Assessing western gull predation on purple sea urchins in the rocky intertidal using optimal foraging theory

C.L. Snellen, P.J. Hodum, and E. Fernández-Juricic

Abstract: Purple sea urchins (*Strongylocentrotus purpuratus* (Stimpson, 1857)) are abundant grazing invertebrates that can have a major impact on the rocky intertidal community. Predators can control the urchin population and indirectly reduce grazing activity. We determined the effects of western gull (*Larus occidentalis* Audubon, 1839) predation on purple sea urchins in the rocky intertidal using the framework of optimal foraging theory and taking into account different prey-handling techniques. We recorded the foraging behavior of gulls, measured urchin availability, and estimated prey caloric content with bomb calorimetry. Western gulls selected purple sea urchins significantly more than other prey items (snails (genus *Tegula* Lesson, 1835), limpets (genus *Collisella* Dall, 1871), sea stars (*Pisaster giganteus* (Stimpson, 1857) and *Pisaster ochraceus* (Brandt, 1835))). Larger urchins contained relatively more calories. Gulls foraged optimally when pecking by frequently selecting the most profitable size class. However, gulls chose smaller urchins than expected when air-dropping, which could have been influenced by group size and age. Gulls selected smaller purple sea urchins when foraging in larger groups likely owing to the risk of kleptoparasitism. Adults chose larger, and juveniles smaller, urchins when air-dropping, suggesting that juveniles are less experienced in foraging techniques. We estimated that gull predation could affect up to one third of the sea urchin populations locally, which could increase species diversity in the rocky intertidal community.

Résumé : Les oursins de mer violets (*Strongylocentrotus purpuratus* (Stimpson, 1857)) sont des invertébrés brouteurs abondants qui peuvent avoir un impact majeur sur la communauté de la zone intertidale rocheuse. Les prédateurs peuvent contrôler la population d’oursins et ainsi réduire indirectement l’activité de broutement. Nous avons déterminé les effets de la prédation par les goélands d’Audubon (*Larus occidentalis* Audubon, 1839) sur les oursins violets de la zone intertidale rocheuse dans le cadre de la théorie de la quête optimale et en tenant compte des différentes techniques de manipulation des proies. Nous avons noté le comportement de recherche de nourriture des goélands, mesuré la disponibilité des oursins et estimé le contenu calorique des proies à l’aide d’une bombe calorimétrique. Les goélands d’Audubon choisissent significativement plus d’oursins violets que d’autres proies (gastéropodes (genre *Tegula* Lesson, 1835), patelles (genre *Collisella* Dall, 1871) et étoiles de mer (*Pisaster giganteus* (Stimpson, 1857) and *Pisaster ochraceus* (Brandt, 1835))). Les oursins plus grands contiennent relativement plus de calories. Lorsqu’ils picorent, les goélands se nourrissent de façon optimale par la sélection fréquente de proies de la classe de taille la plus avantageuse. Cependant, lorsqu’ils laissent tomber leurs proies en vol, les goélands choisissent des oursins plus petits que prévu, ce qui peut être dû à l’influence de la taille et de l’âge du groupe. Lorsqu’ils se nourrissent en groupes plus grands, les goélands sélectionnent des oursins violets plus petits, vraisemblablement à cause du risque de cleptoparasitisme. Lorsqu’ils laissent tomber leurs proies de l’air, les adultes choisissent des oursins plus grands et les jeunes des oursins plus petits, ce qui laisse croire que les jeunes ont moins d’expérience des techniques alimentaires. Nous estimons que la prédation par les goélands peut affecter jusqu’à un tiers des populations locales d’oursins de mer, ce qui pourrait faire augmenter la diversité spécifique dans la communauté intertidale rocheuse.

[Traduit par la Rédaction]

Introduction

The rocky intertidal is characterized by a high diversity of invertebrate species and algae. One common inhabitant is the purple sea urchin (*Strongylocentrotus purpuratus* (Stimpson, 1857)), an herbivorous grazer that can modify benthic communities by removing algal assemblages (Sala et al. 1998). Purple sea urchins may also prevent the establishment and population growth of subordinate invertebrate species (Vance 1979; Marsh 1986). Some predators can reduce the density of urchins and thus enhance community diversity. In subtidal kelp forests, predation of sea urchins by sea otters (*Enhydra lutris* (L., 1758)) (Irons et al. 1986; Estes and Duggins 1995; Reisewitz et al. 2006), sheephead (*Semicossyphus pulcher* (Ayres, 1854)), and spiny lobsters (*Panulirus interruptus* (J.W. Randall, 1840)) (Tegner and Dayton 1981; Tegner and Levin 1983; Tegner 2001) has been well documented; however, relatively little is known about predation on intertidal purple sea urchins.

Gulls of the genus *Larus* L., 1758 have been identified as

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predators on various urchin species (Irons et al. 1986; Hori and Noda 2001), and there has been recent anecdotal evidence of western gull (*Larus occidentalis* (Audubon 1839)) predation on purple sea urchins in rocky intertidal areas (S. Lawrenz-Miller, personal communication (2003)). The goal of this study was to establish how this generalist predator forages on purple sea urchins, considering the effects of handling technique, age, and group size. We used the framework of optimal foraging theory, as it provides insights into the mechanisms behind predator–prey interactions (Schmidt 1999). Understanding the behavioral decision making of gulls at local scales (i.e., rocky intertidal) could allow us to later build models that can predict the effects of gull predation on the population structure of purple sea urchins in the rocky intertidal.

According to optimal foraging theory (Charnov 1976; Stephens and Krebs 1986), organisms are expected to maximize net energy gain or profitability, thereby increasing the probability of survival and production of offspring (van der Steen 1999), which can influence fitness (Schoener 1987; Pierotti and Annett 1991). Several laboratory and field studies have found that generalist foragers behave in an optimal manner by choosing the most profitable prey items (Irons et al. 1986; Campbell 1987; Pierotti and Annett 1987; Norris and Johnstone 1998; Berec et al. 2003). Generalist species that opportunistically specialize on a single prey item, such as northwestern crows (*Corvus caurinus* Baird, 1858) (Zach 1978; Richardson and Verbeek 1986) and kelp gulls (*Larus dominicanus* Lichtenstein, 1823) (Ward 1991), are expected to select the largest individuals, which would have a higher caloric content than smaller individuals.

