

Distribution and reproductive aspects of the pandalid shrimp, *Pandalus eous*, in the deep sea of the East Sea, Korea

Hye-Min Park^a, Chul-Woong Oh^{a,b,*} and Myeong Ho Sohn^c

^aDepartment of Marine Biology, Pukyong National University, Busan 608-737, Korea; ^bKorea Inter-University Institute of Ocean Sciences, Pukyong National University, Busan 608-737, Korea; ^cDokdo Fisheries Research Center, National Fisheries Research and Development Institute, Pohang, 791-119, Korea

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The objective of the study was to investigate if reproductive characteristics of *Pandalus eous* affect the depth distribution in the East Sea of Korea. *P. eous* was found at depths of 500–900 m in the East Sea of Korea, with the highest percentage occurrence (34%) at 500 m. A negative correlation was observed between the number of individuals and the depth. The overall sex ratio also turned out to be significantly correlated with depth. On average, the larger individuals (bigger than 26.37 cm), which included transitional, female, and ovigerous females, were mostly distributed at 700 m depth. The percentage of males increased by depth and ovigerous females were mainly distributed in the shallow water (300 m) during winter.

Ovigerous females were not found at 900 m, which is the deepest depth range in this study. The percentage of transitional individuals was greatest at 500 m and decreased gradually with depth. All ovigerous female individuals were of the spent ovarian stage in winter. Female numbers in the ripe ovarian stage increased with depth and immature females rarely appeared. The gonadosomatic indices of the nonovigerous females and ovigerous females were highest at 700 m in depth. The mean egg size of *P. eous* was $0.83 \pm 0.11 \text{ mm}^3$ in the non-eyed stage and $0.93 \pm 0.17 \text{ mm}^3$ in the eyed stage.

Keywords: *Pandalus eous*; deep water shrimp; vertical distribution; reproduction; East Sea

Introduction

The pandalid shrimp is a cold-water shrimp occurring in shallow to deep sea down to 2000 m (Allen 1959; Holthuis 1980; King and Moffitt 1984; Chace 1985; Bauer 2004; Patricia et al. 2010). Bergström (2000) reported that shrimp of the genus *Pandalus* have attracted considerable scientific interest, mainly due to two reasons: their commercial value and reproductive strategy. The Northern shrimp *Pandalus eous* also attracted special interest because of its protandric life cycle, and as the target of important fisheries in the North Pacific (Koeller et al. 2000; Koeller et al. 2003; Ouellet 2005). In the Japan Sea, sex reversal of *P. eous* begins in July, spawning occurs in April, and hatching out takes place between February and March (Nakame 1991). The shrimp fisheries are one of most valuable marine resources in Korea. *Pandalus* species are also important food items for demersal fish and constitute integral parts of marine food webs found on the continental shelves (Bergström 2000). Although the deep sea area is the largest habitat for *P. eous*, its biology was the least

known and explored, due primarily to the difficulty of sampling. But these days because of the development of large fishing vessels and overexploitation of resources, there is a tendency to reduce the amount of resources gradually when considering the environmental aspects of global warming continues, the cold deep water habitat of the shrimp catch is decreasing (Choi 2002).

The distributions of deep-sea shrimps and reproductive behaviour show a specific characteristic depending on their distribution depth. Coastal, shelf, and upper – or middle – slope habitats are very different, and errors in understanding biological aspects of deep-sea shrimps can arise if they are considered together and general patterns of comparison are drawn between shallow and deep sea processes (Company et al. 2003). Ramirez Llodra (2000) proposed that the mesopelagic zone lies between 200 m and 1000 m depth, where the sunlight is too dim to support phytoplankton growth, but still affects the behaviour of organisms on a diurnal basis. In addition, food availability and predator density are some of the factors which influence the distribution

*Corresponding author. Email: ohcw@pknu.ac.kr

of species dwelling in deep sea and their life-histories. A size-related distribution was observed for the deep water pink shrimp, with juveniles settling in shallower waters (mostly around 100–200 m) and larger individuals moving towards deeper waters (Ardizzone et al. 1990; Abello et al. 2002; Politou et al. 2008). These results confirm the primordial role that depth plays in the distribution of the different life stages of deep water shrimp (Politou et al. 2008). Castilho et al. (2008) suggested that the variation in abundance of those species might at times be related to the physiological demands associated with their reproductive behaviour, such as the migration of adults for copulation and spawning. Therefore distribution and abundance as a function of depth could be influenced by sex ratio and reproductive traits such as larval survival and dispersal.

