Morphological character changes through decapodid-stage larva and juveniles in the ghost shrimp *Nihonotrypaea harmandi* from western Kyushu, Japan: clues for inferring pre- and post-settlement states and processes

Akio Tamaki[a,*], Yuko Saitoh[a,1], Jun-ichi Itoh[b], Yuichiro Hongo[a], Shun-suke Sen-ju[a], Seiji Takeuchi[a], Satoshi Ohashi[c]

[a] Graduate School of Fisheries Science and Environmental Studies, Nagasaki University, Nagasaki 852-8521, Japan

[b] Faculty of Fisheries, Nagasaki University, Nagasaki 852-8521, Japan

[c] Nagasaki Prefectural Institute of Fisheries, Nagasaki 851-2213, Japan

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Authors' contributions: AT supervised the study and wrote the manuscript. YS and SO undertook the laboratory experiments. JI undertook the field experiment. YH and SS conducted the larval sampling at sea. ST assisted in analyzing data and interpretation of results.

[*] Corresponding author. Complete postal address: Faculty of Fisheries, Nagasaki University, Bunkyo-machi 1-14, Nagasaki 852-8521, Japan. Tel.: +81 95 819 2856; fax: + 81 95 819 2799.

E-mail address: tamaki@nagasaki-u.ac.jp

[1] Present address: Crearia Inc., Kita-ku, Tokyo 114-0003, Japan

Abstract

Some decapod crustaceans release larvae from estuarine or coastal shores to coastal oceans. Decapodids (last-stage larvae) return home, settle, and metamorphose into juveniles I, which go through further instars. Several morphological characters degenerate or develop in response to lifestyle transitions. Using a burrow-dwelling callianassid shrimp, *Nihonotrypaea harmandi*, inhabiting an intertidal sandflat in a coastal boundary layer adjacent to coastal ocean, this study described morphological changes and drew inferences about states and processes in its early life history. Decapodid and juveniles were differentiated by linea thalassinica on carapace. In the laboratory, the decapodid stage lasted 3–6 d. Given choice between sandy sediments from coastal ocean bed and adult habitat, decapodids exhibited no preference, suggesting broad receptiveness. The shortest durations of the juvenile-I, -II, and -III were estimated at 6 d each. Starved decapodids normally metamorphosed into juveniles I, showing secondary lecithotrophy. The non-feeding state could be extended through the juvenile I (and possibly juvenile II), where the mean total lengths of shrimps reared in groups with food (diatoms) remained about 4.6 mm. Post-settlement decapodids reared individually resumed feeding. The rostrum lengths in decapodids were ≥ 0.36 mm on the initial two dates (Days 0 and 1), after which the mean values rapidly reduced to 0.30–0.36 mm on Day 2 and below 0.30 mm thereafter. The pereiopod exopods disappeared through the decapodid stage from four pairs to almost zero by Day 4. In the coastal ocean, no juveniles occurred, and almost all decapodids had rostrum lengths ≥ 0.30 mm and 3 or 4 pereiopod exopods, suggesting their pre-settlement state. Of the smallest shrimps collected on the sandflat for their subsequent rearing there, 74% were estimated to be Day-0 or -1 decapodids based on their rostrum lengths. This and the laboratory experimental results suggest (1) the acquisition of competence for settlement by newly-metamorphosed decapodids while in the coastal ocean, which was

nevertheless realized there and (2) their rapid transport by flood tidal currents from coastal ocean to sandflat. The newly-settled decapodids grew steadily at 0.2 mm d^{-1} in total length. The reared juveniles reached the smallest adult size in 80 d. The uropod expod changed from elliptical to sub-circular in shape markedly around the termination of the juvenile II or III, suggesting the acquisition of ventilating function for benthic life. Overall, the post-settlement shrimps can be staged by total-length ranges as 4–5.5 mm for decapodids, 5.5–10 mm for juveniles, 10–20 mm for sub-adults.

Keywords:

Decapod larva, Settlement, Metamorphosis, Intertidal sandflat, Coastal boundary layer, Coastal ocean

1. Introduction

A large proportion of marine benthic macro-invertebrates have a planktonic larval stage in their early life history. As a consequence of larval dispersal through transport by water currents, local adult populations are connected to various degrees, including self-seeding (Strathmann et al., 2002; Cowen and Sponaugle, 2009). The transport and survival processes through pre- and early post-settlement periods become a bottleneck for determining the subsequent population size (Ólafsson et al., 1994; Caley et al., 1996; Hunt and Scheibling, 1997; Metaxas and Saunders, 2009). Larval settlement on the substratum is succeeded by metamorphosis autonomically, with varying time lags (Crisp, 1974). “Competence” and “delay” are frequently used interrelated terms concerning settlement and metamorphosis events, and both terms have been attached to either one

(Crisp, 1974; Pechenik, 1990). If the time lag between settlement and metamorphosis is very short and almost concurrent such as observed for sessile or biofouling species, the state of settling larvae exhibiting exploratory behaviors for appropriate substrata may well be called competent for metamorphosis, capable of delaying it. For species with substantial time intervals between settlement and metamorphosis, the two terms should specifically be applied to either event.

Decapod crustaceans, brachyuran crabs in particular, are among the most intensively targeted taxonomic groups for studies of early life-history population processes (Anger, 2001; Queiroga and Blanton, 2005). Among the planktonic decapod larvae, export-type ones occupy a large part of the planktotrophic group (McConaugha, 1988). They are initially released from shores in estuaries and coasts, transported to offshore coastal oceans, and retained there to grow over a wide range of durations. Finally, the degree of successful transport of larvae at their last developmental stage back to adult habitats on the shore is directly conducive to the abundance of recruits in time and space (Johnson, 1985; Lipcius et al., 1990; Eggleston and Armstrong, 1995; Jones and Epifanio, 1995; González-Gordillo et al., 2003; Miller and Shanks, 2004; Giménez and Dick, 2007; Morgan et al., 2009; Olaguer-Feliú et al., 2010). For decapod crustaceans, it would be appropriate to treat larval settlement and metamorphosis as appreciably separated events both in time (Christy, 1989; Jensen, 1991; Strasser and Felder, 1998; Forward et al., 2001; Hasek and Rabalais, 2001; Moksnes et al., 2003; Anger, 2006; Lecchini et al., 2010) and in space as settlers can move to a distance by swimming (Forward et al., 2001; Moksnes et al., 2003; Lecchini et al., 2010). Although the last-stage larva is often called postlarva, this term assumes ambiguity. Those larvae in their pre-settlement state should not be prefixed with “post”. Only post-settlement individuals should be called the “post”-larvae. In the present study, we follow Felder et al. (1985) and Anger (2001), where the term, decapodid, is defined to denote individuals at the (last larval + first benthic) stage preceding metamorphosis into those at the first juvenile instar (hereafter abbreviated as juvenile I).

However, the synonyms of “postlarva” for specific taxa such as megalopa are so prevalent in the literature that their use is more or less inevitable.

To approach the process of larval transport from coastal ocean toward shore, it is first of all necessary to determine the duration of the decapodid stage of a target species using individuals reared in the laboratory. This duration acts as the temporal window for successful settlement and metamorphosis, which may primarily be determined by water temperatures and salinities encountered in the field but can also be dependent on either feeding or nonfeeding modes adopted by the decapodid [Dawirs, 1981; Harvey, 1996; the latter mode – secondary lecithotrophy known for several decapod taxa (Anger, 1989)]. The response of decapodids to cues at their settlement on substrata and their capabilities of accelerating or delaying metamorphosis into juveniles I can also be different between the two feeding modes (Harvey and Colasurdo, 1993; Harvey, 1996). Thus it is also required to determine which feeding mode the decapodid takes.

The static horizontal distribution pattern in decapodids with different ages (starting from the time of molting completion from the last zoeal stage) and/or its temporally changing pattern with age progression have been examined to draw inferences about their on-shore transport process from coastal ocean to estuarine upstream shore (Lipcius et al., 1990; Wolcott and De Vries, 1994; Paula et al., 2003; Olaguer-Feliú et al., 2010) or to coastal shore (Hatfield, 1983; Jamieson and Phillips, 1988; Moreira et al., 2007). In particular, two-step models for decapodid transport have been proposed for the coastal ocean–estuary setting (Miller and Shanks, 2004; Queiroga et al., 2006; Epifanio and Tilberg, 2008). Concerning the coastal ocean–coastal shore setting, growing attention has been paid to coastal boundary layers recently (Moreira et al., 2007; Morgan et al., 2009; Tamaki et al., 2010; Nickols et al., 2012). In both settings, the entrance to an estuary or to a coastal boundary layer acts as the spatial window for decapodids present in the coastal ocean to cross. In several of the above-mentioned field studies and in laboratory ones testing for a variety of

97 environmental and biological cues to accelerate or delay metamorphosis of decapodids into
98 juveniles I, two standard techniques have been employed to estimate decapodid ages: (1)
99 molt-staging by microscopically examining the integument of some specific parts of live or
100 preserved specimens, with the broadest classification of the postmolt, intermolt, and premolt stages
101 [after Drach (1939) and reviews in Stevenson (1985) and Anger (2001, 81–93)] and (2)
102 measurement of the time to metamorphosis by rearing live decapodids in the laboratory, with
103 shorter times regarded as a proxy for older ages (reviews in Forward et al., 2001). When applied to
104 decapod larval ecological studies, the first technique observes the degree of retraction of epidermis
105 from cuticle (apolysis), the maxillipeds, telson, and uropods most frequently noted (Hatfield, 1983;
106 Lipcius et al., 1990; Hasek and Rabalais, 2001; González-Gordillo et al., 2003; Gebauer et al.,
107 2004; Moreira et al., 2007) and the rostral spine at times (Anger, 1983; Wolcott and De Vries, 1994).
108 This technique is most suited to decapodids which have relatively long developmental durations
109 under normally encountered field conditions (e.g. $\geq$ 10 d) and can be collected in large numbers,
110 enabling subdividion of the three major stages, premolt stage in particular. The second technique
111 can be applied to those with a few-day developmental durations (Christy, 1989; Harvey and
112 Colasurdo, 1993; Strasser and Felder, 1998; Moreira et al., 2007; Olaguer-Feliú et al., 2010) as well
113 as those with longer durations (Lipcius et al., 1990; Fernandez et al., 1994; Zeng et al., 1997;
114 Moreira et al., 2007). When decapodids collected from offshore coastal oceans are involved in
115 research projects, both due sufficient time and appropriate experimental setup on board ship are
116 required (Wolcott and De Vries, 1994; Brumbaugh and McConaugha, 1995). In cases where
117 decapodis with a few-day developmental durations are targeted but a large number of individuals
118 cannot be obtained alive, any morphological characters other than molt stages could also be useful
119 to estimate their ages based on preserved specimens.
120 Since the decapodid stage is transitional from planktonic to benthic phase of life, some

morphological characters associated with swimming or floating functions in the zoeal stages are expected to be gradually lost or reduced in size during the former phase (precisely, resorbed; Felder et al., 1985; Anger, 2006). Decapodid morphological changes could continue also during the latter phase until metamorphosis into juveniles I. The temporally changing pattern in these degenerating characters recorded from rearing experiments in the laboratory may provide a useful set of clues to estimate the age of decapodids with relatively short developmental durations collected in the field. Furthermore, if these morphological characters mirror the immediate past phase of the existence of decapodids there, inference could be drawn regarding their positioning or physiological states in the field such as (1) whether the collected decapodids had remained in the water column as the plankton with a long dispersal potential or they had already stayed on/in the substratum as the benthos between settlement and metamorphosis events [note that secondary dispersal after settlement for a shorter distance is possible (Moksnes et al., 2003)]; (2) which ages of decapodids are competent to settle on the substratum (cf. Lipcius et al., 1990; Jensen, 1991; Wolcott and De Vries, 1994; Zeng and Naylor, 1996; Forward et al., 2001; Gebauer et al., 2004); and (3) how long decapodids accelerate or delay the time to metamorphosis into juveniles I, responding to a variety of cues (Christy, 1989; Pechenik, 1990; Jensen, 1991; O'Connor, 1991; Harvey and Colasurdo, 1993; Forward et al., 2001; Stanley et al., 2012). One notable morphological character is pereiopd exopods, which have a natatory function in the zoeal stages. In the decapodid stage, these are gradually or abruptly lost, their role being replaced by pleopods (Anger, 2006). Another promising character is rostrum size. Though remained as a hypothesis, the elongated rostral spine, in concert with the dorsal spine, could afford buoyancy to zoeal body (Strasser and Felder, 1999a; Anger, 2003). In the decapodid stage, rostrum size becomes reduced, while the dorsal spine disappears at the time of molting from the last zoeal stage. To date there were no detailed laboratory and field studies that described the temporally changing pattern in pereiopod exopods and rostrum through

145 the entire decapodid stage (e.g. exopod distribution in pereiopods and rostrum length on a daily
146 basis).

147 Concerning the events at around the settlement of decapodids and their metamorphosis into
148 juveniles I, some confusing understanding could arise on the following two aspects. First, as
149 premised in the second paragraph, following their settlement on the shore, decapodids may spend
150 some varying period of time before metamorphosis into juveniles I. For several brachyuran crabs,
151 time series data for the abundance of newly-settled megalopae (= settlers) were obtained on an
152 hourly to daily basis by deploying readily retrievable passive collectors equipped with artificial
153 substrates or light traps (Jones and Epifanio, 1995; Oishi and Saigusa, 1997; Moksnes and
154 Wennhage, 2001; Miller and Shanks, 2004). In contrast, for decapodids of burrowing forms, they
155 usually have to be collected by extracting sediment columns (Tamaki et al., 1997; Nates and Felder,
156 1999). If only the latter type of collection at some discrete time intervals is possible, contaminated
157 counts of decapodids and/or juveniles I with respective age composition for each group between
158 two consecutive sampling occasions should be avoided in order to have an accurate estimate of
159 settler density on each occasion. Secondly, juveniles are also considered as a returning component
160 from coastal ocean to estuarine or coastal shore (Epifanio et al., 1984; McConaugha, 1988;
161 González-Gordillo, 2003), which has never been demonstrated. This hypothesis implies that some
162 members of the decapodid assemblage present in the coastal ocean should settle and metamorphose
163 on the bed there and that its substratum properties are at least non-repellent to those competent
164 pre-settlement decapodids. Juveniles are often collected from the shallow water column while they
165 are performing a secondary dispersal in the vicinity of adult habitats (Dittel and Epifanio, 1990;
166 Eggleston and Armstrong, 1995; Feldman et al., 1997; Oishi and Saigusa, 1997; Pereira et al.,
167 2000; Reyns and Eggleston, 2004; Oliveira et al., 2012). These juveniles might be mistaken as a
168 returning component from further offshore. There are at least two steps approaching the above two

169 aspects. The first one is to find some specific morphological characters and/or growth-related
170 dimensions, such as total length, which help distinguish between post-settlement decapodids with
171 different ages and between those decapodids and juveniles I. A combined use of specimens reared
172 in the laboratory and the field would be useful for this purpose. The second step is to
173 experimentally examine competent pre-settlement decapodids' choice between substrata from the
174 coastal ocean bed and from the adult habitat.

175 The survival and growth process through the juvenile stage can act as a final bottleneck in the
176 early life history for determining adult population size in decapod crustaceans (Eggleston and
177 Armstrong, 1995; Tamaki et al., 1997; Giménez, 2010). To elucidate the change in these two
178 parameters with age during this stage, it is first of all necessary to discriminate specimens between
179 different ages within the juvenile I and those between the different instar numbers. As
180 morphological characters in the juvenile stage tend to change gradually, some easily measurable
181 characters might be informative, including total or carapace length, other partial length relative to
182 these lengths, and angle dimensions in specific parts. Such parameters would be obtained from
183 specimens reared in the laboratory and the field. For identifying juveniles derived from different
184 instars, the tracking of molting events is useful, which can be most effectively achieved by rearing
185 individually from the decapodid through juvenile stages in the laboratory.

186 The ghost shrimp (Decapoda: Axiidea: Callianassidae) is a pronounced member on tidal flats
187 and shallow subtidal soft bottoms over the world, considerably affecting both benthic community
188 structure and ecosystem functions through its construction of a deep burrow and intense
189 bioturbating activity (Flach and Tamaki, 2001; Atkinson and Taylor, 2005; Pillay and Branch, 2011).
190 Concerning the formerly treated infraorder Thalassinidea, a major taxonomic revision has been
191 recently made to divide it into two separate infraorders, Gebiidea comprising four families and
192 Axiidea comprising six families including Callianassidae (Dworschak et al., 2012). Despite a rich

193 array of biological and ecological studies on fully benthic aspects for callianassid shrimp, findings
194 on their planktonic and early benthic stages, decapodids and juveniles in particular, are rather
195 limited. The information on callianassid larval stages and morphologies was compiled in a review
196 for larvae of Gebiidea and Axiidea (table 2 in Pohle et al., 2011). The callianassid species can be
197 divided into two groups, one with abbreviated larval development possessing up to two or three
198 zoeal stages and the other with four to six zoeal stages. Larvae of the former group may be retained
199 near adult habitats, while longer-distance transport is expected for the latter (export type into
200 coastal ocean). The morphology of the decapodid was described for nine and ten species for the
201 former and latter groups, respectively, in which no mention was made on its change with age. The
202 duration of the decapodid stage was given for two species in the former group (Sankolli and Shenoy,
203 1975; Abrunhosa et al., 2005) and for two species in the latter group (Strasser and Felder, 2000,
204 1999a; Abrunhosa et al., 2008). The description of the morphology of juvenile I and its duration
205 was given for two species (Sankolli and Shenoy, 1975; Abrunhosa et al., 2005) and one species
206 (Abrunhosa et al., 2005), respectively.

