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Species composition and vertical distribution of chitons (Mollusca: Polyplacophora) in a rocky intertidal zone of the Pacific coast of Costa Rica

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The present study describes the species composition and vertical distribution of chitons in tide pools and on exposed rock areas of the intertidal zone of Samara, Guanacaste, Pacific Costa Rica. Nine different species of chitons were recorded, and their densities and sizes were determined using quadrate sampling. Physical (period of emersion, temperature and salinity range) and biotic (presence and diversity of food resources) factors were examined to assess their influence on distribution and abundance of each species. Ischnochiton dispar *was the predominant species with densities of up to 200 ind* m^{-2}*, representing 85.4% of all sampled individuals (N = 4193). The size of* I. dispar *was positively correlated with the size of the inhabited boulders. Two species (*I. dispar *and* Stenoplax limaciformis*) showed segregation in size:* I. dispar *being negatively and* S. limaciformis *positively correlated to the distance from the shore. Two of the nine species (*Chiton stokesii *and* Acanthochitona hirundiniformis*) occurred mainly on rocky areas outside the tide pools with variable amounts of exposure to air during each tidal cycle. In both species the tide pool specimens were significantly smaller than those collected in the rocky areas. Distribution of all other species was restricted to the tide pools and species had their peak abundance in the zones with more moderate conditions and a higher diversity of algae, resulting in the highest chiton diversity in these areas.*

Keywords: chiton ecology, segregation in size, abundance, zonation, *Ischnochiton dispar*

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INTRODUCTION

Chitons (Mollusca: Polyplacophora) are common members of the intertidal community on the rocky shores of tropical Central America. The majority of studies on chitons in this area have chosen a taxonomic approach, focusing on the species diversity along the Pacific and Atlantic coasts (e.g. Ferreira, 1983, 1987; Bullock, 1985, 1988; Reyes-Gómes, 1999; García-Rios, 2003; García-Rios *et al.*, 2003, 2007; García-Rios & Álvarez-Ruiz, 2007). Comments on the biology of certain species are scarce in these publications. Apart from a few studies (Glynn, 1970; Randall & Martin, 1987; McMahon *et al.*, 1991; Littler *et al.*, 1995; Kleeman, 2003), the ecology of Central American chitons is, thus, poorly understood.

This situation also prevails in Costa Rica. Besides taxonomic works (e.g. Ferreira, 1987; Schwabe & Wehrtmann, in press), only few publications deal with different aspects of the biology and ecology of the chitons present on the Pacific coast. Cruz & Sotela (1984) studied the biology of *Chiton stokesii* Broderip, 1832; Miller (1983) analysed species richness and trophic roles of tropic chitons and compared them to those in temperate zones, and the study conducted by Schmidt-Effing (1980) focused on the homing behaviour and activity rhythm of *C. stokesii*. Willis & Cortés (2001) studied different habitats in the Manuel Antonio National Park, Pacific Costa Rica, and reported the presence of two chiton species, namely *Chiton virgulatus* Sowerby, 1840 and *Lepidozona flavida* (Thiele, 1910) (according to Kaas & Van Belle, 1994 a synonym of *Callistochiton pulchrior* Carpenter MS, Pilsbry, 1893).

The vertical distribution of chiton species in the intertidal zone in sub-Antarctic regions is known to be influenced by a variety of physical factors such as temperature and salinity range (Simpson, 1976) and in general by biotic factors, e.g. food resources (Piercy, 1987). However, similar data from the tropics are not available. Earlier studies (Otaíza & Santelices, 1985; Randall & Martin, 1987) have shown that many chiton species display species-specific vertical habitat stratification. Studies from central Chile (Otaíza & Santelices, 1985), Australia (Smith & Otway, 1997) and the sub-Antarctic (Simpson, 1976) investigated the distribution patterns and the influence of certain abiotic and biotic factors. A comparison of these studies shows that more data are needed to reveal overall patterns in chiton distribution, habitat selection, and abundance, leading to a better understanding of chiton ecology in general. As far as we know, no information has been published either on species composition and vertical distribution of chitons or on the influencing environmental factors along the Pacific coast of Central America.

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The present study was undertaken to remedy this lack and documents the variation of species composition and abundance of chitons on a rocky intertidal zone on the Pacific coast of Central America. We describe distribution patterns of the nine chiton species encountered at the study site in relation to their specific habitats which are characterized by their principal physical and biotic features.

MATERIALS AND METHODS

Study site

The study was carried out from February to June 2004 in Samara (Playa Cangrejal), Guanacaste, on the Pacific coast of Costa Rica (Figure 1). During low tide, an area of approximately 40,000 m^2 of rocky tide pools and elevated rocks surrounded by fine coral sand is exposed at the south-western end of the bay (Figure 2A). The entire bay is protected from strong waves by a coral reef, and affected by a diurnal tidal rhythm and a mean tidal range of 2.28 m (Lizano, 2006).

Sampling lasted two to three days each month and took place during low tide in daylight hours; some additional observations on chiton behaviour were made at night. On sampling days the weather was usually sunny but occasionally overcast by scattered clouds. Air temperatures ranged from 28°C to 34°C, water temperatures varied between 29.3°C to 31.1°C, and salinity fluctuated between 32.4 to 33.8 ppt during high tides.

Tide pools

The tide pools at Samara comprise 5–30 cm deep depressions and channels, eroded into the rock and filled with predominately coarse sand (0.6–2.0 mm). Boulders ranging from <5 to >20 cm occurred in the pools.

