

DESTRUCTION AND OPPORTUNITY ON THE SEA FLOOR: EFFECTS OF GRAY WHALE FEEDING¹

JOHN S. OLIVER AND PETER N. SLATTERY

Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, California 95039 USA

Abstract. Gray whales (*Eschrichtius robustus*) are highly disruptive bottom feeders that remove infaunal invertebrate prey and sediments by suction. The response of the benthos to gray whale feeding was examined in the primary feeding grounds of the Bering Sea and in an ecological analog of these prey communities along the west coast of Vancouver Island. Prey communities were dominated by ampeliscid and other amphipod crustaceans that formed dense tube mats. Large feeding excavations (often 2–20 m²) were rapidly colonized by scavenging lysianassid amphipods, especially *Anonyx* spp., that attacked injured and dislodged infauna. Many of the attacked animals were small crustaceans (<1 cm long) and polychaete worms. *Anonyx* spp. was 20–30 times more abundant inside fresh excavations than in the surrounding tube mat, where they dispersed within hours after the initial feeding disturbance. A smaller species of lysianassid, *Orchomene minuta*, invaded less rapidly and remained much longer in excavations than the larger, *Anonyx* spp. Natural scavenging events outside feeding excavations revealed that lysianassids commonly fed on relatively small crustacean carcasses (<3 cm long). Within days and weeks, gray whale feeding excavations trapped organic debris. Most invading species were much more abundant in debris patches compared to debris-free areas of the same excavations. The numbers of some colonists remained elevated in disturbed areas for >2 mo. Early colonists were characterized by much greater abundances inside excavations relative to the adjacent tube mat. Two numerically dominant groups of tube-dwelling amphipods were not characterized by a large pulse of abundance inside excavations. *Ampelisca* and *Protomedea* gradually colonized pits. They also swam less frequently than the early colonists, and probably had more infaunal habits. Gray whale feeding clearly has a dramatic impact on the structure of benthic communities, and also may enhance the population size of several secondary prey.

Key words: *Ampelisca*; benthic communities; colonization; crustaceans; disturbance; *Eschrichtius robustus*; feeding ecology; gray whale; habitat selection; Lysianassidae; scavengers.

INTRODUCTION

Baleen whales (Mysticeti) usually consume small pelagic crustaceans near the ocean surface (Gaskin 1982). They filter tremendous numbers of prey on the baleen fringe. No other marine or terrestrial mammal has similar foraging habits.

Gray whales (*Eschrichtius robustus*) are unique among the baleen whales. They feed primarily on the sea floor. The major prey are amphipod crustaceans living within the sediment in the southern Chukchi and especially the northern Bering Sea (Rice and Wolman 1971). Gray whales suck sediment and fauna into the mouth, capture prey on the baleen filter, and expel sediment through the baleen. Excavation size is highly variable. Single suction marks are often 1–2 m long, and reworked feeding excavations form distinct features >25 m in diameter (Oliver et al. 1984). Fresh feeding excavations can cover >30% of the sea floor (Oliver and Kvitek 1984), and very large geographic areas (Johnson and Nelson 1984).

Some mammalian grazers (Harper 1977, Noy-Meir 1981) and predators (Platt 1975, Estes et al. 1978) have dramatic effects on vegetation patterns, but none disrupts the primary habitat as extensively as the gray whale during normal feeding activities. The largest terrestrial mammals such as elephant and rhinoceros rarely

excavate soil. Although there is speculation that both groups cause soil erosion by heavy grazing, this is undocumented (Jewell and Holt 1981, Laws 1981). Even when long-term patterns of habitat change are linked to domestic grazing, the link is complicated by concurrent changes in climate (Hastings and Turner 1965).

There is little understanding of how any cetacean influences the structure of prey and nonprey communities. Among all the marine mammals, only the community role of the sea otter is well known (Estes and Palmisano 1974, Dayton 1975, Estes et al. 1978, 1982, Simenstad et al. 1978, Duggins 1980). The highly disruptive feeding activities of gray whales undoubtedly have dramatic and predictable effects on marine bottom communities. This paper considers the population and community consequences of gray whale feeding in soft-bottom habitats, the primary feeding grounds.

METHODS

The two major study areas were the Southeast Cape of St. Lawrence Island in the Bering Sea and Pachena Bay on the western side of Vancouver Island, British Columbia. The Bering Sea area was visited during early July 1980 and 1983. Pachena Bay was visited during July and September 1982 and February, April, July, and August 1983. Gray whales feed in both study areas, and infaunal prey communities are remarkably similar (Oliver et al. 1984). Parallel observations, experiments,

¹ Manuscript received 15 June 1984; revised 17 January 1985; accepted 22 January 1985.

and sampling were done in each area whenever possible. However, because of the accessibility of the feeding ground and the excellent logistic support, field work was more intensive and covered longer periods in Pachena Bay.

Most gray whales migrate along the west coast of Vancouver Island during March and December. The bulk of the population spends the winter in the calving lagoons of Baja California and the summer in the feeding grounds in the northern Bering and southern Chukchi seas (Rice and Wolman 1971). Over 50 animals spend the entire summer along Vancouver Island (Darling 1984), feeding on infaunal and epifaunal invertebrates (Darling 1977, Oliver et al. 1984, Murison et al. 1984). While this summer group is <1% of the gray whale population, it can have a dramatic effect on prey communities and habitats (Oliver et al. 1984). Few whales remain in the Vancouver Island feeding grounds during the winter months (Darling 1984).

Feeding gray whales were present in Pachena Bay during July and September 1982, and April, July, and August 1983. None was present in February 1983 (Oliver et al. 1984).

All field observations, experiments, and sampling were done by divers using SCUBA. Benthic invertebrates were sampled with hand-held corers (75 cm² except July 1980, 180 cm²; the latter core size appears only in Table 6). Sediments were washed over a 0.5-mm screen and residues preserved in a 4% solution of formaldehyde. All macrofauna were identified to species and counted. Biomass of total fauna was determined as wet mass. Benthic animals swimming off the bottom were collected in emergence traps placed over the sediment during light (midday) and dark (including the crepuscular period) hours in Pachena Bay (25–31 July 1982). Each trap covered 0.25 m², was 0.5 m high, and collected animals at the top (Alldredge and King 1980). Trap time was usually 6–8 h. Scavenging lysianassid amphipods were collected in baited, 3.8-L jars placed on the sea bottom for 24 h at depths of 6, 12, and 15 m in July 1982 and April and July 1983. The grain size distribution of the surface sediments (top 5 cm) was measured by a modified Emery tube analysis (Folk 1974).

Natural feeding excavations of gray whales were common at both study areas and were easily distinguished from depressions made by other biological or physical processes (Oliver et al. 1983b, 1984, Johnson and Nelson 1984, Oliver and Kvitek 1984). Artificial feeding excavations were made at both study areas by shoveling sediment and fauna into buckets that were dumped outside the experimental areas. Natural excavations are made by suction, not digging. However, both methods remove the sediment and most of the infaunal animals from an excavation. Experimental excavations were $\approx 1.5 \times 0.75$ m and 10–15 cm in depth. This is morphologically similar to some natural excavations, although there is considerable variation in

excavation size, shape, and depth (Oliver and Kvitek 1984, Oliver et al. 1984).

