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Ditlef Rustad

A SURVEY OF THE INTERTIDAL ZONE OF SOGNEFJORDEN (WESTERN NORWAY) WITH SPECIAL REFERENCE TO *BALANUS BALANOIDES* (L.) (CIRRIPEDIA)

TRONDHEIM 1980

E R R A T A

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PAGE	LINE	FOR	READ
7	9	methane	wood gas
16	15	above 10 m	(0 m)
22	20	3 m	2 m
39		Fotnote no. 7	7) Eastern side of the headland. Temperatures measured in 0, 1, 2, and 5 m.
39		Fotnote no. 8	8) Western side of the headland. Temperatures measured in 0, 1, 2, and 5 m.

E R R A T A

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PAGE	LINE	FOR	READ
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by

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ABSTRACT

Rustad, Ditlef. 1980. A survey of the intertidal zone of Sognefjorden (Western Norway) with special reference to *Balanus balanoides* (L.) (Cirripedia). *Gunneria 36*: 1-74.[1]

The results of biological investigations of the intertidal zone in Sognefjorden, undertaken during the period 1937-1946, are presented. The distributions of *Balanus balanoides* and some other intertidal animals were directly related to the hydrographical conditions. The spat of *B. balanoides* did not survive in the areas where the surface salinity in the actual year fell below 5 o/oo. The horizontal and vertical distribution of *Balanus balanoides* is discussed in relation to physical and biotic factors.

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[1] Zoological Series 10.

PREFACE

I first visited Sognefjorden in 1937 to investigate the biology of the intertidal zone. After a few days, however, the plan had to be abandoned owing to engine trouble.

In 1941, because of war conditions, we were obliged to vacate the biological station at Herdla (near Bergen) and activities were transferred temporarily to Sogn. The prevailing war conditions still hampered our work in several ways, but using the provisional biological station at Hermansverk as a base we collected hydrographical and biological samples as part of an investigation of Sognefjorden. Of the latter only those from the intertidal zone are still extant. The samples from deeper water - the dredge and trawl catches etc. - alas, were for the most destroyed in a fire.

The present paper and a paper on hydrographical observations from Sognefjorden published in Gunneria 30 (1978) are extracts from my original report (Rustad 1977) which is deposited in manuscript form at the library at The Royal Norwegian Society of Sciences and Letters, the Museum.

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INTRODUCTION

It is a well-known fact that vast difference exists in the intertidal floras and faunas found in the outer and inner parts of the major Norwegian west coast fjords. However, the special investigations of these differences have been very few. A few algological investigations have been made (cf. Jorde & Klavestad 1963, p. 3), but with regard to the fauna there is only Brattegard's (1966) investigation of the distribution of the fauna of rocky shores in Hardangerfjorden. The previous, very sparse, information is cited and summarised therein (cf. Brattegard 1966, p. 2).

The purpose of the investigations reported here was: firstly, to ascertain in what respects the fauna of the intertidal zone changes from the outer to the inner part of the fjord, secondly, to detect any possible fluctuations in abundance or distributions from year to year in species distributions; and thirdly to find the reasons for the difference between the outer and inner part of the fjord and for any observed fluctuations.

In the intertidal zone we find continually varying environmental conditions along the shore, and a corresponding marked variation in the development of the intertidal flora and fauna. Thus, as a rule, a marked difference exists between the intertidal fauna of headlands and that of bays. This variability, which may be found even over quite a restricted area, is superimposed on the large-scale variations which caused the difference between the outer and inner part of the fjord, and which is capable at times of disturbing the latter picture. During an investigation of the large-scale variation it is therefore necessary to choose strictly comparable localities. I have therefore chosen the conditions on the protruding headlands as representative of the large-scale variation. The conditions in the larger or smaller bays are then considered as possible deviations caused by local changes in the environmental conditions. Theoretically one might conversely consider the conditions in the bays as the norm, but since the habitat conditions in the sheltered bays seem to be much more complicated than those on the more exposed headlands, it seems both more practical and more reliable to choose the headlands. Jorde & Klavestad (1963, p. 4) and Brattegard (1966, p. 3) made a similar choice. Some features from the more sheltered localities, however, will be included to supplement the picture.

MATERIAL AND METHODS

The positions of the investigated localities (stns 1-110) are shown in Fig. 2.

Observations were made either from the ship, with binoculars, as we passed by close to the shore, or by rowing ashore and making an on-the-spot inspection of the intertidal zone.

The investigation was started in 1937 and was continued during the years 1941-1946.

The 1937 cruise was planned to yield a general picture of the situation, as well as more detailed information on the distribution of *Balanus balanoides**. Because of engine trouble the cruise was unfortunately interrupted and so much delayed that the *Balanus balanoides* investigation could not be completed. Nevertheless, despite all their shortcomings, the observation yield a sufficiently reliable picture of the situasjon in 1937 that they can also be used to supplement the picure give by the later investigations.

When investigations were resumed, in the autumn of 1941, they were hampered by the war conditions. It was impossible, for example, to cruise further out than Stn. 8 on the south side and Stn. 51 on the north side, as fortifications and mine-fields rendered the outer parts of the fjord inaccessible.

As part of the investigation of the intertidal zone, a hydrographical survey of the upper 0-20 m of the water column was also undertaken. The results of this survey have already been published (Rustad 1978).

* Hereafter *Balanus* means the adult (one-year-old or older) *Balanus balanoides*, whereas the younger specimens are referred to as the 0-group.

RESULTS

Distribution of conspicuous animals and plants

In the outermost part of the investigated area - on the south side of Sognesjøen - a well-developed *Balanus* belt is the most conspicuous and characteristic feature of the intertidal zone*.

The *Balanus* belt is especially distinct and well-developed on exposed, smooth, vertical or overhanging rock surfaces, wherever the seaweed vegetation of the intertidal zone is either sparse or wholly absent. In the most extreme cases the whole *Balanus* belt is entirely exposed and uncovered. On sloping rock surfaces, however, the lower part of the *Balanus* belt is completely covered and hidden by a luxuriant seaweed vegetation. Just how much of the *Balanus* belt remains uncovered by seaweed in different places seems to depend upon the degree of wave exposure and the steepness of the rock. The broadest *Balanus* belt is found on the most exposed and steepest localities.

In the *Balanus* belt we usually find many *Patella vulgata* L., both above and within the seaweed zone, and many *Nucella lapillus* (L.) are also present, especially below the upper seaweed limit. In less exposed places one may find many *Littorina saxatilis* (Olivi) above and in the upper part of the *Balanus* belt, sometimes with *L. littorea* (L.) and *L. obtusata* (L.) lower down. The last-mentioned species is usually found browsing on the seaweed fronds, especially on *Ascophyllum nodosum* (L.) Le Jol.

West of Stn. 4 (Fig. 2) I have only found small and solitary specimens of *Mytilus*. Further inwards in the fjord more *Mytilus* gradually occurs. In the *Fucus* zone at Stn. 5 there was a dense population of small *Mytilus* overgrown with crowded *Balanus*.

The most conspicuous change farther inwards in the fjord is that the *Balanus* population decreases (cf. for example Fig. 4), whereas the *Mytilus* population at first increases and thereafter decreases again.

* The expressions 'zone', 'belt', etc. are used in a general way and no precise sociological meaning should be ascribed to them.

As far up the fjord as the mouth of F u g l s e t f j o r d e n *Patella*, *Nucella* and *Littorina obtusata* also become somewhat reduced in numbers, but *L. littorea* and *L. saxatilis* are still numerous.

The seaweed vegetation in the middle part of the fjord was much the same as that further out. The different species still formed fairly distinct belts. In exposed localities there was a belt of *Fucus spiralis* (L.) in the upper part of the intertidal zone. This was replaced lower down by a broader belt of *Fucus vesiculosus* L., and lower still *Fucus serratus* L. and then *Laminaria* sp. occurred. In more sheltered places, such as in the small bays, *Pelvetia canaliculata* (L.) was usually found above the *Balanus* belt, and *F. vesiculosus* was more or less replaced by *Ascophyllum nodosum*.

As regards *Balanus*, conditions seemed to become less favourable inwards up the fjord. On the other hand, both larger individuals and a broader belt of *Mytilus* occurred further inwards up the fjord. East of F u g l s e t f j o r d e n the *Balanus* population became still more markedly reduced. *Balanus* gradually disappeared from the *Mytilus* zone, so that from now on a characteristic white-and-black *Balanus-Mytilus* belt was sometimes visible on steep rocks, until finally becoming the rule. *Balanus* may still be found down in the *Mytilus* zone - especially on sloping rocks where seaweed was also present - but they were more scattered and in general now growed directly on the rock surface and only to a lesser degree on the *Mytilus* shells.

In favourable years the white-and-black *Balanus-Mytilus* belt was developed more or less all over the area between Stns 19 and 26. The *Mytilus* belt gradually broadened, so that at Stns 23 and 26 it spread down to 2-3 m below the upper *Balanus* limit. The animals - especially in the lower part of the *Mytilus* belt - were on the whole somewhat larger than those living nearer the mouth of the fjord.

Littorina littorea and *L. saxatilis* were still numerous, but *L. obtusata*, *Nucella* and *Patella* gradually decreased in number until they disappeared from the intertidal zone. *Nucella* was found as far up the fjord as Stn. 23. Although *Nucella* has not been particularly searched for along the shores between Stn. 23 and F i n n e f j o r d it is hardly conceivable that it extends further in than the mouth of F i n n e f j o r d e n. My innermost finds of *L. obtusata* and *Patella* are from the mouth of A r n a- f j o r d e n.

Beyond the inner limit for *Nucella*, the *Balanus* population did not show any characters which might be ascribed to the absence of this principal predator (cf. Barnes & Barnes 1962, p. 34). The reason may be that the number of *Nucella* specimens, and in consequence the intensity of predation, becomes reduced gradually inwards up the fjord.

Except that *Pelvetia* and *F. spiralis* had gradually become sparser, the seaweed vegetation did not yet show any marked changes. According to Dr Ove Sundene (pers.comm.) who accompanied us for a couple of weeks in 1942 and 1945, the distribution of a number of other algal species also change inwards up the fjord. They extend further inwards on the southern side of the fjord (cf. Jorde & Klavestad 1963, p. 61). I myself have no precise observations concerning the inner limits of the seaweed species, but *Pelvetia* went at least as far as Stn. 26 on the southern side of the fjord, and at all events was present to a point somewhat east of L ø n n e f j o r d on the northern side. *F. spiralis* penetrated further up into the fjord.

Yet further inwards up the fjord, the *Balanus* population decreased rapidly. Its inner limit was found to lie somewhere between Stns 31 and 33, its precise position varying from year to year. In some years the 0-group was found considerably farther inwards (e.g. to the mouth of L u s t e r f j o r d e n and to the head of A u r l a n d s f j o r d e n), but here they later died out and their shells were washed away in the course of the same summer.

The distribution of *Mytilus* also fluctuated. In favourable years there was a *Mytilus* belt at Stn. 35, about 3 m breadth and still one of 1.5 m breadth inwards to Stn. 42. The innermost limit of *Mytilus* (in the intertidal zone) lay somewhere in the outer parts of L u s t e r f j o r d e n and Å r d a l s- f j o r d e n. In other years only a sparse population was found in the area around the mouth of A u r l a n d s f j o r d e n. Below the low-water mark *Mytilus* may be found also further inwards up the fjords on anchored floating buoys or such-like.

L. saxatilis and *L. littorea* were sometimes found - occasionally in large numbers - quite far inwards up the fjord. *L. saxatilis* occurred at least as far in as ca. Stn. 49, and *L. littorea* inwards at least to Stn. 50, which is almost at the head of L u s t e r f j o r d e n.

East of A u r l a n d s f j o r d e n the seaweed belt consists of an upper, narrow belt of *F. vesiculosus*, with a luxuriant belt of *Ascophyllum* covering the rocks below; still lower down, a more or less continuous belt of *F. serratus* occurred. Where the off-shore bottom was gently sloping, a lush zone of a tall-growing type of *F. vesiculosus* could be found below the *F. serratus* belt and below the low-water mark. According to Ove Sundene this would most probably be *F. vesiculosus* f. *vadorum* (cf. Jorde & Klavestad 1963, p. 43). Even as far in as Stns 50 and 110 there is still quite a lot of seaweed. Both *F. serratus and Laminaria* sp. occur in the inner part east of A u r l a n d s- f j o r d e n, although only sparsely.

If we now turn to the northern side of the fjord, the belt limits found on the southern side are here displaced, sometimes quite considerably, towards the mouth of the fjord.

The order of the belts of the intertidal zone, which on the southern side was not encountered until just east of the mouth of F u g l s e t f j o r d e n, is found on the northern side already at Stn. 51. The *Mytilus* belt is well developed and the *Balanus* population so much reduced that, at least in some places, the characteristic white-and-black *Balanus-Mytilus* belt exists. I have no observations from areas situated further out on the northern side of the fjord, but by comparison with the hydrographic conditions found further inwards up the fjord, which indicate that the northern side is much more influenced by typical 'fjord conditions' than the southern side, there is no reason to doubt that *Mytilus* would have been found considerably further out towards the mouth on the northern side as compared to the southern side.

In favourable years the white-and-black *Balanus-Mytilus* belt was encountered on the northern side from stns 51-53 inwards to L ø n n e f j o r d e n, i.e. much nearer the mouth than on the southern side. The same appeared to hold for the optimum area for

Mytilus, viz. the *Mytilus* belt apparently attained its greatest breadth between Stns 63 and 73 on the northern side, compared to between Stns 23 and 35 on the southern side.

The distributions of the other molluscan species were also more or less skewed, with the inner limits laying furthest out on the northern side. Thus, I found that *Nucella* only extended inwards to Stn. 70, *Patella* to Stn. 73, and *Littorina obtusata* to about Stn. 74. In reality the skewness is greater than that indicated by the innermost finds of these species, since the populations present close to the inner limits were a good deal denser on the southern side of the fjord than at the corresponding localities on the northern side. Something similar was also the case with *Balanus*. The inner limits of the species were found at Stn. 99 on the northern side and at about Stn. 33 on the southern side. This does not represent a particularly skewed distribution, but on the other hand considerably more *Balanus* was usually found at Stns 30 and 31 than at Stn. 87 on the northern side.

The innermost limit for regular annual occurrence of *Mytilus* in the intertidal zone seems to be at about Stn. 100. My innermost find of *Mytilus* in the intertidal zone on the northern side came from Stn. 104. According to people living locally *Mytilus* may in some years be found still further inwards (cf. also p. 13/14).

The above statements apply to the more exposed localities (protruding headlands). In sheltered localities a marked reduction of the *Balanus* population was usually noted, but the opposite was occasionally the case in unfavourable years, when the population of the exposed localities had been reduced in numbers. The seaweed vegetation also differed somewhat from that found in exposed localities.

In sheltered localities in the outer part of the fjord *Pelvetia* was usually present above the *Balanus* belt and more or less abundant *Ascophyllum* was found in the *F. vesiculosus* zone, whereas both species were usually absent from exposed localities. *Pelvetia* did not occur in the inner part of the fjord, and its distributional limit perhaps lay somewhere between Stn. 28 and A u r l a n d sf j o r d e n. *Ascophyllum* usually also dominated the vegetation both on the headlands and in the bays.

The *Littorina* spp. also seemed to prefer less-exposed localities. They were certainly also found on rather exposed headlands, but never in such quantities as in the bays.

