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The amphipod *Corophium multisetosum* (Corophiidae) in Ria de Aveiro (NW Portugal). I. Life history and aspects of reproductive biology

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Abstract The population of *Corophium multisetosum* Stock, 1952 in Areão displayed a semiannual, iteroparous life history. Mean longevity was ~6 mo, with the estimated life span longer for overwintering individuals born in autumn than for individuals born in spring. Length-frequency data indicated that the length increment per moult is probably higher in males than females; however females moulted more frequently and achieved a larger body size. Preliminary growth rates were $100 \mu\text{m d}^{-1}$ for juveniles and 19 to $29 \mu\text{m d}^{-1}$ for mature females, with the lower values occurring during the winter. It was estimated that under favourable conditions females may attain reproductive size and mature within 1 mo. Although incubating females were present all year round, recruitment occurred in spring, almost ceased during the summer, peaked in autumn, and decreased again during the winter. Extreme temperatures and very low salinities during winter and summer may have deterred breeding, while moderate temperatures (15 to 20°C) and salinities >1 psu in spring and autumn were apparently favourable for reproduction. The unfavourable summer conditions constrained breeding and synchronised the timing of reproduction. In late-autumn and during the winter, as temperature decreased and brooding time increased, synchrony was progressively lost. Brood size varied as a function of embryonic developmental stage, size of incubating females, and season. The life-history pattern and reproductive fea-

tures of *C. multisetosum* in Areão are closely related to temperature and salinity; other environmental conditions such as oxygen content of the water and food availability may also be relevant.

Introduction

During the first benthic survey of Ria de Aveiro (NW Portugal) in 1985/1986, high densities of the amphipod *Corophium multisetosum* Stock, 1952 were found in the upper reaches of Canal de Mira, one of the main channels of the Ria (Queiroga 1990). The macrobenthic community structure and environmental conditions of this area were further investigated in 1988/1989 (Cunha and Moreira 1995). On this occasion, the *C. multisetosum* population was sampled together with the remaining macrobenthic fauna, and the collected material was further examined. The present contribution describes the life history of *C. multisetosum* over a 1 yr period, and some aspects of its reproductive biology. The field data are interpreted together with some information from laboratory experiments (Ré 1996), and are discussed in relation to other studies on several *Corophium* species. Production estimates and certain aspects of the population dynamics (density and biomass) in relation to environmental factors are considered in the following paper in this issue (Cunha et al. 2000b).

Despite its wide distribution in Europe, and with the exception of some notes on the population at the Dead Vistula (Jazdzewski 1987), available data on the life history of *Corophium multisetosum* are scarce. However, the life histories of other *Corophium* species have been described from field and laboratory data: *C. volutator* was studied from two mud-flats in the Bay of Fundy (Peer et al. 1986) and from the Dovey estuary (Watkin 1941; Fish and Mills 1979) (in the latter area the life history of *C. arenarium* was also investigated; (Fish and Mills 1979); *C. sextoni* living on the hydroid *Nemertisia antennina* and *C. bonnellii* in kelp holdfasts were studied

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in Torbay (Hughes 1978) and Millport (Moore 1981), respectively; the life cycle of *C. insidiosum* was studied under laboratory conditions (Nair and Anger 1979) and in wild populations from the north-east coast of England (Sheader 1978) and the Arcachon lagoon (Labourg 1968).

Reproductive aspects of several species can also be found in the reviews by Nelson (1980) and Sainte-Marie (1991) and in the extensive literature dealing specifically with *Corophium* species or with brackish coastal environments (e.g. Hart 1930; Segestråle 1959; Casabianca 1967, 1975; Muus 1967; Birklund 1977; Möller and Rosenberg 1982).

Materials and methods

The benthic macrofauna was randomly sampled between May 1988 and April 1989 at low water of new-moon spring tides in Areão (upper reaches of Canal de Mira, Ria de Aveiro: 40°40'N, 8°45'W). Ten core replicates (10 × 0.01 m², 20 cm depth) were collected monthly. The samples were sieved in the field through a 0.5 mm mesh, and preserved in 10% formalin. The structure of the macrobenthic community in Areão as well as the temporal variation of several environmental factors and further details on sampling have been described by Cunha and Moreira (1995).

For this study, all *Corophium multisetosum* individuals were counted and classified into five demographic categories: juveniles (J) without distinctive characteristics; non-setose females (F_{ns}) with non-setose oostegites; incubating females (F_{inc}) with fully developed setose oostegites and carrying embryos in their marsupium; empty females (F_e) with fully developed setose oostegites and empty marsupium; males (M) with ventral genital apophyses in the 7th segment of the pereon.

Embryos and juveniles were removed from the marsupia of incubating females and the embryos were separated into three developmental stages: (1) rounded embryos; (2) embryos with ventral cleft and rudimentary appendages; (3) segmented embryos. These three stages plus the newly hatched juveniles in the marsupium correspond, respectively, to Stages 1/2, 3, 4/5 and 6, described in detail by Sheader and Chia (1970) for *Marinogammarus obtusatus* and Stages A, B, C and D described by Peer et al. (1986) for *Corophium volutator*. The number of embryos was counted only in incubating females with undamaged marsupia.

The head length (L_h) was measured from the tip of the rostrum to the posterior margin of the head (dorsal view). In the smaller samples all specimens were measured, but because of the large number of individuals collected in most months, the population size-structure was inferred from the study of a random sub-sample (900 to 2000 measured specimens per monthly sample). Some undamaged specimens were further selected for the measurement of the total length (L_t , measured along the dorsal midline from the tip of the rostrum to the posterior end of the telson). All measurements were taken with a calibrated ocular micrometer under a dissecting microscope.

The ash-free dry weight (AFDW, determined to the nearest 0.1 mg) of the different demographic categories in each replicate was obtained after ignition of the dried specimens in a muffle-oven for 2 h at 450 °C.

Results

Morphological data

Corophium multisetosum is one of the largest species in the genus. Like *C. volutator* and *C. arenarium*, the other

Table 1 *Corophium multisetosum*. Minimum, maximum and mean total body length (L_t , mm) in Ria de Aveiro (J juveniles; F_{ns} non-setose females; F_{inc} incubating females; F_e empty females; M males)

	J	F_{ns}	F_{inc}	F_e	M
L_t min	0.8	2.3	4.1	4.1	1.6
L_t max	3.4	7.4	9.4	9.7	7.6
L_t	1.9	4.2	6.2	6.3	4.0

two large species common in European waters, it has a segmented urosome, but is readily distinguished by the single, large, slender and curved process in Antenna 2 (Peduncle Article 4) and by the produced distolateral angle in the peduncle of Uropod 3. Sexual dimorphism in adult specimens is evidenced by the differing size and proportions of Antenna 2.

