

Effects of temperature and salinity on larval development of *Elminius modestus* (Crustacea, Cirripedia) from Helgoland (North Sea) and New Zealand

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ABSTRACT: Larvae of *Elminius modestus* (Darwin) from four different populations (Portobello, Leigh, Doubtless Bay [New Zealand] and Helgoland [North Sea]) were reared at different salinity and temperature combinations. The larvae of *E. modestus* from Helgoland developed successfully at a wide range of temperature (6° to 24 °C) and salinity (20 to 50 ‰ S). Mortality was highest at 10 ‰ S; only at 12° and 18 °C did a small percentage develop to the cypris. The larvae from New Zealand were reared at a temperature range of 12°–24 °C at 20, 30 and 40 ‰ S; mortality increased in all populations at all salinities with decreasing temperature and was extremely high at 12 °C and 40 ‰ S. The temperature influence on larval duration could be described in all cases by a power function. No significant differences in temperature influences on developmental times between the tested salinities were found, except for the Portobello population at 20 ‰ S. Significant differences were found in the temperature influence on larval development between the populations from Helgoland and the North Island of New Zealand (Leigh, Doubtless Bay). No differences were found between the Helgoland and Portobello population. The pooled data for the temperature influence on the larval development of the three tested New Zealand populations at 20, 30 and 40 ‰ S and the pooled Helgoland data at 20, 30 and 40 ‰ S show highly significant differences.

Larval size (stage VI) was influenced by experimental conditions. The larvae grew bigger at low temperatures and attained their maximum size at 30 ‰ S (Helgoland). There was a strong reduction in larval size at temperatures from 18° to 24 °C. The larvae of the New Zealand populations were smaller than those from Helgoland. The greatest difference in size existed between the larvae from Portobello and Helgoland.

INTRODUCTION

Elminius modestus (Darwin) is a very common species throughout New Zealand (N. Z.), where it occurs on a wide range of substrates in the mid- and shallow sublittoral zones (Luckens, 1976; Foster, 1978; Moore, 1944; Morton & Miller, 1968). The distribution of *E. modestus* in Australia is restricted to shipping ports and it is possible that ship-aided dispersal from N.Z. to Australia has occurred (Foster, 1980, 1982). Similarly, *E. modestus* has also supposedly introduced itself to Europe by settling on ships coming from N. Z. (Bishop, 1947; Crisp, 1958), and was first recorded in 1945 in Chichester

Harbour (England) by Bishop (1947). Since 1945, *E. modestus* has spread rapidly throughout Europe (Barnes & Barnes, 1960, 1961, 1965a, 1969; Barnes & Powell, 1966; Barnes & Stone, 1972; Barnes et al., 1972; Bishop, 1954; Boschma, 1948; Connell, 1955; Crisp, 1959a, 1960; Crisp & Southward, 1959; Den Hartog, 1953, 1956; Fischer-Piette & Forest, 1961; Hiscock et al., 1978; Jones, 1961; Powell, 1960; Stubbings, 1950).

E. modestus was first recorded at Helgoland in 1955 (DenHartog, 1959; Kühl, 1963), and has since become a common species in the inter- and subtidal zone around Helgoland (Anger, 1978; Harms & Anger, 1983; Janke, 1986).

Genetic divergence of these separated populations in N. Z. and Europe, which might be caused by the genetic equipment of the invaders and/or by different natural selection in the two habitats (Crow & Kimura, 1970), has been tested (Flowerdew, 1984; Ritz & Foster, 1968) and no indication of genetic divergence was found (Flowerdew, 1984).

The present study describes and compares the influence of water temperature and salinity on larval development of three populations of *E. modestus* from N. Z. (Portobello – Otago harbour; Leigh – Snells Beach; Doubtless Bay) and one from Europe (Helgoland) (Fig. 1).

MATERIALS AND METHODS

Elminius modestus develops through six nauplius stages. The first larval stage is not considered here because it lasts only a few hours and does not feed (Harms, 1984). Experiments were terminated when the larvae reached the cypris stage. Larvae of *E. modestus* were reared individually in small glass bowls (4–5 ml) at different salinities (10, 20, 30, 40, 50 ‰ S) in constant-temperature rooms (6 °C, LD 14:10 and 9°, 12°, 18° and 24 °C, LD 17:7). The salinities were obtained by mixing concentrated seawater (acquired by deep freezing seawater) with distilled water.

Larvae were not previously adapted to the salinities. The water was changed every second day and the larvae were fed with *Skeletonema costatum* (10⁵ cells per ml). Antibiotics were added at a concentration of 0.3 ml Crystamycin/l seawater (300 mg Penicillin G and 500 mg Streptomycin in 4 ml distilled water). Culture bowls were checked daily for exuviae, though twice daily at 24 °C. 75 larvae were reared for the Helgoland population in each experimental set at 6°, 12°, 18° and 24 °C, and 25 at 9 °C. Experiments were terminated when the larvae reached the cypris stage. For more details see Harms (1984).

For the experiments done at the Marine Institutes of Portobello (University of Otago) and Leigh (University of Auckland) adults of *E. modestus* were collected from the field and ripe eggs were collected. Only larvae which hatched during the first hour were used for experiments. The experiments in Portobello (n = 55 at 12°, 15° and 18 °C; n = 22 at 16° and 24 °C LD 15:9) were done in "temperature controlled water-baths" and in Leigh (n = 36 at 12°, 15°, 18° and 24 °C LD 12:12) in "temperature controlled boxes" at 20, 30 and 40 ‰ S. The relatively small culture bowls (4–5 ml) had to be checked in both cases at room temperature (18 °C), causing temperature changes of the culture medium. Because such variations can have a strong influence on developmental time (Costlow & Bookout, 1971; Sastry, 1979), adult *E. modestus* from Portobello, Leigh and Doubtless Bay were taken to the Marine Station Helgoland (F. R. G., North Sea) to repeat the experiments under conditions identical to those for the Helgoland population at 12°, 18° and 24 °C and 20, 30 and 40 ‰ S.

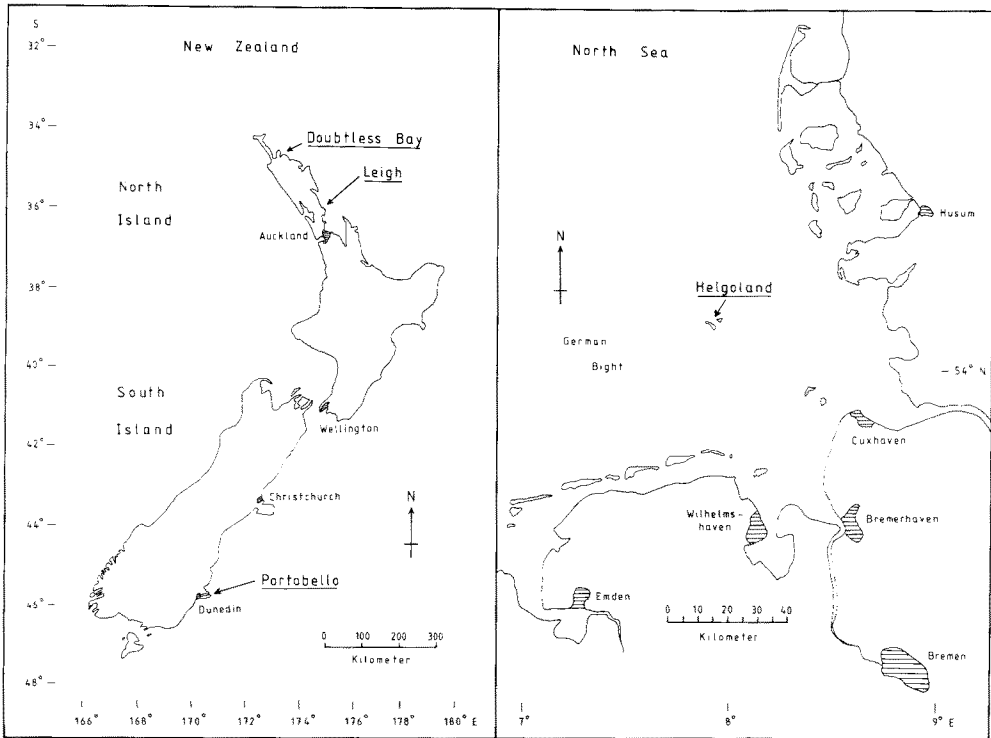


Fig. 1. Map of New Zealand and the German Bight (Europe) with the locations of the tested populations of *Elminius modestus*

The origin of the tested populations is shown in Figure 1. The natural range of water temperatures and salinity at Helgoland, Portobello and Leigh is given in Figure 2. Doubtless Bay conditions resemble those of Leigh.

The adults from N.Z. were kept at the Marine Station Helgoland at constant 15 °C for about three months in a flow-through-system before newly hatched larvae were taken for experiments. 24 larvae of the N.Z. populations were reared at the Marine Station Helgoland at each combination.

The growth rate of the larvae was determined by measuring the breadth of the carapace with an okular micrometer. Carapace breadth is a good indicator because of its relatively small variation within single experimental sets (Harms, 1982).

