PREY CHOICE DECISIONS BY GLAUCOUS-WINGED GULLS: ENERGETIC AND ANTI-PARASITIC HYPOTHESES FOR SIZE SELECTION OF SEA STARS

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Abstract

Gulls are among few reported predators of the Ochre Sea Star *Pisaster ochraceus*, an ecologically important intertidal species. However almost no information exists on rates of sea star predation and factors affecting gull foraging decisions. In this study, I report high (up to 90%) occurrences of sea stars in the diets of intertidal foraging Glaucous-winged Gulls *Larus glaucescens*. Field-based prey choice experiments revealed that the probability of a gull selecting the most energetically profitable sea star sizes was high, but decreased significantly with increasing kleptoparasitism risk. Comparison of optimal diet breadth models suggests that tide related changes in prey availability strongly influence the range of sea star sizes consumed by gulls. Anti-parasitic properties of sea stars, while potentially reducing gull parasite load, appear to have little effect on prey choice decisions. The implications of high rates of size-selective sea star predation by gulls for intertidal community structure are discussed.

Keywords: Glaucous-winged Gull; *Pisaster ochraceus*; prey choice decisions; kleptoparasitism; self-medication; optimal diet breadth

Dedication

To my family – James, Joi Lynn, Anthony, and Angela – who have always supported me and been a source of inspiration

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1: Introduction

The foraging decisions of free-living animals are subject to a complex array of intrinsic and extrinsic influences. Energy acquisition is tightly linked to forager fitness (Hamilton 2010), and optimal foraging models based on energy intake rate-maximization alone have seen considerable success in explaining foraging behaviour in a range of taxa (Stephens and Krebs 1986, Sih and Christensen 2001). However, several factors, including inter- and intraspecific competition (Nilsson et al. 2000), forager experience (Marchetti and Price 1989), temporal fluctuations in the prey distribution (Lucas 1983), digestive constraints (van Gils et al. 2005), and even parasitism and disease risk (Lozano 1991), may interact with prey availability and energetic profitability to drive observed patterns of foraging behaviour. A thorough investigation of the potential role of such factors is therefore important in studies of the foraging decisions of natural populations for which the controlled conditions of the laboratory are not available. This is particularly true when examining economically or ecologically important predator or prey species – the details of the way in which a predator exploits its prey resource (i.e., selectively vs. opportunistically, with or without a substantial social influence) are suggested to play an important role in predator-prey population dynamics (van Baalen et al. 2001, Holt and Kimbrell 2007).

The prey choice behaviour of Glaucous-winged Gulls *Larus glaucescens* when foraging on Ochre Sea Stars *Pisaster ochraceus* provides an excellent example of the need to investigate the potential impacts of diverse influences when attempting to understand forager behaviour. The impetus for the studies described in this thesis was the observation that gulls foraging in coastal areas of southern British Columbia, Canada frequently consume large *Pisaster*, which require exceptionally large amounts of time (> 20 minutes in some cases) to fully ingest. Such long handling times would appear to result in low energetic profitability and substantial costs in terms of missed opportunities to find and consume higher quality prey. However, energetic profitability alone may be particularly misleading in this system: gulls forage in large aggregations and exploit highly variable intertidal environments. They must therefore contend with high rates of intraspecific kleptoparasitism (Brockman and Barnard 1979, Burger and Gochfield 1981) and a prey distribution that changes continually with the ebb and flow of the tide (Lucas 1983, van Gils et al. 2006). Additionally Glaucous-winged Gulls in the study area experience high rates of parasitic infection (Levine 1953; Ching 1978; Hoberg 1981, 1984) and may alter their diets either to avoid exposure to parasites (Hart 1990, Lozano 1991) or to protect themselves against or even treat existing parasitic infections through adaptive self-medication (Clayton and Wolfe 1993, Lozano 1998). Here I use the framework of rate maximizing foraging theory to investigate the role of each of these potential influences in driving gull selection of sea star sizes in the field and the inclusion of large, low profitability stars in their diet.

In Chapter 2, I use data from behavioural observations and laboratory energetic analyses to characterize the relationship between *Pisaster* size and energetic profitability. I then use field-based prey offer experiments to test the hypothesis that, when prey are equally available, profitability is the primary driver of sea star size choice. This design also allowed me to examine the influence of intraspecific kleptoparasitism risk on star size selection. Previous work on gulls (e.g., Hockey and Steele 1990) and other taxa (e.g., Northern Pike *Esox lucius*; Nilsson et al. 2000) indicates that foragers at high risk of kleptoparasitic attack will switch their diet preferences away from the most energetically profitable prey, thereby rendering themselves less desirable targets for food theft. A similar mechanism may act on sea star size choice by gulls in intertidal foraging groups.

In Chapter 3, I use optimal diet breadth models (Charnov 1976, Richardson and Verbeek 1986) to examine the range of sea star sizes taken by gulls at an intertidal site. Encounter rates with available prey types are considered of primary importance in determining diet breadth (Stephens and Krebs 1986). When these rates remain relatively constant or change gradually over time, it is reasonable to assume that foragers can estimate encounter rates with considerable accuracy (Fortin et al. 2002, Berec et al. 2003, Rödel et al. 2004). However, in highly variable environments such as the intertidal zone, the possibility arises that the time required for a forager to update its estimates of prey encounter rates exceeds the time over which these rates actually persist, leading to sub-maximal energetic intake rates. Modelling work by Lucas (1983) has shown that such high environmental variability should select for rapid updating of information regarding the prey distribution, but empirical studies in which the timescale of information updating by foragers is explicitly tested are surprisingly rare (but see Ward 1993). In this chapter I compare two diet models that differ in their assumptions regarding the timescale of information updating by gulls to determine (i) whether these birds are capable of tracking rapid changes in the prey distribution caused by tidal flux, and (ii) whether energy intake rate maximization is sufficient to explain observed gull diet breadth, particularly the consumption of large, low-profitability sea stars.

Finally, Chapter 4 examines the potential for adaptive self-medication by gulls when feeding on *Pisaster* and whether this plays a role in size selection and the consumption of large stars. Self-medication behaviour involves an animal exploiting the antipathogenic properties of other organisms, or the substances they produce, to protect itself against parasites or ameliorate the symptoms of infection (Clayton and Wolfe 1993). While somewhat controversial (Sapolsky 1994, Castella et al. 2008), self-medication behaviour has been implicated in a variety of foraging (e.g., Wrangham and Nishida 1983, Huffman 2001, Singer et al. 2009) and non-foraging (e.g., Gwinner and Berger 2005, Castella et al. 2008) contexts. Sea star consumption may provide anti-parasitic benefits via at least two mechanisms, both of which are likely to scale with star size. Sea stars produce saponins, highly bioactive compounds with known antipathogenic properties (Julien et al. 1985, Hostettmann and Marston 1995), the consumption of which may negatively affect the survival and reproduction of gull gastro-intestinal parasites. Additionally, sea stars are bulky prey and, when swallowed whole (the only means by which gulls consume stars), may serve to dislodged attached endoparasites through mechanical abrasion, as has been observed for chimpanzees *Pan troglodytes* and other great apes swallowing large quantities of coarse plant material (Huffman 2001). I test for both the existence of antiparasitic benefits of sea star consumption and their potential role in driving size selection by gulls through analyses of sea star saponin content and the relationship between gull parasite load and the size of sea star consumed.

In addition to providing an excellent test case for the role of diverse intrinsic and extrinsic factors in driving foraging behaviour in natural populations, the gull-sea star system represents an important ecological interaction due to the widespread co-occurrence of both species and their strong ecological roles. Glaucous-winged Gulls are highly abundant throughout the Strait of Georgia in British Columbia, where this study took place (Badzinski et al. 2006). These generalist foragers take a broad diet, ranging from fish and invertebrates to human refuse (Trapp 1979, Vermeer 1982), yet previous studies have reported low (if any) occurrences of sea stars in the gull diet (Vermeer 1982, Irons et al. 1986, Snellen et al. 2007). A close link between diet quality and reproductive success has been demonstrated for this species (Murphy et al. 1984) and the closely related Western gull *L. occidentalis* (Annett and Pierotti 1999), emphasizing the importance of prey choice decisions for gull fitness.

Pisaster is also highly abundant in the Strait of Georgia and throughout its range from southern Alaska to Baja Califronia (Feder 1959). *Pisaster* is an ecologically important intertidal predator – the original "keystone species" (Menge et al. 1994) – with the ability to significantly affect intertidal community structure and species richness by limiting the distribution of its main prey, mussels (*Mytilus* spp.; Paine 1974, 1976; Robles et al. 1995). The local impact of *Pisaster* on mussel distribution is dependent on sea star density (Paine 1974) and it follows that substantial predation on *Pisaster* would restrict the ability of this species to shape intertidal community structure. However, *Pisaster* has generally been considered a top-predator, experiencing little if any top-down control (Mauzey 1966), a viewpoint consistent with the low rates of gull predation reported in previous studies. In contrast, I report high (up to 90%, Chapter 2) occurrences of sea stars in the Glaucous-winged Gull diet, which suggests a possible role for this species in top-down control of local *Pisaster* populations, and thus an indirect role in structuring intertidal communities. No information currently exists regarding gull prey choice when foraging on *Pisaster*, and several aspects of this interaction, including size-selective predation, may affect the impact of gull predation on local sea star density and recruitment. This study therefore serves both to illustrate a comprehensive approach to understanding foraging behaviour in a complex natural system and to provide information on an undescribed and potentially ecologically important predator-prey interaction of particular interest to intertidal ecologists.

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2: Energetic profitability interacts with kleptoparasitism risk, but not forager age, to drive size selection of Ochre Sea Stars by Glaucous-winged Gulls

2.1 Abstract

Net energy gain is thought to play a central role in the prey choice decisions of most foragers, yet its effect may be masked by factors including food theft avoidance, and the ontogeny of foraging skills. I investigated predation by the Glaucous-winged Gull *Larus glaucescens* on the ecologically important Ochre Sea Star *Pisaster ochraceus*, an only recently reported predator-prey interaction for which no information exists on factors affecting prey choice. I tested the hypothesis that *Pisaster* size selection by gulls was based on energetic profitability. I then examined the degree to which profitability interacts with intraspecific kleptoparasitism risk and age-related foraging efficiency to produce the patterns of prey choice observed in a natural setting. Behavioural observations of free-living gulls revealed moderate to high (32.5% - 91.6%) occurrences of *Pisaster* in gull diets. I used handling time data and bomb calorimetry to determine the relationship between sea star size and energetic profitability, which informed prey offer experiments that allowed me to test hypotheses regarding gull prey choice. I show that gulls readily discriminate between *Pisaster* sizes based on energetic profitability, choosing the most profitable sea star in 60% of trials. Prey discrimination ability does not differ between gull age classes and thus does not contribute to the reduced foraging efficiency of juveniles. However generalized linear modelling revealed a highly significant effect of intraspecific kleptoparasitism risk on prey choice whereby gulls exhibit a non-linear decrease in preference for highly profitable sea stars with increasing risk.

2.2 Introduction

Foraging theory suggests that, in order to maximize the fitness returns from foraging behaviour, an individual must successfully discriminate between available prey types, investing time and energy into the consumption of prey types that maintain a high energy intake rate (or low starvation risk) and ignoring those that don't (Stephens and Krebs 1986, Hamilton 2010). Energetic profitability, defined as the amount of energy provided by a prey item per unit of time required to capture and consume that prey (handling time), is considered an important characteristic by which foragers judge the relative value of different prey types (Elner and Hughes 1978, Richardson and Verbeek 1986, van der Steen 1998, Sih and Christensen 2001). However, due to the potential for alternative dietary considerations (e.g. nutrient intake rate, Pulliam 1975; toxin avoidance, Belovsky and Schmitz 1994; minimization of indigestible material in diet, Bustnes and Erikstad 1990), the possibility of imperfect prey discrimination (Draulans 1984, Ward 1991, Hamilton et al. 1999), and tradeoffs between prey quality and the risk of food theft (Hockey and Steele 1990, Langen and Rabenold 1994, Nilsson et al. 2000), it is often unclear to what extent foragers use information on energetic profitability differences when selecting prey in complex field settings. Thus, while selection of the most energetically profitable prey type suggests adherence to an optimal diet (Berec et al. 2003, Snellen et al. 2007), apparently suboptimal prey choices may not indicate a misapplication of the theory, but rather the presence of an unmeasured factor affecting relative prey value (Sih and Christensen 2001). Investigation of factors that interact with energetic profitability in driving forager prey choice is therefore essential to understanding patterns of resource use in natural populations.

Here I examine predation by the Glaucous-winged Gull *Larus glaucescens* on the Ochre Sea Star *Pisaster ochraceus* (hereafter *Pisaster*), two highly abundant species on the Pacific coast of North America. *Pisaster* is an ecologically important intertidal predator (Menge et al. 1994) whose abundance affects intertidal community structure (Paine 1974, Robles et al. 1995). Gull predation on this sea star may therefore play an important role in the stability of intertidal systems, yet no previous information exists regarding gull prey choice when foraging on *Pisaster*.

Food theft, or kleptoparasitism (Giraldeau and Caraco 2000, Morand-Ferron et al. 2007), can be costly to the host individual in terms of energy and time spent searching for and/or handling prey items that are not ultimately consumed. Additional costs are incurred by species in which kleptoparasitic attack results in energetically demanding high-speed aerial chases or potentially dangerous aggressive interactions, as is the case for gulls (family Laridae) and other sea birds (Brockman and Barnard 1979, Burger and Gochfield 1981, Giraldi 1994). Several species for which kleptoparasitic attacks are common have been shown to shift their prey choices away from the most energetically profitable (and therefore most hotly contested) prey types in situations where the risk of food theft and/or aggressive interactions is high (Hockey and Steele 1990, Langen and Rabenold 1994, Nilsson et al. 2000). Thus foragers may pay a cost in terms of energy intake rate, manifested as the selection of lower quality prey, in order to reduce the risk of theft. Kleptoparasitism risk in this context is the likelihood that potential food thieves will attempt to steal a particular prey item, which is presumably assessed by a forager prior to prey selection. The interaction between kleptoparasitism risk and prey quality is likely to be dependent on the local density of conspecifics, and a characterization of the relationship between local density and risk-related diet shift will improve understanding of resource use for any species that commonly forages in aggregations.

For components of foraging behaviour such as prey capture and consumption, there is a well documented increase in efficiency associated with gull age, such that adult gulls have higher energy intake rates and therefore require less foraging time than juveniles to meet energetic demands (Verbeek 1977, Searcy 1978, Burger and Gochfield 1981, Greig et al. 1983, Skorka and Wojcik 2008). Several species of *Larus* defer breeding for up to four years (Greig et al. 1983, MacLean 1986), and delayed maturation is frequently attributed to the amount of learning required by juveniles to master the complex foraging techniques employed by many gull species (Searcy 1978, MacLean 1986, Marchetti and Price 1989, Forslund and Pärt 1995). Here I am interested in whether the ability to discriminate between prey types based on energetic profitability, and by extension the ability to select an energetically optimal diet, differs between adult and juvenile gulls. Prey discrimination ability could act in concert with prey capture and consumption efficiencies in mediating the decreased energy intake rates of juvenile gulls, and may indeed be one of the skills under development during delayed maturation. However this possibility has not previously been explored.

A sizeable literature exists on the diet of the Glaucous-winged Gull (Barash et al. 1975, Trapp 1979, Vermeer 1982, Murphy et al. 1984, Irons et al. 1986, Skagen et al. 1991, Wootton 1997), and the ecologically similar Western Gull (*L. occidentalis*; Maron 1982, Annett and Pierotti 1999, Snellen et al. 2007). Previous studies either fail to mention *Pisaster* as a prey type for these species (e.g. Trapp 1979, Wootton 1997), or cite extremely low dietary occurrences of sea stars - between 0.4 and ~10% (e.g. Irons et al. 1986, Snellen et al. 2007). However, anecdotal evidence and my preliminary observations suggest that *Pisaster* is a common prey species for Glaucous-winged Gulls in rocky intertidal areas of southern British Columbia. *Pisaster* exhibits indeterminate growth (Paine 1976, Sebens 1987), and a large range of sizes (from < 1 to > 20 cm radius; pers. obs., Paine 1976) occurs at intertidal sites. Thus *Pisaster* does not represent one distinct prey type, but rather a range of prey types that vary continuously in energetic profitability. This may lead to difficulty in distinguishing between prey (Hughes 1979, Ward 1991), particularly for inexperienced foragers.

In this study I use a combination of laboratory energetic analysis, field-based behavioural observations, and prey choice experiments to address the following questions: (i) Does *Pisaster* constitute a major prey species for Glaucous-winged Gulls foraging in the study sites? (ii) Are gulls able to distinguish among sea star sizes on the basis of energetic profitability and are profitability differences the main driver of prey choice? (iii) Does prey discrimination ability differ between gull age classes? (iv) Does kleptoparasitism risk affect the relative value of individual seas stars and active size choice by gulls, and if so how does this effect change with local gull density?

2.3 Methods

2.3.1 Field Sites

Field studies were conducted from April to September 2009 and April to August 2010 at two sites in southern British Columbia: Stanley Park (49°18'10"N, 123°

7'35"W), approximately 2 km from downtown Vancouver, and Robert's Creek (49°25'48"N, 123°40'25"W), a partially wooded, but largely residential area on the Strait of Georgia. Glaucous-winged Gulls and Ochre Sea Stars were abundant at both sites, and preliminary observations suggested that sea stars made up a substantial portion of the gull diet at these sites. Roberts's Creek is a rocky intertidal habitat dominated by rock weed, *Fucus gardneri*, with considerable barnacle (*Semibalanus cariosus* and *Balanus glandula*) cover. Stanley Park has a mixed substrate consisting of mud and sand with small- to medium-sized boulders. This site is located on Burrard Inlet, a major shipping and recreational waterway for the city of Vancouver and is therefore subject to considerable industrial input and human disturbance. The upper shore levels at Stanley Park are dominated by blue mussels, *Mytilus edulis*, while the lower intertidal zone is mainly covered by kelp, *Nereocystis luetkeana* and *Laminaria saccharina*. All fieldwork was conducted from 2 hours before to 2 hours after daily low tide on days when the tidal minimum was ≤ 1.3m. This range represents both the time of day and tidal period when gull intertidal foraging and group size was at a maximum (pers. obs., Irons et al. 1986), thereby reducing the likelihood of obtaining multiple measurements from single individuals. Daily foraging group size peaked, on average, at 37.2 gulls (peak range = 18 to 62 gulls) at Robert's Creek and 38.5 gulls (peak range = 19 to 65 gulls) at Stanley Park.

2.3.2 Behavioural Observations

I conducted approximately 260 hours of behavioural observations over the two field seasons. Data collection was conducted both visually (non-focal prey consumptions; see below) and using a Canon high definition digital camcorder (HDV 1080i; focal individual sampling and group videos; see below). I conducted focal animal sampling (Altman, 1974) on randomly selected gulls foraging in the intertidal zone. Focal samples lasted for a maximum of 10 minutes or until the gull left the intertidal zone. These samples provided a continuous record of all behaviours and prey choices and were used to determine handling times and encounter rates for all common prey types. The behavioural observation method termed "Group Videos" was developed to increase data for handling and search times. This procedure consisted simply of videotaping a group (2 to 10) of foraging gulls rather than following a single individual. Individuals could then be "followed" during video analysis to obtain handling time and encounter rate data. Opportunistic handling time measurements from non-focal gulls were also recorded when observed.

I analyzed all behaviour video data digitally using iMovie HD version 6.0 (© Apple 2006). Handling times and search times were measured to the nearest 0.1 second. For each consumption event, I also noted time of day, tide level (relative to minimum low tide for the site), and age class of the gull. Gulls were divided into two age classes, *juvenile* and *adult*, based on plumage characteristics. The juvenile age class consisted of birds in their second, third, and fourth summer plumages (Howell and Dunn 2007). As this study was conducted during the breeding season, first summer gulls were rare on the foraging grounds, and when they did occur (in mid to late August), they were excluded from analyses.

I developed a method of estimating *Pisaster* size relative to gull beak length using video screen shots and the free image processing software ImageJ. ImageJ allows one to set a specific number of pixels in an image equal to a length of the user's choice and then take subsequent measurements using this predetermined pixels-per-unit-length setting. The procedure involved setting the pixels corresponding to gull beak length equal to the average Glaucous-winged Gull beak length of 5.9 cm (James-Veitch and Booth 1954) and then measuring *Pisaster* size relative to this value. All *Pisaster* sizes were estimated (to 0.1 cm) as the length of the longest ray, essentially the radius of this radially symmetrical animal. I tested the validity of this method by measuring the ray length (using measuring tape) of 58 sea stars (between 0.8 and 6.7 cm radius) and videotaping gulls handling these stars. A size estimate was then obtained for each using the video method. The average of the absolute value of the difference between measured and estimated star size was 0.14 cm (sd = 0. 10 cm, max difference = 0.4 cm). I found no significant difference between the measured and estimated values (one-way ANOVA, F = 0.001, p = 0.98).

Gull fecal samples, collected for a separate study on the relationship between diet choice and parasite load (see Chapter 4), were here analyzed for presence or absence of

Pisaster ossicles (small bone-like structures which pass relatively intact through the gull digestive system). This provided a measure of the occurrence of *Pisaster* in the gull diet. Fecal samples were randomly collected on July 23 and August 8-11, 2010 at Robert's Creek and on July 24 and August 19, 2010 at Stanley Park. Samples were collected in sterile plastic vials (50 ml Falcon Tubes) and stored in 10% formalin at 4° C until analyzed.

2.3.3 *Pisaster* Energetic Content

I used bomb calorimetry to estimate the energetic content of 33 sea stars throughout the range of sizes eaten by gulls (ray length 0.8 to 8.6 cm). Sea stars were collected during summer 2009 from both Robert's Creek and Stanley Park. I brought the sea stars back to the laboratory at Simon Fraser University on the day of collection where I measured their wet mass (to 0.01 g using an electronic balance) and ray length (to 0.1cm). Sea stars were then frozen at -20° C until needed. In preparation for bomb calorimetry, I homogenized individual sea stars in a Waring Blender and then lyophilized these homogenized star samples to ~ 30% original wet mass. Caloric content was then determined for 1 g sub samples from each sea star using a Parr 1341 Oxygen Bomb Calorimeter, following the procedure outline in the Parr manual. The relationships between *Pisaster* size and both energy content (scaled up to body size) and handling time were used to determine energetic profitability for sea stars throughout the edible range.

