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Shelter preference and utilisation behaviour of small benthic octopus *Amphioctopus fangsiao* d'Orbigny for brooding under laboratory conditions

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Abstract

For benthic octopuses, shelter utilisation is a common behaviour to defend their vulnerable soft bodies against predators. Furthermore, most species of octopus exhibit egg-care behaviour, and the brooding females often attach their egg masses on the inside of the shelters to defend their eggs securely. The type of shelter is therefore a matter of concern for brooding females, affecting their reproductive success. This study aimed to investigate the shelter preference and utilisation behaviour of the small benthic octopus *Amphioctopus fangsiao*. Five types of shelters, including empty shells of bivalve *Saxidomus purpurata* and gastropod *Rapana venosa*, and different-sized artificial pottery pots, were introduced into the aquaria where eight female octopuses were individually reared. The types of shelters utilised by the females were recorded twice a day until they started spawning (observation period, 12–28 days). Six females with a body weight (BW) ranging from 68 to 125 g utilised the gastropod shells most frequently, and four females attached their eggs to the inside of the shells. Characteristic shell-wearing behaviour like that of live gastropods was observed for these females. Meanwhile, large two females with 135 and 182 g BW selected the largest artificial pot for spawning, suggesting a body size-dependent shelter preference.

Keywords: octopus; gastropod; bivalve; egg care, reproductive success; conservation

Introduction

Octopuses have soft bodies and versatile skins that enable them to change body shape and colour. These traits facilitate their characteristic performance of predation avoidance through escaping into crevices and gaps, camouflaging themselves against the bottom backgrounds, and mimicking other animals (Hanlon et al. 2008; Hanlon and Messenger 2018). Nevertheless, most benthic octopuses require shelters or dens as refuges to defend their vulnerable bodies, which lack any skeletal protections (Ambrose 1982; Anderson 1997; Finn et al. 2009; Hartwick et al. 1984; Iribarne 1990; Katsanevakis and Verriopoulos 2004; Mather 1982a, 1982b, 1994; Narvarte et al. 2013). It has been reported that shelter abundance is one of the limiting factors for the distribution and survival of octopuses (Aronson 1986; Guerra et al. 2014; Katsanevakis and Verriopoulos 2004; Mather 1982a, 1982b). The significance of shelter availability has also been recognised for brooding females; most octopuses exhibit maternal care of their eggs in shelters or dens, maintaining oxygen levels and protecting against predators, infection and parasites (Boletzky and Villanueva 2014). Because the maternal protection of eggs against predators may depend on the quality of shelters, such as size and shape, females prefer suitable shelters for spawning and brooding inside of which they can fix the egg strings (Boletzky and Villanueva 2014; Iribarne 1990; Narvarte et al. 2013; Van Heukelem 1977). In the natural habitat, the mortality rate of brooding females of *O. bimaculatus* is reported to be high, >70%, presumably due to predation by predators such as moray eels (Ambrose 1988). In addition, the absence of brooding females results in high mortality of eggs of *O. tehuelchus* (Narvarte et al. 2013). Taking into account that most octopuses are semelparous, it can be inferred that the shelter plays an important role in maintaining the octopuses' lineage by providing refuge for females and a substrate for defending eggs.

Amphioctopus fangsiao is a small benthic octopus (typically, 200 mm in total length, 100 g in body weight for an adult) that is distributed coastal waters of Japan, China and Korea (Jereb et al. 2016). This species inhabits mainly on soft sediment such as sandy or muddy bottoms and is an important fishery resource caught by small trawls and octopus pots (Jereb et al. 2016; Sauer et al. 2020; Yamamoto 2021). In the Seto Inland Sea, one of the main fishing grounds of this species in Japan, the spawning occurs during spring and a female spawns 100−200 eggs. The size of *A. fangsiao* eggs is relatively large (7−10 mm in length) among benthic octopuses, and the duration from spawning to hatching lasts 50−60 days (Jiang et al. 2020a, 2020b; Yoshikawa et al. 2016). The offspring commences benthic life immediately after hatching, and the lifespan is about one year (Kitajima and Hayashida 1985; Segawa and Nomoto 2002; Yamauchi and Takeda 1964; Yoshikawa et al. 2016). It has been known that adult *A. fangsiao* utilises empty gastropod and bivalve shells for shelters; therefore, various empty shells of species such as *Rapana venosa*, *Brunneifusus ternatanus* and *Anadara broughtonii* have been traditionally used for fishing (as octopus pots), as well as artificial pottery pots (Abe et al. 1997; Sauer et al. 2020). In recent years, fishery production of this species has been declining rapidly in Japan; however, factors affecting the population size are largely unknown (Yamamoto 2021).

