

Original Article

# Short timescale rate maximization by gulls and implications for predation on size-structured prey

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The timescale over which a predator estimates changes in prey encounter rates will play an important role in maximization of energetic returns from foraging in habitats where prey availability is highly variable through time. However, studies that explicitly test the temporal scale over which foragers track changes in prey availability are surprisingly rare. The increasingly well-recognized impact of terrestrial predators (e.g., birds) on intertidal food webs is likely to depend on their ability to track prey fluctuations in these highly variable environments. Here, we compare the predictions of 2 optimal diet models: a “classic” model in which prey encounter rate estimates are based on long-term, site-level abundance averages, and a model in which encounter rate estimates change at regular intervals throughout the foraging period. We parameterized these models using data from a field study on glaucous-winged gulls (*Larus glaucescens*) foraging on various sizes of the sea star *Pisaster ochraceus*. Predictions from the classic model, which assumes constant diet breadth throughout the tide cycle, did not match field observations of diet breadth. The “tide-sensitive” model, which assumes that gulls track tide-related changes in prey abundance, provided a better fit to observational data, explaining the full range of *Pisaster* sizes consumed by gulls. We conclude that gulls track short-term changes in prey encounter rates within a single low tide period to maximize foraging returns. We also present data for high rates of *Pisaster* removal by gulls, challenging the view of this sea star as a top predator in its intertidal communities. **Key words:** diet breadth, glaucous-winged gull, intertidal ecology, *Pisaster ochraceus*, prey encounter rate. [*Behav Ecol*]

## INTRODUCTION

The foraging decisions of animals have direct implications for a variety of higher-order phenomena, including population dynamics of predators and prey (Abrams 1992; van Baalen et al. 2001; Holt and Kimbrell 2007), and community structure (Roughgarden and Feldman 1975; Hambäck 1998; Kotler and Brown 2007). Theory suggests that adaptive prey choice—selection between prey items (species or individuals) based on some currency or prey characteristic (e.g., energy intake rate or profitability, nutrient content, size)—will alter the impact that a predator has on its prey population and the community as a whole relative to nonselective predation (Fryxell and Lundberg 1994; Schmitz et al. 1997; De Roos et al. 2003). Thus, information regarding the details of animal prey choice decisions should improve our understanding of population and community ecology.

Foraging theory has classically approached the problem of prey choice under the framework of missed opportunity costs, in which the penalty for taking lower quality prey results from the fact that time spent handling such prey is time taken away from searching for better prey (MacArthur and Pianka 1966; Stephens and Krebs 1986). This straightforward reasoning has been formalized in the classic diet model (Charnov 1976;

see Ydenberg 2010 for a concise overview of the model and its assumptions). One of the major predictions of the diet model is that the inclusion of a less profitable prey type in a forager's diet should be independent of its abundance, depending instead on the encounter rate with more profitable prey, and thus that diet breadth should expand as the encounter rate with highly profitable prey decreases (Stephens and Krebs 1986).

Classical foraging theory assumes that foragers are perfectly informed regarding encounter rates with available prey types and will therefore instantaneously adjust their diets to changes in prey density (Stephens and Krebs 1986; Barkan and Withiam 1989; Fortin et al. 2002). In reality, however, animals require time to gather information on changes in prey availability (Abrams 1992), and the timescale over which foragers update information on prey encounter rates is often unclear. In empirical studies, expected encounter rates are commonly estimated using long-term averages (i.e., over the whole foraging period) or site-level estimates of relative abundances (Richardson and Verbeek 1986; Cayford and Goss-Custard 1990; Kaspari and Joern 1993; Berec et al. 2003). These approaches have been successfully applied in several field studies of mammalian herbivores (brown hares [*Lepus europaeus*], Rödel et al. 2004; kudus [*Tragelaphus strepsiceros*], Owen-Smith 1994) and carnivores (honey badgers [*Mellivora capensis*], Begg et al. 2003; african lions [*Panthera leo*], Scheel 1993) which show changes in diet breadth over several months as the abundances of preferred plant and animal species fluctuate seasonally. However, when encounter rates with prey vary over much shorter timescales, such

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long-term averaging may result in suboptimal energy intake rates by over- or underestimating the missed opportunity costs associated with taking less profitable prey (Lucas 1983). Using a 2-prey-type model, Lucas (1983) showed that a forager will overestimate energetic return from specializing on the high quality prey type when the time required to estimate the encounter rate with this prey type is long relative to changes in prey abundance. This suggests that finer-scale estimation of prey encounter rates would lower the threshold for switching between a specialist and a generalist diet when encounter rate variability is high (Lucas 1983). Thus a predator can improve its foraging success by basing diet breadth decisions on short-term rather than long-term estimates of prey encounter rates when foraging in highly variable environments. This result may have substantial implications for predictions of predator impact on prey density, or at multiple trophic levels in a food web, if for instance prey removal rates are only measured under a subset of relevant environmental conditions.

Assumptions regarding the timescale over which foragers track relevant environmental parameters (van Baalen et al. 2001; Stephens 2007), and by extension the temporal scale of foraging optimization, significantly affect predictions regarding prey choice behavior (Barkan and Withiam 1989; Gass and Roberts 1992; Fortin et al. 2002), and the stability of predator-prey systems (Krivan 1997; Abrams 1999; Holt and Kimbrell 2007). However, empirical comparisons of diet models that differ in their assumptions regarding encounter rate information use are surprisingly rare (but see Ward 1993). Here, we present a straightforward extension of the basic multiple-prey diet model (Charnov 1976; Richardson and Verbeek 1986) in which the expected encounter rates with all prey types change at regular intervals throughout the foraging period. Diet breadth predictions from this model are contrasted with those from a “classic” model in which the forager’s expected encounter rates are estimated using prey abundances averaged over the entire foraging period, an approach analogous to the long-term averaging used in many empirical studies.

We investigated prey choice behavior and diet breadth in glaucous-winged gulls (*Larus glaucescens*) foraging on the ochre sea star (*Pisaster ochraceus*, hereafter *Pisaster*). *Pisaster*, the original “keystone species” (Paine 1966; Menge et al. 1994), has long been considered an important predator in rocky intertidal habitats throughout the Pacific coast of North America (Paine 1966, 1969, 1974; Robles et al. 1995; Sanford 1999). *Pisaster* controls the lower distributional limit of its primary prey resource, the mussel species *Mytilus californianus* and *M. trossulus* (Paine 1974; Robles et al. 1995), thereby preventing the mussel monoculture that ensues when these sea stars are experimentally removed (Paine 1966; Menge et al. 1994) and increasing overall community diversity by allowing space for the recruitment and attachment of otherwise excluded species. This sea star has generally been considered a top predator (Mauzey 1966; Navarrete et al. 2000), and no top-down control of *Pisaster* populations has been suggested. However, we have previously shown that glaucous-winged gulls consume large numbers of *Pisaster*, and that this sea star constitutes up to ~90% of prey taken by gulls at intertidal sites along coastal British Columbia, Canada (Suraci and Dill 2011). Given that the impact of *Pisaster* on the mussel distribution is dependent on sea star density (Paine 1974), gull predation has the potential to alter *Pisaster*’s effect on intertidal community structure. The role of birds (gulls in particular) as top predators in intertidal food webs, and their ability to affect intertidal species abundance at several trophic levels, has received recent attention (Marsh 1986; Wootton 1995, 1997; Hori and Noda 2001; Ellis et al. 2005, 2007). While non-selective predation will decrease the density of a prey species,

theoretical work suggests that size-selective predation, particularly preference for small, sexually immature individuals, can lead to less intuitive results, including an overall increase in density of preferred prey sizes (De Roos and Presson 2002; De Roos et al. 2003). A wide range of *Pisaster* sizes co-occur at intertidal sites, representing a continuous range of energetic profitability values to foraging gulls (Suraci and Dill 2011). Elsewhere we showed that gulls exhibited a strong preference for small *Pisaster* sizes, using preference experiments in which several sea star sizes were equally available (Suraci and Dill 2011). In the present study, we expand on this work to examine how size selectivity interacts with environmental variability to determine the actual range of *Pisaster* sizes taken by gulls at an intertidal site along the Strait of Georgia in British Columbia.

