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PROOF
RESEARCH PAPER

Can the Culture Density of the Marine Copepod *Pseudodiaptomus nihonkaiensis* be Improved by Installing an Artificial Substrate?

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Abstract

The understanding of the increasing population density of copepods in culture tanks contributes to establish their stable cultures at high productions for aquaculture industry, which are preferred live feeds for fish larvae. In the present study, the semi-benthic copepod *Pseudodiaptomus nihonkaiensis* were used as target species. This genus is often found from brackish water and its tolerance to a wide range of salinity and water quality has attracted attention as a potential commercial live feed for aquaculture. Population growth and egg production in the semi-benthic copepod *P. nihonkaiensis* are investigated. Copepods were cultured in tanks without mesh, with mesh lining tank walls, and with 2, 4 or 8 mesh partitions in each tank to identify the effect of substratum surface area on copepod population density. Linear regression revealed peaks in nauplius, copepodite, adult and total densities, and the cumulative number of eggs for all sampling events to correlate positively with substratum surface area ($p<0.01$). Greater substratum area within a culture tank may improve egg production by increasing habitat for ovigerous females. The simple installation of inexpensive artificial substrata in existing copepod culture tanks might improve the feasibility of using copepods as a live food in commercial-scale aquaculture

Introduction

Copepods are preferred live food for marine fish larvae in aquaculture (Støttrup 2003). Fish larvae fed copepods survive better (Wilcox et al. 2006), are better pigmented (Næss et al. 1995) and have better growth (Støttrup and Norsker 1997) than those fed *Artemia* and/or rotifers. However, despite the obvious advantages of copepods as a live food, their use remains limited because of low productivity and intensive culture costs. Culture densities of copepod are directly related to its productivity and production costs (Drillet et al. 2011a). But, at high copepod stocking densities, the encounter rates of individuals are greater and competition for food and space is amplified. For example, the high-density conditions can reduce egg production rate, hatching success and respiration rate of copepods even under an excess food supply (Franco et al. 2017; Takayama et al. 2020; Rahman et al. 2022). Mass-scale copepod culture has been limited by the high labor intensity involved as well as by the large number of vessels required to produce sufficient copepod quantities (O'Bryen and Lee 2005; Sarkisian et al. 2019). Therefore, a technology for improving culture density is needed to produce copepod economically and efficiently.

In marine benthic copepod such as *Tigriopus japonicus, Amphiascoides atopus, Tisbe holothuriae*,

previous studies demonstrated that placing artificial substrates such as corrugated plastic sheets, plastic balls, limestone cobbles and nylon mesh in the culture vessel increases copepod culture density and reduces cannibalism loss (Koga 1976; Stottrup and Norsker 1997; Sun and Fleeger 1995; Koga et al. 2021). The authors assumed that the artificial substrates provide large surface area as a habitat and biofilm formed on the substrate as food source. This simple method is effective in such benthic copepods, however, the effects of the substrate on the population density of non-benthic species has not been tested.

Pseudodiaptomus spp. are semi-benthic calanoid copepods; the adults are mostly substrate oriented while the nauplii and copepodites are planktonic. The genus is globally distributed from tropical to temperate waters and is predominantly estuarine (Walter 1989). Later life-history stages also engage in diurnal vertical migration, living on the bottom during the day and migrating to the surface at night (Hirakawa 1997). One such species, *Pseudodiaptomus annandalei* is mass cultured for use as a live feed for larval grouper and other planktivore (Doi et al. 1997; Hagiwara et al. 2001; Liao et al. 2001; Chen et al. 2006; Lee et al. 2010; Celino et al. 2012). However, at high population density condition, reproduction (i.e. ovigerous rate) of the species was reduced due to competition for bottom area in the culture among semi-benthic adults (Rayner at al. 2017). Thus, the placing artificial substrates into the culture vessel may have a potential to improve the competition and reproduction of the semi-benthic species.

