

Inducible responses in the brown seaweed *Ecklonia cava*: the role of grazer identity and season

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Summary

1 Plants must either tolerate consumption or defend themselves against grazer attacks. Selection for phenotypically plastic antiherbivory responses has been suggested for many plants, including a few species of seaweed, but little is known about its specificity or seasonality.

2 Multi-factorial experiments tested the effects of consumer identity (*Littorina brevicula* vs. *Haliotis discus*) and season (summer vs. autumn) on the induction of antiherbivory defences in the brown seaweed *Ecklonia cava*. Following a grazer-free acclimation phase, algae were incubated with grazers (treatment phase) and, subsequently, without grazers (recovery phase). Feeding preference assays, were used to assess differences in consumption rates between grazer-exposed and control plants.

3 In summer, *Littorina*, but not *Haliotis*, induced defence in *Ecklonia*. This defence vanished by the end of the recovery phase. In autumn, neither exposure to direct attack nor to waterborne cues induced defensive responses.

4 Both consumer identity and season of consumption can influence the ability of a given macroalgal species to induce antiherbivory defences. Tailoring such responses to spatial and temporal variation in grazer pressure could have profound ecological implications, for example changing food webs and community structure.

Key-words: consumption, grazer specificity, macroalgae, plant–animal interaction, seasonality

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Introduction

Plants may control their interactions with herbivores via a range of defence mechanisms (Agrawal & Karban 1999), from associational defence (e.g. Atsatt & O'Dowd 1976), which is the least reported, to chemical defence (e.g. Paul *et al.* 2001), the most frequently reported, and perhaps most widespread, type.

Despite their obvious protective benefits, defences may be associated with several disadvantages for their users (Agrawal & Karban 1999), including the risk of self-intoxication by defence compounds, metabolic costs of production and/or storage of chemicals, and

herbivores becoming adapted to constitutive plant traits that would otherwise repel them (but see Schmitt *et al.* 1995; Agrawal 2000). If defence against herbivory incurs a metabolic cost, plant fitness should be enhanced by tolerating herbivory under low grazing load, but inducing defences when grazing intensity is high (Karbon *et al.* 1999). Such an inducible response should allow deactivation or elimination of defensive traits to pre-stimulus levels after consumer activities cease (Zangerl 2003), so that adjustable, rather than permanently expressed (constitutive) defences, could reflect a selective advantage under variable grazing pressure (Agrawal 2001). Additional potential benefits of inducibility could be its lack of predictability (Hay 1996) and its suitability as a cue for predators/parasitoids of plant consumers (Zangerl 2003).

Inducible defences can have important implications in shaping ecological communities (Trussell & Smith 2000; Agrawal 2001; Van Zandt & Agrawal 2004a) and can also structure food webs, either directly, by altering the abundance and distribution of herbivores (references in Agrawal 2001), or indirectly by attracting their enemies (e.g. Turlings *et al.* 1995). Ultimately, even herbivore community richness may thus be controlled by inducible plant defence (Van Zandt & Agrawal 2004a). The specificity of induced defences, which is an important but so far understudied feature, can result from either the dependency of plant responses on grazer identity (Agrawal 1999) or effects being specific to those herbivores that are sensitive to particular compounds (Hay *et al.* 1987; Agrawal 2000; Huntzinger *et al.* 2004). Specificity of plant responses has been reported at the molecular (de Moraes *et al.* 1998; Stout *et al.* 1998) and metabolic pathway levels (Zangerl 2003), for both grazer-emitted (Agrawal 1999, 2000; Van Zandt & Agrawal 2004b; but see Coleman *et al.* 1996), and volatile plant cues (de Moraes *et al.* 1998; Karban *et al.* 2004). Temporal variability in the abundance of a herbivore, as well as in chemical plant properties (Bowers & Stamp 1993), should add an additional level of complexity to plant–animal interactions. Although the time lag of induction should match the temporal variability of consumption pressure, there is very little evidence for such patterns (Turlings *et al.* 1995; Doan *et al.* 2004).

