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Geographical variation in the breeding cycles and recruitment of *Patella* spp.

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Abstract

The effect of geographical differences in breeding cycles on the recruitment variation of the limpets – *Patella vulgata* L., *P. aspera* Röding and (to a limited extent) *P. depressa* Pennant – has been studied over much of their range in Britain and NW. Europe. In spite of considerable annual and local variation in recruitment success, broader patterns can be distinguished, which can be linked to spawning times and factors affecting the survival of newly-settled spat. The breeding cycles of *P. vulgata* and *P. aspera* differ across their ranges in that, in both species, spawning begins, and gametogenesis ends, earlier in the north and east than in the south and west. The cause of these differences can be correlated with geographical and annual differences in sea temperature over the potential breeding periods, and can be related to the regional incidence of conditions found experimentally to be necessary for successful settlement and survival of spat during a critical stage of their growth. The significance of this 'temperature window' in determining the littoral and geographical distribution of the species is discussed.

Introduction

In the 1970's, a study which had begun in 1965 to explain local cycles of interaction of key rocky-shore species expanded to include the causes of their natural population fluctuations, over as wide a geographical range as was feasible. The rationale behind this study has been extensively discussed (Lewis, 1976, 1984; Lewis *et al.,* 1982), and it now forms the core of the rocky-littoral section of the COST 647 programme. This paper describes some of the latest findings on the relation of differences in limpet breeding cycles to recruitment. Though most data derive from British limpet populations, with less regular data from Ireland and N.W. Europe, the results of the more intensive studies of Portuguese limpet populations, published elsewhere in this volume, have been available since their commencement (Guerra & Gaudêncio, *pers. comm.*).

Of the three species of British patellids, much of the work since 1969 has concerned *Patella vulgata* L., and has been published elsewhere, (Lewis & Bowman, 1975; Bowman & Lewis, 1977; Bowman, 1985). Almost as many data exist for *Patella aspera* Röding, but because of early interpretational problems have not till now been published. Both these species occur throughout the British Isles wherever there is suitable habitat, though *P. aspera* is nearing the northern limit of its range in northern Scotland. The third species, *Patella depressa* Pennant, is restricted to the Channel coast and the south-west of the British Isles (excluding Ireland), reaching its northern limit in North Wales. For logistical reasons, this limpet was not included in the programme until the late 1970s and data are fewer, but are recorded here to allow comparison with the more detailed Portuguese studies (*op. cit.*).

Methods

Recruitment data for *P. vulgata* were obtained by *in situ* observations on marked 1 square metre sites chosen, on the basis of early experience, as being likely to have a high settlement potential and low biological variability. Recruitment levels in *P. aspera* were originally assessed from size-frequency analyses of population clearances from mid- to low-shore pools and 'open' rock. After 1973, low/mid-littoral coralline pools of ca. 0.5 – 1 sq. m. area and less than 20 cm. depth were found to make suitable sites for *in situ* observations, since not only are they primary settlement areas but they are more stable biologically than adjacent 'open' rock with its fluctuating populations of mussels, barnacles and algae. In SW. England most *vulgata* sites and all *aspera* pools doubled as *depressa* recruitment sites. Almost all sites were located in the mid-littoral of exposed shores, as *vulgata* sites were positioned wherever possible near *aspera* sites, to maximise use of the restricted sampling time.

Figure 1 shows the number and distribution of the observation sites for the three species around Britain. Each site was visited two to five times each year, mainly in spring and autumn, except in NE. England, where visits were monthly or fortnightly or whenever tides allowed. At each visit the numbers of spat (<1 year-olds), juveniles (1 – 2 year-olds) and adults (the rest) were counted and their size range noted. The annual recruitment for a site was regarded as the highest number recorded of that spawning-year class. Because of differences in time taken for spat to emerge from settlement crevices, this number was recorded from 2 – 24 months after settlement. The observation-site data were supplemented by extra counts and occasional clearances for size-frequency measurement, from similar or lower-littoral habitats.

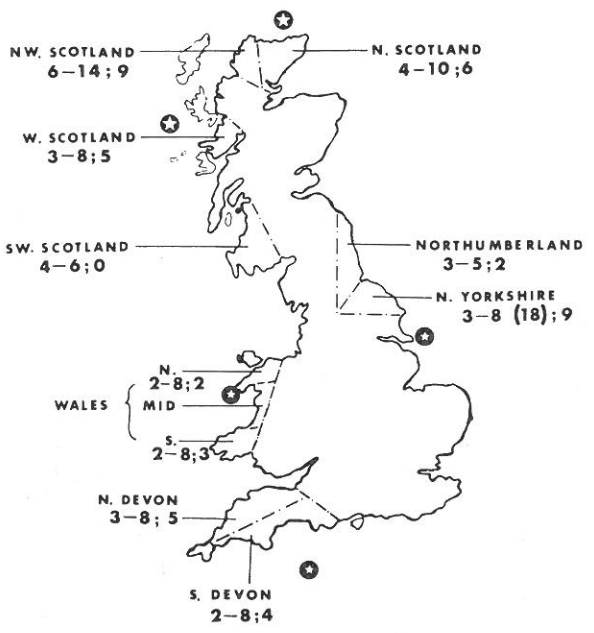


Fig. 1. Map of the British Isles, showing regions studied. Numbers indicate: number of shores studied – total *P. vulgata* observation sites; total *P. aspera* observation sites. Bracketed figure for N. Yorks. indicates total *vulgata* sites 1966 – 70. Stars show location of sea-temperature recording stations referred to in Fig. 4.

Breeding cycles were studied by regularly collecting 50 – 100 animals from the same shore level/habitat at each locality, and assessing the breeding state of the population from morphological examination of the gonad, as described by Orton *et al.* (1956). On the basis of size, colour and abundance of ripe (loose) gametes, each gonad was classified as neuter or in one of five stages of development, spawning or re-development, from which a mean gonad index was calculated: G.I. = 0 if all animals were neuter, G.I. = 5 if all fully developed. Again, frequency of sampling was greater in NE. England, where at the height of the breeding season samples could be taken daily if necessary (for *vulgata* only), to pinpoint spawning time.

Initially, morphological assessment of small early releases was confirmed by histological examination of sectioned gonads; with practice this later proved unnecessary, though since 1980 settlement plates have been used in NE. England to detect spatfalls and thus check for partial spawnings.

Since 1981 an invaluable aid in the understanding of breeding and spawning patterns, and recruitment success, has been the collection of daily sea and pool/shore temperatures by littoral recorders in NE. England, Wales and NW. Scotland.

Results: *Patella vulgata*

Recruitment variation

Table 1 presents the peak annual recruitments for the longest-running Robin Hood's Bay observation sites, which initially showed relative stability of populations other than limpets. However, since 1975, most sites have become increasingly wet, the result of increased mussel cover, loss of old barnacles (and poor recruitment of new), and since 1981 a general increase in algal cover partly because of reduced grazing from declining limpet numbers. Site 1 in particular now bears little resemblance to its original description (see Table 1), being now mostly bare rock with 10% mussel cover, sparse barnacles and thick annual weed cover. In contrast, Sites 7 & 8 proved susceptible to intermittent loss of their seed-mussel cover (and therefore their main limpet spat-settlement habitat) through periodic heavy dogwhelk (*Nucella lapillus*) predation and/or storm scouring. Only Site 3 has not changed appreciably in character, since its wetness derives as much from its lower-shore location as from its mussel etc. cover. Especially on the initially-dry barnacle-dominated sites, a succession of heavy recruitments since 1975 therefore greatly increased the density of adult limpets. For instance, the year-end density (excluding juveniles) on Site 2 was 240 per sq. m. in 1966, 390 in 1974, but rose to >1 000 by 1980; poorer recruitment together with predation by oystercatchers (*Haematopus ostralegus*) then reduced the density to 290 in 1984. The increased grazing from the elevated limpet numbers in 1980 was partly responsible for the decline in barnacle cover at these sites, by preventing the establishment of cyprids.

Table 1. P. vulgata: Peak annual recruitment at Robin Hood's Bay observation sites. All sites 1 sq. metre in area.