P. nihonkaiensis was first reported from Izumozaki Harbour (Hirakawa 1983) and subsequently from Shijiki Bay (Kimoto et al. 1988), Tanabe Bay (Shimode and Shirayama 2004), Akajima Island (Omori et al. 2015) and Sagami Bay (Hirahara 2018; Natori 2018) in coastal water of Japan. This species is also reported from Dolsan Island, and Pyosun in coastal water in Korea (Soh et al. 2001). The extensive distribution of *P. nihonkaiensis* may suggest that it might be a suitable taxon for mass culture. We examine the effects of substratum surface area on *P. nihonkaiensis* egg production, growth and culture density in series of experiments to evaluate the potential of this species for mass culture.

Materials and Methods

Copepod Collection, Isolation, and Stock Culture

Pseudodiaptomus nihonkaiensis were isolated from Manazuru Port in Sagami Bay, Japan (35°09'05" N, 139°08'42" E) between April and August 2021 using a plankton net (mesh size: 180 µm). Upon arrival at the laboratory, adults were identified by light microscopy following Hirakawa (1983) and DNA analysis using the modified lysis buffer method (Kobayashi et al. 2022). DNA was extracted from these copepods via a modified ethanol removal method, with adjustments made to the dilution of the lysis buffer, and incubation time. The mitochondrial cytochrome *b* gene was amplified from these DNA samples by PCR. The nucleotide sequences of the PCR products were analyzed by the Sanger method. The obtained sequences were subjected to homology search against the DNA database using BLAST (Basic Local Alignment Search Tool).

Isolated copepods were cultured in filtered (< 0.22 µm) seawater in several 3 L plastic bottles maintained at 25°C in an incubator (Biotron, NK System) with a 12:12 L/D photoperiod. Copepods were fed sufficient *Isochrysis galbana* algae (2.0 µg-C mL^{-1}) once daily (Hirahara and Toda 2018). Algae were cultured with f/2 medium (Guillard and Ryther 1962) at 25°C in an incubator (FLI-301N, EYELA) with a continuous light regime. Half of the culture water within bottles was exchanged every 2 days. After seven days of culture, healthy copepods were selected for experimentation.

Experimental Design

Artificial Substrata

330-µm nylon meshes were used as a substratum to line tank walls, and for internal partitions within culture tanks (Koga et al. 2021); this mesh allowed for the passage of all *P. nihonkaiensis* developmental stages. A plastic tank (length 83 mm, width 82 mm, height 49 mm, surface area in contact with seawater 142 mm^2) containing 100 mL of filtered (< 0.22 µm) seawater (salinity 35) was used for culture. A control (just tank wall surfaces) and four treatments, one with tank wall inner surfaces lined with mesh, and others with 2, 4 or 8 equally spaced additional mesh partitions within the tank, were prepared. The surface area of the control tank was 142×10^3 mm^2 L^{-1}, and in the four treatments, 363, 440, 516 and 669×10^3 mm^2 L^{-1} (Figure 1). Each treatment was replicated three times.

Culture Experiment

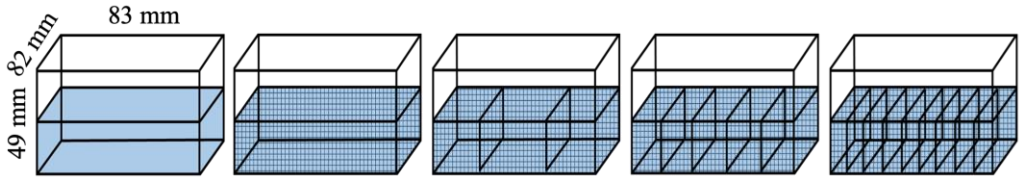
Ten males and ten ovigerous females were inoculated into each replicate tank for each treatment and cultured for 30 days. All tanks were maintained in the incubator at 25°C, with a 12:12 L/D photoperiod. Copepods were fed 2.0 µg-C mL^{-1} of *I. galbana* once daily. Every 3 days, abundance of nauplius, copepodite and adults, clutch size, and number of egg sacs were counted. Ovigerous rate (*O*, %) was calculated as:

$$O = F_{\mathrm{ovi}}/F_{\mathrm{all}} * 100$$

where F_{ovi} is abundance of ovigerous females, and F_{all} is total female abundance.

