ELSEVIER

Journal of Experimental Marine Biology and Ecology
278 (2002) 47–65

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Asexual propagation in the coral reef macroalga *Halimeda* (Chlorophyta, Bryopsidales): production, dispersal and attachment of small fragments

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Received 7 January 2002; received in revised form 6 June 2002; accepted 24 July 2002

Abstract

Siphonous, green macroalgae of the genus *Halimeda* are ubiquitous and ecologically important in tropical and subtropical marine environments. It has been hypothesized that the abundance of *Halimeda* on coral reefs is in part due to the ability of this genus to propagate asexually via vegetative fragmentation. However, vegetative fragmentation has only been documented for *H. discoidea* in a laboratory setting. To test the hypothesis that vegetative fragmentation contributes to field populations of *Halimeda*, we examined three aspects of fragmentation by *H. tuna* (Ellis and Solander) Lamouroux, *H. opuntia* (Linneaus) Lamouroux and *H. goreaui* Taylor on Conch Reef in the Florida Keys: (1) short-term (8 days) and long-term (14 weeks) fragment survival and rhizoid production in the laboratory and field (7 and 21 m), (2) size of the fragment pool and (3) influences of herbivory and water motion on production and dispersal of fragments. Although morphologically similar to *H. discoidea*, only a small percentage of *H. tuna* fragments survived. Fragments of *H. opuntia* and *H. goreaui* were more robust, and survival and rhizoid production were positively correlated with size in short-term trials. In 14-week field trials, one-third or fewer fragments of any species survived at 7 m, potentially because fragments were covered by large amounts of sediment. Survivors included some buried, seemingly dead individuals that turned green when exposed to light, highlighting the remarkable ability of this genus to survive disturbances. There was much less sediment accumulation at 21 m, where more fragments survived. Most (93%) eight-segment fragments of *H. opuntia* produced attachment rhizoids by the end of the 14-week trial. Overall, a

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PII: S0022-0981(02)00335-0

range of 4.7–9.4 fragments of *Halimeda* m^{-2} day^{-1} were found on Conch Reef; most fragments were generated by *H. goreaui*. Fish bite marks were evident on 75–85% of the individuals of *H. tuna* and the number of bites per thallus ranged from 1 to 23. Herbivorous reef fish commonly fed on all three species of *Halimeda*. Some fish consumed the biomass, while others rejected most bites. For example, 83% of bites were rejected by the blue-striped grunt. Dispersal distances for rejected bites ranged from 0 to 31 m. Water motion was also responsible for fragment dispersal; experimentally produced fragments moved up to 48 cm day^{-1}. Results presented here suggest that asexual propagation of fragments of *Halimeda* is an important component of the life-history of this genus and vegetative fragmentation contributes to the abundance of this genus on coral reefs.

Keywords: Asexual reproduction; *Halimeda goreaui*; *Halimeda opuntia*; *Halimeda tuna*; Herbivory; Vegetative fragmentation

1. Introduction

Asexual propagation via vegetative fragmentation occurs when detached, live portions of individuals survive and continue to grow. In the marine environment, fragmentation via fission may be an endogenous part of the life-history of an organism (e.g. fungiid corals: Hoeksema, 1991; Yamashiro and Nishihira, 1998; alcyonacean corals: McFadden, 1986; zoanthids: Karlson, 1986, 1991). Alternatively, fragmentation may be the result of exogenous processes, such as predation (e.g. Walters and Smith, 1994; Walters and Beach, 2000), boring organisms (e.g. Winston, 1983; Correa and Flores, 1995; Meesters and Bak, 1995) or physical disturbance events (e.g. Highsmith, 1980; Tunnicliffe, 1981; Santelices and Varela, 1994; Walters and Smith, 1994; Wulff, 1995; Kramarsky-Winter et al., 1997). A third possibility is that fragmentation is the result of a combination of endogenous and exogenous events (e.g. Lasker, 1984). Fragments that are produced as an integral part of an organism's life history are predicted to have high survivorship, whereas fragments produced by biotic or abiotic factors may or may not be able to survive and grow clonally. In the latter case, it may advantageous for these organisms to develop mechanisms that promote survivorship of fragments.

The importance of fragmentation as a means of asexual reproduction has been documented in many marine taxa, including corals (e.g. Connell, 1973; Tunnicliffe, 1981; Highsmith, 1982; Lasker, 1984; Hunter, 1993; Coffroth and Lasker, 1998; Yamashiro and Nishihira, 1998; Edmunds, 1999; Smith and Hughes, 1999), sponges (e.g. Wulff, 1985, 1991; Maldonado and Uriz, 1999), bryozoans (e.g. Winston, 1983; Winston and Jackson, 1984), hydroids (e.g. Bavestrello et al., 2000), ascidians (e.g. Stoner, 1989), polychaetes (e.g. Oliver, 1984; Wilson, 1985) and macroalgae (e.g. Mshigeni, 1978; Kilar and McLachlan, 1986; Santelices and Varela, 1994; Trowbridge, 1998; Smith and Walters, 1999; Beach and Walters, 2000; Ceccherelli and Piazzi, 2001). Most of this work has focused on the survivorship of large fragments (fragment length: centimeters to tens of centimeters). Little is known about the fate of small algal fragments (length: millimeters to a few centimeters) which are regularly generated by herbivores or disturbance events. Santelices and Ugarte (1987) found that almost 90% of thallus

fragments of the green macroalgae *Enteromorpha compressa* and *Ulva rigida* were not damaged as they passed through the digestive tracts of herbivorous mollusks. After being expelled in fecal pellets, undigested fragments survived and grew (Santelices and Ugarte, 1987). For the green alga *Halimeda discoidea*, Walters and Smith (1994) found that 56–100% of fragments produced by fish grazing and 100% of fragments generated by Hurricane Iniki survived and produced rhizoids. Damage that occurred between segments (nodes) or within segments resulted in either a few fast-growing or many slower-growing rhizoids (Walters and Smith, 1994).

