

Bangor University

DOCTOR OF PHILOSOPHY

Factors influencing competition and mortality in barnacles.

Barnett, Brian E.

Award date: 1979

Awarding institution: Bangor University

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FACTORS INFLUENCING COMPETITION

AND MORTALITY IN BARNACLES

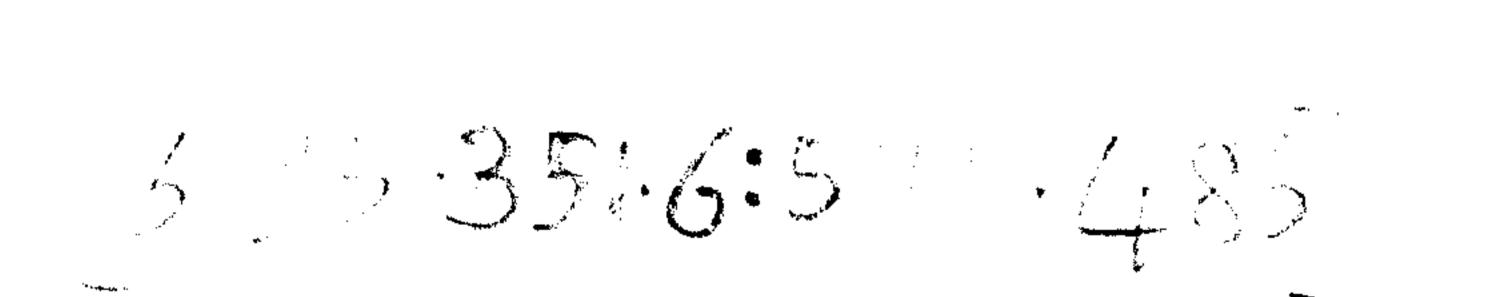
submitted to the University of Wales

Ьу

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June 1979

Third party material to be excluded from digitised thesis:

Section II. Research paper pp27-42 J.Mar.Biol.Ass.UK 1979 59 (4) Section III Research paper pp43-64 J.Mar.Biol.Ass.UK 1979 59 (3) Section IV Research paper pp66-82 J.Mar.Biol.Ass.UK 1979 59 (2)

Readers may consult the original thesis if they wish to see this material

Acknowledgements

I would like to thank Professor D.J. Crisp for his supervision and

guidance and for his help and criticism during the preparation of this thesis.

Thanks are due to Sarah Edwards for conducting some of the counts in

section III, and to Mr. W. Rowntree and Mr. D.C. Williams for assistance

with photographic work. I would also like to record my gratitude for the

help and encouragement received from staff and colleagues, too numerous

to mention.

The work was carried out during the tenure of a N.E.R.C. Grant.

Finally, thanks are due to Mrs. M. Taylor and Mrs. P. Pritchard for typing the manuscript. (Special thanks to Pat for being so helpful

since my departure).

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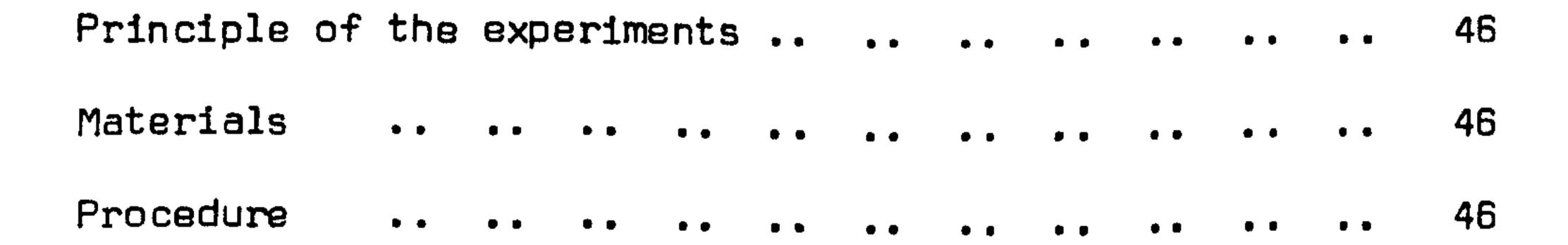
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Competition between <u>Elminius modestus</u> (Darwin) and <u>Balanus balanoides</u> (L) is considered to be an important issue in the invasion of British shores by <u>E.modestus</u> and in explaining the coexistence of both species in the intertidal 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 <u>Hemioniscus balani</u> (Spence

Bate) are also examined to assess their importance in the ecology

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 <u>B.balanoides</u>.

IMTRODUCTION.

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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?

