

Effect of detachment on the palatability of two kelp species

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Key words: defence, dislodgement, detachment, floating, macroalgae, palatability

Abstract

Many species of macroalgae survive after becoming dislodged from their primary substratum, but little is known about their capacity to express anti-herbivore defences after detachment. We examined the effect of detachment on the relative palatability of the two kelp species *Lessonia nigrescens* and *Macrocystis integrifolia* to mesograzers. Laboratory and field experiments were conducted on the northern-central coast of Chile to investigate whether (i) time after detachment and (ii) grazing on detached and attached algae could trigger internal defence mechanisms in the algae, which may have acted as deterrents to grazing. In order to examine palatability, feeding assays were run after each experiment using fresh algal pieces and artificial food. Time after detachment had a significant influence on palatability of *L. nigrescens* but not of *M. integrifolia*. During the first 12 days of detachment, detached *L. nigrescens* held in grazer-free laboratory tanks were not significantly more palatable than attached conspecifics from the field but thereafter detached individuals became more palatable. Floating individuals of *M. integrifolia* showed no effect of detachment, indicating that this alga maintains its defence after detachment. An experiment conducted in the field confirmed these results for *M. integrifolia*. An additional laboratory experiment confirmed that attachment status plays an important role on algal defence reaction for *L. nigrescens* when exposed to grazers. Detached and previously grazed individuals of this species were less palatable than grazer-free control algae, but grazing had no effect on palatability of attached algae. Our results indicate that kelps have varying capacities for development of anti-grazing responses once they become detached, possibly depending on their capacity to float and survive after detachment.

Introduction

Defence mechanisms against herbivorous grazers have been reported for numerous species of marine macroalgae (e.g. Van Alstyne, 1988; Paul & Van Alstyne, 1992; Sotka et al., 2002). These mechanisms include (i) morphological defences such as calcification of structures, increase in tissue toughness and/or modification of growth form (Littler & Littler, 1980; Hay et al., 1988; Hay, 1991) and (ii) chemical defences including the production of noxious or unpalatable chemical compounds, which are termed secondary metabolites, because usually they are not associated with the primary metabolism of the plant (Bazzaz

et al., 1987; Duffy & Hay, 2001). Among chemical defences three mechanisms have been recognized: (1) constitutive defence, where secondary metabolites are produced continuously, independent of attack or presence of grazers (e.g. Pavia & Toth, 2000), (2) inducible defence, where algae enhance production of secondary metabolites when under attack by herbivores (e.g. Sotka et al., 2002), and (3) activated defence triggered by injury and acting extremely rapidly (seconds to minutes) by converting a less potent stored secondary metabolite to a more potent one (e.g. Paul & Van Alstyne, 1992; Cetrulo & Hay, 2000). The three mechanisms function as herbivore deterrents, and they have been reported from a wide diversity of different

macroalgae, including brown, green, and red algae (e.g. Steinberg, 1984; Paul & Fenical, 1986; Van Alstyne, 1988; Peckol et al., 1996; Cetrulo & Hay, 2000; Pavia & Toth, 2000; Van Alstyne et al., 2001; Sotka et al., 2002; Taylor et al., 2002).

Two classical approaches have been employed to test for the presence of chemical defences in marine macroalgae. The first is based on an empirical method where algae that were exposed to either: (i) naturally occurring herbivory, (ii) experimental grazing levels or (iii) artificial injury *in situ*, are collected from the field and evaluated for the presence of chemical or morphological defences, or (iv) they were injured after collection (e.g. Van Alstyne, 1988, 1989; Paul & Van Alstyne, 1992; Peckol et al., 1996; Cronin & Hay, 1996a,b; Pavia et al., 1997; Hammerstrom et al., 1998; Cetrulo & Hay, 2000). In the second type of studies, algae are usually maintained detached in experimental outdoor flow-through systems, where they are grown in tanks of variable sizes and are treated with different grazing regimes and after exposure tested for the presence of defensive mechanisms (e.g. Toth & Pavia, 2001; Sotka et al., 2002; Taylor et al., 2002). Although this allows all algae in a tank to be exposed to the same light and nutrient regimes over time, it does not necessarily reflect the natural condition where algae are growing attached to a firm substratum.

Benthic algae, particularly in shallow areas, are exposed to varying degrees of wave and water currents, which may dislodge them from the substratum. This detachment can cause physical stress for the plants, possibly altering seaweed palatability, as is known in cases of desiccation (Renaud et al., 1990). Stressed algae often show a limited potential for chemical defence (Renaud et al., 1990; Cronin & Hay, 1996b), and it is expected that this is also true for detached algae. However, little is known about the effect of detachment on the presence of defence mechanisms in marine macroalgae even though this appears important in understanding the mechanisms of chemical defence in a natural situation. Understanding the relationship between detachment and defence appears important since assemblages of unattached seaweeds are commonplace in nature (e.g. Benz et al., 1979; Ólafsson et al., 2001; Hirata et al., 2001; Thiel & Gutow, 2004). Storms frequently cause detachment of benthic macroalgae (Norton & Mathieson, 1983), which then contribute to floating or drifting populations. Some macroalgae possess gas bladders (e.g. the giant kelp *Macrocystis pyrifera*) or a plant body that temporarily acts as a balloon (e.g. the entire thallus of *Colpomenia perigrina*)

(Norton & Mathieson, 1983), allowing them to float at the sea-surface. Other species of algae have no floating potential and after detachment sink to the sea-floor where they might contribute to a species-rich assemblage of drifting macroalgae in shallow waters (Benz et al., 1979; Norton & Mathieson, 1983; Norkko & Bonsdorff, 1996).

After detachment, macroalgae may be exposed to intense herbivory (biological stress). For example, floating macroalgae harbour many animals, including herbivores, that have originally been living on them and thus can quickly consume them (Ingólfsson, 1995, 1998). Also drift-algae in shallow waters are commonly inhabited by a wide diversity of mesograzers, in particular amphipods and isopods (Inglis, 1989; Geertz-Hansen et al., 1993; Ingólfsson, 2000; Brooks & Bell, 2001). Floating algae may survive for extended periods at the sea surface (Hobday, 2000) despite high abundances of grazers, but drifting algae often face high grazing pressure from a wide diversity of benthic grazers and may have little chance to survive for long (see e.g. Rodriguez, 2003). Thus, it can be hypothesized that kelp species that float after detachment may be capable of maintaining their defence after detachment, while kelp species that sink after detachment may lose their defence capacity shortly after detachment.

Here we tested whether two kelp species from the SE-Pacific, that differ in their behaviour (floating or drifting) after detachment, maintain their defences, or whether they lose them due to physiological alterations caused by detachment. Plants of *Lessonia nigrescens* are negatively buoyant and sink to the seafloor after detachment where they may contribute to a large pool of drifting algae. In contrast, *Macrocystis integrifolia* floats after detachment and may travel for a long time with ocean currents (e.g. Helmuth et al., 1994). Field and laboratory experiments were conducted on the northern temperate coast of Chile in order to learn how detachment affects the palatability and thus the defence capacity of these two macroalgae.

Materials and methods

Both laboratory and field experiments were carried out to test the changes in palatability following extended detachment of the two kelp species. Laboratory experimentation was done with *Lessonia nigrescens* and *Macrocystis integrifolia* while field experimentation was carried out with *M. integrifolia* only. An additional laboratory experiment was conducted with *L.*