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Effects on the Animal Community of Dislodgment of Holdfasts of *Macrocystis pyrifera*[1]

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ABSTRACT: Effects of natural dislodgment of holdfasts of *Macrocystis pyrifera* (L.) C. Agardh on the associated holdfast community were studied during a 110-day period. Six holdfasts were collected at the beginning of the study and analyzed to determine the abundance of major taxa at time 0. Forty-four holdfasts were detached from the rocky substrate and suspended on three midwater buoys to simulate natural dislodgment and drift in the kelp forest. The most abundant taxa associated with attached and drift holdfasts were decapod crustaceans, mollusks, polychaetes, ophiuroids, echinoids, asteroids, isopods, and amphipods. Only amphipods and isopods increased significantly in density in drift holdfasts during the experimental period. All other invertebrate taxa showed a decrease in abundance during the 3-month experiment.

A RICH AND DIVERSE community of macro- and micro-invertebrates is associated with holdfasts of brown macroalgae. Most of the studies related to the invertebrate fauna associated with holdfasts have a taxonomic emphasis (e.g., Colman 1940, Ghelardi 1971, Moore 1971, 1973*a*, Quast 1971). Ghelardi (1971) identified over 150 species of invertebrates inhabiting the holdfasts of *Macrocystis pyrifera* (L.) C. Agardh off La Jolla, California, representing nine different groups of organisms (Nematoda, Polychaeta, Isopoda, Gammaridae, Caprellidae, Pelecypoda, Gastropoda, Ophiuroidea, and Chelifera). Snider (1985), studying the patterns of emergence of demersal zooplankton associated with *M. pyrifera* holdfasts off Point Loma, California, reported 22 gammarid amphipod species. Other authors have described the ecological interactions of the invertebrate communities occurring in the holdfasts. Holdfasts of brown algae are important to their fauna because they provide mechanical shelter from wave impact and bottom surge, refuge from predators, food supply, and nursery areas (Andrews 1945, Bayne 1964, Jones 1971, 1972, Moore 1972, 1973*b*,*c*, 1974, 1978, Cancino and Santelices 1981, Ojeda and Santelices 1984, Vásquez and Santelices 1984, Snider 1985).

Storms can have a considerable effect on *M. pyrifera* kelp plants by "uprooting" and detaching the plants. Holdfasts are also dislodged as the plants age, and, indeed, many of the animals that burrow and feed upon the holdfasts can eventually disrupt their own "homes." According to Dayton et al. (1984), the most important cause of mortality of established *M. pyrifera* plants is entanglement with drifting plants. The drifters, with their heavy holdfasts suspended in the water column, slowly meander through the kelp forest, entangling additional plants, resulting in a "snowball effect." Dislodged plants with attached holdfasts may drift through an established kelp forest for up to 18 months and cause 50% yearly mortality of the adult *Macrocystis* population in the outer Point Loma kelp forest (Dayton et al. 1984).

Processes related to the rate of change of fauna associated with drifting holdfasts may be influenced by predation, competition, abandonment, and reproduction. Vásquez and Santelices (1984) documented such processes in holdfasts of *Lessonia nigrescens* Bory in central Chile, and Ojeda and Santelices

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(1984) documented similar processes in holdfasts of *M. pyrifera* in the Beagle Channel, southern Chile.

Experimental evidence that addresses the fate of animal communities inhabiting dislodged holdfasts of *M. pyrifera* is lacking. The purpose of this paper is to supply data showing how holdfast communities change after plants are dislodged and the holdfasts are suspended in the water column, sometimes for several months.

MATERIALS AND METHODS

The holdfasts studied in this experiment were collected from a *M. pyrifera* kelp forest located at 15 m depth offshore of Point Loma, California (32° 42′ N, 117° 16′ W). Forty-four holdfasts, with basal diameters ranging from 28 to 64 cm, were detached from the bottom during the period of 16 February to 23 March 1990. The size of each holdfast was determined by measuring the height and the basal diameter in two directions perpendicular to each other. The theoretical volume of each holdfast was calculated assuming the holdfast was an elliptical cone, following Ghelardi (1971). The holdfasts ranged between 2552 and 12,359 cm^3 in size.

