10. 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 Co., 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

10.1 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, as slight changes in elevation translate to large changes in hydrology, geomorphology, and vegetation (Collins et al. 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 (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). As there are few seeds and fruits in the marsh available for foraging terrestrial vertebrates (Greenberg et al. 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 et al. 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]. Data from two studies, one of tidal marsh invertebrates and the other of rocky intertidal invertebrates, are presented here. Most of the previously available invertebrate data from China Camp focus on predation of invertebrates (Dean et al. 2005, Visentainer et al. 2006) rather than on their diversity and distribution. The implications of invertebrate distribution and diversity on the behavioral ecology of their predators are also briefly discussed.

[1] The material in this article is also being published in the National Estuarine Research Reserve Special Issue of the journal *San Francisco Estuary and Watershed Science*, and in the book *Tidal Salt Marshes of the San Francisco Estuary: Ecology, Restoration, Conservation.*

10.2 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 a Mediterranean climate with mild, wet winters and warm, dry summers. The upper part of the 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 et al. 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 is comprised of high-order channels that receive tides twice daily and low-order channels that are smaller, at slightly higher elevation, and, thus, receive less frequent tidal inundation. Pacific cordgrass (*Spartina foliosa*) grows inside the banks of the high-order channels, while 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 and dominated by pickleweed, a low-growing succulent halophyte, with other common

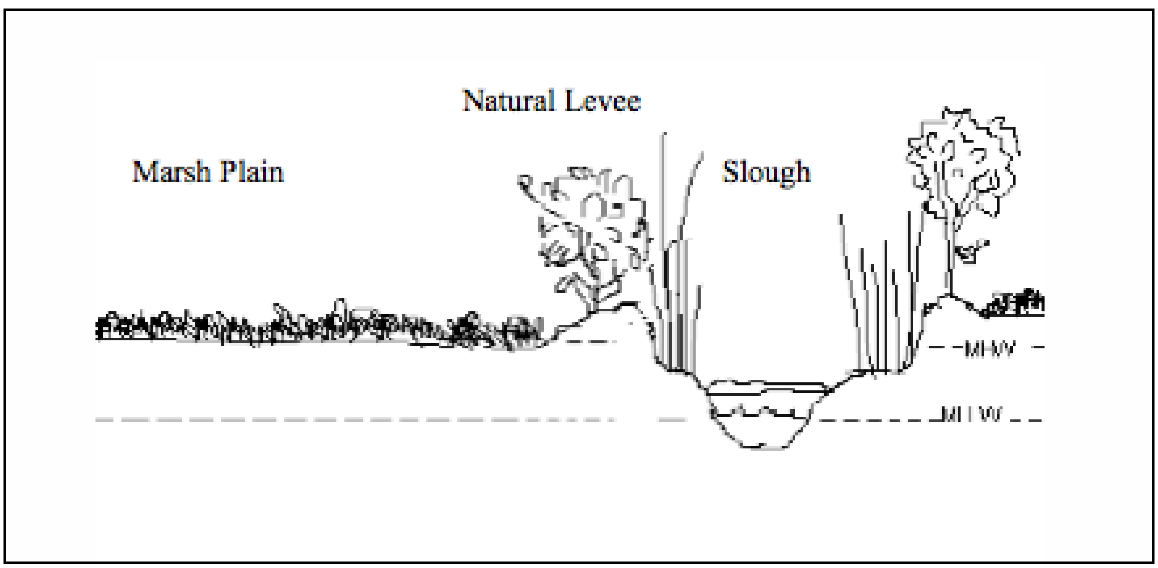

Figure 1. Sub-habitats of the China Camp tidal marsh. Channels are bordered by natural levees with vegetation dominated by Grindelia stricta *and* Sarcocornia pacifica. *The marsh plain adjacent the natural levee is slightly lower in elevation and is dominated by* S. pacifica.

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 overbanking tides (Collins et al. 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 et al. 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. The study was conducted in a 3.3 ha plot within the centennial portion of the marsh, characterized by the simple, less sinuous channels typical of a rapidly formed marsh.

Sample Collection

Sampling was conducted at low tide from May to July, 2001, and consisted of five capture methods: pit trap, sweep net, snail count, mud core, and sticky trap. Equal sampling effort was expended along high-order and low-order channels. For each channel type, random sampling locations were stratified 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. The plant species within 10 cm of each trap were recorded.

