EFFECTS OF THE STIPE-BORING AMPHIPOD
PERAMPHITHOE STYPOTRUPETES (COROPHIOIDEA: AMPITHOIDAE) AND GRAZING GASTROPODS ON THE KELP *LAMINARIA SETCHELLII*

J. R. Chess

ABSTRACT

The ampithoid amphipod *Peramphithoe stypotrupetes* hollows and infests the stipes of the alga *Laminaria setchellii* after intense grazing of its lamina by gastropods. The intensity of gastropod grazing and subsequent levels of amphipod infestation appear to be correlated with calm ocean conditions. Once established in the stipe, a pair of adult amphipods produces multiple cohorts of offspring, which hollow and kill the plant. At a study site off northern California, an entire bed of the alga was infested and no plants survived. Aspects of the natural history of *P. stypotrupetes* are discussed.

Invertebrates that graze on the mature sporophytes of large brown algae (kelps) generally cause only minor damage to the plants (Foster and Schiel, 1985), but there are exceptions. The decimation of kelp forests by echinoids has been well documented (e.g., Lawrence, 1975; Chapman, 1981), but many of these occurrences are believed to be unnatural events that are the result of population explosions stimulated by coastal pollution or the lack of natural predators (North and Pearse, 1970; Estes and Palmisano, 1974; Kain, 1979). Natural population levels of sea urchins commonly have little effect on mature, attached kelp, since the urchins feed mostly on drift material (Foster and Schiel, 1985).

A number of mollusks and crustaceans are known to feed on kelps, but generally they are nonlethal. The European acmaeid *Patina pellucida* (L.) can graze and weaken the holdfast of *Laminaria hyperborea* (Gunn.) Foslie (see Kain, 1963), and the Californian trochids (*Tegula* spp.) can damage kelp lamina when numerous (Foster and Schiel, 1985; personal observation). Other gastropods are damaging only when in abnormally high densities, as, for example, *Lacuna vincta* (Montagu), which can markedly deplete stands of *Laminaria saccharina* (L.) (see Fralick *et al.*, 1974). Crustaceans that burrow into stipes and holdfasts of kelp, usually with nonlethal effects, include the isopods *Limnoria algarum* Menzies and the amphipod *Ampitholina cuniculus* (Stebbing), as well as members of the amphipod

families Biancolinidae, Najnidae, Phliantidae, and Eophliantidae (Menzies, 1957; Myers, 1974; Conlan and Chess, 1992).

Members of the herbivorous corophioidean amphipod family Ampithoidae inhabit self-constructed tubes or chambers in coastal marine algae (Conlan and Bousfield, 1982). Among these, certain species of *Peramphithoe* have developed a partially close relationship with brown algae of the order Laminariales on which they live and feed. *Peramphithoe humeralis* (Stimpson) in the northeastern Pacific and *P. femorata* (Krøyer) in the southeastern Pacific both inhabit *Macrocystis pyrifera* (L.), where they fold and stitch (glue) lamina margins into chambers (Limbaugh, 1955; Kreibolm de Paternoster and Escofet, 1976). Although these species graze the lamina, they are not fatal to the plants.

In the northeastern Pacific, *Peramphithoe stypotrupetes* Conlan and Chess hollows and inhabits the stipes of *Eisenia arborea* Areschoug and *Laminaria setchellii* (see Conlan and Chess, 1992: *L. setchellii* Silva as *L. dentigera* Kjellman). This relationship appears to be unique, in that the alga is almost always destroyed, the destruction sometimes involving entire beds. The amphipod feeds on the medullary and cortical tissues of stipes, forming a hollowed chamber where a pair of adults, and their successive broods, feed and grow, eventually causing the death of the plant (Conlan and Chess, 1992). This report describes how *P. stypotrupetes* infests *L. setchellii*, documents its impact, and pre-

sents additional natural history observations to those reported in Conlan and Chess (1992).

