### Gigartinales symposium

### Applying flow tank measurements to the surf zone: Predicting dislodgment of the Gigartinaceae

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#### SUMMARY

Our understanding of how flow affects the survival of members of the Gigartinaceae has advanced considerably in recent years. In particular, methods have been developed that give phycologists a powerful tool with which to predict mechanistically the survival of waveswept macroalgae. One limitation of such methods, however, is the lack of hydrodynamic data for macroalgae in surf-zone flows. The method instead relies upon the extrapolation of low-velocity flow tank measurements (< 3.5 m s<sup>-1</sup>) to velocities well beyond their measured range (10-20 m s<sup>-1</sup>). Such extrapolation is particularly tenuous for flexible organisms, such as macroalgae, that can reconfigure in flow. This study uses three members of the Gigartinaceae to evaluate two commonly used methods for extrapolation of flow tank data to high water velocities: one that allows for continued thallus reconfiguration at extreme water velocities and one that does not. Limitations of both models are evident and underscore the need for improved measures of force generation on macroalgae exposed to extreme flows. Additionally, the extent to which the mechanical design might influence life history traits of the Gigartinaceae is discussed.

Key words: dislodgment, drag, Gigartinaceae, hydrodynamic force, *Mastocarpus, Mazzaella*, mechanical design, wave exposure.

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### INTRODUCTION

The survival of macroalgae on rocky shores is, in part, due to their ability to weather the hydrodynamic forces generated by breaking waves. In the surf zone, water motion subjects attached macroalgae primarily to the hydrodynamic force of drag, which tends to push a thallus downstream and challenges its strength of attachment (Gaylord 1997). This water motion can range from 10 to 20 m s<sup>-1</sup> for highly wave-exposed shores, 3-7 m s<sup>-1</sup> for moderately protected shores and < 1 m s<sup>-1</sup> for calm harbors and bays (Jones and Demetropoulos 1968; Denny 1985, 1988; Bell and Denny 1994;

Gaylord 1997). How much water motion can a given alga withstand? To address this question, Denny (1995) developed a mechanistic approach that utilizes field measurements of attachment strength and flow tank measurements of hydrodynamic forces to predict dislodgment of wave-swept organisms for a given flow regimen.

While the approach of Denny (1995) is extremely powerful and has greatly improved our understanding of wave-induced disturbance to marine communities, it is not without its limitations. In particular, the approach requires an understanding of the manner in which moving water generates forces on sessile organisms. Such data are typically obtained from flow tank experiments that are limited to velocities below 3.5 m s<sup>-1</sup> [e.g. Carrington ( = Bell) 1990; Dudgeon and Johnson 1992; Gaylord et al. 1994]. Thus, considerable extrapolation of the data is required in order to predict dislodgment of organisms on highly wave-exposed shores. Such extrapolation is particularly tenuous for flexible macroalgae that can reconfigure and assume a more streamlined shape in flow (Carrington 1990; Vogel 1994). How much do flexible macroalgae continue to reconfigure in flows beyond 3.5 m s<sup>-1</sup>?

The purpose of this study is to evaluate two common methods for extrapolating hydrodynamic data to higher water velocities. Three species common to wave-swept shores of the west coast of North America are considered: Mastocarpus papillatus (C. Agardh) Kützing, Mazzaella flaccida (Setchell et Gardner) Fredericq [formerly Iridaea flaccida (Setchell et Gardner) Silva] and Mazzaella leptorhynchos (J. Agardh) Leister (formerly Gigartina leptorhynchos J. Agardh). These species were selected because all of the necessary biomechanical data needed for the present analyses are available from previous studies (Carrington 1990; Gaylord et al. 1994; Denny 1995). Furthermore, they are closely related (as members of the Family Gigartinaceae), yet vary considerably in their morphology and distribution with respect to wave action. Mazzaella

Email: <bell@uri.edu> Communicating editor: S. C. Lindstrom Received 7 February 1999; accepted 25 May 1999. *flaccida* is a broad, smooth, flat alga found on fully exposed shores, *M. leptorhynchos* is a highly textured, multibranched alga restricted to moderately protected shores and *Mastocarpus papillatus* is an intermediately branched and textured alga most commonly found on moderately protected shores, but can be found on exposed shores as well (Abbott and Hollenberg 1976; Bell 1992; Gaylord *et al.* 1994).

