Wave-related abrasion induces formation of extended spines in a marine bryozoan

MICHA M. BAYER*, CHRISTOPHER D. TODD, JANE E. HOYLE
AND JOHN F. B. WILSON

Gatty Marine Laboratory, School of Environmental and Evolutionary Biology, University of St Andrews, St Andrews, Fife KY16 8LB, Scotland, UK (mmb@st-andrews.ac.uk)

SUMMARY

Inducible morphology, the conditional expression of morphological characters under certain environmental regimes, is a trait usually found in organisms subject to discrete environmental variability. In marine invertebrates, inducible changes in morphology are usually linked to unpredictable attack by predators or overgrowth competition. We present here evidence that extended spine formation in the marine bryozoan *Electra pilosa* is inducible by an abiotic cue, wave-related abrasion. In a laboratory experiment, we induced the formation of extended spines by subjecting colonies of *E. pilosa* to abrasion by seaweeds. We also investigated the potential role of *Adalaria proxima*, a specialist suctorial nudibranch predator of *E. pilosa*, in the formation of extended spines. While the presence of the predator does not itself induce extended spine formation, the spines do have a fortuitous anti-predator effect, discouraging predation both by *A. proxima* and another nudibranch, *Polycera quadrilineata*. We suggest that extended spines in *E. pilosa* constitute an adaptation for the protection of feeding polypides in high-energy environments, and that plasticity for the trait is of adaptive value in this passively dispersed organism, which exploits a diverse range of substrata and epifaunal habitats.

1. INTRODUCTION

Amongst invertebrate animals, inducible changes in discrete morphological characters have been reported to be mediated by biotic factors (Adler & Harvell 1990; Harvell 1990). These phenotypic plasticities include defensive structures such as spines (rotifers, bryozoans) or helmets (crustaceans), formed in response to predators, and sweeper tentacles (cnidarians) or stolons (bryozoans) arising from competition for space. We report here on the induction of a discrete morphology (extended median proximal spines, EMPS), which is novel in being mediated by an abiotic factor, wave-related abrasion. Typically, bryozoan colonies are encrusting and comprise interconnected zooids. The cosmopolitan marine bryozoan *Electra pilosa* L. is abundant in north-western Europe, and commonly grows epibiotically on the intertidal macro-alga *Fucus serratus* L. (Ryland & Hayward 1977). Zooids of *E. pilosa* generally have up to 11 short (*ca.* 100 µm) marginal spines and a single short (*ca.* 200 µm) median proximal spine (MPS). In a long-spined zooid morph, however, the MPS is greatly elongated (up to 2100 µm), a feature which is so distinctive that it has led some taxonomic authorities to assign this morph subspecific status (Hincks 1880). Nonetheless, three lines of evidence point to this morph being an ecophe-

notypic variant: (1) long- and short-spined zooids can occur within the same colony (figure 1); (2) the proportions of long- and short-spined colonies within populations vary seasonally (Stebbing 1973); and (3) on wave-exposed shores, there are higher proportions of colonies having long-spined zooids than occur on sheltered shores, and within colonies from exposed shores there is a higher proportion of long-spined zooids than in colonies from sheltered shores (figure 2). Colonies epibiotic on different seaweed species also differ in the percentage of long-spined zooids they display (C. D. Todd, unpublished data).

Given the above observations on the environmental correlation between wave exposure and the long-spined morph, we considered it likely that the formation of extended spines might be inducible by wave action, or perhaps by wave-related abrasion. We therefore subjected replicated genotypes to simulated wave action and algal abrasion in a laboratory experiment. Also, we aimed to investigate the role of a specialist nudibranch predator of *E. pilosa* as a potential inductive cue for the formation of extended spines. In the bryozoan *Membranipora membranacea* L., the formation of spines (as spine-bearing specialist zooids in which feeding and budding functions have been lost) is inducible through a water-borne cue from a nudibranch sea slug predator (Harvell 1984a). *E. pilosa* is preyed upon by a variety of organisms, but in British waters it is predominantly exploited by the nudibranch

*Author for correspondence.

