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FACTORS INFLUENCING COMPETITION AND MORTALITY IN BARNACLES

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ABSTRACT.

Competition between Elminius modestus (Darwin) and Balanus balanoides (L) is considered to be an important issue in the invasion of British shores by E.modestus and in explaining the coexistence of both species in the intertidal barnacle niche.

Competition is discussed by reference to the concept of ecological performance, which is a term describing all adaptations and physiological and behavioural attributes of each species. Much information on the biology of cirripedes already exists, but the importance of predation and settlement behaviour in relation to competition have not been examined satisfactorily. Consequently these two ecological features are investigated in the thesis. The tolerance of developing embryos to extremes of temperature, and the infection frequencies of the castrating parasite Hemioniscus balani (Spence Bate) are also examined to assess their importance in the ecology of each species.

All the available information is then summarised. Comparative assessments of ecological performance are made for each species and for each single feature of their ecology. The assessments are then analysed in an attempt to identify factors which are especially important in regulating competition between the two species. It is acknowledged that the approach is necessarily an over-simplification, but it is broadly concluded that biological mechanisms are more important than actions of the physical environment. Settlement behaviour and susceptibility to predation may be especially significant in influencing competition both during the initial colonisation by E.modestus and in the contest of its coexistence with B.balanoides.

INTRODUCTION.

At about the time when Hitler was contemplating the conquest of Britain, the Australasian barnacle *Elminius modestus* was successfully invading the shores of Southern England. By the end of the war it had become established along the south-east coast and from this foothold, has spread over most of the British Isles. The early stages of this resoundingly successful invasion are well reviewed by Crisp (1958) and subsequent colonisation of British shores has been reported by Crisp and Southward (1959) and Crisp (1960).

The introduction of a new species to an area provides a unique opportunity to observe the resulting ecological interaction. *Elminius* has been so successful in colonising our coasts that inevitably it has made a marked impact on the intertidal community. Two intriguing questions immediately arise: Firstly, why has the invader been so successful? And secondly, what is the result of the ecological disturbance created by the invasion? The answers to both questions hinge around the success of *E.modestus* in competition with the indigenous intertidal barnacle *Balanus balanoides*.

Since *Elminius* has been established around the shores of North Wales for over twenty years (see Crisp 1958), without entirely displacing *B.balanoides* it seems reasonable to assume that some kind of ecological balance has been achieved with the two species sharing the intertidal barnacle niche. This essentially answers the second question concerning the ecological disturbance resulting from the invasion, but instantly raises a new question; namely, how is the balance maintained?

In order to answer these questions it is necessary to make a very thorough examination of the factors which control competition and mortality in the two species of cirripede.

Competition.

For the purpose of this thesis, the general definition of competition as:

"Inferred or proven interaction between species which share a common population-limiting resource", (Macfadyen 1963) seems satisfactory. The definition is equally applicable to intraspecific competition if the word "species" is replaced by the word "individuals".

The factors which influence competition may act directly or indirectly. Competition for food and space will be directly affected by aspects of the organism's biology relating to feeding efficiency, growth rate and size. Other features of the organism's biology such as resistance to dessication, and temperature tolerance may be said to act indirectly since they do not relate to the resource for which the organisms are competing, but affect the activity and survival of the organism and thence its efficiency in competition. For example Crisp and Southward (1956) suggested that temperature changes altered the balance of competition between the barnacles, *Chthamalus stellatus* and *B.balanoides*, by effects on breeding activities and feeding efficiencies.

Competition is not an easy subject to study. Reynoldson (1970) has suggested that five criteria based on comparative distribution and abundance; Identification of a common resource; the performance of competing populations; And results of manipulating resources, and populations in the field, should all be consistent with a competition hypothesis before a competitive interaction is clearly proven. However the sessile nature of intertidal barnacles coupled with their accessibility and abundance make them suitable subjects for studies of competition (Connell, 1959), and a number of important observations have been made. Connell (1961 a) demonstrated the importance of intraspecific competition in B.balanoides as a factor contributing to mortality by smothering and undercutting of individuals and the death of groups of individuals as a result of hummocking. In a parallel study on the ecology of Chthamalus stellatus Connell (1961 b) showed that interspecific competition with B.balanoides was responsible for the restriction of Chthamalus to the upper part of the intertidal region.

The observations of Crisp (1958 and 1964) are of great intertest in describing competition between E.modestus and B.balanoides. In the first paper (Crisp, 1958, p.510) the situation described would suggest the eventual replacement of Balanus by Elminius. However, results from the field experiments on growth-rate described by Crisp (1964) suggest that E.modestus only has an advantage over B.balanoides in what the author describes as extremely rigorous and unnatural conditions, whilst his observations made in the intertidal region show B.balanoides to have a clear advantage. Yet, on the shores of the Menai Straits, both species seem to coexist satisfactorily. Growth rate is an important factor in competition between barnacles (Connell, 1961 a and 1961 b) but clearly there are other factors involved.

Assessment and analysis of interspecific competition.

Considering Reynoldson's (1970) criteria it is quite difficult to prove the existence of competition. The analysis of a competition situation is equally difficult because of the multitude of component factors which contribute to the fitness or ecological performance of a given species. (Since fitness has a specific meaning in evolutionary terms, and will be affected by competition, it is better to use the term ecological performance to describe all the physiological and behavioural attributes which dictate ecological success). The actual mechanics of interspecific competition are even more difficult to investigate because of the complex interplay between the various aspects of ecological performance and the fluctuations and temporal and spatial variations in environmental factors. Connell (1959) summarises the problem, quoting Darwin:

> "Probably in no one case could we precisely say how one species has been victorious over another in the great battle of life."

In fact whilst we can measure most of the individual components which contribute to the ecological performance of an organism (e.g. growth-rate, salinity tolerance), it is still not possible to measure the contribution of each component to the overall success of a species in any given competitive situation. It is therefore necessary to resort to making subjective assessments or value judgments of each component of ecological performance for each of the competing species. Reference to Table 6, p.510 in Crisp (1958) demonstrates this approach. I am effectively re-defining Crisp's term "Ecological requirements" as components of ecological performance. The assessments of performance for each species can be tabulated and compared and hopefully, if sufficient components have been examined, the information can be used to explain the success of one species in competition against the other.

Such an approach is quite straightforward when considering the physical environment. Tolerance to most features of this environment can be measured quite accurately, at least on a comparative basis.

Factors relating to the biological environment, e.g. susceptibility to predation, parasitism and disease are much more difficult to assess.

The Study approach.

