

Postembryonic development of *Aapseudes heroae* and *Allotanaais hirsutus* (Tanaidacea, Crustacea) in Magellanic and sub-Antarctic waters

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Abstract: *Aapseudes heroae* Sieg, 1986 (Family Aapseudidae) and *Allotanaais hirsutus* (Beddard, 1886) (Family Tanaidae) are common Tanaidacea of the southern Magellanic region. The aim of the investigation is to elucidate the postmarsupial development of these tanaid species that differ in their biogeography. Population structures are analysed from size frequency data and from different postembryonic stages of specimens collected in the Atlantic entrance of the Beagle Channel and from the Atlantic continental slope to the south-east. The population of *Aapseudes heroae* shows three age groups, the one of *Allotanaais hirsutus* probably at least three. Some large specimens indicate that the latter sub-Antarctic species might reach an age of several years. Both species are probably gonochoristic, and protandric hermaphroditism was not observed. The fecundity of *Aapseudes heroae* and *Allotanaais hirsutus* was analysed. No significant correlation could be found between cephalothorax width and egg number or number of larvae. For both species hypothetical life cycles are reconstructed. As sub-Antarctic temperatures are low and seasonality is strong in the Magellanic region, it is possible that these species are reasonably adapted in reproduction as shown in some polar species of Isopoda and Cumacea.

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Introduction

Tanaidaceans are an almost entirely marine order of the Peracarida, whose species diversity usually increases with increasing water depth. Families such as Leptocheiliidae exhibit protogynous hermaphroditism with up to four different male stages (Sieg 1984), but the life histories and postembryonic stages of most species of Tanaidacea are not well known. In the Antarctic species from the peracarid order Isopoda tend to grow and develop more slowly than those from boreal regions. Wägele (1988, 1990) assumes that this might be due to the influence of low temperatures and high seasonal input of nutrients. Sub-Antarctic and Antarctic Euphausiacea species tend to grow more slowly and possibly to a larger maximum size with increasing latitude (Siegel 1987). Corey (1981) describes a similar relationship between the development of Arctic Cumacea and temperature and seasonality.

It is possible that Antarctic Tanaidacea may show similarities in their development to these peracarid species but, so far, studies of their population dynamics and postmarsupial development have only been undertaken for subtropical, boreal and one Antarctic species (e.g. Bückle-Ramírez 1965, Messing 1983, White 1987, Hamers & Franke 2001, Błażewicz-Paszkowycz 2001) or deep sea Tanaidacea (Gardiner 1975). For the first time,

morphometric investigations of the postmarsupial development and population structure of the two sub-Antarctic species of Tanaidacea, *Aapseudes heroae* Sieg, 1986 (Aapseudidae) and *Allotanaais hirsutus* (Beddard, 1886) (Tanaidae) have been carried out. Our paper attempts to construct a hypothetical life cycle for these two species.

Materials and methods

The specimens came from five stations in the southern Magellanic region. Three were located at the Atlantic entrance of the Beagle Channel and sampled during the Italian-Chilean-German expedition “Joint Magellan” on board FS *Victor Hensen* in October/November 1994. Two stations lying off the Atlantic continental slope were sampled during the expedition ANT XIII/4 on the RV *Polarstern* from March to May 1996. The standard sampling gear was a modified epibenthic sledge (EBS) (Rothlisberg & Percy 1977, Brandt & Barthel 1995) with the exception of station 40/117, where a small dredge was used. Both epi- and supranet had a mesh size of 500 µm in the forenet and a 300 µm mesh size in the cod end. The mouth opening of the nets measured 1 m. For stations and further information see Fahrbach & Gerdes (1997) and Arntz & Gorny (1996).

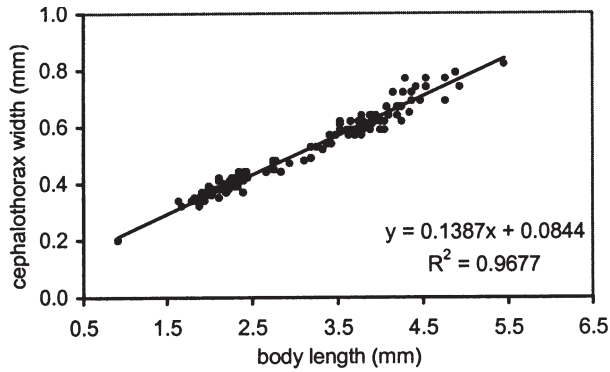


Fig. 1. *Aapseudes heroae*. Relationship between cephalothorax width and body length.

Morphometric measurements

Morphometric measurements were taken of individuals of both species. For consistency only frontal head parts of fragments were counted and considered; the maximal cephalothorax width was determined for all specimens using a Wild M5 stereomicroscope. Additional measurements of total body length were taken from a subset of specimens, (length from tip of rostrum to caudal end of pleotelson). Cephalothorax width was easier to measure than its length, as it was less often damaged and less vaulted. Moreover, biased measurements could be reduced in *Aapseudes heroae*, because the rostrum of this species was deflexed to a varying extent. Measurements were carried out with an accuracy of 0.014 mm at x56 and 0.025 mm at x32 magnification.

As cephalothorax width and body length were significantly correlated in both tanaid species (Figs 1 & 2), the width was used as a measure for the length-frequency distributions of the different stages. The advantage of this measurement was that fragments of the peraeon could also be considered, even if the pleon was broken.

STATISTICA was used to perform the regression analysis with Pearson's correlation coefficient (R). The regression

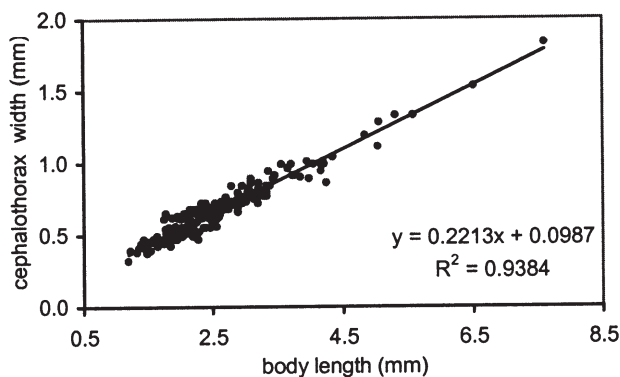


Fig. 2. *Allotanaeis hirsutus*. Relationship between cephalothorax width and body length.

analysis for 123 specimens of *Aapseudes heroae* gave a R value of 0.9837 with a significance of $P < 0.0001$. The regression analysis for 231 specimens of *Allotanaeis hirsutus* showed a correlation coefficient of 0.9687 after Pearson, again with $P < 0.0001$.