Figure 1. (a) Scanning electron micrograph (SEM) of a typical laboratory-grown, short-spined colony of *Electra pilosa*. Zooid length *ca.* 0.6 mm. (b) SEM of laboratory-grown induced colony of *E. pilosa*, showing long- and short-spined zooids. (c) Extended spines and feeding lophophores in a field-collected colony of *E. pilosa*. Fully formed extended spines (here *ca.* 1200 μ m) have a conical tip; spines of intermediate length shown here are blunt-ended and still forming. Short-spined zooids are also present.

mollusc *Adalaria proxima* (Alder & Hancock), a stenophagous specialist (Todd 1981), and, to a lesser extent, the sublittoral species *Polycera quadrilineata* (Müller), which is preferentially associated with *M. membranacea* (Thompson & Brown 1976). The relationship between the predator and its prey is intimate to the extent that larval metamorphosis in

A. proxima is specifically induced by the presence of the bryozoan (Lambert & Todd 1994; Lambert *et al.* 1997).

To investigate whether extended spines in *E. pilosa* zooids are inducible through predation by *A. proxima*, we subjected cloned replicate colonies of *E. pilosa* growing on glass plates to predation by *A. proxima*, and monitored colony development thereafter. We also

Figure 2. Differences in spinosity of *Electra pilosa* colonies from four sites of varying wave exposure. (a) Percentages of colonies including long-spined zooids at each site ('spiny' colonies). (b) Percentages of long-spined zooids within 'spiny' colonies at the same sites. Data shown are back-transformed arcsin means $\pm$ s.e. Sites shown: CS, Clachan Seil, west Scotland, sheltered to very sheltered, Lewis Biological Exposure (LBE) scale 4–5 (Lewis 1964); DD, Dundonnell, north-west Scotland, sheltered, LBE scale 4; GB, Gruinard Bay, north-west Scotland, semi-exposed, LBE scale 3; KB, Kingsbarns, east Scotland, exposed to semi-exposed, LBE scale 2–3.

assessed the effectiveness of extended spines in reducing predation: zooidal spines or specialist spinozooids can be an effective means of hindering or disrupting predation (Cook 1985; Harvell 1984a, 1986). Here, we offered short-spined, long-spined and de-spined *E. pilosa* to both *A. proxima*, a suctorial predator which removes only the soft tissues of individual zooids, and *P. quadrilineata*, a raptorial predator which consumes the soft tissues of the zooids and also the skeletal components.

2. MATERIAL AND METHODS

(a) Abrasion experiments

Recently settled ancestrulae (post-larval 'founder' zooids) of *E. pilosa* were collected on *F. serratus*. Colonies were propagated from the ancestrulae, grown onto glass plates, and replicated by fragmentation (for details of methodology

see Bayer *et al.* (1994)). Six replicate colonies from each of four genotypes (total $n = 24$) were randomly allocated to slots in two complete randomized blocks on a horizontal rack which was held *ca.* 2 cm below the surface of the water in a purpose-built thermostatically controlled tank (18 °C). The flagellate *Rhodomonas* sp. was provided as food at a concentration of 50 000 cells ml⁻¹. The food concentration in the tank was established daily by counting cells in a water sample using a Sedgwick–Rafter counting chamber, and food was added as required to re-establish the above concentration. The water in the tank (75 l of 3 µm-filtered seawater) was changed once a week. To mimic wave action throughout the experiment, a tipping tank mounted 30 cm above the rack discharged 7.2 l of internally pumped water every 20 s.

There were two treatments ('intermittent' and 'permanent' abrasion) and one control ('no abrasion') group. The experiment was subdivided into three periods: period 1 provided a phase of undisturbed growth, allowing colonies to attain a size sufficient to prevent whole-colony mortality during abrasion; at the beginning of period 2, specimens of the filamentous red macroalga *Ceramium rubrum* (Hudson) were attached to the edges of plates allocated to the two treatments ('intermittent' and 'permanent' abrasion) to provide wave-generated mechanical stimulation or abrasion of the underlying colony. The algae were removed from the 'intermittent' abrasion treatment at the end of period 2, whereas colonies in the 'permanent' abrasion treatment remained abraded during period 3. The experiment was carried out twice, with different sets of genotypes. The lengths of the periods were determined by colony growth and varied slightly between experimental repeats (period 1 = 18/12 d, period 2 = 8/9 d, period 3 = 8/8 d, for experiments 1/2, respectively). Throughout each experiment, colonies were drawn on alternate days, using a *camera lucida* mounted on a stereomicroscope, to provide a detailed temporal record of colony growth and of EMPS formation. In addition, colonies were drawn on the last day of each experimental period, thus allowing a direct comparison of the pre- and post-induction status of colonies. EMPS are easily recognizable from the early stages of their formation: a large boss with a visible lumen develops on the zooid bud, which then forms the base of the developing EMPS; in a non-extended MPS, the boss is rudimentary and has no visible lumen.