RESULTS

Helgoland population

The time span for the development of the naupliar stages II–VI at different combinations of salinity and temperature are shown in Figure 3. Developmental time of the naupliar stages increases with decreasing water temperatures, and is shortest between

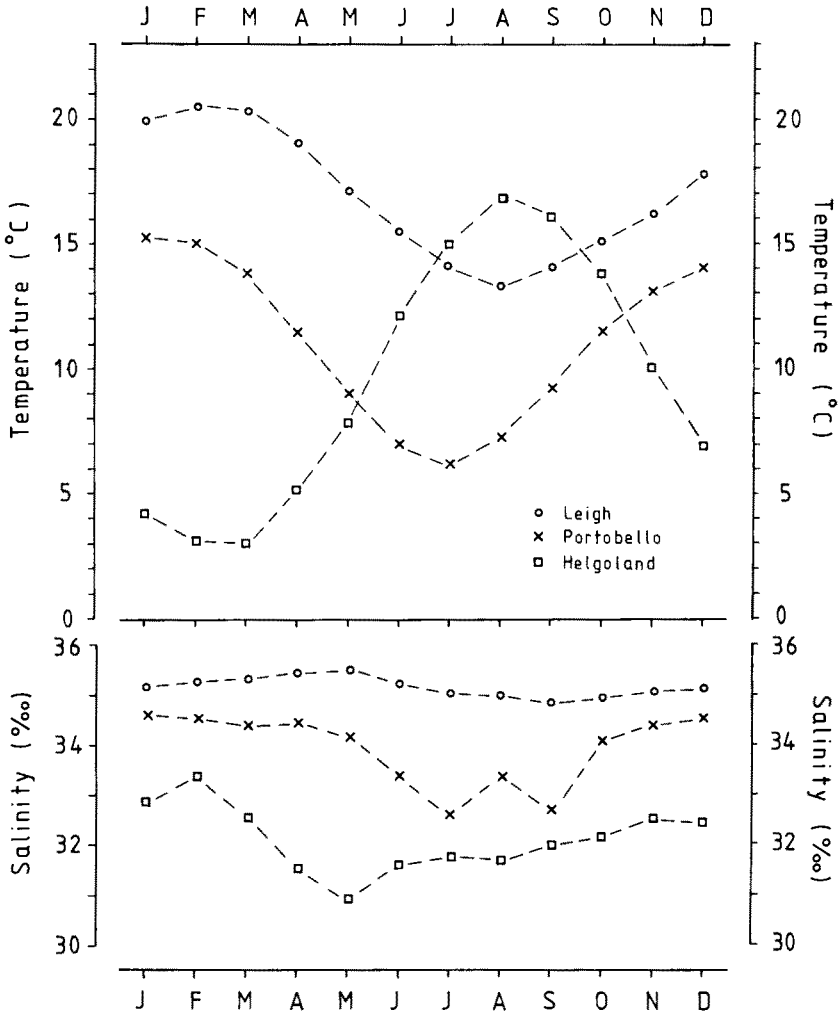


Fig. 2. Annual variation of water temperature and salinity at Helgoland (\square , according to Hickel & Mangelsdorf, 1980), Portobello (\times , according to Slinn, 1968) and Leigh (\circ , according to Ballentine, 1983)

20 and 40 ‰ S. The temperature influence at the different salinities can be described by a power function. Table 1 shows the function constants b and m and correlation coefficient (r) for the developmental time of the single naupliar stages as well as for the total development from nauplius II to the cypris stage. No differences in temperature influence exist between the tested salinities. The Q_{10} -values for the temperature influence between 6°, 12° and 24°C on the duration of total development lie between 2.2 and 3.4, depending on the temperature range and salinity (Table 7). The regression line for the time of total development from nauplius II to the cypris is compared in Figure 11 with the data of the N.Z. populations.

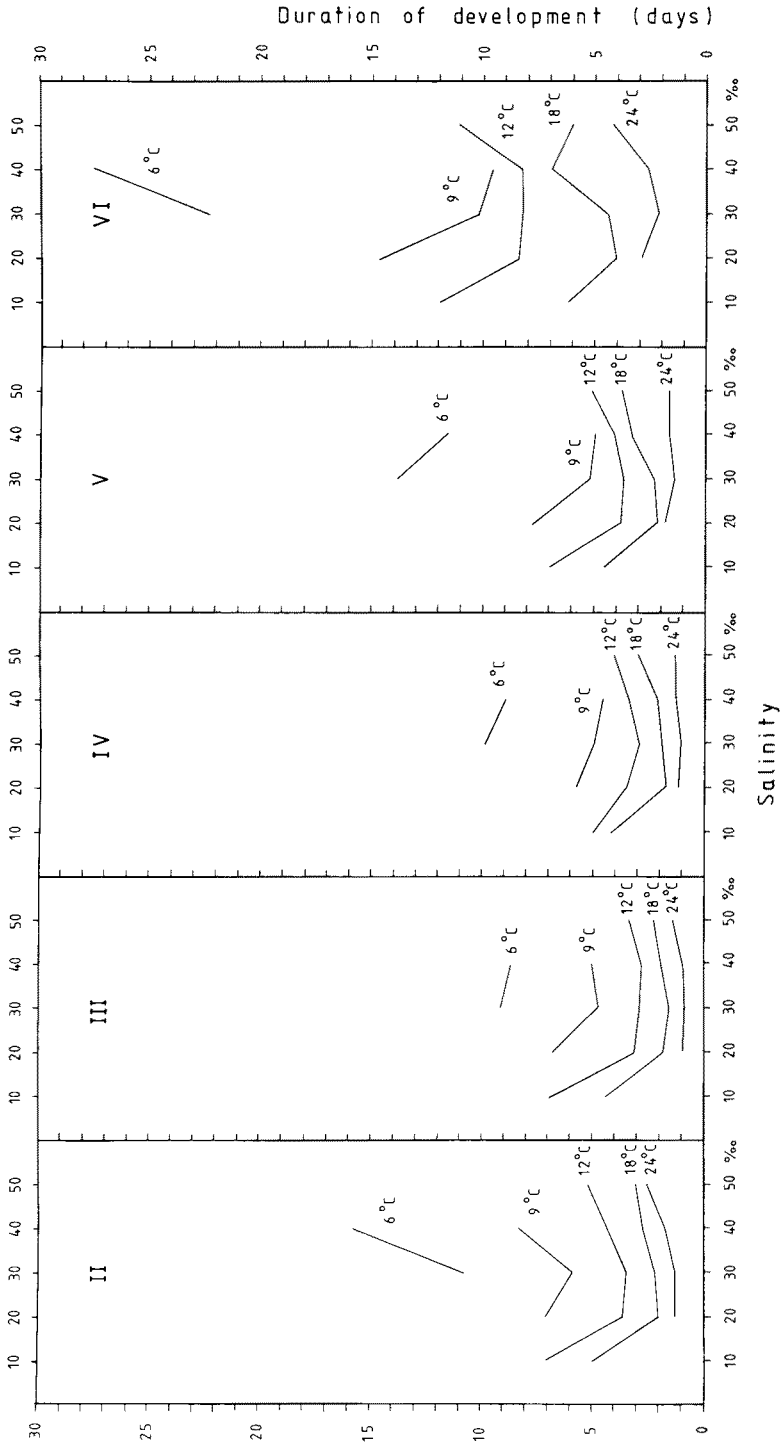


Fig. 3. Developmental time of the naupliar stages of *Elminius modestus* from Helgoland at different combinations of temperature and salinity (days, mean values)

Table 1. Values of power function ($D = b t^m$) for thermal influence (t) on larval development (D) of *Elminius modestus* from Helgoland for the temperature interval 6° to 24°C at 10, 20, 30, 40 and 50‰ S. (b and m are constants, r = correlation coefficient, p = confidence interval)

Salinity (%)	b	m	r	p	Salinity (%)	b	m	r	p
Nauplius stage II					Nauplius stage III				
20	225	-1.63	-0.99	<0.001	20	369	-1.87	-0.94	<0.001
30	158	-1.51	-0.99	<0.001	30	176	-1.65	-0.97	<0.001
40	253	-1.58	-0.99	<0.001	40	155	-1.59	-0.97	<0.001
50	68	-1.05	-0.97	<0.02	50	42	-1.05	-0.90	<0.05
Nauplius stage IV					Nauplius stage V				
20	175	-1.58	-0.95	<0.001	20	119	-1.35	-0.94	<0.001
30	147	-1.52	-0.99	<0.001	30	235	-1.61	-0.98	<0.001
40	103	-1.37	-0.96	<0.001	40	97	-1.24	-0.95	<0.001
50	116	-1.36	-0.88	<0.05	50	238	-1.52	-0.95	<0.02
Nauplius stage VI					Nauplius II to cypris				
20	382	-1.55	-0.95	<0.001	20	1135	-1.58	-0.98	<0.001
30	433	-1.63	-0.98	<0.001	30	1118	-1.58	-0.99	<0.001
40	366	-1.50	-0.94	<0.001	40	933	-1.45	-0.97	<0.001
50	404	-1.44	-0.99	<0.01	50	796	-1.34	-0.99	<0.01

Mortality (except at 6 °C) was lowest at 20 ‰ S (Fig. 4). At 10 ‰ S, most of the larvae died after a few days (at 6°, 9° and 24 °C), and only a small percentage reached the cypris stage at 12° and 18 °C (2 and 6 %, respectively). Mortality at 20–40 ‰ S was lowest at 24 °C and increased with decreasing water temperature.