Although inducible defences in terrestrial plants have been much more extensively studied than in aquatic plants, recent studies indicate that this phenomenon might be common, and taxonomically widespread, among seaweeds (e.g. Hemmi *et al.* 2004, brown algae; Ceh *et al.* 2005, red algae; J. Ceh, unpublished data, green algae). The very few studies testing for specificity of induced defences in macroalgae (Pavia & Toth 2000; Rohde *et al.* 2004), suggested that alga–herbivore combination, as well as the consumer itself, influences the ability of macroalgae to induce defences (Amsler 2001).

The present study investigated the combined effects of timing and specificity of induced defences, which were previously studied only in isolation. It was tested whether inducible defences in the habitat-structuring brown alga *Ecklonia cava* were (i) grazer-specific, (ii) seasonally variable, (iii) due to waterborne cues from neighbouring grazed conspecifics or non-grazing consumers, and (iv) reduced after grazing ceased.

Materials and methods

SPECIES DESCRIPTION

The kelp *Ecklonia cava* Kjellman is commonly found on the southern rocky shores of the Korean peninsula, occasionally forming dense populations in the upper sublittoral. Individuals were collected at a depth of 5 m from the rocky shores at Jeju-Island (Hagui, 33°29' N, 126°23' W; Sungsan, 33°27' N, 126°56' W). Pilot stud-

ies revealed that two snails, the periwinkle *Littorina brevicula* Philippi and the abalone *Haliotis discus* Hannai Ino, readily consumed *E. cava*. Individuals of *L. brevicula* (8–12 mm diameter) were collected in the upper sublittoral around Sangju Bay, where their density declines dramatically between summer (35 individuals 100 cm⁻²) and autumn (8 individuals 100 cm⁻²) (Yang 2002). Due to intense harvesting, field-grown *H. discus* individuals are rare and, consequently, 1-year-old 30 mm long animals were obtained from the aquaculture facilities of the National Fisheries Research and Development Institute (NFRDI).

EXPERIMENTAL DESIGN AND SET-UP

Two three-phase induction experiments were conducted in the laboratory to test the inducibility of defence in *Ecklonia* and whether it depended on grazer identity and season. Consumer species (two levels) and grazing (summer, two levels; autumn, four levels) were manipulated in a factorial design. In summer, *Ecklonia* was either exposed to or protected from consumers, while additional grazing manipulations in autumn comprised the effects of waterborne cues from nearby grazed conspecifics and from non-grazing consumers.

Experiments were conducted at NFRDI, Sangju, South Korea (34°42' N, 127°59' W) in 2003 from 16 June to 27 July (summer) and 1 September to 12 October (autumn). Each of two basins (2.5 × 1.5 × 0.5 m) housed 14 (summer) or 28 (autumn) transparent plastic aquaria (volume 2 L, 12 × 18 × 11 cm), representing single experimental units (EUs), over which all treatments used for one grazer species were randomly distributed (summer, two grazing treatments × seven replicates; autumn, four grazing treatments × seven replicates). Because the two grazer species were tested in different basins, we confirmed that growth rates did not differ ($\pm 1.5\%$) significantly between basins (*t*-test: $t_{26} = 0.75$, $P = 0.753$).

To minimize intrusion of fouling organisms, seawater from Sangju Bay was filtered (1 µm, Micropore filter system) prior to its passage through the aquaria, at the maximum possible flow rate of 40 mL min⁻¹. Seawater temperature in the individually aerated EUs was maintained between 18 and 20 °C. Each EU was divided by plastic mesh (1 mm mesh size) into equal-sized up- and downstream compartments. The entire set-up was positioned underneath a burlap-filtered glass roof so that algae in aquaria were exposed to natural light : dark cycles, closely matching ambient PAR irradiance intensity at 1 m water depth (at bottom of aquaria, $85.02 \pm 1.8 \mu\text{mol s}^{-1} \text{m}^{-2}$ (mean \pm SD); at 1 m depth in Sangju Bay, $94.98 \pm 3.9 \mu\text{mol s}^{-1} \text{m}^{-2}$; underwater quantum sensor LI-192SA (LI-COR, Nebraska, USA).