As a result of the water discharge from the tipping tank deviating slightly from vertical, colony growth was reduced in one of the blocks (i.e. rows in the rack) in experiment 1. Prior to experiment 2, settings on the tipping tank were adjusted slightly to reduce the block effect, and therefore the analysis of the experimental data was undertaken for each experiment separately.

At the end of each experiment, colonies were removed from the tank, cleaned with a paint-brush in fresh water and air-dried. Colonies were then examined under a stereomicroscope, and the numbers of short- and long-spined zooids in each colony were counted. Data were log₁₀-transformed where necessary, and then analysed using Multifactorial Analysis of Variance (SuperANOVA, Abacus Concepts, Inc., Berkeley, California, USA, 1991).

(b) Testing for inductive cues from *Adalaria proxima*

A total of 38 colonies of *E. pilosa* from four replicated genotypes were obtained by fragmentation and grown to a size of approximately 150 mm² (equivalent to *ca.* 915 zooids). Half of these were subjected to a 2–3 d period of continuous predation by *A. proxima* after which the mollusc was removed; during the predation period, colonies were kept in

individual 200 ml polypropylene dishes at 15 °C, the maximum temperature tolerable by the molluscs. Colony development was then monitored for a minimum of 20 d. Except for the period of predation, colonies on their glass plates were held vertically in a randomized array by a circular Perspex rack situated in a round 8 l glass trough. Colonies were fed the flagellate *Rhodomonas* sp. throughout the experiment; the filtered seawater in the tank was changed twice a week.

(c) Prey choice and feeding rate experiments

To standardize the size of colony pieces offered to predators, we punched out with a cork borer 5 mm diameter discs (equivalent to ca. 40 zooids) from *E. pilosa* colonies growing on *E. serratus*. In all cases, discs were cut from the area immediately proximal to the distal growing margin, to avoid possible variation in zooid palatability (Harvell 1984b). Due to the patchiness of extended spines, discs categorized as long-spined rarely consisted exclusively of long-spined zooids; accordingly, the criterion adopted here was a minimum of 50% long-spined zooids. To prepare de-spined discs, extended spines were clipped basally with iridectomy scissors to render the median spines comparable in length to unextended median spines. Short-spined discs comprised exclusively zooids with unextended median proximal spines. The algal discs were then impaled horizontally onto short pieces of fuse wire (three to each piece of wire, one of each prey type) which was then bent to produce a trefoil array of the three discs. The trefoil array eliminated the need for randomization of discs and enabled each individual predator to be in contact with all three discs at the same time, thus offering a choice of the three different types of prey. The disc arrays and molluscs were then introduced at random orientations into separate wells of Corning six-well plates containing filtered seawater.

Positions of feeding molluscs on the disc arrays were recorded at 1 min intervals for the first 6 h of the experiment. The extent of predation was recorded on a WILD M8 stereomicroscope, fitted with a *camera lucida*, at varying intervals during the experiment, depending on the feeding activity of molluscs. A final observation was made after 24 h. *P. quadrilineata* is a raptorial predator that removes whole zooids, and this necessitated measurement of the colony area consumed; this was accomplished by means of drawings made using the *camera lucida*, which were digitized using analySIS 2.0 image analysis software (Soft-Imaging Software GmbH, Münster, Germany). *A. proxima*, a suctorial predator, removes the soft parts of zooids only, leaving the hard skeleton; accordingly, the number of zooids consumed was counted and used in the analysis. Two repeats of the experiment were carried out for each predator species.

Feeding rate data were log₁₀-transformed where necessary, and analysed by Analysis of Covariance (SuperANOVA) using mollusc weight or length as the covariate. Data from the choice experiments were analysed using *G*-tests for goodness of fit (Sokal & Rohlf 1981).

3. RESULTS

(a) Abrasion experiments

It appears that formation of EMPS is a deterministic process, as indicated by spine length frequency distributions: MPS and EMPS show strikingly different mean lengths, with normal distributions

(M. M. Bayer, unpublished data), suggesting that the extended spine is a discrete character rather than one that shows continuous variation.

