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Intertidal benthic resources of the Copper River Delta, Alaska, USA

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Abstract

The Copper River Delta, Alaska is the largest contiguous coastal wetland system along the West Coast of North America. Vast expanses of tidal mud flats formed by sediments carried by the suspended load of the Copper River serve as a connection between the Gulf of Alaska and the extensive network of wetlands, rivers and sloughs of the delta system. In addition to providing habitat for resident fish, shrimp and crabs, these tidal flats serve as critical feeding grounds for up to 5 million migratory shorebirds as well as an entry and exit corridor for three species of commercially fished salmonids. Here we report the first description of the benthic community of these intertidal flats. Between April and September 2000, we conducted three samplings on the Copper River Delta in which we quantified benthic macro-invertebrates inhabiting silt-clay sediments, the dominant substrate in the system, over a range of tidal inundation. Specifically, sampling was performed in two areas on the delta: near the outflows of the Eyak River and Pete Dahl Slough. Pore-water salinity of surficial sediment ranged from 4 psu during peak summer flow of the Copper River to 14 psu in April prior to increased riverine input. Sediment temperatures corresponded to ambient air temperatures with lowest temperatures during the April–September observation period recorded in April (4°C) and warmest in August (16°C). The benthic community of the delta's tidal flats was characterised by low species diversity and was dominated by the tellinid bivalve *Macoma balthica*, which reached densities greater than 4000 m⁻². Age–length relationship of *M. balthica* indicated slow growth and longevity of up to 8 years. Polychaete densities, primarily the phyllodocid *Eteone longa*, were low throughout the study period, reaching a maximum of only 700 m⁻² in August. Amphipod densities, primarily the corophid amphipod *Corophium salmonis*, were high (up to 7000 m⁻²) only during the August sampling. Spatial patterns of benthic invertebrate abundance were best explained by differences in tidal inundation with longer inundation corresponding to greater invertebrate densities. Temporal changes in abundance of polychaetes, amphipods, and *M. balthica* recruits corresponded to increases in sediment temperatures. Natural or human-induced changes to *M. balthica* populations could impact the food web of the delta, which could cascade to larger geographic impacts because of the importance of the delta to migratory species. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Copper River Delta; Mudflats; Benthic community; *Macoma balthica*; Southeastern Alaska

1. Introduction

The vast expanses of intertidal mudflats are one of the more striking features of the south-central Alaskan coastline. Unfortunately, the logistical difficulty asso-

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ciated with sampling these shallow, geographically isolated environments has prevented an adequate assessment of their biological resources. In particular, our knowledge of the benthic invertebrate community residing within the muddy sediments of these systems is poor. Given the importance of benthic invertebrates as prey for a variety of avian and aquatic consumers (e.g., shorebirds, ducks, crabs, and fish) and the vulnerability of these environments in south-central Alaska to petroleum spills (Teal and Howarth, 1984; Peterson, 2001), there is a critical need to assess their value to the local ecosystem.

The tidal flats of the Copper River Delta serve as feeding grounds for a variety of migratory (shorebirds and salmonid fish) and resident demersal (e.g., dungeness crabs, *Cancer magister*) species. Over 5 million shorebirds visit the flats annually between late April and mid-May on their way to breeding grounds in western Alaska. Two species of shorebirds, Western Sandpiper, *Calidris mauri*, and Dunlin, *Calidris alpina pacifica*, comprise more than 90% of these migrants (Bishop et al., 2000). Both species of shorebirds feed on benthic invertebrates residing within the sediments of mudflats (Recher, 1966; Quammen, 1984; Senner et al., 1989; Sutherland et al., 2000). Based on radio-telemetry studies, length of stay on the delta for Western Sandpiper, the most numerous shorebird, averages 2.6 d with a range from 1 to 8 d (Bishop et al., 2000). In addition to shorebirds, major runs of three species of salmonids (sockeye, *Oncorhynchus nerka*, coho, *O. kisutch*, chinook, *O. tshawytscha*), 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). The duration of stay on the delta is unknown for adult and juvenile salmonids. Given that harpacticoid copepods and amphipods make up a significant portion of smolt diets (Willette, in press), the tidal flats of the Copper River Delta could serve as a potentially important feeding ground for these fish.

