

1 DWARF MALES IN THE BARNACLE *ALEPAS PACIFICA* PILSBRY, 1907
2 (THORACICA, LEPADIDAE), A SYMBIONT OF JELLYFISH

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4 BY

5
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15 DWARF MALES IN *ALEPAS*

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ABSTRACT

In the pedunculate barnacle *Alepas pacifica* Pilsbry, 1907 a symbiont of jellyfish, several small individuals were found attached to conspecifics rather than directly to the host. We investigated whether these individuals act as dwarf males, as is known in some other barnacle species. The conspecific-attached individuals had longer penes than juvenile hermaphrodites of similar sizes attached directly to jellyfish, although there was no other morphological difference between these two types of individuals. Only the largest conspecific-attached individual was ovigerous. We conclude that the conspecific-attached individuals are dwarf males, which develop male function at a smaller size than hermaphrodites do, with a small possibility of becoming hermaphroditic. This is the first report of dwarf males, and hence the coexistence of males and hermaphrodites (androdioecy), in the family Lepadidae. In addition, the record of *A. pacifica* attached to *Nemopilema nomurai* Kishinouye, 1922 is new to science.

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INTRODUCTION

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39 Barnacles have an exceptionally diverse array of sexual systems and therefore can
40 be used as model systems for the evolution of sexual systems in animals (Darwin, 1852;
41 Charnov, 1987; Høeg, 1995; Yusa et al., 2012). Most barnacles are self-infertile
42 simultaneous hermaphrodites, for example, the intertidal acorn barnacle *Semibalanus*
43 *balanoides* (Linnaeus, 1767) (cf. Yuen & Hoch, 2010) and the neustonic pedunculate
44 *Lepas anserifera* Linnaeus, 1767 (cf. Inatsuchi et al., 2010). However, in many deep-sea
45 or symbiotic species, pure males coexist with hermaphrodites (called androdioecy) as is
46 known in *Scalpellum scalpellum* (Linnaeus, 1767) (cf. Buhl-Mortensen & Høeg, 2006)
47 and *Koleolepas avis* (Hiro, 1931) (cf. Yusa et al., 2001); males may coexist with females
48 (dioecy) as in *Scalpellum stearnsii* Pilsbry, 1890 (cf. Ozaki et al., 2008) and *Verum*
49 *brachiumcancris* (Weltner, 1922) (cf. Buhl-Mortensen & Høeg, 2013). Male barnacles are
50 attached on conspecific hermaphrodites or females and are always much smaller than
51 the conspecifics (Darwin, 1852). In this paper, the males that are less than half the
52 length of conspecific hermaphrodites or females are defined as dwarf males, even if a
53 small proportion of the males may later become hermaphrodites, following the
54 preceding literature (Crisp, 1983; Buhl-Mortensen & Høeg, 2006; Yusa et al., 2010,
55 2012; Spremberg et al., 2012).

56 Barnacles are sessile organisms, and mating occurs primarily within reach of their
57 penes. Under such conditions, the sex allocation theory predicts that mating group size
58 is the major cause of sexual system variation (Charnov, 1982, 1987; Yamaguchi et al.,
59 2008, 2012). In a confined but relatively large group, as is often observed in intertidal or
60 neustonic habitats, the mating success of males is limited by the number of eggs
61 produced within the group. Therefore, male fitness does not increase linearly with the
62 resource input, and individuals should allocate some resources to egg production as well
63 as male function to maximise fitness; thus, they should become hermaphrodites. When
64 deep-sea or symbiotic habitats limit the size of mating groups, sperm competition
65 among hermaphrodites is less intense, and dwarf males with limited resources can be
66 competitive with male-acting hermaphrodites due to the advantages of having better
67 access to eggs for fertilisation and higher rates of survival to maturity; thus,
68 androdioecy evolves. In further smaller groups, large individuals may give up male
69 function to become pure females because they have almost no mates to inseminate; thus,
70 dioecy evolves. Limited space for attachment and short longevity of the substratum

71 further facilitate the evolution of dwarf males due to their small size and short time to
72 maturity, respectively (Yamaguchi et al., 2013a, b). These theoretical predictions are
73 fairly well supported empirically (Kelly & Sanford, 2010; Yusa et al., 2012). Although at
74 least three species of barnacles broadcast sperm (Barazandeh et al., 2013, 2014), this
75 factor does not appear to affect the general trend of sexual system variation according to
76 mating group size.