Study Areas

Observations and collections were made irregularly between 1972 and 1992 during other investigations along the Mendocino coast of northern California (39°21'N, 123°50'W), Baranof Island (56°03'N, 134°20'W), southeastern Alaska, and off Santa Catalina Island (33°28'N, 118°29'W), southern California. Directed studies on the infestation by Peramphithoe stypotrupetes and attrition rates of Laminaria setchellii were made at Pt. Cabrillo on the Mendocino coast between November 1978 and April 1981, but other observations came from the various sites along that coast throughout the 20-year period.

Pt. Cabrillo, a state biological preserve, is an exposed rock headland with surge channels 3–20 m in depth that are semi-protected from moderate seas by offshore reefs and exposed rocks. The fauna and flora are typical of a northern California wave-swept habitat, with the most conspicuous kelps being Postelsia palmaeformis Ruprecht and Lessoniopsis littoralis (Tilden) in the intertidal, Laminaria setchellii from the lower intertidal to about 10-m depth, and Pterygophora californica Ruprecht and Nereocystis leutkeana Mertens growing from depths of about 8–15 m. The area observed encompassed approximately 1,200 m².

Incidental Observations

The association between Peramphithoe stypotrupetes and kelps was first recognized in 1972 at Santa Catalina Island, where abraded stipes of Eisenia arborea were collected and noted to contain numerous ampithoid amphipods. The same condition was observed in the stipes of Laminaria setchellii in northern California in 1977, and in Alaska during 1980.

Successful stipe infestation by the amphipods appeared to depend upon initial intense grazing by other invertebrates on lamina tissues and to some extent the transition zone (the main region of active cell division, located between the stipe and lamina). If the meristem in the transition zone is destroyed, then the plant is incapable of further growth and dies (Kain, 1971).

Along the Mendocino coast, infested stipes were conspicuous during most years. However, the highest rates of infestation appeared to coincide with years of exceptionally calm fall and winter months. Observations during these calm periods revealed an unusually high degree of grazing on the lamina of L. setchellii by benthic herbivores, primarily gastropods (Fig. 1). The grazers concentrated on the perennial kelps during the winter months when ephemeral algae were scarce or absent. The trochid gastropods Tegula pulligo (Gmelin), and, to a lesser extent Calliostoma ligatum (Gould), were the most prominent grazers during daylight hours. At night, other molluscan grazers became active, as evidenced by observations made in a quiet cove (Little River) about 8 km south of Pt. Cabrillo in March 1984. There, about two h after sunset, the trochids on the stipes and lamina of L. setchellii and Pterygophora californica were joined by several diurnally sedentary grazers, including the abalones Haliotis rufescens Swainson and H. walallensis Stearns and the chiton Cryptochiton stelleri (Middendorff).

These grazing molluscs appear to have limits to their ability to maintain a footing on stipes that are whipped by surge. It was noted that, under conditions of moderate surge (seas 1.5–2.0 m), trochids were absent from L. setchellii at depths shallower than about 7 m, but were present on those in adjacent sites at depths of 12–15 m. Under conditions of heavy surge, these gastropods appeared unable to maintain their position on stipe tips or lamina at any depth.

On the Mendocino coast, annual transition-zone expansion and lamina growth begins during late February and early March. Growth proceeds in the manner typical of other species of Laminaria, where "As the new lamina enlarges, the old one becomes a mere appendage at its apex and ultimately breaks off completely" (Fritsch, 1945, p. 195).