Migrations in *Pandalus* seem to be promoted by breeding, feeding and/or the movement of water masses having different temperatures (Bergström 2000). Migrations of berried female *P. borealis* into shallower water in connection with egg hatching have been observed (Hjort and Ruud 1938; Hørstedt and Smidt 1956; Haynes and Wigley 1969; Bergström 1991, 2000). Similar migrations in *P. eous* in Japanese waters were also reported (Kurata 1981). Therefore the depth distribution of ovigerous females for increasing larval survival is important to larval distribution and recruitment.

Although a study on the fishing conditions of Korean shrimp trawl fisheries and stock assessment of *P. eous* was conducted by Kim and Jo (1985), their depth distribution and reproductive aspects was not known in the East Sea of Korea. The knowledge of animal distribution relative to their environment is of central importance to ecology (Bell et al. 1990, Yimin et al. 1999). The present paper examines the distribution pattern, as well as the differences in the size structure of the population related to depth, to find the depth of the main distribution between 300 m and 900 m, and the reproductive patterns of *P. eous* in the East Sea of Korea.

Materials and methods

Sampling

P. eous were collected from the middle part of the East Sea off Samcheok (Figure 1). Sampling by trawl was performed over five years in June and December 2004, May and November 2005, March and September 2006, April and October 2007, and June and November 2008, at depths ranging from 300 m to 900 m (Supplementary Table 1). Sampling could not be carried out at 900 m depth in June and December 2004, 800m depth in December 2004, or 300–400 m

in April 2007 because of technical problems with gear operation. The abundance and distribution of *P. eous* were recorded at depth intervals of 100 m. The duration of trawling was 60 min for hauls, and each of the seven bottom trawl hauls was performed and the samples were collected with an otter trawl with a 45 mm cod end mesh, towed at a speed of 3 knots. The depth of each bottom was measured using a SCANMAR trawl monitoring system. Shrimps were randomly sampled and preserved in 10% neutral formalin. The overall mean bottom temperature decreased gradually from 0.90°C at about 300 m depth to 0.35°C at 900 m depth, whereas the salinity was relatively constant from 34.06‰ at 300 m depth to 34.08‰ at 900 m depth.

Sampling analysis

The carapace length (CL) of the samples was measured with vernier calipers from the dorsal posterior median edge of the cephalothorax to the rear of the eye socket, with an accuracy of 0.01 mm. Sex was determined under a binocular microscope by the size and shape of the endopodite of the first pleopod and the presence or absence of the appendix masculina (Allen 1959).

Transitional individuals mean males who have transitioned to females with reproductive ability in their lifetime. Transitional individuals were determined from the proportion of appendix interna formed by the appendix masculina. The sex ratio was based on the proportion of females for all years combined.

Ovarian examination and egg size

The ovarian stages were determined according to Meredith's (1952) and Company's (1995) illustrations of size and shape in proportion to the gastric mill and thoracic cavity, and external appearance of the ovary. Four main stages of development were established: immature, maturing, ripe, spent. The body and ovarian dry weight were determined by drying at 80°C for 48 h and weighting to the nearest 0.0001 g using an electronic digital balance. The gonadosomatic index (GSI) was determined with the following formula:

$$\text{GSI} = \left[\frac{\text{ovarian dry weight}}{\text{body dry weight} - \text{ovarian dry weight}} \right] \times 100 \quad (1)$$

Egg size of ovigerous females was recorded as two stages: (1) non-eyed egg; and (2) eyed egg.

For egg volume calculation, five eggs were subsampled. These were measured along the major and minor axes (including the chorionic membrane tightly