77 Recently, sexual expression of barnacles is suggested to be more plastic than
78 previously considered (Yusa et al., 2013). For example, in the acorn barnacle *Chelonibia*
79 *testudinaria* (Linnaeus, 1758), small individuals who are attached to conspecific
80 hermaphrodites develop a penis and act as dwarf males, although some of them may
81 later become hermaphrodites (Crisp, 1983; Zardus et al., 2014). Similar examples have
82 been reported in the pedunculate barnacles *Octolasmis warwickii* Gray, 1825 (cf. Yusa
83 et al., 2010) and *O. unguisiformis* Kobayashi & Kato, 2003 (cf. Sawada et al., in press).

84 Irrespective of the recent findings of dwarf males in otherwise hermaphroditic
85 barnacles (Yusa et al., 2010, 2012), no dwarf males have been reported in the family
86 Lepadidae. This may chiefly be due to their tendency to form large groups on floating
87 objects (wood, sea algae, plastics, etc.; Thiel & Gutow, 2005). However, *Alepas pacifica*
88 (Lepadidae) is symbiotic with jellyfish, and the number of individuals on the same host
89 is relatively small (normally 1 - 3; although sometimes 'numerous' or 'more than 100' per
90 host were recorded in the literature; Pagès, 2000).

91 We found that small individuals were attached to the capitulum and peduncle of
92 conspecifics in *A. pacifica* (fig. 1). Although most dwarf males are attached to the
93 capitulum in other species, Sawada et al. (in press) found that individuals attached to
94 the peduncle also act as dwarf males in *Octolasmis unguisiformis*. Therefore, we
95 hypothesised that these small individuals of *A. pacifica* were dwarf males. However,
96 simply being attached to conspecifics is not a prerequisite for dwarf males, as similar
97 conspecific-attached individuals are not dwarf males but juvenile hermaphrodites in the
98 pedunculate *Poecilasma kaempferi* Darwin, 1852 (cf. Yamaguchi et al., 2014). The
99 purpose of this study was to investigate whether these conspecific-attached individuals
100 in *A. pacifica* are dwarf males or juvenile hermaphrodites by inspecting their male and
101 female sexual status.

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MATERIAL AND METHODS

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105 Fourteen individuals of jellyfish with *Alepas pacifica* were collected aboard or on
106 shore along the western coast of Japan between 2005 and 2009 (table I). All barnacles

107 were fixed in 5 – 10% seawater formalin until further analyses. The exact size of the
108 host is unknown in most cases because only part of the host was cut and preserved due
109 to the large size of the host jellyfish (up to 2 m in diameter in the case of *Nemopilema*
110 *nomurai* Kishinouye, 1922; cf. Uye, 2008).

111 The barnacles were detached from the host jellyfish, and the total length,
112 capitulum length, and capitulum width were measured for all individuals using a
113 Vernier calliper to the nearest 0.1 mm. Next, each individual was dissected, and the
114 presence of an egg mass in the mantle cavity was checked under a binocular microscope;
115 the penis length was measured to the nearest 0.025 mm using a micrometre. There
116 were high correlations between total length and capitulum length (N = 118, $r = 0.99$, $P <$
117 0.001 , both \log_{10} -transformed after adding 0.5) and between capitulum length and width
118 ($r = 0.98$, $P < 0.001$). The capitulum length was used as a measure of body size because
119 it is the most accurate measurement.

120 Parametric tests, including Pearson's correlation, analysis of covariance
121 (ANCOVA) and logistic regression, were primarily used as statistical tests. Before
122 conducting ANCOVA, the lack of the significant interaction between the explanatory
123 variable (attachment site) and the covariate (capitulum length) was checked. All data
124 were \log_{10} -transformed after adding 0.5, but when the assumption of normality was
125 violated even after transformation, non-parametric tests (Kendall's τ or Mann-Whitney's
126 U) were used.

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RESULTS

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130 A total of 91 individuals of *Alepas pacifica* were found attached on 14 host jellyfish
131 (11 *Nemopilema nomurai* and three *Cyanea nozakii* Kishinouye, 1891; Table I). The
132 record of *A. pacifica* attached to *N. nomurai* is new to science. The number of individuals
133 per host varied greatly, from 1 to 38 (mean \pm SD = 6.5 ± 10.5). Even when there were two
134 or more individuals on the same host, they were distantly distributed in most cases (fig.
135 1A). In addition, 62 individuals (27 individuals after metamorphosis and 35 individuals
136 still inside the cyprid shell) were found attached to conspecifics. The capitulum lengths
137 of conspecific-attached individuals (mean \pm SD = 1.59 ± 0.95 mm, N = 27) were much
138 smaller than those directly attached to the host (9.02 ± 6.65 mm, N = 91).

