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Journal of Sea Research 55 (2006) 207–216

JOURNAL OF
SEA RESEARCH

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Distribution of the invasive bivalve *Mya arenaria* L. on intertidal flats of southcentral Alaska

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Received 30 September 2005; accepted 18 October 2005
Available online 22 December 2005

Abstract

The bivalve *Mya arenaria* L. is a common inhabitant of intertidal sediments along the southcentral Alaskan coastline. Its current distribution along the Pacific coast of the continental USA, Canada and Alaska has resulted from a series of intentional and unintentional introductions as well as larval transport between points of introduction over the previous century. Despite the apparent success of *M. arenaria* in intertidal habitats of coastal Alaska, no study has examined its distribution in this environment. We sampled four times over a two-year period (2001–2002) to document the distribution of *M. arenaria* in intertidal sedimentary habitats of the Copper River Delta and adjacent Orca Inlet (southeastern Prince William Sound), Alaska. Sampling was performed along a gradient of tidal elevations at three sites (Hartney Bay, Eyak and Pete Dahl) chosen to represent the range of physical/chemical settings of protected intertidal sand and mud flats within the study area. Among the three sampling sites, abundance of *M. arenaria* was lowest at sites near the outflow of the Copper River (Pete Dahl) and highest in areas of higher salinity and water clarity (Hartney Bay and low tidal elevation plots at Eyak). Within each of the two sites located on the Copper River Delta (Eyak and Pete Dahl), abundances of *M. arenaria* were highest at low tide plots (+1.1 m for Eyak, +1.4 m for Pete Dahl), a pattern consistent with the distribution of *M. arenaria* within tidal flats in Europe (Wadden and White Seas). For the third site located in Orca Inlet (Hartney Bay), *M. arenaria* was found at all tidal elevations; however, distinct differences in the distribution of newly recruited *M. arenaria* (<10 mm shell length [SL]) and older juveniles and adults (>10 mm SL) were evident. Density and growth of *M. arenaria* in southcentral Alaska were most similar to values reported for the White Sea (Russia); both areas are located at similar latitude and represent the northern extreme of *M. arenaria* distribution.

Keywords: Benthic community; Subarctic tidal flats; *Mya arenaria*; Distribution; Copper River; Prince William Sound; Alaska

1. Introduction

The softshell clam *Mya arenaria* L. can be a biomass dominant species on intertidal and shallow, subtidal sand and mud flats in many temperate and subarctic areas along the northeast and northwest coasts of the Atlantic Ocean and the northeast coast of the Pacific Ocean (e.g., Warwick and Price, 1975; Beukema, 1982, 1992; Emmerson et al., 1988; Brey, 1991; Strasser, 1999). This wide geographic range has resulted from a series of intentional and unintentional introductions as well as range expansions over the last

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doi:10.1016/j.seares.2005.10.004