In order to be able to analyse the population structure and composition of both tanaid species, and to consider also potential measuring errors, individuals were grouped into three different cephalothorax width size classes of 0.03 mm increments. Numbers of specimens from stations 1200, 1206 and 1213 were standardized to 1000 m² hauls. For the length-frequency measurements of *Allotanaeis hirsutus* from stations 40/110 and 40/117 the absolute (total) numbers were used.

Postmarsupial development

Sex, developmental and fecundity stages of all specimens were identified, and special morphological characters, such as cheliped shape were documented. In ovigerous females with a marsupium, the number of eggs, embryos or manca 1 stages were identified. Determination of the different postmarsupial developmental stages followed the definitions of Gardiner (1975), Johnson (1982), Messing (1983) and Sieg (1984).

A few damaged individuals could not be definitely assigned a sex or developmental stage and it was impossible to identify individuals with damaged oostegite-bearing pereonites either as juveniles or as females. Under similar conditions, fragments of *Allotanaeis hirsutus* could be defined as female stages due to the cheliped morphology. Due to damage in some cases it was impossible to discriminate between preparatory, "intermediate" or copulatory female stages.

Analysis of composite length-frequency distributions

Analyses of length-frequency data were carried out to find evidence for the existence of potential age groups in the populations of *Aapseudes heroae* and to relate these to the occurrence of developmental stages over the life cycle of the species. The analysis was based on the Macdonald & Pitcher (1979) approach, which tries to separate the single components (normal distributions) of a distribution mixture with the help of the interactive computer software 'MIX'. During this stepwise optimising process means, standard deviations and proportions of the various components are modified until the iterations result in a significant fit between the expected and the observed distribution mixture. The fit is checked by a Chi-square test. In those cases where a significant result cannot be obtained, the input parameters or the number of underlying normal distributions have to be changed. For the composite length-frequency distribution all stations were combined after standardizing data to 1000 m² hauls of the different stations to start from a

quantitative, representative sample of the population. It was intended to analyse the structure of the populations to gain evidence for their possible postmarsupial development.

Fecundity

Fecundity was defined as mean number of eggs per ovigerous female. It was calculated according to Masunari (1983) for *Leptochelia savignyi* (Krøyer, 1848) by the sum of all eggs in the marsupium of each female and later the division by the number of ovigerous females. Females with a damaged marsupium had possibly lost eggs and were excluded, as were females with embryos or manca 1 stages. Fecundity was also calculated using Messing's definition (1983), i.e. the median number of offspring per female, including eggs and retained manca stages. For the regression analysis between fecundity and cephalothorax widths females with a damaged marsupium were excluded because eggs were obviously lost.

Results

Stages of postmarsupial development

Of 343 individuals of *Apseudes heroeae*, 136 specimens were males, 95 females, 74 juveniles, and 32 manca stages. Males, preparatory females (prep♀), copulatory females (cop♀), and juveniles, manca 2 stages and manca 1 stages could be discriminated. Hermaphroditism was not evident as none of the males possessed oostegites, and none of the females showed a male sexual bulb. Only one male showed heterochely, one with typically enlarged, the other small and of juvenile form. Five individuals from stations 1200 and 1213 could not be attributed to either immature males, manca 2 stages or juveniles.

Of 1652 individuals of *Allotanaeis hirsutus* 57 were males, 26 females, and 1507 juveniles. Sixty-three individuals could not be definitely attributed to the juvenile or a female stage, as pereon segments were lacking. Manca stages were absent. The "intermediate female stage" (int♀) as described by Johnson (1982) could not be identified definitively, because no females with scars from lost oostegites were observed nor were females found with male sexual bulbs or males with rudimentary oostegites.

Three additional moulting stages could be differentiated within the preparatory females on the basis of the oostegite size, as in the postembryonic development described for *Tanaeis dulongii* (Audouin, 1826) (Johnson 1982, White 1987, Hamers & Franke 2001). The largest specimen collected was a male of 7.61 mm length.

Analysis of the length-frequency distributions

The composite length-frequency distribution covered all developmental stages including males and females for the

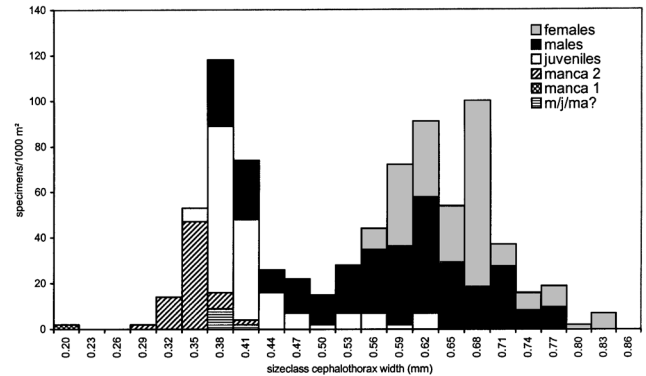


Fig. 3. *Apseudes heroeae*. Length-frequency distribution in November 1994 (southern spring). m/j/ma? = damaged specimens, of which stage could not be determined definitely (males, juveniles or manca 2).

larger size classes (Fig. 3). But the distribution-mixture analysis yielded poor estimates at the 5% significance level. The single female length class of 0.68 mm was strongly over-represented, whereas the neighbouring classes were strongly under-represented. Due to this suspected measurement bias it was decided to run the same analysis excluding the female stage, the results of which are summarized in Table I.

It appears that *Apseudes heroeae* has at least three normal distributions present in the length-frequency data (Fig. 4). The first normal distribution/age group consisted of mancae 2, juveniles and small males, with a cephalothorax width of 0.38 to 0.47 mm. The second normal distribution was mainly represented by larger males and females (if they were included in this size range). The frequency of juveniles decreased for these size groups (mean of 0.57 mm). Juveniles were absent from the third normal distribution. These size classes around 0.69 mm are dominated by males and females. In general the manca stage only occurs in the very first age group, while the juvenile phase extends into the second age group. A few males (and probably females) occur for the first time in age group 1, but they do not dominate the population before age group 2. After they reached the adult stage they even survived for another age group.

