Proceedings of the 6th International Coral Reef Symposium, Australia, 1988, Vol. 2

ENVIRONMENTAL CUES CONTROLLING SPAWNING IN TWO HAWAIIAN CORALS, MONTIPORA VERRUCOSA AND M. DILATATA

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ABSTRACT

The influences of experimental manipulation of lunar phase, seawater temperature, and day length on timing of spawning were investigated in two congeneric Hawaiian corals. Two to nine clones of each species were monitored for 93 days under each of the following treatments: 1) constant artificial "full moon", 2) shifted lunar phase (offset 14 days), 3) constant "new moon", 4) lowered ("winter") seawater temperature for one month, 5) shortened ("winter") day length, 6) controls (ambient summer seawater temperature, day length, and lunar phase). Control colonies of M. verrucosa spawned (1-3 spawnings/colony) between 2045 and 2230 on the nights of the new moon or the two nights following in June and July; M. dilatata colonies spawned (5-8 spawnings/colony) between 2030 and 2100 on or within nine nights after full moon in July and August, as well as one night after new moon in July. Colonies of both species in the constant full moon treatment spawned synchronously with controls. In the shifted moon treatment, all M. verrucosa and M. dilatata spawned on the same nights as controls for the first spawning cycles, but synchrony was disrupted (2-12 days off-cycle) in the second month. Only three out of seven M. verrucosa colonies in the constant new moon treatment spawned, in phase with controls in June and one week prior to new moon in August. M. dilatata colonies in this treatment retained synchrony at the July full moon, but spawned eight days out of phase in August. Decreased seawater temperature apparently precluded spawning in June for M. verrucosa and in July for M. dilatata. One M. verrucosa and both M. dilatata colonies spawned in phase with controls after seawater temperature was raised back to summer levels. In the short-day treatment, M. verrucosa colonies spawned on the same nights as controls, but 1.5-2 hours earlier. M. dilatata colonies spawned in experimental and control chambers about 1.5 hours after sunset. Temperature, lunar phase, and onset of darkness all act to control spawning periodicity in corals. The physiological mechanisms by which these environmental cues are perceived and translated have not yet been determined.

INTRODUCTION

Over 130 Great Barrier Reef coral species in eleven families have now been reported to participate in an annual mass spawning during the week following the full moon in the austral spring (Willis et al. 1985). Synchronous multi-specific spawning has also been reported to occur during fall months in Western Australian corals. In contrast, reports on Caribbean (Szmant 1986), Red Sea (Shlesinger and Loya 1985), and Hawaiian (Hunter unpubl.) corals indicate that, while most species observed spawn annually during fairly narrowly-defined periods, these periods are often non-overlapping among species. In some species, substantial variability in synchrony of spawning has now been documented both within populations and among populations in different geographic regions with spawnings occurring over more than one month, lunar phase, or time of day (Willis et al. 1985, Heyward et al 1988, Oliver et al. this volume, Simpson this volume, Hunter and Richmond unpubl.). Spawning patterns in the scleractinia may not be as constrained or constant as previously inferred.

Environmental cues that may allow or entrain spawning synchrony in corals are not well understood and have not been empirically determined for most species. Inferences that seawater temperature, tidal amplitude, lunar or diel cycles are spawning cues in species which broadcast gametes on an annual basis have been made from such evidence as the occurrence of spawnings either in spring when temperatures and day length are rising or in summer when they are maximal, split spawnings in some years in which full moon falls early within the reproductive season, or spawnings observed at a predictable time of day or night (Fadlallah 1983, Harriott 1983, Krupp 1983, Babcock 1984, Harrison et al. 1984, Heyward and Collins 1985, Shlesinger and Loya 1985, Wallace 1985, Willis et al. 1985, Babcock et al 1986, Chornesky and Peters 1987). Most studies which have addressed reproductive periodicity of corals are those in which timing of spawning is determined from the depletion of gametes from colonies sampled at various intervals and/or direct observation of colonies either in the field or in laboratory aquaria (Marshall and Stephenson 1933, Stimson 1978, Kojis and Quinn 1981ab, Babcock 1984, Harrison et al. 1984, Heyward and Collins 1985, Shlesinger and Loya 1985, Wallace 1985, Willis et al. 1985, Babcock et al. 1986, Szmant 1986). Jokiel et al. (1985) found that manipulation of lunar cues of corals held in laboratory microcosms caused a rapid loss or shift in planulation synchrony in Pocillopora damicornis, a species which normally produces planula on a monthly cycle. Babcock (1984) altered the light:dark cycle for Goniastrea aspera colonies held in the laboratory for several days and found that colonies under the offset photoperiod changed the hour at which they spawned gametes accordingly. The amount of natural variability and flexibility in timing of gamete release in response to manipulation within and among species will provide insight into both the mechanics and selective pressures involved in the reproductive behavior of scleractinian corals.

