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REPRODUCTION AND GROWTH OF *LITTORARIA* (GASTROPODA: LITTORINIDAE) AT ANG SILA, THAILAND

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***ABSTRACT.* –** Little is known of reproductive patterns of molluscs inhabiting mangroves. Yet this is one of the dominant environments in tropical intertidal areas and molluscs are one of the dominant faunal groups in mangroves. Several species of the gastropod genus *Littoraria* are adapted specifically to life in mangrove environments. The present paper examines reproductive periodicity in four species of *Littoraria* from Ang Sila, Thailand, from June 2003 to June 2004. Monthly samples were made to measure reproduction and growth. Ripe or partly spawned animals occurred throughout study, suggesting that these species are capable of either partially spawning frequently or rapidly returning to reproductive condition after spawning. The major spawning occurred in August–September 2003 and January–February 2004. *Littoraria pallescens* had a clear growth pattern with a one-year life cycle. In contrast, there was apparent recruitment failure in *L. melanostoma* and the combination of *L. articulata* and *L. strigata*.

***KEYWORDS.* –** *Littoraria pallescens*, *Littoraria melanostoma*, adaptation, spawning, life cycle, recruitment.

INTRODUCTION

Molluscs are one of the key faunal groups in mangroves in Southeast Asia. Molluscan assemblages in the mangroves are diverse (Macnae, 1968). Many of the molluscs that occur in mangroves are also found on adjacent intertidal shorelines: rocky, sandy and muddy. The molluscs simply use the mangroves as an additional habitat. Cantera et al. (1983) estimated that 80% of the gastropod species in mangroves are incidental to the tree zones; only 20% are adapted to the mangrove system. The few species adapted specifically to life in the mangroves can be abundant and have a high biomass (Wells, 1983, 1984a, 1986). *Littoraria* is one of the few genera of gastropods adapted to living in mangrove systems. Reid (1986) revised the group and recorded 20 species in the Indo-West Pacific; additional species have since been described (Reid, 2001; Stuckey & Reid, 2002). Sanpanich et al. (2004) studied the distribution of the family Littorinidae in Thailand. Ten species of *Littoraria* were recorded, with most occurring widely in both the Andaman Sea and the Gulf of Thailand. Although there have been a number of studies on the systematics, biology and ecology of *Littoraria* in Southeast Asia (Little & Stirling, 1984; Reid, 1985, 1986, 1999; Cook & Garbett, 1989; Ohgaki, 1992; Buckland-Nicks et al., 2000; Sanpanich et al., 2006), there have been few papers (Gallagher & Reid, 1974; Burgett et al., 1987; Jensen et al., 1999; Reid, 2001; Black & Johnson, 2001) on their reproduction and growth. To help fill this gap, the present paper examines seasonal patterns of reproduction and growth in four species of *Littoraria* in the Gulf of Thailand.

MATERIALS AND METHODS

The present study was conducted at a small mangrove habitat at Ang Sila, Thailand (13º19'03"N 155º47'05"E). Wells et al. (2001) provided a detailed description of the area. It is an intertidal sand/mudflat with a disused crab holding area consisting of a low concrete wall about 45 cm high. Portions of the sides of the concrete enclosure are fringed by mangroves, largely *Avicennia* and *Rhizophora*. There is also a small area dominated by the sedge *Sesuvium portulacastrum* (Linnaeus) Linnaeus, 1759. Five species of *Littoraria* are present: *L. articulata* (Philippi, 1846), *L. carinifera* (Menke, 1830), *L. melanostoma* (Gray, 1839), *L. pallescens* (Philippi, 1846), and *L. strigata* (Philippi, 1846). *Littoraria carinifera* was not sufficiently abundant to work with and will not be examined here. The shells of *L. articulata* and *L. strigata* cannot be separated in the field, but Reid (1986) considered them to be distinct species. Relaxed males can be distinguished on the basis of penial morphology; separation is much less reliable in females. For this study, seasonality of gonadal state was determined for males, and a combined size frequency was determined for the two species.

To examine reproductive state, ten individuals each of males and females of *Littoraria pallescens* and *L. melanostoma* were collected at Ang Sila monthly for 13 months from Jun.2003 to Jun.2004; 10 males each of *L. articulata* and *L. strigata* were collected. All specimens were kept alive until dissection in the laboratory. For paraffin sections, the gonads were cut and fixed at 4ºC overnight in Bouin's solution. The gonads were washed in 70% ethyl alcohol to remove the Bouin's fixative then dehydrated in a graded series of ethyl alcohol (70–100%) for 30 min each, cleared with dioxane, infiltrated and embedded in paraffin wax. Blocks of specimens were sectioned at 3–5 µm, stained with haematoxylin-eosin and PAS-haematoxylin, and observed under a light microscope equipped with a camera. Gonadal state was divided into five categories similar to those described by Sobhon et al. (1999): early development, late development, mature (ripe), partly spawned and spawned.

