Journal of Shellfish Research, Vol. 15, No. 2, 421–432, 1996.

THE MANGROVE SNAIL *THAIS KIOSQUIFORMIS* DUCLOS: A CASE OF LIFE HISTORY ADAPTATION TO AN EXTREME ENVIRONMENT

VOLKER KOCH AND MATTHIAS WOLFF
Center for Tropical Marine Ecology
Klagenfurter Str. Gebäude GEO
28233 Bremen, Germany

ABSTRACT This article describes the population ecology of *Thais kiosquiformis* Duclos, the dominant predatory gastropod of the root system of Costa Rican mangroves. *T. kiosquiformis* was shown to cope with the extreme living conditions of its habitat (risk of desiccation and overheating through several hours of daily air and sun exposure, strong salinity, and current changes during the tidal cycle) by using the following strategies: (1) extremely slow growth (~1 mm/y), cessation of growth at the onset of maturity (at ~24 mm in shell length), (2) maintaining high interindividual plasticity in growth and shell thickness as a response to abiotical conditions, food availability, and population density, and (3) migrating ontogenetically for the benefit of lowering desiccation and predation mortality. Because of its high density and biomass (192.2 ± 102.4 g wet weight/m^2), and the predation pressure it exerts mostly on the barnacles of the mangrove roots, *T. kiosquiformis* seems to occupy a central role in maintaining the functioning and productivity of mangroves through "cleaning" their root system from the encrusting fauna.

KEY WORDS: Costa Rica, mangroves, population ecology, gastropods

INTRODUCTION

Thaidid gastropods evolved in the early Miocene (Vermeij 1978) and are distributed worldwide from tropical to boreal areas, indicating the large adaptive potential of this family. They occur in intertidal and subtidal shallow waters, often as a dominant invertebrate predator within their habitats (Menge 1978). Studies on the ecology of thaidid gastropods revealed a complex set of mechanisms to deal with the harsh environmental conditions they encounter in the intertidal habitat. These include prey type selection motivated by energétic considerations (Palmer 1984); prey size choice to minimize the risk of dislodging at wave-exposed sites (Richardson and Brown 1990); optimized foraging behaviour in relation to prey abundance and mortality factors such as predators and desiccation (Menge 1978, Spight 1983, Fairweather 1988); switching to anaerobic metabolism by aperture closing to avoid desiccation (Cantera et al. 1980); size-dependent zonation related to factors like food, predators, shelter, and desiccation (Butler 1979); and modification of shell thickness as a response to different predation pressures by crabs (Kitching 1977, Palmer 1985, Geller 1990). Menge (1978) concluded from his study on predation exerted by *Thais lapillus* on a rocky shore that each snail has to be considered an individual, where life history traits and phenotype are as important as extrinsic factors (e.g., actual habitat conditions). West (1988) also reported high interindividual variation in prey preferences and growth of *Thais melones* on the Pacific Coast of Panama. Great individual plasticity in behavioural, physiological, and morphological responses to a harsh environment seems thus to explain the success of this family.

Thais kiosquiformis Duclos is among the most abundant snail species and probably the most important invertebrate predator in the mangrove swamps of the upper Gulf of Nicoya on the Pacific Coast of Costa Rica (10°N, 85°W). It is distributed along the Pacific and Atlantic Coasts from Baja California to Peru in the intertidal at salinities of 5–30‰, living mainly on mangrove roots, rocks, and rotting trunks (Keen 1971, Cantera et al. 1980). It is strictly carnivorous, preying on balanids, bivalves, and other gastropods by drilling a hole in the prey's shell or by introducing its foot. Cannibalism does not seem to occur. Specimens can survive desiccation up to 9 d by closing the aperture tightly and switching to anaerobic metabolism. The species grows to approximately 50–55 mm in shell length; the strong shell is muddy brownish with well-developed spines. Maturity is reached at 24–32 mm shell length (Cantera et al. 1980).

The objectives of this study were (1) to describe the population structure (density, biomass, horizontal size distribution) of *T. kiosquiformis* at study sites differing in freshwater influence, sediment characteristics, height above low water level, and total mangrove extension; (2) to estimate growth and mortality rates at the different study sites; and (3) to estimate food consumption and identify main prey items. The overall goal of the study was to explain the mechanisms that not only promote survival under the extreme conditions of the mangrove habitat but also allow this species to maintain high abundance and biomass in the mangrove root community.

MATERIALS AND METHODS

Study Area and Sampling Sites

The Gulf of Nicoya is a tectonic estuarine embayment located on the Pacific Coast of Costa Rica, Central America (Fig. 1). The gulf is divided into a shallow upper part (~20 m) and a lower part (>200 m in depth), which is bordered by the Puntarenas Peninsula in the east and San Lucas Island in the west. Because of seasonal upwelling events, this region is the most productive fishery ground in Costa Rica.

Seasonality on the Central Pacific Coast of Costa Rica is very pronounced, with 89% of the annual precipitation occurring from May to October. Average total precipitation for Puntarenas is approximately 1,550 mm/y (Thomas 1988). The annual mean air temperature for Puntarenas is 27.35°C (Janzen 1991); water temperatures in the upper gulf range from 28 to 30°C. The water body of the upper gulf is heavily influenced by freshwater and sediment input of the Rio Tempisque, located at the northern end, and by numerous smaller rivers, especially along the eastern shores (Peterson 1960). The tides are semidiurnal (12.4 h); amplitudes vary between 1.8 and 2.8 m with a mean of 2.3 m (Peterson 1960, Voorhis et al. 1983). During the rainy season, surface salinity in the upper gulf may drop down to 5‰ near river mouths during low

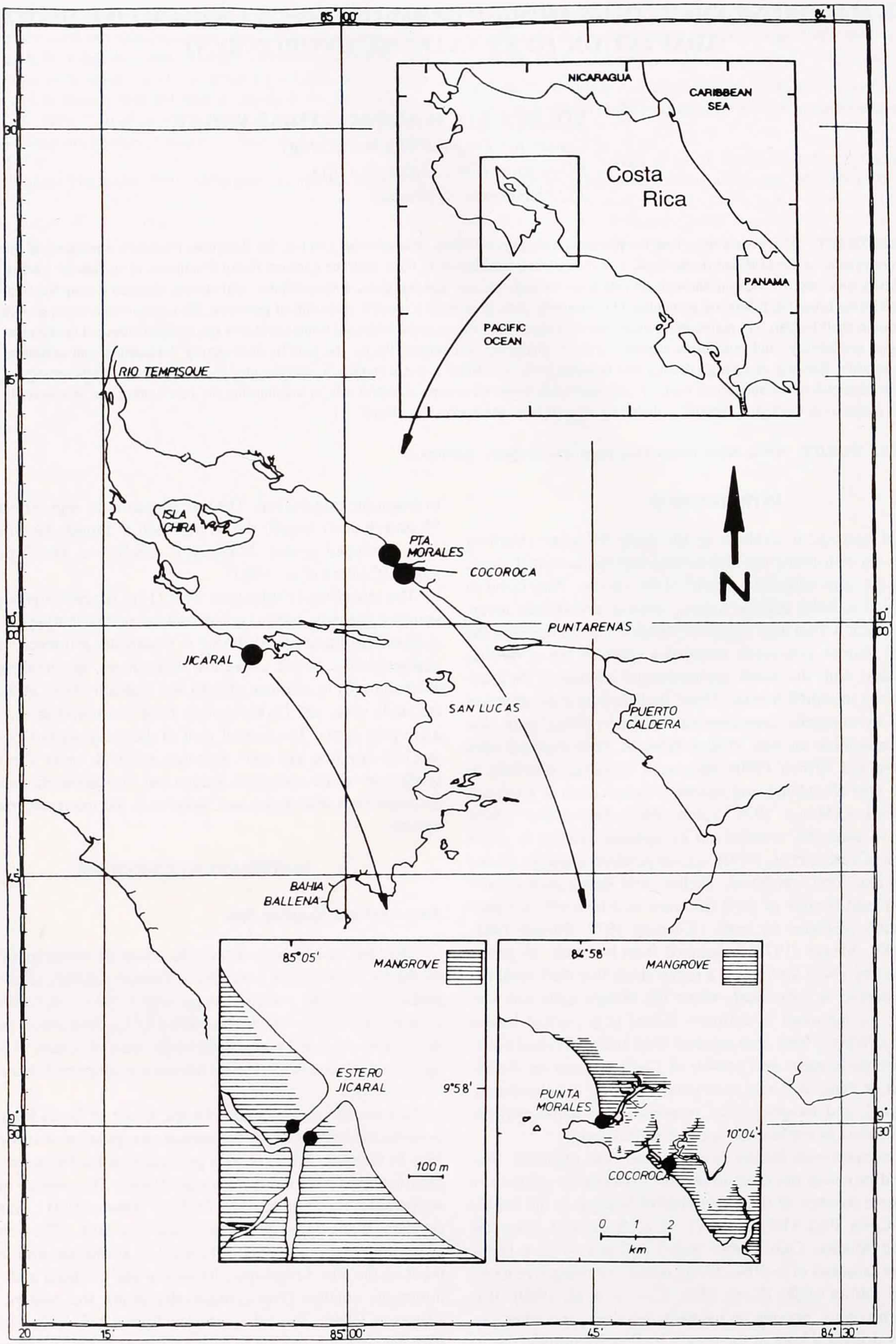

Figure 1. Gulf of Nicoya with the three study sites (solid circles)—Punta (PTA) Morales (P), Cocoroca (C), and Jicaral (J).

tide (this study). The outer coastline of the upper gulf is covered with extensive mangrove stands, dominated by red mangroves (*Rhizophora mangle* and *Rhizophora harrisoni*).