This paper describes an empirical investigation of the effects of altering lunar phase, seawater temperature, and day length on the timing of spawning in two Hawaiian acroporid corals, Montipora verrucosa (sensu Vaughan 1907) and M. dilatata.

MATERIALS AND METHODS

The study was conducted in two concurrent parts: 1) weekly sampling from a field population, and 2) experimental manipulations of clonal replicates of colonies maintained in flow-through microcosms.

Field study

Thirty colonies of Montipora verrucosa were haphazardly chosen from colonies on Coconut Island reef in Kaneohe Bay at weekly intervals from 27 May to 24 August, 1987. M. dilatata, because of its rarity, was not included in the field sampling. Branches of M. verrucosa >5 cm in length (polyps closer to branch tips were often sterile) were removed by finger pressure from colonies >25 cm in diameter. Samples were examined under a stereo dissector microscope within one hour of collection, and scored for the presence or absence of gametes. Oocyte size was estimated from the mean of ten diameters measured with an ocular micrometer at 50x. The presence or absence of zooxanthellae within oocytes and the morphology and mobility of sperm were also recorded for each sample.

Experimental treatments

Response to manipulation of potential spawning cues was tested within and among clones of Montipora verrucosa and M. dilatata. Four to five colonies (assumed to be clonemates based on proximity and similarity in corallum color and morphology) from each of nine patches of Montipora verrucosa were collected from Checker Reef, Kaneohe Bay. Two large colonies of M. dilatata, a much rarer species, were brought back to the lab and gently broken into six clonal replicates each. Colonies were collected on 18 May and allowed to acclimate in continuous-flow microcosms replicating reef flat conditions for 10 days before experimental treatments were begun. Treatments and the number of colonies of each species per treatment are given in Table 1. Experimental treatments were initiated on 28 May (two days after new moon) and maintained for 93 days. Seawater intake was ~1 m below MLW on Coconut Island reef flat.

Table 1. Number of clones of Montipora verrucosa (Mv) and M. dilatata (Md) in each experimental treatment. Clones were not replicated within treatments.

	Mv	Md
Constant Full Moon	5	2
Shifted Lunar Phase	7	2
Constant New Moon	7	2
Lowered Seawater Temperature	4	2
Shortened Day Length	4	2
Control	9	2

In order to limit exposure of experimental colonies to exogenous spawning products or other possible pheromones, seawater was turned off between 1800 and 2400 each night during the week following new or full moon. All three lunar phase chambers were covered each night to eliminate extraneous illumination. An automatic timer-operated bucket-pulley system raised the covers every morning at 0530. Because of the importance of not exposing colonies to incidental light (e.g. flashlights), spawnings in the lunar treatments could not be monitored at night. Therefore, colonies were placed into individual plastic bags, the lower halves of whichs were perforated to allow for water exchange. Bags were left intact from the tops of the colonies (~20-25 cm off the bottom of the chambers) to the surface. As egg-sperm bundles were positively buoyant, the bags caught each colony's spawn on the water surface. The occurrence and extent of gamete release from the previous night could then be recorded each morning without disrupting the experimental treatments.

Constant Full Moon: an artificial moon was constructed from a rheostat-controlled incandescent bulb contained within a glass jar. The "moon" was suspended ~15 cm above the surface of the water of the experimental chamber. Light intensity was measured with a LiCor, Inc. Model L1-188B integrating quantum meter and adjusted to 0.01 uE/m^2/sec, equivalent to full moon irradiance (Jokiel et al. 1985). The "moon" was left on continuously in this treatment.

Shifted Lunar Cycle: a similar artificial moon was used in this treatment, but shifted 14-days out of phase with the natural lunar cycle. On natural new moon, the artificial moon was illuminated and left on for 14 days. At natural full moon, the light was turned off and the chamber experienced no night irradiance for the next 14 nights.

