The effects of the winter of 1962/63 on the British marine fauna

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KURZFASSUNG: **Die Wirkungen des Winters 1962/63 auf die Britische Meeresfauna.** Während des ungewöhnlich kalten Winters 1962/63 herrschten die niedrigsten Temperaturen an der Südostküste Großbritanniens. Die größten negativen Anomalien dagegen wurden an den Küsten von Hampshire und Dorset, im Bristol-Kanal und in Teilen von Nord-Wales festgestellt. Die nördlichen Formen wurden im allgemeinen nicht ernstlich beeinträchtigt, aber einige keltische und südliche Formen erlitten sehr hohe Verluste im Bereich der Gezeitenzone, insbesondere in mehr oder minder abgeschlossenen Buchten im Gebiet der oben erwähnten Lokalitäten. Bei den südlichen Formen der exponierten Küsten der westlichen Vorgebirge war die Sterblichkeit relativ gering; marine Algen wurden ebenfalls nur wenig geschädigt. Der Tod trat nicht nur als direkte Folge der Kälteeinwirkung auf die Gewebe ein, sondern wurde auch durch die zu weit gehende Herabsetzung der Aktivität (etwa unzureichende Zilienaktivität zur Entfernung sedimentierender Schlammpartikel, mangelnde Anhaftungsfähigkeit an die Felsoberfläche oder ungenügendes Eingrabungsvermögen) verursacht. Selbst in Situationen, in denen hohe Sterblichkeitsraten auftraten, überlebten im allgemeinen einige wenige (vielleicht resistentere) Individuen in günstigen Habitaten, so daß die Verbreitungsgrenzen nur geringfügig beeinflußt wurden. Bei vielen Litoralformen spielte zudem ein adaptives Verhalten eine wichtige Rolle für das erfolgreiche Überstehen der Kälteperiode.

CONDITIONS IN BRITAIN DURING JANUARY AND FEBRUARY 1963

From late December 1962 until late February 1963 air temperatures over a large part of southern England averaged between 5 and 6° C below the seasonal average. Figure 1 shows the isobars and winds from a typical weather map for the period. High pressure to the north and low pressure to the south of the British Isles brought an easterly air stream across the southern half of the country. Often, as on the occasion illustrated, the easterly wind was of gale force in many coastal areas and these gales, coupled with the intense cold, were a major factor in damage to marine life (GIBSON 1963). At other times high pressure centred over the British Isles produced calm clear weather with extremely severe frost at night. The isotherms shown in Figure 1 do not refer to any one particular occasion but are intended to show the areas most generally affected by severe cold. They are based on the average of the 6 a. m. temperature readings following four of the coldest nights (Jan. 12, 22; Feb. 4 and 25). It can be seen from the hatched area indicating an average of below −7° C on these four nights that, although the south and south east were the most severely affected areas as in most winters, severe weather extended unusually far westward reaching the coasts of Dorset and Hampshire, the Bristol Channel and North Wales. Figure 2 gives the negative anomalies of the mean minimum temperatures averaged over January and February for a number of coastal and inland stations. From this map it can be seen that the greatest anomalies, exceeding 5 C over the whole period, occurred in a wide band