It is remarkable that very small fragments of any marine algae can survive wounding, attach to the substratum, and continue to grow. Some species in the order Bryopsidales (Chlorophyta) are very successful at this type of propagation, although all members of this siphonous order are unicellular and multinucleate (for review, see Vroom and Smith, 2001). Sexual reproduction by many members of the Bryopsidales, including *Halimeda*, is holocarpic, with dioecious individuals releasing gametes all at once and then dying within hours (Hillis-Colinvaux, 1972; Clifton, 1997; Clifton and Clifton, 1999). If fertilization and recruitment of sexually produced individuals are not successful for this taxa over the long-term, asexual reproduction via vegetative fragmentation may contribute substantially to populations.

In this paper, we tested the hypothesis that asexual reproduction via vegetative fragmentation of *Halimeda* contributes to populations on coral reefs. We investigated the importance of vegetative fragmentation and the potential for fragment dispersal in *H. tuna*, *H. opuntia* and *H. goreaui* commonly found in the Florida Keys reef tract, asking:

1. Is fragment survival and production of attachment rhizoids dependent on fragment size and depth?
2. How large is the fragment pool on the reef?
3. How important are fish herbivory and water motion to fragment production and dispersal?

2. Methods

2.1. Study location and study organisms

Populations of *H. tuna*, *H. opuntia* and *H. goreaui* were sampled at two sites (Shallow Conch: 7 m and The Pinnacle: 21 m) separated by approximately 700 m on Conch Reef (24°56′87″N; 80°27′28″W), approximately 9 km off of Key Largo, FL, USA, using Nitrox (EAN 36) and saturation diving. Laboratory experiments were conducted at the NOAA/National Undersea Research Center facility in Key Largo.

Three morphologically different species of *Halimeda* were examined on Conch Reef: *H. tuna*, *H. opuntia* and *H. goreaui*. Individuals of *H. tuna* are composed of lightly calcified, disk-shaped, ribless segments (up to 20 mm diameter) connected by flexible joints or nodes (Littler et al., 1989). Individuals grow to 25 cm in height on hard surfaces, with branching primarily in one plane (Littler et al., 1989; Littler and Littler, 2000). Segments of *H. opuntia* are highly calcified disks (mean diameter 7.2 ± 0.2 mm), with

three lobes and three radiating ribs visible on the surface of each disk (Littler et al., 1989). *H. opuntia* spreads laterally on sand and on hard surfaces with dense branching to form extensive clumps or mounds (height: 20 cm; diameter: 1 m) with many points of attachment (Littler et al., 1989; Littler and Littler, 2000). Calcified, brittle segments of *H. goreaui* are flat, three-lobed and much smaller (up to 6 mm diameter) than those of *H. opuntia* (Littler and Littler, 2000). Most individuals of *H. goreaui* hang or drape from vertical surfaces, extending 13 cm in deeper waters (Littler and Littler, 2000). *H. tuna* dominated the Shallow Conch site; the Pinnacle site was dominated by *H. opuntia* (Vroom et al., in preparation). Although deeper ($\sim$ 35 m) areas are dominated by *H. goreaui*, it occurred at low percent cover at our study sites (LJW, personal observation).

2.2. Vegetative fragmentation: short-term and long-term trials

Eight-day trials investigating survival and rhizoid production of fragments for all three species of *Halimeda* were simultaneously determined under laboratory conditions and at our 7- and 21-m field sites in October 1994. The laboratory trial was run to determine the potential for fragments of these three species to survive and produce attachment rhizoids with minimal water motion. Lighting in the laboratory was supplied by overhead fluorescent bulbs on a 12 h:12 h light/dark cycle. These lights supplied 50 μmol quanta m^{-2} s^{-1} (Licor 4π Underwater Quantum Sensor attached to LI-1400 data loggers). This amount was 1/8 of the midday solar irradiance at 21 m and 1/400 of the values at our 7-m site.

Crescent-shaped fragments were cut with a sharpened pipette tip in the following size classes: 0.5, 1, 2.5 and 4 segments for *H. tuna*; 1.5, 2, 4.5 and 8 segments for *H. opuntia*; and 2.5, 3, 6.5 and 12 segments for *H. goreaui*. Although segment size differed among species, the lengths of the fragments used were similar (29.3 ± 1.0, 35.9 ± 1.2 and 30.7 ± 1.0 mm for *H. tuna*, *H. opuntia* and *H. goreaui*, respectively). Fragments were created the night before deployment in the laboratory or field. Individuals were collected from the 7-m site for use in the laboratory and the 7-m field experiment. After cutting, fragments were kept in the dark overnight in seawater-filled containers and returned to the reef early the next day. Individuals collected from the 21-m site were transported to the Aquarius Underwater Habitat for manipulation, stored overnight on a reef adjacent to the habitat (20 m) and then deployed to our field location early the following morning.

Plastic, compartmentalized boxes (Tuftainer) without lids were used in the field trials with one fragment placed in each compartment ($52 \times 52 \times 52$ mm). Thirty replicates of each size class were randomly assigned to compartments. All boxes were covered with translucent, non-UV inhibiting, polyethylene mesh (mesh diameter: 1.6 mm) that retained fragments, but allowed water to circulate. All boxes were transported fully assembled and secured to the study sites with cable ties and buried weights. Half of the compartments had 5 mm of sand covering the bottom; the remainder was deployed with no sand. However, in less than 24 h, sand accumulated in all compartments.

For the laboratory trial, fragments ($N = 20$ per treatment) were randomly placed in compartmentalized ice cube trays with 0.45-μm Millipore-filtered seawater and loosely covered with clear plastic wrap. Half of these compartments also contained 5 mm of sand. Although the size of the compartments was smaller than the compartment size for the field

trials (45 × 32 × 25 mm), the fragments were motionless and did not contact more than one edge of a compartment. Water was replaced every 24 h.

