

A population study of *Galathea intermedia* (Crustacea: Decapoda: Anomura) in the German Bight

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The objectives of this study were to assess population biology and dynamics of the squat lobster *Galathea intermedia*. On the basis of nearly regular monthly samples taken with a 2-m beam trawl in the Helgoland trench (HTR) during the period of 1985 until 1992, sex ratio, length composition, relative growth and reproduction were studied. The overall sex ratio deviates significantly from 1:1 with 1♂:1.8♀ ($P \leq 0.001$). On average, sexes are equally large, but adult females attain a slightly larger size than adult males. No sex-specific differences in the length–weight relationship were found. Relative growth of the first abdominal segment is clearly of sexual-dimorphic character. On the basis of the length–frequency distributions, the life cycle of the HTR population lasts between one and two years. According to the appearance of ovigerous females and juveniles, reproduction and recruitment are clearly seasonal. Recruitment takes place between July and December. The main reproduction begins in April and ends in September, with a peak between June and August. A significant increase of specimens showing both male and female morphological characters, referred to as morphological hermaphrodites ($P \leq 0.001$), and males ($P \leq 0.05$) respectively, was detected.

INTRODUCTION

The squat lobster *Galathea intermedia* Lilljeborg, 1851 is distributed along the coasts of north-western Europe up to northern Norway in the north (Christiansen, 1972; D'Udekem D'Acoz, 1996) and to the Atlantic coasts of northern Africa in the south. It is common in the German Bight, particularly in the Helgoland trench (HTR), a depression of more than 50 m depth south of Helgoland (Figure 1).

Recent publications on this species are those by Hall-Spencer et al. (1999), who examined the anterior coloration pattern of *G. intermedia* and Christiansen & Anger (1990), who studied the complete larval development of this species. Other than these studies little is known of its biology, growth and population dynamics. Predominantly, this detritus feeder is found in small groups hiding in the interstices of mearl fragments (Hall-Spencer et al., 1999). According to Christiansen (1972) and Holthuis (1950) it is most common in depths between 8 and 100 m. Extensive collections obtained by the Senckenberg Research Institute from the entire North Sea contain specimens from depths between 9.7 m and 91 m, though most of the specimens originated from depths between 30 and 80 m. It is the smallest North Sea galatheid and is known to be gonochoric.

Regular long-term trawl sampling by the Senckenberg Research Institute in the German Bight revealed that there was a constant high abundance of *G. intermedia* in the HTR, which probably comprises the sole reproducing population in the German Bight (Caspers, 1939).

The HTR is a relatively deep depression south-west of the island of Helgoland. Its average depth is about 50 m, the maximum depth 59 m (54°8.6N 7°53.4'E). While other parts of the German Bight are about 35 m deep or less, the

HTR differs in its hydrographic conditions (Blahudka & Türkay, 2002): bottom temperature and salinity are more influenced by oceanic conditions and oscillate less than in the coastal areas. Therefore, the HTR can be characterized as an isolated relatively deep area within the German Bight (Goedecke, 1968; Berberich, 1989). Sediments differ as well: whereas sandy and muddy bottoms dominate the German Bight, the HTR has secondary hard grounds consisting of molluscan shells (Caspers, 1939). Studies on the faunal composition and occurrence of *G. intermedia* and its size structure in the German Bight were conducted for the first time to gain an insight into its life cycle.

MATERIALS AND METHODS

As part of a qualitative screening of the epibenthic fauna of the German Bight regular sampling was conducted from 1982 (HTR) until 1992 with RV 'Senckenberg'. For all catches a 2-m beam trawl with a tickler chain and mesh size in the cod end of 1×1 cm was used. Each haul covered a distance of about one nautical mile (n.m.) at two knots, which equals a sea bed surface of about 3740 m². Beam trawls are used in shrimp and plaice fisheries and are efficient for qualitative sampling of epibenthic fauna. However, they are less appropriate for quantitative surveys. The mesh size of 1×1 cm limits the size of animals caught and small specimens, such as juveniles, will only be caught incidentally if the meshes become clogged during larger catches. In spite of this, sedentary animals can be caught in large enough numbers to allow statistical treatment (Blahudka & Türkay, 2002). The trawl collected a huge amount of oyster shells and other debris at each sampling. For the sedentary species known to live

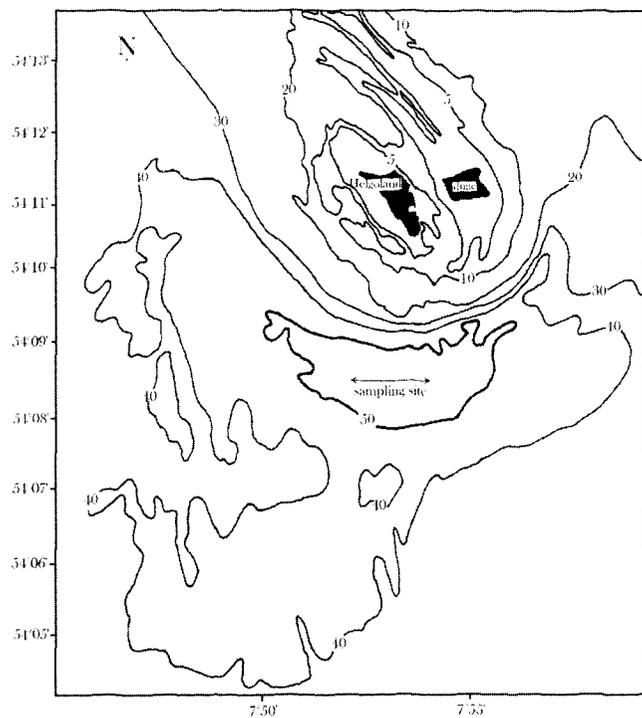


Figure 1. Situation of the Helgolander trench (HTR) and the sampling station.

among this debris and retiring into its fissures and cavities collecting such a large amount of substratum along the pathway of the trawl equates to random sampling. Out of each catch a random sub-sample of ten litres was taken. The sample was fixed in 4% formalin diluted with sea-water, transferred to 70% alcohol, and sorted.

For this study, 4368 specimens collected in the HTR from 1985 until 1992, were analysed. All *Galathea intermedia* were classified as males, females (ovigerous and non-ovigerous), juveniles and morphological hermaphrodites and were measured for morphometric analysis. For sex determination the morphological characteristics were examined (situation of gonopores and presence of first and second pleopods) using a binocular microscope. Carapace length (CL) was measured from the posterior border of the orbit to the mid point of the posterior median margin of the carapace. In addition, the greatest width of the first abdominal segment in dorsal view was determined, in order to examine possible sex-specific differences of relative growth. Measurements were carried out with an ocular micrometer to the nearest 0.1 mm. For wet weight determination a balance (Sartorius A 200S) was used to the nearest 0.1 mg. Specimens with damaged or broken carapaces were excluded from length measurements. For the illustration of the length–frequency distributions size-classes were established with equal class intervals of 0.3 mm (Table 1).