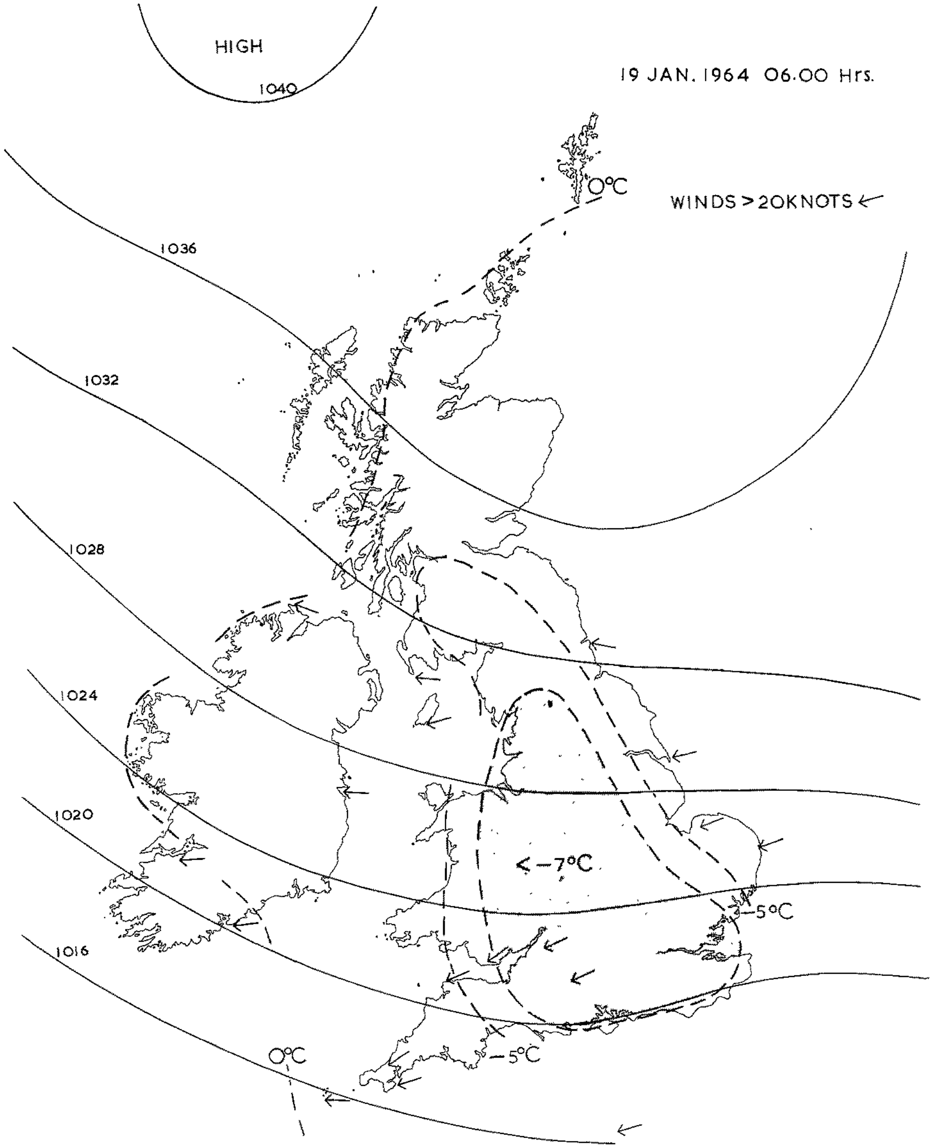

Fig. 1: Weather map illustrating typical conditions in the British Isles during the winter of 1962/63. The isotherms are based on the average 6.0 a.m. temperatures after the four cold nights of Jan. 12, 22, Febr. 4, and 25, and indicate the generally coldest areas throughout the period. Data from daily weather maps, Meteorological Office, London

running from north-west to south-east and affecting the coasts of North Wales, much of the Bristol Channel and the south coast from Devon to Hampshire. Further west, along the peninsulas of south-west England, South Wales, North Wales, throughout northern Scotland, the Hebrides, Shetlands and the whole of Ireland, the extremes of cold, both absolute and relative, diminished considerably. Much of the south-west of Ireland and extreme west of Ireland and Scotland were little affected by freezing conditions. Both temperatures and anomalies were less severe than might have been expected on the north east coast of England and Scotland, perhaps on account of the moderating effect of air flowing almost continuously off the North Sea.

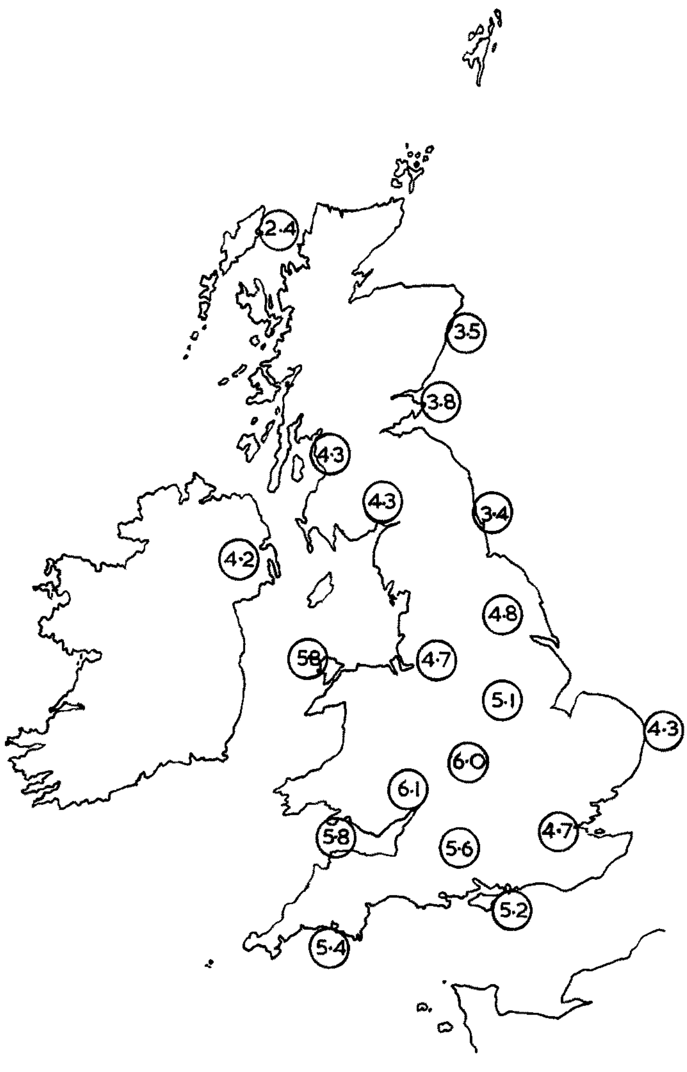

Fig. 2: Negative anomalies of mean minimum temperatures for January and February 1963 (in respect of long term averages for these months)

The winter of 1962/63 therefore provided a large scale natural experiment, the results of which may allow marine organisms to be classified according to their tolerance to cold, and the part played by severe winters in determining their distribution to be assessed. To this end a number of independent observers in Britain jointly reported in detail the effects they had observed on marine organisms at various parts of the coast (Crisp et al. 1964). The account that follows is a summary of these observations and I wish to acknowledge the co-operation of all those who took part.

