Preliminary Report: the Tidal Marsh Food Web

Report to the San Francisco Bay Fund for the grant:

Food web pathways of bird contamination in Bay Area tidal marshes.

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Introduction

Many marsh restoration and enhancement projects are currently planned or underway in the San Francisco Estuary[1]. There is no clear way of assessing the impact of these changes on Pacific coast salt marsh animals because their ecology is poorly understood. In particular, the trophic, or feeding, relationships between most species in the marsh are not known. One reason food web interactions are important is that contaminants are often mobilized from abiotic sources in sediment or water through the biotic pathways of a food web[2]. The outcome of this mobilization into the food web can include the transfer of contaminants by mobile species to new geographical locations in the estuary and upland and the bioaccumulation of contaminants by top predators[3]. Knowledge of the salt marsh food web would help scientists and managers assess the risks, interpret the levels, and possibly minimize the accumulation of contaminants in key wildlife species.

The purpose of our project is to fill this knowledge gap by identifying the likely pathways contaminants take between marsh habitats and wildlife. Our research focuses on the food webs of resident birds and predatory fish. These taxa are high-level consumers in the marsh food web, and they have important conservation concerns relating to contamination. Many resident marsh bird species are listed at the state and federal levels due to habitat loss. Recent research on mercury and selenium in salt marsh birds has generated concern that these elements could be affecting reproductive success[4]. While most salt marsh fish are not threatened, high contaminant levels are a problem in some Bay fish species eaten by humans[5]. When juvenile fish use salt marshes as nurseries, they may accumulate significant contaminant concentrations. We studied the food webs of the San Pablo Song Sparrow (*Melospiza melodia samuelis*) and various predatory fish: juvenile striped bass (*Morone saxatilis*), Pacific staghorn sculpin (*Leptocottus armatus*), and longjaw mudsucker (*Gillichthys mirabilis*).

We used stable isotope ratios of carbon and nitrogen as chemical tracers to elucidate the feeding relationships of marsh organisms. These ratios have been shown to vary naturally among salt marsh primary producers (C_3 and C_4 vascular plants and marine algae)[6]. In some cases, isotopic values for primary producers overlap, making it difficult to distinguish carbon sources in dynamic systems[7]. However, complex isotopic signatures of primary producers are integrated in the tissues of herbivorous primary consumers. The isotopic signature of primary consumers can be traced higher into the food web, because there is little or no trophic enrichment of carbon isotopes; the stable isotope ratio of the predator mirrors that of the prey[8].

Salt marshes comprise a few distinct habitats, each dominated by a different primary producer (Fig. 1). If we can ascertain that an animal obtains most of its energy from a particular primary producer using stable isotopes, we also know which marsh habitat is supporting that animal. This tight spatial relationship should help land managers target specific marsh habitats to achieve goals related to species dependent on those habitats. To extrapolate from the prey eaten by a consumer to the primary producers and associated marsh habitats needed to support that consumer, we must assume that the isotopic signatures of the primary producers are distinct in time and space. Our results will demonstrate that C_3 and C_4 salt marsh plants in the study area had distinct isotopic signatures at one point in time, and data from a more comprehensive study of the Estuary support this assumption for salt marsh C_3 plants, C_4 plants, and marine phytoplankton over the course of one year[7].

Methods

All samples were collected in the tidal salt marsh at China Camp State Park, Marin County, California (38°00'45" N, 122°29'25" W). Most samples were collected in June and July 2001. A few Song Sparrow samples were obtained as early as March, and the fish were collected in September and October. Samples were collected from four plots within the study area.