In the course of this study it was intended to look primarily at biological aspects of the ecological performance of each species. These have generally been neglected, but are obviously important. Some factors such as susceptibility to disease and longevity/senescence were deemed too difficult to investigate, if indeed they exist in natural conditions. Particular attention was given to the effects of predation by Nucella lapillus, the importance of which has been demonstrated by Connell, (1961 a). The occurrence of the castrating parasite Hemioniscus balani was briefly examined because of possible influences on fecundity and population levels. (See Crisp and Southward, 1958).

Direct physical competition for space and food is controlled by the settlement behaviour of the cypris larvae and the growth rates and feeding efficiencies of the adults. The specific spacing behaviour of cyprids at settlement is vitally important, as once settled, the choice of site is irrevocable. Special attention was given to this point as a result of a comment by Knight-Jones and Moyse (1961) that settlement behaviour created a situation where interspecific competition was likely to be more intense than intraspecific competition. According to mathematical theories of competition (Macfadyen 1963, ch.14; Slobodkin 1961) such a situation must result in the eventual exclusion of one species by the other. As previously observed, this does not appear to be the case, at least in the Menai Straits. Furthermore, the idea is in direct conflict with the extensive literature on gregariousness in barnacles (Knight-Jones and Stephenson, 1950; Knight-Jones, 1953; Knight-Jones and Crisp, 1953; Crisp and Meadows, 1962, 1963). Consequently, this point was examined in some detail, both in the laboratory and in the field.

Most of the physical factors concerned in cirripede ecology have already been investigated. Salinity, dessication and tolerance to high temperatures were studied by Foster (1969), whilst low temperature tolerance has been examined by Crisp and Ritz (1967) and Ritz (1968). The only significant gap in our knowledge of the influences of the physical environment was the tolerance of developing embryos to extremes of temperature. This feature was considered to demand investigation because of the possibility that temperature tolerance in embryos is more important than that of adults in dictating ecological performance. Embryonic temperature tolerance is also important because of its interplay with fecundity. The extended breeding season and greater fecundity of E.modestus (Crisp and Davies, 1955) would not confer such a distinct advantage on this species if its embryos were unable to tolerate temperatures experienced during the colder months of the year. In fact Barnes and Barnes (1962) considered that the effects of temperature on breeding may eventually limit the spread of E.modestus in Scotland.

The majority of the work was carried out in the laboratory, as the aim of each investigation was to examine single components of ecological performance. Field studies usually describe the summated effects of several components and were therefore generally employed only as supporting studies to the main investigation. The exceptions to this were the survey of parasitic infection, which necessitated a field study, and the field observations on settlement behaviour.

Arrangement of material.

The thesis therefore comprises six sections. Section I deals with the thermal tolerances of developing embryos. This information in itself describes a component of ecological performance and also facilitates reassessment of fecundity as a component. Sections II and III examine settlement behaviour in relation to competition in order to assess the relative emphasis on interspecific and intraspecific competition. Section IV considers the relative susceptibility to predation by *Nucella* and section V examines the infection frequencies of each species by *H.balani*. All the information is brought together in section VI along with information from the literature and an attempt is made to explain the success of *E.modestus* in its colonisation of British shores, and also to examine factors contributing to its coexistence with *B.balanoides.*

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SECTION I

TEMPERATURE TOLERANCE AT DIFFERENT STAGES OF EMBRYONIC DEVELOPMENT, IN THE CIRRIPEDES *BALANUS BALANOIDES* (L.) AND *ELMINIUS MODESTUS* DARWIN.

Abstract.

The upper and lower median lethal temperatures for the major phases of embryonic development in B.balanoides and E.modestus are measured. No values could be obtained for the earliest stage embryos of E.modestus due to scarcity of material.

The upper median lethal temperature is measured as an instantaneous value, although tolerance of low temperature is measured as the 18 hr. L.M.L.T. Both species exhibit similar patterns of tolerance to high temperature, displaying an increase in tolerance as embryonic development proceeds. Most stages of development are shown to be more tolerant than the adults. Tolerance to low temperatures also increases with embryonic development. However, values for E.modestus embryos suggests a greater tolerance than that of adult barnacles, whilst embryos of B.balanoides appear to be generally less tolerant than adults.

Both species show appropriate adaptation in tolerance of temperature extremes: The boreo-arctic Balanus balanoides is more tolerant of low temperatures; Elminius modestus from sub-tropical waters is more tolerant of high temperatures. The ecological implications of the differences are briefly discussed.

INTRODUCTION.

The lethal effects of high temperature on barnacles have been extensively studied, (Southward, 1958, and 1965, Crisp and Ritz, 1967, and Foster, 1969). Tolerance of low temperatures has also received considerable attention, (Southward, 1958, Crisp and Ritz, 1967, Cook and Gabbott, 1970, and Cook and Lewis, 1971). Most attention has been given to adult barnacles, although the work of Crisp and Ritz, (1967), and Foster, (1969), included Nauplii, cyprids, settled cyprids and spat.

However, very little is known of the temperature tolerance of cirripede embryos. Foster, (1969), says that, "It appears that, throughout the ontogeny of cirripedes, there is a uniform tolerance of temperature and salinity", but he presents no evidence in relation to the embryonic stages. Crisp and Ritz, (1967), were only able to assess the tolerance of almost fully developed embryos of B.balanoides to low temperature. As they point out, the relationship between temperature tolerance and age is not clear, but there is evidence that the harmful effects of temperature are more important during embryonic development than at any other phase of an animal life-cycle. Ushakov, (1968), states -

> "For most of the somatic cells studied, injurious temperatures are many centigrade degrees higher than those lethal for the intact organism. In contrast, temperatures injurious for eggs and zygotes exceed optimal temperatures for embryo development only by 2^{o} to $5^{o}C$. (Andronikov, 1965)."

It follows, therefore, that the embryos may be the most vulnerable stage of the life-cycle, and their limits of temperature tolerance will dictate the survival and distribution of a population. On the same premise, it could reasonably be expected that the earlier stages of embryonic development are more susceptible to extremes of temperature, than are later stages. Consequently, this investigation examines the median lethal temperature of cirripede eggs at different stages of development.

Measurement of Lethal Limits.

The temperature tolerance of an organism is usually expressed as the median lethal temperature, (M.L.T.). Crisp and Ritz, (1967), have briefly discussed the different approaches to measuring the M.L.T. Their procedure for assessing low temperature tolerance was adopted in this investigation.

In assessing tolerance to high temperatures the "instantaneous upper lethal temperature", (Foster, 1969), was employed. As Foster explains, this approach is suitable for comparative work, although the results are not of direct ecological significance. Apart from rapidity and convenience the "instantaneous" value has the added advantage of being comparable with the results of Southward, (1958), and Crisp and Ritz, (1967).

Criteria for establishing mortality.