Two sampling sites were chosen in each of the three estuaries of Punta Morales (P1, P2), Cocoroca (C4, C5), and Jicaral (J6, J7) for a representative cross-section of the upper gulf (Fig. 1). The vegetation consisted exclusively of the two *Rhizophora* species mentioned above. Large mudflats extended seaward at each location. Freshwater input was highest at Cocoroca (Rio Lagarto), followed by the Rio Jicaral and the Rio Quebrada Grande in Punta Morales (Fig. 2). The latter only carries freshwater during the rainy season, and even then, the input is very low (Gocke et al. 1981, this study). The increase in salinity in November marks the end of the rainy season. At high tide, the water level at the sampling sites of C and J was approximately 1–1.5 m; in P, it was 1.5–2 m above the sediment, coinciding with the upper limit where barnacles occurred. The sediment in Punta Morales was coarser than that at the other sampling sites, with stones and rocks contrary to the uniform sandy/muddy Cocoroca and Jicaral sites. Accordingly the ''sink-in depth'' varied considerably: J > C > P.

Sampling Strategy

Twelve length frequency samples were taken at about monthly intervals along transects at P1, P2, and C4 from September 1993 to July 1994. In C5, J6, and J7, only 10 samples were taken from October 1993 to July 1994. An additional sample of tagged snails was taken in February 1995 in P1. Surface water salinity and water temperature were measured at the adjacent water line (refractometer, ±0.5‰; mercury thermometer, ±0.2°C). Each transect consisted of 10 squares of 60 · 60 cm each (0.36 m^2), placed 1 m apart from centre to centre, with a 10-m line tagged at 1-m intervals. This line was positioned vertical to the mangrove edge (Fig. 3). Because a solid frame could not be used because of the mangrove roots, an inch rule was taken instead. All *T. kiosquiformis* found within the square were taken to the laboratory. Total shell length was measured to the nearest 0.5 mm with a caliper. Snails from each square were measured separately to determine length frequency patterns along the transect. After measuring, specimens were returned to the transect to avoid introducing artificial mortality into the population. This was not done in Jicaral because of the large distance to the laboratory (1 h by boat).

On the first sampling date, a different strategy was used to determine the appropriate square size: in addition to the basic design, each square was divided into four subquadrats of 30 · 30 cm each (0.09 m^2). Mean length, standard deviation, and variance of the subsamples were calculated to determine whether the variance changed as a function of sample area. The 60 · 60 cm quadrat size gave homogeneous results even for densities <35 snails/m^2, whereas the smaller quadrat size (30 · 30 cm) did not perform well under low densities, where number of snails, mean length, and standard deviation differed significantly among the subsamples. Therefore, the larger quadrat size was selected for subsequent sampling during the study (length frequency sampling and biomass determination).

Growth and Mortality

The growth of *T. kiosquiformis* was determined from the length frequencies by use of the seasonalized von Bertalanffy growth equation (Pauly and Gaschütz 1979) as implemented in the FiSAT program (Gayanilo et al. 1994):

$$L_t = L_\infty(1 - e^{-(K(t-t_o)+CK/2\pi(t-t_s)}$$

where L_∞ is the asymptotic length, L_t is the length at time t, K is the growth constant, t_o is the age at length zero, C lies between 0 and 1 and describes the growth amplitude (of a sine function), and t_s is the starting point of the growth oscillation.

The program restructures the data by calculating a running average over five length classes, dividing each length class by this value and subtracting 1 from the result, which creates peaks and troughs. The program traces growth curves with different sets of parameters through the length frequencies and selects the curve that hits as many peaks and avoids as many troughs as possible.

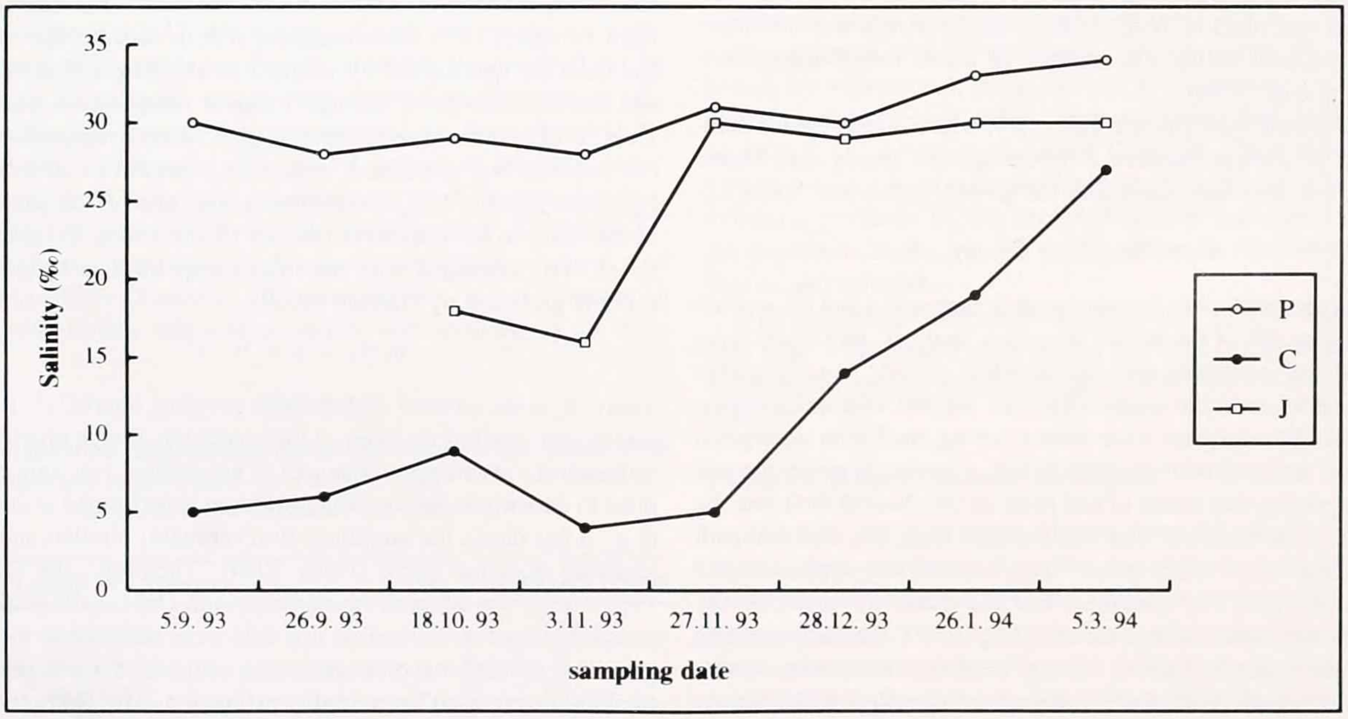

Figure 2. Surface salinity at the study sites P, C, and J during low tide.

