THE PHENOLOGY OF SEXUAL REPRODUCTION BY GREEN ALGAE (BRYOPSIDALES) ON CARIBBEAN CORAL REEFS[1]

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Recent field observations of highly organized, species- and sex-specific patterns of synchronous gamete release by tropical green algae (Bryopsidales) invite a variety of future studies into the ecology and life histories of an important component of tropical reef communities. This paper details sexual reproduction by 22 algal species within five common genera (*Caulerpa, Halimeda, Penicillus, Rhipocephalus,* and *Udotea*), including field observations on the spatial occurrence, timing, and color changes associated with fertility, data on gamete size and behavior, and descriptions of coincident changes in local species abundances.

Ecologically ephemeral episodes of sexual reproduction involved macroscopic changes that reliably indicated developmental state and sexual identity. The time from onset of fertility to gamete release was 36 h (*Halimeda*), 48 h (*Caulerpa, Penicillus,* and *Rhipocephalus*), or 96 h (*Udotea*). All species produced flagellated, negatively buoyant, anisogamous gametes. Microgametes of all species were similar in size; however, considerable species-specific differences were seen in the size of macrogametes. In *Caulerpa, Halimeda,* and *Udotea flabellum (*Ellis and Solander) Lamouroux, the volumetric ratio of macrogametes to microgametes ranged from 2:1 to 45:1, whereas more extreme levels of anisogamy (10^4:1) were observed for *Penicillus* spp., *Rhipocephalus phoenix* (Ellis and Solander) Kuetzing, and other *Udotea* spp. The macrogametes of *Caulerpa* and *Halimeda* showed strong positive phototaxis.

Although only a subset (generally about 5%) of the thalli representing each species released gametes on a given morning, most species underwent bouts of sexual reproduction on numerous occasions during the seasonal peak of reproductive activity (March–May). As might be expected for holocarpic species, dramatic declines in local algal abundance coincided with these periods. The density of sand-dwelling genera such as *Penicillus* fell by 80–90% during this 3-month period in 1997. Similar declines in the cover of sprawling species such as *Caulerpa racemosa* ((Forsskal) J. Agardh) exposed large (35–50 m^2) sections of previously overgrown reef substrate.

Key index words: **Bryopsidales;** *Caulerpa;* **coral reefs; gamete release;** *Halimeda;* **marine algae;** *Penicillus;* **phototaxis;** *Rhipocephalus;* **reproductive ecology; sexual reproduction;** *Udotea*

Siphonous green seaweeds (Bryopsidales) are a ubiquitous and ecologically important feature of many tropical marine environments, including coral reefs, lagoons, mangrove swamps, and seagrass beds (e.g. Bach 1979, Hillis-Colinvaux 1980, Williams 1984, 1990, Bold and Wynne 1985, Hay 1997a, Adey 1998). Representative species, especially the giant coenocytic algae of the Caulerpaceae (*Caulerpa*) and the many calicified members of the Udoteacae (*Halimeda, Penicillus, Rhipocephalus,* and *Udotea*), commonly co-occur within these habitats, where their abundant biomass often makes them a significant source of food, shelter, competition, and calcium carbonate (e.g. Stoner 1985, Tanner 1995, Braga et al. 1996, Hay 1997b, Hillis 1997, and references therein).

Despite their importance to the ecology of tropical marine communities, the basic biology of many siphonous green seaweeds remains poorly understood. Subtle modes of sexual and asexual reproduction obscure basic aspects of their life histories, and field studies of growth and reproduction are uncommon (e.g. Beth 1962, Merten 1971, Price 1992, Rogers 1996). Until recently, a dearth of observed sexual reproduction in the field, coupled with laboratory studies of vegetative reproduction via rhizoid extension (e.g. Hillis-Colinvaux 1973, Friedmann and Roth 1977) or thallus fragmentation (Walters and Smith 1994), supported an inference that asexual processes regulate bryopsidalean biomass on coral reefs (e.g. Friedmann and Roth 1977, Hillis-Colvinaux 1980). However, recent observations of gamete release on Caribbean reefs (Clifton 1997) indicate that sexual reproduction can also play an important role in the dynamics of these algae.

During a 20-month period of nearly continuous daily monitoring, Clifton (1997) observed numerous species-specific bouts of sexual reproduction in which hundreds to thousands of algae released gametes into the water column during a single, brief (5–20 min) pulse of reproductive activity. Although several species often released gametes on the same morning, closely related species did so at different times. Environmental factors such as light level and water temperature subtly influenced the diel timing of gamete release, whereas obvious lunar or tidal cues did not. A broadly seasonal peak of reproductive activity co-

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incided with the annual shift from Panama's dry season to wet season (March–June), a period of increased solar radiation (Cubit et al. 1989).

Such episodic bouts of gamete release are a common, ecologically important feature of reproduction for a wide variety of externally fertilizing marine organisms (Denny 1988, Brawley and Johnson 1992, Levitan 1995). Although the consequences of such bouts of gamete release under natural conditions generally remain poorly understood, a growing body of evidence indicates that bouts of synchronous gamete release yield high levels of fertilization under certain conditions for algae (e.g. Brawley 1992, Pearson and Brawley 1996, Serrão et al. 1996), corals (Oliver and Babcock 1992), gorgonians (Lasker et al. 1996, Coma and Lasker 1997), fishes (Petersen 1991, Petersen et al. 1992), and various echinoderms (Babcock and Mundy 1992, Babcock et al. 1992, Sewell and Levitan 1992).

The phenology of sexual reproduction by tropical green seaweeds thus relates directly to a variety of important questions regarding the ecological significance of sexual versus asexual reproduction, the dynamics of fertilization following gamete release, and the fate of zygotes. These questions, in turn, highlight the need for further investigations into the basic life history and reproductive ecology of tropical green algae in their natural habitats. However, for this work to proceed, ecologists must first be able to detect basic aspects of fertility in the field; we operationally define ''fertility'' as the appearance of consistent macroscopic features consistently related to sexual function that allow visual recognition in the field of imminent sexual reproduction. Within Bryopsidales, these changes involve rapid (typically overnight) gametangial development and the associated conversion of protoplasmic contents into gametes. To date, descriptions of gametogenesis in tropical green algae have come mainly from laboratory studies of a few representative species (summarized for the Caulerpaceae by Goldstein and Morall 1970 and for the Udoteacae by Bold and Wynne 1985; see also Drew and Abel 1988, Littler and Littler 1990), with scant information on the appearance, distribution, and development of fertile algae in the field. A similar paucity of information exists regarding patterns of gamete size, gamete behavior, and the fate of zygotes. This paper provides data on these variables for 22 common species of Caribbean green algae, including details on rates of gamete release and subsequent thallus collapse. As such, this study represents one of the first comprehensive attempts to couple field and laboratory observations on a variety of species within the order, and the comparative data presented here should provide a useful guide to those wanting to examine further the reproductive ecology and life histories of this important group.

