THE POTENTIAL SYNERGISTIC EFFECTS OF CLIMATE CHANGE AND FISHING PRESSURE ON EXPLOITED INVERTEBRATES ON ROCKY INTERTIDAL SHORES

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ABSTRACT

Climate change and fishing are both major determinants of the distribution and abundance of marine species. As the rates of climate change and exploitation accelerate, additive and synergistic interactions between them are becoming increasingly important to the dynamics of marine ecosystems and the sustainability of marine fisheries. We examine the impacts of climate change and fishing pressure on the stocks of three commonly exploited intertidal invertebrates on Northeast Pacific rocky shores. California sea mussels (*Mytilus californianus*) are not likely to experience dramatic population shifts in the face of climate change, and the current low levels of exploitation appear to be sustainable. Owl limpets (*Lottia gigantea*), which grow more slowly, exhibit higher temperature sensitivity, and are preferred targets of fishers, will likely experience considerable reductions in distribution and abundance if temperatures rise and exploitation continues. Black abalone (*Haliotis cracherodii*) have already experienced dramatic declines directly attributable to over-exploitation and indirectly to warming trends that have exacerbated the effects of a devastating disease. Two generalities emerge from these comparisons. First, differences in life history characteristics result in a wide range of climatic and anthropogenic effects among species. Second, the effects of fishing pressure may unexpectedly magnify the effects of climate change, and vice versa. Synergistic interactions between environmental change and exploitation on rocky shores and in other marine ecosystems present considerable challenges for fisheries managers. The key to successful management and restoration in marine systems lies in developing a mechanistic understanding of the interactions between climate change and fishing pressure and how they affect population and ecosystem dynamics.

INTRODUCTION

Climate change and fishing are expected to be dominant drivers of future trends at the population, community, and ecosystem level in marine systems, from tropical coral reefs to polar seas to the deep-sea benthos (McClanahan 2002; Clarke and Harris 2003; Glover and Smith 2003). Although relationships between marine ecosystem dynamics and both climate (Glantz 1992; Beamish 1995; Roemmich and McGowan 1995; Francis et al. 1998) and fishing (Dayton et al. 1998; Pauly et al. 2002; Jackson et al 2001; Botsford et al. 1997; Chavez et al. 2003) are well-known, rarely are fishing and climate change considered together. Indeed, climatic variability is not incorporated into most fisheries management schemes (but see Conser et al. 2001). While more is being learned about how climate change affects fished populations (Glantz 1992; Beamish 1995; Finney et al. 2000; Bjørnstad and Grenfell 2001; McGinn 2002), our understanding of the interactions between exploitation and changing environmental conditions remains poor.

Climate change and fishing can interact in ways that are additive or synergistic (fig. 1). Additive effects occur when environmental conditions and fishing each reduce stock abundance in ways that are independent of one another. When effects are additive, a 20% stock reduction due to environmental impacts and a 50% reduction due to fishing would result in a 70% reduction in stock size (fig. 1A). By comparison, synergistic interactions generate effects that are greater than the sum of their parts, such as when one forcing agent exacerbates the effect of another, or when the combined influence of both factors pushes a population past a threshold abundance level. In these cases, the 20% reduction due to climate and the 50% reduction due to exploitation result in a >70% reduction in stock size (fig. 1B). Although progress is being made (e.g., Jurado-Molina and Livingston 2002), we still know very little about how fishing interacting with climate change affects marine populations, particularly when interactions are synergistic. In most cases, we lack sufficient data to properly address these types of questions (but see Jacobson and MacCall 1995; Hobday and Tegner 2002; Jurado-Molina and Livingston 2002).

Rocky intertidal shores provide a model system for examining the effects of climate change, fishing, and their interactions. Climate change may have substantial direct impacts on intertidal species, many of which live close to their environmental tolerances (Tomanek and Helmuth 2002), and climatically forced changes in the distribution and abundance of intertidal species are well documented (Barry et al. 1995; Southward et al. 1995). Fishing pressure on rocky shores is high in most parts of
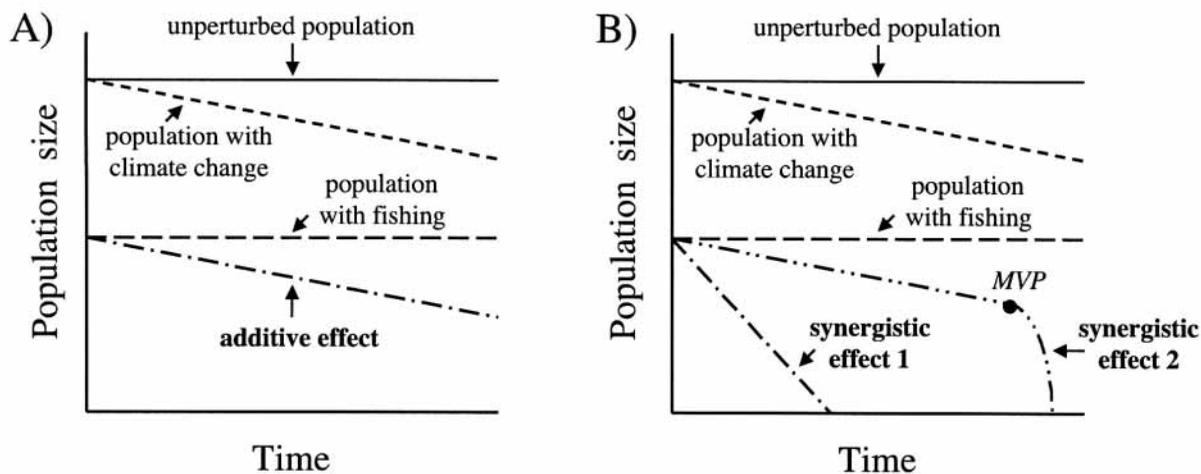
Figure 1.   Additive versus synergistic effects of climate change and exploitation. *A*, The effect of fixed-quota fishing pressure (assuming constant environmental conditions) and monotonic climate change (assuming no fishing). Lower line represents additive effects, which are the sum of fishing and climatically induced reductions in population size. *B*, As in A, except the effects of fishing and climate change are nonadditive. Synergistic effect 1 can arise if fishing pressure increases the vulnerability of the population to climate change, or vice versa. Synergistic effect 2 can arise if the combined impacts of fishing and climate change push the stock below a threshold that would not be reached by climatic or fishing impacts acting in isolation. In the case illustrated here, the population declines below the minimum viable population size (*MVP*) and cannot recover.

the world, with important consequences for intertidal communities (for review, see Thompson et al. 2002). Anthropogenic climate change coupled with rapidly expanding coastal human populations has the potential to intensify both direct and indirect effects in the future and increases the probability of important synergisms between climatic variability and fishing.