At the end of the 8-day period, all fragments (laboratory and field) were examined with a dissecting microscope to determine the percent of individuals that: (1) survived (pigment retention, turgidity and retention of siphonous connections between segments if the fragment contained >1 segment), and (2) produced attachment rhizoids. If the nodes connecting multisegmented fragments were severed, the fragment was not considered to have survived, even if the new, smaller fragments survived and produced rhizoids. The sand depth in all compartments was also recorded in field trials. Data were arcsine square-root transformed to satisfy assumptions of normality and homoscedasicity, analyzed with a two-way ANOVA with location (7 and 21 m, laboratory) and fragment size (number of segments) as fixed factors, and Tukey's a posteriori multiple comparisons tests (Zar, 1996).

To complement the 8-day, short-term, vegetative fragmentation trial, a field trial was run for 14 weeks (12 June to 20 September 1997; $N = 15$ per treatment). The only difference between short-term and long-term trials was that all compartments contained 1 cm of sand at the start of the long-term trial.

2.3. Fragment pool

All unattached fragments of all three species of *Halimeda* naturally occurring on Conch Reef were collected from fifteen 0.25-m^2 quadrats at the 7- and 21-m sites in July, September and October 1998. The October collection occurred 2 weeks after Hurricane Georges (Category 4) passed over Conch Reef on September 25, 1998. Fragments were placed in collecting devices constructed from 500-ml centrifuge tubes with the tip cut off and replaced with nylon stocking mesh. Fragments were submerged in seawater-filled buckets for transport to the laboratory for immediate determination of species and number of segments per fragment. For each species of *Halimeda*, the number of fragments in the fragment pool and the number of segments per fragment were compared with two-way ANOVAs (fixed factor: depth; random factor: date).

2.4. Herbivory on Halimeda and fragment dispersal by fish

Fifty-five individuals of *H. tuna* were collected in July and September 1998 from the 7- and 21-m sites and transported to the laboratory, where the number of crescent-shaped bite marks on each individual was recorded. Bite marks were not clearly visible on the heavily calcified segments of *H. opuntia* and *H. goreaui.* Two-way ANOVAs with date and depth as the random and fixed factors, respectively, were used to compare: (1) the mean percentage of individuals that had at least one bite mark, and (2) the mean number of bites per individual.

The identity of fish herbivores and the outcome of individual herbivory events (consumed or rejected) were determined by observing grazing individuals for 3–5 min after the individual was observed foraging on *Halimeda*. In preliminary trials, we determined which fish species foraged on *Halimeda* and were undisturbed by human

observers. At least 2 m separated observers and fish during the observation periods. Observers recorded: (1) the total number of bites from intact *Halimeda* (three species), (2) the number of *Halimeda* fragments created by fish rejecting these bites and (3) distance from the source to deposition for rejected fragments.

2.5. Fragment dispersal by water motion

The importance of water motion on fragment dispersal was measured by placing 25 fragments of each size/species combination used in the fragment survival trials at three replicate locations at the 7- and 21-m sites in October 1994. Prior to deployment in the field, fragments were air-dried, sputtered with Krylon Colorworks fluorescent orange spray paint, dried and then rehydrated with seawater. To ensure that painting small fragments did not greatly influence their potential dispersal, the sinking rates of 15 fragments of each size class of each species of *Halimeda* was measured before and after painting in a 5000-ml wide-mouth flask (height: 450 cm; width: 325 cm). Sinking rates were then analyzed with ANOVA.

At the 7- and 21-m sites, fragments of all species were placed at a starting point (0, 0) marked with a dive weight and the distance and direction of travel for all fragments was recorded once a day for 4 days using a cloth measuring tape. Direction was recorded as being in one of four quadrats relative to magnetic north (0–89°, 90–179°, 180–269°, 270–359°) delineated with a 1.3-cm diameter PVC pipe "X" (length of

Table 1
Vegetative fragmentation: 8-day trials

	df	SS	MS	*F*	*p*
Halimeda tuna					
Location	2	1.121	0.560	9.17	0.0001
Fragment size	3	0.252	0.084	1.38	0.2502
Location × fragment size	6	0.371	0.062	1.01	0.4182
Residuals	308	18.833	0.061		
Halimeda opuntia					
Location	2	4.739	2.369	13.73	0.0001
Fragment size	3	19.074	6.358	36.83	0.0001
Location × fragment size	6	1.482	0.247	1.43	0.2022
Residuals	308	53.167	0.173		
Halimeda goreaui					
Location	2	24.641	12.321	83.62	0.0001
Fragment size	3	3.088	1.029	6.98	0.0001
Location × fragment size	6	1.325	0.221	1.50	0.1781
Residuals	308	45.383	0.147		

The results of separate two-way ANOVAs for each tested species of *Halimeda* to determine if location (laboratory, 7 and 21 m) or fragment size effected fragment survival and rhizoid production. Fragment sizes of *H. tuna* were 0.5, 1, 2.5 and 4 segments, *H. opuntia* fragments were 1.5, 2, 4.5 and 8 segments, and *H. goreaui* fragments were 2.5, 3, 6.5 and 12 segments.

each arm: 1 m). A two-way ANOVA (fixed factors: depth, fragment size) was run for each species to determine differences in direction of movement and distance.

Mean maximum flow rates at the sites were determined with four maximum velocity flow recorders (Bell and Denny, 1994) that recorded flow rates between 10 and 50 cm s^{-1}. At the start of the dispersal trials, the flow recorders were deployed directly above the surface at each site near the locations where fragments were placed. All flow recorders were checked and reset daily for the 4 days of the trial.

