Organismal defenses versus environmentally mediated protection from herbivores: Unraveling the puzzling case of *Desmarestia viridis* (Phaeophyta)

Patrick Gagnon a,⁎, Louis Vincent St-Hilaire-Gravel 1, John H. Himmelmana, Ladd E. Johnsona

a Département de biologie and Québec-Océan, Université Laval, Québec City, Québec, Canada, G1K 7P4

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Abstract

The role of anti-herbivore organismal defenses in algae–herbivore interaction is frequently investigated without taking into account the potential role of environmental factors in mediating the interaction. Here we reexamine the interaction between the highly acidic, brown alga *Desmarestia viridis* and the green sea urchin, *Strongylocentrotus droebachiensis*, by incorporating a previously overlooked facet, the effect of changes in the wave environment on the ability of the urchin to establish contact with the alga. Factorial experiments in a wave tank (presence versus absence of waves; real versus mimic algae) showed that the aggregation of urchins on *D. viridis* was more than 2-fold greater in the absence than in the presence of waves. Similar numbers of urchins made contact with natural and mimic *D. viridis* plants, both with and without waves, indicating that any external release of chemicals (acid) from the alga had no perceptible repulsive effect on the urchin. The ability of the urchins to climb onto *D. viridis* increased markedly when urchin density attained a critical level. These results were consistent with field observations that urchins readily attack *D. viridis* under conditions of low wave action but do not under conditions of moderate wave action. We conclude (1) that the chemical makeup of *D. viridis* alone is neither necessary nor sufficient to limit contacts by the urchins and that (2) wave action is a major factor explaining the survival of *D. viridis* on urchin barrens, because waves limit the movements of the urchins towards the alga. We recommend that studies addressing marine algal defenses against herbivores be more comprehensive and examine interactions between algal traits, the physical environment, and the abundance and behavioral repertoire of herbivores.

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1. Introduction

Herbivory is ubiquitous in marine communities, and the substantial increase in studies on algae–herbivore interactions over the last two decades has led to a better understanding of the processes regulating populations and communities (e.g. Menge, 1976; Lubchenco and Gaines, 1981; Dayton, 1985b; Hay and Fenical, 1988;
Sousa and Connell, 1992). Although there is a legitimate, growing interest in the study of anti-herbivore organismal (chemical and morphological) defenses in marine algae (Duffy and Hay, 1990; Hay et al., 1994; Borell et al., 2004), less attention has been devoted to other defensive mechanisms, such as spatial and temporal escapes and species associations, which may also be important (Hay, 1986; Pfister and Hay, 1988; Gagnon et al., 2003b).

Even less explored is the potential for variation in environmental conditions to mediate subtidal algae–herbivore interactions in a way that increases the survival of an alga by reducing foraging by herbivores. For example, the potential effect of such factors on the encounter rates between an herbivore and its algal prey—the very first parameter determining the level of possible damages inflicted to an alga (Lubchenco and Gaines, 1981)—has been largely overlooked. Water motion (waves and tidal currents) is an important factor in shallow, marine coastal habitats (Denny, 1988) and has been shown to influence individual behaviors and ultimately shape apex predator–prey interactions (Rochette et al., 1994; Addy and Johnson, 2001; Hunt and Scheibling, 2001; Gagnon et al., 2003a). Thus, models of algal defenses against herbivores that do not incorporate the effect of water motion on the ability of herbivores to establish contact with their algal prey may have only limited applicability.

A classic example of a putative chemical defense is found in the brown algal order Desmarestiales, where certain species produce and store high concentrations of sulfuric acid (H₂SO₄) within cell vacuoles, resulting in extremely low internal pH (down to ~0.5 pH, Eppley and Bovell, 1958; McClintock et al., 1982; Thompson, 1988). A number of studies have proposed that this trait chemically repulses grazers (Anderson and Velimirov, 1982; Dayton, 1985a; Himmelman and Nédélec, 1990; Gagnon et al., 2003b). However, this idea has only recently received experimental support: the addition of sulfuric acid to an agar-based food source reduced urchin feeding rates in the laboratory (Pelletreau and Muller-Parker, 2002). On the other hand, urchins have been observed to feed readily on Desmarestia spp. under conditions of low water motion (Himmelman and Steele, 1971; Cowen et al., 1982; Konar, 2000), suggesting that the chemical nature of the latter works in conjunction with other factors (e.g. aspects of the abiotic environment, availability of alternative prey) to allow their survival in urchin-dominated environments.

