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Host specificity of four corallivorous *Phestilla* nudibranchs (Gastropoda: Opisthobranchia)

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ABSTRACT: Nudibranchs that exclusively eat scleractinian corals provide a rare opportunity to study specialist predation in the marine environment. To measure the diet breadth of 4 *Phestilla* species on Guam, we offered the nudibranchs different corals in choice and no-choice feeding assays. Larval preferences were determined by measuring the percent metamorphosis in response to different coral species. We compared the specificity of larval metamorphosis to adult feeding preferences. *Phestilla sibogae* ate a range of *Porites* species (Poritidae) in the field and would not eat other coral genera in the laboratory no-choice assays. Metamorphosis was approximately 90% in response to 4 *Porites* spp. *Phestilla minor* was found on *Porites lutea* and *Porites annae* in the field. It preferred *P. annae* over *Porites cylindrica* and *P.* (*Synaraea*) *rus* during the choice and no-choice assays. The highest rates of metamorphosis (approx. 80%) were in response to *P. lutea*, *P. annae*, and *P. cylindrica*. *Phestilla* sp. 1 is morphologically similar to *P. minor*, but it eats different *Porites* species. It preferred *P.* (*S.*) *rus*, but would eat *P. cylindrica* during the no-choice assays. The highest rate of metamorphosis (approx. 80%) was in response to *P.* (*S.*) *rus*. *Phestilla* sp. 2 is distinct from the other *Phestilla* species studied, as it is a specialist on corals in the genus *Goniopora* (Poritidae). It preferred *G. fruticosa* and also ate *G. minor* and *G. lobata* during the feeding assays. The highest rates of metamorphosis (approx. 60%) were in response to *G. fruticosa*, *G. minor*, and *G. lobata*. This study documents a range of diet breadth among *Phestilla* species. *Phestilla* spp. larvae could distinguish between coral species within a host genus and showed a tendency to have high metamorphosis on their preferred hosts, but they also metamorphosed in response to non-food coral species.

KEY WORDS: *Phestilla* · Host specialization · Coral predators · Larval metamorphosis

INTRODUCTION

The evolution of host specificity has intrigued ecologists for the last century (Berenbaum 1996). A narrow dietary breadth (defined as feeding on 1 family of plants for insects) requires the evolution of a suite of adaptations, which limits the resources a consumer can use to survive. Insects are well-studied in terms of their dietary breadth and the ecological factors thought to determine specialization (Futuyma & Moreno 1988). Predation, resource partitioning, and host-plant chemistry have been proposed as important factors favoring the close association between insects and their host plants (Bernays & Graham 1988, Schultz 1988).

In the marine environment there are fewer specialists, and these are typically associated with a smaller range of host species as compared to terrestrial ecosystems (Hay et al. 1990, Hay 1992, Hay & Steinberg 1992). Among the best examples of marine specialists are opisthobranch mollusks, including sacoglossans and nudibranchs. Over 80% of the sacoglossan gastropods are specialist herbivores (Hay 1992, Williams & Walker 1999). Nudibranchs in the genus *Phestilla* prey exclusively on scleractinian corals (Harris 1975, Rudman 1981). Adult *Phestilla sibogae* (= *Phestilla lugubris*, Rudman 1981) feed on *Porites compressa* (Poritidae) in Hawaii (Hadfield 1977) and on *Porites somaliensis* and *Phestilla australensis* in the Indian

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Ocean (Tanzania) (Rudman 1981). In Tanzania, *P. minor* was also found on *Porites somaliensis* and *P. australensis*. *Phestilla melanobrachia* feeds on multiple coral genera in the Dendrophyllidae throughout the Indo-Pacific (Harris 1975). In addition to these 3 described *Phestilla* species, 2 additional species are found feeding on *Porites* spp. (Poritidae) and *Goniopora* spp. (Poritidae) in Guam, a region of relatively high coral diversity (Randall 2003).

Phestilla species, like many marine gastropods, have planktonic larvae that settle and metamorphose in response to chemical cues from sessile prey organisms (Hadfield 1977, Lambert & Todd 1994, Krug & Manzi 1999, Trowbridge 2000). In Hawaii, a small (<500 MW), polar, water-soluble molecule released from *Porites compressa* is required for metamorphosis of *Phestilla sibogae* (Hadfield & Pennington 1990). Without this chemical cue, *P. sibogae* will not metamorphose from a planktonic veliger to a juvenile slug. This obligate relationship between *Phestilla* spp. and their coral hosts provides an opportunity to study dietary breadth of these nudibranchs in terms of adult and larval specificity.

In the present study, we examined the host specificity of 4 species of *Phestilla* found on Guam. We determined whether adult feeding choice and larval metamorphosis correspond to preferred prey. Three aspects of specificity were measured: (1) adult distributions on different species of corals in the field, (2) adult consumption of different corals, and (3) larval metamorphosis in response to different corals. In addition to our studies with *P. sibogae* and *P. minor*, we report specificity data for 2 additional species of *Phestilla* that are currently being described (B. Rudman pers. comm.).

MATERIALS AND METHODS

Species studied. *Phestilla sibogae* is an aeolid nudibranch described by Bergh in 1905. This species was synonymized under the name *P. lugubris* by Rudman (1981). However, there is evidence that there are 2 closely related species of *Phestilla* in the eastern tropical Pacific as well as 2 available names, *P. sibogae* and *P. lugubris* (M. Hadfield pers. comm.). We use the name *P. sibogae* to be consistent with the last 25 yr of published research on this species. This species grows to a length of approximately 30 mm and is characterized by cerata covered with irregular nodules ending in a swollen rounded tip (Rudman 1981). The color of the cerata is variable depending on coral host species. *P. sibogae* lays a spiral white egg ribbon with lecithotrophic veliger larvae that are competent for metamorphosis 4 d after hatching (=9 d after fertilization) (Miller & Hadfield 1986). *P. sibogae* is widely distributed throughout the Indo-Pacific (Harris 1975, Rudman 1981).