139 Among the 118 individuals excluding the cyprids (91 jellyfish-attached and 27
140 conspecific-attached individuals), 10 (five from each attachment site) were broken or
141 empty and apparently died before collection; these individuals were excluded from
142 further analyses. Among the 108 intact individuals, the relationship between capitulum

143 length and penis length was studied for the individuals smaller than 6 mm in capitulum
144 length (N = 49) to match the size between jellyfish-attached and conspecific-attached
145 individuals (fig. 2). There was a positive relationship between capitulum length and
146 penis length ($F = 204.20$, $P < 0.001$, ANCOVA). Notably, the conspecific-attached
147 individuals had larger penes than did the jellyfish-attached individuals ($F = 5.29$, $P =$
148 0.026 , ANCOVA), although the largest ovigerous conspecific-attached individual had a
149 penis length similar to that of those attached to jellyfish (fig. 2). Otherwise, there was
150 no difference in morphology between the individuals with different attachment sites.

151 Seven out of the 108 individuals (6.5%) had egg masses in the mantle cavity. The
152 smallest ovigerous individual directly attached to the jellyfish had a capitulum length of
153 9.1 mm. In addition, the largest conspecific-attached individual (5.9 mm capitulum
154 length) had an egg mass. There was a positive relationship between capitulum length
155 and the presence of egg masses (N = 108, likelihood $\chi^2 = 10.51$, $P < 0.01$, multiple logistic
156 regressions), but this relationship was not different between the attachment sites
157 (likelihood $\chi^2 = 3.00$, $P = 0.08$).

158 There was a positive relationship between the capitulum length of
159 jellyfish-attached individuals and the number of conspecific-attached individuals
160 (including cyprids) (N = 91, $\tau = 0.39$, $P < 0.001$, Kendall's rank correlation). The
161 ovigerous hermaphrodites also had more conspecific-attached individuals than
162 non-ovigerous hermaphrodites ($U = 69$, $P < 0.001$, Mann-Whitney's U test).

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DISCUSSION

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166 Individuals of *Alepas pacifica* attached to the conspecifics were on average much
167 smaller than individuals attached to the jellyfish. However, the conspecific-attached
168 individuals had relatively longer penes for their body sizes than those directly attached
169 to the host jellyfish. These results coincide with results in *Chelonibia testudinaria*
170 (Crisp, 1983) and *Octolasmis warwickii* (Yusa et al., 2010), indicating that the
171 conspecific-attached individuals act as dwarf males. This is the first report of dwarf
172 males in the family Lepadidae.

173 There was a tendency that larger or ovigerous hermaphrodites had more dwarf
174 males. A similar tendency has been reported in *Koleolepas avis* (Yusa et al., 2001) and
175 *Octolasmis warwickii* (Yusa et al., 2010). Two general explanations are possible for
176 these relationships. First, dwarf males may be attracted to larger and/or ovigerous
177 hermaphrodites because a greater fertilisation success is expected (Yusa et al., 2010). In
178 barnacles, large individuals tend to lay more eggs (Zann & Harker, 1978; Yusa et al.,

179 2001, 2010; Ozaki et al., 2008), and currently ovigerous individuals are expected to lay
180 eggs more likely than non-ovigerous ones in a near future simply because they are
181 mature. Second, larger (or ovigerous) individuals tend to be old and may have
182 accumulated dwarf males, even if there is no preference by dwarf males for larger
183 individuals. However, the high proportion of dwarf males still inside the cyprid shell
184 (56%; 35/62) suggests that most dwarf males were still very young, presumably just
185 after settlement, rendering the second explanation (accumulation of dwarf males over
186 time) unlikely. Thus, although the mechanism is unknown, the data suggest that dwarf
187 males preferentially settle on larger/ovigerous hermaphrodites.

188 The occurrence of dwarf males in this species is congruent with the sex allocation
189 theory in that dwarf males evolve when mating groups are small (Charnov 1982, 1987;
190 Yamaguchi et al., 2012). In the family Lepadidae, species of neustonic *Lepas* generally
191 form large groups (Inatsuchi et al., 2010; Yusa et al., 2012), and although smaller
192 (consisting of 2 – 7 individuals), *Dosima fascicularis* (Ellis & Solander, 1786) that form
193 their own floats also live in groups (Zheden et al. 2015). *Alepas pacifica* most likely form
194 the smallest mating groups in the family: 67% of the individuals in Pagès (2000) lived
195 solitarily on the host. In the present study, only 9% (8/91) of the individuals lived
196 solitarily, but the great majority of individuals appeared to be too distant from each
197 other to mate (fig. 1A), even if they lived on the same host individual (that can reach 2
198 m in diameter; Uye, 2008). This barnacle is known to feed on the host tissue including
199 the gonads (Pagès, 2000), and it may be disadvantageous for the barnacles to live close
200 to each other for feeding purposes. Thus, small group size due to low density per host
201 and host feeding appear to be the factors for the evolution of dwarf males in this species.
202 The short lifespan of the host jellyfish (less than 1 year; Uye, 2008) may also facilitate
203 the evolution of dwarf males (Yamaguchi et al., 2013a). A similar condition in response
204 to the parasitic or commensal life applies to several androdioecious barnacles (e.g.,
205 species of *Chelonibia*, *Octolasmis warwickii*, *O. unguisiformis*, and *Koleolepas avis*;
206 Crisp, 1983; Yusa et al., 2001, 2010; Zardus et al., 2014; Sawada et al. in press).

