

Distribution of Macroinvertebrates Across a Tidal Gradient, Marin County, California

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ABSTRACT

The distribution of macroinvertebrates across a tidal gradient is described from a study of invertebrate distribution across tidal marsh sub-habitats, a non-quantitative survey of epifauna on intertidal rocky substrate, and a few additional observations and records from China Camp State Park, Marin County, California. In the tidal marsh study, invertebrates were sampled from distinct sub-habitat types: high-order channels, low-order channels, vegetated marsh plain, and natural levees adjacent to channels. Invertebrates were collected using a variety of trapping methods to account for capture biases associated with any one method. All common invertebrate taxa were significantly more abundant in a particular sub-habitat, and within each trapping method a few species accounted for most of the biomass. On intertidal rocks, 79% of the taxa identified to species or genus were exotic, but a few native species were common.

KEY WORDS

Macroinvertebrate, intertidal, food web, tidal marsh, tidal gradient, salt marsh, exotic species, San Francisco Bay, China Camp State Park

INTRODUCTION

Intertidal habitats present a harsh physical environment for resident invertebrates. Twice daily tides subject terrestrial invertebrates to the risk of drowning, and aquatic invertebrates to the risk of desiccation. Inundation periods and sediment properties vary across the intertidal gradient, and environmental conditions change rapidly with inundation and exposure. Physical and biological conditions change over small spatial scales, because slight changes in elevation translate to large changes in hydrology, geomorphology, and vegetation (Collins and others 1986; Pennings and Callaway 1992).

Distribution of rocky intertidal invertebrates varies over both large and small spatial scales as a result of differences in dispersal, recruitment, and response to changes in microhabitat between species (Underwood and Chapman 1996). The small-scale zonation of rocky intertidal invertebrates results from a combination of physiological limitations and ecological interactions (Tomanek and Helmuth 2002).

Within tidal marshes, distinct sub-habitats—from large, high-order channels to small, low-order channels, to marsh plain and natural levee—are found adjacent to each other along the tidal gradient, sometimes changing abruptly from one meter to the next. Marsh invertebrate communities vary by sub-habitat, with many species showing a preference for particular elevations, vegetation zones or substrate types

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(Teal 1962; Davis and Grey 1966; Levin and Talley 2000).

Invertebrates constitute much of the secondary productivity in tidal marshes (Teal 1962), and play a critical role in transferring primary productivity up the food web, forming a substantial part of the diet of many resident marsh vertebrates (Grenier and Greenberg 2005). Because few seeds and fruits in the marsh are available for foraging terrestrial vertebrates (Greenberg and others 2006), the distribution and diversity of invertebrates largely determines the food resources available for secondary consumers, and influences their foraging behaviors. Invertebrates constitute a substantial portion of the diet of many common marsh fish species as well (Visintainer and others 2006).

This paper provides original data on the distribution of macroinvertebrates across a tidal gradient, and reviews what is known about the diversity, distribution, and abundance of intertidal invertebrates at China Camp State Park in Marin County, California, a National Estuarine Research Reserve Site.¹ In this paper, we present data from two studies, one of tidal marsh invertebrates and the other of rocky intertidal invertebrates. Most of the previously available invertebrate data from China Camp focus on predation of invertebrates (Dean and others 2005; Visintainer and others 2006) rather than on their diversity and distribution. We also briefly discuss the implications of invertebrate distribution and diversity on the behavioral ecology of their predators.

METHODS

Study Area

China Camp State Park contains 180 ha of tidal marsh, located on the western edge of San Pablo Bay in Marin County, CA (38°00'45" N, 122°29'25" W). San Pablo Bay is subject to semi-diurnal tides and has a Mediterranean climate with mild, wet winters and warm, dry summers. The upper part of the

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intertidal zone, above roughly mean high water, is occupied by salt marsh, with mudflats below that. Rock outcrops and boulders are exposed on the low intertidal mudflats near a small island known as Rat Rock. The salt marsh is composed of a mix of ancient and centennial marsh, with the centennial marsh having accreted along the bayward edge over the last 150 years, likely due to the deposition of Gold Rush hydraulic mining sediments (Jaffe and others 2007).

The salt marsh at China Camp includes several distinct sub-habitats along a tidal gradient, each with distinct vegetation and hydrology (Figure 1). The dendritic tidal conveyance network comprises high-order channels that receive tides twice daily, and low-order channels that are smaller and at slightly higher elevation, and, thus, receive less frequent tidal inundation. Pacific cordgrass (*Spartina foliosa*) grows inside the banks of the high-order channels; the low-order channels are unvegetated (though they may be overhung by pickleweed, *Sarcocornia pacifica*, or other vegetation). Low-order channels peter out into the marsh plain, which, in turn, receives less frequent tidal inundation than the channels. Marsh plain is the most extensive sub-habitat in the marsh, extending from mean high water to slightly above mean higher high water, dominated by pickleweed, a low-growing succulent halophyte, with other common marsh plants interspersed (primarily *Jaumea carnosa*, *Distichlis spicata* and *Frankenia salina*; Goals Project 2000). Natural levees build up along the edge of channels as coarse sediments are deposited by over-