In the Mingan Islands, northern Gulf of St. Lawrence (Québec, Canada), the green sea urchin, Strongylocentrotus droebachiensis, dominates the rocky subtidal zone and its grazing leads to the formation of extensive “urchin barrens” (Himmelman, 1991), where fleshy macrophytes are mostly absent. One exception is Desmarestia viridis, an annual alga that occurs exclusively on barrens, either individually or in small groups (Fig. 1). It has a small holdfast, a thin, highly flexible stipe, and a profusely-branched, filamentous frond that can measure up to 1.5m in length. The occurrence of D. viridis in this intensively grazed environment, along with its known high acidity (McClintock et al., 1982), suggests that it repels or deters urchins using chemicals. Several observations support this idea. First, field

![Fig. 1. An isolated Desmarestia viridis (~60cm in length) surrounded by a dense aggregation of green sea urchins, Strongylocentrotus droebachiensis, at 5m in depth on a gently-sloped, moderately exposed bedrock platform in the Mingan Islands, eastern Canada.](image-url)
experiments comparing the degree to which urchins move towards monospecific bundles of various algae have revealed that urchins are weakly attracted to *D. viridis* (Himmelman and Nédélec, 1990). Second, *D. viridis* is consumed at low rates in the laboratory compared to preferred algae such as the kelps *Aralia esculenta* and *Laminaria* spp. (Vadas, 1977; Larson et al., 1980; Himmelman, 1984; Himmelman and Nédélec, 1990).

Other characteristics might also explain the survival of *D. viridis* on urchin barrens. Observations and experiments have shown that urchins are much less abundant under a *D. viridis* canopy than in surrounding areas (Himmelman, 1984; Gagnon et al., 2003b), and that urchins may retract to deeper water as dense stands of *D. viridis* develop at the lower edge of kelp beds (Scheibling et al., 1999). This pattern may be because urchins avoid tactile contact with agitated algal fronds (i.e., a mechanical abrasion) as experimentally demonstrated in Alaska (Konar, 2000). Alternatively, it could be that urchins are repelled by chemicals released as the fronds sweep over the bottom (the “acid broom” hypothesis, Dayton, 1985a). These alternatives both represent environmentally mediated defenses in which the efficiency of the organismal trait (chemical or morphological) is mediated by an environmental condition, water motion in these cases. An even simpler hypothesis is that environmental conditions directly control the behavior of the urchin. For example, the urchin *Strongylocentrotus nudus* decreases its displacement in response to increased water motion (Kawamata, 1998). In a similar way, hydrodynamic forces created by water motion may reduce displacement of *S. droebachiensis*, thus indirectly protecting *D. viridis*. However, the degree of protection may be influenced by urchin density as several studies have suggested a threshold density of urchins is needed before urchins can anchor and consume preferred algal species (Bernstein et al., 1981; Scheibling et al., 1999; Gagnon et al., 2004). Thus, there may be a density-dependant relationship in the attack success of *S. droebachiensis* on *D. viridis*.

In this study we use laboratory microcosms and field observations to determine whether the chemistry of *D. viridis*, the intensity of the wave environment, and the density of urchins affect the level of encounters between urchins and *D. viridis*. We show that water motion alone can explain variation in attack success and that the chemical nature of this alga has little effect on the degree to which urchins make contact with it, this initial step in any urchin–algal interaction.

### 2. Methods

Our study was conducted in the Mingan Islands in the northern Gulf of St. Lawrence, eastern Canada (50°13′6″N, 63°41′12″W). Experiments were conducted in an indoor wave tank using the green sea urchin, *S. droebachiensis*, and the brown alga *D. viridis*, both of which were collected at depths of 3–8m around Île aux Goélands, an island located ~5km from the laboratory at Havre-Saint-Pierre.