In this article, we examine the relationships between environmental change and fishing on rocky shores in the Northeast Pacific, with specific reference to California (fig. 2). First, we summarize past and future climatic trends, as well as observed and predicted biological responses. Then, we examine the effects of climate change and fishing on three exploited intertidal invertebrates: the California sea mussel (*Mytilus californianus* Conrad), the owl limpet (*Lottia gigantea* Sowerby), and the black abalone (*Haliotis cracherodii* Leach). We use these case studies to demonstrate the general importance of climate-exploitation synergisms as well as the life-history characteristics that make an exploited species particularly vulnerable to synergistic effects. Finally, we discuss the importance of incorporating climatic variability into fisheries management strategies.

CLIMATE CHANGE AND INTERTIDAL ECOSYSTEMS

Environmental Change

A dramatic warming trend associated with greenhouse gas emissions is expected to be the dominant feature of environmental change over the next 100 years (IPCC 2001). Although this trend has already been detected, it is superimposed on natural environmental variability across a range of temporal scales. Natural environmental
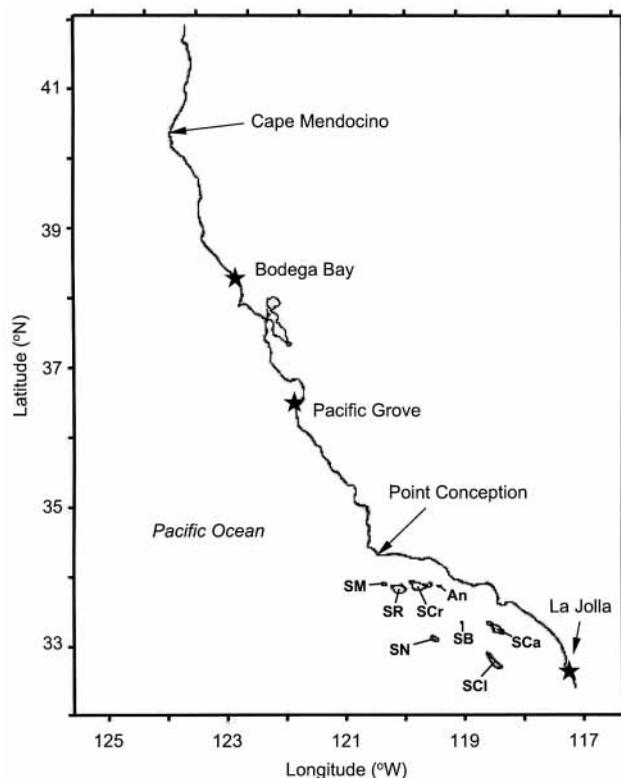

Figure 2.   Map of the California coast. Stars indicate coastal sea-surface temperature recording stations. The Channel Islands, identified by letter codes, are San Miguel Island (SM), Santa Rosa Island (SR), Santa Cruz Island (SCr), Anacapa Island (An), San Nicolas Island (SN), Santa Barbara Island (SB), Santa Catalina Island (SCa), and San Clemente Island (SCl).

variation includes low-frequency 60–80 year oscillations (Ware and Thomson 2000), interdecadal oscillations (20–40 years) such as the Pacific Decadal Oscillation (Mantua et al. 1997), 18.6 year oscillations in the timing
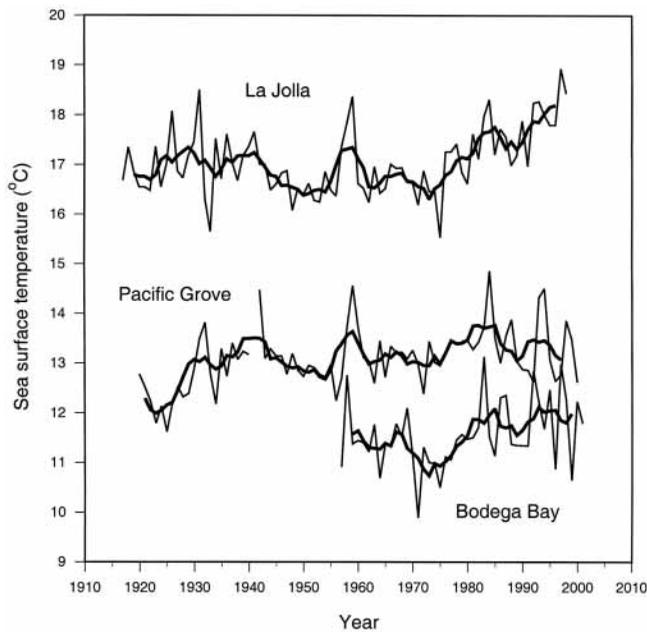
Figure 3. Nearshore sea-surface temperature records for three sites along the California coast: Scripps Institution of Oceanography, La Jolla; Hopkins Marine Station, Pacific Grove; and Bodega Marine Laboratory, Bodega Bay (see fig. 2 for map). Thin lines are annual means. Heavy lines are 5-year running means.

and duration of tidal emersion (Denny and Paine 1998; Helmuth et al. 2002), and high-frequency interannual oscillations such as El Niño Southern Oscillation events (Jones et al. 2001). These oscillations provide natural "experiments" that can serve as proxies for studying the impacts of long-term, nonoscillatory trends such as those predicted by anthropogenic warming scenarios (IPCC 2001).

