

**COEXISTENCE OF *LITTORARIA SCABRA* AND *LITTORARIA PALLESCENS*
(GASTROPODA: LITTORINIDAE) IN NORTHERN SULAWESI, INDONESIA**

By **Farnis B. Boneka**

Faculty of Fishery, Sam Ratulangi University, Manado 95115 A, North Sulawesi, Indonesia.

ABSTRACT

The occurrence of two common littorinid species, *Littoraria scabra* and *Littoraria pallescens* was investigated in a mangrove on North Sulawesi. These two closely related species have similar geographical ranges. They were commonly found coexisting on the same mangrove trees. One way ANOVA gave no difference of the length of *L. scabra* ($p < 0.05$) with respect to 3 study sites at Manado, Bunaken, and Salibabu, while *L. pallescens* showed significant difference. *L. scabra* occupied the lower level, 25-150 cm from ground surface, and were restricted to the bark; conversely, *L. pallescens* occupied wider altitude range, 50-380 cm above ground, and inhabited mainly the leaves. In dry condition, *L. scabra* was more resistant to desiccation than *L. pallescens*. Transplant experiment showed that both species tended to crawl down to the bottom, when moved from one place to another. It seems that specialization in substrate utilization is the most likely factor explaining the coexistence of *L. scabra* and *L. pallescens* in cases of overlapping distributions.

INTRODUCTION

The dominant snails, living on mangrove trees, were formerly known as *Littorina scabra* in the Indo-Pacific, and *L. angulifera* in the Atlantic (Little, 1990; Reid, 1985). Recently the group has been revised under the generic name *Littoraria*, with 20 species found in Indo-Pacific mangroves (Reid, 1986).

The geographical distribution of the "*Littoraria scabra*" group is almost as wide as that of mangrove (Reid, 1985). Since they have a planktonic larval stage, they may occupy a wide geographical area. *L. scabra*, *L. intermedia*, and *L. pallescens* have been recognized as oceanic species in the Indo-Pacific Province and tend to occur at the same localities (Reid, 1985). Cook and Garbett (1989), and Reid (1986), reported that the *L. scabra* occupies bark as well as root and *L. pallescens* occupies the leaves of the mangrove trees.

If the ecological isolation is documented, the important question is causality. To answer by stating that two species have different habitat requirement is merely to restate the question. Such closely related species must have a preponderance of traits in common, and their isolation implies some important differences (Bovbjerg, 1969).

The impetus to study the comparative ecology of *L. scabra* and *L. pallescens* is that:

- (1) They have similar ranges, from the east coast of Africa to the western Pacific (Reid, 1986);
- (2) In north Sulawesi they are abundant and live on the same mangrove trees;
- (3) Gause's principle states that species cannot coexist for long, if they are too identical in their utilization of the resources (Schoener, 1974), which will evolve under stress of competition, for which the species, in order to counteract, may turn to specialization in niche or habitat (Menge, 1972).

Too often field observations reach a point where the ecological data or techniques are inadequate to explain disjunct distributions; competitive exclusion is then invoked with little direct evidence (Bovbjerg, 1969). Examples of active exclusion and niche shift are known for other groups, e.g. fish (Werner and Hall, 1977; Langeland *et al*, 1991), but clear evidence of competitive exclusion is still difficult to obtain.

The aim of the present work is:

- (1) To uncover the coexistence of two closely related species in the light of competitive exclusion principle.
- (2) To gain more insight in the ecology of these two related species.

MATERIALS AND METHODS

The characters used to distinguish *L. scabra* and *L. pallescens* are based on the structure of the penis and shell features. Detailed descriptions may be found in Reid (1986), while reference to a quick guide may be Cook and Garbett (1989).

Samples were collected at three study locations, Manado, Bunaken Island, and Salibabu Island (Fig. 1), during July-August 1993. Specimens were collected in the middle mangrove area, about 50 metres from the seaward edge. *Sonneratia* is the most common species of mangrove tree at the north coast of Manado. At Bunaken Island, *Avicennia* and *Rhizophora* are common mangrove trees. At Salibabu Island *Avicennia* is the common tree. Snails were hand picked during low tide within an area of 10 x 10 m, with two replications. In comparison, Cook and Garbett (1989) presented the density of *L. pallescens* as ind. per leaf, for instance 1 per 40 leaves at Phuket Island. Because of the great size range of trees and shape (branch and aerial root), Reid (1985) counted the number of snails seen in a search time of 2 min.