***Early development.* –** In the ovary, early stage cells are attached to the cell wall of the egg acinus, together with a few mature eggs. Most of the egg acini are small, whereas sperm acini are larger but are composed of many small sperm acini that have immature sperm inside. The hepatopancreas is expanded and begins to pack together.

***Late development.* –** Gonads of both males and females are composed of many acini that have a tendency to expand to fill all the space outside the hepatopancreas. There are many large, mature eggs in the ovary attached to the wall together with a few immature eggs. The sperm acini are expanded.

***Mature (ripe).* –** Gonads of both males and females contain fully mature germ cells with only a few immature gametes along the wall of the acinus. The gonad is full and swollen.

***Partly spawned.* –** Each of the numerous acini has some fully developed and some early oocytes which are loosely packed. There is considerable open space in the ovary as most of the oocytes have been released. Similarly in the testis there are spaces from which sperm had been released. The gonads are composed largely of mature eggs or sperm whereas the earlier stages of gamete cells are still attached to the dilated traberculae of the acini.

***Spawned.* –** In both testis and ovary, fully mature gametes have been discharged. There are large spaces in the gonads. The hepatopancreas is formed in large loops that are widely spaced because the gametes have been released. Residual oocytes and sperm can remain in the gonads.

Six females of *Littoraria pallescens* and *L. melanostoma* were collected monthly five days before the full moon for 13 months and placed individually in small jars for two weeks to allow spawning. Larvae (*L. pallescens*) and eggs (*L. melanostoma*) were collected daily and counted using a counting chamber. Data presented are totals of larvae or eggs released by individuals over the two week period. The snails were returned to the environment after the observations were finished.

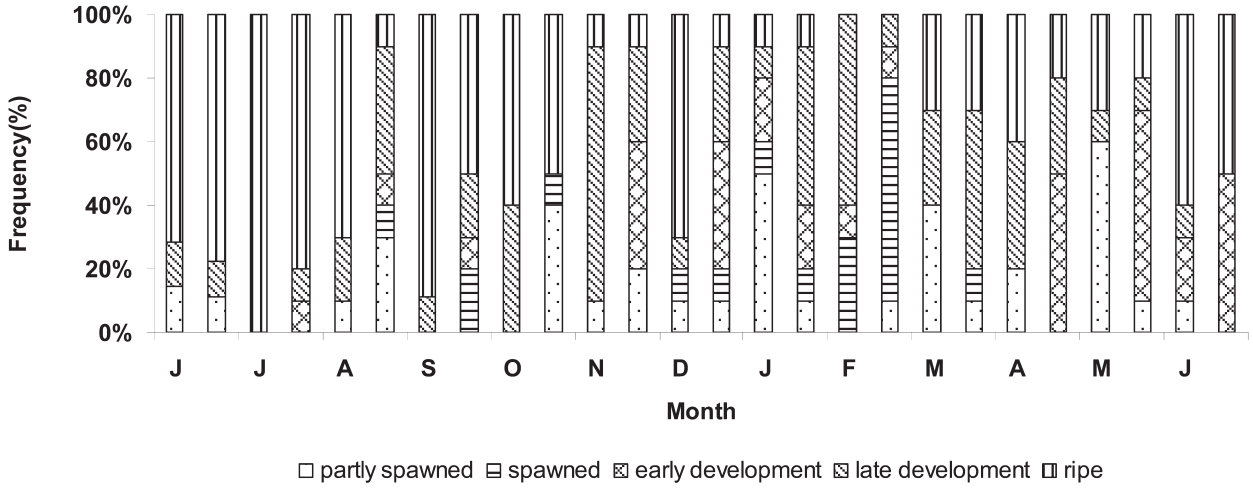
Four hundred individuals each of *Littoraria pallescens*, *L. melanostoma* and mixed specimens of *L. articulata* and *L. strigata* were collected monthly for 13 months to measure size frequency throughout the year. Densities were too low to collect the necessary number of individuals on quantitative transects. Instead, the collectors began at the southeastern corner study site and moved north, parallel to the concrete wall. This strategy ensured all available habitats were searched, including all parts of the mangrove trees, the concrete wall, sediment surface and *Sesuvium.* At the northern extent of the *Sesuvium*, the collector changed direction and collected in a southerly direction further east of the concrete wall. *Littoraria pallescens* occurred primarily in the trees, in both the upper foliage and on the trunks, whereas *L. melanostoma*, *L. articulata* and *L. strigata* all occurred primarily on the lower parts of the trees, near the sediment surface and up the trunk. All three occurred on bamboo poles associated with the former shrimp farm and on the concrete wall. They also occurred in *Sesuvium* and rarely on the open mud surface. All of these habitats were sampled each month. Voucher material is held by the Zoology Museum, Institute of Marine Sciences, Burapha University.