207 In mid-western Kyushu, southern Japan, three species of the callianassid genus *Nihonotrypaea*
208 are distributed in an estuarine system extending from Ariake Sound (estuary), through Tachibana
209 Bay (intermediate waters), to Amakusa-Nada (inner shelf waters of the East China Sea = coastal
210 ocean) (Tamaki et al., 1999; Tamaki and Harada, 2005; Fig. 1A); note that in papers by A. Tamaki
211 and his colleagues published before 1998, the name *Callianassa japonica* was incorrectly applied
212 to *N. harmandi* (Bouvier, 1901) (see Manning and Tamaki, 1998). This water area belongs to a
213 meso-tidal regime, with maximum tidal ranges of 6 m in the innermost part of Ariake Sound and 3
214 m in Amakusa-Nada, and with semidiurnal tides. The main habitat of *N. japonica* is extensive
215 intertidal sandflats in the middle one-third of Ariake Sound, whereas *N. harmandi* and *N. petalura*
216 inhabit small to medium sandflats and boulder shores, respectively, in their common water area

Fig. 1

217 ranging from the outer one-third of Ariake Sound through Tachibana Bay to Amakusa-Nada (Kubo
218 et al., 2006). The complete larval development of the three species has been described based on
219 laboratory-reared specimens, and the number of zoeal stages was five for *N. japonica* (see Miyabe
220 et al., 1998) and *N. harmandi* (see Konishi et al., 1999) and six for *N. petalura* (see Konishi et al.,
221 1990). The nursery ground for larvae of *N. harmandi* and *N. petalura* lies in a part of
222 Amakusa-Nada, with 60–70-m water depths, where no late-stage larvae (Zoeae IV and V) of *N.*
223 *japonica* were found, and *N. harmandi* was estimated to occupy 94% of all collected larvae
224 (Tamaki and Miyabe, 2000; Tamaki et al., 2010). The seabed in this water-depth range is composed
225 of fine, medium, and coarse sands (Japan Coast Guard, Hydrographic and Oceanographic
226 Department, 1994, fig. 33). The analysis in the present study was focused on *N. harmandi*,
227 assuming that the larval abundance of the other two species is negligibly low in Amakusa-Nada. Of
228 26 main local adult populations of *N. harmandi*, the population on the sandflat facing a maximum
229 of 30-m deep Tomioka Bay, located on the northwestern corner of Amakusa-Shimoshima Island,
230 was the largest, with its estimated total number of individuals accounting for 70% of all local
231 populations (Tamaki and Harada, 2005). Tomioka Bay, intervening between two promontories,
232 forms a coastal boundary layer adjacent to the coastal ocean where strong tidal currents flow, their
233 east-west component predominant, with a maximum speed of approximately 140 cm s^{-1} at spring
234 tides (Japan Coast Guard, Hydrographic and Oceanographic Department, 1994) and 75 cm s^{-1} at
235 neap tides (Tamaki et al., 2010). Lecithotrophic larvae of a gastropod species with short planktonic
236 duration (e.g. 3d) on the sandflat are released at neap tides and retained within the bay (Mandal et
237 al., 2010), whereas zoeae I of *N. harmandi* are released toward Amakusa-Nada at nighttime
238 ebb-tide hours of spring tides (Tamaki et al., 2010). Tamaki et al. (2010) also showed that
239 decapodids of *N. harmandi* perform a normal diel vertical migration (i.e. ascent and descent during
240 the night and rest at depths during the day) through the entire range of a 68.5-m water column in

Amakusa-Nada and entered Tomioka Bay at nighttime flood tides. Through the water column in mid-summer, temperature varied from 18.5 °C at the deepest stratum to 26.9 °C at the surface and salinity from 34.2 to around 31.5 [Fig. 1B, adapted from the original data for Tamaki et al. (2010, fig. 2)]; for the deepest part, measurements on other occasions detected values between 17 and 18 °C (A. Tamaki, unpublished data). Our preliminary observation has suggested that the decapodid stage lasts a few days. Following the decapodid settlement on the Tomioka Bay sandflat, the growth, survival, and distribution patterns in the juvenile stage could crucially affect population dynamics there (Tamaki and Ingole, 1993; Tamaki et al., 1997). In these studies, the population was divided into the juvenile and adult stages according to cohort separation, their boundary varying from 10 to 20 mm in total length depending on its frequency-distribution shape on respective sampling occasions. Furthermore, based on our preliminary observations on juveniles, the ontogenetic changes in uropod exopod shape and pleon length relative to total length were notable. With all above findings so far, detailed analysis has yet to be made on such items as (1) morphological keys to differentiate decapodid and juveniles, (2) morphological and body-dimensional keys to distinguish between pre- and post-settlement decapodids and between successive post-settlement decapodids, (3) duration of the decapodid stage, (4) feeding mode of decapodids, (5) decapodid's selectivity between intertidal and coastal ocean sediments, (5) feeding mode of juveniles, (6) morphological or body-dimensional keys to separate juvenile instars, (7) overall growth patterns throughout the decapodid stage and juvenile instars, and (8) more rigorous definition of juvenile and adult stages.

The objective of the present study was to clarify the above eight items by using specimens of *N. harmandi* collected from the water area ranging from Amakusa-Nada to the Tomioka Bay sandflat. The material came from (1) laboratory-rearing of larvae released from ovigerous females and of juveniles that subsequently appeared, (2) field rearing of juveniles derived from newly-settled

decapodids on the Tomioka Bay sandflat to their adult stage, and (3) collection of larvae from Amakusa-Nada and close off Tomioka Bay. The results of the substratum-choice experiments using decapodids were also used to examine the effect of sediment on the duration of the decapodid stage. Of degenerating morphological characters during the decapodid stage, special attention was paid to the daily change in rostrum length and pereiopod exopods. The applicability and limitation of these morphological keys to the estimation of ages of decapodids and their states of existence (pre- or post-settlement) were evaluated. The possibility of total length as a key body dimension for discriminating between different-age post-settlement decapodids and between juveniles of different instar numbers was also examined. Morphological changes gradually added to the juvenile body were noted as a signature for its true benthic life. At the same time, based on the acquired morphological clues, some inferences were drawn for pre- and post-settlement states in the field and for possible related processes. Finally, what are meant by two key words in the final-stage meroplanktonic larvae, settlement and metamorphosis, was considered in the general context of decapod crustaceans that release export-type larvae from estuarine or coastal shore to coastal ocean.

2. Materials and methods

2.1. Rearing of zoeae to decapodids in the laboratory

To obtain decapodids of *Nihonotrypaea harmandi* for morphological examination, zoeae were mass-reared in 2010 and 2011 at Nagasaki Prefectural Institute of Fisheries, which stands by the coastal ocean. This rearing experiment was undertaken also to track the zoeal development process, which will not be mentioned in this paper. About 30 to 200 ovigerous females that seemed to be about to release larvae were collected from the Tomioka Bay sandflat during daytime low tide of spring tide on three occasions from the end of July to early September (mean number of eggs per

289 female = 330: Tamaki et al., 1997). Of all larvae released (Zoeae I) by early morning the next day
290 on each occasion, approximately 5,800–6,600 ones were transferred to a 30-l polycarbonate tank
291 which contained ambient natural seawater passed through a 10-μm mesh filter, with gentle aeration
292 (Day 0 for the zoeal rearing). The water temperature was kept at around 21 °C (Batch 1, in 2010),
293 23 °C (Batch 2, in 2010), and 24 °C (Batch 3, in 2011), using thermoregulator systems. The
294 temperature values were set according to their range experienced by vertically migrating larvae in
295 the water column of Amakusa-Nada during the nighttime in mid-summer (Tamaki et al., 2010; Fig.
296 1B). In addition to the three batches, a water tank set at 17.5 °C, with the initial, 6,600 zoeae I, was
297 established at the same time as in Batch 3 (Batch 4). This temperature value corresponded to that in
298 the deepest stratum of the water column in which decapodids stay during the daytime. The standard
299 deviation about mean temperatures over the course of each rearing set varied from 0.04 to 0.5 °C.
300 The water salinities in the four batches were between 32 and 33, which were within the values for
301 the vertical range encountered in the field. Larvae were fed a combination of the diatom
302 (*Chaetoceros gracilis*), the rotifer (*Brachionus rotundiformis*), and the brine shrimp (newly-hatched
303 *Artemia* spp. nauplii) on respective sufficient rations, following the protocol that had been
304 established for each stage (Miyabe et al., 1998; Konishi et al., 1999). The occurrence of decapodids
305 was checked every morning. In Batch 1, a total of 445 decapodids appeared over 17 d, with the
306 peak (106 individuals) on Day 30. In Batch 2, the total number was 557 over 16 d, with the peak
307 (95 individuals) on Day 28. In Batch 3, the total number was 291 over 15 d, with the peak (49
308 individuals) on Day 30. In Batch 4, the total number was 393 over 27 d, with the peak (55
309 individuals) on Day 52. Unless specifically stated, all procedures described in the following
310 sections were for Batches 1–3; for observations and experiments that started from the
311 newly-metamorphosed decapodids, individuals obtained from these batches were transferred to
312 smaller containers surrounded by waters with temperatures similar to or not so different from those

313 in the zoeal-rearing tanks. For decapodids in Batch 4, those that emerged on Day 0 only were used
314 for observations on morphology [rostrum length and exopods on pereiopods (Section 2.5)].
315
316 *2.2. Treatment of decapodids and juveniles in the laboratory*
317 All decapodids of *N. harmandi* that appeared every morning were collected and each
318 occurrence date labeled as Day 0 (lab) [Day 0 for the ensuing decapodid and juvenile rearing in the
319 laboratory; "(lab)" is affixed to discriminate between laboratory and field rearing (see Section 2.4)].
320 Of the total number 50–60% were used for examining the daily change in morphological characters.
321 Apart from those fixed with 5% neutralized seawater formalin on Day 0 (lab), decapodids were
322 subsequently reared either individually or in groups of two to ten individuals in a small container
323 made of a polyvinyl chloride pipe, 10 cm in diameter and 10 cm in height, with a 70-μm mesh
324 nylon net attached to the bottom. To always keep the inside of the container dark [cf. in the field,
325 values less than 1 μmol quanta m^{-2} s^{-1} in photon flux density at depths occupied by decapodids
326 were recorded during daytime (Tamaki et al., 2010)], two 2-mm mesh black nets were covered on
327 its top. The containers were maintained in a large box soaked with running filtered seawater
328 introduced from the outside of the laboratory, with their water depths adjusted to 7–8 cm.
329 Decapodids and juveniles were retrieved and fixed daily in the morning (as the decapodid and the
330 juvenile cannot necessarily be separately described beforehand in the Materials and methods and
331 Results sections, the two stages are often put together). The water temperatures were recorded
332 twice in the daytime daily as a rule. The rearing individually was conducted for 34 decapodids,
333 which was intended to track individual molting events. Exuviae were searched for every morning,
334 and up to Day 25 (lab) a total of 26 shrimps were retrieved and fixed at some time intervals. For the
335 rearing in groups, a substantial number of shrimps were retrieved and fixed every morning from
336 Day1 to Day 11 (lab); the consecutiveness of dates was achieved when results from the three

337 higher-temperature zoeal-rearing batches were combined (Section 2.1). A fewer number of shrimps
338 were collected discretely for an extended period from Day 13 to Day 57 (lab). The specimens
339 examined for this period came from the rearing in groups, except for the inclusion of a part of
340 individually-reared ones [Day 15 to Day 25 (lab); Section 3.2]. Exuviae were sometimes observed
341 also from containers for the rearing in groups, and the dates of their occurrence recorded.
342 It had been established in a laboratory experiment that the diatom (*Chaetoceros gracilis*) was
343 solely effective for juveniles of *N. harmandi* to grow (Yokoyama et al., 2005; in that study,
344 refrigerator-stored material was used). Our preliminary observation has indicated that decapodids
345 ingest neither *Brachionus rotundiformis* nor newly-hatched *Artemia* nauplii. In the present study,
346 decapodids and juveniles were fed live *C. gracilis* on a ration of approximately $0.4–1 \times 10^8$ cells
347 per container. Although an individual diatom cell is 5 μm in size, cells were forming floccules,
348 adherent to the bottom net. The un-ingested lumps and fecal pellets were cleared every other day.
349 Specifically, to demonstrate the existence of secondary lecithotrophy, four to 12 decapodids per
350 container (26 in total) were kept starved for a period up to Day 16 (lab), during which time
351 decapodids might have metamorphosed into juveniles I.
352 To confirm if there is any selectivity or repellency by decapodids between substrata from the
353 coastal ocean bed (Amakusa-Nada) and from the intertidal adult habitat (Tomioka Bay sandflat), a
354 choice experiment was conducted during August–September, 2011. The age of the target
355 decapodids were Days 0, 1, and 2 (lab). The substrata were sandy sediments. These were collected
356 about 70 d before the experiment, either using a Smith-McIntyre grab on board the TV “Kakuyo”,
357 Nagasaki University, from a 70-m deep bottom above which the occurrence of decapodids in the
358 water column had been recorded (Tamaki et al., 2010) or by hand from the intertidal, and kept
359 frozen at –30 °C until use. The surface sediments to a depth of 3 cm were used, with the grain-size
360 compositions summarized as (1) coastal ocean bed: moderately well-sorted medium sand [median

361 phi (Mdϕ) = 1.51, inclusive graphic standard deviation (σ_I) = 0.52], with 1.65% silt-clay content,
362 and (2) intertidal sandflat: well-sorted fine sand (Mdϕ = 2.10, σ_I = 0.45), with 0.39% silt-clay
363 content. In a temperature-controlled (23–25 °C) room with only dim light, each kind of thawed
364 sediments was placed by half on a polycarbonate cylindrical cup, 5.6 cm in diameter and 3.3 cm in
365 height, to a height of 1 cm from bottom, with the central partition of a 2-mm thick polycarbonate
366 plate, 1.5 cm in height. Filtered seawater was added gently to a height of 2.8 cm. As soon as a
367 single decapodid was released above the partition plate, with no food, the whole cup was covered
368 with a box that cut off light; our observations made on other occasions revealed that given sediment
369 under dim light, decapodids completed burrowing within 1 min. After 24 h, the cup was checked
370 for the presence of any swimming or dead individuals, which were excluded from statistical
371 analysis. The shrimp that had existed within either type of sediments was retrieved and fixed. The
372 total number of runs varied between 23 and 25 for each of the Days-0, 1, and 2 (lab) shrimps, with
373 two sets for Day 0 (lab) and each one set for Days 1 and 2 (lab). Two-tailed binomial tests were
374 performed to detect any significant choice for either type of sediment (α = 0.05: α = 0.025 for
375 either tail). When a substantial number of decapodids actually burrowed into the sediment, all
376 retrieved specimens were also examined for any morphological characters that could have been
377 induced by their burrowing experience. The comparison was made with those of shrimps
378 maintained without sediment for respective identical ages [i.e. Days 1, 2, and 3 (lab) mentioned in
379 the first paragraph].
380
381 *2.3. Collection of decapodids and juveniles from the water column at sea*
382 To compare morphological characters in decapodids and juveniles of *N. harmandi* swimming in
383 the water column at sea with those of shrimps reared in the laboratory, specimens were collected
384 and fixed from Amakusa-Nada and the mouth of Tomioka Bay, about 10 km and 3 km off the

Tomioka Bay sandflat, respectively (Fig. 1A). The former (coastal ocean) sampling was conducted in July–August, 2006 around a 68.5-m deep site, using a MOCNESS (Multiple Opening/Closing Net Environmental System, Biological Environmental Sampling Systems, Inc.) on board the TV "Kakuyo", which covered the water-depth range of 2 to 60 m, with every ca. 10 m. The larval vertical distribution pattern there is given in Tamaki et al. (2010). For the present study, all stored shrimps were re-examined for their morphology. The latter (bay mouth) sampling was conducted around a 35-m deep site on 27–28 September, 2011, using a fisherman's boat. A conical 0.33-mm mesh net, 130 cm in diameter and 440 cm in length, positioned at a depth of 15 m was towed horizontally at a speed of 1 knot for 10 min. A total of 16 tows were made from evening to morning, as decapodids appear in the upper to middle water column mostly at night (Tamaki et al., 2010).

2.4. Rearing of decapodids and juveniles on intertidal sandflat

To complete analysis for morphological character changes and body-growth patterns through the decapodid and juvenile stages of *N. harmandi*, a combined use of laboratory- (Section 2.1) and field-reared specimens was made. To secure a sufficient number of juveniles at advanced instars, small shrimps that were assumed to be newly-settled decapodids were collected on the Tomioka Bay sandflat during daytime low tide on 5 and 8 August and 17 September 1994 and subsequently reared there. Sediment columns collected to a depth of 5–10 cm were passed through a 0.5-mm mesh sieve, from which only the smallest-sized shrimps in appearance were selected while on the sandflat [Day-0 (field) shrimps]. Note that the "Day" and "(field)" combination does not designate the actual or estimated age of that shrimp in contrast to the "Day" and "(lab)" combination (Section 2.2). When it becomes necessary to refer to the age, expressions such as x-d old shrimps or day-x shrimps are adopted (x = 0, 1, 2…); in particular, the latter is used for post-settlement decapodids or juveniles from the time of settlement regardless of how long the pre-settlement duration has been

409 (see the Discussion). A polyvinyl chloride pipe (12 cm in diameter and 33 cm in length, with a
410 1-mm mesh nylon net attached to the bottom) that was filled with sediment passed through a 1-mm
411 mesh sieve was used for the rearing. Five to ten Day-0 (field) shrimps and 15 to 20 ones were kept
412 in each pipe for the periods of 2, 4, 6, and 7 d and 11, 15, 20, 27, 35, 45, 60, and 90 d, respectively;
413 the rearing in mid-September was conducted for the shorter periods only (up to 6 d). The pipe was
414 sealed with a 1-mm mesh nylon net on its top and buried upright in the sediment, with its bottom
415 reaching the depth of 30 cm. Each pipe was retrieved on its predetermined date and the shrimps
416 inside fixed. The ambient subsurface temperature was recorded at some time intervals, using a
417 maximum-minimum temperature buried at 30 cm in the sediment.
418 Actually, Day-0 (field) shrimps could have comprised decapodids and newly-metamorphosed
419 juveniles with different ages for each. The knowledge on the possible range of this initial age
420 composition is indispensable to secure the appropriateness in estimating ages of advanced-instar
421 juveniles. A total of 19 smallest shrimps were collected apart from those used for the above
422 experimental setup and fixed on respective same dates in August (seven shrimps each) and
423 September (five ones). The analysis for their age compositions was made based on several
424 morphological characters selected from those of the laboratory-reared shrimps and on total-length
425 data from both laboratory- and field-reared shrimps. The total-length data were also used to
426 characterize decapodid and juvenile growth patterns.
427
428 *2.5. Morphological characters, measurement, and statistical analysis*
429 Several morphological characters of decapodids and juveniles of *N. harmandi* were examined
430 and measured for their dimensions as listed below [(1)–(6)]. The whole set of characters could not
431 necessarily be observed or measured from each specimen due to their different degrees of damage.
432 The line or curve tracing was made, using a stereomicroscope with drawing apparatus (Nikon

433 SMZ-10) under a magnification of × 21.3 and 57.0 for the dimensions in (1) and (2) and in (3) and
434 (6), respectively. The lines or curves were drawn from side view for (1)–(3) and from dorsal view
435 for (6), which were imported to a computer through a scanner as JPEG file formats. Using Renda!
436 ver. 1.2.1 (open-access software given in Japanese; http://nodakoubou.net/program2/vb/renda.html),
437 points were acquired at a rate of 20 s^{-1} along the line or curve for their two-dimensional coordinates.
438 The total number of points varied according to cursor movement speed and figure size on the
439 display. An average of 117 points per cm was plotted. The length of the line or curve was obtained
440 by summing the distance between two consecutive points. The measurement of angle dimensions
441 was also made on the computer display. The finally estimated value for each actual dimension was
442 calculated to the one or two decimal place.
443 (1) Total length (abbreviated as TL): mid-dorsal curve length from tip of rostrum to posterior
444 margin of telson.
445 (2) Carapace length (abbreviated as CL): mid-dorsal curve length from tip of rostrum to
446 posterior margin of carapace. This dimension is used to calculate pleon length relative to total
447 length: relative pleon length, defined as (TL – CL)/TL.
448 (3) Rostrum length (abbreviated as RL): mid-dorsal curve length from tip of rostrum to base of
449 eyestalk. For this dimension, the side-view drawing was necessary, as the rostrum tends to be bent
450 downward (ventrally). For only the graphical presentation of RL distribution against date, the three
451 decimal-place values were used to avoid too many identical plots. A part of the rostra apparently
452 showed a sign of the premolt stage, with appreciable apolysis. For such rostra, the RLs to both
453 epidermis and cuticle tips were recorded.
454 (4) Linea thalassinica (longitudinal groove or uncalcified line on dorsal part of carapace
455 extending from anterior margin below antennal spine to posterior margin in most thalassinideans:
456 McLaughlin, 1980, 167–168): presence or absence on each side of carapace.

457 (5) Exopods on pereiopods: presence or absence on each side of pereiopods 1–5.

458 (6) Uropod exopod shape: parameterized by dimensions of a pentagon fitted interiorly to the
459 exopod circumference, including the ratio of long axis to short axis lengths and three apex angles.
460 The long axis was defined as the line connecting the mid-point of the proximal side and the distal
461 tip of the posterior, lower plate which is demarcated from the anterior, upper plate by a suture,
462 while the short axis is the longest line perpendicular to the long axis. The distal, left, and right apex
463 angles were defined as those made between every adjacent two sides, with the left and right
464 directions defined for the left uropod exopod.

465 Five adult specimens derived from the ovigerous females that had been used for larval release
466 (Section 2.1) were also examined and several dimensions measured for comparison with those of
467 decapodids and juveniles [mean (± SD) TL = 32.6 (± 1.8) mm; estimated age = two years old, after
468 Tamaki et al. (1997)].

469 To compare the values of any dimension between the decapodid and juvenile specimens set
470 under two or more different conditions, non-parametric, Mann-Whitney *U*-test or Kruskal-Wallis
471 test was conducted, using “R” 2.15.1 (R Development Core Team, 2012).