Six artificial excavations were dug in Pachena Bay on 13 July 1982 (12 m depth). Two excavations were sampled on each sampling date. Two artificial excavations (at 12 m depth) were dug in Pachena Bay on 15 April 1983. One was sampled at 0 and 3 d; the other at 1 d after digging. Divers dug excavations in February, July, and August to observe swarms of lysianassid amphipods that are attracted to the digging disturbance. These excavations were not sampled quantitatively. Two artificial excavations (20 m depth) also were dug at St. Lawrence Island directly off the fish camp on Southeast Cape on 3 July 1983. One was sampled at 0 and 24 h and one at 1 h after digging. The replication of experimental excavations is minimal because of the difficulty of digging large pits underwater.

Groups (5–50 individuals) of scavenging lysianassid amphipods (*Anonyx* spp.) were teased apart with forceps and the prey item collected. These first-attack victims were measured and identified to species in the laboratory. Groups of other lysianassids (*Orchomene* spp.) were collected from natural scavenging events that were found outside feeding excavations. First attack victims and natural scavenging events were observed at both study areas.

A series of laboratory experiments evaluated behavioral responses to sediment with and without a surface layer of organic debris. The debris was a mixture of woody chips (<5 mm long) and detritus collected from natural debris patches in the Pachena River during July 1983. The river debris contained no benthic invertebrates, but was similar to material that was trapped in feeding excavations of gray whales in Pachena Bay (see Results).

Sediment from the Pachena Bay feeding ground (12 m depth) was screened (0.5 mm) and kept in freshwater for several days. A 3-cm layer of this defaunated sediment was placed in each experimental container with a 5-mm layer of woody debris spread on the surface sediment of one side of the container (a plastic dish, diameter = 20 cm, height = 5 cm). The container was enclosed by a mesh corral (0.5 mm) that extended to the air-water interface of the aquarium, allowing animal swimming without escape. A strong water current was directed over each container. Fifty individuals of *Ampelisca agassizi* or *Anisogammarus pugettensis* from Pachena Bay were added to each container (five replicates). After 24 h, the number of individuals was counted from the debris and debris-free sediment. All laboratory experiments were done in aquaria that received raw sea water at the Bamfield Marine Station.

RESULTS

Pachena Bay

Community Patterns.—Gray whales fed in a dense bed of ampeliscid amphipods in the middle of Pachena

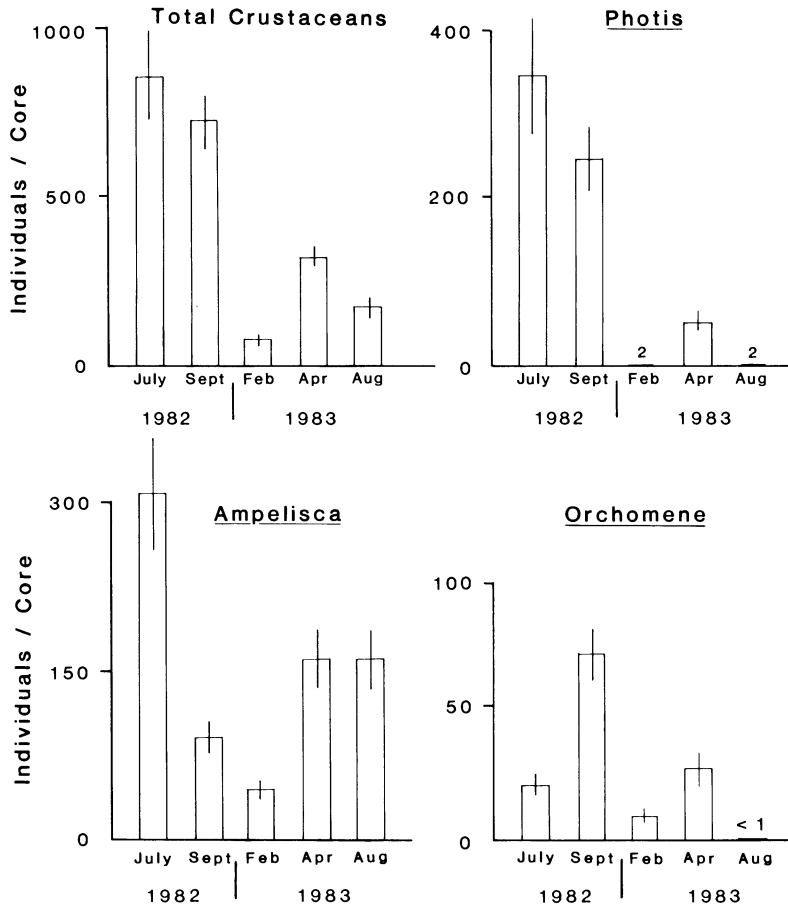


FIG. 1. Seasonal changes in the number of individuals of crustaceans and numerically dominant amphipods in the gray whale feeding ground in Pachena Bay (12 m depth). Mean number of individuals per 75-cm² core and standard errors (N = 6 cores).

Bay. The bed occurred in 10 to 16 m of water. The general zonation of benthic invertebrate communities in the bay was described by Oliver et al. (1984). The primary study area was in the center of the feeding ground, at the 12-m station. All field experiments and most sampling were performed here.

Seasonal patterns of community change were distinct (Fig. 1). During July 1982, 96% of the individuals of infaunal invertebrates were crustaceans; 98% of the crustaceans were amphipods; and 90% of the amphipods were *Ampelisca agassizi*, *Photis lacia*, *Protomeдея penates*, and *Orchomene minuta* in the major feeding area of Pachena Bay (12 m depth). Community patterns were similar in September 1982.

There was a striking decrease in animal abundance during the winter (Fig. 1), but crustaceans still accounted for 77% of the individuals of all invertebrates. By the following August 1983, the two most abundant species of small tube-dwelling amphipods, *Photis lacia* and *Protomeдея penates*, maintained populations that were <1% of the numbers present during the previous summer (Fig. 1). In general, only the largest tube dwell-

er, *Ampelisca agassizi*, had a high abundance by the second summer. Even this species was twice as abundant during the previous summer (Fig. 1).

Emergence traps were placed at the 12-m station to determine which infauna enter the overlying waters during the day and night. Almost all migrations occurred during the night, including the crepuscular period (Table 1). More than 99% of the *Photis lacia*,

TABLE 1. Most abundant invertebrates captured in emergence traps open for 6–8 h periods during either day or night at 12-m depth in Pachena Bay. Means and standard deviations (day, N = 4 traps; night, N = 4 traps).