Phestilla minor (Rudman 1981) can reach a length of 7 mm and has cerata with a swollen distal tip and 1 swollen collar region below this (Rudman 1981). This species has been recorded from Tanzania, Australia, and Hawaii (Rudman 1981). *P. minor* has an average of 44.1 ± 4.59 (mean ± SE, n = 18) eggs in each oval egg mass that are either straight or curved in the shape of a semicircle. The larvae are lecithotrophic and are competent to metamorphose immediately after hatching (5 to 6 d post-fertilization) (S.S. unpubl. data).

Phestilla sp. 1 resembles *P. minor*, but it has morphological characteristics that may be an indication of sibling speciation. *Phestilla* sp. 1 reaches a maximum length of 5 mm and has cerata with 1 swollen region below a tapering distal tip. It produces 24.4 ± 1.27 (mean ± SE, n = 18) eggs per oval egg mass, and has lecithotrophic larvae with immediate metamorphic competence after hatching (see 'Results').

Phestilla sp. 2 is similar in size and morphology to *P. sibogae* and reaches a maximum length of 30 mm. It has smooth cerata that taper and end in a distal swollen bulb. *Phestilla* sp. 2 has a yellow egg ribbon which is layed in a spiral. Its lecithotrophic larvae are competent for metamorphosis after a 4 d larval stage (9 d post-fertilization) (R.R.-W. unpubl. data). This species has been briefly mentioned as a specialist on corals in the genus *Goniopora*, and has been observed in Singapore and Papua New Guinea (Robertson 1970, Gosliner 1992, Gosliner et al. 1996).

Field surveys. Field surveys were conducted using SCUBA or snorkeling at a total of 29 sites on Guam (13° N, 144° E), from 18 January to 5 October 2001. More sites were searched on the western side of the island, because rough seas prevail on the eastern side during most of the year. Field surveys were also conducted at 8 sites in the Republic of Palau (7° N, 133° E), from 1 to 10 August 2002. Habitats searched included the reef flat and the fore-reef slope from 0 to 20 m.

To minimize damage to corals, only fragments and small loose colonies of corals were examined for nudibranchs, which limited the ability to search large coral heads. Corals were turned over and visually searched for adult *Phestilla*. No attempt was made to quantify the population densities of nudibranchs, since only small coral colonies were searched and small juvenile nudibranchs could not be seen. At each location, the species of *Phestilla* and the coral it was found on were recorded. If a coral species was unknown, a small sample was brought back to the laboratory for identification. Coral voucher specimens are kept at the University of Guam Marine Laboratory.

Adult feeding assays. Adult nudibranchs were raised in laboratory aquaria on host corals. Larvae were raised to metamorphic competence (see below), and were then placed in 10.8 l plastic containers with their host coral in aerated standing seawater. To ensure the same feeding history of all *Phestilla sibogae* used for assays, adults were raised on *Porites* (*Synaraea*) *rus*. *Phestilla minor* and *Phestilla* sp. 1 were brought from the field on fragments of *Porites annae* and *P.* (*S.*) *rus*, respectively. Due to the rarity of *Phestilla* sp. 2, it was also raised in the laboratory, on *Goniopora fruticosa*. Water was changed in each container every 3 d until juvenile *Phestilla* spp. were observed. The nudibranchs were then moved to flow-through seawater containers and allowed to feed until they reached an adult size.

The dietary preference of adult *Phestilla* spp. was tested using choice assays in laboratory aquaria. The assays were run for 72 h, because the nudibranchs would begin to die after 72 h without feeding. Individual adult *Phestilla* spp. were maintained in 600 ml plastic containers with flow-through seawater and offered fragments (2 to 6 cm long) of 2 different species of coral. Coral fragments were checked for feeding scars, and the cumulative number of polyps eaten was recorded every 24 h. Containers with the same size and species of corals without nudibranch predators were used to control for autogenous changes in the number of polyps. Separate assays were run in which *Phestilla sibogae* was offered a choice of *Porites cylindrica* versus *Turbinaria reniformis*, and *P. cylindrica* versus *Goniopora fruticosa*. *Phestilla minor* was offered *P. cylindrica* versus *Porites annae*, and *Porites* (*S.*) *rus* versus *P. annae*. *Phestilla* sp. 1 was offered a choice between *P.* (*S.*) *rus* versus *P. annae*, and *P. cylindrica* versus *P.* (*S.*) *rus*. *Phestilla* sp. 2 was offered *P. cylindrica* versus *G. fruticosa*, and *G. fruticosa* versus *G. minor*. These coral species were chosen to determine if there was an overlap of preferred prey among each *Phestilla* species. Coral fragments and individual nudibranchs were only used once in feeding trials.

No-choice assays were conducted to determine if *Phestilla* species would eat other corals in the absence of preferred hosts. The assays were set up as described for the choice assays except that each nudibranch was maintained with 1 coral fragment. Each species of *Phestilla* was offered the same coral species that were used during the choice assays. *Phestilla* sp. 2 was also offered *Goniopora lobata* and *G. eclipsensis* during the no-choice assays. The cumulative number of coral polyps consumed was recorded every 24 h for 72 h. All feeding values are reported as cumulative means ±1 standard error (SE).

Larval metamorphosis assays. Adults were maintained in the laboratory to provide a source of eggs. Adult nudibranchs and live coral fragments were collected from various locations around Guam and maintained in flow-through seawater outdoor aquaria. A total of 5 to 20 adult nudibranchs were supplied with host corals that served as food as well as a substrate for egg deposition. Approximately 10 egg masses were collected from the corals 5 to 6 d after deposition, checked microscopically for complete development (as indicated by fully formed, moving veligers), and artificially hatched in petri dishes by ripping the egg cases with a pair of forceps.