### MATERIALS AND METHODS

# Predicting dislodgment of the Gigartinaceae

A simplified version of the six-step mechanistic approach of Denny (1995) is used in this study. Specifically, a range of water velocities (5–20 m s<sup>-1</sup>) is used to calculate hydrodynamic forces and risk of dislodgment for a given thallus size (steps 5–6). The lengthy calculations of Denny's steps 1–4 do not affect the conclusions of this study and are consequently omitted. The simplified approach that follows is tailored to macroalgae in the surf zone.

The primary hydrodynamic force experienced by macroalgae in the surf zone is drag, which tends to push a thallus downstream and challenge its strength of attachment (Gaylord 1997). As described by Vogel (1994), drag ( $F_{drag}$ ) is traditionally modeled by the equation:

$$F_{\rm drag} = \frac{1}{2} \rho \ U^2 \ C_{\rm d} \ A \tag{1}$$

where  $\rho$  is seawater density (1025 kg m<sup>-3</sup>), *U* is water velocity (in m s<sup>-1</sup>), *C*<sub>d</sub> is the drag coefficient (a dimensionless index of streamlining) and *A* is thallus area (in m<sup>2</sup>). In flow tank experiments by Carrington (1990), Dudgeon and Johnson (1992), Gaylord *et al.* (1994) and others, it has been shown that a macroalgal thallus typically reconfigures and collapses into a more streamlined shape with increasing flow. Following the convention of Vogel (1984), the dependence of drag coefficient on flow can be described by the model

$$C_{\rm d} = S_{\rm d} U^{\rm E} \tag{2}$$

where  $S_d$  is the shape coefficient of drag (Denny 1995) and *E* describes the dependence of drag coefficient on water velocity. *E* for a rigid, bluff body is zero (drag coefficient is constant with flow), while *E* for a flexible, reconfiguring object, such as a macroalga, is typically negative. Vogel (1994) provides a more detailed discussion of *E*. Note that E + 2 is equivalent to the velocity exponent of drag,  $\beta$ , introduced by Denny (1995).

While drag coefficients, and their dependence on U, have been measured for a number of macroalgal species (Carrington 1990; Gaylord *et al.* 1994), they are limited to the relatively low velocities characteristic of protected shores (< 3.5 m s<sup>-1</sup>). In order to predict hydrodynamic forces on macroalgae on more wave-

exposed shores it is necessary to extrapolate these measurements to much higher water velocities (10 or even 20 m s<sup>-1</sup>; Jones and Demetropoulos 1968; Denny 1985, 1988; Bell and Denny 1994; Gaylord 1997). Two different methods of extrapolation are common in the literature and will be compared in this study. In model A, used by Gaylord *et al.* (1994) and Denny (1995), the model of (2) was applied to higher water velocities. That is, a thallus was assumed to continue to reconfigure with ever increasing water velocity. In model B, used by Carrington (1990), Shaughnessy *et al.* (1996), and Blanchette (1997), it is assumed that thallus reconfiguration is a low-velocity phenomenon and that drag coefficient is constant beyond some critical water velocity (e.g. 2.5-3.5 m s<sup>-1</sup>).

