

# The first observations of *Ischnochiton* (Mollusca, polyplacophora) movement behaviour, with comparison between habitats differing in complexity (#20798)

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# The first observations of *Ischnochiton* (Mollusca, polyplacophora) movement behaviour, with comparison between habitats differing in complexity

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Most species of *Ischnochiton* are habitat specialists and are almost always found underneath unstable marine hard-substrata such as boulders. The difficulty of experimenting on these chitons without causing disturbance means little is known about their ecology despite their importance as a group that often contributes greatly to coastal species diversity. In the present study we measured among-boulder distributional patterns of *Ischnochiton smaragdinus*, and used time-lapse photography to quantify movement behaviours within different habitat types. Chitons were significantly overdispersed among boulders, as most boulders had few individuals but a small proportion harboured large populations. *I. smaragdinus* emerge from underneath boulders during nocturnal low-tides and **moves** amongst the inter-boulder matrix (pebbles or rock-platform). Seventy-two percent of chitons in the pebble matrix did not move from one pebble to another within the periods of observation (55-130 minutes) but a small proportion moved across as many as 5 pebbles per hr, indicating a capacity for adults to migrate among disconnected habitat patches. Chitons moved faster and movement paths were less tortuous across rock-platform compared to pebble substrata, which included more discontinuities among substratum patches. Overall, we show that patterns of distribution at the boulder-scale, such as the observed overdispersion, must be set largely by active dispersal of adults across the substratum, and that differing substratum-types may affect the degree of dispersal for this and possibly other under-boulder chiton species.

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## Abstract

Most species of *Ischnochiton* are habitat specialists and are almost always found underneath unstable marine hard-substrata such as boulders. The difficulty of experimenting on these chitons without causing disturbance means little is known about their ecology despite their importance as a group that often contributes greatly to coastal species diversity. In the present study we measured among-boulder distributional patterns of *Ischnochiton smaragdinus*, and used time-lapse photography to quantify movement behaviours within different habitat types. Chitons were significantly overdispersed among boulders, as most boulders had few individuals but a small proportion harboured large populations. *I. smaragdinus* emerge from underneath boulders during nocturnal low-tides and **moves** amongst the inter-boulder matrix (pebbles or rock-platform). Seventy-two percent of chitons in the pebble matrix did not move from one pebble to another within the periods of observation (55-130 minutes) but a small proportion moved across as many as 5 pebbles per hr, indicating a capacity for adults to migrate among disconnected habitat patches. Chitons moved faster and movement paths were less tortuous across rock-platform compared to pebble substrata, which included more discontinuities among substratum patches. Overall, we show that patterns of distribution at the boulder-scale, such as the observed overdispersion, must be set largely by active dispersal of adults across the substratum, and that differing substratum-types may affect the degree of dispersal for this and possibly other under-boulder chiton species.

## Introduction

Dispersal of mobile benthic species can occur by a combination of movement processes occurring as adults (Little 1989, Grantham et al. 2003) and by “supply-side” processes (Underwood & Fairweather 1989) for species with larval stages. Contributions of adult and larval processes to dispersal have been measured for species with easily observable larval processes (e.g. larval settlement/recruitment; Rowley 1989) or adult processes (e.g. movement of slow-moving species on rock platforms exposed during low tide; Underwood & Chapman 1989). There are many species, however, that occur almost exclusively in cryptic/hidden habitats that are not easily observed, such as underneath unstable hard-substrata. The species are mostly hidden from view and in order to observe them it is generally required to disturb the habitat (Chapman & Underwood 1996). Consequently, we have little information about their natural dispersal capacities as adults. Our knowledge about intertidal invertebrate behavioural ecology (see reviews by Grantham et al. 2003, Ng et al. 2013) would be improved by incorporating under-boulder species, because the specialist species there often have high levels of rarity or endemism (Benkendorff & Przeslawski 2008, Chapman et al. 2009, Liversage 2015) and ecological information is needed to inform conservation management.