Amphipods	No. individuals per 0.25-m ² trap	
	Night*	Day
<i>Ischyrocerus</i>	20 090 ± 7058	2448 ± 2412
<i>Photis</i>	19 362 ± 6802	0.8 ± 1.2
<i>Ampelisca</i>	341 ± 100	0.5 ± 1.0
<i>Protomeдея</i>	224 ± 79	0

* Includes crepuscular period.

TABLE 2. Most abundant invertebrates found in cores of woody debris patches and debris-free sand in 6 m of water in Pachena Bay. Means and standard deviations ($N = 8$ cores).

Amphipods	No. individuals per 75-cm ² core	
	Debris	No debris
<i>Anisogammarus</i>	195 ± 198	1 ± 2
<i>Allorchestes</i>	79 ± 68	2.7 ± 3.1
<i>Atylus</i>	7.7 ± 10	0.4 ± 1.3
<i>Tiron</i>	6.8 ± 5.7	0

Protomedeia penates, and *Ischyrocerus anguipes* were recently released young, in the first and rarely the second molt stage. In contrast, 74% of the *Ampelisca agassizi* in the traps were sexually mature adults ($N = 1511$ individuals). Adults of this species accounted for only 5% of the benthic population at the same time and place ($N = 1937$ individuals).

The structure of bottom communities was significantly altered by the presence of organic debris (a mixture of woody chips < 5 mm long, and detritus). In the shallower portion of the bay (6 m water depth), small patches of debris (10–30 cm in diameter and 5 mm thick) occurred on the level bottom and contained highly elevated numbers of several amphipods (Table 2). The four most abundant amphipods (Table 2) and the isopod *Edotea sublittoralis* were rare (usually less than one individual per 75-cm² core) in debris-free areas from the 6 m depth and in the tube mat from the central feeding ground (12 m depth). These five crustaceans accounted for 94% of the infaunal invertebrates in the debris patches at 6 m depth. Two species, *Anisogammarus pugettensis* and *Allorchestes* cf. *malleolus*, also were abundant in debris patches in 3 m of water and especially in debris patches on the intertidal beach, where there were 829 ± 203 *A. pugettensis* and 84 ± 19 *A. cf. malleolus* per 75-cm² core (means and standard deviations; $N = 6$ cores).

Debris patches (30–50 cm in diameter) within recent feeding excavations (12 m water depth) contained much greater numbers of amphipods than debris-free areas within the same excavations (Table 3). Recent feeding excavations were distinguished by their morphology, including exposure of amphipod tubes along the pit border, steep sides, poorly consolidated sediment, and few tubes within the pit (also described in Oliver et al. 1984). Debris patches were only common inside feeding excavations in April 1983. Only one crustacean, *Ampelisca agassizi*, was less abundant inside debris compared to debris-free parts of the same excavations (4.4 ± 1 vs. 33.5 ± 16 individuals per 75-cm² core; $\bar{X} \pm SD$, $N = 9$ cores; also see Experimental Patterns). In addition, the total number of crustaceans and the abundances of numerically dominant species within excavation debris (*Atylus tridens*, *Orchomene minuta*, *Anisogammarus pugettensis*, and *Allorchestes* cf. *mal-*

leolus) were significantly greater than the numbers in the undisturbed tube mat ($P < .005$; Mann-Whitney U test; $N = 9$ and 6 cores, respectively).

Recent feeding excavations contained significantly coarser sediment than the adjacent, undisturbed tube mat ($P < .05$; Mann-Whitney U test, $N = 4$ cores). Excavation sediment had a greater median grain size (0.160 vs. 0.124 mm), contained less very fine sand (39 vs. 53%), and was poorly sorted (sorting coefficient of 0.91 vs. 0.70). The sorting coefficient is a relative measure of the variation in grain sizes. A lower coefficient indicates less variation and greater sorting. Qualitative observations of excavation sediments during April and the previous summer also revealed coarser sediment inside recent feeding excavations.

Experimental Patterns.—The first colonists into the excavations were lysianassid amphipods, *Anonyx* sp. These individuals swarmed into excavations within seconds and were usually gone by the next day (Fig. 2). *Anonyx* sp. was >30 times more abundant inside excavations than in the adjacent tube mat. They invaded all of the experimental excavations. At the same time, thousands of individuals were captured in baited traps placed on the sea floor at the 12 m depth, and hundreds were trapped during similar 24-h exposures in 6 and 15 m of water. In contrast, few *Anonyx* sp. were captured in baited traps or invaded experimental excavations during July and August 1983. The absence of *Anonyx* sp. during 1983 may be related to warm water caused by El Niño (Weare 1983). *Anonyx* sp. primarily inhabit cold waters of the northern cold temperate to arctic seas (Steele 1979).

Anonyx sp. attacked injured and dislodged infauna within excavations. Numerous qualitative observations were made of scavenging events by teasing apart

TABLE 3. Number of infaunal individuals in substrate cores from woody debris patches and debris-free areas inside three recent feeding excavations of gray whales in Pachena Bay (12 m depth). Means and standard deviations ($N = 3$ cores).

	Whole excavations		
	No. 1	No. 2	No. 3
	No. individuals per 75-cm ² core		
Total crustaceans			
Woody debris	841 ± 306	619 ± 82	459 ± 110
No debris	142 ± 74	96 ± 36	66 ± 16
Amphipods			
<i>Atylus</i>			
Woody debris	564 ± 193	23 ± 22	59 ± 49
No debris	1 ± 1.2	1 ± 1.2	0
<i>Orchomene</i>			
Woody debris	113 ± 99	253 ± 60	95 ± 23
No debris	26 ± 25	43 ± 24	25 ± 9
<i>Anisogammarus</i>			
Woody debris	30 ± 13	208 ± 48	207 ± 29
No debris	0.3 ± 1.0	3 ± 2.5	3 ± 2