Allotanaeis hirsutus was the dominant tanaidacean species

Table I. Results for the components of the interactive fitting of mixtures of length-frequency distributions of *Apseudes heroeae* (excluding females).

	Mean length L (mm)	s.e. (m) (standard error of mean)	SD (standard deviation of mean)	s.e. (standard error of standard deviation)
normal distribution1	0.371	0.0023	0.032	0.00018
normal distribution2	0.569	0.0300	0.066	0.00210
normal distribution3	0.692	0.0610	0.050	0.00220

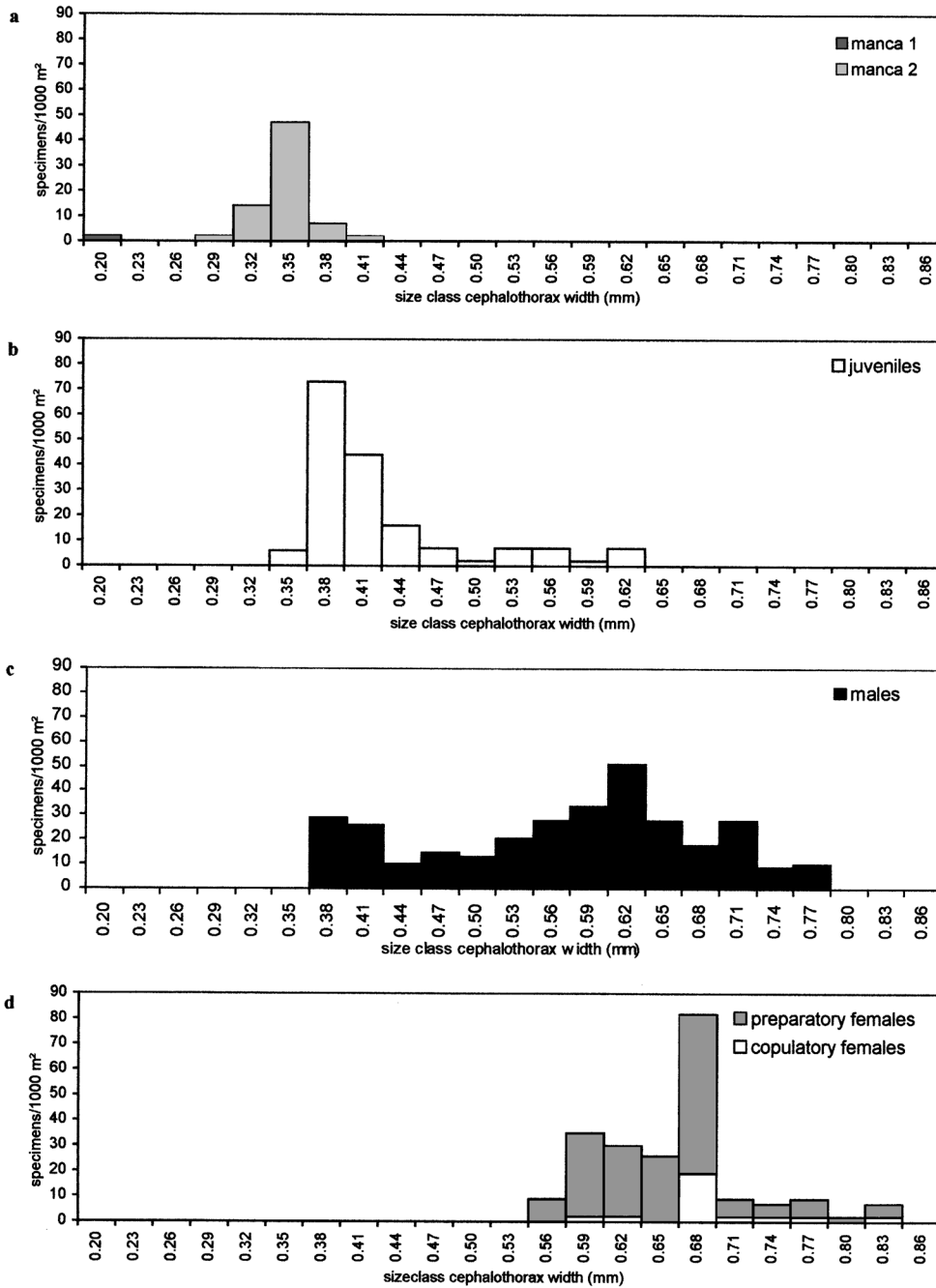


Fig. 4. *Aapseudes heroeae*. Length-frequency distribution of the single stages/sexes in November 1994 (spring), **a.** manca-stages, **b.** juveniles, **c.** males, and **d.** females.

in the November samples. However, the distribution mixture analysis was not able to separate different normal distributions due to the dominating influence of the first normal distribution and the very low numbers of specimens in the larger size classes (Figs 5–7). The size classes 0.38 to 0.71 mm consisted almost exclusively of juveniles (Figs 5 & 6). However, there are indications that a second mode in the length-frequency distribution occurred around 0.96 mm, which could not be clearly separated using this method. This became more obvious if the older stages were treated separately from the juvenile of the size classes (Fig. 6). Small adult males and females were of similar size to juveniles (0.47 to 0.68 mm), whereas the larger size

classes of 0.74 to 0.98 mm may be attributed to a second age group. Single specimens were found of 1.64 to 1.82 and 1.97 mm size, which may indicate age groups beyond the second age group.

The distribution pattern clearly demonstrates the dominance of the juvenile stage with a modal size of 0.68 mm. Only a few larger preparatory stages occur in the samples, while female size classes overlapping with juveniles are completely missing (for comparison see Fig. 5).

