Ovarian maturation, size at sexual maturity and spawning season of
Metapenaeopsis provocatoria owstoni Shinomiya & Sakai, 2000
(Decapoda: Penaeidae)

Md. Mosaddequr Rahman, Jun Ohtomi

Abstract.—Metapenaeopsis provocatoria owstoni (Decapoda: Penaeidae) is distrib-
uted in the waters of Japan, Korea and Taiwan. There is, however, no study available
on the population biology of this species to design its sustainable management and
conservation protocols. We, therefore, studied for the first time its oocyte develop-
ment, ovarian maturation, size at sexual maturity and spawning season using samples
collected from Kagoshima Bay, southern Japan. Histological observation of ovaries
confirmed seven oocyte developmental stages. This species exhibited asynchronous
ovarian development, which indicates multiple spawning in a single reproductive sea-
son. Ovarian maturity stages were classified into three categories based on the devel-
opmental stage of the most advanced oocytes in the ovary: immature, maturing and
mature. Females containing oocytes that either had evidence of germinal vesicle
breakdown or migrating nucleus were defined as mature. The gonadosomatic index
exhibited a positive but gradual relationship with ovarian maturation progression. In
contrast, macroscopic staging showed a sharper relationship with histological stages
of ovarian maturity, which exposed its potential as a maturity index for M. provocato-
ria owstoni. The size at sexual maturity was estimated to be 12.8 mm CL, and the
spawning season appeared to last from April to December, with May to June being the
main part.

Key words: Kagoshima Bay, oocyte developmental stage, macroscopic staging, maturity index,
reproductive biology

Introduction

Metapenaeopsis provocatoria owstoni Shinomiya & Sakai, 2000 is one of the fourteen
species of Metapenaeopsis distributed in Japanese waters (see Sakaji et al., 2000a; Shinomi-
ya & Sakai, 2000; Ohtomi & Nagata, 2004). This species is different from the M. provoca-
toria found in Australia, New Caledonia, Indonesia, the Philippines and South Africa; and M.
provocatoria longirostris distributed in Western Australia (Shinomiya & Sakai, 2000). In
Japan, M. provocatoria owstoni is reported from the Pacific side of Sagami Bay to Mi-
yazaki; the Bungo Strait, the Sea of Japan and Yuya Bay. Outside of Japan, this species has
been reported in the East China Sea from Pusan to Korean Strait, Korea and Taiwanese wa-
ters. M. provocatoria owstoni has a bathymetric distribution ranging from 80–300 m depths
(Shinomiya & Sakai, 2000). In addition to this species, three other species of Metapenaeopsis
are reported from Kagoshima Bay, southern Japan: M. acclivis, M. kyushuensis and M. sibo-
gae (Ohtomi & Nagata, 2004).

In Kagoshima Bay, M. provocatoria owstoni is often caught as “by-catch” of the small-scale
seine fishery and it is marketed together with
The population of *M. provocatoria owstoni* in the bay has been declining in recent years, which has coincided with the rapid increase in the *M. sibogae* population (Rahman & Ohtomi, unpublished). There is, however, no information available on the population biology of *M. provocatoria owstoni* in the literature to aid the initiation of any sort of activities to design and implement its sustainable management and conservation protocols.

The knowledge of the reproductive biology of any marine species can assist in decision making to facilitate the identification of the priority areas needed for proper management and conservation, and to mitigate the impacts caused by various intrinsic and extrinsic factors. Even though *Metapenaeopsis* is the most speciose genus of the family Penaeidae, only a small number of studies have been conducted on their reproductive biology. These include aspects of the population biology of *M. rosea* in Torres Strait, Australia (Watson & Keating, 1989); growth and maturation of *M. barbata* in the Aki-nada area, the Seto Inland Sea, Japan (Sakaji et al., 1992); oocyte development, maturation and spawning of *M. dalei* in Tosa Bay, Japan (Sakaji et al., 2000b; Sakaji, 2001a); oocyte development of *M. aegyptia, M. barbata* and *M. sinica* from Tosa Bay, Japan (Sakaji, 2001b); growth and reproduction of *M. dalei* on the western coast of Korea (Choi et al., 2005); life history of *M. palmensis* off southwestern Taiwan (Chen et al., 2014); reproductive biology, morphological sexual maturity and biometric indices of *M. sibogae* in Kagoshima Bay, Japan (Rahman & Ohtomi, 2017, 2018a, 2018b).

