

ANNUAL FLUCTUATIONS IN THE RECRUITMENT OF *PATELLA VULGATA* L.

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(Figs. 1–10)

Fluctuations in the annual recruitment of *Patella vulgata* at Robin Hood's Bay over 7 years have been analysed in relation to annual variations in gonad cycles and environmental conditions. Evidence to date suggests that short periods of low air temperatures during the first few weeks after settlement of spat in the late autumn exert the greatest influence upon the level of recruitment. Not only are the time and severity of autumnal frosts highly variable from one year to another, but gonad ripening and first spawning, determined respectively by summer temperatures and rough seas, can also vary independently by up to 7 weeks. Although an early reproductive season is more likely than not to lead to successful recruitment, success or failure appears to depend less upon the time of spawning than on the chance occurrence of frost within 4–5 weeks of this variable event. Thereafter the severity of mid-winter conditions appears to be irrelevant.

Regional data from the northern half of the British Isles are less detailed than those from Robin Hood's Bay, especially about the exact spawning time in some areas. Nevertheless there has been no instance of poor recruitment that does not appear to accord with a frost-control hypothesis. Continuing work in these areas suggests that lack of spawning synchrony and a tendency to re-ripen could complicate future interpretation.

In sub-habitats where limpet life-spans are long, several years of above-average recruitment at Robin Hood's Bay have resulted in high adult densities persisting during years of poor recruitment. Where longevity is less, the adult densities respond more closely or irregularly to recruitment fluctuations.

On the basis of the frost-controlled fluctuations, of preliminary data on gonad cycles in northern Norway and Portugal, and on the local distribution towards the species' southern limit in Portugal it is tentatively suggested that geographical limits are set, to the north, by spat intolerance of low temperature and, to the south, by inability of juveniles to withstand heat/desiccation during their first summer after settlement.

INTRODUCTION

In an attempt to identify the causes of the natural population fluctuations on British rocky coasts, an exploratory programme on the recruitment fluctuations of certain 'key species' has been operating for several years. The choice of species and the emphasis upon their recruitment have been discussed elsewhere (Lewis, 1976) and were justified as the most economical means of gaining the ability to (a) 'explain' major changes in the general character of rocky shore communities, and (b) make predictions about natural events against which to detect regional or temporal consequences of man-made changes in water quality. Mussels, barnacles and limpets are being studied but it is the last with which most interpretative progress appears to have been made, and this paper is concerned solely with *Patella vulgata* L. It is, however, essentially a preliminary report in a continuing study and it illustrates the practical and interpretative problems inherent in formulating and substantiating hypotheses in this type of work.

Sampling problems arose first from the considerable variation in recruitment which

results from very local differences in physical and biological conditions (Lewis & Bowman, 1975), and secondly from the fact that the time of year at which the highest numbers of detectable spat (or juveniles) occur on the open rock surface varies locally from a few months to a year or more after the autumnal spawning (Fig. 1). Early maxima and a rapid decline characterize smooth, continuously wet surfaces where direct-settling spat can first be detected usually between December and February and where all juveniles are usually large enough to be seen within another 1–4 months. At the other extreme in dry, upper-shore areas spat survive only in damp cracks and among mussels and barnacles, and few can be seen until they emerge in increasing numbers during summer and autumn.

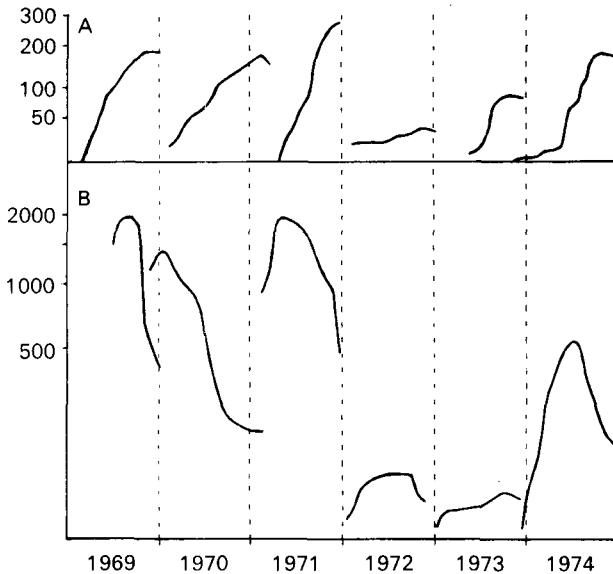


Fig. 1. Illustration of the range of variation between sites and years in the time at which maximum numbers of juveniles occur. (A), A dry 'late-emergence' site; (B), a wet 'direct-settlement' site.

The use of standard settlement panels proved impracticable, and it was not possible to carry out random sampling on a scale sufficient to prevent the annual variation being masked by the spatial differences. Accordingly, marked m^2 sites were used to give constancy in most physical conditions, and the known influence of biological changes on recruitment was minimized as far as possible by placing sites in habitats of high biological stability. Additionally, they were positioned to give a range of limpet densities and of anticipated recruitment levels. The very extended and variable 'recruitment period', together with the possibility of annual variation in the time of recruitment maxima even in the same site, afforded no choice other than regular in situ counts over much of the year.

Local sites at Robin Hood's Bay (on the north-east coast of England) provide most of the data for discussion, but it seemed essential also to cover a wider geographical area. Inevitably the intensity and reliability of the geographical data are less than the local. Furthermore, and contrary to initial expectations that local data might not be interpret-

able unless seen against a broader pattern, it is a locally derived hypothesis that permits interpretation of the geographical data. Accordingly the two sets of data and their interpretation are dealt with separately.

SURVEY DATA AND DISCUSSION

Annual recruitment at Robin Hood's Bay

The total numbers of settling spat (< 0.2 mm length) cannot be determined and so the highest numbers of the 'O' class found at any time during the year following the autumnal spawning have been taken as the measure of 'recruitment'. These annual maxima are shown in Table 1. Because of the close similarity among the replicates of Site 3 all future data here relate to their mean, and Site 5 b, because of its more recent origin, is omitted from further analyses although so far it shows a broadly similar pattern to that of Site 5 a. In Fig. 2 the annual variation at each site is shown as % units of the mean above or below each site mean.

Table 1. *Recruitment of P. vulgata at Robin Hood's Bay*

Season	Sites							
	1	2	3 a	3 b	3 c	4	5 a	5 b
1967/68	13	78				138		
1968/69	23	182				278	1956	
1969/70	34	145	45	58	45	295	1408	
1970/71	58	272	78	93	93	336	1908	2516
1971/72	16	35	40	37	37	44	84	178
1972/73	15	85	16	25	21	101	53	144
1973/74	23	179	28	28	43	278	549	372

These data suggest that the recruitment seasons of 1968/69, 1969/70 and 1970/71 were at or above average, while the two following (1971/72 and 1972/73) were very poor. The 1973/74 season was less distinctive overall, but showed a substantial recovery over the previous two. Analysis of variance for the five sites over the last five seasons (Table 2) confirms that both the between-sites and between-years variance is significant at the $P = 0.001$ level. The site differences were expected and are of no further concern here. Subjecting the annual data to significant difference tests confirms that the two poor seasons (1971/72 and 1972/73) differ from the two preceding seasons, with the status of 1973/74 varying according to which analysis is used (Table 3).