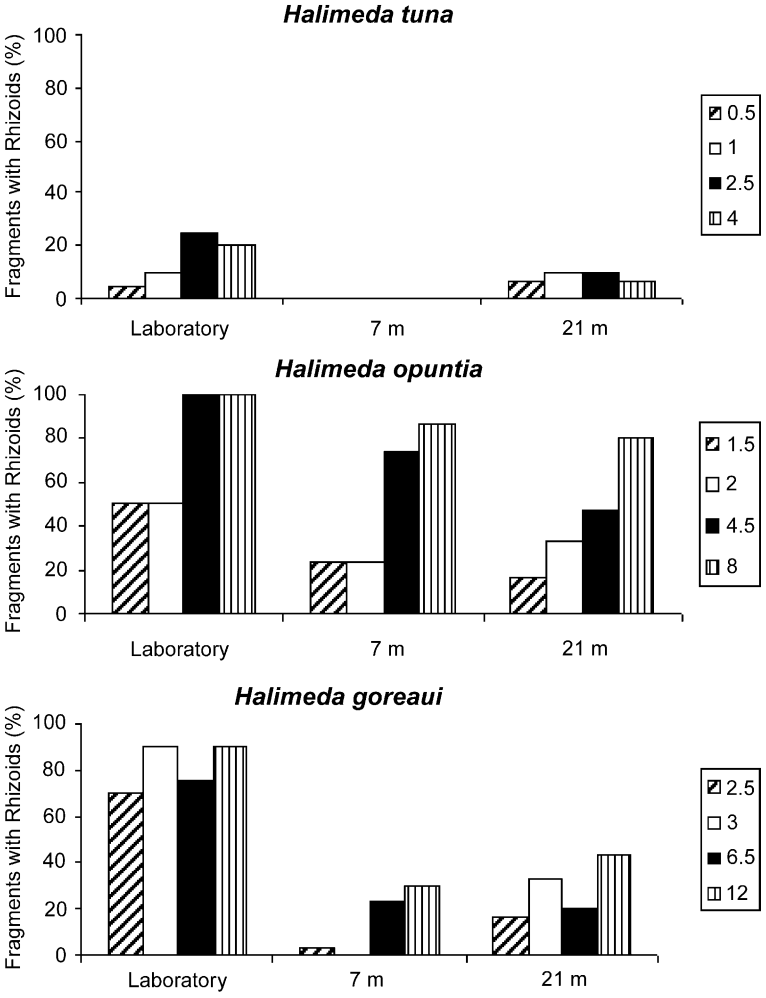

Fig. 1. Asexual reproduction via vegetative fragmentation in the genus *Halimeda*. Percent of fragments of *H. goreaui*, *H. opuntia* and *H. tuna* that survived damage and produced rhizoids during the 8-day trial in the laboratory and at the 7- and 21-m field sites. Tested fragment sizes (i.e. number of segments) for each species are boxed.

3. Results

3.1. Vegetative fragmentation: short-term trials

For all tested species of *Halimeda*, more fragments retained their pigmentation, turgor, connections between segments, and produced rhizoids in the laboratory than in the field, and there were no differences between the 7- and 21-m sites (Table 1, Fig. 1). For *H. tuna*, survival was low in both the laboratory and field and did not differ with fragment size. However, for *H. opuntia* and *H. goreaui*, fragment success and fragment size were positively correlated, and 100% of the 4.5- and 8-segment fragments of *H. opuntia* survived and produced attachment rhizoids (Fig. 1). There was no significant interaction between location and fragment size for any of the tested species of *Halimeda* (Table 1). Mean sand depth in all compartments was 1.9 ± 0.1 mm after 8 days at the 7-m site and 4.7 ± 0.4 mm at the end of the experiment at the 21-m site.

3.2. Vegetative fragmentation: long-term trials

Survival and production of rhizoids was impacted by both fragment size and depth for all three species of *Halimeda* (Table 2). Although most fragments were buried under a layer of sediment at the 7-m site when retrieved (mean sand depth ± S.E.: 20.7 ± 2.4 mm),

Table 2
Vegetative fragmentation: 14-week field trial

	df	SS	MS	*F*	*p*
Halimeda tuna					
Depth	1	0.833	0.833	7.95	0.0057
Fragment size	3	0.867	0.289	2.76	0.0457
Depth × fragment size	3	0.433	0.144	1.38	0.2530
Residuals	112	11.733	0.105		
Halimeda opuntia					
Depth	1	11.408	11.408	83.33	0.0001
Fragment size	3	3.025	1.008	7.37	0.0002
Depth × fragment size	3	0.025	0.008	0.06	0.9802
Residuals	112	15.333	0.137		
Halimeda goreaui					
Depth	1	1.008	1.008	10.72	0.0014
Fragment size	3	3.492	1.164	12.38	0.0001
Depth × fragment size	3	0.958	0.319	3.40	0.0204
Residuals	112	10.533	0.094		

The results of separate two-way ANOVAs for each tested species of *Halimeda* to determine if depth (7 and 21 m) or fragment size effected fragment survival and rhizoid production. Fragments of *H. tuna* were 0.5, 1, 2.5 and 4 segments, fragments of *H. opuntia* were 1.5, 2, 4.5 and 8 segments, and fragments of *H. goreaui* were 2.5, 3, 6.5 and 12 segments.

some fragments of all three species regained pigmentation upon exposure to diffuse irradiance in the laboratory (Table 3). Of these, fragments of *H. opuntia* (4.5 and 8 segments) and *H. goreaui* (12 segments) had produced and retained rhizoids (Table 3). After 14 weeks at the 21-m site, compartments accumulated much less sand (mean sand depth: 5.8 ± 0.2 mm) and a percentage of individuals in all but the smallest size-class fragments of *H. tuna* and *H. goreaui* were pigmented, turgid, and produced rhizoids, including 93% of the 8-segment fragments of *H. opuntia* (Table 3).

3.3. Fragment pool

Halimeda goreaui consistently produced the greatest number of fragments, while the number of fragments of *H. opuntia* and *H. tuna* remained low and similar over time (Table 4). Significantly more individuals of all three species were found at the

Table 3
Fate of fragments in 14-week trials

Species	Fragment size	% Pigmented	% Pigmented + new rhizoids	% Pigmented + new segment
Shallow Conch (7 m)				
Halimeda tuna	0.5	0	–	–
	1.0	0	–	–
	2.5	6.7	0	0
	4.0	13.3	0	0
Halimeda opuntia	1.5	0	–	–
	2.0	0	–	–
	4.5	26.7	20.0	0
	8.0	33.3	33.3	0
Halimeda goreaui	2.5	0	–	–
	3.0	0	–	–
	6.5	6.7	0	0
	12.0	20.0	20.0	0
Pinnacle (21 m)				
Halimeda tuna	0.5	0	–	–
	1.0	33.3	26.7	0
	2.5	20.0	13.3	0
	4.0	33.3	13.3	13.3
Halimeda opuntia	1.5	60.0	46.7	0
	2.0	60.0	46.7	0
	4.5	93.3	80.0	0
	8.0	93.3	93.3	0
Halimeda goreaui	2.5	0	–	–
	3.0	6.7	0	0
	6.5	26.7	13.3	0
	12.0	66.7	40.0	0

Fragment size refers to the number of segments, % pigmented refers to the percentage of fragments that were pigmented or regained pigmentation after exposure to light, % pigmented + new rhizoids refer to fragments that retained/regained pigments and produced attachment rhizoids and % pigmented + new segment refer to fragments that retained/regained pigments and produced new segments.

