CHARACTERIZATION OF ENERGY AND POTENTIAL CONTAMINANT PATHWAYS IN SUBARCTIC ESTUARINE HABITATS: ECOLOGY OF TIDAL FLAT COMMUNITIES OF THE COPPER RIVER DELTA, ALASKA

Final Report to the Prince William Sound Regional Citizens Advisory Council

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Summary

Vast expanses of intertidal sand/mudflats serve as a critical link in the food web of nearshore biological communities in many coastal areas of Alaska. The rich abundance of benthic invertebrates residing within the sediments of intertidal flats and the large network of subtidal channels that bisect these flats provide a significant prey resource for numerous species of fish, crabs, birds, and marine mammals. One of the largest expanses of intertidal mud/sand flats occurs in the Copper River Delta and southeastern Prince William Sound (Orca Inlet). The estuarine nature of this system results in mixing of nutritional sources from riverine, estuarine and marine ecosystems, which fuel secondary productivity. Here, we investigated linkages between riverine and oceanic influences and the nutritional baseline for mudflat food webs in the Copper River Delta and Hartney Bay in Southeastern Prince William Sound, using stable isotopes of naturally occurring carbon (C) and nitrogen (N), which are both essential elements for growth. Isotopes of C and N have been used in numerous studies of marine and freshwater food webs. The proportion of N that occurs as ^{15}N versus ^{14}N, the latter being the more common form, gives information on source of N (marine derived N is enriched in ^{15}N compared to terrestrial derived N) and trophic position (higher ^{15}N are associated with organisms feeding higher in the food web). The ratio of C isotopes is useful in determining the source of energy because the ratio is conserved to a higher degree than N as energy is assimilated up the food web. In general, terrestrial primary producers have lower δ^{13}C values than primary producers in the marine environment. Differences among δ^{13}C (a calculation that relates the relative concentration of ^{13}C to the more common ^{12}C) and δ^{15}N (a calculation that relates the relative concentration of ^{15}N to the more common ^{14}N) were determined for several portions of the food web: particulate organic matter (organic material in the water column), sediment organic material (includes detritus and microalgae that feed benthic invertebrates), macroalagae, benthic invertebrates, and demersal (bottom-feeding) fishes.

Variations in δ^{13}C and δ^{15}N were detected at each trophic level of the food web and tended to indicate differences in nutrient sources between the more oceanic influenced Hartney Bay mud flat community and the mudflat community of the riverine influenced Copper River Delta. Differences among δ^{13}C and δ^{15}N values of suspended particulate organic matter from the oceanic-influenced Hartney Bay versus those collected in the Delta were consistent with variation in intertidal sediment values at the two sites (HB: $\delta^{13}C = -15$ and $\delta^{15}N = 6.5‰$ vs. CRD $\delta^{13}C = –24$ and $\delta^{15}N = 0.3‰$). Thus, the two systems differ in sources of particulate organic matter, which radiate up the food web at both sites. For benthic invertebrates (the clam *Macoma balthica*, one species of marine worm, and two species of amphipods) on the Copper River, δ^{13}C was much heavier (i.e, less negative δ^{13}C ratio) than particulate organic matter and sediment values. This pattern indicates that (1) terrestrial nutritional sources (i.e., organic material suspended in the water column and deposited on the sediment surface), while important for the benthic community on mudflat community on the Delta, are apparently augmented by oceanic derived inputs of nutrients for benthic communities on mudflats and (2) deposit feeders preferentially assimilated benthic microalgal sources as opposed to water column material. The strong reliance of these intertidal food webs on benthic as opposed to free- floating primary producers suggests the sensitivity of these waters to oil spill effects that can have long residence times in the surficial sediments. Stable carbon and nitrogen isotopes of intertidal benthos, demersal fishes, and potential food sources also indicated that the oceanic site (HB) was enriched, suggesting a greater input of oceanic nutrients than terrestrial (riverine) derived. With regard to potential contaminant release, a critical element in future monitoring of the Copper River Delta mudflats is the collection of baseline contaminant levels in sediments and *Macoma balthica*.

Keywords: bivalves, crustaceans, demersal fish, macrophytoplankton, nutritional source, particulate organic matter (POM), primary producers, stable isotope ratio (SIR),

Introduction

The unique interface of land, sea and air characteristic of intertidal habitats serves to promote high biological productivity within the intertidal and adjacent subtidal habitats. The land provides a substratum for the occupation of intertidal organisms, the seawater facilitates import and export of nutrients and larvae, and the air provides a medium for passage of solar energy and a source of physical stress (Peterson 2001). In addition to high levels of internal energy production (e.g., benthic microalgae and macroalgae, Pinckney and Zingmark 1993), many intertidal areas receive substantial energy subsidies because they serve as the interface between the oceanic photic zone and coastal river runoff (Raffaelli and Hawkins 1996). Whereas tidal energy and wind subsidize the intertidal zone with planktonic foods produced in the photic zone, freshwater runoff injects inorganic nutrients from terrestrial communities (Nixon 1986, Peterson 2001). This mix of nutrients coupled with high solar energy levels results in high primary production that is readily transferred to higher trophic levels through a sizeable benthic invertebrate prey base.

Many of the factors that contribute to the high biological productivity also result in heightened sensitivity of intertidal systems to natural and anthropogenic change. Short and long-term changes in sea level resulting from annual or decadal changes in atmospheric pressure and global warming result in changes in tidal inundation, which can lead to changes in the location of the land-sea interface. Changes in habitat boundaries may also result from subsidence and/or elevation of flat areas resulting from tectonic activity (e.g. the 1964 Good Friday Earthquake, Plafker 1990). Spatial and temporal variation in coastal circulation patterns or upwelling/ downwelling intensity can result in shifts in temperature regime or delivery of oceanic nutrients and significantly modify species distributions, primary production and trophic transfer (Andersen and Piatt 1999, Zheng and Kruse 2000, Clark and Hare 2002). Patterns of freshwater inputs, which affect both nutrient levels and ambient salinities, can vary in response to climatic oscillation that in turn effect precipitation levels and transgression or regression of glaciers. Adding to the heightened sensitivity of intertidal habitats is the fact that these areas are often the repository for contaminants released in coastal areas (Short and Heintz 1997, Short et al. 1999, Peterson 2001). As with changes caused by variation in natural forcings, a host of direct and indirect effects may result from acute and chronic exposure to contaminants that ultimately modify the complex ecological network of a coastal system (Peterson 2001). The detection of these effects is often difficult and requires long-term field research that incorporates a web of ecological interactions (Underwood and Peterson 1984, Underwood 1992).

Determining how food web dynamics of coastal systems are influenced by the mix of oceanic and riverine nutrients is critical given our dependence on the resources provided by these nearshore systems. Intertidal mudflats are important as an energy source for coastal food webs . Mudflats have been characterized as important foraging grounds that support higher rates of trophic transfer and subsequent secondary production. For example, mudflats provide foraging habitat for migratory shorebirds, as well as for demersal fish and crustaceans. All of these species forage on infaunal and epifaunal macroinvertebrates which in turn are directly linked to primary production. Investigation of which nutritional sources mediate food web dynamics within estuarine habitats such as mudflats will enhance our ability to determine what is driving secondary production in coastal systems.

Stable isotope ratios (SIR's) have been successfully used to trace the transfer of organic matter from different sources through aquatic food webs (Darnaude et al 2004), provided that the SIR's of the sources are different. In particular, $\delta^{15}N$ data can provide information about trophic position as the $\delta^{15}N$ of the consumer is often 2-5‰ heavier than the prey (Minagawa and Wada 1984). A real concern when undertaking comparative sites studies is that the isotopic signal of the baseline of nutritional support is constant . When comparing systems having different hydrodynamic influences, this case is often violated. By using a uniform indicator organism, however, we can exploit these differences to better understand the coupling between benthic and pelagic nutrient sources.