The tidal nature of the system provides an opportunity to test hypotheses regarding the gulls’ ability to track changes in prey abundance. When foraging on intertidal invertebrates, glaucous-winged gulls focus their efforts almost exclusively at or above the water line (Irons et al. 1986; Suraci JP, personal observations). Changes in tidal height therefore result in changes in prey availability over a relatively short timescale due to the well-described zonation patterns of intertidal species (Raffaelli and Hawkins 1996). Low physiological tolerances to heat and desiccation stress restrict *Pisaster* to the low intertidal zone (Petes et al. 2008) and they are thus only available to gulls during a short period around daily low tide (hereafter “the low tide period”—approximately 2h before to 2h after low tide). Within their intertidal range, *Pisaster* abundance gradually declines with increasing shore height (this study). Given the insights from Lucas’s (1983) opportunity cost model, this combination of factors suggests that gulls could greatly improve their net energetic return by regularly re-estimating the encounter rates with various *Pisaster* sizes throughout the tide cycle and adjusting their diet breadth accordingly, rather than basing prey choice on long-term averages of encounter rates (i.e., across the entire period of *Pisaster* exposure). Here, we compare the 2 diet breadth models described above using data from gulls foraging on *Pisaster*. Support for the “classic” diet model would suggest that gull prey choice decisions are not sensitive to short-term, tide-related variability in prey abundance. Conversely, support for the “tide-sensitive” model would suggest that gulls track short-term changes in prey encounter rates to maximize energetic return.

## METHODS

### Field site

All fieldwork was conducted from April to September 2009 and April to August 2010 at Roberts Creek (49°25′53″N, 123°40′35″W), a rocky intertidal site on the Strait of Georgia in British Columbia, Canada, approximately 40 km northwest of Vancouver. The intertidal zone at this site is composed of large rock outcroppings and small boulders, and is dominated by rock weed (*Fucus gardneri*) with considerable barnacle (*Semibalanus cariosus* and *Balanus nubilis*) cover. *Pisaster* are locally highly abundant and constitute a substantial dietary component for gulls foraging at this site (Suraci and Dill 2011). All fieldwork was conducted from 2h before to 2h after daily low tide on days when the tidal minimum was ≤1.3 m above mean lower low water (MLLW). This range represented both the time of day and tidal period when gull intertidal foraging and group size were at a maximum (Suraci JP, personal observations; Irons et al. 1986), thereby reducing the likelihood of obtaining multiple measurements from single individuals. Maximum daily group size at Roberts

Creek was, on average ( $\pm$ SD), 37.2 ( $\pm$ 12.2) gulls (observed maximum range = 18–62 gulls). During these observation periods, tide level fluctuated between 0.1 and 1.8 m above MLLW. This tidal flux affected approximately 130 m of shore perpendicular to the water line and resulted in substantial changes in relative prey availability (see below).

### Behavioral observations

Methods for determining handling times and search times for all prey types, including all sizes of *Pisaster* throughout the range of sizes eaten by gulls, were described in detail elsewhere (Suraci and Dill 2011). Briefly, we used focal animal sampling (Altman 1974) of randomly chosen gulls and opportunistically observed prey consumptions from nonfocal gulls to determine handling times and search times for all prey consumed. Foraging behaviors were recorded using a Canon high definition digital camcorder (HDV 1080i). Videotaped behaviors were analyzed using iMovie HD version 6.0 (©Apple 2006) and all handling and search times were measured to 0.1 s. For each consumption event, we noted time of day, tide level (relative to MLLW), and age of the gull (juvenile or adult). We developed a method for determining sizes of sea stars consumed by gulls using screenshots from video recordings, also described in detail by Suraci and Dill (2011). Sea star sizes were estimated (to 0.1 cm) relative to an average gull beak length of 5.9 cm (James-Veitch and Booth 1954) and are reported as the length of the longest ray (essentially the radius of this radially symmetrical animal). This method was accurate to within 0.14 cm (Suraci and Dill 2011).

During the 2010 field season, we conducted instantaneous scan samples (Altman 1974) at 25-min intervals throughout each 4-h visit to the field site. During scans, the “instantaneous” behavior of each individual gull was grouped into a behavioral category, essentially foraging (searching for, handling, or consuming prey) or nonforaging (loafing, preening, nonforaging movement, interacting with other gulls, etc.). We also recorded the age class of each individual and the tide level. Scan samples provided an estimate of gull density and overall foraging effort at the site throughout the observed tidal range. Videotaped scan samples provided additional data on sea star sizes consumed at various points throughout the tidal range. The sizes of 95 sea stars were estimated from gull consumptions observed during scan samples using the video size estimation method referred to above. These data were used in conjunction with sea star size estimates from focal observations ( $n = 170$ ) in testing the predictions of the 2 diet breadth models.

### Prey abundance estimates

We estimated the abundance of all prey types by randomly placing 0.25 m<sup>2</sup> quadrats ( $n = 180$ ) along 10 m transect lines (5 quadrats per transect). Transect lines were placed randomly in the intertidal zone, following the low tide line as it shifted throughout the observation period. We recorded the abundance and size (to 0.5 cm) of all *Pisaster* and other major prey types—including nereid polychaetes, limpets, snails, and hermit crabs—deemed available to gulls (Snellen et al. 2007). All prey items that were completely exposed or under small rocks moveable by gulls (based on foraging observations) were considered available, as were items in small crevices that were less than 5.9 cm (the length of a gull beak) from the opening. Prey items under heavy rocks or in crevices too deep to be reached by a gull beak were excluded from abundance estimates. We used prey abundance estimates to calculate relative availability of all prey types exploited by gulls at this site.

### Prey type definitions

Gulls at Roberts Creek consumed a wide range of sea star sizes, from 1.0 to 7.8 cm ray length. This span of *Pisaster* sizes represents an essentially continuous range of prey types that vary nonlinearly in expected energetic profitability (Suraci and Dill 2011). However, for analysis within a foraging theory framework it was necessary to group sea stars into discrete prey types based on size (Osenberg and Mittelbach 1989), and we chose to use 0.5 cm size classes in this study (from 1.0 to 8.0 cm ray length). Therefore, when discussing results from the diet models, a sea star size class of, for example, 2.5 cm actually represents all sea stars of ray lengths 2.25–2.74 cm; the average energetic content and handling time from this range of sizes was used in calculating intake rate for the 2.5 cm size class.

*Pisaster* constituted 91.6% of all observed prey consumptions at this site (see also Suraci and Dill 2011). However, 2 other prey types were taken by gulls on occasion and are included here to accurately depict all foraging options available to gulls at Roberts Creek. Polychaete worms (primarily *Nereis vexillosa*) made up 3.1% of observed prey consumptions and the final 5.3% consisted of “small invertebrates” (SI), a group of prey species that were too small to be accurately identified from behavioral observations, but which abundance estimates suggested to consist mainly of small gastropods (*Tectura scutum*, *Lottia pelta*, *Tegula funebris*) and hermit crabs (primarily *Pagurus hemphilli*). Thus, polychaete worms and SI were included as 2 prey types in addition to the 15 *Pisaster* size classes, for a total of 17 prey types that could potentially occur in the gull diet.

### Energetic profitability estimates for sea stars

Energetic profitability is defined as the amount of energy provided by a prey item per unit handling time, where handling time is the time from prey discovery to the resumption of search. Energetic profitability for all size classes of sea star throughout the range of sizes consumed by gulls was determined by estimating the relationships between sea star size and (1) energy content, and (2) handling time. The procedure and data used to determine energy content of sea stars (through bomb calorimetry) is identical to that presented in Suraci and Dill (2011). Briefly, sea stars throughout the applicable size range ( $n = 33$ , size range = 0.8–8.6 cm) were individually homogenized in a Waring Blender and samples were lyophilized to constant dry weight (~30% original wet mass). Energy content was determined for 1-g subsamples from each sea star using a Parr 1341 Oxygen Bomb Calorimeter. Energy content per unit wet mass was fairly constant across the range of sea star sizes sampled with a mean ( $\pm$ SE) of 2.09 ( $\pm$  0.05) kJ/g wet mass. We also determined the proportion of each subsample of homogenized sea star that consisted of nonmetabolizable material (mainly calcareous ossicles) by taking the mass of the material that was left uncombusted after bomb calorimetry. The mean ( $\pm$ SE) percentage of sea star wet weight (i.e., original mass) that consists of nonmetabolizable material was found to be 16.28 ( $\pm$ 0.85)%. As described elsewhere (Suraci and Dill 2011), a linear regression between sea star size and energy content yielded a highly significant regression equation ( $\ln$  Energy [kJ] = 0.33 + 2.55  $\times$   $\ln$  Size [cm]) [ $P < 0.001$ ,  $R^2 = 0.97$ ], which we used to predict the expected energy available from any given *Pisaster* size.