Before seeking general causes for these differences one must ask whether they reflect changes in local biological conditions. Only two sites warrant comment. On Site 1 the moister conditions resulting from limited colonization by *Mytilus* in 1969 could have culminated in the 1970/71 peak of 58 recruits (Table 1), but the pattern in succeeding years so closely parallels Sites 2, 3 and 4, where no major biological changes took place, as to suggest that the major influence on Site 1 was general rather than local. By contrast, Site 5 a, with the highest recruitment potential, became very much drier in 1973 following predation of nearby mussels that had been reducing drainage of the area. On the formerly pool-like surface small patches of lithothamnia died and the 1973/74 limpet

recruitment was much lower absolutely, and relative to other sites, than the good seasons 1968/69–1970/71. This low result on this single site accounts for the uncertain rating in Table 3 of what was otherwise a good season. Comparisons with other sites and other years suggest that *ca.* 1700–1800 is a reasonable estimate of the probable input had

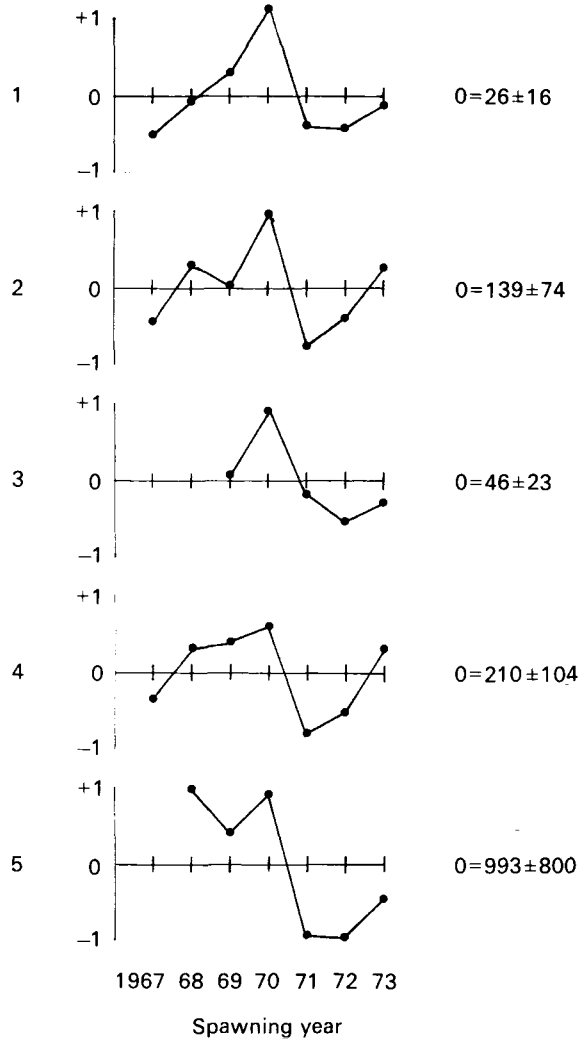


Fig. 2. The variation in annual recruitment at each site relative to the mean and expressed in units of 100% of the site mean.

conditions not changed. Unless mussels re-establish nearby, this site, and its companion 5 b, must now be regarded as 'new sites' with much lower potential maxima. Clearly neither Site 1 nor 5 detracts from the conclusion that significant annual differences have been recorded, so general rather than local factors may now be sought.

Table 2. *Analysis of variance on data in last five years of Table 1, using mean of Sites 3a, 3b and 3c and omitting Site 5b*

Source of variation	D.f.	S.s.	M.s.	F
Between years	4	2.534	0.633	10.49***
Between sites	4	4.311	1.077	17.86***
Residual	16	0.965	0.060	
Total	24	7.812		

$$F, P = 0.001_{(4, 16)} = 7.94.$$

Table 3. *Comparison of annual recruitment using the Student-Neuman-Keuls test and Tukey's w-procedure*

Years not significantly different from each other ($P = 0.05$) are underscored by the same line

Ranked seasons	1971/72	1972/73	1973/74	1969/70	1970/71
S-N-K test	_____		_____		
Tukey's <i>w</i>	_____		_____		

Causes of recruitment variation

Recruitment success or failure may be determined during various distinct phases: gonad development and spawning, planktonic life or the period of settlement, establishment (and emergence) on the shore. With such an abundant species as *P. vulgata* living, as it is at Robin Hood's Bay, in roughly the centre of its geographical distribution, one may reasonably expect the normal range of conditions to lead to regularly high levels of recruitment. But whereas these are the culmination of success at all earlier phases, low recruitment can result from failure at a single sensitive phase. Poor seasons, therefore, are potentially the more informative.

Gonad cycle and spawning

A mean gonad index was calculated from about 100 animals, 28–35 mm in length, a size range which in this protandrous species, and in this area, gave approximately equal sex ratios. The same extensive habitat was used throughout, and the monthly sampling frequency increased as spawning time approached. On the basis of size, colour and surface appearance (Orton, Southward & Dodd, 1956) each gonad was classed as neuter or in one of five stages of development or spawning. Neuter stages are never present during the period of maximum ripeness, nor are ripe stages 4 and 5 present when the index is at its lowest.

The level of maximum ripeness (upper part of Fig. 3) has been relatively constant from year to year (except recently in 1974) but its timing has varied by up to 6 weeks. Spawning and subsequent events have also been very variable. Most commonly there has been a single, sharp spawning fall in the index in October or November, and then a steady decline into the resting phase. In two seasons of early ripening, 1969 and 1973, small index falls in September were followed by apparent re-ripening, and the main spawnings

were respectively three-and-a-half months and one month later. The reality of these September spawnings was confirmed by the presence in both years of 1 mm spat on the shore by early November, much too soon to be attributable to the later spawnings.

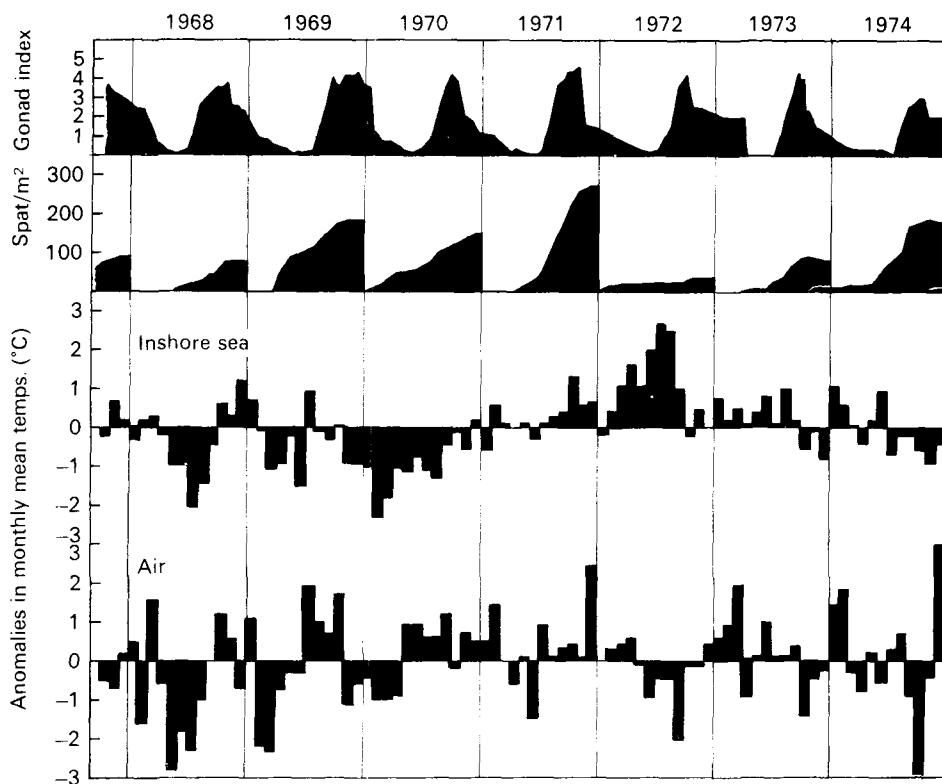


Fig. 3. The gonad index, the local anomalies of sea and air temperature, and the recruitment record as illustrated by site 2. (Note that recruitment is derived from the spawning of the previous autumn.)

