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JELLYFISH BLOOMS

Nudibranch predation and dietary preference for the polyps of *Aurelia labiata* (Cnidaria: Scyphozoa)

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Abstract There is concern that jellyfish blooms may be increasing worldwide. Some factors controlling population size, such as temperature and food, often have been studied; however, the importance of predators is poorly known. Aeolid nudibranchs feed on cnidarians, but their predation on the benthic polyps of scyphozoan rarely has been documented. To understand the potential of nudibranchs to consume polyps, we tested several predation preference hypotheses with the generalist feeding nudibranch, *Hermissenda crassicornis*, and polyps of the common moon jellyfish, *Aurelia labiata*. Of the six prey species tested during feeding experiments, *A. labiata* polyps and the tunicate *Distaplia occidentalis* were significantly preferred. Nudibranch size, diurnal cycle, and ingestive conditioning did not significantly influence prey choice. Nudibranchs showed significant positive chemotaxis toward living polyps, hydroids, and tunicates, but not to sea anemones. Nudibranch chemotaxis was significantly more positive to polar extract of *A. labiata* than of *D. occidentalis.* Consumption of polyps was correlated with nudibranch size, with mean consumption by large nudibranchs (>0.92 g) of about 31 polyps h^{-1}. Three other nudibranch species also ate *A. labiata* polyps. Our results emphasize the potential importance of predation for controlling jellyfish benthic polyp populations and consequent jellyfish blooms.

Keywords Jellyfish · Predator · Selection · Hydroid · Tunicate · Sea anemone · Chemotaxis

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Introduction

There is concern that jellyfish blooms have increased in recent decades and, consequently, have had increased effects on ecosystem dynamics and human enterprises. Large blooms may reduce zooplankton biomass to such an extent that they can alter entire trophic webs (Mills, 1995; Brodeur et al., 2002; Purcell, 2003; Ruzicka et al., 2007; Pauly et al., 2009). They degrade fisheries by consuming ichthyoplankton and potentially competing with fish for food resources (Purcell & Arai, 2001; Purcell & Sturdevant, 2001), and they also impede the fishing industry by clogging fishing nets (Uye & Ueta, 2004; Purcell et al., 2007).

Jellyfish blooms also clog water-intake screens of coastal power and desalination plants and reduce tourism revenues by increased stinging at beaches (UNEP, 1991; Purcell et al., 2007; Mariottini & Pane, 2010). Common moon jellyfish in the cosmopolitan genus *Aurelia* are key problem species around the world.

To understand the causes of large blooms of medusae, increased attention is being paid to the importance of the benthic asexual stage (polyp) of scyphozoan jellyfish. The asexual strobilation of the polyps is directly responsible for producing new jellyfish. Studies on *Aurelia* spp. show that polyp population dynamics are affected by several factors, including environmental and climatic conditions (Lucas, 2001; Purcell, 2005; Purcell et al., 2009, 2012; Holst, 2012; Thein et al., 2012), substrate preference and availability (Lucas et al., 1997; Miyake et al., 2002; Holst & Jarms, 2007; Willcox et al., 2008; Hoover & Purcell, 2009), food availability (Buss, 1990; Gong, 2002), and predation (Hernroth & Gröndahl, 1985a, b; Gröndahl, 1988; Keen, 1991). Predation, the least studied of the above factors, is the topic of our study.

Nudibranchs are a group of shell-less marine gastropods, commonly called sea slugs. Many species from the nudibranch suborders Dendronotacea and Aeolidacea utilize benthic cnidarians as food sources. Those in the Suborder Dendronotacea commonly have generalist feeding habits (McDonald & Nybakken, 1996); species in the Suborder Aeolidacea harvest the unfired nematocysts of their prey and incorporate them into their own tissues for defense (Cargo & Burnett, 1982).

Although very few studies exist, some show important effects of nudibranch predation on *Aurelia* spp. polyp populations. In Gullmar Fjord, Sweden, the nudibranch *Coryphella verrucosa* (Sars, 1829) ingested the polyps of *Aurelia aurita* (Linnaeus, 1758) at rates up to 200 polyps d^{-1} on settling plates; this predation was believed to be responsible for a drastic decline in polyp abundance (Hernroth & Gröndahl, 1985a). Further, Gröndahl (1988) believed that inter-annual variation in ephyra (and thus medusa) abundance was controlled by that predation. A 2-year study by Keen (1991) showed that the effect of predation by the nudibranch *Hermissenda crassicornis* (Eschscholtz, 1831) on *Aurelia* sp. polyps was highly dependent on the density and extent of polyp colonies. Keen (1991) found that large patches of polyps could be broken up into smaller patches by predation and that small patches (<100 cm^2) frequently were consumed within a month. Keen (1991) also observed that the numbers of experimental sites in situ that lost all polyps during monthly census intervals were positively correlated with the numbers of large (>4 cm in length) nudibranchs present.

Hermissenda crassicornis is a common aeolid nudibranch species found in a wide variety of habitats (e.g., rocky intertidal, mud flats, and boat docks) along the Pacific coasts of North America, from Alaska to Mexico, and of Asia (Morris et al., 1980; Behrens, 1991; Thein et al., 2012). Mating animals and egg masses of *H. crassicornis* occur all year in the Puget Sound (Morris et al., 1980). *H. crassicornis* is a generalist, preying on many cnidarians, tunicates, bryozoans, sponges, annelids, and other gastropods, including con-specifics (McDonald & Nybakken, 1996). Because of its availability and generalized diet, *H. crassicornis* was chosen for experiments on nudibranch predation on *A. labiata* (Chamisso & Eysenhardt, 1821) polyps.

It is not known if the polyps of *Aurelia* spp. are a preferred food of *H. crassicornis.* The necessity of harvesting fresh nematocysts to maintain their defenses (Cargo & Burnett, 1982) may influence their dietary preferences, but the use of scyphozoan polyps as food has rarely been studied. Avila et al. (1998) compared *H. crassicornis* growth and survival on three cnidarian diets, the hydroid *Tubularia crocea* (Agassiz, 1862) or either of the sea anemones *Haliplanella luciae* (Verrill, 1870) and *Metridium senile* (Linnaeus, 1761), but did not distinguish preference. In a second study, Avila (1998) used the cnidarians above, as well as the hydroid *Pennaria* sp., the tunicate *Ciona intestinalis* (Linnaeus, 1767), and the mussel *Mytilus edulis* (Linnaeus, 1758), concluding that ingestive conditioning influenced chemotactic preferences of *H. crassicornis*, but ingestive preferences were not tested.