Handling times were obtained for a total of 170 *Pisaster* consumptions observed at Roberts Creek over the 2 field seasons. We examined the relationship between handling time and sea star size using a linear mixed effects model with size as a fixed effect and individual gull as a random effect to

account for multiple handling time observations taken from some gulls. Handling time data were natural log-transformed to approximate a normal distribution and to correct for heteroscedasticity. These analyses were performed using the lme function from the nlme package in R (R Development Core Team 2008). The mixed effects model revealed a strong positive correlation (Figure S1) between sea star size and natural log-transformed handling time (correlation between fitted and observed values [pseudo- $R^2$ , Draper and Smith 1981] = 0.77) with a highly significant slope ( $P < 0.0001$ ). The regression equation from this model (ln Handling Time [s] =  $-0.35 + 0.98 \times \text{Size [cm]}$ ) was then used in conjunction with the regression equation for sea star energy content to produce estimates of energetic profitability for all sea star sizes observed to be consumed by gulls. As energetic profitability is simply the ratio of prey energy content to handling time, we divided predictions from the energy regression by those from the handling time regression to produce profitability estimates for each sea star size. We estimated the error around these profitability estimates using delta method error approximation, as described by Powell (2007). This procedure incorporates error from both the energy content and handling time regressions into a single error estimate for each profitability estimate. Throughout the text, we report sea star profitability as profitability estimate  $\pm$  delta method standard error.

**Energetic profitability estimates for non-sea star prey**

Handling times for all non-sea star prey types were estimated from behavioral observations by taking the mean of all observed handling times for polychaete worms ( $3.82 \pm 0.29$  s SE) and SI ( $3.31 \pm 0.17$  s SE). Estimates of whole prey item energy content for these prey types were taken from the literature and converted from kCal/prey to kJ/prey where necessary. Oftedal et al. (2007) provide an estimated energy content for *N. vexillosa* of 8.38 kJ per individual. We divided this value by the mean polychaete handling time (above) to obtain a worm energetic profitability estimate of 2.19 kJ/s, which was used in parameterizing the diet breadth models.

As SI prey types could not be identified to species during behavioral observations, we used estimates of energy content per prey item for the 3 SI taxa most commonly encountered in abundance quadrats. Oftedal et al. (2007) provide an estimate of 4.26 kJ per individual for the black turban snail (*T. funebralis*) and 5.43 kJ per individual for the maroon hermit crab (*P. hemphilli*). Irons et al. (1986) report an average energy content for common limpet species (the plate limpet *Tectura* [formerly *Notoacmaea*] *scutum* and the shield limpet *Lottia* [formerly *Collisella*] *pelta*) of 2.93 kJ per individual. We took the average of the above 3 energy values to obtain a single SI energy content estimate of 4.21 kJ/prey. We divided this value by mean SI handling time to produce an SI energetic profitability estimate of 1.27 kJ/s.

**The models**

*Classic diet model*

Given all prey types available to a forager, optimal diet breadth models allow one to determine what subset of those prey types a forager should include in its diet in order to maximize its energy intake rate. We used a sequential prey encounter model developed by Richardson and Verbeek (1986) based on the original optimal prey choice model by Charnov (1976) (see also Schoener 1971; Pastorok 1981) to explore the effect of changes in diet breadth on long-term energy intake rate. This model calculates the expected intake

rate from a diet of specified breadth; for a diet including prey types 1 to  $j$ , intake rate is given by

$$\frac{\bar{E}_j}{\bar{T}_j} = \frac{\sum_{i=1}^j e_i P_{ij} - k \bar{TS}_j}{\sum_{i=1}^j h_i P_{ij} + \bar{TS}_j} \tag{1}$$

where  $\bar{E}_j$  is the expected net energy gain and  $\bar{T}_j$  the expected time required to locate and consume any prey item of types 1 to  $j$ .  $e_i$  and  $h_i$  are the average energy gain and handling time of prey type  $i$ , respectively.  $\bar{TS}_j$  is the expected search time to discover any prey item of types 1 to  $j$ .  $P_{ij}$  represents the relative abundance of prey type  $i$  in a diet that includes  $j$  prey types (see below). Finally,  $k$  is the energetic cost of searching, which was set to twice the basal metabolic rate, or 0.057 kJ/s. Basal metabolic rate was calculated using the formula derived by Daan et al. (1990) and an average glaucous-winged gull body mass of 1090.78 g (James-Veitch and Booth 1954). Note that all model symbols and their meanings are identical to those used by Richardson and Verbeek (1986).

$P_{ij}$  was calculated as:

$$P_{ij} = \frac{N_i}{\sum_{i=1}^j N_i} \tag{2}$$

where  $N_i$  is the abundance of prey type  $i$  in the intertidal zone at Roberts Creek.  $P_{ij}$  can also be thought of as the percentage of all available prey consisting of prey type  $i$  in a diet including prey types 1 to  $j$ . Thus, for the most restrictive diet (i.e.,  $j = 1$ ),  $P_{ij} = 1$ . There was no need to correct for availability of prey items to gulls, as this was accounted for by the abundance sampling method (see above).

In a field study where conditions cannot be strictly controlled, it is difficult to determine how many, if any, potential prey a forager encounters and ignores during search before finally taking a prey item. Thus, prey type-specific estimates of mean search time can be misleading. Instead, search time measurements for all observed prey consumptions can be averaged into a site level “search time to prey acceptance.” This measure provides the average search time  $\bar{TS}_x$  for the observed diet, which includes prey types 1 to  $x$ . The search time  $\bar{TS}_j$  for any other diet range 1 to  $j$  can then be calculated, following Richardson and Verbeek (1986, Equation 3), by determining the ratio of the total abundance of prey types in the observed diet to the total abundance of prey types 1 through  $j$ , and multiplying this value by  $\bar{TS}_x$ . We have modified this equation slightly by removing the term relating estimated prey abundance to availability as experienced by the forager. Thus

$$\bar{TS}_j = \left( \bar{TS}_x \right) \frac{\sum_{i=1}^x N_i}{\sum_{i=1}^j N_i} \tag{3}$$

Following the procedure outlined by Stephens and Krebs (1986), all prey types available at the site were ranked by energetic profitability (see Table S1) and sequentially added to the diet in order of decreasing profitability, starting with the most profitable type, then the 2 most profitable, and so on. For any particular diet breadth, the diet includes prey type  $j$  and all prey types of greater profitability. The above model was then used to calculate intake rate for all possible diet breadths ( $n = 17$ ). The diet breadth at which intake rate is the highest is considered the rate maximizing diet, and a forager is expected to ignore all prey types outside of this range.

As in Charnov’s (1976) original optimal foraging model, the inclusion of a prey type in the rate maximizing diet is

a function of its energetic profitability as well as the profitability and encounter rate of all more profitable prey types. Encounter rate with a prey type is commonly calculated as the inverse of the prey type-specific search or arrival time (Stephens and Krebs 1986). However, as noted above, prey type-specific search times can be misleading in field studies. Therefore in this formulation, encounter rate is incorporated by the inclusion of terms for search time to encounter any prey in a given diet breadth category ( $TS_j$ ) and the relative abundance of each prey type in that category ( $P_{ij}$ ).

#### *Tide-sensitive diet model*

Abundance estimates revealed changes in prey type abundance with increasing shore height above MLLW. As the vast majority of prey consumed by gulls in the intertidal zone at Roberts Creek are taken from exposed areas of the shoreline (i.e., above the tide line; Irons et al. 1986; Suraci JP, personal observations), tidal flux effectively causes continuous changes in prey abundance at the site level, which will translate into changes in prey encounter rate throughout the tide cycle. Additionally, site-level search time  $TS_x$  was found to increase with increasing tide level, thereby lowering the encounter rate with all prey types (see Results).