Larvae were raised to metamorphic competence. Newly hatched veligers from different egg masses were combined and transferred from the petri dishes to 2–4 larval chambers constructed as described by Miller & Hadfield (1986). These PVC chambers were placed in 1 l plastic beakers and filled with antibiotic-spiked seawater (90 µg penicillin G ml^{-1}, and 75 µg streptomycin sulfate ml^{-1}). Antibiotic-spiked seawater was changed daily, and beakers were placed in a running seawater bath to maintain ambient ocean temperature (approx. 28 to 32°C). The larvae were not fed in the chambers. The length of time in the larval chambers varied from 1 d for *Phestilla minor* to 4 d for *P. sibogae* and *Phestilla* sp. 2. In separate assays, larval metamorphosis was tested after 0, 1, and 2 d for *Phestilla* sp. 1.

Larval metamorphosis was tested in response to different coral species. For each metamorphosis assay, 10 to 50 larvae were transferred to individual 5 ml wells (*Phestilla minor* and *Phestilla* sp. 1) or 9 ml wells (*P. sibogae* and *Phestilla* sp. 2) of Costar® media culture well-plates (nos. 3513 and 3516). Many assays had a low number of replicates (3 to 5) due to the limited number of larvae available from each culture. Treatments of 1 coral fragment in 3 ml of 0.2 µm filtered seawater (FSW) or the control (only FSW) were added to the individual wells with the larvae. Corals were broken into 1- to 2-cm pieces at least 24 h prior to the assays. The third assay with *Phestilla* sp. 2 used larger 3-cm coral fragments in 100 ml glass beakers, which were filled with FSW to a total volume of 50 ml. Coral species were selected for these assays if they were eaten by the adult *Phestilla* spp. or found in the same habitat as host coral species.

The proportion of larval metamorphosis was scored for each treatment. The culture plates were checked for the proportion of larvae that had metamorphosed after 24 h for *Phestilla sibogae* and after 48 h for the 3 other species. Larvae of *P. sibogae* lose their shells as they metamorphose from the veliger stage into a juvenile slug within 24 h of exposure to the chemical cue produced by *Porites* spp. (Hadfield 1977). The other 3 species had the highest percentage of metamorphosis after 48 h of exposure to host corals. Although small

juvenile slugs were observed in the wells, it was more precise to count the empty shells than the transparent juveniles. Percent metamorphosis was calculated as the number of empty shells/total number of larvae × 100. Larvae not metamorphosed after 48 h were considered unaffected by the coral treatments.

The proportion of metamorphosis was analyzed for significant differences using ANOVA followed by a Tukey (HSD) post-hoc test. If data did not meet the assumptions of ANOVA, they were arcsine-transformed, or the non-parametric Kruskal-Wallis test was used followed by a procedure comparing mean ranks. All figures show untransformed data. All analyses were conducted using Statistix 7 (Analytical Software).

RESULTS

Field surveys

In the field on Guam, *Phestilla sibogae* was found on 6 species of *Porites* (Table 1). It was most commonly found on *Porites lutea* and *P.* (*S.*) *rus* in reef-flat and fore-reef-slope habitats on both sides of Guam (Fig. 1). *Phestilla minor* was found on 2 species of coral, *Porites annae* and *P. lutea*, on both sides of Guam. *Phestilla* sp. 1 was found on *Porites cylindrica* or *P.* (*S.*) *rus* on reef flats and fore-reef slopes on both sides of Guam. *Phestilla* sp. 2 was only found on *Goniopora fruticosa* at 2 locations on the fore-reef slope on the eastern side of Guam, even though this coral is found on both sides of the island. *Phestilla sibogae*, *P. minor*, and *Phestilla* sp. 1 were found sympatrically at 5 reefs that are dominated by multiple species of *Porites*. *P. minor* and *Phestilla* sp. 1 were consistently found on distinct *Porites* species (Table 1). *Phestilla* species were not observed at 12 sites that typically had low coral cover or few host species (Fig. 1).

On Palau, *Phestilla sibogae* was found on 4 species of *Porites* (Table 1). *Phestilla minor* was only found on *Porites lutea*; however, *Porites annae* was rarely encountered. *Phestilla* sp. 1 was found on both *Porites cylindrica* and *P.* (*S.*) *rus*. *Phestilla* sp. 2 was only found on *Goniopora djiboutiensis*, but *G. fruticosa* was never observed.

Adult feeding assays

During the laboratory choice experiments, *Phestilla sibogae* only consumed *Porites cylindrica* (Fig. 2a,b). During the no-choice assays, *P. sibogae* ate *P. cylindrica* and a small amount of *Turbinaria reniformis* (Fig. 3a–c). No coral polyp mortality was observed in the controls, except for 5.6 ± 3.4 (mean ± SE) *P. cylindrica* polyps dead in the no-choice assay, after 72 h.

Phestilla minor strongly preferred *Porites annae* in both choice assays (Fig. 2c,d). During the choice assays, in only 1 replicate, 4 *Porites cylindrica* and 2 *Porites* (*S.*) *rus* polyps were consumed. Only *P. annae* was eaten during the no-choice assays (Fig. 3–f). No coral polyps were found dead in the control containers.

Phestilla sp. 1 only ate *Porites* (*S.*) *rus* during the choice assays (Fig. 2e,f). During the no-choice assay

Table 1. *Phestilla* spp. Summary of host preferences for *Phestilla* nudibranchs (G: Guam; P: Palau)

	Coral species eaten in the field	Coral species eaten in the laboratory	Larval metamorphosis, preferred corals[a]
Phestilla sibogae	*Porites annae* (G, P) *P. australiensis* (G) *P. cylindrica* (G, P) *P. lutea* (G, P) *P.* (*S.*) *rus* (G, P) *P. vaughni* (G)	*Porites cylindrica*	*Porites annae* *P. cylindrica* *P. lutea* *P.* (*S.*) *rus*
Phestilla minor	*Porites annae* (G) *P. lutea* (G, P)	*Porites annae*	*Porites annae* *P. cylindrica* *P. lutea* *Turbinaria reniformis*
Phestilla sp. 1	*Porites cylindrica* (G, P) *P.* (*S.*) *rus* (G, P)	*Porites cylindrica* *Porites* (*S.*) *rus*	*Porites* (*S.*) *rus* *P. annae*
Phestilla sp. 2	*Goniopora fruticosa* (G) *G. djiboutiensis* (P)	*Goniopora fruticosa* *G. lobata* *G. minor*	*Goniopora fruticosa* *G. lobata* *G. minor* *Porites cylindrica*

