INTERTIDAL AMPHIPODS AS POTENTIAL DISPERAL AGENTS OF CARPOSPORES OF IRIDAEA LAMINARIOIDES (GIGARTINALES, RHODOPHYTA)\textsuperscript{1}

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ABSTRACT

Mid and late successional benthic algae have poor dispersal capacities. Mobile herbivores may increase dispersal of some algae because spores can survive digestion by grazers and stick to external body appendages. We show that carpospores are the only type of reproductive unit of the rhodophyte Iridaea laminarioides Bory that survive passage through the digestive tract of the amphipod Hyale sp. The spores also stick to the amphipods' legs and are thus carried by the amphipods in the field. Amphipods significantly increased (P < 0.01) the number of spores settling on artificial substrata in places where barriers prevented the normal ingress of algal propagules. The presence of artificial substrata that act as a refuge for the grazers also caused an increase (P < 0.01) in the number of settled spores. Amphipods also significantly increased (P < 0.01) the number of spores under an Ulva sp. canopy in laboratory experiments.

Key index words: amphipod grazing; Hyale hirtipalma; Iridaea laminarioides; Rhodophyta; spore dispersal; spore resistance to digestion


Mobile amphipods that preferentially consume the cystocarpic algal tissue of I. laminarioides may have an ecological role as spore releasers and dispersal agents (Buschmann and Santelices 1987). Amphipods can release spores by disrupting the cystocarp of I. laminarioides and may also transport the propagules as they move among algal patches (Buschmann 1990). Two mechanisms exist by which the propagules could be transported: 1) by surviving digestion or 2) by becoming attached to the appendages of the amphipods.

We tested the hypothesis that amphipods present on the exposed rocky intertidal region of southern Chile are potentially important dispersal agents of the red alga Iridaea laminarioides by the two mechanisms described above. This study also experimentally assessed the mechanisms by which amphipods can mediate dispersal enhancement of I. laminarioides.

MATERIALS AND METHODS

Iridaea laminarioides plants and the amphipod Hyale hirtipalma (Dana) were collected in rocky intertidal habitats at Pucatrihue Beach in southern Chile (40°33' S, 73°43' W) and transported to the laboratory in temperature-controlled containers. Algae were sorted for reproductive structures as follows: mature cystocarpic fronds with large, brown-red cystocarps; mature tetrasporangial fronds with mature, red-purple tetrasporangial sori; and sterile thalli, lacking all macroscopic reproductive structures. Amphipods were selected by size. Algae and amphipods were washed in sterile seawater and maintained under running sea water and constant temperature (12–14°C), photon fluence rate (35–45 µEmired s\textsuperscript{-1}), photoperiod (12:12 h LD) and salinity conditions. Prior to each experiment, amphipods were starved for 72 h.

The capacity of spores to survive passage through the digestive tract of the amphipods was evaluated by offering reproductive carposporic, tetrasporic and sterile (control) I. laminarioides tissues to starved amphipods maintained in separate groups. After 24 h, 35 fecal pellets were collected from each algal type offered to the amphipods and incubated in sterile seawater in separate Petri dishes under the conditions described above. The number of spores per fecal pellet was counted under a Nikon microscope. Spores were quantified after 1 and 7 days of incubation. The total number of spores found in the fecal pellets was compared between treatments using a chi-square test including the Yates' correction (Sokal and Rohlf 1979).

Fecal pellets from amphipods were also collected in the field and washed in sterile seawater under the controlled conditions described above. After 5 days of incubation, the number of spores in the fecal pellets was counted under a microscope.

The capacity for carrying carpospores stuck to amphipod legs was measured in two ways. First, the number of spores on 15 locomotory appendages of amphipods found over mature cystocarpic fronds of Iridaea laminarioides in the laboratory was counted under a Nikon microscope and compared against controls, i.e. amphipods maintained on sterile algal fronds. Secondly, amphipod legs obtained directly from field collected individuals were observed under a stereomicroscope. Twenty legs obtained from amphipods collected on I. laminarioides and 20 legs from individuals found on Ulva sp. were compared. In all observations just described, only one leg was obtained randomly from each amphipod. The total number of spores on the legs for the different treatments was compared using a chi-square test including the Yates' correction (Sokal and Rohlf 1979).

The hypothesis that Hyale hirtipalma might facilitate spore release and dispersal while grazing and moving between algal patches was tested by placing 30 amphipods each inside replicate plastic
RESULTS

Carpospores were the only reproductive unit of *Iridaea laminarioides* able to survive passage through the digestive tract of *Hyale* (Table 1). However, their number decreased significantly ($\chi^2 = 7.62; P < 0.01$) after 7 days of incubation, presumably due to mortality (Table 1). *I. laminarioides* propagules also germinated in fecal pellets collected in the field; 17 germinating spores were found in 30 fecal pellets from amphipods collected on *Iridaea* patches.

