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Seasonal variation in a low shore *Fucus serratus* (Fucales, Phaeophyta) population and its epiphytic fauna

Gray A. Williams[1]
Port Erin Marine Laboratory, The University of Liverpool, Port Erin, The Isle of Man, U.K.
[1]*Present address: The Department of Ecology and Biodiversity & The Swire Institute of Marine Science, The University of Hong Kong, Hong Kong; Fax: 852–5176082, e-mail hrsbwga@hkucc.hku.hk*

Key words: epiphytes, niche partitioning, rocky shore, seaweed, temporal and spatial variation

Abstract

Seasonal variation in a *Fucus serratus* assemblage was studied on the Isle of Man, UK over a 13-month period. Algal cover varied greatly, related to shedding reproductive fronds and winter storms. Peak reproduction was recorded in the autumn. There was little change in density of plants, the population was dominated by a bank of germlings (<20 cm) and an adult mode between 50–70 cm. An indistinct third component of recruiting juveniles was present when gaps in the canopy formed. Seasonal variation in the algae was reflected in the population dynamics of the mobile epiphytes such as *Littorina mariae* and *Lacuna pallidula,* which exhibited annual life histories. Sessile species (such as bryozoans) utilized the algae year round, dominating the perennial stipes and lower fronds, which were not shed. Other species utilized the algae in a transient fashion: some feeding on the algae (e.g. *Idotea*), or other epiphytic animals (e.g. *Nucella*). *Fucus serratus*, therefore, provides a variety of spatially and temporally variable niches that explain the diversity of epiphytic animal species that exploit this alga.

Introduction

Fucus serratus L. is a dominant low shore alga on sheltered rocky shores on the NE Atlantic coast (Hawkins *et al.*, 1992). This alga has been used as a fertilizer (Knight & Parke, 1950), and more recently as a source of fucoidans, which have been identified as modulating agents of mammalian immune responses (Coughlan, 1977; Ramsden & Rider, 1992). *Fucus serratus* is a perennial alga, usually living for 3–4 years, with seasonal changes in growth associated with reproduction and frond shedding (Knight & Parke, 1950). Over 91 different taxa have been recorded on this species (Boaden *et al.*, 1975), which can sometimes cover over 75% of the algal host's surface area (Williams & Seed, 1992). The epiphyte assemblage found on *F. serratus* has been investigated by numerous workers (reviewed by Seed & O'Connor, 1981; Seed, 1985). Variations in species composition and cover of epiphytic animals have been described for algae under different environmental conditions (Boaden *et al.*, 1975), at different tidal heights (Wood & Seed, 1980) and at different seasons of the year (Seed *et al.*, 1981; Oswald & Seed, 1986). Competition for space between sessile epiphytic animals has also been documented (O'Connor *et al.*, 1975, 1980; Boaden *et al.*, 1976). More recently, studies have investigated host-epiphyte interactions (Williams & Seed, 1992). Encrusting bryozoans have been shown to decrease algal photosynthesis rates (Oswald *et al.*, 1984) but also alleviate the effects of cold temperatures (Oswald & Seed, 1986). Grazing by mobile herbivores has been suggested to benefit the host alga by cleaning fronds of fouling species (Williams, 1990; 1992a).

Much of the previous research has concentrated on the use of the alga as a substratum for epiphyte exploitation and has not accounted for growth or reproductive patterns in the alga. This paper documents seasonal variation in population structure, phenology and cover of *Fucus serratus*, and its epiphytic faunal assemblage on the Isle of Man, U.K.

Materials and methods

Sampling was conducted every month at low water spring tides at St Michael's Island, a sheltered rocky shore on the Isle of Man (O. S. Grid reference SC 296 675) between May 1988 and May 1989. Field work was conducted in the *Fucus serratus* zone (≈ 2.20 m above the lowest astronomical tide), where ten permanent 50 x 50 cm quadrats were located. In each of the ten quadrats percentage cover of *F. serratus* was scored using a 50 x 50 cm perspex sheet drilled with 100 random points. Plants over 5 cm were counted and measured (± 1 cm); those below 5 cm were simply counted. Each month five plants (maximum length ≈ 500–600 mm) were collected from an adjacent area by cutting at the holdfast and then inserting the complete alga into a plastic bag to prevent epiphytic animal loss. In the laboratory each alga was subdivided into stipe and midrib tissue (no frond material), frond tissue (midrib with frond), and reproductive tissue (fronds with receptacles), and these components were wet weighed after rinsing in seawater and allowing to dry for 5 minutes in a sieve.