One of the most widespread groups of boulder habitat specialists are chitons within the *Ischnochiton* genus. While much research has focussed on movement behaviours of other chitons that live on exposed (i.e. non-cryptic) rocky habitats (Thorne 1968, Chelazzi et al. 1983, Chelazzi et al. 1987, Chelazzi et al. 1988) practically nothing is known of natural movement behaviours of *Ischnochiton* that are primarily associated with boulders. Palmer (2012) suggested that patterns of among-boulder overdispersion could be explained by philopatric behaviour, with chitons rarely dispersing from their natal boulders. Chapman (2002) observed high rates of dispersal onto artificially deployed boulders, and questioned whether such dispersal may occur by “drifting” or

“crawling”. Smith & Otway (1997) and Jörger et al. (2008) noted that some chitons readily drop off overturned boulders and fall into the water to be passively transported by water motion. This was considered an “escape-response” that may affect the movements and distribution of species that use this behaviour. Empirical data about movement ecology of *Ischnochiton* is required to determine whether dispersal behaviours such as these are occurring in reality and contributing to distributional patterns such as overdispersion. This pattern occurs when large variation among replicates causes data to not approximate a Poisson distribution (Richards 2008), and has been observed repeatedly for distribution data of other *Ischnochiton* species (Grayson & Chapman 2004, Liversage & Benkendorff 2013).

The only direct observations of *Ischnochiton* movements are notes of movement occurring on exposed rock surfaces, mostly nocturnally (Kangas & Shepherd 1984). Using shell patterns to identify individual chitons, Liversage et al. (2012) found that approximately two-thirds of the individuals emigrate from their original boulder over three days, while an average of three new chiton individuals move onto boulders. Similarly, in an intertidal cobble reef, McClintock et al. (2007) marked and relocated a habitat-generalist chiton species (*Sypharochiton pelliserpentis*) and found that the percentage of chitons that stayed under their original cobble after two tidal cycles varied from 10% (small cobbles) to 45% (large cobbles). These studies suggest chitons may move frequently across boulder habitat patches. The boulders/cobbles in these studies were, however, overturned for sampling and hence physically disturbed (Chapman & Underwood 1996), so the relatively high levels of movement recorded may not fully reflect natural movement patterns. To our knowledge no previous study has quantified undisturbed movement patterns of any *Ischnochiton* species, which was our aim in this study.



Temperate boulder reefs of the south-eastern Australian intertidal-zone harbour populations of *Ischnochiton smaragdinus*. This small chiton attains a maximum length of approximately 2cm and has an atypical carnivorous diet of sponges, bryozoans and ascidians (Kangas & Shepherd 1984). Another unique trait  species is occasionally noted on exposed-rock habitats nocturnally (Kangas & Shepherd 1984).

The present study focused on *I. smaragdinus*, a common chiton in South Australian rock pools  comprised of a variety of substrata including boulders, cobbles, pebbles and rock platforms. First, we measured distributional patterns to test the hypothesis that adult individuals are overdispersed among boulders, similarly to many other representatives of *Ischnochiton* (Grayson & Chapman 2004, Liversage & Benkendorff 2013). These distributions may be caused by movement behaviours. Accordingly, we measured movement paths of chitons using time-lapse photography during nocturnal low tides. To determine the generality of the finding from Liversage et al. (2012), that chitons migrate among habitat patches that have been disturbed by sampling, we tested the hypothesis that chitons will not remain on individual habitat patches, but migrate amongst the boulders, pebbles or cobbles that have been left undisturbed (i.e. not overturned or moved). Measurements of chiton movements were also made within pools that included rock-platform habitat, which includes fewer discontinuities (i.e. interstices and areas of sand between adjacent hard-substrata) among habitat patches compared to rock pools containing pebbles and cobbles. We tested the hypothesis that variables including speed and directionality were affected by the different habitat types.

## Materials and Methods

Distributions and movement patterns of *I. smaragdinus* were measured during diurnal low tides at four sheltered intertidal boulder fields on the Fleurieu Peninsula, South Australia. For distribution measurements, 30 haphazardly selected boulders were overturned and numbers of attached *I. smaragdinus* were counted during October 2007 at two sites (Myponga Beach – 35°22'12.6"S 138°23'18.2"E) and (Second Valley – 35°30'39.6"S 138°12'58.4"E). The boulders at both locations were approximately 30cm long and 15cm high, and were siltstone or sandstone. Sampled boulders were separated from each other by approximately 1m. Frequency distributions of chitons across boulders at each site were compared to a Poisson distribution (expected if chitons are distributed randomly) using a one-sample Kolmogorov-Smirnov test. If patterns of overdispersion produce non-random frequency distributions, this test will indicate a significant difference between observed and expected (Poisson) distributions.