Foraging theory suggests that, as the encounter rate with more profitable prey types decreases, foragers should expand their diet to include less profitable prey (MacArthur and Pianka 1966; Schoener 1971; Stephens and Krebs 1986). To determine how sensitive gulls are to changes in relative prey availability, we sought to incorporate changes in prey encounter rates with tide level into the predicted diet breadth model. We did so by iteratively recalculating 2 model parameters,  $P_{ij}$  and  $TS_j$ , at regular intervals throughout the observed tidal range. Starting at a tide level of 0.2 m above MLLW, we recalculated  $P_{ij}$  and  $TS_j$  at 0.1 m intervals—up to a tide level of 1.4 m (approximately the highest shore level at which gulls were observed to forage)—using mean values of abundance and search time from measurements taken at or above the tide level of interest. Calculations were performed in this way, as all prey above the tide level of interest are expected to remain available to a foraging gull. We assume that the other model parameters, namely expected energy gain and handling time of prey ( $e_i$  and  $h_i$ , respectively) and the energetic cost of searching ( $k$ ), are not affected by tide cycle. Finally, we analyzed the relationship between diet breadth and expected energy intake rate at various tide levels to identify particular tide levels at which the model predicts an expansion in gull diet breadth.

To test whether gulls actually increase their selection of less profitable prey in accordance with the predictions of our tide-sensitive model, we used logistic regression to analyze changes in the resource selection function (RSF) for sea stars in relation to tide level. RSFs are proportional to the probability of a particular resource (e.g., prey type) being used by an animal, and account for the availability of that resource in the environment (Manly et al. 2002; Fortin and Fortin 2009). Logistic regression analysis allows one to model the dependence of the RSF on 1 or more measured variables. In such an analysis, the binomially distributed response variable is coded as 1 for used resource units and 0 for available units (Manly et al. 2002).

In our analyses, used resource units were sea stars observed being consumed by gulls during focal or scan samples. Available resource units were determined using quadrat sampling as described above. The predictor variable in these analyses was a binary variable which was scored as 0 if the sea star was of a size predicted by our diet models to be included in the gull diet at all tide levels (i.e.,  $\leq 6.5$  cm) and 1 for sea star sizes predicted by the tide-sensitive model to be included only at higher tide levels ( $> 6.5$  cm, see below). We also tested for an interaction between

this binary size variable and the tide level at which a sea star was sampled. Following Fortin and Fortin (2009), tide level was included as an interaction term only, rather than as a main effect because both used and available sea stars were associated with the same tide level. Data were grouped into 2 strata based on tide categories, and analyses were performed separately for each stratum. Stratum 1 included used and available sea stars sampled when the tide was between 0 and 0.7 m, and stratum 2 included data sampled at tide levels  $\geq 0.7$  m. This tide level marks the point at which large, low-profitability sea stars were predicted by the tide-sensitive model to be included in the gull diet (see below). Stratifying the data in this way allowed us to compare the interaction between large sea star RSF and tide height between these 2 tide level categories. Logistic regression analyses were performed using the glm function in R (R Development Core Team 2008). We were primarily interested in the interaction between large star RSF and tide level, and  $P$ -values presented for this interaction are those produced by the glm function. To test the validity of the models including an interaction term, we used a likelihood ratio test to compare the full model to a model excluding the interaction term (Manly et al. 2002). The chi-squared test statistic is the difference in deviance and the degrees of freedom (df) is the difference in df between the 2 models.

#### **Changes in foraging effort with tide cycle**

Our tide-sensitive diet model predicts a decrease in energetic return from intertidal foraging with increasing tide height (decrease in “maximum attainable intake rate,” see below), which could lead to changes in gull foraging effort or site use. To validate this prediction, we tested for an effect of decreased energetic return on gull foraging behavior using census data from gulls at Roberts Creek. A total of 195 scan samples (see above) were conducted over 22 days at Roberts Creek in the 2010 field season. Data on the total number of gulls engaged in foraging (searching for, handling, or consuming prey) were plotted against the tide level at which the scan was conducted to estimate the change in foraging effort throughout the tidal cycle. We used a generalized linear model (GLM) with a Poisson error distribution to examine the relationship between number of foraging gulls and tide level. An initial GLM including the date of the scan sample as a covariate showed a significant effect of date on gull counts. We therefore used a generalized linear mixed effects model (GLMM; see Zuur et al. 2009) with date as a random effect to account for the variation in gull count data associated with date. GLMMs were run using the lme4 package in R (R Development Core Team 2008). We produced a measure of goodness-of-fit (a “pseudo- $R^2$ ” value) for the GLMM by taking the square of the correlation between the model predictions (fitted values) and the original data on foraging gull counts.

#### **Biomass of sea stars removed by gulls**

We can use the tide-level-specific estimates of maximum attainable intake rate provided by the tide-sensitive diet model (see below) to determine the amount of energy an individual gull will consume during a single low tide period, assuming optimal foraging. Given the relatively constant energy content per gram body weight across sea star sizes (mean  $\pm$  SE =  $2.09 \pm 0.05$  kJ/g), the quantity of energy consumed by a gull can easily be converted to sea star biomass. This quantity can then be scaled up to the site level by multiplying by the number of gulls engaged in active foraging, while accounting for the effect of tide level on both gull foraging effort and intake rate. The total biomass of sea stars removed by gulls during a single low tide period is therefore given by

$$\frac{\sum I_i T_i N_i}{C} \tag{4}$$

where  $I_i$  is the maximum attainable intake rate over tidal range  $i$  (expressed as kJ/s),  $T_i$  the amount of time the tide level spends within tidal range  $i$  (in s),  $N_i$  the average number of gulls actively engaged in foraging behavior when tide is within this tidal range (determined using scan sample data as described in the previous section), and  $C$  is the average energy content per gram biomass of sea star. (Note that removing  $N_i$  from Equation 4 yields per capita biomass removed.) This calculation ignores the contribution of non-sea star prey to gull energy intake. However, this is unlikely to have a large impact on our results, as these prey types make up a small proportion (<10%) of the gull diet at our study site. As  $T_i$  varies from day to day, we present a calculation of total sea star biomass removed on a particularly favorable (i.e., very low tide) day at Roberts Creek, providing an estimate of the maximum impact of gull predation on the *Pisaster* population in a single low tide period. Equation 4 can be used to calculate biomass removed over any period for which  $T_i$  is known, and we extend our analysis to estimate biomass removal over an 8-day period, representing the time between 2 neap tides when daily low tide is  $\leq 1.3$  m above MLLW (i.e., when *Pisaster* are exposed and gull intertidal foraging is highest [Suraci JP, personal observations]).

**RESULTS**

**Prey energetic profitability**

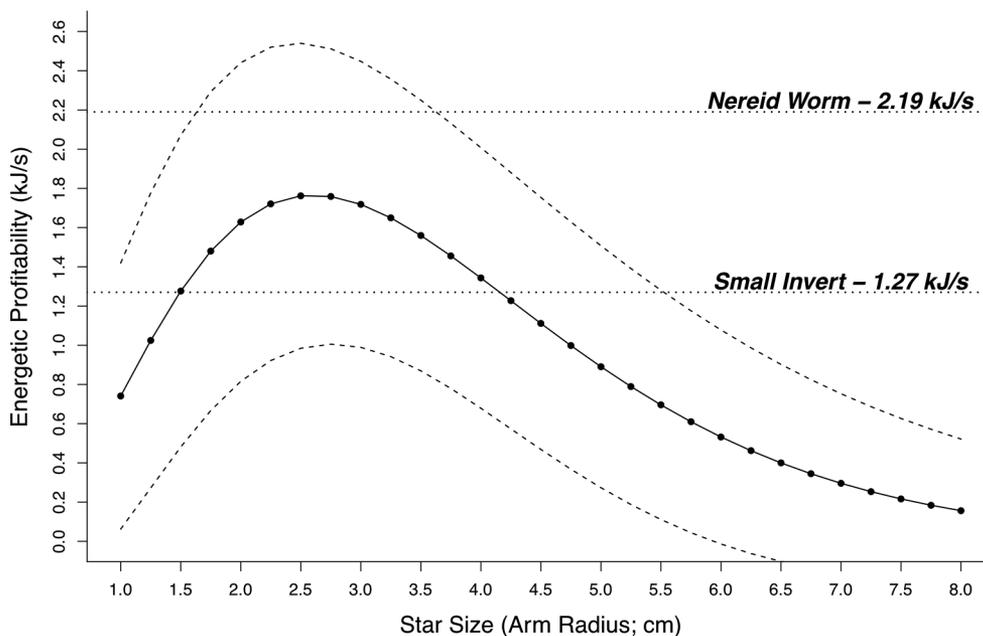
Energetic profitability is a peaked function of sea star size (Figure 1). Profitability reaches a maximum of  $1.75 \pm 0.40$  kJ/s for sea stars of ray length 2.5 cm and declines rapidly thereafter, reaching a minimum of  $0.15 \pm 0.19$  kJ/s at the largest sea star size applicable to this study, 8.0 cm. Figure 1 compares the

profitability estimates of the non-sea star prey types with those of the range of sea star sizes (see also Table S1). The most profitable prey available to gulls at this site are nereid polychaetes (2.19 kJ/s), and SI profitability (1.27 kJ/s) is comparable to that of both 1.5 and 4.5 cm sea stars.

