

Predation by hydromedusae on hydrozoan embryos and larvae: planktonic kin selection?

J. Timothy Pennington*

Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

ABSTRACT: Laboratory experiments were conducted with hydromedusae of *Aequorea victoria* and *Phialidium gregarium* to determine if males or females would prey upon: (1) heterospecific adults (medusae); (2) heterospecific embryos and larvae; (3) conspecific embryos and larvae not genetically related to the predator medusae; or (4) conspecific embryos and larvae genetically related to the predator medusae (their offspring). Adult *A. victoria* ate adult *P. gregarium*, and adult *P. gregarium* ate embryonic and larval *A. victoria*. Neither species of medusae ate conspecific embryos or larvae, regardless of medusa sex or genetic relationship between predator and prey. Results suggest that the intraspecific competitive interactions documented by other workers for benthic hydrozoans are probably not paralleled by analogous predatory interactions between planktonic hydromedusae and their embryos and larvae.

INTRODUCTION

Planktonic cnidarians can be an abundant predator class (Möller 1980a, Mills 1981a, Arai & Mason 1982, Hernroth & Gröndahl 1983, Larson 1985) with substantial impact on prey communities (McCormick 1969, Huntley & Hobson 1978, Möller 1980b, Purcell 1981, Larson 1985). However, relatively little attention has been paid to patterns and mechanisms of prey selection by cnidarian zooplankton. The finding that 'food juices' and mechanical stimulation in combination cause nematocyst discharge (Pantin 1942) has only recently been re-addressed (Lubbock 1979, Thorington & Hessler 1988a), despite an enormous amount of work on the glutathione 'feeding response' in *Hydra* (reviewed by Lenhoff 1974). Greene (1985) categorized zooplanktivores on the basis of their feeding mechanisms (e.g. 'functional groups' of predators) and predicted prey selection on the basis of size and swimming speed in accordance with the encounter rate model of Gerritsen & Strickler (1977). While this construct is clearly of value, the mechanisms underlying observations of cnidarian prey-selectivity remain largely unresolved (Purcell & Mills 1988).

Prey selection by most planktonic cnidarians is pre-

sumably controlled by selective nematocyst discharge. At a minimum, the sensors controlling discharge must discern potential animal prey from self tissues and inanimate or plant materials. In contrast, studies of competitive aggression among benthic hydrozoans have found extremely 'fine-tuned' sensory discrimination at both interspecific and intraspecific levels (reviewed by Buss et al. 1984, Grosberg 1988): hydroids are able to identify genetically distinct colonies as non-self and to compete with them, whether or not the competitor is of the same or another species. The effectors in these interactions are nematocysts (Buss et al. 1984), and the sensory discrimination is genetically based (Ivker 1972, Bigger 1980, Buss et al. 1984, McFadden et al. 1984). While specialized cnidoms and other specifically aggressive structures (modified polyps or stolons; see Buss et al. 1984) not present on medusae are often involved in competitive aggression (see Buss et al. 1984), this is not always the case (Lubbock 1980).

Predatory interactions have also been observed at an intraspecific level between the polyps, planula larvae and ephyrae of several scyphozoan species. Gröndahl (1988) found that scyphistomae of *Aurelia aurita* consumed both conspecific planulae and those of *Cyanea capillata*. Similarly, F. A. Sommer (pers. comm.) observed scyphistomae of *Pelagia colorata* to eat conspecific planulae as well as ephyrae, and R. H. Brewer (pers. comm.) found both *Chrysaora quinquecirrha* and

* Present address: Hopkins Marine Station, Stanford University, Pacific Grove, California 93950, USA

C. capillata scyphistomae to prey on conspecific planulae.

This study documents predatory interactions between the planktonic medusae and embryos and larvae of 2 hydrozoan species, *Aequorea victoria* and *Phialidium gregarium*. In particular, the purpose was to learn if intraspecific medusa:larva predation occurs, and if so, whether similar predatory behaviors might be exhibited by (1) male or female medusae which are (2) genetically related or unrelated to their prey (offspring or nonoffspring). *A. victoria* and *P. gregarium* were used because they were the most abundant local hydromedusa species (Friday Harbor, Washington, USA; see Mills 1981a), and predatory encounters between medusae and planulae are probably common in the plankton.