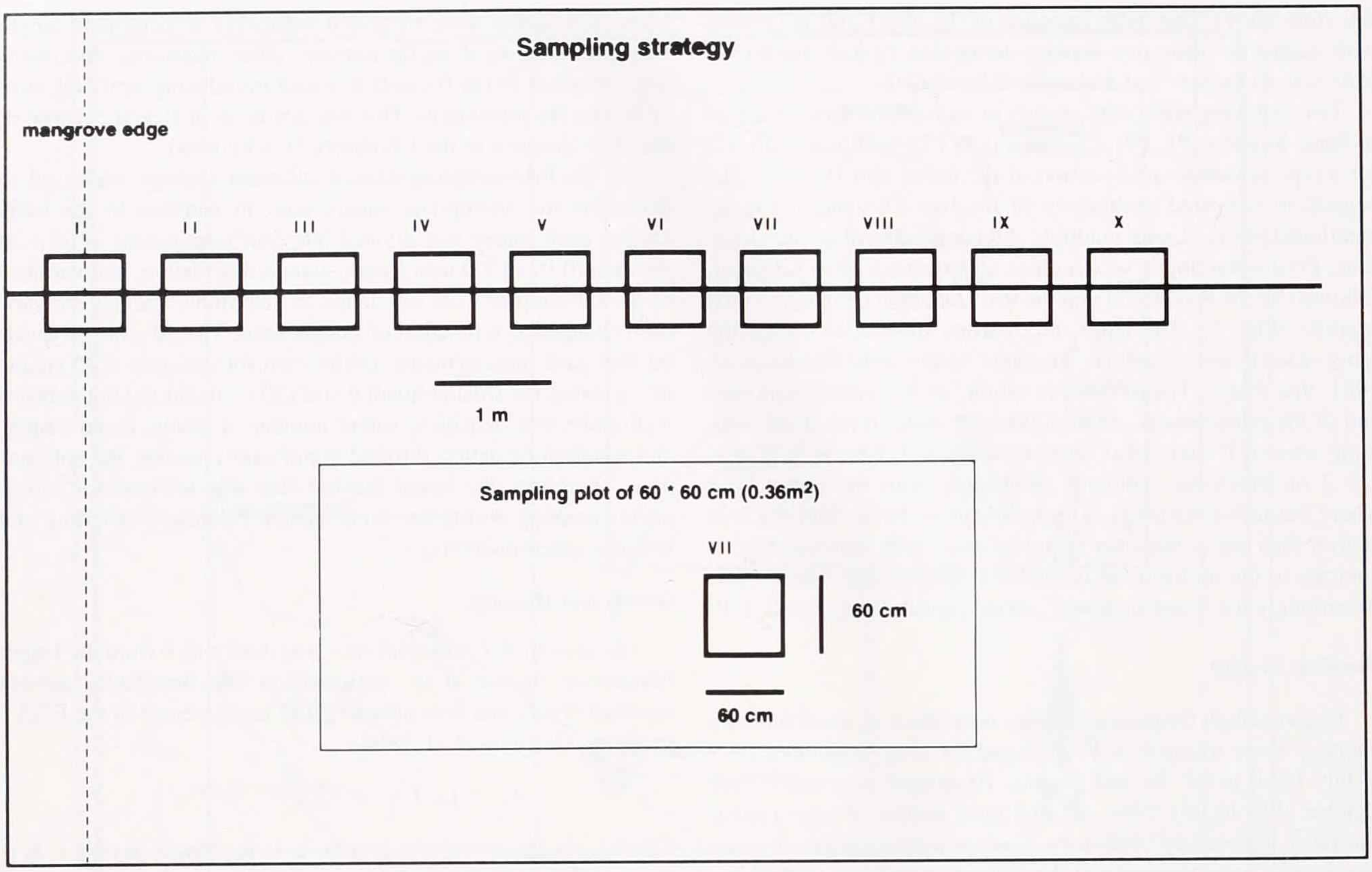

Figure 3. Sampling strategy. Letters (I-X) mark quadrat numbers.

The length measurements of each transect were grouped into 1-mm intervals. Because of the striking differences in biomass and length distributions between the transects, the von Bertalanffy parameters were calculated separately for each transect. Because the analysis of the whole range of length frequencies did not give satisfactory results (goodness of fit, $Rn < 0.2$ in all cases), the youngest visible cohort was determined by eye and reanalysed separately (P1 and P2, ≤23 mm; C4, ≤22 mm; C5 and J6, ≤25 mm), as described in Wolff (1985). In J7, growth was not determined because of the low number of snails found during each sampling date (<30).

The growth performance index (ø′), which allows for the comparison of growth between different species (Pauly and Munro 1984), was then calculated with the growth parameters K and L_∞:

$$ø' = \log_{10} K + 2 \cdot \log_{10} L_\infty$$

As a second method to estimate growth parameters and to compare with the results of the length frequency analysis, 643 snails were marked and monitored over the sampling period. A paint marker was used to mark 230 snails; 186 were marked with quick-drying oil paint. The numbers were written on the shell with waterproof markers. Because both methods failed, a sandwich technique was used, applying two layers of nail paint on the cleaned shell near the aperture. The numbers were written with india ink, and the mark was sealed with "crazy glue." This method was applied to 413 snails, of which 186 specimens had old marks (re-marked). The animals were released near the sampling site P1. On each sampling occasion, a search of about 1 h was conducted for marked snails, which after collection, were measured with a caliper to the nearest 0.1 mm and subsequently released at the same spot.

Estimates of von Bertalanffy growth parameters were derived by the use of the Munro plot (Munro 1982).

$$K_{(t_2-t_1)} = \ln(L_\infty - L_1) - \ln(L_\infty - L_2)$$

where L_1, L_2, t_1, and t_2 are the lengths and times of marking and recapture, respectively, L_∞ is as described above, and $K_{(t_2-t_1)}$ is the growth constant over the time interval. The model allows for calculating the growth constant K for each individual. The sample from February 1995 was treated separately because the transect had been left undisturbed for nearly 1 y, avoiding recapture stress and habitat disturbance through frequent sampling. A linear regression of maximum shell length (L_{max}) versus average density at the transects was calculated, expecting a negative correlation of L_{max} with density. L_{max} was defined as the mean of the largest 3% of the snails at the respective transect (Pauly 1984). Total mortality (Z) was estimated with the mark-recapture data by use of a formula proposed by Gulland (1969):

$$\ln N_r = a + b \cdot r'$$

where N_r is the number of recoveries per time interval r′, a is the y-intercept, and b is the slope of the regression, which provides the estimate of Z (with sign changed). This method can only be applied to data where the marking procedure is performed at one time (e.g., a few days), the sampling effort is roughly similar, and mark shedding does not occur (Pauly 1984). Therefore, the October 1993 census was taken as the starting point. Only snails marked or recaptured (and re-marked) at this date were included in the analysis. This ensured that only specimens with sealed marks (no mark shedding) were used for mortality estimation. The February 1995 recapture data had to be corrected for sampling effort because the area was searched for 4 h, exceeding normal effort by a factor of four.

Population Structure, Biomass, and Density

For each quadrat, the median length was calculated (this was preferred to the mean length because of the lower sensitivity to "outliers") with the pooled data of all samples taken from September to March to prove whether different length groups prefer distinct zones along the 10-m transect from the mangrove border inwards. In addition, the proportion of juveniles ($\leq$20 mm) of the total was calculated for each quadrat to see if they prefer a distinct zone within each transect and to compare the dominance of juveniles between the transects.

Total shell length was converted to dry weight with 87 specimens of *T. kiosquiformis*. To do so, the shell was broken, and the cleaned tissue was placed in aluminum dishes and dried for 100 h to constant dry weight at 65°C. Dry weight was determined with a precision of 0.1 mg. A potential regression of the form $y = a \cdot x^b$ was used (Table 1). The last four samples were excluded from the size distribution and from the biomass calculations because of possible sampling bias because they were not taken by the authors.

Dry weights of all individuals of a length class were calculated from the pooled length frequency data with the regression given above. Biomass values of the length classes were summed and divided by the total area (in square meters) sampled, yielding an average biomass of *T. kiosquiformis* for the upper gulf. The biomass of each sampling quadrat was calculated by pooling the length frequencies for the respective quadrat.

Food Intake

The *in situ* food intake of three size groups of *T. kiosquiformis* (18–22 mm; 23–27 mm; 28–32 mm) was estimated over a period of 14 d in the field (Punta Morales). Ten snails of each group were placed in a mesh wire cage (height, 1 m; Ø, 40 cm), situated approx. 0.5 m above mean low water level at the mangrove edge. The 10 snails were weighed collectively before and after the experiment to the nearest 0.1 g. Wet weight again was converted to flesh weight gain by use of a linear regression of wet weight versus flesh weight (Table 1). Wet weights of each prey species were also registered before the experiment (for balanids that were offered on pieces of aerial roots, percent area covered was estimated). The following eight species (corresponding to the most abundant potential prey in the area) were placed in each of the three cages: *Balanus* sp. (Crustacea), *Littoraria varia, Littoraria fasciata, Anachis, rugosa, Cerithium stercusmuscarum* (Gastropoda), *Brachidontis, puntarensis, Pinctada mazatlantica* (juv.), and *Cardita affinis* (Bivalvia). *P. mazantlantica* is not common in mangrove forests, but a large spatfall had occurred on the mangrove roots shortly before the experiment started, so this bivalve was included. Two months later, this species had disappeared from the area. After the experiment, the surviving prey organisms were counted and weighed together with the empty shells. Because all prey had shells, weight differences measured after the experiment consisted only of flesh weight consumed by the predator. Daily food intake was expressed as % BWD (flesh weight consumed daily/wet (flesh) weight of predator). The weight increment of *T. kiosquiformis* was expressed as % wet weight gain/14 d. Prey preference was not determined; the relative abundance of prey species and their availability in the experiment were not comparable to normal habitat conditions. Some prey specimens (8 of 156) were not found after the experiment and had to be excluded as not eaten.

TABLE 1.

