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LIFE CYCLE OF THE JAPANESE PYGMY SQUID *IDIOSEPIUS PARADOXUS* (CEPHALOPODA: IDIOSEPIIDAE) IN THE *ZOSTERA* BEDS OF THE TEMPERATE COAST OF CENTRAL HONSHU, JAPAN

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ABSTRACT: The life cycle of the Japanese pygmy squid, *Idiosepius paradoxus*, was studied in the *Zostera* beds of the temperate coast of central Honshu, Japan. *Idiosepius paradoxus* was collected monthly from January 1998 to December 1999. This species was sexually dimorphic with females considerably larger than males. The adult size of this species changed with seasons. The small sized generation appeared in the warm season from late spring to early autumn. In the warm season, mature males with spermatophores in the Needham's sac began to appear from late spring, and mature females with ripe eggs appeared from early summer. In the cool season from late autumn to early spring, the individuals appeared to grow slower and larger, with sexual maturity by spring. Although the individuals in the late autumn were larger than those of the warm season, they were not sexually mature. In the present study area, the larger sized generation passed winter matured and spawned at next spring, and moreover, the small sized generation in the warm season matured from late spring to early autumn. In conclusion, it was suggested that *Idiosepius paradoxus* have at least two generations within one year.

INTRODUCTION

The genus *Idiosepius* belongs to the family Idiosepiidae, and consists of seven nominal species occurring in the Indo-West Pacific (Lu and Dunning, 1998). They are the smallest living cephalopods, inhabiting beds of seagrass and algae and posses the unique habit of adhering to substrates with an adhesive organ on the dorsal mantle (Moynihan, 1983; Nabhitabhata, 1998; Sasaki, 1923). The taxonomic position of the genus *Idiosepius* is somewhat problematic (Boletzky, 1995), although it is tentatively grouped in the order Sepioidea (Nesis, 1987; Lu and Dunning, 1998). Recently, it was suggested that the genus *Idiosepius* may be more closely related to the order Teuthoidea than to Sepioidea based on the morphological observations (Hylleberg and Nateewathana, 1991 a, b) and genetic analysis (Bonnaud *et al*., 1997). Many ecological studies have examined *Idiosepius pygmaeus*, which is distributed in the tropics from Southeast Asia to Australia (Moynihan, 1983; Jackson 1989, 1992, 1993; Lewis and Choat 1993).

The Japanese pygmy squid *Idiosepius paradoxus* is the most northern species in the genus *Idiosepius*, distributed in Japan, South Korea and central China (Lu and Dunning, 1998; Nesis, 1987). Previous reports on *I. paradoxus* relate to the species' adhering habit (Sasaki, 1923), a morphological description with a brief note on feeding and mating habits (Sasaki, 1929), the appearance of pelagic juveniles (Okutani, 1968), the egg-laying behaviour (Natsukari, 1970) and the embryonic development (Natukari, 1970; Yamamoto, 1988; Watanabe, 1999). Recently, Shigeno (2002) suggested that *I. paradoxus* is a very suitable model species for developmental studies of cephalopods. We have previously reported in detail the reproductive and feeding behaviours of *I. paradoxus* in an aquarium with the eelgrass *Zostera marina* (Kasugai, 2000, 2001) and a description of egg masses on eelgrass blades (Kasugai and Ikeda, 2003). However, studies of the life cycle of *I. paradoxus* throughout the year in a natural habitat have not been reported. In this study, we collected *I. paradoxus* specimens from

Zostera beds off the temperate coast of central Honshu, Japan over a period of two years from 1998 to 1999, and analyzed the life cycle of this species particularly with respect to seasonal patterns of body size and maturation.

MATERIALS AND METHODS

Idiosepius paradoxus specimens were collected from small *Zostera* beds along the southern coast of Chita peninsula in central Honshu, Japan (34°43′N, 136°58′E, Fig. 1). The *Zostera* beds lie on the sandy bottom at a depth of between 0 and 2 m at low tide. The beds were mainly composed of *Zostera marina*, with some *Zostera japonica* only in certain areas near-shore.

Idiosepius paradoxus specimens were collected at low tide in a small drag net (1x2 m, mesh size: 1.5 mm) once or twice a month from January 1998 to December 1999 (Table 1). The surface water temperature of the collecting sites was recorded every time. Specimens were preserved in buffered 10% seawater-formalin immediately after collection, and mantle length (ML) and wet body weight (BW) were measured soon after transfer to the laboratory. Evidence of copulation was noted based on the existence of spermatangia attached. Sexual maturity was determined after removal of the mantle by the presence of spermatophores in Needham's sac in the males, and of mature oocytes in the females, respectively.