As regards *Balanus* my impression is that even in the outermost part of the fjord, where the *Balanus* specimens were living crowded together, there was practically everywhere more *Balanus* present on the headlands than in the bays. Farther inwards up the fjord this state of affairs usually became even more marked. Dense *Balanus* populations were only found on the more exposed sites, being much sparser in the bays. In the innermost part of its distributional area *Balanus* was preferentially encountered in relatively more exposed places. However, sometimes at localities with only scattered *Balanus* there were often richer *Balanus* populations present on stony substrates in the bays than there were on rocky headlands. It is possible that this is especially true during periods in which the hydrographical conditions are unfavourable to *Balanus* and that in such cases it is especially large, roughly one-year-old, specimens of the 0-group which are found.

In the outermost part of its area where *Mytilus* formed a belt of its own in the intertidal zone, it was perhaps commoner on the smaller headlands than in the smaller bays. Further inwards up the fjord, however, this was hardly the case. At the innermost limit of the annual occurrence of *Mytilus* (at about Stn. 100), and in unfavourable years, *Mytilus* was only found in the small bays and not at all on the headlands. In somewhat larger bays (e.g. Stns 62 and 64) the *Mytilus* population was usually somewhat reduced, but it is questionable whether in those cases the degree of wave exposure was the decisive factor.

In the outer part of the fjord *Nucella* shows a tendency to bunch together in clefts and crevices and wherever the rock surface is uneven, but they may also occur fairly numerously on *Balanus* and *Mytilus*, on smooth, exposed rock surfaces. Towards the inner limit of its distribution, however, *Nucella* was chiefly found in the bays and more rarely on the headlands.

Turning now to the fjord branches we would have expected to find a similar gradual change towards the head as that found in the main fjord. As regards the fauna and flora of the intertidal zone, however, a rather abrupt change occurred when entering the fjord branches. Even in Risnefjorden - the outermost of the fjord branches - the dominant *Balanus* belt disappeared just behind the headland at the mouth of the fjord. In the fjord branches, at most a development of the *Balanus* population corresponding to the conditions found well inwards up the main fjord was encountered - Types III-IV (cf. Table 1) - i.e. there were sparse, only occasionally rather more crowded, strips of *Balanus* above the seaweed belt, with not particularly many *Balanus* present within the seaweed belt. On the other hand, however, *Balanus* did occur right up to the head of some of the outermost fjord branches. In Risnefjorden and Eikefjorden *Balanus* was even found close to the river mouths. We did not investigate the intertidal zone at the head of Vadheimsfjorden, but comparing it with the conditions found in Høyangsfjorden and Lønnefjorden there is no reason to doubt that *Balanus* also occurred right up to the head of Vadheimsfjorden as well. In Fuglsetfjorden we found that the inner limit of *Balanus* lay in the narrow and shallow sound leading to the innermost basin, and in Finnefjorden *Balanus* extended barely beyond the sound into the innermost basin. In the innermost basin itself no *Balanus* specimens were found. These basins are typical 'poller'*, with an upper layer of fresh or brackish water, i.e. the habitat conditions are therefore quite different from those in the innermost parts of the other fjord branches. In Arnafjorden we found no *Balanus* in the innermost parts, but this may perhaps vary from year to year. In Fjærlandsfjorden *Balanus* was found only on the eastern side in the outer part of the fjord, which agrees well with the skewness found in the hydrographical conditions. Adult *Balanus* were found at the mouth of Sogndalsfjorden only in one year (St. 99, 2 June 1943). The rest of the fjord branches lie beyond the inner limit for adult *Balanus* in the main fjord.

The *Mytilus* population was also found to be considerably reduced inwards up the fjord branches, but in many of the branches

* 'Poll' (pl.: Poller) is the Norwegian term for a basin which is separated from the sea (open sea or fjord) by a narrow and shallow sound.

this species did occur right in as far as the head of the fjord.

In R i s n e f j o r d e n *Patella* was found half-way into the fjord. Apart from this and a few exceptional cases, neither *Patella* nor *Nucella* were found in any of the fjord branches. The *Littorina* spp., on the other hand, were found right up to the head of the fjord branches (excepting the inner basins of F u g l s e t-f j o r d e n and F i n n e f j o r d e n). This was also true for *L. obtusata* within its inner limit in the main fjord, i.e. it occurred inwards up to and including L ø n n e f j o r d e n and F i n n e f j o r d e n.

Fluctuations in the distribution of *Balanus balanoides* (L.)

To illustrate the changes in the distribution of *Balanus* balanoides I have grouped my observations into the seven population types described in Table 1. Each population type has its own symbol, depicted in Fig. 3, which are then used on the maps (Figs 4-10) showing the distribution of *Balanus* in the years 1937 and 1941-1946. This method of course produces a discontinuous representation of what is in fact a continuous range of population types, which should be born in mind when studying the maps.

For a picture of the varying success of settlement of *B. balanoides* throughout the period of investigation the 0-group data were similarly subdivided into several population types, as described in Table 2. The annual distributions of these population types (symbols as depicted in Fig. 11) are shown on the maps (Figs 12-18).

For all the years covered by these investigations I have the greatest number of observations from 1941, with considerably fewer observations from the other years. Nevertheless, they are sufficient to provide fairly reliable pictures of the actual conditions. The hydrographical data have been published previously (Rustad 1978).

1937 (Figs 4 and 12):

From the outermost part of the fjord - W of Stn. 8 - I have observations only from 1937. The *Balanus* population was well developed there that year.

The observations from the areas further inwards up the fjord - mostly from the south side of the fjord - indicate that the distribution of adult *Balanus* extended nearly as far inwards in 1937 as in 1941 (Fig. 5). That fewer *Balanus* were found at Stn. 27 in 1937 than in 1941 may be due to the fact that the 1937 observations were most probably made somewhat farther south than in 1941 - i.e. somewhat further into (or inside) in the bay - and even such minor habitat differences may influence the development of the *Balanus* population. The one negative observation made, at Stn. 90, provides no unequivocal evidence about the inner limit of *Balanus* on the northern side of the fjord. Between Stns 88 and 94 the *Balanus* population was rather scattered also in 1941. A single negative observation, therefore, does not exclude the possibility that population existed even further eastwards.

In 1937 we found a rich stock of the 0-group, distributed further inwards up the fjord than in any of the subsequent years (1941-1946). Assuming that the distribution of *B. balanoides* (0-group and adults) is to a great extent influenced by the salinity of the surface water layers (cf. p. 44 ff.), this occurrence of the 0-group may seem surprising, as the supply of freshwater in May 1937 was more than twice the normal value, being from nearly twice to more than three times greater than during the years 1941-1946. The situation may be explained by assuming that the greater part of the supply of freshwater mainly arrived during the latter half of May (this assumption is supported by the observed salinities in 1937, viz.: Stn. 4, 3 May, ca. 31 o/oo; Stn. 68, 6 May, ca. 27 o/oo; and Stn. 32, 7 May, ca. 24,5 o/oo), whereas my 0-group observations were made in the first half of the month. In 1937 the freshwater surplus arrived in May and June, whereas it does not usually come until June and July. Normally the supply of freshwater in June primarily affects the surface salinity in the inner part of the fjord. We may assume, therefore, that the May supply in 1937 chiefly affected the inner part of the fjord; in the outer part of the fjord the 0-group population was found at a higher level than even the adults, whereas in the inner part of the fjord the 0-group seemed to prefer the lower part of the seaweed region, or deeper. This and a similar observation at Stn 39 perhaps indicate the presence of an upper layer of freshwater which prevented the cyprid larvae from settling and developing at a higher level in the intertidal zone.

It seems reasonable to suppose that the freshwater surplus in May and June 1937 caused a marked reduction of the 0-group population - particularly since the decrease in salinity took place earlier on, while the larvae were still small and presumably less resistant to unfavourable habitat conditions (cf. p. 47).

1938-1940:

Regardless of how settlement and the initial growth of the new year-classes progressed, it is most probable that the freshwater surplus in both July 1938 and June and July 1939 (Rustad 1978, Table 2) caused a marked reduction of the 0-group population, which resulted in poor recruitment to the new year-class. In 1940, however, the supply of freshwater was considerably less than normal, which resulted in good recruitment and a well-developed adult *Balanus* population in 1941.

1941 (Figs 5 and 13):

The *Balanus* population in 1941 was really quite large, consisting chiefly of the 1940 year-class, plus the remnants of older and weaker year-classes and the assumed successful settlement of the current year's spat. On the southern side of the fjord we found population type I inwards as far as F u g l s e t f j o r- d e n, succeeded by an intermediate population type inwards to Stn. 19 and a type II population which extended inwards to a point between Stns 26 and 28. On the northern side of the fjord where no observations were made farther out than Stn. 51, we found type II present from this station inwards to Stn. 71.

At the inner limit for *Balanus* in 1941 (Stn. 32) single specimens were found somewhat further in than in 1937, indicating a slight inward shift of the inner species limit. I have no observations from the opposite side of the fjord but, judging from the conditions farther out still, most probably no *Balanus* occurred to the east of S o g n d a l s f j o r d e n.

The supply of freshwater in June and July 1941 was considerably less than normal, and the total supply in that year was also somewhat below normal. It is, therefore, reasonable to assume that conditions were favourable for the 0-group in 1941, although no observations were made before the end of October, and at this time of the year the 0-group could only be identified in a few places since the majority of the *Balanus* found had already attained such size that they were virtually indistinguishable from the older ones. Thus it is impossible to ascertain whether the inwards shift of the inner limit of *Balanus* was due to the distribution of the 1940 or 1941 year-class.

Although it is most probable that some settlement also took place further inwards up the fjord, no traces of the 0-group were found further in than Stns 33 and 100 even as late as October.

1942 (Figs 6 and 14):

In the early spring of 1942 the *Balanus* population probably consisted chiefly of the 1940 and 1941 year-classes, and since both these year-classes were rich ones it is most probable that all favourable surfaces would have been by then more or less completely covered by crowded *Balanus*. The gradually disappearing 1940 year-class would have been in process of being replaced by the forthcoming 1942 year-class. Since that year-class must be supposed to have been a rich one also, judging by the hydrographical conditions, it would fill in all the possible remaining patches of bare rock and to a greater or less degree, would also settle and grow on the shells of the older *Balanus*. In accordance with this assumed course of events, at the end of July (during the period in which salinity was lowest) the *Balanus* population in the outer part of the fjord showed no difference from the population of the preceding year, except that a somewhat richer *Balanus* population was present lower down on the *Mytilus* at Stn. 51 (population type II in 1941 and of the intermediate type I/II in 1942).

Later in the year (6 November), however, the inner limit of *Balanus* had shifted a trifle outwards and a little north of the rounded headland at Stn. 32 only single specimens were now present in place of the patches of scattered *Balanus* found there in 1941. As the supply of freshwater, and accordingly the salinity conditions, too, were even more favourable in 1942 than in 1941 (at least until September), the observed reduction in the *Balanus* population may possibly be explained by the death of some of the two-year-old individuals of the 1940 year-class. For the H e r d l a area, somewhat south of Sognefjorden, Runnström (1925, p. 39) states: "Ich kann also bekräftigen, dass *B. balanoides* gewöhnlich nur ein Alter von zwei Jahre erreicht. Einzelne Individen können möglicherweisen drei Jahre alt werden". This may perhaps also be the case in the outer part of Sognefjorden, but a dying-off of two-year-olds is hardly likely to be a regular occurrence at the inner limit for *Balanus*. During the low salinity period in 1943-1945 the 0-group did not survive in areas where the salinity fell below 5 o/oo (Figs 15-17 and 19) The observations for Stns 32 and 99 in 1943 are from 2 June - i.e. before the period of lowest salinity, and the adults found north of Stn. 32 in 1946 - the remnants of the 1942 class or older - must therefore have been 4-years-old. It should also be mentioned that around Stn. 31, near the *Balanus* inner limit, single, exceptionally large specimens, most probably more than two-years-old were sometimes found (cf. p. 30).

This may mean that, under favourable conditions with adequate new recruitment, the older *Balanus* may succumb during their third year to the competition from younger year-classes. On the other hand, under more or less unfavourable conditions, with insufficient or virtually no recruitment and in consequence reduced competition, many specimens may live for several years longer. This agrees with the observations of Barnes & Barnes (1962, p. 10) from Danish waters, where conditions are generally unfavourable to *Balanus* due to a low tidal range and a more or less low surface salinity. They state that the existing adult population may have "... been built up over a number of years ...", and that the size of many of the adults suggested that they are quite capable of living for between five and 10 years.

In agreement with the favourable hydrographical conditions in 1942 we found a rich settlement and a well-developed stock of the 0-group in July and August in the outer part of the fjord. In the inner part of the *Balanus* area, from stns 29 to 33, we found more of the 0-group than of adults even as late as 6 November. At the same time we also found 0-group populations on both sides of the mouth of

S o g n d a l s f j o r d e n, where no adults were encountered. Earlier in the year (6 August) some live 0-group individuals were found at Stns 40 and 100 and a considerable number of empty shells at Stn. 42. Later a few empty shells were also found at Stn. 38.

The occurrence of the 0-group in 1942 thus indicates an inward shift of the distribution of the species. The final result, however, was a shift of the inner limit on the northern side of the fjord inwards to Stn. 99, and on the southern side an increase in *Balanus* numbers in the inner area and only a slight shift of the inner limit.

The more pronounced reduction in the 0-group stock west of the mouth of S o g n d a l s f j o r d e n may have been caused by the increased supply of freshwater here (cf. p. 46).

1943 (Figs 7 and 15):

The supply of freshwater in June and July was considerably greater than normal. Observations from October and December indicate that in general this had not affected the *Balanus* population in the area occupied by population type I. At Stn. 13 there may even have been a slight augmentation of this population.

A narrower *Balanus* belt at Stn. 10 was caused by a loss of the *Mytilus* individuals with attached *Balanus*. On the other hand, a slight reduction of the *Balanus* population at Stn. 14 between 15 July and 9 December, and the reduction observed on 20-21 October around the mouth of E i k e f j o r d e n were most likely caused by the salinity decrease.

However, most probably some reduction of the *Balanus* population also took place elsewhere, but without quantitative data this is impossible to ascertain. Moreover, the observation made at Stn. 13 may indicate that within this outer area an increase in the 1943 population, due to recruitment from the 1942 year-class, made good the reduction in that population which occurred later on in the year. Within the part of the *Balanus* distribution area where no population of type I was ever found, a population increase was recorded at Stn. 20 on 16 July, and at Stn. 51 no population reduction was observed even as late as 18 August. At Stns 54, 55, 66, 18 and 23 there were markedly fewer *Balanus* present in December than previously. Here I have no observations from 1942, but it is reasonable to suppose that the reduction of the *Balanus* population took place during the summer and autumn of 1943. At Stn. 73, the strip of partly scattered and partly more dense stocks of adults, together with the broad and crowded belt of the 0-group, present in 1942, had by 10 December 1943 been replaced by a broad belt of scattered *Balanus*. This disappearance of the dense patches and the marked thinning-out of the population as a whole had taken place during 1943, although the total number of *Balanus* present was most probably greater at the end of 1943 than in 1942. It thus seems that there, too, the rich 1942 year-class more than compensated for the unfavourable conditions which prevailed in 1943.

Elsewhere in the middle part of the *Balanus* distribution area, a reduction occurred later in the year (October and December). Compared with the conditions at Stn. 99 (cf. below) this indicates that the reduction in the *Balanus* population started in the inner part of the *Balanus* distribution area.