The definition of death is a tricky problem, in biology as in medicine, and yet it is a prerequisite in any study of lethal effects. The problem is further complicated when dealing with invertebrates because of their capacity for regeneration and ability to survive extensive physical damage. In the case of invertebrate embryos, mortality is probably best described as the failure to produce viable larvae. However, this criterion relies on a satisfactory method of identifying "viable larvae."

Such an approach is applicable to work on cirripede eggs, at least, theoretically. In practice, the idea is feasible for E.modestus embryos with their short incubation period (14 days approx.), but the much longer incubation period of B.balanoides (100 days approx), introduces considerable difficulties. Furthermore, there is no reliable means of assessing the viability of the nauplii produced by the eggs. Consequently the criterion of successful development, as used by Crisp and Ritz, (1967) was adopted. For the purpose of these investigations the mortality of any given embryonic stage is defined as the failure to develop (successfully) through four further stages.

The definition holds for all stages 1 to 9, but is obviously inapplicable to late stage eggs. Once again it was decided to adopt the criterion used by Crisp and Ritz, (1967), namely successful hatching of mature embryos. However, preliminary experiments indicated inadequacies in this approach. In some cases the application of hatching substance (Crisp 1956), caused the properly formed but unhatched nauplii to become mobile and attempt to break out of the egg case, although they failed to hatch. In other instances, obviously deformed and presumably non-viable nauplii hatched and began swimming. The first case gives rise to a dilemma. As mobility is usually considered to be evidence of life it is difficult to classify these embryos as dead, but, if the criterion of hatching success is used to establish mortality, they cannot be classified as alive. In general, such cases were ascribed to the category of "significant mortality". The definition of mortality for late stage egg masses is therefore based on a composite criterion of completed embryonic development, mobility and hatching success.

Note: In all assessments of mortality the condition of experimental material was always related to observations on the appropriate control.

METHODS.

Apparatus: For details of thermal treatment concerning the determination of upper lethal temperatures, see Foster (1969). All experiments were performed using a Grant Instruments SB 15X water bath, set to achieve a heating rate of 0.2°C/min.

Full details of the equipment used for investigating low temperature tolerance are given by Crisp and Ritz (1967). However, the thermostablity of the low temperature compartments was re-assessed as ± 1.0 degrees C over a period of 18 hours.

Materials: Rocks bearing adult barnacles were collected at various tidal levels from the shore of the Menai Straits, near the Menai Suspension Bridge.

Procedure: The paired egg masses were carefully removed from the mantle cavity, washed in clean sea-water and examined under the microscope to identify the stage of development, (Crisp, 1954). Each mass was then placed in a 25 mm. diameter specimen tube and covered with sterilised sea-water. The tubes were corked and labelled. One tube was set aside as a control, and subsequent to the experiment, both egg masses were reared in vitro following the method of Crisp (1959). Material was examined at intervals and development of the treated egg mass was compared with that of the control. The condition of the experimental material was recorded under one of three categories; Alive, Dead, Significant mortality.

Results were collected for four groups of developmental stages;

Group 1 : Stages 1 - 4 (Segmentation and epiboly).
Group 2 : Stages 5 - 7 (Endoderm segmentation).
Group 3 : Stages 8 - 10 (Limb bud formation and differentiation).
Group 4 : Stages 11 - 13 (Up to full development of viable stage 1 nauplius).

Data was then analysed using a computer programmed for probit analysis and linear regression.

RESULTS.

Upper Median Lethal temperature (U.M.L.T.)

E.modestus.				*B.balanoides.*			
Group	Stages	L.T.50 ± S.E.		Group	Stages	L.T.50 ± S.E.	
1	1- 4	*		1	1- 4	41.1	± 0.2
2	5- 7	46.6	± 0.2	2	5- 7	42.9	± 0.2
3	8-10	47.1	± 0.1	3	8-10	43.7	± 0.2
4	11-13	47.9	± 0.1	4	11-13	44.3	± 0.2

Lower Median Lethal temperature (L.M.L.T.)

E.modestus.				*B.balanoides.*			
Group	Stages	L.T.50 ± S.E.		Group	Stages	L.T.50 ± S.E.	
1	1- 4	*		1	1- 4	- 10.2	± 0.3
2	5- 7	- 8.0	± 0.3	2	5- 7	- 12.7	± 0.2
3	8-10	- 11.4	± 0.6	3	8-10	- 14.0	± 0.2
4	11-13	- 15.3	± 0.5	4	11-13	- 17.8	± 0.5

* *E.modestus*, group 1 (Stages 1-4): Insufficient data was obtained to provide a result, owing to the scarcity of material.

L.T.50 = Median Lethal temperature.

S.E. = Standard error.

Stages = Stage of development, as defined by Crisp, (1954).

DISCUSSION.

1. Differences between stages of embryonic development, and comparison with figures for other phases of the life-cycle.

A. Upper Median Lethal Temperature (U.M.L.T.).

(i) B.Balanoides.

As anticipated there is an increase in the U.M.L.T. as development progresses. This is most evident after the cleavage stages (1-4) with an increase of 1.8 degrees C. In fact, in the remaining three groups of stages, the M.L.T. only rises by a further 1.4 degrees C.

The value of 43.7°C. for stages 8-10 is in agreement with the observations of Crisp and Ritz (1967), who found virtually no effect with temperatures up to 43°. These results therefore substantiate their view that late stage eggs exhibit a tolerance at least as great as that of the adults. The final stages of development (11-13) are tolerant of temperatures approximately 1 degree greater than that quoted for the adults.

Embryonic development encompasses a wide range of temperature tolerance. The lowest value, predictably that found in the earliest stages, is considerably lower than the M.L.T's cited for adults. However, they are fractionally higher than the figures given for nauplii and cyprids, (Crisp and Ritz, 1967). Therefore these planktonic larvae of <u>B.balanoides</u> are the most susceptible stage of the life-cycle. But, as Southward (1958) has pointed out, shore temperatures may reach considerably higher levels than sea-water temperatures. Consequently the early stage eggs are more likely to be subjected to high temperatures than the planktonic phases of the life-cycle, and therefore the earliest stages of embryonic development, in <u>B.balanoides</u>, are probably the most vulnerable to heat death.

(ii) E.modestus.

E.modestus embryos show the same pattern of increasing tolerance as development progresses. Furthermore, the temperature difference between groups of stages are similar to those found for B.balanoides. It is most regrettable that no value could be obtained for the earliest group of stages.

