Predation by West Coast rock lobsters (*Jasus lalandii*) on two species of winkle (*Oxystele sinensis* and *Turbo cidaris*)

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Rock lobsters, *Jasus lalandii*, may play an important role in structuring the communities on shallow reef ecosystems and have recently increased in density in the area between Cape Hangklip and Danger Point on the south-west coast of South Africa. This has probably resulted in increased predation on natural populations of smooth turban shells (*Turbo cidaris*) and pink-lipped topshells (*Oystele sinensis*), both of which are proposed targets for small-scale commercial fisheries. This study examines the size selectivity, prey species preferences and consumption rates of rock lobsters feeding on these two winkle species. Rock lobsters showed a strong preference for small *O. sinensis*, and were limited to taking a maximum (or critical) size of prey, which increased linearly with rock-lobster size. By contrast, rock lobsters of all size classes tested were able to crack and consume a full size range of *T. cidaris*, and no size preferences were evident. When the two gastropods were offered simultaneously, rock lobsters preferentially consumed the thinner shelled *O. sinensis*. Consumption rates increased linearly with rock-lobster size. Population consumption rates indicate that rock lobsters will have a profound effect on winkle stocks in the area, even if winkles constituted less than 1% of the diet. This in turn suggests that commercial exploitation of these stocks is unlikely to remain sustainable.

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Introduction

The rock lobster *Jasus lalandii* occurs between Walvis Bay, Namibia (23°S, 14°32'E) and East London (East Coast of South Africa, 29°S, 27°50'E) (Heydorn 1969; Pollock & Beyers 1981), but has historically been far more abundant in the cooler waters of the West Coast than in the regions further East (Field, Griffiths, Griffiths, Jarman, Zoutendyk, Velimirov & Bowes 1980; Pollock & Beyers 1981). Since the late 1980's, *J. lalandii* has, however, showed a marked increase in abundance on South Africa's south-east coast (Tarr, Williams & MacKenzie 1996; Mayfield 1998).

Rock lobsters are major predators in shallow marine systems around the southern African coastline, and have a substantial impact on the density and population structure of their prey populations (Pollock 1979; Barkai & Branch 1988), and indeed the composition of entire benthic communities in which they occur (Barkai & McQuaid 1988; Barkai, Davis & Tugwell 1996).

It has been suggested that the increase in rock-lobster numbers between Cape Hangklip (34°23'S, 18°50'E) and Danger Point (34°36'S, 19°18"E, defined here as East of Cape Hangklip, EOCH) has resulted in the dramatic decrease in sea urchin densities in this area (Tarr *et al.* 1996). Rock lobsters have also been observed handling smooth turban shells (*Turbo cidaris*) in the natural environment (S. Mayfield pers. obs.) and empty shells of both *T. cidaris* and *Oxystele sinensis* (the pink-lipped topshell) have been found in front of *J. lalandii* lairs. Furthermore, gut content analyses of *J. lalandii* captured EOCH have contained both *T. cidaris* and *O. sinensis* operculae and shell remains (*ca.* 10% by occurrence, Mayfield 1998). It is possible that the consumption of these winkles by rock lobsters will increase as alternative food resources, such as sea urchins and mussels decline (Mayfield

1998). This could have severe effects on winkle abundance and population structure.

Concurrent with the increase in rock lobster numbers has been an interest in the potential commercial harvest of both *T. cidaris* and *O. sinensis*. Both these species occur on South Africa's South and East coasts, with *O. sinensis* occurring down to a depth of about 5 m and *T. cidaris* to 30 m (Branch, Griffiths, Branch & Beckley 1994).

This study aims to determine rock lobster prey-size selectivity, prey species preference and feeding rate on *T. cidaris* and *O. sinensis*. This information will become of vital importance should the proposed commercial fishery become a reality. Based on published information we predict that: (1) small rock lobsters will be incapable of consuming large winkles; (2) rock lobsters will preferentially consume small winkles when offered a choice; and (3) rock lobsters will preferentially consume *O. sinensis* over *T. cidaris* as the former has a relatively thinner shell.

