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Round-trip Catadromous Migration in a Japanese Amphipod, *Sternomoera rhyaca* (Gammaridea: Eusiridae)

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We conducted a field study of the life cycle of the eusirid gammaridean amphipod *Sternomoera rhyaca* Kuribayashi, Mawatari, and Ishimaru, 1996 in a stream at Gokibiru, Hokkaido, Japan over the course of two non-consecutive years. This species is biennial; it spends most of its life in freshwater, but undertakes a short catadromous migration to the sea for reproduction. Reproduction occurs from March-June. Mature adults drift downstream to the sea singly and in precopulating pairs. Copulation and oviposition in the marsupium occur in mixed water at the stream mouth. Males die after copulation; ovigerous females return upstream by walking or swimming, where their eggs develop and hatch, after which the females also die. Juveniles remain in the stream, growing until they reach sexual maturity. Laboratory experiments showed that survivorship of all stages was lowest in seawater and highest in freshwater, though juveniles survived equally well in mixed water (50% seawater) and freshwater. Eggs developed to hatching only in freshwater; hatchlings in seawater and mixed water died within one and 21 days, respectively. Thus, *S. rhyaca* is well adapted to freshwater. Indeed, the only stages that required elevated salinity were copulation and subsequent oviposition, and we speculate that freshwater inhibits the female pre-reproductive molt. Because the life cycle of *S. rhyaca* has the most ontogenetically and temporally restricted saltwater phase known in any catadromous animal, its origin and maintenance are of evolutionary interest. We discuss two alternative hypotheses for the origin of the migratory life cycle, and discuss its maintenance in terms of fitness costs and benefits.

Key words: adaptation, amphipod, catadromy, diadromy, fitness, migration, osmoregulation, reproduction, salinity, survivorship

INTRODUCTION

The term diadromy (Myers, 1949) means a migration of an aquatic animal between freshwater and the sea. According to McDowall (1997a), a migration must satisfy a number of criteria to be considered a true diadromous migration. It must involve regular, physiologically mediated movements between the two biomes; occur at predictable times and at specific life-cycle stages of a species; include most of a species' populations; and involve two reciprocal migrations, one from freshwater to the sea and another in the opposite direction. Diadromy incorporates three subcategories: anadromy, catadromy, and amphidromy (Myers, 1949; McDowall, 1992, 1997a,b). In anadromy, adult animals migrate to freshwater to reproduce, but the main biome for feeding and growth is the sea. In catadromy, the converse occurs; adult animals migrate to the sea to reproduce, but the main biome for feeding and growth is freshwater. In amphidromy, there is a migration to the sea of larvae produced in freshwater, followed by a return of post-larvae or juveniles to freshwater; thus, both reproduction and the bulk of feeding and growth occur in freshwater.

Diadromous life cycles have originated independently, and sometimes repeatedly, within several taxonomic groups of animals, and how they originate and are maintained are fundamental evolutionary questions (Gross, 1987; McDowall, 1997a; Hendry *et al.,* 2004). Gross *et al.* (1988) argued that the diadromous migrations of fishes, at least, have evolved in relation to differences in primary productivity between freshwater bodies and the seas to which they connect. In fishes, diadromy is widespread across taxa; McDowall (1999) indicated 241 diadromous species across 33 families. Diadromous migrations also occur in some invertebrate groups, including mollusks (*e.g.*, Schneider and Lyons, 1993) and crustaceans, though less commonly in

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these groups than in fishes.

In this paper, we report a reproductive migration in a eusirid gammaridean amphipod, *Sternomoera rhyaca* Kuribayashi, Mawatari, and Ishimaru, 1996. Three of the four known species of *Sternomoera* are restricted to freshwater, inhabiting springs and brooks throughout their life cycle (Labay, 1997; Kuribayashi *et al.,* 1996). A taxonomic investigation of the fourth species, *S. rhyaca*, which is endemic to Japan, showed that it occurs only in coastal streams flowing directly into the sea, rather than inland (Kuribayashi *et al.,* 1996). During a study of the life cycle, we realized that adults migrated between upstream freshwater sites and the sea. Subsequently, we undertook a field investigation of this migration, and conducted survivorship experiments in the laboratory to investigate the salinity tolerance of several ontogenetic stages.

We show herein that *S. rhyaca* has a biennial, migratory life cycle in which mature adults move downstream to the sea for copulation and oviposition in the marsupium, after which postcopulatory ovigerous females return upstream, where their eggs hatch and juveniles grow. No other catadromous animal exhibits such a narrow restriction of the saltwater phase of its life cycle, nor a complete and immediate round-trip by reproductive females. We also show through survivorship experiments that *S. rhyaca* is physiologically highly freshwater-adapted. Finally, we discuss the possible origins of this life cycle, and its maintenance in terms of fitness costs and benefits.

MATERIALS AND METHODS

Reproduction and developmental classes

Like many other gammaridean amphipods (Hynes, 1955; Hartnoll and Smith, 1978), *S. rhyaca* engages in precopulation (amplexis), a behavior in which an adult male clasps the thoracic region of a physiologically attractive preadult female with his gnathopods and holds her beneath him until she molts. Soon after the female molts, the male deposits sperm on her ventral surface, and the sperm are transferred into the marsupium, which is a brood chamber composed of oostegites, each a specialized extension on

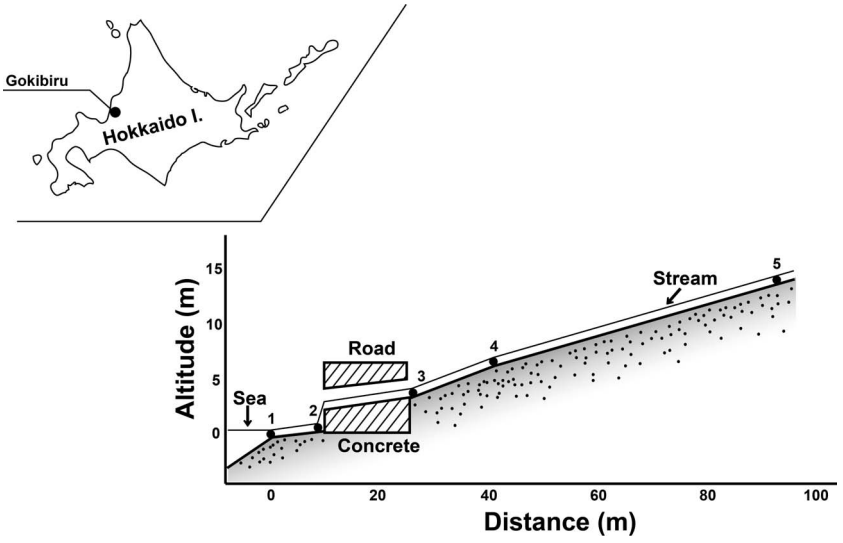


Fig. 1. Above) Location of the stream at Gokibiru, near Atsuta, Hokkaido Island, Japan; **Below)** sectional diagram of the stream, showing the positions of sampling sites (1–5).