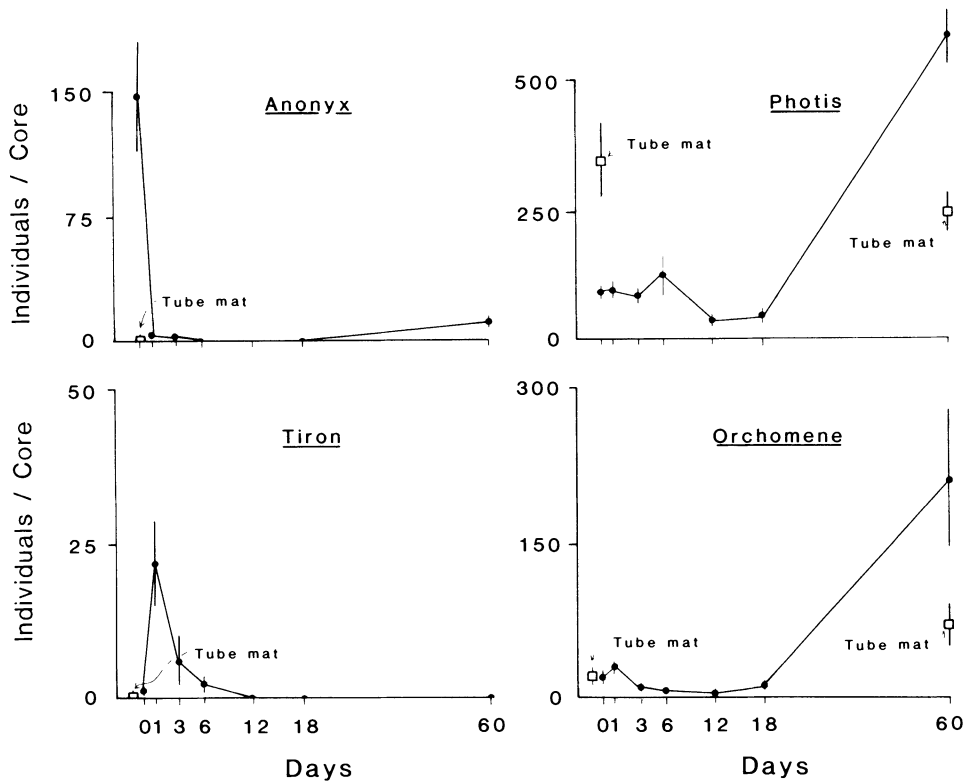


FIG. 2. Colonization of experimental excavations ($\approx 1.5 \times 0.75 \text{ m} \times 10\text{--}15 \text{ cm}$ deep) by numerically dominant amphipods in Pachena Bay (12 m depth). Mean number of individuals per 75-cm² core and standard errors ($N = 6$ cores).

balls of *Anonyx* sp. and revealing the prey. Prey included individuals of *Ampelisca agassizi*, *Protomedea penates*, the polychaete *Nephtys* sp. and other worms, and the bivalve *Psephidia lordi*. In addition to these first-attack victims, we observed numerous scavenging events outside feeding excavations in the bay. Both *Anonyx* sp. and *Orchomene minuta* occurred on algal drift, fish carcasses, fish fecal deposits, and the exoskeletons of larger crustaceans such as crabs and shrimp.

Like *Anonyx* sp., *Tiron biocellata* is a highly motile amphipod that swims and inhabits superficial sediment layers. *Tiron biocellata* rapidly invaded the experimental excavations where it was over 10 times more abundant than in the adjacent tube mat (Fig. 2). Unlike the lysianassids, *T. biocellata* is not a known scavenger.

Photis lacia and *Orchomene minuta* gradually increased inside the experimental excavations from July to September, when they were over twice as abundant within the pits compared to the undisturbed tube mat (Fig. 2). Both species are relatively small. *Photis lacia* is a tube dweller and *O. minuta* is a lysianassid amphipod, much smaller than *Anonyx* sp. (see Bering Sea Patterns). These species accounted for the large total number of crustaceans inside the excavations in September (Fig. 3).

Only two abundant crustaceans did not have elevated numbers inside the experimental excavations.

By September, *Ampelisca agassizi* and *Protomedea penates* (Fig. 3) were about twice as abundant in the tube mat compared to the experimental excavations. *Ampelisca agassizi* accounted for most of the biomass of crustaceans and tube material in the undisturbed bottom community. While the relative abundances of species were quite different inside and outside the experimental excavations, species composition and biomass (Fig. 3) were similar within 2 mo.

By February the next year, all experimental excavations were filled with sediment and could not be distinguished from the surrounding bottom. The plastic stakes that marked the excavations were dislodged, apparently by the activities of whales during the fall. We relocated the station, but not the exact location of individual excavations, so the experimental excavations could not be sampled after September 1982. However, given the colonization patterns in September (Figs. 2 and 3) and the low infaunal abundances in February (Fig. 1), community patterns probably were re-established within the experimental excavations by February.

The presence of organic debris had a significant effect on colonization patterns into artificial excavations in April 1983 (Table 4). Unlike the woody debris found in natural excavations at the same time (Table 3), the debris in the artificial pits was a fine organic matter

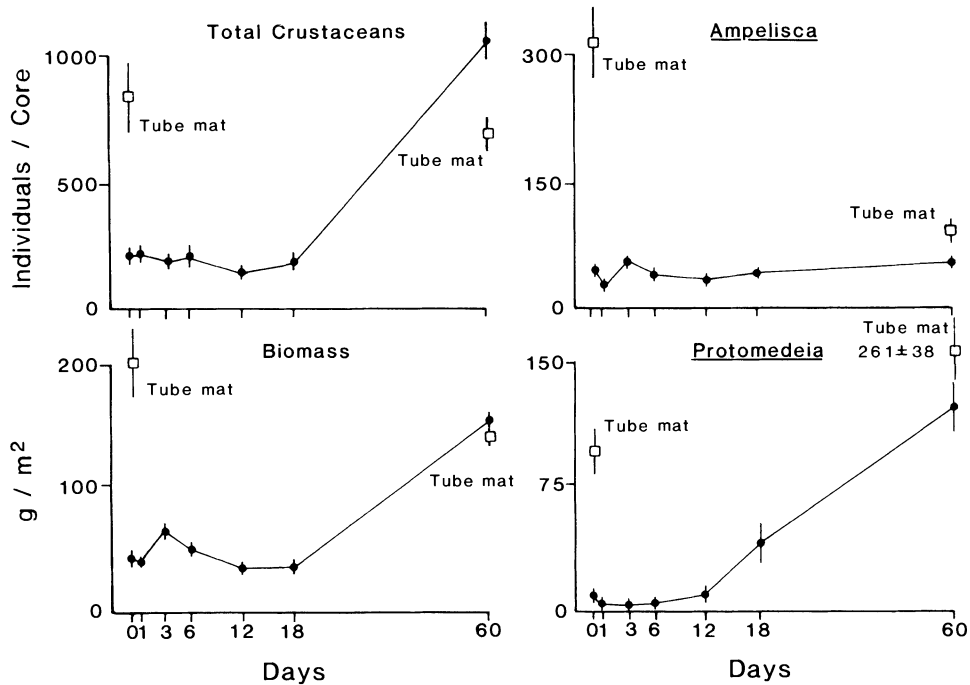


FIG. 3. Colonization of experimental excavations by all crustaceans and the later colonists, *Ampelisca agassizi* and *Protomedeia penates*, and changes in infaunal biomass in Pachena Bay from July to September 1982 (12 m depth). Mean number of individuals per 75-cm² core, mass per square metre, and standard errors ($N = 6$ cores).

trapped from the overlying waters. Woody material was rare, and instead the debris patches (30–50 cm in diameter) were a thin layer (1–2 mm) of flocculent seston which accumulated within 1 d. Infaunal crustaceans showed similar patterns of abundance in the thin flocculent debris and the thicker woody debris (Tables 3 and 4). Invasion of the experimental exca-

vations showed that animals responded rapidly to the presence of debris. Crustaceans were abundant in debris that accumulated 1 d after the experimental digging (Table 4). The total number of crustaceans and the abundances of the species shown in Tables 3 and 4 were always higher inside debris patches within both the natural and experimental excavations compared to debris-free areas in the same pits ($P < .05$; Wilcoxon signed ranks test, $N = 5$ cores). Only *Ampelisca agassizi* had significantly larger numbers in debris-free areas compared to the debris patches within the natural (see Community Patterns) and experimental excavations ($P < .05$; Wilcoxon signed ranks test, $N = 5$ cores).

