

This is an Accepted Author Manuscript of an article published in CBM-Cahiers de Biologie Marine on 26 January 2024, available online:

<https://doi.org/10.21411/CBM.A.F7E539FB>.

1 **A smaller species releases proportionally larger juveniles in *Apseudes***
2 **(Crustacea: Peracarida: Tanaidacea)**

3

4 Keiichi KAKUI*, Chizue HIRUTA

5

6 *Department of Biological Sciences, Faculty of Science, Hokkaido University, Sapporo*

7 *060-0810, Japan*

8

9 *Corresponding author: Keiichi Kakui; kakui@eis.hokudai.ac.jp; Faculty of Science, Hokkaido

10 University, N10 W8 Kita-ku, Sapporo 060-0810, Japan

11

12 Running titles. Juveniles in two *Apseudes* species

13 **Abstract:** We compared the body size (carapace width, CW) of the first free-living instar
14 individuals, or manca 2, and of the smallest ovigerous individuals, between two
15 simultaneously hermaphroditic tanaidacean species, *Apseudes nipponicus* Shiino, 1937 and
16 *Apseudes* sp. The former species is 2.2 times larger, with a CW of 2.61 mm in the smallest
17 ovigerous individual, compared to 1.17 mm in the latter. Average CWs of manca 2 individuals
18 were 0.51 mm (*A. nipponicus*; n = 3, 0.50–0.51 mm) and 0.38 mm (*Apseudes* sp.; n = 9, 0.38–
19 0.39 mm), meaning that *A. nipponicus* manca 2 were 20% as large as the smallest ovigerous
20 individuals, whereas those of *Apseudes* sp. were 32% as large. The proportionally larger
21 juveniles in the smaller species are consistent with the hypothesis that *Apseudes* sp. is
22 progenetic, achieving earlier maturation as females.

23

24 **Keywords:** Apseudidae • manca • life history • Malacostraca • simultaneous
25 hermaphrodite

26 Large size differences among congeneric species are common in Peracarida (Crustacea:
27 Malacostraca), such as in the genera *Neognathophausia* in Lophogastrida (Pequegnat, 1965),
28 *Bathynomus* in Isopoda (Lowry & Dempsey, 2006), and *Apseudes* in Tanaidacea. In *Apseudes*,
29 *A. nipponicus* Shiino, 1937 is relatively large (Fig. 1A), with a body length (BL) of around 12
30 mm at first spawning; in contrast, *Apseudes* sp. sensu Kakui & Hiruta (2013) (hereafter
31 “*Apseudes* sp.”) is relatively small (Fig. 1C), with a BL of around 5 mm at first spawning (Kakui
32 & Hiruta, 2023). Both species are simultaneous hermaphrodites (Kakui & Hiruta, 2013,
33 2023).

34 Upon finding that masculinization in chelipeds was slighter in *Apseudes* sp. (the
35 smaller species) than in *A. nipponicus* (the larger species), Kakui & Hiruta (2023) suggested
36 that *Apseudes* sp. might be progenetic, achieving earlier maturation as females by reducing
37 resource allocation to male secondary traits and growth. This raised the further question
38 whether the large size difference between the species is evident earlier in ontogeny.

39 To address this question, we compared the body size of manca-2 individuals between
40 *A. nipponicus* and *Apseudes* sp. Manca 2 is the stage at which individuals are released from
41 the female brood pouch (i.e., the first free-living instar stage), characterized by lacking
42 pleopods and any traces of pereopod 6, and having pereonite 6 similar in size to a pleonite
43 (Larsen, 2003). As a proxy for body size, we measured the carapace width (CW) of the manca
44 2 individuals, because accurate measurements of BL are difficult due to deformation or
45 lateral curvature of the body. CW correlates well with BL, and the slope of the regression line
46 between BL and CW is the same in the two species (Kakui & Hiruta, 2023). For *A. nipponicus*,
47 three captive-bred mancae 2 were measured; these were descendants of individuals
48 collected in 2015 from an experimental aquarium at the Shimoda Marine Research Center,
49 University of Tsukuba (see Kakui et al., 2017) and had been fixed and preserved in 70%
50 ethanol in 2015. For *Apseudes* sp., nine captive-bred mancae 2 were measured; these were
51 descendants of individuals collected in 2009 and 2010 in the Port of Nagoya Public Aquarium,

52 Japan (see Kakui & Hiruta, 2013) and were fixed and preserved in 99% ethanol on 7 June
53 2023. For both species, we used data from Kakui & Hiruta (2023) on CW in postmanca
54 developmental stages (OL, oostegite lacking; Pr, preparatory; Ovi, ovigerous).

