DISSERTATION

IMPACTS OF AN INTRODUCED MARINE INVERTEBRATE ON WINTERING SHOREBIRDS

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY VERONICA B ESTELLE ENTITLED IMPACTS OF AN INTRODUCED MARINE INVERTEBRATE ON WINTERING SHOREBIRDS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

IMPACTS OF AN INTRODUCED MARINE INVERTEBRATE ON WINTERING SHOREBIRDS

It has been speculated that the introduction of the European green crab (*Carcinus maenas*) along the West Coast of North American may pose a threat to migratory and wintering shorebirds that use similar habitats and prey resources. I conducted a literature review to determine the current state of knowledge on the effects of marine introduced species on shorebirds. I explored potential impacts of green crabs on Dunlin (*Calidris alpina*) prey consumption, foraging behavior, and weight change in Bodega Harbor and Bolinas Lagoon, CA. To do this I used a randomized complete block experiment in which green crab density was the treatment. I further explored potential impacts of green crabs on Dunlin through an observational study of Dunlin diets in these two embayments after the green crab introduction. I compared data on Dunlin diets prior to the arrival of green crabs in these locations with current diet data to assess whether Dunlin diets have changed since the green crab's introduction.

In Chapter 1, I reviewed the literature to assess effects of introduced species (marine plant or animal) on shorebirds. The body of literature addressing this topic is fairly sparse. I found 12 references in which effects of introduced marine organisms on shorebirds are considered; 6 studies considered introduced marine invertebrates and 6 introduced plants. The plant studies were by far the more rigorous, and investigated the question of impact of the introduced species upon shorebirds. Most of these studies took place in England; there is no published research from North America regarding the effects of introduced marine plants on shorebirds. The primary plant effects were related

to loss of habitat and changes in invertebrate prey communities within patches of *Spartina alterniflora* (and its various hybrids) and *Zostera maritima*. Authors specifically discussed the impact and implications of these plant invasions on shorebirds. In contrast, studies on introduced invertebrates in marine environments were more speculative about impacts and implications for shorebirds, and there were no examples of manipulative experiments to investigate causal relationships between these organisms. Of the invertebrate studies conducted, one showed no effect on shorebird abundance and distribution in one embayment in North America, and another showed increased reproductive output of the Black Oystercatcher (*Haematopus moquini*) in one location (South Africa). Because estuaries are among the most heavily and rapidly invaded coastal ecosystems and because shorebirds rely upon the food and habitat resources of these systems, there is a need to evaluate the ecological effects of these novel species on shorebirds. I hypothesize that the primary effects of introduced marine plants and animals will be mediated through space and food resources and will involve indirect effects.

In Chapter 2, I used a manipulative field experiment to examine shorebird responses to the effects of green crab predation on invertebrate prey. I set up a randomized complete block design with green crab density as the treatment. The experiment was conducted in two parts, a crab foraging experiment, followed by a Dunlin foraging experiment. I expected that temporal, spatial, and environmental variation in prey density could affect my ability to detect changes in this response variable, and so I incorporated specific experimental design features (Before After Impact Control, blocking, and paired sampling) to minimize variation from these sources.

I found that green crabs significantly reduced the prey density of a crustacean species, but not of other prey taxa that it previously affected (esp. the clam *Nutricola* spp.). This result was contrary to other studies, and may be related to past effects of green crab predation and to unusually low prey density during the season in which the experiment was conducted. I also found that Dunlin were able to reduce the density of a polychaete in areas where no green crabs had foraged compared to areas where high densities of green crabs had been held. Additionally, Dunlin reduced the density of *Nutricola* spp. in cages where high densities of green crabs were held compared to zero density cages. This result was also contrary to results of previous studies, and it may be related to indirect effects of holding green crabs in a cage at high density or to some other aspect of their foraging behavior. If this treatment effect holds beyond the experimental conditions, this would provide another mechanism by which the green crab negatively impacts *Nutricola* spp.

I detected no effects of green crabs on Dunlin foraging behaviors or weight. However, both Dunlin and green crab diet were different from free-ranging individuals in that fewer Dunlin consumed clams in the experiment than in non-captive conditions, and green crabs foraged on gastropods, not clams, during the experiment. Experimental results combine to suggest that prey conditions (density) affected green crab predation, and this in turn, affected Dunlin prey consumption and dietary composition.

Further implications of this research will need to be evaluated in an energetics context, and with attention to shorebird body condition and winter survival rates as these may affect population parameters. As marine invertebrate communities continue to change with the introduction of marine organisms, it will become important to the management and conservation of shorebirds to consider the ecological role of introduced marine plants and animals, particularly in locations where large numbers of shorebirds congregate during migration or winter.

In Chapter 3, I conclude with an examination of Dunlin diet in Bolinas Lagoon and Bodega Harbor, CA. I compared Dunlin diet prior to the green crab's introduction with that after the crab's arrival to assess whether any changes had occurred in Dunlin diet during this time, with the understanding that any documented changes do not necessarily imply a causative relationship.

Dunlin diet remains highly variable between locations and among years, and all major prey taxa (molluscs, crustaceans, polychaetes and insects) occur presently in their diets. However, when results from previous studies on changes in invertebrate density and size are considered, it is clear that the bivalve component (esp. *Nutricola* spp.) of the Dunlin diet in Bodega Harbor is currently comprised of fewer, smaller individuals than previous to the introduction of the crab. The present diet of Dunlin in Bodega Harbor appears more similar to that in Bolinas Lagoon than it did historically, but number of annual samples is too minimal during each period to be supportive of a causative relationship. Prior to introduction of the green crab in Bolinas Lagoon, the primary prey of Dunlin was polychaetes and crustaceans, not bivalves. Currently in Bolinas Lagoon, the Dunlin diet has a significantly higher percent occurrence of bivalves and a lower percent occurrence of crustaceans than it did prior to the green crab's arrival. In this location, Dunlin may now forage upon smaller individual bivalves, particularly *Nutricola* spp. than before the crab's introduction.

There may be energetic costs to these dietary changes, and these should be examined with regard to effects on shorebird winter body condition and survival rates. I conclude that future research on change in shorebird populations, diets, and foraging should consider changes in invertebrate biota due to introduced marine invertebrates. In the future, shorebird diet should be examined as a function of relative abundance of native vs. non-native prey composition.

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CHAPTER 1

INTRODUCED SPECIES IN MARINE ECOSYSTEMS: AN UNASSESSED THREAT TO SHOREBIRD POPULATIONS?

ABSTRACT

Introduced invertebrates and plants are a pervasive and global threat in marine ecosystems. Marine introductions may have a variety of ecological and evolutionary effects on single and multiple species, communities, ecosystem processes, and multiple trophic levels. However, relatively little research has been conducted on the effects of introduced marine organisms on multiple species or multiple trophic levels.

Shorebirds (Order Charadriformes) depend upon coastal ecosystems and are currently experiencing global population declines. I review the documented effects of introduced marine species on shorebirds and ask whether introductions in marine ecosystems could be deleterious to shorebird populations. Specifically, some marine introductions alter prey dynamics, composition, and abundance, create indirect effects through trophic interactions, and change physical aspects of mudflats important to wintering shorebirds. Given the ecologically complex interactions that arise after some marine introductions, research focused on multi-trophic impacts is needed before we can conclude that marine introductions do not pose a threat for shorebirds.

Keywords: marine invertebrates, marine plants, introduced marine species, shorebirds, Scolopacidae, Charadriidae, impacts, competition, predation, population decline

INTRODUCTION

Introductions of animals and plants in marine environments around the world are increasing at an accelerating rate (Cohen and Carlton 1998, Carlton 2001). In the United States alone, there are at least 400 introduced marine species in coastal environments (Ruiz *et al.* 1997). Marine invaders, like those in terrestrial and freshwater ecosystems, exert ecological effects such as displacement and extirpation of native species, changes in species composition in communities, alterations in population dynamics and structure of age classes, and changes in nutrient cycles (Posey 1988; Alpine and Cloern 1992; Cohen and Carlton 1995; Grosholz *et al.* 2000; Byers 2000, Byers and Goldwasser 2001). With the exception of studies on the Chinese clam (*Potamocorbula amurensis*; Alpine and Cloern 1992) and one study on the European green crab (*Carcinus maenas*; Grosholz *et al.* 2000), research on the impacts of marine introductions in the past focused on direct effects on native, benthic species and communities, generally at single trophic levels (Grosholz *et al.* 2000). Research on marine invasions has recently expanded to examine indirect effects of non-natives on multiple species, food webs, ecosystem properties, and on the properties of native communities that may affect invasion (Grosholz 2002). Historic data in many locations are unfortunately absent, and the lack of these complicates our current understanding of the ecological effects of non-native species. Given the prevalence of introduced marine species, their broad range of effects, and a host of anthropogenic disturbances that occur in marine ecosystems, future studies will likely examine how marine introductions affect multiple trophic levels, and whether their impacts alter food webs or destabilize marine ecosystems.

Because marine introductions commonly affect the abundance and diversity of invertebrate species directly, it is plausible that these invaders also have important indirect effects on populations of marine vertebrates that rely on coastal resources during all or part of their life history. Currently, the effects of introduced marine invertebrates on vertebrate population dynamics are largely unknown, although there are some indications of local multi-trophic effects. For example, the introduced Chinese clam occurs in greater densities and is energetically more valuable than the native clam (*Macoma balthica*) commonly eaten by Lesser Scaup (*Aythya affinis*) in San Francisco Bay (Cohen and Carlton 1995; Richman and Lovvorn 2004). The exotic clam also bio-accumulates selenium, hydrocarbons, and some heavy metals to a much greater degree than do the native clams (Richman and Lovvorn 2004). Scaup on the Pacific Flyway have been undergoing a 20-year population decline, and Austin *et al.* (2000) have questioned whether this decline may be related to deterioration or contamination in the prey base.

Shorebirds are also experiencing global population declines and some rely extensively on coastal environments for nearly two-thirds of their annual cycle (Piersma *et al.* 1997; Brown *et al.* 2001). These birds use marine invertebrate prey to fuel their energetically demanding migratory flights between Arctic breeding and southern wintering grounds and to ensure their survival during the winter season (Myers 1983). The potential for invasive marine species to affect shorebird population dynamics is most likely to arise as a consequence of altered physical habitat quality, changes in prey resources, and multi-trophic interactions (Daehler and Strong 1996; Winemiller and Polis 1996; Grosholz *et al.* 2000). The possible connection between changes in winter food supply caused by marine introductions and shorebird population change has rarely been explored or factored into conservation planning (see Piersma *et al.* 1997; Piersma and Baker 2000; Brown *et al.* 2001) despite the fact that introduced species represent a significant agent of change in marine ecosystems today (Carlton and Geller 1993; Ruiz *et al.* 1997). If invasive species are negatively affecting the abundance, composition, or distribution of shorebird prey in coastal habitats, it is tenable that invasive species are contributing to the observed declines in shorebird populations.

Theory suggests for migratory birds that conditions on the wintering grounds affect the outcome of the breeding season and that the nonbreeding season is extremely important in the regulation of numbers of birds (Fretwell 1972). The linkage between winter conditions and breeding outcome has been difficult to test or document empirically for shorebirds because they are difficult to track between different phases in their annual cycle. However, Goss-Custard (1981) explored the idea that winter food supply could affect population size in migratory shorebirds by demonstrating that even small increases in winter mortality can affect shorebird population size to a disproportionately large degree. Although Goss-Custard envisioned a change in winter food supply through loss of winter habitat, a similar effect could occur with the introduction of species that change food-web dynamics or the composition of invertebrate communities in coastal ecosystems. In an empirical study, Gill *et al.* (2001) demonstrated a link between increased numbers of Black-tailed Godwits (*Limosa limosa*) returning to winter in England and Ireland and high winter prey- intake rates there. It is thus important, especially for declining populations of migratory animals, that we understand factors affecting prey conditions during their nonbreeding season.

Global Population Declines of Shorebirds

The American and Canadian Shorebird Conservation Plans (Brown *et al.* 2001; Hyslop *et al.* 2000) have documented declining population trends for at least 24 of 52 North American shorebird species (Howe *et al.* 1989; Morrison *et al.* 1994, 2001). Morrison *et al.* (2001) updated some of these analyses and found that declines in North American shorebirds "appear to be even more extensive and severe than previously thought." Of 35 species for which there were sufficient data 28 had negative population trends. The decline in shorebird populations is not restricted to North America. Globally, at least 35 of 155 scolopacid and charadrid species considered by Piersma *et al.* (1997) are "in danger of passing away or are extinct."

Though exact causes of these declines in shorebird populations are unknown, BirdLife International has identified primary threats to the persistence of 35 species (Kim Sattersfield, pers. comm.). The highest ranking threats include habitat modification and loss (32 species; mostly due to wetland reclamation), overexploitation (17 species; especially market hunting in the US during the 19th century and small-scale hunting currently in other parts of the world), predation by introduced species (16 species; introductions of goats, rats, hedgehogs, and snakes to islands), disturbance (18 species; human encroachment into coastal wintering areas), and pollution (6 species; bio-accumulated toxins in prey). Of the 16 species for which there were data and that were categorized as "threatened by introduced species," the threat was always predation by a terrestrial mammal. Threats posed by invasive species via competition or indirect effects (e.g., trophic cascades, exploitative competition, habitat alteration) are hard to document, yet increasing numbers of introduced species in marine ecosystems and observed declines in many shorebird populations make it important to explore the relationship between these two phenomena.

Shorebirds in Marine Environments

Shorebirds (Order Charadriformes) are a diverse group of birds found in coastal and inland areas throughout the world. The two most diverse families, Scolopacidae (88 species of sandpipers and snipes) and Charadriidae (65 species of plovers and lapwings) are also the most studied. Approximately 58% of all shorebird species (216) use marine environments for part or all of their annual cycle (Warnock *et al.* 2002) and they comprise 44% of the species diversity of marine birds (Burger 1984). The primary trophic role of shorebirds in marine ecosystems is as a predator. As predators they contribute strongly to the flow of energy and matter through marine food webs (Baird *et al.* 1985). For example, in a variety of estuarine locations in Europe and Africa, shorebirds consumed 6-44% of the total annual invertebrate production in a given location (Baird *et al.* 1985). Because predation is often the primary mechanism by which soft- sediment invertebrate communities are regulated (Lenihan and Micheli 2001), shorebirds may influence invertebrate population dynamics and community structure. However, no explicit studies have demonstrated top-down regulation of an entire invertebrate community by shorebirds.

Life-history Characteristics that Make Shorebirds Vulnerable to Environmental Change

At least three life-history characteristics of long-distance migratory shorebirds make them vulnerable to broad-scale, human-induced environmental changes such as the invasion of non-native invertebrates. First, when these shorebird species migrate they do so *en masse* along traditional routes composed of a network of locations used for resting and feeding. These traditional "staging sites" provide abundant prey at critical times during the migration of shorebirds, and at the same time, they have the potential to serve as "geographic bottlenecks" in the event of an environmental impact at one of these sites (Myers 1983). Second, millions of shorebirds migrate between arctic and sub-arctic breeding grounds and temperate, sub-tropical, and tropical wintering areas each year. Their migrations are energetically demanding and require undisturbed habitat and abundant food at specific times. Third, shorebirds arriving on wintering grounds may be energetically depleted, depending upon their migration strategy and the distance they migrate (O'Reilly and Wingfield 1995). Their winter survival depends upon rapid acquisition and assimilation of food on the wintering grounds (Castro *et al.* 1989). Collectively, these features of shorebird ecology underscore the fact that prey resources at wintering locations and at key staging sites during migration are essential to shorebird long-term viability.

Case Studies of Introduced Marine Species Effects on Shorebirds

Because of current global population declines in shorebirds and an incomplete knowledge of how invasive marine species may affect the abundance and diversity of invertebrate prey, I focus here on the documented and potential effects of introduced marine species (animals and plants) on shorebirds. I do not address the effects of introduced species (terrestrial mammals) as predators of shorebirds and their eggs as this topic has been covered elsewhere (Jackson and Green 2000; Dowding and Murphy 2001; Jackson *et al.* 2004).

A logical first question is whether changes in the prey base can be attributed to the introduction of a marine species and, if so, has this resulted in any documented effects on shorebirds. The existing literature does not allow this question to be addressed rigorously. There are published examples demonstrating or speculating on positive, neutral, negative, and uncertain effects of introduced species on shorebirds (Table 1). These papers examined direct and indirect effects of non-native species on shorebirds using experimental or observational techniques, and they discussed possible effects in terms of changes in shorebird fitness, behavior, abundance, and distribution. Overall, far less attention was given to the effects of introduced marine invertebrates and consequent changes in the prey base than to introduced plants and habitat modification, presumably because it is more difficult to measure the effects of changing food resources than direct habitat alterations on higher trophic levels.

Effects of a Space-dominant Competitor on Shorebird Reproductive Output

In the 1970s a Mediterranean mussel, *Mytilus galloprovincialis*, was introduced accidentally to the West Coast of South Africa (Griffiths *et al.* 1992). This mussel is a superior competitor for space in the mid- and upper rocky intertidal. Its growth rate, reproductive output, and tolerance to desiccation exceed that of the native mussel, *Aulacomya ater*, and *M. galloprovincialis* is now the space-dominant species in the rocky intertidal community of western South Africa (Griffiths *et al.* 1992). The displacement of *A. ater* has resulted in a rocky intertidal with a greater biomass and vertical coverage by *M. galloprovincialis*. The net result is that the non-native mussel provides a superabundant and readily available food source for predators that feed in the upper rocky intertidal.

Along with the change in mussel species has come a change in the flora and fauna within the mussel-bed matrix. Algal diversity within *M. galloprovincialis* beds has declined. *M. galloprovincialis* has a smooth shell whereas *A. ater* has a ribbed shell. Small native limpets easily graze the smooth shells of *M. galloprovincialis* and have thereby effectively eliminated algal species that once inhabited the native mussel beds. Changes in the fauna within the mussel beds include an increase in the density of polychaetes and bivalves and a decrease in the density of barnacles, amphipods, and sea spiders (Griffiths *et al.* 1992). Finally, adults of the native limpet *Patella granularis* have been eliminated by competition for space with *M. galloprovincialis* while the density of small and recruiting limpets has increased markedly.

The overall effect of *M. galloprovincialis* on the African Black Oystercatcher (*Haematopus moquini*) has been an increase in its reproductive output (Griffiths *et al.* 1992; Hockey and Schurink 1992). After invasion of the non-native mussel, the percent of oystercatcher pairs raising two chicks instead of one increased significantly. In comparing pre- and post-invasion diets of oystercatchers, Hockey and Schurink (1992) found a dramatic decrease in the proportion of *P. granularis* in the diet and a substitution of *M. galloprovincialis* for *A. ater*. Although long-term effects of the non-native mussel on the ecosystem and its nutrient dynamics were not explored, Griffiths *et al.* (1992) and Hockey and Schurink (1992) did comment that a greater volume of water is filtered by this non-native mussel. Additional removal of food and nutrients from the water column could affect lower trophic levels and, ultimately, other predators (sea stars, fish, lobsters, whelks, and octopuses) foraging within the ecosystem. Finally, humans extensively harvest this non-native mussel, thus increasing disturbance and competitive effects with oystercatchers (Griffiths *et al.* 1992).

Effects of a Non-native Predator on Shorebird Winter Abundance, Distribution, and Foraging

In Bodega Harbor, CA, Grosholz and Ruiz (1995) and Grosholz *et al.* (2000) studied the effects of the European green crab (*Carcinus maenas*), an invasive predatory crab, on multiple functional groups in a marine food web. Grosholz *et al.* (2000) compared density and relative abundance of a variety of common soft-sediment infaunal and epifaunal invertebrate species and absolute abundance and distribution patterns of shorebird species prior to and after the invasion of the green crab (approximately 4 years pre- and 4 years post-invasion data). They found that green crab predation led to a 5 to10-fold decline of native clam (*Nutricola tantilla* and *N. confusa*) and crab (*Hemigrapsus oregonensis*) species and declines in gammaridean amphipods (*Eohaustorius* and *Paraphoxus* spp.). The depression of prey abundance persisted for 4 years after the green crab's invasion. The species of prey that declined are common in the diets of green crabs and shorebird species in Bodega Harbor and other nearby, local embayments (Recher 1966; Stenzel *et al.* 1976; Ruiz 1987; Grosholz *et al.* 2000). Grosholz *et al.* (2000) also found a 4-fold increase in a small tube-building crustacean, *Leptochelia dubia*, and 70-100 fold increases in species of syllid (*Exogone* spp.) and spionid (*Pseudopolydora* spp.) polychaetes, species uncommon in the diets of green crabs (Grosholz *et al.* 2000). *L. dubia* and *Exogone* are uncommon in the diets of local shorebirds, but *Pseudopolydora* have been frequently reported (Stenzel and Page unpublished data; Stenzel *et al.* 1976; Ruiz 1987).

Despite changes in prey populations, average annual, mid-season abundance of four of the most common shorebird species, Dunlin (*Calidris alpina*), Western Sandpiper (*Calidris mauri*), Willet (*Catoptrophorus semipalmatus*), and Marbled Godwit (*Limosa fedoa*), and pooled abundances of 13 shorebird species did not show any differences before and after the green crab introduction (Grosholz *et al.* 2000). Shorebirds did not shift their distribution among various foraging sites within the Harbor after invasion of the crab, even though there were large changes in abundance of prey species that shorebirds are known to consume in Bodega Harbor (Ruiz 1987). Because they saw no change in the abundance and distribution of shorebird species wintering in the Harbor, Grosholz *et al.* (2000) concluded that there were no multi-trophic effects of the green crab upon shorebirds during their study.

Alternative explanations for the apparent absence of multi-trophic effects include the possibility that shorebirds switched to alternative prey and were not affected by the loss of previously predominant prey items. In addition, the magnitude and time period over which the invasion took place may have been inadequate to elicit a change in shorebird abundance (Grosholz *et al.* 2000). Other variables that were not recorded, such as body condition, molt schedule, foraging rate, or diet composition, might be more sensitive than abundance or distribution to changes in prey species. The biologically relevant question is whether alternate prey will be sufficient to ensure the birds' winter survival and successful migration and reproduction (Goss-Custard *et al.* 2004). For example, the polychaetes and tanaid species that increased in abundance in Bodega Harbor after the green crab invasion are smaller bodied and take longer to capture and consume than the clams and crabs that were previously available and abundant. The physical condition of the birds during the study in Bodega Harbor was unknown. Even though the abundance and distribution of shorebirds apparently did not change, winter survival, body condition, molt schedule, and foraging rates may have been affected.

A second alternative explanation for the lack of changes in shorebird abundance and distribution is that the magnitude and rate of green crab invasion were not sufficient to affect these variables. This explanation seems plausible when the response of shorebirds during the green crab invasion is compared with that during an unusually large, but natural, recruitment of the native Dungeness crab (*Cancer magister*) in Bodega Harbor in 1985 (Ruiz 1987; Grosholz *et al.* 2000). Abundance of Dungeness recruits in 1985 was so great that local prey resources (mostly small native clams, *N. tantilla* and *N. confusa*) were completely consumed by the Dungeness recruits. Ruiz (1987) found a significant decline in Dunlin abundance, weight, body condition, and molt status in response to the prey depletion. Some adult Dunlin also left the Harbor at night, presumably to search for alternative foraging opportunities. Juveniles did not leave the Harbor at night, and these individuals had lower body condition indices than did juveniles at other locations and adults using the Bodega Harbor site during the day. Ruiz (1987) also noted reduced return rates of adult Dunlin and Western Sandpipers over the subsequent 2 years, despite a recovery of prey resources. In contrast, the green crab invasion was smaller in magnitude and occurred over a longer period than did the Dungeness recruitment event. In the green crab example, shorebird abundance and distribution did not change as noticeably as they did during the Dungeness example. Perhaps for green crabs to affect shorebird abundance and distribution, there must be a larger and a more rapid invasion of the green crab than has occurred in Bodega Harbor. The natural recruitment event demonstrates that prey resources can become limiting and that the conditions for exploitative competition can develop when there is a rapid and large-magnitude "bloom" of a predator. Whether the green crab as an invader species can mimic the rate and magnitude of a large natural recruitment event remains to be seen. The Dungeness example provides evidence that prey depletion can have significant impacts on shorebird populations on local and larger scales, and impacts that can persist for a number of years.