Three transect sites 20 m apart from each other were selected in the tide pool area. Transects were laid out in straight lines running from the mean high tide line (MHT) to the mean low tide line (MLT) (Figure 3). Starting at the MHT (defined as 0 m), every five metres a 1 m^2 quadrate was carefully examined for chitons; a total of 89 quadrates were sampled. Chitons were found by removing and inspecting every boulder, carefully checking the solid rock and other present substratum (i.e. algae or coral grid). All chitons were identified in the field according to Kaas & Van Belle (1985, 1987, 1990, 1994) Lyons (1988), García-Ríos *et al.* (2003) and Kaas *et al.* (2006). Their body length was measured with a Vernier caliper to the nearest 0.1 mm.

To determine the potential preferences for stone sizes five randomly selected quadrates in Zone III (see Tables 1 & 3) which was characterized by the highest abundance of *Ischnochiton dispar* (Sowerby, 1832), were analysed. All boulders found in these quadrates were assigned to one of five size-classes (<5 cm; 5–10 cm; 10–15 cm; 15–20 cm; >20 cm). Number and body length of the chitons found on each inhabited stone were recorded. Data were tested (Spearman correlation test; Engel, 1997) for correlation between body length and stone size.

The size distribution of the two most common tide pool species at the study site (*I. dispar* and *Stenoplax limaciformis* (Sowerby, 1832)) was analysed for possible correlation with the distance from the shore by means of the Spearman correlation test (Engel, 1997).

The duration of the 'drought period' (used herein as meaning for the duration each tide pool quadrate was exposed during low tides) was recorded for each quadrate. During this period salinity and temperature were measured in 30 minute intervals and compared to a mean high tide value, measured at different points of the study area. In May 2004, algae were collected from the tide pools and brought to the laboratory of the Escuela de Biología, Universidad de Costa Rica, San José, for identification. According to Steneck & Watling (1982) the algae were sorted into the following functional groups potentially utilized as food resource by chitons: microalgae, filamentous algae (<1 cm) and crustose coralline algae. The density and diversity of these groups of algae were recorded. The quadrates were then grouped into five different habitat zones based on abiotic (duration of drought period, salinity and temperature range) and biotic (presence and diversity of algae) parameters (Table 1). The data provided in Table 1 summarize our observations and measurements and reflect the maximum changes of physical conditions endured by organisms inhabiting these zones on a typical hot sunny day during low tide.

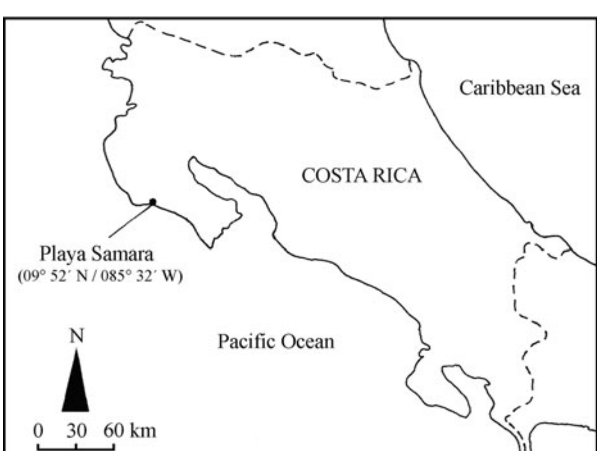

Fig. 1. Location of the study site, Samara (Playa Cangrejal), Pacific coast of Costa Rica.

Exposed rocks

Bare rock plates and elevated rock quadrates differ mainly from the tide pools by their lack of water during low tides and the resulting exposure of the inhabitants to air. However, the surface of the rock walls is uneven with small holes and cracks which retain water at all times. The angle of slope of the elevated rocks ranged from 30° to 80°. The rock plates were usually solid and horizontally orientated with only a few shallow (3–10 cm) cracks.

In June 2004 the rocky area outside the tide pools was sampled by randomly choosing quadrates on elevated rocks and rock plates in different parts of the intertidal zone. One entire, prominent, and exposed rock in Zone IV (equal to an area of 16 m^2) was also sampled, as well as one quadrate (1 m^2) of exposed rocks in the other zones and one quadrate (1 m^2) of bare rock plates in each habitat zone.

Two species (*Chiton stokesii* and *Acanthochitona hirundiniformis* (Sowerby, 1832)) occurred in the tide pools as well as on exposed rocks. Differences in body size between the

