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Growth and Reproduction of the Sea Snake, *Emydocephalus ijimae*, in the Central Ryukyus, Japan: a Mark and Recapture Study

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ABSTRACT—A mark and recapture study was carried out for three years on a population of the Ijima's sea snake, *Emydocephalus ijimae*, in the coastal shallow water of Zamamijima Island, central Ryukyus, Japan. The relatively high recapture (47% of 167 marked snakes) suggests that *E. ijimae* is a particularly philopatric, sedentary species among the sea snakes. The sex ratio (male: female), approximately 1.6:1, significantly skewed from 1:1. The growth rate in SVL declined with growth, with females thoroughly growing better than males. Males and females were estimated to begin reproductive activity in the second or third summer and the third spring after birth, respectively. Frequency of female reproduction is guessed to vary from annual to biennial, or even less frequent.

Key words: sea snake, population biology, growth, reproduction, sex ratio

INTRODUCTION

The sea snake is a group of marine species of the family Elapidae, and mostly inhabits tropical shallow waters of Pacific and Indian Oceans. As one of the two major groups of the extant marine reptiles, the sea snake is an ideal organism to investigate morphological, physiological, and ecological aspects of adaptations to marine life (e.g., see Dunson, [1975] and Heatwole [1999], for review). Ecological aspects of the sea snake biology, however, have been rather poorly investigated yet. Moreover, most ecological studies have dealt with tropical populations of a few species (*Aipysurus laevis*: Burns 1985; Burns and Heatwole, 2000; *Enhydrina schistosa*: Voris,1985; Voris and Jayne, 1979; Voris *et al*., 1978; *Lapemis curtus* and *Hydrophis elegans*: Ward, 2001; *Laticauda* spp.: Shine *et al*., 2002), leaving various ecological properties of sea snake populations under the seasonal environment yet to be studied. For the better understanding of ecological adaptations to the marine life by the sea snake, such a paucity of information regarding populations in subtropical seas needs particular attention, because in terrestrial snakes, differential ecological patterns have been reported for species under tropical and temperate environments (e.g., Fitch, 1982; Seigel and Ford, 1987).

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Emydocephalus ijimae, composing the genus *Emydocephalus* together with its Southern Hemisphere counterpart (*E. annulatus*), is known to be relatively common in shallow waters of East China Sea (Maki, 1931; Smith, 1926; Takahashi, 1984). While most other sea snakes prey on fishes (Voris and Voris, 1983), the two *Emydocephalus* species and another species of a different genus (*Aipysurus eydouxii* from waters adjacent to Australia and Southeast Asia) are known to exclusively feed on eggs of coral reef fishes (Voris, 1966; Voris and Voris, 1983; Guinea, 1996). This suggests that these three species play a peculiar role in coral reef ecosystems in their respective ranges (Voris, 1972).

East China Sea, representing the northernmost extremity of range of the reef-dwelling sea snake community (Toriba, 1994), shows a marked seasonal fluctuation in water temperature with the monthly average ranging from 20.6°C in February to 28.4°C in August (data from the National Sea Level Monitoring Center of Japan between 1978 and 1996: also, see Masunaga *et al*., in press). *Emydocephalus ijimae* in this area thus offers a good opportunity to investigate ecological traits of a sea snake under the seasonal environment.

In the foregoing study, we investigated male and female gonadal patterns in a central Ryukyu population of *E. ijimae* by examining a series of preserved specimens (Masugana *et al*., in press). However, a number of important life history characteristics, such as growth rate and age at maturity, are

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not yet determined. We thus have carried out a field study for a population of this sea snake with a mark and recapture procedure.

