

The effects of exposure to wave action on the distribution and morphology of the epiphytic hydrozoans *Clava multicornis* and *Dynamena pumila**

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SUMMARY: The spatial distribution patterns of two species of epiphytic hydrozoans, *Clava multicornis* and *Dynamena pumila*, on the intertidal alga *Ascophyllum nodosum* were studied in adjacent wave-sheltered and wave-exposed areas. *Clava* were more abundant on the wave-sheltered algae than on the wave-exposed fronds, and in both areas occupied the basal and middle sections of the algae. There was no difference in the abundance of *Dynamena* between the wave-sheltered and wave-exposed areas, but in both areas *Dynamena* were most abundant on the basal and apical sections of the algae than on the central sections. The number of hydranths per colony of *Clava* was higher in the sheltered area than in the exposed area. The hydrocauli of *Dynamena* on the wave-exposed algae bore fewer hydrothecae than those on the sheltered algae. The proportion of *Dynamena* hydrothecae that contained hydranths was close to 100% in the sheltered area, but only 70% in the exposed area. It was concluded that variations in distribution and morphology could be caused by the direct or indirect effects of one or more variables, including wave action, feeding rates, and exposure to solar radiation. Experiments are required to elucidate the specific effects of these variables.

Key words: epiphytic hydrozoans, wave action, distribution, morphology.

INTRODUCTION

The polyp stages of marine hydrozoans may be found on a wide variety of natural and artificial substrata, including seagrasses and intertidal algae (Seed and O'Connor, 1981; Boero *et al.*, 1985; Gili and Hughes, 1995). Some species are found mainly, or only, on specific plant substrata, often in extreme environments, such as the rocky intertidal zone. The epiphytic habit requires the ability to select specific substrata difficult for other species to colonise (Calder, 1991; Hughes *et al.*, 1991a,b; Genzano and

Rodríguez, 1998) and may be an adaptation to reduce interspecific competition, so prevalent in epifaunal communities. However, epiphytism may lead to selective pressures to adapt to special circumstances associated with that host and its environment. Marine plants are flexible, often have a high turnover of leaves or fronds, but may grow continuously, providing new substrata. Seagrasses, for example, are usually found in sheltered conditions, but the leaves are short-lived and the specialist epiphytic hydroids have special growth strategies that help maintain their position on the plants (Hughes, 1991a,b; Rossi *et al.*, 1997). In contrast, fucoid algae have apical meristems and parts of the plants

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may be several years old, providing more long-lived substrata. The problems faced by furoid epiphytes are associated with the highly hydrodynamic environment of the rocky intertidal. Hydroids are small, often delicate, animals that may require special adaptations, either of morphology or habit, to withstand the potential damage caused by wave action. Riedl (1971) reviewed some variations in the morphology of hydroids attributable to variations in water movement and more recently Hughes (1992) described some morphological adaptations of *Dynamena pumila* to enable the hydroids to tolerate wave action.

Differences in distributions of epiphytes may occur at several different scales and are more difficult to interpret. For example, the effects of wave action, which are difficult to measure, are usually studied by relative and fairly unspecific comparisons between obviously wave-exposed and obviously wave-sheltered locations. However, if these areas are separated by large distances there is the further complication of studying different populations and gene pools, and noted differences cannot be attributed with certainty to the environmental variations. This may be especially true for species where the dispersal potential is low because of the absence of planktonic stages. There are further difficulties in explaining the causes of small-scale differences in distributions on the algae, because small-scale variations in the environment occur around the host (e.g. O'Connor *et al.*, 1979). For example, some epiphytes are more abundant in the central areas of seaweed clumps where the effects of wave action are reduced (Ott, 1980), but this may be an effect of the water movement rather than a response to it.

The large furoid alga *Ascophyllum nodosum* is common on relatively sheltered rocky shores of northwest Europe (Vadas *et al.*, 1990) with a large surface area available for colonisation by epiphytes (Peckol 1988). The sessile epiphytic community of *Ascophyllum* consists mostly of hydrozoans, bryozoans, barnacles and algae and shows spatial variations, with height on the shore and with exposure to water movement (Aldrich *et al.*, 1980). This is a study of the differences in distributions and morphology of the hydroids *Clava multicornis* and *Dynamena pumila*, (hereafter referred to only by their generic names), common facultative epiphytes of the seaweed *Ascophyllum nodosum* (see Cornelius, 1979), in relatively wave-exposed and wave-sheltered locations in close proximity (within 50 m) on the Isle of Cumbrae, Scotland.