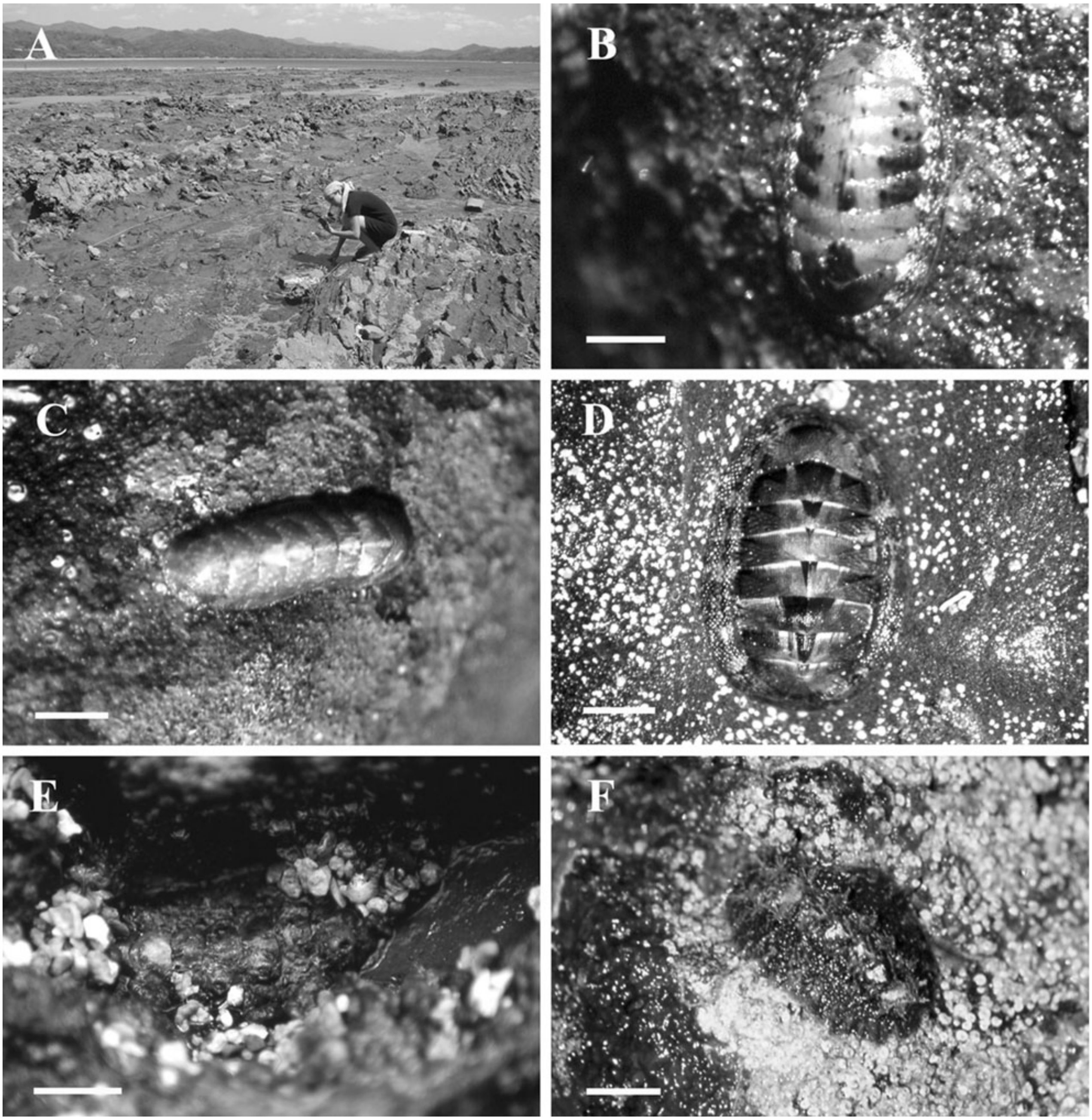

Fig. 2. The study site, Samara (Playa Cangrejal), Pacific Costa Rica, during low tide (A) and the five most common species of chitons at the study site (B–F). (B) *Ischnochiton dispar* (scale bar 0.5 cm); (C) *Stenoplax limaciformis* (scale bar 0.5 cm); (D) *Chiton stokesii* (scale bar 1 cm); (E) *Acanthochitona hirundiniformis* (scale bar 0.5 cm); (F) *Acanthochitona ferreirai* (scale bar 0.5 cm).

individuals from both habitats were tested for significance by means of the Mann–Whitney *U*-test (Engel, 1997).

Reference specimens of all encountered species of the present study were deposited at the Bavarian State Collection of Zoology (ZSM).

RESULTS

1. Habitat diversity

The five zones differed considerably concerning their abiotic and biotic characteristics (Table 1). The duration of the drought period decreased from Zone I to Zone IV; Zone V was never exposed. Salinity varied between 37.0 (Zone I) and 33.0 ppt (Zones VI and V). Water temperature decreased from the shore (Zone I) to the open water (Zone V). Algae were found in all five zones; diversity and density increased with the distance from the shore.

2. Species diversity

Nine species of Polyplacophora were recorded at the study site: *Ischnochiton dispar* (Sowerby, 1832), *Stenoplax limaciformis* (Sowerby, 1832), *Chiton stokesii* Broderip, 1832, *Acanthochitona hirundiniformis* (Sowerby, 1832),

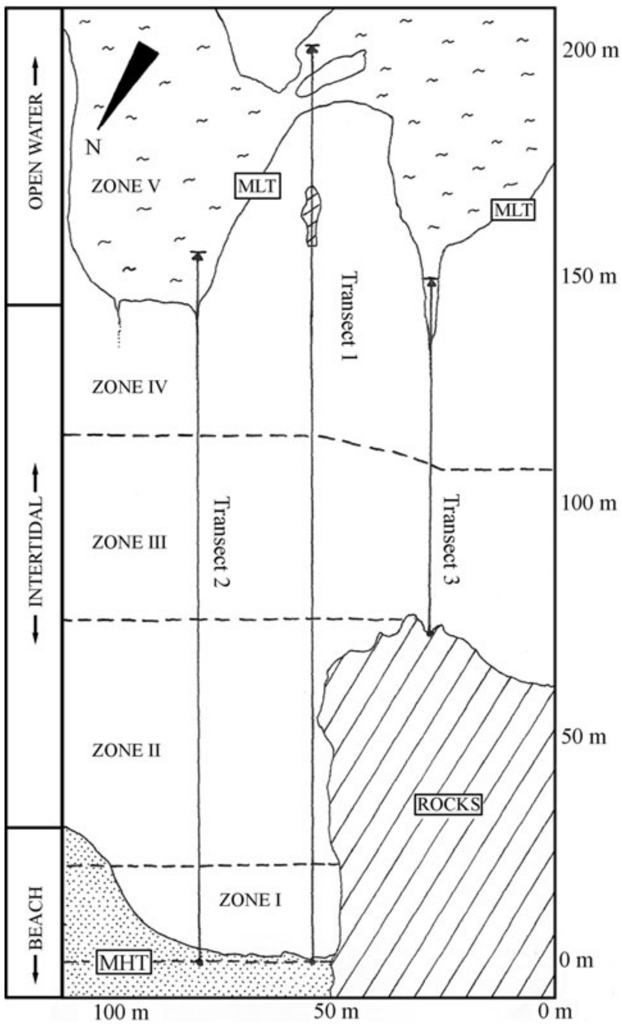

Fig. 3. Topography of Samara (Playa Cangrejal), Pacific Costa Rica, and location of transects and zones. MHT, mean high tide line; MLT, mean low tide line.