THE DISTRIBUTION OF THE MARINE FAUNA IN BRITAIN

The effects of the winter are best considered in relation to the distribution of three main elements comprising the British fauna. The northern forms, whose distribution extends northwards well into the Arctic circle, do not spread far, if at all, to the south of the British Isles. Many extend all round the British coast, but some are more abundant in the north and east. The Celtic forms, whose centre of distribution is located approximately at the latitude of the British Isles, range both to the north and to the south and occur on all parts of the British coast. The southern forms, whose centre of distribution is usually in Mediterranean latitudes, reach their northern limits in Britain and are found only on the west and south west coasts. Some of these forms, such as *Chthamalus stellatus* and *Gibbula umbilicalis,* extend eastward as far as the Isle of Wight and reach the north of Scotland (Fig. 3); others, such as *Paracentrotus lividus,* are confined to the extreme south west and west of Ireland. Southern forms with intermediate limits are shown in Figures 4, 5 and 6.

The distribution of the fauna as a whole, and of such southern forms as *Chthamalus stellatus* in particular (Moore & Kitching 1939, Kitching 1950) reflect the pattern of winter temperature. The milder Atlantic air over the west and south west normally alleviates the colder continental conditions that frequently affect the eastern half of the country. Whether these lower winter temperatures exert a critical influence on the north eastward extension of these forms, or whether some other factor associated with proximity to the Atlantic controls their distribution, has been the subject of debate. Other possible influences are proximity to deep water and wave exposure (Fischer-Piette 1936), the nature of submarine deposits (Smith 1953), and differences in the biological or chemical constituents of Atlantic water (Reid 1935, Moore & Kitching 1939, Powell 1954, Moyse 1963). The results of a long period of negative temperature anomaly should help to discriminate between these alternatives.

MORTALITY OF INTERTIDAL FORMS

South east

In the south and south east where temperatures were minimal, the fauna consists only of northern and Celtic forms. Estimates of mortalities in the intertidal zone made by several observers in this area are summarized in Table 1.