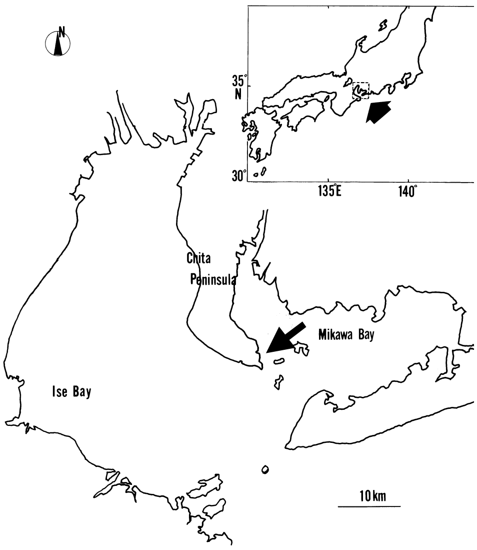

Figure 1. Map of Japan, detailing the location of the study site along the southern coast of Chita peninsula.

RESULTS

Condition of the Zostera bed and data collection

In spring, the eelgrass *Zostera marina* generally grew thick with flowering shoots, making the canopy high. However, from early summer, the flowering shoots drifted and started to be blighted probably because of the effect of high water temperature. In winter, plants grew again and seedlings appeared (Aioi, 1980; Arasaki, 1950ab). The canopy of *Z. marina* was very high from winter to spring in 1998. However, the *Zostera* bed was badly damaged by a typhoon that struck in September 1998. After that, the *Zostera* bed gradually recovered and in 1999, the canopy was still low and the study area was dotted only with small patches of *Z. marina*. The water temperature generally followed a regular seasonal pattern, with the lowest temperature (6.0°C) on 3 February 1999 and the highest (30.0°C) on 22 August 1998 (Table 1). A total number of 739 *I. paradoxus* specimens were caught in the two year period. All specimens could be sexed and the sexual maturity determined (Table 1). Collection dates were classified into cool- and warm- season according to the body size and maturity of specimens (Table 1; see Fig. 3). The cool- and warm- seasons were from November to middle May and from late May to October, respectively.

Relationship between ML-BW and sexual dimorphism

The relationships between ML and BW of females and males collected in this study are shown in Fig. 2. This species exhibits sexual dimorphism with females considerably larger than males. The size for all female specimens collected ranged from 4.2 mm to 18.8 mm in ML and 15 mg to 796 mg in BW, while males ranged from 4.2 mm to 13.8 mm ML and weighed between 10 mg and 280 mg BW.

Table 1. Details of samples collected during this study.

Collectin Date	Water temperature (°C)	Season	Number of sampling specimens Total	Female	Male
28 Jan 1998	9.7	cool	59	35	24
26 Feb 1998	10.3	cool	74	34	40
29 Mar 1998	13.0	cool	107	36	71
29 Apr 1998	18.8	cool	37	12	25
28 May 1998	25.3	warm	10	4	6
25 Jun 1998	24.0	warm	29	10	19
10 Jul 1998	28.0	warm	114	36	78
24 Jul 1998	25.5	warm	16	13	3
22 Aug 1998	30.0	warm	8	1	7
4 Sep 1998	27.2	warm	0	0	0
7 Oct 1998	23.9	warm	0	0	0
20 Nov 1998	16.5	cool	7	6	1
2 Dec 1998	13.5	cool	0	0	0
16 Jan 1999	9.5	cool	1	1	0
3 Feb 1999	6.0	cool	5	3	2
4 Mar 1999	9.8	cool	17	6	11
18 Mar 1999	13.5	cool	25	4	21
15 Apr 1999	16.1	cool	30	9	21
17 May 1999	21.4	cool	15	6	9
15 Jul 1999	23.8	warm	41	15	26
29 Jul 1999	29.4	warm	47	13	34
27 Aug 1999	29.6	warm	15	4	11
27 Sep 1999	25.3	warm	7	4	3
16 Oct 1999	21.0	warm	0	0	0
25 Nov 1999	16.6	cool	49	33	16
24 Dec 1999	10.7	cool	26	16	10
	Total		739	301	438