Long-term changes have now been documented for many environmental variables in the Northeast Pacific. Instrumental sea-surface temperature records indicate both periodicity and general warming trends in California (fig. 3). Mean air temperatures near the northern California coast increased by more than 1.1°C in the past 50 years, although most of this trend is due to warmer temperatures at night (Nemani et al. 2001). An increase in El Niño frequency has been documented (Jones et al. 2001), as has an increase in winter storm frequency (Bromirski et al. 2003).

Climatologists provide several "high-confidence" predictions for future environmental trends (IPCC 2001). Sea level is predicted to rise approximately 30–50 cm over the next 100 years. Air and sea-surface temperatures will continue to increase at the global scale, although local trends along the coast will depend on additional factors such as upwelling and fog. Increased land-sea thermal gradients are expected to increase wind stress, which may in turn result in enhanced upwelling

and increased storminess. Other aspects of oceanic circulation (e.g., California Current advection) and chemistry (e.g., pH) are likely to change in the future (IPCC 2001), but the nature and impacts of these trends are more difficult to forecast and will not be considered here.

Intertidal Responses to Climate Change

Rocky intertidal assemblages, by virtue of their straddling the interface between the marine and terrestrial realms, respond to changes in both oceanic and atmospheric conditions. Intertidal sampling in the 1930s and 1990s in Pacific Grove, California, revealed an increase in the abundance of southern invertebrate species and a concomitant decrease in the abundance of northern invertebrate species—a change attributed to increasing sea-surface temperature (Barry et al. 1995; for a British example, see Southward et al. 1995). Although intertidal populations are expected to keep pace with sea-level rise, warming air temperatures may compress vertical zonation patterns. A comparison of algal upper limits in the Gulf of Maine between 1928 and 1996 revealed that many species had shifted downwards on the shore while none had shifted upwards, which may have been a response to increasing air temperatures in the region (Mathieson et al. 1998). Compressed zonation may result in local extinctions if species are "squeezed out" in an ever-narrowing band of habitable shoreline. This squeeze effect is thought to set the local and regional distributional limits of a turf-forming algae in Washington (Harley 2003) and a barnacle in New England (Wethey 1983). Latitudinal range changes have been documented for intertidal species (e.g., Southward et al. 1995; Connolly and Roughgarden 1998), and many such range shifts are correlated with warming temperatures. Range shifts have also been documented for subtidal invertebrates in response to changes in temperature and/or larval transport (e.g., Zacherl et al. 2003; L. Rogers-Bennett, unpub. data). Poleward range shifts now appear to be a general response to warming at the global scale (Parmesan and Yohe 2003).

CLIMATE CHANGE AND EXPLOITED INVERTEBRATES

Case Study 1: Sea Mussels

Life History. The California sea mussel, *Mytilus californianus*, is a dominant rocky-shore species that forms extensive mid-intertidal and occasionally subtidal beds from Alaska to southern Baja California, Mexico (Suchanek 1985). Individuals grow rapidly and can attain sizes up to 15 cm in as little as 3 years. Sea mussels typically form a mosaic of mature, often multilayered beds interspersed with disturbance patches of various sizes, ages, and stages of recovery. The primary agents
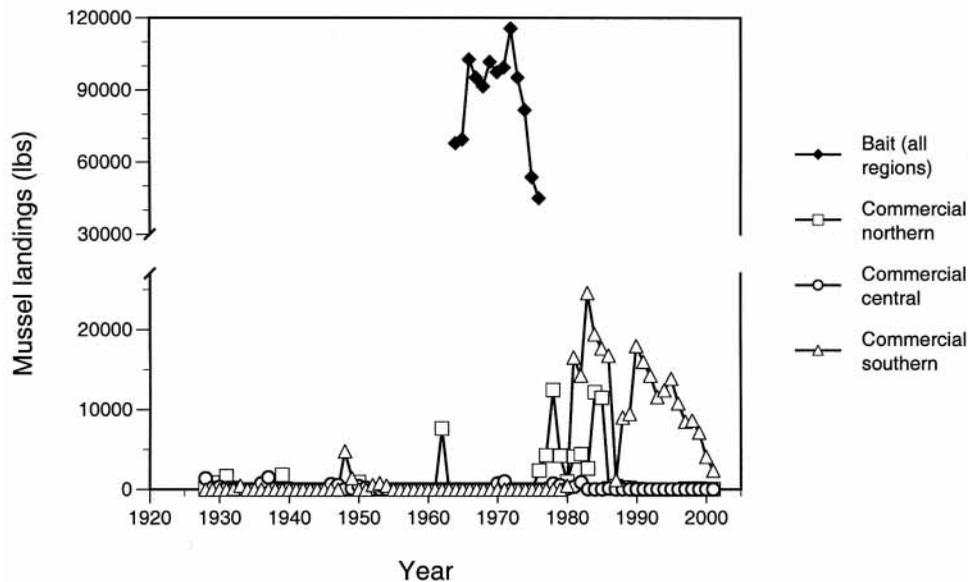
Figure 4. Mussel (*Mytilus* spp.) landings in California. Open symbols are commercial landings, divided into northern (Eureka and San Francisco), central (Monterey), and southern (Santa Barbara, Los Angeles, and San Diego) regions. Solid symbols are bait landings. Because 99.7% of the mussels in this category were landed at Los Angeles and San Diego, the data were not subdivided by region. Commercial landings data were obtained from the Pacific Fisheries Environmental Laboratory. Bait landings data were obtained from California Department of Fish and Game Fish Bulletins and were only available from 1964 to 1976. Note the change in *y*-axis scaling above the axis break.

of gap formation are hydrodynamic forces during storms and wave-born debris such as drift logs (Dayton 1971; Denny 1987). Rates of patch recovery are generally fastest in the low intertidal and at wave-exposed sites (Seed and Suchanek 1992). Depending on local conditions and larval supply, patch recovery may require a few years to several decades (Paine and Levin 1981; Seed and Suchanek 1992).