Table 4
Fragment pool composition

Depth (m)	Species	No. of fragments	Range: no. of fragments	No. of segments	Range: no. of segments
July 1998					
7	*Halimeda goreaui*	4.9 (1.6)	0–18	9.8 (1.8)	1–100
	Halimeda opuntia	0.6 (0.3)	0–5	19.4 (6.8)	1–47
	Halimeda tuna	1.7 (0.6)	0–7	3.7 (0.6)	0.5–10
	Overall	2.4 (0.6)	0–18	9.1 (1.4)	0.5–100
21	*Halimeda goreaui*	11.6 (2.7)	0–37	14.7 (2.1)	1–279
	Halimeda opuntia	2.2 (0.6)	0–9	23.3 (6.3)	1–147
	Halimeda tuna	3.1 (0.8)	0–12	7.5 (1.3)	0.5–45
	Overall	5.6 (1.1)	0–37	14.5 (1.7)	0.5–279
September 1998					
7	*Halimeda goreaui*	2.9 (0.8)	0–9	9.6 (2.6)	0.5–102
	Halimeda opuntia	2.0 (0.5)	0–8	22.0 (6.5)	0.5–134
	Halimeda tuna	1.3 (0.4)	0–5	2.8 (0.6)	0.5–8
	Overall	2.1 (0.4)	0–9	12.1 (2.5)	0.5–134
21	*Halimeda goreaui*	23.1 (1.9)	15–38	13.3 (2.3)	0.5–618
	Halimeda opuntia	2.1 (0.8)	0–8	19.6 (7.3)	0.5–215
	Halimeda tuna	3.0 (0.7)	0–9	4.8 (1.3)	0.5–45
	Overall	9.4 (1.6)	0–38	12.8 (1.9)	0.5–618
October 1998					
7	*Halimeda goreaui*	0.1 (0.1)	0–2	1.8 (0.3)	1.5–2
	Halimeda opuntia	0.0 (0.0)	–	–	–
	Halimeda tuna	1.4 (0.2)	0–2	7.4 (3.2)	0–17.5
	Overall	0.2 (0.1)	0–2	6.0 (2.5)	0–17.5
21	*Halimeda goreaui*	12.3 (2.6)	0–30	21.0 (9.2)	0.5–1656
	Halimeda opuntia	1.3 (0.7)	0–9	26.8 (8.0)	3–147
	Halimeda tuna	0.4 (0.2)	0–3	3.5 (1.6)	0.5–11
	Overall	4.7 (1.2)	0–30	21.0 (8.1)	0.5–1656

The mean number of pigmented, unattached fragments (± S.E.) per square meter, the range of number of fragments per square meter, the mean number of segments per fragment (± S.E.) and the range in the number of segments per fragment collected in fifteen 0.25-m^2 quadrats on three sampling periods in 1998. The final collection date was 2 weeks after Hurricane Georges passed near Conch Reef.

deep site than at the 7-m site, although the number of fragments of *H. goreaui* at both depths was reduced after Hurricane Georges (Tables 4 and 5). Likewise, significantly fewer fragments of *H. tuna* were found after Hurricane Georges (Tables 4 and 5). No temporal or spatial differences were found when the number of segments per fragment was compared separately for each species of *Halimeda* (p>0.1000 in all cases). This is likely due to the wide range of fragment sizes found on all sampling dates (Table 4).

3.4. Herbivory on Halimeda

Most individuals of *H. tuna* at the 7-m site (80–85%) and the 21-m site (75–77%) had at least one segment with a crescent-shaped bite mark and the number of bites per plant ranged from 0 to 23 (Table 6). There were no significant (p>0.1000) temporal or spatial

Table 5
Halimeda fragment pool

	df	SS	MS	*F*	*p*
Halimeda tuna					
Location	1	23.511	23.511	5.19	0.0253
Sampling date	2	70.288	35.144	7.75	0.0008
Location × sampling date	2	12.022	6.011	1.33	0.2710
Residuals	84	380.800	4.533		
Halimeda opuntia					
Location	1	22.500	22.500	4.92	0.0293
Sampling date	2	28.067	14.033	3.07	0.0518
Location × sampling date	2	10.067	5.033	1.10	0.3375
Residuals	84	384.267	4.575		
Halimeda goreaui					
Location	1	3815.511	3815.511	74.43	0.0001
Sampling date	2	725.089	362.544	7.07	0.0015
Location × sampling date	2	680.956	340.478	6.64	0.0021
Residuals	84	4306.267	51.265		

The results of separate two-way ANOVAs for each tested species of *Halimeda* to determine if depth (7 and 21 m) or sampling date (July, September and October 1998) influenced the number of fragments per square meter on Conch Reef.

differences in the percentage of individuals with at least one bite mark or the mean number of bite marks per individual.