207 Dwarf males in *A. pacifica* represent an example of ‘conditional’ dwarf males (Yusa
208 et al., 2013) in that they have no substantial morphological differences from the
209 hermaphrodites and a small proportion of them actually become hermaphroditic.
210 Similar examples have been documented in *Chelonibia testudinaria* (Crisp, 1983;
211 Zardus et al. 2014), *Octolasmis warwickii* (Yusa et al., 2010), and *O. unguisiformis*
212 (Sawada et al., in press). Because simultaneous hermaphrodites in many barnacles tend
213 to develop male function first (i.e., protandric simultaneous hermaphrodites; Inatsuchi
214 et al., 2010), dwarf males in these species can be regarded as potential hermaphrodites

215 that mature earlier as males and arrest growth in response to the attachment to
216 conspecifics. These contrast with dwarf males in the scalpellids, such as *Scalpellum*
217 *scalpellum*, where the males are morphologically distinct from hermaphrodites
218 (Spremborg et al., 2012).

219 The presence of such 'conditional' dwarf males in otherwise hermaphroditic
220 species renders the distinction between hermaphroditism and androdioecy unclear
221 (Yusa et al., 2013). Nevertheless, the 'hermaphrodite' and 'dwarf male' routes are not
222 interchangeable once individuals choose whether to settle on a usual substratum or a
223 conspecific. Because androdioecy is a highly rare phenomenon among animals (Weeks et
224 al., 2006), further research is needed on various 'conditional' dwarf males, which
225 represent an incipient condition of androdioecy.

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330

331 FIGURE LEGENDS

332

333 Fig. 1. (A) Part of the jellyfish *Nemopilema nomurai* Kishinouye, 1922 (host ID = 1)
334 showing a distant distribution of the barnacle *Alepas pacifica* Pilsbry, 1907 (attachment
335 site is indicated by the arrowhead). (B) The largest individual of *A. pacifica* in (A),
336 removed from the jellyfish, with 14 small individuals attached to it. The largest
337 conspecific-attached individual was ovigerous.

338

339 Fig. 2. *Alepas pacifica* Pilsbry, 1907. Relationship between capitulum length (mm) and
340 penis length (mm) for conspecific- (open circles) and jellyfish-attached (closed circles)
341 individuals with a capitulum length of less than 6 mm.

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Table I

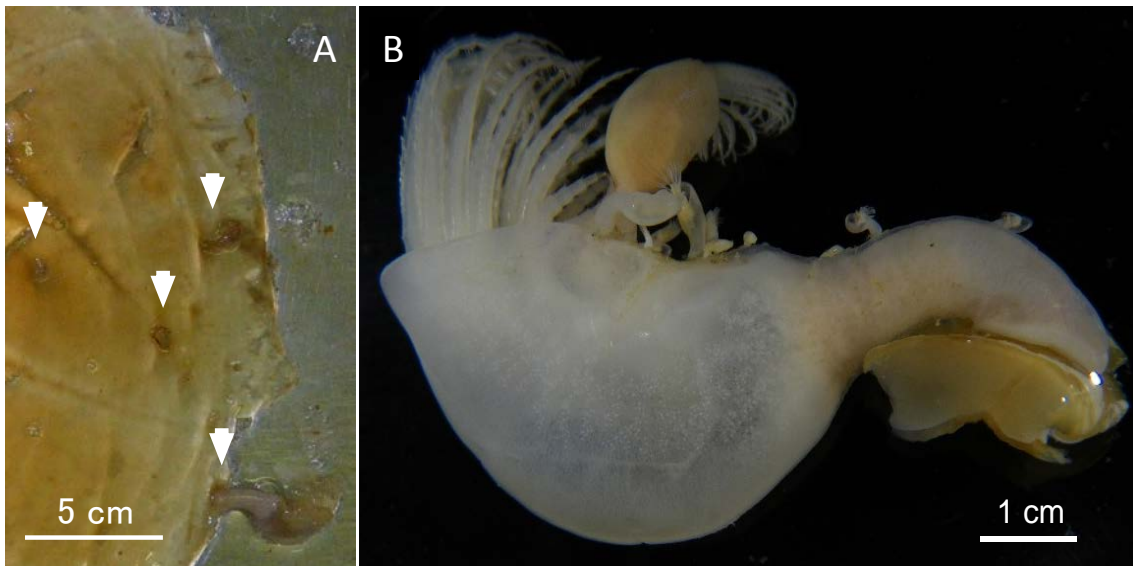
Jellyfish hosts of *Alepas pacifica* Pilsbry, 1907 in this study.