MATERIALS AND METHODS

Field data on algal fertility and gamete release were collected from shallow-water reefs (1–5 m depth) in the vicinity of the Smithsonian Tropical Research Institute's San Blas field station during more than 2760 h of snorkeling comprising three basic periods of study between October 1994 and May 1997: 1) opportunistic observations of gamete release on patch reef WB-12 (for reef locations, see Robertson 1987) during 139 days of early-morning surveys of reef fish reproductive behavior between 26 October 1994 and 12 May 1995 (eight species; Clifton 1997); 2) twice-daily surveys of tagged and untagged representative of 14 species (Table 1), every day, from 6 June 1995 to 12 September 1995 and from 1 October 1995 to 3 July 1996 (Clifton 1997); and 3) daily monitoring of the same 14 species, plus opportunistic observations of eight others (Table 1) on two reefs (WB-12 and House) between 1 March 1997 and 11 May 1997 (total number of study days = 584). When more than one observer (range one to eight, usually two) was present on the reef to observe gamete release, the time of initial release was averaged for that day and treated as a single datum in Table 1.

All species were common and either globally or locally abundant throughout the study area. Tagged algae (Clifton 1997) were visually censused twice daily for any changes in color or morphology that might indicate future sexual reproduction. Monitoring was done by slowly swimming a prescribed route (~700 m) over reef and sand habitat that contained the tagged algae. During this swim, thousands of untagged algae were also cursorily examined.

Species Abundance. We monitored changes in the abundance of several species during the 1997 study period using a variety of methods. For the sprawling *C. racemosa,* we estimated (using a surveyor's tape) the size of numerous discrete algal mats (n = 8–17, Fig. 2) on four different patch reefs (House, Point 24, Point 31, and WB-12; initial surveys done 2–4 March 1997). These reefs were visited daily to look for evidence of fertility in *C. racemosa.* Mats on a specific reef were then remeasured on the day following the detection of any episode of sexual reproduction on that reef. For *P. capitatus,* density within five permanent 1-m^2 quadrats was initially recorded at patch reef Point 24 on 2 March 1997. Subsequent measures of density in the same five 1-m^2 areas were made on each day following an episode of gamete release (n = 4; locations were not mapped).

In early March 1997, a permanent grid (3 × 3 m) was established in a shallow (3–4 m depth) fringing reef/sand habitat near reef WB-12. Although a mix of study species was present within this area, the grid was dominated by *P. lamouroxii.* The location of all siphonous green algae present within the 9-m^2 area was initially mapped on 3 March 1997 by systematically placing a 1-m^2 quadrat, gridded every 10 cm, over the entire region. Algae within these grids were not tagged. Grids were then monitored daily, and locations of all algae were remapped whenever fertility of *P. lamouroxii* was observed (5 days: 17 March; 1, 12, and 23 April; and 3 May). Sexual identity of all fertile thalli was recorded at that time. A final map of the entire grid was made on 12 May 1997.

Gametes. The timing (onset of release) and duration (time needed to expel gametes from gametangia) of gamete release were noted during morning field observations. Gamete size was determined (using a calibrated optical micrometer) from freshly released gametes viewed at 100–400×. For biflagellated gametes (all microgametes and macrogametes from *Caulerpa, Halimeda,* and one species of *Udotea* (*flabellum*)), we measured the length (excluding flagella) and width of at least 20 gametes obtained from three to seven (usually four) algae of each sex. For species producing larger, spheroid macrogametes with stephanokont flagella (*Penicillus, Rhipocephalus,* and other species of *Udotea*), we measured the diameter of the gametic region containing the nucleus and chloroplasts. Observations of gamete behavior and viability were generally made on uncovered glass slides, although aspects of phototaxis and the dispersal of larger gametes (visible to the naked eye) were noted from samples in buckets (20 L) or from the field.

Zygotes of *P. lamouroxii* and *C. racemosa* were obtained by mix-

TABLE 1. Data on aspects of the timing of sexual reproduction and size (μm) of gametes for 22 species of siphonous green algae (ND = no data, NA = not applicable for monoecious species).

