Morphological and genetic adaptation to a lagoon environment: a case study in the bryozoan genus *Alcyonidium*

Abstract The Fleet (southern England) is a stable (ca. 5,000 years) coastal saline lagoon that supports a population of *Alcyonidium* resembling the common coastal epiphyte, *Alcyonidium gelatinosum* (L.). A combination of morphological, reproductive, and ecological characters was used to compare lagoonal and non-lagoonal proximate populations. Comparisons revealed a difference in the timing of spawning, considered to be related to the temporarily restricted availability of viable substrata within the lagoonal basin. Allochronous spawning and spatial separation together suggest that the lagoonal taxon is reproductively isolated. The two populations were further compared with seven other coastal populations of *Alcyonidium* using randomly amplified polymorphic DNA (RAPD) analysis. The results confirm the individuality of the lagoonal taxon but also a close relationship with three *A. gelatinosum* populations. We present and consider four hypotheses that may account for the presence of this genetically distinct taxon: (1) diversification within the Fleet; (2) colonisation from another lagoon; (3) a southern lagoonal species at its northern limit; and (4) introduction by shipping or other anthropogenically mediated dispersal mechanism. Significant diversification on the time scale involved has been demonstrated for isolated freshwater environments and, therefore, is feasible within a saline lagoon. Hypothesis 1 and, to a lesser extent, hypothesis 2 are consistent with the recognition of individual lagoons as ‘biogeographic’ islands of importance for their unique or characteristic biodiversity. The study also represents the first example of concordant morphological, reproductive, and genetic diversification in a marine bryozoan.

Introduction

Saline lagoons often form behind sedimentary barriers associated with microtidal coasts. Seawater and biophysical exchange occur through one or more inlets or by percolation. A typical lagoonal basin is an isolated, low energy ecosystem characterised by extreme shelter from wave action, an attenuated tidal range, weak currents and poor flushing, and a prevalence of shallow sublittoral mud beds often colonised by seagrasses (Barnes 1980). Lagoons are well recognised as being unique in terms of their biodiversity. A range of characteristic invertebrate morphospecies is known to be common to many saline lagoons in north-west European waters (Barnes 1980, 1988, 1989, 1994; Bamber et al. 1992), some of the species being closely related to estuarine or open coastal counterparts. For example, the lagoonal cockle *Cerastoderma glaucum* (Bruguière) and estuarine cockle *Cerastoderma edule* (L.) are only differentiable according to relatively minor morphological, biological, and ecological characteristics; the species co-exist in intermediate environments and can hybridise (Barnes 1980). The existence of characteristic lagoonal morphospecies suggests that physical isolation and low energy regimes may exert strong selective pressures on marine colonisers, fostering the evolution of differentiated taxa. Rapid genetic differentiation has recently been demonstrated for populations of fish isolated within post-glacial freshwater lakes (McPhail 1993; Duvernell and Turner 1998; Foster et al. 1998). Coastal saline lagoons formed behind sedimentary barriers are also post-glacial entities, typically no more than 10,000 years old. It is, therefore, reasonable to hypothesise that rapid genetic differentiation may also occur within saline lagoons.

We used a combination of morphological, reproductive, and ecological characters, in conjunction with randomly amplified polymorphic DNA (RAPD) analy-
sis to compare lagoonal and non-lagoonal populations of the marine bryozoan genus *Aleyonidium* (Lamouroux) as found within and outside the Fleet Lagoon (southern England). This genus is particularly suitable for study because of its tendency to produce cryptic species (Thorpe et al. 1978a, b), partly attributable to the limited dispersal potential of the ephemeral lecithotrophic larvae characteristic of most British species within the genus. Here, we examine the hypothesis that relatively stable saline lagoons may foster the evolution of unique morphological and genetic variants.

The RAPD technique has previously been used to investigate population genetic structure within clonal marine organisms, including cnidarians (Levitan and Grosberg 1993; Grosberg et al. 1997), freshwater bryozoa (Okamura et al. 1993; Hatton-Ellis et al. 1998) and ascidians (Bishop et al. 1996). Although the RAPD technique is not always favoured for technical reasons (Haymer 1994; Reiseberg 1996), recent work has established its value for differentiating taxa, provided that certain assumptions are fulfilled and appropriate control experiments are performed (Haymer 1994; Reiseberg 1996; Perez et al. 1998). The RAPD technique is particularly powerful when used in combination with other characters (Reiseberg 1996).

**Materials and methods**

Ecological studies

The Fleet is a 13-km-long saline lagoon formed between a shingle barrier (Chesil Bank) and the mainland coast of southern England (Fig. 1; 50°40.5′N, 2°34.3′E). The lagoonal basin exhibits classically sheltered conditions with weak tidal circulation and poor flushing (Robinson et al. 1983). The waters of the lagoonal basin are mainly brackish although fully saline conditions can prevail along most of the basin during dry periods (Whittaker 1978). The shallow subtidal bottom (< 1 m) is dominated by organic muds supporting seagrass meadows (two species of *Zostera*, two of *Ruppia*) (Whittaker 1978). A species of *Aleyonidium* colonising mollusc shells within the lagoonal basin was first mentioned by Seaward (1978) and identified only as a member of the *A. mytili/polyoam* 'complex' (Seaward 1981). Recent field surveys have revealed this population to be concentrated within the central section of the lagoon basin (P.E.J. Dyrnda, personal observation). In contrast, *A. gelatinosum* (L.) is absent from the lagoonal basin but occurs intertidally on *Fucus serratus* L. at the lagoon mouth (Fig. 1). Lagoonal *Aleyonidium* was collected by sweep netting at Langton Hive Point (Fig. 1) in winter, and by hand gathering by snorkellers whilst vegetation was dense in summer. Thirty colonies of the lagoonal *Aleyonidium* were collected at 4- to 6-week intervals between January 1995 and January 1997 (31 January 1995, 6 April 1995, 1 May 1995, 9 June 1995, 15 July 1995, 10 August 1995, 7 September 1995, 8 October 1995, 12 November 1995, 28 March 1996, 4 May 1996, 14 January 1997). Fronds of *F. serratus* bearing *A. gelatinosum* were hand collected at ‘Small Mouth’ (Fig. 1) at low tide. Samples were preserved in 70% ethanol. Additional colonies were maintained live for observation, morphometric analysis, and photography. Seasonal monitoring of vegetation cover and intertidal populations within the central lagoon was undertaken over the same period (Fig. 2).

Colonies of *A. gelatinosum* were also collected from the Menai Strait (53°13.4′N, 4°10.2′W) and Camel Estuary (50°32.8′N, 4°55.3′W). Five populations representing two other littoral *Aleyonidium* species were sampled as follows: *A. mytili* (Dalyell) Longniddry (56°3.0′N, 3°49.0′W), Falls of Lora (56°25′N, 5°24′W), Cleddau Bridge (51°42.3′N, 4°55.8′W); *A. reticulatum* Ryland and Porter (2000), Porlock (51°12′N, 3°27′W), Watwick (51°42.0′N, 5°09.3′W).

**Laboratory studies**

* Morphometric analyses

Morphometric analysis of live colonies was undertaken using image analysis [Wild M420 Makroscop, video camera, and PC running...