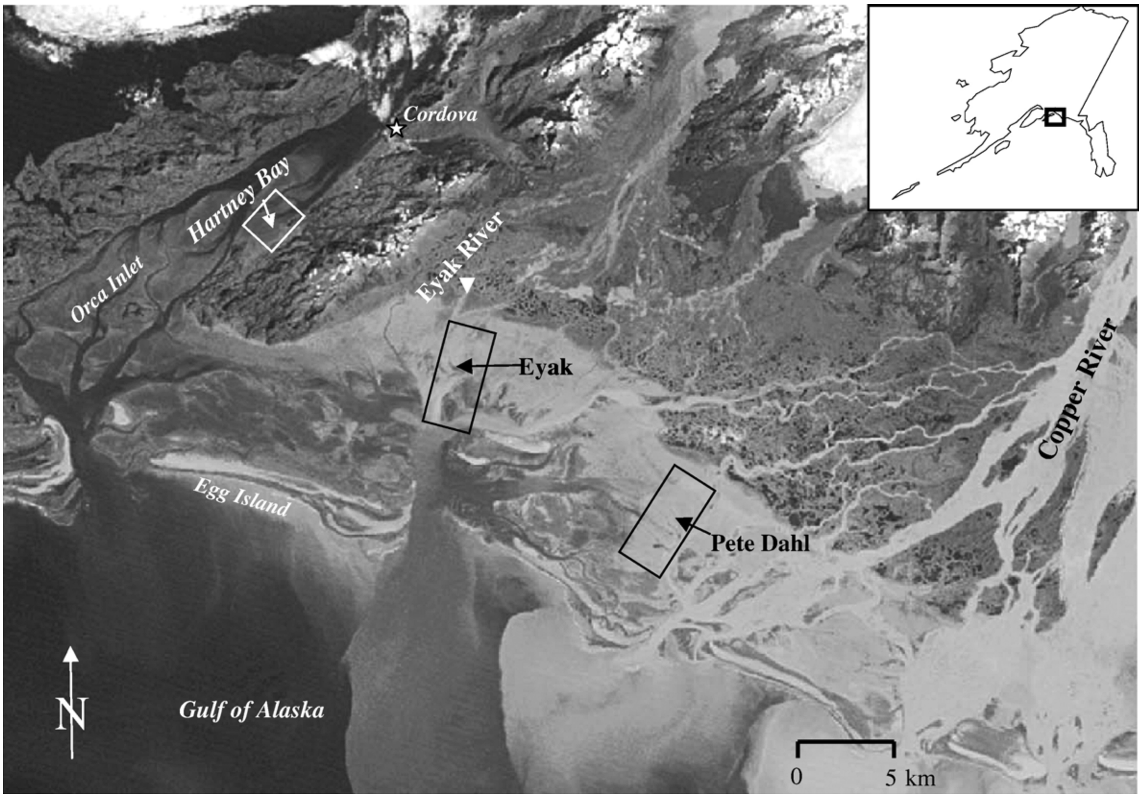

Fig. 1. Aerial image of the western Copper River Delta, Alaska showing the spatial extent of the Copper River outflow (cloudy, grey water vs. deep black water) and the network of mudflats throughout the brackish water portions of the Delta and Orca Inlet. The three sampling areas (Pete Dahl, Eyak and Hartney Bay) are noted on the image.

700 years (Strasser, 1999). Introductions of *M. arenaria* on the northeastern Pacific coast occurred via plantings of eastern oysters, *Crassostrea virginica*, from the Mid-Atlantic Unites States in the late 1800s and early 1900s (Hanks, 1963; Feder and Paul, 1974). Although introduced over the last 130 y to the northeast Pacific coast, the paleontological record suggests that *M. arenaria* occupied many areas in the northeast Pacific during the Miocene and Pliocene. The oldest records of *M. arenaria* date from the mid-late Miocene (22.5–5.0 million y ago) with *M. arenaria* shells found on the Pacific west coast of Japan and the Pacific east coast in California (MacNeil, 1965; Strasser, 1999). Later in the Miocene, *M. arenaria* appeared in Atlantic waters off the North American coast and even later in Europe via an Arctic route (MacNeil, 1965; Bernard, 1979) or a Central American passage (Strauch, 1972). Glaciations during the Pleistocene resulted in survival of *M. arenaria* only on the Atlantic west coast with extinction of all populations in the northeast Pacific and eastern Atlantic (MacNeil, 1965; Strasser, 1999). Over the last 300–700 y, *M. arenaria* successfully reinvaded many areas within its paleontological range through a series of introductions. In many areas where *M. arenaria* has been introduced it has become a dominant member of the infaunal community (Warwick and Price, 1975; Beukema, 1982, 1992; Brey, 1991) and has apparently had little to no negative effects on the endemic fauna (Strasser, 1999).

Despite its apparent success in invading many of the shallow mud and sand flats along the northeast Pacific coast, few studies have examined the distribution of *M. arenaria* within these habitats. Here, we report findings of the first study conducted in intertidal flats of southeastern Prince William Sound and the Copper River Delta, Alaska, designed to examine the distribution of *M. arenaria*. The high suspended sediment load of the Copper River (~69 million metric tons y^{-1}: Brabets, 1997) nourishes an extensive network (~500 km^2) of intertidal sand and mudflats in the nearshore area. This large expanse of intertidal mudflats provide habitat for *M. arenaria* as well as a host of other bivalve species.

2. Materials and methods

2.1. Study sites

Sampling for infaunal invertebrates, including *Mya arenaria,* was conducted on intertidal areas at Hartney Bay (60° 30′ N; 145° 50′ W) in Orca Inlet (south-eastern Prince William Sound) and at two areas on the Copper River Delta (Fig. 1), the outflows of the Eyak River (60° 23′ N; 145° 43′ W) and Pete Dahl Slough (60° 20′ N; 145° 28′ W). We selected these three areas to bracket the range of local physical/chemical settings (e.g., salinity, sediment grain size, turbidity) in which intertidal flats occur. Within each area, sampling plots were established at high, mid and low tidal elevations, with tidal elevation generally decreasing with distance from the shoreline. Tides are semidiurnal with an average range of 3.1 m. Because of the difficulty in reaching many of our sampling plots on the geographically isolated delta (Eyak and Pete Dahl sites were visited via helicopter and Hartney Bay was accessed by foot), the number of sampling plots had to be kept low.

