



## Colonisation and persistence of patches of the crustose brown alga *Pseudolithoderma* sp.

Jane E. Williamson\*, Robert G. Creese

*Leigh Marine Laboratory and School of Biological Sciences, University of Auckland, P.O. Box 349,  
Warkworth, New Zealand*

Received 25 October 1995; revised 11 December 1995; accepted 8 February 1996

### Abstract

Encrusting algae are one of the major occupiers of space on hard marine substrata and are thought to influence the patterns of distribution and abundance of other organisms in intertidal areas of rocky seashores. However, little is known about their ecology and the mechanisms which may affect their distribution and abundance in space and time. *Pseudolithoderma* sp., a brown encrusting alga common on intertidal rocky shores in northeastern New Zealand, occurs in discrete patches on sheets of the honeycomb barnacle *Chamaesipho columna*. Patches of the alga change their size and shape over a wide range of spatial and temporal scales. To identify potential mechanisms that may influence the life-history of this alga, patterns of colonisation and persistence of patches of *Pseudolithoderma* were monitored for 1 year by measuring the colonisation of spores of *Pseudolithoderma* on settlement plates in relation to existing patches of the alga, and measuring the amount of lateral expansion and contraction of established patches. Colonisation of *Pseudolithoderma* occurred at a variable rate throughout the year, but was consistently greater on plates placed on patches of *Pseudolithoderma* than those placed 1 m away from patches and was rare on plates placed 10 m away from established patches. Established patches of *Pseudolithoderma* had a much faster rate of lateral expansion ( $\text{m}^2$  per year) than those previously measured for other species of crustose algae, and declined in area unpredictably. The rapidity and lack of seasonality in the changes of the patches is hypothesised to be due to a variable age structure of the patches of *Pseudolithoderma*, along with localised interactions with small grazers and the underlying barnacles on the rocky shore. This suggests that processes operating at a very localised scale may be equally or even more important in determining the demography of fleshy encrusting algae, such as *Pseudolithoderma*, than processes operating at larger scales.

**Keywords:** Barnacle; *Chamaesipho columna*; Colonisation; Encrusting algae; Intertidal; New Zealand; Persistence; *Pseudolithoderma*; *Ralfsia*; Recruitment; Rocky shore; Settlement

\*Corresponding author. School of Biological Science, The University of New South Wales, N.S.W. 2052, Australia. Tel.: (61-2) 385-2073; Fax: (61-2) 662-2913; e-mail: j.williamson@unsw.edu.au

## 1. Introduction

Sessile animals and plants are major occupiers of space on hard, marine substrata and impart a biogenic dimension to the structure of these habitats. Several general models describing the structure of marine assemblages have been formulated from studies of sessile marine organisms in habitats from temperate waters. Such habitats include kelp forests (e.g., Dayton, 1985; Estes and Steinberg, 1988; Foster, 1990), encrusted subtidal surfaces (e.g., Karlson and Buss, 1984; Sebens, 1985; Wethey and Walters, 1986; Butler and Chesson, 1990) and intertidal rocky shores (e.g., Dayton, 1971; Lubchenco and Menge, 1978; Paine and Levin, 1981). These models have been primarily developed from observations and manipulations of the more prominent species in these assemblages. In mid-intertidal regions, this has resulted in a focus on foliose and turfing algae (e.g., Lubchenco, 1978; Steneck, 1986) or macro-invertebrates such as barnacles (e.g., Connell, 1961; Denley and Underwood, 1979; Jernakoff, 1985) and mussels (e.g., Dayton, 1971; Grant, 1977). Encrusting algae are less conspicuous members of these assemblages and are frequently assumed to have a minor role in influencing the distribution and abundance of other intertidal organisms. However, since their ecology is poorly understood and even basic patterns of distribution and abundance for crusts are often undescribed, the extent of the influence that encrusting algae have on other organisms is relatively unknown. An understanding of the dynamics of such species is fundamental to a greater appreciation of how benthic assemblages on rocky shores are organised.

In parts of New Zealand, unlike most intertidal areas worldwide (see review by Hawkins and Hartnoll, 1983), encrusting algae are prominent on hard substrata and large foliose algae constitute only a minor component of the assemblage of species (Raffaelli, 1979; Creese, 1988). On sheltered to semi-exposed shores in northeastern New Zealand, mudstone reefs are dominated by sheets of the honeycomb barnacle, *Chamaesipho columna* Spengler (Luckens, 1974). A fleshy encrusting brown alga, *Pseudolithoderma* sp.<sup>1</sup>, occurs as a mosaic of patches which typically cover vast areas of *C. columna*. *Pseudolithoderma* is the major occupier of secondary space in this habitat and forms a conspicuous structural element on these shores (Luckens, 1974; Jeffs, 1985; Williamson, 1992). Moreover, although this alga is thought to have an important influence on other co-occurring organisms, little is known about the dynamics of its life-history or its role within the assemblage of species.

Demographic patterns of encrusting algae worldwide are generally considered to be relatively constant over large areas. Typically, they are slow growing compared to other marine plants, with linear rates of lateral spread smaller than those measured for non-crustose algae by several orders of magnitude (e.g., Paine et al., 1979 compared to Littler, 1980; Norton, 1991). In addition, the rates of colonisation of crusts are usually slow, with individual plants persisting for decades (Paine et al., 1979; Steneck, 1986; Dethier, 1987).

---

<sup>1</sup>The taxonomic identity of *Pseudolithoderma* sp. is uncertain. It has previously been identified in New Zealand as a species of *Ralfsia*. This alga is now thought to belong to the genus *Pseudolithoderma*, with closest affinities to *Pseudolithoderma australis* Womersley (Womersley, 1987, Nelson pers. comm.).

*Pseudolithoderma* on New Zealand shores does not appear to have the typical features of life-history observed in other encrusting algae. General observations in New Zealand indicate that patches of *Pseudolithoderma* on mid-intertidal shores rapidly expand in area and dominate extensive portions of reef for several consecutive years, then quickly decline to become much less abundant, a situation which may also persist for several years (Ballantine, unpubl. data). To identify potential mechanisms that may influence this demography, two aspects of the life-history of *Pseudolithoderma* are examined in this study: (1) patterns of colonisation in relation to existing patches of *Pseudolithoderma*, and (2) the persistence of undisturbed patches of *Pseudolithoderma*.