Gamete classification	Timing				N	Gametes				Gamete sex-size ratio (F:M)
	Release time in min relative to sunrise Means ± SE (N)	Duration of release; Range of observed times in min	Sex dif: M before F in Means ± SE (N) min	Thallus persistence; Range of observed times in days		Macrogametes		Microgametes		
						Length Means ± SE (range)	Width Means ± SE (range)	Length Means ± SE (range)	Width Means ± SE (range)	
Family Caulerpaceae										
Caulerpa cupressoides[a]	14.4 ± 0.7 (45)	5–12	NA	0.5–2.0	120	11.5 ± 0.1 (10.3–13.3)	2.9 ± 0.1 (2.3–3.8)	5.4 ± 0.1 (5.3–6.8)	2.5 ± 0.1 (2.3–3.0)	2.9
C. mexicana[b]	−12.4 ± 0.9 (7)	5–10	NA	0.3–1.0	100	12.4 ± 0.1 (10.5–14.3)	2.9 ± 0.1 (2.3–3.5)	6.0 ± 0.1 (4.5–6.8)	2.5 ± 0.1 (2.3–3.0)	3.0
C. racemosa[a]	32.0 ± 0.8 (86)	7–15	NA	0.5–2.0	140	8.1 ± 0.1 (7.3–9.8)	2.8 ± 0.1 (2.3–3.0)	6.3 ± 0.1 (5.3–6.8)	2.3 ± 0.1 (2.0–3.0)	2.0
C. serrulata[b]	−1.0 ± 1.5 (7)	5–10	NA	0.5–2.0	100	8.0 ± 0.1 (6.3–10.5)	2.9 ± 0.1 (2.3–4.5)	5.5 ± 0.1 (5.3–6.8)	2.5 ± 0.1 (2.3–3.0)	2.0
C. sertularioides[b]	79.5 ± 3.2 (11)	7–12	NA	0.5–2.0	100	8.2 ± 0.1 (7.1–12.3)	2.9 ± 0.1 (2.3–3.5)	5.6 ± 0.1 (5.3–6.8)	2.5 ± 0.1 (2.3–3.0)	2.0
C. verticillata[b]	−27.7 ± 1.2 (3)	5–10	NA	0.3–1.0	ND	ND	ND	ND	ND	ND
Family Udoteaceae										
Halimeda discoidea[c]	−51 (1)	10–15	ND	ND	80	7.7 ± 0.1 (6.0–9.0)	2.9 ± 0.1 (2.3–3.5)	5.6 ± 0.1 (4.5–6.8)	2.4 ± 0.1 (2.3–3.0)	2.0
H. goreaui[c]	−65 (1)	10–15	5 (1)	ND	80	7.8 ± 0.1 (6.8–9.0)	3.1 ± 0.1 (2.0–4.3)	5.7 ± 0.1 (4.5–6.8)	2.5 ± 0.1 (2.3–3.8)	2.1
H. incrassata[a]	32.8 ± 1.0 (38)	15–25	6.1 ± 0.5 (12)	1.5–4.0	80	15.5 ± 0.2 (13.5–19.5)	8.7 ± 0.1 (7.0–10.3)	5.5 ± 0.1 (5.3–6.3)	2.5 ± 0.1 (2.3–3.0)	34.1
H. monile[a]	−16.8 ± 1.9 (21)	15–20	4.6 ± 0.5 (8)	1.1–3.5	80	7.7 ± 0.1 (6.0–9.0)	2.9 ± 0.1 (2.3–3.0)	5.6 ± 0.1 (5.0–6.8)	2.4 ± 0.1 (1.5–3.0)	2.0
H. opuntia[a]	−53.1 ± 1.8 (26)	5–10	4.3 ± 0.6 (6)	1.2–4.0	80	7.5 ± 0.1 (5.3–9.0)	3.0 ± 0.1 (2.3–4.5)	5.4 ± 0.1 (5.0–6.3)	2.5 ± 0.1 (2.3–3.0)	2.0
H. simulans[a]	−20.2 ± 1.4 (25)	15–20	5.5 ± 0.7 (6)	1.5–6.0	100	19.7 ± 0.7 (16.5–21.0)	8.9 ± 0.1 (5.3–9.0)	5.5 ± 0.1 (5.0–6.8)	2.5 ± 0.1 (2.3–3.8)	45.4
H. tuna[a]	−14.7 ± 1.4 (9)	15–25	6.3 ± 1.1 (4)	1.5–3.5	80	7.5 ± 0.1 (6.8–9.0)	3.1 ± 0.1 (2.0–4.5)	5.4 ± 0.1 (5.3–6.8)	2.6 ± 0.1 (2.3–3.0)	2.0
Penicillus capitatus[a]	−41.2 ± 8.2 (42)	10–15	6.7 ± 0.5 (28)	0.5–2.5	80	253.2 ± 2.1 (210.0–300.0)	143.6 ± 1.4 (120.0–186.0)	6.1 ± 0.1 (4.5–6.8)	2.5 ± 0.1 (2.3–3.0)	7.8 × 10⁴
P. dumetosus[a]	65.6 ± 5.1 (17)	20–30	8.5 ± 0.7 (6)	0.5–3.0	100	226.3 ± 1.8 (180.0–270.0)	91.7 ± 1.3 (72.0–126.0)	6.1 ± 0.1 (4.5–6.8)	2.4 ± 0.1 (2.3–3.0)	2.2 × 10⁴
P. lamouroxii[a]	17.8 ± 0.8 (34)	20–30	9.1 ± 0.7 (26)	0.5–2.5	100	242.0 ± 1.4 (210.0–288.0)	122.0 ± 1.5 (90.0–168.0)	6.0 ± 0.1 (5.3–6.8)	2.6 ± 0.1 (2.3–3.0)	4.5 × 10⁴
P. pyriformis[a]	5.5 ± 1.4 (21)	25–35	10.6 ± 1.0 (9)	0.5–3.0	100	225.1 ± 1.0 (168.0–210.0)	116.0 ± 0.5 (102.0–132.0)	6.2 ± 0.1 (5.3–6.8)	2.5 ± 0.1 (1.5–3.0)	4.0 × 10⁴
Rhipocephalus phoenix[a]	−23.4 ± 1.9 (25)	5–15	9.0 ± 1.2 (7)	0.4–2.5	80	200.5 ± 2.1 (168.0–252.0)	93.0 ± 0.9 (66.0–114.0)	6.3 ± 0.1 (5.3–6.8)	2.4 ± 0.1 (2.3–3.0)	2.2 × 10⁴

TABLE 1. (Continued).

| | Timing | | | | Gametes | | | | | |
| | | | | | Macrogametes | | | Microgametes | | |
Gamete classification	Release time in min relative to sunrise Means ± SE (N)	Duration of release; Range of observed times in min	Sex dif: M before F in Means ± SE (N) min	Thallus persistence; Range of observed times in days	N	Length Means ± SE (range)	Width Means ± SE (range)	Length Means ± SE (range)	Width Means ± SE (range)	Gamete sex-size ratio (F:M)
Udotea abbottiorum[c]	−4.0 ± 1.3 (8)	15–20	4.4 ± 0.9 (8)	1.5–5.5	80	185.2 ± 1.2 (168.0–222.0)	76.6 ± 1.0 (60.0–102.0)	6.4 ± 0.1 (6.0–6.8)	2.5 ± 0.1 (2.3–3.0)	2.5×10^4
U. caribaea[a]	136.8 ± 3.5 (33)	25–35	9.9 ± 1.3 (18)	1.5–5.5	80	245.9 ± 2.3 (180.0–288.0)	120.8 ± 1.2 (102.0–168.0)	6.3 ± 0.1 (5.3–6.8)	2.4 ± 0.1 (2.3–3.0)	4.9×10^4
U. cyathiformis[c]	−25.5 ± 0.5 (2)	25–35	8.5 ± 0.5 (2)	1.0–3.5	80	248.5 ± 1.7 (198.0–288.0)	125.5 ± 1.3 (102.0–156.0)	6.5 ± 0.1 (5.3–6.8)	2.6 ± 0.1 (2.3–3.0)	4.9×10^4
U. flabellum[a]	−38.2 ± 2.5 (22)	5–10	4.0 ± 0.8 (5)	7.0–19.0	80	10.4 ± 0.1 (9.8–12.8)	2.8 ± 0.1 (2.3–3.0)	6.6 ± 0.1 (6.0–6.8)	2.4 ± 0.1 (2.3–3.0)	2.1

[a] Species monitored beginning in June 1995.
[b] Species monitored after May 1996.
[c] Species monitored after March 1997.

ing gametes within plastic petri dishes. These were initially raised in aquaria (40 L) within a cascade, open-water, seawater system at the field station. In May 1997, these petri dishes were transported to a laboratory at the University of California, Santa Cruz, and transferred to closed-system, heated (26° C) aquaria containing under-gravel filtration and aeration. Observations of zygote development ended in August 1997, following contamination of the aquaria by foreign algae.

