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Latitudinal trends in reproduction, recruitment and population characteristics of some rocky littoral molluscs and cirripedes

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Abstract

This paper reviews progress in the COST 647 rocky littoral programme involving three patellids, two trochids and two cirripedes on European Atlantic coasts. Northern geographical limits are set primarily by repopulation failure, and northern populations are characterised by short, mid-summer breeding periods, high frequency of failed or poor recruitments and low density of large, long-lived individuals. Towards the south molluscan breeding periods lengthen and become later, extending in some cases throughout much of the year but with least or no activity in mid-summer. There are probably fewer recruitment failures and thus higher densities, but individuals are of smaller maximum size and shorter life-span.

The cirripedes show similar latitudinal trends in recruitment timing but *Semibalanus* is restricted to a single annual brood throughout its range.

The two species reaching their southern limits show progressive restriction to the lowest tidal levels.

Recruitment failures do not result from inadequate gonad activity. They arise in cirripedes during the planktonic phase and in the molluscs during settlement and early shore life. The temperature sensitivity of molluscan spat is primarily responsible for the north/south gradient in recruitment times from summer towards winter.

Introduction

A principal objective of COST 647 is distinction between the many biological changes which have local physical and/or biological causes and those which are attributable directly or indirectly to broad-scale agencies such as climatic and/or hydrographic anomalies or trends. To achieve this distinction necessitates appropriately broad-scale, and ideally international, data which in turn inevitably lead towards considerations of a) geographical distribution and its control, and b) the possible extents to which population parameters change along the gradients from one geographical limit to the other. These gradients are seldom smooth, being disrupted by local coastal configuration and hydrography, but essentially they are latitudinal and reflect the broad climatic changes between tropical and polar

regions. Hence in the region of COST 647 studies, i.e. west and north-west Europe, we are dealing primarily with north (cooler)/south(warmer) gradients.

Accepting the basic role of recruitment in population dynamics and the probably high sensitivity of repopulation processes to climatic fluctuations, the rocky littoral programme of COST 647 has concentrated upon annual recruitment in a few species. These were selected on account of their known ecological significance and/or because their geographical distribution afforded high potential for the investigation of climatic influences (Table 1). The accessibility of this habitat permits mobile investigators to obtain broad-scale data more easily than in other habitats, but nevertheless poor national participation in the programme has restricted international comparisons to data primarily

Table 1. Species in the COST 647 rocky littoral programme and their geographical limits occurring within the study area.

	Southern limit	Northern limit
<i>Patella vulgata</i> L.	N. Portugal	N. Norway
<i>Patella aspera</i> Röding	-	S.W. Norway
<i>Patella depressa</i> Pennant*	-	Wales
<i>Monodonta lineata</i> (da Costa)*	-	N. Ireland
		Wales
<i>Gibbula umbilicalis</i> (da Costa)*	-	N. Scotland
<i>Chthamalus montagui</i> Southward*	-	N. Scotland
<i>Semibalanus balanoides</i> (L.)	Biscay	-
	N.W. Spain	

Species marked * have additional northern limits variously along the French and British coasts of the English Channel. The last four species will henceforth be referred to by the generic name only.

from Britain, Portugal and, more recently, Spain.

Some latitudinal trends have been discussed previously (Lewis *et al.*, 1982) and the present purpose is to extend earlier data and review progress so far.

Geographical limits

If geographical limits are to provide reliable insights into the role of latitudinal factors, one must question the extent to which these limits are set by the large-scale intervention of non-latitudinal factors such as unsuitable substrata or salinity, decreased habitat area or larval wastage by offshore currents. Such conditions have long been thought to contribute substantially to the loss of several species in our programme (and in effect to the setting of 'north-eastern limits') as one moves eastwards along the Channel coast of Britain: namely *Gibbula*, *Monodonta*, *Chthamalus*, *Patella depressa* (Crisp & Southward, 1958; Lewis 1964).

The other northern limits (see maps in Lewis, 1964) which occur on the more physically complex western coasts of the British Isles, appear to involve both latitudinal and local factors. Thus in the case of *Gibbula*, dying out on the north coast of Scotland (for details see Lewis *et al.*, 1982), a relative scarcity of suitable sheltered habitats on these mainly exposed and steep coasts might be contributing to a decrease in overall abundance and therefore to fewer planktonic larvae, which in turn would fail to find the suitable shores. By contrast, *Chthamalus*, which also reaches its limits around

northern Scotland, thrives on open coasts yet still declines to extreme scarcity and ultimate extinction in upper shore sites which seem physically suitable and lack both competitors and predators.

Further south, *Monodonta* fails to bridge the 15–25 km gaps from Northern Ireland to south-west Scotland, presumably because of the strength of tidal currents running parallel to the coast. The other northern limit of *Monodonta* in Britain (N. Wales) roughly coincides with that of *P. depressa*, and here offshore currents coming after intermittent stretches of unsuitable shoreline possibly form the final and unsurmountable barrier for both species.