Altitude level, where the snails were resting on the trees, were measured (in cm) from ground surface. Specimens were kept alive in ventilated boxes, and brought to the laboratory and preserved in 10% formalin. Substrate, altitude, and shell length were recorded.

Desiccation and transplant experiments were conducted in the laboratory. Snails were placed in bottles connected to open tubes and their movements were observed to find their altitude orientation. Cook (1986) used closed plastic box. For desiccation treatment, the snails were placed in ventilated bottles for about 3 weeks.

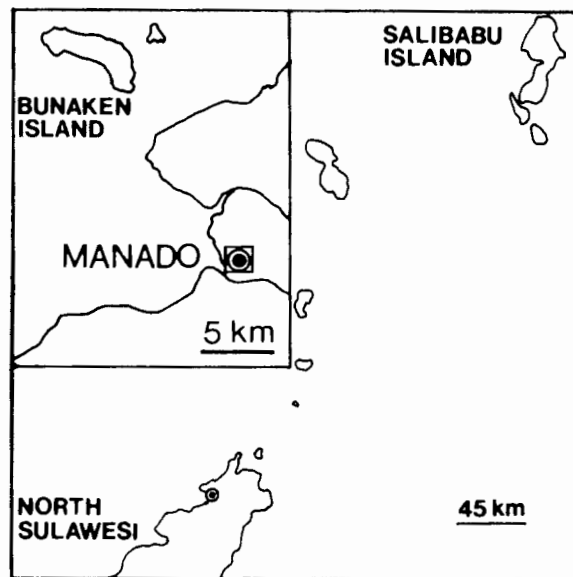


Figure 1. Study sites.

RESULTS AND DISCUSSION

The two littorinid species, *Littoraria pallescens* and *L. scabra*, numerically composed the significant parts of the fauna in mangrove forest at the study locations. *L. pallescens* (546 ind./200m²) dominated the Manado samples (*L. scabra* 1 ind./200 m²). At Bunaken both species occurred in almost equal proportions (Fig. 2).

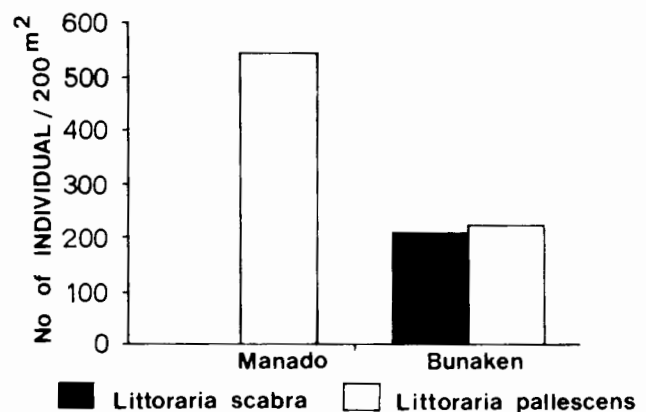


Figure 2. Proportions of *L. scabra* and *L. pallescens* in the mangroves of Manado and Bunaken.

The abundance may be controlled by substrate conditions as discussed below. The abundance could also be controlled by predation (Paine, 1966). Reid (1992) reported that in Cockle Bay (Magnetic Island, North Queensland) there were two important predators: birds and crabs. The latter taxon contained the most important predators on *Littoraria*. There is still little evidence for predation by birds on *Littoraria* species (Reid, 1987).

In agreement with previous studies referred to in the introduction, the present result was that *L. pallescens* mostly occupied leaves (73% of the specimens found), the remaining 17% were found on bark. Surprisingly this ratio was similar for both Manado and Bunaken locations. The abundance of *L. pallescens*, therefore, could be seen as a function of foliage. *L. scabra* was exclusively found on the bark (including root).

Distribution and abundance of the two littorinid species may be related to substrate characteristics as follows:

- (1) The leaves have relatively more surface available than bark;
- (2) The leaves are naturally located at the higher levels of trees, in other words, they are often not present at lower level;
- (3) The tree height (related to its age) may control "the leaf surface supply" for the snails.

The dominance of young *Sonneratia* in Manado mangrove may explain the high abundance of leaf-dwelling species, *L. pallescens*. The young *Sonneratia* will provide more leaf area relative to bark and root area, which will give advantage for *L. pallescens*. The relative high proportion of *L. pallescens* on bark, may reveal its plastic behavior in regard of substrate preference. At Bunaken, where the mangrove trees are taller and older, bark and root (of *Rhizophora*) supported a good surface for *L. scabra*.