To test whether the sex ratio in the samples was significantly different from 1:1, χ^2 -tests ($P \leq 0.001$) were conducted. For the determination of relative growth and length–weight relationship regressions were calculated for both sexes. For further statistical data analysis of regressions the Package R was used. As part of this package the program Lowess was applied (Cleveland, 1981). It is a set of base routines for smoothing scatterplots by robust locally weighted regression.

Table 1. Size-class definition used in this study.

Size-classes	Carapace length (mm)
1	≤ 2.0
2	2.1–2.3
3	2.4–2.6
4	2.7–2.9
5	3.0–3.2
6	3.3–3.5
7	3.6–3.8
8	3.9–4.1
9	4.2–4.4
10	4.5–4.7
11	4.8–5.0
12	> 5.0

Time of reproduction was estimated by the presence of ovigerous females in the samples.

RESULTS

Composition of the HTR population

Between 1985 and 1992 66 samples were taken, in 60 of which *Galathea intermedia* was present. A total of 4368 individuals was studied, 292 (7%) of which were damaged and therefore not taken into account for this study; 1227 were males, 2207 females of which 197 were ovigerous. In addition 243 morphological hermaphrodites, 383 juveniles and 16 megalopa stages were included in the total (Table 2).

Of individuals large enough to sex ($N=3677$), 60% were females, 33% males and 7% showed both male and female morphological characteristics. The male–female proportion in the total sample deviated significantly from the hypothesized 1:1 ratio ($P \leq 0.001$), females dominating 1.8:1 over males. When sex ratio is examined as a function of size a variable pattern emerges (Figure 2).

In small size-classes (1–4) the ratio of ♂:♀ ranges between 0.6 and 0.7. In the two uppermost size-classes (11–12) it ranges between 0.6 and 0.65. In the middle size-classes (6–10), however, this ratio remains below 0.5, with the lowest proportion of males in size-class 8. The average sex ratio is plotted against time in Figure 3.

In April and November the proportion of males is particularly high, with sex ratios of 0.85 in April and 0.65 in November. However, between May and October the proportion of males is lower, ranging between 0.5 (July) and 0.41 (October).

Males and females were most frequent in size-class 3 (2.4–2.6 mm), while ovigerous females peaked in size-class 9 (4.2–4.4 mm). The size of egg-carrying females ranged between 2.4 mm (size-class 3) and 5.9 mm (size-class 12) CL, with the majority of all egg-carrying females measuring between 3–4 mm CL (size-classes 6–9). In the uppermost size-classes (10–12) a clear decrease occurs.

The presumed period of reproductive activity is associated with the appearance of ovigerous females in the samples, while the period of recruitment is associated with the appearance of juveniles. *Galathea intermedia* shows a relatively constant and clearly seasonal cycle of reproduction (Figure 4).

Table 2. Numbers of individuals present in the monthly catches from 1985–1992. Two samples per month, the number indicated is equivalent to the sum of individuals; 0, no *Galathea intermedia* in the samples, *, no samples.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Σ
1985	*	202	*	*	179	*	24	*	198	19	348	*	970
1986	69	*	*	57 ¹	*	73	*	24	38	170	0	*	431
1987	39	17	*	0	14	0	3	26	19	*	106	108	332
1988	*	*	17	*	68	66	12	148	372	*	165	*	848
1989	68	*	112	110	2	17	2	41	218	*	113	275	958
1990	*	*	*	*	*	9	*	142	25	33	60	0	269
1991	20	22	6	*	6	4	8	2	*	7	*	19	94
1992	15	31	3	10	1	*	3	*	44	3	*	64	174

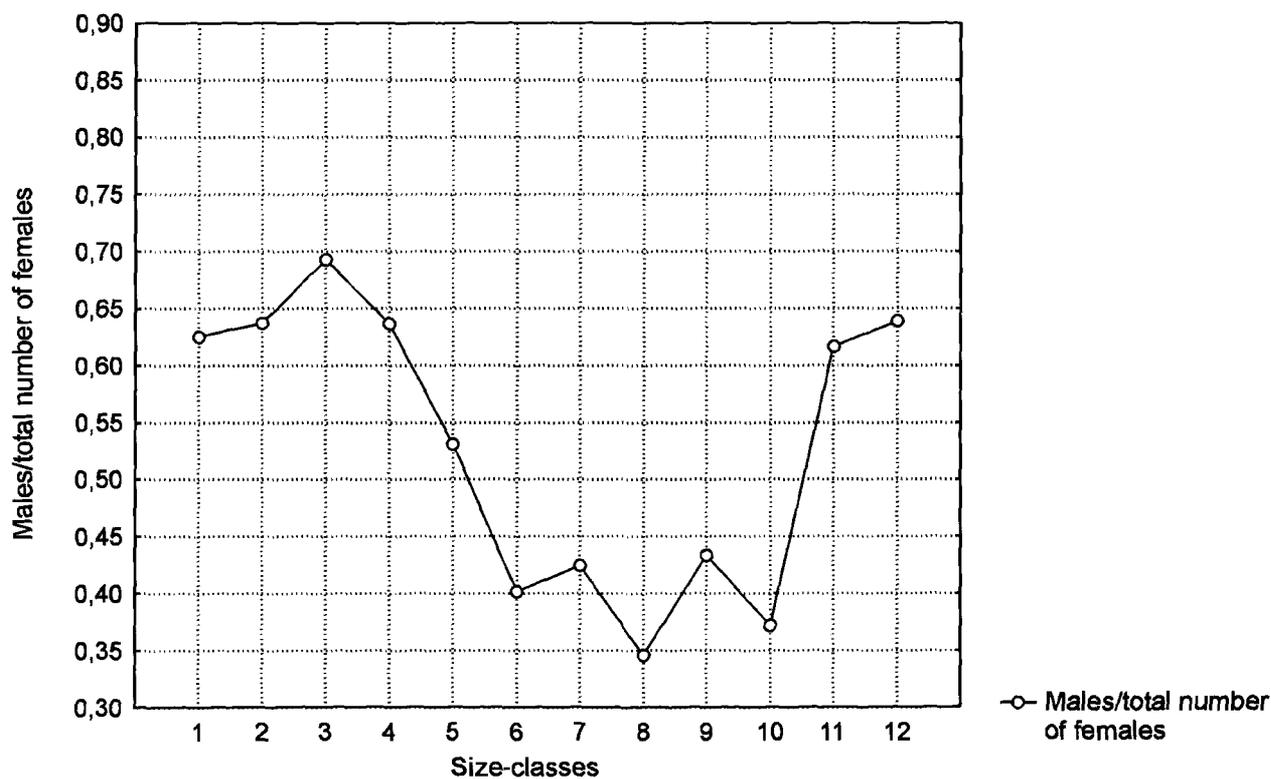
In the samples of 1985 until 1992 ovigerous females were present between January and November: 93% of these egg-carrying females appeared between April and September, and merely 7% between October and March. In July 100% of a total of 30 females were ovigerous (Figure 4). Juveniles in the samples are limited to the time between July and December. In August the relative proportion of juveniles increases to more than 20% of the population. Subsequently, decreasing numbers were caught until the end of the year. Males appear throughout the year, making up 24 to 45% of the population (Figure 4).