Methods

Specimens of *T. cidaris* and *O. sinensis* were collected in the intertidal zone between Danger Point and Cape Point in the south-western Cape. For simplification, only male rock lobsters across the size range available were collected using baited commercial traps to ensure that they were feeding at the time of capture and to prevent unnecessary damage to limbs. They were acclimated to aquarium conditions for seven days prior to any experiments being conducted, during which time they were held in the filtration pond of the recirculating sea water system and fed on an unnatural prey (pilchards, *Sardinops sagax*) to prevent any learning process affecting the results (Wright, Francis & Eldridge 1990; Gosselin & Chia 1996). The aquarium was maintained at 13±1°C

under a 12h:12h light:dark cycle with the light phase starting at 6am, which were the approximate conditions at the time of capture. As all rock lobsters were collected simultaneously during summer 1997, they would all have been in the reserve accumulation phase of the moult cycle and been in similar physiological states (Cockcroft 1997).

Different rock lobsters were used for each experiment. Prior to each experiment, randomly selected individual rock lobsters were transferred from the holding tank to separate (615 x 325 x 325 mm) glass tanks connected to the same circulating sea-water system under the same photo period. These rock lobsters were starved for two days, then offered an opened black mussel to ensure that they were feeding. Each rock lobster was then starved for a further 24h to ensure equal starvation levels and complete clearance of the digestive tract (Zoutendyk 1988), before each of the following experiments was performed. For all experiments described below, winkle measurements refer to the maximum shell width (abbreviated here to width). There is a strong correlation between winkle maximum width and total shell length (Dr A. Pulfrich, unpublished data).

Critical size of prey

To determine the minimum and maximum (or critical) size of *O. sinensis* that *J. lalandii* could consume, 12 rock lobsters of known size (50–105 mm carapace length, CL) were each offered one small *O. sinensis*. Winkles consumed after 24h were replaced with progressively larger individuals of the same species. This process was continued for each rock lobster until 48h passed without further mortality of winkles, after which the respective rock lobsters were supplied with open mussels, to confirm they were still feeding. The largest winkle consumed by each rock lobster was taken as the critical prey size for that size rock lobster. The process was then repeated for *T. cidaris*.

Size preference within each prey species

Six rock lobsters of 53, 69, 74, 82, 90 and 105 mm CL were provided with a constant size range of *O. sinensis*, consisting of four individuals in each 5 mm size class (namely 10–14, 15–19, 20–24, 25–29, 30–34 & 35–39 mm width), randomly positioned within the tank. Consumed winkles were replaced every 24 hours with live individuals of the same size class and species. This was repeated for five days and the total number of each size class consumed per day recorded. The experiment was then repeated by offering *T. cidaris* to the same six rock lobsters in the size classes: 15–19.9, 20–24.9, 25–29.9, 30–34.9, 35–39.9, 40–44.9, 45–49.9 & 50–54.9 mm width.

Species preference

Six rock lobsters were simultaneously provided with five *O. sinensis* and five *T. cidaris* individuals of known size, randomly positioned in the tank. The winkles were all of a size class accessible to every rock lobster. The numbers and sizes of each winkle species consumed per day were recorded for five days. The total number of *O. sinensis* and *T. cidaris* consumed by each rock lobster during the five days was compared to determine if any correlation with rock lobster size was shown.

Feeding rate

Feeding rates for the size preference and species preference experiments for each rock lobster were determined by calculating the mass (g) and energy value (kJ) of winkles consumed each day. Dry weights of each winkle species were obtained by drying (to constant mass) a representative size range in an oven at 60°C for 72h, after which the shell was removed and the dry flesh weighed. The dried flesh was then ground using a 500μm pore size electric mill and the calorific content (kJ.g^{-1}) determined through complete combustion in excess oxygen using a DDS 500 bomb calorimeter. Feeding rates were then converted to kJ.rock lobster^{-1}.day^{-1}.

Method of penetration

Visual observations were made on the method of shell penetration by the rock lobsters on the two prey species. The shells of consumed winkles were also retained and the damage caused by penetration noted and compared to samples of empty shells collected at the study site.

Predatory impact of *Jasus lalandii* on *T. cidaris* populations

Estimates of the possible impacts of predation by *J. lalandii* on populations of *T. cidaris* EOCH were made as follows. The surface area between the shore and the 15 m depth contour was estimated from a SAN 120 navigational chart for the area between Cape Hangklip and Danger Point. The total number of rock lobsters larger than 50 mm CL in this area was then estimated from density information (Mayfield 1998). Rock lobster size-frequency distributions from the same area were used to estimate the total number of rock lobsters in each 10 mm CL size class.