2.3.4 Prey Offer Experiment

I conducted cafeteria-style prey offer experiments in the field from May to August 2010 to test the hypothesis that gulls select between *Pisaster* sizes based on differences in energetic profitability, and to explore how kleptoparasitism risk and age interact with profitability to drive size choice. An experimental trial consisted of placing 4 sea stars of different sizes (see below) in a tight circle on an exposed surface (e.g. rock or sand) in the intertidal zone. Sea stars were placed such that they would be simultaneously encountered by, and equally available to, a foraging gull. The four *Pisaster* size classes used in each trial were SC1 (Arm length = 0.5 – 2.0 cm), SC2 (2.0 – 3.5 cm), SC3 (4.0 – 5.5 cm), and SC4 (6.0 – 7.5 cm). These size classes were chosen such that (i) the edible range of sizes was well represented in each trial and (ii) there was always one size class (SC2) that was distinctly more profitable than the others. A trial began when a foraging gull encountered a prey offering. I recorded the age class of the individual (juvenile or adult), which sea star was selected first, the order of additional sea stars taken (if this occurred), and the number of other gulls within 5 meters (as a proxy for kleptoparasitism risk).

2.3.5 Statistical Analyses

2.3.5.1 Classical Tests

When it was necessary to compare the means and variances of two distributions, I first subjected the data to the Shapiro-Wilks Test for normality. Data that passed this test were analyzed using one-way Analysis of Variance. If the normality assumption was not met, I used the non-parametric Wilcoxon's Rank Sum Test. Differences between proportional data were analyzed using Chi-squared Tests when the number of observations in each category was >5. When this was not the case, Fisher's Exact Test was used.

2.3.5.2 Sea Star Handling Time

I used a linear mixed effects model to analyze the relationship between handling time and sea star size, setting individual gull as a random effect to account for multiple handling time observations taken from some individuals. Parameter estimates derived from the mixed effects model were similar to those derived from a standard generalized least squares (gls) regression, however the AIC value for the mixed model was lower than that for the gls (498.85 vs. 501.34), so the mixed model was used. Handling time data were natural log-transformed to approximate a normal distribution and to correct for heteroscedasticity. Linear mixed effects models were fit using the lmer function from the package lme4 in R (R Development Core Team, 2008). As this function does not provide a measure of goodness-of-fit for the model, I report a "pseudo R^2" value, estimated as the square of the correlation between the predicted values from the model and the actual values of the response variable (ln(Handling Time)). Note that when the response variable is continuous (as is the case in this analysis), the above method is identical to that used to calculate an R^2 value for linear regression.

The decision not to include other covariates for which I have data in the handling time model was made because I am interested in assessing the relationship between handling time and size as generalized across sites, gull age classes, and tide levels. Predictions from this handling time model were to be used in generating estimates of the change in sea star energetic profitability with size and I wished these estimates to be applicable over a range of conditions.

2.3.5.3 Sea Star Energetic Content

I used standard linear regression analysis to determine the relationship between *Pisaster* body size and energy content. Caloric estimates for each sea star sample were first converted to kilojoules, and both variables (energy and body size) were natural log-transformed to linearize the relationship and homogenize the variance. Linear regression was then carried out using the lm function in R (R Development Core Team 2008).

2.3.5.4 Prey Offer Experiments

Chi-squared tests were used to compare selection frequencies of the four size classes (SC1 to 4). I was also interested in whether a particular size class was selected more or less frequently than would be expected due to chance alone. As one sea star of each size class was offered in every trial, the null expectation is that size classes should be selected in accordance with their proportional abundance of 25%. Chi-squared tests were used to determine whether actual selection frequencies differed from this value.

I used logistic regression (generalized linear model with binomial distribution) and stepwise model selection to evaluate several factors with potential effects on sea star size choice and the probability of selecting the most profitable sea star. The response variable in these models was a binomial variable describing whether the most profitable sea star (SC2) was selected first (1 = yes, 0 = no). Explanatory variables tested included (1) site - Stanley Park or Robert's Creek, (2) age of the focal gull – Juvenile or Adult, (3) kleptoparasitism risk – the number of conspecifics within 5 meters, and (4) Amount of time from daily tidal minimum (range = 0.03 to 2.17 hours). The last measure was chosen in place of a direct measurement of tide level to facilitate comparison across sites, as the magnitude of tidal flux during observation periods differed between the two sites (Robert's Creek: range = 0.1 to 1.8 m, Stanley Park: range = 0.3 to 1.6 m). Beginning with a full model that included all of the above terms plus the interaction between kleptoparasitism risk and time from tidal minimum, I followed the stepwise model selection procedure outlined by Zuur et al. (2009) in which the least significant term (the one with the highest p-value) is dropped, the model is refit, and a likelihood ratio test is performed between the new model and its predecessor. A p-value for this test greater than 0.05 suggests that the dropped term does not significantly affect the amount of deviance explained by the model. This procedure is continued until all terms in the model are significant at a confidence level of 0.05. For these models, data from all 75 trials were used. All logistic regression models were fit using the glm function in R (R Development Core Team 2008).

I predicted that the probability of selecting the most profitable sea star first in the prey offer experiments would decline with increasing risk of kleptoparasitism. The most profitable sea star size class (SC2) was not the smallest; it required a longer handling time than SC1, the smallest size class, and therefore allowed a greater opportunity for theft by kleptoparasites. I hypothesized that as the number of potential kleptoparasites in proximity to the focal gull increased, the gull's probability of selecting the most quickly consumed star over the most energetically profitable one would likewise increase. To test this hypothesis I used logistic regression, setting the probability of selecting the most profitable sea star as the response variable and the number of conspecifics within 5 meters of the focal gull as the explanatory variable. For this analysis I was only interested in trials in which either SC2 (the most energetically profitable size class) or SC1 (the most quickly consumed size class) were selected first (n = 70). All trials in which this was not the case (n = 5) were dropped from the analysis. To test the significance of the kleptoparasitism risk model, I performed a likelihood ratio test (with a chi-squared distribution) on the difference in explained (or residual) deviance between this model and a null model with no predictors (Hosmer and Lemeshow 2000). The chi-squared statistic in this test is the difference in residual deviance and the degrees of freedom is the difference in degrees of freedom between the two models.

2.4 Results

2.4.1 Dietary Occurrence of *Pisaster*

The diversity of prey types exploited by gulls and the degree to which they relied on *Pisaster* varied greatly between the two field sites. At Robert's Creek, *Pisaster* was by far the dominant prey type; out of a total of 322 observed prey consumptions, 91.6% (n = 295) of these were *Pisaster*. This predominantly sea star diet was supplemented by polychaete worms (*Nereis* spp.; 3.1%) and a set of small invertebrates (5.3%) which were too small to be identified visually, but consisted mainly of several species of gastropod as well as hermit crabs. Occasionally I observed a gull flying over the site with a cockle (*Clinocardium nuttalii*) or crab (*Cancer* spp.) in its mouth, but they were never observed to obtain these prey types at Robert's Creek. The prey community at Stanley Park is considerably more diverse, and *Pisaster* made up a significantly smaller proportion of the observed prey consumptions ($\chi^2_{[1]} = 279.5$, $p < 0.0001$). Of 526 observed prey consumptions, 32.5% (n = 171) were *Pisaster.* Other major prey types at this site included cockles, crabs (*Cancer productus, C. magister*), polychaete worms, mussels (*Mytilus trossulus*), urchins (*Strongylocentrotus droebachiensis*), and a "small invertebrate group" similar to the one described for Robert's Creek.

Gull fecal samples, randomly collected at the two sites, provide an additional measure of the occurrence of *Pisaster* in gull diets. At Robert's Creek, 90.0% of fecal samples (45 of 50) contained *Pisaster* ossicles, while only 12.5% (6 of 48) contained ossicles at Stanley Park. This difference was again highly significant ($\chi^2 = 55.87$, df = 1, $p < 0.001$).

2.4.2 Profitability Estimates: Handling Time and Prey Energetic Content

Handling times were recorded for a total of 223 sea star consumptions, observed at both sites over the two field seasons. Gulls at the sites consumed sea stars ranging in size from 0.8 to 8.6 cm radius. The linear mixed effects model showed a strong positive relationship between sea star size and gull handling time (T_H) (R^2 = 0.87; Fig. 2.1). Equation 1 shows the regression equation derived from this model.

$$[1] \qquad \ln T_H \text{ (sec)} = -0.17 + 0.93 * \text{Size (cm)}$$

While the statistical package used to fit the linear mixed effects model (see Methods) does not provide p-values for the parameter estimates, the 95% confidence limit for the slope (0.93 ± 0.08) does not cross zero, lending support for the significance of this relationship.

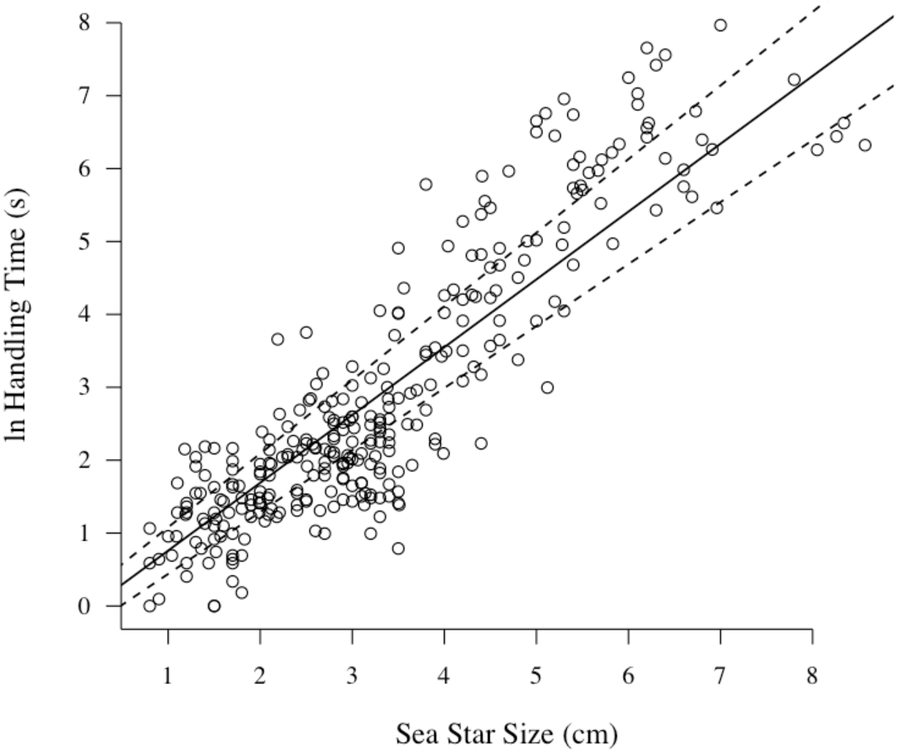

Figure 2.1: Relationship between *Pisaster* size (measured as longest ray length) and gull handling time as fit by linear mixed effects model. Handling time has been natural log-transformed to normalize the data. Dashed lines represent 95% confidence intervals around model fit.

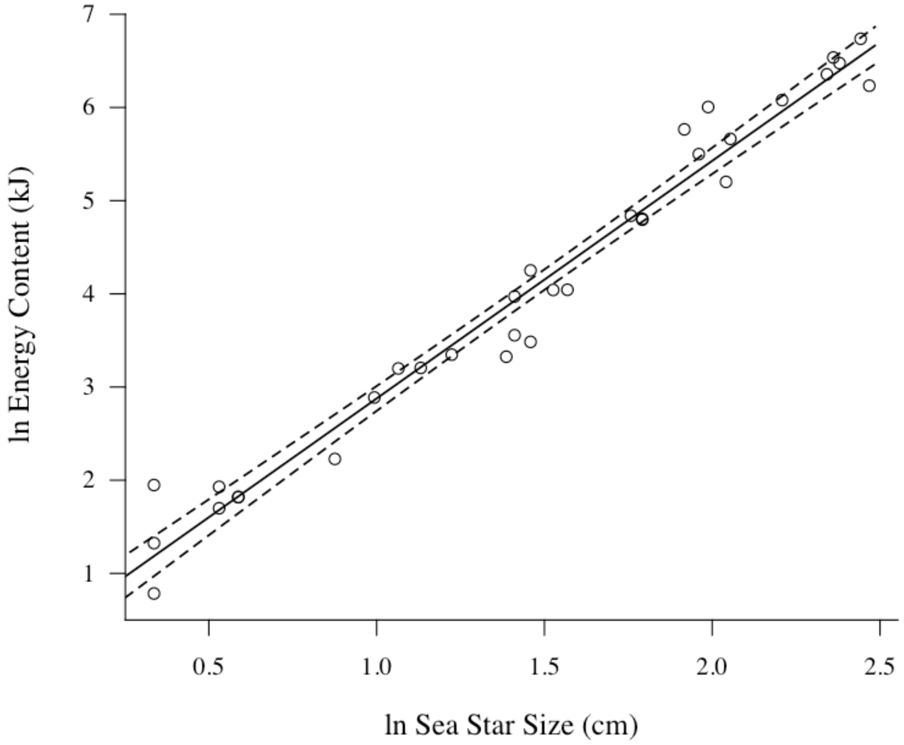

Figure 2.2: Relationship between sea star size (longest ray length) and energy content of the whole star as estimated by linear regression. Both variables have been natural log-transformed to normalize the data. Dashed lines represent 95% confidence intervals.

As expected, there is a strong positive relationship between *Pisaster* energy content (*E*) and body size ($P < 0.001$, $R^2 = 0.97$; Equation 2 and Fig. 2.2). In addition, the parameter estimate for the slope is highly significant at a confidence level of 0.05 (slope ± 95% CI = 2.55 ± 0.16, $p < 0.001$).

$$[2] \qquad \ln E\ (\mathrm{kJ}) = 0.33 + 2.55 * \ln \mathrm{Size}\ (\mathrm{cm})$$

Energetic profitability (*R*) is defined as the quotient of the energetic content (*E*) of a prey type and its handling time (T_H). I therefore calculated the profitability of sea stars throughout the edible range of sizes by dividing predictions from the energetic content regression by predictions from the handling time mixed model. This procedure produced a smooth curve of predicted *Pisaster* profitabilities (Fig. 2.3) and allowed me to estimate profitability for any star size. Sea stars having the highest profitability values are between 2.0 and 3.5 cm in radius, with profitability peaking at a value of 1.67 kJ/sec for

2.7 cm sea stars. Profitability declines quickly with both increasing and decreasing size, reaching a minimum of 0.13 kJ/sec for the largest sea star I saw taken by a gull in this study (size = 8.6 cm radius). I calculated the mean sea star profitability experienced by gulls in this study by averaging the profitability estimates of all observed sea star consumptions (excluding those in which I experimentally offered sea stars to gulls). The mean ± 1 S.E. profitability, when data from both sites are combined, was 1.27 ± 0.04 kJ/s. However, I found a significant difference in average energetic profitability of consumed sea stars at the two field sites (Wilcoxon Rank Sum, W = 1064.5, $p < 0.0001$). The mean ± 1 S.E. profitability at Stanley Park was 1.01 ± 0.08, compared to 1.37 ± 0.03 at Robert's Creek. To prevent pseudo-replication in the above estimates, average sea star profitability per individual was used when more than one sea star consumption was recorded from a single gull.

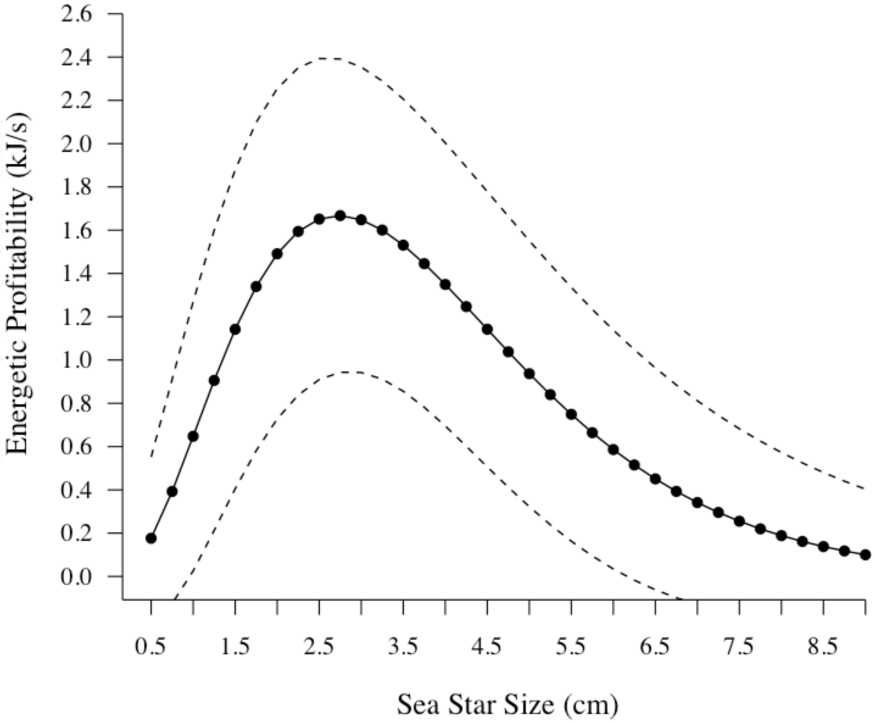

Figure 2.3: Estimated energetic profitability (kJ/s) for sea star sizes (measured as longest ray length) throughout the edible range. Estimates were derived by taking the quotient of predictions from the sea star energy content regression and the handling time mixed model (see text). Dashed lines are 95% confidence limits around mean energetic profitability. Confidence limits were determined using delta method variance approximation (Powell 2007).

2.4.3 Prey Offer Experiments

The most profitable size class, SC2, was selected first by foraging gulls in 60.0% of trials (45 of 75 trials, Fig. 4). This was significantly more than SC1 (33.3%; χ^2 = 9.67, df = 1, p = 0.002), SC3 (6.7%; χ^2 = 45.63, df = 1, p < 0.001), SC4 (0%; χ^2 = 61.46, df = 1, p < 0.001), and all three other size classes combined (40.0%, χ^2 = 5.23, df = 1, p = 0.022).

These results suggest that gulls select sea stars in relation to their energetic profitability. SC2 (profitability ± S.E. = 1.62 ± 0.01 kJ/s) was selected significantly more frequently than would be expected based on its 25% proportional availability (χ^2 = 17.39, df = 1, p < 0.001; Fig. 2.4). The selection frequency of SC1 (profitability ± S.E. = 1.03 ± 0.03 kJ/s), was not significantly different from the null expectation of 25% (χ^2 = 0.90, df = 1, p = 0.35), while both SC3 (profitability ± S.E. = 1.00 ± 0.01 kJ/s) and SC4 (profitability ± S.E. = 0.42 ± 0.01 kJ/s) were selected significantly less frequently than expected based on proportional availability (SC3: χ^2 = 8.13, df = 1, p = 0.004; SC4: χ^2 = 19.20, df = 1, p < 0.001).

For trials in which SC2 was chosen first and the focal gull chose a second sea star (n = 32), SC1 was chosen second (75% of trials) significantly more often than SC3 (25% of trials; χ^2 = 14.06, df = 1, p = 0.0002). There were a total of 25 trials in which SC2 was not chosen first (either SC1 or SC3 was first) and a second sea star was chosen. In 24 of these 25 trials (96%), this second sea star was SC2. SC3 was chosen second in one trial (4%), which constitutes a significantly smaller proportion (χ^2 = 38.72, df = 1, p < 0.0001).

In the logistic regression analysis of several factors with potential effects on sea star size choice, the only model term that, when dropped, resulted in a significant decrease in explained deviance (as determined by likelihood ratio test) was the number of conspecifics within five meters (χ^2 = 18.10, df = 1, p < 0.001). The terms for site, age of focal gull, time from daily low tide, and the interaction between number of conspecifics and time from low tide were excluded from the best model based on stepwise model selection (Zuur et al. 2009).

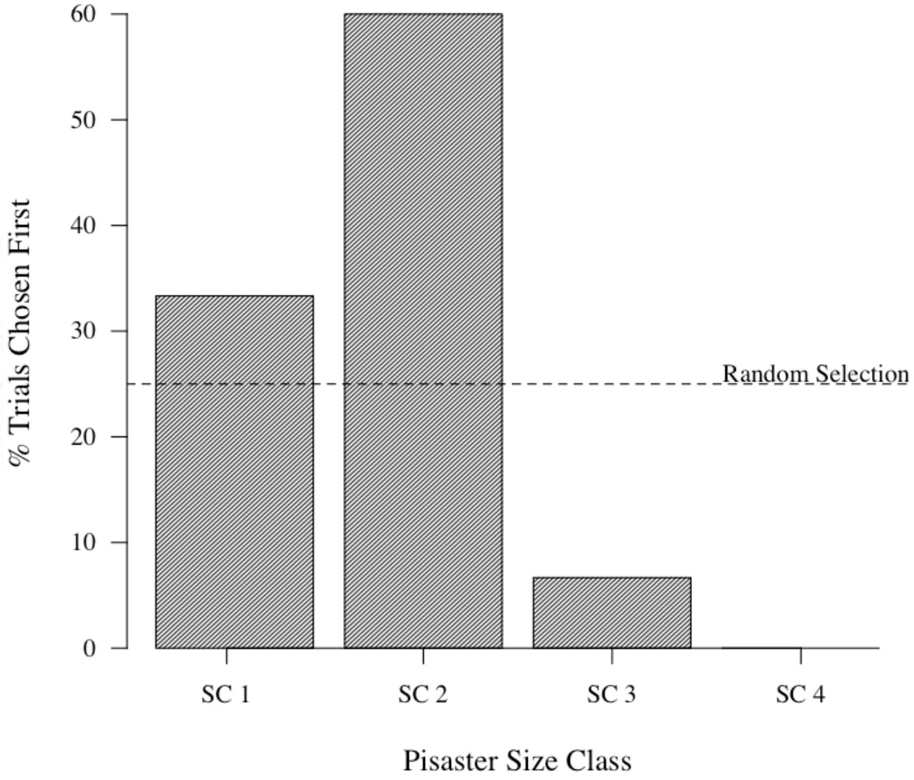

Figure 2.4: Percent of total prey offer trials in which each *Pisaster* size class was selected first. The four *Pisaster* size classes used in each trial were SC1 (Arm length = 0.5 – 2.0 cm), SC2 (2.0 – 3.5 cm), SC3 (4.0 – 5.5 cm), and SC4 (6.0 – 7.5 cm). The dashed line represents the null hypothesis of random selection.

The lack of an effect of both site and gull age on the probability of selecting the most profitable sea star first was confirmed by chi-squared tests. At Stanley Park, SC2 was selected first in 60.6% of trials (20 out of 33), which was not significantly different from Roberts Creek, where SC2 was selected first in 59.5% of trials (25 out of 42; $\chi^2 = 0$, df = 1, p = 1). Adult gulls selected SC2 first in 59.0% of trials (23 out of 39), compared to 61.1% for juveniles (22 out of 36 trials; $\chi^2 = 0$, df = 1, p = 1). When I only used data from trials in which the number of gulls within five meters was zero (i.e. when kleptoparasitism risk was removed), the proportion in which SC2 was selected first increased to 80.0% for adults and 93.3% for juveniles. This difference is again non-significant (Fisher's Exact Test, odds ratio = 0.29, p = 0.365).