Sea mussels play an important role in structuring intertidal communities. Sea mussels are dominant competitors for space and can competitively exclude other large benthic organisms such as kelps and barnacles that require primary space for attachment (Paine 1966). However, mussel beds also provide biogenic habitat for several hundred species of algae and small-bodied invertebrates (Suchanek 1992). Finally, sea mussels provide an important trophic link in intertidal food webs; mussels are consumed by whelks, crabs, lobsters, sea stars, fish, shore birds, and sea otters (Seed and Suchanek 1992). The sea star *Pisaster ochraceus* is a particularly important mussel predator; *Pisaster* predation determines the position of the mussel bed's lower limit (Paine 1966).

Fishing History. Humans have exploited *Mytilus californianus* along the California coast for many thousands of years (Erlandson et al. 1999). In the early decades of the twentieth century, an average of 47,000 pounds of mussels (*Mytilus* spp.) were fished per year until 1927 when a major outbreak of paralytic shellfish poisoning occurred (Richards and Trevelyan 2001). After that, landings declined dramatically and remained low for several

decades. Extensive commercial efforts resumed in the late 1970s but have declined recently (fig. 4). However, landings for bait, for the years in which data are available, far outweighed these commercial landings. Unfortunately, reliable landings data for *M. californianus* are lacking, as commercial records do not distinguish between *M. californianus*, *M. trossulus*, and *M. galloprovincialis*. Recreational landings of mussels, while probably substantial, are not required to be reported in California.

Today, both commercial and recreational mussel collection is legal outside of parks and reserves. Although *M. californianus* is currently of minor economic importance in California, it is still recreationally fished (10 lb bag limit) for bait and, less frequently, for human consumption (Richards and Trevelyan 2001). Unlike the congeneric *M. galloprovincialis*, *M. californianus* is not currently a target species for the California aquaculture industry (Richards and Trevelyan 2001). Commercial fishing of sea mussels occurs in Oregon, and a commercial fishery has been proposed in British Columbia. These more northerly fisheries and the markets they serve may increase the demand for commercially fished sea mussels from California.

Effects of Climate Change. Climate change may affect *Mytilus* populations through a variety of pathways. Individual growth rates in mytilid mussels are positively correlated with water temperature until some threshold is surpassed, at which point growth rates decline abruptly (Seed and Suchanek 1992). Thus, climate change may increase the growth and age-specific fecundity of this

species at the local scale, provided that temperatures do not become extreme. Sublethal stress (Roberts et al. 1997) and even significant mortality (C. Harley, unpub. data) have been observed following spells of hot weather. However, increasing air temperatures may or may not lead to shifts in the vertical range of mussel beds. The upper limit of the mussel bed at one wave-exposed site (Tatoosh Island, Washington) is correlated with emersion time, not thermal stress (Harley and Helmuth 2003). Increasing winter storminess will likely increase rates of disturbance in sea mussel beds and may thus reduce overall population abundance. Finally, although larval recruitment patterns are heavily influenced by patterns of nearshore oceanography, future patterns of larval transport are difficult to forecast.

Climate change is also likely to impact mussel distributions indirectly through the effects of interacting species. The abundance and per capita consumption rate of the predatory sea star, *Pisaster ochraceus*, are both positively correlated with water temperature in short-term (2–6 week) experiments (Sanford 1999). Thus, warming sea-surface temperatures may compress the vertical zone occupied by mussels from below as a result of increased predation pressure. Pisaster do not appear to be negatively influenced by temporal trends in air temperature (Sanford 2002), suggesting that the vertical extent of *Pisaster* foraging will not be influenced by climatic warming. *M. californianus* is also affected by an array of diseases and parasites that can cause mortality or sterility (Bower 1992), but the role of temperature in influencing host-parasite relationships in sea mussels is largely unknown.

Implications for Mussel Populations. Increased frequency and severity of storms and thermal stress events are likely to become increasingly important sources of mussel mortality. If harvesters only remove mussels from the surface layer of the bed, the effects of harvest and hydrodynamic disturbance (which removes all mussels from a patch) are likely to be additive (i.e., neither factor will increase rates of mortality due to the other). Thermal stress typically only kills mussels in the surface layer of multilayered beds (C. Harley, unpub. data). Thus, thermal stress events or surface-layer harvesters operating in isolation will not result in the complete removal of a patch of mussels. However, if fishers remove the top layer of mussels, and the bottom layer is subsequently killed during a heat wave, no mussels will remain as a recruitment surface and nursery habitat for young conspecifics. Because gaps in the mussel bed take longer to recover than areas in which only the superficial layers have been removed, the effects of fishing and climate in this scenario are synergistic (see effect 1 in fig. 1B).

Indirect climatic effects mediated by other species may lead to substantial changes in mussel populations.

Increasing water temperatures may increase sea star predation rates (Sanford 1999), thereby removing the largest, most fecund mussels along the lower limit of the bed. Furthermore, by raising the lower limit of the mussel bed, *Pisaster* would redirect fishing pressure to higher shore levels. Because higher shore levels take longer to recover from disturbance (Seed and Suchanek 1992), elevated *Pisaster* predation could magnify the impact of a fixed level of human exploitation. Conversely, climate change may indirectly enhance mussel populations by reducing the season during which mussels are fit for human consumption. In California, a ban on the recreational fishing of mussels is already imposed from May 1 to October 1 when mussels are most likely to ingest and concentrate toxins associated with harmful algal blooms (HABs). HABs tend to occur during warmer water conditions, and climate change has been suggested as the mechanism underlying recent observed increases in HABs (Mudie et al. 2002). Thus, the seasonal ban on mussel collecting may need to be extended if warm-water events begin to occur earlier in the spring and later in the fall, which would in turn reduce the impact of the fishery on mussel populations.

Although the scenarios outlined above may change the spatial and temporal availability of edible mussels, it would appear that sea mussel populations in general (and the bait fishery they support) are not in danger of decline. This conclusion, however, would need to be reevaluated if fishing pressure increased with, for example, the resumption of extensive commercial fishing operations. In the face of increasing fishing pressure, certain regulations should be instituted to ensure the sustainability of the resource, including hand-picking (as opposed to raking), leaving at least the bottom layer of mussels intact, and focusing collecting activities in the low intertidal and at exposed sites, which experience more rapid rates of recovery (Behrens Yamada and Peters 1988; Paine 1989).