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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

However the sessile nature of intertidal barnacles coupled proven.

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

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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

- 5 -

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 <u>Nucella lapillus</u>, the importance of which has been demonstrated by Connell, (1961 a). The occurrence of the castrating parasite <u>Hemioniscus balani</u> 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 <u>E.modestus</u> (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.

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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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AND ELHINIUS MODESTUS DARWIN.

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STAGES OF EMBRYONIC DEVELOPMENT, IN

THE CIRRIPEDES BALANUS BALANOIDES (L.)

TEMPSKAPURE FOLGRAHUE AT DIFFERENT

DECTION I

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Abstract.

The upper and lower median lethal temperatures for the major

- 11 -

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. Nost 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 3. balanoides appear to be generally less tolerant than adults.

Both species show appropriate adaptation in tolerance of temperature

The boreo-arctic Balanus balanoides is more tolerant of low extremes:

temperatures; Elminius modestus from sub-tropical waters is more

tolerant of high temperatures. The ecological implications of the

differences are briefly discussed.

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INPRODUCTION.

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). Nost 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 entogeny 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 <u>B.balanoides</u> 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° to 5° 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 temporature 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, (K.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.

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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).

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Criteria for establishing nortality.

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

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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.nodestus 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 - 15 -

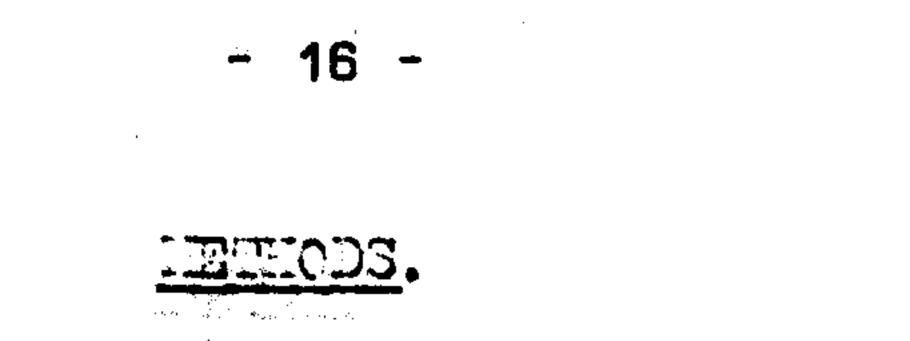
hatching success is used to establish mortality, they cannot be classified as alive. In general, such cases were ascribed to the category of "significant mortality". The definition of mortality for late stage egg masses is therefore based on a composite criterion of completed embryonic development, mobility and hatching success.

Note: In all assessments of nortality the condition of experimental material

was always related to observations on the appropriate control.

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Apparatus: For details of thernal treatment concerning the determination of upper lethal temperatures, see Foster (1969). All experiments vere 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 \pm 1.0 degrees C

over a period of 18 hours.

Rochs bearing adult baimacles were collected at various Laterials: tilal levels from the shore of the Lenai Straits, near the Lenai

Suspension Bridge.

The paired egg masses were carefully renoved from the mantle Procedure: 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). Haterial 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;

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analysis and linear regression.

Group 2 : Group 3 Group 4 Data was then analysed using a computer programmed for probit

Group 1 :

Stages 5-7 : Stages 8 - 10 : Stages 11 - 13

Stages 1 - 4

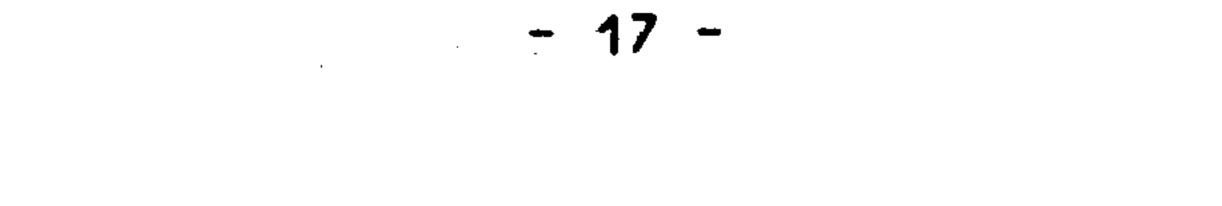
(Segmentation and epiboly).

(Endodern segmentation).

(Limb bud formation and differentiation).

(Up to full development of viable

stage 1 nauplius).