Previous studies have shown the existence of spawning seasonality in *Metapenaeopsis* species, which was reported to be influenced primarily by water depth, water temperature and latitudinal variations of the sampling areas, among other possible factors (Sakaji et al., 1992; Choi et al., 2005; Chen et al., 2014; Rahman & Ohtomi, 2017). Furthermore, the suitability of gonadosomatic index (GSI) as a maturity index for small penaeid shrimp has been put into question due to its dependence on body size (Courtney et al., 1995) and its gradual relationship with the progression of ovarian maturation (Ohtomi et al., 2003; Rahman & Ohtomi, 2017). Rahman & Ohtomi (2017) subsequently proposed a new macroscopic index based on comparisons of ovary width to body width as a simple, cost-effective and reliable maturity index for small penaeid shrimps. The present study, therefore, aimed to delineate oocyte development, ovarian maturation, size at sexual maturity and spawning season of *M. provocatoria owstoni* for the first time using samples collected from Kagoshima Bay, southern Japan. We also tested the suitability of both GSI and macroscopic staging (Rahman & Ohtomi, 2017) as a simple and reliable maturity index in assessing the ovarian maturity status in *M. provocatoria owstoni*.

### Materials and Methods

#### Sampling

Monthly samples of *M. provocatoria owstoni* were collected from experimental trawl surveys conducted in Kagoshima Bay, southern Japan (31°25′N, 130°38′E) at depths ranging from around 80 to 230 m (Fig. 1). Sampling was conducted on-board the training vessel Nansei-Maru (175 t) of the Faculty of Fisheries, Kagoshima University from January 2013 to December 2017 using a simple trawl net carrying canvas kites on the tip of the wings (LC-VI; Nichimo Corporation, Tokyo). The net was 23.5 m long and 8.0 m wide, with a mesh size of 37.9 mm and 20.2 mm at the net body and cod end, respectively (Ohtomi et al., 2004). The net was towed for a preset tow duration of 10 min. at a speed of 2 kt. Individuals of *M. provocatoria owstoni* were sorted for each haul, and then counted and chilled immediately in ice. The samples were transferred to the lab-
oratory on the same day and fixed in 10% formalin pending further analysis.

**Measurements**

The sex of each specimen was determined through the observation of its external traits (i.e. presence of a petasma in males or a thelycum in females), and only females \((N = 640)\) were used in this study. For each female, carapace length (CL) was measured to the nearest 0.01 mm from the posterior margin of the eyestalk to the dorsal midline of the posterior margin of the carapace with slide calipers (CD-15PS; Mitutoyo Corp., Kawasaki, Japan), and body weight was measured to the nearest 0.01 g using an electronic balance (EB-430DW; Shimadzu Corp., Kyoto, Japan). The exoskeleton and muscles above the ovary of each female were removed, and the ovary and body widths were measured to the nearest 0.01 mm at the middle of the first abdominal segment. Ovaries were classified as one of three initial sexual maturity stages based on the ratio of ovary width to body width following Rahman & Ohtomi (2017): Stage I, ovary width < 1/5 body width; Stage II, 1/5 body width ≤ ovary width < 1/3 body width; and Stage III, ovary width ≥ 1/3 body width. The whole gonad was then removed and weighed to the nearest 0.001 g using the electronic balance. The gonadosomatic index was calculated as:

\[
\text{GSI} \, (\%) = 100 \times \frac{\text{ovary weight}}{\text{body weight}}
\]

The performances of macroscopic staging based on ovary width to body width and GSI in assessing ovarian maturity status were verified by histological observation (see next section).

**Histological analysis of ovary**

The ovaries were examined histologically to quantify the degree of ovarian maturation. A small portion of each ovary was extracted from the 81 females collected between January 2013 and December 2017 (CL, 9.2 to 21.2 mm; GSI, 0.14 to 7.78%) and each was dehydrated in an ethanol series, infiltrated with paraffin and sliced into 6 µm sections. The sections were then stained with Mayer’s hematoxylin and eosin, cover-slipped with a mounting medium and examined under a microscope (DMLB; Leica, Wetzlar, Germany). As a preliminary examination, sections from three parts of the ovary (the posterior region of the cephalothoracic lobe, and the anterior and middle regions of the abdominal lobe) from one female shrimp (CL, 17.3 mm; GSI, 6.78%) were examined in order to differentiate the maturity stages in relation to the different positions in the ovary. From our examination, we determined that there was no difference in the maturity stage with respect to ovary position. Therefore, tissue samples ex-
tracted from the anterior regions of the abdominal lobes were used for further histological analysis to determine the oocyte developmental stages following Yano (1988), Sakaji et al. (2000b), Chen et al. (2014), and Rahman & Ohtomi (2017).

