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NATURAL MORTALITY IN NE PACIFIC COASTAL HYDROMEDUSAE: GRAZING PREDATION, WOUND HEALING AND SENESCENCE

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ABSTRACT

Hydromedusae appear in the coastal plankton during defined species-specific periods. In a predictable succession, some species appear shortly after the spring plankton bloom begins, and others follow as ecological conditions continue to change. Most species also have well-defined seasonal terminations. This study explores the programs of mortality in the field other than whole-animal predation of five abundant species of hydromedusae in the San Juan Archipelago, north of Puget Sound in Washington State.

Living specimens were regularly hand-collected and examined for injuries, disease, general deterioration, evidence of damage by parasites or symbionts, and for gut fullness. Young spring medusae of most hydrozoan species were in excellent physical condition. The proportion of damaged individuals increased with time throughout the season. The nature and source of this damage varied according to the species of hydromedusa. The large, long-lived species *Aequorea victoria* and *Mitrocoma cellularia* showed high amounts of grazing damage, caused mostly by hyperiid amphipods and parasitic larval sea anemones, whose negative effects accumulate late in the season. The shorter-lived species *Clytia gregarium* and *Mitrocomella polydiademata* showed lower overall incidence of damage than species with long-lived individuals, and were assumed to be removed largely by whole animal (rather than grazing) predation. Senescence was seen to be the primary factor only in the demise of the population of *Gonionemus vertens*.

Hydromedusae occur in the coastal plankton during defined species-specific periods. Most neritic hydromedusae are seasonally budded off benthic hydroids. The medusae are of separate sexes and represent the sexually reproducing portions of some hydrozoan life cycles. After approaching their "adult" size, medusae usually spawn daily until the end of their lives. In a predictable succession, some species appear after the spring plankton bloom begins, and other species follow as ecological conditions continue to change. In the study area, over 40 species of hydromedusae are found in the plankton (Mills, 1981). The succession of species is similar year after year, with starting times varying widely by species; beyond a general increased availability of food, the cues for release of medusae from their hydroids are not known in most cases.

Most species of hydromedusae also have well-defined seasonal terminations. Population terminations are nearly as clearly marked as their appearances in the spring. Possible sources of mortality for natural populations of hydromedusae include old age, starvation, predation, parasitism, and disease. In this study, I have explored the programs of mortality in the field of five abundant species of hydromedusae in the San Juan Archipelago, north of Puget Sound in Washington State. Assessing the impact of whole-animal predation on medusa populations was beyond the scope of this study, as the physical system is too vast and patchy for simple estimates of population sizes.

Medusae in the Puget Sound region offer a rare opportunity to investigate the general problem of non-predation causes of mortality in plankton populations. The animals are sufficiently abundant and accessible for easy hand collection without damaging the specimens. They are also transparent and of a convenient size for macro- and microscopic examination of individuals, so that injuries,

Table 1. The proportion of hydromedusae of five species having food in their gut at the moment of collection decreases late in the season. Numbers sampled on each date: *Aequorea* N = 50–100, *Mitrocoma* N = 25–75, *Clytia* N = 50–100, *Mitrocomella* N = 75, *Gonionemus* N = 20. A dash indicates the species is no longer present in the plankton

Species	Percent of population with food in the gut		
	Late spring	Mid-summer	Mid-autumn
Aequorea victoria	80%	78%	44%
Mitrocoma cellularia	100	96	66
Clytia gregarium	96	96	45
Mitrocomella polydiademata	80	—	—
Gonionemus vertens	90	80	—

infections (which appear as cloudy areas on otherwise transparent surfaces), and other sorts of deterioration are easily detected.

This project began in the autumn of 1983, at a time when most hydromedusae had disappeared from the plankton after maintaining large summer population levels. Casual observation indicated that a large proportion of individuals of the three remaining common species had sustained systematic morphological damage. Of the large species *Aequorea victoria* and *Mitrocoma cellularia,* only 84% and 73%, respectively, of individuals were damaged in late October. The smaller *Clytia gregarium* showed damage in only 12% of individuals. The study was expanded to include bimonthly sampling (omitting the smallest size classes) from spring through autumn in 1984 and 1991 of the most abundant species, tabulating the extent and type of damage incurred.

