

# LOBSTERS

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Lobsters are a polyphyletic group of crawling decapod crustaceans that have a cylindrical, usually laterally compressed carapace and prominent abdomen with tail fan. The evolutionary origins of lobster-like crustaceans can be traced back at least 245 million years to the early Triassic Period. Of the many extant families in the group, the Nephropidae and Paniluridae stand out as rich in species, geographically widespread, and functionally important in near-shore and intertidal environments.

## TAXONOMY AND NATURAL HISTORY

The family Nephropidae, or clawed lobsters, consists of approximately 118 species in 18 genera. They are characterized by claws on the first three pairs of walking legs, with the first pair often greatly enlarged relative to the other two. The antennae are small and located lateral to a prominent rostrum (forward projection of the carapace between the eyes). The Nephropidae includes the commercially and ecologically important Atlantic clawed lobster, *Homarus americanus*.

The family Paniluridae, or spiny lobsters, consists of approximately 45 species and occurs in all major oceans. Spiny lobsters lack both a rostrum and claws on the anterior walking legs. They defend themselves with long whip-like first antennae covered with sharp spines. A pair of forward projecting horns protect the stalked eyes. Many species emit harsh rasping sounds (stridulation) by rubbing the plectrum, a finely ribbed scale at the base of the antennae, against smooth ridges on the adjacent surface of the carapace. Stridulation apparently functions to startle predators and warn conspecifics. The most species-rich genera, *Jasus* with 9 species and *Panulirus* with 19 species, are found in shallow depths (<100 meters) of cool temperate latitudes (approximately 30–45°) and warm temperate to tropical latitudes (35–0°), respectively.

*Homarus americanus* in the Atlantic and *Panulirus* spp. in the Pacific play an important role in communities of the shallow subtidal zone (depth <35 meters). Acting in concert with other consumers, they hold populations of sea urchins and other herbivorous invertebrates in check, helping to maintain kelp beds and the diverse species assemblages that inhabit them. In some locations, lobster fisheries have severely reduced stocks, incurring outbreaks

of grazing sea urchins and the subsequent loss of the kelp bed community.

Perhaps as a consequence of heavy exploitation reducing their numbers, as well as their secretive habits, lobsters are seldom thought of as intertidal species. However, early accounts of the colonists made reference to Native Americans collecting copious amounts of clawed lobsters from New England tidal flats during low tide. Early twentieth century naturalists on the southwest west coast of North America remarked on the shore-loving tendencies and frequent occurrence in tidepools of spiny lobsters. Contemporary observations on shores of California Channel Islands protected from sport and commercial exploitation reveal that *Panulirus interruptus* remain during the day in subtidal shelters and emerge at night to forage, and if the tide is high, they may roam into the upper levels of the intertidal zone (Fig. 1). Spiny lobsters crush shelled prey with large shearing mandibles on the ventral surface. Intertidal prey include polychaetes, urchins, barnacles, turbin snails, limpets, littorines, and most frequently, mussels (*Mytilus* spp.).



FIGURE 1 *Panulirus interruptus* foraging in the intertidal zone at night. Barnacles, anemones, mussels, and algae comprise the carpet of sedentary species. While foraging, spiny lobsters creep along tapping the substratum with the terminal segments (dactyls) of the forward walking legs. The dactyls pry up the prey, positioning it in front of the mouth on the ventral surface.

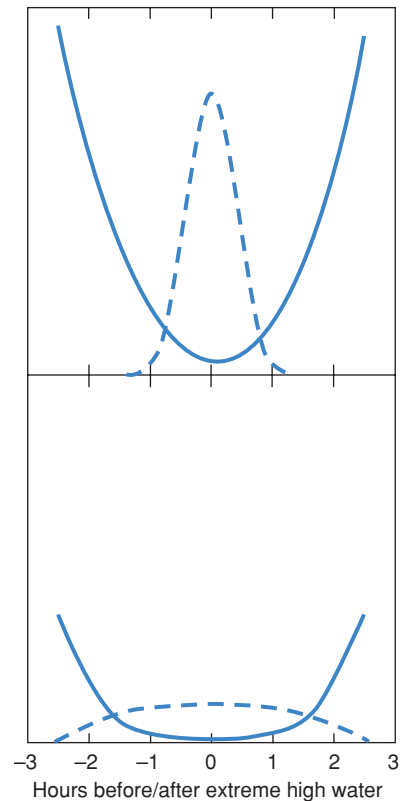
## SPINY LOBSTERS AS KEYSTONE PREDATORS IN THE ROCKY-SHORE COMMUNITY

Keystone predation is confirmed experimentally when removal of the purported keystone predator species allows a prey species to increase sufficiently to eliminate its competitors. On rocky shores of the California