**Size at sexual maturity and spawning season**
The size at sexual maturity was estimated based on the relationship of ovarian maturity progression with CL-class and the minimum size of macroscopically and histologically determined mature females. The spawning season of *M. provocatoria owstoni* was estimated based on the monthly occurrence of mature females (see Results). The main spawning season was defined as the period (months) when a higher percentage of mature females occurred.

**Results**

**Classification of developmental stages of oocytes**
Oocytes were classified into one of seven developmental stages based on their histological characteristics: oogonium, early nucleolus, middle nucleolus, late nucleolus, yolk granule, prematuration, and maturation (Table 1). Oogonium stage: the oocytes were round, basophilic, and of similar sizes (ca. 2–4 μm in diameter) and they were situated in the connective tissue of the ovary (Fig. 2a). Early nucleolus stage: the oocytes were 10–76 μm in diameter. The cytoplasm was thin and weakly basophilic. No prominent follicle cell layer was visible (Fig. 2b). Middle nucleolus stage: the oocytes were 58–129 μm in diameter with strongly basophilic chromatin areas located in the nucleus and a thick layer of follicle cells visible surrounding the oocytes (Fig. 2c). Late nucleolus stage: the cytoplasm was weakly stained with hematoxylin. Circular nucleoli lie peripherally in the germinal vesicle and oocyte diameter ranged from 77 to 197 μm. The thickness of the follicle layers decreased (Fig. 2d). Yolk granule stage: eosin-stained acidophilic yolk granules appeared in the cytoplasm and the oocytes were 168–259 μm in diameter (Fig. 2e). Prematuration stage: acidophilic yolk granules concentrated in and filled the cytoplasm of the oocyte, and germinal vesicle breakdown (GVBD) occurred throughout the cytoplasm at this stage. The oocytes ranged from 173 to 268 μm in diameter (Fig. 3f). Maturation stage: The germinal vesicle shrunk in size and shifted to the edge of the oocyte. The acidophilic yolk granules were concentrated and filled the cytoplasm of the oocyte. The oocytes were 220–254 μm in diameter (Fig. 3g).

**Assessment of stages of ovarian maturity**
This species had asynchronous ovaries, containing oocytes at various developmental stages (Fig. 2h). Therefore, the ovarian maturity stages were classified based on the developmental stage of the most advanced oocytes observed.

| Ovarian maturity stage | Oocyte stage | Histological characteristics | Oocyte diameter (range, μm) |
|------------------------|--------------|------------------------------|-----------------------------|
| Immature               | Oogonium     | Previtellogenesis            | 2–4                         |
|                        | Early nucleolus |                              | 10–76                       |
|                        | Middle nucleolus |                             | 58–129                      |
|                        | Late nucleolus  |                              | 77–197                      |
| Maturing               | Yolk granule  | Progression of vitellogenesis | 168–259                     |
| Mature                 | Prematuration | Germinal vesicle breakdown    | 173–268                     |
|                        | Maturation    | Migratory nucleus            | 220–254                     |

* Developmental stage of the most advanced oocytes in the ovary.
in the ovary, and they were divided into three categories: immature, maturing, and mature (Table 1). Ovaries with oogonium-stage oocytes and/or oocytes in the early-, middle-, or late nucleolus-stages (previtellogenic oocytes) were categorized as immature. Maturing ovaries contained oocytes in the yolk granule-stage (vitellogenic oocytes) in addition to previtellogenic oocytes (except oogonium-stage oocytes). Mature ovaries contained prematuration- and maturation-stage oocytes as well as previtellogenic (except oogonium-stage oocytes) and vitellogenic oocytes. Females of *M. provocatoria owstoni* were defined as mature when their oocytes either had evidence of GVBD or migrating nucleus that would lead them to spawn within a few hours.

**Change in ovarian maturation with progression of gonadosomatic index**

There was no significant correlation found between CL and GSI \( (N=29, r=0.044, P= \)
0.820) for sexually mature females that were determined using the histological method. The percent occurrence of females in each histologically determined stage of ovarian maturity gradually shifted as the GSI increased from most ovaries being immature to a majority being mature (Fig. 3). Females with a GSI < 2% were mostly immature, whereas most females with a GSI of 2 to < 4% were maturing. The mature females first appeared in the GSI 2–3% class. Nearly 50% of the females with a GSI ≥ 4–5% were mature, whereas all the females with GSI ≥ 6% were mature.