Several factors, including handling technique, age of the forager, and kleptoparasitism (food theft among conspecifics, Brockmann and Barnard 1979), can affect foraging efficiency. The use of different handling techniques (e.g., flying and walking in starlings (*Sturnus vulgaris* L., 1758) (Bautista et al. 1998), hammering and stabbing in oystercatchers (*Haematopus ostralegus* L., 1758) (Norris and Johnstone 1998)) affects both the size of the selected prey item and the handling time (Irons et al. 1986; Nilsson and Brönmark 1999; Smallegange and van der Meer 2003), resulting in differences in net energy gain and overall foraging efficiency (Wanink and Zwarts 2001). Regarding age effects, juveniles are generally less efficient in several aspects of their foraging behavior (Ingolfsson and Estrella 1978; Burger 1987; O'Brien et al. 2005) and tend to select less profitable prey (Richardson and Verbeek 1987; Toft and Wise 1999). Thus, juveniles may experience higher foraging costs, which could negatively affect their survival (Newton 1998), although as they gain experience, they can learn complex handling techniques over time (Richardson and Verbeek 1987; Wunderle 1991). Finally, when animals forage in single-species groups, the risk of kleptoparasitism may increase (Giraldeau and Caraco 2000; Krause and Ruxton 2002). To reduce food loss to conspecifics, individuals may modify their foraging strategies (Maron 1982; Steele and Hockey 1995; Nilsson and Brönmark 1999; Ha and Ha 2003); however, this could result in suboptimal foraging and decreased net energy gain (Barash et al. 1975; Maron 1982; Nilsson and Brönmark 1999).

We were interested in five specific aspects of the foraging behavior of western gulls. First, we determined whether western gulls exhibited a preference for purple sea urchins. We predicted that western gulls would select proportionally more purple sea urchins than other common prey items (sea stars (*Pisaster giganteus* (Stimpson, 1857) and *Pisaster ochraceus* (Brandt, 1835)), snails (genus *Tegula* Lesson, 1835), and limpets (genus *Collisella* Dall, 1871)) because of the relatively higher purple sea urchin energetic content (Irons et al. 1986; Pierotti and Annett 1987; Ward 1991). Second, we characterized the energy content of purple sea urchins relative to urchin test size to predict prey caloric content in the field. We expected large purple sea urchins to have higher caloric content than smaller ones (Zach 1979; Caraco et al. 1980) because of an increase in gonadal content (Lawrence 1987), which is a major source of calories (González et al. 2001). Third, we established profitability of purple sea urchins (following Irons et al. 1986; Richardson and Verbeek 1986; Ward 1991; Norris and Johnstone 1998; Wanink and Zwarts 2001) to determine whether western gulls were foraging optimally with two different handling techniques: pecking and air-dropping. We predicted that western gulls would forage optimally when air-dropping, since gulls frequently select larger prey items and handle them for a shorter amount of time with this technique (Barash et al. 1975; Maron 1982). Fourth, we determined the role of group size on prey size selection. The air-dropping technique is expected to increase the risk of kleptoparasitism, since western gulls are not in contact with the prey during air-drops, providing opportunities for conspecifics to steal the prey (Maron 1982). We predicted that western gulls would select smaller urchins and reduce drop height when using the air-dropping technique to minimize the effects of kleptoparasitism. Fifth, we assessed the role of western gull age in prey selection. We predicted that adults using the air-dropping technique would choose larger purple sea urchin sizes than juveniles owing to differences in experience (Irons et al. 1986; Richardson and Verbeek 1986; Burger 1987; O'Brien et al. 2005).

Materials and methods

Study site

Data were collected at Wilder Annex, a rocky intertidal area located along the coast of southern California on the Palos Verdes Peninsula (33°42′50.94″N, 118°18′59.11″W). This location was selected based on the high abundance of both western gulls and purple sea urchins and also because it is one of the few areas in southern California where western gulls actively consume purple sea urchins. The study site extended from the high tide zone to the subtidal and was 500 m in length. Data were collected during the 2004–2005 (September–March) and 2005–2006 (September–November) nonbreeding seasons of western gulls. Sampling was restricted to the nonbreeding period to minimize possible changes in foraging behavior (diet switching and increased foraging effort) associated with provisioning offspring feeding (Annett and Pierotti 1989; Monaghan et al. 1989). The study site was generally visited when maximum low tide occurred during daylight hours (following Irons et al. 1986; Bertellotti and Yorio 1999).

Caloric content of prey

After preliminary observations, which consisted of sampling invertebrates with quadrat sampling (same methods as described below), we established that the most common prey items in the study area were purple sea urchins, snails, limpets, and sea stars. Sea stars were selected by western gulls only once during this study, so we did not include them in the prey caloric content analysis owing to logistic constraints. However, we did include sea stars in the prey selection analysis because they were present across the study area during this study.

We used bomb calorimetry to determine caloric content of 39 purple sea urchins, 21 snails, and 20 limpets collected on site. We determined the size of purple sea urchins by measuring test diameter and that of snails and limpets by measuring shell length. We estimated the caloric content (kcal) of the internal contents for individual purple sea urchins larger than 30 mm in diameter. However, owing to the extremely low mass (i.e., dry mass) of smaller purple sea urchins (<30 mm) and of snails and limpets (all <26 mm), dried internal contents were individually weighed and then combined for analysis, which is a common procedure to establish caloric content of very small items (M. Edwards, personal communication (2006)). We calculated caloric content (kcal) of large and small individuals by multiplying the dry mass (g) of the individual by the estimated kcal/g value.