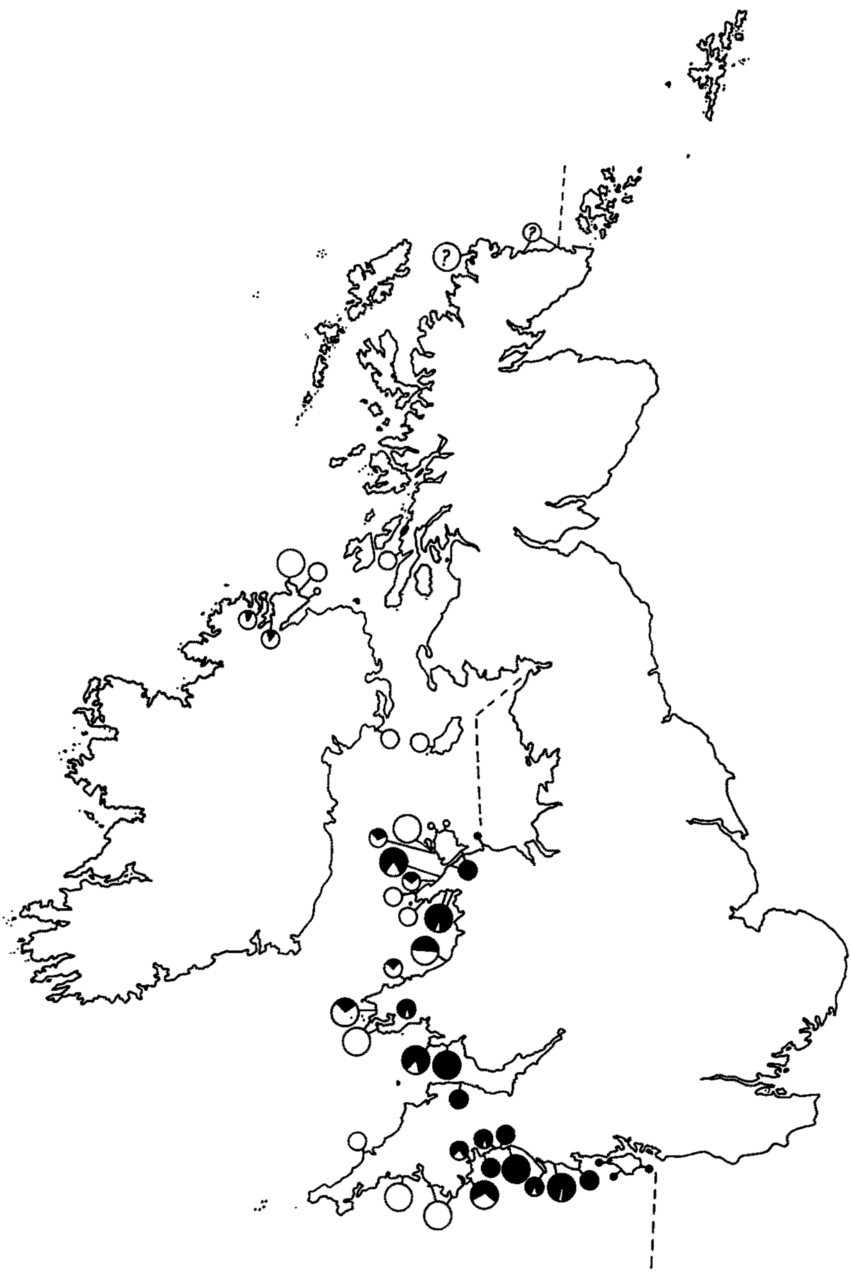

Fig. 3: Mortality observed in the topshell *Gibbula umbilicalis.* Size of circles represent previous abundance; large circles: abundant, medium circles: common or frequent, small circles: rare or local. The fraction of the circle blacked out represents reported mortality. Clear circles: reports that mortality was insignificant. Question marks: absence of relevant data. Broken lines indicate previously established limits of distribution

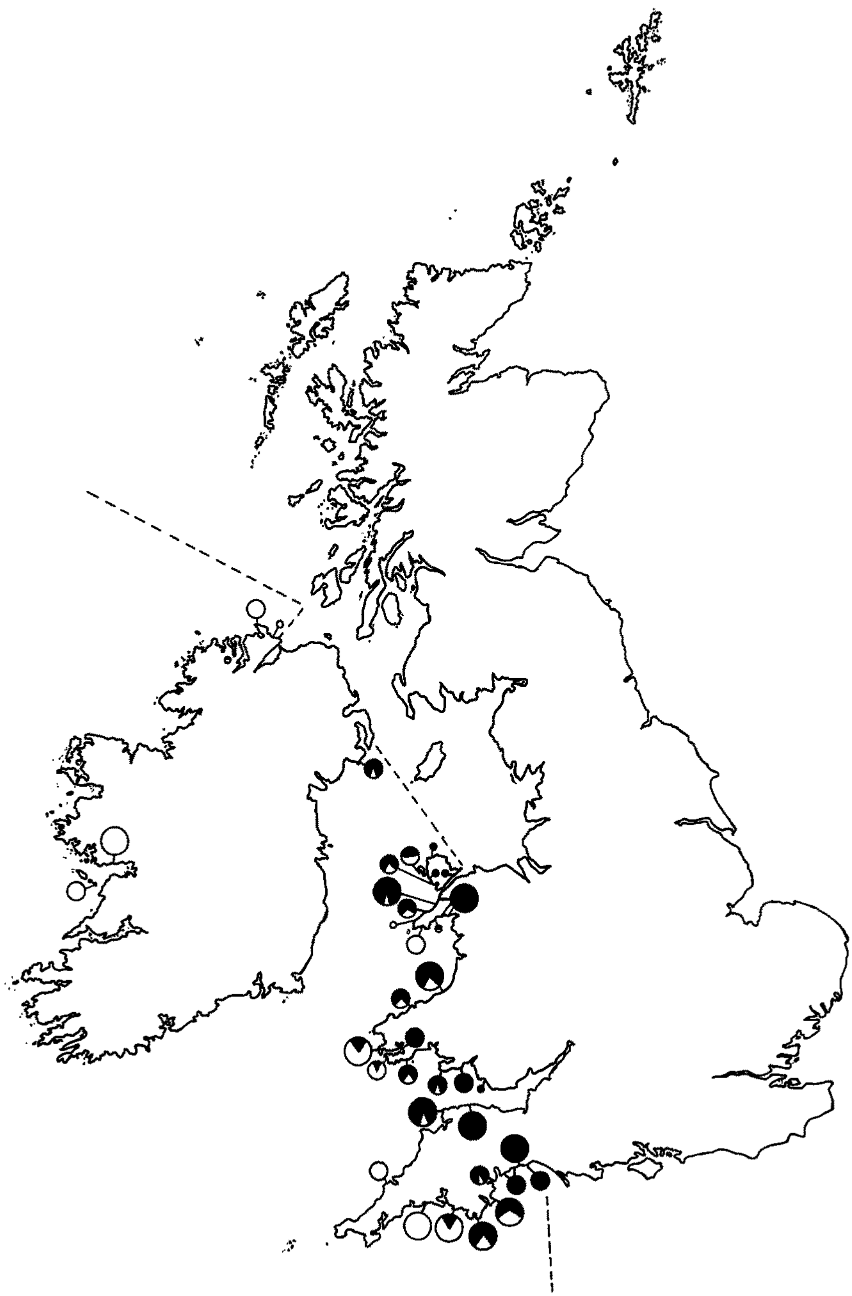

Fig. 4: Mortality of the large topshell *Monodonta lineata.* Symbols as for Figure 3. Northern limits of distribution further south, and mortality generally greater