MATERIALS AND METHODS

Predators and prey. Sexually mature medusae (adults) of *Aequorea victoria* and *Phialidium gregarium* were hand-dipped from surface waters, sexed by examination of gonads under a dissecting microscope, and placed in individual jars containing 400 ml of 3 μ M-filtered seawater 1 d prior to experiments. Adult *A. victoria* were ca 6 cm in diameter, while adult *P. gregarium* were ca 3 cm in diameter. The jars were placed in a 10 °C incubators with photoperiods controlled so that both species of medusae spawned the following morning (see Miller 1980). On the day of experiments eggs and sperm from individual medusae were mixed, resulting in embryos of known parentage. Embryos developed into planula larvae over the next 12 to 24 h (development reviewed by Mills & Strathmann 1987). To facilitate discrimination of prey added at the beginning of experiments from eggs spawned by females during experiments, embryos were dyed for 2 min by adding 2 or 3 drops of 0.01 % Neutral Red vital stain to 50 ml seawater containing the embryos. A control for possible artifacts caused by the stain was conducted during the 'Interspecific medusa:planula' experiments described below.

Throughout treatment medusae were handled gently with plastic or glass utensils and were not lifted clear of the water; medusae handled in this way survived unfed for ca 2 wk in the laboratory if the seawater was changed every few days. During qualitative observations medusae appeared healthy during the first several days following collection, though their tentacles became very long after 3 to 7 d of starvation (see Mills 1981b) and the swimming bells became progressively smaller thereafter.

Predation among medusae. An experiment was conducted to demonstrate that adult *Aequorea victoria* would eat adult *Phialidium gregarium* in the experi-

mental setup. Two freshly-collected *P. gregarium* were placed in each of five 1 l jars nearly full of 3 μ M-filtered seawater. One freshly collected *A. victoria* was added to each of the jars; the jars were then capped and strapped around the horizontal axis of a 'grazing wheel' (see Yen 1982, Bailey & Batty 1983). The grazing wheel rotated slowly (ca 1.6 rpm), keeping the predators and prey suspended. Experiments were conducted for 24 h in a 12:12 h light:dark, 11 °C coldroom, after which the number of survivors were counted. No controls were included in this experiment because preliminary observations indicated that non-predatory mortality did not occur under these conditions.

Interspecific medusa:planula predation. Most experiments with embryos and larvae were similar to those described in Pennington & Chia (1985), Rumrill et al. (1985) and Pennington et al. (1986), where other aspects of predation upon larvae of benthic invertebrates were studied. Two reciprocal experiments were conducted with interspecific predator:prey combinations. In the first experiment, medusae of *Aequorea victoria* were offered *Phialidium gregarium* embryos and planulae as prey. Twenty-five cleaving embryos of *P. gregarium* were counted into each of a series of fifteen 1 l jars nearly full of 3 μ M-filtered seawater. The jars were divided into 3 sets (Sets A to C) of 5 replicates each. Sets A and B received dyed embryos, while Set C received normal transparent embryos. One adult *A. victoria* was added to each jar of Sets B and C. The jars in Set A received embryos but no predators and served to control for background prey mortality and loss through handling. The second experiment was conducted similarly, except that in this case 50 cleaving embryos of *A. victoria* were offered as prey to individual medusae of *P. gregarium*.

Experiments were conducted on the grazing wheel as described for predation between medusae. After 24 h medusae were removed and prey were concentrated by siphoning most of the water away through 73 μ M Nitex mesh. Surviving embryos had developed into planula larvae by this time; these were fixed in dilute formalin (ca 2%) and counted later. A 1-way analysis of variance (ANOVA) was calculated with the data for each predator species and tested for any significant differences between control and treatment means. Where significant differences were found (e.g. Fig. 1C), a Student's t-test was used to test for significant difference in rate of predation on dyed or transparent embryos and planulae.

