CALFED BAY-DELTA PROGRAM

CALFED SCIENCE FELLOWS PROGRAM

Sea Grant California

In cooperation with the

California Sea Grant College Program

FELLOWSHIP APPLICATION COVER PAGE

APPLICANT TYPE ☐ Postdoctoral Researcher ■ Ph.D. Graduate Student

PROJECT NUMBER

PROJECT TITLE Nutrients & benthic invasion dynamics

FINANCIAL SUMMARY

First Year CALFED Funds Requested: $43,125.00

Total CALFED Funds Requested: $107,812.00

Duration: 2.5 Years

Proposed Start/Completion Dates: September 2007-February 2010

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Will animal subjects be used? ☐ Yes ■ No

APPROVAL DATE: PROTOCOL #: PENDING:

Does this application involve any recombinant DNA technology or resea ☐ Yes ■ No

PROPOSED RESEARCH

Nutrients & Benthic Invasion Dynamics in San Francisco Bay

Introduction/Question/Objectives:

This project is designed to investigate the effects of nutrients on invasion success in a marine environment as well as the biotic effects of the invasive species at the onset of their invasion, and once they are part of the system. Specifically, it asks whether nutrient additions confer an advantage on an invasive snail species in a benthic soft sediment west coast estuary (SFB), how invasive snail species in this system affect their habitats, and how competitive interactions between native and invasive species change over time.

The project will address the following three questions:

1) Do nutrients affect invasion success in a benthic marine habitat?
2) What effects do invasive species have on benthic habitats at the onset of their invasion?
3) How do competitive interactions between native and invasive species shift over time?

Globally, biological invasions are responsible for a suite of negative impacts (Pimentel *et al*. 2005). In U.S. coastal waters, there are now more than 500 marine invaders, nearly 300 of which reside in San Francisco Bay (Ruiz *et al*. 1997, Ruiz *et al*. 2000). Aquatic invasive species play a formidable role in the California-Delta system, causing extensive economic and ecological harm to the region. The proposed project is one of the first efforts to examine the critical relationship between nutrient pollution—which the Bay-Delta region has also experienced—and the success of aquatic invasive species. It also examines the effects of a new invader (*Batillaria attramentaria*), and native-invasive species interactions over time.

Nutrients & Aquatic Invasion Success

Our current understanding of the relationship between nutrients and invasive species is limited to terrestrial systems, where studies have shown that invasive species capable of fixing nitrogen or partitioning nutrient resources can edge out their competitors (Ehrenfeld 2003, Fargione *et al*. 2003, Levine *et al*. 2003). In these systems, increased nutrients facilitate the spread of plant invasions. However, these same relationships are relatively unexamined in benthic marine systems. It is known that nutrients can affect benthic microalgae assemblages resulting in the growth of taxa that are potentially toxic to benthic consumers (Armitage and Fong 2004). However, it is not known whether these changes may disproportionately affect native v. invasive species. We have examined the facilitative effects of nutrient additions but not the effects of nutrient pollution. This study is designed to inform our understanding of marine species' responses to nutrients.

Founder Population Analyses to Broaden Understanding of Invasion Success

The Japanese invasive mud snail *Batillaria attramentaria* (Crosse 1862) was found in Loch Lomond Marina in San Francisco Bay during a routine survey in July 2005. While San Francisco Bay is a heavily invaded estuary (Cohen & Carlton 1998), this species is a new and significant invasion that requires immediate attention. It has been documented in estuaries in northern California since the 1930s (Hanna 1966, Byers 1999), arriving via oyster aquaculture in association with the species *Crassostrea gigas* (Bonnot 1935). In estuaries to the north (*e.g.*, Tomales Bay) and south (*e.g*., Elkhorn Slough) of SF Bay, *B. attramentaria* can reach densities of > 10,000 individuals/m^2 (Byers 2000) and may be causing the extirpation of native snail populations (Byers 1999). In addition, this demonstrated invasion success elsewhere in northern California makes it critical that it be studied and eradicated as swiftly as possible in San Francisco Bay.