Materials and Methods

Individuals of four abundant species of hydromedusae, *Aequorea victoria* (Murbach and Shearer, 1902), *Clytia (Phialidium) gregarium* (A. Agassiz, 1862), *Mitrocoma cellularia* (A. Agassiz, 1865), and *Mitrocomella polydiademata* (Romanes, 1876) were individually hand-collected using a plastic beaker fixed to a long handle from surface waters adjoining the floating docks of the Friday Harbor Laboratories, San Juan Island. A fifth species, *Gonionemus vertens* A. Agassiz, 1862 was collected from Mitchell Bay on San Juan Island. Although a few very young individuals of the first four species are present in the plankton beginning in March, sampling was not begun until late April (1984) when the individuals were large enough to collect in substantial numbers or May (1991) when I returned to the study site after a short absence. Medusae persisted in the plankton later in the autumn of 1991 than many other years. In groups of about 25, they were carried into the laboratory in a bucket of sea water and examined live using a dissecting microscope for injuries, disease, general deterioration, and evidence of damage by parasites or symbionts. Depending on availability, the number of each species collected in each sampling period usually varied between 50 and 125, although smaller numbers were infrequently collected either early or late in the season if few specimens were present. All species except *Gonionemus,* which is endemic to a specific location, were collected from several different water masses (usually over a 2–5 day period) during each sampling interval in order to obviate patch effects. Gut fullness was established as part of a separate study of hydromedusan diets (Mills, in prep.); the numbers presented in Table 1 are from samples taken in 1982 for *Gonionemus vertens* and 1989 for all other species.

Manubrium regeneration times were established in the laboratory by isolating either naturally or surgically damaged medusae in 500–1,000 ml sea water at ambient temperatures of 10–13°C. Medusae were not fed during the repair period.

Results

In general, young spring animals of most hydrozoan species are in excellent physical condition. During the period of early somatic growth (Fig. 1), damaged specimens are rare. Toward late spring, proportions of damaged individuals in-