Intraspecific medusa:planula predation. Three experiments were conducted to examine predation by medusae upon conspecific embryos and planulae. In the first experiment, male and female *Aequorea victoria* were offered their offspring as prey. Fifty dyed sibling embryos were counted into each of 3 jars. This

procedure was repeated with offspring from 5 different parent-pairs so that there were 5 sets of 3 jars, each set containing sibling embryos. The father and mother were added to separate jars within each set at the beginning of the experiment; the third jar received no predator and served as control. In the second experiment, adult *A. victoria* were offered 50 dyed conspecific embryos and planulae from other parents. These embryos and planulae were presumably unrelated to the medusae used as predators, unless it is supposed that most or all medusae collected from the plankton on any given day are budded from the same or genetically related polyp colonies. In the third experiment, adult *Phialidium gregarium* were similarly offered dyed conspecific embryos and planulae from other parents as prey. As with *A. victoria*, these embryos and planulae were presumably unrelated to the medusae used as predators. All 3 experiments were conducted and analyzed as described above for interspecific medusa:planula predation.

RESULTS

Predation among medusae

Medusae of *Aequorea victoria* ate half of the *Phialidium gregarium* medusae offered as prey on the grazing wheel (Fig. 1A). Variance in predation rate was high in this experiment because some *A. victoria* ate both *P. gregarium* while others did not feed. For this reason qualitative observations were made of predatory interactions between individuals and groups of medusae over periods of several days. It was found that some *A. victoria* did not eat *P. gregarium*, even to the point of starvation. Additionally, after 5 to 10 d of starvation a few *A. victoria* ingested conspecific medusae, but were never observed to digest them. Instead, after several hours the ingested medusae were regurgitated; these individuals survived, though their bells and tentacles were often tangled in mucus.

Interspecific medusa:planula predation

Medusae of *Aequorea victoria* did not eat significant numbers of *Phialidium gregarium* embryos and planulae, whether or not the prey were naturally transparent or stained with Neutral Red (Fig. 1B, ANOVA, $p = 0.772$). Medusae of *P. gregarium*, however, consumed over half of the *A. victoria* embryos and planulae offered (Fig. 1C, ANOVA, $p = 0.012$). Rate of predation by *P. gregarium* was not significantly different on transparent or stained prey (Fig. 1C, t-test, $p = 0.602$).

Intraspecific medusa:planula predation

Adult *Aequorea victoria* did not eat significant numbers of conspecific embryos and planulae (Fig. 2A, ANOVA, $p = 0.875$; Fig. 2B, ANOVA, $p = 0.412$). This lack of predation was not a function of predator sex or genetic relatedness between predator and prey (offspring or genetically unrelated embryos and planulae). Similarly, neither male nor female medusae of *Phialidium gregarium* ate significant numbers of unrelated but conspecific embryos or planulae (Fig. 2C, ANOVA, $p = 0.698$). Because medusae of *P. gregarium* did not eat significant numbers of unrelated conspecific embryos and larvae, it seemed unlikely that they might have eaten their offspring; an experiment to examine this possibility was therefore not conducted.

DISCUSSION

In jars on the grazing wheel, adult (medusoid) *Aequorea victoria* ate adult *Phialidium gregarium*, but adult *P. gregarium* did not eat adult *A. victoria*. These findings are not new (see Arai 1980, Arai & Jacobs 1980), but serve to demonstrate that *A. victoria* will feed in the experimental setup. However, attempted cannibalism among starving adult *A. victoria* has not been previously noted. Although little is known of the mechanisms by which medusae capture other medusae, recognition of potential prey items presumably occurs at the cellular level via the chemoreceptors controlling nematocyst discharge (see Mariscal 1974,