We sampled sparrows, fish, aquatic and terrestrial invertebrates, and vascular plants. Our study was designed to use primary consumers as integrators of primary producer signals[9], so we did not sample the full host of photosynthetic organisms. We captured sparrows in mistnets and released them after taking small blood samples. Fish and shrimp were captured in minnow traps, beach seines, and fyke nets. Benthic invertebrates on the marsh plain and in the sloughs were captured in pit traps and mud cores. Terrestrial insects on vascular plants were collected in sweep nets. Vascular plant leaves and insect larvae in *Grindelia* leaf buds were collected by hand. Sparrow and plant samples were placed on ice in the field. Sparrow blood was frozen immediately upon return to the laboratory, and plant leaves were refrigerated until processing. Invertebrate samples were kept in the shade in the field. Invertebrates were kept alive in the laboratory from 6 to 24 hours, depending on the taxon, to allow gut evacuation, and then they were frozen.

Tissues analyzed for stable-isotope ratios varied by taxon. We used sparrow blood, white lateral muscle dissected from fish, abdominal muscle from shrimp, foot muscle from clams, green leaves from vascular plants, and whole insects and amphipods. Samples from birds, fish, and shrimp were analyzed individually. For all other taxa, samples were pooled into composites by spatial plot. Organisms in a composite sample were collected in the same spatial plot and habitat type on the same day. On rare occasions, two or three days were required to collect a full sample. Composite samples generally included material from 20-25 individuals. However, for plants that number was difficult to gauge, and some invertebrate samples had only 5-10 individuals. Tissue samples were freeze dried (mudsuckers and clams) or dried in an oven at 50-60°C until constant mass, and then ground to a homogeneous powder.

Samples were combusted in a continuous flow Europa mass spectrometer at the Berkeley Center for Stable Isotope Biogeochemistry. Stable isotope ratios are reported with the delta (δ) symbol, defined as the parts per thousand (‰) deviation from a standard material. Forty-five percent of samples were run in duplicate; the variation in replicates (± 1 SD) was typically less than 0.15‰ for both carbon and nitrogen. The analytical error of the mass spectrometer was less than 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$. Values reported are means ± 1 SE, unless otherwise noted.

Due to concerns about calcium carbonate affecting the carbon signal from whole amphipods[10], we compared the stable isotope ratios of amphipod samples treated with HCl and untreated samples. After grinding, half of each of three amphipod samples was treated with 1N HCl, and then re-dried at 60°C. The acidification treatment depleted the $\delta^{13}C$ by 0.6‰ ± 0.3 and the $\delta^{15}N$ by 0.8‰ ± 0.4. Because the effect was small for carbon and the treatment altered the nitrogen values as well, all subsequent amphipod data reported here are from untreated samples.

Results and Discussion

Individual species

The data from each species grouped into a tight cluster of isotope values (Table 1), with the standard error of the mean δ^{15}N and δ^{13}C values for each species generally being ± 0.4‰ or less (range ± 0.0-0.7‰). This clustering suggests little variation in diet between individuals for species analyzed with individual samples and little variation over space for species analyzed with composite samples. The primary consumers clustered into three distinct groups (Fig. 2): consumers associated with high marsh vascular plants, *Spartina*, and most likely marine algae. Dual isotope plots are interpreted by assessing the relationship between a consumer and a potential food source. Carbon isotopes ratios are enriched (less negative) by approximately 0.5‰ in the tissue of a predator relative to its prey, while nitrogen ratios are enriched (more positive) by approximately 2-5‰ during each transfer up one trophic level.[11,12]

The semi-terrestrial amphipods collected from the marsh plain clustered with *Coleoptera* larvae found in *Grindelia* at the depleted end of the δ^{13}C scale (-21 to -22‰). The larvae live wholly within the Grindelia leaf buds, so their only source of food is the Grindelia plant. The larger than expected carbon fractionation between the plant and the larvae may possibly be explained by a difference in the isotopic signals of the bud tissue the larvae eat and the mature leaf tissue we sampled[13]. Given that the amphipods cluster with the *Coleoptera* larvae that appear to be feeding exclusively on *Grindelia*, amphipods probably obtain much of their carbon from *Salicornia* or *Grindelia*. Amphipods may be eating plant detritus, though, and we sampled only live tissue. A possible symbiotic relationship between this amphipod species and *Salicornia* is being studied[14]. These two invertebrate species integrate the primary producer signal of high marsh vascular plants.