After the amphipods crawled over fertile carposporic fronds of *Iridaea*, 25 spores were found stuck to the 15 amphipod appendages. No spores were found stuck to the appendages when the amphipod crawled over infertile *Iridaea* fronds ($\chi^2 = 46.08; P < 0.001$). Also, 28 spores were found stuck to 20 appendages from amphipods caught on *Iridaea* fronds in the field. This number of spores is significantly higher ($\chi^2 = 22.86; P < 0.01$) than the seven spores found stuck to 20 amphipod legs collected on *Ulva*, suggesting that the spores could be lost as the amphipod travels between different algal patches.

When *Hyale* grazes on mature carposporic tissues of *Iridaea laminarioides* it scratches the carpospore with its maxillipeds and consumes the pericarp tissue. This feeding activity can eventually perforate the pericarp, releasing a large number of carpospores into the water column. This grazing activity significantly increased ($t = 5.53; P < 0.001$) the number of spores released and fixed to the cover slips (Fig. 2). As previously demonstrated (Buschmann and Santelices 1987), the liberated spores are as viable and mature as those spontaneously released by the plant.

The presence of the artificial barriers placed inside the containers significantly reduced ($t = 2.72; P < 0.05$) the number of attached spores per cover slip in the absence of grazing (Fig. 2). However, the presence of amphipods significantly increased the number of spores ($t = 4.08; P < 0.01$) to as much as 50 spores per cover slip (Fig. 2). The presence of filaments acting as amphipod refuges and attaching surfaces further increased ($t = 6.17; P < 0.01$) the number of spores attached to the cover slips present below (Fig. 2), to an average density of 146 spores per slip. Finally, the experiments using *Ulva* as barriers demonstrated that amphipods significantly increased ($t = 4.61; P < 0.001$) the number of spores in the presence of *Ulva* since this alga attracts the amphipods (Fig. 3). Also, the amphipods significantly increased ($t = 3.79; P < 0.01$) the number of spores attached under *Ulva* (Fig. 3).

DISCUSSION

Previous results showed that the amphipod *Hyale media* (Dana) has a marked food preference for ma-
tecture cystocarpic *Iridaea laminarioides* (Buschmann and Santelices 1987, Luxoro and Santelices 1989). While grazing, however, the amphipods cause the release of large numbers of spores (Fig. 2) without affecting their development. Our results confirm those of Buschmann and Santelices (1987) that carpospores are the only type of reproductive unit of *Iridaea laminarioides* which survives passage through the digestive tract of amphipods. Breeman and Hoeksema (1987) also showed that algal tissues can survive passage through the gut of amphipods; however, the *Hyale-Iridaea* interaction shows a higher degree of specificity than previous reports for other algal-grazer interactions (Santelices et al. 1983, Santelices and Correa 1985, Jernakoff 1985, Santelices and Ugarte 1987, Paya and Santelices 1988, Santelices and Martinez 1988) because the consumption by the amphipods was highly specific and restricted to cystocarps of *I. laminarioides* rather than gametophytic tissues (Buschmann and Santelices 1987, Luxoro and Santelices 1989). The evidence presented in this paper suggests that this consumption might not be detrimental to *I. laminarioides*. Amphipods could facilitate the number of carpospores released, and they could also act as an active spore dispersal agent.

Our results also indicate that carpospores can stick to amphipod legs. The mucilage covering algal spores is a very common feature with several possible ecological roles: it may affect settlement efficiency, sinking rates of spores in the water column, or provide protection against desiccation during low tides (Lobban et al. 1985, Hoffmann 1987). Mucilage may also help spores stick to the legs of amphipods. This means that, in general, a close relationship between the alga and the amphipods is not necessarily required to explain the evolution of this adaptation. Indeed, in seed dispersal by adhesion to mobile animals, little structural modification appears to be required to change from wind to adhesive dispersal (Sorensen 1986).

Both methods described in this study, propagation of live carpospores from fecal pellets and the sticking of propagules to amphipod legs, may help to transport the spores to places otherwise made inaccessible by physical barriers. Turf-forming algae can inhibit the settlement of algal spores by acting as a barrier that reduces the number of spores reaching the substratum beneath (Hruby and Norton 1979, Deysher and Norton 1981). Conversely, algal turfs also enable spores already established beneath the turf to withstand longer exposure to air than those that are unprotected (Hruby and Norton 1979, Chapman 1984) since moisture retained by turf-algae can decrease desiccation stress (Hay 1981). Amphipods can potentially act as carpospore transporting agents as they pass through turf algae, such as *Ulva*, and because they can move between algal patches.

Mid and late successional forms of terrestrial plants have more species with adhesive adaptations than early successional ones (Sorensen 1986). *Iridaea laminarioides* is a typically mid successional alga in intertidal communities (Santelices 1990). Since these algae may show a limited propagule dispersal range, this study indicates that mobile amphipods could enhance dispersal of their spores that are incorporated into fecal pellets and attached to appendages.
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