Additional evidence of a link between prey reductions and declines in shorebird body condition, survival, and abundance comes from studies of the overexploitation of prey resources by humans. Goss-Custard *et al.* (2004) found that Black Oystercatchers (*Haematopus ostralegus*) in English estuaries required 3-8 times more shellfish prey (*Cerastoderma edule* and *Mytilus edulis*) than had been allocated to them in management plans. During the course of the winter, shellfish flesh content decreased, oystercatchers' efficiency of extracting the flesh decreased, and oystercatchers did not compensate this loss of prey resource by switching to another type of prey or by supplementing their forage by visiting other nearby sites. Management plans had been developed based on the assumption that oystercatchers could switch to other prey types to compensate for less of their predominant prey, but this was not observed. Oystercatchers in English estuaries were starving and their winter mortality rates increased sharply because humans were depleting their shellfish prey. The importance of this example is that it demonstrates a connection between reduction in winter forage and population-level effects for a shorebird species.

A final example of the effects of prey reduction is the dramatic decline in the Red Knot (*Calidris canutus rufa*), which stages in Delaware Bay, MD during spring migration

(Baker *et al.* 2004; Morrison *et al.* 2004). At Delaware Bay in the spring, the Red Knot exploits horseshoe crab eggs and experiences a rapid rate of fattening (Baker *et al.* 2004). Exploitation of the horseshoe crab eggs for bait by the fishing industry has led to a massive decline in the abundance and availability of horseshoe crab eggs. Apparently in response to this decline in food resource, Red Knot numbers have fallen from 51 000 to 27 000 during 2000–2002 (Morrison *et al.* 2004). If immediate management actions are not taken, demographic modeling predicts that this subspecies faces a high risk of extinction (Baker *et al.* 2004). This example illustrates the potential consequences of reducing prey resources at a key staging site. Baker *et al.* (2004) comment that shorebirds may not be able to adjust their migration strategies and maximize their fitness in light of environmental changes such as global climate change, overexploitation of food resources, habitat destruction, and disturbance at staging sites. It is interesting to note that Delaware Bay has at least 212 known introduced marine species (Ruiz *et al.* 1997), and their ecological role in this example remains unexplored.

Effects of a Suite of Non-native Invertebrate Species on Shorebird Winter Distribution, Abundance, and Behavior

Carlton (1979) noted that the invertebrate prey found in diets of shorebirds in San Francisco Bay (as described by Recher 1966) was composed largely of introduced species (97–100% in the 1960s for birds examined by Recher). Carlton also suggested that the preponderance of historically "new" prey species in San Francisco Bay could have altered shorebird distribution, abundance, and feeding strategies. The presence or extent of alteration in shorebird distribution, abundance, and feeding strategies is impossible to know now, however, without knowledge of the status and trends of shorebird populations and their use of resources prior to introduction of invertebrate species (more than 100 years ago). A lack of historic data on shorebird diet and resource use in San Francisco Bay emphasizes the need for monitoring programs that simultaneously assess changes in shorebird populations and their invertebrate prey. Many of the National Oceanographic and Atmospheric Administration's Estuarine Reserves and the National Park Service's National Seashores are now implementing monitoring programs for invertebrates, but they may not necessarily combine these efforts with shorebird monitoring. Additionally, monitoring shorebirds by counts alone may not be sufficient to detect effects of introductions. Observations on foraging behavior, diet, or body condition rather than count data alone may be needed to detect an impact of a non-native species.

Effects of Introduced Parasites on Shorebird Foraging and Overall Health

Few published studies have investigated the effects of non-native parasites on shorebird populations. Generally however, shorebirds are thought to be susceptible to parasites and pathogens because their immune systems are not broadly adapted to parasitic infection (Piersma and Baker 2000). The effects of non-native parasites on shorebird migrations, foraging, abundance, distribution, mortality rates, and immune systems are unknown, although it has been hypothesized that there may be a trade-off between immunofunction and growth and sustained exercise rates for shorebirds (Piersma 1997). If this is true, then shorebird life-history characteristics could be affected by novel parasites in marine environments.

Non-native species of marine invertebrates sometimes bring along their non-native parasites. The added effect of non-native parasites in marine systems is an area of current research (Lafferty 1993; Lafferty and Morris 1996; Torchin *et al.* 2001, 2003). Non-native digenean trematodes - flukes having more than one intermediate host – are recorded now in West coast embayments (Torchin *et al.* in press). These trematodes initially infect a mollusc, then pass to a fish, crustacean (commonly a crab) or another mollusc, and finally end up in a bird or mammal. Initial and intermediate hosts experience changes in growth rates, survivorship, and behavior, and the definitive host may or may not experience pathenogenic effects from these trematodes.

To date, deleterious effects of non-native digenian trematodes on shorebirds have not been clearly documented in the literature, but rather, there remains speculation about their effects. For example, in California the native mud snail, *Cerithidea californica*, and the non-native mud snail, *Batillaria cumingi* (previously *B. attramentaria*), carry parasites. *Cerithidea* carries a suite of up to 18 native digenean trematodes (Torchin *et al.* in press) and *Batillaria* carries one, non-native digenean trematode. *Batillaria* competitively displaces *Cerithidea* and causes local extirpation of this snail and of its 18 species of parasites. The trematode occurring in *Batillaria* appears to cause behavioral changes in the fish, crustacean, and mollusc species it infests, causing them to be more prone to predation by water birds (waterfowl, grebes, cormorants, and herons), shorebirds (Greater Yellowlegs, *Tringa melanoleuca*), and mammals (Torchin *et al.* in press). Pathology for the final host does not yet appear to be high in this system, although there has been limited research on shorebirds and water birds with respect to this non-native parasite.

In Venezuela, juvenile and adult Greater Yellowlegs exhibited a negative response to infection by digenean trematodes. These shorebirds over-summered instead of migrating to the breeding grounds. It is believed that infection by the trematodes either delayed or suspended pre-migratory molt in the Yellowlegs and prohibited fat deposition necessary for migration. McNeil *et al.* (1994, 1995) linked these effects on shorebirds with infestations by digenean trematodes, and suggested that trematodes may cause a high degree of pathology in shorebirds. However, McNeil *et al.* (1994, 1995) did not evaluate the native vs. non-native status of the trematode species identified in their study sites. Their result may portend consequences of exposure to ecologically and evolutionarily new parasites for shorebirds and other water birds in marine environments.

Effects of Introduced Species that Result in Habitat Modification

Some introduced species directly affect the physical structure and resources of an ecosystem when they create, destroy, or modify habitat. An example is *Spartina alterniflora*, which modifies and reduces the availability of open mudflat habitat, affects infaunal species composition, and increases sedimentation rate in estuaries (Daehler and Strong 1996). This and other non-native *Spartina* species (*S. alterniflora x S. foliosa, S. patens, S. densiflora*, and *S. anglica*) invade open mudflats and transform them into densely vegetated meadows; *Spartina* stem density can be exceptionally high (519-638 stems/m^2; Wonham 2003). *Spartina* species also change the below-surface environment by anchoring into the substrate via concentrated rhizomatous mats. These thickets of below-surface rhizomes change infaunal conditions for many invertebrates. Because many shorebirds do not feed in close proximity to or within dense vegetation (Prater 1981), it has been speculated that *Spartina* will eventually exclude foraging and roosting shorebirds from critical mudflat habitat (Daehler and Strong 1996). The detritus of *Spartina* also often makes conditions inhospitable for invertebrates where it has invaded (Nairn 1986).

It is unknown how much open mudflat space has been invaded by this plant on the Pacific Coast of North America, although efforts are underway to map the native (*S. foliosa*) and non-native (*S. alterniflora, S. alterniflora x S. foliosa, S. patens, S. anglica, S. densiflora*) marshes in the San Francisco Bay area. In Willapa Bay, WA, as much as 20% (approximately 5 000 ha) of open mudflats have been covered by non-native *Spartina* in the last 10 years (D Garcia-Rossi, UC Davis Bodega Marine Lab, pers. comm.). Although there is considerable concern that this introduced cordgrass will affect shorebirds, substantive research on its direct or indirect impacts on shorebirds has only recently begun in San Francisco Bay (Stahlberg *et al* unpublished data; Grosholz *et al* unpublished data). Most of what we know about interactions between *Spartina* and shorebird populations comes from work in Europe.

In England, a negative interaction between shorebirds and *Spartina anglica* (a hybrid of *S. alterniflora* and *S. maritima*) has been observed (Goss-Custard and Moser 1988, Smith and Evans 1973). Goss-Custard and Moser (1988) documented that abundance of wintering Dunlin declined at a higher rate in estuaries where *S. anglica* had spread than in estuaries where *S. anglica* remained constant or decreased. They suggested that *S. anglica* affected shorebirds, especially small-bodied Dunlin, by reducing available feeding area and the amount of time for feeding. As *S. anglica* spreads from the high to low intertidal it covers previously open mudflat and reduces the area and amount of time available to shorebirds for foraging. A decrease in feeding area or feeding time would likely increase emigration and mortality rates of wintering Dunlin (and other shorebird species). Goss-Custard and Moser (1988) made two other important points about this interaction: 1) a 10% reduction in mudflat availability by S. *anglica*, especially in the higher intertidal, had a marked negative effect on Dunlin abundance, whereas a 10% increase in mudflat availability did not produce a marked increase in numbers; and 2) wintering Dunlin displaced from one estuary did not necessarily find accommodations in another estuary. This is because individual carrying capacities of various sites likely differ and because the level of inter- and intra-specific competition increased as density of birds increased (Goss-Custard and Moser 1988). Not only small-bodied shorebirds are affected negatively by *Spartina* stands -- the much larger Bar-tailed Godwit (*Limosa lapponica*) also appears to avoid feeding in dense patches of *S. anglica* (Smith and Evans 1973). However, no similar decline in their winter numbers in English estuaries has been associated with the invasion of *S. anglica.*

No peer-reviewed studies in North America have yet assessed the ecological interactions between *Spartina* and shorebirds. There are studies underway in San Francisco Bay to evaluate the effect of *Spartina* on the behavior and reproduction of Song Sparrows (*Melospiza melodia*) (Cully Norby, UC Berkeley and San Francisco Estuary Institute, pers. comm.), a native species that utilizes *Spartina*-dominated areas for reproduction. Both mechanical and chemical means of control have been instituted for *Spartina* in American and English estuaries, although it is not clear how these control methods influence sediment dynamics or whether they produce toxic effects on non-target species.

CONCLUSIONS

The introduction of species to marine communities is a problem of global scale, and one that shows no indication of decreasing in extent or magnitude (Steneck and Carlton 2001). Marine introductions are found in a variety of habitats, ranging from rocky shores to soft sediments (Carlton 2003), with estuaries being the most frequently and heavily invaded habitat (Ruiz *et al.* 1997; Carlton and Geller 1993). For the marine invasions that have been studied, the literature indicates that the invaders altered food webs, population dynamics and community composition and structure, and ecosystem processes where they have become established (Carlton 1999, 2003; Ruiz *et al.* 1997, 1999; Grosholz *et al.* 2002). Because human-mediated introductions are projected to increase in marine ecosystems (Carlton and Geller 1993), studies of their impacts at multiple trophic levels become an especially important area for future research.

In this review I have summarized what is known of the effects of marine invasions on shorebirds, a group of marine vertebrates whose populations are declining worldwide (Piersma *et al.* 1997). My primary goal was to explore the literature for explicit effects of non-native marine species on shorebirds, and secondarily, it was to illustrate through case studies the ways in which these non-native species may pose a significant threat to shorebird populations. It is clear that the relationship between introduced marine and estuarine species and shorebirds is poorly understood. The primary focus of studies on the effects of introduced species on shorebirds has been from the perspective of predation - how have introduced terrestrial mammals affected shorebird populations by preying on shorebird adults, chicks, and eggs, especially on islands (Jackson and Green 2000; Dowding and Murphy 2001; Jackson *et al.* 2004)? Rarely has the perspective been to examine introduced marine species and their direct and indirect effects on shorebirds through competition and changes in the prey base. In 1927, de Groot, when writing about Clapper Rail (*Rallus obsoletus*) mortality in San Francisco Bay, documented "an incredible number of" rails being entrapped (their beaks and toes) by a widespread introduced mussel and dying by starvation or drowning. De Groot (1927) stated that this type of interaction occurred because of an "invisible foe," and he suggested that it contributed significantly to Clapper Rail population decline in San Francisco Bay. Is it possible that changes in the prey base and other types of interactions with non-native marine species could be an "invisible foe" to shorebird populations?

Effects of non-native marine plants on shorebirds are the more 'visible' problem when one considers effects of marine introductions on shorebirds. Among the plant studies covered in this review (see Nairn 1986 for others) there were both direct and indirect effects of invasive plants on shorebirds. Significant effects on shorebirds resulting from plant introductions included colonization (and thus loss) of open mudflat habitat, negative changes in prey survival and composition, obstruction to feeding, reduction in amount of time for feeding, and reduction in numbers of wintering birds utilizing estuaries invaded by *Spartina*. The plant studies included in this review were all located in England or Ireland.

The studies linking effects of marine and estuarine invertebrate introductions on shorebirds were generally fewer and more speculative than those examining plant effects (Table 1). Of three studies on invertebrate effects, two demonstrated an increase in reproductive output for one shorebird species affected by one introduced species in one location. Another study examining the effect of an invasive crab on shorebirds in a single embayment in North America did not detect an effect on abundance and distribution of shorebirds there. Are the lack of demonstrable effects, however, due to no effect, or due to a lack of study? Is there enough evidence to conclude that marine invertebrates do not affect shorebirds during their winter, migratory or breeding seasons?

Shorebirds are an integral component of marine food webs and ecosystems, and sustaining their populations depends upon how we manage disturbance and impacts in marine and estuarine ecosystems. Shorebird populations are sensitive to the range and conditions of impacts and disturbances that occur within marine ecosystems (see Red Knot, Black Oystercatcher, and Dunlin examples herein), and have been proposed as good indicators of environmental change (Piersma and Baker 2000). The disturbances that are now common in coastal environments include pollution, over-extraction of vertebrate and invertebrate resources by humans, development and alteration of physical habitat, and introduction of species. The interaction of these multiple disturbances for species living in coastal ecosystems is not understood. However, it has been suggested that rapidly occurring and compounding disturbances in ecosystems may change community assembly in surprising ways (Paine *et al.* 1996), and may alter the stability and resilience of an ecosystem (Scheffer *et al.* 2001; Scheffer and Carpenter 2003). The net result of compounding disturbances could include large fluctuations in populations, changes in community composition, and loss of species (Paine *et al.* 1996). It is not currently known whether the introduction of species in marine ecosystems could further compound existing disturbances and cause a sudden or dramatic shift in an ecosystem's stability or resilience, but this has been suggested (Paine *et al.* 1996). As for the effect of introduced marine species on shorebirds, the jury seems to be out still. The literature indicates that there is not yet enough information to conclude that introduced marine species are, or are not, negatively affecting shorebirds and their populations.

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Table 1. List of peer-reviewed papers discussing impacts of introduced marine invertebrates or plants on shorebirds

REFERENCE	SHOREBIRD SPECIES	INTRODUCED MARINE SPECIES	LOCATION	EFFECT ON SHOREBIRD SPECIES
<u>*Invertebrates*</u>				
Carlton 1979	General	General	San Francisco Bay, CA	<u>Speculation</u> on changes in foraging rate, behavior, and abundance and distribution
Griffiths *et al.* 1992	Black Oystercatcher	*Mytilus galloprovincialis* (mussel)	W South Africa[OB]	Increased reproductive success
Hockey and Schurink 1992	Black Oystercatcher	*Mytilus galloprovincialis*	W South Africa[OB]	Increased reproductive success
Grosholz and Ruiz 1995	General	*Carcinus maenas* (crab)	Bodega Harbor, CA	<u>Speculation</u> on indirect trophic effects on shorebirds
Grosholz *et al.* 2000	Multiple (e.g. Dunlin, Western Sandpiper, Willet, Marbled Godwit)	*Carcinus maenas*	Bodega Harbor, CA[NEX]	No effect measured on abundance and distribution
Torchin *et al.* (in press)	General	unspecified trematode parasites (host = *Batillaria cumingi*) (snail)	Bolinas Lagoon, CA	<u>Speculation</u> on changes in shorebird foraging and abundance

Table 1 continued.

REFERENCES	SHOREBIRD SPECIES	INTRODUCED MARINE	LOCATION	EFFECT ON SHOREBIRD SPECIES
Plants				
Prater 1981	General	*Spartina anglica*	England^{OB}	Loss of shorebird prey in areas covered by decomposing *Spartina* detritus
Nairn 1986*	General	*Spartina anglica*	Ireland^{OB}	Loss of open mudflat for feeding
Tubbs and Tubbs 1980 (cited in Nairn 1986)	Redshank and Curlew (*Tringa tetanus* and *Numenius arquata*)	*Zostera* spp. *Ulva lactuca* *Enteromorpha* spp	England^{OB}	Decreases in numbers using estuaries
Goss-Custard and Moser 1988	Dunlin	*Spartina anglica*	England^{OB}	Loss of winter forage habitat and decreases in winter populations of Dunlin in England
Daehler and Strong 1996	General	*Spartina alterniflora*	San Francisco, CA	<u>Comment</u> regarding reduction of open mudflat feeding habitats of shorebirds

* The Nairn 1986 paper is a review of the effects of *Spartina anglica* on waders, and thus I did not include all papers cited in this review.

** Papers located by searching in Web of Science, Wildlife and Ecology Studies Worldwide, and Journal Storage. Searches not restricted to any country or region of the world.

OB refers to an observational study, NEX refers to a natural experiment.

CHAPTER 2

EXPERIMENTAL ASSESSMENT OF THE INDIRECT EFFECTS OF A NON-NATIVE CRAB PREDATOR (*Carcinus maenas*) ON WINTERING SHOREBIRDS

ABSTRACT

We used a manipulative field experiment to examine shorebird responses to the effects of green crab predation on invertebrate prey. We set up a randomized complete block design with green crab density as the treatment. The experiment was conducted in two parts, a crab foraging experiment, followed by the Dunlin foraging experiment. We expected that temporal, spatial, and environmental variation in prey density could affect our ability to detect changes in this response variable, and so we incorporated specific experimental design features (Before After Control Impact (BACI), blocking, and paired sampling) to minimize variation from these sources.

We found that green crabs significantly reduced the prey density of a crustacean species (*Leptochelia dubia*), but not of other prey taxa that it previously affected (esp. the clam *Nutricola* spp.). This result was contrary to other studies, and may be related to past effects of green crab predation and to unusually low prey density during the season in which the experiment was conducted. We also found that Dunlin were able to reduce the density of a polychaete in areas where no green crabs foraged compared to areas where low and high densities of green crabs foraged. Additionally, Dunlin reduced the density of *Nutricola* spp. in cages with high densities of green crabs compared to those with low and zero crab densities. This result was also contrary to results of previous studies, and it may be related to indirect effects of holding green crabs in a cage at high density or to some other aspect of their foraging behavior. If this treatment effect holds beyond the experimental conditions, this would provide another mechanism by which the green crab negatively impacts *Nutricola* spp.

We detected no effects of green crabs on Dunlin foraging behaviors or weight. Both experimental Dunlin and green crab diets were different from those of free-ranging individuals in that fewer Dunlin consumed clams in the experiment than in non-captive conditions, and green crabs foraged on gastropods, not clams, during the experiment. Experimental results combine to suggest that prey conditions (density) affected green crab predation, and this in turn, affected Dunlin prey consumption and dietary composition.

Further implications of this research will need to be evaluated in an energetics context, and with attention to shorebird body condition and winter survival rates as these may affect population parameters. As marine invertebrate communities continue to change with the introduction of marine organisms, it will become important to the management and conservation of shorebirds to consider the ecological role of introduced marine plants and animals, particularly in locations where large numbers of shorebirds congregate during migration or winter.

Keywords: shorebirds, (*Calidris alpina*), green crab (*Carcinus maenas*), foraging, introduced species, invertebrate prey, multi-trophic effects.

INTRODUCTION

Non-native species are now ranked in the top five threats to biodiversity (Wilcove *et al.* 2000). Through predation, competition, and indirect trophic effects non-native species affect resident species, communities, and ecosystems, causing decline in abundance, changes in the population dynamics of native species, and alteration in ecological functions (Vitousek *et al.* 1996, Tillman 1997). Estuaries have been particularly vulnerable and are the most heavily invaded of all coastal habitats (Ruiz *et al.* 1997), and the number of introduced invertebrates and plants in estuaries is increasing at an exponential rate (Cohen and Carlton 1998). In the US alone, at least 400 introduced marine species are now established in Pacific, Atlantic, and Gulf coast estuaries (Ruiz *et al.* 1997).

Coastal habitats are also important foraging areas to more than one half of the world's shorebird species (Warnock *et al.* 2002). Current analyses of shorebird population trends indicate that approximately 23% of the world's shorebird species are experiencing population declines (Piersma and Baker 2000). During shorebird migration and regional movements in the nonbreeding season, many shorebird species rely extensively on coastal ecosystems for winter habitat and food resources. The quality of winter food resources has important consequences for shorebird survival (Goss-Custard 1981, Gill *et al.* 2001, Goss-Custard *et al.* 2004), migration, and breeding success (Baker *et al.* 2004).

To evaluate the food requirements of shorebirds during the nonbreeding season some researchers have tried to estimate the degree to which they deplete prey resources (Schneider and Harrington 1981, Evans and Dugan 1984, Sewell 1996). Based on a study conducted in Africa, shorebirds may consume nearly half of the annual standing crop of invertebrates in a single wintering location (Baird *et al.* 1985). In California, consumption was estimated to be as high as 80% (Quammen 1984). Introduced marine species can impact critical invertebrate prey populations and communities used by shorebirds by altering the size and age distribution, abundance, and species diversity of native invertebrate prey (Vermeij 1982, Posey 1988, Grosholz and Ruiz 1995, Grosholz *et al.* 2000). Introduced marine species may even cause local extirpations of native invertebrates (McKinney 1998) as well as changes in their population (Byers 2000) and community (Ross *et al.* 2004) dynamics. Trophic effects caused within a food web by introduced species may extend beyond invertebrates to vertebrates (Richmond and Lovvern 2004), although trophic linkages to vertebrates have rarely been investigated.