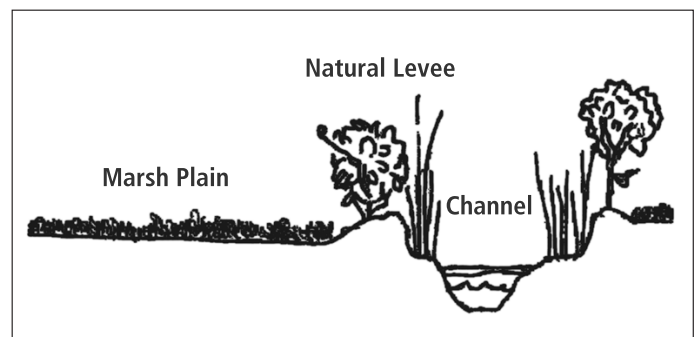


Figure 1 Sub-habitats of the China Camp tidal marsh. Channels are bordered by natural levees with vegetation dominated by *Grindelia stricta* and *Sarcocornia pacifica*. The marsh plain adjacent the natural levee is slightly lower in elevation and is dominated by *S. pacifica*.

banking tides (Collins and others 1986). These levees are dominated by gumplant (*Grindelia stricta*), a short woody shrub. Levees are higher and wider, and *Grindelia* is more abundant, along high-order channels. Consequently, flood tides overflow low-order channels first, wetting the marsh plain near small channels more frequently and for longer periods than near large channels (Collins and others 1986).

Tidal Marsh Invertebrate Study

Invertebrates at China Camp marsh were collected from the channels, marsh plain, and natural levees as part of a food web study reported in greater detail by Grenier (2004). Invertebrates were collected to investigate which taxa were available as potential prey items for the San Pablo Song Sparrow (*Melospiza melodia samuelis*), a tidal marsh obligate, and other marsh vertebrates; and to determine how macroinvertebrates were distributed across the tidal gradient. Because no single method was sufficient to account for all invertebrate locomotion types and habitat preferences, multiple trapping methods were used. We conducted the study in a 3.3-ha plot within the centennial portion of the marsh, which is characterized by the simple, less sinuous channels typical of a rapidly formed marsh.

Sample Collection

We conducted sampling at low tide from May to July, 2001, which consisted of five capture methods: pit trap, sweep net, snail count, mud core, and sticky trap. We expended equal sampling effort along high-order and low-order channels. For each channel type, we stratified random sampling locations across three sub-habitats: within the channel, on the natural levee adjacent to the channel, and on the nearby marsh plain. No samples were taken in standing water. We recorded the plant species within 10 cm of each trap.

We conducted pit trap, sweep net, and snail count methods with equal effort in each of the sub-habitats. Pit traps were cylindrical plastic containers, 11 cm in diameter and 11 cm deep, buried in the sediment, with the top of the trap level with the ground, and no space between the container and the surrounding

sediment. Traps were open for at least 3 hours. Sweep net sampling consisted of 10 strokes with a 15-inch diameter sailcloth net; each stroke sweeping new vegetation. Snail counts consisted of counting all snails within a 22-cm x 22-cm quadrat.

We used mud core and sticky trap methods only in the channels, because (1) on the natural levees and marsh plains, pilot mud core samples consisted of dry, hard-packed sediment devoid of macroinvertebrates, and (2) pilot sticky trap samples replicated results from pit traps and sweep nets in natural levee and marsh plain habitats. Cores were 7 cm in diameter and 10 cm deep, and we collected organisms from them with a 0.5-mm mesh sieve. For each core, we recorded the relative abundance of roots on a scale of 0 to 3, with 0 indicating no roots and 3 indicating very dense roots. Sticky traps were a thin layer of Tanglefoot adhesive spread onto sheets of plastic (20 x 10 cm) that were placed on the sediment. We set the traps for at least 3 hours and checked frequently as the tide rose; if the traps were in jeopardy of flooding, we moved them to adjacent higher ground.

Sample Processing

Common invertebrates were identified to the lowest feasible taxonomic level with assistance from experts (see "Acknowledgements"). We determined average biomass for large or common taxa (<10 individuals per trap method) by weighing between 9 and 115 individuals per taxon, after drying at 55 °C until we achieved a constant weight. Snails were weighed without their shells. Because planthoppers (*Prokelisia marginata*) had such low mass, they were weighed in groups of 10 individuals at a time. We estimated masses for araneid spiders from lycosid spiders of similar size.

Data Analysis

We calculated catch per unit effort (CPUE) as the number of invertebrates of the same taxon caught per trap hour for pit traps and sticky traps, and as invertebrates per trapping event for all other capture methods. We examined differences in CPUE among sub-habitats using non-parametric ANOVA

(Kruskal–Wallis), which was also used to determine the relationship between CPUE and presence of roots, and CPUE and plant community composition. The relationship between CPUE and plant community composition was examined separately for each of the sub-habitats along the tidal gradient, because vegetation varied dramatically among sub-habitats. We tested plant-invertebrate relationships in the channel sub-habitat separately for large and small channels, because *Spartina foliosa* was found only in large channels.

