

Short Communications

Exposure to wave action: some consequences for the sea urchin *Stomopneustes variolaris* on the Natal coast

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Population size structure in the intertidal echinoid, *Stomopneustes variolaris*, has been observed to vary between habitats, in a manner which suggests the influence of factors in addition to variation in recruitment success. This paper reports on an investigation into the hypothesis that exposure to wave action might be a factor accounting for the variation in population size structure between habitats at Sheffield Beach.

Populasiegroottesstruktuur in die tussengety echinoidea, *Stomopneustes variolaris* varieer tussen habitate op 'n wyse wat die invloed van faktore buite en behalwe 'n variasie in aanwerwingsukses aandui. In hierdie artikel word die hipotese ondersoek dat blootstelling aan golfaksie 'n moontlike faktor kan wees in die variasie in populasiegroottesstruktuur tussen die Sheffieldstrandhabitate.

Sedentary intertidal organisms are subject to considerable drag and impact forces (Denny, Daniel & Koehl 1985). As important components of the intertidal physical environment, these hydrodynamic forces have been implicated in the structuring of wave-swept communities (Paine & Levin 1981) and populations (Ebert 1968; Atkinson & Newbury 1984). In addition, exposure to wave action is known to affect growth rates (McPherson 1968; Baker 1973), gonad production (Gonor 1973), choice of attachment site (Lawrence & Sammarco 1982), and feeding strategies (Lawrence 1975) in a number of sea urchin species.

Stomopneustes variolaris is a long-spined echinoid widely distributed throughout the Indo-Pacific. In southern Africa it inhabits the high energy intertidal rocky shores on the East coast, between Inhambane and Preslies Bay. On the Natal coast it is a sedentary, and frequently cryptic, drift feeder (Drummond 1990). The habitat requirements of this species are provided in only a few habitats within the intertidal region on the Natal coast, namely: the wave-swept intertidal shelves of the lower Balanoid zone, deep pools in the low and mid-shore, and channels and gullies extending into the mid and upper-shore.

Subjective observations suggest that several differences exist between populations in the different habitats. Firstly, in the extent to which individuals occupy cryptic positions, including cracks, crevices or hollows in the substratum or pool walls, or burrows excavated by the sea urchins themselves. Secondly, maximum body size and population size

structure vary in a manner which suggests the influence of factors in addition to variation in recruitment success. And lastly, spine length shows considerable variation between habitats.

The hypothesis that these differences are related to the degree of wave action in each habitat was explored by quantifying the flow regime and relating this to the characteristics displayed by a population in each habitat. In addition a translocation experiment was performed to determine whether wave action was responsible for the observed variation in spine length between sea urchins of different habitats.

Three populations inhabiting contrasting habitats within the intertidal at Sheffield Beach (29°30'S / 31°20'E) were selected for study: (i) the shelf population, where the sea urchins occupied shallow hollows in the intertidal shelf of the lower Balanoid; (ii) the burrow population, individuals of which occupied burrows in the sandstone of the mid-shore; (iii) the wall population, where the sea urchins lived exposed (as opposed to cryptically) on the sides of deep pools in the upper Balanoid zone.

The degree of exposure to wave action was compared by determining the relative water flow in each habitat. A simple mechanical flow meter was held under water for 30-s periods, 10 replicates being acquired from each site at three different stages in the tidal cycle. The effect of temporal variation in wave velocity was minimized as measurements from all three sites were acquired within 16 min at each stage. The size structure of the three populations was determined by measuring, with outside calipers, as large a proportion of each population as possible, either *in situ* or after detaching urchins from the rock. In shelf and burrow populations the maximum diameter of the burrow or hollow was measured to ascertain whether there was a relationship between burrow / hollow size and size of inhabiting urchin.

S. variolaris at Sheffield Beach showed considerable variation in spine length across the three habitats. Whether this variation was the result of exposure to wave action was investigated as follows. Firstly, 63 relatively long-spined *S. variolaris* were translocated from a sheltered site at Hibberdene to an exposed site at Oslo Beach. At the same time a control group at Hibberdene was detached, handled and measured in a similar manner to the experimental group, then returned to the approximate area from which they were collected. After six months the control and experimental groups were collected and the mean spine length/cm test diameter was compared with the initial value. Secondly, the test diameter and length of the five longest spines were measured on 50 urchins from a range of size classes in each of the three study populations. From this a mean spine length/cm test diameter was calculated for each population and correlated with the prevailing exposure regime.