Immediately after (1–2 h) collection in the field, urchins were maintained in recirculating seawater aquaria in the California State University, Long Beach, Marine Laboratory. Wet masses were later measured in the Marine Laboratory using an electronic scale (0.01 g). Once the samples were freeze-dried, we measured dry masses using an electronic scale at the Smithsonian Institution National Zoological Park Department of Conservation Biology, Nutrition Laboratory, in Washington, D.C., where bomb calorimetry procedures were conducted. Some sample dry mass values were lost. We used a general linear model (linear regression, n = 17 urchins) to characterize the relationship between the dry mass and the wet mass of urchins. There was a significant and strong relationship between dry and wet mass of purple sea urchins ($F_{[1,16]} = 174.78$, $P < 0.001$, $R^2 = 0.916$), and the model generated an equation ($\log_{10}$ dry mass = –0.448 + 0.724 $\log_{10}$ wet mass) that was used to determine the missing dry masses using the corresponding known purple sea urchin wet masses.

Field observations

During the 2004–2005 season, we recorded the behavior of western gulls through visual observations. In the 2005–2006 season, we used a Sony digital video camera recorder (DCRTRV38) to increase the rate of data acquisition. We recorded foraging western gulls using instantaneous scans and focal observations (see below) to characterize the foraging behavior of western gulls, including prey-handling techniques. From these observations, we identified three prey-handling techniques: pecking, air-dropping, and swallowing intact prey. With the pecking technique, western gulls jabbed at the peristomal membrane of the urchin, dislodging the Aristotle's lantern, and pecked out the soft tissue with the bill. When air-dropping, western gulls dropped the prey over a hard substrate to fracture the urchin test and expose the soft tissue. Gulls also swallowed intact prey, a common handling technique among *Larus* gulls (see Irons et al. 1986). However, this technique was omitted from the present analyses owing to the low number of observations recorded (n = 2).

We determined the availability of western gull prey items by counting the number of purple sea urchins, snails, limpets, and sea stars in 0.25 m^2 quadrats placed randomly along two 50 m transects running parallel to the waterline 10 m apart in the low intertidal zone (where all foraging activity took place). Based on preliminary observations of western gull foraging behavior in the area, on a given quadrat, we sampled for prey that would be accessible to gulls directly. We also counted prey in accessible crevices or slightly hidden under small rocks, as gulls had been observed handling such individuals. However, we did not count prey individuals hidden in crevices that were too small (i.e., <6 mm) to be accessed by the gull's beak or below heavy rocks that the gulls would not be able to displace. Final values were expressed as numbers of individuals per square metre. Prey density measurements were used to determine prey preferences (see below). In addition, test diameter of purple sea urchins, which is an indicator of urchin size, was measured to the nearest 0.1 mm using calipers during density measurements. Test diameter was used to determine size class availability for optimal foraging calculations (see below). Because the spatial distribution of differently sized prey items could affect the availability of prey, we used the standardized Morisita index (I_p) (see details in Krebs 1999) to assess the distribution of purple sea urchins that were classified into three size classes: small (<30 mm), medium-sized (30–50 mm), and large (>50 mm).

To determine prey selection frequency of purple sea urchins, sea stars, snails, and limpets, we conducted instantaneous scans of western gulls for a period of 15 min. These 15 min scanning periods were repeated four times during the course of each 2 h visits to the study site. The number of times each prey item was chosen by gulls was used to determine selection frequency.

To quantify foraging behavior on purple sea urchins, we conducted a total of 171 focal observations on haphazardly selected foraging western gulls until (*i*) the subject consumed a purple sea urchin (i.e., one foraging event), (*ii*) the subject left the intertidal area, or (*iii*) the observation time exceeded 15 min. Irons et al. (1986) found that the pecking technique used by glaucous-winged gulls (*Larus glaucescens* Naumann, 1840) took longer (310 s) than air-dropping or swallowing intact prey. To be conservative, we chose 15 min (900 s) as the length of time to observe one foraging event, regardless of technique. These focal observations were repeated four times on different focal individuals during the course of each visit to the study site. During these focal observations, we recorded handling technique (pecking, air-dropping), handling time (seconds), age of the foraging gull, the number of conspecifics present, and if kleptoparasitism occurred. In addition, we recorded drop height if the focal gull used the air-dropping technique during the foraging event. Drop height was measured indirectly using drop time, the time for a purple sea urchin to fall to the ground after being dropped (following Maron 1982), with a stopwatch to the nearest 0.01 s. Drop time, t, was converted to height, d, using the formula $d = 1/2at^2$, where a is the acceleration that is due to gravity (9.8 m/s^2). When measuring drop height, we included in the analysis only the first drop and omitted cases in which the focal birds were chased by conspecifics because of the higher risk of kleptoparasitism (following Maron 1982).

Individuals that had the white and grey adult plumage typical of western gulls were considered adults (Sibley 2003). Gulls that exhibited at least some aspect of the brown juvenile plumage, including individuals in their third winter, were classified as juveniles. We counted the number of conspecific western gulls located within a 3 m radius around the focal individual. We then categorized group size as one gull (solitary), two gulls, and three or more gulls. This categorization was based on the frequency distribution of observed group sizes.

A successful foraging event was defined as the complete consumption of the selected purple sea urchin. When the air-dropping technique was used, we considered the foraging attempt successful when the western gull broke open the purple sea urchin test on the first drop and consumed it. If more than one drop was used, we recorded the foraging event as a failure (following Maron 1982) because (*i*) gulls may alter their foraging behavior during subsequent drops based on information gained from the previous drop and (*ii*) subsequent drops may also attract conspecifics, causing gulls to further alter dropping behavior. We did not include failure events in the analyses.

We did not individually mark western gulls in the study area owing to logistic constraints. To minimize the possibility of an individual being recorded more than once on a given sampling session, we used (*i*) natural marks (color variations, injuries, and differences in body shape), (*ii*) leg bands of previously tagged individuals (n = 6 or 3.5% of observed individuals), and (*iii*) focal individuals that were separated by at least 10 m. In addition, several western gulls were present at the study site, which reduced the chances of repeated observations on the same individual.