## 2. Materials and methods

### 2.1. Locations studied

This study was done in the mid-intertidal region on two shores, Echinoderm Reef and Matheson Bay, on the northeastern coast of New Zealand (Fig. 1). Details of the ecology of the district can be found in Morton and Chapman (1968); Gordon and Ballantine (1976) and Creese (1988). Both shores are mudstone platforms with small terraces separated by shallow, cobble-filled gutters. These platforms have eroded to form slightly tilted ridges and boulders which support large areas of the barnacle *C. columna* and patches of the crustose alga *Pseudolithoderma* sp. The term 'patch' is used in a variety of ways by different researchers (e.g., Suchanek, 1978; Paine and Levin, 1981; Sousa,

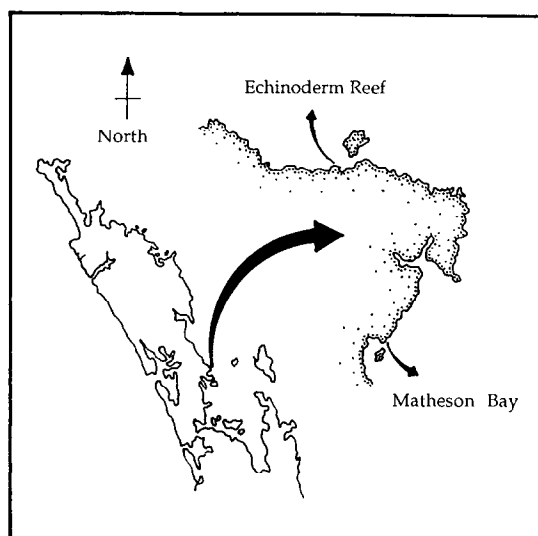


Fig. 1. Location of Echinoderm Reef and Matheson Bay in the Leigh district ( $36^{\circ} 16'S$ ,  $174^{\circ} 48'E$ ) of the Hauraki Gulf on the northeastern coast of New Zealand. The Leigh district is located 100 km north of Auckland, and the distance between Echinoderm Reef and Matheson Bay is approximately 4 km.

1984a,b; Connell and Keough, 1985; White and Pickett, 1985) and requires definition. In this study we have defined a patch of *Pseudolithoderma* as a discrete area of the alga (*sensu* Keough, 1984; McGuinness, 1987a,b; Butler and Chesson, 1990).

## 2.2. Colonisation of *Pseudolithoderma*

Patterns of colonisation of *Pseudolithoderma* in 1991 were monitored at each intertidal shore using settlement plates. Holes (diameter 15 mm; depth 45 mm) were drilled into the mudstone with a pneumatic drill powered by compressed air. Each hole was filled with epoxy resin and left to harden for at least 5 days. Smaller holes (diameter 10 mm; depth 35 mm) were then drilled into the resin and threaded with a tap. Steel bolts (diameter 10 mm; depth 30 mm) were screwed through the centre of settlement plates (15 × 15 cm; made from Hardiflex, a wood fibre/cement mix) into these holes to secure the plates flush with the substratum. This allowed mobile organisms, such as grazers, to move freely across the plates. Further, this enabled plates to be easily removed for sampling in the laboratory and replaced in the field and left only small holes in the rock at the completion of the study.

To test the hypothesis that the colonisation of *Pseudolithoderma* is inversely related to the proximity of existing patches of *Pseudolithoderma*, settlement plates were attached at three distances from existing patches and the amount of *Pseudolithoderma* colonising these plates was recorded over time. The three distances represented areas either on, beside, or away from established patches of *Pseudolithoderma*. One set of plates was placed on patches of *Pseudolithoderma* (i.e., in the centre of patches > 3 m diameter); a second set on rock covered with the barnacle *C. columna* and beside patches of *Pseudolithoderma* (i.e., within 1 m of the edge of patches); and a third set on rock covered with the barnacle *C. columna* and away from patches of *Pseudolithoderma* (i.e., approximately 10 m from the edge of patches).

Each set consisted of 2 groups of 9 replicate settlement plates. The first group was sampled approximately every 8 weeks to monitor colonisation over time (hereafter called bimonthly plates) and were replaced with a new group of plates at each sampling time. During a single low tide, these new plates were screwed into the same position where the old ones had been removed. The second group was also examined every 8 weeks (hereafter called cumulative plates), but were returned to their original positions on the shore within two days to monitor the persistence of the newly established crusts.

Plates brought back to the laboratory for sampling were temporarily stored in tanks of running seawater and immersed in seawater while under the microscope. *Pseudolithoderma* on the settlement plates was examined with a dissecting microscope in the laboratory and its percent cover was estimated by counting its frequency of occurrence through 100 randomly punched holes in an overlaid plastic sheet. To eliminate potential bias from edge effects, cover was not estimated within 1 cm of either the edge of the plate or the central hole. Since it was impossible to distinguish settlement (i.e., the arrival of new spores) from early growth (i.e., vegetative growth from germinated spores), we have used the term colonisation to describe the amount of cover of the crust on a settlement plate at a given sampling time. Estimates of cover on cumulative plates

also included lateral growth of crusts that had colonised plates at previous sampling times.

Analysis of variance was used to determine differences in the percent cover of *Pseudolithoderma*. Prior to analysis, Cochran's test (Winer et al., 1991) was used to examine homogeneity of variances ( $P > 0.05$ ). Bimonthly plates were analysed using a two-factor model at each location, with time and distance as fixed factors. The first factor, time, tested for the consistency of the patterns of colonisation over 12 months; and the second factor, distance, tested for differences in the patterns of colonisation of *Pseudolithoderma* in relation to the distance from existing patches. Locations were analysed separately because at Matheson Bay the initial designations of two treatments for the factor distance (i.e., plates placed on and beside patches) became obscured (see Section 3. At both locations, some bimonthly plates were lost at each sampling time, resulting in unequal numbers of replicates (from six to nine) among treatments. Therefore, the analysis of variance for bimonthly plates was done from March 1991, using data from six randomly chosen replicates per treatment.

Since the replicate plates for the cumulative group were non-independent through time, data from these plates were analysed with separate one-factor models at each sampling time. This allowed the effect of distance on cover to be formally tested at each sampling time, but not over time. Nevertheless, trends through time could still be observed in plots of the data. As with the bimonthly plates, some cumulative plates were lost at each sampling time. Due to the differential loss of plates between locations, Echinoderm Reef and Matheson Bay were analysed separately.

Analyses for cumulative plates were done from January 1991. *A posteriori* multiple comparisons (Student-Newman-Keuls test; Zar, 1984) were used to determine the location of differences among the treatment means after analysis of variance.

### 2.2.1. Colonisation of *Pseudolithoderma* on natural versus artificial substrata

Many field studies have used artificial substrata (e.g., glass, perspex, asbestos, ceramic tiles) to monitor the colonisation of sessile organisms. Since artificial substrata are usually cost effective and easy to manipulate, replication can often be increased. However, patterns of colonisation on artificial substrata may not be indicative of those on natural substrata because it is not known whether organisms settling on these substrata are responding to cues in the environment or to cues from the artificial substratum (McGuinness, 1989; Anderson and Underwood, 1994). Therefore, an additional experiment was set up to determine whether the artificial settlement plates used in this study experienced similar patterns of colonisation of *Pseudolithoderma* to that of natural substrata.