Once the majority of the gonads have reached maximum ripeness, spawning is apparently triggered by onshore gales and heavy seas. In Fig. 4 the black band in each year shows the duration of the sampling interval within which spawning took place. The arrows and letter 'S' above the horizontal time axes indicate 24-h periods of onshore storms and/or rough seas. This relationship confirmed the observations of Orton *et al.* (1956) and sometimes made it possible to fix the date of spawning accurately in the later years. In 1973, for example, the September spawning followed heavy swell unaccompanied by onshore winds, and that in October occurred during a 24-h period of northerly gales on 10 and 11 October.

The later steady declines in the index could indicate either gradual release or resorption of remaining gametes, but sharper falls suggest more definite 'spawnings'; especially that in April 1973 when a severe north-easterly gale, following a remarkably storm-free winter, produced the only 100% neuter condition in 7 years. Neither this late 'spawning' nor that of January 1970 give rise to detectable spat on the shore, and yet artificial

fertilization made in June (Dodd, 1957), using gonads that could only have been relics from the previous season, indicates that some gametes remain viable for a long time. Thus the failure of such late spawnings is perhaps mainly a matter of environmental conditions during mid-winter or early spring.

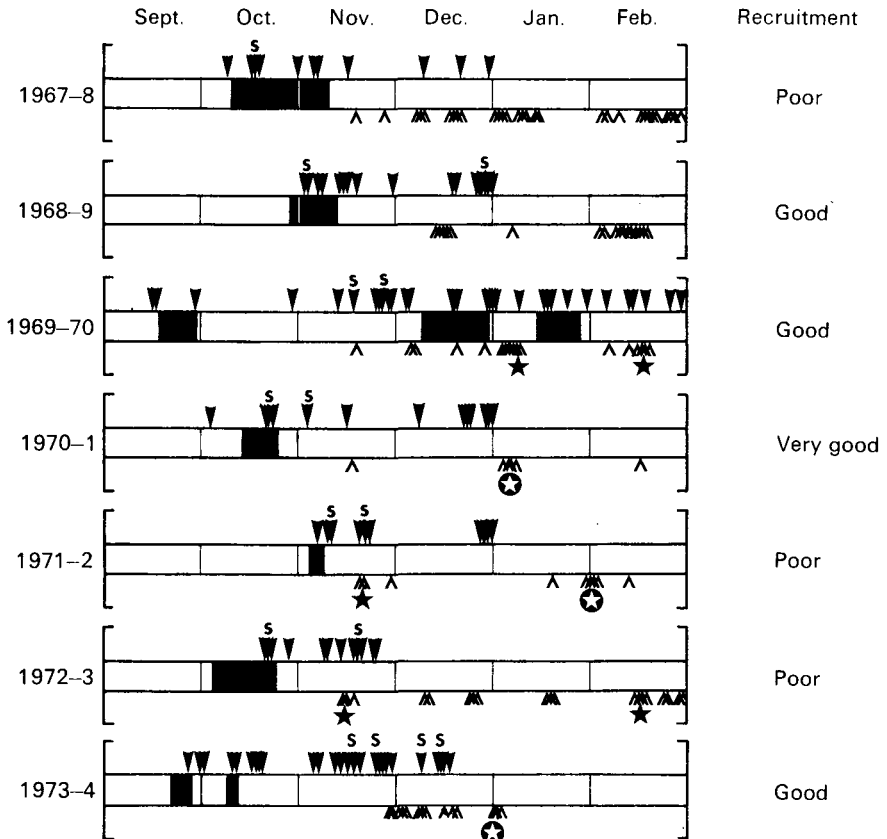


Fig. 4. The incidence of onshore gales and low air temperatures in relation to spawning times and recruitment. (The recruitment rating is derived from the data in Table 1.) ■, interval during which spawning occurred; ▽, 24-hour gales over 20 knots; ▾, 24-hour storms over 45 knots (force 9); ▲, day with minimum air temp. below -1.5°C ; ★, snow on shore/ice on rock pools; ★, ice on pools and max. air temp. below 0°C .

The years of high and low recruitment as illustrated by Site 2 (Table 1) can be compared in Fig. 3 with the gonad cycle of the previous autumn. If there is a direct relationship between the two it is not at once apparent. Although the index may be a rather coarse comparative measure of gametic output the degree of ripeness appears to have been of no consequence since the low value of 1968 (3.5) was followed by good recruitment, while the highest value recorded (4.6 in 1971) preceded the lowest recruitment.*

Turning next to spawning time we find that early spawning and high recruitment

*The moderately good recruitment now recorded after the very poor gonad year of 1974 (index 2.9) reinforces the view that gonad size and ripeness are not the main determinants.

coincided in the 1969/70 and 1973/74 seasons, but late initial spawning has produced both high (1968/69) and low (1971/72) recruitment. Simultaneous release of gametes should lead to a high rate of fertilization, but again there is no constant relationship between recruitment and apparent spawning synchrony. If there were, the 1971/72 season (which also had a high index value) should have been the most successful, whereas it was the worst.

The lack of a recurrent direct relationship with any single aspect of the gonad and spawning cycle does not necessarily mean that they have no influence upon recruitment, but it does suggest that factors operating later in the sequence could be more critical.

The planktonic phase

The duration of the planktonic phase in nature is uncertain, but in artificial rearing torsion was complete in 4–5 days (Smith, 1935), and spat settled 10 days after fertilization (Dodd, 1957). Similar brevity in nature after synchronous spawning could lead to either success or failure if environmental conditions varied annually. Unfortunately, and like Ballantine (1961) working in the Plymouth area, we have failed to take larvae in tow-nettings, and since we also lack information on planktonic food or predators, speculation about this phase is largely pointless. However, the transportation and settling densities of barnacle larvae can sometimes be related to movement of surface waters under the influence of on- or off-shore winds (Barnes, 1956; Lewis, personal observation). Since such water movements have already been demonstrated locally (Newton, 1973) the annual variation in wind direction shortly after spawning has been studied. Some of the early years suggested that high recruitment was indeed associated with onshore winds preventing seaward dispersal of larvae (see 1968 and 1970 in Fig. 4), but lack of correlation in other seasons suggests that while wind direction may be a contributory influence there must be other over-riding factors.

Settlement and early shore life

It is not until 4–6 weeks after spawning that spat (< 1 mm long) can be detected under natural conditions. Since many are not seen then, and indeed some juveniles only 'appear' much later at 2–3 mm length, the total input and possible mortality rates early in shore life cannot be determined. In spite of this it is unlikely that predation, which was doubtless very high during the planktonic phase, continues to play an important and variable role immediately after settlement. The most widespread biological source of spat destruction is probably their accidental removal by grazing adults, but although we have experimentally demonstrated higher recruitment after the total clearance of adults (Lewis & Bowman, 1975) there is no discernible relationship in present data between recruitment and adult density.

Among variable physical conditions the two potentially most important influences upon spat or juveniles appear to be desiccation and temperature.

Desiccation. By the time spat or juveniles are large enough to be seen those in the upper part of the shore are mainly restricted to micro-habitats that remain wet between tides. This is an annual feature, whatever the recruitment level, and unless the much smaller (< 0.2 mm) settling stage can select such physical or biological habitats when tidally

submerged, it can only result from the early mortality of all spat that settle (randomly?) on open, more quickly-drying surfaces. Accepting, therefore, that there is an initially severe desiccation gradient, might not annual variation in its intensity determine the numbers surviving in even the damp situations upshore as well as on open surfaces at lower levels, thereby removing the need to look for any other factor controlling 'recruitment'?