The benthic resources of the delta are under constant threat because of their proximity to major oil shipping lanes in the Gulf of Alaska and the Trans Alaska pipeline. Once thought to be safe from potential oil spills in the shipping lanes of the Gulf of Alaska because of the westward flow of the Alaska Coastal Current, recent studies have shown that this assump-

tion may be flawed, and that the delta is vulnerable to oiling. For instance, preliminary results of a circulation study in the Gulf of Alaska indicate that currents in the vicinity of the Copper River Delta tidal flats can flow eastward from the Gulf toward the delta (Vaughan, 1997). In addition, a survey of local commercial fishermen reported that strong, sustained westerly winds in summer could shift surface currents eastward to areas of the Copper River Delta flats (Allen et al., 1996). An inland spill of the Trans Alaska pipeline in the vicinity of the Tiekel River or its tributary the Tsina River, could flow into the Copper River and result in significant oiling of the tidal flats. Finally, on the eastern side of the delta near Katalla, future onshore oil and gas exploration along with nearby mining of privately owned coal fields could trigger development and increase shipping activities on the delta.

In light of these threats and because of its rich natural resources and ecological sensitivity, the Copper River Delta is in need of ecological assessments and contingency plans in case of catastrophic oiling. Here, we present the results of a study designed to quantify the benthic resources and ultimately assess their importance as prey for avian and demersal consumers within the muddy sediments of the Copper River Delta system.

2. Methods

2.1. Study site

The Copper River Delta, Alaska is the largest contiguous coastal wetland system on the West Coast of North America (Thilenius, 1995). The large delta system includes approximately 500 km² of tidal flats that are fed by several glacial rivers and wetland sloughs. The Copper River provides the largest supply of freshwater and associated sediment load to the delta. Brabets (1997) reported the delivery of 62 million metric tons (69 million tons) of suspended sediments annually to the delta from the 63 000 km² drainage basin of the Copper River. Much of this delivery follows spring ice melt (May–June) and continues into the warmer summer months when the discharge rate of the river can be as high as 5300 m³ s⁻¹ (Brabets, 1997). Tidal flats of the delta are dominated by silt-clay sediments with fine sands increasing in proportion as

one gets closer to the barrier islands that separate the delta from the Gulf of Alaska. The current elevation of the delta results from the Great Alaska earthquake of 1964, an earthquake of Richter magnitude 9.2, which uplifted many sections of the region 2 m or more (Plafker, 1990). As a result of the earthquake, large areas of intertidal mudflats became supratidal and subtidal estuarine substrates became intertidal mudflats (Brabets, 1997).

The delta is characterised by maritime weather, resulting in mild wet summers (July mean air temperature 12 °C) and cool wet winters (January mean air temperature -5 °C). Average annual precipitation increases, moving landward, from 97 cm in nearby areas of the Gulf of Alaska (Searby, 1969) to 236 cm on the uplands, and 417 cm at the mountain bases (Western Regional Climate Center, <http://www.wrcc.dri.edu>). Average annual snowfall is 302 cm (Western Regional Climate Center, <http://www.wrcc.dri.edu>). While snow

and ice may cover the supralittoral areas of the delta intermittently from October to late April, above-freezing temperatures and precipitation limit snow accumulation.

2.2. Benthic invertebrate sampling

Benthic sampling was performed in two areas on the delta: near the outflows of the Eyak River (Eyak) and Pete Dahl Slough (Pete Dahl) (Fig. 1). Both sites are protected from the Gulf of Alaska by barrier islands, with Egg Island and Pete Dahl channels, respectively, the primary entrances to Gulf waters. The two study areas were selected because they represented two areas of high shorebird use and are representative of the entire delta.

To determine the distribution and abundance of major benthic taxa on the tidal flats, we designed a sampling scheme that would cover a range of tidal