Anisogammarus pugettensis showed a significant ($P < .005$; Mann-Whitney U test, $N = 5$ cores) preference for sand with a layer of woody debris in laboratory experiments (48 ± 1.4 individuals per debris side vs. 1.6 ± 1.5 per nondebris side of chambers, $\bar{X} \pm SD$). This species was very abundant in debris patches on the level bottom (Table 2), and in debris within natural and experimental excavations (Tables 3 and 4). In contrast, *Ampelisca agassizi* had no preference ($P > .1$; Mann-Whitney U test, $N = 5$ cores) for sand with or without woody debris in the laboratory (28 ± 6.7 individuals per debris side vs. 20 ± 5.4 individuals per nondebris side of chambers). This species was always more abundant in debris-free areas compared to debris patches inside natural and experimental excavations.

TABLE 4. Colonization of experimental excavations by the numerically dominant invertebrates in April 1983 in Pachena Bay. Samples were taken in flocculent debris patches and debris free areas. Means and standard deviations ($N = 6$ cores at 0 d; $N = 3$ cores at 1 and 3 d).

Amphipods	Time after disturbance (d)		
	0	1	3
No. individuals per 75-cm ² core			
<i>Anisogammarus</i>			
Flocculent debris	1 ± 1.2	47 ± 36	129 ± 72
No debris	...	1.3 ± 1.0	41 ± 17
<i>Atylus</i>			
Flocculent debris	0	151 ± 109	87 ± 31
No debris	...	0	2 ± 2.1
<i>Orchomene</i>			
Flocculent debris	12 ± 18	310 ± 142	206 ± 50
No debris	...	86 ± 32	95 ± 32
<i>Photis</i>			
Flocculent debris	0	39 ± 17	19 ± 5
No debris	...	1.7 ± 1.3	1 ± 1.2

Bering Sea

As in Pachena Bay, lysianassid amphipods rapidly invaded experimental excavations near St. Lawrence Island (Figs. 4 and 5). *Anonyx* spp. was nearly 20 times more abundant inside the artificial excavations compared to the adjacent tube mat. Most individuals left the pits within 1 h after the digging (Fig. 4). *Anonyx* spp. individuals that remained after 1 h were significantly smaller ($P < .05$; Kolmogorov-Smirnov test) than conspecifics that first invaded the excavations (Fig. 5).

Anonyx spp. primarily attacked small amphipod crustaceans and polychaete worms in the experimental excavations (Table 5). The tube dwellers *Ampelisca macrocephala* and *Ischyrocerus latipes* were frequently attacked. Near St. Matthew Island, spionid polychaetes were a numerically dominant member of the infaunal community (J. S. Oliver and P. N. Slattery, *personal observation*) and were often attacked (Table 5). Only the tunicate *Peloniaia corrugata* was attacked and not consumed. These animals remained in the bottom of excavations for the duration of our visit (3 d). They may be protected from lysianassid predation by the heavy tunic or by chemicals (Pierie and Bell 1984).

Natural scavenging events involved the carcasses of crustaceans with persistent exoskeletons including large king crabs and relatively large peracarid crustaceans ($\approx 2-3$ cm in length), such as the amphipods *Ampelisca*, *Acanthostepheia*, *Wecomedon*; the isopod *Tecticeps*; and the cumacean *Diastylis*. These events were easily located by divers and were always colonized by groups of smaller lysianassids, *Orchomene minuta*. None of the carcasses contained fresh soft tissue. If a baited trap or injured animal was placed on the sea floor, *Anonyx* spp. rapidly attacked fresh tissue as in the first attacks

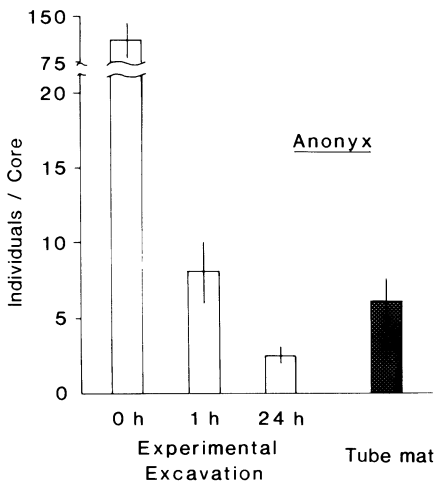


FIG. 4. Colonization of experimental excavations by scavenging lysianassid amphipods, *Anonyx* spp., near St. Lawrence Island. Mean number of individuals per 75-cm² core and standard errors ($N = 6$ cores).

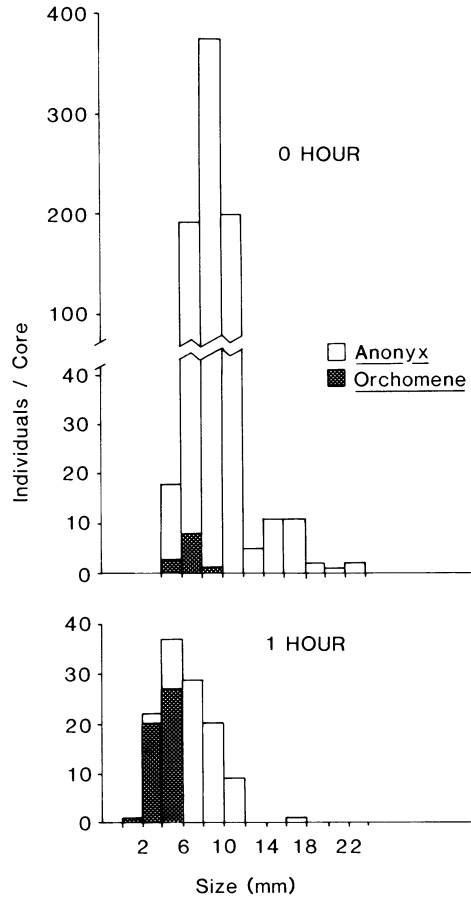


FIG. 5. Change in the number and size of individuals in two groups of lysianassid amphipods invading experimental excavations near St. Lawrence Island at 0 and 1 h after making an experimental excavation.

(Table 5). As in Pachena Bay (Fig. 2 and Table 4), *O. minuta* colonized excavations more slowly than the larger *Anonyx* spp. near St. Lawrence Island (Fig. 5). In addition to lysianassids, other scavengers, such as the isopod crustacean *Tecticeps alascensis*, were attracted to experimental feeding disturbances.