Shells of the patellacean limpet *Cellana radians* were often observed to be covered by *Pseudolithoderma* when residing on or beside patches of the alga. Therefore, these shells could be used as natural substrata for colonising *Pseudolithoderma*. It was hypothesised that the cover of *Pseudolithoderma* on shells of *C. radians* living on or beside existing patches would be greater than the cover on those living away from the alga. To test this hypothesis, the amount of *Pseudolithoderma* covering shells of *C. radians* was recorded in relation to the distance of *C. radians* from patches of *Pseudolithoderma*. Limpets were divided into four arbitrary categories, according to the cover of *Pseudolithoderma*

on their shells: (1) no *Pseudolithoderma*, (2) 1–25% cover of *Pseudolithoderma*, (3) 26–50% cover of *Pseudolithoderma* and (4) 51–100% cover of *Pseudolithoderma*. Grids were placed on the mid-shore at Echinoderm Reef and Matheson Bay and 100 quadrats (50 cm × 50 cm) were randomly positioned. In each quadrat, the percent cover of *Pseudolithoderma*, the number of *C. radians*, the percent cover of *Pseudolithoderma* on their shells, and the shortest distance between the quadrat and the nearest patch of *Pseudolithoderma* were recorded. Data were analysed using a chi-squared goodness-of-fit test.

Movement of *C. radians* is usually restricted to areas with defined boundaries. For example, if placed on bare rock within patches of *Pseudolithoderma* or areas of coralline turf (*Corallina officinalis*), they will not cross the edges of these natural boundaries (Creese unpubl. data). Since coralline turf and *Pseudolithoderma* rarely occur together, they provide natural simulations of the away and on treatments used in the settlement plate experiment, respectively. In May 1991, 186 *C. radians* with no visible traces of *Pseudolithoderma* were collected, tagged and released in equal numbers into areas with either patches of *Pseudolithoderma* or coralline turf. These were collected the following December and their shells photographed. Percent cover of *Pseudolithoderma* on each shell was estimated by placing a piece of clear plastic divided into 2 mm<sup>2</sup> squares over each photograph and scoring the area under each intersection point.

### 2.3. Persistence of patches of *Pseudolithoderma*

To monitor the patterns of persistence (i.e., settlement, vegetative growth, and mortality) of patches of *Pseudolithoderma*, lateral expansion and contraction of isolated patches were monitored monthly during 1991. Patches ranged in size from 300 cm<sup>2</sup> to 8000 cm<sup>2</sup> and were separated from other patches by at least 1 m. Each patch of *Pseudolithoderma* was a continuous, thick crust in areas with a large cover of *C. columna*. Seven patches were monitored at Echinoderm Reef, but only five could be found at Matheson Bay that were comparable to those at Echinoderm Reef.

At each sampling period, three stainless steel rods were positioned into pre-drilled holes in triangular formation around each patch. This allowed plastic sheeting to be placed over each patch in the same position and orientation each month. Patches were tagged and the size of each patch was estimated by tracing the outline of *Pseudolithoderma* on to the overlaid plastic sheeting. If a patch disappeared completely, the same bare or barnacle-covered area was still checked each month for newly colonised *Pseudolithoderma*. If the traced area was larger than a piece of A4 paper (29.7 cm × 21.0 cm), it was reduced to A4 size using a planvariograph prior to quantitative analysis. The area and perimeter of each patch was calculated with a microcomputer digitiser (GTCO Digi-pad PC). Ten calculations of the same tracing estimated coefficients of variation of 0.18% for area and 0.33% for perimeter. To estimate separately the error associated with the tracing of a patch, patch 4 at Echinoderm Reef (see Fig. 4) was traced during three consecutive low tides in March 1991, and its area and perimeter were calculated using the above method. This procedure produced a coefficient of variation of 1.52% for area and 1.91% for perimeter, suggesting an overall margin of error in this method of less than 2%.

### 3. Results

#### 3.1. Colonisation of *Pseudolithoderma*

Data from both groups of plates showed three trends (Fig. 2 and Fig. 3). First, throughout the year *Pseudolithoderma* rapidly colonised plates near patches, but rarely colonised plates away from patches. Second, colonisation of *Pseudolithoderma* on plates at Matheson Bay was slightly greater than on plates at Echinoderm Reef. Third, at both locations, colonisation of *Pseudolithoderma* appeared to peak during late winter to early spring (July–October).

On bimonthly plates at Echinoderm Reef, with the exception of the final sampling date when there was no significant difference between treatments, the cover of *Pseudolithoderma* was significantly greater on plates on patches of *Pseudolithoderma* than on those beside or away from patches (time  $\times$  treatment:  $F_{10,90} = 3.72$ ,  $P < 0.001$ ; Cochran's test,  $C = 0.17$ ,  $P > 0.05$ ; arcsine square-root transformed data) (Fig. 2a). In contrast, on bimonthly plates at Matheson Bay, plates beside patches of *Pseudo-*

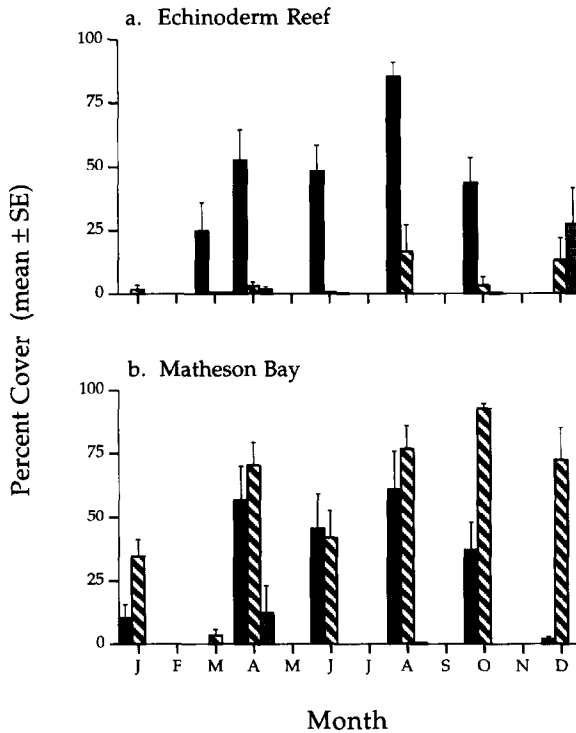


Fig. 2. Colonisation of *Pseudolithoderma* on bimonthly plates at (a) Echinoderm Reef and (b) Matheson Bay. Filled bars (■) represent plates on patches of *Pseudolithoderma*. Cross-hatched bars (▨) represent plates on *C. columna* beside patches of *Pseudolithoderma* (i.e., within 1 m). Stippled bars (▩) represent plates on *C. columna* away from patches of *Pseudolithoderma* (i.e. approximately 10 m from a patch).