At the conclusion of focal observations, we collected and measured the discarded purple sea urchin tests to determine the actual size of the urchin selected during each foraging event. We established size classes in 5 mm increments, with the smallest size class beginning at 5 mm and the largest size class ending at 70 mm (size range of urchins selected by gulls: 26.8–69.2 mm). Some optimal foraging studies employ a continuous range of prey sizes to determine size selection (Elner and Hughes 1978; Irons et al. 1986). Our sample sizes (pecking: n = 92, air-dropping: n = 22) after the 2-year field study only allowed us to use 5 mm increments based on the prey size range (following Smallegange and van der Meer 2003). We determined the number of times urchins from each size class were selected to calculate selection frequency for each handling technique separately. Size class selection frequency was calculated as the number of urchins selected from a size class divided by the total number of urchins selected overall and for each handling technique (Table 1).

Optimal foraging

Using the test size measurements of purple sea urchins (see prey density measurements), we determined size class availability (λ), which was calculated as the number of purple sea urchins within a size class divided by the total number of urchins measured across all size classes (Donovan and Welden 2002) (Table 1). We then calculated profitability (R) using the formula

$$[1] \qquad R = \frac{E}{T_\mathrm{h}}$$

where E is the caloric content (kcal) of the prey item and T_h is time (s) spent handling the prey item (Charnov 1976; Lendrem 1986; Donovan and Welden 2002). We first determined the caloric content of each selected purple sea urchin using the predictive regression equation describing the relationship between urchin size and caloric content. We then used the recorded handling time for the selected purple sea urchin to calculate the profitability of each urchin (kcal/s) and later established profitability for each purple sea urchin size class by averaging these values for each handling technique. Western gulls never selected purple sea urchins <30 mm, so profitability for size classes <30 mm could not be calculated.

We visually compared the size class profitability with the frequency of selected purple sea urchin size classes for each handling technique (following Elner and Hughes 1978; Richardson and Verbeek 1987; Smallegange and van der Meer 2003). If animals are indeed selecting the most profitable prey size class, it can be concluded that they forage optimally on a particular prey item (see Stephens and Krebs 1986).

Table 1. Selection of purple sea urchin (*Strongylocentrotus purpuratus*) size classes (5 mm increments) in the rocky intertidal at Wilder Annex.

Size class (mm)	No. of urchins selected for pecking technique	No. of urchins selected for airdropping technique
5–10	0	0
10–15	0	0
15–20	0	0
20–25	0	0
25–30	3	0
30–35	3	0
35–40	7	1
40–45	20	5
45–50	22	6
50–55	26	3
55–60	11	4
60–65	0	1
65–70	0	2

Note: Number of purple sea urchins selected for each technique represents sample size for profitability calculations of each size class (Fig. 2). The total number of urchins selected was 114. Western gulls (*Larus occidentalis*) often used the pecking technique while foraging on purple sea urchins, which explains the difference in sample sizes between techniques.

Statistical analysis

We first established whether there were seasonal effects in our data by using general linear models for continuous variables (urchin size, handling time, drop height) and χ^2 tests of homogeneity for frequency variables (prey item selection, group size).

A general linear model was used to determine variation in caloric content in relation to prey item (purple sea urchin, snail, limpet). Planned comparisons were used to determine differences between levels of prey item caloric content.

We used general linear models (linear regression design) to assess the following relationships: (*i*) dry mass, as a measure of gonadal volume, and purple sea urchin test size and (*ii*) caloric content and purple sea urchin test size. Sample size for each of these relationships was 39 purple sea urchins.

A log-likelihood test was used to determine if the sample proportion of chosen prey items (i.e., prey selection frequency) was significantly different from the sample proportion of the four available prey items using the following statistic:

$$[2] \qquad \chi^2_{\mathrm{L}} = 2\sum_{i=1}^{I}\left[u_i \log_{\mathrm{e}}\left\{\frac{u_i}{E(u_i)}\right\} + m_i \log_{\mathrm{e}}\left\{\frac{m_i}{E(m_i)}\right\}\right]$$

where u_i is the number of chosen prey items and m_i is the number of available prey items for prey categories 1 to I (Manly et al. 2002). Additionally, $E(u_i) = (m_i + u_i) u_{\mathrm{total}} / (u_{\mathrm{total}} + m_{\mathrm{total}})$ is the expected value of u_i and $E(m_i) = (m_i + u_i) m_{\mathrm{total}} / (u_{\mathrm{total}} + m_{\mathrm{total}})$ is the expected value of m_i on the hypothesis of no selection (Manly et al. 2002). A selection ratio of 1 indicates that a prey item is being selected in proportion to availability. The confidence interval around a selection ratio, constructed using Bonferroni's inequality, determines whether selection of a prey item is either more or less in proportion to availability (Manly et al. 2002). If the lower limit of the confidence interval for a particular prey item is above 1, the prey is selected. If the upper limit of the confidence interval is below 1, the prey item is avoided (Manly et al. 2002). Furthermore, if the confidence interval for the difference between selection ratios does not overlap zero, the selection ratios are considered significantly different (Manly et al. 2002). The validity of the confidence intervals around the selection ratios depends on the assumption that the sample proportions are normally distributed (Manly et al. 2002). A reasonable requirement to ensure normal distribution is that the number of both chosen and available prey items should be five or more for each prey category (Manly et al. 2002). Thus, purple sea urchins (n = 237) were compared with all other prey items combined (n = 18; 1 sea star, 14 snails, 3 limpets) owing to the low number of prey items in each category.

We assessed whether there was a difference in handling time between the two handling techniques (pecking, air-dropping) with a general linear model. We included purple sea urchin size as a covariate to control for its potential confounding effect on handling time. Additionally, we used general linear models to assess the relationship between urchin size and handling time for each of the two handling techniques.