The data were compared between months to examine growth rates.

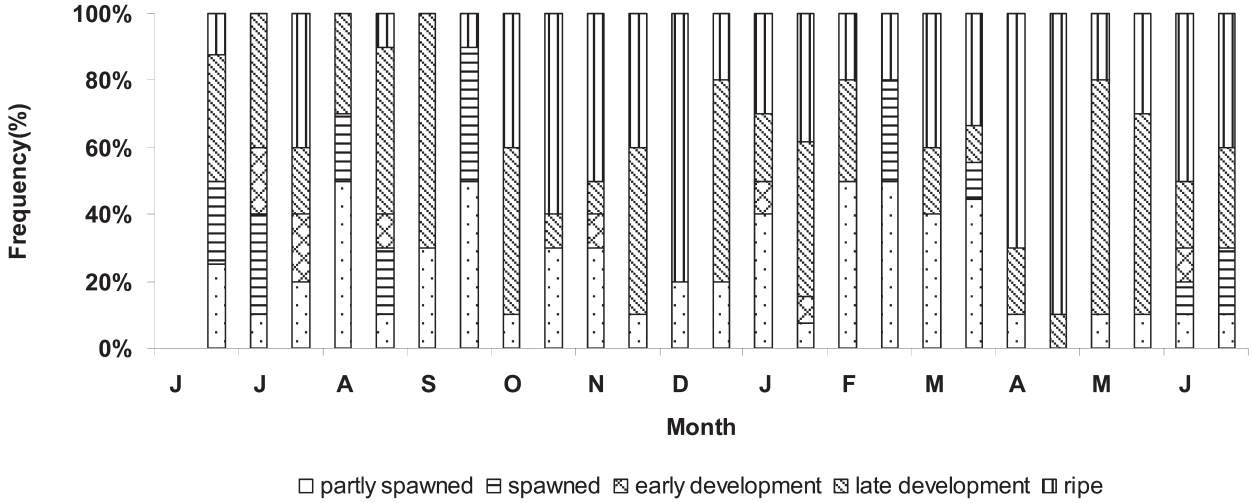
RESULTS

Figure 1 shows the reproductive stages of *Littoraria pallescens*, *L. melanostoma* and the combination *of L. articulata* and *L. strigata* from Jun.2003 to Jun.2004. Although there were fluctuations between months within a species, between sexes and between species, a pattern

L. pallescens



L. melanostoma



L. articulata/strigata

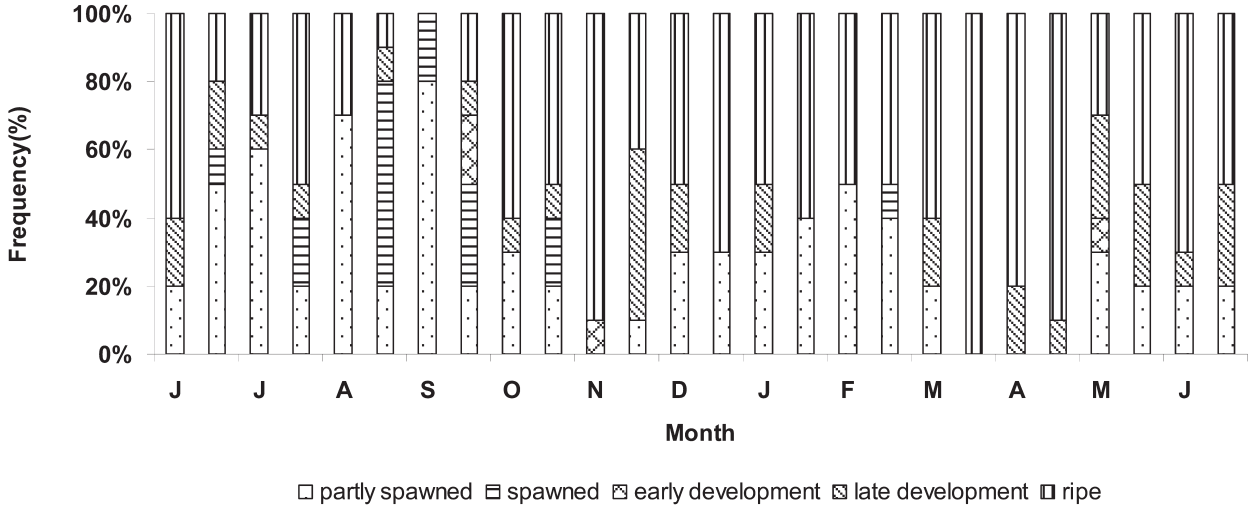


Fig. 1. Reproductive stages of *Littoraria pallescens*, *L. melanostoma* and *L. articulata/strigata* at Ang Sila, Thailand, from Jun.2003 to Jun.2004.