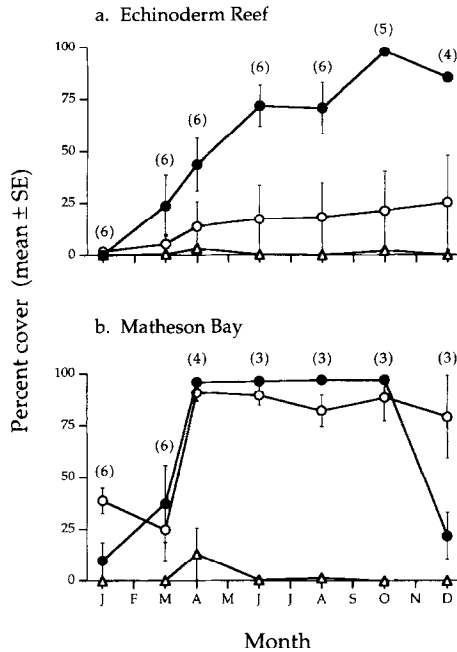


Fig. 3. Colonisation of *Pseudolithoderma* on cumulative plates at (a) Echinoderm Reef and (b) Matheson Bay. Filled circles (●) represent plates on patches of *Pseudolithoderma*. Hollow circles (○) represent plates on *C. columna* beside patches of *Pseudolithoderma* (i.e., within 1 m of a patch). Triangles (△) represent plates on *C. columna* away from patches of *Pseudolithoderma* (i.e., approximately 10 m from a patch). Numbers in parentheses represent the number of replicate plates remaining at each sampling date for each site.

*lithoderma* generally had similar cover to those on patches of *Pseudolithoderma*, and both treatments had greater cover of *Pseudolithoderma* than plates away from patches of *Pseudolithoderma* (Fig. 2b). This difference among treatments (i.e., between plates on and beside patches) between locations was primarily due to a major change in the distribution of *Pseudolithoderma* at Matheson Bay during December 1990, one month after the plates were placed on the shore. At this time, large reductions in algal cover occurred in some of the patches that contained plates. This was so severe that in several cases plates initially positioned in the middle of a patch were finally situated 50–100 cm away from the new perimeter of the patch. At the same time, several smaller patches with plates beside them expanded laterally, growing around the plates of these treatments. By April 1991, three of the nine patches at Matheson Bay originally positioned to be beside patches were now located on patches. Similarly, six of the nine plates initially located on patches were now located beside patches.

The continued use of initial designations confounded our ability to detect differences in cover between treatments on or beside patches of *Pseudolithoderma* at Matheson Bay. It was impossible to reassign the treatments of these plates *post hoc*, therefore three plates from each treatment on or beside patches of *Pseudolithoderma* were randomly chosen and pooled and a two-factor analysis of variance was done comparing the cover

between these pooled plates to the cover on plates away from patches over time. Except for plates collected in March, the cover of *Pseudolithoderma* was significantly greater on plates pooled from treatments on or beside patches of *Pseudolithoderma* than on those away from patches (time  $\times$  treatment:  $F_{5,60} = 2.98$ ,  $P < 0.05$ ; Cochran's test,  $C = 0.32$ ,  $P < 0.01$ ; arcsine square-root transformed data) (Fig. 2b), a pattern similar to that at Echinoderm Reef.

Plates left to accumulate *Pseudolithoderma* for approximately 12 months showed similar patterns of colonisation among treatments to the bimonthly plates (Fig. 2 and Fig. 3). Except for the last sampling time at Matheson Bay, plates on patches of *Pseudolithoderma* sampled at both locations after March 1991 had significantly greater cover of *Pseudolithoderma* than on those beside or away from patches (Table 1, Fig. 3). Further, plates beside patches of *Pseudolithoderma* had significantly greater cover of than those away from patches, especially at Echinoderm Reef (Fig. 3a).

### 3.1.1. Colonisation of *Pseudolithoderma* on natural versus artificial substrata

A chi-squared goodness-of-fit test showed that the amount of *Pseudolithoderma* on shells of *C. radians* was not distributed randomly with respect to the distance from patches of *Pseudolithoderma* ( $\chi^2 = 60.08$ , 6 d.f.,  $P < 0.01$ ). Shells of limpets on bare areas in patches had substantially more *Pseudolithoderma* than those in bare areas away from patches (Table 2). Moreover, shells beside patches had greater cover than those located more than 10 m away from patches (Table 2).

Of the 186 *C. radians* tagged in May 1991, only 13 were found in December 1991. All were within 75 cm of their initial point of release. Of these, seven were found near *Pseudolithoderma* and had an average cover of  $27.28 \pm 3.23\%$  (mean  $\pm$  SE) of *Pseudolithoderma* on their shells. The other six were found near coralline turf and had no *Pseudolithoderma* on their shells. These data support the pattern of colonisation observed on the artificial settlement plates: greater colonisation of *Pseudolithoderma* on plates near patches of *Pseudolithoderma* than on those away from patches. Moreover, it

Table 1

Results of Student-Newman-Keuls (SNK) tests for one-factor analyses of variance of the percent cover of *Pseudolithoderma* at various sampling times on the cumulative settlement plates

Echinoderm Reef		Matheson Bay	
Month	SNK	Month	SNK
January	ns	January	B A C
March	ns	March	ns
April	A B C	April	A B C
June	A B C	June	A B C
August	A B C	August	A B C
October	A B C	October	A B C
December	A B C	December	B A C

Means are ranked in descending order; the underlying horizontal line shows a non-significant result at  $P < 0.05$ . A = plates in the middle of a patch of *Pseudolithoderma*; B = plates 1 m from the nearest patch of *Pseudolithoderma*; C = plates 10 m from the nearest patch of *Pseudolithoderma*; ns = no significant treatment effect in analysis of variance.

Table 2

Percent of limpet shells in three distances from patches of *Pseudolithoderma*, relative to the percent cover of *Pseudolithoderma* on their shells

Distance	Sample size	Percent cover of <i>Pseudolithoderma</i> on limpet shell			
		0	1–25	26–50	51–100
On	(125)	47.2	17.6	20.0	15.2
Beside	(107)	64.5	8.4	15.9	11.2
Away	(119)	92.4	0.8	4.2	2.4

Percentages represent the cover of *Pseudolithoderma* on each shell. On = one third to whole quadrat covered by *Pseudolithoderma*. Beside = less than one third of quadrat covered by *Pseudolithoderma*. Away = no *Pseudolithoderma* in quadrat. Numbers in brackets represent the sample size for that distance.

supports the hypothesis that plates made of wood fibre/cement are likely to experience similar patterns of colonisation of *Pseudolithoderma* to those on natural substrata (i.e., limpet shells).

### 3.2. Persistence of patches of *Pseudolithoderma*

All patches of *Pseudolithoderma* at Echinoderm Reef and Matheson Bay decreased in area from the start of monitoring to the end of the year. However, during this period, many patches showed localised lateral expansion in area. Generally, when patches of *Pseudolithoderma* expanded in size, such expansion occurred at a constant rate of 5–7 cm per month, with the largest recorded expansion of 11 cm per month. This gives a conservative annual estimate of expansion of approximately 60 cm.

Each patch was described by the percentage of the maximum area it attained and by its perimeter-to-area ratio (Fig. 4 and Fig. 5). The former measure shows the general changes in the area of each patch and the latter gives an indication of whether the patch was fragmenting into several smaller patches, because a patch composed of small fragments will have a greater perimeter-to-area ratio than an intact patch of the same area.