B. attramentaria is both critical and feasible to eradicate in San Francisco Bay, yet much can be learned about its impacts during this process. Documented interactions with other species include competition with the native horn snail *Cerithidea californica* (Byers 2000), the introduction of a novel parasite to the infaunal and fish communities (Torchin *et al.* 2005), facilitation of other invasive species (Wonham *et al.* 2005), and changes to habitat structure via the addition of hard substratum in previously open mudflats (Wonham *et al.* 2005). Interestingly, even with this information, we have little understanding about how the snail affects nutrients and the benthic microalgal community, though preliminary results of our investigation suggest these interactions are significant. We will investigate the immediate changes brought about by this invasion. This is a rare opportunity to investigate the impacts of an invasive species in a benthic habitat during the initial stages of the invasion.

In addition to the immediate ecological consequences of this invasion, we are also interested in these populations from an evolutionary standpoint. Founder populations of invasive species present a unique opportunity to investigate the relative effects of deterministic (Fisher 1930) v. stochastic (Wright 1932) processes on the evolutionary trajectory of an invasive species. In addition, they can provide insights into both ecological and evolutionary explanations for invasion success. Relatively little is known about founder populations of invasive species, as most invasion events are discovered many generations after the species has become established. Theory originally predicted that founder populations were often small and genetically depauperate, and therefore more subject to evolutionary processes such as genetic drift (Wright 1932). However, substantial evidence is now emerging that populations that experience a bottleneck do not in fact suffer from a loss of genetic diversity (Wares *et al*. 2005). In these populations, natural selection is likely to have a stronger influence on the evolution of the species, and even to promote rapid evolution (Kingsolver *et al*. 2001). In some instances, rapid evolution may be a stronger explanation for invasion success than plasticity of what some researchers term a "general-purpose genotype" (Dybdahl & Kane 2005). Though we expect to successfully eradicate this *B. attramentaria* population, knowledge about its initial genetic and demographic characteristics will provide invaluable insights for future invasions.

Behavior Shifts in Native-Invasive Species Interactions over Time

Behavioral responses in native species can be influenced by multiple factors, including parasites (see Lafferty 1993 on *Cerithidea californica*, the native mud snail), environmental conditions (Trussell 1997), and invasive species (Monello *et al.* 2006). Similarly, invasive species can change in response to new environments (for terrestrial plant examples see Clements *et al.* 2004 and Richards *et al.* 2006). These dynamics are not well-understood in marine systems. Historically, the interactions between two dominant snails in San Francisco Bay have been characterized as negative, and favoring the invasive species *Ilyanassa obsoleta* (Race 1982). However, recent pilot data suggest these interactions may be shifting. This study will quantify the interactions between the native and invasive mud snails, and determine if there has been a significant change in the interactions over time and among populations within San Francisco Bay.

Approach/Plan of Work:

Study System

San Francisco Bay is influenced by multiple disturbances including nutrient influx and invasive species, as well as development, contaminant inputs, salinity changes, and sedimentation. The largest estuary on the west coast of the U.S., it drains more than 40 percent (163,000 km^2) of California's surface area, much of that coming from mining and agricultural areas with high contaminant and nutrient levels (Cohen and Carlton 1998). Salinity fluctuates from 34 psu near the Golden Gate Bridge to near 0 in the Delta, and temperatures can range anywhere between 23 and 6°C (USGS 2006). Ninety-five percent of the marshes surrounding SF Bay have been filled or diked (Atwater *et al.* 1979). More than 68 million gallons of ballast water are pumped into it every year, containing thousands of non-native species and their larvae (Cohen and Carlton 1995).

The nutrients found in San Francisco Bay originate from multiple sources, including nitrogen from Central Valley farms and atmospheric deposition. Hydraulic mining in the Sierra Nevada Mountains in the 1800s caused excessive amounts of sediment to flow into the system, concurrent with the beginnings of industrialized travel and increased propagule pressure from exotic species (Gilbert 1917; Carlton 1979). Freshwater diversions and seasonal runoff from farms are still responsible for the greatest increase in nitrogen to the system, however (Horne and McCormick 1977), and most of this arrives as inorganic nitrate, readily available for primary producers.