Pit trap, sweep net, and snail count methods were conducted 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” diameter sailcloth net, sweeping new vegetation with each stroke. Snail counts consisted of counting all snails within a 22 cm x 22 cm quadrat.

Mud core and sticky trap methods were used 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 7.0 cm in diameter and 10 cm deep, and organisms were collected from them with a 0.5 mm mesh sieve. For each core, the relative abundance of roots was recorded on a scale of 0--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. The traps were set for at least three hours and checked frequently as the tide rose; if the traps were in jeopardy of flooding, they were moved to adjacent higher ground.

Sample Processing

Common invertebrates were identified to the lowest feasible taxonomic level with assistance from experts (see Acknowledgements). Average biomass was determined for large or common taxa (greater than 10 individuals per trap method) by weighing between 9 and 115 individuals per taxon, after drying at 55 degrees Celsius until a constant weight was achieved. 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. Masses for araneid spiders were estimated from lycosid spiders of similar size.

Data Analysis

Catch per unit effort (CPUE) was calculated as the number of invertebrates of the same taxon caught per trap hour for pit traps and sticky traps, and calculated as invertebrates per trapping event for all other capture methods. Differences in CPUE among sub-habitats were examined using nonparametric 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 the vegetation varied dramatically among sub-habitats. Plant-invertebrate relationships in the channel sub-habitat were tested 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, organisms on and around a low intertidal rocky outcrop and boulders near Rat Rock at China Camp State Park were collected by hand and identified in the field by A. Cohen using 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.

10.3 Results

Tidal Marsh Invertebrates

A total of 4597 invertebrates were captured in 787 trapping events, representing seven taxonomic classes and at least 14 orders (Table 1). Six of the 7 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

Table 1. Number of invertebrates collected in the tidal marsh study by each capture method (* = exotic species).

						Number of Individuals Collected (by 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	Nereidae	*Neanthes succinea**	Polychaete worm	2	-	-	-	-
		Other Polychaetes			Polychaete worm	131	-	-	-	-
Mollusca	Gastropoda	Basommatophora	Ellobiidae	*Myosotella myosotis**	European marsh snail	1	3	22	886	2
	Bivalvia	Veneroida	Tellinidae	*Macoma petalum**		39	-	-	-	-
Anthropoda	Crustacea	Amphipoda	Corophiidae	*Corophium alienense**	Aquatic amphipod	195	3	-	-	-
			Corophiidae	*Grandidierella japonica**	Aquatic amphipod	98	-	-	-	-
			Talitridae	*Traskorchestia traskiana*		-	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	-	-
			Bembidion		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
			Otitidae		Picture wing fly	-	-	25	-	-
			Other Diptera			-	-	86	-	99
		Homoptera	Delphacidae	*Prokelisia marginata**	Planthopper	-	-	703	-	1
			Other Homoptera		Leafhopper	-	1	11	-	-
		Hemiptera				-	-	9	-	-
		Lepidoptera			Moth	-	-	4	-	-
		Other Insecta			**Insect**	**1**	**1**	**6**	**-**	**-**

captures for most trapping methods. The amphipod *Traskorchestia traskiana* comprised 77% of the individuals caught by pit trap, while the planthopper *Prokelisia marginata* comprised 64% of the individuals 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 (+/- 1 SD) of common taxa ranged from 0.26 (+/- 0.07) mg/individual for *Prokelisia marginata* to 8.65 (+/- 6.70) mg/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 invertebrate 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 were 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, $n = 36$, $p < 0.001$).

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 horsemussel *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.