At Echinoderm Reef (Fig. 4), four patches disappeared completely (numbers 1, 4, 6 and 7), and in two others only traces of *Pseudolithoderma* remained (numbers 2 and 5) by the end of the sampling period. Patches 4 and 7 peeled off the substratum, taking the majority of underlying barnacles with them. Patches 1 and 6 appeared to dry out, curl up at the edges and flake off, each leaving an exposed surface of a continuous sheet of barnacles. Interestingly, patch 6 was the only area at either location where recolonisation (i.e., small areas of colonising *Pseudolithoderma* were recorded in November 1991) occurred in the same position where the initial patch had disappeared (Fig. 4). The pattern of patch persistence at Matheson Bay is similar to that of patches at Echinoderm Reef. At Matheson Bay (Fig. 5), four patches disappeared completely (numbers 1, 3, 4 and 5), taking most of the underlying barnacles with them. Only one patch at each location had not disappeared by the end of the sampling period (numbers 3 in Fig. 4 and 2 in Fig. 5).

Patches varied greatly in their maximum area (Table 3). Patches at Matheson Bay were larger than those at Echinoderm Reef, but this did not seem to effect their

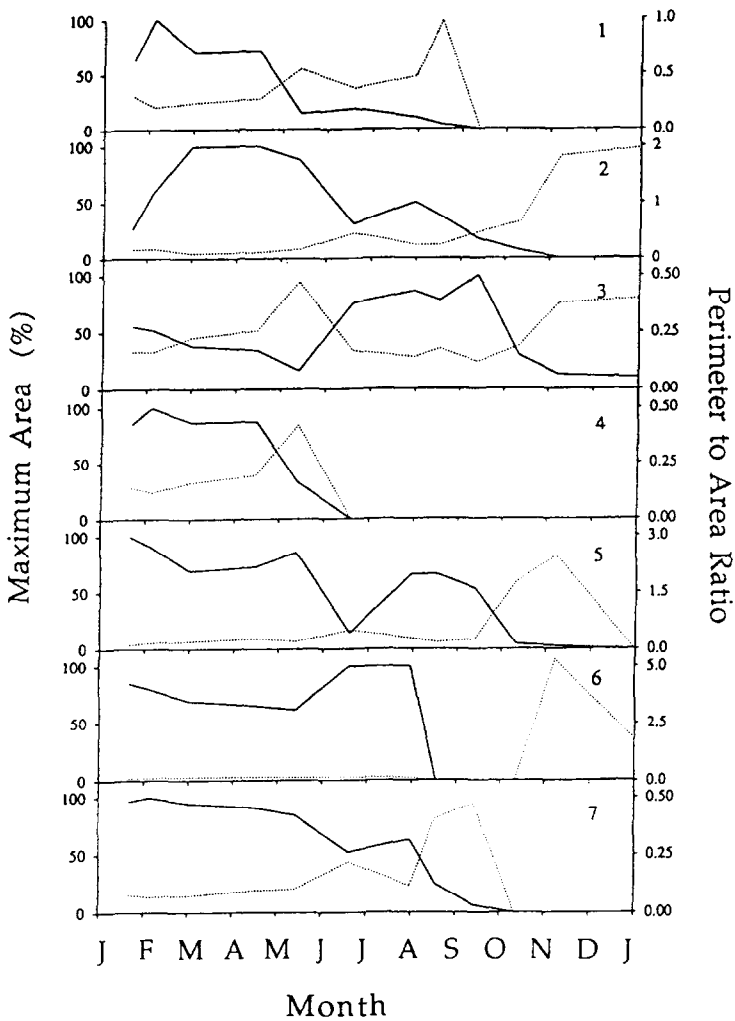


Fig. 4. Expansion and persistence of seven patches of *Pseudolithoderma* at Echinoderm Reef. Maximum area (—) represents the ratio of the area of a particular patch in a given month divided by the maximum area for that patch during the year and is expressed as a percentage. Perimeter-to-area ratio (· · · · ·) represents the ratio of the perimeter of a particular patch in a given month divided by the area of that patch for the same month.

persistence. Furthermore, the change in area of a patch did not appear to be influenced by the size of the patch. For example, patch 5 at Echinoderm Reef (a relatively small patch) increased by over 50% of its original area during 1 month (June–July; Fig. 4). Similarly, patch 5 at Matheson Bay which was five times larger than patch 5 at Echinoderm Reef, experienced an equivalent increase in area from March to April 1991 (Fig. 5). This example also shows the lack of obvious temporal trends to changes in the size or area of patches at either location. Patches usually declined in area by splitting

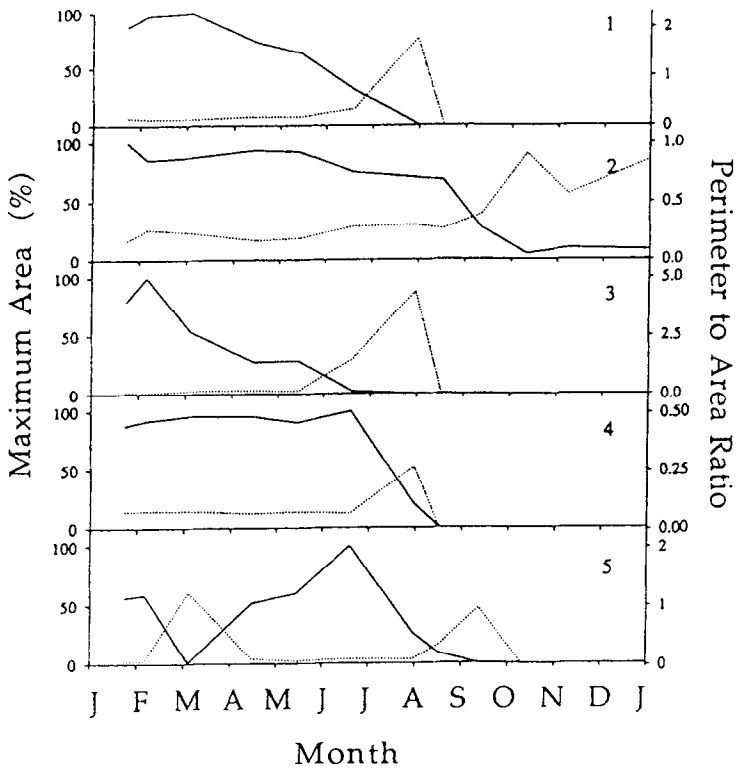


Fig. 5. Expansion and persistence of five individual patches of *Pseudolithoderma* at Matheson Bay. Maximum area (—) represents the ratio of the area of a particular patch in a given month divided by the maximum area for that patch during the year and is expressed as a percentage. Perimeter-to-area ratio (·····) represents the ratio of the perimeter of a particular patch in a given month divided by the area of that patch for the same month.

Table 3

Maximum area for individual patches of *Pseudolithoderma* at Echinoderm Reef and Matheson Bay. The number of each patch corresponds to the numbered patches in Figs. 4 and 5

Patch	Maximum area (cm <sup>2</sup> )	
	Echinoderm Reef	Matheson Bay
1	953	2556
2	5286	1353
3	1693	5106
4	3537	5122
5	2599	13 690
6	3331	
7	7432	
Mean (±SE)	3547 (±834)	5565 (±2159)

into a number of smaller patches, resulting in an increase in the perimeter-to-area ratios of the patches (Fig. 4 and Fig. 5). An exception to this was patch 6 at Echinoderm Reef, where the perimeter-to-area ratio remained constant until the sudden disappearance of the patch during August 1991 (Fig. 4).

