Spatial distribution in relation to life history in the neritid gastropod *Clithon retropictus* in the Kanzaki River Estuary, Osaka, Japan

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Abstract: Population structure, growth, reproductive activities and spatial distribution in a population of the neritid gastropod *Clithon retropictus* are described, and the effects of habitat stones on distribution and individual activities are investigated. Monthly changes in coupling behavior and abundance of egg capsules indicated that the main reproductive season is June. The occurrence of small juveniles indicated that recruitment occurred mainly between August and September in the lower intertidal region of the adult distribution range. Recruits grew to a large size (ca. 9 mm SL), reaching maturity in June of the second year (ca. 1 year old). Longevity was estimated to be at least 3.3 years. More than 90% of snails occurred on stones throughout the year, predominantly underneath stones on exposed substratum rather than those on submerged substratum. Snail abundance was significantly influenced by stone coverage, water condition and time of year (month). Stone manipulation revealed a positive relationship between snail abundance and stone abundance. Mating behavior occurred mainly on the upper or lateral surface of stones. The occupancy periods of individual snails on stones were positively correlated with stone size in autumn, but not in the other three seasons. Distances moved by individual snails per day were significantly shorter in winter than in the other seasons.

Key words: *Clithon retropictus*, density, life history, spatial distribution, stones

Introduction

The utilization of pebbles, cobbles and/or boulders as habitats by benthic invertebrates may positively influence the distribution of the latter by reducing physical stress, and providing feeding and egg-laying sites. The relationships of distribution with size and abundance of stones has been investigated for snails (Wada et al. 1983, Takada 1999, Kurihara 2000, Kobayashi et al. 2003, Kurihara 2007), crabs (Takada 1999, Lohrer et al. 2000), sea cucumbers (Sloan 1979, Wada 1992, Takada 1999), and starfish and sea urchins (Wada et al. 1983). However, few field studies have been conducted wherein the abundance or size of stones have been manipulated (see Takada 1999, Lohrer et al. 2000). Furthermore, so far as we know, no studies have examined the effects of stone size on suitability for occupation by or movements of individuals.

The gastropod *Clithon retropictus* (Martens, 1878) (Ne-ritidae) occurs on hard substrata, such as stones and concrete blocks, in brackish or freshwater riverbeds (Furujo & Tomiyama 2000, Ohara & Tomiyama 2000) in Japan, Korea, southern China and Taiwan (Nishiwaki 1996, Noseworthy et al. 2013). Many ecological studies, including salinity tolerance (Furujo & Tomiyama 2000, Hirata et al. 2001), reproductive activity (Nishiwaki et al. 1991a, Hirata et al. 2000, Shigemiyi & Kato 2001) and amphidromous migration (Ondo & Nakamoto 1964, Abe 1981, Abe 1983, Nishiwaki et al. 1991b, Shinkawa 1987, Furujo & Tomiyama 2000, Shigemiyi & Kato 2001, Kobayashi & Iwasaki 2002), have been conducted on the species. However, temporal changes in spatial distribution in relation to substratum and intertidal height have not been addressed. In addition, although stones are known to be essential for the habitat of *C. retropictus*, few studies have investigated the effects of stones on its spatial distribution of the latter, except for those which have suggested an association of snail occurrence with stone presence (Hirata et al. 1999, Furujo & Tomiyama 2000, Ohara & Tomiyama 2000).
This study aimed to clarify (1) the effect of stone size on abundance and movements of *C. retropictus*, and (2) the spatial distribution and movement patterns of *C. retropictus* in relation to life stage and seasonal activity.

**Materials and Methods**

**Study site**

The study was conducted during daytime low tide around spring tide on a tidal flat in the Kanzaki River Estuary, Osaka Prefecture (34°68′N, 135°41′E, Fig. 1), an area of significant *Clithon retropictus* abundance.

