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AQUARIUM EXPERIMENTS COMPARING THE FEEDING BEHAVIOUR OF ROCK LOBSTER *JASUS LALANDII* ON ABALONE AND SEA URCHINS AT TWO SITES ON THE WEST COAST OF SOUTH AFRICA

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Predation by the rock lobster *Jasus lalandii* is influential in regulating the composition of shallow-reef communities on the west coast of South Africa. Two previous and independent studies addressing this topic, but conducted 600 km apart (one in Cape Town and the other in Port Nolloth on the west coast of South Africa) and using different experimental protocols, revealed contradictory results regarding the feeding behaviour of *J. lalandii*. The Port Nolloth study showed that juvenile abalone *Haliotis midae* hiding under sea urchins *Parechinus angulosus* were safe from predation by rock lobsters, which seemed to prefer the sea urchins as food. However, the Cape Town study showed that rock lobsters preferentially selected juvenile abalone over sea urchins. Because of the importance of these results to abalone ranching and the South African abalone fishery, the experiments were repeated at the two study sites, using a standardized experimental protocol. Rock lobsters from both sites showed a strong preference for juvenile abalone over sea urchins, even in the presence of kelp *Ecklonia maxima*. There was no significant difference ($F_{3,92} = 0.09$, $p > 0.1$) in abalone consumption by rock lobsters between the two sites. Therefore, at least in the absence of preferred prey such as mussels, sea urchins appear to provide only limited protection to juvenile abalone from rock lobsters.

Key words: abalone *Haliotis midae*, *Jasus lalandii*, predation, sea urchins

The distribution of the West Coast rock lobster *Jasus lalandii* ranges between Walvis Bay, Namibia (23°S, 14°50´E), and East London (29°S, 27°50´E) on the south-east coast of South Africa (Heydorn 1969). Historically, they have been more abundant along the South African west and south-east coasts (Field *et al.* 1980, Pollock and Beyers 1981), but recently there has been a marked increase in their abundance on the South-East Coast (Tarr *et al*. 1996, Mayfield 1998). The species is an important predator in shallow marine systems, strongly influencing prey density and population structure (Pollock 1979, Barkai and Branch 1988, Mayfield 1998), to the extent of being able to alter the composition of benthic communities (Barkai and McQuaid 1988, Barkai *et al.* 1996).

The abalone *Haliotis midae* is commercially harvested off South Africa, principally along the Southern Cape coast between Cape Hangklip (34°23´S, 18°49´E) and Quoin Point (34°47´S, 19°38´E) near Cape Agulhas (Tarr 1992). Field observations (Tarr *et al*. 1996), coupled with field and laboratory experiments (Day and Branch 2000a, b, 2002a, b), have demonstrated that juvenile abalone (<35 mm shell breadth) are rarely found outside the spine canopy of the Cape sea urchin *Parechinus angulosus*. Furthermore, areas experimentally cleared of sea urchins showed marked increases in siltation and significantly lower densities of abalone recruits (Day and Branch 2002a). Sea urchins are an important component in the diet of rock lobsters (Newman and Pollock 1974, Pollock 1979, Griffiths and Seiderer 1980, Barkai and Branch 1988, Zoutendyk 1988, Mayfield *et al.* 2000), and the marked increase in abundance of rock lobster since 1990 along the South-East Coast has caused concern that it may negatively impact the commercial abalone fishery in that region (Tarr *et al*. 1996, Mayfield and Branch 2000).

Laboratory studies have demonstrated that *J. lalandii* shows clear prey-size and prey-species preferences, consuming mostly small ribbed mussels *Aulacomya ater* and black mussels *Choromytilus meridionalis* (Pollock 1979, Griffiths and Seiderer 1980). Van Zyl *et al.* (1998) also demonstrated their preference for small winkles *Oxystele sinensis*.

Two separate laboratory experiments, carried out at different locations on the West Coast (Cape Town and Port Nolloth) and using different methods, investigated the feeding behaviour of *J. lalandii* on juvenile abalone in the presence or absence of sea urchins. The intention was to quantify the protection offered

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by sea urchins to abalone. However, the results differed markedly. At Port Nolloth, Scott (1997) showed that *J. lalandii* readily consumed juvenile abalone, but feeding on them ceased when sea urchins were offered as alternative prey. In contrast, at Cape Town (some 600 km south of Port Nolloth), Mayfield *et al.* (2001) showed that *J. lalandii* readily consumed sea urchins and juvenile abalone whether offered singly or in combination; in the latter case, juvenile abalone were preferred over sea urchins. This contrast in feeding behaviour could be a result of differences in experimental procedure or possibly locality. The presence of kelp *Ecklonia maxima* also appears to influence the activity patterns of juvenile abalone. Day and Branch (2002b) showed that, in aquaria, juvenile abalone were more likely to remain concealed beneath urchins if the latter had access to drift kelp. Similarly, De Beer (1998) found that *J. lalandii* consumed fewer juvenile abalone in the presence of kelp because they more frequently remained under urchins during these conditions.