The aim of this study was to provide information about the shelter preference and utilisation behaviour of brooding females of *A. fangsiao* as a basis for understanding the cause of the decline in population size and its corresponding conservation measure. We assessed the behaviour of eight *A. fangsiao* females by supplying different types (size and shape) of shelters under individually reared conditions, and the selectivity of shelters by females for hiding and spawning was recorded. The results illustrated that *A. fangsiao* females prefer a certain type of shelter depending on their body size and exhibited characteristic behaviour of shelter utilisation, suggesting the significance of shelters for their reproductive success.

Materials and methods

Female octopuses

Female octopuses that were caught in the central area of the Seto Inland Sea, off Okayama (34°26'N, 133°48'E), during the period from 15 to 21 February 2019 were stocked once in a tank with a flow-through water system at the Fisheries Cooperative Association of Daiichi-Tanoura-Fukiage (Kurashiki, Okayama). Because most females have already received spermatophores from males in this area in February, males were not collected. The females were transferred to the laboratory at Tokyo University of Marine Science and Technology by the Shinkansen on 22 February 2019. The octopuses were weighed and then stocked individually into an aquarium (water volume, 32 L; inner dimensions, W480 × D315 × H300 mm; white-translucent polypropylene) filled

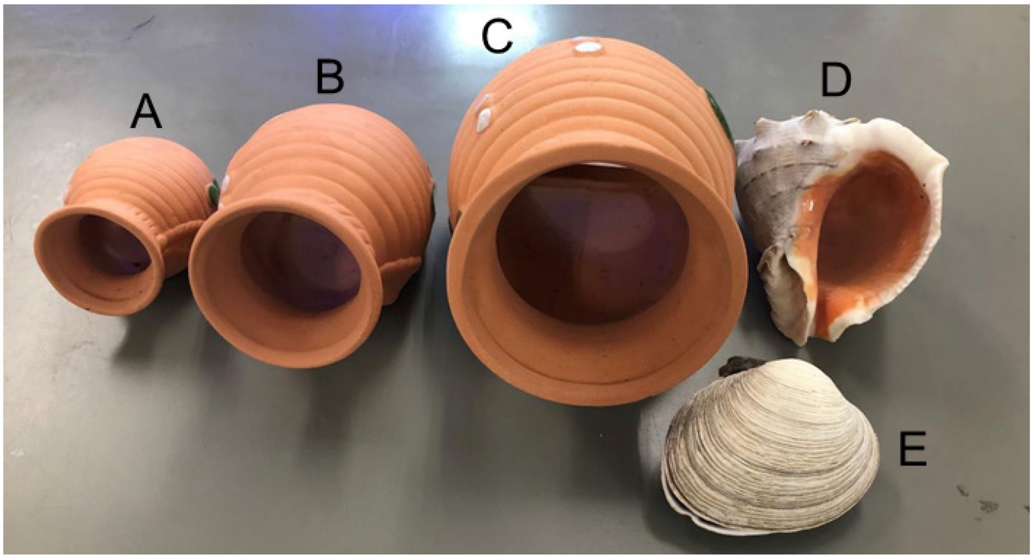

Fig. 1. Photographs of different types of shelters: (A) artificial pot-S, (B) artificial pot-M, (C) artificial pot-L, (D) gastropod *Rapana venosa* shell and (E) bivalve *Saxidomus purpurata* shell.