Elevated nutrient levels can increase primary production and thus provide more food for grazers. In benthic marine systems, this effect can trigger greater grazer abundance, which, at certain densities, further increases productivity as the diatoms themselves are resuspended and re-exposed to nutrients and light (Admiraal *et al.* 1982, Connor and Teal 1982). Primary production in a system is a critical metric of ecosystem function, and healthy ecosystems often have high levels of productivity. However, excessive plant production, due to elevated nutrient levels, can result in detrimental low oxygen levels. In addition, increased nutrients can shift the species distribution of benthic microalgae from diatoms to cyanobacteria and purple sulfur bacteria (Armitage and Fong 2004). Thus, nitrogen loading can cause unexpected and significant changes in community and ecosystem function in marine systems (Turner and Rabalais 1994; Mack and D'Antonio 1998). Depending on how the system responds to the nutrients, the resultant changes in productivity could increase the success of invaders or native species, depending on which organisms are present. In marine systems, the relationship between invasion success and productivity remains to be explored (Levine and d'Antonio 1999).

Among the most common snail species on the SF Bay mudflats are the introduced Atlantic mud snail *Ilyanassa obsoleta* (Say 1822), and the native *Cerithidea californica* (Haldeman 1840). Introduced to the west coast via aquaculture of the oyster *Crassostrea virginica*, *Ilyanassa* was first reported in San Francisco Bay in 1907 and is found as far north as the Canadian border (Carlton 1979). It can tolerate temperatures from 13-22° C, and withstand salinities from 10-32 ppt. *I. obsoleta* often burrows 1-2 centimeters below the surface, and can crawl several meters during a single low tide (Weiskel, pers. observation). Both *C. californica* and *I. obsoleta* consume benthic diatoms, though *I. obsoleta* is an obligate omnivore and therefore also consumes bacteria and animal material (Curtis and Hurd 1979). *Ilyanassa* grazing has been shown to change primary production rates and diatom community composition (Pace *et al.* 1979; Connor and Teal 1982), and its bioturbation and grazing are substantially more disruptive to the sediment surface than the equivalent grazing behavior in *C. californica* (Weiskel, pers. observation). *I. obsoleta* also consumes *C. californica* egg masses and physically disturbs the native mud snail by literally "walking over it" during *I. obsoleta's* annual migration in spring from subtidal regions to the intertidal mudflats and creeks (Race 1982). Past studies go so far as to suggest it has successfully displaced *C. californica*, restricting the native snail to higher, vegetated areas (Race 1982). The larvae of *I. obsoleta* are planktonic, while *C. californica* are direct developers. They are both reproductive during the summer months, though the invasive is also reproductive in winter (Weiskel, unpublished data).

I propose to determine how nutrient inputs influence both the native and invasive snails, as well as primary production and other sediment characteristics, and how these effects in turn influence the population growth and interactions between *C. californica* and *I. obsoleta*. In addition, I propose to examine the initial effects of the newly arrived *Batillaria attramentaria* population in San Francisco Bay.

Experiment 1: Nutrients & Aquatic Invasion Success

I am conducting a factorial experiment on the eastern side of San Francisco Bay to quantify the impact of elevated nutrients on resource utilization and whether the addition of nutrients changes growth rates or reproductive activity for either *C. californica* or *I. obsoleta*. Factors for the experiment include two nutrient levels (present or absent), 2 snail species (*C. californica* or *I. obsoleta*), and 6 snail densities (0, 50, or 100, with no one cage containing > 100 snails), plus appropriate open and cage controls for destructive sampling purposes (following Silliman and Zieman 2001 and references therein). The study will run for 6 months and be repeated over 2 summers.

My response variables include a suite of sediment characteristics, as well as snail growth and fecundity. Specifically, I will measure infaunal community composition, oxygen levels in the sediment (REDOX potential), carbon:nitrogen ratios, and changes in the benthic microalgal community (using High Performance Liquid Chromatography, or HPLC, per Pinckney *et al.* 1999 and C. Janousek, dissertation 2005.) at time zero and throughout the experiment. At the beginning and conclusion of the experiment I will measure growth of individually marked snails, and will record egg cases and size-specific snail mortality (as per Armitage and Fong 2004) as the study continues. I will analyze the results of the experiment using MANOVA and repeated measures ANOVA as appropriate. This comprehensive design will allow me to compare native and invasive species' responses to elevated nutrient levels as well as examine changes in the microphytobenthos.