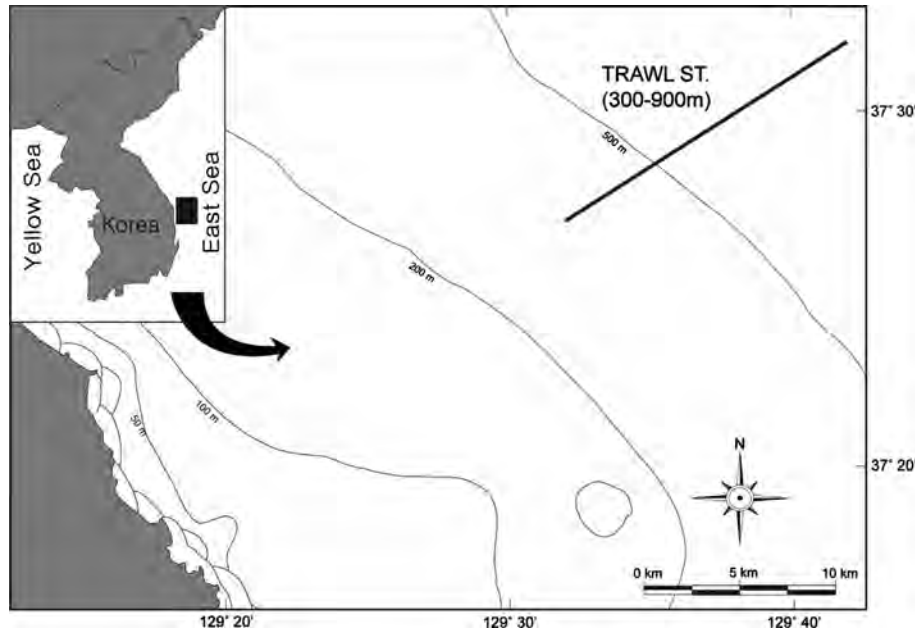


Figure 1. Map showing sampling areas.

adhering to the egg surface), using a binocular microscope with a calibrated eyepiece. The eggs were treated as ellipsoids and the volume quantified with the formula:

$$\text{Volume} = 4/3\pi r_1 r_2^2 \quad (2)$$

where r_1 is half the major axis and r_2 half the minor axis.

Abundance and distribution

Abundance was standardised to number of individuals per 100 m². To determine the mean depth of shrimp in any given profile, the center of mass (ZCM) was calculated according to Fortier and Leggett (1982):

$$\text{ZCM} = \sum_{i=1}^n p_i z_i \quad (3)$$

where p_i is the proportion of the total number of shrimps caught within the i th depth interval; and z_i is the mid depth of the i th interval.

Statistical analysis

A chi-square test was used to look at differences in the occurrence of males, females and ovigerous females with depth over the sampling period. The differences in the size–frequency distributions between depths were determined by the Kolmogorov–Smirnov two sample test. The differences in carapace length between depths were tested using an analysis of variance (ANOVA). If the variance of the data was not homogeneous, a nonparametric test (Kruskal–Wallis test) was used to evaluate the differences. The regression of body weight on body measurement (CL) was analysed with log-transformed data. The Kruskal–Wallis test was used to look at differences in the GSI by depth, and the Kolmogorov–Smirnov two sample test was used to look at differences in the distribution of GSI by depth. The statistical

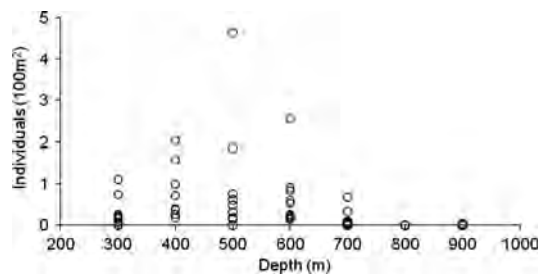


Figure 2. Relative abundance (%) of *Pandalus eous* per depth range (number per 100 m²) in the East Sea.

analyses were performed with MINITAB version 12 and SYSTAT version 10.

Results

Distribution with depth

The highest numbers of individuals occurred in June 2004, and most individuals occurred at around 500 m (Figure 2). Fewer individuals were caught in 2006 and 2007 than in the other sampling years. *P. eous* occurred between depths of 300 m to 800 m depth in all sampling years except in November 2005. When combined all year, the percentage occurrence was very high (34%) within the 500 m depth. *P. eous* were distributed with 26% at 400 m depth and 24% at 600 m depth. The shrimp was not found at 800 m and only 98 individuals were collected at 900 m in November 2005. A significantly negative correlation between the number of individuals and depth was observed in *P. eous* ($r = -0.305$, $P < 0.05$) (Figure 3). *P. eous* occurred mainly in shallow water with a ZCM of 489 m depth. This species is distributed from shallow to deep water (from 300 m to 900 m) separately for each sex. The total numbers of females, males, and ovigerous females had different distribution patterns at different depths (Supplementary Table 2). When combined over all depth ranges, the overall sex ratio of *P. eous* was female dominant, but the proportion of males was higher at 400–500 m (Supplementary Figure 1). A chi-square test showed that there was a significant difference in sex ratio ($\chi^2 = 356.833$, $df = 5$, $P < 0.001$).