***T. kiosquiformis:* Regression Parameters of Dry Weight Versus Shell Length and Flesh Weight Versus Wet Weight Used for Biomass Estimation and Calculation of Daily Ration.**

Total Length/Dry Weight	Wet Weight/Flesh Weight
$a = 0.00010$	$a = -0.00700$
$b = 3.187$	$b = 0.129$
$r^2 = 0.976$	$r^2 = 0.937$
$n = 87$	$n = 87$

RESULTS

Growth and Mortality

The length frequency analysis yielded similar parameters for the different sampling sites (Fig. 4), where the ranges are: K, 0.18–0.2; L_∞, 48–50 mm; C, 0.575–0.65; W_p, 0.775–1.0. The goodness of fit (R_n) of the growth curves ranged between 0.171 (C5) and 0.341 (J6). The average growth performance (ϕ') was 2.66, with values for K and L_∞ of 0.19 and 49 mm, respectively.

The tagging experiment conducted in Punta Morales yielded results that differed from those of the length frequency analysis. Recapture data from September 1993 to March 1994 and from March 1994 to February 1995 are presented separately, because the latter consisted of individuals that were left undisturbed for 1 y (Fig. 5). The points can be divided roughly into three groups: specimens with positive K values, >0.02 (I); others with K values around zero, $0.02 > K > -0.02$ (II); and snails with negative K values, < -0.02 (III). Between September and March, only six juvenile and subadult snails (<24 mm) showed positive K values. Most specimens did not grow at all; snails larger than 25 mm tended to show negative K values. For the period from March to February, the smaller animals had the highest K values, decreasing more or less linearly to zero at a shell length of 24 mm. The same division of points was applied here, but because no negative K values occurred (and no specimens >26 mm), only the first two groups are represented. Mean density at the transects was negatively correlated ($R^2 = 0.944$) with maximum shell length (Fig. 6). Highest $L_{max.}$ values occurred at J7 and J6, where density (and biomass) were lowest, whereas high densities (P1 and C4) related to low $L_{max.}$ values. P2 was excluded from the calculation because the population at this transect consisted almost exclusively of juveniles and subadults.

The estimation of the total mortality rate (Z) from the tagging data (Fig. 7) yielded a value of 0.178/y (c.i. 0.132–0.225). The resulting fit of the regression was good ($R^2 = 0.951$; $p = 0.0002$).

Population Structure, Biomass, and Density

The distribution of length classes along the transects (Fig. 8) shows a clear prevalence of smaller animals in the inner zone. The median length decreases from the mangrove border to the interior part, stabilizing 5–8 m inwards from the mangrove edge. The graph also demonstrates the large differences in median shell length between the transects. The subpopulation in J7 consisted of the largest snails, followed by J6, C5, C4, P1, and P2. In P2, the

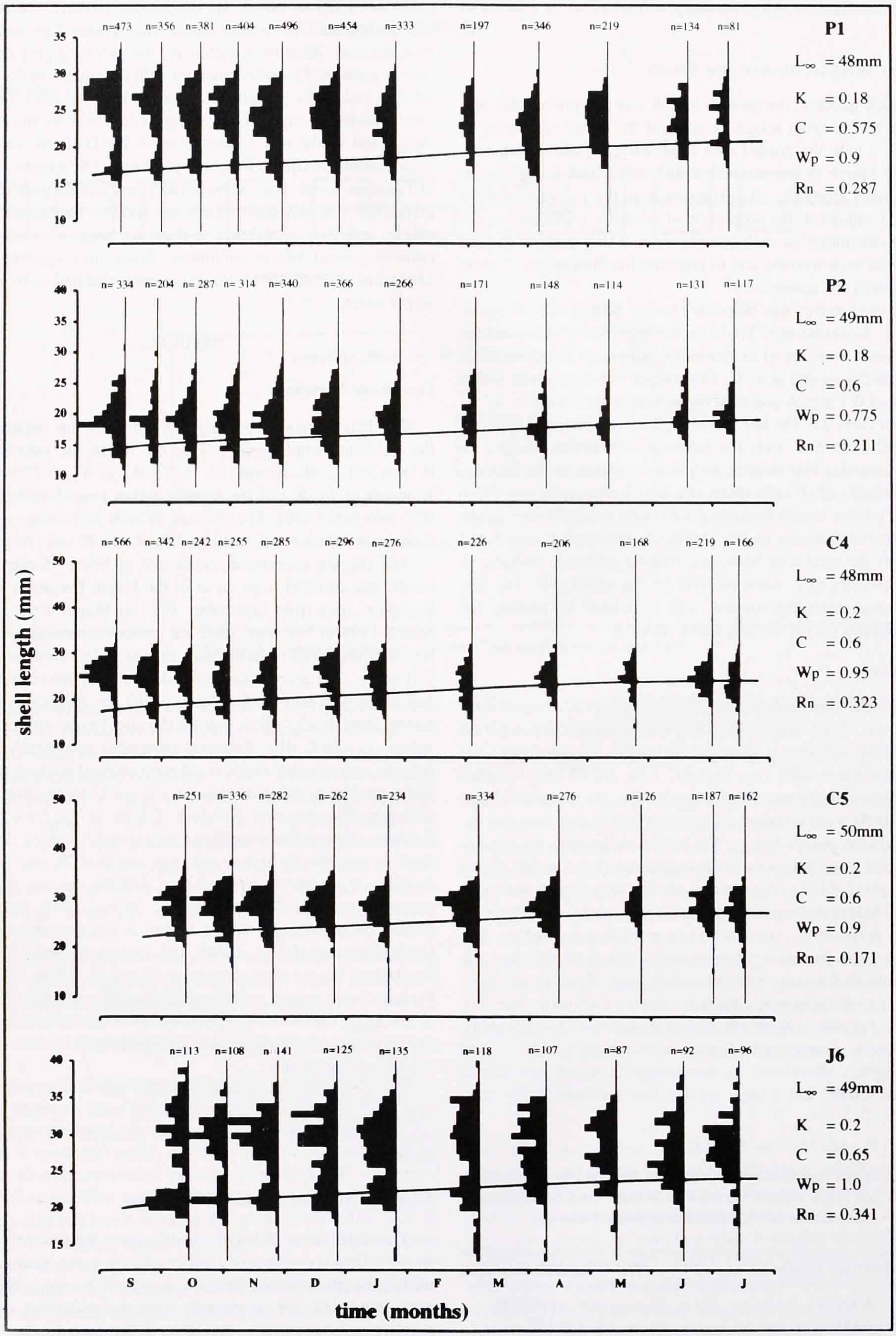

Figure 4. *T. kiosquiformis:* growth at the five transects, calculated from the length frequencies with ELEFAN. L_∞ and K von Bertalanffy growth parameters; C, constant of growth oscillation; Wp, winterpoint; Rn, goodness of fit.

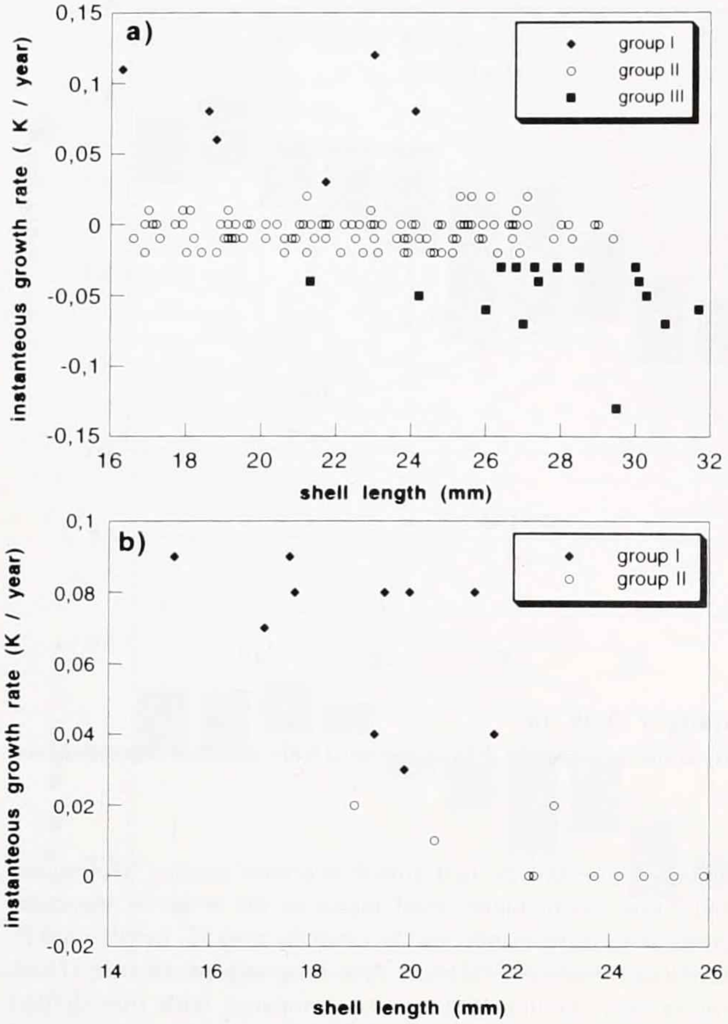

Figure 5. *T. kiosquiformis:* growth constant K as related to shell length for individuals of the marking experiment. (a) Sampling period from September 1993 to March 1994. (b) Sample taken in February 1995. Group I, $K > 0.02$; group II, $0.02 < K < -0.02$; group III, $K < -0.02$.

decrease in median length was not very pronounced, but because it was the transect with the smallest snails, large changes in size frequency distribution could not be expected. The dominance of juveniles ≤20 mm is therefore clearly strongest in P2, followed by P1 and C4 (Fig. 9). At the other transects, only 0–10% juveniles were found. At the first three transects, the dominance of juveniles increased inwards from the mangrove edge, indicating a gradient along which snails of different age classes are distributed. Highest density values (ind./m^2), obtained at the transects, were: 222 at P1, 139 at P2, 194 at C4, 111 at C5, 56 at J6, and 19 at J7.

