J. mar. biol. Ass. U.K. (1991), **71**, 495-513
Printed in Great Britain


# FORTY YEARS OF CHANGES IN SPECIES COMPOSITION AND POPULATION DENSITY OF BARNACLES ON A ROCKY SHORE NEAR PLYMOUTH

A.J. SOUTHWARD

Leverhulme Unit, Marine Biological Association, The Laboratory, Citadel Hill, Plymouth, PL1 2PB

The abundance of the common intertidal barnacles, *Chthamalus montagui*, *Chthamalus stellatus*, *Semibalanus balanoides* and *Elminius modestus* has been monitored since 1951 at a site near Cellar Beach, River Yealm, south Devon. Counts are made at 12 levels on a transect between high tide and low tide. The two chthamalids are of warm-water distribution while *S. balanoides* is a boreo-arctic species; changes in the abundance of these species are linked to environmental temperature. Maximum fluctuations occur in the lowermost third of the intertidal zone. The proportion of *Chthamalus* adults is correlated with annual mean inshore sea temperature two years earlier, while the proportion of *S. balanoides* adults is negatively so correlated. This relationship accounts for over 40% of the variance. A smaller part of the variance (<20%) is explained by intensity of larval settlement, also related to climate. The fourth barnacle, *E. modestus*, is an Australasian immigrant that arrived in England during World War II and reached south Devon in 1948. It increased during the 1950s on the transect but has since stabilized at a low level of abundance that shows large interannual variations not directly related to temperature. Between 1951 and 1975, coinciding with a secular decline in sea temperature, there was a long-term trend towards reduction of *Chthamalus* and increase in *S. balanoides*; this trend has reversed since. Removal of the long-term trend reveals a short-term fluctuation of approximately 10-y frequency that correlates with a cycle in sea temperature two years earlier. These cycles are close to the 10-11 y solar (sunspot) cycle between 1951 and 1975. The biological data have since diverged from the solar cycle and now show less fit with annual mean sea temperature. Changing weather patterns and other effects of global climate shift may be involved.

## INTRODUCTION

In south-west Britain the typical intertidal barnacle zone is made up of four balanid cirripedes with membranous bases (Figure 1). Of these the commonest are *Chthamalus montagui* Southward and *Semibalanus balanoides* (L.), the other two, *Chthamalus stellatus* (Poli) and *Elminius modestus* Darwin, being less abundant (Bassindale, 1964; Newman & Ross, 1976; Southward, 1976; Crisp, Southward & Southward, 1981). Three other cirripedes can be encountered on the shore, but two of them, *Balanus crenatus* Bruguière and *Verruca stroemia* (O.F. Müller) are basically sublittoral forms that can exist in cryptic habitats at low tide; the other, *Balanus perforatus* Bruguière, occurs on open rock in the lower half of the intertidal zone, but is often sparse and contributes significantly to the barnacle zone only in specially favoured places (Fischer-Piette, 1933, 1936).

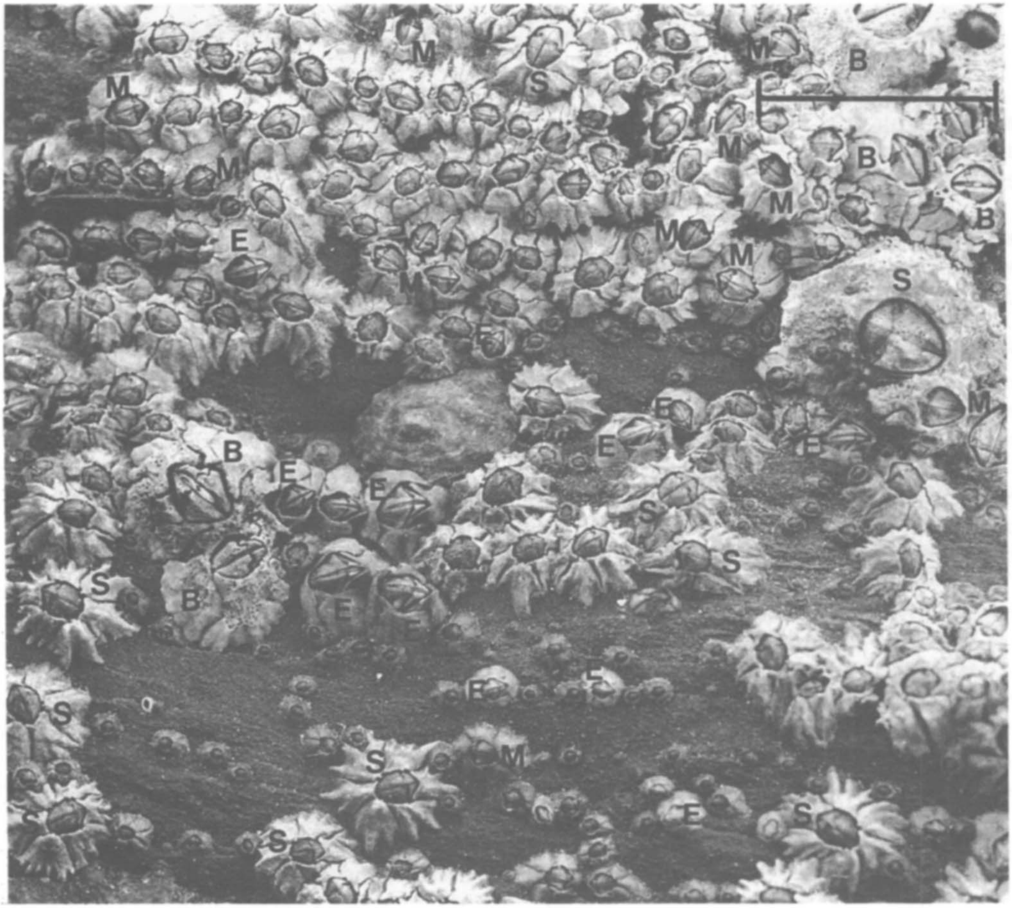

Figure 1. Field photograph illustrating the co-existence of all four common barnacle species on the transect near Cellar Beach. Taken 20 August 1989 in the low tide region, 2·2 m above chart datum. Scale bar 1 cm. Some of the barnacles are labelled to show the species: M, *Chthamalus montagui*; S, *Chthamalus stellatus*; B, *Semibalanus balanoides*; E, *Elminius modestus*; most of those not labelled are 1-and 2-y old *Chthamalus stellatus*, plus recently settled *Elminius*. A large and very old *C. stellatus* is present on the upper right-hand side. At the left and at the upper right are a few old *Semibalanus balanoides* surviving from the spring 1988 settlement. A small limpet, *Patella vulgata*, is in the centre of the picture.

*Chthamalus montagui* is the most abundant in Devon and Cornwall where it dominates the upper half of the barnacle zone (Southward, 1976; Dando *et al.*, 1979). Its relative, *C. stellatus*, possibly belonging to a different sub-genus (Dando & Southward, 1980), is found mostly in the lower half of the intertidal zone but can occur higher up the shore in wave-washed or otherwise wet or shaded places (Crisp *et al.*, 1981). These two chthamalids are both of warm-water distribution and reach their northern limits in the British Isles (*ibid.*). The second most common intertidal barnacle in south-west Britain, *S. balanoides*, is an arctic-boreal species that reaches its southern and western limits in Cornwall, Brittany and in the cold Galician rias of north-western Spain (Fischer-Piette & Prenant, 1956; Crisp *et al.*, 1981). *Semibalanus balanoides* is the major constituent of the intertidal barnacle zone away from the western and southern shores of the British Isles,

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occupying a restricted region between high water of neap tides (MHWN) and low water of neap tides (MLWN) (Lewis, 1964). The fourth common inhabitant of the intertidal barnacle zone, *E. modestus*, is an immigrant from Australasia that arrived in Europe during World War II and reached south Devon in 1948 (Bishop, 1947; Crisp, 1948; Crisp & Southward, 1959). *Elminius modestus* can occasionally survive higher in the intertidal than *S. balanoides*; it is usually commonest below MHWN, but differs from the other three in being able to colonize the sublittoral and in tolerating quite low salinities (Foster, 1970). *Elminius modestus* contributes substantially to the barnacle zone in estuarine and sheltered localities in south-east England, the Bristol Channel and the Irish Sea, but is not as common as the other three species on the open coast in south-west Britain.

Changes in the relative abundance of *C. montagui* and *S. balanoides* (reported as *C. stellatus* and *Balanus balanoides*) were detected in 1950-51, in comparison with surveys made in 1934 (Moore, 1936; Southward & Crisp, 1954) and further fluctuations were noted in later years (Southward & Crisp, 1956; Southward, 1967), when accumulating evidence indicated a climatic relationship. Crapp (1970) reported comparable fluctuations in relative abundance of barnacles and other intertidal animals during the 1960s in Milford Haven in south Wales, also linked to climatic factors. Regular monitoring of barnacle abundance was put into effect from 1953 as part of a long-term programme aimed at elucidating the factors responsible for such biological fluctuations. It was also hoped to provide an early-warning system, through observation of easily accessible short-lived organisms, of changes in other marine habitats, and in longer-lived species of economic importance. The barnacle survey was carried out in two components: a less detailed study over a wide area of south-west Britain each spring, and a more detailed study in the autumn of certain of the stations established by H.B. Moore (Moore, 1936). Originally four localities were examined in detail each autumn, eventually reduced to three. After Natural Environment Research Council funding for this project was stopped in 1987/88 only one station has been continued, as well as a little coastal monitoring elsewhere in south-west Britain. The station selected in 1988 for continuation is at the mouth of the River Yealm and is the site that had shown most fluctuation in the previous 37 years. This report includes observations from 1951 to 1990 and compares the fluctuations in species and abundance with changes in the environment. A later report will cover fluctuations in the barnacle populations of the whole south-west peninsula as detected by the wider-ranging survey made in the spring months.