Constant New Moon: colonies in this treatment received no night irradiance for the three month period of study.

Lowered Seawater Temperature: seawater temperature was decreased 0.5° C every three days for 2 weeks with an immersible MinnowCool chiller to 22.0° C, approximating winter conditions (about 4.4° C below ambient in June). Temperature was allowed to return to ambient after 30 days.

Shortened Day Length: the experimental chamber was covered ten minutes earlier every night for 12 nights until winter daylength was approximated (11.3 h light:12.7 h dark). Covers were removed nightly, after dark and before moonrise (~1930-2000), to provide exposure to natural night irradiance. Colonies in this treatment were maintained under this cycle for the duration of the experiment.

RESULTS

Field Sampling

Both species are simultaneous hermaphrodites, with polyps containing ovaries and testes in separate, alternating mesenteries, and produce egg-sperm

bundles (~8 eggs/bundle). All Montipora verrucosa colonies examined contained eggs and sperm in late May when sampling was initiated (Figure 1). Over the next three weeks, the percentage of fecund colonies dropped to 80%, and then to 20% during the week following new moon in June. Approximately 10-20% of colonies retained gametes over the next month, until new moon in July, after which fewer than 2% still had gametes (100 colonies were examined on 9 August). Oocyte size remained relatively constant (350 ± 22.85 um) between late May and the week prior to new moon in June, during which mean egg diameter increased to 425 ± 14.52 um (Figure 1). Mean egg size gradually declined through the remainder of the summer, with the range in sizes being large (140-420 um). Slicks of gametes were observed in wind-rows around Kaneohe Bay on 26 June and 28 July, indicating two major field spawning events.

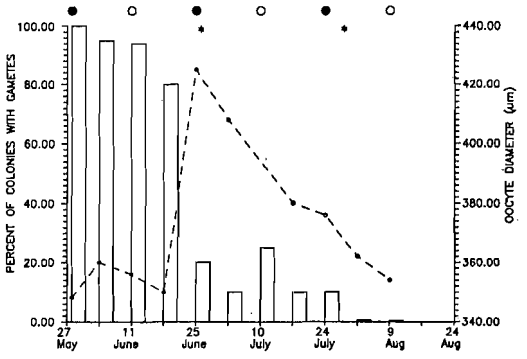

Figure 1. Proportion of colonies with gametes (bars) and mean oocyte diameters (dashed line) from weekly field samples from 30 Montipora verrucosa colonies in summer, 1987. Asterisks indicate observations of gamete slicks in Kaneohe Bay. Lunar phases are shown at top.

Oocytes were pale pink in color. During the week before new moon, zooxanthellae became so numerous within the mesenterial walls as to make the ovaries appear golden-brown. Zooxanthellae moved into the eggs one to two days prior to spawning. Condensation of sperm heads was observed four days prior to spawning. Tails became visible about one day later at which time sperm motility was first noted. Egg-sperm bundles were collected from laboratory spawnings and monitored for several hours. After a period of 45-90 minutes, bundles began to break up. When agitated by swirling, a negatively buoyant sperm "packet" could be separated from the bundle. If left undisturbed in a still beaker, sperm were observed to stream downward away from the bundle, while the eggs remained floating near the surface.

Experimental treatments

Controls: All nine Montipora verrucosa control colonies spawned on 26-27 June (Figure 2) between 2045-2230 (new moon on 25 June). Two colonies spawned on both nights. Three colonies spawned again on 25-27 July (new moon on 25 July), with one colony spawning three nights in a row. Both M. dilatata clones spawned at 2045 on 12 July (full moon on July 11, moonrise at 2028). One colony spawned again on 13 July at an unrecorded time. Both colonies also spawned on 26 July between 2030-2100, one night after new moon. At the second full moon (9 August, moonrise at 1950), colonies again released large numbers of gametes on three to five nights between 9-18 August at unrecorded times.