Rocky Intertidal Invertebrates

During low tide on November 15, 2005, A. Cohen collected by hand and identified organisms on and around a low intertidal rocky outcrop and boulders near Rat Rock at China Camp State Park with a 10-power hand lens. The sampling was conducted as a component of ongoing surveys for the State of California’s Marine Invasive Species Program, with the goal of characterizing and monitoring the

distribution and abundance of exotic species in California’s coastal waters. Some of these samples, along with quantitative samples from nearby quadrats, were preserved for identification in the laboratory. We report here only on the initial field identifications.

RESULTS

Tidal Marsh Invertebrates

A total of 4,597 invertebrates was captured in 787 trapping events, representing seven taxonomic classes and at least 14 orders (Table 1). Six of the seven taxa identified to species (85.7%) were exotic (most of the arthropods were not identified to species). As expected, community composition of invertebrates differed notably by capture method, and one taxon dominated captures for most trapping methods. The amphipod *Traskorchestia traskiana* comprised 77% of the individuals caught by pit trap; the planthopper *Prokelisia marginata* comprised 64% of the individu-

Table 1 Number of invertebrates collected in the tidal marsh study by each capture method

Phylum	Class	Order	Family	Genus and Species	Common Name	Mud Core	Pit Trap	Sweep Net	Snail Count	Sticky Trap
Annelida	Oligochaeta				Oligochaete worm	655	–	–	–	–
	Polychaeta	Phyllodocida	Nereididae	<i>Alitta succinea</i> ^a	Polychaete worm	2	–	–	–	–
		Other Polychaetes				Polychaete worm	131	–	–	–
Mollusca	Gastropoda	Basommatophora	Ellobiidae	<i>Myosotella myosotis</i> ^a	European marsh snail	1	3	22	866	2
	Bivalvia	Veneroida	Tellinidae	<i>Macoma petalum</i> ^a		39	–	–	–	–
Arthropoda	Crustacea	Amphipoda	Corophiidae	<i>Corophium alienense</i> ^a	Aquatic amphipod	195	3	–	–	–
			Corophiidae	<i>Grandierella japonica</i> ^a	Aquatic amphipod	98	–	–	–	–
			Talitridae	<i>Traskorchestia traskiana</i>		–	602	4	–	4
	Arachnida	Araneae	Araneidae		Orb spider	–	4	44	–	–
			Lycosidae		Wolf spider	–	26	2	–	–
			Other Arachnida		Spider	2	7	38	–	1
	Insecta	Coleoptera	Heteroceridae		Mud-living beetle	41	3	–	–	–
			Curculionidae		Weevil	–	–	7	–	–
			Carabidae	<i>Bembidion sp.</i>	Ground beetle	–	65	1	–	–
			Chrysomelidae		Spotted cucumber beetle	–	–	13	–	–
Other Coleoptera				Beetle adult	1	5	17	–	–	
				Beetle larvae	14	52	–	–	–	
Diptera		Dolichopodidae			Long-legged fly	–	–	116	–	544
		Ulidiidae			Picture-winged fly	–	–	25	–	–
		Other Diptera				–	–	86	–	99
Homoptera	Delphacidae	<i>Prokelisia marginata</i> ^a		Planthopper	–	–	703	–	1	
	Other Homoptera			Leafhopper	–	1	11	–	–	
Hemiptera					–	–	9	–	–	
Lepidoptera				Moth	–	–	4	–	–	
Other Insecta				Insect	1	1	6	–	–	

^a Indicates an exotic species.

als caught by sweep net. Oligochaete and polychaete worms made up 67% of mud core captures and dolichopodid flies made up 83% of individuals caught by sticky trap.

Pit trap biomass was dominated by one species across all sub-habitats, while sweep net biomass was dominated by different taxa in each sub-habitat (Figures 2 and 3). Mass (\pm 1 SD) of common taxa ranged from 0.26 (\pm 0.07) mg/individual for *Prokelisia marginata* to 8.65 (\pm 6.70) mg per individual for *Traskorchestia traskiana* (Table 2). The mean biomass per quadrat for the snail *Myosotella myosotis* was 15.7 mg on the marsh plain, and 25.5 mg on the natural levee, with no snails observed in the channels.

The abundance of common taxa differed by sub-habitat (Table 3). Channel size also influenced inver-

tebrate community composition, with several common taxa being more abundant near either low-order or high-order channels (Table 4). The burrowing amphipod *Corophium alienense* was the only species whose abundance was related to the density of plant roots, being more abundant in areas with lower root density (Kruskal-Wallis; $H = 14.57$, $n = 72$, $p = 0.02$).

The abundance of *Corophium* amphipods, *Macoma petalum* clams, and *Prokelisia* planthoppers was related to plant distribution. The burrowing amphipods and clams were more likely to be found in large channels where *Spartina foliosa* was not present (*C. alienense*: Mann-Whitney $U = 223.5$, $n = 36$, $p < 0.001$; *M. petalum*: Mann-Whitney $U = 223$, $n = 36$, $p < 0.001$), while planthoppers were more likely to be found in channels where *S. foliosa* was present (Mann-Whitney $U = 94$, $n = 36$, $p < 0.001$).