In the innermost distributional area for *Balanus*, adults were found at Stn. 99, which represents an inward shift of the inner limit on the northern side of the fjord. On 10 january a belt of partly scattered and partly crowded *Balanus* was found here above the *Mytilus* belt, but the population had already become somewhat reduced by 2 June, by which time the surface salinity had fallen to 8.31 o/oo (cf. p. 46).

The few *Balanus* found at Stn. 92 on 2 May may also indicate an increase of the population here on the northern side, but no observations were made at this locality in 1942, and only a negative one excists from 1941.

On the opposite side of the fjord, at Stn. 31, on 30 January and 2 February, and on the north side of the rounded headland at Stn. 32 on 2 June, the *Balanus* population was markedly richer in 1943 than in 1942, obviously as a result of the favourable conditions which prevailed in 1942, but I have no record of any shift of the inner limit here on the southern side of the fjord.

On 12-17 April there was no sign of the 1943 class in the outer half of the fjord, but the dense stock of 0-group found at Stns 53 and 63 on 28 May indicates that a successful settlement of the new year-class had taken place in the outer part of the fjord.

The supply of freshwater in 1943 was considerably greater than normal. Accordingly, surface salinity had decreased to 11.92 o/oo and 8.31 o/oo at Stns 31 and 99, respectively, already by 2 June and at that time only a few and scattered specimens of the 0-group were found at Stns 32 and 99. Unfortunately, the observations are so scattered in space and time that it is impossible to decide whether this was a result of a reduced settlement, or of a reduction in a formerly richer stock. Nor do the observations make it possible to tell whether the absence of the 0-group at Stn. 92 on 2 May was due to the complete obliteration of a former stock of the 0-group or to the fact that the settlement of the new year-class had not yet started.

Further inwards up the fjord no trace of the 0-group was found.

From the middle of July and later on in the year only a few and scattered specimens were left of the supposedly abundant original stock in the outer part of the fjord. In more sheltered localities the 0-group populations were, however, richer.

On the whole, a marked reduction in the old *Balanus* population took place in the course of 1943 and a poor recruitment from the new year-class occurred.

1944 (Figs 8 and 16):

My 1944 observations indicate that the *Balanus* population became somewhat reduced in the course of the year, but in the outer *Balanus* area (with population types I and I/II) it is impossible without quantitative data to demonstrate the scale of the reduction. I noted that the situation at Stn. 10 (24 October) was about the same as that recorded at the time of the previous observation (9 December 1943), except for the occurrence of a scattered stock of *Balanus* on formerly bare rock surfaces below the *Balanus/Mytilus* belt and which therefore must have been due to settlement by the 1944 0-group. At this time of the year spat recruitment may therefore have concealed any possible reduction in the adult *Balanus* population. At Stn. 56 (26 July) I did not observe any reduction of the *Balanus* population living on the sloping rocks, but on a steep rock face in the vicinity there was a belt of numerous, but not crowded *Balanus* present above the *Mytilus* belt. Not even patches of former, crowded, *Balanus* population remained, which may indicate either that a more pronounced reduction occurred here in 1943 than took place between Stns 54 and 55, or that a further reduction of the *Balanus* population took place in the course of 1944. At Stn. 18 the *Balanus* population in 1944 was possibly somewhat reduced compared to that present in December 1943.

At Stn. 66, which from an ecological viewpoint lies considerably further inwards up the fjord than Stn. 18, the population found on 20 January 1944 were only somewhat poorer than that recorded on the previous visit (9 December 1943), but later in the year (25 October) a more obvious reduction in the *Balanus* population was found.

At localities where a population increase was recorded during the first half of 1943, a distinct reduction of the *Balanus* population took place in 1944, At least some - perhaps most - of these reductions however, may have taken place during the latter half of 1943.

Localities which had not been visited since 1941 or 1942 also showed a reduction in their *Balanus* populations. At Stn. 69 the population on 20 January was already reduced in comparison with that found in 1942, indicating a reduction during 1943, and later in the year (26 October) the population was found to have decreased even further. For this period I also have some observations from the area between H ø y a n g s f j o r d e n and L ø n n e f j o r d e n, and everywhere the *Balanus* population on exposed localities was reduced as compared with that present in 1941 and 1942.

At Stn. 22, where the shore consists of rough and fissured rocks, the population position on 26 October was about the same as that found on 31 October 1941, inasmuch as a narrow, and at least partly crowded *Balanus* belt was present. This may perhaps be explained by the fact that the hydrographical conditions here in 1944 were much the same as those in the area with population types I and I/II and much the same as, or perhaps somewhat better than, those which prevailed in 1942. Most probably, however, a larger population may have been present here during the first half of 1943 (owing to the rich 1942 year-class) which became reduced during the latter half of 1943. The observations are insufficient to decide whether or not the population had been reduced as compared with that in 1941, as might be expected considering the conditions recorded elsewhere.

At Stn. 76 on 21 January 1944, we found much the same population present as in 1941 and 1942 (Type IV). Judging from the stock of the 0-group found on 1 August 1942, there was most probably a richer *Balanus* population here during the first half of 1943, which became reduced during the latter half of that year. On the same day only few and scattered *Balanus* were found at Stn. 26, on the steeply sloping rocks on which crowded *Balanus* were found in 1941 and 1942.

Around Stn. 87, where the *Balanus* populations as a rule was poorely developed, the conditions along the shore varied considerably, but the observations from 31 October indicate that no change had occurred since the preceding year. At Stn. 87 itself no *Balanus* was found.

At Stn. 32 on 5 August only a few *Balanus* remained. The scattered stock from 2 June 1943 had most likely already been reduced during the low salinity period in 1943.

Since the first observations concerning the 0-group in 1944 date from the end of July, they cannot tell anything about the settlement of the new year-class. Observations from 1937, 1942 and 1943 indicate that in Sognefjorden cyprid settlement takes place sometime between the middle of April and the middle of May. In 1944 the supply of freshwater was about normal in April, below normal in May, and again about normal in June, and surface salinities at the turn of April/May was considerably more favourable in the outer part of the fjord in 1944 than in 1943. It is therefore, most likely that the conditions for settlement and the early development stages of the 1944 0-group were favourable. In July and August, however, the supply of freshwater was considerably above normal and the 0-group probably became much reduced in numbers thereafter.

The onset of the lowest surface salinities was delayed in 1944, in comparison with 1942 and 1943. The salinity conditions in the outer part of the fjord were not so favourable in 1944 as in 1942, but somewhat better than in 1943. As far out as Stn. 56 the lowest salinity value recorded in 1944 (at the turn of July/August) was only a little higher than that recorded in 1943 (in the middle of July) and even on 26 July only a scattered stock of the 0-group was found here. The data from Stn. 51 on 31 July 1945 indicate some contribution from the 1944 year-class, which may have transformed a type II population to type I, but during June and July 1945 this had once more changed to a defective type I.

My observations in the outer part of the fjord clearly show that the development of the 0-group after the time of the lowest surface salinity values in 1944 was considerably poorer than in 1942. In 1943 and 1944 the development of the 0-group stock varied considerably from place to place, and as observations were few and only three of the same localities were sampled in both years, no reliable differences between the two years can be demonstrated.

Close to the inner *Balanus* limit markedly lower minimum salinities were recorded in 1943 and 1944, than in 1942, and the minimum values were fairly similar in 1943 and 1944. Accordingly, the development of the 0-group was also rather poor in 1944. Already on 5 August no traces of the 0-group were visible, neither around the mouth of S o g n d a l s f j o r d e n nor on the opposite side of the fjord. As in 1943, and in contrast to 1942, none of the 1944 year-class were found farther inwards up the fjord in 1944.

1944 was thus another unfavourable year for *Balanus*. Further decrease in the *Balanus* population in the outer part of the fjord was noticeable (perhaps with the exception of the area containing population types I and I/II) and a distinct reduction of the population size in the inner part of the *Balanus* area - with a slight outward shift of the inner limit of *Balanus* on the northern side of the fjord.

1945 (Figs 9 and 17):

The observations from 1945 show a continuing reduction in the *Balanus* population. The reduction was now obvious also in the outer area and affected both the population types I and I/II.

Already on 22 March the *Balanus* population at Stn. 10 was distinctly lower than that recorded on 14 October 1944. Since no period of low surface salinity had intervened, the population decline was most probably due to the dying-off of the older year-classes (1942 and ? 1943). On the other hand, the decline of the populations at Stns 8, 13 and 51 (31 July to 1 August) may have been intensified by the influence of lowered surface salinities.

Within the former areas of population type II no population reduction was discernible so early as March. It is reasonable, however, to suppose that some reduction also took place here. The apparent increase in the *Balanus* population at the mouth of Høyangsfjorden (type IV in 1944 and type III in 1945) hardly witnesses any genuine population increase, but is most probably due to the fact that the specimens of the 1944 0-group had by then grown larger and were more conspicuous.

Later on (3 August), a reduction in the *Balanus* populations at Stns 22, 23 and 73 was found.

At Stns 26, 28 and 76 the population declined between March and August.

On 19 March I got the impression that fewer *Balanus* than previously were present on both sides of Stn 87.

In the inner part of the *Balanus* area it was obviously by 6 March that the inner limit had shifted somewhat further outwards on the southern side of the fjord and the situation was found to be much the same on 28 July, when moreover no *Balanus* were found at Stns 99 and 100. It seems reasonable to suppose that the inner limit would also have been shifted a little further outwards on the northern side of the fjord.

The values for the supply of freshwater and the surface salinity may indicate that somewhat less favourable conditions for *Balanus* prevailed at the turn of April/May compared with the conditions in 1943, but this is uncertain. The few available observations indicate that the development of the 0-group in the outer part of the fjord was approximately the same in 1945 as in 1943.

In late July no 0-group were found at Stns 31, 32 and 99 (the inner limit of *Balanus*) or further inwards up the fjord; nor did we find any on the western side of Stn. 28 on 4 August. In other words 1945 would also seem to have been an unfavourable year for *Balanus*.

1946 (Figs 10 and 18):

In 1946, after moving back to the biological station at Herdla, I had only one opportunity to revisit Sognefjorden and take samples from the area around the inner limit for *Balanus*.

On 11 September, from Stn. 30 to about 100 m north of the headland at Stn. 32 we only found a few scattered adult *Balanus* and none at all on the opposite side of the fjord at Stn. 99. On the chart (Fig. 10) I have indicated a population type similar to that present in 1945, but it is very probable that a quantitative investigation would have shown a diminution in population size. If my surmise that none of the 0-group in this area survived the low salinity period during the summers of 1943, 1944, and 1945 is correct, then the animals found in 1946 must have been the survivors of the 1942 year-class, or older, i.e. at least 4 years old, but I cannot rule out the possibility that I may have overlooked a few specimens of the 0-group in both 1944 and 1945.

I have no salinity observations from 1946. The supply of freshwater was somewhat less than normal, but not as low as in 1941 or 1942. My few 0-group samples indicate a rich 1946 year-class, but not as rich as the 1942 year-class. We also found some trace of 0-group settlement further in beyond the inner limit for adult *Balanus*, but not as far up the fjord as in 1942. On 11 September we found that they had died out as far out as Stns 32 and 99, i.e. the 1946 year-class did not result in any inward shift of the inner *Balanus* limit.

From my results it appears that the inner limit of *B. balanoides*, especially on the southern side of the fjord, shows only small changes from year to year, despite of great variations in the hydrographical conditions. On the northern side shifts in the position of the inner limit are somewhat more obvious from year to year.

It seems that the hydrographical conditions primarily have an influence on the development of the new year-class and that the observed variations in the populations of adult *Balanus* depend upon the annual balance between recruitment from the new year-class and the adult death rate, which in turn are also probably influenced by the hydrographical conditions, primarily the salinity of the surface layers. The adults are obviously more tolerant of low salinity than are the 0-groups. Correspondingly, at the time of lowest salinity in 1944 and 1945, adult *Balanus* were found further inwards up the fjord than were the 0-group. Both years were obviously unfavourable for *Balanus*.

DISCUSSION

The influence of the environmental factors on the distribution of *Balanus balanoides*

In Sognefjorden *Balanus* is restricted horizontally to the outer half of the fjord and vertically to a rather narrow belt in the intertidal zone.

Horizontal distribution

Plankton hauls show that in the spring *Balanus* larvae are carried to the heads of the fjord branches by inflowing undercurrents, and larvae are present below the lower limit of the *Balanus* belt, as well as above it at high tide. Thus every year *Balanus* should be able to spread further up into the fjord, or to form a broader belt. Since it nevertheless has a restricted distribution this cannot be due to any lack of time for migration, the presence of any kind of topographical barrier, or to reproductive failure. Even if *Balanus* is unable to reproduce in its inner distributional area, the innermost parts of the fjord still receive a supply of larvae from elsewhere every year. The restricted distribution must therefore be due to unfavourable habitat conditions.

The conditions prevailing around the inner area for *B. balanoides* in Sognefjorden would seem to differ from those in the inner area for the species on the northern and north-eastern coasts of Zealand in Denmark, for which Barnes & Barnes (1962, pp. 33-34) state: "Each relatively discrete centre has to maintain itself and the spat-fall is a measure of dispersion from that centre without any supplement from nearby populations". A few lines further on, however, they state: "This view is probably somewhat exaggerated; in places larvae from adjacent adult populations may mix and settlement be recruited from several places". - Considering the long planktonic life of the *Balanus* larvae, however, it would seem reasonable to suppose that in these southern areas the stock might be amply augmented from the cyprids which are most likely present in the soutward-flowing under-current. On the other hand, the conditions may perhaps be such that the spat from the local populations are capable of living and developing in the surface water layers, where they must also be more or less held together by some sort of eddy, whereas the cyprids in the under-current are prevented from reaching the surface because of the well-developed vertical salinity gradient (cf. below, p. 55-56 and Brattström 1941, p. 80).

Substrate type, wave action, currents and nutritional conditions

As a sessile animal *B. balanoides* is absolutely dependent on the presence of a solid substrate; i.e. a hard bottom of rocks or stones, if the latter they must be so large, or so firmly fixed, that they cannot be moved about by wave action.

The cyprids of *B. balanoides* are most probably capable of selecting the most favourable substrate type for settlement, cf. Barnes, Crisp & Powell 1951, p. 240: "Clearly smooth surfaces, such as occur on mobile pebbles would be most undesirable for intertidal forms".

Looking at Sognefjorden as a whole the substratum cannot be a factor restricting the distribution of *B. balanoides*; an abundance of suitable hard bottom substrates is present. Locally, however, soft bottom areas (mud, sand or gravel) may exclude the presence of *Balanus*.

Obviously a hard bottom substrate alone does not offer equal possibilities for life, and the occurrence of the animals within the area is therefore dependent on the nature of the shore, its underwater topography and orientation. For example, where small clefts in the rocks force the water upwards when the waves are lapping the shore, the *Balanus* belt extends higher up the intertidal zone than on adjacent areas of smooth rock.

In the outermost part of the investigated area the actual topography of the shore is less important. Here *Balanus* is numerous, to a great extent crowded, practically everywhere.

Further inwards up the fjord, or in the fjord branches, the *Balanus* is noticeably better developed on smooth and exposed rock surfaces, than in more sheltered places, or on stones or rough rocks. In the outer part of the fjord, however, exspecially when the hydrographical conditions were unfavourable to *Balanus*, it may be more abundant in bays than in the neighbouring exposed localities. In its innermost distributional area, *Balanus* shows a marked preference for exposed, smooth, vertical or overhanging rock surfaces. - The estimation of the degree of exposure in the following section is based on a purely subjective evaluation (cf. Brattegard 1966, p. 10).