**Spatial distribution and seasonal population change**

Vertical distribution and size structure of *Clithon retropictus* were surveyed monthly from March 2012 to March 2013. Four transects were established (Lines A–D), each with 4 sampling points at different intertidal heights (SP. 1–4), running at right angles to the shoreline. The lowermost points of Lines B–D were in tidal pools (water depth: 6–7 cm) (Fig. 1). The substratum of the sampling points was composed of pebbles and cobbles on muddy sand and their intertidal heights ranged from −24 cm to +51 cm relative to mean tide level (MTL).

Snails within a 1 m×1 m quadrat at each sampling point were collected and their positions (on mud substrate, upper or lateral surfaces of stones, and underneath stones) recorded. Shell lengths of the snails were measured with calipers to the nearest 0.1 mm. The shell lengths of coupling snails (one snail mounted on the other) were measured and the respective position of each snail noted. All snails collected were subsequently released to the original site. Environmental conditions, such as intertidal height (height above datum line), coverage of substrate by stones (three ranks; I: 0–25%, II: 25–50%, III: 50–75%) and degree of water submergence (water-logged or exposed) were recorded for each sampling point.

Cohort analysis was based on size frequency histograms of the snails collected from the 16 sampling points. Normal curves were fitted to the histograms and size classes determined using Bhattacharya’s method in the FISAT II package (FAO 2002).

A general linear model (GLM) was used to determine the effects on snail density of intertidal height, degree of water submergence, coverage of stones and time of year (month), utilizing data from August, September 2012 and March 2013, when all environmental data were available. Interactions among these 4 factors were not examined. A generalized linear model with logistic regression was used to determine the effects of submerged or exposed conditions and time of year on the proportion of snails occurring underneath stones.

As for the coupling snail where one snail mounted on the other snail, the shell length relationship between the upper and lower snails was analyzed in the spawning (from June to August 2012) and non-spawning seasons (from October 2012 to March 2013), using Pearson’s product-moment correlation analysis or Kendall’s rank correlation analysis. The spawning season was determined from a survey of egg capsules (as explained below). Intertidal heights inhabited by individual snails were compared between the newly-settled juveniles smaller than 7 mm in shell length and adults recorded in September, using Mann-Whitney’s U-test assuming that individual data are independent.

Data analysis was conducted by parametric test when the residual of data showed a normal distribution. If the residual did not show a normal distribution, data were transformed into square-root, logarithmic or inverse values. Subsequently, a non-parametric test was conducted if the
transformed data also failed to show a normal distribution. All statistical analyses were conducted by JMP 9 (SAS Institute 2010).

Reproductive activity

Seasonal changes in the frequency of coupling snails were determined from monthly sampling along the four transects. Some of the coupling snails were collected in June and July 2012 (52 pairs) and in October 2013 (57 pairs), and sexed (determined by the presence or absence of a globular bursa copulatrix, following dissection), separately for upper and lower snails of each pair.

Seasonal changes in spawning activity were based on the number of egg capsules each month from October 2012 to October 2013 at SP. 3 (Line D), where snails were abundant. Egg capsule numbers on each of four stones were also counted (maximum and minimum lengths were; Stone 1, 13×8 cm; Stone 2, 20×15 cm; Stone 3, 27×21 cm; Stone 4, 11×5 cm).

Movements of individual snails

Daily movements of individual snails and overall seasonal patterns were determined from individually marked snails in May, July and September 2012, and January 2013. An area (4 m×4 m) (St. 3, Fig. 1) of variously sized stones was established, snails occurring within a 1 m radius from the center of that quadrat being individually marked on their shells by paint and the size (maximum length) of stones inhabited by the respective snails recorded. The snails were then replaced in their original position. The marker paint did not have any detectable influence on the snails. Marked snails were tracked for five days during each season, the position of individual snails within St. 3 and the sizes (maximum length) of stones inhabited by them being recorded. The distances moved by individual snails recovered within a 2 m radius from the release site were determined as the direct distance between the recovery site and the release site. The distances moved by individual snails per day were compared between the four seasons by the Kruskal-Wallis test. For each season, correlations between stone occupancy periods and respective stone sizes were tested by Kendall’s rank correlation analysis.