Acanthochitona ferreirai Lyons, 1988, *Callistochiton expressus* (Carpenter, 1865), *Chaetopleura lurida* (Sowerby in Broderip & Sowerby, 1832), *Lepidochitona beanii* (Carpenter, 1857) and *Callistoplax retusa* (Sowerby in Broderip & Sowerby, 1832). A total of 4193 individuals were identified and measured; the overwhelming majority (85.4%) of the analysed individuals belonged to *I. dispar* (Table 2). The diversity of chiton species increased from the shore to the MLT (see Table 1).

3. Distribution of each species

ISCHNOCHITON DISPAR (SOWERBY, 1832) (FIGURE 2B)

Ischnochiton dispar was by far the most abundant chiton at the study site. A total of 3580 individuals were sampled (85.4% of all chitons recorded). The presence of the species was limited to the tide pools; it was never observed on exposed rocks. During daylight hours it was found exclusively on the undersurfaces of boulders while during the night it was frequently observed crawling and feeding along the sides and surfaces of the submerged rocks. Highest abundance was recorded in Zone III with a density of 214 specimens per m^2 (Table 2). The species was also abundant in Zone IV. Considerably fewer individuals were sampled in Zones I–II and Zone V (Figure 4).

The mean body length was 11.6 mm ($\pm$4.2 mm SD; N = 3580), ranging from 1.5 mm to 23.1 mm. The sizes of the specimens were negatively correlated to the distance from the shore (i.e. the body length of the individuals decreased significantly with the increasing distance from the shore; $r = -0.183$; $P < 0.001$; N = 3580, Spearman correlation test).

In general, *I. dispar* showed a clustered distribution and was sometimes found in accumulations of up to 11 individuals on the underside of stones 10–15 cm in size. The range of the mean stone number of each size-group present in the tide pools of the five selected quadrates of Zone III is shown in Table 3. These quadrates were densely inhabited by 119 to 158 individuals of *I. dispar* which occupied boulders of all size-ranges (Table 3). Although small boulders (<5 cm) were not uncommon in Zone III, only few individuals were encountered on these rocks. The specimens preferred large stones, especially those ranging between 15 and 20 cm (81.5% occupied). The mean body length of *I. dispar* increased significantly with the size of the boulders ($r = 0.177$; $P < 0.0001$; N = 629; Spearman correlation test).

In two quadrates of Zone IV an accumulation of young individuals (<5 mm) was encountered in May 2004, representing up to 40% of the population of these quadrates.

STENOPLAX LIMACIFORMIS (SOWERBY, 1832) (FIGURE 2C)

The species was commonly found in tide pools of Zones III to V; only scattered individuals were recorded in Zone II (Figure 5). No individuals occurred in Zone I and the species was never found in the rocky areas outside the tide pools. This species occurred underneath or on the sides of boulders of different sizes which were firmly and relatively deeply embedded in the coarse sand substrate. Specimens were encountered at the base of the boulders surrounded by sand but were absent from the subsurface deoxidized blackened boulder bottom. The mean body length was 20.0 mm ($\pm$6.86 mm SD), varying between 3.5 mm and 36.0 mm (N = 320). The mean size of individuals increased significantly towards the open water zone ($r = 0.30$; $P < 0.0001$; N = 320; Spearman correlation test) (see Table 4).

CHITON STOKESII BRODERIP, 1832 (FIGURE 2D)

The body length of *C. stokesii* varied between 8.8 mm and 71.3 mm (mean 42.5 mm; $\pm$14.3 mm SD; N = 149). This species was found in all tide pool zones except Zone V and on the rocky areas outside the tide pools. Individuals encountered under boulders in tide pools were significantly smaller (mean 33.6 mm; $\pm$14.6 mm SD; N = 38) than those in the rocky areas outside the pools (mean 45.5 mm; $\pm$12.9 mm SD; N = 111) ($P < 0.0001$; Mann–Whitney *U*-test). Moreover, this species occurred far more abundantly in the rocky areas (74.5% of the sampled specimens), even though the tide pool area sampled was four times larger. Outside the pools *C. stokesii* spent the daylight hours mainly hidden in shaded crevices both exposed to air and covered with some rest water. Specimens were found up to 1.7 m above the low water line on exposed rocks which resulted in 4–5 hours of air exposure during each tidal cycle.

Table 1. Description of the different habitat zones of Samara, Pacific Costa Rica. MHT, mean high tide line; salinity and water temperature: increase of these parameters compared to the values measured at high tide and maximum value reached.