I will use 0.5 x 0.5 m cages made of 1/4 inch Vexar mesh and PVC and place the cages 1.0 m apart. Nutrients will be added using Jobes fertilizer sticks, 19:6:12 (Nitrogen:Phosphorus:Potassium ratio) or ammonium chloride, which will be hammered either directly into the mud or packed in centrifuge tubes. This nutrient addition technique results in strong initial nutrient peaks (Worm *et al*. 2000) and mimics a sudden nutrient influx. Twenty percent of the snails in each cage will be marked using paint and superglued wire tags, and weighed and measured at the start and conclusion of the experiment.

In preliminary method trials conducted this summer, I found that fertilized cages with snails had higher chlorophyll_*a* levels than the unfertilized cages. This result may be due to increased grazing, which can trigger faster diatom generation (Admiraal *et al.* 1982). Further, though the overall differences were not significant ($p = 0.78$), it appears that some treatments are positively affecting chlorophyll_*a* levels more than others early on in the experiment. For example, the disproportionately stronger effect in the high-density, *I. obsoleta*-only treatment is consistent with the invader's more disruptive and aggressive grazing behavior.

Based on these pilot data and other studies (*e.g*., Armitage and Fong 2004 on *C. californica*), I hypothesize that increasing nutrients will result in a shift in benthic microalgae from benthic diatoms to cyanobacteria and purple sulfur bacteria. I predict that this micro-community change will have substantial negative effects on the native *C. californica*, while the elevated nutrient levels will have a positive impact on *I. obsoleta*, due its broader diet and bioturbation-grazing behavior, which disturbs the top sediment layer and potentially breaks up harmful bacterial mats, exposing the non-toxic diatoms below.

I plan to pair this experimental approach with a spatial scale survey to determine if nutrient level effects on microalgal communities that I measured in controlled experiments predict species distributions in San Francisco Bay. I will identify multiple sites (n=12) that have either populations of Ilyanassa and/or Cerithidea and measure chlorophyll levels, microalgae functional groups, and sediment characteristics on a monthly to bimonthly basis to determine what correlates at a broader scale with species distributions. Predators are not considered to be particularly important in determining the distribution of snails in central California estuaries (Sousa 1993). This study will allow me to see if there is any pattern of native-invasive species distributions that matches the microalgal communities patterns.

I hypothesize that areas with high nutrient inputs and higher abundances of cyanobacteria will have a higher abundance of invasive snails than the native snails.

Experiment 2: Founder Population Analyses to Broaden Understanding of Invasion Success

To address the effects of initial invasion and eradication, we are collecting demographic information on the new invasive *B. attramentaria* populations. In addition, we are attempting an eradication in Loch Lomond Marina (LLM). In May 2006 we surveyed the population and in July we began eradication. We took monthly pre-eradication samples to determine the effects of the eradication on density estimates.

We used an asymmetric BACI (Before-After-Control-Impact) experimental design (Underwood 1994) to measure the habitat characteristics in 1 snail-invaded and 3 control areas. The BACI areas were divided into high (above 1ft tidal height) and low (below 1 ft tidal height) and samples were taken from both areas. We measured chlorophyll_*a* (a standard proxy for standing microalgal biomass and primary production in benthic systems), REDOX potential (oxygen levels in the sediment), and carbon:nitrogen ratios (to determine food quality) every month prior to the eradication efforts. We also sampled infaunal diversity at the beginning and conclusion of the eradication season. High-impact eradication effects (multiple volunteers stomping in mud) were controlled for by trampling the control sites after samples were taken.

To date, we have surveyed *the B. attramentaria* population in San Francisco Bay and begun eradication attempts. The population size is approximately 137,500 within the eradication—or high density—area, and in 5 days we were able to remove > 69,200 of them, or just over 50 percent. The parasitism rate of the population is 2.31 percent. Preliminary habitat results indicate that *B. attramentaria* removal significantly decreases chlorophyll_*a* levels, a proxy for standing microalgal biomass in the system ($p < 0.001$). I recently presented a talk on this work at the Fifth Annual Marine BioInvasions Conference at MIT in Cambridge, MA.