Field manipulation experiment

A field manipulation experiment was conducted from May 28 to June 26, 2013 to evaluate the effect of stones on the abundance of Clithon retropictus. A transect, 15 m long and running parallel to the shoreline (21 cm below MTL), was established at St. 1 (Fig. 1). The transect was selected on the basis of: (1) a suitable abundance of C. retropictus; (2) similar abundance of similarly sized stones (diameter: 2–5 cm) occurring throughout; and (3) absence of human disturbance. Thirty quadrats (50×50 cm) along the transect were randomly assigned to one of three treatments: T0 (zero stone density; no stones in the quadrat following manipulation); T1 (normal stone density; natural density of stones following manipulation); and T2 (double stone density; twice the normal density of stones in the quadrat following manipulation). There were ten replicates for each treatment type.

Quadrats were placed on alternating sides of the transect line to minimize potential edge effects and sampling disturbance. In each quadrat, the number of stones was noted, stones then being removed individually and resident snails counted. In T0 quadrats, stones were removed into a tray. Following sampling, they were not returned to their original quadrats. After each T2 quadrat was sampled, the stones removed from it were returned and stones from a T0 quadrat also added. After examination of the T1 quadrat stones, the latter were returned to their respective quadrats. All 30 quadrats were examined three times, initially before stone manipulation and subsequently 1 and 4 weeks following manipulation. T1 quadrats served as controls for the effects of sampling disturbance since there was no subsequent manipulation of stone density. All snails within each quadrat were collected and counted, subsequently being returned to their respective quadrat. Snail densities were analyzed by ANOVA or the Kruskal-Wallis test to examine any effects of the differing levels of stone density.

Results

Monthly changes in size distribution and growth pattern

Monthly changes in population structure from March 2012 to March 2013 resulted in all of the frequency histograms being polymodal, with three or four peaks (Fig. 2). Newly recruited juveniles (mean shell length 4.8 mm) appeared in September 2012, growing to a mean shell length of 7.4 mm in October, but with little subsequent growth until the following March (Fig. 3). Size groups of approximately 13, 17 and 21 mm observed in September were regarded as 1, 2 and 3 years old, respectively. Longevity was therefore estimated as being at least 3.3 years, given that egg deposition occurred during the peak period of reproductive activity (June).

Seasonal pattern of reproductive activity

Egg capsules were found from April to September, peaking in June (Fig. 4). Coupling snails were observed all year round, but the proportion peaked in June and July (Fig. 5). Most coupling pairs (49/52) collected in June and July 2012 were heterosexual, compared with only half (29/57) collected in October 2013. The proportion of heterosexual pairs was significantly higher in the summer months compared with autumn months (likelihood ratio $\chi^2 = 28.2$, df=1, $P<0.0001$).

The shell lengths of the upper and lower snails of coupling pairs were significantly positively correlated with each other in both the spawning and non-spawning seasons.
Spatial distribution

The mean density (snails m²) from 16 sampling points ranged from 30 (August 2012) to 15 (February 2013). Vertical distribution differed among the 4 transects (Fig. 6), the lower snails being significantly larger than their partners (spawning season, likelihood ratio χ²=118.60, df=1, P<0.0001; non-spawning season, likelihood ratio χ² =8.56, df=1, P=0.0034).

**Fig. 2.** Size frequency distributions of *Clithon retropictus* from March 2012 to March 2013 in the Kanzaki River Estuary. Arrowhead indicates mean shell length of each size class.

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7). Along Line A, the density was low at each point in spring and summer, and highest at SP. 3 in autumn and winter. Along Lines B and C, the density was highest at the lowermost point in spring and summer, the peak shifting to SP. 3 in autumn and winter. Along Line D, the density remained high at SP. 2 (8 cm below MTL) throughout all seasons.

