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Cover

Hingebeak shrimps (family Rhynchocinetidae) are widely distributed in marine subtropical and tropical rocky and coral reef habitats. Some species have striking coloration and are commercially important as "ornamental" shrimps in the tropical aquarium trade. A unique character of the family is the articulated rostrum, or "beak," on which the common name "hingebeak shrimp" is based.

In many species of hingebeak shrimps, males develop into large dominant "robustus" males, with highly developed claws, or pincers, as well as a pair of spearlike appendages. These robustus males guard and defend smaller females during copulation, while subordinate "typus" males attempt sneak matings whenever receptive females are unguarded. All previously studied hingebeak species are gonochoric—that is, they have separate sexes and individuals retain the same sex throughout life. However, everything is different in *Rhynchocinetes uritai*: the current study by Osawa and colleagues (pp. 125–136) confirmed that this species is a protandric sequential hermaphrodite in which males change sex, becoming females. As males, individuals are smaller than females and engage in only very brief mating interactions with females.

Rhynchocinetes uritai inhabits subtidal rocky habitats. Like other hingebeak shrimps, its members commonly aggregate in crevices. Groups are often found in crevices with sea urchins or feather stars, but the individuals in the cover image gathered at the entrance of a cave inhabited by the beach conger, *Conger japonicus*.

This extensive study on the life history of *R. uritai* indicates that these shrimps enter benthic habitats during the summer months. They grow during the fall and winter months, reach sexual maturity in the coming spring, and reproduce as males during their first reproductive season. During the following winter they change sex and reproduce as females during their second reproductive season.

The life-history patterns of *R. uritai* and other sex-changing species do not appear strikingly different from those of gonochoric caridean shrimp species from similar latitudes. The findings of this study raise the question of why protandry has not evolved in more caridean species with small males and larger females.

Credits: Photo, Martin Thiel, Universidad Católica del Norte, Coquimbo, Chile; layout, Beth Liles, Marine Biological Laboratory.

Reference: *Biol. Bull.* **228:** 125–136. (April 2015)

Analysis of Life-History Traits in a Sex-Changing Marine Shrimp (Decapoda: Caridea: Rhynchocinetidae)

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Abstract. The hypothesis of protandrous (male to female) sex change was tested for the first time in a rhynchocinetid shrimp, *Rhynchocinetes uritai*, with an analysis of life-history traits. Samples were taken monthly for 2 years in Oura Bay, Japan, using a combination of bait and refuge traps. Breeding was seasonal but extended from spring through autumn, with female-phase individuals (FPs) producing broods successively, with their ovaries maturing for a new spawn during incubation of a previous brood. Females incubated numerous (~500–4000) embryos that suffered insignificant mortality before hatching. Recruitment of juveniles after planktonic larval development began in summer and peaked during the autumn, with negligible recruitment during winter and spring. Cohort analysis confirmed the hypothesis of protandric sex change in this species, with juveniles maturing into the male phase (MP) during their first reproductive season at an age of 6–10 mon, depending on the time of recruitment. Sex change occurred during the following winter when transitional individuals matured into FPs during their second reproductive season at an age of ≥18 mon. Two cohorts were followed from recruitment until the end of the study, indicating a life span of 21–25 mon. Aside from its sexual system, this sex-changing species showed no obvious differences in reproductive and other life-history traits from those of gonochoric species from similar latitudes and habitats.

Introduction

Caridean shrimps, with over 3200 species (De Grave and Fransen, 2011), display a diversity of life styles in a variety of marine and freshwater habitats (Bauer, 2004). Although the majority of carideans are gonochoristic (separate sexes), there are numerous species that are sex changers (Chiba, 2007). Sequential hermaphroditism in shrimps varies among caridean species from (i) simple protandry, in which all individuals first develop into a male phase (MP) and then, when older and larger, change into a female phase (FP) (*e.g.,* Baeza, 2010; Baeza and Piantoni, 2010); to (ii) partial protandry, in which only some individuals are sex changers (Bergström, 2000; Bauer, 1986, 2000); to (iii) protandric simultaneous hermaphroditism, in which individuals first develop as MPs but later change to functional simultaneous hermaphrodites with a primarily female phenotype (Bauer and Holt, 1998; Fiedler, 1998; Laubenheimer and Rhyne, 2008; Braga *et al.*, 2009; Onaga *et al.*, 2012). Detailed studies on the reproductive ecology and other life-history traits of caridean species are revealing previously unknown examples of protandrous species (Bauer and Conner, 2012). Increased knowledge about the sexual systems and reproductive biology of protandrous species will contribute to an understanding of the evolution of hermaphroditic shrimps.

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Abbreviations: CL, carapace length; FP, female-phase hermaphrodite; MP, male-phase hermaphrodite; SR, sex ratio.

The caridean shrimp family Rhynchocinetidae, comprising 24 species in two genera, *Rhynchocinetes* and *Cinetorhynchus* (Okuno, 1997a, b; De Grave and Fransen, 2011), has a cosmopolitan distribution in marine subtropical and tropical rocky or coral reef habitats. Some species have striking coloration and are commercially important as "ornamental" shrimps in the tropical aquarium trade (Calado, 2008). A unique character of the family is the articulated rostrum (Chace, 1997; Okuno, 1997a, b) on which the common name "hingebeak shrimp" (McLaughlin *et al.*, 2005) is based.

Species of both rhynchocinetid genera show a dichotomy in sexual dimorphism and mating system (Baeza *et al.,* 2014). Some species appear to have populations composed of smaller females and similar-sized males but include larger, sexually dominant males with hypertrophied weaponry (third maxillipeds, first chelipeds, or both) (Correa *et al*., 2000; Bauer *et al*., 2014). Other species appear to have small males and larger females (*e.g.*, *R. uritai*, Bauer and Thiel, 2011), as do many caridean species (Bauer, 2004). Typically, such caridean species are not sexually dimorphic in weaponry and exhibit a "pure searching" mating system (Wickler and Seibt, 1981; Correa *et al.*, 2003; Bauer, 2004; Bauer and Thiel, 2011), without male agonistic behavior and without defense of females.

Sexual systems of rhynchocinetids may vary as well. *Rhynchocinetes typus*, *R. brucei* (Correa and Thiel, 2003; Thiel *et al*., 2010), and two *Cinetorhynchus* species from Hawaii (Bauer *et al*., 2014) are gonochoristic. However, based on morphological evidence from a limited single sample, Bauer and Thiel (2011) hypothesized that *R. uritai* from the western Pacific is protandric.

The timing of sex change in protandric shrimps may be controlled by just ontogeny and growth—that is, the MP changes to FP when it has grown large enough to support the higher energetic needs of a reproductive female. On the other hand, studies on pandalid and *Lysmata* (Hippoltyidae) species (*e.g.,* Charnov *et al.*, 1978; Lin and Zhang, 2001; Baeza and Bauer, 2004) have indicated that the size at sex change may be under the influence of demographic factors—that is, the relative abundance of MPs and FPs in the population (environmental sex determination, or ESD) (Charnov, 1981, 1982; Charnov and Anderson, 1989). Population and life-history analyses of other protandric carideans should shed more light on this question.

Similar to their sexual systems, the life-history strategies of caridean shrimps also vary considerably (Bauer, 1992, 2004). In caridean shrimps, particular attention has been given to latitudinal variation in life-history characteristics such as seasonality of reproduction, spawning frequency, fecundity, embryo mortality, age at first reproduction, adult size, and life span (Thorson, 1950; Sastry, 1983; Bauer, 2004). Perhaps because of the nocturnal behavior and difficulty in the collection of most rhynchocinetid species, no such analyses have been done on rhynchocinetid shrimps to determine how their biological and ecological characteristics agree with or vary from general paradigms that have been proposed about invertebrate and caridean life-history traits (Orton, 1920; Thorson, 1950; Sastry, 1983; Pearse *et al.*, 1991; Bauer, 1992, 2004; Ramirez-Llodra, 2002; Marshall *et al.*, 2012).

Relatively few life-history studies have been done on sex-changing shrimps (*e.g.,* Bauer, 1986, 2002; Zupo, 1994) other than commercially important protandric species (*e.g.,* crangonids: Gavio *et al.*, 2006; pandalids: Bergström, 2000). In this study, life-history traits of a rhynchocinetid shrimp were analyzed for the first time with *Rhynchocinetes uritai* Kubo 1942 from Oura Bay, Japan, using the results from a monthly sampling program, cohort analysis, and morphological observations. Specifically, we tested the hypothesis of protandry and analyzed the ontogenetic and temporal pattern of sex change. We report on the annual cycle of reproduction, as well give estimates of other life-history traits (age of first reproduction, spawning pattern and frequency, fecundity, embryo mortality, growth, and life span).