Fecundity

Table II shows the cephalothorax widths, numbers and

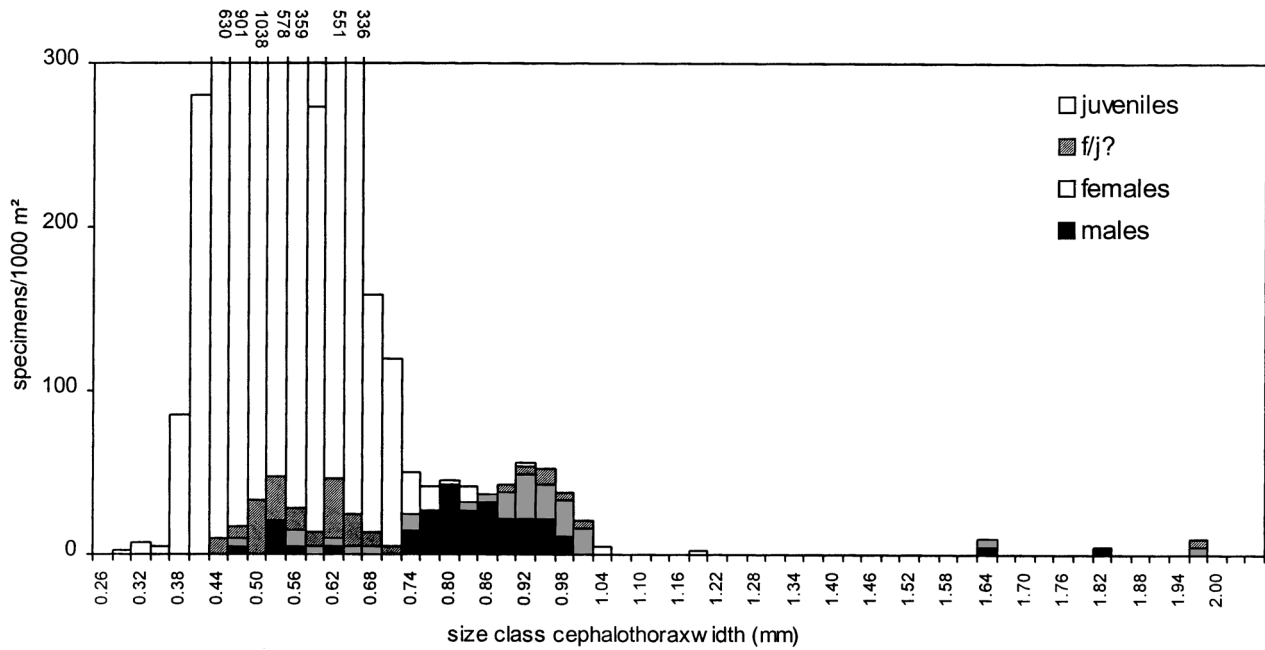


Fig. 5. *Allotanis hirsutus*. Length-frequency distribution of all specimens from stations 1200, 1206 and 1213 from November 1994 (southern spring). flj? = damaged specimens, of which stage could not be determined definitely (females or juveniles).

stages of copulatory females of *Apseudes heroae* and *Allotanis hirsutus*. These are the absolute numbers at stations 1200 (*Apseudes heroae*) and 1206 (*Allotanis hirsutus*), and it was only at these stations that copulatory females of these species were sampled. Females with brood pouch embryos (= BPE) or manca 1 stages were only found for *Apseudes heroae*, and not for *Allotanis hirsutus*. Ovigerous females of *Apseudes heroae* carried 9 to 15 eggs in their marsupia. Three had 9–12 BPEs in their brood pouches. Only one female was found with two individuals of manca 1 stages. Masunari's (1983) definition of fecundity was 12 for *Apseudes heroae*, if those females with only four eggs in the marsupia were neglected (some eggs were probably lost due to a damaged marsupium). Whilst *Apseudes heroae* has only one brood sac, females of *Allotanis hirsutus* possess two brood sacs. So egg numbers of females with only one brood sac were excluded. Average fecundity for *Allotanis hirsutus* was 27 eggs per female but ranged from 19 to 31 eggs in both brood sacs, with 8 to 18 eggs in single brood sacs. One additional single detached brood sac was found to contain 21 eggs.

Possibly due to insufficient data no significant correlation could be found between cephalothorax width and egg number or number of larvae for *Apseudes heroae*. The suspected positive correlation between number of eggs and larvae and cephalothorax width could not be verified statistically (Table II).

Egg bearing females of *Allotanis hirsutus* show no significant relationship between cephalothorax width and total numbers of eggs (Fig. 9, Table II). In the Tanaidae, brooding females generally bear two brood pouches, into

which the eggs are released. For an additional analysis only that brood pouch was considered, which showed the highest number of eggs. Then with increasing female size (Fig. 9) a decrease in egg numbers was observed.

Discussion

Population structure

Figure 4a shows that the manca 2 stage in *Apseudes heroae*

Table II. *Apseudes heroae* and *Allotanis hirsutus*. Number of eggs, BPEs (= brood-pouch-embryos) or manca 1 stages in marsupium of copulatory females and their cephalothorax width.

<i>Apseudes heroae</i>			<i>Allotanis hirsutus</i>			
width (mm)	number of eggs	brood stage	width (mm)	eggs in left broodsac	eggs in right broodsac	total eggs
0.59	0	-	0.55	15	15	30
0.62	4	eggs	0.56	13	18	31
0.67	12	BPEs	0.90	15	14	29
0.67	9	BPEs	0.91	16	14	30
0.67	2	manca I	0.91	14	14	28
0.69	12	BPE	0.94	15	14	29
0.69	13	eggs	0.94	10	9	19
0.69	12	eggs	0.99	14	14	28
0.69	9	eggs	0.99	14	15	29
0.69	0	-	0.99	10	14	24
0.72	4	eggs partly lost	1.01	12	13	25
0.74	12	eggs	1.01	lacking	13	
0.78	12	eggs	1.65	8	lacking	
0.82	15	eggs	cephalothorax lacking	10	11	21
			torn single broodsac		21	