Movement paths of *I. smaragdinus* were measured using time-lapse photography techniques involving photography from above the water surface in randomly selected rock-pools. Observations were made at night during seven low-tide periods at two sites at Myponga Beach between August and December 2006. One site (35°22'12.6"S 138°23'18.2"E) had rock-pools with pebble substrata (Fig 1a); the mean length of pebbles was measured from four rock-pools to be 4.14cm (SE = 0.35) and all measured rock-pools had pebbles of similar length (ANOVA  $F_{(3, 36)} = 0.88$ ,  $P > 0.25$ ). The pebbles were flattened with their height about half their length, and were partially buried in sand. The second site (35°22'01.9"S 138°24'19.1"E) had rock-pools with a substratum of unbroken rock-platform (Fig. 1b). At each rock-pool, a camera (Olympus C5050<sup>®</sup>) was positioned on a tripod directly above to photograph an area of approximately 50x50cm. The camera took digital images at one minute intervals. Periods of photography were

initiated when the tide had receded and there were no visual distortions of the substratum from moving water. Observations were ended when distortion from increasing water depth during the advancing tide again prevented resolution of the substratum. This method provided an observation time that varied from 55 to 130 min.

Images were processed using Photoshop CS<sup>®</sup> imaging software. The locations of all chitons within the rock-pool in the first image in a given time series was marked on a Photoshop<sup>®</sup> workspace layer separate from the image, then the next image in the time series was superimposed on the first. The next image was adjusted in scale to offset the effects of changes in water level (which magnifies or reduces the view of the substratum when viewed above the water surface), and the subsequent position of all chitons was then added to the layer onto which the initial positions were marked. This process was used for all subsequent images in the time series until the entire movement paths of all chitons were delineated. To ensure each chiton followed was an independent replicate, they were only included if no interaction occurred with other chitons (i.e. direct contact or movement across another chiton's path). Studies using photographs to measure habitat characteristics on larger boulder habitats have used techniques to correct for the curvature of boulders (e.g. applying a corrective factor of  $\approx 1.2$  to area measurements from boulder edges; Liversage et al. 2012). While no distortion would be caused when delineating movement paths leading around edges of pebbles, there may be distortion of paths leading from edges over the pebble tops. However, because the pebbles were flattened in shape, and the chitons were large (mean 0.64cm) in relation to the pebbles (mean 4.14cm), it was not considered necessary in this case to apply any corrective adjustments.

Three movement variables were measured as well as the length of each chiton. Net speed was calculated as the total distance travelled divided by the total time observed. Maximum speed was considered as the largest distance travelled by an individual in any five minute period. We calculated the net:gross displacement ratio to provide an indication of the tortuosity of movement paths, as done for sea stars (Swenson & McClintock 1998), copepods (Buskey 1984), fish (Parrish et al. 2002) and seals (Davis et al. 2001). This metric is calculated as net displacement (the straight distance between the start and end point of a movement path) divided by gross displacement (the actual distance travelled; Fig 1). A net:gross displacement ratio close to 0 indicates the movement path is highly tortuous, and most movement has not contributed to dispersal away from the starting point. A value close to 1 indicates the path is straighter with most movement having resulted in dispersal. The net:gross displacement ratio was measured only for chitons that moved a minimum of 30mm during the period of observation.