But away from the geographical limits such non-latitudinal factors seem to be less potent; areas of unsuitable habitat cause gaps in distribution but do not set limits. Individuals become more abundant southwards and situations are occupied that would remain empty further north. It appears, therefore, that where a species is abundant there are sufficient larvae to bridge unsuitable stretches of coastline, but where densities are declining or larvae are regularly scarce for any other reason, the presence of adverse currents or unsuitable habitats may then present unsurmountable barriers to species that are already under pressure. What then are the pressures which have a latitudinal component, and at what stage do they operate? Are population densities reduced and limits finally set by biological factors that increase northwards but which, being biological, must vary in intensity with time and lead to fluctuating limits? Or are there occasional catastrophic mortalities which cut back the range and

are then followed by progressive re-occupation of lost ground? Conversely are there less obvious factors which lead directly to an inadequate repopulation rate?

Competition for space is very evident between the lusitanian *Chthamalus* spp and the boreal *Semibalanus*, and their fluctuations have long been linked with broadscale climatic oscillations which favour them alternately (Southward & Crisp, 1954; Southward, 1967). But while *Chthamalus* is usually the poorer competitor in the north its greater vertical range on the shore gives it a high level refuge from *Semibalanus* (and predators) over west and north Scotland. Within these 'safe' levels *Chthamalus* still declines for other reasons. While the barnacles replace each other to north or south, this is not the case with the molluscs. All five species co-exist in northern Portugal, but from south-west Britain northwards one loses first *P. depressa* and *Monodonta*, then *Gibbula*, and finally *P. aspera* until *P. vulgata* alone occurs in west and north Norway. The mid/upper shore trochid microhabitats remain vacant, *P. vulgata* (and possibly *Littorina* spp?) expand into the *depressa* and *aspera* territory, but there are no obvious replacing competitors.

The other alternatives, catastrophic mortality or repopulation failures, have been discussed previously (Lewis *et al.*, 1982) and so I briefly reiterate here the main considerations leading to the conclusion that for our species northern limits are primarily set by repopulation failure. They are:

- Although severe mortalities occurred in coastal faunas around the British Isles in the winter of 1962/63 they did not affect *Chthamalus* anywhere, nor *Gibbula* at its northern limits (Crisp, 1984); and although *Monodonta* (and to a lesser extent *P. depressa*) did suffer some cut-backs in range there has been no repetition of such mortalities since that date (i.e. in 22 years).
- Experimental transferences to North Sea coasts (i.e. outside their geographical range) of *Chthamalus* (Southward & Crisp, 1954) and of *Monodonta* and *Gibbula* (Williamson & Kendall in prep.) did not result in increased mortality, even though in 1978/79 the two topshells experienced the most severe North Sea winter since 1962/63.
- Mortality of *Chthamalus* around north Scotland averaged only 8% over 4 years.
- In all species, populations close to northern

limits have always contained, and sometimes been dominated by, old animals and have frequently lacked young age-classes for a time.

- A population of *Monodonta* about 80 km from its northern limit, and abundant in the mid-70's, died out by 1983 as more recent recruitments failed to offset the deaths of the '75 and '76 year-classes.

Accepting therefore that repopulation failures appear most likely to set geographical limits to the north, it is most unlikely that the conditions causing failure will be restricted to those limits. Rather they can be expected to occur over varying extents of the adjacent coastline and therefore to affect repopulation well inside a species' range. Geographical-scale data amply confirm that this is so. Fluctuations inside the range are usually synchronous, but less severe, reflections of events at the northern limit. This is shown most strikingly by *Gibbula* (Kendall & Lewis this volume; Lewis *et al.*, 1972), with synchronous patterns of success or failure covering sites up to 700 km from the northern limit. Although it has been suggested above that the north-east limit of this species on the Channel coast is probably set more by local rather than latitudinal factors, the poorest years here (1978, 1981 inputs) nevertheless coincided with the broadscale recruitment failures elsewhere.

The failures in *Chthamalus* around north and north-west Scotland have been more limited spatially (< 150 km) but of greater frequency, some areas having significant recruitment since 1970 only in 1975 and 1983.

As has been shown by Bowman & Lewis (this volume) populations of *P. aspera* at latitudes, in Britain, near to the northern limit in south-west Norway lacked the 1968 class over virtually the northern two-thirds of the British Isles; while in *P. vulgata* poor recruitment in northern parts of Britain coincided with apparent failure years 2000 km further north at the geographical limit in northern Norway. While this species, in Britain, has not experienced such frequent or widespread failure as the other species it still shows considerable fluctuations that are synchronous over much of northern Britain.

But it is also evident that the controlling factors do not act in smooth north/south gradients of intensity on all occasions. *P. vulgata* and *P. aspera* both show regional asynchrony, with northern

areas occasionally being more successful than some further south (e.g. 1977 and 1978, Bowman & Lewis this volume), and *Semibalanus* has shown much local asynchrony within the same region (Kendall *et al.*, 1982).

Despite such irregularities it remains apparent that general declines in abundance northwards primarily reflect an increasingly inadequate rate of repopulation which finally culminates in the setting of the limit of distribution.

Sources of repopulation fluctuations

The successful establishment of an 'O' class in the adult habitat is the end of a long series of consecutive processes or phases, and while overall success doubtless requires that each should be successful, there is increasing evidence that some are more sensitive than others to environmental factors.

