Title

Reestablishment of trophic interactions in restored coastal wetlands: the relative importance of top-down and bottom-up forces in structuring Cerithidea californica (Gastropoda) abundance

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Reestablishment of trophic interactions in restored coastal wetlands: the relative importance of top-down and bottom-up forces in structuring Cerithidea californica (Gastropoda) abundance.
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Summary

The few remaining coastal wetlands in California are heavily impacted by development, pollution, and eutrophication. Habitat restoration is an increasingly important method for preserving wetland species, but reestablishment of plant infrastructure does not necessarily result in the recovery of habitat functions. Assessment of interactions that cross multiple trophic levels can provide important insights into restored site functions at the community level. Food web support for both resident and migratory species is a critical function of coastal wetlands, so I focused on the development of trophic dynamics in restored wetlands. Many wetland species, such as wading shorebirds and commercially important fish, have high public profiles and fill keystone ecological roles, illustrating the importance of this type of project for ecological, management, commercial, and public audiences.

I used both long-term monitoring and short-term experimental approaches to investigate the functional recovery of wetlands. In the first stage of the project, I followed the population dynamics of a common mud snail, *Cerithidea californica*, in a restored tidal mudflat and an adjacent natural mudflat in a southern California coastal wetland. To explain the consistently lower snail abundances that I observed in the restored area, I then initiated a series of experiments designed to compare the relative roles of top-down (predation) and bottom-up (food availability) forces on *C. californica* density and fitness in the restored and natural areas. The

combination of monitoring and experimental approaches allowed direct comparisons between natural and restored sites, providing valuable insight into whether restoration projects that nominally fill mitigation criteria are truly functioning wetlands. This understanding will contribute to the development of mitigation goals that include functional criteria and will facilitate the functional assessment of restoration success.

The University of California Marine Council Coastal Environmental Quality Initiative Graduate Fellowship facilitated the execution of these studies, the completion of my doctoral degree at University of California Los Angeles in 2003, and the publication of two manuscripts, with a third in preparation. In addition, I presented data from this project at six national and international conferences between 2001 and 2003. These studies were performed in cooperation with my graduate advisor, Dr. Peggy Fong (UCLA), who is a co-author on all publications resulting from this project.

Population dynamics: Are natural and restored communities similar?

The first component of this project investigated one of the basic assumptions of coastal wetland restoration: that populations of epibenthic macroinvertebrates will readily establish in created habitat once tidal flow has been restored and vegetation has been planted. I quantified habitat characteristics and the spatial and temporal patterns of *Cerithidea californica* (California horn snail) density in a newly created wetland and an adjacent natural area in Mugu Lagoon, southern California, USA for 3.5 years. Though the created site vascular plant cover gradually approached natural site levels, sediment characteristics markedly differed between sites. In the created area, grain size was coarser, salinity was higher, and moisture and organic content were lower than in the natural area. Densities of *C. californica* in the created site changed little during the study period, and were often 25-50% lower than in the natural site. The influences of habitat suitability and dispersal limitation on *C. californica* colonization of the created site varied among snail age classes. Sediment moisture and organic content explained some of the variability in subadult (47%) and adult (55%) density and relative abundance, but none of the variability in juvenile abundance. Adult snail density was also strongly influenced by distance from the natural/created site transition zone, explaining about 50% of the variability in adult abundance. Juvenile and subadult snail densities were not related to distance from the natural site, possibly due to greater dispersal ability. Overall, these trends suggest that adult *C. californica* were affected by both habitat characteristics and dispersal ability, subadults were influenced to a lesser degree by habitat characteristics, and juveniles were not related to either factor. Accordingly, the influence of habitat characteristics and dispersal ability on created site colonization may change with snail age. Successful restoration of benthic invertebrate communities requires consideration of ontogenetic shifts in both habitat characteristics and dispersal ability of the target species, even in created sites in close proximity to natural areas.

