

Primary Research Paper

## Toward using *Margaritifera falcata* as an indicator of base level nitrogen and carbon isotope ratios: insights from two California Coast Range rivers

Jeanette K. Howard\*, Kurt M. Cuffey & Madeline Solomon

Department of Geography, University of California, Berkeley, 507 McCone Hall, Berkeley, CA 94720-4740, USA  
(\*Author for correspondence: Tel.: +510-642-3946, Fax: +510-642-3370, E-mail: jhowie@uclink4.berkeley.edu)

Received 20 May 2004; in revised form 20 October 2004; accepted 29 October 2004

**Key words:** freshwater mussels, stable isotope, baseline conditions, trophic, California

### Abstract

Measurements of freshwater mussel tissue are potentially very useful for determining base-level isotopic values for food web studies in aquatic environments. As long-lived, filter-feeding organisms, mussels have the potential to spatially and temporally average the isotopic baseline signal. Following from earlier studies that focused on lake environments, this study investigates the stable carbon and nitrogen isotope ratios in tissue of the river dwelling freshwater mussel, *Margaritifera falcata*, in two extensively studied northern California coast range rivers, the South Fork Eel and Navarro. We highlight advantages and challenges for using riverine mussel isotopes as indicators of baselines.  $\delta^{13}\text{C}$  of primary producers is known to vary with habitat along the South Fork Eel channel, but our measurements show no such variations, demonstrating that riverine mussels do preserve a spatially averaged measure of instream derived food sources. Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are shown to be markedly different in the two rivers, reflecting differences in food sources and possibly watershed land use. We also found that  $\delta^{15}\text{N}$  of mussel tissue increased by approximately 2‰ with mussel age in both rivers. This suggests it is important to consider age and size effects when estimating baseline values from mussel tissues.

### Introduction

Stable isotope analysis techniques provide insight about food webs in both terrestrial and aquatic ecosystems. Nitrogen isotope ratios ( $\delta^{15}\text{N}$ ) have been used to estimate the trophic position of consumers in food webs, as  $\delta^{15}\text{N}$  generally increases by an average of 3.4‰ with each rise in trophic level (Managawa & Wada, 1984; Owens 1987; Cabana & Rasmussen, 1994). Carbon isotope ratios ( $\delta^{13}\text{C}$ ) generally do not change significantly with differences in trophic position, but instead provide insight into the food sources of consumers (DeNiro & Epstein, 1978; France, 1996).

Although the most direct way to measure the isotopic base level of a system's food web is to measure the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of primary producers, primary producers in aquatic systems have large

temporal variations, complicating their use for measuring base levels over long periods (Cabana & Rasmussen, 1996; Vander Zanden & Rasmussen, 1999; Post, 2002). In addition, baseline  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  are also spatially variable in aquatic and terrestrial systems. For example, McKinney et al. (1999) found that the base isotopic signature of  $\delta^{15}\text{N}$  in six lakes within a 40 km radius varied from 4.9 to 11.9‰. Vander Zanden & Rasmussen (1999) also found that the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of primary consumers in Canadian lakes varied significantly as a function of lake habitat ( $\delta^{15}\text{N}$  ranged from -2 to 9‰ and  $\delta^{13}\text{C}$  from -27 to -30‰). Within a stream ecosystem, Finlay (1999) found that herbivore  $\delta^{13}\text{C}$  (a proxy for algal  $\delta^{13}\text{C}$ ) varied from -18 to -26‰ between low and high velocity (pool and riffle) habitats along the same river channel.

This seasonal and spatial variability highlights the importance of understanding controls on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic baselines for food web studies, and motivates further development of methods for measuring baseline characteristics (Cabana & Rasmussen, 1996; Vander Zanden & Rasmussen, 1999; Finlay et al., 2002; Post, 2002). Baselines provide a benchmark for both food chain length ( $\delta^{15}\text{N}$ ), and diet tracers ( $\delta^{13}\text{C}$ ) related to bottom-up mass transfer. Without baseline estimates of  $\delta^{15}\text{N}$  it is difficult to ascertain if the  $\delta^{15}\text{N}$  signature of an organism reflects trophic position or a variation of inputs to the ecosystem. Additionally, without baseline  $\delta^{13}\text{C}$  measurements, it is difficult to interpret an organism's  $\delta^{13}\text{C}$  signature in terms of diet.