Year	Site 1	2	3	4	5	6	7	8
1967	13	78	138	(25)				
1968	28	182	278	(90)			1956	
1969	34	145	295	45	58	45	1408	
1970	58	272	336	78	93	93	1908	2516
1971	16	35	44	40	37	37	84	211
1972	15	85	101	16	25	21	53	144
1973	23	179 M+	278	28	38	43	549 M−	372
1974	28	301	172	37	58	37	260	160
1975	10	203	196	24	42	30	228	158
1976	M+ 77	358	515	38	B− 92	56	1728 W+	1110
1977	86	434 B−	572	62	84	94	509	195
1978	B− 82	528	717	68	84	77	1447 M+	962
1979	78	281	456	80	97	70	654	603
1980	71	293	369	33	32	29	243 M−	189
1981	B− 27	80	85 B+	17	24	12	319	229
1982	W+ 72	102 B−	161	78	B− 98	W+ 76	496	263
1983	67	268	247	102	153	93	3130 W+	2088
1984	103	391	332				465	554
1967 – 75 mean:	25	165	204	42	50	44	805	594
1967 – 84 mean:	49	234	294	51	68	54	908	650

Key to sites:
1: HL dense barnacles, ca. MHWN. }
2: HL barnacles/mussels, ca. MHWN. } exposed north headland of R.H. Bay.
3: ML mussels/barnacles, ca. MLWN. }
4 – 6: ML dense barnacles, ca. MTL.-replicates, moderate exposure, S side bay.
7, 8: ML bare wet rock/mussels, MTL.-replicates, partial shelter, central bay.
M+; −: Mussel % cover doubled; lost. B+; −: barnacle % cover ±25%. W+: appearance or marked increase in weed cover (*Enteromorpha* and *Fucus* spp.).
NB. Year is spawning/settlement year, not that in which peak counts were recorded. Bracketed figures from similar site further S on same reef.

Increased wetness and, particularly, increased small-mussel cover (which provides primary-settlement habitat for limpet spat), have been shown to elevate *vulgata* settlement/recruitment numbers (Lewis & Bowman, 1975), and these changes must have markedly increased the sites' potentials – compare, for instance, the sudden difference in recruitment among the replicate Sites 4 – 6 in 1976, following increased wetness because of loss of barnacle cover on Sites 5 & 6 but not 4. This, together with differences in timing of site changes, devalues the usefullness of assessing comparative annual settlement/recruitment from deviations from the sites' long-term recruitment means, as was generally possible until 1975. Thus, for the initially-dry Sites 1, 2 and 4–6, though recruitments in 1968–70 were judged 'good' by pre-1976 standards, only those of 1970 exceed the long-term means. 1976–78 were definitely above-average recruitment years but where direct comparison was possible in the absence of major wetness etc. changes, it seems likely that without such changes they might have been more equivalent to 1968–70 than the recruitment figures suggest. This supposition is strengthened by observations on *vulgata* spat numbers in other, unchanged, habitats such as the midshore *aspera* observation pools.

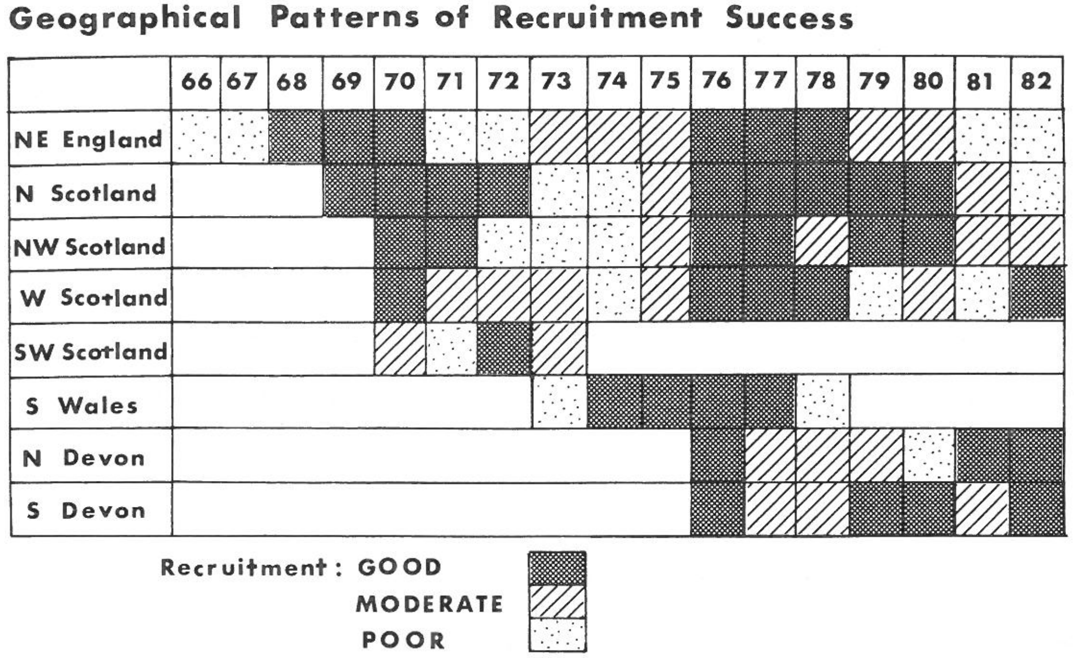
The other difficulty in assessing the relative success of annual settlement is the time elapsing before a site's peak recruitment figure is reached. The sites tabled peak variously after ca. 6 months (Sites 7 & 8), 9–12 months (2 & 3), and 12–18 months (1 & 4–6). The longer the time lag, the more the final recruitment figure can be affected by climatic extremes, or other causes of mortality, and for this reason settlement plates were eventually developed.

This latter problem was greatest at many of the Scottish locations, where peak recruitment was often not recorded until 18–24 months after settlement. All the regional sites were chosen to resemble Site 2 where possible, as (supposedly) combining habitat stability with high settlement/recruitment potential. In practice, they were found to have lower recruitment than that of Site 2, and lower annual variation: compare the mean input per square metre (± S.D.) for the longest-running sites in N. Scotland (62±21); NW Scotland (20±18); W. Scotland (37±23); NE. England (Site 2) (234±137). They also experienced much greater biological variation than the NE sites, because of unstable barnacle and mussel populations, and heavier predation of limpets, barnacles and mussels by oystercatchers, dogwhelks and eiders (*Somateria mollissima*) respectively. The lower limpet densities permitted variable cover of *Fucus vesiculosus* and ephemeral algae and diatoms, and all these factors considerably altered the sites' settlement/recruitment potential. Assessment of relative success was therefore more difficult than in the NE, so, to achieve a better basis for comparison, also taken into account were changes in spat numbers during the build-up to peak recruitment, and the numbers of spat recorded nearer settlement time in less variable habitats where spat emerged earlier, such as mid- and low-shore coralline pools. The raw regional recruitment data are too numerous to be included here (though they are available on request) and would require a lengthy analysis of the sites' vicissitudes. Instead, Fig. 2 presents an interpretation of relative settlement/recruitment success for all regions, based on the above criteria, though the classification has necessarily to be less precise.

The regions in the figure are arranged in order of coldest winter sea temperatures, and the year indicated is the spawning year, not that of peak recruitment (as this might occur up to 18 months after settlement). There is broad similarity in recruitment success between adjacent regions, particularly over much of northern Britain, where the 1976–1978 recruitments were all above-average. In all northern regions the 1975 class was well-represented in spring 1976, but the unexpectedly-low peak numbers recorded (see Table 1 for NE England) almost certainly resulted from high mortality in the abnormally-hot summer of 1976 (Bowman, 1978). Severe cold together with considerable storm damage on sites in northern Britain in the winters of 1978/9 and 1980/1 must also have depressed the eventual totals for these years: in the NE, Sites 7 & 8 suffered severe sand-scouring in storms immediately following the 1980 settlement, which was at least partly responsible for their poor recruitment. In 1976 all regions had good recruitment, and in 1982 there was a gradient of increasing success from NE backing to SW. The limited data we have from outside Britain suggest that the 1980 and 1981 recruitments in NW Brittany were both 'good', as was that of 1982 in Galway, which broadly match the appropriate S. or W. British pattern for those years. The existence of such regional patterns suggests that broadscale climatic, rather than local, factors control recruitment. These might operate at some stage of the breeding cycle, in the planktonic stage, at settlement, or during early shore life.