Algae were searched in the field using surgical (Tru-touch) gloves to which small gastropods stick (Williams, 1992b, 1995), and the littorinids found were measured using vernier calipers (± 0.5 mm). Littorinids below 2.5 mm were simply counted (Williams, 1992b). In the laboratory the longest axis of the five plants collected was divided into Y-segments (dividing the alga into pieces containing a single dichotomy, after Boaden *et al.*, 1975) and traced on acetate sheets. The surface areas of sessile epiphytic animals were also traced. These surfaces were then digitized to obtain areas and percentage cover values for epiphyte loads. No distinction was made between convex and concave frond surfaces. All mobile species were removed by hand searching and recorded; the presence of any sessile species not previously recorded along the longest axis was also noted.

Results

Algal population dynamics

The density of *Fucus serratus* was variable within the range 10–14 plants 0.25 m $^{-2}$ for the majority of the year (June to March) but increased (range 18–22 plants 0.25 m^{-2}) in April and May when new recruits were recorded (Figure 1). The population had two major size classes (Figure 1); a germling 'bank' of plants between 0 - 10 cm, which accounted for 30–40% of the population, and a second mode of adult plants above 40 cm in size. There was no clear mode of individuals between these size classes although individuals in the size range 10–40 cm were present throughout the year (Figure 1). The largest mode was very stable with a peak of abundance at a size of 50–70 cm throughout the year (Figure 1), although annual peaks within this mode could not be differentiated.

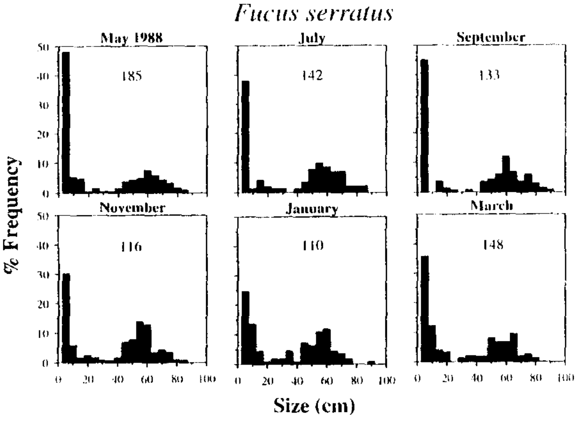

Figure 1. Bi-monthly size frequency histograms for a *Fucus serratus* population between May 1988 to May 1989 from St Michael's Island, Isle of Man (total from 2.5m^2). Individuals below 5 cm in height were grouped in the smallest size class. Numbers represent total number of plants 2.5 m $^{-2}$.

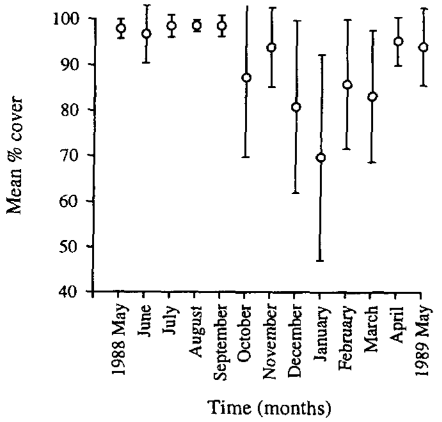

Figure 2. Mean (± S.D.) cover of *Fucus serratus* (n=10) between May 1988 to May 1989 from St Michael's Island, Isle of Man.

Throughout the summer, algal cover was uniformly high (>95% cover, Figure 2), but decreased and became patchy with the onset of autumn (September). The lowest cover (*c.* 70%) was recorded in January 1989. In the spring, algal cover increased to reach

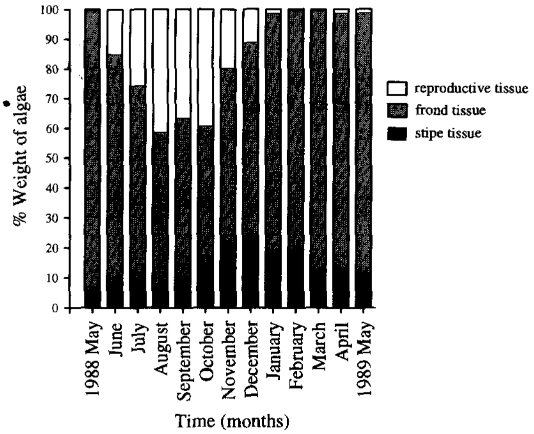

Figure 3. Mean monthly percentage wet weight of *Fucus serratus* allocated to stipe tissue (filled bars); frond tissue (hatched bars) and reproductive tissue (open bars) (n=5 plants) between May 1988 to May 1989 from St Michael's Island, Isle of Man.

