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12 Sea-otters and shellfisheries

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Introduction

Competition between humans and marine mammals for exploitation of the world's fishery resources is an issue of increasing concern. However, the consequences of these interactions remain largely undocumented from both biological and economic standpoints. This is mainly because of the immense logistical difficulties in studying the habitats where marine mammals typically feed. For example, all but a few species feed on the high seas, either in the water column or the deep benthos where their prey species are often patchily distributed, highly mobile, or both. Therefore, the prey communities of most marine mammal species are inaccessible, and their distributions unpredictable in space and time, thus making in-situ observations difficult and field experiments nearly impossible.

The sea-otter (*Enhydra lutris*) provides a notable exception to this troublesome situation. Sea-otters prey on benthic invertebrate species that inhabit shallow coastal waters of the temperate and boreal north Pacific region, most of which are sessile or weakly motile. Thus the system is accessible, observable, describable, and amenable to experimental study. These qualities have been instrumental in placing coastal marine communities among the most successfully utilised arenas of basic ecological research.

Recent historical events have added further to our understanding of how sea-otters influence benthic communities. Before the mid-1700s, otters probably occurred in most shallow habitats through the temperate and boreal north Pacific. During that time, populations of abalones, clams, crabs, and perhaps other invertebrate forms, were probably limited largely by the effective nature of sea-otter predation. Subsequently, overexploitation of sea-otters through the 18th and 19th centuries not only eliminated the otters but their ecological rôle as well, so that, by earlier standards, dense populations of their invertebrate prey developed. These high-density prey populations in turn encouraged the development of numerous commercial and recreational shellfisheries as the west coast of North America became increasingly populated and industrialised. Then, following their protection in 1911, sea-otter populations began to recover. In some areas (most notably central California) the expanding range of sea-otter populations came into direct conflict with shellfisheries. As sea-otters drove their prey populations downward toward earlier levels, certain local shellfisheries were driven to extinction.

During the past few decades, two quite different perspectives of sea-otter predation have emerged. One is purely ecological and concerns the intricate network of organisational processes whereby nearshore communities are influenced by sea otters as consumers. The other is social and economic, and has arisen through exploitation competition between sea otters and humans for shellfish resources.

This Chapter will consist of three parts. First, there is a review of the salient features of the biology of sea otters and the ecological consequences of sea-otter predation. (This section will be brief since much has already been written on the subject.) Next, a consideration of the interactions between sea-otters and shellfisheries beginning, in each instance, with a summary of the relevant biological characteristics of the species involved in the fisheries. Then follows a discussion of the current status of fisheries for the species. Where conflicts with otters have already occurred, the supporting evidence is presented and evaluated. Where they have not yet occurred because of non-overlapping distributions with sea otters, we speculate on the likelihood of future conflicts should these distributions eventually overlap one another. Last, some general conclusions are drawn concerning the interaction between sea-otters and shellfisheries deriving from comparisons across species or between geographical areas.

Biology and ecology of sea otters

Sea-otters of the genus *Enhydriodon*, not greatly dissimilar from the extant species (*Enhydra lutris*), are known from the late Miocene (Repenning 1976). These early forms were widely distributed in the Northern Hemisphere. *Enhydra* apparently arose in the North Pacific Ocean some time during the early Pleistocene. It has never ranged beyond that area.

At the time of the arrival of Europeans in the North Pacific, sea otters occurred from the northern Japanese archipelago to the central coast of Baja California (Kenyon 1969). Through most of the Pleistocene, it is likely that they were abundant wherever rocky or soft-sediment habitats offered them suitable food resources. There is evidence that aboriginal people limited otter populations, but this probably occurred only near village sites (Simenstad *et al.* 1978). More extensive exploitation began with the arrival of European fur traders, resulting in near extinction of the species by the beginning of this century. Subsequently, under the protection of an international treaty and, more recently, national and local laws, populations have grown in range and numbers.

Recovery of populations has been most complete in Alaska and the Soviet Union, where much of the aboriginal range is now reoccupied (Estes 1980, Johnson 1982). A translocated population has been established in south-eastern Alaska. Of more tenuous status are small, translocated populations in British Columbia and Washington State. A similar translocated population in southern Oregon is extinct (Jameson *et al.* 1982). The California population has grown slowly during most of the 20th century. It presently ranges from Santa Cruz to Pismo Beach and numbers about 1300 animals (J. A. Estes & R. J. Jameson, unpublished). Apparently the California population has not grown in numbers over the past decade (US Fish and Wildlife Service 1982). Because of the sensitivity of sea-otters to oil contamination, the presence of offshore petroleum development and transport in California caused the designation of the resident sea-otter population as 'threatened' (Greenwalt 1977).

Sea-otters forage in the rocky and soft-bottom benthos, from the lower littoral zones to depths of at least 55 fathoms (Newby 1975). In most areas, the majority of foraging dives seem to occur to depths less than 20 fathoms (Kenyon 1969, Estes *et al.* 1981). Many prey species are consumed, most of which are molluscs, echinoderms, and crustaceans. Fish are also important prey in some parts of the Aleutian, Commander, and Kurile islands, but not in California.

Sea-otters are effective predators and limit many of their prey populations with

remarkable success, which is largely due to their great mobility compared with the sluggish or sessile nature of most of their prey. Indeed, the only ways in which most prey species can escape from otter predation are by taking refuge in cracks and crevices in rocky substrata (Lowry & Pearse 1973), or by taking advantage of their small size, deep water, or some combination thereof. This interaction appears to have numerous and far-reaching consequences to the organisation of coastal marine communities. Perhaps the most well documented of these comes from studies in Alaska where one of the principal effects of sea-otter predation is to limit the intensity of grazing of kelp by herbivorous sea urchins (Estes & Palmisano 1974, Duggins 1980). The broader consequences of these interactions to coastal food webs are less clearly understood, although they are probably both numerous and important. Most of these consequences appear to result from the physical structure or biological productivity of kelp. For example, kelps serve to nourish or protect numerous species inhabiting the coastal zone. From an energetic standpoint alone, kelp appears to be the major contributor to rocky coastal systems. The mere presence of dense beds of surface-canopy-forming kelps can have a substantial limiting influence on the intensity of wave shock which eventually reaches the shore, in turn influencing the structure and organisation of littoral communities (Palmisano & Estes 1977).

The effectiveness with which sea-otters limit grazing by sea urchins has been clearly demonstrated as far south as Point Buchon, California, in the eastern North Pacific. Interactions of the same general kind probably occur, or could occur, even further to the south. Indeed, 'urchin barrens', as Lawrence (1975) has referred to localities from which kelp has been stripped by sea urchins, are known from outside the sea-otters' range as far south as northern Baja, California. Although these barren areas are not so widespread there as they are further to the north, they could never have developed in the presence of sea-otters.

To conclude this section, we summarise two accounts of the complex ways in which sea otters may influence coastal community organisation. The first is from the western Aleutian Islands and concerns the way in which the otters' effect on their prey community influences their own behaviour (Estes *et al.* 1982). By limiting populations of sea urchins, sea-otters: (a) reduce the availability of their invertebrate prey resources, and (b) stimulate the development of kelp assemblages and associated populations of kelp bed fishes. These changes in prey resources bring about a shift in the otter's diet, from one which consists entirely of invertebrates to one which consists of invertebrates and fish. The addition of fish to their diet seems to enhance the abundance of otters to levels significantly above those which would be possible on a diet of invertebrates alone. Furthermore, it causes the otters to alter their foraging behaviour radically. That is, where their diet consists solely of invertebrates, they invest a relatively small amount of time foraging during daylight hours, and they distribute that effort uniformly over time. However, where fish are important prey items, they invest substantially more time in foraging, and distribute that effort disproportionately toward dawn and dusk to correspond with those times when fish are most vulnerable to predation.

The second account comes from central California, where the surface kelp canopy is composed mainly of two species, *Macrocystis pyrifera* (a perennial) and *Nereocystis leutkeana* (an annual). Historical reconstruction of the distribution of kelp, based on maps prepared at various times from the early part of this century, indicate a general expansion of kelp beds in various areas subsequent to the range expansion of sea-otters (VanBlaricom & Jameson 1979, VanBlaricom 1984, G. R. VanBlaricom, unpublished data). Furthermore, the overall trend has included a change in canopy composition –

from *Nereocystis* to *Macrocystis* – over these same areas and times. These changes are thought to have resulted from a reduction in the intensity of herbivory, brought about by otter predation. That is, in the absence of otters, grazing by sea urchins both limited the distribution of kelp beds and favoured *Nereocystis* as an annual species. Following the re-establishment of otters in any particular area, herbivory was essentially eliminated and the kelp beds expanded in size. Furthermore, *Macrocystis* survival was probably increased, which, in conjunction with its perennial life history, perhaps allowed it to inhibit competitively or exclude *Nereocystis* in many areas. Although anecdotal, the model makes good intuitive sense and there is now experimental evidence to support the proposed competitive mechanisms (G. R. VanBlaricom, unpublished data).

Equally intriguing stories undoubtedly will be discovered in time. Indeed, the influences of sea-otters on coastal communities are so dramatic and far reaching that ecological and evolutionary interpretations of these systems can scarcely be made without considering them.

Fishery conflicts

Sea otters are of varying importance to fisheries for each of the subsequently discussed species. In some instances, such as for abalones and Pismo clams, the problem has been acute and widely publicised. In others, such as for spiny lobsters, the problems are merely anticipated pending further range expansion of sea otters. In still others, there is neither biological evidence nor the human perception of a conflict, even though the species may co-occur with and be consumed by sea-otters. The order in which we present the following case studies is arbitrarily taxonomic, molluscs being first, crustaceans second, and echinoderms last. The detail given to each species largely reflects our perception of the severity of existing or potential fishery conflicts with sea-otters.

Dungeness crab: *Cancer magister* (Dana)

Biology and fishery

Dungeness crabs range from around Point Conception, California, north to the Aleutian Islands (Dahlstrom & Wild 1983). Mating in California occurs from about March through June. Sperm are stored by the females until about October when the females spawn and the eggs are fertilised. One to two million fertilised eggs are carried by the females until December or January, at which time they hatch into planktonic larvae. During the early zoeal stages, the larvae migrate vertically in the water column, and although little is known of their movements at this stage, apparently they are carried seaward and northward by the Davidson Current (Reilly 1983). The larval stages last from 125 to 130 days. The megalopae (the final larval stage) become concentrated in certain areas close to shore where they settle and metamorphose to the young crab stage. The crabs molt 11 to 15 times during their 2–6-year lifespan (Program Staff 1983).

The commercial fishery for Dungeness crab began in the San Francisco area in 1848 (Dahlstrom & Wild 1983). By 1892, 1 250 000 kg of crab were landed in California (all of which were from the area near San Francisco Bay). A prohibition against the taking of female crabs was imposed in 1897, and size limits were begun in 1905. Fisheries further to the north developed with new technology and increasing market demands.

For example, significant catches in northern California began about 1935, thereafter increasing to make up the majority of the state's catch by 1945. Fishing presently occurs in waters from 4 m to 90 m in depth – most commonly between 36 m and 65 m.

In California, the major commercial fishing areas occur from Half Moon Bay to Bodega Bay, and from Cape Mendicino to the Oregon border. Smaller fisheries exist near Morro Bay, in Monterey Bay, and near Fort Bragg. Heavy fishing occurs along the entire coast of the State of Oregon, except for small areas near Cape Blanco and south of Cascade Head. In Washington, Dungeness crab fishing extends from the Columbia River to Destruction Island. The fishery is scattered in British Columbia, occurring in various bays and inlets throughout the province. The major fishery area in British Columbia is near Hecate Strait. Commercial fishing is also scattered throughout south-east and south central Alaska, extending westward along the Alaska Peninsula to near Sandman Reefs.

Dungeness crab landings undergo distinct cycles at about 10-year intervals. Since 1954, total landings have ranged between about 7 and 30 million kg/year (Table 12.1). It was recently demonstrated that fluctuations in total landings show a remarkable correlation with mean annual sunspot number (Love & Westphal 1981). In general, the cyclical fluctuations in landings appear to be most pronounced at the southern end of the fisheries' range. Temporally, cyclical patterns in crab landings in California, Oregon, and Washington are well correlated. Landings in Alaska are less distinctly cyclic and not correlated with those farther to the south. Cyclical patterns are not apparent in landings' data from British Columbia. In part, landings' fluctuations in Alaska are influenced by market conditions to the south (Kimker 1981). That is, there is increased incentive to fish in Alaska during periods when landings elsewhere are depressed.

South of Point Arena, Dungeness crab landings failed in the early 1960s, and remain depressed at present. The failure followed a change in oceanographic conditions, most notably an increased warming and intensification of the Davidson Current (Wild *et al.* 1983). Laboratory studies have shown that although elevated water temperatures of the observed range increase growth rates of fertilised crab eggs, they also cause a substantial decline in survival (Wild 1983). Intensification of the Davidson Current may also have caused crab larvae to drift further northward.

Failure of the fishery has been attributed to other causes or contributing factors as well. For example, the nemertean worm (*Carcinonemertes errans*) has been found in a high percentage of crab egg masses (Wickham 1979a). Egg parasitism, together with heavy human exploitation, are thought to produce population cycles of increasing amplitude (Botsford & Wickham 1978) which may have led to the eventual collapse of the central California crab fishery (Wickham 1979b). Increased pollution of San

Table 12.1 Ranges in reported commercial landings of Dungeness crab by state or province.

Location	Landings (kg/year)	
	Minimum	Maximum
California	0.4	9.8
Oregon	1.2	6.7
Washington	2.0	7.9
British Columbia	1.2	2.0
Alaska	0.8	5.1

Francisco Bay, the major nursery area for young crabs, has also occurred over the appropriate time period, as has increased predation by hatchery-reared salmon on the megalopae. Although the fishery probably has been intensively exploited, overexploitation does not appear to have caused its failure directly, since males only are caught, and female impregnation rates have remained high and independent of male landings (Dahlstrom & Wild 1983).

Interactions with sea-otters

A conflict between sea otters and the Dungeness crab fishery developed recently in Orca Inlet, eastern Prince William Sound, Alaska. Landings in Prince William Sound declined initially following the 1964 earthquake, due to reductions in the extent of sublittoral habitat and prey abundance which were caused by tectonic shifts in elevation (Kimker 1982a). Some recovery was expected, based on a strong recruitment of juvenile crabs in 1978. However, in 1980 the fishery was not opened due to a low pre-season crab abundance. This coincided with about 180 sea-otters moving into the area in the process of their natural range expansion (Kimker 1982b). On the basis of this evidence, there may be a substantial potential for conflict between sea-otters and the Dungeness crab fishery along much of the Pacific coast of North America. At a present ex-vessel price of something more than \$2.20 per kg, the economic consequences of this conflict could range into the tens of millions of dollars per year, far exceeding the potential loss from sea-otter depredation on any other shellfishery.

Rock Crabs: *Cancer* spp.