Zone	Distance from MHT [m]	Maximum range of physical conditions			Algae diversity and density	Species of chitons
		Drought period [hrs]	Salinity [ppt]	Water temperature [°C]		
I	Transects 1 & 2: 0–20	4–5 h	+3.2; maximum 37.0	+9.9; maximum 40.7	slight green algae film	*Ischnochiton dispar*, *Chiton stokesii*
II	Transects 1 & 2: 20–75	3–4 h	+2.1; maximum 35.9	+8.7; maximum 39.5	green algae film; first crustose coralline algae	*I. dispar*, *Stenoplax limaciformis*, *C. stokesii*, *Acanthochitona hirundiniformis*
III	Transects 1 & 2: 75–115; Transect 3: 75–110	2–3 h	+1.8; maximum 35.6	+6.2; maximum 37	dense algae film, crustose coralline algae	*I. dispar*, *S. limaciformis*, *C. stokesii*, *A. hirundiniformis*, *Callistochiton expressus*
IV	Transect 1: 115–190; Transect 2: 115–140; Transect 3: 110–130	1–2 h	+0.9; maximum 33.3	+2.2; maximum 34.9	high density and diversity of filamentous and coralline algae	*I. dispar*, *S. limaciformis*, *C. stokesii*, *A. hirundiniformis*, *Acanthochitona ferreirai*, *C. expressus*, *Chaetopleura lurida*, *Lepidochitona beanii*
V	Transect 1: 195; Transect 2: 140–155; Transect 3: 130–150	none	+0.0; maximum 33.0	+0.0; maximum 32.5	high density and diversity of filamentous and coralline algae	*I. dispar*, *S. limaciformis*, *A. hirundiniformis*, *A. ferreirai*, *C. expressus*, *C. lurida*, *L. beanii*, *Callistoplax retusa*

ACANTHOCHITONA HIRUNDINIFORMIS (SOWERBY, 1832) (FIGURE 2E)

The 62 individuals of *A. hirundiniformis* had a mean body length of 19.6 mm (±6.0 mm SD; minimum: 6.3 mm; maximum: 30.7 mm). The majority of the individuals encountered in the tide pools occurred in Zone III (N = 13; maximum density: five individuals per m^2); only five specimens were collected in Zone IV, and just one individual each in Zones I and V. In the tide pools, *A. hirundiniformis* spent the daylight hours underneath or on the sides of the boulders. The individuals were found on boulders of all size-groups, the exception were stones being smaller than 5 cm. The majority of *A. hirundiniformis* (67.7% of all sampled specimens) were encountered in the rocky areas outside the tide pools, mainly in shallow cracks and holes. Usually these individuals were covered by a thin layer of water but they were also observed being air exposed. On elevated rocks they occurred up to a height of 1.2 m above the low water line. The specimens inhabiting the underside of boulders of the tide pool areas were significantly smaller (mean size 14.7 mm; ±6.2 mm SD; N = 20) than those outside the tide pools (mean size 23.1 mm; ±3.7 mm SD; N = 42) ($P < 0.00001$; Mann–Whitney *U*-test). Young individuals (body size < 10 mm) were exclusively found in tide pools on the undersurface of boulders.

Table 2. Number of specimens of each chiton species (N), their maximum densities, and percentage in relation to the total number of individuals sampled during February to June 2004 in Samara, Pacific Costa Rica.

Species	N	%	Maximum density (ind/m^2)
Ischnochiton dispar	3580	85.4	214
Stenoplax limaciformis	320	7.6	21
Chiton stokesii	149	3.6	12
Acanthochitona hirundiniformis	62	1.5	5
Acanthochitona ferreirai	36	0.9	6
Callistochiton expressus	27	0.6	4
Chaetopleura lurida	9	0.2	2
Lepidochitona beanii	8	0.2	2
Callistoplax retusa	2	<0.1	1
Total	4193	100	

ACANTHOCHITONA FERREIRAI LYONS, 1988 (FIGURE 2F)

Representatives of this species varied in body length between 6.0 mm and 32.3 mm (mean body size: 18.3 mm; ±7.36 mm SD; N = 36). In contrast to *A. hirundiniformis*, *A. ferreirai* was collected (with the exception of one individual) in the tide pool quadrates. The highest abundance occurred in Zone IV with a maximum density of 6 ind/m^2; various individuals (N = 16) were also present in Zone V. Individuals were usually encountered underneath or on the sides of the boulders of all size-groups, excluding stones <5 cm. Boulders occupied by *A. ferreirai* were firmly embedded in the substrate and densely covered with different types of macroalgae.

CALLISTOCHITON EXPRESSUS (CARPENTER, 1865)

The species was present in Zones III to V, and body length ranged from 1.7 mm to 13 mm (mean body size: 7.3 mm; ±3.0 mm SD; N = 27). Their maximum density (4 ind/m^2) occurred in Zone V. They did not show a preference for a certain stone size but were usually on stones stuck firmly in the substrate. Specimens were found on the sides or underneath the stones. When a stone occupied by *C. expressus*