During early March (1992) at Mendocino, many Tegula pulligo and Calliostoma ligatum were observed feeding on the old lamina tissue, but not on the adjacent new growth of expanding lamina tissue (Fig. 2). This suggests that snail-induced damage to the transition zone takes place before the new growth begins, and that the damage is probably not lethal to the plant.
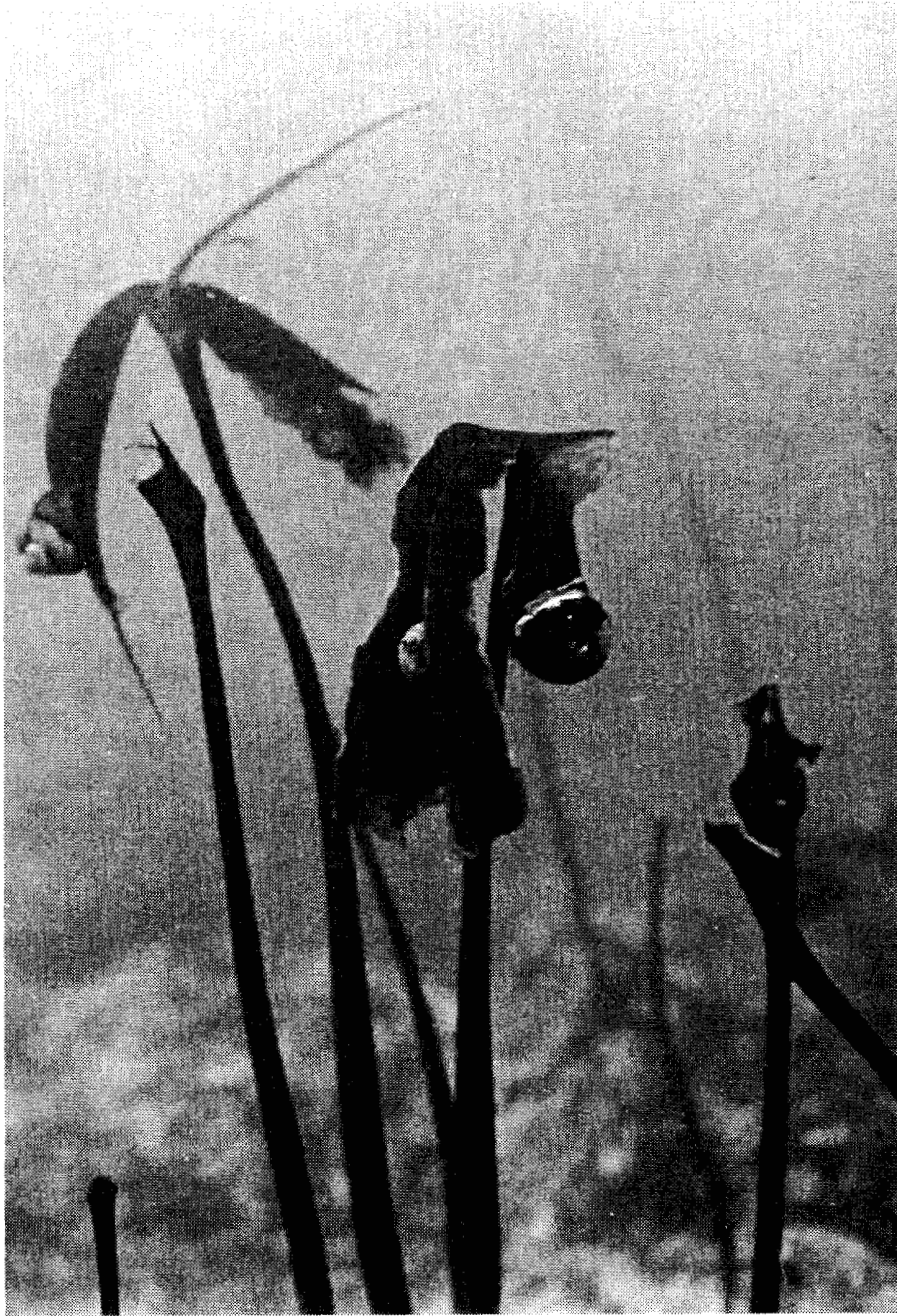
Fig. 1. *Tegula pulligo* grazing the lamina of *Laminaria setchellii* during a calm winter period (December).

Fig. 2. Expanding new lamina (light area) in *Laminaria setchellii* with *Tegula pulligo* feeding on old lamina tissue during early spring (March).

All infestations of *L. setchellii* by *P. stypotrupetes* occurred on stipes that had lost lamina. However, stipes with the gastropod *T. pulligo* still attached often were grazed into the distal areas of the transition zone, whereas those abraded by physical forces retained at least a remnant of lamina and an intact transition zone. It appeared that only the gastropod grazers removed entire lamina, thus exposing stipe tissues to amphipod infestation.

MATERIALS AND METHODS

Directed observations and measurements of the effects of *P. stypotrupetes* on *L. setchellii* were initiated at the Pt. Cabrillo site during 1978, and monitored irregularly until 1981. This site was assessed occasionally during the following years.