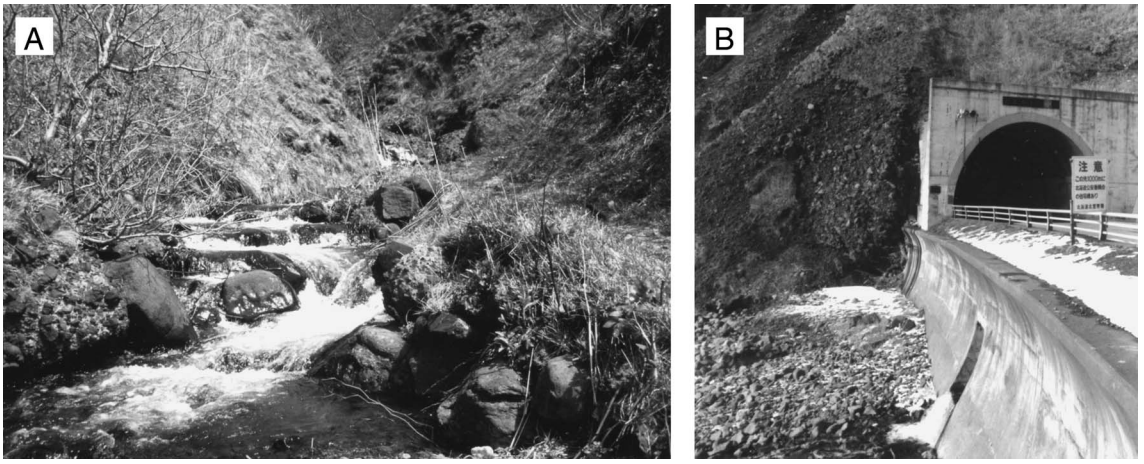


Fig. 2. A) The stream at Gokibiru in the vicinity of Site 5; **B)** emergence of stream (bottom, center) onto cobble beach from culvert through road embankment. Both photographs taken in spring.

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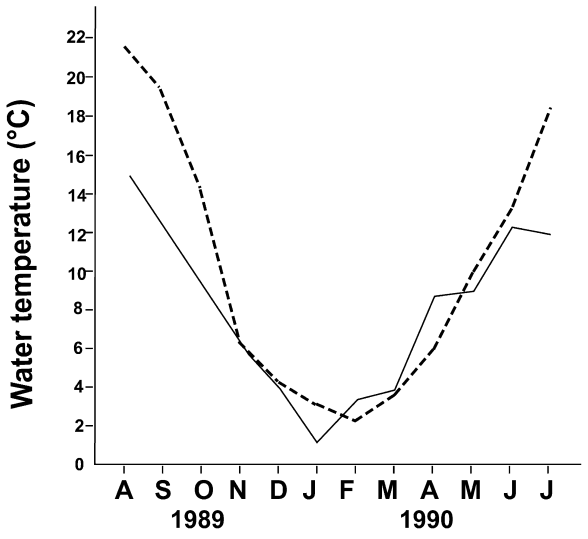


Fig. 3. Water temperature of the stream at Gokibiru (solid line), measured once a month from August 1989 to July 1990 at Site A at around midday, and sea-surface temperature (dashed line) plotted from monthly averages in 1989–1990 from data collected at Atsuta, near Gokibiru (HAPC, 1989, 1990).

the coxae from the second gnathopod to the fifth pereopod. After copulation, the female breaks away from the male and lays her eggs into the marsupium before her cuticle hardens; fertilization occurs in the maruspium. The ovigerous female retains the eggs in her marsupium until they complete development and hatchlings are released.

To investigate the life cycle of *S. rhyaca*, we distinguished five developmental classes among animals collected: (1) mature males identified by having calceoli (a secondary sexual character in both sexes) on antennae 1–2, and genital papillae; (2) immature males, with genital papillae but lacking calceoli; (3) mature females, with calceoli and fully developed oostegites or eggs; (4) immature females, with poorly developed oostegites and lacking calceoli, and

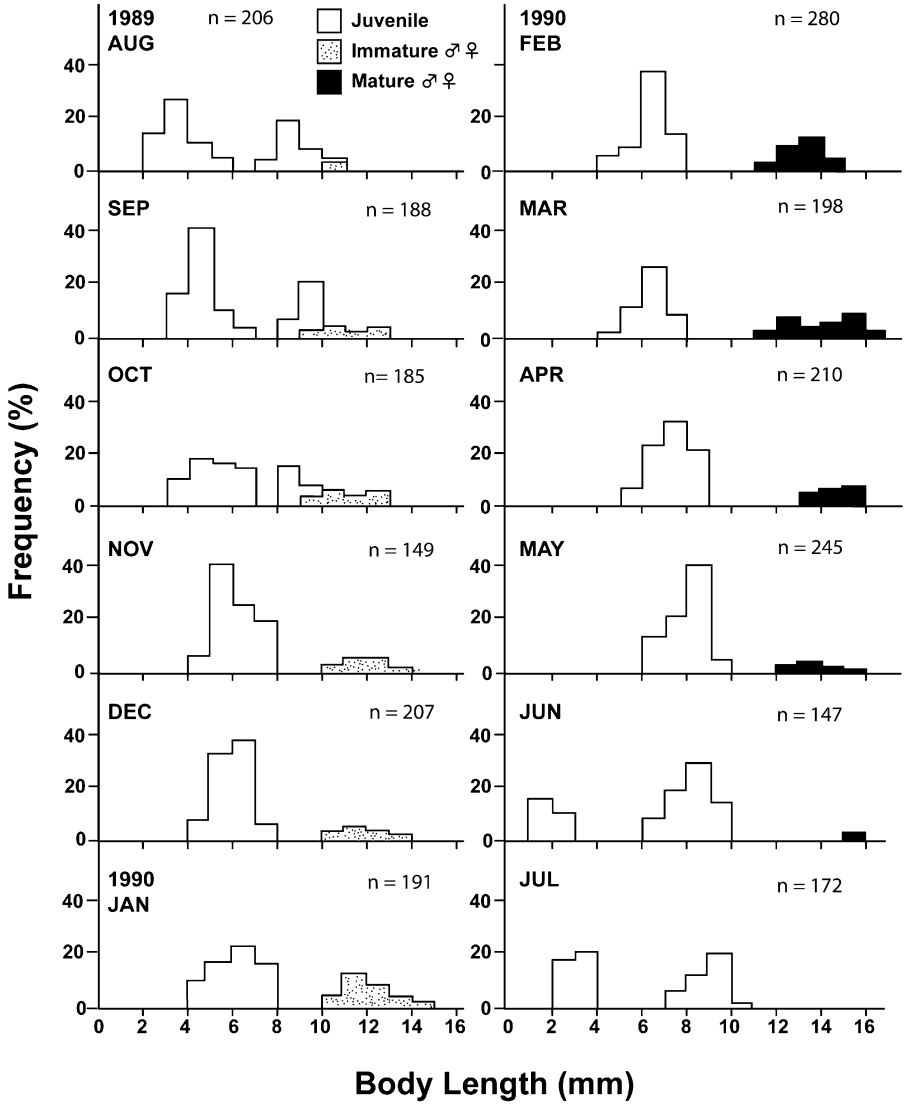


Fig. 4. Length-frequency distributions of *Sternomoera rhyaca* from samples taken once a month from August 1989 to July 1990 at around midday at Site A in the stream at Gokibiru. Both sexes are pooled for the classes of immature and mature individuals. This figure is based on the same data set as Fig. 5.