3.5. Fragment dispersal by fish

Although the suite of grazers differed with depth, on Conch Reef many species of reef fish grazed all three species of *Halimeda* (Table 7). Some fish were primarily grazing on epiphytes (e.g. ocean surgeonfish *Acanthurus bahianus*), whereas others, such as the blue-striped grunt *Haemulon sciurus* and the porkfish *Anisotremus virginicus*, winnowed large amounts of *Halimeda* spp. in search of associated invertebrates. Some species (e.g. redband parrotfish *Sparisoma aurofrenatum*) readily consumed *Halimeda*, while others rejected *Halimeda* spp. (Table 7). For example, the yellowtail parrotfish *Sparisoma rubripinne*, the redtail parrotfish *S. chrysopterum*, the blue-striped grunt and the porkfish

Table 6
Evidence of fish grazing on *H. tuna*

Date	Depth (m)	*N*	Mean no. of bites (± S.E.)	Range: no. of bites	Mean percent with bites (± S.E.)
July	7	55	2.1 (0.5)	0–8	80.0 (5.0)
July	21	51	3.3 (0.8)	0–12	76.5 (6.0)
September	7	53	4.9 (1.7)	0–23	84.9 (5.0)
September	21	64	4.0 (1.5)	0–19	75.0 (5.5)

The mean number and range of crescent-shaped bite marks per plant on individuals of *H. tuna*, as well as the mean percentage of individuals with at least one bite mark, are presented.

Table 7
Fish observations

Species	*N*	Bites/min (mean ± S.E.)	Percent bites rejected	Distance (m) until contact (mean ± S.E.)	Range of distances until contact
Shallow Conch (7 m)					
Parrotfish					
Redband (*Sparisoma aurofrenatum*)	33	1.8 (0.2)	4.1	1.3 (1.3)	0–10
Princess (*Scarus taeniopterus*)	18	0.5 (0.2)	24.1	2.2 (0.8)	0–5
Stoplight (*Sparisoma viride*)	27	0.6 (0.2)	17.0	0.5 (0.1)	0–1
Redtail (*Sparisoma chrysopterum*)	15	1.8 (0.5)	20.0	0.0	0
Yellowtail (*Sparisoma rubripinne*)	12	1.7 (0.4)	25.0	0.01 (0.01)	0–0.1
Queen Angelfish (*Holocanthus ciliaris*)	11	0.1 (0.1)	0.0		
Surgeonfish (*Acanthurus bahianus*)	21	3.3 (1.1)	5.2	1.7 (1.0)	0–1
Pinnacle (21 m)					
Parrotfish					
Redband (*Sparisoma aurofrenatum*)	43	2.7 (0.3)	5.2	3.1 (1.4)	0–25
Princess (*Scarus taeniopterus*)	30	1.4 (0.5)	9.6	2.1 (0.8)	0–10
Stoplight (*Sparisoma viride*)	27	1.1 (0.3)	10.2	5.3 (2.8)	0–31
Redtail (*Sparisoma chrysopterum*)	4	1.2 (0.5)	50.0	5.0 (0.0)	5
Queen angelfish (*Holocanthus ciliaris*)	14	0.5 (0.2)	23.8	6.8 (4.6)	0–25
Blue-striped grunt (*Haemulon plumieri*)	23	2.0 (0.3)	82.6	5.6 (2.0)	0.1–25
Porkfish (*Anisotremus virginicus*)	10	2.3 (0.4)	70.0	0.7 (0.4)	0.1–30
Surgeonfish (*Acanthurus bahianus*)	16	2.2 (0.6)	37.5	0.8 (0.8)	0–5

After divers observed individual fish grazing on *Halimeda*, they recorded the number of additional bites of *Halimeda* taken for 3–5 min, the number of *Halimeda* fragments rejected by the fish and distance covered by the fragment from the time a bite was taken until the time the fragment contacted the ocean bottom. *N* = number of individuals observed; distances are in meters.

rejected over 20% of bites at both depths (Table 7). When fish rejected *Halimeda*, some expelled the alga immediately (distance: 0 m), whereas other expelled bites were dispersed up to 31 m from the source (Table 7).

3.6. Fragment dispersal by water motion

The weight of the paint used to mark fragments had no significant effect on fragment sinking rates. Specifically, the weight of *H. tuna* was 0.020 ± 0.004 prior to painting and 0.022 ± 0.008 after treatment and there was no increase or decrease in sinking rates when unpainted and painted fragments were compared with ANOVA ($F_{1,39} = 0.1142$; $p = 0.7373$). For *H. goreaui,* the weight of segments prior to paint treatment was 0.006 ± 0.001 and 0.007 ± 0.001 after treatment ($F_{1,39} = 0.2889$; $p = 0.5940$). For *H. opuntia,* weights of segments prior to and after painting were 0.015 ± 0.002 and 0.018 ± 0.002, respectively ($F_{1,39} = 0.8006$; $p = 0.3765$).

The range of distances that marked fragments moved at the 7-m site was 10–48 cm day^{-1}; the range of distances that marked fragments moved at the 21-m site was 7–47 cm day^{-1}. At both the 7- and 21-m sites, fragment movement was primarily in the south/southwest direction (Table 8), although the dispersal shadow was wider at 7 m than at 21 m.

Table 8
Fragment dispersal and direction

Species	No. of segments	*N*	Mean distance	Direction	Maximum distance
Shallow Conch (7 m)					
Halimeda tuna	0.5	9	40.2 (17.0)	240.3 (33.3)	167.0
	1.0	18	35.5 (7.1)	230.4 (19.8)	95.0
	2.5	17	38.2 (6.9)	259.2 (15.3)	99.0
	4.0	16	30.1 (5.0)	270.0 (21.6)	68.0
Halimeda opuntia	1.5	18	30.4 (7.1)	185.4 (23.4)	131.0
	2.0	22	19.7 (2.4)	245.7 (17.1)	39.0
	4.5	12	31.6 (15.2)	232.2 (30.6)	193.0
	8.0	30	27.1 (3.7)	252.0 (18.9)	120.0
Halimeda goreaui	2.5	9	52.3 (5.4)	182.7 (9.9)	167.0
	3.0	18	51.4 (8.4)	182.7 (16.2)	153.0
	6.5	17	47.0 (13.6)	204.3 (22.5)	151.0
	12.0	16	49.3 (11.2)	163.8 (16.2)	147.0
Pinnacle (21 m)					
Halimeda tuna	0.5	4	12.8 (5.1)	202.5 (22.5)	27.0
	1.0	57	39.8 (4.0)	213.3 (8.1)	129.0
	2.5	55	34.6 (4.2)	219.6 (9.0)	148.0
	4.0	48	33.8 (4.5)	216.0 (10.8)	125.0
Halimeda opuntia	1.5	50	15.2 (1.7)	181.8 (9.9)	52.0
	2.0	75	15.2 (1.6)	185.4 (8.1)	81.0
	4.5	68	20.0 (2.0)	177.3 (9.0)	79.0
	8.0	46	23.1 (2.4)	180.0 (11.7)	73.0
Halimeda goreaui	2.5	21	52.8 (3.3)	225.0 (5.4)	187.0
	3.0	67	50.4 (3.1)	228.6 (5.4)	106.0
	6.5	37	56.9 (5.0)	218.7 (9.5)	135.0
	12.0	17	50.1 (6.9)	233.1 (13.5)	93.0