Biology and fishery

Three broadly sympatric species are known collectively as rock crabs: *Cancer antennarius* (Stimpson), *C. anthony* (Rathbun), and *C. productus* (Randall). Rock crabs range from Alaska to Baja California, Mexico, and overlap with much of the original range of sea otters (Morris *et al.* 1980). *Cancer antennarius* is the most abundant rock crab in shallow waters of the exposed rocky coast of California where sea-otters presently occur (Carroll 1982). *C. antennarius* ranges from Oregon to Baja (Morris *et al.* 1980).

The life histories of rock crabs are generally similar to that of the Dungeness crab, *Cancer magister* (see above). Major differences include a preference for a rocky substrate and, for *C. antennarius*, presence of ovigerous females in all seasons of the year (Carroll 1982).

Annual commercial landings for rock crabs in California averaged about 80 000 kg from 1950 to 1970, increasing to 545 000 kg by 1975 (Hardy *et al.* 1982). Rock crabs are also taken by recreational fishermen, primarily with baited hoop nets and traps set from piers, jetties, and skiffs. The recreational fishery seems to be fairly large, but landings data are not available. The total fishery for rock crabs is thought to be near maximum sustainable yield (Hardy *et al.* 1982).

Interaction with sea-otters

Cancer antennarius is one of the most important foods for sea-otters in California (Wild & Ames 1974, Estes *et al.* 1981). However, the impact of sea-otters on rock crab fisheries is not clear. A small (1 fisherman) commercial harvest of *C. antennarius* survives in Estera Bay in spite of the presence of sea-otters in the area (Hardy *et al.*

1982). Rock crabs are regularly taken by sport fishermen at several locations within the range of sea-otters in California.

Populations of *C. antennarius* were studied near Diablo Canyon, California, from 1976 to 1981 (Carroll 1982). Sea-otters were present during the entire study and frequently ate rock crabs near sampling stations. Based on catch per unit effort in bimonthly trap samples, numbers declined gradually from 1976 (7–16 crabs/trap-day) until January 1981 (2–4 crabs/trap-day), but then increased somewhat (4–6 crabs/trap-day) until the study was terminated in April 1981. Since long-term population data are generally not available for rock crabs, it is not possible to determine if the trends described by Carroll are part of a cyclical pattern of the kind seen for *Cancer magister*, or are a result of the cumulative effects of sea-otters.

However, it seems that the effects of sea-otters on harvestable stocks of rock crabs are far less precipitous than those on abalone, sea urchins, or Pismo clams. We suggest that certain behavioural traits of rock crabs may account for the difference. Rock crabs are quite cryptic, especially during daylight hours when they generally are immobile and remain in deep crevices. The utilisation of such refuges probably reduces the efficiency of otter foraging and may contribute to the survival of harvestable stocks in the presence of sea-otters. Other explanations are plausible, however, and there is much to be learned about interactions between sea-otters and rock crabs.

California spiny lobster: *Panulirus interruptus* (Randall, 1840)

Biology and fishery

Spiny lobsters are common in the southern portion of the aboriginal range of the sea otter in North America. Lobsters typically occupy rock substrata at depths of 0–75 m along the open coast, often in association with kelp forests. Lobsters are also found in embayments, rock jetties, surf grass beds, and submarine canyons.

The life history of *Panulirus interruptus* has been summarised by Frey (1971). In California, spiny lobsters typically mate in winter or early spring. Females carry the sperm packet on the ventral surface of the abdomen. Eggs are fertilised at the time of extrusion – usually May or June. Fertilised eggs are carried by the abdominal appendages until hatching, about 10 weeks after fertilisation. Egg production increases with female size; large females may produce up to 800 000 eggs. Hatched phyllosoma larvae are capable of long-range dispersal in the plankton. The phyllosome phase is followed by a deeper-dwelling puerulus which in turn metamorphoses to the adult form.

Growth is typically slow in spiny lobsters. Females mature at age 4–5 years (Mitchell *et al.* 1969). The legal size for harvest is reached in 10–11 years (Frey 1971). Lobsters are omnivorous, feeding on sea urchins, mussels, clams, polychaetes, and various other living and dead organic matter.

Spiny lobsters range from Monterey, California, to Bahia Magdalena, Baja California Sur, Mexico, and an isolated population occurs in the northern Golfo de California (Duffy 1973). There are few recorded sightings of spiny lobsters in Monterey Bay (Schmitt 1921, Faro 1970). The northernmost populations currently known occur at Cayucos Point, Shell Beach, and Point Sal, California. These populations are known only from anecdotal information and appear to be small. Commercial harvesting of spiny lobsters presently occurs from Purisima Point, California, southward to Laguna San Ignacio, Baja California Sur (Guzman del Proo 1975, Barrera *et al.* 1976, California Department of Fish and Game 1976). In California, the best fishing grounds for spiny lobster are the offshore islands and the mainland from Point La Jolla to Point

Loma in San Diego county (Duffy 1973). The bulk of the Mexican harvest comes from the offshore islands and the central Pacific coast of the Baja California peninsula (Guzman del Proo 1975). Lobsters are taken by sport fishermen from Cayucos Point southward in California. The size of the sport harvest is poorly documented (Duffy 1973), but is apparently small relative to the commercial harvest (Hardy *et al.* 1982).

Commercial landings of spiny lobsters in California peaked in the late 1940s, then declined steadily until 1977 (Fig. 12.1a). For 1968–77, annual landings averaged about 120 000 kg/year, about one-third of the figure for 1948–57, in spite of increased fishing effort and consumer demand (Heimann & Carlisle 1970, Pinkas 1970, 1974, 1977, Bell 1971, Duffy 1973, Oliphant 1973, 1979, McAllister 1975, 1976, Hardy *et al.* 1982, California Department of Fish and Game, unpublished). Declining landings were attributed to overexploitation of lobster stocks, particularly as a result of poaching and illicit capture of animals below the minimum size limit (Duffy 1973, Duffy, personal communication, Hardy *et al.* 1982). As a result, fishery laws were changed in 1972, requiring escape ports in all lobster pots so that undersize animals could escape before

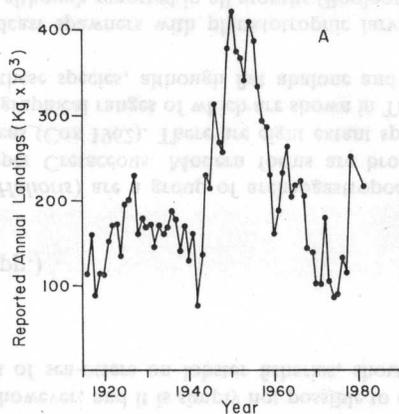


Figure 12.1a Commercial landings of spiny lobster (*Panulirus interruptus*) in California, 1916–78 and 1981 (data for 1979 and 1980 not available.) (From California Department of Fish and Game.)

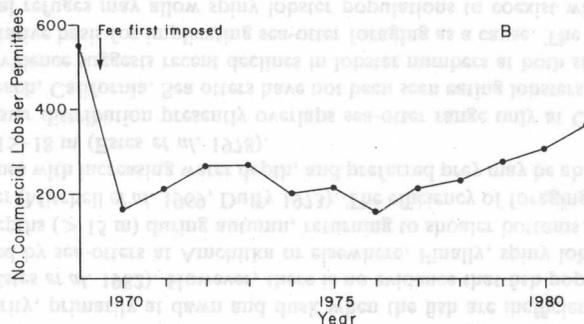


Figure 12.1b Numbers of permits for commercial lobster harvesting in California, 1961–81 (From California Department of Fish and Game.)

the pots were pulled to the surface. Annual landings increased to 254 000 kg in 1978 and 217 000 kg in 1981 (California Department of Fish and Game, unpublished). Increased landings probably resulted from the modified pot design, although the relationship has not been unambiguously established (Duffy, personal communication). A lag of 5–6 years between the imposition of escape-port regulations and increased landings is consistent with known growth rates of spiny lobsters in California, and the size distribution of lobsters at the time regulations were changed.

The numbers of commercial fishermen with state lobster permits dropped markedly in 1970 when fees were first charged for permits. But the numbers of permits began to increase again in the late 1970s (Fig. 12.1b), apparently in response to the increased success of other fishermen (Duffy, personal communication).

In Mexico, annual landings rose from 752 000 kg in 1959 to 1.3 million kg in 1966, and have varied little since that time (Fig. 12.2).

Interaction with sea-otters

There is concern that continued southward expansion of the sea-otter population in California will damage the lobster fisheries (California Department of Fish and Game 1976, Hardy *et al.* 1982). At present, however, there is very little data on which to base predictions of interactions between spiny lobsters and sea-otters. Four captive sea-otters caught and ate 10 live spiny lobsters over a period of 5 hours (Antonelis *et al.* 1981). The extent to which such data apply to natural foraging abilities of sea-otters is unknown. In a field study of sea-otter foraging near Point Lobos, California, 3 of 455 prey items taken were reported to be spiny lobsters (Hall & Schaller 1964). Boolootian (1965) also observed occasional takes of lobsters by sea otters in the Monterey area. These observations are also difficult to interpret, in terms of potential fishery conflicts, because they occurred so far north of commercially significant populations of spiny lobsters. Faro (1970) has suggested that other prey items, such as crabs, were erroneously identified as spiny lobsters by Hall and Schaller and Boolootian.

The potential impact of sea-otters on natural lobster populations is clearly an open question. Spiny lobsters hide in crevices or caves during daylight hours. Other invertebrates which use such microhabitats are protected from consumption by sea-otters (Lowry & Pearse 1973). Lobsters emerge at night, but are capable of swimming rapidly

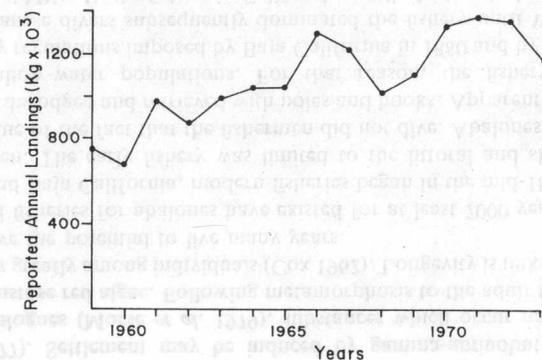


Figure 12.2 Commercial landing of spiny lobsters (*Panulirus interruptus*) along the Pacific coast of Baja California, Mexico, 1959–73. (From Guzman del Proo 1975.)

and forcefully when disturbed. Sea-otters appear to have limited effects on mobile or nocturnal prey. Those at Amchitka Island, Alaska, eat sluggish epibenthic fish with some regularity, primarily at dawn and dusk when the fish are inefficient at escaping predators (Estes *et al.* 1982). However, there is no evidence that fish populations have been depleted by sea-otters at Amchitka or elsewhere. Finally, spiny lobsters migrate to greater depths (> 15 m) during autumn, returning to shoaler bottoms in spring and early summer (Mitchell *et al.* 1969, Duffy 1973). The efficiency of foraging by sea otters clearly declines with increasing water depth, and preferred prey may be abundant below a depth of 15–18 m (Estes *et al.* 1978).

Spiny lobster distribution presently overlaps sea-otter range only at Cayucos Point and Shell Beach, California. Sea otters have not been seen eating lobsters at either site. Anecdotal evidence suggests recent declines in lobster numbers at both sites, but there is no quantitative basis for implicating sea-otter foraging as a cause. The use of spatial and temporal refuges may allow spiny lobster populations to coexist with sea-otters, but this possibility cannot be evaluated on the basis of existing data. It appears that overexploitation, habitual disregard for the minimum size limit, and changing fishery regulations account for at least part of the historical between-year variation in commercial landings of spiny lobsters in California. Much of the life history of spiny lobsters is poorly understood, however, and it is simply not possible to offer confident predictions regarding effects of sea-otters on lobster fisheries, should the two come into contact.

Abalone (*Haliotis* spp.)

Biology and fishery

The abalones (genus *Haliotis*) are a group of archeogastropods whose fossil record dates back to the upper Cretaceous. Modern forms are broadly distributed from subarctic to tropical seas (Cox 1962). There are eight extant species in the north-east Pacific Ocean, the geographical ranges of which are shown in Table 12.2. Commercial fisheries exist for all these species, although flat abalone and threaded abalone are rarely taken.

Abalones are broadcast spawners with planktotrophic larvae (Webber 1977). In California, spawning, although reported in all months (Booolootian *et al.* 1962, Young

Table 12.2 Geographical distribution of abalone species along the west coast of North America.

Species	Range	
	from north	to south
pinto (<i>Haliotis kamtschatkana</i>)	Southeast Alaska	Poiint Sur, California
flat (<i>H. walallensis</i>)	British Columbia	La Jolla, California
red (<i>H. rufescens</i>)	Sunset Bay, Oregon	Bahia Tortuga, Baja California
black (<i>H. cracherodii</i>)	Coos Bay, Oregon	Cabo San Lucas, Baja California
pink (<i>H. corrugata</i>)	Point Conception, California	Bahia Tortuga, Baja California
green (<i>H. fulgens</i>)	Point Conception, California	Bahia Magdalena, Baja California
white (<i>H. sorensenii</i>)	Point Conception, California	Bahia Tortuga, Baja California
threaded (<i>H. assimilis</i>)	Point Conception, California	Bahia Tortuga, Baja California

& DiMartini 1970), occurs mainly from late spring to early fall (Cox 1962). The fertilised eggs form veliger larvae which probably remain in the plankton for a week or less (Webber 1977). Settlement may be induced by gamma-aminobutyric acid and its chemical analogues (Morse *et al.* 1979), substances which occur naturally in certain species of crustose red algae. Following metamorphosis to the adult form, growth rate seems to vary greatly among individuals (Cox 1962). Longevity is unknown; individuals probably have the potential to live many years.

Aboriginal fisheries for abalones have existed for at least 7000 years (Orr 1960). In California and Baja California, modern fisheries began in the mid-1800s with Chinese pole fishermen. The early fishery was limited to the littoral and shallow sublittoral zones by virtue of the fact that the fishermen did not dive. Abalones spotted from the surface were dislodged and retrieved with poles and hooks. Apparently the pole fishery depleted shallow-water populations. For that reason, the fishery was effectively eliminated by regulations imposed by Baja California in 1880 and by the United States in 1900. Japanese divers subsequently dominated the fishery until World War II.

Before World War II, the fishery in California was limited exclusively to red abalone. It was centered in Monterey until about 1930, switching thereafter to Morro Bay and expanding southward to southern California after the war. With the advent of rubber diving suits, the fishery also moved into deeper water after the war. British Columbia and Alaska support commercial fisheries for pinto abalones. These fisheries greatly intensified in the mid-1970s in response to the development of a Japanese market. There have never been commercial abalone fisheries in Oregon or Washington.

The Mexican abalone fishery occurs exclusively within the historical range of the sea-otter. Baja California Sur currently produces about 80% of the landings (Anonymous 1978). There are four management zones for abalone in Baja California (see Luch Belda *et al.* 1973 for map of zone boundaries), from which five species are exploited. Landings data are available by zone from 1956 (we have been unable to obtain zone-specific data subsequent to 1970). Overall, the fishery reached maximum production in about 1950, at around 6 million kg per year (Luch Belda *et al.*, 1973, Guzman del Proo 1975), followed by a sharp decline to about 3 million kg per year by 1955 (Fig. 12.3a). Landings continued to decline, reaching about 2 million kg per year by 1974. Around 4 million kg were landed in 1978 (Anonymous 1978). Red abalone are common only in Zone I (Table 12.3). White abalone also comprise a significant part of the landings in this zone. Pink and green abalone comprise the bulk of reported landings in the other three zones.