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(5) juveniles of both sexes, lacking genital papillae, oostegites, and calceoli. Mature females could further be identified as breeding females, with long setae on the margin of oostegites, and non-breeding females, lacking such setae.

Field studies of life cycle and migration

We studied *S. rhyaca* in a small coastal stream at Gokibiru, Atsuta (43°24'N, 141°26'E), on the Sea of Japan coast of Hokkaido (Fig. 1). Flowing down between the steep slopes of a narrow valley, the stream (Fig. 2A) varies in width from around 4 m in less-rapid areas to 1 m in constricted rapids; maximum depth is generally around 0.4 m in pools below small falls, though this may increase during floods. The banks are lined with vegetation and large boulders, and the bottom consists of rocks and gravel. At the seaward terminus, parallel to the shore, is a wide road embankment (illustrated schematically in Fig. 1), with concrete walls on the landward and seaward sides. The stream flows under the road through the embankment by a long, concrete-lined culvert that is rectangular in cross section and about 1.5 m high by 2 m wide. The stream exits this culvert (Fig. 2B) above a cobbled beach and flows over the beach to the sea. The cobble beach remains mostly exposed; maximum tidal range at Gokibiru is <0.5 m, and the maximum high tide level above MLLW is around 0.4 m. However, during storms, waves can reach the seaward wall of the embankment, completely submerging the beach in seawater.

An initial sampling site (Site A, located near Site 5 shown in Fig. 1) to study the overall life history was located 100 m upstream from the mouth. Animals were collected and water temperature recorded at this site at around midday once a month from August 1989 to July 1990. Sea-surface temperature at the mouth of the stream was not measured, as readings in the zone of mixing were unreliable. For a comparison of stream and sea-surface temperatures, average monthly sea-surface temperatures measured at Atsuta (near Gokibiru) published by HAPC (1989, 1990) were used.

At each sampling, mud and dead leaves on the bottom of the stream were stirred up with the hands, and floating animals detached from the detritus were collected by scooping with a hand net (0.5-mm mesh; mouth size 30×20 cm). Animals thus collected were regarded as representing the age structure of the population, although the sampling was by no means quantitative. Animals were fixed in 5% neutralized formalin in freshwater. In the laboratory, within a few weeks after fixation, body lengths were measured to the nearest 0.1 mm with the aid of an ocular micrometer on a dissecting microscope, and specimens were sorted into the five developmental classes defined above. The sorted animals were washed with freshwater and then preserved in 70% ethanol.

To study the migration of *S. rhyaca*, five sampling sites (Fig. 1) were established along the stream, and sampling was conducted once a month at each site from January to December 1994. Site 1 was located at the mouth of the stream, where salinity was about half that of undiluted seawater in the vicinity; Site 2, below a small waterfall from the concrete culvert running under the road; Site 3, just above the culvert; Sites 4–5, in steep areas upstream. In this census, quantitative sampling was employed to enable direct comparisons among the sites. At each sampling, a quadrate (30×30 cm) was set on the bottom. Mud and dead leaves within the quadrate were stirred up with the hands, and floating animals and detritus were collected by hand net (0.5-mm mesh; mouth size 30×20 cm) and fixed in 70% ethanol. The number of precopulating pairs in the samples was counted immediately after sampling, because pairs were easily separated by fixation. In the laboratory, numbers of individuals belonging to respective developmental stages were counted. Body size was not measured.

Laboratory study of salinity tolerance

To examine the effect of salinity on the survivorship of various developmental stages of *S. rhyaca* and on oviposition, four series of experiments were conducted in a laboratory at Hokkaido University using animals collected at Gokibiru in the manner described above. Survival was examined for three salinity conditions: (1) freshwater; (2) mixed water, a 1:1 mixture of freshwater and seawater (salinity ~16 ‰); and (3) seawater (salinity 31–32 ‰). Water used for the experiments was transported weekly from the study area: freshwater from the stream and undiluted seawater from the shore a distance from the stream. Survivorship experiments were continued for 60 days.

During the experiments, amphipods were maintained in plastic containers (for sizes, see below) in an incubator, with the water temperature of each experiment set according to the ambient water temperature at the sampling site in the stream on the date the animals were collected. Animals were fed to repletion on decaying leaves and commercial artificial fish food (Tetra Conditioning Food®). The food and water in the containers were replaced every other day.

For survival data, Kaplan-Meier analyses were performed, with statistical comparisons by the Wilcoxon test and following Holm's method for multiple comparisons implemented in JMP IN 5.1.2 software (SAS Institute Inc., Cary, North Carolina, USA). The four series of rearing experiments conducted were as follows.

Juveniles, males, and females. Juveniles (7–9 mm length) and mature males and females were collected at Site 4 on 25 February 1994, and the survivorship experiment commenced the same day. For each age/sex-class replicate, five animals were maintained in a 100-ml container (8 cm in diameter and 4 cm deep) at 6±1°C with a photoperiod of 12L:12D. Five replicate containers were prepared for each of the three water conditions for each age/sex class. The containers were inspected daily, and any dead animals were removed after being recorded.

Precopulating pairs. Precopulating pairs were collected on 12 April 1994, and the survivorship experiment commenced the same

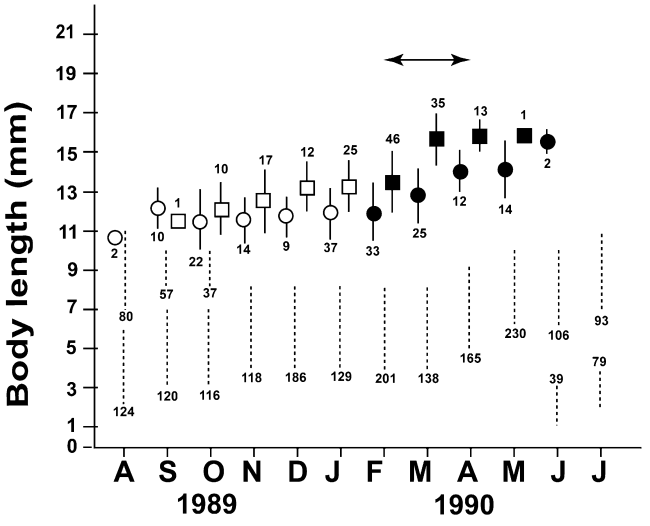


Fig. 5. Body length of mature and immature *Sternomoera rhyaca* from samples taken once a month from August 1989 to July 1990 at around midday at Site A. This figure is based on the same data set as Fig. 4. Circles and squares indicate mean values (■, mature males; ●, mature females; □, immature males; ○, immature females); bars attached to the symbols indicate ±SDs. For juveniles, only the ranges of body lengths are shown by dashed bars; two dashed bars for June-October indicate two size classes of juveniles. Double-headed arrow indicates the period when precopulating pairs were observed. Numbers above or below bars indicate sample sizes.