Snail density was influenced by substrate moisture conditions, stone coverage and month, but not by intertidal height (Table 1), snails being more abundant at wetter sites than at well drained sites, as well as on sites with greater stone coverage (Fig. 8). Over 90% of snails occurred on stones, particularly in the autumn and winter months (Fig. 9). The proportion of snails occurring underneath stones was influenced by water condition and month (Generalized linear model: likelihood $\chi^2=150.3$, $P<0.0001$; water condition: likelihood $\chi^2=11.7$, $P<0.001$; month: likelihood $\chi^2=117.4$, $P<0.0001$). Snails occurring underneath stones were more abundant on exposed substratum (Range: 8.6–43.7%, mean±SD = 26.6±9.5) than on submerged substratum (6.4–37.3%, mean±SD = 20.5±11.4). The proportion of snails underneath stones was low in summer, but high in autumn and winter (Fig. 10).

Almost all coupling snails occurred on stones (June: 208/214 = 97.2%; July: 188/204 = 93.1%; August: 105/115 = 91.3%), coupling snails on stones being significantly more frequent than non-coupling in June (442/474 = 93.2%) (likelihood ratio $\chi^2=6.70$, df=1, $P=0.01$). However, in July and August the proportion of snails on stones was similar between coupling and non-coupling snails (July: 391/418 = 93.5%; August: 545/583 = 93.5%) (July: likelihood ratio $\chi^2=0.07$, df=1, $P>0.05$; August: likelihood ratio $\chi^2=0.82$, df=1, $P>0.05$). Most coupling snails occurring on stones were found on the upper or lateral surfaces (June: 184/208 = 88.5%; July: 157/188 = 85.5%; August: 88/105 = 83.8%). Coupling snails on the latter surfaces in June were significantly more frequent than non-coupling snails on the same surfaces (361/442 = 81.7%) (likelihood ratio $\chi^2=7.17$, df=1, $P=0.01$), whereas in July and August, the proportions of coupling and non-coupling snails (July: 328/391 = 83.9%; August: 439/545 = 80.6%) were similar (July: likelihood ratio $\chi^2=0.02$, df=1, $P>0.05$; August: likelihood ratio $\chi^2$
Newly-settled juveniles smaller than 7 mm in shell length occupied the lower region (mean ± SD = 18 ± 14 cm below MTL) within the adult snail distributional range (mean ± SD = 7 ± 15 cm below MTL) (Fig. 11) and were also distributed in lower intertidal zones than adults (Mann-Whitney's U-test, Z = −5.57, P < 0.0001).

Table 1. Results of general linear model for effect of intertidal height, stone-coverage, water-logged condition and month on snail density (R² = 0.47).

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<td>Intertidal height</td>
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<td>Stone-coverage</td>
<td>9.26</td>
<td>&lt;0.001</td>
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<tr>
<td>Water-logged condition</td>
<td>12.88</td>
<td>&lt;0.001</td>
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<td>Month</td>
<td>3.71</td>
<td>0.03</td>
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= 0.75, df = 1, P > 0.05).

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Fig. 7. Snail densities at 4 stations from the landward (SP. 1) to seaward (SP. 4) sites on 4 transects in March, June, September and December 2012.

Daily movements of individual snails and seasonal patterns

The distance moved by snails per day was 50–70 cm in spring, summer and autumn, with no significant difference among the three seasons, but was significantly shorter in winter (Kruskal-Wallis test, $\chi^2 = 125.98$, P < 0.0001, Fig.

Fig. 8. Mean snail density (+SD) in relation to stone-coverage (I: 0–25%, II: 25–50%, III: 50–75%) at water-logged (solid circles) and well drained sites (open circles) in August and September 2012, and March 2013.

Fig. 9. Monthly changes in the proportion of snails occurring on stones from May 2012 to May 2013. Vertical bars indicate 95% confidence limits based on a normal distribution.

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The time spent on the same stone was significantly positively correlated with the stone size in autumn, but not in other seasons (Table 2).