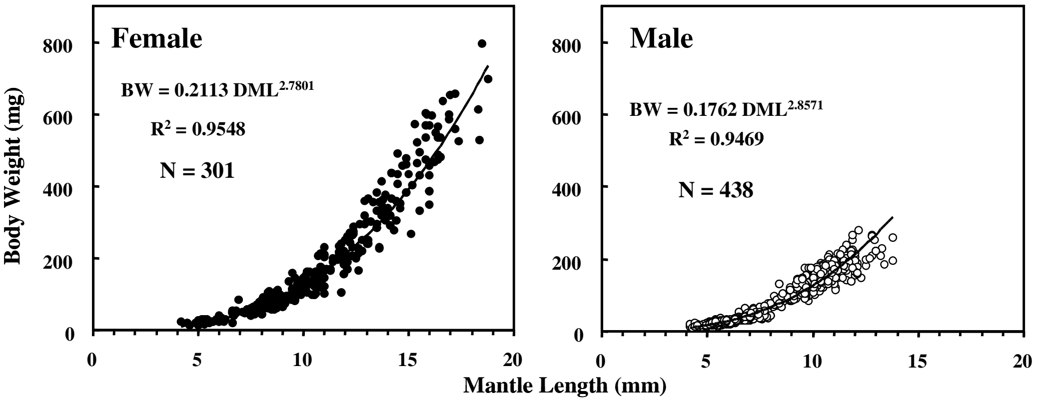

Figure 2. The relationship between ML and BW of *Idiosepius paradoxus.*

Seasonal change in ML

The seasonal change in size (ML) structure is shown in Fig. 3 and the monthly change in the mean ML is also plotted for the 2yr period (Fig.4A). Mean ML of *I. paradoxus* showed similar seasonal variation for both males and females. In the late cool-season (late March to middle May), mean ML reached a maximum for both sexes. In the beginning of the warm-season (28 May 1998 and 15 Jun 1999), a minimum size of specimens was evident on the *Zostera* beds, and mean ML gradually increased until the late cool-season. However, in between the late warm-season and the early cool-season, especially in October, almost no specimens were collected.

Maturation

In the cool-season, mature male specimens appeared from late December and mature females from late February. In the warm-season, mature males and females appeared from late May and middle June respectively. There was a great difference in mean ML of mature specimens between the cool and warm-seasons for both sexes (Fig. 4B). In the cool-season, the minimum size of mature females was 11.1 mm ML (collected on 29 April 1998) and the minimum size of a mature male was 7.7 mm ML (collected on 24 December). On the other hand, the maximum size of females from the warm-season was 6.9 mm ML (collected on 24 July 1998) and males 4.2 mm ML (collected on 25 Jun 1998).