During ontogenic development, the external sexual characters appear earlier in males than in females. Males of ~1.6 mm total length (L_t) were already recognisable by the presence of genital apophyses, while females of ~2.3 to 2.8 mm L_t had just begun to develop oostegites. The minimum body size of incubating females was 4.1 mm; females reached larger sizes than males. Maximum length was observed in specimens collected in March and April 1989: 9.7 and 7.6 mm for females and males, respectively (Table 1).

The allometric relation between total length (L_t in mm) and head length (L_h in mm) is expressed as (Fig. 1):

$$L_t = 8.820L_h^{1.238} (n = 235; r = 0.984; 0.183 \leq L_h \leq 1.000),$$

where the exponent is significantly higher than 1 ($t_{obs} = 18.19$; 233 df; $P < 0.001$). Despite this slight positive allometry, head length was used as individual size reference because it can be measured more accurately than total body length.

A slight sexual dimorphism is apparent from Fig. 1 (in general, males were shorter than females with the same head length), but the difference between the allometric coefficients, estimated for females and males separately, was not statistically significant.

Demographic structure of the population

The demographic structure of the population underwent considerable fluctuations during the annual cycle. These are shown in Fig. 2, together with the water temperature and salinity fluctuations throughout the study period.

All demographic categories were present all year round, but only very few incubating females (<0.5% of total abundance, A, and biomass, B) were collected in May, July and August when salinity was very low (<1 psu). In the latter two months, the low salinity coincided with the maximal annual water temperature (~24 °C). The percentage of juveniles was low (A = 5 to 9%, B < 1%) in mid-summer (July/August) and winter (February/March) and higher (A = 30 to 72%, B = 3 to 10%) during the autumn (September to December).

Fig. 1 *Corophium multisetosum*. Relationship between total length and head length. (*J* juveniles; *F_{ns}* non-setose females; *F_{inc}* incubating females; *F_e* empty females; *M* males)

The empty females showed an opposite trend with lower percentages ($A = 2$ to 5% , $B = 10$ to 13%) in autumn and higher percentages ($A = 16$ to 20% , $B = 28$ to 31%) in summer. The sex ratio favoured males only when the population was dominated by small-sized individuals (October to January and April).

In September, an important recruitment pulse took place that markedly changed the population structure (Fig. 2). The abundance of juveniles in the population rose to 72.9% and the biomass of incubating females to 48.9% , while the male population dropped to minimal percentages of both abundance and biomass (11.9 and 21.6% , respectively). This pulse accompanied a slight decrease in temperature (24.4 down to 23.1 °C) and an increase in salinity (1.8 to 6.5 psu at high water). The smaller recruitment pulse in June also coincided with an increase in salinity (0.5 to 3.0 psu at high water).

Size structure

The length-frequency analysis of the *Corophium multisetosum* population used $\sim 16\,700$ measurements. The annual average density (individuals m^{-2}) of each size-class (ungrouped head-length measurements to the nearest $1/60$ mm) is plotted in Fig. 3, with the frequencies of juveniles adjusted to a population sex ratio of $1:1$ (estimated value for total data set). The highest modal abundance corresponds to the size (L_h) of 0.417 mm, indicating that a large number of smaller individuals

might have been lost by sieving the samples through 500 μm mesh. Several modal values are clearly evident in both the female and male populations. The difference between the modal values may be interpreted as to the size increase in consecutive moult stages (see Sheader and Chia 1970), implying that males of $L_h > 0.417$ mm probably went through four successive moults. In the female population the pattern is not so clear, but it appears that the number of moulting stages is higher and that the length increase between consecutive moults is smaller than in the male population.

Size-specific survival in the studied population can also be estimated from data in Fig. 3. Where individuals can not be aged reliably and in populations where changes in composition can not be followed because of overlapping of successive cohorts, monthly size-frequency data over a period of 1 yr provide an indication of size-specific survival and of the annual population mortality pattern (Fenwick 1984). However, it should be noted that: (1) these plots contain data for several cohorts which might have differed in mortality pattern; (2) size-specific survival cannot be literally interpreted as age-specific survival, since the relationship between size and age may not be linear nor constant throughout its range. In Fig. 3, the difference between the modal densities of 0.417 and 0.500 mm indicates a high mortality associated with the size of females reaching maturity, followed by a period of high survival and finally by a decline to low numbers at larger sizes ($L_h > 0.767$ and 0.667 for females and males, respectively).

Fig. 2 *Corophium multisetosum*. Evolution of demographic structure throughout sampling period in Areão in relation to variation in some environmental factors. Intensity of recruitment indicated by size of letter R, [T water temperature (°C); S salinity (psu); W water balance (difference between rainfall and evapotranspiration); other abbreviations as in Fig. 1]

Fig. 3 *Corophium multisetosum*. Annual average size-structure of female and male populations in Areão. Frequencies of juveniles were adjusted by population sex ratio of 1:1 (Horizontal lines size range of different demographic categories; ind. individuals; further abbreviations as in Fig. 1) Modal head lengths are interpreted as mean size of consecutive moult stages

Life history

Head lengths were grouped into 12 size-classes in order to produce the length-frequency histograms in Fig. 4. In May, despite the low number of incubating females, juveniles represented 13.2% of the population, indicating that recruitment was already taking place. Small-sized juveniles (1st and 2nd size-classes; $L_t \approx 1.0$ and 1.6 mm, respectively) were recorded during the spring, mainly in June. The population reached minimum density in August as a result of the small spring recruitment and the gradual disappearance of the larger individuals from the population. Large non-setose and setose empty females were recorded during the summer, but very few incubating females were present. Yet, in September, almost all the large females (9th and 10th size-classes; $L_t \approx 7.0$ and 7.9 mm, respectively) were incubating. Empty females in the 11th and 12th size-classes ($L_t \approx 8.8$ and 9.7 mm, respectively) were observed in October and November but not in December, indicating a probable longevity of ~ 5 to 6 mo for the June recruits.