Seven *Ecklonia* individuals were collected in the field and macroscopic epibionts removed with a soft sponge. Cleaned algae were rinsed with seawater, spun-dry in a salad spinner and weighed. Twenty (summer) and 40

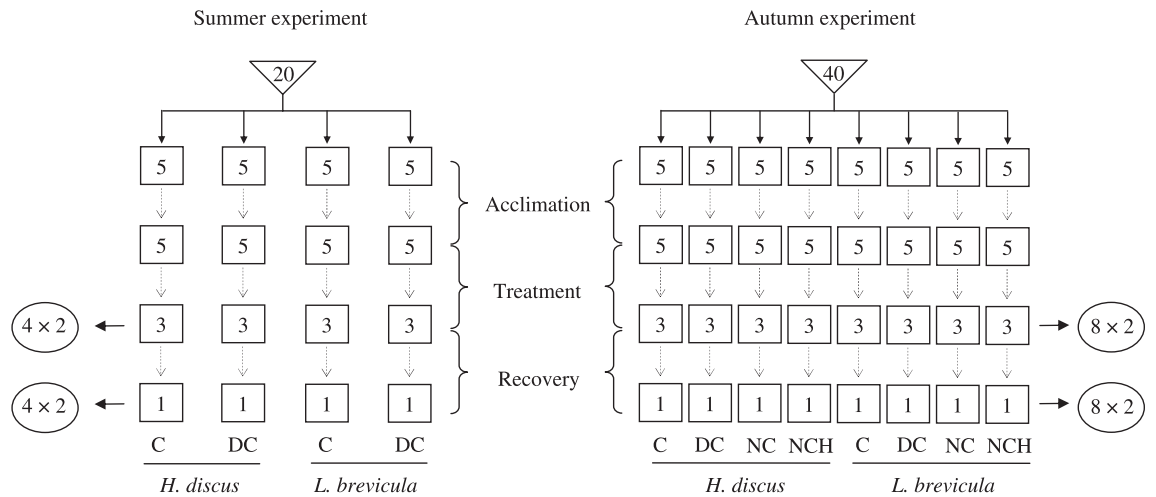


Fig. 1 Allocation of algal pieces from a single *Ecklonia* individual to aquaria comprising all treatment combinations of one replicate, and changes of numbers of algal pieces as a result of withdrawal for feeding assays. Numbers of algal pieces are shown prior to allocation (inverted triangle), in aquaria during the induction experiment (square), and feeding assays (oval). Solid and broken arrows indicate spatial and temporal transitions, respectively. Letters reflect grazing treatments: C = control, DC = direct consumption, NC = waterborne cues from nearby consumed conspecifics, NCH = waterborne cues from non-consuming herbivores.

(autumn) pieces (wet mass 3.0 ± 0.5 g) were cut from each individual to provide sufficient pieces to perform multiple bioassays at different phases of the experiment on one replicate of all treatments. To control for genetic variability between algal pieces from the same EU, each downstream compartment was stocked with five genetically identical plant pieces at the beginning of the experiment (Fig. 1).

Plant pieces were acclimated for 14 days to allow adaptation to experimental conditions and to neutralize grazing histories from the field. During treatment phase (a further 14 days), *Ecklonia* was either left without grazers (controls, C, summer and autumn experiment) or was exposed to direct grazing (DC, summer and autumn), waterborne cues from grazed neighbouring conspecifics (NC, autumn) or waterborne cues from non-grazing consumers (NCH, autumn). The response variable in all cases was the change in *Ecklonia* wet mass, an indicator of algal palatability. The effect of direct snail grazing was assessed by incubating the algae in seven of the EUs in each basin with *Littorina* or *Haliotis* and seven without herbivores (control). In the autumn experiment, 10 *Littorina* or three *Haliotis*, together with *Ecklonia* pieces, were added to the upstream compartment of a further seven, randomly selected EUs in each basin, to test the effects of waterborne cues from consumed *Ecklonia* on the palatability of non-grazed conspecifics in the downstream compartment. The effects of waterborne cues from non-grazing consumers were tested by placing non-grazing *Littorina* or *Haliotis* in the upstream compartments of the remaining seven aquaria in each basin. At the end of the treatment phase, two plant pieces were withdrawn from the downstream compartment of each EU. One plant piece was used for feeding preference assays, while the second piece was used to assess repulsive effects of non-polar *Ecklonia* extracts (reported in Körner 2004).