Materials and Methods

Sampling methods

This two-year study was carried out in rocky sublittoral habitats in Nabeta Cove, Oura Bay (34°39′52′N; 138°56′19′E), facing the University of Tsukuba's Shimoda Marine Research Center (SMRC), which is situated on the southern end of the Izu peninsula, Japan. Water temperature at 10 m depth was taken hourly at a SMRC monitoring station in Nabeta Cove, and the temperature values reported here are monthly means of the daily means. Water temperature varied seasonally from lows of 14.0 °C in January 2011 and 14.4 °C in 2012, to highs of 23.5 °C in September 2010 and 24.6 °C in 2011 (Fig. 1). Likewise, monthly means of daily mean measures of electrical conductivity (EC) of surface water (30 cm depth) were recorded at SMRC and converted to salinity values. Due to equipment

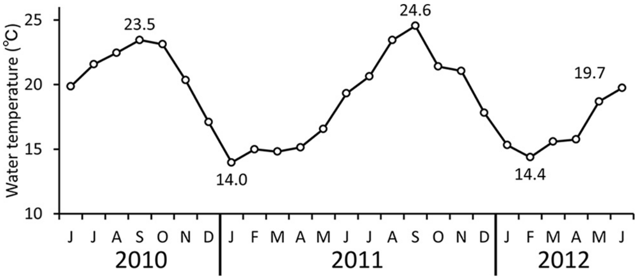

Figure 1. Seasonal variation in water temperatures at 10 m depth in Nabeta Cove, Oura Bay, Japan, during the study.

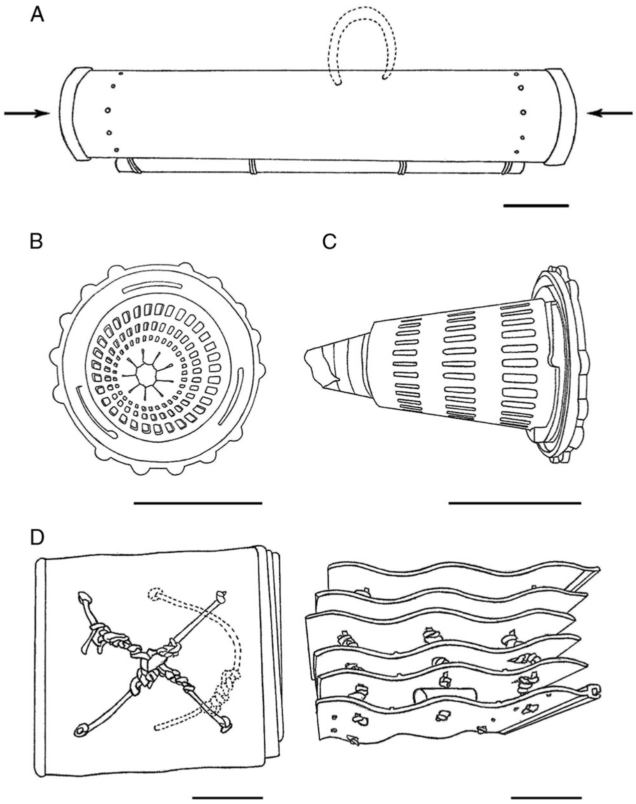

Figure 2. Traps used in sampling of *Rhynchocinetes uritai*. (A) Bait trap, side view; arrows point to ends where funnels shown in B and C are inserted. (B) End view of funnel. (C) Side view of funnel. (D) Refuge trap for small juveniles from top (left) and side (right) views. Dotted lines in A and D represent rope loops used to carry and retrieve the traps. Scale bars represent 10 cm.

problems, EC/salinity measures are not available from January 2012 to the end of the study. Salinity varied little from June 2010 to December 2011, ranging from 31.5 to 34.8 ppt, with a mean and standard deviation of 34.7 ± 0.8. Primary productivity in the waters offshore of Shimoda, as indicated by values of chlorophyll *a*, was highest from March to May and in July during the year from November 2011 to November 2012 (unpubl. data, Shigeki Wada, SMRC).

Sampling of *Rhynchocinetes uritai* was done twice a month from June 2010 to June 2012 with four bait traps (Fig. 2A–C) that sampled adults and larger juveniles. The sampling procedure may have affected collection of smaller, newly recruited individuals. Therefore, two refuge traps (Fig. 2D), which attracted more of the smaller individuals compared with bait traps, were used from February 2011 until the end of the study. During the time period January 2012–June 2012, two of the four bait traps received a light source to test for the effects of light on shrimp captures, but our previous studies verified that the catch efficiency was not significantly different compared with normal bait traps (Y. Osawa, unpubl. data). As *R. uritai* occurs in groups of several individuals in crevices and small caves during the day, all traps were deployed by two scuba divers at locations where such groups of shrimps had been observed. Rocks were placed at the entrances of bait traps and surrounding refuge traps to maintain them in place. Bait traps with two 0.5-mm-mesh bags (60 cm h × 35 cm w) covering both entrances were collected after 22–26 h. After the first year of sampling, refuge traps were left in the field for 11–41 days, and placed in 6-mm-mesh nets upon removal. Shrimps were poorly attracted to traps in late fall to winter (November to February); thus shrimps were also captured by hand nets by two scuba divers from November 2010 to March 2011, and December 2011 to March 2012. Collected shrimps were placed in a cooler box (88 cm L × 42 cm W × 44 cm H) with seawater and immediately transported to the laboratory of SMRC. All specimens were preserved with 10% neutralized seawater formalin as soon as possible after sampling.

Measurements and data analysis

In all specimens, the carapace length (CL) was measured from the base of the supraorbital spine to the posteromedial end of the carapace using digital calipers under a binocular stereomicroscope. Specimens with CL smaller than 4.0 mm were measured using a stereomicroscope with a video micrometer (Olympus VM-60 with magnification of 380×). Sexual condition was determined from external sexual characteristics. Individuals in the male phase (MP) were identified by the presence of prominent lateral lobes on the endopods of the first pleopods, as well as an appendix masculina located next to the appendix interna on the endopods of the second pleopods. Individuals in the female phase (FP) were recognized by the absence of MP pleopod characteristics and the presence of vitellogenic ovaries or broods of embryos, and especially by characters of the "breeding dress" (Höglund, 1943; Bauer, 2004). The latter consists of adaptations for spawning and incubating embryos: expanded flanges on the endopods of the first to third pleopods and enlarged side plates (pleura) on abdominal segments 1–3. Individuals with an appendix masculina and larger pleopod flanges were identified as "transitional"—that is, in the process of sex change (Bauer and Thiel, 2011). All individuals with CL smaller than 4.0 mm and without either MP or FP external characteristics were classified as juveniles.

The reproductive period of the population was identified by calculating the percentage of FPs carrying embryos (breeding FPs) relative to the total numbers of FPs collected (Pakhomov *et al.*, 2000). As in Bauer (1986), ovarian condition and embryonic development of the breeding FPs from March 2011 to June 2012 were visually determined by external inspection and staged to determine the spawning pattern of incubating FPs. The ovarian maturation stage was scored as stage 1 (no vitellogenic oocytes visible), stage 2 (the developed vitellogenic oocytes were observed in less than half of the cephalothoracic space available for oocytes), stage 3 (more than half of the space filled), and stage 4 (space available completely filled). Development of embryos incubated by FPs was scored from stages 1 to 4: stage 1 (newly spawned), stage 2 (blastoderm distinct, no eye development), stage 3 (eye development observed), and stage 4 (close to hatching).

The relative frequency (%) of breeding FPs in each size class was plotted, and the logistic function $y = 1/1 + e^{r\ (\mathrm{CL}\text{-}\mathrm{CL}_{50})}$ was fitted to data according to Castilho *et al.* (2007). $\mathrm{CL}_{50\%}$ represents the carapace length at which 50% of the individuals are considered mature, and *r* describes the slope of the curve. Fitting of the curve was carried out following the least-squares method (Castilho *et al.*, 2007).

Fecundity measures consisted of brood size (number of embryos) and embryo size (volume). All embryos were removed from females carrying stages 1 and 4 embryos ($n = 25$ females for each stage) and counted. After log10 transformation of embryo number and carapace length (female size), ANCOVA was used to test the null hypothesis of equal embryo mortality during incubation between females with stages 1 and 4 embryos by comparison of regression lines of embryo number on carapace length.