Measurements of drag coefficient as a function of velocity were obtained from the literature (Carrington 1990; Gaylord *et al.* 1994) and pooled for each of the three test species. The model of (2) was fitted to the data, using a non-linear, iterative regression of the form  $y = ax^b$  (SigmaPlot 4.01, SPSS Inc., N. Chicago, IL, USA). For subsequent analyses, this curve-fit was used: (i) to predict a decreasing  $C_d$  as a function of water velocity (model A); and (ii) to calculate a constant  $C_d$  for a given  $U_{crit}$  (Model B).  $U_{crit}$  was assumed to be 3.5 m s<sup>-1</sup>, the upper velocity limit of the flow tank data. For each species, hydrodynamic force was calculated according to (1) for a range of water velocities and thallus planform areas.

$$F_{\text{break}} = \mathbf{j} + \mathbf{m}A^{\mathbf{q}} \tag{3}$$

The probability that a given hydrodynamic force would dislodge a thallus from its substrate was calculated from field measurements of attachment strength obtained from Denny (1995). The force required to break a thallus,  $F_{\text{break}}$ , was modeled to be an allometric function of thallus area:

where j, m and q are allometric constants reported by Denny (1995) and are listed for each species in Table 1. Each  $F_{drag}$  estimate was divided by its corresponding  $F_{break}$  prediction, yielding a normalized force,  $F_n$ . Note that  $F_n$  is a dimensionless force ratio and follows the convention of Denny (1995). The probability,  $P(F_n)$ , that an individual chosen at random will be dislodged by a given  $F_n$  was then calculated using the cumulative probability distribution:

$$P(F_{\rm n}) = \exp\{-[(a - bF_{\rm n})/(a - bc)]^{1/b}\}$$
(4)

where a, b, and c are parameters derived from measurements of attachment strength. Parameter values for each species were obtained from Denny (1995) and are listed in Table 2.

For comparison with the model predictions, mean thallus size of a field population was obtained for each species from Bell (1992) and Gaylord *et al.* (1994). The locations of these populations were similar (or even identical) to those used by Bell and Denny (1994) to

quantitate water velocities in the surf zone. Thus, it was possible to assign a typical winter water velocity for the moderately protected populations of *M. papillatus* and *M. leptorhynchos* and the wave-exposed population of *M. flaccida.* These data are summarized in Table 3.

## Monitoring field populations of *Mastocarpus papillatus*

For a more detailed evaluation of the model predictions, rates of dislodgment and standing biomass were monitored for three populations of *M. papillatus* in Monterey County, California. Two of the sites were adjacent to Hopkins Marine Station (36°37′N, 121°54′W): Agassiz Beach (protected from direct wave exposure by an off-shore rocky outcrop) and West Beach (often exposed to large breaking waves). A third site was located on the wave-exposed open coast approximately 20 km to the south (36°27′N, 121°56′W), either adjacent to the Granite Canyon Marine Laboratory (dislodgment rate monitoring) or Garrapata State Beach (standing biomass monitoring).

To monitor dislodgment rate at each of the three sites, five permanent  $0.35 \times 0.25$  m rectangular quadrats that contained a healthy abundance of *M. papillatus* thalli were established in October 1989. Within each quadrat, 10 thalli were haphazardly selected and tagged, for a total of 50 tagged thalli at each site. Approximately every 2 weeks, each thallus was counted and a new thallus was tagged to replace any that could not be found (to maintain 10 thalli in each quadrat). A census was repeated bimonthly until February 1991 and dislodgment for each quadrat was calculated as the fraction of thalli missing since the previous census.

Thalli were tagged around the stipe with vinyl

 Table 1. Model parameters for breaking force as a function of thallus area (equation 3) obtained from Denny (1995)

Species	j	m	q
Mastocarpus papillatus	2.634	0	_ a
Mazzaella flaccida	12.09	0	_ a
Mazzaella leptorhynchos	2.231	31.936	0.353

 $^{a}\textsc{Breaking}$  force is size-independent for this species, thus m=0 and the computation of q is unnecessary.

