

aspects for success are teamwork; minimum and essential biological-ecological fishery knowledge; social and economic understanding of the resources/systems to be co-managed; use of adaptive strategies; and mutual trust among players (not only between government and users but also, importantly, among users). Delegated co-management is welcomed by small-scale fishers, and the system has shown success in shoreline/inshore fisheries, where strong and long-standing fishery traditions on marine resources extraction and management are deeply rooted in the culture. Collaborative co-management has proven successful in small-scale commercial benthic fisheries, where explicit Territorial User Rights for Fisheries (TURFs) have been assigned to organized small-scale fishery communities.

SMALL-SCALE SUBSISTENCE FISHERY ECONOMICS AND HUMAN WELL-BEING

Worldwide, the shoreline/inner-inshore subsistence fishery is a key, though as yet unquantified activity, and as such it is impossible to be economically evaluated. In shoreline subsistence fishery resource sustainability is amenable to regulations via co-management schemes, in which fishers, still un-technologized, are the central management drivers. Subsistence fishery management models should be sociologically, rather than economically, oriented, and fishers' well-being must be central. Older, single-species fishery management strategies, as well as purely biophysical ecosystems-integral prescriptions for fishery sustainability, appear to be less amenable, or unrealistic, for these fisheries. In small-scale subsistence fisheries, humans have played a central role for thousand of years, as opposed to large-scale fisheries, in which mechanization, technology, and subsidies appear as the managerial drivers to be controlled. Therefore, it is unacceptable to approach the rational management of shoreline/inshore small-scale subsistence fisheries using the same tools as for commercial fisheries.

SEE ALSO THE FOLLOWING ARTICLES

Algal Economics / Food Uses, Modern / Management and Regulation

FURTHER READING

- Berkes, F., R. Mahon, P. McConney, R. Pollnack, and R.S. Pomeroy. 2001. *Managing small-scale fisheries: alternative directions and methods*. IDRC publication 1-320. Ottawa, Canada: International Development Research Centre. http://www.idrc.ca/en-ev-9328-201-1-DO_TOPIC.html.
- Caddy, J.F., and O. Defeo. 2003. Enhancing or restoring the productivity of natural populations of shellfish and other marine resources. FAO Fisheries Technical Paper No. 448. Geneva: UN Food and Agricultural Organization.

- Castilla, J.C. 1994. The Chilean small-scale benthic fisheries and the institutionalization of new management practices. *Ecology International Bulletin* 21: 47–63.
- Castilla, J.C., and M. Fernández. 1998. Small-scale benthic fisheries in Chile: on co-management and sustainable use of benthic invertebrates. *Ecological Applications* 8: S124–S132.
- Castilla, J.C., and O. Defeo. 2001. Latin American benthic shellfisheries: emphasis on co-management and experimental practices. *Reviews in Fish Biology and Fisheries* 11: 1–30.
- Castilla, J.C., and O. Defeo. 2005. Paradigm shifts needed for world fisheries. *Science* 309: 1324–1325.
- Gelcich, S., G. Edwards-Jones, and M.J. Kayser. 2005. Importance of attitudinal differences among artisanal fishers towards co-management and conservation of marine resources. *Conservation Biology* 19: 865–875.
- Johannes, R.E. 2002. The renaissance of community-based marine resource management in Oceania. *Annual Review in Ecology and Systematic* 33: 317–340.
- McClanahan, T., and J.C. Castilla. 2007. *Fisheries management: progress toward sustainability*. Oxford, UK: Blackwell Publishers.
- McConney, P.A., R. Pomeroy, and R. Mahon. 2003. *Guidelines for coastal resource co-management in the Caribbean: communicating the concepts and conditions that favor success*. Caribbean Conservation Association and University of West Indies.

ECOSYSTEM CHANGES, NATURAL VERSUS ANTHROPOGENIC

KAUSTUV ROY

University of California, San Diego

Intertidal communities are incredibly dynamic, exhibiting natural fluctuations on many different spatial and temporal scales. These habitats are also easily accessible and subject to increasing human impacts as more and more people inhabit coastal areas. Such impacts can directly or indirectly affect intertidal species and communities. Separating natural from anthropogenic changes is important both from a scientific as well as a management perspective. Yet as more and more people use resources from the tidepools, it is becoming increasingly difficult to separate these effects.