472 Through the decapodid and juvenile stages, the temporal changes in TL, relative pleon length,
473 and several dimensions related to the uropod’s exopod shape were examined. The growth patterns
474 based on TL were obtained separately for the laboratory- and field-reared specimens. For the other
475 dimensions, a combined data from both kinds of rearing were used; those specimens for up to 25 d
476 were derived from the former rearing [real dates – Days 0 to 25 (lab); Section 2.2] and those for the
477 subsequent dates from the latter [estimated dates – Days 27 to 90 (field); Section 2.4]. The reason
478 for the adoption of field data for the latter period only was to diminish the influence from possible
479 errors in age estimation. For the Day-0 (lab) data, 20 specimens were randomly chosen from the
480 maximally available 128 ones. For the subsequent data from Day 3 to Day 25 (lab), a total of 25

specimens was used from batches reared either in groups or individually. To draw a smoothing curve of each variable against age (in days), Loess regression was conducted, using "R" 2.15.1 (R Development Core Team, 2012; parameter values: span = 3/4, degree = 1, evaluation = 100).

3. Results

3.1. Temperature and salinity in the laboratory

The ranges of running seawater temperature in the laboratory aquaria for rearing decapodids and juveniles of *Nihonotrypaea harmandi* were: (1) Batch 1 – 29.0–26.9 °C from Day 0 to Day 10 (from 21 August to 10 September, 2010) and 28.3–23.6 °C from Day 11 to Day 57 (from 11 September to 18 October, 2010); (2) Batch 2 – 25.3–23.6 °C (from 1 to 18 October, 2010); and (3) Batch 3 – 27.9–24.2 °C (from 24 August to 24 September, 2011). Although no measurement was made for the corresponding salinity, some mean (± SD) values of the seawater in the 30-l tank used for the concomitant zoeal rearing are available as a reference: (1) for Batch 1 – 32.3 ± 0.2 (number of measurements = 1388) from 21 to 30 August, 2010; and (2) for Batch 3 – 32.6 ± 0.2 (number of measurements = 22640) from 24 August to 24 September, 2011.

3.2. Individual molting events and occurrence of linea thalassinica in fed shrimps

In the batch of 34 decapodids reared individually with food and without sediment in the laboratory to track their molting events, exuviae were found for the first time on Day 3 [*N* (number of specimens observed) = 7] and subsequently on Day 4 (*N* = 4) (Fig. 2A, solid circles). Of these newly-appeared juveniles I, seven were fixed (three from Day 3 and four from Day 4), and all these possessed the linea thalassinica. In contrast, it was absent in the six decapodids that had not yet molted and fixed on Day 4. The second group of dates when exuviae were found comprised Days 9

Fig. 2

505 (*N* = 3) and 10 (*N* = 6). The third group of dates ranged more widely, including Days 15 (*N* = 1), 16
506 (*N* = 1), 19 (*N* = 2), 20 (*N* = 2), 21 (*N* = 1), and 25 (*N* = 1). Of the second and third groups, 13
507 shrimps were fixed (two from Day 9, six from Day 10, and each one from Days 15, 16, 19, 20, and
508 25), and all these possessed the linea thalassinica. Through the first to third groups, two sets of
509 discrete occurrence of exuviae were found for identical shrimps, with one on Days 3 and 15 and the
510 other on Days 9 and 19.
511
512 *3.3. Molting and occurrence of linea thalassinica in fed shrimps reared in groups*
513 In the shrimps reared in groups with food and without sediment in the laboratory, exuviae were
514 found for the first time on Days 3 and 4 (number of individuals = 10), with the furthest records for
515 one on Day 38 and the other one on Day 46. The linea thalassinica never appeared during Day 0 to
516 Day 2 [*N* (total number of specimens) = 55 to 120; Fig. 2B, circles]. The subsequent daily change
517 in the proportion of occurrence was 17.6% on Day 3 (*N* = 51), 63.6% on Day 4 (*N* = 66), 83.3% on
518 Day 5 (*N* = 60), and 97.4% on Day 6 (*N* = 38) and 100% thereafter (cumulative total *N* for Days 7
519 to 13 = 156). When linearly interpolated between Day 3 and Day 4, the 50% proportion was
520 reached on Day 3.7.
521 The shrimps showing appreciable apolysis in their rostra and thus apparently indicating the
522 premolt stage occurred around the first and second groups of molting events [Fig. 2A, blank
523 circles*; N* (total number of shrimps examined on each date) is indicated in Fig. 2B]. The values of
524 rostrum length for these shrimps measured to its epidermis tip were about half those to the cuticle
525 tip [Fig. 2C: 52% on Days 2 to 5 inclusive (*N* = 58) and 48% on Days 8 and 11 inclusive (*N* = 4)].
526 The linea thalassinica was absent in all shrimps in the first group, in which their premolt stage was
527 recorded for the first time on Day 2, followed by the peak on Day 3. The second group of shrimps
528 appeared on Days 8 and 11, which was at around the second group of exuviae occurrence. In

particular, Day 8 was just prior to the earliest emergence of exuviae on Day 9. The linea thalassinica was present in all these shrimps. Thereafter, no shrimps at the apparent premolt stage were found. Moreover, in any other cases encountered in both laboratory and field, shrimps with appreciable apolysis in their rostra were never found.

3.4. Molting events and survivorship in starved shrimps

Of the 26 decapodids maintained starved in four groups without sediment in the laboratory, three exuviae were found for the first time on Day 3. The shrimps were fixed on Days 5, 10, 13, and 16, when all of them possessed the linea thalassinica. Their survival rates on these dates were 75% (9/12), 100% (5/5), 40% (2/5), and 50% (2/4), respectively.

3.5. Substratum choice by decapodids and occurrence of exuviae and linea thalassinica

In the laboratory experiment testing for alternative choice by decapodids between sediments from the Amakusa-Nada bed (coastal ocean) and from the Tomioka Bay sandflat inhabited by adults, 91 of a total of initially released 97 decapodids were found buried alive in either type of sediment 1 d later. Usually one or two burrow openings had emerged on the sediment surface, with discarded sediment around. At times burrows had been constructed along the transparent cup wall, through which their cemented inner lining was seen. In U-shaped burrows with two surface openings, the lowest part of the U ran on the cup bottom. These retrieved shrimps had neither selected nor repelled either type of sediment significantly: (1) Day-0 decapodids, experimental set 1: $p = 0.095$ (eight from subtidal sediment vs. 13 from intertidal sediment, with one swimming in the water column and one dead on the sediment surface); (2) Day-0 decapodids, experimental set 2: $p = 0.047$ (15 subtidal vs. eight intertidal, with one swimming and one dead); (3) Day-1 decapodids: $p = 0.42$ (12 subtidal vs. 12 intertidal); and (4) Day-2 decapodids: $p = 0.20$ (13 subtidal

553 vs. 10 intertidal, with one swimming and one dead). Of these four sets, exuviae were found only
554 from the Day-2 set (five ones collected on Day 3). The linea thalassinica was absent in all shrimps
555 retrieved on Day 1 [*N* (number of shrimps from both sediment types inclusive) = 41; three of the 44
556 shrimps became damaged at the time of retrieval and were excluded from morphological analysis]
557 and on Day 2 (*N* = 24) but was present in 52% of those retrieved on Day 3 (*N* = 23) (Fig. 2B,
558 crosses). The latter value was 2.7 times greater than the proportion in the specimens reared without
559 sediment (and with food) and retrieved on Day 3. Thus, with sediment, the 50% proportion was
560 reached 0.7 d earlier (Section 3.3).
561
562 *3.6. Daily change in rostrum length in fed shrimps reared in groups or individually*
563 The range and mean (± SD) values for rostrum length of the decapodids that had been reared in
564 groups with food and without sediment and emerged on Day 0 in the laboratory were 0.32–0.59 Fig. 3
565 mm and 0.43 (± 0.06) mm [*N* (total number of specimens) = 120; Fig. 3A,B]. The mean RL values
566 became smaller slightly to 0.42 mm on Day 1 but precipitously to 0.32 mm on Day 2, 0.27 mm on
567 Day 3, and 0.22 mm on Day 4. The values stayed around 0.20 mm on Days 5–7 and rapidly became
568 smaller to reach 0.16 mm on Days 8–10 inclusive. After Day 8, the mean + SD values were almost
569 below 0.2 mm. The mean value became much smaller on Day 11, from which on to Day 57 it was
570 around a grand mean value of 0.13 mm [note that specifically, data for Days 15 to 25 were derived
571 from shrimps reared individually (Section 3.2); for all other cases, shrimps reared in groups were
572 used]. The mean (± SD) RL for the five adult specimens was 0.24 (± 0.04) mm. For the specimens
573 at the premolt stage, the RLs measured to the cuticle tip were apparently greater than those of the
574 specimens with no signs of apolysis on each corresponding date (Fig. 2C), suggesting the transient
575 expansion in rostrum immediately prior to the molting event. The RLs from the premolt-stage
576 specimens were not included in the above-mentioned values (Fig. 3).

From the characteristic dropping pattern in the mean (± SD) and median RL values of shrimps during Day 0 to Day 5, the 0.36- and 0.30-mm RLs appear to disjunctively demarcate the three rostrum-length groups: (1) long RL group, with RLs ≥ 0.36 mm; (2) intermediate RL group, with 0.36 mm > RLs ≥ 0.30 mm; and (3) short RL group, with 0.30 mm > RLs. The RLs of most shrimps on Days 0 and 1 belonged to the long RL group, accounting for 95.8 and 90.9% of the specimens, respectively, with the remainders in the intermediate RL group (N = 55 on Day 1; Fig. 3C). Of the RLs on Day 2 [N = 47; for all Day numbers including Day 2, shrimps at the premolt stage were excluded (Section 3.3)], 19.1% belonged to the long RL group (12.8% RLs = 0.36 mm), 46.8% to the intermediate RL group, and 34.1% to the short RL group. Of the RLs on Day 3 (N = 26), 50.0% belonged to the intermediate RL group, with the other half in the short RL group. Of the RLs on Day 4 (N = 59), 10.2% belonged to the intermediate RL group, with 89.8% in the short RL group. Of the RLs on Day 5 (N = 50), 2.0% belonged to the intermediate RL group, with 98.0% in the short RL group. For shrimps at the premolt stage on Days 2–5 inclusive, the mean (± SD) RL measured to the epidermis tip was 0.19 ± 0.03 mm (N = 58).

Of the shrimps retrieved on Days 3–6, all rostrum lengths for those possessing the linea thalassinica belonged to the short RL group. In the shrimps lacking the linea thalassinica on Day 3 (N = 17; those at the premolt stage on this date and later were excluded), 76.5% RLs belonged to the intermediate RL group, with the 23.5% in the short RL group. On Day 4 (N = 17), these percentage values were 29.4% and 70.6%, respectively. On Days 5 and 6, only one specimen without the linea thalassinica was present, with its RL being 0.16 mm.

3.7. Daily change in pereiopod exopod distribution in fed shrimps reared in groups

In the shrimps reared with food and without sediment in the laboratory, the exopods were distributed on pereiopods 1–4 but not on pereiopod 5. The number of exopod-equipped pereiopods

601 listed below was from either side of the body, as their distribution pattern appeared the same
602 between both sides in intact specimens. The highest and second highest proportions were recorded
603 on the three and two pereiopods on Day 0 and on the one and two pereiopods on Day 1 (Fig. 4A). Fig. 4
604 The specimens that had lost all pereiopod exopods emerged as early as on Day 1, occupying 2% of
605 the total number. This proportion rapidly increased to 74% on Day 2. The exopods were almost lost
606 on Day 4 (in 97% of the specimens) and completely on Day 6. With dates, the exopods were lost
607 successively from pereiopod 4 toward anteriorly (Fig. 4B). The proportion of the specimens that
608 had exopod-equipped pereiopod 4 accounted for 17% on Day 0 and became zero on Day 2. Those
609 pereiopod 3s accounted for 63 and 16% on Days 0 and 1, respectively, and became zero on Day 2.
610 Those pereiopod 2s accounted for 91 and 49% on Days 0 and 1, respectively, with the proportion
611 sharply dropping to 5% on Day 2. Those pereiopod 1s accounted for over 98% on Days 0 and 1,
612 with the proportion dropping to 28 and 20% on Days 2 and 3, respectively, and to 1.5% on Day 4.
613 Along with the appearance of their linea thalassinica, the shrimps had lost all exopods (N = 9 on
614 Day 3, N = 42 on Day 4, N = 50 on Day 5, and N = 38 on Day 6).
615
616 *3.8. Effects of sediment on rostrum length and pereiopd exopod distribution*
617 Once having experienced the burrowing into the sediment, the process of both shortening of
618 rostrum length and losing of pereiopod exopods in shrimps was generally accelerated as compared
619 with those reared without sediment. The materials for this comparison came from those listed in
620 Sections 3.5–3.7.
621 The proportions of shrimps in the three rostrum-length groups (defined in Section 3.6) to the
622 total number of shrimps (N) with sediment on each of the three retrieval dates were: (1) Day 1 (N =
623 41) – 68.3% in the long RL group and 31.7% in the intermediate RL group; (2) Day 2 (N = 24) –
624 12.5% in the long RL group, 62.5% in the intermediate RL group, and 25.0% in the short RL group;

and (3) Day 3 (N = 22) – 4.5% in the intermediate RL group and 95.5% in the short RL group (Fig. 3C). On Day 1, the proportion in the intermediate RL group was 3.5 times greater in the treatment with sediment than without it. On Day 3, the proportion in the short RL group was 1.9 times greater in the treatment with sediment. The overall mean (± SD) RLs with and without sediment on the three dates were: (1) Day 1 – 0.38 ± (0.04) mm (N = 41) and 0.42 ± (0.05) mm (N = 55); (2) Day 2 – 0.31 ± (0.03) mm (N = 24) and 0.32 ± (0.05) mm (N = 47); and (3) Day 3 – 0.20 ± (0.05) mm (N = 22) and 0.27 ± (0.05) mm (N =26) (Fig. 3B). Mann-Whitney U-tests detected significant differences between the two treatments for Days 1 and 3 ($p < 0.001$) but not for Day 2 ($p = 0.57$). Such more rapid shortening of rostrum length with sediment was particularly evident on Day 3, when its mean RL value was nearly the same as that without sediment on Day 4.

The highest proportions of pereiopods with exopods on Day 1 lay on the zero exopod-equipped pereiopod in the treatment with sediment [54% of N (= 41)] and on the one exopod-equipped pereiopod in the treatment without sediment [49% of N (= 57)] (Fig. 4A). The frequency distributions of pereiopods with exopods were significantly different between the two treatments ($p < 0.001$, χ^2-test, $d.f.$ = 3; data for three and four exopod-equipped pereiopods combined). On Days 2 and 3, the highest proportions were on the zero exopod-equipped pereiopod for both treatments: (1) Day 2 – 54% of N (= 24) with sediment and 74% of N (= 58) without sediment; and (2) Day 3 – 87% of N (= 23) with sediment and 82% of N (= 51) without sediment. The frequency distributions were not significantly different between the two treatments on Day 2 ($0.2 < p < 0.3$, $d.f.$ = 2; data for the one and two exopod-equipped pereiopods combined). For Day 3, the χ^2-test was not applicable to the frequency distributions due to too low values for the one to three exopod-equipped pereiopods.

3.9. Morphological characters in larvae collected from water column at sea

649 In the decapodid (and possible juvenile) specimens collected from the water column at the
650 coastal ocean site and the bay (= Tomioka Bay) mouth site (Fig. 1A), no one possessed the linea
651 thalassinica. Almost all shrimps belonged to the larger two of the three rostrum-length groups (Fig.
652 5). The proportion of shrimps in each group to the total number of shrimps (*N*) were: (1) coastal
653 ocean site (*N* = 276) – 49.6% in the long RL group and 50.4% in the intermediate RL group; and
654 (2) bay mouth site (*N* = 58) – 70.7% in the long RL group, 25.9% in the intermediate RL group,
655 and 3.4% in the short RL group (one 0.28 mm and one 0.26 mm).

Fig. 5

656 The shapes of the frequency distribution of the number of exopod-equipped pereiopods were
657 similar between the two sites for each of the two larger rostrum-length groups (Fig. 6A,B). In both
658 groups, the frequencies were the highest for the four exopod-equipped pereiopods, successively
659 decreasing with fewer exopod-equipped pereiopod numbers. When the frequency distributions are
660 compared between shrimps from the coastal ocean site and from the laboratory rearing in groups
661 with food and without sediment, the tendency for more exopod-equipped pereiopod numbers in the
662 field is obviously found for both RL groups. In the laboratory, (1) the highest frequency in the long
663 RL group was for the two and three exopod-equipped pereiopods, followed by the one exopod, and
664 (2) the highest frequency in the intermediate RL group was for the zero exopod-equipped pereiopod,
665 successively decreasing with more exopod numbers. The χ^2-tests detected a significant difference
666 in the frequency distributions between field (data from two sites combined) and laboratory for each
667 RL group (for both groups, $p < 0.001$, *d.f.* = 4).

Fig. 6

668

669 *3.10. Morphological characters of decapodids derived from the lowest-temperature tank*

670 Of the Day-0 decapodids that were derived from the zoeal rearing tank set at 17.5 °C in the
671 laboratory (Batch 4), morphology was examined for 45 specimens. No shrimps possessed the linea
672 thalassinica. Except for one individual belonging to the intermediate rostrum-length group (RL =

673 0.33 mm), all decapodids were in the long RL group, with the range and mean (± SD) of 0.36–0.63
674 mm and 0.45 (± 0.07) mm. No significant difference in median RL was detected against the Day-0
675 decapodids derived from Batches 1–3 reared at higher temperatures (Fig. 3A,B; Mann-Whitney
676 *U*-test, $p = 0.25$). In contrast, the higher number of pereiopod exopods were retained in the shrimps
677 from Batch 4, with 96% on the four and 4% on the three (cf. Fig. 4A).
678
679 *3.11. Morphological character changes and growth patterns through decapodid and juvenile stages*
680 In the 3-mo period from August to November, 1994 for the field rearing of decapodids and
681 juveniles on the Tomioka Bay sandflat, the maximum and minimum temperatures of the ambient
682 subsurface sediment gradually decreased from 29.3 to 24.2 °C and from 26.8 to 19.9 °C, Fig. 7
683 respectively (Fig. 7A; values plotted from 5 August as Day 0; initially set values were excluded
684 from description).
685 Of the 19 smallest-sized shrimps collected on 5 and 8 August and 17 September 1994 inclusive
686 for estimating their initial age composition as a reference to the subsequent field rearing, both linea
687 thalassinica and all pereiopod exopods were absent in 14 ones, and the linea thalassinica present but
688 all exopods absent in five ones [Group 1 and Group 2 on Day 0 (field), respectively]. In Group 1,
689 the rostrum lengths of nine shrimps belonged to the long RL group, ranging from 0.37 to 0.43 mm
690 (Group 1-1), and those of the other five shrimps to the intermediate RL group, ranging from 0.30 to
691 0.35 mm (Group 1-2). The ranges for Groups 1-1 and 1-2 were almost within the mean (± SD) RLs
692 for the Day-1 and Day-2 (lab; with sediment) shrimps, respectively (Fig. 3B). In Group 2, the
693 rostrum lengths belonged to the short RL group, ranging from 0.17 to 0.23 mm, which was within
694 the mean (± SD) RL for the Day-3 (lab; with sediment) shrimps. The morphological characteristics
695 of shrimps in Group 2 were also shared by those in the Day-3 (lab; without sediment) and several
696 older shrimps possessing the linea thalassinica (Figs. 2B, 3A, and 4).