Length frequency distribution with depth

Segregation of intraspecific size by depth exists in both sexes and the transitional stage. *P. eous* is the only species with a spent period which can change sex and function as female. The carapace length by depth were

significantly different for all kinds of sexes (Kruskal–Wallis test, $P < 0.05$) (Supplementary Figure 2). There was a significant difference in the size frequency distribution between depths in all kind of sexes (Kolmogorov–Smirnov test, $P < 0.05$). As seen in Supplementary Figure 2, on average, the largest male occurred at 400 m while the smallest size of male appeared at 900 m depth. Carapace length of males ranged from 7.41 mm to 29.73 mm CL, and most of them fell into the size range 15.12 mm to 28.26 mm CL. On average, the largest individuals of transitional, female, and ovigerous females occurred at 700 m. The average size of transitional individuals was greater than males with the size range of 15.83–31.90 mm CL, with specimens of 23.28–26.37 mm CL predominating. The size range of females ranged from 15.85 mm to 36.67 mm, with specimens of 27.43–29.65 mm CL predominating. The minimum size of ovigerous female was 18.98 mm, and maximum size was 35.78 mm CL, with specimens of 27.79–29.36 mm CL predominating. At 900 m depth, where only a small number of individuals was caught, the smallest male and transitional individuals were found.

Reproductive pattern

The distribution depths of deep water shrimp are related most specifically to their reproductive patterns. The reproductive characteristics of the species *P. eous* were examined over two years, in December 2004 and November 2005. The distribution of these features within a limited season may represent a distinct reproductive pattern. *P. eous* ovigerous females mainly distributed at shallow water around 300–400 m depth. Also ovigerous females did not distribute within the deepest depth range. These results showed that the percentage of *P. eous* males increased by depth, and ovigerous females mainly distributed in shallow water, represented only in this

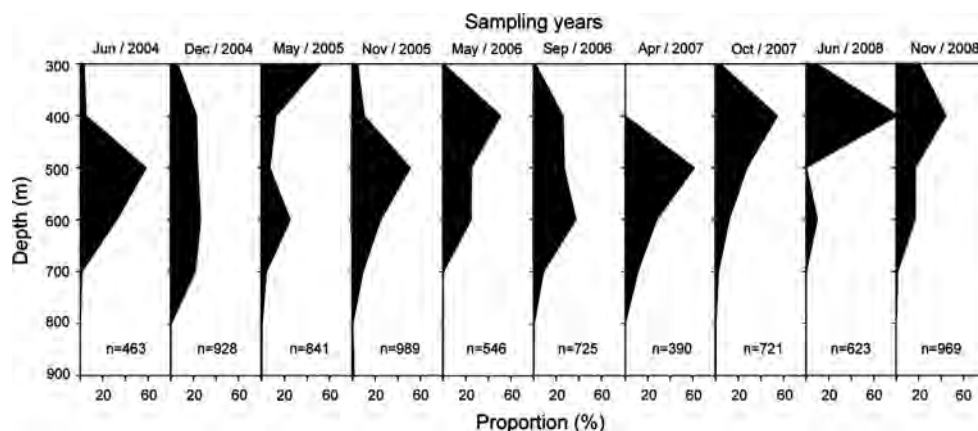


Figure 3. Correlation between the abundance and depth in *Pandalus eous* during the sampling period.