For the Eyak and Pete Dahl areas, three 10-m^2 plots, spaced >200 m apart, were established per tidal elevation, for a total of nine sampling plots per area. The majority of intertidal flats occur within an elevation range +1.0 to +2. 7 m, all elevations are based on MLLW (Powers and Bishop, unpubl. data). Tidal elevations for our sampling plots at Pete Dahl were as follows: high +2.4 m, mid +1.8 m, and low +1.4 m. Tidal elevations at Eyak plots were: high +2.3 m, mid +1.6 m, and low +1.1 m. 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. Intertidal habitat at both Eyak and Pete Dahl included both sand and mud flats, with no mussel beds detected at either area. At Hartney Bay, two 10-m^2 plots, separated by 0.5 km, were established at: high (+2.2 m), mid (+2.0) and low (+1.0 m), for a total of six sampling plots. Two additional sampling plots were established at this site within a broad band of mussels (*Mytilus trossulus*) located between mid and low elevations at +1.7 m and referred to as mid-mussel plots.

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). 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). Salinity at all Hartney Bay sampling sites was relatively high ranging from 23–32 psu. Salinities at both 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 plots in the Eyak and Pete Dahl areas. Salinity ranges from 0–22 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 14 to 32 psu at mid and high tide sites and from 14 to 32 psu at low tide sites (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 y^{-1}, Brabets, 1997) in the area as well as storm-induced suspension of silt/clay sediments. Turbidity during summer months is lowest, typically <20 nephelometer 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 NTUs at high and mid tide plots near Pete Dahl and decreases to between 50 and 100 NTU at Pete Dahl low sites (Powers and Bishop, unpubl. data).

The overall climate of the Copper River Delta region is maritime with mild, wet summers and cool, wet winters. Mean air temperature in July is 12°C and −5°C in January. Precipitation in the form of snow or rainfall is high throughout the year ranging from 97 cm in nearby areas of the Gulf of Alaska to 417 cm at mountain bases surrounding the Copper River

Table 1
Results of three-factor analyses of variance testing the effects of sampling area (Pete Dahl, Eyak and Hartney Bay), sampling date (April 2001, June 2001, September 2001, and September 2002), and tidal elevation (high, mid, and low) on the transformed ($\sqrt{m^{-2}+0.5}$) abundance of *Mya arenaria* ≤10 mm and >10 mm in shell length

Variable	Factor	df	Sum of Squares	F	p
Mya ≤ 10 mm	Area	2	208.1	12.6	<0.001
	Date	3	45.6	1.8	0.149
	Elevation	2	284.9	17.2	<0.001
	Area * Date	6	126.6	2.6	0.029
	Area * Elevation	4	193.7	5.9	<0.001
	Date * Elevation	6	29.0	0.6	0.740
	Area * Date * Elevation	12	69.2	0.7	0.747
	Residual	60	495.7		
Mya > 10 mm	Area	2	193.8	20.5	<0.001
	Date	3	14.6	1.0	0.149
	Elevation	2	36.8	3.9	0.026
	Area * Date	6	40.6	1.4	0.220
	Area * Elevation	4	388.3	20.5	<0.001
	Date * Elevation	6	24.5	0.9	0.528
	Area * Date * Elevation	12	48.2	0.8	0.601
	Residual	60	495.7		

Delta (Western Regional Climate Center, http://www.wrcc.dri.edu). From November to early April snow and ice may intermittently cover high and mid-tidal areas of the tidal flats (M. Bishop, pers. obs.). Frequent periods of above-freezing temperatures and rainfall limit snow and ice accumulation in tidal flat areas for extended time periods. Sediment temperatures at low tide generally correspond with ambient air temperatures with warmest temperatures found during July and August (10–16°C) (Powers et al., 2002).

2.2. Bivalve collections

We made three collections (April 22–26, June 6–16 and September 6–11) in 2001 and one collection (September 7–10) in 2002. At Hartney Bay we collected three replicate 15-cm diameter cores, inserted to a depth of 10 cm, at each of the 8 plots. After removal of the cores, the hole resulting from the core was excavated an additional 5 to 10 cm (depending on the presence and depth of a hard shell layer) by hand to capture any large *M. arenaria* that were deeply burrowed. For the Pete Dahl and Eyak sampling areas we used a combination of small, 10-cm diameter cores and large, 15-cm diameter cores to sample infaunal bivalves. In 2001 we collected four small cores at each mid and high tide plot and both large cores (n = 3 per plot) and small cores (n = 4 per plot) at each low tide plot. In 2002 we collected three large cores from each plot. We made additional collections in June and September 2001 from areas adjacent to the sampling plots to increase the number of *M. arenaria* specimens for age-length determinations. All cores were washed onto a 0.5 mm sieve. All material retained on the sieve was placed in a solution of 10% formalin/rose Bengal for at least 48 h and then transferred to a 70% ethanol solution. Animals were identified to species and shell length (SL) was measured for all bivalves.