## METHODS

The site is close to the mouth of the River Yealm, a small ria-type estuary near Plymouth where fresh water input is very small (Marine Biological Association, 1957). The fauna at the site is fully marine. The original transect of Moore (1936), at Misery Point, a little farther inside the Yealm, is difficult of access without a boat and the transect was moved 200 m to the west in 1955, closer to Cellar Beach, from which it is reached by a short scramble eastward (National Grid reference SX531477). The steeply sloping rocks, Dartmouth Slates of Devonian age, are on the south side of the ria and face north-north-west. Even in summer they receive minimal sunshine and for the rest of the year are

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shaded. The entrance to the Yealm is sheltered by Wembury reef and additional shelter is provided at low tide by a sand bar, so that the transect is exposed to wave action only at high tides in windy weather from the west.

Each autumn the barnacles are counted at approximately 0·5 m intervals along a line from a fixed rock spur at the upper limit of the barnacle zone, just above mean high water of spring tides (MHWS), down to the lower limit of the barnacle zone, just above mean low water of spring tides (MLWS). The levels have been related to revised Admiralty Chart Datum (CD) by measurement from the observed low tide, using tidal height predictions with corrections for angle of slope of the tape, and meteorological conditions (Admiralty Tide Tables, 1989). This has been checked several times.

Counts are made according to species size and abundance on grids with contiguous squares: spat (metamorphosed settled larvae) and very abundant juvenile and adult *Chthamalus montagui* are counted on 10 or 20 squares of 1 $cm^2$; less abundant *C. montagui*, *C. stellatus* and *Semibalanus balanoides* on 25 squares of 1 $cm^2$, or 2-4 squares of 25 $cm^2$; scarcer numbers of *C. stellatus*, adult *Elminius modestus* and *S. balanoides* on 5 squares of 100 $cm^2$; results are recorded as mean number $cm^{-2}$ for the barnacle-covered rocks. In previous publications (Southward, 1967; Southward *et al.*, 1975) use was made of a 'barnacle index' for comparison of the biological data with changes in climate. This index was simply the proportion of *Chthamalus* in the total population of barnacles; other indices have been prepared and are discussed later (see Table 7 and pp. 506, 508, 510). Spat of *Chthamalus*, less than 1 mm length, are separated from juveniles by eye; juveniles are separated from adults, when possible, by a subjective procedure based on experience. Spat of *Chthamalus* are found from August to October (Southward, 1976; Burrows, 1988), usually with a peak in September and can thus be assessed from autumn counts. However, settlement is very patchy and the records are converted to scores based on half-log groups of pooled abundance at several levels. No attempt has been made to separate spat, juveniles and adults of the rapidly growing species *E. modestus*, which settles predominantly in late summer and autumn. The settlement of *S. balanoides* occurs in April and counts made in the autumn show only those surviving the heavy mortality of juveniles in summer. Mortality of adults of *Chthamalus* and *S. balanoides* takes place mostly in winter and spring. At this site, as at many other places around Plymouth (Burrows, 1988) there is always free rock space for new settlement. Although there are patches of contiguous individuals and some crowding occurs (*cf.* Hui & Moyse, 1987) the rock is never coated 100% by barnacles and none of the four species shows hummock formation that occurs when settlement and survival exceed rock space available for adults (*cf.* Barnes & Powell, 1950).

Records have been made of macro-algal abundance, as local percentage cover of the rock, and some data are available on abundance of limpets (mostly *Patella vulgata* (L.)) and of the dog-whelk *Nucella lapillus* (L.), though not on an annual basis.

Sea temperature records noted are mostly taken from the results of two or three times weekly measurements in Plymouth Sound (Cooper, 1958; Southward, 1960), a series now the responsibility of Plymouth City Environmental Health Officer. Additional inshore temperature data for a few missing months were provided by measurements taken from

Table 1. *Abundance of total adult* Chthamalus *each autumn on the transect near Cellar Beach, River Yealm, as mean number cm*$^{-2}$ *at each of 12 levels. The levels are given as heights in metres above chart datum. The counts are of* Chthamalus stellatus *and* Chthamalus montagui *combined.*

| level | 5.40 | 5.04 | 4.68 | 4.32 | 3.97 | 3.62 | 3.27 | 2.91 | 2.55 | 2.20 | 1.70 | 1.20 | total | mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ↓HWS | | | ↓HWN | | | ↓MTL | | | ↓LWN | | | | |
| 1951 | 0.45 | 4.60 | (nd) | 4.12 | 7.76 | 3.00 | (nd) | 2.12 | 0.08 | 0.00 | (nd) | (nd) | 22.13 | 2.46 |
| 1952 | | | | | | | | | | | | | | |
| 1953 | 0.12 | 2.00 | 4.80 | (nd) | 6.00 | 1.60 | 1.60 | (nd) | 0.74 | 0.40 | (nd) | (nd) | 17.26 | 1.92 |
| 1954 | 0.24 | 1.60 | 8.00 | 6.80 | (nd) | 2.64 | (nd) | 1.20 | 2.40 | 0.32 | 0.04 | (nd) | 23.24 | 2.32 |
| 1955 | (nd) | (nd) | 6.40 | (nd) | (nd) | (nd) | 3.36 | (nd) | (nd) | 0.60 | 0.56 | (nd) | 10.92 | 2.18 |
| 1956 | 0.37 | 3.34 | (nd) | 4.64 | 3.80 | 2.40 | (nd) | 3.88 | (nd) | 1.40 | 0.02 | (nd) | 19.85 | 2.21 |
| 1957 | 0.60 | 6.20 | 6.20 | 3.80 | 5.00 | 5.40 | 6.20 | 2.80 | 0.00 | (nd) | 0.02 | (nd) | 36.22 | 3.62 |
| 1958 | 4.00 | 6.40 | 5.60 | 2.40 | 2.00 | 2.80 | 1.60 | 1.50 | (nd) | 0.02 | (nd) | (nd) | 26.32 | 2.92 |
| 1959 | 1.40 | 3.50 | 4.20 | 6.00 | 6.60 | 4.00 | 1.10 | 2.80 | 2.40 | 1.92 | 0.10 | (nd) | 34.02 | 3.09 |
| 1960 | 4.00 | 6.00 | 5.50 | 5.40 | 6.20 | 3.80 | 3.20 | 5.00 | 5.00 | 1.20 | 0.00 | (nd) | 45.30 | 4.12 |
| 1961 | 4.00 | 5.70 | 7.00 | 6.50 | 7.50 | 5.00 | 5.50 | 5.00 | 3.20 | (nd) | 0.24 | (nd) | 49.64 | 4.96 |
| 1962 | 5.20 | 7.70 | 10.00 | 7.60 | 4.50 | 3.00 | 2.00 | 2.10 | 2.60 | (nd) | 0.04 | (nd) | 44.74 | 4.47 |
| 1963 | 0.50 | 1.60 | 4.50 | 3.20 | 3.60 | 1.00 | 0.40 | 0.20 | 0.10 | 1.40 | (nd) | (nd) | 16.50 | 1.65 |
| 1964 | 3.30 | 5.00 | 4.00 | 2.70 | 0.92 | 0.32 | 0.14 | 0.11 | 0.15 | 0.00 | 0.00 | (nd) | 16.64 | 1.51 |
| 1965 | 2.40 | 3.40 | 3.30 | 1.20 | 0.49 | 0.06 | 0.12 | 0.07 | 0.14 | 0.06 | 0.01 | 0.00 | 11.25 | 1.02 |
| 1966 | 1.16 | 3.60 | 3.30 | 0.87 | 0.20 | 0.40 | 1.00 | 0.24 | 0.20 | 0.08 | (nd) | 0.14 | 11.19 | 1.02 |
| 1967 | 1.80 | 6.00 | 3.00 | 5.50 | 2.15 | 1.00 | 3.00 | 2.50 | 2.70 | 2.80 | 1.20 | (nd) | 31.65 | 2.88 |
| 1968 | 0.48 | 4.00 | 3.00 | 5.00 | 1.36 | 2.33 | 1.75 | 1.60 | 2.15 | 1.30 | (nd) | 0.44 | 23.41 | 2.13 |
| 1969 | 2.22 | 3.60 | 3.80 | 1.60 | 2.00 | 0.48 | 1.28 | 1.46 | 0.70 | 0.05 | (nd) | 0.05 | 17.24 | 1.57 |
| 1970 | 0.48 | 3.70 | 3.40 | 1.10 | 2.60 | 0.90 | 0.90 | 0.40 | 0.22 | 0.00 | 0.08 | 0.08 | 13.86 | 1.16 |
| 1971 | 0.30 | 2.84 | 3.60 | 3.40 | 1.60 | 1.50 | 2.00 | 2.00 | 1.70 | 1.50 | 0.40 | 0.14 | 20.98 | 1.75 |
| 1972 | 1.58 | 3.30 | 4.20 | 2.80 | 2.40 | 1.80 | 1.20 | 1.70 | 1.60 | 0.40 | (nd) | 0.01 | 20.99 | 1.91 |
| 1973 | 1.40 | 2.50 | 2.60 | 0.85 | 1.04 | 0.28 | 0.56 | 0.36 | 0.20 | 0.00 | (nd) | 0.00 | 9.79 | 0.89 |
| 1974 | 0.75 | 4.00 | 3.50 | 1.00 | 0.15 | 0.01 | 0.01 | 0.04 | 0.01 | 0.00 | 0.01 | 0.00 | 9.48 | 0.79 |
| 1975 | 1.60 | 4.40 | 4.80 | 0.76 | 0.32 | 1.40 | 0.20 | 0.40 | 0.02 | 0.46 | 0.04 | 0.01 | 14.41 | 1.20 |
| 1976 | 0.70 | 1.88 | 2.00 | 0.90 | 0.46 | 0.42 | 0.20 | 0.18 | 0.17 | 0.48 | 0.00 | 0.00 | 7.39 | 0.62 |
| 1977 | 0.56 | 3.10 | 4.10 | 3.90 | 1.00 | 1.10 | 2.50 | 0.36 | 1.36 | 0.68 | 0.00 | 0.00 | 18.66 | 1.65 |
| 1978 | 0.80 | 3.10 | 3.50 | 1.20 | 1.10 | 0.70 | 1.40 | 0.70 | 0.16 | 0.32 | (nd) | 0.00 | 12.98 | 1.18 |
| 1979 | 0.78 | 2.90 | 3.60 | 2.00 | 1.90 | 1.10 | 1.00 | 0.85 | 0.28 | 0.36 | 0.00 | 0.00 | 14.77 | 1.23 |
| 1980 | 1.60 | 3.00 | 4.20 | 1.20 | 2.00 | 0.60 | 1.10 | 0.50 | 0.70 | 0.04 | 0.00 | 0.00 | 14.94 | 1.25 |
| 1981 | 0.57 | 4.20 | 4.10 | 4.50 | 1.80 | 0.80 | 0.45 | 0.52 | 0.24 | 0.16 | (nd) | 0.00 | 17.34 | 1.58 |
| 1982 | 0.44 | 3.80 | 3.40 | 2.00 | 1.30 | 1.70 | 2.10 | 0.60 | 0.30 | 0.40 | 0.04 | (nd) | 16.08 | 1.46 |
| 1983 | 0.92 | 3.20 | 3.60 | 2.40 | 2.00 | 1.30 | 2.10 | 0.90 | 0.80 | 0.20 | 0.20 | 0.00 | 17.62 | 1.47 |
| 1984 | 1.36 | 2.68 | 2.70 | 2.20 | 2.04 | 1.20 | 1.20 | 0.00 | 1.20 | 0.48 | 0.02 | (nd) | 15.08 | 1.37 |
| 1985 | 1.52 | 3.90 | 3.40 | 2.40 | 2.95 | 1.50 | 1.20 | 0.84 | 0.40 | 1.10 | 0.44 | 0.05 | 19.70 | 1.64 |
| 1986 | 2.68 | 4.30 | 5.20 | 4.50 | 3.60 | 1.80 | 2.10 | 0.80 | 1.70 | 1.50 | 0.01 | 0.01 | 28.20 | 2.35 |
| 1987 | 2.10 | 4.80 | 4.10 | 5.60 | 2.40 | 0.40 | 0.60 | 0.24 | 0.60 | 0.20 | 0.00 | 0.00 | 21.04 | 1.75 |
| 1988 | 1.44 | 4.20 | 4.50 | 2.00 | 0.40 | 0.20 | 0.00 | 0.40 | 0.00 | 0.00 | 0.01 | 0.00 | 13.15 | 1.10 |
| 1989 | 2.08 | 3.20 | 6.50 | 2.20 | 3.10 | 1.60 | 0.56 | 0.04 | 0.80 | 0.60 | 0.65 | 0.00 | 21.33 | 1.78 |
| 1990 | 2.56 | 4.80 | 4.11 | 3.12 | 2.63 | 0.74 | 1.16 | 0.65 | 1.04 | 1.18 | 1.80 | 0.08 | 23.87 | 1.99 |
| mean | 1.50 | 3.80 | 4.31 | 3.09 | 2.55 | 1.55 | 1.48 | 1.19 | 0.97 | 0.57 | 0.21 | 0.04 | 20.23 | 1.69 |