The total number of *T. cidaris* over the same area was estimated from the density surveys conducted by Pulfrich (1997). Size-frequency distributions for this species from the same
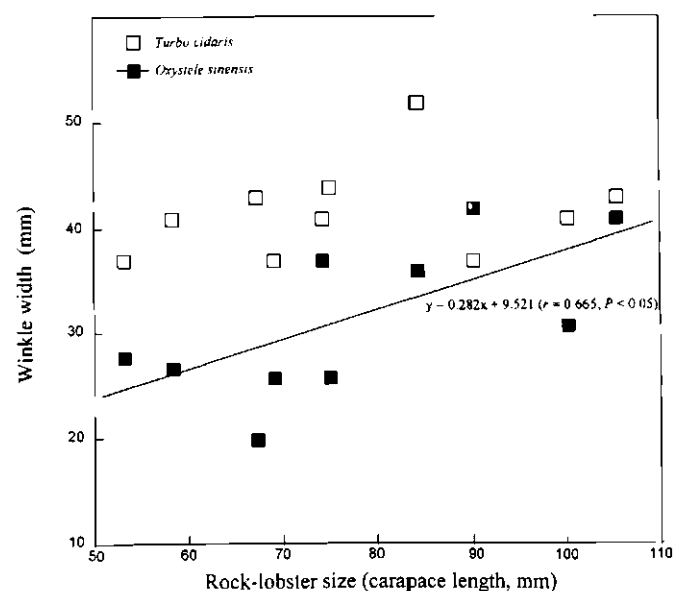
Figure 1 Maximum (or critical) size of the two winkle species consumed by *Jasus lalandii* between 51 and 105 mm carapace length. N = 10 because 2 rock lobsters did not eat.

study were used to estimate the most abundant size classes.

Results

Critical size of prey

The maximum, or critical, size of *Oxystele sinensis* consumed by rock lobsters showed a significant positive linear relationship (n = 10, r = 0.665, P < 0.05) with increasing rock lobster CL (Figure 1). However, no significant relationship was found between the maximum size of *Turbo cidaris* eaten and rock lobster size. Rather, all rock lobsters were able to crack and consume all sizes of *T. cidaris*. Sample size (n) was 10 because two rock lobsters did not feed.

Size preference within each prey species

All rock lobsters preferentially consumed *O. sinensis* well below the critical size (Figure 2a) with a clear size preference for the smallest size class offered (10–14mm width). Larger rock lobsters ate successively larger winkles (Figure 2a) and large rock lobsters consumed *O. sinensis* up to about 40 mm width. Although the largest size classes of *T. cidaris* were avoided, there was, however, no suggestion of a systematic relationship between *T. cidaris* size preference and rock lobster carapace length (Figure 2b). The total number of *T. cidaris* consumed over the four days did, however, increase significantly with rock lobster size (n = 6, r = 0.933, P < 0.01) as described by the equation:

number consumed = 0.375 rock lobster size (CL, mm) – 14.69.... (1)

Species preference

Four out of five rock lobsters tested consumed more *O. sinensis* than *T. cidaris* when offered both species simultaneously (Figure 3). The 53 mm CL rock lobster ate nothing. More
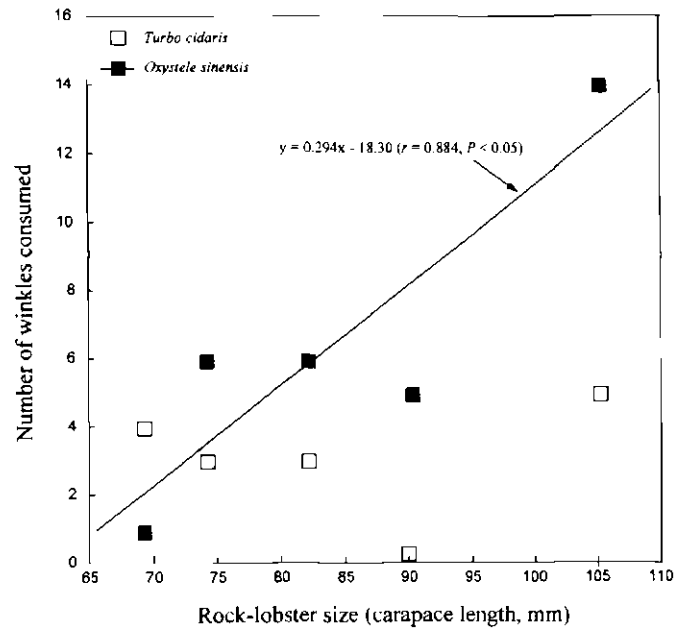
Figure 3 Number of each of the two winkle species consumed over 120 hours by five rock lobsters of differing sizes (CL, mm).