MATERIALS AND METHODS

Thestudy site (300 m×250 m) was set in the coastal water of

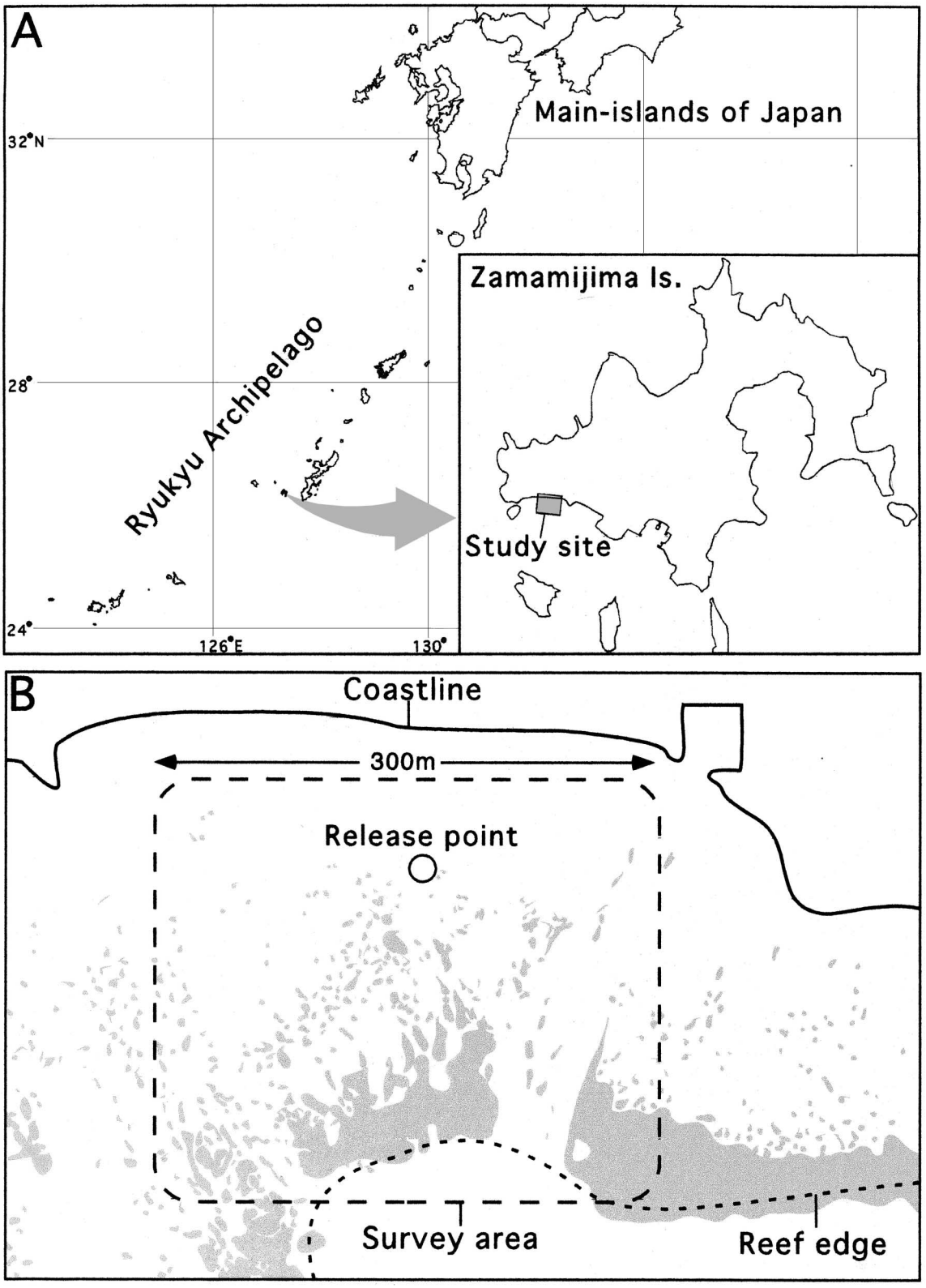


Fig. 1. Maps showing the location of Zamamijima Island (A), and details of the study site (B). Shaded portions in the latter denote reef corals.

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Zamamijima Island, Okinawa Group, central Ryukyus, Japan (Fig. 1). The site was located mostly within the reef edge (1–3 m), but partially extending outside of the reef (3–5 m). Bottom of the site was largely sandy, flat, forming a slightly descending slope outward, although there were two large colonies of branching corals near the reef edge and the bottom outside of the reef constituted a rather steep slope. Numerous smaller colonies of corals were scattered within the study site exclusive of a portion close to the coastline. No topographical differences were evident between the study site and surrounding area of shallow water.

The field survey was carried out every month from April 1994 to July 1997 exclusive of September 1994, August, September and November 1995, May 1996, and April and June 1997. During each survey period, which consisted of 1–8 successive days (Appendix 1), snakes were searched for by 1–5 men, each slowly swimming for 60–120 minutes almost everyday with the aid of snorkel. An effort was made to survey as randomly as possible within the study site in each survey. Snakes encountered were captured by hand, and were checked for marks coding their individual reference numbers. Individuals having no marks were marked by ventral clipping. Newly captured snakes, as well as recaptures not yet captured during a same survey period, were then examined for snout-vent length (SVL, in mm), body weight (BW, in g), subcaudal scale count, and the presence or absence of conical protrusion on the rostral scale (i.e., secondary sexual characters in males: Heatwole *et al*., 1978). Finally they were released from a fixed point, which was located 50 m offshore from the middle of the nearest coastline (Fig. 1). Individuals already captured in a same survey period were released immediately at points of encounters.

Previous gonadal and external investigations of preserved specimens revealed that male and female *E. ijimae* attain sexual maturity at 500 mm and 550 mm SVL, respectively (Masunaga *et al*., in press), and that mature males invariably have a conical rostral protrusion (male secondary sexual character: see above)(Masunaga *et al*., unpublished data). We thus considered individuals 500 mm ≤ SVL with conical rostral protrusion as adult males, those 500 ≤ SVL <550 mm without this character as subadult females, and those 550 mm ≤ SVL without the rostral protrusion as adult females.