#### 2.1. Algal chemistry and the wave environment

To determine the possible impact of any external release of chemicals by *D. viridis* and of hydrodynamic conditions on encounters between the urchin and the alga, we quantified the tendency of the urchins to move and the extent to which they aggregated on *D. viridis* and on an algal mimic in a wave tank. The algal mimics were cotton mop heads, which reproduced both the filamentous nature and the water-induced movements of *D. viridis*. To experimentally assess the relative importance of these factors, we used a wave tank to conduct a laboratory experiment involving a factorial design with six treatments: (1) the absence of *D. viridis* and waves as a control for urchin displacement, (2) the presence of waves alone to quantify the effect of water motion on urchin displacement, (3) the presence of a cotton mop without waves to measure the tendency of urchins to aggregate on a *D. viridis*-like mimic, (4) the presence of a cotton mop and waves to measure the tendency of urchins to aggregate on a sweeping *D. viridis*-like mimic, (5) the presence of *D. viridis* without waves to quantify the vulnerability of *D. viridis* to urchin contact in the absence of wave action, and (6) the presence of *D. viridis* with waves that caused a 10cm sweep of the fronds to investigate wave-induced changes in protection. We defined “sweep” as the amplitude of the back and forth movement of the tips of peripherally protruding algal filaments across the bottom in the direction of the wave surge (i.e. the marginal extension of the area touched by the alga). The sweep was small relative to the total length of the alga. For example, a 50–60cm *D. viridis* plant had a sweep amplitude of about 10cm during moderate wind conditions (~30km h⁻¹). Given that the mop head was 100% cotton, we assumed that its release of chemicals (especially sulfuric acid) was negligible.

The wave tank has been described previously (Gagnon et al., 2003a). In brief, a pulley system controlled the back-and-forth water motion and thus...
the sweeping motion of \textit{D. viridis}. The tank was 1.94 m in length, 1.22 m wide and 0.48 m deep, and the depth of the water column in each trial was 23 cm. The bottom was completely covered with concrete tiles which had their upper surfaces sculpted with undulations, holes and cracks to simulate the irregularities of a natural rocky bottom. Each corner of the tank was illuminated by a 150W floodlight positioned 90 cm above the bottom. For treatments with \textit{D. viridis} and the algal mimic, either a new plant (50–60 cm in length) or a mop head with 50 cm long cotton filaments was attached with a plastic cable tie to an eye-bolt at the center of the tank. For the treatments with water motion, the system was set up to generate 23 wave cycles per minute, equivalent to the wave frequency under moderate winds at our collection site (Île aux Goélands). The tank was 1.94 m long × 2.5 m high) were exposed during the trials with waves only (the same wave amplitude that caused a 10 cm sweep by \textit{D. viridis}) were determined as described by Gagnon et al. (2003a). The urchins experienced a moderate degree of turbulence that was mainly due to longitudinal (\textit{x}-axis) flow (\textit{Re}=5106; mean current velocity was \textasciitilde 0.19 m s\(^{-1}\)) and peak velocity was \textasciitilde 0.30 m s\(^{-1}\)), and to a lesser extent to lateral (\textit{y}-axis) flow (\textit{Re}=2553) (a flow with \textit{Re}>2000 is considered turbulent, Denny, 1988). Vertical flow (\textit{z}-axis) was weaker (\textit{Re}=798). These hydrodynamic forces were similar to summer conditions observed at our collection site (Gagnon et al., 2003b) but less than those observed in similarly wave-exposed systems (e.g. Eckman et al., 2003).