697 The total lengths of shrimps in Group 1-1 on Day 0 (field) ranged from 4.1 to 4.7 mm, with
698 mean (± SD) of 4.5 (± 0.2) mm [*N* (number of specimens) = 9]. Those TL values for Group 1-2 and
699 Group 2 on Day 0 (field) were 4.6–4.9 mm and 4.8 (± 0.1) mm (*N* = 5), and 4.5–5.0 mm and 4.8 (±
700 0.2) mm (*N* = 5), respectively. The mean (± SD) TL for Groups 1 and 2 on Day 0 (field) inclusive
701 was 4.6 (± 0.3) mm (*N* = 19) (Fig. 7B,C). Those values on Days 2 and 4 (field) were 5.0 (± 0.2) mm
702 (*N* = 12) and 5.5 (± 0.4) mm (*N* = 9), respectively. Considering these fairly constant standard
703 deviations about means, the daily growth rate of decapodids and juveniles during the initial four
704 days in the field can be estimated using mean TLs, yielding 0.2–0.25 mm d^{-1}. This value is
705 consistent with growth rate estimates for the entire rearing period up to Day 90 (field), derived
706 from the linear regression equations of TL (mm) on cumulative days: (1) TL = 0.19 × (Day number)
707 + 4.89 (R^2 = 0.90; $p < 0.001$) for all TL data [Fig. 7C, solid line (plots not shown); *N* (expressed as
708 *N*′) on each date given in Fig. 7B,C]; and (2) TL = 0.19 × (Day number) + 4.97 (R^2 = 0.99; $p <$
709 0.001) for the mean TLs (*N* = 13; line not shown in the figure). At a daily growth rate of 0.2-mm
710 TL d^{-1}, Day-0 (field) shrimps could reach 20-mm TL in ca. 80 d. On Day 90 (field), the TLs ranged
711 from 16.3 to 28.5 mm, with mean (± SD) of 21.5 (± 4.5) mm (*N* = 8). The breeding season of the *N.*
712 *harmandi* population on the Tomioka Bay sandflat spanned from June through October, during
713 which time the subsurface temperature exceeded 20 °C, and the minimum TL of ovigerous females
714 was 17.9 mm, with a grand mean value of 20.9 mm for all sampling occasions (Tamaki et al., 1997).
715 In the present field rearing, a total of 21 shrimps with TLs ≥ 17.0 mm were retrieved from the
716 Day-45, -60, and -90 (field) samples, in which 13 females were contained. All their ovaries were
717 undeveloped.

718 The growth rates of decapodids and juveniles reared in groups with food and without sediment
719 in the laboratory were much lower than those reared in the field (Fig. 7B,C, stars). The range and
720 mean (± SD) TL on Day 0 (lab) were 4.0–5.7 mm and 4.8 (± 0.35) mm (*N* = 119), and those values

721 on Day 1 (lab) were 4.1–5.2 mm and 4.6 (± 0.3) mm (N = 55). There was a significant reduction in
722 the median TL from Day 0 (lab) to Day 1 (lab) (Mann-Whitney U-test, $0.001 < p < 0.01$), with the
723 proportion of TLs > 5.0 mm having decreased from 28.6 to 7.2% (Fig. 8). A significant positive
724 correlation existed between TL and CL for each date [Day 0 (lab): $r = 0.55$ and $p < 0.001$; Day 1
725 (lab): $r = 0.37$ and $0.001 < p < 0.01$], and the linear regression equations of TL on CL were: (1) TL
726 = 1.18CL + 3.27 [$p < 0.001$; Day 0 (lab)]; and (2) TL = 0.64CL + 3.84 [$0.001 < p < 0.01$; Day 1
727 (lab)]. Thus, the shortening of both carapace and pleon lengths combined to bring about the
728 decrease in total length from Day 0 to Day 1 (lab). The TL-value distribution and its mean (± SD)
729 for the Day-1 (lab) shrimps were very close to and equal to those for Group 1 of the Day-0 (field)
730 shrimps, respectively. On Day 2 and Day 3 (lab), the mean (± SD) TLs were 4.65 (± 0.3) mm (N =
731 47) and 4.6 (± 0.3) mm (N = 26), respectively. There was no significant difference in median TLs
732 among Days 1–3 (lab) (Kruskal-Wallis test, $p = 0.77$). Although a slight increase in TL took place
733 on Days 4 and 5 (lab) [5.0 (± 0.4) mm (N = 54) and 4.9 (± 0.3) mm (N = 50)], the mean TLs on
734 Days 6–8 (lab) returned to the former low level of 4.6–4.7 mm (Fig. 7B). After Day 9 (lab),
735 however, the TL began to increase at a constant rate of 0.06 mm d^{-1}, which can be confirmed by a
736 significant linear regression equation of TL on cumulative dates from Day 9 (lab) [TL = 0.06 ×
737 (Day number) + 4.51 ($R^2 = 0.88$; $p < 0.001$); data from Days 9, 10, 11, 13, 43, 50, and 57 (lab) were
738 used for the calculation (Fig. 7C, broken line; only a single individual on Day 43 was due to the
739 death of other ones)]. An exceptionally high growth rate for the laboratory-reared shrimps was
740 recorded for those reared individually with food and without sediment and retrieved on Days 15, 16,
741 19, 20, and 25 (lab) (Fig. 7B,C, triangles; each N = 1; Section 3.2). Their TL values lay close to the
742 linear regression line for the field-reared shrimps.

Fig. 8

743 The smoothing curve for the relative pleon length of decapodids and juveniles based on Loess
744 regression gradually ascended with age from the initial value of 0.73 on Day 0 (lab) to a reflection

745 point around Days 25 (lab) – 27 (field) (Fig. 9A). When all CL and TL data for the specimens on
746 Day 0 (lab) and Day 1 (lab), respectively, were used (*N* = 119 and 55; Fig. 8), the mean values were
747 also 0.73 for both dates (mean TL/CL ratios = 3.75 and 3.74). From Days 25 (lab) – 27 (field) on,
748 the relative pleon lengths more gradually approached the mean value of 0.80 for adults.

Fig. 9

749 Observations on the uropod exopod of several shrimps without the linea thalassinica retrieved
750 up to Day 3 (lab) revealed the shape as elliptical, with the suture present between anterior and
751 posterior plates on a same plane. In shrimps with the linea thalassinica from Day 4 (lab), the
752 posterior plate became somewhat convex along its left side and slightly elevated from the anterior
753 one. The smoothing curve for the short-axis length/long-axis length ratio ascended with age from
754 the initial value of 0.57 to a reflection point around Days 25 (lab) – 27 (field), passing the value of
755 1.0 on Day 60 (field) and approaching the mean value of 1.09 for adults (Fig. 9B). On Day 0 (lab),
756 the distal apex angle was acute (value on the smoothing curve = 55.0°), while the left and right
757 apex ones were obtuse and nearly the same (values on the curve = 117.9° and 121.4°; Fig. 9C).
758 There was a reflection point also around Days 25 (lab) – 27 (field) in each curve for the three
759 angles. The distal apex and two other angles came nearer with age, the curve for the former passing
760 that for the left apex angle on Day 60 (field) and approaching that for the right apex angle on Day
761 90 (field). On this date, the mean values for the three angles converged at 79.2–94.0°, which were
762 close to those values for adults (82.0–88.2°). These changes in both length and angle dimensions of
763 the uropod exopod with age indicate the transition in shape from elliptical to sub-circular.
764
765 **4. Discussion**
766
767 The water temperature and salinity in the laboratory rearing or substratum-choice experiments
768 for decapodids of *Nihonotrypaea harmandi* largely corresponded to the values recorded for the

769 water column between the surface and 30 m in Amakusa-Nada in mid-summer (Sections 3.1 and
770 3.5; Fig. 1B). In the field water column, substantial numbers of decapodids were collected from this
771 depth range during the night but only very few during the day (Tamaki et al., 2010, fig. 4). Thus,
772 the development and behavior of decapodids in their deepest positions below 60 m during the day,
773 with the lowest temperature and highest salinities, were not reproduced under the present
774 experimental conditions except for the one rearing experiment set at 17.5 °C (Section 3.10). The
775 water temperature and salinity in both laboratory and field rearing of juveniles (Section 3.1; Fig.
776 7A) also largely corresponded to the values recorded for the August–October section of a two-year
777 benthic population monitoring on the Tomioka Bay sandflat, which were 20–28 °C and 32.0–33.8,
778 respectively (Tamaki et al., 1997).

779 The convincing evidence for the occurrence of metamorphosis from the decapodid to the
780 juvenile I in the present *N. harmandi* specimens reared in the laboratory was the emergence of
781 exuviae, which was always accompanied by the first appearance of the linea thalassinica on their
782 carapaces (Sections 3.2–3.5). Thus, for the smallest shrimps with TLs around 4–5 mm (Fig. 7), the
783 linea thalassinica is the character enabling us to most easily distinguish the juvenile I from the
784 decapodid. The explicit descriptions on the linea thalassinica for callianassid decapodids and
785 juveniles are limited: (1) for the decapodid – absent in *N. petalura* (see Konishi et al., 1990), *N.*
786 *japonica* (see Miyabe et al., 1998), *N. harmandi* (see Konishi et al., 1999), and *Lepidophthalmus*
787 *sinuensis* and *L. louisianensis* (see Nates et al., 1997) but present in *Sergio mirim* [as *Callichirus*
788 *mirim*; Rodrigues, 1984]; and (2) for the juvenile I – present in *Callichirus masoomi* [as
789 *Callianassa* (*Callichirus*) *kewalramanii*; Sankolli and Shenoy, 1975].

790 The duration of the decapodid stage of *N. harmandi* can be estimated based on the daily change
791 in the proportion of specimens with the linea thalassinica reared with food and without sediment in
792 the laboratory and on the occurrence of those specimens at the premolt stage, as evident in

793 appreciable apolysis in their rostra (Fig. 2A,B). The duration spanned from 3 to 6 d, with half the
794 decapodids becoming juveniles I in 3.7 d. However, it must be noted that this measure should be
795 regarded as one of the possible ranges, shortened or lengthened in response to various stimuli such
796 as the presence of sediment (Fig. 2B). The duration estimated for decapodids of *N. harmandi* is
797 comparable to those values recorded for a few other callianassid species: (1) 3.0–3.5 d (Strasser
798 and Felder, 1999a) and 4–6 d (Abrunhosa et al., 2008) for *Callichirus major*; (2) 4.3–6.6 d for *C.*
799 *islagrande* (see Strasser and Felder, 2000); and (3) 8 d for *Lepidophthalmus sinuensis* (see
800 Abrunhosa et al., 2005).

801 Following the decapodid stage in *N. harmandi*, two or three juvenile instars could be tracked
802 using the daily record on the emergence of exuviae in the laboratory (Sections 3.2 and 3.3). Since a
803 fair number of exuviae were retrieved on Days 9 and 10, it is most probable that the shortest
804 duration of the juvenile I was 6 d (starting from Day 3 or 4). The pattern for appearance of the
805 premolt stage would also support this estimate (Fig. 2A). A less convincing value was available for
806 the duration of the juvenile II, as a fewer number of exuviae were retrieved from Day 9 (or 10) to
807 Day 15–21, with the possible shortest duration being 6 d. The final date of the juvenile II might be
808 extended to Day 25. Alternatively, with the possible fastest developmental speed, the juvenile III
809 could span from Day 15–16 to Day 21–25, lasting a minimum of 6 d. It is uncertain which juvenile
810 instars the exuviae retrieved on Days 38 and 46 came from. The records on the rearing of
811 callianassid juveniles thus far have been up to the juvenile II, with no durations for respective
812 instars explicitly stated: (1) to the juvenile I for *Callichirus masoomi* [as *Callianassa* (*Callichirus*)
813 *kewalramanii* (see Sankolli and Shenoy, 1975)] and *Lepidophthalmus siriboia* (see Abrunhosa et al.,
814 2005); and (2) to the beginning of the juvenile II for *C. major* and *C. islagrande* (see Strasser and
815 Felder, 1999c, 1998).

816 In the laboratory, decapodids of *N. harmandi* became juveniles I in as short as 3 d even in the

absence of food (Section 3.4), indicating the existence of secondary lecithotrophy known for several decapod taxa (Anger, 2001, 112–113). By contrast, starved zoeae I survived only for a maximum of 5 d and never proceeded to the zoea II (Y. Saitoh and A. Tamaki, unpublished data). As for other callianassid decapodids, secondary lecithotrophy has been recorded only for *Lepidophthalmus siriboia*, which was facultative, feeding on *Artemia* nauplii when provided; its zoeae (up to stage III) also underwent lecithotrophic development (Abrunhosa et al., 2008). Decapodids of *L. sinuensis* and *L. louisianensis* were carnivorous as well as the preceding zoeae with up to two stages (Nates et al., 1997). Regarding decapodids of callianassids with four to six zoeal stages that undergo planktotrophic development, lowered feeding activity (on *Artemia* nauplii) compared with zoeae was noted for *Callichirus major* (see Strasser and Felder, 1999a) and *C. islagrande* (see Strasser and Felder, 2000).

The results of the rearing experiment using starved decapodids and juveniles of *N. harmandi* in groups without sediment in the laboratory also indicate that beyond the decapodid stage, secondary lecithotrophy could be extended until some point at the juvenile II [Day (lab) 16; Section 3.4 and preceding paragraph]. Even fed decapodids and juveniles reared in groups without sediment in the laboratory exhibited no substantial growth throughout the juvenile I [until Day (lab) 9; Fig. 7]; a transient, slight increase in TL on Days 4 and 5 (lab) would most probably be due to water uptake, associated with molting from the decapodid to the juvenile I (cf. Anger, 2001). The little or no growth suggests that both decapodids and juveniles I could not effectively ingest diatoms when individuals were put together. In this case, juveniles resumed feeding activity from Day 9 (lab), which would be the beginning date of the juvenile II (preceding paragraph).

The non-feeding habit of decapodids and juveniles I of *N. harmandi* was not necessarily the rule. In the field-rearing of shrimps, the majority (74%) of the Day-0 (field) shrimps were decapodids, with the linea thalassinica absent (Group 1 in Section 3.11; based on first paragraph of

841 the Discussion). Subsequently, the Day-0 (field) shrimps as a whole began to grow steadily at a
842 constant rate of 0.2-mm TL d^{-1} (Fig. 7). In the laboratory, the shrimps that were reared individually
843 with the diatom *Chaetoceros gracilis* and without sediment and retrieved on Days 15–25 (lab)
844 attained nearly the same total lengths as in the field-reared shrimps. These results, together with the
845 findings for the shrimps reared in groups in the laboratory (preceding paragraph), strongly suggest
846 that (1) the live *C. gracilis* were a right food item in terms of both quality and quantity, (2) only
847 when solitary, decapodids and juveniles of *N. harmandi* were able to feed on diatoms deposited on
848 the bottom net of the container to grow normally even without sediment to burrow into, and (3) in
849 the field, as soon as their settlement and burrow construction in the sediment were accomplished,
850 decapodids resumed feeding activity well prior to metamorphosis into the juvenile I. In an earlier
851 study, a mean daily growth rate of 0.032-mm CL d^{-1} was obtained for decapodids and the
852 subsequent juveniles of *N. harmandi* isolated individually in sterile sediment and fed with
853 refrigerator-stored *C. gracilis* spread on the sediment surface at a daily ration of 2.1×10^8 cells
854 (more than double the number provided in the present study; Yokoyama et al., 2005, table 1); using
855 the TL/CL ratio of 3.75 found in the present study (Section 3.11), this rate is equivalent to 0.12-mm
856 TL d^{-1}. Furthermore, for adult specimens of *N. harmandi* collected from the Tomioka Bay sandflat,
857 their dependence only on planktonic and benthic microalgae was demonstrated using carbon and
858 nitrogen stable isotope analysis (Shimoda et al., 2007). When confined and reared in groups in a
859 narrow container, decapodids and juveniles I would interfere with each other or compete for food,
860 both resulting in limited or no growth. Based on the experimental findings for fed and starved
861 decapodids and juveniles I together, their non-feeding mode may appear facultative. However,
862 caution must be used for differences between pre- and post-settlement states. Under restricted
863 conditions in the laboratory container, decapodids would perceive the surrounding environment as a
864 kind of sediment and thus have decided to become the benthos (“quasi”-settlement: new term

865 coined in this study to stand for forced settlement state in the laboratory). This explains the feeding
866 activity of individually reared decapodids even without sediment. It is possible that decapodids
867 present in the free water column at sea would regard themselves as the plankton, exhibiting obligate
868 secondary lecithotrophy. Decapodids perform a normal diel vertical migration, but not tidally-timed
869 vertical migration during the night (Tamaki et al., 2010). At some phase of the tidal cycle, flood
870 tides occur twice during one night in the present water area. It may cost the non-feeding decapodid
871 an expenditure of stored energy to make ascent migration for several tens of meters in response to
872 each flood tide. The adaptive significance of decapodids' non-feeding habit at sea has been
873 interpreted for megalopae of the pagurid hermit crab (Dawirs, 1981; Anger, 1989) and the hippid
874 sand crab (Harvey, 1993) in light of their strategy of concentrating on locating and selecting
875 suitable habitats to settle on rather than partially spending time for feeding.

876 In the callianassid larval morphology literature, (1) disappearance of dorsal spine
877 on the second pleonal segment, (2) shortening of rostrum, and (3) shrinkage or
878 disappearance of pereiopod exopods are commonly described as one distinct set of
879 transitional changes from last zoeal to decapodid stages. Newly-metamorphosed juveniles I
880 of the present *N. harmandi*, with their linea thalassinica, had RL values below 0.30 mm and had
881 lost all pereiopod exopods (Sections 3.6 and 3.7). The present study is the first to give quantities for
882 these characters through the course of the decapodid stage (Figs. 3 to 6). Possible functional roles
883 that the elongated dorsal spine and rostrum play during the zoeal stages have yet to be established.
884 Using Chinese mitten crab zoeae reared at different salinities, Anger (2003) suggested that rostrum,
885 in concert with dorsal spine, afford buoyancy to the body. By comparing the dorsal spine lengths
886 for two conspecific populations of *Callichirus major* zoeae from different-salinity water regimes,
887 Strasser and Felder (1999a) raised the same hypothesis. It remains unknown for decapodids of *N.*
888 *harmandi* whether their relatively long rostra as compared with juveniles' (Fig. 3) still contribute to

889 floating. The natatory function of pereiopod exopods during the zoeal stages is replaced by
890 pleopods in the decapodid stage. In the literature on callianassid shrimp to date, the most posterior
891 exopod-equipped pereiopod has been recorded as the fourth one, including the present *N. harmandi*,
892 except for the fifth one for *C. major* (see Strasser and Felder, 1999a). It must be noted that the
893 distribution of the remnant pereiopod exopods can vary depending on the age of the decapodid
894 specimens used for respective descriptions (Fig. 4). The argument that follows is based on a
895 premise that the above morphological changes are the process through which those parts with no
896 longer functional roles for benthic life become degenerated and that rostrum size and pereiopod
897 exopod distribution and numbers, together with body dimensions such as total length, can be useful
898 clues to estimate the ages of field-collected decapodids (and juveniles I) and to infer their states in
899 the immediate past such as pre- or post-settlement states.
900 Comparing results for the laboratory-rearing of decapodids of *N. harmandi* between without-
901 and with-sediment treatments, development rates toward the metamorphosis into the juvenile I
902 appeared accelerated with sediments by ca. 1 d, as evident in: (1) shortening of rostrum length (Fig.
903 3B,C), (2) reduction of pereiopod exopod numbers (Fig. 4A), and finally (3) emergence of the linea
904 thalassinica (Fig. 2B). The effect of sediment was pronounced for the Day-0 to Day-1 set and the
905 Day-2 to Day-3 set in the rostrum-length change and for the Day-0 to Day-1 set in the
906 pereiopod-exopod change. Substantial promotion was not observed for the other sets, suggesting
907 that decapodids confined to the narrow container without sediment for 1 d (from Day 0) had
908 perceived the surrounding environment as a kind of sediment, as mentioned previously. For
909 decapod crustacean decapodids, a fair amount of research have been done to detect a variety of
910 cues to shorten or lengthen the time to metamorphosis (Christy, 1989; Jensen, 1991; O'Connor,
911 1991; Harvey and Colasurdo, 1993; Harvey, 1996; Gebauer et al., 2004; Lecchini et al., 2010;
912 Stanley et al., 2012). In these studies, glass bowls containing clean offshore seawater (e.g. filtered,