Extended spine formation was observed to be a two-stage process. Initially, a large basal boss forms on the zooid wall, and the boss then either develops an extended spine, or, in exceptional circumstances, calcifies and forms a spine of length intermediate between the lengths of unextended and extended MPS. The development of EMPS commenced within 24 h of exposure to the abrasion stimulus, and was completed within a minimum of 4 d. Figure 3 shows the back-transformed arcsin mean ($\pm$ s.e.) per cent of zooids that formed in each experimental period, and that displayed the induced morphology (bosses, intermediate length spines and EMPS). Extended spines formed in all colonies that received algal abrasion, but only for zooids budded and fully formed during the treatment periods (figure 3). Some colonies in the 'intermittent' abrasion treatment did produce a small number of EMPS following the removal of algal abrasion (period 3, figure 3), but zooid maps showed that these were all peripheral buds that were forming while still being subject to the stimulus up to the end of period 2. Thus, there appears to be a period only early on in their ontogeny when zooids can form EMPS. No EMPS were formed in control colonies subjected only to wave-crash: EMPS do not, therefore, form in response to water movement alone and in *E. pilosa* they probably are not an adaptation to modulating water flow over the colony surface (cf. Whitehead *et al.* 1996).

ANOVA revealed a significant difference ($p < 0.001$) in the percentage of induced zooids between the periods in experiment 1, but showed no significant period effect for experiment 2 ($p = 0.271$) due to an increase in the number of zooids induced during period 3 in the 'permanent' abrasion treatment. A significant block effect ($p = 0.015$) was also observed for experiment 2.

The final size range of colonies was 80–2506 zooids and 121–669 zooids for experiments 1 and 2, respectively. As expected, final colony size varied strongly with genotype, but there were also block and treatment effects; growth of colonies in the 'permanent' abrasion treatment was significantly reduced when compared to that of control colonies ($p = 0.003$, ANOVA), with control colonies attaining approximately twice the final size of 'permanent' abrasion treatment colonies. This was possibly attributable to a reduction in the availability of suspended *Rhodomonas* cells to feeding zooids of the treatment colonies, due to a simple screening effect of the algal tufts; alternatively, the observed reduction in colony growth might have been attributable to the energetic costs of EMPS production. Additional sources of variation in colony growth might be increased frequencies or duration of feeding polypide retraction in abraded colonies, but alternative experimental designs will be necessary to distinguish these sources of variation.

(b) Testing for inductive cues from *Adalaria proxima*

A. proxima is a major predator of *E. pilosa* in the intertidal and sublittoral, but none of the zooids in either the

Figure 3. Induction of EMPS formation in *Electra pilosa*. Data are percentages of zooids newly formed in each period for two repeats. Experiment 1 (a) and experiment 2 (b) of the wave-crash abrasion experiment (two treatments and control): (i) control: wave-crash throughout, no abrasion (all values zero); (ii) permanent abrasion: wave-crash throughout, abrasion in periods 2 and 3 (black fill). (iii) intermittent abrasion: wave-crash throughout, abrasion in period 2 only (hatched fill).

treatment or the control colonies developed EMPS during predation or over the post-predation observational period. The formation of EMPS in *E. pilosa* is thus unrelated to predation by this major predator, and probably others. As expected, EMPS did not develop in pre-existing zooids, and thus colony growth is a requirement for the expression of this inducible character; here, colony growth rate was temporarily reduced during the predation period, possibly indicating a shock response to predation itself and/or an effect of the temperature reduction (see §2). Nonetheless, colonies in the predation treatments budded a total of approximately 1600 zooids during the predation period, none of which formed EMPS. Colonies also continued to bud new zooids after predation, with colony area increasing by 215–431% over the period between exposure to predation and the conclusion of

the experiment, and remained active and healthy throughout. There were no significant differences in colony area between treatments at the end of the experiment.