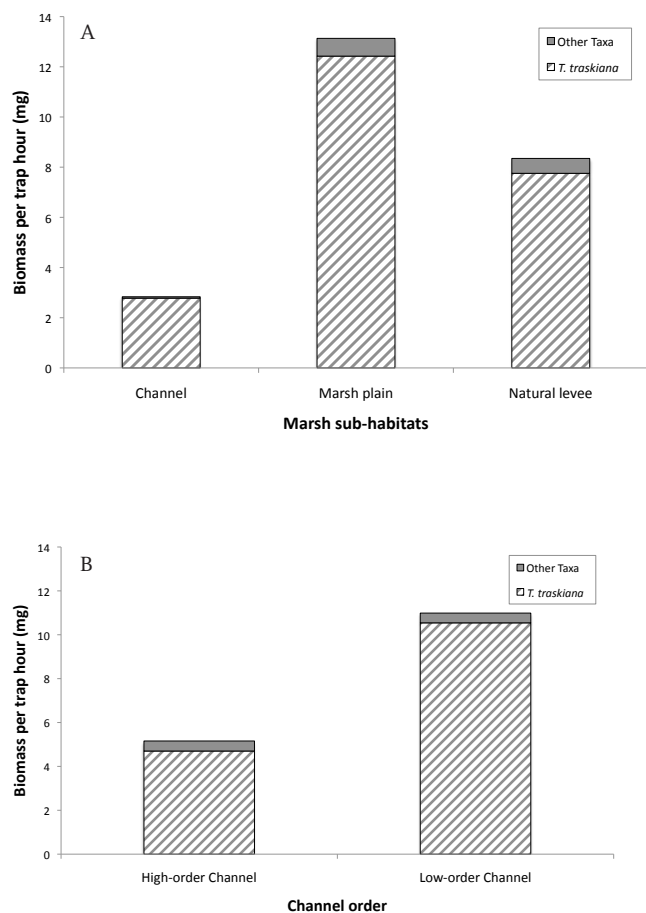


Figure 2 Mean biomass per trap hour for pit traps by (A) marsh sub-habitat and (B) channel order

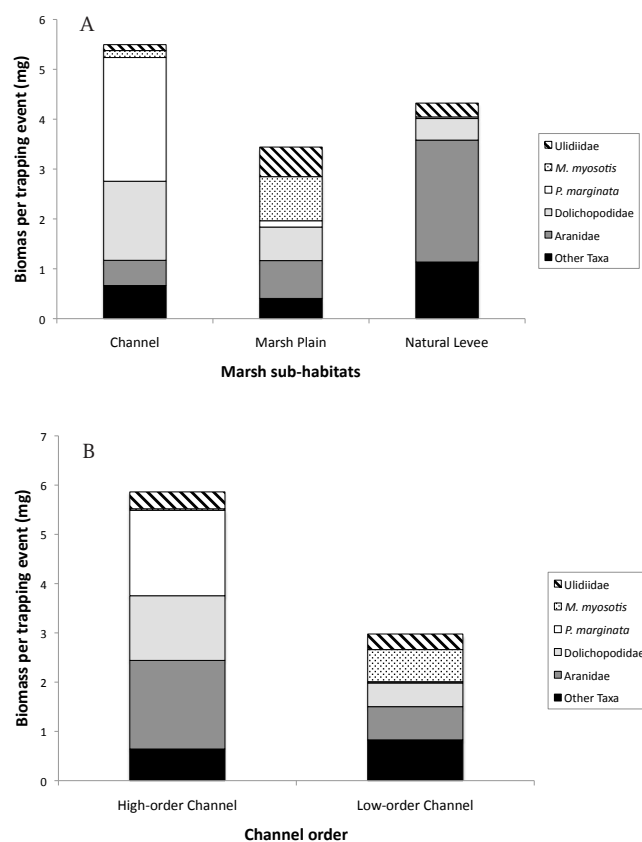


Figure 3 Mean biomass per trapping event from sweep netting by (A) marsh sub-habitat and (B) channel order

Table 2 Individual mass (± 1 SD) for common taxa caught by sweep net and pit trap

Taxon (Order)	n (Weighted)	Mean biomass	(mg)
<i>T. traskiana</i> (Amphipoda)	99	8.65	± 6.70
Chrysomelidae (Coleoptera)	26	7.15	± 2.06
Lycosidae (Araneae)	26	6.07	± 4.20
<i>M. myosotis</i> (Basommatophora)	60	3.35	± 1.44
Ulidiidae (Diptera)	25	2.85	± 1.16
Curculionidae (Coleoptera)	9	2.49	± 0.28
Heteroceridae (Coleoptera)	16	1.96	± 0.75
Dolichopodidae (Diptera)	113	1.73	± 0.61
<i>Bembidion</i> sp. (Coleoptera)	42	1.68	± 0.42
Corophiidae (Amphipoda)	11	0.45	± 0.25
<i>P. marginata</i> (Homoptera)	40	0.26	± 0.07

Rocky Intertidal Invertebrates

Invertebrates from nine classes and at least 16 orders were observed in the epifaunal survey (Table 5). Of the 28 taxa identified to genus or species, 22 (78.6%) are known to be exotic.

Additional Records

In addition to the taxa above, several invertebrates that had been seen but not captured during the quantitative tidal marsh study were hand-collected for identification. These taxa included the European green crab (*Carcinus maenas*), the yellow shore crab (*Hemigrapsus oregonensis*), two species of shrimp (*Palaemon macrodactylus* and *Crangon franciscorum*), the Eastern mud snail (*Ilyanassa obsoleta*), stinkbugs in the family Pentatomidae, and mites in the family Tetranychidae.

