.21 | 1 | 7.46 | 1 | | | | | −16.49 ± 1.85 | 2 | 12.15 ± 0.34 | 1 | 1 |
| *Harmathoe extenuata* | −14.98 | 1 | 8.72 | 1 | | | | | | | | | 1 |
| *Harmathoe imbricata* | −14.52 | 1 | 7.97 | 1 | | | | | | | | | 1 |
| *Heteromastus filiformis* | −13.40 | 1 | 5.81 | 1 | | | | | | | | | 1 |
| *Lumbrinereis fragilis* | | | | | | | | | −14.96 ± 0.61 | 2 | 10.22 ± 1.45 | 2 | 1 |
| *Neanthes succinea* | | | | | −13.48 | 1 | 8.47 | 1 | −14.75 | 1 | 8.00 | 1 | 1 |
| *Notomastus latericeus* | | | | | −21.53 | 1 | 8.89 | 1 | −18.43 ± 1.87 | 2 | 10.32 ± 0.33 | 2 | 1 |

Table 1 (continued)

| Species | Sage Lot Pond δ¹³C | n | δ¹⁵N | n | Quashnet River δ¹³C | n | δ¹⁵N | n | Childs River δ¹³C | n | δ¹⁵N | n | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Polychaeta (continued)** | | | | | | | | | | | | | |
| *Orbinia ornata* | −14.34 ± 1.07 | 2 | 4.84 ± 0.33 | 2 | −13.98 ± 0.16 | 2 | 7.31 ± 0.45 | 2 | | | | | 1 |
| *Pectinaria gouldii* | | | | | | | | | −16.24 | 1 | 6.75 | 1 | 1 |
| *Podarke obscura* | −13.74 | 1 | 8.15 | 1 | −12.73 ± 0.65 | 2 | 9.20 ± 0.15 | 2 | −15.36 | 1 | 10.33 | 1 | 1 |
| *Polycirrus eximius* | −16.57 | 1 | 4.38 | 1 | | | | | −15.72 | 1 | 8.17 | 1 | 1 |
| *Sabellaria vulgaris* | | | | | | | | | −14.94 | 1 | 9.24 | 1 | 1 |
| *Tharyx acutus* | −14.08 | 2 | 4.97 | 2 | | | | | | | | | 1 |
| **Teleostei** | | | | | | | | | | | | | |
| *Anguilla rostrata* | | | | | −14.40 ± 0.08 | 2 | 10.27 ± 0.30 | 2 | | | | | 1 |
| *Cyprinodon variegatus* | −11.50 ± 0.90 | 3 | 5.20 ± 0.50 | 3 | | | | | −14.00 ± 0.50 | 3 | 9.80 ± 0.30 | 3 | 2 |
| *Fundulus heteroclitus* | −14.00 ± 0.40 | 3 | 8.70 ± 0.32 | 3 | −14.64 | 1 | 10.95 ± 0.24 | 15 | −14.60 ± 0.50 | 3 | 11.64 ± 0.27 | 3 | 2, 5 |
| *Fundulus majalis* | | | | | −14.49 ± 0.48 | 2 | 10.30 ± 0.40 | 2 | | | | | 1 |
| *Gasterosteus aculeatus* | −16.90 | 1 | 9.00 | 1 | −14.52 | 1 | 11.39 | 1 | −15.40 ± 0.40 | 3 | 12.30 ± 0.40 | 3 | 1, 2 |
| *Gobiosoma bosc* | | | | | −13.77 ± 0.20 | 2 | 11.25 ± 0.20 | 2 | | | | | 1 |
| *Menidia menidia* | −16.50 ± 0.50 | 4 | 9.02 ± 0.11 | 11 | −13.81 | 1 | 10.64 ± 0.15 | 16 | −17.70 ± 0.80 | 4 | 11.33 ± 0.18 | 14 | 2, 5 |
| *Pseudopleuronectes americanus* | | | | | −14.37 | 1 | 9.21 | 1 | | | | | 1 |
| *Tautogolabrus adspersus* | | | | | −14.29 | 1 | 10.82 | 1 | | | | | 1 |
| **Zooplankton** | | | | | | | | | | | | | |
| *Acartia tonsa* (adults) | −20.31 ±0.90 | 4 | 7.08 ± 2.45 | 4 | | | | | | | | | 1 |
| *Acartia tonsa* (copepodites) | −20.33 ± 0.51 | 2 | 5.37 ± 0.39 | 2 | −22.02 | 1 | 7.03 | 1 | −21.59 ± 0.16 | 4 | 6.17 ± 0.50 | 4 | 1 |
| *Acartia tonsa* (nauplii) | −20.19 ± 0.42 | 4 | 6.06 ± 1.41 | 4 | −21.59 ± 0.22 | 6 | 7.20 ± 0.39 | 6 | −21.00 ± 0.27 | 5 | 7.44 ± 0.06 | 5 | 1 |
| *Mnemiopsis leidyi* | −20.19 ± 0.50 | 3 | 11.33 ± 0.45 | 3 | −20.25 ± 0.64 | 3 | 10.27 ± 2.14 | 3 | −18.74 | 1 | 7.03 | 1 | 1 |
| Polychaete larvae | | | | | −18.90 ± 0.30 | 4 | 8.63 ± 0.77 | 4 | −19.77 ± 0.16 | 3 | 7.82 ± 0.98 | 3 | 1 |

values in the water column and in benthic species due to nutrient supply and to trophic position.