A correct balance of all the influences contributing to desiccation is not possible without a series of micro-meteorological stations on the shore. Nevertheless, from such data as were available on cloud cover, air temperature, wind strength and direction, relative humidity, sea spray and rainfall we have classed each post-settlement period of eight weeks in terms of high, average or low desiccating influences. This exercise does not suggest that desiccation is the principal controlling factor. The years in which drying influences were respectively the highest and lowest (1969 and 1973) were both followed by high recruitment, whilst the post-settlement period leading to lowest recruitment (1971-72) did not experience strong sunshine until after a long and cold damp period. But the strongest circumstantial evidence against invoking desiccation is: (a) early spawning, which would normally expose spat to warmer and drier autumnal conditions, has so far resulted in high recruitment, and (b) recruitment fluctuations in the lowest and wettest site (no. 5) have been both in phase with those on the drier sites and also of greater relative scales.

Although early desiccation produces the initial distribution *pattern* of survival (wet/dry; tidal gradient) it does not, therefore, seem to play a major role in determining the actual *numbers* that survive and reach a detectable size. In the drier sites the 'increase' in juveniles throughout the first year suggests that individuals most susceptible to desiccation are eliminated at the outset. By contrast, in the lower or wetter habitats, most of the mortality due to desiccation appears to be delayed until well into the first year, when numbers may fall by up to 60% during summer and autumn (Lewis & Bowman, 1975).

Temperature. Air temperature influences desiccation, but both sea and air temperatures could have an independent effect, and the fact that shore life commences in the late autumn suggests that the varying severity of winters might hold the key. Alternatively, initial growth rates influenced by sea temperatures in November or December might determine the ability of juveniles to withstand mid-winter cold or spring desiccation.

The lower parts of Fig. 3 show anomalies of monthly mean sea and air temperatures relative to the period 1962-1972. Air data were supplied by the Meteorological Office (Whitby Coastguard Station) and shore-line sea data were obtained weekly in Robin Hood's Bay by Laboratory staff. The inconsistency between sea and air temperatures in 1972 arose from possible procedural errors that were not detected until late that year, but even when those sea data are discounted there appears to be no recurrent relationship between recruitment and temperatures up to 3-6 months after spawning. Above-average temperatures astride the year-end has accompanied both high recruitment (1968/69, 1970/71) and the lowest recorded (1971/72, 1972/73). Not only did the good 1969/70 recruitment take place when temperatures were below average from November to April inclusive, but the second highest recruitment (1968/69), although associated with above-

average conditions until January, occurred in spite of the coldest February and March yet experienced. These inconsistencies suggest that, if juvenile survival is indeed influenced by winter conditions, the general temperature régime over several months is irrelevant and that one should look perhaps for a short period of high stress and/or high spat sensitivity. That such a period would be early in shore life is a reasonable assumption, and is supported by data from Site 5, the only one on which recruitment is mainly by direct surface-settlement. Although the small size of spat makes the accuracy of early counts rather uncertain, this site usually gives a good indication of how successful each season will be as early as December or January (Fig. 5). This suggests that if control is indeed exerted after settlement it operates very early, and probably when most spat are too small to be seen.

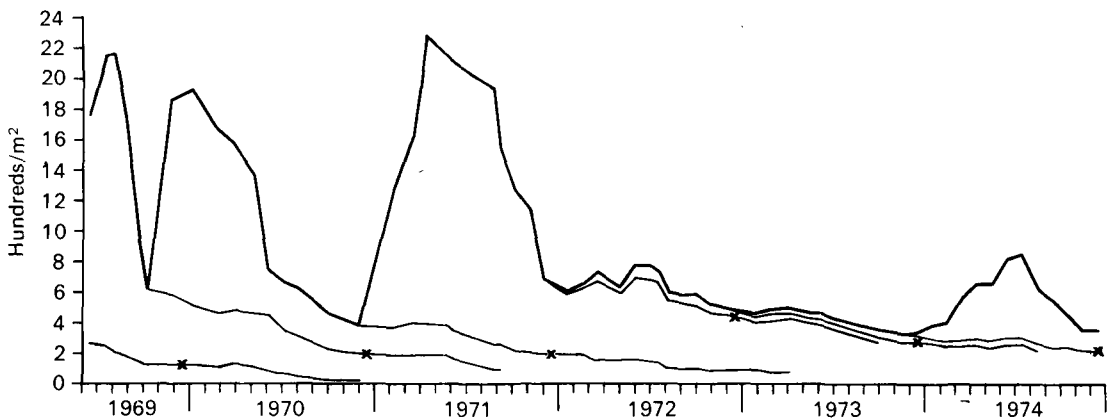


Fig. 5. The detailed record of population levels at site 5 where the recruitment potential, the juvenile mortality and the effects of frost have been the maximum. The 1973/4 recruitment reflects the change to drier conditions. 'X' marks the 'adult' numbers recorded in Fig. 9 and used in Fig. 10.

Consideration of climatic conditions generally, and air temperatures in particular during early shore life now shows there to be a convincing relationship between recruitment and the incidence of low air temperature (frost) in the first few weeks after spawning. From Fig. 4 it can be seen that in the three poor seasons (1967/68, 1971/72 and 1972/73) frosts of varying severity and frequency occurred within four to five weeks of spawning, while in the four good seasons there has been only one (1970/71) with a slight frost during this period. Moreover, this particular frost was during a night when high spring tides at 06.00 hours would have protected most of the shore over the crucial time.

Events in 1971/72 first suggested that this relationship might exist. In that year two consecutive nights of frost (-2.4°C and -3.3°C) were recorded about two weeks after spawning, thin ice was seen to have formed on upper shore pools and very poor recruitment was later recorded. In the following season gonad ripening and spawning were earlier, but even so several frosts down to -2.5°C and thin ice were again experienced about three weeks later, and recruitment was only marginally better than in the season before. The earliest poor season (1967/68) is less informative because at that time sampling was not directed to fixing the exact spawning date. Assuming that it was about

the beginning of November there were two single frosts (-2.3°C on the 18th; -3.0°C on the 27th) but we have no ice or snow data. These frosts were later and less concentrated than in 1971, and the recruitment was somewhat higher (Table 1).

Among the good recruitment seasons two show successional spawnings. In 1973 both resulted in settlement, but both were very early and even the second was about 7 weeks before the first frosts. In 1969 the September spawning was about 7 weeks before the first slight frost but the two later spawnings were followed by temperatures down to

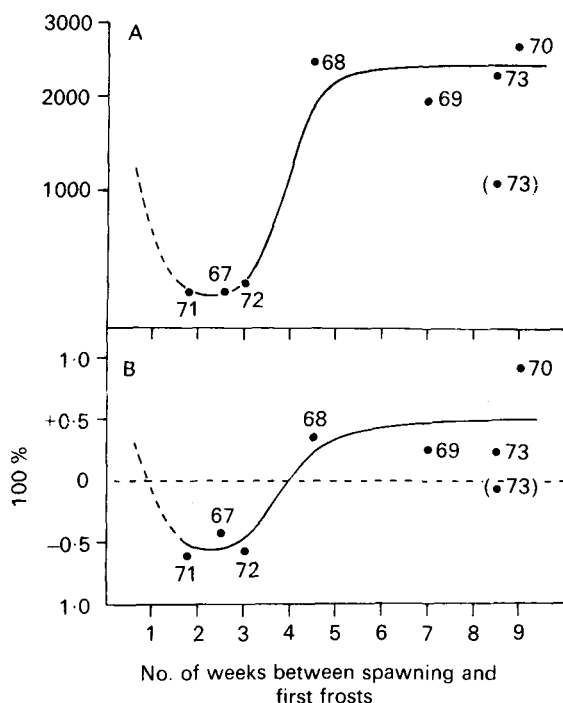


Fig. 6. The relationship between annual recruitment levels and the duration of frost-free time after spawning. (A) annual total of juvenile maxima on all sites; (B) summation of individual site variations astride their means expressed in % units of the mean. Data for 1967 and 1968 are based on 3 and 4 sites respectively, all other years on 5 sites. Unbracketed 1973 data incorporate the 'correction' for Site 5 on p. 796.