The number of chitons in each rock-pool was variable, so comparisons among treatments were done with univariate PERMANOVA, using PRIMER v6 (Anderson & Walsh 2013). We considered substratum-type as a fixed factor and the different rock-pools as a random factor. There was only one substratum type in each of the rock-pools, so the rock-pool factor was nested in substratum-type. Attempts were made to find rock-pools with different substratum-types within the same area, but appropriate substratum-types were only found separated spatially. Distributional patterns vary over small spatial scales (i.e. among boulders) for *Ischnochiton* (Grayson & Chapman 2004, Liversage & Benkendorff 2013), but few differences in other among-boulder movement patterns have been found during comparisons of separate larger-scale locations (Liversage et al. 2012). This suggests that spatial confounding between the sites can be considered unlikely in our comparisons between these substratum-types. The analyses used

Euclidean distances and 9999 permutations. Homogeneity of variances was tested with PERMDISP, using medians, which in univariate analyses is equivalent to Levene's test (Anderson et al. 2008). If the  $P$  values of the random factor was  $> 0.25$ , it was eliminated to provide a more powerful test for the relevant null hypothesis (Underwood 1997).

## Results

At our two study sites, most boulders had no *Ischnochiton smaragdinus* or only a small number (1-3 individuals; Fig. 2) living under them. A small percentage of boulders harboured large population sizes, reaching up to 30 individuals at Myponga beach and 13 at Second Valley (Fig. 2). These right-skewed frequency distributions differed strongly to the Poisson distributions expected if chitons were distributed randomly for analyses of data from both sites (Myponga Beach Kolmogorov-Smirnov goodness-of-fit test  $P < 0.001$ ; Second Valley  $P < 0.001$ ). These measurements were taken diurnally, and all 143 individuals were sheltering underneath the boulders and cobbles. None occurred in exposed areas that were visible without overturning the substrata.

Movement paths of 113 individuals were analysed. Only 2 individuals did not move. The frequency of movement generally did not result in dispersal across substratum units (pebbles or cobbles), but a smaller proportion of individuals displayed more extensive dispersal (Fig. 3). Substratum-type appeared to affect all movement variables measured (Table 1). Significantly lower speeds were observed in rock-pools with a pebble substratum, and this difference was particularly evident regarding the maximum speeds attained (Fig. 4a). The fastest individual

overall speed over a five min period was  $55\text{cm}\cdot\text{hr}^{-1}$  on a rock-platform surface. Although mean sizes of chitons varied among random rock-pools, they did not vary between the two habitat types (Table 1), so this variable did not affect differences in speed between fixed factor treatments.

The net:gross displacement ratio was significantly greater in rock-pools with a rock-platform substratum (Table 1; Fig. 4b), indicating more directional, less tortuous movement paths. Although chitons on pebble substrata often had highly tortuous paths, in no instances was it observed that a given chiton returned to the same position where it had previously been resting.

## Discussion

Movement patterns of mobile intertidal species vary from almost no movement (e.g. Branch 1975), to movement to and from a “home” position (e.g. Mackay & Underwood 1977, Chelazzi 1990), to regular and widespread dispersal among habitat patches (e.g. Underwood 1977). The results from the present study show for the first time that the undisturbed movement behaviour of *Ischnochiton smaragdinus* involves dispersal among multiple patches of substrata. Many individuals did not move across pebbles and cobbles during the observation periods, but a small proportion moved across as many as five within an hour. These individuals clearly did not remain in their natal habitat, thus such behaviour is unlikely to explain patterns of overdispersion in this species. No instances of chitons being “drifted” in the water were observed, indicating that adult dispersal occurs via “crawling”, at least during low tide (Chapman 2002). It is possible that movements are similar to those of the intertidal limpet *Cellana tramoscerica* which alternates between homing behaviour and randomly directed movement (Mackay & Underwood 1977). The

observations here could be explained by *I. smaragdinus* individuals remaining in a “home” patch (i.e. pebble) for a certain time and then subsequently moving quickly through adjacent patches.



Similar to other intertidal molluscs (Underwood & Chapman 1989, Chapman & Underwood

1994, Erlandsson et al. 1999, Underwood 2004), movements of *I. smaragdinus* appear to be

affected by topography of the substratum. A discontinuous layer of pebbles and cobbles was

associated with reduced speed of movement and resulted in more convoluted movement paths.



Complex topographies are known to reduce movement speeds of some gastropods and result in

faster population turn-over rates in less complex areas with greater immigration and emigration

(Underwood & Chapman 1989). It may be advantageous for chitons to minimise time spent on



exposed rock-platforms to avoid predation, especially from fish and brachyurans known to prey

on *Ischnochiton* (Shepherd & Clarkson 2001, Mendonça et al. 2016).