(c) Prey choice and feeding rate experiments

P. quadrilineata predation was reduced by EMPS, as indicated both by the significantly lower number of long-spined discs consumed over the duration of the experiment (*G*-test for goodness of fit, $p < 0.025$; figure 4), and the significantly lower proportion of long-spined discs attacked during the first feeding bout (*G*-test, $p < 0.025$; figure 4). In those cases where *P. quadrilineata* did consume long-spined discs, feeding rates were significantly lower than on short-spined and de-spined discs (ANCOVA, $p = 0.002$). Similarly, *A. proxima* showed a clear preference for short-spined and de-spined prey (figure 4), with a significantly lower number of long-spined discs attacked (*G*-test, $p < 0.001$) and a significant preference for short-spined and de-spined discs over long-spined discs during the first feeding bout (*G*-test, $p < 0.001$). *A. proxima* feeding rates were not significantly different amongst treatments (ANCOVA, covariate mollusc length), which was most likely due to only two nudibranchs feeding on long-spined discs, but the mean feeding rate on long-spined discs was still lower than that for short-spined and de-spined *E. pilosa* (long-spined: $1.52 \text{ zooids h}^{-1} \pm 1.40$, s.e.; short-spined: 2.20 ± 0.64 ; de-spined: 2.97 ± 1.10). Observed predation rates were lower than previously reported for adult *A. proxima* (Todd & Havenhand 1989) and can probably be explained by the present individuals being reproductive.

4. DISCUSSION

The rapid—and presumably energetically costly—formation of extended spines raises questions about the potential adaptive significance of this character in *E. pilosa*. Bryozoans are suspension feeders, and zooids capture particles by means of their tentaculate and ciliated lophophore. In the everted position (figure 1c), lophophores in *E. pilosa* project above the colony into the water column, and are essentially unprotected. It is probable that selective pressure for protection of the lophophore is high, as indicated by the fast lophophore retractor reflex, which is triggered by contact with solid objects (Thorpe *et al.* 1975). Fully formed extended spines can be several times the length of everted lophophores (EMPS length *ca.* 1200 μm ; lophophore length *ca.* 470 μm ; M. M. Bayer, unpublished data) and, at least in clusters, may afford considerable protection against mechanical disturbances. EMPS are uncalcified hollow projections of the chitinous cuticle (Ryland & Hayward 1977), a material which combines high mechanical strength with flexibility to the extent that they are essentially unbreakable (M. M. Bayer, personal observations).

The plastic expression of the trait begs the question why it should not be expressed constitutively, rather

Figure 4. Feeding preferences of two nudibranchs, *Adalaria proxima* (a) and *Polycera quadrilineata* (b), preying upon *Electra pilosa*. Individuals were offered a choice of three different types of *E. pilosa* colony: long-spined discs (white fill); short-spined discs (hatched) and de-spined discs (black fill). Records were made of the molluscs' choice of prey in the initial feeding period (left-hand section of graphs) and the total number of discs in each category that had been fed upon by the end of the experiment (right-hand section of graphs). Data shown are from two experimental repeats, represented by left-hand and right-hand columns of each pair of bars (sample sizes: *A. proxima*, $n = 20/23$; *P. quadrilineata*, $n = 34/40$; for repeats 1/2, respectively).

than facultatively. Phenotypic plasticity is typically found in organisms that inhabit environments that are unpredictably variable both spatially and temporally (Adler & Harvell 1990). There has been considerable controversy over whether phenotypic plasticity is itself a selectable trait or a by-product of selection on phenotypic values. A recent synthesis of conflicting theory has resolved some of the controversy (Via *et al.* 1995), with the conclusion that phenotypic plasticity can itself be an adaptive trait. Adaptive plasticity appears to be a widespread phenomenon and has been reported for all major taxonomic groups (Dudley 1996; Dudley & Schmitt 1996; Ebert 1996; Gotthard & Nylin 1995; Hazel *et al.* 1987; Kingsolver & Wiernasz 1991; Stearns 1989; Vasseur & Aarsen 1992). The plastic expression of