The benthic *Coleoptera* larvae clustered with the planthoppers at the enriched end of the δ^{13}C scale (-14 to -15‰). These δ^{13}C values suggest that these insects feed on *Spartina* in the low marsh. The nitrogen data support this interpretation for the planthoppers, and the planthopper specialization on *Spartina* is well documented[15]. However, the beetle larvae had a δ^{15}N value that was more depleted than that of *Spartina*, which is the opposite of expected for a feeding relationship. This may be due to an error in sampling, an unusual fractionation of nitrogen in the larvae, or evidence of an unsampled food source that is very enriched in δ^{13}C.

The *Macoma* clams, which are capable of filter-feeding and grazing on benthic sediment, had a strikingly more positive δ^{15}N than the other primary consumers, indicating that the baseline nitrogen value for marine primary producers is several per mil higher than that of vascular plants in the marsh. The δ^{15}N of shrimp was 4‰ higher than that of clams. This difference in nitrogen values of shrimp and clams may indicate that shrimp specialize on a higher trophic level food than phytoplankton or that the clam signal includes some input from high and low marsh vascular plant production. If *Macoma* were to ingest some terrestrial detritus with a signature similar to that of the high marsh plants, we would expect lower δ^{15}N for bivalves feeding in marshes than for those in the open Bay. To the contrary, bivalves collected by the RMP in 2000 from the open waters of San Pablo Bay had similar values (δ^{15}N = 11.8‰ ± 2.7; n = 2) to the clams we sampled. Based on this evidence, we interpret the data as indicating that clams ate mainly marine-derived foods.

The three fish species clustered together, with juvenile bass and sculpin more enriched in δ^{15}N than mudsuckers. The sample size for bass and sculpin was small ($n = 2$), and considerably more effort was required to capture these fish than other species in this study. Bass and sculpin were caught in a fyke net set across the mouth of a large tidal channel from high slack tide until the channel had almost completely dewatered. We used the fyke net only after several beach-seining attempts failed to capture either species. The difficulty of obtaining bass and sculpin suggests that these fish were not common in the China Camp salt marsh at that time of year. More data on fish use of the salt marsh is needed before making definitive conclusions about their role in the food web.

Sparrows were more depleted in δ^{13}C and δ^{15}N than fish. Sparrow sample size was relatively large ($n = 35$), yet individual sparrows had very similar carbon and nitrogen isotope values (± 0.1‰ SE). This tight clustering most likely indicates that sparrows have a very specific diet; most individuals are eating the same foods in similar proportions.

The salt marsh food web

These results suggest that the salt marsh food web is divided into three relatively distinct parts -- high marsh, low marsh, and channel -- with few biotic pathways linking the different habitats. The evidence for separation between high and low marsh is the strong difference in δ^{13}C between the C_3 and C_4 vascular plants. The evidence for separation between channels and the other habitats is the large difference in δ^{15}N between the high and low marsh primary consumers and the channel primary consumers. At the higher trophic levels, a few vertebrates that we did not sample (rails, wading birds, and raccoons) may have diets that span two or more of the high marsh, low marsh, and channel food webs.

The high marsh food web is based on primary production by *Salicornia* and *Grindelia*. Terrestrial insects and other invertebrates in the high marsh (e.g. *Coleoptera* larvae and amphipods; Fig. 2) feed on these plants and are eaten, in turn, by sparrows. Sparrows are a secondary consumer, and other non-sampled species likely to feed at this level are carnivorous small mammals and passerines (e.g. shrews and Marsh Wrens).

In the low marsh food web, *Spartina* is eaten by planthoppers, *Coleoptera* larvae, and other invertebrate primary consumers. Sparrows and other secondary consumers (see end of previous paragraph) prey on the primary consumers.