Balanus does not seem to have any special orientation preference with regard to the force of gravity, it is indifferent whether the available rock surface is vertical or horizontal, or faces upwards or downwards. The decisive factor seems above all to be the degree of exposure to wave action. "It has frequently been noted that the growth of *B. balanoides* is greater in exposed situations and least under sheltered conditions" (Barnes 1955, p. 113). The degree of development of the population also depends on whether the rock surface is smooth or rough. On smooth rock the degree of exposure will be the same everywhere, favouring a uniform population development. On rough rock surfaces or on stony shores conditions will be very heterogeneous. The exposure to the wave action will vary very much according to the orientation of the local surface, causing wide differences in population development over short distances. This effect is not equally important throughout the investigated area. Wave action in the outermost part is probably so strong that even a fairly great degree of rugosity along the shore does not reduce the degree of exposure sufficiently. Further inwards up the fjord, wave action diminishes and the effect of surface rugosity becomes more obvious and pronounced. If wave actions becomes still weaker, then even on smooth surfaces the degree of exposure will be so low that the degree of inclinations instead becomes important. *Balanus* then thrives better on vertical or overhanging rock surfaces than on sloping surfaces, as the influence of the waves will be greater on the former than on the latter. It is also possible that the more uniform distribution of *Balanus* found in the outermost area is partly due to the fact that here *Balanus* is in better general condition than elsewhere and therefore does not respond to minor differences in the degree of wave action. This means that the effect of exposure to wave action also depends on the degree of susceptibility of the local *Balanus* population.

It is easily ascertained, and generally accepted, that *Balanus* populations are better developed in exposed localities than in more sheltered places. However, it is considerably more difficult to explain why this is so.

With strong wave action more detritus will be stirred up than in calmer water, and violent water movements may also increase the supply of plankton, but bearing in mind the delicate limbs of these animals it is difficult to see that strong wave action would offer particularly suitable feeding conditions. When wave action is moderate the animals are kept busily at work, not only needing to beat with their cirri as in calm water. Within short periods they may need to hold their cirri out as a sieve at one moment turned to face the inflowing current and the next moment turned 180° to face the outflowing current (cf. Moore 1935, p. 298, Barnes, Crisp & Powell 1951, p. 227). Nevertheless, when the waves are breaking at their worst the animals are hardly at their most active.

Strong wave action may also be likely to maintain a high oxygen content of the water, which may be of some importance where the animals are living crowded together. Wave action may also have a favourable effect on salinity, since any surface fresh water will fairly rapidly be mixed with saltier water from below.

Referring to his experiments on the growth of *B. balanoides* on panels with and without algae (cf. below, p. 55 ff.) Barnes (1955, p. 113) suggests that the greater growth of *B. balanoides* in exposed situations "... may not be entirely the result of the exposure conditions upon the barnacles themselves; greater exposure leads to a poorer development of small closely adherent algae and this in turn could permit a more rapid growth of the barnacles".

There is another circumstance which also may be of great importance in this connection. In sheltered localities I have seen examples of heavy *Balanus* mortalities, which involuntarily reminded one of the effects of infectious diseases. For example, I have seen hundreds of crowded *Balanus* shells filled with a reddish, decaying, matter. In sheltered localities the dead animals may remain for some time attached to the rock surface, whereas in exposed localities they will be washed away quite soon, and thus the chances of spreading of infectious deseases will be considerably better in sheltered localities than in exposed ones, and it is not at all improbable that a species exhibiting such mass occurrences as *Balanus*, is exposed to one or more epizootic diseases. The favourable effect of strong wave action therefore - at least to some extent - may be due to a rapid removal of sick and dead animals, preventing further spreading of infection.

The effect of the waves decreases inwards up the fjord, and one might imagine that the inner limit of *B. balanoides*, is determined by the reduction in wave action. (Lack of exposure seems to be a limiting factor for other species, cf. Brattegard 1965, p. 49.)

Brattegard (1966, p. 39) states from Hardangerfjorden: "The relatively high number of species found in localities situated on protruding headlands and other situations subject to wave action in the main fjord, indicate that exposure has a favourable effect on the fauna also in these inner sheltered areas".

Most probably the decrease in wave action does have some influence upon the population size of *Balanus* found inwards up the main fjord, but other factors must determine its absolute inner limit. On the other hand I am inclined to believe that in the fjord branches the degree of exposure is responsible for the rapid decline in the size of the *Balanus* populations. True enough the wind as a rule blows up or down the fjord branches as in the main fjord, but in the former cases the wind has a much shorter distance open for its action and is unable to raise such high waves as in the main fjord.

The following example may illustrate the difference in conditions in the main fjord and in a fjord branch:

On 21 August 1942, at 0 m we found a rapid decrease in salinity values inwards up F u g l s e t f j o r d e n: 17.14 o/oo and 17.86 o/oo on the W and E sides, respectively, at the mouth of the fjord. From mid-fjord inwards the values were 15.41 o/oo N of Stn. 17, 13.48 o/oo off Stn. 16, and 12.80 o/oo in the middle of the inner basin.

In the main fjord we found (22 August 1942) surface salinities of 8.24 o/oo off Stn. 26, and 7.72 o/oo off Stn. 76, - i.e. lower salinities than those recorded at the same time in the innermost basin of F u g l s e t f j o r d e n.

I have no *Balanus* observations from Fuglsetfjorden from 1942, but, as mentioned above (p. 21), the *Balanus* populations in the outer part of the main fjord were very similar in 1941 and 1942, and we may well presume that this was also the case in the fjord branches in the outer area. In 1941 the *Balanus* population changed from types II and III in the outer part of F u g l s e t f j o r- d e n to types IV and V in the inner part of the fjord, and no *Balanus* at all was found in the innermost basin, whereas in 1941 and 1942 we found type II at Stn. 26 and type IV at Stn. 76 (Figs 5 and 6), i.e. nearly the same as those in the outermost part of F u g l- s e t f j o r d e n.

Decreased salinity most likely causes a diminution in the strength of the *Balanus* populations in the fjord branches as well, but since the decline occurs so rapidly, one or more other limiting factors (perhaps occurring, also in the main fjord, but not so actively) need to be sought for in the fjord branches, and the degree of exposure to wave action may be of vital importance here.

Reduced wave action may bring about a reduced supply of food, a lowered oxygen content of the water, increase the possibilities for lowered surface salinity and a greater danger of infection. For *Balanus* the result will be poorer condition with a reduced power of resistance to e.g. low salinity and infection, and the final effect will be a reduced population size. The weaker currents prevailing in the fjord branches will produce similar effects.

The assumption that in the fjord branches it is not only the decrease in salinity, but also some other factor which leads to the reduction in the *Balanus* population seems to be confirmed to a certain degree by the distribution of *Littorina obtusata*. This species, which seems to require a higher salinity than *Balanus* and which as a rule prefers more sheltered localities, occurs at least equally far inwards up the fjord branches as *Balanus* does. In F i n n e f j o r d e n, i.e. near its inner limit in the main fjord, *L. obtusata* was found even somewhat further inwards in the innermost basin than *Balanus* was. In some cases, however, it seems that *L. obtusata* penetrates so far up into the fjord branches because the surface freshwater layer is here so thin that *L. obtusata* - in contrast to *Balanus* - is able to maintain itself below the freshwater layer.

Patella and *Nucella* were only found exceptionally in the fjord branches, and only in their outer parts. Like *L. obtusata*, both these species seem to require a higher salinity than *Balanus* does. It is therefore possible that the reduction of the salinity in the fjord branches may explain the reduction in the population sizes of these species. Brattegard (1965, p. 49) found "... a positive correlation between their distribution and the summer salinity distribution in the surface".

With regards to *Nucella*, the reduction in the stocks of *Balanus* and *Mytilus*, which form the main prey of *Nucella*, may perhaps suffice to explain the scarcity of *Nucella* in the fjord branches.

On the basis of the available data it is more difficult to account for the decrease in the *Mytilus* population inwards. In the main fjord this species does not show any preference for exposed localities. On the contrary, some observations from the innermost part of its distributional area seem to indicate that *Mytilus* under certain conditions prefer more sheltered localities (see p. 16). *Mytilus* tolerates a decrease in salinity better than *Balanus* does, but the *Mytilus* population is also diminished inwards up the fjord branches and much more than one might expect from the observed decrease in salinity, at least as compared with the main fjord. It is possible that food conditions in the fjord branches are poorer than those of the main fjord, thus causing the observed reduction in the *Mytilus* population in the fjord branches. It seems a reasonable supposition that this should also influence the occurrence of *Balanus* - perhaps to an even higher degree than for *Mytilus*. My impression is that the currents never are so strong in the comparatively shorter fjord branches in the outer part of Sognefjorden as in the main fjord. Weaker currents lead to a reduction in the supply of food, but this hardly plays any decisive role in limiting the distribution of these two species in the main fjord. Food conditions as a whole are probably, at most, of only secondary importance in determining the inner limit of *Balanus* in the main fjord. Plankton samples from the upper layers show that ample quantities of plankton are present right up to the heads of the main and branch fjords. The supply of organic compounds by the rivers is greatest in the inner part of the fjord and it moreover seems likely that growth conditions for the plankton are good here. Such conditions are most probably also found in the fjord branches and to a greater or lesser degree they will counteract the reduction of food supply due to the weaker strength of the currents there. On the other hand it is possible, or perhaps even probable, that during the summer there is not much plankton present in the upper 1-2 m when salinity is extremely low. When the salinity reaches its lowest value, however, the food content of the upper water layers will be of no consequence to *Balanus*, since the animals then remain closed. But if the decrease in salinity during the spring or early summer leads to a poor plankton content of the upper water layers already before *Balanus* is forced to close up because the salinity value has reached its critical minimum value, then it is very probable that food shortage will lead to an impoverished condition of the *Balanus* population, which will most likely be of decisive importance later in determining how long *Balanus* is able to remain closed and unable to feed until surface salinity once again rises above til critical survival value.

In the above survey of the intertidal fauna the conditions around the headlands have mainly been described, because the conditions here are more uniform and more readily comparable than those in the bays. In Sognefjorden, where the wind as a rule blows along the fjord - inwards or outwards - the headlands will of course be more exposed to wave action than the bays. This, in its turn, will result in more favourable conditions for *Balanus* on the headlands. One does not have to go very far in beyond a straight line drawn between headlands before the shelter effect becomes obvious, especially in the middle and inner parts of the *Balanus* area of distribution. Conditions around the headlands themselves are also comparatively more favourable - especially on smaller promontories - since these very often consist of protruding, smooth rocks, whereas the shoreline in the bays more often consists of stones or rugged rocks. Off the headlands we also as a rule find the strongest currents, which implies more rapid water exchange and therefore better feeding conditions and oxygenation. In the bays, the current is generally weaker, whether it continues to run in the same main direction as off the headland or forms an eddy. Due to the keen competition for food it is very probable that the prevailing current conditions are very important for the animals. Referring to his own observations and those of Fischer-Piette (1929) Moore (1935, p. 284) states: "... that the advantageous effect of wave-action on the growth of barnacles may be reproduced by a current of water".

Current conditions do not seem to be of similar importance for *Mytilus*, at least within its optimal distributional area. This may mean that *Mytilus* is less susceptible to variations in current strength and feeding conditions than *Balanus* is. If so, this may either be due to a more selective choice of food items by *Balanus*, or to the fact that *Balanus* is only able to catch its food in the water stream which flows within the reach of the cirri, whereas *Mytilus* is able to actively draw in and filter a larger quantity of water from a wider area. With regard to food accessibility, every *Balanus* is wholly dependent on its position within the micro-current systemt of the water layer flowing past close to the rock. Some animals will be more favourably placed than others, which lie in the 'food shadow' of their competitors and only have access to a more or less depleted water flow (cf. Moore 1935, p. 293).

The nutritional state of the animals most likely influences their resistence to harmful influences, e.g. poorly nourished specimens will more easily succumb to disease. Little is so far known about whether nutritional state influences physiological tolerance or not. Barnes, Finlayson & Piatigorsky (1963, p. 238) found that under anaerobic conditions lactic acid production is reduced by starved animals, but undoubtedly well-fed animals will be better off than poorly-nourished ones during any periods when they are forced to remain closed. In particular, it is conceivable that nutritional state may become important towards the inner limit of *Balanus*, where the animals are more often forced to close their shells for protection during periods of unfavourable hydrographical conditions. In this case, too, the most favourable conditions will exist on the smooth rock surfaces of promontories and headlands - a supposition in agreement with the observed distribution of *Balanus*.

As regards the horizontal distribution of *Balanus* in Sognefjorden, however, food conditions are most likely of only secondary importance, whereas for the vertical distribution they seem to have a decisive influence, determining both the upper and lower limit of the *Balanus* belt (p. 48 ff).

Ice

It is not uncommon for the inner parts of the fjord branches to freeze over in winter. Regular ice formations and ice erosion along the shores may restrict the distribution of *Balanus* inwards up the fjord (Dons 1946, Brattström 1948). Throughout the period covered by my investigations, however, the fjord never froze as far out as the *Balanus* limit, and it is hardly likely that this ever happens.

Silt content of the water and pollutants

There are indications that the silt content, especially of the water film which covers the surface of the rocks during the settling period, may influence the distribution of *Balanus* (Brattegard 1966, pp. 44-45), but other observations indicate that *Balanus* is well able to withstand muddy conditions (Barnes & Barnes 1962, p. 32).

No observations were made on a possible effect of the silt content on the distribution (inner limit) of *Balanus* in Sognefjorden, but because the time of maximum of silt content generally coincides with that of the lowest salinity it may perhaps play som part, together with the low salinity of the upper water layers, in causing the subsequent death of any 0-group *Balanus* which settle further inwards than the normal limit (1937, 1942. 1946).

During the actual investigation period Sognefjorden was not subject to pollution of any importance, perhaps except for some biocidal residues from the fruit-growing districts in the inner half of the fjord.

pH

Changes in the pH of the sea water due to a lowering of the salinity, have no influence on oxygen uptake by *Balanus*, whose shells serve as an alkali buffer, which maintains the body fluids at a constant pH (Kreps 1929a).

Oxygen

As a rule there is a sufficiency of oxygen in the upper water layers. In general, variations in the oxygen content do not influence the horizontal limits of *Balanus*.

However, it is possible that oxygen content, and/or the CO_2-content, of the water may play some part in determining the lower limit of *Balanus* within the area in which a typical *Balanus-Mytilus* belt is present.

Possibly, local exception may arise, when extensive exchange of the deeper water with a high H_2S content occurs in the innermost basins of some of the fjord branches. Some observations indicate that such a change occurred in the innermost basin of N æ r ø f j o r d e n. On 7 August 1942 the dredge samples indicated that a rich bottom fauna was present in the sound at Stn. 36. In the latter half of June 1943 there were only few animals left, most probably owing to the disastrous effects of an out-flowing current with a high H_2S-content. On 6 June 1945 we found a greater number of benthic species present than in 1942, but no mass occurrence of certain species, as in 1942. N æ r ø f j o r d e n, however, is situated beyond the inner limit of *Balanus*, and no exchange of such bottom water was ever observed within the *Balanus* distributional area. An oxygen shortage, however, may occur at times when the animals are forced to close their opercular valves, e.g. at times of low water levels, or when the salinity of the surface water falls too low.

Air temperature

The physiological tolerance of *Balanus* to temperature variations is undoubtedly great, since the animals hardly possess any effective means of protecting themselves against the great variations to which they may be exposed at low tides, viz. burning sun in the summer and below zero temperature in the winter.