Some nudibranchs exhibit ingestive conditioning based on dietary history (Hall et al., 1984; Avila, 1998). Early ingestive conditioning may occur when larval *H. crassicornis* complete metamorphosis on several species of hydroids that it later consumes (Harrigan & Alkon, 1978); however, adult *H. crassicornis* also lives well on a diet of tunicates (Harrigan & Alkon, 1978), which would provide more energy-efficient foraging.

In one study, *H. crassicornis* displayed chemotaxis toward the hydroid *Pennaria* sp., which it had never fed on, but not toward the conditioned diet of the sea anemone *M. senile* (Avila, 1998).

Several nudibranch species use chemotaxis in choosing prey items (Willows, 1978; Todd, 1981; Seavy & Muller-Parker, 2002). *H. crassicornis* exhibits chemotaxis to several species of hydroids in a simple Y-maze, and choices via chemotaxis have been observed (Tyndale et al., 1994; Avila, 1998). Because *H. crassicornis* is a generalist feeder, many known prey items have not been tested for chemotaxis by the nudibranch. Whether any nudibranch species shows chemotaxis to scyphozoan polyps of any species is unknown. Furthermore, to our knowledge, chemotaxis has never been compared to ingestive preference in nudibranchs.

Factors affecting the polyp stage could greatly affect medusa abundances of species globally. Our study examined how the predatory behavior of the nudibranchs could affect scyphozoan polyp populations by testing the following null hypotheses: H_{01} *H. crassicornis* preference does not differ between paired food choices; H_{02} *H. crassicornis* shows no preferences among six food choices; H_{03} nudibranch size does not affect food preference; H_{04} feeding preferences do not differ between daytime and nighttime; H_{05} ingestive conditioning does not affect food preferences of *H. crassicornis*; H_{06} *H. crassicornis* shows no taxis to living food choices or to seawater controls; H_{07} *H. crassicornis* shows no taxis to polar or non-polar prey extracts or to control seawater blanks; H_{08} *H. crassicornis* shows no chemotactic preference between the polar extracts of *A. labiata* polyps and *D. occidentalis*; H_{09}, H_{10}, and H_{11} nudibranch size, polyp size, and polyp density do not affect the total number of *A. labiata* polyps consumed; and H_{12} nudibranch size does not affect the polyp size class consumed. We tested six additional nudibranch species to determine if consumption of *A. labiata* polyps was common.

Methods

Collection and maintenance of organisms

The food organisms used in ingestion and chemotaxis experiments were chosen based on field observations near a large colony of *A. labiata* polyps and known foods of nudibranchs (McDonald & Nybakken, 1996). Animals were collected from various sites surrounding Shannon Point Marine Center (SPMC) in Anacortes, Washington (48°30′N, 122°41′W). The collection sites were intertidal or slightly subtidal and chosen only for the abundance of the desired organisms found there.

Experimental organisms were maintained at SPMC in sea tables with a constant supply of flow-through ambient seawater. Water temperatures averaged 12.4 ± 1.3°C and salinities averaged 30.3 ± 1.1 ppt during experimentation. Organisms to be used as food were separated by species into 33 × 25.4 × 15 cm flow-through plastic mesh baskets. All food organisms were offered newly hatched *Artemia* sp. nauplii once per week. *H. crassicornis* nudibranchs were kept individually in 25 × 17 × 13 cm flow-through plastic mesh baskets to prevent cannibalism.

Maintenance diets of the nudibranchs differed among experiments. For the 30-min, 2-choice experiments, nudibranchs were maintained on mixed diets of the hydroid *Obelia geniculata* (Linnaeus, 1758), the tunicates *Distaplia occidentalis* Bancroft, 1899 and *Corella willmeriana* Herdman, 1898, and *A. labiata* polyps. The test species were used in the diet regimen, but the nudibranchs to be tested were not fed their test prey species. For the more robust 6-choice, 24-h ingestive preference testing, individual *H. crassicornis* were maintained on the predetermined diets described below to test for possible effects of ingestive conditioning. For single-choice chemotaxis experiments, nudibranchs were not fed between collection and testing 3 days later. For 2-choice chemotaxis experiments, the nudibranchs were maintained on a diet of *O. geniculata* hydroids. All organisms were used within 3 weeks of collection and determined to be in healthy condition.

Ingestive preference: 30-min, 2-choice experiments

We first tested the prey choices of *H. crassicornis* in short experiments with pairs of four prey species: *O. geniculata* (hydroid), *D. occidentalis* (colonial tunicate), *Epiactis prolifera* Verrill, 1869 (sea anemone), and polyps of *A. labiata* (jellyfish). Nudibranchs were unfed for 24 h before testing in order to standardize conditions for each nudibranch (Hall et al., 1984;

Avila et al., 1998). The testing arenas were 21-cm-diameter × 10-cm-deep glass bowls filled with seawater filtered to 50 μm. To maintain ambient water temperature, the bowls were placed nearly immersed in a flow-through sea table. Two prey specimens were placed on opposite sides of the testing arena 15 min before each test began to allow their scents to disperse in the bowl.

Each unfed nudibranch was transferred in a large spoon from its holding pen to the test arena immediately before the 30-min testing period. One nudibranch was placed in the middle of the bottom of each bowl, equidistant and oriented away from both prey items. The prey that was fed upon first and the duration of time each nudibranch spent eating each prey item was recorded. Due to the limited number of nudibranchs available, subsequent tests were conducted at 48-h intervals with the same nudibranchs using different prey choices. The order of the test treatments was determined by availability and freshness of prey items collected. In total, 26 nudibranchs were tested for the polyp-tunicate choice, and 16 nudibranchs each for the polyp-hydroid and polyp-anemone choices. The data were analyzed using paired *t* tests. The null hypothesis (H_{01}) was that *H. crassicornis* feeding shows no differences between paired food choices.

Ingestive preference: 24-h, 6-choice experiments

To assess the food preferences of *H. crassicornis* when offered a wider selection of foods over a longer period, 6-choice ingestive preference experiments ($n = 18$) were run for 24 h per trial. Nudibranchs were placed in the center of a circular flow-through arena (diameter = 40 cm, height = 15 cm) containing six food choices that included the polyp, hydroid, and tunicate species used in the 2-choice tests, plus the sea anemone *Anthopleura elegantissima* (Brandt, 1835), the bryozoan *Bugula* sp., and the sponge *Halichondria bowerbanki* Burton, 1930. The arena apparatus was adapted from Seavy & Muller-Parker (2002). To eliminate any bias from currents or gradients present in the sea table, the arena was surrounded by a circular seawater delivery hose that introduced water into the arena from all directions through small holes at 10-cm intervals around the circumference. Water flow within the arena was tested prior to each trial by adding food coloring to the food choice locations and observing mixing patterns. Food choice locations appeared to receive similar flows and the water in the arena was well mixed.