Landings in Zone I reached a maximum of about 450 000 kg per year in 1957, declined to near zero in 1964, and then increased to about 150 000 kg per year in 1970. Landings in Zone II reached a maximum of about 1.5 million kg per year in 1956, then declined to about 900 000 kg per year by 1970. Zone III contains a younger fishery than zones I or II. It produced maximum landings (about 2 million kg per year) in the early 1960s, followed by a moderate decline. Zone IV contains the youngest fishery. It began at about 500 000 kg per year in 1956 and increased slowly to about 700 000 kg per year in 1971. At that time there was no evidence of a decline in landings, although the catch now appears to be composed mostly of small individuals.

In addition to these patterns of growth and decline in the fisheries, analyses of CPUE and size composition of landed abalones support the view that stocks in Baja California have been overexploited. For example, at Isla de Cedros (Zone II), landings of pink and green abalones declined from 165 kg/diver per day in 1964 to 105 kg/diver per day in 1975. At Punta Abreojos (Zone IV), the catch per unit effort declined from

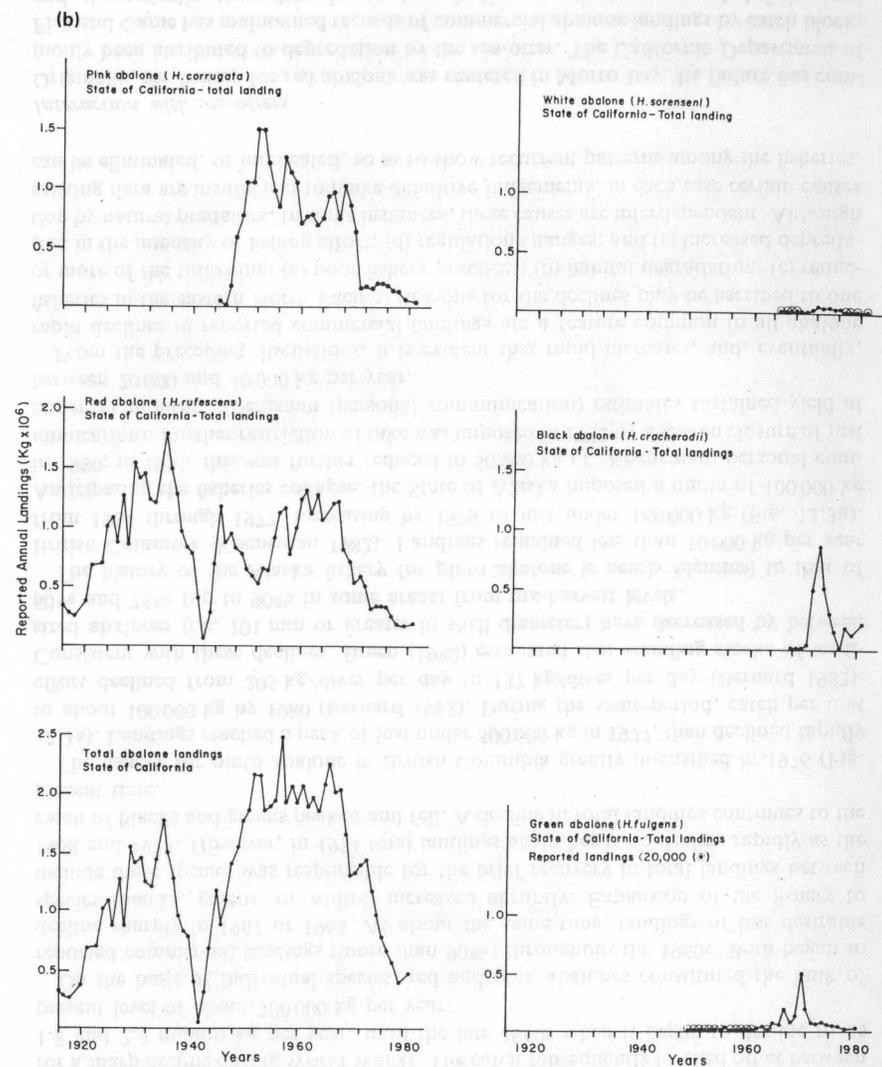
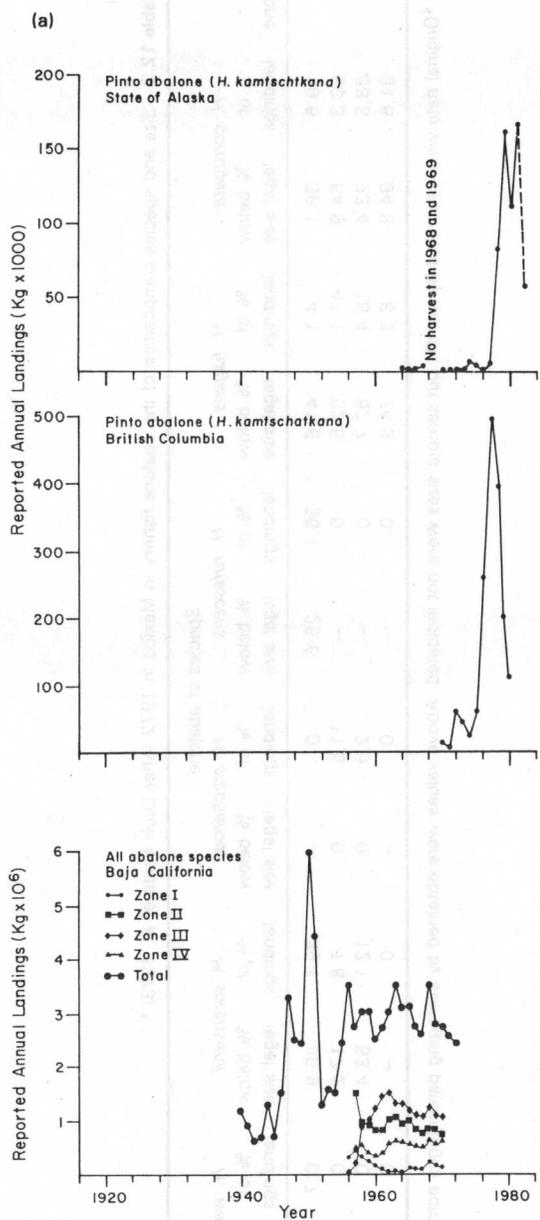


Figure 12.3 Commercial landings of abalones along the west coast of North America, 1916–81. (a) Mexico, British Columbia and Alaska; (b) California. (From: Mexico, Luch Belda *et al.* 1973; California, Cox 1962 and California Department of Fish and Game; British Columbia, Breen 1980 and Bernard 1982; Alaska, Koeneman 1982.)

Table 12.3 Size and species composition of the abalone fishery in Mexico in 1972 (after Luch Beida *et al.* 1973).^a

zone	Species of abalone												
	<i>H. corrugata</i>		<i>H. fulgens</i>		<i>H. rufescens</i>		<i>H. cracherodii</i>		<i>H. sorensenii</i>		<i>H. walallensis</i>		
	% of landings	% below legal size	% of landings	% below legal size	% of landings	% below legal size	% of landings	% below legal size	% of landings	% below legal size	% of landings	% below legal size	
I	19.6	38.1	4.1	41.6	36.1	25.6	0	11.5	0	39.4	25.9	0.7	0
II	53.3	64.9	41.1	52.5	0	—	—	17.2	1.8	—	—	—	—
V	68.5	73.4	18.4	62.7	0	—	2.9	53.4	12.1	0	—	0	—
	91.6	94.8	8.3	74.8	0	—	0	—	0	—	—	0	—

^aOriginal data were separated by month, but sample sizes were not indicated. Above values were obtained by averaging percentages across months.

90 kg/diver per day to 60 kg/diver per day during the same period (Doi *et al.* 1977). For all species of abalones in all areas, animals below minimum legal size make up a substantial portion of the landings (generally between 40% and 80% of the catch — (Table 12.3). In Zone IV, where annual landings had not declined by 1971, nearly the entire catch was below minimum legal size in 1972.

Landings data for abalone from California show similar patterns (Fig. 12.3b). Total landings increased gradually from the early part of this century until about 1950, except for a sharp decline during World War II. The catch subsequently levelled off at between 1.8 and 2.3 million kg per year, until the late 1960s when it began to decline to its present level of about 700 000 kg per year.

On the basis of individual species, red and pink abalones constituted the bulk of reported commercial landings (more than 90%) throughout the 1960s. Both began to decline sharply in 1967 or 1968. At about the same time, landings of less desirable species (blacks, greens, or whites) increased abruptly. Expansion of the fishery to include these species was responsible for the brief recovery in total landings between 1968 and 1973. However, in 1974 total landings again began to decline rapidly as the catch of blacks and greens peaked and fell. A decline in total landings continues to the present time.

The fishery for pinto abalone in British Columbia greatly intensified in 1976 (Fig. 12.3a). Landings reached a peak of just under 500 000 kg in 1977, then declined rapidly to about 100 000 kg by 1980 (Bernard 1982). During the same period, catch per unit effort declined from 205 kg/diver per day to 137 kg/diver per day (Bernard 1982). Consistent with these declines, Breen (1980) estimated that standing stocks of legal-sized abalones (i.e. 101 mm or greater in shell diameter) have decreased by between 60% and 75% (up to 90% in some areas) from pre-harvest levels.

The history of the Alaska fishery for pinto abalone is nearly identical to that of British Columbia (Koeneman 1982). Landings remained less than 10 000 kg per year from 1964 through 1977, increasing by 1979 to just under 160 000 kg (Fig. 12.3a). Anticipating the fisheries collapse, the State of Alaska imposed a quota of 100 000 kg in 1980; in 1981, this was further reduced to 50 000 kg (T. Koeneman, personal communication). Further restriction of take was imposed in 1982 by a season closure of just under 11 months. Koeneman (personal communication) estimates sustained yield at between 20 000 and 40 000 kg per year.

From the preceding discussions, it is evident that rapid increases, and, eventually, rapid declines in reported commercial landings are a feature common to all abalone fisheries in the eastern North Pacific. Reasons for the declines may be ascribed to one or more of the following: (a) poor fishery practices; (b) habitat degradation; (c) reduction in the intensity of fishing effort; (d) regulation changes; and (e) increased depredation by natural predators. In some instances, these causes are interdependent. Although existing data are insufficient to make definitive judgements, in each case certain causes can be eliminated, or implicated, so as to show recurrent patterns among the fisheries.

Interaction with sea-otters

Originally, the fishery for red abalone was centered in Morro Bay. Its failure has commonly been attributed to depredation by the sea-otter. The California Department of Fish and Game has maintained records of commercial abalone landings by catch block, and, theoretically, these data should show declines as sea otters expanded their range into areas occupied by the fishery. However, fishermen apparently did not adhere to accurate reporting, so that early in the period during which otters are thought to have

depressed the commercial fishery, many fishermen simply worked further to the south while continuing to report landings from their original catch blocks. Later, as they became aware of the problems this was creating in data interpretation, there was a rapid shift in the location of reported landings. Consequently the data do not provide an accurate view of how sea-otters influenced the fishery. In this specific instance it is difficult to separate the effects of sea-otters from the effects of human exploitation, although it seems likely that otters contributed substantially both to the rate and to the extent of the fisheries' collapse.

Populations of black abalone in central California are also thought to have been greatly reduced by sea-otter predation. Again, unfortunately, the history of this fishery is difficult to interpret, except in a general way. There has never been a commercial fishery for black abalone in central California, and since records are not kept of sport landings, documentation of population declines following range expansion of sea otters is mainly a subjective one. There are stretches of private coast south of the Big Sur area from which the public has been largely excluded. These areas supported abundant standing stocks of black abalone before the arrival of sea-otters. Because most of the populations declined following the arrival of sea-otters, it has been inferred that otter predation was the principal cause (E. E. Ebert, personal communication).

Perhaps the most objective analysis of the sea-otter's influence on populations of red abalones comes from habitat survey data obtained by the California Department of Fish and Game in the Point Estero region. From 1965 to 1967, abalone density in this area ranged from about 0.075 to 0.085 individuals/m². After sea otters reoccupied the area, red abalone density declined to about 0.01 individuals/m² (Wild & Ames 1974).

Collectively, these data and observations leave little doubt that sea-otters have eliminated or hastened the decline of certain abalone fisheries. However, the history of abalone fisheries from outside of the sea-otters' range in California (i.e. commercial fisheries for pink, green, white, and black abalones) and elsewhere (Canada and Mexico) demonstrates that other factors have also been important. Among these, commercial exploitation was probably the most important. In retrospect, it seems unfair to place the blame for this solely on poor management practices because abalone appear to possess life history characteristics which make them especially susceptible to over-exploitation (Harrison 1969, Sainsbury 1977, Breen 1980). Initial landings were probably all composed of accumulated stocks of old individuals. Consequently, initial catch characteristics were in no way indicative of their sustainable productivity (Breen 1980).

Since abalones appear to be long-lived, slow-growing species, high initial rates of human exploitation quickly drove the fisheries to the left side of their yield-biomass curves (i.e. beyond MSY). It is not surprising, therefore, that the commercial fishery never persisted long in any given area, since it was not economically feasible for it to do so. This point is exemplified by the extremely concentrated nature of fishing effort at any specific time in the recent history of the fishery. For example, when Bissell and Hubbard (1968) reported on the status of the red abalone fishery in California, 59% of the commercial landings (composing 32% of the total statewide) were from Morro Bay. At that time, 70% of the Morro Bay landings (22% of the total state landings) came from about 9 miles of coastline between Point Estero and Cambria.

As might be expected of such fisheries, perturbations which influenced catch availability also produced immediate and dramatic effects on reported landings. The two most obvious of these perturbations were depredations by sea-otters and regulation changes. The influence of regulation changes can be clearly seen in several instances. For example, in 1959, when the minimum legal size for commercial take of red abalone

was reduced from 20.3 cm to 19.7 cm (maximum shell diameter), landings increased sharply. In 1971, minimum legal size for green abalone was reduced from 18.4 cm to 17.8 cm. This resulted in a substantial increase in landings of green abalone initially, although since growth rate in this species is thought to be very low as individuals approach minimum legal size (E. E. Ebert, personal communication), landings declined again after the largest size-class was reduced. The sharp reduction in landings of pink abalone in 1971 was mainly the result of increasing the minimum size limit from 15.25 cm to 15.9 cm. If abalone populations were being exploited at levels such that they existed on the right slope of their yield-biomass curves (i.e. exploitation rate < than MSY), perturbations of these types would not be expected to have such extreme and immediate effects on the fishery.

To complicate matters, the following factors contribute to the difficulties in managing abalone fisheries at the desired level of MSY (Hardy *et al.* 1982).

