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Growth, reproduction and recruitment of the endangered brackish water snail *Iravadia* (*Fairbankia*) *sakaguchii* (Gastropoda : Iravadiidae)

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Abstract

The population structure and reproductive activity of the brackish water snail *Iravadia* (*Fairbankia*) *sakaguchii*, which lives under partially buried stones on intertidal mudflats, were investigated monthly in the Waka River Estuary, Wakayama, central Japan. Observations of the reproductive organs indicated the main reproductive season as being from June to July. Maturation size was estimated to be approximately 4.0 mm in shell length (SL) in females and 3.9 mm SL in males, there being no significant sexual dimorphism in adult body size. The occurrence of snails smaller than 2 mm SL indicated that recruitment occurred between August and October, all the recruits co-occurring with adults under stones. The recruits grew to a large size (>3 mm SL) and reached maturity in August of the second year (1 year old), longevity being estimated as at least 37–38 months. Throughout the study period of 28 months, the population mostly comprised individuals between 3 and 5 mm SL, with recruits being fewer than older snails. The population density decreased each year, this being attributable to a low level of recruitment.

Additional keywords: tidal flat.

Introduction

Iravadia (*Fairbankia*) *sakaguchii* (Kuroda & Habe, 1954) is a small (usually less than 6 mm in shell length (SL)) gastropod belonging to the family Iravadiidae (superfamily Rissooidea). The family occurs worldwide, although most species are found in the Indo-West Pacific region, their habitat usually being in estuaries or enclosed bays (Ponder 1984). Although some taxonomic studies of the family have been conducted (e.g. Ponder 1984, 1994; Beu and Maxwell 1990; Dockery 1993), there appear to have been no ecological studies on life history or population dynamics.

Iravadia sakaguchii is endemic to Japan and has been recorded at several locations, including Wakaura Bay, Wakayama (type locality), Ariake Sound, Sea of Suou, the Seto Inland Sea, Ise Bay and Mikawa Bay (Kimura 1987, 1989; Fukuda *et al*. 1990; Murohara 2000; Kimura *et al*. 2001). Because of its limited distribution, the species has been assessed as 'endangered' (Wada *et al*. 1996). Nevertheless, there have been only fragmentary studies on habitat conditions undertaken to date (Fukuda *et al.* 1990; Kimura and Kimura 1999; Kobayashi *et al*. 2003).

Iravadia sakaguchii is known to live under partially buried stones or hard materials on mudflats in brackish water (Fukuda *et al*. 1990; Hosaka and Fukuda 1996; Kobayashi *et al*. 2003). Ecological studies of benthos in this type of habitat have not received much attention because of the inherent difficulties in field observations. The aim of the present study was to reveal the life history and provide an understanding of the population ecology of *I. sakaguchii*.

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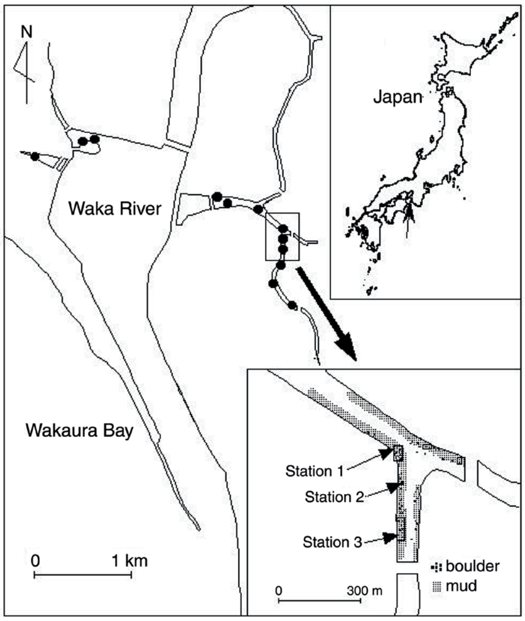

Fig. 1. Map showing locations of the study sites (stations 1–3) in the Waka River Estuary, central Japan. Solid circles indicate where *Iravadia sakaguchii* occurred.