The mean distance in centimeters (± S.E.), mean compass direction in degrees (± S.E.) and maximum distance (cm) of painted fragments of *Halimeda tuna*, *Halimeda opuntia* and *Halimeda goreaui* at the end of the 4 days of observations. Seventy-five fragments of each size-class of each species were deployed at each depth on day 0. *N* = number located on day 4.

Differences in distance traveled by fragments of each size class were similar in most cases for each species (Table 8). Only the smallest size fragments of *H. opuntia* (1.5 segments) differed between depths (ANOVA: $p = 0.0036$); individuals moved further in shallow water (Table 8). Mean flow rates directly above the reef at the 7- and 21-m sites were 13.8 ± 4.0 and < 10 cm s^{-1}, respectively, in October 1994.

4. Discussion

Although not extensively studied, asexual propagation via vegetative fragmentation may be very common for tropical macroalgae. It has been documented in all three algal divisions (e.g. Rhodophyta: Kilar and McLachlan, 1986; Wick et al., in preparation; Phaeophyta: Beach and Walters, 2000; Walters and Beach, 2000; Chlorophyta: Walters

and Smith, 1994; Smith and Walters, 1999; Ceccherelli and Cinelli, 1999; Ceccherelli and Piazzi, 2001). Kilar and McLachlan (1986) found that 43–93% of fragments of the wiry, red alga *Acanthophora spicifera* >30 mm length recruited to the coral reef, and the limiting factor was encountering a surface on which a fragment could snag. It took <2 days for *A. spicifera* to attach to the substratum and 25% of the fragments remained in quadrats for greater than 3 days (Kilar and McLachlan, 1986). Fragment arrival rates for *A. spicifera* ranged from 0.8 to 9.6 m^{-2} day^{-1}. These results are similar to our Conch Reef results with *Halimeda* in terms of survival and fragment pool size (Table 4, Fig. 1).

Although very different in their morphology and degree of calcification, *H. tuna*, *H. opuntia* and *H. goreaui* successfully reproduced by vegetative fragmentation. The most successful species was *H. opuntia* (Table 2, Fig. 1). For *H. tuna*, small numbers of short rhizoids were only produced from cuts, while both *H. opuntia* and *H. goreaui* could produce numerous, fast-growing rhizoids where cuts were made and from the tips of lobes on all segments (LJW, personal observation). Success of *H. goreaui* was greatly reduced in the field when compared to the laboratory results (Table 2, Fig. 1). This was in part due to disarticulation of segments. Our definition of success stated that all segments must remain connected. In the laboratory, all *H. goreaui* segments remained intact. However, with this delicate alga, nodal regions were frequently severed in the field. Thus, our estimates of successful asexual reproduction may be very conservative for this species.

We predicted that the propensity for fragmentation for *H. tuna* would be similar to the very successful Hawaiian *H. discoidea* (Walters and Smith, 1994), based on morphological similarities. However, *H. tuna* was the least successful species in Florida waters, with only a limited number of rhizoids produced on a few fragments (Table 3, Fig. 1). This difference was potentially due to differing responses to wounding. Even without a dissecting microscope, you could see large amounts of cytoplasm oozing from cuts of *H. tuna* when fragments were created in the laboratory (LJW, personal observation). Some smaller fragments lost so much cytoplasm immediately upon cutting that they died within the 8 days of the short-term trial. Many individuals of *H. tuna* that survived the initial cutting had large, visible, cytoplasm plugs that harbored substantial microbial communities. None of these fragments produced rhizoids. *H. tuna* was, however, the only species to generate new segments during the 14-week trial (Table 2).

4.1. Fragment success

Fragmentation studies to date have focused primarily on corals, especially hard corals, and fragment size has frequently been found to be positively correlated with both success and dispersal distances. Most of these studies involved fragments much larger than those used in our research (e.g. Loya, 1976; Highsmith, 1980). Bruno (1998), however, followed the fate of 60 small fragments (length: 2–13 cm, diameter: <1 cm) of the branching coral *Madracis mirabilis* for 11 months. He found limited dispersal (most <20 cm, maximum: 58 cm) in this species at 10 and 20 m after 11 months and distance was not related to fragment size (Bruno, 1998). There was also no relationship between fragment size and survivorship for fragments greater than 5 cm in length and he predicted that fragments died if buried. Unlike Bruno (1998), we found that larger

fragments of *Halimeda* were significantly more successful than small segments and that sedimentation did not necessarily kill fragments (Table 2, Fig. 1). Additionally, *Halimeda* fragments covered much greater distances, even under calm summer conditions on Conch Reef. The minimum distance covered after 4 days at 21 m was 13 cm for 0.5-segment fragments of *H. tuna* (diameter: 10 mm), while the maximum distance covered after 4 days was 57 cm for 6.5-segment, 15 mm long, fragments of *H. goreaui* (Table 8).

In the genus *Halimeda*, water motion can both create fragments (Walters and Smith, 1994) and disperse individuals. At our 21-m site on Conch Reef, flow rates between 10 and 30 cm/s have been recorded 3 m above the substratum and were associated with shoreward-moving internal waves 10 m in height (Leichter et al., 1996). Although flow rates recorded during our study at this depth were less than 10 cm/s, the higher flow rates as described by Leichter et al. (1996) would enable fragments to disperse over longer distances, and potentially increase genetic diversity of *Halimeda* on Conch Reef. Intense water motion associated with hurricanes, however, may significantly reduce the number of fragments on reefs, if fragments are lost from the system.