The recovery phase of the experiment tested whether grazer-mediated changes in algal palatability disappeared within 14 days of removal of all grazers and any algae in the upstream compartment. Two algal pieces were withdrawn from the downstream compartment of each EU and one was used in feeding preference assays.

FEEDING PREFERENCE ASSAYS

Grazer-mediated changes in algal palatability were assessed in 72-h long choice (summer, control and grazed) or multichoice (autumn, control, grazed, waterborne cues from grazed conspecifics and from non-grazing snails) feeding assays. Grazers were 10 *Littorina* or three *Haliotis* contained within 300 mL seawater in transparent plastic Petri dishes (\varnothing 15 cm, 3 cm height, $n = 7$), maintained at a constant temperature of 19 °C and with the water exchanged every 12 hours. To avoid confounding effects by grazer adaptations to food quality, different grazer individuals were used for treatment and feeding assays. Algal palatability, represented by consumption rates, was determined by weighing food items at the beginning and end of feeding assays. To account for algal mass changes that occur independently of herbivory (autogenic change), additional algae were incubated without grazers for the duration of the feeding assay (Peterson & Renaud 1989). The assayed alga and its autogenic control were from the same EU, thus, their experimental history was identical. Actual consumption during feeding assays was calculated as

$$F_b \times (C_e \times C_b^{-1}) - F_e$$

where F and C indicate wet mass of the assay alga and the autogenic control, respectively, and the subscripts b

and *e* indicate measurements at the beginning and end of feeding assays, respectively.

STATISTICAL ANALYSIS

Homogeneity of variances was only tested on significant results, using Levene’s test, because heteroscedasticity leads to increased probability of a type 1 error, thus not affecting the logical interpretation of non-significant results (Underwood 1997). Where appropriate, data were log-transformed to meet the assumptions.

Summer: Data were analysed by two-factorial repeated-measures ANOVA with consumption of treated vs. control piece from one feeding assay as the repeated (within-subject) measure (two levels, fixed). Within each analysis, consumer identity was used as a grouping factor (two levels, fixed). Due to ambiguous selection of an appropriate error term for post-hoc tests involving within-subject by between-group interactions, no post-hoc tests were computed for consumer species–grazing interactions (Winer *et al.* 1991). Instead, one-tailed paired *t*-tests were performed for each grazer species separately, to elicit indirectly which treatment combination caused significant interactions.

Autumn: The multichoice assays were analysed by resampling without replacement, using a Monte Carlo analysis with 10 000 permutations (Bärlocher 1999) for each grazer species separately.

Results

SUMMER EXPERIMENT

Total consumption of *Ecklonia* pieces by *Littorina* was significantly higher than by *Haliotis* at the end of the treatment phase (Fig. 2a), when there was also a significant consumer–grazing interaction (Table 1). In *Littorina* assays, control algae were strongly and significantly more consumed than *Littorina*-exposed *Ecklonia* pieces (paired *t*-test, $t_6 = 2.52$, $P = 0.045$, Fig. 2a). In contrast, *Haliotis*-exposed *Ecklonia* were not significantly more consumed than control specimens (paired *t*-test, $t_6 = 1.66$, $P = 0.148$). No significant effects remained at the end of the recovery phase (Table 1, Fig. 2b).

AUTUMN EXPERIMENT

Littorina assays

Exposure to direct and waterborne grazing cues by *Littorina* did not reveal any significant effect at the end of the treatment phase (resampling, $P = 0.760$). In contrast to summer experiments, direct *Littorina* exposure increased *Littorina* consumption in autumn relative to controls but the 2.3-fold effect was not significant (Fig. 3a). The general pattern of differences in feeding preferences, although non-significant (resampling, $P = 0.090$), persisted until the end of the recovery phase (Fig. 3b).