Materials and methods

Seasonal changes in population structure

The present study was conducted on an intertidal mudflat in the Waka River Estuary, Wakayama, central Japan (34°10′N, 135°10′E; Fig. 1). Three stations (stations 1, 2 and 3) where *I. sakaguchii* occurred were selected along a tributary of the Waka River, with intertidal heights varying from –29 to 14 cm above mean sea level. Stations 1 and 3 were areas of stones on mud (station 1: 1.5×2 m^2 (number of stones: 32); station 3: 1.6×8 m^2 (number of stones: 181)), whereas station 2 consisted of an artificial block ($55 \times 44 \times 4.5$ cm in height) on mud. Water salinity near the stations, recorded over 24 h on 3 and 4 July 2000, varied from 1.6 to 29.4. The silt-clay content of the mud, recorded by grain size analysis according to the Wentworth classification, ranged from 16.3% to 73.4% (n = 15; Kobayashi *et al*. 2003).

Populations of *I. sakaguchii* at the three stations were monitored during periods of daytime low tide every 2 months from March 2000 to April 2001 and once a season (August, October, January, April and August) from August 2001 to August 2002. At each station, all stones were overturned and snails found underneath the stones or on the mud were picked up with tweezers. Each of the snails collected was set on a Petri dish (90 mm in diameter), aperture facing upwards, with 1-mm graph paper to measure the SL (from the apex to the anterior margin of the aperture) to the nearest 0.5 mm. After being measured, the snails were replaced carefully in their original positions under the stones.

Reproductive activities

To investigate the reproductive stages of the snails, 19–24 snails larger than 3 mm SL were collected near station 1 monthly from December 2001 to November 2002. These specimens were preserved in the laboratory at –5°C. The SL of each snail was measured (from the apex to the anterior margin of the aperture) to the nearest 0.1 mm with a vernier micrometre. Measured specimens were then soaked in 70% hydrochloric acid solution for approximately 30 min to dissolve the shell. Specimens were then dissected under a binocular microscope, sex being determined according to the presence of female or male reproductive organs. Snails were classified into five groups according to reproductive stage, which was determined by the relative sizes of the reproductive organs (female: albumen gland, capsule gland and bursa copulatrix; male: prostate, penis and testis) as shown in Tables 1 and 2.

Table 1. Reproductive stages classified according to the relative size of reproductive organs and gonad conditions in female *Iravadia sakaguchii*

Ag+Cg	Bursa copulatrix	Ovary	Stage
iv	iv	iv	f1
s	iv	iv	f2
s	iv	v	f3
l	iv	v	f4
l	v	v	f5

Ag, Albumen gland; Cg, capsule gland; iv, invisible; v, visible; s, small; l, large.

Table 2. Reproductive stages classified according to the relative size of reproductive organs and gonad condition in male *Iravadia sakaguchii*

Penis	Prostate	Testis	Stage
s	iv	iv	m1
m	iv	iv	m2
m	s	v	m3
l	s	v	m4
l	l	v	m5

iv, Invisible; v, visible; s, small; m, middle; l, large.

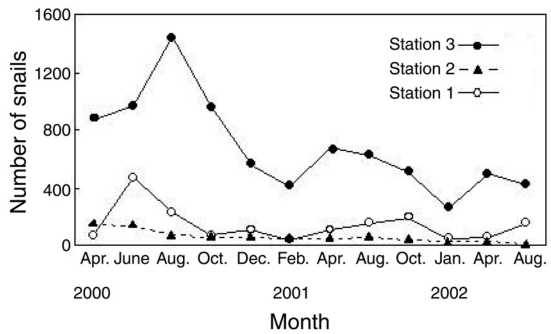

Fig. 2. Monthly changes in snail numbers at stations 1–3 from April 2000 to August 2002.

Results

Seasonal and yearly changes in population density

Numbers of *I. sakaguchii* showed seasonal fluctuations during the study period at stations 1 and 3, increasing between spring and summer and declining between autumn and winter (Fig. 2). However, at station 2, the number of snails did not exhibit any particular seasonal fluctuation.