Invertebrate prey resources affect the distribution and abundance of shorebirds on local and regional scales during nonbreeding seasons (Evans and Dugan 1984, Goss-Custard 1984, Piersma 1987). This fact suggests that profound, widespread changes to shorebird habitat or food resources during the winter months have the potential to affect shorebird populations, possibly leading to population declines (Goss-Custard and Moser 1988, Baker *et al.* 2004). For example, in Delaware Bay, MD a historically superabundant prey resource (horseshoe crab eggs, *Limulus polyphemus*) that many species of shorebird rely upon annually is being overexploited by humans. Red Knots (*C. canutus rufa*) are showing significant population declines presumably in response to diminished food resources at this critical migratory stop (Baker *et al.* 2004). In another example linked more specifically to introduced marine species, San Francisco Bay is the most heavily invaded estuary in the world and in some areas has entire "introduced communities" of invertebrates. Currently more than 200 introduced species (plant and invertebrate) inhabit San Francisco Bay (Cohen and Carlton 1995). Annually, this estuary is a significant migratory and wintering location for over one million shorebirds (Page and Gill 1994). Unfortunately, little is known about how changes in the biota of San Francisco Bay have affected shorebirds. At this time, there is no evidence that the abundance and distribution of shorebirds in this estuary have significantly declined. However, there have been no experimental studies in San Francisco Bay to evaluate the impact of non-native invertebrates on shorebirds, although observational studies on the impacts of an introduced plant, *Spartina alterniflora*, on shorebirds are underway (E.D. Grosholz, pers. comm.). Given changes to invertebrate prey populations such as has occurred in San Francisco Bay, it is plausible that populations of vertebrates at higher trophic levels (e.g., shorebirds) have experienced some impacts. To date, only one study in North America has evaluated the effect of an introduced marine invertebrate on local abundance and distribution of shorebirds (Grosholz *et al.* 2000). Most foraging or prey studies involving shorebirds have examined the effects of shorebirds on prey, rather than prey on shorebirds (but see Weber and Haig 1997). In addition, these studies have not identified the native vs. non-native status of prey items in shorebird diets, nor do they consider the question of indirect effects on shorebirds arising from introduced marine species.

In 1989, the European green crab (*Carcinus maenas*) (hereafter green crab) was accidentally introduced to San Francisco Bay (Cohen and Carlton 1995). Within 10 years it spread rapidly along the Pacific Coast with established populations now documented in every major embayment between Elkhorn Slough, CA and Gray's Harbor, WA. The green crab arrived in Bodega Harbor, CA in 1993, and within 8 months its abundance was estimated at 1.7-6 crabs /trap in the mid-intertidal (~ +1.2m above Mean Lower Low Water (MLLW); Grosholz and Ruiz 1995). In the period since its introduction, green crabs have caused significant declines in some invertebrate prey populations (Grosholz *et al.* 2000). In particular the crab has had a strong negative effect on small venerid clams, *Nutricola* spp., and on a small native grapsid crab, *Hemigrapsus oregonensis.* Through indirect effects of the green crab's predation there has been an increase in some species of polychaetes (spionids and syllids), crustaceans (amphipods and the tanaid *Leptochelia dubia*), and another introduced species, the small clam *Gemma gemma* (Grosholz 2005).

The green crab forages in the same intertidal habitats and on many of the same invertebrate taxa consumed by over-wintering Long-billed Curlew (*Numenius americanus*), Greater Yellowlegs (*Tringa* melanoleuca), Marbled Godwits (*Limosa fedoa*), Dunlin (*Calidris alpina*), Least and Western Sandpipers (*C. minutilla*, *C. mauri*), Sanderling (*C. alba*), and other shorebirds. Despite use of shared prey resources (in particular, *Nutricola* spp. and *H. oregonensis*) between the green crab and shorebirds, shorebird abundance and distribution in Bodega Harbor, CA, does not appear to have changed with the crab's invasion (Grosholz *et al.* 2000). An apparent lack of response in the local abundance and distribution of shorebirds following the green crab invasion is in contrast to dramatic changes seen in shorebird populations following a natural recruitment event by the Dungeness crab (*Cancer magister*) in Bodega Harbor. During this massive predator 'bloom' in spring 1985, nearly all *Nutricola* and *L. dubia* within the harbor were consumed, presumably by the Dungeness crab recruits (Ruiz 1987). As these food resources plummeted to a near $0/m^2$ density, there was a significant decline in the abundance of winter shorebird populations in Bodega Harbor. Many shorebird individuals that remained in the harbor had poor body condition in comparison to those in other nearby harbors. In the spring following the Dungeness recruitment event, prey returned to normal densities. However, in the second winter after the recruitment the effect of prey depletion persisted on shorebirds. Abundance of shorebirds returning to the harbor remained low in the winter of 1986-87, body condition of over-wintering Dunlin and Western Sandpipers continued to be poor in comparison to others in the region, and the adult:juvenile ratio of these species was low in comparison to previous years (Ruiz 1987). A low adult:juvenile ratio in 1986-87 indicates increased mortality for adults that wintered in Bodega Harbor in 1985-86.

Occasionally, dramatic changes in populations can be traced to a single cause (Savidge 1987, brown tree snake extirpation of avian species). In other cases, causes of dramatic population declines remain elusive and even equivocal for years (e.g., the global decline of amphibian populations). Causes for population declines that occur more slowly than the aforementioned examples (e.g., declines of neotropical and grassland birds and shorebirds) can be exceedingly difficult to discern (Bart 2005). Such declines may result from the long-term cumulative effects of a number of factors (e.g., habitat loss, changes in populations of both predators and competitors, pathogens). We speculate that changes in the invertebrate prey base of over-wintering shorebirds caused by introduced species could play a role in the decline of shorebird populations. Possible mechanisms include altered energetics of individuals resulting in declines of their winter and migratory survival rates as well as subsequent declines in breeding success. To detect these kinds of effects, metrics other than abundance and distribution will need to be evaluated.

In this paper, we describe the approach we used to determine if green crabs were affecting shorebird consumption of prey, foraging behavior, changes in body mass, or diet. Given that green crabs in Bodega Harbor consumed similar prey species to shorebirds, we hypothesized that green crabs have the potential to indirectly affect wintering shorebird populations through competition for shared food resources. We proposed that one mechanism for this effect is by a decrease in the quality of shorebird foraging habitat due to prey depletion and diffuse interspecific competition with the green crab. To evaluate this research hypothesis we: **(i)** quantified experimentally the impacts of green crab and shorebird predation on shared food resources, and **(ii)** quantified shorebird foraging behavior, mass, and diet in areas with and without green crabs and in areas of differing green crab density, and **iii**) compared presence and absence of prey taxa in stomach contents of caged and free-roaming green crabs and shorebirds. We predicted that green crab and shorebird predation would most affect the abundance of bivalve prey. We also predicted that increasing the density of green crabs would affect the rate of shorebird foraging behaviors and lower shorebird mass. Finally, we predicted that in areas treated with a high density of green crabs, shorebirds and green crabs would forage on different invertebrate prey from each other, suggesting a shift in diet due to diffuse competitive interactions.

The approach we describe here represents the first field experiment in North America to evaluate the effects of an introduced marine predator on shorebirds through indirect trophic interactions. Controlled experiments using enclosures (2m x 2m x 1.5m cages) set up in natural habitats were central to this effort because they offered a means to evaluate causal relationships between shorebird response to varying levels of green crab predation. We incorporated design and implementation recommendations from Sewell (1996) and Virnstein (1978) that were expected to improve a soft-sediment cage experiment. For example, Sewell (1996) recommended that a Before-After-Control-Impact (BACI) approach be used so as to minimize variation in invertebrate density due to temporal heterogeneity. Virnstein (1978) cautioned against conducting these experiments in areas of high flow due to sediment accretion within and around cages, and thus changes in invertebrate density that could confound predator effects. We experienced both success and unexpected outcomes from this experiment. In this paper we report on the most interesting insights arising from our experiments and offer suggestions for changes in design that would improve future experiments.

METHODS

Study Site and Natural History of Bodega Harbor

Bodega Harbor is a 2km^2 embayment approximately 70km north of San Francisco, CA (Figure 1). It receives little freshwater input and has a single opening to the Pacific Ocean through a jetty. The volume of water in the harbor flushes nearly completely during the lowest tidal periods except for water held within a deep, central shipping channel and a few smaller channels that cut through mudflats. The harbor, therefore, is a marine-dominated system whose waters are similar in temperature and salinity to the ocean throughout the year. In the fall of the year, ocean surface water temperature and salinity are approximately 10-15C and ~33.0 – 33.5ppt (Bodega Marine Lab (BML) archived data).

There are approximately 320ha of mudflat within Bodega Harbor, and these support approximately 10,000 thousand foraging shorebirds during the fall, winter, and spring each year, and a diverse benthic invertebrate community. The Doran flat (180ha) is the largest of all mudflats within the harbor, and its surface sediments experience relatively little disturbance as the tides exchange. This flat is easily accessible to walking at low tide. Close to shore sediments have a sandy texture and are composed of 92-94% sand. Near the shipping channel, sediments change to a loamy texture and are composed of 82-90% sand (data from this study). Invertebrate composition changes along this gradient of sediment composition and tidal height. Close to shore the invertebrate composition is dominated by molluscs and crustaceans and farther from shore, close to the shipping channel, the invertebrate community becomes a near monoculture of Spionid polycheates (annelids). The Doran flat is divided twice by shallow-water channels, thus dissuading the public from visiting the outer reaches of it. Because so many shorebirds forage on this flat and because it receives low public visitation, we chose to locate our field experiment on the Doran flat.

Study Overview

The primary goal of this study was to determine if the introduced green crab alters foraging (either consumption or behavior) by Dunlin. As a part of this effort, we also examined green crab effects on the invertebrate prey base. Specifically, we first tested whether density of benthic invertebrates changed as a function of green crab density (hereafter "green crab experiment"). Based on previous work (Grosholz *et al.* 2000), we expected green crabs to significantly decrease prey resources, particularly *Nutricola* spp., within the cages in which they were held. We anticipated that we could use crab-induced prey densities as treatments in a Dunlin foraging experiment (hereafter "Dunlin foraging experiment"). Assuming these prey conditions had been established, we tested whether shorebird prey consumption, foraging behavior, or mass varied among the areas treated with differing crab densities.

The Experiments and Their Design

We conducted these experiments using a complete randomized block design with paired sub-sampling, four experimental units in each of four blocks (block as a random factor), and a single fixed-factor treatment (crab density) with four levels. We collected sub-samples within each experimental unit to obtain a less variable estimate of prey density for each unit (pairing will be described below). Within a block each experimental unit was $4m^2$ and 15m apart. In each block, 3 experimental units were covered with cages (see description below), and one was left uncaged. We marked the uncaged unit in each block with 2 pieces of PVC (extending 20cm above the mud surface) placed on diagonal corners. Blocks were separated by 50m. In this experiment we utilized blocking in order to control for the effect of a spatially heterogeneous invertebrate distribution and a gradient of sediment characteristics in the experimental area (Table 1).

In the crab foraging experiment there were four treatment levels of crab density. These levels included ambient crab density (uncaged units), 0, 1.2, and 6 green crabs/m^2 (caged units). We chose these density levels for a variety of reasons. First, comparison of ambient and zero density levels in this experiment allowed us to examine the data for a cage effect. The zero density treatment served as a control for crab effects. 'Low' and 'high' crab densities fall within the range of normally occurring green crab densities measured in Bodega Harbor (Grosholz, *unpub. data*) and provided in the literature (Coleman 2000, Floyd and Williams 2004). Coleman (2000), using a mark-recapture study, reported an ambient density of green crabs of 1.2/m^2 in the Gulf of St. Lawrence, Canada. In other green crab cage experiments, researchers have set "moderate" densities of green crabs at $4/m^2$, and "high" densities of green crabs at $6/m^2$ (Floyd and Williams 2004) and $7/m^2$ (Davis *et al.* 1998). We chose to set the 'high' crab density at 5 times ambient level because we expected this level to produce prey depletion, and we chose to incorporate a high density level to evaluate the effects of increasing crab densities over time.

For the Dunlin foraging experiment, the logistics of acquiring and handling birds allowed a test of bird responses in only two levels of crab density per block (0 and high density). The Dunlin experiment was run in two parts, with birds placed in zero and high density cages ($n = 4$ cages) of two blocks on one day, and then placed in the zero and high density cages ($n = 4$ cages) of the remaining two blocks on the next day.

For both the green crab and Dunlin foraging experiments, the response variable was the average difference in density of 16 invertebrate taxa between the beginning and end of an experiment (e.g., before and after predation by crabs or birds). Differences were calculated from counts of invertebrates within sediment-cores taken at three times: (1) before putting crabs on the plots (time 1), (2) after removing crabs from the plots and before putting birds on the plots (time 2), and (3) after removing birds from the plots (time 3). For the Dunlin experiment there were two additional response variables: foraging behavior and change in body mass. We also examined stomach contents of selected experimental animals (both birds and crabs). Because the goal of this experiment was to examine responses of Dunlin to prey conditions created by the introduced green crabs, we chose to run the experiment in the two parts described.

Further, back-to-back experiments with crabs and then birds allowed an evaluation of each predator's effect on invertebrate prey.

We measured three covariates that varied across the experimental area and could potentially confound a treatment effect: % cover of standing water at low tide, % cover of algae, and % sand, silt, and clay in sediments. Because water flow across the Doran mudflat in Bodega Harbor is extremely slow-moving, we did not expect these covariates to change during the month-long period of the experiment. We also did not want to disturb the substrate within an experimental unit by taking measurements because we were concerned this could affect prey availability and prey consumption by green crabs or Dunlin. We therefore recorded visual estimates of % water and algal cover at the beginning of the experiment, and collected sediment 'plugs' and determined % sand, silt, and clay content at the end of the experiment. We used field observations of the sediments (e.g., how firm or soft an area was) as well as the estimates of % cover by water and algae to systematically assign placement of the blocks beginning from a random location on the Doran mudflat.

We conducted the foraging experiments during October and November 2001. This was an optimal time for the experiment for two reasons. First, fall migration of Dunlin occurs from late September – December, with peak numbers occurring in Bodega Harbor during October – mid-January (BML, archived data). Second, by late November, green crabs begin moving into the subtidal to spend the winter months (LeRoux *et al.* 1990). A disadvantage in conducting these experiments during the late fall, however, was that the lowest low tides, which provide the greatest exposure of mudflats (both time and extent), never occur during the daylight hours. We had to work during the higher of the semi-diurnal low tides so that we could easily observe the birds' behaviors during the daylight hours. These tides limited exposure of the mudflat where the experiment was conducted to ~2.5 hours (tidal height +1.2-1.4m MLLW). We chose this tidal height because this is where the greatest abundance of green crabs in Bodega Harbor occurred (Grosholz and Ruiz 1995).

Cage Design and Construction

We constructed 12 cages to keep experimental animals within each experimental unit. Each cage consisted of 4 styrene strips (17.75cm x 2m) buried in the substrate, a PVC frame, and, for the top and sides, either hardware cloth (crab experiment) or mosquito netting (Dunlin experiment). The ends of the styrene strips were attached to one another with cable ties so that they formed a square foundation to which we later attached the wire bottom of a cage. Holes (6.3mm) drilled across the surface of each strip allowed water to percolate between the inside and outside of the cages so infauna would not suffocate. We hammered the plastic styrene foundation into the mudflat until it was flush with the sediment surface. Green crabs could not dig their way out of a caged area. The 2m x 2m x 1.5 m frame was made of 1.3cm diameter schedule 40 PVC. The frame was secured to the mudflat by sliding the frame's vertical PVC tubes over 8 pieces of rebar (0.9cm x 1.7m), with 1.25m of rebar extending above the mudflat and 0.25m of the PVC extending into the mudflat. As the final stage in cage construction, we attached pre-measured 1.3-cm hardware cloth (for the crab experiment) or mosquito netting (for the Dunlin experiment) to the frame and foundation of each cage. The cages appeared to work exactly as designed.

For soft-sediment studies, our enclosure cages are relatively large ($4m^2$; Virnstein 1978). However, cages had to be at least this size because it was necessary to enclose enough space so that shorebirds would forage. In a previous field season used for pilot studies, we found that Dunlin held inside experimental units of only $1m^2$ spent all of their time trying to escape the small enclosures.

Implementation of the Experiments and Data Collection

We took the first of three sets of sediment cores (representing initial or background invertebrate density) before crabs were introduced to the plots, taking care to minimize sediment disturbance within each plot. In each experimental unit we randomly selected three coring locations following the rule that individual cores could not be collected within 10cm of the inside edge of a cage nor within $0.5m^2$ of each other. This size of core ($10cm^2$ in diameter and 5cm deep) was used in previous soft-sediment studies (Myers *et al.*1980, Ruiz 1987, Grosholz *et al.* 2000), and, importantly, had a depth that encompassed the vertical foraging range of both green crabs and Dunlin. After coring, we placed plastic markers in each cored location, flush with the substrate, so that subsequent cores could be paired spatially with the initial cores. Through the use of paired sampling, we tried to minimize variation due to patchy invertebrate distributions. On the day after taking the initial cores, we finished installing the cages to protect these experimental units from mudflat predators.

We placed individual core samples in bags upon collection and carried them to the lab for processing. Each core sample was sieved through a 0.5mm mesh sieve, and the core remains were fixed in 10% buffered formalin. After two weeks the samples were transferred to 70% ethanol for storage. All invertebrate taxa within cores were identified to the lowest taxonomic level possible, and enumerated in the lab. Because green crabs select *Nutricola* larger than 2mm (adults) over those that are smaller than 2mm (juveniles) (Grosholz and Ruiz 1995), we enumerated these size classes of *Nutricola* clams.

After the initial set of invertebrate cores was taken, we put 6 and 24 green crabs into each low and high density cage, respectively. We used only adult male green crabs (70-80mm carapace width) for this experiment. Females are commonly gravid during the fall and may not forage regularly (LeRoux *et al.* 1990). We trapped adult male green crabs in baited traps in Bodega Harbor during the month preceding the experiment. These were maintained in an outdoor tank at BML and fed bits of squid 3 times/week until a week before the experiment began. Crabs remained in the low and high density cages for 13 days, an amount of time used in a previous green crab foraging experiment in Bodega Harbor (Grosholz and Ruiz 1995).

At the end of the crab foraging experiment we removed all crabs from the cages. Since the crabs did not bury themselves deeply in the sediment, we were able to retrieve them with little disturbance to the sediment inside each cage. Out of the crabs retrieved, we randomly chose 2-5 from each cage and immediately injected them with 10% buffered formalin to stop their digestion. In the lab we removed stomachs from the green crabs and stored these in 70% ethanol for diet analysis. We later examined these stomach contents under a 6.7-40x microscope, and identified undigested hard parts as polychaete, crustacean, or mollusc. We scored each grouping for presence or absence.

At the same time we removed green crabs from the low and high density cages, we collected the second set of 48 cores (time 2, after crab foraging) from all experimental units. We took the second set of cores within 2.5 to 7.5cm of the original cored locations, and thus, paired our sub-samples. The difference in invertebrate counts between a core pair collected at time 2 and time 1 indicated the amount of change in a given invertebrate taxa during the crab foraging experiment. The three sub-sample pairs of counts for each cage were ultimately averaged to give an estimate of the average change in invertebrates by taxa for each experimental unit.

Due to inclement weather and logistics of bird handling, we were forced to allow 3.5 days to pass after removal of crabs and collection of the second set of cores before we began the Dunlin foraging experiment. We captured 68 Dunlin in mist nets during this period and maintained them in a covered, outdoor aviary at BML, feeding them meal worms *ad libitum* and providing ample drinking water. Once the weather improved, and the tide was low, we introduced 8 birds to each zero and high density cage in two randomly selected blocks (32 birds total). On the following day, we repeated this with 32 additional birds and the remaining 2 blocks.

As the low tide approached on each of these days we removed wire cage structures from the low and high density cages and replaced them with bird-safe covers (a soft, mosquito net camping tent (Wolf 2001) positioned over top of the PVC frame). The netting was held above the mudflat in its center with a PVC pole, and it was secured around the edge of each cage so that no birds could escape. We also placed 8-10 Dunlin decoys within each cage during this part of the experiment to encourage foraging (J. Kelly, pers. comm.). At no point before bird foraging did we walk inside any of the experimental units.

Once we positioned the netting over the PVC frames, two teams of two people weighed individually-banded Dunlin with Pesola scales to the nearest 0.5g, and then released them into the appropriate cages. After Dunlin were released, 4 observers moved 50m away and each began recording foraging observations on birds in separate cages. After a 2hr observation period, which was the extent of time allowed by the tides, observers worked in pairs to catch and remove birds from cages before the rising tide reached them. We placed each bird in an individual cotton bag to limit its stress during handling, and we carried them in 4 boxes to BML where we measured their final weights. We returned birds to the mudflats for release on the following morning. Unfortunately, we could not conduct the Dunlin foraging experiment for longer than 2hr (tidal limitations) or conduct more runs of the experiment. It would have been unlikely for us to have caught another large group of Dunlin, thus allowing a second run of the experiment under similar conditions. It was also not possible to continue to hold these birds and then try multiple predation trials with them because we were uncertain that we could maintain their weight in captivity.

We observed foraging behaviors of an individual bird (focal bird) through spotting scopes set at 25X. A bird's foraging behavior was recorded every 3sec during repeated 2min observation bouts for the 2hr period. Each observer set a timer for 2min so that they would be aware of the end of the observation interval without being visually interrupted. During each 2min interval, an observer counted out 3sec intervals, and scored the behavior performed by the focal bird in a field notebook. Observers noted whether birds were 'stitching,' 'probing,' or 'not feeding' during the 2min observation period, and we did not stop watching a bird during these intervals. We used symbols for each behavior to make the recording as easy as possible. We defined 'feeding' as the bird's bill touching or being inserted into the mud, and 'not feeding' as the bill not touching the mud. Feeding was further resolved as either 'probing' (slow, single insertions of the bill in the mud), or 'stitching' (rapid insertions of the bill in the mud either in a single location or across a wider location as the bird walked). Non-feeding behaviors included standing, preening, and roosting.

Observers chose focal birds for each 2min observation bout as randomly as possible because birds were not individually identifiable. Selection of a focal bird occurred with the constraint that observations could not be made on the same individual in back-to-back 2min bouts. Individual birds were certainly observed multiple times within the 2hr observation period for any given cage.

At the end of the foraging behavior experiment and after weighing the experimental birds, we pumped the stomachs of 16 randomly selected individuals, 2 from each zero and high density cage. Stomach pumping is an alternative technique for acquiring gut samples from wild birds without having to sacrifice them. Ramer (1985) estimated that it produced results that were 85% similar to those obtained from examining gut contents of sacrificed birds. Methods for this technique are described in Ramer (1985) and Chapter 3. We analyzed bird stomach contents in the same manner as the crab stomach contents, and again we recorded presence and absence of polychaetes, crustaceans, and molluscs. For comparison of diet between Dunlin and green crabs, we calculated the proportion of stomachs (either Dunlin or green crab) that contained a particular taxon (polychaete, crustacean, mollusc) or other items (e.g., algae, beetles).

While half of the field crew was taking care of the Dunlin, and before the tide rose, the other half of the crew collected the final set of sediment cores (*n* = 48, time 3). These cores were paired with earlier cores as described above, and samples were collected and processed in the same manner.

After completing the experiments, we collected sediment plugs from each experimental unit to determine the % sand, silt, and clay composition. To estimate % cover of standing water and algae, we randomly selected 5 of 16 possible $0.5m^2$ areas within an experimental unit, and placed a $0.5m^2$ quadrat on top of the substrate in each of those locations. One person visually estimated the values. A second person randomly acquired three sediment plugs (taken in 30cc disposable syringes) within each experimental unit. The sediment samples were analyzed by the Colorado State University Soils Lab using methods described by Sheldrick and Want (1993).

Data Analysis

Original counts per core of each invertebrate taxon were log transformed (ln(x+1)) to better meet the assumptions of normality and equality of variances assumed by ANOVA. The response variable estimated for each cage from the benthic invertebrate samples was the change in density of invertebrate taxon between time 1 and time 2 (for the crab experiment) and time 2 and time 3 (for the Dunlin experiment). Differences between cores in a pair (*n* = 3 per cage), either in the crab or the Dunlin foraging experiment, were averaged to arrive at a single estimate of change in density for each invertebrate taxon for each experimental unit. We averaged the paired core differences instead of treating them as a nested factor because variability among the paired core differences within an experimental unit was no different from the variability among paired cores for a given treatment across blocks. Similarly, changes in bird weights were averaged over all 8 birds in a cage. For foraging behavior, the total number of observations of a given behavior was divided by the total observation time to yield an average rate per cage. The rate was used in subsequent analyses comparing treatment levels.