Atylid amphipods were abundant inside natural excavations containing broken shell debris (Table 6). Dense shell deposits were observed below the infaunal tube mats around St. Lawrence Island and were probably exposed by gray whale feeding. Shell debris also occurred within the tube mat. At the Penuk Islands, we found a thick pavement of broken shells covering the sea floor. *Atylus collingi* was very abundant here (Table 6) and apparently preferred bottom substrates formed by shell fragments, taking refuge under the fragments and using them as a movable shelter or perhaps in feeding.

Atylids were also highly motile. In July 1980 and 1983, we encountered large swarms of sexually immature animals swimming near the sea floor and

TABLE 5. Benthic invertebrates that were dislodged in experimental excavations and attacked by groups of lysianassid amphipods (*Anonyx* spp.) in the Bering Sea.

First attack victims	St. Lawrence		St. Matthew
	No. 1	No. 2	
	No. individuals attacked		
Crustaceans			
<i>Ampelisca</i>	15	4	1
<i>Anonyx</i>	6
<i>Ischyrocerus</i>	...	12	...
<i>Synidotea</i>	...	1	...
Polychaetes			
<i>Nephtys</i>	1	3	3
Ampharetid	4
<i>Spiophanes</i>	6
<i>Travisia</i>	1
Bivalves			
<i>Yoldia</i>	...	2	...
<i>Tellina</i>	1
Others			
Tunicates*	24
<i>Edwardsia</i>	1
Nemertean	...	1	...

* Attacked but not eaten.

throughout the water column. While *Anonyx* spp. frequently swam several metres from the sea floor, atylid amphipods were the most abundant benthic crustacean found in the water near St. Lawrence Island.

DISCUSSION

The feeding disturbance of gray whales produces similar responses in prey communities from the Bering Sea and Vancouver Island. Feeding is highly disruptive, scavengers are major colonists, and various animals are attracted to debris within pits. Although our work is concentrated in Pachena Bay, the structure of prey communities and the feeding behavior of whales in Pachena Bay and Bering Sea are also alike (Oliver et al. 1984).

Scavenging lysianassid amphipods invade feeding excavations and consume injured and dislodged invertebrates. The two major genera of lysianassids have different scavenging responses to gray whale feeding. The first invaders are species of *Anonyx* that are relatively large. They form dense swarms that disperse within hours into the surrounding and relatively undisturbed tube mat. *Anonyx* are the first to attack stranded animals, fresh bait, and unsuspecting divers. Smaller species such as *Orchomene minuta* invade excavations more slowly than *Anonyx*, but remain in pits for a longer time. They are not the first scavengers to attack fresh carcasses, nor do they swarm on the surface or above the bottom. *Orchomene minuta* is the most abundant scavenger on relatively old carcasses located outside feeding pits but inside the major feeding grounds.

Lysianassid amphipods are voracious scavengers and

predators (Bousfield 1973). Although they are abundant and widespread (Gurjanova 1962), their feeding habits are largely known from baited traps (e.g., Thurston 1979). As a result, attention has focused on their activities near large baits (Hessler et al. 1978) and on the ecological role of infrequent falls of large carcasses to the sea floor (Dayton and Hessler 1972, Stockton and DeLaca 1982). There is little qualitative or quantitative information on natural scavenging events. Fortunately these events are common in the shallow, cold-water habitats where gray whales feed. Our observations of first-attack victims and older carcasses illustrate that many small animals (<3 cm) are consumed by lysianassids. Similar observations are difficult or impossible to make in less dense communities and in habitats inaccessible to divers. Nevertheless, small invertebrates may be the most important source of food for lysianassids in other environments, including the deep sea.

Organic debris accumulates in excavations within days after gray whale feeding. Debris may persist for many days or weeks. Old excavations may trap new patches of debris for months after feeding disturbance. Much larger numbers of animals colonize debris patches compared to debris-free areas of the same excavations. Colonization patterns are remarkably similar in a thick layer of woody debris and in a thin layer of flocculent material. Since there are considerable differences between the potential shelter offered by the two kinds of debris, animals may be attracted to debris for the food more than shelter. Laboratory experiments clearly illustrate a behavioral attraction to debris patches. Even shallow pits made by feeding rays on wave-swept sands accumulate organic matter that is potential food for invertebrate colonists (VanBlaricom 1982). While all our debris samples are from Pachena Bay, Bering Sea excavations are likely to trap organic matter and cause similar patterns.

Patches of shell debris are common in feeding excavations near St. Lawrence Island. Atylid amphipods are most abundant in shell substrates and inside pits containing shell debris exposed at the sediment surface. Atylids nestle between shell fragments which they use for shelter or perhaps to aid in feeding. In Pachena

TABLE 6. Abundance of *Atylus collingi* in feeding excavations containing shell debris and in the adjacent tube mat near St. Lawrence Island, and in a shell bottom at the Penuk Islands. Means and standard deviations (number of cores is given in parentheses).

	1983	1980*
	No. individuals per 75-cm ² core	
Tube mat	0.2 ± 0.3 (6)	2 ± 2 (6)
Feeding excavation with shell debris	18 ± 16 (6)	14 ± 11 (5)
Penuk shell bottom	101 ± 23 (12)	...

* Data from 180-cm² cores converted to 75 cm².

Bay, another species of atyid is abundant in patches of organic debris.

Scavengers and animals attracted to debris are 2–30 times more abundant inside feeding excavations compared to the adjacent tube mat. With the exception of *Anonyx*, these early colonists maintain high local abundances for at least several days and probably weeks after the feeding disturbance. Even in the absence of obvious debris patches, some early colonists have higher numbers inside pits than in the tube mat after 2 mo.

Unlike the early colonists, two groups of tube dwellers are not characterized by a large pulse of individuals into feeding excavations. The numbers of *Ampelisca* and *Protomedeia* gradually increase inside pits. There are no early peaks in abundance. Although the colonization patterns of these species are only documented in Pachena Bay, Nerini and Oliver (1983) make the same argument for the Bering Sea. *Ampelisca* accounts for most of the biomass of infaunal crustaceans in the feeding grounds, and is a major gray whale prey (Oliver et al. 1983b, 1984). In contrast to the observations that the juveniles of *Ampelisca abdita* invade open space in an intertidal community (Mills 1967, 1969), all sizes of *Ampelisca* invade feeding excavations in both the Bering Sea and Pachena Bay.

Infaunal patterns inside the experimental excavations were similar to patterns observed in natural feeding excavations in both the Bering Sea and Vancouver Island. Oliver et al. (1984) were able to follow a feeding whale underwater in Pachena Bay and observed swarms of lysianassid amphipods invade natural feeding excavations immediately after the disturbance. We made similar observations in the Bering Sea (J. S. Oliver and P. N. Slattery, *personal observation*). The same scavengers invaded experimental excavations in both areas. Like the experimental excavations, the natural excavations that we sampled in Pachena Bay contained elevated numbers of several less transient early colonists, and relatively low numbers of the later colonists. The differences between infaunal patterns in and out of debris patches also were similar for the natural and experimental excavations in Pachena Bay. Nerini and Oliver (1983) also found elevated numbers of early colonists and relatively low numbers of later colonists in natural feeding excavations in the Bering Sea.