Food availability: the critical role of microalgae

The monitoring study described above demonstrated that lower *C. californica* abundance in the restored site was due in part to both dispersal ability and habitat characteristics, but variability among and within age classes of snails suggested that other factors likely limited *C. californica* abundance in the restored site as well. Thus, the second segment of this project investigated the role of food availability on *C. californica* density and fitness. *C. californica* are herbivorous, primarily consuming benthic microalgae on tidal flats. I installed enclosures on the tidal flats in both the created and natural sites and added nutrients (N and P) to half of them to increase food availability; the other half of the enclosures were unenriched to maintain ambient food levels. I then added snails to half of the enriched and half of the unenriched plots. After eight weeks, I collected the snails to assess survival and used high-performance liquid chromatography to determine the relative abundance of each of the components of the microalgal community. This experiment was repeated in summer 2000, fall 2000, and spring 2001. Diatom biomass increased slightly (~30%) in response to nutrient treatments but was not affected by snail herbivory. Blooms of cyanobacteria (up to 200%) and purple sulfur bacteria (up to 400%) occurred in response to nutrient enrichment, particularly in the sandier site, but only cyanobacterial biomass decreased in response to snail grazing. Snail mortality was 2-5 times higher in response to nutrient addition, especially in the sandier site, corresponding to a relative increase in cyanobacterial biomass. However, nutrient-related snail mortality occurred only in the spring and summer, when the snails were most actively feeding on the microalgal community. In the cooler fall months, *C. californica* enter a period of decreased activity and a reduction in food consumption. Accordingly, the snails showed no response to nutrient-induced cyanobacterial growths in the fall. These experiments demonstrated strongly negative upward cascading effects of nutrient enrichment through the food chain. The strength of this upward cascade was closely linked to sediment type and microalgal community composition, resulting in a stronger negative effect of nutrient addition in the sandier created site. Thus, it became apparent that even at the microalgal level, differences in community composition can have dramatic impacts on food web dynamics and community responses to anthropogenic influences such as nutrient enrichment.

Predators: consumers and agents of disturbance

Herbivores generally face a number of predators, and *C. californica* is no exception. One of its most common predators is the burrow-excavating crab *Pachygrapsus crassipes*. Predation can indirectly benefit primary producers by reducing herbivore abundance, a pattern known as a trophic cascade. Alternatively, in an ecosystem where potentially toxic blooms of benthic microalgae can occur, a burrowing predator such as *P. crassipes* may be able to mitigate the negative effects of nutrient addition through bioturbation and subsequent removal of harmful algal mats. Thus, in the next segment of this project I increased community complexity to evaluate how nutrient enrichment altered indirect trophic (trophic cascades) and non-trophic (bioturbation) interactions as well as direct trophic interactions. In the same natural and created tidal flats as in the previous experiments, we crossed *P. crassipes* addition and nutrient enrichment in cages containing *Cerithidea californica* and benthic microalgae in summer 2002. Crab predation on snails was intense, but there was no evidence of a trophic cascade, as crab reduction of snail density did not increase benthic microalgal biomass. To the contrary, crab bioturbation of the sediment decreased diatom and cyanobacterial biomass by up to 80% in the sandflat. Subadult snail lengths increased 15-20% over five weeks in treatments with neither crabs nor nutrients. Only 5% snail growth occurred in the presence of crabs in the mudflat, possibly a result of crab alterations of microalgal abundance as well as sediment properties, including reductions of substratum tensile shear strength, sediment redox potential, and sediment nutrient content. As in the previous series of studies, nutrient addition increased snail mortality in both sites but also decreased snail growth to less than 5% in the sandflat, likely a result of nutrient-induced development of toxic or poor nutritive quality cyanobacterial mats. Overall, the coupling between top-down and bottom-up forces within the trophic food web was generally weak, as nutrient addition did not strongly alter the impacts of predators. However, the community was shaped by trophic interactions acting in concert with the nontrophic impacts of crab bioturbation. The stronger effects of crabs in the natural area and the stronger effects of nutrients in the restored area demonstrated striking contrasts in both the trophic and nontrophic interactions between the two sites.

Related publications

Armitage, A.R. and P. Fong. 2004. Upward cascading effects of nutrients: shifts in a benthic microalgal community and a negative herbivore response. *Oecologia* 139: 560-567.

Armitage, A.R. and P. Fong. 2004. Gastropod colonization of a created coastal wetland: potential influences of habitat suitability and dispersal ability. *Restoration Ecology* 12: 391-400.

Armitage, A.R. and P. Fong. In prep. The complex influences of a marsh decapod through trophic and habitat modification pathways.

Related presentations

Armitage, A.R. and P. Fong. September 2003. Effects of habitat-modifying crabs on community structure in muddy and sandy tidal flats. Estuarine Research Federation 17th Biennial Conference.

Armitage, A.R. and P. Fong. August 2003. Trophic-level effects of habitat-modifying crabs in muddy and sandy tidal flats. Ecological Society of America 88th Annual Meeting.

Armitage, A.R. and P. Fong. April 2003. Successes and shortcomings in habitat restoration: a case study of *Cerithidea californica* (Gastropoda) colonization and fitness in a created tidal mudflat. California Estuarine Research Society Inaugural Meeting.

Armitage, A.R. and P. Fong. November 2002. Interactive effects of nutrient enrichment and predation on the gastropod *Cerithidea californica* differ in natural and restored coastal wetlands in southern California. Western Society of Naturalists 83rd Annual Meeting.

Armitage, A.R., P. Fong, and R.R. Vance. November 2001. Top-down and bottom-up forces in restored and natural mudflats in a southern California estuary. Estuarine Research Federation 16th Biennial Conference.

Armitage, A.R., P. Fong, and R.R. Vance. November 2001. Top-down and bottom-up forces in restored and natural mudflats in a southern California estuary. Western Society of Naturalists 82nd Annual Meeting.