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day. Each pair was maintained separately in one of the three water conditions in a 50-ml container (6 cm in diameter and 3 cm deep) maintained at 6±1°C and 12L:12D. Sample size was 37 precopulating pairs per treatment. Duration of survival of the female and male, occurrence of oviposition, and duration of precopulation were recorded for every pair.

Ovigerous females. Seven or eight ovigerous females, all within 7 days after ovipositing in the laboratory, were maintained in each replicate 300-ml container (10 cm in diameter and 4.5 cm deep) at 10±1°C and 13L:11D. Five replicate containers were tested for each water condition, with total n=37 per treatment. Survival of females, and of broods to the hatching and juvenile stages, were recorded. This experiment commenced on 26 April 1994.

Hatchlings. Twenty hatched juveniles were maintained in each replicate 50-ml container (6 cm in diameter and 3 cm deep) at 10±1°C and 13L:11D. Ten replicates were prepared for each water condition, and the survival of hatchlings was recorded. This experiment commenced on 31 May 1994.

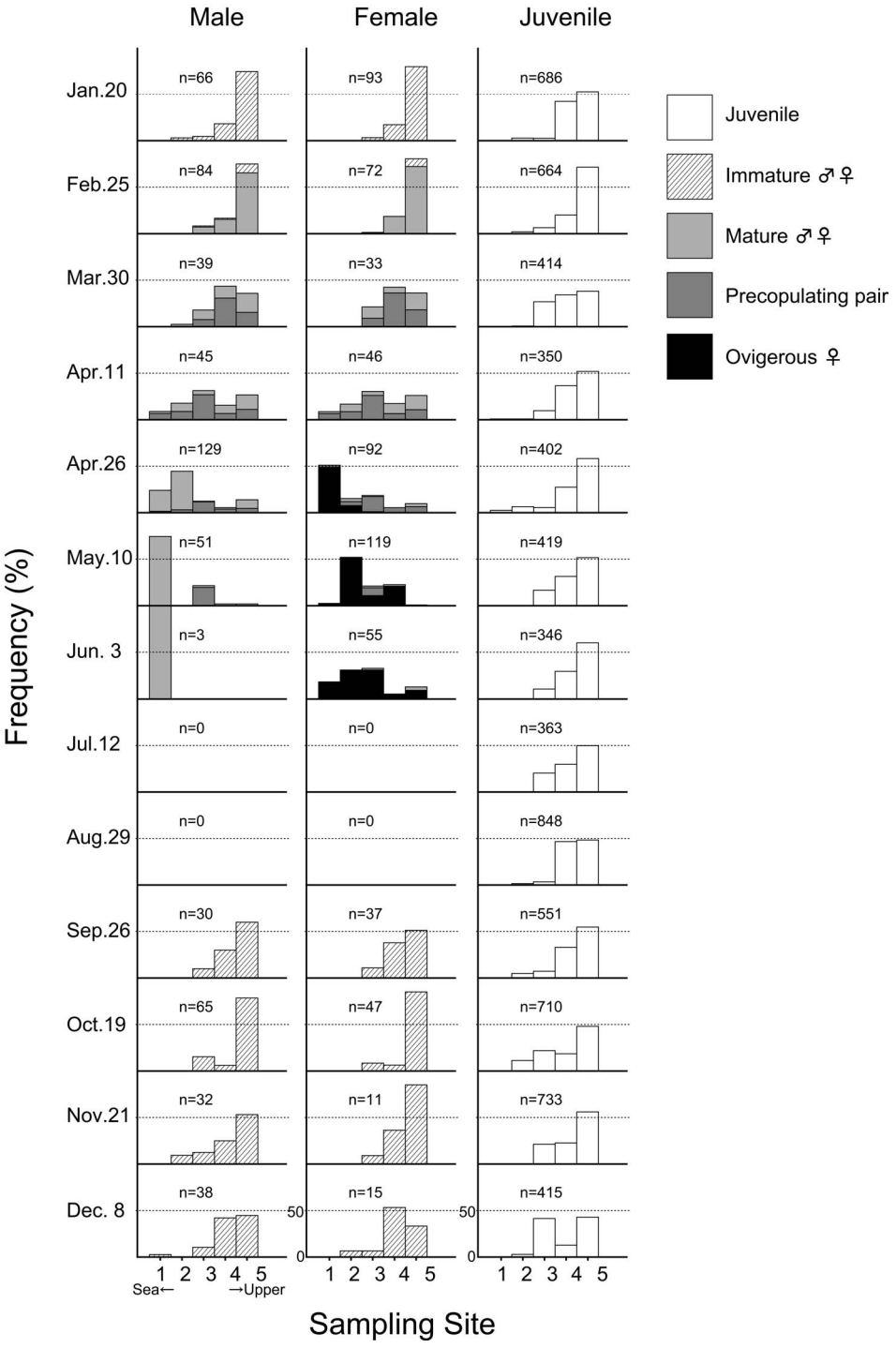


Fig. 6. Frequency distributions of five classes of *Sternomoera rhyaca* from samples taken from January to December 1994 at Sites 1–5 in the stream at Gokibiru.

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RESULTS

Life history

Figs. 3–5 show the results of the field study conducted at upstream Site A in 1989-90. Stream water temperature ranged from 15 °C in August to 1 °C in January (Fig. 3). Average monthly sea-surface temperature (HAPC, 1989, 1990) showed greater annual variation, ranging from 21.44 °C in August to 2.15 °C in February. The differences between stream and sea-surface temperatures were most pronounced from July through October. From November to June, stream and sea-surface temperatures were similar, differing by 0–3 °C. A stream-temperature curve showing monthly averages rather than individual measurements might show even less difference from sea-surface temperatures during this period.

The length-frequency histograms in Fig. 4 show contributions to the population of annual cohorts, as well as the maturation of these cohorts over the course of a year, and indicate that the life cycle is biennial. Three cohorts were evident in June: a few mature females recruited two years previously, a primary cohort of larger juveniles recruited the previous year, and the first monthly appearance of a cohort of small, post-hatching juveniles recruited in 1990. By July, mature adults had disappeared, leaving two cohorts of juveniles. By August, some of the older cohort of juveniles became identifiable as immature males or females by secondary sexual characters. By November, all members of this cohort were identifiable to sex. Sexually mature males and females appeared in February, and mature individuals were evident in the population until June. Precopulating pairs (not shown) were observed from February to April; paired females were always virgin, that is, before their preadult molt. Ovigerous females (not shown) were collected from April to June, and newborn juveniles appeared in the stream after early June.