Because isotopes of short-lived primary consumers are sensitive to seasonal and spatial differences, they generally provide insufficient baseline information for studies that require quantitative estimates of trophic position or comparison across multiple ecosystems. As an alternative, long-lived primary consumers, such as freshwater mussels, can provide information about baseline conditions that is better averaged over time and space (Cabana & Rasmussen, 1996; McKinney et al., 1999; McKinney et al., 2002; Post, 2002).

Mussels have been used in a variety of studies to estimate baseline conditions in lentic habitats (lakes) (Cabana & Rasmussen, 1996), but few studies have used mussels to estimate baseline conditions in stream ecosystems. Freshwater mussels are potentially very useful for measuring isotopic baselines in rivers. As long-lived, nearly stationary organisms that filter-feed from flowing river water, mussels build tissue that has the potential to both temporally and spatially average variations in the isotopic signatures of primary production and decomposition. As primary consumers with a soft tissue turnover time of approximately one year (Raikow & Hamilton, 2001), mussels are considered good indicators of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  baselines in pelagic food webs in lakes (McKinney et al., 1999; Vander Zanden & Rasmussen, 1999; Post, 2002). Because baseline isotopic issues are more complex in rivers than in lakes, we concentrated our studies in a system where numerous isotopic studies have been conducted to spatially delineate the energy sources of the river food web (Finlay et al., 1999; Finlay, 2001; Finlay et al., 2002).

## Objectives

The purpose of this study is to examine several aspects of riverine mussel isotope signatures that are relevant to their use as baseline indicators. We analyze and compare  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures in the freshwater mussel, *Margaritifera falcata*, in two watersheds in the Northern California Coast Ranges where we have conducted extensive measurements and analyses of mussel populations (Howard & Cuffey, 2003; Howard, 2004). The watersheds are different in certain respects, both in terms of land use history and hydro/geomorphology, and we wish to ascertain whether the baseline isotopic signatures differ accordingly. In addition, the study explores whether the isotopic signatures vary spatially with position in the river (low vs. high velocity areas), in response to known variations of  $\delta^{13}\text{C}$  of primary producers and algivorous insects (Finlay et al., 1999). Finally, we document an unexpected relationship between mussel ages and isotopic composition of their tissues, a relationship that can impact baseline assessments.

## Study sites

Thirty-four *M. falcata* were collected from the South Fork Eel, and 13 from the North Fork Navarro rivers (Fig. 1). Although similar in hydrologic regime, native vegetation type and geologic setting, the two study rivers have different land use histories. The South Fork Eel site is located within the Angelo Coast Range Reserve, part of the University of California Natural Reserve System, a relatively pristine watershed of old growth Douglas fir (*Pseudotsuga menziesii*) and redwood (*Sequoia sempervirens*) forest with only minor human modifications (Table 1). The area contained within this study site totals 15,000 ha, extending from the headwaters to the confluence with Ten Mile Creek. Some logging occurred in the drainage basin from the early to mid 1900s, but since 1950 the 5000-ha Angelo Reserve has been protected as a conservation site (Johnson, 1979). This study area is the site of nearly two decades of ecological research (Power, 1990a–c, 1991).

The North Fork Navarro River site totals 19,000 hectares, and includes the entire North