METHODS

The study site is at the southern end of Ballochmartin Bay on the east coast of the Island of Great Cumbrae, in the Firth of Clyde, Scotland. The shore faces east across the Fairlie Channel to the mainland about 1 km away and has the flora characteristic of a sheltered shore. The wave-exposed area and wave-sheltered area are on the east and west side of an isolated rock promontory. The wave-exposed site receives wave action predominantly when easterly winds blow across the Fairlie channel; the wave-sheltered site is protected from these waves by the rocky promontory.

Whole plants of *Ascophyllum* that bore colonies of *Clava* or *Dynamena* were selected randomly from within a horizontal transect, 1 m wide and 50 m long parallel to the waters edge at the same tidal height in the two areas. The selected plants were either collected for laboratory examination or examined *in situ*. The distributions of the epiphytes were mapped on sections of the *Ascophyllum* plants which were categorised according to the approximate dichotomous structure of the algae (Fig. 1). The number of colonies of *Clava* in each section were counted. Colonies of *Dynamena* were less discrete because of their extensive hydrorhizal growth and could not be separated. Instead their abundance was measured by counting the number of hydrocauli in each section. The number of hydranths on thirty randomly selected colonies of *Clava* from each area were counted. The number of hydrothecae on thirty randomly

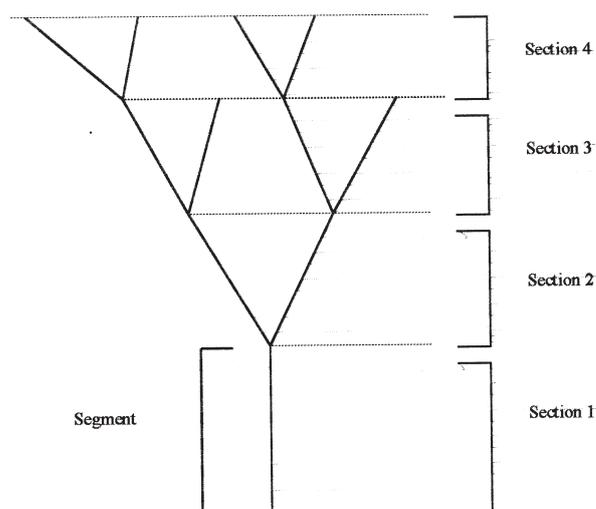


FIG. 1. – Diagram of *Ascophyllum* showing how the sections of the algae were categorised.

selected hydrocauli of *Dynamena* from each area were counted and the number of hydrothecae that contained hydranths and were empty were counted on 15 randomly selected hydrocauli from each area. The distances between adjacent pairs of hydrothecae on 15 randomly selected *Dynamena* hydrocauli from each area were measured.

RESULTS

Clava had a higher density of colonies on *Ascophyllum* in the wave-sheltered area than in the wave-exposed area (Fig. 2a) ($F(1, 247)=18.0, p<0.0003$), while *Dynamena* had a significantly higher density of hydrocauli in the exposed area than the sheltered (Fig. 2b) ($F(1, 499)=9.11, p<0.005$). In both the exposed and sheltered areas *Dynamena* was more abundant on the basal and apical sections of the algae than on the central sections (Fig. 3b). *Clava* did not show this pattern of distribution and was equally abundant on sections 1-4, rarer on sections 5 and absent on more distal sections. (Fig. 3a).