'fingerling' thread (0.4 mm diameter, Floy Tag and Manufacturing Inc., Seattle, WA, USA). Approximately 5 cm of thread was knotted loosely around each stipe and a 0.3 mm length of aluminum tubing (2.5 mm outer diameter, numbered individually with a small wire marker and coated with lacquer) was crimped around the thread ends. The tags did not visibly abrade the stipe and, when attached to nearby anchored objects as a control, remained intact for months (longer than any single thallus remained tagged during the experiment).

Standing biomass was monitored monthly from October 1988 to February 1991. At each site, a 10 m horizontal transect was placed at approximately + 1.0 m above MLLW (the vertical position of maximal biomass). A square quadrat  $(0.125 \times 0.125 \text{ m}, \text{ or } 0.0156 \text{ m}^2)$  was placed at 10 random positions along the transect and all of the thalli falling within the quadrat were collected. At Garrapata, where the population density was lower than the other two sites, a larger quadrat  $(0.25 \times 0.25 \text{ m}, \text{ or } 0.0625 \text{ m}^2)$  was used. The collected thalli were pooled by site, rehydrated in sea water for 6–24 h, blotted dry and weighed to the nearest 0.01 g. Standing biomass was calculated as the total fresh weight of the thalli divided by the total area sampled.

### RESULTS

### Predicting dislodgment of the Gigartinaceae

Drag coefficient measurements obtained from the literature are shown in Fig. 1. For water velocities up to  $3.5 \text{ m s}^{-1}$ , a substantial reduction in drag coefficient with increasing velocity occurs in all three species. E is negative for each species, indicating thallus reconfiguration with increasing flow (Table 4). On extra-

 
 Table 2.
 Model parameters for cumulative probability distributions of normalized force (equation 4) obtained from Denny (1995)

Species	а	b	С
Mastocarpus papillatus	0.5015	0.0596	0.7585
Mazzaella flaccida	0.3926	0.1599	0.8971
Mazzaella leptorhynchos	0.3757	0.1290	0.8808

Table 3. Mean thallus area and wave exposure for field populations of the three test species

Species	Thallus area (cm <sup>2</sup> )	Wave exposure	Velocity (m s <sup>-1</sup> ) <sup>a</sup>	Source
Mastocarpus papillatus Mazzaella flaccida	80 83	Moderately protected	5 10–20	Bell (1992) Gaylord <i>et al.</i> (1994)
Mazzaella leptorhynchos	39	Moderately protected	5	Gaylord <i>et al.</i> (1994)

<sup>a</sup>From Bell and Denny (1994), where 'moderately protected' and 'exposed' correspond to Agassiz Beach and West Beach, California, respectively.



**Fig. 1**. Drag coefficient as a function of water velocity. Data obtained from flow tank experiments of Carrington (1990) and Gaylord *et al.* (1994). Model A (—) and model B (----) were used to extrapolate the data to higher water velocities. (a) *Mastocarpus papillatus*, (b) *Mazzaella leptorhynchos*, (c) *Mazzaella flaccida*.

 Table 4.
 Model parameters for drag coefficient as a function of water velocity (equation 2)

Species	$S_{d}$	E	<b>r</b> <sup>2</sup>	п
Mastocarpus papillatus	0.1564	-0.3665	0.175	139
Mazzaella flaccida	0.1118	-0.8768	0.728	6
Mazzaella leptorhvnchos	0.1655	-0.5637	0.870	5

polation of the data to higher water velocities, model A yields lower predictions of drag coefficient than model B (Fig. 1a–c). For the extreme water velocity of 20 m s<sup>-1</sup>, the difference between the two models is 1.9, 2.7 and 4.6-fold for *M. papillatus*, *M. leptorhynchos*, and *M. flaccida*, respectively.