-6.0°C , snow on the shore and inshore sea temperatures briefly as low as 0.6°C . No settlements attributable to these late spawnings were detected, and while these failures might have had other causes they are both compatible with a frost-control hypothesis. The high recruitment resulting from the small index fall in September 1969 suggests that the index is non-linear, a fall from about 4.0 to 3.5 producing a disproportionately large output of gametes.

The relationship between recruitment and the number of frost-free weeks elapsing each year after the first or sole spawning date is shown in Fig. 6.

Low-temperature control of recruitment

The annual variation so far at Robin Hood's Bay appears to be most reasonably explained by the susceptibility of very young juveniles to the low air temperatures occasioned mostly by frost, but also by snow and sleet. Present evidence suggests that the susceptible period lasts about 3 weeks, i.e. up to 4–5 weeks after spawning, but this will be tested further as future seasons permit. Low temperatures in the first week or so after spawning, during the planktonic phase, will presumably be too early to have an effect, hence the dotted line in Fig. 6.

Frost control entails various qualifications and conclusions. First, it seems improbable that complete recruitment failure would occur. Not only might some spat have settled in protecting microhabitats but also, as apparently happened here in 1971, some could be protected by high tide during the night. Moreover, although spawning synchrony probably aids fertilization, a moderate lack of synchrony would extend the potential settlement period and so increase the probability of some spat each year escaping the earliest and generally infrequent frosts. In this context the spawning stimulus itself, onshore waves, is such that populations along a highly irregular coastline could be affected at different times with potentially beneficial consequences for recruitment, but a confusing lack of correlations. Since the spawning stimulus in very sheltered waters remains unknown, it is perhaps fortunate that this work began on an open and uniform coastline.

Assuming that there is good synchrony, the lack of direct correlation between spawning time and recruitment success (p. 800) was inevitable because the crucial relationship is the chance interval between two independent events: spawning–storms and frosts. Early spawning increases the probability that spat become established before the first frosts (usually mid- to late November here), but even mid-November spawnings have been very successful when first frosts were also late (e.g. 1968). A December spawning followed by a long frost-free period has not yet occurred here, but it could conceivably be successful. Viable gametes retained until spring might also be productive, so it is unfortunate that the only presumed spawning at this time of year (April 1973, see p. 798) was followed by a period of frost.

The time at which gonads reach maximum ripeness is also variable (by up to 6 weeks) and although this is the least critical event in the entire sequence early ripening clearly facilitates early spawning and improves recruitment prospects. Early ripening (i.e. in late September) has coincided with above-average air temperature during July/August/September (1969, 1973 and recently 1975 – not shown in Fig. 3), while the latest ripening occurred after a cold summer (1968). But there are some rather anomalous years (1970 and 1971) which suggest that other factors are involved.

The combination of events and conditions most propitious for a high level of recruitment appears to be:

- (a) early ripening of the gonad (probably resulting from a warm summer);
- (b) heavy seas as soon as the gonads ripen, so that spawning takes place late September/early October;
- (c) a $1\frac{1}{2}$ – 5 week period after spawning that is free from severe air frosts or lying snow.

Of these three (c) is most crucial, with (a) and (b) serving only to enhance the probability of (c).

Both frost and autumnal desiccation appear to act when spat are so small that precisely what happens in the field can never be known. We judge desiccation to be the predictable factor setting the initial distribution pattern, and frost mortality the main but irregular

Table 4. Comparison of effect of frost in different sites

Site	Mean recruitment		% reduction in frost years	Site description
	Frost-free years	Frost years		
1	34	14	58	High. <i>Balanus</i> (few <i>Mytilus</i>)
2	194	66	66	High. <i>Balanus/Mytilus</i>
3	57	30*	47	Mid. Dense <i>Balanus</i>
4	297	94	68	Mid. <i>Mytilus</i> (few <i>Balanus</i>)
5	1757	73*	96	Mid. Bare. Wet

* 2 frost-free years only. Other sites 3 years.

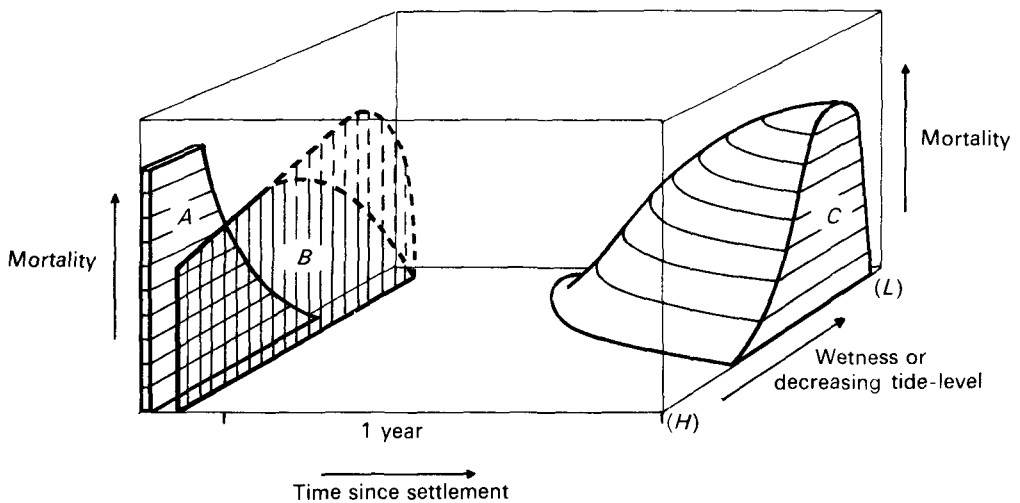


Fig. 7. Diagrammatic representation of the degree of mortality resulting from A, desiccation at initial settlement, B, frost shortly after settlement and C, desiccation during the following year, in relation to wetness of the habitat or the tidal level. A and C are recurrent, B is intermittent and operates only upon survivors of A.

event that reduces the numbers of spat within this pattern. Susceptibility to frost, as to desiccation, should show a tide-level correlation but the limited comparison that is possible between 'frost-free' and 'frost' years shows the higher (or drier) sites to have suffered the least (Table 4). This suggests that spat on the drier sites which have survived early desiccation because of their position in cracks or among mussels and barnacles are also somewhat protected there from frost. By contrast, spat in lower, more open and wetter sites are less subject to autumnal desiccation but appear there to lack protection from frost – as indeed they also do to the greater desiccation of the following summer.

At very low tide levels the short period of emersion probably affords regular protection

against both desiccation and frost – even on smooth, bare rock – but no site was low enough to test this. The severity of the effects of desiccation and frost, and the time at which they influence different habitats during the 15-month period after spawning are diagrammatically represented in Fig. 7.