**Field manipulation experiment**

Prior to stone manipulation, snail densities were similar among the treatments (ANOVA, \( F=1.30, P>0.05 \)). However, one week and four weeks after stone manipulation, the snail densities showed significant differences among the three treatments (Fig. 13), being highest where stones were doubled and lowest where stones were removed (after

<table>
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<th>Season</th>
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<tr>
<td>Spring</td>
<td>209</td>
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<tr>
<td>Summer</td>
<td>256</td>
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<td>0.12</td>
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<tr>
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<td>186</td>
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<td>0.049</td>
</tr>
<tr>
<td>Winter</td>
<td>159</td>
<td>0.04</td>
<td>0.52</td>
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1 week: Kruskal-Wallis test, \( \chi^2=22.74, P<0.0001 \); after 4 weeks: \( \chi^2=21.96, P<0.0001 \).
Discussion

Egg capsules of Clithon retropictus in the Kanzaki River Estuary were observed from April to September, with the peak in June, indicating that the reproductive season occurs in the summer. Most coupling pairs of C. retropictus in the summer were heterosexual, in contrast to the lower frequency of heterosexual pairs in October, which indicates that coupling behavior observed in the summer was, in fact, mating behavior. Furthermore, the frequent observation of coupling behavior in June and July reflected that the peak of mating behavior occurred in those months. Oviposition was also peaked in June, and newly-settled juveniles appeared in September. Thus, recruitment occurred approximately 3 months after the main breeding season.

In the Isuzu River, Mie Prefecture, oviposition was found mainly in May and June, with newly-settled juveniles being found in August (Abe 1981). Similarly, oviposition behavior in the Egawa River, Hiroshima Prefecture, was observed from May to August by Shinkawa (1987). The reproductive season of a population in the Saigo River, Fukuoka Prefecture, occurs from April to September, peaking in June and July (Kobayashi & Iwasaki 2002), and newly-settled juveniles have been observed from August to September in the Goino River, Kagoshima Prefecture, (Furujo & Tomiyama 2000). Thus, the reproductive and recruitment seasons of the Kanzaki River population of C. retropictus are similar to those of other populations of the species in western Japan.

In contrast, Hirata et al. (2000) reported the reproductive period for a population in the Naka River, Shizuoka Prefecture, as occurring from February to August, peaking in May, on the basis of monthly changes in the number of spermatophores in the globular bursa copulatorix. Previously, Nishiwaki et al. (1991a) had reported that egg capsules from the same river population were found from March to August, with a peak in April, indicating that the reproductive season of the C. retropictus population in Shizuoka Prefecture is earlier by 1 to 2 months than that of populations in western Japan.

The smallest snail that exhibited coupling behavior during the main reproductive season had a shell length of 6.9 mm, well within the maximum shell length (9.0 mm) attained by newly-settled juveniles by the main reproductive season (June) of the following year and indicative of C. retropictus in the Kanzaki River reaching maturity at age one year. Maturation of similar aged individuals has already been established for another neritid snail Nerita japonica (Nakano & Nagoshi 1980).

Results from the present study suggested that the longevity of C. retropictus in the Kanzaki River is at least 3.3 years. The longevity of C. retropictus in the Saigo River, Fukuoka Prefecture can be estimated to be at least 3 years from the size frequency histogram in Kobayashi & Iwasaki (2002). The longevity of other neritid species, estimated from size frequency histograms, is 3 years for Nerita japonica (Nakano & Nagoshi 1980) and 2 years for Nerita squamulata (Kurihara 2007). In contrast, Shigemiya & Kato (2001), examining a growth line of shells, estimated longevity in C. retropictus as up to 20 years. The shorter life span estimated in the present study compared to Shigemiya & Kato (2001) is attributed not only to the different methods of age estimation, but also to the fact that the population treated in the present study did not include any freshwater populations, which are composed of older individuals.

Coupling behavior observed during the reproductive season was considered to be mating behavior, since most of the snails involved were male–female pairs. If so, the positive correlation in body size between such coupling snails can be explained by assortative mating resulting from mate choice, mate availability or mating constraints (Crespi 1989).