2.3. Data analysis

We performed three-factor analysis of variance (ANOVA) with a factorial design to determine whether the abundance of *M. arenaria* differed among the three sampling areas (Pete Dahl, Eyak, and Hartney Bay), tidal elevation (high, mid, or low) and/or sampling date (April 2001, June 2001, September 2001, and September 2002). Because differences in the distribution of small (≤10 mm SL) and large (>10 mm SL) *M. arenaria* were evident in the samples, we performed separate ANOVAs for these two size categories. Based on age-length relationships in Feder and Paul (1974) and this study, *M. arenaria* ≤10 mm SL would be inclusive of all possible age 0 clams. For the two ANOVAs, we used the average abundance of each size class of *M. arenaria* from the three to four cores collected at each plot on each sampling date as the dependent variable and standardised the abundances to number per m^2. Significant interactions with sampling area in the three-factor ANOVAs were examined by performing separate two-factor ANOVAs testing the effects of tidal elevation and sampling date within each area. For the two-factor ANOVA for *M. arenaria* collected from Hartney Bay, tidal elevation had four levels (high, mid, mid-mussel and low), whereas only three levels (high, mid and low) were used in the two-factor ANOVA for Eyak. Abundances were too low at the Pete Dahl site for an ANOVA to be performed. All data were square root transformed ($\sqrt{x+0.5}$) after Cochran's test detected heterogeneity of variances in both the ≤10 mm and >10 mm data sets. After transformations, Cochran's test failed to detect heterogeneity of variances. Student-Neuman-Keuls (SNK) post-hoc contrasts were performed for each significant main effect.

To document *M. arenaria* growth patterns in our study area, age was estimated by counts of external annuli for 300 *M. arenaria* collected. Shell length (maximal distance between ventral and dorsal margins of the valves) was measured for all clams aged. For

Table 2
Results of a two-factor analysis of variance testing whether sampling date (April 2001, June 2001, September 2001, and September 2002), tidal elevation (high, mid, mid-mussel, and low) or their interaction affect the transformed ($\sqrt{\#\,\mathrm{m}^{-2}+0.5}$) abundance of *Mya arenaria* $\leq$10 mm and $>$10 mm in shell length at Hartney Bay

Variable	Factor	df	Sum of Squares	F	p	SNK post hoc summary
Mya $\leq$10 mm	Date	3	169.8	5.0	0.012	Apr 01 > Jun 01, Sep 01, Sep 02
	Elevation	3	364.4	10.8	$<$0.001	Low > high, mid, mid-mussel
	Date * Elevation	9	79.3	0.8	0.635	ns
	Residual	16	180.0			
Mya $>$10 mm	Date	3	29.0	2.2	0.126	ns
	Elevation	3	322.4	24.6	$<$0.001	Mid > high > mid-mussel, low
	Date * Elevation	9	63.3	1.6	0.194	ns
	Residual	16	69.9			

M. arenaria in Prince William Sound, annuli counts have been shown to be a useful proxy for age (Feder and Paul, 1974). Aging of older clams ($>$7 y) has proved difficult (MacDonald and Thomas, 1980); however, few clams above this age were found in our study.

3. Results

Mya arenaria was present in all three sampling areas (Hartney Bay, Pete Dahl and Eyak). Abundances varied among sampling areas and tidal elevation within an area. Significant interactions between sampling area and tidal elevation were detected by the three-way ANOVA for both small ($\leq$10 mm) and large ($>$10 mm) *M. arenaria* (Table 1). Two-factor ANOVAs performed to examine the effects of sampling date and tidal elevation within the Eyak and Hartney Bay sampling areas revealed significant effects of tidal elevation with no interaction between tidal elevation and date for both size classes of *M. arenaria* (Tables 2 and 3). Abundance of *M. arenaria*$\leq$10 mm SL at Hartney Bay was the only variable to vary by date (Table 2).