than twice the total number of *O. sinensis* than *T. cidaris* (32 compared to 15) were consumed by all the rock lobsters combined. The total number of *O. sinensis* consumed over the five days showed a significant positive linear correlation (n = 5; r = 0.884; P < 0.05) with rock lobster CL (Figure 3), while the total number of *T. cidaris* consumed showed no correlation with rock lobster CL (r = 0.08; P > 0.05).

Feeding rates

Calorific value (flesh only) in both prey species followed an exponential relationship with shell width, with *Turbo cidaris* having a slightly higher calorific value than *Oxystele sinensis* for any given shell width. The relationships between shell width (x, mm) and calorific value (y, kJ.g^{-1}) were described by the equations:

$$y = 0.962 \exp^{(0.088x)} \quad \text{for } T. \, cidaris$$

and

$$y = 0.084 \exp^{(0.136x)} \quad \text{for } O. \, sinensis$$

Figure 4 shows the relationship between feeding rate (kJ.day^{-1}) and rock lobster size with data derived from both the size-preference and species-preference experiments. A close positive linear relationship was found between feeding rates (both species combined) and rock lobster size (n = 18, r = 0.857, P < 0.05).

Method of penetration

Rock lobsters captured the winkles with their first pair of walking legs and then rotated them, pausing periodically, presumably to test for penetrability with their mandibles. Smaller *Oxystele sinensis* were cracked at the apex and totally opened to expose the flesh (Figure 5a). Small *Turbo cidaris* were cracked in the centre of one of the whorls and the flesh
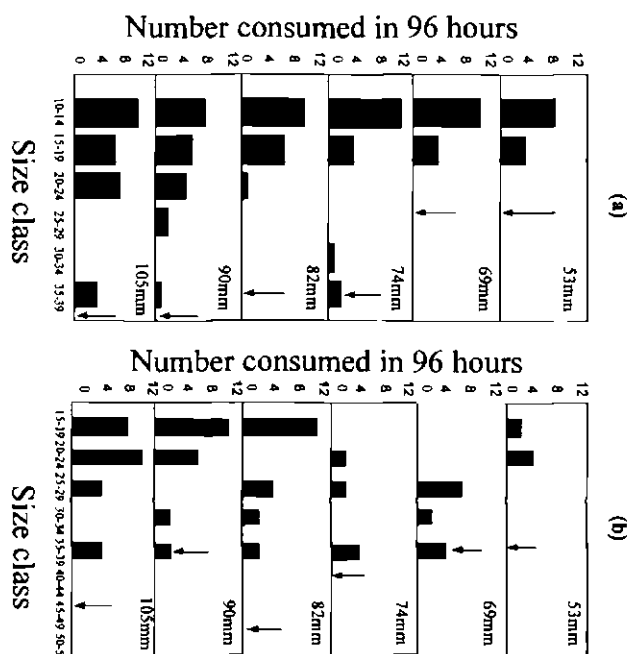
Figure 2 Numbers of each size class of (a) *Oxystele sinensis* and (b) *Turbo cidaris* consumed by six different-sized rock lobsters in 96 hours. Arrows indicate the maximum size of winkle consumed (see Figure 1).
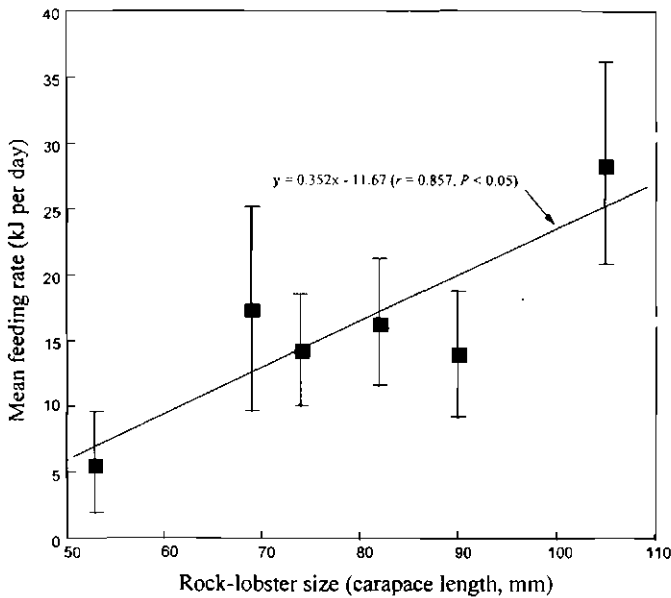
Figure 4 Average feeding rate of *Jasus lalandii* on both *Oxystele sinensis* and *Turbo cidaris* in relation to rock-lobster size.