Embryo size is a basic life-history trait that indicates larval development (abbreviated, lecithotrophic, planktotrophic) and a key factor influencing fecundity (brood size = number of embryos) (*e.g.,* Terossi *et al.*, 2010). To measure embryo size, the median of the lesser (d_1) and greater (d_2) diameters of 10 embryos, chosen haphazardly from each brood, were taken and measured to calculate embryo volume [oblate spheroid, $V = 1/6\ (\pi \times d_1^{\,2} \times d_2)$] (Turner and Lawrence, 1979).

All samples from different traps (bait and refuge traps; hand nets) were pooled to compose the monthly sample. Monthly size-frequency distributions were constructed using 0.5-mm size classes. The size-frequency data in each sampling month were used for cohort analysis using Bhattacharya's method and NORMSEP of FAO-ICLARM Stock Assessment Tool (FiSAT ver. II) (Gayanilo *et al.*, 2005). Cohorts were identified using frequencies perceived to belong to one age group by Bhattacharya's method. The size/age points of cohorts and choice of best results were based on three criteria: (a) separation index (SI) values for the different age groups (cohorts), (b) the number of the recognized age groups, and (c) the standard deviation (SD) (Amin *et al.*, 2009). Monthly data with more than 100 individuals were analyzed using NORMSEP, which applies the maximum likelihood concept to SEParation of the NORMally distributed components of size-frequency samples based on the results from Bhattacharya's method (Gayanilo *et al.,* 2005).

Progression of cohorts through time and life-span estimates was done using the best-fitted growth curve utilizing the Powell-Wetherall Plot routine and Electronic LEngth-Frequency ANalysis (ELEFAN I) routine of FiSAT II to identify the Von Bertalanffy Growth Function (VBGF): $\mathrm{CL}_t = \mathrm{CL}_\infty\ (1 - \exp - K(t - t_0))$, where CL_∞ is the asymptotic carapace length, CL_t is the carapace length at time *t*, *K* the growth coefficient (year^{-1}) and t_0 the theoretical age at zero length (with no biological significance) (Than, 2006; Semensato and Di Beneditto, 2008). Firstly, initial values of CL_∞ and Z/K (Z = total mortality and K = growth coefficient) were estimated using the Powell-Wetherall method. The value of estimated CL_∞ fell in the range of the 95% confidence interval of predicted extreme CL, using the Maximum Length Estimation routine in FiSAT II. Secondly, the best optimized CL_∞ and *K* were calculated using *K*-value scans and automatic search routine in ELEFAN I. CL_∞ and *K* with the highest *Rn* value (ranging from 0 to 1), which indicates the goodness of fit, were selected. Monthly recruitment was defined as percentage of juveniles (recruits) in the monthly sample (number of juveniles/total number of individuals × 100). In the first year of sampling, refuge traps were not used, which may have resulted in lower recruitment values.

The mean CLs of the newly recruited cohorts were plotted over time following Baldwin and Bauer (2003). The upper and lower 95% confidence limits of each cohort were calculated based on cohort mean CL, and regression lines were plotted. Monthly sex ratios were calculated as the number of MPs divided by the total number of MPs and FPs. A binomial test was used in each sampling month to test deviations from a 1:1 sex ratio (Wilson and Hardy, 2002; Baeza *et al.*, 2010). The monthly proportions of transitionals were calculated as the number of transitionals divided by the total number of individuals including juveniles, MPs, transitionals, and FPs.

Results

Sample base for population data

A total of 3106 specimens were collected during the study: 205 were classified as juveniles; 1340 were classified as MPs; 660 and 452 individuals as FPs incubating embryos and nonbreeding FPs, respectively; and 449 individuals (15%) as transitionals (individuals changing sex). The CL ranged between 4.2 and 10.6 mm (mean ± SD: 6.8 ± 1.0) for MPs, 6.8 and 13.0 mm (mean ± SD: 9.5 ± 0.9) for nonbreeding FPs, and 8.1 and 12.6 mm (mean ± SD: 9.9 ± 0.8) for breeding FPs. The size of transitionals ranged between 5.7 and 11.3 mm (mean ± SD; 8.4 ± 0.9). The mean CLs of sexual types were significantly different (Kruskal-Wallis statistical test: $H = 2305.9$, df = 4, $P < 0.001$).

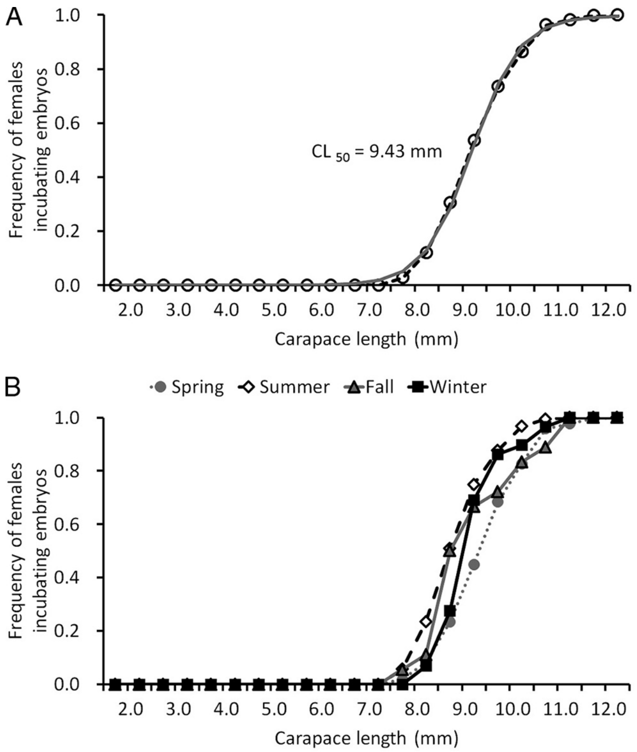

Figure 3. Size of sexual maturity in reproductive females of *Rhynchocinetes uritai*. (A) Sexual maturity of total breeding FPs (female phase, black dotted line) with the logistic function $y = 1/1 + e^{r\,(CL-CL_{50})}$ (solid gray line). (B) Seasonal differences in the size of sexual maturity based on the $CL_{50\%}$ of breeding FPs from June 2010 to June 2012.

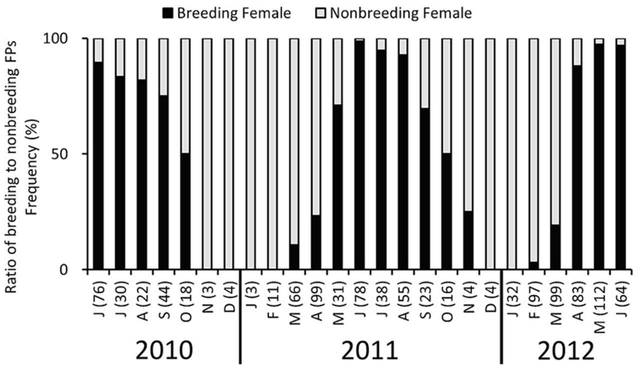

Figure 4. Frequency of breeding FPs (female phase) and nonbreeding FPs from June 2010 to June 2012. The total numbers of FPs are shown in parentheses for each month.

Reproductive characteristics and breeding patterns

The smallest FP observed with a brood of embryos was 8.1 mm CL. The mean $CL_{50\%}$, a reproductive parameter showing average size of reproductive FPs (those incubating embryos), was 9.43 mm in FPs of *Rhynchocinetes uritai* in Oura Bay (Fig. 3A). The proportion of breeding FPs in 0.5-mm size classes increased logistically with CL. The size at sexual maturity of females did not differ significantly among seasons (Fig. 3B).

Breeding (spawning and embryo incubation) was seasonal and extended in this population of *R. uritai*, taking place from spring into autumn in both years of the study (Fig. 4). Beginning with the start of the study in June 2010, breeding declined from peak values in summer (June–August) toward low values in autumn, and no more reproductive females were found in November 2010. In 2011, when sampling covered the entire year, breeding FPs first appeared in March, increasing to a peak nearing 100% in June–August, and declining steadily until December, when breeding ceased. Breeding then began again in February–March 2012, increasing to nearly 100% in June, the last month of sampling (Fig. 4).