The breeding cycle

a) NE England At Robin Hood's Bay the breeding cycle has been followed closely since the start of the study, and though the gonads never failed to develop there were considerable annual differences in both peak Gonad Index (ie. maximum mean gonad



Geographical Patterns of Recruitment Success

	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
NE England	░	░	▩	▩	▩	░	░	▨	▨	▨	▩	▩	▩	▨	▨	░	░
N Scotland				▩	▩	▩	▩	░	░	▨	▩	▩	▩	▩	▩	▨	░
NW Scotland					▩	▩	░	░	░	▨	▩	▩	▨	▩	▩	▨	▨
W Scotland					▩	▨	▨	▨	░	▨	▩	▩	▩	░	▨	░	▩
SW Scotland					▨	░	▩	▨									
S Wales								░	▩	▩	▩	▩	░				
N Devon											▩	▨	▨	▨	░	▩	▩
S Devon											▩	▨	▨	▩	▩	▨	▩

Recruitment: GOOD ▩
MODERATE ▨
POOR ░

Fig. 2. P. vulgata: Geographical patterns of recruitment success. Assessment of data from size-frequency analyses, settlement pools, and all observation sites (allowing for gross changes in sites' settlement potential caused by biological variation – see text).

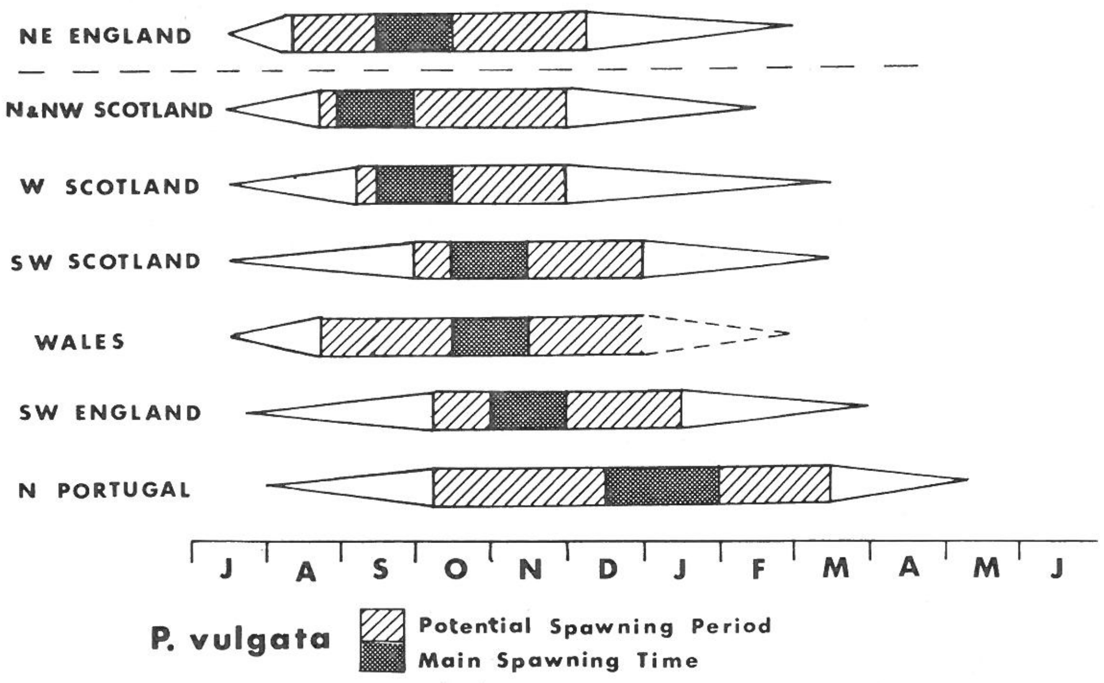


Fig. 3. P. vulgata: Regional differences in breeding periods. Bars indicate duration of breeding period when sex is morphologically distinguishable. Dark shading shows period when most of the gametes are released (main spawning time); light shading shows period when other, usually small, spawnings have occurred: decline of gonads after this is probably through resorption of gametes. Dashed lines indicate only one or two years' data. Period of observations: NE. England, 1968–85; other British regions, 1973–84; N. Portugal, 1974 and 1980–83 (Guerra & Gaudêncio, pers. comm.).

size) and the timing, extent and frequency of spawnings (Bowman & Lewis, 1977; Bowman, 1985). In NE England, the gonads begin to develop in July, as shown in Fig. 3, and some gametes become mature in August. Maximum gonad size is usually reached by October and most gametes are released during September and October. However, spawning can occur well before all gametes are fully-developed (eg. in August), in which case only the ripe gametes are shed. Such releases often do not result in a decrease in gonad size but, with experience and frequent sampling, can be detected by a sudden disappearance from the gonad samples of 'loose' (ie. ripe) gametes. These partial spawnings are followed by continued development of unripe gametes (gonad re-ripening), or occasionally by a new burst of gametogenesis (redevelopment), resulting in an increase in gonad size followed by later spawning, and such gonads can be distinguished by colour or histology from unspawned gonads until ripe gametes are present again. Very high Gonad Indices are therefore attained only when most of the season's gametes ripen before any release occurs, and so tend to be associated with 'late' spawning.

However, the data showed (Bowman & Lewis, 1977) that good recruitment was not attributable to gonad size nor to size of release. Until 1981 there was, however, very good correlation between time of first release and success of recruitment, so that 'early' = good and 'late' = poor. In a Multiple Linear Regression analysis, using 28 variables possibly affecting recruitment, >70% of recruitment variation could be attributed to earliness of release, while much of the remainder related to variation in mussel cover (M. A. Kendall & P. Williamson, *pers. comm.*). This correlation was initially explained by supposing that late-settling spat were likely to be killed by early-winter frosts, but this hypothesis has now been modified after using settlement plates to catch spatfalls and follow their fates directly.

A detailed account of the growth and survival of newly-settled spat is currently in preparation, but their relation to recruitment is summarised in Bowman (1985). It was found that spat are highly susceptible to growth retardation and shell deformities induced by excessively high and low temperatures, as well as to detachment from the substrate during rough seas, during a critical period lasting from settlement until production of the 'true' calcified shell and growth of the mantle tentacles, at a size of ca. 0.7 mm. shell diameter. The temperature range for optimal growth in the laboratory was 10–14 °C, and as growth all but ceases at temperatures below 6 °C, the critical period can vary in length from 6 weeks to 5 months (ie. over the winter). Once past this critical period the spat are much hardier, and a clear relationship has been demonstrated since 1980 between the number of spat passing this stage *before* the onset of winter and the eventual numbers of recruits (Bowman, 1985). Since spat either fail to settle, or die very quickly, when shore temperatures are too high, as in August/September 1981 and 1982, the recruitment at Robin Hood's Bay derives almost entirely from settlements during September/October, and the hypothesis can be reformulated thus: good recruitment follows when spawning results in settlement coinciding with a restricted temperature range, optimal at ca. 10–14 °C, during early shore life.

b) Geographical variation In NE England this narrow range, the temperature 'window', normally occurs during September/October, but there is clearly going to be a north/south gradient in any such climatic factor. Since it must be to the species' advantage to recruit successfully every year, it is perhaps not surprising to find a geographical gradient in time of the main gametic release, from August/September in N. Scotland to November in SW. England. Figure 3 is based mainly on our own data, since in order to prove such differences are geographical it is necessary to compare data for different localities in the same year. Samples received in 1974 from near the European limits of *vulgata*'s range (Tromsø, Norway and Portô, Portugal) suggested that the main release started even earlier (July/August) in Norway, later (after December) in Portugal. The latter observation has been confirmed by Guerra & Gaudêncio (q.v. this volume). Data from S. Britain, Eire and France (Evans, 1953; Orton *et al.*, 1956; Choquet, 1966; Thompson, 1980; Hatch, 1977) and from Orkney (Baxter, 1982) fit into this gradient of spawning times, though hitherto the pattern for SW. England has been regarded as the norm.