- (a) Although largely undocumented, there seems to be a great deal of geographical variation in growth rate and recruitment success, even within species. In fact, substantial variation of these factors frequently occurs over very short distances (E. E. Ebert, personal communication). In some areas, abalones appear to recruit infrequently. Yet, due to their long life span, large standing stocks accumulated over the years before exploitation, consequently producing high initial yields but resulting in virtually no potential for a sustained fishery. Assessment of recruitment success is complicated by the fact that small size-classes of abalones are highly cryptic in their behaviour.
- (b) Beyond the effect of exploiting large adults, it is still unknown to what extent mortality at various stages in the life history of abalones is capable of limiting production. Conceivably, by increasing the abundance of larvae or the survival of recently metamorphosed juveniles, or by enhancing successful metamorphosis, one could enhance the productivity of abalone fisheries. However, it is equally conceivable that one or more of their life-history stages is not critical to potential population growth (e.g. if they show density independence at that particular stage over some range in density). Until this question is resolved, there is little reason to expect that management directed at the enhancement of any one of these stages is very likely to increase production of the fisheries.
- (c) A final problem with the management of abalones stems from the fact that market values have soared with declining availability. For example, ex-vessel prices for red abalones have experienced a 200-fold increase, from \$0.50/dozen during the 1930s and 1940s to \$100/dozen at the present time (Pleschner 1982). One consequence of this is that there is little chance that abalone fisheries will become self-regulating. A more stable market, in contrast, could be expected to limit commercial exploitation once the density of legal-sized adults was reduced to some particular level (Clark 1973). Another consequence of a high market value is the development of poor fishery practices. For example, the taking of undersized specimens almost certainly has increased with the prospect of windfall profits. It also is thought that fishermen, by excessively handling and examining slightly undersized individuals, have increased the mortality of already heavily exploited populations.
- (d) Information on landings by the recreational fishery is lacking, although it is speculated that their total equals or exceeds that of the commercial fishery (E. E. Ebert, personal communication).

Northern razor clam: *Siliqua patula* (Dixon, 1789)

Biology and fishery

Northern razor clams are abundant through much of the present and former ranges of sea-otters in the North Pacific. Razor clams are solenid bivalves found from Pismo Beach, California, northward through the Aleutian Islands, occurring from the low intertidal to 40 m depth (Blunt 1980, Morris *et al.* 1980), along sand beaches exposed to oceanic swell or strong tidal currents. Razor clams are suspension feeders capable of rapid burrowing in loosely consolidated sands; permanent burrows are not constructed.

The sexes are separate and fertilisation is external in northern razor clams (Morris *et al.* 1980). Spawning begins when water temperature exceeds 13°C, which occurs in May and June in Washington (Morris *et al.* 1980), and in July and August in Cook Inlet, Alaska (Nosho 1972). Larvae remain mobile for about 8 weeks. They are able to swim but spend much of the time resting on the sand (Morris *et al.* 1980, Rudy & Rudy 1983). Successful recruitments produce juvenile densities of up to 16 000/m², but juvenile mortality rates are very high, particularly during storms (Amos 1966, Rudy & Rudy 1983).

Growth rates of northern razor clams vary across latitude, and on small spatial scales as well. Sexual maturity (shell length 10 cm) is reached in 5–7 years in Alaska (Weymouth *et al.* 1931, Nickerson 1975), and in 3–4 years farther south. Minimum size for commercial harvest (11.4 cm) is reached in about 4 years in Washington and Oregon, 3–4 years in British Columbia, and 5–9 years in Alaska (Weymouth *et al.* 1931, Amos 1966, Nickerson 1975, Paul & Feder 1976, Bernard 1982).

Historically, the harvest of northern razor clams was a substantial commercial enterprise. Annual landings in Alaska exceeded 2.2 million kg in 1917, but fluctuated wildly in subsequent years as a result of localised stock depletion and variable market conditions (Orth *et al.* 1975). More recently, the Alaskan commercial harvest has been hindered by competition with north-west Atlantic clam fisheries, occasional outbreaks of paralytic shellfish poisoning, and severe habitat degradation associated with the calamitous 1964 earthquake (Baxter 1971, Orth *et al.* 1975). Annual landings averaged 134 000 kg for 1960–63, falling to 23 000 kg during 1964–74 (Fig. 12.4). Commercial

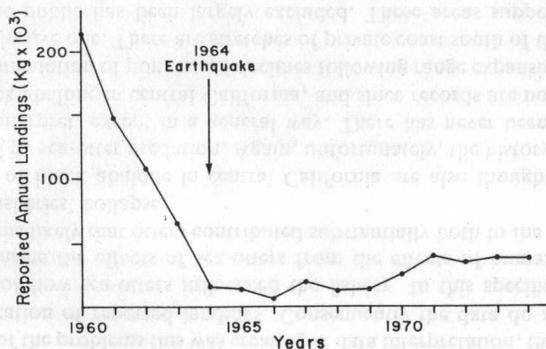


Figure 12.4 Commercial landings of northern razor clams (*Siliqua patula*) in Alaska, 1960–74. (From Orth *et al.* 1975.)

gathering of razor clams in Alaska now occurs at scattered locations on the Alaska Peninsula, Cook Inlet, Prince William Sound, and the Copper River Delta. Over 90% of the harvest is used to supply bait for the Dungeness crab fishery of the North Pacific (Orth *et al.* 1975).

In British Columbia, razor clams are abundant only at Long Beach on the west coast of Vancouver Island, and on beaches near Masset on the north-east coast of Graham Island in the Queen Charlotte Group (Bernard 1982). The commercial harvest of the Province occurs entirely at Masset. Commercial clamming began in 1924, primarily to produce canned clams for human consumption. Substantial fluctuations in landings over the years were caused by variable stock size, changing market conditions, and changing availability of labour and shipping facilities (Bernard 1982). Commercial canneries closed in the late 1960s, and the bulk of commercial landings since that time have been used as bait for the Dungeness crab fishery. Since 1970, annual landings have been variable, ranging from 18 000 kg to 100 000 kg (Bernard 1982).

Limited commercial harvesting is carried out in Washington and Oregon. The Washington fishery is located in the Willapa Spits area, producing annual landings of 3500–14 000 kg which are used primarily for Dungeness crab bait (Northup personal communication, Burge, personal communication). In Oregon, most commercial digging is done between Tillamook Head and the Columbia River. Annual landings have ranged from 18 000 kg to 55 000 kg in recent years, and most of the harvest is marketed as fresh meat for human consumption (Snow, personal communication).

Northern razor clams are collected throughout their range by sport diggers. Sport harvesting is particularly intensive in Washington and Oregon. During the period 1974–80, annual sport landings averaged 941 000 clams in Oregon (Snow, personal communication), and 10.1 million in Washington (Burge, personal communication). Recent recruitment failures in Washington and Oregon, possibly resulting from excessive harvests, have led to the imposition of foreshortened seasons and reduced daily bag limits by management agencies (Snow, personal communication). Important sport harvests also occur in California between Humboldt Bay and the Smith River (Blunt 1980), in British Columbia at Long Beach, Vancouver Island (Bernard 1982), and in Alaska in the Clam Gulch area of the Kenai Peninsula (Paul & Feder 1976).

Interaction with sea-otters

Sea-otters consume razor clams with some regularity in Alaska (Johnson 1982), but there is no documentation of the impact of sea-otters on clam populations. Sea-otter numbers have increased markedly in eastern Prince William Sound and off the Copper River Delta within the past decade (Pitcher 1975, Johnson 1982, Kimker, personal communication). Clam stocks in these areas were severely damaged by tectonic uplift and tsunami scour during the 1964 earthquake (Baxter 1971, Hanna 1971, Noerenberg 1971). There is no evidence that damaged stocks had recovered significantly when sea otters moved into the area in the late 1970s (Paul & Feder 1976). Therefore, the depressed status of razor clam stocks in the Prince William Sound–Copper River Delta areas cannot be attributed solely to the activities of sea-otters.

Sea otters have been seen eating razor clams in southern Oregon (Jameson, personal communication), and in California at Atascadero Beach, near Morro Bay (Burge, unpublished; Fitch, unpublished). There is some evidence that razor clam densities were reduced by sea-otter foraging at Atascadero Beach (California Department of Fish and Game 1976).

Pismo clam: *Tivela stultorum* (Mawe, 1823)

Biology and fishery

Pismo clams are venerid bivalves overlapping in range with the southern portion of the aboriginal distribution of sea otters in North America. Pismo clams are known from Halfmoon Bay, California, southward to Isla Socorro, Islas Revillagigedos, Mexico (Fitch 1950, 1953, Morris *et al.* 1980), occurring on surf-swept sand beaches from the intertidal zone to 25 m depth. In recent years, few Pismo clams have been seen north of Monterey Bay. Pismo clams are filter feeders. Unlike northern razor clams, which also occur on exposed beaches, Pismo clams have thick, heavy shells and are unable to burrow rapidly.

The natural history and ecology of Pismo clams have been reviewed by Fitch (1950). The sexes are separate; fertilisation is external, and spawning occurs annually in summer and autumn, generally following a rise in sea surface temperature. Spawning females may release up to 20 million eggs in a single season. Larvae apparently remain in the plankton for several weeks before settlement and metamorphosis. Major recruitments are often separated by many years, may be site specific, and do not appear to correlate with the size of breeding stock.

Growth rates of individual Pismo clams can vary substantially between years and between sites, even on a small scale (Coe 1947, Fitch 1950). Pismo clams typically become sexually mature at the age of 1 year and at a size of 3–5 cm (maximum shell length). Growth to minimum size for legal sport harvest in California (12.7 cm in Monterey Bay, 11.4 cm at Pismo Beach and Morro Bay) requires 3–9 years (Fitch 1950).

Pismo clams were harvested commercially in California from 1916 to 1947. Annual landings peaked at 302 000 kg in 1918 (Aplin 1949) and declined thereafter, except for moderately increased landings in 1923–5 and 1934–7 (Fig. 12.5). Commercial harvesting of Pismo clams still occurs in Mexico, but species-specific landings data for bivalves are not available at present. From 1935 to 1947, up to 24 million kilograms per year of fresh Pismo clams were imported from Mexico into California (Aplin 1949). Most of the commercial harvest in California was taken from beaches near Morro Bay and at Pismo Beach and Oceano (Herrington 1929). Pismo clams are harvested from

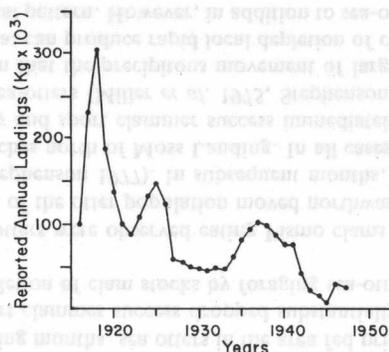


Figure 12.5 Commercial landings of Pismo clams (*Tivela stultorum*) in California 1916–47. (From California Department of Fish and Game.)

many locations in Mexico; beaches near Bahia San Quintin are perhaps the best known (Aplin 1947).

The ultimate collapse of the commercial Pismo clam harvest in California was apparently due to a combination of infrequent recruitment, poor juvenile survival, and chronic overexploitation. Management authorities expressed concern over these problems as early as 1923, and frequently thereafter (Weymouth 1923, Herrington 1926, 1929, Clark 1928, 1929, 1931, 1932, Scofield 1931, Croker 1932, Roedel 1939, 1942), calling for increased restrictions of harvesting and better enforcement of management policies. Each of the three peak periods of commercial harvest (1917–19, 1924–6 and 1935–9) was sustained largely on the strength of a few dominant year-classes. Recruitments in intervening years were not adequate to maintain commercial exploitation at high levels. Occasional pollution problems and natural disasters may have contributed to declining clam stocks (Weymouth 1919, Anonymous 1922). Pismo clams are apparently capable of concentrating the toxins of paralytic shellfish poisoning, but traditional processing techniques seem to remove toxic tissues. No cases of human poisoning from Pismo clams are known (Fitch 1950).

Pismo clams are harvested throughout their range in California by sport fishermen. Historically, the most popular sport clamming sites in central California have been the beaches in Monterey Bay, near Morro Bay, and near Pismo Beach (Miller *et al.* 1975). The best clamming locations in southern California are in Ventura, Los Angeles, and Orange counties (Knags *et al.* 1976, 1977).

Following the closure of the commercial fishery, the success of sport harvesting of Pismo clams in central California has been plagued by infrequent recruitment success and poor juvenile survival. Of particular concern is the chronically high mortality rate of small clams, apparently resulting from improper sport digging (Fitch 1950). Recruitment failures have occurred at all clamming beaches, but the problem is most acute at Atascadero Beach, just north of Morro Bay. Here, major recruitments have been recorded only in 1944 and 1972. Minor settlements occurred in the intervening years, but rates of juvenile survival were poor (Fitch 1952, 1954, Baxter 1962, Carlisle 1966, 1973). In a 1971 census effort, no Pismo clams of any size were found at Atascadero Beach (Carlisle 1973). However, the recruitment of 1972 produced a dense population of juveniles (Burge 1979). The above patterns are based on data from beach transect censuses traditionally used by the California Department of Fish and Game (review in Fitch 1950). In recent years, the Department has used interviews with sport clambers to develop indices of catch per unit effort as a second method of stock assessment (Miller *et al.* 1975, Burge 1979). Clammer interview data have suggested a more positive picture of the status of Pismo clam stocks in California, in some cases contradicting results of transect censuses. For example, clammer interviews at Atascadero Beach indicated relatively high success rates before 1973 (Burge 1979), in marked contrast to the dismal status reports based on transect data (Carlisle 1973).

Interaction with sea-otters

Sea otters began to re-enter Pismo clam habitat in the early 1970s. At the southern end of their range, sea-otters were first seen eating Pismo clams in February 1973 at Atascadero Beach (Wild & Ames 1974, Wade 1975). Otters foraging along the beach ate Pismo clams almost exclusively. Clam stocks appeared to be depleted at Atascadero Beach by autumn 1974, a loss attributed to foraging by sea-otters (Miller *et al.* 1975). Sea otters began eating Pismo clams at Morro spit (south of Atascadero Beach) in

February 1975 (Miller *et al.* 1975). In January 1979, sea otters moved in numbers south of Point San Luis and began feeding on Pismo clams near Pismo Beach and, later Oceano. In the following months, sea otters in the area fed primarily on Pismo clams. Clam density and sport clammer success dropped substantially during this time, suggesting significant depletion of clam stocks by foraging sea-otters (Burge 1979, Hardy *et al.* 1982).

In April 1973, sea-otters were observed eating Pismo clams near Moss Landing, as the northernmost part of the otter population moved northward across Monterey Bay (Miller *et al.* 1975, Stephenson 1977). In subsequent months, otters were seen eating these clams along beaches north of Moss Landing. In all cases, substantial reductions of Pismo clam density and sport clammer success immediately followed the onset of foraging activity by sea-otters (Miller *et al.* 1975, Stephenson 1977).