From the water movement values obtained on three separate occasions it appears that the shelf habitat is more exposed to wave action than either the wall or burrow habitats (Table 1). In addition the area inhabited by the burrow population is subject to stronger water movement than the walls of the pools (Table 1).

The Sheffield beach shelf population (Figure 1C) was composed almost entirely of individuals 3–5 cm in test diameter, with less than 5% of the population in smaller or larger size classes. By contrast there was a wider range of

Table 1 Relative water flow in the study habitats at Sheffield Beach recorded on three occasions

Date	Stage in tidal cycle	Habitat	Relative water flow
18/04/92	outgoing tide	shelf	51,9 SD 6,4
		wall	9,9 SD 4,8
		burrow	28,8 SD 9,4
17/05/92	low tide	shelf	65,0 SD 25,7
		wall	16,0 SD 6,8
		burrow	25,4 SD 11,8
01/06/92	low tide but high swell	shelf	74,4 SD 30,8
		wall	22,5 SD 10,9
		burrow	41,7 SD 13,5

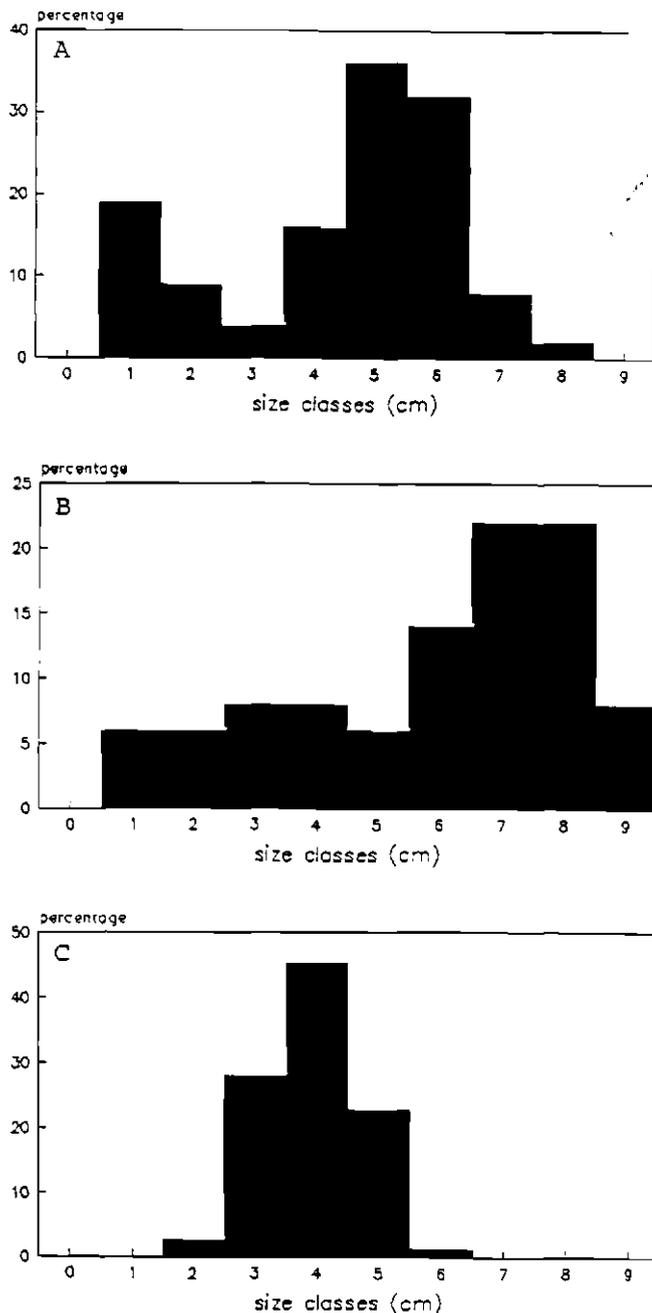


Figure 1 The size structure of the three study populations at Sheffield Beach. (A) Burrow population $n = 75$; (B) wall population $n = 65$; (C) shelf population $n = 80$.