with artificial seawater (34 ppt salinity) (Sealife, Marinetech Co. Ltd., Tokyo, Japan). Each of the 12 aquaria were connected with a server tank (water volume, 150 L) equipped with a recirculating system, and 30% volume of the rearing water was renewed every week. The octopuses were fed frozen shrimp, *Plesionika semilaevis*, every morning. Until the starting experiment, the shelters, made of PVC pipe (inner diameter, 40 mm; length, 100 mm), were provided for all females.

Shelter selectivity experiment

After acclimation for 11 days, eight females ranging from 68 to 182 g in body weight (BW) were selected and applied to the experiment. The experiment was carried out using the same aquaria and feeding conditions as those used during the acclimation period, but the PVC-pipe shelters were removed from the aquaria. As test shelters, five types of shelters, including empty shells of bivalves and gastropods, and artificial pottery pots, were selected (Fig. 1). The bivalve *Saxidomus purpurata* and the gastropod *R. venosa* were adopted because they are distributed orthotopically with *A. fangsiao* on the sandy and muddy bottoms in the Seto Inland Sea. The shell length, weight and inner volume of the *S. purpurata* were 81 ± 2 mm (mean ± SD; range 79–84 mm), 66.7 ± 8.4 g (52.1–80.2 g) and 57.7 ± 3.8 mL (53.1–63.8 mL; in the case of closed shells), respectively. The *S. purpulata* shells were used as a pair connected by a hinge. The size dimensions of the *R. venosa* were 107 ± 4 mm (100–112 mm) in shell height, 70 ± 3 mm (65–75 mm) in aperture length, 159 ± 9 g (143–173 g) in weight and 132 ± 11 mL (117–151 mL) in inner volume. Three different sizes of artificial pottery pots with a similar design (Takotsubo-Large, Takotsubo-Middle and Takotsubo-Mini, Sudo Co. Inc., Aichi, Japan) were used, and their sizes (inner volume, weight) were W195 × D140 × H140 mm (995 mL, 460 g) for Takotsubo-Large (hereafter, artificial pot-L), W140 × D110 × H110 mm (335 mL, 164 g) for Takotsubo-Middle (hereafter, artificial pot-M) and W105 × D80 × H80 mm (95 mL, 62g) for Takotsubo-Mini (hereafter, artificial pot-S). These five shelters of different types were introduced into each aquarium where the female *A. fangsiao* were