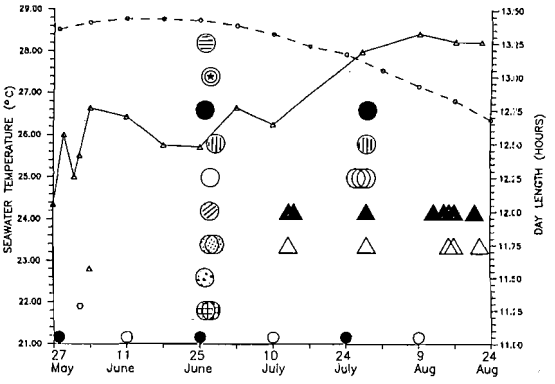

Figure 2. Spawnings in nine colonies of Montipora verrrucosa (large circles) and two colonies of M. dilatata (triangles) under control conditions. Shadings indicate individual clones. Ambient seawater temperatures (solid line) and day length (dashed line) are shown. Small triangle denotes mean winter (February) reef flat temperature; small circle shows winter (February) day length.

Constant Full Moon: Four of the five experimental M. verrucosa colonies in this treatment spawned, two with controls in June and two with the controls in July (Figure 3). M. dilatata clones spawned one to eight nights after full moon in July and August.

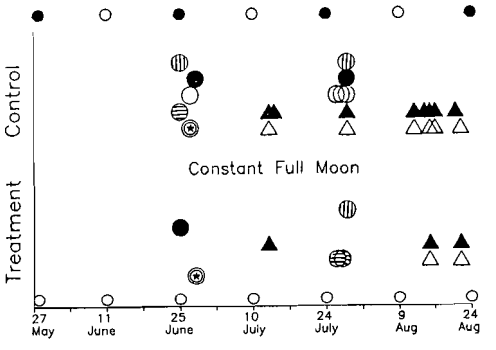

Figure 3. Spawnings of control and experimental colonies in full moon treatment for M. verrucosa (circles) and M. dilatata (triangles). Lunar phase for control (top) and treatment (bottom) are indicated.

Shifted Lunar Phase: All seven experimental M. verrucosa colonies spawned at least once during the summer, synchronously with controls the first lunar cycle, and five to twelve days out of phase with controls the second month (Figure 4). Similarly, both M. dilatata colonies spawned with controls at full moon in July, and then eight days prior to controls in August (one colony).

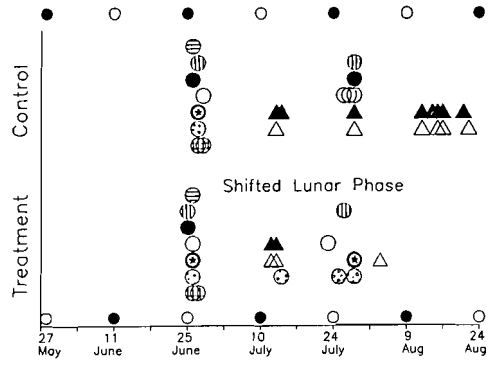

Figure 4. Spawnings of control and experimental colonies in shifted moon treatment for M. verrucosa (circles) and M. dilatata (triangles). Lunar phase for control (top) and treatment (bottom) are indicated.

Constant New Moon: Only three of the seven M. verrucosa colonies which received no night irradiance spawned during the 93 day experimental period, although all had gametes at the outset (Figure 5). Two colonies spawned synchronously with controls at the first new moon; one of these spawned again one week prior to new moon in July along with a third colony. No gametes were found in the four colonies which did not spawn, indicating that resorption may have occurred. M. dilitata colonies spawned, one to two days prior to controls, at full moon in July, and eight to ten days prior to controls in August.

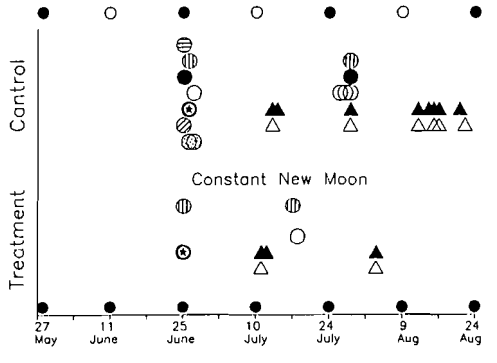

Figure 5. Spawnings of control and experimental colonies in new moon treatment for M. verrucosa (circles) and M. dilatata (triangles). Lunar phase for control (top) and treatment (bottom) are indicated.

Lowered Seawater Temperature: Spawning was apparently precluded for M. verrucosa and M. dilatata clones maintained at winter water temperatures (Figure 6). One month after seawater temperature was returned to ambient, one M. verrucosa and both M. dilatata clones spawned after new moon and full moon, respectively.