There were no observations in 1952, and in some other years certain levels were omitted, indicated as (nd) in the table.

the Marine Biological Association's research vessels, fitted with calibrated electronic thermometers, and a new weekly series was started for the Eddystone station (L5) in 1984. This source of environmental data also ceased in 1987.

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## RESULTS

### *Changes in individual species*

The actual annual abundances of total *Chthamalus* (including *Chthamalus stellatus* as well as *C. montagui*), *C. stellatus*, *Semibalanus balanoides* and *Elminius modestus* are shown in Tables 1-4 as means of the counts at each tidal level.

### *Chthamalus montagui*

It can be seen from Table 1 that *Chthamalus montagui*, which dominates the total *Chthamalus* counts, is essentially a high water species, and through the whole period its maximum continuous abundance occurred between MHWS and MHWN. In the first decade of the survey *Chthamalus* extended down to MLWN in densities exceeding 1 $cm^{-2}$. In the mid 1960s and 1970s *Chthamalus* became considerably less common below MHWN. Although there have been increases in abundance since 1975 it was not until 1989 that the former abundance was seen again. Particular reductions in density of *Chthamalus* occurred in 1964-66, 1974 and 1988, corresponding to peaks in abundance of *S. balanoides* (*qv*). Below MTL on this transect there is a higher proportion of *C. stellatus* in the total number of *Chthamalus*, often more than 50% at MLWN (see Figure 1). Hence changes of *Chthamalus* at these levels refer as much to *C. stellatus* as to *C. montagui*, as noted in the next section.

### *Chthamalus stellatus*

After 1975, when *C. montagui* was first recognised as a distinct species, *C. stellatus* was recorded separately. The annual numbers are shown in Table 2. The variation from year to year at the upper levels of the transect, where the species is uncommon and patchily

Table 2. *Abundance of adult* Chthamalus stellatus *each autumn on the transect near Cellar Beach, River Yealm, as mean number* $cm^{-2}$ *at each of 12 levels. As noted in Table 1, the heights are given in metres above chart datum and levels not counted in certain years are shown as (nd).*

| level | 5.40 ↓HWS | 5.04 | 4.68 | 4.32 ↓HWN | 3.97 | 3.62 | 3.27 ↓MTL | 2.91 | 2.55 | 2.20 ↓LWN | 1.70 | 1.20 | total | mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1976 | 0.00 | 0.00 | 0.04 | 0.04 | 0.10 | 0.05 | 0.12 | 0.20 | 0.18 | 0.24 | 0.00 | 0.00 | 0.97 | 0.08 |
| 1977 | 0.00 | 0.00 | 0.00 | 0.07 | 0.17 | 0.24 | 0.32 | 0.32 | 0.32 | 0.20 | 0.01 | 0.00 | 1.65 | 0.14 |
| 1978 | 0.00 | 0.00 | 0.08 | 0.08 | 0.20 | 0.30 | 0.90 | 0.03 | 0.12 | 0.08 | 0.00 | (nd) | 1.79 | 0.16 |
| 1979 | 0.00 | 0.00 | 0.00 | 0.04 | 0.12 | 0.12 | 0.20 | 0.11 | 0.42 | 0.14 | 0.06 | 0.00 | 1.21 | 0.10 |
| 1980 | 0.00 | 0.00 | 0.02 | 0.06 | 0.06 | 0.22 | 0.24 | 1.00 | 0.16 | 0.16 | 0.01 | 0.00 | 1.93 | 0.16 |
| 1981 | 0.00 | 0.00 | 0.00 | 0.32 | 0.90 | 1.30 | 0.55 | 0.56 | 0.16 | 0.16 | 0.00 | (nd) | 3.95 | 0.36 |
| 1982 | 0.00 | 0.01 | 0.03 | 0.20 | 0.40 | 0.50 | 0.02 | 0.04 | 0.06 | 0.04 | 0.10 | 0.00 | 1.40 | 0.12 |
| 1983 | 0.00 | 0.00 | 0.20 | 0.14 | 0.40 | 0.30 | 0.33 | 0.30 | 0.73 | 0.40 | 0.06 | 0.00 | 2.86 | 0.24 |
| 1984 | 0.00 | 0.01 | 0.14 | 0.05 | 0.28 | 0.07 | 0.60 | 0.00 | 0.40 | 0.04 | 0.05 | 0.00 | 1.64 | 0.14 |
| 1985 | 0.00 | 0.01 | 0.12 | 0.12 | 0.03 | 0.36 | 0.18 | 0.12 | 0.70 | 1.00 | 0.60 | 0.07 | 3.31 | 0.28 |
| 1986 | 0.00 | 0.01 | 0.01 | 0.10 | 0.30 | 0.12 | 0.11 | 0.06 | 0.48 | 0.14 | 0.02 | 0.08 | 1.43 | 0.12 |
| 1987 | 0.00 | 0.03 | 0.16 | 0.12 | 0.10 | 0.12 | 0.08 | 0.20 | 0.48 | 0.10 | 0.00 | 0.01 | 1.40 | 0.12 |
| 1988 | 0.00 | 0.03 | 0.08 | 0.08 | 0.08 | 0.60 | 0.10 | 0.03 | 0.05 | 0.27 | 0.03 | 0.00 | 1.35 | 0.11 |
| 1989 | 0.00 | 0.16 | 0.04 | 0.10 | 0.22 | 1.20 | 0.48 | 0.96 | 2.30 | 1.20 | 3.87 | 0.09 | 10.62 | 0.89 |
| 1990 | 0.00 | 0.01 | 0.01 | 0.27 | 0.12 | 0.10 | 0.06 | 0.05 | 0.09 | 0.23 | 1.30 | 0.08 | 2.32 | 0.19 |
| mean | 0.00 | 0.02 | 0.06 | 0.12 | 0.23 | 0.37 | 0.29 | 0.27 | 0.44 | 0.29 | 0.41 | 0.03 | 2.52 | 0.21 |

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distributed, is probably an artefact of counting less than the minimal area of reproducibility (see Burrows, 1988), a procedure dictated by the broken nature of the rock. In the middle shore there has been a trend comparable with that of *C. montagui* at high water, with reductions in the same years and a recent increase in adults following good settlement and recruitment of juveniles.