The data support this interpretation of the high and low marsh food webs, because the isotopic differences between vascular plants, the primary consumers listed above, and sparrows are appropriate for the expected fractionation between trophic levels. The position of sparrows closer to the C_3 plant δ^{13}C than to *Spartina* δ^{13}C indicates that a greater proportion of their nutrients are derived from high marsh plant production than from *Spartina*. This conclusion makes sense from a resource availability perspective, given that *Spartina* and the sediment beneath it are only available to sparrows at low tide, while the high marsh plants and sediment are accessible during all but the highest tides of the year. Biomass from the low and high marsh food webs is transported out of the marsh to the upland by raptors (hawks, owls, kites, falcons, vultures), wading birds (herons and egrets), snakes, and mammals (raccoon, striped skunk, rodents) that feed on the secondary consumers and their offspring.

Although we did not directly sample marine phytoplankton and benthic diatoms, the tidal channel food web is most likely based on primary production from these photosynthetic organisms[7]. Aquatic primary consumers, including the clams we sampled, feed on these primary producers. Secondary consumers in the channels, such as mudsuckers and possibly shrimp as discussed previously, prey on the primary consumers. Juvenile striped bass and sculpin had more enriched $\delta^{15}N$ values than mudsuckers, suggesting that they may be tertiary consumers. The $\delta^{13}C$ signal in the channel food web varies little between trophic levels, suggesting that the web is based on a single primary producer signal (marine algae). Biomass from this food web is likely transported out of the marsh to the Bay and upland by transient fish and shrimp, semi-aquatic birds (wading birds, waterfowl, grebes, cormorants), raccoons, and the direct action of the tides.

We did not sample Clapper Rails, but an educated guess based on the literature is that they sit between the secondary and tertiary consumer levels of the channel food web. Although rail dietary source proportions are not known, prey items with the highest biomass are from channel habitat (e.g. bivalves and fish)[16]. These birds also eat spiders and insects from the vegetated marsh habitats[16], however, and their preferred habitat is low marsh[17]. Therefore, the rail diet probably spans the low marsh and channel food webs, but from a contaminants perspective the main pathway of biomass intake is likely to be in the tidal channel habitat.

Interestingly, we detected division of the marsh food web into habitat-based components during the season when trophic interactions across the elevational gradient might be expected to peak. In June and July, the tidal range reaches extremes[18]. Fish have access to the marsh plain during high tide, and birds can access the channels during low tide. Young of the year have increased population sizes of sparrows and fish, which might require individuals to forage over larger areas to meet metabolic needs. The tissues we sampled from sparrows[19], juvenile bass, and juvenile sculpin[20,21] reflect the diet during a recent enough time period that seasonal dietary changes could be detectable.

Implications for management of contaminants

Contaminants may be transferred to marsh fish and birds via the biotic pathways described in the previous section. The evidence for separation between food webs in different marsh habitats suggests that contaminants originating in the high marsh are not likely to be exported through the food web to bay fish (Fig. 3). Similarly, toxicants in the tidal channels will probably not bioaccumulate in sparrows. However, rails and other birds subsisting on aquatic animals would be at risk for exposure to contaminants in the channel food web.

Sparrows and mudsuckers appear to be secondary consumers, while the nitrogen data indicate that juvenile bass and sculpin may be tertiary consumers. This result provides a basis for interpreting the concentration of contaminants found in these species using models of bioaccumulation. Adult striped bass are not known to frequent marshes, but there is concern that juveniles may take on significant contaminant loads while foraging in marshes. The tertiary consumer level of juvenile bass is significant, because it means bioaccumulation is more intense during the time bass are in marshes than if bass were secondary consumers. Channel habitat is only available to bass during high tides, so a significant proportion of bass foraging is likely to occur in other habitats. Our data do not indicate what proportion of the bass energy budget (and,

thus, potential contaminant exposure) comes from tidal marsh. What we can glean from the data is that the bass stable isotope signal is consistent with a diet of foods available in the marsh.

Future Directions

The results presented here provide an initial understanding of the salt marsh food web. We plan to augment the data in this report with other taxa and more spatial and temporal replicates collected from the same study area. This research will be submitted to a peer-reviewed journal within the next year. That publication will contain mathematical models for source proportions in the diets of vertebrates and for trophic levels. For this report, the food web model is qualitative, because sample sizes are small and all taxa have not yet been analyzed. As with all food web studies of one area at one point in time, extrapolation of our results to other marsh systems and others years or seasons should take into consideration the possible variation over space and time.