Plant and algal isotopic contents are dependent on the concentration and isotopic signatures of assimilated dissolved substrates. Carbon stable isotope values of primary producers will vary depending on factors that affect growth rate such as water temperature, irradiance, and nutrients (concentration and isotopic content; MacLeod and Barton 1998). Though much less data exist, $\delta^{15}N$ values undoubtedly depend on similar factors. Regionally (within 200 km), we expect organismal SIR values to change mostly as a function of season (i.e., irradiance and corresponding changes in temperature and runoff). Isotopic differences between sites which are exposed to similar climatic conditions suggest a difference in the regional supply of initial substrates (Alexander et al. 1996). In general, terrestrial primary producers have lower $\delta^{13}C$ values than primary producers in the marine environment (Darnaude et al. 2004).

In this study, we investigated the nutritional sources for two benthic food webs in intertidal mudflats of southcentral Alaska that differ in productivity and species diversity. Specifically our study had two objectives: (1) compare the principal sources of energy for the two benthic food webs (Copper River Delta and Hartney Bay), including detritus, macroalgae, benthic microalgae and phytoplankton and (2) examine C and N isotope ratios for key invertebrate prey species and predator species at the two sites during fall (September-October) to determine the fate of these nutrient sources. Our goal was to characterize the flow of energy through a food web so as to provide valuable insight into the potential pathways of contaminants, if they were released into the nearshore environment.

Methods

Study Site

One of the largest expanses of intertidal and shallow subtidal flats occurs at the terminus of the Copper River. Large expanses of mudflats also occur throughout Cook Inlet and Controller Bay with more modest expanses of intertidal mudflats scattered throughout small embayments along the Alaska coastline. Located at the eastern edge of Prince William Sound near the port of Cordova, the vast 500-km^2 mudflats of the Copper River Delta stretch almost continuously for 80 km from Egg Island to Grass Island and from Kokinhenik Island to Softuk Bar (Fig. 1). Extensive mudflats also occur in Orca Inlet, a large bay in southeast Prince William

Sound influenced by the Copper River. The vast network of intertidal mudflats and shallow sloughs that meander through the flats serve as a critical connection between the Gulf of Alaska and the vast expanse of freshwater wetlands, rivers, lakes and glaciers. The tidal flats of the Copper River Delta provide foraging habitat for a variety of migratory (shorebirds and salmonid fish) and resident demersal species (e.g., Dungeness crabs, Pacific halibut, lingcod). Over 4 million shorebirds, the largest spring concentration of shorebirds in the Western Hemisphere (Isleib 1979, Bishop et al. 2000) visit the Copper River flats annually between late April and mid-May on their way to breeding grounds in western Alaska. The Delta also supports a substantial commercial and subsistence fishery that is an integral element of the local economy: some 549 gillnet fishers commercially harvest 3 species of salmon in the estuarine and nearshore waters. The tidal flats serve as both an entry and exit corridor for these salmon. The fish migrate through the delta first as smolts (i.e., late-stage juveniles) leaving freshwater habitats and then again as adults attempting to return to the same freshwater habitats to spawn (Christensen et al., 2000).

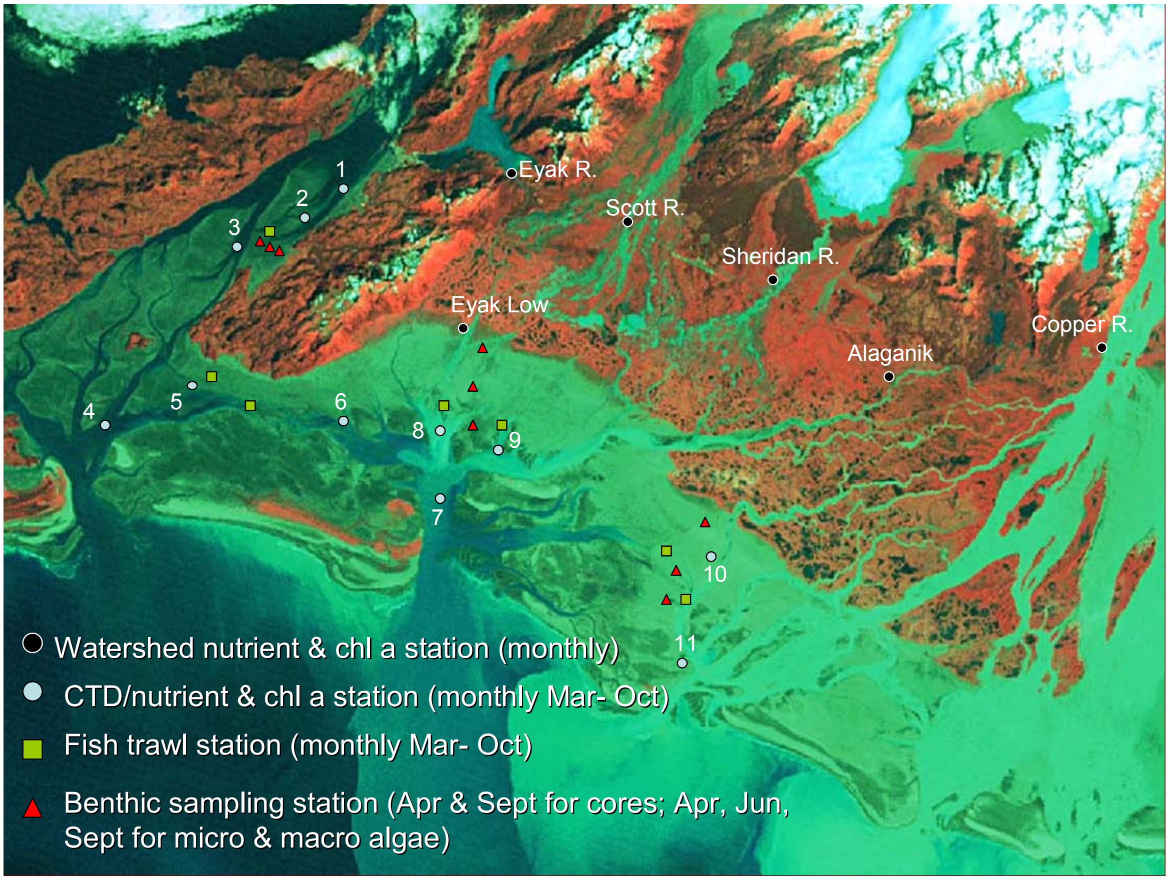


Figure 1. Aerial image of the Copper River Delta and Southeastern Prince William Sound indicating stations for the Copper River Delta study led by M. Bishop and S. Powers. Samples for stable isotopes were collected at benthic stations (triangles) and fish trawl stations (squares) in September 20033.

Climate for the Copper River Delta is maritime with approximately 2,350 mm of precipitation annually with heaviest input during September and October . Salinity varies both temporally in relation to discharges from rivers and sloughs as well as spatially with distance from the Gulf of Alaska, Prince William Sound and the plume of the Copper River (Fig. 1). Salinities ranged in Orca Inlet from 33 ppt (April) to 21 ppt (July). Salinities at both Eyak and Pete Dahl generally increase with distance from the shoreline and proximity to the Gulf of Alaska. From late April to August extensive snow and ice melt in the Copper and Eyak River drainage basins results in elevated river discharge (up to 5,300 m^3 s^{-1} for the Copper River during this period, Brabets, 1997). The large discharge of freshwater within the semi-enclosed area of the Copper River Delta results in system-wide lowering of salinities particularly near the high and mid tide elevations in the Eyak and Pete Dahl areas. Salinity ranges from 2 to 10 psu from mid-May to mid-September with lowest salinities found at the Pete Dahl sites. During periods of reduced river discharge (mid-September to early May) salinity ranges from 15 to 24 psu at these same mid and high tide plots, and from 17 to 28 psu at low tide plots (Powers et al. 2002, 2005).