Initial expectation of frequently inadequate gonad development at or near the northern limits has not been realised. Crips *et al.* (1981) similarly anticipated that summer temperatures around northern Scotland would seldom allow breeding in *Chthamalus montagui*, but there has been no year since 1970 in which nauplii have not been produced and released. Indeed, the previously mentioned transplants of *Chthamalus* and *Monodonta* to beyond their geographical limits still resulted in apparently normal gonad activity. Nor have levels of activity correlated with annual recruitment fluctuations in *Semibalanus*, naupliar production slowly increasing during a six year period in which annual metamorph numbers fluctuated strongly (Kendall *et al.*, 1985). In *Patella* spp gametic production and output are difficult to assess because releases often overlap with development. Nevertheless, and despite an initial belief of a positive link between gonad size and recruitment in *P. aspera* (see Bowman & Lewis this volume) we are now satisfied that factors other than total gametic output are of much greater importance in determining ultimate recruitment. Indeed, in some British limpet populations it now appears that the major releases of each year's gametes may contribute very little to the next season's 'O' class, this being derived frequently from the relatively few eggs released early in the season (Bowman, 1985).

The planktonic phase is one in which large and

annually varying mortalities of larvae can be envisaged (Thorson, 1950), but about which we have been unable to obtain much data. However, the possibility that whatever larvae exist may be driven towards or away from the shoreline by wind-induced currents or drift is more amenable to assessment, and there are several reports of high settlement densities in cirripedes when onshore winds occur (Barnes, 1956; Hawkins & Hartnoll, 1982; Kendall *et al.*, 1985). The generally higher recruitment rates on coastlines facing prevailing winds compared with coasts of different orientation is further circumstantial support (Kendall *et al.*, 1982). If this is correct for cirripedes it is also possible that larvae of the other species are similarly influenced, even though no evidence yet exists. On the other hand much will surely depend upon the duration of the planktonic phase, and cirripedes (4–6 weeks duration) would be more vulnerable than the molluscs (4–10 days). But since wind direction just before and during the settlement period is not only one of the least predictable of environmental factors but also lacks a latitudinal component, we must look elsewhere for a physical gradient that links with geographical distribution.

Settlement and early shore life expose spat/juveniles to new and potentially severe conditions, and our studies point increasingly to the critical sensitivity of these phases, especially in the molluscs. In a species at its northern limit or within the northern part of its range – as most of our species are in Britain – reproduction takes place in summer or early autumn, and the cause of failure is most likely to be temperatures too low for successful establishment. Where there is most information, as in *Patella* spp (Bowman, 1985; Bowman & Lewis, this volume), it is now clear that the strength of the future 'O' class (first recognisable in the field as 1–2 mm spat) depends not on the total numbers of veligers settling on the shore in late summer or autumn but on the numbers which chance to meet sea/air temperatures within the limited range that is suitable initially for metamorphosis, and thereafter for fast growth and attainment of a size sufficient to withstand the coming winter. *P. vulgata* spat from north-east England fail to metamorphose at pool temperatures of 17 °C and above, and growth is best between 10–14 °C, ceasing completely in the field at 6 °C.

Settling veligers of 0.25 mm length and

metamorphosed spat can be studied only by using settlement panels that can be examined microscopically and returned to the field. Such direct observation and experimentation have not yet been possible with trochid larvae, but there are indirect pointers to a similar sensitivity to cold, for the two smallest 'O' classes in eight years have coincided with below-average temperatures during their initial autumn and winter (1978/79, 1981/82, Kendall & Lewis, this volume).

Whereas the molluscan larvae settle (survive?) best in microhabitats protected from desiccation and temperature extremes, cyprids attach to open rock and would appear to be highly vulnerable to aerial conditions. We have not observed *Chthamalus* settlement as it happens and can only report that in the many failure years around northern Scotland nauplii were released each August but no, or few, juveniles could be found next spring. *Semibalanus*, a boreo-arctic species, settles in the spring and there is much heat death of cyprids and new metamorphs, especially in the upper shore (Foster, 1970; Wethey, 1985), but during four years of observation in north-east England the annual variation in initial mortality showed no correlation with metamorph maxima (Kendall *et al.*, 1985). Nevertheless when *Semibalanus* and *Chthamalus* occur together and compete for space, as in north-west Scotland, such heat deaths of *Semibalanus* spat (and adults) in 1975 and 1976 made it possible for the high-level *Chthamalus* to become established lower down the shore (Bowman, in prep.). The fact that *Semibalanus* spat are immediate and fast-growing occupiers of rock surface also influences 'recruitment' data in a manner that does not appear to arise among the molluscs. If circumstances lead to a highly synchronous settlement a high density results, whereas with an extended settling period the growth of the earliest spat reduces the space available for late-comers. And since spat occupy the same habitat as adults, another contrast with *Patella* and the trochids, a high adult density may oblige spat to settle in misleadingly large numbers in the restricted areas of vacant space – including those cleared experimentally! (Kendall *et al.*, 1985).