exposed (Figure 5b). Larger individuals of both species were cracked sequentially from the shell lip until the damage extended behind the operculum and the muscular foot could be reached and extracted (Figure 5c). Very large winkles,
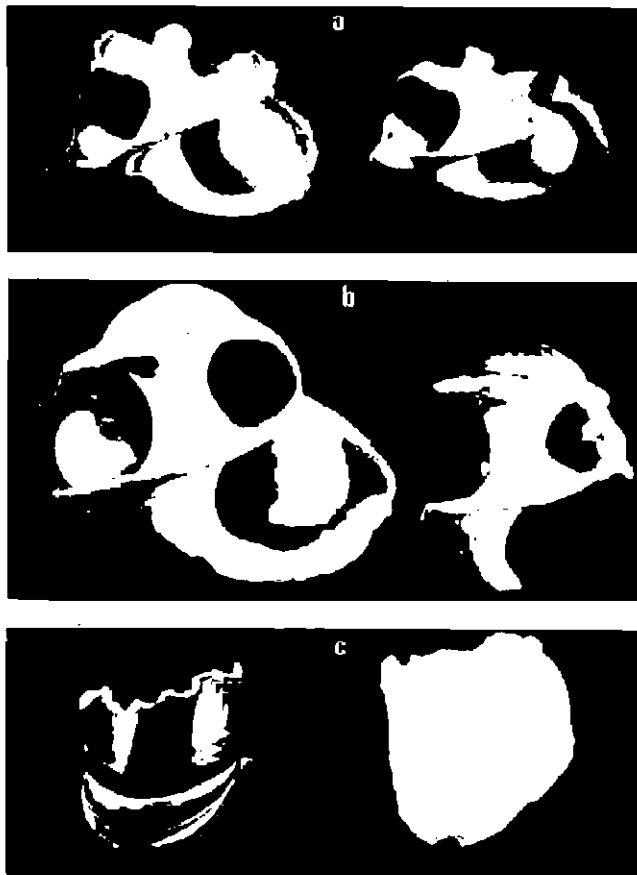
Figure 5 Winkles consumed by rock lobsters in the laboratory (left-hand side) and specimens collected from rock-lobster lairs EOCH (right-hand side) for (a) small *O. sinensis* (3×), (b) small *T. cidaris* (3×) and (c) large *T. cidaris* (2×).

especially the larger *T. cidaris* that were too large to crack, showed bite marks only at the rim of the lip, and only some of the flesh was removed. The rock lobsters were observed holding these large winkles upside down for long periods, perhaps waiting for them to emerge so that they could grasp the exposed foot. This is a likely scenario as numerous consumed winkles had limited shell damage.

Predatory impact of *J. lalandii* on *T. cidaris* populations

The total length of coastline between Cape Hangklip and Danger Point was estimated at 81 km, of which approximately 56 km are hard substratum. This distance was used in further calculations, as both rock lobsters and winkles are restricted to rocky substrata. The average distance offshore to the 15 m depth line was 870 m (n = 60). The average density of rock lobsters between Cape Hangklip and Danger Point (to a depth of 15 m) was 0.67 lobsters.m^{-2} (SE = 0.10; n = 160). This multiplied by the total area (56 km x 0.87 km) gave a total number of 33 x 10^6 rock lobsters. The average density of *T. cidaris* for the same area was taken as 0.91 ± 0.23 winkles.m^{-2}, giving an estimated total number of 44 x 10^6 individuals. The estimated total number of *T. cidaris* consumed per year by rock lobsters if they were to feed solely on this prey, was estimated to be 36460 x 10^6 individuals (Table 1). These figures greatly exceed the current standing stock EOCH. Thus, even if winkles make up only a small proportion of the diet, their populations could be severely impacted by rock lobster predation (Table 1).