Data Analysis

All data were verified to have met parametric test assumptions. Differences in density, clutch size, and



Condition	Non substrate	Covered the inner walls	Covered the inner walls + 2 pieces	Covered the inner walls + 4 pieces	Covered the inner walls + 8 pieces
Specific surface area ($\times$ 10 mm^2 L^{-1})	142	363	440	516	669

Figure 1. *Pseudodiaptomus nihonkaiensis* culture tank experimental design.

ovigerous rate were analyzed using one-way analysis of variance (ANOVA). A Tukey–Kramer post hoc test was performed when ANOVA showed a significant difference at $p<0.05$.

Results

Population Growth and Density

Second generation nauplii and copepodites appeared in all treatments from days 3 and 6, respectively (Figure 2). Adult density initially, gradually decreased in all treatments over time, but tended to increase after days 9–12. In all treatments, nauplius density peaked before the first 15 days (875.0±72.8, 1458.0±176.0, 1376.7±140.6, 1661.3±190.3 and 2235.3±236.2 nauplii L^{-1} at 142, 363, 440, 516 and 669×10^3 mm^2 L^{-1}, respectively), and copepodite density peaked after 9–12 days (565.2±74.4, 958.7±86.7, 1190.0±131.4, 1167.7±138.9, 1138.7±156.5 copepodites L^{-1} at 142, 363, 440, 516 and 669×10^3 mm^2 L^{-1}, respectively). Adult density peaked after 18–24 days in all treatments (202.7±25.8, 226.0±13.3, 270.7±27.3, 261.3±26.4, 331.3±33.7 adults L^{-1}, at 142, 363, 440, 516 and 669 × 10^3 mm^2 L^{-1}, respectively). On days 6–12, total density peaked in all treatments (1110.7±176.7, 2176.0±197.9, 2669.3±269.8, 2683.3±292.6, 3528.0±358.7 inds. L^{-1} at 142, 363, 440, 516 and 669×10^3 mm^2 L^{-1}, respectively). Linear regression revealed maximum nauplius, copepodite adult, and total densities to correlate positively ($p<0.01$) with volume specific substratum surface area (Figure 3).

Egg Production

The ovigerous rate decreased over time in all treatments, with no significant difference among treatments (Figure 4). The same culture dates trended toward higher ovigerous rates in condition with higher substratum surface area. Maximum ovigerous-female densities per culture volume tended to be higher in treatments with more substratum (38.7±1.9, 60.7±7.4, 93.3±9.4, 93.3±9.4 and 136.7±9.4 ovigerous females L^{-1} at 142, 363, 440, 516 and 669×10^3 mm^2 L^{-1}, respectively) (Figure 5a). Maximum ovigerous female density per substratum surface area (0.21±0.035×10^{-3} ovigerous females mm^{-2}) (Figure 5b) and average egg sac size (10.8±4.2 eggs sac^{-1}) (Figure 6) were relatively consistent over time, with no significant differences among treatments.

Linear regression revealed the cumulative number of eggs during periods when only first generation adults produced eggs (days 0–9), when second generation adults joined the population (days 12–30), and throughout the entire cultivation period (days 0–30), to correlate positively ($p<0.01$) with substratum surface area (Figure 7).

Discussion

Population size generally changes by way of birth, death, immigration, and emigration. Because our culture of *Pseudodiaptomus nihonkaiensis* represents a "closed population" with neither emigration nor immigration, birth and death must be responsible for changes in population dynamics. We measured egg production (ovigerous rate, density of ovigerous females, clutch size) as indicators of reproduction and birth. The ovigerous rate and density of ovigerous females tended to be higher with increased substratum surface area. In ovigerous females in particular, the egg sac not only increases body weight by 40% (Mauchline 1998) but it also increases the effects of gravity (Strickler 1982). Therefore, compared with other developmental stages, ovigerous females are more likely to attach to a substratum (Dur et al. 2010). Several pseudodiaptomid species commonly utilize long antennule setae to attach to detritus (Fancett and Kimmerer 1985). Because adult *P. annandalei* occur near the sediment surface and/or detritus during the day (Blanda et al. 2015), adult competition for habitat can occur and the ovigerous rate can decrease (Rayner et al. 2017). Our nylon mesh increased the surface area of habitat available for *P. nihonkaiensis*, especially adults, which may have led to