RESULTS

Recapture rate

From five to 42 snakes ($\bar{x}$=16.5) were captured in each survey period (Appendix 1). During the first (23–25 April 1994) and second periods (1–4 May 1994), 14 and 12 snakes, the latter being still all new captures, were found, respectively. Marked snakes were first recaptured in the third survey period (4–7 June 1994). The proportion of recaptures (the number of recaptures per the total number of individuals captured) was (9/31)×100=29.0%. The recapture rates increased rapidly from the third to the fifth periods (25 August 1994: 85.7%), and then stabilized to relatively high scores (45.0–100%, $\bar{x}$=79.5%: Appendix 1). A total of 45 individuals continued to be recaptured over one year. During the whole study period, 167 snakes were marked and 79 were recaptured at least one time. Thus, the overall recapture rate was 47.3%. There were no significant differences in the recapture rate between adult males (33/63=52.4%) and adult females (15/28=53.6%)(χ^2 test, χ^2 = 0.003, p>0.05). Of 97 snakes first marked as immature individuals, 41 (42.3%) were subsequently recaptured at least one time.

Sexual dimorphism in subcaudal count and sex ratio

Subcaudal counts differed significantly between adult males ($\bar{x}$=26.7, SD=1.3, range: 24-30, n=62) and subadult/adult females ($\bar{x}$=20.9, SD=1.2, range: 19-24, n=29) (Student's t-test, t=20.37, p<0.0001). The mark and recapture practice revealed no ontogenic changes in the subcaudal count at all. Sexes of individuals, yet 500 mm > SVL at final capture, were determined: individuals having 25 or more subcaudals were considered as males, whereas those with 23 or fewer subcaudals as females. The one snake of this size group, having 24 subcaudals, was recorded as a juvenile of unknown sex. The sex ratio (no. of males: no. of females) of the marked snakes (1.6:1, n=169) was significantly skewed in favor of males (χ^2-test, χ^2=4.56, p<0.05).

Growth in snout-vent length

Individual trajectories of SVL in recaptured females and males are presented in Fig. 2. The smallest individual was 311 mm in SVL at initial capture. This individual and 54 others, all 400 mm > SVL and found between February and July, were considered as juveniles not long after birth at initial capture, because SVL of *E. ijimae* at birth is reported to range from 266 mm to 342 mm (Moriguchi, 1991; Uehara, 1993; Masunaga *et al*., in press). Moreover, those 55 individuals had traces of navels (a mark of umbilical cord). Of these putative newborns, those 350 mm > SVL at initial capture in April grew to as large as or even larger than 450 mm in SVL by the next April (Fig. 2). Female sometimes exceeded 800 mm in SVL, with the largest one reaching as large as 855mm. In contrast, male was usually smaller than 750 mm in SVL, and even the largest male was no greater than 785 mm (Fig. 2).

Growth rates in SVL (mm/day) were calculated for the individuals recaptured at intervals ≥ 300 days (Table 1). In either sex, the growth declined with body size. Snakes greater than 700 mm in SVL showed growth rates no more than 20% (females) or even less (males) of those in snakes smaller than 500 mm in SVL. In matured individuals, growth rate was significantly greater in females (550 mm ≤ SVL) than in males (500mm ≤ SVL), when the growth rate (dependent variable, log-transformed) was analyzed against mean of SVLs at two successive captures(covariate, log-transformed) by ANCOVA (n=14 for females, 24 for males, df=1,35; F=29.95, p<0.001 for elevation; F=2.55, p>0.05 for slope).

Growth rates during a same warmer period (from April to October 1994) and a cooler period (from October 1994 to April 1995) showed no distinct differences in males. In females, the rate tended to be greater in the warmer period than in the cooler period, although limited sample size did not permit any statistical confirmation (Fig. 3).

Temporary fluctuation in body weight

Individual trajectories of BW in recaptured females and males are presented in Fig. 4. BW in adult females and males ranged from 170 to 600 g and from 70 to 350 g,