is relatively clear. There was a tendency for spawning to have occurred in Aug.–Sep.2003. Males of *L. pallescens*, *L. melanostoma* and *L. articulata* and females of *L. pallescens* all spawned in August. Females of *L. melanostoma* and males of *L. strigata* spawned in September. This pattern was repeated in Jan. and Feb.2004. Males of *L. pallescens* spawned in January, and the remaining classes in February.

In the laboratory, females of *Littoraria pallescens* released between 254,000 ± 100,000 and 408,000 ± 88,000 larvae per month in the period of Jul.–Nov.2003 (Fig. 2). There were no further releases until 396,000 ± 22,000 were released in Jun.2004. Females of *L. melanostoma* released larvae in only three months: means of 119,000 ± 70,000 in Nov.2003; 141,000 ± 98,000 in Feb.2004; and 128,000 ± 0 in Jun.2004.

Growth data for *Littoraria pallescens* are convincing, and are consistent with the interpretation that there was a major spawning late in 2003. During the period of Jul.2003 to Feb.2004, the size frequency curves for the population were unimodal, with an average size that ranged slightly between 17.1 and 17.6 mm (Fig. 3). In March, for the first time, the curve was bimodal. There was a substantial cohort of young individuals, which comprised 39% of the population and had a mean length of 6.6 mm; year-old individuals were 61% of the population and had a mean length of 17.6 mm. The young grew rapidly, reaching a mean size of 9.6 mm in April, when they were 69% of the population. They increased further to a mean length of 12.0 mm and 75% of the population in May. By June the population was again unimodal, with a mean length of 14.8 mm. This suggests that the adults died out and were replaced by young individuals within the year. In contrast, the size frequency curves for *L. melanostoma* and the combination of *L. articulata* and *L. strigata* were unimodal throughout the year (Figs. 4–5); there was no period of influx of large numbers of juveniles, although there were small numbers of juvenile *L. melanostoma* in Aug. and Oct.2003 and Feb.2004.

DISCUSSION

Most tropical species of *Littoraria* release planktotrophic veligers but a few species brood embryos (Reid, 1986, 1999). Berry (1986) studied semilunar and lunar spawning periodicity in tropical littorinid gastropods. *Littoraria strigata*, *Echinolittorina vidua* (Gould, 1859) (as *Nodilittorina millegrana* (Philippi, 1848) and *E. trochoides* (Gray, 1839) (as *N. pyramidalis* Quoy & Gaimard, 1833) spawned regularly in a Malaysian bay during March to June, but not from July to October. *Echinolittorina vidua* showed the least precise timing, spawning between two days before and seven days after the new or full moon and their associated spring tides. Spawning of *E. trochoides* was more strictly confined to spring tides with ~90% of eggs appearing between two days before and five days after the new or full moon. *Littoraria strigata* also spawned regularly on the spring tides with ~89% of eggs appearing between one and five days after the new and full moon. However, full moon spawnings (when spring tides are highest) yielded an average of seven times more eggs than the weaker new moon tides (Berry, 1986). Burgett et al. (1987) reported *L. angulifera* (Lamarck, 1822) spawned through at least 10 months of the year, peaking in the spring and autumn between June and December and being minimal in December and March. Berry & Chew (1973) reported that egg capsules of *L. melanostoma* were released almost entirely during the full moon spring tides and occurred at all seasons of the year. Thus the general pattern appears to be that whereas spawning can be seasonal, it tends to occur over a wide period, but is closely related to the lunar phases. Our size frequency samples were collected