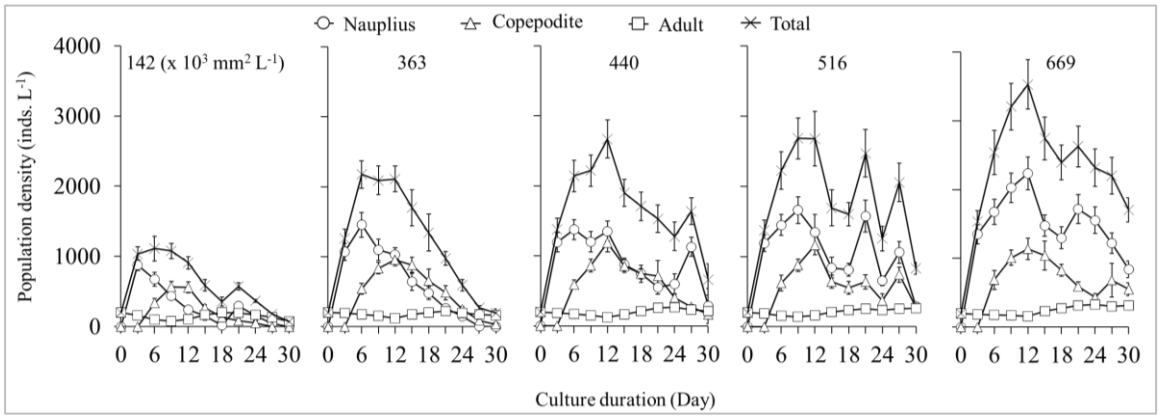


Figure 2. Temporal variation in *Pseudodiaptomus nihonkaiensis* density in cultures with different specific surface areas. Cultures were inoculated with ten adult males and ten adult ovigerous females. Error bars indicate standart deviations (n=3).

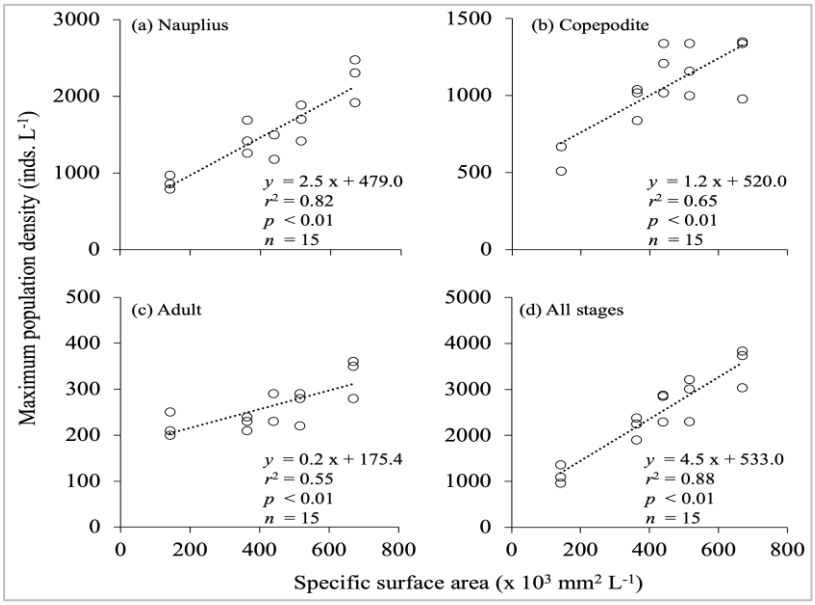


Figure 3. Relationship between specific surface area of culture tanks an maximum population density of (a) nauplius, (b) copepodite, (c) adult and (d) all stages in *Pseudodiaptomus nihonkaiensis*