There is no question that the precipitous movement of large numbers of sea-otters into Pismo clam habitat can produce rapid local depletion of clam stocks. Indeed, this appears to be the typical pattern. However, in addition to sea-otter predation, there are other influences, in a long-term sense, on the demography of Pismo clam populations. As a specific case in point, we question the importance of sea-otter predation in the apparent failure of the 1972 clam cohort at Atascadero Beach to survive to harvestable size (Burge 1979). As noted above, juvenile survival rates of Pismo clams have been historically low at Atascadero Beach, regardless of the presence of sea otters. In 1974, high mortality rates were reported for clams of the 1972 year-class at Atascadero Beach, not because of sea-otter predation, but because of disturbance by sport clammers seeking northern razor clams (California Department of Fish and Game, unpublished). We suggest that other mortality sources may have contributed to the demise of the 1972 clam cohort, and that sea-otter predation is not the only explanation consistent with available data, both current and historical. A second case in point is the relatively recent discovery of a population of Pismo clams at Port San Luis, northwest of Pismo Beach (California Department of Fish and Game, unpublished). This area has been within the sea-otter range since 1979. Little is known about the dynamics of the population, but sea-otter predation apparently has not occurred.

An additional unresolved issue is the possible effect of motor vehicle traffic on survival rates of juvenile clams. At present, vehicular traffic is permitted on Pismo clamming beaches south of Pismo Beach. Traffic levels are often high, particularly on holiday weekends, when traffic jams and collisions are frequent. Vehicular travel extends across the intertidal zone during low tide, overlapping with tidal zones in which juvenile Pismo clams are most abundant (Baxter 1961). Vehicular disturbance may contribute to reduced survival of young clams; to date, however, there has been no documentation of the effects of motor vehicles on Pismo clams (L. Laurent, personal communication).

The recognition that sea otters can reduce Pismo clam densities to low levels raises two additional issues of a more general nature, both relevant to the development of management schemes for Pismo clams and sea-otters. The first involves the economic consequences of substantial reduction of a relatively localised sport fishery. In the mid-1970s, the prospect of 'reoccupation' of the Pismo Beach area by sea-otters caused widespread expressions of concern for the local tourist-based economy, thought to rely heavily on visitors attracted to the area by the opportunity to dig or dive for Pismo clams. A recent socioeconomic analysis suggests, however, that the economic impact of a loss of clam resources may be small, perhaps insignificant, in the Pismo Beach area (Holt 1982, Holt *et al.* in press). While these analyses are by no means the last word,

they raise the intriguing hypothesis that it is the beach, not the clams, that draws people and dollars to Pismo Beach. The second issue is the extent to which depletion of Pismo clam stocks by sea-otters will persist in time. Fundamental to this question are certain aspects of the life histories of Pismo clams and sea-otters, which we will now review.

Pismo clam recruitment occurs primarily on beaches exposed at low tide, and individual clams produce identifiable annual growth rings in the shell. Thus, age structure and recruitment success can be determined more readily in Pismo clams than in most other shellfish subject to predation by sea-otters. Samples of clams were gathered annually by the California Department of Fish and Game at most major clamming beaches from 1923 to 1965 and from 1971 to the present. Data collected through 1971 have been summarised by Fitch (1952, 1954, 1955), Baxter (1961, 1962), and Carlisle (1966, 1973). These data indicate that major settlements of clams can be separated by up to 18 years on beaches south of Pismo Beach, and up to 28 years on Atascadero Beach. As noted by Tomlinson (1968), there appears to be no correlation between adult breeding stock size and annual recruitment of juvenile Pismo clams. Finally, we note that Pismo clams reach sexual maturity at an age corresponding to a shell length of 3–5 cm (Fitch 1950). For unknown reasons, sea otters are apparently unwilling or unable to eat clams smaller than about 6–7 cm in length (Miller *et al.* 1975, Stephenson 1977). Thus, some reproductive clams survive in the presence of sea-otters.

Occupation of new areas by sea-otters tends to occur in a predictable sequence of events in California. First occupants are typically dense groups of males which often congregate at range peripheries. The male groups tend to forage on a few relatively abundant prey species of high energy value when an area is first occupied. As readily available food declines in abundance, male groups move to new areas and are replaced by breeding females, territorial males, and dependent pups (Wild & Ames 1974, Estes *et al.* 1981, R. Jameson personal communication). This transition is accompanied by a drop in sea-otter density, often by a factor of ten or more. In sand beach areas, the transitional decline in density may be even greater because breeding otters seem to avoid permanent residence in open sand areas, at least in California (California Department of Fish and Game 1976).

Given the above information, we believe that the long-term influences of sea otters on Pismo clam populations remain uncertain. At present, high-density male groups occur in California in relatively close proximity to all major Pismo clam beaches. Should male groups move away from clam beaches in the course of continued expansion of the sea-otter population, predatory pressure on Pismo clams could decline substantially. As noted, clam stocks affected by foraging sea otters retain the potential to generate successful recruitments. Given sufficient time for successful recruitment (perhaps a decade or more), depleted clam stocks should increase in density, possibly to a level adequate to sustain a limited sport harvest. The time course of these events is entirely uncertain. The movement of male groups of sea otters may be related to continued growth of the population, a process very much in doubt at present (US Fish and Wildlife Service 1982). Recruitment frequency of clams cannot be predicted, nor can we predict how quickly sea otters might 're-discover' recovered clam stocks and again increase foraging effort and reduce the stocks. We offer this view as a plausible alternative to the argument of Hardy *et al.* (1982), that sea otters have irrevocably eliminated Pismo clam fisheries in central California. At present, we suggest that data are insufficient to select a model most appropriate to describe the long-term fate of the clam fishery. However, we reiterate our agreement that recent precipitous reductions in Pismo clam stocks in central California have been caused by sea otters, and we doubt

that recovery of depleted stocks will occur as long as high-density groups of male otters remain near major clamming beaches.

Butter clam: *Saxidomus giganteus* (DeShayes, 1839)

Biology and fishery

The butter clam is an infaunal venerid bivalve which occupies mud, mud-sand, or mud-gravel substrata in bays or, more rarely, along semi-protected beaches from the Aleutian Islands to San Francisco (Morris *et al.* 1980, Rudy & Rudy 1983). Butter clams are found from the low intertidal to depths of 30 m, living from a few centimetres to 30 cm below the sediment surface. Butter clams are filter feeders. Mobility is limited, although siphons can be retracted when disturbed (Morris *et al.* 1980, Rudy & Rudy 1983).

The sexes are separate in butter clams. Spawning occurs in summer or autumn when water temperatures reach 12–20°C (Nosho 1972, Rudy & Rudy 1983). Fertilisation is external. Larvae are planktonic, reach veliger stage in about 2 weeks, and metamorphose and settle about 4 weeks after fertilisation. Because spawning is apparently temperature dependent, successful recruitment may be infrequent and variable between locations, particularly in more northerly populations (Nosho 1972). In some instances, significant recruitments may be separated by up to 20 years (Quayle & Bourne 1972).

Butter clams become sexually mature at shell lengths of about 40 mm (Quayle & Bourne 1972). Growth rates are typically very slow. In Alaska, maturity is reached in 5–6 years, harvestable size (64 mm) in 8–20 years (Fraser & Smith 1928, Baxter 1965, Paul & Feder 1976).

Butter clams are rare in California south of Humboldt Bay, where a small commercial harvest occurs (Morris *et al.* 1980). Commercial harvests are also small in Oregon (J. Lannon, personal communication), although they are common in coastal bays and estuaries (Rudy & Rudy 1983). Clam stocks in Puget Sound and coastal bays in Washington provide 99% of commercial landings of butter clams in the United States (Amos 1966). From 1975 through 1978, annual landings of butter clams in Puget Sound averaged 24 000 kg (Burge, personal communication).

The largest commercial fishery for butter clams is in British Columbia (Amos 1966), where annual landings averaged 600 000 kg during the 1970s (Bernard 1982). Between-year variations in landings are substantial, but no long-term trend has been apparent in Canadian landings since 1970 (Bernard 1982).

Commercial harvesting of butter clams in Alaska is largely undeveloped (Paul & Feder 1976). A small fishery developed in southeastern and south central Alaska in 1930, producing annual landings of about 10 000 kg until the mid-1940s. In 1946, changes in regulations occurred in response to problems with paralytic shellfish poisoning. The economic consequences of the regulations were such that the fishery collapsed in 1955 (Nosho 1972). At present, the Alaskan commercial harvest survives on a very small scale in a portion of Cook Inlet, where problems with paralytic shellfish poisoning occur infrequently (Orth *et al.* 1975).

Commercial exploitation of this species has been severely retarded by several factors. Butter clams concentrate the toxins of paralytic shellfish poisoning to a greater degree and for longer time periods than most other commercially harvested bivalves (Orth *et al.* 1975). Toxins are concentrated in the siphon and gills and may remain at high levels for up to 2 years after ingestion of the plankton (Quayle & Bourne 1972). In areas where blooms of *Gonyaulax* occur annually, butter clams may contain toxins con-

tinuously. Processing methods are available for removal of toxic clam tissues, but they are economically unattractive because they are labour intensive and involve considerable loss of clam meat. Since 1951, 22 cases of paralytic shellfish poisoning of people in Alaska have been attributed to consumption of butter clams; 2 of the cases were fatal (Orth *et al.* 1975). The threat of paralytic shellfish poisoning forces frequent seasonal closures of fisheries in some areas, and has led to permanent closure of some coastal areas in British Columbia (Bernard 1982).

Full development of butter clam fisheries is also restricted by techniques currently used in commercial harvests. Most commercial clamming is done with hand-operated forks or shovels, although some mechanised digging is carried out in Puget Sound (Paul and Feder 1976, Bernard 1982, Burge, personal communication). Annual landings of butter clams are apparently far below potential yields in British Columbia and Alaska, but the economic status of the clam fishery is sufficiently precarious that harvesting interests are unwilling to make the capital investments necessary to convert to more efficient and productive mechanical techniques (Orth *et al.* 1975, Bernard 1982).

Butter clam stocks are susceptible to natural catastrophic mortalities. The great earthquake of 1964 damaged most stocks of butter clams in Prince William Sound, Alaska (see below), and recovery of populations has not occurred (Paul & Feder 1976).

Butter clams are gathered by sport clammers throughout their range in California, Oregon, Washington, and British Columbia, and along the entire southern coast of Alaska. There are no published records of sport landings.

Interaction with sea-otters

The butter clam is an important prey item for sea otters in Prince William Sound, Alaska (Calkins 1978, Estes *et al.* 1981, Johnson 1982), and for the translocated population of sea-otters off Vancouver Island, British Columbia (Morris *et al.* 1981). Sea-otters translocated to Oregon also ate butter clams (Jameson 1975), but the Oregon population of sea-otters now appears to be extinct (Jameson *et al.* 1982).

Local depletion of butter clam stocks has been associated with foraging by the expanding sea-otter population in Prince William Sound (Paul & Feder 1976, Johnson 1982). However, there is no quantitative documentation of large-scale depletion of clam stocks unequivocally attributable to the activities of sea-otters. On the other hand, there is reason to suspect that long-term coexistence of sea-otters and harvestable butter clam stocks can occur on a regional scale in Prince William Sound. The most direct evidence is the observation that butter clams remain a relatively important prey item for sea-otters in areas that have been occupied by otters for many years (A. Johnson, personal communication, Estes *et al.* 1981). This notion is consistent with some novel evidence provided by the 1964 earthquake. Intertidal substrata in many parts of Prince William Sound were tectonically uplifted by several metres during the earthquake (Pflaker 1972). Infaunal bivalves in these areas were stranded well above normal tidal levels, and died in place (Baxter 1971). Sediment scour produced by tsunamis and seiches associated with the earthquake caused many stranded bivalves to be exposed or partly exposed at the sediment surface (Reimnitz & Marshall 1972). As a result, one can now find populations of 'earthquake fossil' clam shells, still positioned in the posture where they died, partly buried in the sediment in the upper intertidal throughout Prince William Sound (photographs in Hanna 1971, Harry 1973). Censusing of live butter clam populations is difficult and time consuming, but stranded shells can easily be enumerated and measured.

VanBlaricom (unpublished) has censused earthquake-stranded populations of butter

clam shells at Green Island (sea otters present in 1964) and Orca Inlet (sea otters absent in 1964). At Green Island, stranded butter clam shells can be found in dense patches, typically several metres in diameter and separated by 10–20 m. Densities of large clams (> 50 mm shell length) reach 25/m² in the patches. In Orca Inlet, stranded clams from comparable pre-earthquake tidal levels are distributed on a comparable spatial scale. Peak within-patch densities of large butter clams are somewhat higher (to 75/m²) than at Green Island. Further study of earthquake-stranded shell populations is in progress, but available data suggest that sea-otters and significant butter clam stocks can coexist, albeit at somewhat reduced clam densities.

Several factors may contribute to the survival of butter clam stocks in the presence of sea-otters. First, the ability to excavate and consume butter clams varies markedly among sea-otters of different ages. Specifically, juvenile sea otters foraging in clam habitat are more frequently unsuccessful at obtaining prey than adults in the same habitat (Estes *et al.* 1981, A. Johnson, personal communication). Furthermore, sea otters of all ages foraging on infaunal clams make a greater proportion of unsuccessful foraging dives than those feeding on epibenthic invertebrates such as mussels (Estes *et al.* 1981). Apparently, the infaunal habits of butter clams constitute a refuge from easy capture and consumption by sea-otters. Second, butter clams in Prince William Sound are particularly abundant within beds of the eelgrass, *Zostera marina* L. (R. Rosenthal, unpublished data). Eelgrass beds are widespread in low intertidal and shallow subtidal depths in the Sound; dense networks of rhizomes in such areas almost certainly inhibit the ability of sea-otters to dig out butter clams.

It is not clear to what extent sea-otters will interfere with future development of butter clam fisheries in the north-east Pacific. Because of low rates of growth and maturation of clams, and infrequent recruitment success, significant expansion of butter clam fisheries almost certainly will run the risk of rapid overexploitation of clam stocks, much in the manner of fisheries for abalone (see above). At present, problems with paralytic shellfish poisoning and uncertain market conditions restrain the expansion of the fishery, and far outweigh any known effect of sea-otters. Should barriers to expansion of the fishery be overcome, resource depletion and conflicts with sea-otters may arise unless conservation management schemes are applied by regulatory agencies. Successful management of butter clam fisheries is complicated by site-specific differences in growth and recruitment which seem to be typical of the species (e.g. Paul & Feder 1976).

Washington clam: *Saxidomus nuttalli* (Conrad, 1837)

Biology and fishery

Washington clams occur in muddy or sandy substrata, primarily in protected bays and lagoons, from Humboldt Bay, California, southward to Isla San Geronimo, Baja California Norte, Mexico (Morris *et al.* 1980). Washington clams grow to a slightly larger maximum size than the congeneric butter clams, but life-history patterns are otherwise similar and will not be repeated here (see above discussion of *Saxidomus giganteus*).

Washington clams are particularly abundant in Morro Bay, Elkhorn Slough, Bodega Bay, Tomales Bay, and Humboldt Bay, California, and are relatively rare south of Morro Bay (Fitch 1953). Large-scale commercial harvesting of Washington clams occurred in California from 1931 to 1947. Annual landings increased to a peak value of 20 000 kg in 1935, and subsequently declined (California Bureau of Marine Fisheries

1949). To our knowledge, the only presently active commercial fishery for Washington clams occurs in Humboldt Bay, where a small annual harvest is marketed in local restaurants (C. Toole, personal communication). Washington clams are popular with sport diggers wherever they are abundant in California.