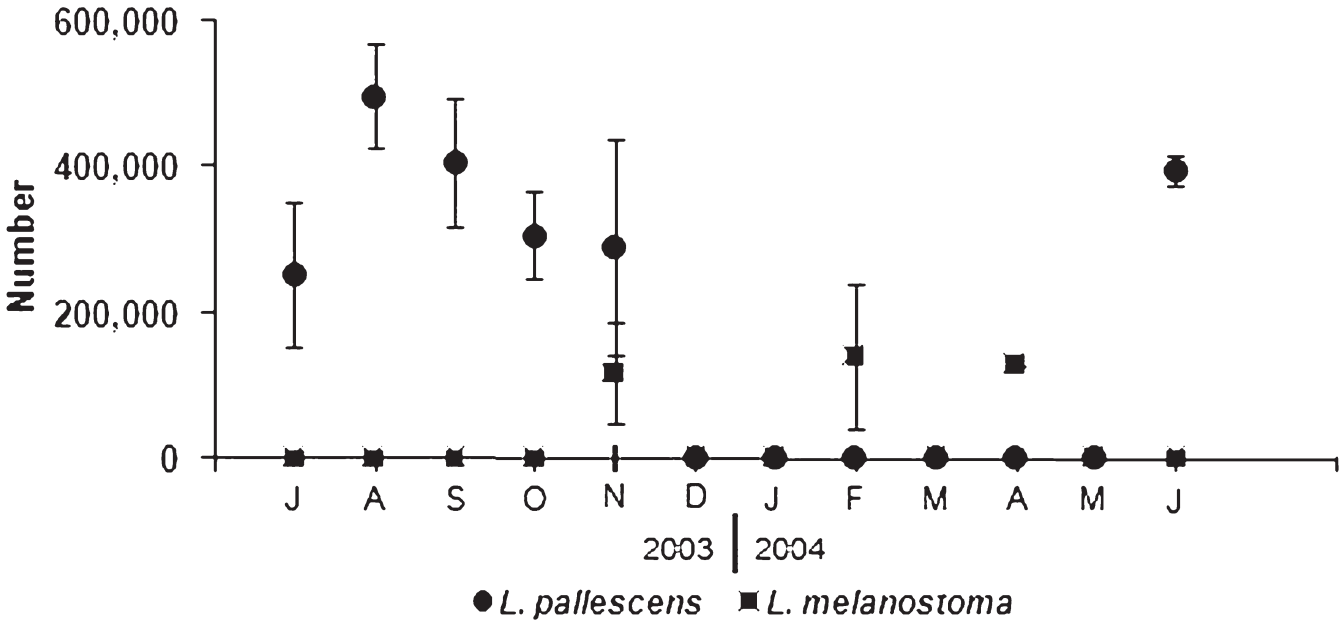


Fig. 2. Number of larvae of *Littoraria pallescens* and eggs of *L. melanostoma* released in the laboratory by females collected at Ang Sila, Thailand, from Jun.2003 to Jun.2004.

at the middle of each month and were thus not tied to lunar periodicity. If individuals mature rapidly and spawned completely over a short period, we might have missed the spawning. However, it is more likely that individuals do not mature every month in time for the appropriate phase of the moon. There was a general pattern of at least some individuals appearing histologically to be ready to spawn at any given period. Individuals of *L. pallescens* and *L. melanostoma* were collected at the same lunar phase and left in the laboratory to spawn. Spawning was clearly seasonal, from June to November, in *L. pallescens,* but there was no apparent seasonality in *L. melanostoma.*

One interesting feature of the present study was the lack of a clear spawning and growth pattern in three of the four species examined. Reproduction essentially failed during the year of the study, and population densities declined significantly (Sanpanich, pers. obs.). This parallels the finding