Predicted probability of dislodgment as a function of thallus area and water velocity is shown for each species in Fig. 2. For a given thallus area and water velocity, model A yields a lower predicted probability of dislodgment than model B (compare solid and dashed lines for a given water velocity). However, there is very little difference between the predictions using model A and model B for *M. papillatus*. For a thallus of mean size on a moderately protected shore (8 cm<sup>2</sup>, 5 m s<sup>-1</sup>; Table 3), the probability of dislodgment is 0.08 and 0.10 using model A and model B, respectively. Only very small *M. papillatus* thalli are predicted to survive on fully exposed shores.

Compared to *M. papillatus*, there is a greater difference between the predicted probabilities using model A and model B for *M. leptorhynchos*. For a thallus of mean size on a moderately protected shore (39 cm<sup>2</sup>, 5 m s<sup>-1</sup>; Table 3), the probability of dislodgment is 0.02 and 0.06 using model A and model B, respectively.

For *M. flaccida*, the difference between the predictions using model A and model B is considerable. For example, a thallus of mean size (approximately 80 cm<sup>2</sup>) exposed to a 10 m s<sup>-1</sup> water velocity has a probability of dislodgment of 0.02 using model A, and 0.85 using model B.

### Monitoring field populations of Mastocarpus papillatus

Dislodgment in natural populations of *M. papillatus* was extremely variable, typically ranging from 10 to

40% (data not shown). No differences in dislodgment between the three populations were evident, so the populations were pooled to increase sample size and emphasize seasonal trends (Fig. 3). The mean biweekly dislodgment rate typically fell within the range of 15–20%, with occasional peaks in dislodgment in winter, early summer and early fall. All three populations of *M. papillatus* showed seasonal trends in biomass, with peaks in late summer to early fall and reduced biomass in winter and spring (Fig. 4).



**Fig. 2**. Probability that a thallus of a given area will be dislodged by a given water velocity (5, 10 or 20 m s<sup>-1</sup>). Model A (—) and model B (----) were used to extrapolate drag coefficient to higher water velocities. Dotted vertical line represents mean thallus area. (a) *Mastocarpus papillatus*, (b) *Mazzaella leptorhynchos*, (c) *Mazzaella flaccida*.



**Fig. 3**. Dislodgment of *Mastocarpus papillatus* thalli in Monterey County, California, pooled from three populations. Data are mean  $\pm$  SE, n = 14.



**Fig. 4**. Monthly biomass measurements of three *Mastocarpus* papillatus populations in Monterey County, California. (●) Agassiz Beach, (○) West Beach, (▼) Garrapata State Beach.

### DISCUSSION

In the mechanistic approach to predicting the probability of dislodgment, is model A or model B more appropriate for the extrapolation of drag coefficient to higher velocities? A proper evaluation of the predictions presented here would require simultaneous measures of thallus size, water velocity and survival rates for field populations of each of the three test species. Such data are simply unavailable for the Gigartinaceae. However, general estimates of thallus area and water velocity can be extracted from the literature and rates of dislodgment in field populations of *M. papillatus* are provided by this study. While these latter data are highly variable and do not specify thallus size, they do provide a crude guideline with which to evaluate the predictions. For the three species considered in this study, a 'typical' probability of dislodgment of 0.20 is assumed for a thallus of mean size.

The two models for extrapolating drag coefficient to higher water velocities yield very similar predictions of dislodgment probability for *M. papillatus*, both of which appear reasonable. For a thallus of mean area on a moderately protected shore (80 cm<sup>2</sup>, 5 m s<sup>-1</sup>), a predicted probability of approximately 0.10 is only slightly lower than the assumed typical value of 0.20. Furthermore, both models predict larger thalli (25 cm<sup>2</sup>) to be present (albeit infrequently) on moderately exposed shores, but only small thalli to be present on exposed shores (< 4 cm<sup>2</sup> for model A; < 2.5 cm<sup>2</sup> for model B; 10–20 m s<sup>-1</sup>). These predictions, particularly those of model A, are consistent with the general observations of Bell (1992), where very large thalli are restricted to sheltered shores.