For the two sampling areas on the Copper River Delta (Eyak and Pete Dahl), *M. arenaria* were largely restricted to low tidal elevations. Because *M. arenaria* were rare at Pete Dahl (combined densities of both size classes averaged across all sampling dates equalled 0 m^{-2} at high and mid plots and 3.2 m^{-2} at low tide plots) no statistical analysis was performed for *M. arenaria* for this area. At Eyak, *M. arenaria* were found almost exclusively at low tidal elevations. Abundances of both size classes of *M. arenaria* at Eyak were higher at low tide plots than at either mid or high tide plots ($p < 0.05$ for both post hoc contrasts) with no difference detected between high and mid tide plots ($p > 0.05$ for post hoc contrast). For *M. arenaria* $\leq$10 mm, the average abundance over all collection dates was 44.0 ± 22.1 m^{-2} (± 1 standard error) at low, 2.6 ± 2.6 m^{-2} at mid and 0 m^{-2} at high tide plots at Eyak (Fig. 2). Abundances of *M. arenaria* $>$10 mm averaged over all collection dates were 44.3 ± 16.5 m^{-2} at low, and 0 m^{-2} at mid and high tide plots (Fig. 2).

For the Hartney Bay sites, the two size classes of *M. arenaria* showed strikingly different patterns with tidal elevation. Highest abundances of *M. arenaria* $\leq$10 mm at Hartney Bay were consistently found at low tide plots (129.3 ± 58.7 m^{-2}; Fig. 3) compared with 7.0 ± 7.0 m^{-2} at high, 12.8 ± 9.5 m^{-2} at mid, and 7.0 ± 7.0 m^{-2} at mid-mussel plots. Irrespective of tidal elevations (no interaction between date and elevation was detected, Table 3), abundances of *M. arenaria*$\leq$10 mm were higher in April 2001 than in

Table 3
Results of a two-factor analysis of variance testing whether sampling date, tidal elevation or their interaction affect the transformed ($\sqrt{\#\,\mathrm{m}^{-2}+0.5}$) abundance of *Mya arenaria* $\leq$10 mm and $>$10 mm in shell length at Eyak

Variable	Factor	df	Sum of Squares	F	p	SNK post hoc summary
Mya $\leq$10 mm	Date	3	10.0	0.3	0.858	ns
	Elevation	2	92.2	3.5	0.046	Low > high, mid
	Date * Elevation	6	8.3	0.1	0.995	ns
	Residual	24	317.2			
Mya $>$10 mm	Date	3	6.5	0.3	0.856	ns
	Elevation	2	77.5	9.1	0.001	Low > high, mid
	Date * Elevation	6	2.2	0.3	0.952	ns
	Residual	24	204.2			

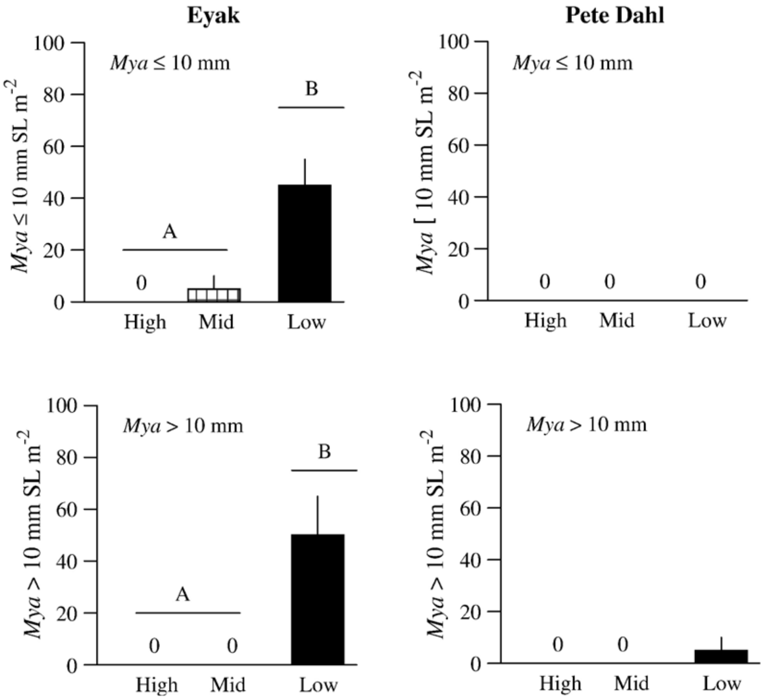

Fig. 2. Mean abundances of *Mya arenaria* + 1 standard error averaged across all sampling dates at Eyak and Pete Dahl sites. High, mid, and low refer to differing tidal elevations (see text for a full description).

June 2001, September 2001, and September 2002 ($p < 0.05$ for all SNK post hoc contrasts). Abundances of *M. arenaria* >10 mm (Fig. 3), which did not differ among collection periods, were lower at low (0 m^{-2}) and mid-mussel plots (2.3 ± 2.3 m^{-2}) than at mid (81 ± 19 m^{-2}) and high tidal elevation plots (29.1 ± 11.9 m^{-2}, $p < 0.05$ for all SNK post hoc contrasts). Mid tidal elevation plots had higher abundances of *M. arenaria* than high tide plots ($p < 0.05$ for all SNK post hoc contrasts).

