

POLISH POLAR RESEARCH	22	1	35–44	2001
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## Remarks on the population structure of two Antarctic peracarid crustaceans: *Eudorella splendida* Zimmer, 1902 (Cumacea) and *Nototanais antarcticus* (Hodgson, 1902) (Tanaidacea)

**ABSTRACT:** This paper presents preliminary data on the population structure of two Antarctic crustaceans *Eudorella splendida* and *Nototanais antarcticus*, commonly occurring in Admiralty Bay (South Shetland Islands). From analysis of the material studied it can be concluded that *N. antarcticus* is a progynous hermaphrodite with a life cycle lasting at least two years. The life cycle of *E. splendida* lasts probably 3–4 years. It is a semelparous species, but some females after brooding moult and revert into the intermediate stage.

**Key words:** Antarctic, Peracarida, Cumacea, Tanaidacea, population structure.

### Introduction

Cumacea and Tanaidacea, as other members of the Peracarida, carry their eggs and larval stages in the marsupium (brood pouch) formed by the epipodites of the pereopoda, the oostegites. Both groups have epimeric development. In the marsupium the larvae moult three times, with the last larval stage called manca being similar to the adult but devoid of the last pair of peraeopods (McLaughlin 1980). Manca moult at least once (usually 2 times, maximum 5 times) resulting in a juvenile stage. In Tanaidacea juveniles are often called neutrum. These individuals can not reproduce even though they superficially resemble a female. Juveniles usually pass through one preparatory stage (occasionally two or three) becoming finally, a copulatory (= mature) instar with fully developed secondary sexual characters. Fe-

males of the iteroparous species, after hatching manca, moult and proceed to next brooding. Successive copulatory stages are separated by one or two (rarely three) precopulatory instars (= intermediate stages).

Hermaphroditism has never been observed in cumaceans (Duncan 1984) but has been observed in the Tanaidacea and originally called progyny (Forsman 1956, Lang 1958). In some tanaid species two types of males are known (Bückle-Ramirez 1965, Jazdzewski 1969). Smaller, so called gonochoric males, develop directly from the manca stage while larger individuals (progynous) can develop in three ways: (I) from unfecundated females, (II) from females, which moulted after reproduction, and (III) from females which became precopulatory females after reproduction and which after the next moult change into males.

The developmental biology and life histories of Cumacea and Tanaidacea are rather poorly known. Life cycles were described for only few cumacean species (Forsman 1938, Krüger 1940, Harada 1967, Corey 1969, Gnewuch and Crocker 1973, Corey 1976a, b, Granger *et al.* 1979, Bishop 1982, Duncan 1984, Persson 1989). Only few tanaid life cycles were analysed (Lang 1953, 1958, Bückle-Ramirez 1965, Jazdzewski 1969, Makkavyeyeva 1970, Masunari 1983, Messing 1983, Modlin and Harris 1989). To date no life history study of any Antarctic cumacean has been published. One such study, devoted to the postmarsupial biology of Antarctic tanaids, *Heterotanais antarcticus* Lang, 1953, was published by Lang (1953). It was based on one sample and excluded the possibility of observation for sex reverse.

## Material and methods

Materials for the present study were collected during several Polish Antarctic Expeditions to the *H. Arctowski* Station (Admiralty Bay, King George Island, South Shetlands) in the years 1977–93. Sampling was performed using a dredge or Van Veen grab. In this material two peracarid crustaceans were comparatively abundant: *Eudorella splendida* Zimmer, 1902 (Cumacea) and *Nototanais antarcticus* Hodgson, 1902 (Tanaidacea). The length of all specimens in the sample were measured to the nearest of 0,1 mm. *E. splendida* was measured from the tip of the pseudorostrum to the the end of the telson, while *N. antarcticus* was measured from the tip of the rostrum to the end of the pleotelson. Males, females, and manca were determined along with specific developmental stages.