Average differences in invertebrate density, foraging behavior, and weight were all analyzed by ANOVA with the General Linear Module procedure (PROC GLM) in SAS 9.2 (SAS Institute, Cary, NC). Covariates were included in the models for invertebrate density when the parameter estimates for both the treatment and the covariate were significant.

RESULTS

Prey Taxa and Background Prey Density

We found numerous invertebrate taxa in sample cores from the Doran mudflat of Bodega Harbor (Table 2). Within these cores, polychaetes (marine annelids) were most abundant, followed by crustaceans and then molluscs (particularly bivalves) (Figure 2a). Of the polychaetes, members of the family Spionidae and the genus *Exogone* (Syllidae) were dominant; for crustaceans, a tanaid, *Leptochelia dubia*, was the most abundant species followed by members of the gammaridean amphipods and the cumacean *Cumella vulgaris*; for molluscs, *Nutricola* spp. and *Protothaca staminae* were the most common bivalves. The introduced bivalve *Gemma gemma* was absent from our samples, as was the polychaete family Maldanidae.

Out of the total fauna collected at the beginning of the experiment, *Nutricola* spp., *L. dubia,* and *Exogone* spp. comprised 43% of the fauna in sediment cores (Figure 2b).

This is in contrast to 80% dominance for these same taxa in control cores taken during a cage experiment conducted by Grosholz and Ruiz (1995) in Bodega Harbor just after the introduction of green crabs. Reductions of prey taxa during the period of 1994–2000 have been fully described by Grosholz *et al.* (2000), and our observations of the % composition of *Nutricola* spp. in sediment cores are in agreement with their post-invasion findings.

We found that the initial mean density (ln(x+1) transformation) of juvenile (<2mm) and adult (<2mm) *Nutricola* spp. was no different among treatments (ANOVA, $F_{\text{juv}} = 0.56$, df = 3,6, $P = 0.65$; $F_{\text{adult}} = 0.51$, df = 3,9, $P = 0.69$), and that there were fewer adult *Nutricola* spp. than juveniles in the initial cores (Figure 3a). Average density (original scale) of juvenile adult *Nutricola* spp. was 6.78 ($n = 48$, SE = 0.91) and that of juveniles was 51.6 ($n = 48$, SE = 11.2).

Green Crab Foraging Experiment

Across the 13 days of the green crab foraging experiment we observed an unexpected increase in prey density across all treatments for nearly all taxa tested. A prey increase (also referred to as prey enrichment) also occurred in some taxa and treatments during the Dunlin foraging experiment. Although we do not know the mechanism(s) causing these increases, this phenomenon appears similar to increases observed by Ruiz (1987). He witnessed an increase of nearly an order of magnitude in *L. dubia* and *Nutricola* spp. during the fall season. As a result of these across-the-board prey increases, several of the treatment effects we detected occurred when prey enrichment was significantly less in one treatment compared to the other. During the

Dunlin experiment, we saw some decreases in prey density, which we will refer to as prey reduction.

In the green crab experiment, crustaceans (all crustacean taxa lumped) and *L. dubia* (a crustacean taxon) were the only taxonomic groupings analyzed that experienced a significant treatment effect, and for whom the covariate % cover standing water explained a significant amount of variation (Table 3). The tanaid *L. dubia* comprised 60% of the initial crustacean density (at time 1), so this species may be responsible for the significant treatment effect that we witnessed for the lumped group. Prey densities increased for crustaceans across all treatment levels (Figure 4a). The increase in the zero crab density cages was significantly greater than in uncaged areas (suggesting a cage effect for crustaceans), but among caged treatments there were no significant differences (Fisher's LSD Test, $t = 2.31$, df = 8, LSD = 0.32, $P < 0.05$). For *L. dubia*, prey density increased significantly more in the zero and low crab density cages than in the uncaged areas and the high crab density cages (Fisher's LSD Test, $t = 2.31$, df = 8, LSD = 0.45, $P < 0.05$; Figure 4b). This again suggests a strong cage effect, but the significantly lower change in prey density in the high crab density cages indicates that crabs consumed the increasing prey in this treatment. Prey density increases were no different between zero and low density cages for *L. dubia* ($P > 0.05$), nor was there a difference between uncaged areas and high density cages.

We also found no significant difference in the change in juvenile or adult *Nutricola* spp. density during the green crab experiment (ANOVA, df = 3,9, $F_{\text{juvenile}} = 0.77$, $P = 0.54$; $F_{\text{adult}} = 0.71$, $P = 0.57$, Figure 3b). However, the data suggest a trend in the direction of change that we would expect given the size selection that green crabs have exhibited on *Nutricola* from other studies (Grosholz and Ruiz 1995).

For all other taxa analyzed there were no discernable differences ($P > 0.05$) in prey density changes across treatments, and the covariates % sand and % cover algae were unrelated to variation in prey density. As with *Leptochelia* and other crustaceans, we primarily witnessed prey enrichment across all treatments, including the cages where green crabs had been added (except for *Lumbrineris* sp. in the low crab density cage). We suspect that these unanticipated increases in prey densities may have decreased our ability to detect differences among crab treatments. Because we detected limited treatment effects on multiple prey taxa, green crab density did not result in the widely different prey densities we had anticipated for the subsequent Dunlin experiment. However, *L. dubia* density varied with green crab treatment. There were also green crab treatment effects on two additional prey taxa, *Lumbrineris* sp. and *Nutricola* spp. However, we were unable to detect these treatment effects statistically during the green crab foraging experiment. Changes in prey density for these taxa were not detected until the Dunlin foraging experiment (see results below).

Across taxa and treatment levels there was a high degree of variability in the prey density changes during the crab foraging experiment, which also contributed to the difficulty in detecting small treatment effects. We attempted to control the inherent variability in invertebrate samples by pairing cores spatially, anticipating that spatial correlation between paired cores would be high (Krebs 1999). We tested this design feature by ANOVA in which paired cores were treated as a nested factor within the block by treatment interaction term (difference in prey density remains the response variable).

The results of this ANOVA indicated that the variability among pairs within a given experimental unit for a given treatment was similar in magnitude to the variability among all pairs within that treatment across blocks. This unexpected result indicates that the spatial pairing of core samples did not reduce variation around estimates of change in prey density.

Dunlin Foraging Experiment

Our goal in this experiment was to assess whether prey conditions following green crab predation would affect various aspects of Dunlin foraging. We evaluated a number of metrics that could potentially express the effect of prey reduction by green crabs on shorebirds, including: changes in the prey taxa consumed by Dunlin, their foraging behavior, body weight, and diet composition. As noted above, we discovered *a posteriori* that the varying crab densities did not create the large differences among prey and across treatments as we expected. Nonetheless, we observed several treatment effects during the Dunlin foraging experiment.

Changes in prey density - First we analyzed changes in prey density caused by 8 Dunlin foraging in the zero and high density green crab cages, which we also compared to the uncaged treatment. We found significant treatment effects on changes in prey density of *Lumbrineris* sp., molluscs (all mollusc taxa combined), and *Nutricola* spp. (Table 3). The covariate % standing water was significant only for *Lumbrineris* sp.. Changes in prey density of *Lumbrineris* sp. in the high crab density cages differed significantly from the zero or uncaged treatments (Fisher's LSD Test, $t = 2.57$, df = 5, LSD = 0.49, $P < 0.05$; Figure 5a). *Lumbrineris* sp. density increased (i.e., there was prey enrichment) in the high crab treatment, while it decreased (prey reduction) in the uncaged areas and in the zero crab density cages. Changes in *Lumbrineris* sp. density did not differ between uncaged and zero crab density treatments. In contrast, the change in mollusc density did not differ between uncaged and high crab density treatments, yet the change in the zero crab density treatment differed from the other two (Fisher's LSD Test, $t = 2.45$, df = 6, LSD = 0.27, $P < 0.05$; Figure 5b). Density of molluscs increased in the zero crab density treatment, while it decreased slightly in the uncaged and high crab density treatments. The pattern of changes in prey density of the clams *Nutricola* spp. (*N. confusa* and *N. tantilla*) was similar to that of the molluscs, but there were some important differences. Changes in *Nutricola* spp. density in the high crab density treatment differed significantly from the uncaged or the zero crab density cages (Fisher's LSD Test, $t = 2.45$, df = 6, LSD = 0.41, $P < 0.05$; Figure 5c). Prey reduction occurred in the high crab density treatment, while there was slight prey enrichment in the uncaged treatment and even more prey enrichment in the zero crab density treatment. Although the apparent increase in *Nutricola* spp. in the zero crab density treatment was greater than the uncaged treatment, there was not a significant difference between the two. We also did not find a significant difference in change of density for either size class of *Nutricola* examined (ANOVA, $F_{\text{juveniles}} = 3.18$, df = 3,6, $P = 0.11$; $F_{\text{adult}} = 1.05$, df = 3,6, $P = 0.41$; Figure 6).

For all other taxa tested, Dunlin did not significantly affect prey density from the level following green crab foraging. As with the crab foraging experiment, variation in prey density changes was large, and small sample sizes have limited our ability to detect smaller treatment effects expressed through Dunlin predation ($n = 3$ sub-samples/cage; $n = 4$ cages/treatment level). However, other factors that may have contributed to our finding few treatment effects include: (i) effects of low prey density in comparison to previous years when green crab predation effects were larger (Grosholz 2005 and *unpub. data*), and (ii) unanticipated crab responses within the high density cages (see below, green crab stomach contents section).

Dunlin Foraging Behavior - We tested for differences in Dunlin foraging behavior between zero and high green crab density cages. No significant differences in the rate of Dunlin foraging behaviors (probing or stitiching) were found between zero and high crab density treatment levels (ANOVA; $F_{Probe} = 3.66$, df = 1, 3, $P > 0.15$; $F_{Stitch} = 3.19$, df = 1, 3, $P > 0.17$; Figure 7). In addition, the rate at which non-feeding behaviors (e.g., preening, standing, walking) occurred was no different among crab treatment levels ($F_{nonfeeding} = 0.16$, df = 1, 3, $P > 0.71$).

Dunlin Weight Changes - Dunlin weight change did not differ between the zero and high crab density treatment levels (ANOVA; $LSMEAN_{zero} = 1.31$, SE = 0.24, $LSMEAN_{high} = 1.92$, SE = 0.24; $F_{treatment} = 8.51$, df = 1,3; $P > 0.06$). In addition, none of the covariates (% sand, % cover standing water, or % cover algae) explained a significant amount of variation in the dunlin weight change data.

Green Crab Stomach Contents

Our analysis of green crab stomach contents yielded some interesting insights into prey density changes during the green crab foraging experiment. A key finding was that 65% of the green crabs in the high density cages had empty stomachs at the end of the experiment (Figure 8), while only 30% of the crabs in the low density treatment had empty stomachs. Together with the limited changes in prey density we measured during the green crab experiment, this finding suggests that although there were 5 times more crabs in the high density treatment, they did not eat 5 times as much prey as the crabs in the low density cages. This finding may partially explain why we did not find more significant differences in density among prey taxa between the low and high crab density cages.

Molluscs (particularly the gastropod *Lacuna marmorata*, but not bivalves) were found in the highest percentage and crustaceans (primarily amphipods) in the lowest percentage of green crab stomachs. Polychaetes and algae were found in nearly equal percentage of green crab stomachs in the low (20%) and in the high (40%) density treatments. In another analysis of green crab stomachs in Bodega Harbor (Grosholz *et al.* 2000), polychaetes and algae were found only 3% and 10% (respectively) of green crab stomachs. These findings on stomach contents combine to suggest a preferred food source (molluscs) of green crabs was less available in previous years.

Experimental Dunlin Stomach Contents

Polychaetes were found in > 85% of experimental Dunlin stomach samples in both high and zero crab density cages (Figure 9). A variety of polychaete taxa were present and identifiable in these samples including *Lumbrineris* sp., *Platynereis bicaniculata, Polydora socialis and P. nuchalis*, Spionidae (*Boccardia* sp, *Streblospio* sp.) and *Capitella capitata* (each taxa identified via the shape of their setae; L. Stenzel and G. Page *unpub. data*, and Hartman 1969). Molluscs (particularly bivalves) and crustaceans (primarily amphipods) were found in less than 30% of Dunlin stomachs. The percent of experimental Dunlin stomachs containing bivalve molluscs was much lower than expected based on previous studies of non-captive Dunlin at this location prior to the green crab invasion (Ruiz 1987). Prior to the arrival of green crabs, 100% of the non-captive Dunlin stomach samples (*n* = 10) examined in Bodega Harbor contained large numbers of mollusc bivalves, *Nutricola* spp. (Ruiz 1987; mean no. *Nutricola* spp./Dunlin stomach = 95.5, SD = 75.1).

DISCUSSION

Prey Dynamics and Green Crab Effects

The introduction of the green crab to Bodega Harbor in 1993 has had significant impacts on intertidal macroinvertebrates. Results from an enclosure experiment, conducted 8 months after the green crab arrived in Bodega Harbor, demonstrated that green crabs can significantly reduce prey density of *Nutricola tantilla*, *N. confusa*, *Cumella vulgaris*, *Corophium* sp., and *Leptochelia dubia* (Grosholz and Ruiz 1995). Further, invertebrate monitoring data collected at fixed transects in the harbor indicate that green crabs have been responsible for harbor-wide declines in some prey populations, especially *Nutricola* spp. and *Hemigrapsus oregonensis* (Grosholz *et al.* 2000, Grosholz 2005). An empirically-derived path model describing the food web of Bodega Harbor (Grosholz *et al.* 2000) documented significant direct effects of green crabs on *Nutricola* spp. (negative), and indirect effects on polychaetes (negative), *L. dubia* (negative) and amphipods (positive).

Because of the results of these previous studies, we expected that green crabs in the current foraging experiment would produce similar effects on prey seen by Grosholz and Ruiz (1995), and that the crabs would create prey conditions (for the subsequent Dunlin foraging experiment) that were related to green crab density. Our results corroborated only one portion of their cage experiment findings, a decline in *L. dubia* density due to green crab predation. In our experiment, *L. dubia* rather than *Nutricola* was the most abundant species. We did not find the expected declines in *Nutricola* spp., *Cumella vulgaris*, or *Corophium* spp. The reasons why we think we had these results are two-fold. First, prey conditions in Bodega Harbor have continued to change since the introduction of green crabs (Grosholz 2005). Second, prey density during the fall of 2001 reached a near 30-year record low, and the cause of this is unrelated to physical variables and remains unexplained (Grosholz 2005). It is plausible that unusually low prey density during this experiment (for whatever causes) may have limited or weakened the predation effect of green crabs.

An indication that invertebrate populations have continued to change since the introduction of the green crab and that these changes may affect green crab predation effects currently lies in comparisons of sediment samples between previous studies (Grosholz and Ruiz 1995, Grosholz *et al.* 2000) and the present one. In 1994, *Nutricola* spp., *L. dubia*, and *Exogone* spp. comprised 80% of the fauna collected in core samples (Grosholz and Ruiz 1995). In the current study these same invertebrate species now comprised 44% of the invertebrate fauna in cores. *Nutricola* spp., a previously dominant clam important in shorebird diets in Bodega Harbor and one of the species most heavily impacted by green crabs (Grosholz and Ruiz 1995), represented only 5% of the total fauna in cores collected at the initiation of our green crab experiment. The density of adult (size > 2 mm) *Nutricola* spp. recorded in the experimental area, ~7 / 0.01m^2, was even lower than the 2001 value, ~21 / 0.01m^2, reported by Grosholz (2005). Grosholz and Ruiz (1995) demonstrated that green crabs selectively forage on adult *Nutricola.* Although there were 7.5 times as many juvenile (< 2mm) as adult *Nutricola* in our initial sediment cores, it appears that green crabs experienced a low threshold density of adult

Nutricola, and that they either switched to alternative prey or stopped foraging. Except for the possibility of maintaining prey (especially *Nutricola* spp. and *Hemigrapsus oregonensis*) at an overall reduced density and in the current compositional state, green crabs may now exhibit an overall weakened predation effect in comparison to their post-invasion effect.

Results from a crab trapping study conducted during the weeks before our experiment (Estelle, *unpub. data*) indicate that green crabs were nearly absent from the mudflats during August and September in Bodega Harbor. During this time we found green crabs in the marshes and marsh channels. This habitat shift indicates that the crabs were using different foraging areas from previous years (Grosholz *et al.* 2000). We believe their abandonment of the mudflats was related to the greatly reduced prey populations in 2001.

Although we had not anticipated unusually low prey density conditions in the experimental area, this situation, combined with the various densities of green crabs, may have influenced treatment effects. It is possible that intraspecific interactions -- specifically, antagonistic interactions -- among the crabs may have inhibited their foraging in the high crab density cages. Evidence for this arises from the green crab stomachs that we dissected. Two-thirds of the crab stomachs that we examined from individuals in the high density cages were empty. This number is nearly twice as high as that previously observed for free-ranging crabs (Grosholz *et al.* 2000). The number of empty crab stomachs recorded in the low density cages (~30%) is similar to that observed of free-ranging crabs. These observations support the suggestion that the crabs in the high density cages were not foraging normally and thus treatment effects may have been reduced in the high density cages. Unfortunately, we did not record any behavioral observations of green crabs held at high density. It was common, however, for us to find dismembered legs and chelae on the sediment surface more often in the high than the low density cages (*pers. obs.*). Another indication of intraspecific interactions among crabs would be mortality records from the two density treatments. However, we did not record mortality data of crabs in the different treatments because this did not appear strikingly different in the field. Negative intraspecific interactions would explain why this and other experiments (Floyd and Williams 2004) did not detect density-dependent effects of green crabs on prey. Using a similar experimental design and the same crab density treatments, Floyd and Williams (2004) did not detect a difference in soft shell clam densities between high and low green crab treatments, but they did detect declines of these clams in cages with crabs compared to controls.

The temporal trend of increasing prey density from the beginning to the end of the crab foraging experiment may also have contributed to our inability to detect many changes in density of prey by adding to sample variability. It is not uncommon to see prey increases within experimental cages (review by Virnstein 1978), particularly when the experiment spans a significant part of the year (3 – 9 months) (Thrush *et al.* 1994a). We anticipated that natural prey dynamics could affect the outcome of the crab experiment, so we kept the experiment's duration to a minimal level (13 days for crabs). This duration was chosen because green crabs produced a significant treatment effect on prey in a previous cage experiment in Bodega Harbor in 12 days time (Grosholz and Ruiz 1995).

Despite our efforts to minimize the effects of natural fluctuations in prey populations on our response variable, we saw surprisingly large increases in prey density across nearly all taxa during the crab foraging experiment and across many taxa during the very short Dunlin foraging experiment. There are several reasons why this may have occurred. First, mudflat invertebrates are known to move for natural reasons or in response to human disturbance. For example, *Cumella vulgaris* is believed to undergo diurnal migrations into the water column (Virnstein 1978). Prey movements have been documented but the scale over which they occur and what prompts them are not well understood (Lenihan and Micheli 2001). Installation of cages and subsequent disturbance during sampling may have prompted individuals from adjacent areas to move into cages. Additional coreing in these locations before and after our disturbance would have aided our understanding of the scope of this potential effect. Second, growth of prey and increased retention of individuals on sieves may have occurred, and thus, prey density would have appeared to increase. Given the short length of our crab experiment, we do not think growth contributed much to the prey increases we witnessed. Third, so-called 'cage effects' occur when prey move inside them, perhaps seeking refuge from predators (Virnstein 1978), but the fact that we saw dramatic increases in uncaged as well as caged areas suggests this dynamic did not cause our results. Because changes in mudflat invertebrate populations are so notoriously difficult to detect, measures taken to reduce sample variance are particularly warranted. As such, we suggest research into the causes of these significant population changes as a precursor to complicated experiments that rely on invertebrate measures.

Dunlin Foraging and Dunlin-Green Crab Interactions

Although Dunlin and other shorebirds have a wide-ranging diet (Stenzel *et al.* 1983, Skagen and Oman 1996), previous work (Ruiz 1987) has documented that small clams, particularly *Nutricola* spp., comprise an important part of the Dunlin diet during the winter months in Bodega Harbor. We expected this overlap in prey use of *Nutricola* spp. between Dunlin and green crabs to result in treatment effects on Dunlin. We found significant effects of green crabs on Dunlin consumption of *Lumbrineris* (a polychaete) and *Nutricola*, but these effects were not in the expected direction. In the treatment where green crabs had been present at a high density, Dunlin reduced the density of *Nutricola* but not *Lumbrineris*. We expected that Dunlin would reduce *Nutricola* density in areas without green crab predation, but not in the high-density treatment. In the treatment without green crabs, Dunlin reduced the density of *Lumbrineris* but not *Nutricola*. The biological interpretation of these effects is unclear.

Although these results are difficult to explain based on the available evidence, we speculate that in addition to green crabs impacting prey density, that they may also affect its availability. For example, when green crabs forage, they turn and loosen near-surface sediments (Ropes 1968). This physical action may make some prey items more accessible and others less accessible. Given the treatment effect on *Nutricola* in cages where crabs were held at high compared to zero density, it appears that crabs could be facilitating the ability of Dunlin to consume *Nutricola* (particularly *Nutricola* <2mm since those >2mm occurred in low density). If so, the green crabs may be having an even greater negative impact on *Nutricola* than previously thought, through both direct and indirect mechanisms. The crabs are directly impacting the clams by consuming those

>2mm and reducing their adult breeding populations. They may also be impacting the clams indirectly by making those individuals <2mm more available to shorebirds.

In the cages without green crabs, *Lumbrineris* were eaten by Dunlin in greater numbers than in the high density cages. We believe this result is directly related to the low background prey density. Given the relatively low density of adult *Nutricola*, and with no facilitation by crabs for foraging on juvenile *Nutricola*, the Dunlin would have little choice but to select another prey item common in their diet (i.e., polychaetes).

Under the conditions of low *Nutricola* density that occurred in 2001, we found no evidence of current competition between experimental Dunlin and green crabs. The prey affected by crab foraging (Crustacea and *Leptochelia*) differed from those affected by Dunlin foraging (*Nutricola* and *Lumbrineris*) in this experiment. At the same time, however, we found additional evidence that green crabs have affected soft-sediment prey populations in Bodega Harbor, and that these changes may have affected diets of both crabs and birds over the time since the invasion. It is plausible given what we know of green crab and Dunlin diets and historic invertebrate populations, however, that crabs and birds competed for prey resources early in the invasion process before invertebrate populations were altered by green crab foraging. Ongoing monitoring of invertebrate populations and shorebird diets after an invasion of green crabs may provide a more clear understanding of the role of competition in these species' interactions.