**Histological verification of macroscopic ovarian stages**

The maturity status of the three ovarian stages that were determined macroscopically was verified by histological analysis (Fig. 4). Nearly 80% of Stage I ovaries were immature. Stage II ovaries included all of the three maturity stages; however, the dominant stage was maturing (nearly 60%). Of the Stage III ovaries, approximately 84% were mature, and the remaining were maturing. The percentage of mature females steeply increased when classified macroscopically. Females with Stage III ovaries were considered mature in the present study.

**Size at sexual maturity**

The percent occurrence of females within each macroscopic ovarian maturity stage showed that all the females having a CL < 10.0 mm and around 90% of the females having a CL 10 to < 12 mm were immature (Fig. 5). Maturing females first appeared in the
10–11 mm CL-class whereas mature females first appeared in the 12–13 mm CL-class. The percentage of mature females was low (<20%) throughout the CL-class range. Both macroscopic staging and histological observation of the ovaries confirmed that the minimum size of mature females was 12.8 mm CL, which is the size of sexual maturity for *M. provocatoria owstoni*.

**Spawning season**

Mature females occurred from April to December with a comparatively higher prevalence from May to June (Fig. 6). These findings indicate that *M. provocatoria owstoni* spawns from April to December in Kagoshima Bay with May-June being their main spawning season.

**Discussion**

The sequential collection of a large number of specimens is of utmost importance for studying the biological aspects of a population (Ohtomi *et al*., 1998). Even though it is difficult to collect a long-time series of samples from deep waters, in the present study, it was possible to collect monthly samples of *M. provocatoria owstoni* for a period of over 5 years from Kagoshima Bay. However, the number of specimens caught per month was relatively small compared to the desired number to obtain credible population biological information. Therefore, specimens collected for the same months over the 5-years sampling period were combined. This decision was supported by the relatively stable environmental parameters (*e.g.*, the bottom water temperature and salinity) of Kagoshima Bay over these years (Farhana & Ohtomi, 2016; Rahman & Ohtomi, 2017; Ohtomi *et al*., 2018; Rahman & Ohtomi, 2018c). The combined data set allowed us to study some major reproductive aspects of *M. provocatoria owstoni*, including size and age at sexual maturity, and spawning season for the first time.

Chen *et al*. (2014) and Rahman & Ohtomi (2017) reported six oocyte developmental stages in both *M. palmensis* and *M. sibogae*. In the present study, we have detected seven oocyte developmental stages in *M. provocatoria owstoni*. In the case of *M. sibogae*, the authors could not detect the migratory nucleus stage, whereas in the case of *M. palmensis*, the authors did not separate the yolk granule stage from the GVBD stage. In the present study, it was possible to detect the oogonium, early-nucleolus, middle-nucleolus, late-nucleolus, and GVBD stages together with the yolk granule and migratory nucleus stages (maturation stage). Sakaji *et al*. (2000b) also detected seven oocyte developmental stages in *M. dalei* including the ovulation stage, characterized by a vitelline envelope surrounding the oocyte instead of the follicle cells. However, in our study, it was impossible to differentiate between the migratory nucleus and the ovulation stages. There were no cortical crypts, which are widely recognized as a sign of oocyte pre-maturation in penaeoid shrimps (*e.g.*, Yano, 1988; Ohtomi & Yamamoto, 1997; Ohtomi *et al*., 1998, 2003; Yamada *et al*., 2007; Farhana & Ohtomi, 2016), found in the periphery of oocyte cytoplasm. Similar outcomes were also reported in other species of *Metapeneaopsis*, including *M. aegyptia*, *M. barbata*, *M. dalei*, *M.
**sinica, M. palmensis and** M. *sibogae* (Sakaji *et al.*, 2000b; Sakaji, 2001a, 2001b; Chen *et al.*, 2014; Rahman & Ohtomi, 2017). This further supports the idea that the absence of cortical crypts and/or rods in oocyte development is a general characteristic of the genus *Metapenaeopsis* as compared to other penaeid shrimps. Initiation of GVBD was considered as a sign of prematuration, whereas the migrating nucleus was considered as a sign of maturation in *M. provocatoria owstoni*.