Based on classification of Duncan (1984) for *E. splendida* five developmental groups were distinguished: (I) manca, (II) nonmarsupial females (including preparatory and intermediate stages of Duncan's classification), (III) marsupial females, (IV) juvenile males and (V) mature males. The sex of individuals smaller than 3.5 mm (in some cases larger) was difficult to determine. Because they are superficially similar to preparatory females these specimens were included as non-

marsupial females. A part of the material was damaged; therefore only a few females were ovigerous.

For *N. antarcticus* five groups were also distinguished: (I) manca, (II) non-copulatory females (without oostegites), (III) precopulatory females (with rudimental oostegites), (IV) copulatory females (with developed brood pouches) and (V) males. The brood pouches of individuals in last category were usually empty (regardless on the season), but this is supposedly an artefact.

## Results and discussion

The materials used for the present population analysis of *Eudorella splendida* and *Nototanais antarcticus* are heterogeneous and incomplete. The author had at her disposal not a set of single year-round regularly sampled materials but rich samples collected in different years, in various parts of Admiralty Bay and using different equipment. Taking into account the nearly constant water temperature at the bottom of Admiralty Bay throughout the year, mostly between  $-1.5$  and  $1^{\circ}\text{C}$  (Lipski 1987), and further considering light and primary production as the main factors influencing the life cycle, the data from various years were set in a season's sequence.

The author is aware that the presented analysis does not make a classical life cycle. However, taking into account the poor knowledge of the life cycle of Antarctic tanaids and cumaceans, even such preliminary results seem to be worth publishing.

### Population structure of *Eudorella splendida*

Histograms of the population structure of *E. splendida* are presented in Fig. 1. Mancas in the population of *E. splendida* were observed from December until the beginning of March; those from the December samples represented two cohorts (2 mm and 3.5 mm). Nonmarsupial females with a body length from 4.5 to 8.5 mm were found in all months from December to May, but in April, and in May they were represented by two cohorts: 4.5–5.5 mm and 6–8.5 mm. Marsupial females were observed from December to May, however they were less abundant in December and January than at the end of March, April, and May. In the end of January juvenile males were more abundant than mature males while these proportions were reversed in March, April and May. At the end of March and in December specimens with a body length of 8.5 mm were observed: these were juvenile males and nonmarsupial females larger than mature males and marsupial females respectively.

From this analysis it can be concluded that *E. splendida* most likely begins to reproduce in December/January. Males die after reproduction, as mature males were not found at the beginning of January. Females live longer than males due to