Table 3. *Abundance of adult* Semibalanus balanoides *each autumn on the transect near Cellar Beach, River Yealm, as mean number* $cm^{-2}$ *at each of 12 levels. As noted for Table 1 the levels are given as heights above chart datum; there were no counts in 1952 and certain levels were omitted in other years, marked (nd).*

| level | 5.40 ↓HWS | 5.04 | 4.68 | 4.32 ↓HWN | 3.97 | 3.62 | 3.27 ↓MTL | 2.91 | 2.55 | 2.20 ↓LWN | 1.70 | 1.20 | total | mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1951 | 0.00 | 0.00 | (nd) | 0.01 | 0.00 | 0.00 | 0.00 | (nd) | 0.00 | 0.00 | (nd) | (nd) | 0.01 | 0.00 |
| 1952 | | | | | | | | | | | | | | |
| 1953 | 0.00 | 0.00 | 0.00 | (nd) | 0.00 | 1.10 | 0.72 | (nd) | 0.16 | 0.04 | (nd) | (nd) | 2.02 | 0.25 |
| 1954 | 0.00 | 0.00 | 0.12 | 0.60 | (nd) | 1.20 | (nd) | 0.80 | 0.56 | 0.16 | 0.08 | (nd) | 3.52 | 0.39 |
| 1955 | (nd) | (nd) | 0.82 | (nd) | (nd) | (nd) | 1.56 | (nd) | (nd) | 1.10 | 1.16 | (nd) | 4.64 | 1.16 |
| 1956 | 0.00 | 0.00 | (nd) | 0.16 | 1.00 | 1.20 | (nd) | 0.48 | (nd) | 0.68 | 0.48 | (nd) | 4.00 | 0.50 |
| 1957 | 0.00 | 0.00 | 0.20 | 1.60 | 2.20 | 2.00 | 1.40 | 4.60 | (nd) | (nd) | 0.40 | (nd) | 12.40 | 1.38 |
| 1958 | 0.00 | 0.00 | 0.36 | 1.60 | 0.65 | 2.40 | 1.76 | 0.80 | (nd) | 0.56 | (nd) | (nd) | 8.13 | 0.90 |
| 1959 | 0.00 | 0.00 | 0.00 | 0.18 | 0.16 | 0.35 | 0.12 | 0.25 | 0.12 | 0.20 | 0.11 | (nd) | 1.49 | 0.14 |
| 1960 | 0.00 | 0.00 | 0.09 | 0.02 | 0.32 | 0.12 | 0.03 | 0.01 | 0.01 | 0.00 | 0.00 | (nd) | 0.60 | 0.05 |
| 1961 | 0.00 | 0.00 | 0.20 | 0.43 | 0.54 | 0.30 | 0.56 | 0.32 | 0.08 | (nd) | 0.14 | (nd) | 2.57 | 0.26 |
| 1962 | 0.00 | 0.00 | 0.30 | 0.30 | 0.64 | 0.18 | 0.09 | 0.04 | 0.06 | (nd) | 0.00 | (nd) | 1.61 | 0.16 |
| 1963 | 0.00 | 0.00 | 0.00 | 0.09 | 0.08 | 0.05 | 0.07 | 0.01 | 0.00 | 0.07 | (nd) | (nd) | 0.37 | 0.04 |
| 1964 | 0.00 | 0.00 | 0.92 | 3.60 | 8.00 | 4.00 | 4.80 | 4.10 | 2.70 | 1.00 | 0.64 | (nd) | 29.76 | 2.71 |
| 1965 | 0.00 | 0.24 | 2.10 | 7.50 | 6.60 | 8.40 | 5.50 | 6.50 | 5.50 | 6.50 | 5.50 | 0.68 | 55.02 | 4.59 |
| 1966 | 0.00 | 0.16 | 0.32 | 1.50 | 1.25 | 2.30 | 2.30 | 0.80 | 1.30 | 1.50 | (nd) | 0.12 | 11.55 | 1.05 |
| 1967 | 0.00 | 0.00 | 1.00 | 1.55 | 2.50 | 4.50 | 1.70 | 1.00 | 1.70 | 2.40 | 0.20 | (nd) | 16.55 | 1.50 |
| 1968 | 0.00 | 0.00 | 0.60 | 0.60 | 2.25 | 0.46 | 1.40 | 1.30 | 0.75 | 3.50 | 3.00 | 0.08 | 13.94 | 1.16 |
| 1969 | 0.00 | 0.00 | 0.40 | 2.87 | 1.85 | 3.15 | 1.36 | 0.56 | 2.09 | 3.95 | (nd) | 0.10 | 16.33 | 1.48 |
| 1970 | 0.00 | 0.00 | 0.84 | 2.80 | 2.00 | 1.90 | 2.00 | 0.90 | 1.10 | 1.70 | 0.19 | 0.12 | 13.55 | 1.13 |
| 1971 | 0.00 | 0.00 | 0.32 | 1.90 | 1.80 | 2.85 | 3.20 | 1.40 | 2.50 | 2.40 | 0.80 | 0.14 | 17.31 | 1.44 |
| 1972 | 0.00 | 0.15 | 0.44 | 2.90 | 2.70 | 3.20 | 4.10 | 2.60 | 3.50 | 5.60 | (nd) | 0.15 | 25.34 | 2.30 |
| 1973 | 0.00 | 0.00 | 1.48 | 3.50 | 4.50 | 4.80 | 4.30 | 3.60 | 4.60 | 2.00 | (nd) | 2.70 | 31.48 | 2.86 |
| 1974 | 0.00 | 0.00 | 2.00 | 3.50 | 4.50 | 6.50 | 6.00 | 6.00 | 6.00 | 7.50 | 5.00 | 3.70 | 50.70 | 4.23 |
| 1975 | 0.00 | 0.00 | 0.24 | 3.40 | 2.40 | 2.40 | 4.00 | 2.90 | 3.40 | 3.30 | 0.16 | 0.80 | 23.00 | 1.92 |
| 1976 | 0.00 | 0.00 | 0.20 | 1.32 | 0.82 | 1.40 | 1.20 | 0.52 | 0.76 | 1.40 | 0.01 | 0.12 | 7.75 | 0.70 |
| 1977 | 0.00 | 0.00 | 0.01 | 0.64 | 0.20 | 1.70 | 0.90 | 0.76 | 0.20 | 0.14 | 0.52 | 0.02 | 5.09 | 0.42 |
| 1978 | 0.00 | 0.00 | 0.00 | 2.30 | 1.90 | 1.40 | 0.40 | 2.00 | 2.00 | 2.80 | (nd) | 0.90 | 13.70 | 1.25 |
| 1979 | 0.00 | 0.00 | 0.01 | 0.50 | 1.70 | 2.20 | 0.68 | 2.20 | 1.60 | 2.70 | 1.00 | 0.60 | 13.19 | 1.10 |
| 1980 | 0.00 | 0.00 | 0.10 | 2.10 | 3.50 | 3.30 | 3.30 | 3.60 | 3.50 | 4.50 | 1.75 | 1.50 | 27.15 | 2.26 |
| 1981 | 0.00 | 0.00 | 0.16 | 0.60 | 1.10 | 2.00 | 2.10 | 0.84 | 1.50 | 3.20 | (nd) | 0.68 | 12.18 | 1.11 |
| 1982 | 0.00 | 0.00 | 0.20 | 0.72 | 2.40 | 2.50 | 2.80 | 3.80 | 2.30 | 3.10 | 1.20 | (nd) | 19.02 | 1.73 |
| 1983 | 0.00 | 0.00 | 0.40 | 1.50 | 2.30 | 1.70 | 1.50 | 1.10 | 1.40 | 2.50 | 0.32 | 0.28 | 13.00 | 1.08 |
| 1984 | 0.00 | 0.00 | 0.46 | 0.70 | 1.92 | 3.20 | 3.40 | 0.00 | 2.20 | 4.40 | 1.50 | (nd) | 17.78 | 1.62 |
| 1985 | 0.00 | 0.00 | 0.24 | 0.00 | 0.52 | 1.36 | 1.20 | 0.72 | 0.88 | 0.68 | 0.48 | 0.20 | 6.28 | 0.52 |
| 1986 | 0.00 | 0.00 | 0.01 | 1.60 | 1.50 | 2.40 | 3.20 | 2.80 | 2.40 | 1.40 | 0.47 | 2.60 | 18.38 | 1.53 |
| 1987 | 0.00 | 0.00 | 0.06 | 0.64 | 0.88 | 0.96 | 2.30 | 1.60 | 2.80 | 2.80 | 1.30 | 0.45 | 13.79 | 1.15 |
| 1988 | 0.00 | 0.00 | 0.00 | 2.20 | 3.20 | 4.40 | 3.00 | 3.20 | 2.00 | 4.00 | 1.06 | 0.44 | 23.50 | 1.96 |
| 1989 | 0.00 | 0.00 | 0.07 | 2.24 | 0.88 | 0.56 | 0.44 | 0.18 | 0.12 | 0.16 | 0.54 | 0.58 | 5.77 | 0.48 |
| 1990 | 0.00 | 0.00 | 0.05 | 1.80 | 2.30 | 2.00 | 2.30 | 1.20 | 0.95 | 2.05 | 2.80 | 1.10 | 16.55 | 1.38 |
| mean | 1.68 | 4.04 | 4.93 | 4.85 | 4.59 | 3.84 | 3.65 | 3.04 | 2.64 | 2.75 | 1.38 | 0.85 | 13.98 | 1.16 |

