

The neozoan *Elminius modestus* Darwin (Crustacea, Cirripedia): Possible explanations for its successful invasion in European water

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ABSTRACT: Comparison of data from the literature has provided evidence that eurythermal and euryhaline adaptation of larvae and adults in combination with a long seasonal breeding period, high fecundity and short generation time have given *Elminius modestus* an advantage over indigenous cirripede species, allowing a rapid spread throughout European waters.

INTRODUCTION

Elminius modestus Darwin, a natural inhabitant of waters around New Zealand and southern Australia, was first recorded in European waters in 1945 on fouling plates in Chichester harbour in West Sussex, England (Bishop, 1947). From there, *E. modestus* spread rapidly along the English coast and was soon found in France and Holland. It is suggested that this species was introduced by shipping during World War II and also that its further spread was due to shipping and natural drift of larvae.

The spread of *E. modestus* is well documented and has been summarized by Harms & Anger (1989). Since then, the settling area has extended further to places along the west coast of Ireland (King et al., 1997). No information is available on whether and to what extent *E. modestus* is settling along the coast of the Kattegat. It is now considered to be a permanent member of the fouling communities from the Shetland Islands down to Portugal. The variation of abundances has been documented over 40 years for a rocky shore near Plymouth (Southward, 1991).

Why could *E. modestus* spread so successfully around Europe? A comparison of available information on *E. modestus* with the one of the native species, *Semibalanus balanoides* (L.), on larval and adult survival strategy might provide an answer to this question. This paper is an attempt to summarize the widely spread information about these two species, which are considered to be competitors for settling space in the intertidal zone.

DATA COMPARISON AND DISCUSSION

Larval development

The time of larval development is a sensitive period during the life cycle of every species. Developmental success has a major influence on spat fall and therefore on the

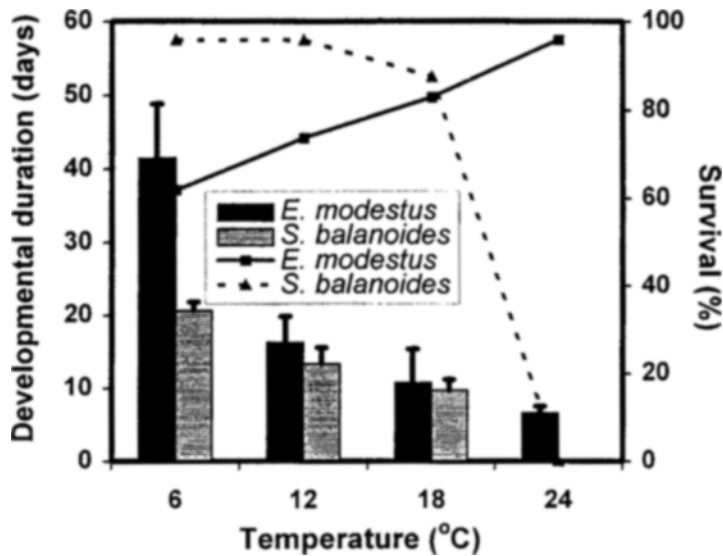


Fig. 1. Temperature influence on larval development up to the cypris stage in *Elminius modestus* and *Semibalanus balanoides* (after Harms, 1984). Developmental duration in days (mean value and standard deviation) from hatching to metamorphosis to the cypris stage is shown by columns. Survival (%) up to the cypris stage is shown by the lines

population size of the next generation. The main environmental factors influencing developmental duration are temperature, salinity and food availability.

The influence of water temperature was examined by Harms (1984) for *E. modestus* and *S. balanoides* (Fig. 1). *S. balanoides* is a cold-water species (Hutchins, 1947; Bousfield, 1954), and thus it has its temperature optimum at low temperatures. It was found that none of the larvae of *S. balanoides* developed beyond the second nauplius stage at 24 °C (Harms, 1984).

The survival of larval stages of *E. modestus* increases with temperature. Unfortunately no temperatures higher than 24 °C were tested. Because temperatures in the natural environment in New Zealand vary between 4 °C and 21 °C (Ritz & Foster, 1968), 24 °C seems to be close to the upper limit of tolerance.