Although the earliest spawnings have been recorded in NE. England, this might simply reflect the more frequent sampling there, over a longer period, and the difficulty of widespread synchronous sampling. In the NE, August releases were not recorded until 1981 and 1982 (September spawning being previously earliest), when other localities could not be visited. A very small mid-August release in mid-Wales in 1985 suggests that all British *vulgata* populations might be capable of spawning from August onwards, though where regular runs of gonad data are available over several years it is clear that release normally starts earlier in the north than in the south (Bowman, 1985). Consequently, gonad redevelopment and multiple release were most common in northern Scotland, whereas gonads were regularly found to be more-fully developed in late October in southern Britain, suggesting an absence of early spawning.

The length of the potential breeding period also showed a north/south gradient: except very rarely few ripe gametes remained unspawned by mid-December in the north, whereas in the south major spawnings regularly occurred as late as January, and the Portuguese study (q.v.) extends this into March. After the last release, any remaining gametes were re-absorbed over the resting period, as described by Orton *et al.*, (1956), so that sex became morphologically indiscernible. Whereas 'resting' gonads in other regions resembled those described by Orton in being also histologically unsexable, through complete regression of the germinal epithelium, in NE England this was not the case: the germinal epithelium for the following season's gametes here appeared towards the end of the current breeding season and persisted over the resting period. These over-wintering gonads were therefore of appreciable thickness, in contrast to those of other populations, and their past and/or future sex could usually be identified histologically. In such a condition, sex-change could be seen to have occurred in a high percentage of previously-male gonads. Thus, although there appears to be in any given year no appreciable geographical difference in time of onset of gametic proliferation, in NE England it begins from an already-present germinal epithelium which elsewhere has first to be produced. This might explain the apparently-faster rate of gamete development in NE populations, though it is not easy to compare development rates accurately, because of local and annual differences in energy budgets and partitioning (Workman, 1983; Wright & Hartnoll, 1981).

Spawning & redevelopment

Spawning in *P. vulgata* had previously been linked to rough seas (Orton *et al.*, 1956), but though this was undoubtedly true in many years at Robin Hood's Bay (Bowman & Lewis, 1977) it was not totally convincing, nor did suggested differences in 'ripeness' of gonads/gametes satisfactorally explain the observed spawning differences. There was also no explanation for annual (and regional) differences in the frequency and amount of redevelopment after an initial major release. Yet in some years a very broad pattern of breeding and spawning time existed: thus in 1977 and 1978 spawning began earlier than usual throughout Scotland and NE England, and these breeding periods were unusually prolonged, with considerable redevelopment, especially at Robin Hood's Bay. By contrast, in 1973 and 1974, spawning in all Scottish regions began relatively late and little or no redevelopment followed (Bowman, 1985). The scale of such events suggested that again a climatic factor might be involved.

Comparison of the regions' potential spawning periods (Fig. 3) with the mean sea temperatures in each area (Fig. 4) shows a rough coincidence with the time from the annual peak of monthly mean

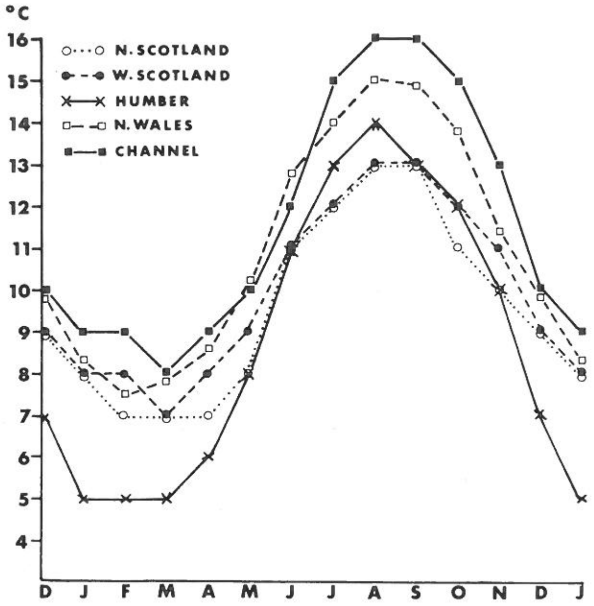


Fig. 4. Inshore sea temperatures around the British Isles. Mean monthly temperatures at the stations shown in Fig. 1, for the period 1966–75 (Meteorological Office data).

temperature to when it drops below about 10 °C. Since on exposed coasts, even in S. England, the peak sea temperature rarely exceeds 16 °C, the spawning period therefore coincides with the proposed temperature 'window' optimal for spat settlement and survival. It also appears that the main spawning time for each region occurs during the period when mean sea temperature drops below 12 °C.

Spawning of molluscs in response to a rise in sea temperature occurs in the limpets *Nacella concinna* Strebel (Picken, 1980; Picken & Allen, 1983) and *Acmaea* spp. (Fritchman, 1962a, 1962b), and several bivalves (Nelson, 1928; Ansell & Lander, 1967; Lammens, 1967). Spawning in response to a drop in temperature past a critical level is rarer, but found in the Bay scallop (Barber & Blake, 1983) and possibly in the South African *Patella oculus* (Branch, 1974). At Robin Hood's Bay the sea temperatures could originally be taken only at low tide in shallow water in the bay, where considerable inshore warming was known to occur. Though storms usually produced a drop in sea temperature, no correlation between this and spawning could be demonstrated. When, however, the nearest available daily inshore sea temperature records (for Humber, about 100 kms south and 0.7 km. offshore) were compared with the Robin Hood's Bay breeding cycles from 1967 to 1980, two connections became obvious (Table 2): a) The season's first spawning was recorded by the first gonad sample taken after the Humber sea temperature first fell below 12 °C. With rare exceptions, spawning had been pinpointed even to the day of occurrence because gonad samples were always taken at the first opportunity after a rough sea, to check for release, and 90% of the spawning drops in temperature accompanied the heavy swell set up by north-westerly gales (either locally or further north). b) After an initial spawning, gonads redeveloped only in years when the sea temperature rose above 12 °C after the spawning drop: later spawning(s) occurred when the temperature next fell to <12 °C. Altogether 20 out of 24 recorded spawnings followed drops to <12 °C, 3 of the remainder being end-of-season spawnings during storms when the sea temperature was already <12 °C.

Table 2. P. vulgata: Relations between Humber sea temperatures (Meteorological Office data), spawning and re-ripening at Robin Hood's Bay, N. Yorks.

	Sea temp. fell <12 °C on:	Spawning first found on:	Sea temp. then rose above 12 °C	Gonads re-ripened
67	18 Oct	10 Nov	No	No
68	12 Oct	14 Oct	Yes	Yes
69	29 Sept	29 Sept	Yes	Yes
70	9 Oct	13 Oct	No	No
71	27 Sept	6 Oct	Yes	Yes
72	21 Oct	23 Oct	No	No
73	26 Sept	27 Sept	Yes	Yes
74	30 Sept	1 Oct	No	No
75	29 Sept	2 Oct	Yes	Yes
76	9 Sept	10 Sept	No	No
77	18 Sept	21 Sept	Yes	Yes
78	19 Sept	21 Sept	Yes	Yes
79	21 Sept	1 Oct	No	No
80	16 Sept	17 Sept	Yes	Yes

Since 1981, temperature recorders installed at MTL on the shore at Robin Hood's Bay have shown 'actual' sea temperature, (ie. that experienced by the mid-littoral for 85% of the high-water period) to be up to 6 °C colder (in summer/autumn) than that taken by hand at the sea's edge. The connection between storms, changes in sea temperature and spawning has therefore been compared directly, as shown in Fig. 5. The figure shows no consistent connection between spawning and temperature drops *per se:* the first spawning occurs only when the sea temperature first drops to <12 °C. This is shown particularly well in Sept. 1984. The August 1982 release was the earliest yet recorded, but small because few gonads had ripe gametes so early in the season. These gonads continued to develop during September, with no further release, despite a few storms, until the next time the temperature fell below 12 °C. It did not rise significantly above 12 °C that season, and redevelopment was minimal, the Gonad Index falling during storms in early October, then at the final release in mid-November. In 1984, after the first (major) release, most of the populations' gonads redeveloped when the temperature rose again above 12 °C. The next release followed a subsequent drop to <12 °C, after which the temperature stayed below 12 °C and there was no further redevelopment, only a limited amount of reripening in some males, before the final spawning after a mid-November storm. Similar relationships were found in 1981 and 1983 (Bowman, 1985), so that during 1981–1984 11 out of 14 spawnings were recorded immediately after a drop to <12 °C at Robin Hood's Bay, the remainder being late-season releases when sea temperature was already <12 °C and were recorded after storms.