The comparison between the water bottom temperature pattern in the HTR (measured in 40–47 m depth) and the occurrence of ovigerous females between 1986 and 1988 (Figure 5), shows that the increase in temperature [$^{\circ}\text{C}$] between April and May coincides with the first appear-

ance of ovigerous females. Maximum ratios of ovigerous females are attained between water temperatures of 12–15 $^{\circ}\text{C}$, which was the case from mid-June to the beginning of August. Numbers decline again during and after the maximum temperatures, which are attained from mid-August to mid-September.

On the basis of χ^2 -tests ($P \leq 0.05$) the ♂:♀ ratio was significantly different during and outside the presumed reproductive season. This ratio was 0.5 between April and September, while outside the reproductive season it was 0.6.

Morphological hermaphrodites appeared regularly in all samples. No temporal periodicity was apparent. A significant increase ($P \leq 0.05$) of the mean number of morphological hermaphrodites within the population of the HTR was noted from 5% in 1985–1986 to 13% in 1991–1992.

**Figure 2.** Ratio of the total number of males to the total number of females in size-classes 1–12; 1985–1992.

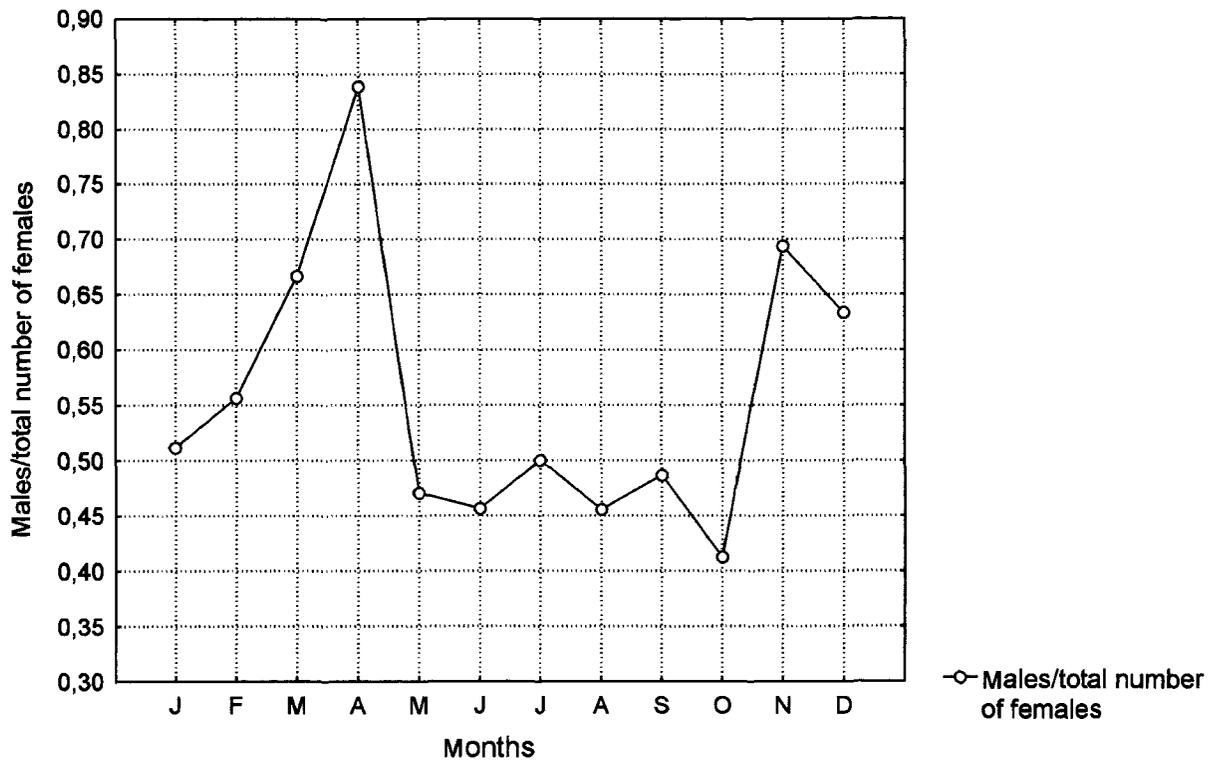


Figure 3. Ratio of the total number of males to the total number of females from January to December; 1985-1992.