Date of collection	Species	Host ID	No. of barnacles (excluding dwarf males)
2009/10/30	<i>Nemopilema nomurai</i>	1	38
2005/7/15	<i>Nemopilema nomurai</i>	2	20
2005/11/4	<i>Nemopilema nomurai</i>	3	8
2006/11/21	<i>Nemopilema nomurai</i>	4	1
2006/12/12	<i>Nemopilema nomurai</i>	5	1
2006/12/12	<i>Nemopilema nomurai</i>	6	1
2009/7/22	<i>Nemopilema nomurai</i>	7	1
2009/7/23	<i>Nemopilema nomurai</i>	8	1
2009/7/3	<i>Nemopilema nomurai</i>	9	1
2009/7/4	<i>Nemopilema nomurai</i>	10	1
2009/7/4	<i>Nemopilema nomurai</i>	11	1
2005/7/10	<i>Cyanea nozakii</i>	12	7
2009/11/5	<i>Cyanea nozakii</i>	13	7
?	<i>Cyanea nozakii</i>	14	3

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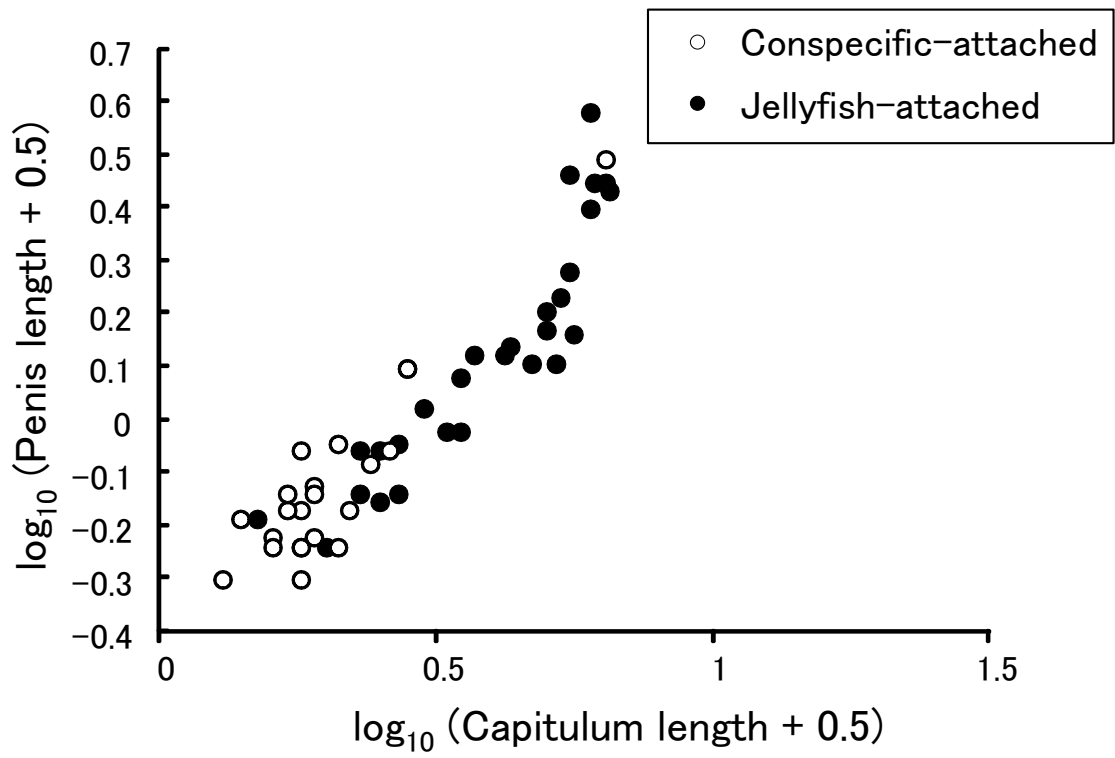
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Fig. 1.



355 Fig. 2.

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