The differences in dispersal capacity between the habitat types may also be useful in

understanding processes involving disturbance and restoration ecology. Disturbance in the form

of movement or overturning of boulders, or disruption of the under-boulder substratum, reduces

densities of chitons before a subsequent process of re-colonisation (Chapman & Underwood

1996, Smith & Otway 1997, Liversage et al. 2012). Similarly, when boulders are artificially

added to a shoreline for habitat restoration, it is important to know how species such as chitons

will colonise those boulders (Chapman 2012, 2013). The present study suggests adult

colonisation will occur most readily when the substratum among boulders is a rock-platform or



other substrata of low complexity.

Smith & Otway (1997) showed that *I. smaragdinus* is less sensitive to disturbance (boulder overturning) compared to other chiton species. Nevertheless, our results indicate it has a highly overdispersed distribution among boulders, similar to most other species of *Ischnochiton* (Grayson & Chapman 2004, Liversage & Benkendorff 2013). Adults of other species may disperse in similar ways to *I. smaragdinus*, but less frequently, explaining why no other species except *Callochiton crocinus* were visible during the present study.

## Conclusions

This study shows that dispersal by adults of an *Ischnochiton* species occurs via active benthic movement during nocturnal low tides, with the extent of dispersal dependent on the type of substratum. This provides information necessary to predict responses to changes in habitat and the potential to colonise new areas during habitat restoration (e.g. Chapman, 2012; Chapman, 2013). The novel methods in this study will be useful in additional studies as there is increasing interest in evaluating movements of mobile intertidal invertebrates in natural (Martinez et al. 2017) and artificial (Browne & Chapman 2014, Evans et al. 2016, Firth et al. 2016) rock-pools.

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# Table 1 (on next page)

Univariate PERMANOVA comparing the length, movement speed, and tortuosity of movement paths for *Ischnochiton smaragdinus* individuals on a pebble or rock-platform substratum.

Measurements were taken from 7 randomly selected rock-pools. Substratum-type was a fixed factor and rock-pool was random and nested. PERMDISP tests determined if variances were significantly heterogenous. When the *P*-value of the random factor was  $>0.25$  it was eliminated from the analysis to provide a more powerful test for the relevant null hypothesis (Underwood 1997). “–” designates eliminated term; \**P* < 0.05; \*\**P* < 0.01.

1

| source             | Chiton length            |       |          | Net speed               |      |          | Maximum speed           |        |          | Net: gross displacement ratio |       |          |
|--------------------|--------------------------|-------|----------|-------------------------|------|----------|-------------------------|--------|----------|-------------------------------|-------|----------|
|                    | df                       | MS    | <i>F</i> | df                      | MS   | <i>F</i> | df                      | MS     | <i>F</i> | df                            | MS    | <i>F</i> |
| Substratum-type    | 1                        | 0.001 | 0.11     | 1                       | 3937 | 6.12 **  | 1                       | 121.44 | 9.28 **  | 1                             | 0.412 | 7.978 *  |
| Rock-pool (nested) | 5                        | 0.130 | 2.84 *   | 5                       | –    |          | 5                       | –      |          | 5                             | 0.007 | 2.304    |
| residual           | 106                      | 4.687 |          | 112                     | 643  |          | 112                     | 13.08  |          | 80                            | 0.003 |          |
|                    | PERMDISP <i>P</i> > 0.75 |       |          | PERMDISP <i>P</i> > 0.1 |      |          | PERMDISP <i>P</i> > 0.1 |        |          | PERMDISP <i>P</i> > 0.1       |       |          |