size classes present in the burrow and wall populations (Figures 1A & B). While both of these populations had a significant proportion of individuals 3 cm and smaller, the burrow population was dominated by individuals 4–7 cm in test diameter and the wall population by individuals 6–9 cm in test diameter. A chi-squared test established that the differences between the size structures of shelf and wall and shelf and burrow populations were highly significant at $p < 0,001$. The size structures of wall and burrow populations did not differ significantly. The narrow range of size classes and smaller body size (Figure 1C) in the shelf habitat suggests that limiting factors are operating in this habitat.

The investigation into the relationship between hollow size and size of inhabiting sea urchin in the shelf population revealed a weaker correlation ($r = 0,67$; $df = 29$) than between burrow size and size of occupying urchin in the burrow population ($r = 0,88$; $df = 21$). This difference was highly significant at $p < 0,001$ ($t = 18,37$; $df = 48$).

Of the 63 *S. variolaris* translocated to Oslo Beach in March 1991, 45 were recovered in August 1991. Comparing the mean spine length/cm test diameter for March and August 1991 (Table 2) revealed a decrease which was significant at $p < 0,001$ ($t = 5,02$). The control group at Hibberdene showed no significant change over the same time period. That this 24,4% decrease in spine length/cm test diameter can be attributed to increased exposure to wave action was further supported by the observation that the spines of 86% of the recovered urchins had blunt tips or showed signs of recent breakage. The presence of more extensive macroalgal beds at Oslo Beach than at Hibberdene eliminated the possibility that a reduced food supply might have inhibited spine growth and repair. The differences in spine length/cm test diameter between the three Sheffield beach populations were significant at $p < 0,001$. The individuals of the wall population in the most protected habitat, had the longest spines (Figure 2), while the shelf urchins in the most exposed habitat had the shortest spines. In terms of spine length and exposure to wave action the burrow population fell between these two extremes (Figure 2). This evidence points to the destructive effect of wave action on spine length, with possible negative consequences for feeding efficiency and overall growth rate, perhaps contributing to the differences in body size between the three study populations.

Table 2 Change in spine length following translocation of relatively long spined *S. variolaris* from a sheltered site at Hibberdene to an exposed site at Oslo Beach

	Translocated 02/03/91	Recovered 23/08/91
Test diameter	5,34 SE 0,23	5,29 SE 0,21
Spine length/cm test	0,45 SE 0,02	0,34 SE 0,01
	$t = 5,02 \quad p < 0,001$	
Control group at Hibberdene		
Test diameter	5,75 SE 0,24	5,69 SE 0,23
Spine length/cm test	0,46 SE 0,01	0,45 SE 0,01

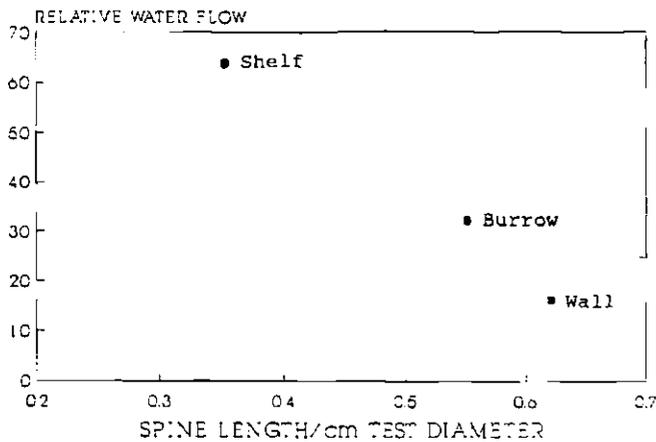


Figure 2 The relationship between relative water flow and the spine length/cm test diameter for the three study populations at Sheffield Beach.