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## *Semibalanus balanoides*

In 1951 *S. balanoides* was only just represented on the transect, but was commoner farther up the Yealm in Newton Creek. The fall in abundance of *S. balanoides* between the original survey of 1934 (Moore, 1936) and the start of the present series in 1951 is documented by Southward & Crisp (1954) and attributed to the general warming of

Table 4. *Abundance of* Elminius modestus *each autumn on the transect near Cellar Beach, River Yealm, as mean number per cm² at each of 12 levels. As noted in Table 1 there were no observations in 1952 and certain levels were omitted in other years, marked (nd).*

| level | 5.40 | 5.04 | 4.68 | 4.32 | 3.97 | 3.62 | 3.27 | 2.91 | 2.55 | 2.20 | 1.70 | 1.20 | total | mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ↓HWS | | | ↓HWN | | | ↓MTL | | | ↓LWN | | | | |
| 1951 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 1952 | | | | | | | | | | | | | | |
| 1953 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.08 | (nd) | 0.04 | 0.08 | (nd) | (nd) | 0.21 | 0.00 |
| 1954 | 0.00 | 0.00 | 0.00 | 0.00 | (nd) | 0.00 | (nd) | 0.01 | 0.00 | 0.00 | 0.00 | (nd) | 0.01 | 0.00 |
| 1955 | (nd) | (nd) | 0.00 | (nd) | (nd) | (nd) | 0.00 | (nd) | (nd) | 0.28 | 0.00 | (nd) | 0.28 | 0.07 |
| 1956 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.13 | (nd) | 0.20 | (nd) | 0.48 | 1.28 | (nd) | 2.09 | 0.26 |
| 1957 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.07 | 0.12 | 0.16 | (nd) | (nd) | 1.10 | (nd) | 1.47 | 0.16 |
| 1958 | 0.00 | 0.00 | 0.12 | 0.20 | 0.16 | 0.32 | 0.48 | 0.16 | (nd) | 0.80 | (nd) | (nd) | 2.24 | 0.25 |
| 1959 | 0.00 | 0.00 | 0.00 | 0.02 | 0.04 | 0.12 | 0.12 | 0.16 | 0.30 | 1.60 | 0.65 | (nd) | 3.01 | 0.27 |
| 1960 | 0.00 | 0.00 | 0.02 | 0.16 | 1.08 | 1.00 | 0.80 | 1.80 | 2.30 | 2.00 | 4.00 | (nd) | 13.16 | 1.20 |
| 1961 | 0.00 | 0.00 | 0.00 | 0.01 | 0.04 | 0.16 | 0.16 | 0.28 | 0.40 | 1.00 | 0.26 | (nd) | 2.31 | 0.21 |
| 1962 | 0.00 | 0.00 | 0.00 | 0.56 | 0.74 | 0.62 | 1.30 | 2.00 | 1.00 | (nd) | 0.28 | (nd) | 6.50 | 0.65 |
| 1963 | 0.00 | 0.00 | 0.02 | 0.34 | 0.35 | 0.43 | 0.15 | 0.25 | 0.50 | 0.21 | (nd) | (nd) | 2.25 | 0.23 |
| 1964 | 0.00 | 0.00 | 0.08 | 0.16 | 0.08 | 0.40 | 0.12 | 1.12 | 1.50 | 2.50 | 2.00 | (nd) | 7.96 | 0.72 |
| 1965 | 0.00 | 0.01 | 0.24 | 0.24 | 0.12 | 0.04 | 0.07 | 0.24 | 0.48 | 0.56 | 0.60 | 0.00 | 2.60 | 0.22 |
| 1966 | 0.00 | 0.00 | 0.12 | 0.20 | 0.22 | 1.20 | 0.90 | 1.30 | 0.50 | 1.20 | (nd) | 0.08 | 5.72 | 0.52 |
| 1967 | 0.00 | 0.01 | 1.00 | 0.48 | 0.24 | 0.32 | 0.36 | 1.40 | 1.20 | 1.50 | 0.46 | (nd) | 6.97 | 0.63 |
| 1968 | 0.00 | 0.00 | 0.00 | 0.05 | 0.25 | 0.16 | 1.55 | 2.00 | 2.00 | 2.50 | 5.00 | 0.20 | 13.71 | 1.14 |
| 1969 | 0.00 | 0.00 | 0.04 | 0.48 | 0.40 | 0.28 | 0.54 | 1.02 | 1.20 | 1.80 | (nd) | 0.36 | 6.12 | 0.56 |
| 1970 | 0.00 | 0.00 | 0.08 | 0.20 | 0.20 | 0.20 | 0.40 | 0.03 | 1.20 | 0.80 | 1.50 | 0.04 | 4.65 | 0.39 |
| 1971 | 0.00 | 0.00 | 0.14 | 0.10 | 0.12 | 0.06 | 0.20 | 0.10 | 0.00 | 0.36 | 0.20 | 0.05 | 1.33 | 0.11 |
| 1972 | 0.00 | 0.00 | 0.00 | 0.08 | 0.08 | 1.08 | 1.42 | 1.02 | 1.05 | 1.52 | (nd) | 1.48 | 7.73 | 0.70 |
| 1973 | 0.00 | 0.00 | 0.02 | 0.02 | 0.16 | 0.60 | 0.56 | 1.28 | 0.96 | 1.00 | (nd) | 0.40 | 5.00 | 0.45 |
| 1974 | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 0.04 | 0.05 | 0.03 | 0.06 | 0.05 | 0.14 | 0.30 | 0.72 | 0.06 |
| 1975 | 0.00 | 0.00 | 0.00 | 0.16 | 0.06 | 0.20 | 0.40 | 0.40 | 0.40 | 1.00 | 0.52 | 0.40 | 3.54 | 0.30 |
| 1976 | 0.00 | 0.00 | 0.24 | 0.24 | 0.24 | 0.24 | 0.88 | 0.64 | 0.72 | 1.00 | 0.18 | 0.60 | 4.98 | 0.42 |
| 1977 | 0.00 | 0.00 | 0.00 | 0.12 | 0.64 | 0.90 | 0.90 | 2.70 | 2.60 | 2.60 | 3.80 | 3.00 | 17.26 | 1.44 |
| 1978 | 0.00 | 0.00 | 0.00 | 0.16 | 0.12 | 0.12 | 0.45 | 0.20 | 0.80 | 0.50 | (nd) | 1.50 | 3.85 | 0.35 |
| 1979 | 0.00 | 0.00 | 0.06 | 0.05 | 0.07 | 0.05 | 0.13 | 0.22 | 0.90 | 1.00 | 1.20 | 0.48 | 4.16 | 0.35 |
| 1980 | 0.00 | 0.00 | 0.01 | 0.01 | 0.05 | 0.08 | 0.15 | 0.08 | 0.05 | 0.10 | 0.45 | 0.20 | 1.18 | 0.10 |
| 1981 | 0.00 | 0.00 | 0.04 | 0.08 | 0.01 | 0.02 | 0.02 | 0.00 | 2.12 | 4.01 | (nd) | 2.08 | 8.38 | 0.76 |
| 1982 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 | 0.08 | 0.00 | 1.54 | 3.05 | (nd) | 0.30 | 5.07 | 0.46 |
| 1983 | 0.00 | 0.00 | 0.00 | 0.04 | 0.02 | 0.04 | 0.14 | 0.13 | 0.18 | 0.84 | 0.35 | 0.36 | 2.10 | 0.18 |
| 1984 | 0.00 | 0.00 | 0.00 | 0.01 | 0.02 | 0.06 | 0.02 | 0.00 | 0.16 | 1.45 | 3.00 | (nd) | 4.72 | 0.43 |
| 1985 | 0.00 | 0.00 | 0.00 | 0.00 | 0.14 | 0.12 | 0.92 | 0.12 | 0.56 | 1.00 | 1.70 | 0.60 | 5.16 | 0.43 |
| 1986 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.02 | 0.06 | 0.10 | 0.02 | 0.12 | 0.07 | 0.07 | 0.48 | 0.04 |
| 1987 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.30 | 1.20 | 2.00 | 0.90 | 0.90 | 4.50 | 0.20 | 13.00 | 1.08 |
| 1988 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.40 | 0.60 | 0.05 | 0.06 | 0.10 | 0.04 | 1.27 | 0.11 |
| 1989 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.14 | 0.80 | 0.44 | 0.70 | 1.50 | 0.80 | 1.24 | 5.62 | 0.47 |
| 1990 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.01 | 0.08 | 0.15 | 0.60 | 0.50 | 1.20 | 2.62 | 0.22 |
| mean | 0.00 | 0.00 | 0.06 | 0.11 | 0.15 | 0.32 | 0.41 | 0.57 | 0.68 | 1.02 | 0.89 | 0.39 | 4.60 | 0.41 |

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climate in the northern hemisphere over the period. This trend appeared to end in the mid 1950s when *S. balanoides* increased, but numbers fell again at the end of the decade as temperatures increased once more (Table 3). After the cold winters of 1961/2 and 1962/3 and the poor summer of 1963 *S. balanoides* built up rapidly to become the dominant barnacle for a decade, with peaks in 1964-65 (Crisp & Southward, 1964; Southward, 1967) and 1971-74. Thereafter it became generally less abundant but there were peaks in 1980, 1984 and 1988 following years of good settlement. The population was much reduced in 1989.