Comparison of these results with figures quoted for adult E.modestus. (Foster 1969), shows that the lowest M.L.T. for eggs, 46.6°C. is 2 degrees higher than the M.L.T. of the adult. B.balanoides shows a 2 degrees difference in the U.M.L.T. between group 1 and group 2 eggs. However, a similar difference in the case of E.modestus would scarcely suffice to make the U.M.L.T. of early stage E.modestus embryos lower than that of the adults. The obvious inference is that all stages of embryonic development in E.modestus are more resistant to high temperature than the adult. Such a conclusion may, however, be incorrect due to experimental conditions. Ritz (1968) observed that the rate of heating has a profound influence on the U.M.L.T. of E.modestus but not B.balanoides. Consequently a fractional difference between the heating rate in these experiments and the rate achieved by other workers may have produced the observed pattern. If actual data were available for stages 1-4, and the heating rate was identical with that used in tests on adult E.modestus, it is quite possible that the earliest stages of development would again be observed as the most susceptible to heat damage.

B. Lower Median Lethal temperature (L.M.L.T.).

(i) B.balanoides.

As with the U.M.L.T., the tolerance of the embryos tested shows an increase as development progresses. The greatest increase in resistance occurs when eggs reach the final stages of development, although the figure of -17.8°C. may be an over-estimate due to the difficulty of establishing mortality in late stage eggs. (See "Criteria for establishing mortality"). This value is several degrees lower than that given by Crisp and Ritz (1967), and approximates to the L.M.L.T. of the adult at this time of year. All other embryonic stages are considerably more susceptible to death by freezing than the adults. But, with a M.L.T. of -5.1°C., (Crisp and Ritz, 1967), the cypris larva is clearly the most vulnerable stage in the life-cycle.

(ii) E.modestus.

As discovered with B.balanoides, there is a pattern of increasing cold tolerance as the embryos develop. The largest increase is again shown by the late stage eggs, although this may be due to over-estimation of the L.M.L.T. for this group as previously explained. Ritz (1968) gives the L.M.L.T. of adult E.modestus as -4.3°C. There is therefore a similarity with the situation observed for the U.M.L.T., whereby eggs are more resistant than the adults. However, it is worth noting that Southward (1958) shows that E.modestus could survive 12-24 hours at -10°C., suggesting that the L.M.L.T. of E.modestus adults may be lower than -4.3°C. If this were so, then at least some egg stages would be more vulnerable to death by freezing than the adults

2. Comparison between species.

(a) U.M.L.T.

The figures for all stages of embryonic development in E.modestus are higher than those for B.balanoides. This is in keeping with findings for the adults of these two species, (Foster, 1969), and is consistent with their different natural habitats. A similar pattern is shown in both cases: Increments in the U.M.L.T. for each group of stages are similar in both species, and the U.M.L.T. for all but the earliest embryonic stages is higher than values given for adults of the same species. It therefore seems likely that the mechanism of heat death is the same in the two species studied.

The information suggests that the last nine stages are more tolerant to high temperature than the parent barnacle.

As previously mentioned this confirms the view of Crisp and Ritz (1967), that the resistance of eggs to high temperature is at least as great as the resistance of the adult.

(b) L.M.L.T.

The eggs of B.balanoides are clearly more resistant to low temperature than those of E.modestus. Again, this is consistent with the different natural habitats of the two species.

Unlike the situation with heat tolerance, E.modestus and B.balanoides show different patterns of cold resistance. The increases in the L.M.L.T. with stage of development show less similarity than the increments of the U.M.L.T. Furthermore, the eggs of E.modestus are more resistant to low temperatures than the adults, whereas eggs of B.balanoides are not as resistant as the adult, (at the same time of year). These differences could suggest a different mechanism of cold tolerance in the embryos of the two species. However, a more likely explanation is a difference in the mechanism of cold tolerance in the adult. B.balanoides adults show considerable changes in cold tolerance during the year, (Crisp and Ritz 1967), whereas E.modestus does not seem to show the same seasonal variation in temperature resistance. (Ritz 1968, and Foster 1969). Of course it is quite possible that both these explanations are correct and both the adult and embryonic stages possess a different mechanism of cold tolerance.

(c) General observations and ecological implications.

Consideration of both the U.M.L.T. and L.M.L.T. figures suggests a basic difference between E.modestus and B.balanoides. In the former the eggs are generally more resistant than the adults to the effects of temperature, whilst in the latter the embryonic stages seem to be the most vulnerable part of the life-cycle. This effectively widens the range of temperature tolerance in E.modestus as compared to B.balanoides and may have contributed to its successful spread in North-West Europe, (Crisp 1958).

Both species show an appropriate adaptation in the temperature tolerance of their embryos: E.modestus, breeding primarily in the summer has embryos which are most tolerant of high temperatures; B.balanoides, breeding from late autumn to early spring has embryos which not only exhibit considerable tolerance to low temperature, but also show increasing tolerance as the seasonal temperatures fall. These differences in temperature tolerance of the embryos coupled with the more profound direct and indirect effects of temperature on breeding activities of E.modestus, (Crisp and Davies, 1955), produce an effective temporal separation of the breeding seasons. It may therefore be suggested that the effects of temperature on the reproduction of E.modestus and B.balanoides contribute to the co-existence of these two species on our coasts.

Summary.

(1) Instantaneous values for the U.M.L.T. of E.modestus and B.balanoides are given for the major stages of embryonic development. (For E.modestus no value could be obtained for the earliest phase of development).

(2) 18 hr., L.M.L.T. values are given for the same stages of embryonic development as examined in the investigation of tolerance to high temperatures.

(3) Both species show similar patterns of tolerance to high temperatures. Tolerance increases as development progresses. Later stages of embryonic development are more tolerant than adults.

(4) Tolerance to low temperature also increases throughout embryonic development. However, the patterns of cold tolerance are different. B.balanoides embryos are generally less tolerant than adults, whilst most embryonic stages of E.modestus survived temperatures below those cited as lethal to the adult. It is postulated that different mechanisms of cold tolerance may exist in the two species.

(5) B.balanoides displays greater tolerance of low temperature than E.modestus.

(6) E.modestus exhibits a greater tolerance of high temperature than B.balanoides.

(7) The findings are consistent with the different zoogeographic origins of the two species. It is concluded that differences in temperature tolerance may assist coexistence of the two species by reinforcing temporal separation of the breeding seasons.

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SECTION II

A FIELD STUDY OF SETTLEMENT BEHAVIOUR IN *BALANUS BALANOIDES* (L.) AND *ELMINIUS MODESTUS* DARWIN (CIRRIPEDIA, CRUSTACEA) IN RELATION TO COMPETITION BETWEEN THEM.

SECTION III

LABORATORY STUDIES OF GREGARIOUS SETTLEMENT IN *BALANUS BALANOIDES* (L.) AND *ELMINIUS MODESTUS* (DARWIN) IN RELATION TO COMPETITION BETWEEN THESE SPECIES.