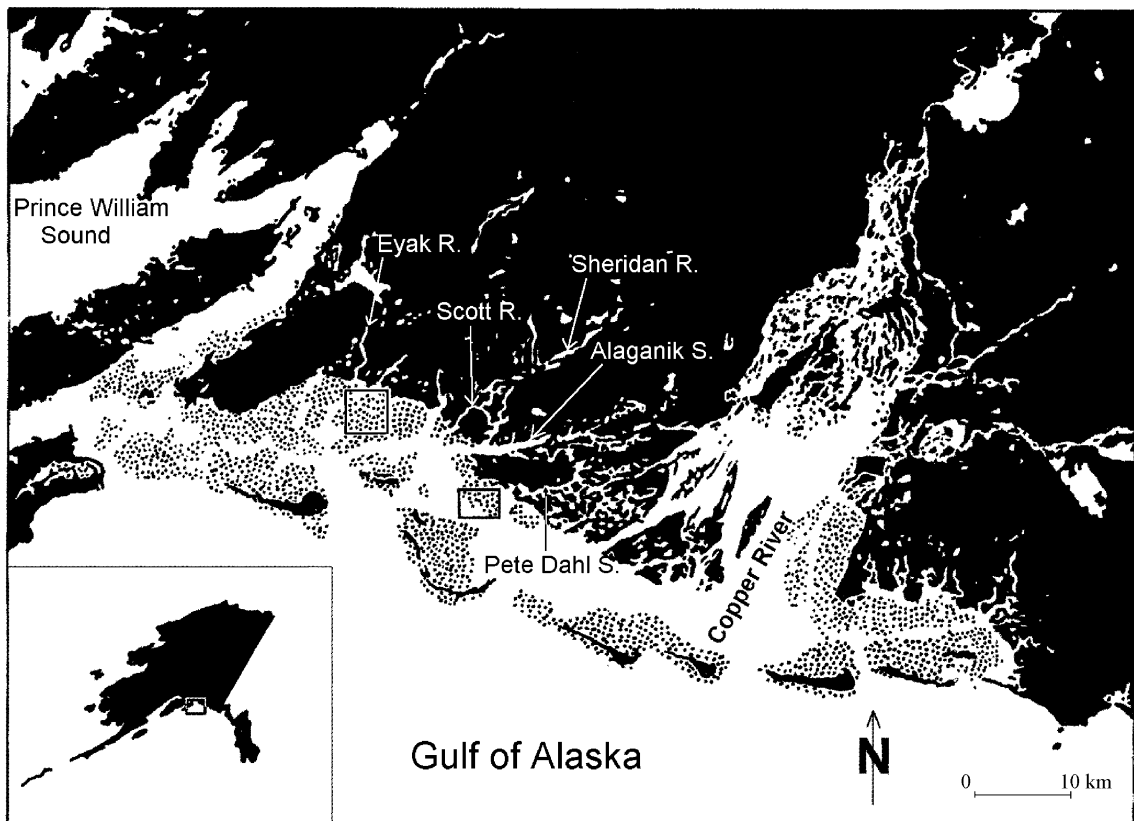


Fig. 1. Copper River Delta, Alaska study area. Small squares highlight the sampling areas used in this study.

inundation over the silt-clay substratum, the dominant bottom type in the system. Within each area we established two sets of four 100 m²-plots with each set of plots representing a different degree of tidal inundation. Within each set, plots were approximately 200 m apart and marked with wooden stakes or buoys. The first set of four plots at Pete Dahl was located within 0.5 km of the terminus of the shoreline. While unvegetated mudflats were the dominant substrate, the grass *Puccinellia pumila* occurred in small patches throughout these plots. The elevation of these plots resulted in the plots being submerged about 5% of a typical summer month (all tidal inundation estimates are based on almost daily observations from helicopter or fixed-wing aircraft fly-overs conducted at various tidal stages from April to June 2000). The second set of four plots at Pete Dahl was located approximately 2.0 km from the terminus of the wetland vegetation and was inundated about 20–22% of the time. At the Eyak site, the first set of plots was established 0.5 km from the terminus of the vegetation zone and the second set approximately 2.0 km. Tidal inundation differed from that of the Pete Dahl site: the first set of four plots at Eyak was inundated 17–18% of the time and the second about 35% of the time.

To determine temporal changes in benthic community structure, we sampled all plots three times during 2000: April 21–24, June 7–10, and August 28–30. These sample periods were selected because they represented the warmest period of the year and the likely time for recruitment of most invertebrate taxa (see McGreer, 1983), and because the April and June dates bracketed shorebird migration on the delta. Two core types, each processed to target different size groups of benthic invertebrates, were collected from each plot during all three sampling periods. A helicopter was used to transport personnel to and from each plot and all cores were collected at low tide.

Once at the plot, we collected three large samples (each sample consisting of two 15-cm diameter cores) by inserting the core to a depth of 10 cm at haphazardly selected locations within each 100-m² plot. The 10-cm depth was selected based on the findings of McGreer (1983) that 93 to 100% of *Macoma balthica* were found in the upper 10 cm from April to October. The contents of the large samples were then placed in a pre-labelled, plastic bag. Within 12 h the contents of each bag were washed with gentle water pressure onto a 1.0-

mm sieve. To quantify smaller invertebrates (e.g. polychaetes, amphipods, chironomid larvae), four smaller cores (10-cm diameter) were inserted to a depth of 10 cm, removed and their contents placed in pre-labelled Ziploc[®] bags. These samples were then washed onto a 0.5-mm sieve within 12 h. The contents of all remaining material on either size sieve were preserved in 10% buffered formalin. After one week, the formalin was removed and replaced with a solution of 70% ethanol/rose Bengal.