## Coupling of different producer and consumer taxa to land-derived N sources

The δ¹³C and δ¹⁵N signatures of producers and consumers varied considerably among taxonomic groups, individual species, and across estuaries (Table 1). Distribution of species differed among the estuaries, with some species not present in all 3 estuaries. Overall, δ¹³C values of different species varied within estuaries due to their C source, but the values did not change across estuaries within the same species. δ¹⁵N values of different species varied within estuaries and across estuaries within the same species, increasing from low to high N load.

The δ¹⁵N isotopic signatures of macrophytes, sediment, and POM significantly increased with N load (Fig. 2a,c,e) and with the percent contribution of wastewater to total N load (Fig. 2b,d,f). These relationships suggest that these specific components of the estuarine ecosystems appear coupled to land use on the watersheds emptying into the area in which they were sampled. In addition, the regression slopes for macrophytes, sediment, and POM all differed significantly, with macrophytes showing the largest slope response to increasing N loads, followed by sediment,

and then POM (Table 2). This result indicates that macrophytes may be the most sensitive indicator of eutrophication that could be used in monitoring land-derived N load.

All taxonomic groups of benthic invertebrates and fishes consistently and significantly increased in δ¹⁵N isotopic signatures with increasing N load. This remarkably consistent response of all these taxa indicates that they were well coupled to the watersheds and estuaries in which they were collected (Fig. 3). The responses of polychaetes, bivalves, decapods, and teleosts were the most pronounced (Fig. 3, Table 3). Polychaetes showed the greatest variation in δ¹⁵N values within each estuary, with a range from 4 to 10‰ in Sage Lot Pond and 6 to 12‰ in Childs River (Fig. 3a). This variation is probably derived from the variation in feeding types among polychaetes (Appendix 1).

The teleost δ¹⁵N signatures were much heavier overall than those of all other groups (Fig. 3h). There was considerable variation in fish δ¹⁵N signatures, probably associated to temporal and spatial variability for some species, flexible food habits (Davenport & Bax 2002), and inclusion of different feeding types (e.g. the predator *Menidia menidia* and the grazer *Cyprinodon variegatus*) among the fishes.

In strong contrast, the isotopic signature of zooplanktonic organisms did not vary with N load (Fig. 4). The range in δ¹⁵N of zooplankton was approximately 3 to 13‰. Adults, copepodids, or nauplii of *Acartia tonsa*,
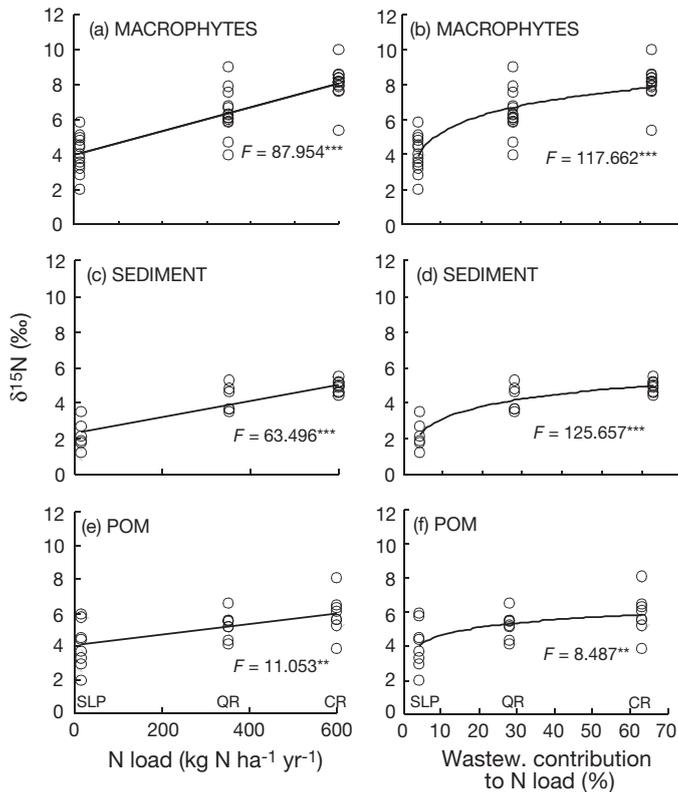
Fig. 2. $\delta^{15}$N of macrophytes, sediment, and particulate organic matter (POM) vs. (a,c,d) N-loading rate and (b,d,f) percentage of wastewater in Sage Lot Pond (SLP), Quashnet River (QR), and Childs Rivers (CR). Wastewater percentages are from McClelland et al. (1997). Regression analysis using N load generates: for macrophytes $y = x \times 0.007 + 3.956$, for sediment $y = x \times 0.005 + 2.276$, and for POM $y = x \times 0.003 + 4.053$; using wastewater percentage generates: for macrophytes $y = 2.911 \times \ln(x) - 3.754$, for sediment $y = 1.880 \times \ln(x) - 2.646$, and for POM $y = 1.322 \times \ln(x) + 0.560$. Asterisks indicate significant regressions, $F$-test (\*\*\*p < 0.001, \*\*p < 0.010)