In Press. J. mar. biol. Ass. U.K. 1979

SECTION IV

A LABORATORY STUDY OF PREDATION BY THE COMMON DOG-WHELK *NUCELLA LAPILLUS* (GASTROPODA : PROSOBRANCHIA) ON THE BARNACLES *ELMINIUS MODESTUS* DARWIN AND *BALANUS BALANOIDES* (L.).

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SECTION V

A NOTE ON THE INFACETION OF *BALANUS BALANOIDES* AND *ELMINIUS MODESTUS* BY THE PARASITIC ISOPOD HEMIONISCUS BALANI (BATE.)

INTRODUCTION.

Barnacles infected by Hemioniscus balani exhibit a significant reduction in growth rate (Crisp 1960), and are usually rendered sterile (Crisp and Davies, 1955 and Crisp 1968). This may affect population levels in succeeding host generations as discussed by Crisp and Southward (1958). Hemioniscus is not a completely specific parasite (Perez 1923), and both E.modestus and B.balanoides are potential hosts (Crisp and Davies, 1955, Crisp and Southward, 1958 and Crisp 1968). If one species were more susceptible than the other infection by H.balani could influence the populations of these two cirripedes and consequently affect the balance of competition between them. A survey was therefore conducted to examine the frequency of occurrence of the parasite in a mixed population of E.modestus and B.balanoides.

Infection of E.modestus and B.balanoides.

On the Anglesey shore of the Menai Straits, adults of both species were examined for the presence of Hemioniscus. Only the occurrence of the adult female parasite was recorded as explained by Crisp (1968). The figures obtained in this way are satisfactory for comparative purposes.

E.modestus was observed to have a frequency of infection of 1.96% ($^{11}/571$) compared to a frequency of 1.25% ($^{6}/486$) for B.balanoides. Comparison of the figures by χ^2 showed that the differences are not significant. ($\chi^2 = 0.80$. p approx., 0.4). On this evidence the susceptibility of the two species is roughly equal. However, the greater facundity of E.modestus (Crisp and Davies, 1955), would still give this species an important advantage in competition with B.balanoides.

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SECTION VI

SYNTHESIS

INTRODUCTION.

The aim of the preceeding sections of this thesis is to examine several aspects of the ecology of the two species of cirripede. Most of the work relates to the biological environment and considers the effects of predation, parasitism and gregarious settlement. Section I concerns the physical environment (the effects of temperature), although it does allow a re-assessment of the importance of the high fecundity of E.modestus (Crisp and Davies, 1955). The information can now be used to make assessments of the ecological performance of the two species with respect to the various factors investigated.

For convenience ecological performance is considered under two headings according to the nature of the environmental factors concerned.

Responses to features of the physical environment are termed "Physical aspects". The biological environment concerns reactions to all other organisms including members of the same species and these are referred to as "Biological aspects." This heading also includes items which are not strictly responses to the biological environment, but are more accurately described as intrinsic biological properties such as fecundity. (Since each individual aspect represents a component of ecological performance, the terms aspect and component are equivalent. For details refer to Table 1).

An important difference between the two types of aspects is the effect of temperature. Physical aspects are not greatly affected by temperature as many are in fact measures of its effects. For example, the median lethal temperatures of a species are necessarily independent of environmental temperature. Other physical factors which do not directly concern temperature show relatively little variation with different temperatures. For example Crisp and Costlow (1963) showed that the effect of salinity on developing cirripede embryos was not appreciably influenced by temperatures normally encountered by the animals. However, since all invertebrates are poikilothermic, most biological aspects of their ecology must inevitably be affected by temperature, although measurements of biological components are not invalidated as long as they adequately relate to temperatures in the natural environment. The significance of this difference between physical and biological components is that the latter are more likely to vary in time and space. Variability in nature is often important in making "fine adjustments" to ecological situations.

All the available information is summarised in Table 1. The table is adapted from Crisp (1958) and up-dated by the relevant sections of this thesis and by the following :

(1) Barnes and Barnes (1962) on growth-rate, (including feeding efficiency and tolerance of siltation).

(2) Barnes, Read and Topinka (1970) on resistance to mechanical damage.

(3) Bhatnager and Crisp (1965) on larval salinity tolerance.

(4) Crisp (1960 and 1964) on growth rates.

(5) Crisp and Davies (1955) on breeding of Elminius.

(6) Crisp and Ritz (1967) on low temperature tolerance.

(7) Davenport (1976) on responses to fluctuating salinity regimes.

(8) Foster (1969 a) on tolerance of high temperatures.

(9) Foster (1969 b.) on effects of salinity dessication and high temperatures.

(10) Larman and Gabbott (1975) on discrimination during settlement.

(11) Ritz (1968) on Low temperature tolerance.

Table 1. An ecological comparison between E.modestus and B.balanoides.

Basic Facts.	E.modestus.	B.balanoides
Tidal zone occupied	M.H.W. to below L.W.S.	H.W.N. to L.W.S.
Settlement season	May to October	March to April
Adult size (Diameter)	5 to 10 mm.	5 to 15 mm.

Components of Ecological performance:	E.modestus.	B.balanoides.	Reference No.*
A. Physical Aspects			
Tolerance of salinity extremes (adult)	+ + + +	+ + +	6 and 9
Tolerance of salinity extremes (larval)	+ + +	+ +	3
Tolerance of high temperature (adult)	+ + +	+ +	8 and 9
Tolerance of high temperature (embryonic)	+ + +	+ +	Thesis
Tolerance of low temperature (adult)	+ +	+ + +	6 and 11
Tolerance of low temperature (embryonic)	+ +	+ + +	Thesis
Tolerance of dessication	+ + + +	+ + + +	9
Tolerance of siltation	+ + +	+ +	1
Resistance to mechanical damage	+ +	+ + +	2
B. Biological Aspects			
Susceptibility to parasitism	-	-	Thesis
Susceptibility to predation	- - -	- - - - -	Thesis
Growth rate	+ + +	+ + + +	4
Feeding efficiency	+ + +	+ +	1
Discrimination during settlement	+ + +	+ + + +	10
Gregariousness during settlement	+ + + +	+ + + + +	Thesis
Fecundity	+ + + + +	+ + +	5

Maximum Score 5 + or -

- signs are used only where the feature is deleterious in its effect. As predation can only act to eliminate individuals, it is given a negative score. All other features except parasitism are described in such a way that they will aid survival and therefore positive scores have been allocated.

* Reference No. Key to numbers is given in text.

"Basic facts" are taken from Southward and Crisp (1963).