NATURAL CHANGES

Natural changes in the distribution and abundance of intertidal species can result from a number of abiotic as well as biotic factors ranging from changes in temperature, coastal upwelling, and circulation to variations in larval supply and recruitment. Temperature and coastal

circulation patterns are important determinants of the geographical distributions of many intertidal species and can influence compositions of intertidal communities on a variety of time scales. A common biological response to changes in temperature is a shift in the distributions or abundances of species or both. During episodes of climatic warming, many species extend their ranges northward, and others show an increase in abundance near their northern distributional limits. The reverse is true during cooling events. Depending on the nature and magnitude of the climatic change, such distributional shifts can separate co-occurring species or lead to formation of new species associations, thereby changing the composition and diversity of local intertidal communities. These changes can happen over a variety of time scales, from short-term fluctuations to decades to geological time. For example, during El Niño Southern Oscillation (ENSO) events, populations of some warm-water species can be found much farther north of their normal distributional limits, but such shifts are ephemeral in that these populations rarely persist much beyond the duration of the ENSO event. Over longer time scales, warming of coastal waters over multiple decades has led to increases in the abundances of warm-water species in temperate intertidal communities such as in Monterey Bay. On even longer time scales, major fluctuations in global climate during the Pleistocene and Holocene (the last 1.8 million years) led to large changes in the compositions of intertidal communities. For example, during warm interglacial periods, such as around 125,000 years ago, intertidal habitats in California harbored many species that today are only found much farther south; the resulting communities have no modern analogs. Such climate-driven changes in community compositions are well documented from many parts of the world. In addition to changes in community composition, such range shifts can also lead to changes in the morphology and genetic population structures of intertidal species. In the Northern Hemisphere, more northerly populations of many species exhibit lower genetic diversity compared to more southerly ones. This is because the northern populations went extinct during Pleistocene glaciations and these regions were recolonized by individuals from southern refugia only after the glacial period was over. Thus these northern populations are too young (less than 20,000 years old) to have accumulated much genetic diversity.

Although changes in species distributions and abundances are a common response to changes in the ambient environment, it is important to note that not all species show these responses; distributions and local

abundances of many species can be remarkably stable even in the face of substantial environmental change. Similarly, species that do respond to changes in climate differ in terms of the magnitude of the responses. The ecological and life history characteristics that drive such individualistic responses remain poorly understood. What is clear is that although responses of some species to climate change are predictable from their thermal physiology alone, those of others reflect more complex interactions between biotic and abiotic factors. For example, even small changes in water temperature (such as those resulting from changes in coastal upwelling patterns) have been shown to influence the rate of predation by the sea star *Pisaster ochraceus* on its mussel prey. Since *Pisaster* is a keystone predator that controls the local abundance of mussels, thereby maintaining a diverse intertidal assemblage of algae and invertebrates, in this case change in temperature has the potential to influence community composition by affecting predator–prey interactions.

HUMAN ACTIVITIES AND INTERTIDAL ECOSYSTEMS

Human activities can impact the easily accessible habitats at the land–sea interface in a number of different ways. Our impacts on intertidal ecosystems range from sewage discharge and industrial pollution to more episodic disturbances such as trampling of the intertidal by foot traffic; harvesting of intertidal organisms for food, fish bait, aquariums, and other needs; and moving of rocks and other material such as dead shells that serve as habitats for many invertebrates. Each of these activities, by itself or in conjunction with other impacts, can substantially change species compositions and the nature of intertidal ecosystems. In addition, introduced species can also change the nature and composition of intertidal communities.

Harvesting

Plants and animals living in intertidal habitats are not only a source of food for people, but they are also used in a variety of other ways. For example, many species of molluscs provide the basis for a thriving ornamental shell trade. Because of such diversified use, a large variety of intertidal species ranging from fish and shellfish to algae are harvested by humans. Such harvesting ranges from localized recreational or subsistence collecting to more organized and widespread fisheries, and the species involved varies from one part of the world to another. Harvesting of intertidal organisms for food and cultural

use has been going on for thousands of years in many coastal areas, although as coastal human population densities continue to increase rapidly, so does the harvesting pressure and its impact on intertidal species. In effect, humans insert themselves into the intertidal ecosystem as top predators, leading to both direct and indirect impacts on other species.

Human harvesting of intertidal species is highly selective; not all species that live in intertidal habitats are directly targeted for harvesting and those that are harvested are not all harvested to the same extent. Furthermore, harvesting of many species tends to be strongly size selective, with larger individuals preferentially taken. The ecological effects of such removal are complex and vary from one region to another, depending on which species are taken and the harvesting methods. Nonetheless, some general trends are clear on a global scale.