913 coastal ocean seawater beyond estuarine plume) are generally accepted as one standard control that
914 is served against experimental treatments (for a review, see Forward et al., 2001): (1) this control
915 setup has been expected to be most neutral or inactive for competent decapodids, and
916 metamorphosis can be affected even by plasticizers and catalysts, which leach into seawater from
917 the plastics such as the container material used in the present study; (2) decapodids confined to the
918 control bowl eventually come to the metamorphosis within some limited time frame, probably
919 responding to tactile stimuli [presumably, an autonomic sequence triggered by the
920 “quasi”-settlement; such boundary effects may be alleviated by the use of a large container, which
921 is rare in cue-detecting experiments [e.g. > 100 l (Wolcott and De Vries, 1994)]; and (3) that limited
922 time can be regarded as a reasonable measure of the maximum duration of the decapodid stage. For
923 megalopae of anomurans and burrowing brachyurans, adult habitat-associated sediments induced
924 shorter times to metamorphosis by ca. 3 d in the diogenid hermit crab (Harvey, 1996) and in the
925 varunid crab (Gebauer et al., 2004), and ca. 8 d in the ocypodid fiddler crab (Christy, 1989; see also
926 O’Connor, 1991). For megalopae of that varunid crab, the receptiveness to sedimentary cues was
927 most valid in the earlier half of their molting cycle. For a congeneric species of that ocypodid crab,
928 water-soluble substances released by adults could also be a shortening factor, which was effective
929 only during the earlier period of the megalopal stage (O’Connor and Gregg, 1998). In the
930 alternative substratum choice by decapodids of the present *N. harmandi*, there was no significant
931 difference between sediments from the coastal ocean bed and from the intertidal adult habitat
932 (Section 3.5). There is a possibility that some water-soluble substances from the adult-inhabited
933 sediment might emanate to be adsorbed by coastal ocean sediment particles in the experimental cup.
934 At least it is certain that the grain size composition of the latter sediment was non-repellent. In a
935 previous laboratory rearing, decapodids placed on sterile silica sand swiftly made burrows in it and
936 maintained them stably [Mdϕ = 2.4, QDϕ (quartile deviation) = 0.4; Yokoyama et al., 2005]. All

these observations suggest fairly broad acceptability by decapodids for sandy sediments. The absence of the requirement for sediment organic matter may come from the feeding habit of adults, not relying on subsurface food but subducting surface-deposited fresh microalgae through the burrow openings (Shimoda et al., 2007). The burrow construction in sterile sediment has also been confirmed for newly-metamorphosed decapodids of two congeneric callianassid species (Strasser and Felder, 1999b): (1) decapodids of *Callichirus islagrande* accepted combusted sand as equally as the natural one; and (2) although, in *C. major*, combusted sand was less preferred than the natural one, its attractiveness was restored with immersion in seawater not necessarily containing adult-derived cues. Such receptiveness of sandy sediment even deprived of organic matter suggests that callianassid decapodids of some species simply need substrata suitable for their quick burrowing. This situation seems similar to behaviors of portunid crab megalopae, readily clinging to inorganic substrata such as air-conditioning filter material hung in the water column (Hasek and Rabalais, 2001; Moksnes et al., 2003). The prime significance of these kinds of substrata for those settling decapodids might be the provision of micro-habitats that serve to conceal them from predators as quickly as possible (Moksnes et al., 2003). In decapodids of *N. harmandi*, not alike to the case for sandy sediments, muddy sediments and boulder shore substrata would be rejected probably due to difficulty in constructing burrows there. Three species of *Nihonotrypaea* never occur in muddy tidal flats, and boulder shores around Tomioka Bay are inhabited by *N. petalura* only (Tamaki et al., 1999; Shimoda and Tamaki, 2004; Shimoda et al., 2007). Experimentally tested decapodids of the callianassid shrimp *Neotrypaea californiensis* exhibited significant preference for bare sediment versus shelly one (Feldman et al., 1997).

The distinctly long rostrum lengths in the Days-0 and 1 (lab; without sediment) decapodids of *N. harmandi* suggest that the “quasi”-settlement effect would not have become evident for this morphological character on the initial two dates and that the shortening tendency appeared

accelerated first on Day 2 (Fig. 3). By contrast, tactile stimuli seem to be more rapidly exerted on pereiopod exopods and reflected on their fewer numbers already on Day 0 (Fig. 4). Thus, the estimation of the two earliest decapodid ages for field-collected shrimps, with their linea thalassinica absent, would be more reliably made based on rostrum length. The 0-d old decapodids consisted of pre-settlement individuals and newly-settled ones (= settlers), while the 1-d old decapodids comprised pre-settlement individuals, newly-settled ones with 1-d pre-settlement duration (= 1-d old settlers), and post-settlement ones with 0-d pre-settlement and 1-d post-settlement durations (= 1-d old post-settlers). The last members can alternatively be called day-1 post-settlers derived from the 0-d old settlers. The settlers and post-settlers could be distinguished from each other based on their total lengths. Provided that the total lengths of newly-settled decapodids are within a narrow range regardless of ages owing to their pre-settlement non-feeding habit (Fig. 7B), a daily 0.2-mm increment in TL to post-settlement decapodids would help separate the previous settlers from successive newcomers. The rostrum lengths for the Group 1-1 decapodids collected from the Tomioka Bay sandflat on Day 0 (field) were closest to those for the Day-1 (lab) shrimps that had stayed in sediment for 1 d [i.e. Day-1 (lab; with sediment) shrimps], and the values for the Group 1-2 decapodids were so to those for the Day-2 (lab; with sediment) shrimps (Section 3.11). All these Group-1 decapodids had completely lost their pereiopod exopods, as compared with about half the shrimps on Day 1 (lab; with sediment) and only 2% on Day 1 (lab; without sediment) (Fig. 4A). The mean (± SD) total length for the Group-1-1 (field) decapodids was almost equal to that for Day 1 (lab; without sediment) which had been reduced from that for Day 0 (lab; without sediment) (Section 3.11; Fig. 7). The mean total length for the Group-1-2 (field) decapodids was greater than that for Day 1 (lab; without sediment) by 0.2 mm. Here, it should be taken into account that the collection of shrimps on the sandflat was conducted during daytime low tide. Tidal currents in Tomioka Bay are strong enough for all

985 zoeal-stage larvae of *N. harmandi* to be carried back and forth between the sandflat and the nearby
986 Amakusa-Nada within a one-night tidal cycle (Tamaki et al., 2010, figs. 1 and 7). Although, in that
987 study, the number of collected decapodids was too few to draw any inferences about their transport
988 process, it would be similar to that of the last-stage zoeae; based on the latter's diel and tidal
989 occurrence pattern at a point 2 km interiorly from the bay mouth site and 0.5 km off the sandflat,
990 the newly-settled decapodids that were collected on the sandflat would have had settled there
991 around the nighttime flood-tide hours ca. 9–10 h before in the possible shortest case. Thus, within a
992 single flood tide, some pre-settlement decapodids present on the eastern edge of the coastal ocean
993 could reach the sandflat (cf. Johnson and Gonor, 1982). In the portunid green crab *Carcinus*
994 *maenas*, the molting event of the last zoea into the megalopa was timed to flood-tide hours in the
995 laboratory, which was considered as adaptive in enhancing settlement on the intertidal zone (Zeng
996 et al., 1997). The molting to the megalopa in the cancrid Dungeness crab *Cancer magister* took
997 place mainly at night, which was considered as adaptive for reducing the risk from visual predators
998 (Fernandez et al., 1994). Although the time lag between actual larval settlement and sampling for
999 the present *N. harmandi* shrimps on the sandflat would be shorter than 1 d, it might have an
1000 identical effect on the rostrum length and total length of the 0-d old settlers and 1-d old settlers to
1001 be reduced to such levels as reached by decapodids on Day 1 (lab; without sediment; for RL and
1002 TL) and Day 2 (lab; without sediment; for RL) or Day 1 (lab; without sediment; for TL),
1003 respectively (Section 3.11). A similar possibility for time-lag influence on morphology (molt stage)
1004 of decapodids was pointed out for megalopae of the portunid blue crab *Callinectes sapidus* that
1005 settled on artificial substrata during the preceding night (Hasek and Rabalais, 2001). In the present
1006 study, 1-d old post-settlers of *N. harmandi* may have the same RL value as that for the 1-d old
1007 settlers but would reach the greater TL value by a 1-d increment. To conclude, the decapodids of
1008 Group 1-1 would be 0-d old settlers, whereas those of Group 1-2 would most probably be 1-d old

1009 post-settlers (derived from 0-d old settlers).

1010 The involvement of newly-metamorphosed 0-d old decapodids of *N. harmandi* in the
1011 successive transport and settlement events ranging from Amakusa-Nada to the Tomioka Bay
1012 sandflat suggests that these larvae have already become competent to settle shortly after their
1013 molting from the last zoeal stage while in the coastal ocean. Those decapodids that have
1014 successfully settled on the sandflat have to wait for at least 3 days to metamorphose into juveniles I,
1015 during which time they may stay buried in the sediment or change locations by swimming for a
1016 short distance. By contrast, of those incoming planktonic decapodids that have failed in
1017 encountering the adult-inhabited sandflat would not settle on habitats of very different types and be
1018 carried by ebb tidal currents back toward the coastal ocean, for which at least a 1-d delay in
1019 settlement chance until the next night ought to be entailed within their competence time window.
1020 When this time limit is expired, decapodids may settle indiscriminately on bottoms with
1021 unfavorable substrata such as coastal ocean bed and muddy or boulder intertidal shore, as is
1022 generally observed for meroplanktonic larvae (Pechenik, 1990; Forward et al., 2001). The
1023 settlement on the substratum by decapodids immediately after metamorphosis from their last zoeal
1024 stages has been demonstrated by laboratory and/or field experiments for the fiddler crab *Uca*
1025 *pugilator* (see Christy, 1989), the porcelain crab *Petrolisthes cinctipes* (see Jensen, 1991), the
1026 pagurid hermit crab *Pagurus maclaughlinae* (see Harvey, 1996), and the callianassid shrimp
1027 *Callichirus major* and *C. islagrande* (see Strasser and Felder, 1999b). The larval settlement even at
1028 the last zoeal stage was reported for the sand crab *Emerita talpoida* (see Harvey, 1993). For
1029 brachyuran crabs in general, it has not been established yet how early in the megalopal (postmolt or
1030 intermolt) stage megalopae become competent and respond to settlement cues (Forward et al.,
1031 2001). Although megalopae at their intermolt stage have been referred to as receptive in the field or
1032 used for experiments detecting cues to accelerate or deter metamorphosis (Hasek and Rabalais,

2001; Gebauer et al., 2004; Stanley et al., 2012), the relatively short duration of the postmolt stage might be a cause to be missed. In relatively sedentary brachyuran crabs with export-type larvae, adult distributions would be determined basically by habitat selection at the time of settlement by megalopae that have returned from coastal oceans (O'Connor, 1993; Paula et al., 2003). By comparison, some highly mobile forms such as portunid crabs perform secondary dispersal in their post-settlement megalopal stage (Moksnes et al., 2003). The migration by megalopae of other brachyuran species including *Callinectes sapidus* from estuary mouth toward upstream adult habitats using nocturnal flood tides or from entrance to coastal boundary layer toward coastal shore is believed to be done by pre-settlement megalopae at their later molt stage such as premolt stage (Lipcius et al., 1990; Morgan et al., 1996; Paula et al., 2003; Moreira et al., 2007; Olaguer-Feliú et al., 2010). In this scenario, the competence for settlement becomes activated first at some later molt stage upon receipt of appropriate cues in the course of approaching the final destination with specific vegetation or hard substrata such as stones. The underlying logic in these studies is that the nearer those pre-settlement megalopae are to adult habitats, the more advanced their molt stages are and the shorter the times to metamorphosis become. However, the molt stage of a decapodid merely suggests its age regardless of pre- or post-settlement states, not serving as a measure directly linked to competence for settlement (Jensen, 1991; Hasek and Rabalais, 2001). The time to metamorphosis for pre-settlement decapodids occurring away from the adult habitat can be longer even if they are already competent; they may simply be young or have never been exposed to molting-accelerating factors associated with adult habitats. Thus it remains to be determined whether the migration by the above-mentioned megalopae is in the pre-settlement substratum-selection process or in the post-settlement secondary dispersal process. In this vein, one term that confounds the understanding of settlement and metamorphosis processes in decapod crustaceans is "competence for metamorphosis" (e.g. Paula et al., 2003; Moreira et al., 2007). Since

the settlement triggers autonomic development with varying speeds toward the metamorphosis, which are basically separate events in decapodids, “competence” would better be attached to “settlement” only. Furthermore, what is meant by “delay in metamorphosis” should be specified to either “delay in settlement” or “delay between settlement and metamorphosis”. Some morphological characters which have had natatory functions and degenerate markedly from pre- to post-settlement states in the decapodid stage such as observed for pereiopod exopods in the present *N. harmandi* would render us to largely discriminate between assemblages in the two states (Fig. 6). Combined with a supposed adaptive significance for early-stage decapodids to quickly settle on broadly acceptable substrata to avoid predators as mentioned previously, their subsequent migration as post-settlers may be regarded as a fine-tuning behavior seeking for more favorable micro-habitats (Lecchini et al., 2010) or a further escape behavior from predators that nocturnally forage on surface-dwelling benthos (Moksnes et al., 2003).

In the specimens of *N. harmandi* larvae collected through the field water column at coastal ocean and bay mouth sites, only zoeae and decapodids were found, with no juveniles, as judged from the absence of the linea thalassinica on their carapaces (Fig. 1A; Section 3.9). Thus, decapodids would never settle on the coastal ocean bed. This result negates the applicability to the case of *N. harmandi* of the view that juveniles in decapod crustaceans are another returning component from coastal ocean to estuarine or coastal shore (Epifanio et al., 1984; McConaugha, 1988; González-Gordillo et al., 2003). Both rostrum length and pereiopod exopod distribution in the decapodids were nearly the same between the two sampling sites (Figs. 5 and 6), suggesting that both sites are parts of a common nursery ground for decapodids in Amakusa-Nada (Tamaki and Miyabe, 2000; Tamaki et al., 2010). Between the two sites, the eastward tidal residual currents are flowing at a speed of 15 cm s^{-1} in the weighted mean depth layer for decapodids situated at around 20 m (Tamaki et al., 2010). At this rate, larvae present at the coastal ocean site could reach the bay

mouth site in 1.5 d (no daytime horizontal transport of decapodids assumed, being close to the seabed with presumably much reduced current velocities). Compared with decapodids that were reared with food and without sediment in restricted space of the laboratory container, the distinct morphological traits for those derived from the free field water column were (1) almost exclusive occurrence of specimens belonging to the long and intermediate rostrum-length groups and (2) retention of the greater number of pereiopod exopods. In the laboratory, the ages of the decapodids in the long and intermediate RL groups are highly likely to have been 0 or 1 d and 2 or 3 d, respectively (Fig. 3). However, a fairly large proportion of specimens was present also in the short RL group on the age of 2 or 3 d, and the zero exopod was the most dominant in the intermediate RL group (Fig. 6B). All these differences between field-collected and laboratory-reared specimens suggest that (1) decapodids confined to the laboratory container had become the benthos, with their developmental process from “quasi”-settlement toward metamorphosis ongoing through Days 2 and 3 and (2) those present at sea might have become competent (preceding paragraph) but were still deciding to remain the plankton, with settlement on the coastal ocean bed suppressed for some reason. Thus, the intermediate RL group of decapodids collected at sea could contain specimens of a wide range of ages, not only 2 to 3-d but also 4 to 6-d (= possible longest duration recorded in the laboratory) old pre-settlement individuals (Fig. 5). The age of a post-settlement decapodid is the sum of its preceding pre-settlement duration (T_{pre}) and the present post-settlement duration (T_{post}), which is also limited to 6 d. It remains to be determined for a newly-metamorposed juvenile I whether (1) T_{post} can take the possible shortest time (i.e. ≤ 3 d; Fig. 2B) and (2) T_{post} is a simple decreasing function of T_{pre}. If these two assumptions are met, the combination of T_{pre} and T_{post} will be (0 and 3) d, (1 and 2) d, (2 and 1) d, and (3–6 and 0) d. However, if T_{post} can be extended to the limit of 6 d, the combination will vary such that (0 and 3–6) d, (1 and 2–5) d, (2 and 1–4) d, and (3, 4, 5, and 6 & 0–3, 0–2, 0–1, and 0, respectively) d. The possibility for variable T_{post} has been

suggested for megalopae of the fiddler crab *Uca pugnax* (see O'Connor and Judge, 1997). The above-mentioned formulae can be used to estimate the age of the five juveniles I of Group 2 collected on Day 0 (field), with their linea thalassinica present and RLs belonging to the short rostrum-length group (Section 3.11). The mean total length for the group suggests a 1-d lapse from the time of settlement (0.2-mm increment from the settlers' mean TL; 1-d T_{post}). Based on the first formula, the age of these juveniles I would be 3 days, with 2-d T_{pre}. Based on the second formula, it could vary from 3 to 6 d, with corresponding T_{pre} being 2 to 5 d, respectively.

Concerning pre-settlement and possibly already competent decapodids of *N. harmandi* present in the coastal ocean, one riddle is what factors could act as suppressors to prevent them from making settlement to burrow into the sediment there in spite of its potential non-repellent nature detected under laboratory conditions (Section 3.5). One hint can be found in the decapodid's diel vertical migration pattern such that (1) during the night, decapodids ascend into the middle to uppermost water column with the warmer and less haline waters (20–27 °C and 34–31.3 in salinity) and (2) the 1-d and older pre-settlement decapodids have at least once experienced the coldest, saltiest, and highest hydrostatic-pressure conditions in their deepest positions, resting in the depths between 60 m and 70 m (= seabed) during the day (e.g. 18.5–19.0 °C and 34.2) [Fig. 1B; Tamaki et al. (2010, figs. 2–5)]. In particular, since the reproduction of *N. harmandi* takes place during the warm season (June–October) with water temperatures above 20 °C on the Tomioka Bay sandflat (Tamaki et al., 1997), individuals with a preference for sediment lying below this threshold temperature will be selected out. Under such low temperatures, settlement performance might be arrested transiently, during which time developmental clock would also become slowed. In the present laboratory study, the Day-0 decapodids derived from zoeae reared at 17.5 °C (Batch 4) retained an almost full set of pereiopod exopods as compared with those possessing fewer numbers reared at 21–24 °C (Batches 1–3; Section 3.10), suggesting the pre-settlement state kept for the

1129 former and the “quasi”-settlement state triggered for the latter. Provided that the metamorphosis
1130 into decapodids in the 30-l tank occurred during the night preceding our retrieval conducted in
1131 morning hours, this time lag might have caused some reductions in pereiopod exopods in response
1132 to tactile stimuli only under the higher temperatures. Extreme temperatures and salinities are listed
1133 as a cue that can delay the time to metamorphosis for brachyuran megalopae (Forward et al., 2001).
1134 Sulkin and Van Heukelem (1986) demonstrated for *Callinectes sapidus* that the exposure of day-1
1135 megalopae to reduced temperature and higher salinity typical of deep continental shelf water
1136 reduced survival and delayed development to the juvenile I (see also Costlow, 1967). For
1137 megalopae of the same species, the higher salinity in coastal ocean water caused a longer time to
1138 metamorphosis by 10–20% compared with the lower salinity in estuarine water (Wolcott and De
1139 Vries, 1994; Forward et al., 1994). In the field, megalopae of *Carcinus maenas* settled
1140 preferentially on artificial collectors deployed at the surface, with very few on those placed at 9-m
1141 depth (Moksnes et al., 2003). The hypothesis raised in the present study implies that decapodids of
1142 *N. harmandi* in the coastal ocean come to decide to settle only when exposed to a combination of
1143 (1) higher temperature (and possibly lower salinity also) and/or lower hydrostatic pressure
1144 associated with the shallow water and (2) an appropriate sandy substratum encountered within the
1145 coastal boundary layer.