The table is intended merely to provide a simple comparative summary of all known features of the ecology of E.modestus and B.balanoides. It is necessarily subjective since there is no reasonable means of estimating the importance of any one component to the ecological performance of the species. Each component is allocated a rating and the score received by each species for a particular component is directly comparable. Scores received for different components are not strictly comparable although some attempt has been made to weight components according to their probable importance. For example, amongst the physical aspects, tolerances to salinity and dessication would seem to be more important than tolerance of siltation or resistance to mechanical damage, since the latter are probably more localised in their occurence and scores have been weighted accordingly. Similarly, amongst biological components, susceptibility to parasitism is clearly less significant than susceptibility to predation and these aspects have also been weighted accordingly.

Summarising the information in this way avoids the problem of comparing sets of figures in different units and takes account of the qualifying comments of the workers whose results have been used. The data is thus easier to evaluate without the constant need to interpret a wide range of different measurements. (It also helps to obviate the otherwise excessive need for references in the text).

Using the table as a basis for discussion it is possible to examine all features of the ecology of E.modestus and B.balanoides and attempt to identify those which have allowed Elminius to be so successful in invading the intertidal habitat on British coasts. Similarly, since Elminius has not completely replaced Balanus on our shores, the table can be used as a basis for discussing their coexistence. It therefore seems appropriate to examine the information in two sections: Section 1 - Ecological features contributing to the success of E.modestus in competition with B.balanoides during it's colonisation of British shores; Section 2 - Ecological features affecting competition between E.modestus and B.balanoides in the context of their coexistence on British shores. Some overlap between sections is inevitable because it is necessary to consider the consequences of components in relation to both colonisation and coexistence in order to assess their effect.

The discussions are based on the situation in North Wales, where most of the observations have been made, and may therefore not apply throughout the entire geographical range of Elminius in the British Isles.

Discussions also tend to overlook the two extreme habitats which are especially favourable to one species, (i.e. sheltered estuaries where E.modestus is dominant, and exposed coasts where B.balanoides is dominant). Their omission is intentional, since most rocky shores provide intermediate conditions between the two extremes, and competition will be most important where the overlap of fundamental niches is greatest. Furthermore, Elminius is so widespread throughout the intertidal environment that the habitats produced by environmental extremes may be comparatively unimportant except during the earliest stages of the Elminius invasion. Crisp (1958) described the importance of sheltered areas such as harbours and estuaries in providing suitable habitats for the establishment of Elminius colonies, from which subsequent dispersal took place. The success of Elminius in these habitats could be ascribed to advantages in tolerance of siltation and lowered salinity, coupled with its greater feeding efficiency which may be very important in areas of reduced water movements. However, the situation is complicated by the considerable fluctuations in abundance of indigenous intertidal barnacles (Southward and Crisp, 1956) during the early years of the spread of *Elminius*. The decline of *B.balanoides* at this time may have significantly assisted colonisation of many areas.

In fact consideration of environmental extremes involves many complications, since competition with other species, (*Chthamalus stellatus* on exposed coasts and *Balanus improvisus* in estuaries) will presumably have an influence in these habitats. The difficulties of analysing competition between two species are sufficient to be convinced that attempts at explaining competition between three or four species would be decidedly over-ambitious.

Discussion is therefore largely confined to intermediate coastal habitats for simplicity, and because these habitats may reasonably be deemed to represent the majority of the intertidal rocky shore environment.

The concept of ecological performance.

The original intention of this thesis was to investigate the ecological interaction between Balanus and Elminius by analysing competition between the species. Analysis involves the assessment and comparison of all aspects of the ecological performance of the two species and consideration of the likely effects of each aspect on competition. It must be emphasised that such an approach is by no means the same as a consideration of the effects of environmental factors on ecology. The concept of ecological performance describes the suitability of organisms to the environment, whereas examination of environmental factors concerns the suitability of the environment to the organisms. Consideration of environmental factors is perhaps more applicable to zoogeography and studies of faunal distribution. For instance, factors such as high temperatures or poor food supply may explain why a species is absent from a certain locality, but wherever the species is found it is the tolerances or adaptations of the species to these factors which govern its success in that environment. It therefore seems more strictly accurate to consider ecological performance when analysing competition, since competition can only occur when both species meet together in the same environment. (There is a great danger of circular argument here and the preceeding remarks may merely reflect a personal viewpoint. However, since we are primarily interested in the organisms it seems more appropriate to discuss the success of a species by reference to its ecological capabilities than by considering the environment).

The approach is probably more valid than a consideration of environmental factors because some biological components of ecological performance do not directly relate to environmental factors. As explained previously, such features as fecundity are not a direct response to an environmental factor, but are intrinsic to the organism. Thus the concept of ecological performance encompasses more than just responses to the environment. Consequently I have used the concept of ecological performance throughout the ensuing discussion.

DISCUSSION.

Section 1 - Ecological features contributing to the success of E.modestus in competition with B.balanoides during its colonisation of British shores.

(A) Physical Aspects.

These are more easily dealt with as they show little variation with time, space or biological conditions, although B.balanoides has the unusual ability of being able to adjust its tolerance to low temperature in accordance with the season of the year (Crisp and Ritz, 1967). In terms of response to the physical environment it is difficult to separate the two species, as concluded by Foster (1969 b). E.modestus is slightly more tolerant of high temperatures and occurs slightly higher on the shore - probably assisted by its greater feeding efficiency. Occupation of this narrow zone free from competition with B.balanoides could provide a useful spatial refuge for Elminius. Once the first arrivals had colonised this region of the shore substantial stocks could be built up facilitating more extensive colonisation. The greater tolerance of siltation by E.modestus could also provide a refuge in sheltered areas. Personal observations in the Conway estuary tend to support this idea. Silt is deposited on rocky surfaces during early Spring and either prevents settlement of Balanus cyprids or covers and kills the young spat. Most adult Elminius which settled later in the year when rock surfaces are comparatively clean survive the period of heavy siltation. However, the specific adaptation of E.modestus to sheltered areas has been questioned by Barnes and Barnes (1962).

(B) Biological components.

The limited advantages of *E.modestus* over *B.balanoides* in physical aspects of its ecological performance imply that its success must lie in biological aspects. It certainly appears to have no advantage in terms of growth rate, nor in its avoidance of castrating parasitism. (The latter in fact does not seem to be a significant feature in the ecology of either species, at least in the Menai Straits). *Elminius* appears to have an advantage over *Balanus* in feeding efficiency as suggested by Barnes and Barnes (1962), although this is probably counteracted by deficiencies in growth rate. The benefits may manifest themselves in allowing *E.modestus* to occupy higher levels on the shore as considered above, and also in enhanced reproductive activity as discussed below.