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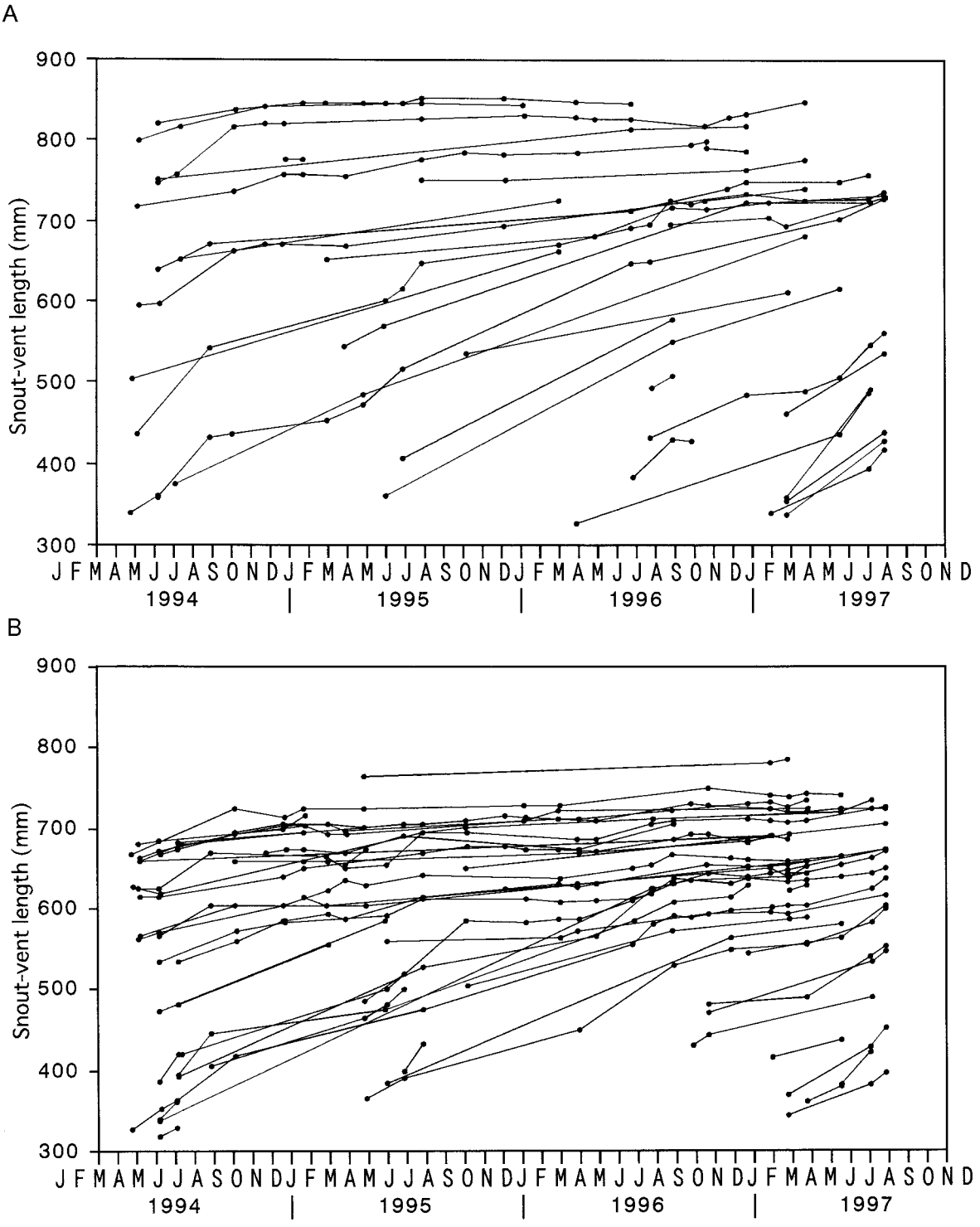


Fig. 2. Individual growth trajectories for SVL of *Emydocephalus ijimae* from Zamamijima, central Ryukyus. (A) females. (B) males.

respectively. Both individual variation and temporary fluctuation in adult BW tended to be much greater in females than in males. In a few adult females, rapid reduction and more or less substantial increase of BW were recognized from November to March or April, and the remaining season of the year, respectively. Change in BW in one individual (No. 1 in Fig. 4A) typically showed weight loss in winter and gain from spring to summer. That is, BW substantially dropped from December 1994 to March 1995 (ca 9% loss of original BW per month), followed by its gradual increase to October1995 (ca 6% gain per month), very rapid decrease to December 1995 (ca19% loss per month), substantial increase to October 1996 (ca 10% gain per month), and rapid decrease, again, to December 1996 (ca 15% loss per

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Table 1. Growth rates in SVL (mm/day) of male and female *Emydocephalus ijimae* from the central Ryukyus ($\bar{x}$ ±SD, followed by sample sizes (n), and ranges in parentheses).

	Size class in SVL		
	<500mm	500–700mm	700mm<
Female	0.35 (n=2, –)	0.20±0.09 (n=6, 0.07–0.34)	0.07±0.030 (n=8, 0.03–0.12)
Male	0.27±0.04 (n=3, 0.25–0.32)	0.13±0.07 (n=17, 0.04–0.24)	0.04±0.02 (n=7, 0.02–0.06)
Combined	0.30±0.05 (n=5, 0.25–0.35)	0.15±0.08 (n=23, 0.04–0.24)	0.05±0.03 (n=15, 0.02–0.12)