Discussion

Several factors may influence a predator's choice of prey. These include cost benefits (Brunner, Kacelnik & Gibbons 1992), risk (Hughes, Ward & Perrin 1995), considerations of long-term energy and mineral intake (Lankford & Targett 1997) and food quality (Irons, Oswood & Bryant 1988; Chambers, Hanson & Prepas 1991). Because food quality of each prey species was kept constant (all individuals of each prey species were collected simultaneously), and predation risk was zero during these experiments, only cost-benefit and long-term considerations should have influenced the rock lobster's choices. The phase of the moult cycle also influences choice of prey (Mayfield 1998), but all rock lobsters were in the same phase of their moult cycle, namely the reserve accumulation phase prior to moulting in October (Cockcroft 1997). Rock lobsters vary their diet according to their moult stage (Mayfield 1998), but in all samples across all seasons EOCH, winkle remains were consistent components of the gut contents.

The positive linear relationship found between rock lobster size and critical size of *O. sinensis* (Figure 1) indicates that larger *O. sinensis* have refuge in size from predation by small rock lobsters, while smaller individuals are vulnerable to predation by all rock lobster size classes. Only rock lobsters larger than 90 mm CL were able to consume the largest *O. sinensis*. However, in the field, small individuals of both winkle species occur in the intertidal zones, while larger specimens extend their distribution well below the low water mark (Pulfrich 1997). Thus, small intertidal *O. sinensis* are not exposed to predation by rock lobsters, but as they grow and migrate downshore, they become increasingly available to rock

Table 1 Estimated population of rock lobsters of different sizes EOCH. [1] refers to data obtained from Mayfield 1998. The number of *T. cidaris* consumed rock lobster^{-1}.year^{-1} was estimated from equation (1). This value multiplied by the number in each size class gave the total predicted consumption of *T. cidaris* in one year. Data on the current density of *T. cidaris* EOCH were obtained from Pulfrich (1997).

Rock-lobster carapace length (mm)	Estimated population EOCH (millions)[1]	Predicted number of *T. cidaris* eaten pert year per rock lobster	Predicted total number of *T. cidaris* eaten in one year (millions)	Total number consumed if *T. cidaris* comprises 1% of the diet (millions)	Total number consumed of *T. cidaris* comprises 0.1% of the diet (millions)
51–60	5.6	538.98	3018.30	30.18	3.02
61–70	11.2	880.76	9864.46	98.64	9.86
71–80	8.4	1222.53	10269.24	102.69	10.27
81–90	4.8	1564.30	7508.65	75.09	7.51
91–100	2.3	1906.08	4383.97	43.84	4.38
101–110	0.63	2247.85	1416.14	14.16	1.42
111–120	0.13	2589.62	336.65	3.37	0.34
Totals		8360.49	36460.76	364.61	36.46

% of *T. cidaris* standing stocks

lobsters.

By contrast, *T. cidaris* seemed not to have any refuge in size from predation by rock lobsters, as even small rock lobsters were able to consume large prey individuals. This is in contrast to our first prediction. Perhaps more importantly, juvenile *T. cidaris* are already exposed to rock lobster predation as they occur in both the subtidal and intertidal zones (Pulfrich 1997).

The preference by *J. lalandii* for small *O. sinensis* (in support of our second prediction), well below the critical size, may be due to the lower energetic cost required to penetrate these smaller winkles. Consumption of small prey is a common observation in similar size-selectivity experiments involving *J. lalandii* feeding on other prey species, including mussels (Griffiths & Seiderer 1980) and sea urchins (Mayfield 1998). This trend is also shown by other lobster species feeding on a variety of prey (for example Tegner & Levin 1983; Robles, Sweetham & Eminke 1990; Andrew & MacDiarmid 1991). The lack of such a clear-cut size preference when feeding on *T. cidaris* is surprising, particularly as this species has a thicker and more robust shell than *O. sinensis* (Van Zyl, unpublished data).