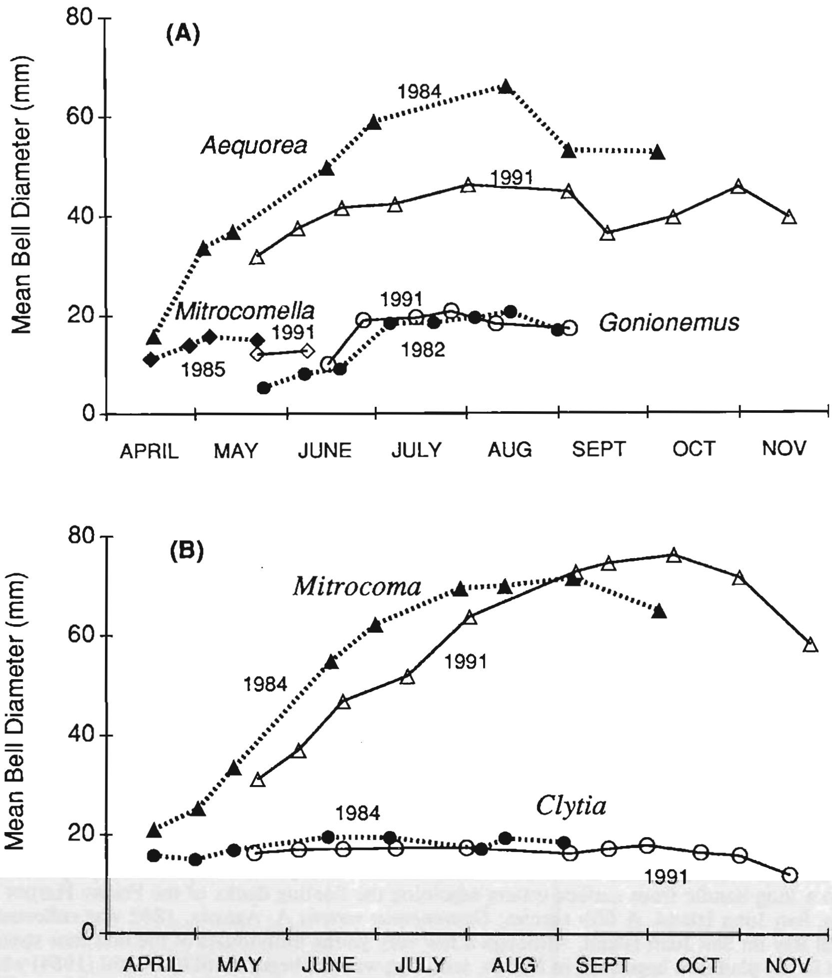

Figure 1. Seasonal changes in mean individual size in five species of hydromedusae. (A) *Aequorea victoria* = ▲, △; *Mitrocomella polydiademata* = ◆, ◇; *Gonionemus vertens* = ●, ○. (B) *Mitrocoma cellularia* = ▲, △; *Clytia gregarium* = ●, ○.

crease as populations of grazing predators rise. At the same time most hydromedusae are beginning to develop gonadal tissue. The effects of grazing predation during periods of high nutrition are rapidly repaired; when isolated in the laboratory, most species produce new feeding structures within a few days. Gonadal tissue is also readily replaced given sufficient food. The progressive seasonal damage to the 5 species studied are summarized below. The observed patterns of injury were remarkably similar for the years 1984 and 1991 (Fig. 2).

Aequorea victoria (Figs. 1a, 2a; Table 1).—Very small individuals of this species are first seen in March; they are thought to live about 6 months (Mills, pers. obs.). The late summer–early autumn drop in mean individual size probably reflects death of the oldest animals and reduced feeding of younger individuals; the population usually persists well into October or November. The proportion of damaged individuals increases from late spring through the summer and autumn,