L. scabra obviously occupied the lower level, 20 to 160 cm from ground surface, while *L. pallescens* was found from 50 to 380 cm. The result corresponds to data in Reid (1985) who reported that the species did not occur below 20-50 cm. The maximum high-

level recorded for *L. pallescens* was 4.5 m (MHWST 3.4 m Phuket Island (Reid, 1985)).

After a period of 528 hours with desiccation treatment, few individuals were still alive, *L. scabra* 16 (32%) and *L. pallescens* 6 (12%) individuals. Chi-square test ($X^2 = 4.55$, $p > 0.05$) revealed that the former was relatively more resistant to desiccation. In nature, however, the latter species was encountered at higher levels of altitude, where the risk of desiccation may be more severe than at lower levels. It suggests that the vertical zonation, with *L. pallescens* living higher up in the trees than *L. scabra*, does not coincide with the physiological endurance for dry conditions. The transplant experiment showed that both species tend to move down to the bottom of the tubes (Table 1). The response of *L. pallescens* did not agree with Cook (1986) where this species moved towards the top of the closed plastic box.

Table 1. Altitude orientation of *L. scabra* and *L. pallescens*.

Treatment	move up ind.(%)	move down ind.(%)	inactive ind.(%)
Each species separated			
<i>L. scabra</i>	10 (20%)	35 (70%)	5 (10%)
<i>L. pallescens</i>	-	42 (84%)	8 (16%)
Two species together (30 ind. each)			
<i>L. scabra</i>	4 (13.3%)	25 (83.3%)	1 (3.3%)
<i>L. pallescens</i>	2 (6.7%)	19 (63.3%)	9 (30.0%)

It seemed that some unknown substrate requirement allowed them to coexist on the same mangrove tree. To demonstrate the evidence of resource partitioning among groups of closely related species, Schoener (1974) referred to competition leading to segregation by habitat. Differences may be related to morphological characters and predation dynamics in a given location.

There is no indication of relationship between shell size and altitude level (or degree of exposure) within species (Fig. 3), as demonstrated in *Littorina littorea* (Hylleberg and Christensen, 1978).

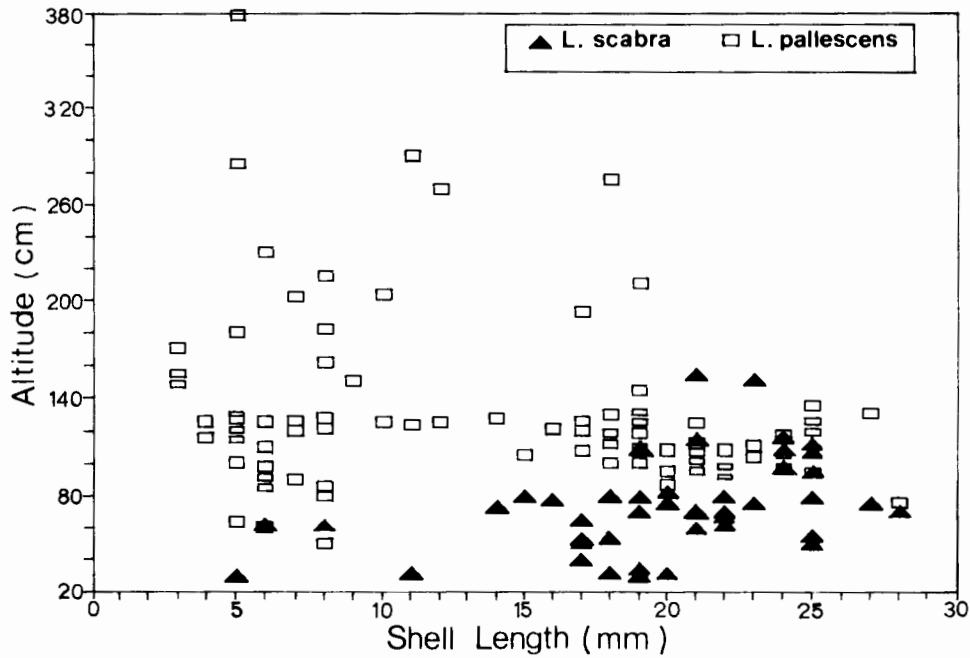


Figure 3. Altitude (cm) versus shell length (mm) of *L. scabra* and *L. pallescens*.