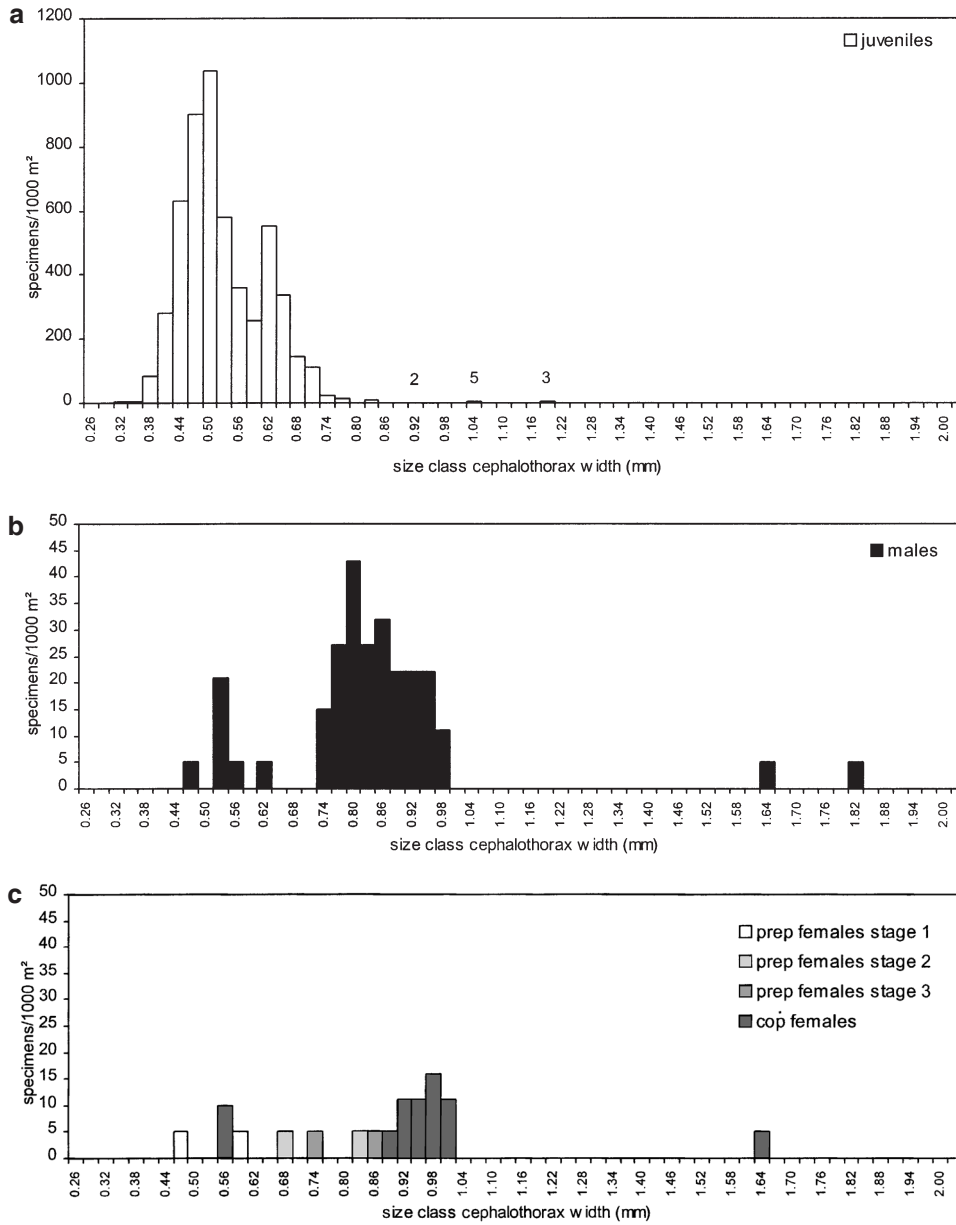


Fig. 6. *Allotanis hirsutus*. Length-frequency distribution of the single stages/sexes from stations 1200, 1206 and 1213 from November 1994 (southern spring); **a.** juveniles, **b.** males, **c.** females, prep = preparatory, cop = copulatory.

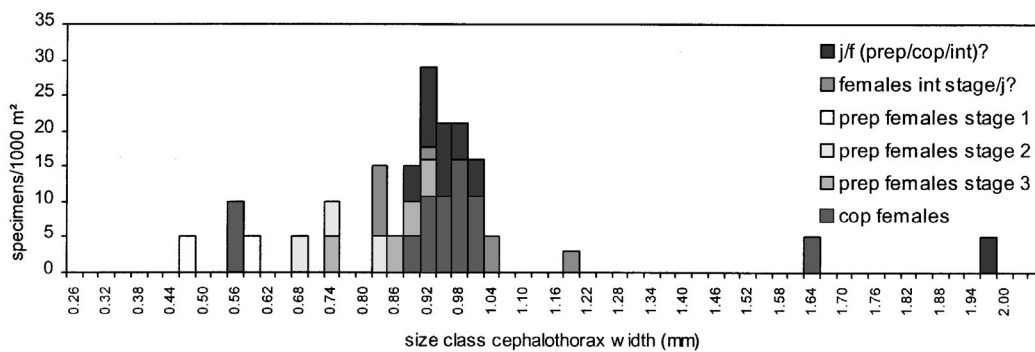


Fig. 7. *Allotanis hirsutus*. Length-frequency distribution of all females from stations 1200, 1206, and 1213 from November 1994 (southern spring) with their several stages of adolescence: int-stage? = probably females of intermediate stage (= “large juveniles”), prep = preparatory, cop = copulatory, j/f (prep/cop/int?) = juveniles or females, of which stage could not be determined definitely (preparatory, copulatory or, intermediate stage).

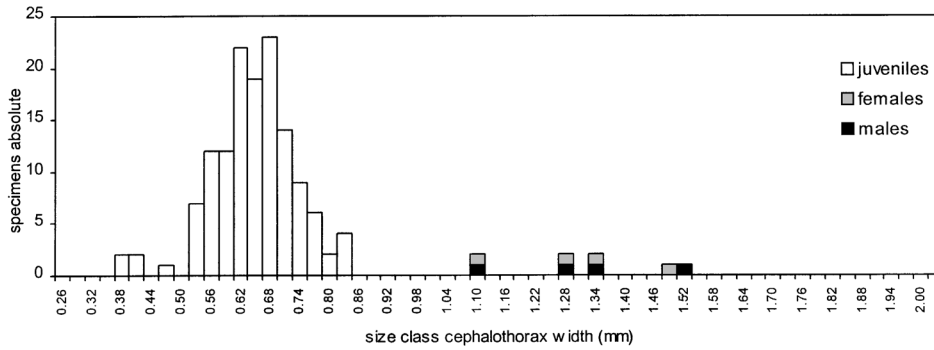


Fig. 8. *Allotanais hirsutus*. Length-frequency distribution for the population of stations 40/110 and 40/117 in May 1996 (southern autumn), absolute numbers of specimens.