Acknowledgements

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Habitat and scientific name	Taxonomic group	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
All marsh habitats				
Melospiza melodia	song sparrow	35	-20.6 ± 0.1	12.2 ± 0.1
High marsh (marsh plain)				
Salicornia virginica	pickleweed	[3]	-25.8 ± 0.2	7.8 ± 0.5
Grindelia humilis	gumplant	[3]	-25.2 ± 0.4	5.6 ± 0.1
Traskorchestia traskiana	amphipod	[3]	-22.1 ± 0.2	10.6 ± 0.1
Coleoptera larvae in *Grindelia*	beetle	[2]	-21.7 ± 0.7	10.4 ± 0.4
Low marsh (sides of high-order slough)				
Spartina foliosa	cordgrass	[2]	-14.6 ± 0.0	8.5 ± 0.2
Prokelesia marginata	planthopper	[2]	-13.9 ± 0.1	10.0 ± 0.5
Coleoptera larvae on sediment	beetle	[2]	-14.9 ± 0.1	7.8 ± 0.4
Channel				
Morone saxatilis	bass (juvenile)	2	-19.5 ± 0.1	18.3 ± 0.2
Leptocottus armatus	sculpin (juvenile)	2	-19.2 ± 0.3	17.5 ± 0.1
Crangon franciscorum	bay shrimp	8	-17.8 ± 0.2	17.1 ± 0.1
Palaemon macrodactylus	Asian shrimp	1	-17.5	16.9
Low marsh and channel				
Macoma bathica	Baltic clam	[2]	-18.0 ± 0.3	12.9 ± 0.6
Coleoptera larvae on sediment	beetle	[2]	-14.9 ± 0.1	7.8 ± 0.4
Gillichthys mirabilis	longjaw mudsucker	5	-17.8 ± 0.5	16.0 ± 0.2