Latitudinal trends in the molluscs: settlement times

The detailed settlement/survival studies on *Patella* spat have so far only taken place in Britain and are still far from complete there, but the sensitivity of the settlers has considerable latitudinal implications. At their extreme northern limits seasonally reproducing species can be expected on theoretical grounds (Hutchins, 1947) to breed during the summer (i.e. maximum sea temperatures), and if gametes are being produced each year at these limits (as they are in our case) the repopulation failures must be arising during a later phase in the autumn and winter. Admitting our ignorance of planktonic events and dealing only with the spat and juveniles, widespread failure will arise when settlement is too late and/or autumn temperatures are too low too early for the growth needed to withstand the coming winter. It will therefore be advantageous to mature and release some eggs early in the summer; and this will remain so moving towards the south wherever the late autumn and winter temperatures can fall low enough to have strong adverse effects.

But to continue spawning in the mid-summer further to the south exposes the sensitive young to the opposite danger of high temperatures, avoidance of which can come only from later settlement. Ultimately at the extreme southern limits temperatures could be damagingly high for settlers over much of the year, and successful recruitment would therefore have to be accomplished astride mid-winter.

Stages in such a north/south switch are clearly discernible in the settling times of British limpets. In north-east Britain the most successful settlements have generally been relatively early in their respective seasons, i.e. July/August in *P. aspera* which is close to its northern limit, and September in *P. vulgata* which is nearing the middle of its range. The spat of both species can first be found in south-west Britain about two months later than in the north-east, and they overwinter in the south-west at smaller sizes as a result.

Patella spp settlement data from Oviedo, North Spain (M. P. Miyares pers commun.) and Portugal (Guerra & Gaudencio, this volume) cover only 2–3 years as yet, and being derived solely from size-frequency analyses without detail of early growth rates they indicate settlement times much less pre-

cisely than when settlement plates can be used. Nevertheless, they suggest successful settlement of *P. vulgata* (at its southern limit in Portugal) taking place some time between late October and January, with greatest success towards the end of this period, i.e. up to about two months later than in south-west England. In the other two *Patella* species, not at their southern limits, the situation is more confused, for there are probably several settlements per season, especially in *P. depressa*. Nevertheless, the most discrete emergence of 2–4 mm *P. aspera* spat from cracks, mussel patches etc began in March 1983 and February 1984, suggesting major settlements between October and January. *P. depressa* less than 5 mm are present throughout the year (slow growth or frequent settlement?) but their numbers are highest from January to March, indicating maximum settlement success in the autumn.

For the trochids we are not yet able to record later settlement moving south in Britain, comparable to that in *Patella*. However, preliminary data from northern Spain (Bode *et al.*, this volume) and Portugal (Gaudencio & Guerra, this volume), and again based solely on size-frequency analyses,

point to first settlements of *Gibbula* and *Monodonta* occurring from September–November in Spain, and of *Gibbula* about November in Portugal. These compare with August and early September for *Monodonta* and *Gibbula* respectively in Britain (Wales).

Although it would be helpful to have data from North Africa and the Mediterranean, where *P. depressa*, *P. aspera* and the two trochids reach their southern limits, it is clear that all five molluscs in our programme are functioning as predicted, the most successful settlements becoming progressively later in the year towards the south, apparently in response to the needs of the spat.

Latitudinal trends in the molluscs: gonad cycles

The changes in settling times are accompanied by changes in gonad cycles, but these do not fully conform to expectation based solely upon the times of successful settlement. The commonest pattern is for gametogenesis and spawning at or near northern limits to be completed in 3–4 months astride the summer (in *P. aspera*, *Gibbula*, *Monodonta* in

Britain; *P. vulgata* in northern Norway). *P. depressa* differs somewhat in that the potential for multiple spawnings and redevelopment is much stronger in this than in the other two limpets, and gonad activity may last from May/June to October/November, with little predictability in the time(s) of spawning.

Moving south there is a common tendency for extension of the breeding season into winter or spring, with or without a change in the onset of gametogenesis (Fig. 1). Marked differences exist between species, however. Thus whereas the breeding season in *P. vulgata* in northern Spain and in Portugal extends from about August to March/April and still leaves a discrete inactive period from April/May to July, *P. aspera* is reproductively active for most of the year and its resting period, not always well defined, is confined to June or July. Erratically fluctuating gonad indices characterise *P. depressa* and suggest frequent spawnings and near-continuous development throughout the year with, however, some years showing least or no activity in June/July. This tendency for mid-summer to be the least active period is shown most strongly in both *P. depressa* and *P. aspera* in the southernmost samples available (south Portugal), perhaps foreshadowing a contraction of breeding towards winter only further south. Whether or not this does occur, the almost year-round breeding in Portugal in the middle of the range contrasts strongly with the latitudinal pattern in *P. vulgata*, in which the breeding period just lengthens steadily from north to south.

Monodonta and *Gibbula* similarly show a lengthening of the breeding period, so that although animals in spawning condition first appear at about the same time as in Britain (i.e. July/August) they remain abundant until November/December in northern Spain and October/November in Portugal. Some loss of synchrony is also apparent, especially in *Gibbula*, with ripe individuals occurring both much earlier and later than the main period.

The above brief summaries are based on data from P. M. Miyares (pers. commun.), Bowman (1985), Garwood & Kendall (1985) and from papers in this volume by Bode *et al.*, Bowman & Lewis, Gaudencia & Guerra, Guerra & Gaudencio, Ibañez *et al.*, Kendall & Lewis.