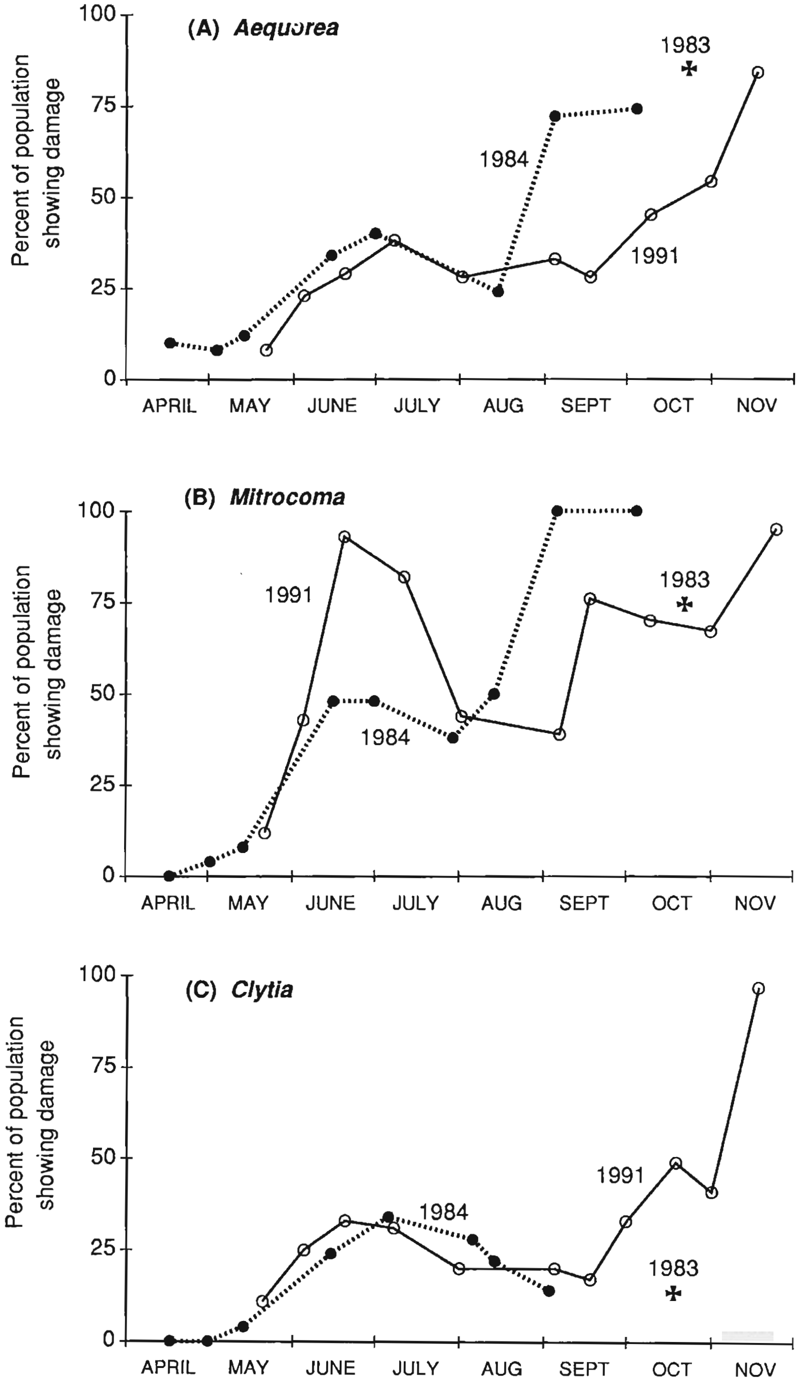

Figure 2. Progressive seasonal damage to three medusa populations in 1983, 1984, 1991. (A) *Aequorea victoria,* (B) *Mitrocoma cellularia,* (C) *Clytia gregarium.*

when over 75% of the population eventually shows some damage. Injuries appear to be mostly attributable to immature hyperiid amphipods *Parathemisto pacifica* Stebbing, 1888 which in their smallest stages live inside the stomach and canal system presumably feeding on partially digested prey of *Aequorea*; larger specimens are later found on the exumbrella, grazing on subumbrellar structures, or burrowed into the jelly. The proportion of *Aequorea* medusae carrying living juvenile hyperiids within their guts rose to a maximum of 9–15% of the population in early August through November 1991. Larger immature hyperiids are present on the bells of nearly all medusae in the field, but they readily hop off during collection, and are therefore difficult to count.

Damage to medusae is concentrated on the mouth and stomach regions (occurring in 54–100% of damaged animals throughout the season), in many cases removing all such tissues (in 6–26% of damaged animals throughout the season), and to a lesser extent includes grazing on the gonads (to 42% of damaged animals) and bell margin. The incidence of pits and tunnels in the jelly (which often also damages the gonads) rises sharply in the summer including 40–45% of damaged individuals by July and 52–78% of damaged individuals in the autumn.

When food is plentiful, the regenerative capabilities of *Aequorea* allow for rapid repair of damage. Specimens that have lost their mouth can regenerate a fully functional feeding structure in an average of 6 days in the laboratory. In the autumn as gut fullness decreases (Table 1), repair rates seem to be much slower. Sick animals with unhealed wounds and infections on the epithelia or in the mesogloea that are brought from the field into the laboratory and fed can be revived to a healthy condition within a few days. Starvation combined with high rates of damage appears to cause the demise of this species in the autumn. Parasitic larval sea anemones *Peachia quinquecapitata* McMurrich, 1913 are sometimes seen on *Aequorea*, but the infestation rate was never over 1%.

Aequorea medusae are harvested for their bioluminescent protein, aequorin, in the late summer in Friday Harbor. Although 100,000–200,000 medusae are taken annually in late August and September (J. Blinks, pers. comm.), there is no evidence that this extensive, but highly localized, collection has significantly impacted the population through its annual occurrence over the past 20 years.

Mitrocoma cellularia (Figs. 1b, 2b; Table 1).—First appearing in March, most individuals are intact until late May, after which the proportion of damaged individuals rapidly increases as they grow throughout the summer. *Mitrocoma* medusae probably live about 6 months (Mills, pers. obs.). Typical damage to this species involves grazing on the manubrium (seen in 30–100% of damaged individuals throughout the season), gonads (proportion of damaged individuals showing grazed gonads rose gradually to a late summer high of 92% in 1984 and 79% in 1991), and bell margin, as well as some erosion of the upper bell surface. The proportion of the population showing damage to the bell or bell margin gradually rises from 10–25% in early summer to 67–100% by autumn. Virtually the entire population is damaged by grazing predation by autumn. Most of the damage is attributable to immature hyperiid amphipods *Parathemisto*, which may be present on most medusae by mid-summer until autumn, but as in the case of *Aequorea*, are hard to quantify. *Mitrocoma*, however, rarely harbors the youngest hyperiids which seem to be found only inside *Aequorea* guts. *Peachia* larvae infested 10% of the *Mitrocoma* population by the anemone larva's mid-summer peak in 1984, but peaked at only 5% in 1991. Some of the missing mouths and bites in the bell margins and on the gonads of *Mitrocoma* may also be due to grazing predation by fish, but this has not been documented.