Channel Islands, dense populations of mussels (*Mytilus californianus*) and the other shelled invertebrates are restricted to wave-beaten headlands. Areas of shore that lie in the lee of the headlands are covered by a dense algal turf comprised of fleshy red algae (principally *Chondrocanthus* (= *Gigartina*) *canaliculata* and *Gelidium coulteri*) and articulated coralline algae (*Corallina pinnatifolia*). Exclusion of *Panulirus interruptus* by cages over plots arrayed on mid-shore levels along the horizontal wave exposure gradient caused changes in the composition of attached life to varying degrees. Plots on a wave-exposed headland that were initially covered with mussels showed further increases in this competitively dominant prey species. Plots in the moderately wave-exposed (middle) segment of the array showed the rapid replacement of the algal turfs by a continuous cover of mussels; those in the most wave-protected areas showed a continuing dominance of the algal turfs, with only slight increases in mussels. The spiny lobsters are, therefore, important intertidal predators in the Channel Islands shore community, but they exert keystone predator effects only in a portion of the horizontal wave exposure gradient.

### INFLUENCE OF HYDRODYNAMIC FACTORS ON THE IMPACT OF PREDATION BY SPINY LOBSTERS

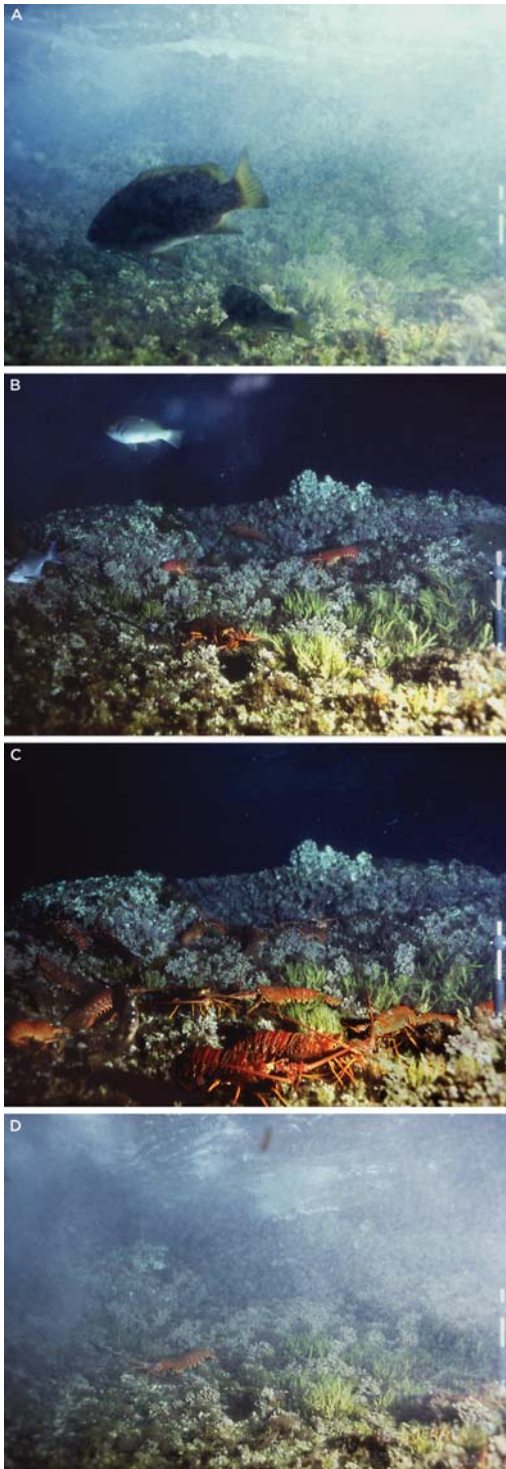
The differences along the shoreline in the apparent effect of lobsters in the California Channel Islands study result from the influence of hydrodynamic factors on both lobster foraging and the recruitment of the mussels. As waves pass over, the oscillatory flow across the rock surfaces of the intertidal zone subject the lobsters to the hydrodynamic stresses of drag and lift, which can damage or dislodge them. These hydrodynamic stresses are proportional to the square of the flow speeds. In turn, the flow speeds are proportional to the wave energy reaching the site and inversely proportional to the depth of the tide. Thus, for any point along the shoreline, maximum bottom flow speed traces a U-shaped curve over the course of a high tide, a consequence of the changing water levels: Water velocity is high when the tide first covers the rocks, but velocities decrease as the tide rises to its maximum height (Fig. 2). The values of the maximum speeds reached during the cycle of tidal immersion increase from wave-protected (relatively low energy) sites to seaward (relatively high energy) sites (Fig. 2). The differing time courses of flow speed, and hence stresses, over the horizontal gradient of wave exposure allow the lobsters prolonged access to wave-protected shores, but only a relatively brief window of opportunity to forage on wave-exposed shores, as