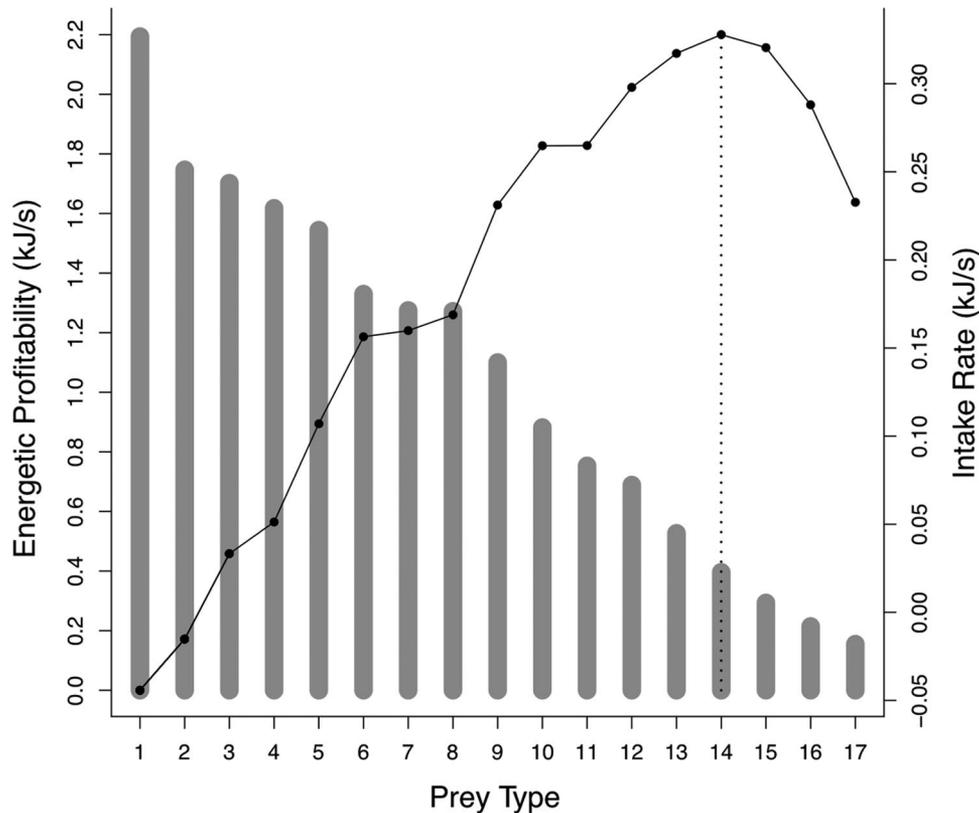
**Diet breadth—classic model**

All available prey types were ranked in descending order of energetic profitability (Table S1). In general, energetic profitability declines with sea star size, although the smallest sea star size classes (1.0, 1.5, and 2.0 cm) have profitability values comparable to those of larger sea stars. The site-level average search time to prey acceptance ( $TS_x$  in Equation 3) was found to be  $44.5 \pm 4.2$  s (mean  $\pm$  SE). This value was used to calculate expected search time to encounter an acceptable prey for each diet breadth category ( $TS_j$  in Equation 1); these values are presented in Table S2 along with relative abundance values for the newly added prey type in each category ( $P_{ij}$  in Equation 1). Equation 1 was then used to determine the effect on energy intake rate of sequentially adding less profitable prey types to the diet. Energy intake rate reaches a maximum of 0.33 kJ/s at profitability rank 14, which corresponds to sea stars of 6.5 cm ray length (Figure 2). This sea star size class had a substantially lower profitability value (0.40 kJ/s) than the most profitable items (e.g., nereid worms [2.19 kJ/s] and 2.5 cm sea stars [1.75 kJ/s], see Table S1). However, the long predicted search times (and consequently low prey encounter rates) associated with specializing on highly profitable prey would result in lower net energy gain than could be realized by expanding the diet to include larger sea stars. The classic model therefore indicates that gulls will maximize energetic intake rate by including sea stars of 6.5 cm and smaller in their diet, as well as nereid worms and SI, but excluding all sea stars larger than 6.5 cm.

We obtained size estimates for a total of 265 sea stars consumed by gulls. Of these, 97.0% (257) fell within the upper



**Figure 1** Estimated energetic profitability (kJ/s) in relation to sea star size (measured as longest ray length). Estimates were derived by taking the quotient of predictions from the sea star energy content regression and the handling time mixed model (see text). Dashed lines are 95% confidence limits around mean energetic profitability calculated using delta method variance approximation (Powell 2007). Dotted lines indicate mean profitability values for nereid polychate worms and SI.



**Figure 2**

Prey type profitability and predicted intake rate from the classic diet model. The energetic profitability values (gray bars, left axis) for all prey types available at Roberts Creek are presented in decreasing order (Profitability Rank, see also Table S1), illustrating the order in which prey types are sequentially added to the diet when calculating intake rate from the diet model. Energetic intake rate predictions from the classic diet model (solid line with closed circles, right axis) are shown as a function of increasing diet breadth, from a diet that includes just the most profitable prey type (Rank 1) to a diet that includes all 17 available prey types. The dotted line indicates the diet breadth (14) at which intake rate is maximized (0.33 kJ/s). Foragers are expected to exclude all less profitable prey types (Ranks 15–17) from their diet.

6.5 cm size limit of the predicted rate maximizing diet (Figure 3a), leaving only 3.0% of observed prey consumptions unexplained. Sea stars  $\leq 6.5$  cm in radius constitute 75.2 ( $\pm 4.3$  SE)% of all available sea stars within the 1.0–8.0 cm size range, as determined by abundance quadrats ( $n = 73$ , quadrats in which no stars were found were excluded). The mean proportion of the *Pisaster* population consisting of stars  $\leq 6.5$  cm in radius differs significantly from the proportion in the gull diet (1-tailed  $t$ -test,  $t = -5.02$ ,  $df = 72$ ,  $P < 0.0001$ ), supporting the assumption of selective, rather than opportunistic feeding.

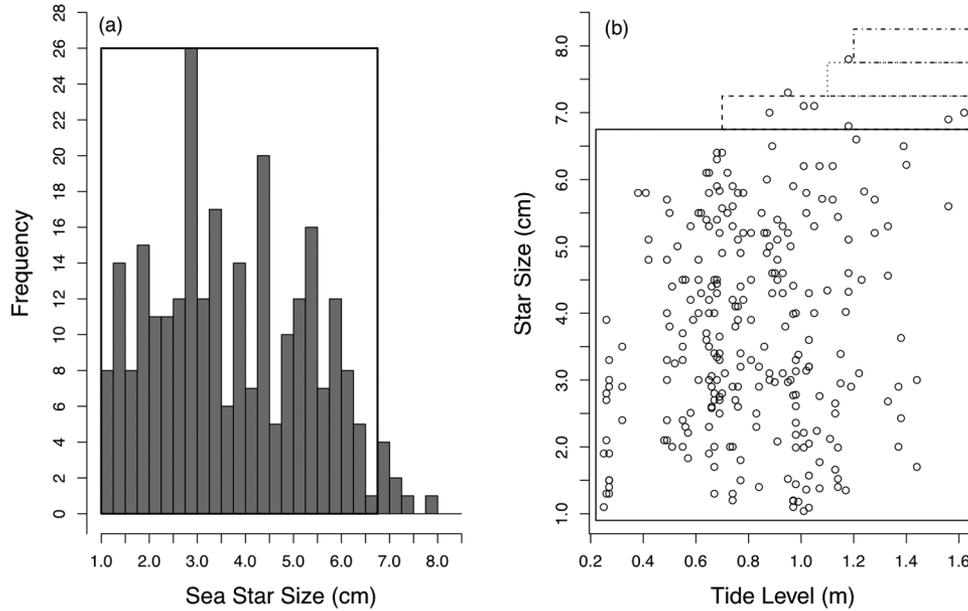
#### Diet breadth—incorporating the effect of tide on prey encounter rate