>95% in April 1989. *Fucus serratus* began to reproduce in early summer (June 1988) and reached a peak in August–October (Figure 3). Over the winter months, the post-reproductive fronds were shed, and as a result stipe tissue accounted for a greater proportion of plant biomass than at other times of the year (November–February). In early spring plants started producing new frond tissue prior to reproduction.

Epiphyte dynamics

Over 20 macrofaunal (>0.5 mm) species were found on *Fucus serratus* (Table 1). Dominant species were the mobile gastropods *Lacuna pallidula* and *Littorina mariae*, the bryozoan *Flustrellidra hispida*, the hydroid *Dynamena pumila*, the tube worm *Spirorbis borealis* and the crustaceans *Ampithöe rubricata* and *Idotea granulosa*. There was some evidence of temporal partitioning between epiphytic species (Table 1). Some species were common all year round (e.g. *Spirorbis*, *Flustrellidra*, *Dynamena*, *Idotea* and the gastropod *Gibbula cineraria*) whereas other species were more transient. The blue-rayed limpet *Patina pellucida*, the isopods *Dynamene bidentata* and *Jaera* spp., and juvenile dogwhelks *Nucella lapillus* were found in the early to late summer but few were found from November 1988 to March-April 1989.

The surface area of individual plants varied along their length (Figure 4). At the base of the alga (Y segments 1–2) the stipe supported the greatest epiphyte cover (30–50%, Figure 4). Further along the alga, the previously defoliated fronds, now comprised of midrib material, also supported an epiphytic fauna despite having a small surface area. Towards the apex of the alga the surface area available increased as this was mostly frond material (>Y segment 5; except at the last dichotomy, which represented the growing tip), but little of this space was utilized by sessile epiphytic animals (<30%). Algae had the greatest surface area in May–July 1988, and after these months there was a decrease in the frond area above Y segment 5 (e.g September - November, Figure 4). After February 1989 there was an increase in the surface area of algae.

Both *Littorina mariae* and *Lacuna pallidula* showed large temporal variation in abundance (Table 1). Both species reached maximum numbers (245 m^{-2} for *Littorina* in June and 309 m^{-2} for *Lacuna* in July) in the summer and decreased dramatically in early autumn to reach very low densities in the late winter. *Littorina* started increasing in May 1989, when a slight increase was noted for *Lacuna*. Populations of both species were dominated in late spring to summer (May onwards) by small individuals (Figures 5 and 6), presumably hatched from egg masses laid in late winter. Towards the end of the year this cohort had grown and matured into adults (e.g. January 1989, *Littorina*). Recruitment of *Littorina* was greatest between March–July whereas that of *Lacuna* appeared to peak in June–September. The amphipod, *Ampithöe rubricata*, showed an annual fluctuation similar to that recorded for the two Littorinidae, decreasing in numbers in the winter months (Table 1).

Ten different macroalgal species were recorded on *F. serratus* (Table 1). *Palmaria palmata* was the dominant species, being present in all months except in the winter (December–March). The other species appeared sporadically and did not show any seasonal pattern.

Discussion

Fucus serratus had a patchy distribution; clumps of mature plants dominated some areas, and patches of juveniles were found beneath adults in other areas. The population structure was dominated by two principal components; a germling 'bank' of algae below 10 cm in size and a temporally stable component of mature algae in the size range 50–70 cm. Although this species has been recorded as living for 3–4 years on the Isle of Man (Knight & Parke, 1950), annual year classes were not readily distinguishable in this study. There was some temporal variation in the population structure, as plants were lost in the winter months due

Table 1. Mean numbers (*) of dominant epiphytes on *Fucus serratus* (numbers m $^{-2}$) and presence/absence data for less common species (scores from 1–5 represent the number of plants of the five replicates that those species were found on; except for *Ampithöe*, where values represent mean number plant $^{-1}$). n.a. = data not available.