Physical/chemical parameters known to influence infaunal populations (i.e., sediment grain size, salinity, tidal inundation) varied among sampling areas and among tidal elevations within sampling areas. Sediments at the high and mid tide plots of all three areas were dominated by silts and clays with very little sand present (< 5 % at Eyak and Pete Dahl and < 10 % at Hartney Bay). Sediments at the low tide plots were coarser with 20 – 35 % sand (i.e. particles retained on a 63 µm sieve) at Eyak and Pete Dahl and 80-90 % at Hartney Bay (Powers et al. 2002, Powers and Bishop unpubl. data). Water clarity within the study area is influenced by the high suspended sediment load of river discharge (average suspended sediment load of the Copper River is 69 million metric tons yr^{-1}) in the area as well as storm-induced resuspension of silt/clay sediments. Turbidity during summer months is lowest, typically < 20 nephlometer turbidity units (NTU), at Hartney Bay, where phytoplankton and some suspended sediment contribute to turbidity levels. Turbidity increases with proximity to the Copper River. Turbidity is highest, between 100 and 400 NTU's at high and mid tide plots near Pete Dahl and decreases to between 50 and 100 NTU at Pete Dahl low sites (Powers et al. 2005).

Sample Collection and Preparation

Benthic invertebrates and primary producers were collected on intertidal mudflats using 15-cm diameter core samples collected in September 2003. All collections were made at low tide when the mudflats were exposed. Three locations were sampled: Hartney Bay (HB), an oceanic-influenced site in Orca Inlet (southeastern Prince William Sound) and on the Copper River Delta near the outflow of the Eyak River (EY) and Pete Dahl Slough (PD), respectively (Fig. 1). Within each site, sampling plots were established at high, mid and low tidal elevations, with tidal elevation generally decreasing with distance from the shoreline. For the Eyak and Pete Dahl areas, three 10-m^2 plots, spaced > 200m apart, were established per tidal elevation, for a total of nine sampling plots per site. Tidal elevations (based on MLLW) ranged from + 2.8 to 3.2 m for high, + 1.8 to 2.0 m for mid, and + 0.8 to 1.2 m for low tide plots with the lower and higher values for each tidal elevation corresponding to Eyak and Pete Dahl respectively. High-tide plots were located within 0.5 km of the shoreline (defined by a distinct break between silt/clay sediments and marsh grasses), mid-tide plots were 1.5 to 2.0 km and low-tide plots 3.0 to 4.0 km from the shoreline. At Hartney Bay in Orca Inlet, three 10-m^2 plots, separated by 250 m, were established at: high (+ 3.5 m MLLW), mid (+ 2.9 m MLLW) and low (+ 0.9 m MLLW). Multiple whole organisms (3-10) of dominant species were combined for both invertebrates and macroalgae from each plot, except in rare case when not available. A composite SIR value for sediment particulate organic matter and benthic microalgae was measured. For invertebrates, tissue was separated from calcareous hard parts to avoid biasing carbon isotope values.

A description of the benthic invertebrate community can be found in Powers et al. (2002, 2004). Briefly, the infaunal community of the Copper River Delta is a low diversity system (4 species account for > 95 % of the biomass) dominated by the deposit feeding bivalve *Macoma balthica*. The suspension feeding bivalve *Mya arenaria*, the corophid amphipod *Corophium salmonis* and the polychaete *Eteone* account for the majority of the remaining benthic animals on the Delta. Diversity of infaunal organisms is greater at Hartney Bay, however, all four species are also found in high abundance at Hartney Bay. Diversity of macroalgae follows a similar pattern with only one species green algae commonly found on the Delta, *Enteromopha sp.*, and one species of brown filamentous algae. Multiple species of brown and green algae are found at Hartney Bay including *Enteromopha* sp.

Fish and mobile invertebrates were collected using a 4-m wide otter trawl from six sites (west to east: Hartney Bay, Eel Grass [EG], West Hump [WH], Seal Bar [SB], Johnson Hole [JH], Racetrack [RT], and Pete Dahl [PD; Fig. 1). Specifically, we analyzed stable isotope ratios of four species of demersal fishes and two mobile crustaceans: starry flounder (*Platichthys stellatus*), Pacific staghorn sculpin *(Leptocottus armatus*), Pacific halibut (*Hippoglossus stenolepsis*), lingcod (*Ophidon elongatus*), Dungeness crab (*Cancer magister*), *Crangon* spp. shrimp. For fish samples, we sampled the upper anterior muscle tissue exclusive of skin. Unlike for birds and mammals, isotopic analysis of muscle and liver tissues of fish suggests that turnover rates are similar for different tissue types in fish . All tissue samples were immediately frozen (-20ºC) upon dissection, then freeze-dried. Dried tissue was homogenized first with a coffee grinder and then with mortar and pestle as needed. Ground biota samples were left unacidified, weighed (~1 mg) into tin boats (5x7mm, Costech Analytica). Sediment and seston filters were acidified prior to SIR analysis for removal of inorganic carbon.

Stable carbon and nitrogen isotope ratios were measured on a isotope ratio mass spectrometer (Finnigan MAT 252, Thermo Finnigan, Bremen, Germany) interfaced in continuous flow to a elemental analyzer (Carlo-Erba NA 1500, CE Instruments, Milan, Italy). Carbon and nitrogen isotope ratios are expressed in the delta notation (δX) and calculated in units of parts per thousand (‰) as follows:

$$\delta X = [(R_{sample}-R_{std})/R_{std}] \times 10^3 \quad (1)$$

where X is ^{13}C or ^{15}N and R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio in sample or standard. Throughout this study, $\delta^{13}C$ and $\delta^{15}N$ refer to the isotopic values of particulate organic matter (POM).

Working gas standards for the mass spectrometer were calibrated using isotope ratio reference gases for CO_2 (UNC-452C, $\delta^{13}C$ = -3.4‰ vs. PDB) and N_2 (UNC-12N, $\delta^{15}N$ = -3.2‰ vs. air) manufactured by OzTech Trading Corporation (Dallas, TX). The primary solid phase reference materials were ammonium sulfate ($(NH_4)_2SO_4$, NIST Reference 8550) and sodium bicarbonate ($NaHCO_3$, provided by Neal Blair, North Carolina State University, Raleigh, NC).

Daily calibration curves were conducted using a secondary standard (acetanilide, Eastman-Kodak). Referencing strategies are detailed in Clesceri in accordance with Werner and Brand .

Data Analysis

Differences in mean $\delta^{13}C$ and $\delta^{15}N$ of the main organic matter reservoirs (i.e., sediments) and primary producers were tested using two-way analysis of variance (ANOVA) using site and elevation as factors. *Macoma balthica* was the only macrobenthic organism distributed widely enough to analyze the effects of site and elevation on isotope values using separate two-way ANOVAs for $\delta^{13}C$ and $\delta^{15}N$. The effect of site on isotope values of the polychaete *Eteone longa* were analyzed using one-way ANOVAs. The amphipod *Corophium salmonis* was collected at both the oceanic- (HB) and riverine-influenced sites (EY and PD). However, the samples from Eyak and Pete Dahl were pooled to account for low densities at these sites and then analyzed with separate one-way ANOVAs.