The differences between the predicted probability of dislodgment using model A and model B are more apparent for *M. leptorhynchos* than for *M. papillatus*. While model A was perhaps more appropriate for *M. papillatus*, this does not appear to be the case for *M. leptorhynchos*. For example, the predicted probabilities based on model A suggest that thalli approximately 100 cm<sup>2</sup> are common on moderately protected shores and thalli approximately 20 cm<sup>2</sup> are common on exposed shores. These predictions are not consistent with the general observations of Gaylord *et al.* (1994), where *M. leptorhynchos* was absent on exposed shores. Thus, the predictions using model B best match the limited observations of field populations that are currently available for *M. leptorhynchos*.

The differences between the predicted probability of dislodgment using model A and model B are most striking for *M. flaccida*. Model B leads to the absurd prediction that a thallus of mean size could not survive in its typical habitat. The predictions based on model A are more reasonable, but probably overestimate the typical size of a thallus on a fully exposed shore. Thus the 'correct' model is likely somewhere in between. The large discrepancy between the two models is due to the four-fold difference in predicted drag coefficient at extreme water velocities  $(10-20 \text{ m s}^{-1})$ .

Upon visual inspection of the measured drag coefficients as a function of water velocity, it is not clear why one model for extrapolation should be more appropriate for one species than another. At high water velocities, model A yields consistently lower drag coefficients than model B for each of the three test species. The difference between the two extrapolations is fairly modest for *M. papillatus* and *M. leptorhynchos*, but guite striking for M. flaccida. Thus the species with the most negative E (M. flaccida) leads to the greatest discrepancies between the two models. It is interesting to note that the estimation of E for *M. flaccida* is strongly influenced by the rapid decrease in drag coefficient measured at very low water velocities  $< 0.5 \text{ m s}^{-1}$ , where the flat, flexible thallus initially comes into alignment with the oncoming flow. Once a flat thallus has achieved this alignment with flow, however, it seems unlikely that additional flow could accomplish substantial further thallus reconfiguration. The unreasonable predictions of model B indicate that a  $U_{\rm crit}$  of 3.5 m s<sup>-1</sup> is insufficient to accomplish this reconfiguration process in M. flaccida. The addition of drag coefficients measured at higher water velocities (perhaps even to 5 m s<sup>-1</sup>) may greatly improve the extrapolation process for this species. Until such data are available, the influence of thallus morphology and flexibility on reconfiguration and drag remain poorly understood.

Vogel (1994) includes a stern warning against the extrapolation of drag coefficients to velocities well beyond their measured range. Yet, in order to evaluate the mechanical limitations of surf-zone organisms and their pivotal role in structuring marine communities, even the crudest of predictions can be of value. That the predictions of the mechanistic approach presented here are consistent with fairly limited observations of field populations is encouraging. However, the discrepancy between the two models used in the predictions for M. flaccida underscore the need for a better understanding of reconfiguration and force generation in macroalgae at high water velocities  $(10-20 \text{ m s}^{-1})$ . Two experimental devices have recently been developed that can address this issue: (i) Utter and Denny (1996) describe a 'wing' to tow objects, such as macroalgae, alongside a boat traveling at a known speed; and (ii) Gaylord (1997) developed instrumentation capable of simultaneous measurements of force generation on a macroalga and water velocity in the surf zone. These devices have produced promising results, but have yet to be applied to the Gigartinaceae.

Note that drag is the only hydrodynamic force considered in this study. The relative contribution of accelerational forces, once thought to be very important for macroalgae in the surf zone (Gaylord *et al.* 1994), has recently been questioned by Gaylord (1997). The

present study provides a reanalysis of the data of Gaylord *et al.* (1994) with the accelerational forces omitted and indicates that drag alone can limit the maximum size of all three species. This is contrary to the conclusions of Gaylord *et al.* (1994), but consistent with the more recent study of Gaylord (1997).