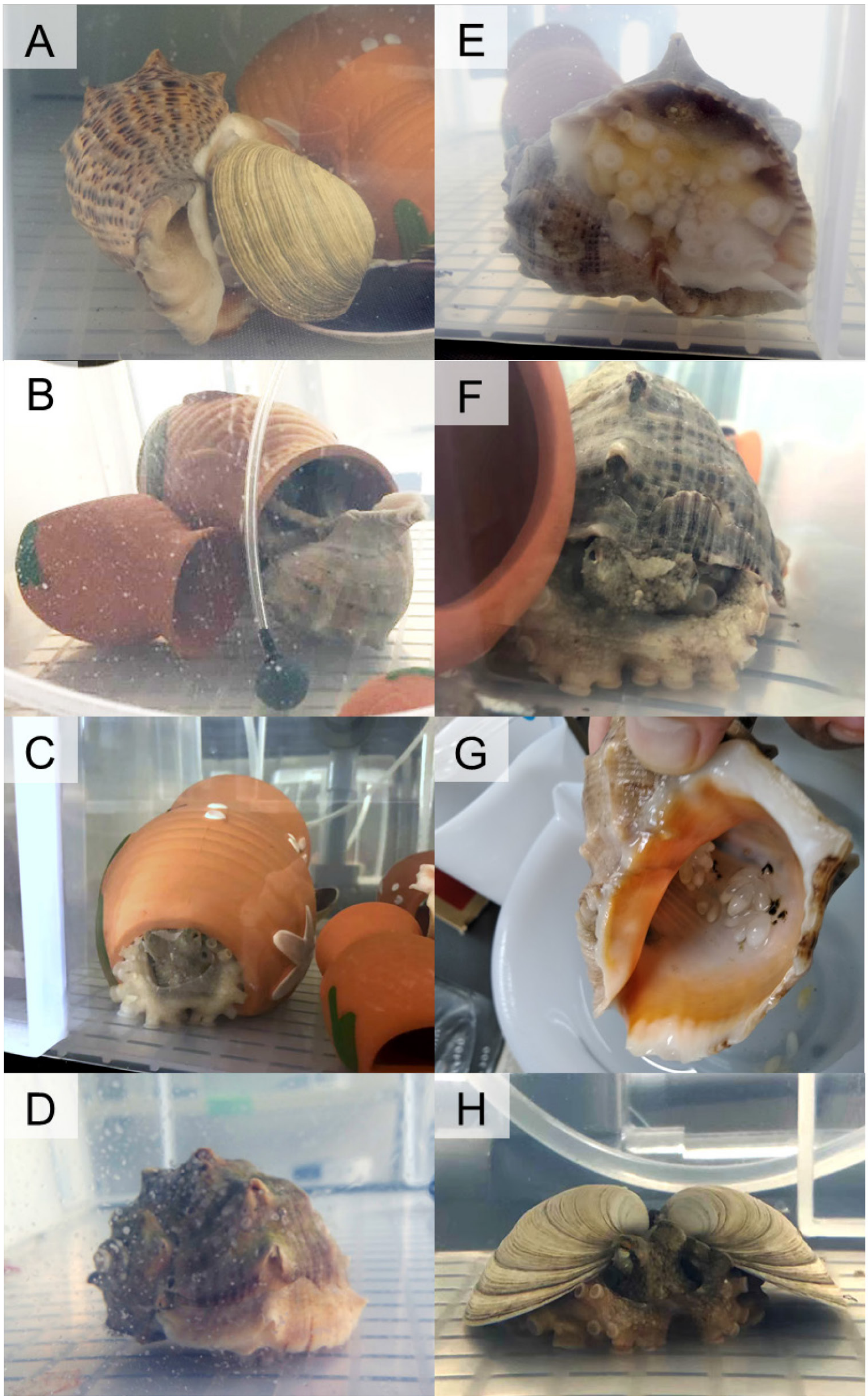

Fig. 2. Shelter utilisation behaviours of *Amphioctopus fangsiao* females observed during experiment (A−G) and preliminary rearing (H). (A) a female hiding in a gastropod shell and barricading with a bivalve shell. (B) a female hiding in artificial pot-L and barricading with a gastropod shell. (C) a female hiding in artificial pot-L. A female completely wearing a gastropod shell and clinging to the bottom (D) and wall (E) of an aquarium. (F) a female looking around while wearing a gastropod shell. (G) eggs attached to the ceiling of the inner space of a gastropod shell. (H) a female hiding underneath bivalve shells.

reared individually. The shelter-utilising behaviour of the octopuses was observed twice a day, every day, at 10 am and 3 pm. Two types of shelter-utilising behavioural patterns were observed during the experiment: one in which the octopus put her body inside (i.e. main shelter), and the other in which she used the shelter to cover the aperture of the main shelter (i.e. barricade) (Fig. 2A, B). The experiment was terminated when the females commenced spawning in any shelter because brooding females did not leave their shelters thereafter. Six of the eight females spawned their eggs until 28 days after starting the experiment, but two females did not spawn even after passing 30 days. Therefore, behavioural observations were terminated at 28 days for the two non-spawning females. Water temperature, pH, dissolved oxygen concentration, light intensity and salinity were measured once a day at 10 am, and they were 15.3 ± 2.0 °C, 8.09 ± 0.10, 10.32 ± 0.45 mg L^{-1}, 440 ± 51 lx and 33.0 ± 0.9 psu, respectively.