Logistic regression showed a significant negative relationship between the number of conspecifics in proximity to a focal gull (i.e., level of kleptoparasitism risk) and the gull's probability of selecting the most profitable sea star (SC2) over the most quickly consumed (SC1; Fig. 2.5). Both the slope and intercept of this model were highly significant (Intercept: $p < 0.001$, Slope: $p = 0.002$), as was the amount of deviance explained by the model (Likelihood Ratio Test between residual and null deviance: $\chi^2 = 14.99$, $df = 1$, $p < 0.001$). According to the logistic regression model, the probability of a

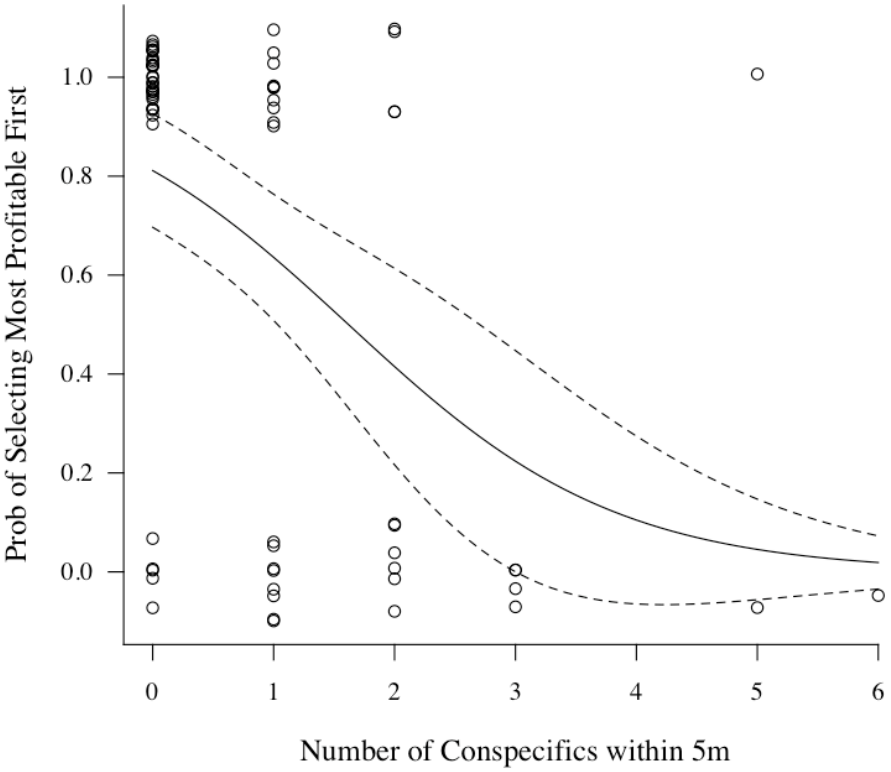

Figure 2.5: Probability of a gull selecting the most energetically profitable sea star in the prey offer trials given the number of other gulls within 5 meters. Data points correspond to individual trials in which the focal gull either selected the most profitable sea star (One) or the smallest, most quickly consumed sea star (Zero). A small amount of random noise has been added to the data to differentiate individual data points. The solid line represents predictions from a logistic regression model regarding the change in probability of a gull selecting the most energetically profitable sea star over the most quickly consumed as number of conspecifics (and therefore kleptoparasitism risk) increases. The dashed lines are 95% confidence intervals around these probability predictions, also produced by the logistic regression model.

gull selecting the most profitable sea star first declines from 81.1 ± 11.5% (95% CI) when no other gulls are within 5 meters, to 1.9 ± 5.4% when 6 gulls are in proximity (the maximum number of conspecifics I observed in the trials; see Fig 2.5).

2.5 Discussion

2.5.1 Occurrence of Sea Stars in Gull Diet

Previous studies suggest that sea stars, including *Pisaster ochraceus*, are not major prey types for gulls in the Northeastern Pacific, citing estimates of sea star occurrence in gull diets between 0 and 10% (Trapp 1979, Vermeer 1982, Irons et al. 1986, Wootton 1997, Snellen et al. 2007). This study, however, shows *Pisaster* is in fact an extremely common prey species, constituting more than 90% of the prey items consumed by Glaucous-winged Gulls at at least one intertidal site. The difference between my estimates and those of Vermeer (1982), who found the maximum occurrence of "starfishes" in gull diet to be 5.0%, are particularly interesting considering that he was also studying the diet of Glaucous-winged Gulls in the Strait of Georgia. Whether this difference is due to site selection, sampling method (he estimated prey occurrence from adult pellets and chick regurgitations), or an actual change in the use of sea stars as prey over the last three decades is unknown. Pearse et al. (2010) report an apparent increase in gull predation on *Pisaster* in Monterey Bay, California. However gulls in their study were observed to pick out the ambulacral regions of overturned stars, rather then swallow stars whole as reported here. Interestingly, the apparent increase in gull predation on sea stars coincides with an epizootic of the ciliate parasite *Orchitophyra stellarum*, which began infecting southern British Columbia *Pisaster* populations in high numbers around 1987 (Leighton et al. 1991). Infection with the ciliate, which causes castration and morbidity in male sea stars, results in reduced strength and rigidity of the sea star body wall (B.J. Leighton, pers. comm.). This may make stars easier for gulls to swallow, thus rendering them more attractive prey items.

The finding that *Pisaster* constitutes a major gull prey species is perhaps unsurprising, as the calculations of energetic profitability for this species, which range from 0.13 to 1.67 kJ/s, are comparable to those reported for other major prey types. Irons et al. (1986) found that the most profitable prey type taken by Glaucous-winged Gulls at intertidal sites in the Rat Islands, Alaska, was the chiton *Katharina tunicata*, which provided an energetic return of 2.06 kJ/s. Snellen et al. (2007), studying Western Gulls - a closely related species (Chu 1998) that commonly interbreeds with the Glaucous-winged Gull (Hoffman et al. 1978, Good et al. 2000) - found that the most energetically profitable size of purple urchin (*Strongylocentrotus purpuratus*) taken at a coastal site in southern California provided 0.48 kJ/s.

Pisaster is considered a keystone intertidal predator along the Pacific coast of North America (Menge et al. 1994) with the ability to regulate the distribution of mussels (*Mytilus californianus* and *M. trossulus*), its primary prey (Paine 1974, Robles et al. 1995), and thereby affect the structure and diversity of intertidal communities. Substantial gull predation on *Pisaster* may therefore have indirect consequences for intertidal community structure at the local scale. However, further work is needed to determine (i) how prevalent the high rates of *Pisaster* predation observed in this study are at other sites in the region and along the Pacific coast of North America, and (ii) whether the observed levels of predation by gulls are sufficient to limit *Pisaster* population size and thereby influence the distribution of mussel beds.

2.5.2 Optimal Size Choice and Age Effects

The ability of a forager to discriminate between prey sizes based on energetic profitability (or any other currency that scales with body size; e.g., nutrient or protein content) is key to choosing an optimal diet (Ward 1991, Hamilton et al. 1999). One might therefore expect prey discrimination ability to be a target of natural selection as it acts to maximize fitness returns from diet choices, an implicit assumption of foraging theory (Stephens and Krebs 1986, Sayers et al. 2010, Ydenberg 2010). However theoretical work on foragers in general (Hughes 1979) and empirical work on birds in particular (Draulans 1984, Ward 1991, Hamilton et al. 1999) suggests that, for many species, the ability to distinguish between prey types or between sizes of a single prey species is imperfect, leading to “suboptimal” prey selection.

The results indicate that Glaucous-winged Gulls are able to readily discriminate between sea star sizes on the basis of energetic profitability and that profitability plays a primary role in driving size choice. Gulls selected the most profitable size class in 60.0% of trials, a proportion that increased to 87.5% for trials in which no other gulls were in proximity to the experimental set up. This study was limited to two sites along the southern Strait of Georgia, however no difference was found between these sites in probability of selecting the optimal prey size, despite the large disparity between sites in dietary occurrence of this sea star. The ability to discriminate between sea star sizes based on profitability may therefore be a common characteristic among the local gull population.

Furthermore I present evidence that the ability to distinguish the energetically optimal prey size does not differ between gull age classes. This is in contrast to overall foraging efficiency and energy intake rate, which have consistently been found to increase with gull age (Verbeek 1977, Searcy 1978, Burger and Gochfield 1981, Greig et al. 1983, Skorka and Wojcik 2008). I found no difference between juveniles and adults in the probability of selecting the most profitable size class in feeding trials. Both age classes choose SC2 in ~60% of trials, and this proportion increased (to 80.0% for adults and 93.3% for juveniles) when no other gulls were in proximity to the prey choice experiment. This suggests that the discrepancy in foraging efficiency documented between juveniles and adults is not due to differential prey recognition ability in this species, and that by their second summer (the youngest age I observed in this study), Glaucous-winged Gulls are able to discriminate between prey sizes at an adult level. This is a novel finding, as previous studies have concentrated on age differences in ability to capture and consume prey, rather than ability to discern the most profitable prey types (Verbeek 1977, Searcy 1978, Burger and Gochfield 1981, Greig et al. 1983, MacLean 1986, Skorka and Wojcik 2008; but see Snellen et al. 2007).

2.5.3 Kleptoparasitism Risk and Optimal Size Choice

I found a significant negative relationship between the number of gulls within 5 meters of the prey offer trial and the probability that the focal gull would select the most profitable *Pisaster* size over the smallest size class (see Fig. 2.5). Recall that the smallest size class (SC1) was less profitable but required a shorter handling time. Two related conclusions can be drawn from this result. Firstly, the likelihood of successfully consuming the smallest sea star must be greater than that of consuming the most profitable sea star when the risk of food theft or displacement by other gulls is high. This is probable, as the greater handling time associated with the more profitable sea star will allow more time for potential kleptoparasites to locate and attack the focal gull. Secondly, the greater probability of successful consumption for the small sea star must progressively outweigh the cost of an energetically suboptimal prey selection (profitability cost = 1.62 kJ/s [best star] – 1.03 kJ/s [smallest star] = 0.59 kJ/s) as the number of conspecifics increases. The generalized linear modelling approach allowed examination of the shape of the relationship between kleptoparasitism risk and perceived prey value, showing that preference for the most profitable sea star declines rapidly with increasing local gull density.

High rates of intraspecific kleptoparasitism are well documented among members of the Laridae (Brockman and Barnard 1979, Burger and Gochfield 1981, Steele and Hockey 1995, Bertellotti and Yorio 2001, Galván 2003), and *L. glaucescens* is no exception (Barash et al. 1975, Rockwell 1982). As it is likely that the loss of prey to kleptoparasites is costly in terms of energy and time expended in locating and/or processing prey prior to theft (Giraldeau and Caraco 2000), it seems reasonable that gulls would be highly sensitive to kleptoparasitism risk when choosing between prey items. Previous work on gulls (Rockwell 1982, Steele and Hockey 1995, Bertellotti and Yorio 2001) and other species (e.g. Curlews *Numenius arquata*, Ens et al. 1990; Northern Pike *Esox lucius*, Nilsson et al. 2000) has shown that kleptoparasitic individuals preferentially target hosts with larger prey items, as this increases both probability of success (Rockwell 1982, Steele and Hockey 1995) and energetic return (Thompson 1986). Potential hosts in turn have been shown to switch their foraging preferences towards smaller, less energetically profitable prey items in situations where kleptoparasitism risk is high (Thompson and Barnard 1984, Hockey and Steele 1990, Nilsson and Brönmark 1999, Snellen et al. 2007). For gulls foraging in the Strait of Georgia, where site-level group sizes commonly exceed 40 individuals (this study), the effect of kleptoparasitism risk on *Pisaster* size preference may significantly affect the size distribution of sea stars removed from the population by predation. This could potentially limit the positive influence of sea star consumption by gulls on intertidal biodiversity (discussed above). However, confirmation of such an effect will require further investigation.

Additionally, it is possible that selecting the smallest, most quickly consumed sea star first when kelptoparasitism risk is high represents an energetically efficient strategy for exploitation of simultaneously encountered prey. Assume that the time between the discovery of a clump of sea stars by a foraging gull and arrival/attack by a kleptoparasite is a predictable function of conspecific group size. A gull will then improve its net energy gain from the clump as a whole by first taking the smallest sea star followed by the most profitable sea star whenever the time between clump discovery and attack is greater than the handling time required to consume the small star. Had the forager instead taken the most profitable sea star first, it would risk being attacked or displaced from the clump before securing another prey item. It is notable that, of the 25 trials in which SC1 was taken first, SC2 was taken second 88% of the time (22 trials). It should be noted, however, that selection of the most profitable sea star was not perfect, even when the effect of kleptoparasitism risk was removed (gulls selected SC2 in 87.5% of prey offer trials in which there were no other gulls within five meters). Whether this results from perceptual errors in distinguishing prey items or an additional unmeasured variable that interacts with energetic profitability in determining size preference is unknown.

Both profitability and kleptoparasitism risk appear to play key roles in *Pisaster* size selection by gulls, illustrating the importance of the interaction between these two factors in determine resource use in this system. These findings may prove useful to future studies of Pacific intertidal community ecology as the details of predator foraging decisions are known to have a substantial impact on prey population dynamics (Schmitz et al. 1997). The high rates of sea star consumption observed in this study and the ecological importance of *Pisaster* in shaping intertidal community structure warrant further investigation of this predator-prey interaction.

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3: Short timescale rate maximization by Glaucous-winged Gulls: Opportunity costs and the consumption of time-consuming prey

3.1 Abstract

The timescale over which a predator estimates changes in the encounter rate with various prey types is known to play an important role in the maximization of energetic return from foraging, particularly in habitats such as the intertidal where prey availability is highly variable through time. However, studies that explicitly test the temporal scale over which foragers track changes in the prey distribution are surprisingly rare. Here I compare the predictions of two optimal diet models: a "classic" model in which 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. I parameterized these models using data from a field study on Glaucous-winged Gulls *Larus glaucescens* foraging on various sizes of the Ochre Sea Star *Pisaster ochraceus* at an intertidal site in southern British Columbia. Large *Pisaster* required exceptionally large amounts of time (20 minutes or more) to consume, resulting in low energetic profitability and a seemingly high potential for missed opportunities to find and consume higher quality prey. However, gulls were observed to regularly take large sea stars, particularly when the tide level was high. Predictions from the classic diet model, which assumes that gulls use long-term estimates of prey encounter rates in their prey choice decisions and thus maintain a constant diet breadth throughout the tide cycle, did not match observations of diet breadth in the field, and the model was unable to explain the inclusion of large sea stars in the diet. The "tide-sensitive" model, which assumes that gulls have perfect information on prey encounter rates and changes in relative prey abundance throughout the tide cycle, predicted an expansion in diet breadth to include

large, low-profitability sea stars at higher tide levels, when the availability of high-quality prey was low. This model's predictions generally coincided with observed increases in the maximum sea star size taken by gulls with increasing tide level. I conclude that gulls are able to track short-term changes in prey encounter rates within a single low tide period in order to maximize energetic return from prey choice.

3.2 Introduction

The foraging decisions of animals have long been of primary interest to biologists due to the fundamental role such decisions play in the population dynamics of predators and prey (Abrams 1992, van Baalen et al. 2001, Holt and Kimbrell 2007), competition within and between species (Jaeger et al. 1983, Sih 1993, Murray et al. 2006, Fortin and Fortin 2009), and community structure (Roughgarden and Feldman 1975, Hamback 1998, Kotler and Brown 2007), among other phenomena. Prey choice, in which a predator determines which potential prey to exploit and which to ignore, is perhaps the most fundamental type of foraging decision with direct implications for higher-order population and community questions (Fryxell and Lundberg 1994, Schmitz et al. 1997). 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). This prediction has held up reasonably well in empirical tests (e.g., Elner and Hughes 1978, Bigger and Fox 1997, Berec et al. 2003, Sayers et al. 2010; for a current review, see Sih and Christensen 2001).

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 the prey distribution (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 of prey arrival (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). This approach has 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. Indeed, Perry and Pianka (1997) suggest that the prediction of a broader diet in seasons of low food abundance may be foraging theory's "most robust theorem to date." However, when encounter rates with prey vary over considerably shorter time scales, such long-term averaging may result in sub-optimal energy intake rates by over- or underestimating the missed opportunity costs associated with taking less profitable prey (Lucas 1983, Ward 1993). Using a two-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 rate when foraging in highly variable environments.

Assumptions regarding the timescale over which foragers track relevant environmental parameters (van Baalen 2001, Stephens 2007), and by extension the temporal scale of foraging optimization, significantly affect predictions regarding prey choice behaviour (Barkan and Withiam 1989, Gass and Roberts 1992, Fortin et al. 2002), and may have substantial implications for 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 I 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.

I investigated prey choice behaviour and diet breadth in Glaucous-winged Gulls *Larus glaucescens* foraging at an intertidal site along the Strait of Georgia in southern British Columbia, Canada. The predominant prey species at this site is the Ochre Sea Star *Pisaster ochraceus*, which constituted approximately 90% of the prey items consumed by gulls during this study (Chapter 2). A wide range of *Pisaster* sizes co-occur at the site, and the various sizes differ substantially in energetic profitability (Chapter 2). Small sea stars between 2.0 and 3.0 cm in radius are among the most energetically profitable prey, providing a relatively small amount of energy (~8 to 23 kJ), but requiring only 5 to 13 seconds to consume. Profitability declines quickly with sea star size, however, and large sea stars (e.g., 6.5 to 8.0 cm radius), while energy rich, require handling times between 7 and 25 minutes (Chapter 2). This includes a period in which the gull remains relatively inactive with the sea star partially swallowed and partially projecting from the mouth. The sea star is then gradually swallowed with a series of gulps that, depending on star size, may be spread over several minutes. Such lengthy handling times would seem to result in substantial missed opportunity costs, yet anecdotal accounts and personal observations indicate that large *Pisaster* are commonly taken by local gulls.

This system, in which a substantial proportion of available prey items require several minutes to consume, provides an interesting test case for the missed opportunity framework and its ability to predict prey choice decisions in free-living animals. In addition, 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, pers. obs.). 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 (Rafaelli 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 2 hours before to 2 hours after low tide). Additionally, 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).

In the present study I examine the ability of foraging theory to explain the range of gull prey choices observed in the field, including large *Pisaster* with extremely long handling times, and the timescale over which gulls re-estimate prey encounter rates and adjust their diet breadth. I compare the two 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. Previous work on intertidal foraging birds has shown that several species switch foraging habitats on a tidal schedule to maximize site-level profitability (Connors et al. 1981, van Gils et al. 2006, Schwemmer and Garthe 2008). Here I also investigate between-site foraging optimization by Glaucous-winged Gulls and compare this to the within-site optimization described by the diet models. Finally, I present data to test the hypothesis that the inclusion of large *Pisaster* in the diet results from digestive constraints on prey consumption.

3.3 Methods

3.3.1 Field Site

All fieldwork was conducted from April to September 2009 and April to August 2010 at Robert's Creek (49°25'53"N, 123°40'35"W). This is 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 dominated by rock weed (*Fucus gardneri*) with considerable barnacle (*Semibalanus cariosus* and *Balanus nubilis*) cover. Ochre Sea Stars are locally highly abundant and constitute a substantial dietary component for gulls foraging at this site (Chapter 2). All fieldwork was conducted from 2 hours before to 2 hours after daily low tide on days when the tidal minimum was $\leq$ 1.3m (see Chapter 2 for justification). During these observation periods, tide level fluctuated between 0.1 and 1.8 m above lowest low tide. 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).

3.3.2 Behavioural 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 Chapter 2. Briefly, I used focal animal sampling (Altman 1974) of randomly chosen gulls, as well as opportunistically observed prey consumptions from non-focal gulls to determine handling times and search times for all prey consumed. Foraging behaviours were recorded using a Canon high definition digital camcorder (HDV 1080i; primarily for focal animal sampling). Videotaped behaviours were analyzed using iMovie HD version 6.0 (© Apple 2006) and all handling and search times were measured to 0.1 seconds. For each consumption event, I also noted time of day, tide level (relative to lowest low tide for the site), and age of the gull, assessed as described in Chapter 2. Also in Chapter 2 I describe a method I developed for determining sizes of sea stars consumed by gulls using screenshots from video recordings. Sea star sizes were estimated (to 0.1cm) 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 (see Chapter 2).

I also conducted instantaneous scan samples (Altman, 1974) at 25-minute intervals throughout each 4-hour visit to the field site. During scans, the "instantaneous" behaviour of each individual gull at the field site was grouped into a behavioural category, essentially foraging (searching for, handling, or consuming prey) or non-foraging (loafing, preening, non-foraging movement, interacting with other gulls, etc.). I recorded the age class of each individual and the tide level at the time of sampling. 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 described above. These data were used in conjunction with sea star size estimates from focal observations (n = 170) in testing the predictions of the two diet breadth models.

3.3.3 Prey Abundance Estimates

I estimated the abundance of all prey types by randomly placing 0.25 m^2 quadrats (n = 180) along 10 m transect lines. Transect lines were placed randomly in the intertidal zone, following the low tide line as it shifted throughout the observation period. I 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. Prey abundance estimates were used to calculate relative availability of all prey types exploited by gulls at this site.

3.3.4 Prey Type Definitions

Gulls at Robert's 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 non-linearly in expected energetic profitability (see Chapter 2). 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 I have chosen 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 e.g., 2.5 cm actually represents all sea stars of ray lengths 2.25 to 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 in this study. However two other prey types were taken by gulls on occasion and are included here to accurately depict all foraging options available to gulls at Robert's 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 behavioural observations, but which abundance estimates suggested to consist mainly of small gastropods (*Tectura scutum, Lottia pelta*, *Tegula funebralis*) and hermit crabs (primarily *Pagurus hemphilli*). Thus polychaete worms and SI were included as two prey types in addition to the 15 *Pisaster* size classes for a total of 17 prey types that could potentially be included in a foraging gull's diet.

3.3.5 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 using a methodology similar to that described in Chapter 2. This procedure involved estimating the relationships between sea star size and (i) energy content, and (ii) handling time. The procedure for determining energy content of sea stars through bomb calorimetry is identical to that presented in

Chapter 2, and yielded a highly significant regression equation (*ln Energy (kJ) = 0.33 + 2.55 * ln Size (cm)* [$P < 0.001$, $R^2 = 0.97$]) that could be used to predict expected energy intake from each of the *Pisaster* size classes (see Chapter 2, Fig 2.2).

I also determined the proportion of each subsample of homogenized sea star that consisted of non-metabolizable material (mainly calcareous ossicles) by taking the mass of the material that was left not combusted after bomb calorimetry. The mean (± SE) percentage of sea star dry weight that consists of non-metabolizable material was found to be 51.19 (± 2.24)%. When calculated as a percentage of sea star wet weight, this yields 16.28 (± 0.85)%.