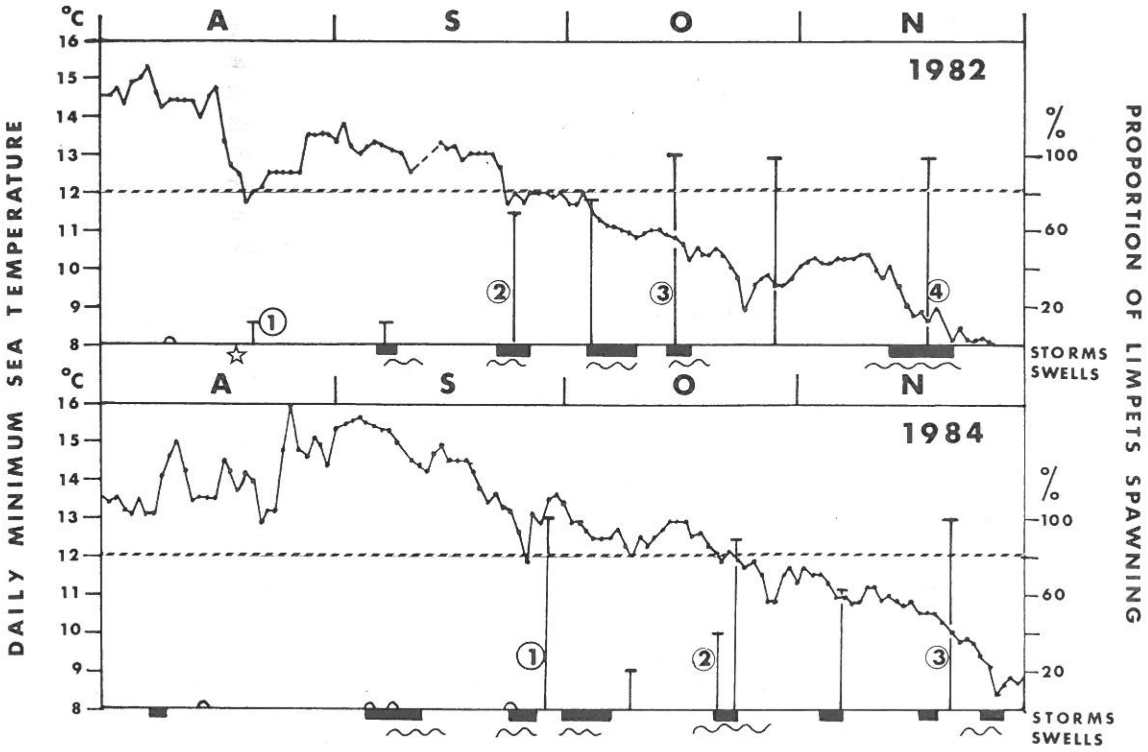


Fig. 5. P. vulgata: Correlation between sea temperature and spawning at Robin Hood's Bay, N. Yorks. Graphs show the daily minimum sea temperature; vertical bars = percentage of spawned limpets in the sample (bumps on the baseline indicate a sample with no spawned limpets) – when this percentage decreases between samples, redevelopment has occurred. Symbols below the baseline indicate occurrence of seiches (star), and duration of storms and heavy swells.

The connection between sea state and temperature was also clarified. Thus, in August, considerable warming of inshore water could occur during spells of calm sunny (anticyclonic) weather, only to cool as quickly when the calm spells ended, as in August 1984. Similarly, marked drops in sea temperature could occur in late autumn during calm cold anticyclonic spells, often with night frosts, as in late October in 1982 and 1984. These falls in temperature did not result in spawning. Temperature drops causing spawning were almost always associated with heavy swells, set up by NW gales either locally or in more northerly waters (N/NW storms off northern Scotland usually produced at Robin Hood's Bay, three days later, a tidal elevation of 0.2–1 m. and a heavy swell even without an accompanying wind, as in mid-August 1982). Such swells presumably brought inshore a body of colder bottom or offshore water, whereas the rough seas produced by local easterly gales presumably resulted in mixing of inshore water which did not always result in a drop in temperature, particularly on the open coast, hence presumably the mismatches with early spawnings.

A comparison of spawning on adjacent exposed and embayed shores suggests that spawning is not induced by a change in some character of the water mass other than temperature. In September 1983 the season's first release occurred simultaneously at exposed shores along 200 km. of the NE coast, when the sea temperature fell to <12 °C for the first time that year. However, in embayed positions, with sea temperatures 4–6 °C above 'true' sea temperature, the fall left bay temperatures still >12 °C and spawning did not occur: similar phenomena had previously been recorded in Scotland. A similar event in October 1985 followed a swell which introduced a body of visibly 'different' (less turbid) water into the bays under observation. The marked separation of warm embayed water from cold deep water on either side of Filey Brigg (N. Yorks.) has regularly resulted in asynchronous spawning, the time-lag between first releases on its exposed and sheltered sides has been 48 days (1981), 25 days (1983), ca. 36 days (1984) and 12 days (1985).

Recent data from NW Scotland not only provide further examples of local exposure/shelter spawning differences, and confirm that 12 °C appears to be critical there, but also indicate the widespread effect of a major NW storm. Thus, in September 1983, >80% spawning was found in both NW Scotland and NE England immediately after the same storm, while in early September 1984 a storm causing heavy spawning in N and NW Scotland also caused a temperature drop in NE England (though not to <12 °C on this occasion – Fig. 5). In August 1982, a severe northerly storm in the N. Atlantic not only set up the seiche which produced a large temperature drop and triggered spawning in NE England (Fig. 5, starred) but also caused temperature falls of similar magnitude in northern Scotland and Portugal.

Whether or not 12 °C is critical in the SW remains undecided, because of recorder breakdowns and collection difficulties, but it is suspected that a slightly higher temperature might be involved.

Patella aspera

Recruitment variation and breeding

Unlike *P. vulgata* which occurs throughout the littoral zone on exposed and sheltered shores in the British Isles, *P. aspera* has a much more limited distribution, being restricted to exposed shores and confined to permanently-wet rock and coralline pools in the mid- and low-littoral. In SW. Britain and Ireland the main population and primary settlement areas occur below MLWN, but towards the north of Britain (and therefore in most of our study areas) the greatest numbers and most regular recruitment are found in mid-littoral pools. Most recruitment data described here were obtained from such pools, though breeding and recruitment in a variety of habitats was studied wherever possible, and their differences are still being elucidated.