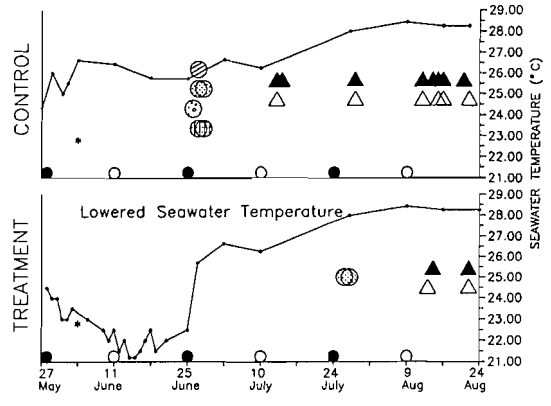

Figure 6. Spawnings of control and experimental colonies in lowered seawater temperature treatment for M. verrucosa (circles) and M. dilatata (triangles). Solid lines indicate seawater temperature in microcosms. Asterisks show winter (February) mean reef flat temperature.

Shortened Day Length: Colonies of M. verrucosa and M. dilatata spawned on the same nights as controls (Figure 7), but all four M. verrucosa colonies released gametes between 1830-2000, 1.5-2 h earlier than controls, indicating that onset of darkness is the final releasing cue for this species. M. dilatata control and experimental colonies spawned between 2030-2100 in July (time of gamete release was not recorded for August spawnings).

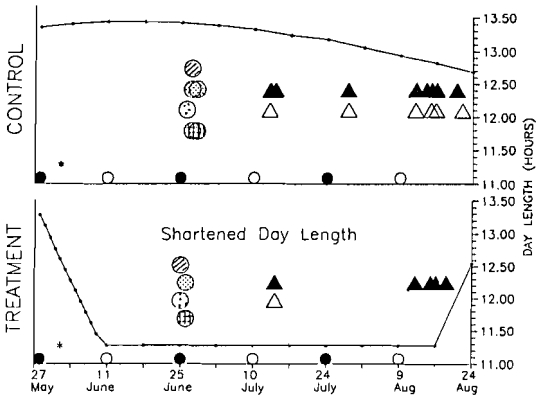

Figure 7. Spawnings of control and experimental colonies in shortened day length treatment for M. verrucosa (circles) and M. dilatata (triangles). Solid lines indicate seawater temperature in microcosms. Asterisks show winter (February) mean day length.

DISCUSSION

Experimental manipulations and field observations revealed that two Hawaiian congeners, Montipora verrucosa and M. dilatata have distinct reproductive schedules and responses to environmental stimuli. Both species release gametes during the summer, prior to maximal seawater temperatures. M. verrucosa had two major spawning episodes and M. dilatata had three during the summer (1987) in which this study was conducted. M. verrucosa spawned within 2-3 days of new moon in June and July. There was much greater variability in M. dilatata, with gamete release occurring at both new and full moon and spawning spread over more nights. Heyward (1985) reported single spawning events for both species in July, 1983, based on weekly field sampling of five colonies each. In 1984, however, he observed multiple spawnings in M. dilatata and spawning at full moon in M. verrucosa (A. Heyward pers. comm.). Both species exhibit a great deal of variability and flexibility in timing of spawning.

Lunar phase was experimentally demonstrated to be an important cue for spawning behavior in both Montipora verrucosa and M. dilatata. An interesting result of these manipulations was that synchronicity was disrupted or shifted after only five to eight weeks under experimental conditions. Shifting of lunar phase had a greater disruptive effect on spawning than either constant full moon or constant new moon treatments, suggesting that night irradiance may normally be perceived as a threshold signal.

Babcock et al. (1986) suggested that timing of spawning may be related to the concentration and retention of gametes at low or slack tide. During the summer in Kaneohe Bay, tidal amplitudes are at their greatest, and lowest tides occur between 2200-2400 and 0700-0900 at new and full moon. In the present study, the effect of tidal influence was absent in all experimental microcosms. Spawnings in the field and in all experimental colonies, with the exception of those in the shortened day length treatment, occurred between 2030 and 2230 (1.5-2 hours before each low tide), supporting the gamete concentration hypothesis. Surveys of additional populations of Montipora verrucosa and M. dilatata in Hawaii, where tidal minima and maxima vary by up to two hours between different coastal locations, would provide evidence to determine if tidal stage is an important selective factor effecting timing of spawning in these species.