The females, probably born in spring, gave birth to numerous juveniles in September and initiated the intense and continuous recruitment that took place during the autumn. The abundance of juveniles was high from September to December, and decreased thereafter till February. A large number of small-sized incubating females (7th and 8th size classes; $L_t \approx 5.3$ and 6.2 mm, respectively) was observed in the population from October to December. In February, recruitment was low despite the relatively high percentage of incubating females. The proportion of large non-setose females was

also high from January to March. Maximum body length was attained in March and April by the overwintering individuals, indicating a probable longevity of ~ 6 to 7 mo for the autumn recruits. Spring recruitment was resumed in March/April.

Hence, two peak-recruitment periods were recognisable in the population of *Corophium multisetosum*: in spring from April to June, and in autumn from September to December. The length-frequency histograms of ungrouped data for incubating females (Fig. 5) show that the autumn recruitment was initiated in September by the large females born during the spring. In October and November there were two groups of incubating females, and by December the old females had died out. The group of smaller females increased in abundance from October to December, but the modal head length remained the same because of the continuous input of young females attaining maturity. It was impossible to recognise the successive cohorts contributing to this group of smaller females. In January recruitment decreased, and in the following months there was a clear shift in the modal head length. The overwintering females gave birth to new recruits in April, but the small size of the incubating females observed in June of the previous year indicates that the spring recruitment may have generated from two different generations. Hence, in both seasons, breeding was commenced by the large females born in the previous season, but within 1 to 2 mo a new generation of females, recognisable by their smaller size, was able to contribute with new recruits.

Breeding activity was more intense when the water temperature lay between 15 and 20 °C and salinities were > 1 psu (Fig. 2). The continued recruitment during the autumn produced a population with an average density more than three times higher than the spring recruitment. The increasing abundance was followed by a similar trend in biomass, which continued to increase until February (Fig. 2), when the population was dominated by large individuals.

Spring recruitment was observed mainly in June 1988, when the estimated population density was double that in May (Table 2). This population growth resulted also from increases in the density of all size-classes that can only be explained by putative migration from other areas. The highest recruitment of juveniles (1st and 2nd size-classes) was observed in September, November and December. Increases in the density of successive size-classes throughout the sampling period (Table 2) were interpreted as a result of individual growth, and depict the evolution of the dominant cohorts.

The growth of incubating females was inferred from the displacement of modal values in the monthly length-frequency histograms of ungrouped data (Fig. 5). Mean values of $29 \mu\text{m d}^{-1}$ (from September to November) and $19 \mu\text{m d}^{-1}$ (from December to April) were estimated for females from the spring and autumn recruitment, respectively (Table 3).

Fig. 4 *Corophium multisetosum*. Length-frequency distribution in Areão, grouped into 12 size-classes. Abbreviations as in Fig. 1

Fig. 5 *Corophium multisetosum*. Length-frequency histograms of incubating females: ungrouped data

Table 2 *Corophium multisetosum*. Size-frequency data in Ria de Aveiro (individuals m^{-2}). Underlined values indicate increasing densities and depict the dominant cohorts (L_h head length class mark, mm)

L_h	May 88	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan 89	Feb	Mar	Apr
0.167	0	<u>531</u>	0	<u>32</u>	<u>2542</u>	1743	<u>6134</u>	1508	<u>2880</u>	550	<u>2578</u>	151
0.250	1000	<u>2063</u>	226	455	<u>39 262</u>	5698	<u>32 112</u>	29 106	4273	572	<u>1214</u>	2388
0.333	1884	<u>7621</u>	2364	1196	<u>4174</u>	<u>36 777</u>	25 703	<u>34 913</u>	15 013	1842	<u>727</u>	<u>8311</u>
0.417	2722	<u>8975</u>	4888	958	<u>4702</u>	<u>35 976</u>	48 174	33 713	20 927	12 193	1674	<u>6686</u>
0.500	5149	<u>7941</u>	<u>7988</u>	2004	1941	<u>7810</u>	<u>17 953</u>	<u>32 872</u>	23 853	18 542	4318	4027
0.583	6309	<u>7288</u>	<u>13 947</u>	3247	1032	<u>10 346</u>	<u>17 003</u>	<u>33 988</u>	24 030	13 001	6872	2388
0.667	4454	<u>10 118</u>	9540	7098	542	<u>7392</u>	<u>13 855</u>	<u>22 681</u>	26 642	15 597	8959	2687
0.750	767	<u>6787</u>	6096	5022	1859	<u>2883</u>	<u>6214</u>	<u>8402</u>	<u>17 288</u>	<u>19 856</u>	11 123	4181
0.833	65	<u>760</u>	<u>2065</u>	1474	2504	1279	<u>1391</u>	<u>1843</u>	<u>6003</u>	<u>11 628</u>	10 350	4961
0.917	0	<u>169</u>	0	94	<u>736</u>	<u>1741</u>	777	409	<u>1041</u>	<u>1886</u>	<u>2744</u>	1960
1.000	10	<u>52</u>	46	0	<u>144</u>	<u>1038</u>	856	114	<u>191</u>	106	<u>282</u>	<u>598</u>
1.083	0	<u>26</u>	0	0	0	<u>147</u>	137	0	0	<u>87</u>	39	<u>83</u>
Total	22 360	52 330	47 160	21 580	59 440	112 830	170 310	199 550	142 140	95 860	50 880	38 420

Fecundity and brooding

Despite the presence of females of reproductive size, breeding almost ceased during the summer months, and the production of offspring by the females born in June

did not take place until September, when recruitment was resumed (Fig. 4). In July and August, the proportion of large non-setose females was high.

The smallest incubating females were observed from October to December. Moreover, the large number of

Table 3 *Corophium multisetosum*. Growth estimates for incubating females [L_h modal head length (from Fig. 5); L_t total length (estimated from allometric equation); ΔL_t length increment]

Date	L_h (mm)	L_t (mm)	ΔL_t (mm)	Number of Days	Growth ($\mu\text{m d}^{-1}$)
13 Sep	0.817	6.87			
10 Oct	0.917	7.92	1.05	27	39
07 Nov	0.967	8.46	0.54	28	19
Total			1.59	55	29
07 Dec	0.683	5.50			
05 Jan	0.783	6.52	1.02	29	35
06 Feb	0.833	7.03	0.51	32	16
08 Mar	0.850	7.21	0.18	30	6
05 Apr	0.900	7.74	0.53	28	19
Total			2.24	119	19

small-sized incubating females observed in October indicates that the fastest developing individuals born in September may have attained reproductive size and matured within 1 mo.

