Size at sexual maturity of male *Lucensosergia lucens* (Decapoda: Sergestidae) in Suruga Bay, Japan

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Abstract.— This study investigated size at sexual maturity of the male sergestid shrimp *Lucensosergia lucens* (“Sakura-ebi” in Japanese). The shrimps were captured in the inner part of Suruga Bay, Japan in August 2013 using experimental trawls. Carapace length (CL), body length (BL), development of petasma, and presence of spermatophores in the terminal ampoule were documented. Probabilities of maturity as a function of CL were modeled using general linear models with a binomial and logit link function and predicted the CL at which 50% of individuals were mature (CL_{50}). Morphologically mature males had a petasma connected with the pars astringens, and the basal part of the pars media was developed. In physiologically mature males, chambers in terminal ampoules were filled with spermatophores, including spermatozoa and appendages. CL_{50} (mm) was estimated to be 8.87 (=27.86 mm BL) and 7.84 (=24.65 mm BL) based on the morphological and physiological criteria, respectively. It is believed that most of the age-0 males attain sexual maturity within the first year and mature males are exploited in the autumn fishing season (October–December).

Key words: petasma, spermatophore, terminal ampoule

■ Introduction

Lucensosergia lucens (known as “Sakura-ebi” in Japanese), a small pelagic shrimp belonging to the family Sergestidae, is distributed only in the western Pacific area from Tokyo Bay, Japan, to Tung-kang, southwestern Taiwan, and presumably off the coasts of Borneo, the Philippines, and New Guinea (Omori & Hashimoto, 2020). This species is an important target of commercial fisheries in Suruga Bay (Omori, 1969), Tung-kang, and around Gueishan Island, Taiwan (Omori *et al.*, 1988; Imai *et al.*, 2013). In Suruga Bay, *L. lucens* has been caught by pelagic trawl fishing since 1894 (Omori, 1995), but the annual catch has gradually decreased with some fluctuations (Kobayashi, 2002). Catch data analysis suggested that these catch fluctuations reflect the annual changes in the abundance and biomass of

shrimp (Fukui *et al.*, 2004; Sakuma *et al.*, 2010). During the 2010s, the annual catch remained at ca. 1,000 tons, but abruptly decreased to the historic low of 300 tons in 2018 and has been <100 tons since 2019 (Shizuoka Fisheries Research Institution, 2021). The fishery for this shrimp in Suruga Bay is currently managed under stricter self-regulation by fishermen (Shizuoka Prefecture, 2021).

Overfishing not only diminishes stock size but also causes changes in life history characteristics. Numerical models have suggested that size variation at the onset of sexual maturity can be caused by fishing pressure (Charnov, 1981; Ernande *et al.*, 2004). In fact, size at maturity (SAM) for females is used as an index to assess the impact of fishing on the stock (Shin *et al.*, 2005). Although SAM concurrently declines with spawning stock size in some commercially exploited decapods (Lipcius &

Stockhausen, 2002; Kodama *et al.*, 2004), environmental factors (mainly temperature) are thought to be the main cause of SAM variation (Chiba *et al.*, 2000; Little & Watson, 2005; Koeller *et al.*, 2007). It has been suggested that the SAM of recent cohorts of female *L. lucens* has become smaller than that of the 1960s and the 1990s (Omori, 1969; Suzuki *et al.*, 2012) as stated by Tanaka & Saitou (2008), Washiyama *et al.* (2017), and Doi *et al.* (2018a). However, factors causing smaller SAM in female *L. lucens* remain unknown, and male SAM has yet to be studied.

Several studies have described the reproductive biology of *L. lucens* other than female SAM: spawning season begins in late May and lasts until the middle of November, with the greatest spawn occurring in July and August (Omori, 1969; Suzuki *et al.*, 2012; Doi *et al.*, 2018a). Spawning occurs in the upper layers at night, where one female can release approximately 1,700–2,300 eggs (Omori, 1969; Kaneko & Omori, 2012). Compared to females, aspects of male reproductive biology are poorly understood. First, morphological sexual dimorphisms and secondary sexual characteristics of males have been described (Omori, 1969). Second, mating seems to occur in spring and early summer, because females inseminated with sperm plugs could be observed in May and June (Suzuki *et al.*, 2012). During copulation, male penaeoids emit right and left spermatophores from their terminal ampoules (ejaculatory ducts; Bell & Lightner, 1988; Chow *et al.*, 1991; Fransozo *et al.*, 2016; Feng *et al.*, 2018), after which they are transferred and deposited into the thelycum (female modified posterior thoracic sternites) by using the petasma (male modified endopods of the first pleopods) (Bauer, 1991). The presence of spermatophores in the terminal ampoule and a complete petasma indicate physiological and morphological sexual maturity of males. A better understanding of the basic male reproductive biology is critical for improving our under-

standing of the biology of the commercially important *L. lucens*. The aim of the present study was to first reveal the SAM of male *L. lucens* in Suruga Bay using morphological (petasma) and physiological (spermatophores in terminal ampoule) traits and their availability as determinants of maturity.