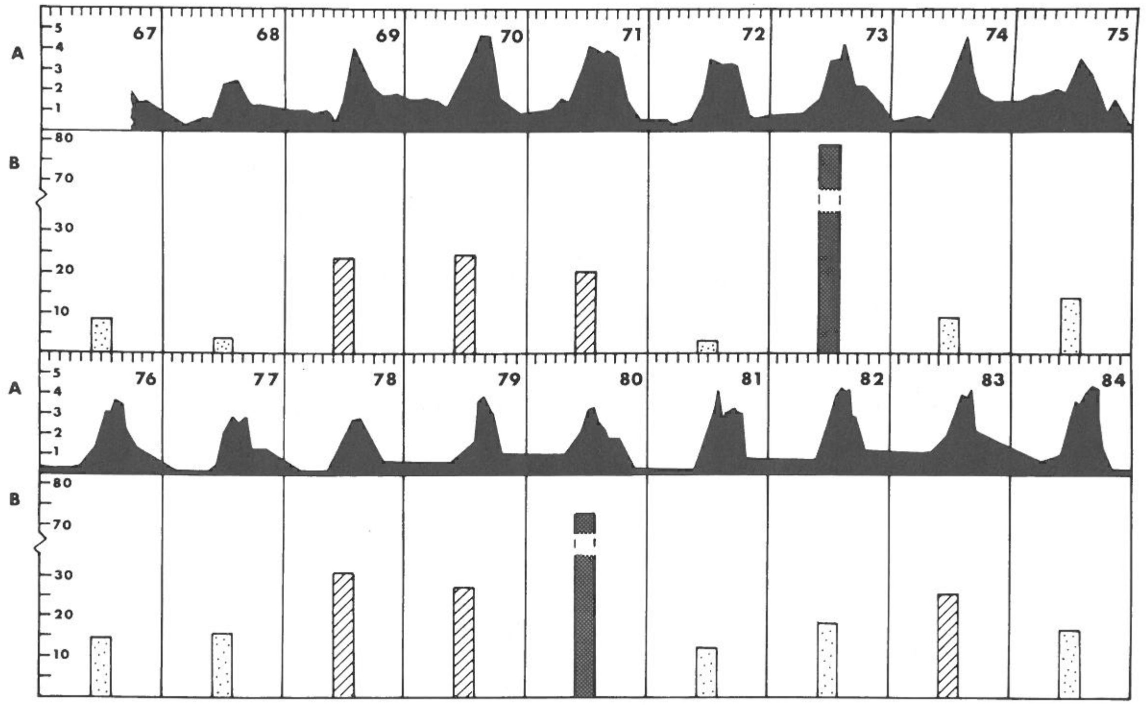


Fig. 6. P. aspera: Annual breeding cycles and recruitment at Robin Hood's Bay, N. Yorks. A: Gonad Index. B: Recruitment – peak number per square metre recorded of each year class. Data from size-frequency analyses, 1967–69, and as the mean of the two main observation pools, 1970–84. Shading indicates percentage deviation of recruitment from the long-term mean: stippled = –25 to –100%; striped = ±20%; hatched = >100%.

Whereas *vulgata* was regarded as a winter breeder (Orton *et al.,* 1956), *aspera* was reputedly a summer breeder, and, as it approaches its northern geographical limit (S. Norway) in northern Britain, local populations in N. Yorkshire were confidently expected to show frequent recruitment failure, possibly as a result of incomplete gonad development. From 1967 to 1972 this expectation seemed to be confirmed, as there were considerable annual differences in peak Gonad Index – much greater than in *vulgata* – which showed a marked similarity to the size of the subsequent recruitment (Fig. 6).

The size-frequency histograms of the local (NE) population for these years (Fig. 7A) show clearly the prolonged effect of the 'missing' 1968 year-class, exacerbated by a poor 1967 crop, on the population structure. Samples collected from around the British Isles in April/May 1971 (Fig. 7B) showed a similar scarcity of mid-sized animals in most northern and western populations, but those in the south (exemplified by SW Eire in Fig. 7B) had no such missing year-class(es), their size-frequency structure being typical of popula-

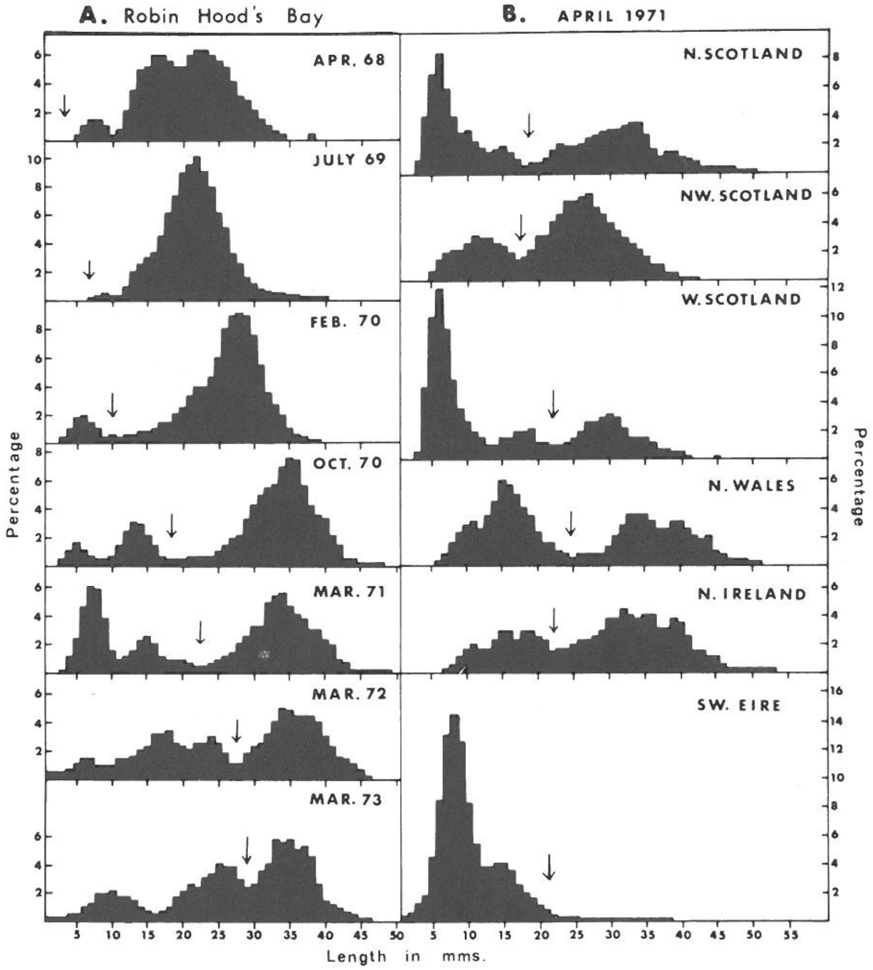


Fig. 7. P. aspera: Recruitment variation as shown by population size-frequency distributions. A: At Robin Hood's Bay, N. Yorks., 1968–73. B: Regional populations in spring 1971. Sample size = ca. 400; arrows indicate position of the 1968 year-class. Samples from N. Ireland and Eire kindly collected by Dr. R. Seed and Dr. G. B. Thompson.

tions with regularly-high recruitment, fast growth and short life (cf. low-littoral *vulgata* populations: Lewis & Bowman, 1975). Such a widespread recruitment failure around the north, and its coincidence with poor gonad development in NE. England in a summer now on record as the coldest in the last 23 years (deviations from monthly mean air temperatures, Whitby, 1968: May −2.7 °C; June −0.8 °C; July −2.5 °C; August −1.3 °C) convincingly substantiated the original prediction.

Though there is probably an element of truth in this explanation of the 1968 recruitment failures, after 1972 the correlation between gonad development and recruitment success broke down, demonstrating (if nothing else!) the need for long-term data in such studies. Fig. 6 shows that there was nothing exceptional about the G.I.s preceding the very good recruitments of 1973 and 1980, or the poor inputs of 1974 and 1981. Though in 1977 (the next-coldest summer after 1968) a low G.I. preceded poor recruitment, the small gonad size here resulted from early spawning of incompletely-ripe gonads, followed by continued development and release of the rest of the gametes, as described earlier for *vulgata.* In fact it became clear that in *aspera* such multiple spawnings are very common, especially in pool-dwelling populations, which tend to be the first to spawn.

When spat first appeared on the shore in early autumn, good recruitment usually followed: in poor recruitment years spat were not found in the observation pools until the following spring, and were often stunted and atypically coloured (Bowman, 1981), continuing to grow unusually slowly and often dying in their second or third year. After the initial regional pattern shown in Fig. 7B, it proved difficult to distinguish any consistent regional similarities. Though the 1973 recruitment was of record proportions in NE. England, N. and NW. Scotland, it failed in W. Scotland; the 1980 recruitment, again very good in NE. England, failed in all other observed regions except S. Devon, Brittany and Portugal. There was a tendency towards similar recruitment throughout the Scottish regions, and (from the limited data available) also throughout S. Britain, Europe and possibly Eire, though the picture was occasionally confused by contrasting recruitment success at different shore levels/habitats. As *aspera* is regarded as a 'southern' species it was expected that hot summers might boost its breeding and recruitment in the north, but in the exceptionally-hot summers of 1975 and 1976 this did not occur: in the NE., although spawning began early (July/August), poor recruitment resulted, which negated a simple 'early = good, late = poor' spawning/recruitment relationship. The Scottish data also seemed anomolous, in that poor recruitment tended to follow hot, sunny summers whereas good recruitment followed dull summers.