Statistical analysis

To assess the preference for the main shelter by the female octopuses, we used Friedman's test, which evaluates the disproportionality of shelter utilisation with an F-test, while the shelter type was ranked based on the frequency of shelter utilisation (Alldredge and Ratti 1986; Kiyota et al. 2005; Poole et al. 1996). The frequency of shelter utilisation was calculated for each shelter type based on the accumulated observation data (twice a day) for individual females throughout the experimental period. For the respective shelter types, their availability to the octopuses was assumed to be equal. The females used any shelters almost all of the time during the observation period (see Results section). Therefore, the data of no-shelter utilisation could be negligible and were eliminated from the analysis. Differences between shelter types were then evaluated using the Holm-Bonferroni method at a 5% significance level. The analysis was performed using R statistical software (R4.0.3; R Core Team 2020), applying a programme available from Okamura et al. (2004).

Results

Temporal changes in the shelter utilisation of the eight females are summarised in Fig. 3. Three females with 68, 79 and 107 g BW selected the gastropod shells as a main shelter on the second day of the experiment, after which they did not change their shelter until spawning (Fig. 3A, B, D). The gastropod shell was also selected by a female with 125 g BW for a long period after the fifth day, and spawning occurred on the 28th day (Fig. 3F). The females with 88 and 110 g BW also utilised gastropod shells as a main shelter for a long period across the experiment, but they did not spawn in the aquaria (Fig. 3C, E). Meanwhile, the largest (182 g BW) and the second largest (135 g BW) females selected the artificial pot-L for spawning, although the largest female often changed shelters from the artificial pot-L to the bivalve and gastropod shells (Figs. 2C, 3G, H).

The frequency of utilisation of each shelter type is shown in Fig. 4. The statistical analysis revealed that the females utilised shelters disproportionately ($F_{4,28}$ = 6.023, p = 0.0013) and that the gastropod shell was a more preferable shelter than the bivalve shell and the artificial pots-S and -M. The artificial pot-L was used frequently by large two females; thus, no significant difference was detected between the utilisation of the gastropod shell and the artificial pot-L.

For the females using the gastropod shells as a main shelter, they barricaded the mouth of the shell using other substrates or completely wore the shell (Fig. 2A, D). These females seemed like live gastropod *R. venosa*; they occasionally lifted the