For both species there were significant differences in size between the exposed and sheltered areas (Fig. 4). The *Clava* colonies had a larger number of hydranths in the sheltered area (22.4 ± 9.13

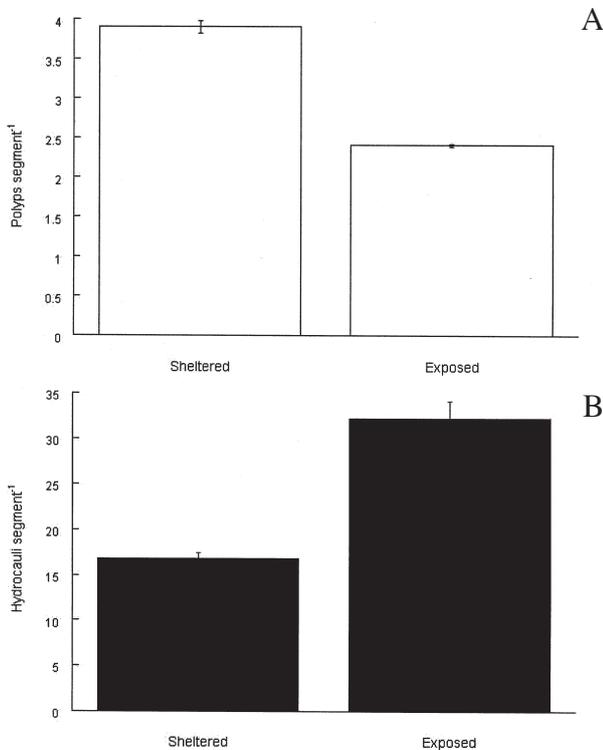


FIG. 2. – The mean number (and standard error) of colonies of *Clava multicornis* (A) and hydrocauli of *Dynamena pumila* (B) on *Ascophyllum* from the wave-sheltered and wave-exposed areas.

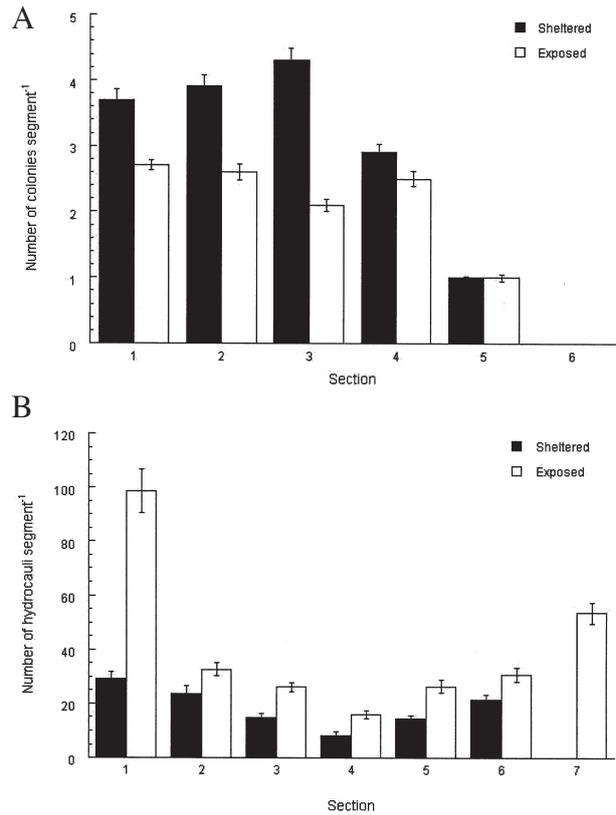


FIG. 3. – The mean number (and standard error) of (A) colonies of *Clava multicornis* (B) hydrocauli of *Dynamena pumila* on each of the numbered sections of *Ascophyllum* in the wave-sheltered and wave-exposed areas.

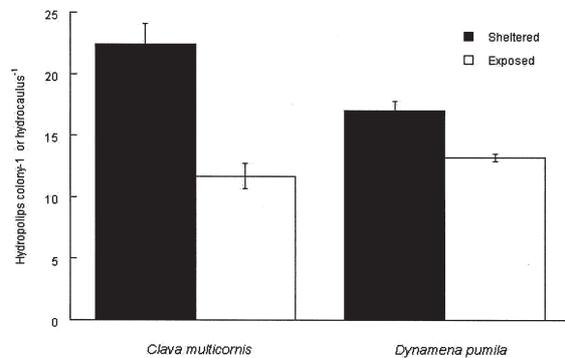


FIG. 4. – The mean number (and standard error) of hydranths per colony of *Clava multicornis* and number of hydrothecae per hydrocaulus of *Dynamena pumila*, on *Ascophyllum* in the wave-sheltered and wave-exposed areas.