Annual variations in temperature have been inferred to be important in timing of gametogenesis and spawning in many scleractinian species (Kojis and Quinn 1981a, Fadlallah 1983, Harriott 1983, Krupp 1983, Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986, Oliver et al. this volume). Synchronization of spawning may be disrupted in populations which do not experience annual fluctuation in seawater temperature (Oliver et al. this volume). In Hawaii, ambient reef flat temperatures range from monthly means of 22.8-26.8° C, with a rapid rise (24.0-26.4° C) in April/May and a drop (26.3-23.3° C) in November/December. Winter seawater temperatures approach lower tolerance limits for most Hawaiian reef-building corals (Jokiel and Coles 1977). Highest seawater temperatures (September/October in Hawaii) may cause stress in corals as indicated by slower growth (Jokiel and Coles 1977).

Winter seawater temperatures were found to arrest or eliminate spawning in both M. verrucosa and M. dilatata. Recovery of spawning synchrony within one month after temperatures were raised in the experimental treatments indicates that temperature plays a pivotal role in the reproductive behavior in these species. These species may utilize increasing temperatures to cue initiation of gametogenesis in spring and spawn during months (June-August) when temperatures are optimal for growth and respiration (Coles and Jokiel 1977, Jokiel and Coles 1977). Seawater temperature may act directly to inhibit gametogenesis and/or spawning when conditions are too cold to support more than basal physiological demands. It is not known whether experimental colonies, perhaps having acclimatized, would have spawned had seawater temperatures been maintained at winter levels for a longer time. Investigation of the relationships between gametogenesis and metabolic function (e.g. growth rate) over a range of temperatures will give better insight into the mechanics of this environmental stimulus.

Spawning period for both species is limited to about two hours per night and appears to be cued by onset of darkness for M. verrucosa. The final releasing cue for M. dilitata is not known as colonies spawned at both new and full moon and did not alter their time of spawning when onset of darkness was brought forward. It is possible that diel entrainment is very strong in this species and a longer period of time is necessary to shift the timing of spawning.

It was thought that increasing or long day-length periods during spring and summer might serve as cues for gametogenesis and spawning in Hawaiian corals. The short time (one month prior to field spawnings) during which day length was experimentally altered in this study was not sufficient to shift seasonality of spawning in Montipora. Longer day-lengths in spring, however, may initially stimulate gametogenic cycles, alone or in conjunction with increasing seawater temperatures, and thus set up the resultant period of maturation.

The extent of overlap or divergence in month, lunar day, or hour of spawning among congeners is of great interest. Within some genera, even those as speciose as the Acropora, there exists substantial partitioning of spawning windows among coral species in Australia (Babcock et al. 1986), the Red Sea (Shlesinger and Loya 1985), the Caribbean (Szmant 1986), Guam (Hunter and Richmond, unpubl.) and Hawaii (this paper). Such partitioning may be interpreted as reproductive isolating barriers in closely related species. The taxonomic relationships of Hawaiian Montipora are not known. In general, speciation events within the scleractinia in Hawaii have apparently been very few (Jokiel 1987), and, although M. dilatata is believed to be an endemic (J. Maragos pers. comm.), it does not appear to have been derived from an extant Hawaiian lineage (Jokiel 1987). Cross-fertilization trials between M. verrucosa and M. dilatata which spawned naturally or by experimental manipulation resulted in abnormal and inviable zygotes (Hodgson this volume). The

evolutionary implications of timing and synchrony of spawning await better understanding of the genetic relationships and reproductive isolating barriers which exist in scleractinian corals.

I thank P.L. Jokiel, L. Watarai, G. Hodgson, D.D. Templin, U. Schober, and R.A. Kinzie III for their kind assistance during many phases of this study. The excellent critical comments of J.Pearse, A.J. Heyward, P.L. Jokiel, and two anonymous reviewers added greatly to the coherency of the manuscript. The Charles H. and Margaret B. Edmondson Fellowship, Alvin Y. Yoshinaga Fund, and the Hawaii Institute of Marine Biology are gratefully acknowledged for their generous financial support.

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