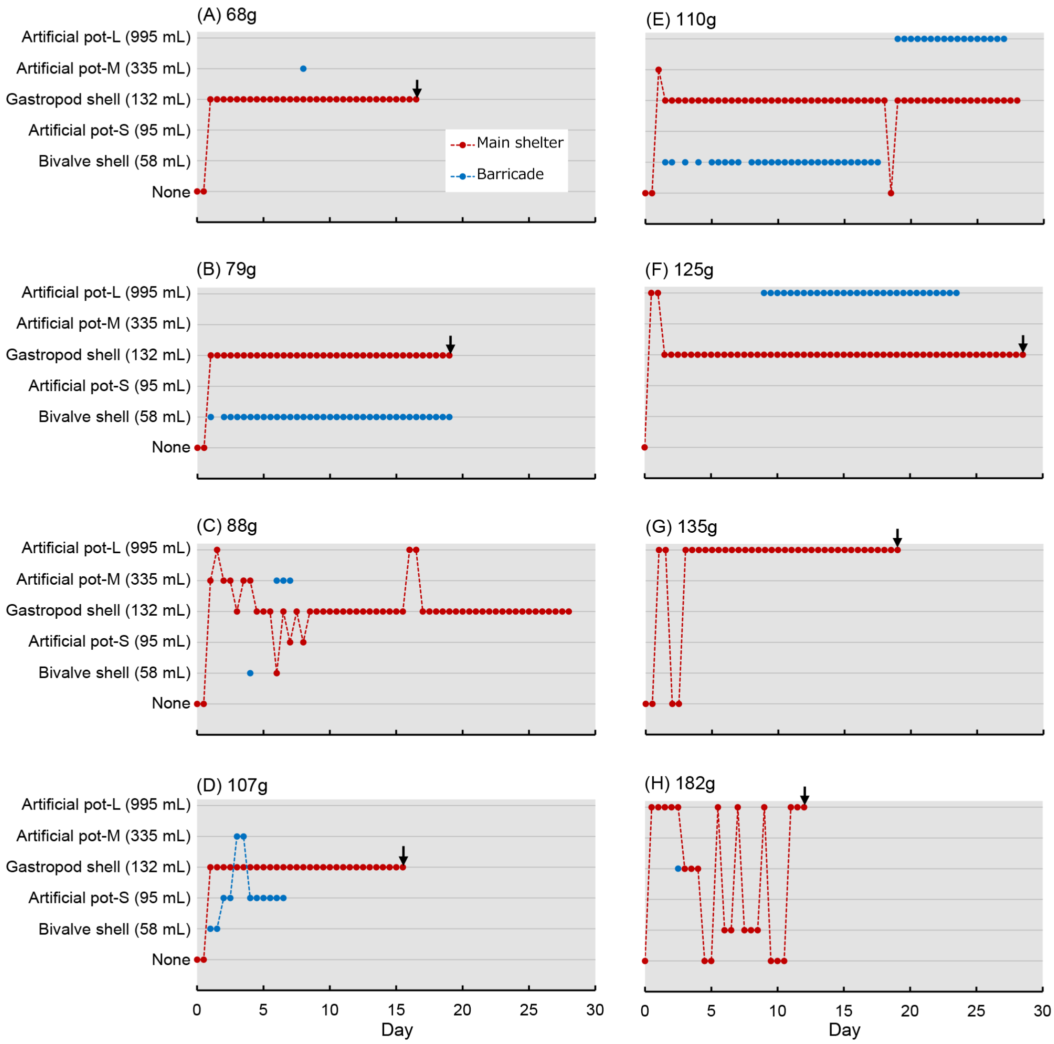

Fig. 3. Temporal changes in utilised shelters by eight individually reared *Amphioctopus fangsiao* females (A−H). Black arrows indicate commencements of spawning.

shell slightly to look around from the rim of the shell aperture and moved (crawled) once in a while by using arm suckers (Fig. 2D−F). In cases where the females spawned their eggs in the gastropod shell, the egg-strings were attached to the ceiling of the inner space of the shell (Fig. 2G).

Discussion

Amphioctopus fangsiao exhibits excellent camouflage performance and burying behaviour, diving their whole body into sand or mud substrata (Yamauchi and Takeda 1964). These characteristics may be instrumental in concealing their vulnerable soft bodies from predators in soft sediment. However, brooding females are not able to bury themselves while protecting their eggs and thus it is a matter of concern to the females whether they can obtain a good shelter to defend both their bodies and their eggs. Although it has been empirically known that *A. fangsiao* prefer empty shells of various bivalves and gastropods as well as artificial pots based on fishery experiences dating back more than two thousand years (Abe et al. 1997; Sauer et al. 2020), it remains unknown what kinds of shelters are preferred by *A. fangsiao* females for spawning or how they utilise shelters