The diameter of recently laid eggs varied from 0.30 to 0.35 mm regardless of female size. Juveniles ($L_t \approx 1.0$ mm) were often found inside the marsupium (8% of the examined F_{inc}), sometimes occurring together with earlier developmental stages (1.6% of the examined F_{inc}). Frequently, 1 to 5 sand particles, about the same size of the embryos, were observed inside undamaged marsupia of incubating females (19% of the examined F_{inc}). These grains were also observed inside the marsupia of empty females.

From September to December, 46 to 79% of the females bearing fully setose oostegites were carrying embryos (Fig. 6). The number of incubating females reached a peak in December (17 260 individuals m^{-2} ; 66% of the mature females), and decreased thereafter following the general trend of the population.

More than 50% of all examined incubating females were carrying embryos in an early developmental stage.

Reproductive synchrony was higher in June, September and October, when 71 to 97% of the examined F_{inc} were carrying Stage 1 embryos.

Maximum egg production (number of $F_{inc} \times$ average brood size) occurred from September to December. In October, despite the decrease in the average size of incubating females, brood size remained high. In December, when the largest females disappeared from the population, the average size of the incubating females was further reduced and the brood size decreased. However, the high egg production was maintained through the steep increase in the number of incubating females. Small brood size and low egg production prevailed during the winter, despite the increasing average size of incubating females.

Brood size was related both to the developmental stage of the embryos and the size of the incubating females, but seasonal variation in the size-specific fecundity was also observed (Fig. 7). Highest fecundity was recorded in October, with a mean salinity (high-water/low-water) of 3.5 psu and a mean water temperature of 18 °C. Smaller broods occurred always at lower salinities. Figure 7 presents data on brood size versus head length as a function of water temperature for each sampling occasion: <15 °C (December 1985, January and February 1986), 15 to 20 °C (October and November 1985, March 1986) and >20 °C (September 1985). In general, larger females had larger broods, but the largest broods were laid at temperatures in the 15 to 20 °C range. Smaller broods coincided both with higher and lower water temperatures. However, the average size of incubating females did not show a clear trend in relation to temperature or salinity.

The smaller brood size of females carrying late embryos (F_3) in comparison with females carrying early embryos (F_1) is illustrated in Figs. 7 and 8. Intramar-supial loss of embryos ranged from 16.5 to 39.5%. These values were estimated for different size-classes only when a sufficient number of both F_1 and F_3 females with undamaged marsupia were available (Fig. 8).

Fig. 6 *Corophium multisetosum*. Trends in brood size (average $\pm$ SE) and density of mature females throughout sampling period (F_1 , F_2 , F_3 females with embryos in Stage 1, 2 and 3, respectively; F_j females carrying juveniles; F_e empty setose females)

Fig. 7 *Corophium multisetosum*. Brood size variation in relation to head length of incubating females, development stage of embryos and water temperature ($\circ$ $T > 20^\circ\text{C}$; Δ , $\blacktriangle$ $20^\circ\text{C} > T > 15^\circ\text{C}$; $\square$, $\blacksquare$ $T < 15^\circ\text{C}$) No Stage 3 embryos found at $T > 20^\circ\text{C}$

Discussion

Breeding period and generations

Although incubating females were present all year round in the *Corophium multisetosum* population, recruitment occurred in spring, almost ceased during the summer, peaked in autumn, and decreased again during the winter. The high proportion of large non-setose females during the summer and winter months indicates that the immature females delayed the onset of maturity and/or the breeding females moulted into a resting stage (sexual quiescence), losing the characteristic fringing setae of the oostegites. A resting stage, separating two successive growing seasons, is characteristic of seasonal breeders, especially at high latitudes (Steele 1967). Its functional significance seems to be linked to the need to release the

juveniles at the most appropriate time for successful recruitment (Wildish 1982).

Extreme temperatures and very low salinities during the winter and summer deterred breeding of *Corophium multisetosum*, while moderate temperatures (15 to 20°C) and salinities > 1 psu during the spring and autumn were apparently favourable for reproduction. Under laboratory conditions, breeding occurred only at intermediate salinity values (between 2 and 18 psu) (Ré 1996). In the Ythan estuary, *C. volutator* occupies a wide range of temperature and salinity, but the onset of breeding coincides with an increase in temperature above 7°C , and occurs only where salinity rises above 7.5 psu (McLusky 1968). In northern temperate regions, the reproduction of amphipods is constrained mainly by the low winter temperatures, and the breeding season occurs mainly in late spring and during the summer. As

Fig. 8 *Corophium multisetosum*. Brood size (average $\pm$ SE) of different size-classes of incubating females. Percentage of intramarsupial loss (value above bars) in each size-class was estimated only when sufficient number of females carrying early embryos and females carrying late embryos was examined

latitude decreases, the breeding season widens, but the high summer temperatures may prove a constraint on reproduction. A negative effect of high temperatures (near 30 °C) on breeding of *C. insidiosum* at the Biguglia Lagoon (42°N) was reported by Casabianca (1967). In the population of *C. triaenonyx* at Visakhapatnam (18°N), breeding does not take place in summer, and peaks during the autumn (Shyamasundari 1972), as with *C. multisetosum* at Areão. The good physiological condition of *C. multisetosum* in autumn (Cunha et al. 2000b) certainly favoured the reproductive activities during this period.

The latitudinal variation in temperature enables an extended breeding period, allowing the production of a large number of cohorts and two or more generations per year at low latitudes. Because of the short maturity and brooding times and the possibility of consecutive broods per female, the recruitment in the *Corophium multisetosum* population was practically continuous during the periods of intense breeding. Moreover, females of different sizes, probably from different generations, contributed to the same cohorts, and the cohorts frequently overlapped because of the high growth rates of the juveniles. A more suitable sampling programme, with shorter periods between sampling occasions and using finer sieves to efficiently collect the smaller individuals, is needed to ascertain further details of the life history of *C. multisetosum* in Areão. Given the complexity of amphipod life histories, an agreement in the definition of the terms “brood”, “cohort” and “generation” is essential to enable comparisons of life-history patterns. This terminology, frequently used with different meanings by different authors, was criticised by Moore (1981) as unwieldy and imprecise.

