THE EFFECTS OF LOCAL DIFFERENCES ON THE POPULATION DYNAMICS OF THE INTERTIDAL PULMONATE LIMPET *SIPHONARIA PECTINATA* (L).

Terence Ocaña / Marine Section, The Gibraltar Ornithological & Natural History Society.

Abstract

The population dynamics of Siphonaria pectinata *inhabiting two areas of shoreline exhibiting distinct topographical differences was investigated. The population at site 2 showed a greater growth rate, increased reproductive effort, larger size structure and lower mortality than the population at site 1.*

The differences observed are attributed to distinct topographical features which may be responsible for producing a different set of biotic and abiotic conditions at each site.

The manner in which all such factors may interact to cause the differences in population dynamics observed is discussed.

INTRODUCTION

The population biology of prosobranch limpets has been the focus of much attention by researchers (see review by Branch, 1981). However, most studies on the pulmonate limpet *Siphonaria* have focused on aspects such as activity rhythms and homing behaviour (Cook, 1976; Thomas, 1973; Cook & Cook, 1978, 1981; Garrity & Levings, 1983; Verdeber *et al.*, 1983; Branch & Cherry, 1985; Branch, 1988) and competition (Creese & Underwood, 1982; Ortega, 1985; Lasiak & White, 1993).

Little information is available on the population dynamics of *Siphonaria*. A notable exception is a study done by Quinn (1988a, b) who studied the ecology of *S. diemenensis* Quoy & Gaimard with respect to population dynamics and food availability and reproductive patterns and energetics.

Comunicaciones

Most studies do not fully consider the effect that the topography of the shore may have on the population dynamics of a limpet species. Recently, however, a study by Liu (1994) attempted to show how two species of *Siphonaria* responded to a variety of hydrographical conditions on three different Hong Kong shores.

This study attempts to show how the population dynamics of *Siphonaria pectinata* (Linnaeus) may show considerable variation between sites separated only by a short distance and discusses ways in which topographical differences between sites may contribute to such variation.

MATERIALS AND METHODS

Study sites

Sampling was carried out at Sandy Bay South, Gibraltar. Site 1 consisted of a steep smooth cliff-face with an overall slope of 90%. The angle of exposure was 130%. Barnacle cover was very low (3% of area sampled). The mean density of *S. pectinata* was 88/m2 and the mean density of Patella sp. was 67/m2. Apart from the microbial film there were only small patches of the macroalgae *Pterocladia* sp. and *Codium* sp. near mean low water (MLW)

Site 2 consisted of a horizontal wave cut platform approximately 1m long with a shallow basin (ca. 70mm deep) which then joined with a boulder approximately 1m in height. The overall slope of the boulder was 50%. The surface of both the platform and boulder had numerous slight depressions (ca. 5-7mm deep). The angle of exposure was 40% although there was a boulder approximately 1m tall directly in front of the platform. Barnacle cover was moderate (50% of area sampled). The mean density of *S. pectinata* was 62/m2 and the mean density of *Patella* sp. was 19/m2. Apart from the microbial film, *Pterocladia* sp. was very abundant on the fringes of the basin and on the platform. There were also tufts of *Ulva* sp.

Population size structure

At each site the shell lengths of 50 individuals chosen at random between 0.25 and 0.75m above MLW were measured to the nearest mm using calipers. The mean shell length and standard deviation were calculated for each census. T-tests were carried out to determine the significance of any differences observed.

Growth

At each site 10 individuals of shell lengths between 7 and 15mm were labelled using numbered paper tags attached to their shells with loctite super-glue. Approximately once a month their shell lengths were measured to the nearest 0.1mm using calipers. The mean increment in shell size was calculated for each census. T-tests were carried out to determine the significance of any differences observed.

Reproductive effort

At each site a permanent quadrat measuring 1 x 0.5m was marked between 0.25 and 0.75m above MLW, with the lowest point being 0.25m above MLW. Approximately once a month the number of *S. pectinata* and the number of egg masses present inside the quadrat were counted and expressed as a Spawning Index (number of egg masses divided by the number of *S. pectinata*).