1146 Summarizing the above, hypothetical on-shore transport paths for a decapodid of *N. harmandi*
1147 from Amakusa-Nada (coastal ocean) to the intertidal sandflat in Tomioka Bay (coastal boundary
1148 layer) with time are illustrated in Fig. 10. The newly-metamorphosed decapodid occurs at Point A
1149 in the coastal ocean. This shrimp must pass Point B in the entrance to the coastal boundary layer (=
1150 spatial window), reach a point on the sandflat, Point C, and metamorphose into juvenile I there. If
1151 the shrimp reaches a point in the inappropriate habitat (Point D), it must return to Point E in the
1152 spatial window and come back to Point B later. Thus the T_{pre} (in day units) can be given as: T_{pre} =

Fig. 10

1153 T_1 (time from Point A to Point B) + 0.25 (from Point B to Point C or D = 6 h; flood tide hours
1154 postulated) + [0.25 (from Point D to Point E; ebb tide hours postulated) + T_2 (from Point E to Point
1155 B) + 0.25 (from Point B to Point C or D)] × *n* (= 0, 1, 2, …). The shortest case is realized when T_1
1156 = 0 and *n* = 0, leaving only 0.25 d. The third, circuit term is repeated as long as the shrimp arrives
1157 at Point D until finally reaching Point C, with $T_2 \geq 1$ for $n \geq 1$. The T_{post} is the time from settlement
1158 to metamorphosis, during which the post-settler may stay in the sediment or swim in the water
1159 column for a short duration to resettle the sandflat. The (T_{pre} + T_{post}) must be within the maximum
1160 time window for metamorphosis (= 6 d).

1161 For some decapod taxa, time series data for settlers (newly-settled decapodids) on an hourly to
1162 daily basis can be obtained relatively easily using collectors equipped with replaceable artificial
1163 substrata or light traps (Jones and Epifanio, 1995; Oishi and Saigusa, 1997; Moksnes and
1164 Wennhage, 2001; Miller and Shanks, 2004). This method is not applicable to decapodids of other
1165 taxa such as callianassids and ocypodid fiddler crabs, which need sediment to burrow into (Tamaki
1166 et al, 1997; Paula et al., 2003). When the extracting or excavating sediment columns is laborious
1167 and its continuation for several months is feasible only discretely, both settlers and post-settlers
1168 collected on one occasion must be discriminated from those on the next. Of the present decapodids
1169 of *N. harmandi*, only those without the linea thalassinica belonging to the long or intermediate
1170 rostrum-length groups can be convincingly identified as 0 or 1-d old individuals. To restrict the
1171 collected specimens to these ages, sampling must be carried out every other day. With longer time
1172 intervals, there arises inevitable uncertainty of contamination from older ages. The use of total
1173 length data to overcome this difficulty has also some limitation due to increased variances with
1174 post-settlement growth. Since the constancy of standard deviation about mean TL seems to be
1175 limited to the initial three dates (i.e. up to 0.3-mm SD; Section 3.11), the collection of shrimps on
1176 the sandflat at least every three days will be required in order to achieve a minimum level of

resolution. One criterion for the correspondence between age and total length would be raised using the 0-d old settlers of Group 1-1 mentioned in Section 3.11, with their initial TLs ranging from 4.1 to 4.7 mm. Adding 0.2 mm d^{-1} on both edges, the range of TL on the next sampling occasion that comes 3 d later (fourth date) is 4.7–5.3 mm. In this case, some overlap in TL values between dates becomes unavoidable. When determining the cohort composed of settlers and post-settlers occurring between two consecutive sampling occasions, the upper critical TL value should be set at 4.9 mm in order to eliminate all specimens on the fifth date (day-4 post-settlers). With this treatment applied to the target cohort, all individuals of 0-d old settlers, 1-d old settlers, and day-1 post-settlers collected on one sampling occasion are included, but undesirably, (1) of the potential day-2 post-settlers with 4.5–5.1-mm TL, those with 4.9 mm < TL ≤ 5.1 mm are excluded and (2) of the potential day-3 post-settlers with 4.7–5.3-mm TL, those with 4.7 mm ≤ TL ≤ 4.9 mm collected on the preceding sampling occasion (3 d before) is contaminated.

The initial daily growth rate of 0.2-mm TL d^{-1} during summer to autumn estimated for the field-reared settlers of *N. harmandi* (Section 3.11) is consistent with a value estimated for the natural population on the Tomioka Bay sandflat (Tamaki et al., 1997). In that study, a regular sampling of the population on the sandflat was carried out every two weeks or month over nearly two years and cohort analysis conducted for total-length frequency distributions with 2.0-mm TL intervals in each sex. The smallest shrimp was 4.1 mm in TL, which would be a decapodid. Of all individuals of the smallest TL class (4.1–6.1 mm) throughout the study period (N = 363), those with < 5.1-mm TL accounted for 44.6%, further suggesting the settlement of substantially large numbers of decapodids on the sandflat. The smallest female was identified by the presence of bud-like second pleopods, of which TL was 5.4 mm. Since settlers with a mean TL of 4.6 mm subsequently grew at a rate of 0.2 mm d^{-1} (Section 3.11), the 5.4-mm TL suggests a day-4 post-settler, which would most probably be a newly-metamorphosed juvenile I (Sections 3.2 and

3.3). The initial growth rate of 0.2-mm TL d^{-1} was achieved by the largest individuals in each cohort. The modes of the cohorts that were recruited in July attained 20-mm TL in December, with a growth rate of approximately 0.1 mm d^{-1}. Those of the cohorts recruited in August reached that size in April the next year, with a growth rate of approximately 0.06–0.07 mm d^{-1}. All these individuals recruited the previous year became mature for the first time in June.

The mean growth rate of juveniles II (and subsequent instars) of *N. harmandi* which had been reared in groups with no substantial growth during the juvenile I was 0.06-mm TL d^{-1} over ca. 40 days (Fig. 7B). The lower growth rate compared with that of juveniles reared individually might be ascribed to the smaller body size at the beginning of the juvenile II, which had been caused by starvation during the juvenile I. In *Carcinus maenas*, the effect of food availability during the larval period was carried over through megalopal stage to juvenile instars, affecting both size of settlers and their subsequent growth rates (Giménez, 2010). Juveniles of *N. harmandi* have sometimes been contained in samples for plankton that were collected close off the Tomioka Bay sandflat, in which the water depth of the sites was ≤ 10 m (A. Tamaki, unpublished data). The maximum total length of juveniles recorded so far was 9.8 mm, which could be a day-26 post-settler (starting from the initial decapodid TL of 4.6 mm and growing at a rate of 0.2 mm d^{-1}) at the juvenile II or III instar (previous paragraph). Video cameras fixed at a point on the sandflat for several hours of submergence during both day and night captured pictures of two swimming shrimps at night, one juvenile with ca. 8.0-mm TL and one ovigerous female (S. Sen-ju and A. Tamaki, unpublished data). The occurrence of migration by post-settlement juveniles and adults on the sandflat has been inferred from the change in density and TL composition with time, especially from the lower high-density zone to the upper low-density zone (Tamaki and Ingole, 1993; Tamaki et al., 1997). Adult shrimps, males in particular, severely fight each other for burrow space and probably for mates also, resulting in defeated individuals expelled out on the sediment surface (Shimoda et al.,

2006). Some of these shrimps would be preys to predators and survivors would become emigrants. Adult burrows are utilized as micro-habitats for newly-settled decapodids and juveniles to branch off their own burrows (Tamaki et al. 1992a); the diameters of two resin casts of such juvenile burrows suggest that the shrimps were day-16 (8-mm TL) and day-58 (16-mm TL) post-settlers. The latter one's burrow would soon become separated from the burrow of the "host" adult (≥ 20-mm TL, with 30–60-cm deep burrow). Newly-settled decapodids themselves can reach only the shallower parts (< 5–10 cm) of the sediment column, which are subjected to scouring induced by large waves (Tamaki, 1987) and surface-foraging predators (Tamaki et al., 1992b) and thus thrown into the water column. This could explain the highest density of juveniles recorded in the lower zone densely inhabited by adults (Tamaki and Ingole, 1993; cf. Feldman et al., 1997, fig. 4). If secondary lecithotrophy in the decapodid stage could be extended to some early juvenile instars (Section 3.4; Fig. 10), those juveniles may still be capable of searching for appropriate habitats at the expense of time for feeding. The occurrence of juveniles of callianassid shrimp in the water column around adult habitats has been recorded for populations under natural conditions [*Neotrypaea californiensis* (see Feldman et al., 1997) and *Lepidophthalmus siriboia* (see Oliveira et al., 2012)] and that inhabiting a penaeid shrimp culture pond [*L. sinuensis* (see Nates and Felder, 1999)]. Also, juveniles of other decapod taxa have been collected frequently from the vicinity of adult habitats (Dittel and Epifanio, 1990; Eggleston and Armstrong, 1995; Oishi and Saigusa, 1997; Pereira et al., 2000). Juveniles I of *Callinectes sapidus* dispersed from densely-settled seagrass beds to lower-density areas, probably minimizing predation by other juvenile crabs (Reyns and Egglestone, 2004). The secondary dispersal for more favorable micro-habitats beyond the metamorphosis into some juvenile instars to correct the broad habitat selection made at the time of settlement by decapodids would be widespread across decapod crustacean taxa.

To examine the change in morphological characters and growth patterns of *N. harmandi*

1249 through the decapodid and juvenile period, the consistency of dates that lapsed from 0-d old
1250 decapodids (day-0 post-settlers) between laboratory- and field-reared specimens is required (day 0
1251 to 25 from laboratory and day 27 to 90 from field in Fig. 9). The age composition of the day-0
1252 post-settlers was represented by Groups 1-1, 1-2, and 2 on Day 0 (field) (Section 3.11), and the
1253 members of these groups were previously estimated as either day-0 settlers (Group 1-1) or day-1
1254 post-settlers (Groups 1-2 and 2). For the present objective, the contamination by the latter group
1255 with only a 1-d delay would not significantly affect those of the advanced juvenile instars. Both
1256 relative pleon length and uropod exopod shape changed markedly on around days 25 to 27, which
1257 were the final dates of either juvenile II or III instars at ca. 10 mm in their total lengths (Fig. 7). The
1258 lengthening of the pleon may reflect the change in feeding habit from omnivory (both carnivory
1259 and herbivory) by zoeae to exclusive herbivory by decapodids and juveniles as post-settlers. There
1260 is a widespread finding that animals sustaining themselves on poorer food have longer intestines
1261 (Sibly and Calow, 1986, ch. 2). Whether or not benthic diets are poorer than planktonic ones under
1262 natural conditions is unknown for *N. harmandi*. The wider space between first and second pleopods
1263 would afford a female a larger number of eggs attached to them. Callianassid shrimps are well
1264 known for their ventilating activity using pleopods to raise oxygen concentration inside deep
1265 burrow galleries, which tends to become hypoxic or anoxic [for *N. japonica* (as *Callianassa*
1266 *japonica*; Mukai and Koike, 1984) and for the family in general (Atkinson and Taylor, 2005)].
1267 During ventilation in *C. subterranea*, the uropods are extended to the round burrow wall to which
1268 exopods' round outer margin tightly fit, leaving only a small opening for effective flow ventral
1269 from the telson toward thoracic gills (Stamhuis and Videler, 1998). The ontogenetic change in
1270 uropod exopod shape from elliptical to sub-circular would reflect its functional shift from
1271 swimming in the plankton to ventilating in the benthos. Overall, individuals of *N. harmandi* in their
1272 entire benthic phase can be staged by total-length ranges roughly as 4–5.5 mm for post-settlement

decapodids, 5.5–10 mm for juveniles, 10–20 mm for sub-adults, and over 20 mm for adults.

Finally, ten essential points from the findings in the present study and for future directions in research on pre- and post-settlement processes by decapodids and juveniles of decapod crustaceans initially releasing their larvae from estuarine or coastal adult habitats on the shore into the coastal ocean are summarized below.

(1) Of typical water settings for those export-type larvae, studies have been conducted most intensively for the estuary–coastal ocean system, in which two-step models for decapodid transport were presented. The coastal boundary layer–coastal ocean system will also be a promising target for research, where the upstream transport process of pre- or post-settlement decapodids in the estuary (second step) is non-existent and some of the pre-settlement state in the coastal ocean can be retained in settling or newly-settled larvae in the water column and/or on the substratum of the adult habitat owing to the relatively short distance from the entrance to the coastal boundary layer to its head. The *N. harmandi* population in the Tomioka Bay–Amakusa-Nada water area provides one example.

(2) Laboratory-rearing of decapodids and juveniles is a basis for inferring their states in the field, but artifacts caused by the confinement to containers are inevitable. For pre-settlement decapodids, a forced, “quasi”-settlement state may be induced by tactile stimuli, eventually leading to metamorphosis into juveniles I autonomically. The speed of development and morphological change, and feeding mode can also be affected, which becomes some limitation to the application of laboratory findings to the interpretation of field processes.

(3) It needs to be established where and how early in the decapodid stage decapodids become competent and respond to settlement cues. Observations on newly-settled decapodids of some species including *N. harmandi* suggest the acquisition of their competency immediately after molting from the last zoeal stage while in the coastal ocean. They may settle on the substratum at

some early time following the ingress into the estuary or coastal boundary layer and spend a substantial time there before metamorphosis. Thus the shallow water column near the adult habitat tends to contain a mixture of pre-settlement decapodids conducting exploratory touchdown and refloatation behaviors, and post-settlement decapodids and juveniles of the early instars swimming for secondary dispersal. In particular, these pre- and post-settlement decapodids are hardly distinguishable from each other in both morphology and behavior. The definition of settlement can also be blurred by seemingly similar swimming behaviors of pre- and post-settlement decapodids. The delay in settlement and that between settlement and metamorphosis should not be put together. The determination of molt stages and the measurement of the time to metamorphosis would not give measures directly linked to competence for settlement.

(4) Some signatures in morphologies that had natatory functions in the zoeal stages and are degenerating markedly from pre- to post-settlement states in the decapodid stage can be used to discriminate between the two states. The pereiopod exopods in the decapodid of *N. harmandi* provide one example of such clues to infer for the decapodid assemblage level but not for the individual level.

(5) Other degenerating morphologies during the decapodid stage could change more slowly than those related to natatory functions in response to the state change from pre- to post-settlement. Such clues may help identify the earliest ages of post-settlement decapodids individually. One example is found in the rostrum length of *N. harmandi*. In this case, the limitation of the applicability to the older ages can be solved to some extent using body length dimensions. In these decapodids, the secondary lecithotrophy most probably associated with their pre-settlement state limits the settler sizes to a narrow range irrespective of their ages, and a constant post-settlement growth rate makes it possible to estimate the time that has elapsed from the settlement event.

(6) When estimating the age of newly-settled decapodids by morphological clues, it should be

taken into account possible effects of a time lag between the actual settlement event and our collection of benthos on rapid morphological changes induced by the decapodids' settlement act.

(7) It needs to be clarified how the pre-settlement duration of decapodids affects the time from their settlement to metamorphosis. The point is whether or not the longer the pre-settlement duration is, the shorter the time to metamorphosis becomes. This was uncertain for the present case of *N. harmandi*.

(8) It needs to be clarified how broad the acceptability by settling decapodids of a variety of cues and how long the time to metamorphosis is shortened responding to these cues. The receptiveness to sandy sediments with a range of grain-size compositions and the shortening of the time to metamorphosis by 1 d in the decapodid of *N. harmandi* give one example.

(9) It needs to be established what factors in the coastal ocean act as suppressors preventing pre-settlement decapodids from doing settlement on the seabed there. This is particularly true for decapodids that perform a long-range diel vertical migration in the coastal ocean, which lie close to the seabed during their resting phase such as observed for *N. harmandi*. This thinking is based on a premise that juveniles are not a retuning component from the coastal ocean toward the adult habitat.

(10) The rearing of newly-settled decapodids in the field for a period up to the adult stage will provide useful clues not only to the discrimination of juvenile instars by body dimensions but also to the functional morphology related to true benthic life. The example of *N. harmandi* given in the present study indicates that the juveniles I and II are the final transitional stages between planktonic and benthic modes of lifestyle, still possessing the potential for secondary lecithotrophy and secondary dispersal and thus enabling them to correct micro-habitat locations broadly made at the time of settlement.

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Figure captions

Fig. 1. A. Coastal water part of the Ariake Sound estuarine system, Kyushu, Japan, with depth contours (m) adapted from Japan Coast Guard, Hydrographic and Oceanographic Department (1994). The sampling for *Nihonotrypaea harmandi* larvae was conducted at two sites in Amakusa-Nada. The intertidal sandflat inhabited by adults is located on the western edge of Tomioka Bay. **B.** Vertical profile of water temperature and salinity recorded at the time of larval sampling (July–August) at coastal ocean site in panel A; all original daytime and nighttime data used for Tamaki et al. (2010, fig. 2) were combined.

Fig. 2. A. Daily occurrence of exuviae from the batch of decapodids of *Nihonotrypaea harmandi* reared individually with food and without sediment (solid circles) and daily change in proportion of shrimps with premolt-stage rostra that were reared in groups with food and without sediment (blank circles; total number of specimens given in panel B) in the laboratory. **B.** Daily change in proportion of decapodids and juveniles with linea thalassinica reared in groups with food and without sediment (circles) and of shrimps used for substratum-choice experiments (crosses; number of specimens on Days 1 and 2 given after commas) in the laboratory. **C.** Rostrum lengths of premolt-stage shrimps in panel A, with measurements to cuticle and epidermis tips shown for respective identical individuals on each date.

Fig. 3. A. Daily change in plots of rostrum length for decapodids and juveniles of *Nihonotrypaea harmandi* reared in groups with food and without sediment in the laboratory. **B.** Daily change in mean (± SD) and median rostrum lengths for shrimps in panel A (solid circles) and for shrimps used for substratum-choice experiments (blank circles; number of specimens given in panel C). **C.**

Daily change in the proportions of the three rostrum-length groups for shrimps demarcated by broken lines in panel B, with (–) and (+) indicating without and with sediment, respectively.

Fig. 4. A. Daily change in the proportions of the number of pereiopods with exopods (0 to 4) for decapodids and juveniles of *Nihonotrypaea harmandi* reared in groups with food and without sediment (–) and for shrimps used for substratum-choice experiments (+) in the laboratory. **B.** Daily change in the proportions of shrimps with pereiopods 1 to 4 (expressed as I–IV) possessing exopods and with no pereiopod exopods for the specimens reared without sediment in panel A.

Fig. 5. Rostrum-length frequency distributions of decapodid (and possible juvenile) specimens of *Nihonotrypaea harmandi* collected from the water column at two sites in Amakusa-Nada (Fig. 1A). The broken lines demarcate the three rostrum-length groups as in Fig. 3.

Fig. 6. A. Frequency distributions of the number of pereiopods with exopods in decapodids of *Nihonotrypaea harmandi* belonging to the long rostrum-length group for the specimens reared in groups with food and without sediment in the laboratory and for those collected from the water column at two sites in Amakusa-Nada (Fig. 1A). **B.** Those frequency distributions in decapodids (and possible juveniles) belonging to the intermediate rostrum-length group.

Fig. 7. Temporal change in mean (± SD) or individual total lengths of decapodids and juveniles of *Nihonotrypaea harmandi* reared on the Tomioka Bay sandflat **(**circles in **B**, **C**) under subsurface (below 30 cm) temperatures (**A**; 5 August 1994 set as Day 0**)** and of those shrimps reared individually with food and without sediment (triangles in **B**, **C**) or reared in groups with food and without sediment (stars in **B**, **C**) in the laboratory. The numbers of specimens in the field and the

laboratory are shown by *N*′ (upper) and *N* (lower), respectively. The Day 0 has different meanings between field and laboratory; the total length in the field on Day 0 came from data for three dates inclusive (i.e. 5 and 8 August, and 17 September 1994), when each rearing started using shrimps that were presumed to be newly-settled decapodids; and the laboratory-reared shrimps did appear as new decapodids on Day 0. In panel C, the solid line indicates the linear regression for all total length data versus day numbers in the field, and the broken line for all total length data of shrimps reared in groups in the laboratory versus Day 9 and thereafter.