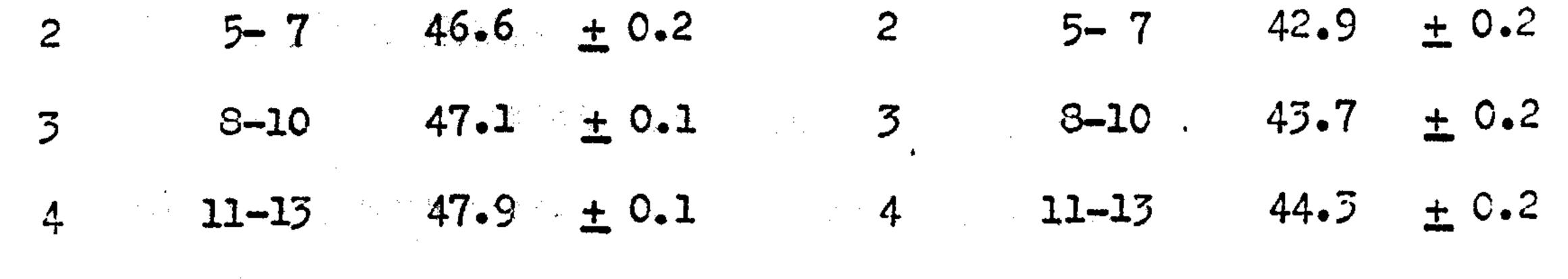
RESULTS.

Upper Hedian Lethal temperature (U.H.L.T.)

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E.modestus. B.balanoides. L.T.50 + S.E.Stages Stages L.T.50 + S.E. Group Group 1-4 * 1-4 41.1 ± 0.2 1



Lover Median Lethal temperature (L.N.L.T.) .

E.nodestus. <u>B.balanoides</u>.

Group Stages L.T.50 \pm S.E. Group Stages L.T.50 \pm S.E. 1 - 1 - 10.2 + 0.3 $2 - 7 - 8.0 \pm 0.3$ $2 - 5 - 7 - 12.7 \pm 0.2$

$3 - 10 - 11.4 \pm 0.6 \qquad 3 - 8-10 - 14.0 \pm 0.2$ 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 = Nedian Lethal temperature. S.E. = Standard error. Stages = Stage of development, as defined by Crisp, (1954).

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Differences between stages of embryonic development,

and comparison with figures for other phases of the

life-cycle.

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

(i)

B.Balanoides.

As anticipated there is an increase in the U.H.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 N.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 H.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 B. balanoides 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.



I.nodestus. (ii)

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 Carlo I. the earliest group of stages.

Comparison of these results with figures quoted for adult

I.nodestus. (Foster 1969), shows that the lowest H.L.T. for eggs, 46.6°C. is 2 degrees higher than the L.L.T. of the adult. B.balanoides shows a 2 degrees difference in the U.H.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 <u>B.nodestus</u> embryos lover than that of the adults. The obvious inference is that all stages of embryonic development in <u>I.modestus</u> 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.H.L.T. of <u>I.modestus</u> but not <u>B.balanoides</u>. 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 <u>I.modestus</u>, it is quite possible that the earliest stages of development would again be observed as the most susceptible to heat damage. B. Lover Median Lethal temperature (L.I.L.T.).

B.balanoides. (i) As with the U.H.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

- 20 -

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mortality"). This value is several degrees lower than that given by Crisp and Ritz (1967), and approximates to the L.H.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 H.L.T. of -5.1°C.,

(Crisp and Ritz, 1967), the cypris larva is clearly the most vulnerable

stage in the life-cycle.

(ii) <u>E.modestus</u>.

As discovered with <u>B.balanoides</u>, 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.H.L.T. for this group as previously explained.

Ritz (1968) gives the L.H.L.T. of adult <u>E.modestus</u> as -4.3°C. There is therefore a similarity with the situation observed for the U.H.L.T.,

whereby eggs are more resistant than the adults. However, it is worth noting that Southward (1958) shows that <u>E.modestus</u> could survive 12-24 hours at -10° C., suggesting that the L.N.L.T. of <u>E.modestus</u> 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 Comparison between species. 2. U.M.L.T. (a)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.H.L.T. for each group of stages are similar in both species, and the U.H.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.

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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.I.L.T. ··· . The eggs of <u>B.balanoides</u> 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.

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(c)

Unlike the situation with heat tolerance, E.modestus and B.balanoides show different patterns of cold resistance. The increases in the L.H.L.T. with stage of development show less similarity than the increments of the U.H.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 nore 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.

General observations and ecological implications.

Consideration of both the U.H.L.T. and L.H.L.T. figures

suggests a basic difference between E.nodestus 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 seen 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-Nest Europe, (Crisp 1958).