Fig. 4 shows distinguishable size distributions between *L. scabra* and *L. pallescens*. But only the latter showed variation of length with respect to locations; and juveniles almost entirely composed the samples from Manado and Salibabu. Statistical test (one way analysis of variance) showed that there is no significant difference of *L. scabra* length size with respect to study sites ($p < 0.05$). The differences of length size distribution of animals versus sampling sites suggest at least two explanations:

1. the species come from genetically different populations, and
2. the differences are related to predation and competition dynamics at each location.

The shells of *L. pallescens* are relatively thin and more fragile than those of *L. scabra*. Perhaps the life of *L. pallescens* living on leaves is an adaptive response to its vulnerability to unknown predators living in the biotope. Thickness of shells may be responsive to effects of predation (Cook and Kenyon, 1993).

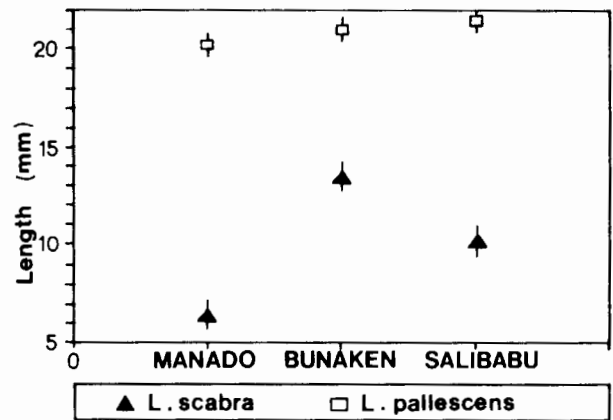


Figure 4. Length size distribution (mm) of *L. scabra* and *L. pallescens* at the three locations.

ACKNOWLEDGEMENTS

I thank Rini Kumaat and Trisje Salim for field assistance.

REFERENCES

- Bovbjerg, R.V. 1969. Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). *Ecology*, **51**(2): 225-236.
- Cook, L.M. 1986. Site selection in a polymorphic mangrove snail. *Biol. Jour. Linn. Soc.* **29**: 101-103.
- Cook, L.M. and S.B. Garbett. 1989. Patterns of variation in mangrove littorinid mollusc on Phuket Island. *Phuket mar. biol. Cent. Res. Bull.* **53**: 1-14.
- Cook, L.M. and D. Kenyon. 1993. Shell strength of colour morphs of the mangrove snail *Littoraria pallidescens*. *J. Moll. Stud.* **59**: 29-34.
- Hylleberg, J. and J.T. Christensen. 1978. Factors effecting the intra-specific competition and size distribution of the periwinkle *Littorina littorea* (L.). *Natura Jutlandica*, **20**: 193-202.
- Langeland, A., J.H. L'abee-Lund, B. Jonsson and N. Jonsson. 1991. Resource partitioning and niche shift in arctic charr, *Salvelinus alpinus* and brown trout *Salmo trutta*. *Jour. Anim. Ecology*. **60**: 895-912.
- Little, C. 1990. *The terrestrial invasion*. Cambridge, Cambridge University Press.
- Menge, B.A. 1972. Competition for food between two intertidal star species and its effect on body size and feeding. *Ecology*, **53**(4): 635-644.
- Paine, R.T. 1966. Food web complexity and species diversity. *Amer. Natur.* **100**: 65-75.
- Reid, D.G., 1985. Habitat and zonation patterns of *Littoraria* species (Gastropoda: Littorinidae) in the Indo-Pacific mangrove forest. *Biol. Jour. Linn. Soc.* **26**: 39-68.
- Reid, D.G., 1986. *The littorinid mollusc of mangrove forest in the Indo-Pacific region*. London. British Museum Nat.Hist. Publ. 228 p.
- Reid, D.G. 1987. Natural selection for apostasy and crypsis acting on the shell colour polymorphism of a mangrove snail, *Littoraria filosa* (Sowerby)(Gastropoda: Littorinidae). *Biol. Jour. Linn. Soc.* **30**: 1-24.
- Reid, D.G. 1992. Predation by crabs on *Littoraria* species (Littorinidae) in a Queensland mangrove forest. In: J. Grahame, P.J. Mill & D.G. Reid (eds.). *Proceeding of the Third International Symposium on Littorinid Biology*, 141-151. London: the Malacological Society.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science*, **185**: 27-39.
- Werner, E.E. and D.J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology*, **58**: 869-876.