Extension of the period of gonad activity overall

or of the period of 'ripeness' does not necessarily mean that spawning is taking place over an equally extended time, either continuously or in short bursts. Spawning which occurs as synchronously as it does in *Patella* spp (Bowman, 1985) or *Gibbula* (Kendall, pers. commun.) requires an environmental trigger, and until it is received ripe *Patella* eggs are stored, other eggs complete their maturation and gonads continue to increase in size. Adaptational logic decrees that spawning should be timed for settlers to meet the optimum conditions, as in the settlement-timing hypothesis of Todd & Doyle (1981); hence it too should be triggered by an environmental stimulus which arrives later towards the south. Spawning stimuli have proved to be very difficult to identify; they are still not known for the trochids and only imperfectly so for *P. aspera* (Bowman & Lewis, this volume), but for *P. vulgata* in Britain there is now overwhelming evidence that it is (or is accompanied by) a fall in sea temperature to below 12°C. This occurs as a result of the normal autumnal decline or when early gales and swells break the thermoclines and bring colder bottom water to the surface for a time. As sea temperature maxima are higher in the south than the north, falls to below 12°C (for whatever reason) tend to be progressively later towards the south, and thus account for the broadly north/south pattern of first spawnings around Britain (Bowman, 1985). A further illustration of the same phenomenon which also indicates the geographical scales that may be involved was the major North Atlantic storm of mid-August, 1982, which caused sea temperatures to fall by up to 3°C as far south as northern Portugal, but only brought them below the critical 12°C, and caused early spawning, in northern Britain.

Since climatic events do not follow orderly sequences there can be no certainty that the spawning trigger will necessarily be followed at the appropriate time by the optimum or even acceptable conditions for the settlers. Hence the more spawnings per season the better, as this increases the possibility of a good match. To some extent this is a matter of chance – the frequency and severity of storms in any region in any year. But there must also be gametes available for release and here a strong latitudinal difference is probable. In the north, with a short breeding season, one- or at most two-spawnings per season are possible, and these are not always successful; this is especially so for the

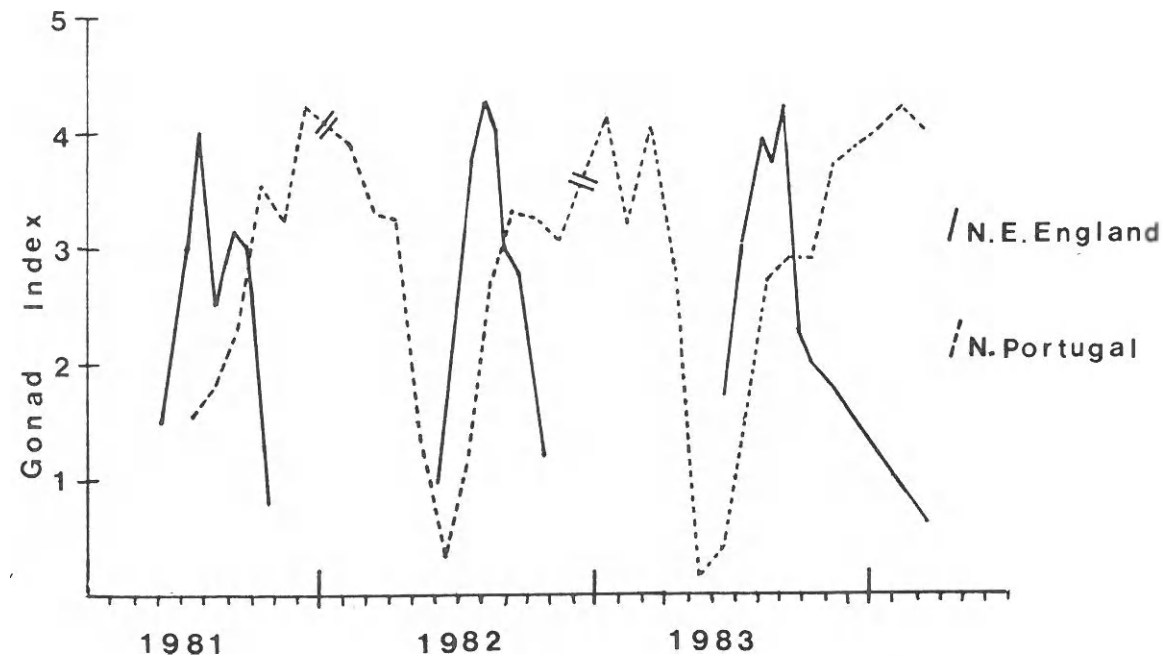


Fig. 1. *Patella aspera*: changes in time and duration of the gonad cycle from near its northern geographical limits to the centre of its range in Portugal.

second one (Bowman, 1985). Where gonads are active longer, in the south or centre of distribution, a succession of storm-induced spawnings and further ripenings could occur (as in *P. depressa* in Spain and Portugal?). Those spawnings which are too close to the summer may fail (in spite of probable selection for larvae and spat with higher temperature tolerances) but others will surely succeed so that the chances of regularly poor recruitment would still appear to be much less than in the north.