Both species show an appropriate adaptation in the temperature

tolerance of their embryos: E.nodestus, breeding primarily in the summer

has embryos which are most tolerant of high temperatures; <u>B.balanoides</u>,

breeding from late autuan 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 <u>I.nodestus</u> and <u>B.balanoides</u> contribute
- to the co-existence of these two species on our coasts.

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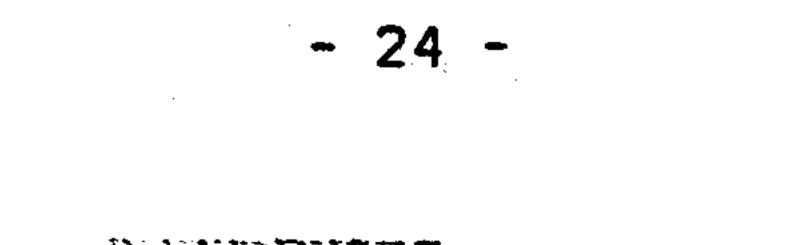


- Instantaneous values for the U.H.L.T. of <u>E.modestus</u> and <u>B.balanoides</u> are given for the major stages of embryonic development.
 (For <u>E.modestus</u> no value could be obtained for the earliest phase of development).
- (2) 18 hr., L.M.L.T. values are given for the same stages of embryonic

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. <u>B. balanoides embryos are generally less tolerant than adults</u>, whilst most embryonic stages of <u>E. modestus</u> 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) <u>B.balanoides</u> displays greater tolerance of low temperature than E.modes tus.
- (6) <u>E.modestus</u> exhibits a greater tolerance of high temperature than <u>B.balanoides</u>.
- (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.

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COMPETITION BETWEEN THESE SPECIES.

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MODESTUS (DARWIN) IN RELATION TO

IN BALANUS BALANOIDES (L.) AND ELMINIUS

LABORATORY STUDIES OF GREGARIOUS SETTLEMENT

SECTION III

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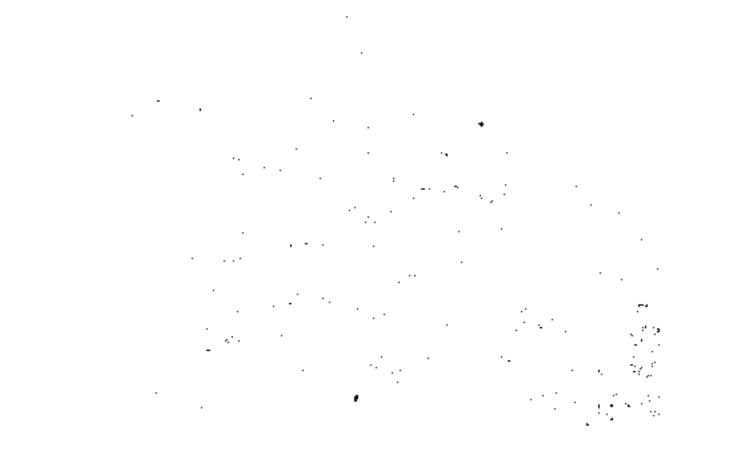
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A LABORATORY STUDY OF PREDATION BY THE

COMMON DOG-WHELK NUCELLA LAPILLUS

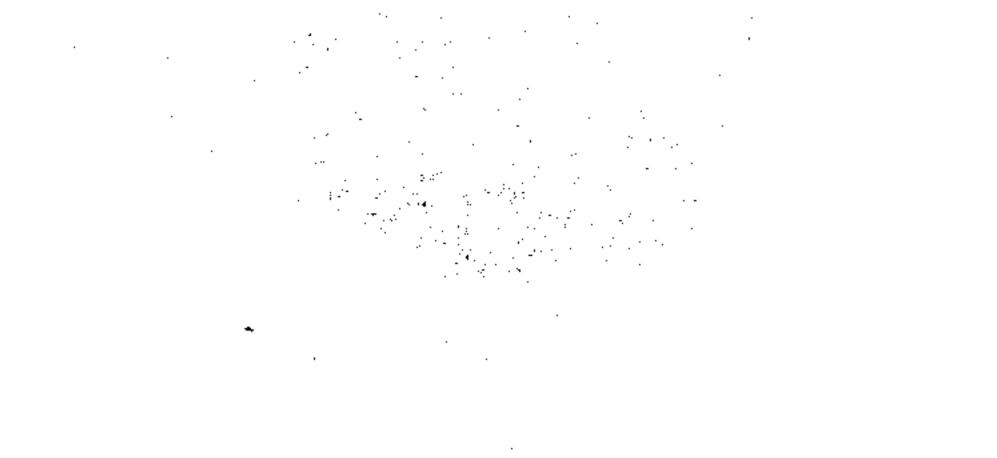
(GASTROPODA : PROSOBRANCHIA) ON THE

BARNACLES ELMINIUS MODESTUS DARWIN AND

BALANUS BALANDIDES (L.).