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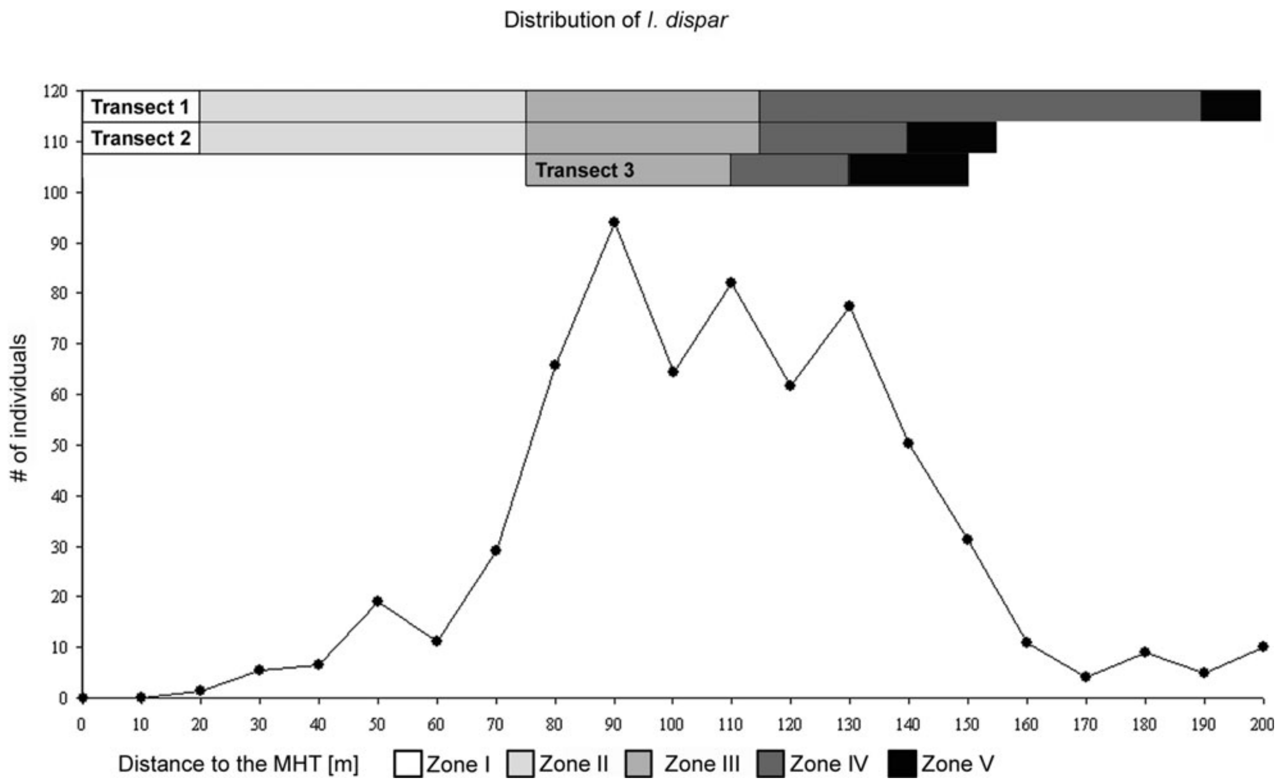

Fig. 4. Vertical distribution of *Ischnochiton dispar* at Samara (Playa Cangrejal), Pacific Costa Rica.

was lifted up, they presented a reaction different from the other chiton species: 70% of the specimens of *C. expressus* curled up immediately and fell off the stone.

CHAETOPLEURA LURIDA (SOWERBY IN BRODERIP & SOWERBY, 1832)

Nine individuals of *C. lurida* were collected in Zones IV and V, ranging in size from 5.9 to 25.1 mm in length (mean 13.0 mm; ±6.3 mm SD). They were found often hidden in cracks and holes of submerged boulders of larger sizes (>15 cm).

LEPIDOCHITONA BEANII (CARPENTER, 1857)

Eight individuals of *L. beanii* were recorded, with a mean body length of 4.7 mm (±2.0 mm SD; min. 2.1 mm; max. 7.7 mm). Almost all individuals were found in Zone V, only one specimen in Zone IV. The stones on which the specimens were encountered were all smaller than 10 cm and typically covered with darkish-red crustose coralline algae.

Table 3. Preferences of stone size and correlation between stone size and body size of *Ischnochiton dispar* in five selected quadrates within the densely populated Zone III in Samara, Pacific Costa Rica.

Stone size [cm]	Mean number of stones per quadrate	± SD	% of stones occupied	Mean number of individuals per stone	Mean size of individuals [mm]	± SD
<5	53.4	32.1	7.5	1.1	9.5	4.7
5–10	46.2	20.6	38.5	3.2	11	4.1
10–15	17.6	3.7	54.5	4.5	11.4	3.9
15–20	5.4	2.2	81.5	5.2	13	3.6
>20	1.8	1.3	55.6	1	11.2	4.4

CALLISTOPLAX RETUSA (SOWERBY IN BRODERIP & SOWERBY, 1832)

The two individuals of *C. retusa* measured 11.0 mm and 10.8 mm in length. They were encountered in tide pool quadrates of the Zones IV and V, underneath boulders of the size-groups '10–15 cm' and '15–20 cm', which were embedded in the substrate.

DISCUSSION

A total of 24 chiton species have been reported from the Pacific coast of Costa Rica (Schwabe & Wehrtmann, in press), most of them occurring in the intertidal. At the study site in Samara we collected nine chiton species, representing 37.5% of the known species from Pacific Costa Rica. In contrast, Willis & Cortés (2001) studying along 36 transects the mollusc diversity in the Manuel Antonio National Park, Pacific Costa Rica, encountered only two chiton species in the low rocky intertidal zone: *Chiton virgulatus* and *Lepidozona flavida*. Thus, our study site can be considered as a fairly species-rich area.