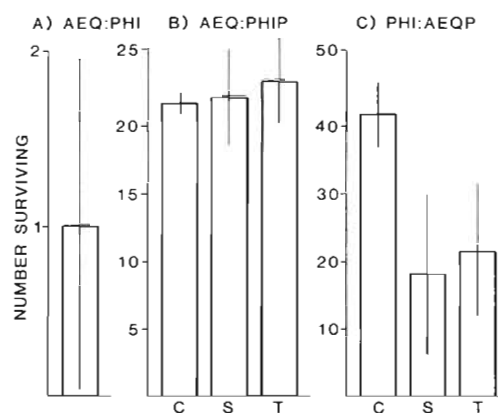


Fig. 1. *Aequorea victoria* and *Phialidium gregarium*. Mean numbers of prey (± 1 standard deviation) surviving experiments with heterospecific predators: (A) medusoid (adult) *A. victoria* offered 2 adult *P. gregarium* as prey (AEQ:PHI); (B) adult *A. victoria* offered 25 *P. gregarium* embryos and planulae as prey (AEQ:PHIP); (C) adult *P. gregarium* offered 50 *A. victoria* embryos and planulae as prey (PHI:AEQP). C: controls (no predators present); S: stained prey; T: transparent (unstained) prey

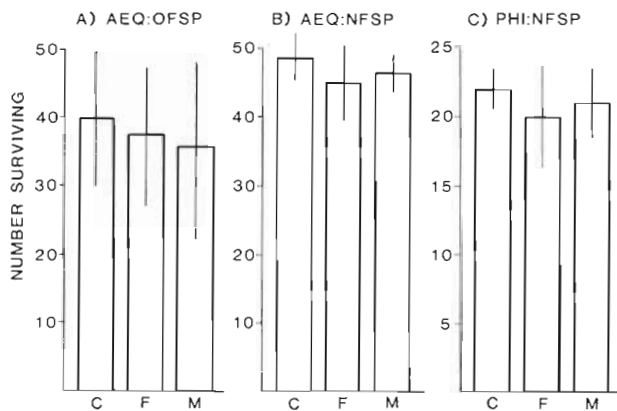


Fig. 2. *Aequorea victoria* and *Phialidium gregarium*. Mean numbers of prey (± 1 standard deviation) surviving experiments with conspecific predators; (A) medusoid (adult) *A. victoria* offered 50 of its offspring (embryos and planulae) as prey (AEQ:OFSP); (B) adult *A. victoria* offered 50 genetically unrelated embryos and planulae as prey (AEQ:NFSF); (C) adult *P. gregarium* offered 25 genetically unrelated embryos and planulae as prey (PHI:NFSF). C: controls (no predators present); F: female predators; M: male predators

Hildeman et al. 1979, Thorington & Hessinger 1988a). Such sensors are at least partially subject to nervous control and their sensitivity can vary with hunger (Mariscal 1974, Thorington & Hessinger 1988b); starving medusae may attack an increasingly wide range of prey, perhaps including conspecific medusae. It nevertheless remains unclear why *A. victoria* should ingest but fail to digest conspecific medusae.

When offered heterospecific embryos and planulae as prey, adult *Phialidium gregarium* ate *Aequorea victoria* embryos and planulae, but adult *A. victoria* did not eat significant numbers of *P. gregarium* embryos and planulae. I had expected medusae of *P. gregarium* to feed in these experiments because they are known to eat other small and poorly motile prey (Larson 1985, Pennington & Chia 1985, Pennington et al. 1986, Purcell & Mills 1988). However, I had also expected medusae of *A. victoria* to feed because they are known to eat adult *P. gregarium*. Because *A. victoria* preys at low rates or not at all on immotile or weakly-swimming echinoid embryos (Pennington et al. 1986), it may be that *A. victoria* nematocysts are not discharged in response to small, relatively immotile prey in general (see Hyman 1940 for a list of prey taken by *A. victoria*). If so, *P. gregarium* embryos and planulae may not have been eaten because their size or motility was insufficient to stimulate discharge of *A. victoria* nematocysts.