Table 2. Results of $t$-tests comparing pairs of regression slopes constructed using $\delta^{15}$N of primary producers vs. N loads from different estuaries of Waquoit Bay (data in Fig. 2)

| Comparison | df | $t$ | p |
|---|---|---|---|
| Macrophytes vs. POM | 60 | 18.5 | <0.001 |
| Macrophytes vs. Sediment | 57 | 22.0 | <0.001 |
| Sediment vs. POM | 41 | 5.0 | <0.001 |

Table 3. Results of $t$-tests comparing linear regression slopes constructed using $\delta^{15}$N data of taxa vs. N loads from different estuaries of Waquoit Bay (data in Fig. 3)

| Comparison | | df | $t$ | p |
|---|---|---|---|---|
| **Polychaeta** | vs. Holothuroidea | 39 | 2.833 | <0.001 |
| | vs. Gastropoda | 39 | 0.583 | 0.169 |
| | vs. Bivalvia | 57 | 0.833 | 0.101 |
| | vs. Decapoda | 58 | 0.750 | 0.004 |
| | vs. Amphipoda | 42 | 0.667 | 0.117 |
| | vs. Isopoda | 39 | 2.833 | 0.081 |
| | vs. Teleostei | 76 | 0.417 | 0.320 |
| **Holothuroidea** | vs. Gastropoda | 14 | 2.050 | <0.001 |
| | vs. Bivalvia | 32 | 2.200 | 0.004 |
| | vs. Decapoda | 33 | 1.250 | 0.030 |
| | vs. Amphipoda | 17 | 1.300 | 0.062 |
| | vs. Isopoda | 14 | 0 | 1.000 |
| | vs. Teleostei | 51 | 1.450 | 0.030 |
| **Gastropoda** | vs. Bivalvia | 32 | 0.176 | 0.787 |
| | vs. Decapoda | 33 | 0.941 | 0.054 |
| | vs. Amphipoda | 17 | 0.882 | 0.152 |
| | vs. Isopoda | 14 | 2.412 | 0.011 |
| | vs. Teleostei | 51 | 0.706 | 0.236 |
| **Bivalvia** | vs. Decapoda | 51 | 3.167 | <0.001 |
| | vs. Amphipoda | 35 | 3.000 | <0.001 |
| | vs. Isopoda | 32 | 7.333 | 0.088 |
| | vs. Teleostei | 69 | 2.500 | <0.001 |
| **Decapoda** | vs. Amphipoda | 36 | 0.111 | 0.620 |
| | vs. Isopoda | 33 | 2.778 | 0.264 |
| | vs. Teleostei | 69 | 0.444 | 0.049 |
| **Amphipoda** | vs. Isopoda | 16 | 3.714 | 0.295 |
| | vs. Teleostei | 53 | 0.429 | 0.677 |
| **Isopoda** | vs. Teleostei | 51 | 2.841 | 0.232 |

the most abundant copepod species, did not show any relationship between $\delta^{15}$N values and N load. In addition, we did not find any pattern in signatures among the different copepod life stages. In Sage Lot Pond, adult *A. tonsa* were heavier, while nauplii and copepodids were lighter. In Quashnet River, adults had a lighter signature than copepodids or nauplii. Fortuitously, there were no adult copepods in our samples from Childs River, and polychaete larvae were not found in Sage Lot Pond. There was, however, no significant increment in $\delta^{15}$N of polychaete larvae from samples collected in Quahsnet River and Childs River. Therefore, zooplankton in our estuaries appear to be largely uncoupled to the N entering from land-derived sources, in strong contrast to what we found so consistent for benthos.