55 Body size is larger in *A. nipponicus* than in *Apseudes* sp. at both the manca 2 and
56 ovigerous stages, though the size difference is greater at the ovigerous stage. Average CWs
57 for mancae 2 were 0.51 mm (0.50–0.51 mm, $n = 3$) for *A. nipponicus* and 0.38 mm (0.38–
58 0.39 mm, $n = 9$) for *Apseudes* sp. (Fig. 1E); the value in the former was thus about 1.3 times
59 that in the latter. The CW of the smallest ovigerous individual was 2.61 mm in *A. nipponicus*
60 and 1.17 mm in *Apseudes* sp. (Kakui & Hiruta, 2023); CW in the former was about 2.2 times
61 that in the latter. The *A. nipponicus* manca 2 is 20% the size of the smallest ovigerous stage,
62 whereas the *Apseudes* sp. manca 2 is 32%. Compared to *A. nipponicus*, *Apseudes* sp.
63 releases relatively large mancae 2.

64 Relatively few studies have provided size data on both mancae 2 and the smallest
65 ovigerous individuals for species in Apseudidae (e.g., Schmidt et al., 2002; Esquete et al.,
66 2012; Kakui et al., 2019). We are unaware of any previous comparison of the size difference
67 between the manca 2 stage and the smallest ovigerous individuals among congeneric
68 apseudid species. Our observation of a smaller species releasing proportionally larger
69 juveniles, however, should be treated with caution, as our data are limited and knowledge
70 on reproduction and life cycles among apseudids remains insufficient. Many abiotic/biotic
71 factors, such as temperature, age, intermolt lengths, or growth increment per molt, may
72 affect the size of eggs or hatchlings and the length of the period from the juvenile to
73 ovigerous states. In any case, producing relatively large mancae 2 is consistent with the
74 hypothesis that *Apseudes* sp. is progenetic.

75

76 **Acknowledgements**

77 We thank Shin Tochinal for providing breeding facilities and Matthew H. Dick for reviewing

78 the manuscript and editing our English. This study was supported by the Japan Society for
79 the Promotion of Science (JSPS) under KAKENHI grants JP19K06800 to KK and JP20J40122 to
80 CH.

81

82 **References**

83 Esquete P., Bamber R. N., Moreira J. & Troncoso J. S. 2012. Redescription and postmarsupial
84 development of *Apseudopsis latreillii* (Crustacea: Tanaidacea). *Journal of the Marine*
85 *Biological Association of the United Kingdom*, 92: 1023–1041. Doi:
86 10.1017/S0025315411002086

87 Kakui K. & Hiruta C. 2013. Selfing in a malacostracan crustacean: why a tanaidacean but not
88 decapods. *Naturwissenschaften*, 100: 891–894. Doi: 10.1007/s00114-013-1079-5

89 Kakui K. & Hiruta C. 2023. Differential masculinization of the chelipeds in two simultaneously
90 hermaphroditic *Apseudes* tanaidaceans (Crustacea: Malacostraca). *Zoologischer*
91 *Anzeiger*, 305: 23–27. Doi: 10.1016/j.jcz.2023.05.004

92 Kakui K., Suzuki A., Nakano H. & Kohtsuka H. 2017. Habitat of a tanaidacean *Apseudes*
93 *nipponicus* Shiino, 1937. *Bulletin of the Kitakyushu Museum of Natural History and*
94 *Human History Series A (Natural History)*, 15: 1–3.