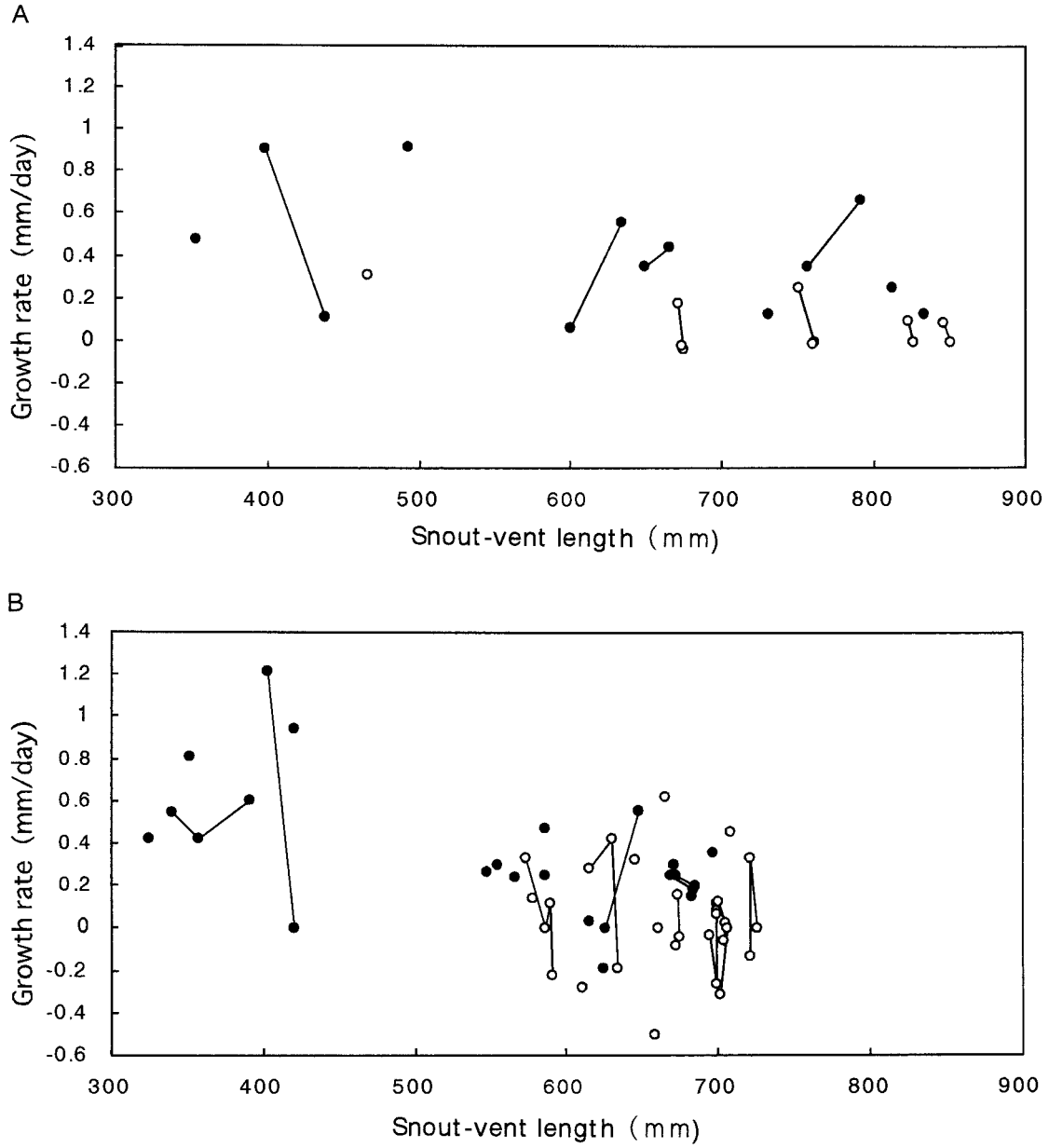


Fig. 3. Relationship between mean SVL and growth rate in *Emydocephalus ijimae* calculated from two successive captures. Closed and open circles represent scores from captures in a warmer (from April to October 1994) and cooler periods (from October 1994 to April 1995), respectively. Scores from more than two successive captures of same individuals are connected by lines. (A) females. (B) males.