The largest tidal flux observed in 1 low tide period was 0.98 m. Tidal flux resulted in substantial changes in prey abundance (Figure 4), with all sea star size classes declining in abundance as tide level increased. Thus prey encounter rate decreases with increasing tide level. Additionally, we found significant differences between the statistical distribution of sea star sizes at the lowest tide level observed (0.2 m above MLLW) and the distributions at higher tide levels (tide = 1.1 m: Wilcoxon Rank Sum Test,  $W = 178.5$ ,  $P = 0.005$ ; tide = 1.2 m:  $W = 207.5$ ,  $P < 0.001$ ), meaning that prey relative abundance also changes with increasing tide height. We recalculated relative prey abundance  $P_{ij}$  and expected search times  $TS_j$  for all prey types at several tide levels (see Table S2) and examined the effect on intake

rate as predicted by the tide-sensitive diet breadth model (Figure 5). This procedure was performed at tide level intervals of 0.1 m from 0.2 to 1.4 m above MLLW. However for illustrative purposes, we present only a subset of these tide levels (0.2, 0.7, 1.1, and 1.2 m), as this scale is sufficient to capture all predicted changes in diet breadth. For all tide levels not presented (e.g., 0.3–0.6 m, 0.8–1.0 m), diet breadth was predicted to remain unchanged from that of lower tide levels.

For all tide levels less than 0.7 m, energy intake rate peaks at a diet breadth that includes 6.5 cm sea stars (Profitability Rank 14) and everything more profitable (smaller sea stars, worms, and SI), a prediction comparable with that of the classic diet breadth model with no tide information. Maximum attainable intake rate is highest at a tide level of 0.2 m, reaching 0.33 kJ/s, and declines gradually thereafter. When tide level reaches 0.7 m, intake rate peaks at 0.29 kJ/s for diet breadth category 15, predicting an expansion of the diet to include sea stars in the 7.0 cm size class. At a tide level of 1.1 m above MLLW, intake rate peaks at 0.18 kJ/s for a diet containing 16 prey types. This indicates that a forager will attain a maximal energetic intake rate by including sea stars up to 7.5 cm in its diet, despite the exceptionally long handling time associated with these stars (see Figure S1). Finally, at a tide level of 1.2 m, a diet that includes 8.0 cm sea stars (prey type 17, Figure 5) provides the maximal energetic return (0.13 kJ/s).

The diet breadth model incorporating information on tide-related changes in prey encounter rate explains 99.2% of the

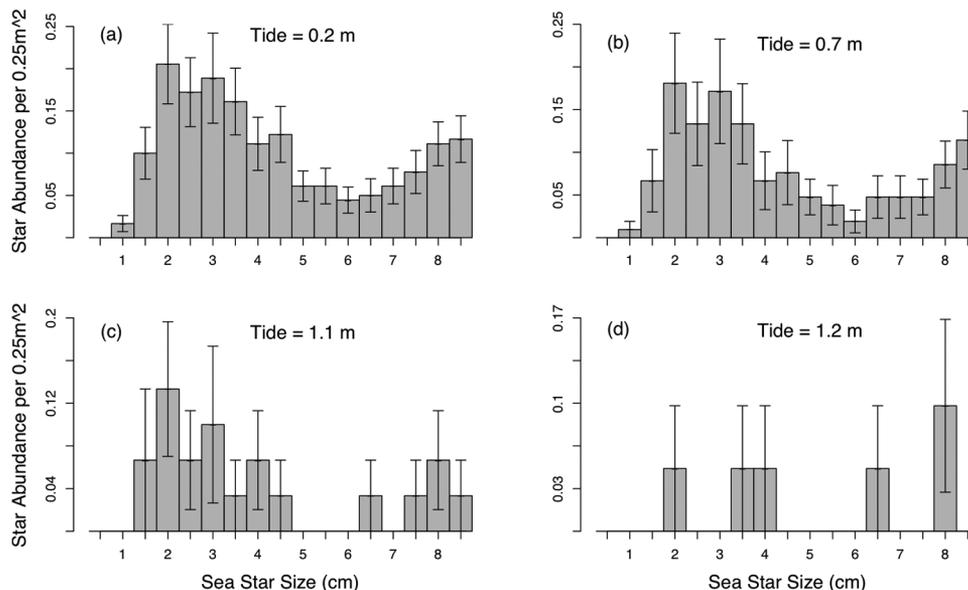


**Figure 3**

(a) Histogram showing the range of sea star sizes consumed by gulls at Roberts Creek and the number of consumptions observed for each size. Sea star sizes were estimated to 0.1 cm, and here have been collapsed into 0.25 cm bins. The box contains all sea star size consumptions that are explained by the classic diet model. (b) The sizes of all sea stars consumed by gulls during this study plotted against the tide level at which each star was taken. Boxes indicate sea star sizes that are predicted by the tide-sensitive model to be included in the gull diet. The solid box indicates the sea star sizes that are predicted (by both the classic and tide-sensitive models) to be included in the diet at all tide levels. Star sizes contained by the dashed box are included at tide levels of 0.7 m and above, sizes contained by the dotted box are included at levels of 1.1 m and above, and sizes contained in the dashed-dotted box are included at levels of 1.2 m and above.

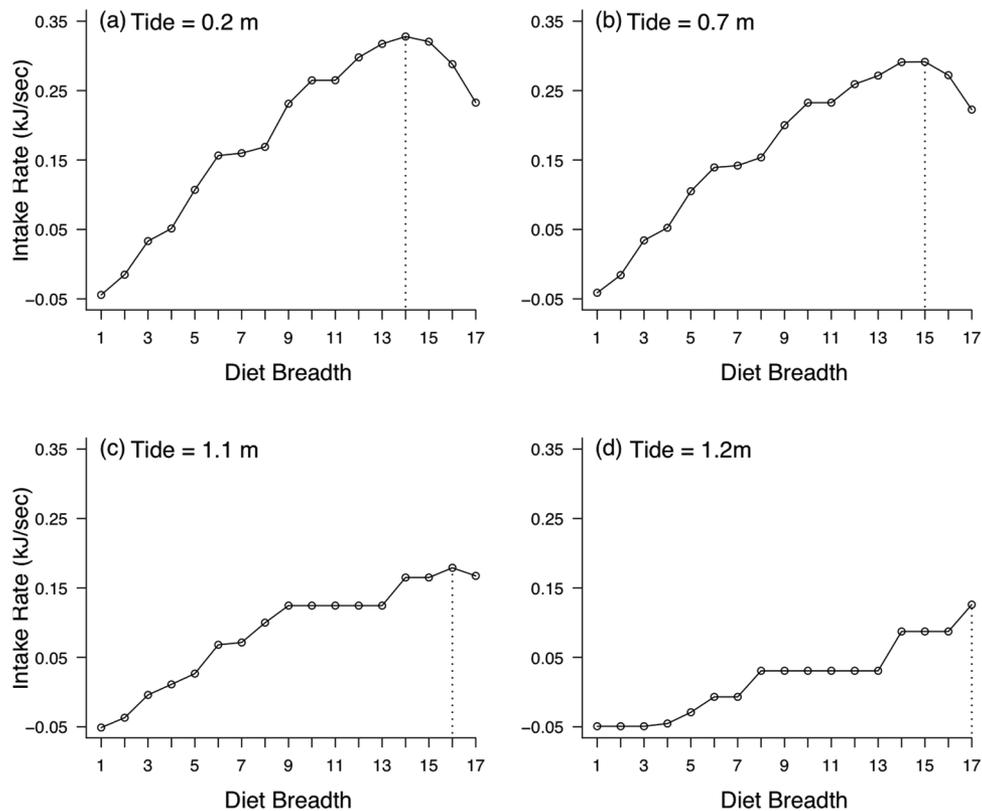
265 sea star consumption observations (Figure 3b). Although this is not a significant increase from the proportion of observations explained by the classic diet model (97.0%;  $\chi^2_{[1]} = 2.54$ ,  $P = 0.11$ ), our RSF analyses indicate that gulls do increase their selection of large (>6.5 cm) sea stars when foraging at higher tide levels. Using logistic regression, we found that the interaction between large sea star RSF and tide level was non-significant ( $P = 1.00$ ) when tide height was <0.7 m, an unsurprising result, given that no large sea stars were taken in this

tide range (Figure 3b). However, at tide levels  $\geq 0.7$  m, we found a significant ( $P = 0.016$ ) positive interaction between large sea star RSF and tide level, indicating that, within this higher tide category, tide height has a positive effect on the likelihood of a gull selecting large, low-profitability sea stars. The high tide category logistic regression model including the interaction term described the data significantly better than a model excluding this term (likelihood ratio test:  $\chi^2_{[2]} = 8.58$ ,  $P = 0.014$ ). Furthermore, an increase in maximum acceptable