Life span and mortality

Mean longevity of *Corophium multisetosum* in Areão was ~6 mo, but the estimated life span was longer for the overwintering individuals born during the autumn than for those born in spring. A similar seasonal difference was reported by Moore (1981) for the *C. bonnellii* population at Millport. Various populations of *C. insidiosum* displayed a reduction in life span with decreasing latitude and increasing temperature (Table 4). This influence of temperature on longevity was confirmed by the experimental work of Nair and Anger (1979), who reported that an increase of 10 °C shortened the life span of *C. insidiosum* by ~2 mo.

Environmental disturbance, predation and competition may increase mortality risk and lead to life-history adaptations, including shortening the interval between successive broods and reducing female maximum longevity (Fenwick 1984; Jensen and Kristensen 1990; Matthews et al. 1992). The inferred age-specific mortality of *Corophium multisetosum* agrees with the patterns described by Wildish (1982) and Fenwick (1984) for several amphipod species: high juvenile mortality is

followed by a period of high survival and, finally, senescent mortality of adults. Nair and Anger (1979) observed high mortality in juvenile stages (36 to 42%) and again in the last 2 to 4 wk of the total life span of *C. insidiosum*.

During the summer in Areão, the high temperatures and low oxygen content of the water (Cunha and Moreira 1995) probably increase the metabolic costs and reduce longevity of *Corophium multisetosum*. At the end of the summer, the density of adults is drastically diminished and intraspecific competition decreases (see Jensen and Kristensen 1990 for *C. volutator* and *C. arenarium*); this may have contributed to the high recruitment success in September (72.9% of juveniles in the population) in the present study.

Growth and moulting

The estimated growth rates of *Corophium multisetosum* indicate that the daily increment of adult females in Areão is 19 to 29 µm, with lower values during the winter and higher values in autumn. The large increase in the population biomass observed from September to December (Fig. 2) also indicates of high growth rates during this season. On the other hand, the larger average length of incubating females and the small increase in the population biomass during the winter (January to March) may be interpreted as a result of longer maturation periods and slower growth rates. It was estimated that, under favourable temperature conditions, *C. multisetosum* females may take only 1 mo to reach reproductive size, i.e. with a body-length increment from 1.0 to 4.1 mm, representing a maximal growth rate of 100 µm d⁻¹ for the juvenile stages. Furthermore, the length-frequency data implied that length increment per moult is probably higher in males than in females, but that females moult more frequently and achieve a larger body size.

These inferences agree with the results obtained by Nair and Anger (1979) for *Corophium insidiosum*: males underwent 4 to 6 moults and females 8 to 14; the observed daily increment in body length was 30 to 87 µm for the juvenile stages, 14 to 43 µm for the females and 7 to 10 µm for the males. For the same species, Birklund (1977) estimated a daily increment of 40 µm. Growth estimates for *C. sextoni* were 17 µm d⁻¹ (Hughes 1978), and for *C. volutator* 110 to 220 µm d⁻¹ and 80 µm d⁻¹ for juveniles and adults, respectively (Möller and Rosenberg 1982). The latter values are much higher than those estimated for *C. multisetosum*, considering that the two species are about the same size.

Sexual maturity and brooding

The interpretation of the size-structure of the *Corophium multisetosum* population indicated that, at warm temperatures, the fastest growing individuals may attain

Table 4 *Corophium* spp. Reproductive traits at different localities [*S* salinity; *M* marine; *B* brackish; *T* temperature; *G* number of generations; *BP* breeding period; *LS* life span, *MT* maturation time; *BT* brooding time; *RT* residence time; $L_{\min}/L_{\max}$ minimal and maximal body length of incubating females, respectively; *NB* number of broods; *BS* brood size (average numbers in parentheses); *IML* intramarsupial loss; *EØ* embryo diameter; *RS* recruit size]

Species, Locality	S	T (°C)	G	BP	LS (mo)	MT (d)	BT (d)	RT (d)	$L_{\min}$ (mm)	$L_{\max}$ (mm)	NB	BS	IML (%)	EØ (mm)	RS (mm)	Source
<i>C.acherusicum</i>																
North Carolina	36N 76W	M							1.9	6.0	>1	(8)		0.34		Nelson (1980)
Fukuyama Harb.	36N 135E	M									>1	(19)				Onbé (1966) ^b
<i>C.arenarium</i>																
Højer	55N 08E									6.4	?	49				Jensen and Kristensen (1990)
Dovey Estuary	53N 04W	B	2	Apr–Oct	8–13		14	>1	4.6	9.0	>1	(6–22)	26		0.9–1.0	Fish and Mills (1979)
							18	5–7								Vaughan (1938) ^c
<i>C. bonnellii</i>																
Millport	52N 05W	M	2	Apr–Oct	5–10		14		3.4		3	(3–8)	10–27	0.36		Moore (1981)
Millport ^a	52N 05W						10–12	1								Shillaker and Moore (1987)
<i>C. curvispinum</i>																
Lower Rhine	B	5–24	3		9	28										Rajagopal et al. (1999)
<i>C. insidiosum</i>																
Kysing Fjord	57N 09E	B		Apr–Nov					2.0	4.0		4–21		0.21	0.8	Muus (1967)
Holbæk Fjord	56N 12E	18–20	>2	May–Aug		25			1.8	5.0					0.85	Birklund (1977)
Cullercoats	55N 01W	M	2	Jan–Oct	10–12	30–60	11–39	1	1.7	4.4	>1	1–21	5–30	0.28	0.75–0.95	Shearer (1978)
Kiel Bay	54N 10E		3						2.0							Anger (1975) ^d
Helgoland Harb. ^a	45N 08E	29–33	10–20		3–8	29–99	4–17	<1	3.0	5.3	3–7	5–40		0.30–0.42		Nair and Anger (1979)
Arcachon	45N 01W	5–30	5–22	4 Feb–Nov	<12	<30	8–16		2.0	6.0	2	4–25				Labourg (1968)
Biguglia	42N 09W	7–25	5–34	>5 All year	1–2	9–20					>1	5–22			0.8	Casabianca (1967, 1975)
<i>C. sextoni</i>																
Torbay	50N 04W	M	1	Apr–Sep	12				3.0	5.8	>1	1–34			0.75	Hughes (1978)
<i>C. multisetosum</i>																
Dead Vistula	54N 19E	5–7		Apr–Oct					5.0	9.0		17–138		0.30		Jazdzewski (1987)
Ria de Aveiro	41N 09W	0–15	>2	Sep–Jun	5–7				4.1	9.4	>1	8–72	16–40	0.30–0.35	0.8	This study
Ria de Aveiro ^a	41N 09W	5–6				28–49		>1							0.9	Ré (1996)
<i>C. triaenonyx</i>																
Visakhapatnam	18N 83E		3	Aug–Apr	4		6–23		3.0	4.5					1.0	Shyamasundari (1972)
Visakhapatnam ^a	18N 83E	30	10–35		2–5											Shyamasundari and Hanumantha (1974)
<i>C. volutator</i>																
Inner Baltic			1	May–Oct	12		<28		4.5		2–5					Segestråle (1959)
Gullmarsvik	58N 12E	4–30	2	May–Sep	<12	35–50	14		4.0		>1				0.8–0.9	Möller and Rosenberg (1982)
Nivå Bay			4	Apr–Nov	6–12	25–30	19	5	4.0	8.5	1–3	10–70			1.2–1.4	Muus (1967)
Højer	55N 08E									8.3		?	115			Jensen and Kristensen (1990)
Bay of Puck	55N 18E								5.0	9.0		9–66		0.40		Jazdzewski (1987)
Whitby Harb.	54N 01W	22–35	1	Apr–Sep			21	5	5.5	8.5	>1	4–48				Hart (1930)
Dovey Estuary	53N 04W	B	2	May–Oct	8–13	90	14	>1	5.0			(15–54)	26		0.9–1.0	Fish and Mills (1979)
Dovey Estuary	53N 04W	B	2	Feb–Sep	<12	60	>17		5.0	9.0	>1				1.0–1.5	Watkin (1941)
Cumberland	46N 64W	B	2	May–Aug			19		5.4	10.5	>1	10–172			1.0	Peer et al. (1986)