2

3

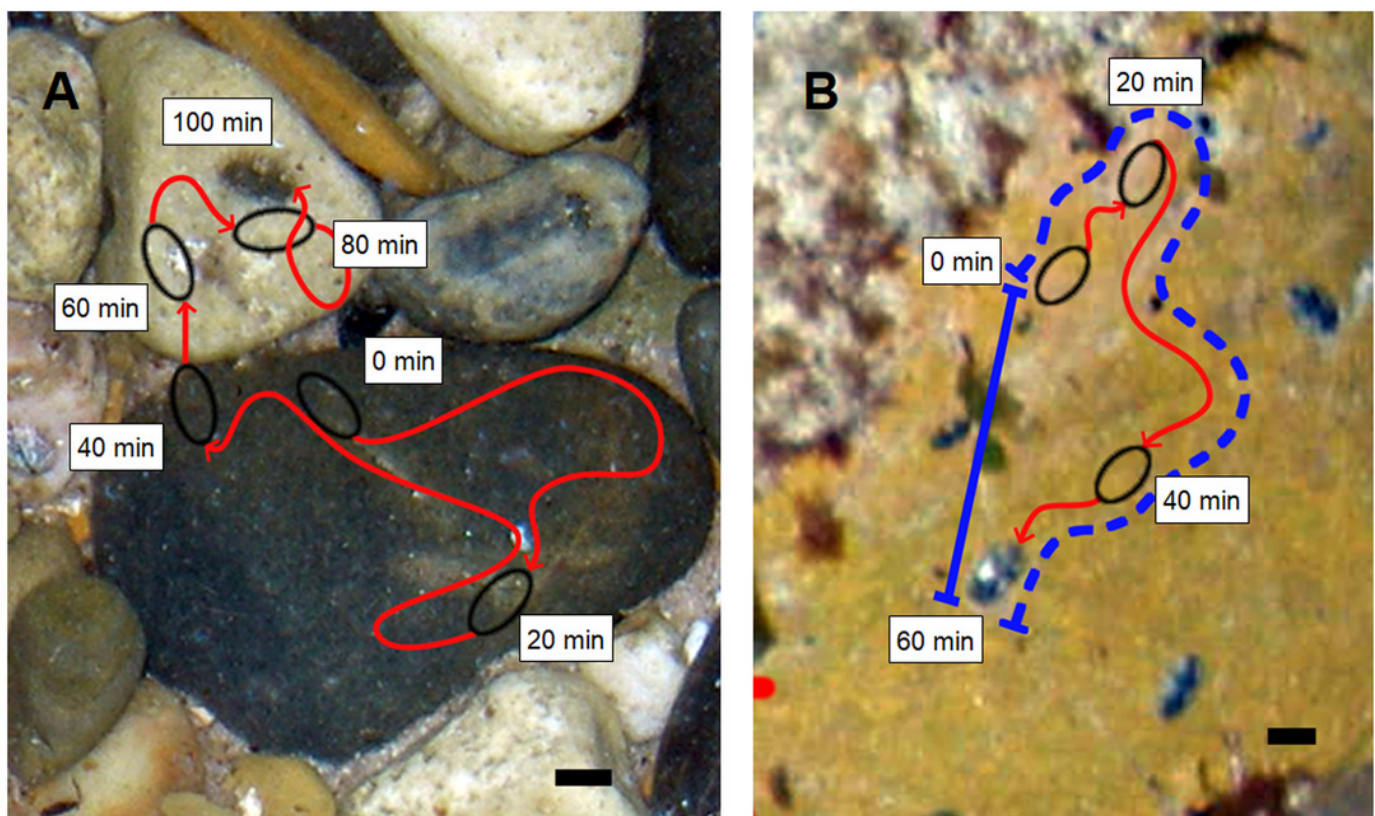
4

5

# Figure 1

Representative movement paths of *Ischnochiton smaragdinus*.