#### 4. Discussion

On both natural and artificial substrata, colonisation of *Pseudolithoderma* was directly related to the distance from existing patches of *Pseudolithoderma* on the shore. Plates on patches of *Pseudolithoderma* had greater colonisation than those 1 m away from patches. Further, plates 10 m away from patches were rarely colonised. This pattern is likely to be related to the life-history of the alga, particularly the dispersal abilities of its spores and possibly their survivorship during germination. If spores of *Pseudolithoderma* have limited dispersal, one would expect to observe greater colonisation of propagules close to existing plants. Enhanced colonisation close to the parent plant is common in foliose brown algae (Paine, 1979; Schiel, 1985; Hoffmann, 1987; Santelices, 1990; Kendrick and Walker, 1991; Norton, 1992; Vadas et al., 1992, but see Reed et al., 1992), presumably because the propagules are not dispersed far from the receptacles of the parent plant. We are not aware of any studies on the dispersal of spores of encrusting algae, but it is likely that the patterns of colonisation observed here are due to the limited ability of spores of *Pseudolithoderma* to disperse.

Alternatively, spores of *Pseudolithoderma* may have been widely dispersed over the entire area, and differential survival of spores or germlings within the first 1 or 2 months of settlement explain the observed patterns of colonisation. In this case, the survival of spores would be directly related to their proximity to patches of *Pseudolithoderma*. Differential survival of spores on rocky shores is often attributed to the escape of propagules in refuges such as between barnacle tests (e.g., Underwood and Jernakoff, 1981) over which grazers have restricted mobility (Creese, 1982; Underwood et al., 1983). On both shores, the barnacle *C. columna* covers the substratum at great densities both within 1 m of ( $31 \pm 0.1$  individuals  $\text{cm}^{-2}$ ; mean  $\pm$  SE;  $n = 170$ ) and greater than 1 m ( $20 \pm 0.1$  individuals  $\text{cm}^{-2}$ ; mean  $\pm$  SE;  $n = 160$ ) from established patches of *Pseudolithoderma*. Consequently, large molluscan grazers are scarce in such areas both near and away from patches of *Pseudolithoderma* (Jefferies, 1985; Creese, 1988). In contrast, small molluscan grazers such as *Siphonaria zelandica* tend to be associated with patches of *Pseudolithoderma* and may enhance the survivorship of the alga (Jefferies, 1985; Beovich and Quinn, 1992). Therefore, grazers are unlikely to have a differential effect on the survivorship of *Pseudolithoderma* at these mid-shore regions.

Another experiment at Echinoderm Reef (Williamson, 1992) supported the explanation that the limited dispersal of spores of *Pseudolithoderma* accounts for their pattern of colonisation. Boulders with established patches of *Pseudolithoderma* were placed within areas with no *Pseudolithoderma* for several metres and where dense populations of barnacles not covered by *Pseudolithoderma* blanketed the substratum. Whereas in previous months no *Pseudolithoderma* colonised these areas (and colonisation was occurring away from these areas), colonisation of *Pseudolithoderma* onto these barnacles

would always occur when such boulders with *Pseudolithoderma* were transplanted into these areas. If large grazing molluscs were solely responsible for controlling the colonisation of *Pseudolithoderma*, then such extensive areas of barnacles without *Pseudolithoderma* would be rare. However, such areas are common at Echinoderm Reef and Matheson Bay, suggesting that limited dispersal would best explain our observations. Nevertheless, more information is needed on the relative contribution of dispersal versus other factors affecting post-settlement survivorship (e.g., desiccation) in determining patterns of colonisation of *Pseudolithoderma*.

Long-term photographic records (Ballantine, unpubl. data) and a study by Jeffs (1985) indicate that the average cover of *Pseudolithoderma* in this study during 1991 falls within the range of cover of *Pseudolithoderma* in the same areas over the past 12 years. Although colonisation of *Pseudolithoderma* occurred throughout 1991, the cover of *Pseudolithoderma* at mid-shore regions showed considerable spatial and temporal variation. For example, the cover of *Pseudolithoderma* on some cumulative plates decreased by more than 75% over a 2 month period. Concurrently, the cover on other plates increased. Such variations in abundance, resulting in a patchy distribution, are common for many sessile species (e.g., Dayton, 1971; Russ, 1980; Ayling, 1981; Underwood and Jernakoff, 1981, 1984; Stocker, 1984; Butler and Chesson, 1990).

When expansions in the size of patches occurred, the rate of expansion was far greater than the estimated expansion of 1 cm per year for *Petrocelis middendorffii*, an algal crust from the Pacific northwest. This alga, unlike *Pseudolithoderma*, does not appear to be in close association with large densities of barnacles or other sessile invertebrates (Paine et al., 1979). The barnacles underlying *Pseudolithoderma* have been shown to provide a source of inorganic nitrogen which enhances the growth of the alga (Williamson and Rees, 1994). Therefore, this rapid expansion of *Pseudolithoderma* may be due to an exchange of nitrogen from barnacle to alga. Further support for such a nutritional association is shown by the lack of seasonal fluctuations in the rate of expansion of *Pseudolithoderma*, despite distinct fluctuations in the concentration of ambient inorganic nitrogen previously recorded in the vicinity of our locations (e.g., Taylor, 1981, Williamson unpubl. data). Such a situation is uncommon for temperate marine algae where the seasonal supply of inorganic nitrogen is typically correlated with the growth rate of the alga (Rosenberg et al., 1984; Thomas et al., 1985; Thomas and Harrison, 1987). Still, there may be alternate factors associated with the life-history of *Pseudolithoderma* which also influence this rapid rate of expansion.

In general, all established patches of *Pseudolithoderma* decreased in area during 1991, albeit at varying rates. Such reductions may be due to the age of the crust, in which case the variable rate of decrease may be due to the patches being of different ages. Loss of patches of *Pseudolithoderma* has previously been attributed to the death of the alga following reproduction, based on a change in the colour of *Pseudolithoderma* just prior to the alga flaking off the substratum (Jeffs, 1985). Distinct changes in the colour of some brown crusts have been positively correlated with mortality following the production of fruiting bodies (Fletcher, 1978). However, no such changes in colour were seen in patches of *Pseudolithoderma* that could be correlated with algal senescence and exfoliation during this study. *Pseudolithoderma* that curled up at the edges just prior to

removal did assume a slightly darker shade, but this appeared to be from the physical drying of the alga after it had begun to flake, rather than a physiological change in the alga before flaking.