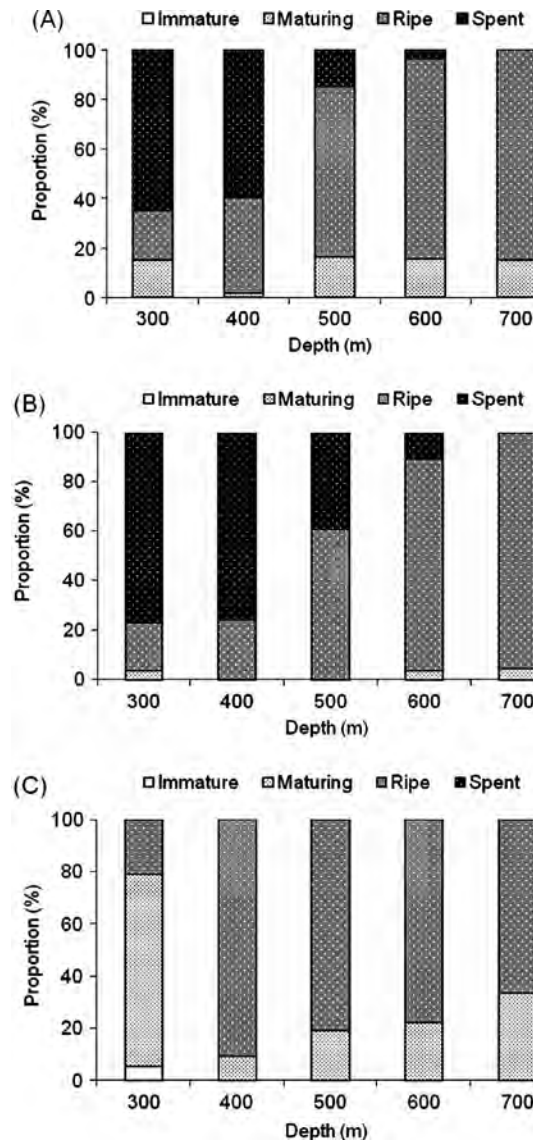


Figure 4. Relative abundance of *Pandalus eous* according to ovarian conditions and sampling depth; (A) total females, (B) nonovigerous females and ovigerous females, (C) transitional individuals.

season. But the percentage of transitional individuals showed a peak at 500 m, and then decreased with depth during this season.

P. eous females of spent ovarian stage consisted of ovigerous female in the winter season. A decreased proportion of the spent stage with depth implies that ovigerous females mainly distributed in shallow water (Figure 4A). *P. eous* females with ripe ovarian stage increased with depth, and immature females rarely appeared (Figure 4B). Overall the highest proportion of maturing females were transitional (Figure 4C). *P. eous* transitional individuals with maturing ovary stage distributed mainly at 300 m depth. The proportion of maturing female slowly increased with increasing depth from 400 to 900 m. The ovarian

stage of transitional individuals differs from that observed in *P. eous* females (Figure 4B, 4C).

The GSI did not significantly differ between 2004 and 2005 winter seasons (Kruskal–Wallis test, $P > 0.05$). GSI was determined for pooled data over two years to express common reproductive patterns of winter season by the depth. For this species, GSI increased with ovarian maturity (Supplementary Table 3). The GSI of transitionals, females and ovigerous females were significantly different with depth (Kruskal–Wallis test, $P < 0.05$) (Figure 5). A significant difference was also found between distribution of GSI and depth (Kolmogorov–Smirnov test, $P < 0.05$). The GSI acrossall individuals was relatively higher at 700 m depth.

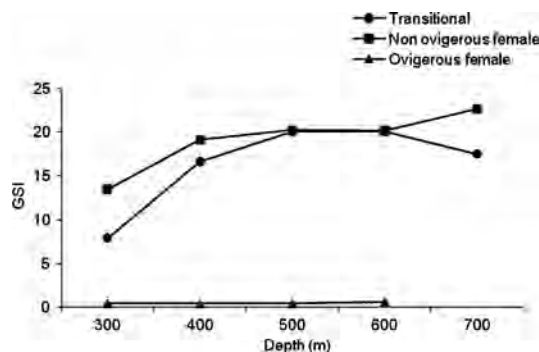


Figure 5. Variation in gonadosomatic index (GSI) of *Pandalus eous* with depth.

Nonovigerous females had higher GSI than those of transitional individuals in all depths. There was higher GSI at 500 m depth in transitional shrimp, and GSI decreased from 500 to 700 m depth in *P. eous*. The result is associated with the proportion of transitional individuals with ripe ovarian stage (Figure 4C).

The mean egg size of *P. eous* was $0.83 \pm 0.11 \text{ mm}^3$ in the non-eyed stage, and $0.93 \pm 0.17 \text{ mm}^3$ in the eyed stage.