When the sensitivity of the settling and juvenile phases first became apparent it seemed likely that recruitment failures could occur throughout a species' range, and not just near the geographical (in this case, northern) limits. This now seems less likely. Nevertheless, fluctuations clearly occur in Portugal but many years' data are required to judge how the frequency and severity of poor years there compare with the north. Meanwhile in *P. vulgata* there have been exceptionally poor years as much as 2000 km from the northern limit, whereas in *Gibbula* the frequency of failure has decreased dramatically within the 6–700 km from northern Scotland to south-west England (Kendall & Lewis, this volume).

Latitudinal trends in cirripede breeding

Both *Semibalanus* and *Chthamalus* show similarities to the molluscan species in conforming to the expected latitudinal patterns of settlement time. Thus *Semibalanus* settles late February/early March at its southern limit and in mid-summer in the Arctic (Feyling-Hansen, 1953), while *Chthamalus*, breeding in the Mediterranean from February to April (Crisp *et al.*, 1981), settles at its northern limit in Scotland about September. However the similarities now cease, for whereas the sequence in *Patella* spp involves settlement becoming progressively later in the autumn from north to south, the cirripede sequence becomes earlier in the spring. There are sound reasons for such differences.

Semibalanus, a boreo-arctic species, is much more constrained by having a single brood per year. Gamete production occurs in summer and autumn, copulation is cued by photoperiod, while embryo development rates during winter and release mechanisms are adapted to releasing nauplii when

highly seasonal planktonic food is likely to be most abundant in different latitudes (Crisp, 1959; Barnes & Barnes, 1976). Annual recruitment fluctuations appear to be much less sensitive than in *Patella* to direct temperature effects and to arise primarily from mismatches (probably nutritional and/or dispersal) during the planktonic phase (Kendall *et al.*, 1985).

Chthamalus, by contrast, is a warm-temperate species with an opportunistic strategy in which production of successive small broods is both temperature- and food-dependent (Hines, 1978). Northward these conditions become adequate progressively later in the spring and early summer, until at the northern limits around Scotland probably only one brood is possible each year, and this succeeds only in especially warm summers e.g. 1975 and 1983. Since nauplii are released every year the final failure lies in the planktonic or settling phase, but the proximal cause may still be reproductive if gonad and embryo development of a single brood are too slow in cold summers to release larvae sufficiently early for completion of the later phases.

Latitudinal trends in population characteristics

Latitudinal comparisons of life span, size and abundance among near-sedentary animals need caution, not only because many local habitat factors operate with possibly greater effect, but also because of the interactions of these three parameters. Nevertheless it is clear that maximum life-spans decrease from north to south, a feature that has been noted before (Dehnel, 1955; Frank, 1975). This is most strongly shown by our trochids, *Gibbula* ranging from 8–12 years in northern Scotland to about 2 years in Portugal, and *Monodonta* from 10–15 years to 4–5 in Spain (see Lewis *et al.*, 1982 and Gaudencio & Guerra, this volume for further details and references). Current limpet data from Portugal (Guerra & Gaudencio, this volume) possibly do not cover the full range of local habitats, so perhaps longer life-spans occur; but they do suggest that all three species live for only 3–4 years, which is variously about 1–4 years less than in similar habitats in Britain. Barnacle life-spans are so often cut short by predation or competition that comparisons can be especially confusing. We therefore simply place on record that upper

shore mortality of *Chthamalus* in northern Scotland (8% in four years), plus other Scottish age/growth/size observations (Lewis, unpublished) suggest that life-spans up to 20 years may not be uncommon in the north. This appears to be the maximum recorded or estimated.

Limpet sizes similarly appear to be smaller in northern Spain and Portugal than in Britain, maximum lengths being up to 5–10 mm less in the fastest growth habitats. *Gibbula* perhaps provides the most interesting data, for while there is an overall decline of maximum base diameter from 20–21 mm at the extreme northern limit to 13–14 mm in Portugal, populations with similar small maxima occur locally throughout Britain and Ireland, apparently as a result of high density and intraspecific competition (Kendall & Lewis, this volume). But it has also been shown in Britain that in broadly similar habitats the density virtually doubles from north to south, and is accompanied by a size reduction from 20–21 mm to 15–17 mm maxima.

We have also seen that settlement failure in *Gibbula* in Britain decreases from north to south, and this could well be the reason for the higher density. Further south still, the potential for more regularly high levels of recruitment increases with the lengthening period of gonad activity; and densities in Portugal are 2–4 times greater than in Britain so that still greater intraspecific competition and smaller maximum sizes could result. While firm evidence of regularly higher recruitment there may still be lacking, we are obliged to accept it does occur; otherwise with a maximum life-span of about 2 years Portuguese populations would be in considerable danger of local extinction.

Thus we have hypotheses that may account for most of the north/south trends. In the north a short breeding period leads to frequent recruitment failures, low density, low intraspecific competition and large maximum sizes. To the south the longer breeding season tends to ensure more regular recruitment, leading to higher densities and small maximum size. But the other major difference, the greater life-span in the north (which almost certainly contributes to the greater sizes there), appears to be less directly related to latitude, for it follows gradients in density which are local as well as latitudinal. The mechanism linking longevity and density remains unresolved.