Alternatively, the variable reduction in patch size may have been due to differential affects of localised forces. For example, the density of small grazers which appear to affect the integrity of a patch are often patchily distributed (Williamson and Creese, 1996). Alternatively, some loss of patches may have been caused by the death of underlying barnacles. Empty barnacle tests adhere to the rock for only a limited time (Williamson, 1992) and any *Pseudolithoderma* on such tests would be removed with the displacement of empty tests. Predation by whelks is a common source of mortality for barnacles (e.g., Fairweather, 1988), but the only carnivorous whelk likely to affect *C. columna* in the area studied (*Lepsiella scobina*) was seldom observed on patches of *Pseudolithoderma* (Williamson, 1992) and, moreover, it is unlikely to drill through such patches to attack the underlying barnacles. For monitored patches in this study, however, we were unable to unequivocally determine the ratio of live to dead barnacles under *Pseudolithoderma* without disrupting the patch.

Patches of *Pseudolithoderma* were dynamic at localised scales and fluctuations were not synchronous between locations. Moreover, patches within 5–10 m of each other (e.g., patches 2 and 4 at Echinoderm Reef) showed no similarity in their patterns of change over time. Although further details of the life-history of *Pseudolithoderma* are needed, our preliminary findings suggest that demographic parameters for *Pseudolithoderma*, such as the rate of patch expansion, are noticeably different from other encrusting algae (e.g., Paine et al., 1979; Dethier, 1987). Research thus far on *Pseudolithoderma* on shores in northeastern New Zealand show that the patchy distribution and abundance of the crust appears to be due to a combination of localised interactions with smaller grazers (Jeffs, 1985; Williamson and Creese, 1996) and the underlying barnacles (Williamson and Rees, 1994) and characteristics of the life-history of the alga (this study). Therefore, it appears that processes operating at a scale of individual patches may be more influential in determining fluctuations in the distribution and abundance of *Pseudolithoderma* than processes operating between patches or at a larger scale.

### Acknowledgments

We thank Sue Clearwater, Sean Handley, Tony Larson and Craig Syms for their assistance in the field. We are grateful to Bill Ballantine (Leigh Marine Laboratory, Leigh) for making his data available for reference and to Wendy Nelson (Natural History Museum, Wellington) for taxonomic identification. Suggestions from Todd Minchinton, Nick Otway, Greg Skilleter and Richard Taylor were invaluable in maintaining the focus of this manuscript. Comments from two anonymous reviewers enhanced the clarity of the manuscript. This study was supported by funds from the University of Auckland Research Committee.

## References

- Anderson, M.J. and A.J. Underwood, 1994. Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. *J. Exp. Mar. Biol. Ecol.*, Vol. 184, pp. 217–236.
- Ayling, A.M., 1981. The role of biological disturbance in temperate subtidal encrusting communities. *Ecology*, Vol. 62, pp. 830–847.
- Beovich, E.K. and G.P. Quinn, 1992. The grazing effects of limpets on the macroalgal community of a rocky intertidal shore. *Aust. J. Ecol.*, Vol. 17, pp. 75–82.
- Butler, A.J. and P.L. Chesson, 1990. Ecology of sessile animals on subtidal hard substrata: the need to measure variation. *Aust. J. Ecol.*, Vol. 15, pp. 521–531.
- Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, Vol. 42, pp. 710–723.
- Connell, J.H. and M.J. Keough, 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. In *The ecology of natural disturbance and patch dynamics*, edited by S.T.A. Pickett and P.S. White, Academic Press, New York, pp. 125–152.
- Creese, R.G., 1982. Distribution and abundance of the Acmaeid limpet *Patella latistrigata*, and its interaction with barnacles. *Oecologia*, Vol. 52, pp. 85–96.
- Creese, R.G., 1988. The ecology of molluscan grazers and their interactions with marine algae in northeastern New Zealand: a review. *N.Z. J. Mar. Freshwat. Res.*, Vol. 22, pp. 427–444.
- Dayton, P.K., 1971. Competition, disturbance, and community organisation: the provision and subsequent utilisation of space in a rocky intertidal community. *Ecol. Monogr.*, Vol. 41, pp. 351–389.
- Dayton, P.K., 1985. Ecology of kelp communities. *Annu. Rev. Ecol. Syst.*, Vol. 16, pp. 215–245.
- Denley, E.J. and A.J. Underwood, 1979. Experiments on factors influencing settlement, survival and growth of two species of barnacles in New South Wales. *J. Exp. Mar. Biol. Ecol.*, Vol. 36, pp. 269–293.
- Dethier, M.N., 1987. The distribution and reproductive phenology of intertidal fleshy crustose algae in Washington. *Can. J. Bot.*, Vol. 65, pp. 1838–1850.
- Estes, J.A. and P.D. Steinberg, 1988. Predation, herbivory and kelp evolution. *Palaebiology*, Vol. 14, pp. 19–36.
- Fairweather, P.G., 1988. Consequences of supply-side ecology: manipulating the recruitment of intertidal barnacles affects the intensity of predation upon them. *Biol. Bull.*, Vol. 175, pp. 349–354.
- Fletcher, R.L., 1978. Studies on the family Ralfsiaceae around the British Isles. *Syst. Assoc. Spec.*, Vol. 10, pp. 371–398.
- Foster, M.S., 1990. Organisation of macroalgal assemblages in the north east Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia*, Vol. 192, pp. 21–33.
- Gordon, D.P. and W.J. Ballantine, 1976. *Cape Rodney to Okakari Point Marine Reserve. Review of knowledge and bibliography to December 1976*. University of Auckland Press, Auckland, 146 pp.
- Grant, W.S., 1977. High intertidal community organisation on a rocky headland in Maine, USA. *Mar. Biol.*, Vol. 44, pp. 15–25.
- Hawkins, S.J. and R.G. Hartnoll, 1983. Grazing of intertidal algae by marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 21, pp. 195–282.
- Hoffmann, A.J., 1987. The arrival of seaweed propagules at the shore: a review. *Bot. Mar.*, Vol. 30, pp. 151–165.
- Jeffs, A., 1985. *The ecology of Siphonaria on Echinoderm Reef, with special reference to its association with the encrusting alga, Ralfsia verrucosa*. Unpubl. M.Sc. thesis, University of Auckland, New Zealand, 103 pp.
- Jernakoff, P., 1985. An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on the algal diversity and cover in an intertidal barnacle zone. *J. Exp. Mar. Biol. Ecol.*, Vol. 88, pp. 287–302.
- Karlson, R.H. and L.W. Buss, 1984. Competition, disturbance and local diversity patterns of substratum-bound clonal organisms: a simulation. *Ecol. Modelling*, Vol. 23, pp. 243–255.
- Kendrick, G.A. and D.I. Walker, 1991. Dispersal distances for propagules of *Sargassum spinuligerum* (Sargassaceae, Phaeophyta) measured directly by vital staining and venturi suction sampling. *Mar. Ecol. Prog. Ser.*, Vol. 79, pp. 133–138.