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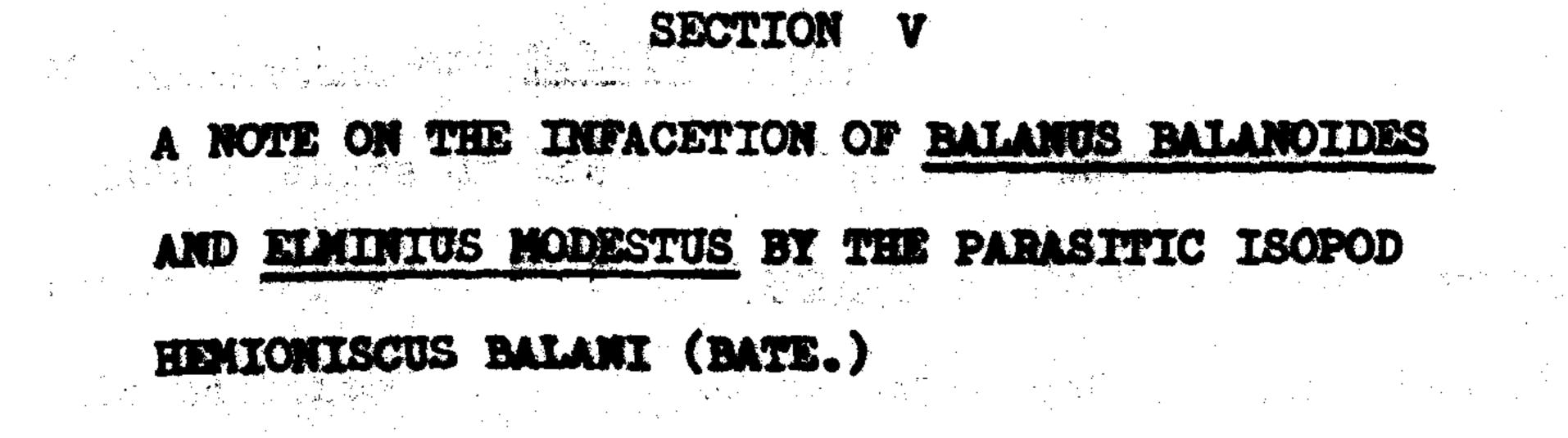
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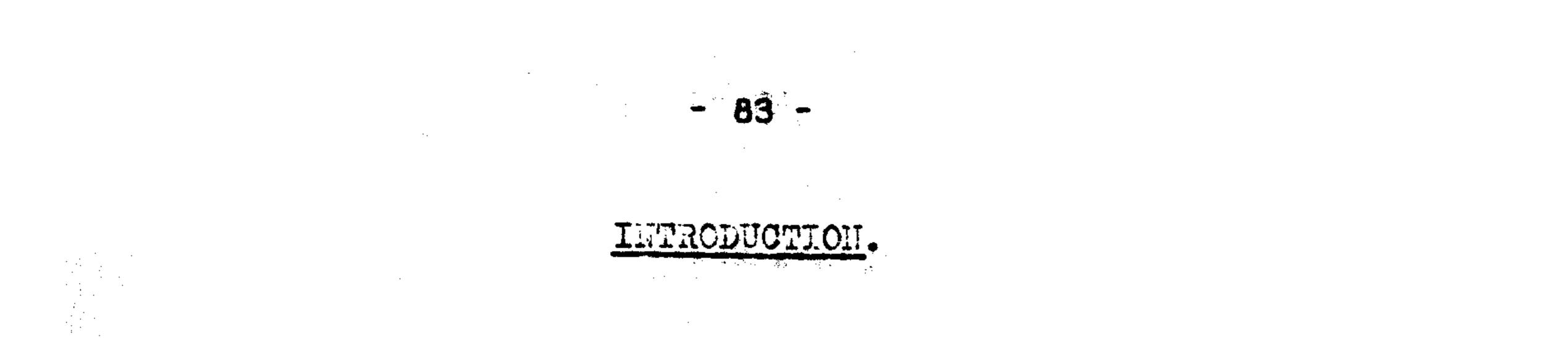
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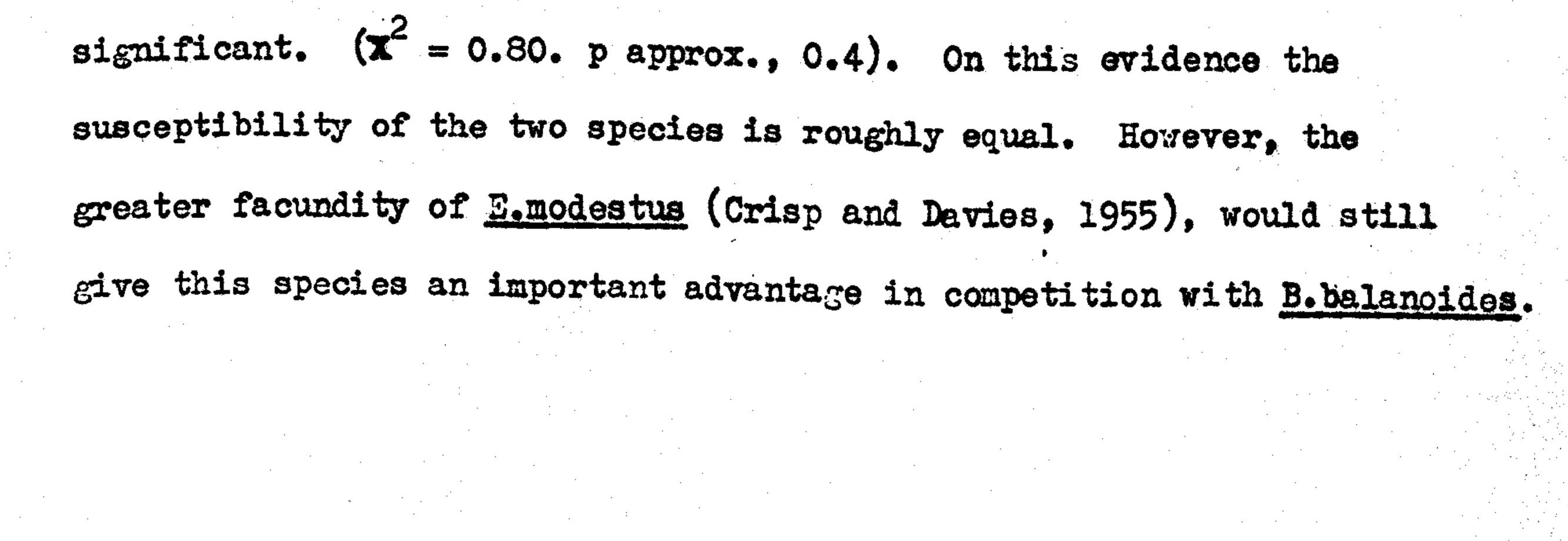
Barnacles infected by <u>Hemioniscus balani</u> exhibit a significant reduction in growth rate (Crisp 1960), and are usually rendered sterile (Crisp and Davies, 1955 and Crisp 1968). This may affect population levels in succeeding host generations as discussed by Crisp and