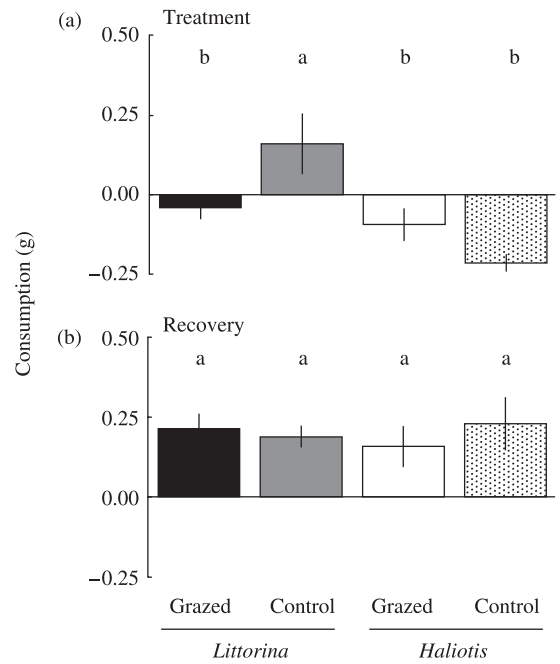


Fig. 2 Mean (± SE) consumption in summer experiment by periwinkles (*Littorina*, black bars) and abalone (*Haliotis*, open bars) determined in 72 hour long feeding assays for intact algae at the end of the (a) treatment and (b) recovery phase. Treatments sharing letters are not significantly different. Grazed (solid bars) indicates snail-exposure during the treatment phase and control (shaded bars) lack of grazing.

Table 1 Results of repeated measures ANOVA from the summer experiment, comparing the effects of herbivore species (*Littorina* and *Haliotis*) and grazing (control and direct exposure to grazers) on *Ecklonia* consumption (treatment phase) and 14 days after exposure to grazers ceased (recovery phase). Consumption was assessed during 72 hour long choice feeding assays using 10 or 3 individuals of *Littorina* or *Haliotis*, respectively. d.f. = degrees of freedom of factor and error terms

Source	Treatment phase			Recovery phase		
	d.f.	F	P	d.f.	F	P
Consumer (C)	1, 12	12.26	0.004	1, 12	0.01	0.907
Grazing (G)	1, 12	0.55	0.472	1, 12	0.23	0.644
C × G	1, 12	8.88	0.012	1, 12	0.99	0.339

Haliotis assays

At the end of the treatment phase, *Haliotis* differentiated among *Ecklonia* pieces exposed to direct and waterborne grazing cues (resampling, $P = 0.018$). Consumption of *Ecklonia* exposed to waterborne cues from non-grazing *Haliotis* was significantly less than consumption of specimens exposed to waterborne cues from nearby grazed conspecifics (Fig. 4a). At the end of the recovery phase, *Haliotis* preference decreased to non-significant levels (resampling, $P = 0.983$, Fig. 4b).

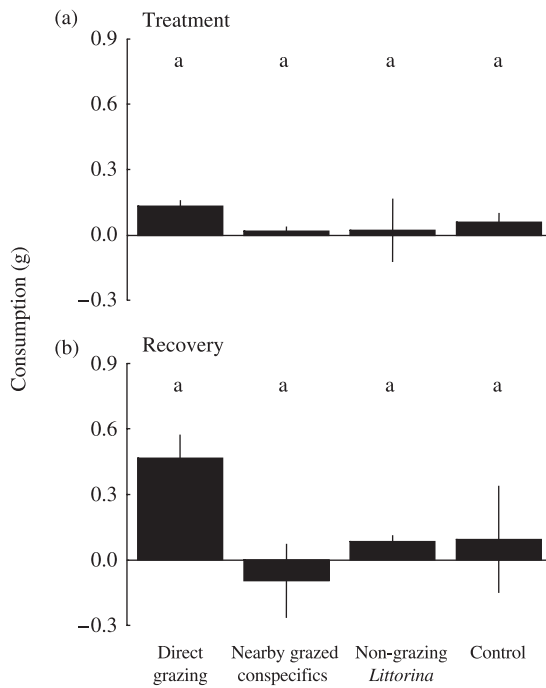


Fig. 3 Mean (\pm SE) consumption in autumn feeding assays using 10 periwinkles (*Littorina*). Single intact algal pieces from each of the four grazing treatments were offered simultaneously in multichoice feeding assays for 72 hours to naive periwinkles, at the end of the treatment (a) and recovery phase (b). Treatments sharing letters were not significantly different.