The Q_{10} value for the overall developmental duration up to the cypris (see Harms, 1984) was lower in *S. balanoides* (1.9) than in *E. modestus* (3.1), but *E. modestus* larvae develop successfully in a wider temperature range; they are more eurythermal than the larvae of *S. balanoides*.

The influence of salinity on larval development was examined in detail for the European and New Zealand populations of *E. modestus* (Harms, 1986). Unfortunately no comparable information is available for larvae of *S. balanoides*. Larvae of *E. modestus* showed lowest mortality, at all temperatures tested, at 20 PSU. Only slightly higher mortality was found for 30 PSU at 18 °C and 24 °C (Harms, 1986). No such clear trend could be observed in comparison with other experiments (Fig. 2). The overall larval developmental duration to the cypris is shortest in the range 20 to 32 PSU, which corre-

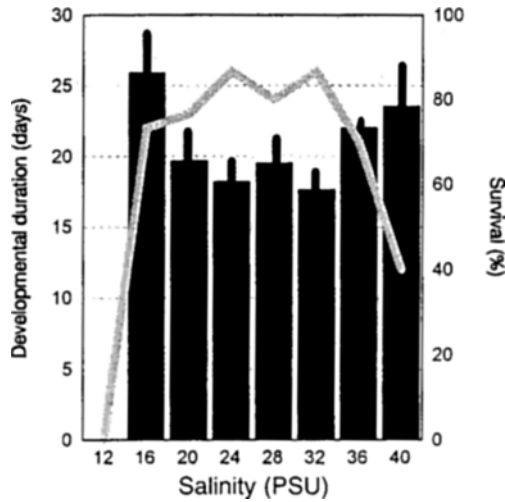


Fig. 2. Effect of salinity on development duration (columns) from hatching to metamorphosis to the cypris stage and development success (line) up to the cypris stage in *E. modestus* (after Harms, 1982)

sponds to the range of highest survival. According to these experiments *E. modestus* larvae are moderately euryhaline.

It is known from experiments by Cawthorne (1978) and Cawthorne & Davenport (1980) that larvae of *S. balanoides* are less tolerant to changes in salinity than those of *E. modestus* (Table 1). Differences in salinity tolerance are more pronounced in nauplius stage I than in the cypris. Both species settle in the intertidal and therefore the cypris stage, during which suitable habitats are found for metamorphosis, has to be adapted to at least periodic dilution of seawater. This might be the reason why differences in tolerance levels in the cypris between rapid and slow changes of salinity are less distinct than in the nauplius stage examined.

It was found by Cawthorne & Davenport (1980) that liberation of larvae ceases at salinities of approximately 21 PSU in *E. modestus* and at 27 PSU in *S. balanoides*. Larval development at constant salinity for *E. modestus* was possible until 16 PSU (Fig. 2), and occasionally even down to 10 PSU (2–6% at 12 °C and 18 °C; see Harms, 1986).

Biomass, respiration rate and food uptake of *E. modestus* were examined for each larval stage at three temperatures (12, 18, 24 °C) by Harms (1987). Comparable data for *S. balanoides*, except food uptake, are given by Lucas (1979) and Lucas et al. (1979). The data on dry weight accumulation, weight-specific respiration rate and net growth efficiency (K_2) are given for both species in Fig. 3. *S. balanoides* accumulates over three times more biomass during larval development than *E. modestus*, but in both species weight-specific respiration rate and especially net growth efficiency, which denotes the proportion of assimilated food converted to growth, lay in comparable ranges. The decrease in weight-specific respiration rate indicates that energy reserves, especially glycogen, are accumulated during larval development, to be used later by the non-feeding cypris stage (Holland & Walker, 1975).