Both crabs and birds appear to have a moderate to high degree of flexibility in their diets. Green crab stomachs contained higher percentages of polychaetes and algae when compared to previous studies, and the most common mollusc consumed was the gastropod *Lacuna marmota*, not the bivalve *Nutricola*. The gastropod (*L. marmota*) is not normally consumed by Dunlin in Bodega Harbor (Estelle *unpub. data*), suggesting diet partitioning rather than competition under these current prey conditions. Dunlin diets in the experiment also appear to have shifted from that previously reported (Ruiz 1987), possibly as an indirect effect of green crab foraging over time. More Dunlin stomachs than expected from these previous results contained polychaetes and beetles, and only 20% of the experimental bird stomachs examined contained *Nutricola.* Of the 20% that did contain *Nutricola*, none contained large numbers of *Nutricola* (*pers. obs.*, indicated by few broken shell remains and hinges of clams in bird stomachs). Ruiz (1987) noted large numbers of *Nutricola* in all Dunlin stomachs that he examined. Although the number of Dunlin he examined was small ($n = 10$), we believe his sample correctly documented the importance of *Nutricola* to the Dunlin's diet in Bodega Harbor prior to the green crab invasion. At the time of Ruiz' study, *Nutricola* were more abundant (1000 to 10,000 per m^2). We do not know if polychaetes were a common Dunlin diet item prior to the green crab's introduction to Bodega Harbor, but Ruiz does mention presence of *Nereis* sp. in the stomach samples he examined.

Potential Green Crab Effects on Shorebirds

Green crabs along the Pacific Coast of the United States certainly could affect the prey resources of over-wintering shorebirds in a number of ways. Green crabs may consume preferred or energetically valuable prey items (Grosholz and Ruiz 1995), they may facilitate population growth of less palatable prey species such as *Gemma gemma* (Schneider and Harrington 1981, Grosholz 2005), or they may facilitate or inhibit shorebird access to prey items through physical disturbance of the substrate (this study).

Ultimately, these changes in prey are important to the birds only insofar as they affect the fitness of individuals and consequently, shorebird population dynamics.

Based on studies to date, we conclude that the overall net effect of foraging in altered prey conditions for shorebirds, partially created by green crabs over the course of their invasion and possibly exacerbated by stochastic events, is still unknown. Changes in prey density can provide only a starting point for hypothesizing effects on birds. Grosholz *et al.* (2000) have investigated shorebird abundance over the years spanning the green crab invasion event, but their metric was only a rough measure of effect. While this work has been helpful, we believe more direct and individual-based measures of effects on shorebirds is necessary.

During this experiment, we employed two metrics that we believed would yield insight into potential energetic effects on Dunlin: weight changes and changes in foraging methods. If green crabs and Dunlin were competing for *Nutricola* spp., or other shared prey items (polychaetes, amphipods), we predicted that we would see a greater weight gain in Dunlin in zero than high crab density cages. Though not significant, the weight gain of Dunlin in the high crab density cages was greater than that in the zero crab density cages. This weight gain may have resulted from the unexplained positive effect of crabs on the ability of Dunlin to prey on small *Nutricola*. The density of *Nutricola* was not very high on average, however, so we would not have expected to see large weight gains in any of the experimental birds.

In our experiment, we also considered potential energetic costs associated with the experimental treatments with respect to foraging techniques. Dunlin and many other shorebirds use multiple methods of foraging. Dunlin use primarily stitching (rapidly linking together many probes) and probing (slower, single insertions of the bill into the sediments, or surface pecks) to obtain their prey. Stitching is expected to be energetically costly compared to probing (Wolf 2001). As such, we predicted that Dunlin would stitch in areas where more prey (more energy) was available and probe where less prey was available. The only prey item whose density changed as a function of crab density was *L. dubia.* However, Dunlin did not reduce density of *L. dubia* in places where there were no green crabs compared to where there was a high density of green crabs. This taxa is only occasionally as compared to commonly found in Dunlin stomach contents (Stenzel *et al.* 1983).

We believe the lack of significant treatment effects on either weight gain or foraging behavior were primarily a result of the fact that prey resources did not respond to crab treatments as we had anticipated (e.g., *Nutricola* would be significantly reduced by crabs). We cannot, however, conclude based on the results of this experiment that alterations in prey resources caused by crabs are not having an impact on shorebirds wintering in Bodega Harbor. We believe that an understanding of the impacts of non-native invertebrates (esp. the green crab) on shorebirds as mediated through prey resources would now greatly benefit from a study that evaluated the energetics of prey choices and prey switching (e.g., what are the costs of a diet dominated by polychaetes vs. bivalves, *Nutricola* vs. *Gemma*) by shorebirds, with an assessment of winter survival, annual return rates, and body condition (e.g., fat content).

Design of Multi-predator, Multi-trophic Experiments to Assess Introduced Species Effects

Our experiment represents a novel approach for conducting experiments with multiple predators (crabs and birds) across trophic levels (predator and prey) in an attempt to assess impacts of introduced species on native species. This experiment was conducted on organisms that historically have not been easily amenable to experimentation (shorebirds and soft-sediment macroinvertebrates). As with most novel approaches, particularly complicated ones using difficult organisms in challenging habitats, there where aspects of the experiment that worked well and other aspects that offer lessons for future work.

Many previous cage experiments investigating shorebird foraging have been unable to detect an effect (Thrush *et al.* 1994a, Sewell 1996). This may be because they have excluded rather than enclosed shorebirds. We attempted this experiment from an exclosure perspective during a pilot study, and it was not effective because Dunlin would not forage near the experimental exclosures, nor would they go near open uncaged units. Enclosing Dunlin was the only way to address the questions we had, and this appeared to work well.

Our use of mosquito netting over relatively large enclosures ensured no harm to the birds during the experiment, and they did not try to escape or otherwise not forage because the enclosure inhibited them. Immediately after release into the experimental cages, most Dunlin began foraging, and they continued to do so for the duration of the experiment. It was interesting to note that some Dunlin preened after release and prior to feeding. In these cases, they commonly bathed in puddles of standing water, or they stood on the mudflat and used small amounts of water to preen their feathers. In experimental units where there was less standing water, it appeared to us that birds did not preen as vigorously, and that it may have taken them longer to initiate foraging. Although there was no statistical support that % cover of standing water explained a significant amount of variation in foraging or nonforaging behaviors, we believe that the amount of standing water in an experimental unit may affect the initiation and continuance of foraging in this type of experimental setting.

The great benefit of getting Dunlin to forage normally in an enclosed setting was that we were able to expose them to prey resources that had been impacted by a known level and duration of predation (this would not be possible in an exclosure experiment). Unfortunately, we had not anticipated the effects of the already depleted resource present in the experimental area. Nonetheless, we believe this experimental arrangement may prove to be an effective tool for other studies trying to evaluate the multi-trophic effects of an introduced invertebrate predator on shorebirds.

Even with the Dunlin behaving normally, this experiment hinged on our ability to assess density of soft sediment invertebrates, a task that many researchers have found difficult (Woodin 1974, Virnstein 1978, Thrush *et al.* 1994b). One of the greatest difficulties with soft-sediment invertebrate assessments is that they are characterized by high variability at small spatial scales. In the design phase of the experiment, we anticipated a large degree of spatial variability, and potential temporal variability in invertebrate densities. We incorporated features in our experimental design that were intended to reduce this challenge. Invertebrate prey are known to be distributed in patches in soft sediments (Thrush 1991), and to have variable population densities because of dynamic recruitment and predation processes (Lenihan and Micheli 2001). We tried to minimize the uncontrollable variation in the experiments by using a Before-After-Control-Impact approach to experimental design, blocking, and paired sampling (Virnstein 1978, Sewell 1996, Krebs 1999).

Acquiring samples prior to the crab predation experiment was essential to establish the initial density of prey. The core samples taken 'before' crab or Dunlin predation documented the overall increase in prey density during the crab experiment, and confirmed decreases in density of some prey taxa during the Dunlin foraging experiment. Without the 'before' predation measures of prey density, the increase in prey abundance over the course of the experiments would have gone undetected. The increase in abundance either signals an external biological event (recruitment or growth of invertebrates) or a condition related to experimental implementation (e.g., cages as refugia, movements of prey in response to sediment disturbance). Our interpretation of a lack of predation effect by crabs would have been complicated further without the knowledge that prey actually increased during this part of the experiment.

We also employed paired sampling within a cage as a way to minimize among sample variation in prey density estimates owing to the spatially patchy distribution of marine invertebrates. This pairing was intended to take advantage of the patchy distributions of invertebrate densities across the mudflat. That is, we expected changes in prey density between paired cores to more accurately represent treatment effects and be less impacted by variation in the spatial distribution of prey than cores taken at random within an experimental unit. Surprisingly, our ANOVA analyses indicated no less variability among paired cores within a cage than among all of the cores within a given treatment across blocks. The lack of improvement from paired sampling suggests that either disturbance related to the process of coreing affected prey densities in subsequent core collection, or that the grain of spatial variability of the prey populations is on an even smaller scale than our 0.01 m^2 core area. Wolf (2001) found evidence that prey, particularly amphipods, were aggregated on a scale less than 10cm. Cores smaller than 10cm in diameter may be useful for sampling invertebrates distributed in small scale patches, especially if paired sampling is to be used.

A larger sample size may also have reduced variation around the density estimates for each treatment level, but there are several reasons why this was not desirable. A large number of core samples would have removed a substantial amount of prey while also creating excessive surface disturbance within experimental units. Also, processing invertebrate samples in mudflat sediments consumes large amounts of time and money. We suggest that future experiments of this type focus on a small number of target taxa (preferably ones that are easy to remove from samples, identify, and count), rather than attempting to quantify all taxa in the sample.

As with the pairing of cores, we used blocking as another technique to minimize the effect of environmental heterogeneity. Generally it did not provide any benefit. We blocked on sediment characteristics (% sand, silt, and clay) because these were clearly different from one end of the experimental area to the other, and these characteristics can affect the composition of invertebrate communities (Lenihan and Micheli 2001) and foraging flocks of shorebirds (Quammen 1984). Because the experimental array spanned 330m of mudflat, it was not possible to place all the experimental units or blocks within an area of uniform sediment characteristics. We established the blocks in the field, without perfect knowledge of the exact measure of each component of sediment. We used a surrogate index for % sand (e.g., how much we sank into the mudflat at various locations along the experimental array; see Myers *et al.* (1980) and his “penetrability” indices), and we made visual estimates of the initial % cover of water and algae in the experimental area in order to place the blocks. Cages within blocks, however, were often different from one another. Because of within block heterogeneity, % cover by sand, water and algae were treated as covariates in the analyses. In the future it would worth the effort to more carefully measure the variables upon which the blocking is based prior to the experiment so that one can ensure reduced within block heterogeneity. For example, % sand could be assessed more precisely by dropping a 9-lb nail from a set height and measuring its depth of penetration as Myers *et al.* (1980) did in their study of shorebird foraging on a beach.

CONCLUSIONS

Green crabs appear to have had significant impacts on prey resources in Bodega Harbor, and they have contributed to the reduction in prey densities of prey species preferred by shorebirds, particularly small clams in the genus *Nutricola* (Grosholz and Ruiz 1995, Grosholz *et al.* 2000, Grosholz 2005). Seven years after the green crab invasion and given the environmental conditions during which our experiment was conducted, we observed differences in the composition of crab and bird diets. These differences appear to be in the direction of non-overlapping resources, which would reduce the chance for competition between these species that otherwise share some prey species (esp. *Nutricola*). In the case of *Nutricola* at low prey density and after years of green crab predation effects on this species, we speculate that size partitioning may keep

Dunlin and green crabs from competing with one another for. *Nutricola* (birds eat the clams <2mm, but crabs do not). The partitioning of resources may also be occurring on a larger scale based on the fact that crabs moved off the mudflats in the late summer of 2001 and birds remained there and foraged.

Although there have been no observed changes in shorebird abundance in Bodega Harbor since the introduction of the green crab, this experiment provides some evidence that birds and crabs have changed their resource use of *Nutricola* so that overlap on this species is less than it used to be. It remains unknown what interactions occurred between shorebirds, crabs, and their prey during the time before prey species reached the low densities observed in this study. A challenge remains in evaluating the degree to which changes in resources caused by non-native species translate into effects on body condition and winter survival rates of shorebirds. These metrics will be important in fully understanding the impact of any non-native species on shorebirds.

The approach we took with our experimental design has much promise. We were able to successfully enclose birds, allowing us to expose them to a specific set of conditions in an otherwise natural setting. Our use of a BACI sampling scheme helped us to detect treatment effects in a setting (soft sediments) where changes in invertebrate density have often been difficult to assess. We suggest using this experimental approach in an area of recent green crab invasion (prey communities have not yet been altered) where green crabs and shorebirds will share the mudflats and its resources. We also suggest using this experimental approach to assess impacts of specific prey resources (native or not) on shorebirds.

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Table 1. Sediment characteristics of blocks and cages as arranged along a single tidal height, spanning 330m from near the shipping channel to shore.

Experimental Location	**Mudflat Location**	**% Sand**	**% Silt**	**% Clay**	**Sediment Texture**
Block 1, Cage 1	Near shipping channel	90	2	8	Loamy Sand
Block 1, Cage 2	Near shipping channel	82	8	10	Loamy Sand
Block 1, Cage 3	Near shipping channel	86	4	10	Loamy Sand
Block 1, Cage 4	Near shipping channel	88	2	10	Loamy Sand
Block 2, Cage 1		88	2	10	Loamy Sand
Block 2, Cage 2		92	2	6	Sand
Block 2, Cage 3		92	2	6	Sand
Block 2, Cage 4		94	0	6	Sand
Block 3, Cage 1		94	0	6	Sand
Block 3, Cage 2		92	2	6	Sand
Block 3, Cage 3		94	0	6	Sand
Block 3, Cage 4		94	0	6	Sand
Block 4, Cage 1	Near shore	94	0	6	Sand
Block 4, Cage 2	Near shore	92	2	6	Sand
Block 4, Cage 3	Near shore	92	2	6	Sand
Block 4, Cage 4	Near shore	92	2	6	Sand

Table 2. List of all invertebrate taxa found in sample cores. Taxa in bold print were selected for statistical analyses and had an average density > 2 individuals/core (1 core = $0.01m^2$). Other taxa were considered too rare in samples to be included in statistical analyses.

POLYCHAETA	CRUSTACEA	MOLLUSCA	MISCELLANEOUS
Capitellidae sp. indet.	*Accedomoera vagor*	*Clinocardium nuttalli*	Arachnid
Dorvilleidae sp. indet.	*Allorchestes angusta*	*Cryptomya californica*	Beetle
Exogone sp. indet.	*Americorophium* sp. indet.	*Cumacea vulgaris*	Fly
Glycinde picta	*Ampelisca unsocalae*	Gastropoda	**Foraminifera tests**
Goniadidae sp. indet.	**Amphipoda sp. indet.**	*Gastropteron pacificum*	Insecta
Hesionidae sp. indet.	*Ampithoe sectimanus*	*Hiatella arctica*	Nematoda sp. indet.
Lumbrineridae sp. indet.	*Ampithoe* sp. indet.	*Lacuna* sp.	Nemertinea sp. indet.
***Lumbrineris* sp.**	*Aoroides intermedius*	*Macoma nasuta*	Oligochaeta sp. indet.
Maldanidae sp. indet.	*Aoroides* sp. indet.	*Macoma* sp. juvenile	Phoronida sp. indet.
Nephtyidae sp. indet.	*Aoroides spinosus*	Mactridae juvenile	Platyhelminthes sp. indet.
Nereidae sp. indet.	*Cancer gracilis*	*Mactrotoma californica*	Sipunculida sp. indet.
Opheliidae sp. indet.	*Caprella californica*	*Musculista senhousia*	
Orbiniidae sp. indet.	Corophiidae sp. indet.	*Mya arenaria*	
Oweniidae sp. indet.	*Crangon alaskensis*	**Mytilidae sp. juvenile**	
Phyllodocidae sp. indet.	*Crangon* sp.	***Nutricola* spp.**	
Platynereis bicanaliculata	***Cumella vulgaris***	*Odostomia* sp.	
Polynoidae sp. indet.	*Eualus townsendi*	*Ostracoda*	
Sabellidae sp. indet.	*Exosphaeroma inornata*	*Petriciola carditoides*	
Spionidae sp. indet.	*Gnorimosphaeroma* sp. juv.	*Petricolaria californiensis*	
Syllidae sp. indet.	***Grandiderella japonica***	***Protothaca staminea***	
Terebellidae sp. indet.	***Grandifoxus* sp. indet.**	*Rochefortia tumida*	
	Harpacticoida sp. indet.	*Saxidomus gigantea*	
	Hemigraspsus sp. juv.	*Semele* sp.	
	Hyale anceps	*Tellina* sp.	
	Hyale sp. indet.	Veneridae juv.	

Table 2 (continued).

POLYCHAETA	CRUSTACEA	MOLLUSCA	MISCELLANEOUS
	Leptochelia dubia		
	Monocorophium acherusicum		
	Monocorophium insidiosum		
	***Monocorophium* sp. indet.**		
	Nebaliidae sp. indet.		
	Photis brevipes		
	Photis sp. indet.		
	Phoxocephalidae sp. indet.		

Table 3. ANOVA results from green crab and shorebird predation experiments. a) invertebrate taxa in bold font were those that showed a significant response to the treatment of green crab density. Those in regular type did not show a significant response to green crab density, but are included as they are relevant for comparison of results in this study to previous studies. b) invertebrate taxa in bold font showed a significant response to dunlin predation after being exposed to green crab density levels of zero and high. For multiple comparisons following significant ANOVA results, Fisher's least significant difference test results are provided (SAS 9.1); $\alpha = 0.05$.

	Prey Taxa	**SAS Model***	**Source of Variation**	**Df**	**Mean Square**	**F**	**P-value**	**LSD Test**	**P-value**
a) Crab Predation	**All Crustacea**	B T W	Block	3	0.56	14.20	0.001		
	(Crustacea)		**Treatment**	**3**	**0.19**	**4.77**	**0.03**	**z, l, h > uc**	**< 0.05**
			Water	1	0.03	8.22	0.02		
			MS(Error)	8	0.04				
	Leptochelia dubia	B T W	Block	3	0.20	2.61	0.12		
	(Crustacea)		**Treatment**	**3**	**0.36**	**4.77**	**0.03**	**z, l > uc, h**	**< 0.05**
			Water	1	0.56	7.44	0.03		
			MS(Error)	8	0.13				
b) Dunlin Predation									
	***Lumbrineris* sp.**	B T W	Block	3	0.64	8.90	0.02		
	(Polychaeta)		**Treatment**	**2**	**0.61**	**8.37**	**0.03**	**h > uc, z**	**< 0.05**
			Water	1	0.84	11.60	0.02		
			MS(Error)	5	0.07				
	All Mollusca	B T	Block	3	0.05	2.17	0.02		
	(Mollusca)		**Treatment**	**2**	**0.15**	**6.17**	**0.04**	**z > uc, h**	**< 0.05**
			MS(Error)	6	0.02				
	***Nutricola* spp.**	B T	Block	3	0.05	0.81	0.53		
	(Bivalvia)		**Treatment**	**2**	**.031**	**5.38**	**0.04**	**z > h, uc**	**< 0.05**
			MS(Error)	6	0.06				

* B = block, T = treatment, W = % cover water; uc = uncaged, z = zero, l = low, h = high crab density treatment levels.

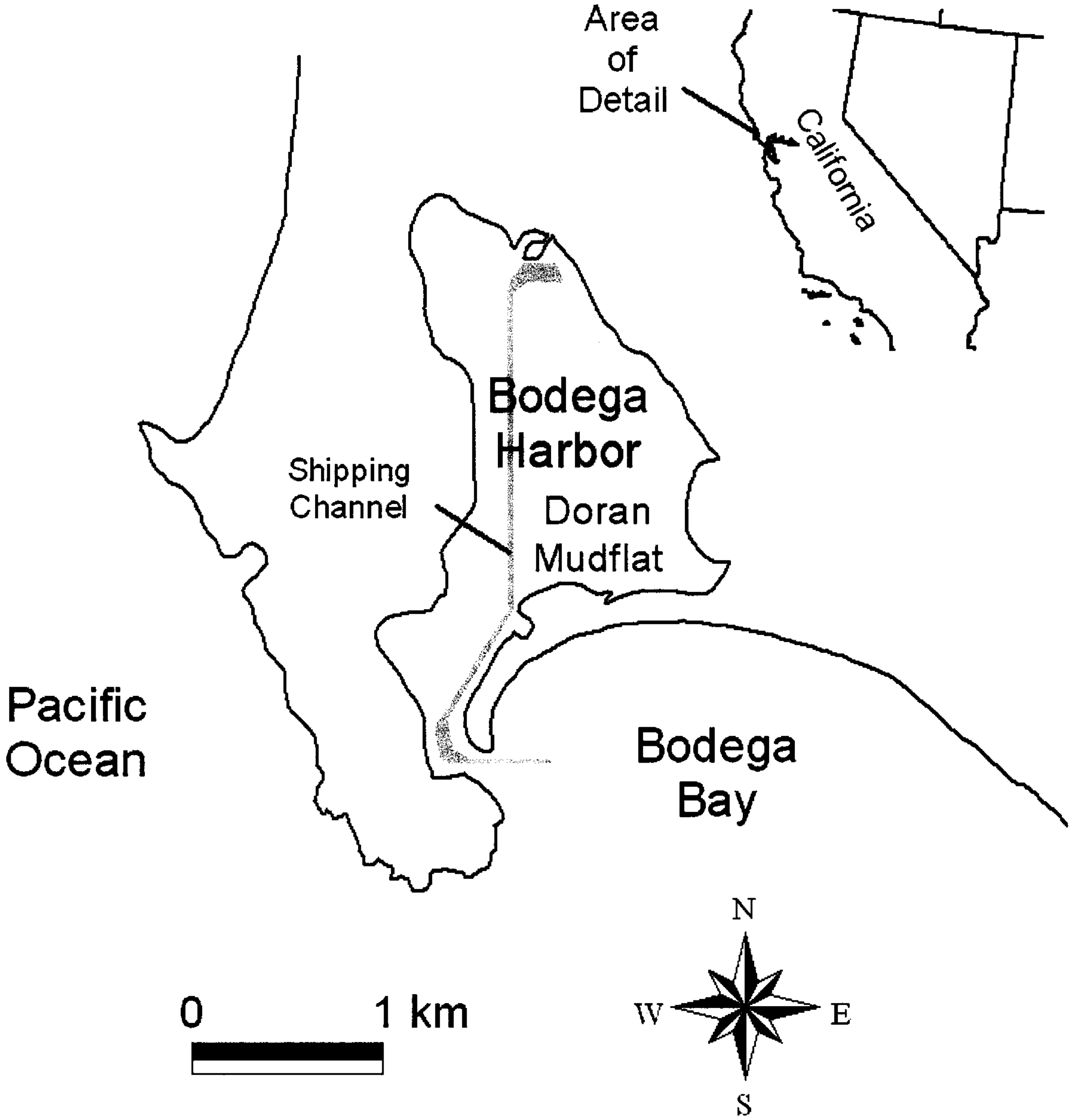

Figure 1. Bodega Harbor study site in northern California.