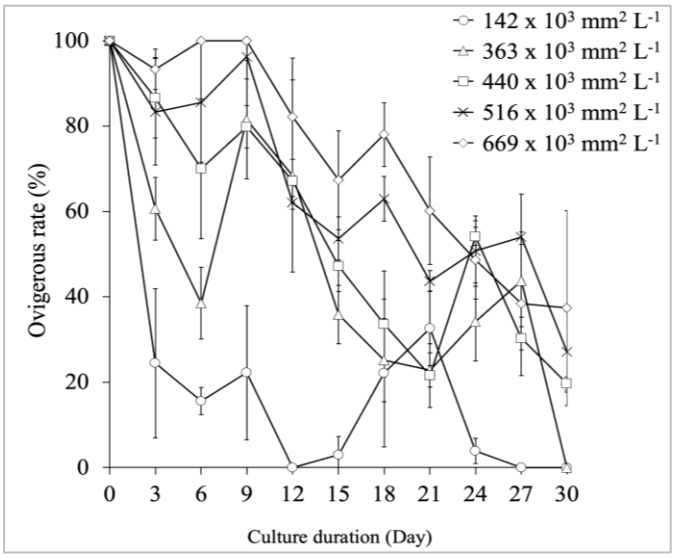


Figure 4. Temporal variation in ovigerous rate of *Psedodiaptomus nihonkaiensis* in tanks with different areas. Symbols indicate the specific surface area within treatments. Tanks were inoculated with ten adult males and ten ovigerous females. Error bars indicate standard deviations (n=3).

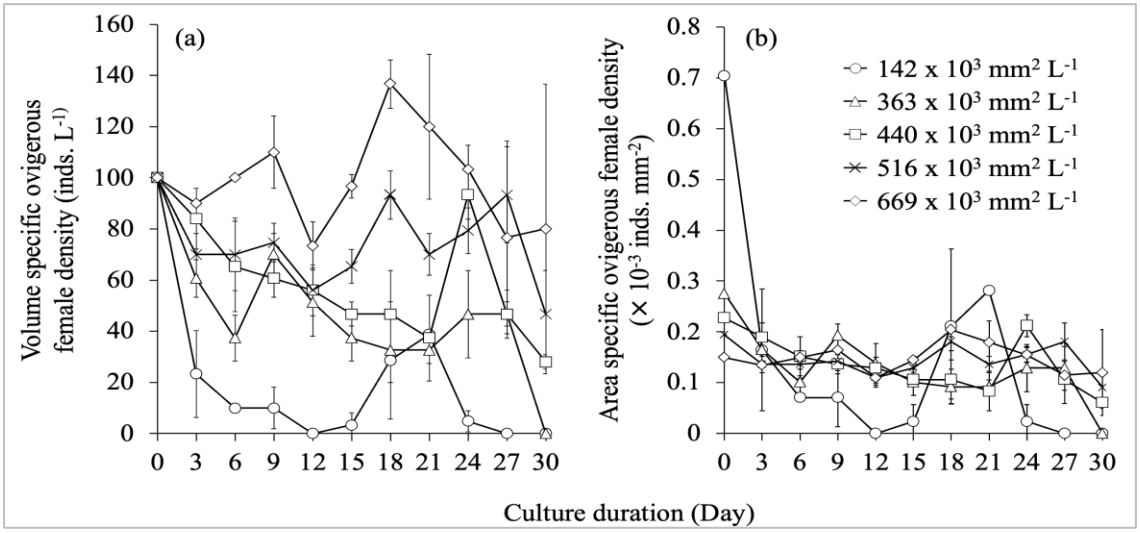


Figure 5. Temporal variation in (a) culture volume specific and (b) surface area specific ovigerous female density in *Pseudodiaptomus nihonkaiensis* when cultured in tanks with different specific surface areas. Tanks were inoculated with ten adult males and ten ovigerous females. Error bars indicate standard deviations (n=3).