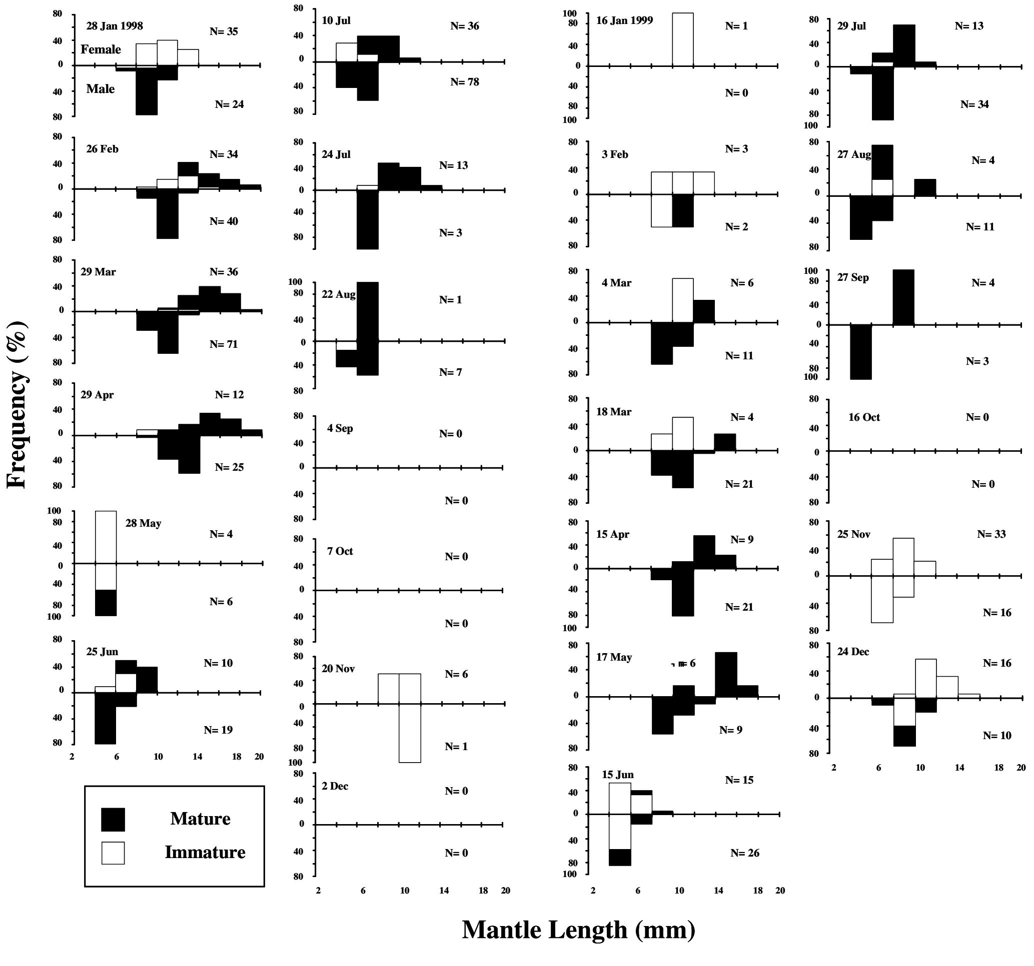

Figure 3. The seasonal change in size (ML) structure of *Idiosepius paradoxus.*

Copulation

The ratio of copulated: uncopulated female specimens changed seasonally (Fig. 4C). Although the ratio of copulated females was low at the beginning of both cool- and warm-seasons, immature specimens were already copulated over the same period. The ratio increased from the middle to late period of both seasons. Spermatangia present on copulated females were attached to the arms, head, neck, buccal membrane and mantle. A total of 46 copulated male specimens were recorded in two years, which was 5.6–33.3 % of the males. The seasonal change in the ratio of copulated males was similar with that of females.

DISCUSSION

The present study suggested that *I. paradoxus* have at least two generations a year in the *Zostera* beds of central Honshu, Japan; namely, the cool-season generation which had a large sized body, and the warm-season generation which had a small body (Fig. 5). *I. paradoxus* collected in the present study showed sexual dimorphism with females considerably larger than males in both the cool and warm seasons, just like other *Idiosepius* (Nesis, 1987). The spawning season, as determined by the appearance of mature females with mature oocytes, is from late February to mid May in the