Biomass, averaged over transects and sampling period, was highest in quadrats III–V (2–4 m from the mangrove border) (Fig. 10). The high standard errors are partly explained by the high variation of biomass values between transects, differing by a factor of up to 6. Average biomass and standard deviation of *T. kiosquiformis,* calculated over transects and sampling period, were 6.37 ± 3.41 g dry weight/m^2 (192.2 ± 102.4 g wet weight/m^2).

Food Intake

The average daily ration was lowest in the medium group (1.3% BWD wet weight; 10.7% BWD flesh weight), followed by the smallest group (1.6% BWD wet weight; 13% BWD flesh weight) (Table 2). The largest animals had the highest daily ration (2.0% BWD wet weight; 16% BWD flesh weight). *Littorina* spp. accounted for nearly 70% of prey eaten in the experiments, followed by the pearl oyster *P. mazatlantica* with 19% and the small mytilid *B. puntarensis* with 10%. Under natural conditions, however, *T. kiosquiformis* primarily feeds on balanids (pers. obs.). The results of the field experiment (Table 2) show that only the smallest size group had slight positive growth in wet weight (0.6%/14 d), whereas the larger groups (23–27 and 28–32 mm) lost weight during the experiment (−1.9 and −1.3%/14 d, respectively).

DISCUSSION

Growth and Mortality

The length frequency analysis yielded very low K values (0.18–0.2) for *T. kiosquiformis* for all transects when compared with the reports of Cantera et al. (1980), who gave growth rates of approximately 0.5 mm/mo (K/y ≈ 0,29) for this species on the Colombian Pacific Coast. Although the goodness of fit (Rn) was rather low for our K estimates (0.171–0.341), the calculated parameters are very similar between transects and seem reliable.

The growth performance index ($ø' = 2.66$) is correspondingly low and seems more comparable to that of boreal than of tropical gastropods, which normally exhibit values between 3.2 and 4.7. Only two boreal thaidids and some *Littorina* species are reported to have similar low values (Wolff 1994).

The results of the marking experiment indicate still much lower growth rates than were found with the length frequency analysis. Of nearly 300 recaptured snails, only a few showed positive growth during the sampling period. One might suspect marking and/or recapture stress to be the cause, but this does not seem probable for the following reasons: (1) marking was conducted by three different methods (see Materials and Methods); (2) marking procedure and recapture never lasted longer than 2 h, whereas snails are naturally exposed for up to 5 h during low tide; (3) many marked snails were recaptured the first time alive after 3–5 mo without showing any measurable growth; and (4) the sample taken in February 1995 yielded basically the same results, although the transect had been left undisturbed for nearly 1 y. The decrease in total shell length in some specimens is due to shell erosion at the apex, where the periostracum can be damaged, especially in older animals, leaving the calcareous shell structures in this part uncovered. The interindividual variability in growth—seen in the wide scatter of individual K values—is very high, but several authors report similar variabilities for other molluscs (e.g., Moore 1972, Broom 1982, Sainsbury 1982, Wolff 1987). This variability can probably be explained through small-scale differences in habitat structure but possibly also by genotypical differences between specimens (Wolff 1987).

Unexpectedly, K, generally considered to be constant for a species over its whole life cycle, clearly decreased with size, and it seemed reasonable to divide the individual K values into three groups: positive values for snails ≤24 mm, values around 0 (occurring in the whole size range), and negative K values for snails >24 mm [one exception]. It thus seemed that 24 mm, which marks the lower limit for the onset of maturity (Cantera et al. 1980), can be taken as the turning point for the snails in P1, where growth ceased completely. This suggests ontogenetically based metabolic changes related to the onset of maturity. This pattern can be described for the study site P1, where population densities were highest. However, for the other study sites, L_{max} values were

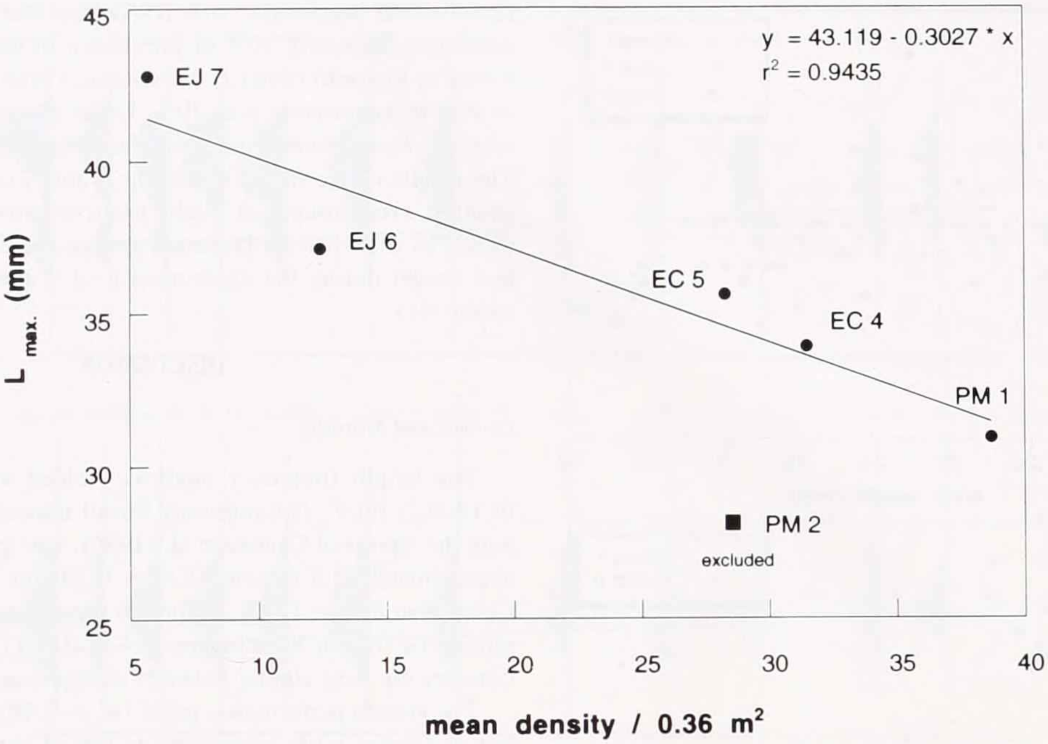

Figure 6. *T. kiosquiformis:* **maximum shell length ($L_{max.}$) vs. average density at the six transects. P2 was excluded from the fitted regression (see text).**

significantly higher, which suggests that growth in these areas continues in older individuals. Thus, it might be speculated that somatic growth ceases early under high population densities (resulting in smaller maximum length) in response to limiting food supply. Under these conditions, energy may be used exclusively for gonad formation and maintenance metabolism. A negative effect of high densities on growth and maximum length through intraspecific competition for microhabitats and food resources has also been reported for other intertidal gastropods (e.g., Underwood 1978). This phenomenon could naturally not be detected by the length frequency analysis because only juvenile specimens, which were still growing, were used.

The thick shell of *T. kiosquiformis,* being the most robust among the snails occurring at Punta Morales (Borjesson and Szelitowski 1989), is energetically costly (Palmer 1985, Kitching 1986) and might be another factor explaining the very slow growth rate of *T. kiosquiformis.* In related species, thick-shelled morphs were also shown to have a decreased tissue growth (*Thais lamellosa,* Palmer 1981); slower shell growth (*Purpura* species, Wellington and Kuris 1983); higher food intake as the result of increased production, maintenance, and locomotion costs (*T. lapillus* and *T. lamellosa,* Palmer 1992) and less offspring production (*Thais emarginata,* Geller 1990) when compared with thin-shelled morphs. Finally, energy costs for adaptations to environmental stress, which is supposed to be very high in tropical intertidal areas (Moore 1972, Vermeij 1978, Garrity 1984), may contribute a significant part to the total energy budget, further reducing energy available for growth (Russell-Hunter 1985).