To record the ingestive preferences of the nudibranchs, a Sony DCR-TRV900 digital video camera was mounted 180 cm above the sea table. The 24-h experiments were recorded using the time-lapse video function, which recorded for 2 s at 30-s intervals. Tests were conducted in natural light, which averaged 14.3 h of daylight and 9.7 h of darkness during experimentation. The low light exposure setting was used to ensure adequate exposure during darkness. An 80-min Sony miniDV cassette was used at LP speed (120 min) to record each trial.

Experimental food organisms were chosen based on records of known *H. crassicornis* foods (McDonald & Nybakken, 1996) and food resources near the nudibranchs when collected. To standardize the amounts of different foods presented, all samples were gently scooped in a small spoon from the holding baskets and placed it into seawater-filled plastic weighing boats on a Mettler Toledo digital balance tared to include the weight of the seawater and weighing boat. The samples were then adjusted to as similar wet weights as possible without damaging the organisms. The food choices were in 30-ml glass Petri dishes that were placed at equidistant marks 5 cm from the perimeter of the arena. To further reduce potential bias, the position of each food choice was chosen from a random number table for each new trial and the nudibranch was always placed with its head oriented to the north. After each trial, the arena was removed and nudibranch waste and slime trails were cleaned from the arena using hot freshwater and an abrasive pad. Each nudibranch was unfed for 24 h before testing (Avila et al., 1998) and its wet weight (g) measured as above.

The data determined from the recordings were the times spent ingesting each food in daylight and in darkness, and the total time spent ingesting each food. The data were analyzed using log likelihood *G* tests to rank preferences, paired *t* tests to test day/night patterns in feeding, a Wilcoxon signed-rank test for day/night data that were not normally distributed, and a type II regression to examine the effect of nudibranch size on food choice. Three null hypotheses were tested: (H_{02}) *H. crassicornis* shows no preferences among 6 food choices, (H_{03}) nudibranch size does not affect food preference, and (H_{04}) feeding

preferences do not differ between daytime and nighttime.

Ingestive conditioning

To ensure the reliability of the preference testing, we tested the potential for ingestive conditioning to bias food preference. The nudibranchs were divided into six groups of three individuals, and each group was conditioned to one of the experimental foods (the polyp, hydroid, tunicate, sea anemone, bryozoan, or sponge species above) for 1 week. The conditioning was limited to 1 week because nudibranch mortality increased greatly with prolonged exposure to a single food. The food preferences of the nudibranchs were then tested for positive preference for the conditioned food and top preference (most-preferred) for the conditioned food. To examine if ingestive conditioning affected preference, the multidimensional non-parametric statistical program PRIMER was used to map nudibranch preference. The null hypothesis (H_{05}) was that ingestive conditioning does not affect food preferences of *H. crassicornis*.

Food preference analysis

Microsoft Excel™ was used to calculate the maximum likelihood ratio (G) for food preference tests. The G statistic is used to evaluate goodness of fit much the same way as Chi-square (χ^2) values and is used specifically in preference testing whenever any observed outcome is more than twice the expected outcome (Williams, 1976). Zar (1996) calculates G for an individual treatment as:

$$G_i = f_o[\ln(f_o/f_e)]$$

and G for all treatments is calculated as:

$$G_T = 2\sum f_o[\ln(f_o/f_e)]$$

where f_o is the number of observed outcomes and f_e is the number of expected outcomes for each treatment in the preference test. Expected outcomes were calculated by dividing the total time spent feeding by six. For further exploration of the degree and direction of preference (i.e., preference for vs. preference against), the normal standard deviates (d) for each G_i were calculated by adjusting the calculated standard residuals (e) by variance (v) and comparing the result to a z statistic:

$$e = (f_o - f_e)/\sqrt{(f_e)}$$
$$v = \left[1 - \left((f_o + f_e)/\left(2\sum f_o\right)\right)\right] \times \left[1 - \left(\left(\sum f_o\right)/\left(2\sum f_o\right)\right)\right]$$
$$d = e/\sqrt{(v)}$$

If the normal standard deviate (d) has a greater absolute value than 1.96 ($p = 0.05$), then a positive value for d represents preference for a treatment and a negative value represents preference against. The greater the absolute value of d, the greater the degree of preference.

Chemotaxis by *Hermissenda crassicornis*: experimental Y-maze

To test the chemotactic preferences of *H. crassicornis*, we tested chemotaxis to living prey items and to the polar and non-polar extracts of selected prey species. Because the classic Y-maze design has been found to hinder natural behavior due to constriction of movement (Zimmer-Faust et al., 1996), preference testing was conducted using a modified Y-maze designed by Seavy & Muller-Parker (2002). The modified Y-maze consisted of a circular, clear, 30-cm-diameter plexiglass arena connected to two flow-through catch chambers. During experimentation, ambient seawater from the flow-through seawater system constantly filled a 30-l tank that was connected by valved 1.27-cm-diameter surgical tubing to two flow-through holding boxes that contained the prey items. The holding boxes had opaque sides to prevent visual response and contained baffles with screened holes near the bottom to ensure that seawater flowed directly over the prey items. The seawater then flowed from the holding boxes into the Y-maze arena catch chambers via valved 0.95-cm-diameter surgical tubing. The seawater drained from the arena through two screened outlets at the rear of the arena.

To ensure proper Y-conformation flow with minimal mixing in the arena, dye tests using food coloring were performed before each treatment. Dyes of different colors were placed in each respective holding box and allowed to flow through the catch chambers into the arena. The valves attached to the catch

chambers were adjusted to equalize flow and a center line and small circle marking the point of convergence were used to calibrate the flow to be identical for each treatment. The small circle was also used to ensure consistent positioning of the nudibranch for each trial. Once Y-conformation flow was established, the entire apparatus was flushed with seawater for 10 min before the start of a trial.

The entire apparatus was disassembled and cleaned rigorously with hot freshwater and brushes after each trial to remove nudibranch mucus trails and chemical residue to eliminate those potential biases. After thorough rinsing and reassembly, the Y-flow was recalibrated. In addition, the order of prey species presentation and which basket held prey were randomized for each set of trials and for each nudibranch. The time between trials was approximately 1 h. To minimize handling effects, nudibranchs were transferred to and from the experimental chamber in new 60 × 15 mm plastic Petri dishes filled with seawater. Each nudibranch was unfed for 3 days before testing to ensure a rapid response (Seavy & Muller-Parker, 2002).