Mitrocoma can regenerate a functional mouth in the laboratory in 4 days. If the bell damage includes a hole through the jelly from exumbrella to subumbrella including the entire manubrium (a common sort of injury), the wound can heal and a functional mouth form in 7 days. Like *Aequorea,* the mean individual size of *Mitrocoma* (Fig. 1b) decreased in late summer and autumn of both years. This probably indicates the death of the oldest members of the population.

Clytia gregarium (Figs. 1b, 2c; Table 1).—Individuals of this species are thought to live 2–3 months (Mills, pers. obs.), although the population persists from March into October or November. In general, this species sustained a much lower incidence of damage than the two larger species with which it coexists; damage peaks occurred both years in early July (mid-season) when 33–34% of the population was damaged. Very late in the season in 1991 (late November), the incidence of damage to individuals rose precipitously, to virtually 100%. Over 80% of these late survivors exhibited bacterial infections on their bells.

Nearly all of the grazing predation to this species involves removal of one or more gonads. This occurs in 65–100% of the damaged *Clytia* medusae mid-season, dropping to around 40% in the autumn. Less frequently, the mouth is also grazed; peaking mid-season at 40% of damaged individuals. Most such predation is attributable to the parasitic larval sea anemone *Peachia,* which had mid-summer peak infestation rates of 16% in early July 1984 and 6% in late June–early July 1991. Spaulding (1972) described *Peachia* infestation on *Clytia* (*Phialidium*) in Friday Harbor peaking at 14% in mid-July 1967 and 33–62% in late June 1970. Grazing by immature hyperiid amphipods, which may occur in numbers on nearly all medusae in late summer and autumn, is probably also important, but is difficult to distinguish in mid-summer from *Peachia* damage. The lower autumnal grazing rates are probably nearly all attributable to amphipods.

Schmid and Tardent (1971) demonstrated the fast regenerative powers of *Clytia* medusae (as *Campanularia*) in response to all sorts of laboratory surgical manipulations. *C. gregarium* at Friday Harbor was able to regenerate a small functional manubrium in 2–7 days following its surgical or natural removal, depending on the amount of associated tissue damage.

The low levels of grazing predation on *Clytia* do not seem sufficient to explain the disappearance of large numbers of individuals throughout the summer, which also rarely display signs of aging in the field. Predation of whole animals by other hydromedusae, and probably by fish as well, is most likely a primary cause of death in this species. Infections combining with poor nutrition appear to claim the last survivors, which by late autumn have outlived most of their medusan predators.

Gonionemus vertens (Fig. 1a; Table 1).—This mid-sized medusa is unusual in that it is semi-benthic, living associated with algae or seagrass in certain shallow bays. It feeds nearly exclusively on small copepods including *Eurytemora* and *Acartia* and their eggs (Mills, in prep.). The *Gonionemus* population is fairly synchronous, living from late April or early May until late July through (rarely) early September (Mills, unpubl.); individuals probably survive about 3 months. Few individuals (less than 5%) show any sort of damage attributable to grazing—nearly all recorded damaged medusae exhibited infections and deterioration of the bell typical of old age and senescence (seen in 16–37% of the population late in the season in August to early September), which seems to be the primary cause of death in this species.

Another source of mortality for *Gonionemus* is intertidal stranding and desiccation during low tides. There is no doubt that some percentage of the population succumbs in such a manner, but its relative importance to the population as a whole has not been established.