Motility patterns of the fauna are related to colonization of feeding excavations. Better swimmers invade pits first. The most active swimmers are shallow burrowers near the sediment-water interface. They are characterized by large peaks in abundance inside pits. Lysianassids (Gurjanova 1962), *Atylus* and *Tiron* (Oliver et al. 1980), and *Anisogammarus* (Bousfield 1981) are early colonists that frequently swim. Among the tube dwellers, the young *Photis* and *Ischyrocerus* are good invaders that often swim. In contrast, the other abundant tube dwellers, *Ampelisca* and *Protomedeia*, swim much less frequently and reestablish populations more gradually inside feeding excavations.

Recovery of infaunal communities inside feeding excavations probably takes a longer time in the Bering Sea than in Pachena Bay. Biomass recovers within 2 mo in Pachena Bay. The structure of bottom communities in summer excavations probably recovers by the winter, when pits are refilled with sediment in the bay. Unlike prey in Pachena Bay, some of the major gray whale prey in the Bering Sea, such as *Ampelisca macrocephala*, live for 2 yr (Kannevorf 1965). However, since all the crustaceans are motile and good colonizers, bottom communities inside Bering Sea excavations probably can recover within a year. Patterns of faunal recovery in both areas are certainly influenced by spatial and temporal changes in bottom communities, as well as the frequency and intensity of feeding disturbance. Redisturbance of feeding excavations by whales (Oliver et al. 1984) and reworking by currents (Johnson and Nelson 1984) produce a complex mosaic of relatively old and new excavations that further complicates the recovery process.

Johnson and Nelson (1984) argue that gray whale feeding may help to maintain the sand substrate where the ampeliscid amphipods, which are the primary prey, form dense beds. Whales suspend fine sediments that can be transported from the feeding ground. Our observations of significantly coarser deposit inside recent natural feeding excavations support this hypothesis. In addition, we observed elevated numbers of several secondary gray whale prey inside experimental and natural feeding excavations. Perhaps periodic disturbance by feeding whales may produce larger populations of these prey on a larger spatial scale.

None of the other baleen whales is likely to influence prey communities like the gray whale. The other species feed in highly dynamic pelagic environments where baleen feeding has only a minor effect on the physical habitat. There are no planktonic scavengers comparable to the lysianassid amphipods and no evidence suggesting that zooplankton colonize the ephemeral patches of water filtered by the whales. In terrestrial habitats, army ants may be one of the few groups that disrupt many animals during foraging and attract scavengers such as birds to a relatively large habitat area (Willis and Oniki 1978). In addition to highly disruptive and widespread bottom disturbances, gray whales also bring benthic invertebrates to the sea surface (Oliver et al. 1984), where they are consumed by a variety of birds (Harrison 1979, Gill and Hall 1983).

Like the gray whale, several other predators disrupt bottom communities while they excavate soft sediment for prey. They include blue crabs and horseshoe crabs (Young et al. 1976, Virnstein 1977, Woodin 1978, 1981), walrus (Oliver et al. 1983a), and sea otters (Shimek 1977, Calkins 1978, Hines and Loughlin 1980, Oliver et al. 1983a). However, only rays produce feeding excavations that are also colonized by large pulses of infaunal animals, primarily amphipod crustaceans (VanBlaricom 1982). Amphipods may be able to in-

vade relatively small areas of open space, such as the feeding excavations of gray whales and rays, better than most infaunal groups. Species with pelagic larvae, on the other hand, may be more adept at colonizing larger areas of open space. The relationship between the spatial scale of disturbance and the life history of infaunal animals is unexplored (e.g., Thistle 1981). Nevertheless, compared to rays, a large number (15 000–20 000; Rugh 1984) of large whales forage intensively (Johnson and Nelson 1984) in one general feeding ground for only several months (Rice and Wolman 1971). Here gray whales are disruptive bottom feeders that have a major effect on the spatial patterns of the benthic community.

ACKNOWLEDGMENTS

We thank our co-workers A. Fukuyama, R. Kvitek, J. Oaken, and M. Silberstein, and La Asociación de Biólogos Ambulantes for their essential contributions. A. Baldrige, D. Canestro, R. Clevenger, S. Dearn, J. Heine, B. Matson, B. Pierson, B. Stewart, and G. Van Dykhuizen helped in the field. S. Baldrige, S. Gaines, D. Helms, and G. VanBlaricom improved the manuscript. Special thanks to R. Nelson, L. Lowry, and K. Frost, and the Alaska Department of Fish and Game for continuing support and education, and to R. Foreman, S. Leader, and A. Bergy at the Bamfield Marine Station. We are grateful for a grant from the National Science Foundation (DPP-8121722) and the support of the *Alpha Helix*. All this is done in memory of Edmund F. O'Connor.