Chemotaxis: living prey items

Hermissenda crassicornis nudibranchs first were tested for chemotaxis to whole, living prey items using single-choice (prey vs. control) experiments. The prey items tested were *A. elegantissima* sea anemones ($n = 9$), *A. labiata* polyps ($n = 9$), *D. occidentalis* tunicates ($n = 9$), and *O. geniculata* hydroids ($n = 8$). With the exception of one nudibranch that was not tested on *O. geniculata*, each was tested for chemotaxis toward each prey item in a randomized series. The chemotaxis testing procedure was as follows: With the Y-maze calibrated and flowing, a prey item was placed in one of the holding boxes while the other remained empty (control). The scent of the prey item was then allowed to effuse into the arena for 1 min. A trial was initiated by carefully positioning a nudibranch in a Petri dish with its head toward the back of the arena on the circle marking the point of flow convergence. Chemotaxis (choice) was defined as entry of the nuibranch's head (including rhinophores) into one of the catch chambers. If no choice was made by 1 h, the trial was deemed "no choice" and removed from analysis. Results were analyzed using a χ^2 contingency table. The null hypothesis (H_{06}) was that *H. crassicornis* shows no taxis to living food choices or to seawater controls.

Chemotaxis: polar and non-polar extracts

Based on results of the living prey tests, polar and non-polar extracts were made from *A. labiata* polyps and *D. occidentalis* tunicates. For extraction of the polar and non-polar compounds from the test species, 6-ml samples were first frozen at −70°C in a So-Low Ultra Low Freezer, then soaked in a 2:1 dichloromethane:methanol solvent solution for approximately 5 min inside an explosion-proof Isotemp Fisher Scientific refrigerator. Remaining solids were removed using a Buckner funnel, and the eluate was placed in a separatory funnel with a small amount of reverse osmosis (RO) water until the polar and non-polar layers separated. To ensure complete separation, samples were centrifuged using a Jouan Inc. Br4i centrifuge for 1 min at 1,000 rpm. A glass Pasteur pipette was used to transfer the methanol layers to separate containers. Complete separation of the two layers was verified by centrifuging again for 2 min at 1,000 rpm. The polar and non-polar extracts were then recovered by evaporating the solvents using a Büchi Rotovapor R-114 in a 40°C water bath. To further remove impurities, methanol was added to the non-polar extracts and the samples were again centrifuged for 2 min at 1,000 rpm. The solutions were then filtered using a 0.2-μm 20-ml syringe and dried using a Savant SpeedVac Plus concentrator. To standardize volume for testing, the polar and non-polar extracts were diluted in RO water and methanol, respectively.

Preliminary single-choice tests (polar or non-polar extract vs. seawater control) were run to determine if the nudibranchs exhibited chemotaxis to the extracts. Then, 2-choice tests between the polar extracts of *A. labiata* polyps and *D. occidentalis* were performed to determine chemotactic preference. Testing procedures were as follows for single-choice tests: 160 μl of extract was randomly injected in one of the holding boxes while the other was left empty (control). For 2-choice tests, 160 μl of the two extracts were injected simultaneously into the two holding boxes, which were alternated for each new trial. The trial then was immediately initiated by carefully positioning a nudibranch in a Petri dish with its head facing the back of the arena on the circle marking the point of flow convergence. Chemotaxis (choice) was defined as the

entry of the nudibranch's head (including rhinophores) into one of the catch chambers. If no choice was made within 5 min, the trial was deemed "no choice" and removed from analysis. Results were analyzed using χ^2 contingency tables. The null hypotheses were (H_{07}) that *H. crassicornis* shows no taxis to polar or non-polar prey extracts or to control seawater blanks and (H_{08}) that *H. crassicornis* shows no chemotactic preference between the polar extracts of *A. labiata* polyps and *D. occidentalis.*

Feeding potential

Hermissenda crassicornis was used to estimate the feeding potential of nudibranchs on *A. labiata* polyps. Thirty-five 1-h feeding experiments were conducted during which individual nudibranchs were allowed to feed on a known number of polyps. Brown algal blades with attached *A. labiata* polyps were harvested and used for feeding potential experiments. Polyp colony densities were determined by cutting the algal blades into known areas and counting the polyps in each area. To ensure that feeding was not limited by food availability, each of the 35 algal blades contained more than 100 polyps, which exceeded nudibranch consumption during preliminary feeding tests. Polyp size was determined by measuring diameters with a caliper tool. Polyps were categorized into "small" (<3 mm diameter) or "large" (>3 mm diameter) size classes based on an apparent discontinuity in size. The algal blades with polyps then were attached perpendicular to the water flow with dissection pins to the bottom of individual 25 × 17 × 13 cm plastic flow-through experimental cages in a sea table with flowing seawater.

To avoid possible ingestive conditioning to other prey, the nudibranchs were supplied with only *A. labiata* polyps as a food source for 1 week. Each nudibranch was then unfed for 24 h before testing to standardize feeding conditions (Avila et al., 1998). The wet weight (g) of each nudibranch was measured as described above immediately before testing. A separation of large and small nudibranchs was set as the median value of 0.912 g for ease of analysis.

After weighing, each nudibranch was placed in an experimental cage with polyps as detailed above. Feeding was allowed for 1 h beginning with first contact with the polyps. After 1 h, the nudibranch was removed and the polyps were recounted and remeasured to determine the numbers of small, large, and total polyps consumed. A multiple stepwise major axis regression was used to determine the relative importance of nudibranch sizes, polyp sizes, and polyp colony densities to the total numbers of polyps consumed. The null hypotheses (H_{09}, H_{10}, H_{11}) were that nudibranch size, polyp size, and polyp density do not affect the total number of *A. labiata* polyps consumed. The null hypothesis (H_{12}) was that nudibranch size does not affect the polyp size class consumed.

Predation on *A. labiata* polyps by other nudibranchs

During monthly surveys of a large colony of *A. labiata* polyps from January 2004 to April 2006 (Hoover & Purcell, 2009; Purcell et al., 2009), six additional nudibranch species found near or on the colony were collected and tested for predation on the polyps. The nudibranchs were unfed for 24 h and then each was placed individually inside an experimental arena with a known number of polyps, as in the feeding potential experiments. The polyps were recounted after 24 h and examined for evidence of predation.

Results

Ingestive preference: 30-min, 2-choice experiments

Two-choice tests indicated that the polyps of *A. labiata* were the preferred prey of *Hermissenda crassicornis* nudibranchs among the 4 choices offered in 30-min trials. The polyps were the first prey chosen in 66% of *Distaplia occidentalis* versus polyp trials, 81% of *Epiactis prolifera* versus polyp trials, and 75% of *Obelia geniculata* versus polyp trials. The nudibranchs also spent significantly more time feeding on polyps than any other prey item ($t_{25} = -2.83$, $P = 0.009$ vs. *D. occidentalis*; $t_{15} = -3.81$, $P = 0.002$ vs. *E. prolifera*, and $t_{15} = -3.34$, $P = 0.004$ vs. *O. geniculata*; Fig. 1). The null hypothesis H_{01}, that no preferences existed between prey pairs, was rejected.

