Introduction

Ecological studies in subtropical sea areas have focused on coral reefs (e.g., Karlson 1999), mangroves (e.g., Lacerda 2002) and seagrass beds (e.g., Hemminga & Duarte 2001). These studies cover the population dynamics and community ecology of corals, mangroves, seagrasses and the inhabitants thereof. The studies have led to new concepts in ecology and fishery science (e.g., high species diversity in a non-equilibrium state (Connell 1978), plant-animal symbiosis as a tool for aquaculture (Heslinga et al. 1984, Shokita et al. 1991)).

Far fewer studies, however, have focused on other habitats in subtropical sea areas. One such habitat is cobbled shores (Baron 1992, Baron & Clavier 1992, Kurihara et al. 2001, Kurihara 2002, 2003). Many of the cobbled shores in subtropical Japan are smaller than 10,000 m² (Kurihara personal observations). In addition, these shores are often covered and disturbed by sand which terrestrial runoff transports (Kurihara et al. 2001, Kurihara 2002). Apparently, small habitat leads to small population size and severe disturbance results in high mortality, which may cause extinction of most species (Begon et al. 2006).

On subtropical cobbled shores, however, do many endemic species occur (e.g. several gastropod species in Neritidae, Turbinidae, Cerithidae, Siphonariidae; several bivalve species in Arcidae, Psammobiidae, Veneridae; Kubo & Kurozumi 1995 and Kurihara et al. 2000). How these species live in such a harsh environment is of significant ecological interest. The present study focuses on the gastropod, *Nerita squamulata* Le Guillou 1841, a dominant species on the cobbled shores (maximum density at Ishigaki Island, Japan: 500 m⁻², Kurihara et al. 2000, 2001).

Life-history traits of a gastropod, *Nerita squamulata* Le Guillou 1841, on a subtropical cobbled shore disturbed by sand

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Received 17 December 2006; Accepted 19 October 2007

Abstract: Cobbled shores in subtropical Japan are small and disturbed by sand transported from terrestrial runoff. How benthic organisms live in such a harsh environment has been seldom studied. On a cobbled shore at Ishigaki Island, the present study investigated the life-history traits of the gastropod, *Nerita squamulata* Le Guillou 1841. Seasonal quadrat samplings showed that the neritid density decreased when and where sand covered cobbles, indicating impact of sand on the neritid. Monthly frequency histograms of the shell width suggested that the neritid lives less than 2 years and recruits as individuals of 1–4 mm shell width in both May–August and February. With the possible short longevity and frequent recruitments, the neritid population may quickly recover after the disturbance by sand.

Key words: disturbance by sand, growth, longevity, neritid, recruitment period

Materials and Methods

Study site

The study site was a cobbled shore (124° 13’ 29” E, 24° 28’ 3” N, ca. 8,000 m²) at Ishigaki Island, Okinawa, subtropical Japan. The tides are semidiurnal with a mean range of 1.6 m from the mean high-water springs to the mean low-water springs. Around the mean tide level, one to two layers of cobbles (diameter = 3 cm) were distributed on a sandy bottom layer. Above the highest sea level, a brook flowed. When this brook was flooded by heavy rain, it tended to transport sand, which covered the cobbles. The temperatures during the survey period were high in July to August (air temperature: 30.2–30.3°C, surface water temperature: 31.9–33.3°C) and low in January (18.8°C,
20.4°C). The wave height was generally low (10 cm at most; measured at low tide at ≈50 cm depth), because the shore is protected by an offshore coral reef. Epifauna on the shore consisted mainly of Gastropoda (for details, see Kurihara et al. 2000).

**Sampling methods**

Seasonal surveys were conducted to examine how the distribution pattern of *Nerita squamulata* changes before and after disturbance by sand. Neritid densities and percent coverages of the cobbles not covered by sand were estimated in June, namely the rainy season around the study site, and in March and September 1998. An $8 \times 2$-m² plot consisting of four $2 \times 2$-m² subplots was set at each of 6 shore levels (defined as “the heights from the mean sea level” + 1 m, Fig. 1). In each subplot, a quadrat ($0.30 \times 0.30$ m² for the lowest 2 shore levels and $0.50 \times 0.50$ m² for the others) was thrown in each month, so that the position of the quadrat differed according to month. In the quadrat, all neritid individuals visible to the naked eye were counted. Sediments in the quadrat were categorized into cobbles and sand, and the cobble coverage was estimated after Kurihara et al. (2001).

At a location ca. 30 m eastward from these plots, monthly surveys were also made to investigate distribution pattern, growth pattern, and recruitment period for the neritid. In a similar manner to the foregoing survey, four $0.25 \times 0.25$-m² quadrats were set monthly from April 1998 to March 1999 at each of 10 shore levels, “SL1” to “SL10” (Fig. 1). From the quadrat, all neritid individuals found were temporarily moved to the laboratory for the measurement of the shell width (Fig. 2) with a digital calipers ($\pm 0.01$ mm; Mitutoyo Digimatic Caliper). The measurer could stabilize the sample between the teeth of the calipers more easily when measuring the shell width than when measuring the shell height, a frequently-used index of body size of gastropods.