[a]Preferred corals were selected if their percentage metamorphosis was significantly different from the control (filtered seawater), as shown in Fig. 4

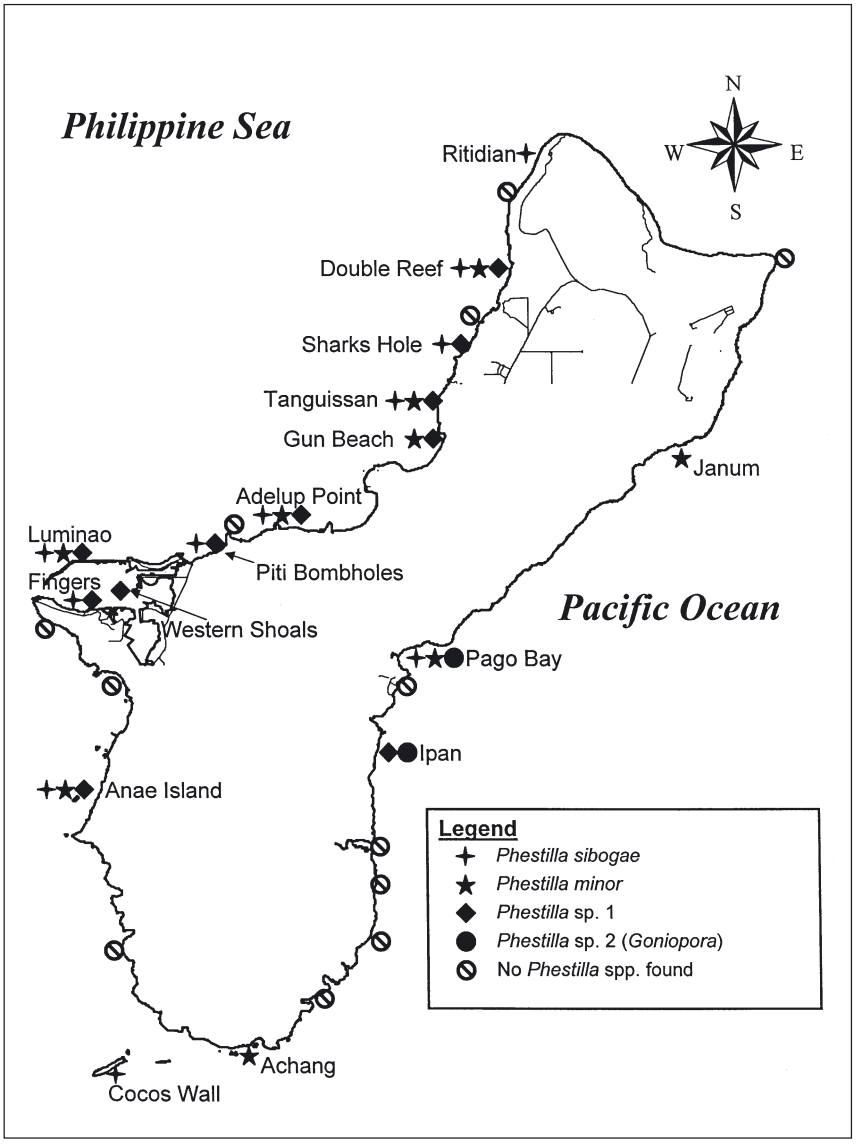

Fig. 1. *Phestilla* spp. Distribution of 4 *Phestilla* species on Guam. Symbols indicate locations where at least 1 adult *Phestilla* sp. was observed. At each location small coral colonies and fragments were inspected for *Phestilla* spp. Guam was searched between 18 January and 5 October 2001

Phestilla sp. 1 ate approximately 9 *P.* (*S.*) *rus* polyps and 4 *P. cylindrica* polyps after 72 h (Fig. 3g–i). There was no consumption of *P. annae*. There was no coral polyp mortality in the controls.

Phestilla sp. 2 ate *Goniopora fruticosa* and *G. minor*, but not *Porites cylindrica* during the choice assays (Fig. 2g,h). It consumed *G. fruticosa*, *G. minor*, and *G. lobata* polyps, but would not feed on *P. cylindrica* or *Goniopora eclipsensis* during the no-choice assays (Fig. 3j–n). In the controls during the no-choice assays 1.8 ± 0.8 *G. fruticosa* and 3.4 ± 3.4 (n = 5) *P. cylindrica* polyps were dead after 72 h. There was no mortality for the other coral controls.

Larval metamorphosis assays

Phestilla sibogae had >90% metamorphosis in response to *Porites annae* and *P. cylindrica* (Kruskal-Wallis, $p < 0.001$) (Fig. 4a); however, means were not significantly different from those of *Turbinaria reniformis* and *Goniopora fruticosa*. In the second assay, all 4 *Porites* species induced high percentages of metamorphosis (Kruskal-Wallis, $p < 0.001$) (Fig. 4b). In both assays there was 40 to 60% metamorphosis in response to *T. reniformis*, which was not significantly different from the filtered seawater (FSW) control in either assay (Fig. 4a,b).