Case Study 2: Owl Limpets

Life History. The owl limpet (*Lottia gigantea*) occupies exposed rocky shores from Crescent City, California, to Baja California, Mexico, although the species is most abundant south of San Francisco (P. Fenberg, pers. comm.). *L. gigantea* is the largest limpet on the west coast of North America, reaching lengths up to 10 cm and living for 15 years or more (Morris et al. 1980; Lindberg et al. 1998). Owl limpets are sequential protandric hermaphrodites, changing sex from male to female as they grow older and larger (Wright and Lindberg 1982). Female gonad mass, and presumably fecundity, increases exponentially with size (Kido and Murray 2003).

Owl limpets are territorial grazers, and can exclude many species of plants and animals through consumption, bulldozing, or harassment (Stimson 1970; Lindberg
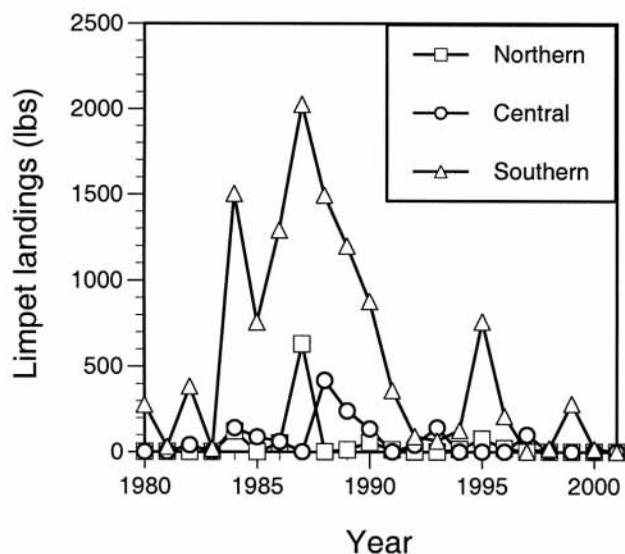
Figure 5. Commercial limpet landings (all species). Northern, central, and southern designations as in fig. 4. Data were obtained from the Pacific Fisheries Environmental Laboratory.

et al. 1998). Owl limpets "garden" their territories, maintaining a high biomass of microalgal biofilm relative to nongardened areas. The main predators of owl limpets are shorebirds and humans (Lindberg et al. 1987; Pombo and Escofet 1996; Lindberg et al. 1998; Kido and Murray 2003).

Fishing History. Limpets were historically fished by coastal Native Americans and have been fished recreationally and commercially in recent times. Commercial limpet fishing in California peaked in the mid to late 1980s, and has declined thereafter (fig. 5) due to a lack of market demand (I. Taniguchi, pers. comm.). Although the limpets, like mussels, were not identified to species in landing records, it is likely that the large individual size of owl limpets has made them the primary target of the limpet fishery. Owl limpets have been protected from commercial fishing in California since 1999. Sport fishing (35-limpet bag limit) is legal outside of state and national parks and other marine protected areas.

Artisanal fishing has reduced owl limpet population size and mean individual size along accessible shorelines in Mexico (Pombo and Escofet 1996). Recreational fishing (for food and occasionally for bait) is poorly documented in California, but indirect evidence suggests that it is substantial. Limpet shell lengths are negatively correlated with site accessibility and with the number of human collectors per unit shoreline in Orange County (Kido and Murray 2003). The mean size of adult owl limpets in southern California has declined significantly by approximately 6% over the past 150 years in all sampled areas except for a tightly regulated marine reserve, suggesting that human take has been influencing owl

limpet populations for some time (Roy et al. 2003). Even reserves are vulnerable; poaching in central and southern California can remove hundreds of owl limpets in a single low tide (Lindberg et al. 1998).

Effect of Climate Change. Unlike sea mussels, owl limpets are likely to suffer severe stress in the face of increasing air temperatures. Owl limpet mortality has been observed following extended spells of hot, calm weather in Pacific Grove (C. Harley, per. observ.), and the upper distributional limit of owl limpets at this site is negatively correlated with temperature (Harley and Denny, unpub. data). Increasing air temperatures are therefore likely to force the upper limit of this species downwards through time. Thermal impacts may be most severe for small limpets, which have less visceral and extravisceral water available for evaporative cooling and higher rates of water loss due to a larger surface area to volume (and circumference to volume) ratio (Branch 1985). Increased storminess is unlikely to impact owl limpet populations, as hydrodynamic forces do not appear to be an important source of owl limpet mortality (Denny and Blanchette 2000).

Relationships with other species are likely to shift. Although changes in limpet food resources may occur, the precise nature of these changes is poorly understood. Perhaps more important will be the barrier to downshore migration represented by the mussel bed. Owl limpets require primary space to graze, and compete with mussels for this space (Stimson 1970). If the upper limit of the mussel bed is set by emersion time, it may remain relatively constant even as increasing thermal stress drives limpet distributions downshore. Because owl limpets are territorial and intraspecific competition is fierce, a reduction in habitable shoreline may lead to a reduction in owl limpet numbers. Declining densities and increased fragmentation of local populations could trigger further population declines by reducing fertilization success.

Owl limpet populations may be most severely impacted by climatic warming in the southern portions of their range, where thermal stress is already high. The degree to which declines of owl limpet populations at southern sites will be balanced by population increases at northern sites remains unknown. The northern range limit of owl limpets may be defined by patterns of larval transport, rather than temperature, as has been proposed for another high intertidal limpet (*Collisella scabra*) found along the California coast (Gilman 2003). If this scenario holds true for owl limpets, rising temperatures may result in both vertical and latitudinal range contractions.

Implications for Owl Limpet Populations. If fishing effort does not decrease in the coming decades, climate change will focus fishers on fewer and smaller local owl limpet populations, resulting in important additive effects.

However, it is likely that the effects of fishing will exacerbate the effects of climate change on *L. gigantea* in a synergistic fashion. Future increases in the frequency of high-temperature extremes may disproportionately affect smaller limpets, which have a limited capacity for evaporative cooling (Branch 1985). From the population perspective, this will increase the relative importance of reproductive output by large individuals that have reached a size refuge from brief temperature spikes. However, these large individuals will be the primary targets of human collectors. In addition to reducing population-level reproductive output, the removal of large individuals may further decrease the success of climatically impacted smaller size classes, which rely to some extent on raiding the gardened territories of larger limpets (Shanks 2003). Finally, by selecting larger individuals, fishers disproportionately reduce the number of females in local populations, which may further reduce population-level reproductive output.