Distribution patterns were analyzed for shell-width classes of 0–4, 4–8, and 8-mm with the index $I_\delta$ (Morishita 1959). $I_\delta$ exceeding 1 indicates an aggregated distribution pattern. This index was calculated in two ways: (1) across the 10 shore levels to analyze aggregation at certain shore levels and (2) across the 4 quadrats within each shore level to analyze aggregation within a shore level. These $I_\delta$ were calculated only when the number of individuals summed across the 10 shore levels or 4 quadrats exceeded 1. The vertical distribution pattern of each size class was also analyzed by calculating the relative density for each shore level: $100 \times$ (density at a shore level)/(sum of densities across all the shore levels).

A shell-width frequency histogram (interval: 1 mm) showed 1 to 4 peaks in each month (see Results), and these peaks were in general defined as the typical shell width of each cohort. In the analysis of shell-width frequency histograms, no algorithm (e.g. Aizawa & Takiguchi 1999) was used. This is because many cohorts determined by such algorithms were unlikely to reflect the true cohorts in each histogram: the cohorts determined did form a bell-shaped curve whose peak greatly (2–3 mm) differed from any peaks in the raw data.

**Results**

Sand covered the cobbles in June due to heavy rain, resulting in low cobbles coverage (Fig. 3). The density of *Nerita squamulata* was correspondingly lower in June (mean±SD: $21.6 \pm 28.8$ m⁻²) than in March ($207.0 \pm 130.0$ m⁻²) and September ($194.1 \pm 222.3$ m⁻²). For each season, the density was higher where cobbles coverage was higher.

The vertical distribution pattern of the neritid in the monthly surveys is shown in Fig. 4. The pattern was non-unimodal for most months. In April 1998, for example, relative density showed maximal values at SL2 and SL7 for the 0–4 mm class; at SL1 and SL3 for the 4–8 mm class; and at SL1, SL4, SL6 for the 8-mm class. The shore level
with each size class showing the highest relative density changed frequently from one month to the next. From December 1998 to January 1999, for example, such shore level changed from SL2 to SL7 for the 0–4 mm class; from SL3 to SL7 for the 4–8 mm class; and from SL1 to SL2 and SL9 for the 8-mm class. Both $I_d$, calculated across the shore levels (Table 1) and within each shore level (Table 2), always had the median exceed 1, indicating aggregated distribution pattern of the neritid.

In shell-width frequency histograms (Fig. 5), the neritid showed 1 to 4 peaks for each month. Most of these peaks were grouped into Cohorts A to D. The typical shell width of Cohort A increased from 2–3 mm in May 1998 to 8–9 mm in March 1999, intermittently stopping the growth apparently. The typical shell width of Cohort B increased from 8–9 mm in April 1998 to 9–10 mm in August 1998, also with apparent intermittent halts in growth. Although Cohort B was not discerned in September 1998, it possibly existed until November 1998 and showed a typical shell width of 12–13 mm. The typical shell width of Cohort C increased from 3–4 mm in February 1999 to 5–6 mm in March 1999. Cohort D existed in April 1998 and possibly in June to July, keeping the typical shell width being 5–6 mm.

### Discussion

*Nerita squamulata* is likely to be disturbed by sand. This is suggested from the seasonal surveys in which the density was lower when and where sand covered cobbles. The disturbance explains in part the neritid’s distribution patterns in the monthly surveys: sand covered cobbles at certain shore levels and quadrats (Kurihara, personal observation), which may result in the aggregated distribution patterns among shore levels and quadrats; and the shore levels with

<table>
<thead>
<tr>
<th>Table 1. Morishita’s index of dispersion, $I_d$, calculated across shore levels. “n” denotes the number of $I_d$ calculated.</th>
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<tbody>
<tr>
<td><strong>Shell width (mm)</strong></td>
</tr>
<tr>
<td>Maximum</td>
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<td>3rd quartile</td>
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<td>Minimum</td>
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<td>n</td>
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<th>Table 2. Morishita’s index of dispersion, $I_d$, calculated across quadrats within a shore level. “n” denotes the number of $I_d$ calculated. Note that $I_d$ was calculated only when the number of individuals summed across the quadrats exceeded 1.</th>
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<td><strong>Shell width (mm)</strong></td>
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<td>Minimum</td>
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<td>n</td>
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abundant sand changed from month to month (Kurihara, personal observation), which results in the unstable and non-unimodal patterns of the neritid’s vertical distribution. Such influences of sand have been also suggested for the gastropods, *Clypeomorus subbrevicula* and *Patelloida striata*, on subtropical cobbled shores (Kurihara 2000, 2002).