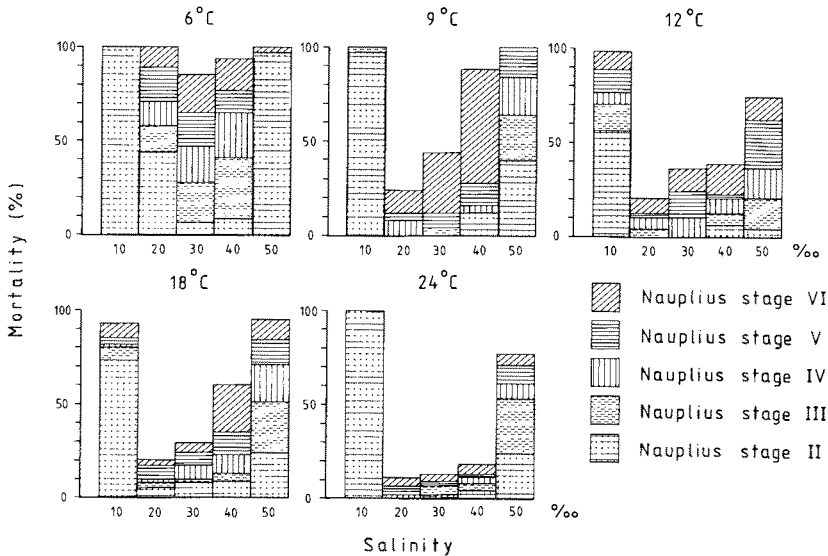


Fig. 4. Mortality of the naupliar stages of *Elminius modestus* from Helgoland in relation to water temperature and salinity

Table 2. Carapace size (breadth, μm) of the naupliar stages II to VI and carapace length (μm) of the cypris stage at different combinations of water temperature and salinity for *Elminius modestus* from Helgoland (mean values \pm 95 % confidence intervals)

Larval stage		II	III	IV	V	VI	Cypris
T ($^{\circ}\text{C}$)	Salinity (‰)						
6	20	176 \pm 3	206 \pm 5	251 \pm 8	305 \pm 20	380	
	30	175 \pm 3	209 \pm 4	252 \pm 6	317 \pm 12	403 \pm 18	566 \pm 32
	40	173 \pm 2	205 \pm 5	253 \pm 8	314 \pm 15	387 \pm 27	552 \pm 67
	50	176	211				
9	20	177 \pm 4	204 \pm 4	240 \pm 7	304 \pm 9	385 \pm 12	556 \pm 21
	30	176 \pm 4	210 \pm 3	247 \pm 5	313 \pm 8	393 \pm 11	597 \pm 36
	40	178 \pm 2	200 \pm 4	240 \pm 5	304 \pm 7	387 \pm 36	550
	50	169 \pm 5	186 \pm 7	247			
12	10	173 \pm 6	213 \pm 9	243 \pm 11	309 \pm 8	366	586
	20	178 \pm 4	215 \pm 7	263 \pm 4	317 \pm 7	387 \pm 9	570 \pm 15
	30	175 \pm 4	209 \pm 5	264 \pm 6	327 \pm 7	392 \pm 10	567 \pm 14
	40	172 \pm 4	203 \pm 4	250 \pm 6	312 \pm 7	384 \pm 8	569 \pm 21
	50	174 \pm 4	200 \pm 6	249 \pm 9	311 \pm 12	389 \pm 9	574 \pm 19
18	10	173 \pm 4	209 \pm 7	265 \pm 9	306 \pm 16	373 \pm 35	484 \pm 24
	20	175 \pm 4	212 \pm 5	293 \pm 5	317 \pm 8	385 \pm 8	562 \pm 26
	30	179 \pm 4	204 \pm 6	257 \pm 9	314 \pm 9	390 \pm 9	583 \pm 39
	40	172 \pm 3	202 \pm 5	251 \pm 5	313 \pm 5	380 \pm 9	558 \pm 12
	50	173 \pm 4	186 \pm 8	239 \pm 10	306 \pm 8	368 \pm 22	537 \pm 17
24	20	174 \pm 2	218 \pm 3	266 \pm 4	317 \pm 6	365 \pm 7	537 \pm 11
	30	173 \pm 4	210 \pm 3	260 \pm 5	311 \pm 6	367 \pm 7	542 \pm 12
	40	169 \pm 4	209 \pm 3	251 \pm 4	309 \pm 6	356 \pm 7	511 \pm 14
	50	173 \pm 5	201 \pm 6	251 \pm 6	307 \pm 5	360 \pm 9	520 \pm 13

Carapace size of the naupliar stages and the carapace length of the cypris larvae at different combinations of water temperature and salinity are given in Table 2. The effect of temperature and salinity on carapace size was most obvious in the nauplius stage VI. There was generally a gradual decrease in size from 6° to 18 °C and a stronger reduction from 18° to 24 °C. The largest exuviae for each temperature were always found at 30 ‰ S (Fig. 5). Towards lower and higher salinities there was a clear reduction in size. Carapace size varied little at 24 °C, although there was a trend towards smaller carapace size at higher salinities.

New Zealand populations

The influence of water temperature and salinity in the experiments carried out at Helgoland on single naupliar stages II–VI of the three N.Z. populations is shown in Figure 6. Developmental time and the salinity influence thereon increased with decreasing water temperature. The temperature influence on total larval development from nauplius II to the cypris could be described for all populations with a power function (Table 3A, Fig. 11). The regression lines for the Helgoland experiments concur well with

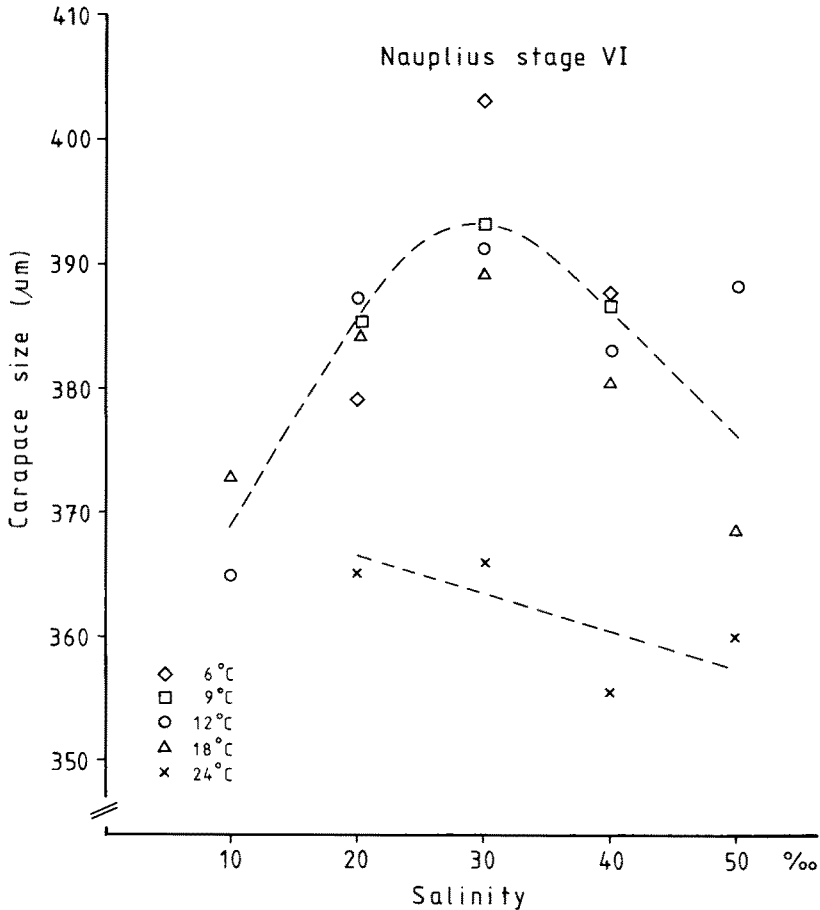


Fig. 5. Carapace size of the VI. nauplius stage of *Elminius modestus* from Helgoland at different combinations of temperature and salinity

the developmental duration of the experiments at the Marine Institutes in Portobello and Leigh at 18 °C (Figs 7 and 8). The shift in developmental time towards shorter spans at low water temperatures and prolonged development at high temperatures may have been caused by temperature changes due to handling of the culture bowls (see Materials and Methods). A comparison of the temperature influence at the three tested salinities for the Portobello, Leigh, and Doubtless Bay population gave no significant differences, except for the Portobello population between 20 ‰ S and 30 ‰ S or 40 ‰ S (Table 4 A). There were no significant differences between the two North Island populations (Table 4 B), so that these data could be pooled (regression constants see Table 3 B). The Portobello population was significantly different from the Leigh and Doubtless Bay populations at 30 ‰ S (Table 4 B). A comparison of the Portobello data with that of the North Island (pooled data of Leigh and Doubtless Bay) showed no significant differences,