	1988								1989				
Species	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Mollusca													
*Littorina mariae** Sacchi & Rastelli	212.8	244.8	210	113.2	62.8	39.2	22.4	31.2	43.2	24.8	30.8	42.4	130
Littorina obtusata L.	2	0	1	1	1	2	0	1	1	0	0	0	0
*Lacuna pallidula** (da Costa)	31.6	n.a.	309.2	267.2	220.4	80	48.8	64.4	33.2	16.8	13.6	5.2	18.8
Gibbula cineraria L.	2	2	4	5	4	2	1	1	1	1	1	4	3
Nucella lapillus L.	2	4	2	2	1	0	0	0	0	0	1	4	3
Patina pellucida L.	1	1	1	0	2	0	0	0	0	0	0	0	2
Acanthodoris pilosa (Muller)	0	0	0	0	0	0	0	0	0	0	1	0	0
Rissoids	0	0	1	1	1	0	0	0	0	0	0	3	1
Crustacea													
Ampithöe rubricata (Montagu)	6.4	8.2	12.4	7.8	6.2	5	2.6	0.6	2.8	1.8	4.4	2	13.4
Idotea granulosa Rathke	2	0	1	3	4	3	4	2	2	2	2	4	4
Jaera spp.	1	2	1	2	0	1	0	0	1	2	0	2	2
Dynamene bidentata (Adams)	0	0	2	4	3	1	0	0	0	1	0	0	2
Carcinus meanas L.	0	0	1	0	0	0	0	0	0	0	0	0	2
Copepod spp.	1	1	1	1	0	0	0	0	0	0	0	0	0
Annelida													
Spirorbis borealis Daudin	4	5	5	5	5	5	4	5	5	5	5	5	5
Polyzoa													
Flustrellidra hispida (Fabricus)	5	5	5	5	5	5	5	5	5	5	5	5	5
Electra pilosa L.	1	1	2	1	0	0	4	2	0	1	2	2	1
Alcyonidium spp.	0	1	1	0	0	0	2	3	3	2	1	1	0
Coelenterata													
Dynamena pumila (L.)	2	4	4	2	1	1	3	3	3	4	3	4	5
Actinia equina L.	0	0	0	0	0	0	0	1	0	1	0	0	0
Clava spp.	0	0	0	0	1	3	3	3	3	1	1	5	4
Algae													
Palmaria palmata (L.) Kuntze	1	2	5	3	3	2	4	0	0	0	1	5	3
Elachista fucicola (Vell.) Aresch.	0	1	0	1	1	0	0	1	1	1	3	2	2
Ceramium rubrum (Huds.) C. Ag.	1	0	0	0	0	0	0	0	0	0	0	1	0
Ulva lactuca L.	0	1	1	2	0	1	1	1	0	0	0	3	2
Membranoptera alata (Huds.) Stackh.	0	1	2	1	1	0	1	1	0	0	1	0	2
Cladophora sp.	1	0	0	0	0	0	1	0	0	0	0	1	0
Fucus serratus L.	1	0	0	2	0	1	0	1	1	1	1	1	1
Lomentaria articulata (Huds.) Lyngb.	0	0	0	1	0	0	0	0	0	0	0	0	0
Unidentified red filament	0	0	0	0	0	0	0	0	0	1	1	0	0
'Lithophyllum'	0	0	0	0	0	0	0	0	0	0	1	1	1