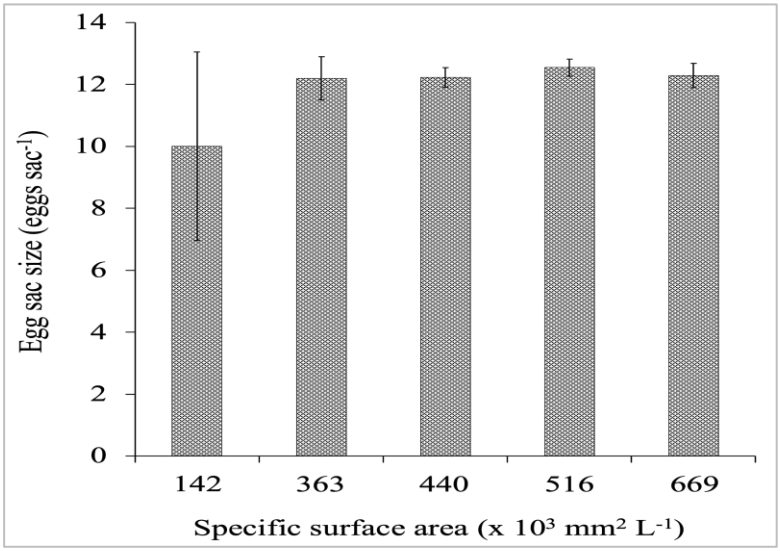


Figure 6. Average egg sac size over 30 days culture of *Pseudodiaptomus nihonkaiensis* in culture tank treatments with different specific surface areas. Error bars indicate standard deviations (n=3).

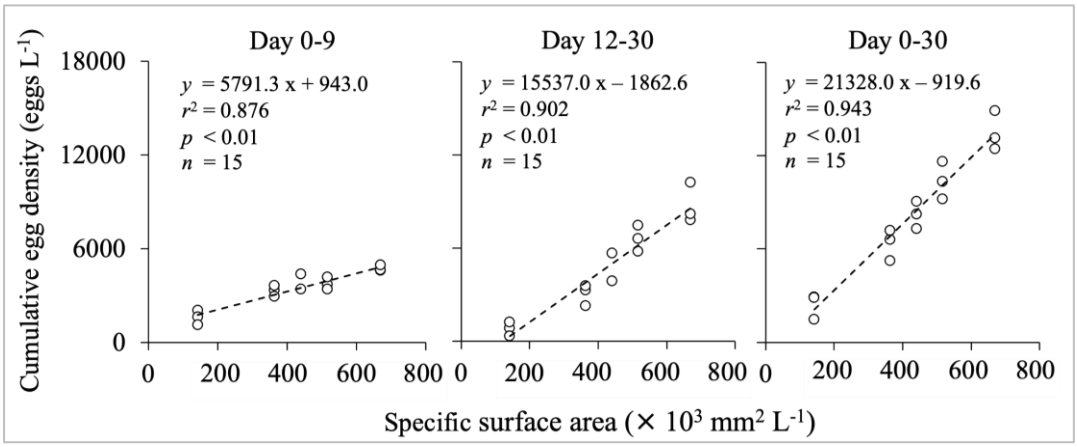


Figure 7. Relationship between specifi surface area of culture tank and cumulative egg density observed during culture experiments in *Pseudodiaptomus nihonkaiensis.*

increase egg production (Figure 7). Additionally, ovigerous female density per surface area after 3 days culture was similar in different treatments (Figure 5b). Therefore, we consider that the number of ovigerous females of the species is highly surface-area dependent under sufficient food condition.

In benthic copepod culture, some previous studies reported that placing artificial substrates such as corrugated plastic sheets, plastic balls, limestone cobbles and nylon mesh in the culture vessel increases copepod culture density (Koga 1976; Stottrup and Norsker 1997; Sun and Fleeger 1995; Koga et al. 2021). The authors assumed that the artificial substrates provide large surface area as a habitat and biofilm formed on the substrate as food source. In the present study, culture experiment was performed under sufficient food condition. In addition, the oviposition rate was already clearly different under different experimental conditions immediately after the start of incubation, when no biofilm was formed. Therefore, it would be unlikely that the biofilm formed on the substrate affected the egg production of *P. nihonkaiensis* in the present study.