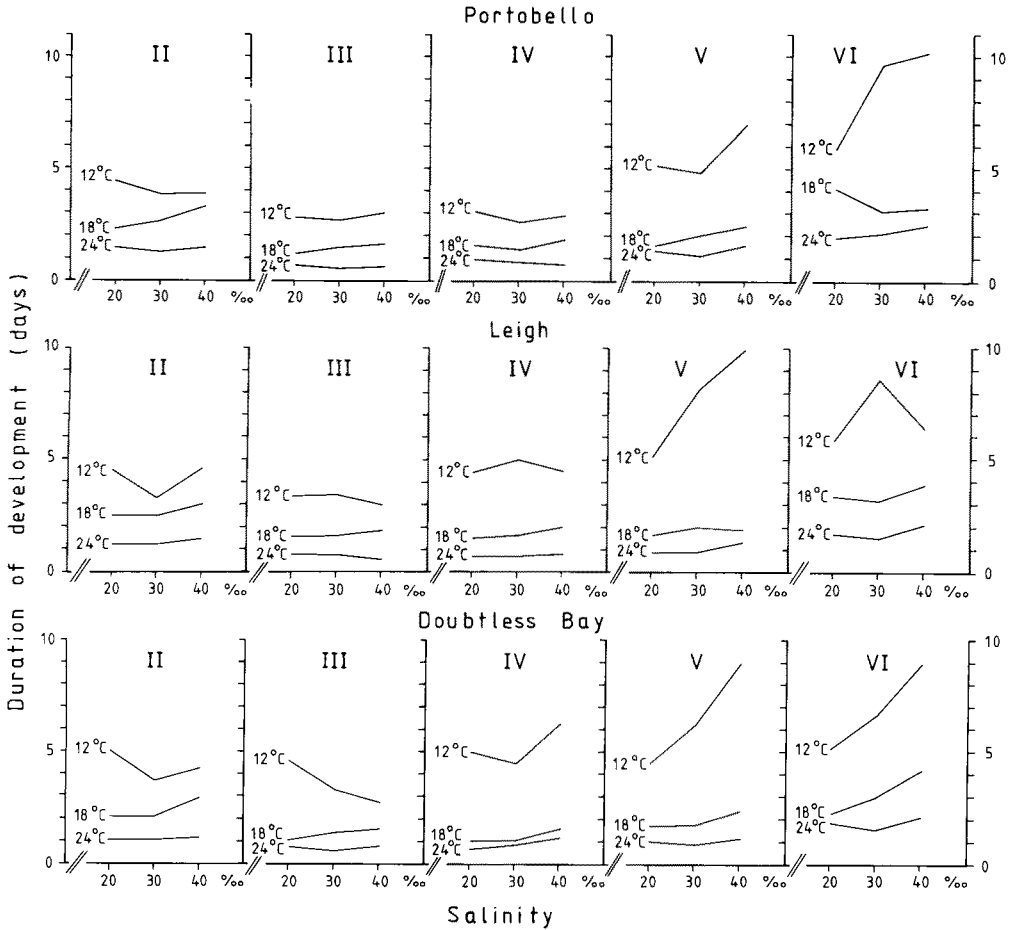


Fig. 6. Developmental time of the naupliar stages of *Elminius modestus* from New Zealand (experiments carried out at Helgoland) at different combinations of temperature and salinity (days, mean values)

and all data of the three N.Z. populations were pooled for comparison with the Helgoland data (Table 3 C, Fig. 11).

Mortality of the single naupliar stages of the N.Z. populations are given in the Figures 9 (experiments carried out in N.Z.) and 10 (experiments carried out in Helgoland). The extremely high mortalities in the Portobello experiments at 12°, 15°, 18° and 24 °C (Fig. 9) might have been caused by contamination with formalin, which had previously been used in the culture room. The developmental duration did not seem to be affected by this (Fig. 7). The experiments at 16 °C, carried out in a constant-temperature room, showed much lower mortality, although it was still higher than in the control experiments in Helgoland (Fig. 10). Normally, mortality was lowest at 24 °C and increased with decreasing temperature. In both experiments, mortality was highest considering all temperatures at 40 ‰ S, and it was extremely high at 12 °C.

Table 3. Values of the power function ($D = b t^m$) for thermal influence (t) on the duration of larval development (D) of *Elminius modestus* from three New Zealand populations (experiments carried out at Helgoland) for the temperature interval 12° to 24°C at 20, 30, and 40‰ S (b and m are constants, r = correlation coefficient, p = confidence interval). Comprehension of the data for the North Island populations (Part B) is based on comparison of the regression slopes (Table 4). Since there were no significant differences between the pooled data of the North Island populations and Portobello all data could be comprehended (Part C)

Salinity (‰)	b	m	r	P
(A) Portobello				
20	1910	-1.79	-0.9999	<0.001
30	3381	-1.99	-0.9998	<0.02
40	3587	-1.97	-0.9999	<0.001
Leigh				
20	4647	-2.12	-0.9980	<0.05
30	12695	-2.45	-0.9997	<0.02
40	5580	-2.12	-0.9991	<0.05
Doubtless Bay				
20	4767	-2.16	-0.9884	<0.1
30	7266	-2.29	-0.9998	<0.02
40	10260	-2.32	-0.9991	<0.05
(B) Comprehended data for the North Island populations:				
20	4770	-2.14	-0.9906	<0.001
30	9604	-2.37	-0.9951	<0.001
40	7570	-2.22	-0.9979	<0.001
(C) Comprehended data for the New Zealand populations:				
	5203	-2.13	-0.9821	<0.001

Table 4. Comparison of the regression slope (m) given in Table 3 for the thermal influence on larval development for the three tested populations of *Elminius modestus* from New Zealand (experiments carried out at Helgoland). Comparison of regression coefficients after Sachs (1976). A: thermal influence at the tested salinities, B: between populations

A	B
Salinity (‰)	Salinity (‰)
Portobello	Portobello vs. Leigh
20 vs. 30 p <0.05	20 n.s.
20 vs. 40 p <0.05	30 p <0.05
30 vs. 40 n.s.	40 n.s.
Leigh	Portobello vs. Doubtless Bay
20 vs. 30 n.s.	20 n.s.
20 vs. 40 n.s.	30 p <0.05
30 vs. 40 n.s.	40 n.s.
Doubtless Bay	Leigh vs. Doubtless Bay
20 vs. 30 n.s.	20 n.s.
20 vs. 40 n.s.	30 n.s.
30 vs. 40 n.s.	40 n.s.

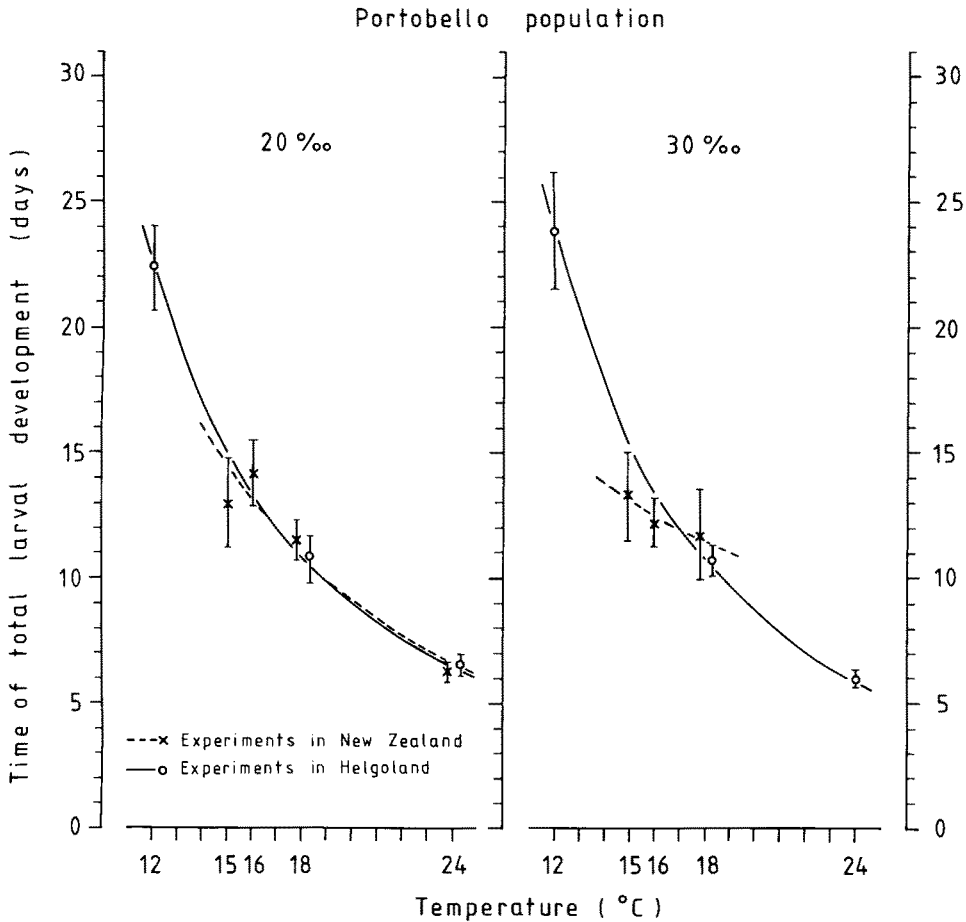


Fig. 7. Comparison of the time span for total larval development in the Portobello experiments (x) and in the control experiments at Helgoland (o) (mean value \pm standard deviations)

The salinity influence on growth rate was in general similar to the Helgoland population (Harms, 1985), but because of the smaller temperature and salinity ranges these trends were less obvious. In all experiments, the carapace size decreased with increasing temperature. The larvae from the Portobello population were always much smaller than larvae from the North Island populations (Fig. 12).