Handling times were obtained for a total of 170 *Pisaster* consumptions observed at Robert's Creek over the two field seasons. I 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 (Fig. 3.1) between sea star size and log-transformed handling time (pseudo-$R^2 = 0.77$, see Chapter 2) with a highly significant slope ($p < 0.0001$). The regression equation from this model [*ln Handling Time (s) = -0.35 + 0.98*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, I divided predictions from the energy regression by those from the handling time regression to produce profitability estimates for each sea star size. I 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. In the text, sea star profitability will be reported as profitability estimate ± delta method standard error.

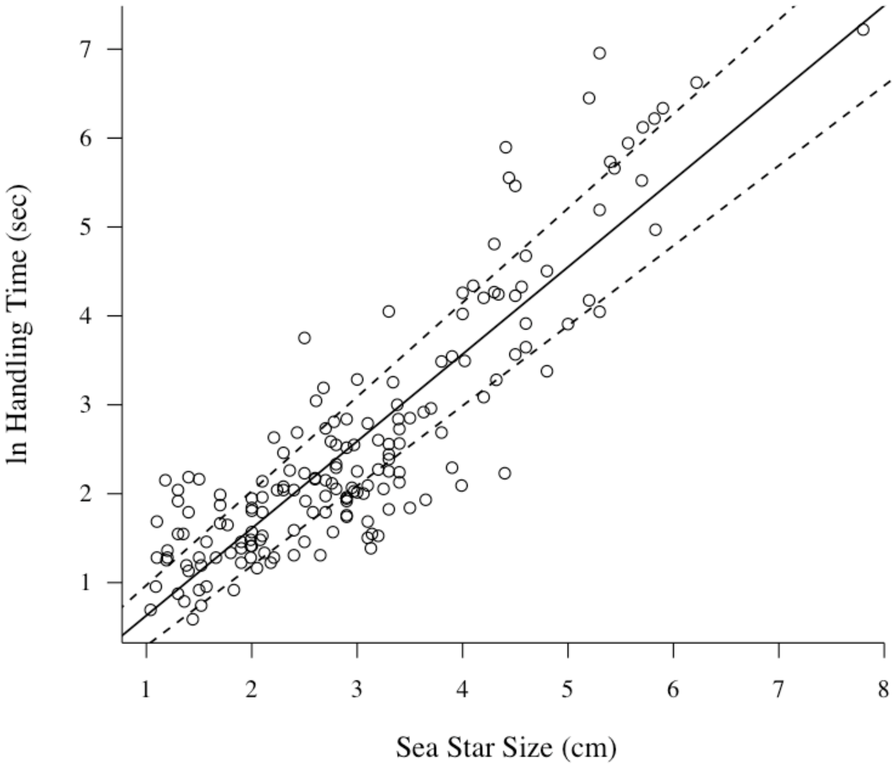

Figure 3.1: Relationship between sea star size (measured as longest ray length) and gull handling time as fit by linear mixed effects model. Handling time has been natural log transformed to normalize the data. Dashed lines represent 95% confidence intervals around mean handling time.

3.3.6 Energetic Profitability Estimates For Non-Sea Star Prey

Handling times for all non-sea star prey types were estimated from behavioural observations by taking the mean of all observed handling times for polychaete worms (3.82 s ± 0.29 s SE) and SI (3.31 s ± 0.17 s SE). Estimates of whole prey item energy content for theses 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. I 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 behavioural observations, I used estimates of energy content per prey item for the three 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 (*Tegula funebralis*) and 5.43 kJ per individual for the maroon hermit crab (*Pagurus 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. I took the average of the above three energy values to obtain a single SI energy content estimate of 4.21 kJ/prey. I divided this value by mean SI handling time to produce an SI energetic profitability estimate of 1.27 kJ/s.

3.3.7 Changes in Foraging Effort with Tide Cycle

I investigated changes in foraging habitat use throughout the tide cycle by quantifying the relationship between tide level and the number of gulls engaged in active foraging. A total of 195 scan samples (see above) were conducted over 22 days at Robert's Creek in the 2010 field season. Data on the total number of gulls engaged in foraging behaviour (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. I 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. I 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). I 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.

3.3.8 The Models

3.3.8.1 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. I 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

$$[1] \qquad \frac{\overline{E}_j}{\overline{T}_j} = \frac{\sum_{i=1}^{j} e_i * P_{ij} - k * \overline{TS}_j}{\sum_{i=1}^{j} h_i * P_{ij} + \overline{TS}_j}$$

$\overline{E}_j$ is the expected net energy gain and $\overline{T}_j$ is the expected time require 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. $\overline{TS}_j$ is the expected search time to discovery of 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 2 x 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 gm (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:

$$[2] \qquad P_{ij} = \frac{N_i}{\sum_{i=1}^{j} N_i}$$

where N_i is the abundance of prey type *i* in the intertidal zone at Robert's Creek. 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 $\overline{TS}_x$ for the observed diet, which includes prey types 1 to x. The search time $\overline{TS}_j$ 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 $\overline{TS}_x$. I have modified this equation slightly by removing the term relating estimated prey abundance to availability as experienced by the forager. Thus

$$\overline{TS}_j = \overline{TS}_x * \frac{\sum_{i=1}^{x} N_i}{\sum_{i=1}^{j} N_i} \qquad [3]$$

Following the procedure outlined by Stephens and Krebs (1986), all prey types available at the site were ranked by energetic profitability (see Table 3.1) and sequentially added to the diet in order of decreasing profitability, starting with the most profitable type, then the two 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}).

3.3.8.2 Changes in Prey Availability with Tide Level

Abundance estimates revealed changes in prey type abundance with increasing shore height above the lowest low tide line. As the vast majority of prey consumed by gulls in the intertidal zone at Robert's Creek are taken from exposed areas of the shoreline (i.e., above the tide line; Irons et al. 1986, pers. obs.), tidal flux effectively causes continuous changes in relative 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, I sought to incorporate changes in prey encounter rates with tide level into the predicted diet breadth model. I did so by iteratively recalculating two model parameters, P_{ij} and $\overline{TS}_j$, at regular intervals throughout the observed tidal range. Starting at a tide level of 0.2 m above lowest low tide, I 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. I 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), were not affected by tide cycle. Finally I 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.

3.4 Results

3.4.1 Prey Energetic Profitability

Energetic profitability is a peaked function of sea star size (Fig. 3.2). Profitability reaches a maximum of 1.75 ± 0.40 kJ/s for stars of ray length 2.5 cm and declines rapidly thereafter, reaching a minimum of 0.15 ± 0.19 kJ/s at the largest star size applicable to this study, 8.0 cm. Figure 3.2 compares the profitability estimates of the non-sea star prey types with those of the range of sea star sizes (see also Table 3.1). The most profitable prey available to gulls at this site are nereid polychaetes (2.19 kJ/s), while small invertebrate profitability (1.27 kJ/s) is comparable to that of both 1.5 and 4.5 cm sea stars.

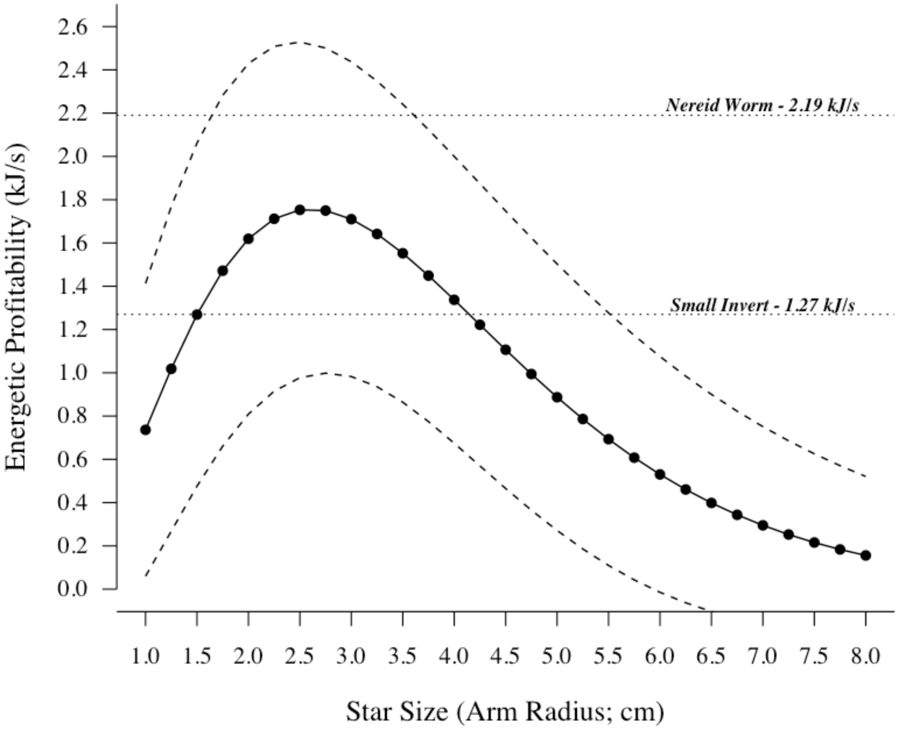

Figure 3.2: Estimated energetic profitability (kJ/s) in relation to sea star size (measured as longest ray length). Estimates were derived by taking the quotient of predictions from the sea star energy content regression and the handling time mixed model (see text). Dashed lines are 95% confidence limits around mean energetic profitability calculated using delta method variance approximation (Powell 2007). Dotted lines indicate point estimates of the profitability of non-sea star prey.

3.4.2 Diet Breadth – Classic Model

All available prey types were ranked in descending order of energetic profitability (Table 3.1). In general, energetic profitability declines with sea star size. However, since profitability peaks at size 2.5 cm, 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 ± 4.2 seconds (mean ± 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 3.2 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

Table 3.1: All prey types available at Robert's Creek, ranked in descending order of profitability. Rankings are the same as those used in the two intake rate figures (Fig. 3.3 and Fig. 3.6). Energetic profitability estimates for each prey type are displayed in the right hand column and represent the values used in the diet models to calculate intake rate.

Profit Rank	Prey Type	Profitability
1	Nereid Worm	2.19
2	Pisaster (2.5 cm)	1.75
3	Pisaster (3 cm)	1.70
4	Pisaster (2 cm)	1.62
5	Pisaster (3.5 cm)	1.54
6	Pisaster (4 cm)	1.33
7	Pisaster (1.5 cm)	1.27
8	Small Invert	1.27
9	Pisaster (4.5 cm)	1.10
10	Pisaster (5 cm)	0.88
11	Pisaster (1 cm)	0.75
12	Pisaster (5.5 cm)	0.69
13	Pisaster (6 cm)	0.53
14	Pisaster (6.5 cm)	0.40
15	Pisaster (7 cm)	0.29
16	Pisaster (7.5 cm)	0.21
17	Pisaster (8 cm)	0.15

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 (Fig. 3.3). 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 3.1). However the high 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.

Table 3.2: Estimates of TS_j and P_{ij} used to calculate intake rate for the classic diet model and at four tide levels used in the tide-sensitive diet model. See text for explanation of terms. Profit ranks are those shown in Table 3.1.

	No Tide Information		**Tide = 0.2 m**		**Tide = 0.7 m**		**Tide = 1.1 m**		**Tide = 1.2 m**	
Profit Rank	TS_j	P_{ij}*	TS_j	P_{ij}	TS_j	P_{ij}	TS_j	P_{ij}	TS_j	P_{ij}
1	651.2	1.000	651.2	1.000	531.8	1.000	1378.6	1.000	1059.6	1.000
2	281.6	0.568	281.6	0.568	273.5	0.486	590.8	0.571	1059.6	0.000
3	173.6	0.384	173.6	0.384	168.4	0.384	318.1	0.462	1059.6	0.000
4	122.5	0.295	122.5	0.295	119.8	0.289	196.9	0.381	706.4	0.333
5	99.5	0.188	99.5	0.188	98.8	0.175	179.8	0.087	529.8	0.250
6	88.1	0.115	88.1	0.115	90.8	0.081	153.2	0.148	423.8	0.200
7	79.9	0.093	79.9	0.093	84.0	0.075	133.4	0.129	423.8	0.000
8	65.0	0.186	65.0	0.186	64.5	0.232	64.6	0.516	84.8	0.800
9	59.5	0.085	59.5	0.085	60.5	0.061	62.7	0.030	84.8	0.000
10	57.1	0.041	57.1	0.041	58.3	0.037	62.7	0.000	84.8	0.000
11	56.5	0.011	56.5	0.011	57.9	0.007	62.7	0.000	84.8	0.000
12	54.3	0.039	54.3	0.039	56.2	0.029	62.7	0.000	84.8	0.000
13	52.8	0.027	52.8	0.027	55.4	0.014	62.7	0.000	84.8	0.000
14	51.2	0.030	51.2	0.030	53.5	0.034	60.8	0.029	81.5	0.038
15	49.4	0.035	49.4	0.035	51.8	0.033	60.8	0.000	81.5	0.000
16	47.3	0.043	47.3	0.043	50.1	0.032	59.1	0.029	81.5	0.000
17	44.5	0.058	44.5	0.058	47.4	0.054	55.9	0.054	75.7	0.071

* The diet breadth model recalculates P_{ij} values for each prey type 1 to j every time a new prey type is added to the diet. The P_{ij} value for a given profit rank will therefore change with each iteration of the diet model. Values shown are for the most recently added profit rank only.

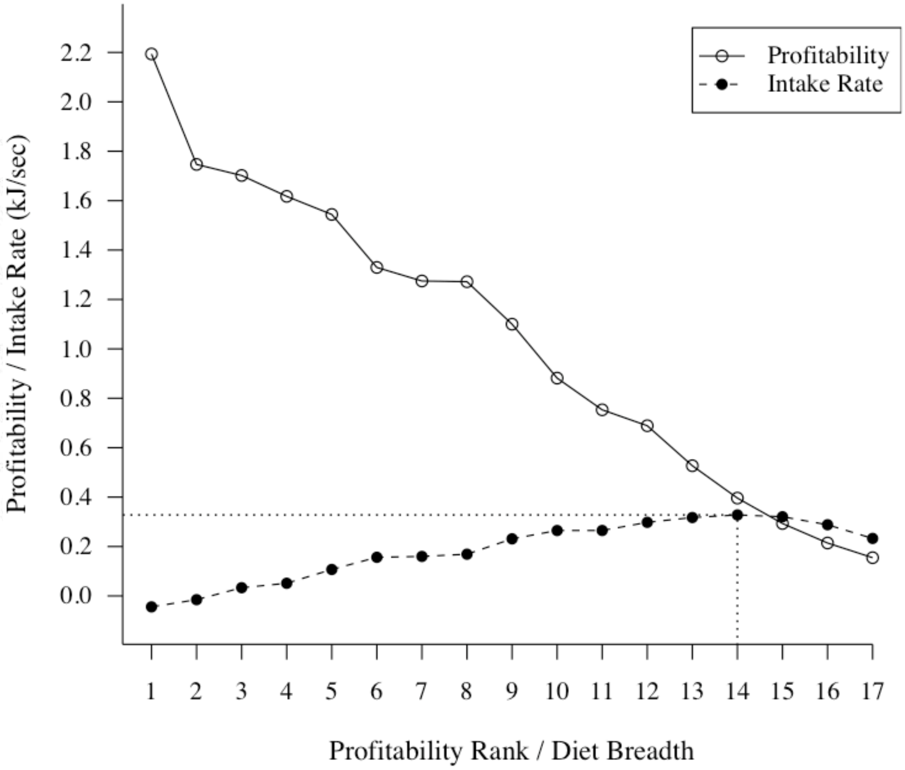

Figure 3.3: Prey type profitability and predicted intake rate from the classic diet model. The energetic profitability values (solid line, open circles) for all prey types available at Robert's Creek are presented in decreasing order (Profitability Rank, see also Table 3.1), illustrating the order in which prey types are added to the diet when calculating intake rate from the diet model. Energetic intake rate predictions from the classic diet model (dashed line, closed circles) 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 lines indicate 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 through 17) from their diet.

I obtained size estimates for a total of 265 sea stars consumed by gulls. Of these, 97.0% (257) fell within the upper 6.5 cm size limit of the predicted rate maximizing diet (Fig 3.4), leaving 3.0% of observed prey consumptions unexplained. Sea stars ≤ 6.5 cm in radius constitute 75.2 (± 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 ≤ 6.5 cm in radius differs significantly from the proportion in the gull diet (One-sided t-test, t = -5.02, df = 72, p < 0.0001), supporting the assumption of selective, rather than opportunistic feeding.

3.4.3 Diet Breadth – Incorporating the Effect of Tide on Prey Encounter Rate

The largest tidal flux observed in one low tide period was 0.98 m. Tidal flux resulted in substantial changes in average abundance of the various prey types (Fig. 3.5a). However, while abundance for all prey types generally declined with increasing tide level, smaller, more profitable sea stars (solid line in Fig. 3.5a) experienced a greater decline with increasing tide than did larger, less profitable stars (dotted line in Fig 3.5a). Thus the encounter rate with the most profitable sea star sizes experiences the greatest decrease with increasing tide level. Figure 3.5b shows the change in site-level search

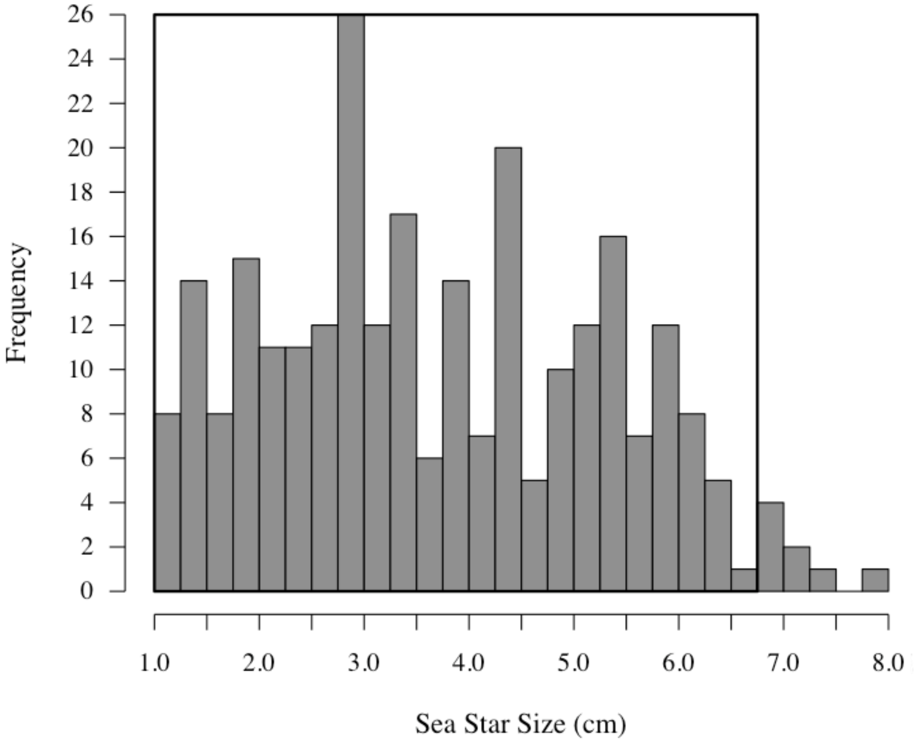

Figure 3.4: Histogram showing the range of sea star sizes consumed by gulls at Robert's Creek and the number of consumptions observed for each size. Sea star sizes were estimated to 0.1 cm, and here have been collapsed into 0.25 cm bins. The box contains all sea star size consumptions that are explained by the classic diet model (all sea stars of ray length 6.75 cm and smaller).

time to prey acceptance (TS_x) with tide height. The general increase in TS_x with increasing tide level results in an overall decrease in encounter rate with all prey types as the tide rises.

I recalculated relative prey abundance P_{ij} and expected search times TS_j for all prey types at several tide levels (see Table 3.2) and examined the effect on intake rate as predicted by the tide-sensitive diet breadth model (Fig 3.6). This procedure was performed at tide level intervals of 0.1 m from 0.2 to 1.4 m above lowest low tide. However for illustrative purposes, I 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 present (e.g., 0.3 to 0.6 m, 0.8 to 1.0 m), diet breadth was predicted to remain unchanged from that of lower tide levels.

For all tide levels up to 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 lowest low tide, intake rate peaks at 0.18 kJ/s for a diet breadth with 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 arm length in its diet, despite the exceptionally long handling time associated with these stars (see Fig. 3.1). Finally, at a tide level of 1.2 m, a diet breadth that includes 8.0 cm sea stars (prey type 17, Fig. 3.6) provides the maximal energetic return, with intake rate peaking at 0.13 kJ/s.

The diet breadth model incorporating information on tide-related changes in prey encounter rate explains 99.2% of the 265 sea star consumption observations (Fig. 3.7). 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). However, an increase in maximum acceptable sea star size with increasing tide level is evident in Figure 3.7. 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 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.

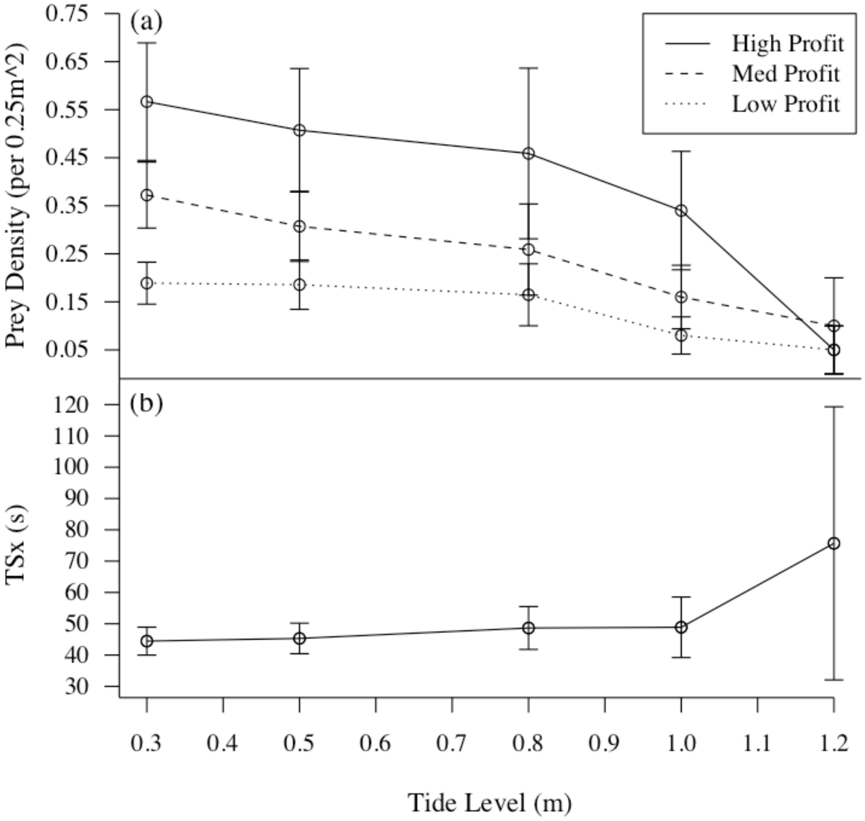

Figure 3.5: Changes in sea star abundance and site-level search time to prey acceptance (TS_x) with tide level. (a) The average summed abundance (per 0.25 m^2) of the three most profitable sea star size classes (2.0, 2.5, and 3.0 cm; solid line), the three least profitable sea star size classes (6.5, 7.0, and 7.5 cm; dotted line), and three size classes of medium profitability (1.5, 3.5, and 4.0 cm; dashed line) are plotted against increasing tide level. Note that the most profitable sea stars show the greatest decline in mean abundance with increasing tide. (b) TS_x shows a gradual increase with increasing tide level, lowering the encounter rate with all prey types. Note that the large error bars around TS_x at a tide level of 1.2 m are due to an extremely low sample size (n = 6) of search time observations at this tide level. Error bars in (a) and (b) are ± 1 SE.