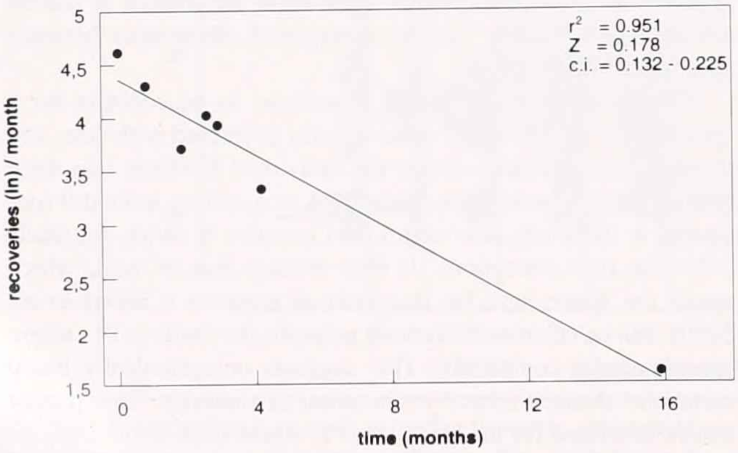

Figure 7. *T. kiosquiformis:* **total mortality rate (Z) as derived from Gulland's (1969) method.**

We believe that a combination of the above-mentioned factors is responsible for the extremely slow growth of *T. kiosquiformis.* The results of the length frequency analysis possibly reflect the growth potential of this species when conditions are favourable and food supply is not limiting. In J6, this may have been the case, because density was low, animals grew near to their asymptotic size, and goodness of fit (Rn) for the resulting growth curve was very good.

If high population density and biomass are maintained while individual growth is very slow, survival must be maximized. Our mortality estimate (Z = 0.178), which is at the low end of the range reported for tropical and subtropical gastropods (0.1–1.66) (Sainsbury 1982, Appeldoorn 1987, Appeldoorn 1988, Prince et al. 1988, Wolff 1989, Debrot 1990), is an indication thereof. This low mortality is probably due to: (1) the strong antipredatory characteristics of the shell (thick shell, narrow aperture, stout spines), which reduce predation pressure by crabs and fish (Vermeij 1978, Palmer 1979, Palmer, 1985, Bertness and Cunningham 1981, Wellington and Kuris 1983); (2) the high tolerance against desiccation (Cantera et al. 1980); and (3) the ability to minimize energy expenditure (extremely slow growth, growth inhibition at the onset of maturity), using a ''sit and wait'' strategy. These results contradict Alongi's (1989) general assumption that turnover rates as well as predation mortalities in the tropics are higher than in temperate latitudes.

The method used may even have overestimated mortality, be-

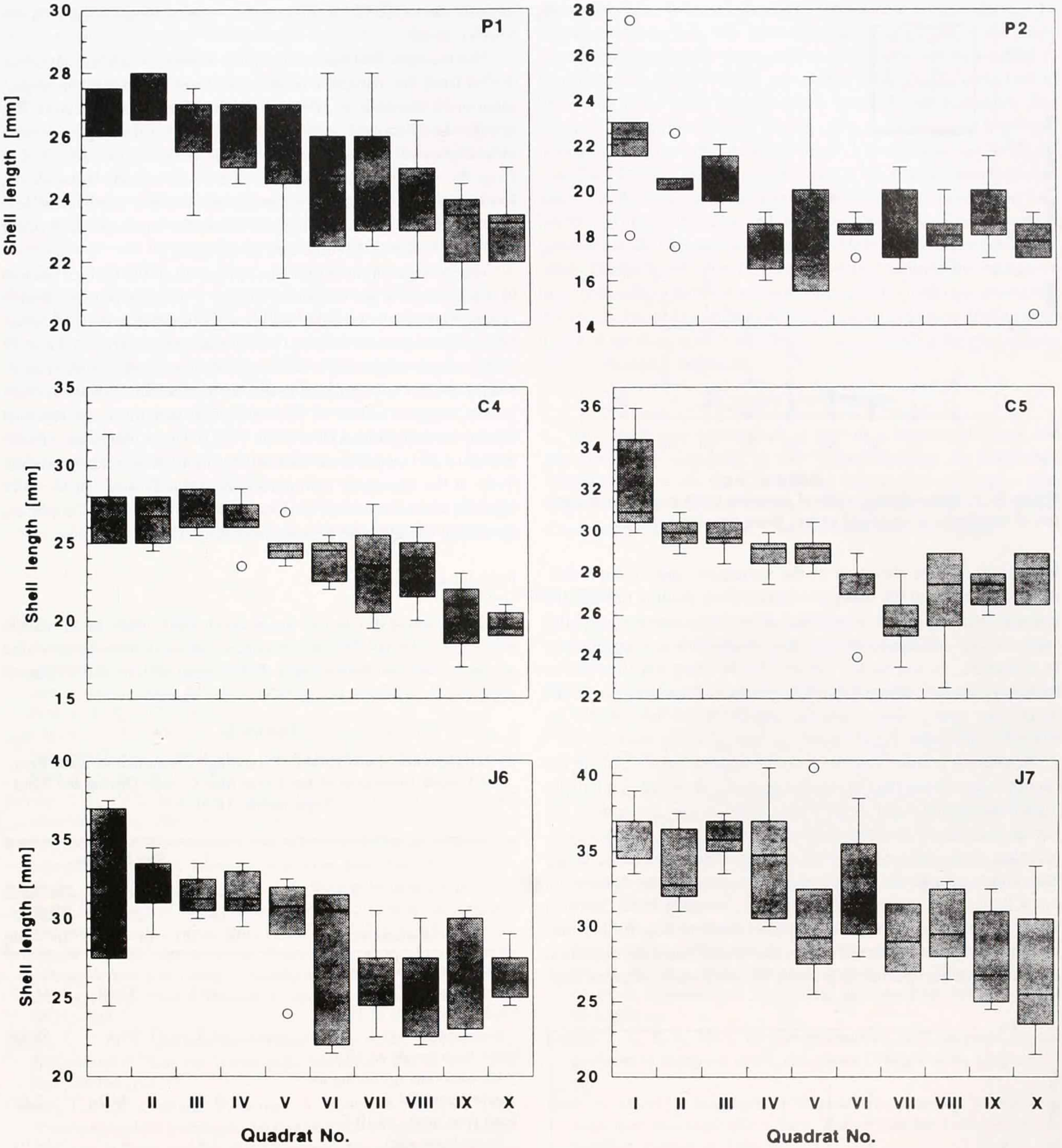

Figure 8. ***T. kiosquiformis:*** **box plots of the size distributions along the six transects, with the combined data of all sampling dates. Horizontal line within the box indicates the median, first upper and lower quartiles are given by the vertical edges of the box, vertical bars indicate the whole data range, and open circles are extreme outliers, which were excluded from the calculation.**

cause mark shedding may have occurred to a small extent and because snails could have migrated out of the area. In addition, specimens well hidden might not have been found.

Population Structure, Biomass, and Density

The observed distributional pattern—with the juveniles predominating mangrove inwards and the larger specimens towards the mangrove edge—probably results from the active distribution of the respective size groups along a gradient of predation and desiccation, as described for several gastropods (e.g., Vermeij 1972, Butler 1979, Garrity 1984). The most important gastropod predators in the area are puffer fish (*Sphoeroides* species and *Diodon* species) and rays, which were frequently observed foraging in Punta Morales (Jerome 1987, Whitey 1990, pers. obs.). Predation pressure is probably more severe at the mangrove border than inside the forest for the following reasons: (1) the root system is much denser inside, making foraging more difficult here; (2) foraging time is reduced inside the forest because of shorter tidal

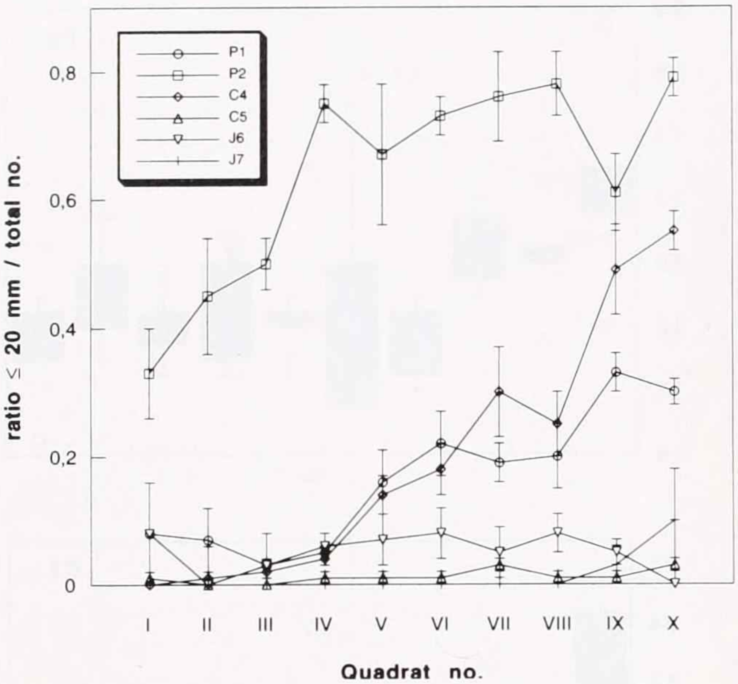

Figure 9. ***T. kiosquiformis:*** **ratio of juveniles (≤20 mm) to total number of specimens ± standard errors along the six transects.**

inundation (higher elevation of the sediment); and (3) light conditions are better at the mangrove border (less shading through the canopy), making visual recognition of prey specimens easier. Because large *T. kiosquiformis* are less susceptible or even immune to predation, as shown by Palmer (1979), they can live at the mangrove border, where barnacles are more abundant than in the inner zone (pers. obs.), whereas smaller snails are largely restricted to the inner forest, where predation is less intense.