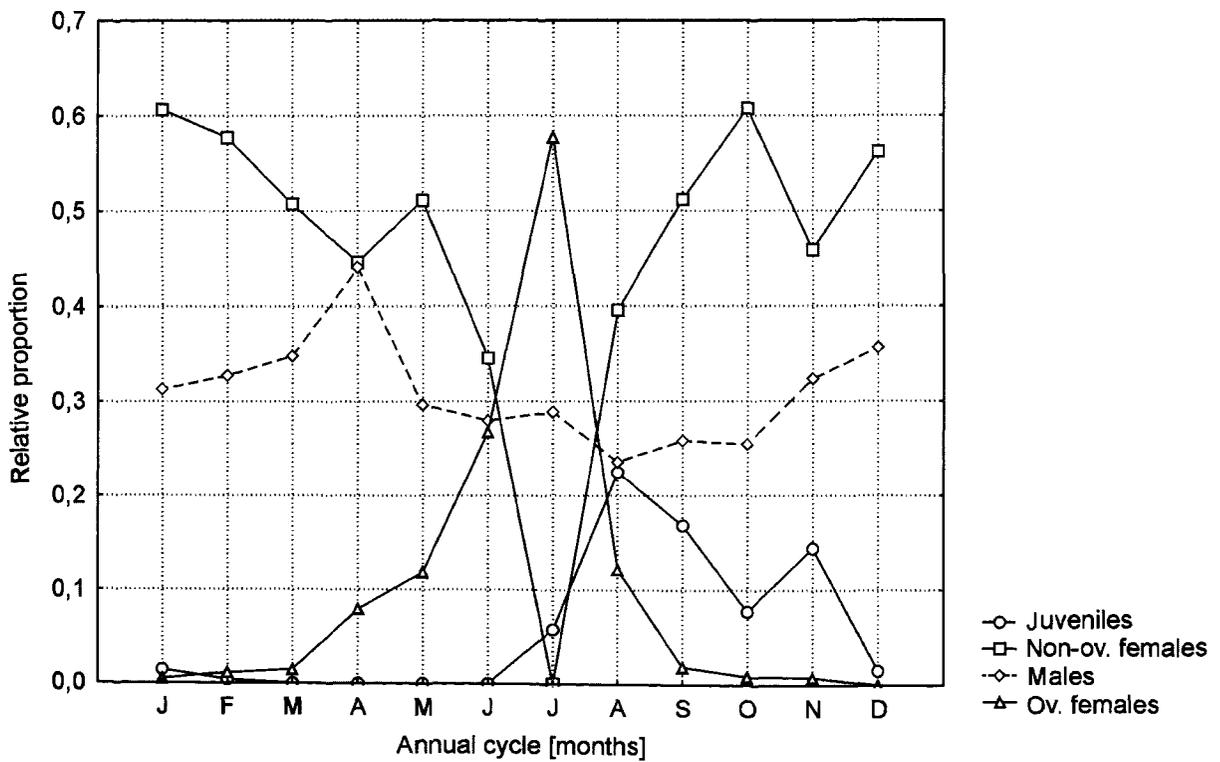


Figure 4. The relative proportion of ovigerous and non-ovigerous females, males and juveniles with reference to the total catch in an annual cycle.

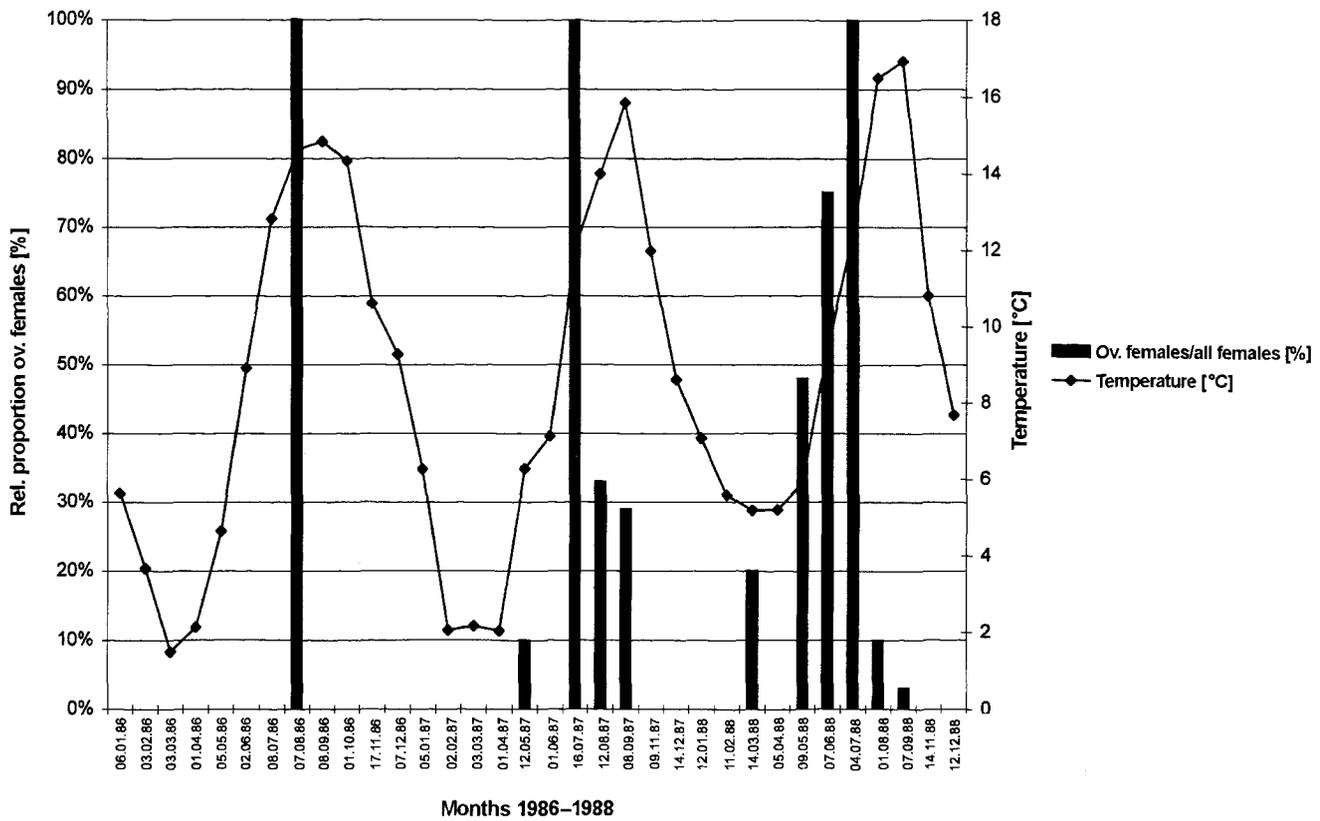


Figure 5. Temperature curve of HTR bottom water compared to relative proportions of ovigerous females in *Galathea intermedia*.