Fig. 5 contains some of the same information as Fig. 4, but additionally shows the larger mean size of males that is evident almost as soon as the sexes are discernable, and that becomes increasingly pronounced with age. The range in body length of mature males was 11.5–17.0 mm (average 15.02±1.12 mm SD, n=95); of mature females, 11.2–16.0 mm (13.61±1.07 mm, n=86); of immature males, 10.5–14.8 mm (12.53±0.95 mm, n=65); of immature females, 9.8–14.0 mm (11.59±0.86 mm, n=94); of juveniles, 1.5–11.0 mm (6.45±1.91 mm, n=2,018). The range in clutch size was 164–261 eggs per clutch (196.46±33.33 eggs, n=13). The best-fit relationship between clutch size and female body length is expressed by the following simple linear regression equation: clutch size=16.37(body length in mm) – 38.81, with r=0.47.

Fig. 5 also shows that males markedly outnumbered females in samples taken in February and March; however this difference was not statistically significant (Chi square, $p>0.05$). In May, females significantly outnumbered males (Chi square, $p<0.001$), and the only two mature animals collected in June were females. This apparent change in sex ratio is understandable in the context of the reproductive migration, in which males die at the stream outlet after mating, but ovigerous females return upstream (see below).

Down- and up-stream movements

Fig. 6 shows seasonal changes in the frequency distribution of developmental stages of *S. rhyaca* at the five sampling sites. Throughout the year, juveniles were almost entirely restricted to freshwater at Sites 3–5, were rarely collected at Site 1 at the mouth of the stream, and were generally most abundant in the upper stream (Sites 4 and 5). A similar pattern obtained for immature individuals of both sexes present in January and from September to December.

In contrast, the distribution of mature individuals, including precopulating pairs and ovigerous females, showed a restricted seasonal pattern. Mature individuals of both sexes were collected from February to June. They first appeared at Sites 3–5 in February, began to form precopulating pairs in March, and by mid-April expanded their range from the upper stream to the mouth of the stream at the seashore. In May, most mature males were found at Site 1, and in June the few mature males collected were all at Site 1.

The distribution of mature females differed somewhat from that of mature males. Ovigerous females (*i.e.*, with eggs in the marsupium) were first observed in late April, when they occurred predominantly at the stream mouth. In May, the peak frequency shifted upstream to Site 2, and in June was split between Sites 2 and 3, with ovigerous females reaching Site 5. Swarms of ovigerous females were occasionally observed creeping up the wall to the entrance of the culvert under the road (Fig. 7; see also movie as supplementary information at http://dx.doi.org/10.2108/zsj.23.763), and through the culvert along a low, sloping buttress flanking the stream, in a long line up to five or six

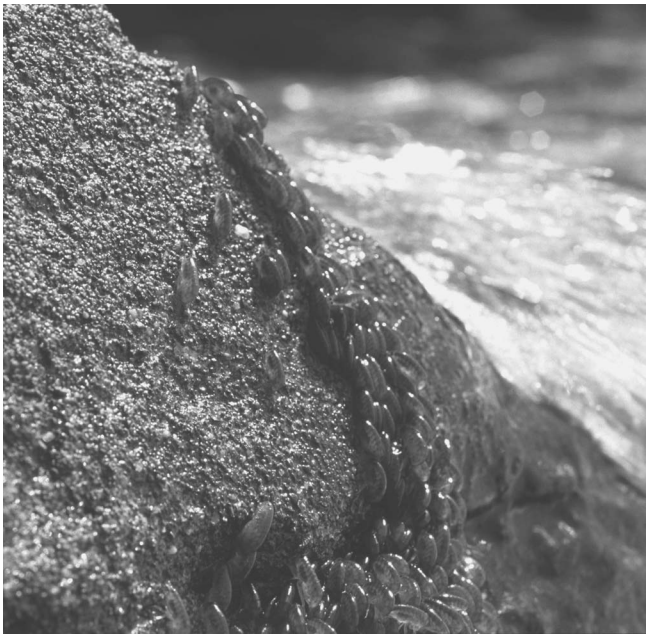


Fig. 7. A swarm of postcopulatory ovigerous females entering the seaward opening of the concrete culvert running under the road embankment at Gokibiru. A line of amphipods up to 5–6 animals wide continued through the whole length of the culvert along a low, curved buttress flanking the stream. The rushing water seen at upper right is fresh streamwater leaving the culvert.

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females wide. Once they had emerged from the culvert, the amphipods were observed creeping upstream along the bottom of the stream; they also swam upstream in less-rapid areas. Furthermore, the amphipods were observed to circumvent rapids by creeping on rocks along the fringes of the stream, similarly to their movement through the culvert, though as small groups and scattered individuals rather than in the dense lines observed in the culvert. This systematic and extensive upward movement was not observed for non-ovigerous females, mature males, or juveniles, although a few immatures were observed creeping upstream along the bottom after floods washed them downstream in late summer and autumn. In July and August, the only amphipods collected were juveniles, found mostly at Sites 3–5.

Effects of three salinity conditions on survivorship and reproduction

Survivorship of hatchlings, juveniles, males, and females. Fig. 8 shows survivorship curves for several developmental stages under each water condition. At all stages, survivorship was significantly higher in freshwater and mixed water than in seawater, and except for juveniles, significantly higher in freshwater than in mixed water (Kaplan-Meier analysis, $p<0.05$). In seawater, males, females, and juveniles all died within 57, 48, and 48 days, respectively. Hatchlings were particularly vulnerable to seawater, as all individuals died within one day. On the 60th day, survivorships in mixed water of males, females, juveniles, and hatchlings were 44%, 8%, 80%, and 0%, respectively; in