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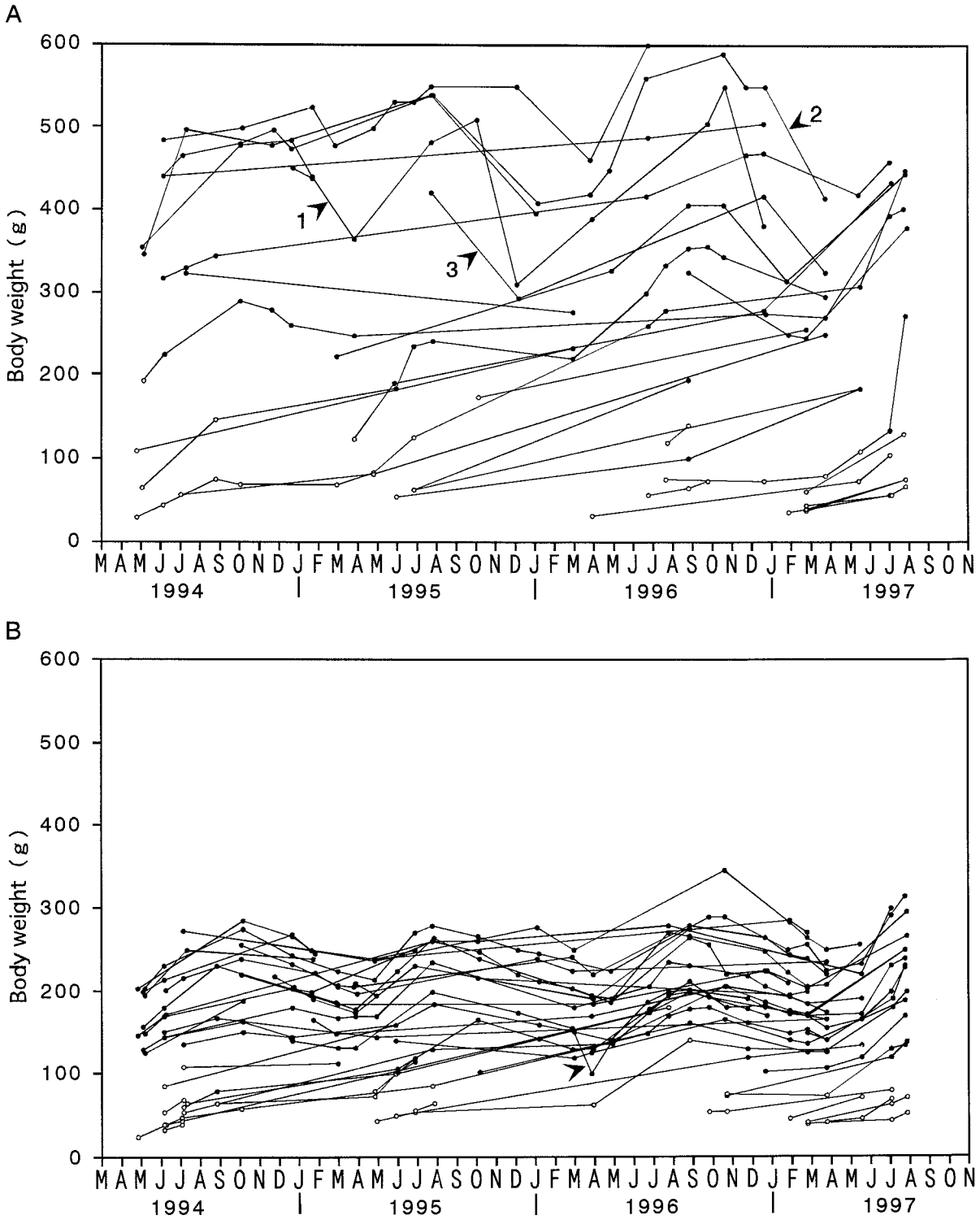


Fig. 4. Individual trajectories for BW fluctuation of *Emydocephalus ijimae* from Zamamijima, central Ryukyus. (A) females. (B) males. Open and filled circles represent immature and mature states, respectively. Arrows indicate individuals referred to in the text.

month) in order. In adult males, on the other hand, BW mostly decreased from August or September to the next March or April and increased from March or April to the next August or September. The ratio of the decrease did not exceed 5% of original BW per month. One exception might be an abnormal case (see an arrow in Fig. 4B). The increase in BW during the spring usually exceeded 10%, often reaching above 15% per month. In juveniles, there were no prominent fluctuations in BW (Fig. 4).

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DISCUSSION

Recapture rate

Several previous authors applied the mark and recapture method to study sea snake populations, but resultant recapture rates were much lower than in the present study. Kropach (1975), for example, reported that less than 1% of 961 marked snakes were recaptured in the pelagic species, *Pelamis platura*, whereas Voris (1985), on the basis of mark and recapture practice for a sea snake assemblage in Malaysia, listed overall recapture rates as 8.8% (46/520) for *Enhydrina schistosa*, 0%(0/69) for *Hydrophis melanosoma*, 3.4% (2/53) for *H. brookii*, and 4.5% (1/22) for *H. torquatus.* With respect to the oviparous sea snake, Lading and Stuebing (1991) reported a value of 30% (83/275) for *Laticauda colubrina*. The high overall recapture rate obtained in the present study (47.3%) suggest a remarkably philopatric, and sedentary nature of *E. ijimae* as compared to other sea snake species.

Sex ratio

Observed sex ratio in the present population was 1.6 in favor of males. Possible factors responsible for such a skewed sex ratio include (1) a bias in actual sex ratio at birth (primary sex ratio), (2) sexually differential mortality after birth, and (3) sexually differential ratio of capture (Shine and Bull, 1977). From the result of our mark and recapture practice that indicates similar rates of recaptures between sexes, factor (3) does not seem to be the case. This, along with the absence of significant difference in sex ratio between juveniles (400 mm ≥ SVL: ca 1.5 in favor of males) and adults, also seems to negate contribution of factor (2), although the presence of sexually biased mortality in neonates may remain possible. Thus, the male biased sex ratio is presently most likely to reflect the primary sex ratio in the central Ryukyu population of *E.ijimae*.