2.2. Urchin density

We also explored the influence of urchin density on their ability to aggregate on \textit{D. viridis} by counting the number of urchins in contact with the alga in trials at three densities, 78, 136, and 194 urchins m\(^{-2}\). These trials were run with water motion that produced a 5 cm sweep of the \textit{D. viridis} fronds. On each of six consecutive sampling days, the urchins (2 to 6 cm in diameter) were collected near Île aux Goélands and divided into 3 groups. The urchins were maintained in running seawater for 3–5 h prior to the trials. The
procedure was as in the previous experiments, except that each trial lasted 40 min, and each group of urchins was only used in a single trial. The order of the trials was randomly chosen. In each trial we recorded the number of urchins in contact with the *D. viridis* plant after 20 and 40 min. Water temperatures varied between 3 and 7°C during the trials.

### 2.3. Field observations

To compare patterns in our wave tank with those in the field, we compared the number or urchins in contact with 8 haphazardly chosen *D. viridis* plants (37–61 cm in length) at Île aux Goélands when water motion was moderate and the sweep of *D. viridis* plants was from 10 to 15 cm (slack tide and \( \sim 29 \text{ km h}^{-1} \) winds), with the number 4 days later when there was low water motion and the sweep was <2 cm (slack tide and \( \sim 9 \text{ km h}^{-1} \) winds). We selected a persistent barrens site known to contain urchin populations of \( \sim 110–140 \text{ individuals m}^{-2} \), a density similar to that used in the first set of wave tank experiments.

### 2.4. Statistical analysis

We analyzed the changes in the aggregation of urchins on *D. viridis* and the tendency of urchins to move within the wave tank using three-way ANOVAs (Zar, 1999) with the factors Block (the 6 days of the trials), Algae (none, algal mimic and *D. viridis* for the analysis on the tendency of urchins to move, but only algal mimic and *D. viridis* for the analysis on the aggregation of urchins, since aggregations were not possible when the algae or mimics were absent), and Waves (with and without). Whereas we applied the first analysis (changes in the aggregation of urchins) to the raw data, we applied the second analysis (tendency of urchins to move) to the log-transformed data, to correct for heteroscedasticity.

The effect of urchin density on the aggregation of urchins on *D. viridis* was analyzed using a repeated measures (split-plot) ANOVA (Hand and Taylor, 1987) with the factors Block (the 6 days of the trials), Density (low, intermediate and high urchin density; randomized within each block), and Time (measurements taken after

![Fig. 2. Mean number (+SE) of green sea urchins, *Strongylocentrotus droebachiensis*, in contact with real and mimic plants of *Desmarestia viridis*, and on the walls of the wave tank, after 45 min. Bars not sharing the same letters are different (LS means tests, \( p<0.05 \)).](image-url)
20 and 40 min). Since variances were similar over time within the different treatments, and the correlation in the data over time was similar for all treatments, we used a pooled covariance structure in the ANOVA (Proc Mixed, Type = CSH, SAS Institute Inc., 1999). We applied the analysis to the raw data as the data for each observation time were normally distributed.

In the above analyses, normality was verified using Shapiro–Wilk’s statistic (SAS Institute Inc., 1999) and homoscedasticity by examining the graphical distribution of the residuals and by using Levene tests (Snedecor and Cochran, 1989). To detect differences among levels within a factor, we used least-square means multiple comparison tests (LS means, SAS Institute Inc., 1999). A significance threshold of 0.05 was used for all statistical tests.

3. Results

Our laboratory experiments indicated that any external release of chemicals by the alga had no perceptible repulsive effect on the urchins. Indeed, similar numbers of urchins were in contact with *D. viridis* and its mimic, both in the presence and absence of waves (Fig. 2). However, wave action appeared to have a strong effect on the displacement of urchins since there were 3–4-fold more urchins on the walls of the tank in treatments with no water movement than in treatments with water movement (Table 1; Fig. 2). There was also a slight, almost significant effect of Algae (pooling the two levels of Waves, \( p = 0.055 \), Table 1) due to higher numbers of urchins on the walls of the tank in the absence than in the presence of *D. viridis* (\( p = 0.050 \)) or the mimic (\( p = 0.03 \)). There was no difference between the mimic and *D. viridis* (\( p = 0.76 \)). Patterns of urchin aggregation paralleled those for urchin displacement. Indeed, almost twice as many urchins were in contact with the alga or the mimic in the absence than in the presence of waves, and slightly more than 3 times more urchins were on the walls of the tank in the absence than in the presence of waves (Table 1, Fig. 2), and there was no significant effect of Algae (i.e., *D. viridis* vs. mimic; \( p = 0.83 \)).