Size-selective harvesting changes the population size structures and abundances of the targeted species; large individuals of harvested species become very rare in areas under heavy exploitation. Such changes have been documented over large stretches of coastlines covering tens to hundreds of kilometers and over many decades (Fig. 1). Removal of large individuals also leads to a decrease in the biomass of the species and can negatively affect its reproductive output. For some species, decreases in spawning biomass as a result of overexploitation have been shown to be responsible for dramatic declines of local populations. Changes in the size distribution and abundance of individual species also lead to changes in the structure of intertidal ecosystems. For example, grazers such as limpets control the abundance of algae and help maintain bare space on the rocks. Removal of these species, a common food item in many parts of the world, can lead to a rapid increase in algal cover and thus loss of space that can be used by other species. Similarly, harvesting of important intertidal predators can lead to a dramatic increase in the abundance of their prey, which in turn can change the nature of the local ecological community. In Chile, *Concholepas concholepas*, a large gastropod, is a prized local food item and heavily harvested. But it is also a keystone species that preys on mussels and creates bare space on the rocks, some of which are then colonized by barnacles. Since the removal of *Concholepas* favors mussels, human harvesting of this key species changes an intertidal community characterized by open space and few mussels into one with a thick cover of mussels (Fig. 2). Mussels themselves are commonly harvested along many coasts, and removal of clumps of mussels indirectly kills many smaller species that live in the complex structures created

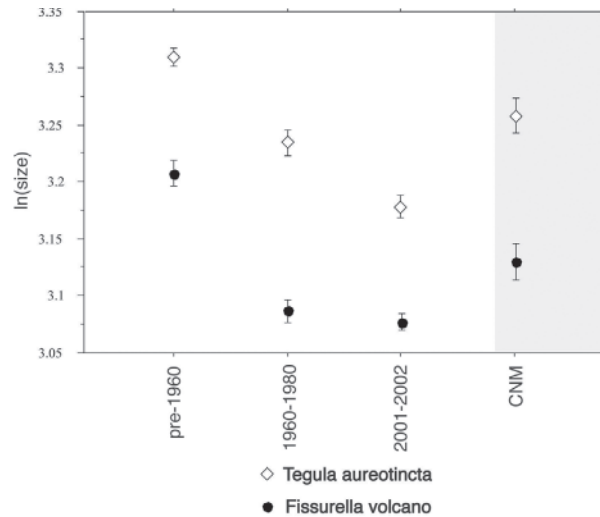


FIGURE 1 Declines in body sizes of two intertidal gastropod species, a turban snail and a small limpet, over time in Southern California in response to human harvesting. Each data point represents the average size (log transformed) across multiple populations in Southern California. For each species, largest individuals were found before 1960. The shaded region of the plot shows data from Cabrillo National Monument in San Diego, one of the few intertidal reserves in Southern California with a human-exclusion zone. That today the largest individuals of these species are found in the only reserve where human harvesting is prevented indicates that size-selective harvesting rather than natural changes have caused the temporal decline in body size. Modified from Roy *et al.* (2003).

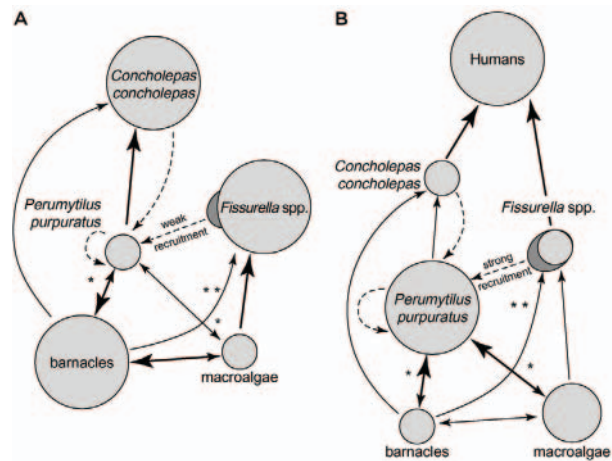


FIGURE 2 Changes in the intertidal community structure in Chile as a result of human harvesting. The size of the circles are proportional to the density of each species shown. Single-headed arrows indicate predation, with the direction of the arrowhead indicating the direction of energy flow. Double-headed arrows indicate that the species involved compete with each other. Broken lines indicate settlement of juveniles with the arrowhead pointing toward the species benefiting. Panel (A) shows the natural condition with no harvesting when *Concholepas* and *Fissurella* dominate. Panel (B) shows the effects of human harvesting of *Concholepas* and *Fissurella*. The mussel *Perumytilus* and various macroalgae increase in abundance at the expense of the barnacles and the harvested snails. Reprinted from Castilla (1999), with permission from Elsevier.

