WHAT DETERMINES PREY SELECTION BY KELP GULLS *LARUS DOMINICANUS* IN MULTISPECIES MUSSEL COMMUNITIES?

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SUMMARY

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Predation of mussels by Kelp Gulls *Larus dominicanus* was studied in South Africa and southern Chile, with particular reference to the choice of prey species and sizes. At both sites one smooth-shelled and one ribbed mussel were present. In South Africa Kelp Gulls preyed on the two species in proportion to their relative abundance, whereas in Chile, one species comprised 98% of the diet but only 69% of the mussel population. Mussels eaten in Chile were much smaller than those eaten in South Africa. We suggest that the differences in predation strategy, which could not be predicted from Optimal Foraging Theory, reflect differences in prey dispersion.

INTRODUCTION

Many species of mussels (Mytilidae) settle in dense cohorts of uniform age, forming beds which blanket the substratum, and mortality of young mussels through predation normally is insignificant compared with mortality due to intraspecific competition for space during growth (Griffiths & Hockey 1987). The Kelp Gull *Larus dominicanus* is a widespread generalist predator of nearshore and intertidal regions that includes small mussels of several species within its prey spectrum (Bahamondes & Castilla 1986, Hockey & Bosman 1988). Mussels are torn from the beds either singly or in clumps and are swallowed whole; following digestion, the empty shells are regurgitated in pellets (Hockey & Bosman 1988).

This study compares predation by Kelp Gulls on two species of mussels in South Africa and on two different mussel species in Chile, and tests the hypothesis that prey choice is determined by physical attributes of the prey and relative prey abundance. We examine differences in prey selection at the two sites, and discuss hierarchies of prey selection by the gulls in relation to prey dispersion.

STUDY AREAS AND METHODS

Observations were made at Marcus Island (33 02S, 17 58E), South Africa, between 1979 and 1984, and 30 km south of Punta Arenas (53 09S, 70 55W), in the Magellan Straits, Chile, during November 1985. The mussels *Choromytilus meridionalis* and *Aulacomya ater* were present at Marcus Island, and to a large extent were separated vertically on the shore, with *A. ater* occurring at higher elevations. At Punta Arenas, a mixed bed of *Perumytilus purpuratus* and *Mytilus (edulis) chilensis* was studied. The study area at Marcus Island (1,5 km of granitic shore) was much more extensive than the Chilean site (58,3 m^2), which was an isolated rocky outcrop in sandy and pebbly beach. The relative abundance of the two mussel species at Marcus Island was calculated from abundance ratings made at 1 m intervals along 18 transects running from the high to low water marks. At Punta Arenas, three distinct sub-assemblages of mussels were recognized, and their distribution was mapped. Relative abundance of the two mussel species at Punta Arenas was calculated by extrapolation from subsamples of 100 to 200 cm^2 cleared within the three sub-assemblages in areas of 100% cover. Mussel length refers to maximum shell length (mm).

Selection of prey species and sizes by Kelp Gulls was determined from whole shells and complete single valves extracted from regurgitated pellets. Where single valves were extracted from an individual pellet, they were separated into left and right valves and only those in the more abundant class were measured.

RESULTS

At Marcus Island, *A. ater* occurred higher on the shore than did *C. meridionalis* and therefore was exposed for longer during each tidal cycle. Numerically, *C. meridionalis* was the more abundant species on the shore (75%). Both species were found in Kelp Gull pellets in similar proportions to their abundance on the shore (Table 1). At Punta Arenas, *M. chilensis* was the most abundant species (69% by numbers). However, this species accounted for nearly 98,4% of all mussel remains in gull pellets (Table 1).

At both sites, one species of mussel, *C. meridionalis* in South Africa and *M. chilensis* in Chile, was smooth-shelled; the other being ribbed and having a stronger shell. At both sites, the smooth-shelled species was more common both on the shore and in the diet of Kelp Gulls (Table 1).