Mortality

At each site 20 individuals of shell lengths between 7 and 15mm were labelled using plastic coloured tags affixed to their shells with J & B Marine weld. Approximately once a month the number of labelled individuals lost were noted and expressed as a percentage of the total population labelled. New individuals were labelled to replace those lost whenever necessary so that the labelled population was restored to 20 after each census.

All sampling was carried out between March 1993 and May 1994.

RESULTS

Population size structure

The population size structure at site 2 was larger than at site 1. Figure 1 one shows that for each census the mean shell length of the population at site 2 was greater than at site 1. T-tests carried out revealed significant differences in mean shell size between populations at site 1 and site 2 (Table. 1).

Growth

The mean growth increment of labelled individuals at site 2 was greater than at site 1 for each census (Fig. 2). T-tests showed that the mean growth increment of individuals at site 2 was significantly greater than at site 1 for 8 out of 10 census points (Table. 2). The remaining 2 census points did not show a significant difference in mean growth increment between sites, but the mean growth increment at site 2 was nevertheless 52% greater than at site 1.

Reproductive effort

Figure 3 shows that the reproductive effort at site 2 was considerably greater than at site 1. Site 2 had a higher spawning index throughout the sampling period. There was a higher number of egg masses at site 2 than at site 1 and the size of the spawn deposited was greater at site 2 than at site 1 (pers. obs.).

Mortality

The mortality rate at site 1 was considerably higher than at site 2 for the duration of the sampling period (Fig. 4). In most cases the difference amounted to over 50%.

DISCUSSION

Distinct topographical features may, in part, be responsible for the differences in population dynamics observed between the two sites. Site 1 may be classified as a rapidly draining site due to its steep slope and low barnacle cover. During ebb tides the rock surface may dry quickly increasing the probability of desiccation stress on the animal. Opportunistic wave action caused by the wash of passing boats would not wet the rock surface for very long particularly on hot, dry days. Death from desiccation could account for the high mortality figures observed for site 1 particularly during the summer months (Fig. 4).

Table 1.- Statistical analysis of populations.

| Date	Mean shell length (mm)		Standard deviation		Number in sample		T-test value
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	
Mar-1993	8.44	11.56	2.18	2.33	50.00	50.00	6.903**
Apr-1993	8.58	10.78	2.04	1.73	50.00	50.00	5.820**
May-1993	8.32	10.82	2.27	2.32	50.00	50.00	5.447**
Jun-1993	8.16	10.78	2.23	2.32	50.00	50.00	5.758**
Aug-1993	7.62	10.50	1.99	2.44	50.00	50.00	6.472**
Oct-1993	8.14	9.58	2.04	2.30	50.00	50.00	3.318**
Dec-1993	7.24	9.48	2.12	2.25	50.00	50.00	5.126**
Jan-1994	7.00	9.38	1.83	2.84	50.00	50.00	4.990**
Feb-1994	7.36	9.78	2.27	2.55	50.00	50.00	5.010**
Mar-1994	7.92	10.96	1.82	2.86	50.00	50.00	6.333**