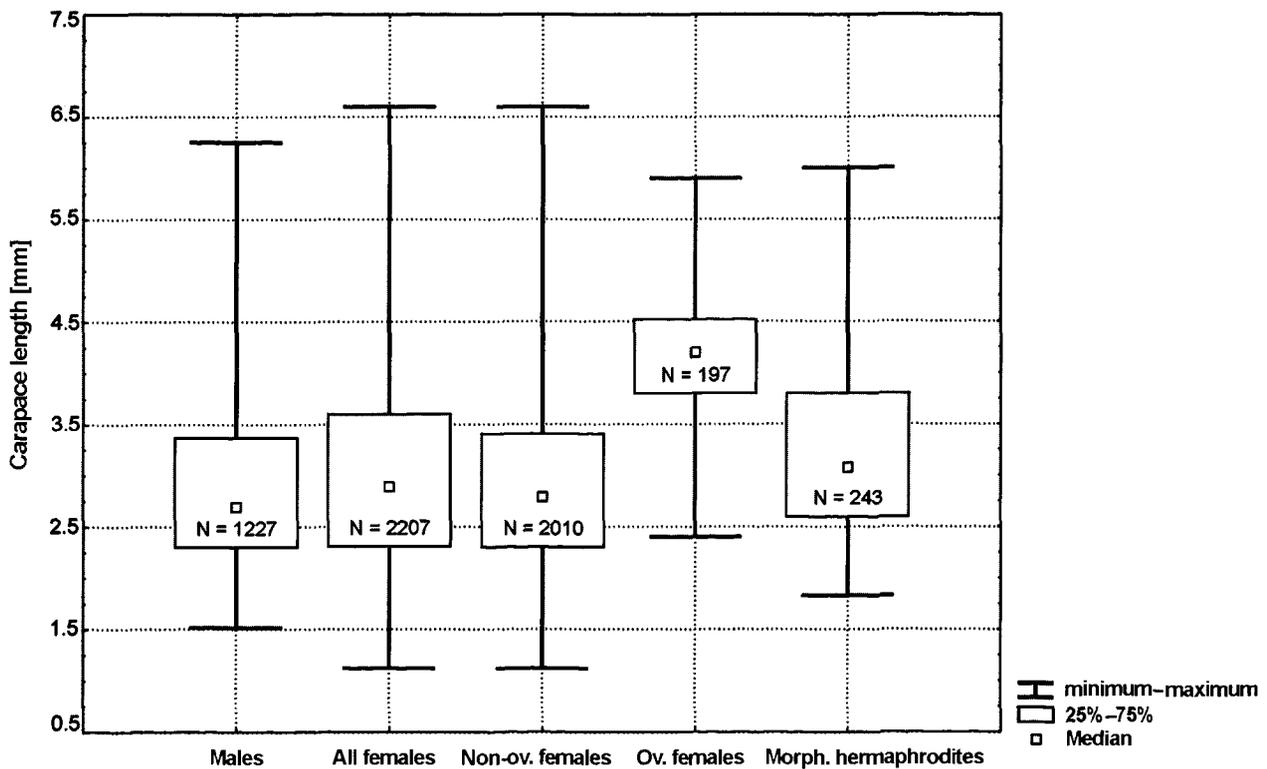


Figure 6. Length distribution of males, females and morphological hermaphrodites between 1985 and 1992.

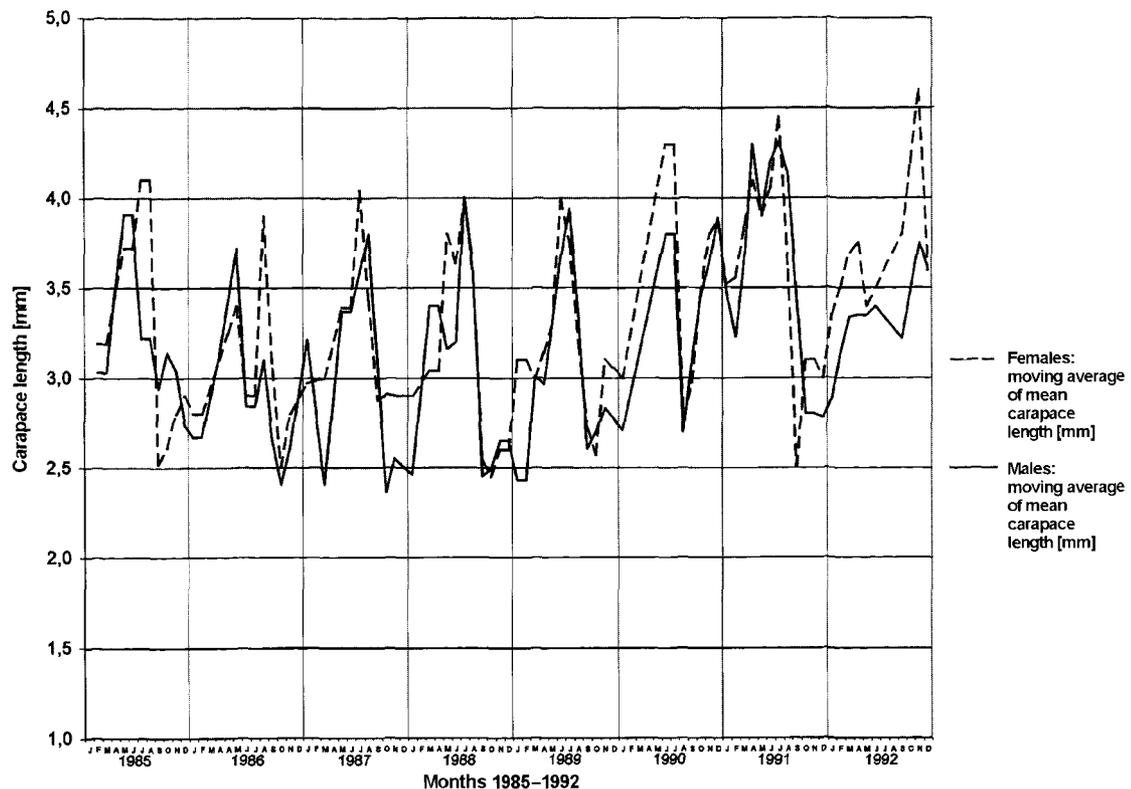


Figure 7. Monthly mean carapace length [mm] between 1985 and 1992.

Growth related characteristics

The smallest and largest females had carapace widths of 1.1 and 6.6 mm respectively. Males were smaller with minimum and maximum sizes of 1.5 and 6.3 mm. Small individuals, in which distinct sexual characteristics are difficult to determine, were classified as juveniles: their CL ranged between 0.8 and 2.2 mm. Morphological hermaphrodites had a mean CL of 3.24 mm and were thus on average larger than non-ovigerous females, but 0.93 mm

Table 3. Estimated standard error for the slopes of log-transformed data of the length-weight relationship for males, non-ovigerous and ovigerous females.

	slope	standard error
♂	2.64	0.0550
non-ovigerous ♀	2.59	0.0503
ovigerous ♀	2.80	0.1939

Table 4. Size distribution of *Galathea intermedia* (1985-1992).