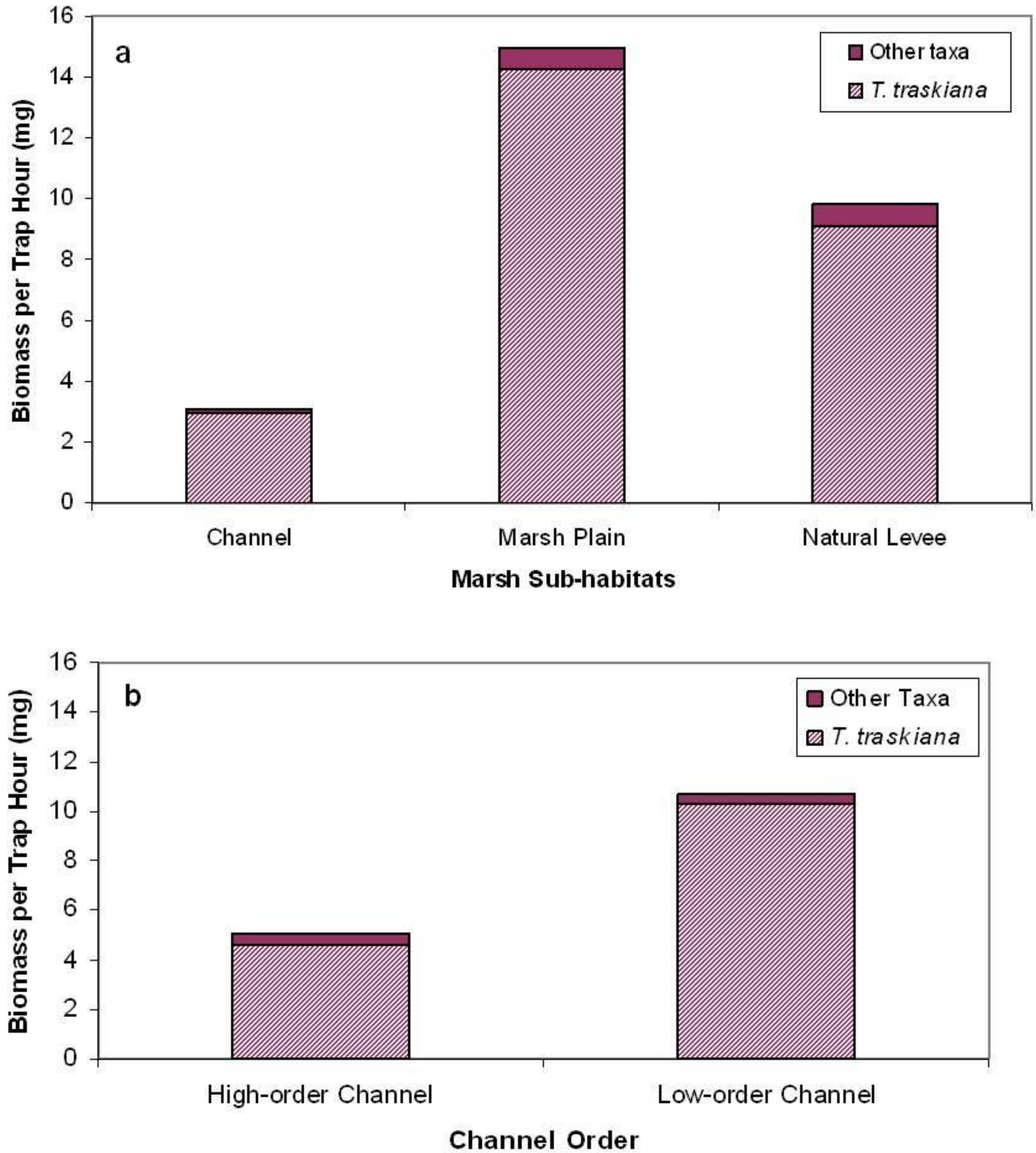

Figure 2. Mean biomass per trap hour for pit traps by a) marsh sub-habitat and b) channel order.