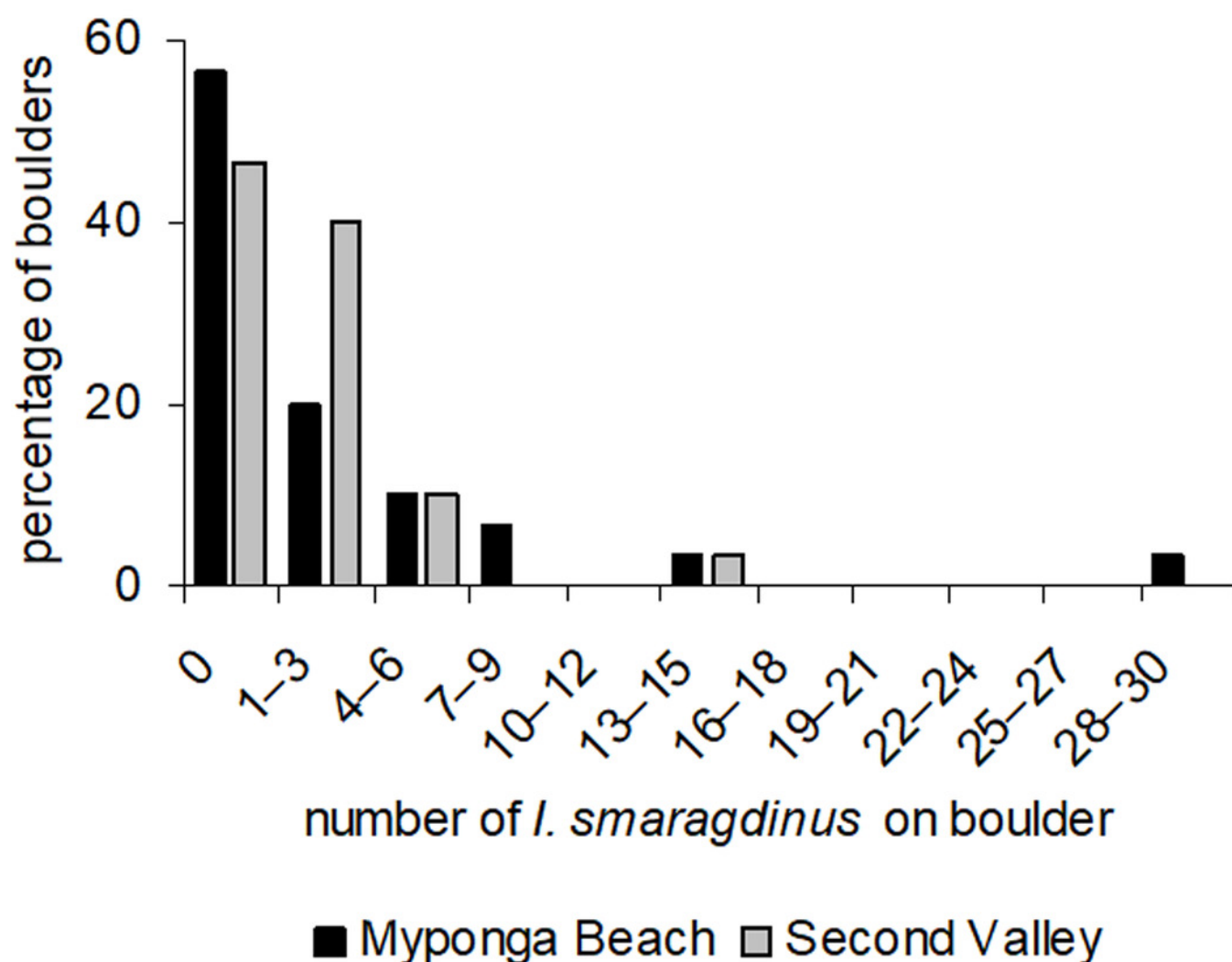
Movement paths are from (A) pebble substratum (100 min) and (B) rock-platform substratum (60 min). The dashed blue line shown in (B) represents the Gross Displacement and the solid blue line indicates Net Displacement, with the ratio of these measures calculated to indicate the tortuosity of the movement path. Black lines at bottom right = 1cm.



# Figure 2

Frequency distributions of *Ischnochiton smaragdinus* among boulders.