Table 1. Effects of salinity decrease (fast and slow) on swimming activity of larval stages of *Eliminus modestus* and *Semibalanus balanoides*. Shown are salinity ranges where 50% of the larvae stopped swimming (according to Cawthorne & Davenport, 1980)

Rates of salinity change	16.74 PSU/h	4.81 PSU/h
<i>E. modestus</i> , nauplius stage I	8.8 ± 0.9 PSU	6.6 ± 0.3 PSU
<i>S. balanoides</i> , nauplius stage I	12.3 ± 1.0 PSU	9.3 ± 1.0 PSU
<i>E. modestus</i> , cypris	9.0 ± 1.3 PSU	8.3 ± 0.9 PSU
<i>S. balanoides</i> , cypris	10.9 ± 1.0 PSU	9.1 ± 1.1 PSU

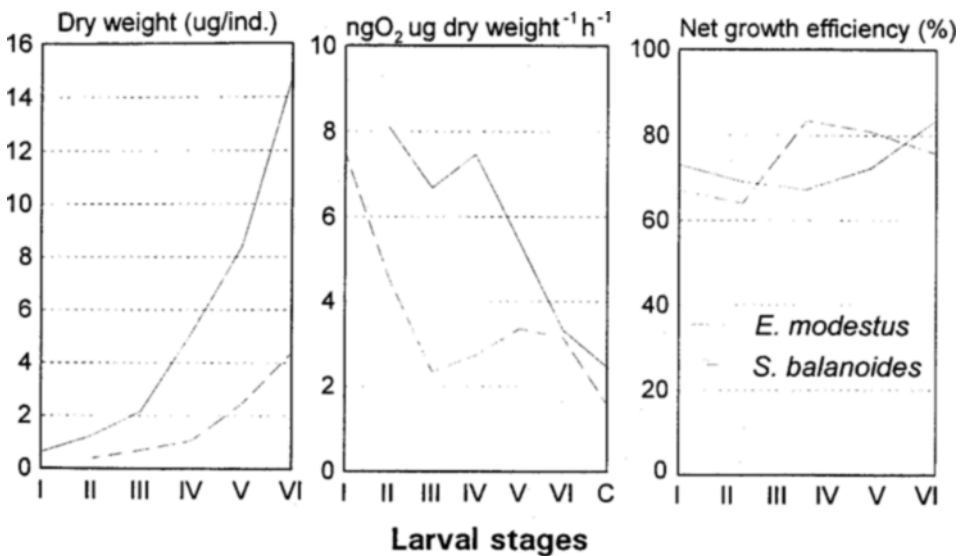


Fig. 3. Growth parameter for larval development of *E. modestus* and *S. balanoides* (after Harms, 1987; Lucas, 1979). Shown are weight increment (μg dry weight/ind.) during larval development (nauplius I–VI), weight-specific respiration rate related to dry weight and net growth (ng) efficiency (K_2)

Adult behaviour

Both species settle in the intertidal zone. Hence they encounter rapid fluctuations of physical environmental parameters. Sessile intertidal organisms, like cirripedes, must be able to tolerate severe conditions during emersion. A parameter to describe environmental stress is desiccation, which combines the effect of temperature, humidity and wind speed with the rate of water loss from the integument of organisms.

The influence of desiccation on intertidal zonation in barnacle species was studied in detail by Foster (1971). Figure 4 summarizes the survival times of three barnacle species of various sizes in drying conditions in the intertidal zone. It is obvious that the smaller individuals are more susceptible to drying out. The two intertidal species *E.*

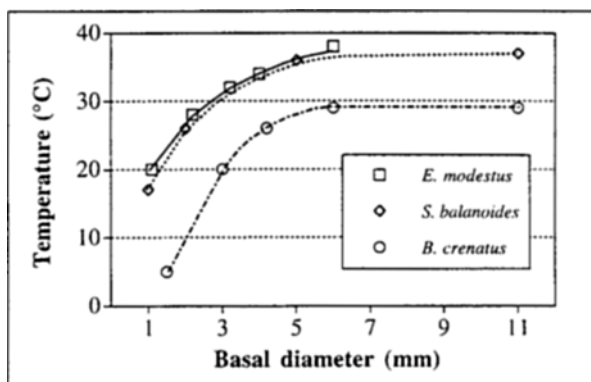


Fig. 4. Temperature influence on desiccation resistance for adult cirripedes of different sizes. Shown are temperature curves at which 50% of tested individuals died after 6 h (maximum emersion period during low tide) at zero humidity (Foster, 1971). In all three species tested, desiccation resistance increased with size and was highest in intertidal species