RESULTS

In the days immediately preceding gamete release, all species underwent specific, chronologically ordered, macroscopic changes in color and morphology that could be easily detected in the field, although considerable interspecific variation existed in both the conspicuousness and the timing of these changes. The first indication of fertility was typically associated with the overnight development of gametangia (Fig. 1). Fertility was most easily detected in species with specialized gametangia (*Halimeda* spp. and most *Udotea*), but could also be determined from changes in thallus color (e.g. *Udotea flabellum*) and the migration of cell contents out of rhizomes (e.g. *Caulerpa*) or stipes (*Penicillus* spp., *Rhipocephalus phoenix*). All algae released anisogamous (to varying degrees; see the following discussion), negatively buoyant, flagellated gametes that stopped moving shortly (1–2 min) after fertilization. The unfertilized gametes of all species remained motile for 40–90 min as determined by repetitive sampling of gametes released in buckets or aquaria. In dioecious species (Udoteacae), males released their gametes several minutes before females (Table 1), but there were no indications that this delay was due to chemical signaling or inducement by male gametes; isolated females (placed in buckets the night before) released their gametes at the same time as other females on the reef. Fusion typically began occurring within minutes of gamete mixing and was observed up to 60 min after gamete release. All species were confirmed to be holocarpic, and bouts of sexual reproduction appeared to influence local abundance on reefs, as algal density and percentage cover dropped quickly during periods of peak reproduction (Fig. 2). General aspects of sexual reproduction by these algae are summarized in Table 1, and additional details regarding each genus are provided in the following discussion.

Caulerpa

Six species of *Caulerpa* underwent sexual reproduction during the study. Gametogenesis by all six was a relatively inconspicuous process involving the migration of the cytoplasm into a netlike lattice of unspecialized gametangia concentrated at the terminal ends of blades and bulbs (Fig. 3; see also Kajimura 1977, Ohba et al. 1992). Migration of the cytoplasm occurred overnight, 48–60 h before gamete release (Fig. 1). Although the resultant transparency of rhizomes was a good indicator of fertility, this trait was generally masked either by burial (for

FIG. 1. A time line of fertility for five genera of tropical green algae, based on field observations, from the first reliable indicators of imminent gamete release (typically the overnight development of gametangia; hatched bars) to the period, prior to gamete release, during which an alga's sex can be reliably predicted (stippled bars). Black and white regions of the x-axis denote periods of night and day, respectively.
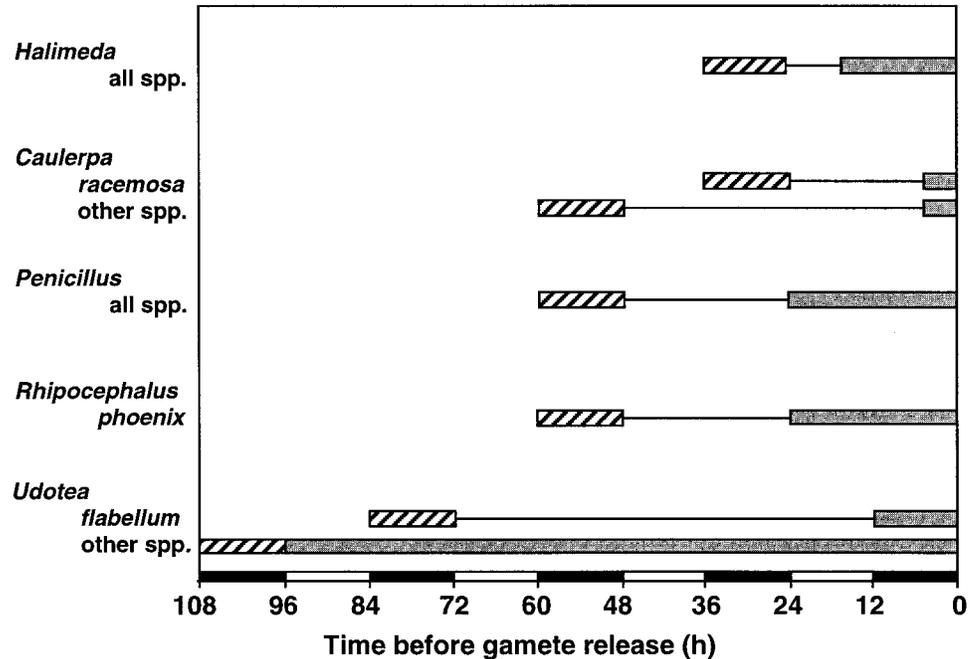
the four sand-dwelling species (*C. cupressoides, C. mexicana, C. serrulata,* and *C. sertularioides*), small size (*C. verticillata*), or the density of overlying branch tips (*C. racemosa*). As gametogenesis progressed and gametes concentrated, larger species, such as *C. racemosa* and *C. cupressoides,* typically acquired a lighter, yellowish-green bicolored appearance that was noticeable from a distance of 1–3 m. However, this characteristic was a reliable indicator of fertility only within the last 12 h before gamete release because earlier it could be confused with a general yellowing of the thallus that often accompanies high levels of solar radiation.

All *Caulerpa* were found to be monoecious, releasing relatively small, motile, biflagellated gametes of moderate anisogamy (Table 1) from different parts of the same thallus. As reported by others (Goldstein and Morall 1970), light-green sections of gametangia released microgametes, whereas brownish-orange-colored gametangia released macrogametes. These color differences were reliably apparent in the field only just prior (1–2 h) to gamete release. For all species, gametes were shed from siphonous tubes 5–15 mm in length (Fig. 3B, C) that developed 12–36 h prior to gamete release. All *Caulerpa* expelled their gametes quickly, with gametangia typically emptying in 5–10 min. Resultant gamete clouds, especially those from sprawling mats of *C. racemosa,* were often large (50–100 m³) and initially conspicuous but dissipated within 10–15 min. Under the microscope, both gamete types remained motile for 40–60 min, with microgametes typically spinning rapidly and with no apparent directionality. In contrast, macrogametes (with eyespots) swam toward the light, rotating in a clockwise manner with

the flagella directed forward. In large aquaria (400 L), macrogametes covered relatively large (0.5–2.0 m) distances in 5–10 min.