All field observations and collections were made using scuba or snorkel. At Pt. Cabrillo, individual plants of *L. setchellii* were marked with numbered disc tags in order to determine rates of infestation by the amphipod and stipe longevity after infestation. Stipes were measured (to the nearest 0.5 cm) from the base of the holdfast to the distal tip of the stipe. Collections of amphipods were made by severing infested stipes near the base, placing each stipe in a separate plastic bag and sealing with rubber bands.

RESULTS

Infestation by the Amphipod

During the fall and winter of 1978–1979 infestations became rampant when particularly calm ocean conditions prevailed from September through April.

Laminaria setchellii occurring in the shallowest depths appeared considerably healthier and less infested with the amphipod than those at greater depths. This relationship was measured during August 1980 at Pt. Cabrillo, when infested and healthy plants were tallied within depth-stratified, adjacent 1 × 25-m belt transects at depths of 1–2 m, 2–3 m, and 3–4 m on a vertical face of a deep surge channel. Within the shallow belt, 5 of 386 stipes (1.3%) were infested, and within the middepth, 12 of 54 (22.2%) were infested. In the deepest belt, only 2 bored-out stipe stumps and no intact plants were found.

Two groups of healthy, uninfested plants were tagged to determine rates of infestation. One group of 14 stipes (on an isolated boulder at a depth of 3 m) was tagged on 16 November 1978. Seven months later, one stipe was infested and five others were

missing. After another 14 months, four more plants were infested, and the one infested earlier was a mere stump. Thus, after 21 months, only four of the original 14 plants remained uninfested. A group of 29 stipes in a surge channel at 2–4-m depth was tagged on 3 July 1979. Fourteen months later all 11 that remained were infested, and after another eight months no remnants of these plants remained. During subsequent observations in 1983 and 1985, no *L. setchellii* could be found in the study area, and by 1990 only a few plants with approximately 1-cm diameter stipes were present.

Throughout the study period, infested stipes were common and sometimes abundant at other sites along the Mendocino coast, but nowhere was the destruction of *L. setchellii* as severe as that observed at Pt. Cabrillo.