Table 1. $\delta^{13}C$ and $\delta^{15}N$ values (mean ± 1 SE) of salt marsh organisms listed by the habitat in which each was abundant (but see text for discussion of bass and sculpin abundance). Sample sizes in brackets are of composite samples.
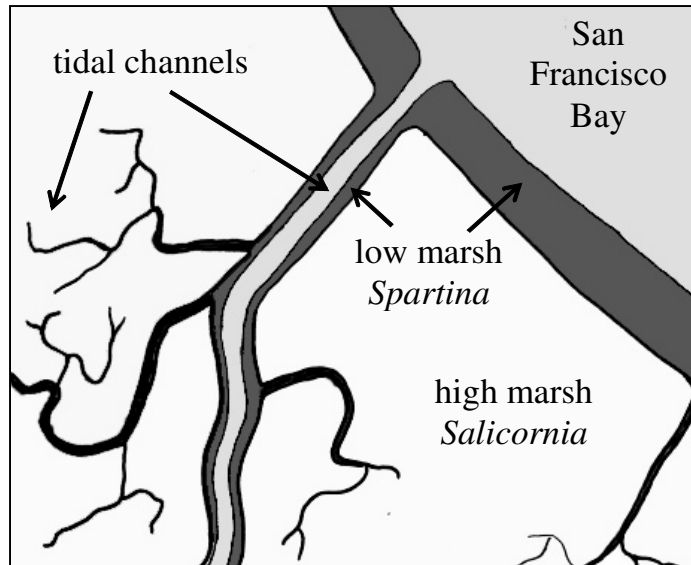
Figure 1. Typical layout of tidal salt marsh habitats in San Francisco Bay. The high marsh plain slopes gently toward low-order tidal channels, which drain into high-order channels connected to the Bay. *Spartina foliosa*, a C_4 grass, grows in low marsh areas along the sides of high-order channels and the Bay edge. *Salicornia virginica*, a C_3 succulent, covers the high marsh plain. *Grindelia,* a C_3 relative of the daisy, grows along the banks of channels. Marine algae, with carbon isotope ratios intermediate to C_3 and C_4 plants, are the main primary producers in the tidal channels.