Comparison of the antipodean populations

The regression constants for the Helgoland population (pooled data) are given, for better comparison, for the same temperature interval (12°–24 °C, Table 5) as for the N.Z. populations. The populations of Leigh and Doubtless Bay showed significant differences to the Helgoland population at 20 and 30 ‰ S (Table 6), which is the natural salinity range for larvae of *Elminius modestus* in the field. Comparison of the pooled North

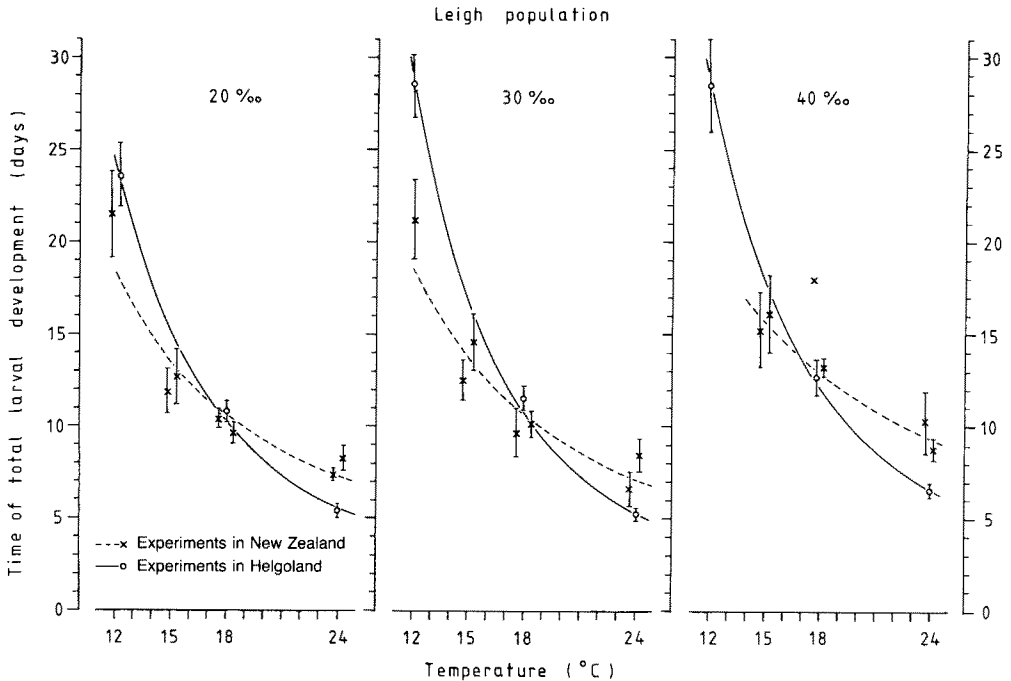


Fig. 8. Comparison of the time span for total development in the Leigh experiments (x) and in the control experiments at Helgoland (o) [mean values \pm standard deviations]

Island populations data, however, showed significant differences at all tested salinities. No differences were found between the Portobello and Helgoland population, which have similar natural temperature ranges. As the data for the Portobello population were not significantly different from the pooled North Island populations data, it was possible to compare the N.Z. populations as a whole with the Helgoland population (Table 6, Fig. 11). The antipodean populations showed highly significant differences in the

Table 5. Values of the power function ($D = b t^m$) for thermal influence (t) on the duration of larval development (D) of *Elminius modestus* from Helgoland for the thermal interval of 12° to 24°C and 20, 30 and 40‰ S. Comprehension of the data based on comparison of regression slopes, which showed no significant differences in temperature influence at the tested salinities

Salinity (‰)	b	m	r	p
Helgoland 12–24°C				
20	620	-1.36	-0.973	<0.01
30	990	-1.54	-0.962	<0.01
40	892	-1.44	-0.911	<0.02
Helgoland 12–24°C (all data comprehended)				
	1225	-1.56	-0.892	<0.001

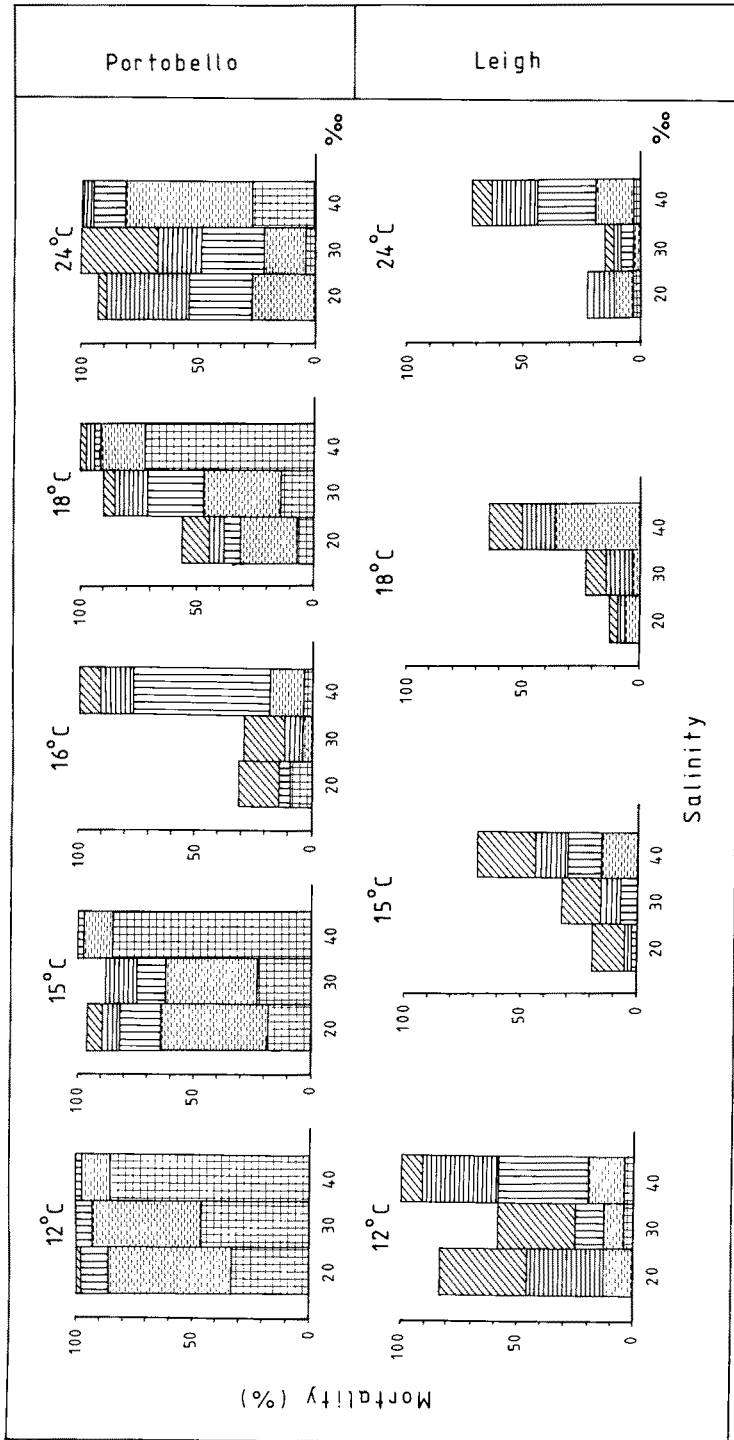


Fig. 9. Mortality of the naupliar stages of *Elminius modestus* in the Portobello and Leigh experiments in relation to water temperature and salinity (for further explanations see Fig. 4)

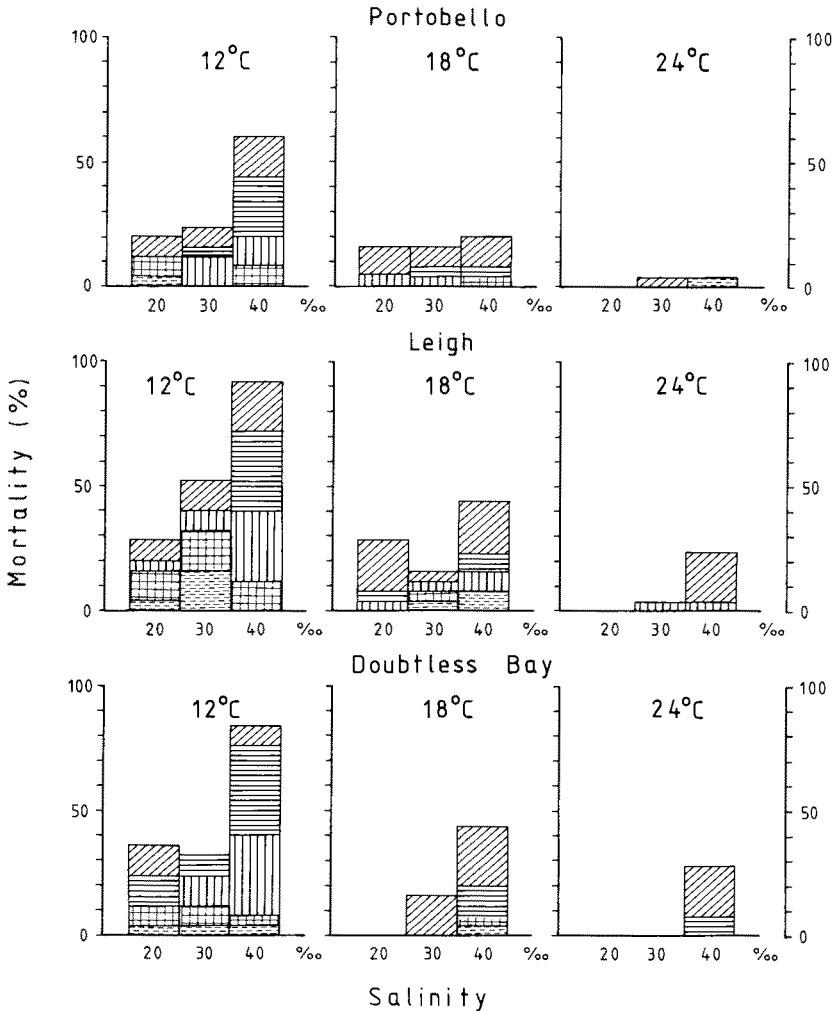


Fig. 10. Mortality of the naupliar stages of *Elminius modestus* from New Zealand (experiments carried out at Helgoland) in relation to water temperature and salinity (for further explanations see Fig. 4)

temperature influence on the duration of the larval development. Similarly, the Q_{10} -values (12°–24 °C) showed a stronger temperature influence in the N.Z. population than in the Helgoland population (Table 7).