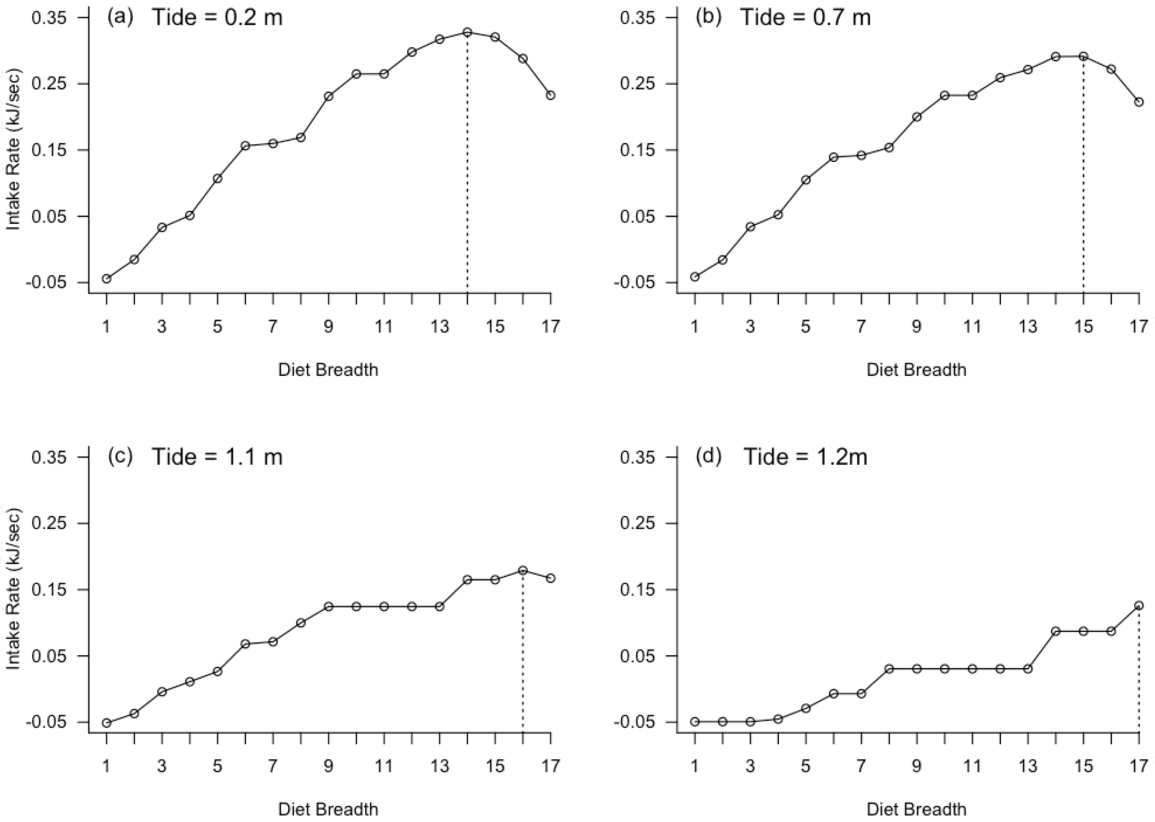

Figure 3.6: Change in energetic intake rate with diet breadth at 4 tide levels, as predicted by the tide-sensitive diet model. Intake rate is shown for tide levels of (a) 0.2 m, (b) 0.7 m, (c) 1.1 m, and (d) 1.2 m above lowest low tide. The dotted line in each plot indicates the diet breadth at which intake rate is maximized. See text for values of maximum attainable intake rate at each tide level.

3.4.4 Foraging Effort and the Tide Cycle

Poisson GLMM showed a highly significant negative relationship between tide level and the number of foraging gulls at Robert's Creek (slope and intercept p-values both < 0.0001, pseudo-$R^2 = 0.564$, Fig. 3.8). This result indicates that an increasing proportion of the total gulls at the site on a given day are either leaving for alternative foraging grounds or switching to non-foraging behaviours as tide level increases and maximum attainable intake rate decreases.

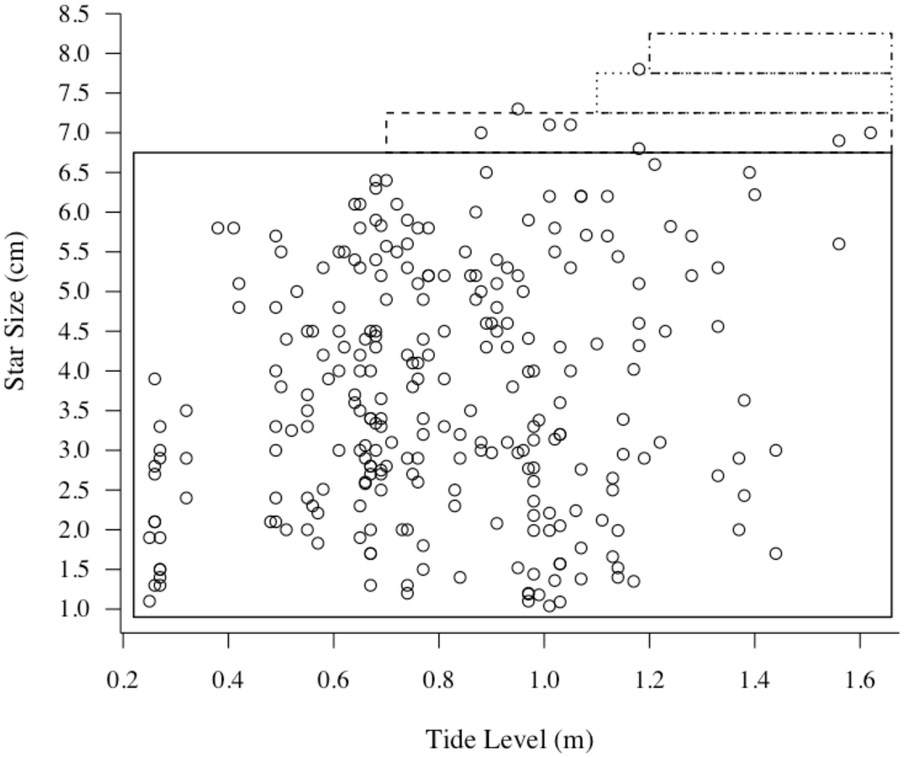

Figure 3.7: The sizes of all sea stars consumed by gulls during this study plotted against the tide level at which each star was taken. The solid box indicates the sea star sizes (up to 6.75 cm) that are predicted (by both the classic and tide-sensitive models) to be included in the diet at all tide 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.

3.5 Discussion

The 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 the site. Although the proportions of observed sea star consumptions explained by the classic and tide-sensitive models (97.0% and 99.2% respectively) were not significantly different, the classic model provides no explanation for the observed increase in maximum acceptable sea star size with increasing tidal height evident in Figure 3.7. This effect is accounted for, at least partially, by the tide-sensitive model. Gulls indeed appear to expand their diet with

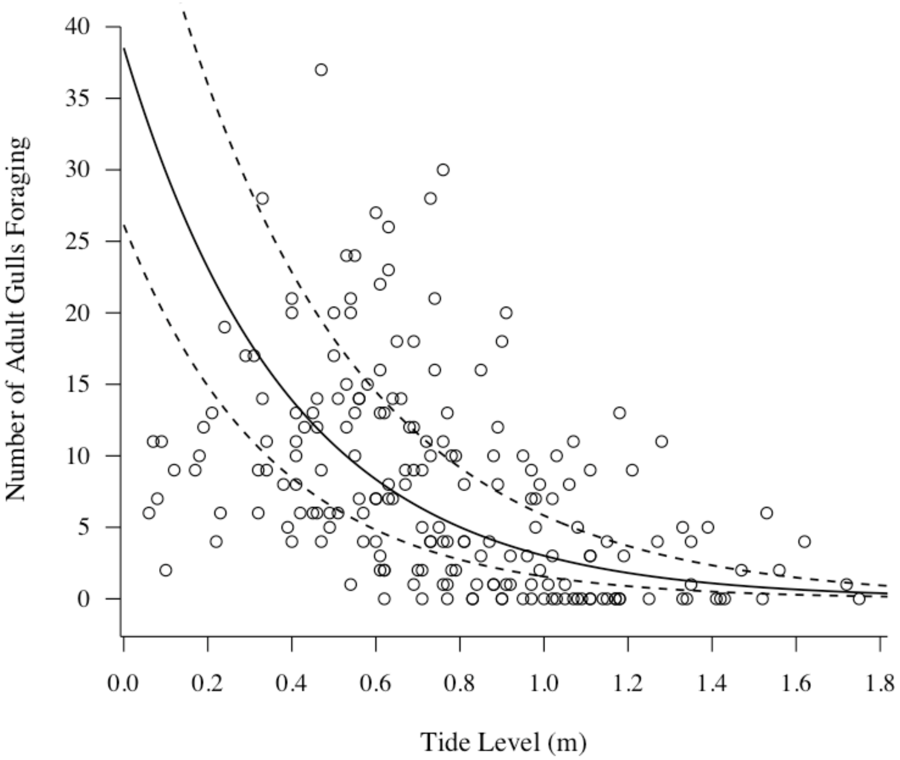

Figure 3.8: The relationship between tide level and the number of gulls engaged in foraging behaviour at Robert's Creek, as estimated from 195 scan samples taken over 22 days. The solid line is the mean decline in number of foraging gulls with increasing tide level determined using a Poisson generalized linear mixed effects model. Dashed lines are 95% confidence intervals determined by the model.

increasing tide level, taking larger, less profitable sea stars as the encounter rate with more profitable prey items decreases. 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.

Additionally, 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 (see Fig. 3.1 and Chapter 2), 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 at all tide levels (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 sub-maximal energy intake rate due to the likelihood of encountering a more profitable prey type if this time were instead used for searching, and that these prey items should therefore be ignored when encountered. However, observations of gulls consuming sea stars in the 7.0 cm and larger size classes are not uncommon; I 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 video-taped scan samples (2010 only).

The tide-sensitive diet model, on the other hand, accounts for the decreasing availability of highly profitable small sea stars with increasing tide height (Fig. 3.5a) and indicates that, at tides levels of 0.7 m and above, a gull will achieve a maximal intake rate by including large sea stars in its diet. This effect is also a function of the gradual increase with tide height in the search time required to locate any acceptable prey item (TS_x).

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, Fortin et al. 2002, van Gils et al. 2005). Other considerations that, when taken together with energetic concerns, have improved predictions of forager diet choice include digestive constraints on the amount of material consumed (Verlinden and Wiley 1989, Jeschke et al. 2002, van Gils et al. 2005) and the balance of various nutritional components through dietary diversity (Belovsky 1984, Doucet and Fryxell 1993, Hirakawa 1995). The latter is unlikely to play a substantial role in this system. *Pisaster* constitutes the vast majority of prey taken at the field site, and all dietary components (e.g., energy, protein, essential minerals, etc.) are likely to scale with sea star body size in a similar way, particularly since the majority of stars taken by gulls are pre-reproductive (see Chapter 5). Digestive constraints, however, 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). While models that explicitly account for the digestive capacity of the forager have only recently been applied to avian predators foraging on intertidal and marine invertebrates (mainly mollusks, e.g., van Gils et al. 2005, Heath et al. 2010), several authors have found evidence that diet choice in these predators 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). It seems probable that gulls in this study are subject to a similar digestive constraint when foraging on *Pisaster*, however this factor was not considered by either of the diet models. Sea stars are bulky prey items, are consumed at a fairly high rate during periods of low water, and contain a substantial amount of non-metabolizable calcareous material (mean ± SE = 16.28 ± 0.85% by wet weight). This leads to one possible explanation of large star consumption. Once a gull reaches its digestive capacity it may require a pause to process consumed prey before it can continue foraging (see Heath et al. 2010). At this point, regardless of tide level, a large star may be a reasonable prey choice, as the obligatory digestive pause could be simultaneously devoted to the long handling time required to consume this energy rich (though low profitability) item. Under this hypothesis, one would expect that time since arrival at the foraging site, rather than tide level, would drive the inclusion of large sea stars into the diet, as gulls would be expected to first reach their digestive capacity by foraging on more profitable prey items before taking a large sea star. However, the data are inconsistent with this explanation of large star consumptions. Fig 3.9 shows the maximum sea star size taken by a gull during my observations as a function of time relative to daily low tide; large *Pisaster* are taken both early and late in the low tide period (when tide level is the highest) and sea stars in size classes greater than 6.5 cm are only ignored from approximately 1 hour before to 1 hour after low tide. This result, while not negating the possibility of a digestive constraint on gull prey choice, is consistent with the hypothesis that tide-related changes in the availability of small, profitable sea stars drive the inclusion of large sea stars in the diet.

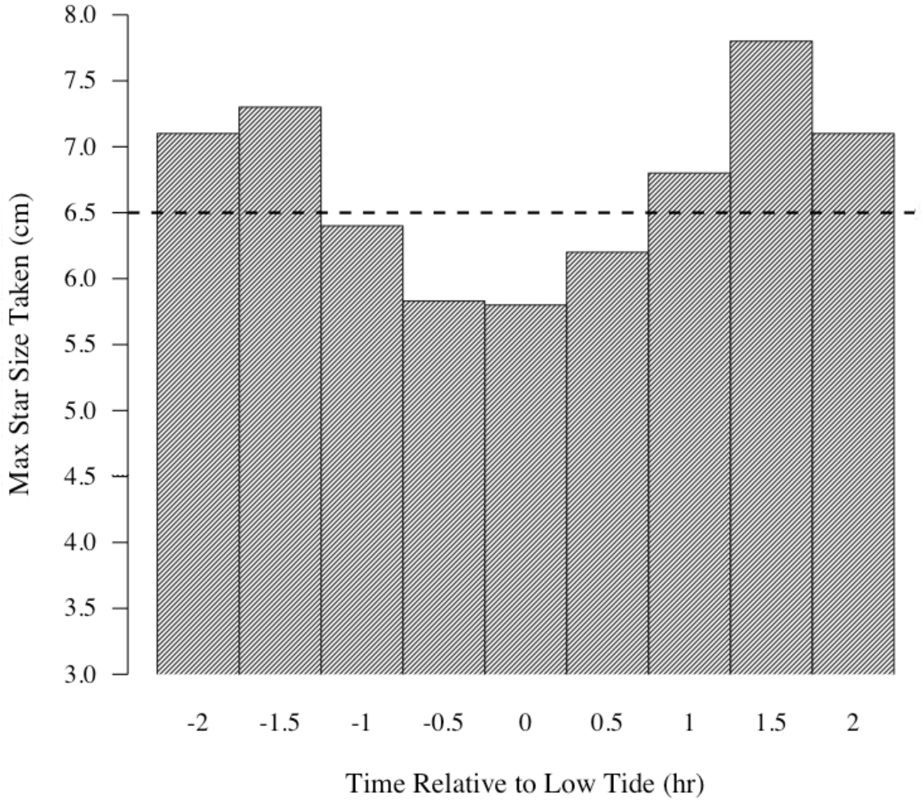

Figure 3.9: The relationship between time relative to low tide and the maximum sea star size taken by gulls during observations. Negative values on the x-axis indicate time (in hours) before daily tidal minimum and positive values indicate time after tidal minimum. The dashed line shows the upper limit of sea star sizes predicted to be included in the diet at all tide levels, and illustrates that, in general, large (i.e., size class 7.0 cm and greater) sea stars are only excluded from the diet during a 1.5 to 2 hour period around daily low tide.

The discrepancies between the predicted and observed diet may result from three possible causes: (i) energy intake rate maximization is an inappropriate or insufficient currency with which to explain the range of Glaucous-winged Gull diet choices, (ii) error associated with energy content, handling time, and abundance estimates led to inaccuracy in predictions of the tide levels at which diet breadth should expand, and (iii) the ability of the gulls to discriminate between sea star sizes and/or track tide related changes in prey encounter rates is imperfect. The first potential cause seems unlikely, considering the high degree of correspondence between predicted diet breadth and observed prey consumptions. Energy intake rate maximization appears sufficient to explain the majority of diet choices for gulls foraging at the field site and indeed provides at least an approximation of the way in which diet breadth changes with prey availability throughout the tide cycle. It appears that the cognitive abilities of the gulls (explanation (iii) above) are also not to blame. Figure 3.7 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. The most probable explanation for the lack of complete agreement between the model and observations and my inability to predict the fine scale of diet breadth expansion is (ii). All of the components of the diet model – prey energy content and handling time, relative abundance, search time, 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 seems highly likely. Additionally, stochastic changes in the prey distribution, which would obscure the exact relationship between shore height and relative prey abundance, along with daily variation in the magnitude of tidal flux make estimation of the rate-maximizing diet breadth at various tide heights difficult.

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 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, theoretical work by Lucas (1983) shows that prey choice decisions based on long-term averages will not yield maximal energetic return when encounter rates vary over short timescales, and a forager will improve its energy intake rate by instead basing prey choice decisions on short-term averages (see also Barkan and Withiam 1989, Gass and Roberts 1992, Fortin et al. 2002).

I used a straightforward extension of the classic foraging algorithm that allows short-term re-estimation of prey encounter rates in a complex field situation (for a related methodology, see Ward 1993). By applying the same restrictions to prey abundance estimates that the incoming tide would apply to gull prey availability, I achieved a qualitatively 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 behaviour accordingly to maximize energetic return. Such a methodology may prove useful for other diet studies in which prey encounter rate varies in a predictable fashion.

Several other studies on birds foraging in tidally structured environments have demonstrated that these predators adjust their foraging behaviour throughout the tide cycle. Sanderlings *Calidris alba* (Connors et al. 1981), Red Knots *C. canutus* (van Gils et al. 2006), and Black-headed Gulls *Larus ridibundus* (Schwemmer and Garthe 2008) have all been shown to switch foraging habitats on a tidal schedule in a way consistent with maximizing overall site profitability. Glaucous-winged Gulls are likely to use a similar site-switching tactic; Figure 3.8 shows a steady decline in the number of foraging gulls at the field site as tide level increases (and maximum attainable intake rate decreases), suggesting that individuals are abandoning this intertidal site for more productive foraging grounds. However, my analysis extends the finding of tide-related changes in foraging site use to show that, even within a site, prey choice behaviour is dynamic over the course of a single low tide period, with gulls adjusting their diet breadth to adaptively exploit changes in prey availability.

Additionally, the decrease in foraging aggregation size with increasing tide height may feed back on prey choice behaviour in this system. As discussed in Chapter 2, kleptoparasitism risk, in the form of local conspecific density, induces gulls to shift prey choice toward smaller sea star sizes, as these sizes are more quickly consumed and less likely to be contested by potential food thieves. Kleptoparasitism risk presumably decreases with decreasing aggregation size, and gulls may therefore be more likely to take a large star when the tide level is high due to the decreased probability of having this prey item stolen. This effect may act in conjunction with decreased opportunity costs in driving large star consumption.

Zwarts and Esselink (1989) found that Curlews *Numenius arguata* changed their foraging behaviour in a predictable manner throughout the tide cycle when feeding on the polychaete *Nereis diversicolor* on intertidal mud flats, probing in *Nereis* burrows during ebb and flow tides and pecking worms off the surface of the mud at low tide. However, the shifts in Curlew foraging were attributed to changes in *Nereis* behaviour – worms spend more time out of their burrows at low tide – and these authors did not document any change in prey choice (i.e., worm size selectivity) throughout the tide cycle. De Vlas et al. (1996) demonstrated that individual oystercatchers *Haematopus ostralegus* that specialize on *N. diversicolor* will take smaller worms or switch to searching for clams *Macoma balthica* when large worms are scarce, however their largely descriptive study did not present theoretical predictions for when such changes in prey acceptance should take place. Finally, taking an approach similar to my own, Ward (1993) determined the distribution of Wedge Clam *Donax serra* size classes at different levels on an intertidal beach. He then analyzed size selection by African Black Oystercatchers *H. moquini* and showed that a model incorporating non-random changes in clam availability throughout the tide cycle predicted oystercatcher prey choice better than a model assuming clams were randomly distributed. Thus, to my knowledge the only two studies on intertidal foraging avian species in which the timescale of encounter rate estimation has been explicitly tested, rather than assumed, both show that these predators are able to track short-term changes in prey abundance and adjust their diets accordingly.

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4: A hard pill to swallow: Do Glaucous-winged Gulls self-medicate by feeding on Ochre Sea Stars?

4.1 Abstract

Parasites are ubiquitous among free-living animals and have the potential to exact substantial fitness costs. Animals have therefore evolved myriad behavioural mechanisms for reducing their exposure to parasites and mitigating the effects of parasite infection. In one particularly intriguing, yet controversial class of behaviours, self-medication, animals exploit the antipathogenic properties of other organisms to protect themselves against parasites and disease. In chemical self-medication, toxic or volatile compounds, generally derived from plants, are used to treat a parasite infection or as deterrents against parasitic colonization of nests. Mechanical self-medication involves the use of abrasive plant or animal material to physically remove attached endoparasites. Here I investigate the potential for adaptive self-medication behaviour against gastro-intestinal parasites by the Glaucous-winged Gull *Larus glaucescens* through its consumption of the sea star *Pisaster ochraceus*. Sea star consumption may constitute either chemical self-medication via highly bioactive saponin compounds produced by *Pisaster*, or mechanical self-medication via physical removal of parasites attached to the digestive tract lining when calcareous sea stars are swallowed whole. I tested for both potential forms of self-medication using a fecal egg flotation procedure to assess parasite load in free-living gull populations. Poisson-distributed mixture models were used to test for a relationship between the size of sea star consumed and parasite load, under the hypothesis that the potential for mechanical removal of parasites increases with star size. I also examined the relationship between *Pisaster* size and saponin content to test the hypothesis that gulls select sea star sizes based on saponin intake rate. I found evidence for a negative effect of the inclusion of sea stars in the diet on gull parasite load. However, neither mechanical parasite removal nor saponin dosage appear to affect sea

star size choice in gulls, leading to the conclusion that adaptive self-medication does not contribute to the foraging decisions of gulls when consuming *Pisaster*.