Materials and Methods

Sampling

The shrimps were collected around their spawning ground (offshore the Fujikawa River) in the inner part of Suruga Bay (Fig. 1) on August 26th, 2013, during their main spawning season (Omori, 1969; Suzuki *et al.*, 2012; Doi *et al.*, 2018b). Sampling was conducted on-board the Research Vessel *Suruga-Maru* of the Shizuoka Prefecture Fisheries Research Institute using a MOHT net. The net was 8.30 m long, with a mouth opening of 1.43 m × 1.43 m and a mesh size of 3.18 mm. The net was towed from 19:54 to 20:11 at a speed of 2.0 kt at 50–58 m depth. The shrimps spawn their eggs mainly in the upper layers at night (Omori, 1969). Individuals of *L. lucens* were sorted for each haul, immersed in 10% seawater formalin on-board, and transported to the laboratory.

Fig. 1. Map showing a sampling site (circle) in Suruga Bay, Japan.

Measurements

After the species of each specimen was confirmed by Hayashi (1992), sex was determined by the presence or absence of petasma. The carapace length (CL) (from the base of the rostrum to the posterior edge of the carapace) and body length (BL) (from the base of the rostrum to the posterior end of the telson) were measured to the nearest 0.01 mm. Measurements of small structures were performed with the aid of a stereomicroscope fitted with an ocular micrometer and camera lucida. BL was used to compare with the results of previous studies. BL in the previous studies was converted to CL based on Omori *et al.* (1973).

The life span of *L. lucens* is about 15 months (Omori, 1969). During the spawning season, the population of *L. lucens* consists of cohorts hatched in recent years (Doi *et al.*, 2018b). For morphological maturity analysis, 96 males with a CL between 4.41–8.56 mm, and 15 males with a CL between 10.25–12.32 mm were selected as a group of males hatched in the current year (2013 year class) and previous year (2012 year class) (Omori, 1969). The petasma (symmetrically paired and jointed copulatory endopods on the first pleopod), which transfers spermatophores from gonopores to the female thelycum (Omori, 1969), stained with methylene blue, was examined under a binocular microscope to quantify the degree of ontogenetic development.

For physiological maturity analysis, 56 males with a CL between 4.41–8.56 mm and 11 males with a CL between 10.25–12.32 mm were selected from the 2013 and 2012 year classes, respectively (Omori, 1969). To confirm the presence of spermatophores within the terminal ampoules, a series of horizontal sections were made for the males. After excision of the abdomen and appendages, the cephalothorax was immersed in Davidson's solution for 1 week for demineralization. Thereafter, it was dehydrated in ethanol, embedded in paraffin wax, sectioned at a thickness of 5–6 μm from

the ventral side, stained with Mayer's hematoxylin and 1% eosin and then observed under a light microscope.

Statistical analysis

To estimate the probability of maturity (ProMat) as a function of CL at the population level, a logistic model was used for the morphological maturity (completed petasma on the first pleopods) or physiological maturity (presence of spermatophores in the terminal ampoule): $\text{ProMat} = 1 / \{1 + \exp[-(\alpha + \beta \cdot \text{CL})]\}$ (e.g., Mollet *et al.*, 2000). The model was fitted using a general linear model (GLM) with a binomial and logit link function by the stats package in R version 4.0.2 (R Core Team, 2020). Overdispersion in the data was assessed by comparing the ratio of Pearson's chi-square statistics to the residual degrees of freedom, deeming a value considerably larger than 1.0 to represent evidence of overdispersion (Hosmer *et al.*, 2013). Overdispersion was also assessed using a chi-squared test fitting a model, using a quasibinomial model (Kabacoff, 2011). Two parameters (α , β) of the logistic models were used to predict the CL at which 50% of individuals were mature ($\text{CL}_{50} = -\alpha/\beta$) (Mollet *et al.*, 2000).