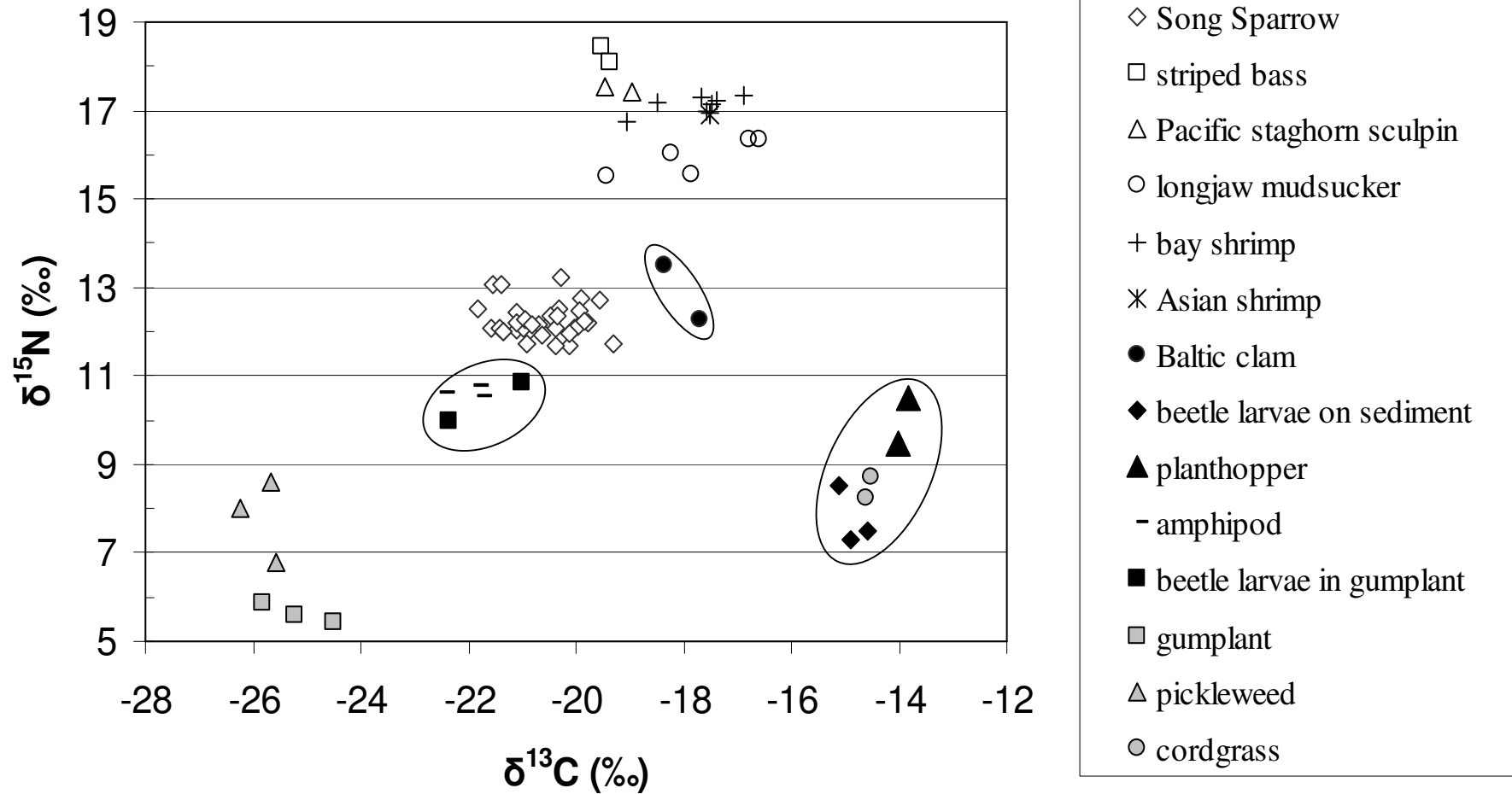
Figure 2. Dual isotope plot of salt marsh primary producers (gray symbols), primary consumers (black symbols), and secondary and tertiary consumers (open and line symbols). Distinct groups of primary consumers are circled.
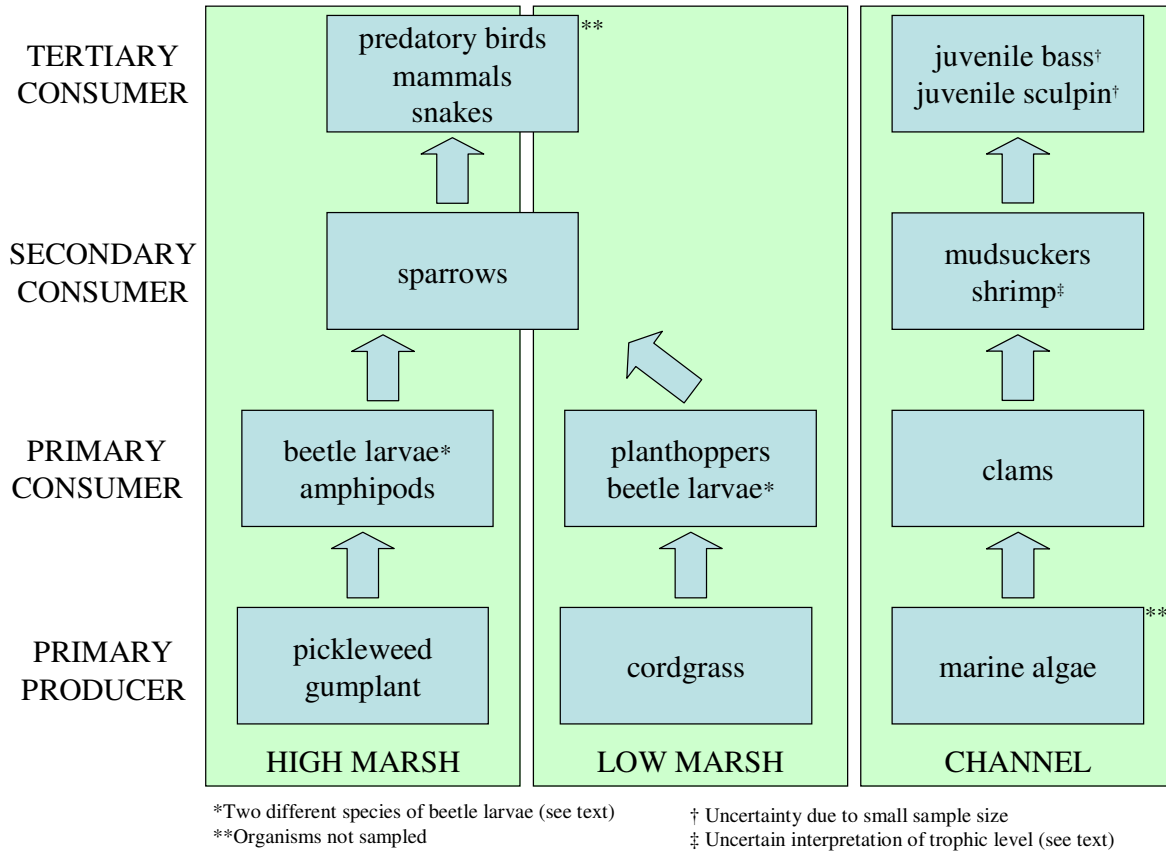
Figure 3. Working model of bioaccumulation pathways in the tidal salt marsh. Large boxes represent marsh habitats. Small boxes represent groups of organisms at the same trophic level. Arrows indicate the direction of bioaccumulation, but not necessarily direct feeding relationships between the species listed. The placement of organisms not sampled is based on natural history information. Note that humans would be a likely endpoint of the channel pathway but not of the high and low marsh pathways.