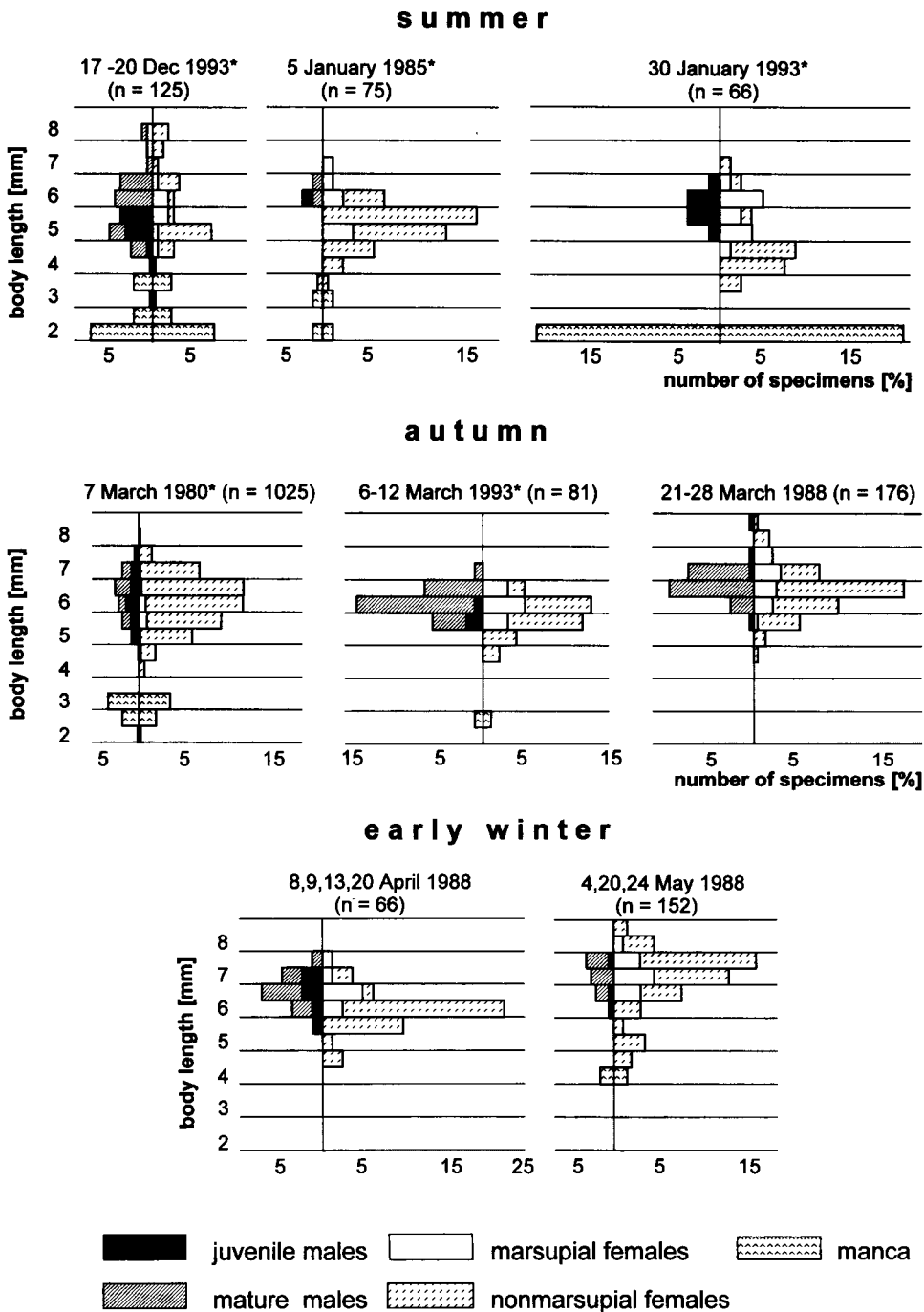


Fig. 1. Population structure of *Eudorella splendida* Zimmer, 1902. \* Van Veen sample. Explanation of categories in legend see Material and methods.

their holding embryos in marsupium and die most likely in February. Manca develop successively, becoming nonmarsupial (= preparatory) females with a body size of 4.5–5.5 mm in early winter. In each month nonmarsupial females, both small and large, constituted a significant percentage of the population. The length of time for development of gonads and the gametogenesis of Antarctic Cumacea is not known. Bishop and Shalla (1994) suggested that the development of gonads of a deep-water species *Leucon profundus* Hansen, 1920 lasts 8 months. Assuming a similar development time for *E. splendida*, gametogenesis would be completed in the next reproductive year and copulation would take place in early summer, i.e., in the third reproductive year. Bishop and Shalla (1994) showed that the development of manca in *L. profundus* lasts 12–15 months, with larvae potentially leaving the marsupium in the beginning of the next reproductive year (i.e. in the beginning of 4th reproductive year). Such a life history model, if assumed for *E. splendida*, would not explain the presence of juvenile males in January and mature males in March. One could rather suggest that fertilisation takes place at the end of summer (second reproductive season). Therefore the gametogenesis of *E. splendida* is probably completed in March and mancas would occur in January/ February in the next (third) reproductive season.