Geographical variation of breeding cycles

Compared to *aspera* in NE. England, the size of juveniles in their first spring, and their later emergence onto 'open' rock or in the observation pools, in Scotland and southern Britain (Bowman, 1981) suggested that they settled later and/or grew more slowly over-winter, and this was found to apply to Irish and Breton populations also. Figure 8 shows that *aspera* does breed earlier in NE. England than in the other regions; it also has the shortest potential spawning period. Thus in NE. England >80% of gametes have been discharged by the end of September in most years, whereas in Scotland and SW. England the gonads usually contain abundant gametes until the end of October and November respectively. Since multiple spawnings regularly occur during the breeding season in these other regions, redevelopment must here be able to recur later in the year than is possible in the NE. Nowhere else has a gonad development as poor as that of 1968 in NE. England been recorded: on the contrary, the Gonad Index in other regions, including N. Scotland, regularly peak at a value of >4.0, despite multiple releases. The spawning pattern is therefore not a simple north/south one as in *vulgata,* as the NE. English population is behaving as though it was further 'north' than the Scottish ones.

The other major difference in the regional breeding cycles of *aspera* compared to *vulgata* is that in any given year there is a marked difference in time of onset of gametic proliferation, starting (in Britain) earliest in SW. England and getting progressively later clockwise towards NE. England. Time of onset also varies annually, within each region (see Fig. 6 for NE. England), proliferation seeming to begin later in years with below-average spring sea temperatures. The possibility of a temperature link with gonad development fits the pattern of regional spring sea temperatures (see Fig. 4), which are markedly colder in NE. England than in N. Scotland from autumn to spring. The later maturation of gonads in N. Scotland compared with NE. England could reflect the lower summer temperatures. Despite their later start, gonads apparently mature faster in Scotland and NE. England than in the south, because the germinal epithelium for the next season's gametes is produced towards the end of the current season, as it is in local (NE.) *vulgata.* As in *vulgata* this 'pre-development' enables the gonads to be sexed histologically during the 'resting period', and sex-change can be seen occurring in a high proportion of males – a situation previously only inferred (Thompson, 1979).

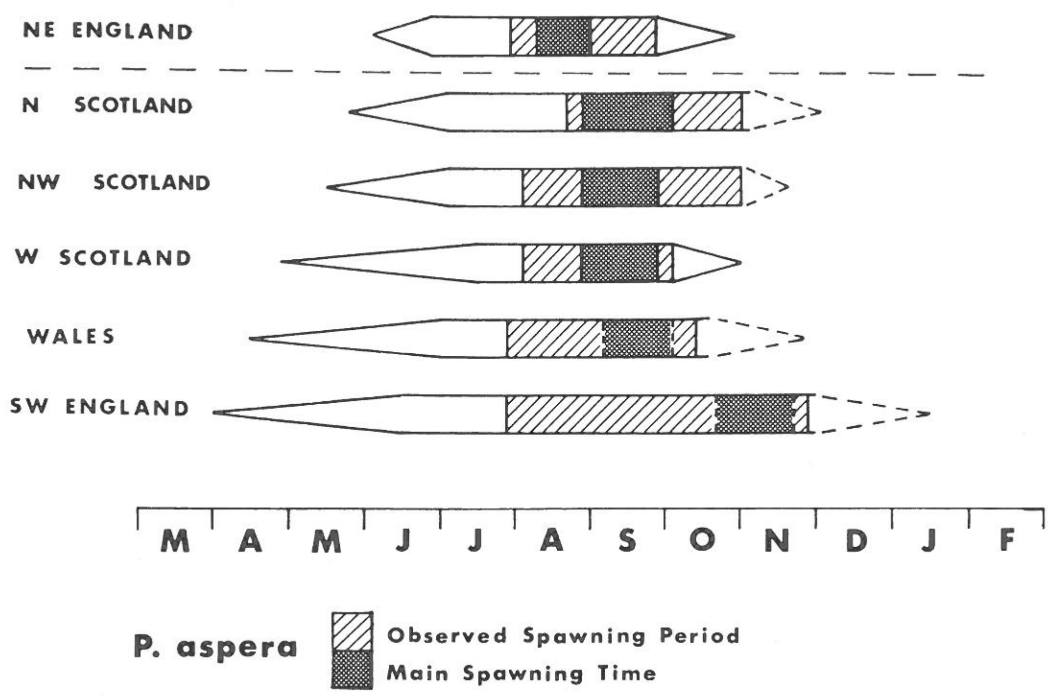


Fig. 8. P. aspera: Regional differences in breeding periods, 1973–85. Key as for Fig. 3.

Because of the relative inaccessibility of the local (NE) *aspera* populations during neap tides and rough weather, it has proved difficult to pinpoint spawning as accurately as with *vulgata.* Early evidence again suggested storms as a possible trigger (cf. Thompson, 1979), and in recent years the *aspera* have certainly spawned during the same swells as caused first release in *vulgata.* In 1983 first release in *aspera* preceded that of *vulgata,* occurring between 10th and 13th August when a moderate NW wind and heavy swell arose during a very calm period; the sea temperature fell but remained above 12 °C and *vulgata* did not spawn. However, in August 1982, the large temperature drop which triggered *vulgata* spawning was not accompanied by swells or gales (see Fig. 5) and *aspera* did not spawn. Recent evidence from the sea-temperature recorder suggests that spawning requires a protracted (>18 hours?) period of exposure to surf plus continuous (lowered) sea temperature, resulting from swells breaking across the mid-littoral during nominal low-water, but the data are still too few to be conclusive.

Determination of the effect of temperature and settling time on *aspera* spat, using settlement plates, has been hindered by a succession of poor recruitments, so experimental laboratory studies are still lacking. However, studies in progress in NE. England, in littoral pools with known differences in temperature regimes during low water, are indicating that the rules governing *vulgata* spat establishment also apply to *aspera* spat, but that *aspera* spat are less tolerant of temperature variation, and more susceptible to storm damage, than *vulgata* spat. They grow more slowly than *vulgata* spat at any given temperature, growth being optimal between ca. 12–16 °C and effectively ceasing at <10 °C. Low temperatures produce severe shell deformities in *aspera* spat even as large as 2 mm. diameter, so spat in regions with lowest winter sea temperatures must reach a larger pre-winter size to maximise their chances of over-winter survival, sea rather than air temperature being important in this respect as the main *aspera* habitats are rarely uncovered over the winter. Larger pre-winter size is achieved in NE. England when spawning/settlement occurs early in the breeding season when the sea temperature is >12 °C and still rising, and/or in habitats such as pools where temperature, and therefore spat growth, are boosted by insolation, though over-heating can adversely affect growth and survival, as found for *vulgata* spat. Although this evidence is not yet complete, it seems to explain the observed settlement/survival and recruitment variations, and strongly suggests that, once again, geographical differences in breeding times might mirror the time of year when the temperature range optimal for growth is likely to occur.

P. depressa

Recruitment variation

In Britain, good *depressa* populations are confined to SW. England, so this species could be studied only briefly, between 1976 and 1983. Significant recruitments were recorded only on the North Devon shores studied: as shown in Table 3, recruitment varied similarly in the two habitat types monitored, though the range of variation differed. 1979 was clearly an outstandingly-good recruitment year, and (significantly?) also a year when large numbers of very young spat appeared on the shore in late autumn. It is difficult to assess the relative success of the earlier years' recruitment, as primary-settlement observation sites were not established till 1979, when the numbers given were recorded; however, earlier counts and clearances at a variety of habitats and levels suggest that probably only 1976 can be regarded as 'good'. The 1981–1983 recruitments were clearly 'failures'. In June 1982, poor 1980 and worse 1981 *depressa* recruitments were found on various shores in Brittany, which agreed with the Devon pattern. The 1979 crop in Brittany was also sparsely represented; this might not disagree with the Devon pattern as the very good 1979 recruitment which peaked in Devon in March 1980 had virtually disappeared from the sites by October 1980. This disappearance, almost certainly mortality induced by over-heating, highlights both the need for regular, and well-timed, sampling, and the dangers of assessment based on data taken too long after settlement.