The maximum number of snails was recorded in spring–summer in each of the study years at stations 1 and 3 (Fig. 2). The peak number of snails decreased each year, being highest in 2000 and lowest in 2002 with only half the number of snails found in 2002 compared with 2000. At station 2, the number of snails decreased continuously throughout the study period, dropping to only three snails by August 2002.

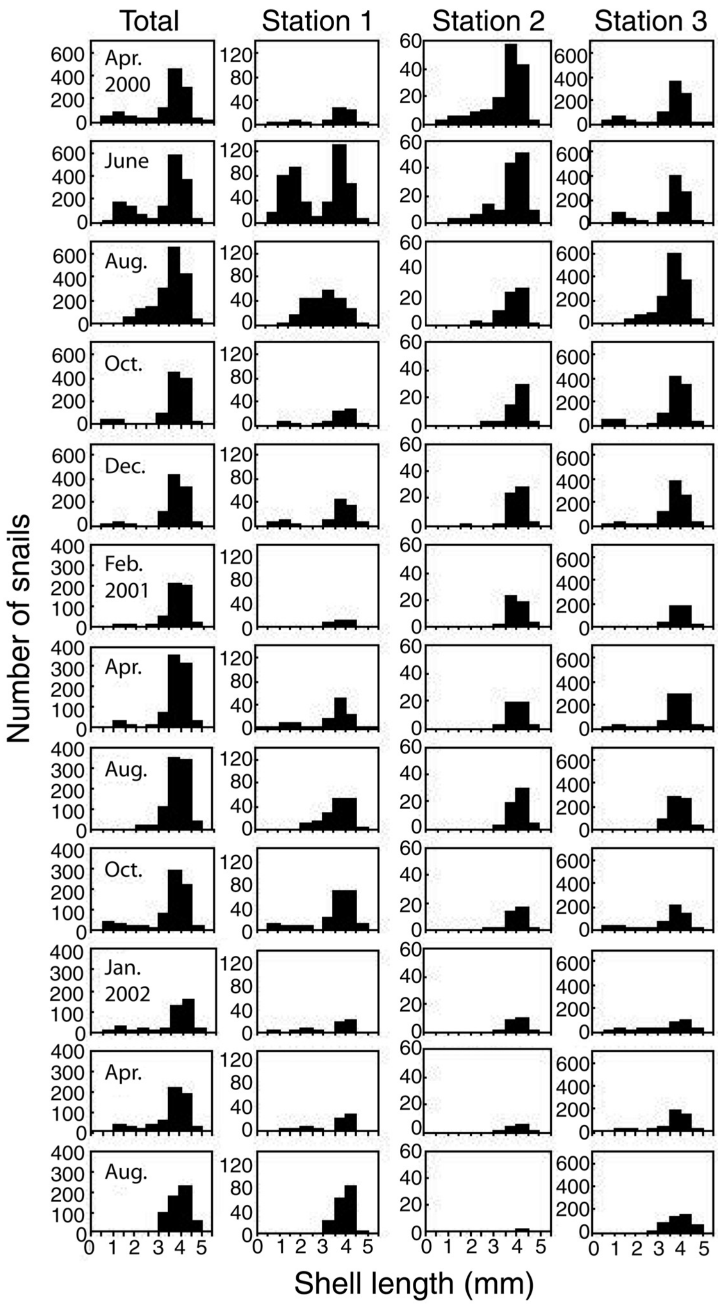

Fig. 3. Frequency distributions of shell lengths of *I. sakaguchii* at stations 1–3 from April 2000 to August 2002.

Seasonal changes in size structure

The populations at the three stations consisted mostly of individuals of 3–5 mm SL during the study period (Fig. 3). The occurrence of snails smaller than 2 mm SL at stations 1 and

3 between August and October in both 2000 and 2001 indicated that recruitment occurred during these periods. Successive changes in length–frequency histograms (Fig. 3) showed that recruits scarcely grew until the following April, but then grew to a large size by the following August (1 year old). After the snails were 1 year old, growth could not be determined from histograms.