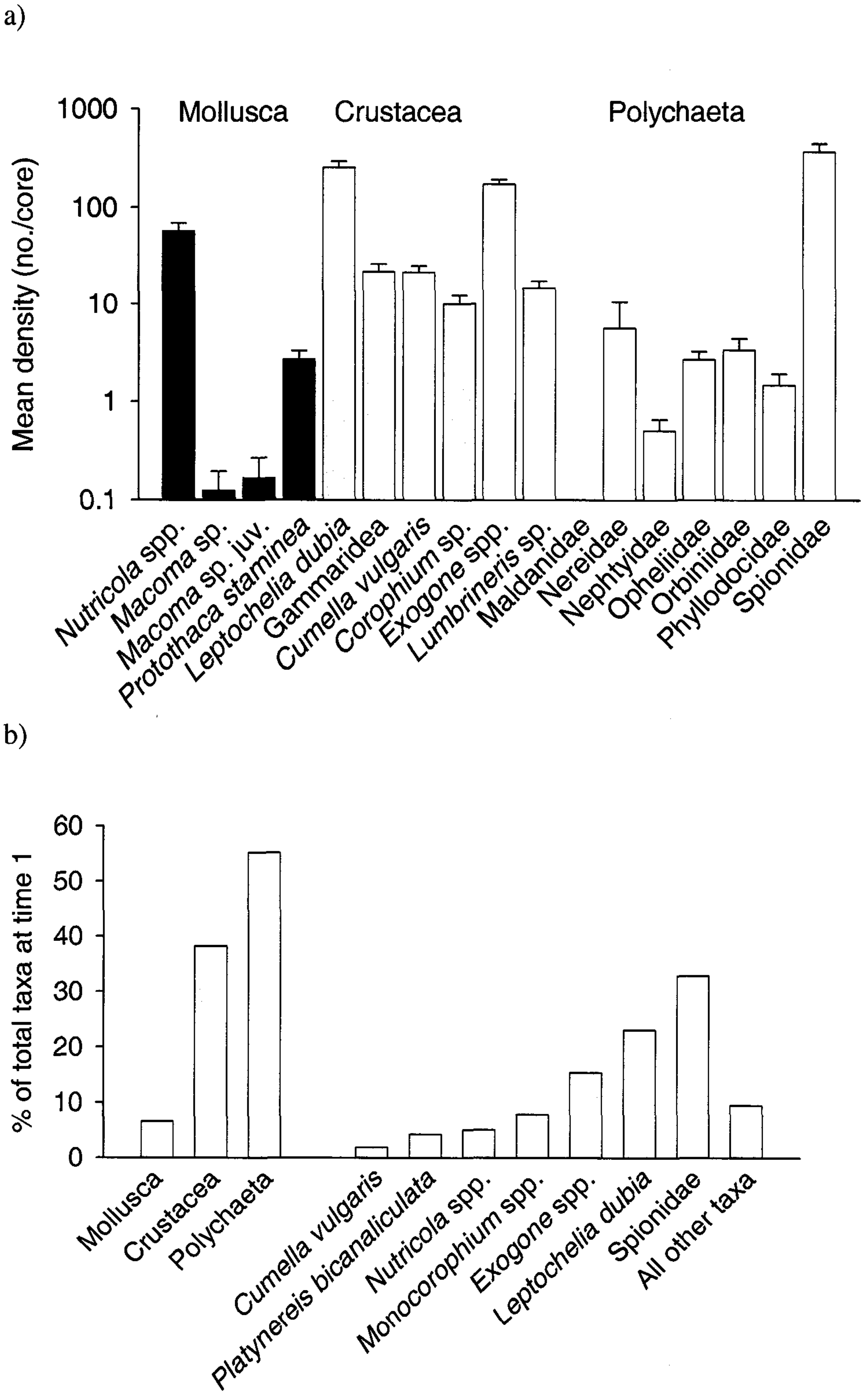

Figure 2. a) average density of invertebrate taxa with >2 individuals per core at the beginning of the crab foraging experiment on Doran Mudflat in 2001; cores were taken at tidal height = +1.2 m above MLLW. Average density is plotted with error bars = 1 SE and b) percent of total number of individuals at the beginning of crab foraging experiment for a given taxonomic grouping.

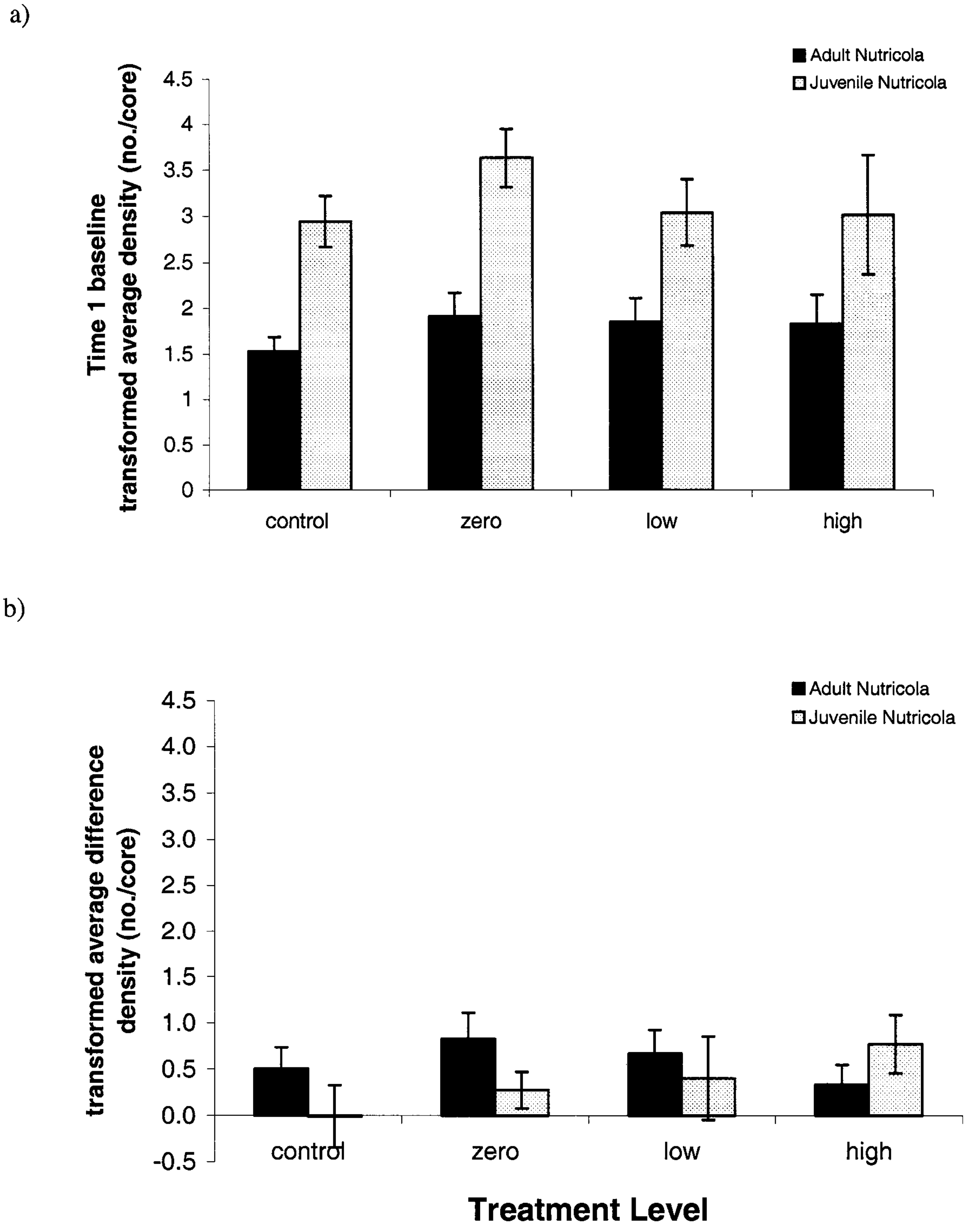

Figure 3. a) Mean density, in ln transformed scale, (with 95% CI) of juvenile and adult *Nutricola* spp. per core at the initiation of the green crab foraging experiment and b) mean change in density (ln transformed scale) of juvenile and adult *Nutricola* spp. during the green crab foraging experiment. No significant difference among treatment levels for either juveniles or adults (ANOVA, df = 3,9, $F_{\text{juvenile}} = 0.77$, $P = 0.54$; $F_{\text{adult}} = 0.71$, $P = 0.57$).

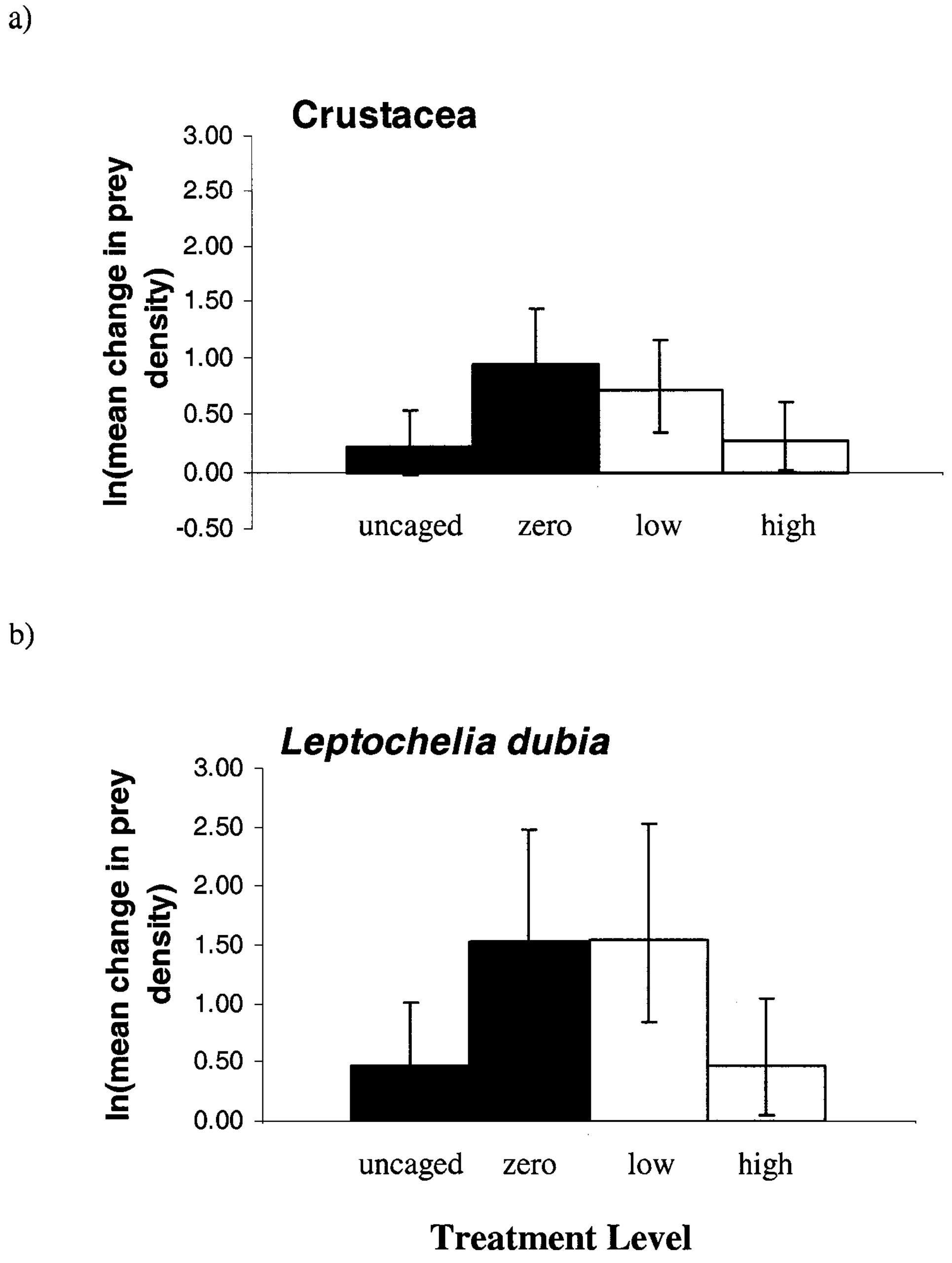

Figure 4. Back-transformed LSmeans with 95% confidence intervals (CI) for all treatment levels in the crab foraging experiment (effect of various densities of green crabs on invertebrate density). LSMeans and 95% CI calculated in SAS Proc GLM were back-transformed via ($e^{(\text{lsmeans})}$-1). The response variable for this analysis was constructed by transforming the original counts with ln(x+1), taking the difference in the transformed invertebrate density between time 2 and time 1 (e.g., time 2 – time 1) for all core pairs, and then averaging the transformed difference among sub-sample cores within a cage. All crustacean taxa lumped (a) and *L. dubia* (b) were the only two taxa showing a significant treatment effect in the crab foraging experiment ($P < 0.05$).

a)

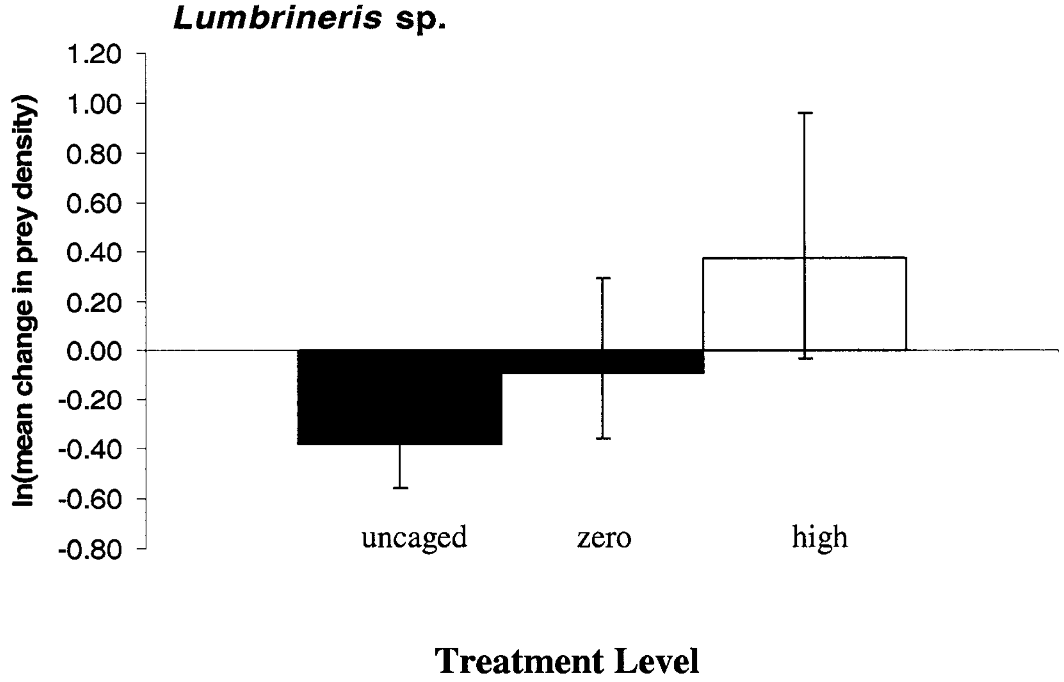

Figure 5. Backtransformed LSmeans with 95% confidence intervals (CI) for all treatment levels in the Dunlin predation experiment (effect of Dunlin on invertebrate density, following green crab predation on invertebrates). LSMeans and 95% CI were backtransformed via ($e^{(\text{lsmeans})}$-1). The response variable for this analysis was calculated by taking the difference in invertebrate density between time 3 and time 2 (e.g., time 3 – time 2) for all core pairs, averaging the differences of the sub-sample cores within a cage, and then transforming the average difference for all cages with ln(x+1). Negative changes indicate prey reduction between time 3 and time 2, and positive changes indicate prey enrichment between time 3 and time 2. Taxa shown in the graphs a-c were the only taxa showing significant treatment effects in the Dunlin predation experiment ($P < 0.05$).

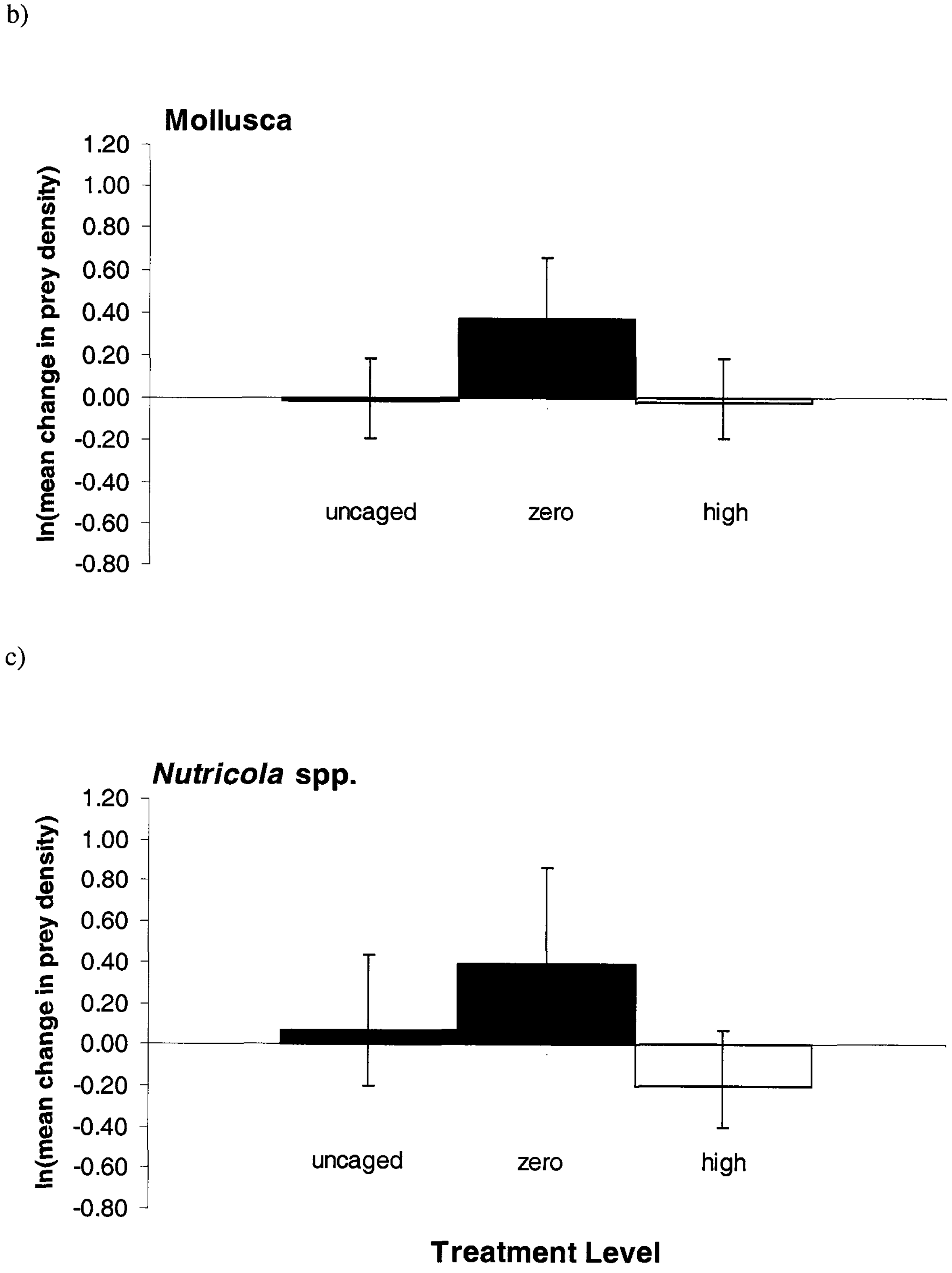

Figure 5. continued.

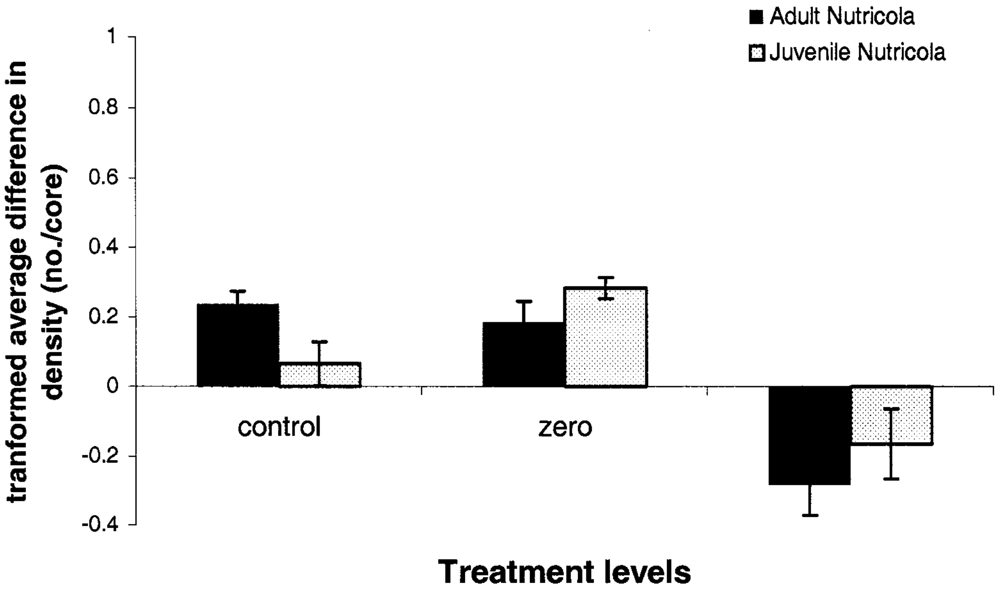

Figure 6. Mean change in density (ln transformed scale) of juvenile and adult *Nutricola* spp. during the Dunlin foraging experiment. No significant treatment effects were observed (ANOVA, $F_{\text{juveniles}} = 3.18$, df = 3,6, $P = 0.11$; $F_{\text{adult}} = 1.05$, df = 3,6, $P = 0.41$).

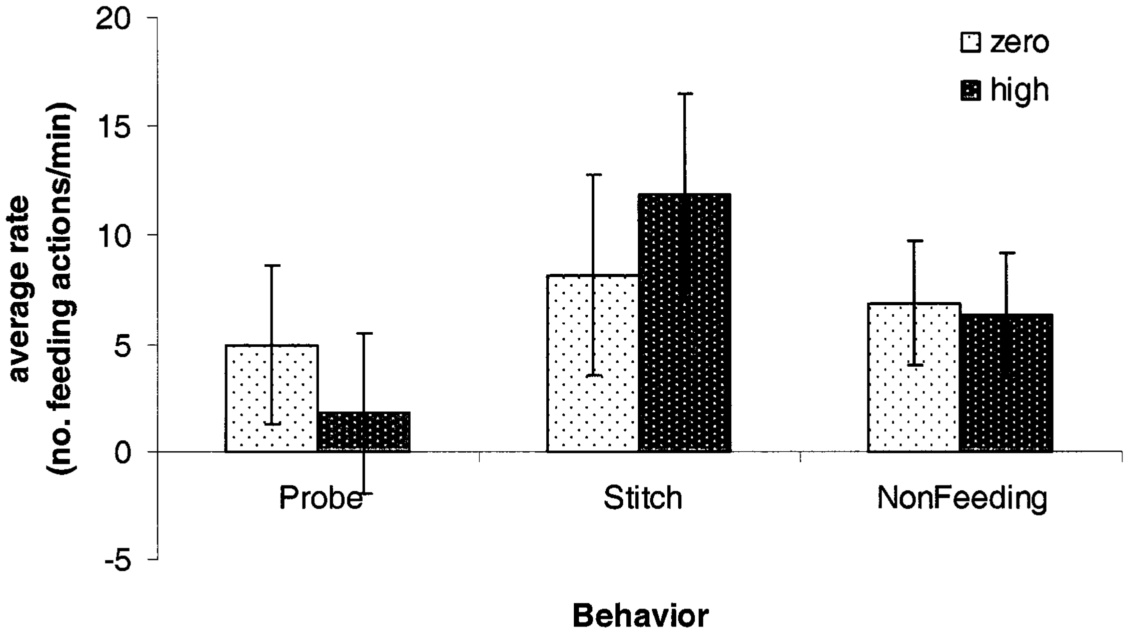

Figure 7. LSMEANS of probing, stitching, and nonfeeding foraging behaviors of Dunlin held in cages with zero or high densities of green crabs. Error bars are 95% CI.