One of the assumptions of our study is that the probability of kleptoparasitism is affected by group size. We tested this assumption with a generalized linear model, controlling for the potential confounding effects of purple sea urchin size. As kleptoparasitic incidents never occurred when the focal western gull was foraging alone, we only included group sizes of two gulls and three or more gulls (see above) in the analysis. We then used a general linear model to establish how western gulls modified purple sea urchin size selection relative to both group size (solitary, two gulls, three or more gulls) and handling technique (pecking, air-dropping). Finally, we assessed the effects of group size (solitary, two gulls, three or more gulls) on drop height, controlling for purple sea urchin size, with a general linear model. Planned comparisons were used in the last two analyses to determine differences between levels of group size.

We assessed the effects of age (juvenile, adult) and handling technique (pecking, air-dropping) on the size of the purple sea urchins selected by western gulls with a general linear model. Planned comparisons were used to determine differences between levels of age and handling technique. We did not analyze the effects of both group size and age in the same analysis because of the low sample sizes of combinations between these two factors.

Some variables were $\log_{10}$-transformed to meet normality assumptions: caloric content, test size, dry mass, and drop height. All statistical analyses were conducted with a 0.05 level of significance (α). We report results as mean ± SE throughout.

Results

A total of 255 foraging events were first used to determine prey selection frequency and subsequent prey type preference. Optimal foraging on purple sea urchins was tested using a total of 164 foraging events. Measurements of urchin test size were feasible in 117 of foraging events. However, three events involved tests so fragmented that they could not be used in the analysis. Drop height was recorded for 44 urchin foraging events in which urchins were air-dropped. Gull foraging group size during this study ranged from one to five gulls. A total of 45.33 ± 4.27 gulls were present at the study site during each sampling day, with 9.53 ± 1.80 individuals selected for focal observations.

Seasonal differences

There was no significant difference in size of selected purple sea urchins between the first and second seasons ($F_{[1,169]}$ = 1.94, P = 0.166; 2004–2005 season: 49.3 ± 0.93 mm, 2005–2006 season: 47.6 ± 0.67 mm). Additionally, there was no significant difference in handling time between seasons ($F_{[1,112]}$ = 0.77, P = 0.382; 2004–2005 season: 310.12 ± 39.90 s, 2005–2006 season: 278.20 ± 13.19 s). No significant differences were detected in drop height between seasons ($\log_{10}$ drop height, $F_{[1,52]}$ = 0.001, P = 0.970; 2004–2005 season: 7.91 ± 1.13 m, 2005–2006 season: 7.85 ± 1.11 m). Frequency of prey item selection was not different between the two seasons ($\chi^2_{[1]}$ = 2.48, P = 0.115) as was group size ($\chi^2_{[2]}$ = 3.36, P = 0.186). Owing to the lack of statistical differences, we pooled the data from both years.

Prey caloric content

Caloric content differed significantly among prey items (urchins: 9.76 ± 1.55 kcal, snails: 0.62 ± 0.08 kcal, limpets: 0.43 ± 0.08 kcal; $F_{[2,78]}$ = 124.32, P < 0.001). Furthermore, using planned comparisons, we found that purple sea urchin caloric content was significantly higher than for both snails and limpets combined ($F_{[2,59]}$ = 124.32, P < 0.001).

There was a significant positive relationship between purple sea urchin size and caloric content ($F_{[1,38]} = 920.99$, $P < 0.001$; $\log_{10}$ caloric content = –4.204 + 3.082 $\log_{10}$ urchin size) (Fig. 1*a*), with the model accounting for 96% of the variability. We also found a significant positive relationship between purple sea urchin size and dry mass ($F_{[1,37]} = 97.29$, $P < 0.001$, $R^2 = 0.724$; $\log_{10}$ dry mass = –5.170 + 3.783 $\log_{10}$ urchin size) (Fig. 1*b*). Overall, larger sea urchins had greater dry mass and higher caloric content.

Foraging choices

Western gulls selected purple sea urchins during 92.9% of foraging choices as opposed to limpets (5.5%), snails (1.2%), and sea stars (0.4%). The proportion of chosen prey items was significantly different from the proportion of available prey ($\chi^2_{[1]} = 230.66$, $P < 0.001$). Western gulls significantly avoided sea stars, snails, and limpets relative to their availability, as the upper limit of the confidence interval was <1 (Table 2). Moreover, western gulls significantly selected purple sea urchins in relation to their availability, as the lower limit of the confidence interval was >1. The confidence interval for the difference between the selection ratios for purple sea urchins and other prey items did not overlap zero (1.69 ± 0.15), indicating that the ratios were significantly different.

Spatial distribution of purple sea urchins

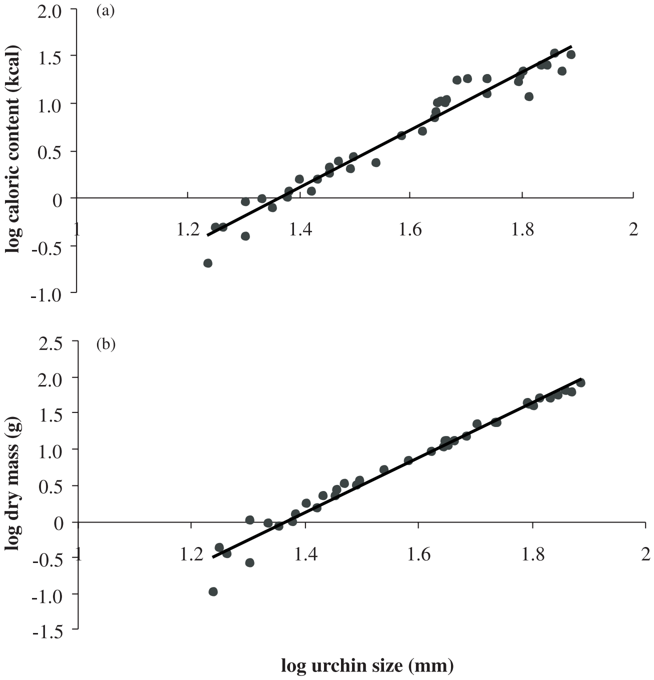
We found that the Morisita index for each of the three purple sea urchin size classes (small (<30 mm), medium (30–50 mm), and large (>50 mm)) was positive and higher than 0.5 ($I_{\mathrm{p(small)}} = 0.520$, $I_{\mathrm{p(medium)}} = 0.534$, $I_{\mathrm{p(large)}} = 0.529$), which is the 95% confidence interval around the zero value that corresponds to a random distribution (Krebs 1999). Thus, the three sea urchin size classes were distributed in a clumped fashion. Furthermore, taking into account the quadrats in which sea urchins were found, we did not find any significant relationship between average test size per quadrat and number of individuals per quadrat (linear regression, $F_{[1,15]} = 0.26$, $P < 0.619$).