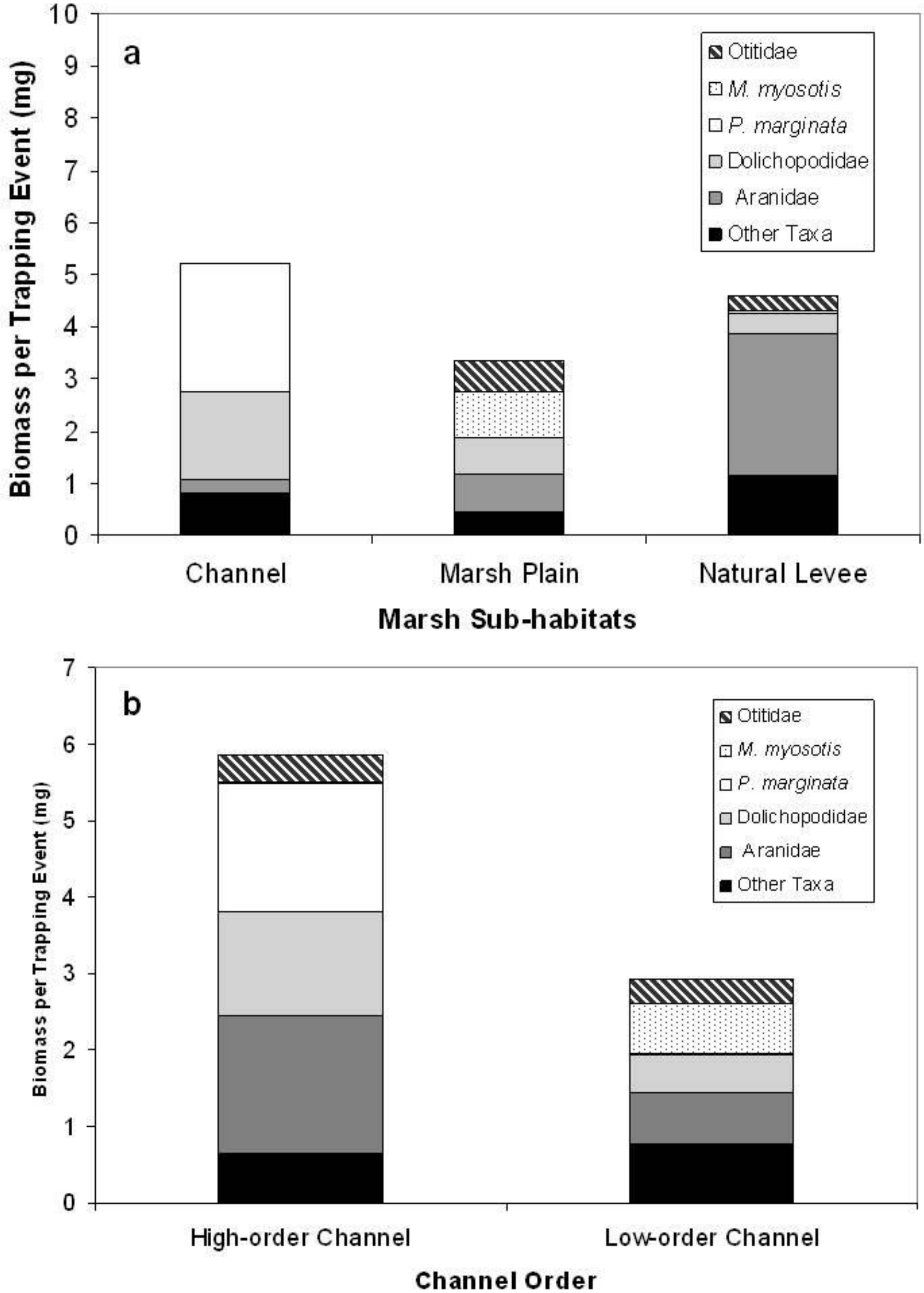

Figure 3. Mean biomass per trapping event from sweep netting by a) marsh sub-habitat and b) channel order.

Table 2. Individual mass (+/- 1 SD) for common taxa caught by sweep net and pit trap.

Taxon (Order)	$n_{weighed}$	Mean biomass (mg)	
T. traskiana (Amphipoda)	99	8.65	+/- 6.70
Chrysomelidae (Coleoptera)	26	7.15	+/- 2.06
Lycosidae (Araneae)	26	6.07	+/- 4.20
M. myosotis (Basommatophora)	60	3.35	+/- 1.44
Otitidae (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
Bembidion (Coleoptera)	42	1.68	+/- 0.42
Corophiidae (Amphipoda)	11	0.45	+/- 0.25
P. marginata (Homoptera)	40	0.26	+/- 0.07

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 (# trap hours or trapping events)			
		Channel	Marsh Plain	Natural Levee	*p*
Pit Trap	Lycosidae (Araneae)	0 (234)	**13 (230)**	**13 (236)**	**0.001**
	Bembidion (Coleoptera)	0 (234)	**44 (230)**	21 (236)	**<0.001**
	T. traskiana (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**
	Otitidae (Diptera)	3 (72)	**15 (72)**	7 (72)	**0.002**
	P. marginata (Homoptera)	**689 (72)**	5 (72)	9 (72)	**<0.001**
	Dolichopodidae (Diptera)	**70 (72)**	28 (72)	18 (72)	**0.016**
Snail Count	*M. myosotis* (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 (# trap hours or trapping events) Low-order Channel	High-order Channel	p
pit trap	*T. traskiana* (Amphipoda)	**418 (349)**	187 (350)	**<0.001**
	Bembidion (Coleoptera)	37 (349)	28 (350)	0.673
	Lycosidae (Araneae)	12 (349)	14 (350)	0.91
sweep net	*M. myosotis* (Basommatophora)	**21 (108)**	1(108)	**0.01**
	Aranidae (Araneae)	12 (108)	**32 (108)**	**0.014**
	P. marginata (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
	Otitidae (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**
	C. alienense (Amphipoda)	26 (36)	72 (36)	0.801
	M. petalum (Veneroida)	13 (36)	26 (36)	0.822
	G. japonica (Amphipoda)	80 (36)	115 (36)	0.868
sticky trap	Dolichopodidae (Diptera)	278 (36)	266 (36)	0.83
snail count	*M. myosotis* (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 (* = exotic species).