### Table 1

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F-value</th>
<th>p</th>
</tr>
</thead>
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<td><strong>In contact with the algae (or mimic)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Block</td>
<td>5</td>
<td>53.34</td>
<td>1.20</td>
<td>0.35</td>
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<td>Algae</td>
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<td>2.04</td>
<td>0.05</td>
<td>0.83</td>
</tr>
<tr>
<td>Waves</td>
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<td>477.04</td>
<td>10.77</td>
<td>0.005</td>
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<tr>
<td>Algae \times waves</td>
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<td>57.04</td>
<td>1.29</td>
<td>0.27</td>
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<tr>
<td>Error</td>
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<td></td>
</tr>
<tr>
<td>Corrected total</td>
<td>23</td>
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<td></td>
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<table>
<thead>
<tr>
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<th>df</th>
<th>MS</th>
<th>F-value</th>
<th>p</th>
</tr>
</thead>
<tbody>
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<td><strong>On the walls of the tank</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
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<td>0.63</td>
<td>10.31</td>
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<td>0.19</td>
<td>3.26</td>
<td>0.055</td>
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<tr>
<td>Waves</td>
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<td>21.67</td>
<td>353.80</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Algae \times waves</td>
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<td>0.013</td>
<td>0.21</td>
<td>0.81</td>
</tr>
<tr>
<td>Error</td>
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<td>0.061</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corrected total</td>
<td>35</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Raw data were used in the first analysis and log-transformed data for the second analysis.

* Two levels: *D. viridis* and mimic.
* Three levels: *D. viridis*, mimic, and no alga.

### Table 2

Summary of three-way ANOVAs showing the effect of Block (the 6 days of the trials), Algae (none, *D. viridis*, and algal mimic), and Waves (with and without) on the number of urchins in contact with the alga (*Desmarestia viridis*).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F-value</th>
<th>p</th>
</tr>
</thead>
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<td>Density</td>
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<tr>
<td>Time</td>
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<td>6.55</td>
<td>0.0090</td>
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<tr>
<td>Error</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td></td>
<td></td>
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</tbody>
</table>

* Error = Block \times Time + Block \times Density \times Time.

## Fig. 3

Mean number (+SE) of green sea urchins, *Strongylocentrotus droebachiensis*, in contact with *Desmarestia viridis* after 20 min and after 40 min in trials in a wave tank at low (78 m\(^{-2}\)), intermediate (136 m\(^{-2}\)) and high (194 m\(^{-2}\)) urchin densities. Values expressed as a percentage of the total number of urchins in the tank are shown within the bars. Bars not sharing the same letters are different (LS means tests, \( p < 0.05 \)).

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The experiment on the effect of urchin density on their ability to aggregate on _D. viridis_ showed that urchin contacts with the alga increased with increasing urchin density, although in a non-linear fashion. Indeed, the number of urchins in contact with _D. viridis_ was similar at low and intermediate densities (LS means, \( p = 0.49 \)), but more than 2-fold greater at the highest density (Table 2; Fig. 3). The number of urchins on _D. viridis_ also increased more rapidly during the high-density trials, as values after 20 min in the high-density treatment (9.6±2.9 SD) were nearly identical to values after 40 min in the low (7.8±4.4, \( p = 0.45 \)) and intermediate (6.2±3.9, \( p = 0.16 \)) density treatments.

Our observations of urchins in contact with _D. viridis_ in the field indicated a striking difference between plants that had a <2 cm sweep (low wave action) and plants with a 10–15 cm sweep (moderate wave action), 17.8 (±2.9 SD) and 0 urchins per plant, respectively. Although this paralleled our observations in the wave tank experiments, the difference between the two wave conditions was somewhat greater. Most of the urchins (~75%) in contact with the _D. viridis_ with a small sweep had filaments of the alga in their jaws.