** Significant at 0.01 level,
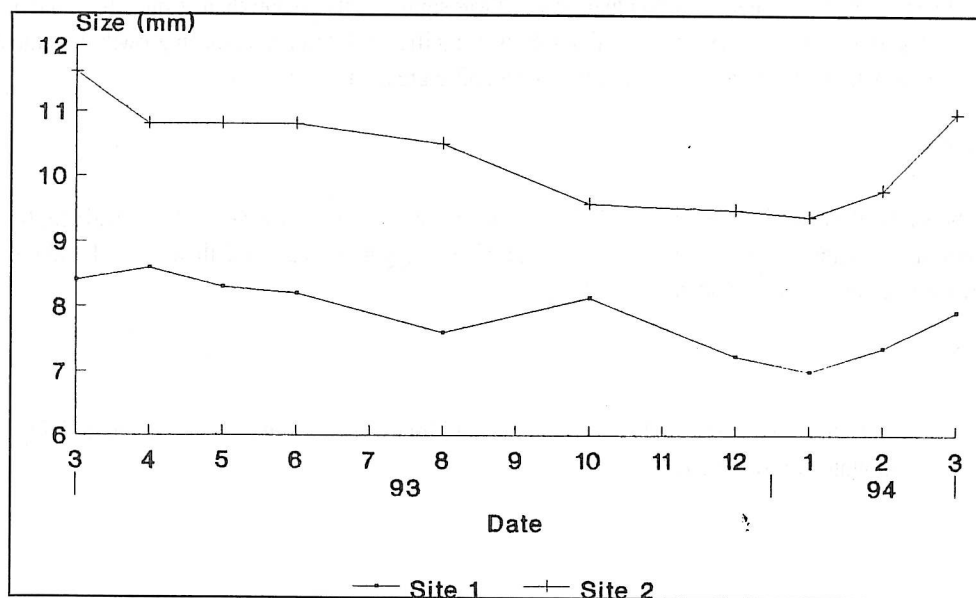
Fig. 1. Mean shell length. Sandy Bay

Other research carried out by the author has shown that foraging excursions by *S.pectinata* occur only if the animal is exposed to air or awash provided that the relative humidity of the rock surface is greater than 75%. It may well be that these conditions do not arise too often and thus feeding opportunities may be restricted at site 1. Site 2 has a more gentle slope, a pockered surface and a higher barnacle cover which tend to keep the rock surface wetter for longer during ebb tides or when splashed by passing boats thus providing more suitable conditions for foraging. It would appear that the risk of desiccation is also considerably less.

It is conceivable that because of the drier conditions at site 1, *S. pectinata* spends more time clamped tightly onto the rock surface in order to reduce the risk of desiccation. Clamping requires energy so a greater part of its energy budget may be directed to this process. If feeding opportunities are reduced at site 1 then the amount of energy available for somatic growth and reproductive effort may be significantly reduced. This is exactly what the results indicate. The drier conditions at site 1 together with decreased feeding opportunities may weaken the animal to a point where it succumbes to desiccation or starvation. This may be reflected in the higher mortality rate at site 1, particularly during the dry season (Fig. 4).

The differences in growth rates between sites may be attributed to differences in food availability (Creese & Underwood, 1982; Underwood, 1984a, b; Bosman & Hockey, 1988; Quinn, 1988a). Although primary productivity was not measured, the fringe of the basin at site 2 supports lush growths of *Pterocladia* and *Ulva* over which *S. pectinata* graze (pers. obs.). This food resource is available throughout the year. Individuals at site 1 would probably have to rely on the microbial film which tends to show considerable patchiness and seasonal variation (Hill & Hawkins, 1991). It would seem that site 2 may have a more dependable and permanent food supply which can be exploited by *S. pectinata*. Quinn (1988a) demonstrated that in areas where the food supply was more constant, *S. diemenensis* was larger and grew faster than in areas where the food supply showed seasonal variation.

Comparable effects can be observed in this investigation. Individuals at site 2 grew faster and were larger than those at site 1. Moreover, a greater food availability means that more resources may be directed to reproduction without sacrificing growth. The constant availability of macroalgae at site 2 may be conducive to a high reproductive effort. In addition, in this species large individuals produce a greater number of egg masses than smaller ones (Ocaña, in prep.) thus contributing to the enhanced reproductive effort observed at site 2 (fig. 3).

Interspecific competition has also been shown to greatly affect the growth and mortality of limpets (Black, 1979; Creese & Underwood, 1982; Ortega, 1985; Lasiak & White, 1993). In a separate study the author showed that the removal of *Patella coerulea* (L) caused a significant increase in somatic growth and reproductive effort in *S. pectinata*. The high density of patellids at site 1 may be placing considerable competitive stress on *S. pectinata* in view that they share the same food resource - the microbial film. The patellid radula is capable of excavating rock and removing embedded microflora (Hawkins & Hartnoll, 1983). However, The radula of Siphonaria consists of numerous fine teeth, uniform in size and with no apparent mineralization, that are unable to dig into rock (Creese, 1978; Creese & Underwood, 1982; Ortega, 1985; Ocana, in prep.). It would seem that *S. pectinata* needs to rely on algal spores and sporelings of macro-algae for its food - a limited resource which it shares with a large population of generalist grazers. This restricts their food availability with possible detrimental effects on growth, reproductive output and mortality. At site 2 the density of patellids is much lower and *S. pectinata* has access all year round to soft frondose algae which their teeth are perfectly adapted to tear small bits off. It may well be possible that site 2 shows enhanced somatic growth, greater reproductive output and decreased mortality due to the constancy of food avilability and a lower level of intraspecific competition.