This paper presents the results obtained by repeating similar feeding experiments at both Cape Town and Port Nolloth. Identical experimental protocols were used, and local rock lobsters were used in an attempt to resolve the conflicting conclusions of the previous experiments.

MATERIAL AND METHODS

At both sites, all experiments were conducted in parallel. Rock lobsters captured at both locations were used simultaneously, but held in separate tanks. The lobsters were held in flow-through aquarium tanks (615 × 325 × 335 mm) in a controlled environment (water temperature maintained at 13 ± 1°C) with a 12:12 h light:dark cycle.

Male rock lobsters of 65, 70, 75 and 80 mm carapace lengths (*CL*) were collected at each site using baited commercial traps to ensure that they were feeding at the time of capture and to prevent unnecessary damage to limbs. Experiments were first conducted at Port Nolloth and then repeated at Cape Town. To equalize the stress endured by the transported animals, rock lobsters collected from the area in which the experiment was conducted were simultaneously held on ice, as were the lobsters transferred between sites. After transportation, all animals were slowly released into holding tanks and allowed two days to acclimatize. Rock lobsters were fed *ad lib* on unnatural prey (sardine *Sardinops sagax*) to prevent any learning process affecting the results (Wright *et al.* 1990, Gosselin and Chia 1996).

Juvenile abalone of 10–15 mm shell length were obtained from abalone farms at Port Nolloth and Cape Town. The sea urchins were collected by hand. Large urchins (>40 mm test width) were chosen because rock lobsters >65 mm *CL* are able to consume sea urchins of this size (Mayfield and Branch 2000). Also, such sea urchins were large enough to offer protection to the juvenile abalone (Day and Branch 2000a, b).

Prior to each experiment, rock lobsters were transferred from the holding tanks to individual glass aquaria, where they were starved for two days and then offered an opened black mussel to confirm that they were feeding. They were then starved for 24 h to ensure complete clearance of the digestive tract and equal starvation levels (Zoutendyk 1988).

At each site, a lobster from each size-class was offered 10 sea urchins and five juvenile abalone. This procedure was repeated in tanks in which kelp fronds were added to determine whether their presence influenced feeding behaviour. Roughly equal amounts of kelp were used for all the kelp experiments. Abalone and sea urchin numbers were recorded and consumed prey were replaced daily, for three consecutive days. This experiment was repeated three times; in each case a different rock lobster was used.

An experimental tank containing 10 sea urchins and five juvenile abalone, but no rock lobster, was used as a control. None of the animals in the control escaped or died throughout the study period.

Statistical analysis

The average number of abalone and sea urchins consumed per day at each site by each size-class of rock lobster was determined in the presence (+k) and absence of kelp (–k). Analysis of variance (ANOVA) was performed on the data to assess differences in consumption between sites, between +k and –k treatments and between size-classes (Zar 1996). Differences between size-classes were not significant ($p > 0.25$) and the data for the four size-classes were therefore pooled for all subsequent analyses.

After pooling the data, the mean numbers of abalone and sea urchins consumed per day was calculated for each individual site for the following conditions: CT–k, CT+k, PN–k and PN+k (where CT = lobsters captured at Cape Town and PN = lobsters captured at Port Nolloth). ANOVA with fixed factors capture locality and kelp presence or absence was performed on these data to examine differences between abalone and sea urchin consumption for each group (Zar 1996).

Finally, ANOVA was done on the combined data from both sites to analyse the average overall consumption of abalone and sea urchins by rock lobsters in each of the four treatments.

RESULTS

For the Cape Town experiments, rock lobsters consumed between 2.5 and 3.5 abalone and 0 and 1.5 sea urchins per day (Fig. 1). There were no significant differences in abalone consumption between the different rock lobster groups (CT+k, CT–k, PN+k and PN–k; $F_{3,44} = 0.66$, $p > 0.05$). However, a multirange Newman-Keuls test revealed that Port Nolloth rock lobsters consumed significantly fewer sea urchins in the absence of kelp compared with the other three groups ($F_{3,44} = 5.22$, $p < 0.01$).