The uncoupling of zooplankton from watershed influences in Waquoit Bay estuaries is not a straight-

forward feature. We know, for example, that female *Acartia tonsa* respond to the relative availability of food in the different Waquoit Bay estuaries, and increase their egg production in proportion to N load (Cubbage et al. 1999). Nonetheless, this response did not translate into a parallel effect on copepod abundances (Lawrence et al. 2004), nor, which is more relevant to the present paper, on isotopic signatures (Fig. 4). The uncoupling from the influence of watersheds shown by *A. tonsa* may be related to the short residence time of water in Waquoit Bay (Valiela et al. 2001, Lawrence et al. 2004). The estimated residence time in these estuaries is ~2 d (Valiela et al. 2004),

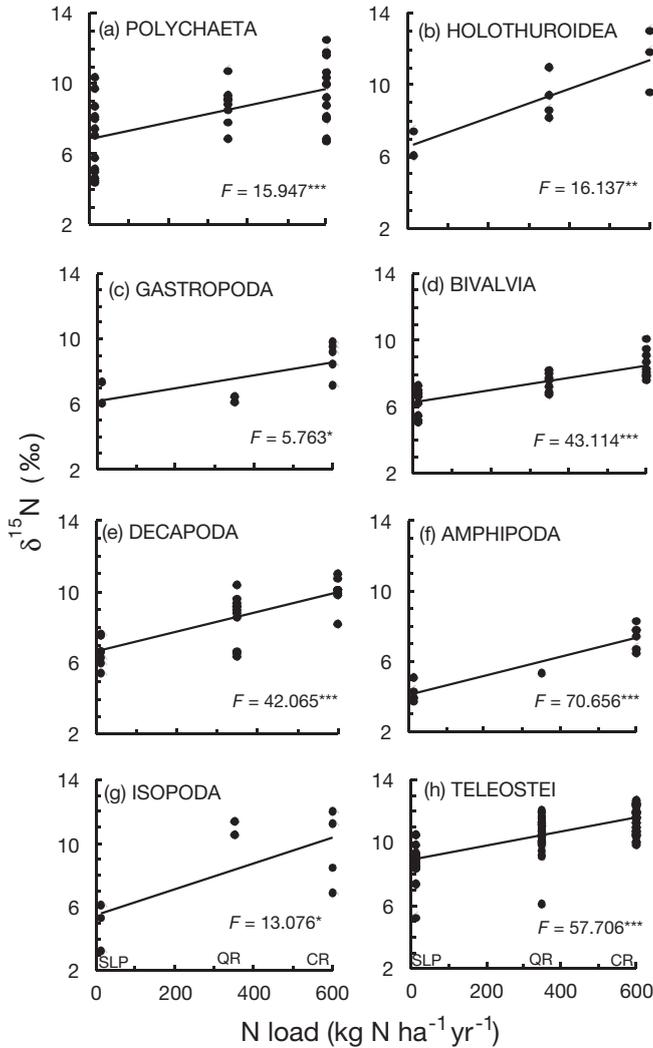Fig. 3. $\delta^{15}N$ of organisms grouped by major taxa vs. N-loading rate in Sage Lot Pond (SLP), Quashnet River (QR), and Childs Rivers (CR). Asterisks indicate significant linear regressions, $F$-test (***p < 0.001, **p < 0.010, *p < 0.050)

Our data consistently demonstrate that primary producers, benthic invertebrates, and fishes were clearly coupled to the watersheds and estuaries in which they were found. In contrast, zooplanktonic organisms may be more subject to advective movements so that they were not as coupled.

## Coupling of trophic groups to land-derived N sources

All trophic groups examined consistently increased their $\delta^{15}N$ signatures with N load (Fig. 5). Grazers showed an increment in $\delta^{15}N$ from low to high N-loaded estuaries similar to that showed by macrophytes (df = 10, $t$ = 2.634, p = 0.292), but they did not increase their signature compared to the macrophytes (ANCOVA: $F$ = 0.606, p = 0.440; Fig. 5a) nor to *Cladophora vagabunda* (ANCOVA: $F$ = 2.563, p = 0.133). This is puzzling, but suggests that these grazers were not strictly feeding on macrophytes. The Waquoit Bay food web seems to lack strict herbivores. In fact, we know, for example, that *Cyprinodon variegatus*, probably the most herbivorous species of fish on our list, also feeds on detritus and meiofauna (Werme 1981). Amphipod diets are largely algae (Hauxwell et al. 1998), but also include detritus (Zimmerman et al. 1979), so that the isotopic signature of 'grazers' could be lower due to consumption of detritus and sediment.
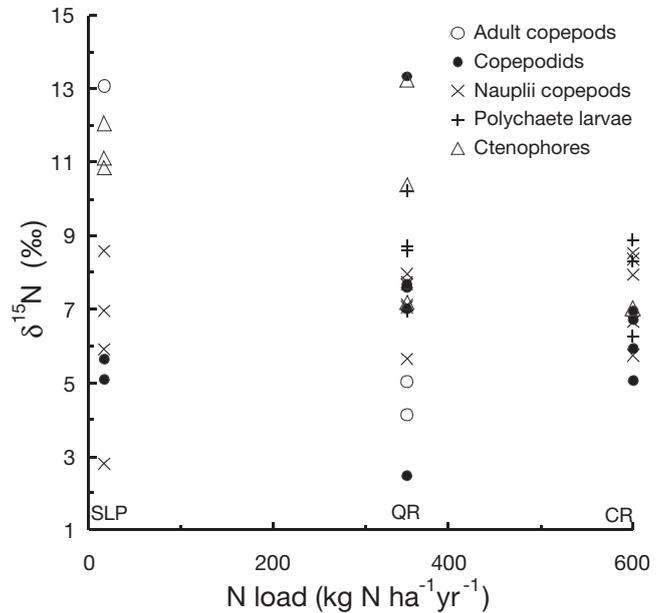
which may be too brief for plankton to take advantage of the available food supply and increase their abundances. The short residence time may not be long enough either to allow zooplankton to assimilate the specific isotopic signature associated with specific watersheds. The uncoupling of copepods from land-derived N loading occurs in spite of clear evidence that phytoplankton do acquire nitrogen signatures characteristic of each estuary (J. K. York, I. Valiela & D. J. Repeta unpubl. data). Plankton feeding in one estuary may find themselves in altogether different places 2 d later, moved by tide and other hydrodynamic advection. This means that the plankton found at any one time may be a mixture of specimens that have experienced quite different feeding and geographic histories and, consequently, bear quite variable isotopic ratios.