The excavation of burrows or occupation of cryptic attachment sites by sea urchins is considered to be a response to high water energy (Otter 1932; Goss-Custard, Jones, Kitching & Norton 1979). The results from the investigation at Sheffield Beach support this conclusion, as sea urchins in the two most exposed habitats, the shelf and mid-shore channels and gullies, were cryptic or had excavated burrows, while urchins in the relatively sheltered pool habitat did not seek shelter but lived exposed on the pool walls.

Denny *et al.* (1985) argue that the flow of water, such as experienced by sedentary organisms in wave-swept habitats, effectively places mechanical limits on the potential size of these animals. It is therefore possible that the degree of shelter provided by the burrow or cryptic attachment site has influenced the maximum body size and size structure of the study populations. It is apparent from work done by Ebert (1968) on *Strongylocentrotus purpuratus* that sea urchins grow to the capacity of their suitable space. The poor correlation between hollow size and size of occupying urchin in the shelf population suggests that these individuals have not grown to the capacity of their hollows. While this may be a function of the age of the population, observations of other shelf populations lead me to suggest that the unpredictable deposition of sand, which occurs in the shelf habitat and not in the other two habitats, has reduced the capacity of the hollows to provide protection. Not only does the presence of sand interfere with respiration and feeding (de Ridder & Lawrence 1982), but it has been observed that accumulation of sand in the hollows and crevices occupied by *S. variolaris* causes the urchin to alter its position (Drummond 1990). As sand accumulates the urchin is forced further from its optimal position within the hollow, and becomes vulnerable to displacement by water movement. Therefore small size would have considerable survival value in this habitat, as it would permit a greater range of movement within hollows to avoid the accumulation of sand, while remaining adequately protected by the attachment site. The area of the intertidal occupied by the burrow population also experiences considerable water movement, but here the substratum is an easily eroded immature sandstone. The excavation of

burrows by *S. variolaris* occupying this habitat has probably occurred in the absence of suitable naturally occurring protection. A positive correlation between urchin size and burrow size suggests complete construction of a burrow by a single individual. This is significant, because if individual sea urchins are able to modify their attachment sites as they grow their ultimate body size is not limited by the size of the available protection. This perhaps accounts for the observed population size structure which comprises a range of size classes including a significant component of large individuals. The depth of the pools (1.5–2.0 m) occupied by the urchins of the wall population effectively absorbs much of the energy of the wave action in this habitat. The consequent absence of mechanical limits to potential size is reflected in a size structure comprising a range of size classes, a significant component of large individuals and a relatively larger maximum body size.

Although these ideas require further investigation, the present study does suggest that the observed differences in population size structure, maximum body size and spine length between the three populations might be attributed to exposure to wave action. It is possible that differences in size structure may arise from variation in growth rates, however, any biological factors implicated in this variation will operate under the constraints imposed by the physical environment, which is dominated by water movement (Denny *et al.* 1985). Factors known to reduce growth rates in echinoids include limited feeding time owing to exposure at low tide (Leighton 1968), excessive turbulence (McPherson 1968), and damage to tests and spines resulting in diversion of resources into repair (Ebert 1968; Baker 1973).

Perhaps the most valuable point to emerge from this study is an increased awareness that *S. variolaris* is capable of considerable ecological plasticity.

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The karyotype and taxonomic status of *Cryptomys hottentotus darlingi* (Rodentia: Bathyergidae)

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Cytogenetic analyses were performed on twenty specimens referable to *Cryptomys hottentotus darlingi* from north eastern Zimbabwe. In comparison to the southern subspecies *C. h. hottentotus* (aFN = 102) and *C. h. natalensis* (aFN = 100), *C. h. darlingi* showed the same diploid number (2n = 54), but a striking reduction in the fundamental number (aFN = 80). C-banding analysis suggests that chromosome differentiation arose most probably by pericentric inversions. The magnitude of the karyotypic differences is assumed to represent reproductive isolation and consequently the specific status for the *darlingi* cytotype is recommended.