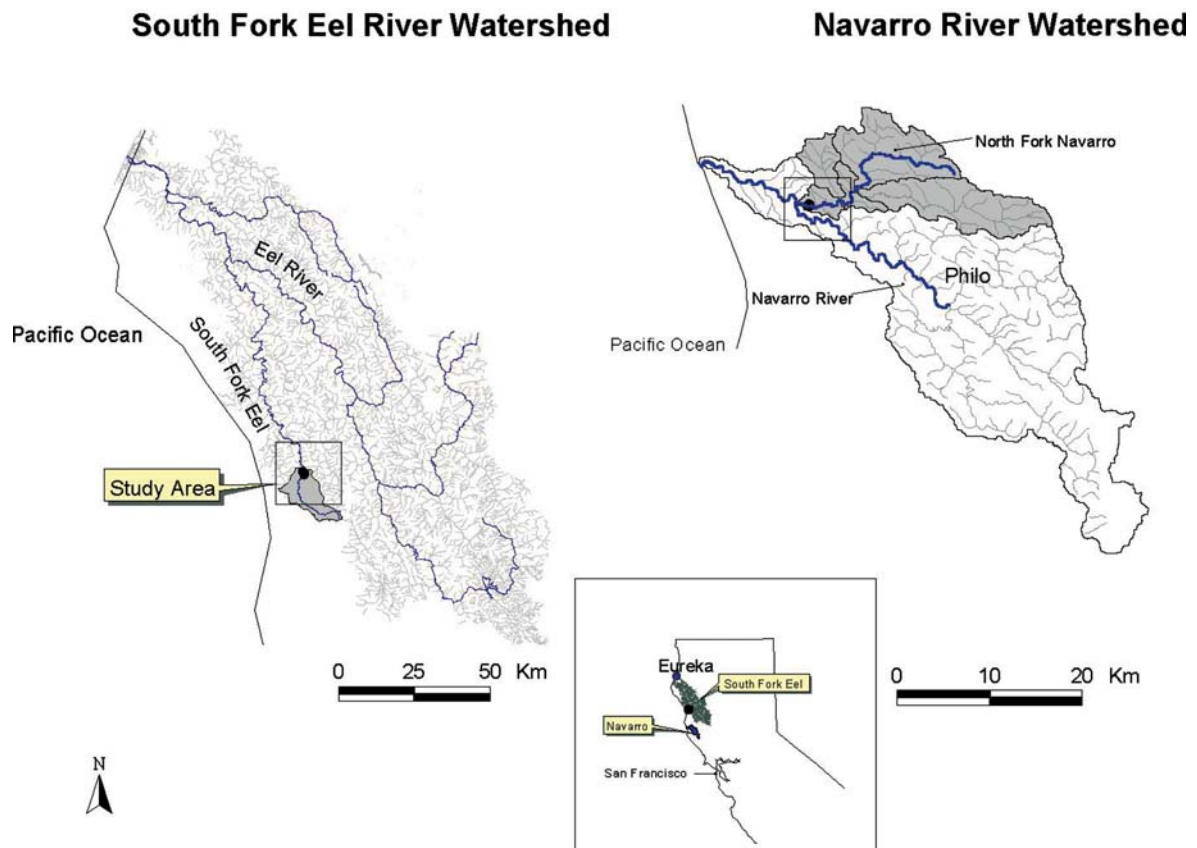


Figure 1. Study area of the South Fork Eel and North Fork Navarro rivers. The black dots indicate the areas of the channels where *M. falcata* were collected for this study. Shaded area of watershed corresponds to landuse statistics listed in Table 1.

Fork Navarro River drainage from the headwaters to the confluence with the Navarro mainstem. In contrast to the South Fork Eel River site, logging and agriculture (livestock grazing, viticulture, and

orchard style fruit cultivation) have been very active in the Navarro River watershed since the mid-1800s. In addition, State Highway 128 was built adjacent to the river between 1933–1963 and

Table 1. Landuse calculated for the North Fork Navarro and South Fork Eel rivers from the USGS Geographic Information Retrieval and Analysis System (GIRAS) landuse system based on available aerial photography from the 1990s

	North Fork Navarro		South Fork Eel	
	Hectares	% of total	Hectares	% of total
Cropland and pasture	293	2	0	0
Deciduous forest	644	3	0	0
Evergreen forest	17,364	90	11,469	77
Herbaceous rangeland	196	1	413	3
Industrial	0	0	56	0
Mixed rangeland	0	0	363	2
Shrub and brush rangeland	718	4	2699	18
Totals	19,215	100	14,999	100

closely follows the river through the Anderson Valley. This rich agricultural valley is currently undergoing extensive conversion from orchard to vineyard. Since the early 1970s, the Nork Fork Navarro River has suffered severe declines in fish populations (Adams, 2001). The North Fork Navarro River is currently listed with the Environmental Protection Agency for exceeding sediment and temperature thresholds necessary for viable fish populations.