All animals in the samples were identified to the lowest practical taxon (usually species or genus) and enumerated under 10 × magnification. Because of its dominance both by number and biomass and our ability to age these bivalves, we measured growth parameters for *M. balthica*. The length along the anterior-posterior axis of the shell was measured using digital callipers to the nearest 0.1 mm for a randomly selected subset of 500 *M. balthica* from each sampling period. Age determinations were made for *M. balthica* by counting annual growth rings on the outside of the shell (see Gilbert, 1973, and McGreer, 1983, for validation of the methodology) and placing clams into year classes from ≤ 1 to 8 y old. Clams from small cores were used for estimation of age-frequency distributions because the smaller mesh size would insure capture of new recruits. In some cases (~ 20% of clams) growth lines were unresolvable because of severe compaction between successive bands that prevented those clams from being aged.

2.3. Physical/chemical measurements

At each sampling plot, we quantified physical and chemical parameters known to influence benthic community structure (i.e., temperature, salinity, sediment grain size, and sediment organic content). Temperature and salinity were measured during all collections. At each plot, pore-water salinity was measured with a Vista Model A366ATC refractometer and sediment temperature recorded using a mercury thermometer. Salinity and temperature of nearby sloughs or rivers were also recorded where appropriate. Surficial sediment samples (upper 2.5 cm) were collected for sediment-grain-size analysis using 5 cm diameter cores during the April sampling period. Analysis for sediment grain size and total organic content (TOC, ash-free dry weight) followed the methods

given in Carver (1970) for wet-sieving (sands) and decantation (silts and clays).

2.4. Data analyses

We performed a two-way analysis of variance (ANOVA) to determine if the density of benthic taxa differed with sampling area (Eyak shorter inundation, Eyak longer inundation, Pete Dahl shorter inundation, Pete Dahl longer inundation), sampling period (April, June, August) or the interaction between sampling period and sampling area. Date was treated as a fixed factor in the analysis because sampling was designed around spring shorebird migration. Because of the low abundance of many invertebrates, we used higher taxonomic groupings for many of the dependent variables (i.e., polychaetes, amphipods, chironomid larvae) in the analyses. Only the density of the bivalve *M. balthica* was analysed at the species level. Polychaete, amphipod, and chironomid densities were obtained from analysis of small cores, whereas *M. balthica* densities were based on analysis of large cores. Prior to performing ANOVA's, data were tested for homogeneity of variances using Cochran's test. Based on the results of these tests, polychaete, amphipod, and chironomid larvae densities were square-root transformed prior to analysis. Transformation was not needed for *M. balthica* densities. Post-hoc analyses of significant

main effects of the ANOVA were performed using Student-Newman-Keuls (SNK) test (Day and Quinn, 1989).

Regressions were performed to examine *M. balthica* growth rates as well as relationships between densities of benthic taxa and sediment grain size. Growth rate of *M. balthica* was examined by regressing age in years against shell length. Linear regressions were performed between density of *M. balthica* measured in April 2000 and % TOC, % sand, % silt, % clay, and % silt + clay. For these regressions, we used the average April densities of *M. balthica* in each plot as the dependent variable and sediment properties of each plot as the independent variable(s) in the analyses. Similar regressions for polychaetes, amphipods, and chironomids were based on densities measured in August 2000 because abundances of these animals peaked in August. Prior to regression analyses, homogeneity of variances (Cochran's test) and normality (Kolmogorov-Smirnov tests) were confirmed for the dependent variables.

3. Results

Sediment temperature and salinity varied with plot location and sampling period. Overall variation in temperature and salinity among plots within a sam-

Table 1

Sediment parameters, sediment temperature and pore-water salinity measurements taken at each sampling plot on the Copper River Delta during 2000