Discussion

Life history and reproductive strategies of species appear to be selective compromises with respect to combination of biotic and abiotic factors in a particular environment (Sastry 1983). As their own reproductive strategy of each species, distribution will be able to vary according to sex and stage of development. The distribution and abundance of *P. eous* as functions of depth, population parameters and aspects of reproductive biology were investigated in this study. Individuals of the *P. eous* were mainly distributed around at 500 m depth and decreased with depth during sampling period. This result indicates that *P. eous* seem to be shallow-dwelling species relatively as compared with other deep water shrimp species in sampling areas (Park 2010). Shumway et al. (1985) reported that *P. borealis* and *P. eous* mainly occurred at between 50 and 500 m depth range. Several authors suggested that this result was correlated between high organic content of seafloor sediments and high biomass (Haynes and Wigley 1969; Shumway et al. 1985; Bergström 2000).

In *P. eous* male and transitional individuals were numerous at smaller size classes while females were dominant at largest size classes. This result also was observed in *Pandalus gracilis* in coastal waters of Korea, it shows that clear sexual dimorphism in the growth, faster growth in females (Oh 2011). Company and Sarda (1997) found that 4 species of 5 deep water pandalid species showed intraspecific size segregation by depth and interspecific size segregation was the rule

in the Mediterranean Sea. A size-related bathymetric distribution was observed for this shrimp in the East Sea of Korea. In present results, large individuals of transitional and female and ovigerous female were mostly distributed at deep water (700 m depth). However, this result is not consistent with that of crangonid shrimps, *Neocrangon communis* and *Argis toyamaensis* in the East Sea of Korea (Park 2010). Herring (2002) reported that the larvae of deep water squid, fish, and shrimps can be found closed to the surface and as they grow they tend to live deeper and deeper in the water column, sinking either gradually over their whole development period. This is similar to Daoud's (2007) observations that juvenile of *P. borealis* generally found in shallow water than older shrimps, and then they migrate offshore by that they mature.

Crustaceans living in the deep water, experience no seasonal variations in their physical environment, except possibly for seasonal variations in the food supply (Vinogradov 1962; Mauchline 1972; Marshall 1979; Sastry 1983). Possibly the most important limiting factor in deep sea ecology is food availability, and all production in the deep sea is fuelled, either directly or indirectly, by the import of organic matter to the bottom, the major part consisting of 'new' production sinking from the process of carbon production by photosynthesis in the euphotic zone (Gage and Tyler 1991). According to Morley et al. (2006), evidence was presented that closely related sympatric species may employ quite different reproductive strategies that suit their depth distribution while indicating the overriding evolutionary adaptation of reproductive traits to temperature and food availability. Sastry (1983) noted that competition for resources, avoidance of predators, and the behaviours for locating food and mate, may become more important to the life history and reproductive strategies of species.

Reproductive patterns affected by external factors, could be interacting with selective depth each species. Higher percentage of *P. eous* ovigerous females occurred mainly at shallow water during winter season.

Ovarian development stages from 300 to 400 m depth was composed dominantly of the spent stage and this stage dramatically decreased by the depth. These results suggest that females have already laid eggs in the shallow depth (300–400 m), and ovigerous females migrate to shallow water for hatching. In addition, the increased GSI by depth provides the evidence that ovigerous females of shallow water species mainly distribute in shallowest depth range for hatching, and sexual maturity is achieved in deeper depth range. In case of *P. eous*, it has been reported that the fishery has been seasonal in nature, peaking in late–winter when ovigerous females move into inshore waters and terminating in spring under regulatory closure (Clark et al. 2000). In the deep water lobster, *Polycheltes typhlops*, the highest proportion of ovigerous females was recorded for the shallowest levels of the bathymetric distribution range of the species and this suggests reproductive migrations related to egg laying and or spawning (Abello and Cartes 1992). These results were also observed in the deep water anomuran crab (*Lithodes ferox*). Their move toward shallow water phenomenon mainly related to reproductive biology were reported (ovigerous females account for most females in winter in the shallowest stratum) (Abello and Macpherson 1991). Vertical migration in the pelagic environment or horizontal movements in the benthic environments serve not only for feeding, avoidance of predators, and locating the preferred environment for survival, but also for locating mates for breeding purposes, a behaviour that is common to many species (Sastry 1983). And a behaviour pattern is observed as pre–hatching migration in many species (Hazlett 1983). A life–history strategy is determined by many environmental factors in the deep sea environment.

Living in deep water species is to have a special strategy unlike the coast. As there are currently no deep water decapods study in the East Sea of Korea, the present study provides insight into reproductive traits of population of *P. eous* and more research is needed to evaluate the effects of inbreeding with depth all seasons.

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