SD) than in the exposed area (11.7 ± 5.3 SD) ($F(1, 60)=31.6, p<0.00001$), while the *Dynamena* hydrocauli bore a larger number of hydrothecae in the sheltered area than in the exposed ($F(1, 53)=17.4, p<0.0001$). There was a significant greater proportion of *Dynamena* hydrothecae that contained hydranths in the sheltered area (1 ± 0.14 SD) than in the exposed area (0.7 ± 0.29 SD) ($F(1, 209)=42.79, p<0.00001$). There was no significant difference in the distance between adjacent pairs of hydrothecae

of *Dynamena* between the exposed (1.1 ± 0.14 mm SD) and sheltered (1.1 ± 0.23 mm SD) ($F(1, 28) = 0.03$, $p < 0.9213$), nor in the distance between adjacent hydrocauli on the hydrorhiza which was consistently close to 3 mm ($F(1, 179) = 0.01$, $p < 0.9043$).

DISCUSSION

If the abundance of hydroids reflected only the length of time the substrata have been available for colonisation then the epiphytes would be most abundant on the oldest, basal, sections of the algae. However, both *Clava* and *Dynamena* had different distributions, which indicates that other environmental variables affected their distributions. The most significant variables in the environment of a rocky shore that could affect hydroids are the direct and indirect effects of water movement, and the effects of exposure to solar radiation, particularly desiccation and heat stress. Responses to, or the effects of, these variables may explain the distributions of *Dynamena* and *Clava* on the algae. Seed *et al.* (1981) and Seed *et al.* (1983) considered the effects of interspecific competition on the spatial disposition of hydroids and other epiphytes on fucoid algae. In this study the abundance of other epiphytes was much lower than experienced by these authors and no direct effect of competition would have affected the distribution of these hydroids.

Williams (1965) and Orlov (1996a) have shown that the planulae of *Clava* attached mostly on the sheltered parts of *Ascophyllum*, because the larvae were unable to settle when the water movement was too great. Although this may be one explanation for the rarity and absence of *Clava* from the apical sections of the algae, the deleterious effects of wave action subsequent to the settlement of the larvae may also be important because the water movement conditions experienced by planulae, and by recently metamorphosed hydroids, will vary with weather conditions. It is possible that settlement of planulae on calm days may occur on all sections of the algae, and that the most exposed hydroids are removed by subsequent storms. Hydroids are small, delicate passive filter feeders that need to project into moving water to feed. However, on a rocky shore such exposure to moving water makes the hydroids susceptible to damage by breaking waves, particularly athecate hydroids unprotected by an external perisarc. This too may help explain why *Clava* were more abundant on the wave-sheltered shore than on the wave-exposed shore.

That the thecate hydroid *Dynamena*, by contrast, was most abundant on the wave-exposed shore and abundant on the apical sections of the algae may reflect a greater tolerance to wave action, through various morphological adaptations of the perisarc, described by Hughes (1992). *Dynamena*, by surviving in relatively wave-exposed locations, may benefit from feeding in the faster moving tidal currents that sweep across the apical parts of the algae. Moreover, the planula larvae of *Dynamena* tend to be photophilic and not negatively influenced by strong hydrodynamic conditions (Burykin, 1989; Orlov, 1996a). Rapid hydrorhizal growth following settlement (Orlov, 1996b) gives *Dynamena* the potential to colonise new substrata, including the apical sections of *Ascophyllum*, relatively rapidly. This may be interpreted as an opportunistic characteristic as *Dynamena* is a poor competitor in the presence of other epiphytes (Seed and O'Connor, 1981).

Dynamena were less abundant on the central sections of *Ascophyllum* than on the apical and basal sections. The reasons are unknown but these sections of the algae are the most dense and here the proximity to neighbouring algal fronds may reduce feeding opportunities, directly by mechanical abrasion, and indirectly by reducing the water movement around the hydroids. The basal sections of the algae are the oldest and least dense (as there are only a few per alga). When the algae are supported in the water column these basal sections are protected from the worst of the wave action, by the denser more distal parts of the algae, but the tidal currents that flow around them are relatively unrestricted. This, together with the age of these sections, may explain why both species of hydroid were relatively abundant here.