4.2. Grazing on Halimeda

Halimeda is chemically and structurally protected from predation (e.g. Ogden and Lobel, 1978; Littler and Littler, 1980; Paul and Fenical, 1983; Hay, 1984; Paul and Hay, 1986; Hay et al., 1988; Paul and Van Alstyne, 1988a,b). Younger segments have the highest concentrations of deterrent compounds, while older segments are protected by heavier calcification (Hay et al., 1988; Overholtzer and Motta, 1999). However, in the present study and studies by Targett et al. (1986) and Overholtzer and Motta (1999), certain herbivorous reef fish continuously grazed on *Halimeda.* Targett et al. (1986) found that individual fish persisted in foraging on *Halimeda* and bites were immediately rejected, suggesting rapid detection of antifeedant compounds. Overholtzer and Motta (1999) further determined that foraging was not random on shallow patch reefs in the upper-middle portion of the Florida Keys reef tract and that *H. opuntia* composed >50% of the diets of three species of juvenile scarids (blue parrotfish *Scarus coeruleus*, redband parrotfish *S. aurofrenatum*, stoplight parrotfish *S. viride*). Older, more-heavily calcified segments were preferentially consumed and fish became aggressive to obtain this resource when foraging in groups (Overholtzer and Motta, 1999). The mean number of bites ($\pm$ S.E.) of *H. opuntia* per 15-min intervals was 54.7 ± 18.7 for *S. viride*, 55.0 ± 28.5 for *S. aurofrenatum*, and 58.9 ± 31.9 for *S. coerulus* (Overholtzer and Motta, 1999). Our parrotfish foraging rates were very similar to these values (Table 7). This dietary choice by scarids may be the result of altered food availability on Florida reefs in recent years, with *Halimeda* being a better alternative than other available macroalgae. On Conch Reef, the brown alga *Dictyota* presently dominates the study areas (Beach et al., in preparation). Although fish continuously sampled *Dictyota*, most bites were immediately rejected and the dispersal shadow of *Dictyota* fragments was much smaller than that of *Halimeda* (Walters et al., in preparation).

In recent years, many coral reefs worldwide have changed from coral and sponge domination to being covered primarily by macroalgae (e.g. Lapointe, 1997). Researchers continue to debate if this change in reef community structure is the result of nutrient alterations in the water column (e.g. Lapointe, 1997, 1999), changes in the number and types of reef herbivores (e.g. Hughes et al., 1999; Miller et al., 1999), or both. In the Caribbean and Florida Keys, herbivorous sea urchins, in particular *Diadema*, removed large amounts of algal biomass on coral reefs until populations were wiped out by disease (e.g. Hughes et al., 1987). Macroalgae have since flourished in these waters, at least in part because herbivorous reef fish do not consume as much biomass as the urchins once did. Additionally, herbivorous reef fish may actually be propagating *Halimeda* on the reef when individuals reject and disperse fragments that can then continue to grow clonally. Damselfish "gardens" are the only other example of which we are aware where reef fish increase macroalgal abundances (Brawley and Adey, 1977).

4.3. Is fragmentation adaptive?

Is fragmentation adaptive for sessile invertebrates and algae? Are there differences between species that can have multiple reproductive events (e.g. corals) versus semelpareous organisms that reproduce only once (e.g. holocarpic species in the genus *Halimeda*)? Advantages of fragmentation may include: (1) extension of the distribution of genets and the species, (2) increases in the abundance of the organism and individual biomass and (3) colonization of areas where sexual propagules are unable to settle or early postsettlement mortality rates are high. Although early research found that fragmentation was beneficial (for review, see Bruno, 1998), more recently, researchers are finding that even if a large percentage of fragments are successful, overall fecundity is reduced in a variety of species (e.g. Zakai et al., 2000). For example, fecundity was significantly reduced in fragments of the coral *Acropora* spp. relative to source colonies and fragment mortality was high, especially when fragments dispersed to unfavorable habitats (Smith and Hughes, 1999). Likewise, Zakai et al. (2000) found that fragmentation reduced larval output by reducing tissue volumes in the coral *Pocillopora damicornis,* and Nagelkerken et al. (2000) found fragmentation of the coral *Madracis mirabilis* had significant detrimental effects on growth and survival. Thus, the costs of fragmentation outweigh the benefits for some marine organisms and this may be related to the organism's potential to successfully sexually reproduce. Additional research is needed to determine the costs and benefits of fragmentation for tropical macroalgae, especially species like *Halimeda*, which reproduce once and die.

In conclusion, the apparently simple life-history of *Halimeda* that is illustrated by a free-living phase that reproduces sexually (e.g. Clifton, 1997) can now be seen to also have a dynamic, asexual, fragmentation component that allows for long-term viability and reestablishment of fragments. Both short and long distance dispersal are promoted by hydrodynamic flow and fish grazing in reef settings. Species of *Halimeda* we have studied in Florida (*H. tuna*, *H. opuntia*, *H. goreaui*) and in Hawaii (*H. discoidea*) differ in capabilities for these fragmentation characteristics, suggesting strong selective advantages for at least some species traits.

Acknowledgements

Funding for this research was provided by N.O.A.A./National Undersea Research Center grants 94-19, 97-20, 98-14 and 99-27 to the authors. We are especially grateful for the tremendous day boat and Aquarius support while working at the NURC Florida Keys research program; Dr. S. Miller, C. Cooper, O. Rutten, D. Ward and the entire NURC staff made our work much more efficient and productive. We also thank C. Roberts, Dr. G. Bernaldi, D. Stellar, Dr. B. Konar, N. Crane, D. Pence, J. Zamzow and Dr. P. Sacks for help in the field and laboratory, and two anonymous reviewers for reading drafts of this manuscript. **[AU]**

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