4.2 Introduction

Every free-living species on earth, and many species of parasite, is subject to parasitism (Windsor 1998). The potentially large fitness costs exacted by parasites on their hosts (Anderson and May 1979) has led to a range of evolved mechanisms, both immunological and behavioural, for reducing parasite load or avoiding exposure (Clayton and Wolfe 1993, Rolff and Siva-Jothy 2003). Behavioural strategies range from the avoidance of fecal-contaminated food (Ödberg and Francis-Smith 1977) to selection of mates based on signals indicating parasite resistance (Folstad and Karter 1992; for a review of antiparasitic behavioural strategies, see Hart 1990). In a class of behaviours termed "self-medication" (Clayton and Wolfe 1993, Lozano 1998), animals exploit the antipathogenic properties of other organisms, or the substances they produce, to protect themselves against parasites (prophylactic) or ameliorate the symptoms of infection (therapeutic). Prophylactic behaviours are expected to be a population response to parasite risk, displayed by both infected and uninfected individuals, while therapeutic behaviours are a response by an individual to a specific parasite infection or the symptoms that it causes (Lozano 1998, Lefèvre et al. 2010).

Some controversy exists as to what constitutes adaptive self-medication (Lozano 1998, Castella et al. 2008), particularly given that the consumption of material with medicinal properties may provide nutritional benefits as well (Sapolsky 1994). Clayton and Wolfe (1993) have outlined three criteria that adaptive self-medication behaviours should meet: (i) the host should deliberately contact the putatively medicinal substance to exploit its antipathogenic properties, (ii) the substance should be detrimental to one or more of the host's pathogens, and (iii) the substance should thereby have a positive effect on host fitness (Clayton and Wolfe 1993, Castella et al. 2008). Singer et al. (2009) additionally suggest that an animal should only engage in self-medication behaviour when faced with parasite infection, or a sufficiently high risk of infection, due to costs associated with the behaviour (e.g., time taken away from other essential behaviours, toxicity of medicinal substances, etc.).

The properties of medicinal substances exploited by self-medicating animals fall into two broad categories, chemical and physical. The most commonly invoked form of self-medication, which I term "chemical self-medication," involves the use of volatile secondary metabolites, generally from plants, to prevent or treat parasitic infection. Studies on a range of taxa have shown increased consumption of such compounds in response to parasite exposure with a corresponding reduction in parasite load (Phillips-Conroy 1986, Huffman and Seifu 1989, Huffman et al. 1993, Lisonbee et al. 2009, Singer et al. 2009). The use by birds (Clark and Mason 1985, 1988; Gwinner and Berger 2005) and ants (Christe et al. 2003, Chapuisat et al. 2007, Castella et al. 2008) of fresh herbage or conifer resin containing volatile compounds as nest material constitutes another, largely prophylactic form of chemical self-medication.

A less commonly described form of antiparasitic behaviour, which I term "mechanical self-medication," occurs when an animal makes use of the physical properties of an organism or object to mechanically remove attached endoparasites. The primary example of such behaviour is whole-leaf swallowing by chimpanzees *Pan troglodytes* (Wrangham and Nishida 1983, Wrangham and Goodall 1989, Huffman et al. 1996, Huffman and Hirata 2004) and other African Great Apes (Huffman 2001). Individuals swallow the hispid leaves of *Aspilia* plants, which pass whole through the digestive tract and dislodge adult nematodes from the intestinal lining, resulting in reduced parasite burden (Huffman and Caton 2001).

Glaucous-winged Gulls *Larus glaucescens* living on the southern coast of British Columbia, Canada have recently been shown to include large numbers of the common intertidal sea star *Pisaster ochraceus* in their diet (Chapter 2). The present study investigates the potential antiparasitic benefits derived by gulls when feeding on *Pisaster* and whether sea star consumption constitutes self-medication behaviour. Glaucous-winged Gulls are host to a number of helminth and coccidian gastro-intestinal parasites (Levine 1953; Ching 1978; Hoberg 1981, 1984), and consumption of *Pisaster* may lead to reduced parasite burden through at least two mechanisms. Saponins, highly bioactive compounds (Hostettmann and Marston 1995) produced by this sea star, may have a negative effect on the survival and reproduction of some or all gastro-intestinal parasite species. Saponins exhibit a range of pharmacological properties (Killeen et al. 1998, Simoes et al. 1999,Yun 2003, Sautour et al. 2005) including antiparasitic activity (Julien et al. 1985, Lopez-Alban et al. 2007). Although widespread in the plant kingdom (Gubanov et al. 1970, Hostettmann and Marston 1995), animal-derived saponins have only been found in two classes of echinoderms, Holothuroidea and Asteroidea (Hashimoto and Yasumoto 1960, Minale et al. 1982, Hostettmann and Marston 1995). *Pisaster* is one such saponin-producing asteroid (Zollo et al. 1989), and several specific saponin compounds shared by this and other sea star species have proven to exhibit antipathogenic properties, including anti-microbial and anti-parasitic activity (Komori 1997).

Alternatively, *Pisaster* consumption may reduce parasite burden through mechanical removal of attached parasites, particularly adult nematodes and cestodes. Gulls feed on sea stars by swallowing individuals whole, and will take stars up to ~ 9 cm in radius (Chapter 2). The large size of these sea stars may serve to dislodge adult parasites, particularly in the upper digestive tract before mechanical breakdown of the sea star begins in the gizzard. Additionally, sea stars contain substantial proportions (~ 16% by wet mass; Chapter 3) of indigestible ossicles, calcareous structural units that pass, often intact, through the digestive tract. This calcareous material may function in mechanical parasite removal while passing through the intestines.

The efficacy of both potential antiparasitic mechanisms is likely to depend on the size of the sea star consumed. Larger sea stars are expected to be more effective at mechanical removal of attached parasites, as such stars present a larger surface area for physical contact with attached worms when swallowed whole. Additionally, larger stars have larger ossicles (see below), which may be more efficient than small ossicles at removing endoparasites. The putative negative effect of *Pisaster*-derived saponins on the gull parasite community is likely to increase with dose. The sea star sizes that maximize saponin intake rate or minimize the time required to reach a certain dose are those with the highest "saponin profitability" (saponin content divided by the time required to consume the star). The relationship between *Pisaster* size and saponin profitability will be examined here.

In addition to investigating the potential antiparasitic benefits that sea stars provide to gulls, I am interested in whether *Pisaster* consumption constitutes an adaptive behavioural strategy in the context of self-medication (i.e., whether this behaviour satisfies the three criteria put forward by Clayton and Wolf [1993] and outlined above). To demonstrate adaptive self-medication, it is necessary to show that gulls choose sea star sizes based on the medicinal benefits they provide, rather than for nutritional or other reasons. I examine two non-exclusive hypotheses regarding size selection and self-medication by gulls. The chemical self-medication hypothesis states that gulls harboring large parasite loads or at high risk of parasite infection will choose sea star sizes so as to maximize their intake rate of saponins. The mechanical self-medication hypothesis assumes that large sea stars are more effective than small stars at removing gastrointestinal parasites, and thus that some relationship exists between the size of sea star consumed and parasite load. This relationship may take two forms, leading to two sub-hypotheses. Firstly, high gastrointestinal parasite loads (or the associated physical discomfort) may trigger the consumption of large sea stars, in which case one expects to see a positive relationship between parasite load and the size of sea star consumed. Secondly, if a gull incorporates large sea stars in the diet for sufficiently long to have a negative impact on parasite infrapopulation size, one would expect to see a negative relationship between the size of star consumed and parasite load. Thus, tests of the mechanical self-medication hypothesis are inherently two-tailed.

4.3 Methods

4.3.1 Assessing Parasite Load from Fecal Propagule Counts

I analyzed a total of 98 *L. glaucescens* fecal samples for number and diversity of gastro-intestinal parasite propagules in an effort to determine the effects of gull diet on parasite load. Fecal samples were collected on July 23 and August 8-11, 2010 at Robert's Creek (n = 50) and on July 24 and August 19, 2010 at Stanley Park (n = 48). Samples were collected opportunistically from the low intertidal zone between 1 hour before and 1 hour after low tide. Thus fecal samples were a maximum of two hours old when collected. Although samples were not taken from individually identified birds, I attempted to minimize the possibility of collecting multiple samples from a single individual by systematically following the low tide line during collection and by taking only one sample from groups of droppings that occurred within 1 m^2 of each other. Samples were collected using plastic coffee stir sticks and were immediately deposited into sterile plastic vials (15 ml Falcon Tubes). I measured the wet mass of each sample (to 0.01 g) on the day of collection using a digital balance. Sample vials were then filled with 10% formalin and stored at 4° C to prevent degradation of parasite eggs (Seivwright et al. 2004).

I developed a fecal flotation protocol, modified from Dryden et al. (2005) and Villanúa et al. (2006), to concentrate and then count all parasite propagules in a fecal sample. Sample vials containing formalin were centrifuged at 1500 rpm for 5 minutes. I then decanted the formalin into a waste container, washed samples with distilled water, and centrifuged again at 1500 rpm for 5 minutes. The water was decanted and sample vials filled to ¾ full with flotation medium (Zinc Sulfate, specific gravity 1.19-1.2; Dryden et al. 2005) and homogenized by vigorous shaking. I centrifuged the samples a third time at 1500 rpm for 5 minutes. I then filled each sample vial with flotation medium to a slight positive meniscus and placed a standard microscope slide cover slip on top. These preparations were allowed to sit for 30 minutes so that all propagules in the fecal sample could float to the top and concentrate on the cover slip. After 30 minutes cover slips were lifted off of the vials and placed directly onto microscope slides, which were then analyzed systematically to quantify all parasite propagules in the samples.

After the fecal flotation procedure, all remaining material from a sample (i.e., everything but parasite propagules) was washed with distilled water onto a piece of Whatman No. 1 filter paper, vacuum filtered to remove excess water, and placed into a drying oven. Samples were dried to constant mass at 60° C (for a minimum of 24 hours) and then weighed (to 0.01 g) using a digital balance to obtain dry mass. Estimated parasite load for each fecal sample was expressed as propagules per gram dry mass (PPGDM) for all analyses. If a fecal sample contained *Pisaster* ossicles, these were removed after drying and stored in a 15 ml vial to be analyzed as described below.

Table 4.1: Average size of grooved and elongate ossicles for sea stars throughout the range of *Pisaster* sizes consumed by gulls. Data are means and standard errors of all ossicles of a given type measured from each sea star (n = 10 of each type). Sea star size (measured as longest ray length) is presented in the leftmost column. Mean ossicle sizes presented here were used to derive the predictive equation for estimating sea star body size from ossicles found in gull fecal samples (see text and Fig. 4.2).

Ray Length (cm)	**Grooved Ossicle (mm)**	**Elongate Ossicle (mm)**
1.6	2.32 ± 0.05	1.21 ± 0.04
1.9	1.88 ± 0.04	1.05 ± 0.04
2.4	2.93 ± 0.04	1.28 ± 0.08
2.8	3.04 ± 0.08	1.39 ± 0.05
3.6	3.70 ± 0.08	1.54 ± 0.05
4.0	3.68 ± 0.11	2.05 ± 0.12
4.5	3.81 ± 0.13	1.93 ± 0.12
5.1	3.39 ± 0.09	1.84 ± 0.09
5.5	4.02 ± 0.21	2.19 ± 0.16
6.5	4.34 ± 0.16	2.34 ± 0.06
7.0	4.46 ± 0.24	2.40 ± 0.04
7.7	6.53 ± 0.23	2.62 ± 0.10
7.9	5.85 ± 0.15	2.44 ± 0.15
9.3	6.30 ± 0.14	3.54 ± 0.17

4.3.2 Sea Star Ossicle Measurements

Pisaster ossicles are small (~ 2 to 10 mm), calcareous, structural elements embedded within the soft tissue of the sea star. They pass, often intact, through the gull digestive tract and are easily identified in fecal samples. Preliminary studies suggested that ossicle size increases continuously with sea star body size. Therefore measuring the size of ossicles found in a gull fecal sample would provide an estimate of the size of sea star consumed by that gull. However, the exact relationship between ossicle size and body size was previously unknown. It was therefore necessary to isolate and measure ossicles from sea stars of known size. Sea stars for this study were collected from Stanley Park in July 2009, and again in May 2010 from both Robert's Creek and Stanley Park. They were taken immediately back to the laboratory at Simon Fraser University where wet mass was taken (to 0.01 g) on a digital balance and length of the longest ray was measured (to 0.1 cm) using measuring tape. Sea stars were then frozen at -20° C

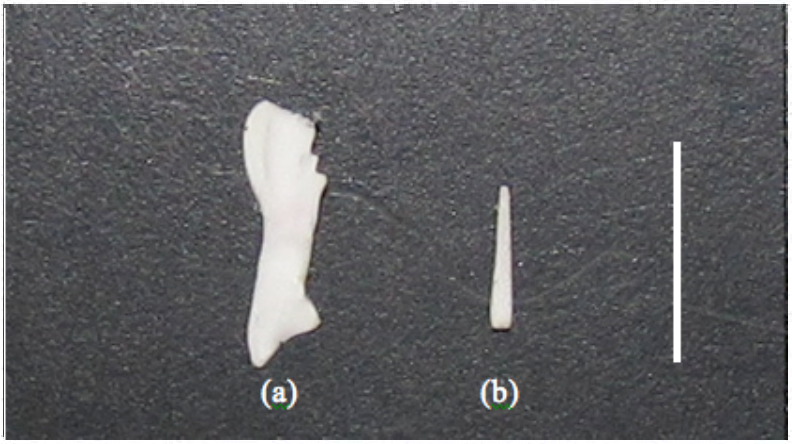


Figure 4.1: *Pisaster* ossicle types used in determining the relationship between ossicle size and sea star body size. (a) Grooved ossicle. (b) Elongate ossicle. Scale bar = 5 mm. Ossicles were taken from a sea star measuring 7.9 cm in radius.

until needed. The 14 *Pisaster* individuals processed for ossicle measurements ranged in size from 1.6 to 9.3 cm ray length (Table 4.1), which approximates the size range of sea stars that gulls were observed to consume in my foraging behaviour study (see Chapter 2).

I used a bleach digestion procedure adapted from Gooding et al. (2009) to obtain intact ossicles from sea stars. Sea stars were dried in an oven at 60° C for 48 hours and a sub sample of each was then submerged in 10% bleach in a 50 ml tube. Tubes were shaken vigorously and allowed to sit for several hours. This process was repeated, with daily bleach changes, for several days until all of the soft tissue had been dissolved away and only ossicles remained. I then vacuum filtered the ossicles on Whatman No. 1 filter paper and dried them in an oven at 60° C for 24 hours. *Pisaster* has several distinct ossicle types (LeClair 1993), however preliminary studies suggested that two ossicle types, termed “grooved” and “elongate” (Fig. 4.1), exhibit a stronger relationship between ossicle length and body size than the others. I measured 10 grooved and 10 elongate ossicles from each of the 14 sea stars. Ossicles were measured to 0.01 mm along the longest axis using a dissecting microscope ocular micrometer. Means and standard errors of ossicle measurements are presented in Table 4.1. Simple linear regression showed a highly significant positive relationship between mean ossicle size for each sea star and body size (measured as length of the longest ray) for both ossicle types

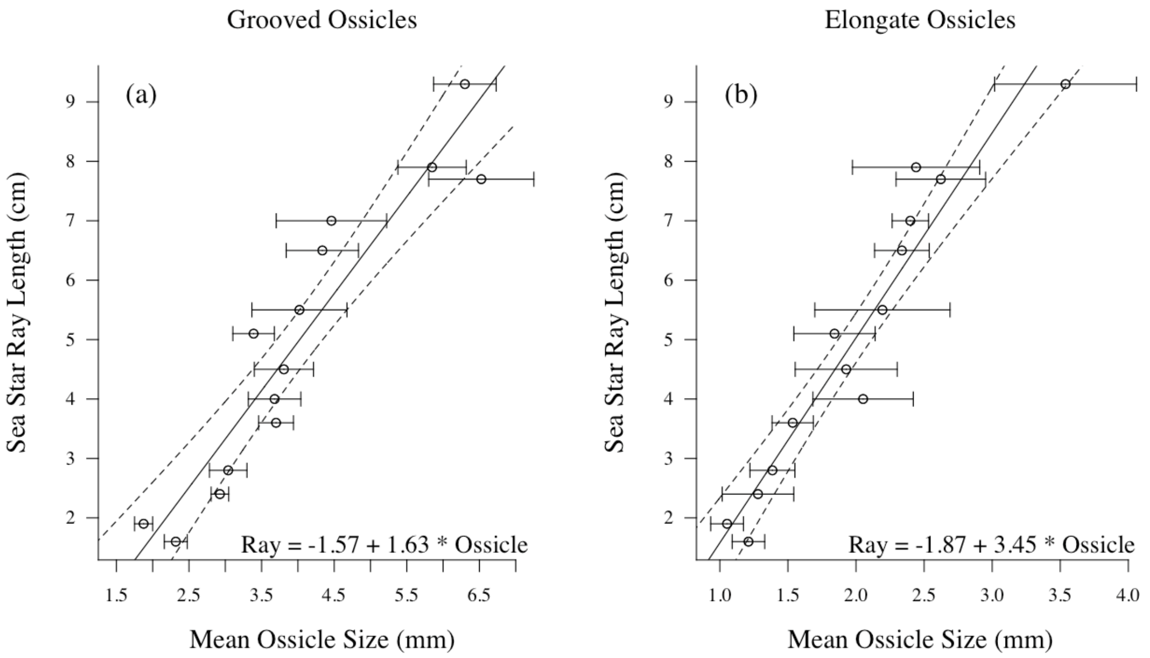


Figure 4.2: Relationship between ossicle size and sea star body size (measured as length of longest ray) for (a) grooved and (b) elongate ossicles. Points are mean sizes of all ossicles measured for a given sea star size (n = 10, see Table 4.1). Horizontal error bars are ± 1 standard deviation and are included to illustrate the magnitude of variation in ossicle size for a given sea star size. Solid lines are linear regression best fit lines for the relationship between mean ossicle size and body size (used to predict sea star size from ossicles found in fecal samples) and dashed lines are 95% confidence intervals.

(Grooved: $R^2 = 0.91$, $p < 0.0001$; Elongate: $R^2 = 0.88$, $p < 0.0001$) (Fig. 4.2). Regression equations from these two linear models where then used to estimate the sizes of sea stars consumed by gulls from ossicles found in fecal samples.

4.3.3 Sea Star Size Estimates from Ossicles in Fecal Samples

Of the 98 fecal samples analyzed, 51 (52%) contained ossicles. Where possible, I haphazardly selected 10 *intact* ossicles of each type (grooved and elongate) for measurement from each of these 51 samples. Intact ossicles showed no evidence of fracture. For some samples it was not possible to find 10 intact ossicles of one or both types, and I instead selected as many as I could find. Ossicles were measured to 0.01 mm as described above. Mean ossicle length values for a given fecal sample were then entered into the regression equations shown in Figure 4.2 to estimate the average size of sea stars consumed. This process provided two estimates of sea star size for most samples (one for each ossicle type), and I used the larger of the two in all analyses. Measurements derived in this way provide an estimate of the relative size of sea stars consumed by gulls with varying levels of parasite infection, but should not be considered accurate estimates of absolute star size. The estimated size of sea star consumed was highly correlated with site; average estimated size was significantly larger at Stanley Park (mean size ± SE = 7.09 ± 1.74) than at Robert's Creek (3.71 ± 0.19; ANOVA: F = 18.65, df = 48, $p < 0.0001$). Thus site was included as a covariate in models relating estimated sea star size to parasite load (see below).

4.3.4 Ethanol Extractions of Pisaster Saponins

Sea stars were collected in June 2009 from Robert's Creek and Stanley Park, and length and wet mass were measured as described above. I used a saponin extraction procedure adapted from Bryan et al. (1996) to determine the relationship between saponin content (per individual sea star) and *Pisaster* body size. This simple ethanol extraction is aimed at isolating all polar compounds from sea stars, however the majority of these compounds are saponins and saponin-like molecules with high bioactivity (Bryan et al. 1996). Samples of lyophilized sea star (~ 1.5-3.5 g) were extracted for 24 hours in an 80:20 ethanol to water solution at a 6:1 solvent volume to sample mass ratio. Extractions were agitated frequently throughout the 24-hour period by vigorous shaking, and the solvent from each sample was then decanted and filtered through Whatman No. 1 filter paper. This filtrate was evaporated under reduced pressure in a rotary evaporator, resolublized in methanol to bind any remaining water, and then re-evaporated. The remaining dry saponin extract was weighed to 1 mg on a digital balance. The mass of the saponin extract was divided by the dry weight of the original sample to determine saponin concentration, expressed as mg per gram dry weight. I then used known dry weight and wet weight values from sea star samples to estimates saponin content per whole individual sea star (Table 4.2). Linear regression showed a highly significant positive relationship between *Pisaster* size (longest ray length) and saponin content ($R^2 = 0.98$, $p < 0.0001$) (Fig. 4.3). Both explanatory and response variables were natural log-transformed to linearize the relationship.

Table 4.2: Data used in estimating the saponin content of whole *Pisaster* individuals. Saponin content was calculated per gram dry weight (fifth column). This value was then converted to an estimate of saponin content per gram wet weight using the individual star-specific dry weight-to-wet weight conversion factor in column four ("% WW"). Finally, the wet weight value was scaled up to an estimate of whole individual saponin content (rightmost column).

Sea Star Size	**Sea Star Mass (g)**	**Mass sub sample (g DW)***	**% WW^{+}**	**mg Saponin/g DW**	**mg Saponin/g WW**	**mg Saponin, Whole Star**
2.8	8.8	1.45	0.341	91	31	271.62
3.1	10.2	1.5	0.333	115	38	391.29
3.5	16	2.9	0.288	105	30	485.45
4.1	20.1	3.02	0.368	75	28	555.21
4.3	30	2.77	0.317	120	38	1139.83
4.4	24	2.7	0.275	112	31	741.23
4.8	38.7	3.3	0.355	91	32	1242.05
5.8	60.9	2.77	0.345	92	32	1929.69
6	61.4	2.98	0.319	92	29	1797.11
6	65.6	3.14	0.311	99	31	2023.72
6.8	131.1	3.08	0.297	115	34	4487.91
7.1	115.7	3.14	0.35	95	33	3866.21
7.8	163	3.06	0.292	87	25	4151.16
10.6	284.1	2.99	0.297	116	35	9816.77
11.5	334.7	3.01	0.294	120	35	11768.99

* DW = Dry Weight
$^{+}$ WW = Wet Weight

4.3.5 Statistical Analyses

4.3.5.1 Data Groupings

Propagule count data (PPGDM) were divided into seven categories based on taxonomic grouping and each category was treated separately for all statistical analyses. These categories were (i) All Propagules, (ii) Nematode Eggs, (iii) Digenean Eggs, (iv) All Helminth (Nematode and Digenean) Eggs, (v) Large Coccidian Oocysts, (vi) Small Coccidian Oocysts, and (vii) All Coccidian Oocysts.