For the limpets there are less firm data on latitudinal population trends, and indeed the dependence of growth, size and life-span upon local habitat factors (Lewis & Bowman, 1975) suggests that demonstration of latitudinal trends comparable to those in *Gibbula* could be more difficult. But cautious comparisons do point to Portuguese limpets probably being more numerous and smaller than in Britain, and this accords with expectations based on the undoubted latitudinal changes in gonad cycles and settlement times.

Zonation and latitude

While southern limits could be set by excessive heat damaging either settlers or gonad activity per se, the only two southern limits among our species, *P. vulgata* and *Semibalanus*, experience no bar to reproduction in the south (Barnes & Barnes, 1972; Guerra & Gaudencio, this volume). They do show, however, that an additional aspect, the 'zonational environment' in the littoral zone, has also to be considered.

All littoral species are limited upshore by aerial conditions. Sometimes low temperatures are harmful but most are limited by intolerance of heat, desiccation or strong light, and it is commonplace to find upper limits lower down the shore in sunny, quick-drying situations, either locally or geographically. It is therefore no surprise to find that *P. vulgata* at its southern limits in northern Portugal is confined to shaded low-level positions. Even in north-east Britain spat are sensitive to heat and desiccation, and remain in damp micro-habitats for many months in the upper shore (Lewis & Bowman, 1975). In south-west England, Ballantine (1961) reported that 1½–2 years elapsed before small animals moved onto open rock surfaces in the upper levels. There is no specific information about the shore levels within which *P. vulgata* settles and survives in Portugal, but it is logical to assume that the low levels are the best (only?) places for spat to establish in winter, and for all-sized animals to survive in summer.

Semibalanus, in its isolated and fluctuating southernmost populations in south-west France and north-west Spain (Barnes & Barnes, 1966, 1972) and also further north in Brittany, south-west Britain and southern Ireland, is similarly most

abundant in shaded or lower shore positions. Although our north-east England studies (Kendall *et al.*, 1985) showed no correlation between heat death of spat and annual repopulation maxima we did record significant heat deaths of adults as well as spat in north-west Scotland in some years. The potential for such deaths must increase towards the south and restrict *Semibalanus* to lower levels. Thus in both species their littoral habitat is being compressed to extinction southwards, and as they vacate the scene their roles, physically and ecologically, are taken over by *P. depressa* and *Chthamalus* spp, processes that perhaps illustrate a common pattern in other boreal species.

For *P. vulgata* the progressive decrease in total population stocks and gametic output southwards must offset to some degree whatever increase in recruitment levels or regularity might result from the longer breeding period, with its potential for more settlements per season (see above); but the resultant between these opposing forces remains unknown. In *Semibalanus*, however, with its single brood, maximum settlement densities in south-west England are well below those further north where the species occupies much of the littoral zone (Kendall *et al.*, 1985).

Littoral gradients may also impinge upon mollusc recruitment more directly. Pools and other damp situations in which *Patella* spat can only survive in mid- and upper-shore levels respond much more quickly to insolation and air temperatures than do the sea or low-level pools. Thus early settlers may fail in the upper shore because pool temperatures become too high by day, whereas late settlers may find low-level pools and sea temperatures too cold and may then succeed, if at all, only in uppershore pools that warm up enough. Thus it is even possible that towards its northern limits *P. aspera*, usually regarded as a lower-shore species extending upshore northwards only as summer temperatures and desiccation decline, is becoming more dependent upon mid-shore pool recruitment than that on open rock at lowest shore levels (Bowman, pers. commun.).

Conclusion

No one species in our programme has been studied in adequate detail throughout its range for a

long enough period. Nevertheless the total amount of information about different species in different regions builds up to suggest features that may prove to be broadly similar in all our molluscan species, when future work fills present gaps and puts very local or short-term data into broader perspectives.

Thus northern populations are known to be characterised by short reproductive periods in the summer, frequent recruitment failures and individuals of large size and potentially long life-spans. Towards the south (note that Portugal is *not* the southern limit of four of our species) the partially confirmed expectations are for longer periods of (possibly) less synchronous gonad activity involving more or all of the winter period, a lower frequency of recruitment failures, and probably higher densities of individuals of smaller size and shorter life-span (when allowances are made for effects of very local factors). Despite the different pattern of gonad activity these same population trends apply also to *Chthamalus*.

Closer to the southern limit the most characteristic feature among the molluscs will probably be a marked decline in abundance as the habitable environment retreats downshore.

From the monitoring viewpoint it is important to note that population stability depends to the north on high longevity, which minimises the effects of recruitment failures. On the other hand, the occasional very good settlement may result in a sudden increase in numbers which then persist conspicuously for several years. To the south, continuity depends upon regular recruitment to offset the short life-spans, and densities will primarily reflect the scale of each input. Between these extremes (i.e. over much of a species' range) the various fluctuations in recruitment and mortality rates preclude any characteristic density patterns until a persistent trend develops. But it is important to note that 'northern'-type stability and 'southern'-type annual oscillations can occur in respectively the upper and lower levels of the same shore at the same time in species of wide vertical range, e.g. *P. vulgata* and *P. depressa*, or among topshells in which recruitment is confined to limited 'nursery areas'.