Climatic warming, coupled with fishing pressure, is likely to reduce or eliminate local populations of owl limpets. Low individual growth rates suggest that the replacement of large, fecund individuals following a significant environmental or fishing-induced mortality event will require years. Depending on the magnitude of owl limpet declines, additional restrictions on take may need to be established if populations are to persist.

Case Study 3: Black Abalone

Life History.   Black abalone, *Haliotis cracherodii*, occur in the rocky intertidal and shallow subtidal zones from Oregon to Baja California. Individuals grow slowly to lengths of 20 cm or more, and may live for over 25 years (Haaker et al. 1995). Small abalone graze benthic micro- and macro-algae, but larger individuals capture and eat drift kelp. In addition to humans, the predators of black abalone include sea stars, octopuses, cabezon, crabs, spiny lobsters, and sea otters (Tegner and Butler 1985; Shepherd and Breen 1992).

Baseline abundances prior to intensive commercial exploitation were estimated to be a minimum of 3.5 million black abalone in the 1960s (Rogers-Bennett et al. 2002). Black abalone occurred at extremely high densities (hundreds of thousands per hectare) in aggregations that were stacked several animals high. In the mid-1980s, black abalone began to suffer from withering syndrome (WS), a chronic wasting disease caused by a Rickettsiales-like prokaryote (Moore et al. 2001). Large numbers of dying abalone and empty shells were first observed in the central Channel Islands (Haaker et al. 1992). The disease spread throughout the islands (Lafferty and Kuris 1993; VanBlaricom et al. 1993) and along the southern California mainland (Steinbeck et al. 1992; Altstatt et al. 1996). Although the origins of the disease are still unknown, high abalone densities may have exacerbated the onset, virulence, and spread of WS (Moore et al. 2002).

It is unclear whether dense aggregations of black abalone occurred prior to the local extirpation of the southern sea otter, *Enhydra lutris*, in the nineteenth century (Davis et al 1992). Abalone in southern California have lived for hundreds of years without sea otters. In the late 1930s the remnant southern sea otter population near Point Sur began a range expansion moving north to Monterey and south to Point Piedras Blancas by 1956. This population has now expanded south of Point Conception into the Southern California Bight (Vogel 2000) and in the future they may move further south along the mainland or out to the Channel Islands. The impact on black abalone of sea otter reoccupation is likely to be at least as dramatic as it was for red abalone populations, which declined from 1,000 individuals per hectare to <100 individuals per hectare at Point Estero in 8 years (Wendell 1994).

Fishing History.   Black abalone live higher in the intertidal than other species of abalone, making them particularly vulnerable to human foragers. Abalone fishing dates back to the late Pleistocene (*ca.* 10,500 years B.P.) in the Channel Islands (Erlandson et al. 1996). More recently, an extensive intertidal fishery was developed by Chinese immigrants in the 1800s, which largely collapsed due to overexploitation by 1900 (Rogers-Bennett et al. 2002). After 1968, when laws prohibiting the export of abalone were repealed, there was a rapid increase in black abalone landings. In 1973, landings from southern California and the Channel Islands peaked at 870 mt (fig. 6). Restrictions on black abalone fishing were implemented in 1974, including diver quotas of 240 abalone/day, an increase in the minimum legal size from 140 to 146 mm, and closure of certain areas (Parker et al 1992). However, in just 5 years, landings declined nearly 10-fold (Karpov et al. 2000). The commercial abalone catch declined on the Channel Islands closest to the mainland (e.g., Santa Cruz and Santa Catalina) first, and at more distant islands (e.g., San Miguel and San Nicolas) later (fig. 6), suggesting that human fishing played a major role in the collapse of the populations (see also Karpov et al 2000). After landings in the fishery declined (1979) and WS devastated remaining populations (mid- and late 1980s), the black abalone fishery was closed in 1993.

