

GROWTH AND MORTALITY OF *LITTORARIA PALLESCENS*,
WITH EMPHASIS ON TWO COLOUR MORPHS,
IN NORTHERN SULAWESI, INDONESIA

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ABSTRACT

Growth and mortality of dark and yellow colour morphs of *Littoraria pallescens* (Philippi, 1846) were studied at Bunaken Island, northern Sulawesi, Indonesia. The dark morph grew faster ($k = 2.536$), than the yellow ($k = 0.624$), though the latter grew to a larger size ($L_{\infty} = 21.367$) than the dark morph ($L_{\infty} = 14.231$). The dark morph had a higher instantaneous rate of mortality ($Z = -0.490$) than the yellow ($Z = -3.340$). It is speculated that the dark shell colour is selected for by biological pressure (e.g., predation), and the yellow morph by physical stress (e.g., desiccation).

INTRODUCTION

The "*Littorina scabra* species complex" encompass 21 members recorded in Indo-Pacific mangroves; 11 of these reveal polymorphism in shell colour. The species are assigned to the subgenus *Littorinopsis* except *L. albicans* (Metcalf, 1852) referred to the subgenus *Littoraria* (Reid 1986). *Littoraria pallescens* (Philippi, 1846) is the most common and the most highly polymorphic species in northern Sulawesi mangroves (Boneka 1994).

Several studies have been carried out on shell colour morphs in various localities (e.g., Cook 1990; Cook & Garbett 1992; Cook & Kenyon 1993; Boneka 1996). The colour morphs are dark, yellow, and orange, in decreasing order of frequency. The morph proportion is fairly constant throughout wide geographical ranges and tropical seasons. In general, however, there are no significant shell property difference and no ecological segregation among the three major colour morphs, with the exception of shells being stronger in the dark morph (Cook & Kenyon 1993).

In the present study area *Littoraria pallescens* live on the same mangrove trees as *Littoraria scabra* (Linné, 1758); the former mainly live on leaves whereas the latter exclusively occupy bark and roots (Boneka 1994). The leaf-living species are generally polymorphic in shell colour,

whereas the bark-living species are monomorphic and cryptic (Reid 1986). Cryptic colouring could be a mechanism by which to avoid visual predators, and bright shell colour could be an adaptation to avoid some solar radiation particularly for the ones living in exposed areas. Increased heat loss occurs when the organisms are light in colour, while the dark organisms gain heat by absorption (Nybakken 1993). Mangrove foliage as a habitat may be seen as an evolutionary response to biological pressure such as predation from the ground, aquatic parasites, competition, or a combination of these factors. The most important agent controlling the littorinid populations in mangroves comes from aquatic predators (Boneka 1995).

The purpose of the present work is to examine the assumption that the difference in shell colour may have biological consequences, especially on growth and mortality which have never been tested in previous studies. Growth and survival in nature are important components of fitness. Fitness is ultimately measured in terms of the phenotype's relative success in converting resources to reproductive products, in which growth can be viewed as the developmental means of achieving the reproductive stage (Calow & Townsend 1981). It is assumed that organisms with similar phenotypes may

respond in a similar way to the same selective pressure, whereas organisms with different phenotypes may respond differently. The comparative approach was applied to examine how colour morphs have adapted to their environments (Harvey & Purvis 1991).

MATERIAL AND METHODS

The study area

The investigation was carried out in a mangrove area in the southern part of Bunaken Island, northern Sulawesi, Indonesia (Boneka 1994). The dominant mangrove species belong to *Avicennia* intermingled with *Rhizophora* and *Sonneratia*. The area is fairly sheltered. The tide is semidiurnal with a spring tide amplitude of about 200 cm. Seawards there is more than 100 m width of seagrass beds, then the coral reef drops off at the edges. Landward the study site is bordered with a coconut plantation and areas for tourists. However, there is no evidence that the visitors collect *Littoraria pallescens*. The study location is a part of Marine National Park, thus the wild life in general, such as birds, lizards, snakes, and crabs still exist.

Littoraria pallescens mainly live on the mangrove leaves. Characteristics of the substratum are (1) higher exposure to solar radiation, (2) higher surface availability (though the tree height may control substrate supply), (3) "an island" structure where the snails must move down onto branches to reach other leaves, (4) unstable ground for climbing crabs which may hunt the snails. Four *Avicennia* trees with a number of *L. pallescens* were selected. Since the species particularly lives on the leaves, high numbers were always found on trees with a heavy canopy layer 80 - 200 cm above the ground surface (Boneka 1994: Fig. 3). Snail density was increased by transplantation of individuals from neighbouring trees.

A total of 443 dark and 337 yellow snails of various lengths were marked individually. The dark or brown shells were marked with black oil paint, and the yellow morphs with

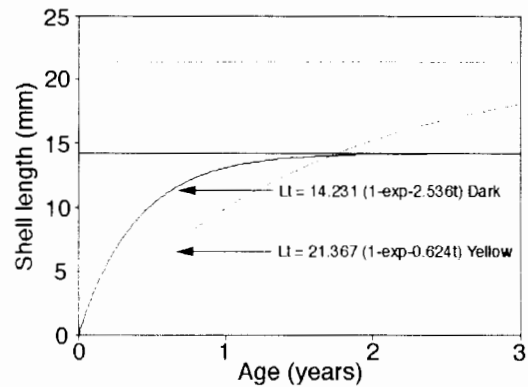


Figure 1. *Littoraria pallescens*, growth of dark and yellow colour morphs.