The uncalcified thalli of *Caulerpa* quickly degraded following gamete release, and, depending on wave action and currents, all remnants of an alga disappeared from the reef within 3 h. More typically, shreds of the yellowish-whitish husks of emptied thalli persisted for 24–48 h after gamete release. Embryogenesis was very slow when observed in the laboratory, with little or no cellular differentiation observed up to 4 months after gamete fusion.

Halimeda

Fertility within *Halimeda* was easily detected by the appearance overnight of small, grapelike clusters of specialized gametangia extending from calcified blade margins and the associated migration of cytoplasm into the gametangia (Meinesz 1972). The resulting white thallus, edged with green, is easily noticed in the field (Clifton 1997). Transparent gametangia developed overnight, 22–36 h before gamete release, before rapidly turning green just prior to sunrise (22–24 h before gamete release; Fig. 1). Differences in gametangial color that indicated sexual identity in these dioecious algae became increasingly distinct during the day, and field identification of an alga's sex was possible in the afternoon (12–18 h before gamete release; Fig. 1); macrogametes were released from the darker green gametangia of females, whereas microgametes were produced in the lighter-green gametangia of males.

Levels of anisogamy and the rate of gamete release varied among the seven species of *Halimeda* monitored (Table 1). As with *Caulerpa,* both micro-

and macrogametes from *Halimeda* were biflagellated (Fig. 4), and the macrogametes showed strong positive phototaxis. Microgametes from all species were similar in size, but macrogametes ranged from 2–45 times the size of microgametes (Table 1). The reef-associated *Halimeda opuntia* released gametes more rapidly than its sand-dwelling congeners. Following gamete release, the white calcified segments of *Halimeda* typically persisted, intact, for 1–2 days, although under conditions of heavy wave action, they sometimes fell apart within 8 h.

Penicillus

The rather inconspicuous onset of fertility in four species of *Penicillus,* manifested by a whitening of the stipe as the cytoplasm migrated and a slight yellowing of the capitulum caused by the extension of uncalcified siphons (Meinesz 1980), occurred overnight, 48–60 h before gamete release. The sex of individuals in these dioecious algae could be reliably identified 24 h before gamete release (sometimes as early as 48 h in the relatively large siphoned *P. lamouroxii*). The capitulum of males was a distinctly lighter and greener color than the darker, grayer coloration of females. A mixture of both sexes was observed within the permanent grid on WB-12 during each period of sexual reproduction. Males produced biflagellated microgametes similar in size and morphology to other genera; however, female *Penicillus* (also *Rhipocephalus* and three species of *Udotea: abbottiorum, caribaea,* and *cyathiformes;* see the following discussion) produced large (100 μm diameter) spheroid gametes with stephanokont flagella arrayed along a membranous, sheetlike ''tail'' (Fig. 4). These negatively buoyant gametes were nonmotile and sank quickly despite flagellar motion that drove water past the gamete. The flagella were rapidly absorbed within 1–2 min of fertilization. Gamete release typically lasted 15–20 min, and resultant gamete clouds were inconspicuous. The dead thalli of postreproductive *Penicillus* disappeared quickly in the field (often within 12 h), especially the capitulum. This resulted both from thallus disintegration of the thallus associated with water motion and from consumption by several species of parrotfish (*Sparisoma aurefrenatum, S. chrysopterum, S. rubripinne,* and *S. viride*). When cultured in the laboratory, zygotes of *P. lamouroxii* showed noticeable growth and differentiation within 3 days of gamete fusion, forming elongated, macroscopically visible cells similar to the ''espera'' form described by Roth and Friedmann (1977). Although these continued to grow during 3 months of observation (reaching lengths of over 5 cm within aquaria), their form never approached that of an ''adult'' thallus.
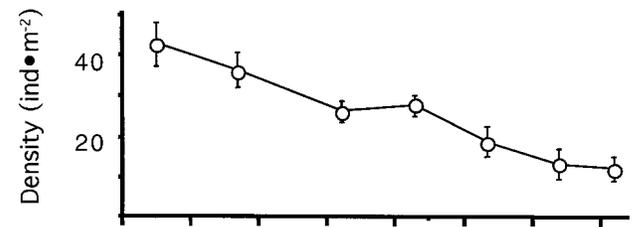
Rhipocephalus

Fertile *Rhipocephalus phoenix* were easily detected in the field, as, much like *Penicillus,* uncalcified extensions of the siphons give each blade a distinctive,
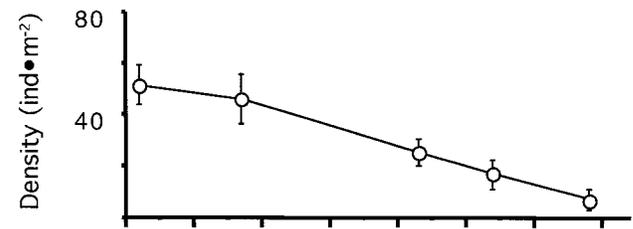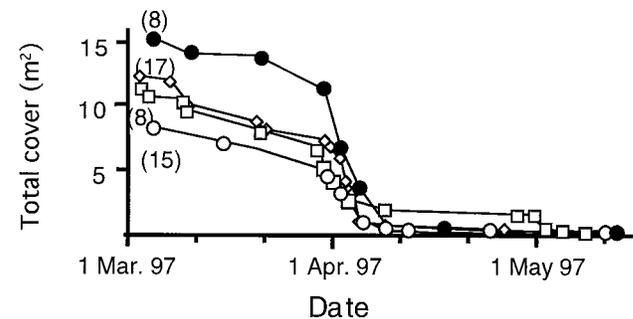

FIG. 2. Changes in the abundance of three species of tropical green algae during periods of sexual reproduction as shown by: (A) Mean declines ($\pm$ 1 SE, n = 5) in the density of *Penicillus capitatus* within 1 m² quadrats on patch reef Point 24; (B) mean declines ($\pm$1 SE; n = 9 for each) in the density of *Penicillus lamouroxii* within 1 m² quadrats on patch reef WB-12; and (C) drops in the total cover of *Caulerpa racemosa* on four patch reefs (number of plants measured on each reef given in parentheses; initial individual cover varied from 0.3 to 2.4 m²). For *C. racemosa,* cover on all reefs had dropped over 99% by 11 May 1997.

bicolored appearance (Fig. 5). The phenology of sexual development also resembled *Penicillus,* with siphon extension and cytoplasmic migration occurring 48–60 h before gamete release. Sexual identity (based on color differences; males are greenish, females are gray) became obvious 24 h prior to gamete release. The anisogamous gametes of *Rhipocephalus* were similar to those of *Penicillus* (described previously), and gamete release generally lasted 10–15 min. Thalli typically disappeared within 24 h of gamete release, often because of parrotfish grazing.