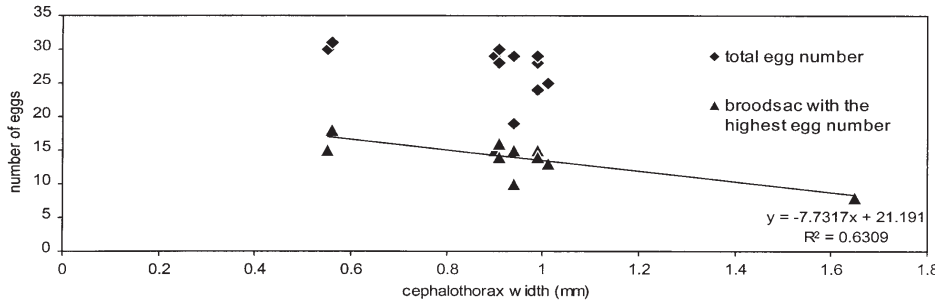


Fig. 9. *Allotanais hirsutus*. Relationship between the total number of eggs of copulatory females and the width of the cephalothorax and relation between the number of eggs in the broodsac with the highest egg number in each case of copulatory females and the width of the cephalothorax.

was represented by a single mode in the overall length-frequency distribution, corresponding with the pattern given by Messing (1983) and probably applying to most Tanaidacea (Sieg 1972, 1984). The occasional observation of a slight differentiation in the cheliped, the length composition of juveniles (Fig. 4b) and the wider range of cephalothorax widths indicates that juveniles have two moulting stages. Two or possibly three juvenile instars have been documented by Messing (1983) for *Pagurapseudes largoensis* McSweeney, 1982 (Family Pagurapseudidae). Most Tanaidacea show two separate juvenile stages, juvenile 1 and juvenile 2. Whilst the first cannot yet be attributed to any sex, the second stage develops female gonads and should therefore be defined as "immature". However, this differentiation can only be identified histologically (Sieg 1984).

Preparatory females of *A. heroae* had a cephalothorax width of ≥ 0.56 mm. Most probably the juvenile 2 stage is followed by two preparatory female instars before the initial copulatory stage as in *P. largoensis* (Messing 1983).

Interestingly, the first normal distribution within *A. heroae* length frequencies includes males from size class 0.38 mm onwards along with frequent juveniles and manca 2 stages. It is possible that some manca 2 stages develop directly into males whereas others moult into a juvenile-1 stage (sex undetermined) before they become males, as in *P. largoensis* (compare Messing 1983). Whilst these small males of *A. heroae* show no cheliped differentiation, possess pleopods and a sexual bulb, the isochelous postmanca male instars of *P. largoensis* do not develop pleopods. Because Messing (1983) did not study gonadal maturation he could not properly attribute certain instars to

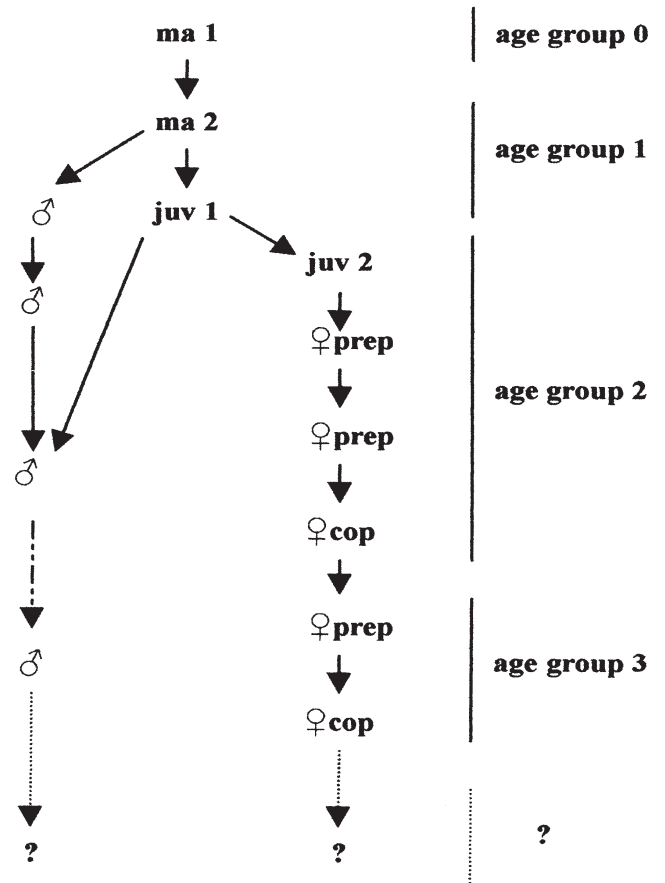


Fig. 10. Possible life cycle of *Apseudes heroae*. ma = manca, juv = juvenile, cop = copulatory stage, prep = preparatory stage, dashed/dotted lines = several moultings.

preparatory or copulatory male stages. After two additional subsequent moults the postmanca males of *P. largoensis* develop heterochely and pleopods like the other postjuvenile males. They also moult up to 14 times during their postmarsupial development. The large range of cephalothorax widths for *A. heroae* (Fig. 4c) suggests that these males also moult several times. The increasing cheliped differentiation with length makes this assumption more likely. They probably develop from manca stage 2 or juvenile stage 1 and moult throughout their lives as in *P. largoensis*.

D.B. Fonseca (personal communication 2002) believes that within the species *Kalliapseudes schubartii* Mañé-Garzón, 1949, two male types exist with a puberty moult. Mañé-Garzón, 1949 noted differences in the cheliped morphology, and considered type II males to be the reproductive male phase. In *Aapseudes chilensis* Chilton, 1923 Vengayil *et al.* (1988) discriminate between “preparatory” and “copulatory males”, considering the different chela size to represent two different types of secondary males, indicating protogyny (see below). However, a male development with successive chelipedal differentiation (fig. 3, page 101) as in *P. largoensis*, could be an alternative explanation. For *A. heroae* it is difficult to decide at which stage males develop into copulatory stages without histological investigations. We can only assume that copulatory males develop synchronically with adult females. If this was true, these males should show a cephalothorax width of about 0.56 mm like females. Immature males possibly moult to copulatory ones in the second year (Figs 3 & 10).