According to Barnes (1958) the southern limit of *B. balanoides* on the Pacific coast of North America depends only on the competitive pressure of two southern species. Favourable temperature conditions extend considerably farther south.

On the European coasts temperature is of primary importance in determining the southern limit of the species. The two most important factors are firstly, an autumnal drop in air temperature to about 10°C, which allows the final maturation of the gametes, and secondly high summer temperatures which effect the survival of the adults and/or the spat. Only locally may competition with a warm-water species be of some importance. On the Atlantic coast of North America the southern limit of *B. balanoides* is determined by both high summer temperatures and competition with two southern species. The air temperature in November is low enough to enable satisfactory maturation of the gametes to take place considerably further south. In the Woods Hole district, Barnes (1958, p. 146) found indications of the adverse effects of high summer temperature on *B. balanoides*. In the late summer of 1956 vast numbers of empty shells were found, and "... all the shells were very uniform in size, some 5 mm basal diameter. Now this is the size reached at such places on the shore by June-July following spring settlement and this is the time when air temperatures rose from 17.2° in May to 20° in June and 25° in July, the maxima in the second two of these months being 26° and 27°C. Measurement had shown that the temperature at the rock surface may be 5-10° higher than the air temperature and there is little doubt that this excessive air temperature was fatal to those relatively young individuals of the current year's spat".

From Sønderborg on the east coast of Jutland Barnes & Barnes (1962, p. 33) found a large number of old empty shells which were considered to be the result of a considerable mortality which had occurred when the water level was exceptionally lowered (during a series of gales) at the same time as the air temperature was high. Extreme low water-levels "... in the spring when the spat are newly settled, and possibly then more sensitive to desiccation, is believed to account for empty spat in other places".

In Sognefjorden air temperatures above 25°C were only recorded on 28 July 1945 at Stns 91, 93 and 99, and the temperature on the rock surface may well have been about as high as in the case mentioned above. No 1945 0-group was found at Stns 31 and 99, and most probably the 0-group was not present on the shores west of S o g n d a l s f j o r d e n either. In this case surface salinity had already fallen to below 5 o/oo during the first few days of July and I am inclined to think that the 0-group then succumbed to the low salinity, but high air temperatures also will certainly have an adverse effect in reducing the length of time the animals are able to remain closed.

On the other hand it seems that under natural conditions *B. balanoides* is never exposed to lethal low temperatures. Kanwisher (1955) investigated the responses of variety of intertidal and sub-tidal animals, to experimental exposure to low temperatures, and he states (loc.cit. p. 62): "No animal was found to stand low temperatures and large internal ice formation that is not faced with these conditions in nature. The large hardiness towards ice formation may be the principal reason allowing intertidal species to successfully invade the shores".

As regards the limits of distribution of *Balanus* in Sognefjorden, air temperature is most probably only of secondary importance, merely modifying the influence of salinity. The autumnal drop in air temperature, which allows the final maturation of the gametes, does not represent a limiting factor in Sognefjorden, since adequately low, but not lethal, air temperatures regularly occur in the autumn.

Salinity

We have seen that in Sognefjorden the *Balanus* population decreased from the outermost part inwards, and also that it decreased more rapidly along the northern side of the fjord than along the southern side. On the other hand I have shown (Rustad 1978) that the salinity of the surface water also decreased inwards up the fjord and that this decrease was more pronounced along the northern side than along the southern side. A marked parallelism thus exists between the occurrene of *Balanus* and the salinity distribution of the surface water. A natural assumption therefore is that the distribution of *Balanus* and surface salinity are interrelated (cf. Brattegard 1966, p. 44, and Jorde & Klavestad 1963, p. 61).

Balanus is known to tolerate a wide range of variation in salinity, and *Balanus* can even be found off river-mouths. This does not imply that the range of physiological tolerance of *Balanus* extends as low as 0 o/oo, however. The explanation must be that the fresh-water from rivers can be restricted to a thin surface layer. I have repeated observations showing this to be true. At high-water *Balanus* is more or less regularly submerged by water with a sufficiently high salinity value, whereas at low-water the animals can close their opercular valves when submerged by the fresh-water. At the same time the metabolic rate is lowered and more anaerobic conditions arise.

Kreps (1925 and 1929b) and Borsuk & Kreps (1929) found that *B. balanoides* and *B. crenatus* tolerated even rapid variations in salinity values between 0 o/oo and 70 o/oo, but 6-7 o/oo was found to be critical, at lower salinities the animals became motionless and were considered to have entered a state of 'Salz-schlaf'. In this state of 'salt sleep' the animals could survive for up to three weeks in completely fresh-water. Below 6 o/oo their oxygen uptake remained at a constant low value, but above 6 o/oo their oxygen uptake increased and over the salinity range 12-35 o/oo oxygen uptake was independent of the salinity.

Barnes *et al.* (1963, pp. 247-248) investigated lactic acid production by *B. balanoides* in water of different salinities. At low salinities *Balanus* closed its opercular valves. No change in lactic acid production was found in salinities from 8 to 0 o/oo, which agrees with the constant oxygen uptake below 6 o/oo found by Borsuk & Kreps (1929). Barnes *et al.* (*loc. cit.*) state that "... it may be assumed that during much of the time an anaerobic regime is established in animals subjected to such low salinities. This is clearly because for much of the time the operculum is tightly closed and ventilation of the mantle cavity greatly reduced. That some exchange with the external medium takes place ... is indicated by the fact that Borsuk & Kreps found a low but significant oxygen uptake at low salinities".

It has been shown that *B. balanoides* shows a decrease in the rate of oxygen uptake when transferred to water of high salinity (Barnes *et al.* 1963, p. 245) and it seems natural to suppose that by closing their shells the animals can also protect themselves for some time against too high salinities.

The ability of the animals to shut themselves off from adverse environmental conditions is surely only practicable within certain limits, however, since at the same time they also shut themselves off from their food supply. The length of time the animals are able to remain shut off most probably depends on other factors, e.g. temperature, pH, state of nutrition, and the rates of production and accumulation of toxic substances which ultimately may kill the animals (Barnes *et al.* 1963, p. 236).

The seasonal decrease in salinity starts earlier and lasts longer the further up the fjord one comes, i.e. the time during which *Balanus* is obliged to remain closed up in the summer increases from the fjord mouth inwards, ultimately limiting the distribution of *Balanus*. The low salinity surface layer is thicker along the northern side of the fjord than along the southern side. This means that on the southern side *Balanus* more often may have daily access to water of higher salinity and containing larger amounts of plankton than on the northern side, and it is thus possible for the animals to rapidly dispose of any accumulated toxic substances. The possibilities for settlement and survival are thus favourable for *Balanus* further inwards on the southern side of the fjord than on the northern side which corresponds with the observed distributional limits.

Dealing with *B. balanoides* in the waters around the coasts of Denmark, southern Sweden and north-eastern Germany, Barnes & Barnes (1962, p. 25) state: "It is generally believed that lower salinity is the most important factor restricting the spread of *B. balanoides* into the Baltic, although ... increasing summer temperatures at low salinity levels may be of some importance". Concerning the influence of the salinity they state (*loc. cit.* p. 35): "In the Öresund the population density falls off sharply once the mean salinity drops below 14-15 o/oo, and since the values fluctuate widely a constant value of 10-12 o/oo is probably the limiting value tolerated by the species".

The 0-group did not survive in the areas in which the salinity values during the year fell below 5 o/oo, usually occurring in July/August, whereas they were found in the areas with 5-10 o/oo, although at reduced numbers compared to those recorded in areas of higher salinity (Figs 14-17 and 19). It is therefore most probable that in Sognefjorden the limiting salinity value for *Balanus* lies between 5 and 10 o/oo, perhaps around 8 o/oo (cf. Stn. 99, p. 24), which corresponds well with the finding mentioned above, that the metabolic rate remained constant below 8 o/oo.

The few salinity observations which I have from 1942, from the area between S o g n d a l s f j o r d e n and F j æ r l a n d s f j o r d e n shortly after the period with lowest salinity, include two occasions on which the salinity fell below 5 o/oo: 19 August, 3.62 o/oo in 0 m at H15 off Stn. 87, and 22 August, 4.92 o/oo in 0 m at H17 off Stn. 91 (Rustad 1978, Table 4). This fresher layer was probably fairly thin (7.41 o/oo at 2 m at H15 - no obs. at 2 m at H17). The salinity decrease in this area was most probably due to freshwater influxes from both S o g n d a l s - f j o r d e n and F j æ r l a n d s f j o r d e n. The observations made off the biological station at H e r m a n s v e r k (Stn. 91) indicate marked fluctuations in the salinity values (*loc. cit.* Table 4). The influx of low-salinity water from S o g n d a l s- f j o r d e n may have been restricted to short periods only, and this may be the reason why some 1942 0-group were nevertheless able to survive.

The records from Stns 23 and 73 in 1943 (Fig. 7), i.e. from localities close to the 5 o/oo outer limit (Fig. 19), are from December that year, and the lack of records of 0-group finds (Fig.15) may be due to the fact that, even if present, they were perhaps indistinguishable from the adults so late on in the year.

From 1944 I have no records of *B. balanoides* from the 5-10 o/oo area.

Since the temperature, by modifying the rate of metabolism, effects the length of time for which the animals can remain closed-up, it may also modify the control low salinities exert on the inner limit of the species up the fjord and on the number of specimens which survive within the area affected by salinity values of 5-10 o/oo.

The inner limit of each year-class is most probably determined during the first period of low salinity after the settlement of the cyprid larvae. It seems reasonable to suppose that these rapidly-growing young stages, which also possess more limited metabolic reserves than older stages, are more sensitive to the unfavourable conditions.

Salinity conditions may somtetimes also be disastrous for adult *Balanus*. At Stns 32 and 99 for example, scattered populations of the 1942 year-class were found on 2 June 1943. By 5 August 1944, however, only 3-4 solitary specimens of *Balanus* were present at Stn. 32, and at Stn. 99 only an empty shell was found. A reasonable supposition is that the population reduction mainly occurred during, and in consequence of, the low salinity period which occurred in 1943.

Algae

For the waters around the Isle of Man Moore (1935, p. 229) states: "The presence of large algae such as *Fucus* spp., *Ascophyllum nodosum*, etc., is definitely harmful to the barnacles, and in most places they are not found within touching distance of them", and as regards the conditions at Plymouth, he suggests "... that the harmful effect of the algae is at least in part due to their screening the barnacles from adequate food supply". - In Sognefjorden, in the Herdla area and in Trondheimsfjorden, I have regularly found numerous, even crowded, *Balanus balanoides* in the seaweed zone on fairly wave-exposed shores. The only examples of a harmful effect of seaweeds on *Balanus* I have ever observed were in the vicinity of solitary *Fucus* plants in the *Balanus* belt which were surrounded by a circular area of bare rock, obviously the cyprid larvae or young 0-group had been dislodged here by the to-and-fro motion of the algal fronds by the waves.

Vertical distribution

For *B. balanoides* around the Isle of Man, Moore (1935, p. 302) states: "The upper limit of distribution is high water neaps in a sheltered place, and up to high water of extreme spring tides at greater wave-exposure. The lower limit similarly drops with increasing exposure".

In Norway this relationship between the tide-levels and the *Balanus* zone limits has, so far as I know, never been referred to in the literature. According to the results of earlier, not published, investigations, which I made at the biological station at Herdla 1935-1941, it appeared that the upper *Balanus* limit approximately coincided with the mean high water spring tide. The locality was not particularly wave-exposed. The uppermost specimens were smaller than those found below, and the former obviously seemed to be living under less favourable conditions. Most probably the upper specimens had a slower growth rate, due to a diminished food supply, because they have access to food only at the time of high tide. In Sognefjorden the size difference between the upper and the lower specimens is as a rule not so marked. It might therefore with some uncertainty seem reasonable to assume that the upper limit of the *Balanus* belt in Sognefjorden coincides with mean high water or mean high water neap tide.

The height of the tides may be of decisive importance for the vertical distribution of any organisms living in the intertidal zone and for a few metres below. As the daily water-level rises and falls so the isotherms and isohalines shift up and down. In this way, the tides, especially when a marked discontinuity layer is present, cause great and rapid changes in the environmental conditions in and somewhat below the intertidal zone, which may have a decisive influence on the vertical distribution of sessile or slowly-moving animals.

Nor is it improbable that such marked fluctuations in one of the hydrographical factors influence the distributions of these animals. Even if the members of the intertidal fauna are obliged to have a wide tolerance to changes in such environmental factors, this does not necessarily mean that the animals are also able to tolerate great and/or excessively frequent fluctuations, even within the ranges of tolerance of the species. In the first place, intertidal species may have physiological races, each having a range of tolerance which is narrower than that of the entire species. In such cases great fluctuations in environmental factors may easily give rise to conditions which lie outside the tolerance range of some of the races. Such fluctuations, even when infrequent, may seem intolerable for the entire species in areas from which suitable physiological races are for some other reason missing. In the second place, it is most probable that individual members of a species, or physiological race are adapted to the normal conditions of the biotope. Should environmental changes then occur too rapidly or with too great frequency that it becomes impossible for the animals to adapt themselves to the new conditions, then such changes will be intolerable for that species as a whole, even if they are within the range of tolerance of the species, where they occur more slowly or more infrequently.

However, there is yet another aspect of water movements which is surely of greater importance for *Balanus* and other intertidal animals. The sea surface forms the boundary between two biocycles: L a n d and O c e a n (Hesse *et al.* 1937, p. 136), the habitat conditions of which are fundamentally different. Furthermore, within each of these biocycles the environmental conditions may vary considerably even within short distances above, e.g. air temperature or relative humidity, or below, e.g. salinity, the sea surface.

The distribution of a species within the intertidal zone will depend on the range of tolerance possessed by that species, or competing species, to the environmental changes chaused by a daily repetition of the change from terrestrial to oceanic conditions. The upper limits of marine organisms will be directly dependent on their tolerance to desiccation at the time of low water, and its duration.

We assume, therefore, that the upper limit of the *Balanus* belt is dependent on the range of tolerance of *Balanus* to desiccation. *Balanus* is unfitted to live under wholly terrestrial conditions. Tolerance of desiccation depends on the animal's ability to screen itself off from the unfavourable environmental conditions by closing its shell. Any further adaptations only serve to perfect this ability.

Barnes & Barnes (1957) state that intertidal barnacles, such as *B. balanoides*, on exposure to air expel any water from the mantle cavity and close the opercular valves in such a way that the underlying noncalcified folds of the membrane form a small 'micro-pylarlike' opening, which intermittently puts the mantle cavity in communication with the external atmosphere. In this way the animals as far as possible control the balance between two opposing factors, viz. water loss and oxygen supply.

As the tissues become dehydrated the rate of metabolism is reduced and the valves finally remain closed for much of the time. The animals then resort to an anaerobic metabolism, accompanied by a further fall in the metabolic rate. In a later paper, however, Barnes *et al.* (1963, p. 250) state: "Since direct observations show that over a normal intertidal period the mantle cavity is for much of the time open to the air at the micropyle and since analyses indicate that there is little accumulation of lactic acid during such a period, it may be assumed that the considerable capacity to live under anaerobic conditions is a feature whose survival value lies in allowing the animal to withstand somewhat abnormal conditions. Such may include periods of exposure to excessive heat or low-salinity water, both of which are not uncommonly experienced by intertidal organisms".

The period of time the animal may remain shut-off must depend upon such other external factors as air temperature and food supply. The higher up within the intertidal zone the animals are situated the shorter the time at their disposal for feeding. Although ... "Starvation results in a lower metabolic rate, aerobic or anaerobic, and a reduced demand of substrates now mobilized from reserves" (Barnes & Barnes 1964, p. 27), a limit must somewhere be found where the supply of food is no longer sufficient to compensate for even these reduced metabolic processes.