Amongst biological components the greatest attribute of *E.modestus* is its remarkable fecundity coupled with its extended breeding season, as described by Crisp and Davies (1955). Obviously these features are very important in colonisation and must largely explain the rapidity with which the invasion took place. Crisp (1958) explains how the vast supply of larvae and long settlement season allowed *Elminius* to take over large areas of the habitat previously occupied by *B.balanoides*. The effectiveness of rapid colonisation is also demonstrated by the predominance of *Elminius* on loose stones. Observations in the Menai Straits and Conway estuary showed that these stones are turned over from time to time by storms or human activity, and the existing barnacle population is suffocated. The new, bare surface becomes available for colonisation and since *Balanus* has such a restricted settlement season the surface is usually colonised by *E.modestus*.

Fecundity and a prolonged settlement season explain the rapid spread of *Elminius* and the creation of small isolated populations. However, both species occur together throughout most of the intertidal zone. This could result entirely from continuous settlement of E.modestus recruited from these isolated stocks and from those occupying the spatial refuge between M.H.W. and H.W.N. (Such individuals are then presumably eliminated by direct physical competition from the established population of B.balanoides.) The hypothesis is not entirely satisfactory since the existence of Elminius in the intertidal zone does not appear to be so completely opportunistic and in many cases Elminius seems to survive in direct physical competition with B.balanoides. It is thus reasonable to conclude that in spite of limitations on growth-rate and size, Elminius uses its advantages of fecundity and feeding efficiency to compete satisfactorily with B.balanoides.

But two other factors have probably contributed to its success. As explained in Section IV, the predatory behaviour of Nucella lapillus could have given E.modestus a great advantage when first colonising new areas of shore. Removal of large numbers of B.balanoides through predation by Nucella would firstly create considerable areas for the settlement of E.modestus. Subsequently the preference shown by Nucella for the larger faster growing species would negate the advantages of B.balanoides in this respect, allowing E.modestus to grow without hindrance from its competitor. Thus the high fecundity of Elminius coupled with its comparative immunity to predation by Nucella would have enabled very rapid and highly successful colonisation.

Finally, there are strong indications that the settlement behaviour of the two species has played a small but vital role in the success of E.modestus. The comparatively low discrimination at settlement shown by Elminius (Larman and Gabbott, 1975) suggests that the presence of the competitor need not hinder settlement of the invader. This would be of great importance in the earliest stages of colonisation where existing populations of Elminius were very small or non-existent. Subsequently, the tendency towards gregarious settlement would not only perform its probable evolutionary function in aiding cross-fertilisation, but would lead to a situation where intraspecific competition would be more pronounced than interspecific competition. In other words, the effects of crowding would be more deleterious within one species than between the competing species as suggested in Section III. Thus it may well be that settlement behaviour has created a situation whereby E.modestus could largely avoid the problem of direct physical competition with the larger, faster-growing indigenous species. (The consequences of this situation are discussed further in Section 2.)

Summary, Section 1.

Advantages in physical aspects of the ecology of E.modestus, namely tolerance of high temperatures and siltation may have contributed to the success of Elminius in colonising British shores. The feeding efficiency of E.modestus has probably supplemented these benefits in physical components, facilitating the occupation of a spatial refuge.

Advantages in biological aspects have probably been more important in the rapidity of the Elminius invasion. High fecundity in conjunction with greater feeding efficiency and a degree of success in direct physical competition with B.balanoides have allowed rapid and effective colonisation of rocky shores. It is suggested that the principal factors contributing to this success in competition are the lower susceptibility of Elminius to predation by Nucella and the tendency for gregarious settlement to minimise the extent of direct physical interspecies competition.

Section 2 - Ecological features regulating competition between E.modestus and B.balanoides in the context of their coexistence on British shores.

(A) Physical Aspects.

It has already been observed that the ecological performance of the two species is difficult to separate when assessed in terms of the physical environment. In fact, as Foster (1969 b) observed, there appears to be a contradiction of Gauses axiom, that two species with similar ecology can not coexist indefinitely. Thus it seems unlikely that physical components of ecological performance can explain coexistence because the overlap of fundamental niches would be too great to allow continuous coexistence. Furthermore, any particular adaptation to the physical environment would be unlikely to change with time or population levels. Southward and Crisp (1956) demonstrated that changes in environmental factors could influence competition between barnacle species, but this is completely different to a change in the organisms ecological performance with respect to the physical factor concerned. Consequently, a physical component contributing towards coexistence must produce a retarding effect on the evident success of E.modestus during colonisation. (It also follows that any advantage conferred by physical components must necessarily make a negative contribution to coexistence). Thus it is very difficult to ascribe coexistence to physical aspects of the ecology of either species because their adaptations to physical factors overlap to such a high degree and because there is no evidence of changes in these factors or the ecological performance of either species with respect to these factors during the short period of time involved.

(B) Biological Aspects.

As in section 1 it appears that biological components must have more influence on competition than physical components of the animals' ecology. Both species compete for space and food, and yet those components which have the greatest effect on direct physical competition, namely size, feeding efficiency and growth rate seem unlikely to encourage coexistence. The experiments of Crisp (1964) indicate that *B.balanoides* is considerably more successful in direct physical competition with *E.modestus* except at high population densities or in conditions of severely restricted water flow, (i.e. limited food availability). It would be reasonable then to suppose that some form of spatial or temporal separation of the species exists in order to explain how both may survive utilising the same resources. Spatial separation as considered in section 1 is very limited and whilst it may be evoked to explain the continued survival of *Elminius* by virtue of a spatial refuge between H.W.N. and M.H.W., it cannot explain the continued survival of *Balanus* since *E.modestus* occurs throughout most of the zone occupied by *B.balanoides*. The hypothesis that *Elminius* survives by means of a spatial refuge and *Balanus* survives by being superior in direct physical competition (on account of its greater size and faster growth rate,) is one possible explanation. However, this idea seems unsatisfactory as explained in Section 1 because of its inconsistency with the rapid spread of *E.modestus* and its observed success in many areas where both species are found together.

Temporal separation resulting from different settlement seasons is perhaps a better explanation. *B.balanoides* settling slightly earlier in the year has chance to become established before the swarms of *Elminius* larvae begin their search for settlement sites. Any space unoccupied by *B.balanoides* can be colonised by *Elminius* and attempts at settling in areas where large numbers of Balanus already exist may also be quite successful. There is an intrinsic suggestion here that E.modestus may be the more successful species in direct physical competition since it must compete against an established Balanus population. Interestingly this is the complete converse of the implications involved in the spatial refuge explanation. Furthermore, the idea of temporal separation can be criticised as it again implies that Elminius is merely an opportunistic coloniser surviving like some ephemeral plant occupying a refuge in time (and space). Whilst it must be accepted that all barnacle species are to some extent opportunistic, this argument suffers the same objections as those discussed in connection with spatial separation of the species. It is difficult to reconcile the rapid and successful spread of E.modestus and evidence of its success in direct physical competition with B.balanoides if its survival is purely the result of opportunistic fortune.