Although the nutritional value of *T. cidaris* for any particular size is higher than the corresponding value for *O. sinensis*, the suspected easier penetrability of *O. sinensis*, which has a thinner and lighter shell than *T. cidaris*, probably explains the preference by rock lobsters for this species when given a choice. This data upheld the third prediction. Despite a lower nutritional yield per prey item, it may be energetically more cost effective for a rock lobster to consume higher numbers of *O. sinensis*, rather than spending time and energy penetrating the thicker-shelled *T. cidaris*. Previous experiments involving prey choice by *J. lalandii* have also demonstrated clear prey selection. These include a preference for abalone (*Haliotis midae*) over keyhole limpets (Scott, Sweijd, Cook & Smullen in press), for black over ribbed mussels (Griffiths & Seiderer 1980) and for abalone over sea urchins, *Parechinus angulosus* (Mayfield 1998). Thus this experiment continues to pro-

vide support to the hypothesis that *J. lalandii* is a selective predator (Barkai *et al.* 1996). As with prey size selection, active prey species choice is not limited to this lobster species. For example, *Homarus americanus* (the American lobster) demonstrated clear preference for crabs over sea urchins (Evans & Mann 1977), and for the urchin *Strongylocentrotus purpuratus* over another urchin. *S. franciscanus* (Tegner & Levin 1983).

The juveniles of *O. sinensis*, as well as other winkles (*Oxystele tigrina* and *Turbo sarmaticus*), seek refuge from subtidal predators, such as rock lobsters, by remaining in the intertidal regions (Pulfrich 1997). However, although small *T. cidaris* find sanctuary under boulders and beneath sea urchins, they are largely confined to the infratidal and subtidal areas and thus unable to avoid rock lobster predation pressure (Pulfrich 1997) except in turbulent areas (Tarr *et al.* 1996). Thus, the high predation rate on this winkle species by *J. lalandii* (Mayfield 1998) may have important consequences for the continued survival of *T. cidaris* in areas where rock lobster numbers have recently increased. Such an area lies EOCH, where in the late 1970's rock lobster abundance was so low as to be recorded as zero (Field *et al.* 1980), but where they are currently abundant (Tarr *et al.* 1996; Mayfield 1998).

Predation by rock lobsters probably plays an important role in restricting *T. cidaris* population sizes, especially when other (often preferred) prey organisms are rare (for example mussels). The extent of the effect of predation will depend on the abundance of rock lobsters, their size-frequency distribution, the prey species available to them and rock lobster food preferences. Barkai *et al.* (1996) state that rock lobsters may be capable of eliminating most of their prey if present in sufficiently high densities, thereby substantially altering the benthic subtidal community. Barkai & Branch (1988) concluded that *J. lalandii* are opportunistic predators and scavengers, and Barkai *et al.* (1996) suggest that rock lobster predation may be an important factor in determining prey species diversity and richness. Tarr *et al.* (1996) proposed that the collapse in the abundance of sea urchins EOCH may in fact be a direct

result of predation by the increased numbers of rock lobsters in the area. The results of this study suggest that when other favoured prey items are low in numbers, rock lobsters could turn towards *O. sinensis* and *T. cidaris* as alternative food sources – as already is occurring sporadically EOCH (Mayfield 1998). This could lead to a marked decline in the winkle populations, especially of *T. cidaris*, which is both vulnerable throughout its life span and to all size classes of rock lobster.

Based on equation (1), it can be calculated that 36×10^9 winkles or c.a. 800 times the estimated total population of *T. cidaris* EOCH ($44 \ 10^6$) would be consumed annually if rock lobsters fed only on *T. cidaris*. This assumption is certainly invalid – the diet of rock lobsters EOCH is comprised mainly of sponges, mussels and barnacles with winkles being rare (Mayfield 1998). However, even if winkles comprised 1% or even 0.1% of the diet of *J. lalandii*, they could still consume respectively 827% and 83% of the standing stocks annually (Table 1). This begs the question of why winkles and rock lobsters currently co-exist EOCH. Behavioural observations show sea urchins to aggregate in the presence of a predator (Bernstein *et al.* 1981, Hagen & Mann 1994). Similar observations here showed that winkles aggregated in the presence, but not absence, of rock lobsters. Although this is unlikely to have influenced the results above (because they have no protective cover), winkles in the field do show a clumped distribution (Pulfrich 1997), frequently occupying narrow crevices. Perhaps this behaviour moderates predation by rock lobsters in the field and permits co-existence.

In conclusion, rock lobsters do consume both winkle species in laboratory experiments and in the field. Even though selection was for small winkles over large ones, and for *O. sinensis* over *T. cidaris*, it is likely that if rock lobster numbers continue to increase EOCH, a collapse of the winkle populations may occur. Furthermore, our results suggest that commercial exploitation of *O. sinensis* and *T. cidaris* in this area would be unwise and unlikely to be sustainable, since these populations may already be in decline through natural predation.

Acknowledgements

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