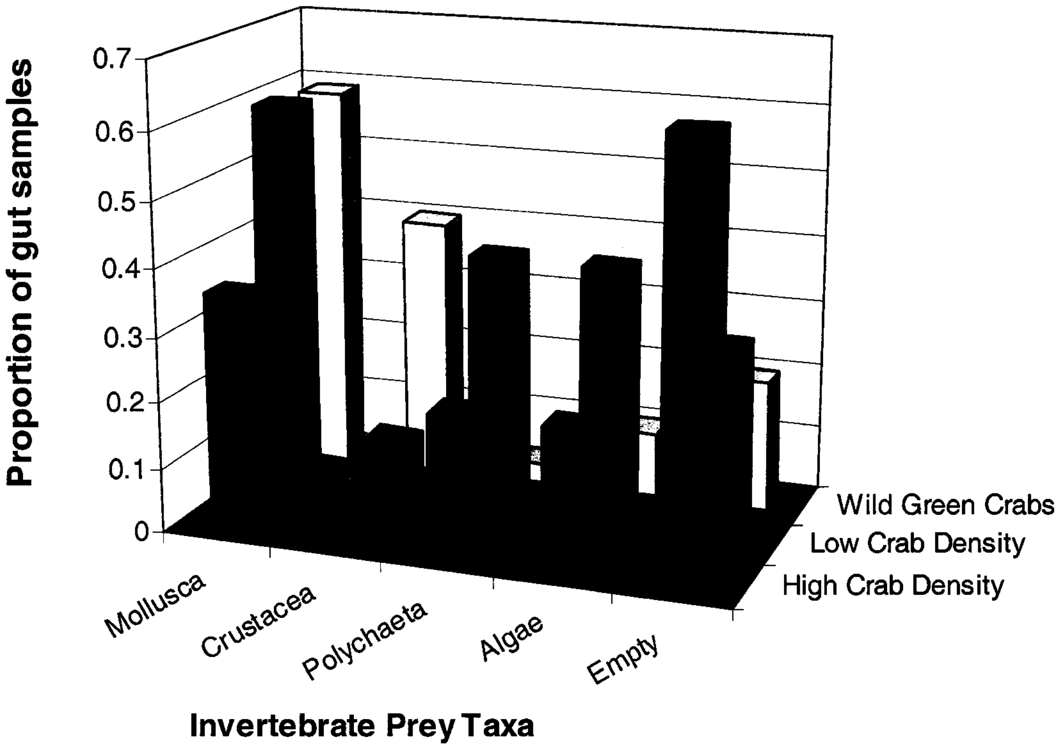

Figure 8. Proportion of stomach samples from experimental green crabs that were empty or contained various invertebrate taxa and algae. Green crabs were collected from experimental cages where their densities were at low (1.2 green crabs/m^2; n = 10 stomach samples) and high (6 green crabs/m^2; n = 14 stomachs) levels. For comparison, stomach samples from free, actively foraging green crabs collected in Bodega Harbor in the late 1990's are included (Grosholz *et al.* 2000; n = 30 stomachs). Note in the current study, molluscs in experimental green crab stomachs were mostly gastropods (*Lacuna marmorata*), not bivalves (*Nutricola* spp.), as reported by Grosholz *et al.* 2000.

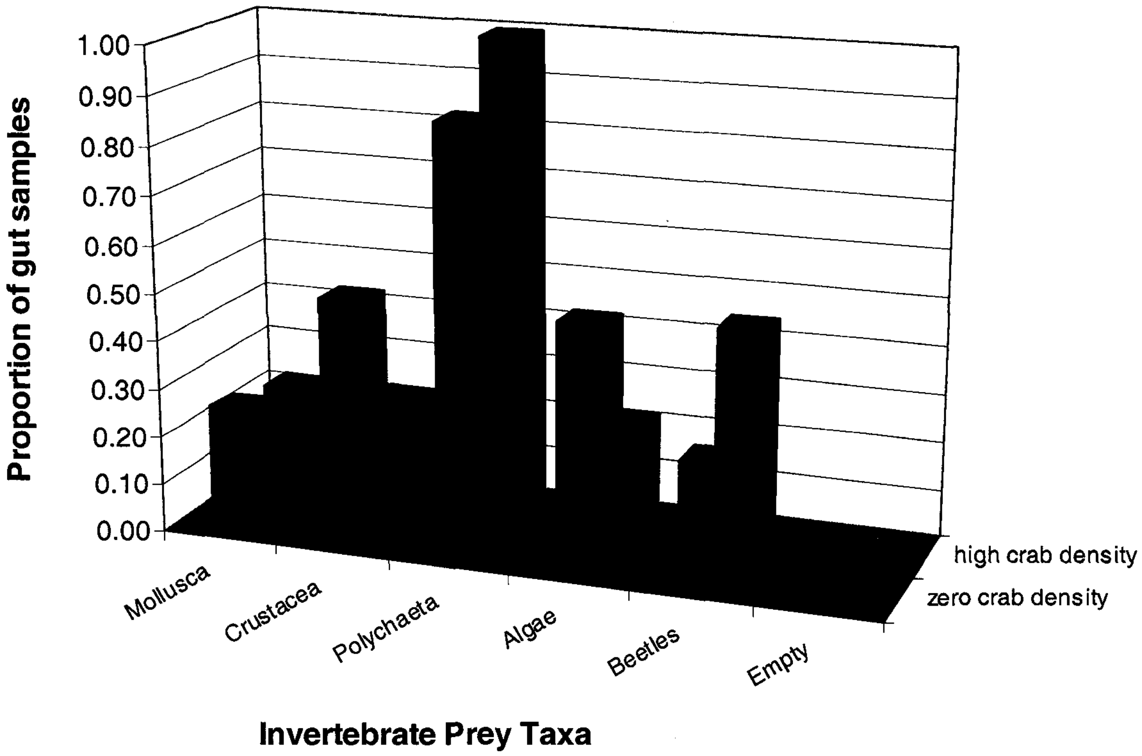

Figure 9. Proportion of Dunlin stomachs containing various prey taxa and algae in the Dunlin foraging experiment. Note that mollusca was comprised of bivalvia (mostly *Nutricola* spp.) not gastropoda (mostly *Lacuna marmorata*) as for green crab results.

CHAPTER 3

ASSESSMENT OF A SHOREBIRD'S DIET PRIOR TO AND AFTER INTRODUCTION OF A MARINE PREDATOR

ABSTRACT

The diet of Dunlin (*Calidris alpina*) prior to and after the introduction of the European green crab (*Carcinus maenas*) was examined in Bolinas Lagoon and Bodega Harbor, CA. My objective was to determine whether Dunlin diet in these two embayments has changed since the introduction of the green crab, with the understanding that changes do not necessarily imply a causative relationship.

Dunlin diet remains highly variable between locations and among years, and all major prey taxa (molluscs, crustaceans, polychaetes and insects) occur presently in their diets. However, it is clear that the bivalve component (esp. *Nutricola* spp.) of the Dunlin diet in Bodega Harbor is currently comprised of fewer, smaller individuals than previous to the introduction of the crab. The present diet of Dunlin in Bodega Harbor appears more similar to that in Bolinas Lagoon than it did historically, but number of annual samples is too minimal during each period to be supportive of a causative relationship. Prior to introduction of the green crab in Bolinas Lagoon, the primary prey of Dunlin was polychaetes and crustaceans, not bivalves. Currently in Bolinas Lagoon, the Dunlin diet has a significantly higher percent occurrence of bivalves and a lower percent occurrence of crustaceans than it did prior to the green crab's arrival. In this location, Dunlin may now forage upon smaller individual bivalves, particularly *Nutricola* spp., than before the crab's introduction.

There may be energetic costs to these dietary changes, and these should be examined with regard to effects on shorebird winter body condition and survival rates. We conclude that future research on shorebird diets and foraging should consider changes in local biota due to introduced marine invertebrates, and that shorebird diet should be examined as a function of the relative abundance of native vs. non-native prey composition.

Keywords: *Calidris alpina*, shorebirds, marine invertebrates, introduced invertebrate, *Carcinus maenas*, green crab, predation, foraging, multi-trophic.

INTRODUCTION

Prominent aspects of the winter ecology of shorebirds concern the prey they consume and the mortality risks they encounter while on their wintering grounds. Shorebird diets exhibit considerable breadth, and for coastal species, commonly include the orders Veneroida (mollusca, small clams), Amphipoda (crustacea), and Phyllodocida (polychaeta) (Skagen and Oman 1996). Shorebirds have been described as both opportunistic (taking prey in relation to its availability) and selective (primarily for size) in their dietary choices (Lifjeld 1984, Wilson 1989). They also exhibit an ability to switch prey types as prey density declines during winter (Goss-Custard 1980).

Possibly the most important impact on shorebird populations wintering in temperate to subtropical coastal environments is the significant habitat loss and degradation that has occurred there (Page and Gill 1994). Filled wetlands, increased development, disturbance, enhanced predation, and pollution comprise the key threats to shorebirds in these locations. These habitat changes are obvious and they are easy to document. Less obvious degradation of native coastal habitats may occur with the invasion of non-native marine invertebrates. Novel species in marine environments can affect the size distribution and population dynamics of native invertebrates as well as local diversity (Posey 1988, Ruiz *et al.* 1997). However, few studies have evaluated the indirect effects of non-native marine invertebrates on wintering shorebirds (Grosholz *et al.* 2000). These effects are most likely to occur in relation to prey resources and to be difficult to document.

For shorebirds wintering on the West Coast, a potentially important introduction occurred with the arrival of the European green crab, *Carcinus maenas*, in San Francisco

Bay, CA in 1989 (Cohen and Carlton 1995). After the green crab's initial introduction, it spread northward to Bolinas Lagoon and Bodega Harbor, CA by 1993 (Cohen and Carlton 1995). The crab's impacts on invertebrates have been studied extensively in Bodega Harbor, CA (Grosholz and Ruiz 1995, Grosholz *et al.* 2000, Grosholz 2005), but not at all in Bolinas Lagoon. It preys upon similar invertebrate taxa that wintering shorebirds rely upon (esp. bivalves and crustaceans; Ropes 1968). In particular, the crab has negatively affected *Nutricola* spp., a venerid clam that it and shorebirds consume. To date, the crab's effects on shorebird diets have not been evaluated in any location.

In this study, we examined Dunlin (*Calidris alpina*) diet in Bolinas Lagoon and Bodega Harbor prior to and after the introduction of the green crab. Relative abundance of the green crab in Bolinas is believed less than in Bodega Harbor (Grosholz and Ruiz 1995, Estelle *unpub. data*), and density of *Nutricola* spp. is reported lower in Bolinas than in Bodega (Stenzel *et al.* 1983, Grosholz *et al.* 2000). Researchers have collected data on shorebird diets from 1973-1976 (Bolinas Lagoon) and 1983-1986 (Bodega Harbor). Prior to the introduction of the green crab, wintering Dunlin in Bolinas Lagoon were described as having a polychaete and amphipod diet with bivalves occurring in a lower percent of stomachs (Stenzel *et al.* 1983). In Bodega Harbor, Dunlin diet was described as completely dominated by *Nutricola* spp. with one genus of polychaete also of importance (Ruiz 1987). With this background information, the objective of this study was to assess whether there have been changes in the Dunlin diet coinciding with introduction of the crab in Bolinas and Bodega.

Historic comparisons of diet data and information on prey resources are key to understanding shorebird diet breadth and how the prey base has changed over time.

Using previous information from these two sites on Dunlin diet and on density of some invertebrate prey, we hypothesized that we would see no difference in percent occurrence of *Nutricola* in Dunlin stomachs currently between Bodega and Bolinas. We also hypothesized a large decline in percent occurrence of *Nutricola* prior to and after the green crab introduction in Bolinas and Bodega, although the historic records for Bodega are minimal (Ruiz 1987).

In this paper we describe briefly a method for collecting stomach samples that was first employed in the 1980's (G. Page and L. Stenzel, Point Reyes Bird Observatory), and refined in this study. Stomach pumping was developed so that shorebirds would not have to be sacrificed to examine their stomach contents. Many people have used various methods to collect diet information on shorebirds. The most direct and least intrusive method is to observe birds and record what prey they are consuming (Stenzel *et al.* 1976). This is obviously difficult and time consuming because it is nearly impossible to identify the consumption of small prey items. The most invasive method of stomach sample collection is to kill birds and quickly preserve the contents of their digestive tracks (Lifjeld 1983, Ramer 1985). This method, while probably the least biased method of diet identification, is rarely used today because of the conservation status of most shorebirds. Other methods involve collection and examination of feces or pellets (Dekinga and Piersma 1993). These methods are biased against small and soft-bodied prey species that are quickly digested. A final group of methods involves either "flushing" or "pumping" the stomach or causing birds to regurgitate with the use of emetics (Stenzel *et al.* 1983, Martin and Hockey 1993). These methods may be difficult to apply without injury to birds, and they may be biased toward prey with hard, indigestible parts. However, aside from bird collection, stomach flushing, pumping, and the use of emetics are the only methods that allow examination of soft and hard bodied prey, particularly if a stomach sample is collected soon after a bird has foraged (Verkuil 1996).

Study Sites and Species

Bolinas Lagoon is a shallow 587ha estuary; 70% of the area exposed at mean low water is classified as tidal flats (Shuford *et al.* 1989). The lagoon is surrounded by high hills, marshy pastures, and a sandspit. There is one dominant freshwater drainage into the Lagoon, and one small jetty opening from the Lagoon to the Pacific Ocean. Kent Island is a 40ha island within Bolinas Lagoon that is dominated by a *Salicornia virginica, Spartina foliosa,* and *Distichlis spicata* salt marsh. The tidal flats and Kent Island are important foraging and roosting locations for the nearly 6,000 shorebirds wintering in Bolinas Lagoon each year. Bolinas Lagoon hosts 14 common species of shorebirds throughout the non-breeding season and in numbers large enough to reduce abundance of invertebrate prey (Stenzel *et al.* 1983).

Bodega Harbor is a 2km^2 marine-dominated harbor with a central shipping channel and approximately 320ha of tidal flats. It is surrounded by pastured hills, marsh, sand dunes, beach, and coastal headlands. It receives very little freshwater input and has a single opening to the Pacific Ocean through a jetty. The tidal flats and the marsh site in this harbor are important foraging and roosting locations for up to13 common species of shorebirds, reaching estimated abundances of 13,000 during the non-breeding season (Bodega Marine Lab - BML - archived data). Bodega Harbor and Bolinas Lagoon share the same assemblage of shorebirds (Stenzel *et al.* 1983, BML data).

METHODS

During November-December 2000 and October–December 2001, we captured 75 Dunlin in Bolinas Lagoon (in 2000, $n = 15$; in 2001, $n = 20$) and Bodega Harbor (in 2000, $n = 20$; in 2001, $n = 20$). We set 3-5 mist nets (0.635cm mesh and 9 or 12m long) on the edge of the marsh and mudflats, across marsh channels, or within the *Salicornia*-dominated marshes of these two embayments on 11 evenings. We set mist nets at the rising high tides at sunset and also during falling low and low tides at night (in 2000, 3 tides in Bodega, 1 in Bolinas; in 2001, 4 tides in Bodega and 3 in Bolinas). During these times birds were flocking and either entering or leaving their night roost, depending upon the state of the tide. We removed shorebirds from nets as they were caught, and released species other than Dunlin. Dunlin were placed two or three at a time in covered laundry baskets and carried to a banding station away from mist nets for processing.

Typically, 1 person on the 3-person field team monitored mist nets while 2 others collected stomach samples from Dunlin. We collected stomach samples by intubation, or stomach pumping (Stenzel *et al.* 1983). Stenzel *et al.* (1983) originally used a plastic straw (3mm inside diameter) affixed to the end of a disposable syringe to collect stomach samples from small sandpipers. In this study, we used a number 10 feeding or urethral catheter tube cut to a length of 20cm and attached to a 10cc disposable syringe. In comparison to the straw, this tube was highly flexible with a soft, rounded and closed end (3.3mm inside diameter). Additionally, instead of one opening on its end like the straw, the catheter tube had openings on either side of the tube, one set above the other, to more effectively sample stomach contents.

Two people performed the stomach pumping procedure as follows. At least 4cc of tepid water (water was held in a thermos) was drawn up into the syringe and feeding tube before the tube was inserted into the esophagus and digestive system of a Dunlin. One person held a Dunlin in a 'bander's hold' with its bill pointed upward in alignment with its spine for the entirety of the procedure. The second person opened the bill of the Dunlin, inserted, and gently guided the tube down its throat, through its proventriculus, and into the stomach. Once the tube was inside the stomach, the person slowly pushed 1-2cc of water from the syringe. Using a slight pumping action with the syringe plunger, the sample was aspirated and placed in a 25ml scintillation vial. Unless an individual Dunlin showed signs of distress or discomfort (coughing, gagging, closed eyes, or uneven breathing), we refilled the syringe and repeated the stomach pumping procedure two more times. We placed all extractions from an individual bird in one vial, and immediately fixed the sample with 10% buffered formalin. The following day, we decanted the formalin and transferred the sample to 70% alcohol for storage.

We used a 6.7-40x dissecting scope to view the preserved stomach samples, and one person examined all samples. We did not attempt to count invertebrate species in the samples because of strong inherent bias associated with differential digestibility of prey (Lifjeld 1983, Martin and Hockey 1993). For example, small or soft-bodied prey tend to be underestimated in stomach samples because they are rapidly digested by shorebirds (less than 15 min; Verkuil 1996), and in many cases no evidence of their presence remains. Numbers of hard-bodied prey with exoskeletons or other characteristic hard parts (bivalve shells or hinges, polychaete jaws) may be overestimated because of a long residence time in the stomach (Rundle 1982, Goss-Custard 1983). Thus, for each sample, we recorded the presence of polychaetes, crustaceans, and molluscs, and when possible, diagnostic parts of invertebrates were identified to a lower taxonomic level. We used Smith and Carlton (1975), Hartman (1969), Fauchald (1977), Keen and Coan (1974), and Barnard (1981), as well as consultation with L. Stenzel and G. Page (Point Reyes Bird Observatory) for identification and nomenclature of tidal flat organisms in stomach samples.

We used Fisher's Exact Test (two-sided, $\alpha = 0.05$) to test for differences in the percent occurrence of prey taxon (beetles, gastropods, bivalves, crustaceans, and polychaetes) in (i) Dunlin stomach contents between years (2000 and 2001) within a site (Bodega and Bolinas) and between sites within pooled years (2000 and 2001), (ii) between historic (Stenzel *et al.* 1983) and recent Dunlin diet in Bolinas Lagoon, and (iii) between Dunlin (2000-01) and green crab stomach contents (1996-98; Grosholz *et al.* 2000) in Bodega Harbor. Historic percent occurrence for each prey taxon found in wintering Dunlin stomachs from Bolinas Lagoon was available as a mean percent occurrence for the period of 1973-75 (Stenzel *et al.* 1983). To compare our data with theirs, we averaged our percent occurrence values across 2000 and 2001 for Bolinas for each taxon.

RESULTS

Stomach Pumping

We pumped the stomachs of 75 Dunlin and were able to conduct this method without causing injury or casuality to the birds. On average it took 3min (SE = 0.4, $n = 11$) to pump a bird's stomach under quiet conditions with two people working together. When noise or activity increased in the presence of a bird whose stomach was being pumped, average time to acquire the sample increased to 5min (SE = 0.7, $n = 5$).

Invertebrate Composition of Stomach Samples

I found diagonostic fragments of prey in Dunlin stomach samples that included jaws and setae from polychaetes, hinges and shells from molluscs, claws and exoskeletal parts from crustaceans, and jaw parts and claws from beetles. In total, I found 5 families (6-12 species) of polychaetes, 2 families (3-5 species) of bivalves, 2 families of gastropods (at least 2 species), and at least 5 families (3-5 species) of crustaceans in the Dunlin stomach samples from Bodega Harbor and Bolinas Lagoon in 2000 and 2001 (Table 1). Three non-native prey species were found in the stomach samples from the two embayments (*Pseudopolydora kempi, Gemma gemma,* and *Gradidierella japonica*). All but three taxa (*Cumella vulgaris*, an unidentified decapod and an unidentified ostracod) were common to the diet samples from both Bodega Harbor and Bolinas Lagoon. Finally, I found an unidentified beetle (possibly of the family Heteroceridae) in 21 of 75 stomach samples. The beetle was reported previously in Bolinas Lagoon shorebird diets, but not in Bodega Harbor diets (Stenzel *et al.* 1983, Ruiz 1987).

Current Diet

Bodega Harbor - In 2000, bivalves, crustaceans, and polychaetes were found in 75-90% of the Dunlin sampled ($n = 20$) (Figure 1a). By 2001 ($n = 19$), crustaceans were recorded in 37%, bivalves in 100%, and polychaetes in about 79% of Dunlin sampled. Beetles were recorded in 35%, whereas gastropods were present in less than 20% of the birds sampled in both years. In 2000, a significantly higher percentage of Dunlin sampled in Bodega Harbor had crustaceans in their stomachs compared to 2001 (Fisher's

Exact Test; df = 1; $P = 0.02$). For all other taxa, no difference in percent occurrence of prey taxa between years was evident (Fisher's Exact Test, df = 1, $0.32 < P < 1.0$).

The dominant venerid clam in Bodega stomach samples in both years was *Nutricola* spp. (77%), although *G. gemma* was also present (5%). In 8% of the samples I could not distinguish *Nutricola* from *Gemma*. Typically, these clams can be distinguished by the color of the hinge if it does not fade during preservation and by the absence of an anterior lateral tooth on the *G. gemma* hinge. However, clams were rarely whole within Dunlin stomach samples, and their hinges were not always in tact. Thus, acutal number of *Nutricola* consumed by Dunlin could not be determined. Based solely on the number of hinges about which I was certain, *Nutricola* never exceeded 7 individuals in a stomach sample.

Bolinas Lagoon - In 2000 I found bivalves in 67%, crustaceans in 60%, and polychaetes in 93% of the Dunlin stomachs sampled ($n = 15$, Figure 1b). In 2001 ($n = 21$), I found crustaceans, bivalves and polychaetes in 80-100% of the stomach samples. Both gastropods and beetles occurred in relatively few stomach samples in 2000 (7%), but these taxa increased to 24% and 38%, respectively, of the stomach samples in 2001. In 2001, a higher percentage of Dunlin sampled in Bolinas Lagoon had beetles in their stomachs compared to 2000 (Fisher's Exact Test, df = 1, $P = 0.05$). For all other taxa, no difference in percent occurrence of prey taxa between years was evident (Fisher's Exact Test, df = 1, $0.06 < P < 0.42$). Similarly, there was no significant difference in percent occurrence of prey taxa between locations (Bodega vs. Bolinas) when data was pooled among years (2000 and 2001) (Fisher's Exact Test, df = 1, $0.11 < P < 0.75$).

Finally, in Bolinas Lagoon in 2000 and 2001 I found that *Nutricola* was the dominant bivalve in the stomach samples (64%), followed by an unidentified mussel (22%), and *Gemma* (3%). We never observed more than 3 *Nutricola* hinges in any one of the Bolinas samples.

Historic Diets

Bodega Harbor - Historic diets of Dunlin and other shorebirds from Bodega Harbor are poorly known. However, prior to the introduction of green crabs in Bodega Harbor, 100% of Dunlin sampled (*n* = 10) contained on average 95.5 *Nutricola* spp. in their stomachs (Table 2, cited from Ruiz 1987). *G. gemma* was not mentioned as a prey item found in Dunlin stomachs by Ruiz (1987). *Nereis* was the only polychaete genus mentioned in the Dunlin stomach contents, and there was no indication in how many samples it occurred (Ruiz 1987).