In *Allotanaeis hirsutus* manca 1 and 2 stages as well as females with BPEs were lacking in the samples, with only egg-bearing females present. *Allotanaeis hirsutus* populations contained neither manca stages nor females with larvae from autumn (Fig. 8), and only preparatory females were sampled. Unfortunately, Shiino (1978), Delille *et al.* (1985) and Sieg (1986) do not describe stages of *A. hirsutus*.

According to evidence from *T. dulongii* (Audouin, 1826) (Johnson 1982, Sieg 1984, White 1987) Fig. 6a shows only one juvenile stage to be present in *A. hirsutus*. Histological studies of these juveniles, however, might reveal different stages. Hamers & Franke (2001) document in females of *T. dulongii* 2–5 and in males 1–3 neutrum stages histologically. *Allotanaeis hirsutus* shows three moulting stages within precopulatory females as does *T. dulongii* (Johnson & Attramadal 1982, White 1987, Hamers & Franke 2001). However, Hamers & Franke (2001) observe 1–3 additional juvenile female instars with minute oostegites before the preparatory phase.

Many of the specimens classified as juveniles of *A. hirsutus* are rather large (cephalothorax width of 0.59–1.19 mm), overlapping with females (Figs 5 & 6a). The second mode in the length-frequency and the several

larger individuals in Fig. 6a might be females in the intermediate stage, which Johnson (1982) described for *T. dulongii*, and Gardiner (1975) for the Neotanaidae. These individuals of *A. hirsutus* bear no scars at coxal plates indicating the loss of oostegites. Here histological investigations would be necessary (Hamers & Franke 2001). There exists confusion over the instar after the copulatory stage, when ovisacs are lost after manca release (intermediate stage). Johnson & Attramadal (1982) describe one intermediate female moulting instar with oostegite scars after the copulatory female stage, whilst White (1987) concluded that those females lacking oostegites/ovisacs are late stage copulatory instars, not separate moulting instars. Observations of Borowsky (1983) and Hamers & Franke (2001) confirm this. Following the first copulatory stage after White (1987) females in *T. dulongii* develop only two preparatory (here intermediate) stages before moulting to the second copulatory female instar. The term “intermediate stage” in White (1987) may lead to confusion here, because this stage had oostegites and corresponded to the “preparatory stage.”

The differences in investigations on laboratory cultured *T. dulongii* (Johnson & Attramadal 1982, White 1987, Hamers & Franke 2001) show that sequences and numbers of developmental stages might vary and probably depend on laboratory environmental conditions.

Thus those size classes > 0.56, but without external morphological characteristics, probably belong to the female stage but appear to be juveniles.

Analysis of the length-frequency distribution

A polymodal length-frequency distribution is usually an indication of the existence of several normal distributions within a mixture. In Crustacea this usually indicates either different moult stages or different age groups in samples. Moulting stages usually hardly overlap in their length-frequency composition, but generally represent a sequence of normal distributions similar in their width to the relatively narrow standard deviation (e.g. Childress & Price 1978). Assuming that the reproductive period and the growth season in temperate or polar species are short compared to the annual cycle (e.g. Mauchline & Fisher 1969, Siegel 1987), we can expect a cohort passing through the population to have a normal length distribution. Furthermore, if we find several moult stages under one normal distribution of the length-frequency, it is most likely that they represent different age groups. In species living for more than one year, growth normally slows for older animals/age groups, and consequently the normal distributions of older age groups would finally overlap in the length-frequency distribution of the population. Each normal distribution would then represent one age group.

The analysis of the population length-frequency distribution of *Aapseudes heroae*, without females, consisted

Table III. Fecundity of several species of Tanaidacea, as number of eggs, BPEs or manca 1 stages in the marsupium (partly from Messing (1983); updated). Ø = average.

family	species	reference	number
Apseudidae	<i>Apseudes latreillei</i> Milne Edwards, 1840	Salvat 1967	60
	<i>A. heroae</i> Sieg, 1986	this paper	9–15 (Ø 12)
Metapseudidae	<i>Synapseudes idios</i> Gardiner, 1973	Gardiner 1973	5–11
	<i>Metapseudes aucklandiae</i> Gardiner, 1973	Gardiner 1973	9
Pagurapseudidae	<i>Pagurapseudes largoensis</i> McSweeney, 1982	Messing 1983	4–17
Leptocheliidae	<i>Heterotanais oerstedii</i> (Krøyer, 1842)	Bückle-Ramírez 1965	6–16
Tanaidae	<i>Tanais dulongii</i> (Audouin, 1826)	Johnson & Attramadal 1982	up to 46
	<i>Allotanais hirsutus</i> (Beddard, 1886)	this paper	19–31 (Ø 27)
Pseudotanaidae	<i>Cryptocope abbreviata</i> G.O. Sars, 1868	Greve 1965	7
Anarthruridae	<i>Leptognathia breviremis</i> Lilljeborg, 1864	Greve 1965	3–8

of three normal distributions. The first component contained manca 2 stages, juveniles and males, (which develop over at least 2–3 moults), and represents the first age group, i.e. the one year old animals. Assuming that offspring are produced annually and considering the fact that large females carry well developed larvae in their marsupia (which are age group 0), we conclude that the subsequent age groups are two- and three-year old specimens.

In the second year of their life cycle almost all individuals moult to males or females, so only a few juveniles were present in the samples. In the third year of the life cycle only males or females were found.

Sex-ratios and fecundity

The sex ratio of *A. heroae* shows almost a 1:1 male: female relationship in southern spring, similar to *P. largoensis* (Messing 1983). Jazdzewski (1969) assumes that the individuals with heterochely in *Heterotanais oerstedii* (Krøyer, 1842), a hermaphrodite, are intermediate stages between male and female. Only one male of *A. heroae* had different chelipeds, and this was considered to be due to developmental anomalies. Whilst Leptocheliidae may show protandric hermaphroditism and develop one primary and three secondary male stages, Apseudomorpha are primarily gonochoristic (Sieg 1984). Because of fully developed mouthparts in males of *A. heroae* and the sex ratio 1:1, *A. heroae* probably only has gonochoristic males.

For *A. hirsutus* the sex ratio cannot be given exactly since a reliable count of females was not possible. Johnson (1982) documents for *T. dulongii* a sex ratio of 6:1 in favour of females in summer. For the Brazilian species *Zeuxo coralensis* Sieg, 1980 females dominated almost throughout the year (Masunari & Sieg 1980).