Interaction with sea-otters

Sea-otters have been seen digging and eating Washington clams in the subtidal sediments at Monterey Harbor, California (Hines & Loughlin 1980). During 1976–7, Washington clams were the dominant prey item for sea-otters foraging in the area. Densities of clams were 8–14/m² in areas regularly foraged by sea-otters. In an adjacent area thought to be free of otter foraging because of debris in the sediment, mean clam densities were 17/m² (Hines & Loughlin 1980).

The range of the California sea-otter population overlaps with the popular sport fishing grounds for Washington clams only at Morro Bay and Elkhorn Slough. There is no quantitative documentation of the impact of sea-otters in these areas on stocks of Washington clams harvested by man.

Littleneck clam: *Protothaca staminea* (Conrad 1837)

Biology and fishery

Littleneck clams (family Veneridae) range from the Aleutian Islands, Alaska, to Cabo San Lucas, Baja California Sur, Mexico, occurring in sand or sandy mud in bays and estuaries, and in gravel under cobble on open coastline (Fitch 1953, Morris *et al.* 1980). Littlenecks are filter-feeding clams which occupy shallow burrows in the lower and middle intertidal. They are virtually immobile and, because their siphons are short, live relatively close to the sediment surface (Rudy & Rudy 1983).

The sexes are separate in Littleneck clams. Individuals capable of spawning can be found throughout the year in Alaska (Paul & Feder 1976). In British Columbia, spawning occurs from April through September (Quayle 1943). Recruitment success varies from year to year (e.g. Paul & Feder 1973), but strong year-classes occur with greater frequency than in butter clams, with which Littlenecks frequently coexist.

Growth rate of Littleneck clams vary markedly among years, beaches, and tidal heights, and across latitude (Bernard 1982). Size at sexual maturity (shell length of 2–3 cm; Quayle 1943) is reached in 1–2 years in British Columbia, 3–4 years in southeastern Alaska, and 6–7 years in Prince William Sound, Alaska (Paul & Feder 1973, 1976). Harvestable size (3 cm) is reached about 1 year later in each area.

Primary commercial fisheries for Littleneck clams are located in British Columbia and Washington. Commercial landings have been influenced historically by many of the same factors which affect landings of butter clams (Bernard 1982; see above discussion), although difficulties with paralytic shellfish poisoning are somewhat less frequent. During 1970–9, annual landings of Littleneck clams in British Columbia ranged from 144 000 kg to 631 000 kg (Bernard 1982). Landings in Puget Sound, Washington, increased from 158 000 kg in 1975 to 416 000 kg in 1978 (R. Burge, personal communication). Littleneck clams were harvested commercially in southeastern Alaska until 1946, when regulatory changes forced closure of the fishery (Paul & Feder 1973; see discussion under butter clams, above). Potential harvests in Alaska appear to be large, particularly in Prince William Sound, where outbreaks of paralytic shellfish poisoning in Littleneck clams are rare (Feder & Paul 1973). This

species is harvested on a small scale in Humboldt Bay, California (C. Toole, personal communication).

Littleneck clams are heavily exploited by sport clambers throughout their range. Landings data are not available for sport harvests.

Stocks of Littleneck clams in Prince William Sound, Alaska, were seriously damaged by the great earthquake of 1964. Recovery was relatively rapid, due to successful recruitments, in areas where the substratum was not severely modified (Paul *et al.* 1976). The history of Littleneck clam fisheries and the recovery of earthquake-damaged populations suggest that the clam populations may be more tolerant of exploitation than most other molluscan species examined in this review. This supposition will be tested if market conditions favour continued expansion of commercial harvesting in Washington and British Columbia.

Interaction with sea-otters

Sea-otters have been seen eating Littleneck clams in California near Cayucus Point (Wild & Ames 1974), in Oregon at Simpson Reef (Jameson 1975), and at several locations in Prince William Sound, Alaska (Calkins 1978, Estes *et al.* 1981, Johnson 1982). There are anecdotal reports that Littleneck clam stocks have been depleted locally by sea otters in California and Prince William Sound, but quantitative documentation of the interaction is lacking. Because of the relative shallowness of their burrows, Littleneck clams are probably more accessible to foraging sea-otters than butter clams, gaper clams, and other deeply buried infaunal bivalves.

However, relationships of sea-otters and Littleneck clams in Prince William Sound seem to parallel those of the butter clams (see above) in several respects. Littleneck clams remain a relatively important component of sea-otter diet in the Sound, and sport harvest can be successful in portions of the Sound occupied by sea-otters for many years (Calkins 1978, Estes *et al.* 1981, Johnson 1982, A. Johnson, personal communication). Densities of *Protothaca* shells stranded by the 1964 earthquake uplift (see detailed discussion in section on butter clams) at Green Island are locally high, approaching 60 harvestable clams/m² in some patches (VanBlaricom, unpublished). Sea otters had been present for a number of years at Green Island at the time of the earthquake. Although it is likely that some Littleneck populations have been reduced in size by otter foraging (Johnson 1982), it is also apparent that human exploitation of Littleneck clams can continue, at least on a recreational scale, within the range of sea otters in Prince William Sound.

Gaper clam: *Tresus nuttallii* (Conrad 1837)

Biology and fishery

Gaper clams are large, infaunal macruid bivalves that range from the Strait of Georgia, British Columbia, to Laguna Ojo de Liebre, Baja California Sur, Mexico, overlapping with much of the aboriginal range of sea otters in North America. As adults, gaper clams live 1 m or more below the surface of sandy or mud-sand substrata in bays or along protected coastline, ranging in depth from the low intertidal to 30 m (Morris *et al.* 1980). Gaper clams are filter feeders with little mobility (Amos 1966).

The sexes are separate in gaper clams. Spawning occurs year-round in Elkhorn Slough, California; peak activity is in February–April (Clark *et al.* 1975). Larvae remain planktonic for 21–30 days before settlement and metamorphosis (Clark *et al.* 1975). The females mature sexually at 2 years of age.

Gaper clams are harvested commercially on a small scale, primarily for local marketing as fresh meat in restaurants. In recent years, commercial landings have been made in Humboldt Bay, California, and in several bays in Oregon (Amos 1966, Frey 1971). From 1950 to 1970, peak annual landings in California were 2700 kg (Frey 1971).

Gaper clams are intensively harvested in intertidal habitats by sport fishermen (Frey 1971, Clark *et al.* 1975). Sport harvest is particularly heavy in California from Morro Bay northward. Sport landings data are not available.

Interaction with sea-otters

Sea-otters have been seen eating gaper clams in California at San Simeon (Ebert 1968a, Jameson, personal communication), Cayucus Point (Wild & Ames 1974), and Morro Bay (Jameson, personal communication). Dense subtidal populations of gaper clams in Monterey Harbour were apparently depleted by foraging sea-otters (California Department of Fish and Game 1976, Hines & Loughlin 1980), although quantitative documentation is lacking. At present, sea-otter distribution overlaps important sport fishing sites for gaper clams only at Morro Bay and Elkhorn Slough. In neither area is there any evidence that sea otters have affected the success of sport harvests of this species (California Department of Fish and Game 1976).

Horse clam: *Tresus capax* (Gould, 1850)

Biology and fishery

Horse clams overlap with much of the aboriginal range of sea otters in North America, occurring from Kodiak Island, Alaska, southward to San Francisco, California (Morris *et al.* 1980, Rudy & Rudy 1983). They are most abundant in bays and estuaries; habitat selection and life history are similar to the congeneric gaper clam, discussed above.

Like gaper clams, horse clams have separate sexes and external fertilisation. Spawning occurs during winter in Humboldt Bay, California, and in early spring in Yaquina Bay, Oregon (Machell & DeMartini 1971, Rudy & Rudy 1983). Larvae apparently remain in the plankton for several weeks (Bourne & Smith 1972). Populations of horse clams in Humboldt Bay are dominated by a few year-classes, probably reflecting variable recruitment success or post-recruitment mortality (Wendell *et al.* 1976).

Small-scale commercial harvesting of horse clams occurs in Humboldt Bay, California (C. Toole, personal communication, R. Warner, personal communication). In Oregon, horse clams comprise about 60% of the annual harvests of clams from coastal estuaries (Rudy & Rudy 1983). During 1975–9, horse clam landings ranged from 7000 kg to 58000 kg in Oregon (D. Snow, personal communication). Primary fishing grounds are Coos Bay, Netarts Bay, Tillamook Bay, and Yaquina Bay (Rudy & Rudy 1983, J. Richards, personal communication, J. Lannon, personal communication), where both intertidal and subtidal stocks are exploited. In Puget Sound, a horse clam fishery has recently developed, with annual landings of less than 1000 kg through 1978 (Burge, personal communication). The commercial fishery for this species in British Columbia is also recent, occurring primarily as a by-product of subtidal harvesting of geoducks (*Panope generose* {Gould, 1850}). Landings were 37000 kg in 1979 and 128000 kg in 1980, primarily from the southern strait of Georgia (Bernard 1982). Intertidal stocks in British Columbia are also harvested, primarily by hand digging; landings have been limited by low market price and handling difficulties (Bernard 1982). Horse clams are not harvested commercially in Alaska, and little is known regarding harvest potential (Paul & Feder 1976).

Interaction with sea-otters

Horse clams are gathered throughout their range by recreational fishermen. Sport landings can be substantial, as in Humboldt Bay, California (C. Toole, personal communication, R. Warner, personal communication), but landings data are unavailable. To our knowledge, sea-otters have been reported consuming horse clams only in Prince William Sound, Alaska (Johnson 1982). There are no data available with which to evaluate the impact of sea otters on horse clam populations, or on exploitation of horse clams by man.

Softshell clam: *Mya arenaria* (Linnaeus, 1758)*Biology and fishery*

Mya arenaria is an infaunal myid bivalve which currently ranges from Point Barrow, Alaska, southward to Elkhorn Slough, California (Fitch 1953, Paul & Feder 1976, Morris *et al.* 1980). These clams native to the North Atlantic were introduced to San Francisco Bay in the 1870s, possibly with early transplants of the eastern oyster (Morris *et al.* 1980). They spread northward along the Pacific coast, reaching southeastern Alaska in 1956 and Prince William Sound in 1958 (Gross 1967).

Softshell clams occur in muddy substrata of quiet back-bays and estuaries, including areas of brackish water. Individual clams are relatively immobile, and live up to 30 cm below the sediment surface (Amos 1966). The sexes are separate. Spawning occurs in spring and autumn (Rudy & Rudy 1983). Sexual maturity (shells 2.5–4.5 cm long) is reached in about 3 years in Alaska (Feder & Paul 1974, Paul & Feder 1976). Harvestable size (5 cm) is reached in 6–7 years in Alaska (Feder & Paul 1974). Successful recruitment apparently occurs with some regularity; recovery was relatively rapid in clam stocks devastated by the 1964 earthquake (Paul & Feder 1976).

The softshell clam fishery is a large industry in the north-west Atlantic, but only small-scale commercial harvesting presently occurs in Pacific North America. There was a large softshell clam fishery in California from 1916 through 1947. Annual landings were large in the early years of the fishery (Fig. 12.6). Maximum annual harvest was 156 000 kg in 1922. The fishery declined steadily after 1925 (Fig. 12.6). At present, minor commercial harvests occur in Humboldt Bay, California, and in coastal

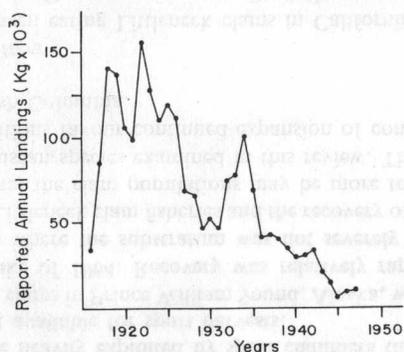


Figure 12.6 Commercial landings of softshell clams (*Mya arenaria*) in California, 1916–47. (From California Department of Fish and Game.)

bays of Oregon (C. Toole, personal communication, R. Warner, personal communication, J. Lannon, personal communication). In Puget Sound, Washington, annual landings have been as high as 150 000 kg in recent years, but the commercial take is now small (R. Burge, personal communication). Commercial landings in British Columbia are generally incidental inclusions in the harvest of other species (Bernard 1982). No commercial harvesting occurs in Alaska, although the potential harvest may be large (Feder & Paul 1973, Paul & Feder 1976).

Softshell clams are frequently harvested throughout their range by sport clammers. Non-commercial harvesting is apparently intensive in the eastern Bering Sea (Paul & Feder 1976). Sport landings data for softshell clams have not been published.

Interaction with sea-otters

Sea-otters are known to eat softshell clams in Prince William Sound, Alaska (Estes *et al.* 1981, Johnson 1982). There is no quantitative documentation of the impacts of otter foraging on populations of these clams, nor is there any firm evidence that sea otters have in any way influenced human exploitation of the species.

Basket cockle: *Clinocardium nuttallii* Conrad, 1837)*Biology and fishery*

Basket cockles are filter-feeding cardiid bivalves that range from San Diego, California, northward into the Bering Sea (Fitch 1953). They live on or just below the surface of mud or sand substrate in bays, estuaries, and along semi-protected coastline, ranging in depth from the low intertidal to 200 m (Morris *et al.* 1980).

Basket cockles are simultaneously hermaphroditic (Amos 1966). Fertilisation is external and spawning occurs in spring and summer. Growth rates are apparently inversely related to latitude (Amos 1966). Basket cockles become sexually mature in 2 years (Morris *et al.* 1980). In Alaska, harvestable size (shell length 5 cm) is reached in about 4–5 years (Paul and Feder 1976).

This species was commercially harvested from 1944 to 1962 in Alaska (Nosho 1972). Annual landings ranged from zero (four different years) to 576 000 kg in 1960 (Nosho 1972). The large fluctuations in annual landings and the ultimate demise of the fishery

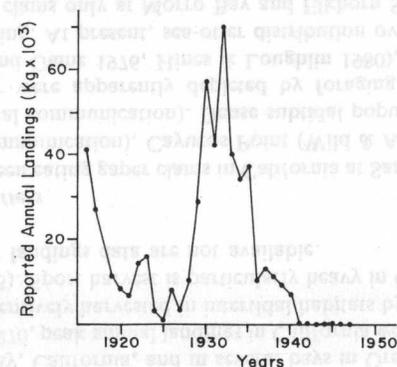


Figure 12.7 Commercial landings of cockles (*Clinocardium nuttallii*) in California, 1916–47. (From California Department of Fish and Game.)

were caused by low rates of meat recovery and intensive labour needs in processing, and by ongoing problems with paralytic shellfish poisoning (Paul & Feder 1976). No commercial harvesting occurs in British Columbia, although basket cockles are occasionally included in harvests of other bivalves (Bernard 1982). In California, a commercial fishery existed from 1916 to 1947. Landings fluctuated substantially over the years (Fig. 12.7): maximum annual harvests were 57 000 kg in 1930 and 70 000 kg in 1932. Landings declined drastically during World War II (California Bureau of Marine Fisheries 1949). Basket cockles are not presently harvested commercially in Washington, Oregon, or California, apparently because of low densities (Fitch 1953, Amos 1966).