Fig. 8. Scatter plots for total length versus carapace length of decapodids of *Nihonotrypaea harmandi* reared in groups with food and without sediment in the laboratory on Day 0 and Day 1, with respective linear regression lines (equations given in text, Section 3.11).

Fig. 9. Temporal change in relative pleon length (**A**), ratio of short-axis length to long-axis length for uropod exopod (**B**), and three angles for uropod exopod (**C**) of decapodids and juveniles of *Nihonotrypaea harmandi*, with smoothing curves versus day numbers based on Loess regressions; Day 0 is set as the date of occurrence of new decapodids. See text, Section 2.5, (6) for the definition of parameters regarding uropod exopod. The data for Days 0 to 10, Days 15 to 25, and Days 27 to 90 were derived from specimens reared in groups in the laboratory, individually in the laboratory, and in the field, respectively. The data for adults were from five ovigerous females that had been used for the subsequent larval rearing in the laboratory.

Fig. 10. Hypothetical paths with time for a decapodid of *Nihonotrypaea harmandi* which has newly appeared at an arbitrary Point A in Amakusa-Nada (coastal ocean). There, it performs a long-range diel vertical migration, occurring in the middle to upper water column only at night. To successfully

settle on the final destination inhabited by adults, the decapodid, at its first step, must be transported to a point (Point B) in the entrance to Tomioka Bay (coastal boundary layer: CBL). It takes T_1 d from Point A to Point B. The decapodid can then reach some point on the intertidal sandflat (Point C) in 6 h (= 0.25 d), riding nighttime flood tidal currents, or arrive at an inappropriate habitat (Point D). In the latter case, the decapodid is carried back to Point E in the entrance to CBL, riding nighttime ebb tidal currents in 0.25 d, from which a circuit transport process continues until the final settlement at Point C within the time window of the decapodid stage (i.e. 6 d). It takes T_2 d from Point E to Point B, with $T_2 \geq 1$ including the case in which the resting-phase decapodid stays close to the bottom in the entrance to CBL. The post-settlement decapodid must wait for T_{post} d to metamorphosis into the juvenile I. The post-settlement shrimp, whether at its decapodid or juvenile stage (most probably up to the juvenile II), either maintains a burrow in the sediment or performs a short secondary dispersal within the sandflat.

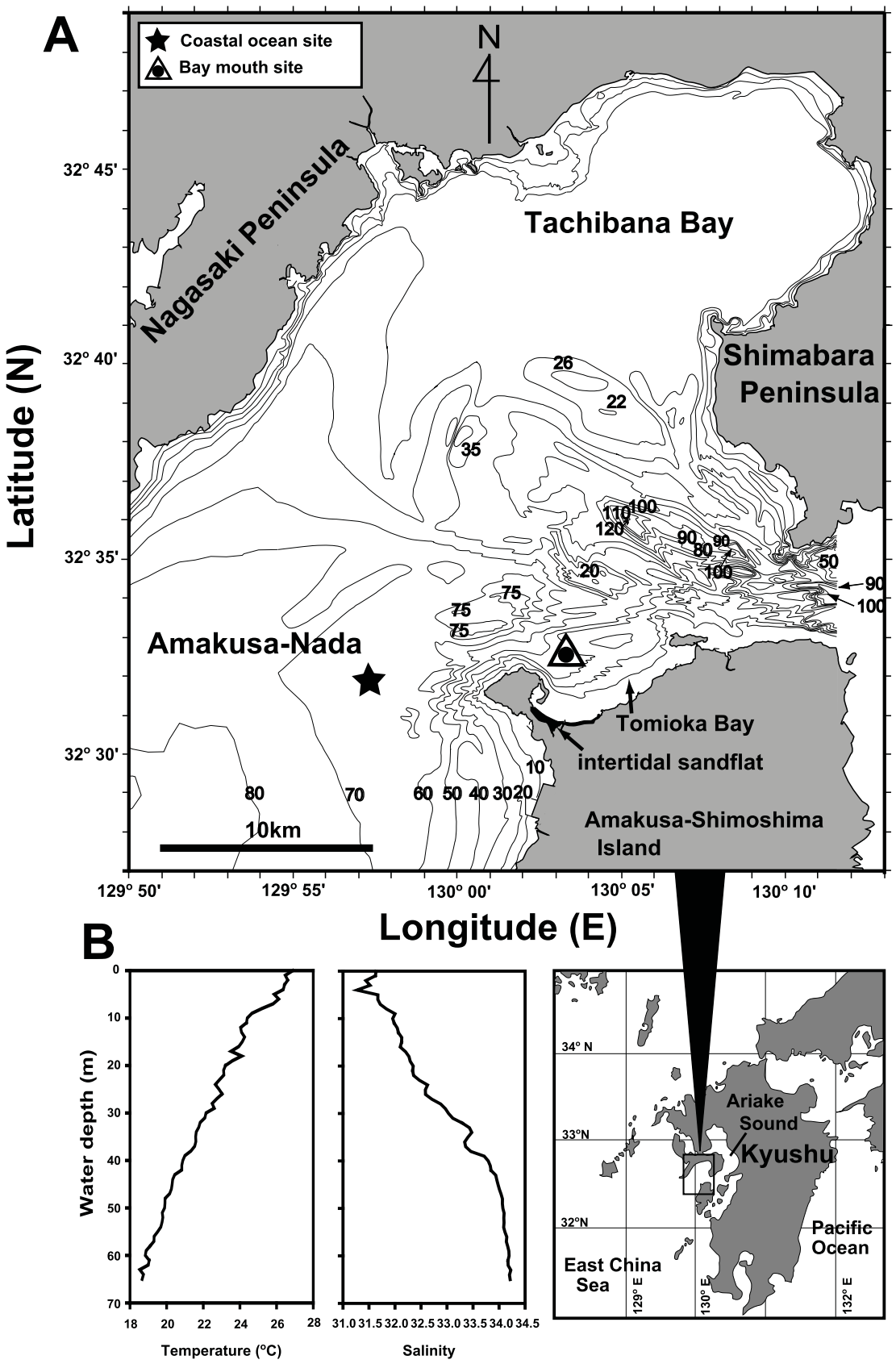

Fig. 1 (Tamaki *et al.*, revised)

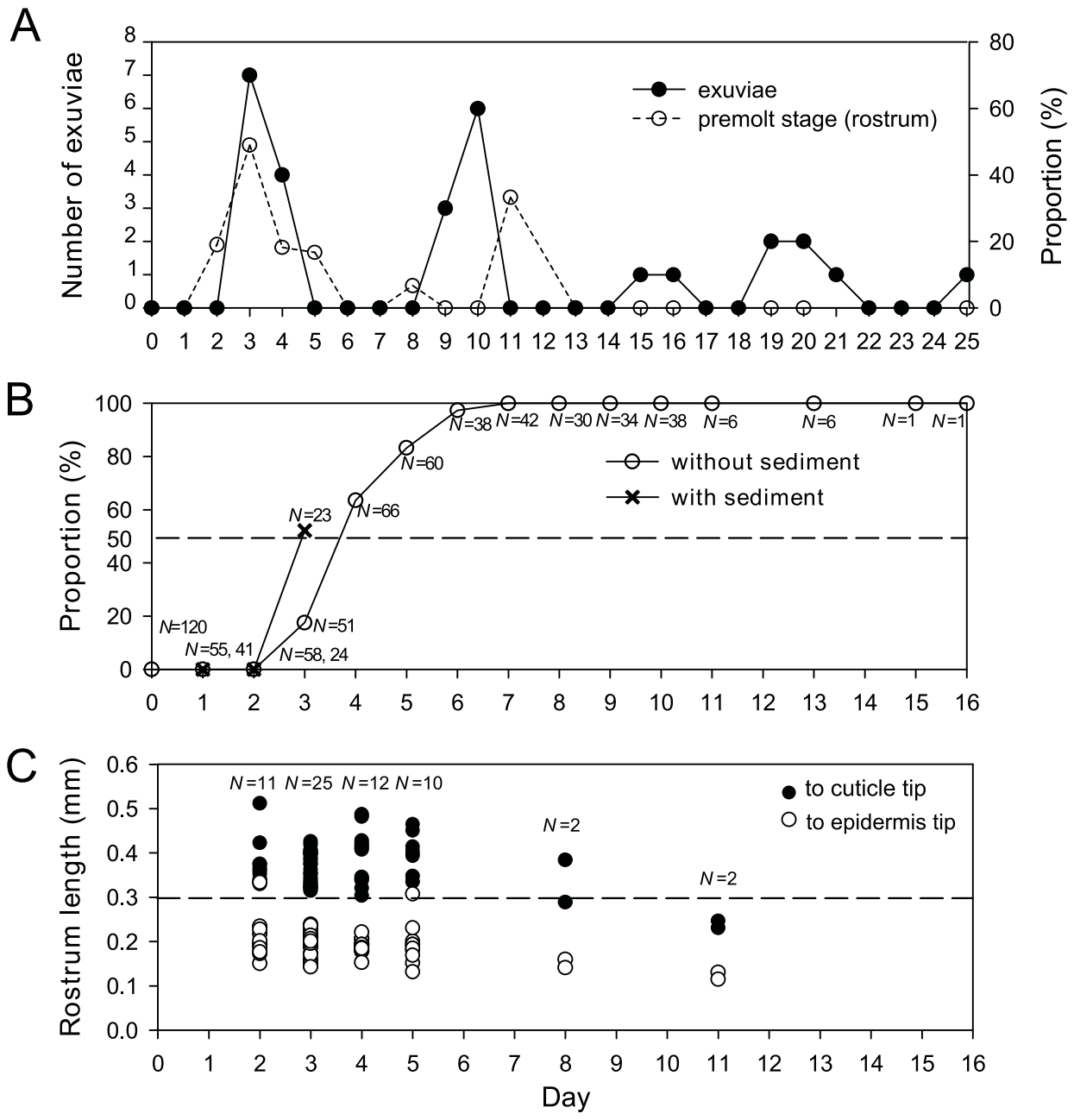

Fig. 2 (Tamaki *et al.*, revised)

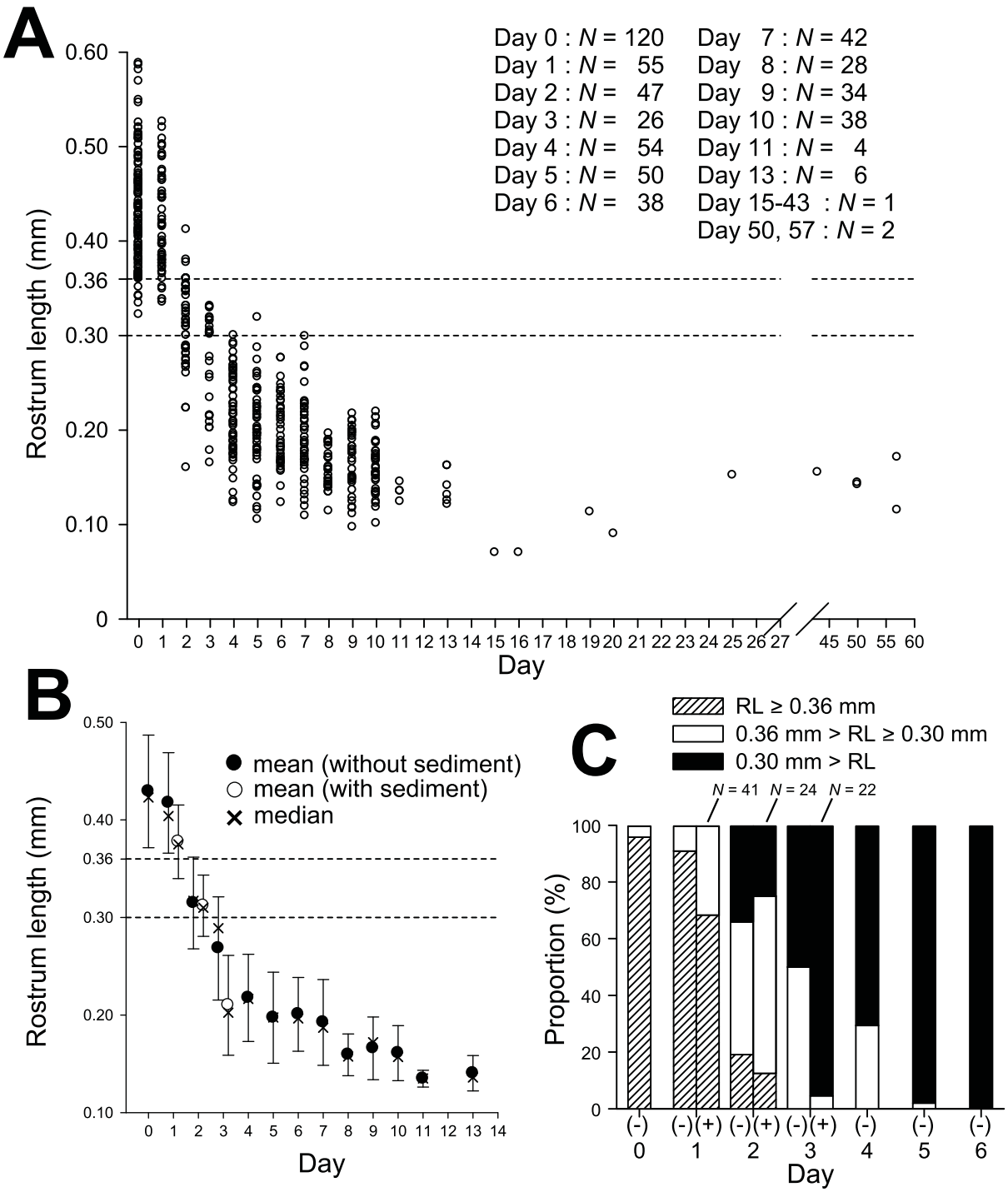

Fig. 3 (Tamaki *et al.*, revised)

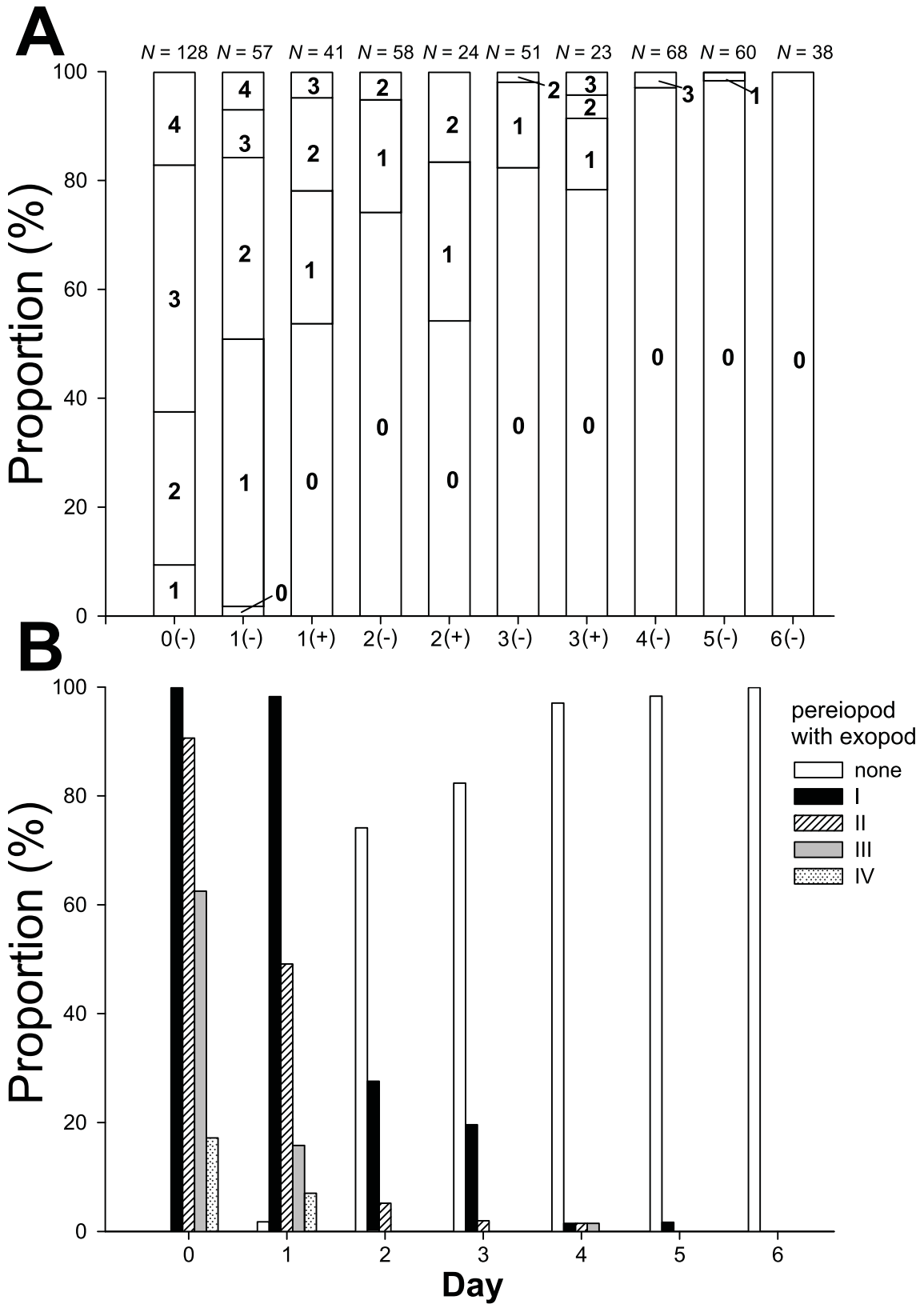

Fig. 4 (Tamaki *et al.*, revised)

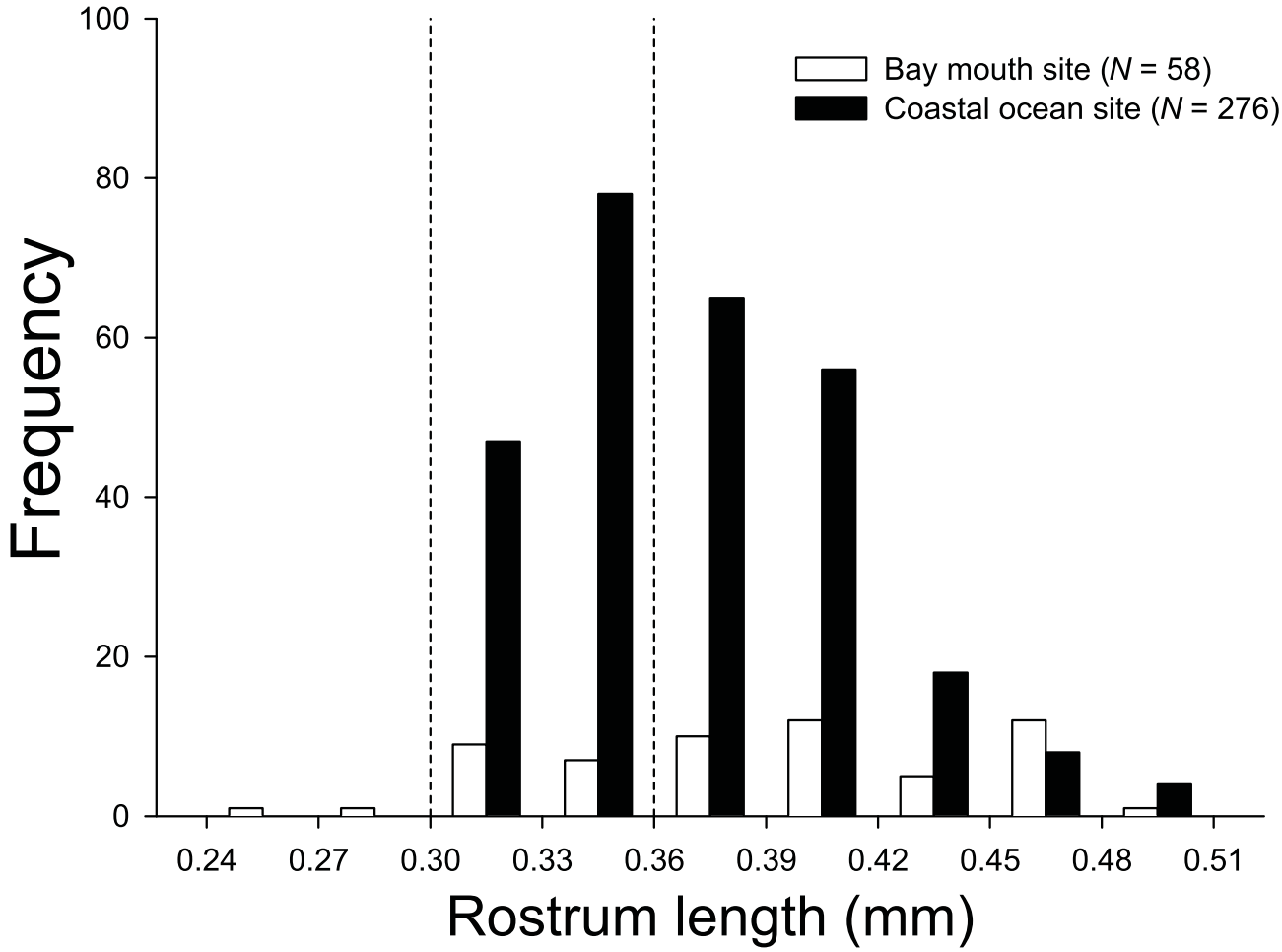

Fig. 5 (Tamaki *et al.*, revised)