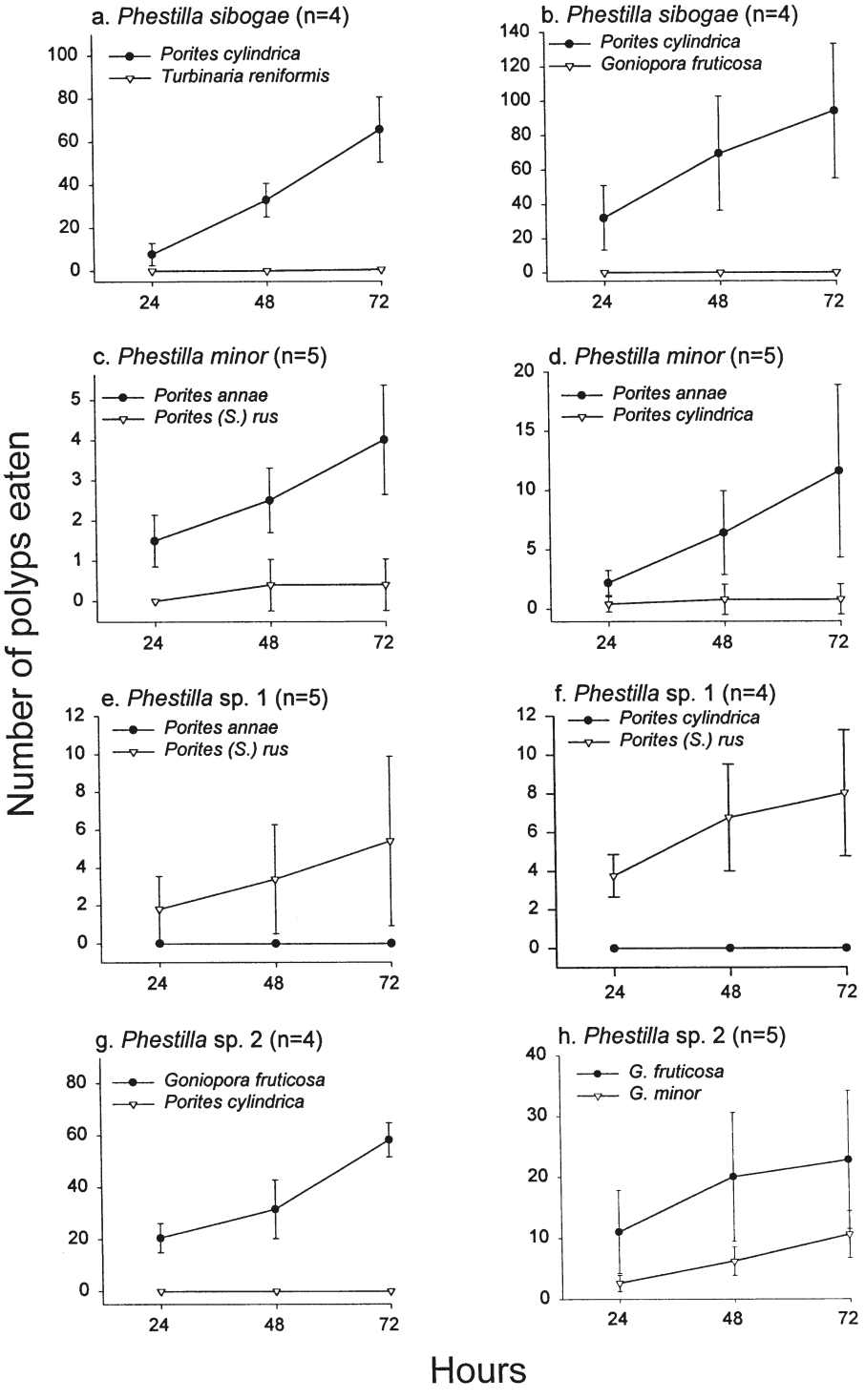

Fig. 2. *Phestilla* spp. Feeding choices of individual *Phestilla* spp. adults when offered both species of corals simultaneously. Graphs show the mean cumulative number of coral polyps eaten every 24 h for 72 h. Error bars are ±1 SE. No mortality in control corals was observed; these data are not shown for clarity. Note different scales on individual graphs