LITERATURE CITED

- Allredge, A. L., and J. M. King. 1980. Effects of moonlight on the vertical migration patterns of demersal zooplankton. *Journal of Experimental Marine Biology and Ecology* **44**: 133–156.
- Bousfield, E. L. 1973. Shallow water gammaridean Amphipoda of New England. Cornell University Press, Ithaca, New York, USA.
- . 1981. Evolution in North Pacific coastal marine amphipod crustaceans. Pages 69–89 in G. G. E. Scudder and J. L. Reveal, editors. *Evolution today*. Proceedings of the Second International Congress of Systematics and Evolutionary Biology. Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, Pennsylvania, USA.
- Calkins, D. G. 1978. Feeding behavior and major prey species of the sea otter, *Enhydra lutris*, in Montague Strait, Prince William Sound, Alaska. *United States National Marine Fisheries Service Fishery Bulletin* **76**:125–131.
- Darling, J. 1977. The Vancouver Island gray whales. *Waters, Journal of the Vancouver Aquarium* **2**:1–19.
- . 1984. Gray whales, *Eschrichtius robustus*, off Vancouver Island, British Columbia. Pages 267–287 in M. L. Jones, S. Leatherwood, and S. Swartz, editors. *The gray whale*. Academic Press, New York, New York, USA.
- Dayton, P. K. 1975. Experimental studies of algal canopy interactions in a sea otter-dominated kelp community at Amchitka Island, Alaska. *United States National Marine Fisheries Service Fishery Bulletin* **73**:230–237.
- Dayton, P. K., and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep-Sea Research* **19**:199–208.
- Duggins, D. 1980. Kelp beds and sea otters: an experimental approach. *Ecology* **61**:447–453.
- Estes, J. A., R. J. Jameson, and E. B. Rhode. 1982. Activity and prey selection in the sea otter: influence of population status on community structure. *American Naturalist* **120**: 242–258.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* **185**:1058–1060.
- Estes, J. A., N. S. Smith, and J. F. Palmisano. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* **59**:822–833.
- Folk, R. L. 1974. *Petrology of sedimentary rocks*. Second edition. Hemphill, Austin, Texas, USA.
- Gaskin, D. E. 1982. *The ecology of whales and dolphins*. Heinemann, London, England.
- Gill, R. E., and J. D. Hall. 1983. Use of nearshore and estuarine areas of the southeastern Bering Sea by gray whales (*Eschrichtius robustus*). *Arctic* **36**:275–281.
- Gurjanova, E. F. 1962. Amphipods of the northern part of the Pacific Ocean (Amphipoda, Gammaridea) Part 1. *Opredejiteji po faune SSSR, Akademii Nauk SSSR* **74**:1–143.
- Harper, S. L. 1977. *Population biology of plants*. Academic Press, New York, New York, USA.
- Harrison, C. S. 1979. The association of marine birds and feeding gray whales. *Condor* **81**:93–95.
- Hastings, J. R., and R. Turner. 1965. *Changing mile*. University of Arizona Press, Tucson, Arizona, USA.
- Hessler, R. R., C. L. Ingram, A. A. Yayanos, and B. R. Burnett. 1978. Scavenging amphipods from the floor of the Philippine Trench. *Deep-Sea Research* **25**:1029–1047.
- Hines, A. H., and T. R. Loughlin. 1980. Observations of sea otters digging for clams at Monterey Harbor, California. *United States National Marine Fisheries Service Fishery Bulletin* **78**:159–163.
- Jewell, P. A., and S. Holt, editors. 1981. *Problems in management of locally abundant wild mammals*. Academic Press, New York, New York, USA.
- Johnson, K. R., and C. H. Nelson. 1984. Side-scan sonar assessment of gray whale feeding in the Bering Sea. *Science* **225**:1150–1152.
- Kannework, E. 1965. Life cycle, food, and growth of the amphipod *Ampelisca macrocephala* Liljeborg from the Øresund. *Ophelia* **2**:305–318.
- Laws, R. M. 1981. Large mammal feeding strategies and related overabundance problems. Pages 217–232 in P. A. Jewell and S. Holt, editors. *Problems in management of locally abundant wild mammals*. Academic Press, New York, New York, USA.
- Mills, E. L. 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. *Journal of the Fisheries Research Board of Canada* **24**:305–355.
- . 1969. The community concept in marine zoology, with comments on continua and instability in some marine communities: a review. *Journal of the Fisheries Research Board of Canada* **26**:1415–1428.
- Murison, L., D. Murie, K. Morin, and J. S. Curiel. 1984. Aspects of feeding observed in the gray whale (*Eschrichtius robustus* Lilljeborg) along the west coast of Vancouver Island. Pages 451–463 in M. L. Jones, S. Leatherwood, and S. Swartz, editors. *The gray whale*. Academic Press, New York, New York, USA.
- Nerini, M. K., and J. S. Oliver. 1983. Gray whales and the structure of the Bering Sea benthos. *Oecologia (Berlin)* **39**: 224–225.
- Noy-Meir, I. 1981. Responses of vegetation to the abundance of mammalian herbivores. Pages 233–246 in P. A. Jewell and S. Holt, editors. *Problems in management of locally abundant wild mammals*. Academic Press, New York, New York, USA.
- Oliver, J. S., and R. G. Kvitek. 1984. Side-scan sonar records and diver observations of gray whale (*Eschrichtius robustus*) feeding grounds. *Biological Bulletin (Woods Hole)* **167**:264–269.

- Oliver, J. S., P. N. Slattery, L. W. Hulberg, and J. W. Nybakken. 1980. Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California. United States National Marine Fisheries Service Fishery Bulletin **78**:437-454.
- Oliver, J. S., P. N. Slattery, E. F. O'Connor, and L. F. Lowry. 1983a. Walrus, *Odobenus rosmarus*, feeding in the Bering Sea: a benthic perspective. United States National Marine Fisheries Service Fishery Bulletin **81**:501-512.
- Oliver, J. S., P. N. Slattery, M. A. Silberstein, and E. F. O'Connor. 1983b. A comparison of gray whale, *Eschrichtius robustus*, feeding in the Bering Sea and Baja California. United States National Marine Fisheries Service Fishery Bulletin **81**:513-522.
- Oliver, J. S., P. N. Slattery, M. A. Silberstein, and E. F. O'Connor. 1984. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. Canadian Journal of Zoology **62**:41-49.
- Pierie, B. J. S., and M. V. Bell. 1984. The localization of inorganic elements, particularly vanadium and sulphur, in haemolymph from the ascidians *Ascidia mentula* (Muller) and *Asciidiella aspersa* (Mueller). Journal of Experimental Marine Biology and Ecology **74**:187-195.
- Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs **45**:285-305.
- Rice, D. W., and A. A. Wolman. 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). American Society of Mammalogists Special Publication Number **3**: 1-142.
- Rugh, D. J. 1984. Census of gray whales at Unimak Pass, Alaska Nov.-Dec.-1977 to 1979. Pages 225-248 in M. L. Jones, S. Leatherwood, and S. Swartz, editors. The gray whale. Academic Press, New York, New York, USA.
- Shimek, S. J. 1977. The underwater foraging habits of the sea otter, *Enhydra lutris*. California Fish and Game **63**: 120-122.
- Simenstad, C. A., J. A. Estes, and K. W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. Science **200**:403-411.
- Steele, D. H. 1979. Zoogeography of the genus *Anonyx* (Crustacea, Amphipoda). Bulletin of the Biological Society of Washington **3**:47-53.
- Stockton, W. L., and T. E. DeLaca. 1982. Food pods in the deep sea: occurrence, quality, and significance. Deep-Sea Research **29**:157-169.
- Thistle, D. 1981. Natural physical disturbances and communities of marine soft bottoms. Marine Ecology Progress Series **6**:223-228.
- Thurston, M. H. 1979. Scavenging abyssal amphipods from the northeast Atlantic Ocean. Marine Biology **51**:55-68.
- VanBlaricom, G. D. 1982. Experimental analysis of structural regulation in a marine sand community exposed to oceanic swell. Ecological Monographs **52**:283-305.
- Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology **58**:1199-1217.
- Weare, B. C. 1983. The possible link between net surface heating and El Niño. Science **221**:947-949.
- Willis, E. O., and U. Oniki. 1978. Birds and army ants. Annual Review of Ecology and Systematics **9**:243-263.
- Woodin, S. A. 1978. Refuges, disturbance, and community structure: a marine soft-sediment example. Ecology **59**:274-284.
- . 1981. Disturbance and community structure in a shallow water sand flat. Ecology **62**:1052-1066.
- Young, D. K., M. A. Buzas, and M. W. Young. 1976. Species densities of macrobenthos associated with seagrass: a field experimental study of predation. Journal of Marine Research **34**:577-592.