Fig. 4. $\delta^{15}N$ of zooplanktonic organisms vs. N-loading rate in Sage Lot Pond (SLP), Quashnet River (QR), and Childs Rivers (CR). Adults, copepodids and nauplii are *Acartia tonsa*. Regression analysis generates: for adults p = 0.590, $r^2$ = 0.219; for copepodids p = 0.103, $r^2$ = 0.004; for polychaete larvae p = 0.109, $r^2$ = 0.211; and for ctenophores p = 0.171, $r^2$ = 0.205
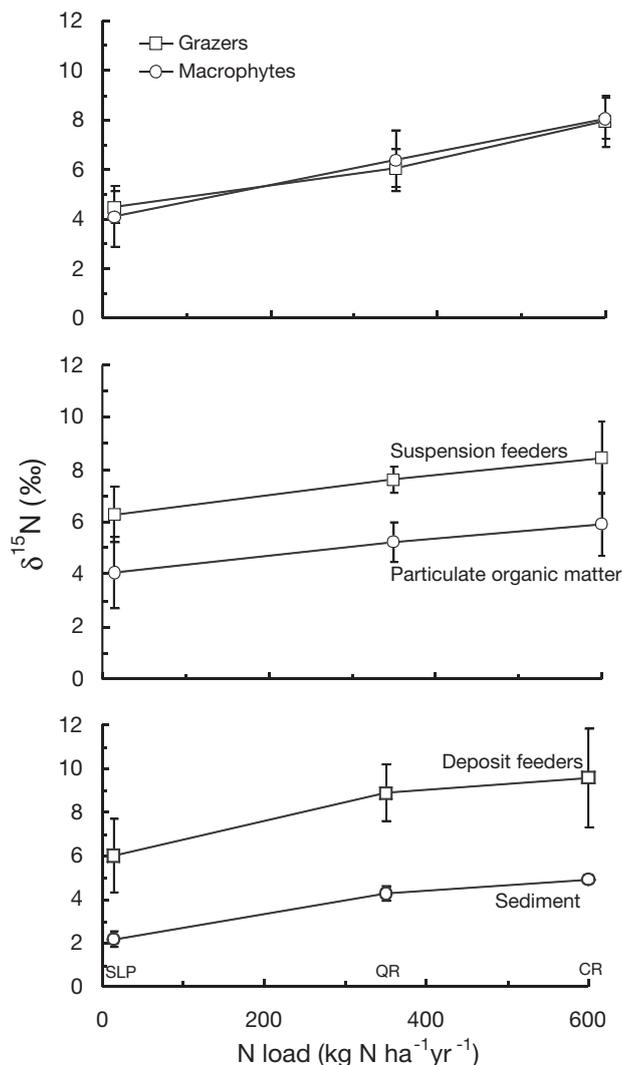
Fig. 5. $\delta^{15}N$ (means ± SE) of primary producers and consumers vs. N-loading rate in Sage Lot Pond (SLP), Quashnet River (QR), and Childs Rivers (CR). Here and and in other figures grazers are: *Cyprinodon variegatus*, *Cymadusa compta*, *Microdeutopus gryllotalpa*, *Erichsonella filiformis*, and *Gammarus mucronatus*; suspension feeders are: *Crepidula fornicata*, *Polycirrus eximius*, *Argopecten irradians*, *Geukensia demissa*, *Mercenaria mercnaria*, *Mya arenaria*, *Molgula manhattensis*, and *Sabellaria vulgaris*; deposit feeders are: *Sclerodactyla briareus*, *Leptosynapta tenuis*, *Tharyx acutus*, *Cyrratulus grandis*, *Orbinia ornata*, *Heteromastus filiformis*, *Notomastus latericeus*, *Neanthes succinea*, *Pectinaria gouldii*, and *Clymenella torquata*

The nearly similar isotopic signatures of macrophytes and the presumptive herbivores suggest that our 'herbivores' must use food items whose signatures are lighter than those of macrophytes to the extent that they mask the 2 to 4‰ fractionation to be expected of consumers of the macrophytes.