Another difference was found by comparing the carapace size of the naupliar stages. The N.Z. populations were much smaller in nauplius II (Fig. 12), which is especially true for the Portobello larvae. This difference in carapace size was found throughout the larval development up to the VI. nauplius stage (Harms, 1985). The variation in size of the VI. nauplius stage (Fig. 12) was caused by the influence of temperature and salinity.

Table 6. Comparison of the thermal influence on larval development of *Elminius modestus* from New Zealand with those from Helgoland (after Sachs, 1976)

Helgoland vs. Portobello		Helgoland vs. Leigh	
20 ‰	n.s.	20 ‰	p < 0.02
30 ‰	n.s.	30 ‰	p < 0.05
40 ‰	n.s.	40 ‰	n.s.
Helgoland vs. Doubtless Bay		Helgoland vs. Leigh and Doubtless Bay	
20 ‰	p < 0.02	20 ‰	p < 0.01
30 ‰	p < 0.05	30 ‰	p < 0.01
40 ‰	n.s.	40 ‰	p < 0.05
Helgoland (all data comprehended) vs. Portobello 20 ‰		n.s.	
Helgoland (all data comprehended) vs. Portobello 30 and 40 ‰		n.s.	
Helgoland vs. Leigh (all data comprehended)		p < 0.05	
Helgoland vs. Doubtless Bay (all data comprehended)		p < 0.05	
Helgoland vs. Leigh and Doubtless Bay (all data comprehended)		p < 0.005	
Helgoland vs. New Zealand (all data comprehended)		p < 0.001	

Table 7. Q_{10} -values for the influence of temperature on the duration of total larval development from nauplius II to the cypris stage of *Elminius modestus*

Salinity (‰)	10	20	30	40	50
Helgoland 6–24 °C	2.32	3.38	3.38	3.06	2.85
Helgoland 12–24 °C		2.20	2.45	2.25	2.23
Portobello 12–24 °C		2.81	3.16	3.11	
Leigh 12–24 °C		3.42	4.12	3.41	
Doubtless Bay 12–24 °C		3.41	3.75	3.85	

All four populations showed similar growth rates during larval development (Harms, 1985).

Observation of individual larvae showed that occasionally an intermediate stage between nauplius VI and the cypris occurred [Helgoland population: 12 °C, 30 ‰ S (1×); Portobello population: 16 °C, 30 ‰ S (1×); Leigh population: 12 °C, 30 ‰ S (4×); 15 °C, 40 ‰ S (2×), 15 °C, 20 ‰ S (1×); 24 °C, 30 ‰ S (1×)]. This stage had the limbs of the nauplius and the thoracic appendages of the cypris. The carapace was more or less cypris-like. Tighe-Ford (1977) described a similar intermediate stage for the larval development of *E. modestus* in the presence of juvenile hormones. A similar stage was also found in *Semibalanus balanoides* (Harms, unpublished observation) at 12 °C and 30 ‰ S (1×). This stage was mainly inactive with no further moulting, and larvae always died after a couple of days.

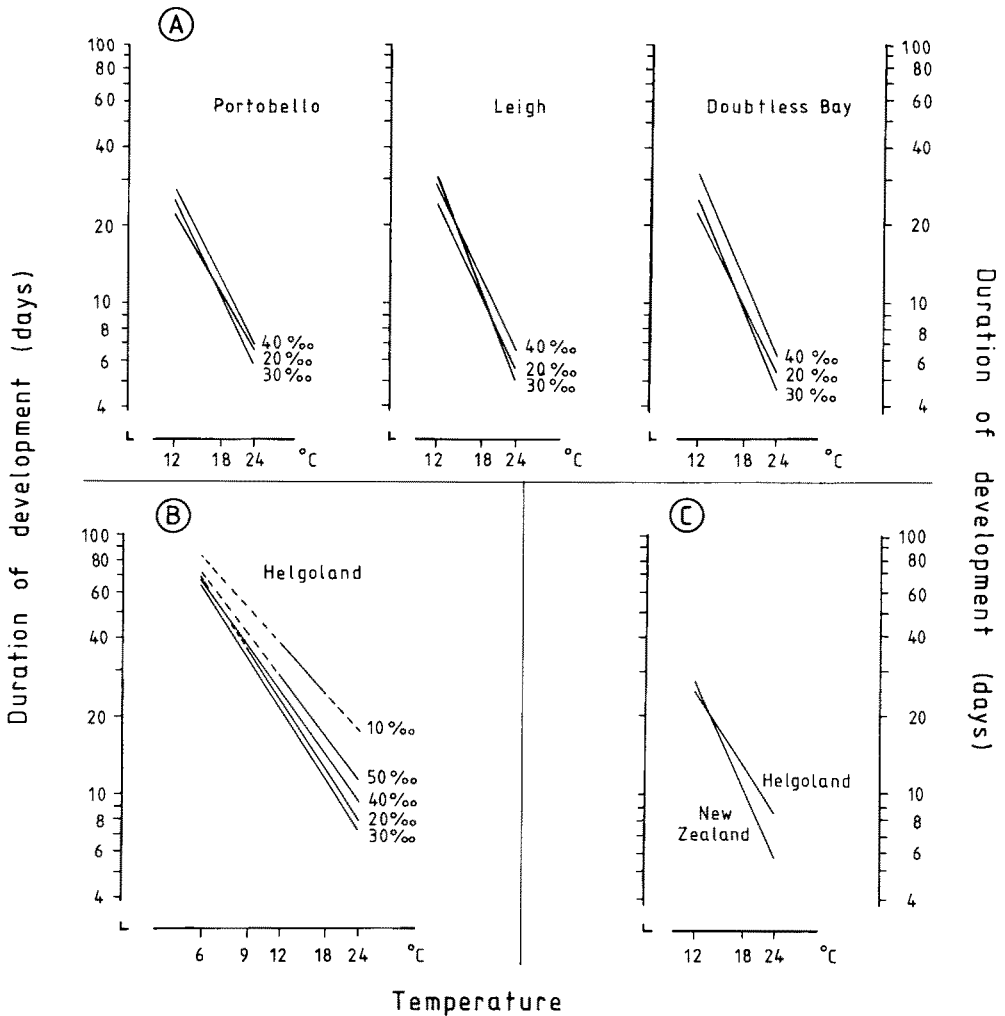


Fig. 11. Duration of total larval development (days) from nauplius II to the cypris stage, calculated from the power functions (Tables: 1, 3 and 5), for *Elminius modestus* from Helgoland and New Zealand

DISCUSSION

The adults of *Elminius modestus*, a euryhaline species, are active between 19 to 40‰ S (Barnes & Barnes, 1974; Davenport, 1976). *E. modestus* larvae hatch only at salinities above 21‰ S, but are still mobile at 9‰ S (Cawthorne & Davenport, 1980). Data of the salinity range in which the larvae of *E. modestus* develop successfully to cypris are missing. Only little is known about the salinity tolerance of the first nauplius stage. Bhatnagar & Crisp (1965) proposed a tolerance limit of 12 to 15‰ S. Davenport & Cawthorne (1978) reported that larvae which are adapted to low salinities had a