Deterioration of Infested Stipes

Individual stipes varied considerably in their degree of infestation or deterioration. The most recently infested contained only one or two adult amphipods in excavations only a few cm deep, while adjacent stipes, apparently infested earlier, were severely damaged with tattered tips and perforations through the outer wall (Fig. 3). It was impossible to determine the number of amphipods in residence or the depth of the excavations in the more severely damaged stipes without dissecting them. However, as noted earlier (Conlan and Chess, 1992), the larger stipes with large chambers generally contained the most amphipods (Fig. 3). Nine of 11 infested stipes, tagged and measured along with the 14 healthy plants during November 1978, persisted for seven months before being remeasured in June 1979. Initially these plants varied in length from 33–55 cm ($\bar{x} = 46.3$ cm) and during the period were reduced to between 6 and 41 cm ($\bar{x} = 22.8$ cm), a mean rate of stipe reduction of 3.01 cm/month. The largest of the infested stipes (55 cm) was reduced at the greatest rate (6.71 cm/month), and the smallest at the lowest rate (1.10 cm/month), but this relation did not hold with intermediate-sized plants. The deterioration rate of the second (surge channel) group of stipes was not calculated, because it was not known when they had become infested.
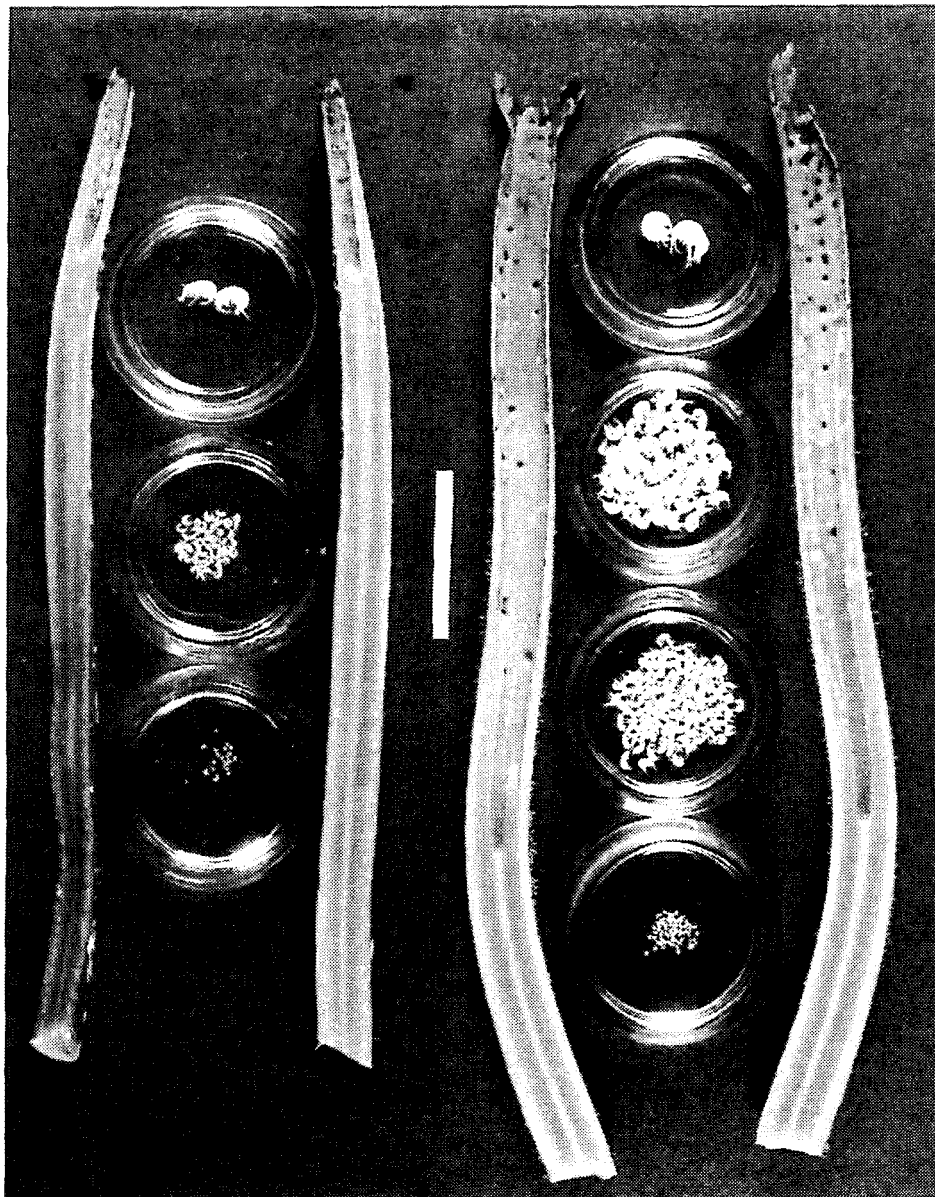
Fig. 3. Two infested stipes of *Laminaria setchellii*, the larger with lateral perforations, each with its complement of adults and offspring cohorts of *Peramphithoe stypotrupetes*, both collected 27 February 1992. (Scale bar = 5 cm; small chamber 6 cm long, larger 24 cm.)

Amphipod Reproduction Within Stipe Chambers

Brooding females were found within infested stipes during all seasons. The size of brood or number of offspring within cohorts was variable, with the largest females tending to have the most and the smallest the fewest. Fecundity of females 20–24 mm in

length ($N = 3$) was 85–145, $\bar{x} = 111.0$; among those 16–19 mm ($N = 8$) was 30–120, $\bar{x} = 69.0$; and from those 14–15 mm ($N = 2$) was 33–60, $\bar{x} = 46.5$. The smallest brooding female found was 14 mm. There appeared to be some mortality or loss of members of any cohort, as suggested by the numerical composition of those found in the large stipe of Fig. 3. Here, the number of offspring in three cohorts of a 19-mm female and 18-mm male were: 62 individuals in the 1.7–2.0-mm cohort, 94 at 5.5–7.0 mm; and 58 at 9–11 mm. The mother was carrying 120 embryos.