Three lines, with surface and midwater buoys, were used to suspend the "experimental drifters." The stipes were cut off, and the holdfasts were tagged and attached to the buoy lines at depths of 5 and 10 m (reported by Dayton et al. [1984] as the main depth of drifter encounters). Four holdfasts were collected from the line approximately every 10 days between 26 February and 30 May 1990. The collected holdfasts were dissected, and the resulting invertebrates larger than 5 mm in body length were counted and grouped into eight main taxa.

Six holdfasts, with basal diameters ranging from 33 to 40 cm, were collected at the beginning of the study to evaluate invertebrate abundance in attached plants before they were dislodged (time 0). The volume of these holdfasts ranged from 3955 to 6591 cm^3. Invertebrate abundance in the attached plants was compared with abundance in the holdfasts suspended from the experimental lines and the temporal changes were recorded.

Because the volume of a holdfast increases as it grows, the values of invertebrate relative abundance were standardized to compare abundance among holdfasts of different sizes. Thus, an index of abundance was calculated as the ratio of invertebrate numbers to holdfast volume times 100, according to Ojeda and Santelices (1984).

RESULTS

Fifty *M. pyrifera* holdfasts, ranging in size from 2552 to 12,359 cm^3, were sampled at Point Loma from February through June 1990. During that period, four holdfasts with an average size of 5766 cm^3 (SD = 2480) were collected from the experimental lines approximately every 10 days. Decapod crustaceans, mollusks, polychaetes, ophiuroids, echinoids, asteroids, isopods, and amphipods were the most frequent and abundant taxa in the holdfasts at the beginning of the experiment (time 0) before the holdfasts were dislodged. The same taxa were the most frequent and abundant in holdfasts that were suspended (Figure 1).

Decapod crustaceans (Figure 1*A*), mollusks (Figure 1*B*), polychaetes (Figure 1*C*), and asteroids (Figure 1*F*) did not show clear temporal patterns of variation during the experimental period. These groups did decrease in density during the course of the study. Decapods and asteroids showed the highest variability in density (> SE).

Ophiuroids (Figure 1*D*) and echinoids (Figure 1*E*) showed clear patterns of abandonment or loss during the experimental period. Both groups decreased significantly during the first 10 to 20 days of the study. Ophiuroids decreased in density from 63 to 10 individuals per holdfast volume in the first 10 days, after which there was no significant variation (Figure 1*D*). Sea urchin densities, on the other hand, continually decreased from 2.3 to 0.4 individuals per holdfast volume during the 110-day study (Figure 1*E*).