$\delta^{15}N$ signatures of suspension feeders, excluding the zooplankton taxa, and their POM food increased

as N load increased (Fig. 5b). The slopes were similar (df = 18, $t$ = 2.445, p = 0.623), but, as evident in the $y$-intercepts, the isotopic signature of the suspension feeders was enriched in $^{15}N$ by 2.3‰, compared with the POM values (ANCOVA: $F$ = 15.838, p < 0.001). Deposit feeders and sediment $\delta^{15}N$ signatures also increased as N load increased (Fig. 5c), with similar slopes (df = 25, $t$ = 3.361, p = 0.264). The enrichment in $^{15}N$ in deposit feeders was 3.9‰ relative to the signature in the sediment along the N-load gradient (ANCOVA: $F$ = 30.241, p < 0.001; Fig. 5c). These results suggest that both suspension and deposit feeders show signatures corresponding to the 2 to 4‰ fractionation expected of trophic steps (Fig. 6). Thus, the trophic groups found in the benthos are clearly coupled to the watershed that input N into the estuary, and, to their food sources.

$\delta^{15}N$ signatures of benthic-associated predators increased as N load increased, in contrast to the $\delta^{15}N$ of zooplanktivore predators (Fig. 7). Benthic predators, such as polychaetes and crabs, were clearly coupled to the watersheds and estuaries, and reflected the isotopic signatures of their prey. Pelagic predators that actively fed on benthic prey, detritus, or plants, like the fishes, also assimilated the specific $\delta^{15}N$ signature of the respective estuary in which they were living. The time spent in the estuaries by these species seems to be long enough to assimilate the particular signature of each estuary, and they, being active swimmers, are not influenced by the residence time of the water, in contrast to planktonic organisms.

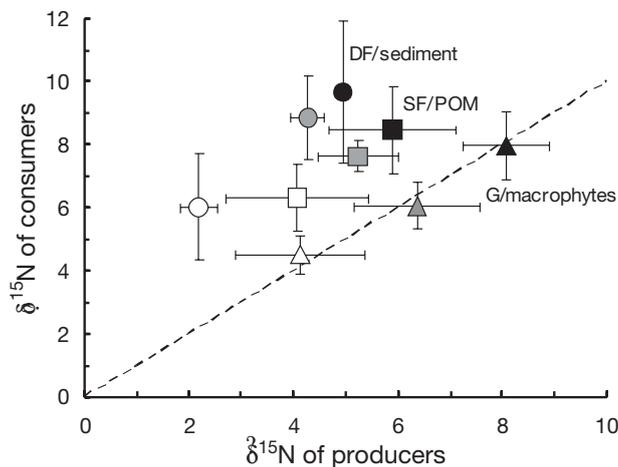Some species we collected in Waquoit Bay have been described as zooplanktivores, but isotopic signa-



Fig. 6. $\delta^{15}N$ (means ± SE) of primary producers vs. those of consumers in Sage Lot Pond (open symbols), Quashnet River (grey symbols), and Childs River (black symbols). DF: deposit feeder (circles); SF: suspension feeders (squares); POM: particulate organic matter; G: grazers (triangles)
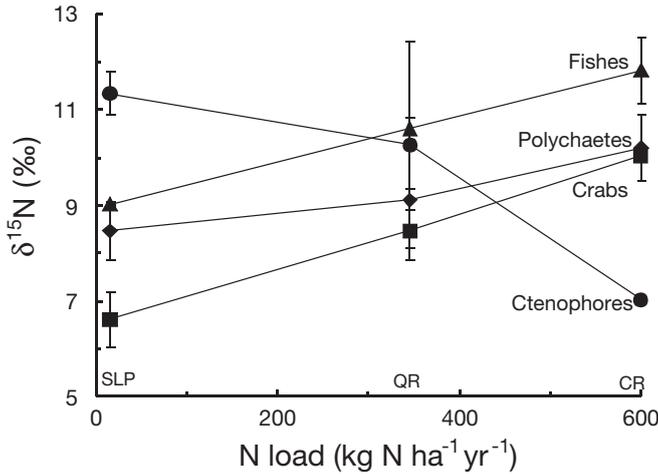
Fig. 7. $\delta^{15}N$ (means ± SE) of predators vs. N-loading rate in Sage Lot Pond (SLP), Quashnet River (QR), and Childs Rivers (CR). Fishes are: *Menidia menidia, Fundulus majalis, Gobiosoma bosc, Tautogolabrus adspersus,* and *Anguilla rostrata*; polychaetes are: *Harmathoe imbricata, H. extenuata, Arabella iridicolor,* and *Podarke obscura*; crabs are: *Carcinus maenas, Rhitropanopeus harsii,* and *Callinectes sapidus*

tures suggested otherwise. For example, *Menidia menidia* do feed on copepods, but they must also prey on benthic invertebrates (Griffin & Valiela 2001). Benthic prey appeared to dominate the diet of *M. menidia*, since the $\delta^{15}N$ signatures of *M. menidia* follow the estuary signature (Table 1). *M. menidia*, although an active swimmer independent of water movements, nevertheless appears to remain within a single estuary long enough to assimilate the $\delta^{15}N$ signature of that estuary.