For the Hartney Bay low tide plots, the vast majority (98%) of *M. arenaria* were 0 age class (no annuli formed) and ranged from 1.5 mm to 5 mm in SL. Only two clams were found that were >10 mm SL and both were <20 mm SL. A similar size distribution was found at the mid-mussel plots, although only nine clams were collected over the study period (Fig. 4). For high and mid tide plots at Hartney Bay, *M. arenaria* representing the full range of 2 to 65 mm were collected. The vast majority of clams at the low tidal elevation site at Eyak ranged in size from 2 mm to 25 mm SL (0–2 y old clams, see Table 4) with only two clams found at 45–50 mm SL (5 and 6 y old). The oldest clam collected in our study was aged at 11 y and had a shell length of 80.5 mm.

4. Discussion

Mya arenaria has successfully colonized areas in the estuarine portion of the Copper River Delta and southeastern Prince William Sound. Abundances of *M. arenaria* were lowest at Pete Dahl, an area that experiences high turbidity and low salinities (2–26 psu, Powers et al., 2002) due to its proximity to the Copper River. In contrast, abundances of *M. arenaria* were highest at Hartney Bay, an area of low turbidity and high, stable salinity (23–34 psu, Powers and Bishop, unpubl. data), and at low tidal elevation sites at Eyak, an area of higher salinity (10–30 psu) and less turbid waters than Pete Dahl. This pattern suggests that the distribution of *M. arenaria* among our three areas may be influenced by low salinity and high turbidity levels associated with riverine outflow. Nichols et al. (1990) in their study of the benthic community of San Francisco Bay suggested a similar mechanism for changes in the distribution of *M. arenaria*. A review of relevant literature on physiology of *M. arenaria* indicates that both low salinity and increased turbidity reduce *M. arenaria* growth and may lead to reduced survivorship (Grant and Thorpe, 1991; Kube et al., 1996). Alternative explanations for differences among our areas include differential larval supply and settlement and/or predation pressures (Strasser et al., 1999; Hunt and Mullineaux, 2002; Armonies and Reise, 2003). Because of the difficulty in working in this geographically isolated area, experimental tests of these competing hypotheses could not be conducted. However, otter trawl surveys conducted in 2002 and 2003 revealed a similar suite of fish and invertebrate predators among the three areas (Powers and Bishop, unpubl. data) and thus provide no indirect support for the predation hypothesis.

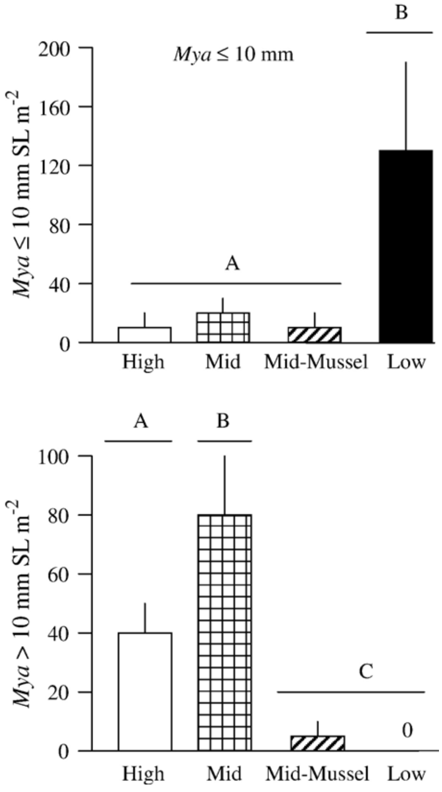

Fig. 3. Mean abundances of *Mya arenaria* + 1 standard error averaged across all sampling dates at Hartney Bay sites. High, mid, mid-mussel and low refer to differing tidal elevations (see text for a full description).