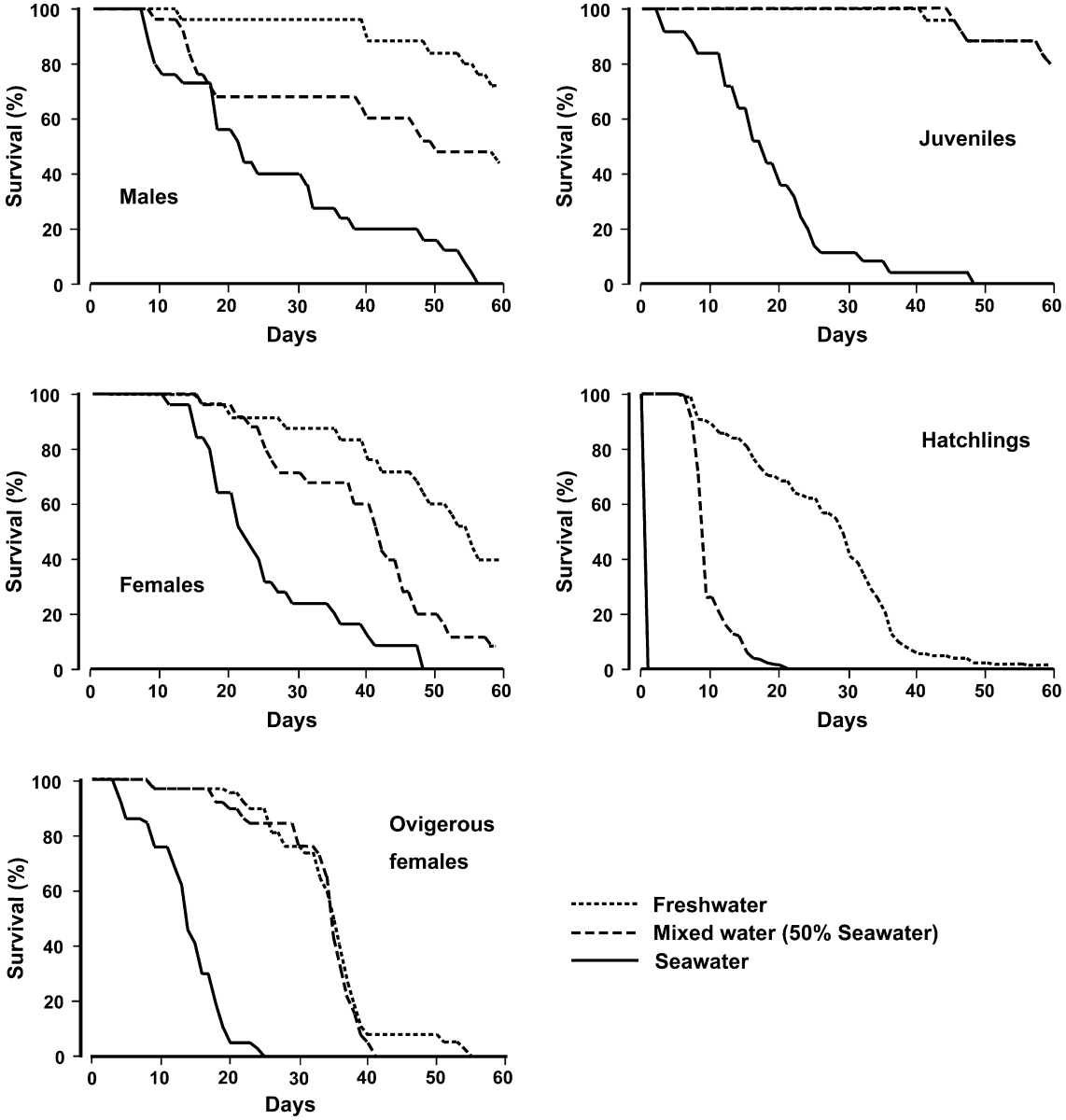


Fig. 8. Survivorship (%) of adult males, non-ovigerous adult females, juveniles, hatchlings, and ovigerous females of *Sternomoera rhyaca* maintained in three water conditions in the laboratory. The percent values are based on the pooled values of 10 replicates per water condition for hatchlings (total n=200 individuals per water condition) or five replicates each per water condition for males, females, juveniles (for each, total n=25 individuals per water condition), and ovigerous females (total n=37 individuals per water condition).

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Table 1. The number of females ovipositing, mean days to oviposition, and mean duration of precopulation of *Sternomoera rhyaca* under three salinity conditions.

% seawater	Number of precopulating pairs tested	Duration (days) of precopulation Mean±SD (range)	Number of females ovipositing	Duration (days) of precopulation for ovipositing females Mean±SD (range)	Days to oviposition Mean±SD (range)
100	37	1.16±0.76 (0– 3)	22	0.86±0.77 (0–3)	1.41±1.84 (0–6)
50	37	2.46±2.81 (0–13)	26	2.19±2.17 (0–6)	2.19±2.17 (0–6)
0	37	8.92±7.65 (1–32)	0	- - -	- - -

freshwater, 72%, 40%, 80%, and 1%, respectively.

Frequency and duration of oviposition. Results are summarized in Table 1. Among precopulating females, 59.5% oviposited in seawater and 70.3% in mixed water; however, this difference was not significant (Chi square, $p>0.05$, 1 df). No females oviposited in freshwater. Duration of precopulation, including both females that oviposited and those that eventually dissolved precopulation without subsequent oviposition, was nearly twice as long in mixed water, and almost eight times as long in freshwater, as in seawater. Among females that oviposited, mean duration of precopulation and overall days to oviposition were likewise shorter in seawater than in mixed water. In seawater, females oviposited on average about 0.6 da after dissolving precopulation (the difference between 1.41 and 0.86 da); in mixed water, females tended to oviposit immediately after dissolving precopulation.

Brood success and survivorship of ovigerous females. Survivorship of ovigerous females (Fig. 8) was not significantly different between freshwater and mixed water, but significantly higher in both than in seawater (Kaplan-Meier analysis; $p<0.05$). In freshwater, 75.7% of ovigerous females (n=37) released juveniles within 30 days. These females kept eggs in their marsupia for about 30 days after oviposition, and released juveniles soon after hatching. The females died not long after the release of juveniles. Other females in freshwater that did not release juveniles died within 54 days. In contrast, no females in seawater or mixed water released juveniles. In seawater, all eggs carried by ovigerous females died within seven days, and all the females died within 24 days. In mixed water, no eggs released juveniles and all died within 41 days, and all the females died within 41 days. Mean survival of ovigerous females in freshwater, mixed water, and seawater was 33.2±8.8, 32.2±7.5, and 12.9±5.4 days, respectively.

DISCUSSION

Summary of the life cycle

The life cycle of *S. rhyaca* is shown schematically in Fig. 9, reconstructed from the data in Figs. 4–6. The life cycle is biennial; juveniles hatched in the stream in June begin to reach maturity the second February after hatching. The breeding season extends from February to June. In March, mature adults (males and virgin females) begin to form precopulating pairs and to move downstream toward the sea (A in Fig. 9). Copulation and oviposition occur in mixed water at