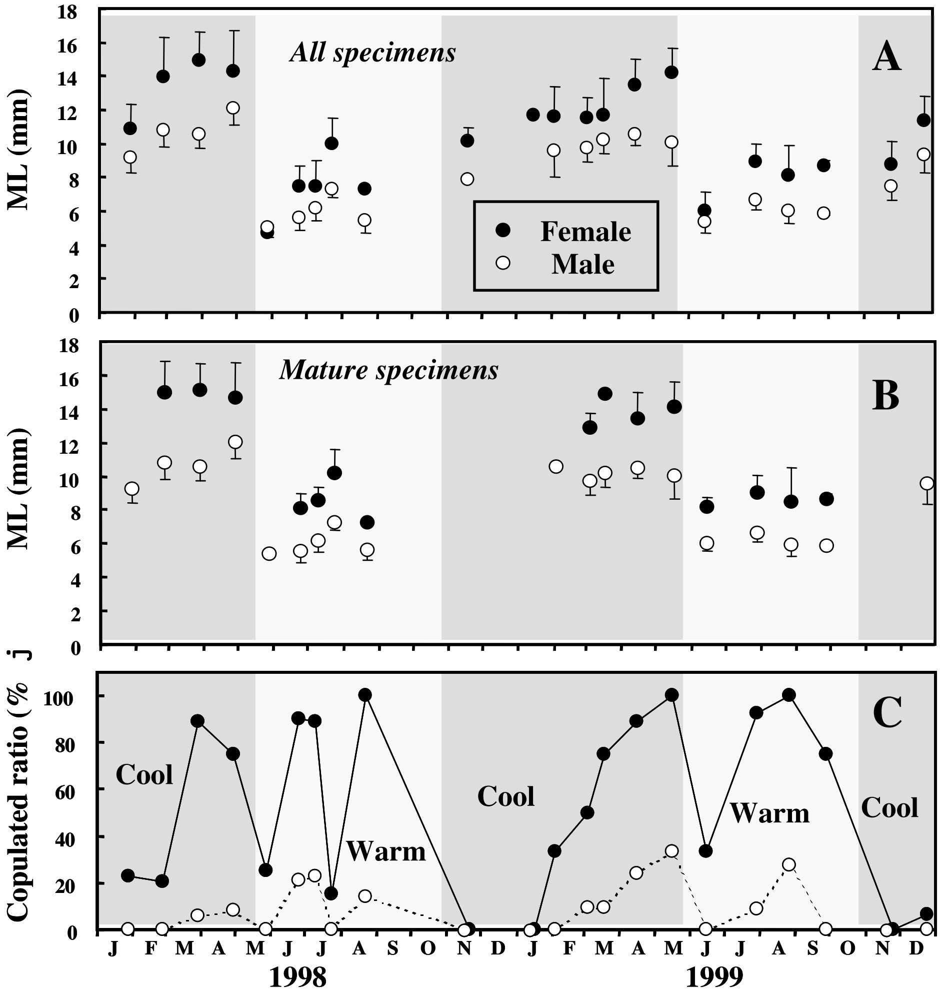

Figure 4. A. Seasonal change in ML of *I. paradoxus* (Mean±SD). B. Seasonal change in ML of mature specimens (Mean±SD) of *I. paradoxus*. C. Seasonal change in the copulated ratio of *I. paradoxus*.

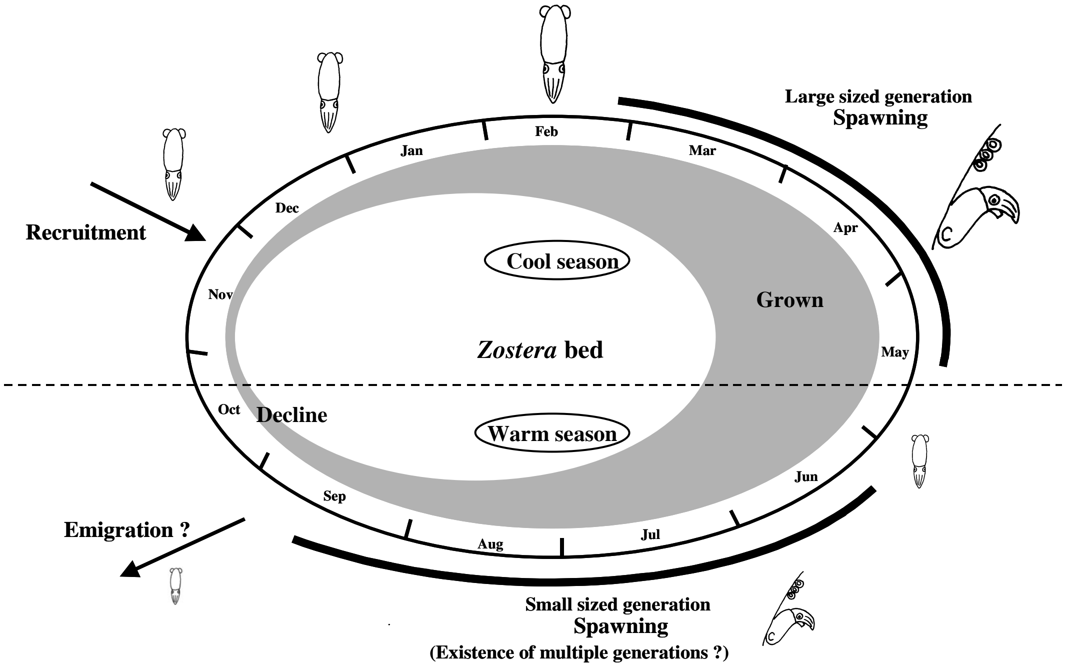

Figure 5. Schematic presentation of the life cycle of *Idiosepius paradoxus* in the *Zostera* beds.

cool-season and from mid June to late September in the warm-season, respectively. The small specimens that occurred in late May might be the offspring of the large sized generation of the cool-season. Natsukari (1970) reported the observation of egg-laying behaviour of captive *I. paradoxus* collected in late July from Kyushu, west Japan. These females were of a small size (6.2–8.4 mm ML), and might be the small size generation as they are of a similar size to the warm-season's mature females in the present study. Specimens from the warm-season probably have a short life span compared with that of the cool-season and thus, multiple generations are thought to exist in the warm-season from March to September. The specimens hatched late in the warm-season are possibly the cool-season generation which will be restrained in sexual maturity during winter. All the specimens of both sexes that appeared in late November were immature, while their body size was larger than the mature specimens from the warm-season.