Phylum	Class	Order	Family	Species	Common Name
Porifera	Desmospongiae	Halichondrida	Halichondriidae	*Halichondria sp.* [1] *	sponge
		Haplosclerida	Chalinidae	*Haliclona sp.* [1] *	sponge
		Other Desmospongiae			sponge
Cnidaria	Hydrozoa				hydroid
	Anthozoa	Actiniaria	Diadumenidae	*Diadumene sp.* [2] *	anemone
			Diadumenidae	*Diadumene lineata**	Orange-lined anemone
					anemone
Annelida	Polychaeta	Phyllodocida	Nereidae	*Neanthes succinea**	pile worm
			Polynoidae	*Harmothoe praeclara* [3] *	scale worm
		Other Polychaeta			polychaete worm
Mollusca	Gastropoda	Cephalaspidea	Philinidae	*Philine sp.* [4] *	Tortellini snail
		Other Opisthobranchia		unidentified opisthobranch	sea slug
	Bivalvia	Ostreoida	Ostreidae	*Ostrea lurida*	Olympia oyster
		Mytiloida	Mytilidae	*Geukensia demissa**	Ribbed horsemussel
			Mytilidae	*Musculista senhousia**	Green bagmussel
			Mytilidae	*Mytilus galloprovincialis*/trossulus* [5]	Bay mussel
		Myoida	Corbulidae	*Corbula amurensis**	Overbite clam
			Myidae	*Mya arenaria**	Atlantic softshell clam
		Veneroida	Tellenidae	*Venerupis philippinarum**	Japanese littleneck clam
		Other Bivalvia		unidentified clam	clam
Arthropoda	Crustacea	Balanomorpha	Chthamalidae	*Chthamalus sp.* [6]	barnacle
			Balanidae	*Balanus glandula*	barnacle
			Balanidae	*Balanus sp.*	barnacle
		Isopoda	Sphaeromatidae	*Gnorimosphaeroma oregonense*	isopod
		Amphipoda	Gammaridae		amphipod
			Corophiidae or Aoridae	unidentified *Corophiid* or *Grandidierella japonica* [7] *	amphipod
		Decapoda	Portunidae	*Carcinus maenas**	Green shore crab
			Varunidae	*Hemigrapsus oregonensis*	Yellow mud crab
Bryozoa	Gymnolaemata	Ctenostomata	Nolellidae	*Anguinella palmata**	bryozoan
			Vesiculariidae	*Bowerbankia sp.**	bryozoan
		Cheilostomata	Membraniporidae	*Conopeum sp.**	bryozoan
			Cryptosulidae	*Cryptosula pallasiana**	bryozoan
			Schizoporellidae	*Schizoporella sp.* [8] *	bryozoan
Chordata	Ascidiacea	Pleurogona	Styelidae	*Botryllus schlosseri**	sea squirt
			Molgulidae	*Molgula manhattensis**	sea squirt

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.

10.4 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 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*, while the marine-derived invertebrates included sponges, cnidarians, polychaete worms, opisthobranch 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, capture for most trapping methods was dominated by one taxon, 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, while factors such as plant biomass and oxygen concentration affect invertebrates over shorter time 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 dipterans and homopterans, 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 et al. (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, while 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 are more shaded, which does seem to be the case based on personal observations of 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 et al. 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 due to reduced flow speeds near vegetation (Levin et al. 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*, as *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 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 are lung-breathing 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 shorecrab *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 & b and 3a & b), 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 parvipinis)* 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 (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 impact predator foraging patterns. Dean et al. (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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10.6 Literature Cited

Brusati ED, Grosholz ED. 2006. Native and introduced ecosystem engineers produce contrasting effects on estuarine infaunal communities. Biological Invasions 8(4):683-695.

Cohen AN. Guide to the exotic species of San Francisco Bay. [Internet]. Oakland, CA: San Francisco Estuary Institute. Available from: www.exoticsguide.org

Cohen AN, Carlton JT. 1995. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. Washington, D.C.: U.S. Fish and Wildlife Service. 246 pages plus appendices.