Similarly to some other *Metapenaeopsis* shrimps, such as *M. aegyptia, M. barbata, M. dalei, M. sinica, M. palmensis* and *M. sibogae* (Sakaji *et al.*, 2000b; Sakaji, 2001a, 2001b; Chen *et al.*, 2014; Rahman & Ohtomi, 2017), *M. provocatoria owstoni* also had asynchronous oocyte development in its ovary. This species is supposed to have multiple spawning during a single reproductive season (Bauer, 1989; Yamada *et al.*, 2007; Rahman & Ohtomi, 2017), even though we could not detect their spawning frequency. The ovarian maturity stages were thus classified into three categories based on the developmental stage of the most advanced oocytes in the ovary: immature, maturing, and mature. Females of *M. provocatoria owstoni* were determined to be mature if their oocytes either had evidence of GVBD or a migrating nucleus that would lead them to spawn within a few hours (Yano, 1988).

We tested the suitability of both GSI and macroscopic index (Rahman & Ohtomi, 2017) in determining the ovarian maturity status of *M. provocatoria owstoni* to see which was a more simple, cost-effective and reliable index. The gonadosomatic index has been used extensively in reproductive studies of shrimps. However, its usefulness as a maturity index in penaeid shrimps is often scrutinized due to its dependence on body size (Courtney *et al.*, 1995) and its gradual relationship with the progression of ovarian maturation (Ohtomi *et al.*, 2003). We did not detect any significant relationship between CL and GSI in mature females of *M. provocatoria owstoni*; however, the relationship between the two variables was gradual and similar relationships have also been reported for other shrimps, including *M. palmensis* (Chen *et al.*, 2014), *M. sibogae* (Rahman & Ohtomi, 2017) and *M. japonicus* (Ohtomi *et al.*, 2003). The gradual relationship between GSI and ovarian maturity stages indicated that GSI is not an appropriate index for assessing the sexual maturity status of female *M. provocatoria owstoni*. On the contrary, macroscopic staging showed a steeper relationship with the histological stages of ovarian maturity observed. Histological observation revealed that the percentage of mature ovaries increased abruptly in Stage III ovaries (nearly 84%) compared to that in Stage II (nearly 23%). Such a steep relationship between macroscopic and histological maturity stages assured the suitability of the macroscopic index as a simple and reliable maturity index for *M. provocatoria owstoni*.

It was not possible to fit the logistic equation to the percentage occurrence of mature females against the CL-class data due to the low percent occurrence of mature females. Several authors questioned the accuracy of the estimation of size at sexual maturity through this logistic equation in penaeid shrimps (Gab-Alla *et al.*, 1990) and the suitability of fitting a logistic equation to obtain maturity information especially in short-lived organisms (Hossain & Ohtomi, 2008). In our study, the relationship between ovarian maturity progression with CL-class and the minimum size of macroscopically and histologically determined mature females were used to estimate the size at sexual maturity of *M. provocatoria owstoni*. The estimated size at sexual maturity was 12.8 mm CL. We have calculated the age at sexual maturity by transforming the CL at maturity value to its respective age class following the CL frequency distribution and the estimated growth equation of *M. provocatoria owstoni* (Rahman & Ohtomi, unpublished data).
individuals were found to become sexually mature within their first year and they possibly experienced two spawning seasons during their lifetime. There is no information available on the size at sexual maturity of this species, therefore, the results will be helpful for future comparative studies. Moreover, depending on the characteristics of the fishery and its management approach, our information will aid to set the mesh size necessary to restrict catching the first mature shrimps and thus leaving the smallest mature shrimps to spawn within Kagoshima Bay (Chen et al., 2014; Rahman & Ohtomi, 2017).