Survivorship is estimated from station 2 data as follows. Because station 2 was isolated by approximately 50 m from other populations owing to a lack of suitable habitat, migration of snails into the station was unlikely, considering the data on individual movement obtained by Kobayashi *et al*. (2003), in which the maximum movement observed for 228 marked snails during 4 months was 1.6 m at most. Furthermore, recruitment scarcely occurred at station 2 in 2000 and 2001 (Fig. 3), with large-sized snails found at the end of the study period (August 2002) appearing to have survived throughout the study period (28 months). If this was the case, the large-sized snails in April 2000 at station 2 can be regarded as having been recruited in 1999 and must be at least 9–10 months old. Consequently, longevity can be estimated as at least 37–38 months (=3.1–3.2 years).

The number of small-sized individuals (<3 mm SL, <1 year old) varied among stations as well as among years (Fig. 3). At station 3, small-sized snails were recorded in all three years (1999, 2000 and 2001), although their abundance was low relative to that of large-sized snails (3–5 mm SL). At station 2, no small-sized snails were observed after February 2001. At station 1, smaller snails were collected in all three years, but their abundance in June 2000 was greater than in other periods, indicating that recruitment at station 1 in 1999 was greater than in the other years and greater than that at stations 2 and 3 over the 3-year period.

Distribution of recruits

The small-sized snails appearing in October (recruits) were found under 17 of 181 stones (9.4%) in 2000 and under 15 of 181 stones (8.3%) in 2001. Those stones were inhabited by both recruits and adults (larger than 4 mm SL). The number of recruits and adults under the same stone were significantly positively correlated in 2001 ($r^2 = 0.69$, $P < 0.05$, $n = 15$), whereas no significant correlation was found in 2000 ($r^2 = 0.02$, $P > 0.05$, $n = 17$).

Reproductive activities

All snails dissected had either female or male organs and the sex ratio was significantly female biased (92 males *v.* 162 females; Binomial test: $P < 0.05$). The size frequency distribution of each sex in snails larger than 3 mm SL indicated that no significant difference in size existed between males and females throughout the year (Mann–Whitney *U*-test: $P > 0.05$; Fig. 4).

Developmental conditions of the reproductive organs showed seasonal changes in both males and females (Fig. 5), the range of body sizes at different reproductive stages overlapping widely (Table 3). From the smallest snail sizes at stage 5, maturation was determined as having been attained at 4.0 mm SL in females and 3.9 mm SL in males.

Female snails at stage 5 occurred in January and February and April–October, with a peak in July. Male snails at stage 5 occurred in May–December, with a peak in June.

Discussion

Monthly changes in the development of the reproductive organs in *I. sakaguchii* showed that the most developed stage occurred most frequently in June (males) and July (females), indicating that those summer months were the main reproductive season. The reproductive

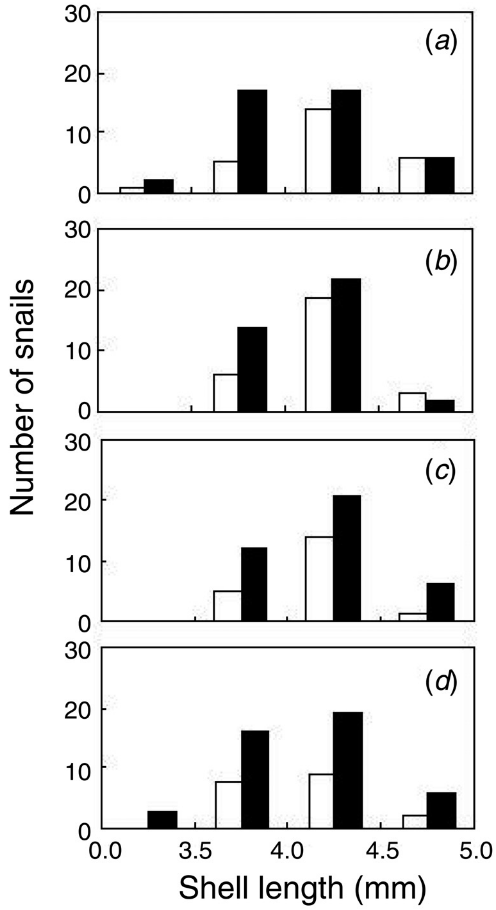

Fig. 4. Seasonal changes in frequency distributions of shell lengths of *I. sakaguchii* females (solid) and males (open). (*a*) December to February; (*b*) March to May; (*c*) June to August; (*d*) September to November.