Data on the biology of the Cumacea indicate that their life cycle depends on water temperature; therefore breeding periods of different species occur in various seasons. Forsman (1938) and Krüger (1940) observed that the population of the cold-water species *Diastylis rathkii* (Kröyer, 1841), found at depths of 13–20 m, reproduces from October to February, i.e., the coldest period in the Northern Hemisphere. The same species, living in a depth range of 30 to 180 m, where the water temperature is generally lower, reproduces almost all year. Year-long reproduction was also observed for *Leucon nasica* (Kröyer, 1941), an Arctic – boreal species which is found in constant water temperatures of 1.6°C (Granger *et al.* 1979). Corey (1981), summarising the knowledge of some Cumacea occurring in temperate, Subarctic, and Arctic waters concluded that most of the species living in temperate waters have a one year life cycle and reproduce once or twice during their life times. For *Cumopsis goodsiri* (Van Beneden, 1861), living in the shallow waters of Europe, Corey (1969) observed two generations: winter and summer ones. The winter generation matures in spring and reproduces twice, producing a summer generation in May and a next winter generation in October. The summer generation of *Cumopsis goodsiri* quickly matures and also reproduces twice, producing another summer generation in July/August and another winter generation in October. Therefore the winter population of *C. goodsiri*, appearing at the end of summer, comes from both the previous winter generation as well as from the summer generation.

Duncan (1983, 1984), who studied the life history of *Almyracuma proximoculi* Jones *et* Burbanck, 1959, presented different observations. Similar to Corey (1969, 1976a, b, 1981), Duncan noticed winter and summer generations. The winter generation, consisting of females fertilised in the fall, becomes the summer generation

in the next season. That summer generation quickly matures and reproduces in summer, giving rise to a winter population. Although *A. proximoculi* has two breeding periods per year (in spring and fall), it is a semelparous species.

Corey (1981) observed that the Arctic cumacean *Diastylis goodsiri* (Bell, 1855) has a three-year life history, with reproduction taking place once, in the third year. Bishop and Shalla (1994) presented similar results. They measured the rate of development of ovaries and embryos in the marsupium and observed that the deep-water species *Leucon profundus* had a minimum life history of three years. Models of the life span proposed for *D. goodsiri* and *L. profundus* appear similar to that of *E. splendida*. The length of gametogenesis and development of embryos in this species are not known, so it is difficult to conclude the length of its life cycle, although the population studied would indicate that these cumaceans have a 3–4 year life cycle.

Cumacean males die after copulation, whereas cumacean females live at least to the moment of manca hatching. Corey (1969) observed that some females were able to produce a second brood after moulting, together with regeneration of their reproductive systems. This was also noted in populations of other cumaceans where, after a peak of breeding activity, clearly larger individuals were found (Gnewuch and Crocker 1973, Corey 1976a,b, Granger *et al.* 1979, Bishop 1982, Duncan 1984). A similar situation is observed in the population of *E. splendida*. Along with mature males and marsupial females (body size 4–6 mm) larger nonmarsupial (= intermediate) females (body length 7.5–8.5 mm) and juvenile males were observed. According to Corey (1969) these larger individuals did not die after brooding, but moulted and reverted to the nonmarsupial (= intermediate) stage. Corey (1976b) mentioned that 2% of the population of *Diastylis sculpta* Sars, 1871 could produce a second brood.

### Population structure of *Nototanais antarcticus*

In the population of *Nototanais antarcticus* (Fig. 2) mancas less than 1 mm and of 1.5 mm in length were observed from November to March. Although their developmental stage (manca 1 or manca 2) was not determined, these two growth classes evidently represented two successive moults. Noncopulatory females were present in the population in each month. Also precopulatory females and males were observed in each month, but the number of males in the population was insignificant in May. The reverse was true for copulatory females. They were found in each month beginning from February and their number in the population was clearly higher in May. In May copulatory females lacked eggs, but 18 broods that seemed to be intact contained 10–20 eggs. Copulation likely occurs in March when copulatory females appear in the population. Males probably die in late summer, but fertilised females overwinter and reproduce in early summer. Also non-copulatory females without oostegites survive winter and probably change into progynous males the following spring.