The breeding pattern of FPs on an individual basis—that is, single *versus* multiple broods (successive breeding)—was determined by analysis of size-frequency distributions of ovarian maturation stages of FPs incubating embryos in various developmental stages from recently spawned to near larval eclosion (hatching) (Fig. 5). The frequency of FPs with stage 1 ovaries decreased dramatically in FPs incubating stages 2–3 embryos (blastoderm distinct, no eye development); no FPs incubating stage 4 embryos (nearly hatching) had stage 1 ovaries. The frequency of FPs with stage 4 ovaries (ovary completely filling the available cephalothoracic space) increased dramatically in FPs incubating stages 3–4 embryos (Fig. 5). More than 80% of FPs incubating stage 3 (eye development first observed) and stage 4 embryos had completely developed ovaries (ovary stage 4), indicating an imminent spawn, about 1 day after hatching, during which mating and the subsequent spawning occur (Bauer and Thiel, 2011). The hypothesis of no correlation between ovarian stage and embryo stage was rejected (Pearson's Chi-squared test, $\chi^2 = 346.7$, df = 9, $P < 0.001$). Thus, females of *R. uritai* produced one brood after another (successively) during the breeding season.

Females incubated large numbers of small embryos, and brood size (number of embryos) increased with female size

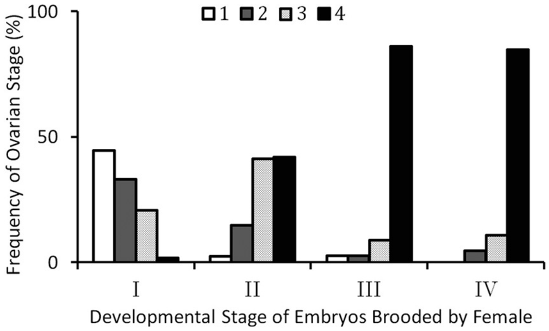

Figure 5. Degree of ovarian development in FPs (female phase) carrying embryos at stage 1 (recently spawned) to stage 4 (near hatching). Stages of ovarian development range from stage 1 (no noticeable ovarian development) to stage 4 (fully developed ovary) are given above the histogram bars.

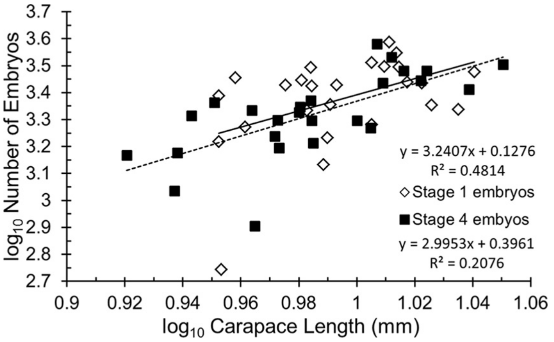

Figure 6. Comparison of brood size (embryo number) regressed on female size (carapace length) between females incubating stage 1 (recently spawned; solid line) and stage 4 (near hatching; dashed line) embryos.

(Fig. 6). Females incubating stage 1 embryos carried from 555 to 3878 embryos (= 2504 ± 732; $n = 25$) while those with stage 4 embryos carried from 804 to 3808 ($\bar{x} = 2215 \pm 725$; $n = 25$). Stage 4 embryos were significantly larger ($\bar{x} = 0.061 \pm 0.008$ mm^3) than those in stage 1 ($\bar{x} = 0.038 \pm 0.006$ mm^3). The hypothesis of no difference in size (volume) between stage 1 and stage 4 embryos was rejected (Student's *t*-test; $P < 0.0001$; $n = 25$). Given that stage 4 embryos were larger, and thus more subject to dislodgement than stage 1 embryos, a comparison of regression lines of $\log_{10}$ embryo number on $\log_{10}$ carapace length was made to test for differences in embryo number between females incubating stage 1 and stage 4 embryos. The assumption of homogeneity of slopes was met (interaction term, stages × carapace length: $F_1 = 0.03$; $P = 0.86$), permitting a test of the hypothesis of equal mortality between stages, which is accepted (ANCOVA: $F_1 = 0.43$; $P = 0.51$). Thus, no significant embryo mortality occurred during development.

Cohort analysis and life span

Recruitment, measured as the percentage of juveniles (individuals < 4.0 mm CL) in the population, began in mid-summer in 2010 and 2011, and strongly peaked during the autumn and extended into December in both these years of sampling (Fig. 7). Little or no recruitment occurred during the winter months or during the spring (Fig. 7).

The optimized values for CL_∞ and K were 13.67 mm and 0.460 y^{-1}, respectively, with the highest *Rn* value of 0.22. Five cohorts were identified and followed during the study period, from "a" (oldest cohort) to "e" (most recently recruited cohort) (Figs. 8, 9) . Recruitment of cohorts c, d, and e began in August 2010, July 2011, and May 2012, respectively. Juveniles matured into males during the autumn and winter of their first year, reproducing as males the following spring and summer. Although transitional individuals were collected throughout the year, most males matured into transitionals from winter to spring of their second year: from December 2010 through March 2011, and November 2011 to February 2012 (Fig. 9).

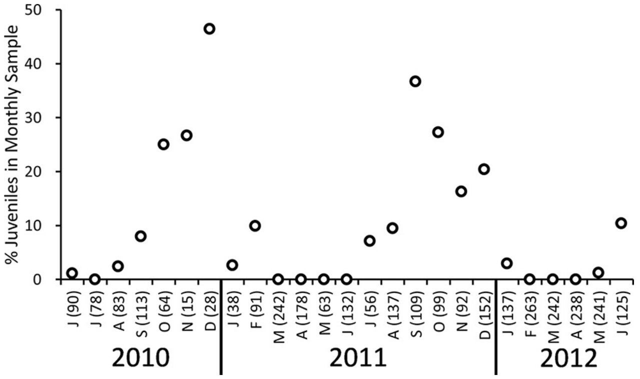

Figure 7. Monthly recruitment defined as percentage of juveniles (recruits) in the monthly sample. Juveniles were defined as individuals <4.0 mm carapace length. Total numbers of juveniles are shown in parentheses for each month. In the first year of sampling, refuge traps were not used, which may have resulted in lower recruitment values.

Cohort a, composed of FPs when the study began in June 2010, disappeared in December 2010. Cohort b was also present in June 2010 but comprised mostly MPs; they became transitionals during the winter of 2010–2011, most were FPs by spring of 2011, and were reduced to very low abundance by December 2011 (Fig. 9).

Two cohorts, c and d, recruited during the study and were followed to its end. Individuals of cohort c, recruited in late summer 2010, matured as MPs from December 2010 and reproduced as MPs until November 2011 (Fig. 9). Some individuals started to change sex by November 2011, and all individuals completed their sex transition into transitionals or FPs in January 2012. Cohort d, recruited in July 2011, began maturing as MPs from December 2011 and survived until the last month of the study, June 2012. From February 2012, the individuals from cohort c reproduced as FPs together with the MPs of cohort d. The period from recruitment until maturation as FPs was 18 mon in cohort c. The disappearance of the cohorts recruited during this study could not be observed before the end of sampling in 2012.

The combined growth data for cohorts c and d were plotted from their recruitment until June 2012 to estimate their age and life span (Fig. 10A). The first appearance of cohort c in August 2010 was considered as the second month of recruitment based on mean CL > 3.0 mm; cohort d, which was first observed in July 2011, was considered as the first month of recruitment based on the smaller mean CL (< 3.0 mm). A linear regression of mean cohort age (months) on size (CL) was calculated using monthly CL means for cohorts c and d: Cohort age = 3.53 (CL) − 12.09 ($r^2 = 0.882$) (Fig. 10B). Regressions of lower and upper 95% confidence limits of the age/size regression were calculated based on the 95% confidence limits of mean cohort

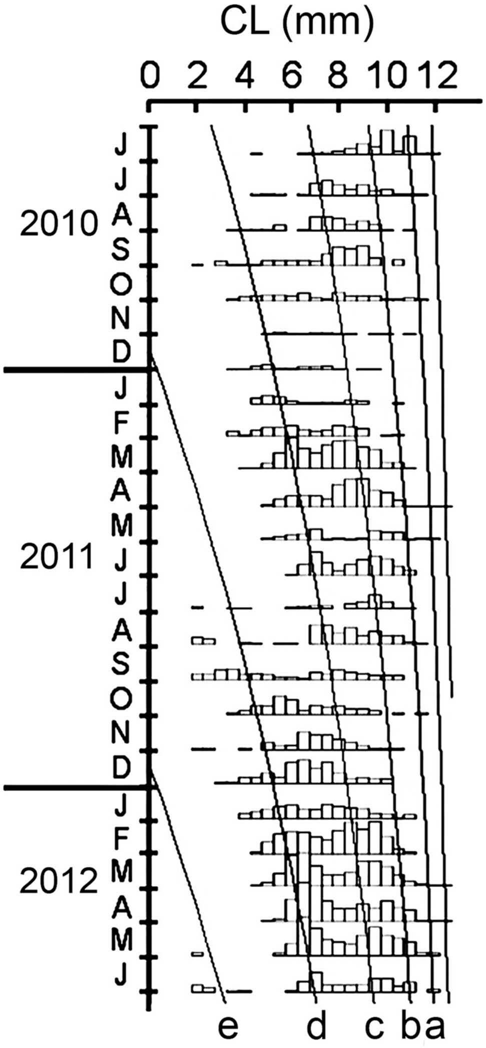

Figure 8. Von Bertalanffy growth function (VBGF) plot and length frequency of cohorts identified from size-frequency distributions. Letters below (a–e) indicate the cohorts identified. Best fitted ($Rn = 0.217$) asymptotic carapace length ($CL_\infty = 13.67$ mm) and VBGF growth constant ($K = 0.460$ year^{-1}) by ELEFAN I routine were used to fit in VBGF growth curve to identify the cohorts.

size [Fig. 10B; Cohort age = 3.22 (CL) – 13.23, and Cohort age = 3.56 (CL) – 8.81].