Irradiation is more intense at the mangrove border, where the canopy is less dense than mangrove inwards, resulting in relatively higher temperature and desiccation. Wind is also stronger at the border because air movements are dampened by roots and leaves, reducing desiccation stress in the inner zone. Generally, larger individuals of a given gastropod species can tolerate desiccation much better than juveniles (Moore 1972, Vermeij 1972, Vermeij 1978, Underwood 1978), which allows them to stay further outside than juveniles. Personal observations confirmed the migration pattern of smaller specimens towards the inner zone, whereas large animals dispersed in all directions or stayed at the border (Koch unpubl. obs.).

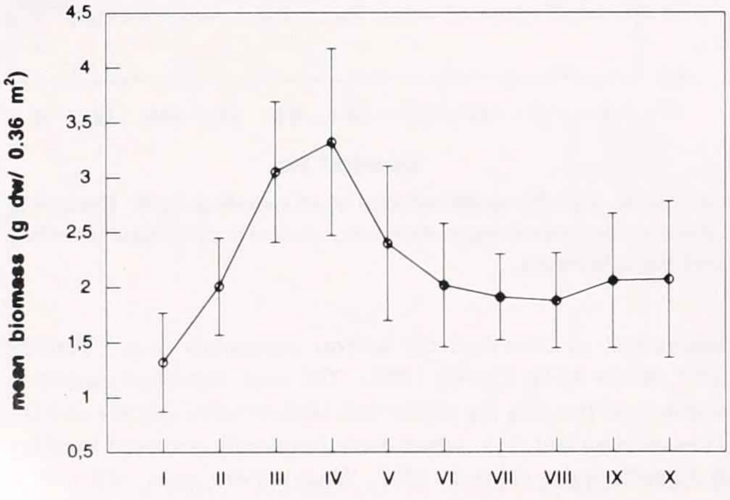

Figure 10. ***T. kiosquiformis:*** **average biomass distribution ± standard errors for each quadrat along the transect. Data from all transects combined.**

The biomass distribution along the transect, with its maximum 2–4 m from the mangrove border, can be explained by the above-mentioned mechanisms affecting the distribution of respective size groups. Middle-sized snails, which account for the largest portion of total population biomass, were found in highest densities 2–4 m from the mangrove border, where stress is already reduced but food supply is still high. Further inwards, where food seems less abundant but where stress is minimized, the smallest snails occur and survive the most vulnerable life stages.

The average biomass of *T. kiosquiformis* in the Gulf of Nicoya of 6.37 ± 3.41 g dry weight/m^2 (192.2 ± 102.2 g wet weight/m^2) is very high when compared with values of other mangrove areas. Lalana Rueda and Gosselck (1986) found values between 8 and 17 g dry weight/m^2 for the whole epifauna during the rainy season, with much lower biomasses in the dry season. In Taiwanese mangroves, biomass values of 131–406 g wet weight/m^2 are reported for the whole epifauna (Wu et al. 1992). These values are similar to that of *T. kiosquiformis* and reflect the high secondary productivity of the mangrove community in the study area. In terms of biomass and abundance, *T. kiosquiformis* is the most important species in the mangrove root community of the study area.

Food Intake

The overall estimate for the average food intake of 1% BWD wet weight (9% BWD flesh weight) is similar to that of the related species. *Thais carinifera* (10% BWD flesh weight and to that of

TABLE 2.

T. kiosquiformis: **Food Intake, Percentage Consumed of Each Prey, and Weight Increment of the Three Size Groups During the Field Experiment (14 d).**

	Size Groups (mm)		
Parameter	**18–22 (n = 10)**	**23–27 (n = 10)**	**28–32 (n = 10)**
Starting weight (wet) of 10 *T. kiosquiformis* (g)	14.71	32.02	44.43
Final weight (wet) of 10 *T. kiosquiformis* (g)	14.8	31.4	43.84
Mean flesh weight of 10 *T. kiosquiformis* (g) during the experiment (14 d)	1.83	4.02	5.62
Total food intake of 10 *T. kiosquiformis* (g)	3.33	6	12.61
Daily ration in % wet weight/day	1.6	1.3	2
Daily ration in % flesh weight/day	13	10.7	16
Weight contribution of each prey species in %			
L. varia	0	2	13
L. fasciata	56	78	54
B. puntarensis	16	3	11
Pinctada sp.	28	17	12
C. affinis	0	0	10
A. rugosa	0	0	0
C. stercusmuscarum	0	0	0
Balanids	0	0	0
Total weight gain of *T. kiosquiformis*/14 d (%)	0.6	−1.9	−1.3

the naticid snail *Natica maculosa* (7.5% BWD flesh weight), which occurs in tropical mudflats (Broom 1982). By the use of average biomass and daily ration, the population of *T. kiosquiformis* consumes approx. 2.5 g flesh weight/m^2 per day. We do not have any reasonable explanation for the differences in daily rations (%BWD) found between the three size groups, with the largest specimens having the highest food intake, followed by the smallest and the middle sized.

The strong preference for littorinid snails in the experiment is most probably not representative of field conditions, where *T. kiosquiformis* was found to feed primarily on barnacles (Cantera et al. 1980, Perry 1988, pers. obs.). Littorinids are not readily available as prey because they occur much higher in the mangroves of Punta Morales (Jerome 1987, Withey 1990) and escape when *T. kiosquiformis* is present (pers. obs.), a behaviour also reported for other littorinid snails (McKillup 1982, Fairweather et al. 1984). Furthermore, thaidid and muricid snails are reported to be capable of choosing the most profitable prey (in terms of energy per unit of effort) and readily switch their preferences when a prey species yielding higher profit is made available (Bayliss 1982, Palmer 1984, Carroll and Wethey 1990).

The weight changes during the experiment seem to confirm the results of the growth analysis, because only the smallest specimens gained weight, whereas the larger snails lost weight during the experimental period. The growth of mangrove trees in the study area is possibly highly dependent on the density and biomass of *T. kiosquiformis*. Perry (1988) reported a 50% growth reduction in the aerial roots of *R. mangle* when covered with barnacles. She found *T. kiosquiformis* and hermit crabs to be the most important predators, but the latter occurred in much lower densities along the transects studied (Koch unpubl. obs.). A similar situation was found in Belize, where mangrove growth also depended on barnacle coverage (Ellison and Farnsworth 1992). The dominant predator in that system was the snail *Melongena melongena*. Our study thus suggests that *T. kiosquiformis* structures the mangrove root community in the study area through the predation pressure it exerts on the community and maintains or enhances the productivity of the mangrove trees by constantly cleaning the root system of its encrusting epifauna.

ACKNOWLEDGMENTS

This study was undertaken as part of a Masters' Degree and was financially supported by the "Studienstiftung des Deutschen Volkes." We thank the Costa Rican friends and colleagues who helped with the practical work and the logistics, especially Rocío Cordoba, Sergio "Cuñado" Segura, and Jose A. Vargas.

LITERATURE CITED

Alongi, D. M. 1989. Ecology of topical soft-bottom benthos: a review with emphasis on emerging concepts. *Rev. Biol. Trop.* 37(1):85–100.

Appeldoorn, R. S. 1987. Assessment of mortality in an offshore population of queen conch, *Strombus gigas* L., in Southwest Puerto Rico. *Fish. Bull.* 85(4):797–804.

Appeldoorn, R. S. 1988. Age determination, growth, mortality and age of first reproduction in adult queen conch, *Strombus gigas* L., off Puerto Rico. *Fish. Res.* 6:363–378.

Bayliss, D. E. 1982. Switching by *Lepsiella vinosa* (Gastropoda) in South Australian mangroves. *Oecologia* 54:221–226.

Bertness, M. D. & C. Cunningham. 1981. Crab shell-crushing, predation and gastropod architectural defense. *J. Exp. Mar. Biol. Ecol.* 50:213–230.

Borjesson, D. L. & W. Szelitowski. 1989. Shell utilization and predation in the hermit crab *Clibanarius panamensis,* Stimpson, in a tropical mangrove estuary. *J. Exp. Mar. Biol. Ecol.* 133:213–228.

Broom, M. J. 1982. Size-selection, consumption rates and growth of the gastropods *Natica maculosa* (Lamarck) and *Thais carinifera* (Lamarck) preying on the bivalve *Anadara granosa*. *J. Exp. Mar. Biol. Ecol.* 56:213–233.

Butler, A. J. 1979. Relationships between height on the shore and size distributions of *Thais spp.* (Gastropoda: Muricidae). *J. Exp. Mar. Biol. Ecol.* 41:163–194.