Profitability and optimal foraging

Optimal foraging was determined by visually comparing two distinct but important aspects of foraging: the most profitable size class and the most frequently selected size class. We found that the size classes of the most profitable urchins, as defined by kcal/s, varied by handling technique (Fig. 2). The most profitable size class for pecked purple sea urchins included individuals in the 50–55 mm size category; these urchins contained 0.051 kcal/s. The most profitable size class for air-dropped purple sea urchins included larger individuals in the 60–65 mm category, which contained 0.113 kcal/s. The low number of samples and the high variability in handling times for the air-dropping technique likely influenced its high degree of variability in profitability (Fig. 2*b*; Table 2).

Foraging western gulls frequently selected the most profitable purple sea urchins (50–55 mm) when pecking (Fig. 2*a*), which indicated that western gulls foraged optimally with this technique. However, when air-dropping, they often selected purple sea urchins that were smaller (45–50 mm) than the most profitable ones (60–65 mm) (Fig. 2*b*). Purple sea urchins ranging from 25 to 35 mm were pecked open, but never air-dropped, and prey items <25 mm were never selected (Fig. 2). When large purple sea urchins (>60 mm) were selected, western gulls always used the air-dropping technique (Fig. 2).

Fig. 1. Relationships between (*a*) size and caloric content and (*b*) size and dry mass of purple sea urchins (*Strongylocentrotus purpuratus*) in the rocky intertidal at Wilder Annex. All data were normalized with a $\log_{10}$-transformation.



There was no significant relationship between purple sea urchin size and handling time for either technique (pecking: $F_{[1,91]} = 1.97$, $P = 0.16$; air-dropping: $F_{[1,20]} = 0.17$, $P = 0.68$). Visual inspection of the data failed to indicate the presence of any linear or nonlinear relationship.

However, handling time was significantly different between the pecking and air-dropping techniques ($F_{[1,112]} = 25.45$, $P < 0.001$), controlling for purple sea urchin size ($F_{[1,112]} = 1.31$, $P = 0.25$). It took longer to peck open a purple sea urchin than to air-drop it (pecking: 307.97 ± 13.64 s, air-dropping: 162.98 ± 18.81 s).

Group size effects

Both group size and handling technique had a significant effect on the probability of kleptoparasitism (Fig. 3). Kleptoparasitism was more likely to occur in larger foraging groups ($W_1 = 6.73$, $P = 0.009$) and when the western gull used the air-dropping technique ($W_1 = 6.26$, $P = 0.012$). However, there was no interaction between group size and foraging technique ($W_1 = 1.98$, $P = 0.159$) after controlling for purple sea urchin size ($W_1 = 1.06$, $P = 0.302$).

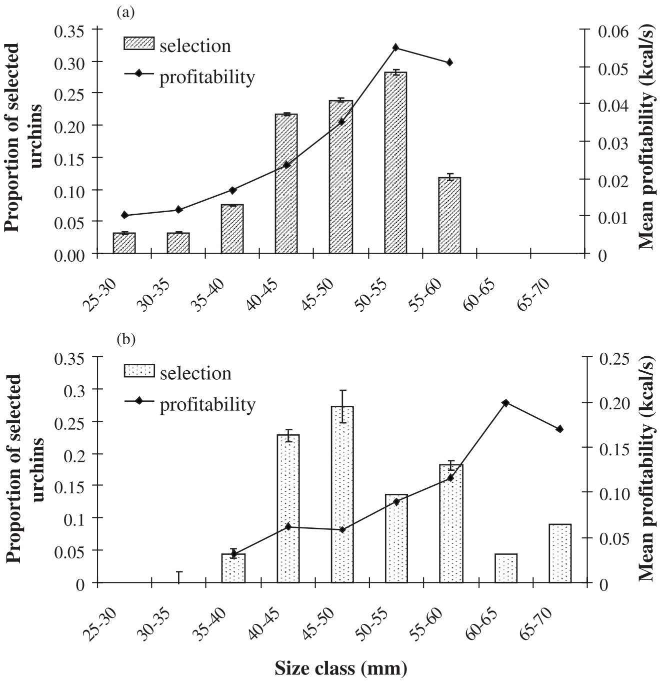
Group size significantly influenced purple sea urchin size selection ($F_{[2,108]} = 3.28$, $P = 0.042$). As group size increased, western gulls selected smaller purple sea urchins (solitary: 48.88 ± 1.29 mm, two gulls: 48.80 ± 1.00 mm, three or more gulls: 45.14 ± 1.35 mm). We found that western gulls selected significantly smaller urchins when foraging in large groups (three or more gulls) in relation to

Table 2. Estimated selection indices for prey items available to western gulls foraging in the rocky intertidal at Wilder Annex.

								Confidence interval	
Prey item category	m_i	π_i	u_i	o_i	ω_i	β_i	SE(ω_i)	Lower	Upper
Purple sea urchins	21.42	0.506	237	0.929	1.836	0.928	0.280	1.28595	2.38532
Other	20.89	0.494	18	0.071	0.143	0.072	0.044	0.05781	0.22816
Total	42.31	1.000	255	1.000	1.979	1.000			

Note: m and u represent available and used units, respectively, while π and o represent the corresponding proportions. The selection ratio and standardized selection ratio are represented by ω and β. SE(ω), the standard error of the selection ratio, was used to calculate confidence limits (Manly et al. 2002). The confidence intervals for each selection ratio have a confidence level (100 – 5/2) = 97.5% to ensure that there is a 0.95 probability that both intervals include the population selection ratio.