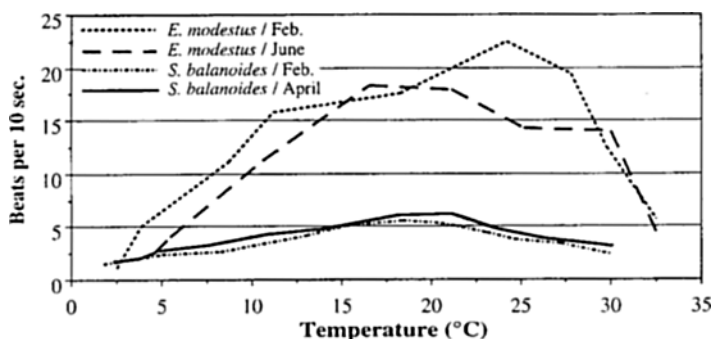


Fig. 5. Cirral activity of adult *E. modestus* and *S. balanoides* related to temperature at different seasons (after Southward, 1955a).

modestus and *S. balanoides* do not show major differences in desiccation resistance. A lower level of tolerance is found in the sublittoral species *Balanus crenatus* Brugière.

Although Foster (1971) found some evidence that *S. balanoides* may survive slightly longer than *E. modestus* in similar desiccating conditions at non-lethal temperatures, this is not reflected in the respective intertidal distribution of these two species. *E. modestus* extends along the European coast to more southern shores compared to the indigenous species *S. balanoides* and reaches slightly higher upper limits in the intertidal, which indicates that *E. modestus* survives better under warmer and, presumably, dryer environmental conditions compared to the indigenous species.

The most obvious activity of a barnacle, and one that plays an important role in both feeding and respiration, is the rhythmic beating of the cirri and the associated movements of the terga and scuta (Crisp & MacLean, 1990; Crisp & Southward, 1961; Ritz &

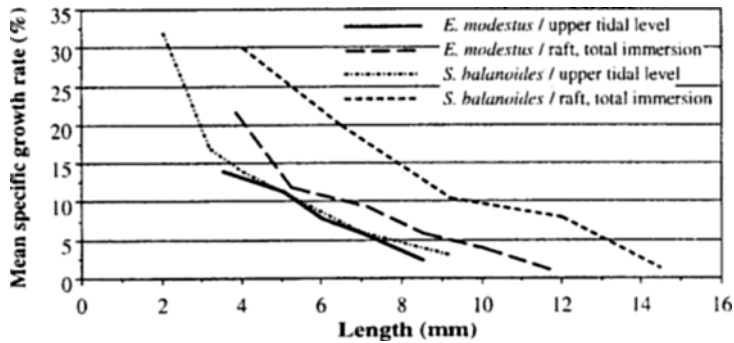


Fig. 6. Mean specific growth rate (percentage increase in length per day) at different tidal levels for juvenile and adult *E. modestus* and *S. balanoides* (after Barnes & Barnes, 1962)

Foster, 1968; Southward, 1955a,b, 1957, 1962, 1964). The most pronounced differences between *E. modestus* and *S. balanoides* are summarized in Fig. 5.

Southward (1955a) stated in his summary that the immigrant *E. modestus* was more active at lower temperatures than were the native southern species and at higher temperatures than were the native northern species, and over the whole of its range showed a much greater frequency of cirral beat than any of the native species examined (see Fig. 5).

The consequences of this high cirral activity are shown by an experiment done by Barnes & Barnes (1962; Fig. 6), who examined the growth rate of *E. modestus* and *S. balanoides* at different levels of submersion. Populations of the same species were examined, settling in the upper tidal region and on fouling plates hanging from a raft permanently in the water. *E. modestus* showed much smaller differences in the growth rate between the two habitats than *S. balanoides*. It can be speculated, due to high cirral activity in *E. modestus* (see Fig. 5), that food intake during a relatively short period of immersion is still adequate to maintain a growth rate close to the one under full immersion.