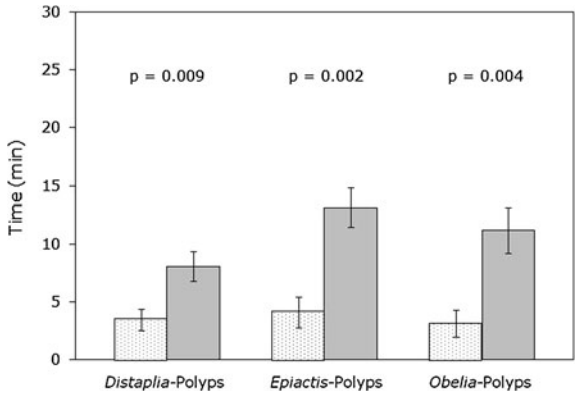

Fig. 1 Feeding times of *Hermissenda crassicornis* nudibranchs during 30-min, 2-choice ingestive preference experiments testing *Distaplia occidentalis* (colonial tunicate), *Epiactis prolifera* (sea anemone), and *Obelia geniculata* (hydroid) against polyps of *A. labiata* (jellyfish). Data are mean ± standard error for 26, 16, and 16 trials, respectively

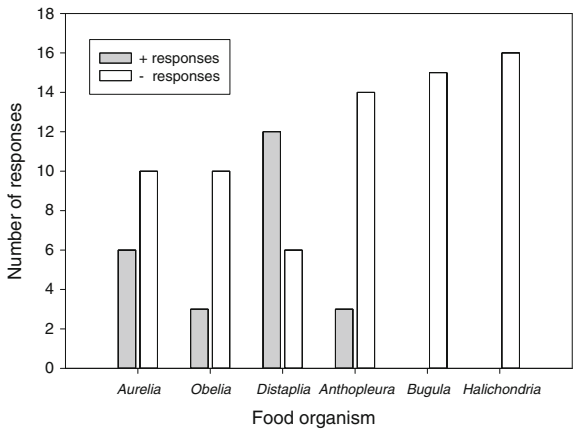

Fig. 2 Numbers of food preference responses by prey type for 17 *Hermissenda crassicornis* nudibranchs. Prey species were *A. labiata* polyps, *Obelia geniculata* hydroids, *Distaplia occidentalis* colonial tunicates, *Anthopleura elegantissima* sea anemones, *Bugula* sp. bryozoans, and *Halichondria bowerbanki* sponges. *Gray bars* indicate preference toward (+) and *white bars* indicate selection against (−) the prey items

Ingestive preference: 24-h, 6-choice experiments

We tested the null hypothesis that no significant differences existed in the preferences of *H. crassicornis* nudibranchs among six food choices. Sixteen of 18 nudibranchs explored the arena before making a choice and all nudibranchs actively traversed the arena during the 24-h trial. One nudibranch did not eat and that trial was omitted from analysis. The remaining 17 nudibranchs averaged 9.0 ± 7.2 h d^{-1} feeding. *D. occidentalis* tunicates, *O. geniculata* hydroids, and *A. labiata* polyps all were consumed by more than half of the nudibranchs tested (Table 1).

The log likelihood G_T values were greater than the critical χ^2 of 11.07, indicating significant preferences in food choice in all 17 trials. Calculation of the normal standard deviates of the G_i values for each food type permitted determination of the degree and direction (+/−) of each nudibranch's preference. *D. occidentalis* was the only food choice for which more than half of the 17 nudibranchs (58.8%) showed a positive preference (Fig. 2). The polyps of *A. labiata* were the second-most-preferred food, with 35.3% of nudibranchs showing a positive preference (Fig. 2); however, only three nudibranchs chose polyps as their most-preferred prey (Table 1), and 58.8% showed selection against the polyps (Fig. 2). All nudibranchs that exhibited a positive preference for the polyps had a very strong preference toward them (Table 2). The nudibranchs showed 17.6% positive preference for *O. geniculata* hydroids and *Anthopleura elegantissima* sea anemones, but there were no positive responses to *Bugula sp.* bryozoans or *Halichondria bowerbanki* sponges (Fig. 2). H_{02}, that no preferences existed among six prey species, was rejected.

To determine if food preference was influenced by nudibranch size, regressions were run between the wet weights (g) of the *H. crassicornis* nudibranchs and the

Table 1 Indices of *Hermissenda crassicornis* nudibranch predation on six test food organisms

Food organism	Nudibranchs consuming (%)	Feeding time (%)	Top preference (% of nudibranchs)
A. labiata polyps	52.9	18.4 ± 35.8	17.6
Obelia geniculata hydroids	58.8	6.7 ± 26.1	11.8
Distaplia occidentalis tunicates	64.7	56.2 ± 42.9	52.9
Anthopleura elegantissima sea anemones	35.3	18.3 ± 38.1	17.6
Bugula sp. bryozoans	17.6	0.2 ± 1.4	0
Halichondria bowerbanki sponges	0	0	0

Table 2 Results of log likelihood *G* preference tests for all *Hermissenda crassicornis* nudibranchs that showed positive preference for the polyps of *A. labiata*

Conditioning prey type	Wet weight (g)	Feeding time on polyps (%)	Standard deviate	*P* value
Distaplia occidentalis tunicates	2.23	22.4	2.997	0.003
A. labiata polyps	1.53	83.9	18.382	<0.001
A. labiata polyps	1.48	16.4	2.449	0.014
Anthopleura elegantissima anemone	0.892	85.7	22.553	<0.001
Halichondria bowerbanki sponges	0.373	34.5	5.498	<0.001
Obelia geniculata hydroids	0.285	99.1	133.386	<0.001

Standard deviates were used to measure the direction (+ or −) and strength of preference; large numbers indicate stronger preferences. Wet weights are included to display the range of nudibranch sizes showing positive preference to polyps. The variety of conditioning prey types illustrates the lack of conditioning effects

G_i preference value standard deviates for each food. Nudibranch size did not significantly affect preferences of any food choice (Table 3); H_{03} was not rejected. All sizes of nudibranchs, from the smallest (0.285 g) to the largest (2.230 g) tested, consumed *A. labiata* polyps.