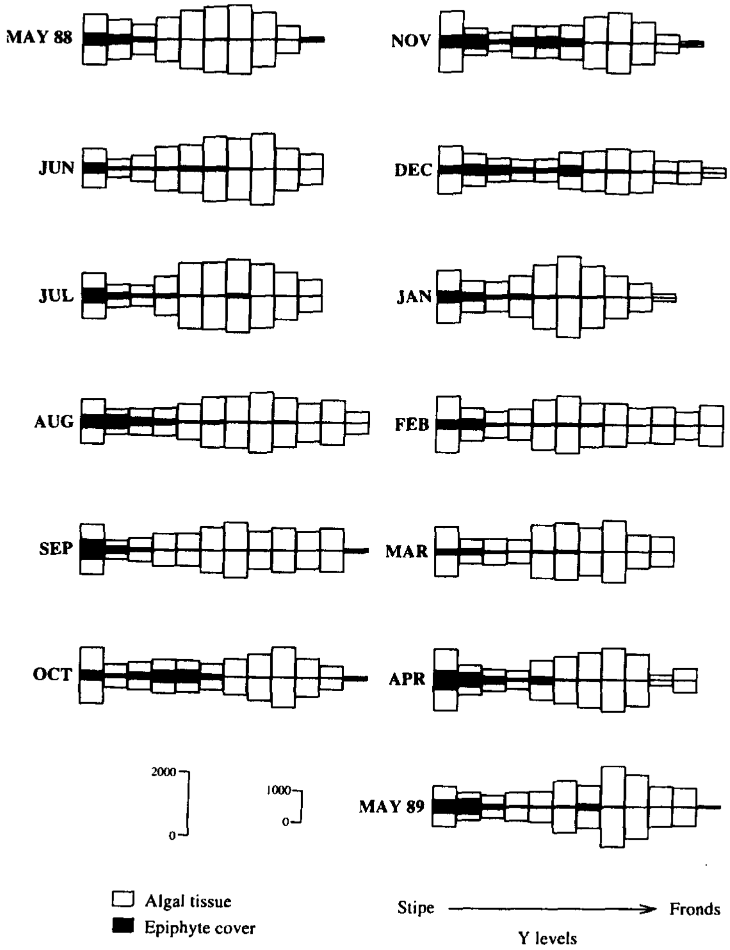

Figure 4. Mean surface area (mm^2) of *Fucus serratus* (convex and concave surfaces combined, open bars; $n = 5$) available along the longest frond divided into Y segments (after Boaden *et al.*, 1975) and percentage cover of sessile epiphytes (shaded bars).

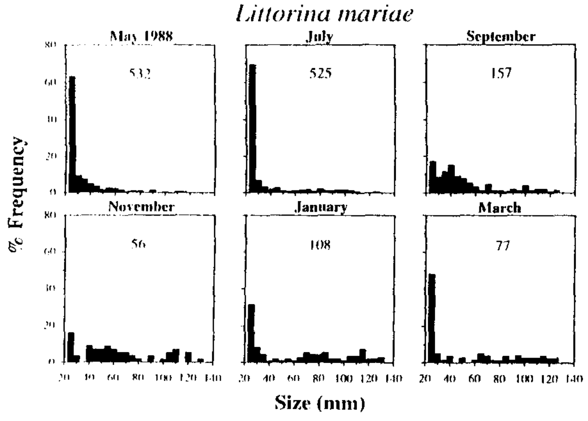

Figure 5. Bi-monthly size frequency histograms for *Littorina mariae* recorded on *F. serratus* (total from 2.5 m^2) between May 1988 to May 1989 from St Michael's Island, Isle of Man.

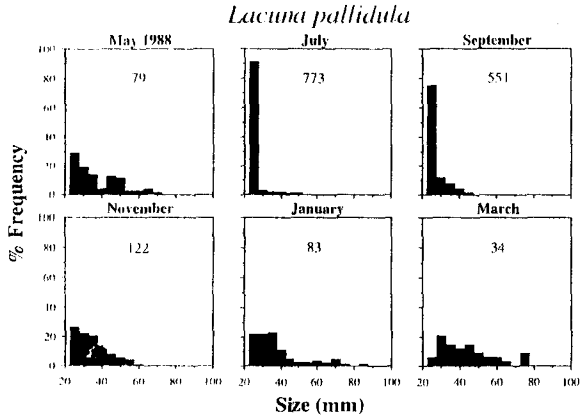

Figure 6. Bi-monthly size frequency histograms for *Lacuna pallidula* recorded on *F. serratus* (total from 2.5 m^2) between May 1988 to April 1989 from St Michael's Island, Isle of Man.

to storms and heavy wave action. When gaps in the canopy were created, juvenile germlings grew rapidly to fill the space (personal observation). There appears, therefore, to be a perennial bank of juvenile algae waiting to recruit to the population when the opportunity arises. Knight & Parke (1950) also recorded high proportions of plants <10 cm in size at Port Erin, Isle of Man, and they suggested that the adult canopy might inhibit juvenile development.

Gaps in the canopy were also created by the annual shedding of reproductive fronds. Cover of *F. serratus* was reduced from c. 95% in the late summer to 70% in the winter months (25% loss). At Sawdern Point, west Wales, Williams (1992b) recorded even higher losses of cover on slightly more exposed shores (from 90% to 40%, a loss of 50%). Reproduction in *F. serratus* at St Michael's Island reached a peak in the autumn (recorded as October at Port Erin, Knight & Parke, 1950) and fronds were shed in October to January. Knight and Parke commented that reproduction is initiated earlier and growth rates are faster on more sheltered shores, which may account for differences between *F. serratus* at St Michael's Island and Port Erin.