Table 2.- Mean growth increment for both populations.

| Date	Mean growth increment		Standard deviation		Number in sample		T-test value
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	
Apr-1993	0.15	0.26	0.07	0.11	11.00	5.00	2.047*,
May-1993	0.05	0.34	0.07	0.30	10.00	10.00	2.977**
Jun-1993	0.03	0.27	0.07	0.10	8.0	7.00	5.333**
Aug-1993	0.10	0.23	0.11	0.13	10.00	8.00	2.257*
Oct-1993	0.14	0.27	0.13	0.17	9.00	9.00	1.831
Dec-1993	0.12	0.23	0.07	0.10	9.00	10.00	2.821*
Jan-1994	0.08	0.24	0.08	0.10	9.00	10.00	3.902**
Feb-1994	0.11	0.21	0.12	0.12	9.00	10.00	1.820
Mar-1994	0.04	0.04	0.07	0.05	8.00	9.00	5.667**

** Significant at 0.01 level; * Significant at 0.05 level.,
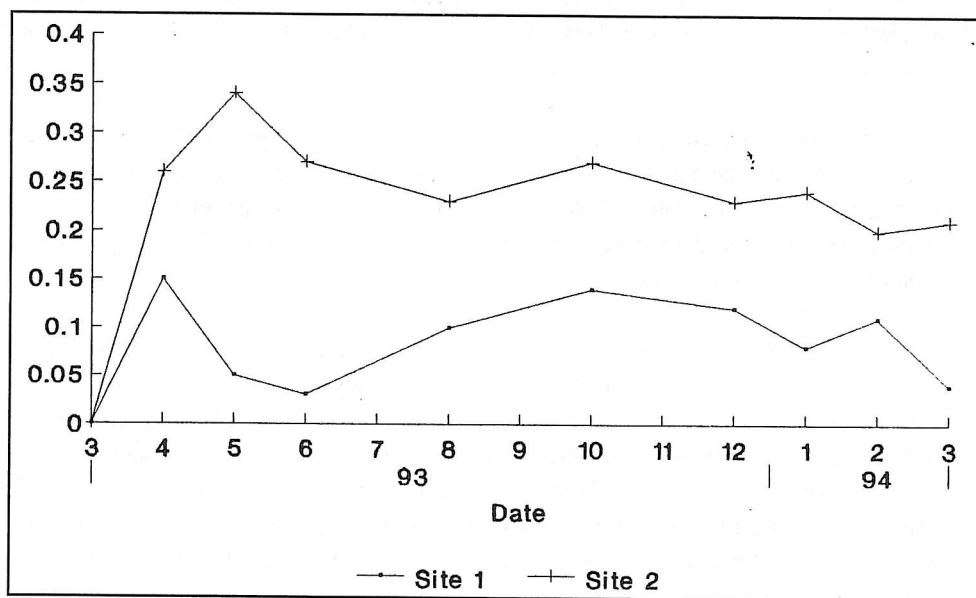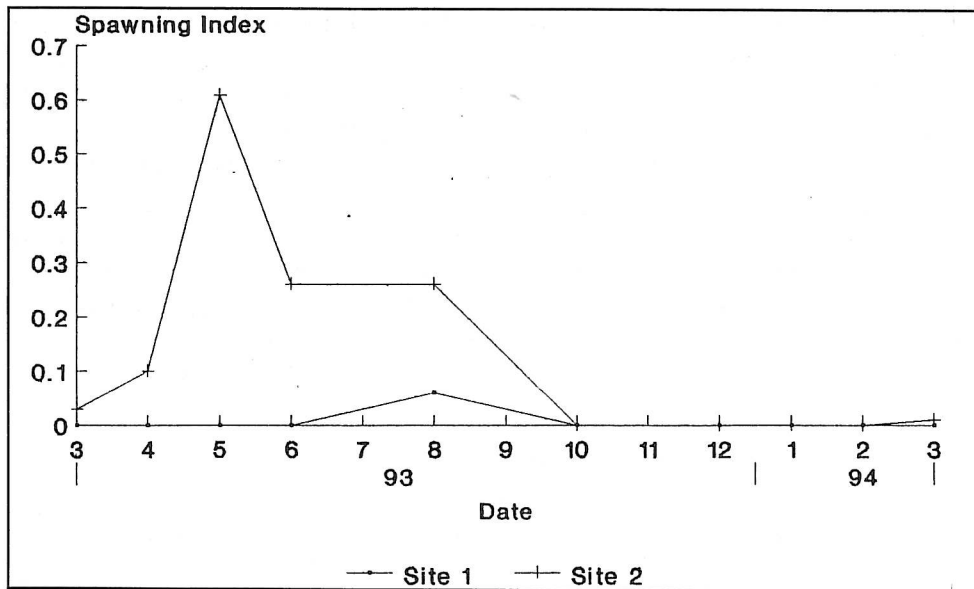