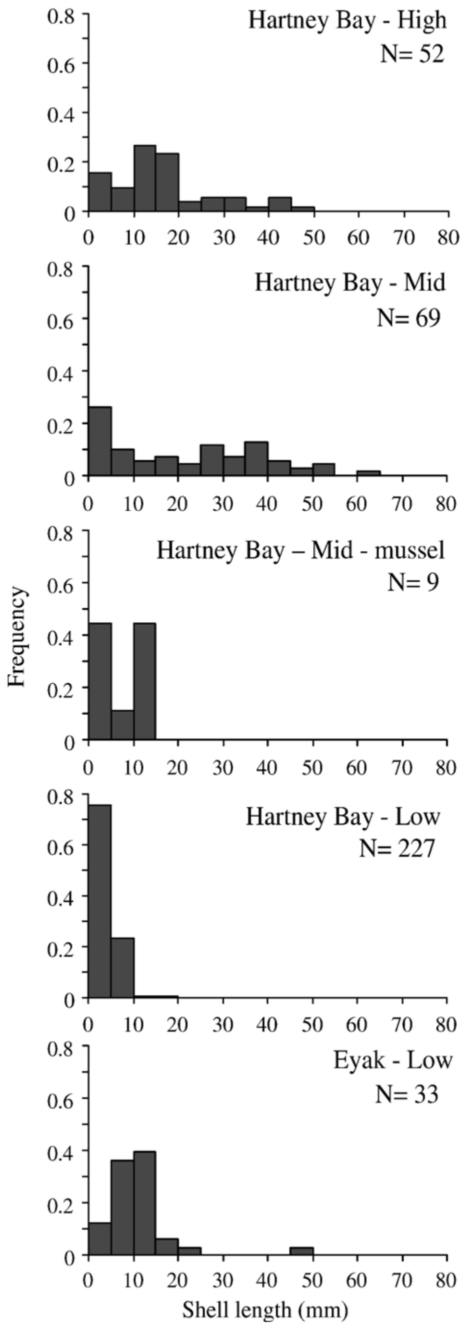

Fig. 4. Relative frequency distributions for *Mya arenaria* by shell length for the four tidal elevations sampled at Hartney Bay and the low tide plots for Eyak. *M. arenaria* were rare at mid and low tidal elevation plots at Eyak and at all Pete Dahl sites. Data presented are inclusive of all sampling dates with N denoting the total number of clams that were measured for each site.

Smaller-scale distributions of *M. arenaria* (i.e., among tidal elevations within an area) at the two Copper River Delta sites also suggest reduced suitability of areas that experience low salinity and high turbidity. Within the Pete Dahl area, *M. arenaria* was found only at the low tide plots, which were furthest away from the influence of the Copper River and closest to the Gulf of Alaska waters. Within the Eyak area, *M. arenaria* was found primarily at low tide plots, although a few individuals were found at mid tide plots. As was the case with Pete Dahl, low tide plots were the furthest away from the influence of the Copper River as well as the Scott and Sheridan Rivers, all glacial-fed rivers with high suspended solid loads. The only bivalve that was present in high densities within all three tidal elevations at both Pete Dahl and Eyak areas

Table 4
Number of individuals aged, average size and age of *Mya arenaria* collected on tidal flats at Hartney Bay and the Copper River Delta, Alaska during the present study and Simpson Bay (North of the study area) by Feder and Paul (1974)

Year Class	This Study			F & P			M & G
	N	Mean shell length (mm)	SD shell length (mm)	N	Mean shell length (mm)	SD shell length (mm)	
0*	199	3.5	1.6	4	9.87	1.8	–
1	31	9.5	3.1	33	13.41	1.1	9.1
2	14	14.0	4.0	13	17.73	2.8	14.5
3	28	19.25	5.3	9	26.04	2.4	19.6
4	12	28.9	8	13	30.87	2.4	23.5
5	6	33.6	8.9	24	39.01	3.2	27.1
6	10	42.1	4.1	21	48.15	3.8	30.6
7	4	44.8	5.8	7	57.5	4.7	33.4
8	2	45.8	9.2	16	64.96	3.4	–
9	2	50.9	13.0	19	73.42	3.1	–
10	0	–	–	11	77.95	4.4	–
11	1	80.5	–	5	76.88	3.3	–
12	0	–	–	3	85.07	1.9	–

Average shell length at is also given for the White Sea (Maximovich and Guerassimova, 2003) an area at a similar latitude to our study.
* Age 0 in Feder and Paul (1974) is equivalent to age 1 in our study and Maximovich and Guerassimova (2003).

was *Macoma balthica*, a species which tolerates much lower salinity values than other marine bivalves (Segerstråle, 1960).

In contrast to the two Copper River Delta sampling areas, *M. arenaria* was present at all tidal elevations at Hartney Bay. However, differences were found between the distribution of small (≤10 mm SL) and large (>10 mm SL) *M. arenaria* among the four tidal elevations sampled (high, mid, mid-mussel and low). Small *M. arenaria* were found in greatest abundance at the low tidal elevation sampling plots, whereas larger individuals (size range of 10 to 65 mm, Fig. 4) were found in greatest number at the mid and high tide plots. Differences in the distribution of the two size classes of *M. arenaria* are likely to result from post-settlement movement and/or size-selective predation.