GROWTH RATES

Ecklonia pieces grew a significant 7% faster in autumn than in summer experiments (t -test, $t_{14} = 10.86$, $P < 0.01$).

Discussion

This study revealed that a defence induction mechanism exists in *Ecklonia*, but depends on the type of mesoherbivore, and that the alga reduced this defence shortly after grazing ceased. The response varied seasonally, being present in summer and absent in autumn, and could not be induced by waterborne cues.

Previously attacked individuals were less palatable than ungrazed controls, indicating that direct *Littorina* grazing induced *Ecklonia* to express a herbivore-repulsive morphological or chemical trait. While the induced plant trait may play multiple functions (e.g. antifouling and antiherbivory Schmitt *et al.* 1995) the fact that it was switched on and off by grazer activity hints at its primary antigrazing role. Although a reduction of previously induced defences is suggested to be an integral part of inducible responses (Zangerl 2003), this has, to date, been reported for very few algae (Hemmi *et al.* 2004; Rohde *et al.* 2004; Weidner *et al.* 2004). Inducible defences under variable grazing regimes may confer a higher fitness than is possible for constitutively defended or undefended species (*sensu*

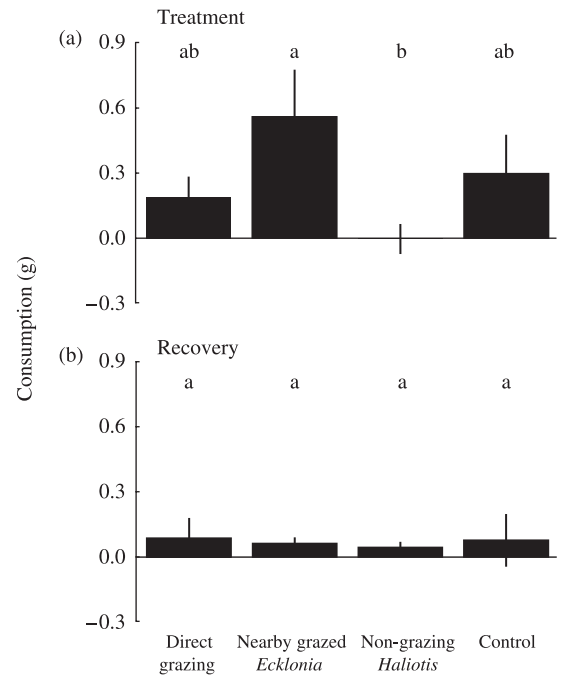


Fig. 4 Mean (\pm SE) consumption in autumn feeding assays using three abalone (*Haliotis*) individuals; symbols as in Fig. 3.

Karban *et al.* 1999). Species with inducible defences are also phenotypically more variable than non-induced species and this should lower the risk of coevolution by their enemies (Agrawal & Karban 1999).

Ecklonia individuals responded differently to the two herbivore species used, reflecting a threat-dependent response by the alga. Higher *in situ* densities of *Littorina* than *Haliotis* (Yang 2002) suggest that natural grazing pressure of the former is more important, although identical consumption rates in most feeding assays demonstrate that both grazers could exert similar feeding pressure on *Ecklonia*. While rigorous experimental evidence of grazer-specific induction of defences in macroalgae is scarce (Pavia & Toth 2000; Rohde *et al.* 2004), more support for specificity of inductive responses and effects comes from studies on leaf-chewing insects (e.g. Stout *et al.* 1998; Agrawal 1999, 2000). Here, specific induction is triggered by salivary constituents (Mattiacci *et al.* 1995; Alborn *et al.* 1997) or the type of feeding damage (Stout *et al.* 1998). Similarly, Pavia & Toth (2000) hypothesized that differences between the snail *L. obtusata* and the isopod *Idotea granulosa* in their ability to induce herbivore defences in the brown alga *Ascophyllum nodosum* might stem from the relatively more concentrated damage caused by snail attacks leading to a higher risk of losing complete thallus parts. However, Rohde *et al.* (2004) demonstrated an equal ability by *L. littorina* and *I. baltica* to induce defence in *Fucus vesiculosus*, suggesting that the specificity of induction may differ between algal species. The present study adds a new level of specificity, because *Ecklonia* induction differed between grazer species with the same grazing mode.