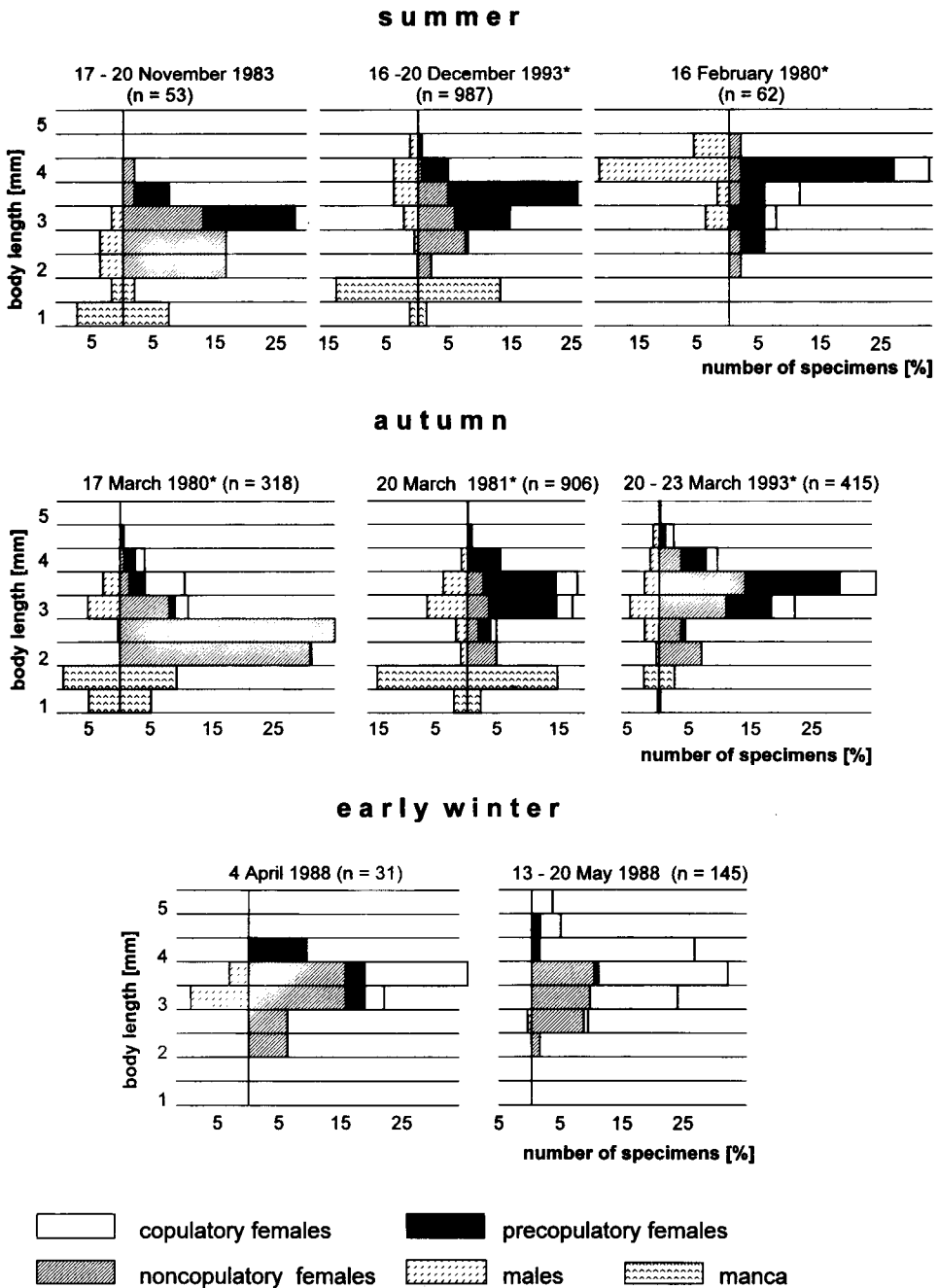


Fig. 2. Population structure of *Nototanais antarcticus* (Hodgson, 1902). \* Van Veen sample. Explanation of categories in legend see Material and methods.