Mitrocomella polydiademata (Fig. 1a, Table 1).—Individuals of this species seem to live about 2 months (Mills, pers. obs.) and are among the first in a succession of species of hydromedusae in these waters; the population is fairly synchronous. Damage rates to individuals are low, and damage is usually restricted to minor grazing on the gonads. Incidence of infestation by the parasitic larval sea anemone *Peachia* may reach over 25%, but these larvae are usually young and still appear to be living off internal digestive fluids prior to adopting their ectoparasitic existence of feeding on gonads and mouth tissues (they are able to transfer hosts at this later stage). In late May and early June the *Mitrocomella* population terminates precipitously; at the same time, the rapidly growing *Aequorea* population feeds heavily on small hydromedusae and *Mitrocomella* is an important component of its diet in Friday Harbor (Mills, unpubl.). The extent to which such predation accounts for the disappearance of *Mitrocomella* has not been established.

Discussion

Three different patterns of natural mortality have emerged for the species examined in this study—mortality due to the long-term and cumulative effects of associated symbionts or parasites, mortality apparently due primarily to whole-animal predation, and mortality due to senescence; these are discussed below. It is beyond the scope of this study to assess the effects of grazing predation on fecundity or general fitness of medusae. However, most medusae spawn daily for long periods and will continue to do so in spite of minimal gonad damage, or after regenerating new tissue, so long as sufficient food is available in the plankton.

Representing the first pattern, the large, long-lived species *Aequorea victoria* and *Mitrocoma cellularia* sustain high amounts of grazing predation throughout the summer with no apparent ill effects in terms of immediate mortality. The burrowing into or general occupancy of medusae by hyperiid amphipods and anemone larvae does not appear particularly harmful to swimming or feeding abilities of the medusae. Obviously, damage incurred to the mouth and manubrium will affect the ability to retain and digest captured prey, but when food is plentiful, the regenerative capabilities of hydromedusae allow for rapid (2–7 days) replacement of grazed feeding structures. In the autumn, the proportion of medusae with food in their guts drops substantially and repair rates seem to be much slower, apparently leading to the ultimate demise of these species.

Secondly, causes of the demise of populations of short-lived individuals such as *Clytia gregarium* and *Mitrocomella polydiademata* are not well-revealed by this study. The effects of grazing predation on these medusae are evident, but appear to be sub-lethal. Availability of food seems also not to be a serious problem until late autumn, yet large numbers of individuals continuously disappear from the plankton. Predation of whole animals by other hydromedusae (Mills, unpubl.; Arai and Jacobs, 1980; Purcell, 1991a, 1991b) and probably by fish is most likely the primary cause of death in these species. Preliminary studies by the author of the sympatric small hydromedusae *Eutonina indicans* (Romanes, 1876), *Sarsia* spp. and *Aglantha digitale* (O. F. Müller, 1776) have been limited by patchiness of populations and low sampling numbers and therefore are not reported here in detail, but these short-lived species appear similar to *Clytia* and *Mitrocomella* in disappearing from the plankton while damage rates remain quite low, suggesting an overriding cause of mortality other than grazing predation or old-age.

The third pattern is exemplified by the semibenthic species *Gonionemus vertens,* which lives only in certain shallow bays and appears to have no associates that damage individual medusae. This was the only species examined in which the medusa population seems to decline by natural senescence.

Although each species has a predictable and rather precise termination in the field, aging and senescence are rarely observed in the field for most species. Most species of hydromedusae, however, can be maintained by regular feeding in the laboratory for weeks to months beyond their normal disappearance in the field, and during this prolonged period, specific patterns of aging not seen in the field have emerged (Mills and V. Schmid, work in progress). The disappearances of field populations seem to be mostly the result of the cumulative bad effects of grazing predation by parasites and symbionts that use the medusae as temporary substrata, combined with decreased food availability and rising bacterial infection rates in the autumn, in addition to presumed whole animal predation. Feeding on whole hydromedusae by other medusae, fish, and probably other predators, is beyond the scope of this study, but is probably at least as important as the grazing predation described here in affecting the population dynamics of each species of hydromedusa.

The principal sources of grazing damage to hydromedusae vary by species. *Mitrocomella, Clytia, Mitrocoma,* and rarely *Aequorea,* are all hosts to the parasitic sea anemone larvae of *Peachia quinquecapitata,* which is ingested as a planula larva by a medusa. The growing *Peachia* eventually moves out of the gastrovascular system of its host, after which it feeds on the host gonads and may also eat the manubrium (stomach). *Peachia* larvae are especially abundant in the early to mid-summer. *Mitrocomella,* which matures early in the spring, may provide initial sites of settlement for the youngest *Peachia* larvae, which grow within the manubrium or radial canals, presumably feeding on body fluids rather than tissues at this stage. *Peachia* is known to transfer hosts frequently (Spaulding, 1972), and it appears to be *Mitrocoma* and *Clytia* which suffer most of *Peachia*'s grazing predation. The frequent host transfers seem to preclude killing most host medusae, which should subsequently be able to repair the damage, at some energetic and reproductive cost.