In the south-west of Britain *S. balanoides* becomes mature the first year after settlement and there is usually extensive mortality of older adults in spring and summer. In years of abundance this species extends from MHWN to MLWN, but in lean years the maximum densities tend to be restricted to around MTL where some adults can survive for more than a year. The upper limit is below that of *Chthamalus*, as long recognised (Moore & Kitching, 1939), but it accompanies *C. stellatus* to the lower limit of the barnacle zone.

### *Elminius modestus*

The immigrant species, *E. modestus*, which is the least abundant of the four barnacles studied here, was not present on the transect before 1953, though seen in 1951 in Newton Creek. As shown in Table 4 the population built up slowly from 1953, to a peak in the mid-1960s, but then declined somewhat during the period of abundance of *S. balanoides*. From 1978 to 1986 it was quite scarce at the upper and middle levels of the transect and common only in MLWN-MLWS region. Numbers have increased recently, coincident with some of the increases in *Chthamalus*, but the species is still less abundant than in the mid to late 1960s. *Elminius* is an ephemeral component of the barnacles on the transect, mostly represented by younger individuals (including spat) that have settled the same summer, and very few survive to the following year. Thus the violent fluctuations in density between years shown in the table probably reflect the number of larvae available for settlement on the transect. This will depend on breeding success of the species elsewhere, as for example in the sublittoral or in the nearby Tamar and Plym estuaries where the lowered salinity encourages greater population density of *Elminius* than in the Yealm.

### *Changes in settlement*

Variation in the strength of settlement of total *Chthamalus* and surviving juvenile *S. balanoides* is shown in Table 5. There are years without observations, when settlement of *Chthamalus* was either slight or took place late, after the adult counts were made. The observations on *S. balanoides* juveniles are incomplete, for various reasons, and offer no guide to initial spatfall, which would be considerably higher. The *Chthamalus* settlement has been compared with the adult abundance by simple linear regression (Table 6). The values of the correlation coefficient ($r$) are quite small. There is some correlation (not quite significant at the 5% level) the same year at the high tide levels, suggesting that aggregated spatfall is stimulated by high adult densities. Correlation significant at the 5% level is found when the settlement is compared with the adult population at the lower

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Table 5. *Relative abundance of settling* Chthamalus *and relative abundance of surviving juvenile* Semibalanus balanoides, *determined each autumn (see text)*

| year | *Chthamalus* | *Semibalanus* | year | *Chthamalus* | *Semibalanus* |
|---|---|---|---|---|---|
| 1951 | nd | nd | 1970 | 4 | nd |
| 1952 | nd | nd | 1971 | 4 | nd |
| 1953 | 3 | 3 | 1972 | 2 | 3 |
| 1954 | 3 | 2 | 1973 | 2 | 4 |
| 1955 | nd | 2 | 1974 | 4 | 3 |
| 1956 | nd | nd | 1975 | 4 | nd |
| 1956 | nd | nd | 1976 | 1 | 2 |
| 1957 | 4 | nd | 1977 | 2 | 1 |
| 1958 | 5 | 3 | 1978 | 3 | 3 |
| 1959 | nd | 1 | 1979 | 4 | 3 |
| 1960 | 4 | 1 | 1980 | 3 | 4 |
| 1961 | 4 | 1 | 1981 | 4 | 2 |
| 1962 | nd | 1 | 1982 | 4 | 2 |
| 1963 | nd | 1 | 1983 | 4 | 2 |
| 1964 | 3 | 4 | 1984 | 3 | 3 |
| 1965 | 4 | 4 | 1985 | 4 | 2 |
| 1966 | 4 | nd | 1986 | 2 | 3 |
| 1967 | 4 | nd | 1987 | 3 | 2 |
| 1968 | 4 | nd | 1988 | 2 | 4 |
| 1969 | 2 | nd | 1989 | 4 | 2 |

As grouped numbers per $cm^2$. 1 = <0.3; 2 = 0.3-1.0; 3 = 1.0-3.0; 4 = 3.0-10; 5 = >10. nd = no observations

Table 6. *Correlation coefficient* (r) *between intensity of settlement of* Chthamalus *spat in a particular year and the abundance of total* Chthamalus *adults the same year and in following years.*

| tide level | same year | 1 y later | 2 y later | 3 y later |
|---|---|---|---|---|
| HWN | 0.32 | 0.11 | 0.10 | 0.15 |
| MTL | 0.23 | 0.29 | 0.40* | 0.25 |
| LWN | 0.28 | 0.36* | 0.40* | 0.04 |

Values of $r$ significant at the 0.05 level of probability are indicated by *

tide levels, 1 and 2 years later, and a similarly significant correlation occurs between settlement and the mid-tide adults two years later. Presumably a good settlement is one of the factors leading to increases in the adult population at these levels, but since this relationship accounts for less than 20% of the variance, other factors must be more important in controlling adult abundance. At high tide levels the population of *Chthamalus montagui* consists mostly of very old individuals, and changes in settlement in one year are unlikely to have a significant effect on the total number of adults.

The data for *S. balanoides* are too incomplete for correlation analysis, but attention is drawn to the high survival of juveniles (and presumably high initial settlement) in the 'cool' periods of climate *viz.* 1963-64, 1973-74, 1978-80, when the adults flourished for a number of years.

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*Changes in total barnacle density and species composition*

In spite of the oscillations in species abundance, the total density of barnacles has remained fairly constant, though there have been fluctuations from year to year (Figure 2). Reductions of one species have been balanced by increases in another. A smoothed curve drawn through the 5-y running means shows a slight rise of overall barnacle density from 1956 to 1970, apparently the result first of a temporary increase in *Chthamalus* then of increased settlement of *S. balanoides*. Thereafter the total density seems to have stabilized, even though bare rock was present, indicating that some other factor than substratum availability was limiting the stockholding capacity of the habitat.

The comparative stability of total barnacle density allows transformation of the data into indices which give a better picture of long-term changes in relative abundance of the species and simplifies comparison with environmental factors. The indices are listed in Table 7. The first of these, called the barnacle index, and used in previous publications

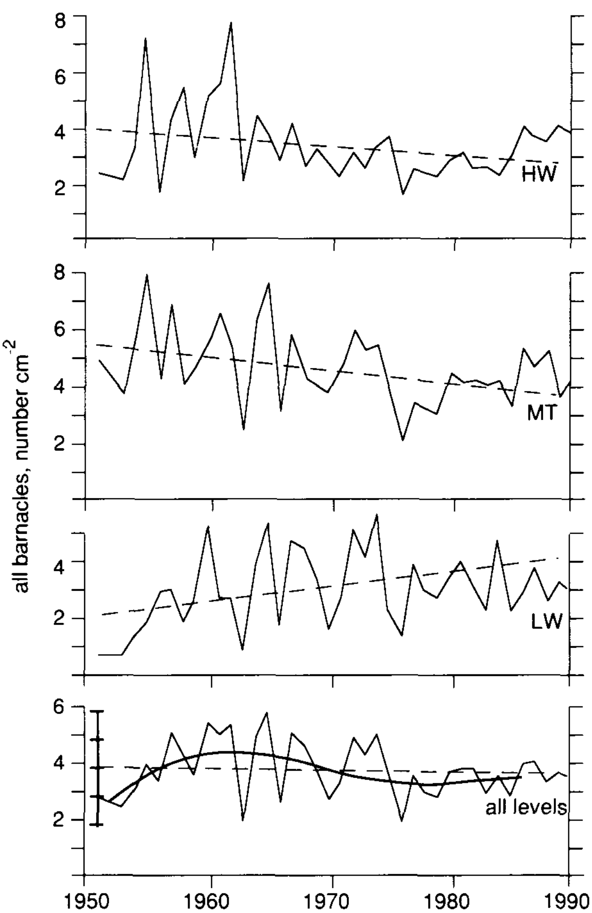


Figure 2. Trends in the total barnacle population at the Cellar Beach station, as mean number cm$^{-2}$ at three different tidal levels and as overall mean for all levels on the transect. The data for the three tidal levels are averages from the counts on the transect: high water, from 5·40 to 4·68 m; mid tide, from 4·32 to 3·27 m; and low water, 2·91 to 1·20 m; all relative to chart datum (see Tables 1-4).