Fig. 5: Mortality of the barnacle *Balanus perforatus*. Symbols as for Figure 3. This species is absent from Ireland (CRISP & SOUTHWARD 1953)

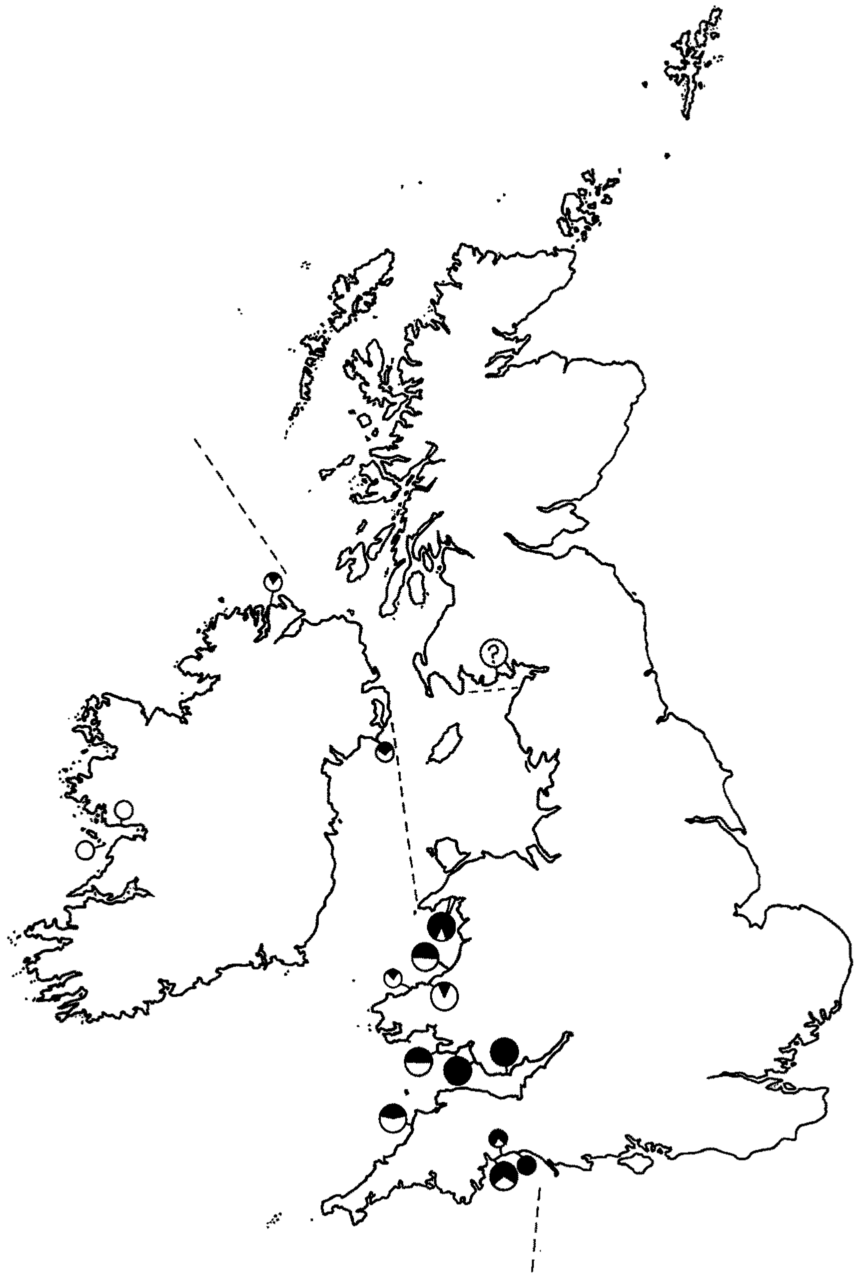

Fig. 6: Mortality of *Sabellaria alveolata*. Symbols as for Figure 3. This species was widely affected, perhaps because it is found on sandy gently shelving shores

Table 1

Intertidal mortalities reported from south and south east England. (100 % mortality implies that dead individuals only were found in the intertidal zone after the frosts. Individuals below low water mark may have survived)

Indigenous forms		Immigrants	
Lanice conchilega (PALLAS)	100 %	*Crassostrea angulata* LAMARCK; from Biscay	100 %
Gibbula cineraria (L.)			
Anomia ephippium L.		*Ostrea edulis* L.; Brittany race	100 %
Scrobicularia plana (DA COSTA)			
Ensis siliqua (L.)		*Elminius modestus* DARWIN; Australasia	50– 80 %
Ensis ensis (L.)			
Pholas dactylus L.	95 %		
Ostrea edulis L.	50–100 %	*Crepidula fornicata* (L.); E. United States	25 %
Venerupis pullastra (MONTAGU)			
Cardium edule L.	50– 60 %		
Mytilus edulis L.	0– 30 %	*Venus mercenaria* L.; E. United States	5 %
Balanus balanoides (L.)	10– 20 %		
Polydora ciliata (JOHNSTON)	Negligible	*Urosalpinx cinerea* SAY; E. United States	Negligible
Hyas araneus (L.)			
Asterias rubens L.			