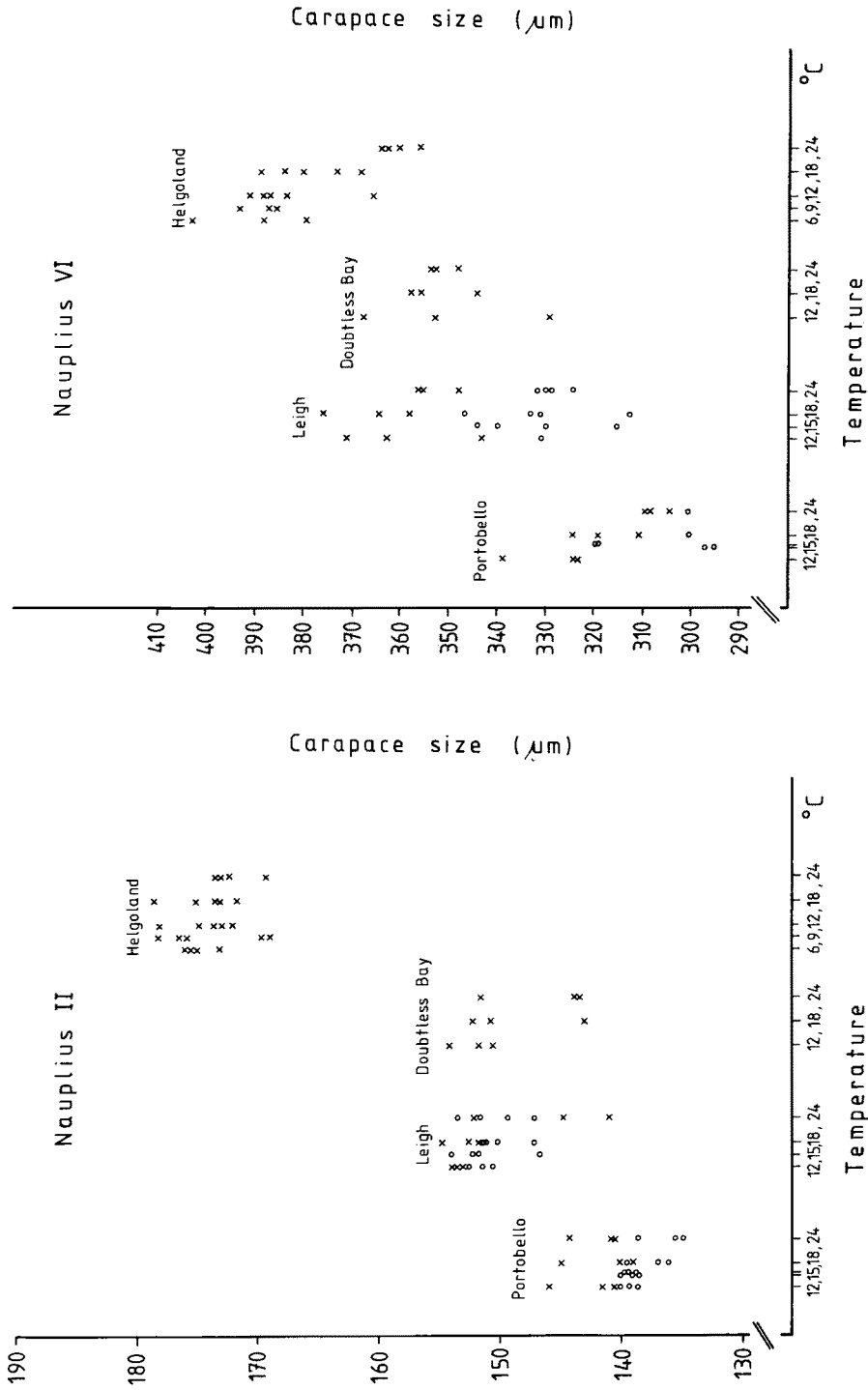


Fig. 12. Carapace size of the nauplius stages II and VI of *Elminius modestus* of three populations from New Zealand and Helgoland (o: Experiments carried out in New Zealand; x: Experiments carried out at Helgoland)

tolerance limit of 6.7 ‰ S. Lance (1964) gave 10.3 ‰ S as the lower tolerance limit of the VI. stage of *E. modestus*. All these experiments were carried out with freshly hatched larvae or those from plankton hauls, data for the other naupliar stages are lacking. These present experiments showed that the larvae of *E. modestus* can be reared to the cypris without any adaptation in a salinity range of 10 to 50 ‰ S (12°–18 °C). The reduced salinity tolerance at extreme temperatures (6°, 9° and 24 °C), and low mortality of the nauplius stages between 20 to 40 ‰ S correspond to the salinity ranges of the adults (Barnes & Barnes, 1974; Davenport, 1976). Judging from the successful cypris metamorphosis to juveniles in all experimental sets (except at 10 and 50 ‰ S), cypris seem to have similar tolerance limits as adults. The rearing of the larvae showed that developmental time at salinities which are normally found in the natural environment was slightly shorter than at extreme salinities (10, 40 and 50 ‰ S).

At the beginning of the experiments, nauplii (stage II) showed a temporary lack of activity at the extreme salinities (10 and 50 ‰ S), and recovered normally after 10 to 30 min. Some of the larvae lived for a long time (up to 25 days) without any further development. Low salinities in natural environments can be observed near water surfaces. Because of this inactivity, the larvae in nature are likely to sink from such low salinity conditions to deeper, more saline water layers. Similar behaviour was observed in decapods (Anger, 1985; Roberts, 1971). Larvae of *E. modestus* also tolerate high salinities, which may occur through evaporation in intertidal areas. This is especially important for *E. modestus* which settles in the upper part of the intertidal zone (Foster, 1971 a, b).

Larval growth rate is influenced both by temperature and salinity. Tighe-Ford et al. (1970) and Crisp (1962) found similar temperature effects on larval size in laboratory culture and field studies. The largest carapace sizes were always found at 30 ‰ S, which is close to natural salinity (Fig. 2).

The differences in larval size between the N.Z. populations are surprising, because the smallest larvae were found in the relatively cool area of the South Island. These results contrast with those of Barnes & Barnes (1965 b) and Crisp (1962), who found increased larval size in cooler geographic areas. No differences in the carapace size of the nauplii occurred between the two North Island populations. The Helgoland larvae, which are subject to occasionally harsh winters (Crisp, 1964 a; Dörjes, 1980; Harms & Anger, 1983; Ziegelmeier, 1964) and relatively low summer temperatures (Hickel & Mangelsdorf, 1980), were always larger than those from N.Z.

Non-genetic adaptation during early stages can have a strong influence on later acclimation (for definition see Crisp & Ritz, 1967; Kinne, 1964) and may influence the differences in naupliar size and developmental time between the antipodean populations. Acclimation to various predominate temperatures might also be responsible for the differences between the North and South Island populations of N.Z. (Table 4). The time span of three months at 15 °C in a flow-through-system at Helgoland might not have been enough to reach identical acclimation conditions for the N.Z. populations. Although more than half the eventual level of acclimation in many groups is achieved in the first week (Crisp & Ritz, 1967).

Earlier experiments, such as a comparison of cirral activity (Ritz & Foster, 1968), and gel-electrophoretic examinations (Flowerdew, 1984) failed to find differences between populations of *E. modestus* from N.Z. and Europe. These results, the differences in larval

development and larval size of the antipodean populations of *E. modestus*, are indications of a diverse temperature influence. The first evidence of a separation of *Semibalanus balanoides* into two distinct races in Europe and North America were based on differences in egg size (Crisp, 1964 b), time of embryonic development (Barnes & Barnes, 1976; Crisp, 1959 b) and on different cirral activities (Southward, 1964). Only recently could these results be confirmed genetically by variations in allele frequencies (Flowerdew & Crisp, 1975, 1976).

Extreme winters may act as a strong factor in the natural selection towards lower temperature adaptation in the Helgoland population. There have always been heavy reductions in population size of *E. modestus* during such winters in the inter- and subtidal area around Helgoland (Harms & Anger, 1983; and unpublished observations for 1981, 1985 and 1986). Survival of the fittest seems to play a significant role in the development of temperature adaptation in the Helgoland population of *E. modestus*.

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LITERATURE CITED

- Anger, K., 1978. Development of a subtidal epifaunal community at the island of Helgoland. – *Helgoländer wiss. Meeresunters.* 31, 457–470.
- Anger, K., 1985. Influence of salinity on larval development of the spider crab, *Hyas araneus*, reared in the laboratory. – In: *Marine biology of polar regions and effects of stress on marine organisms.* Ed. by J. S. Gray & M. E. Christiansen. Wiley, Chichester, 463–473.
- Ballentine, W. J., 1983. Leigh climate report, the climate in 1983. – *Leigh Lab. Bull.* 17, 1–120.
- Barnes, H. & Barnes, M., 1960. Recent spread and present distribution of the barnacle *Elminius modestus* Darwin in north-west Europe. – *Proc. zool. Soc. Lond.* 135, 137–145.
- Barnes, H. & Barnes, M., 1961. Recent spread and present distribution of the barnacle *Elminius modestus* Darwin in south-west Europe. – *Glasg. Nat.* 18, 121–129.
- Barnes, H. & Barnes, M., 1965a. *Elminius modestus* Darwin: Further European records. – *Progr. Oceanogr.* 3, 23–30.
- Barnes, H. & Barnes, M., 1965b. Egg size, nauplius size, and their variation with local, geographical, and specific factors in some common cirripedes. – *J. Anim. Ecol.* 34, 391–402.
- Barnes, H. & Powell, H. T., 1966. Notes on the occurrence of *Balanus balanoides*, *Elminius modestus*, *Fucus serratus* and *Littorina littoralis* at Arcachon, France, in 1963 and 1964. – In: *Some contemporary studies in marine science.* Ed. by H. Barnes. Allen & Unwin, London, 107–111.
- Barnes, H. & Barnes, M., 1969. *Elminius modestus* Darwin: Records of its present distribution and abundance in the Baie de St. Malo and in the region of St Jean-De-Luz. – *J. exp. mar. Biol. Ecol.* 3, 156–161.
- Barnes, H. & Stone, R. L., 1972. New record for *Elminius modestus* Darwin, 1854, in western Scotland (Cirripedia, Thoracica). – *Crustaceana* 23, 309–310.
- Barnes, H. & Barnes, M., 1974. The responses during development of the embryos of some common cirripedes to wide range of salinity. – *J. exp. mar. Biol. Ecol.* 15, 197–202.
- Barnes, H. & Barnes, M., 1976. The rate of development of the embryos of *Balanus balanoides* (L.) from a number of European and American populations and the designation of local races. – *J. exp. mar. Biol. Ecol.* 24, 251–269.