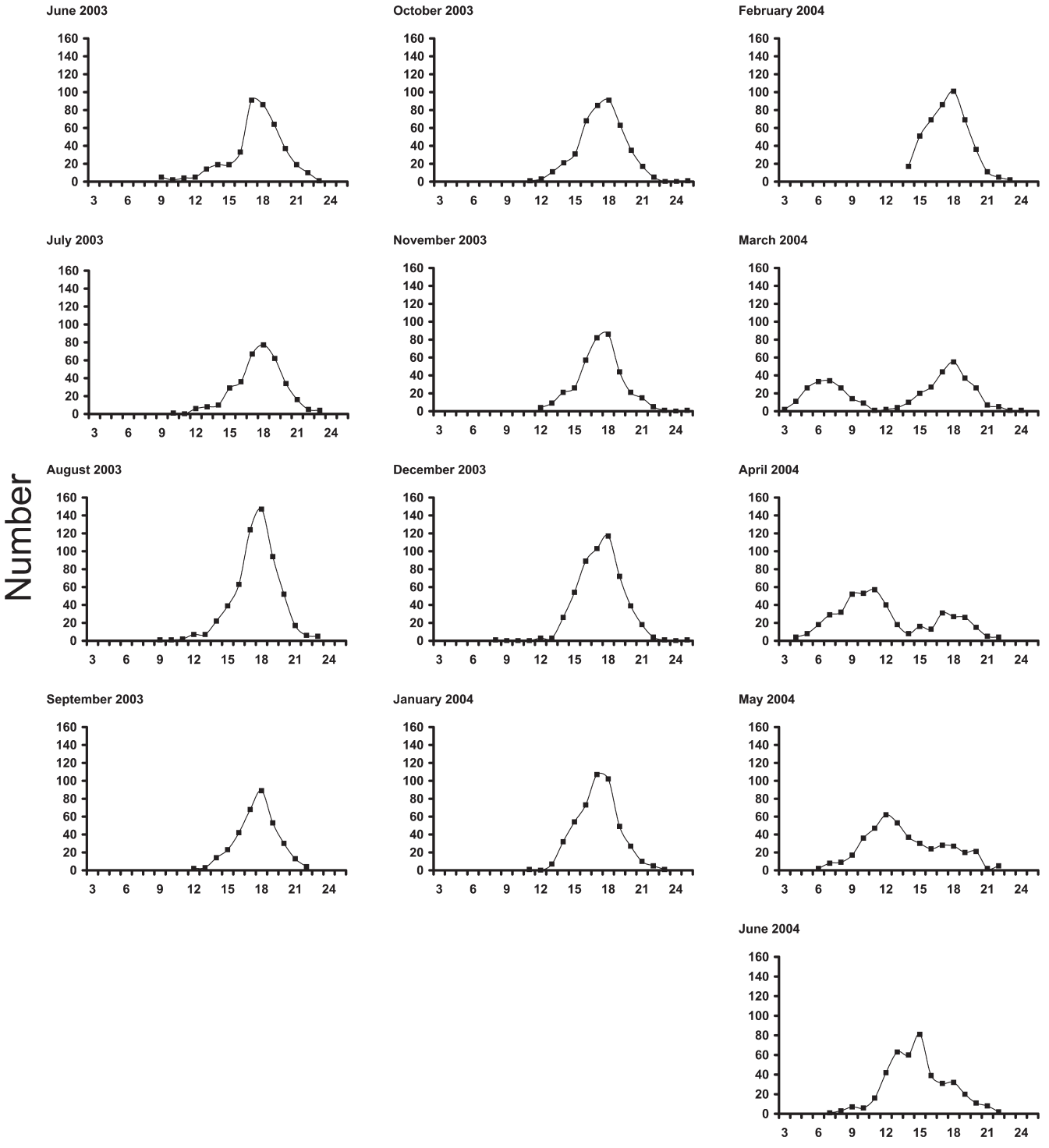


Fig. 3. Size frequency data for *Littoraria pallescens* at Ang Sila, Thailand, from Jun.2003 to Jun.2004.

of Wells (1984b) that *Nodilittorina unifasciata* (Gray, 1826) in Western Australia has a one-year life cycle. Reproduction failed in *N. unifasciata* during the period of his study and population densities declined.

The life cycle of *Littoraria pallescens* was shown to be annual at Ang Sila, with the adults being removed from the population and being replenished by young individuals from the next year class. Whereas little recruitment was demonstrated in the remaining species, their declining abundance is consistent with a lifespan on the order of one year. A similar rapid turnover of the population was found in *L. intermedia* (Philippi, 1846) at Phuket by Jensen et al. (1999). Black & Johnson (2001) studied the life histories of eight species of littorines at Ningaloo Reef, Western Australia. There were three species of *Littoraria* from mangroves for which sufficient data were available. *Littoraria cingulata* (Philippi, 1846), *L. filosa* (Sowerby, 1832), and *L. scabra*