Other invertebrates we commonly observed at China Camp include the isopod *Sphaeroma quoiana*, whose pencil-diameter burrows riddle the channel banks and may contribute to their slumping and erosion, and the small, commensal isopod *Iais californica*, which lives on *Sphaeroma*'s ventral surface. Both of these species are from Australia. The ribbed horse mussel *Geukensia demissa*, an import from the Atlantic, lives in the lower channels and at the marsh edge, attached by byssal threads to subsurface *Spartina* stems or other objects.

DISCUSSION

The data presented in this paper demonstrate the unequal distribution of invertebrates across intertidal sub-habitats at China Camp State Park in San Francisco Bay. Relatively few species made up the majority of the invertebrate biomass in the tidal marsh, and the majority of both the rocky intertidal invertebrates and the tidal marsh invertebrates identified to species level were exotic. The strong association of certain invertebrate groups to specific sub-habitats suggests that predators with different feeding specializations may forage primarily in one part of the marsh or another.

Invertebrate Diversity

Two general groups of intertidal invertebrates were collected at China Camp: those that belong to taxonomic groups that are primarily land-dwelling (terrestrial-derived invertebrates), and those belonging to taxonomic groups that are mostly marine-dwelling (marine-derived invertebrates). While only marine-derived invertebrates were found in the rocky intertidal habitat, both marine- and terrestrial-derived invertebrates were found in the tidal marsh. The terrestrial-derived invertebrates included spiders, insects, oligochaetes, and the pulmonate snail *Myosotella myosotis*; the marine-derived invertebrates included sponges, cnidarians, polychaete worms, opistho-

Table 3 Catch per unit effort (CPUE) by sub-habitat for pit trap and sweep net samples. *P*-values are from Kruskal–Wallis tests (alpha = 0.05). Bold text indicates the zone with the highest CPUE.

Capture method	Taxon (Order)	Total count (No. of trap hours to trapping events)			<i>p</i>
		Channel	Marsh plain	Natural levee	
Pit Trap	Lycosidae (Araneae)	0 (234)	13 (230)	13 (236)	0.001
	<i>Bembidion</i> sp. (Coleoptera)	0 (234)	44 (230)	21 (236)	< 0.001
	<i>T. traskiana</i> (Amphipoda)	69 (234)	318 (230)	215 (236)	< 0.001
	Heteroceridae larvae (Coleoptera)	52 (234)	0 (230)	0 (236)	< 0.001
Sweep Net	Chrysomelidae (Coleoptera)	1 (72)	3 (72)	9 (72)	0.014
	Aranidae (Araneae)	3 (72)	9 (72)	32 (72)	< 0.001
	Ulidiidae (Diptera)	2 (72)	15 (72)	7 (72)	0.002
	<i>P. marginata</i> (Homoptera)	689 (72)	5 (72)	9 (72)	< 0.001
	Dolichopodidae (Diptera)	70 (72)	28 (72)	18 (72)	0.016
Snail Count	<i>M. myosotis</i> (Basommatophora)	0 (72)	339 (72)	547 (72)	< 0.001

Table 4 Comparison of catch per unit effort (CPUE) of common taxa by channel order, summed across all sub-habitats. *P*-values are from Kruskal–Wallis tests (alpha = 0.05). Bold text indicates the channel size with the greatest CPUE, where results are significant.

Capture method	Taxon (Order)	Total Count (No. of Trap Hours to Trapping Events)		<i>p</i>
		Low-order Channel	High-order Channel	
Pit Trap	<i>T. traskiana</i> (Amphipoda)	418 (349)	187 (350)	< 0.001
	<i>Bembidion</i> sp. (Coleoptera)	37 (349)	28 (350)	0.673
	Lycosidae (Araneae)	12 (349)	14 (350)	0.91
Sweep Net	<i>M. myosotis</i> (Basommatophora)	21 (108)	1 (108)	0.01
	Aranidae (Araneae)	12 (108)	32 (108)	0.014
	<i>P. marginata</i> (Homoptera)	11 (108)	692 (108)	< 0.001
	Curculionidae (Coleoptera)	0 (108)	7 (108)	0.007
	Dolichopodidae (Diptera)	30 (108)	86 (108)	0.013
	Chrysomelidae (Coleoptera)	9 (108)	4 (108)	0.154
	Ulidiidae (Diptera)	12 (108)	13 (108)	0.827
Mud Core	Oligochaeta	108 (36)	19 (36)	0.001
	Polychaeta	424 (36)	231 (36)	0.011
	Heteroceridae (Coleoptera)	3 (36)	38 (36)	0.035
	<i>C. alienense</i> (Amphipoda)	26 (36)	72 (36)	0.801
	<i>M. petalum</i> (Veneroida)	13 (26)	26 (36)	0.822
	<i>G. japonica</i> (Amphipoda)	80 (36)	115 (36)	0.868
Sticky Trap	Dolichopodidae (Diptera)	278 (36)	266 (36)	0.83
Snail Count	<i>M. myosotis</i> (Basommatophora)	641 (108)	245 (108)	< 0.001