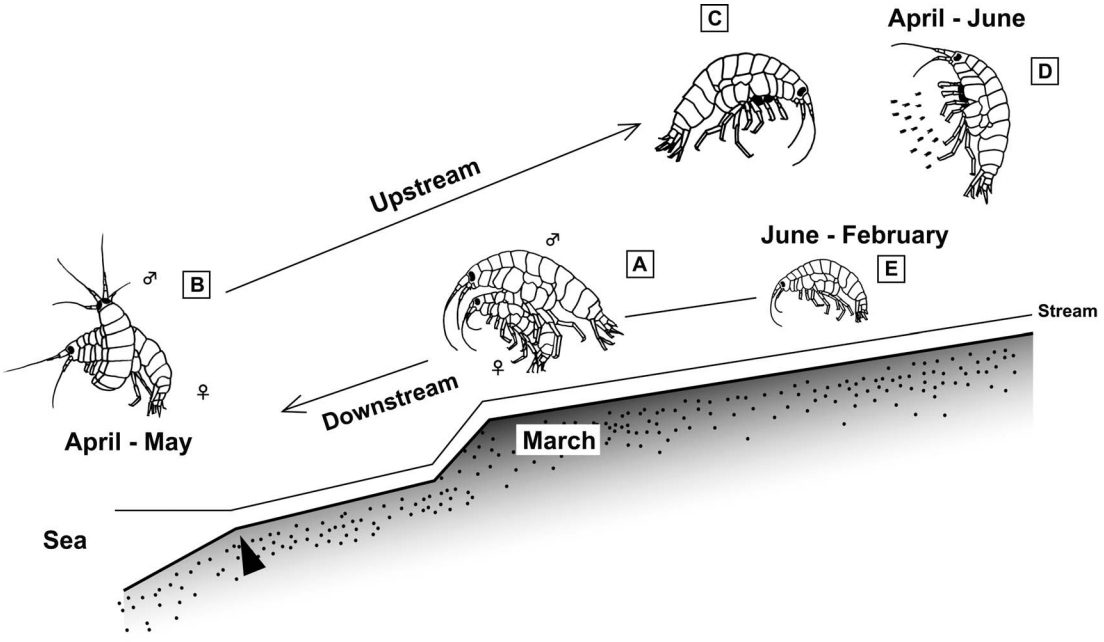


Fig. 9. Diagram of the life cycle of *Sternomoera rhyaca* illustrating the catadromous reproductive migration between the stream and the sea (see Discussion for details): **A)** precopulation; **B)** copulation and oviposition; **C)** ovigerous females; **D**) release of hatchlings; **E)** immatures and juveniles. Arrowhead marks the boundary between freshwater (to right of arrowhead) and mixed freshwater and seawater (to left of arrowhead) at the stream outlet. Ontogenetic stages are illustrated in the relative positions along the stream-to-sea gradient in which they can be found during the life cycle.

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the stream outlet beginning in April (B in Fig. 9), and ovigerous females are found there from late April to early June. This is during the period of the year in which the difference between stream and sea-surface temperature is minimal, ranging from 0–3 °C (Fig. 3). From late April to early June, only ovigerous females return upstream (C in Fig. 9), where their eggs develop and hatch, and juveniles grow (D, E in Fig. 9). Since no mature individuals were found from mid July through August in the field, *S. rhyaca* must reproduce only once in its life; males die after copulation at the stream outlet, and females die after releasing hatchlings upstream. That all females in precopulating pairs were pre-adult-molt virgin individuals also supports this conclusion. The same biennial life cycle, with reproduction from late winter to early summer, was confirmed at another site, Furubira, approximately 70 km southwest of Gokibiru (data not shown).

Diadromy in crustaceans

The taxonomic distribution of diadromous species is narrower in crustaceans than in fishes. Eleven species of diadromous freshwater shrimps studied by Fièvet (1999) and Fièvet *et al.* (2001) on a Caribbean island are distributed among the families Atyidae, Palaemonidae, and Xiphocarididae; all are amphidromous. Five amphidromous representatives of two of the same families, Palaemonidae and Atyidae, occur in Japan (Miya and Hamano, 1988; Hamano and Hayashi, 1992; Hamano, 1996). Among crabs, diadromous species are particularly prevalent in the family Grapsidae (Anger, 1995), and tend to be catadromous (Watanabe and Kajiyama, 1987; Schubart *et al.,* 2000; Diesel and Schuh, 1998).

Diadromous life cycles are also known in a few amphipods. Among the best-studied migratory life cycles of any crustaceans are those of the amphipods *Gammarus zaddachi* and *G. chevreuxi* in coastal rivers in Europe (Dennert *et al.,* 1969; Girisch *et al.,* 1974; Dennert and van Maren, 1974; Hough and Naylor, 1992). In these species, mature adults seasonally drift downstream from more liminic reaches of rivers to estuarine or mixohaline reaches, where reproduction and the bulk of embryogenesis occur, and where animals spend the early post-hatching stage. Most reproduction takes place from December through March. After a period of summer growth in estuarine or mixohaline water, juveniles of both species undertake mass migrations to more liminic reaches upstream in the late summer or autumn.

The life cycles of *G. zaddachi* and *G. chevreuxi* fulfill in broad terms the definition of a truly catadromous life cycle (see Introduction). The life cycle of *S. rhyaca* is also catadromous, though not classically so. In most catadromous crustaceans, reproduction in the saltwater biome includes not only copulation, oviposition, and fertilization, but also development of the eggs, hatching, and a period of post-hatching growth before juveniles migrate upstream. In contrast, *S. rhyaca* migrates to the sea only for copulation, oviposition, and fertilization; it completes virtually all embryogenesis, and subsequent growth from hatching to maturity, in freshwater. Indeed, seawater is lethal to the eggs and hatchlings of *S. rhyaca*, and even mixed water completely inhibits egg development to hatching and greatly reduces the survivorship of hatchlings.

Origin of the life cycle

Sternomoera rhyaca has the most ontogenetically and temporally restricted saltwater phase known in any catadromous animal; hence, the evolutionary origin and maintenance of this unusual life cycle are of interest. Species of the genus *Sternomoera* are restricted in distribution to surface (epigean) freshwaters of Japan and the Russian Far East (Tattersall, 1922; Ueno, 1933; Stephensen, 1944; Hiroki, 1984, 1988; Honma *et al.,* 1988; Ishimaru, 1990; Kikuchi *et al.,* 1993; Kuribayashi *et al.,* 1994; Kuribayashi *et al.,* 1996; Labay, 1997). Barnard and Karaman (1982) established this genus to encompass sternobranchiate freshwater species of *Paramoera,* another eusirid genus that includes marine to sub-surface (hypogean) freshwater species. Barnard and Barnard (1983) suggested that *Sternomoera* evolved from a marine stock of *Paramoera*.

In Japan, *Sternomoera* is currently represented by three species: *S. japonica* (Tattersall, 1922), *S. yezoensis* (Ueno, 1933), and *S. rhyaca*. Among these, *S. rhyaca* has the broadest distribution; it occurs in coastal streams from the northern tip of Hokkaido Island southward to southeastern Honshu Island on the Sea of Japan side, and to Sagami Bay on the Pacific side. In contrast, *S. yezoensis* and *S. japonica* are inland forms, restricted to freshwater springs and brooks throughout their life cycles (Kuribayashi *et al.,* 1996). Their distributions are disjunct, with *S. japonica* on Honshu Island and *S. yezoensis* on Hokkaido. The fourth known species is *S. moneronensis* Labay, 1997, reported from freshwater on Moneron Island in the northern Sea of Japan. Thus, *S. rhyaca* is the sole diadromous species in a clade of otherwise completely freshwater-adapted species.

We propose two hypotheses for the origin of the migratory life cycle of *S. rhyaca*. One is that this species independently evolved diadromy within a lineage restricted to freshwater. In support of this hypothesis is *S. rhyaca*'s absolute requirement of freshwater for embryogenesis, which suggests a high degree of freshwater adaptation; in contrast, broods of the estuarine species *G. zaddachi* and *G. chevreuxi* have low survivorship in freshwater (Girisch *et al.,* 1974).

The alternative hypothesis is that *S. rhyaca* represents an intermediate stage in the evolutionary adaptation to freshwater from a marine or migratory estuarine ancestor. By this hypothesis, *S. rhyaca* should represent the ancestral life cycle in the *Sternomoera* clade, showing considerable freshwater adaptation but tied to the sea for reproduction; other species of *Sternomoera* should represent the derived form of the life cycle, which is completed entirely in freshwater. Similarities of *S. rhyaca*'s life cycle to those of *G. zaddachi* and *G. chevreuxi* in Europe suggest it could have evolved from an ancestor that migrated in larger, estuarine rivers. The generally high survivorship of both juveniles and adults of *S. rhyaca* in salinities ranging from seawater to freshwater, and especially of juveniles in freshwater and mixed water, is characteristic of estuarine species, rather than marine or freshwater species (*e.g.*, Beadle and Cragg, 1940).