**Figure 4**

Mean abundances (per 0.25 m<sup>2</sup>) of edible sea star sizes at 4 tide levels, as determined by quadrat sampling. Error bars are  $\pm 1$  SE. Note scale of the y axis differs between plots. Panels show mean sea star abundance at tide levels of (a) 0.2 m ( $n = 180$  quadrats), (b) 0.7 m ( $n = 105$ ), (c) 1.1 m ( $n = 30$ ), and (d) 1.2 m ( $n = 20$ ).



**Figure 5**

Change in energetic intake rate with diet breadth at 4 tide levels, as predicted by the tide-sensitive diet model. Intake rate is shown for tide levels of (a) 0.2 m, (b) 0.7 m, (c) 1.1 m, and (d) 1.2 m above lowest low tide. The dotted line in each plot indicates the diet breadth at which intake rate is maximized. See text for values of maximum attainable intake rate at each tide level.

sea star size with increasing tide level is evident in [Figure 3b](#). Sea stars in the 6.5 cm size class were first taken at a tide level of 0.68 m and sea stars in the 7.0 cm size class were first taken at a tide level of 0.88 m. The only observed sea star in a size class greater than 7.0 cm (a 7.8 cm sea star) was taken at a tide level of 1.18 m, which is close to the tide level (1.2 m) at which this size was predicted to be included in the diet.

#### Foraging effort and the tide cycle

The decrease in maximum attainable intake rate predicted by the tide-sensitive model indicates that the intertidal zone becomes an increasingly less profitable foraging habitat with increasing tide height. If gulls are tracking short-term environmental changes, they should gradually switch habitats or switch to nonforaging activities as habitat quality decreases. Indeed, there was a highly significant negative relationship between tide level and the number of actively foraging gulls at Roberts Creek (Poisson GLMM, slope and intercept  $P$ -values both  $<0.0001$ , pseudo- $R^2 = 0.564$ , [Figure 6](#)), indicating that an increasing proportion of the total gulls at the site on a given day either leave for alternative foraging grounds or switch to nonforaging behaviors as tide level increases. A similar analysis was performed using data on number of gulls present at the site (regardless of behavior), which showed an equally strong inverse relationship with tide level.

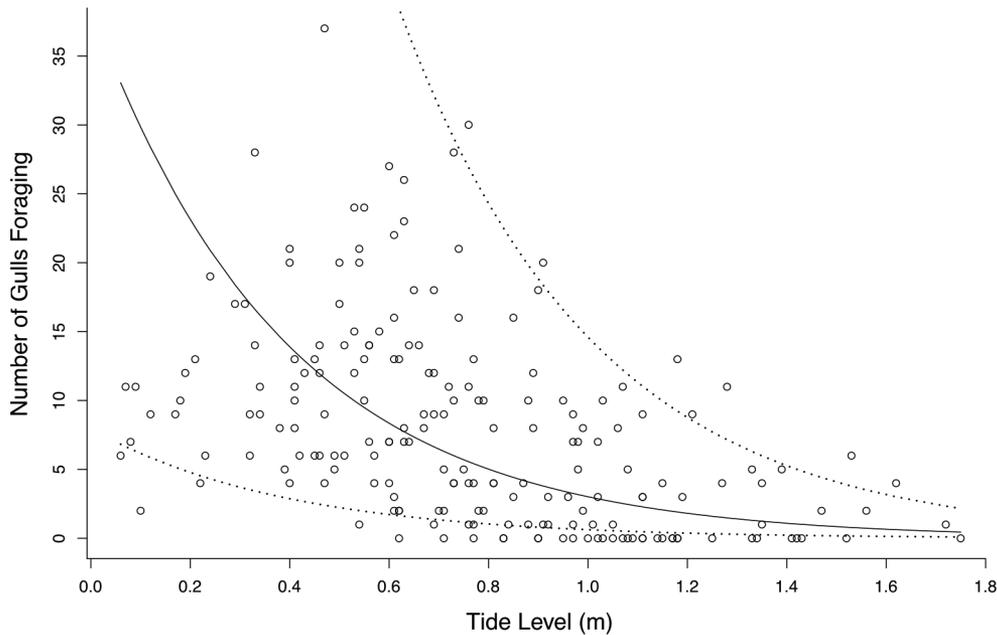
#### *Pisaster* biomass removed

We used Equation 4 to calculate the total biomass of sea stars removed by gulls on a particularly low tide (thus favorable for sea star foraging) day at Roberts Creek. On 11 July 2010, the

tide was between 0.7 and 1.1 m (intake rate = 0.29 kJ/s) for a total of 60 min and between 0.2 and 0.7 m (intake rate = 0.33 kJ/s) for a total of 180 min. Scan sample data revealed that a mean ( $\pm$ SE) of 8.2 ( $\pm 1.6$ ) gulls were actively engaged in foraging when the tide was high (between 0.7 and 1.1 m) and 11.8 ( $\pm 0.8$ ) gulls were foraging when tide was low (between 0.2 and 0.7 m). Substituting these values into Equation 4 yields an estimated 24127.3 g of sea star biomass removed on this date. Using the same procedure, we calculated biomass removal for 8 low tide periods around the above date (8–15 July 2010), representing the period between 2 neap tides when daily low tide was  $\leq 1.3$  m above MLLW. Over this range, gulls were estimated to remove 117091.3 g of sea star biomass.

#### DISCUSSION

In order to select a diet that provides the maximal energetic return, an animal must acquire information on its encounter rate with different prey types. The timescale over which a forager tracks changes in prey encounter rates should depend on how quickly the abundance of prey types in the environment changes ([Lucas 1983](#)). While long-term averages may be appropriate when prey abundance changes slowly (e.g., seasonally; [Scheel 1993](#)), encounter rates should be tracked over considerably shorter timescales in highly variable environments, such as the intertidal zone, where fluctuating tide levels can result in effectively continuous changes in prey abundance. Our data suggest that gulls foraging in intertidal areas of British Columbia track changes in prey encounter rates and adjust their diets over relatively short timescales in response to cyclical, tide-related changes in prey availability.



**Figure 6**

The relationship between tide level and the number of gulls engaged in foraging behavior at Roberts Creek, as estimated from 195 scan samples taken over 22 days. The solid line is the mean decline in number of foraging gulls with increasing tide level determined using a Poisson GLMM. Dashed lines are 95% confidence intervals determined by the model.

Our tide-sensitive diet model, which assumes that gull foraging decisions are based on changing prey encounter rate information rather than static estimates of prey abundance across the low tide period, provides an improvement relative to the classic diet model in explaining gull prey choice at Roberts Creek. The RSF analyses indicate that gulls increase selection on larger, less profitable *Pisaster* at higher (i.e., >0.7 m) tide levels, a result consistent with the predictions of the tide-sensitive model. The maximum acceptable sea star size therefore increases with tide height, as illustrated in Figure 3b. The tide levels at which diet expansion occurs are predicted with reasonable accuracy by the tide-sensitive diet model, and the discrepancies between prediction and observation are small relative to the applicable range of sea star sizes and tide levels.