Pacific staghorn sculpin, shrimp, and starry flounder were the most abundant species captured in bottom trawl samples (except EG and WH sites). Therefore, we analyzed the effect of site (all except EG and WH sites) and species (Pacific staghorn sculpin, shrimp, and starry flounder) on each stable isotope ratio with separate two-way ANOVAs. The effect of site on stable isotope ratios of Pacific halibut was analyzed using separate one-way ANOVAs. Homogeneity of variance was first tested prior to each analysis using Cochran's test when balanced, and normality was tested using Bartlett's test for unbalanced datasets (Underwood 1981). Data violating these assumptions were transformed using arcsine transformations and reanalyzed. Student-Newman-Keuls (SNK) post-hoc tests were utilized to compare means of significant interactions and main effects for balanced analyses, whereas Tukey's post-hoc tests were utilized for unbalanced datasets (Day and Quinn 1989). Finally, to assess the relationship between demersal fish length and stable isotopes, regression analyses were performed.

Results

Isotopic Signature of Potential Food Sources and Organic Matter Reservoirs

The dominant macroalga, *Enteromorpha*, was found at all sites except at the Eyak mid-tide elevation. Average $\delta^{13}C$ values of *Enteromorpha* ranged from –19.6 (PD) to –13.0‰ (HB). Average $\delta^{15}N$ values had a smaller range, 4.9 [EY] to 9.2‰ (HB; Table 1). Both the $\delta^{13}C$ and $\delta^{15}N$ values of *Enteromorpha* were significantly different ($p = 0.003$ and $p < 0.0001$, respectively) among the three sites (one-way ANOVA, Table 2). Post-hoc analyses indicated that Pete Dahl had lighter $\delta^{13}C$ values (-17.7 ± 0.9‰ SE) than either Hartney Bay or Eyak, which had equivalent values (~ -14‰). *Enteromorpha* was more enriched in ^{15}N at Hartney Bay (8.9 ± 0.24‰ SE) than the Copper River Delta sites (~5.3‰). Pete Dahl was the only site where *Enteromorpha* was found at enough stations to test the effect of elevation. Neither $\delta^{13}C$ ($p = 0.08$) nor $\delta^{15}N$ ($p = 0.23$) signals varied significantly with elevation, however, there was a slight trend of reduced *Enteromorpha* $\delta^{13}C$ values at lower elevations (Table 1).

Table 1. Stable carbon and nitrogen isotopes and elemental analysis (mean and 1 SE) for *Enteromorpha* and surficial sediments (0-2 cm depth) at the high (H), mid (M), and low (L) tidal

elevations of Hartney Bay (HB), Eyak (EY), and Pete Dahl (PD) sites. % OC = % organic carbon, % TN = % total nitrogen.

Sample	Location	Elevation	n	δ^{13}C	*se*	δ^{15}N	*se*	%OC	*se*	%TN	*se*
Algae *Enteromporha*	B	H	2	-13.07	*0.92*	9.17	*0.27*	35.25	1.38	2.60	0.12
		M	3	-13.89	*0.87*	8.87	*0.54*	28.50	2.61	2.99	0.34
		L	1	-13.05	*na*	8.99	*na*	39.73	na	4.51	na
	EY	H	2	-13.80	*1.15*	5.46	*0.07*	25.62	1.03	2.71	0.47
		M	na	na	*na*	na	*na*	*na*	*na*	*na*	na
		L	1	-15.14	*na*	4.94	*na*	34.94	na	2.41	na
	PD	H	3	-15.09	*1.39*	5.50	*0.24*	35.90	0.46	2.10	0.03
		M	3	-18.41	*1.21*	5.33	*0.12*	30.87	1.34	2.22	0.03
		L	3	-19.66	*0.92*	5.05	*0.10*	26.93	1.85	1.96	0.18
S Sediment (0-2 cm)	HB	H	3	-22.54	*0.45*	4.74	*0.52*	0.33	0.01	0.03	0.00
		M	3	-23.13	*0.45*	4.57	*0.28*	0.46	0.07	0.04	0.00
		L	3	-20.11	*0.18*	4.49	*0.06*	0.18	0.01	0.03	0.00
	EY	H	3	-22.32	*0.11*	2.57	*0.12*	0.37	0.02	0.04	0.00
		M	3	-22.89	*0.04*	2.64	*0.05*	0.29	0.01	0.03	0.00
		L	3	fill in	fill in	fill in	fill in	fill in			
	PD	H	3	-21.67	*0.13*	3.59	*0.31*	0.21	0.01	0.02	0.00
		M	3	-22.22	*0.60*	1.85	*0.31*	0.22	0.01	0.02	0.00
		L	3	-21.06	*0.21*	1.54	*0.08*	0.12	0.02	0.01	0.00

Table 2. ANOVA results on the effect of site (Hartney Bay, Eyak, and Pete Dahl on stable isotope ratios of the macroalga *Enteromorpha*.

		DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
δ^{13}C	Site	2	75.756	37.878	8.661	0.003	17.322	0.941
	Residual	16	69.975	4.373				
δ^{15}N	Site	2	57.506	28.753	136.272	< 0.001	272.544	1.000
	Residual	16	3.376	0.211				

For surficial sediments, both elevation and site influenced δ^{15}N, percent organic C and percent total N. Elevation was the only source of significant variation in surficial sediments for δ^{13}C (Table 3). Percent organic C and total N ranged from 0.12 and 0.01% to 0.46 and 0.07%, respectively (Table 1). At all sites, organic carbon was greatly reduced at the lower tidal elevations. Sediment δ^{13}C values (two-way ANOVA, $p = 0.62$) did not differ among sites, but were heavier at lower tidal elevations (mean of -20.7 ± 0.237‰) than at mid and high tidal elevations (~-22‰; $p = 0.001$, Table 3). ANOVA revealed that δ^{15}N sediment signals varied among sites ($p < 0.0001$), primarily a result of lighter δ^{15}N sediment signals (~2.3‰; SNK test) on the Copper River Delta (EY and PD) than at HB (4.60 ± 0.30‰). Variation in sediment δ^{15}N values was greatest at PD, whereas δ^{13}C signals from these sediments were indistinguishable (Fig. 2).

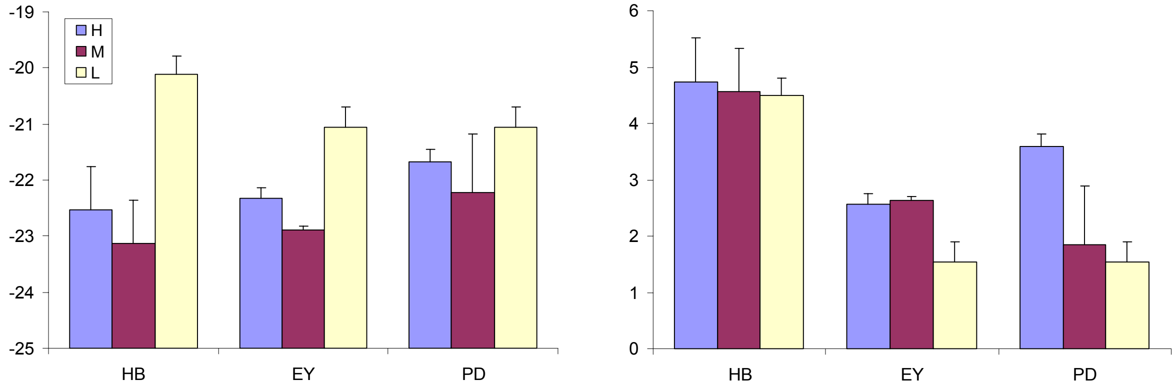
Table 3. ANOVA results on the effects of site (Hartney Bay, Eyak, and Pete Dahl) and tidal elevation (high, mid, low) for stable isotope ratios, percent organic carbon (% OC), and percent total nitrogen (%TN) of surficial (0-2 cm) sediments.

		DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
$\delta^{13}C$	site	2	0.885	0.442	0.486	0.623	0.972	0.115
	elevation	2	19.230	9.615	10.560	0.001	21.121	0.979
	site * elevation	4	3.485	0.871	0.957	0.455	3.828	0.239
	Residual	18	16.388	0.910				
$\delta^{15}N$	site	2	32.166	16.083	28.156	<0.001	56.312	1.000
	elevation	2	5.611	2.805	4.912	0.020	9.823	0.736
	site * elevation	4	4.166	1.041	1.823	0.168	7.293	0.440
	Residual	18	10.282	0.571				
%OC	site	2	0.087	0.043	6.708	0.0067	13.416	0.871
	elevation	2	0.174	0.087	13.461	0.0003	26.921	0.996
	site * elevation	4	0.05	0.012	1.924	0.15	7.697	0.462
	Residual	18	0.117	0.006				
%TN	site	2	0.001	0.001	15.1	0.0001	30.2	0.998
	elevation	2	0.001	0.001	17.2	<.0001	34.4	1
	site * elevation	4	0.001	1.65E-04	4.45	0.0112	17.8	0.863
	Residual	18	0.001	3.70E-05				

Isotopic Signatures of Macrobenthos

The isotopic signatures of the benthic organisms at each site differed significantly for both $\delta^{13}C$ and $\delta^{15}N$ values (Table 4). A greater diversity of benthic organisms was found at Hartney Bay, the oceanic-influenced site, than at the two Copper River Delta sites (EY or PD). Benthos at Hartney Bay included: the amphipod *Corophium salmonis*; bivalves *Macoma balthica*, *Mya arenaria*, and *Mytilus trossulus*; and polychaetes *Nephtys* sp. and *Eteone longa*. At Hartney Bay, filter and deposit feeders (*Mya*, *Mytilus*, *Corophium*, and *Macoma*) had the lowest $\delta^{15}N$ values (9.4 to 10.7‰) of the macrobenthos. In contrast, polychaetes contained significantly higher $\delta^{15}N$ values of 13-15‰ ($p < 0.05$, SNK). At Hartney Bay, $\delta^{13}C$ values of *Mya* and *Mytilus* were significantly lighter (by ~3‰, $p < 0.05$, SNK) than the remaining deposit feeders or polychaetes (~ -13‰, Fig. 3).

Figure 2. Mean (+ 1 standard error) values for $\delta^{13}C$ (a) and $\delta^{15}N$ (b) values (+1 SE) in surficial sediments by site and elevation (high, mid, and low tidal elevation). HB = Hartney Bay, EY = Eyak, PD = Pete Dahl. .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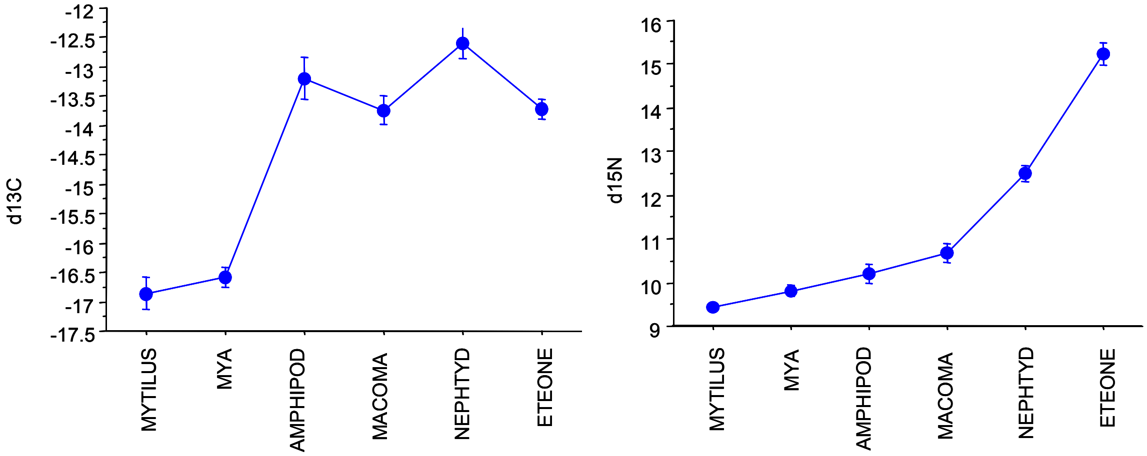


Table 4. Values (mean and 1 SE) for stable carbon and nitrogen isotopes, % organic carbon (OC), and % total nitrogen (TC) for macrobenthic consumers at Hartney Bay (HB) and two sites on the Copper River Delta: Eyak (EY) and Pete Dahl (PD).

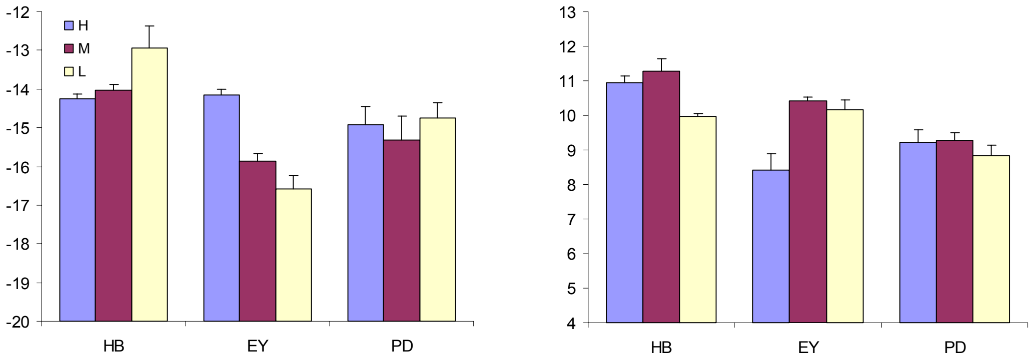
Sample	n	Location	$\delta^{13}C$	$\delta^{15}N$	%OC	%TN	C/N
Total	77						
Deposit Feeders							
Macoma balthica	10	HB	-13.74	10.68	40.35	9.17	4.42
			0.24	0.21	0.41	0.20	0.11
	9	EY	-15.54	9.66	37.69	8.61	4.37
			0.38	0.35	1.35	0.21	0.10
	9	PD	-15.00	9.11	34.98	8.35	4.19
			0.27	0.17	1.27	0.26	0.09
Corophium salmonis	5	HB	-13.19	10.20	37.92	7.70	4.94
			0.37	0.21	0.47	0.21	0.12
	1	EY	-14.76	6.12	37.19	7.34	5.07
			na	na	na	na	na
	6	PD	-14.44	6.53	38.43	7.85	4.90
			0.21	0.29	0.51	0.15	0.07
Filter Feeders							
Mytilus trossulus	5	HB	-16.85	9.43	40.70	8.32	5.31
			0.26	0.09	1.15	1.14	0.81
Mya arenaria	6	HB	-16.94	9.59	40.20	10.56	3.81
			0.42	0.27	0.82	0.22	0.06
Polychaete							
Eteone longa	6	HB	-13.71	15.23	46.47	12.09	3.85
			0.17	0.26	0.64	0.26	0.07
	5	EY	-16.00	13.63	45.12	11.30	4.00
			0.24	0.39	0.54	0.13	0.04
	6	PD	-14.10	13.01	43.72	11.32	3.86
			0.29	0.22	0.32	0.19	0.04
Nephtys	9	HB	-12.60	12.50	35.64	9.71	3.68
			0.20	0.12	0.52	0.31	0.07

Table 5. ANOVA results on the effects of site (Hartney Bay, Eyak, and Pete Dahl) and tidal elevation (high, mid, low) on stable isotope ratios of *Macoma balthica*.

		DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
δ^{13}C	Site	2	15.384	7.692	16.967	<0.001	33.935	0.999
	Elevation	2	1.768	0.884	1.949	0.171	3.899	0.340
	Site * Elevation	4	11.025	2.756	6.080	0.003	24.320	0.956
	Residual	18	8.160	0.453				
δ^{15}N	Site	2	12.233	6.117	24.539	<0.001	49.078	1.000
	Elevation	2	3.243	1.621	6.505	0.008	13.009	0.860
	Site * Elevation	4	7.032	1.758	7.052	0.001	28.210	0.979
	Residual	18	4.487	0.249				

Site location and elevation influenced isotope values for bivalve *Macoma balthica*, the dominant infaunal species. *Macoma* δ^{13}C and δ^{15}N values differed with site, elevation and the interaction of site and elevation (Table 5). In general, δ^{13}C values were lower (indicating more terrestrial inputs of nutrients) at Eyak and Pete Dahl than Hartney Bay. δ^{13}C values of *Macoma* at the Pete Dahl site did not differ among tidal elevation. δ^{13}C values of *Macoma* at the Eyak site differed among tidal elevation such that values at high tide plots were greater than mid and low tidal plots. However, as elevation increased and tidal inundation subsequently decreased, δ^{13}C values of *Macoma* approached –14.5‰ at all high tide plots regardless of site (Fig. 3). The δ^{15}N values of *Macoma* at EY and HB were similar at the low and mid elevations (mean ~10‰). Conversely, PD *Macoma* δ^{15}N values, which were uniform ($P > 0.05$, SNK tests) at all tidal elevations, were significantly lighter (~8.5‰) at the low and mid elevations than at HB or EY. In contrast to the lower elevations, Eyak δ^{15}N values for *Macoma* at the high elevation were equal to Pete Dahl (~8-9‰) while *Macoma* collected at the high elevation plots at HB (~11‰) were greater than those at the two sites on the Delta. This overall pattern of lower δ^{15}N at Pete Dahl and to a lesser extent Eyak than Hartney Bay reflects the more oceanic and less terrestrial input of nutrients into Hartney Bay.

Figure 3. Mean δ^{13}C (a) and δ^{15}N (b) variability (+1 SE) of *Macoma balthica* at Hartney Bay (HB), Eyak (EY), and Pete Dahl (PD) and tidal elevation (high, mid, low).



Stable isotope ratios of both the polychaete *Eteone longa* and the amphipod *Corophium salmonis* generally varied among sites. ANOVA revealed that both δ^{13}C and δ^{15}N values of *Eteone* differed among sites ($p = 0.0004$ and $p < 0.0001$, respectively), and that both isotope values at Hartney Bay were heavier than either PD or EY. Again this pattern is indicative of a more oceanic and less terrestrial input of nutrients into Hartney Bay compared to Eyak and Pete Dahl. Site also significantly influenced both δ^{13}C and δ^{15}N values of *Corophium* ($p = 0.004$ and $p < 0.0001$, respectively). *Corophium* contained lighter δ^{13}C values in the Delta or riverine influenced sites (-14.6 ± 0.2‰) than at HB (-13.2 ± 0.4‰). Variation between the sites was greater for δ^{15}N than the δ^{13}C (~4 vs. 1.4‰, respectively). In particular, δ^{15}N values of *Corophium* were higher at the oceanic-influenced site (10.2 ± 0.2‰) than on the Delta (6.4 ± 0.2‰).

Table 6. Stable carbon and nitrogen isotopes (mean and 1 SE) for demersal fish and mobile crustaceans at six trawl sites.

Sample	n	Location	δ^{13}C (‰)	SE	δ^{15}N (‰)	SE
Total	*102*	*mean*	*-15.54*		*12.55*	
		se	*0.23*		*0.19*	
Starry Flounder	5	HB	-13.59	1.46	13.18	0.26
	5	SB	-15.87	1.41	12.39	0.77
	5	JH	-19.02	1.47	12.13	2.16
	6	RT	-15.68	1.27	12.50	1.07
	5	PD	-15.52	1.49	12.87	0.92
Pacific Staghorn Sculpin	5	HB	-15.08	1.46	14.22	0.81
	5	SB	-15.64	1.41	13.85	0.31
	5	JH	-15.10	1.44	12.85	0.70
	5	RT	-16.23	1.38	12.94	1.33
	5	PD	-14.03	1.49	11.52	0.67
Pacific Halibut	1	HB	-14.72	na	13.70	na
	3	EG	-15.01	0.52	13.53	0.19
	4	WH	-15.49	0.18	12.21	0.15
	1	SB	-15.95	na	13.02	na
	2	JH	-15.66	0.23	13.13	0.32
Dungeness Crab	5	SB	-15.28	0.41	11.64	0.14
	1	JH	-14.87	na	11.40	na
	5	RT	-15.15	0.25	11.50	0.22
	5	PD	-15.75	0.20	11.58	0.11
Crangon Shrimp	3	HB	-13.51	0.16	12.29	0.03
	5	SB	-15.69	0.53	11.86	0.35
	5	JH	-16.39	0.49	11.63	0.72
	4	RT	-15.91	0.69	12.14	0.37
	5	PD	-15.70	0.61	10.93	0.50
Lingcod	2	WH	-17.65	0.59	14.625	0.47

Stable Isotopic Composition of Demersal Fishes

Site location generally influenced stable isotope values of demersal fishes and mobile crustaceans collected from bottom trawls. Average $\delta^{13}C$ data of these species ranged from –19.0 (starry flounder, JH) to – 13.5‰ (crangon shrimp, HB) with an average $\delta^{13}C$ of –15.5 ± 0.2‰ SE (Table 6). Variation in $\delta^{15}N$ values was substantially less than that of $\delta^{13}C$ values (3.3‰ vs. 5.5‰, respectively). The minimum average $\delta^{15}N$ value was 10.93‰ (*Crangon* shrimp, PD) and the maximum was 14.2‰ (Pacific staghorn sculpin, HB; mean 12.5 ± 0.2‰ SE). This pattern reflects trophic position in that *Crangon* shrimp consume Enteromorpha spp. or other algae species, whereas Pacific staghorn sculpin feed on shrimp, clam and small fishes. Linear regression analysis showed no relationship between $\delta^{13}C$ or $\delta^{15}N$ values of fish tissue with body length ($r^2 < 0.05$) indicating that no major diet shifts with increasing length of fish were present.

The effect of site significantly influenced $\delta^{13}C$ values of the three most common trawl species (sculpin, starry flounder, shrimp; $p = 0.017$, Table 7). Post-hoc analyses (SNK) revealed heavier $\delta^{13}C$ values at HB (~-13‰) than the other sites (< -15‰). ANOVA results for $\delta^{15}N$ values of these three fish were significant for species ($p = 0.0002$) and site ($p = 0.003$), but not the site*species interaction. Pacific staghorn sculpin, *Crangon* shrimp, and starry flounder $\delta^{15}N$ values were only distinguishable (SNK) at HB. Pacific staghorn sculpin was the only trawl species that showed within-site variation. Sculpin captured at PD contained lighter $\delta^{15}N$ values (~11‰) than those collected at HB or SB (13-14‰), whereas the $\delta^{13}C$ values of these same tissues did not differ (mean –15.21 ± 0.37‰).

Table 7. ANOVA results of the effects of species (Pacific staghorn sculpin, *Crangon* shrimp, and starry flounder) and site on stable isotope ratios of demersal fishes and mobile crustaceans captured in bottom trawl samples.

		DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
$\delta^{13}C$	Species	2	6.703	3.351	0.840	0.437	1.681	0.181
	Site	4	52.669	13.167	3.302	0.017	13.207	0.812
	Species * Site	8	50.022	6.253	1.568	0.155	12.543	0.635
	Residual	57	227.321	3.988				
$\delta^{15}N$	Species	2	19.896	9.948	9.795	0.0002	19.589	0.986
	Site	4	18.540	4.635	4.563	0.003	18.253	0.934
	Species * Site	8	10.510	1.314	1.293	0.265	10.347	0.534
	Residual	57	57.894	1.016				

The commercially relevant fishes, Pacific halibut and lingcod, were less abundant than Pacific staghorn sculpin, starry flounder, and shrimp in trawl samples. Pacific halibut ranging in size from 84 to 261 mm were found at the 5 of the 8 trawl sites. Site did not significantly affect halibut $\delta^{13}C$ (mean –15.4 ± 0.2‰ SE, $p = 0.48$) or $\delta^{15}N$ (mean 13.0 ± 0.2‰ SE, $p = 0.12$) values. Only two lingcod were found during the study, both at the WH site. Mean $\delta^{13}C$ values were slightly lighter than the other species (-17.7± 0.6‰), whereas $\delta^{15}N$ values of lingcod were substantially heavier (14.6 ± 0.5‰) than the remaining demersal species. Dungeness crabs were not found at HB but were collected at PD, JH, and SB with δ^{13}C and δ^{15}N means of –15.4 ± 0.1‰ SE and 11.6 ± 0.6‰ SE, respectively.

Discussion

Previous (Powers et al. 2002, 2005) and ongoing research on the estuarine portion of the Copper River Delta have documented a highly productive benthic community residing within the tidal flat community. The majority of benthic biomass is composed of one species, *Macoma balthica.* These small clams serve as a conduit that transfers benthic primary production and organic matter to higher trophic levels, e.g. fish, crabs, and shorebirds. In effort to better understand this flow of energy, and potentially the flow of contaminants, we compared nutritional sources and trophic interactions at three sites with differing degrees of oceanic and fresh water influence. Hartney Bay (Orca Inlet) is most heavily influenced by tidal flow from Prince William Sound and to a lesser extent the Gulf of Alaska (GOA). Small freshwater inflow from stream into Hartney Bay is likely minor in comparison to its tidal influence from Prince William Sound. In contrast, the influx of fresh water on the Delta from the series of rivers and feeder sloughs dampens the impact of the GOA. In particular, the Pete Dahl site was influenced most heavily by the Copper River, while Eyak received primary inflow from the smaller Eyak River. Molar N to P ratios indicate P limitation in the Eyak and Copper Rivers (> 20), while surface water N to P ratios at in the estuarine and oceanic waters indicate N limitation throughout most of the year. Lower N/P ratios (i.e. increased phosphorous concentrations) at the surface water stations suggest that GOA waters are at least partly influencing all three sites (Powers and Bishop, unpublished data).

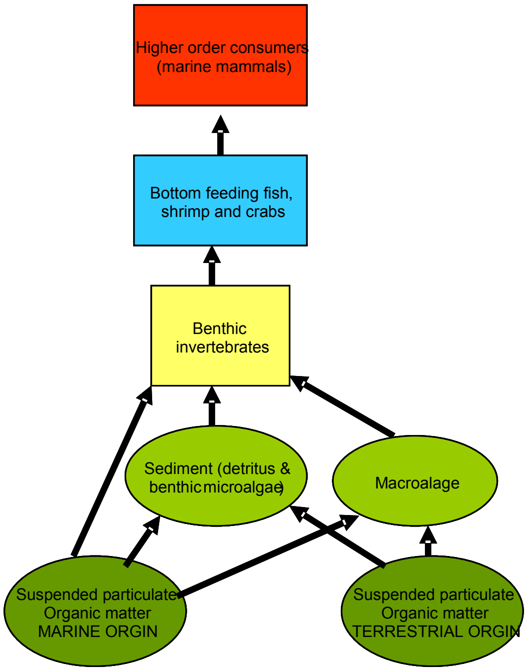


Figure 4. Conceptual diagram of energy flow in intertidal mudflats of the Copper River Delta. The relative importance of the two suspended particulate organic matter pools differ among sites.

Particulate organic matter available for incorporation into the food web is typically derived from the dominant primary producer within each site (Harrigan et al. 1989). In subtidal Alaskan bays, demersal fishes and benthic consumers either directly or indirectly derive their C and N from phytoplankton and submerged macrophytes such as kelp. Several additional sources of organic matter such as attached macroalgae and microphytobenthos become important in intertidal mudflats, like those of the Copper River Delta and Orca Inlet (Fig. 4). Unlike the southeastern United States, these mudflats do not have high densities of *Spartina* salt marsh grasses, as seen in some European intertidal systems . In freshwater-influenced mudflats, particulate terrestrial matter and dissolved exudates from decaying organic matter in the watershed can also be important (Darnaude et al.

2004). The SIR values of consumers from our Delta mudflat sites (δ^{13}C values averaging –15‰) were substantially heavier than those at the higher salinity Hartney Bay (δ^{13}C values from –18 to –24‰). Therefore, our results suggest that the Delta mudflats are primarily supported by benthic macroalgae, microalgae, and terrestrial exudates.

Sediments from stations in the Copper River Delta (Eyak and Pete Dahl) exhibit δ^{15}N values near 0‰, that is, about 6‰ lower than from HB. Low sediment δ^{15}N values on the Delta probably represent an increased abundance of nitrogen derived from N_2 fixing sources. Riverine phytoplankton is likely a minor source of organic matter to the Delta as no phytoplankton was found in feeder sloughs and rivers which were laden with glacial till . Symbiotic N_2 fixation by Sitka alder (*Alnus crispa*) is an important N subsidy to riparian vegetation in Alaskan forests, as evidenced by the low δ^{15}N values (-1.5‰) of foliage samples . The uptake of δ^{15}N-depleted DIN by bacteria or benthic microalgae that do not fix N_2 (e.g. Diatoms) would result in low δ^{15}N values of the sediment-microbial aggregate. Given the higher δ^{13}C values of *Enteromorpha* found at PD than HB and EY ($p = 0.003$), *Enteromorpha* ostensibly assimilates a lighter source of dissolved inorganic carbon (DIC), feasibly fed by the Copper River, if we assume similar concentrations of DIC at all sites. The lower δ^{15}N signals in *Enteromorpha* on the Delta (EY and PD) compared to Hartney Bay is also indicative of greater terrestrial input .

Although it is difficult to determine both trophic structure and food sources when the stable isotopic baseline of primary producers vary, our study suggests that these differences can be exploited to identify trophic interactions within coastal food webs. *Macoma* δ^{13}C was substantially higher (> 9‰) than its presumed detrital food source of surficial sediments at the Pete Dahl site. Conversely, a typical C trophic fractionation factor of about 1‰ was found between *Macoma* and sediments in HB. This divergent behavior of the same organism (*Macoma*) between two sites suggests a preferential selection of a particular food source in the more terrestrially influenced Delta than the oceanic HB site. Fiddler crabs selectively assimilate specific particles of sediments, which could account for large (i.e., up to 6‰) disparities in δ^{13}C from their presumed food source . Preferential selection of algal components of sediments and/or an avoidance of terrestrially sourced organics in estuarine systems has also been observed previously for polychaetes , oysters , and zooplankton . In the marine dominated estuaries, the use of river derived C is viewed as minimal when the δ^{13}C values of bivalve stomach contents and muscle tissue does not vary with distance from the source of terrestrial OM (Chanton and Lewis 2002). Similarly, our δ^{13}C muscle tissue values are higher (-15 and –13‰) than for those systems receiving ^{13}C-depleted POM or DIC.