Maintenance of the life cycle

The migration of *S. rhyaca* undoubtedly entails fitness costs (see Hendry *et al.* (2004)), both in the energy for

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upstream movement diverted from developing embryos, and in brood mortality, as we observed that not all females are able to successfully return to freshwater after mating at the stream outlet. These costs are hypothetically higher than those incurred by passively migratory estuarine species such as *G. zaddachi* and *G. chevreuxi*, and certainly higher than for *S. rhyaca*'s completely freshwater-adapted congeners, which avoid them altogether. It is thus unclear why *S. rhyaca* retains its unusual migratory life cycle. A possible explanation for the requirement of saltwater for reproduction might be that *S. rhyaca* has simply been unable to evolve a solution to this constraint. This might result, for example, from adaptive inertia due to a pleiotropic effect (Baatz and Wagner, 1997), at one of the steps in the reproductive process, of a gene (for examples, see Charmantier, 1998) involved in the osmoregulatory adaptation to freshwater.

The step in the reproductive sequence that requires elevated salinity may be the female pre-reproductive molt. In the brackish-water species *Gammarus duebeni*, decreasing salinity (at a given temperature) increases the length of the molt cycle (Kinne, 1959; Hartnoll and Smith, 1978), which in turn increases the length of precopulation, since copulation and oviposition follow and are contingent upon the female pre-reproductive molt. In *S. rhyaca*, the mean length of precopulation similarly increases with decreasing salinity (Table 1). The total failure of oviposition in freshwater might thus be due to complete freshwater inhibition of the female pre-reproductive molt, though we did not observe whether this was the case. A counterargument is that all other molts of *S. rhyaca* take place in freshwater. However, the pre-reproductive molt is likely coordinated with the hormonal system involved with ovarian maturation (Hartnoll and Smith, 1978), so it may be different.

Balanced against the apparent fitness costs of *S. rhyaca*'s migration, there may well be undetected fitness benefits. As an example, Hynes (1955) reported freshwater populations of *Gammarus lacustris* and *G. duebeni* in Britain that are infected with larvae of the acanthocephalan *Polymorphus minutus*. Mass infections can nearly eliminate populations of these amphipods in lakes, but populations in streams are much less susceptible. Although we have no relevant data on parasites in *Sternomoera*, this example illustrates how *S. rhyaca*, by exclusively inhabiting small coastal streams, could derive as-yet-undetected fitness benefits that help explain maintenance of the life cycle. In this context, the same behavior driving *S. rhyaca* females to move upstream following copulation may be adaptive in preventing individuals of any age from being lost to the population after they are washed to the sea by floods. Coastal streams in Japan are subject to intermittent floods due to heavy rains, and we have observed a few immature individuals returning upstream after floods in late summer and autumn.

In fact, we believe it is highly unlikely that *S. rhyaca* maintains its migratory life cycle solely due to an evolutionarily constrained requirement for seawater during a narrow window of ontogeny. Girisch *et al.* (1974) pointed out that the migratory life cycles of *G. zaddachi* and *G. chevreuxi* do not exist simply to accommodate osmoregulatory limitations at different stages of ontogeny; indeed, the animals move to the osmotically suboptimal condition of freshwater for at least part of the life cycle. Instead, these estuarine life cycles themselves are likely complex adaptations in response to biotic and abiotic factors in addition to salinity that vary along estuarine-riparian gradients. These species have evolved behaviors such as endogenous swimming rhythms coordinated with tidal cycles to accomplish movement in the appropriate direction (upstream or downstream) at the appropriate stage of the life cycle (juvenile or adult) (Girisch and Dennert, 1975; Dieleman, 1977; Hough and Naylor, 1992). Their behavior also includes presumably adaptive responses to exogenous cues such as changes in salinity, temperature, and water currents. As with *G. zaddachi* and *G. chevreuxi*, the life cycle of *S. rhyaca* undoubtedly involves seasonally coordinated, ontogenetic-stage-specific behavioral responses (*e.g.*, seasonally timed swimming behavior necessary for the downstream drift of mature adults; positive rheotaxis or negative geotaxis for upstream migration), similarly suggesting that the life cycle itself is a complex adaptation to inhabiting coastal streams.

Finally, we note that downstream migration of *S. rhyaca* might be advantageous for the species' dispersal. Although our laboratory experiments demonstrated that survivorship in seawater was the lowest of the three water conditions tested, the 50% survival time of juveniles and adults in seawater was nonetheless 18 and ~22 days, respectively (Fig. 8). This means that individuals swept into the sea during the breeding season or by floods very likely live long enough to be dispersed by currents to nearby streams. This dispersibility may be reflected in the broad distribution of *S. rhyaca* compared its inland congeners.

Physiological ecology

In its quite different tolerances to elevated salinity among ontogenetic stages, and the highly ontogenetically restricted saltwater phase of the life cycle, *S. rhyaca* is quite interesting from the standpoint of physiological ecology. This species shows a type-2 pattern in its ontogeny of osmoregulation, in which adults can hyper-hypo-osmoregulate and develop this capability at the earliest post-hatching stage (Charmantier, 1998; Charmantier and Charmantier-Daures, 2001). Pattern 2 is characteristic of species in environments where salinity is very high, very low, or variable, and thus includes both freshwater and estuarine species. In this pattern, the ability to hyper-hypo-osmoregulate temporarily becomes weak in hatchlings immediately post-hatch, possibly due to a switch in osmoregulatory sites at hatching. This is consistent with the observation that hatchlings of *S. rhyaca* live less than a day in seawater.

Charmantier and Charmantier-Daures (2001) hypothesized that the ability to osmoregulate may develop during embryogenesis in some crustaceans. This may be the case in *S. rhyaca*, the embryos of which not only tolerate, but require, freshwater. However, experiments will be necessary to determine whether the embryos gain osmotic protection from the egg envelope, from maternal regulation of the closed environment of the marsupium, or by themselves achieving the ability to hyper-osmoregulate. What is curious about *S. rhyaca* is that although juveniles can hypo-osmoregulate moderately well in seawater, and iso- or hypo-osmoregulate very well in mixed water, embryos and hatchlings cannot; the latter two die quickly in seawater and

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less quickly in mixed water.

Future studies

The obvious next step in elucidating the origin of the unusual migratory life cycle of *S. rhyaca* is to conduct a molecular phylogenetic analysis of *Paramoera* and *Sternomoera* to determine the ancestral life cycle in *Sternomoera*. In addition, *S. rhyaca* has several advantages for studying the factors involved in the origin and maintenance of a catadromous life cycle: 1) it belongs to a phylogenetically well-defined group; 2) its life cycle has well-defined temporal stages and occurs over a relatively short distance (<100 m); and 3) the species has a broad latitudinal distribution in coastal streams in Japan. Finally, the unusual pattern of ontogeny of osmoregulation in *S. rhyaca* is worthy of future study.

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