Southward (1958). <u>Hemioniscus</u> is not a completely specific parasite (Perez 1923), and both <u>E.modestus</u> and <u>B.balanoides</u> 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 <u>H.balani</u> 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 <u>E.modestus</u> and <u>B.balanoides</u>.

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 <u>Hemioniscus</u>. 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.

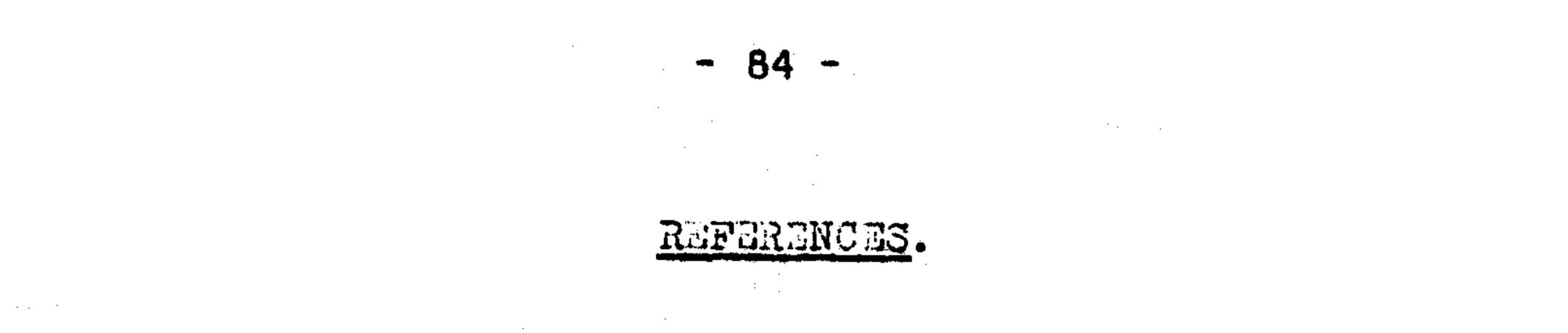
<u>E.modestus</u> was observed to have a frequency of infection of 1.96% (¹¹/571) compared to a frequency of 1.25% (⁶/486) for <u>B.balanoides</u>. Comparison of the figures by \mathbf{x}^2 showed that the differences are not