Sitogenetiese ontleding is uitgevoer op 20 individue van *Cryptomys hottentotus darlingi* van noord-oostelike Zimbabwe. In vergelyking met die suidelike subspesies *C. h. hottentotus* (aNF = 102) en *C. h. natalensis* (aNF = 100) vertoon *C. h. darlingi* dieselfde diploïde getal (2n = 54), en 'n verbasende vermindering in die *nombre fondamentale* (aNF = 80). C-band-analise impliseer dat chromosoomdifferensiering heel waarskynlik ontstaan het deur middel van perisentriese inversies. Daar word aangeneem dat die grootte van die kariotiepverskille reprodutiewe isolasie verteenwoordig, en gevolglik word spesifieke status vir die *darlingi* sitotipe aanbeveel.

Mole-rats of the genus *Cryptomys* are a group of subterranean rodents (Family Bathyergidae), endemic to central and southern Africa. Systematic relationships and taxonomic delimitations among most of the taxa within the genus

remain obscure. The common mole-rat, *Cryptomys hottentotus*, is a geographically variable species which occurs from the western part of central Tanzania southwards into Zambia, Malawi, Zimbabwe, Mozambique and South Africa. At present, five subspecies are recognized within its distributional range (Honeycutt, Allard, Edwards & Shluter 1991). *Cryptomys h. hottentotus* inhabits the south and west of South Africa, *C. h. natalensis* occurs in the east and north of South Africa, *C. h. darlingi* occurs in eastern Zimbabwe and western parts of Mozambique, *C. h. amatus* and *C. h. whytei* occur in the northern part of the distributional range, being reported from eastern Zambia, northern Malawi and southwestern Tanzania (De Graaff 1981; Ansell 1978; Ansell & Dowsett 1988).

Although there is some literature on the systematics of the genus *Cryptomys*, most of the information concerns those taxa living in the southern part of its distributional range (Allard & Honeycutt 1992; Honeycutt, Edwards, Nelson & Nevo 1987; Nevo, Shlomo, Beiles, Jarvis, & Hickman

Table 1 Mean relative length, arm ratio, centromeric index and type of metaphase chromosomes of *Cryptomys h. darlingi* from Goromonzi, north-eastern Zimbabwe

Chromosome pair	Mean relative length \pm SE	Arm ^b ratio	Centromeric ^c index	Type ^d
1	6,85 \pm 0,27	–	0,00	t
2	6,36 \pm 0,23	2,9	0,26	sm
3	5,76 \pm 0,45	1,5	0,40	m
4	4,89 \pm 0,22	–	0,00	t
5	4,71 \pm 0,22	–	0,00	t
6	4,40 \pm 0,30	1,9	0,34	sm
7	4,23 \pm 0,07	1,7	0,37	sm
8	4,13 \pm 0,22	1,4	0,42	m
9	4,00 \pm 0,29	–	0,00	t
10	3,80 \pm 0,22	1,3	0,43	m
11	3,40 \pm 0,19	1,3	0,43	m
12	3,38 \pm 0,13	–	0,00	t
13	3,30 \pm 0,20	1,4	0,42	m
14	3,22 \pm 0,08	–	0,00	t
15	3,13 \pm 0,14	–	0,00	t
16	3,09 \pm 0,08	1,3	0,44	m
17	2,89 \pm 0,09	–	0,00	t
18	2,80 \pm 0,09	–	0,00	t
19	2,80 \pm 0,12	1,5	0,40	m
20	2,79 \pm 0,11	1,4	0,42	m
21	2,50 \pm 0,12	1,2	0,45	m
22	2,41 \pm 0,12	–	0,00	t
23	2,40 \pm 0,16	1,5	0,40	m
24	2,30 \pm 0,19	–	0,00	t
25	2,15 \pm 0,15	–	0,00	t
26	1,97 \pm 0,32	1,2	0,45	m
X	3,95 \pm 0,62	1,6	0,39	m
Y	2,36 \pm 0,46	1,4	0,41	m

Karyotypical descriptors based on 12 metaphase chromosome plates:

^a Mean relative length as a percentage of the haploid genome length with its standard error. ^b Arm ratio is the proportion between the short and the long arm of the chromosome. ^c Centromeric index determined by dividing the length of the short arm by the total length of the chromosome. ^d Type of chromosome determined by the position of the centromere: (t) telocentric/acrocentric, (sm) submetacentric and (m) metacentric chromosome.