^a Laboratory experiments; ^b Cited by Sainte-Marie (1991); ^c Cited by Shillaker and Moore (1987); ^d Cited by Nair and Anger (1979)

reproductive size and mature within 1 mo. Laboratory reared females took 4 wk to lay their first brood at 22 °C and 7 wk at 10 °C (Ré 1996). Both maturity time (period between the birth of the females and laying of their first brood) and brooding time in *Corophium* species display temperature-related seasonal and latitudinal variations: sexual maturity and embryonic development are accelerated at warmer temperatures. The estimated maturity time for *C. insidiosum* was 30 to 60 d at Cullercoats (Latitude 55°N; temperature = 4 to 13 °C), but in the Biguglia Lagoon (45°N; 5 to 34 °C) it was only 9 to 20 d (Casabianca 1967, 1975; Sheader 1978). The effect of temperature on maturity and brooding time was also confirmed by laboratory experiments with *C. insidiosum* (Nair and Anger 1979) and *C. triaenonyx* (Shyamasundari and Hanumantha 1974).

The minimum size of incubating females in *Corophium* species (Table 4) is about half the maximum size. This wide size range in incubating females implies the occurrence of several moults during maturity and enables possible consecutive broods. A maximum of seven broods was observed for *C. insidiosum* under laboratory conditions (Nair and Anger 1979), and although direct evidence from field populations is scarce, most authors agree that the occurrence of multiple broods is plausible in *Corophium* species.

Lunar rhythmicity of breeding, observed in several *Corophium* populations (Sheader 1978; Fish and Mills 1979), is enabled by the short brooding time, in general ~2 to 3 wk, and the possibility of multiple broods. The high percentage of incubating females carrying embryos in an early developmental stage (F₁) collected during the present study was probably associated with the time of sampling in the lunar cycle (± 2 d around new moon), and may be interpreted as a lunar-induced rhythm. The unfavourable summer conditions constrained breeding and synchronised the timing of reproduction, so that in September the percentage of F₁ females was particularly high. Later in autumn and during the winter, as temperature decreased and brooding time increased, synchrony was progressively lost.

Fecundity, intramarsupial loss and parental care

Brood size in *Corophium multisetosum* was related to the developmental stage of embryos and the size of incubating females, but the results also showed that the observed seasonal variation in fecundity was not solely due to the variation in the average size of incubating females. Several authors have reported seasonal changes in the size-specific fecundity of brackish amphipods (Sheader 1978, 1983; Fish and Mills 1979; Naylor et al. 1988). Environmental factors such as temperature, salinity, photoperiod, oxygen concentration and food availability may be important in determining brood size (Kinne 1959; Vlasblom 1969; Fish 1975; Van Dolah and Bird 1980; Sheader 1983). This issue is further discussed by Cunha et al. (2000a).

Brood size in *Corophium* species is large, and varies according to the maximum size of each species (Table 4). A maximum of 40 embryos was reported for *C. insidiosum* (Nair and Anger 1979), but a higher number was reported for larger species: 138 for *C. multisetosum* (Jazdzewski 1987) and 172 for *C. volutator* (Peer et al. 1986). There is less variation in the size of early embryos and recently hatched juveniles from species to species (Table 4). Corophioids have large broods (relative to their body size) and the smallest embryos among gammaridean amphipods (Sainte-Marie 1991). The observation that the size of recently laid eggs is not related to the size of incubating female in *C. multisetosum* was also verified for *C. bonnellii* (Moore 1981), but not for *C. insidiosum* (Nair and Anger 1979).

The number of early embryos is frequently used for comparisons of brood size, partly because of the variation in intramarsupial losses among amphipods, which can range from 0 to over 50% of the initial number of eggs laid (Moore 1981). Intramarsupial loss in *Corophium multisetosum* is high, but comparable to values estimated for other *Corophium* species (Table 4). The morphology of the oostegites is an important factor for the protection of the eggs and, in the corophiids, the long interlacing setae are essential to the flexibility and reinforcement of the marsupium formed by narrow oostegites (Moore 1981; Leite et al. 1986). Intramarsupial losses may result from accidental spillage caused by somersaulting of the females within the tubes and/or aggressive interactions with other individuals, active removal by the female, and/or decomposition of moribund embryos or unfertilised eggs (Shillaker and Moore 1987). Moore (1981) suggested that the presence of sand grains in the marsupium may also damage the embryos. The presence of sand particles in the marsupia of 19% of the *C. multisetosum* females collected during the present study appears not to have been accidental. Moore mentioned that sand grains were observed in *C. bonnellii* marsupia but never in *Lembos websteri* (the other species considered in his study). However, it remains unknown if sand particles are introduced into the marsupium while females interact with their brood. Shillaker and Moore (1987) described the brooding behaviour of *C. bonnellii* and observed that females interact with their broods, removing or replacing embryos, and are capable of distinguishing embryos of its own species. Moreover, recently hatched juveniles frequently re-entered the marsupium, sometimes assisted by the mother.