4.3.5.2 Effect of Presence/Absence of Ossicles on Parasite Load

I analyzed the effect of the presence or absence of ossicles in fecal samples on parasite load, expressed as PPGDM, using Wilcoxon's Rank Sum Test. As there were substantial ties in the data (multiple zero observations of PPGDM for each data grouping), I used the function wilcox.exact from the package exactRankTests in R (Hothorn and Hornik 2006), which is capable of computing exact p-values with ties. For each data grouping, comparisons were run with data from both sites pooled, as well as for each site individually. It should be noted that site-specific tests were heavily unbalanced. At Robert's Creek, where sea stars are the main prey species, the majority of fecal samples contained ossicles (45 of 50 with ossicles). At Stanley Park the opposite trend occurred with the majority of samples lacking ossicles (6 of 48 with ossicles). However, when data were pooled from both sites, sample sizes with and without ossicles were similar (51 with ossicles and 47 without). Confidence intervals (95%) around mean parasite load were calculated via bootstrapping.

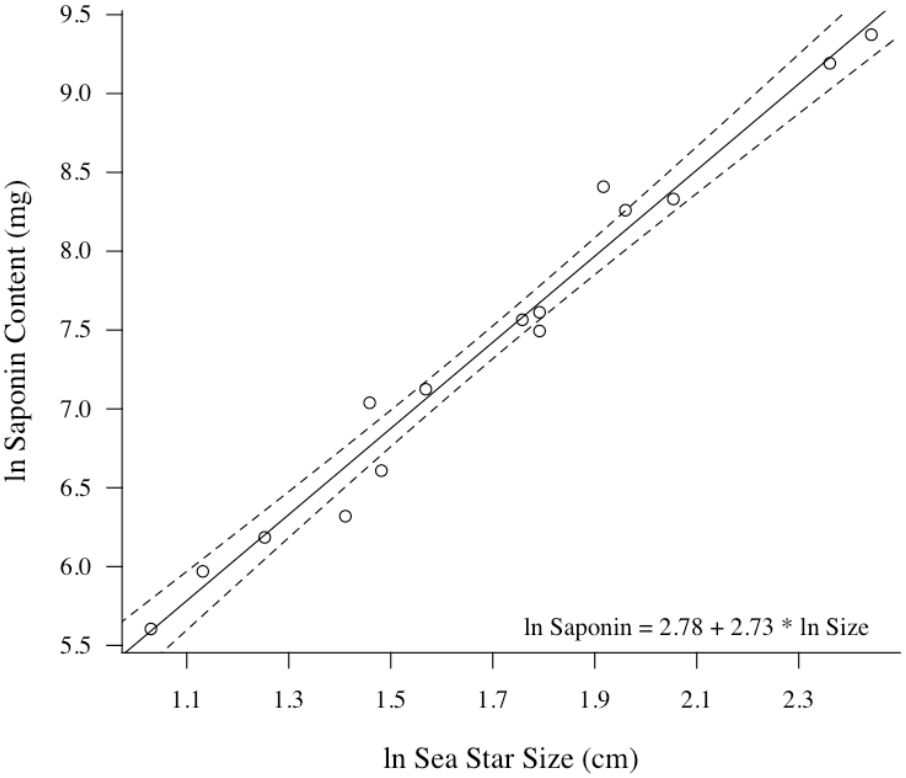


Figure 4.3: Relationship between sea star size (measured as longest ray length) and saponin content. Both variables are natural log-transformed. Solid line is the linear regression best fit line. Dashed lines are 95% confidence intervals.

4.3.5.3 Propagule Count Model Selection

I used a model selection procedure to investigate the effect of size of sea star consumed (estimated from fecal ossicles) on parasite load. For these analyses, only data from fecal samples containing ossicles were used. The propagule count data (PPGDM) were highly zero-inflated, meaning that there were far more zeros than would be expected based on the Poisson distribution. I therefore used zero-inflated models to account for the excess (Martin et al. 2005). Zero-inflated (or "mixture") models treat zero and non-zero counts separately by first modeling the probability of measuring a zero using the binomial distribution. The full dataset is then analyzed with a Poisson or negative binomial distribution, allowing for a proportion of zero counts appropriate to that distribution (Martin et al. 2005, Zuur et al. 2009). If there is overdispersion in the non-zero portion of the data set (variance is significantly different from the mean; Cox 1983), this can be overcome by modeling the data using the negative binomial distribution (Potts and Elith 2006). Likelihood ratio tests (Zuur et al. 2009) revealed significant overdispersion in all of the data groupings except for Nematode Eggs, therefore all datasets but this one were modeled using the negative binomial distribution.

Zero-inflated models allow for specification of covariates in both the binomial (zero counts) and Poisson/negative binomial (all counts) portions of the model (Zuur et al. 2009). Seivwright et al. (2004) suggest that the storage duration of fecal samples (time between collection and processing) can have a substantial effect on propagule counts. Therefore, in addition to estimated sea star size, I included the number of days between fecal sample collection and processing as an explanatory variable in the models. I also included a term for site (either Stanley Park or Robert's Creek) as a third covariate. I used all three covariates in modeling expected propagule counts μ (the Poisson/Negative binomial portion of the model). However, I had no *a priori* reason to expect that estimated sea star size or collection site would affect the probability π of measuring a zero (binomial portion of the model). Therefore this portion of the model was fit using the sample storage duration term or a constant term calculated by the model. I used AIC model selection (Burnham and Anderson 2002) to assess the relative power of different covariate combinations in explaining fecal propagule counts. The candidate models for each data grouping consisted of all possible additive combinations of covariates (n = 16). I calculated AIC scores (Akaike, 1973) and ΔAIC values (the difference between a given model's score and that of the lowest-scoring model) for all candidate models fit to each data grouping. All models were fit in R using the zeroinfl function from the pcsl library (R Development Core Team, 2006).

The AIC model selection methodology allows one to compare the relative explanatory power of models with various combinations of predictor variables and determine which model best explains the data. However, my primary interest in this analysis was whether estimated sea star size affects parasite propagule count. I used likelihood ratio tests (Zuur et al. 2009) to compare the best model for each data grouping, as determined by AIC, with and without a term for sea star size (i.e., if the top model did not include the size term, it was compared with a model having the same covariates with an additional term for size). These tests compare the amount of variance explained by the two models, providing a p-value for the significance of the sea star size term in predicting fecal propagule counts while accounting for the statistical effect of other important covariates. I also report p-values for covariates in the top models, which were estimated by the zeroinfl function used to fit these models.

4.3.5.4 Comparing Saponin Profitability and Energetic Profitability

In Chapter 2 I describe a method for estimating the energetic profitability of sea stars throughout the range of sizes consumed by gulls. I first determined (i) the relationship between sea star body size and energy content using ln-ln transformed linear regression, and (ii) the relationship between sea star size and gull handling time using a mixed effects model (Chapter 2). Energetic profitability was then determined for any sea star size by dividing the predicted energy value for that size by the predicted handling time. In order to demonstrate adaptive chemical self-medication, it will be necessary to show that gulls choose sea star sizes based on their saponin content rather than energetic profitability and it is therefore necessary to compare the sizes that maximize energetic profitability with those that maximize saponin profitability. As the denominator in calculations of both types of profitability will be the same (gull handling time) one can simply compare the slope of the relationship between energy and size with that of the relationship between saponin content and size (described above). I did so using a two-sample t-test (Draper and Smith 1998) in which the test statistic is the difference between slopes divided by the standard error of this difference (SED):

$$SED = \sqrt{SE(Slope_1)^2 + SE(Slope_2)^2}\ .$$

The degrees of freedom for this test are the sum of the residual degrees of freedom from the two regressions.

4.4 Results

4.4.1 Site-Level Parasite Prevalence

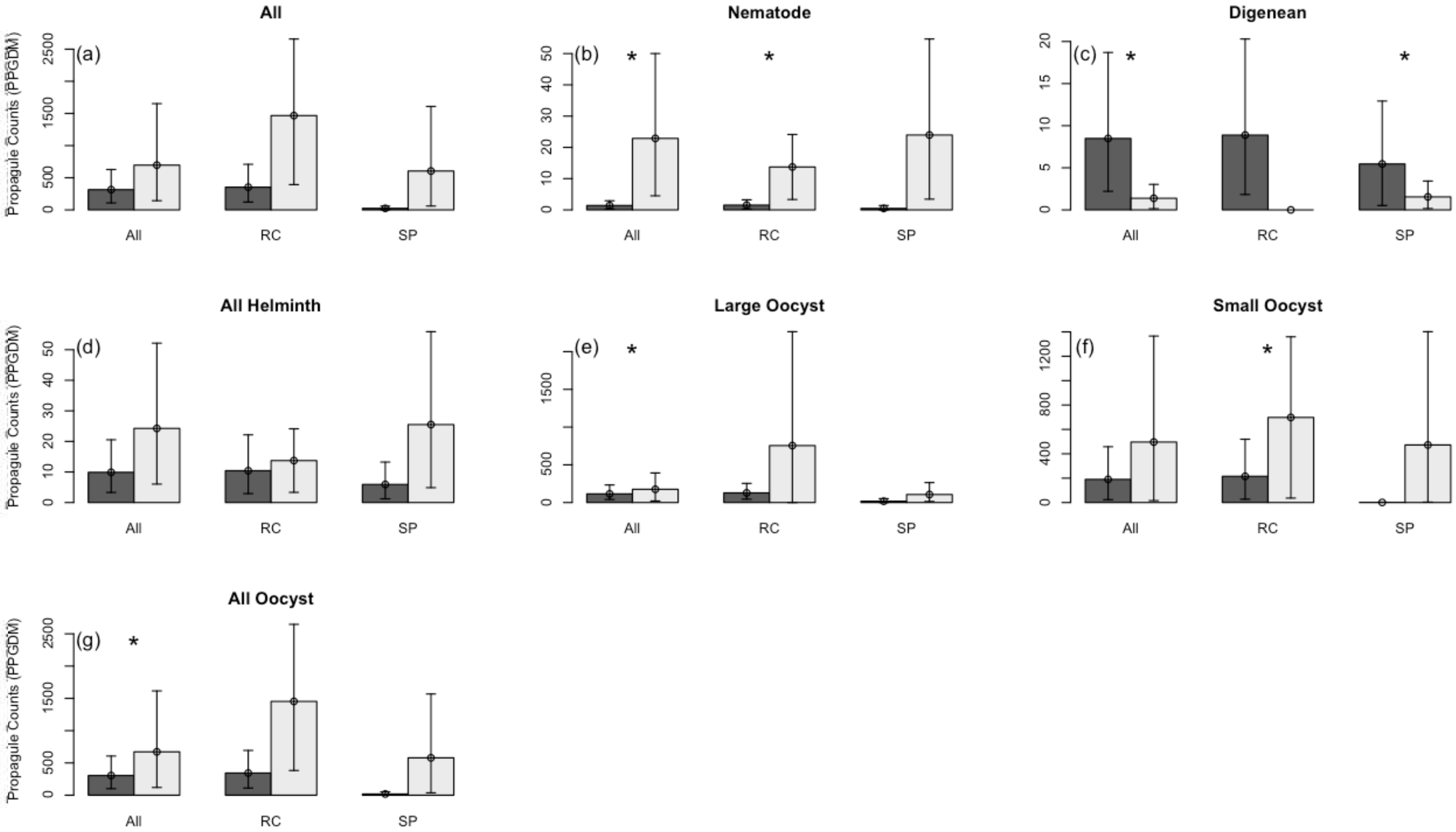
At Robert's Creek, 78.0% of fecal samples (39 of 50) contained propagules of one or more parasite species. This prevalence was not significantly different from that at Stanley Park, where 64.6% of samples (31 of 48) contained propagules ($\chi^2_{[1]} = 1.553$, p = 0.213). Pairwise chi-squared tests revealed that prevalence was only significantly different between sites for two of the data groupings, All Oocysts (RC prevalence = 72.0%, SP prevalence = 35.4%; $\chi^2_{[1]} = 11.766$, p = 0.0006), and Large Oocysts (RC prevalence = 48.0%, SP prevalence = 25.0%; $\chi^2_{[1]} = 4.629$, p = 0.031). The prevalence of Small Oocysts was slightly higher at Robert's Creek as well (26% vs. 14.6% at SP), but this difference was not significant. Neither helminth parasite taxon showed significantly different prevalence levels between sites.

4.4.2 Propagule Counts in the Presence or Absence of Ossicles

Figure 4.4 compares mean propagule counts (expressed as PPGDM) between fecal samples with and without *Pisaster* ossicles. In general, fecal samples without ossicles had higher mean propagule counts than samples containing ossicles, although differences were not always significant (see below). However one data grouping, the digenean egg group (Fig. 4.4c), showed the opposite pattern - higher mean propagule counts in samples containing ossicles. This pattern held across sites and at the individual site level.

Wilcoxon Rank Sum tests comparing propagule counts between samples with and without ossicles revealed several significant differences when data from both sites were

Figure 4.4: Barplots of mean propagule counts from fecal samples with and without *Pisaster* ossicles. Counts from each data grouping are presented separately. Dark bars are mean propagule counts from fecal samples without ossicles and light bars are mean counts from samples with ossicles. For each data grouping, means are plotted for both sites combined (“All”) as well as separately for Robert’s Creek (“RC”) and Stanley Park (“SP”). Error bars are 95% confidence intervals around mean propagule count computed via bootstrapping. An asterisk (*) above the bars indicates a significant difference in mean propagule counts between samples with and without ossicles, as determined by Wilcoxon Rank Sum tests (see Table 4.3).


All
(a)
Propagule Counts (PPGDM)
0
500
1500
2500
All
RC
SP
Nematode
(b)
*
*
0
10
20
30
40
50
All
RC
SP
Digenean
(c)
*
*
0
5
10
15
20
All
RC
SP
All Helminth
(d)
Propagule Counts (PPGDM)
0
10
20
30
40
50
All
RC
SP
Large Oocyst
(e)
*
0
500
1500
All
RC
SP
Small Oocyst
(f)
*
0
400
800
1200
All
RC
SP
All Oocyst
(g)
*
Propagule Counts (PPGDM)
0
500
1500
2500
All
RC
SP

pooled (Table 4.3). When all propagule types were combined (Fig. 4.4a), I found no difference in propagule count between samples with and without ossicles. However when individual propagule types were considered, I found significantly lower counts in fecal samples containing ossicles for nematode eggs (Wilcoxon's W = 1004, p = 0.050; Fig. 4.4b), large coccidian oocysts (Wilcoxon's W = 1460.5, p = 0.031; Fig. 4.4e), and the "All Oocyst" grouping (Wilcoxon's W = 1467.5, p = 0.044; Fig. 4.4g). Digenean egg counts, however, were significantly *higher* in samples with ossicles (Wilcoxon's W = 1444.5, p = 0.015; Fig. 4.4c).

Table 4.3: Results of Wilcoxon's Rank Sum Tests comparing propagule counts from fecal samples with and without *Pisaster* ossicles. Count data were partitioned into Data Groupings (leftmost column, see text) and comparisons performed on combined data from both sites as well as at the individual site level. Test statistics (Wilcoxon's W) and p-values are presented for each comparison. P-values in bold and italic are significant at $\alpha = 0.05$.

Data Grouping	**Sites Combined**		**Robert's Creek**		**Stanley Park**	
	Wilcoxon's W	p-value	Wilcoxon's W	p-value	Wilcoxon's W	p-value
All Propagule	1337	0.319	57	0.073	118	0.816
Nematode	1004	***0.050***	54	***0.005***	113	0.594
Digenean	1444.5	***0.015***	142.5	0.323	191	***0.007***
All Helminth	1180	0.880	77	0.199	166	0.159
Large Oocysts	1460.5	***0.031***	136	0.446	115.5	0.757
Small Oocysts	1220	0.828	62	***0.023***	126	1.000
All Oocysts	1467.5	***0.044***	54.5	0.057	118	0.755

As noted above, sample sizes were highly unbalanced for Wilcoxon Rank Sum tests performed on site-specific propagule count data due to a significant difference between field sites in the proportion of haphazardly collected fecal samples containing ossicles (90% at Robert's Creek and 12.5% at Stanley Park; $\chi^2_{[1]} = 55.87$, $p < 0.0001$).

Despite this, significant site level differences in propagule counts between samples with and without ossicles were still detectable (Table 4.3). Again, the difference in ossicle counts was not significant at either site when counts for all propagule types were combined. For fecal samples collected at Robert's Creek, nematode egg counts were significantly lower in samples containing ossicles (Wilcoxon's W = 54, p = 0.005), as were small coccidian oocyst counts (Wilcoxon's W = 62, p = 0.023). The only significant difference found for Stanley Park data was in digenean egg counts where counts were significantly *higher* in samples containing ossicles (Wilcoxon's W = 191, p = 0.007).

4.4.3 Effect of Sea Star Size on Propagule Count

Zero-inflated model comparisons suggest that there is no relationship between sea star size, as estimated from the average size of ossicles in fecal samples, and fecal propagule counts. For all data groupings, the model with the lowest AIC score consistently excluded sea star size as a covariate (Table 4.4). Likelihood ratio tests for each data grouping comparing the AIC top model with and without term for sea star size showed that size had no effect on propagule counts ($p > 0.1$ for all tests, see Table 4.4).

The top model in five of the seven data groupings (All Propagules, Nematode, Digenean, Small Oocysts, and All Oocysts) included terms for both site and sample storage duration in the all-counts (μ) portion of the model. In all cases (except for sample storage duration in the All Propagules model) the model terms for site and sample storage duration were significant at the 0.05 confidence level, indicating a real effect of both on propagule counts. However, for each of these data groupings, the top model excluded sample storage duration as a predictor for the binomial (π) portion of the model, suggesting that storage duration does not have a substantial effect on the probability of measuring a zero propagule count. The top model for the All Helminth grouping (combining nematode and digenean egg counts) included only the term for sample storage duration in the all-counts portion, which was significant (p = 0.019). Storage duration was also included in the binomial portion of the top model, but the effect was non-significant (p = 0.510). Model comparison for the final data grouping, Large Oocysts, suggests that the best model includes only a term for site in the all-counts

Table 4.4: Comparison of Zero-Inflated Poisson/Negative Binomial models describing fecal propagule count data. Sixteen models were compared for each data grouping, using all combinations of three covariates – star size, site, and storage duration – as well as an intercept-only model (~1) in the count-data portion of the model (μ) and one covariate (storage duration) or a constant fit by the model (1) in the binomial portion (π). AIC scores and ΔAIC values are presented for each model in each data grouping. Values in bold and italic correspond to the top model in that data grouping. Empty cells (…) represent models that could not be fit (i.e., failed to converge). Using likelihood ratio tests, the top model in each data grouping was then compared to the same model including an additional term for sea star size.

Model Covariates*		**All Propagules**		**Nematode**		**Digenean**		**All Helminth**		**Large Oocysts**		**Small Oocysts**		**All Oocysts**	
μ	π	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
sz,d,st	d	550.56	0.56	90.34	3.83	181.12	3.98	223.60	5.34	368.13	5.61	216.18	3.27	506.63	2.62
sz,d,st	1	551.98	1.98	88.44	1.93	179.13	1.99	221.61	3.35	366.36	3.84	214.67	1.76	505.32	1.31
d,st	d	552.60	2.60	88.43	1.92	179.14	2.00	221.91	3.65	366.28	3.76	214.26	1.35	505.36	1.35
d,st	1	***550.00***	***0.00***	***86.51***	***0.00***	***177.14***	***0.00***	219.91	1.65	364.52	2.00	***212.91***	***0.00***	***504.01***	***0.00***
sz,st	d	554.43	4.43	118.88	32.37	190.85	13.71	224.30	6.04	366.13	3.61	216.36	3.45	508.46	4.45
sz,st	1	552.44	2.44	116.89	30.38	189.20	12.06	224.71	6.45	364.37	1.85	215.79	2.88	507.92	3.91
sz,d	d	551.89	1.89	94.51	8.00	181.25	4.11	222.40	4.14	372.29	9.77	217.03	4.12	511.73	7.72
sz,d	1	553.19	3.19	92.83	6.32	179.28	2.14	220.41	2.15	370.87	8.35	215.17	2.26	511.00	6.99
sz	d	…	…	124.01	37.50	189.63	12.49	222.53	4.27	370.29	7.77	218.39	5.48	512.94	8.93
sz	1	555.83	5.83	122.01	35.50	187.96	10.82	222.95	4.69	368.87	6.35	217.97	5.06	513.09	9.08
d	d	554.93	4.93	94.70	8.19	183.32	6.18	***218.26***	***0.00***	370.55	8.03	215.99	3.08	510.40	6.39
d	1	552.92	2.92	92.81	6.30	181.46	4.32	220.73	2.47	369.15	6.63	214.68	1.77	509.81	5.80
st	d	…	…	116.88	30.37	…	…	223.40	5.14	364.28	1.76	215.66	2.75	…	…
st	1	550.54	0.54	114.89	28.38	189.28	12.14	224.09	5.83	***362.52***	***0.00***	…	…	506.43	2.42
~1	d	556.76	6.76	122.96	36.45	189.28	12.14	221.76	3.50	368.55	6.03	217.16	4.25	511.20	7.19
~1	1	…	…	120.96	34.45	…	…	222.42	4.16	367.15	4.63	216.68	3.77	…	…
		χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value
LRT$^+$		0.021	0.884	0.067	0.795	0.011	0.915	2.139	0.144	0.150	0.699	0.244	0.621	0.694	0.405

* Model Covariate Abbreviations: sz = sea star size, d = storage duration in days, st = site

$^+$ Results of likelihood ratio tests between top model and model containing a term for star size (sz). Chi-squared statistics and p-values for these tests are shown.

portion and no predictor variables in the binomial portion. The term for site, however, was non-significant (p = 0.935).