Udotea

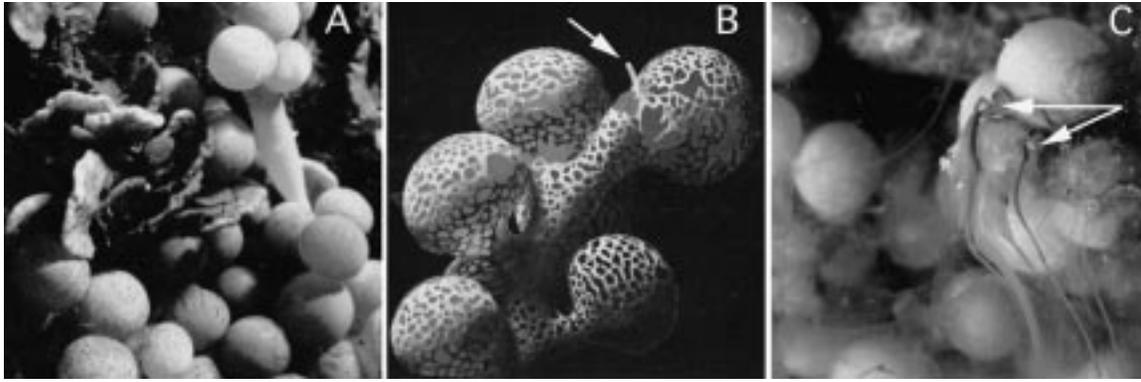Four species of *Udotea* (*U. abbottiorum, U. caribaea, U. cyathiformis,* and *U. flabellum*) underwent bouts of

FIG. 3. Macroscopic features of gametogenesis in *Caulerpa racemosa:* (A) Nonfertile specimen; note uniform, opaque coloration of bulbous, ''pealike'' blades; calcified blades of *Halimeda opuntia* are also visible (image 0.8×); (B) fertile *C. racemosa* 3 h before gamete release, showing netlike lattice of unspecialized gametangia along blades; siphonous tubes extending away from blade (arrow) typically develop 12–24 h before gamete release in this species (image 4×); (C) release of microgametes from two siphonous tubes (arrows). Although initially cohesive, gamete streams quickly disperse with water motion. Simultaneous release occurs from many parts of the alga (image 3.5×).

sexual reproduction during the study. Fertility of all four was conspicuous, although the sexual phenology of *U. flabellum* was quite different from its three putative congeners. Whereas *U. abbottiorum, U. caribaea,* and *U. cyathiformis* showed dramatic morphological changes involving the rapid development of gametangia along terminal blade margins and obvious cytoplasmic migration (Fig. 6; also described by Littler and Littler 1990), *U. flabellum* showed only color changes. Indications of fertility (either a general lightening in color for *U. flabellum* or gametangial development for the others) occurred at least 4 days prior to gamete release (Fig. 1). Sexual identity became apparent for the latter three species at this time, based on the form of gametangia: Female algae attained a ''spikey'' appearance, whereas the gametangia of males were smoother and rounder (Fig. 6). Sexual identity in *U. flabellum,* based on color differences, became evident 24 h prior to gamete release. Males became light green in color over the entire thallus, whereas females became gray.

Gamete release by *U. flabellum* was extremely rapid and conspicuous. Both sexes produced small, biflagellated micro- and macrogametes that most closely resembled the gametes of *Halimeda* and *Caulerpa* (Table 1). In contrast, the other three species of *Udotea* produced large, spheroid macrogametes that resembled those released by *Penicillus* and *Rhipocephalus.* The duration of gamete release in these three species was typically more protracted (Table 1) and much less conspicuous. The thalli of postreproductive *Udotea* tended to remain on the reef longer than other genera, with the intact blade of *U. flabellum* sometimes persisting for weeks (Table 1).

DISCUSSION

Siphonous green algae play a vital ecological role within tropical reef communities worldwide, and understanding the factors that govern their distribution and abundance on and near reefs is important. To date, the basic ecology of these algae remains poorly understood, and studies that examine aspects
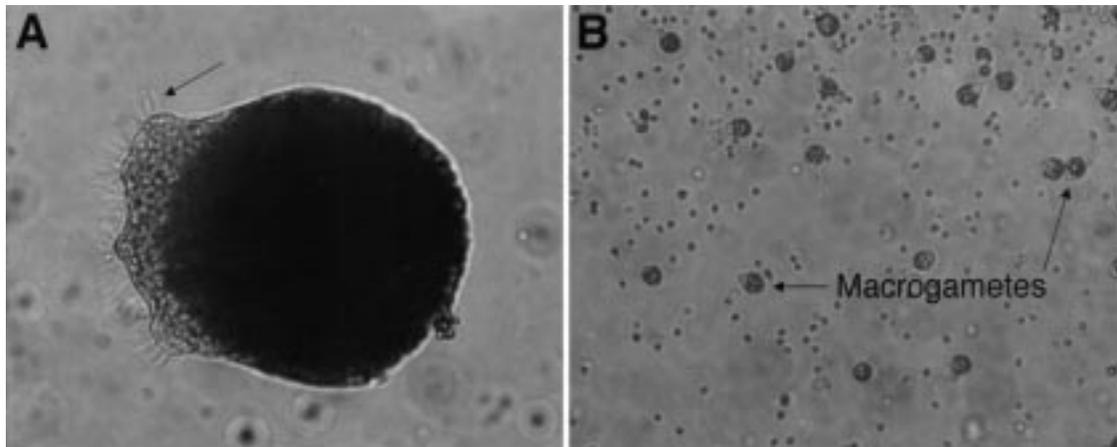