Jackson (1988) reported that the life span of the tropical *I. pygmaeus* from the central Great Barrier Reef of North Queensland Australia is quite short, with the oldest specimens aged being 67 days and 79 days for males and females respectively, based on statolith age analysis. *I. pygmaeus* also exhibited slower growth during the cooler seasons of the year (Jackson and Choat, 1992). However, slower growing cool-season individuals lived longer and had comparatively larger gonads than their warm-season counter parts, despite no difference in body size between the two seasons (Jackson, 1993). It was suggested that *I. pygmaeus* appeared to be employing a "trade-off" in its reproductive strategy by partitioning a greater amount of energy into gonad tissue over a longer lifespan during the cooler period of the year (Jackson, 1993). On the other hand, *I. paradoxus* in the present study exhibits a large difference in mature individual's body size between cool-seasons (large) and warm-seasons (small). *I. pygmaeus* is a tropical species, and the surface water temperatures just offshore from the central Great Barrier Reef (Jackson, 1998, 1993; Jackson and Choat, 1992) fluctuates between 19.3 and 30.9 °C (Walker, 1981 see Jackson, 1992). In these water temperatures, it may be possible for *I. pygmaeus* to spawn and develop eggs through the year. *I.*

paradoxus is a temperate species, with the water temperature in the present study fluctuating between 6.0 and 30.0°C (Fig. 2). The hatching rate of *I. paradoxus* eggs is 40d or less in temperature of 15.0°C (Shigeno personal communication), and so reproduction may be impossible in the winter with under 10.0°C water temperature. For this reason, *I. paradoxus* must survive over the coldest season without reproducing. Although, it is supposed that the warm-season generation of *I. paradoxus* reach sexual maturity quickly at a small body size. The existence of a small size generation (s) in warm-seasons and a large sized generation in cool-seasons had been reported in some small shrimp species inhabiting Japanese water (Yasuda, 1956; Kikuchi, 1962, 1966; Yamashita and Shiota, 1970) and also in mysids inhabiting coastal water from 20°to 50°latitude (Mauchline, 1980). In the present research, sexual maturity was determined only by the presence of spermatophores in the Needham's sac of the males and mature oocytes in the females. Further study could observe the seasonal development of gonads by detailed histological investigation. Moreover, the comparative observations of age analysis, morphological characteristics, spawning output and so on between warm and cool-season generations are necessary to understand the reproductive strategies of *I. paradoxus*.

The body size of *I. paradoxus* was clearly separated at late May in 1998 and early June in 1999 (Fig. 3, 4A). However, on the same *Zostera* beds as in this study, a small number of large specimens, which might have passed the winter, and small mature specimens simultaneously appeared in early June in 2000 and 2001 (Kasugai personal observation). Thus, there may not be complete isolation between the cool and warm-season generations. Cross-mating between two generations (one and two year classes) has also been reported in the European cuttlefish *Sepia officinalis* (Gauvrit *et al*., 1997, 1998).

The numbers of specimens appeared to decrease from August with no specimens present in October with regression of the *Zostera* beds. A similar finding was reported in the *Zostera* beds located on the coast of the Seto Inland Sea of Japan (Yamamoto, 1988). An interesting question is where do *I. paradoxus* live before their recruitment onto the *Zostera* beds in late December.

The egg masses of *I. paradoxus* are spawned on the surface of eelgrass blades on the *Zostera* beds (Kasugai and Ikeda, 2003). The eggs spawned by the cool-seasons generation will hatch on the *Zostera* beds because the eelgrass is intact on the beds in this season. However, egg masses spawned by warm-season generations may leave the *Zostera* beds with the drifting leaves before hatching. These drifting plants may result in dispersion of the hatchlings and juveniles of *I. paradoxus*. We suggest that *I. paradoxus* restrict their life to the drifting plants when the *Zostera* beds are declining, and recruit to the *Zostera* beds with the restoration of eelgrass. It was reported that a lot of floating eelgrass appeared from July to December in the Seto Inland Sea, Japan (Yamamoto *et al*, 2002). We have knowledge that the hipolyichid shrimp *Latreutes acicularis*, which is the typical crustacean species that inhabits beds of algae and seagrasses in Japan, have a small size generation with a short life span in the warm seasons and a large size generation with a longer life staying over the coldest season (Yasuda, 1956; Kikuchi, 1962, 1966; Yamashita and Shiota, 1970). On the *Sargassum* beds of the Seto Inland Sea of Japan, *L. acicularis* move from near the *Zostera* beds only from summer to autumn. The juveniles born in the *Sargassum* bed migrate to the *Zostera* bed with a decrease of the water temperature (Mukai, 1970). The prey organisms of *I. paradoxus* are mainly small crustaceans living in the *Zostera* beds (Kasugai, 2001). A high abundance of *L. acicularis* live in the *Zostera* beds at this study area, and have been observed to be preyed upon by *I. paradoxus* on the spot (Kasugai, 2001). *I. paradoxus* may migrate to other areas such as the *Sargassum* beds while looking for these crustaceans during periods of eelgrass decline. It needs further study to understand the migration of *I. paradoxus,* in relation to the appearance of the crustaceans as food organisms.