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SECTION VI

SYNTHESIS

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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 offects 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).

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INTRODUCTION.

An important difference between the two types of aspects is the affect 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 mimals. 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 nechanical damage.

Enatnager and Crisp (1965) on larval salinity tolerance. (3) Crisp (1960 and 1964) on growth rates. (4) (5) Crisp and Davies (1955) on breeding of Elminius. Crisp and Ritz (1967) on low temperature tolerance. (6) Davenport (1976) on responses to fluctuating salinity (7) regines, regines, a second de la seconda

(8) Foster (1969 a) on tolerance of high temperatures. Foster (1969 b.) on effects of salinity dessication and (9) high temperatures. Larman and Gabbott (1975) on discrimination during (10)settlement.

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

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

B. Biological Aspects

| Basic Facts. | <u>E.modestus</u> . | |
|-----------------------|------------------------|------------------|
| Tidal some 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 sise (Diameter) | 5 to 10 mm. | 5 to 15 mm. |

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| Components of Boological 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 |

Susceptibility to parasitism -Thesis -Susceptibility to predation - - -Thesis . • 4 Growth rate + + + + + + +Feeding afficiency + + + 1 + + Discrimination during settlement + + + 10 + + + + Gregariousness during settlement + + + ++ + + + +Thesis Feoundity + + + + +5 + + +

Nazizum 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 parasities 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.

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"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



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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

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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 <u>Elminius</u>. The decline of <u>B.balanoides</u> 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

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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).

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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

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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.

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Section 1 - Ecological features contributing to the success of

<u>E.modestus</u> in competition with <u>B.balanoides</u> 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

<u>B.balanoides</u> 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). <u>E.modestus</u> 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 <u>B.balanoides</u> could provide a useful spatial refuge for <u>Elminius</u>. 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 <u>E.modestus</u> 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 <u>Balanus</u> cyprids or covers and kills the young spat. Most adult <u>Elminius</u> 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).

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(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 <u>B.balanoides</u>. 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 <u>Balanus</u> has such a restricted settlement season

the surface is usually colonised by E.modestus.

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Fecundity and a prolonged settlement season explain

the rapid spread of Elminius and the creation of small isolated

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populations. However, both species occur together throughout most of the intertidal zone. This could result entirely from continuous settlement of <u>E.modestus</u> 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 <u>B.balanoides.</u>) 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 <u>B.balanoides</u>. 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 <u>B.balanoides</u>.

But two other factors have probably contributed

to its success. As explained in Section IV, the predatory behaviour

of <u>Nucella lapillus</u> could have given <u>E.modestus</u> a great advantage when first colonising new areas of shore. Removal of large numbers of <u>B.balanoides</u> through predation by <u>Nucella</u> would firstly create considerable areas for the settlement of <u>E.modestus</u>. Subsequently the preference shown by Nucella for the larger faster growing species would negate the advantages of <u>B.balanoides</u> in this respect, allowing <u>E.modestus</u> to grow without hindrance from its competitor. Thus the high fecundity of <u>Elminius</u> coupled with its comparative immunity to predation by <u>Nucella</u> 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 <u>E.modestus</u>. The comparatively low discrimination at settlement shown by <u>Elminius</u> (Larman and Gabbott, 1975) suggests - 96 -

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.)

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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

Advantages in biological aspects have probably been

more important in the rapidity of the <u>Elminius</u> invasion. High fecundity in conjunction with greater feeding efficiency and a degree of success in direct physical competition with <u>B.balanoides</u> 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 <u>Elminius</u> to predation by <u>Nucella</u> and the tendency for gregarious settlement to minimise the extent of direct physical

interspecies competition.

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Section 2 - Ecological features regulating competition between

E.modestus and B.balanoides in the context of their coexistence on British shores.