The only pelagic species that appears to be a strict zooplanktivore was the ctenophore *Mnemiopsis leidyi*. *M. leidyi* was uncoupled to the watersheds and the estuaries (Fig. 4), as well as to the zooplankton. This confirms that species that fed strictly within the water column food web were not affected by their watersheds.

So far we have referred to the $\delta^{15}N$ data, but the $\delta^{13}C$ information also provides a perspective on the link between the benthic and pelagic components of the food webs. The carbon sources in our food web seem to be divided into 2 pathways (Fig. 8). Suspension feeders had lighter $\delta^{13}C$ values than scavengers, grazers, predators, and deposit feeders, across all 3 estuaries (Fig. 8a). A reasonable explanation for this contrast may be that $\delta^{13}C$ values are linked to the food source and by these feeding types. In these estuaries, macroalgae may be consumed by scavengers, grazers, predators, and deposit feeders (Fig. 8a). Evidence for this conclusion is given by the similarity in the $\delta^{13}C$ signatures of these consumers and the macroalgal $\delta^{13}C$ signature (Fig. 8b). In contrast, suspension

feeders showed $\delta^{13}C$ signatures that matched the $\delta^{13}C$ values of POM (Fig. 8b). These results corroborate the $\delta^{15}N$ results and confirm that the benthic and water column parts of Waquoit Bay food webs are relatively independent.

The isotopic nitrogen data thus suggest that there are powerful links between land use on watersheds and those parts of the estuarine food webs that are associated with the benthos. Those components of the estuarine environment that are pelagic and feed on zooplankton seem to be uncoupled to the land and the benthos, as made evident by the N and C isotopic information.

The results of this study have applied and basic implications. In terms of application, it is apparent that taxa associated with the benthos are likely to be more appropriate indicators for monitoring eutrophication of estuarine waters. The basic implications of our results include the suggestion that understanding the structuring of estuarine food webs must involve partitioning the components into those whose controls might depend on external terrestrial factors and whose control may lie elsewhere.
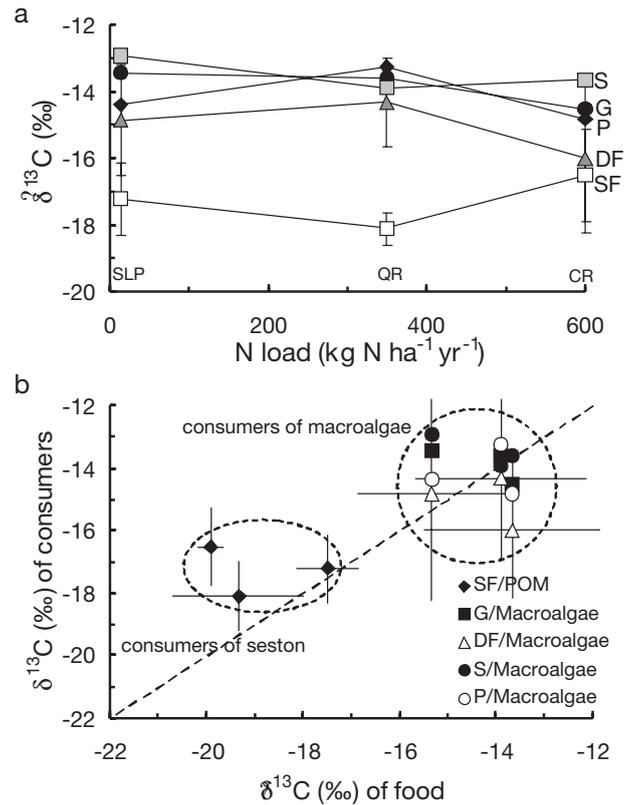


Fig. 8. $\delta^{13}C$ of major trophic groups vs. (a) N-loading rate in Sage Lot Pond (SLP), Quashnet River (QR), and Childs Rivers (CR) and vs. (b) $\delta^{13}C$ of presumed food sources. S: scavengers; G: grazers; P: predators; DF: deposit feeders; SF: suspension feeders; POM: particulate organic matter