- Barnes, H., Barnes, M. & Klepal, W., 1972. Some cirripedes of the French Atlantic coast. – J. exp. mar. Biol. Ecol. 8, 187–194.
- Bhatnagar, K. M. & Crisp, D. J., 1965. The salinity tolerance of nauplius larvae of cirripedes. – J. Anim. Ecol. 34, 419–428.
- Bishop, M. W. H., 1947. Establishment of an immigrant in British coastal waters. – Nature, Lond. 159, 501.
- Bishop, M. W. H., 1954. *Elminius modestus* in France. – Nature, Lond. 173, 1145.
- Boschma, H., 1948. *Elminius modestus* in the Netherlands. – Nature, Lond. 161, 403.
- Cawthorne, D. F. & Davenport, J., 1980. The effect of fluctuating temperature, salinity, and aerial exposure upon larval release in *Balanus balanoides* and *Elminius modestus*. – J. mar. biol. Ass. U.K. 60, 367–377.
- Connell, J. H., 1955. *Elminius modestus* Darwin, a northward extension of range. – Nature, Lond. 175, 954.
- Costlow, J. D. & Bookhout, C. G., 1971. The effect of cyclic temperatures on larval development in the mud crab *Rhithropanopeus harrisi*. In: Fourth European Marine Biology Symposium. Ed. by D. J. Crisp. Univ. Press, Cambridge, 211–220.
- Crisp, D. J., 1958. The spread of *Elminius modestus* Darwin in north-west Europe. – J. mar. biol. Ass. U.K. 37, 483–520.
- Crisp, D. J., 1959a. A further extension of *Elminius modestus* Darwin on the west coast of France. – Beaufortia 82, 37–39.
- Crisp, D. J., 1959b. The rate of development of *Balanus balanoides* (L.) embryos in vitro. – J. Anim. Ecol. 28, 119–132.
- Crisp, D. J., 1960. Northern limits of *Elminius modestus* in Britain. – Nature, Lond. 188, 681.
- Crisp, D. J., 1962. The planktonic stages of the Cirripedia *Balanus balanoides* and *Balanus balanus* from north temperate waters. – Crustaceana 3, 207–221.
- Crisp, D. J., 1964 a. The effect of the severe winter of 1962–63 on marine life in Britain. – J. Anim. Ecol. 33, 165–210.
- Crisp, D. J., 1964b. Racial differences between North American and European forms of *Balanus balanoides*. – J. mar. biol. Ass. U.K. 44, 33–45.
- Crisp, D. J. & Ritz, D. A., 1967. Temperature acclimation in barnacles. – J. exp. mar. Biol. Ecol. 1, 236–246.
- Crisp, D. J. & Southward, A. J., 1959. The further spread of *Elminius modestus* in the British Isles to 1959. – J. mar. biol. Ass. U.K. 38, 429–437.
- Crow, J. F. & Kimura, M., 1970. An introduction to population genetics theory. Harper & Row, New York, 591 pp.
- Davenport, J., 1976. A comparative study of the behavior of some balanomorph barnacles exposed to fluctuating seawater concentrations. – J. mar. biol. Ass. U.K. 56, 889–907.
- Davenport, J. & Cawthorne, D. F., 1978. An apparatus for the laboratory stimulation of environmental fluctuations in temperature, salinity and oxygen tension. – Lab. Pract. 27, 281–284.
- DenHartog, C., 1953. Immigration, dissemination and ecology of *Elminius modestus* (Darwin) in the North Sea, especially along the Dutch coast. – Beaufortia 33, 9–20.
- Den Hartog, C. 1956. Speculations on the immigration of the barnacle *Elminius modestus* in France. – Beaufortia 56, 141–142.
- DenHartog, C., 1959. Die Seepocke *Elminius modestus* auf Helgoland. – Beaufortia 86, 207–209.
- Dörjes, J., 1980. Auswirkungen des kalten Winters 1978/1979 auf das marine Macrobenthos. – Natur Mus., Frankf. 110, 109–115.
- Fischer-Piette, E. & Forest, J., 1961. Nouveaux progrès du cirripede austral *Elminius modestus* Darwin sur les côtes atlantiques françaises et iberiques. – Crustaceana 2, 293–299.
- Flowerdew, M. W., 1984. Electrophoretic comparison of the antipodean cirripede, *Elminius modestus*, with immigrant European populations. – J. mar. biol. Ass. U.K. 64, 625–635.
- Flowerdew, M. W. & Crisp, D. J., 1975. Esterase heterogeneity and an investigation into racial differences in the cirripede *Balanus balanoides* using acrylamide gel electrophoresis. – Mar. Biol. 33, 33–39.
- Flowerdew, M. W. & Crisp, D. J., 1976. Allelic esterase isozymes, their variation with season, position on the shore and stage of development in the cirripede *Balanus balanoides*. – Mar. Biol. 35, 319–325.

- Foster, B. A., 1971a. Desiccation as a factor in the intertidal zonation of barnacles. – *Mar. Biol.* 8, 12–29.
- Foster, B. A., 1971b. On the determinants of the upper limit of intertidal distribution of barnacles. – *J. Anim. Ecol.* 40, 33–48.
- Foster, B. A., 1978. The marine fauna of New Zealand: Barnacles (Cirripedia: Thoracica). – *Mem. N.Z. oceanogr. Inst.* 69, 1–160.
- Foster, B. A., 1980. Biogeographic implication of a re-examination of some common shore barnacles of Australia and New Zealand. – *N.Z. DSIR Inf. Ser.* 137, 613–623.
- Foster, B. A., 1982. Two new intertidal balanoid barnacles from eastern Australia. – *Proc. Linn. Soc. N.S.W.* 106, 21–32.
- Harms, J., 1982. Untersuchungen zur Larvalentwicklung und zum Wachstum von Seepocken der Deutschen Bucht. *Dipl. Arb.*, TH Darmstadt, 118 pp.
- Harms, J., 1984. Influence of water temperature on larval development of *Elminius modestus* and *Semibalanus balanoides* (Crustacea, Cirripedia). – *Helgoländer Meeresunters.* 38, 123–134.
- Harms, J., 1985. Untersuchungen zum Lebenszyklus von *Elminius modestus* Darwin (Crustacea, Balanoidea). *Diss.*, TH Darmstadt, 146 pp.
- Harms, J. & Anger, K., 1983. Seasonal, annual, and spatial variation in the development of hard bottom communities. – *Helgoländer Meeresunters.* 36, 137–150.
- Hickel, W. & Mangelsdorf, P., 1980. Phytoplankton, micronutrients, and salinity at Helgoland Roads in 1978. – *Annls biol. Copenh.* 35, 118–119.
- Hiscock, K., Hiscock, S. & Baker, J. M., 1978. The occurrence of the barnacle *Elminius modestus* in Shetland. – *J. mar. biol. Ass. U.K.* 58, 627–629.
- Janke, K., 1986. Die Makrofauna und ihre Verteilung im Nordost-Felswatt von Helgoland. – *Helgoländer Meeresunters.* 40, 1–55.
- Jones, D. H., 1961. *Elminius modestus* on the south east coast of Scotland. – *Nature, Lond.* 190, 103–104.
- Kinne, O., 1964. Non-genetic adaptation to temperature and salinity. – *Helgoländer wiss. Meeresunters.* 9, 433–458.
- Kühl, H., 1963. Die Verbreitung von *Elminius modestus* (Darwin) (Cirripedia, Thoracia) an der Deutschen Küste. – *Crustaceana* 5, 99–111.
- Lance, J., 1964. The salinity tolerances of some estuarine planktonic crustaceans. – *Biol. Bull. mar. biol. Lab., Woods Hole* 127, 108–118.
- Luckens, P. A., 1976. Settlement and succession on rocky shore at Auckland, North Island, New Zealand. – *Mem. N.Z. oceanogr. Inst.* 70, 1–63.
- Moore, L. B., 1944. Some intertidal sessile barnacles of New Zealand. – *Trans. Proc. R. Soc. N.Z.* 73, 315–334.
- Morton, J. E. & Miller, M. C., 1968. *The New Zealand Sea shore*. Collins, London, 638 pp.
- Powell, H. T., 1960. *Elminius modestus* Darwin on the isle of Cumbrae. – *Nature, Lond.* 185, 119–120.
- Ritz, D. A. & Foster, B. A., 1968. Comparison of the temperature responses of barnacles for Britain, South Africa and New Zealand, with special reference to temperature acclimation on *Elminius modestus*. – *J. mar. biol. Ass. U.K.* 48, 545–558.
- Roberts, M. H., 1971. Larval development of *Pagurus longicarpus* Say reared in the laboratory. II. Effects of reduced salinity on larval development. – *Biol. Bull. mar. biol. Lab., Woods Hole* 190, 104–116.
- Sachs, L., 1976. *Angewandte Statistik*. Springer, Berlin 545 pp.
- Sastry, A. N., 1979. Metabolic adaption of *Cancer irroratus* developmental stages to cyclic temperatures. – *Mar. Biol.* 51, 243–250.
- Slinn, D. J., 1968. Some hydrological observations in Auckland and Otago harbours. – *Trans. R. Soc. N.Z.* 2, 79–97.
- Southward, A. J., 1964. The relationship between temperature and rhythmic cirral activity in some Cirripedia considered in connection with their geographical distribution. – *Helgoländer wiss. Meeresunters.* 10, 391–403.
- Stubbings, H. G., 1950. Earlier records of *Elminius modestus* (Darwin) in British waters. – *Nature, Lond.* 166, 277.
- Tighe-Ford, D. J., 1977. Effects of juvenile hormone analogues on larval metamorphosis in the

- barnacle *Elminius modestus* Darwin (Crustacea: Cirripedia). – J. exp. mar. Biol. Ecol. 26, 163–176.
- Tighe-Ford, D. J., Power, M. J. D. & Vaile, D. C., 1970. Laboratory rearing of barnacles larvae for antifouling research. – Helgoländer wiss. Meeresunters. 20, 393–405.
- Ziegelmeier, E., 1964. Einwirkungen des kalten Winters 1962/63 auf das Makrobenthos im Ostteil der Deutschen Bucht. – Helgoländer wiss. Meeresunters. 10, 276–282.