FIG. 4. Microscopic view of gametes from two species of siphonous green algae: (A) *Penicillus capitatus* macrogamete with flagella arrayed along membranous ''tail'' (arrow); flagellar motion drives water back over the gamete; (B) biflagellated gametes of *Halimeda incrassata.* Both macrogametes (arrows) and microgametes (smaller dots) are visible. Both images are at the same scale (800×).
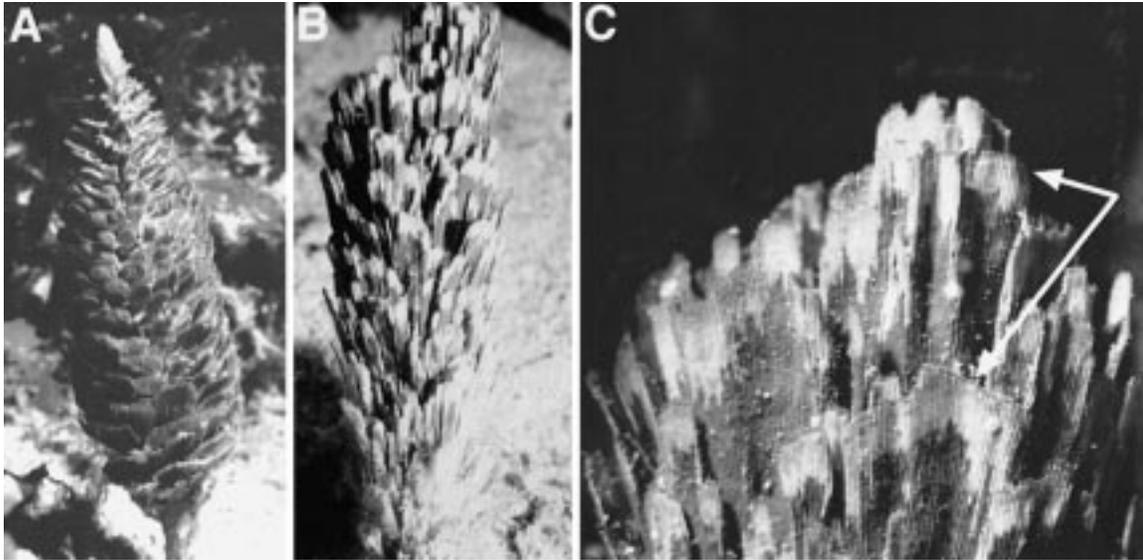
FIG. 5. Fertility in *Rhipocephalus phoenix:* (A) Typical, nonfertile alga with uniform coloration along blades (image 0.75×); (B) fertile female, 16 h before gamete release; the lighter coloration of blade margins is diagnostic of fertility; males are similar in appearance, but gametangia are light green rather than gray (image 0.5×); (C) close-up of fertile female. Note uncalcified siphonous tubes (arrows) that give each blade its bicolored appearance. Gametes are extruded from the terminal ends of these tubes (image 2×).

of green algal growth, reproduction, and survival, especially under natural conditions, should be encouraged. The current study provides some of the first comparative field data on the timing, appearance, and consequences of fertility within the Bryopsidales. These data, coupled with the results of previous laboratory studies, reveal that many features of sexual reproduction (e.g. timing of gametogenesis on different temporal scales and aspects of gamete release, size, and behavior) vary consistently and predictably between species within the order. Given the important role that these variables presumably play in determining the success of sexual reproduction, their differences might ultimately relate to patterns of algal distribution and abundance on a variety of spatial and temporal scales. Thus, the details
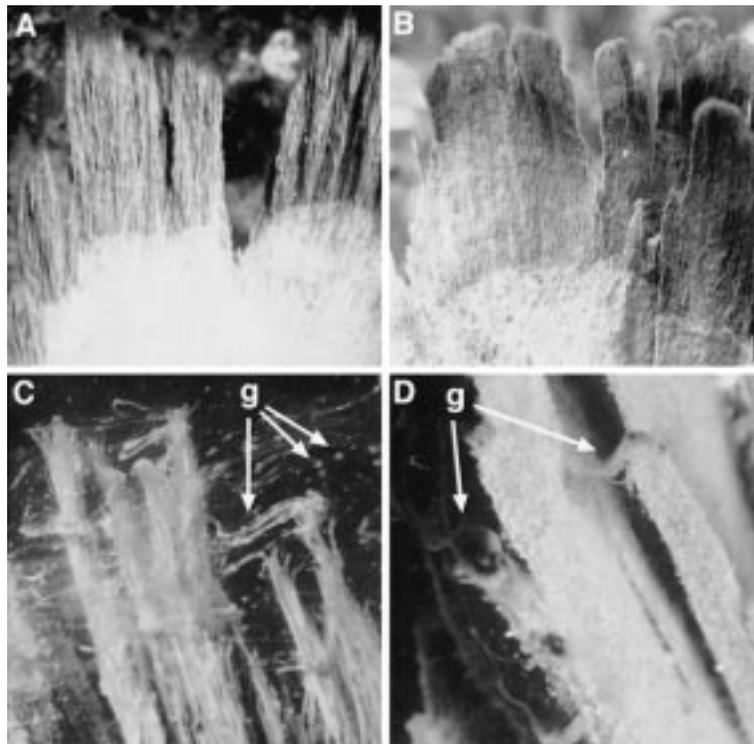

FIG. 6. Sexual dimorphism in *Udotea caribaea:* (A) Fertile female with ''spiky'' gametangia extending along the blade margin; this condition developed overnight as gametangia grew and cytoplasmic contents migrated out of blade and into the gametangia, exposing the calcified nature of the blade, below (image 1×); (B) fertile male with ''rounded'' gametangia extending along blade margin; this condition arose as in (A) (image 1×); (C) release of macrogametes within mucilaginous discharge from female; individual gametes (arrows) are visible as small spheres (image 4×); (D) release of microgametes (arrows) from terminal blade margins of male alga (image 4×).

of algal sexual phenology presented here should not only help researchers who want to detect fertile algae in the field and anticipate the release of gametes but also raise a number of new questions regarding the reproductive ecology and life history of these important members of tropical marine communities.

From an ecological perspective, bouts of sexual reproduction by these algae are a remarkably transient phenomenon, with most species becoming fertile, releasing their gametes, and dying in less than 60 h. Given the brief, often inconspicuous nature of fertility and the generally rapid disappearance of postreproductive thalli, it is perhaps not surprising that episodes of sexual reproduction by tropical green algae have not been widely reported in the literature despite being a prevalent and frequent occurrence in some places and times (Drew and Abel 1988, Clifton 1997). Until the factors that induce fertility are better understood, daily monitoring of algal populations represents the best means for accurately assessing temporal patterns of reproductive activity.