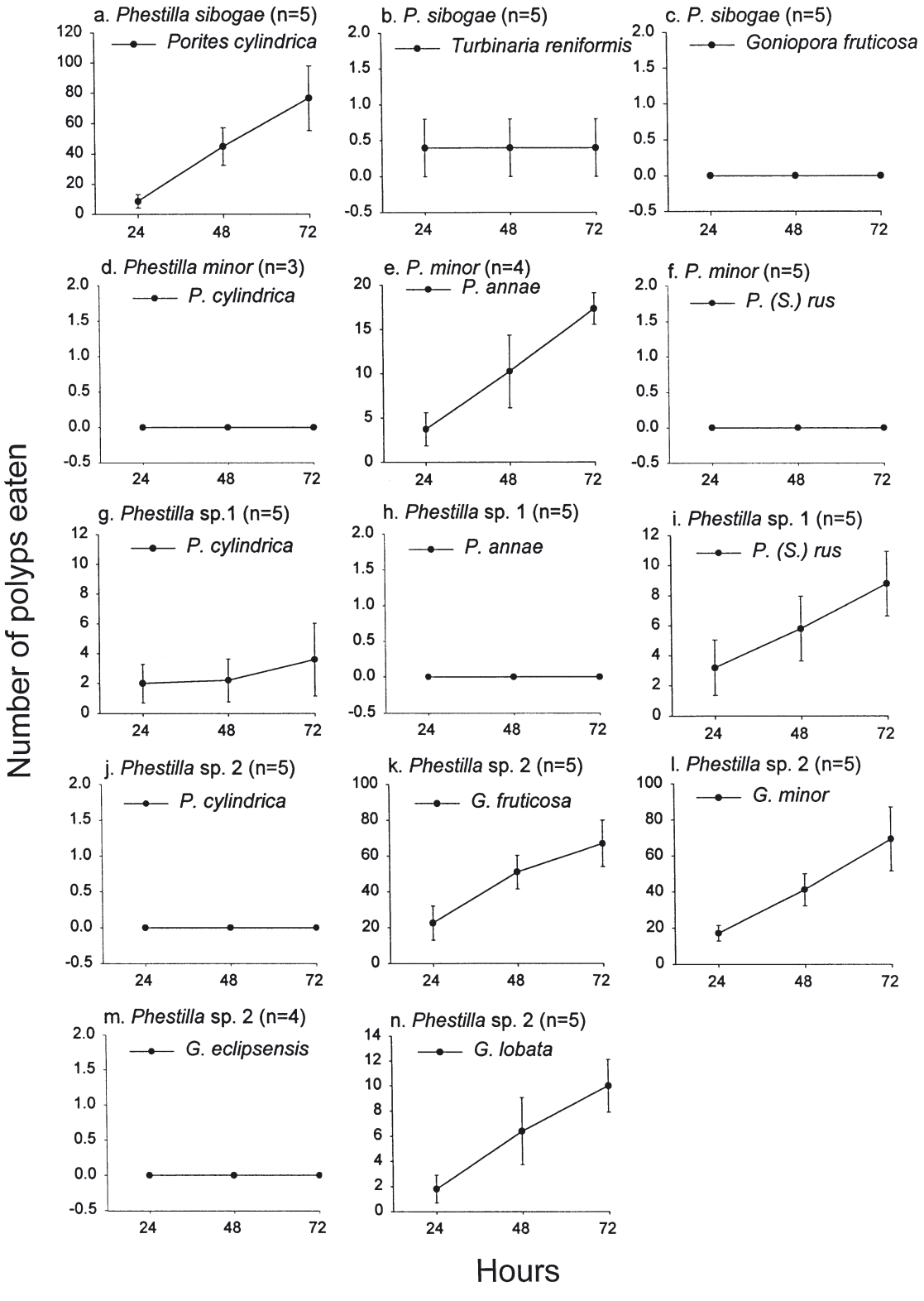

Fig. 3. *Phestilla* spp. Feeding of *Phestilla* spp. adults when no choices were offered. Graphs are the mean cumulative number of coral polyps eaten every 24 h for 72 h. Error bars are ±1 SE. Polyp mortality in controls is not shown (see 'Results'). Note different scales on individual graphs

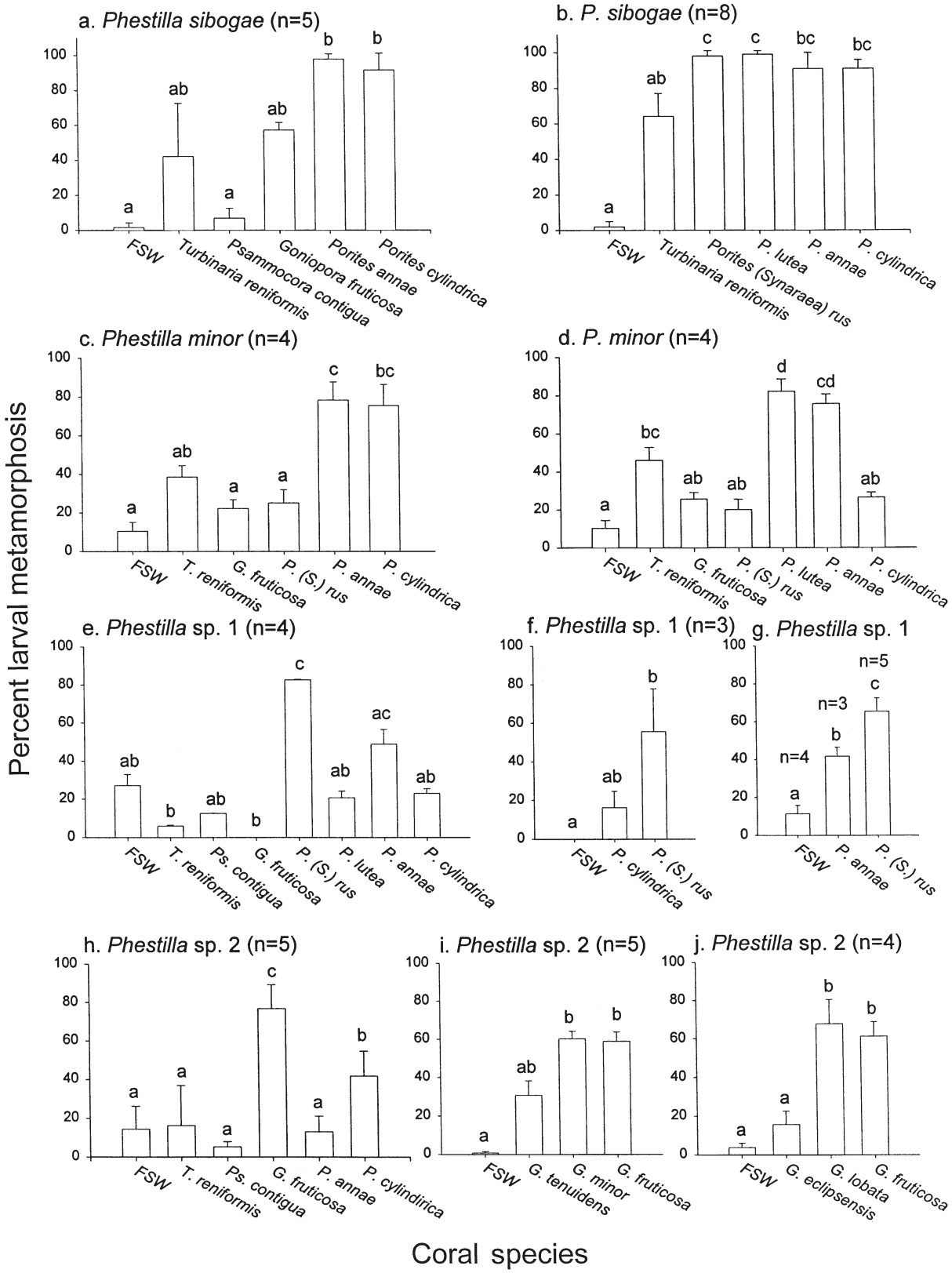

Fig. 4. *Phestilla* spp. Larval metamorphosis in response to live coral fragments in 4 *Phestilla* species. Individual graphs are separate assays with different larval cultures. Bars represent mean percentage metamorphosis with +1 SE. Controls are 0.2-µm-filtered seawater (FSW). Larval age varied for each species; 4 d after hatching for *P. sibogae* and *Phestilla* sp. 2, 1 d for *P. minor*, and 0, 1, and 2 d for *Phestilla* sp. 1 in f, e, and g, respectively. Mean percentage of metamorphosis was measured after 24 h for *P. sibogae* or 48 h for *P. minor*, *Phestilla* sp. 1, and *Phestilla* sp. 2. Significant groupings are indicated by the letters above bars, analyses are by 1-way ANOVA or Kruskal-Wallis tests