by the mussels. Despite region-specific differences in harvesting practices and species compositions, it is clear that human harvesting of intertidal species leads to predictable changes in community compositions; exploited localities tend to have higher dominance by algae and consequently higher abundances of species associated with algae, but reduced open space and lower abundance and biomass of harvested species as well as many grazers and animals that use the primary substrates.

Trampling

Trampling by humans is another significant yet underappreciated threat to the health of intertidal ecosystems. People can change the composition of intertidal assemblages simply by walking on them. The force exerted by human footsteps crushes many species of algae as well as small invertebrates (e.g., barnacles and small molluscs) and so the direct effect of trampling is a reduction in or a loss of various types of algae including species that form thick turfs and reduced densities of animals associated with the turf. Susceptibility of algal and invertebrate species to trampling does vary, as does the ability of species to recover if and when trampling is discontinued. In places with high human visitation, trampling can transform an intertidal area with a thick cover of algal turf (e.g., coralline turf) to one that is essentially bare rock. Trampling also has indirect effects; densities of limpets and other grazers can increase as algal turf disappears and more bare rock becomes available. Like harvesting, impacts due to trampling are increasing as densities of coastal populations increase on a global scale and more people use the intertidal habitats for recreational or other usage.

Other Impacts

Many other anthropogenic activities ranging from pollution, eutrophication, and oil spills to the presence of introduced species affect the health of intertidal assemblages. Episodic disturbances such as oil spills generally have localized effects, but recovery can be slow, and not all species may come back. Pollution is becoming an increasing problem for intertidal habitats near rapidly growing coastal cities, but the effects of various pollutants on the health of intertidal ecosystem remain poorly known. Some pollutants impair immune response and make intertidal species more vulnerable to diseases, whereas endocrine disruptors (e.g., tributyl tin, TBT) associated with antifouling paints can cause female sterility in some species, leading to reduced reproductive output and the potential for local extinctions.

A number of plants and algae have been intentionally or accidentally introduced by humans into intertidal

habitats that are outside the natural distributions of these species. Such introductions have the potential to change the nature and composition of the recipient assemblage, although the effects vary depending on the nature of the introduced species. In some cases introduced species simply increase local diversity without displacing the native species, but in other cases such invasions affect the abundances of native species either directly or indirectly.

SYNERGIES AND THE FUTURE OF INTERTIDAL ECOSYSTEMS

Few ecosystems today are buffered from anthropogenic impacts, and tidepools, being easily accessible, are particularly vulnerable. Also in a world dominated by human activities, the distinction between natural and human-mediated change is increasingly becoming blurry; even changes in global climate are now driven by anthropogenic emissions of greenhouse gases, and the dynamics of global climate in the future are likely to be very different from the conditions under which the species living in the tidepools evolved. Of particular concern is the problem of synergistic interactions between many of these stressors; as populations of many species decline as a result of direct or indirect effects of human harvesting, climate warming, or both, they may become particularly vulnerable to diseases or other disturbances. The dramatic decline of the black abalone (*Haliotis cracherodii*) in California, where overexploitation, climatic warming, and disease have all been implicated, already provides one example of such synergistic interactions. How tidepool ecosystems will look in the future depends largely on our abilities to understand and manage these threats.

SEE ALSO THE FOLLOWING ARTICLES

Climate Change / Economics, Coastal / Habitat Alteration / Introduced Species / Predation / Upwelling

FURTHER READING

- Castilla, J. C. 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends in Ecology and Evolution* 14: 280–283.
- Hellberg, M. E., D. P. Balch, and K. Roy. 2001. Climate-driven range expansion and morphological evolution in a marine gastropod. *Science* 292: 1707–1710.
- Roy, K., A. G. Collins, B. J. Becker, E. Begovic, and J. M. Engle. 2003. Anthropogenic impacts and historical decline in body size of rocky intertidal gastropods in southern California. *Ecology Letters* 6: 205–211.
- Thompson, R. C., T. P. Crowe, and S. J. Hawkins. 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation* 29: 168–191.