**FIGURE 2** Diagram of idealized relationship between maximum bottom flow speed (solid lines) and lobster densities (dashed lines) as water levels change over the course of a high tide. Curves depict relationships for midshore levels from the beginning of submergence on the rising tide to reemergence on the falling tide. (Top) Time courses for wave-exposed site. (Bottom) Time courses for wave-protected site. The duration of foraging is longer on wave-protected sites, but the peak abundances of lobsters are lower in these prey-sparse areas. These relationships obtain in the calm summer season. Little foraging occurs on exposed sites in the stormy winter months.

evidenced by the shifting abundances of intertidal foragers (Figs. 2 and 3).

Mussel recruitment (accumulation of juveniles on the shore following their settlement from plankton stocks) increases over the wave exposure gradient from wave-protected to wave-exposed sites. Therefore, the mussels' capacity to replenish their populations increases from protected to wave-exposed sites, as the accessibility of these populations to the predatory lobsters decreases over the same span. Hydrodynamic factors influence relative levels of these crucial processes such that one observes predatory elimination of sparse mussel recruits along midshore levels in protected areas, keystone predation at midshore levels of moderately exposed sites, and predatory reduction of otherwise dominant mussel beds on wave-exposed headlands.



**FIGURE 3** Time-lapse photographic sequence; four successive frames of a fixed plot on a midshore level recorded over the course of a high tide in summer. (A) During late afternoon, fishes enter midshore levels on the rising tide. (B) As night falls and the water levels rise still higher, maximum flow speeds decrease, and lobsters move onto the algal turfs. (C) Peak lobster abundances occur at extreme high water. (D) As water levels fall with the receding tide, maximum flow speeds and turbulence mount, and the lobsters leave the site well in advance of emergence. Photographs by the author.

## SEE ALSO THE FOLLOWING ARTICLES

Algal Turfs / Hydrodynamic Forces / Predation / Recruitment / Tides / Wave Exposure

## FURTHER READING

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# LOCOMOTION: INTERTIDAL CHALLENGES

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The rocky-intertidal zone poses a unique set of challenges for locomotion. An animal is subject not only to periodic immersion and emersion, high water velocity, and uneven substrata but also to an extraordinary level of heterogeneity in water flow conditions—factors with the potential to assist, constrain, or even prevent locomotion. Furthermore, for animals using a form of pedestrian locomotion, in which thrust is generated by pushing or pulling on the substratum, the characteristics of the substratum will affect the animal's ability to hold on in waves or to gain purchase for forward motion.

## ENVIRONMENTAL CONDITIONS ENCOUNTERED

An animal in the intertidal zone may encounter three basic types of environmental conditions that present different sets of forces affecting locomotion. Above the water line, but not in a tidepool, an animal experiences terrestrial conditions for locomotion, where buoyancy and fluid dynamic forces (due to the relative movement of air) are minimal and weight of the animal is the defining force. Within a tidepool that is above the reach of waves,

[AQ1] Figure 111.3 is reduced to 15.7% to fit in a column.