Table 5 Marine invertebrates collected on intertidal rocks at China Camp in November 2005 and identified in the field

Phylum	Class	Order	Family	Species	Common name	
Porifera	Desmospongiae	Halichondrida	Halichondriidae	<i>Halichondria</i> sp. ^{1,a}	sponge	
		Haplosclerida	Chalinidae	<i>Haliclona</i> sp. ^{1,a}	sponge	
		Other Desmospongiae			sponge	
Cnidaria	Hydrozoa				hydroid	
	Anthozoa	Actiniaria	Diadumenidae	<i>Diadumene</i> sp. ^{2,a}	anemone	
Diadumenidae			<i>Diadumene lineata</i> ^a	orange-lined anemone		
Annelida	Polychaeta	Phyllodocida	Nereididae	<i>Alitta succinea</i> ^a	pile worm	
			Polynoidae	<i>Harmothoe praeclara</i> ^{3,a}	scale worm	
		Other Polychaeta			polychaete worm	
Mollusca	Gastropoda	Cephalaspidea	Philinidae	<i>Philine</i> sp. ^{4,a}	tortellini snail	
		Other Opisthobranchia		unidentified opisthobranch	sea slug	
	Bivalvia	Ostreoida	Ostreidae	<i>Ostrea lurida</i>	Olympia oyster	
			Mytiloida	Mytilidae	<i>Geukensia demissa</i> ^a	ribbed horse mussel
		Mytiloida	Mytilidae	<i>Musculista senhousia</i> ^a	green bag mussel	
			Mytilidae	<i>Mytilus galloprovincialis</i> ^a / <i>trossulus</i> ⁵	bay mussel	
			Myoida	Corbulidae	<i>Corbula amurensis</i> ^a	overbite clam
		Veneroida	Myidae	<i>Mya arenaria</i> ^a	Atlantic softshell clam	
			Tellenidae	<i>Venerupis philippinarum</i> ^a	Japanese littleneck clam	
			Other Bivalvia		unidentified clam	clam
Arthropoda	Crustacea	Balanomorpha	Chthamalidae	<i>Chthamalus</i> sp. ⁶	barnacle	
			Balanidae	<i>Balanus glandula</i>	barnacle	
			Balanidae	<i>Balanus</i> sp.	barnacle	
		Isopoda	Sphaeromatidae	<i>Gnorimosphaeroma oregonensis</i>	isopod	
		Amphipoda	Gammaridae			amphipod
			Corophiidae or Aoridae		unidentified Corophiid or <i>Grandidierella japonica</i> ^{7,a}	amphipod
		Decapoda	Portunidae	<i>Carcinus maenas</i> ^a	green shore crab	
			Varunidae	<i>Hemigrapsus oregonensis</i>	yellow mud crab	
Bryozoa	Gymnolaemata	Ctenostomata	Nolellidae	<i>Anguinella palmata</i> ^a	bryozoan	
			Vesiculariidae	<i>Bowerbankia</i> sp. ^a	bryozoan	
		Cheilostomata	Membraniporidae	<i>Conopeum</i> sp. ^a	bryozoan	
			Cryptosulidae	<i>Cryptosula pallasiana</i> ^a	bryozoan	
			Schizoporellidae	<i>Schizoporella</i> sp. ^{8, a}	bryozoan	
Chordata	Ascidiacea	Pleurogona	Styelidae	<i>Botryllus schlosseri</i> ^a	seasquirt	
			Molgulidae	<i>Molgula manhattensis</i> ^a	seasquirt	

a exotic species

Taxonomic notes:

- 1 The sponges in San Francisco Bay in the genera *Halichondria* and *Haliclona* have been identified in many texts as the Atlantic species *Halichondria bowerbanki* and *Haliclona loosanoffi*, respectively, but some taxonomists have recently questioned these identifications.
- 2 Of the four exotic *Diadumene* species in San Francisco Bay, this is the orange- or salmon-colored one that has sometimes been listed as *D. cincta*, but according to Dr. Daphne Fautin of the University of Kansas is not that species.
- 3 Based on its abundance in other studies in San Francisco Bay, this is probably the Australian species *Harmothoe praeclara* and not the native (and primarily outer coast) species *H. imbricata*, but no morphological characters were examined that would distinguish the two.
- 4 At least four exotic *Philine* species have been reported in Central California: *P. auriformis* from New Zealand and *P. orientalis* from the Philippines and Hong Kong in San Francisco Bay and other waters; and *P. aperta* from South Africa and *P. japonica* from Japan in other Central California bays. This seems an unlikely convergence of multiple species in this one genus from distant corners of the world, and we consider the taxonomy of exotic *Philine* species on the west coast of North America to be yet unresolved.
- 5 The native species *Mytilus trossulus*, the Mediterranean species *M. galloprovincialis*, and hybrids of the two have all been reported in San Francisco Bay. Characters were not examined to distinguish among these. Based on the frequency of the exotic or hybrid forms in San Francisco Bay, these specimens were counted as exotic (see Results).
- 6 The native species *Chthamalus fissus* and *C. dalli* are both present in Central California; characters were not examined to distinguish between them.
- 7 The Corophiidae reported in San Francisco Bay west of the Carquinez Strait are *Corophium alienense*, *C. heteroceratum*, *Monocorophium acherusicum*, *M. insidiosum*, and *M. uenoi*—all of them exotic. The native Corophiidae reported in the San Francisco Bay watershed, *Americorophium spinicorne* and *A. stimpsoni*, are only found east of Carquinez Strait, usually in fresh water. The native *A. brevis*, once present in San Francisco Bay, is believed to be extinct south of Humboldt Bay. The Aoridae species *Grandidierella japonica*, from Japan, resembles the Corophiidae and is common in San Francisco Bay. Morphological characters were not examined to distinguish among these various species.
- 8 The *Schizoporella* species in San Francisco Bay was formerly identified in many texts as the Atlantic species *S. unicornis*, but may comprise more than one species. We consider the taxonomy of *Schizoporella* in San Francisco Bay to be unresolved.