Neither species of medusa preyed upon conspecific embryos or planulae at detectable rates, suggesting that intraspecific aggression may not occur among the planktonic life-history stages of these hydrozoans. As discussed above, for *Aequorea victoria* this may have

been due to the relative immotility of embryos and planulae in general. However for *Phialidium gregarium*, which ate *A. victoria* embryos and planulae, some feature of the surface chemistry of conspecific embryos and planulae apparently protects conspecific larvae by averting or not stimulating nematocyst discharge. Because intraspecific predation was not observed, my questions concerning predation by male or female medusae on genetically related or unrelated conspecific larvae became irrelevant. However, these considerations might again become pertinent if future work should reveal that starvation of medusae broadens the range of stimuli that cause nematocyst firing to include conspecific prey – a possibility that may be suggested by the failed cannibalistic attacks among *A. victoria*.

The observed lack of intraspecific aggression between planktonic medusae and larvae stands in contrast to its ubiquity in those benthic hydrozoans so far studied (reviewed by Buss et al. 1984). However, *Aequorea victoria* and *Phialidium gregarium* were chosen for use here because of their co-occurrence in the plankton. The ecologies of the benthic colonies of these species are not well known (see Roosen-Runge 1970, Arai & Brinckmann-Voss 1980) and although unlikely, it is possible that the colonies of these species are unique in that they do not engage in intraspecific aggression. Regardless, the potential for intraspecific aggression also appears to be lacking in the medusae of another hydrozoan species. Bührer & Tardent (1980) and Tardent & Bührer (1982) found that manubrial transplants were uniformly successful between medusae of 2 strains of *Podocoryne carnea*, even though similar interstrain grafts rejected one another as polyps or stolons. For *P. carnea*, these results demonstrate that the histoincompatibility reactions characteristic of aggression between benthic colonies are absent or suppressed in the medusa stage.

If at least some scyphozoan polyps cannibalize conspecific planulae (Gröndahl 1988, R. H. Brewer & F. A. Sommers pers. comm.) and ephyrae (F. A. Sommers pers. comm.), and all benthic hydrozoans engage in intraspecific interference competition (reviewed by Buss et al. 1984), why don't the planktonic medusae studied here eat conspecific embryos and larvae? It can be argued that the competitive aggression of benthic colonies bears little relation to the predatory aggression of planktonic medusae. This argument is only partly valid. Where both types of aggression are mediated by the same 'sensor-effector systems' (nematocysts and their sensors; Buss et al. 1984), the distinction between competition and predation is arbitrary (Bigger 1980, Lubbock 1980). For example, scyphistomae may well cannibalize planulae and ephyrae because they use the same sensor-effectors in both predatory and competi-

tive interactions. Conversely, where specialized competitive structures bear unique cnidae (reviewed by Bigger 1988), predatory and competitive aggression may be decoupled.

On an evolutionary level, the contrasting patterns of intraspecific aggression between planktonic and benthic life-history stages probably occur because planktonic organisms cannot benefit through 'interference' competition. The benefits of aggression in this type of competition are restricted to circumstances where interaction between individual competitors occurs predictably and repeatedly, so that energetic investments in aggression are likely to produce future benefits (e.g. maintenance of territory or avoidance of fusion; Grosberg 1988). The spatial instability of planktonic habitats prevents such interaction. The resulting lack of selection for intraspecific competition has apparently produced barriers to aggression in medusae at the species level, even though, in principal, medusae might still benefit by preying on conspecific but unrelated prey.

Acknowledgements. I thank G. Freeman and C. Mills for advice concerning hydromedusae and their larvae, R. Brewer and F. Sommer for their unpublished observations, and A. Harrington, S. Miller, A. Ringwood and S. Rumrill for comments on the manuscript. The work was supported by an NSERC of Canada grant to F. S. Chia.

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This article was presented by Dr M. R. Landry, Honolulu, Hawaii, USA

Manuscript first received: May 28, 1989
Revised version accepted: November 10, 1989