Both shorter and extended spawning seasons have been reported for various species of Metapenaeopsis. Shallow water species like M. acclivis and M. barbata from Kasaoka Bay in the Ariake Sea and Aki-nada in the Seto Inland Sea, Japan, respectively and M. palmensis in the waters off Taiwan exhibited relatively shorter spawning seasons (Yasuda, 1949; Ikematsu, 1963; Sakaji et al., 1992; Chen et al., 2014). Whereas deep-water species like M. sibogae in Kagoshima Bay exhibited an extended spawning season (Rahman & Ohtomi, 2017). Interestingly, the same species of penaeid shrimps inhabiting different water depths had different spawning periodicities. For example, the spawning season of P. fissuroides lasted from July to October in the East China Sea near Taiwan, at a depth of 60–100 m (Song et al., 2002), whereas its spawning season in Kagoshima Bay (at a water depth of around 135 m) was found to be much longer (July to February) (Farhana & Ohtomi, 2016). A similar phenomenon had been reported for Metapenaeopsis shrimps as well. M. dalei collected from 15 to 65 m water depths in Tosa Bay, which exhibited a year-long spawning season (Sakaji, 2001a), while M. dalei in the shallower western sea of Korea (water depth <30 m) spawned from July to August (Choi et al., 2005). This clearly shows the role of water depth in determining spawning periodicity. Several studies have indicated that an extended reproductive period may be a typical feature of deep-water species (Harrison, 1988; Gage & Tyler, 1991). It is also important to note that the spawning periodicity of a species may vary significantly among habitats despite having similar water depths. For instance, mature females of M. dalei were reported to occur from July to August in Suo-nada in the Seto Inland Sea, and Sendai Bay (Yatsuyanagi & Maekawa, 1957; Kosaka, 1977), whereas this same species spawned throughout the year in Tosa Bay (Sakaji, 2001a). This shows the importance of habitat-specific population biology information of a species to formulate sound management strategies. Furthermore, earlier research demonstrated the influence of water temperature on spawning seasonality and indicated that Metapenaeopsis species do not spawn at water temperatures below 10°C (Onbe & Kakuda, 1962; Sakaji, 2001a; Tabata et al., 2015). Seasonality in the reproduction of penaeids is also influenced by the availability of the planktonic larvae they use as food (Giese & Pearse, 1974; Sastry, 1983; Tyler, 1986; Bauer, 1989, 1992; Bishop & Shalla, 1994).

The spawning season of M. provocatoria owstoni extended from April to December with May to June being the main season. Kagoshima Bay is a deep water bay with relatively stable water temperatures at deeper depths throughout the year (>15°C, Rahman & Ohtomi, 2017) owing to the intrusion of the warm Kuroshio Current into the bay during winter (Kohno et al., 2004). Furthermore, phytoplankton is reported to be predominant throughout the year within the bay (Kohno et al., 2002). Deep-water habitats, relatively constant bottom-water temperatures, and the availability of larval food might influence the extended spawning season of M. provocatoria owstoni. Similar factors were also reported to influence the spawning periodicity of M. sibogae in Kagoshima Bay (Rahman & Ohtomi, 2017). However, it was not possible to identify the factors responsible...
for triggering the initiation and cessation of spawning and these should be revealed in future studies. Furthermore, future studies on the spawning frequency and fecundity, as well as a breeding stock assessment, are recommended to gain a broader understanding of the reproductive potential of the population, which in turn will establish the basis for sustainable management regimes.

Acknowledgements

We are grateful to Dr. Miguel Vazquez Archdale, Faculty of Fisheries, Kagoshima University for his valuable comments and improvements on this manuscript, and to the crew of the training vessel Nansei Maru, of the same institution, for their help during the experimental trawl surveys. Thanks are due to the students of the Fisheries Biology laboratory, Faculty of Fisheries, Kagoshima University for their relentless assistance throughout the study. The work was supported in part by JSPS KAKENHI Grant Number 19K02297.

Literature Cited

Bauer, R. T., 1989. Continuous reproduction and episodic recruitment in nine shrimp species inhabiting a tropical seagrass meadow. Journal of Experimental Marine Biology and Ecology, 127: 175–187.

Bauer, R. T., 1992. Testing generalizations about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species. Invertebrate Reproduction & Development, 22: 193–202.

Bishop, J. D. D., & Shalla, S. H., 1994. Discrete seasonal reproduction in an abyssal peracarid crustacean. Deep Sea Research, Part I: Oceanographic Research Papers, 41: 1789–1800.

Chen, H. S., Chen, C. Y., & Chen, M. H., 2014. Life history tactics of southern velvet shrimp Metapenaeopsis palmensis (Crustacea, Decapoda) in the waters off southwestern Taiwan. Hydrobiologia, 741: 177–191.

Choi, J. H., Kim, J. N., Ma, C. W., & Cha, H. K., 2005. Growth and reproduction of the kishi velvet shrimp, Metapenaeopsis dalei (Rathbun, 1902) (Decapoda, Penaeidae) in the western sea of Korea. Crustaceana, 78: 947–963.

Courtney, A. J., Montgomery, S. S., Die, D. J., Andrew, N. L., Cosgrove, M. G., & Blount, C., 1995. Maturation in the female eastern king prawn Penaeus plebejus from coastal waters of eastern Australia, and considerations for quantifying egg production in penaeid prawns. Marine Biology, 122: 547–556.

Farhana, Z., & Ohtomi, J., 2016. Ovarian maturation, size at sexual maturity, and spawning season of Parapenaeus fissauroides Crosnier, 1985 (Decapoda: Penaeidae). Journal of Crustacean Biology, 36: 815–822.