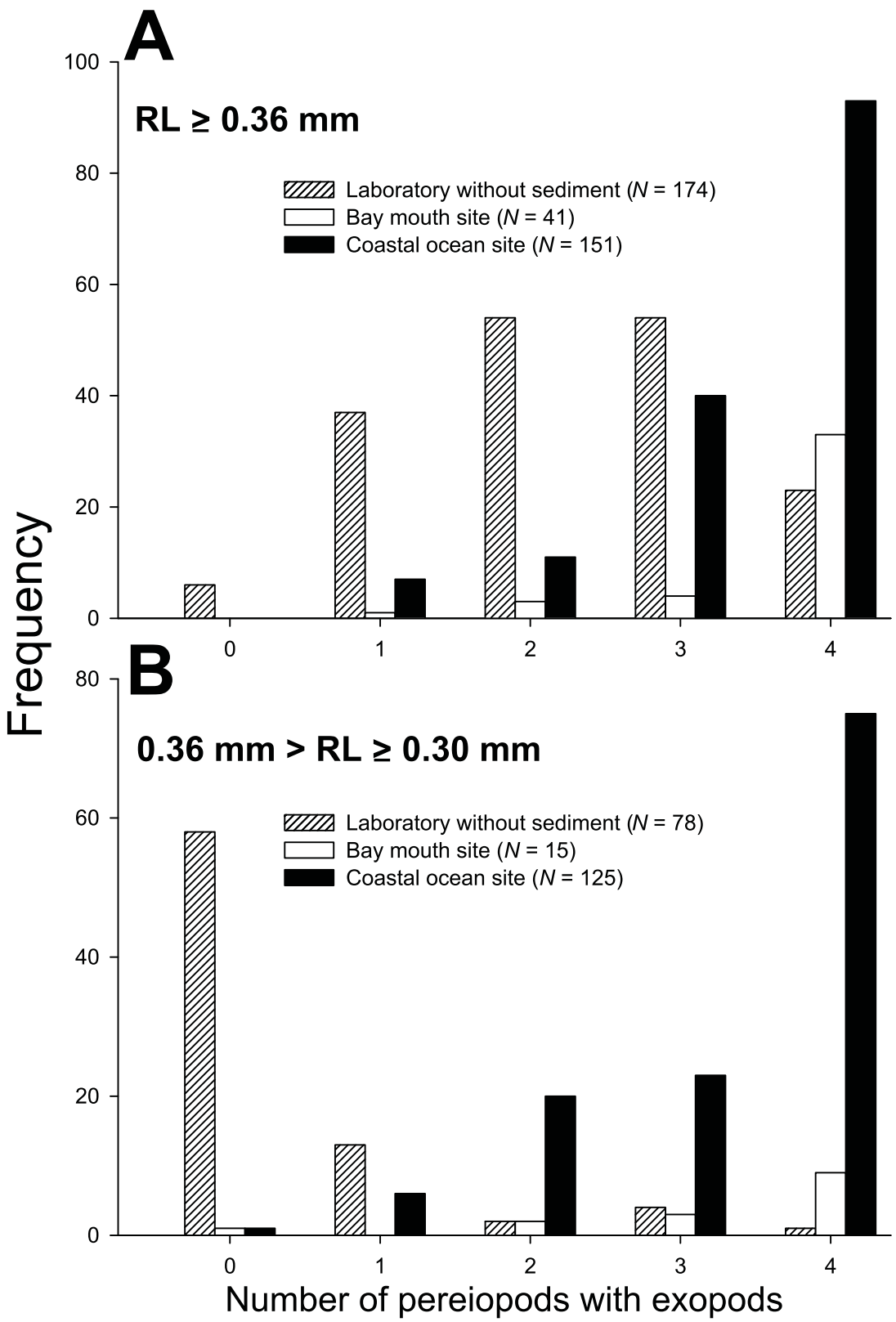

Fig. 6 (Tamaki *et al.*, revised)

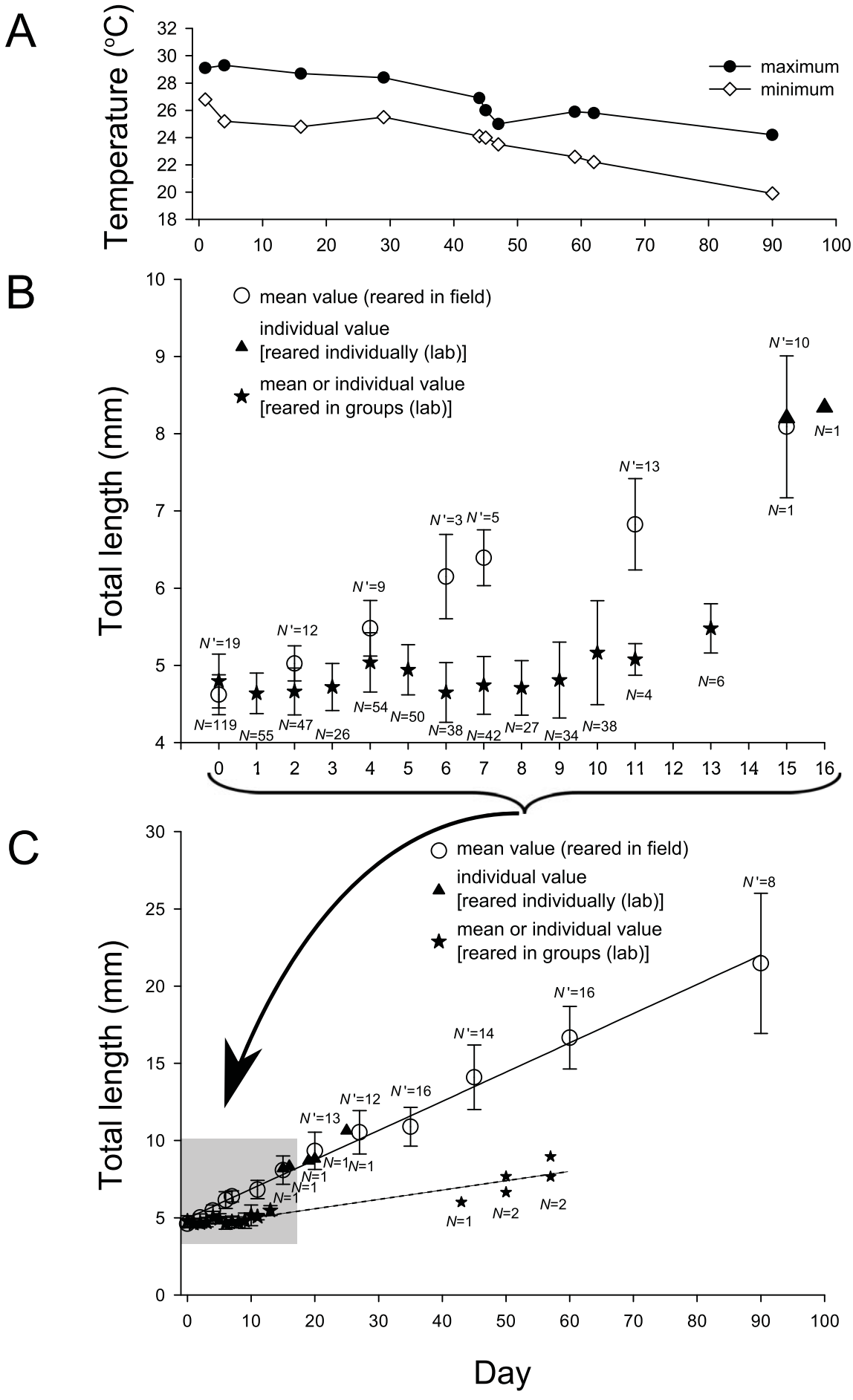

Fig. 7 (Tamaki *et al.*, revised)

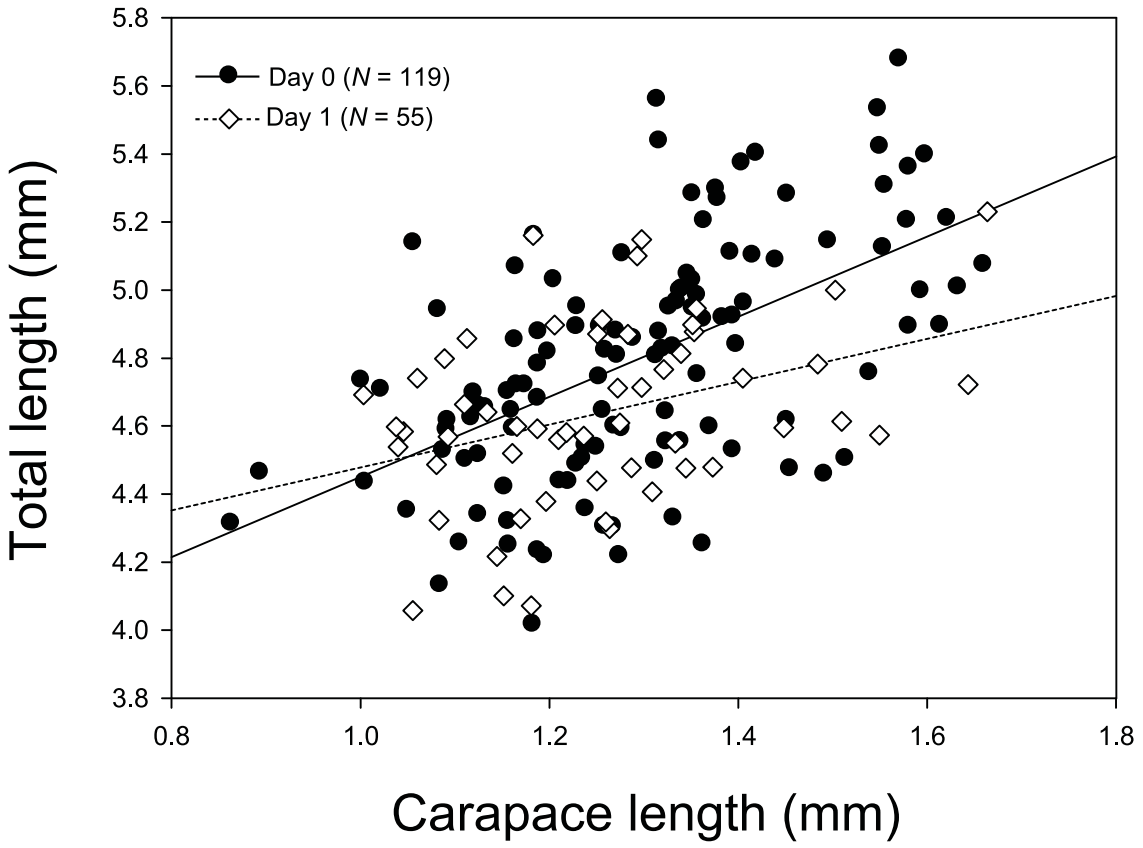

Fig. 8 (Tamaki *et al.*, revised)

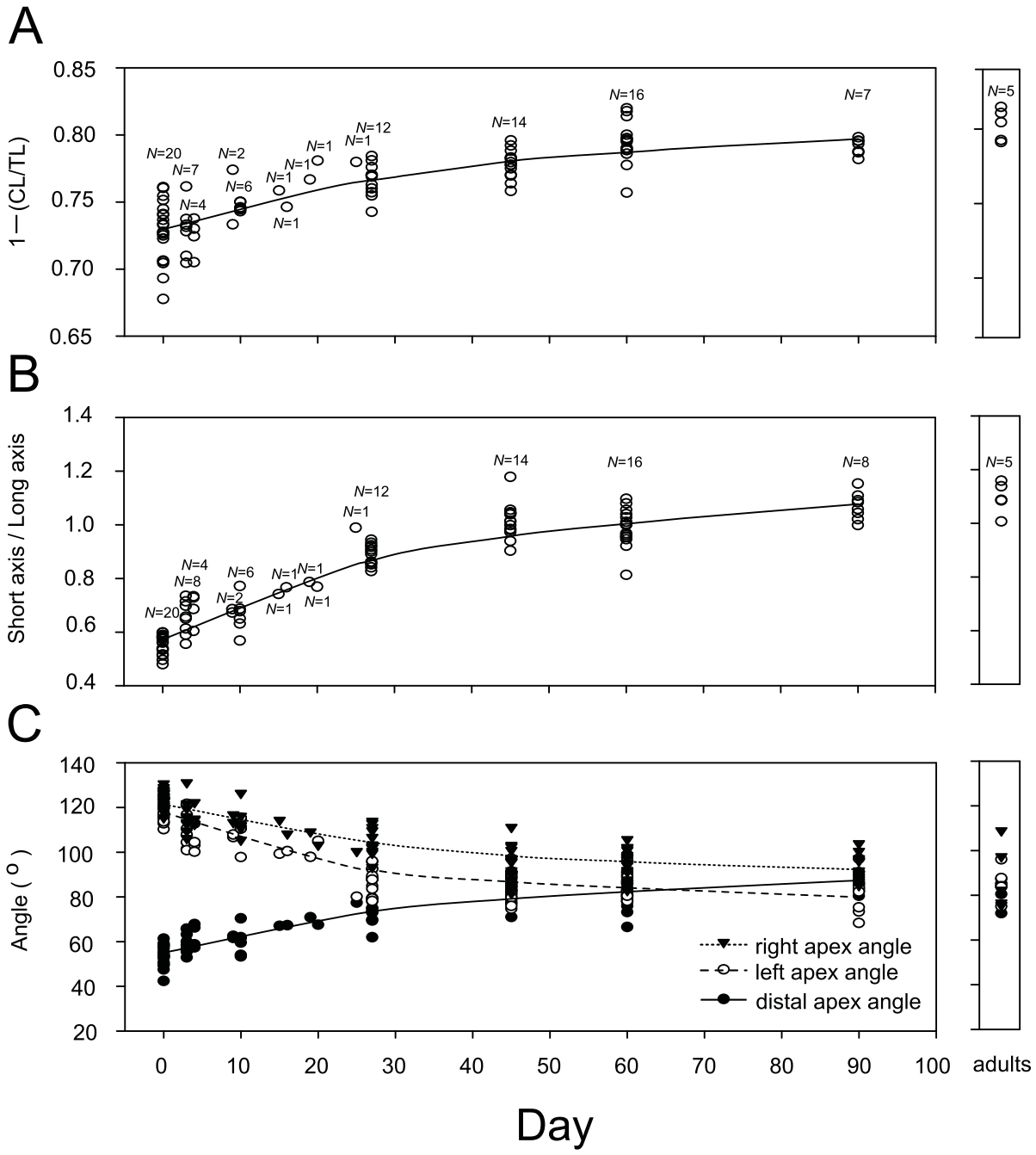

Fig. 9 (Tamaki *et al.*, revised)

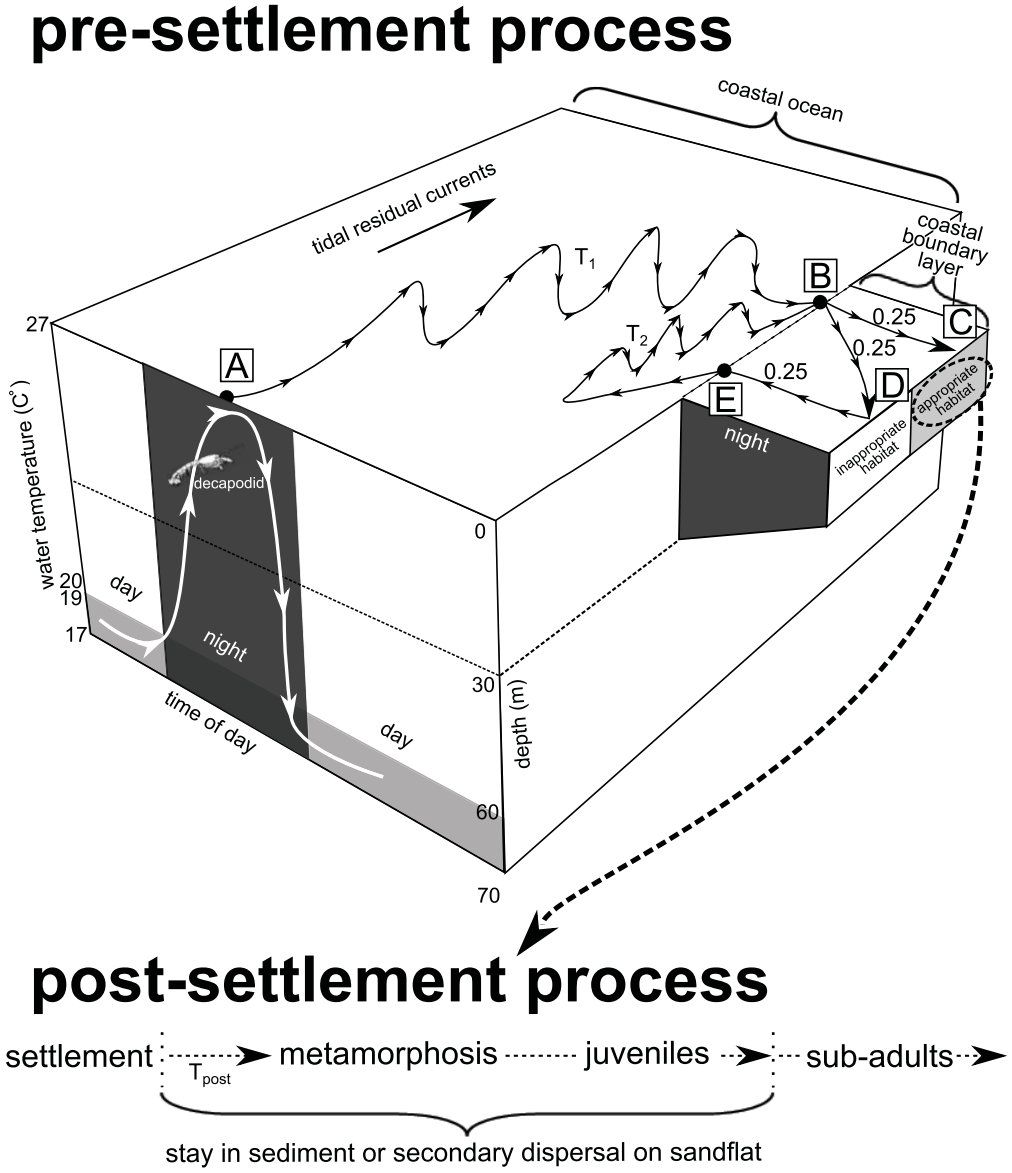

Fig. 10 (Tamaki *et al.*, revised)