Sex ratio and sex change

Throughout most of the sampling period, sex ratios (SR) tended to be skewed in favor of MPs, with the highest values during the winter months, that is, January 2011 and December 2011 (Fig. 11A). SR varied from 0.15 in June 2010 to 0.94 in December 2011 (Fig. 11A), but from April to July 2011, SRs were skewed in favor of FPs. From July 2011, SR started to increase and reached 0.5 (equal number of MPs and FPs) in August 2011, after which it further increased and was heavily biased towards MPs by December 2011. Sex ratios started to decrease from January 2012 and stabilized around 0.5 in February to May 2012.

The proportion of transitionals—individuals in the process of sex change—showed a distinct seasonal pattern (Fig. 11B), with low values in summer and autumn and high values during winter and early spring. The highest proportions of transitionals were observed soon after or during the same months when the SR was skewed toward MPs.

Discussion

Breeding in *Rhynchocinetes uritai* was seasonal and extended from spring into autumn, taking place during the months of rising and warmer water temperatures, similar to that of other shallow-water carideans from Japanese waters (*e.g.,* Kikuchi, 1962; Oya, 1987; Omori and Chida, 1988) and other warm-temperate (subtropical) seas (*e.g.,* Alon and Stancyk, 1982; Bauer and VanHoy, 1996; Bauer and Abdalla, 2000; Bauer, 2004). As in other such carideans, females of *R. uritai* are successive breeders on an individual basis. Caridean females usually molt, mate, and spawn a new brood within a few hours to a day of hatching a previously incubated brood, and those from subtropical and tropical waters produce at least two and up to several broods during the breeding season (Bauer, 2004). In this study, most female-phase (FP) individuals of *R. uritai* carrying embryos ready to hatch also had a mature ovary with yolk-filled oocytes, indicating an upcoming spawning and successive spawns throughout the breeding season.

Bauer (1989, 2004) hypothesized that the adaptive reason for successive breeding of tropical and warm-temperate species carideans is to increase reproductive output during their relatively short reproductive life spans. In shrimps from higher (boreal, polar) latitudes, females typically produce only a single brood per year and sometimes every other year (Bauer, 2004).

Females of *R. uritai* produced numerous small embryos that hatch, as in other carideans with similarly sized embryos (Bauer, 1991, 2004), into larvae with extended development in the plankton (10 zoeal stages; Maihara, 2002). Fecundity (number of stage 1 embryos), which is directly influenced by embryo size, increased with female size, as in other carideans (Corey and Reid, 1991; reviewed in Bauer, 2004). Embryo volume typically increases somewhat during development due to water uptake (*e.g.,* Cory and Reid, 1991; Lardies and Wehrtmann, 2001; Terossi *et al.*, 2010). An increase in brood volume during development, and subsequent possible dislodgement of embryos as females move about in the environment, is suspected of being one of the causes (Bauer, 2004) of the often high embryo mortality reported in many caridean species (*e.g.,* Corey and Reid, 1991; Wehrtmann and Lardies, 1999; Lardies and Wehrtmann, 2001; Li *et al.*, 2011). In *R. uritai*, embryo volume

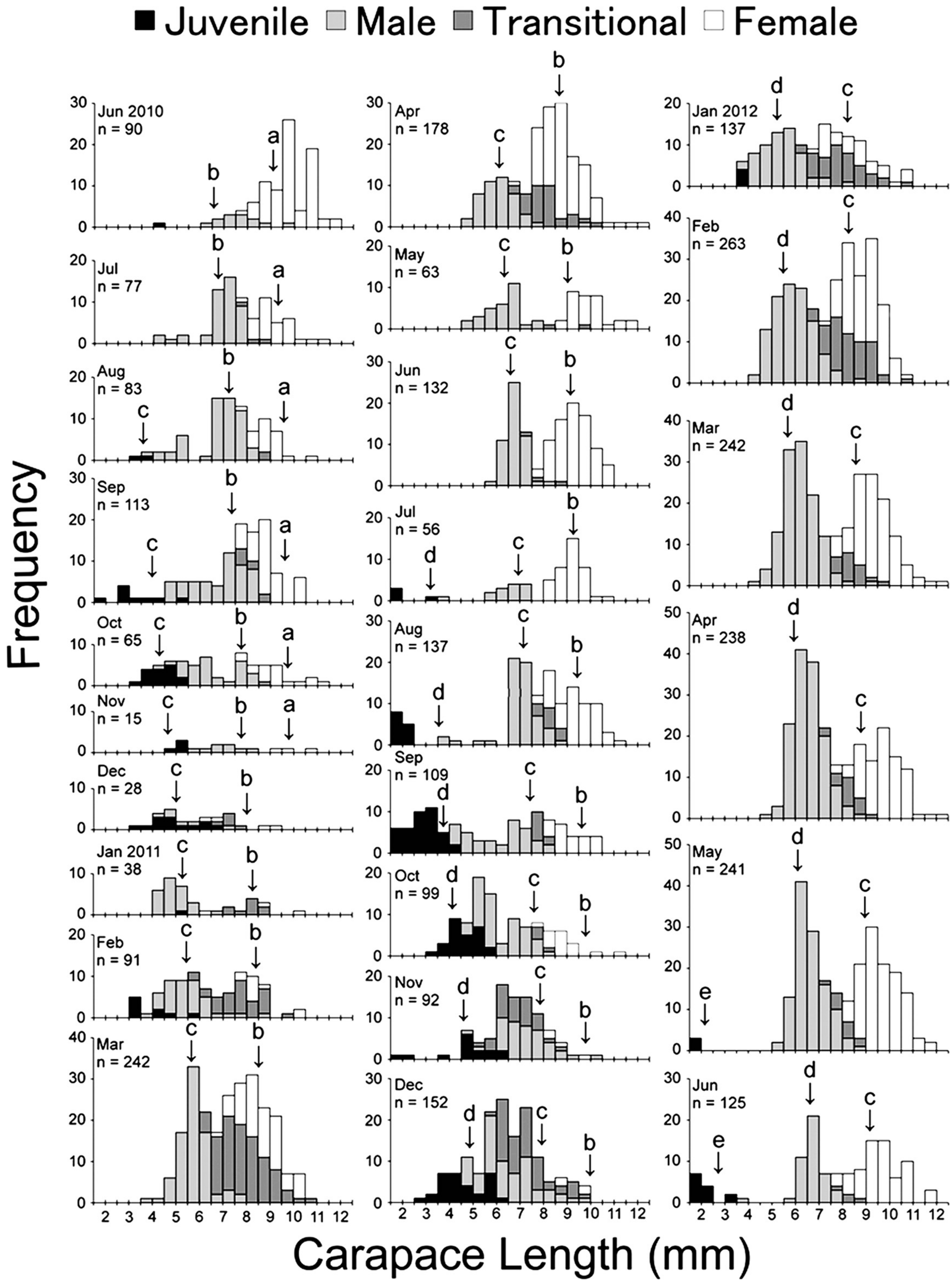

Figure 9. Monthly size-frequency distributions showing sexual stage composition of cohorts (a–e): Black = juvenile, light gray = male, dark gray = transitional, and white = FPs (female phase).

nearly doubled from stage 1 (recently spawned) to stage 4 (near hatching) embryos. However, no significant embryo mortality was detected in our study.