Collins L, Collins J, Leopold L. 1986. Geomorphic processes of an estuarine marsh: preliminary results and hypotheses. International geomorphology 1:1049-1072.

Davis LV, Gray IE. 1966. Zonal and seasonal distribution of insects in North Carolina salt marshes. Ecological Monographs 36(3):275-295.

Dean AF, Bollens SM, Simenstad C, Cordell J. 2005. Marshes as sources or sinks of an estuarine mysid: demographic patterns and tidal flux of *Neomysis kadiakensis* at China Camp marsh, San Francisco estuary. Estuarine, Coastal and Shelf Science 63(1-2):1-11.

Denno R, Schauff M, Wilson S, Olmstead K. 1987. Practical diagnosis and natural history of two sibling salt marsh-inhabiting planthoppers in the genus Prokelisia (Homoptera: Delphacidae). Proceedings of the Entomological Society of Washington 89(4):687-700.

Doyen JT. 1976. Marine beetles (Coleoptera excluding Staphylinidae). In: Cheng L, editor. Marine insects. [Amsterdam and New York]:[North-Holland Publishing Company]. p. 497-519.

Goals Project. 2000. Baylands ecosystem species and community profiles: Life histories and environmental requirements of key plants, fish and wildlife. Oakland (CA): San Francisco Bay Regional Water Quality Control Board. [xvi, 408 p]

Greenberg R, Maldonado JE, Droege S, McDonald M. 2006. Tidal marshes: a global perspective on the evolution and conservation of their terrestrial vertebrates. BioScience 56(8):675-685.

Grenier J. 2004. Ecology, behavior, and trophic adaptations of the salt marsh song sparrow *Melospiza melodia samuelis*: the importance of the tidal influence gradient. Berkeley (CA): Environmental Science, Policy and Management, University of California, Berkeley. [vi, 139]

Grenier JL, Greenberg R. 2005. A biogeographic pattern in sparrow bill morphology: parallel adaptation to tidal marshes. Evolution 59(7):1588-1595.

Jaffe BE, Smith RE, Foxgrover AC. 2007. Anthropogenic influence on sedimentation and intertidal mudflat change in San Pablo Bay, California: 1856-1983. Estuarine, Coastal and Shelf Science 73(1-2):175-187.

Kneib R. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries and Coasts 7(4):392-412.

Kreeger DA, Newell RIE. 2002. Trophic complexity between producers and invertebrate consumers in salt marshes. In: M. P. Weinstein and D.A. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology, Kluwer Press, New York, pp. 183-216..

Levin LA, Neira C, Grosholz ED. 2006. Invasive cordgrass modifies wetland trophic function. Ecology 87(2):419-432.

Levin LA, Talley TS. 2002. Influences of vegetation and abiotic environmental factors on salt marsh invertebrates. In: M. P. Weinstein and D.A. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology, Kluwer Press, New York, pp. 661-707.

Mitsch W, Gosselink J. 2000. Wetlands. 3rd edition. New York (NY): John Wiley & Sons.

Page H. 1997. Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California salt marsh. Estuarine, Coastal and Shelf Science 45(6):823-834.

Pennings SC, Callaway RM. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology [73(2)]:681-690.

Teal JM. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43(4):614-624.

Tomanek L, Helmuth B. 2002. Physiological ecology of rocky intertidal organisms: a synergy of concepts. Integrative and Comparative Biology 42(4):771.

Underwood A, Chapman M. 1996. Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107(2):212-224.

Visintainer TA, Bollens SM, Simenstad C. 2006. Community composition and diet of fishes as a function of tidal channel geomorphology. Marine Ecology Progress Series 321:227-243.

West JM, Zedler JB. 2000. Marsh-creek connectivity: fish use of a tidal salt marsh in southern California. Estuaries and Coasts 23(5):699-710.

Whitcraft CR, Levin LA. 2007. Regulation of benthic algal and animal communities by salt marsh plants: impact of shading. Ecology 88(4):904-917.

Wyatt TD. 1986. How a subsocial intertidal beetle, Bledius spectabilis, prevents flooding and anoxia in its burrow. Behavioral Ecology and Sociobiology 19(5):323-331.

A Profile of the
San Francisco Bay National Estuarine Research Reserve

China Camp State Park

Rush Ranch Open Space Preserve

December 14, 2011

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