Comparison of *H. crassicornis* feeding during daylight and nighttime showed that the nudibranchs spent the same amount of time eating in daylight (29.6 ± 13.0% of total time feeding) as at nighttime (33.1 ± 10.5% of total time feeding). No significant difference was found between daytime and nighttime preferences ($t_{16} = -0.112$, $P = 0.913$ for *A. labiata* polyps and $T = 429$, $N = 102$, $P = 0.172$ for all foods, Fig. 3). H_{04} was not rejected.

The potential for ingestive conditioning to affect the ingestive preferences of the *H. crassicornis* nudibranchs was tested. Although nudibranchs eating the three most-consumed foods (tunicates, polyps, and hydroids) appeared to show predation responses based on ingestive conditioning, only 6 of 17 (35.3%) of all nudibranchs exhibited a positive preference toward their conditioned food source. All three nudibranchs conditioned to *D. occidentalis* tunicates preferred it to all other food choices. Two of three nudibranchs conditioned to *A. labiata* polyps showed a positive preference for polyps, but polyps were the top preference for only one of them. One of three nudibranchs conditioned to *O. geniculata* hydroids showed a positive preference for the hydroid, but it was not its top preference (Fig. 4). The multidimensional non-parametric statistical program PRIMER analyzed similarity by proximity of like treatments on a two-dimensional plane. The absence of significant clusters with a goodness-of-fit stress level of 0.07 indicated that ingestive conditioning did not affect preference and H_{05} was not rejected.

Table 3 Probabilities that the size of the nudibranch *Hermissenda crassicornis* ($n = 17$) affected preferences for six food choices

Food organism	r^2	$F_{1,16}$	*P*
A. labiata polyps	0.175	3.393	0.084
Obelia geniculata hydroids	0.018	0.299	0.592
Distaplia occidentalis tunicates	0.023	0.381	0.546
Anthopleura elegantissima sea anemones	0.002	0.024	0.879
Bugula sp. bryozoans	<0.001	0.005	0.947
Halichondria bowerbanki sponges	0.033	0.544	0.471

Probabilities were determined with regressions between the wet weights (g) and the G_i preference value standard deviates for each food

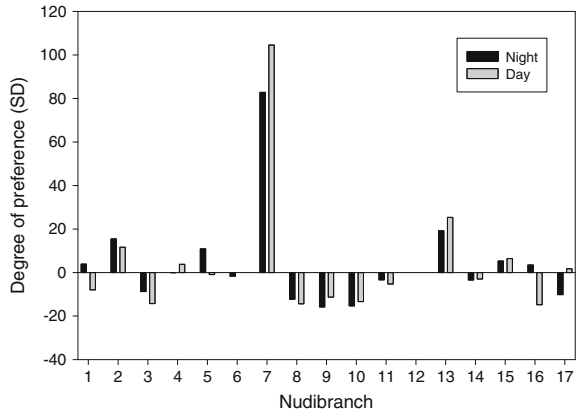

Fig. 3 Day versus night preferences of *Hermissenda crassicornis* nudibranchs for the polyps of *A. labiata.* The calculated standard deviates (SD) of *G* statistics for daytime and nighttime preferences are compared for 17 nudibranchs

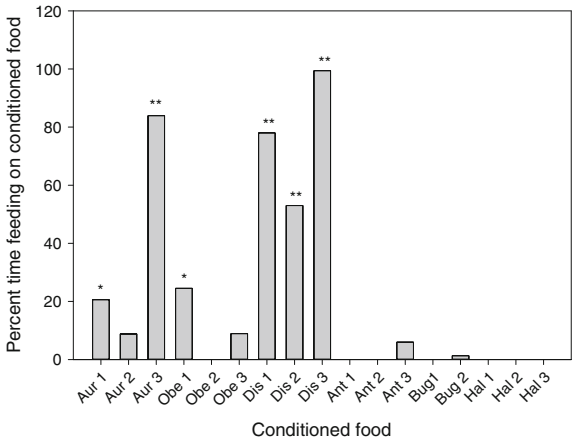

Fig. 4 Percent of total time individual *Hermissenda crassicornis* nudibranchs spent feeding on conditioned foods. Aur, *A. labiata* polyps; Obe, *Obelia geniculata* hydroids; Dis, *Distaplia occidentalis* tunicates; Ant, *Anthopleura elegantissima* sea anemones; Bug, *Bugula* sp. bryozoans; Hal, *Halichondria bowerbanki* sponges. Two or three nudibranchs were tested for each prey species. *Positive preference; **top preference

Chemotaxis: whole, living prey

Chemotaxis of *H. crassicornis* nudibranchs to living prey was observed during single-choice tests between prey items and seawater. Significant responses were observed for *A. labiata* polyps ($\chi^2_7 = 8$, $P = 0.005$), *D. occidentalis* tunicates ($\chi^2_8 = 9$, $P = 0.003$), and *O. geniculata* hydroids ($\chi^2_6 = 7$, $P = 0.008$). The null hypothesis H_{06}, that no chemotaxis to living prey occurred, was rejected. By contrast, no responses were observed in tests using *A. elegantissima* sea anemones ($n = 8$). The seawater blank was not chosen during any trial. One nudibranch from *A. labiata* trials and one nudibranch from *O. geniculata* trials did not make a choice and these trials were excluded from analysis. Nudibranchs responded more quickly to *A. labiata* and *D. occidentalis* (within 5–10 min of prey introduction) than to *O. geniculata* (20–30 min).

Chemotaxis: polar and non-polar extracts

Preliminary single-choice tests using *H. crassicornis* showed that the nudibranch exhibited chemotaxis to the polar extracts of *A. labiata* polyps and *D. occidentalis* tunicates. Immediate responses to the polar extracts occurred in all trials ($n = 4$ for each extract) and H_{07} was rejected; however, no responses were observed toward the non-polar extracts ($n = 4$ for each extract). Therefore, the polar extracts of *A. labiata* and *D. occidentalis* were chosen for use in 2-choice chemotaxis experiments.

Two-choice tests showed a significant chemotactic preference of *H. crassicornis* for the polar extract of *A. labiata* polyps over that of *D. occidentalis* tunicates ($\chi^2_{10} = 7.36$, $P = 0.007$; Fig. 5). H_{08} was rejected. One nudibranch that had just finished laying an egg mass before the trial did not make a choice and was excluded from analysis.