Explanations for the recent arrival of the invasive mud snail *B. attramentaria* founder population in Loch Lomond Marina, San Francisco Bay and Bodega Harbor remain elusive. Starting this summer (2007), we will characterize the Bodega Harbor population by conducting a similar survey to that conducted for the LLM population. In addition, we will simulate the eradication efforts in LLM in the older, established population of *B. attramentaria* in Tomales Bay, measuring the same habitat characteristics at all sites. If the habitats and/or demographics are different among these populations, we might expect our new San Francisco Bay and Bodega Harbor populations to have different effects on the benthic community, as well as to take a different evolutionary trajectory. This study provides a rare opportunity to examine two founder populations of a familiar invasive species. It is designed to broaden our knowledge about initial genetic and demographic characteristics of successful aquatic invaders, and to lend some insight into the mechanisms for these unexpected habitat changes caused by this important marine invasive species.

Experiment 3: Behavior Shifts in Native-Invasive Species Interactions over Time

Behavioral responses in native species can be influenced by multiple factors, including parasites (see Lafferty 1993 on *Cerithidea*), environmental conditions (Trussell 1997), and invasive species (Monello *et al.* 2006). Similarly, invasive species can change in response to new environments (for terrestrial plant examples see Clements *et al.* 2004 and Richards *et al.* 2006). These dynamics are considerably less well-understood in marine systems.

To address this question of plasticity or potential rapid evolution, I am conducting a series of behavioral trials between *I. obsoleta* and *C. californica* from multiple populations under controlled conditions. I use isolated 5-gallon buckets, with Tupperware containers that allow snails to interact in a constant light-temperature environment that is similar to summer conditions in northern California, when both species are most actively grazing and interacting. I use mud from Bodega Harbor, which has no snails and is therefore free of gastropod scents which could bias the interactions. I am currently establishing a baseline of behavioral responses and determining proper observation times. Following this trial period, I will test different populations of each species. I will use both naïve and sympatric populations of both snails, to determine whether prior exposure confers an advantage to either species in historically competitive native-invasive interactions (Race 1982). I have conducted the experiments thus far on moist mud not covered in water, and focusing on the behavioral responses that occur during simulated low tide conditions. However, I will also conduct behavioral trials under water. Response variables include distinct behaviors, such as crawling in a particular direction relative to the other snail, withdrawing the operculum, burrowing, or changes in grazing.

Preliminary results indicate that the historical negative interactions between the snail species are not occurring; indeed, I have not been able to recreate the previously observed predation and disturbance behaviors reported in the literature. Further trials will provide an opportunity for comparison between current and historical observations and should provide insight into the mechanisms behind these shifting competitive interactions.

Output/Anticipated Products and or Benefits:

Results from this collection of experiments will serve to inform the CALFED community and others about the relationship between nutrients and invasion success in benthic habitats. Nutrient loading and invasive species are unlikely to disappear as threats to estuarine systems but a greater understanding of their interactions and effects on native species can facilitate better protection for native species and the habitats on which they depend.

Year 1 Outcomes

By the completion of my first year as a CALFED science fellow, I will have conducted the experiments described in this proposal, and be starting to analyze them. Depending on what the results indicate, a further year of the studies in the field is likely to be important. I intend to have developed strong collaborations with my existing community mentor, as well as begun to communicate across the agencies focused on water quality and invasive species. I also plan to be farther along with the *B. attramentaria* eradication, and to have submitted a manuscript characterizing the incipient *B. attramentaria* populations and their ecological effects. I should also be able to have some indication as to whether nutrients are affecting invasion dynamics in the system.

Year 2 Outcomes

By the end of my second year as a CALFED science fellow, I will be done with all of my field experiments, and will likely be finishing some lab analyses and writing up the rest of my results for publication.

Year 3 Outcomes

I have asked for a half-year of funding forYear 3. I intend to graduate in December of 2009, but anticipate having further analyses or follow-up to do on my final experiments. I plan to use the Winter of 2010 to finish writing up my results and look for an academic postdoc position to start in the Fall of 2010. By the completion of my tenure as a predoctoral student, I plan to have contributed to answers for my initial 3 questions about nutrients and benthic invasion dynamics. I will prepare my results in formats that can be submitted for peer-reviewed publication as well as sent to managers and other CALFED stakeholders for their direct use.

In conclusion, my research examines the effects of nutrients on native and invasive gastropod species, and the species' effects on each other and on benthic habitats in San Francisco Bay. My research may highlight an important linkage between nutrient pollution and invasion success that could provide greater urgency for reducing nutrient inputs in San Francisco Bay and other coastal estuaries.

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