Site	Tidal Inundation	Plot	% Sand	% Silt	% Clay	% TOC	Sediment Temperature (°C)			Pore-water Salinity (psu)		
							Apr	June	Aug	Apr	June	Aug
Pete Dahl	Shorter	1	10.82	57.55	31.58	1.64	4	9	15	14	2	11
	Shorter	2	11.11	57.48	31.40	0.81	4	9	15	14	2	11
	Shorter	3	16.25	63.17	20.58	1.20	4	9	15	14	2	11
	Shorter	4	14.30	61.12	24.31	1.15	4	10	14	14	2	12
	Longer	1	7.37	54.42	37.84	1.15	4	9	15	14	5	11
	Longer	2	6.59	54.57	38.83	0.89	4	9	15	14	5	11
	Longer	3	7.55	65.74	26.71	1.69	4	8	15	14	5	12
	Longer	4	7.76	64.77	27.47	1.36	4	9	15	15	5	11
Eyak	Shorter	1	24.51	52.03	23.30	0.98	4	9	16	18	7	8
	Shorter	2	21.51	57.54	38.83	0.88	4	9	16	18	7	8
	Shorter	3	33.42	49.65	16.93	1.64	5	9	16	18	8	8
	Shorter	4	39.47	45.59	14.94	1.42	4	9	16	18	7	8
	Longer	1	14.95	57.36	27.71	1.68	5	10	16	19	8	8
	Longer	2	16.46	57.05	26.49	1.48	4	9	15	18	8	8
	Longer	3	37.54	45.01	17.46	1.30	5	9	15	19	9	8
	Longer	4	29.18	54.33	16.49	1.21	4	10	16	20	8	8

Table 2

Results of two-way analyses of variance testing the effects of sampling area, sampling period and their interaction on the densities of *Macoma balthica*, polychaetes, amphipods, and chironomid larvae. Polychaete, amphipod and chironomid densities were square-root transformed prior to analysis, *M. balthica* density did not need to be transformed

Dependent variable	Source of variation	df	Mean square	F-value	p
<i>Macoma balthica</i> density	Sampling area	3	35864182	133.3	<0.001
	Sampling period	2	437153	1.6	0.211
	Sampling area * period	6	356409	1.3	0.271
	Residual	36	68952		
Polychaete density	Sampling area	3	486	19.7	<0.001
	Sampling period	2	171	6.9	0.003
	Sampling area * period	6	26	1.1	0.397
	Residual	36	24		
Amphipod density	Sampling area	3	1892	13.7	<0.001
	Sampling period	2	5534	40.1	<0.001
	Sampling area * period	6	1169	8.4	<0.001
	Residual	36	137		
Chironomid density	Sampling area	3	177	2.1	0.105
	Sampling period	2	36	0.5	0.639
	Sampling area * period	6	36	0.5	0.835
	Residual	36	80		

pling period was small compared to variation among sampling periods (Table 1). Highest salinities (14–20 psu) and lowest sediment temperature (4 °C) were recorded during April 2000. Salinities were lower during the subsequent sampling trips in June (2–9 psu) and August (8–12 psu), presumably as a result of

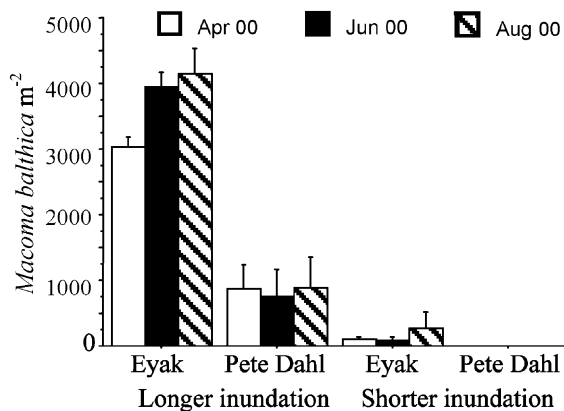


Fig. 2. Densities of *Macoma balthica* (mean + SE) at each sampling area for each sampling period. ANOVA revealed a significant effect of sampling area (with SNK post hoc contrasts showing longer inundation Eyak sites > longer inundation Pete Dahl sites > shorter inundation Eyak sites > shorter inundation Pete Dahl sites), but no effect of sampling period or the interaction between sampling period and area.

increased river and slough discharge during ice melt. Temperatures increased throughout the summer with warmest sediments detected in August (14–16 °C; Table 1). Sediments at all plots were dominated by fine silts and clays (60 to 90%, mean = 82%). Sand accounted for a greater percentage of the sediments at Eyak plots than at Pete Dahl plots. A trend of increasing sand content with reduction in tidal inundation was also apparent.