Fig. 2. Mean profitability of purple sea urchins and proportion of purple sea urchins selected for each handling technique: (*a*) pecking and (*b*) air-dropping. Urchin size was determined by test diameter (mm). Values without error bars represent size classes with only one sample. Sample sizes for the calculation of profitability are presented in Table 1.



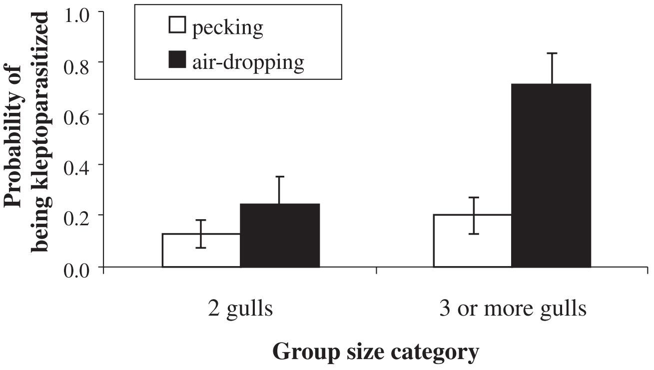
solitary and two-gull group conditions combined ($F_{[1,108]}$ = 5.78, P = 0.018). Although handling technique was not significant ($F_{[1,108]}$ = 2.97, P = 0.089), we found a trend towards selecting relatively larger purple sea urchins with the air-dropping technique (air-dropping: 51.00 ± 1.77 mm, pecking: 46.91 ± 0.75 mm). There was no significant interaction between group size and handling technique ($F_{[2,108]}$ = 1.93, P = 0.151).

Group size did not have a significant effect on drop heights when western gulls air-dropped ($F_{[2,40]}$ = 2.91, P = 0.066), controlling for purple sea urchin size ($F_{[1,40]}$ = 0.08, P = 0.779).

Age effects

Neither age ($F_{[1,110]}$ = 0.09, P = 0.770) nor handling technique ($F_{[1,110]}$ = 0.61, P = 0.436) alone significantly affected purple sea urchin size selection. However, we found a significant interaction between the two factors ($F_{[1,110]}$ = 6.13, P = 0.015) (Fig. 4). Juvenile western gulls selected smaller purple sea urchins when air-dropping than when pecking ($F_{[1,110]}$ = 818.61, P < 0.001). Adults showed the opposite pattern: when air-dropping, they selected significantly larger purple sea urchins than when pecking ($F_{[1,110]}$ = 2450.35, P < 0.001).

Fig. 3. Probability of kleptoparasitism relative to western gull (*Larus occidentalis*) group size (two gulls and three or more gulls) and handling technique (pecking and air-dropping).

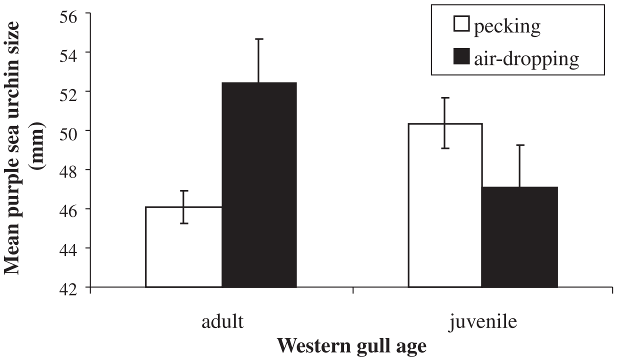


Discussion

Our results show that western gulls (*i*) exhibited significant selection for the energy-rich purple sea urchins, (*ii*) foraged optimally when pecking but not when air-dropping, and (*iii*) tended to select smaller purple sea urchins when foraging in larger groups. Furthermore, (*iv*) adult gulls selected relatively larger purple sea urchins when air-dropping than when pecking, but the pattern reversed in juveniles.

Some authors have argued that energy (i.e., kcal), as used in this study, may not be the correct currency to assess optimal foraging (Pierotti and Annett 1987; Smallegange and van der Meer 2003) and that other currencies should be used such as nutrient content (O'Brien et al. 2005), detoxification (Toft and Wise 1999), and rate of digestion (Schoener 1987). However, optimal foraging theory assumes that the maximization of some currency accrued during foraging activity will increase fitness (Caraco et al. 1980; Stephens and Krebs 1986; Pierotti and Annett 1991). This currency has frequently been identified as energy because an organism's ability to meet its metabolic requirements depends on its energy intake (Heinemann 1992; Bautista et al. 1998). Given that overall energy intake is considered a limiting factor for higher trophic level species (Begon et al. 2006), we deemed

Fig. 4. Mean purple sea urchin size selection relative to age (adult and juvenile western gulls) and handling technique (pecking and air-dropping).



the use of energy as currency to be appropriate and discuss our results in the in the context of the behavioral mechanisms affecting gull foraging decisions and later derive some ecological implications.

While at Wilder Annex, western gulls specialized on purple sea urchins, which had the highest caloric content. Other species have been found to select high caloric content prey in field and laboratory conditions. For instance, great tits (*Parus major* L., 1758) forage optimally by actively selecting the more energy-rich item 95% of the time when presented with different types of mealworms on a conveyor belt (Berec et al. 2003). Optimal foraging also predicts that energy-poor prey will be ignored regardless of their abundance in the environment (Begon et al. 2006). We corroborated this prediction in western gulls, which avoided prey items with lower caloric content, despite similar availability. Although *Larus* gulls are ecological generalists that exploit a wide variety of prey items (Moriera 1995; Bertellotti and Yorio 1999; Hori and Noda 2001), specialization on a single prey item has been previously documented at a local scale in herring gulls (*Larus argentatus* Pontoppidan, 1763) (Pierotti and Annett 1987).