Laboratory observations revealed an interval of up to 7 d between the liberation of the first- and last-hatched juveniles in a single brood of *Corophium multisetosum* (Ré 1996). The presence of hatched juveniles in the marsupium has been observed in several *Corophium* species, and the reported residence times of intramarsupial individuals vary between a few hours and 7 d (Table 4). In Areão, a higher percentage of *C. multisetosum* females carried juveniles during the winter, probably because in the warmer months the juveniles are forced to leave the marsupium sooner because of the

higher frequency of moulting and the rapid succession of broods.

Final remarks

Like other *Corophium* species and many low-latitude/warm-water amphipods, *C. multisetosum* population in Areão has a semiannual iteroparous life-history. Multivoltinism, accelerated maturity and short lifespan (resulting in increased reproductive tempo) typify low-latitude/warm-water populations and are also the predicted *r*-selected attributes of species living in shallow, brackish habitats that are frequently disturbed and unpredictable (Greenslade 1983; Southwood 1988; Sainte-Marie 1991). The general trends in the attributes of *Corophium* populations, gathered from published data and summarised in Table 4, support the predicted habitat and latitudinal distribution of life-history patterns. As an example, the comparison of *C. insidiosum* populations from Cullercoats (Sheader 1978) and Biguglia (Casabianca 1967, 1975) clearly shows the wider breeding period, higher number of generations, accelerated maturity and reduced longevity in the latter population from a lower-latitude locality, with higher temperatures and lower salinities. The importance of temperature was also emphasised by Gratto et al. (1983), who ascribed the life-history differences between the *C. volutator* populations of Avonport and Musquash Harbour (same latitude) to the lower temperature ($\sim 10^\circ\text{C}$ less) at the latter locality. Temperature, through its control of metabolic rates and linked effects on reproductive effort, and salinity, through its effect on moulting and reproductive success (Wildish 1982), may be important physiological constraints to reproduction and determinants of life-history patterns of amphipods in estuaries. The life-history pattern and the reproductive features of *C. multisetosum* in Areão showed an important relationship to temperature and salinity, but other environmental conditions such as oxygen content or food availability may also be relevant (see also Cunha et al. 2000a, b). Nair and Anger (1979) allude to the role of the “status of the brood” (origin from an early or late brood of the mother animal), but this characteristic is probably very difficult to assess in wild populations.

In his interesting review on the reproductive bionomics of gammaridean amphipods, Sainte-Marie (1991) concluded that phylogenetic or physiological constraints, and not only selection, may be useful for the interpretation of gammaridean life-history patterns. He found that, among gammaridean amphipods, corophiids and gammarids were unique in retaining iteroparity even at high latitudes, a trait that enhances their reproductive potential, the highest among amphipods. The lack of viable alternatives for a given reproductive trait may be due to phylogenetic constraints (Fenwick 1984). The reproductive bionomics of corophiids is characterised by numerous broods, large brood size (in relation to body size) and small egg size (Sainte-Marie 1991). These traits

contribute to their high reproductive potential, and are probably the reason of their success in colonising coastal habitats where they establish dense and highly productive populations.

References

- Anger K (1975) Benthos und Abwasser. Dissertation, Universität Kiel, Kiel, Germany (Cited by Nair and Anger 1979)
- Birklund J (1977) Biomass, growth and production of the amphipod *Corophium insidiosum* Crawford, and preliminary notes on *Corophium volutator* (Pallas). *Ophelia* 16: 187–203
- Casabianca M-L (1967) Sur la biologie de *Corophium insidiosum* Crawford dans l'étang de Biguglia (Corse). *Bull Soc zool Fr* 91: 401–405
- Casabianca M-L (1975) Méthode de calcul de la production par estimation de la mortalité. Application à une population à structure complexe du crustacé *Corophium insidiosum* Crawford (Lagune de Biguglia, Corse). *C r hebdomadaire, Acad Sci. Paris* 280: 1139–1142
- Cunha MR, Moreira MH (1995) Macroenthos of *Potamogeton* and *Myriophyllum* beds in the upper reaches of Canal de Mira (Ria de Aveiro, NW Portugal): community structure and environmental factors. *Neth J aquat Ecol* 29: 377–390
- Cunha MR, Moreira MH, Sorbe JC (2000a) Predicting amphipod's brood size variation in brackish environments: an empirical model for *Corophium multisetosum* Stock, 1952 (Corophiidae) in Ria de Aveiro (NW Portugal). *J exp mar Biol Ecol* 248: 207–223
- Cunha MR, Moreira MH, Sorbe JC (2000b) The amphipod *Corophium multisetosum* (Corophiidae) in Ria de Aveiro (NW Portugal). II. Abundance, biomass and production. *Mar Biol* 137: 651–660
- Fenwick GD (1984) Life-history tactics of brooding Crustacea. *J exp mar Biol Ecol* 84: 247–264
- Fish JD (1975) Development, hatching and brood size in *Bathyporeia pilosa* and *Bathyporeia pelagica* (Crustacea: Amphipoda). *J mar biol Ass UK* 55: 357–368
- Fish JD, Mills A (1979) The reproductive biology of *Corophium volutator* and *Corophium arenarium* (Crustacea, Amphipoda). *J mar biol Ass UK* 59: 355–368
- Gratto GW, Thomas MLH, Bleakney JS (1983) Growth and production of the intertidal amphipod *Corophium volutator* (Pallas) in the inner and outer Bay of Fundy. *Proc Nova Scotia Inst Sci* 33: 47–55
- Greenslade PJM (1983) Adversity selection and the habitat templet. *Am Nat* 122: 352–365
- Hart TJ (1930) Preliminary notes on the bionomics of the amphipod, *Corophium volutator* Pallas. *J mar biol Ass UK* 16: 761–790
- Hughes RG (1978) Life-histories and abundance of epizotes of the hydroid *Nemertesia antennina* (L.). *J mar biol Ass UK* 58: 313–332
- Jazdzewski K (1987) *Corophium multisetosum* Stock in the southern Baltic – some notes on its morphology, ecology and biology. In: Jazdzewski K, De Broyer C, Stock JH (eds) *Proc. 4th Symposium of the Baltic Marine Biologists*. Sea Fisheries Institute, Gdynia, Poland, pp 245–247
- Jensen KT, Kristensen LD (1990) A field experiment on competition between *Corophium volutator* (Pallas) and *Corophium arenarium* Crawford (Crustacea: Amphipoda) effects on survival, reproduction and recruitment. *J exp mar Biol Ecol* 137: 1–24
- Kinne O (1959) Ecological data on the amphipod *Gammarus duebeni*. *Veröff Inst Meeresforsch Bremerh* 6: 177–202
- Labourg P-J (1968) Cycle reproducteur annuel à Arcachon de *Corophium insidiosum* Crawford, amphipode Corophiidae. *Act Soc linn Bordeaux* 105: 1–16
- Leite FPP, Wakabara Y, Tararam AS (1986) On the morphological variations in oostegites of gammaridean species (Amphipoda). *Crustaceana* 51: 77–94