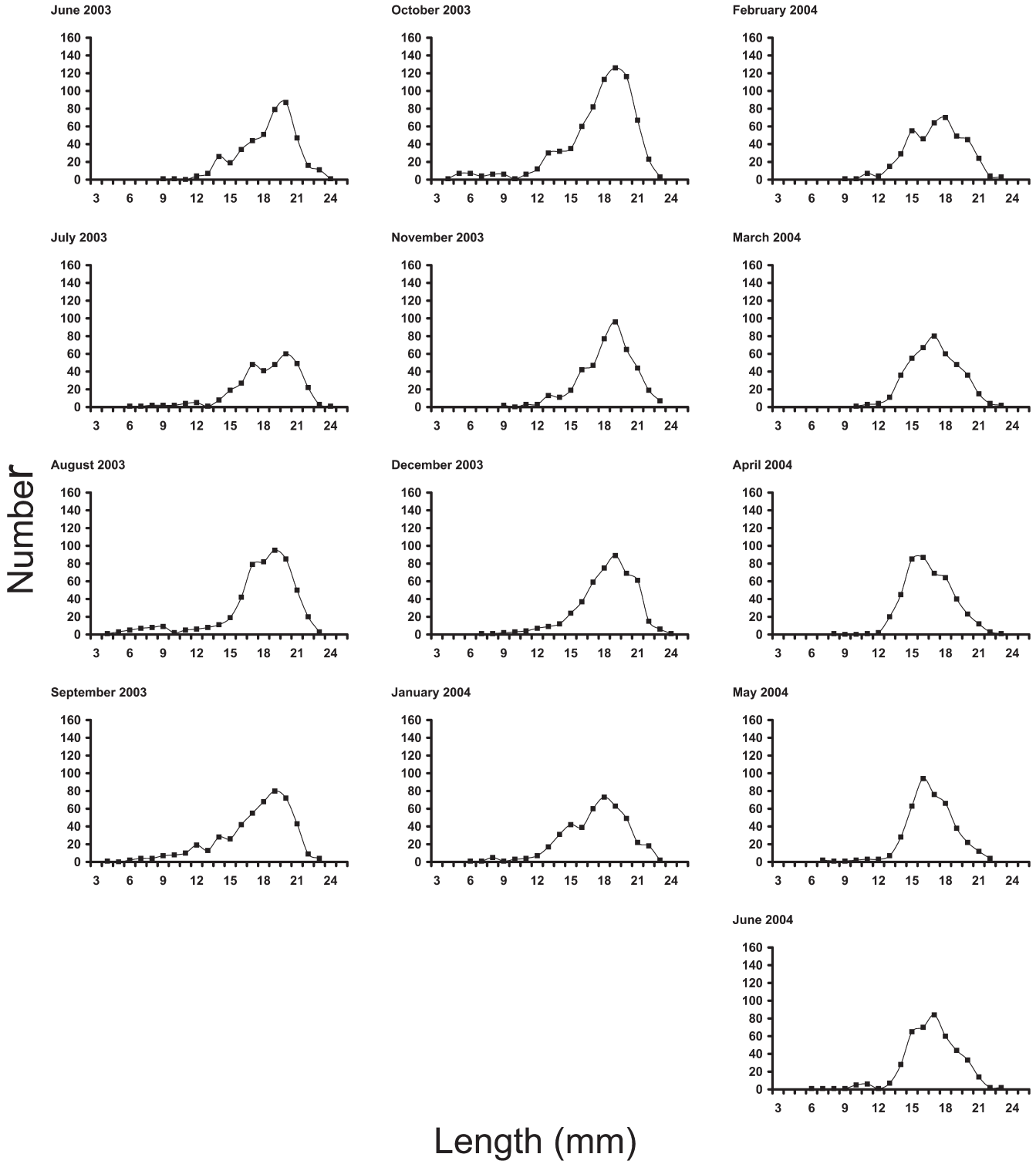


Fig. 4. Size frequency data for *Littoraria melanostoma* at Ang Sila, Thailand, from Jun.2003 to Jun.2004.

(Linnaeus, 1758) reached half of their maximum size of 22-27 mm in 0.94, 0.35, and 0.75 yr, respectively. In contrast, rocky-shore littorines were smaller (10–17 mm), but took much longer to reach half of their maximum size: 1.23, 2.87, and 1.28 yr, respectively, for *Nodilittorina australis* (Gray, 1826), *N. trochoides*, and *L. undulata* (Gray, 1839), respectively. In fact, some *N. millegrana* captured in 1988 were recovered alive in 1995.