Clearly many Celtic forms suffered heavy mortality but northern forms, as a whole, escaped. Immigrants from the eastern coast of the United States, where extremes of temperature are regularly encountered, were also little affected. Conditions very similar to those of the south east were experienced on the shallow sandy coasts of the eastern Irish Sea and the Solway Firth where the resident fauna is similarly depleted of southern forms.

Land influenced western and south western coasts

Under this heading I include those parts of the west and south west coast that lie nearest to the centre of the main land mass of the British Isles over which the coldest air was located (Fig. 1). They comprise the coast from Hampshire to east Devon, the coasts of the Bristol Channel and parts of the coast of North Wales. These areas are of particular interest not only because they mark the limits of distribution of certain southern forms (CRISP & KNIGHT-JONES 1954, CRISP & SOUTHWARD 1958) but also because they experienced the largest negative temperature anomalies during the cold spell (Fig. 2). It is not surprising therefore that some southern forms suffered complete or nearly complete mortality in these areas. These animals are listed in Table 2.

Farther west, where conditions were milder, an increasing proportion of the population of these same animals survived. Hence extreme temperature in winter appears to be one factor, and probably the main one, limiting their distribution. However, other forms with similar limits of distribution, such as the barnacle, *Chthamalus stellatus,* and the algae, *Cystoseira granulata* and *C. ericoides,* were unaffected by the cold. Furthermore, many of the Celtic forms which suffered high mortality in the south east were killed in these land influenced western areas also. High mortalities between the tide marks were recorded for *Actinia equina, Cereus pedunculatus, Sabella pavonina* and *Portunus puber,* in addition to those animals listed in Table 1.

Table 2

Southern forms which experienced heavy mortality in the intertidal zone on land influenced coasts

Species	Regions where heavy mortalities were observed
Anemonia sulcata (PENNANT)	Hampshire–Dorset, Bristol Channel
Branchiomma vesiculosum (MONTAGU)	Bristol Channel
Audouinia tentaculata (MONTAGU)	North Wales, Cardigan Bay
Sabellaria alveolata (L.)	Dorset, Bristol Channel and Tremadoc Bay
Patella intermedia JEFFREYS	Hampshire–Dorset
Monodonta lineata (DA COSTA)	East Devon, Bristol Channel, North Wales
Gibbula umbilicalis (DA COSTA)	Hampshire–Dorset, Bristol Channel, North Wales
Pharus legumen (L.)	Bristol Channel, North Wales
Balanus perforatus BRUGUIÈRE	Hampshire–East Devon, Bristol Channel (absent from North Wales)

Atlantic influenced western coasts

Under this heading are included the peninsulas of south west England and Wales and the west coasts of Ireland and Scotland. The negative anomaly was not as great as elsewhere because these areas are at all times under the influence of the open sea, but the winter was nevertheless exceptional, except perhaps in west Scotland and in the Hebrides. Surprisingly, none of the forms investigated that were typically restricted to these western shores showed any evidence of exceptional mortality. These included *Bifurcaria rotunda*, *Cystoseira* sp., *Paracentrotus lividus* and *Xantho incisus*. Table 3 lists all the southern forms which did not appear to have been influenced by the cold and whose distribution limits, therefore, probably should not be attributed to winter extremes of climate.

Table 3

Southern forms which did not experience exceptional mortality

Bifurcaria rotunda (HUDS.) PAPENF.	*Chthamalus stellatus* (POLI)
Cystoseira ericoides (L.) AG.	*Xantho incisus* LEACH
Cystoseira granulata AG.	*Clibanarius misanthropus* RISSO
Cystoseira fibrosa (HUDS.) AG.	*Paracentrotus lividus* (LAMARCK)

It is interesting to note that, except for *Patella intermedia*, most of the cold sensitive forms shown in Table 2 occur more abundantly in sheltered or embayed areas, where greater extremes of local heating and cooling occur, than on the more equable exposed coasts of the western promontories. These promontories thus function as refuges where survival is possible during and after extreme winters as can be seen from the changed distributions shown in Figures 3 to 6. The apparently cold tolerant forms (except *Cystoseira granulata*) are by contrast more common on or near these exposed promontories, so that their most favoured habitats are seldom visited by severe frosts. However, there can be little doubt that *Chthamalus stellatus,* at least, is a genuinely cold tolerant form, since it can survive transplantation to the east coast of Britain (Crisp 1950) and artificial exposure for over 12 hours to temperatures of -10^0 C (Southward 1958). Apart from the high proportion of southern forms that were unaffected the mortalities experienced by each of the three faunal groups (Table 4) followed the expected pattern.