branch snails, bivalves, crustaceans, bryozoans, and sea squirts (Tables 1 and 5). As is typical of San Francisco Bay, many of the marine-derived invertebrate species at China Camp have been introduced from other parts of the world, including the coasts of the North Atlantic Ocean, Pacific Asia, and Australia (Cohen and Carlton 1995).

Invertebrate Distribution

Tidal Marsh

Most taxa in this study showed a preference for a particular sub-habitat or channel order. In addition, one taxon dominated the catch for most trapping methods, reflecting whether the capture method was most likely to catch ground-crawling, flying, canopy-dwelling, or benthic invertebrates. These results suggest clear niche partitioning. Competition, predation, food resources, and limits of physiological tolerance likely all play a role in maintaining this uneven distribution of invertebrates.

Each tidal marsh sub-habitat differs in the frequency and duration of tidal inundation, and consequently varies in sediment moisture, oxygen, and salinity; sediment particle size and organic content; and vegetation (Levin and Talley 2000). Levin and Talley (2000) suggest these interrelated factors influence invertebrate distribution in tidal marshes on different spatial and temporal scales. Parameters such as marsh age, salinity, and elevation act over large time-scales to determine which species are present in a marsh; factors such as plant biomass and oxygen concentration affect invertebrates over shorter time-scales and smaller spatial scales, determining where in the marsh certain species will be found. The results from this study are consistent with previous studies showing that the community composition of invertebrates differs by elevation and vegetation zone (reviewed in Levin and Talley 2000).

The channels, being most frequently inundated, support invertebrates that prefer moist environments. Our study found that benthic epifauna were more abundant in the channel than in the higher-elevation sub-habitats. Similarly, studies of southern California

tidal marshes have found benthic infauna to be most abundant at lower elevations (Levin and Talley 2000). Risk of desiccation increases at higher elevation for these invertebrates (Kneib 1984).

The channels also supported the greatest number of insects at China Camp, particularly homopterans and dipterans. Davis and Gray (1966) found that many marsh insects respond to tidal flooding and drying with behavioral rather than physiological adaptations. Even species able to withstand long periods of submersion in laboratory experiments preferred to escape the rising tide by flying, swimming, or running along the water surface whenever possible. The ability of flying and hopping insects, such as homopterans and dipterans, to quickly escape rising tide waters and predators may explain their abundance in the channels, despite being taxa of terrestrial origin. Heterocerid beetles, found in the channels at China Camp, are one of the few families of Coleoptera with marine representatives (Doyen 1976). Wyatt and others (1986) suggest the shape of their burrows, which takes advantage of the surface tension effects of small air-filled openings, allows these beetles to protect their larvae from flooding in intertidal habitats.

Oligochaetes and polychaetes were most abundant in small channels; heterocerid beetles, Dolichopodid flies, and planthoppers were more frequently found in large channels. These invertebrates may be responding to physical differences among channel orders, or biotic differences in food resources, predation, or competition. The narrow width and overhanging vegetation of small channels may reduce drying, limit temperature increases, provide protection from terrestrial predators, or affect food availability by changing the composition of microalgae. Whitcraft and Levin (2007) found more insects and fewer amphipods and oligochaetes in unshaded than shaded plots in a southern California marsh, which they hypothesized was related to the presence of more cyanobacteria in unshaded plots and more diatoms in shaded plots. A similar mechanism could produce the trend seen at China Camp, if the smaller channels at China Camp were more shaded, which does seem to be the case, based on personal observations by the authors.

While the inner banks of the small channels at China Camp were unvegetated, scattered stands of Pacific cordgrass, *Spartina foliosa*, grew inside the banks of large channels. Planthoppers specialize on *Spartina* sap (Denno and others 1987), so it is not surprising that they showed a strong association with *Spartina*. *Corophium alienense* and *Macoma petalum* showed a significant negative association with *Spartina*. *Corophium* abundance was also negatively correlated with plant root density. Brusati and Grosholz (2006) found differences in the invertebrate community between the low-elevation *Spartina* marsh and the nearby mudflat at China Camp and other San Francisco Bay marshes, with greater infaunal density in the mudflat overall, although invertebrate density was higher in the *Spartina* zone at China Camp in one year of their study. Previous studies in California marshes have attributed decreases in abundance of some taxa near marsh vegetation to either a reduced availability of suspended particulates resulting from reduced flow speeds near vegetation (Levin and others 2006) or rhizomes interfering with burrowing (Brusati and Grosholz 2006). Flow of suspended particles would be important to both species that appeared to avoid *Spartina*, because *C. alienense* is a suspension feeder, and *M. petalum* is both a suspension feeder and a surface deposit-feeder.