In *R. uritai*, Bauer and Thiel (2011) found that incubation of embryos in three females took 13 days at 23 °C. Maihara (2002) found that the larvae of *R. uritai* took 31–48 days to

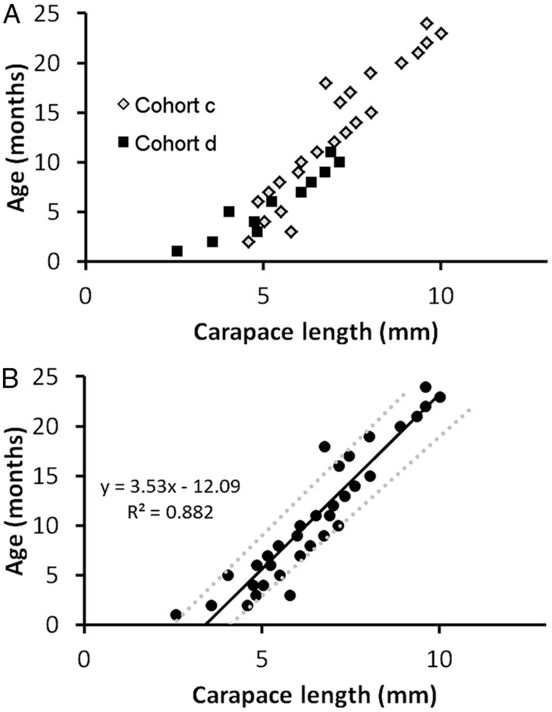

Figure 10. Age and life-span estimation of *Rhynchocinetes uritai* cohorts recruited during the study. (A) Cohort age (time from recruitment) plotted on the mean size (carapace length, CL) of individuals in cohorts c and d. (B) Regression of age on mean cohort CL (solid line) for cohorts c and d combined ($n = 40$). R^2, square of Pearson correlation coefficient. Upper and lower 95% confidence limits on regression line shown by dotted gray lines [$y = 3.56$ (CL) – 8.81 and $y = 3.22$ (CL) – 13.23, respectively].

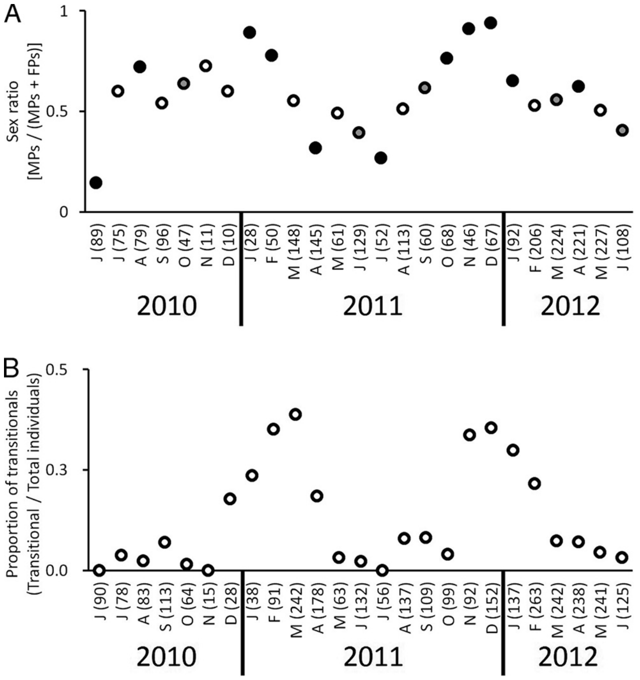

Figure 11. Temporal variation in sex ratio and proportion of sex-changing individuals (transitionals) in the *Rhynchocinetes uritai* population at Oura Bay, Japan. MP, male phase; FP, female phase. (A) Monthly sex ratios (MP/MP + FP) from June 2010 to June 2012. The numbers in parentheses next to the months are the total number of MPs and FPs. The hypothesis of a 1:1 sex ratio (SR = 0.5) was assessed using the binomial test, and results of the test are shown with dots of different fill: black ($P \leq 0.01$), gray ($P > 0.01 < 0.05$), white (no fill) ($P \geq 0.05$). The hypothesis is rejected when probability values are <0.05. (B). Monthly proportion of transitionals from June 2010 to June 2012. The numbers in the *x*-axis after the months are the total number of individuals in each month.

develop from hatching until the juveniles reached 1.31–1.39 mm in carapace length; the period of planktonic larval development after hatching is thus estimated at 1–2 mon. Therefore, the time between spawning and recruitment may be estimated at about 2–3 mon.

The seasonal data showed that FPs were breeding continuously from June to October 2010, March to November 2011, and February until June 2012 (the last month of the study), with a peak between May and August. Recruitment began in summer in the first 2 years of study, with a strong peak in the autumn, and ceased during the winter. Thus, there is a relatively good correspondence, with the expected lag of a few months for larval development, between the time period when most (at least 50%) females were ovigerous (April–October) and when most recruitment took place.

An important causal factor in the seasonality of breeding patterns in marine invertebrates with feeding planktonic larvae has been hypothesized to be the supply of larval food, that is, phyto- and zooplankton abundance (Thorson, 1950; Castilho *et al.*, 2007; Marshall *et al.*, 2012). *Rhynchocinetes uritai* has extended larval development, consisting of 10 zoeal stages and 1 decapodid stage, which occurs in the nearshore plankton (Maihara, 2002). The pattern of planktonic productivity (food for larval shrimps) is higher during the spring and summer in warm-temperate seas, when water temperatures are higher (Thorson, 1950; Longhurst, 1981). In the waters off Oura Bay, our study site, primary productivity (chlorophyll *a* values) is highest during the time period from spring to midsummer (Shigeki Wada, SMRC, unpubl. data). Serisawa *et al.* (2001) found a similar seasonal pattern of chlorophyll *a* in Nabeta Cove of Oura Bay, our study site. Thus, *R. uritai* females are releasing larvae during the time of the year when there is a high probability of abundant food for larvae.

The larger sample sizes and continuous sampling throughout the year in this study allowed us to confirm the preliminary hypothesis of Bauer and Thiel (2011), which was based on a single small sample, that *R. uritai* is a protandric hermaphrodite. In all cohorts recruited into the Oura Bay population, juveniles first developed as males (male phase: MP), and then passed through a sex-changing (transitional) phase before becoming females (female phase: FP). Cohort analysis allowed us to estimate the total life span of two cohorts (at least 23 mon for cohort c; cohort d

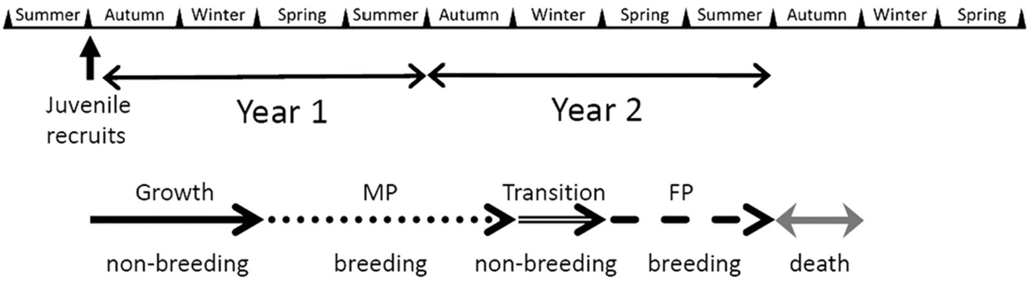

Figure 12. Population cycle of *Rhynchocinetes uritai*: recruitment, growth, sexual maturation of juveniles into the male phase (MP), with later change to the female phase (FP), and then disappearance (death) from the population.

was 12-mon-old with its individuals in MP stage at the end of the study). These figures are within the range reported for carideans from warm-temperate waters around the world and much less than the life spans of caridean species from higher latitudes (Bauer, 2004).

We were also, through cohort analysis, able to determine the time an average individual spends in each sexual phase. A typical individual functions as an MP only in its first year (Year 1), changing sex between reproductive seasons in the winter and early spring to FP in the second year (Year 2), with most individuals disappearing from the population before or early in their third year (Fig. 12). Sex change thus occurs during the winter months, the non-reproductive season. Because fecundity increases with larger size in *R. uritai*, it appears advantageous for individuals to remain male during the first reproductive season in order to grow and accumulate energy before changing to female during their second winter.

In this study, we have confirmed with extensive sampling over 2 years that *R. uritai* is a protandric hermaphrodite, as suggested by Bauer and Thiel (2011). We found that most MPs change sex at the time when the sex ratio becomes biased toward MPs because of the decrease (presumed mortality) of adult FPs after the reproductive season. The life-history traits discussed above for *R. uritai* fit the pattern typical of warm-temperate carideans worldwide (reviewed in Bauer, 2004), supporting the latitudinal paradigm in life-history traits for this and other crustacean taxa (Thorson, 1950; Sastry, 1983; Bauer, 2004).