Copepods can be cannibalistic (Hada and Uye 1991; Gallucci and Ólafsson 2007; Camus and Zeng 2009; Drillet et al. 2014; Takayama et al. 2021), and the cannibalism rate can depend on a range of factors such as adult density (Camus and Zeng 2009; Drillet and Lombard 2015; Drillet et al. 2015), and food (Drillet et al. 2014; Vu et al. 2017) and prey density (Gallucci and Ólafsson 2007; Drillet et al. 2014). Attachment substrata increased the surface area within tanks by 7.8 times, reduced the cannibalism rate of benthic *Tigriopus japonicus* by up to ~17%, and increased total *T. japonicus* density by up to 1.7 times (Koga et al. 2021). While cannibalism may contribute to mortality in closed populations, it was not observed during culture of *P. incises* or *P. hessei* (Noyon and Froneman 2013; Nguyen et al. 2020). Post-hatchling nauplii of *Pseudodiaptomus* species exceed 100 µm length, and the maximum prey size of *P. hessei* is 39 µm (Pagano et al. 2003) and *P. marinus* 63 µm (Uye and Kasahara 1983). Therefore, cannibalism of *P. nihonkaiensis* was unlikely to have occurred in our culture tanks. Increased substratum surface area within culture tanks may have improved egg production by increasing appropriate habitat for ovigerous females.

In this study, the density of adults initially decreased gradually in all treatments over time, but it tended to increase after days 9–12. Nauplius density peaked before the first 15 days in all treatments. Additionally, the ovigerous rate tended to decline over time in all treatments, even under the condition with the largest surface area in the vessel. The suitable culture conditions allowed the individuals to grow and reproduce quickly, which likely kept the density of adults low or resulted in fewer adults in the first 9 days. However, when culture conditions, particularly water quality due to metabolite accumulation, were disrupted, the reproduction and growth rates decreased. This disruption may have led to an increase in the number of adult individuals in the tank instead of nauplius and copepodites. Continuous water quality maintenance may be important for achieving stable high-density culture of *P. nihonkaiensis*.

In aquaculture of benthic organisms such as shellfish, use of substrates for settlement is common technique (e.g. Rodríguez-Pesantes et al. 2020). We cultured *P. nihonkaiensis* in tanks with different substratum surface areas and report densities to increase significantly with increased substratum surface area (Figure 3). These results are the first to demonstrate a relationship between population density and surface area for a semi-benthic copepod that spends a large part of its life cycle in the water column. In the present study, the largest surface area condition showed a 3.2 times higher total density of all development stages than the condition without substrate (i.e. control condition), and achieved a relatively high copepod density compared to previous reports. Therefore, installing artificial substrata in culture tanks may be simple and effective method to improve the productivity of *Pseudodiaptomus* mass culture. Towards the implementation of this technology, further study of material and design of the artificial substrates are required to maximize copepod stocking density and minimize cost for installing it.

Conclusion

This study investigated the effect of increasing the specific surface area in the culture tank on the population of the semi-benthic copepod *Pseudodiaptomus nihonkaiensis* by placing substrates in the tank. The increase in specific surface area increased the number of ovigerous females per volume of water in the culture tanks, resulting in the increase in maximum population density in the tanks of all developmental stages (nauplius, copepodites, and adults). These results suggest that the substrate in the culture tanks provided area for attachment for *P. nihonkaiensis* and increased the maximum population density in the tanks. We propose that the installation of substrates in culture tanks is a fundamental technology for the development of new bioreactors for the intensive culture of *P. nihonkaiensis*.

Ethical Statement

All copepod samples were collected according to national legislation in Japan, and all necessary permits were obtained prior to conducting this research

Author Contribution

Shinichi Koga, Yoshiki Takayama and Tatsuki Toda designed the study. Shinichi Koga conducted the experiments and sample measurements. Shinichi Koga

and Yoshiki Takayama drafted the manuscript. Yoshiki Takayama and Tatsuki Toda contributed to revising the manuscript critically for important intellectual content. All the authors read and accepted the final manuscript before submission

Conflict of Interest

The authors have no conflict of interest to declare.

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