Some aspects of the mechanical design of other members of Gigartinaceae have been addressed as well. Dudgeon and Johnson (1992) compared the risk of dislodgment of *Chondrus crispus* Stackhouse and *Mastocarpus stellatus* (Stackhouse) Guiry on New England shores and Shaughnessy *et al.* (1997) compared the risk of dislodgment of *Mazzaella linearis* (Setchell *et* Gardner) Fredericq and *Mazzaella splendens* (Setchell *et* Gardner) Hommersand on the coast of British Columbia, Canada. While the data in these studies are not sufficient to include in the analyses presented here, they do allow for some broad generalizations about the mechanical design of the Gigartinaceae to be drawn:

1. The stipe is the most common location of mechanical failure (Carrington 1990; Shaughnessy *et al.* 1996).

2. The stipe does not increase substantially with thallus size. As a result, attachment force is relatively fixed and dictates a mechanical limit to thallus size for each species (Carrington 1990; Dudgeon and Johnson 1992; Shaughnessy *et al.* 1996).

3. Maximum thallus size decreases with increasing water velocity. For any given species, only relatively small blades are able to persist on wave-exposed shores (Shaughnessy *et al.* 1996).

4. Dislodgment is seasonal. Thalli may grow without mechanical constraint during calm periods (e.g. summer), but suffer high mortality during extreme storm conditions (Bell 1992; present study).

Thus, for the members of the Gigartinaceae considered here, flow is predicted to affect both the size and survival of a thallus. Heavy winter storms are effective in removing the 'annual' thallus, while a 'perennial' holdfast is left behind to maintain space on the shore and generate new thalli year after year. For *M. papillatus*, this perennial holdfast is haploid and is distinct from the diploid 'petrocelis' stage (a perennial crust).

The above scenario, where an increase in mechanical failure during extreme flow conditions, rather than senescence, leads to an effectively annual life span, does not necessarily apply to all surf-zone algae. In *Fucus gardneri* Silva, for example, thallus failure occurs in the distal branches rather than the stipe (Blanchette 1997). With this alternative mechanical design, extreme flows merely prune back the thallus, but do not cause dislodgment. The result is a perennial thallus whose size, but not survival, is affected by extreme flow.

Based on these observations, it appears that the mechanical design of a macroalga and its life history strategy may be intertwined (Table 5). An annual

Table 5. Comparison of the mechanical design and life history characteristics of members of the Gigartinaceae and *Fucus gardneri* 

	Gigartinaceae	Fucus gardneri
Location of 'weak link'	Stipe	Distal branches
Result of mechanical failure	Dislodgment	Size reduction
Life span	Annual	Perennial
Size-dependent survival	Yes	No

thallus is not necessarily one that senesces each winter, but instead may be one that suffers catastrophic mortality during periods of extreme flow. Because the weakest portion of the thallus is in the stipe, mechanical failure results in the loss of the entire thallus. Mortality is likely to be particularly high when relatively calm periods that have allowed for extensive growth (increasing A) are followed by periods of extreme flow (increasing U). Many members of the Gigartinaceae fit this general model (C. crispus, M. papillatus, M. stellatus, M. flaccida, M. leptorhynchos, M. linearis, *M. splendens*), and it may prove to apply to many other genera in this group as well. The alternative mechanical design of F. gardneri, where pruning of excessive growth allows for survival in extreme flows, leads to a sturdy perennial thallus (Blanchette 1997).

Note that the model for seasonal increases in dislodgment of Gigartinaceae assumes that the stipe strength is constant, as has been shown for *M. papillatus* (Carrington 1990). However, the thallus tissue of this species has been shown to degenerate in winter (Bell 1992) and this degeneration may be an important factor in the observed seasonal loss of biomass. Further studies with other genera, evaluating the effects of season, reproductive status, life history phase and nutritional state on tissue strength, are sorely needed, and will likely blur the strong distinctions between an annual and perennial thallus drawn in this study.

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