Considerably fewer prey were consumed by rock lobsters in the Port Nolloth experiments compared with those at Cape Town (Fig. 1), between 0.6 and 1.2 abalone and 0.1 and 0.8 sea urchins being consumed per day. There were no significant differences in abalone consumption between the rock lobster groups ($F_{3,44} = 0.82$, $p > 0.1$). Neither the CT-captured nor the PN-captured rock lobster revealed any significant differences in sea urchin consumption in the presence or absence of kelp ($p > 0.5$). However, a multiple range Newman-Keuls test revealed that all the PN animals (in the presence or absence of kelp) consumed significantly fewer sea urchins than the CT animals. ($F_{3,44} = 3.25$, $p < 0.05$).

Combining the data for both sites, PN- and CT-caught rock lobsters consumed similar numbers of abalone per day in the groups ($F_{3,92} = 0.09$, $p > 0.1$; Fig 1). Sea urchins consumption was about half of juvenile abalone. A multiple range Newman-Keuls test revealed that PN rock lobsters (with or without kelp) consumed significantly fewer sea urchins compared to the other groups. ($F_{3,92} = 6.94$, $p < 0.01$).

DISCUSSION

Several factors influence a predator's selection of prey. Only male rock lobsters were used in the present study to avoid sex as a possible bias. However, Mayfield *et al.* (2000) found no differences between the diets of male and female *J. lalandii*. Also, the experiments were conducted during the same phase of

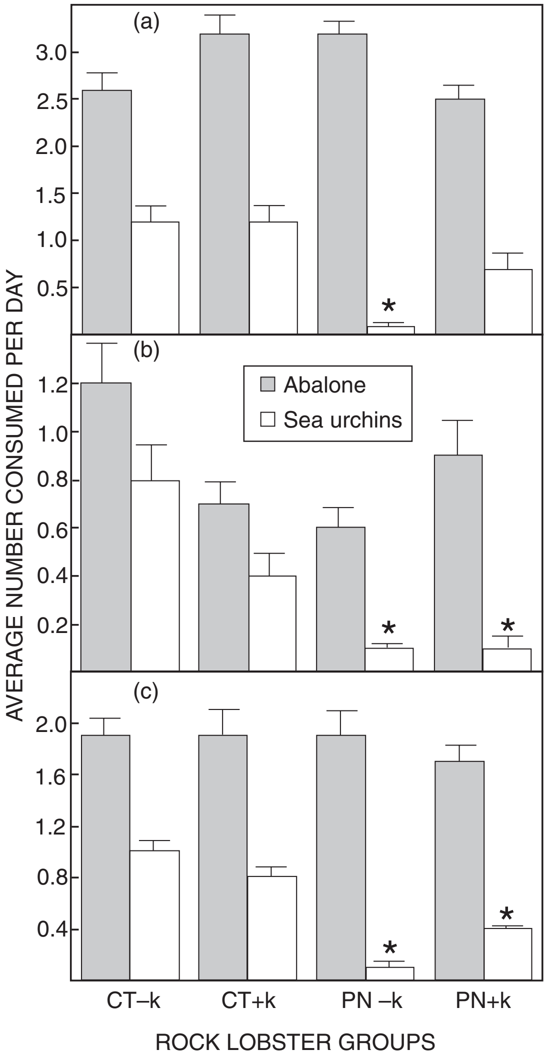

Fig. 1: Average numbers of juvenile abalone and sea urchins consumed per day by rock lobster in the experiments conducted in (a) Cape Town, (b) Port Nolloth and (c) both sites combined. Rock lobsters were captured at Cape Town (CT) or Port Nolloth (PN), and held with (+k) or without (–k) kelp. Error bars indicate one standard error. Note the differences in the scales on the y-axis. There were no significant differences between rates of consumption of abalone in any of the three sets of data. An asterisk above the bars indicates significantly lower rates of consumption of urchins than in other treatments

the moulting cycle, i.e. the reserve accumulation phase before moulting in October, to ensure that differences in moult phase did not influence prey choice (Mayfield 1998) or feeding rate (Cockcroft 1997).