Isopods and amphipods, the most abundant groups in the holdfasts, showed very

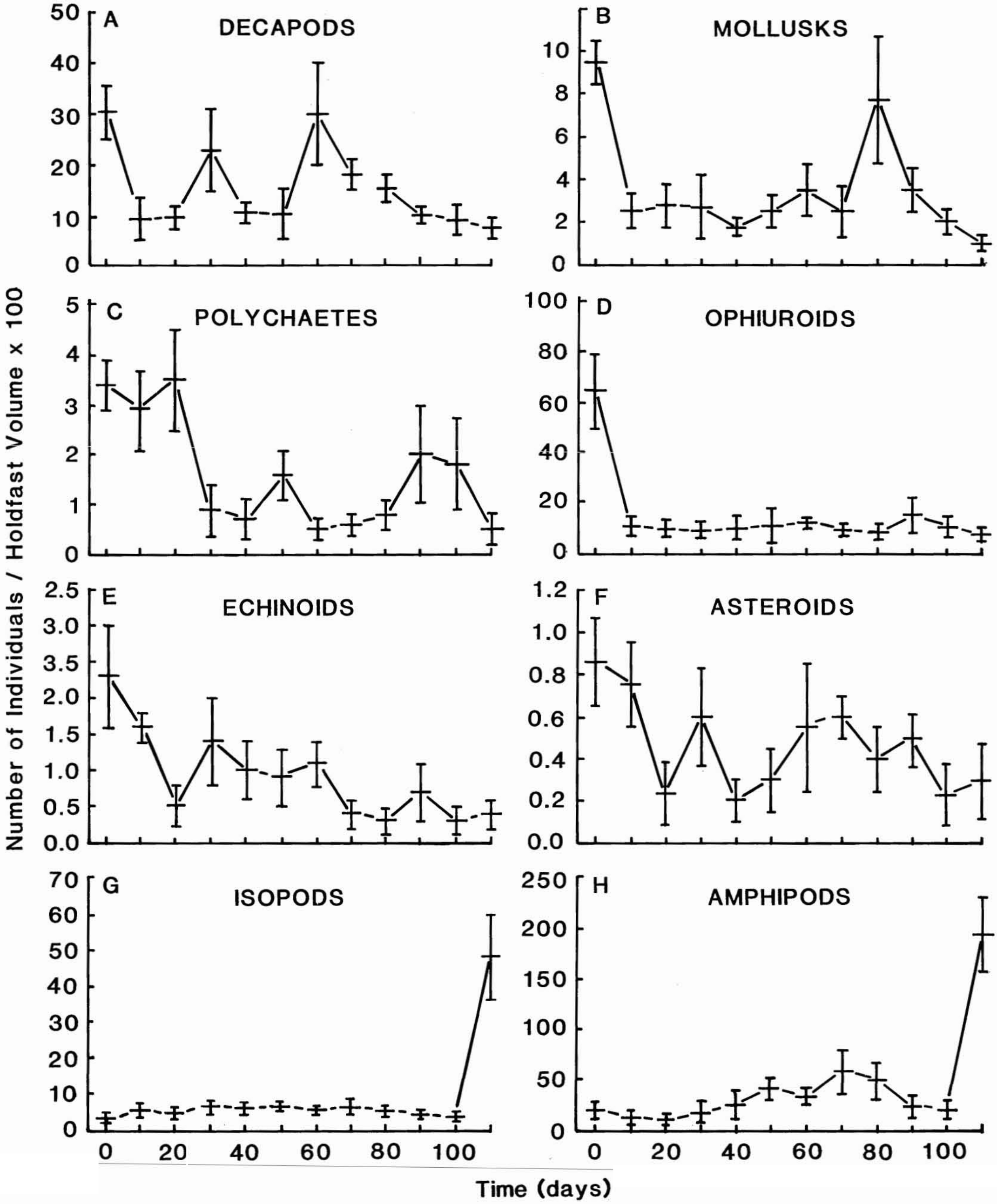

FIGURE 1. Temporal variation of major taxa of invertebrates found in the experimental holdfasts of *Macrocystis pyrifera* ($\bar{x} \pm 2$ SE).

different trends from all other taxa (Figures 1*G*, 1*H*). Both taxa increased significantly in density during the experiment. Isopods reached densities of up to 40 individuals per holdfast volume at the end of 110 days of observation, and amphipods increased from 20 to 200 individuals per holdfast volume.

DISCUSSION

Abundance results of invertebrates inhabiting the holdfasts of *M. pyrifera* generally agreed with those reported by Ghelardi (1971) and by Snider (1985). There were, however, some differences in the abundance and frequency of echinoids, mollusks, and asteroids from those reported by Ghelardi (1971). These differences can be attributed to the small sample device used by Ghelardi and the high variability in the mean density as discussed by Snider (1985).

The temporal patterns of variation of the experimental drifter holdfasts show that decapods, mollusks, asteroids, ophiuroids, polychaetes, and echinoids decreased in abundance with time. Isopods and amphipods, on the other hand, increased in abundance in the detached holdfasts during the course of this study. It is interesting to note that both of these groups are brooders and reproduce inside the holdfasts (Snider 1985). Major changes in the groups that decreased were observed during the first 20 days of the experiment. Fish predation (pers. obs.) and loss of organisms during detachment may explain some of the major changes during the early part of the experiment.

The experimental period used in this study was only 3.5 months; after that the holdfasts began to disintegrate. The maximum longevity estimates of *M. pyrifera* drifters (with stipes remaining on the plant) are up to 18 months in the Point Loma kelp forest (Dayton et al. 1984). Other patterns of density variability in the animal population inhabiting the drifter holdfasts would likely have been seen with a longer experimental period.

The results show that some abandonment (by predation or migration) and colonization or reproduction occur in the detached *M. pyrifera*. Also, without substrate limiting the vertical growth, drifting holdfasts acquire a cilindrical morphology (pers. obs.). The growth form of drifting holdfasts may account for changes in the diversity and density of the fauna from that commonly found in attached holdfasts.

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