## Methods

### *Field collections*

*M. falcata* were collected from four sites along the South Fork Eel River and one site on the North Fork Navarro River in August and September 2002. The South Fork Eel sites are located within a ~20 m-wide channel reach with ~20% forest canopy cover. The North Fork Navarro River site is within a ~10 m-wide channel reach with ~60% canopy cover. The forest cover on adjacent hillslopes in both rivers is similar (redwood, douglas fir forest). Individuals were collected by hand while wading in water approximately 30–60 cm deep. Collection sites were selected based on previous work conducted in the two rivers that extensively documented mussel abundance and habitat character (Howard & Cuffey, 2003). From the South Fork Eel, we collected mussels from two low and two high velocity (run) habitats (pool velocities <0.05 m/s; run velocities between 0.05 and 0.5 m/s). In the North Fork Navarro mussels were collected from only one site due to the small total population there. Although ideally we would have collected mussels from multiple sites in the North Fork Navarro, only one site in this system contained a high enough abundance (>300) whereby sacrificing individuals would not compromise the population. Care was taken to ensure that the variety of specimen sizes collected from each site spanned the size distribution of the local populations. Shell lengths were measured to the nearest 0.5 mm using dial calipers from the umbo to the ventral margin, following the vector of maximum growth. Wet weights (shell and tissue) were measured to the nearest 0.1-g using a field balance.

### *Mussel ages*

Mussel ages were calculated by counting annual rings on shell thin sections (Howard, 2004). Shells were cut with a diamond saw from the umbo region to the ventral margin, and mounted on glass slides with epoxy. Thin sections were then cut, sanded with successively smaller grit sizes, and polished with fine lapidary powders of 3 and 1  $\mu\text{m}$  – diameter grit sizes.

Annual rings were counted and growth between years measured under a compound microscope with 10 $\times$  and 40 $\times$  magnification. On these thin sections, growth increments appear as light bands separated by dark narrow lines. The dark lines mark winter seasons when little shell growth occurs. The counting of rings is facilitated by the fact that growth increments are continuous from the prismatic layer to the external nacreous sublayer. The increments from initial growth are thick, and become progressively thinner as the mussel matures. To ensure accuracy, growth increment counting was repeated five times for each thin section.

### *Lab processing*

#### *Drying and processing mussel tissue*

Mussel samples were allowed to evacuate gut contents in potable tap water for 48 h. The mussels were then rinsed, frozen, and stored at  $-5\text{ }^{\circ}\text{C}$  until further processing. Whole mussel tissues were dried at  $40\text{ }^{\circ}\text{C}$  for 72 h in a drying oven, and ground into a fine powder using an SPEX Certiprep 6800 Freezer Mill.

#### *Lipid extraction*

Because lipids are known to be relatively depleted in  $\delta^{13}\text{C}$  (Parker, 1964; Kling et al., 1992), we removed the lipids from the mussel tissue samples with a 2:1 methylene glycol and methanol mixture, and analyzed the residual fraction (Stewart, 2001). Dry sample material from individual mussels was placed in tin capsules for subsequent element and stable isotope analyses.

#### *$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements*

Stable carbon and nitrogen isotope ratios, and carbon and nitrogen content, were measured on a

Europa Continuous Flow Mass Spectrometer interfaced with a Carlo Erba Elemental Analyzer. Analyses were conducted at the Center for Stable Isotope Biogeochemistry, U.C. Berkeley ([ib.berkeley.edu/groups/biogeochemistry/index.html](http://ib.berkeley.edu/groups/biogeochemistry/index.html)). Stable isotope ratios are reported in delta ( $\delta$ ) notation, which represents the parts per thousand ( $\text{‰}$ ) deviation of the sample from an internationally recognized standard material.  $\delta^{13}\text{C}$  values are reported in reference to the Pee Dee Belemnite standard;  $\delta^{15}\text{N}$  values are reported in reference to atmospheric nitrogen. Measurements of variable weight standards were used to correct for any non-linear response to variation in sample size. Ten percent of the mussel tissue samples were analyzed in duplicate.

#### Statistical analysis

Differences in mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic values between high and low velocity sites within the South Fork Eel River (intra-river variability), and between the South Fork Eel and Navarro rivers (inter-river variability) were statistically assessed using Student's *t*-test. The relationship between mussel age and stable isotopic values was quantified using linear regression, and the significance of the slope being different from zero was tested using the analysis of variance (ANOVA) procedure (Zar, 1999).