The number of cohorts cohabiting a chamber was positively correlated with the length of the hollowed stipe chamber. Offspring cohorts in chambers 2–4-cm long ($N = 7$) varied from zero–one, $\bar{x} = 0.29$; those from 5–10-cm chambers ($N = 13$) varied from zero–3, $\bar{x} = 1.23$. All chambers from 15–25 cm ($N = 5$) contained four cohorts, and the largest chamber observed, 116 cm, contained four or possibly five. Separating large individuals into cohorts was often difficult, because older amphipods appear to grow at a slower rate and their size groupings become more obscure. When the cohort size-classes were easily distinguished, the smallest were always found in the lowermost part of the chamber.

Several stipes that were variably hollowed out and decomposing contained no amphipods, and others that had been reduced to mere stumps (<10 cm high) often harbored only a few *P. stypotrupetes* of mixed sizes, and at times other species of gammarideans as well.

DISCUSSION

Peramphithoe stypotrupetes appears to be one of the few crustaceans known to be capable of large-scale killing of mature kelp sporophytes. However, other gammaridean amphipods, primarily *Peramphithoe humeralis*, have been described inflicting considerable damage to large areas of a forest of *Macrocystis pyrifera* off San Diego following a period of elevated sea temperatures (Tegner and Dayton, 1987). *Amphitholina cuniculus* burrows into the medullary region of the stipes of *Alaria esculenta* off Ireland (Myers, 1974). It was reported to have infested up to 82% of a bed of *A. esculenta* with a large proportion "so badly damaged

... that it was unlikely that the alga would survive the winter" (Lewis, in Myers, 1974, p. 469). *Amphitholina cuniculus*, which is morphologically highly modified for burrowing (Conlan and Chess, 1992), enters the stipe laterally rather than through an abraded or grazed distal end as does *P. stypotrupetes* (see Myers, 1974).

Conditions for Infestation

The relationship between increased grazing by gastropods on off-bottom kelp lamina and low water turbulence is probably wide spread. The brown sea hare *Aplysia californica* Cooper has been seen on the tops of *Pterygophora californica* when seas were calm (Foster and Schiel, 1985), and a one-day period of heavy surge dislodged all *Norrisia norrisi* Sowerby and *Tegula aureotincta* Forbes from the upper portions of plants of *M. pyrifera* (see Bakus, unpublished, cited in Lowry *et al.*, 1974). Surge from wave action is considered to be maximal in the subtidal fringe and to decrease gradually with depth, and the vertical distribution of many organisms is determined chiefly by these forces (Kitching, 1941). The reported observations thus indicate that less turbulent conditions in deeper water have allowed more intense gastropod grazing pressure on *L. setchellii*, and subsequently higher levels of infestation by *P. stypotrupetes*, than for plants at shallower depths. The extended period of calm ocean conditions during the fall and winter of 1978–1979, with intense gastropod grazing even at shallow depths, was probably the primary cause of the high level of stipe infestation and subsequent decline of the populations of *L. setchellii* at Pt. Cabrillo.

The relative tenderness of lamina tissue, as compared to the stipe and holdfast, may account for its apparent preference by grazing gastropods. Steinberg (1985) suggested that "stipes and holdfasts ... are often much tougher than the blades of the same plant and that many herbivores, including *Tegula*, probably find it physically very difficult to consume these plant parts."

The avoidance of the newly expanding transition zones and laminae by gastropod grazers observed during March 1992 suggests that these tissues may produce higher levels of herbivore-deterrent chemicals than the older, degraded lamina. In studies of

food preference, species of phaeophytes with high levels of phenolic compounds were avoided by *Tegula funebralis* (A. Adams), while those with low levels were preferred (Steinberg, 1985). In other studies, it was found that the young growing tips and reproductive structures of tropical green algae contained higher concentrations of noxious compounds than mature plant tissues (Paul and Fenical, 1986; Paul and Van Alstyne, 1988). A similar condition may exist with the new spring growth in *Laminaria*. It is also possible that trochid gastropods are incapable of maintaining a footing on the slippery new surfaces. Kain (1971) suggested that this "highly mucilaginous surface is not a very hospitable substratum for most organisms."