The population structure (Fig. 2) of *N. antarcticus* suggests that mancas leave the marsupium in early summer. Lang (1953) observed another Antarctic tanaid, *Heterotanais antarcticus* (Paratanaidae), and found that females, after reproduction, moult twice and again become a precopulatory instar (= intermediate stage). The first precopulatory stage is devoid of oostegites while the second has rudimentary oostegites. Also two precopulatory instars were observed by Messing (1983) in the life cycle of the tropical species *Pagurapseudes largoensis* McSweeney, 1982 (Pagurapseudidae), although in contrast to *N. antarcticus* and *H. antarcticus* both precopulatory instars had rudimentary oostegites.

As mentioned earlier the males of Tanaidacea can develop in two ways: (I) directly from manca and/or juvenile that is superficially similar to females (gonochoric males) and (II) from females after their reproduction, after hatching of mancas (progynous males). This phenomenon was observed by many authors and was usually related to the number of males in the population. In the case of an absence or low number of males in the population the ability to reverse sex arises (Bückle-Ramirez 1965, Highsmith 1982, 1983, Stoner 1986, Modlin and Harris 1989). However, gonochoric males can appear in the population when the abundance increases (Modlin and Harris 1989). The data presented in Fig. 2 does not suggest *N. antarcticus* is a progynous hermaphrodite; however Makkavyeyeva (1970) and Messing (1983) have shown that all taxa with males that have a rudimentary digestive system, also have the same developmental strategy. Therefore it is probable that *N. antarcticus* is a progynous hermaphrodite. In the model of the life cycle of *Hargeria rapax* (Harger, 1879) presented by Modlin and Harris (1989), small gonochoric males appeared early in the reproductive period, while progynous individuals were present in almost each month of the cycle. However, Makkavyeyeva (1970) observed in *Leptochelia savignyi* (Kröyer, 1842) that gonochoric males were present in summer and fall, while progynous individuals were present only in spring. The presence or absence of gonochoric and progynous males in the population of *N. antarcticus* (Fig. 2) would be related to the model proposed by Modlin and Harris (1989): small gonochoric males (body length 2.5 mm) are present only in the beginning of the reproduction period while progynous individuals occur during the entire summer (from December to April).

In April and May, specimens for the present analysis were collected by a dredge with a relatively large mesh size, so it is quite probable that the absence of mancas in these months is an artefact of the sampling method. Therefore it cannot be excluded that *N. antarcticus* winters also as a manca stage. The presence in November of noncopulatory females as well as mancas indicates such a possibility.

The present incomplete material does not allow the author to precisely evaluate the length of the life cycle of *N. antarcticus*; more observations are needed to assess it definitely. However, it seems to be out of question that the complete life cycle of this common west Antarctic species lasts at least two years.



**Acknowledgements.** — Thanks are due to my two colleagues: Dr. Piotr Presler and Dr. hab. Jacek Siciński for making material available for this study. I am also very grateful to Prof. Dr. hab. Krzysztof Jazdzewski for critical comments offered during the preparation of this paper.

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Received January 30, 2001

Accepted March 25, 2001

## Streszczenie

Artykuł przedstawia wstępne dane na temat struktury populacji dwóch antarktycznych gatunków *Eudorella splendida* i *Nototanaeis antarcticus* pospolicie występujących w Zatoce Admiralicji (Szetlandy Południowe). Analiza materiałów pozwala wnioskować, że *N. antarcticus* jest progynicznym hermafrodytą, którego cykl życiowy trwa przynajmniej dwa lata. Drugi z badanych taksonów, *E. splendida*, jest gatunkiem semelparycznym i ma prawdopodobnie 3–4 letni cykl życiowy.