## Results and discussion

### Intra-river variability – South Fork Eel

#### $\delta^{13}\text{C}$ Isotopic Signature

The  $\delta^{13}\text{C}$  signatures of mussels collected from pool and run habitats within the South Fork Eel are not statistically different at  $p = 0.05$  (Student's *t*-test) (Fig. 2). The mean  $\delta^{13}\text{C}$  of mussel tissue from the two pool sites is  $-22.89\text{‰}$ , whereas from the riffle sites it is  $-22.81\text{‰}$ . Previous stable isotope studies of aquatic food web structure and carbon dynamics on the South Fork Eel River have highlighted the spatial variability along the river. Finlay et al. (1999, 2002) found that the  $\delta^{13}\text{C}$  of epilithic algae and invertebrate herbivores collected from pool habitats were 8–9 $\text{‰}$  less negative

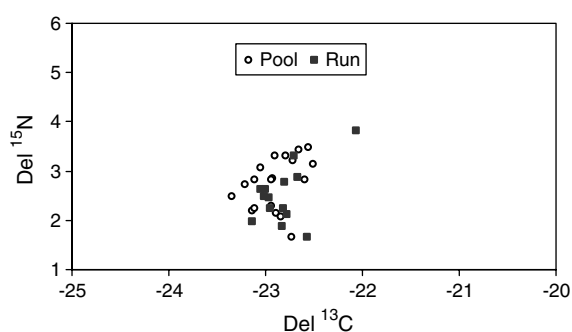


Figure 2. *Margaritifera falcata*  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope signatures for pool (low velocity, open circles) and run (high velocity, squares) sites within the South Fork Eel River.

than the  $\delta^{13}\text{C}$  of epilithic algae and invertebrate herbivores from adjacent riffle habitats (mean  $\delta^{13}\text{C}$  in pools is  $\sim -18\text{‰}$ , riffles  $\sim -25\text{‰}$ , terrestrial detritus  $\sim -28\text{‰}$ ). Furthermore, Finlay et al. (1999) found that these differences persisted throughout the high winter and low summer baseflows, although the differences were much less pronounced in winter.

Given this observed variability, our results demonstrate that freshwater mussels do contain a spatially averaged measure of the stable isotope signatures of the river system. Of course this average is weighted according to preferred diet sources. Several scenarios of diet sources are possible and it is difficult to ascertain what mix of food sources mussels are utilizing. The  $\delta^{13}\text{C}$  signature of mussels is intermediate between the riffle and pool habitats, and suggests that mussels may be consuming food sources derived from a variety of instream habitats. Alternatively, these results may indicate that mussels are consuming a mix of terrestrial and pool derived carbon sources. However, given that algal productivity is highest in this system during the summer months, the time when mussels are consuming but when terrestrial sources are low, it seems likely that instream food sources dominate the mussels' diet.

Indeed other researchers have found evidence for selective feeding by mussels (Raikow & Hamilton, 2001), and it is quite possible that mussel  $\delta^{13}\text{C}$  values preferentially reflect the algal component of seston in general. This will need to be further investigated in efforts to establish methodology for mussels as baseline indicators. As Finlay (2001) demonstrated in the South Fork Eel, the  $\delta^{13}\text{C}$  values

of collectors, filter feeders and predators in small headwater streams closely match terrestrial detritus. But as watershed size increases, the three functional feeder groups reflect algal carbon sources of  $\delta^{13}\text{C}$ . In addition, in most free flowing river systems the seston contribution to food webs increase with river size (Whiles & Dodds, 2002; Paul & Hall, 2002). These suggest that mussels are most useful as baseline indicators in larger or seston rich streams, and may be less useful in headwater streams.

#### $\delta^{15}\text{N}$ isotopic signature

There is no significant difference in the  $\delta^{15}\text{N}$  isotopic signatures of mussels collected from pool or run habitats in the South Fork Eel (Student's *t*-test,  $p = 0.05$ ) (Fig. 2). The mean  $\delta^{15}\text{N}$  is 2.5‰ the range is 1.6 to 3.8‰. We have also sampled algae and seston at a variety of places within the river. For these the  $\delta^{15}\text{N}$  averages  $-0.9$  to  $-1$ ‰, consistent with a one trophic level difference between primary production and mussels.