Results

Petasma

The five developmental stages of petasma are divided based on distinctive morphological features (Fig. 2A–E): Stage I (Fig. 2A), undivided rod-like structure; Stage II (Fig. 2B) is divided into three parts: pars astringens (pa), pars externa (pe), and pars media (pm), with the processus ventralis (pv) and lobus connectens (lc) elongating shortly at the distal part of the pm; Stage III (Fig. 2C), pa becomes less round and sharper, pe and pm are more elongated (tip of pv extends further than that of lc); Stage IV (Fig. 2D), lobus terminalis (lt) are clearly divided from lc and all structures are

Fig. 2. Photographs of five developmental stages (I–V) of the petasma of male *Lucensosergia lucens*. Ventral-view of the right petasma at stage I–IV (A–D) and the jointed right and left petasmas at stage V (E). plp1, first pleopod; pa, pars astringens; pe, pars externa; lc, lobus connectens; lt, lobus terminalis; pm, pars media; pv, processus ventralis; Scale bars = 0.1 mm (A) and 0.5 mm (B–E).

Fig. 3. Relationship between carapace length (CL) and development of the petasma of male *Lucensosergia lucens*. (A) Proportion of five developmental stages (see Fig. 2) of the 2 mm CL class. Brackets and parentheses mean that end of the range is inclusive and exclusive, respectively. (B) Probability of morphological maturity (0 = immature; 1 = mature, having stage V petasma) against CL. The curve and shaded area are logistic equations for the proportion of maturity against CL and its 95% confidence intervals, respectively.

more elongated, but the right and left petasmas are not jointed; Stage V (Fig. 2E), the right and left petasmas are jointed with pa.

The proportion of males with a more developed petasma increased with larger CL ranges (Fig. 3A). Males with stage V petasmas had CL ranges between 6.36–12.32 mm ($n = 20$). A portion of males with CL ranges 5–9 mm and all males with CL ranges ≥ 9 mm had complete

petasmas, showing that a part of age-0 (2013 year class) and all the age-1 males (2012 year class) attained morphological maturity. All males with stage V petasmas had spermatophores in their terminal ampoule, except for five males which did not receive a histological examination.

The logistic function of the ProMat for morphological maturity was estimated by the GLM as fol-

lows (Fig. 3B): $ProMat = 1 / \{1 + \exp[-(-14.293 + 1.612 \cdot CL)]\}$, and CL_{50} (mm) based on the morphological maturity was estimated to be 8.87 (= 27.86 mm BL) with the 8.26–10.21 range (= 26.38–31.22 mm BL) having a 95% confidence interval. The ratio of Pearson's chi-square statistics to the residual degrees of freedom suggested that there was no overdispersion in the data ($103.65/109.00 = 0.95$). A chi-square test for overdispersion comparing the binomial and quasibinomial models resulted in $p = 0.63$, suggesting a lack of evidence for overdispersion.

Terminal ampoule

The terminal ampoule was surrounded by a muscular layer and consists of chambers lined by epithelial cells (Fig. 4). Typhlosoles, secretory epithelium of duct structures did not reach from vas deferens. There was no content within the chambers of the immature males (Fig. 4A). In mature males, the primary and appendage chambers contained spermatophores, including sperm mass and glutinous material (plugs and adhesives connecting the right and left spermatophores, respectively) (Fig. 4B).

Histological observations showed no spermatophores inside the terminal ampoule, nor the terminal ampoule itself, in a series of longitudinal sections for 45 males with CL ranges be-

tween 4.74–8.56 mm, although the presence of spermatophores inside the terminal ampoule was confirmed in 22 males with CL ranges between 7.02–12.32 mm (Fig. 5A). A part of age-0 and all age-1 males attained physiological maturity. Among these physiological mature males, 7 males with CL ranges of 7.10–8.53 mm possessed stage IV petasmas.

The GLM for the proportion of physiological maturity was as follows (Fig. 5B): $ProMat = 1 / \{1 + \exp[-(-18.041 + 2.302 \cdot CL)]\}$, and CL_{50} (mm) based on the physiological maturity was estimated to be 7.84 (= 24.65 mm BL) with the 7.50–8.82 range (23.92–26.07 mm BL) having a 95% confidence interval. There was no evidence of overdispersion ($39.30/65.00 = 0.60$; chi-square test for overdispersion, $p = 1.00$).