Physical Aspects. (\mathbf{A})

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 axion, 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.

components must have more influence on competition than physical components of the animals' ecology. Both species compete for space and food, and yet those componants which have the greatest effect on direct physical competition, namely size, feeding efficiency and

As in section 1 it appears that biological

Biological Aspects. **(B)**

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growth rate seem unlikely to encourage coexistence. The experiments of Crisp (1964) indicate that <u>B.balanoides</u> 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. <u>B.balanoides</u> 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 <u>B.balanoides</u> can be colonised by <u>Elminius</u> 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.

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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

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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

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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 111. (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

<u>Elminius</u>. As the population of <u>Elminius</u> increased (at the expense of <u>B.balanoides</u>), intraspecific competition between individuals of <u>Balanus</u> declined, leaving <u>B.balanoides</u> 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 <u>Nucella</u>. Connell(1961 a) has clearly shown that predation by <u>Nucella</u> is important in regulating <u>Balanus</u> populations. The experiments described in section \overline{IV} indicate that prey selection may change according to the populations of the prey species present. Furthermore, the tendency shown by <u>Nucella</u> to take

the larger individuals (Connell, 1961 a) would create space for both species probably at the expense of <u>B.balanoides</u>, thus negating some of the advantages of this species resulting from its greater size, growth-rate and earlier settlement season. (Even if predation became - 103 -

random, <u>Mucella</u> 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 specier 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.

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Summary, Section 2.

The ecological components contributing to the co-existence

of <u>B.balanoides</u> and <u>E.modestus</u> 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.

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- 105 -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 <u>liminius</u> 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. The second s Obviously competition must involve to verying 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 attempted. 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

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and the second showed a high level of similarity. Thilst the approach can not completely explain the competitive interaction between <u>liminius</u> and <u>Bolanus</u> 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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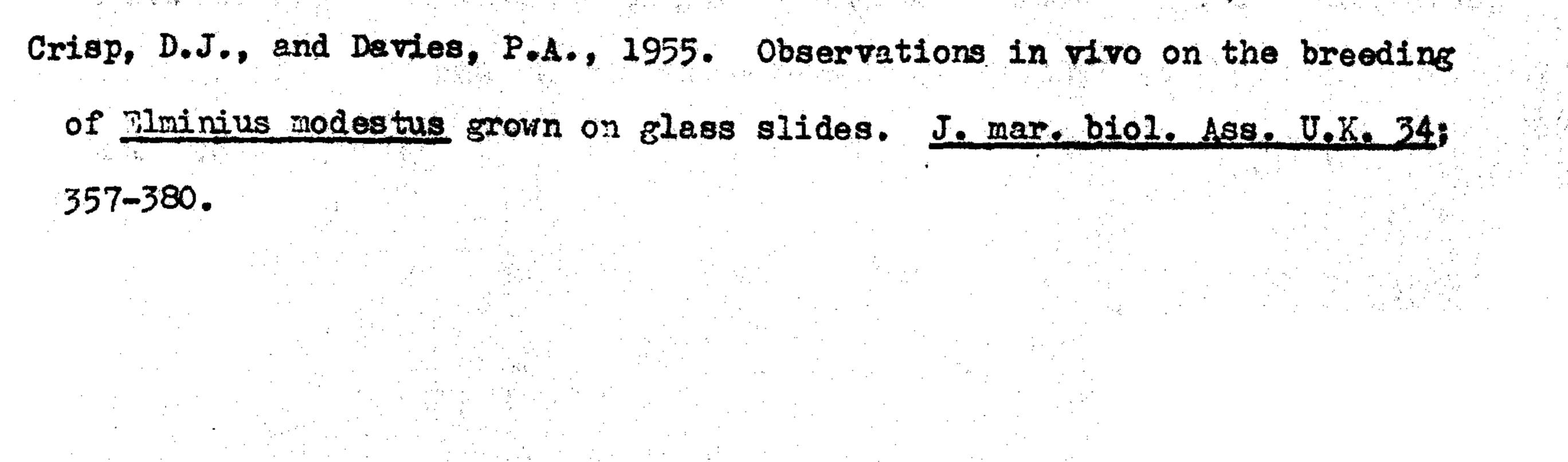
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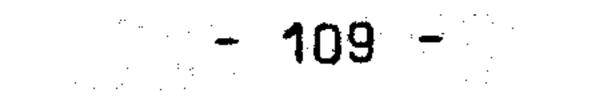
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<u>SUHARY</u>.

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 cregarious settlement

in relation to competition are investigated (sections II to $\overline{\underline{V}}$ inclusive.)

Terperature 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 $\overline{\mathbf{YI}}$. 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 <u>Elminius</u> in colonisation and the coexistence of both species on British shores.