Usually the size of the specimens in the upper part of the *Balanus* belt more or less decreases upwards. From the lower part of the *Balanus* belt and for some way upward, the supply of food is so abundant that it is not only sufficient to compensate for the resting metabolism, but also permits a rate of growth characteristic of the species. In the upper part of the *Balanus* belt, however, the supply of food decreases, the surplus which maintains growth gradually disappears, and finally the food supply in the uppermost part of the belt eventually becomes insufficient even to compensate for the resting metabolism.

It seems reasonable to suppose that a well-fed animal will be able to remain closed-up for a longer time than an animal with less food reserves. In favourable places within the existing micro-current system, the animals will be able to tolerate desiccation for a longer time, i.e. are able to survive higher up than in less favourable places. Because conditions in nature are hardly ever uniform over long distances horizontally, this will result in an irregular upper *Balanus* limit. The rougher and more uneven the substrate, i.e. the less uniform the current and food conditions are, the more irregular will the upper *Balanus* limit be. This agrees with my observations on the *Balanus* limit in Sognefjorden.

Even if the rate of metabolism is greatly reduced while *Balanus* remains closed, it is hardly probable that metabolic rate is independent of the air temperature. An increase in the temperature during that period would thus shorten the time *Balanus* is capable of remaining closed. High summer temperatures might then lead to a lowering of the upper *Balanus* limit. Moreover, the upper limit would then be expected to be lower on the more sun-exposed northern side of the fjord. Observations on the *Balanus* upper limit made within an hour of each other on the southern and northern sides of the fjord, seem to confirm this assumption. The upper limit should, on the whole, also be lower in the sunniest sites on either side of the fjord. One might also expect that the upper limit should in general be lower in the inner part of the *Balanus* distributional area than further out near the open coast, since the mean July air temperature (normal period 1901-30) is 13.6°C, at Kinn, on the coast, whereas at Leikanger (Stn. 90), near the inner limit for

Balanus in Sognefjorden, 15.7°C.

In the inner part, or possibly especially in the middle part, of the *Balanus* distributional area, the upper limit of *Balanus* may perhaps also be lower than usual in some places due to the presence of a thin layer of freshwater at the surface during the settlement period of the cyprids, or somewhat later. The cyprids would not penetrate into such a layer, but remain below it or, if already settled, they would be obliged to close up for so long a period that they would die of starvation or oxygen deficiency etc.

As regards the lower limit of the *Balanus* belt, the situation is quite different. If the lower limit of a marine species depends on the tidal level a most likely supposition is that such species are incapable of withstanding permanent submersion.

About *Balanus* balanoides Broch (1924, p. 113) states: "... dass es eine Lebensbedindung für die Individuen ist, zeitweise trocken gelegt zu werden". Dons (1944, p. 141 and 1946, p. 197) has expressed similar opinion. According to this the lower limit of the *Balanus* belt would be dependent on the tolerance time of the species to subersion.

During my investigations at Herdla, however, I found that *B. balanoides*, when settled on experimentally suspended slate panels could develop to sexual maturity and produce larvae, apparently quite normally, even when the panels were permanently situated below the lowest tide level. Barnes & Powell (1953, p. 124) found in their experiments that "Quite evidently it is not the unsuitability of complete submersion for growth and development that usually limits *B. balanoides* to the intertidal zone". Moreover, Barnes & Barnes (1962), in their description of the distribution of *B. balanoides* along the Danish and south-western Swedish coasts, state that from the intertidal zone *Balanus* extended below low-water level and well into the sublittoral.

As a rule, however, the species is restricted to the intertidal zone, and it is difficult to pinpoint the limiting factor.

The cyprid larvae possess numerous oil droplets in the anterior part of their bodies (Runnström 1925; Visscher 1928), and the latter author supposed that the droplets serve to increase buoyancy, thus aiding the cyprids in reaching and remaining in the surface layers. However, these oil droplets disappear towards the end of the free-swimming period of the larvae, and personally I have never observed any, apparently normal, cyprids passively floating up towards the surface. The importance of the oil droplets in aiding the cyprids to reach the upper water layer and finally the intertidal zone therefore seems questionable.

On the other hand, the cyprid larvae of *B. balanoides* are markedly positively phototropic up to the time of settlement (Runnström 1925; Pyefinch 1948). Runnström (p. 14) states: "Dieser starke positive Heliotropismus ist sicher die Ursache des Aufenthaltes der Larven an der Oberflache und kann vielleicht auch erklären, warum sich *Balanus balanoides* bloss in der Gezeitenzone festsetzt".

If the cyprids only settle at the time of high-water, and if, due to their positive phototropism at the time of settlement, they are restricted to an upper water layer which does not exceed the tidal range, this may explain why *B. balanoides* is as a rule restricted to the intertidal zone.

Barnes & Powell (1953, p. 110) state: "It is postulated that intertidal settlement takes place most readily from a thin layer of water, ... On vertically exposed panels this occurs while the tide is rising and falling past the panel .... The "Clinging reaction" of *B. balanoides* cyprids described by Pyefinch (1948) (in contrast to *B. crenatus* which is mainly a sublittoral species) lends support to this hypothesis". I once (1934, unpublished) made a single experiment concerning this question. I had noticed that when the water-level in a 'tidal-aquarium' fell, (the 'tides' were more or less synchronized with those in the sea) numerous cyprid larvae were held back under the film of water which was left on the glass walls of the aquarium. To see whether this phenomenon might have any influence upon the settlement of cyprids, a large number of cyprid larvae (from a plankton haul) were put into a large glass jar filled with sea water. The sides of the jar were shaded with paper, and by using vertical illumination from above the cyprids were concentrated near the surface. A slate panel was then lowered into the jar and slowly hauled up again. A considerable number of cyprids were found to be retained under the water film on the slate. It was now left standing dry for four and a half hours and then placed into the 'tidal-aquarium' about 5 minutes after the time of low-water. The next day only one cyprid was left on the panel and on the following day this, too, had disappeared. The results of this, admittedly single experiment, do not harmonize with the above-mentioned statments. One might consider the explanation to be that the cyprids used in the experiment were not yet ready for settling, but that is not very likely since I had already observed similar cyprids settling on the pillars of the quay. Also the cyprids in the 'tidal-aquarium' later on settled and metamorphosed on the slate panels and on the bottom of the aqarium. Those on the bottom had undoubtedly settled below the low-water mark.

During my investigations at Herdla in the years 1935-1941, I had several series of slate panels hanging under the quay at the biological station. Most of the panels were at first hung in the *Balanus* zone during settlement period of the cyprid larvae. Later on, these panels were suspended at levels ranging from a little above the *Balanus* zone down to 1 1.5 m below the low-water mark. Similar vertical series of test panels had already been suspended at the time of settlement. From the result of the latter series it was seen that the *B. balanoides* cyprids will also readily settle below the low-water mark, at least on such a clean substrate.

Most of the panels in these series were from time to time brought into the laboratory, where other sedentary organisms - mainly algae - were removed from the panel surfaces and from the shells of already settled *Balanus*, and the *Balanus* specimens were then measured. Two other vertically suspended test series, however, were left untouched until the settlement time of the following year. This cleaning, as well as the desiccation which occurred while the panels were hanging up dry in the laboratory, resulted in a marked reduction in the growth of algae on the first series of panels, whereas the latter, undisturbed series soon had a heavy algal cover.

The following year I got the impression that the number of *Balanus* specimens left on the undisturbed panels was lower than on the cleaned ones, although the size of the surviving *Balanus* seemed to be much the same on both series of panels. It is therefore very possible that algal growth may have been reduced during the summer, as it was in the experiments described by Barnes (cf. below). A reasonable supposition was that the reduction of the *Balanus* population on the undisturbed panels was due to the algal growth.

Barnes (1955) has investigated this particular question. After describing the results of his experiments on the growth of *B. balanoides* on cleaned as well as on algal-covered panels under conditions of continuous immersion, Barnes (*loc. cit.* p. 112) concluded: "It is quite evident from these results that the presence of algae is a most important factor in controlling the growth of *B. balanoides*. ... , it cannot be doubted that the presence of algal cover, when it forms a close adherent mass, will seriously affect the growth rate. It is also evident that had the algal cover persisted throughout the season (in the experiments the algal growth had proved to be markedly reduced in July, followed by a marked increase in the growth rate of *Balanus*) the animals of these submerged panels would have reached a mean length of about 5 mm by the end of the summer, a value which approximates to that attained under natural conditions". (On the cleaned panels the animals had attained a length of some 12 mm by July.) Barnes continues: "It is less certain how growth is restricted in this way; it may be by restricting the access of food or it may act by mechanically interfering with cirral beat and hence with the feeding activities; if the latter were the case, it would seem that the young and less robust stages of the barnacle would be most seriously affected and that under extreme conditions survival would be impaired".

I am inclined to think that algal competition decisively influences the vertical position of the lower limit of the *Balanus* belt in the outermost part of its distribution area. Further up the fjord, the lower part of the broad *Balanus* belt was found to overlap a belt of small-sized *Mytilus*. Here, the environmental conditions obviously favour *Balanus* rather than *Mytilus*. It is possible that it is competition between the two species which here explains the lower growth rate of *Mytilus*. The lower limit of *Balanus* here most likely also depends on the distribution of small algal species.

In the middle part of the *Balanus* area, i.e. in the optimal area for *Mytilus*, where we find the characteristic white and black *Balanus*-*Mytilus*-belt developed, it seems more likely that the lower limit of *Balanus* is displaced somewhat upwards, by some form of competition with *Mytilus*, but the nature of the decisive factors is unknown. Perhaps competition for food, oxygen, or some other intraspesific relationships are involved.

The lowering of the upper limit for *Mytilus*, as compared with *Balanus*, is because the former is less well able to withstand desiccation (Runnström 1925, p. 15).

In the description of the *Balanus* population found in Sognefjorden (Rustad 1977) I frequently stated that we also found *Balanus* growing on the shells of large *Mytilus* specimens. As a rule, however, these *Balanus* seemed to belong to the 0-group, and would presumably gradually die out later, owing to competition with *Mytilus*.

Further inwards up the fjord, where *Balanus* is more scattered, it was as a rule difficult, if at all possible, to define a lower limit; presumably the presence of algae, or of *Mytilus*, excludes *Balanus* from the lower levels of the intertidal zone hereabouts.

It might perhaps be possible for *Balanus* to thrive at a lower level - below *Mytilus* and the harmful algae. When, nevertheless, as a rule no *B. balanoides* are found below the intertidal zone, this is most likely because the positive phototropism of the cyprid larvae prevents them from settling sufficiently deep, or that food conditions, or some other environmental conditions, become too unfavourable at these depths.

On the other hand, at least the 0-group may occasionally be found living somewhat deeper down than usual. This is most likely caused by the presence of an upper water layer of low salinity.

To get some idea of the reaction of *Balanus* cyprids to salinity I once made the following simple experiment: Cyprids, caugth with plankton net in water with a salinity of 30.6 o/oo, were apportioned among seven aquaria containing water of the following salinities: 17.1 - 19.2 - 22.6 - 26.4 - 32.7 - 35.0, and 37.1 o/oo.

In the aquaria containing water of the lower salinities, the cyprids closed up their shells and sank to the bottom, whereas at the higher salinities the cyprids scattered and swam about lively in the water. After about 5 minutes, in the aquaria with salinities of 17.1 and 19.2 o/oo all the cyprids were lying on the bottom. In water of 22.6 o/oo only a few were swimming about. In the higher salinities (26.4 o/oo or above) the greater proportion of the cyprids were actively swimming about and they continued to swim for several days more, until they eventually gradually collected together at the bottom of the aquarium, where they sometimes lay quiet, or crawled around, or swam just above the bottom. The cyprids which kept on swimming for the longest time were those in the 32.7 o/oo water, i.e. at the salinity closest to that in which they were caught. At a salinity of 22.6 o/oo some degree of adaption was observed, viz. after 3 hours the greater proportion of cyprids were swimming about and continued doing so for 3 days, but after that only a few cyprids were still seen swimming. At a salinity of 19.2 o/oo a small increase in the number of swimming cyprids was observed after about 5 days, but later on only some few cyprids were still seen swimming. At a salinity of 17.1 o/oo only solitary cyprids were swimming during the first week, a few more the next week, but later on once again only solitary specimens were now and then observed swimming close to the bottom.

After 40 days, a large number of the cyprids in some of the aquaria had settled on the bottom and metamorphosed. At a salinity of 17.1 o/oo none had metamorphosed and out of the original ca. 650 cyprid larvae 50-100 specimens were still alive. In the aquaria with 19.2, 22.6, and 26.4 o/oo salinities, which initially contained ca. 625, 1.000, and 1.200 cyprid larvae respectively 15, 8, and 16.7% had metamorphosed. At salinities of 32.7, 35.0, and 37.1 o/oo with initial populations of ca. 1.300, 1.325, and 870 cyprid larvae, 31, 24.5, and 31% respectively had metamorphosed. In the 22.6 o/oo aquarium a lot of the cyprids and all of the metamorphosed specimens were dead, whereas in the other aquaria most of the animals were still alive.

To sum up the results: At a salinity of 22.6 o/oo and below, all the cyprid larvae closed-up their shells and sank to the bottom. After 40 days none had metamorphosed in the aquarium with water of 17.1 o/oo salinity, whereas in those of 19.2 and 16.4 o/oo some had metamorphosed, and at 32.7 o/oo and higher salinities a greater proportion of the original cyprids had metamorphosed.

This behaviour of the cyprids could well explain the occasional presence of 0-group *Balanus* below the usual vertical distribution level in nature, mentioned previously.

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Table 1. Description of the different population types of *Balanus balanoides*. (Cf. Fig. 3.)

Type	Description
B.	*Balanus balanoides* present. (No records of population type exists).
I.	Sloping rocks: Crowded, broad or narrow *Balanus* belt above *Fucus vesiculosus*. *Balanus* also crowded in the *F. vesiculosus* zone; somewhat more scattered only in the lowest part of the zone. Where there is a luxuriant zone of *F. spiralis* this covers the lower part of the *Balanus* belt above the *F. vesiculosus* zone. Where a *Mytilus* belt is present, the *Mytilus* shells are as a rule more or less covered by *Balanus*. Steep rocks (seaweeds sparse or lacking): Crowded *Balanus* belt, corresponding in breadth with that above and within the *F. vesiculosus* zone on sloping rocks. When a *Mytilus* belt is present this is more or less completely covered by the *Balanus* belt, which may also extend below the *Mytilus* belt.
II.	Sloping rocks: Crowded, broad or narrow *Balanus* belt above the *F. vesiculosus* zone, more scattered lower down. Occasionally *Balanus* (as a rule the current year's spat) more or less crowded in the upper part of the *F. vesiculosus* zone. Where a luxuriant zone of *F. spiralis* is present this may more or less completely cover the *Balanus* belt, with often only a narrow strip of *Balanus* visible above the *F. spiralis* zone.

cont.

Table 1. cont.