In the habitat disturbed greatly by sand, the neritid possibly has advantageous traits, namely, short longevity and multiple recruitment periods, as follows.

The longevity of the neritid may be <2 years, as indicated from the inferences below. (1) Cohort A suggests that the neritid grows from 2–3 mm to 8–9 mm in shell width over a period of 10 months from May to the next March. (2) Cohorts A and B suggest that the neritid grows minimally for 1 month from March to April. (3) Cohort B suggests that the neritid grows from 8–9 mm to 12–13 mm over a pe-

To recruit onto the habitat shortly after the disturbance by sand and grow rapidly to be able to reproduce. Short longevity and frequent recruitments bring about a high intrinsic rate of increase, which is considered to be advantageous in habitats with severe abiotic disturbance (Begon et al. 2006). The traits explain the high density of the neritid on cobbled shores at Ishigaki Island (Kurihara et al. 2000).

Estimates and analyses in the present study possibly contain errors. A growth pattern and recruitment period estimated from size frequency histograms tend to include more errors, when the bell-shaped curves in the histograms have a large variance as in the present study (Yamakawa 1997). The differences of (Nagoshi & Berndt 1980, 1983) from other confamilial species (Table 3) reflect not only the uniqueness of cobbled shores but also other factors (e.g. high temperature in subtropical region including the studied cobbled shore). These problems should be addressed through further investigations such as mark-recapture experiment to estimate growth rate; histological observation to estimate recruitment period; and comparison between (Nagoshi & Berndt 1980, 1983) and closely related taxa on different sediments with many factors (e.g. climatic region) controlled.

Acknowledgements

I thank Dr. Y. Nakamura for his comments on this paper; Dr Y. Takada for his help in the field; and Mrs. M. Ogura and Mrs. Y. Hosokawa for their help in the laboratory.

References


Baron J (1992) Reproductive cycles of the bivalve molluscs Atactodea striata (Gmelin), Gafarium tumidum Roeding and

### Table 3. Longevity, recruitment mode, and habitat type of the species in Neritidae.

<table>
<thead>
<tr>
<th>Species</th>
<th>Maximum longevity (yr)</th>
<th>Frequency of recruitment (/yr)</th>
<th>Substratum of study site</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heminerita japonica</td>
<td>3</td>
<td>1</td>
<td>Rock</td>
<td>Nakano &amp; Nagoshi 1980, 1983</td>
</tr>
<tr>
<td>Nerita atramentosa</td>
<td>3 to 5.5</td>
<td>1</td>
<td>Rock</td>
<td>Underwood 1975</td>
</tr>
<tr>
<td>Nerita albicilla</td>
<td>12</td>
<td>1</td>
<td>Beach rock</td>
<td>Frank 1969</td>
</tr>
<tr>
<td>Nerita polita</td>
<td>4</td>
<td>No report</td>
<td>Beach rock</td>
<td>Frank 1969</td>
</tr>
<tr>
<td>Nerita squamulata</td>
<td>2</td>
<td>2</td>
<td>Cobble</td>
<td>The present study</td>
</tr>
</tbody>
</table>

Nerita squamulata at the present study site possibly recruits at least twice a year. This is because the size frequency histograms twice showed a peak at small shell widths, 2–4 mm, in May–August 1998 and February 1999, although the latter peak was somewhat unclear. Multiple recruitment periods for this species are also suggested from seasonal measurements of its shell width on cobbled shores near the study site (Kurihara et al. 2001). Multiple recruitment periods and/or long recruitment periods (>0.5 yr) are also suggested for the molluscs Turbo coronatus coronatus (Fuse 1993), Atactodea striata and Gafarium tumidum (Baron 1992) which often inhabit subtropical cobbled and sandy shores (Kubo & Kurozumi 1995). The intermittent and long recruitment periods may be possible owing to the gradual seasonal changes of environmental factors (e.g. temperature) in subtropical area. In contrast to the above-mentioned molluscs, only one short recruitment within a year is indicated for (Nagoshi & Berndt 1980, 1983); May for (Nagoshi & Berndt 1980, 1983); and May to June for (Nagoshi & Berndt 1980, 1983).

The short longevity and multiple recruitments within a year suggested for only (Nagoshi & Berndt 1980, 1983) among the confamilial species can be related to its unique habitat, namely, cobbled shores. The two traits enable (Nagoshi & Berndt 1980, 1983) to recruit onto the habitat shortly after the disturbance by sand and grow rapidly to be able to reproduce. Short longevity and frequent recruitments bring about a high intrinsic rate of increase, which is considered to be advantageous in habitats with severe abiotic disturbance (Begon et al. 2006). The traits explain the high density of the neritid on cobbled shores at Ishigaki Island (Kurihara et al. 2000).