Basket cockles are frequently taken by sport fishermen, but landings data are not available (Bernard 1982).

Interaction with sea-otters

Sea-otters have been seen consuming basket cockles in Prince William Sound (Johnson 1982) and a related species (*Clinocardium ciliatum*) has been found in sea-otter stomachs at Amchitka Island, Alaska (Kenyon 1969). There are presently no published data regarding the impact of sea-otters on cockle populations. In a 1971 study in Montague Strait, Prince William Sound, sea otters did not consume basket cockles although they were present in the area (Calkins 1978).

Rock scallop: *Hinnites giganteus* (Gray, 1825)

Biology and fishery

Rock scallops are pectinid bivalves ranging from the Queen Charlotte Islands, British Columbia, to Punta Abreojos, Baja California Sur, overlapping with a large portion of the historical range of sea-otters in North America (Fitch 1953). They occur on hard substrata from the intertidal to 50 m in depth, primarily along exposed outer coasts (Morris *et al.* 1980). The juveniles are capable of swimming to evade predators; larger individuals are attached permanently to rock surfaces. Growth rates of rock scallops are very low. Individuals may require up to 25 years to reach maximum size (5–15 cm in the intertidal, 25 cm subtidal; Morris *et al.* 1980). The sexes are separate and fertilisation external. Spawning occurs in April in central California (Morris *et al.* 1980).

Rock scallops are taken by sport fishermen throughout their range. At present there is no commercial fishery, although experimental mariculture is under development in southern California (J. Richards, personal communication). Available data suggest that rock-scallop harvesting is a minor sport fishery in California (Miller *et al.* 1972). However, excessive harvesting by sport fishermen has been implicated in apparent depletions of *Hinnites* populations in some areas (Morris *et al.* 1980).

Interaction with sea-otters

Sea-otters have been seen eating rock scallops in California and Oregon (Limbaugh 1961, Ebert 1968a, Faro 1970, Jameson 1975, Estes *et al.* 1981, Ostfeld 1982). In both areas, the rock scallops were a relatively minor portion of the sea-otter diet. In 1967, rock scallops were most abundant in portions of the California sea-otter range most recently reoccupied by otters (Ebert 1968b). Faro (1970) described rock scallop densities as low in the Point Pinos area near Monterey, California, and suggested that both sea-otters and sport fishermen were responsible. Low densities of rock scallops at Del Monte Reef, near Monterey, have been tentatively attributed to sea-otter foraging (Minter 1971). However, densities of scallops at Del Monte before the return of sea-

otters are unknown, although it is likely that sea-otter foraging does have an effect. Details of the relationship have not been documented, and the relative effects of predation on rock scallops by man and sea-otters are entirely unknown.

Oysters

Biology and fishery

In natural conditions, oysters are filter-feeding bivalves which live attached to rocks, shells, or other hard substrata on tidal flats in protected, back-bay habitats. Most commercially harvested oysters come from mariculture operations where they grow on ropes, racks, poles, or other artificial substrata more suited to efficient maintenance and harvest. Four species of oyster are now harvested in Pacific North America, three of which are non-native. All are in the family Ostreidae.

The Japanese oyster (*Crassostrea gigas* {Thunberg, 1795}) was introduced to North America early in the century. Populations capable of reproduction and successful recruitment are now established in Puget Sound, Washington, and the Strait of Georgia, British Columbia (Morris *et al.* 1980, Bernard 1982). *C. gigas* now ranges from Morro Bay, California, to British Columbia. The sexes are separate, but individuals may be sequentially hermaphroditic, changing sex over winter. In Puget Sound, spawning occurs in July or August. Larvae are free swimming for about 4 weeks. In many areas, post-larvae juvenile 'seed' oysters must be imported and planted regularly to maintain populations large enough to sustain commercial harvests (Morris *et al.* 1980).

Japanese oysters now dominate the commercial oyster harvest in the north-east Pacific. In California, Japanese oysters are cultured in Morro Bay, Elkhorn Slough, Drakes Estero, Tomales Bay, and Humboldt Bay (Conte & Dupuy 1981). Annual landings in California averaged 407 000 kg during 1970–9, primarily from Humboldt Bay (Conte & Dupuy 1981); those in Oregon during the same period averaged 103 000 kg (D. Snow, personal communication). Most oysters harvested in Oregon come from Tillamook Bay, Yaquina Bay, and Coos Bay (J. Lannon, personal communication). The annual harvest of Japanese oysters in Washington has been about 2.3 million kg in recent years (Burge, personal communication). About half the Washington harvest comes from Puget Sound, the remainder from Grays Harbour and Willapa Bay. Recent annual landings in British Columbia have been about 2 million kg, primarily from the southern part of the Strait of Georgia (Bernard 1982). *C. gigas* was cultured near Ketchikan, Alaska, with marginal success from early in the century until 1961 (Yancy 1966), when market conditions apparently forced failure of the business.

Wild populations of *C. gigas* are harvested by sport fishermen in Washington and British Columbia. Landings data are not available. Local depletion of wild oyster stocks by sport fishermen is a chronic problem, particularly in Puget Sound.

Olympia oysters (*Ostrea lurida* {Carpenter 1864}) are native to Pacific North America and ranged historically from Sitka, Alaska, to Cabo San Lucas, Baja California Sur, Mexico. They are sequentially hermaphroditic, each animal changing sex frequently during its life. Sexual phases may overlap such that some animals are simultaneously hermaphroditic for short periods (Morris *et al.* 1980). Males shed sperm clusters into the water, but females retain eggs in the mantle cavity, where fertilisation occurs. Larvae are brooded for 10–14 days, then released. The free-swimming larval period is 30–40 days, after which settlement and metamorphosis occur (Morris *et al.* 1980). *O. lurida* reaches sexual maturity 5 months after metamorphosis and produces

two broods (up to 300 000 larvae per brood) per year. Growth to harvestable size (3–5 cm) requires 3–5 years in California (Morris *et al.* 1980).

Ostrea lurida was the original mainstay of the commercial oyster industry in western North America. Habitat degradation and introduction of other more marketable species have led to the virtual extinction of Olympia oysters as a commercial entity (Morris *et al.* 1980, Conte & Dupuy 1981). At present, the remnant commercial culture of *O. lurida* is centered in Puget Sound, Washington. Annual landings averaged 11 000 kg during 1970–9 (R. Burge, personal communication); the trend is one of continued decline.

The eastern oyster (*Crassostrea virginica* [Gmelin, 1971]) was introduced to San Francisco Bay in 1870, following completion of transcontinental rail lines. It quickly became the dominant commercial species in California because of its large size and better flavour than *Ostrea lurida* (Conte & Dupuy 1981). Repeated 'seeding' was necessary to maintain stocks of *C. virginica*. Annual landings peaked at 1.2 million kg of meat in 1899. Problems with pollution and habitat degradation caused a subsequent decline in production, and commercial culture of *C. virginica* in San Francisco Bay collapsed during the 1930s (Conte & Dupuy 1981). In recent years, eastern oysters have been cultured on a small scale in Elkhorn Slough, Tomales Bay, and Humboldt Bay. Annual landings in California have been less than 500 kg since 1978 (Conte & Dupuy 1981).

A fourth species, the European oyster (*Ostrea edulis* L.), was recently introduced to California. It is now cultured on a small, experimental basis at Elkhorn Slough (Conte & Dupuy 1981).

Interaction with sea-otters

Current sea-otter range now overlaps with oyster culture operations at Morro Bay and Elkhorn Slough, California. Sea-otters frequently forage on crabs and clams in the seaward portion of Morro Bay, but none has been seen near oyster beds in back-bay tidelands (L. Laurent, R. Hardy, and R. Jameson, personal communications). Although systematic observations have not been made, sea-otters apparently forage frequently within Elkhorn Slough, occasionally passing near oyster culture racks. Consumption of oysters by sea-otters has not been reported. In Coos Bay, Oregon, a sea otter from a translocated population (see Jameson *et al.* 1982) foraged on crabs but did not feed on nearby oysters (Mate, unpublished).

Sea-otters are capable of shucking and eating oysters given them by man (California Department of Fish and Game 1976), but natural foraging has not been observed anywhere. In our view, the potential for damage to the oyster industry by sea otters is limited. Sea-otters have had no rôle in the substantial variation between years in landings of oysters in the north-east Pacific. Pollution, habitat alteration, changing market conditions, episodic outbreaks of paralytic shellfish poisoning, the availability of shipping facilities, the price and availability of oyster 'seed', and problems with disease have been the principal causes of the historically variable success of the oyster industry (Paul & Feder 1976, Conte & Dupuy 1981).

Mussels

Biology and fishery

Two species of mussel (family Mytilidae) are common and ecologically important within the aboriginal range of sea otters in North America. The California sea mussel

(*Mytilus californianus* [Conrad, 1837]) dwells primarily on rocky intertidal substrata along shores exposed to oceanic swell from the Aleutian Islands to southern Baja California. Isolated subtidal populations are also known (Paine 1976). The bay mussel (*Mytilus edulis* [Linnaeus, 1758]) ranges in western North America from the Arctic Ocean to Isla de Cedros, Baja California Sur, Mexico, primarily in intertidal areas protected from heavy wave action. *M. edulis* may also be found on outer coast habitats in close association with *M. californianus* (Suchanek 1978, Morris *et al.* 1980).

The sexes are separate and fertilisation external in both species. *M. californianus* populations may include some spawning individuals throughout the year; peaks occur, for example, in July and December in California (Morris *et al.* 1980). Spawning in *M. edulis* is seasonal, the spawning season varying substantially from place to place.

Individual growth rates vary substantially over all spatial scales. For example, young *M. edulis* typically grow 7–8 cm in length in 1 year in southern California (Morris *et al.* 1980), but less than 2 cm in Prince William Sound, Alaska (VanBlaricom, unpublished data). Growth rates of this species also vary with tidal height and microhabitat type (VanBlaricom, unpublished data).

The commercial harvesting of mussels is presently a minor industry in Pacific North America. In California, small-scale mussel culturing operations are in experimental phases (J. Richards, personal communication). Minor commercial harvesting of natural populations of *M. californianus* and *M. edulis* occurs in Oregon near Cannon Beach and Newport (D. Snow, personal communication, J. Lannon, personal communication). Culturing of *M. edulis* occurs in Puget Sound, Washington, where landings reached 18 000 kg in 1980 (R. Burge, personal communication). Commercial landings of mussels in British Columbia include both natural and cultured harvests (P. Breen, personal communication, G. Jamieson, personal communication). Landings averaged 4000 kg per year in 1979 and 1980 (Bernard 1982). The potential commercial harvest of mussels in Alaska is substantial, but no such harvest now exists (Paul & Feder 1976). The commercial potential for mussel harvesting for human consumption is severely limited by the continuing threat of paralytic shellfish poisoning (PSP) along the North American Pacific coast. Mussels are notorious for their concentration and storage of PSP toxins. In 1980, for example, there were 98 cases of paralytic shellfish poisoning of people in Marin and Sonoma counties, California, including two fatalities. Most of the cases resulted from consumption of mussels by recent Asian immigrants unfamiliar with the toxic potential of Pacific coast bivalves (J. Richards, personal communication).

Both mussel species are harvested on a recreational basis wherever they occur. Sport harvests are used both for food and fishing bait.

Interaction with sea-otters

Sea-otters are known to consume both *M. californianus* and *M. edulis*. Otters typically gather mussels by diving during high tide, but occasional emergent foraging occurs during low water (R. Jameson, personal communication). Mussels were apparently an important component of sea-otter diet near Monterey, California, early in the 1960s (Limbaugh 1961, Hall & Schaller 1964, Booloottian 1965, Faro 1970, Hines & Loughlin 1980). In general, however, mussels form a small portion of sea-otter diet in California (Ebert 1968a, Wild & Ames 1974, Estes *et al.* 1981, Ostfeld 1982). Mussels are occasionally taken by translocated sea-otter populations in Oregon and British Columbia (Jameson 1975, Morris *et al.* 1981). *Mytilus edulis* is an important component of sea-otter diet in Prince William Sound, Alaska (Estes *et al.* 1981, Johnson 1982).

There is no published documentation of the impact of sea-otters on commercial or sport landings of mussels anywhere within the present range of sea-otters. Otters clearly are capable of reducing mussel density on a local scale through foraging activity. For example, when sea-otters returned to the north shore of Monterey Peninsula in the 1960s, mussel biomass on rocky intertidal substrata in the area declined sharply (Faro 1970, Wilde & Ames 1974, Hines & Loughlin 1980, D. Abbott, personal communication). However, the effect of sea-otters on mussel populations is less significant elsewhere along the coast of central California, much of which is more exposed to oceanic swell than the Monterey area. Dense stands of *Mytilus californianus* are particularly common on exposed rocky headlands within the range of the California sea-otter population (Fisher 1939, Ebert 1968a,b, G. VanBlaricom, personal observations).

Since 1978, VanBlaricom has studied patches of *M. californianus* on intertidal rocks exposed to seasonally heavy surf at Point Piedras Blancas, near San Simeon, California. Sea-otters have been present at Point Piedras Blancas since 1959 (Wild & Ames 1974). From May 1978 through February 1982, virtually no mussels were taken from study plots or nearby mussel patches by sea-otters. In March 1982, sea otters removed mussels from study areas with some regularity, creating cleared patches up to 1 m² in size within study plots. During this period, one of three mussel patches was reduced in size by 10–20% by sea-otter foraging. A second patch received little damage, and a third was untouched. Since April 1982, sea-otter foraging on mussels has again become infrequent in the study plots.

Episodic creation of cleared patches in mussel beds is of some interest from an ecological perspective (e.g. Paine & Levin 1981). However, consumption of mussels by sea-otters in California appears to be sufficiently scattered in time and space that regional-scale depletion of harvestable stocks does not occur. The exposure of much of the central California coast to heavy surf probably provides an important refuge for mussels from foraging sea-otters. Consumption by other predators (e.g. the sea star, *Pisaster ochraceus*, and the black oystercatcher, *Haematopus bachmani*) and dislodgement by storm waves are probably at least as important as sea-otter predation in limiting the availability of mussels for human use in California.

Sea-otters are capable of reducing mussel biomass on a local scale in Alaska (Johnson 1982, VanBlaricom & Johnson, unpublished), but there is no evidence that sea-otter foraging has interfered with human harvest of mussels in Alaska.

Red sea urchins (*Strongylocentrotus franciscanus*)

Biology and fishery

The genus *Strongylocentrotus* has five extant species in the north-east Pacific. Only one of these, *S. franciscanus* (the red sea urchin), is exploited in a commercial fishery. Red urchins occur in northern Japan and along the west coast of North America from south-east Alaska to central Baja California. They range in depth from the lower littoral zones to about –90 m (Morris *et al.* 1980).