Western gulls that air-drop their prey are able to extract relatively more meat than those that use the pecking technique (Maron 1982). Larger hard-shelled prey are also relatively easy to break open with the air-dropping technique, resulting in less time (and thus less energy) spent in obtaining the soft tissue inside (Zach 1979; Maron 1982; Ward 1991). Handling times for the air-dropping technique were significantly shorter than for pecking, which may have affected the slightly higher profitability of air-dropping. Although western gulls selected relatively larger urchins when air-dropping, our results (Fig. 2) indicated that they did not select the most profitable size class within this particular technique and thus failed to forage in the expected optimal manner. However, western gulls did forage optimally when pecking by selecting the most profitable size class for this technique. This partial lack of correspondence to the optimal foraging predictions resulted from western gulls selecting smaller urchins than expected only when air-dropping; this conclusion could be influenced by many factors, including the two that we studied: kleptoparasitism and age (see below).

Western gulls are social organisms that often forage in aggregations (Maron 1982), which can increase the risk of kleptoparasitism (Campbell 1987; Nilsson and Brönmark 1999). Previous studies in glaucous-winged gulls and kelp gulls determined that the likelihood of food theft increases with the air-dropping technique (Barash et al. 1975) and when conspecifics are within 10 m of a foraging gull (Siegfried 1977). Similarly, we have demonstrated for the first time with western gulls that the probability of kleptoparasitism increases when air-dropping and in larger groups. The higher costs of foraging in larger groups may account for the smaller prey size selection when air-dropping their prey.

To minimize the chances of kleptoparasitism, individuals can air-drop prey items from a lower altitude (Zach 1978, 1979; Maron 1982). However, western gulls apparently did not follow this strategy. This result may reflect a trade-off between the costs of losing the prey item via kleptoparasitism and the benefits of successfully breaking it open with conventional drop heights. If an individual chooses a lower dropping height and is unable to break open a purple sea urchin on the initial drop, it will probably try again. This would increase the foraging costs by raising the attention of conspecifics (Maron 1982) and reduce the prey value owing to the extra energy required to air-drop a second time (Ingolfsson and Estrella 1978; Kent 1981). This trade-off between risk avoidance and optimal foraging (Nilsson and Brönmark 1999) may be particularly important in larger groups, since the risk of spending energy for little or no profit with decreased initial drop height (suboptimal foraging) is greater than the risk of kleptoparasitism during the initial drop.

We did not find variations in purple sea urchin size selection between ages, but each age used different behavioral strategies to handle prey. The foraging experience of adults may account for the selection of larger purple sea urchins when air-dropping, which may also increase the chances of breaking them open (Kent 1981). However, when juveniles air-dropped, they chose smaller purple sea urchins than when pecking, which could partly explain the lack of fit of optimal foraging predictions with the air-dropping technique. The different strategies suggest that juveniles are inexperienced and have not yet refined their foraging skills. Previous studies indicate that avian foragers must learn appropriate foraging behavior through a trial-and-error process (Barash et al. 1975; Siegfried 1977; Zach 1979; Richardson and Verbeek 1987). Gamble and Cristol (2002) concluded that play activity among juvenile herring gulls may actually provide practice for future foraging events. We frequently observed juvenile western gulls handling old empty urchin tests, golf balls, sparkplugs, and other discarded items at the study site and sometimes even air-dropping these objects.

Other energetic factors may be involved in the lack of fit of optimal foraging predictions for the air-dropping technique. Western gulls must apply a great deal of force to remove an individual purple sea urchin from a rock, particularly if it is large, as the tube feet suction to the rock is extremely strong (Irons et al. 1986, Lawrence 1987). Hence, these extra costs in both energy expenditure and handling time could reduce the profitability of larger urchins, thereby encouraging gulls to select smaller individuals than predicted. Furthermore, air-dropping involves flying and hovering energetic costs (Tucker 1972; Maron 1982; Marsh

1986), which could be higher for larger sea urchins, also leading to reductions in profitability (Kent 1981).

Ecological implications

Urchin grazing within the rocky intertidal can negatively affect habitat structure by removing turf algae (Palacín et al. 1998). Additionally, urchins remove newly settled invertebrate recruits, thus reducing community diversity (Vance 1979). Purple sea urchins, owing to the nature of their grazing activity, are also partly responsible for the erosion of the rock substratum and the loss of habitat relief (Sala 1997). However, the abundance of purple sea urchin populations is largely determined by predation in kelp forests and subtidal rocky habitats (Tegner and Dayton 1981; Sala 1997; Reisewitz et al. 2006).

To evaluate the potential local effects of gull predation in the rocky intertidal, we first estimated the daily energetic requirement of an individual western gull as 1202.26 kJ/d applying the equation developed by Birt-Friesen et al. (1989) and using an assimilation efficiency of 75% (see Furness et al. 1988). Assuming a diet composed purely of purple sea urchins, a western gull would need to consume 32.29 urchins per day based on a mean profitability of 49.65 kJ (this study). Given that western gulls only forage on purple sea urchins during the nonbreeding season (September–March) and during low tidal ranges (≤1.0 MLLWL), we determined that an individual western gull may consume 3229 urchins each year (approximately 100 foraging days). When considering the mean flock size of western gulls present at Wilder Annex during the course of this study (45.33 ± 4.27 gulls), we determined that 145 305 purple sea urchins could potentially be consumed by western gulls each year. We estimated the purple sea urchin population at Wilder Annex to be approximately 400 000 individuals based on our own density measurements, which were corroborated with data from a long-term study (S. Lawrenz-Miller and A. Miller, unpublished data). Thus, we conclude that the potential upper limit of purple sea urchin predation could affect 36% of this population.

Consequently, western gulls could potentially affect the local spatial distribution and abundance of purple sea urchins. By removing them from the substratum, gulls might increase patchiness at microhabitat scales and indirectly provide opportunities for subordinate invertebrate species to colonize (Marsh 1986; Wootton 1992). This conclusion cannot be generalized to other areas, but it suggests potential localized effects of western gull predation that could maintain or even enhance community diversity and structural complexity of the rocky intertidal.

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