- Matthews SL, Boates JS, Walde SJ (1992) Shorebird predation may cause discrete generations in an amphipod prey. *Ecography* 15: 393–400
- McLusky DS (1968) Some effects of salinity on the distribution and abundance of *Corophium volutator* in the Ythan estuary. *J mar biol Ass UK* 48: 443–454
- Möller P, Rosenberg R (1982) Production and abundance of the amphipod *Corophium volutator* on the west coast of Sweden. *Neth J Sea Res* 16: 127–140
- Moore PG (1981) The life-histories of the amphipods *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards in kelp holdfasts. *J exp mar Biol Ecol* 49: 1–50
- Muus BJ (1967) The fauna of Danish estuaries and lagoons. *Meddr Danm Fisk-og Havunders* 5: 1–316
- Nair KKC, Anger K (1979) Life cycle of *Corophium insidiosum* (Crustacea, Amphipoda) in laboratory culture. *Helgoländer wiss Meeresunters* 32: 279–294
- Naylor C, Adams J, Greenwood P (1988) Population dynamics and adaptive sexual strategies in a brackish water crustacean, *Gammarus duebeni*. *J Anim Ecol* 57: 493–507
- Nelson WG (1980) Reproductive patterns of gammaridean amphipods. *Sarsia* 65: 61–71
- Onbé T (1966) Observations on the tubicolous amphipod *Corophium acherusicum* Costa in Fukuyama Harbor area. *J Fac Fish Anim Husb Hiroshima Univ* 6: 323–338 (cited by Sainte-Marie 1991)
- Peer DL, Linkletter LE, Hicklin PW (1986) Life history and reproductive biology of *Corophium volutator* (Crustacea: Amphipoda) and the influence of shorebird predation on population structure in Chignecto Bay, Bay of Fundy, Canada. *Neth J Sea Res* 20: 359–373
- Queiroga H (1990) *Corophium multisetosum* (Amphipoda: Corophiidae) in Canal de Mira, Portugal: some factors that affect its distribution. *Mar Biol* 104: 397–402
- Rajagopal S, van der Velde G, Paffen BGP, Bij de Vaate A (1999) Growth and production of *Corophium curvispinum* G.O. Sars, 1895 (Amphipoda) an invader in the lower Rhine. In: Schram FR, von Vaupel Klein C (eds) *Crustaceans and the biodiversity crisis*. Vol. 1. Brill, Leiden, pp 457–472
- Rê A (1996) Estudo da utilização de *Corophium multisetosum* (Amphipoda: Corophiidae) na avaliação ecotoxicológica de sedimentos estuarinos e marinhos. MSc thesis. Universidade de Aveiro, Aveiro, Portugal
- Sainte-Marie B (1991) A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. *Hydrobiologia* 223: 189–227
- Segestråle SG (1959) Synopsis of data on the crustaceans *Gammarus locusta*, *Pontoporeia affinis* and *Corophium volutator* (Amphipoda Gammaridea). *Commentat biol* 20: 1–23
- Shearer M (1978) Distribution and reproductive biology of *Corophium insidiosum* (Amphipoda) on the north-east coast of England. *J mar biol Ass UK* 58: 585–596
- Shearer M (1983) The reproductive biology and ecology of *Gammarus duebeni* (Crustacea: Amphipoda) in southern England. *J mar biol Ass UK* 63: 517–540
- Shearer M, Chia F-S (1970) Development, fecundity and brooding behaviour of the amphipod, *Marinogammarus obtusatus*. *J mar biol Ass UK* 50: 1079–1099
- Shillaker RO, Moore PG (1987) The biology of brooding in the amphipods *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards. *J exp mar Biol Ecol* 110: 113–132
- Shyamasundari K (1972) Studies on the tube building amphipod *Corophium triaenonyx* Stebbing from Visakhapatnam Harbour. Annual life cycle. *Riv Biol* 65: 203–216
- Shyamasundari K, Hanumantha R (1974) Effect of temperature on embryonic and post-embryonic stages of *Corophium triaenonyx* Stebbing (Crustacea, Amphipoda). *Broteria (Ser Ciênc nat)* 43: 187–194
- Southwood TRE (1988) Tactics, strategies and templets. *Oikos* 52: 3–18
- Steele VJ (1967) Resting stage in the reproductive cycles of *Gammarus*. *Nature, Lond* 214: p 1034
- Van Dolah RF, Bird E (1980) A comparison of reproductive patterns in epifaunal and infaunal gammaridean amphipods. *Estuar cstl mar Sci* 11: 593–604
- Vaughan AK (1938) Studies on the biology of certain species of the amphipod genera *Corophium* and *Bathyporeia*. MSc thesis. University of Wales, UK (cited by Shillaker and Moore, 1987)
- Vlasblom AG (1969) A study of a population of *Marinogammarus marinus* (Leach) in the Oosterschelde. *Neth J Sea Res* 4: 317–338
- Watkin EE (1941) The yearly life cycle of the amphipod, *Corophium volutator*. *J Anim Ecol* 10: 77–93
- Wildish DJ (1982) Evolutionary ecology of reproduction in gammaridean Amphipoda. *Int J Invert Reprod* 5: 1–19