season of other temperate region species of rissooideans (approximately 5–15 mm SL) living in brackish water varies considerably as follows: spring for *Assiminea japonica* Martens, 1877 (Kurata and Kikuchi 2000), summer for *Hydrobia ventrosa* (Montagu, 1803) (Barnes 1990) and *Angustassiminea castanea* (Westerlund, 1883) (Kurata and Kikuchi 2000), and late winter–spring and summer–autumn for *Hydrobia ulvae* (Pennant, 1777) (Anderson 1971; Fish and Fish 1974; Bachelet and Yacine-Kassab 1987; Barnes 1990; Haubois *et al*. 2002).

Simultaneous hermaphroditism and protandry are known in some gastropods (Sumikawa 1994), but there is no indication of this in *I. sakaguchii*.

The occurrence of snails smaller than 2 mm SL indicated that recruitment occurred from August to October (Fig. 3). The abundance of recruits recorded in October was much lower than that of older snails at all stations in both 2000 and 2001, suggesting a low level of recruitment in both years. There were fewer small-sized snails in June 2000 than large-sized snails, indicating a low level of recruitment relative to adult abundance in 1999. This low

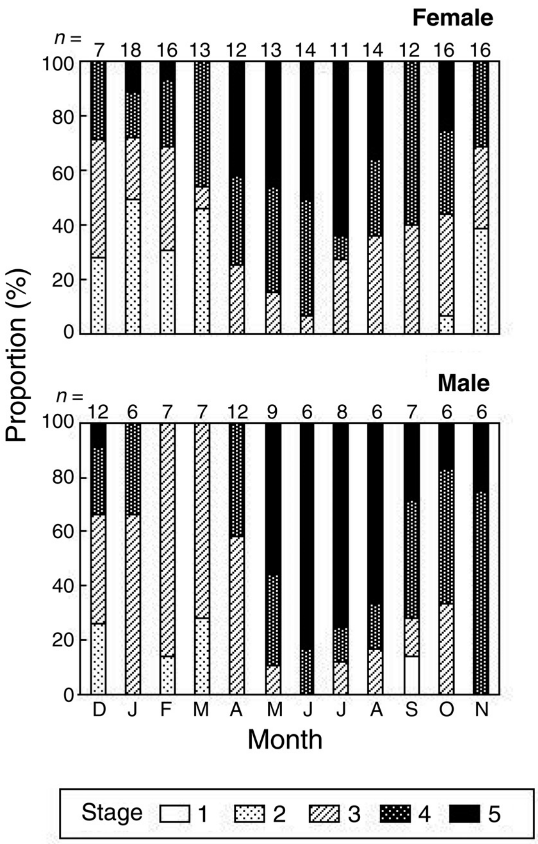

Fig. 5. Monthly changes in reproductive stages of females and males from December 2001 to November 2002. Reproductive stages (1–5) classified according to reproductive organ condition.

Table 3. Range of shell lengths for each reproductive stage in male and female *Iravadia sakaguchii*

Stage	Shell length (mm)	
	Male	Female
1	3.0	–
2	3.8–4.0	3.5–4.4
3	3.5–4.4	3.2–4.8
4	3.5–4.8	3.6–4.9
5	3.9–4.5	4.0–4.7

level of recruitment may be caused by low levels of reproductive activity and/or high mortality of larvae and juveniles. Life history studies of other rissooid species have shown that the abundance of recruits is generally higher than that of large-sized snails, although the number of recruits fluctuated with time and place (e.g. *H. ulvae* (Chatfield 1972; Anderson 1971; Fish and Fish 1974; Bachelet and Yacine-Kassab 1987; Barnes 1990; Drake and Arias 1995; Sola 1996; Cardoso *et al*. 2002), *H. ventrosa* (Siegismund 1982;