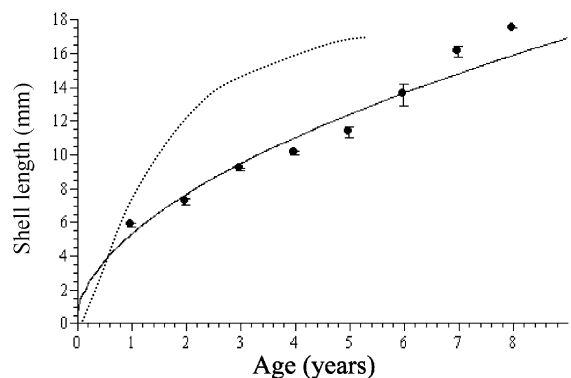


Fig. 3. Growth rate of *M. balthica* estimated from shell annuli for clams on the Copper River Delta, AK. Points (mean ± SE) are fitted to a power curve ($y = \exp 1.67 * x^{0.529}$, $R^2 = 0.954$). The dashed-line curve is the growth curve reported in McGreer (1983) for *M. balthica* on mudflats in the Fraser River Estuary, British Columbia.

Macoma balthica was the dominant infaunal organism (in number and biomass) found on the delta. None of the regressions between sediment properties and *M. balthica* densities of each plot was significant ($p > 0.16$; $R^2 < 0.14$ for all regressions). The two-way ANOVA for densities of *M. balthica* revealed a significant effect of sampling area ($p < 0.001$), but no effect of sampling period ($p = 0.211$) or the interaction between sampling period and area ($p = 0.271$; Table 2). All sampling areas differed significantly from each other with respect to *M. balthica* densities ($p < 0.05$ for all SNK tests). Eyak longer inundation plots had the highest densities of *M. balthica* (mean ± 1 SE = 3709 ± 205 m⁻²), followed by Pete Dahl longer inundation plots (831 ± 218 m⁻²), Eyak shorter inundation plots (151 ± 70 m⁻²), and Pete Dahl shorter inundation plots (0.71 ± 0.71 m⁻², Fig. 2).

The best prediction (based on R^2 values from a series of curves) for growth rate of *M. balthica* on the Copper River Delta was provided by a power curve (Fig. 3, $R^2 = 0.954$). Average size of clams at the end of 1 y of growth was 5.86 mm ± 0.09 (1 SE). Clams appeared to grow at a rate of 1.4 to 1.9 mm y⁻¹ after year 1. The oldest *M. balthica* collected was 8 y old.

Benthic invertebrates other than *M. balthica* showed a distinct pattern of increasing abundance from April to August. Significant effects of sampling period and sampling area were detected for polychaetes and amphipods in the ANOVAs ($p < 0.01$, Table 2), but not for chironomid larvae. Polychaete density was highest at longer inundation Eyak plots, followed by longer inundation Pete Dahl plots (Fig. 4). Density of polychaetes was higher in August ($p < 0.05$ for SNK tests of August vs. April and August vs. June) than densities in April and June, which did not differ ($p > 0.05$ for SNK test). One species, the phyllodocid polychaete *Eteone longa*, accounted for the majority ($\sim 90\%$) of polychaetes in the study plots. The interaction for sampling period and sampling area was significant only for amphipods ($p < 0.01$). Amphipods were present in high densities at only longer inundation plots in the August sampling (Fig. 4). The corophid amphipod *Corophium salmonis* accounted for 80–90% of all amphipods. Though not significantly different from other areas used in the ANOVA, shorter inundation plots at Pete Dahl were the only plots that had high densities of chironomid larvae. Chironomid densities were extremely low at all other plots. This pattern appeared to intensify as the