traits is assumed to be adaptive under the following three conditions (Adler & Harvell 1990): (1) the selective agent is unpredictable and carries a reduction in fitness for the organism; (2) environmental cues tied to the selective agent are reliable and non-fatal; and (3) there is a cost that partly offsets the fitness benefits of the inducible morphology. With specific reference to *E. pilosa*, (1) larval dispersal is passive and, except for larval microhabitat choice, carries an element of unpredictability with respect to the quality of the habitat encountered at the time of larval competence to metamorphose; exposure to wave-related abrasion probably carries a cost in terms of reduced growth (see above) and possibly reduced reproductive value too. In bryozoans, reproductive value is closely linked to colony growth due to their modular construction (Thorpe 1979). Third, wave exposure can be variable not only spatially but also on a temporal scale, ranging from daily to seasonally. (2) Cues are reliable predictors in that the cue and the selective agent are identical in the present case (wave-related abrasion); although partial mortality is widespread amongst bryozoan colonies due to competition, predation or physical disturbance, the cue is potentially fatal to the genotype. This is in contrast to, for example, the case of the bryozoan *M. membranacea*, in which the selective agent (predation by a nudibranch predator) and the cue (a waterborne chemical) are separate entities (Harvell 1984a, 1986), and where the cue itself is harmless. (3) Costs may occur in terms of the metabolic expenses of EMPS formation and possibly increased risk of micro-fouling and siltation of the zooid skeleton: Marcus (1926) observed that EMPS can entrap significant amounts of sand and silt, which can in turn prevent polypides from everting and feeding.

Although extended spines can be an effective anti-predator device against two mollusc species with contrasting feeding strategies, it is clear that in contrast to the spinozooids of *M. membranacea*, the spines of *E. pilosa* zooids are not inducible by the predators themselves. *A. proxima*, a specialist predator of *E. pilosa*, occurs both intertidally and subtidally, but intertidal populations show clear distributional variations in association with wave action. On the wave-exposed east and west coasts of Scotland the nudibranchs occur beneath stable rocks (where *E. pilosa* is comparatively rare), whereas on the sheltered coasts (especially sealochs) of western Scotland the molluscs are found exclusively on *F. serratus* and *Laminaria digitata* (Todd *et al.* 1997). It is apparent, therefore, that in locations characterized by long-spined colonies (e.g. on macroalgae on wave-exposed shores), the bryozoan is not exploited by *A. proxima*, and that epibiotic populations of the mollusc are most frequent in locations where short-spined colonies predominate. Selective pressure on the evolution of anti-predator defences can thus be assumed to be of minor importance to *E. pilosa*. Although inducible morphology is generally adaptive with respect to a primary causative agent, this does not preclude the existence of a fortuitous adaptive function with respect to other, secondary agents: for example, just as spines in *E. pilosa* may also reduce predation, structural reinforcements in conifer needles, induced by wind exposure,

may also be adaptive in increasing resistance to herbivory and frost (Ennos 1997).

We thank Tara Graham, Jennifer Shaw and Laura Gamwell for laboratory assistance. Scott Lidgard, Keith Sillar, Anne Magurran and an anonymous reviewer provided valuable comments on the manuscript, and Janette Duck, Peter Baxter and the staff of the Bute Medical Building Workshop gave excellent technical assistance. This research was funded by Natural Environment Research Council grant GR3/9512 to C.D.T.