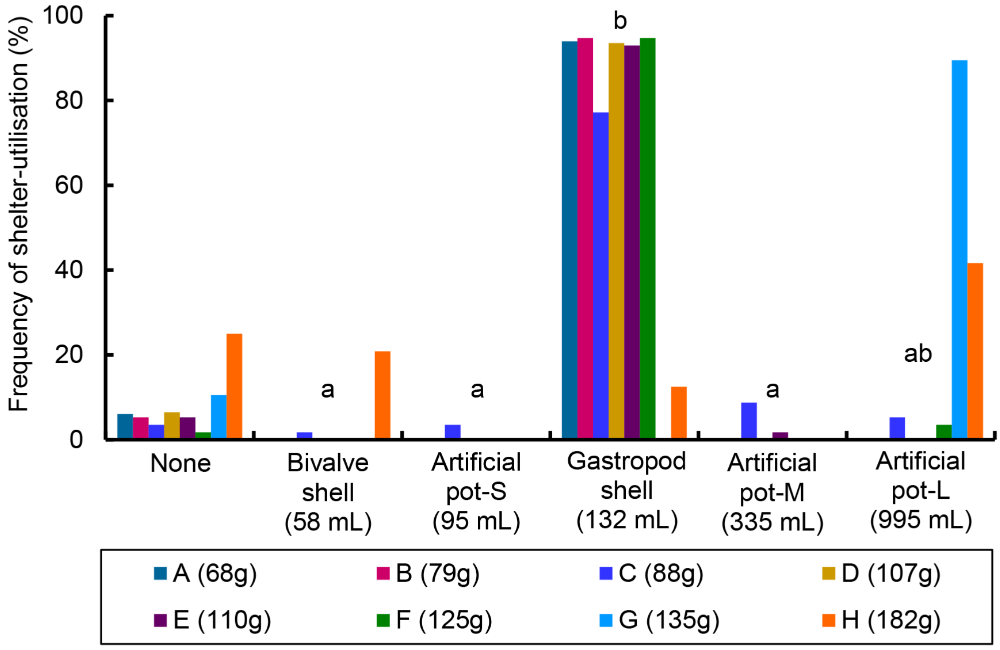

Fig. 4. Comparison of utilisation frequency of different shelters by eight *Amphioctopus fangsiao* females (A−H) during the experimental period. Significant differences amongst the shelters are indicated by different lowercase letters ($p < 0.05$).

for brooding. Our results suggest that females smaller than 125 g BW prefer gastropod *R. venosa* shells for brooding and exhibit the characteristic behaviour of wearing the shell like a live gastropod and attaching the egg-strings to the ceiling of the inner space of the shell.

Bivalve shells are known to be preferred by *A. fangsiao* as various bivalve shells have been used as fishing gears (Abe et al. 1997; Sauer et al. 2020). Nevertheless, the empty shells of the bivalve *S. purpurata* were not utilised by the females in the present study. It is reasonable to infer that the females did not choose the *S. purpurata* shells because of their small inner volume (95 ml in the case of closed shells), but we observed that the females did use the *S. purpurata* shells when there was no available alternative shelter during the preliminary rearing (Fig. 2H). This suggests that the female *A. fangsiao* can use various shelter types but carefully choose a more preferable one presumably based on shelter function and size-matching between inner volume of the shelter and body size. Indeed, two large females with more than 135 g BW did not utilise the gastropod shells but instead chose the artificial pot-L for spawning. There is a high possibility that the gastropod shell was too small for these females because the gastropod shells had only 132 ml of the mean inner space volume; thus, both of the large females used the larger shelters presumably due to the body size-dependent shelter preference.

In the natural habitat, it has been reported that *A. fangsiao* females utilise empty pen shells of *Atrina pectinate* for brooding (Yamauchi and Takeda 1964). Because *A. pectinate* grow large, up to 300 mm in shell length (Awaji et al. 2018), their shells can provide sufficiently large inner space for brooding female octopuses. *Atrina pectinate* and *R. venosa* are both large species of Bivalvia and Gastropoda that can be found on sandy and muddy bottoms in the temperate coastal waters of the western North Pacific Ocean where *A. fangsiao* occurs. The shells of *R. venosa* tested in the present study (mean shell height, 107 mm) can be classified as regular-sized adults in Japanese waters (Okutani 2017). Additionally, in the Seto Inland Sea, the BWs of most *A. fangsiao* are less than 125 g during the breeding season from March to May, but the maximum BW can reach 283 g in March (Yamamoto 2021). Taken together, the shells of *R. venosa* may be a preferable shelter for the greater part of the brooding *A. fangsiao* females in the Seto Inland Sea; however, body size-dependent shelter selection might occur for large females in their natural habitat.