4. Discussion

Our studies of the interactions between the highly acidic, brown alga _D. viridis_ and the green sea urchin, _S. droebachiensis_, showed that the chemical makeup of the alga is neither necessary nor sufficient to limit contacts with the urchins. Certainly, a significant component of the survival of _D. viridis_ in dense urchin barrens is explained by wave action, which substantially reduces the displacement of the urchins, thus reducing encounter rates between the two organisms, and ultimately attacks on the alga. This finding furthers our understanding of this puzzling, and still unresolved, algae–herbivore interaction. It also illustrates the need to examine marine algal defenses in a broader context.

Traditionally, studies of algal defenses against herbivores have focused on the defensive role of chemical compounds (e.g., phenolics and phlorotannins, Hay and Fenical, 1988; Van Alstyne et al., 1999; Taylor et al., 2003) and structural characteristics (e.g., calcification, Steneck and Watling, 1982; Watson and Norton, 1985; Paul and Hay, 1986). Most studies mainly compared the feeding response of herbivores to natural and artificial (e.g., agar-based) foods. Although such an approach can indicate the nature and potential effectiveness of chemical and structural agents, it overlooks the first two components of foraging (1) the behavior that allows foragers to reach a prey, and (2) their response to the prey upon contact (Chapman and Underwood, 1992). Our results indicate that failure to consider at least the first component can be misleading.

The urchins responded directly to water motion, as indicated by the 3-fold greater number of urchins on the walls of the tank in the absence than in the presence of waves. Most urchins were firmly attached to the bottom of the tank at the end of the trials with waves, indicating that _S. droebachiensis_ stops moving at current speeds of \( \sim 0.30 \text{ m s}^{-1} \). This current speed was less than half the threshold speed reported to stop movement in the congener, _S. nudus_ (\( \sim 0.70 \text{ m s}^{-1} \), Kawamata, 1998). Thus, water motion provides indirect, yet obvious protection to _D. viridis_ from contact by _S. droebachiensis_. Indeed, it substantially decreases movement of urchins towards the alga under hydrodynamic conditions commonly found in habitats where _D. viridis_ is found (Gagnon et al., 2003b). Although we assumed that the movement of urchins onto tank walls reflected foraging activity, it must be kept in mind that laboratory conditions cannot completely reproduce field conditions. It is possible that the behavior we recorded was influenced by other conditions in the tank environment. Nevertheless, given the strong changes in behavior between the treatments with and without water motion, it seems unlikely that other important parameters related to water motion (e.g., oxygenation) co-varied among the treatments.

Twenty years ago, Dayton (1985a), in a study of the mechanisms regulating kelp communities in the southeast Pacific, suggested that _Desmarestia ligulata_ acts as an ‘acid broom’ that prevents the sea urchin _Loxechinus albus_ from consuming kelp plants (_Macrocystis pyrifera_) recruiting beneath the kelp canopy (recruits were more abundant inside than outside the canopy). That is, the sulfuric acid might be released when the alga abrades the bottom, and the acid would repel urchin attacks (i.e., the “environmentally mediated chemical defense hypothesis”). Our results do not support this hypothesis as the number of urchins in contact with _D. viridis_ plants and mimics was similar in the presence (and absence) of waves. If the urchins were responding negatively to chemicals released by moving _D. viridis_, the number of urchins in contact with _D. viridis_ should have been less than the number on the mimics, but this was not the case. Our results indicated that _D. viridis_ is more vulnerable to contact with urchins in the absence of waves but its chemical makeup seems to contribute little or nothing in preventing urchin aggregations, at least under low-to-moderate wave conditions.

Previous reports have suggested that wave-induced mechanical contact with algal fronds (including _D.
viridis) can prevent urchin attacks (the “environmentally mediated tactile defense hypothesis”) (Himmelman and Steele, 1971; Velimirov and Griffiths, 1979; Gagnon et al., 2003b; Konar and Estes, 2003). Here we found no clear-cut evidence of this type of effect, but only a tendency for urchins to form larger aggregations on D. viridis in calm than in agitated waters. Additional experiments with varying duration, wave intensity, D. viridis size, urchin density and hunger state would be needed to clarify the situation.