The fecundity of *A. hirsutus* and *A. heroae* is similar to that of other Tanaidacea (Table III). Besides the Spelaeogriphacea the Tanaidacea are a peracarid taxon with low fecundity (Messing 1983). In several Tanaidacea, i.e. *Leptochelia dubia* (Krøyer 1842) or *L. savignyi* (Krøyer 1842), the number of eggs increases linearly with female size (Mendoza 1982, Masunari 1983), a feature also found

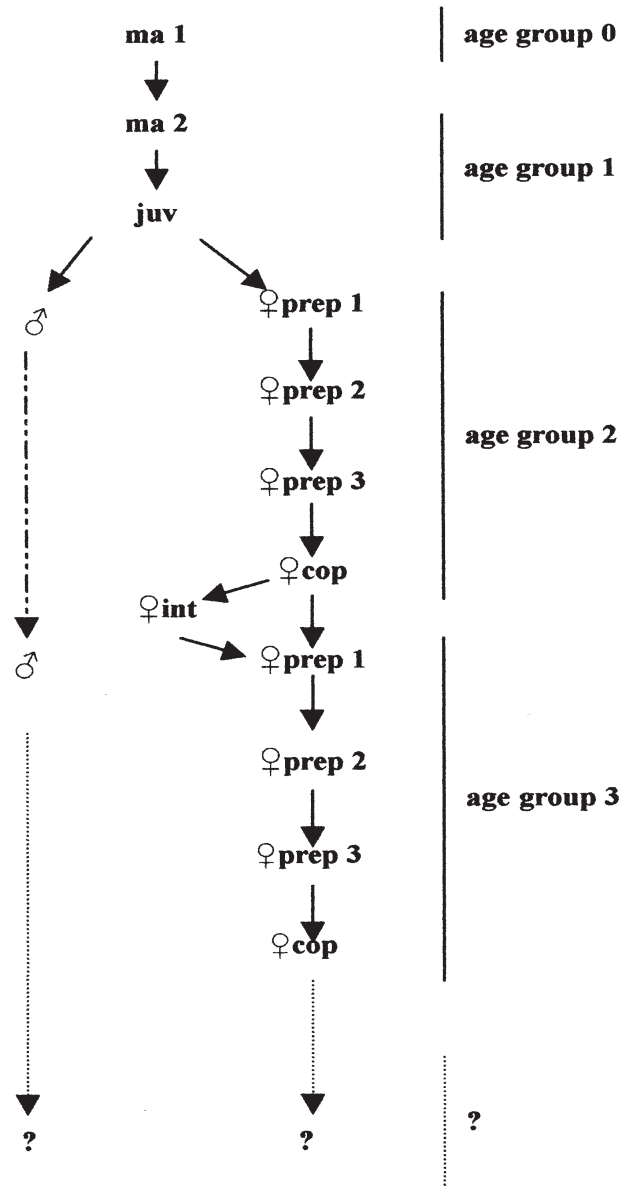


Fig. 11. Possible life cycle of *Allotanais hirsutus*. ma = manca, juv = juvenile, cop = copulatory stage, prep = preparatory stage, int = intermediate stage, dashed/dotted lines = several moultings.

in many Cumacea (Corey 1981). The observed decrease of egg numbers with increasing female size in *A. hirsutus* (Fig. 9) seems to be unusual. The egg diameter does not increase with increasing cephalothorax length.

Life cycles

The limited sampling allows only a hypothetical construction of the life cycle for the two species. That *A. heroae* shows all stages of the postembryonic development at the same time allows several options. One is that this species reproduces continually throughout the year, like the subtropical *P. largoensis*, whilst an alternative is that the intermoult periods are prolonged so that the complete developmental cycle to copulatory specimens cannot be performed during one year. If the latter is true, manca 1 stages must leave the marsupium at a time when food availability is favourable, in southern spring or in summer. As the southern Magellan region is characterized by low sub-Antarctic temperatures and strong seasonality (Hartmann-Schröder & Hartmann 1962, Brattström & Johansen 1983), it seems more prudent to assume a prolonged seasonally adapted lifecycle. Investigations of the reproductive biology and postmarsupial development of Antarctic isopods (Wägele 1987, 1988, 1990) show that their life cycles are prolonged compared to closely related species from boreal or more temperate regions. Arctic Cumacea also have a longer life span and tend to mature at higher ages than species from subtropical or tropical waters (Corey 1981). The fact that in the southern autumn no copulatory females of *A. hirsutus* with eggs were present in the samples, but only precopulatory stages, might indicate that the development of these stages takes at least half a year. Under these circumstances copulatory females are present in the spring samples (October/November), with manca stages released in summer.

Since the length-frequency distribution of *A. hirsutus* shows some very large males (up to a length of 7.61 mm) and females, both in spring and in autumn, this might indicate that this species can reach an age of several years. Beddard (1886) found sub-Antarctic specimens of *A. hirsutus* with lengths up to 9 mm. Błazewicz-Paszkowycz (2001) assumed that the complete life cycle of the west Antarctic species *Nototanais antarcticus* lasts at least two years.

Messing (1983) observed that intermoult duration subsequently increased. Under laboratory conditions males of the subtropical species *P. largoensis* lived up to 15 months and passed through about 14 instars, whilst life span of females were estimated at nine months. In nature the intermoult periods were shorter, giving estimated life spans of seven months in females, and between nine and ten months in males.

Figures 10 & 11 summarize schematically the proposed

developmental sequence for *A. heroae* and *A. hirsutus*. Manca 1 stages of *A. heroae* are released in spring/summer and represent the O-group (less than one year of age).

This is the first attempt to describe the postmarsupial development of sub-Antarctic species of Tanaidacea. These reconstructions of the life cycles of *A. hirsutus* and *A. heroae* are preliminary but offer a basis for future sampling to test their reliability.

Future perspectives

The present paper is based on only two species of Tanaidacea from different stations, sampled within a short period of time. Thus there is little direct evidence with regard to seasonal development of the different life-history stages. Future research needs to collect a time-series at a specific location throughout the year, supplemented by laboratory experiments on growth. The present study also indicated difficulties in the identification of juvenile stages versus immature stages. Since internal development seems to precede changes in external morphology, histological studies would probably be advantageous.

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