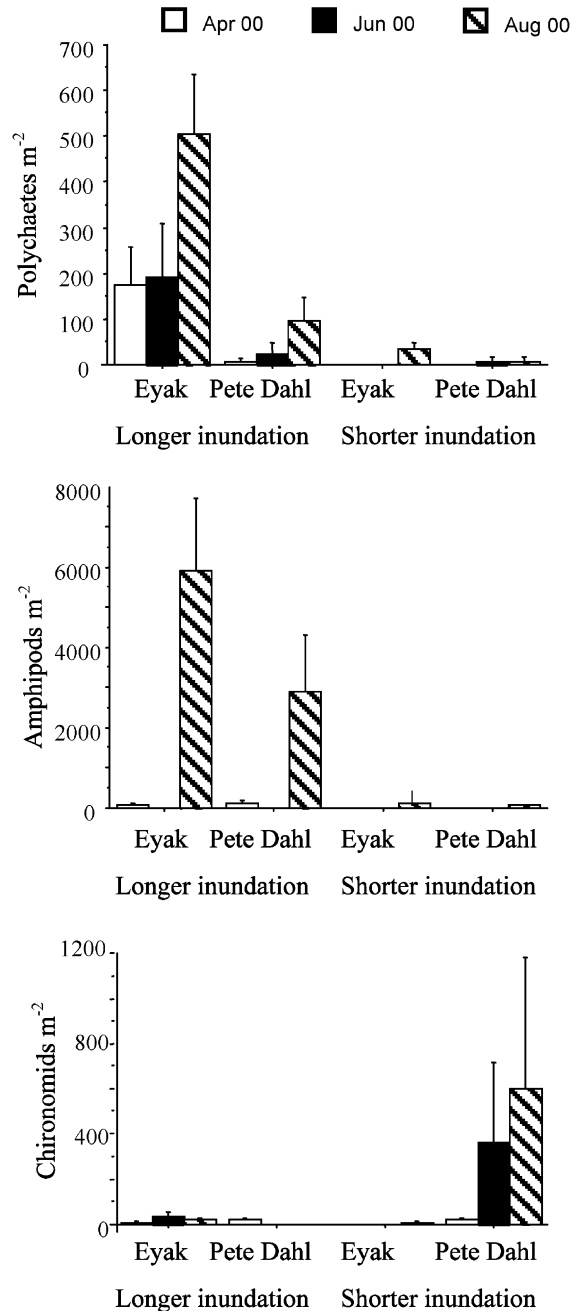


Fig. 4. Densities of polychaetes, amphipods, and chironomids (back transformed mean \pm SE) at each sampling area for each sampling period. ANOVA revealed a significant effect of sampling area and sampling period for polychaetes and amphipods, a significant interaction between the two effects for amphipods, but no effect of sampling area, sampling period, or their interaction for chironomids.

summer season progressed (Fig. 4). As was the case for *M. balthica*, none of the regressions between sediment parameters and August densities of polychaetes, amphipods, or chironomids were significant (all p values >0.15).

4. Discussion

The vast expanses of intertidal flats within the Copper River Delta system support a dense assemblage of infaunal invertebrates with low species diversity. Three species, the tellinid bivalve *Macoma balthica*, the corophid amphipod, *Corophium salmonis*, and the phyllodocid polychaete *Eteone longa*, accounted for over 95% of the individuals identified on the mudflat. The numerical and biomass dominance of *M. balthica* in the silt-clay sediments of the delta's tidal flats is characteristic of many brackish water tidal flats at higher latitudes (e.g., Segerstråle, 1962; Gilbert, 1973). Densities of *M. balthica* found at the longer inundation, Eyak plots ($\sim 4000 \text{ m}^{-2}$) are similar to those reported by Myren and Pella (1977) in their study of tidal flats near Port Valdez, Alaska, but substantially higher than those reported for the Fraser River Estuary, British Columbia ($\sim 1800 \text{ m}^{-2}$) by McGreer (1983). Geographic comparisons for the densities of polychaetes and amphipods are difficult because of the lack of published findings on these taxa from similar habitats in the region. Polychaete abundances were low, ranging from 0 in the April sampling period to less than 700 m^{-2} in August. Amphipod abundances were also low in the April and June sampling periods; however, abundance did increase markedly by the late August sampling (6000 m^{-2}).

Tidal inundation appeared to be the best correlate for spatial patterns of benthic invertebrate abundance, whereas sediment grain size and sediment organic content failed to predict spatial variability in benthic invertebrates. The four sampling areas differed primarily with respect to tidal inundation and not sediment grain size: all plots were within the silt/clay bottom type. Longer inundation Eyak plots, which had the highest submergence time of all plots, had the highest densities of *M. balthica* (Fig. 2), polychaetes, and amphipods (Fig. 4). Longer inundation Pete Dahl plots had the second highest submergence time and densities of *M. balthica*, polychaetes and amphipods. The

shorter inundation plots at both Eyak and Pete Dahl had few polychaetes or amphipods. Although much lower than either set of longer inundation plots, densities of *M. balthica* were higher at the shorter inundation Eyak plots than those at the shorter inundation plots at Pete Dahl. Similar findings of increased abundance of *M. balthica* as inundation time increases have been reported by Myren and Pella (1977) and others (see citations in Myren and Pella, 1977). The overall pattern of highest species density at intermediate tidal levels and sediment composition has also been documented by Beukema (1976, 1988, this issue) and Beukema and Cadée (1997) in their studies of tidal flats in the Dutch Wadden Sea and probably represent a generic pattern for temperate and subarctic tidal flats. Chironomid larvae were the only taxa in our study that showed the opposite trend with respect to tidal inundation, i.e. high densities only at the shorter inundation plots (Fig. 4).