Phestilla minor had 80% metamorphosis in response to *Porites annae* and *P. cylindrica* (Fig. 4c). Metamorphosis on *Porites* (*S.*) *rus* and *Goniopora fruticosa* was less than that on *P. annae* and *P. cylindrica* (ANOVA, $p < 0.001$). Metamorphosis on *P.* (*S.*) *rus*, *T. reniformis*, and *G. fruticosa* was not significantly different from the FSW control. Metamorphosis on *P. cylindrica* was as high as on *P. annae* in the first assay, but not the second (Fig. 4c,d). In the second assay *Phestilla minor* had greater metamorphosis in response to *Porites lutea* and *P. annae* than to *P.* (*S.*) *rus* and *P. cylindrica* (ANOVA, $p < 0.001$). There was approximately 40% metamorphosis in response to *T. reniformis*, which was also significantly different from the FSW control. In both assays about 10% of the larvae metamorphosed in the FSW treatment (Fig. 4c,d).

In all 3 assays, *Phestilla* sp. 1 had the highest metamorphosis in response to *Porites* (*S.*) *rus* (ANOVA, $p < 0.001$) (Fig. 4e–g). The percentage of metamorphosis on *P.* (*S.*) *rus* was consistently higher than that on *P. annae*, and was significantly greater in the third assay (ANOVA, $p < 0.001$) (Fig. 4g). Metamorphosis in response to *P.* (*S.*) *rus* was significantly greater than that on *P. cylindrica* in the first assay (Fig. 4e), but not in the second (Kruskal-Walllis, $p = 0.003$) (Fig. 4f). No change in the rates of metamorphosis 0, 1, or 2 d after hatching were observed for *Phestilla* sp. 1 (Fig. 4f,e, and g respectively). Metamorphosis on *Porites lutea*, *P. cylindrica*, *Goniopora fruticosa*, *Turbinaria reniformis*, and *Psammacora contigua* was not different from the FSW controls in any of the assays (Fig. 4e–g). Rates of spontaneous metamorphosis in the FSW controls were relatively high in some assays (Fig. 4e).

Metamorphosis in *Phestilla* sp. 2 was greatest in response to *Goniopora fruticosa*, but there was also approximately 40% metamorphosis to *Porites cylindrica* (ANOVA, $p < 0.001$) (Fig. 4h). The percentages of metamorphosis on *Turbinaria reniformis*, *Psammacora contigua*, and *Porites annae* were not different from the FSW control. In the second assay (Fig. 4i) there was high metamorphosis on *G. minor* and *G. fruticosa*. The congener *G. tenuidens* induced approximately 30% metamorphosis, but was not different from the FSW control (Kruskal-Wallis, $p < 0.001$). During the third assay, conducted in 100 ml beakers, there was approximately 60% metamorphosis in response to *G. lobata* and *G. fruticosa* (ANOVA, $p < 0.001$) (Fig. 4j). *G. eclipsensis* induced only approximately 16% metamorphosis, which was not significantly different from the FSW control.

DISCUSSION

With over 400 species (from 21 families) of corals to choose from on Guam, larval settlement for *Phestilla* spp. is an important process that determines host availability for juveniles and adults. Survival of these nudibranchs is dependent upon finding the specific host corals that induce metamorphosis. With few exceptions (mentioned below), larval metamorphosis corresponded to adult feeding preferences (Table 1). *Phestilla sibogae* only ate *Porites* spp. (Poritidae) in the laboratory and the field, and had high rates of larval metamorphosis in response to all the *Porites* species tested. The chemical cue necessary for *P. sibogae* metamorphosis is produced by at least 4 species of *Porites* from Guam and *Porites compressa* on Hawaii. There was variable, but always less metamorphosis on *Turbinaria reniformis* (Dendrophyllidae) and *Goniopora fruticosa* (Poritidae). These 2 species are not eaten by *P. sibogae*, but *G. fruticosa* is preferred by *Phestilla* sp. 2. Our observations are consistent with previous records of *P. sibogae* eating and settling in response to *Porites* species (Harris 1973, Hadfield 1977, Rudman 1981). Due to the high diversity of coral species on Guam and Palau we are able to broaden the documented range of corals eaten by *P. sibogae* from the 3 *Porites* species previously recorded (Hadfield 1977, Rudman 1981) to at least 8 species.

In the field *Phestilla minor* was only found on *Porites annae* and *P. lutea*. In the laboratory this species preferred *P. annae*, and would not eat *P. cylindrica* and *P.* (*S.*) *rus*. Larval metamorphosis was highest in response to *P. annae* and *P. lutea*. *P. minor* had variable metamorphosis in response to *P. cylindrica* and *Turbinaria reniformis*, which may be a result of natural variation in the rates of metamorphosis among different batches of larvae (Wieczorek & Todd 1998). There was also some spontaneous metamorphosis in the seawater controls (Fig. 4c,d: Shjegstad 2002). This has not been previously reported for *P. minor*, but is known to occur in some opisthobranchs (Gibson & Chia 1995, Krug 2001). *P. minor* was found on *Porites compressa* in Hawaii and on *P. somaliensis* and *P. australensis* in Tanzania (Rudman 1981). New records of this species from different regions may broaden the number of preferred hosts; however, we observed similar levels of specificity on both Guam and Palau.