Prediction of recruitment, albeit in terms as broad as 'good', 'moderate' and 'poor' was, and remains, the objective. To an extent this may be done simply at extreme northern limits (e.g. *Chthamalus*, *Gibbula*, *Monodonta*) by the now known correla-

tion of warm summers with good recruitment (as in 1975, 1976, 1983) without knowing why. However, for *P. vulgata* and *P. aspera* (even though this is close to its northern limit) the confident prediction of 'failure', which in monitoring terms is the most significant natural event, has necessitated gaining a deep insight into all the phases involved together with accurate environmental data.

Even in Britain (for trochids and *P. depressa*), but more especially in south-west Europe for all species, there is need of precise data on spawning times, storms and sea temperatures; on speed and frequency of gonad re-ripening; on number and exact times of settlements per season and the fate of early or late settlers, together with experimental work on the temperature requirements and tolerances of spat and juveniles. Such data would resolve current uncertainties resulting from the longer breeding seasons which, because they encounter higher temperatures than in the north, suggest either higher values for spawning triggers and settler tolerances, or frequent larval and spat mismatches and wastage, or long retention of ripe gametes before spawning (or a combination of all three).

Finally, how do our current data and hypotheses accord with the generality of data on invertebrate reproduction? The latitudinal reversals of breeding times shown by our *Patella* spp have previously been reported extensively in temperate zone polychaetes by Bhaud (1972). They are also implicit in the different breeding times shown by species of different geographic affinity living in the same location, i.e. summer breeders being at their northern limits and vice-versa (in the northern hemisphere). Such examples are provided by ascidians (Millar, 1958), echinoderms (Falk-Petersen, 1982) and in Australasian mussels, a southern hemisphere observe (Wilson & Hodgkin, 1967).

The longer breeding period southwards appears to be an accepted principle of biogeography dating back to Orton (1920). When linked with earlier spawning to the south (or later northwards depending upon one's own position!) it shows the breeding pattern of a warm-water species in which the temperature and nutritional requirements of the gonad are the main determinants of the timing of the overall repopulating process. Such needs in such species are satisfied sooner and for longer in the south (Seed, 1976).

Clearly, similar needs exist in limpets and trochids, but their food supply is much less seasonally and regionally varying than in the bivalve plankton feeders which figure often in molluscan gonad studies. Hence the longer breeding of *Patella* spp, *Gibbula* and *Monodonta* in south-west Europe probably owes most to the warmer temperatures, even if these operate as much via increased grazing activity as upon metabolic processes. But whatever the environmental or endogenous conditions that initiate gametogenesis and control its duration in our molluscs, the significant point is that the increased duration southwards (or at least to the centres of their ranges) results primarily from extension *later*, i.e. through autumn into winter and the following spring. The accompanying move away from mid-summer breeding in the north finally, as in *P. vulgata*, brings repopulation firmly into the winter period.

A similar pattern of later breeding southwards in the scallop *Argopecten irradians* was attributed by Sastry (1970) to geographical differences in food availability and temperature, and Barker & Blake (1983) elaborated this in terms of energy available for reproduction from the balance of input and reserves relative to latitudinal changes in metabolic rate. Accepting the more critical nutritional requirements of bivalves, and that some workers find that these over-ride temperature or other latitudinal factors (Newell *et al.*, 1982), it is nevertheless particularly interesting in *Argopecten* to observe the latitudinal temperature regimes. Gonad initiation begins in Massachusetts at about 10°C (April), in North Carolina at 20°C, and in Florida about 28°C (July), but spawning temperatures are about 23°C in the north (July) and were induced at 25°C (October) in the south. These data indicate that the gonads function adequately over a very wide range of temperatures, whereas the larvae and settlers are meeting very similar conditions throughout the species range.

The existence of latitudinal (by implication temperature-controlled) gradients or reversals in breeding/recruitment times implies a narrow optimum range for some crucial phase, even accepting probable adaptation by local races. Although it is axiomatic that the entire process from gametogenesis initiation to establishment of the 'O' class has evolved to give the best chance of repopulation success under regionally varying conditions, the major

research emphasis by far is placed upon studies of gonad development and spawning, with the implication that later phases or events are of little significance. Yet the molluscs in this COST 647 programme point to a different conclusion. Various within this group we find northern limits set primarily by recruitment not gonad failure, breeding in animals transplanted beyond geographical limits, and recruitment fluctuations and even failures well inside distributional limits that show no correlation with gamete production. Such facts, reinforcing increasing information on the narrow temperature range within which spat are successful, point overwhelmingly to spat being the more sensitive phase and most in need of the latitudinal gradient in settling times. The seasonality of gametogenesis and the shorter duration northwards point clearly to strong temperature sensitivity in gonads, but within the overall reproductive/recruitment sequence the annual timing of gonad cycles appears to have become geared primarily to meeting the needs of spat.

Although the patterns of gonad development and spawning in *Modiolus modiolus* differ greatly from those in *Patella*, Brown (1964) concludes that here too, spawning and larval development operate within a narrower range of temperature regimes than gametogenesis. It seems probable that this will prove to be the case in many other species, provided that studies on 'reproduction' are extended to cover the later and possibly most critical phases within 'repopulation'.

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