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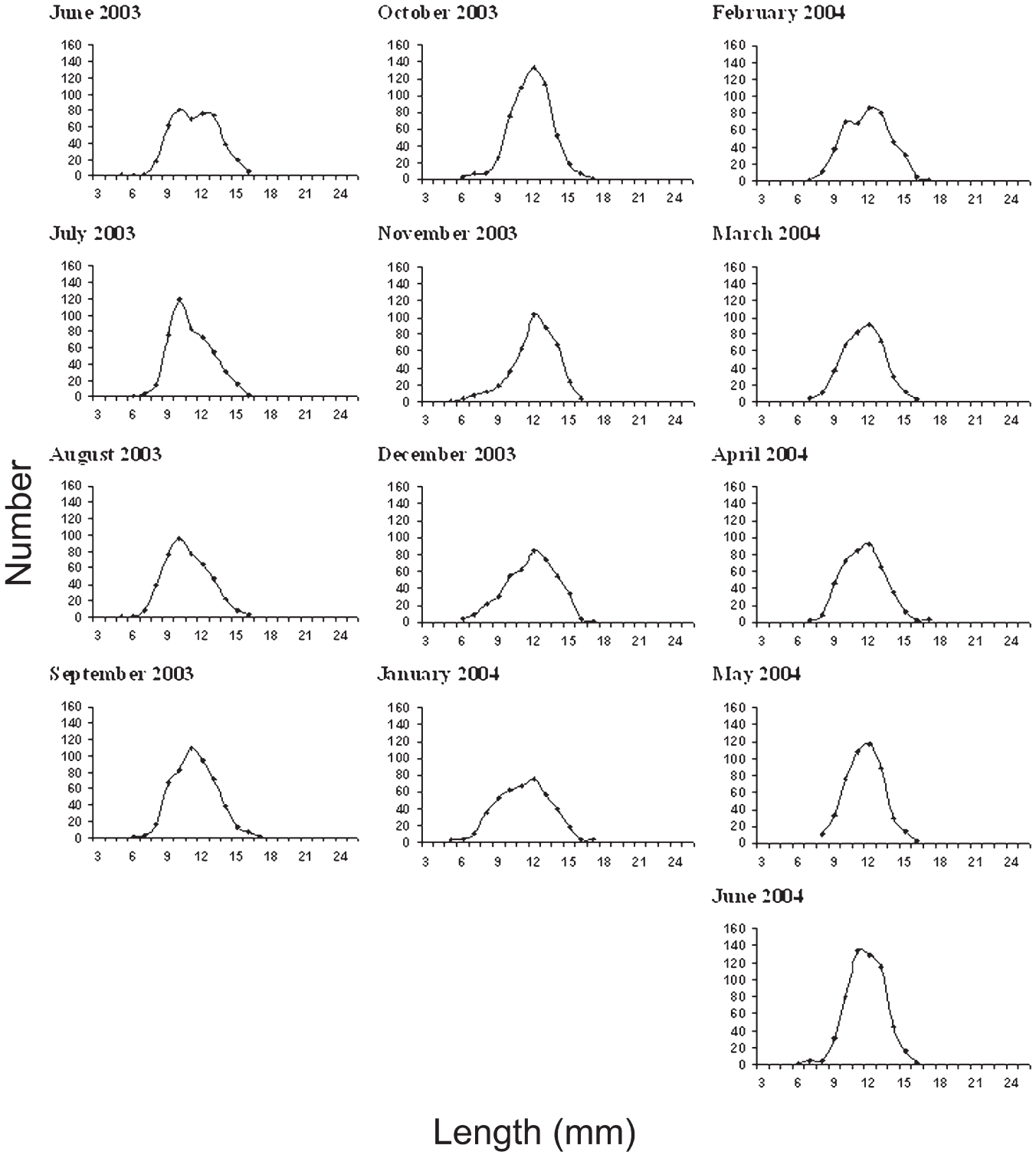

Fig. 5. Combined size frequency data for *Littoraria articulata* and *L. strigata* at Ang Sila, Thailand, from Jun.2003 to Jun.2004.

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THAI ABSTRACT

ปัจจุบันพบว่ายังมีข้อมูลน้อยเกี่ยวกับรูปแบบการสืบพันธุ์ของหอยที่อาศัยอยู่ในป่าชายเลน ซึ่งเป็นระบบนิเวศที่สำคัญในเขตน้ำขึ้นน้ำลงของเขตร้อนรวมทั้งในประเทศไทย หอยทั้งหอยสองฝาและหอยฝาเดียวเป็นกลุ่มของสิ่งมีชีวิตที่สำคัญกลุ่มหนึ่งในป่าชายเลน หอยฝาเดียวในสกุล *Littoraria* หลายชนิดมีการปรับตัวเพื่อการใช้ชีวิตในป่าชายเลน รายงานวิจัยฉบับนี้ให้รายละเอียดถึงช่วงเวลาการสืบพันธุ์ของหอย *Littoraria* ทั้งหมด 4 ชนิดจากบริเวณอ่างศิลาในประเทศไทย ระหว่างเดือนมิถุนายน พุทธศักราช 2548 ถึง มิถุนายน 2549 คณะผู้วิจัยได้ทำการเก็บตัวอย่างหอยทุกเดือนเพื่อศึกษาการเจริญพันธุ์และการเจริญเติบโต หอยที่สมบูรณ์เต็มที่และหอยที่ปล่อยเซลล์สืบพันธุ์แล้วบางส่วนมีอยู่ตลอดระยะเวลาการศึกษา แสดงให้เห็นว่าหอยในสกุลนี้สามารถสืบพันธุ์ได้ตลอดทั้งปี ส่วนช่วงระยะเวลาที่หอยมีการสืบพันธุ์มากที่สุดคือช่วงเดือนสิงหาคม ถึง กันยายน 2548 และ มกราคม ถึง กุมภาพันธ์ 2549 หอย *Littoraria pallescens* มีรูปแบบการเจริญเติบโตที่ชัดเจนในรอบ 1 ปี ในทางตรงกันข้ามในช่วงเวลาดังกล่าวไม่มีการให้กำเนิดลูกหอยในหอยฝาเดียวชนิด *L. melanostoma*, *L. articulata* และ *L. strigata*

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