At Marcus Island, both species of mussel grow too large for Kelp Gulls to swallow them (pers. obs.), but Kelp Gulls preyed on larger *C. meridionalis* than *A. ater* (Fig. 1). The maximum sizes swallowed by gulls were 40 mm for *A. ater* and 60 mm for *C. meridionalis* (Table 1, Fig. 1). At Punta Arenas, the largest mussels swallowed were only 20 mm, although mussels of up to 35 mm in length were present (Fig. 2). Predation on *M. chilensis* at Punta Arenas was confined to size classes in which *M. chilensis* made up more than 75% of all mussels present (Fig. 2). At Punta Arenas, 78% of all mussels were < 20 mm in length, and 80% of these were *M. chilensis*. *Mytilus chilensis* comprised only 33% of all mussels > 20 mm. Kelp Gulls therefore selected the more abundant, but smaller, species. Byssal growth of *P. purpuratus* is not as extensive as that of *A. ater* (pers. obs.). The forces required to remove *A. ater* of the mean and maximum sizes eaten by gulls from the substratum were calculated as 16 N and 34 N respectively. Corresponding values for mean and maximum sized *C. meridionalis* were 10 N and 26 N (Griffiths & Seiderer 1980).

DISCUSSION

At each site, two species of mussels were available as prey to Kelp Gulls; one smooth, thin-shelled species and one ribbed, thick-shelled species. At both sites, the thin-shelled mussel was the most abundant species both in the mussel community and in the diet of the gulls. Differences in the relative abundances of the mussel species between the two sites were small, yet at Marcus Island prey were taken in proportion to their abundance, whereas at Punta Arenas one species made up nearly the whole diet.

The bimodal size distributions of mussel species at Punta Arenas suggest that *P. purpuratus* is the faster-growing species which could withstand greater predatory pressure than *M. chilensis* by virtue of more intense intraspecific competition for space and hence higher natural mortality (Griffiths & Hockey 1987). The greater abundance of *M. chilensis* may reflect settlement patterns, but the selection for small individuals by gulls, in a situation where prey morphology cannot be considered as a limiting factor, is unexpected: at Marcus Island Kelp Gulls select larger mussels than at Punta Arenas. More effort is required to remove large mussels from the substratum (Griffiths & Seiderer 1980), but the energetic rewards of selecting larger mussels also are potentially greater because the ratios of flesh:shell mass and flesh:shell volume

TABLE 1

RELATIVE ABUNDANCE OF MUSSELS ON THE ROCKS AND IN GULL PELLETS, AND PREY SIZE SELECTION BY KELP GULLS AT MARCUS ISLAND AND PUNTA ARENAS

		Percentage frequency		n	Size selection by Kelp Gulls (mm)		
Site	Species	On rocks	In pellets	(in pellets)	Range	Mean	Median
Marcus Island	*C. meridionalis*	74,8	78,8	6 623	1 - 60	25	24
	A. ater	25,2	21,2	1 785	1 - 40	17	16
Punta Arenas	*M. chilensis*	69,0	98,4	183	1 - 20	12	12
	P. purpuratus	31,0	1,6	3	-	-	-

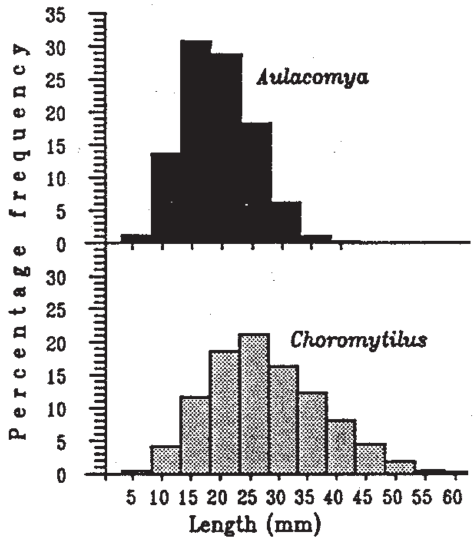

Figure 1

Sizes of *C. meridionalis* and *A. ater* recovered from Kelp Gull pellets at Marcus Island