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Table 7. *Indices used in describing changes in abundance and species composition of intertidal barnacles. Calculated from the sums of the average density of the species at each level for the whole transect or for the grouped levels (HW, MT & LW).*

| | |
|---|---|
| Barnacle index | BI = CT/(CT + SB + EM) |
| Warm index | WI = CT/(CT + SB) |
| Boreal or cold index | CI = SB/(CT + SB + EM) |
| Neritic index | NI = EM/(CT + SB + EM) |

CT = total *Chthamalus* (*C. montagui* + *C. stellatus*), SB = *Semibalanus balanoides* and EM = *Elminius modestus*

(Southward, 1967; Southward *et al.*, 1975), is simply the ratio of total *Chthamalus* to total barnacles. Examples are shown in Figure 3 for three tide levels. At HW there was a dip in the index during 1964-1974, but it has since returned to the previous level; the long-term trend, as a linear regression of the index against time, shows no change. At MTL and at LW the long-term trend suggests a decline in the index; at these levels there was a slight fall in the index in the mid 1950s, followed by a rise in the late 1950s. At both levels the index fell rapidly in 1964, when *S. balanoides* replaced *Chthamalus* as the dominant barnacle in the MT and LWN regions. The index increased again in the late 1960s, but there was another sharp fall in 1973. From 1976 onwards the index has shown less fluctuation, with the proportion of *Chthamalus* being about 50% at MTL and about 20% at LWN.

The existence of an approximate ten-year cycle in these data was noted previously (Southward *et al.*, 1975). The temperature data also show a 10-y cycle, and the phase lag

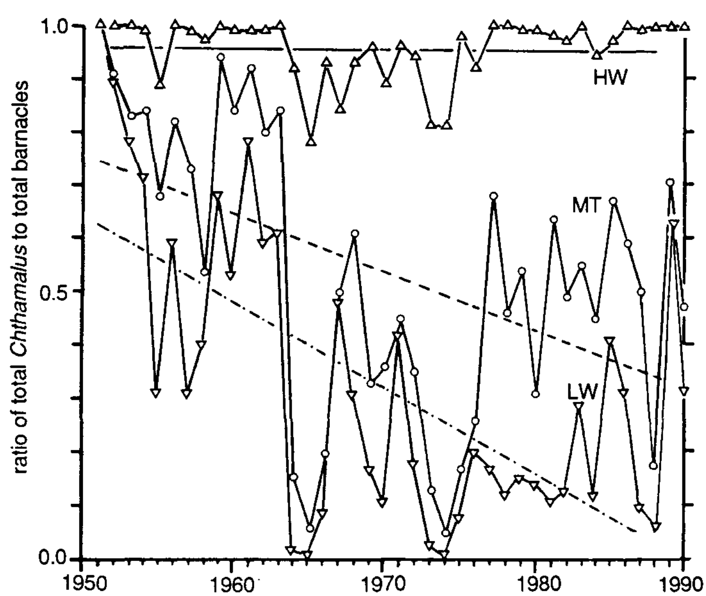


Figure 3. Changes in the proportion of species in the barnacle population at the three grouped tidal levels (see Figure 2) on the transect near Cellar Beach. The index used here is the ratio of total *Chthamalus* to total barnacles. The trends over the whole period are shown as linear regressions against time. Triangles, high water; circles, mid-tide; inverted triangles, low water.

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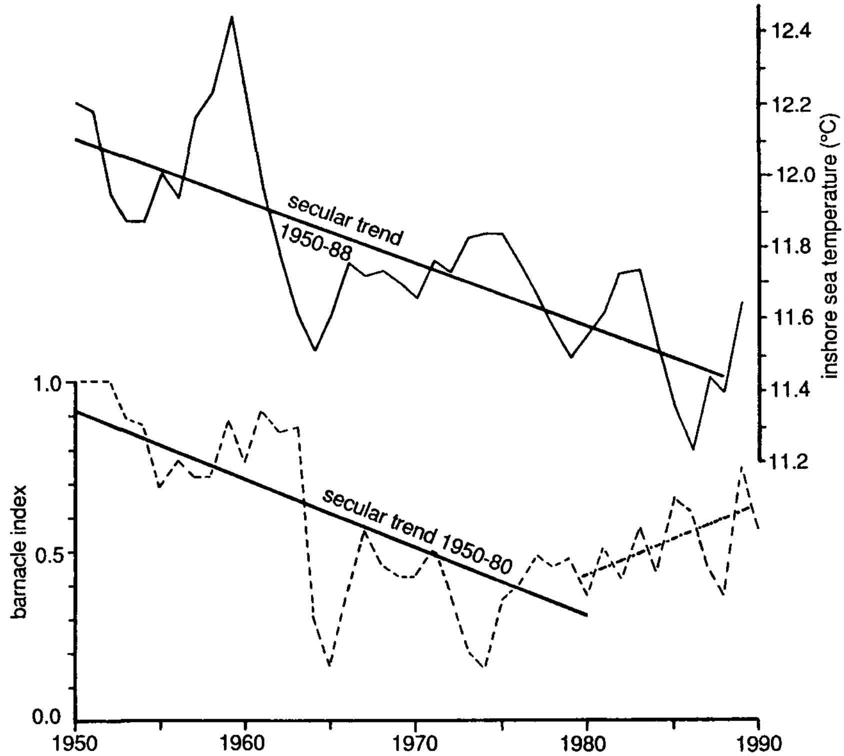


Figure 4. Comparison of changes in inshore sea temperature (upper graph) and fluctuations in the barnacle index (lower graph). The temperature, for Plymouth Sound, is shown as 5-y running means of the annual means, with the long-term ('secular') trend shown as a linear regression of the annual means against time. The barnacle index is the annual value for all levels on the Cellar Beach transect; the long-term trend from 1950 to the 1970s agrees with the temperature trend, but has diverged since.

of about two years between the two data sets (Southward, 1967), corresponds to the time for *Chthamalus* to reach adult size from settlement. Figure 4 is a continuation of the graphical method used in these earlier publications and compares annual changes in the barnacle index for the whole transect with smoothed (5-y running mean) annual mean sea temperature inshore.

As already noted, the abundance of *E. modestus* has fluctuated more than that of any of the other three species of barnacles on the transect, apparently dependent on 'good' years for reproduction and survival. As far as can be seen the good years for *Elminius* correspond to the slightly warmer summers within the cool phase dominated by *S. balanoides*. Removal of the fluctuations of *Elminius* from the barnacle index, to produce a ratio of total *Chthamalus* to *S. balanoides*, called the warm index, produces a slightly better correspondence between major changes at all tide levels, except for one or two 'odd' years, *e.g.* 1980 and 1988 when reductions in *Chthamalus* at MT and LW were not seen at the HW levels. There was a periodic rise and fall in the warm-water component of the barnacles, superimposed on a much longer trend shown by a 10-y filter (Figure 5). The decadal trend, if we can call it this, was first a long decline from the start of counts to a trough in the 1970s, then a rise to about half way between the previous peak and trough. If this long-term trend is subtracted from the annual values, the shorter-term fluctuations then emerge and can be compared with environmental factors. The extracted shorter-term trend is shown in Figure 5, as annual deviations from the long-term trend. It is evident that there has been a cycle of approximately 10-y frequency. This cycle is easily seen in the first three decades but since the late 1970s it has been reduced or replaced by a greater amplitude of year-to-year variations, combined with an apparent overall upward trend.

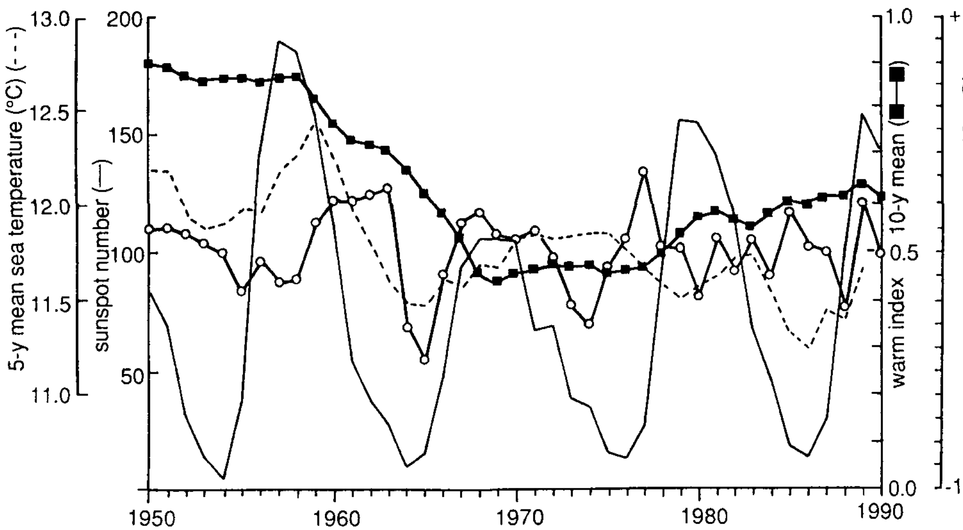


Figure 5. Comparison between environmental factors and changes in the proportion of barnacle species on the transect near Cellar Beach. The heavy line with square symbols is the long-term trend in the 'warm index', as 10-y running means. The line with open circles shows the shorter-term trends as deviations of the annual warm index from this long-term trend. The broken line is the 5-y running means of sea temperature in Plymouth Sound (see also Figure 4), and the thin solid line is the annual mean sunspot number. Note that the long-term trend in barnacle species has not yet returned to the values found in the 1950s. The correlation between the short-term barnacle fluctuations and sea temperatures two years earlier, and a lesser correlation between the barnacle fluctuations and sunspots three years earlier, is not obvious after 1975, as discussed in the text.