Given that unrelated caridean species from a number of different families inhabiting nearshore, warm-temperate seas show similar population dynamics, these life-history traits do not appear to be phylogenetically constrained within the Caridea. Reproductive and recruitment patterns of *R. uritai* and other sex-changing species (Bauer and VanHoy, 1996; Bauer, 2002; Fransozo *et al.*, 2005; Baeza *et al.*, 2010) do not appear strikingly different from those of gonochoric carideans from similar latitudes. The protandric life cycle in *R. uritai* (Fig. 12) begins with recruitment, followed by development of individuals as MPs during their first reproductive season; these overwinter as transitionals, putting energy into growth for the sex change to FP during the non-reproductive season. Ovarian maturation, spawning, and larval development then take place during the spring-summer reproductive season, as in gonochoric warm-temperate carideans with small males and larger females. The findings of this study raise the question of why protandry has not evolved in more caridean species.

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Literature Cited

Alon, N. C., and S. E. Stancyk. 1982. Variation in life-history patterns of the grass shrimp *Palaemonetes pugio* in two South Carolina estuarine systems. *Mar. Biol.* **68:** 265–276.

Amin, S. M. N., A. Arshad, S. S. Siraj, and B. J. Sidik. 2009. Population structure, growth, mortality and yield per recruit of sergestid shrimp, *Acetes japonicus* (Decapoda: Sergestidae) from the coastal waters of Malacca, Peninsular Malaysia. *Indian J. Mar. Sci.* **38:** 57–68.

Baeza, J. A. 2010. Observations on the sexual system and the natural history of the semi-terrestrial shrimp *Merguia rhizophorae* (Rathbun, 1900). *Invertebr. Biol.* **129:** 266–276.

Baeza, J. A., and R. T. Bauer. 2004. Experimental test of socially mediated sex change in a protandric simultaneous hermaphrodite, the marine shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae). *Behav. Ecol. Sociobiol.* **55:** 544–550.

Baeza, J. A., and C. Piantoni. 2010. Sexual system, sex ratio, and group living in the shrimp *Thor amboinensis* (De Man): relevance to resource-monopolization and sex-allocation theories. *Biol. Bull.* **219:** 151–165.

Baeza, J. A., A. A. Braga, L. S. López-Greco, E. Perez, M. L. Negreiros-Fransozo, and A. Fransozo. 2010. Population dynamics, sex ratio and size at sex change in a protandric simultaneous hermaphrodite, the spiny shrimp *Exhippolysmata oplophoroides. Mar. Biol.* **157:** 2643–2653.

Baeza, J. A., R. T. Bauer, J. Okuno, and M. Thiel. 2014. Molecular phylogeny of hinge-beak shrimps (Decapoda: Caridea: *Rhynchocinetes* and *Cinetorhynchus*) and allies: a formal test of familiar and generic monophyly using a multilocus phylogeny. *Zool. J. Linn. Soc.* **172:** 426–450.

Baldwin, A. P., and R. T. Bauer. 2003. Growth, survivorship, life-span, and sex change in the hermaphroditic shrimp *Lysmata wurdemanni* (Decapoda: Caridea: Hippolytidae). *Mar. Biol.* **143:** 157–166.

Bauer, R. T. 1986. Sex change and life history pattern in the shrimp *Thor manningi* (Decapoda: Caridea): a novel case of partial protandric hermaphroditism. *Biol. Bull.* **170:** 11–31.

Bauer, R. T. 1989. Continuous reproduction and episodic recruitment in nine shrimp species inhabiting a tropical seagrass meadow. *J. Exp. Mar. Biol. Ecol.* **127:** 175–187.

Bauer, R. T. 1991. Analysis of embryo production in a caridean shrimp guild from a tropical seagrass meadow. Pp. 181–192 in *Crustacean Egg Production,* A. Wenner and A. Kuris, eds. Balkema, Rotterdam.

Bauer, R. T. 1992. Testing generalizations about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species. *Invertebr. Reprod. Dev.* **22:** 193–202.

Bauer, R. T. 2000. Simultaneous hermaphroditism in caridean shrimps: a unique and puzzling sexual system in the Decapoda. *J. Crustac. Biol.* **20:** 116–128.

Bauer, R. T. 2002. Reproductive ecology of a protandric simultaneous hermaphrodite, the shrimp *Lysmata wurdemanni* (Decapoda: Caridea: Hippolytidae). *J. Crustac. Biol.* **22:** 742–749.

Bauer, R. T. 2004. *Remarkable Shrimps: Adaptations and Natural History of the Carideans.* University of Oklahoma Press, Norman, OK.

Bauer, R. T., and J. H. Abdalla. 2000. Patterns of brood production in the grass shrimp *Palaemonetes pugio* (Decapoda: Caridea). *Invertebr. Reprod. Dev.* **38:** 107–113.

Bauer, R. T., and S. L. Conner. 2012. Gonochoric sexual system in the caridean shrimps *Processa riveroi* and *P. bermudensis* (Decapoda: Processidae) inhabiting a tropical seagrass meadow. *J. Mar. Biol. Assoc. U.K.* **92:** 521–529.

Bauer, R. T., and G. J. Holt. 1998. Simultaneous hermaphroditism in the marine shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae): an undescribed sexual system in the decapod Crustacea. *Mar. Biol.* **132:** 223–235.

Bauer, R. T., and M. Thiel. 2011. First description of a pure-search mating system and protandry in the shrimp *Rhynchocinetes uritai* (Decapoda: Caridea). *J. Crustac. Biol.* **31:** 286–295.

Bauer, R. T., and R. VanHoy. 1996. Variation in sexual systems (protandry, gonochorism) and reproductive biology among three species of the shrimp genus *Thor* (Decapoda: Caridea). *Bull. Mar. Sci.* **59:** 53–73.

Bauer, R. T., J. Okuno, and M. Thiel. 2014. Inferences on mating and sexual systems of two Pacific *Cinetorhynchus* shrimps (Decapoda: Rhynchocinetidae) based on sexual dimorphism in body size and cheliped weaponry. *Zookeys* **457:** 187–209.

Bergström, B. I. 2000. The biology of *Pandalus. Adv. Mar. Biol.* **38:** 55–245.

Braga, A. A., L. S. López-Greco, D. C. Santos, and A. Fransozo. 2009. Morphological evidence for protandric simultaneous hermaphroditism in the caridean *Exhippolysmata oplophoroides. J. Crustac. Biol.* **29:** 34–41.

Calado, R. 2008. *Marine Ornamental Shrimp: Biology, Aquaculture and Conservation.* Wiley-Blackwell, Oxford.

Castilho, A. L., M. A. Gavio, R. C. Costa, E. E. Boschi, R. T. Bauer, and A. Fransozo. 2007. Latitudinal variation in population structure and reproductive pattern of the endemic South American shrimp *Artemesia longinaris* (Decapoda: Penaeoidea). *J. Crustac. Biol.* **27:** 548–552.

Chace, F. A., Jr. 1997. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907–1910, Part 7: Families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae, and Hippolytidae. *Smithson. Contrib. Zool.* No. 587. 106 pp.

Charnov, E. L. 1981. Sex reversal in *Pandalus borealis:* effect of a shrimp fishery? *Mar. Biol. Lett.* **2:** 53–57.

Charnov, E. L. 1982. *The Theory of Sex Allocation.* Princeton University Press, Princeton.

Charnov, E. L., and P. J. Anderson. 1989. Sex change and population fluctuations in pandalid shrimp. *Am. Nat.* **134:** 824–827.

Charnov, E. L., D. W. Gotshall, and J. G. Robinson. 1978. Sex ratio: adaptive response to population fluctuations in pandalid shrimp. *Science* **200:** 204–206.

Chiba, S. 2007. A review of ecological and evolutionary studies on hermaphroditic decapod crustaceans. *Plankton Benthos Res.* **2:** 107–119.

Corey, S., and D. M. Reid. 1991. Comparative fecundity of decapod crustaceans. I. The fecundity of thirty-three species of nine families of caridean shrimp. *Crustaceana* **60:** 270–294.

Correa, C., and M. Thiel. 2003. Population structure and operational sex ratio in the rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *J. Crustac. Biol.* **23:** 849–861.

Correa, C., J. A. Baeza, E. Dupré, I. A. Hinojosa, and M. Thiel. 2000. Mating behavior and fertilization success of three ontogenetic stages of male rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *J. Crustac. Biol.* **20:** 628–640.