Table 4

Mortalities of three main faunal elements in Britain

Distribution and no. of species in sample	Severe mortality	Less severe mortality	Unaffected
Southern (21)	57 %	24 %	19 %
Celtic (36)	39 %	47 %	14 %
Northern (26)	0 %	15 %	85 %

MORTALITIES BELOW THE TIDE MARKS

Deaths of fish and of sub-littoral invertebrates, though most obvious in relatively shallow parts of the sea near the coast, were also evident over large areas of the North Sea. Most obviously affected, both among vertebrates and invertebrates, were southern forms such as the fish, *Conger conger, Solea vulgaris, Gobius paganellus, Labrus bergylta,* and *L. ossifagus;* the crustacea *Maia squinado, Palinurus vulgaris, Porcellana longicornis, Corystes cassivelaunus* and species of *Portunus;* and the cephalopods *Octopus vulgaris* and *Sepia officinalis.* Bivalves suffered particularly heavy mortality and included such forms as *Nucula nucleus, Ostrea edulis, Pecten maximus, Cardium echinatum, Spisula solida, Mactra corallina, Lutraria lutraria,* all British species of *Ensis* and *Pharus legumen.* Considerable numbers of *Echinocardium cordatum* and *Psammechinus miliaris* were reported killed in the more severely affected areas.

CAUSES OF DEATH

Mortality may result either from the direct effect of low temperature on the tissues or from the indirect results of lowered metabolism and consequent disorganization of vital processes. Direct tissue damage may result from the intrusion of ice crystals, the formation of air bubbles, or from the raised osmotic pressure of the unfrozen tissue fluids (Scholander et al. 1953). Some cold hardy forms can tolerate the freezing of 60 to 70 % of their water, provided that the ice crystals form in the intercellular spaces (Kanwisher 1955). Hence intertidal forms such as *Chthamalus stellatus, Elminius modestus* and *Balanus balanoides,* which are subject to desiccation by evaporation in summer, may be pre-adapted to withstand the effects of dehydration of the tissue fluids by freezing in winter.

Although temperatures within the intertidal zone fell to values at which ice crystals might be expected to form in the tissues of many organisms, and although deaths immediatly following the hard frosts were observed on some occasions, there was much evidence to indicate that the indirect effects of the cold weather were also a frequent cause of death. The evidence is summarized below.

a) Algae, even those such as *Pelvetia canaliculata* growing at the highest tidal levels, were not seriously affected. The mortality observed was almost entirely confined to animals. Animals exhibit a greater degree of physiological complexity and therefore would be more likely to become disorganized by prolonged cold (see KANWISHER 1955, 1957).

b) Severe mortality in many animals did not coincide with the coldest period but was delayed until later in, or even after, the cold spell.

c) Many fish and sub-littoral invertebrates were killed at temperatures above zero and appeared externally to be in perfect condition.

d) In some instances the younger and more active individuals were less affected than the older ones.

e) Fatal results of cold torpor and debilitation were obvious in flat fish (dermal sores), bivalves (failure to clear debris and mud from the mantle space), topshells (buried in gravel), razor shells (inability to burrow), and limpets and anemones (loss of adhesion).

f) Many organisms were stranded and left open to attack by predatory birds because their normal activities were slowed down.

FACTORS IN SURVIVAL

Despite heavy mortalities to certain organisms, particularly in the intertidal zone, the complete destruction of a species over a significant length of shore, even at the extreme limits of its range, was unusual. *Gibbula umbilicalis, Monodonta lineata, Balanus perforatus* and *Sabellaria alveolota,* southern forms with a limited vertical range on the shore, afford some of the few examples of extensive and complete mortality (Figs. 3–6). Even in these species, however, the distribution limits were not necessarily modified because isolated populations survived on the milder promontories (see above). In most species studied however some individuals escaped in almost every locality by one of the following means.

Individual variations in tolerance

Not only were young forms of certain species found alive more commonly than adults (e. g. *Carcinus maenas, Anomia ephippium, Pholas dactylus*) but the existence of racial differences in tolerance can also be inferred. *Ostrea edulis* of the Britanny race died more readily than native oysters. *Actinia equina,* although it extends as far north as the White Sea, suffered heavy mortality in South Wales (93 % in an area carefully observed by MOYSE & NELSON-SMITH) and elsewhere (CRISP et al. 1964). Similarly SOUTHWARD (1958) found that 50 % of the population of British specimens of *Balanus balanoides* could not survive for more than a day below -10^{0}C whereas PETERSEN

(1962) reports survival of the same species in Greenland after having remained in the ice foot over the winter at temperatures falling to -35^{0} C. It therefore seems likely that more tolerant races must exist in Arctic waters. If such racial variations in tolerance have evolved in different areas, individual differences must presumably exist in any one area.