The results of the present study show the different spatial patterns of abundance for these species. They can be divided into two groups according to their presence in the intertidal zone: (1) species (almost) exclusively found in tide pools (*I. dispar*, *S. limaciformis*, *A. ferreirai*, *C. expressus*, *C. lurida*, *C. retusa* and *L. beanii*); and (2) species that occurred

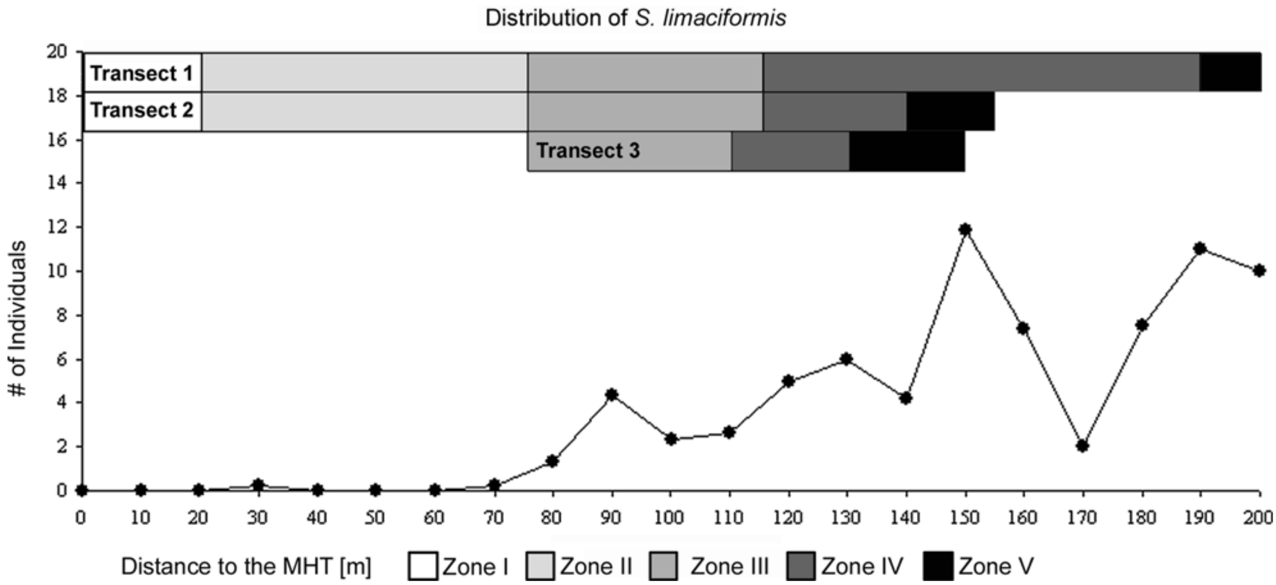

Fig. 5. Vertical distribution of *Stenoplax limaciformis* at Samara (Playa Cangrejal), Pacific Costa Rica.

mainly in the rocky areas outside the pools (*C. stokesii* and *A. hirundiniformis*). Since physical conditions (especially duration of air exposure) differed greatly between the two habitats, the results of the species groups will be discussed separately.

Tide pool species

The environmental stress and consequently the biota of intertidal rock pools vary with the distance from the shore (Newell, 1979). In the study area, the physical conditions closer to the MHT showed greater variation in temperature, salinity, and period of exposure as compared to those near the MLT, which are characterized by relatively stable conditions (see Table 1). The combination of increasing temperature and salinity together with decreasing algae diversity is most likely responsible for the observed trend of lower chiton diversity toward the shore area (Table 1). This conclusion is supported by similar observations from Central Chile (Otaíza & Santelices, 1985) and Australia (Kangas & Shepherd, 1984).

Food availability is unlikely to limit abundance and distribution of chitons inhabiting Zones II to IV. In accordance with the results obtained by Kangas & Shepherd (1984), food resources were abundant and probably more than sufficient in these zones to maintain the chiton populations. At Samara we observed that the rise in algal diversity was correlated with an increase in chiton diversity (see Table 1). Thus, e.g. the absence of crustose coralline algae in Zone I might have limited the distribution of species feeding on this group of algae to deeper zones. It can be assumed that the presence of specialist feeders is closely related to the presence of their food resource (Kangas & Shepherd, 1984). During our study *L. beanii* was exclusively encountered on darkish red crustose algae and might therefore be a specialist feeder of these algae. Chitons have traditionally been considered to be herbivorous grazers (e.g. Simpson, 1976; Steneck & Watling, 1982). However, analyses of gut contents have shown that some chiton species are also omnivorous or even carnivorous (Kangas & Shepherd, 1984; Piercy, 1987). Therefore, gut content analysis as well as direct feeding observations of the chiton species studied herein are recommended to verify the assumptions about specialized feeders, and to allow further conclusions concerning the role of food resources on the vertical distribution of chiton species, taking into consideration that some species might not be herbivorous, but carnivorous or omnivorous.

Desiccation stress is a major factor for the distribution of chiton species in rocky areas outside the tide pools (see discussion below). Tide pool species of the present study, however, were protected from desiccation by behavioural means, as they were encountered exclusively on the undersurface of boulders, surrounded by water, and in this way protected from sunlight and exposure to air. A correlation between greater size of the individuals and a higher position on the shore has been previously reported for some chiton species living on rocks outside tide pools (e.g. Murdoch & Shumway, 1980). Schmidt-Effing (1980) assumed that the same pattern is valid for the tide pool species *I. dispar*. However, our data regarding the segregation in size of the common tide pool species seem to indicate that such a pattern is not necessarily evident in chitons inhabiting tide pools: two species (*I. dispar* and *S. limaciformis*) showed a weak, but statistically highly significant correlation between body length and distance from the shore, but while *I. dispar* showed a negative correlation (i.e. the size of the

Table 4. Size distribution in *Stenoplax limaciformis* from Samara, Pacific Costa Rica.