Phestilla sp. 1 is morphologically similar to *P. minor*, but it feeds on different coral species. *Phestilla* sp. 1 was found on *Porites* (*S.*) *rus* and *P. cylindrica* on both Guam and Palau, but preferred *P.* (*S.*) *rus* in the laboratory feeding assays. The highest metamorphosis was also on *P.* (*S.*) *rus*, but this was not consistently different from *P. annae*, which it would not eat. There was lower metamorphosis in response to *P. cylindrica* and *P. lutea*, which were not different from the FSW controls. *Phestilla* sp. 1 was found on *P. cylindrica* in the field, but did not prefer it in the laboratory assays. This sug-

gests that *P. cylindrica* is not a preferred host, but this may be an indication of population level preferences, or conditioning, as the *Phestilla* sp. 1 in our assays were all raised on *P.* (*S.*) *rus*. After being raised on 1 host the opisthobranch might be physiologically acclimated, making it difficult to switch hosts during the laboratory assays (Hall et al. 1982, Trowbridge 1991). The distinct host utilization observed between *P. minor* and *Phestilla* sp. 1 is a characteristic of sibling species in both marine and terrestrial ecosystems (Feder & Bush 1989, Knowlton 1993, 2000, Funk et al. 1995, Leebens-Mack et al. 1998). The short larval competence period for *Phestilla* sp. 1 and *P. minor* would imply less dispersal, potentially leading to resource partitioning of distinct *Porites* species.

Phestilla sp. 2 ate and metamorphosed on some of the *Goniopora* species, but not *G. eclipsensis*. It preferred *G. fruticosa* during the choice assays, but was observed by Gosliner et al. (1996) in Papua New Guinea on other *Goniopora* species. During the no-choice assays there was a similar amount of *G. fruticosa* and *G. minor* eaten, but less *G. lobata*; however, *G. lobata* has large polyps that probably provide more biomass than polyps of either *G. fruticosa* or *G. minor*. Why *Phestilla* sp. 2 did not eat all of the *Goniopora* species is unknown; however, rates of larval metamorphosis consistently matched adult feeding behavior.

The specificity of *Phestilla melanobrachia* on corals in the Dendrophyllidae was well studied by Harris (1973, 1975). *P. melanobrachia* has a wide dietary breadth of multiple genera in the Dendrophyllidae. *P. minor* and *Phestilla* sp. 1 ate 1 or 2 *Porites* species. *P. sibogae* eats at least 8 *Porites* species, indicating a broader dietary breadth than that of *P. minor* and *Phestilla* sp. 1. Adult dietary breadth of opisthobranchs is often thought to be specific to 1 genus or even 1 species of prey; however, field observations do not necessarily reveal their potential dietary breadth (Williams & Walker 1999, Ginsburg & Paul 2001). Our field observations of *Phestilla* sp. 2 on Guam suggested that it only ate *Goniopora fruticosa*. We found that it would eat 2 other *Goniopora* species in the laboratory, which is potentially important for survival in habitats with little or no *G. fruticosa*, such as the areas searched in Palau.

Many marine larvae use chemotaxis to locate the appropriate host organisms (Pawlik 1992, Zimmer-Faust & Tamburri 1994, Morse et al. 1996, Williamson et al. 2000, Browne & Zimmer 2001). *Phestilla sibogae* requires a chemical cue produced by *Porites compressa* for metamorphosis from a planktonic veliger to a benthic slug (Hadfield & Scheuer 1985, Hadfield & Pennington 1990). Our results found that metamorphosis in the laboratory did not always match feeding preferences. Larvae metamorphosed at high rates on preferred coral species, but sometimes also metamorphosed in response to non-food corals. For example, *Turbinaria reniformis* and *P. cylindrica* induced significant metamorphosis in multiple *Phestilla* species that would not eat them. This may provide a potential mechanism for host switching in a dynamic community (Trowbridge & Todd 2001); however, adult *Phestilla* from the field were not observed on these species, and our results may be an experimental artifact. Different species and genera of corals may have similar chemical cues or variable ratios of multiple cues, which can be distinguished by the larvae in the field. Unfortunately, laboratory assays expose larvae to high concentrations of the chemical cues that may induce unnatural metamorphosis (Zimmer & Butman 2000). This may explain why the larvae metamorphose in response to a broader range of corals than they consume.

The water-soluble settlement cue from *Porites compressa* that induces metamorphosis in *Phestilla sibogae* is well studied, but is not chemically described (Hadfield & Scheuer 1985, Hadfield & Pennington 1990). Other *Phestilla* spp. studied also respond to a water-soluble metamorphic inducers (R.R.-W. & S.S. unpubl. data). The specificity of adult *P. minor* and *Phestilla* sp. 1 to 1 or 2 coral species suggests that *Porites* spp. are producing distinctive and recognizable settlement cues. *Phestilla* sp. 2 also distinguishes among coral species in the same genus. Neural pathways are known to increase sensitivity to chemical cues in specific hosts for insects (Hay & Steinberg 1992, Bernays & Wcislo 1994), and are implicated in the ability of *P. sibogae* to recognize chemical cues in corals (Murphy & Hadfield 1997, Hadfield et al. 2000). To better understand the developmental biology and cellular process of metamorphosis in *Phestilla* spp., it is important to describe the chemical cues responsible for metamorphosis.

Host chemistry is an important ecological aspect of specialization for many terrestrial insects and marine invertebrates (Ehrlich & Murphy 1988, Hay et al. 1990, Hay 1992, Stachowicz & Hay 2000). For insects the chemical features of the host are selected by the mother, who locates an appropriate site for oviposition. For marine larvae, including *Phestilla* spp., host chemistry may serve as a cue for larval recruitment to the appropriate habitat. Many marine invertebrates rely on chemically defended hosts for refuge and as a source of deterrent secondary metabolites (Hay et al. 1990, Cimino & Sodano 1994, Becerro et al. 2001, Cruz-Rivera & Paul, in review). Predator avoidance, response to specific metamorphic inducers, and larval life-history together have probably influenced specialization in *Phestilla* nudibranchs.

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