Immature hyperiid amphipods seem to be the primary sources of late season damage to *Aequorea* and *Mitrocoma.* Most are immature *Parathemisto pacifica*; *Hyperia medusarum* is much less common, but does more extensive damage on an individual basis. Hyperiids are found on the exumbrellas and even within the stomachs of hydromedusae, and are responsible for the tunnels cut through the jelly and for the sometimes-extensive grazing damage on the mouth and gonads of medusae. The long-term destructive potential of these associations was revealed only by a continuous series of systematic physical examinations and is not evident from incidental or casual observations.

Other sources of damage to hydromedusae in NE Pacific coastal waters include trematode larvae and nematodes, which occur from time to time in the mesogloea of jellyfish (Mills, unpubl.). These occasionally do great damage, but seem not to be important at the population level.

Another medusan parasite that occurs primarily in winter and early spring is the trophozoite stage of the dinoflagellate *Oodinium* sp. This species attaches to and derives nutrients from several species of ctenophores and at least the hydromedusa *Euphysa* sp. (Mills and McLean, 1991). This dinoflagellate does little apparent damage to its hosts, however, and is present at a time of year when few hydromedusae are in the water column. It is not thought to influence the population dynamics of any of its host species.

Single-celled green flagellates (Class Prasinophyceae) sometimes colonize the exumbrellar surface of hydromedusae in the Friday Harbor vicinity (Mills, unpubl.). This association may be seen anytime during the jellyfish season (affecting up to 2% of the *Clytia* population), although it occurs most frequently in late-summer or autumn, and the medusae involved are often, but not always, visibly in poor health. In addition to Clytia, such infestations have been seen regularly on the bells of *Polyorchis penicillatus,* and rarely on *Catablema multicirrata* and *Leuckartiara nobilis.* More than one species of green flagellates have been recognized as colonizers on the bells of hydromedusae (C. Mills, L. Goff and C. O'Kelly, unpubl.); the long-term effects of this association on medusan survival is not known.

In the absence of critical published information on the subject, it was the goal of this paper to investigate some of the causes of the regular and rather abrupt autumnal terminations of medusan populations in the field. It is the general conclusion that senescence is rarely the cause of death of these animals. The late season decrease in individual bell size exhibited by *Aequorea, Mitrocoma,* and *Clytia* might have several explanations including death of the largest and oldest specimens. Another possible contributor to the decrease in average size is bell shrinkage due to inadequate food, as has been documented for the scyphomedusa *Aurelia* (Hamner and Jenssen, 1974); the reality of that effect taking place among these hydromedusae has not been explored.

The intimate associations of amphipods with gelatinous zooplankton have been well-documented in the past (summarized especially by Harbison et al., 1977; Madin and Harbison, 1977; Laval, 1980), but it is surprising to discover that the long-term effects of such associations can have such profound population consequences for hydromedusae. In fact Laval (1972) carefully documented the parasitic aspects of an association between a *Hyperia* and a species of *Clytia* (*Phialidium*) in the Mediterranean, but the possibly universally deleterious nature and large-scale implications of such associations were not apparent from his report. Metz (1967), in studying the population dynamics of *Hyperia galba,* also found that an amphipod contributed "to a great extent" to the disappearance of its host scyphomedusae *Aurelia aurita* and *Cyanea capillata* in the autumn.

The effects of grazing predation on hydromedusae, as well as other damage caused by symbionts or parasites, can be mitigated by wound-healing and regeneration during periods of high nutrition. However, later in the season when food becomes limited, damage by predation appears to be aggravated by infectious disease and starvation, resulting in a progressive inability of wounds to heal and then death. As predicted by Laval (1980), the results of the present study clearly demonstrate "that animal associations among the pelagic ecosystem are more important than previously thought."

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