Effects of Climate Change.   As with mussels and limpets, climate change may affect black abalone populations via several pathways. Although no information is available on the link between air temperature and black abalone performance, black abalone do possess behavioral adaptations that may facilitate evaporative cooling (Hines et al. 1982), which suggests that they occasion-
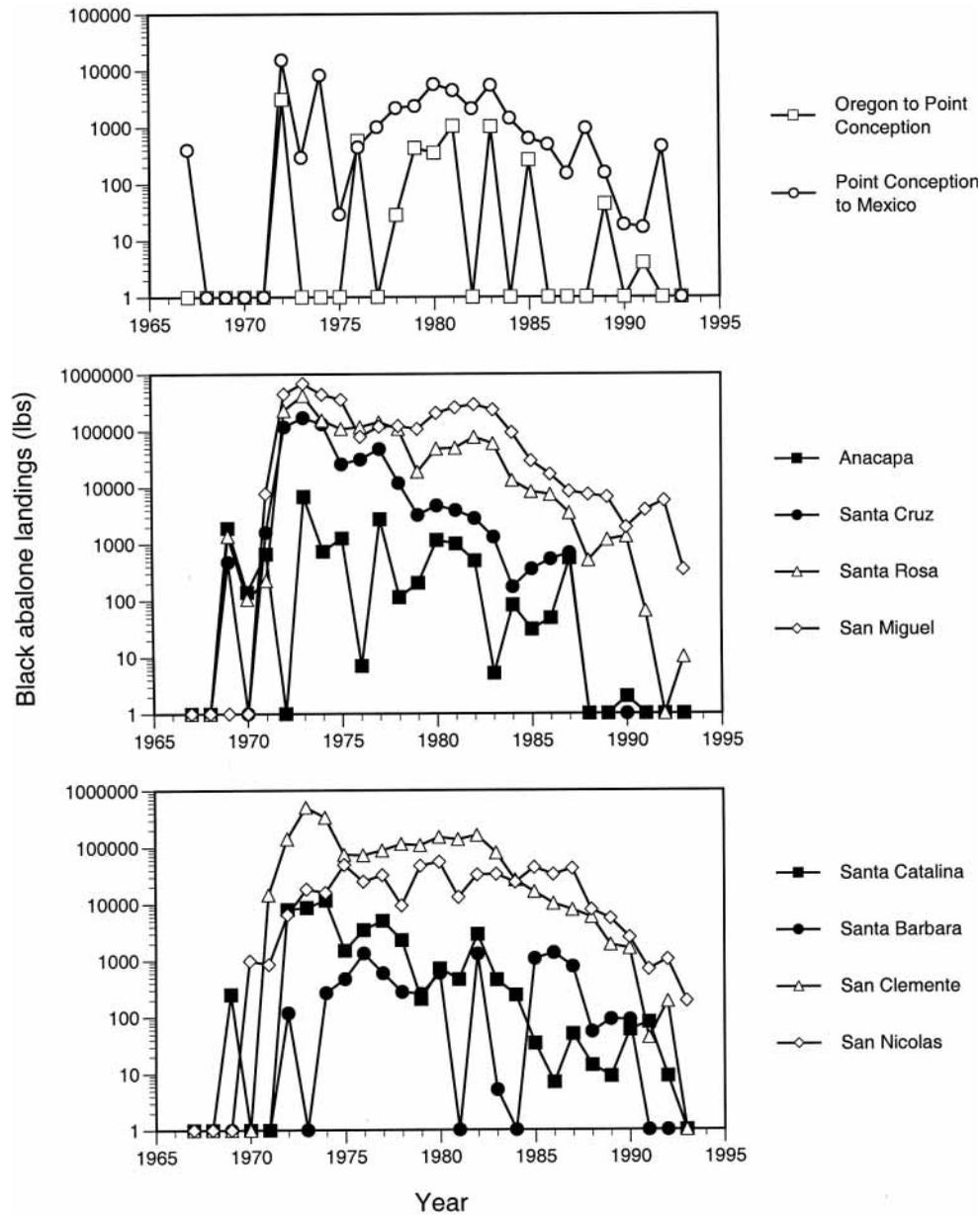
Figure 6.   Commercial black abalone landings for mainland sites (top panel), the northern Channel Islands (middle panel), and the southern Channel Islands (bottom panel). The data (x+1 on the log scale) were obtained from the California Department of Fish and Game, using only those dive blocks adjacent to the coastline. Note that landings from nearshore islands (solid symbols) declined before landings from more distant islands (open symbols). See fig. 2 for map.

ally experience thermally stressful conditions. It is therefore conceivable that continued atmospheric warming will force black abalone into the very low intertidal and subtidal zones, where they will compete with other herbivores such as sea urchins. The direct effects of water temperature on black abalone are also largely unexplored (but see Haaker et al. 1995). However, elevated temperatures are associated with reduced growth, condition index, and reproduction in other abalone species (Haaker et al. 1998; Vilchis et al. 2005; Guzmán del Próo, pers. comm.).

Indirect effects of climate change will likely outweigh the direct effects. Abalone growth is reduced during El Niño conditions (Haaker et al. 1998), and this is likely the result of a reduction in food quantity or quality (Vilchis et al. 2005). Increasing water temperatures, storm frequency, and El Niño frequency in the future could all serve to reduce the supply of drift algae food resources. More importantly, there is a positive relationship between water temperature and the expression of the fatal WS in black abalone in the lab (Friedman et al. 1997) and in the field (Tissot 1995). Mortality

associated with WS during warm-water events has been slowly spreading north from Point Conception over the past 10 years (Raimondi et al. 2002). Warming trends in water temperatures are expected to allow the disease to continue its northward expansion and affect populations that are not currently symptomatic (Moore et al. 2002). This problem is particularly severe in light of the southern expansion of the sea otter population. Black abalone may be caught in a squeeze between the spreading of the disease from the south and the range expansion of otters from the north.

Implications for Abalone Populations. Climate-related disease outbreaks and overexploitation have already had tremendous impacts on black abalone populations, which have collapsed in the southern portion of their range. The recovery of black abalone populations is likely to be a slow process due to low growth rates and limited dispersal from potential source populations (Hamm and Burton 2000). The dramatic nature of the population crash and the uncertainties surrounding population recovery have prompted NOAA fisheries to convene workshops exploring the potential listing of black abalone as an endangered species (M. Neuman, pers. comm.). If they are listed, they would join their congener the white abalone, *H. sorenseni*, which was listed in 2001 (*Federal Register* 66 (103) 29046, 29 May 2001) as a result of overfishing.

The magnitude of exploitation and warming-related disease mortality make climate-exploitation synergisms particularly likely for black abalone. The combination of heavy fishing and disease may have reduced black abalone populations to such low levels that Allee effects will hinder natural recovery (see synergistic effect 2 in fig. 1B). Recovery from exploitation may be further slowed by reductions in food supply and warmer temperatures in the future, both of which have the potential to reduce growth and fecundity. Conversely, recent (post-1980s) overexploitation may have particularly tragic consequences for abalone populations in the face of WS if fishers removed individuals that had survived the disease by virtue of having some degree of genetic resistance (synergistic effect 1 in fig. 1B). The synergistic interactions between recent fishing and ongoing climate change may seriously delay or prevent the recovery of this species.

DISCUSSION

Climate Change, Exploitation, and Recovery

Climate change can enhance species' vulnerability to overexploitation, just as exploitation has made species particularly vulnerable to changes in climate. The combined influence of exploitation and adverse environmental change will tend to reduce and fragment exploited populations, making them more vulnerable to Allee effects. Fishing pressure may reduce population sizes sufficiently that additional stresses from rare environmental catastrophes (e.g., extreme high temperatures, winter storms) place populations at risk of local extinction. Increasing population fragmentation may also alter metapopulation dynamics, with potentially serious consequences for local and global populations of exploited species.