Avoidance of the new growth by gastropods suggests that whatever damage they cause to the lamina and distal transition zone must occur prior to new growth during the fall and winter months. Therefore, it seems unlikely that *P. stypotrupetes* could successfully invade stipes of *L. setchellii* during early spring and summer, when rapid lamina growth is in progress.

Amphipod Infestation

The infestation of only those stipes of *L. setchellii* that have been previously grazed to or into the transition zone indicates that *P. stypotrupetes* is probably incapable of penetrating, or possibly using, the tissues of the lamina or outer stipe. The amphipod is, however, capable of entering and using the tissues of the transition zone and inner stipe, as the gut contents showed (Conlan and Chess, 1992).

In the Monterey Bay area, an ampithoid gammaridean, probably referable to *P. stypotrupetes*, was described as burrowing into the sides of stipes of *Pterygophora californica* (much as *Amphitholina cuniculus* enters *Alaria esculenta* (L.)), hollowing a chamber in the interior and producing successive broods of offspring. Mortality to these plants occurred when surge-induced turbulence broke the stipe off at the area of the chamber. Infestation levels were described as variable, at times as high as 20%, but at other times none could be found (Michael Foster, Moss Landing Marine Laboratories, personal communication, 24 March 1992). Schroeter (cited in Conlan and Chess,

1992) found this same relationship occurring off the coast of Santa Barbara. Although *P. californica* is a major component of the sublittoral off the Mendocino coast, there was no evidence of it being infested there, but it could easily have been overlooked if infestations occur infrequently or at low levels.

Hollowing of stipes of *Laminaria setchellii* by *Peramphithoe stypotrupetes* and the subsequent rate of stipe shortening undoubtedly accelerates with the development, growth, and increased feeding of successive broods. The mean rate of shortening (3.01 cm/month) would be much lower during initial infestation and much higher during later stages, the rate probably being proportional to the cumulative biomass of amphipods occupying a chamber.

The tendency for the crowded amphipods to perforate the distal portions of stipe chambers would allow increased water circulation inside, and thus enhance respiration and waste removal. It is unknown if the perforations are formed specifically or are simply the result of heavy grazing on the interior of the stipe. In either case, lateral stipe perforations would seem beneficial to amphipods occurring in high densities. However, the loss of a fraction of newly hatched juveniles, suggested above, may be proportional to the number of perforations present. On the other hand, the strong tendency of offspring cohorts to segregate by size (the smallest occurring deepest in the chambers where there are no perforations) must offset their potential loss.

The circumstances that stimulate the amphipod's abandonment of stipes is unknown, but is most likely related to the lack of available food, when the inner stipe tissues are gone, or to the noxious environment of the chamber when the remaining tissues begin to decompose. The length of time for the death of stipe tissue to occur and for decomposition to begin seems quite long, since actively infested stipes persisted for at least 223 days.

It appears that, for high levels of infestation to occur, extended periods of calm ocean conditions, coupled with extensive lamina grazing by gastropods, are required to permit the invasion of stipes by *Peramphithoe stypotrupetes*. At Pt. Cabrillo the infestation of stipes seemed to increase nearly

exponentially during the 1978–1980 period. This was probably caused by rapid infestation of neighboring stipes by offspring of the initial invaders.

The original shallow-water community of *Laminaria* at Pt. Cabrillo was dramatically modified by the mortalities caused by the gastropod—*P. stypotrupetes* invasion. Although there have been subsequent low levels of recruitment, *L. setchellii* remains a minor component of the biota there after 12 years. However, at various sites in the vicinity of Pt. Cabrillo, *L. setchellii* is abundant and luxuriant. The situation at Pt. Cabrillo may be explained by its being a biological preserve where unusually high densities of the red abalone *Haliotis rufescens* occur. Although this abalone relies primarily on drift algae for nutrition (Leighton, 1971), intense grazing by these herbivores has probably precluded the reestablishment of *L. setchellii*. Even though plants of *L. setchellii* were virtually eliminated at Pt. Cabrillo, *P. stypotrupetes* appears to have little lasting effect on the structure of algal communities over time.