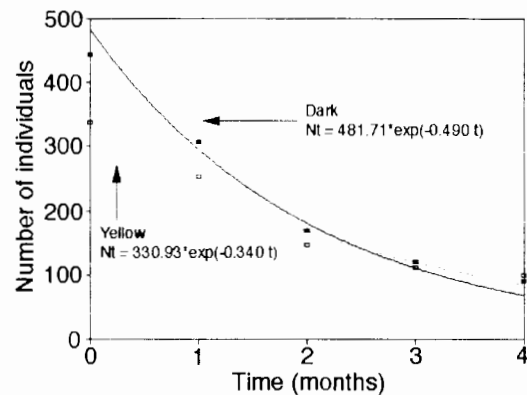


Figure 2. Mortality of dark and yellow colour morphs.

yellow paint. The experimental animals could be identified, but the numbers did not change the general impression of shell colour. The pink morph was neglected since it was hard to obtain in appropriate numbers (statistical requirements). Shell length was measured to the nearest 0.05 mm with Vernier callipers, and the individual numbers were recorded monthly for five months (August-December 1995). The neighbouring trees were observed in order to detect if the snails migrated.

From the increments in shell mean length on each *Avicennia* tree during five months, the parameters of the von Bertalanffy growth equation were estimated for dark and yellow morphs.

$[L_t = L_\infty (1 - e^{-K(t-t_0)})]$, where L_t = shell length at age t , L_∞ = asymptotic shell length, K =

growth coefficient, and t_0 = theoretical age when shell length is zero]

The K and L_∞ parameters were estimated by the linear methods of Gulland (1969). Since the von Bertalanffy equation is valid for age t , it is also valid for age $t+T$ (in this case, T = five months or 0.4167 year), and is written as $L_{t+T} = L_\infty (1 - e^{-k(t+T-t_0)})$. The linear equation can be found by subtracting L_t from this equation: $L_{t+T} - L_t = L_\infty (1 - e^{-kT}) - L_t (1 - e^{-kt})$ and plotting $L_{t+T} - L_t$ as y -axis, L_t as x -axis, $L_\infty (1 - e^{-kT})$ = intercept, and $(1 - e^{-kT})$ = slope.

The number of snails (N) alive at time t is given by $N_t = N_0 e^{-Zt}$, where N_0 = the number of snails at $t = 0$, and Z = the instantaneous rate of mortality. The Z parameter was estimated from a previously logarithmic transformation of this equation: $\ln N_t = \ln N_0 - Zt$.

RESULTS

Growth rates of the dark and yellow *Littoraria pallescens*, were examined on the basis of 91 dark and 99 yellow morphs, since the main part of the marked snail population had disappeared from the study area, probably due to natural mortality. There was no evidence that the snails migrated to the neighbouring trees, indicating that snails have a small tendency to migrate.

During the five months of study there was a moderate increase of shell lengths resulting in sigmoid growth curves. Fig. 1 shows that the dark and yellow morphs of *L. pallescens* had different growth rates. The von Bertalanffy growth equation, and estimated parameters, were $L_t = 21.367 (1 - e^{-0.624t})$ for yellow morph, and $L_t = 14.321 (1 - e^{-2.536t})$ for dark morph. The dark morph obviously grows faster with a value of $k = 2.536$ compared to the yellow morph with $k = 0.624$. On the other hand, the dark morph has a smaller asymptotical size ($L_t = 14.321$) than the yellow morph ($L_t = 21.367$). Thus the dark morph reached maximum size earlier than the yellow.

The colour morphs have different instantaneous rates of mortality as shown in Fig. 2. The dark morph disappeared faster from the

study area with $Z = -0.48958$, than the yellow, with $Z = -0.33957$.

DISCUSSION

Species inhabiting the supratidal zone must be capable of coping with aquatic and terrestrial predators, and physical stress, such as temperature and desiccation. We suggest that the colour morphs of *Littoraria pallescens* reflect differentiation in life history strategy in response to complexity of natural pressure in the environment.

One weakness of the present procedure is that we did not record shell length increments of individual snails. Therefore the growth analysis is based on the mean length size of four groups from the *Avicennia* trees. It can be accepted if the mortality occurs at random with respect to shell size. The dark morph revealed faster individual growth and attained asymptotic size earlier than the yellow morph. However, it had a smaller asymptote size and a faster instantaneous rate of mortality than the yellow morph. This may illustrate that fast growth can be associated with a mortality cost.

The dark morph has a stronger shell (Cook & Kenyon 1993) as well as a rapid growth. This is thought to be the best defence mechanisms in connection with biological pressure such as predation. It has been proposed by a number of authors (e.g., Calow & Townsend 1981) that rapid growth can reduce predation during the early vulnerable stage. A thick shell may be of adaptive significance reducing the risk of being crushed by crab predators. Yet, so far no reliable evidence of crushing attempts has been seen on the snails (Boneka 1996). It seems that the dark morphs allocate the energy to growth, pigmentation, and shell strength instead of obtaining a large size. The yellow morph has no advantage considering predation in early stages, but with increasing body size this morph may obtain some protection. A relationship was found between body size and predation in temperate periwinkles. Shell crushing crabs could only handle the smaller sizes of *Littorina littorea* (Hylleberg &

Christensen 1978). Faster growth also means that the organism sooner becomes reproductive, and should be correlated with fitness (Calow & Townsend 1981).

Large body size means less surface area relative to volume and hence less area to gain heat, and it takes longer time to heat up (Nybakken 1993: 227). The water loss as a result of increasing temperature can also be reduced by bigger body size with ability to store more water. The yellow shell morph seems to conserve more energy for longevity and increasing body size. The shell characteristics and the biological consequences of the yellow colour likely reveals a balance between biological and physical pressures

in nature. The dark morph might be at a disadvantage under physical stress compared with the yellow morph. Cook & Kenyon (1993) suggested that these morphs could be good candidates for the study of relationships between organisms and their environment.

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