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**Appendix 1.** Trophic groups of the analyzed species based on literature data

| Species | Trophic group | Source |
|---|---|---|
| **Amphipoda** | | |
| *Cymadusa compta* | Grazer | Hauxwell et al. (1998) |
| *Gammarus mucronatus* | Grazer | Cruz Rivera & Hay (2000), Zimmerman et al. (1979) |
| *Gammarus oceanicus* | Grazer/detrivore | Hudon (1983), Denton & Chapman (1991) |
| *Microdeutopus gryllotalpa* | Grazer | Hauxwell et al. (1998) |
| **Ascidiacea** | | |
| *Molgula manhattensis* | Suspension feeder | Peterson & Svane (2002) |
| **Bivalvia** | | |
| *Argopecten irradians* | Suspension feeder | Lu et al. (2000) |
| *Geukensia demissa* | Suspension feeder | Huang et al. (2003) |

**Appendix 1** (continued)

| Species | Trophic group | Source |
| --- | --- | --- |
| **Bivalvia (continued)** | | |
| *Mercenaria mercenaria* | Suspension feeder | Weiss et al. (2002) |
| *Mya arenaria* | Suspension feeder | Weiss et al. (2002) |
| **Decapoda** | | |
| *Callinctes sapidus* | Predator | Hsueh et al. (1992) |
| *Carcinus maenas* | Predator | Elner (1981) |
| *Crangon septemspinosa* | Predator/detritivore | Wilcox & Jeffries (1974) |
| *Libinia dubia* | Predator/grazer | Oakes & Haven (1971), Stachowicz & Hay (1999) |
| *Neopanopeus sayi* | Predator/detritivore | Gibbons (1984) |
| *Pagurus longicarpus* | Predator/detritivore | Gibbons (1984), Tettelbach (1985) |
| *Palaemonetes pugio* | Predator/detritivore | Chambers (1981) |
| *Palaemonetes vulgaris* | Predator/detritivore | Chambers (1981) |
| *Rhitropanopeus harssi* | Predator | Milke & Kennedy (2001) |
| **Gastropoda** | | |
| *Crepidula fornicata* | Suspension feeder | Lesser et al. (1992) |
| *Haminoea solitaria* | Detrivore | Chester (1993) |
| *Nassarius obsoletus* | Oportunistic deposit feeder | Ray (1982) |
| **Holothuroidea** | | |
| *Leptosynapta tenuis* | Deposit feeder | Plante & Shriver (1998) |
| *Sclerodactyla briareus* | Deposit feeder | McAloon & Mason (2003) |
| **Isopoda** | | |
| *Cyathura polita* | Detrivore | Ray (1982) |
| *Erichsonela filiformis* | Grazer | Hauxwell et al. (1998) |
| **Polychaeta** | | |
| *Aglaophamus circinata* | Predator/omnivore | Kozloff (1990), Noyes (1980) |
| *Arabella iridicolor* | Predator | Rouse & Pleijel (2001) |
| *Cirratulus grandis* | Deposit feeder | Rouse & Pleijel (2001) |
| *Clymenella torquata* | Deposit feeder | Luckenbach & Orth (1999) |
| *Eteone lactea* | Predator/scavenger | Rouse & Pleijel (2001) |
| *Glycera americana* | Opportunistic deposit feeder | Ray (1982) |
| *Harmothoe extenuata* | Predator | Rouse & Pleijel (2001) |
| *Harmothoe imbricata* | Predator | Daly (1973) |
| *Heteromastus filiformis* | Deposit feeder | Ray (1982) |
| *Lumbrinereis fragilis* | Predator | Valderhang (1985) |
| *Neanthes succinea* | Deposit feeder | Pardo & Dauer (2003) |
| *Notomastus latericeus* | Deposit feeder | Martin et al. (2000) |
| *Orbinia ornata* | Deposit feeder | Rouse & Pleijel (2001) |
| *Pectinaria gouldii* | Deposit feeder | Whitlatch & Weinberg (1982) |
| *Podarke obscura* | Predator | Kozloff (1990) |
| *Polycirrus eximius* | Suspension feeder | Rouse & Pleijel (2001) |
| *Sabellaraia vulgaris* | Suspension feeder | Rouse & Pleijel (2001) |
| *Tharyx acutus* | Deposit feeder | Rouse & Pleijel (2001) |
| **Teleostei** | | |
| *Anguilla rostrata* | Predator | Werme (1981) |
| *Cyprinodon variegatus* | Grazer | Werme (1981) |
| *Fundulus heteroclitus* | Predator/detritivore | Werme (1981) |
| *Fundulus majalis* | Predator | Werme (1981) |
| *Gasterosteus aculeatus* | Predator | Sanchez-Gonzales et al. (2001) |
| *Gobiosoma bosc* | Predator | Nero (1976), Dahlberg & Conyers (1979) |
| *Menidia menidia* | Predator | Griffin & Valiela (2001) |
| *Pseudopleuronectes americanus* | Predator | Stehlik & Meise (2000) |
| *Tautogolabrus adspersus* | Benthivore | Ojeda & Dearborn (1991) |
| **Ctenophora** | | |
| *Mnemiosis leidyi* | Zooplanktivore | Costello et al. (1999) |
| **Copepoda** | | |
| *Acartia tosa* | Phyto-microzooplanktivore | Kleppel (1993) |