	N	O	Median	Min.	Max.	Range	Variance	Standard deviation
♂	1227	2.88	2.69	1.52	6.25	4.73	0.74	0.86
♀	2207	3.01	2.89	1.12	6.60	5.50	0.78	0.88
non-ovigerous ♀	2010	2.89	2.79	1.12	6.60	5.50	0.67	0.82
ovigerous ♀	197	4.18	4.20	2.40	5.90	3.50	0.39	0.63
morph. hermaphr.	243	3.25	3.18	1.83	6.00	4.12	0.69	0.83

N, number of individuals; O, arithmetic mean; min., minimum; max., maximum; morph. hermaphr., morphological hermaphrodites.

smaller than the average size of the ovigerous ones (Figure 6).

The monthly mean CLs of male and female *G. intermedia* over the period of 1985-1992 show steady seasonal variation (Figure 7).

As a rule, at the beginning of each year between January and July the mean CL increases in both sexes, declines during the second half and by the end of the year increases slightly again (Figure 7).

In Figure 8A D the ratio of males and the ratio of females, as a proportion of the total population, is plotted for size-classes against time.

Length-frequency distributions of both sexes are principally unimodal. Progressions of frequency per size-class over time, which would indicate growth of age groups, are recognizable for males and females throughout the year. In the 1st quarter of the year more than 60% of the total number of males appear in size-classes 1 to 4, and thus are smaller than 3 mm CL (size-class 5), whereas in the 2nd quarter only 45% of males are apparent in the small size-classes. The frequency of males has shifted to the middle

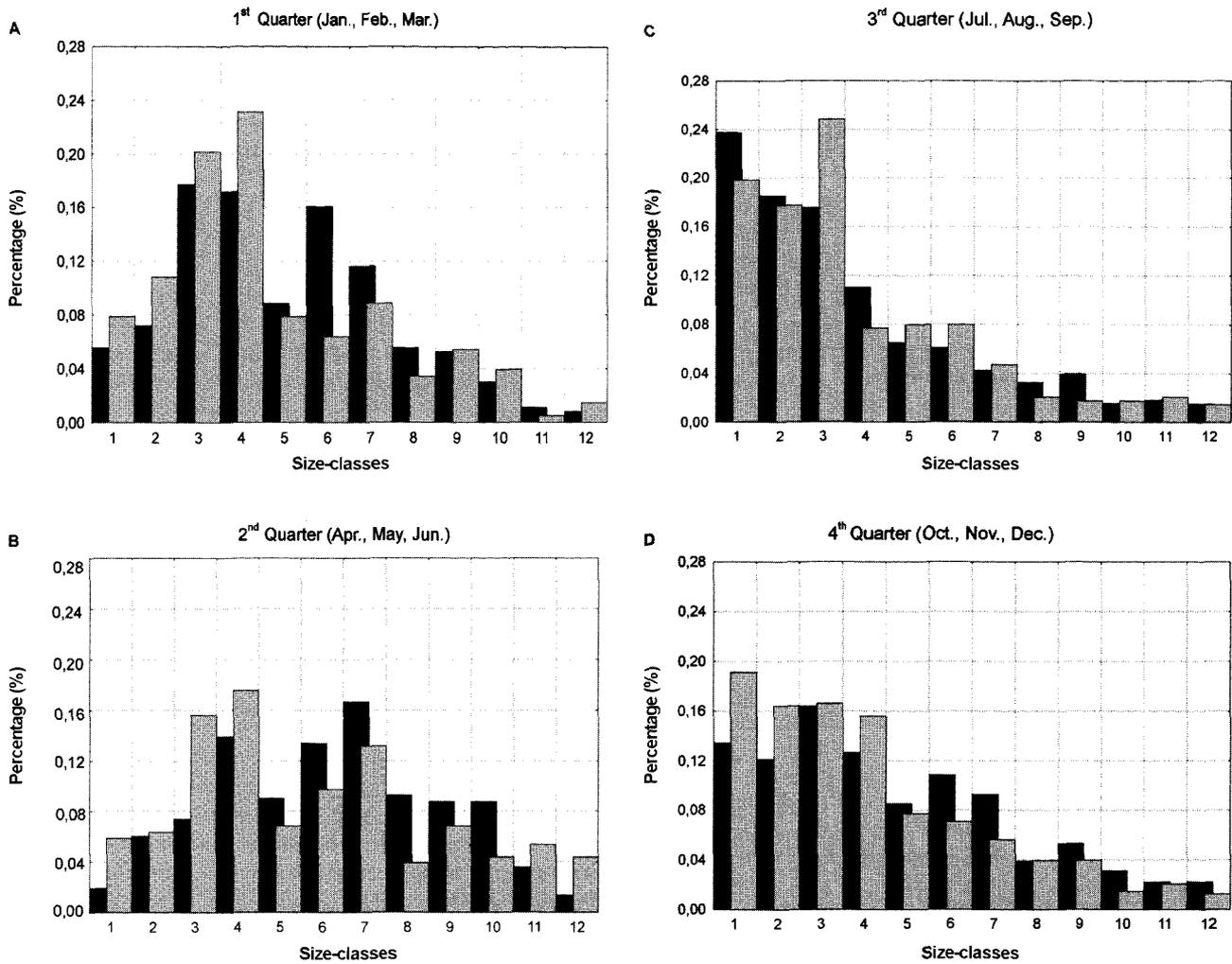


Figure 8. (A–D) Length–frequency distribution of males and females per quarter in an annual cycle. ■, females; ▨, males.

and large size-classes (Figure 8B). Subsequently, between July and August (3rd quarter) the number of males in large size-classes make up only 7% of all males in that period of time. In contrast to the male length–frequency distribution females in the 1st and 2nd quarters are most abundant in the small and middle size-classes (3–7). Female length–frequency distribution in the 3rd and 4th quarters of the year almost resemble that of the males (Figure 8C,D).

Length–weight relationship

A linear regression analysis was applied to the measured parameters of CL and weight. The following regression equations describe the relationship between log-transformed data of weight and CL for:

- males: $y = 2.64x - 2.97 (r^2 = 0.85)$ (1)
- non-ovigerous females: $y = 2.59x - 2.95 (r^2 = 0.86)$ (2)
- ovigerous females: $y = 2.80x - 3.00 (r^2 = 0.77)$ (3)

where r^2 is the coefficient of determination, x is \log_{10} CL [mm] and y is log weight [g].

For males a mean length increment of 1% corresponds to a weight increment of 2.6% with a coefficient of determination $r^2=0.85$. The relationship for non-ovigerous

females is very similar. For ovigerous females a length increment of 1% corresponds to a weight increment of 2.8% ($r^2=0.77$), not significantly different from the other groups. However, ovigerous females are heavier than non-ovigerous females and males: thus, the majority of the data points referring to them are situated above the log–log regression line (Figure 9).