A specific response to waterborne grazer cues might represent a mechanism by which plants could anticipate impending grazing and therefore induce defences before incurring damage. Incubation with non-grazing snails and isopods failed to induce defences in *F. vesiculosus*, while waterborne cues from grazing isopods, but not snails, were effective (Rohde *et al.* 2004). In the present study, palatability of control pieces was not significantly different to *Ecklonia* individuals that had been exposed to waterborne cues. However, this interpretation might be confounded by seasonal effects, as responses of waterborne cues were only tested in autumn, i.e. the season when direct exposure to *Littorina* no longer induced defence.

Littorina induced defences in the summer but not in the autumn experiment, while *Haliotis* did not induce defences in either season. Such a temporal variability in the ability to induce defences might reflect a seasonal pattern, although this conclusion has to be viewed cautiously as only one experiment could be conducted at each season. Seasonal patterns in the ability of macroalgae to induce defences have not been previously studied, although examples are known from terrestrial (Turlings *et al.* 1995; Doan *et al.* 2004; Van Zandt & Agrawal 2004a), freshwater (Stibor & Lampert 2000) and marine habitats (Raimondi *et al.* 2000). On a smaller temporal scale, diurnal induction patterns controlled by herbivore activities have been reported from insect-damaged plants (Turlings *et al.* 1995). Several seasonally variable factors may explain the observed temporal variability of inducible defences in *Ecklonia*. *Littorina* density is fourfold lower in autumn than in summer, while that of *Haliotis* is very low year round (Yang 2002). Coupled with lower water temperatures, grazing intensity of *Littorina* in the field is strongly, and that of *Haliotis* moderately, reduced in autumn relative to summer months. Our set-up exposed *Ecklonia* to identical grazer densities at both seasons and grazing intensity was presumably similar, as *Littorina* consumption rates did not differ significantly between summer and autumn feeding assays. The general lack of defence induction by *Haliotis* might reflect that response to the notoriously low grazing pressure by this species as compared with other herbivorous molluscs (e.g. Scheibling 1994) has minor selective value. The same grazing intensity of *Littorina* induced defences in summer but not in autumn, apparently contradicting models that suggest that a fitness-related threshold of grazing impact is required to induce defences (Karban *et al.* 1999) and suggesting that factors other than feeding pressure must be considered, at least in the *Littorina*–*Ecklonia* interaction. Water temperature at the study site decreases from 24.9 °C in August to 16.4 °C in November (unpublished data, J.H. Kim), very likely affecting metabolic rates in algae and grazers, as reported for *Patella* species (Jenkins *et al.* 2001). Such changes may affect defence response patterns (Cronin 2001). However, identical water temperatures were maintained during the summer and

autumn experiment, eliminating this as a potential driver of season-related responses. Growth rates of *Ecklonia* pieces were higher in the autumn compared with the summer experiment, but this could be the result of a trade-off against lower investment in defence when herbivore pressure is reduced.

The influence of seasonal patterns of grazing pressure on grazer-specific induction of antiherbivore defence, together with rapid reduction of defences after grazing ceases, strongly suggests that *Ecklonia* might use inducible defence responses as a cost-saving mechanism. The occurrence of inducible defences in *Ecklonia* might reflect a finely adjusted algal response, adding new levels of complexity to plant–animal interactions, presumably with strong ecological implications for food web structure and community composition of herbivores.

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