- Keough, M.J., 1984. Effects of patch size on the abundance of sessile marine invertebrates. *Ecology*, Vol. 65, pp. 423–437.
- Littler, M.M., 1980. Morphological form and photosynthetic performances of marine macroalgae: tests of a functional form hypothesis. *Bot. Mar.*, Vol. 23, pp. 161–165.
- Lubchenco, J., 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat.*, Vol. 112, pp. 23–39.
- Lubchenco, J. and B.A. Menge, 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.*, Vol. 48, pp. 67–94.
- Luckens, P.A., 1974. Removal of intertidal algae by herbivores in experimental frames and on shores near Auckland. *N.Z. J. Mar. Freshwater Res.*, Vol. 8, pp. 637–654.
- McGuinness, K.A., 1987a. Disturbance and organisms on boulders. I. Patterns in the environment and the community. *Oecologia*, Vol. 71, pp. 409–419.
- McGuinness, K.A., 1987b. Disturbance and organisms on boulders. II. Causes of patterns in diversity and abundance. *Oecologia*, Vol. 71, pp. 420–430.
- McGuinness, K.A., 1989. Effects of some natural and artificial substrata on sessile marine organisms at Galeta Reef, Panama. *Mar. Ecol. Prog. Ser.*, Vol. 104, pp. 201–208.
- Morton, J.E. and V.J. Chapman, 1968. *Rocky shore ecology of the Leigh area, North Auckland*. University of Auckland Press, Auckland, 44 pp.
- Norton, T.A., 1991. Conflicting constraints on the form of intertidal algae. *Br. Phycol. J.*, Vol. 26, pp. 203–218.
- Norton, T.A., 1992. Dispersal by macroalgae. *Br. Phycol. J.*, Vol. 27, pp. 293–301.
- Paine, R.T., 1979. Disaster, catastrophe and local persistence of the sea palm, *Postelsia palmaeformis*. *Science*, Vol. 205, pp. 685–687.
- Paine, R.T. and S.A. Levin, 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.*, Vol. 51, pp. 145–178.
- Paine, R.T., C.J. Slocum and D.O. Duggins, 1979. Growth and longevity in the crustose red alga *Petrocelis middendorffii*. *Mar. Biol.*, Vol. 51, pp. 185–192.
- Raffaelli, D., 1979. The grazer-algae interaction in the intertidal zone on New Zealand rocky shores. *J. Exp. Mar. Biol. Ecol.*, Vol. 38, pp. 81–100.
- Reed, D.C., C.D. Amsler and A.W. Ebeling, 1992. Dispersal in kelps: factors affecting spore swimming and competency. *Ecology*, Vol. 73, pp. 1577–1585.
- Rosenberg, G., T.A. Proyben and K.H. Mann, 1984. Nutrient uptake and growth kinetics in brown seaweeds: response to continuous and single additions of ammonium. *J. Exp. Mar. Biol. Ecol.*, Vol. 80, pp. 125–146.
- Russ, G.R., 1980. Effects of predation by fishes, competition and structural complexity of the substratum on the establishment of a marine epifaunal community. *J. Exp. Mar. Biol. Ecol.*, Vol. 42, pp. 55–70.
- Santelices, B., 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr. Mar. Biol. Ann. Rev.*, Vol. 28, pp. 177–276.
- Schiel, D.R., 1985. Growth, survival and reproduction of two species of marine algae at different densities in natural stands. *J. Ecol.*, Vol. 73, pp. 199–217.
- Sebens, K.P., 1985. Community ecology of vertical rock walls in the Gulf of Maine, U.S.A.: small scale processes and alternative community states. In *The ecology of rocky coasts*, edited by P.G. Moore and R. Seed, Hodder and Stoughton, London, pp. 346–371.
- Sousa, W.P., 1984a. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.*, Vol. 15, pp. 353–391.
- Sousa, W.P., 1984b. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology*, Vol. 65, pp. 1918–1935.
- Steneck, R.S., 1986. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annu. Rev. Ecol. Syst.*, Vol. 17, pp. 273–303.
- Stocker, L.J., 1984. Recruitment, growth and mortality in the subtidal ascidian *Pseudodistoma novaezelandiae* (Ascidiacea: Polyclinidae). Unpubl. M.Sc. thesis, University of Auckland, New Zealand, 91 pp.
- Suchanek, T.H., 1978. The ecology of *Mytilus edulus* L. in exposed rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.*, Vol. 31, pp. 537–551.
- Taylor, F.J., 1981. Phytoplankton and nutrients in Goat Island Bay, New Zealand. *Int. Rev. Gesamten Hydrobiol.*, Vol. 66, pp. 377–406.

- Thomas, T.E., P.J. Harrison and E.B. Taylor, 1985. Nitrogen uptake and growth of the germlings and mature thalli of *Fucus distichus*. *Mar. Biol.*, Vol. 84, pp. 267–274.
- Thomas, T.E. and P.J. Harrison, 1987. Rapid ammonium uptake and nitrogen interactions in five intertidal seaweeds grown under field conditions. *J. Exp. Mar. Biol. Ecol.*, Vol. 107, pp. 1–8.
- Underwood, A.J., E.J. Denley and M.J. Moran, 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia*, Vol. 56, pp. 202–219.
- Underwood, A.J. and P. Jernakoff, 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia*, Vol. 48, pp. 221–233.
- Underwood, A.J. and P. Jernakoff, 1984. The effects of tidal height, wave exposure, seasonality and rock pools, and the distribution of macroalgae in New South Wales. *J. Exp. Mar. Biol. Ecol.*, Vol. 75, pp. 71–96.
- Vadas, R.L., S. Johnson and T.A. Norton, 1992. Recruitment and mortality of early post-settlement stages of benthic algae. *Br. Phycol. J.*, Vol. 27, pp. 331–351.
- Wetley, D.S. and L.J. Walters, 1986. Quantifying spatial patterns of overgrowth in epibenthic communities. *Mar. Ecol. Prog. Ser.*, Vol. 29, pp. 271–278.
- White, P.S. and S.T.A. Pickett, 1985. Natural disturbance and patch dynamics: an introduction. In *The ecology of natural disturbance and patch dynamics*, edited by S.T.A. Pickett and P.S. White, Academic Press, Orlando.
- Williamson, J.E., 1992. Distribution patterns and life-history features of the intertidal encrusting alga *Pseudolithoderma*. Unpublished M.Sc. thesis, University of Auckland, 158 pp.
- Williamson, J.E. and R.G. Creese, 1996. Small invertebrates inhabiting the crustose alga *Pseudolithoderma* sp. on rocky intertidal shores in northeastern New Zealand. *N.Z. J. Mar. Freshwater Res.*, Vol. 30, pp. 223–234.
- Williamson, J.E. and T.A.V. Rees, 1994. Nutritional interaction in an algal-barnacle association. *Oecologia*, Vol. 99, pp. 16–20.
- Winer, B.J., D.R. Brown and K.M. Michels, 1991. *Statistical principles in experimental design*, McGraw-Hill, New York, third edition, 1057 pp.
- Womersley, H.B.S., 1987. *The marine benthic flora of southern Australia. Part II*. South Australian Government Printing Division, Adelaide, 484 pp.
- Zar, J.H., 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ, second edition, 718 pp.