The positive correlation between shell lengths of coupling snails during the non-reproductive season could reflect an aggregative tendency due to reasons other than mating. In fact, the lower snails were significantly larger than those on top, possibly due to the inclination of the upper snails to treat larger snails as a substitution for stones.

Factors affecting the abundance of C. retropictus included substrate moisture condition, stone coverage and time of year. The importance of stones as the substrate is also implicated from our observations that more than 90% of snails occurred on stones irrespective of the season. The field manipulation experiment also confirmed the importance of stones for snail occurrence, since snail abundance increased with increasing stone abundance. There are also other reports showing that C. retropictus occurs more frequently on stones than on mud or sand (Ohara & Tomiyama 2000; Furujo & Tomiyama 2000).

Time of year was an important factor in snail abundance owing to the increase in snail density in autumn and winter, particularly at SP. 4 on transect Lines B and C. This decrease was concurrent with an event in which stones became covered with sand at those sites. Similar decreases in snail density following sand-covering of stones has also been recorded for Nerita squamulata (Kurihara 2007) and Clypeomorus subbrevicaula (Kurihara 2000) on a subtropical cobbled shore.

The present finding that snails were more abundant on a wet substrate than on a well-drained substrate, suggests that the former condition is important for C. retropictus, snails avoiding the latter. Dependency on substrate moisture conditions appeared to be greater in smaller snails because most juveniles were found in lower zones of the adult distributional range.

In the potamid Cerithidea rizophorarum living in an estuarine salt marsh, small individuals occur in puddles or lower intertidal zones, whereas the habitat of large individuals extends to higher zones (Wada & Nishikawa 2005). In
some batillarid and potamidid snails, including Batillaria multiformis, Cerithidea djadiariensis, C. cingulata and C. rhizophorarum, living near a mangrove forest, small snails occur in a lower intertidal area more frequently than large snails (Wakamatsu & Tomiyama 2000), whereas small individuals of Batillaria cumingi (Adachi & Wada 1999) and Hydrobia ulvae (Haugeois et al. 2002) occur at higher intertidal areas within their distributional range. Clearly, therefore, the recruitment sites of brackish water snails vary among species.

The following reasons for the preference of C. retropictus for stones as habitat are proposed: (1) provision of a source of food such as algae on the surface, (2) reduction of physical stress (including heat, desiccation, freezing, osmotic fluctuations and wave action), (3) provision of egg-laying sites, (4) provision of coupling sites and (5) provision of shelter from predators. Clithon retropictus is known to feed on epilithic microalgae (Antonio et al. 2010), the high density of snails on stones being due to the abundant epilithic microalgae growing on the stone surfaces (Ohara & Tomiyama 2000). The shelter from desiccation provided by stones is seen in the spatial distribution of C. retropictus being closely related to water presence, more snails occurring beneath exposed stones than under submerged ones. In addition, stones may provide shelter from cold, as indicated by the presence of a greater proportion of snails underneath stones in winter.

Stones are also used for oviposition sites, egg capsules having been observed on stones during the present study. Nishiwaki et al. (1991a) also reported C. retropictus eggs laid on a concrete block, a hard surface being a necessary factor. It was noted that stones were used for mating sites, most coupling snails in the reproductive season having been recorded on stones, especially on the upper or lateral surfaces. Coupling behavior underneath stones was clearly difficult.

Daily movements of individual snails revealed that the period spent on the same stone increased with stone size in autumn, not so in spring, summer or winter. In winter, this may reflect inactivity of snails at low temperatures. However, the lack of any relationship between time spent on a stone and stone size in spring and summer may be attributed to more active movement, irrespective of stone size.

In conclusion, the abundance of C. retropictus is influenced mainly by the amount of stones and the substrate moisture condition. The seasonal pattern of their distribution is a result of seasonal variation in individual activity as well as by seasonality of reproductive activities.

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