We generally observed a greater isotopic divergence among primary consumers than secondary consumers (benthic invertebrates and fish). Often in food source- apportionment studies only the herbivores reflect the differences in isotopic content of the host primary producers. For example, Stephenson et al. (1986) found that when they collected the herbivorous snail *Lacuna vincta* from kelp and seagrass dominated sites, carbon isotope ratios varied by site. In our study, Hartney Bay, the more oceanic-influenced site, contained more diverse communities of macroinvertebrates, which permitted comparison of the dietary sources of filter feeders (i.e., *Mytilus* and *Mya*) and deposit feeders (*Macoma* and amphipods). We found that *Mytilus* and *Mya* have lighter δ^{13}C values than the predominantly deposit feeding *Macoma balthica* and amphipods (mean -16.9 vs. –13.5‰). This pattern suggests that filter feeders are consuming disproportionately more isotopically depleted phytoplankton than deposit feeders. We also found that δ^{15}N enrichment was greatest for *Corophium salmonis*(3-4‰) at the oceanic site, and decreased somewhat with increasing trophic position. Given that the trophic enrichment factor for this amphipod and *Enteromorpha* (~1‰) is much less that the predicted average of 3.4‰ (Minagawa and Wada 1984), *Corophium* is probably utilizing other dietary sources.

At the oceanic site, δ^{13}C values of the demersal fishes (-14.2‰) are tightly coupled with *Macoma* values (-13.7‰, trophic fractionation of 0.5), suggesting the importance of this bivalve species for top predators. However, lighter δ^{13}C values of *Mya* and *Mytilus* (-16.9‰) indicates that these two bivalves are likely a smaller component of fish diet. The benthic community of the Delta's tidal flats is characterized by low species diversity and is dominated by *Macoma balthica*, which reaches densities of over 4000 m^{-2}. Polychaete densities, primarily the phyllodocid *Eteone longa*, are low on the delta reaching a maximum of only 700 m^{-2} in August (Powers et al. 2002). Amphipod densities, primarily the amphipod *Corophium salmonis*, are high (up to 7000 m^{-2}) only during the August sampling. All of these species are important in the diet of fish on the Delta (Powers and Bishop unpubl. data). Slow-growing populations will integrate stable isotopes over a longer period of time . In the case of juvenile fishes, isotopic composition reflecting changes in diet will alter at time scales of about 1 month (Hesslein et al. 1993). Low mean isotopic variability of demersal species among sites is expected if the fish integrate diet from a range of sources (Kline 1999). Fish serve to transfer carbon in the form of feces from the sessile invertebrates to the water column (Kline 1999).

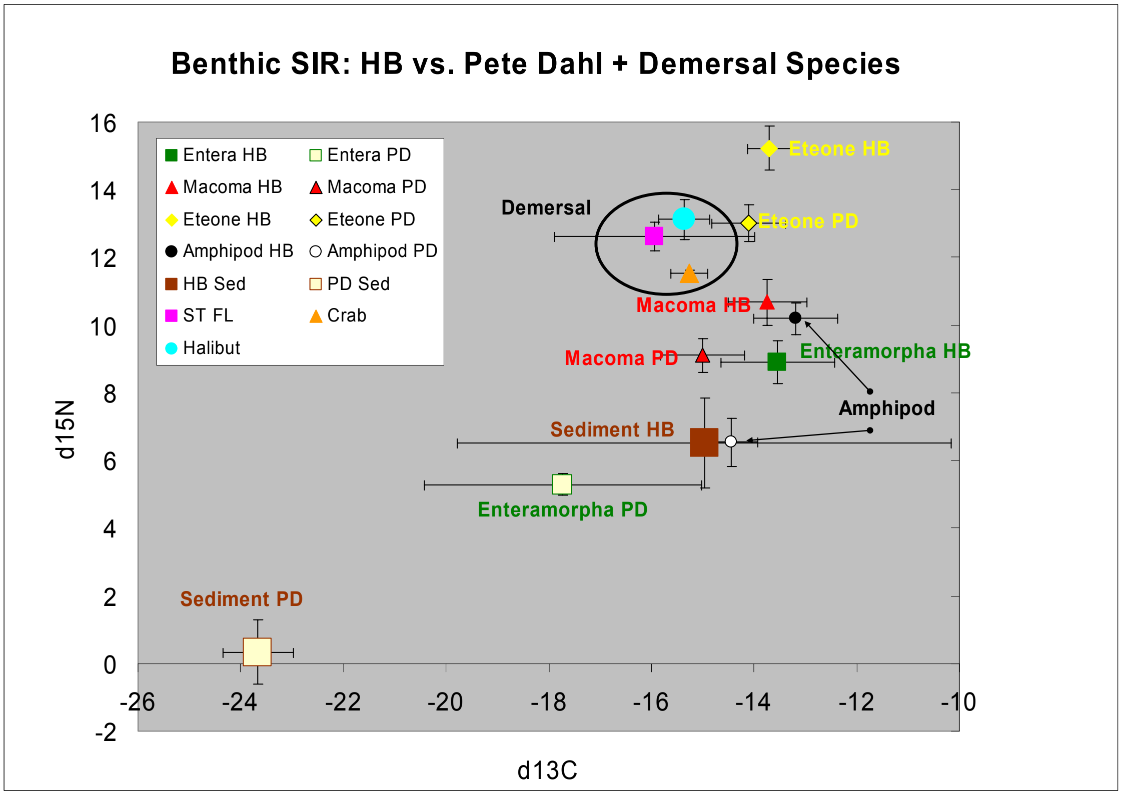


Figure 5. Summary of mean δ^{13}C and δ^{15}N signature for selected species in intertidal mudflats of the Copper River Delta, Alaska.

Summary & Conclusion

Vast expanses of intertidal sand/mudflats serve as a critical link in the food web of nearshore communities within the Copper River Delta and southeastern Prince William Sound. The rich abundance of benthic invertebrates residing within the sediments of intertidal flats and the large network of subtidal channels that bisect these flats provide a significant prey resource for numerous species of fish, crabs, birds, and marine mammals. Transfer of primary production and organic matter to the predator community occurs through a few dominant benthic invertebrate species, *Macoma, Mya, Mytilus,* amphipods and polychaetes (Powers and Bishop, unpublished data). Based on the isotopic signature of key species measured in this study, the energy source (food) for these benthic prey taxa varies along a gradient from the Copper River. Pete Dahl, and to some extent Eyak site, showed higher levels of terrestrial organic matter in the sediments than the more oceanic Hartney Bay sites. This $\delta^{13}C$ and $\delta^{15}N$ signature was also reflected in the sediments that contain benthic microalgae, the suspended organic matter in the water column and the macroalgae *Enteromorpha* sp. These groups of primary producers appear to support the dense *Macoma* populations of the Delta and Hartney Bay. The large differences in sediment and POM values $\delta^{13}C$ was not completely reflected in *Macoma* isotopic composition between delta and Hartney Bay sites (Fig. 5). *Macoma* $\delta^{13}C$ was much heavier than POM and sediment values only at the most riverine influenced site (Pete Dahl), suggesting that deposit feeders preferentially assimilated benthic microalgal sources. Thus terrestrial nutritional sources, while important, are apparently augmented by marine derived nutrients inputs for benthic communities on mudflats. Stable carbon and nitrogen isotopes of intertidal benthos, demersal fishes, and potential food sources also indicated that the oceanic site (Hartney Bay) was enriched and provide evidence for the greater importance of marine derived nutrients to the Hartney Bay benthic community. Regardless of the relative dependency on marine versus terristrally derived nutrients sources, the strong reliance of these intertidal and demersal food webs on benthic as opposed to freely floating primary producers suggests the sensitivity of these waters to oil spill effects that can have long residence times in the surficial sediments.

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