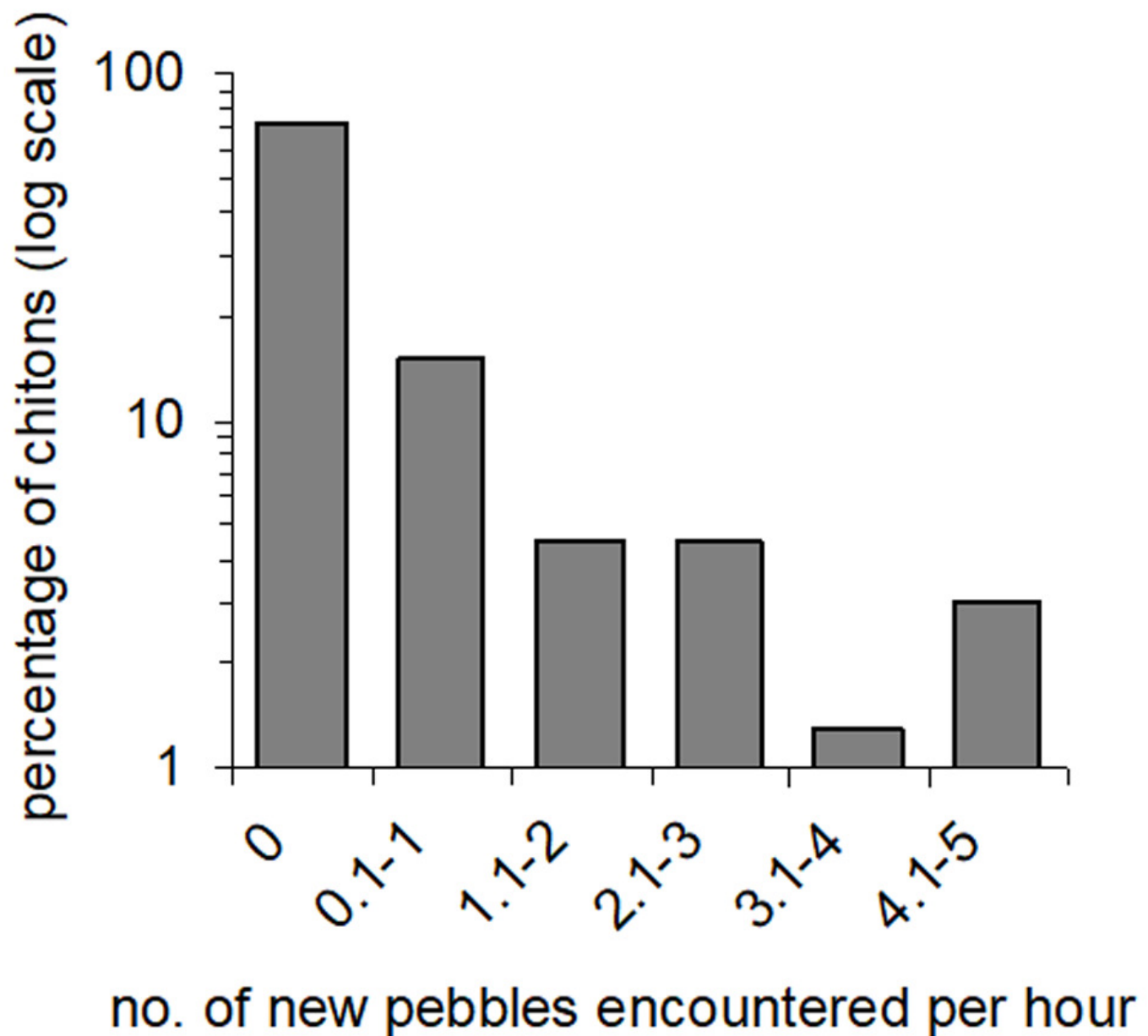
Percentages are shown of the total number of boulders that harboured different numbers of *Ischnochiton smaragdinus* individuals, from the sites Myponga Beach and Second Valley.



# Figure 3

Amounts of movement across pebble habitat patches.

Percentages of *Ischnochiton smaragdinus* individuals that had different rates of movement across pebbles in rock pools with a pebble substratum.



# Figure 4

Movement characteristics of *Ischnochiton smaragdinus* in habitats of differing complexity.

Mean ( $\pm$ SE) (A) speed of movement and (B) tortuosity of the movement path (measured as net:gross displacement ratio; see Fig. 1). “Net speed” refers to the speed averaged over the entire observation period (55 - 130 minutes) and “max. speed” refers to fastest rate of movement by a chiton in any five minute period. Data are from four rock-pools with pebble substratum and three with rock-platform substratum. The number of chitons per rock pool ranged from 3-32. \* $P < 0.05$ .