Growth parameters related to reproduction

A linear regression analysis was applied to the measured parameters of CL and abdominal width. The regression of abdominal width against CL for females was:

females: $y = 1.14x - 0.06 (r^2 = 0.96)$ (4)

where r^2 is the coefficient of determination, x is \log_{10} CL [mm] and y is \log_{10} abdominal width [mm].

The slope greater than 1 (1.14) indicates a positive allometric relationship of both parameters: the ratio of abdominal width to CL increases disproportionately, that is with increasing size.

When the residuals from the regression are smoothed using the Lowess procedure (Cleveland, 1981) with default smoothing parameter $f=\frac{2}{3}$, a change point at CL 3 mm is

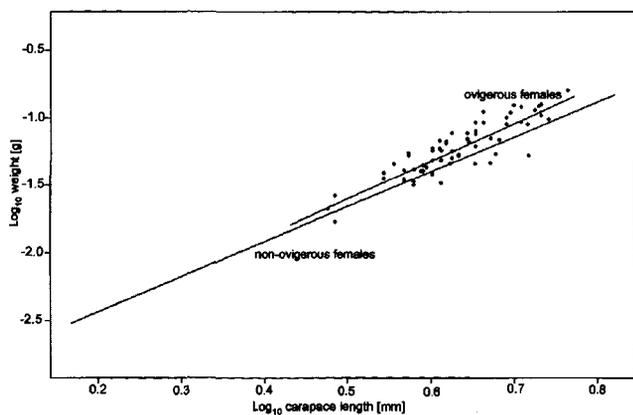


Figure 9. Log weight [g] plotted against log carapace length [mm]; ovigerous and non-ovigerous females (data analysis conducted by Dr B. Ferebee).

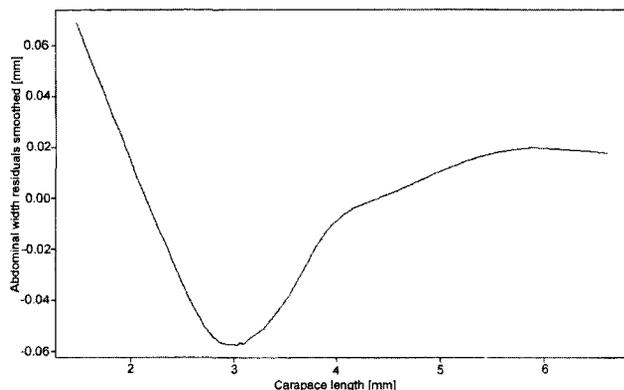


Figure 10. Smoothed residuals of regression analysis: abdominal width [mm] plotted against carapace length [mm] for females (data analysis conducted by Dr B. Ferebee).

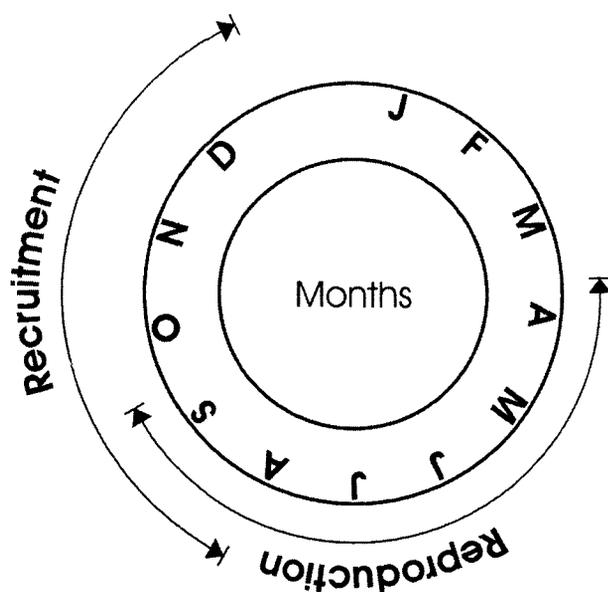


Figure 11. Presumed life cycle of *Galathea intermedia* in the German Bight.

revealed (Figure 10): the ratio of abdominal width to CL grows more rapidly for larger individuals.

To test the significance of this apparent change of slope, regression analyses were performed separately for females below 3 mm CL and for those above 3 mm CL. The following regression equations describe the relationship between the log transformed data of abdominal width and CL in both groups:

$$\text{♀} \leq 3 : y = 1.086x - 0.24 (r^2 = 0.82) \quad (5)$$

$$\text{♀} \geq 3 : y = 1.176x - 0.46 (r^2 = 0.87) \quad (6)$$

where r^2 is the coefficient of determination, x is \log_{10} CL [mm] and y is \log_{10} abdominal width [mm].

The slope for females above 3 mm CL ($a_2=1.176$) is greater than for small individuals ($a_1=1.086$). This difference is small, but according to the methods described by Sachs (1984), statistically significant.

DISCUSSION

Compared to the yearly range of temperature in the HTR of up to 15°C, the salinity (30–33) is relatively constant (Blahudka & Türkay, 2002): thus an effect of salinity variation on the pattern of reproduction seems unlikely. In fact Figure 5 suggests that it is probable that the temperature rise in April initiates the main reproductive period of the species. The appearance of ovigerous females and juveniles in the samples at only definite periods indicates seasonal variation of reproductive activity. In addition, recruitment, indicated by the occurrence of more juveniles in the catches, is not continuous: it is mainly limited to the time between July and December, reaching a maximum from September to November. Supported by the asymmetrical length–frequency distribution revealing a moderate bimodal progression, the presence of two different year groups (cohorts) is indicated.

The wide size range of egg-carrying females (CLs between 2.4 and 5.9 mm) suggests the possibility of alternative strategies of reproduction. Early reproduction involves slower growth and consequently the production of fewer eggs. However, the larvae of these broods have the advantage of hatching under more favourable environmental conditions than those hatching at a later date. Whereas females mating and brooding later, attaining a considerable body size first, are capable of producing and carrying a larger number of offspring with correspondingly higher chances of larval survival. However, brooding later might be to the disadvantage of the larvae hatching under less positive environmental conditions and furthermore larger females will have undergone substantial mortality, whilst growing to this reproductive size.

In contrast to crustaceans with determinate growth (see Hartnoll, 1983, 1985), *Galathea intermedia* follows the indeterminate growth pattern. Females of *G. intermedia* seem to attain sexual maturity at a relatively early age at the expense of rapid growth. Obviously, the proportion of ovigerous females and hence the reproductive activity of *G. intermedia* is higher in larger than in smaller size-classes. To determine the sexual maturity of *G. intermedia*, the relative growth of the first abdominal segment was investigated (see Aiken & Waddy, 1980). As indicated by our results the ratio of abdominal width to CL increases

more rapidly above 3 mm CL. This may be an indication of the transition from immature to mature females. This interpretation is supported by the fact that most ovigerous females are larger than 3 mm. The relative abdominal width of males does not reveal any change in allometry at a specific CL. Therefore, the abdominal width can be considered as a dimorphic secondary sexual character in *G. intermedia*.