In many species of cephalopod, males copulate with immature females (Mangold, 1987). In *I. paradoxus*, males mature earlier than females in both warm and cool-seasons, and immature females were implanted with spermatangia by early matured males. Males copulate with not only females but also males. A total number of 46 copulated males out of 438 males were found in the two years of sampling. Under captive conditions, male-male copulation has been observed in *I. paradoxus* (Kasugai, personal observation) and *I. thailandicus* (Nabhitabhata, 1998). Copulations between males in captivity had been reported in the Japanese cuttlefish *Sepia esculeata* (Arakawa, 1960), and male-male copulation in natural conditions has been reported in the oceanic squid *Illex coindetii* (Lordan and Casey, 1997). In this report, only one copulated male was found among 179 caught males, thus it was suggested to be 'accidental' copulation between males. Observations of male-female mating behaviour of *I. paradoxus* show the males to dart ostensibly looking for a female in an unguarded moment without pair formation and complete copulation within a short time (Kasugai, 2000). Moreover, male *I. paradoxus* also copulates with females while they are laying eggs (Kasugai, 2000). Male *I. paradoxus* may choose the strategy not to form courtship but copulate with females whenever the occasion may arise during their short life, and sometimes the male may misjudge males as females and thus implant his spermatangia to males.

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REFERENCES

Aioi, K. 1980. Seasonal change in the standing crop of eelgrass (*Zostera marina* L.) in Odawa Bay, central Japan. Aquat. Bot. **8**: 343–354.

Arakawa, K. 1960. Miscellaneous notes on mollusca (2). Mating and spawning habits of some marine molluscas. Venus **21**: 72–78.

Arasaki, M. 1950a. Studies on the ecology of *Zostera marina* and *Zostera nana* (I) Bull. Jpn. Soc. Sci. Fish. **15**: 567–572.

Arasaki, M. 1950b. Studies on the ecology of *Zostera marina* and *Zostera nana* (I) Bull. Jpn. Soc. Sci. Fish. **16**: 70–76.

Boletzky, S.v. 1995. The systematic position of the Sepiolidae (Mollusca: Cephalopoda). Bull. Inst. oceanogr. Monaco n special **16**: 99–104.

Bonnaud, L., R. Boucher-Rodoni, and M. Monnerot. 1997. Phylogeny of cephalopods inferred from mitochondrial DNA sequences. Molecu. Phyloge. Evol. **7**: 44–54.

Chotiyaputta, C., T. Okutani and S. Chaitiamvong. 1991. A new pygmy cuttlefish from the Gulf of Thailand *Idiosepius thailandicus* n. sp. (Cephalopoda: Idiosepiidae). Venus **50**: 165–174.

Hylleberg, J. and A. Nateewathana. 1991a. Morphology, internal anatomy, and biometrics of the cephalopod *Idiosepius biserialis* Voss, 1962. A new record for the Andaman Sea. Phuket mar. Biol. Cent. Res. Bull. **56**: 1–9.

Hylleberg, J. and A. Nateewathana. 1991b. Redescription of *Idiosepius pygmaeus* Steenstrup, 1881 (Cephalopoda: Idiosepiidae), with mention of additional morphological characters. Phuket mar. Biol. Cent. Res. Bull. **55**: 33–42.

Jackson, G. D. 1989. The use of statolith microstructuresto analyzelife-history events in the small tropical cephalopod *Idiosepius pygmaeus*. Fish. Bull., U.S. **87**: 265–272.

Jackson, G. D. 1992. Seasonal abundance of the small tropical sepioid *Idiosepius pygmaeus*. The Veliger **35**: 396–397.

Jackson, G. D. 1993. Seasonal variation in reproductive investment in the tropical loliginid squid *Loligo chinensis* and the small tropical sepioid *Idiosepius pugmaeus*. Fish. Bull., U.S. **91**: 260–270.

Jackson, G. D. and J. H. Chort. 1992. Growth in tropical cephalopods: an analysis based on statolith microstructure. Can. J. Fish. Aquat. Sci. **49**: 218–228.

Kasugai, T. 2000. Reproductive behavior of the pygmy cuttlefish *Idiosepius paradoxus* in an aquarium. Venus **59**:37–44.

Kasugai, T. 2001. Feeding behaviour of the Japanese pygmy cutlefish *Idiosepius paradoxus* (Cephalopoda: Idiosepiidae) in capitivity: evidence for external digestion? J. Mar. Biol. Ass. U.K. **81**: 979–981.

