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Local elimination of *Codium fragile* ssp. *tomentosoides*: indirect evidence of sacoglossan herbivory?

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A local population of the introduced green macroalga *Codium fragile* ssp. *tomentosoides* was investigated in Oban in the district of Argyll, western Scotland. Periodic surveys demonstrated that sacoglossan densities (*Elysia viridis* and *Placida dendritica*) were unusually high in 1997 and early 1998, slug herbivory noticeably damaged algal thalli, and the local algal population was decimated. These patterns provide indirect evidence of the significance of slug herbivory on the introduced alga.

The introduced green macroalga *Codium fragile* ssp. *tomentosoides* (Van Goor) Silva thrives on rocky shores around the British Isles (Trowbridge & Todd, 1999). The abundance of the alga has fluctuated considerably since its appearance on English, Irish, and Scottish shores; these fluctuations may be due to environmental and ecological variations. The role of herbivory by sacoglossan sea slugs that feed selectively on *Codium* spp. merits further investigation because slugs can locally reduce macroalgal hosts (e.g. Trowbridge, 1992, 1993). During a comprehensive investigation of sacoglossan—*Codium* interactions on Scottish shores, quantitative observations provided indirect evidence that sacoglossan slugs may contribute to the reported decline of the alga in many areas of western Scotland.

The shore along the Oban Bay Esplanade was investigated for *Codium fragile* ssp. *tomentosoides*; this site and the Argyll region were colonized by the invasive alga several decades earlier and native congeners are exceedingly rare in Scotland (reviewed by Trowbridge & Todd, 1999, 2001). All slugs discovered on the invasive alga were collected and used for laboratory experiments; details of their population structure are reported elsewhere (e.g. Trowbridge & Todd, 2001). In October 1996, only four thalli were found during 1 h of searching; these were mature plants and were not attacked by sacoglossan grazers (Figure 1). In March 1997, the site was revisited and 18 thalli were found directly downshore of the Oban Bay Hotel (OS grid reference NM 853304). All the thalli were attacked by the large sacoglossan *Elysia viridis* (Montagu, 1804) (Figure 1). In May, the majority of thalli were attacked by adult slugs, with a mean of seven and maximum of 38 *E. viridis* per thallus (Figure 2). In July, densities of *E. viridis* had declined significantly although the maximum value was still unusually high. Few individuals of the smaller sacoglossan *Placida dendritica* (Alder & Hancock, 1843) were observed in 1997 (Figure 2). Thus, the extensive grazing damage observed (Figure 1) was due to *Elysia viridis*. (Slug grazing is visually distinct from crustacean or prosobranch gastropod feeding: Trowbridge, 1992, 1993.) In February 1998, 100% of the thalli were attacked by sacoglossans, 94% were severely damaged, and densities of both sacoglossan species were extremely high (Figures 1 & 2). No *Codium* thalli (upright fronds or undifferentiated vaucherioid stages) or slugs were found in extensive resurveys of Oban in March 1998, May 1999 or June 2000.

These observations collectively suggest that the high slug densities in 1997 and early 1998 caused the local decimation and elimination of *C. fragile*. The high slug densities, the observed severe grazing damage, and the disappearance of the alga at Oban Esplanade are indirect evidence that sacoglossan herbivory has important ecological consequences at local levels. In Loch Sween and Loch na Cille, Argyll, algal populations persisted in 1998, 1999, and 2000. How is the Oban site different? Oban is wave-sheltered yet has high water flow between closely situated islands. Thus, slug dislodgement from algal hosts may be low and the supply of planktotrophic larvae may be quite high. In fact, the two other known sites in western Scotland where dense populations of *Elysia viridis* form are on the native green alga *Cladophora rupestris* (Linnaeus) Kützing in tidal rapids at Clachan Seil, Argyll (OS grid reference NM 785197) and Spanish Rapids, Loch Maddy, North Uist (NF 922695) in the Outer Hebrides (Trowbridge & Todd, 2001; Trowbridge, unpublished data).