Correa, C., J. A. Baeza, I. A. Hinojosa, and M. Thiel. 2003. Male dominance hierarchy and mating tactics in the rocky shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *J. Crustac. Biol.* **23:** 33–45.

De Grave, S., and C. H. J. M. Fransen. 2011. Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). *Zool. Meded.* **85:** 195–588.

Fiedler, G. C. 1998. Functional, simultaneous hermaphroditism in female-phase *Lysmata amboinensis* (Decapoda: Caridea: Hippolytidae). *Pac. Sci.* **52:** 161–169.

Fransozo, V., R. C. Costa, G. Bertini, and V. J. Cobo. 2005. Population biology of spine shrimp *Exhippolysmata oplophoroides* (Holthuis) (Caridea, Hippolytidae) in a subtropical region, São Paulo, Brazil. *Rev. Bras. Zool.* **22:** 1078–1084.

Gavio, M. A., J. M. Orensanz, and D. Armstrong. 2006. Evaluation of alternative life history hypotheses for the sand shrimp *Crangon franciscorum* (Decapoda: Caridea). *J. Crustac. Biol.* **26:** 295–307.

Gayanilo, F. C., P. Sparre, and D. Pauly. 2005. *FAO-ICLARM Stock Assessment Tools II: User's Guide.* Food and Agriculture Organization of the United Nations, Rome.

Höglund, H. 1943. On the biology and larval development of *Leander squilla* (L.) forma typica De Man. *Svenska Hydrografisk-Biologiska Kommissionens Skrifter Ny Serie Biologie. Band II, No. 6:* 1–44.

Kikuchi, T. 1962. An ecological study on animal community of *Zostera* belt in Tomioka Bay, Amakusa, Kyushu. II. Community composition (2) Decapod crustaceans. *Rec. Oceanogr. Works JPN* **Series 6:** 135–146.

Lardies, M. A., and I. S. Wehrtmann. 2001. Latitudinal variation in the reproductive biology of *Betaeus truncatus* (Decapoda: Alpheidae) along the Chilean coast. *Ophelia* **55:** 55–67.

Laubenheimer, H., and A. L. Rhyne. 2008. Experimental confirmation of protandric simultaneous hermaphroditism in a caridean shrimp outside of the genus *Lysmata. J. Mar. Biol. Assoc. UK.* **88:** 301–305.

Li, H. Y., S. Y. Hong, and H. J. Jin. 2011. Fecundity and brood loss of sand shrimp, *Crangon uritai* (Decapoda: Crangonidae). *J. Crustac. Biol.* **31:** 34–40.

Lin, J., and D. Zhang. 2001. Reproduction in a simultaneous hermaphroditic shrimp, *Lysmata wurdemanni:* Any two will do? *Mar. Biol.* **139:** 1155–1158.

Longhurst, A. R. 1981. *Analysis of Marine Ecosystems.* Academic Press, New York.

Maihara, Y. 2002. Larval stages of the rhynchocinetid shrimp, *Rhynchocinetes uritai* Kubo, 1942 (Decapoda, Caridea, Rhynchocinetidae) reared under laboratory conditions. *Sci. Rep. Mus. Tokai Univ.* **4:** 59–77 (in Japanese with English abstract).

Marshall, D. J., P. J. Krug, E. K. Kupriyanova, M. Byrne, and R. B. Emlet. 2012. The biogeography of marine invertebrate life-histories. *Annu. Rev. Ecol. Evol. Syst.* **43:** 97–114.

McLaughlin, P. A., D. K. Camp, M. V. Angel, E. L. Bousfield, P. Brunel, R. C. Brusca, and D. Cadien. 2005. *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Crustaceans.* American Fisheries Society, Bethesda.

Okuno, J. 1997a. A new shrimp of the genus *Rhynchocinetes* from the Great Australian Bight (Crustacea: Decapoda: Rhynchocinetidae). *Rec. S. Aust. Mus.* **30:** 13–18.

Okuno, J. 1997b. Crustacea Decapoda: review on the genus *Cinetorhynchus* Holthuis, 1995 from the Indo-West Pacific (Caridea: Rhynchocinetidae). Pp. 31–58 in *Les Fonds Meubles des Lagons de Nouvelle-Calédonie (Sédimentologie, Benthos),* B. Richer de Forges, ed. ORSTOM, Paris.

Omori, M., and Y. Chida. 1988. Life history of a caridean shrimp *Palaemon macrodactylus* with special reference to the difference in reproductive features among ages. *Nippon Suisan Gakkaishi* **54:** 365–375.

Onaga, H., G. C. Fiedler, and J. A. Baeza. 2012. Protandric simultaneous hermaphroditism in *Parhippolyte misticia* (Clark, 1989) (Caridea: Hippolytidae): implications for the evolution of mixed sexual systems in shrimp. *J. Crustac. Biol.* **32:** 383–394.

Orton, J. H. 1920. Sea-temperature, breeding and distribution in marine animals. *J. Mar. Biol. Assoc. U.K.* **12:** 339–366.

Oya, F. 1987. Growth, stomach contents and parasites in a tidepool population of the hippolytid shrimp *Heptacarpus futilirostris,* with reference to reproduction. *Mar. Biol.* **96:** 225–234.

Pakhomov, E. A., P. Kuun, and C. D. McQuaid. 2000. Biology of the bottom-dwelling shrimp *Nauticaris marionis* Bate, 1888 at the sub-Antarctic Prince Edward Islands. *Polar Biol.* **23:** 522–530.

Pearse, J. S., J. B. McClintock, and I. Bosch. 1991. Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. *Am. Zool.* **31:** 65–80.

Ramirez-Llodra, E. 2002. Fecundity and life-history strategies in marine invertebrates. *Adv. Mar. Biol.* **43:** 87–170.

Sastry, A. N. 1983. Ecological aspects of reproduction. Pp. 179–270 in *The Biology of the Crustacea,* Vol. 8, *Environmental Adaptations,* F. J. Vernberg and W. B. Vernberg, eds. Academic Press, New York.

Semensato, X. E. G., and A. P. M. Di Beneditto. 2008. Population dynamic and reproduction of *Artemesia longinaris* (Decapoda, Penaeidae) in Rio de Janeiro State, south-eastern Brazil. *Bol. Inst. Pesca* **34:** 89–98.

Serisawa, Y., H. Takaki, A. Kurashima, and Y. Yokohama. 2001. Seasonal change in nitrate concentration in seawater and photosynthetic activity of bladelets of *Ecklonia cava* in Nabeta Bay, Shimoda, southern part of Izu Peninsula, Japan. *Nippon Suisan Gakkaishi* **67:** 1065–1071.

Terossi, M., I. S. Wehrtmann, and F. L. Mantelatto. 2010. Interpopulation comparison of reproduction of the Atlantic shrimp *Hippolyte obliquimanus* (Caridea: Hippolytidae). *J. Crustac. Biol.* **30:** 571–579.

Than, S. K. 2006. Population dynamics of *Gerres abbreviatus* Bleeker, 1850 from the Parangipettai waters, southeast coast of India. *Sri Lanka J. Aquat. Sci.* **11:** 1–19.

Thiel, M., S. T. C. Chak, and C. P. Dumont. 2010. Male morphotypes and mating behavior of the dancing shrimp *Rhynchocinetes brucei* (Decapoda: Caridea). *J. Crustac. Biol.* **30:** 580–588.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev. Camb. Philos. Soc.* **25:** 1–45.

Turner, R. L., and J. M. Lawrence. 1979. Volume and composition of echinoderm eggs: implications for use of egg size in life-history models. Pp. 25–40 in *Reproductive Ecology of Marine Invertebrates,* S. E. Stancyk, ed. University of South Carolina Press, Columbia, SC.

Wehrtmann, I. S., and M. A. Lardies. 1999. Egg production of *Austropandalus grayi* (Decapoda, Caridea, Pandalidae) from the Magellan region, South America. *Sci. Mar.* **63:** 325–331.

Wickler, W., and U. Seibt. 1981. Monogamy in Crustacea and man. *Z. Tierpsychol.* **57:** 215–234.

Wilson, K., and I. C. W. Hardy. 2002. Statistical analysis of sex ratios: an introduction. Pp. 48–92 in *Sex Ratios: Concepts and Research Methods,* I. C. W. Hardy, ed. Cambridge University Press, Cambridge.

Zupo, V. 1994. Strategies of sexual inversion in *Hippolyte inermis* Leach (Crustacea, Decapoda) from a Mediterranean seagrass meadow. *J. Exp. Mar. Biol. Ecol.* **178:** 131–145.