REFERENCES

- Adler, F. R. & Harvell, C. D. 1990 Inducible defenses, phenotypic variability and biotic environments. *Trends Ecol. Evol.* **5**, 407–410.
- Bayer, M. M., Cormack, R. M. & Todd, C. D. 1994 Influence of food concentration on polypide regression in the marine bryozoan *Electra pilosa* (L.) (Bryozoa: Cheilostomata). *J. Exp. Mar. Biol. Ecol.* **178**, 35–50.
- Cook, P. L. 1985 Bryozoa from Ghana—a preliminary survey. *Sciences zoologiques, Ann. vol. 238*. Tervuren, Belgique: Musée Royale de l'Afrique Centrale.
- Dudley, S. A. 1996 Differing selection on plant physiological traits in response to environmental water availability: a test of adaptive hypotheses. *Evolution* **50**, 92–102.
- Dudley, S. A. & Schmitt, J. 1996 Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *Am. Nat.* **147**, 445–465.
- Ebert, T. A. 1996 Adaptive aspects of phenotypic plasticity in echinoderms. *Oceanol. Acta* **19**, 347–355.
- Ennos, A. R. 1997 Wind as an ecological factor. *Trends Ecol. Evol.* **12**, 109–111.
- Gotthard, K. & Nylin, S. 1995 Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* **74**, 3–17.
- Harvell, C. D. 1984a Predator-induced defense in a marine bryozoan. *Science* **224**, 1357–1359.
- Harvell, C. D. 1984b Why nudibranchs are partial predators: intracolony variation in bryozoan palatability. *Ecology* **65**, 716–724.
- Harvell, C. D. 1986 The ecology and evolution of inducible defenses in a marine bryozoan: cues, costs and consequences. *Am. Nat.* **128**, 810–823.
- Harvell, C. D. 1990 The ecology and evolution of inducible defenses. *Quart. Rev. Biol.* **65**, 323–341.
- Hazel, W., Brandt, R. & Grantham, T. 1987 Genetic variability and phenotypic plasticity in pupal colour and its adaptive significance in the swallowtail butterfly *Papilio polyxenes*. *Heredity* **59**, 449–455.
- Hincks, T. 1880 *A history of the British marine polyzoa*. London: John Van Voorst.
- Kingsolver, J. G. & Wiernasz, D. C. 1991 Seasonal polyphenism in wing-melanin pattern and thermoregulatory adaptation in *Pieris* butterflies. *Am. Nat.* **137**, 816–830.
- Lambert, W. J. & Todd, C. D. 1994 Evidence for a water-borne cue inducing metamorphosis in the dorid nudibranch mollusc *Adalaria proxima* (Gastropoda: Nudibranchia). *Mar. Biol.* **120**, 265–271.
- Lambert, W. J., Todd, C. D. & Hardege, J. D. 1997 Partial characterization and biological activity of a metamorphic inducer of the dorid nudibranch *Adalaria proxima* (Gastropoda: Nudibranchia). *Invert. Biol.* **116**, 71–81.
- Lewis, J. R. 1964 *The ecology of rocky shores*. London: The English Universities Press Ltd.
- Marcus, E. 1926 Beobachtungen und Versuche an lebenden Meeresbryozoen. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* **52**, 1–102.
- Ryland, J. S. & Hayward, P. J. 1977 *British anascan bryozoans*. Synopses of the British Fauna (New Series). London: Academic Press.
- Sokal, R. R. & Rohlf, F. J. 1981 *Biometry*. New York: W. H. Freeman.
- Stearns, S. C. 1989 The evolutionary significance of phenotypic plasticity. *BioScience* **39**, 436–445.
- Stebbing, A. R. D. 1973 Observations on colony overgrowth and spatial competition. In *Living and fossil bryozoa* (ed. P. G. Larwood), pp. 173–183. London: Academic Press.
- Thompson, T. E. & Brown, G. H. 1976 *British opisthobranch molluscs*. Synopses of the British Fauna. London: Academic Press.
- Thorpe, J. P. 1979 A model using deterministic equations to describe some possible parameters affecting growth rate and fecundity in Bryozoa. In *Advances in bryozoology* (ed. G. P. Larwood & M. B. Abbott), pp. 113–120. London and New York: Academic Press.
- Thorpe, J. P., Shelton, G. A. B. & Laverack, M. S. 1975 Colonial nervous control of lophophore retraction in cheilostome bryozoa. *Science* **189**, 60–61.
- Todd, C. D. 1981 The ecology of nudibranch molluscs. *Oceanogr. Mar. Biol. A. Rev.* **19**, 141–234.
- Todd, C. D. & Havenhand, J. N. 1989 Nudibranch bryozoan associations: the quantification of ingestion and some observations on partial predation among Doridoidea. *J. Moll. Stud.* **55**, 245–259.
- Todd, C. D., Lambert, W. J. & Thorpe, J. P. 1997 The genetic structure of intertidal populations of two species of nudibranch molluscs with planktotrophic and pelagic lecithotrophic larval stages: are pelagic larvae 'for' dispersal? *J. Exp. Mar. Biol. Ecol.* (Submitted.)
- Vasseur, L. & Aarsen, L. W. 1992 Interpretation of adaptive plasticity in *Lemna minor*. *Oikos* **65**, 233–241.
- Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D. & Van Tienderen, P. H. 1995 Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.* **10**, 212–217.
- Whitehead, J. W., Seed, R. & Hughes, R. N. 1996 Factors controlling spinosity in the epialgal bryozoan *Flustrellidra hispida* (Fabricius). In *Bryozoans in space and time* (ed. D. P. Gordon, A. M. Smith & J. A. Grant-Mackie), pp. 367–375. Wellington, New Zealand: National Institute of Water & Atmospheric Research Ltd.

Received 16 July 1997; accepted 8 August 1997