In contrast to the channels, the marsh plain receives relatively fewer inundation events. Ground-crawling invertebrates such as the amphipod *Traskorchestia traskiana*, *Bembidion* beetles, and lycosid spiders were most abundant on the marsh plain. *T. traskiana* is one of the few salt marsh species able to feed on *Sarcocornia detritus* (Page 1997), which could explain its high population density and domination of invertebrate biomass on the marsh plain. *T. traskiana* was found in greater abundance in the marsh plain near smaller channels, suggesting that this species may prefer the more frequent wetting of this habitat, either to remain moist or to find richer bacterial and algal feeding deposits.

The natural levee, with the least frequent inundation of the three sub-habitats, had the greatest plant diversity of all the sub-habitats, and featured the only woody plant in the marsh: gumplant (*Grindelia stricta*). *Myosotella* snails were most abundant on

natural levees and were absent from the channels. These snails breathe through their lungs like their upland relatives (Cohen 2005); their low mobility likely puts them at risk of drowning in rising tidal waters, and may increase their risk of predation in open areas. The natural levee, with its relatively high elevation and abundant vegetative cover, may provide these snails with refuge from both tides and predators. However, these snails show a preference for the natural levee and marsh plain near low-order channels where inundation is more frequent than near high-order channels, suggesting they prefer a moist environment, despite their avoidance of channels. Araneid spiders were most abundant on the natural levee along large channels. The woody structure of the channel-side gumplant provides these spiders with support for their webs near channels where flying insects are most abundant.

Rocky Intertidal

A relatively diverse community of epifaunal invertebrates lives on low intertidal rocks near Rat Rock (Table 5), including a variety of attached filter-feeders (sponges, hydroids, anemones, oysters and mussels, barnacles, bryozoans, and sea squirts) and a few mobile worms and crustaceans. A handful of clam species were also found in the sediment at this site. While exotic species dominate this community, some natives are common. The dominant barnacles are the white acorn barnacle *Balanus glandula*, and a small, brown barnacle in the genus *Chthamalus*, both of which are native. The small native shore-crab *Hemigrapsus oregonensis* and the native isopod *Gnorimosphaeroma oregonense* are both common on or underneath rocks, and *Hemigrapsus* can also be abundant in the marsh channels. Native Olympia oysters, *Ostrea lurida*, were abundant on these rocks in the fall of 2005, but low salinities during the subsequent unusually wet winter and spring apparently eliminated the population.

Invertebrates as Food Resources

Salt marsh invertebrate communities are typically species poor but may be biomass rich (Kreeger and Newell 2000). Only a few species comprised the bulk

of macroinvertebrate biomass in the tidal marsh study (Figures 2A, 2B, 3A, 3B), although some other species not captured (e.g., *G. demissa* and *S. quoiana*) probably also accounted for significant invertebrate biomass in the marsh.

The strong association of certain invertebrate groups to specific sub-habitats suggests that predators with different feeding specializations may forage primarily in one part of the marsh or another. The distribution of invertebrates among the sub-habitats in our study suggests that the channels offer greater food resources for predators seeking aerial or benthic infaunal prey, while the marsh plain and natural levees offer the greatest resources for predators of surface-dwelling invertebrates. Studies of salt marsh Song Sparrow behavior and trophic ecology suggest that sparrows assimilate the majority of their carbon and nitrogen from invertebrates found on the marsh plain and natural levee (Grenier 2004). However, the dietary composition of most terrestrial marsh predators relative to the marsh sub-habitats has been little studied.

Marsh-feeding fish, on the other hand, have received slightly more attention. While high-marsh invertebrates were found to be an important source of food for fish such as longjaw mudsucker and killifish (*Fundulus parvipinnis*) in a southern California tidal marsh (West and Zedler 2000), stable isotope data suggest that longjaw mudsucker at China Camp were not assimilating invertebrates from the marsh plain as a significant proportion of their diet (Grenier 2004). Visintainer and others (2006) found that copepods, amphipods, mysids, and isopods made up a large portion of the diet of the most common fish species feeding in the China Camp marsh. They further found that stomach fullness and prey taxa richness in these fish varied with channel order in a species-specific way. This pattern supports the hypothesis from our tidal marsh study that unequal distribution of invertebrates by channel order may affect predator foraging patterns. Dean and others (2005) suggest that China Camp is a sink for mysid shrimp, with large mature mysids being heavily preyed upon by marsh fish and birds. Further study is needed to better understand how invertebrate distributions influence both predation patterns and trophic transfer between the China

Camp tidal marsh and adjacent upland and marine habitats.

Future Research

The results presented here contribute to understanding invertebrate diversity and distribution in the intertidal habitats of San Francisco Bay. However these short-term studies do not shed light on seasonal and inter-annual variation in invertebrate community structure. Future field studies on the diversity, distribution, and ecology of the intertidal invertebrate community of San Francisco Bay in various seasons and over longer time scales would improve our understanding of this fauna and its significance in the food web.

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