LITERATURE CITED

Chapman, A. R. O. 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, eastern Canada.—Marine Biology 62: 307–311.

Conlan, K. E., and E. L. Bousfield. 1982. The amphipod superfamily Corophioidea in the northeastern Pacific region. Family Ampithoidae: systematics and distributional ecology.—National Museum of Natural Science (Ottawa) Publications in Biological Oceanography 10: 41–73.

———, and J. R. Chess. 1992. Phylogeny and ecology of a new kelp-boring amphipod, *Peramphithoe stypotrupetes*, new species (Corophioidea: Ampithoidae).—Journal of Crustacean Biology 12: 410–422.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities.—Science 185: 1058–1060.

Foster, M. S., and D. R. Schiel. 1985. The ecology of giant kelp forests in California: a community profile.—United States Fish and Wildlife Service Biological Report 85 (7.2), pp. 1–152.

Fralick, R. A., K. W. Turgeon, and A. C. Mathieson. 1974. Destruction of kelp populations by *Lacuna vincta* (Montagu).—Nautilus 88: 112–114.

Fritsch, F. E. 1945. Structure and reproduction of the algae. Vol. 2.—Cambridge University Press, Cambridge, England. Pp. 1–939.

Kain, J. M. 1963. Aspects of the biology of *Laminaria hyperborea*, II. Age, weight and length.—Journal of the Marine Biological Association of the United Kingdom 43: 129–151.

———. 1971. Synopsis of biological data on *Laminaria hyperborea*.—FAO Fisheries Synopsis 87: 1–74.

———. 1979. A view of the genus *Laminaria*.—Oceanography and Marine Biology Annual Review 17: 101–161.

Kitching, J. A. 1941. Studies in sublittoral ecology. III. *Laminaria* forests on the west coast of Scotland; a study of zonation in relation to wave action and illumination.—Biological Bulletin 80: 324–337.

Kreibolm de Paternoster, I., and A. Escofet. 1976. La fauna de anfipodos asociado a los bosques de *Macrocystis pyrifera* en el chabut: *Ampithoe femorata* (Krøyer) (Ampithoidae) and *Bircenna fulva* Chilton (Eophliantidae).—Physis A 35: 77–91.

Lawrence, J. M. 1975. On the relationship between marine plants and sea urchins (Echinodermata: Echinoidea).—Oceanography and Marine Biology Annual Review 13: 213–286.

Leighton, D. L. 1971. Grazing activities of benthic invertebrates in southern California kelp beds.—Nova Hedwigia 32: 421–453.

Limbaugh, C. 1955. Fish life in kelp beds and the effect of kelp harvesting.—University of California Institute of Marine Resources, IMR ref. 55.9, pp. 1–158.

Lowry, L. F., A. J. McElroy, and J. S. Pearse. 1974. The distribution of six species of gastropod molluscs in a California kelp forest.—Biological Bulletin 147: 386–396.

Menzies, R. J. 1957. The marine borer family Limnoridae (Crustacea, Isopoda).—Bulletin of Marine Science 7: 101–200.

Myers, A. A. 1974. *Amphitholina cuniculus* (Stebbing), a little known marine amphipod crustacean new to Ireland.—Proceedings of the Royal Irish Academy 74: 463–469.

North, W. J., and J. S. Pearse. 1970. Sea urchin population explosion in southern California coastal waters.—Science 167: 209.

Paul, V. J., and W. Fenical. 1986. Chemical defense in tropical marine algae, order: Caulerpales.—Marine Ecology Progress Series 34: 157–169.

———, and K. L. Van Alstyne. 1988. Use of ingested algal diterpenoids by *Elysia halimedae* Macne (Opisthobranchia: Ascoglossa) as anti-predator defenses.—Journal of Experimental Marine Biology and Ecology 119: 15–29.

Steinberg, P. D. 1985. Feeding preferences of *Tegula funebralis* and chemical defenses of marine brown algae.—Ecological Monographs 55: 333–349.

Tegner, M. J., and P. K. Dayton. 1987. El Niño effects on southern California kelp forest communities.—Advances in Ecological Research 17: 243–279.