As demonstrated by the case studies presented here, the effects of climate change and fishing depend on the characteristics of exploited species, including resistance to various forms of disturbance (e.g., thermal extremes, storm-induced disturbance, and human collection) and resilience, or ability to recover following a disturbance. Species such as sea mussels, whose distribution appears to be largely independent of temperature, will be resistant to certain climatic trends and thus less susceptible to synergisms between climate and fishing. For owl limpets and black abalone, whose populations may be strongly linked directly and indirectly, respectively, to temperature, climatic warming may have large impacts and increase the likelihood of synergisms with exploitation.

The vital rates of exploited species will be a major factor in their resilience to climate- and fishing-induced reductions in population size. For organisms with low turn-over rates and slow growth (e.g., black abalone), exploitation and climatic fluctuations may reduce populations much more quickly than they naturally replenish. In these cases, the risk of multiplicative effects is high because populations may be pushed below abundance thresholds from which they may never recover. For species with more rapid growth and higher population recovery rates (e.g., sea mussels), the synergistic risks of climate change and fishing are reduced because population resilience is high and there is a greater likelihood of recovery between extreme events. In intermediate cases (e.g., owl limpets), the impacts of climate change and exploitation may be sustainable for years to decades, but risks are still substantial as rare climatic (or poaching) events could collapse entire populations.

Challenges of Uncertainty

Reducing Uncertainty. Several gaps in our current knowledge hamper our ability to understand, manage, and restore exploited populations in the face of climate change. First and foremost is the considerable uncertainty underlying the specifics of future climate (IPCC 2001). Although broad-scale trends, such as warming air and sea-surface temperatures, are virtually assured, cycles of warming and cooling complicate the picture. Furthermore, broad-scale global trends may not be representative of local or even regional-scale patterns. This is apparent in the patterns of sea-surface temperature variability at different sites in California (see, for example,

fig. 3) and in the inverse production regimes in the California Current and the Gulf of Alaska (Hare et al. 1999). Even if environmental change were spatially uniform, biological responses may still be site specific. For example, the upper limit of intertidal barnacles is only influenced by temperature at a subset of sites in Washington (Harley and Helmuth 2003), suggesting that climate change may shift barnacle zonation patterns in some places but not in others. Finally, changes in many variables, such as current velocity, upwelling intensity, mass transport, and coastal fog are difficult to forecast given current information but are fundamentally important to coastal populations. Improvements in climatic forecasting at regional and local scales will be crucial if we hope to use environmental information to improve fisheries management strategies (Walters and Collie 1988).

Biological processes add an additional layer of uncertainty. Future species assemblages and community characteristics may not be easily inferred from present data or historical records since there may be no present or past analog (e.g., Overpeck et al. 1992). In order to predict potential ecological relationships under future environmental conditions, we must supplement correlative time-series information with novel approaches to research. Progress is being made through experimental manipulations during shorter-term natural fluctuations (e.g., Sanford 1999), monitoring of "nonscientific" manipulations such as localized sea-water warming near nuclear power stations (e.g., Steinbeck et al. 1992), and mathematical models of the relationships between organisms and the environment (Helmuth 1998; Hobday and Tegner 2002). A particularly important focus of future research will be the behavior of populations at low abundances and their ability to rebound under future climate scenarios. Such research will be of primary importance in predicting the prospects for restoration of depleted species and is seldom the focus of fisheries research.

Accepting and Incorporating Uncertainty. Although scientists are gradually reducing the uncertainties surrounding climate-fisheries interactions, management will always proceed in the absence of perfect knowledge. Management procedures with feedbacks from stocks to management may be one way to cope with uncertainty (Parma 2002). Model simulations have been used to examine whether fixed or variable fishing strategies are optimal under conditions of environmental fluctuations (Walters and Parma 1996; Spencer 1997). Fixed strategies performed well (within 15% of optimal) in situations with a Beverton-Holt stock recruitment relationship and relatively high productivity at low stock abundances (Walters and Parma 1996). In contrast, Spencer (1997) found that variable fishing policies outperformed fixed strategies in most cases incorporating depensation at low adult abundances. For species such as abalone, where depensatory effects become important at low population sizes (Shepherd and Brown 1993) and recruitment overfishing has been observed (Rogers-Bennett et al. 2004), recovery may be very slow or nonexistent during unfavorable environmental conditions.

For heavily exploited and overexploited populations, marine protected areas (MPAs) provide a conservative approach that may be vital to long-term population viability. Indeed, given the unavoidability of climate change, the only way to prevent synergistic effects between climate and fishing is to curtail fishing in some areas. MPAs, either explicit or de facto, will enhance the local abundance of many exploited species and increase the likelihood that at least some populations will survive the vagaries of environmental variability (Hughes et al. 2003). MPAs may also allow populations currently affected by both fishing and environmental change to recover, although recovery is by no means guaranteed (Tegner 1993). MPAs also provide opportunities for distinguishing between the effects of fishing and climate change as drivers of the dynamics of marine populations (Moser et al. 2000). However, MPAs are only effective if there is adequate enforcement (Daniels and Floren 1998), as is readily apparent from the effects of continued collection of owl limpets (Kido and Murray 2003) and remnant black abalone (I. Taniguchi, pers. comm.) in protected areas. Finally, MPAs are themselves vulnerable to climate change. An adaptive approach to siting new MPAs has been suggested as a way to optimize reserve-network performance as environmental conditions change (Soto 2002).

Conclusions and Recommendations

Human impacts on marine systems are increasing, both directly through fishing and indirectly through anthropogenic warming. The effects of either climate change or fishing alone are sufficient to dramatically alter marine populations and ecosystems and may drive heretofore abundant species to extinction (Roberts and Hawkins 1999; Dulvy et al. 2003). However, the synergistic effects of environmental change and exploitation may be more severe than the effects of either one in isolation. This is evident from our examples on rocky shores and may hold for other marine ecosystems. Managers need to be aware of these potential synergisms, which may lead to unwelcome surprises when anthropogenic impacts and global change interact (Paine et al. 1998). The intertidal examples highlighted here, along with a growing body of other evidence (e.g., Walters and Collie 1988; Walters and Parma 1996; McCall 2002), suggest that future management strategies must shift their emphasis from correlative data to a more mechanistic understanding of the effects of environmental variability and its interactions with fishing.

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