Feeding potential

Feeding rates of *H. crassicornis* nudibranchs on *A. labiata* polyps were determined to assess their effect on polyp populations. Feeding data were $+1$ $\log_{10}$ transformed to include zero values in the analysis. The numbers of polyps consumed increased with the wet weights of the nudibranchs. The percentages of large (>3 mm) and small (<3 mm) polyps consumed both increased proportionally with the wet weight of the nudibranchs ($r^2 = 0.156$, $F_{1,34} = 6.08$, $P = 0.019$ and $r^2 = 0.124$, $F_{1,34} = 4.68$, $P = 0.038$, respectively; Fig. 6) and H_{09} was rejected. There was no significant difference between the slopes of the two regression lines ($F = 2.33$, $P = 0.132$), therefore H_{10} was not rejected. Results of the multiple stepwise major axis regression indicated that only nudibranch size significantly affected the total number of polyps consumed ($r^2 = 0.341$, $F_{3,34} = 5.334$, $P < 0.001$); therefore, polyp colony density (10–65 polyps cm^{-2};

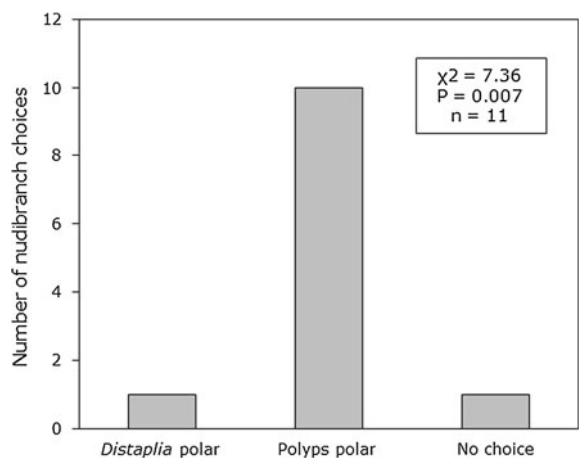

Fig. 5 Chemotactic choices made by *Hermissenda crassicornis* between the polar extracts of *Distaplia occidentalis* colonial tunicates and *A. labiata* polyps

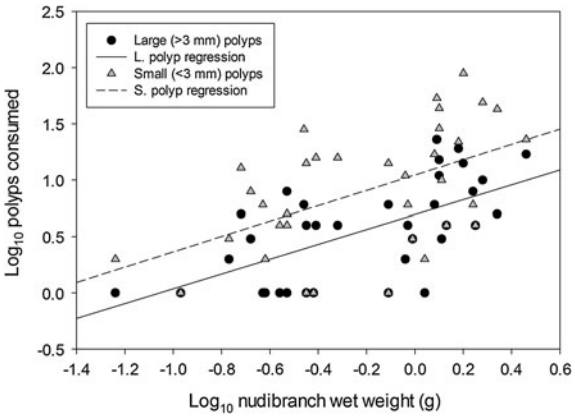

Fig. 6 Effect of the size of *Hermissenda crassicornis* nudibranchs on the numbers of large and small *A. labiata* polyps consumed. Data were +1 Log_{10} transformed to account for zeros in the data

$P = 0.621$) and polyp size class ($P = 0.498$) were removed from the regression, and H_{11}, H_{12} were not rejected. The greatest consumption was 102 polyps in 1 h by a nudibranch weighing 1.576 g. The mean rate ± standard error of consumption for large nudibranchs weighing more than 0.912 g (median) was 31.3 ± 28.9 polyps h^{-1} ($n = 17$), while the mean rate of consumption for nudibranchs weighing less than 0.912 g was 8.6 ± 9.7 polyps h^{-1} ($n = 18$). The mean rate of consumption for all nudibranchs was 19.6 ± 23.9 polyps h^{-1} ($n = 35$). The total number of polyps (p) that would be consumed in an hour by a *H. crassicornis* nudibranch could be approximated from its wet weight (ww) based on the following equation:

$$\log_{10}(p) = 1.337 + (1.347 * \log_{10}(\mathrm{ww})).$$

Predation on *A. labiata* polyps by other nudibranchs

Six species of nudibranchs, in addition to *H. crassicornis*, were tested for predation on *A. labiata* polyps in the laboratory. Four of the species consumed polyps (Table 4), but five arminid nudibranchs (*Janolus fuscus* O'Donohue, 1924) collected in March, April, and September and two nudibranchs in each of the aeolid species, *Dirona albolineata* MacFarland, 1905 (March and August) and *Dirona aurantia* Hurst, 1966 (March), did not. Nudibranchs were observed near or on the *A. labiata* colony during the spring, summer, and autumn when the colony was most actively adding individuals through budding and possible planula recruitment (Purcell et al., 2009). No nudibranchs were observed during the winter. Few other nudibranch species are known to be predators of scyphozoan polyps (Table 4).

Discussion

Nudibranch preference for the polyps of *A. labiata*

Our results clearly demonstrate feeding preference by *Hermissenda crassicornis* nudibranchs for *A. labiata* polyps among several prey taxa in live prey choice and chemotaxis experiments. Thus, null hypotheses H_{01}, H_{02}, H_{06}, H_{07}, and H_{08} concerning choices were rejected. Preferences were unaffected by nudibranch size, day versus night, or ingestive conditioning; therefore, H_{03}, H_{04}, and H_{05} were not rejected.

The ingestive preferences of the nudibranch on *A. labiata* polyps and other foods differed somewhat in 2-choice and 6-choice tests. During the 2-choice tests, the nudibranchs greatly preferred *A. labiata* polyps over the three other food choices, including the colonial tunicate *Distaplia occidentalis*. The polyps were chosen first in ≥66% of the trials and were fed on longest (≥70% of total feeding time). In contrast, in the 6-choice tests the nudibranchs preferred *D. occidentalis* to all other food choices (58.8% of nudibranchs showed positive preference), and *A. labiata* polyps were the second-most-preferred food (~50% of the nudibranchs tested consumed polyps, but only 35.3% showed a positive preference for polyps). Apparently, the availability of additional food items and the longer foraging time during 6-choice testing influenced preferences for these two organisms. Alternatively, the preferences observed during 6-choice testing may have been related to the costs versus benefits of foraging on the dense tissues of the tunicate versus the more diffuse tissues of the other organisms. *H. crassicornis* has been shown to survive and grow well on a diet exclusively of tunicates (Harrigan & Alkon, 1978).