Table 3. P. depressa, N. Devon: Mean Peak Annual Recruitment at observation sites. Recruitment expressed as mean numbers per sq. m. for high/mid-littoral pool sites and mid/low littoral rock sites. Brackets indicate counts taken well before or after expected time of peak recruitment.

	Pools	Rock	Rank
1976	(15)	(24)	2
1977	8.0	11.3	4
1978	3.2	4.0	5
1979	170.0	47.0	1
1980	8.6	13.0	3
1981	0	3.0	7
1982	0	3.0	7
1983	(0)	(4)	6
Mean	25.6	15.0	

Breeding cycles

Our gonad data are intermittent, but agree with Orton & Southward (1961) and Hatch (1977) that *depressa* in Britain can breed from May/June to October/November, with multiple spawnings and redevelopment similar to those found in *aspera* and *vulgata* but sometimes so extensive that they resemble separate breeding seasons. Thus in 1978 (and probably similarly in 1980) a large spawning in June/July, dropping the G.I. to 2.9, was followed by marked redevelopment and a later spawning in October/November, whereas in 1979 spawning in early July was apparently not followed by redevelopment. No spat were recorded on the sites from the June 1978 spawning, but that in July 1979 was presumably responsible for the abundant spat found that autumn. In the absence of any data from settlement/survival/growth studies using settlement plates, the fate of spat from these spawnings remains speculative. Better information on spawning times, over a wider geographical range than is available in the British Isles, is needed before any conclusions can be reached for this species, and in this context the Portuguese studies (*op. cit.*) provide a valuable contribution.

Discussion

The breeding cycles of *P. vulgata* and *P. aspera* show shifts in spawning time, relatively earlier towards regions of cold winter-sea temperatures, later towards regions of high summer temperatures. Considering that the temperature tolerance range of the adults of both species is <0 °C to ca. 42 °C (Evans, 1948), the spat of both species apparently have a remarkably low tolerance of temperature variation and a narrow temperature range for optimal growth. Since survival depends on fast initial growth during the vulnerable phase immediately after settlement, it seems unlikely to be a coincidence that regional spawning periods bracket the time of year when the optimal temperature is most likely to be experienced. In the 'north' (not necessarily geographic north), earlier spawning lessens the debilitating effects of severe or prolonged winter cold and rough weather; in the 'south' delayed spawning avoids the equally-disastrous effects of high shore (and sea?) temperatures: particularly for pool-settling spat overheating from strong insolation is the problem, not desiccation. Yet even in 'northern' populations there is evidence that early settlements can fail because of experiencing too-high temperatures, and late settlements in the 'south' could certainly fail in stormy or unusually-cold winters. Because of this, and because of annual climatic differences, an extended breeding period with several releases might increase the chance of some settlement success, particularly towards the limits of a species' range. Since, in the 'north', early settlements have a disproportionately better chance of survival, the breeding cycles here have apparently adapted to produce gametes as fast as possible, by starting next season's gametogenesis before the end of the current season.

Spawning of *P. vulgata* in response to a sea-temperature drop to below the critical 12 °C, whatever the physiological mechanism involved, tends to synchronise local spawning and ensures that the young limpets experience optimal sea temperatures at least while in the plankton. In NE. England, especially during warm summers, such a temperature drop is usually produced only by the strong NW gales which follow in the wake of a deep depression passing over the British Isles. Such storms, which also appear to have been responsible for some *aspera* releases, tend to affect a wide area, and are likely therefore to cause widespread spawning, probably explaining supra-regional patterns of recruitment success, particularly in the north. It is uncertain whether a higher critical temperature is involved in the extreme south of *vulgata*'s continental range, where the winter sea temperature rarely drops below 12 °C. Conversely, it is not clear what triggers spawning in the extreme north if the summer sea temperature does not exceed 12 °C, though very recent data suggest that in such a situation spawning (and rates of gonad development) are unusually asynchronous in different habitats across the shore (for *vulgata* and *aspera*).

The asynchrony of spawning found at adjacent exposed and sheltered shores (in *vulgata*) or at different shore levels (in *aspera*) also increases the spread of the potential settlement period, which may be advantageous in years (or localities) when conditions curtail the period of gonad development in some habitats. Though the evidence indicates that *vulgata* populations tend to spawn first, and early settlements survive better, on exposed shores, it is uncertain whether early or late settlements are more likely to contribute most to sheltered-shore recruitment, where the spat will encounter less wave action but more extreme temperature variation (in summer and winter). Conceivably, the low *vulgata* recruitment/density on sheltered shores, and the absence of *aspera* even if littoral coralline pools are present, indicates that conditions in shelter are much less favourable for settlement or survival of spat of either species.

As the shore is not a uniform environment, the time when conditions favour spat survival must vary with habitat as well as seasonally. For example, a temperature 'window' requiring moderately-warm sea and equable shore temperatures would be more likely to occur in the lower-littoral and in shaded mid-littoral pools in summer; in autumn, if sea temperatures were only marginally warm enough, spat might be able to grow fast enough to survive only in pools whose temperatures were boosted during low-water by solar heating. The littoral distribution of a species over its geographical range would therefore be set by the tolerance range of its spat and the ability of its adults to migrate from the main recruitment areas. This would explain why limpets in the south become progressively restricted to the low-littoral of exposed shores (eg. *vulgata* in Portugal, *aspera* in the Mediterranean), but in the north occupy progressively higher shore levels (eg. *aspera* in NE. England and northern Scotland). Geographical limits of a species' range would then be reached when a temperature 'window' was not available somewhere on the shore with sufficient frequency for recruitment to maintain a population. As limpets seem to have a remarkable ability to adjust their breeding period to cope with the seasonal vagaries of a littoral environment, the onus for setting their geographical limits is thus shifted from breeding failure to spat survival.

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Aspects of the ecology of *Patella* spp. on the Portuguese coast

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Keywords: gastropods, *Patella* spp., ecology, breeding cycles, longevity

Abstract

Three species of the genus *Patella* were studied on the Portuguese coast as a specific contribution to the COST 647 programme. With little prior information existing, this paper presents new basic data on the geographical distribution, relative abundance, habitats, size-structure of populations, and reproductive cycles of *P. depressa* Pennant, 1777, *P. aspera* Roding, 1798, and *P. vulgata* L. 1758. Comparisons with N.W. Europe provide evidence of distinct latitudinal trends in the population dynamics and reproductive biology of these species.

Introduction

Limpets play a fundamental ecological role in controlling the quantity of algae on the shore. As grazers, they destroy large quantities of algae, mainly at the early sporeling stages (Lewis, 1964). They are widely distributed around the coasts of western Europe and the British Isles, variously inhabiting moderately-sheltered to fully-exposed shores, making them ideal candidates for inclusion in the rocky-littoral studies of the COST 647 programme.

In Portugal, limpets are abundant over all the intertidal rocky shore. Together with mussels and trochids, they form part of the staple diet of the poorer populace, especially in the north. Apart from Nobre's work on Molluscs (1931, 1938–40), there were no general studies on limpets in Portugal, and no information on population dynamics. In 1981, the Instituto Nacional de Investigação das Pescas started to collaborate with COST 647 by studying the three limpet species already under investigation by the rocky-shore group in England, i.e. *Patella depressa* Pennant, 1777, *P. aspera* Roding, 1798, and *P. vulgata* L. This paper presents some aspects of the ecology of these species.

Geographical distribution and habitat

The distribution of the three species on the Portuguese coast is shown in Fig. 1.

P. depressa

This species extends from N. Africa to S.W. England and Wales (Fretter & Graham, 1976). In Portugal it replaces *P. vulgata* as the dominant intertidal limpet on exposed and sheltered shores, occurring at all shore levels, on horizontal and vertical surfaces, and in pools lined with *Lithophyllum incrustans* (where it usually co-exists with *P. aspera*).

In the upper shore the shells are usually steeply-conical, and very thick, whereas at lower levels they are polygonal, very flattened, and thin. Shell length also varies according to shore level, thus at high levels, particularly those with dense *Chthamalus* cover, the maximum length is 25 mm, but at low levels it reaches 30–35 mm. On very exposed shores the shells of limpets on verticals are frequently almost completely eroded.

Juveniles are found mainly at low levels and always in damp situations e.g. in small pools or cracks, around the edges of mussel patches, on *Mytilus* or on wet, bare rock.