Postlarval transport of *M. arenaria* (2 mm to 15 mm SL) has been reported in several tidal flat areas (Baggerman, 1953; Matthiessen, 1960; Günther, 1992; Armonies, 1996; Hunt and Mullineaux, 2002) and is more common in higher energy, sandy sediments (Emmerson and Grant, 1991). Sediments at the low tidal site at Hartney Bay are dominated by coarse sands, whereas sediments at higher tidal elevations are dominated by silts and clays. This sediment pattern is probably due to differences in current velocities suggesting that erosive conditions exist at low tidal elevations but not mid and high tide. The large peak in the density of small *M. arenaria* in April 2001 did not persist into the June 2001 sampling, indicating that mortality or emigration from low tidal plots was substantial during this two-month window. In their investigation of the effects of both size-selective predation and post-settlement dispersal on *M. arenaria* in a New England tidal flat community, Hunt and Mullineaux (2002) concluded that the loss due to predation was considerably larger than the flux due to transport for individuals >2 mm. At Hartney Bay, predation by the several thousand migrating shorebirds that visit this area between late April and early May (Senner et al., 1989; Bishop et al., 2000) or by flatfishes and *Crangon* shrimp, both of which have been collected in large numbers near the study area (Powers and Bishop, unpubl. data), could have contributed to the decreased abundance of small *M. arenaria* (Pihl, 1982; Pihl and Rosenberg, 1984).

Distribution of *M. arenaria* within intertidal sediments on the Copper River Delta is similar to patterns reported from intertidal areas in the Wadden and White Seas in Europe. The pattern we observed at Eyak and Pete Dahl of high densities at low tidal elevation is similar to that reported by Günther (1992), Armonies (1996), Strasser et al. (1999), and Maximovich and Guerassimova (2003). The results of our Hartney Bay surveys are consistent with this pattern in that recently settled juveniles (≤10 mm SL) were most abundant at low tide plots; however, *M. arenaria,* particularly those >10 mm SL, were abundant at mid and high tide plots. Matthiesen's (1960) study of the intertidal benthos along the USA northeast Atlantic coast noted that small *M. arenaria* (2–15 mm SL) changed their distribution with tidal elevation: small *M. arenaria* migrated from low tidal elevation plots to higher intertidal elevations. In contrast, Günther (1992) reported no such redispersal of *M. arenaria*, but did report shoreward migration of *M. balthica*. It should be noted that while there is similarity in our distributional patterns with the above referenced studies, both the density and length at age measured on the Copper River Delta and Hartney Bay are considerably lower than those reported in the Wadden Sea and the Northeast coast of North America. *M. arenaria* density in our study averaged 30 m^{-2} over all tidal ranges with a range of 0–280 m^{-2}; a density 1 to 2 orders of magnitude lower than those reported in the Wadden Sea (e.g., Günther, 1992) and much more similar to those reported for the White Sea where mean density ranges from 10 to 260 m^{-2} (Table 1 in Maximovich and Guerassimova, 2003). Length at age measurements from our study are also similar to those reported for the White Sea by Maximovich and Guerassimova (2003) for the first 4–5 y of life, but our values tend to be higher for the remaining years (Table 4).

M. arenaria appears to have established persistent populations within the Copper River Delta and southeastern Prince William Sound based on Feder and Paul's (1974) and Senner et al.'s (1989) earlier work and the range of year classes represented in our study (Fig. 4, Table 4). Although densities are relatively low compared to more temperate areas, the distributional patterns seem to have a high degree of similarity with patterns recorded in European estuaries. A major limitation to the study of *M. arenaria* in Alaska is the lack of research on the spawning cycle of this animal. This void may explain the difference in length at age estimates between our study and Feder and Paul (1974), which was conducted in Simpson Bay, an area 40 km N of our study site. Feder and Paul (1974) reported an average size of 9.5 mm for age 0 clams collected in mid-May; however, settlement of *M. arenaria* would be expected to occur much later in the summer based on the May–June peak in larval supply observed in the Wadden Sea (Strasser and Günther, 2001) or mid-summer peak in the White Sea (Maximovich and Guerassimova, 2003). These observations coupled with the difficulty in observing the first over-winter annulus in *M. arenaria* (Maximovich and Guerassimova, 2003) suggests that clam age is off by one year in Feder and Paul (1974). If this is the case, then our length at age estimates would be in general agreement with Feder and Paul (1974).

Acknowledgements

This research was funded by a grant from the Prince William Sound Oil Spill Recovery Institute. John Tucker (Wilderness Helicopters) was critical to the success of this project in providing transportation to and from the Delta field sites. We also acknowledge the help of Erica Clesceri in field collections and Melissa Boykin, Christina Talent and Kevan Gregalis for their assistance in the processing of samples. This manuscript was improved by the comments of J.J. Beukema and three anonymous reviewers.

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