## *Changes in predator abundance*

The dog-whelk, *Nucella lapillus*, which preys on barnacles and mussels, was always present on the transect up to the 1970s, and at low tide there were sometimes quite large numbers of its relative *Nassarius incrassatus*, which is both a predator and scavenger. The dog-whelk was as ubiquitous as the common limpet, *Patella vulgata*, and no consistent counts were made of either. Going back through the field notes in the light of the discovery that the species is sensitive to organotin-based antifouling paints (Bryan *et al.*, 1986; Gibbs & Bryan, 1986) it is evident that *Nucella* was present at over 100 $m^{-2}$ at the low-water levels in the 1950s and 1960s and has gradually disappeared from the Yealm transect in the past twenty years. It declined by an order of magnitude between 1968 and 1972 and a similar decrease occurred in 1974. A further decline took place after 1974, and currently, since 1985, there are no *Nucella* on or near the transect. Even on the extensive reefs at Wembury, nearby, an hour's search in 1987 produced only three living dog-whelks, and few dead shells (*cf.* Southward & Southward, 1988).

### *Changes in algal cover of the rocks*

In the 1950s the lichen *Lichina pygmaea* and the alga *Pelvetia canaliculata* were present at high-tide level close to the transect, with *Fucus serratus* and *Laurencia pinnatifida* sparse at MTL, more abundant at LWN. In 1960-61 there was an unusually dense settlement of *Fucus vesiculosus* (>50% cover) at MTL; this thinned out in 1965, but a population persisted through to 1976, from 5 to 15% cover. It then vanished from the immediate area of the transect, and only a few tufts were noted in one year, 1982. From 5 to 25% cover of *Fucus spiralis* was seen from 1964 to 1972, but is not now found on or close to the transect. *Laurencia pinnatifida* has always been present on the transect in patches of varying extent and position on the steep shaded faces between MHWN and MLWN, the cover varying from 5 to 50% without evident trends from year to year. *Fucus serratus* is always present from MTL, at 2-15% cover, increasing to 50% in places at MLWN. Among other algae, the kelps *Laminaria digitata* and *L. saccharina* occur only below the lowest level sampled, 1·2 m above CD, but patches of *Chondrus* and *Rhodymenia* occur in shady spots, from MTL down. Very occasionally, at certain levels between MT and LW, the algae mentioned can jointly occupy all the rock space for a metre each side of the transect, thus excluding barnacles, but the normal situation is for the barnacle cover to be greater than 50% of the rock surface. The counts reported here refer to this barnacle-covered surface.

## TRENDS IN RELATION TO THE ENVIRONMENT

The forty years' data show that the variations in abundance of *Chthamalus* and *Semibalanus balanoides* correspond with minor fluctuations in sea temperature. The inverse relationship between the warm-water species and the cold-water species is quite evident from the data, even though, as already noted, the two are not in full competition for space on the rock since there is always some free space for settlement. It was suggested on the basis of the observations up to 1975 (Southward *et al.*, 1975) that the approximate 10-y cycle in the barnacle index and temperature data was linked to the well-known 10-11 y solar cycle, of which the sunspot index is an external and easily observed manifestation (shown in Figure 5), and that the proportions of the barnacle species were varying in accordance with climate, warm phases favouring *Chthamalus* and cold phases *S. balanoides*. After adding the additional 15 years' observations now available the data set continues to show significant correlation with the mean inshore sea temperature and to a lesser extent with the solar cycle (Table 8). As might be expected from a longer series, other causes of variability reduce the correlation between sea temperature and the barnacle indices. At its best, with a 2-y lag, temperature accounts for more than 40% of the variance and is thus still the major factor in determining the ratio of the warm-water species to the cold-water species. The occurrence of such a relationship is evident from the quick response shown in years when there has been unusually rapid cooling of the climate *e.g.* from the winter of 1961-62 through to the summer of 1963; or during a sudden warming *e.g.* in 1988 and 1989.

https://doi.org/10.1017/S002531540005311X Published online by Cambridge University Press

Table 8. *Correlation coefficient (r) between annual mean sea temperatures (Plymouth Sound), solar activity (mean annual sunspot number) and changes in the proportion of the barnacle species (as 'indices') on the transect near Cellar Beach, River Yealm. The indices are listed in Table 7.*

| | Sea temperature annual | Sea temperature 5-y smoothed | Sunspots |
|---|---|---|---|
| Same year | | | |
| BI | 0.28 | 0.55 | 0.11 |
| WI | 0.25 | 0.50 | 0.12 |
| NI | -0.11 | -0.27 | -0.03 |
| CI | -0.24 | -0.47 | -0.11 |
| 1-y lag | | | |
| BI | 0.46 | 0.62 | 0.24 |
| WI | 0.46 | 0.58 | 0.23 |
| NI | -0.16 | -0.27 | -0.12 |
| CI | -0.43 | -0.54 | -0.20 |
| 2-y lag | | | |
| BI | 0.58 | 0.67 | 0.33 |
| WI | 0.60 | 0.63 | 0.31 |
| NI | -0.02 | -0.25 | -0.16 |
| CI | -0.60 | -0.60 | -0.28 |
| 3-y lag | | | |
| BI | 0.36 | 0.64 | 0.40 |
| WI | 0.34 | 0.59 | 0.39 |
| NI | -0.14 | -0.30 | -0.15 |
| CI | -0.31 | -0.55 | -0.36 |

The lesser factors that influence the relative abundances of the barnacles and which might be responsible for the increased variance of the data in the long-term, include both biotic and abiotic factors. On the present data there seems to be no obvious relationship between the small changes in algal cover of the rocks and the fluctuations in barnacle species abundance. When algal cover increases rapidly to 100%, as after removal of grazing herbivores (Southward & Southward, 1978), barnacles decline almost to zero within a year or two. But, as noted on p. 498, the transect always carries some bare rock available for colonisation, and any exclusion by algae was very localised.

However, the great decrease in abundance of the predacious dog-whelk, *Nucella lapillus*, from the transect and from most shores around Plymouth (p. 508) could be an important biotic factor. The role of *Nucella* as a structuring factor on the barnacle zone and its species composition in south-west Britain cannot now be tested by exclusion experiments (Burrows, 1988) owing to the overall low population density. It is conceivable that a high population density of dog-whelks might increase the turn-over rate of all barnacles, even if no particular species was actually selected for food, and that the amplitude of changes of species composition might be reduced when dogwhelks are absent.

Another possibly important factor affecting species composition would be an overall change in climate superimposed on the 'normal' fluctuations already seen. In assessing correlations between the biota and the annual mean sea temperature we are assuming that the seasonal range of temperature and the temperature extremes remain similar during small increases or decreases in the mean. This might hold good for stochastic variations or for changes linked to the steady solar cycle. It might not be true during major shifts of climate, for example, such as is expected from the increasing concentration in the atmosphere of carbon dioxide, methane and the chlorofluorocarbons. This 'greenhouse' effect might well produce shifts in the extremes and in the annual range of temperature, and cause changes in the general weather pattern; such changes might precede or mask the emergence of a definite upward trend in mean sea temperature. It is conceivable that the combined effect of such changes might result in increases in short-term climate variability that would lead to destabilisation of dominance by one particular species of barnacle, given the 2-y phase-lag that exists between trends in temperature and trends in adult barnacle abundance. Indeed it is possible that the barnacle populations are already responding to climatic change of this sort, too subtle to be discernable from the averaged temperature data. The onset of the changes in the proportions of the barnacle species, leading to lesser amplitude fluctuations and an apparent upward trend in the barnacle index and the warm index (Figures 4 & 5), can be placed in the mid 1970s. The dog-whelk was already in decline, and the concentration of 'greenhouse gases' had begun to change much earlier (Hansen *et al.*, 1981). On present data it is difficult to separate the effects of these two factors and determine the causes of the changed relationships after 1975. There is evidence for a change in UK weather patterns since the mid 1970s, including decreasing spring and early summer rainfall, and the decade just ending has seen some surprising extremes of heat and cold as well as severe storms.

Continuance of the barnacle observations could help to distinguish the other biotic and abiotic factors involved in controlling the relative proportions of the species in relation to changes in temperature and climate and provide an early-warning system for the biological effects of global change in climate. If a significant rise in mean sea temperature does occur in our latitudes as a result of global warming, then factors other than change of temperature become less important and confident predictions can be made of further increases in abundance of *Chthamalus* at the expense of *S. balanoides*. We could also predict that comparable changes in species composition, leading to replacement of cold-water species by warm-water species, would occur generally in shelf seas and would involve longer-lived organisms such as demersal and pelagic fish.

Thanks are due to Dr Eve Southward for help with the field observations; to Dr A. Koeckelenbergh, Sunspot Centre, Observatoire Royal de Belgique, Bruxelles B-1180, for sunspot numbers; and to an anonymous referee for constructive comments. An award under the NERC small grants scheme helped to put the data into computer-compatible form.

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Submitted 9 January 1991. Accepted 12 February 1991.