Kasugai, T. and Y. Ikeda. 2003. Description of the egg mass of the pygmy cuttlefish, *Idiosepius paradoxus* (Cephalopoda: Idiosepiidae), with special reference to its multiple gelatinous layers. The Veliger 46: 105–110

Kikuchi, T. 1962. An ecological study on animal community of *Zostera* belt, in Tomioka Bay, Amakusa, Kyushu. (II) Community composition, (2) Decapodan crustaceans. Res. Oceanogr. Wrk. Jap., spec. (6): 135–146.

Kikuchi, T. 1966. An ecological study on animal community of *Zostera marina* belt, in Tomioka Bay, Amakusa, Kyushu. Publ. Amakusa Mar. Biol. Lab. **1**: 1–106.

Lewis, A. R. and J. H. Choat. 1993. Spawning mode and reproductive output of the tropical cephalopod *Idiosepius pygmaeus*. Can. J. Fish. Aquat. Sci. **50**: 20–28.

Lu, C. C., and M. C. Dunning 1998. Subclass Coleoidea. **In**: P. L. Beesley, G. J.B. Ross, A.. Wells (eds.). Mollusca: The southern synthesis. Fauna of Australia Vol 5 Part A xvi. CSIRO Publishing, Melbourne. pp. 499–563.

Lordan, C and J. Casey. 1997. The first record of “accidental” copulation between male squid of the genus *Illex*. J. Moll. Stud. **63**: 556–558.

Mangold, K. 1987. Reproduction. **In**: P. R. Boyle (ed.). Cephalopod life cycle vol.II Comparative reviews. Academic Press, London. pp. 157–200.

Mauchline, J. 1980. The biology of mysids and euphausiids. Advances in Marine Biology **18**: 1–681.

Moynihan, M. 1983. Notes on the behaviour of *Idiodepius pygmaeus* (Cephalopoda: Idiosepiidae). Behabiour **85**: 42–57.

Mukai, H. 1970. Life histories of the shrimps in the *Sargassum* region. Hirosima Daigaku Seibutu Gakkaisi **35**: 7–13.

Nabhitabhata, J. 1998. Distinctive behaviour of Thai pygmy squid, *Idiosepius thailandicus* Chotiyaputta, Okutani and Chaitiamvong, 1991. Phuket mar. Biol. Cent. Special Publ. **18**: 25–40.

Natsukari, Y. 1970. Egg-laying behaviour, embryonic development and hatched larva of the pygmy cuttlefish, *Idiosepius pygmaeus paradoxus* Ortmann. Bull. Fac. Fish. Nagasaki Univ. **30**: 15–29.

Nesis, K. N. 1987. Cephalopods of the world., Squids, cuttlefishes, octopuses, and allies. T. F. H. Publ. Inc., Neptune City, N. J. 351pp.

Okutani, T. 1968. Studies on early life history of decapodan mollusca III. Systematics and distribution of larvae of decapod cephalopods collected from the sea surface on the Pacific coast of Japan, 1960–1965. Bull. Tokai Reg. Fish. Res. Lab. **55**:9–57.

Sasaki, M. 1923. On an adhering habit of a pygmy cuttlefish, *Idiosepius pygmaeus* Steenstrup. Annot. Zool. Jap. **10**: 209–213.

Sasaki, M. 1929. Monograph of the recent dibranchiate cephalopods of the Japanese and adjacent waters. J. Fac. Agr. Hokkaido Imp.Univ. 29, suppl. **10**: 1–357.

Shigeno, S. 2002. Study on the brain development in the Coleoid Cephalopod: fundamental process, adaptive design, and evolutionary sophistication. Doctoral Thesis Okayama Univ.

Watanabe, K. 1997. Comparative embryology of debrachian cephalopos during the early life history. Doctoral Thesis Tokyo Univ. Fish.

Yamamoto, M. 1988. Normal embryonic stages of the pygmy cuttlefish, *Idiosepius pygmaeus paradoxus* Ortmann. Zool. Sci. **5**: 989–999.

Yamamoto, M., M. Tochino, K. Yamaga and M. Fujiwara. 2002. Juvenile fishes associated with floating seaweeds in thecentral Seto Inland Sea, Japan. Nippon Suisan Gakkaishi **68**: 362–367.

Yamashita, K and A. Shiota. 1970. An ecological study of the shrimps on the *Zostera* belt off Miyajima Aquarium, Miyajima. AKI, nature and culture of Miyajima. **2**: 1–14.

Yasuda, J. 1956. Naiwanni okeru ebiruino sigenseibutugakuteki kenkyu (II) kakuron kakusyuruino seitaini kansuru kenkyu. [Biological study of shrimp resources in Seto Inland Sea (II). Ecological study of each species]. Bulletin of Naikai Regional Fisheries Research Laboratory (9):1–81.