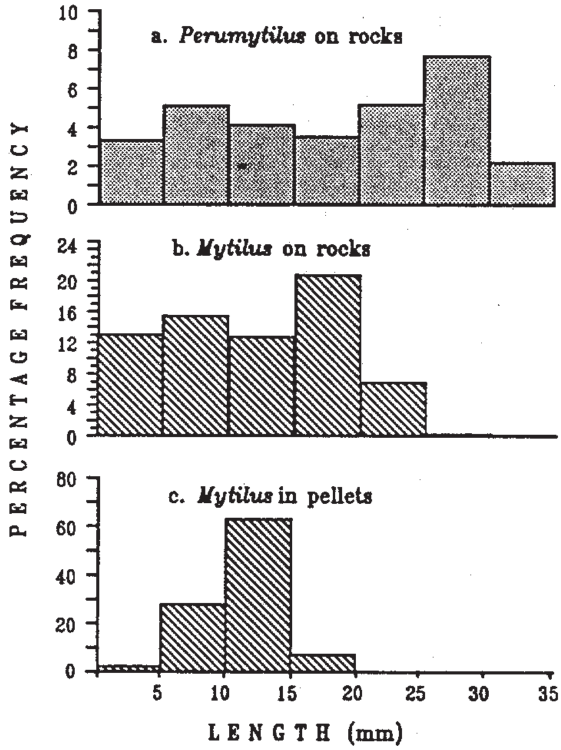

Figure 2

Size frequency distributions of (a) *Perumytilus purpuratus* and (b) *Mytilus chilensis* on rocks at Punta Arenas, Chile. Histograms reflect relative abundance by size classes (summed frequencies for the two species = 100%). (c) Size frequency distribution of *M. chilensis* in Kelp Gull pellets increase with increasing mussel size (Griffiths 1981). The much smaller Surfbird *Aphriza virgata* selects the smooth and weaker-shelled mussel *Semimytilus algosus* at sites where *S. algosus* and *P. purpuratus* are sympatric in southern Chile: this may be due to differences in shell strength (Navarro *et al.* in press). Surfbirds do not regurgitate pellets, and selection for *S. algosus* may reflect the relative ease with which shells of the two species can be crushed in the gizzard.

It appears that Kelp Gulls, presented with two sets of prey species of similar relative abundances and morphologies, have adopted different predation strategies in two geographically separate areas. At Marcus Island, the two mussel species largely are parapatric within the intertidal region: one grows higher on the shore than the other. At Punta Arenas, the mussel species occur in mixed beds. If Kelp Gulls capture both mussel species at similar rates at Marcus Island, gulls at this site divide their foraging activities in direct proportion to habitat availability. Once a decision as to where to forage has been taken, only the decision as to prey size selection remains. At Punta Arenas, on the other hand, a foraging gull presumably is faced with two decisions at each feeding attempt: which species to take and what sizes to select. The fact that both species of mussel are available at Punta Arenas in the size range preyed upon, but that only one species is taken, strongly suggests that initial selection is for the more abundant species and selection for size is secondary. The unexpected selection for small individuals of the most common mussel species probably is due to the birds selecting patches in which the ratio of *M. chilensis* to *P. purpuratus* is largest, corresponding to patches of densely packed, relatively small mussels.

Differences in patterns of prey selection by Kelp Gulls at these two sites serve to highlight the importance of prey dispersion (patchiness) in influencing prey choice by predators. Failure to consider this factor at even small spatial scales may lead to erroneous interpretations of Optimal Foraging Theory. The use of relative prey abundance *per se* is inadequate for predicting the responses of a predator.

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