Other factors affecting feeding behaviour include energy cost benefits (Brumner *et al.* 1992), considerations of long-term energy and mineral intake (Lankford and Targett 1997), risk (Hughes *et al.* 1995) and food quality (Irons *et al.* 1988, Chambers *et al.* 1991). Only cost benefits and long-term considerations should have influenced prey choice of the rock lobsters in this study, because food quality of each prey species was similar (by collecting all individuals of each prey species simultaneously and standardizing prey sizes). It is clear that abalone were the preferred prey over sea urchins, concurring with the findings of Mayfield *et al.* (2001). Juvenile abalone have a higher calorific value than sea urchins (Field *et al.* 1980, Mayfield *et al.* 2001), so rock lobsters enhance their gain per unit effort by feeding on abalone (Mayfield 1998).

All size-groups of rock lobster at both sites consumed sea urchins. This finding concurs with that of Mayfield (1998), but contrasts with the observations of Scott (1997), who found that, over a 30-day period, sea urchin were not eaten by rock lobster, even when they were the only prey available to them. The main difference between the experimental protocols used by Mayfield (1998) and Scott (1997) was the density of sea urchin.

Juvenile abalone appear to take both fewer and shorter foraging trips from underneath sea urchins when kelp is present (Day and Branch 2002b), probably because sea urchins provide a potential food source for the abalone by trapping kelp and other debris (Andrew and MacDiarmid 1991). However, the present experiments failed to demonstrate any reduction in abalone consumption by rock lobsters in the presence of kelp. They seemed to pursue juvenile abalone actively from underneath the sea urchins. This contrasts with the findings of De Beer (1998), who found fewer abalone consumed in the presence of kelp.

In the PN experiments, all PN-captured rock lobsters (in both PN–k and PN+k) consumed significantly fewer sea urchins than CT-caught rock lobsters ($p < 0.05$, Fig. 1). The only significant difference in average sea urchin consumption in the CT experiments was that the PN–k animals consumed fewer sea urchins (average 0.1± 0.04 per day) than the other treatments (average 1.0 ± 0.5 per day).

The average number of abalone consumed by all treatments combined (CT–k, CT+k, PN–k and PN+k) was significantly greater in the CT experiments than in the PN experiments. In the CT experiments, all treatments combined consumed more abalone per day than did the lobsters in the PN experiments. Conversely, the average sea urchin consumption in all these groups combined showed no significant differences between the CT and PN experiments. The higher abalone consumption in the CT experiments may be related to differences in sea urchin behaviour. In the PN experiments, the sea urchins were more mobile and aggregations more pronounced than the in CT experiments. This, combined with the fact that the PN sea urchins also crowded together in corners, could also have provided extra protection from predation for the abalone hiding underneath them, because the rock lobsters had to remove more sea urchins to get to the abalone. Juvenile abalone in both the PN and CT experiments seemed actively to choose clumps of sea urchins and were most often found underneath these clumps. Scott (1997) and Mayfield (1998) also observed such clumps of sea urchins. In the field, juvenile abalone also actively choose such clumps for protection (SM pers.obs), possibly for this very reason.

The PN-captured rock lobsters seemed to be less active than the CT-caught animals, which could have contributed to their lesser consumption of sea urchins at that site (and to their lesser consumption when the results were pooled for experiments at both sites). The cause of the lesser consumption of both abalone and sea urchins in the Port Nolloth experiments (involving both PN- and CT-caught rock lobsters) compared to those in the Cape Town experiments (also involving rock lobsters caught at both sites) remains unexplained.

At first glance, the present results appear to contradict the hypothesis that juvenile abalone gain protection under sea urchins (Tarr *et al.* 1996, Mayfield and Branch 2000, Day and Branch 2000b, 2002b). However, during the experiments, rock lobsters were given no choice of prey other than sea urchins and abalone. In their natural environment, rock lobsters have a much wider prey selection. The average ratio of juvenile abalone to sea urchins east of Cape Hangklip is about 1:20 (Mayfield 1998), so juvenile abalone there could protect themselves from predation by hiding under sea urchins. Mayfield (1998) found no juvenile abalone remains in the gut contents of wild-caught rock lobsters, but those in aquaria clearly have the ability to source and consume juvenile abalone. More important, mussels rank among the most preferred prey of rock lobsters (Pollock 1979, Griffiths and Seiderer 1980). In their absence, it is possible that juvenile abalone have to gain protection through concealment beneath the sea urchins.

In conclusion, although the results presented here seem to be rigorous, they do need to be viewed in the light that any laboratory experiment risks introducing artificial conditions, and the absence of alternative highly preferred prey such as mussels may, in particular, have influenced the results.

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