Temporal changes in the benthic community appeared to correlate best with changes in sediment temperature. Sediment temperature increased from April to August, as did densities of polychaetes and amphipods at the longer inundation plots. Sediment temperature increased presumably in relation to ambient air temperatures. Salinity decreased from April to June at all plots and then increased slightly from June to August at Pete Dahl plots and remained unchanged at Eyak Plots (Table 1). Changes in salinity are most likely a function of increased freshwater inputs from the Copper, Eyak, and Sheridan Rivers. Amphipod and polychaete abundances may have also increased in response to increases in epibenthic algae. Between the June and August sampling periods we noted the appearance of epibenthic algae, primarily *Enteromorpha* sp., on the mudflats. This species would provide both a substrate and a food source for amphipods and polychaetes. The increase in the abundance of algae may also be a function of increased temperatures.

Growth and longevity of *M. balthica* on the Copper River Delta are similar to other higher latitude populations of this bivalve. The age-length curve illustrated in Fig. 3 is similar to those that Gilbert (1973) presents for populations in the Gulf of Finland, which is located at the same latitude as the Copper River Delta (60° N). McGreer's (1983) study in the Fraser River, British Columbia, (dashed line on Fig. 3) found substantially higher growth rates than we report here. According to

McGreer's (1983) data, the length of a clam at 3 y would be approximately 15 mm, whereas in our study a clam of this same age would only be 10 mm in length. Clam longevity also differed between our results for the Copper River Delta and those reported by McGreer (1983) for the Fraser River Delta: the oldest clam found in our study was 8 y compared to 5 y in McGreer's study. Both patterns, decreased growth and increased longevity, agree with Gilbert's (1973) predictions that the more northern populations of *M. balthica*, which experience relatively lower temperatures and shorter growing seasons, should have reduced growth and increased longevity. Similar results, decreased growth and increased longevity with increasing latitude, have been reported for other intertidal bivalves from the West Coast of North America, e.g., *Mya arenaria* (Feder and Paul, 1974), *Mytilus californianus* (Dehnel, 1956), and *Protothaca staminea* (Paul and Feder, 1973).

M. balthica is sensitive to the presence of oil (Shaw et al., 1976, 1986), and is particularly susceptible to bioaccumulation of petroleum hydrocarbons (Broman and Ganning, 1986; Mageau et al., 1987). A major oil spill originating from either the Trans Alaska pipeline or from the Gulf of Alaska shipping lanes could result in significant oiling of the Copper River Delta's mudflats. The acute, chronic and indirect effects of oiling on *Macoma* could impact the food web of the delta, which could expand to larger geographic areas because of the importance of the delta to migratory species. For Pacific Flyway shorebirds, the Copper River Delta and the adjoining Bering River Delta together comprise one of the few sizeable coastal wetlands available as a stopover between the Fraser River Delta (southern British Columbia) and their western Alaskan breeding grounds (Senner et al., 1989). Shorebirds are directly vulnerable to oil both through oiling of feathers and the transfer of hydrocarbons through the food chain (see Martin, 1994, for a review). Oiled plumage can cause direct mortality or impaired physiological condition of adults through loss of insulation and subsequent hypothermia (Hartung, 1967; Vermeer and Vermeer, 1975) and altered foraging and preening behaviour (Burger, 1997). Shorebirds also can ingest oil by preening or by consuming contaminated foods. Bivalves such as *M. balthica* are a staple for many shorebirds, including the Western Sandpipers and Dunlin, the most numerous shorebirds stopping over on the Copper River Delta.

Ingestion of oil even at sublethal doses can lead to altered endocrine function (Holmes et al., 1978). Thus, the loss or degradation of key staging areas such as the Copper River Delta through development or catastrophic events such as oil spills could severely affect reproductive success and survival of shorebirds unable to shift to alternative feeding areas (Myers, 1983; Senner and Howe, 1984).

Continued monitoring of the benthic invertebrate populations with the goal to better understand and ultimately predict temporal and spatial patterns of invertebrate abundance is critical to assessing the resilience of this community to major disturbance events. Equally important is the need to better understand and quantify trophic linkages from the benthic invertebrate community. The Copper River Delta supports a huge abundance of migratory shorebirds and salmonids; however, its importance for resident species such as the dunghen crab is largely unknown. Whereas benthic communities and their predators at more temperate latitudes may show rapid (~ 1 y) recovery from large-scale disturbances (e.g. Powers et al., in review), the effect of similar disturbances at more northern latitudes may require substantially longer recovery times because of the slow growth rates and longevity of the dominant taxa of the system.

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