Type	Description
	Steep rocks (seaweed sparse or lacking): White-and-black *Balanus-Mytilus* belt. Scattered *Balanus* may be found on the *Mytilus* shells. Occasionally the *Mytilus* belt may be more or less covered by the current year's spat of *Balanus*.
III.	Sloping rocks: *Balanus* forms a comparatively even, but scattered, only occasionally somwhat more crowded, belt above the *F. vesiculosus* zone. (More or less covered by *F. spiralis*.) Scattered *Balanus* in the upper part of the *F. vesiculosus* zone. Steep rocks (Seaweeds sparse or lacking): *Balanus-Mytilus* belt, with comparatively scattered, only occasionally more crowded, *Balanus*. *Mytilus* may occasionally be more or less covered by the current year's spat of *Balanus*.
IV.	Sloping rocks: Some patches of scatterede *Balanus* connected by a strip of scattered *Balanus* around the upper limit of *F. vesiculosus*. Steep rocks (seaweeds sparse or lacking): A strip of scattered *Balanus* with some large patches of scattered *Balanus* above the *Mytilus* belt.
V.	Small patches of few and scattered *Balanus* around the level of the upper seaweed limit - especially on steep surfaces. - Few or single specimens.
E.	Only som empty shells of *Balanus* present.
O.	No *Balanus* present.

Table 2. Description of the different population types of the 0-group of *Balanus balanoides*. (Cf. Fig. 11)

Type	Description
P.	The 0-group present.
I.	Crowded. Less crowded but forming a broad belt. Very many.
II.	Numerous.
III.	Narrow, crowded, strip. Sparse population, but a relatively broad belt.
IV.	Narrow strip of scattered specimens. Scattered strips and patches.
V.	A few small patches of scattered specimens. Very few.
VI.	None of the 0-group present.
VII.	Empty shells. (No numerical records.)
VIII.	A few empty shells.
IX.	A considerable number of empty shells.

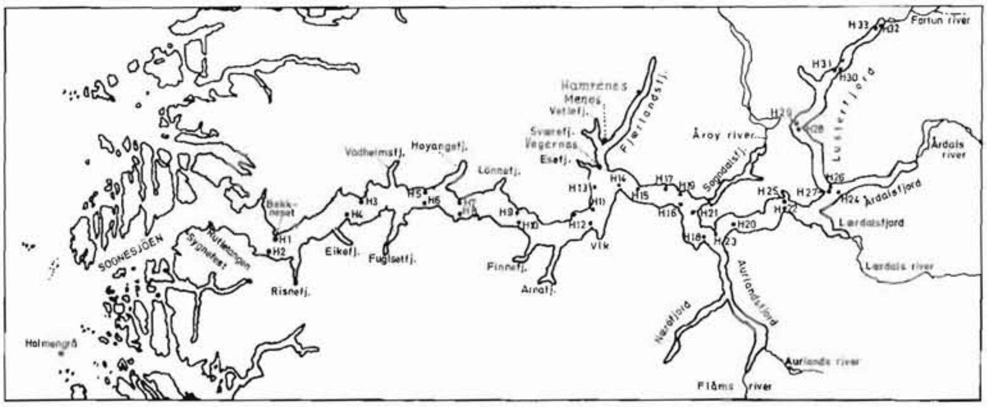

Fig. 1. Map of Sognefjorden showing the fjord branches, main rivers, and hydrographical stations (cf. Rustad 1978).

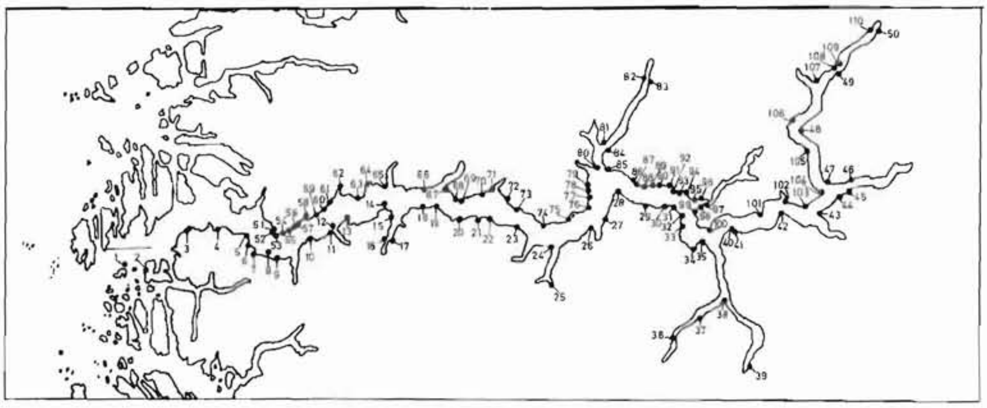

Fig. 2. Map of Sognefjorden showing the position of the 110 investigated localities.

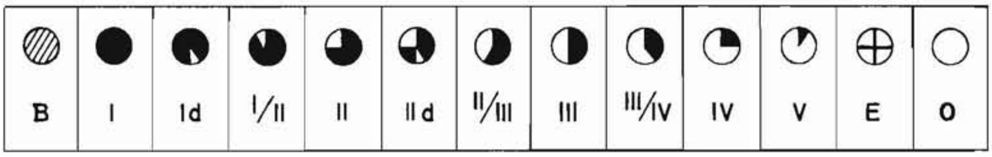

Fig. 3. Symbols used for the different population types of adult *Balanus balanoides*. B, E, O, and roman numerals refer to the types described in Table 1, whereas d denotes defective populations of the type indicated by the roman numerals. I/II, II/III, and III/IV represent intermediate types, as described in Table 1.

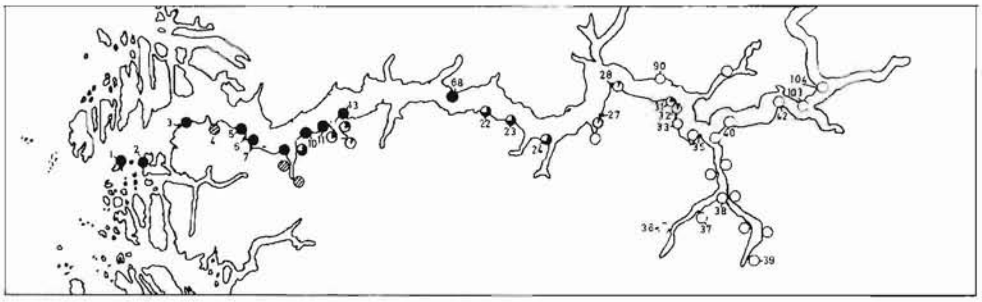

Fig. 4. Distribution of the different population types of adult *Balanus balanoides* in 1937.

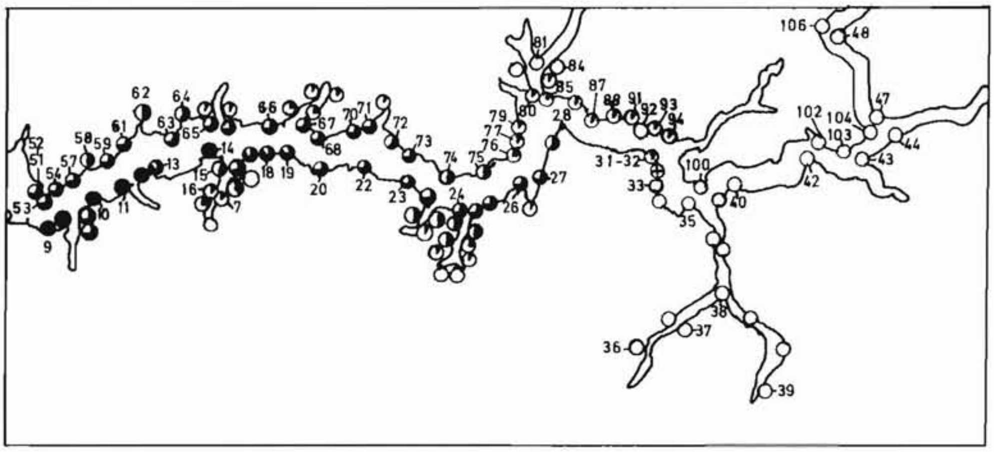

Fig. 5. Distribution of the different populations types of adult *Balanus balanoides* in 1941.

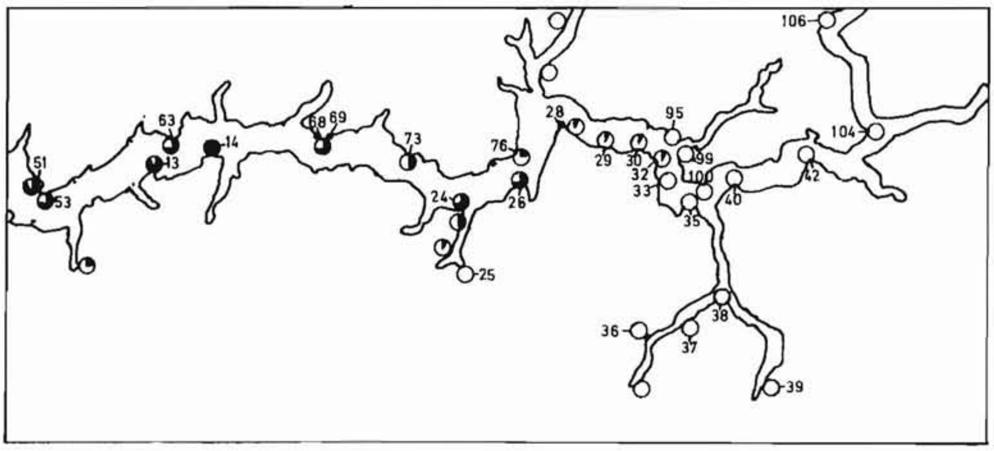

Fig. 6. Distribution of the different population types of adult *Balanus balanoides* in 1942.

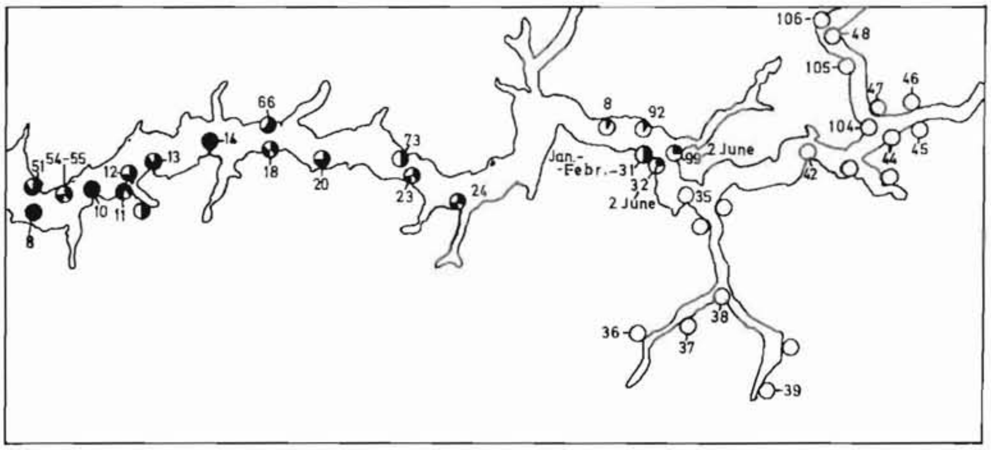

Fig. 7. Distribution of the different population types of adult *Balanus balanoides* in 1943.

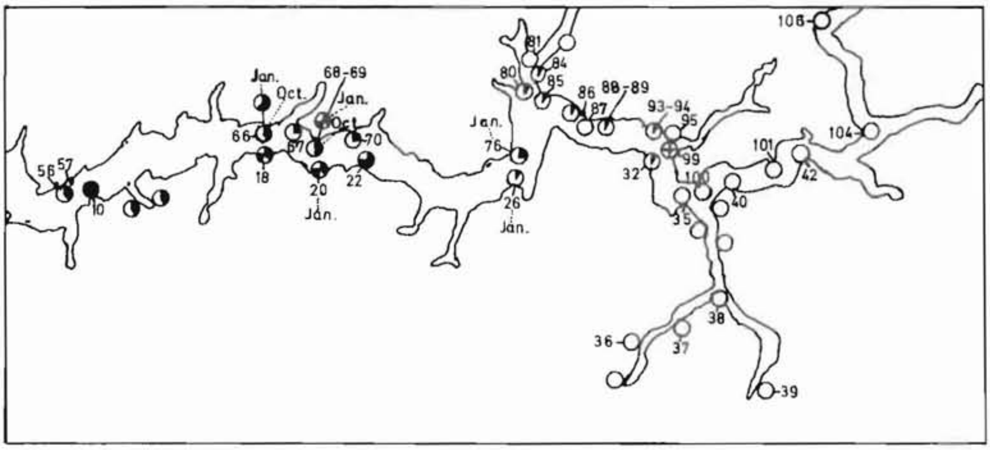

Fig. 8. Distribution of the different populations types of adult *Balanus balanoides* in 1944.

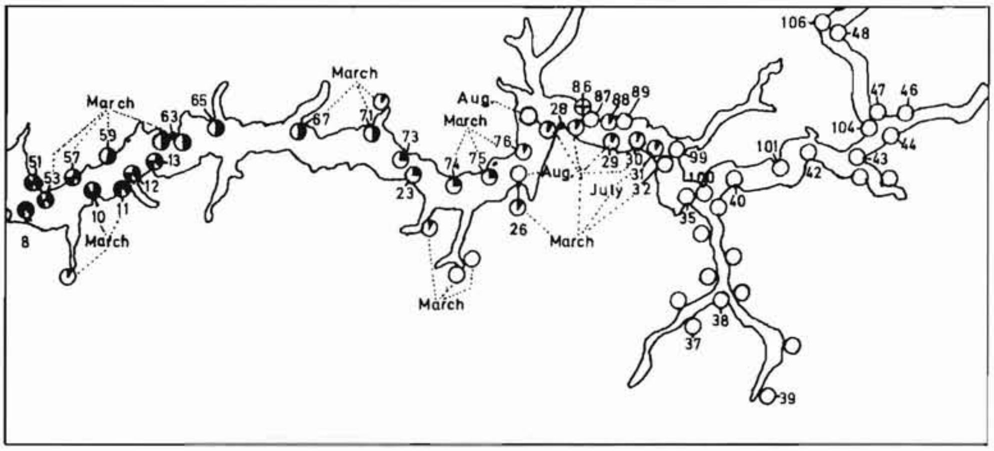

Fig. 9. Distribution of the different population types of adult *Balanus balanoides* in 1945.

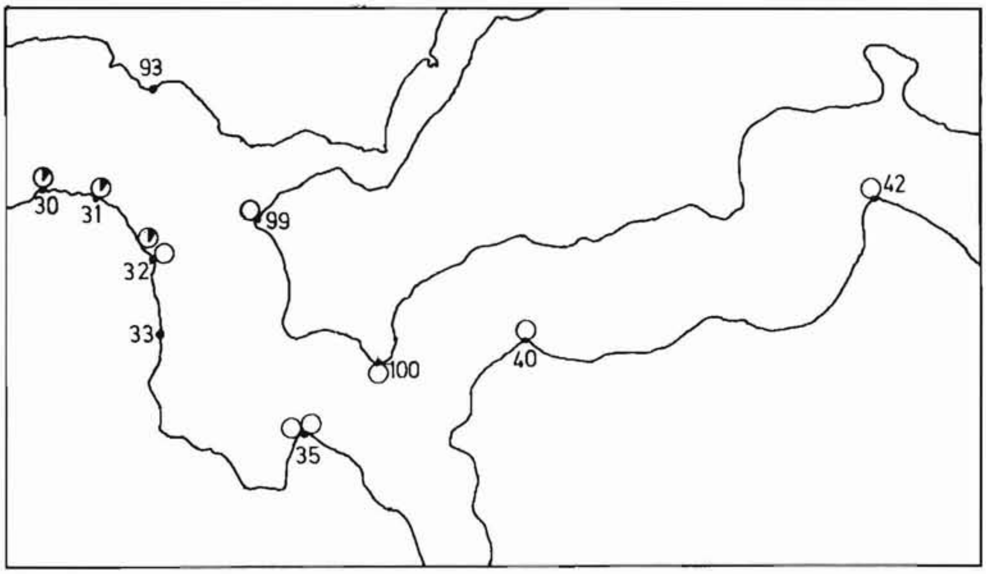

Fig. 10. Distribution of the different population types of adult *Balanus balanoides* in 1946.