According to the length–frequency distributions, males and females recruit equally to the population within the presumed recruitment period from July to December. By April of the following year the number of large males has increased strikingly. Up until June more than 80% of males fall into the uppermost size-class. The subsequent decline of numbers of these large animals, which is reflected by the maximum sizes attained from June onwards, is most probably caused by mortality. We assume that mating occurs when large males are at a maximum, thus before the maximum number of ovigerous females are recorded. The result of a χ^2 -test ($P \leq 0.05$) corresponds well with these observations: noticeably fewer males compared to females occur between April and September than outside the reproductive season. Migration is unlikely as the reason for the variable proportion of males, especially as there is no evidence for migration of this species neither within nor outside the German Bight. The length–frequency distributions indicate a shorter period of growth and an earlier death for males compared to the females—a possible explanation for the female biased sex ratio of the population. In contrast to males, females reveal relatively constant growth. No abrupt rise in the number of females occurs at any time, such as seen for large males between February and April. After sexual maturity females grow slower than males, but finally become slightly larger than males, suggesting a higher life expectancy in females. If the proportion of males and females is plotted as a function of size, a variable pattern, termed anomalous by Wenner (1972), emerges. This results in different strategies: for males it is advantageous to quickly attain a large size, while females grow relatively slower, since they mature sexually quite early and delay moulting each time they are ovigerous. Thus an accumulation of the females in the intermediate size-classes emerges.

In total 6% (243) of 4076 sexable individuals of *G. intermedia* studied between 1985 and 1992 featured both female and male external morphological characteristics. Since such individuals appear only occasionally, for *G. intermedia* one can basically assume gonochorism. A change of sex, characteristic of protandric and protogynous hermaphrodites occurred: no accumulation of one sex within the small or the large size-classes was evident. Whether the individuals revealing both male and female sexual characteristics are functional hermaphrodites needs to be investigated. There was a tendency for an increase in numbers of morphological hermaphrodites of the population in the HTR from 1985 to 1992. Presently it remains unclear if this can be correlated with any environmental features.

From our observations we conclude the life cycle presented schematically in Figure 11.

According to this, *G. intermedia* is a short lived species in the German Bight and completes its life cycle in just over a year, males being shorter lived than females.

Thanks are due particularly to Christa Rensing (Senckenberg-Institute, Wilhelmshaven) for her efforts in collecting and preserving the material for this study at regular monthly intervals over the years whenever one of us was not on-board. We also thank the captain and crew of RV 'Senckenberg' for their careful handling of ship and gear which largely contributed to the success of our work. Temperature and salinity data were received from Professor B.W. Flemming and Dr A. Bartholomä (both Senckenberg-Institute, Wilhelmshaven) and F. Nast (German Oceanographic Data Centre, DOD, Hamburg). The statistical analyses were performed by Dr B. Ferebee from the Department of Mathematics of the Frankfurt University, who also gave us advice in all mathematical questions, which we gratefully acknowledge. Special thanks are due to Dr R. Hartnoll (Port Erin Marine Laboratory, Isle of Man, UK) for critical reading and commenting on an earlier version and for streamlining our English. This work was financially supported by the Senckenberg Natural History Society (Frankfurt am Main).

REFERENCES

- Aiken, D.E. & Waddy, S.L., 1980. Reproductive biology. In *The biology and management of lobsters: physiology and behaviour*, vol. 1 (ed. J.S. Cobb and B.F. Philipps), pp. 2–72. New York: Academic Press.
- Berberich, D., 1989. *Vergleichende Untersuchungen zur Artenzusammensetzung, Abundanz und Biomasse des Makrozoobenthos der Helgoländer Tiefen Rinne von 1936/37 und 1988/89*. Unpublished diploma thesis, Fachbereich Biologie der Technischen Hochschule Darmstadt, 142 pp.
- Blahudka, S. & Türkay, M., 2002. A population study of the shrimp *Crangon allmanni* in the German Bight. *Helgoland Marine Research*, published online: 16 July 2002.
- Caspers, H., 1939. Die Bodenfauna der Helgoländer Tiefen Rinne. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **2**, 1–353.
- Christiansen, M.E., 1972. *Crustacea Decapoda: Zoologische Bestimmungstabeller*. Oslo: Universitetsforlaget.
- Christiansen, M.E. & Anger, K., 1990. Complete larval development of *Galathea intermedia* Lilljeborg reared in laboratory culture (Anomura: Galatheaidae). *Journal of Crustacean Biology*, **10**, 87–111.
- Cleveland, 1981. LOWESS: a program for smoothing scatterplots by robust locally weighted regression. *The American Statistician*, **35**, 54.
- D'Udekem D'Acoz, C., 1996. Contribution a la connaissance des crustacés décapodes helléniques. II. Peneidea, Stenopodidea, Palinuridea, Homaridea, Thalassinidea, Anomura, et note sur les Stomatopodes. *Bios (Macedonia, Greece)*, **3**, 51–77.
- Goedecke, E., 1968. Die hydrographische Struktur der Deutschen Bucht im Hinblick auf die Verschmutzung der Konvergenzzone. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **17**, 108–125.
- Hall-Spencer, J.M., Moore, P.G. & Sneddon, L.U., 1999. Observations and possible function of the striking anterior coloration of *Galathea intermedia* (Crustacea: Decapoda: Anomura). *Journal of the Marine Biological Association of the United Kingdom*, **79**, 371–372.
- Hartnoll, R.G., 1983. Strategies of crustacean growth. *Memoirs of the Australian Museum*, **18**, 121–131.
- Hartnoll, R.G., 1985. Growth, sexual maturity and reproductive output. In *Factors in adult growth* (ed. F.R. Schram and A.M. Wenner), pp. 101–128. Rotterdam & Boston: A.A. Balkema. [Crustacean Issues, no. 3.]
- Holthuis, L.B., 1950. *Decapoda en Stomatopoda*. Leiden: A.W. Sijthoff. [*Fauna van Nederland*, **15**, 1–166.]
- Sachs, L., 1984. Comparing two regression coefficients § 5.5.8. In *Applied statistics: a handbook of techniques*. New York, Berlin: Springer.
- Wenner, A.M., 1972. Sex ratio as a function of size in marine crustacea. *American Naturalist*, **106**, 321–350.

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