Exposure to solar radiation may also restrict the colonisation of the apical sections of *Ascophyllum*, particularly by the athecate *Clava*. The apical sections are those most exposed to solar radiation when the algae lie flat after the tide has ebbed. Desiccation and heat stress may affect *Clava* more than *Dynamena*, as the hydranths of *Dynamena* may be withdrawn into their thecae which are then closed by operculae. The perisarc may also reduce the amounts of UV radiation reaching the cells of *Dynamena*. Further experiments on the relative susceptibility of the two species to UV radiation, prevention or tolerance of desiccation, and tolerance of heat stress are required to ascertain the importance of these variables in affecting their distributions.

Phenotypic variations in morphology of hydroids have been reported in response to variations in water

movement, food availability and temperature (see review by Gili and Hughes, 1995). Hydroid size is often inversely related to degree of water movement, and this is the case here for both *Clava*, which had fewer hydranths in the wave-exposed area, and *Dynamena*, which had shorter hydrocauli on the wave-exposed algae. Flow velocities may also have an indirect effect on hydroid morphology through feeding rates. Hydroids may feed efficiently in only a narrow range of current velocities, because if the currents are too slow the amounts of food brought to the vicinity of the hydroid is low, and if the currents are too fast the hydranths and the tentacles may be deformed and flattened reducing the surface area presented across the current and reducing feeding efficiency. Further, the potential food particles may be moved past the hydranths too quickly for them to be captured. There is experimental evidence that feeding rates alone may affect hydroid morphology. For example, *Dynamena* and *Gonothyrea* increased hydrorhizal growth and branching in response to increased food supply (Burykin 1980a, b). In *Laomedea* a shortage of food led to shorter and more widely spaced hydrocauli (Berrill, 1950; Crowell, 1957). Thus, water movement may affect hydroid morphology directly and indirectly, and further experiments would be required to ascertain the effects of these different variables. There were no differences between any of the other morphological features evaluated in the two areas, including the distance between hydrocauli of *Dynamena*, which has been postulated to be shorter in exposed areas, thus packing the hydrocauli closer together into a more compact structure (Seed and O'Connor, 1981). Such an effect or response may be seen if samples are taken from shores with a higher degree and range of wave action than those examined here. Alternatively in *Dynamena* the distance between hydrocauli may not be a variable character.

The proportion of *Dynamena* hydrothecae that contained hydranths was lower in the exposed area than in the sheltered area. This may reflect damage to the delicate hydranths by waves, the repair of which may necessitate resorption and regrowth of the hydranths. Further observations of the variations in the proportions of empty hydrothecae may provide further evidence, for example by examining hydroids on a wider variety of wave-exposed shores and by examining variations between hydrocauli on different sections of the same alga. Loss of hydranths in other thecate and atehcate hydroids has been attributed to an intrinsic cycle of growth, feed-

ing and resorption as a mechanism to avoid hydranth ageing. Hughes (1987) argued against this hypothesis, and the almost complete presence of hydranths on the wave-sheltered *Dynamena* in this study supports the view that it is not necessary for hydranths to be resorbed after only a few days to avoid senescence. A difference in food availability may contribute to the difference in hydranth presence between the exposed and sheltered areas, as one response of some hydroids to scarcity of food is for some hydranths to regress, while more peripheral hydranths are generated (see Gili and Hughes, 1995). The amounts of food in the water will be the same because of the proximity of the two areas, but in the exposed area the wave-generated currents may reduce feeding rates (for the reasons outlined above). However, differences in feeding rates are probably not responsible because other data on abundance and distribution do not indicate a relative food scarcity in the wave-exposed area (see above). This work is a good example of how phenotypic variation caused by responses to different water movement may be observed even in a short-space scale. Differences in morphology of hydroids were such that they can be used as indicators of different regimes of water movement (Gili and Hughes, 1995). Hydroids are adapted to high exposed habitats not only by decreasing their size but also by developing structures that either strengthen the hydrocaulus or increase its flexibility, in both cases to prevent fracture of the perisarc or detachment. Such adaptations should be also associated with feeding efficiency and prey availability.

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