All snake species so far studied karyologically by appropriate experimental arrangements have exhibited the ZZ/ZW sex chromosome system (e.g., see Olmo [1986] for review). This usually predicts equality in male and female ratios in newborns and, indeed, published sex ratios for broods of most snake species are not significantly skewed from 1:1 (Shine and Bull, 1977). In a few species including one sea snake *Enhydrina schistosa*, however, significantly skewed sex ratios were reported even for neonates (eg, Shine and Bull, 1977; Lemen and Voris, 1981; Gutzke *et al*., 1985; Dunlao and Lang, 1990), and Burger and Zappalorti (1988) attributed this phenomenon in the oviparous colubrid species, *Pituophis melenoleucus*, to sexually differential mortalities in developing embryos, which result from their sex-specific tolerances of incubation temperature. We thus suspect that the putative skewed sex ratio in newborn *E. ijimae* may possibly be derived from higher embryonic mortality in females than in males. This assumption needs careful verification by examining sex ratios in developing embryos and neonates.

Growth and maturity

A few previous studies estimated growth rates in SVL for several tropical sea snakes. In a series of publications by R. A. M. Bergman, for example, the first year growth rates in *Lapemis hardwickii,Thalassophis anomalus*, and *Hydrophis fasciatus* from Indonesian waters were estimated to be 0.3 mm/day (Bergman, 1949), 0.3 mm/day (Bergman, 1954), and 0.5 mm/day (Bergman, 1962), respectively. Voris and Jayne (1979) also estimated the first year growth rate in *Enhydrina schistosa* from Malaysia to be approximately 1.0 mm/day, whereas Burns and Heatwole (2000) gave values up to 0.32 mm/day for juveniles of the Great Barrier Reef population of *Aipysurus laevis*. Estimated overall growth rate in SVL of immature *E. ijimae* (individuals smaller than 500 mm in SVL) ($\bar{x}$ = 0.30 mm/day) is similar to corresponding values for some tropical sea snakes.

SVL in newborn *E. ijimae* is reported to range from 266 mm to 342 mm (Moriguchi, 1991; Uehara, 1983; Masunaga *et al*., in press). On the other hand, average growth rates were estimated from our data to be 0.27 mm/day in immature males (<500 mm in SVL), and 0.36 mm/day in immature females (<550 mm in SVL). Taking these into considerations, males and females seem to attain maturity at similar ages, i.e., between 19 and 28 months after birth for males, and between 19 and 26 months after birth for females. Because neonates appear from November to January, and spermatogenesis in males and ovulation in females commence in August and May (Masunaga *et al*., in press), they seem to actually start reproductive activity in the second or third summer and the third spring after birth, respectively.

Ward (2001) assumed *L. hardwickii* to mature at 2-4 years of age, and *H. elegans* at 3–5 years, whereas Burns (2000) suspected that male and female *A. laevis* mature during the third year, and the fourth or fifth year after birth, respectively. These suggest that *E. ijimae* mature relatively fast among sea snakes.

Our previous study demonstrated that *E. ijimae* exhibits sexual size dimorphism (SSD) in favor of females (Masunaga *et al*., in press) like a majority of other snakes examined so far (Shine, 1978, 1994). Shine (1993) argued that earlier maturation of males and prominent lowering of the growth rate after maturation in both sexes are the major proximate causes of such an SSD. Besides these, higher mortality in males might also be responsible for the female large SSD observed in a wild population (e.g., Shine *et al*., 2002). However, our results seem to negate all these possibilities and suggest that the higher overall growth rate in females mostly contributes to the female large SSD in this species.

The female large SSD in reptiles, as well as many other organisms, is often attributed to the operation of selective forces that favor large females due to their greater fecundity (Shine, 1978; Fitch, 1985). Recently, evolution of SSD (especially in snakes) is also often explained on the ground of partitioning of food resource between sexes (e.g., Shine, 1989, 1991; Shine *et al*., 2002). However, these do not

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explain the observed SSD in *E. ijimae*, because in this species maternal body size does not correlate with brood size or with reproductive frequency (Masunaga *et al*., in press), and both sexes exclusively feed on fish eggs that are much smaller than their gape sizes (Voris, 1966; Voris and Voris, 1983; Guinea, 1996). Further studies are needed to specify ultimate factors responsible for the female large SSD in *E.ijimae*.

Body weight fluctuation and reproductive frequency

Adult male *E ijimae* prominently increases BW from early spring to late summer. Increase in frequency of spawning by coral reef fishes with the raise of water temperature in spring (Yamamoto, 1976; Thresher, 1984) increases food availability. The temporary increase of BW in adult males might track temporal fluctuation in food availability in their habitat.