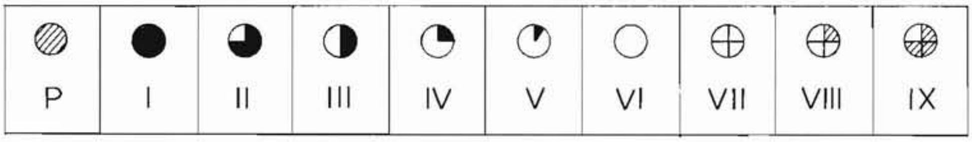

Fig. 11. Symbols used for the different population types of the 0-group of *Balanus balanoides*, as described in Table 2.

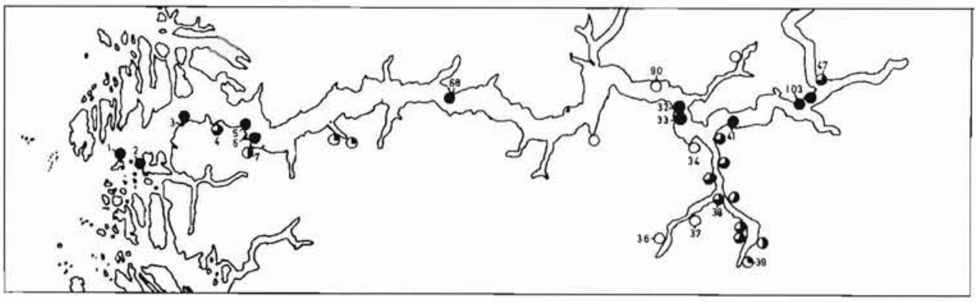

Fig. 12. Distribution of the 0-group types of *Balanus balanoides* in 1937.

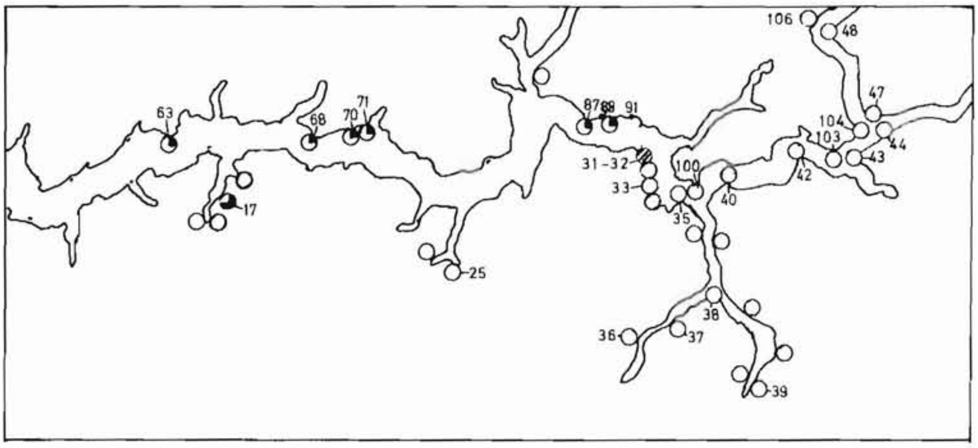

Fig. 13. Distribution of the 0-group types of *Balanus balanoides* in 1941.

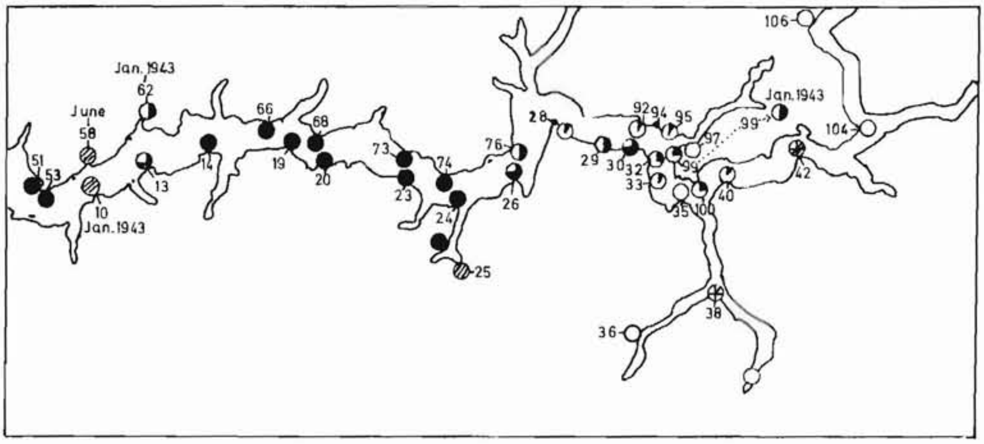

Fig. 14. Distribution of the 0-group types of *Balanus balanoides* in 1942.

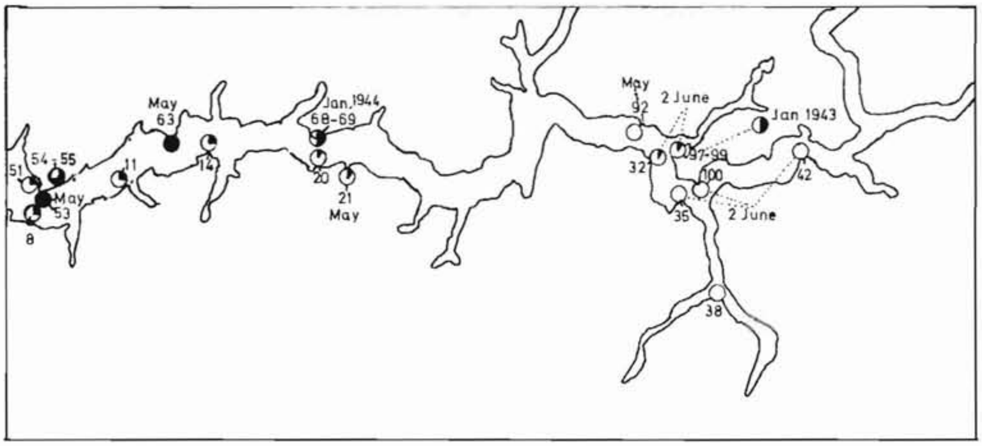

Fig. 15. Distribution of the 0-group types of *Balanus balanoides* in 1943.

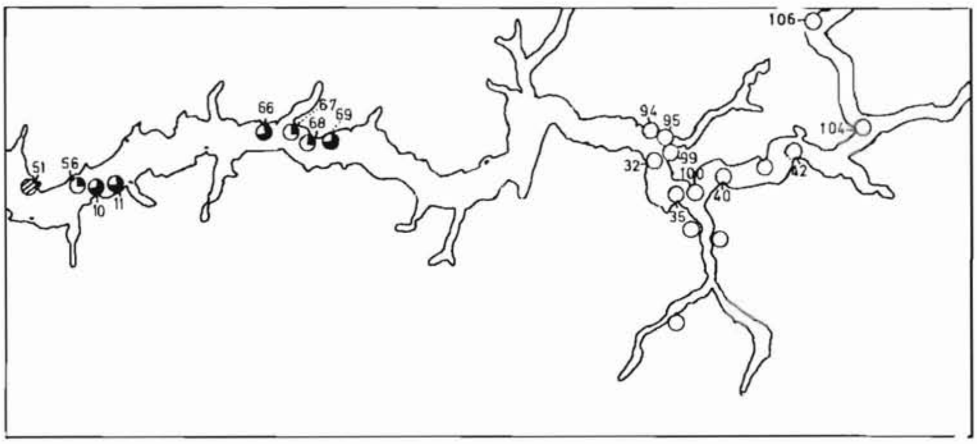

Fig. 16. Distribution of the 0-group types of *Balanus balanoides* in 1944.

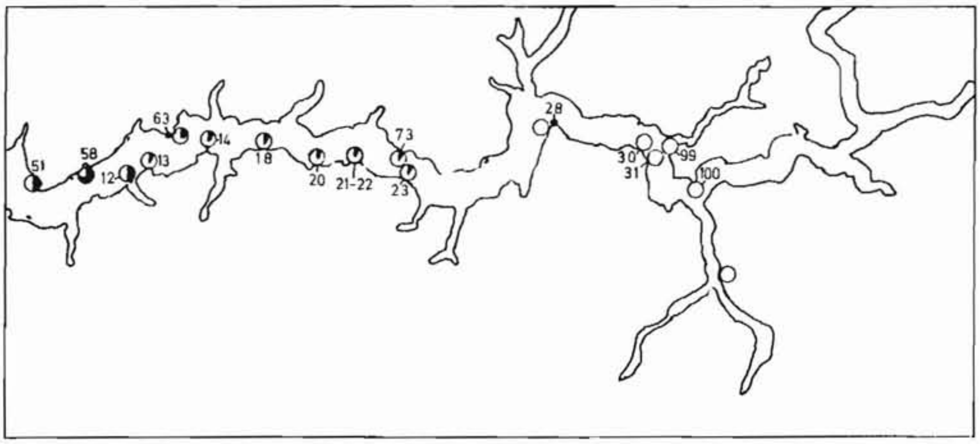

Fig. 17. Distribution of the 0-group types of *Balanus balanoides* in 1945.

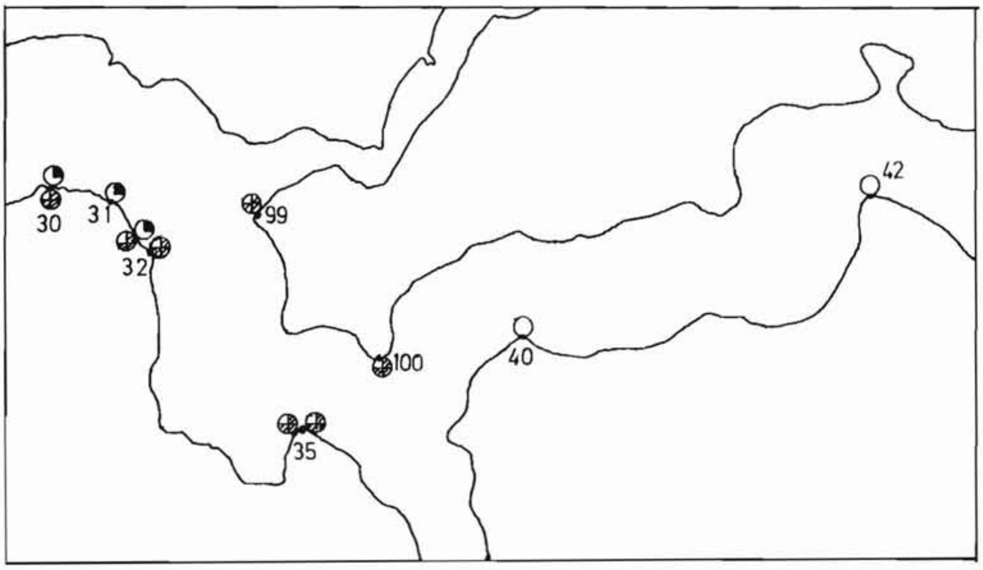

Fig. 18. Distribution of the 0-group types of *Balanus balanoides* in 1946.

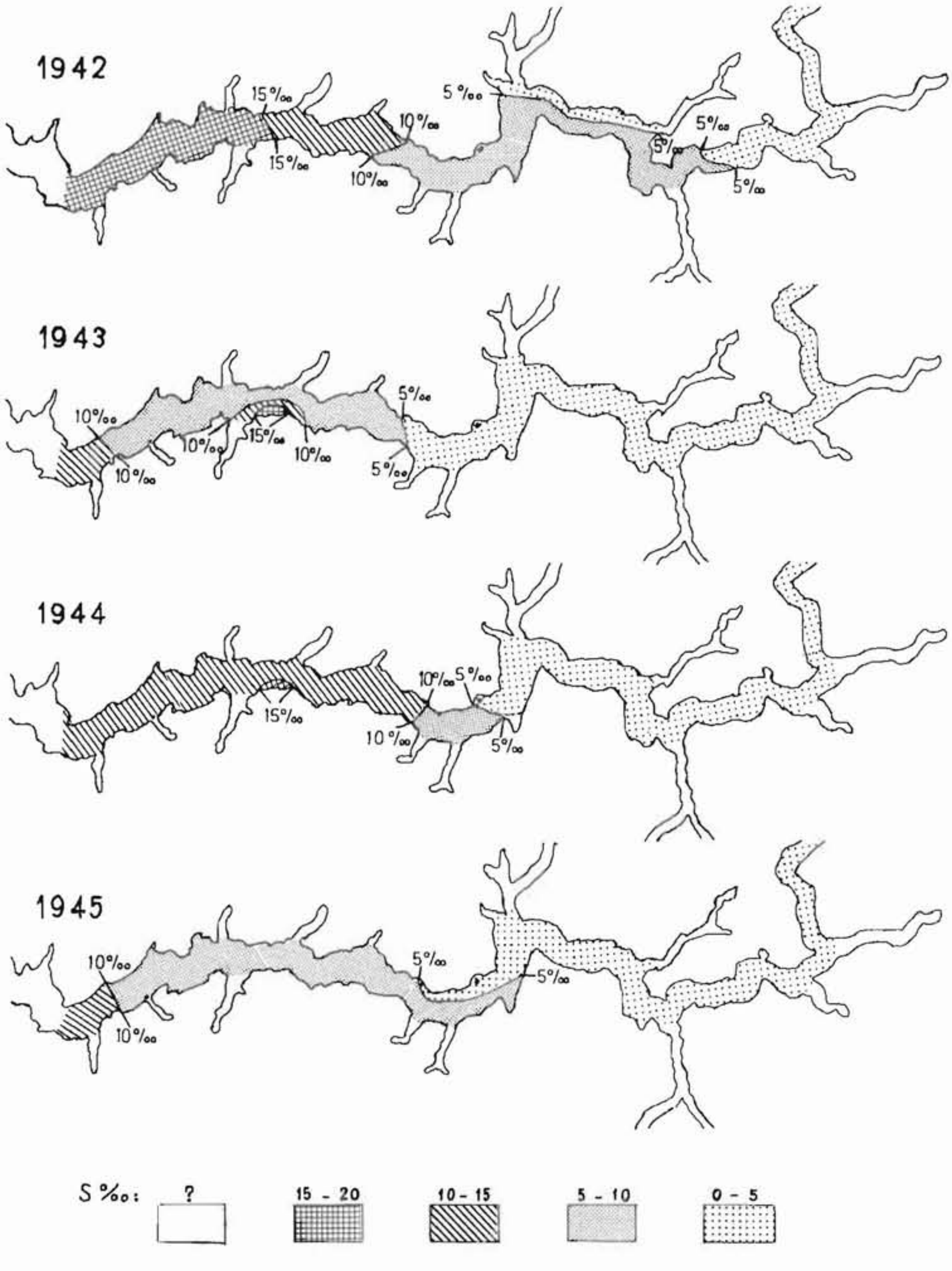

Fig. 19. Surface salinity distribution in Sognefjorden at the turn of July/August in the years 1942-1945.