Fig. 2. Mean growth increment. Sandy Bay

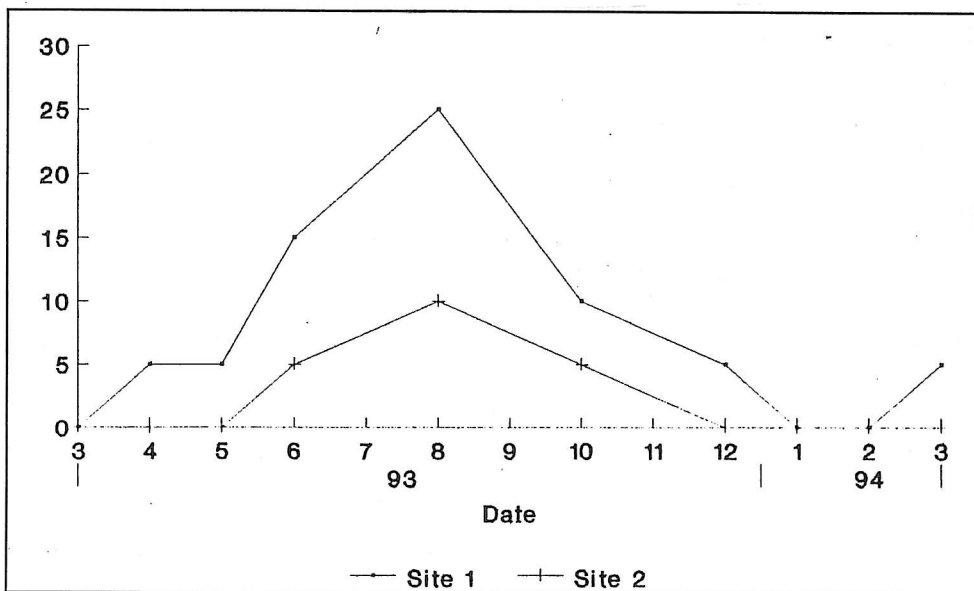**Fig. 3.** Reproductive effort. Sandy Bay

Fig. 4. Percentage mortality. Sandy Bay

Comunicaciones

Wave action may also play an important part in shaping the population dynamics of *Siphonaria* at both sites. The angle of exposure and the steepness of the slope at site 1 means that wave impact is considerable. Since *S. pectinata* adheres weakly onto the rock when moving, it would tend to remain on its home scar during periods of moderate and rough wave action, further reducing feeding opportunities. It would appear that the risk of dislodgement by wave action is greater at site 1, an effect which may be reflected in the higher mortality rate experienced at this location. The reduced angle of exposure and the boulder directly in front of site 2 would tend to dissipate wave action considerably, possibly creating opportunities for feeding, but almost definitely reducing the risk of dislodgement. This could partly account for the reduced mortality rate at site 2.

The growth and population dynamics of the same species of limpets may be expected to vary among different habitats (Branch, 1975, 1976; Creese, 1981; Workman, 1983; Fletcher, 1984). This same expectation needs to be applied to all situations where populations of a single species inhabit shores which exhibit distinct topographical features. Otherwise the effects of localised heterogeneity on the population dynamics of a species may be overlooked.

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