One only has to imagine the intense competition for space that would result if the settlement seasons coincided to be convinced that temporal separation of spat-fall, whilst not complete, must enhance the possibilities of coexistence. Elminius with its prolonged breeding and settlement season expresses the advantages of its greater fecundity, but B.balanoides, settling earlier in the year has chance to establish that particular year class before the new generation of E.modestus arrives.

So far nothing has been found which can greatly alleviate the extent of competitive exclusion resulting from crowding. Nor have any mechanisms been considered which can vary to maintain a balance in competition thus allowing coexistence.

A feature of paramount importance in competition is settlement behaviour. Whilst such ecological components as growth-rate and size govern the outcome of direct physical competition, settlement behaviour controls the incidence of contacts which give rise to such interactions between the two species. Earlier consideration of spatial separation related to the general pattern of distribution (and survival) whereby the only effective separation of the species is a narrow band of the upper shore dominated by E.modestus. In general, throughout the intertidal, both species occur together. The only noticeable discontinuities are a form of patchiness rather than zonation, again reflecting the likelihood that biological mechanisms rather than physical factors are at work. Presumably this patchy distribution is a direct consequence of gregarious settlement as considered in section III. (The environmental heterogeneity responsible for creating these patches can only be assumed). It is thus easily arguable that small scale spatial separation of the species does occur, and that this makes a significant contribution to coexistence. Concommitent with the spatial separation resulting from gregarious settlement is the effective increase in direct intraspecific competition and consequent reduction of direct interspecific competition since most of the competitive effort of the individual becomes directed against its own species. As described in theoretical terms, (Slobodkin 1961, ch., 7), such a situation can enable coexistence even when there is considerable overlap of the fundamental niches, because the effect of each species on the other one is minimised. Thus the effect of gregarious settlement in tending to make intraspecific competition more intense than interspecific competition and creating small scale spatial separation of the species may promote coexistence of the two species in the same habitat.

The actual intensity of intraspecific competition can vary according to population density as shown by Crisp (1960, 1964), and the role of direct physical competition in regulating barnacle populations has been demonstrated by Connell(1961 a, 1961 b). Hence there is an ecological mechanism which can and will vary according to the relative success of either species. Crisp (1958, p.510) describes a change in competitive interaction between *Balanus* and *Elminius*. As the population of *Elminius* increased (at the expense of *B.balanoides*), intraspecific competition between individuals of *Balanus* declined, leaving *B.balanoides* which were "individually large, healthy and successful."

The fluctuations and variations in the intensity of direct physical competition within and between species are difficult if not impossible to assess, but it seems that the balance between the two must be very important in maintaining coexistence. If the theoretical considerations mentioned earlier can be said to apply to real situations then the gregarious settlement of both species may be fundamental in controlling competitive interactions in such a way as to achieve coexistence.

The final component which may play a part in coexistence is the predatory behaviour of *Nucella*. Connell(1961 a) has clearly shown that predation by *Nucella* is important in regulating *Balanus* populations. The experiments described in section IV indicate that prey selection may change according to the populations of the prey species present. Furthermore, the tendency shown by *Nucella* to take the larger individuals (Connell, 1961 a) would create space for both species probably at the expense of *B.balanoides*, thus negating some of the advantages of this species resulting from its greater size, growth-rate and earlier settlement season. (Even if predation became random, Nucella would still tend to remove the numerically dominant species thereby helping to restore a balance between the populations and encourage coexistence).

Paine (1966) has shown that predation can significantly affect the balance of competition between species in the intertidal environment and encourages diversity. It therefore seems likely that the susceptibility of both species to predation by Nucella is an important feature in the coexistence of Elminius and Balanus on our shores.

Summary, Section 2.

The ecological components contributing to the co-existence of B.balanoides and E.modestus seem to be biological rather than physical. As in section 1 the major features are identified as the settlement behaviour of the two species and the predatory activity of Nucella lapillus. Both of these factors can act to reduce the extent of direct physical competition between the two species and also have the capacity to vary according to the state of balance between populations of the two species. Temporal separation of the breeding seasons may also be important in facilitating co-existence.

Conclusions.

It is difficult to ascribe success in competition or coexistence to individual components of ecological performance. However, it seems reasonable to conclude that in the situation existing between Elminius and Balanus biological mechanisms are more important than influences of the physical environment in regulating competition. In particular, fecundity, settlement behaviour and susceptibility to predation all seem to be highly significant. Temporal separation of spat-fall may also be important.

Obviously competition must involve to varying degrees all components of ecological performance both singly and by means of a complex interplay of factors acting in combination. Consequently any assessment of the situation is bound to be an over-simplification. Some factors are completely ignored, and small fluctuations and variations in the environment may have influences which are almost impossible to detect. As observed in the introduction to this thesis, the interaction between ecological performance and environmental variation makes the actual mechanics of interspecific competition very complicated indeed. It is therefore to be hoped that the concept of ecological performance simplifies the issue sufficiently to make helpful deductions without over-simplifying to the point where such deductions are meaningless. There is certainly scope for more experimental field ecology to test some of the ideas put forward here. For example much could be learned from observations on artificially introduced populations of one species into areas where they are absent or very low in numbers. The subsequent elimination or survival of such a population could shed much light on the factors controlling ecological success. It would be especially interesting to introduce B.balanoides to Australasian shores and thus observe the situation in reverse so to speak.

The ecological performance approach is a useful preparation for such ecological experimentation, although a great deal of information is required before such an analysis can be a ttempted. The general conclusion that biological factors are more important than physical ones is not altogether surprising, since such extensive competition could only result if the physical aspects of the ecology of the two species showed a high level of similarity. Whilst the approach can not completely explain the competitive interaction between Elminius and Balanus I hope that this synthesis has revealed the major features of the ecology of both species which allowed the former to be so successful in its invasion of British shores, and which now allow both species to coexist as established members of the rocky-shore community.

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SUMMARY.

Factors affecting competition between Elminius modestus and Balanus balanoides are briefly reviewed.

The situation is investigated by considering single components of the ecology of both species. Most attention is given to features of the biological environment which have not been adequately examined before.

The effects of parasitism, predation and gregarious settlement in relation to competition are investigated (sections II to V inclusive.) Temperature tolerance of developing embryos is considered in section I.

Parasitism is shown to be comparatively unimportant, but predation and gregarious settlement may be significant factors in cirripede ecology. since they can influence the balance of competition between species. Embryonic temperature tolerances probably reinforce the temporal separation of settlement seasons.

The consequences of all aspects of the ecology of both species are discussed in section VI. It is concluded that biological features of ecology are more important than influences of the physical environment. Predation and settlement behaviour may be particularly significant in explaining both the initial success of Elminius in colonisation and the coexistence of both species on British shores.