Due to the shedding of spent reproductive fronds and subsequent thickening of the remaining midrib, individual *F. serratus* plants vary along their longest axis in their surface area, and hence niches available for colonization (Boaden *et al.*, 1975). The bases of the plants (first Y segments) are made up of stipe tissue, thickened midrib material from initial fronds. The first basal segments have a larger surface area than later basal segments. These represent a large, permanent surface area that is not subject to shedding. Towards the apex of the plant the surface area available for utilization increases initially due to the presence of frond tissue. At the apex are the growing tips, which present small surface areas at the beginning of the growing season and which bear the receptacles during the reproductive season.

Epiphytic animals, therefore, utilize different areas of the plant. The dominant sessile species, bryozoans (principally *Flustrellidra*) and spirorbid worms, were most dense near the base of the plant. Sessile species have to settle on parts of the algae that will not be shed or need to have short life histories (i.e. be fugitive species). Competition for such space can be high (Boaden *et al.*, 1976), but species-specific settlement preferences and temporal partitioning of recruitment is thought to allow niche partitioning along the fronds of *F. serratus* (O'Connor *et al.*, 1975; Seed & Boaden, 1977; O'Connor *et al.*, 1980; Seed & O'Connor, 1981). Despite this, loss of the epiphytic fauna due to frond shedding is known to occur in *F. serratus* (up to 40% of spirorbid worms have been lost due to frond shedding at Y-levels 4–5, Seed & O'Connor, 1981) and other algae that shed fronds (e.g. some *Sargassum* species, Norton & Benson, 1983). Competitive interactions can also account for epiphyte mortality (e.g. up to 75% of spirorbids at Y level 2 suffer overgrowth interactions with bryozoans, Seed & O'Connor, 1981), but these interactions can be reduced by the seasonal growth of fronds, which effectively creates new resources. Many species direct settlement and growth towards young fronds (Ryland & Stebbing, 1971; Seed *et al.*, 1981). Perennial species like *Flustrellidra* were found on the lower Y segments (Wood & Seed, 1980; Seed *et al.*, 1981) and therefore avoided the risk of seasonal shedding. *Flustrellidra* is a strong competitor and excludes other bryozoan species from utilizing this resource (Stebbing, 1973) although it is outcompeted by sponges and tunicates in more sheltered habitats (Boaden *et al.*, 1976; Seed & O'Connor, 1981). Other species, therefore, have to settle on other parts of *F. serratus* (e.g. *Alcyonidium*, Seed & O'Connor, 1981) or grow and reproduce very quickly on the ephemeral resource of reproductive fronds (Wood & Seed, 1980). In general, however, space does not seem to be a limiting factor on *F. serratus* at St Michael's Island as the maximum cover of any Y segment was only 55%.

Mobile epiphytic animals are not limited in their position on the host plant and can utilize the alga in a more transient manner. Mobile species tend to inhabit fronds on which they graze or browse micro-epiphytes (Williams, 1990). Many species are seasonal on *F. serratus* and utilize the alga as a nursery ground, e.g. juvenile *Nucella lapillus* feeding on spirorbids and then migrating from the alga to feed on barnacles (Crothers, 1985). The isopod *Dynamene bidentata* shows a similar life history, seasonally migrating to other habitats (Holdich, 1959). *Patina pellucida* migrates from the fronds to the holdfasts of *Laminaria* prior to frond shedding (Kain & Svendsen, 1969), and this behaviour may account for the records of this species in May - July on *F. serratus*. Other species do, however, spend their entire life history on *F. serratus*. The littorinids *Littorina mariae* and *Lacuna pallidula* exhibit annual life cycles. Juveniles hatch from benthic egg masses laid on young fronds of *F. serratus* in winter (Smith, 1973; Williams, 1992b) and develop rapidly to maturity at a small body size by late autumn / early winter. The amphipod *Ampithöe rubricata* exhibits a similar pattern of abundance. These life histories have been associated with algal variability, storm losses and predation pressure from crabs and fish (Smith, 1973; Grahame, 1985; Williams, 1992b). Therefore the life histories of these species parallel the temporal changes in the resource that they inhabit.

The assemblage of species found on *Fucus serratus* on the low shore is extremely dynamic. Seasonal patterns of algal reproduction, frond shedding and growth result in a highly variable and diverse range of niches for exploitation by epiphytes. Epiphytic animal species utilize these resources via a number of different strategies that accommodate temporal and spatial patterns of host variability.

Acknowledgments

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