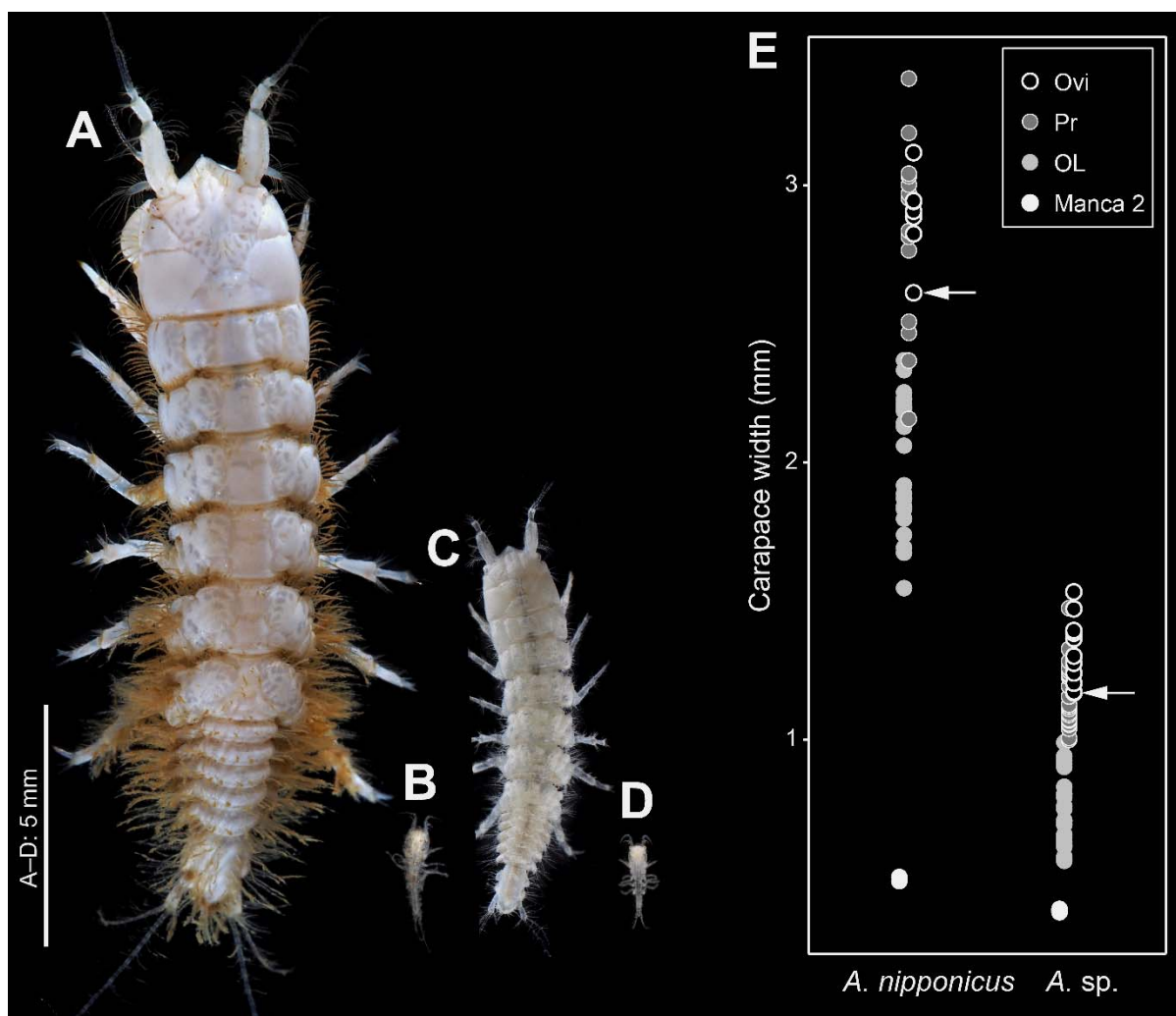
95 Kakui K., Hiruta C. & Uyeno D. 2019. Sexual system in the tanaidacean *Falsapseudes*
96 *bowmani* (Crustacea: Malacostraca: Peracarida). *Invertebrate Biology*, 138: e12257.
97 Doi: 10.1111/ivb.12257

98 Larsen K. 2003. Proposed new standardized anatomical terminology for the Tanaidacea
99 (Peracarida). *Journal of Crustacean Biology*, 23: 644–661. Doi: 10.1651/C-2363

100 Lowry J. K. & Dempsey K. 2006. The giant deep-sea scavenger genus *Bathynomus* (Crustacea,
101 Isopoda, Cirolanidae) in the Indo-West Pacific. *Mémoires du Muséum National*
102 *d’Histoire Naturelle*, 193: 163–192.

103 Pequegnat L. H. 1965. The bathypelagic mysid *Gnathophausia* (Crustacea) and its

- 104 distribution in the Eastern Pacific Ocean. *Pacific Science*, 19: 399–421.
- 105 Schmidt A., Siegel V. & Brandt A. 2002. Postembryonic development of *Apseudes heroae* and
106 *Allotanais hirsutus* (Tanaidacea, Crustacea) in Magellanic and sub-Antarctic. *Antarctic*
107 *Science*, 14: 201–211. Doi: 10.1017/S0954102002000019
- 108 Shiino S. M. 1937. On *Apseudes nipponicus* n. sp. (Crustacea: Tanaidacea). *Annotationes*
109 *Zoologicae Japonenses*, 16: 53–62.
- 110



111

112 **Captions for figures**

113 **Figure 1.** Habitus and the relationship between carapace width and developmental stage
 114 in *Apseudes nipponicus* and *Apseudes sp.* **A, B.** *Apseudes nipponicus*, postmanca individual
 115 (CW = 3.38 mm) (A) and manca 2 (B). **C, D.** *Apseudes sp.*, postmanca individual (CW = 1.52
 116 mm) (C) and manca 2 (D). **E.** Relationship between carapace width and developmental stage
 117 in the two species. OL, oostegite lacking; Ovi, ovigerous; Pr, preparatory. Arrows, the
 118 smallest ovigerous individual observed for each species.