The classic diet model cannot account for the seemingly excessive handling times that gulls devote to large (>6.5 cm) sea stars. Gulls consume *Pisaster* exclusively by swallowing individuals whole, regardless of sea star size. *Pisaster* handling time is an exponentially increasing function of body size (Figure S1, see also Suraci and Dill 2011), and there is thus an appreciable difference in handling time between sea stars predicted by the classic diet model to be included in the diet (upper size class = 6.5 cm, handling time = 6.9 min) and the largest sea star applicable to this study (7.8 cm, handling time = 24.5 min). The classic diet model suggests that handling large sea stars will result in submaximal energy intake rates due to the likelihood of encountering a more profitable prey type if this time were instead used for searching. However, observations of gulls consuming sea stars in the 7.0 cm and larger size classes are not uncommon; we report 8 such observations in this study, and these only include sea star consumptions that were recorded during random focal samples (2009 and 2010 field seasons) or videotaped scan samples (2010 only) (i.e., only observations for which sea star size could be estimated from video). This behavior occurred in both years of the study and throughout all months of the field season (May–August).

The tide-sensitive diet model accounts for the decreasing availability of highly profitable small sea stars with increasing tide height (Figure 4) and indicates that, at tide levels of 0.7 m and above, a gull will maximize its intake rate by including larger sea stars in its diet.

Energy intake rate maximization appears sufficient to explain the majority of diet choices for gulls foraging at our field site and provides an approximation of the way in which diet breadth changes with prey availability throughout the tide cycle. However, there were some discrepancies between the predicted and observed diets. For example, Figure 3b suggests that gulls adjust their diet breadth with changes in tide level at a finer scale than that predicted by the model, apparently ignoring all sea stars larger than 6.0 cm at tide levels less than 0.6 m. All of the components of the diet model—prey energy content and handling time, relative abundance, search time, and metabolic cost of searching—are estimates (averages or predictions from statistical models) with their own inherent error, which is not accounted for by the model. That this would lead to some inaccuracy in the ability to predict energetic intake rates and the exact tide levels at which diet breadth should change is likely.

Energetic intake rate is not the only factor affecting animal prey choice decisions, and models based solely on this currency have failed to adequately predict diet in several consumer–resource systems (Belovsky 1984; Sih and Christensen 2001; van Gils et al. 2005). Consideration of digestive constraints on the amount of material consumed often improves predictions of forager diet choice (Verlinden and Wiley 1989; Fortin et al. 2002; Jeschke et al. 2002; van Gils et al. 2005), though exceptions exist (e.g., Babin et al. 2011). Digestive constraints are expected to play a role in diet selection in the majority of foragers, whenever prey are handled and consumed more rapidly than they are digested (Jeschke et al. 2002). Several authors have found evidence that diet choice by avian predators foraging on marine invertebrates is affected by the large volumes of indigestible material that they must process to extract energy from their hard-bodied

prey (Bustnes and Erikstad 1990; Zwarts and Blomert 1990; Guillemette 1998; Hamilton et al. 1999; Heath et al. 2010). Gulls in our study may have been subject to a similar digestive constraint when foraging on *Pisaster*, a factor that was not considered by either diet model and may have affected our ability to accurately predict changes in diet breadth.

The classic foraging theory prediction that a predator should include less profitable prey types in its diet as the encounter rate with more profitable types decreases (MacArthur and Pianka 1966; Pulliam 1974; Charnov 1976) has found support from several studies on both laboratory (Elner and Hughes 1978; Perry 1987; Sih and Petranka 1988; Berec et al. 2003) and field systems (Richardson and Verbeek 1986; Scheel 1993; Rödel et al. 2004; Fontaine et al. 2008; for more exhaustive lists, see Stephens and Krebs 1986; Sih and Christensen 2001). These studies generally calculate prey encounter rates using site-level abundance estimates or averages of encounter rates across the entire foraging period, either for logistical reasons or due to an implicit assumption that this timescale matches that at which foragers update encounter rate information (Fortin et al. 2002). However, when encounter rates vary over short timescales, a forager will improve its energy intake rate by instead basing prey choice decisions on short-term averages (Lucas 1983; Barkan and Withiam 1989; Gass and Roberts 1992; Fortin et al. 2002). We used a straightforward extension of the classic foraging algorithm that allows short-term re-estimation of prey encounter rates in a complex field situation. By applying the same restrictions to prey abundance estimates that the incoming tide would apply to gull prey availability, we achieved a better fit between the diet breadth model predictions and observed prey choice than was possible when tide was ignored. This approach shows that gulls are capable of closely tracking changes in the prey distribution over short timescales and adjusting their behavior accordingly to maximize energetic return. Ward (1993) found a similar effect of tide on black oystercatcher (*Haematopus moquini*) diet, though over a spatial rather than temporal scale (i.e., through prey zonation rather than tidal flux).

Several previous studies on birds foraging in tidally structured environments have demonstrated that these predators adjust their foraging behavior throughout the tide cycle, switching foraging habitats on a tidal schedule in a way consistent with maximizing overall site profitability (Connors et al. 1981; van Gils et al. 2006; Schwemmer and Garthe 2008). Our data suggest that glaucous-winged gulls use a similar site-switching tactic, gradually moving away from the intertidal zone as habitat quality (i.e., maximum attainable intake rate) decreases with increasing tide level (see Figure 6). This study extends the finding of tide-related changes in foraging site use to show that, even within a site, prey choice behavior may be dynamic over the course of a single low tide period, with gulls adjusting their diet breadth to adaptively exploit changes in prey availability. Theoretical work by McNamara et al. (1993) suggests that, when foragers have the option of exploiting multiple patches, as is likely the case here, prey choice will be independent of patch composition, leading to a constant diet within and between patches. However in our system, the optimal tactic is likely to depend on time constraints placed on foraging by the tide cycle (time constraints were not considered in the McNamara et al. models), as well as the extreme differences in quality/productivity of available foraging habitats (e.g., intertidal zone, offshore habitats, human refuse dumps). An assessment of foraging habitat alternatives was beyond the scope of this study, but our findings indicate that gulls combine adaptive diet breadth and patch selection when foraging in the intertidal zone.

This study contributes to a growing literature identifying birds as major players in many rocky intertidal communities (e.g., Marsh 1986; Wootton 1995, 1997; Hori and Noda 2001; Ellis et al. 2005, 2007). For instance, Ellis et al. (2007) demonstrated an intertidal trophic cascade generated by gull (*Larus marinus* and *L. argentatus*) predation on crabs (*Cancer borealis*) that impacts species densities over at least 3 trophic levels and may affect primary productivity. The present study expands on this body of work in 2 ways. Firstly, we offer an alternative to the common interpretation of *Pisaster* as a top predator in its community (Paine 1963, 1966; Navarrete et al. 2000) with “no important predators of its own” (Mauzey 1966, p. 128). We found that, when daily tidal fluctuations are particularly favorable for sea star foraging, gulls at Roberts Creek can remove up to 24 kg of sea star biomass in a single 4 h low tide period, and up to 117 kg over a span of 8 days. We suggest that such high levels of gull predation may impact *Pisaster* population structure and affect this sea star’s well-described ability to promote intertidal biodiversity through consumption of mussels (Paine 1966; Menge et al. 1994; Robles et al. 1995; Sanford 1999). Gulls exhibit a strong preference for small sea stars (Suraci and Dill 2011) and the majority of gull predation pressure is concentrated on sexually immature individuals; Menge (1975) found that *Pisaster* mature at approximately 90 g, corresponding to a radius of approximately 5.0 cm (Suraci J, unpublished data), and thus 73% of the 265 observed sea star consumptions reported here were of immature juveniles. Additionally, despite tide-related expansion of the gull diet to include larger *Pisaster* sizes, gulls only exploit a fraction of the sea star population at Roberts Creek. The most abundant *Pisaster* sizes, adults of  $\geq 10$  cm radius, are completely excluded from the diet at all tide levels (Figure S2). Future investigations of the impact of gull predation on the *Pisaster* population should account for size selectivity, and how it changes with tide level, as this may have substantial consequences for sea star demography (De Roos and Presson 2002; De Roos et al. 2003) and mussel consumption rates.

Secondly, our finding of diet optimization over time frames shorter than a single low tide period is likely to generalize to other intertidally foraging birds and to diet sets containing multiple prey species (rather than sizes of single species). Understanding the impact of avian predators on marine invertebrate prey abundance is necessary for a complete understanding of intertidal food web structure (Marsh 1986; Ellis et al. 2005). Our results suggest that, when estimates of avian impact on a prey species are based on observations of prey removal rates (e.g., Wootton 1997), it may be necessary to account for changes in these rates as prey abundance fluctuates with tide level. This may lead to an improvement relative to estimates based on average removal rates over an entire tide cycle, illustrating the importance of incorporating information on foraging decisions into studies of community-level processes.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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