Results of chemotactic preference testing indicated that the *H. crassicornis* actively uses chemotaxis in determining prey choice and that the polar compounds extracted from *A. labiata* polyps were significantly preferred to those from *D. occidentalis* tunicates. Of interest in these experiments is the complete and

Table 4 Known nudibranch predators of scyphozoan polyps

Nudibranch species	Months observed	Number	Scyphozoan species	Reference
Dendronotacea				
Dendronotus dalli (Bergh, 1879)	Aug	1	*A. labiata*	This study
Dendronotus rufus (O'Donoghue, 1921)	Sep, Oct	3	*A. labiata*	Kozloff (1983) This study
Aeolidacea				
Flabellina fusca (Bergh, 1894)	Mar	12	*A. labiata*	This study
Hermissenda crassicornis	Mar, Aug, Sep	5	*A. labiata*	This study
Cratena pilata (Gould, 1870)			*Chrysaora quinquecirrha* (Desor, 1848)	Schultz & Cargo (1971)
Austraeolis catina (Marcus, 1962)			*Cassiopea* sp.	Clark & Goetzfried (1978)
Flabellina verrucosa (Sars, 1829) (as *Coryphella verrucosa*)	Oct–Nov		*A. aurita*	Hernroth & Gröndahl (1985a, b)
Dondice parguerensis (Brandon & Cutress, 1985)	Nov–Feb		*Cassiopea xamachana* (Forsskal), *C. frondosa*	Brandon & Cutress (1985)

definitive nature of the choices made. These results suggest that chemotaxis plays a strong role in nudibranch foraging behavior.

Also of interest in the chemotaxis results was the complete lack of response to the anemone, *Anthopleura elegantissima*, and to the non-polar extracts of *A. labiata* and *D. occidentalis*. Our results for polar and non-polar extracts are consistent with previous studies showing that many of the compounds that elicit chemoreception in marine organisms are polar (Croll, 1983; Purcell & Anderson, 1995). This may be due to their water-soluble nature, or the fact that polar compounds are generally metabolites such as proteins, carbohydrates, and amino acids (Croll, 1983; Christie, 1993). Studies have confirmed amino acids as feeding stimulants in other marine gastropods such as *Aplysia* sp., and they are thought to be stimulants for the snail, *Nassarius obsoletus* (Say, 1822) (reviewed in Croll, 1983). In contrast, many non-polar compounds are composed of lipids that are not water soluble (Christie, 1993).

The combined results of the prey choice experiments suggest that *A. labiata* polyps, along with *D. occidentalis* tunicates, are top prey choices of *H. crassicornis*. As they are both highly preferred, it is likely that the nudibranch preys upon the two food sources to fulfill different biological needs. While the tissues of the tunicate may be consumed to provide simple nourishment, the polyps are consumed, in part, to harvest nematocysts. Because aeolid nudibranchs utilize harvested nematocysts of their cnidarian prey in their own defense mechanisms, it is necessary for the nudibranchs to periodically replenish nematocysts to the cnidosacs (Martin, 2003).

The results of our prey choice experiments suggest that among cnidarian prey, *H. crassicornis* nudibranchs prefer feeding on small, soft-bodied (athecate), colonial cnidarians, such as scyphozoan polyps. Ingestive preference experiments showed that *A. labiata* polyps were preferred twice more than any other cnidarian food choice. In chemotaxis experiments, no chemotaxis was exhibited toward *A. elegantissima* anemones. Despite its generalist feeding habits on organisms from different phyla, *H. crassicornis* has distinct favorites within phyla. Other species of aeolid nudibranchs, such as *Aeolidia papillosa* (Linnaeus, 1761), specialize on one class of cnidarian prey; for example, *A. papillosa* eats sea anemones, such as *A. elegantissima* (Waters, 1973; Edmunds et al., 1974; Hall et al., 1984; Seavy & Muller-Parker, 2002). In addition, *H. crassicornis* fed exclusively on the soft tissue of hydroid polyps, but ignored the harder stalks when offered a choice (Avila et al., 1998). Small, soft-bodied, colonial cnidarians would provide the most cost-effective foraging for nudibranchs that include cnidarians in their diets.

Two sources of potential error were unavoidable in our nudibranch food preference experiments. First, ingestive conditioning may have occurred prior to capture of the nudibranchs. We tested for ingestive

conditioning, which was negligible for diets assigned after capture; however, the feeding habits of the nudibranchs pre-capture were unknown. The potential of larval stage conditioning also cannot be discounted. It would be preferable to start with laboratory-reared naive subjects. Second, although all food organisms used in testing appeared healthy, their health and attractiveness to the nudibranchs may have been compromised during <3 weeks in the seawater table. Unfortunately, analysis of how the duration of captivity affected preference was not possible.

Nudibranch feeding potential on the polyps of *A. labiata*

We assessed the potential for *H. crassicornis* nudibranchs to affect the population dynamics of *A. labiata* polyps. Data from laboratory feeding trials support previous findings that *H. crassicornis* can be a significant predator of *Aurelia* spp. polyps (Keen, 1991). Only one of the four null hypotheses tested (H_{09}) was rejected; the number of polyps consumed increased with nudibranch size, but were unaffected by polyp size or density. Large *H. crassicornis* (>0.912 g wet weight, $n = 17$) consumed a mean of 31.3 polyps h^{-1}, with a maximum of 102 polyps h^{-1}. Because *H. crassicornis* consumed prey for an average of 9 ± 7.2 h d^{-1}, the maximum feeding potential of the nudibranchs appears to be substantially greater than previously measured (120 polyps d^{-1}) for a $\sim$5.7 g nudibranch (Keen, 1991).

Polyp colony density and size may play significant roles in limiting predation pressure. In laboratory experiments, Keen (1991) found significantly greater effects of *H. crassicornis* predation on polyp mortality at low densities (2 polyps cm^{-2}) than at high densities (10 polyps cm^{-2}). Those results would give consumption rates by a $\sim$2.4 g nudibranch of 49.6 polyps d^{-1} at low polyp density but only 5.0 polyps d^{-1} at high polyp density. By contrast, our results indicated that polyp densities (10–65 polyps cm^{-2}) did not affect nudibranch consumption rates; however, we suspect that the small sizes of the polyp clusters on algal blades used in our experiment allowed nudibranchs access to the polyps without being stung. Field surveys by Keen (1991) on a large polyp colony where nudibranchs were present showed that 27% of areas with polyp patches <100 cm^2 had losses each month, but only 16% of areas with patches 100–1,000 cm^2 had losses. In our own field surveys, nudibranchs were observed only at the edges of the polyp colony or where the polyps were sparse.

The potential for nudibranch predation to control scyphozoan polyp populations may be underappreciated. Nudibranch predation may be important in controlling establishment and early growth of polyp colonies along with small, fringe populations of large colonies. During our experiments, we confirmed that four nudibranch species were predators of *A. labiata* polyps, two of which were new records of polyp predation. Because there are hundreds of aeolid and dendronotid nudibranch species that consume cnidarians, and hundreds of scyphozoan polyps and hydroid species that produce jellyfish, further studies of other nudibranch species and their feeding potentials are needed to better understand the potential of predation to control jellyfish blooms.

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