Zone	Number of individuals	Mean body size [mm]	Maximum density (ind/m²)
I	–	–	–
II	10	13.5	3
III	86	18.4	9
IV	156	20.9	21

individuals decreased with increasing distance from the shore), *S. limaciformis* was positively correlated (i.e. the size of the individuals increased with increasing distance from the shore). Thus, the above mentioned correlation between size and position on the shore cannot be generalized for tide pool species. Otaíza & Santelices (1985) suggested that small species and small individuals of large species generally occur in areas of less water movement while large chitons occur in the zones of greatest wave impact. It can be assumed that chitons inhabiting the rocky zones outside the tide pools are generally more exposed to wave impact than the species living on the underside of boulders. According to Otaíza & Santelices (1985), wave impact might be another explanation for the size-dependent habitat selection of *C. stokesii* and *A. hirundiniformis* (see discussion below). But the contrasting segregations in size of *I. dispar* and *S. limaciformis* show that wave impact probably has little effect on the segregation of size of tide pool species. To explain these results, more data are needed on larval recruitment, mortality, and behavioural response to habitat of these two species.

Small scale variation in abundance expressed in abrupt changes from one quadrate to the next was observed in *I. dispar* (Zone III; see Figure 4), and especially in *S. limaciformis* in Zone VI (see Figure 5). Such abrupt changes can hardly be explained by differences of physical or biotic conditions described in Table 1. Physical disturbances, especially by human impact, are more likely to explain these sudden changes in abundance (Smith & Otway, 1997). These authors showed that overturning boulders resulted in a significant decline in species richness, overall abundance and species density. Since our study location is a popular recreation area during the weekends, we assume that anthropogenic impacts may affect the small scale abundance of species such as *I. dispar* and *S. limaciformis*.

Specimens of the abundant species *I. dispar* did not occupy each boulder, even in the extremely dense populated quadrates, but appeared rather clustered on a few boulders. Even though *I. dispar* occupied stones of all size-groups, specimens showed a tendency to avoid small boulders (<5 cm) and a certain preference for large boulders (see Table 3). Clustered patterns of dispersion are relatively common in molluscs on rocky intertidal shores and have shown to be a consistent pattern in some chiton species irrespective of their average abundance (Grayson & Chapman, 2004). The mean densities of chitons declined following disturbance, and larger boulders are less frequently overturned than smaller ones (see Smith & Otway, 1997). This higher rate of disturbance in boulders <5 cm is possibly the reason why they are generally avoided by most chiton species (see results) and might explain the preference of *I. dispar* for larger boulders (Table 3).

The mean body length of *I. dispar* increased significantly with the size of the boulders they occupied. Earlier studies have shown that such a relationship between the body length of chitons and the size of boulders or the type of substrate is generally rare (e.g. Smith & Otway, 1997; Grayson & Chapman, 2004). However, in some species (e.g. *Ischnochiton australis* (Sowerby, 1840) and *I. elongates* (de Blainville, 1825)) a similar positive correlation does exist (Smith & Otway, 1997). Since both of these species were highly sensitive to disturbance (i.e. presented an escape response by curling up and falling off the boulder), we assume that the correlation between body size and boulder size might also be related to the rate of disturbance. However, among the species in our study site only *C. expressus* exhibited this type of escape response. All the other species (including *I. dispar*) displayed a more sluggish response, showing no immediate reaction to disturbance, but eventually moving slowly to the other side of the overturned rock. These behavioural differences may affect the spatial distribution of the chitons since species that fall off the boulder are passively transported by water movement to a different region. Its effect on the correlation of body length and boulder size, however, seems questionable on the basis of our data.

Species occurring mainly in rocky areas outside the tide pools

Different size-groups of *C. stokesii* and *A. hirundiniformis* occupied different ecological niches in the study area. Both species were encountered in tide pools as well as in the rocky areas outside the pools. The individuals inhabiting the tide pools, however, were significantly smaller than those encountered in the rocky areas outside the pools. Effects of desiccation are known to be size dependent with smaller individuals being more strongly affected than large specimens (Murdoch & Shumway, 1980). This may explain the observation that larger specimens of both species have been found more frequently outside the rock pools while smaller specimens were restricted to the tide pool environment. Such ontogenic differences in habitat selection are in contrast to the conclusion of Otaíza & Santelices (1985) that species are usually limited to either tide pools or rocky areas. But desiccation or thermal stress cannot explain why larger individuals are usually found outside of tide pools. An alternative hypothesis is that larger individuals are more respiration stressed in oxygen-depleted tide pools and are found outside of them in order to engage in aerial respiration.

Outside the tide pools, both species were usually hidden in shaded crevices or under small overhangs. Choosing this more thermally stable and cooler microhabitat during daylight exposure reduces the thermal load and desiccation stress (McMahon *et al.*, 1991). By this behaviour *C. stokesii* is protected to some extent from extreme heat stress, leaving air exposure as the predominant intertidal stress factor (McMahon *et al.*, 1991). *Acanthochitona hirundiniformis* was encountered in a similar habitat but on a lower level of the rocks, thus suffering shorter periods of air exposure during each tidal cycle (maximum of four hours) than *C. stokesii* (maximum of five hours). However, *C. stokesii* is known to cope with even longer emersion periods (up to six hours), and 93% of 30 individuals tested under laboratory conditions survived 18 hours of air exposure (McMahon *et al.*, 1991). The results of McMahon *et al.* (1991) as well as the results of the present study contradict the assumption presented by Cruz & Sotela (1984) that *C. stokesii* has only limited capacity to cope with desiccation.

The spatial patterns documented by the results of the present study are only indicative of what may be found in other intertidal chiton communities along the Pacific coast of Central America. Further studies at different sites and periods of the year (dry and rainy season) are needed to indicate whether the patterns observed at Samara can be generalized to similar habitats elsewhere in the tropics.

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