Following enlargement of the gonads during autumn and winter, most spawning occurs in April and May with the gametes being released into the water column (Bennett & Giese 1955, Giese 1959). The larvae are planktotrophic (Strathmann 1971), and, on the basis of laboratory studies, appear to remain as free-swimming forms for 61–131 days (Strathmann 1978). There appears to be no habitat selectivity by the recently metamorphosed young (Cameron & Schroeter 1980). However, settlement in the

natural environment is seen only sporadically, and, in some areas at least, juveniles are found almost exclusively beneath the spine canopy of large adults (Tegner & Dayton 1977). Maximum size varies greatly among areas, occasionally reaching more than 200 mm in test diameter. Although red urchins may live to be more than 20 years old (Morris *et al.* 1980), under suitable conditions most of their growth is probably attained during the first 5–7 years (Benech 1977).

Sea urchins are among the most important of marine herbivores (see reviews by Lawrence 1975, Lubchenco & Gaines 1981). Their grazing activities often result in areas becoming entirely devoid of fleshy algae – these have been referred to by Lawrence (1975) as 'urchin barrens'. In the North Pacific, such barren areas appear to have been caused by recent population increases of red, purple (*S. purpuratus*), and green (*S. drobachiensis* and *S. polyacanthus*) sea urchins (Leighton *et al.* 1966, North & Pearse 1970, Estes & Palmisano 1974). These increases have been attributed to the following factors.

- (a) *Release from predation.* Sea otters are the most commonly implicated predatory species, and indeed, the otters' range expansion has greatly reduced urchin densities in many areas (for examples, see McLean 1962, Lowry & Pearse 1973, Estes & Palmisano 1974, Benech 1977, Duggins 1980, Breen *et al.* 1982). In southern California, the exploitation in sport and commercial fisheries of other predatory species, such as sheephead (*Semicossyphus pulcher*) and spiny lobsters (*Panulirus interruptus*), is thought to have contributed to the problem (Tegner 1980, Tegner & Dayton 1981). The importance of sheephead has been corroborated by Cowen (1982, 1983), who, by experimentally removing sheephead from part of an isolated reef, demonstrated a trend of increased urchin density compared with an unmanipulated control area in which the density of urchins did not change.
- (b) *Release from competition.* Since abalones and sea urchins occupy the same habitats and consume the same algal food resources, there has been speculation that they limit one another through exploitation competition (Haaker & Wilson 1975). On the basis of this proposed interaction, and because abalone populations have been reduced by the fishery, urchin population increases were perhaps facilitated by release from competition with abalones. Although intuitively appealing, there are still no data to support the proposed mechanism.
- (c) *Pollution.* Kelp bed declines have been particularly dramatic near sewage effluents deriving from the large population centres in southern California (Leighton *et al.* 1966). Some of the discharged materials (e.g. dissolved amino acids) can be directly absorbed by urchins (North 1964a,b, Pearse *et al.* 1970), and at moderate concentrations these materials are thought to enhance sea-urchin growth. In addition, sewage effluents appear to cause the deterioration of kelp (North 1964a,b). Evidence in support of this explanation is mainly anecdotal, and although sewage may well have been of substantial importance in certain localised areas, it is unlikely to have been of any real consequence at many of the more remote locations throughout the North Pacific where urchin barrens also commonly occur.

Whatever their cause, the urchin barrens, once established, tend to maintain themselves through time. To some extent this appears to result from fundamental changes in the foraging behaviour of sea urchins, which cause them to switch from non-destructive to destructive grazing in the absence of a large standing biomass of kelp.

More specifically, when kelp is abundant, even moderately high densities of sea urchins tend to be largely sessile while feeding on detrital matter that falls out of the kelp canopy (Reed & Harrold 1981), and they seem to have little, if any, influence on living plants. However, where kelp is absent, urchins tend to be more highly mobile in their efforts to find food (Mattison *et al.* 1977, Reed & Harrold 1981, J. Estes unpublished data). In this active foraging mode they destructively graze the living plants that they encounter, thereby also inhibiting the successful re-establishment of newly settled plants and thus maintaining the system as a barren area.

Perturbations of this state of community organisation, in the form of disturbances which temporarily reduce the intensity of herbivory, often seem to provide the plant association an opportunity to achieve a stable refuge in size or abundance. For example, Leighton *et al.* (1966) found that by removing sea urchins from a sufficiently large area, the resulting kelp patch, once established, not only persisted but actually continued to expand its distribution into areas where urchin densities remained high. Duggins (1981) documented a similar phenomenon following an unusual accumulation of salps (*Salpa fusiformis*) and benthic diatoms (*Melosira* sp.) in the shallow coastal waters near Glacier Bay, Alaska. In this situation, the urchins preferentially fed on diatoms and salps, thereby allowing kelp plants to settle and achieve a refuge in size. The plant assemblage persisted thereafter through the summer field season. This same pattern seems to occur following numerous events that may temporarily reduce the intensity of herbivory (e.g. see Paine & Vadas 1969, Pearse & Hines 1979). Perhaps of paramount importance among these events is the depredation of sea urchins by sea otters.

In the north-east Pacific, fisheries for red sea urchins occur in British Columbia, Washington, California, and Baja California. At the present time these fisheries serve an exclusively Japanese market for urchin roe (Kato 1972). The North American fishery has developed recently. Landings data are available for the states of California and Washington, and the Province of British Columbia (Fig. 12.8). The Washington fishery is located mainly in the Strait of Juan de Fuca and the San Juan Archipelago. Reported landings increased by well over an order of magnitude between 1975 and 1978, and have remained roughly constant since that time. The urchin fishery in California began in 1971. Although a sporadic fishery has operated out of Fort Bragg in northern California, the majority of reported landings are from the northern Channel Islands. Annual landings rose from 81 kg in 1971 to 1.6 million kg in 1973 and reached 11.1 million kg in 1981. Current harvest levels are thought to be above MSY (E. E. Ebert, personal communication).

The British Columbia fishery was established in 1970; landings data are available since 1972. Initially, the fishery was concentrated near Tofino (Bernard 1982), but it collapsed after several years (Fig. 12.8), possibly as a result of competition with the then-emerging California fishery. A sporadic fishery also occurred in Georgia Strait, which increased sharply to 324 000 kg in 1980. This may have been due to an ever-increasing demand together with a stabilisation in landings by the fisheries in Washington and California. At the present time there is concern over the possibility of overexploiting the fishery in British Columbia. We have been unable to locate statistics on the Mexican fishery, although in recent years we have seen evidence of its existence at various sites from the Mexican/US border south to at least Punta Baja, Baja California Norte, Mexico.

Red sea urchin fisheries are currently undergoing rapid expansions along the Pacific coast of North America. They all are, however, too recent to allow proper interpreta-

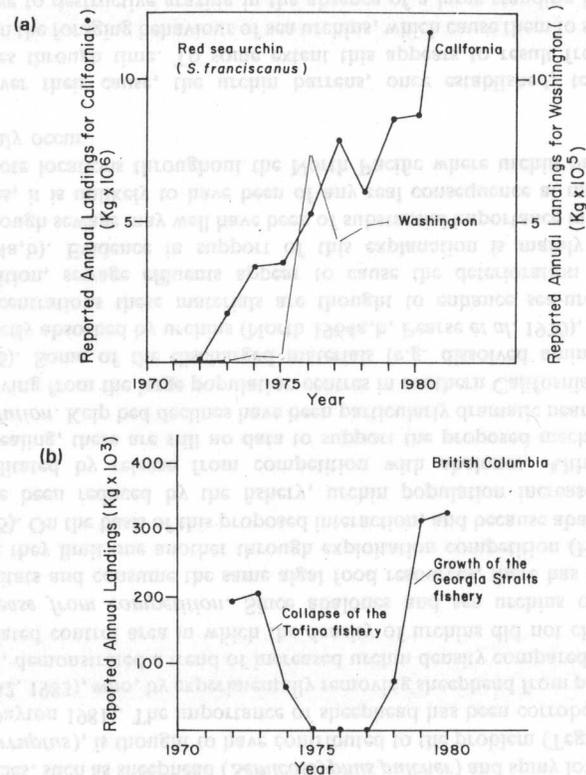


Figure 12.8 Commercial landings of red sea urchins (*Strongylocentrotus franciscanus*) along the west coast of North America. (a) California and Washington; (b) British Columbia. (From California, California Department of Fish and Game; Washington, Washington Department of Fisheries; British Columbia, Bernard 1982.)

tion of their status from landing patterns. There does seem to be the potential for overexploitation. For example, Bernard (1982) reported that areas heavily exploited in the early 1970s by the Tofino, British Columbia, fishery have been slow to recover, perhaps because there were insufficient numbers of adult-sized individuals under which the juveniles normally successfully settle.

Many areas appear suitable for urchin exploitation along the west coast of North America. Most of these are not currently being harvested because of processing and marketing problems. Nearby processing units are needed to make local fisheries feasible. Yet processing units themselves require an adequate fishery potential to operate at a profit, and this seems to be excluding the development of a fishery throughout much of the potential range.

Interaction with sea otters

Benech (1977) convincingly argued that sea-otters contributed to the failure of a developing urchin fishery in San Luis Obispo County, California. Other than this single

instance, there is no overlap at the present time between sea urchin fisheries and sea-otters. Sea urchins appear to be one of the first species consumed after sea-otters expand their range into new habitats to feed, and there is abundant evidence that urchin populations are reduced both in density and mean size by otter predation (Lowry & Pearse 1973, Estes & Palmisano 1974, Gotshall *et al.* 1976, Laurent & Benech 1977, Duggins 1980, Breen *et al.* 1982). There can be little doubt that the presence of sea-otters is incompatible with red urchin fisheries.

Discussion

In reviewing these case studies, we now are faced with the task of drawing from them some sort of synthesis. Our title delineates two common themes. One of these is that invertebrate species (as distinguished from fin fishes) are exploited in each of the fisheries. However, this apparent thread of cohesiveness should be regarded with caution. Actually, the group is remarkably diverse taxonomically consisting of at least 28 species from three different phyla. In this sense, these species differ more from one another than do those comprising the whole of the world's fin fisheries. The other common theme is the actual or potential depredation of shellfish by sea-otters. This latter theme may well be unique in the sense that those same qualities that make the interaction between sea otters and shellfisheries demonstrable in some cases (see introductory remarks) also may set them apart in nature from the same kinds of interactions involving other species of marine mammals.

Based on the results of this review, we have drawn together a long list of conclusions. Not all of these explicitly concern sea otters, although in our view they are implicitly quite relevant to the problem of sea-otter-shellfishery conflicts because they help to provide a comprehensive perspective of the problems facing shellfish fisheries. We hold no illusion that the list is complete. Yet it does point out, as we have interpreted the evidence, a variety of important matters which must be drawn into any consideration of shellfish resources, and how fisheries for these resources are affected by sea-otter depredations. These conclusions follow.

- (a) In nearly all cases, the quality of evidence implicating or exonerating sea-otters in the decline or failure of various shellfisheries is poorer than one might hope for. Usually, this is because: (i) available records or data are insufficient to indicate declines, or (ii) where well-documented declines have occurred, the relative contributions of sea-otters and overfishing cannot be separated. Certainly sea-otter depredations remain an important factor in the minds of most people, but seldom has their effect been demonstrated unequivocally. Contrary to popular belief, our review suggests that some kinds of shellfisheries do survive in the presence of sea-otters (e.g. rock crabs, northern razor clams, butter clams, littleneck clams, and mussels). Others, such as commercial abalone and sea urchin fisheries, clearly do not.
- (b) Different species of shellfish seem to be of widely varying susceptibility to sea-otter predation, depending on factors such as life-history characteristics, mobility, or the use of cryptic habitats. For example, abalone and sea urchin populations have been reduced to very low levels by sea otters, especially in areas offering no habitat refuges in the form of substrate cracks and crevices. Overall, crustaceans are probably less vulnerable than are molluscs and echinoderms (sea urchins). Perhaps this

- is because crustaceans are, comparatively speaking, much more mobile than are most molluscan and echinoderm species, and therefore it is likely that otters must make use of visual cues to capture crustaceans. Furthermore, crustaceans are usually nocturnally active (when visual cues are apparently least effective), and some species (e.g. spiny lobsters and Dungeness crabs) spend part of the year in deep water. It also appears that estuarine shellfisheries are less severely affected (or often unaffected) by sea otter foraging compared with fisheries of the open coast.
- (c) Most shellfish populations are exploited at or beyond the level of MSY. Except for those that are newly emerging, most shellfisheries have been unable to maintain a sustained level of high productivity, regardless of whether they were also subject to predation by sea otters. As a result, yields are sharply responsive to factors affecting available stock size (such as predator depredation or regulation changes).
 - (d) All the shellfish species discussed here have complex life histories in which their reproductive products are broadcast into the plankton where they undergo various metamorphoses before entering fishable adult populations. The larvae are planktotrophic in most instances, which greatly extends the potential time they can spend in the water column. In most species, little is known of these early life stages. In no case is it known how events acting on these various life-history stages affect the abundance of the adult populations that derive from them.
 - (e) Frequently, shellfish populations exhibit substantial variation between areas or over time in several aspects of their life history. For example, recruitment may occur regularly in some areas and very rarely in others; for other species it may be episodic everywhere. Similarly, growth rates and maximum sizes for a given species often vary among areas. Seldom are there sufficient data available to incorporate these sources of variation into management programmes. Consequently, following Larkin's (1977) general view of the problem, different stocks certainly have been differentially affected by exploitation, even if the intensity of exploitation was spatially uniform and low enough to be accommodated by the species as a whole.
 - (f) There are both commercial and recreational fisheries for most species. In some cases, landings from the recreational fisheries are thought to equal or exceed commercial landings. Yet often, usually for simple practical reasons, recreational fisheries are unmonitored or effectively unregulated.
 - (g) Natural disasters have greatly affected a few local fisheries. For example, the earthquake of 1964, by altering coastal elevations, caused a decline in some of Alaska's clam fisheries. Similarly, paralytic shellfish poisoning precipitated the collapse of others.
 - (h) Economic factors often have a powerful influence on shellfisheries. These may be manifested in several ways. For example, market conditions may make it unprofitable to participate in a fishery, which would seem to be true for sea urchin fisheries along most of the coast of North America. In circumstances where price is strongly dictated by supply, it may be profitable to continue fishing even after the stock has been severely depleted (e.g. abalone).
 - (i) Many shellfisheries have developed rapidly. This was especially true of recent ones (e.g. the pinto abalone and red urchin fisheries). There are several consequences of this sort of rapid growth. One is that a fishery can exceed MSY while landings are still in a growth phase (e.g. Ricker 1973). Another is that the fisheries may

quickly become overcapitalised or otherwise overcommitted, thus making regulations difficult to impose. Yet another consequence is that, with such rapid growth, management has neither the time nor the information to impose well-thought-out regulations. More often than not, this results in regulations being implemented when it is too late.

We conclude that shellfisheries of the coastal north Pacific region are, in their history and behaviour, not unlike many other of the world's fisheries. Some species, due to slow growth or infrequent recruitment, seem especially susceptible to overexploitation. Indeed, the Pacific shellfisheries have to contend with a variety of pressures brought about by heavy human utilisation of the coastal environment. Of particular significance among these pressures is the prospect of predation by the sea otter, whose near extinction permitted the development of those fisheries in the first place.

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