Variations within the habitat in the degree of exposure to cold

At the shore level where the lowest ebb tides coincide with severe frosts, an abrupt change must occur in the temperature minimum experienced by the habitat. Beyond this point the habitat is continuously immersed and the temperature cannot therefore fall below -1.9^{0} C, the freezing point of sea water of normal salinity, except in the very unlikely event of super-cooling. Not surprisingly, therefore, many populations that were completely eliminated within the intertidal zone survived below low water mark (e. g. *Lanice conchilega*, *Sabella pavonina* and *Pharus legumen*).

The higher the shore level the longer is the rock exposed to radiation cooling during frost. Clearly marked increases in mortality at higher shore levels could be observed in such forms as *Patella vulgata* growing on exposed rock, *Tanais chevreuxi* living in crevices, and *Sabellaria alveolata* living in its own sand tubes. On parts of the coast where the shore line was steep and deep water not far distant, the mortalities of intertidal forms were considerably lower than those on flat sandy shores nearby where the water was shallower and therefore colder. Animals that had been able to retreat into crevices, below the surface of deep pools or beneath thick beds of algae, survived better than those remaining on bare rock surfaces. There was some evidence that lowered salinity and the associated silt in estuarine waters tended to increase mortality.

Adaptive behaviour

Many free-living intertidal forms, particularly shore fish, crustacea and gastropods, move down the shore during winter, sometimes entering deep pools and sometimes penetrating into deep water beyond the tide marks (Yonge 1949, Jannsen 1960, Naylor 1963). Species that were observed to have disappeared after the frosts but which returned during the following spring and summer were *Blennius pholis, Gobius paganellus, Ligia oceanica* and *Diogenes pugilator*. One member at least of the fauna inhabiting rock crevices, *Tanais chevreuxi*, was observed to have moved deeper down the crevice and away from the region of ice crystal formation at its entrance. In contrast many individuals of *Audouinia tentaculata*, for reasons not understood, emerged from their burrows and were in consequence completely exposed to the cold. It is thus clear the behaviour of the animal may play an important part in its survival during exceptionally cold winters.

SUMMARY

1. During the exceptionally cold winter of 1962/63 the south east coasts of Great Britain suffered the coldest conditions, but the coasts of Hampshire and Dorset, the Bristol Channel and parts of North Wales the greatest negative anomalies.
2. Northern forms were not generally seriously affected, but some Celtic and southern forms suffered very high mortality in the intertidal zone, particularly in embayed situations in the areas mentioned above.
3. Southern forms limited to exposed western promontories did not suffer much damage; marine algae were also little affected.
4. Death was caused, not only as a direct result of exposure of the tissues to extreme cold, but also from the general lowering of the animals' activity; for example, failure to remove silt by ciliary action, to cling to rock surface, and to burrow, led to many deaths.
5. Even where high mortality was experienced, a few, perhaps more resistant, individuals of the species generally survived in favourable habitats, so that distribution limits were little affected. Adaptive behaviour played an important part in the survival of many littoral forms.

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Discussion following the paper by CRISP

BOOKHOUT: Was there any evidence that northern animals moved southward as a result of the severe winter of 1963? At Beaufort, North Carolina (USA), *Mytilus edulis* moved in and covered the pilings. This has not been the case at Beaufort before.

CRISP: No, I don't think there was any evidence of northern forms becoming more common. The only effect observed of this nature was that some of the northern forms, such as *Balanus balanoides* and *Mytilus edulis,* had a particularly heavy spat fall in the following spring.

WELLS: When the rising tide arrives, a littoral animal may experience a sudden change of temperature. Have you data on the difference between air and water temperature in various places, which would show whether such shocks, as distinct from the actual temperature levels, have had significant effects?

CRISP: What we could give are the differences in mean temperature of air and sea but not the absolute or relative values at the time the tide was rising. The intertidal temperatures on the shore itself were not measured. It would be very interesting to know just what these are and to what extent they act as a limiting factor and whether any part is played by temperature shocks. Many animals live almost buried in the sand, and these would not suffer such a sudden change as the animals living on the rocks.

BOOLOOTIAN: How did you ascertain your figures for mortality rates?

CRISP: I have presented the results of the cooperation of many people, including Dr. Alan J. SOUTHWARD, Mr. MOYSE, Mr. Nelson SMITH and Dr. Duncan WAUGH. Various methods have been used. One hundred per cent mortality is easy to measure: one didn't find any animals alive. The lower mortalities were more difficult. In some cases we compared counts made at different times, previous to the cold winter, with counts made subsequently. In other cases counts were made of the number of living and dead organisms during and just after the cold spell.

WIESER: Did the small animals survive better than the large ones because they could hide better (in crevices, for example) or because they were more resistant?

CRISP: I can only guess as to the answer to that. I suspect that the young ones may survive because the hungry gulls would not notice them, if they could conceal themselves. This would not, however, apply to animals, like the piddocks, that remain concealed in any case.