#### Inter-river variability – South Fork Eel and Navarro rivers

##### $\delta^{13}\text{C}$ Isotopic Signature

The difference in means of stable isotope measurements (both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of the Navarro River samples compared to those from the South Fork Eel River were statistically significantly at  $p = 0.05$  (Student's *t*-test) (Fig. 3). The mean  $\delta^{13}\text{C}$  signature for Navarro river mussels was approximately 6‰ more negative than the mean  $\delta^{13}\text{C}$  of South Fork Eel river samples. The mean  $\delta^{13}\text{C}$  of mussels collected from the Navarro is  $\sim -28$ ‰ (Fig. 3), which is similar to values for terrestrial detritus (Finlay et al.,

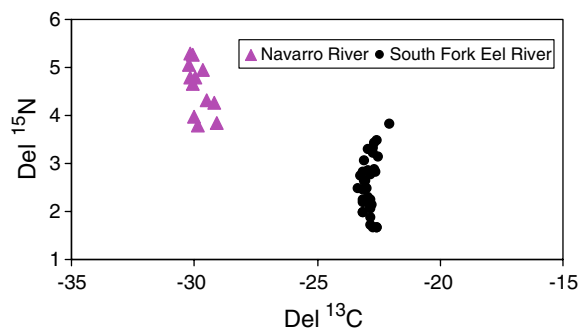


Figure 3. Freshwater mussel  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope signatures for South Fork Eel (circles) and Navarro (triangles) river sites.

2002). This suggests that mussels in this area of the North Fork Navarro may be obtaining their energy from terrestrially derived sources instead of instream sources as in the South Fork Eel.

The differences in  $\delta^{13}\text{C}$  values may be attributed to the canopy cover in each study area, and thus the composition of particulate matter in the water column. In the South Fork Eel River, the channel is wide with little vegetation and instream energy sources dominate (algal blooms). In contrast, the Navarro channel has a dense forest canopy cover, allowing terrestrial carbon inputs to dominate seston even in summer, the time when mussels are feeding.

#### $\delta^{15}\text{N}$ isotopic signature

In the Navarro, the mean  $\delta^{15}\text{N}$  signature is 2‰ heavier than in the South Fork Eel (4.6 in the Navarro compared to 2.6 in the South Fork Eel), ranging from 3.8 to 5.3‰ (Fig. 3). The difference in mean  $\delta^{15}\text{N}$  signature values between watersheds is the equivalent of approximately one half of a trophic level. This difference between rivers may reflect differences in source nitrogen input, differences in utilization and fractionation of nitrogen by mussels, or differences in feeding patterns of mussels. Because the mussels are the same species, and located within the same seasonal hydrologic regime, the first hypothesis seems most plausible. Agriculture (Table 1), and particularly the current conversion from orchard to vineyards, may be causing increased nitrogen flux to the river associated with synthetic fertilizer use as has been documented in other studies (Cabana & Rasmussen, 1996; Fry & Allen, 2003). As documented by other researchers  $\delta^{15}\text{N}$  values of terrestrial vegetation are generally lower than those of algae (Mambelli, personal communication), and fine particulate organic matter (FPOM) (Christian et al., 2004). Therefore, differences in terrestrially and instream derived food sources alone does not explain the higher  $\delta^{15}\text{N}$  values of mussels from the Navarro River, and in fact would generate a  $\delta^{15}\text{N}$  difference opposite to that measured here.

#### Intra-river variability related to age

Within both systems, the  $\delta^{15}\text{N}$  values vary by approximately 2‰ (Figs. 3 and 4).  $\delta^{13}\text{C}$  values did

not show this same variability (Figs. 3 and 4). We have found an explanation for part of this variability, which is that there is a relationship between  $\delta^{15}\text{N}$  and mussel age. As Fig. 5 shows, the correlation between  $\delta^{15}\text{N}$  and age is moderately strong ( $r^2 = 0.58$ ,  $p = 0.004$  for the Navarro;  $r^2 = 0.64$ ,  $p = 0.001$  for the South Fork Eel populations).

Although the mechanism for this relationship is not known, one possible explanation is that *M. falcata* are gape-limited by the size of their incurrent siphons. Older and larger *M. falcata* individuals, with larger inhalant siphons, may eat organisms that feed higher on the food chain, such as drifting invertebrates. This has been documented in another filter feeder, the zebra mussel (MacIsaac et al., 1995). In that study, researchers showed a significant relationship between shell length (a proxy for organism age) and the diameter of the inhalant siphon. That study demonstrated that larger zebra mussels were capable of sup-