Bolinas Lagoon - Winter diet (November to February) of Dunlin in Bolinas Lagoon was examined during 1973-1975 (Stenzel *et al.* 1983). Polychaetes and crustaceans (mostly amphipods) had the highest percent occurrence of the prey taxa (93-96%, repectively), and bivalves (mostly *Nutricola*) were present in only 48% of the Dunlin stomachs sampled (*n* = 29; Figure 2). Beetles were present in more stomachs (35%) than were gastropods (3%). The number of hinges of *Nutricola* spp. was not reported in Stenzel *et al.* (1983).

The most notable difference between the 1973-76 and the 2000-01 Dunlin stomach samples was a change in the percent occurrence of bivalves and crustaceans. Percent occurrence of bivalves in the samples from the 1970's was significantly less than that in the 2000-01 samples (*P* = 0.004). Crustaceans were opposite to bivalves, and they occurred in a significantly lower proportion in the 2000-01 samples than in the earlier samples ($P = 0.02$).

Comparison of Green Crab and Dunlin Stomach Contents

Diets of freely foraging green crabs (Grosholz *et al.* 2000) and Dunlin in Bodega Harbor shared bivalves (primarily *Nutricola* spp.) and crustaceans (primarily amphipods), and less so polychaetes. The proportion of Dunlin stomachs containing bivalves and polychaetes was significantly greater than the proportion of green crab stomachs containing these same prey taxa (Figure 3; $P_{\text{Bivalve}} = 0.001$; $P_{\text{Polychaete}} < 0.0001$). The proportion of crustaceans I found in Dunlin stomachs (56%) pooled across 2000-01 was not significantly different from that reported in green crab stomachs (40%; $P = 0.23$) (Grosholz *et al.* 2000). Finally, beetles and gastropods were not specifically reported as green crab prey taxa in Bodega Harbor. However, green crabs may forage on gastropods when density of other prey taxa is low (Chapter 2).

DISCUSSION

The introduction of non-native invertebrates in coastal ecosystems has the potential to alter trophic interactions among organisms, particularly if invasive species are able to affect prey population and community dynamics through predation (Davis 2003) or competition (Byers 2000), or if they provide positive facilitation to other non-native species (Simberloff and Von Holle 1999, Grosholz 2005). The European green crab is a particularly interesting invasive species because it is a significant predator on molluscs (Ropes 1968), which are important prey for shorebirds (Piersma *et al.* 1993, Skagen and Oman 1996). The extent and strength of indirect effects of green crabs on shorebirds are relatively unknown. This study provides an initial examination of a shorebird's diet in a location where green crabs are known to have impacted shared prey (Bodega Harbor), and in a location where data on shorebird diets prior to the introduction of green crabs (Bolinas Lagoon) are available.

Green crabs invaded Bodega Harbor in 1993 and have had a significant negative effect on *Nutricola* spp. (Grosholz *et al.* 2000), which is a common prey item for Dunlin (Ruiz 1987, this study). In Bodega Harbor, density of large (>2mm) *Nutricola* has declined from 122 to 26/0.01m^2 since the crab's invasion (Grosholz *et al.* 2000). Data collected in 2001 indicate that *Nutricola* density can be depressed periodically to 7/0.01m^2 (Chapter 2). In Bolinas Lagoon, density of *Nutricola* spp. (~2/0.01m^2, sizes unknown) was low even before the green crab's invasion (these numbers in Bolinas Lagoon were last evaluated in the 1970's by Stenzel *et al.* 1983).

Given the significant decline in *Nutricola* spp. in Bodega Harbor after the introduction of the green crab, and the historic difference in *Nutricola* density between Bodega Harbor (high density) and Bolinas Lagoon (low density), I hypothesized that there would be no difference in percent occurrence of *Nutricola* in Dunlin stomachs currently between Bodega and Bolinas. I also hypothesized a large decline in percent occurrence of *Nutricola* over the period of the green crab's introduction in Bolinas. I confirmed no difference in Dunlin stomach contents (for all prey taxa) between Bodega and Bolinas currently, but there was a significant temporal change in Dunlin diet in Bolinas Lagoon. Bolinas Dunlin currently have a higher, not lower, percent occurrence of bivalves (mostly *Nutricola* spp.), and a lower percent occurrence of crustaceans in their stomachs in comparison to data in 1970's before green crabs arrived.

The smaller percent occurrence of crustaceans in the stomach samples of Dunlin from Bolinas is consistent with the direction of change we expected after the arrival of green crabs because this predator is known to forage on and reduce the density of crustaceans (Grosholz *et al.* 2000). However, the increase in *Nutricola* in Dunlin stomachs is not as we anticipated and requires further explanation. Because both sets of stomach samples in Bolinas (1970's and 2000's) were acquired with nearly the same size tube (~3mm), we know that the apparent increase in percent occurrence of bivalves means that more Dunlin have clams <3mm in their stomachs currently than in the 1970's. However, we do not know whether size distribution of *Nutricola* has changed in Bolinas Lagoon as it has in Bodega Harbor. In Bodega, the change in size distribution toward more smaller *Nutricola* is linked to green crab predation effects (Grosholz *et al.* 2000), but in Bolinas, if there has been a decline in density of *Nutricola*, the cause could either be due to green crabs or some other environmental effect.

Green crabs may affect the size class of *Nutricola* consumed by Dunlin when *Nutricola* density is low, but this effect also appears to be related to crab density (Chapter 2). In Chapter 2 we saw some evidence that green crabs may facilitate Dunlin consumption of small (<2mm) *Nutricola* when crabs occur in high density, however there is no data to suggest that green crab density is high in Bolinas Lagoon. Measures of relative abundance between the two sites indicate that there are fewer green crabs in Bolinas than Bodega (Grosholz and Ruiz 1995 and Estelle, *unpub. data*). The mechanism by which a higher percent of Dunlin sampled have *Nutricola* in their stomachs remains unknown. A measure of change and annual variability in prey density and size classes of prey (esp. *Nutricola* and crustaceans) as well as green crab density would improve our ability to interpret whether the dietary change in Dunlin in Bolinas Lagoon is related to the introduction of green crabs or not.

Prior to arrival of green crabs in the area there was a pattern of difference in diet composition of Dunlin between sites, but his study indicates currently there is no statistical difference between sites. Wintering Dunlin in Bolinas Lagoon, where bivalve density was low compared to Bodega Harbor (Stenzel *et al.* 1983 vs. Ruiz 1987), primarily consumed polychaetes and amphipods, not bivalves. In Bodega Harbor, where bivalve density was high, they primarily consumed bivalves (*Nutricola* spp.), not amphipods or polychaetes. From these observations prior to green crab arrival, it appeared that diets between Bolinas and Bodega were different. The observed differences prior to the arrival of the crab, whether significant or not, were probably related to differences in composition of the invertebrate prey base between locations. Currently, however, Dunlin diets in Bolinas Lagoon and Bodega Harbor are no different in the percent occurrence of the various prey taxa examined in this study.

We were surprised to find that the percent of Dunlin with bivalves in their stomach was still high at Bodega Harbor despite significant declines in *Nutricola* density following the introduction of green crabs. This suggests that even when density of large *Nutricola* is low, Dunlin are still able to forage on this species. Data from an exclosure experiment (Chapter 2) suggest this may be possible because Dunlin can take any size class of *Nutricola* that is available, whereas green crabs preferentially forage on *Nutricola* >2mm (Grosholz and Ruiz 1995), leaving the smaller ones behind. However, the number of bivalves in Dunlin stomachs in Bodega Harbor currently appeared to be far less than when Ruiz (1987) sampled. He found on average 95 *Nutricola* per stomach with a minimum of 26 and a maximum of 213. We found at most 7 *Nutricola* in Dunlin stomachs in Bodega Harbor, and these were < 3.3 mm, as dictated by our stomach sampling device. No size measurements for *Nutricola* spp. are available from the Ruiz (1987) data.

The diet of Dunlin in this area of central California appears to be diverse and variable. At the same time, results from this study combined with that from a predation experiment (Dunlin and green crabs) in Bodega Harbor (Chapter 2) suggest that the introduction of the green crab may be responsible for a dietary change in Dunlin. This change is manifested as fewer Dunlin stomach samples containing *Nutricola* of a small size in Bodega Harbor, and more Dunlin samples with *Nutricola* of a small size in their stomachs in Bolinas. Unlike the variability in Dunlin diets prior to the invasion of the green crab when the possibility of all taxa and all size classes was present, green crabs may have permanently altered the bivalve component of the Dunlin diet today because larger *Nutricola* are no longer present in large densities (see Grosholz 2005). If Dunlin are spending time foraging on small *Nutricola* that green crabs do not eat, this may come at an energetic cost to the birds, and it may lead to additional negative effects on *Nutricola* spp. An investigation of the energetics and winter body condition or survival rates of Dunlin under various diets should be a research priority.

As exotic species invasions in coastal ecosystems continue to increase, the implications of possible changes in the abundance and diversity of prey species on local to regional scales will be of greater interest. The methods of diet estimation used in this study are an efficient and non-lethal approach to assessing changes in diet over time. The approach allowed us to infer, generally, that Dunlin diets are compositionally similar to those prior to the green crab invasion, but, with regard to individual taxa, diets appear to have changed in some substantive ways (e.g., size of prey, numbers of individuals taken). Our conclusions required that we have access to current as well as prior information on invertebrate populations and prior shorebird diets (Stenzel *et al.* 1983, Ruiz 1987, Grosholz *et al.* 2000, Chapter 2). To further test the observations and conclusion we have made, an important step would be a standard method of quantifying prey taxa in shorebird stomachs. Since *Nutricola* and crustaceans appear to be the taxa changing most obviously in abundance, size, and percent occurrence in Dunlin stomach contents, these would be the obvious taxa to quantify. Bivalves may be easier than crustaceans to quantify. A sampling bias for prey items <3.3mm will always be present with the necessary non-lethal stomach pumping procedures described herein.

Our understanding of multi-trophic effects in marine ecosystems would be increased by evaluating shorebird body condition as a function of diet mediated by non-native invertebrates. Changes in either the size class or the prey taxa consumed by shorebirds could be driven by competition with a non-native species or by non-native invertebrates directly or indirectly affecting native invertebrates. In contrast, the invasion into some systems by non-native invertebrates may have positive, short-term effects. For example, *Potamocorbula amurensis* (clam) and *Mytilus galloprovincialis* (mussel) that some ducks and shorebirds prey upon have occurred in such high densities that they have increased the winter forage available to scaups (Richman and Lovvorn 2004) and breeding success for oystercatchers (Hockey and Schurink 1992). In the case of the ducks, however, the non-native clam that they consumed in large abundance also accumulated a high amount of heavy metals, something that did not occur from the consumption of native clams.

In Bodega Harbor, it appears that green crabs have facilitated an increase in abundance and consequent spread of *G. gemma*, another non-native venerid clam that has been present since the 1920's (Grosholz 2005). *G. gemma* appears similar to *Nutricola* in size (<2mm – 8mm) and availability (also a surface dweller). On the East coast, where the clam is native, Schneider and Harrington (1981) found that many species of shorebirds consume large numbers of *Gemma*, but the shorebirds do not appear to digest them readily. Schneider and Harrington (1981) speculated that *Gemma* may have a thicker shell than other venerid clams and that this might prevent efficient digestion by shorebirds. If *G. gemma* population increases are leading to a decline in *Nutricola* populations in Bodega Harbor (Grosholz 2005), it will be important to monitor shorebird diets in this harbor and to examine *Nutricola* population effects on shorebird body condition and survival rates.

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TABLE 1. List of taxa found in Dunlin stomachs in Bodega Harbor and Bolinas Lagoons during 2000 and 2001.

Phylum Annelida,
Class Polychaeta:
Lumbreneridae
    (possibly *Lumbrineris zonata*)
Spionidae
Polydora nuchalis
Polydora socialis
Pseudopolydora kempi (**non-native; introduced with Japanese oysters***)
Boccardia proboscidea
    Nereidae
Platynereis bicanaiculata
Syllidae
    Exogone sp.
Capitellidae
    Capitella capitata
    (possibly *Mediomastus californiensis* and *Notomastus magnus*)
Phylum Mollusca,
Class Bivalvia:
Veneridae
Nutricola spp. (*tantilla* and *confusa*, possibly *lordi*)
Gemma gemma (**non-native; introduced from Atlantic***)
Mytilidae
    Unidentified Mytilidae
Class Gastropoda:
Lacunidae
Lacuna marmorata
Unidentified Gastropoda
Phylum Arthropoda,
Class Crustacea:
Order Amphipoda:
Gammaridea
Allorchestes angustus
Unidentified Corrophiidae
Grandidierella japonica (**non-native; introduced from Japan***)
Order Malacostraca:
Cumacea
Cumacea vulgaris
Order Decapoda:
Unidentified Decapoda
Order Ostracoda:
    Unidentified Ostracoda
Other:
foraminifera, diatoms, nematodes, oligochaetes, beetles, pieces of algae, plastic fibers, styrofoam bits, and pebbles.

(* Smith and Carlton 1975)

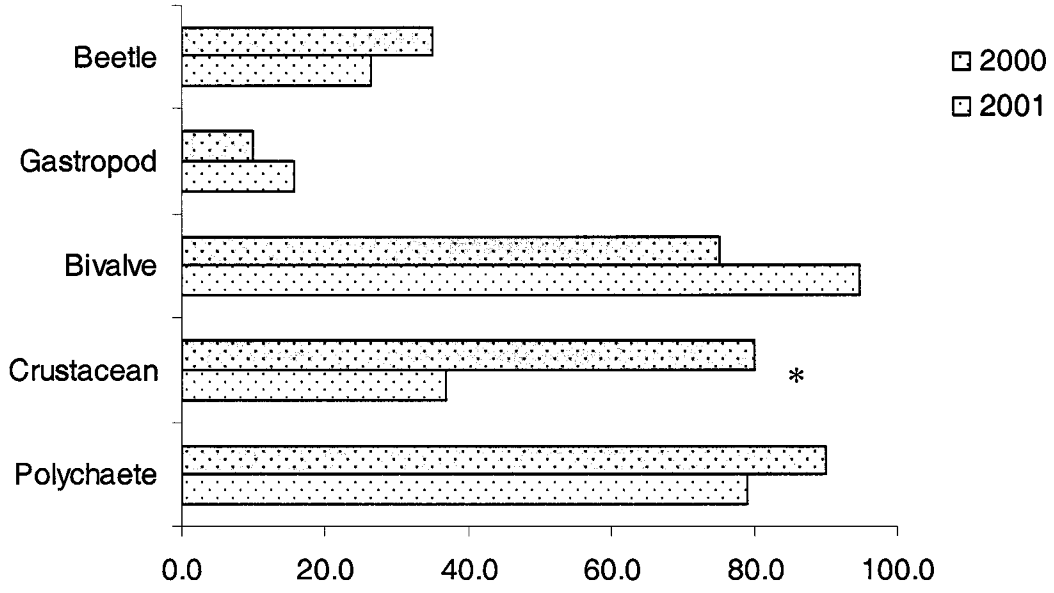
TABLE 2. Diet of shorebirds in Bodega Harbor in 1985-1986 (borrowed from Ruiz 1987[1]).

Species	N	% with *Nutricola* spp.	Mean no. *Nutricola*/stomach	SD	Range
BBPL	2	100	42.0	4.2	39-45
DUNL	10	100	95.5	75.1	26-213
SPPL	6	83	9.1	15.8	0-41
WILL	8	88	92.4	101.7	0-254
WESA	9	78	14.4	20.0	0-54

BBPL = Black-bellied Plover, DUNL = Dunlin, SPPL = Semi-palmated Plover, WILL = Willet, WESA = Western Sandpiper.

1 Another invertebrate found in Dunlin stomachs by Ruiz (1987) was identified as *Nereis diversicolor* (a polychaete). This is likely a misidentification and was probably *Neanthes limnicola (*Smith and Carlton 1975*). N. diversicolor* is a European species not known in Bodega Harbor or the West Coast. Ruiz did not mention any other invertebrates identified in Dunlin stomachs, but did indicate that *Nutricola* and the polychaete were dominant.

a) Bodega



b) Bolinas

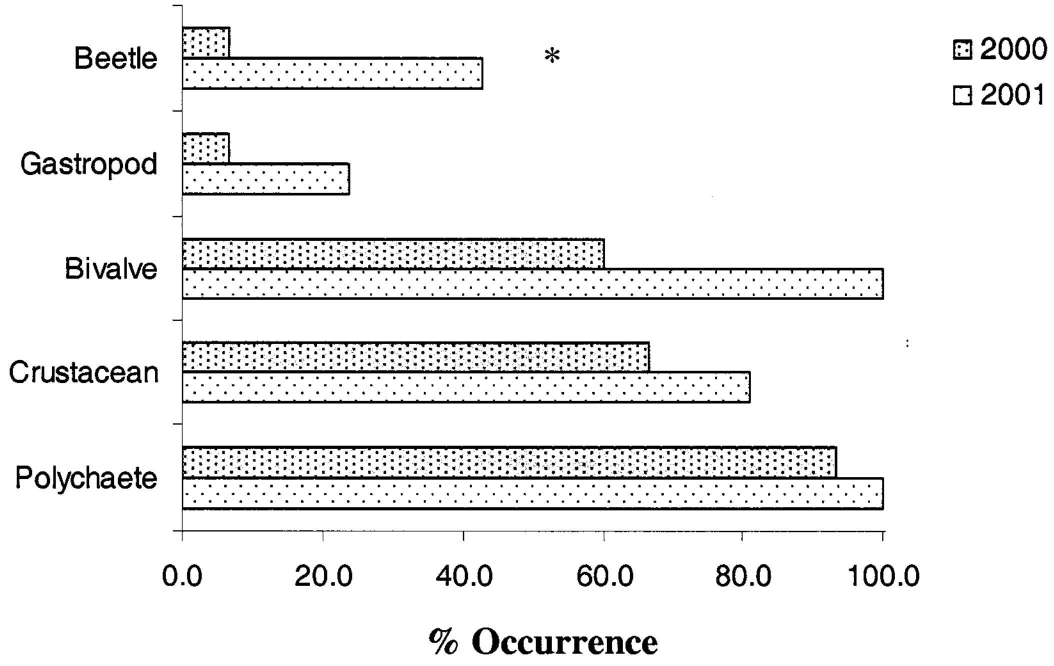


Figure 1. Comparison of % occurrence of prey taxa in wintering Dunlin stomachs between years in a) Bodega Harbor (*P = 0.02, n_{2000} = 20, n_{2001} = 19) and b) Bolinas Lagoon (*P = 0.05, n_{2000} = 15, n_{2001} = 21).

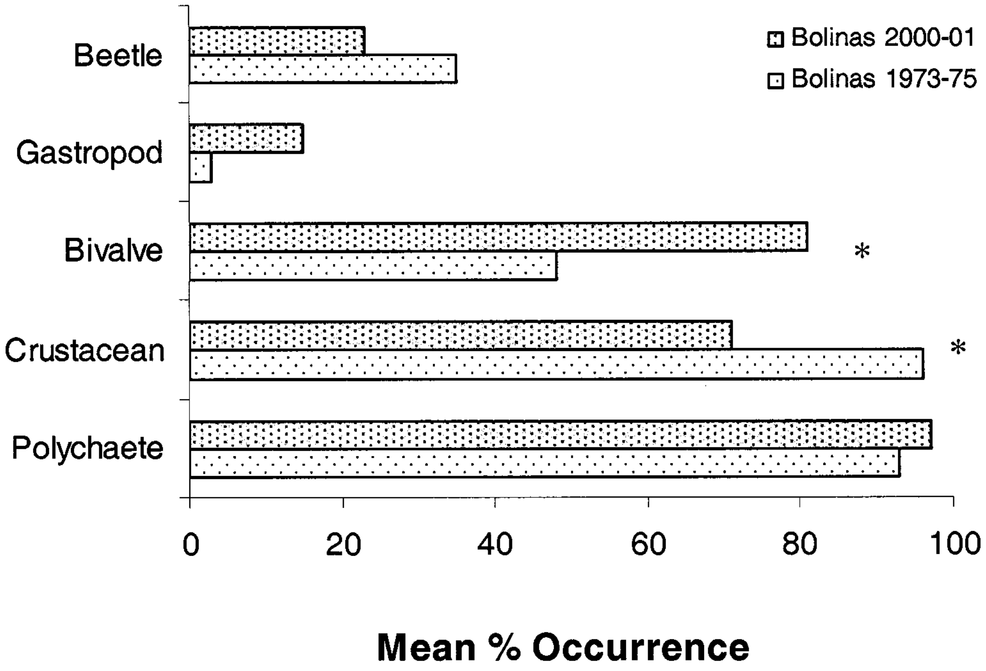


Figure 2. Mean percent occurrence of prey taxa in wintering Dunlin stomachs in Bolinas Lagoon. Comparison of data from Bolinas Lagoon 2000-02 (average %; *n* = 36) with 1973-75 (average %; *n* = 29). (*$P_{\text{Bivalve}} = 0.004$, *n* = 65 and *$P_{\text{Crustacean}} = 0.02$, *n* = 65)

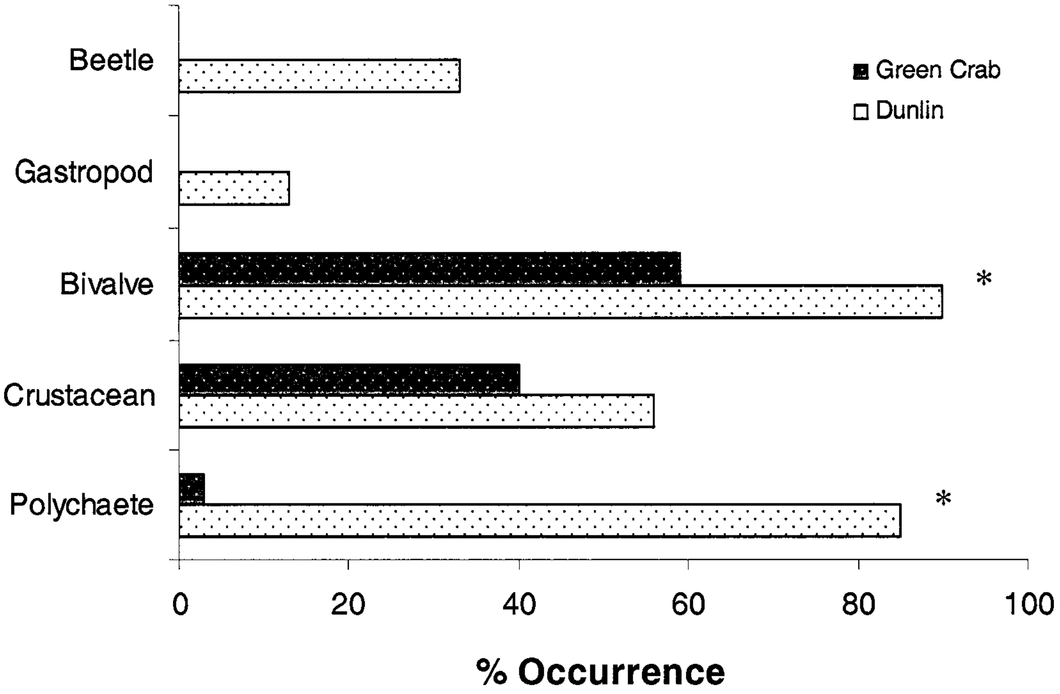


Figure 3. Percent occurrence of selected invertebrate taxa in Dunlin (*n* = 39) and green crabs in Bodega Harbor. Dunlin and green crab samples were acquired from actively foraging individuals. Data for green crab stomach contents (*n* = 30) from Grosholz *et al.* (2000). ($^*P_{Bivalve} = 0.001$, $n = 69$; $^*P_{Polychaete} < 0.0001$, $n = 69$).