Drake and Arias 1995), *Hydrobia neglecta* Muss, 1963 (Siegismund 1982; Drake and Arias 1995), *A. japonica* (Kurata and Kikuchi 1999; Tashiro *et al*. 2001) and *Assiminea grayana* Fleming, 1828 (Fortuin *et al*. 1981)). In the case of *A. castanea*, recruits were much less abundant than large-sized snails over a 2-year period (Kurata and Kikuchi 1999), as observed for *I. sakaguchii.*

Recruitment occurred at stations 1 and 3 in both 2000 and 2001, but did not occur at station 2 in either year. No recruitment at station 2 may be due to the artificial substrate at this station, but comparisons of recruitment between artificial and natural substrate at the same location are needed to clarify this.

The co-occurrence of adults and recruits in the same living space and the positive relationship between adults and recruit abundance suggest that recruitment may be related to the presence of adults. *Iravadia sakaguchii* is assumed to have a pelagic larval veliger stage based on the figure of the protoconch in Fukuda *et al*. (1990, fig. 2). If this is the case, our data suggest that veligers may settle preferentially in an adult habitat.

Snails grow to a large size (>3 mm SL) by August of the second year (1 year old). Because the shell length at maturity is approximately the same in both sexes (4 mm in females, 3.9 mm in males), it is likely that snails reach maturity during their second summer. Barnes (1990) reported that *H. ulvae* matured after approximately 0.8 of a year of benthic life. However, other estimates gave maturation in this species at almost 2 years (Anderson 1971) or at approximately 1 year (Chatfield 1972; Fish and Fish 1974). Kurata and Kikuchi (2000) estimated that *A. japonica* matured at 1.4 years and that *A. castanea* matured at 0.8 of a year. Thus, the age at maturity of *I. sakauchii* is somewhat similar to those of other rissooid species.

The longevity of *I. sakaguchii* was estimated to be approximately 3.1–3.2 years, whereas that of *H. ulvae* has been estimated as approximately 2.0–2.5 years (Fish and Fish 1974) or approximately 1–2 years (Sola 1996; Cardoso *et al*. 2002). Longevity has been estimated as approximately 1.0–1.5 years in *H. ventrosa* and *H. neglecta* (Drake and Arias 1995), 2.6–3.0 years in *A. japonica* and 4.6 years in *A. castanea* (Kurata and Kikuchi 1999) and 1.5–2.0 years in *Assiminea grayana* (Fortuin *et al*. 1981). Therefore, *I. sakaguchii* may have greater longevity than most other species of Hydrobiidae and Assimineidae.

The number of *I. sakaguchii* individuals found at the sampling sites increased in warm seasons and decreased in cold seasons. The increase in the number of snails from winter to spring may be due to recruitment during this period or differences in sampling success between winter and spring. However, data on size structure make the former possibility unlikely, whereas observations on activity patterns in the laboratory, which showed that the proportion of active snails, whether floating or crawling, was higher in summer than in winter (Kobayashi *et al*. 2003), support the latter. Low activity in cold seasons would lead to a low discovery rate.

The number of snails in warm seasons decreased in subsequent years during the study period, this being attributable to low levels of recruitment in 2000 and 2001. If *I. sakaguchii* is characterised by low levels of recruitment, low mortality or extended longevity is required to maintain the population. In fact, the species has greater longevity than most other related species, although mortality rates were not examined in the present study. Nevertheless, the population density decreased during the duration of the study. Thus, sporadic successful recruitment, which is known in other long-lived benthos (Bouman and Lewis 1977; Peason and Munro 1991; Nakaoka 1993), is required to maintain this species population. However, another possible reason for the decrease in population density is mortality caused by repeated sampling disturbance and this requires further testing in future studies.

Our observations on the life history traits of *I. sakaguchii* have some relevance to the conservation of this endangered species. A low level of recruitment, positive co-occurrence of recruits and adults and greater longevity suggest that the long-term conservation of adults is critically important for maintaining populations. Consequently, even temporal modification or removal of adult habitat, which is often sparse and widely separated, will probably lead to the rapid decline or local extinction of populations. Thus, protection of the adult habitat against human disturbance is required to assure the long-term survival of this species.

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