Discussion

The present study successfully described the ontogenetic development of the petasma. In Sergestidae, an enlarged and elongated petasma and epi- or mesopelagic taxa is associated with the colonization of the water column where the water turbulence and currents cause mating interference (Lunina & Vereshchaka, 2017). Moreover, the species have an intricately sculptured “open thelycum”, a spermatophore with a

Fig. 4. Light micrographs of horizontal sections of a left terminal ampoule both without (A) and with a spermatophore (B) in *Lucensosergia lucens*. ch, chamber; ep, epithelium; gm, glutinous material; ml, muscular layer; sm, sperm mass.

Fig. 5. Relationship between carapace length (CL) and absence (A)/presence (P) of spermatophores in terminal ampoule of male *Lucensoergia lucens*. (A) Proportion of males with/without spermatophores in terminal ampoules of 2 mm CL class. Brackets and parentheses mean that end of the range is inclusive and exclusive, respectively. (B) Probability of physiological maturity (0 = immature; 1 = mature, having spermatophores in terminal ampoule) against CL. The curve and shaded area are logistic equations for the proportion of maturity against CL and its 95% confidence intervals, respectively.

complex appearance (Bauer, 2013). The thelycum of female *L. lucens* is of this open type (Hayashi, 1992), and the spermatophores have specialized accessory structures such as wings, flanges and plates (sperm plug) to assist with attachment to a female (Doi *et al.*, personal observation). The complex development process in the petasma of *L. lucens* provides an easier index for assessment of morphological maturity.

Morphological features of the terminal ampoule of *L. lucens* (Fig. 4) are similar to those of *Eusergestes similis*, the only species for which histological observations of the terminal ampoule have been performed in Sergestidae (Genthe, 1969; as *Sergestes similis*). The terminal ampoule of Sergestidae, including the present species, contains elliptic or pear-shaped chambers and do not have typhlosoles or incomplete tissue folds, which keep their contents isolated in ducts, as seen in some penaeids (e.g., King, 1948; Bell & Lightner, 1988; Chow *et al.*, 1991; Fransozo *et al.*, 2016). The male reproductive system including testis and vas deferens of *L. lucens* needs to be

analyzed microscopically to understand the mechanism underlying spermatophore formation.

Both morphological and histological observations confirmed that the 2012 year class (> 12 mm CL) and a portion of the 2013 year class (6–10 mm CL) were sexually mature in males as well as females (Doi *et al.*, 2018a). The morphological SAM was larger than the physiological SAM, and some physiological mature males did not have stage V petasmas. From these facts, it is thought that the stage V petasma is a good indicator of mature males, although physiological maturity may precede morphological maturity. The estimated BL_{50} in males (24.65–27.86 mm BL) is smaller than that of females (30–34 mm BL; Doi *et al.*, 2018a) (= 8–9 mm CL). Smaller modes in the length frequency distribution of the catch in October 1964 and 1965 were 28–30 mm or 30–32 mm BL bins (= 7.7–8.3 or 8.3–8.8 mm CL), respectively (Omori, 1969). Sakuma *et al.* (2010) analyzed the catch data between 1998 and 2008 and indicated that the mean BL of

age-0 males in November and December was 28.9–32.9 mm and 29.1–33.9 mm BL respectively (= 8.0–9.1 and 8.0–9.3 mm CL). It is inferred that some age-0 males attain sexual maturity before October, and the age-0 mature males are exploited in the autumn fishing season (October–December). Laboratory rearing experiments showed that the effects of temperature on molt frequency and size increment in *L. lucens* (Omori, 1971; Fukui *et al.*, 2003). A statistical model showed that sea surface temperature in the bay between August and September could explain average BL in the annual autumn fishing season and the presence of optimal temperature for growth of *L. lucens* (Ohnishi, 2004). Thus, the SAM should be studied in the annual fishing season to confirm the fishing pressure on immature/mature age-0 males.

The present study demonstrates that mature males can be identified by confirming the joint between the right and left petasmas (Fig. 2E), as observed in *E. similis* (Genthe, 1969). For female *L. lucens*, ovarian color aided the classification of immature and mature shrimps (Doi *et al.*, 2017). Using these simple methods to discriminate mature shrimps, their occurrence can easily be monitored. These results will contribute to a better understanding of the mechanism and variation in the temporal variation of SAM of *L. lucens* and their stock management in Suruga Bay, Japan.

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