Gab-Alla, A. A. F. A., Hartnoll, R. G., Ghobashy, A. F., & Mohammed, S. Z., 1990. Biology of penaeid prawns in the Suez Canal lakes. Marine Biology, 107: 417–426.

Gage, J. D., & Tyler, P. A., 1991. Deep-sea biology: A natural history of organisms at the deep-sea floor. Cambridge University Press, London.

Giese, A. C., & Pearse, J. S., 1974. Introduction: general principles. In: A. C. Giese, & J. S. Pearse, (eds), Reproduction of marine Invertebrates, Acoelomate and Pseudocoelomate Metazoaons. Academic Press, New York, pp. 1–49.

Harrison, K., 1988. Seasonal reproduction in deep-sea Crustacea (Isopoda: Asellota). Journal of Natural History, 22: 175–197.

Hossain, M. Y., & Ohtomi, J., 2008. Reproductive biology of the southern rough shrimp Trachysalambria curvirostris (Penaeidae) in Kagoshima Bay, southern Japan. Journal of Crustacean Biology, 28: 607–612.

Ikematsu, W., 1963. Ecological studies on the fauna of Macrura and Mysidacea in the Ariake Sea. Bulletin of the Seikai Regional
REPRODUCTION OF *METAPENAEOPSIS PROVOCATORIA OWSTONI*

Fisheries Research Laboratory, 30: 1–124. (in Japanese with English abstract).

Kobari, T., Habano, A., & Ichikawa, T., 2002. Seasonal variations in phyto-and zooplankton biomass in Kagoshima Bay. Memoirs of Faculty of Fisheries-Kagoshima University, 51: 19–25.

Kohno, J. I., Hosotani, K., Ono, Y., & Kikukawa, H., 2004. Warm ocean water intrusion into Kagoshima Bay. *Journal of Visualization*, 7: 331–340.

Kosaka, M., 1977. On the ecology of the penaeid shrimp, *Metapenaeopsis dalei* (Rathbun), in Sendai Bay. Journal of the Faculty of Marine Science and Technology, Tokai University, 10: 129–136. (in Japanese with English abstract).

Ohtomi, J., Ahamed, F., Rahman, M. M., & Fukushima, H., 2018. Distribution patterns and population dynamics of the pandalid shrimp *Plesionika izumiae* (Decapoda, Caridea) in a unique semi-enclosed deep-water bay environment. *Crustaceana*, 91: 1073–1096.

Ohtomi, J., Fujieda, S., Higashi, M., & Habano, A., 2004. Preliminary trawl survey for estimating distributions of benthic animals and marine debris in Kagoshima Bay. Bulletin of the Japanese Society of Fisheries Oceanography, 68: 158–164. (in Japanese with English abstract).

Ohtomi, J., & Nagata, M., 2004. First record of *Metapenaeopsis sibogae* (De Man, 1907) (Decapoda, Penaeidae) from Japanese Waters. *Crustaceana*, 77: 333–339.

Ohtomi, J., Tashiro, T., Atsuchi, S., & Kohno, N., 2003. Comparison of spatiotemporal patterns in reproduction of the kuruma prawn *Marsupenaeus japonicus* between two regions having different geographic conditions in Kyushu, southern Japan. *Fisheries Science*, 69: 505–519.

Ohtomi, J., & Yamamoto, S., 1997. Change in gonadosomatic index with ovarian matura- tion in jack-knife shrimp *Haliporoides sibogae* off south-western Kyushu, Japan. *Fisheries Science*, 63: 1044–1045.

Onbe, T., & Kakuda, S., 1962. Ecology of fishes of Kasaoka Bay as observed from the catch of pound nets. Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University, 4: 21–45.

Rahman, M. M., & Ohtomi, J., 2017. Reproductive biology of the deep-water velvet shrimp *Metapenaeopsis sibogae* (De Man, 1907) (Decapoda: Penaeidae). *Journal of Crustacean Biology*, 37: 743–752.

Rahman, M. M., & Ohtomi, J., 2018a. Relative growth and morphological sexual maturity of the deep-water velvet shrimp *Metapenaeopsis sibogae* (Crustacea, Decapoda, Penaeidae). *Invertebrate Reproduction & Development*, 62: 125–132.

Rahman, M. M., & Ohtomi, J., 2018b. Biometric relationships of the deep-water velvet shrimp *Metapenaeopsis sibogae* (Crustacea, Decapoda, Penaeidae) in Kagoshima Bay, Japan. *Zoology and Ecology*, 28: 365–375.