Fecundity and settling period

It was calculated by Crisp & Davies (1955) that assuming a life span of three breeding seasons for *E. modestus*, an average number of 500 nauplii in each brood, and 12 broods per season the total output of young approaches 20 000 per individual. This is equivalent to the output over the same period of three broods of a large specimen of *S. balanoides*, occupying a considerably greater area than one individual of *E. modestus*. The rapid production of numerous broods, as long as water temperatures exceed 6 °C, and the shorter generation time are important features, putting *E. modestus* at an advantage in its competition with the indigenous *S. balanoides* (Crisp & Davies, 1955).

The generation time was calculated by Crisp & Davies (1955) to be about 14 weeks. This is very short compared to that of *S. balanoides*, which is about 1 year. Therefore small eggs produced in successive though smaller broods, which will settle and reach maturity quickly and so contribute to further egg production, mean the eurythermal

species *E. modestus* is at a tremendous advantage over species such as *S. balanoides* (Barnes & Barnes, 1968).

Related to this successive breeding, larvae of *E. modestus* can be found in plankton throughout most of the year. The settling season of juveniles starts at Heligoland in June and lasts until October (Harms & Anger, 1983). Assuming that there is always competition for free settling space in benthic communities, this long period of larval abundance increases the chance of finding space to maintain the population. *S. balanoides* has only one larval release, related to the spring diatom bloom (Barnes, 1962). Spat fall occurs around March and April, in a relatively short period.

It follows from the increase in population density of *E. modestus* in many areas that there must have been a great increase of nauplii during the summer months. This must have affected the growth of other planktonic larvae. Although this point has already been outlined by Crisp (1958), up to now no detailed studies have been carried out on this subject.

CONCLUSIONS

As shown by data available in the literature, there are several factors which in total might explain the successful spread of *E. modestus* throughout the Western European coastal area (Table 2). The larval stages are eurythermal and euryhaline, which enable the larvae to survive in a wide range of habitats. Also, the adults are tolerant of changes in temperature and salinity, but this is less surprising for a sessile intertidal species. The effective utilization of food by high cirral activities in conjunction with the high fecundity over much of the year and the relative short generation time might be the major adaptations responsible for the successful invasion of European waters.

Table 2. Ecological requirements of *E. modestus*, compared with native species (summarized according to Crisp, 1958). X = month of the year; LWN = low water nip, LWS = low water spring, HWN = high water nip, MHW = mean high water, HWS = high water spring; tolerance levels are given from none (-) through low (#) to high (####)

	<i>Elminius modestus</i>	<i>Semibalanus balanoides</i>	<i>Chthamalus stellatus</i>	<i>Balanus crenatus</i>	<i>Balanus improvisus</i>
Season of settlement	V-X	III-IV	VII-IX	IV-IX	V-IX
Tidal levels occupied	MHW. to below LWS	HWN to LWS	HWS to LWN	Below LWN	Below LWN
Tolerance of low salinity	###	#	-	#	####
Tolerance of silt	##	#	#	#	###
Tolerance of temperature (< 0 °C)	##	###	#	##	###
Tolerance of temperature (> 20 °C)	###	-	####	-	##
Tolerance of desiccation	###	##	####	-	-
Resistance to mechanical damage	#	##	####	###	###
Cirral beats at 20 °C per 10 sec	17-18	5-6	ca. 6	ca. 10	ca. 9

Can the results for *E. modestus* obtained from the European population still be extrapolated to the situation in New Zealand and Australia? Comparison of cirral activity (Ritz & Foster, 1968) and examination of isoenzymes by gel electrophoresis (Flowerdew, 1984) did not show significant differences between the populations. Only some rare alleles present in the New Zealand population could not be found in the European one. This might be an indication of a relatively small founder population or a later specific selection process. Cultivation experiments at different temperatures and salinities (Harms, 1986) did show differences in larval development and larval size in the two antipodean populations of *E. modestus*. It was suggested that especially extreme winter conditions may act as a kind of natural selection regarding adaptation to lower temperatures in the Northern European population of *E. modestus*. Up to now it has not been examined whether differences within the European population have been established due to such selection mechanisms.

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