Various animals, such as bivalves, crabs, seastars and sharks, are known to eat octopus eggs (Batham 1957; Cosgrove 1993; Villanueva and Norman 2008). In addition, chitons are also reported to reduce egg survival by removing eggs from the substrata (Narvarte et al. 2013). To avoid predation and to defend their eggs, females of small octopus species, such as *Hapalochlaena* spp. and *Amphioctopus burry*, carry their egg masses to escape from dangers (Forsythe and Hanlon 1985; Villanueva and Norman 2008). It remains unknown whether *A. fangsiao* females escape from predators while wearing gastropod shells in their natural habitat. However, we observed that the females wearing the gastropod shells sometimes crawled in the aquaria, suggesting that they have the potential to escape by walking with their shelters. In addition, the shelter-wearing females looked very much like live *R. venosa* (Fig. 2D−F); this suggests the possibility that they wear gastropod shells for mimicking.

Besides the main shelter for hiding their bodies, some females exhibited the characteristic behaviour of blocking the apertures of the main shelters (gastropod shells) using other substrates in the present study. Similar barricading behaviour has been reported in many octopus species; these species barricade the entrance or aperture of their dens and holes with solid materials such as empty mollusc shells and stones (Guerra et al. 2014; Hanlon and Messenger 2018; Mather 1994). This barricading behaviour may also help to conceal and defend the octopuses and their eggs from predators. Taken together, *R. venosa* shells are a high-performance shelter for regular-sized *A. fangsiao* females, providing not only visual concealment (primary defence, sensu Hanlon and Messenger, 2018) but also an easy-to-defend space for eggs even if they are detected by predators; these females wear the shell, perhaps escape by walking, and can block the shell aperture by barricading.

In shelter-utilising animals, such as hermit crabs, brachyuran crabs and spiny lobsters, it has been reported that the availability of shelters is an important factor limiting recruitment success and post-settlement survival, thereby impacting population dynamics (Asakura 1991, 1995; Beck 1995; Eggleston et al. 1990; Inutsuka et al. 2020; Mintz et al. 1994). Likewise, in octopuses inhabiting soft sediment, their distribution and abundance are known to depend on shelter abundance (Aronson 1986; Guerra et al. 2014; Katsanevakis and Verriopoulos 2004; Mather 1982a, 1982b). In the Seto Inland Sea, fishery production of *A. fangsiao* started to decline in 2009, becoming more rapid after 2015 (Yamamoto 2021). According to the statistics of the Takamatsu City Central Wholesale Market, which is one of the largest markets located in Kagawa Prefecture facing the Seto Inland Sea, the annual handling weight of *A. fangsiao* was 176 ± 44 t (range, 98–200 t) during 2005–2009, but it declined 23 ± 15 t (range, 11–47 t) during 2015–2019 (Takamatsu City 2021). Correspondingly, the annual fishery production of gastropods and bivalves also declined from 4285 ± 455 t (range, 3643–4664 t) during 2005–2009 to 1852 ± 276 t (range, 1630–

2316 t) during 2015–2019 in the Seto Inland Sea (Ministry of Agriculture, Forestry and Fisheries 2021). It is known that *A. fangsiao* consume gastropods and bivalves as food (Ebisawa et al. 2011); however, our results suggest that their empty shells may also play an important role in their reproductive success. There is the possibility that the recent decline of gastropod and bivalve resources is affecting the population size of *A. fangsiao* in the Seto Inland Sea through a decrease in the supply of preferable shelters for brooding. In this context, the artificial supplementation of shelters, such as the empty shells of gastropods and bivalves or artificial pots, into the breeding area of this species appears to be one of the possible measures for the conservation of this species.

Acknowledgments

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Ethical approval

This study followed all applicable international guidelines for the care and use of animals and was approved by the Committee on the Ethics of Animal Experiments at Tokyo University of Marine Science and Technology (permission number: R2-S1).

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