4.4.4 Comparing Saponin Profitability and Energetic Profitability

The slope of the linear regression between sea star energy content and body size (Chapter 2) was not significantly different from the slope of the regression between saponin content and body size (t = 1.25, df = 44, P = 0.22). This suggests that the relationship with sea star size will be highly similar for both saponin profitability and energetic profitability, as gull handling time for any star size will be identical in both cases. To illustrate this point, I calculated saponin profitability following the procedure outlined in Chapter 2. Comparison of the relationships between saponin profitability and energetic profitability (reprinted from Chapter 2) and sea star size reveals that they are indeed nearly identical, with both profitability types reaching a maximum between sea star sizes of 2.5 and 3.0 cm (Fig. 4.5).

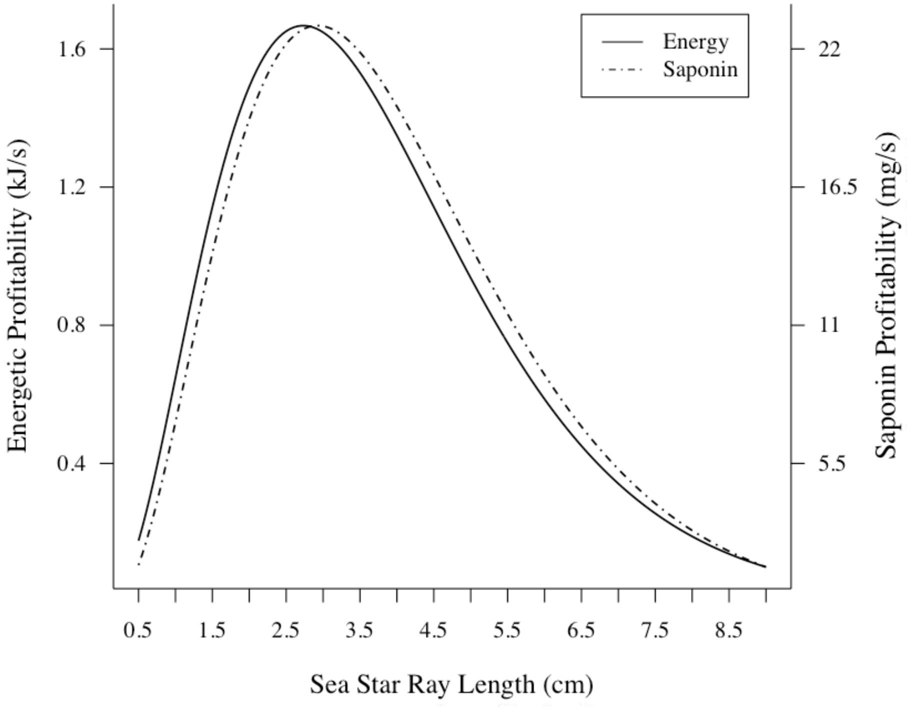


Figure 4.5: Energetic profitability (solid line) and saponin profitability (broken line) plotted as a function of sea star size. Note that the two profitability curves have extremely similar shapes and both reach a maximum between sea star sizes of 2.5 and 3.0 cm.

4.5 Discussion

The results of the Wilcoxon Rank Sum tests comparing propagule counts between fecal samples with and without ossicles suggests that the inclusion of sea stars in a gull's diet does have some effect on parasite load, although the strength and direction of this effect are inconsistent. For the majority of parasite propagule types occurring in gull fecal samples, I found lower mean propagule counts in samples containing *Pisaster* ossicles, with several of the differences in propagule count being significant (see Table 4.3). The co-occurrence of low parasite loads and sea star remains suggests that the consumption of sea stars may indeed reduce infection intensity of certain common parasite taxa, namely nematodes and coccidians. This finding, however, does not directly support either of the hypotheses presented in this study as the mechanism relating sea star consumption to reduced parasite load remains unclear.

Not all parasite species appear to be negatively affected by sea star consumption. Digenean egg counts were actually higher in fecal samples containing ossicles (Fig. 4.3c), an effect that was significant for Stanley Park data and when data from both sites were pooled. It is possible that gastrointestinal discomfort caused by generalized endoparasitic infection stimulates increased levels of sea star consumption, but that star consumption has no actual effect on digenean parasite load in particular. In this case star consumption and high digenean infection intensity would be associated, as observed here. Additionally, while a direct positive effect of sea star consumption on digenean infrapopulation size seems unlikely, a potential indirect mechanism exists whereby the negative effect that *Pisaster* consumption appears to have on nematode and coccidian parasites reduces competition on the digeneans, allowing their population size to increase. The effects of interspecific parasite competition on infrapopulation dynamics have been well demonstrated in other systems (see Dobson 1985 for a review).

4.5.1 Mechanical Self-Medication Hypothesis

I assume that large sea stars are more effective than small stars at physically removing attached endoparasites. The mechanical self-medication hypothesis therefore states that parasite load will correlate with the size of sea star consumed. However, the direction this relationship should take is unclear, leading to the two sub-hypotheses outlined in the Introduction and discussed in detail below. Likelihood ratio tests between zero-inflated propagule count models with and without a term for sea star size indicated that there is no association, either positive or negative, between the size of sea star consumed and parasite load for any of the data groupings (see Table 4.4). Similar analyses (not presented here) on propagule count data in which zero counts were removed and data were log transformed (allowing analysis within a simple linear regression framework) corroborated this finding. These results provide evidence against the mechanical self-medication hypothesis and suggest that antiparasitic benefits do not play a role in the selection of large sea stars as prey.

In some cases the AIC scores for zero-inflated models including sea star size were within 2 units of the top model's score (i.e., $\Delta AIC < 2$; Table 4.4) and an analysis based on multi-model inference and weighted parameter estimates (Burnham and Anderson 2002) could be used to incorporate an appropriately small effect of sea star size into predictions of parasite load. However, such an analysis is beyond the scope of this study, as I am only interested in testing the significance of the relationship between sea star size and parasite load.

I presented two sub-hypotheses regarding the direction of the relationship between the size of sea star consumed and parasite load. If gulls take larger-than-average sea stars in response to parasite infection, large sea star consumption would correlate with high parasite loads in a gull that had just begun to self-medicate, due perhaps to the onset of physical discomfort associated with infection. Alternatively, if a gull had been incorporating large sea stars in its diet for a sufficient length of time to cause a decrease in adult parasite numbers, one would expect large sea star remains to occur in fecal samples with low propagule counts. The analyses presented here provide no support for either sub-hypothesis. However, while these two conditions cannot co-occur within the same individual, they are not mutually exclusive at the site or population levels, and really represent two endpoints on a continuum of parasite infection intensity. This situation may have prevented me from detecting a relationship between sea star size and parasite load if one does indeed exist. Without tracking changes in parasite load in individual gulls, I have no way of distinguishing where along this continuum a particular gull lies.

It was impossible to tell if the ossicles in a given fecal sample came from one or multiple sea stars, particularly when the sizes of all ossicles fell within the range of variation for a single sea star size (see Fig. 4.2). If ossicles in a fecal sample were indeed derived from more than one sea star, it would perhaps be most appropriate to use only ossicles from the largest star in estimating sea star size consumed, as larger stars are hypothesized to have greater parasite-removing potential. My inability to distinguish between multiple sea stars required that I simply take the mean size of all ossicles in a fecal sample, which may have obscured the relationship between sea star size and parasite load. However, I think this is unlikely. All analyses were initially run using sea star size estimates derived from only those ossicles whose size measurements fell within the top 25% for a given fecal sample. This process yielded estimates of sea star size for some fecal samples (up to 13 cm ray length) that were well beyond the maximum size that gulls were actually observed to consume and was therefore abandoned in favor of taking the mean size of all ossicles in a fecal sample. However, analyses run using the large sea star size estimates produced results similar to those presented here, with no evidence of a significant relationship between sea star size and parasite load.

Additionally, verification of one of the sub-hypotheses – that large sea star remains should co-occur with low parasite loads due to removal of adult worms – may be exceedingly difficult using fecal samples from wild gull populations. Prey processing by the gull digestive tract and changes in fecal propagule counts due to actual changes in adult parasite infrapopulation size are likely to operate on vastly different time scales. Hilton et al. (2000) report that cumulative fecal production tends to reach an asymptote at approximately 19 hours post feeding for many seabird species, including Herring Gulls *L. argentatus*. Thus the maximum time one would expect between consumption of a sea star and occurrence of that sea star's ossicles in a fecal sample is perhaps 24 hours. Measurable fluctuations in population size of intestinal parasite fauna due to the anti-parasitic effects of diet choice, however, are likely to require more than 24 hours. Furthermore, the fecal sampling procedure provides only a snapshot of the gull diet. Even if an individual gull were frequently incorporating large sea stars in its diet in response to high parasite infection intensity, a one-day hiatus in large star consumption by the individual would be sufficient to prevent detection of this phenomenon. All of the problems with this study could be overcome by performing experiments on captive gulls in which diet could be controlled and parasite load could be closely monitored through time. Unfortunately such experiments were not logistically feasible.

I know of only two putative examples of self-medication via a physical, rather than chemical, mechanism. The first involves the swallowing of whole leaves, a behaviour that is associated with fecal expulsion of adult nematodes and/or tapeworm proglottids in a range of taxa (e.g., geese, bears and dogs; Huffman and Caton 2001), but which has only been investigated in depth in chimpanzees *Pan troglodytes* (Wrangham and Nishida 1983, Huffman et al. 1996, Huffman 1997, Huffman and Caton 2001). In addition to stimulating digestive function and reducing gut transit time, whole leaves are associated with the presence of adult nematodes in the feces, leading Huffman and colleagues (Huffman et al. 1996, Huffman and Caton 2001) to posit that the rough surfaces of the leaves abrasively remove adult parasites from the lining of the lower digestive tract. Leaf swallowing is exhibited to a significantly higher degree by individuals showing symptoms of parasite infection (e.g., malaise, diarrhea) and is therefore considered an adaptive antiparasitic behaviour (Huffman and Caton 2001). The second example comes from a study of small stone swallowing by Double-crested Cormorants *Phalacrocorax auritus*. Robinson et al. (2008) suggested that ingestion of small stones may result in the mechanical removal of *Contracaecum* spp. nematodes from the lining of the stomach, however their results were equivocal and appeared to be confounded by cormorant sex. Thus the existence of mechanical self-medication behaviour, while well supported for chimpanzees, has yet to be adequately demonstrated for non-hominid species.

4.5.2 Chemical Self-Medication Hypothesis

I found the slope of the relationship between sea star size and saponin content to be statistically indistinguishable from the slope of the size and energy content relationship, suggesting that both saponin profitability and energetic profitability will undergo similar changes with changes in sea star size. Figure 4.5 illustrates this, showing that both profitability types reach a maximum between sea star sizes of 2.5 and 3.0 cm. In Chapter 2, I used field-based prey selection experiments to show that gulls exhibit a strong preference for sea stars in this size range. However, it is impossible in this system to distinguish between prey selection based on energy - the most commonly invoked currency in studies describing prey choice (Stephens and Krebs 1986, Sih and Christensen 2001) – and prey selection based on putative medicinal content, a less intuitive and perhaps less parsimonious prey choice criterion.

Even if gull prey choice decisions are independent of the medicinal content of prey, this does not preclude the possibility that gulls experience an anti-parasite benefit from sea stars as a by-product of energetically optimal prey choice. Comparisons of mean propagule counts between fecal samples with and without *Pisaster* ossicles (described above) suggest a relationship between parasite load and sea star consumption that is not dependent on sea star size. For all but one parasite species, average propagule counts were lower in samples containing ossicles, and it remains possible that this apparent reduction in parasite load is due to non-deliberate saponin ingestion by gulls that are foraging on sea stars for their energetic value. However, such an indirect mechanism violates one of the three criteria for adaptive self-medication, namely that the animal deliberately contacts the medicinal substance in order to exploit its anti-pathogenic properties (Clayton and Wolfe 1993, Castella et al. 2008). In the absence of evidence demonstrating that gulls specifically choose sea stars for the purpose of saponin ingestion, independently of the nutritional value they provide, and without experimental work demonstrating an actual negative effect of *Pisaster* saponins on parasite survival and/or reproduction, I am forced to conclude that chemical self-medication does not play a role in *Pisaster* size choice by gulls.

4.5.3 Conclusion and Future Directions

The three criteria outlined by Clayton and Wolfe (1993) to assess adaptive self-medication are (i) that the host should deliberately contact the medicinal substance to exploit its antipathogenic properties, (ii) that the substance should have a negative effect on one or more pathogen species, and (iii) that the host should thereby experience increased fitness. Testing for criterion (iii), an effect of *Pisaster* consumption on gull fitness, was beyond the scope of this study. I found some evidence for criterion (ii) in that fecal samples containing sea star remains generally exhibited lower parasite loads, although the mechanism driving this effect remains unclear. However, I found no evidence to support criterion (i), namely that exploitation of the medicinal properties of sea stars drives size choice by gulls. The lack of a relationship between sea star size and parasite load indicates that mechanical self-medication plays no role in driving consumption of large *Pisaster*, and the confounded nature of energetic and saponin profitability does not support a role for chemical self-medication in overall *Pisaster* size selection by gulls. In Chapter 3 I show that *Pisaster* consumption and the range of sea star sizes consumed by free-living gulls can largely be explained by an adaptive prey choice strategy aimed at maximizing energetic intake rate. When taken together with the findings of the present study, these results strongly suggest that adaptive self-medication does not contribute to the foraging decisions of Glaucous-winged Gulls when selecting between *Pisaster* sizes.

However, the inherent weaknesses in testing for self-medication using an uncontrolled, largely observational field study mean that these conclusions are only tentative. Future work on this problem would benefit greatly from access to a colony of captive birds. In this situation, individuals could be cleared of any preexisting parasitic infections, experimentally re-infected, and monitored for parasite load through periodic fecal sampling. Any anti-parasitic benefits of sea star consumption could thereby be directly observed through changes in fecal propagule counts within an individual [criterion (ii)]. Binary preference experiments in which trained gulls are offered a sea star and another non-medicinal prey type of similar energy value could be used to demonstrate active choice of the medicinal item by comparing preference between infected individuals and non-infected controls [criterion (i)]. Finally, even the fitness consequences of *Pisaster* consumption could be determined by comparing breeding success of parasitized individuals with and without access to stars [criterion (iii)].

There is growing evidence for the widespread occurrence of self-medication behaviours and their importance in the antipathogenic behavioural repertoire of a taxonomically diverse set of animals. However, convincing demonstration of such behaviours remains elusive (Lozano 1998, Castella et al. 2008). As highlighted in this study, it is crucial to look beyond plausibility toward actual behavioural decisions when examining putative cases of animal self-medication.

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5: General Discussion

Despite the widespread co-occurrence of Glaucous-winged Gulls and Ochre Sea Stars throughout the Pacific coast of North America, and the breadth of the literature on both of these species, virtually no information previously existed on their predator-prey relationship and the factors influencing gull prey choice when feeding on stars. Intertidal foraging gulls exploit heterogeneous, temporally variable prey resources and must contend with substantial intraspecific competition and food theft within the large foraging groups that form at intertidal sites. I show that both of these factors – prey variability and kleptoparasitism risk – contribute directly to the prey choice decisions of Glaucous-winged Gulls when foraging on sea stars, and that the range of observed prey consumptions, including large, low-profitability stars, can thereby be explained.

In this thesis, I show that gulls engage in high rates of *Pisaster* predation (up to 90% dietary occurrence) and that predation rates are site-dependent, presumably based on the availability of alternative prey. Differences in energetic profitability between sea star sizes is a primary driver of size selection, with gulls exhibiting a distinct preference for 2.5 to 3.5 cm radius stars, which are among the most energetically profitable prey items available at the study sites. However, kleptoparasitism risk had a significant negative effect on the probability of a gull selecting the most profitable star sizes in field-based prey offer experiments, with preference gradually switching to smaller (< 2.0 cm), more quickly consumed stars as kleptoparasitism risk increased (Chapter 2). Optimal diet breadth models suggest that gulls maximize energetic intake rate through size selection when foraging on *Pisaster* at Robert's Creek, British Columbia, and that large, low profitability sea stars become acceptable in the rate maximizing diet at higher tide levels when the availability of more profitable star sizes is reduced (Chapter 3). Finally, I present some evidence that gulls may derive medicinal benefits from sea star consumption in the form of reduced parasite loads, but find little evidence to suggest that these benefits contribute to *Pisaster* size selection (Chapter 4).

The optimal diet model comparison presented in Chapter 3 indicates that diet breadth is finely tuned, within a given low tide period, to tide-related changes in sea star availability. Thus, gulls appear able to optimize their diet – through short-term updating of prey encounter rate information – at a single intertidal site, which may constitute only one stop on a daily foraging itinerary (see e.g., van Gils et al. 2006, Schwemmer and Garthe 2008). Schwemmer and Garthe (2008) show that Black-headed Gulls *Larus ridibundus* switch between terrestrial and marine/intertidal foraging habitats on a daily basis and that habitat use patterns are based on the tide cycle. Glaucous-winged Gulls are also known to use a variety of foraging habitats, including the pelagic zone (when exploiting fish schools; Hoffman et al. 1981) and human refuse tips (Vermeer 1982). The results of the generalized linear mixed model relating gull foraging effort to tide level at Robert's Creek (Chapter 3, Fig. 3.8) suggest that foraging habitat switching is based on tidal prey availability in this species as well. This study therefore extends previous work showing that the daily habitat use patterns of several seabird and shorebird taxa constitute use of the most profitable habitat at a given point in the tide cycle (Connors et al. 1981, van Gils et al. 2006, Schwemmer and Garthe 2008) – essentially a patch use problem – to demonstrate that, within a given site, prey choice may be optimized based on even shorter-term changes in tide level.

Apparent prey choice optimization by gulls in a habitat in which (i) they spend only a portion of their foraging time (use of intertidal sites appears to be limited to approximately four hours around low tide), and (ii) sea stars are by far the dominant diet item raises the question of what proportion of their daily energy needs gulls are able to satisfy by feeding on *Pisaster*. Daan et al. (1990) provide an allometric equation relating avian body mass to daily energetic expenditure (DEE) by parent birds during the nesting season, which corresponds to the season in which this study was conducted. Energy expenditure is highest in the nesting season due to the energetic demands of provisioning young (Daan et al. 1990), leading to estimates of DEE near the maximum for a given body size. For the Glaucous-winged Gull, with an average body mass of 1090.8 gm (James-Veitch and Booth 1954), the Daan et al. (1990) equation yields a DEE of 3910.7

kJ. This value represents the minimum amount of energy a gull would have to acquire in one day in order to maintain a positive energy budget.

To determine the amount of energy a gull could feasibly acquire from sea star foraging during one low tide period, we can use the tide level-specific estimates of maximum attainable intake rate provided by the tide-sensitive optimal diet model (Chapter 3). However, the amount of time that the tide will spend at or near a given level varies from day to day. Thus, to simplify the calculation, I will determine the maximum attainable energy from sea star foraging for a particularly favorable (i.e., very low tide) day at Robert's Creek. On July 11, 2010 the tide was between 0.7 and 1.1 m (intake rate = 0.29 kJ/s) for a total of 60 minutes and between 0.2 and 0.7 m (intake rate = 0.33 kJ/s) for a total of 180 minutes. However, even when present at intertidal foraging sites, gulls do not spend 100% of their time actively searching for and consuming prey. Scan sample data (see Chapter 3) provide an estimate of the proportion of gulls present at Robert's Creek who where actively engaged in foraging/feeding behaviour at a given tide level, and this value may be used to estimate the amount of time an individual gull spends foraging. At higher tides (i.e., between 0.7 and 1.1 m) gulls spend a mean of 38.4% of their time foraging, while at lower tides (0.2 to 0.7) this value is 44.0%. For tide levels 1 to *i*, the total energy acquired from sea star foraging is given by

$$E = \sum I_i \bullet T_i \bullet P_i$$

where I_i is the maximum attainable intake rate, T_i is the amount of time at tide level *i*, and P_i is the proportion of time spent foraging (between 0 and 1). For our example day of July 11, 2010, this calculation provides a value of 1969.3 kJ. Thus, under favorable tide conditions, a gull could recoup roughly 50% of its DEE by foraging on sea stars within a single low tide period.

Pisaster has long been considered an important keystone 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. While abiotic factors including ocean acidification (Gooding et al. 2009) and fluctuations in water temperature (Sanford 1999, 2002) are known to affect the strength of the *Pisaster*-mussel interaction, 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 previously been suggested. *Pisaster* was a major prey resource for Glaucous-winged Gulls at both field sites considered here, with predation on sea stars being especially intense at Robert's Creek. It is feasible that the high rates of star consumption observed in this study would limit the ability of local *Pisaster* populations to control the mussel distribution. Under this scenario, one would expect the indirect positive effect of gull predation on mussels to result in decreased local biodiversity through exclusion of species that compete with mussels for space. However, as summarized by Schmitz et al. (1997), adaptive prey selection by a predator can substantially alter consumer-resource dynamics relative to non-selective consumption. Gulls exhibit size-selective predation on *Pisaster*, showing a distinct preference for smaller sea stars and only incorporating large sea stars in the diet at high tide levels (Chapters 2 and 3). Thus gulls will preferentially remove the sea star sizes with the smallest impact on local mussel biomass (though reduced predation on small mussels by removal of small stars may have downstream demographic effects). However, size-selective predation by gulls may affect recruitment and demography of local sea star populations. *Pisaster* reaches sexual maturity at a weight of approximately 90 g (Menge 1975), which corresponds to a radius of approximately 5.0 cm (JPS, unpublished data). The majority of sea stars taken by gulls will therefore be immature juveniles (73% of 265 observed sea star consumptions reported in Chapter 3 were < 5.0 cm). In fact, the 2.5 to 3.5 cm size range preferred by gulls corresponds to the sizes of one-year old *Pisaster* recruits (Sewell and Watson 1993). Thus I suggest that, at a site where the full range of *Pisaster* sizes is well represented, gull predation will have only a minor effect on sea star control of the mussel distribution in the short term. However, if star consumption rates remain high and uninterrupted for a sufficient length of time, the effect of gull predation on juvenile *Pisaster* recruitment may eventually lead to a decrease in the density of large adult stars, thereby reducing predation pressure on mussels and decreasing overall community diversity.

Understanding the impact of gull foraging on intertidal diversity is beyond the scope of this study, and further work is necessary to demonstrate a real community level effect of *Pisaster* predation by gulls. Additionally, given that both species discussed here co-occur in substantial numbers, not just in southern British Columbia, but throughout their shared ranges from Alaska to northern Mexico, future work should attempt to determine whether the high rates of sea star predation observed in this study are geographically widespread. Finally, and more generally, my explicit test of assumptions regarding the timescale of information updating by foragers indicates that, when environmental variability is high, estimating changes in prey encounter rates over an appropriately short time frame will improve the predictions of optimal foraging models – by more closely emulating the actual experience of the forager – relative to the site level abundance averages frequently used to estimate encounter rates in field studies. Such an approach is likely to be applicable in any situation in which the prey distribution changes rapidly, including variable environments and when exploiting mobile prey.

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