Aggregation has been proposed as a functional mechanism in the foraging of S. droebachiensis (Garnick, 1978; Bernstein et al., 1983; Vadas et al., 1986). Fronts of grazing urchins that can advance through kelp beds only appear to form once urchins attain a critical density or biomass (Breen and Mann, 1976; Scheibling et al., 1999; Gagnon et al., 2004). Our experiments demonstrated a key role of density in determining the rate of contact of urchins with D. viridis. We observed a 2-fold increase in the number of urchins on D. viridis in trials with high compared to low (and even intermediate) densities of urchins, indicating that increases in urchin densities result in aggregations that are more effective (and faster) in anchoring D. viridis. Assuming that urchins moving about in random directions (Dumont, 2005; Lauzon-Guay et al., in press), the encounter rates with D. viridis should have increased more or less linearly with urchin density and time. However, contact success was not linearly related to urchin density but increased markedly above a threshold (between ~135 and 195 urchins m⁻¹). The threshold density, however, likely increases with increasing wave action. Indeed, the number of urchins aggregating on a motionless D. viridis can be more than an order of magnitude greater than for D. viridis with a 5 cm sweep, and two orders of magnitude greater than for D. viridis with a 10 cm sweep (Gagnon, 2003), indicating that D. viridis becomes less vulnerable to urchins with increasing wave action. Although wave action is likely beneficial for D. viridis, the associated decrease in vulnerability may have to be balanced against the greater risk of being dislodged by waves, a common threat for plants and animals in coastal habitats (Witman and Suchanek, 1984; Dayton, 1985b; Trussell et al., 1993; Denny, 1995). Following storms, dislodged and broken D. viridis are often found on exposed sites in the Mingan Islands.

Although our data further our understanding of how D. viridis survives on wave-exposed urchin barrens, they do not explain why many algae are absent in this environment. Numerous studies have shown that species of Desmarestiales, including D. viridis, weakly attract urchins and are consumed at low rates (Vadas, 1977; Larson et al., 1980; Himmelman, 1984; Himmelman and Nédélec, 1990). The reduced palatability, whether due to the acids or other factors (see Konar, 2000; Pelletreau and Muller-Parker, 2002), would reduce grazing once contact with the alga is established, thus acting as a second mechanism (after wave action) limiting urchin attacks. The urchins are likely more inclined to move towards and anchor down preferred algal foods, so that the attraction to the algae leads to the formation of destructive feeding aggregations, as often seen at the lower edge of kelp beds in wave-agitated shallower waters (Scheibling et al., 1999; Gagnon et al., 2004). Our results also do not explain the occasional persistence of patches of D. viridis in relatively wave-protected urchin barrens. Possibly, this phenomenon arises when urchin density is too low (e.g., below a threshold density) or when D. viridis exists along with more palatable algae. Indeed, the acid in D. viridis may help it to escape urchin grazing for a certain period of time (as long as other resources are available) by reducing its attractiveness relative to other species (see Himmelman and Nédélec, 1990 for a comparison of the palatability of D. viridis with other algal species consumed by the urchin). Hay (1996) emphasizes the need to investigate additive and synergistic effects of multiple types of defenses in studies of algal defenses against herbivores. We agree, but caution that studies of plant defenses must also consider the possible role of external factors in providing algae with protection from herbivory. We have shown that water motion alone can severely restrict both urchin displacements and aggregations on D. viridis which, ultimately, should lead to reduced attack rates and to greater survival and reproduction by D. viridis. Future studies addressing marine algal defenses should examine the interactions between algal defense mechanisms (e.g., chemical, morphological traits), the physical environment (e.g., water motion, temperature), and herbivore-related traits (e.g., abundance, behavior). Failure to do so could lead to incomplete, if not erroneous, conclusions on the ability of algal species to withstand herbivores.

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