Cantera, J. R., R. Contreras, F. Borrero, E. Buttkus & F. Zapata. 1980. Historia natural del gastrópodo del mangle *Thais kiosquiformis* Duclos, 1832, en la costa del Pacifico Colombia. Memorias del seminario organizado por UNE SCO (Cali, 27.11-01.12.1978):170–194.

Carroll, M. L. & D. S. Wethey. 1990. Predator foraging behaviour: effect of a novel prey species on prey selection by a marine intertidal gastropod. *J. Exp. Mar. Biol. Ecol.* 139:101–117.

Debrot, A. 1990. Temporal aspects of population dynamics and dispersal behaviour of the West Indian topshell *Cittarium pica,* at selected sites in the Exuma Cays, Bahamas. *Bull. Mar. Sci.* 47(2):431–447.

Ellison, A. M. & E. J. Farnsworth. 1992. The ecology of Belizean mangrove root fouling communities: patterns of epibiont distribution and abundance, and effects on root growth. *Hydrobiologia* 247(1–3):87–98.

Fairweather, P. G. 1988. Movements of intertidal whelks (*Morula marginalba* and *Thais orbita*) in relation to availability of prey and shelter. *Mar. Biol.* 100:63–68.

Fairweather, P. G., A. J. Underwood & M. J. Moran. 1984. Preliminary investigations of predation by the whelk *Morula marginalba*. *Mar. Ecol. Prog. Ser.* 17:143–156.

Garrity, S. D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* 65(2):559–574.

Gayanilo, F. C., P. Sparre & D. Pauly. 1994. The FAO-ICLARM Stock Assessment Tools (FiSAT) user's guide. Final draft. FAO, Rome. ICLARM Contr. 1048.

Geller, J. B. 1990. Consequences of a morphological defense: growth, repair and reproduction by thin- and thick-shelled morphs of *Nucella emarginata* (Deshay es). *J. Exp. Mar. Biol. Ecol.* 144:173–184.

Gocke, K., M. Vitola & G. Rojas. 1981. Oxygen consumption patterns in a mangrove swamp on the Pacific Coast of Costa Rica. *Rev. Biol. Trop.* 29:143–154.

Gulland, J. A. 1969. Manual of methods for fish stock assessment. Part I. Fish population analysis. *FAO Man. Fish. Sci.* 4, 154 pp.

Janzen, D. H. (ed.). 1991. Historia natural de Costa Rica. ISBN 9977-67-169-9, Editorial de la Universidad de Costa Rica, San José, Costa Rica. 822 pp.

Jerome, T. G. R. L. 1987. Vertical distributions, shell morphologies and predation of mangrove snails. Associated Colleges of the Midwest, 34 pp.

Keen, A. M. 1971. Sea Shells of Tropical West America. Marine Mollusks from Baja California to Peru. 2nd ed. Stanford University Press, Stanford, California. 1064 pp.

Kitching, J. A. 1977. Shell form and niche occupation in *Nucella lapillus*. *J. Exp. Mar. Biol. Ecol.* 26:275–289.

Kitching, J. A. 1986. The ecological significance and control of shell variability in dogwhelks from temperature rocky shores. pp. 234–248. *In:* P. G. Moore and R. Seed (eds.). The Ecology of Rocky Coasts. Columbia University Press, New York.

Lalana Rueda, R. & F. Gosselck. 1986. Investigations of the benthos of mangrove coastal lagoons in southern Cuba. *Int. Rev. Gesamt. Hydrobiol.* 71(6):779–794.

Menge, B. A. 1978. Predation intensity in a rocky intertidal community. Effect of algal canopy, wave action and desiccation on predator feeding rates. *Oecologia* 34:17–35.

Moore, H. B. 1972. Aspects of stress in the tropical marine environment. *Adv. Mar. Biol.* 10:217–269.

Munro, J. L. 1982. Estimation of the parameters of the von Bertalanffy growth equation from recapture data at variable time intervals. *J. Cons. CIEM*. 40:199–200.

Palmer, R. A. 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* 33(2): 697–713.

Palmer, R. A. 1981. Do carbonate skeletons limit the rate of body growth? *Nature* 292:150–152.

Palmer, R. A. 1984. Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. *Oecologia* 62: 62–72.

Palmer, R. A. 1985. Adaptive value of shell variation in *Thais lamellosa:* effect of thick shells on vulnerability to and preference by crabs. *Veliger* 27(4):349–356.

Palmer, R. A. 1992. Calcification in marine molluscs: how costly is it? *Proc. Natl. Acad. Sci. USA* 89(4):1379–1382.

Pauly, D. 1984. Fish Population Dynamics in Tropical Waters: A Manual for Use With Programmable Calculators. Studies and Reviews. ICLARM, Philippines. 325 pp.

Pauly, D. & G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. I.C.E.S. C.M. 1979/G, Demersal Fish Cttee, 24, 24 pp.

Pauly, D. & J. L. Munro. 1984. Once more on the comparison of growth in fish and invertebrates. *Fishbyte* 2:21.

Perry, D. M. 1988. Effects of associated fauna on growth and productivity in the red mangrove. *Ecology* 69(4):1064–1075.

Peterson, C. L. 1960. The physical oceanography of the Gulf of Nicoya, a tropical estuary. *Bull. InterAmerican Trop. Tuna Commission* 4(4), 37 pp.

Prince, J. D., T. L. Sellers, W. B. Ford & S. R. Talbot. 1988. Recruitment, growth, mortality and population structure in a southern Australian population of *Haliotis rubra* (Mollusca: gastropoda). *Mar. Biol.* 100:75–82.

Richardson, T. D. & K. M. Brown. 1990. Wave exposure and prey size selection in an intertidal predator. *J. Exp. Mar. Biol. Ecol.* 142(1–2): 105–120.

Russell-Hunter, W. D. 1985. Physiological, ecological and evolutionary aspects of molluscan tissue degrowth. *Am. Malacol. Bull.* 3(2):213–221.

Sainsbury, K. J. 1982. Population dynamics and fishery management of the paua, *Haliotis iris*. I. Population structure, growth, reproduction and mortality. *N.Z. J. Mar. Freshwater Res.* 16:147–161.

Spight, T. M. 1983. Risk, reward and the duration of feeding excursions by a marine snail. *Veliger* 24(4):302–308.

Thomas, P. 1988. Die Niederschlagsverhältnisse in Costa Rica. Master's Thesis, University of Augsburg, Augsberg, Germany, 88 pp.

Underwood, A. J. 1978. The ecology of intertidal gastropods. *Adv. Mar. Biol.* 16:111–210.

Vakily, J. M. 1992. Determination and comparison of growth in bivalves, with emphasis on the tropics and Thailand. *ICLARM Tech. Rep.* 36: 125.

Vermeij, G. J. 1972. Intraspecific shore-level size gradients in molluscs. *Ecology* 53:693–700.

Vermeij, G. J. 1978. Biogeography and adaptation. Harvard University Press, Cambridge, Massachusetts. 332 pp.

Voorhis, A. D., C. E. Epifanio, D. Maurer, A. I. Dittel & J. A. Vargas. 1983. The estuarine character of the Gulf of Nicoya, an embayment on the Pacific Coast of Central America. *Hydrobiologia* 99:225–237.

Wellington, G. M. & A. M. Kuris. 1983. Growth and shell variation in the tropical Eastern Pacific intertidal gastropod genus *Purpura:* ecological and evolutionary implications. *Biol. Bull.* 164:518–535.

West, L. 1988. Prey selection by the tropical snail *Thais melones:* a study of interindividual variation. *Ecology* 69(6):1839–1854.

Withey, J. 1990. Predation and Vertical Distribution of Four Snail Species in a Tropical Mangrove Estuary. Associated Colleges of the Midwest, 38 pp.

Wolff, M. 1985. Fischerei, Ökologie und Populationsdynamik der Pilgermuschel *Argopecten purpuratus* (L.) im Fischereigebiet von Pisco (Peru) unter dem Ein-fluβ des El Niño 1982/83. Ph.D. Thesis, University of Kiel, 113 pp.

Wolff, M. 1987. Population dynamics of the peruvian scallop *Argopecten purpuratus* during the El Niño Phenomenon of 1983. *Can. J. Fish. Aquat. Sci.* 44:1684–1691.

Wolff, M. 1989. Estimates of growth, mortality and recruitment of the Loco *Con cho-lepas concholepas* (Bruguiere, 1789) derived from a shell mound in northern Chile. *Stud. Neotrop. Fauna Env.* 24(2):87–96.

Wolff, M. 1994. Population Dynamics, Life Histories and Management of Selected Invertebrates of the SE Pacific Upwelling System. Habilitation at the University of Bremen, Bremen, Germany. 210 pp.

Wu, Q., Z. Fengwu, L. Lin, J. Jingxiang, L. Rongguan, C. Erxi, H. Minghai & H. Xinguang. 1992. Benthic communities of mangrove area in Daya Bay. *J. Oceanogr. Taiwan Strait Taiwan Haixia* 11(2): 161–166.