Success in predicting the general level of recruitment since 1973 suggests that unless there has been a remarkable coincidence in the operation of completely unsuspected factors the hypothesis of low temperature control is soundly based. There remains a lesser level of variability, especially in successful years, which probably reflects the cumulative influence of several unknown factors, and about which our data contribute little as yet except in one instance. Early spawning is advantageous, but the earliest experienced (September 1969) did not produce the outstandingly successful recruitment that might have been expected on this basis alone. The absence that year of onshore winds for a month after spawning raises again, especially in comparison with 1968 and 1970 (Fig. 4), the possibility that the degree of larval dispersal is a secondary factor of some importance.

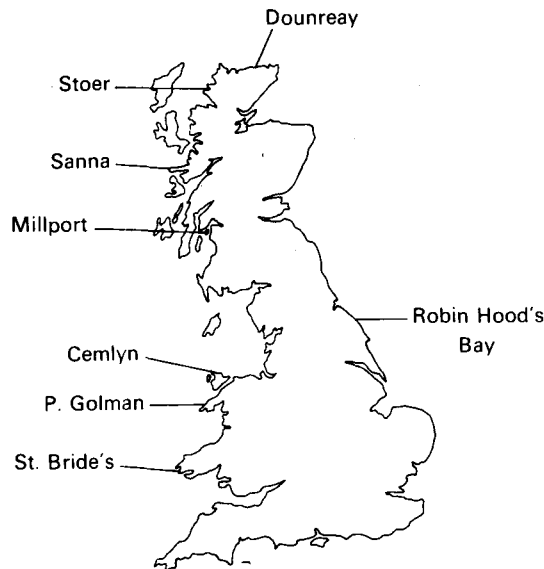


Fig. 8. The localities where regular data are being collected.

Geographical recruitment data and their interpretation

The number of localities suitable for both this and parallel studies, and which could be investigated while maintaining the regular programmes at Robin Hood's Bay, has inevitably been small. Furthermore, since it seemed preferable initially to have more 'northern data' than possible contrasts from southwestern areas, information to date comes mainly from a few areas of Scotland and more recently from Wales (Fig. 8). Sites as similar as possible to those at Robin Hood's Bay were established, but after 1–2 years some proved unsuitable and were replaced, so that the number giving data on relative performance from year to year (see Table 5) is disappointingly low. Furthermore,

although visits are made when juvenile maxima are expected there can be no certainty of this. Supplementary data on recruitment have sometimes come from size-frequency analyses of samples collected near the observation sites, but these data too are tentative as we do not know the local growth rates.

Table 5. *Geographical recruitment data (nos./m²)*

	Sites						Supplementary data
	1	2	3	4	5	6	
Dounreay							
1970/71	101						165
1971/72	63	69	48				43
1972/73	70	71	95				
1973/74	41	28	31	15	54		
Stoer							
1970/71	24						35. 36.
1971/72	21	47	14				
1972/73	7	5	2				
1973/74	2	10	3	14			
Sanna							
1970/71	17	19	52				
1971/72	—	0	41	32	13		32
1972/73	—	0	30	31	19		
1973/74	14	9	36	27	23		23. 26. 13.
Millport							
1970/71	11	6	47				
1971/72	0	0	0	0	0		
1972/73		13	225	46	498	236	
1973/74			12	15	52	11	
Cemlyn							
1971/72			27				
1972/73	0.2	1	16	19			
1973/74	0.3	4	10	11			
P. Golman							
1971/72	2	10					
1972/73	1	12	0.5	40			
1973/74	0	6	1.2	42			
St Bride's							
1973/74	620			120	20		
1974/75	1200	920	960	500	90		

N.B. Sites 4 and 5 St Bride's were not identical over the two years but are presented to indicate general levels. The 1974/75 data are given for this one locality in view of their possible relevance to the discussion on p. 813.

Although longer runs are needed to put the relative position of some of the data in Table 5 into perspective we have attempted, for the Scottish localities, to identify (Table 6) the 'good' and 'poor' seasons locally and to compare them with Robin Hood's Bay. The 1969/70 ratings are based upon the size-frequency structure of early samples, and some compensatory interpretations have been made in later years following changes in site conditions, e.g. 1973/74 at Sanna is now judged to have been a good year.

The initial premise, when expecting correlations with general climatic events was that broadly similar or regionally different patterns of results would supplement those at

Robin Hood's Bay and facilitate interpretation. As Table 6 shows the early years were generally similar, but thereafter the pattern was irregular, even unexpected, and as with the previous analyses for Robin Hood's Bay no widely applicable correlation with any general patterns of climatic conditions has been found. Accordingly the regional data must be considered in the light of the locally-derived low-temperature hypothesis.

Table 6. *Simplified summary of the occurrence of 'good', +, and poor', -, recruitment at the Scottish sites and Robin Hood's Bay*

Season	Dounreay	Stoer	Sanna	Millport	Robin Hood's Bay
1969/70	+	+	+?	n.d.	+
1970/71	+	+	+	-?	+
1971/72		+		-	-
1972/73		-		+	-
1973/74	-	-	+	-?	+

Crucial to that hypothesis is the time between spawning and first frosts, but for practical reasons we rarely know the precise spawning dates in these localities. Probable dates can be inferred from local wind data assuming the gonads are ripe, but gonadal state too is known only imperfectly or not at all. Leaving Millport for later consideration, intermittent samples suggest that gonad development is similar to that at Robin Hood's Bay, or up to 2-3 weeks earlier. Using Robin Hood's Bay data as the general baseline, the good and poor seasons for localities other than Millport can be considered relative to possible spawning times (based on local wind data) and known periods of local frost.

In the generally good season of 1969/70 spawning was very early at Robin Hood's Bay (September) and probably everywhere, and no locality had frosts until mid- or late November. Next season spawning was probably later everywhere, but again first frosts were either slight or about 5 weeks later and recruitment was again good everywhere. In 1971/72, a very poor season at Robin Hood's Bay, major geographical differences appeared, with Dounreay experiencing similar but less severe conditions than Robin Hood's Bay, while the two west coast localities were virtually frost-free until the end of December. Recruitment at the latter was good to average by present criteria. Dounreay recruitment fell appreciably from the previous year, but only to levels which so far appear to be 'average'; the effect of frosts was not therefore as severe as might have been predicted.

In the second very poor season at Robin Hood's Bay, 1972/73, the only notable feature elsewhere was the poor result at Stoer, and this locality alone experienced several consecutive nights of frost (down to -3.0°C) in mid-November within 4 weeks of presumed spawning. Early spawning was probable everywhere in 1973 (late September), so good or at least average recruitment should have resulted. However, the two northernmost localities, Dounreay and Stoer, experienced three days of frost in mid-October (the earliest frosts in our records) and both had low recruitment.

Summarizing these results it seems that poor recruitment has always coincided with frosts within the first 4-5 weeks after the estimated spawning time. Although there has been one case of these conditions not leading to a particularly poor result there is no

case of poor recruitment that does not accord with the frost hypothesis. Lack of frost has not always led to very high recruitment, but what constitutes 'high' or 'average' is still in doubt.

The Millport results need separate comment because not only are the fluctuations unusually wide (Table 4) but also the contrasting seasons of 1971/72 and 1972/73 appeared to be completely at variance with the frost control hypothesis. Estimated spawning times, based on local winds and Robin Hood's Bay gonad data, relative to local frosts, point to high recruitment in 1971/72 and poor recruitment in 1972/73 – the opposite of what actually happened. To throw possible light retrospectively upon this contradiction, Millport gonads have since been sampled through the collaboration of Dr P. G. Moore. These analyses are showing that differences of up to 3–4 weeks exist between gonadial cycles at Millport and Robin Hood's Bay, and that re-ripening and secondary spawning are possibly more frequent there, as appears to have been the case in 1946 and 1947 (Orton *et al.* 1956). Although the events of the two 'problem seasons' can never be known, appreciation of the apparently more variable gonad cycle at Millport enables one to envisage entirely plausible sequences of events that could have led to the results obtained. Furthermore, it is significant that when, in the 1973/74 season, more gonadial data were available at Millport, the modest recruitment recorded was in line with hypothesis expectations.