Occasional rapid decrease of BW from the late autumn to early spring in adult females (Fig. 4A) can not be explained solely on the ground of temporary fluctuation in food availability. Previous captive observations and gonadal examinations of preserved specimens indicated that in *E. ijimae* of the central Ryukyus parturition occurs from late autumn (November) to mid winter (January)(Moriguchi, 1991; Uehara, 1993; Masunaga *et al*., in press). The prominent BW reduction in an adult female can be due to parturition.

A few previous authors predicted that in some sea snakes having long gestation periods, such as *A. laevis* and *H. elegans*, reproduction occurs biennially or even less frequently due to an otherwise much limited period left for each female to restore energy for production of the next brood after parturition (Burns, 1985; Ward, 2001). A relatively long gestation period (6–8 months) and participation of no more than half of adult females to reproduction in each year (Masunaga *et al*., in press) suggested that *E. ijimae* also reproduced less than annually. Nevertheless, some adult females monitored in the present study (nos. 1–3 in Fig. 4A) exhibited BW reduction in two or more successive parturition seasons, suggesting that not all females reproduced less than annually.

Gonadal examination of preserved specimens demonstrated that almost all adult females of *E. ijimae* had well developed ovarian follicles just before ovulation season (Masunaga *et al*., in press), unlike *A. laevis* in which ovarian follicles in non-reproductive females in a given year cease to grow a few months before ovulation season (Burns, 1985). Masunaga *et al*. (in press) interpreted the former ovarian pattern as indicative of “delayed decision” for reproduction in a given year by each female *E. ijimae*.

Presence of individuals that reproduce every year support this view, and we, therefore, suspect that reproductive frequency of a female *E. ijimae* is largely or predominantly determined by her foraging success just before ovulation season. Animals that depend directly on the temporal energy intake for brood production are often referred to as “income breeders”, whereas species that commence secondary vitellogenesis (Aldridge, 1979) only after accumulation of sufficient body reserves (in the form of fat bodies, etc.) as “capital breeders”. Of the tetrapods, most endotherms are “income breeders”, whereas a majority of ectotherms are considered “capital breeders” (Pough, 1980; Bonnet *et al*., 1998, 2002; Bronson, 1998). Results of our present and previous studies (Masunaga *et al*., in press) suggest that *E. ijimae* is an “income breeder” like a few terrestrial snakes (Wharton, 1966; Seigel and Ford, 1987; Bonnet *et al*., 1998). Longer monitoring (Madsen and Shine, 2001) of more females is essential to elucidate factors responsible for temporal and individual variation of reproductivefrequency in this sea snake.

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Appendix 1. Summary of results of mark and recapture practice for *Emydocephalus ijimae* in Zamamijima Island, the central Ryukyus, Japan.

Year	Survey period	No. of persons engaged	No. of snakes captured	No. of snakes recaptured	No. of snakes newly marked	Proportion of recaptured snakes (%)	Cumulative no. of snakes marked
1994	Apr. 23–25	1–2	14	–	14	–	–
	May 1–4	2	12	0	12	0.0	14
	June 4–7	1–3	31	9	22	29.0	26
	July 2–9	1–2	21	10	11	47.6	48
	25–Aug	2	7	6	1	85.7	59
	Oct. 1–4	1	16	12	4	75.0	60
	Nov. 19–21	1	5	4	1	80.0	64
	Dec. 17–22	1	13	12	1	92.3	65
1995	Jan. 18–22	1	13	11	2	84.6	66
	Feb. 24–Mar. 1	1	16	11	5	68.8	68
	Mar.24–28	1	13	8	5	61.5	73
	Apr. 24–27	1	17	10	7	58.8	78
	May 28–30	1	15	9	6	60.0	85
	June 26–27	1	12	9	3	75.0	91
	July 25–27	1	20	16	4	80.0	94
	Oct. 2–4	1	9	6	3	66.7	98
	Dec. 3–5	1	7	7	0	100.0	101
1996	Jan. 3–5	1	8	8	0	100.0	101
	Feb. 26–29	1	12	12	0	100.0	101
	Mar. 27–30	1	15	12	3	80.0	101
	Apr. 26–27	1	9	8	1	88.9	104
	June 22–24	1	12	11	1	91.7	105
	July 22–24	1	12	9	3	75.0	106
	Aug. 24–26	2	23	18	5	78.3	109
	Sep. 23–24	2	11	9	2	81.8	114
	Oct. 18–20	3	12	9	3	75.0	116
	Nov. 22–24	3	12	12	0	100.0	119
	Dec. 20–22	4	18	17	1	94.4	119
1997	Jan. 25–27	4	18	14	4	77.8	120
	Feb. 22–24	4	40	18	22	45.0	124
	Mar. 24–27	1–5	34	21	13	61.8	146
	May 16–18	2	18	14	4	77.8	159
	July 2–7	1	23	19	4	82.6	163
	July 26–29	5	42	39	–	92.9	167

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