The degree to which genets versus ramets participate in sexual reproduction on a given morning remains unknown. The presence and proximity of both males and females of *P. lamouroxii* within the permanent grid on WB-12 suggests that, at a minimum, at least two genets are present. The fact that thalli from distant parts of a reef (i.e. a relatively large spatial area, >100 m²) simultaneously undergo sexual reproduction similarly argues that at least some genets are participating in bouts of gamete release. However, even for the monoecious species of *Caulerpa,* the likelihood that gametes from different sources actually mix probably diminishes with distance. Molecular investigations of genetic structure within populations would help resolve the extent to which sexual versus vegetative modes of reproduction contribute to overall patterns of algal demography. Recent genetic analyses of various species of *Caulerpa* (Benzie et al. 1997) suggest that both modes of reproduction might play a role that varies spatially and perhaps temporally.

It also remains unclear which environmental triggers induce a specific alga to undergo sexual reproduction. Changes in temperature, light, and nutrients (important environmental variables for these algae; e.g. Littler et al. 1988, Williams and Dennison 1990, McGlathery et al. 1992, Terrados and Ros 1992, Lobban and Harrison 1994, Rogers 1996) as well as demographic variables (e.g. age, size, and local density) might all play a role. As with other algal species (see Brawley and Johnson 1992), changes in light intensity associated with sunrise probably coordinates the diel timing of gamete release, although water temperature might also play a role (Clifton 1997). Shifts in blue and near-blue light might be especially important (e.g. Lüning and Dieck 1989, Lüning 1992). The consistently precise timing of gamete release in the early morning on Caribbean reefs, regardless of tide height or lunar phase (Clifton 1997), suggests that larger-scale patterns of water motion have little influence on when siphonous green algae shed their gametes.

Other algal species also release gametes at dawn (e.g. Ngan and Price 1983, Amsler and Neushul 1989; see also the review by Brawley and Johnson 1992). Assuming that changing light levels organize reproductive events, it remains unclear whether the early-morning (as opposed to evening) timing of gamete release in Bryopsidales ultimately relates to proximal aspects of changing light intensity, photosynthetic requirements of zygotes, the potential for herbivory, or other factors. This warrants further investigation.

The temporal patterns of gamete release summarized in Table 1 bolster the original finding (Clifton 1997) that, within the Bryopsidales, each species releases gametes at a specific time of morning, with more closely related species releasing gametes at different times. Conspecific synchrony presumably increases fertilization rates (see introduction), whereas heterospecific asynchrony reduces the potential for hybridization between species. As a reproductive isolating mechanism, such temporal patterns of gamete release (Palumbi 1994) might ultimately contribute to species-level evolution within the group.

The well-established holocarpic nature of these tropical green seaweeds (Hillis-Colinvaux 1984), coupled with the frequency of sexual reproduction observed during this study, indicates that sexual reproduction can play an important role at both the population and the community level. In the short term, sexual reproduction has a clear, negative impact on local algal abundance (Fig. 2), especially following major reproductive events. In the longer term, the apparently lengthy terms of zygote development noted in this study and in others (e.g. Meinesz 1972, 1980, Roth and Friedmann 1977) suggest that recruitment of sexually derived algae into the population occurs months after bouts of gamete release, with a possible cryptic stage of life history occurring before the production of an ''adult'' form (Meinesz 1972, Bold and Wynne 1985). This delay might allow green algae to persist through unfavorable (possibly seasonal) periods in a manner analogous to terrestrial seed banks (Hoffmann and Santelices 1991). Seasonality in Panama (Cubit et al. 1989) is known to be ecologically significant for herbivorous reef fishes and their algal foods (e.g. Robertson 1990, Clifton 1995).

Levels of anisogamy should relate directly to the reproductive ecology and evolution of benthic marine organisms that release gametes directly into the water column (e.g. Levitan 1991, 1996a). Although the phenomenon has yet to be explored for siphonous green algae, the range of gametic differences noted in this study indicates that this group represents a superb opportunity to further examine patterns of sexual allocation and gamete size versus a suite of ecologically relevant factors (e.g. monoecious vs. dioecious life history, thallus size, adult

density, and habitat type). Further study of species-level variation among algae that share similar habitats and phylogenetic history (e.g. *Halimeda incrassata, H. monile,* and *H. simulans*) might prove especially fruitful.

Differences in gamete size might also influence fertilization success (e.g. Levitan 1993, 1996b, Levitan and Petersen 1995, Podolsky and Strathmann 1996) as well as zygotic dispersal (Reed et al. 1992, Babcock et al. 1994). Given the negative buoyancy of gametes observed in this study, zygote dispersal might be relatively limited (as in other algae; e.g. Santelices 1990, Pearson and Brawley 1996), especially for the species of *Penicillus, Rhipocephalus,* and *Udotea* with larger, nonmotile macrogametes. However, observations of gamete clouds drifting many meters downcurrent from reefs suggest that dispersal of smaller gametes and, potentially, zygotes might be greater in other species despite the negative buoyancy of gametes. Gamete behavior, especially phototaxis by the macrogametes of *Caulerpa* and *Halimeda,* might further influence fertilization rates by keeping gametes in the water column for extended periods of time. This might provide a gamete-level mechanism for outcrossing or influence subsequent levels of dispersal, as it apparently does in some kelps (e.g. Reed et al. 1988). How fertilization success is affected by varying taxis between micro- and macrogametes in these two genera deserves further investigation.

Except for *Udotea,* the phenology of sexual reproduction was relatively conserved within genera, reinforcing currently perceived phylogenetic relationships within Bryopsidales. Observations during this study generally corroborated previous observations of fertility by the more abundant and conspicuous species (e.g. *Halimeda*) while adding detail to our understanding of less conspicuous species (e.g. *Caulerpa* and *Penicillus*). The phenology of sexual reproduction by *Rhipocephalus phoenix,* not previously described in detail, resembled the reproduction of *Penicillus* in many respects.

In contrast to the other four genera, intriguing differences in the phenology of sexual reproduction within *Udotea* suggest that phylogenetic relationships within the genus require further examination. In many respects, patterns of gametogenesis, gamete morphology, and gamete behavior in *U. flabellum* appear more closely allied with the patterns observed within *Halimeda* and *Caulerpa* and also in the uncalcified *Flabellia petiolata,* another large-bladed siphonous green alga formerly placed in *Udotea* (Meinesz 1980). In contrast, sexual reproduction in *U. abbottiorum, U. caribaea,* and *U. cyathiformis* more closely resembles that seen in *Penicillus* and *Rhipocephalus.* This latter link matches the phylogenetic relationships proposed by Hillis-Colinvaux (1984). If the current placement of *U. flabellum* is correct, the cladistic analyses of Littler and Littler (1990) suggests that smaller, biflagellated gametes are a derived character within the genus and one that has evolved

more than once within the order. Molecular investigations of the siphonous green algae should help resolve these evolutionary relationships.

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