High densities of the sacoglossans *Elysia maoria* Powell, 1937 and *Placida aoteana* (Powell, 1937) on Australasian shores periodically caused grazing damage and thallus loss to *Codium fragile* ssp. *tomentosoides* (reviewed by Trowbridge, 1998). High densities of *P. dendritica* have been noted for two other locations: Clare Island, Co. Mayo, Ireland (Colgan, 1911) and Lincoln Co., Oregon (Trowbridge, 1992, 1993). At high densities, *P. dendritica* causes

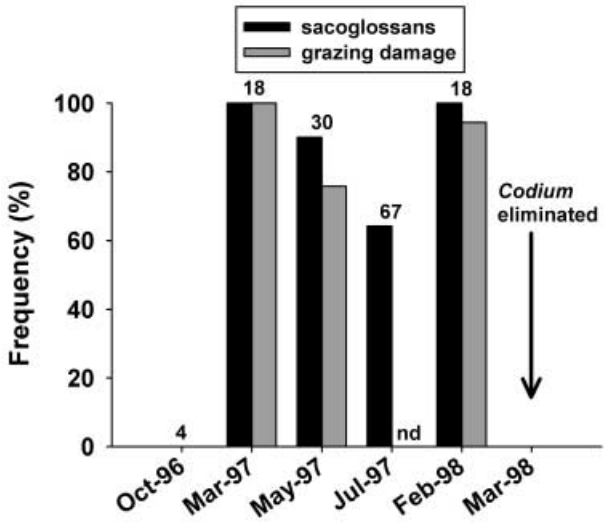

Figure 1. Percentage of *Codium fragile* ssp. *tomentosoides* thalli attacked by sacoglossans and damaged by sacoglossan herbivory on the rocky littoral area at Oban, Argyll, Scotland. Numbers above bars indicate the number of thalli examined; nd denotes no data collected.

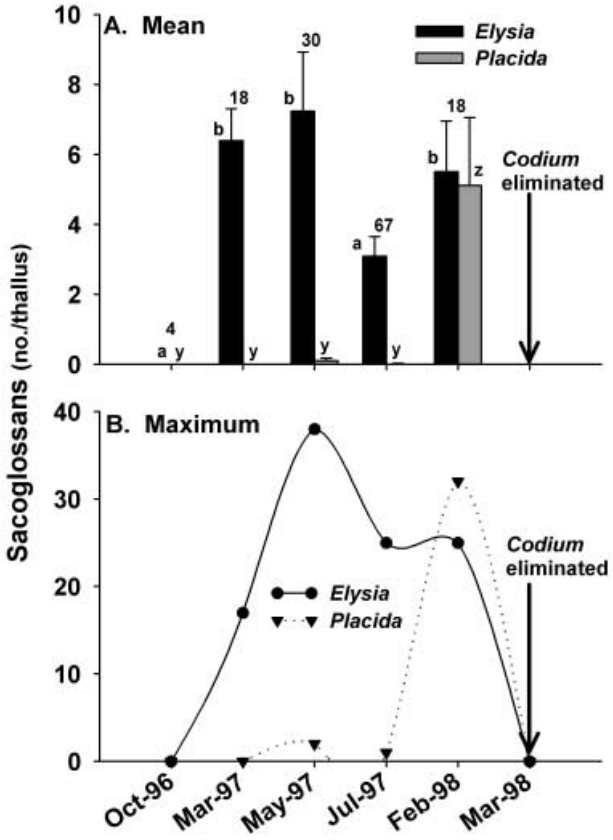

Figure 2. Densities of sacoglossans (*Elysia viridis* and *Placida dendritica*) on *Codium fragile* ssp. *tomentosoides* at Oban, Argyll, Scotland. (A) Bars indicate mean values; error bars indicate 1 SE; values above bars indicate number of algal thalli sampled; different letters denote slug abundances that differed significantly based on Kruskal–Wallis and Dunn tests (analyses were separate for each slug species). (B) Curves indicate spline-curves connecting maximum monthly densities to allow visual estimates of peak slug densities over time.

extensive damage to differentiated and undifferentiated *Codium* hosts, including branch loss and thallus fragmentation (Trowbridge, 1992, 1993, 1998; Harris & Mathieson, 1999). In the case of Oban, sacoglossan abundance on *Codium* was high, and sacoglossan herbivory weakened and destroyed the local host-plant population.

Codium fragile ssp. *tomentosoides* has relatively limited dispersal via short-lived parthenogenetic female gametes (Trowbridge, 1998). Recolonization of the alga to Oban shores is contingent on marginal dispersal of floating thalli and/or anthropogenic introductions (inadvertently from shellfish transplants, ship hull-fouling, etc.). Transplant experiments necessary to measure sacoglossan herbivory directly at Oban would not be ethical given the Wildlife & Countryside Act 1981 which explicitly prohibits planting in the wild or translocating listed plant species, including *C. fragile* ssp. *tomentosoides*. Thus, indirect evidence in the field or laboratory is the only ethical approach for assessing the role of sacoglossan herbivory.

In conclusion, my observations suggest that high densities of marine specialists can locally reduce macroalgal populations. Based on published evidence for congeners around the world, the slug densities at which this local eradication occurred are unusually high. Thus, while sacoglossan herbivory can occasionally control invasive hosts, the generality of this intense herbivory may be restricted to regions with high slug densities.

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