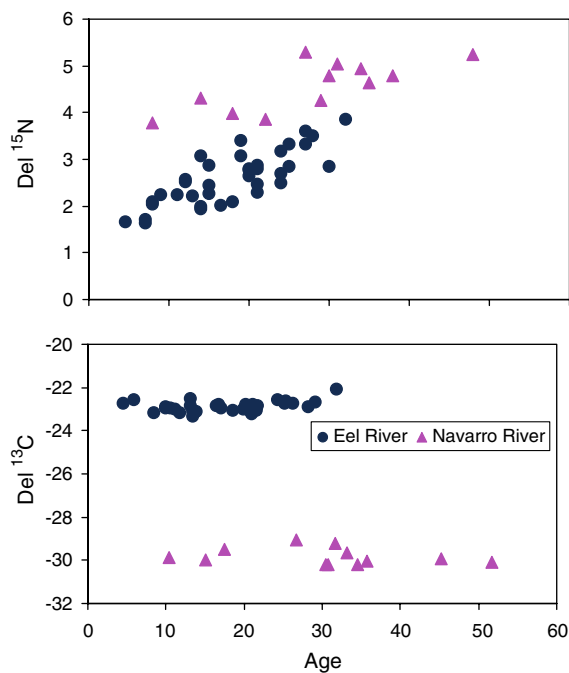


Figure 4. (a) Relationship between age of mussel and tissue  $\delta^{15}\text{N}$  for the South Fork Eel River (circles,  $r^2 = 0.64$ ,  $p = 0.0001$ ), and Navarro River (triangles,  $r^2 = 0.58$ ,  $p = 0.004$ ). (b) Relationship between age of mussel and tissue  $\delta^{13}\text{C}$  for the South Fork Eel River (circles,  $r^2 = 0.05$ ,  $p = 0.19$ ), and Navarro River (triangles,  $r^2 = 0.05$ ,  $p = 0.47$ ). Statistical results are for linear regression models.

pressing zooplankton abundance, primarily rotifers.

## Conclusion

Our examination of stable isotopic ratios of mussels from within river reaches of varying velocity and between rivers (South Fork Eel and Navarro rivers) led to several conclusions:

1. There is no significant difference in the  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  signatures of mussels collected from pool and run habitats within the South Fork Eel. The mean value of mussel  $\delta^{13}\text{C}$  and its absence of variability imply that mussel tissues provide a spatially integrated measure of the stable isotope signature of the river system. This value will be weighted according to preferential diet sources for mussels, which introduces a substantial complexity in interpreting mussel isotopes as baseline indicators.
2. Between the two rivers studied, there are significant differences in both the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic signatures of mussels. On average, the  $\delta^{13}\text{C}$  signature of the South Fork Eel mussels is  $\sim 6\%$  heavier than those in the Navarro River. This reflects instream/algal vs. terrestrially derived food sources in the South Fork Eel and Navarro, respectively. In addition, the  $\delta^{15}\text{N}$  of mussels in the South Fork Eel is on average  $\sim 2\%$  lighter than the Navarro, which suggests different source inputs perhaps resulting from agriculture practices.
3. In both the South Fork Eel and Navarro populations,  $\delta^{15}\text{N}$  demonstrably increases with age of mussel, with the  $\delta^{15}\text{N}$  values varying by approximately  $2\%$  as a function of age. Therefore, it is important to consider the specimen's age when using mussels to infer baseline values in aquatic environments.
4. As filter feeders, mussels are well suited to establish baseline conditions of food webs that utilize seston at the first trophic level. Because the seston contribution to river food webs increases with stream size, mussels may be most useful as baseline indicators in large and/or seston rich rivers rather than small river systems where CPOM most likely dominates food sources.

## Acknowledgements

We are grateful to Paul Brooks, Stefania Mambelli, and Todd Dawson for assistance with isotopic analysis of mussel tissue, for use of their laboratories, and helpful comments on earlier drafts. This research was supported by Grant 24924 from the California Center for Water Resources.