Rahman, M. M., & Ohtomi, J., 2018c. Recruitment, growth patterns, and longevity of the deep-water velvet shrimp *Metapenaeopsis sibogae* (Decapoda: Penaeidae) in Kagoshima Bay, Japan. *Zoology and Ecology*, 28: 365–375.

Ohtomi, J., Yamamoto, S., & Koshio, S., 1998. Ovarian maturation and spawning of the deep-water mud shrimp *Solenocera melantho* De Man, 1907 (Decapoda, Penaeoidea, Solenoceridae) in Kagoshima Bay, southern Japan. *Crustaceana*, 71: 672–685.

Sakaji, H., 2001a. Maturation and spawning of the small penaeid shrimp *Metapenaeopsis dalei* in Tosa Bay, Pacific coast of southern Japan. *Fisheries Science*, 67: 444–448.

Sakaji, H., 2001b. Observations of the oocytes of the small penaeid shrimps *Metapenaeopsis aegyptia*, *M. barbata*, and *M. sinica*. *Benthos Research*, 56: 81–85.

Sakaji, H., Tokai, T., & Sato, R., 1992. Growth and maturation of whiskered velvet shrimp *Metapenaeopsis barbata* (De Hann) in Aki-nada area, the Seto Inland Sea. *Nippon Su-
isan Gakkaishi, 58: 1021–1027. (in Japanese with English abstract).

Sakaji, H., Tsuchiya, K., & Segawa, S., 2000a. Penaeid fauna (Crustacea, Decapoda) of Tosa Bay and Urado Bay, Pacific coast of southern Japan. Bulletin of the National Research Institute of Fisheries Science, 15: 11–39.

Sakaji, H., Tsuchiya, K., & Segawa, S., 2000b. Oocyte development of Metapenaeopsis da-lei (Penaeidae, Decapoda, Crustacea). Invertebrate Reproduction & Development, 38: 7–12.

Sastry, A. N., 1983. Ecological aspects of reproduction. In: F. J. Vernberg, & W. B. Vernberg (eds.), The biology of Crustacea. vol. 8. Academic Press, New York, pp. 179–270.

Shinomiya, S., & Sakai, K., 2000. A new Japanese subspecies of Metapenaeopsis: Metapenaeopsis provocatoria owstoni subsp. nov. (Crustacea: Decapoda: Penaeidae). Senckenbergiana maritima, 30: 123–140.

Song, H. T., Yao, G. Z., Yu, C. G., & Xue, L. J., 2002. The quantitative distribution and biological characteristics of Parapenaeus fisuroides in East China Sea. Progress in Fishery Sciences 2002: 8–12. (in Chinese with English abstract).

Tabata, T., Hiramatsu, K., & Harada, M., 2015. Assessment of the water quality in the Ariake Sea using principal component analysis. Journal of Water Resource and Protection, 7: 41–49.

Tyler, P. A., 1986. Studies of a benthic time series: reproductive biology of benthic invertebrates in the Rockall Trough. Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences, 88: 175–190.

Watson, R. A., & Keating, J. A., 1989. Velvet shrimps (Metapenaeopsis spp.) of Torres Strait, Queensland, Australia. Asian Fisheries Science, 3: 45–56.

Yamada, R., Kodama, K., Yamakawa, T., Horiguchi, T., & Aoki, I., 2007. Growth and reproductive biology of the small penaeid shrimp Trachysalambria curvirostris in Tokyo Bay. Marine Biology, 151: 961–971.

Yano, I., 1988. Oocyte development in the kuruma prawn Penaeus japonicus. Marine Biology, 99: 547–553.

Yasuda, D., 1949. A biological note on the shrimp, Trachypenaeus curvirostris (Stimpson). Nippon Suisan Gakkaishi, 15: 180–189. (in Japanese with English abstract).

Yatsuyanagi, K., & Maekawa, K., 1957. Ecological studies on the useful sea animals off Yamaguchi Pref. Inland Sea. 15. Ecological studies on the Metapenaeopsis da-lei (Rathbun). Yamaguchi Prefectural Inland Sea Fisheries Experimental Station, 9: 13–20 (in Japanese).

Addresses
(MMR) Graduate School of Agriculture, Forestry and Fisheries, Kagoshima University, 1–21–24 Korimoto, Kagoshima 890–8580, Japan

(JO) Faculty of Fisheries, Kagoshima University, 4–50–20 Shimoarata, Kagoshima 890–0056, Japan

Email address of corresponding author
(JO) ohtomi@fish.kagoshima-u.ac.jp