Nevertheless the extreme contrast between the 1971/72 and 1972/73 seasons, and especially the total failure in the former, remain surprising and have prompted speculative search for other causes. The most promising of these appeared to be wind direction because it was in the Clyde that this influenced the settlement of barnacles strongly (Barnes, 1956). Wind strength and direction have been analysed for the critical months each year, but have produced no evidence to support the view that differences in mass transportation of larvae could have been responsible.

In general, these geographical data provide rather less convincing support for the frost hypothesis than those from Robin Hood's Bay, but this is due mainly to difficulties of interpretation when the vital information about local gonad cycles and spawning times is lacking. Yet the practicalities of virtually simultaneous sampling on a wide front – ideally, immediately after storms – make it probable that only a few localities can ever be followed in detail. A further complication to appear recently is that spawning synchrony is indeed poor along irregular coastlines, a factor that not only hampers interpretation but could also damp recruitment fluctuations. This might account for the relative uniformity of recruitment at Sanna (Table 5) where the larval catchment area is very irregular; but similar conditions in the Firth of Clyde have not prevented the violent fluctuations at Millport.

The second major geographical need now is clearly an extension to south-western regions, where, since autumnal frosts are less common, recruitment should be consistently good unless spat thresholds of sensitivity are higher than in the north. Regularly high recruitment there would suggest that population levels are controlled later in juvenile life. While an increase in the number of sites per locality would be desirable, it is reassuring that even with the apparently low numbers used so far (4–8) all sites in a locality show the same relative trend, especially in the poor seasons which are the more

informative. Hence in the intensive/extensive dilemma of geographical fieldwork an increase in localities with few sites appears of higher priority than an increase in sites at fewer localities.

Influence of recruitment variation upon population density at Robin Hood's Bay

Implicit in studying recruitment is the contention that numbers of the adult (post 'O' class) animals are more dependent upon the level of the initial recruitment than on later mortality influences. Earlier work (Lewis & Bowman, 1975) has shown that there is no

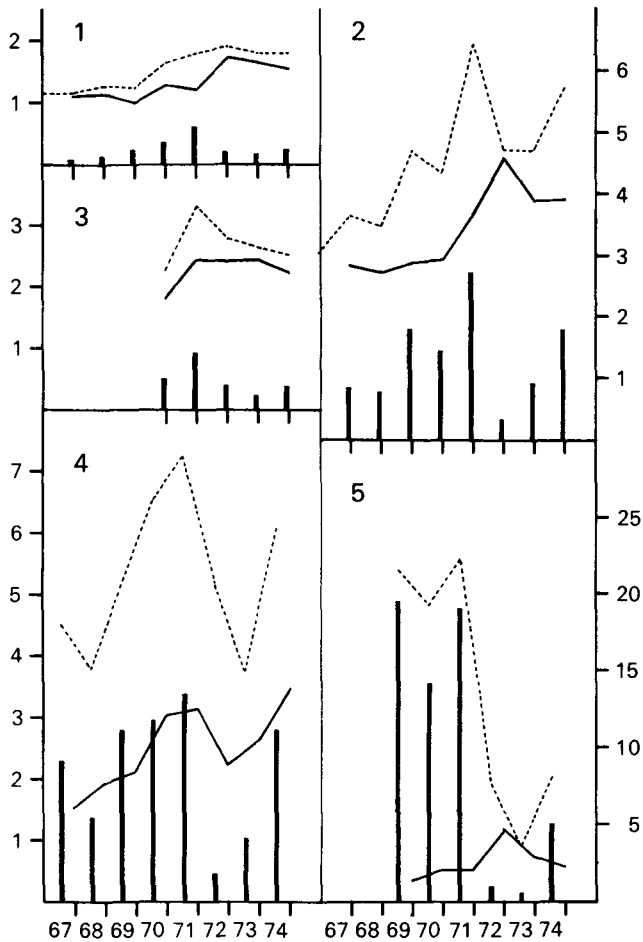


Fig. 9. Annual population maxima (---), year-end adult numbers (—) and recruitment (vertical bar) at the 5 Robin Hood's Bay sites. (Scales in 100's of individuals.)

major and widely acting external cause of general mortality, maximum life spans varying inversely with the growth rate which is itself variable among habitats. In this study, so far, there has been no persistent recruitment trend, only fluctuations, but three consecutive good seasons in the years 2-4 have brought about increases of between 25% and 130% in the adult stock, the lowest in the latest-established sites. The annual recruit-

ment, the total population level when juveniles reach their maxima, and the year-end total of adults are shown in Fig. 9. The adult numbers to which the survivors of each input first contribute are those of the following year-end. Thus at Site 2, the peak of adults in December 1972 owes much to the juveniles recorded in December 1971 and

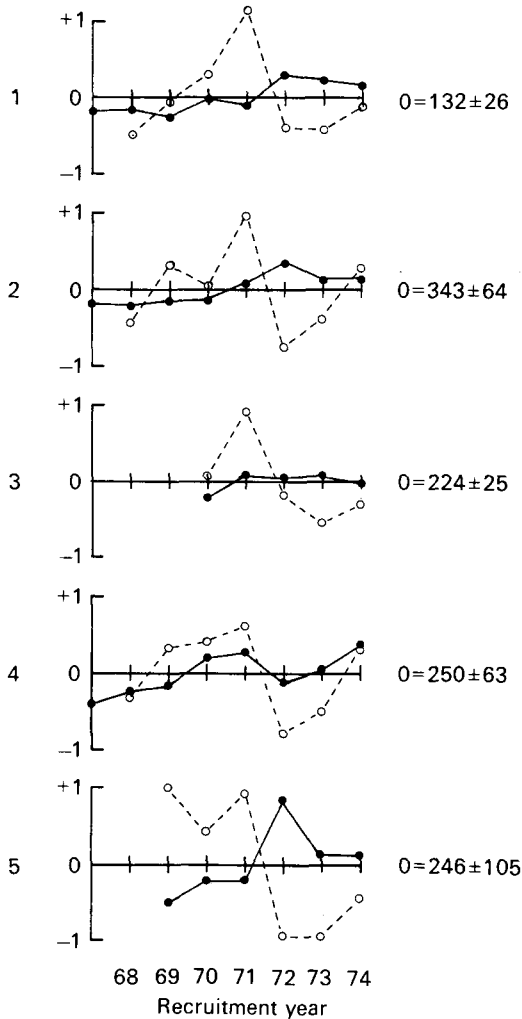


Fig. 10. Progressive changes in year-end adult numbers expressed in units of 100% astride the site mean, in relation to the recruitment fluctuations shown in Fig. 2. —, Adults; - - -, juveniles. The mean and standard deviations quoted refer to adults; values for recruitment are given in Fig. 2.

spawned in the autumn of 1970. (The 1974 juveniles, included for completeness, make no contribution to the adult numbers shown in this figure.) The progressive adult changes relative to recruitment fluctuations are compared in terms of the percentage annual variation astride the respective means in Fig. 10.

The total population (Fig. 9) naturally reflects the recruitment fluctuations closely,

but the adult variations are rather more complex because they reflect both the survival characteristics of limpet populations in different habitats and chance influences.