## References

- Adams, H., 2001. What is the fate of the Navarro? The Eel River Reporter 4: 3–6.
- Cabana, G. & J. B. Rasmussen, 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372: 255–257.
- Cabana, G. & J. B. Rasmussen, 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Sciences* 93: 10844–10847.
- Christian, A. D., B. N. Smith, D. J. Berg, J. C. Smoot, and R. H. Findlay, 2004. Trophic position and potential food sources of 2 species of unionid bivalves (Mollusca: Unionidae) in 2 small Ohio streams. *Journal of the North American Benthological Society* 23: 101–113.
- DeNiro, M. J. & S. Epstein, 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42: 495–506.
- Finlay, J. C., M. E. Power & G. Cabana, 1999. Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. *Limnology and Oceanography* 44: 1198–1203.
- Finlay, J. C., 2001. Stable carbon isotope ratios of river biota: implications for carbon flow in lotic food webs. *Ecology* 82: 1052–1064.
- Finlay, J. C., S. Khandwala & M. E. Power, 2002. Spatial scales of carbon flow in a river food web. *Ecology* 83: 1845–1859.
- France, R. L., 1996. Absence or masking of metabolic fractionations of  $^{13}\text{C}$  in a freshwater benthic food web. *Freshwater Biology* 36: 1–6.
- Fry, B. and Y. C. Allen, 2003. Stable isotopes in zebra mussels as bioindicators of river-watershed linkages. *River Research and Applications* 19: 683–696.
- Howard, J. K., 2004. Freshwater mussels in California Coast Range rivers: abiotic controls and functional role. PhD dissertation, University of California, Berkeley.
- Howard, J. K. & K. M. Cuffey, 2003. Freshwater mussels in a California North Coast Range river: occurrence, distribution, and controls. *Journal of The North American Benthological Society* 22: 63–77.
- Johnson, S. G., 1979. The land-use history of the Coast Range Preserve, Mendocino County, Masters' Thesis. San Francisco State University, California.
- Kling, G. W., B. Fry & W. J. O'Brien, 1992. Stable isotopes and planktonic trophic structure in Arctic lakes. *Ecology* 73: 561–566.
- MacIsaac, H. J., C. J. Lonner & J. H. Leach, 1995. Suppression of microzooplankton by zebra mussels – importance of mussel size. *Freshwater Biology* 34: 379–387.
- Managawa, M. & E. Wada, 1984. Stepwise enrichment of  $^{15}\text{N}$  along food chains: further evidence and the relation between  $\delta^{15}\text{N}$  and animal age. *Geochimica et Cosmochimica Acta* 48: 1135–1140.
- McKinney, R. A., J. L. Lake, M. Allen & S. Ryba, 1999. Spatial variability in mussels used to assess base level nitrogen isotope ratio in freshwater ecosystems. *Hydrobiologia* 412: 17–24.
- McKinney, R. A., J. L. Lake & M. A. Charpentier, 2002. Using mussel isotope ratios to assess anthropogenic nitrogen inputs to freshwater ecosystems. *Environmental Monitoring and Assessment* 74: 167–192.
- Owens, N. J. P., 1987. Natural variations in N-15 in the marine environment. *Advances in Marine Biology* 24: 389–451.
- Parker, P. L., 1964. The biogeochemistry of the stable isotopes of carbon in a marine bay. *Geochimica et Cosmochimica Acta* 28: 1155–1164.
- Paul, M. J. & R. O. Hall, 2002. Particle transport and transient storage along a stream-size gradient in the Hubbard Brook Experimental Forest. *Journal of The North American Benthological Society* 21:195–205.
- Post, D. M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703–718.
- Power, M. E., 1991. Shifts in the effects of tuft-weaving midges on filamentous algae. *American Midland Naturalist* 125: 275–285.
- Power, M. E., 1990c. Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. *Ecology* 71: 897–904.
- Power, M. E., 1990b. Benthic turfs vs. floating mats of algae in river food webs. *Oikos* 58: 67–79.
- Power, M. E., 1990a. Effects of fish in river food webs. *Science* 250: 811–814.
- Raikow, D. F. & S. K. Hamilton, 2001. Bivalve diets in a midwestern U.S. stream: a stable isotope enrichment study. *Limnology and Oceanography* 46: 514–522.
- Stewart, R., 2001. Lipid extraction for isotope analysis. United States Geological Survey.
- Vander Zanden, M. J. & J. B. Rasmussen, 1999. Primary consumer  $^{13}\text{C}$  and  $^{15}\text{N}$  and the trophic position of aquatic consumers. *Ecology* 80(4): 1395–1404.
- Whiles, M. R. & W. K. Dodds, 2002. Relationships between stream size, suspended particles, and filter-feeding macroinvertebrates in a Great Plains drainage network. *Journal of Environmental Quality* 31: 1589–1600.
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.