In Sites 1, 2 and 3, where recruitment rarely exceeds 50% of the standing crop and is usually very much lower, maximum life spans of up to 15–17 years are possible. As would be expected, the effect of good recruitment years has here persisted into the succeeding poor years. (Data for Site 3 relate to the good recruitment years and later, so the baseline here is disproportionately high.) Where the potential recruitment levels equal or greatly exceed the standing crop (Site 4 and 5 respectively) they are also associated with shorter maximum life spans (*ca.* 8 and 4–5 years respectively). This leads to the expectation that adult numbers will reflect the recruitment fluctuations more closely. This seems to have happened at Site 4, but in reality the trough of adults in 1972 and 1973 (Fig. 9) was due less to the smaller input than to unusually high adult mortality. Without this the previous high recruitments would probably have sustained a steady or rising population in spite of the more moderate life span. Site 5 reflects chance influences more strongly. The survivors of the high recruitments in 1969 and 1970 just maintained the adult density, but higher proportions of the 1971 input survived into the second and third years. These numbers, double those of the previous seasons and more than the existing adults, delayed the effect of the next two very low inputs. (For details of each year's survival patterns see Fig. 5.)

Assuming that these sites reflect the general situation, the increase in limpets has had little effect on the biological character of the shore as a whole. This is, however, only to be expected since it is limpet *decrease* which would allow algae to become established and thereby entrain repercussions among the barnacles and mussels.

RECRUITMENT FLUCTUATIONS AND GEOGRAPHICAL DISTRIBUTION

Geographical limits may be set by inability to withstand physical conditions directly or to compete successfully where efficiency is somewhat impaired; or they can be set by a failure in the reproductive/recruitment process. The higher sensitivity of reproductive than somatic processes to temperature conditions has long been known in marine species (Orton, 1920; Thorson, 1949; Kinne, 1963; Naylor, 1965), and postulated or inferred to be one of the major factors influencing geographical distribution (Hutchins, 1947; Ekman, 1953).

The recruitment fluctuations in *P. vulgata* in apparent response to the low air temperatures of the British Isles, far from the species' northern limit in northern Norway (Vader, 1976), suggest strongly that increasingly frequent recruitment failure at progressively higher latitudes could impose the northern limit. But spat susceptibility is a late event in re-population, and parallel work on *P. aspera* (reported briefly in Bowman & Lewis, 1974) has provisionally related poor recruitment in that species to a much earlier stage, i.e. incomplete gonad development in some years. *P. aspera* at Robin Hood's Bay is fairly close to its northern limit (south-western Norway), and if *P. vulgata* were to behave similarly one might find with increasing latitude that the source of repopulation failure shifts from the settling spat to the gonad. On the other hand, the more northerly populations of *Balanus balanoides* adapt to shorter growing seasons and longer winters by earlier maturation and fertilization (Crisp, 1959), and a similar process might occur

in *P. vulgata*. One year's samples from northern Norway, kindly provided by Dr W. Vader of Tromsø, suggest that such adaptation does occur with gonads ripening in 1974 about 6–8 weeks in advance of those at Robin Hood's Bay. Further confirmation of this difference is required, but whatever the outcome the absence of small individuals in sample populations indicates clearly that recruitment is not an annual event in all localities in northern Norway.

Low temperature effects, on either gonads or spat, can, however, set only northern limits. Thresholds of spat susceptibility might be at a higher level in southern populations, but the possibility that low temperatures limit recruitment becomes ever more unlikely towards the southern limit. Even within the British Isles doubts must arise when south-western shores are considered. At present we have only the limited data from North and South Wales shown in Table 5, and although these localities have yet to show a temporal pattern, the very recent (1974/75) recruitment in South Wales (St Bride's) appears unusually high. This might reflect chance lack of shoreline frosts, but with their general improbability there in October, November or early December such high recruitment may be normal. If so, the population must be controlled by a later-operating factor, which with increasing severity further south might also set the southern geographical limit.

By contrast with northern Norway where it is the sole limpet present, *P. vulgata* is joined towards the south first by *P. aspera* (south-western Norway and north-eastern Scotland) and then by *P. depressa* (North Wales) and becomes progressively subordinated to these two species towards its southern limit in south-west Portugal (Fischer-Piette & Gaillard, 1959). Competition might therefore be involved, and the abundance or restriction of *P. vulgata* to tidal levels largely above these two species in south-western France (Evans, 1957) and on the north coast of Spain (Fischer-Piette & Gaillard, 1959) appear to support this. But an increasing effect of heat or desiccation towards the south is also implicit in the species' increasing depression to low tide levels and avoidance of a southerly aspect along the west coast of Spain and Portugal (Fischer-Piette & Gaillard, 1959). Even on the north coast of Spain one of us (J.R.L.) found *P. vulgata* largely confined to shaded, damp situations.

In the latter an abundance of '0', '1' and '2' classes indicated clearly that gonadal failure does not occur regularly. Yet in samples from Oporto (Portugal), kindly obtained by Dr Mario Galhano, gonads in 1974 were unspawned and still developing in November i.e. about 6 and 13 weeks later than spawning at Robin Hood's Bay and Tromsø respectively that year. Just as early breeding in the north could be advantageous, so could regularly late breeding in the south since it would ensure that newly settled spat were subjected to a minimum of autumnal desiccation.

In southern Britain neither competition nor desiccation are sufficiently severe to limit the species' general ubiquity. Yet some controlling factor must exist and in the probable absence of frost, desiccation is the most convincing alternative. Ballantine (1961) stresses the juveniles' need of damp habitats at Plymouth, the heavy mortality after July, of the first year, and that a 'home' on open, dry rock may not be established until year two when greater size increases resistance to desiccation. In some South African limpets Branch (1975) found high level desiccation and spat mortality so severe that populations

were maintained by upshore migrations of old animals. Although Ballantine reported that this was not the case at Plymouth, there nevertheless remain sufficient grounds for suggesting that whatever the role of competition the direct role of desiccation increases further towards the south. It might result in higher autumn mortality (although not if spawning becomes progressively later) but probably the greatest effect will be in the summer of the first year. Perhaps the first evidence of desiccation effects along the north/south gradient would be decreasing density and changing age structure in the upper shore.

These speculations linking fluctuating recruitment and geographical distribution may be summarized as follows. Northern limits could be set by recruitment failure originating possibly in the gonad, but more probably from the susceptibility of spat to low air temperatures. Moving south this susceptibility remains and results in recruitment fluctuations in accordance with autumnal frost conditions. Further south, where frost recedes as a feasible shore-line factor, increasing insolation plays an increasing role: first, by reducing the number of protected microhabitats suitable for initial survival of spat in the autumn, then by increasing greatly the mortality of juveniles during their first spring and summer of shore life, and ultimately by limiting the total population to shaded situations as the southern limit of temperature tolerances is reached. Towards the south there may also be increasing competition from other *Patella* species better adapted to higher temperatures. Within this north/south gradient recruitment fluctuations occur in the British Isles, and can be deduced from the size-structure of populations in northern Norway. There seems no reason why these fluctuations arising from autumnal weather variations should not be paralleled in the south by fluctuations in the numbers joining the adult stock as a result of chance variations in summer conditions.

It is a great pleasure to record our appreciation of the invaluable assistance of Dr Maria Galhano (Oporto), Dr P. G. Moore (Millport) and Dr W. Vader (Tromsø) in providing samples and information at times or from areas that would otherwise have been unavailable to us. This work, and the earlier studies that facilitated it, were financed by the Natural Environment Research Council to which we are greatly indebted.

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