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- Contribution No. 120 from the Catalina Marine Science Center.

## The Effect of Food Density and Dispersion on Patch Selection by Foraging Black Surfperch

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**Abstract.** – Response to patterns of food density and dispersion was examined in young-of-year black surfperch (*Embiotoca jacksoni* Agassiz). Field studies of foraging revealed that the density of invertebrate prey on a substrate type was positively correlated with preference (selectivity). Forager responses to prey dispersion patterns varied with prey density. In both the field and the laboratory, when choosing among types of substrates containing equal mean prey but differing in variability, young-of-year black surfperch showed a declining preference for the more variable type as prey density increased. Laboratory experiments revealed that the surfperch employed a simple feeding mechanism involving random visits to patches, a higher probability of initiation of feeding on food-rich than food-poor patches, and few bites taken per patch, regardless of food level.

### Introduction

An issue of great importance in predicting which patches will be chosen by a forager regards how characteristics of the feeding patches other than food density impact selection. For example, variation in physical structure among patches can alter the harvesting of food or provide differing degrees of protection to the forager from its predators (Stein 1979; Savino & Stein 1982; Cerri 1983; Schmitt & Holbrook 1985; Holbrook & Schmitt 1988a). The presence or density of predators can greatly reduce the value of an otherwise acceptable food patch (Milinski & Heller 1978; Sih 1980; Cerri & Fraser 1983; Werner *et al.* 1983a, 1983b; Schmitt & Holbrook 1985; Holbrook & Schmitt

1988b). One goal of field investigations of foraging behavior is to understand how these various constraints, in conjunction with underlying patterns of food distribution, influence patch choice.

Most studies of patch selection have concentrated on food density as the criterion influencing the behavior of foragers. Usually, the average density of food items is compared among types of patches. An additional way in which patch types might differ from one another is in the dispersion of food items. Two patch types that have the same average food level can have very different distributions of food items among patches. Since search time or other components of foraging behavior could be affected by the degree of prey dispersion, the relative value to a forager of patches that are similar in prey density but not in prey dispersion might be quite different.

Natural environments are often characterized by patch types with different spatial distributions of prey. Yet few studies have attempted to measure response of foragers to food dispersion patterns (Weissburg 1986), despite some theoretical interest (Oster & Wilson 1978; Real 1980; Caraco 1980, 1983; Weissburg 1986). In this paper, I explore response to patterns of food density and dispersion by young-of-year black surfperch (*Embiotoca jacksoni* Agassiz). Individuals feed on crustaceans harvested from the surfaces of foliose algae and other benthic substrates in reef environments. Although the size structure and species composition of prey are similar among species of algae used by juvenile black surfperch for feeding (Schmitt & Holbrook 1984b), the species of algae differ substantially in mean densities of prey they contain (Schmitt & Holbrook 1985). The species of algae (patch

types) also differ in degree of prey dispersion. Food is never uniformly distributed (among plants) on any patch type used by black surfperch, but food items tend to be much more clumped on some patch types than on others. Below I first establish that foragers selectively feed from patch types containing high food levels. Then I show how food dispersion patterns affect selectivity for patches containing similar prey levels. Finally, I investigate feeding mechanisms that account for the responses of feeding surfperch to patches that differ in mean density or dispersion of prey.

### Methods

Field observations and laboratory experiments were conducted at the Catalina Marine Science Center, Santa Catalina Island, CA (33°28'N: 118°30'W).

**Response to Food Density:** Juvenile black surfperch harvest prey from a variety of benthic substrates, including rock surfaces and various species of foliose algae. I first determined that there was a positive relationship between density of food on substrates and intensity of their use during feeding. To do this, I observed 40 young-of-year black surfperch on the west side of Big Fisherman Cove for 10 min each and recorded bites directed toward benthic substrates [foliose algae, turf, the vascular plant *Phyllospadix torreyi*, and sand (see Holbrook & Schmitt 1984; Schmitt & Holbrook 1984b for detailed methods)]. Availability of substrates was assessed by line transects as previously described (Holbrook & Schmitt 1984; Schmitt & Holbrook 1985). Selectivity was determined by comparing use of substrate types by the local population of juvenile black surfperch (all bites combined) with their relative availability using Manly's Index (Manly 1974; Chesson 1978, 1983) as:

$$\alpha_i = \frac{r_i / n_i}{\sum_{j=1}^m r_j / n_j}, i = 1, \dots, m \text{ (Chesson 1978)}$$

where  $r_i$  and  $n_i$  are the proportions of substrate type  $i$  used by fish and in the environment respectively. This measure removes any bias introduced by differences in availability of substrate types. Alpha values can range between 1 (total preference for that patch) and 0 (total avoidance) and, for the  $n$  patch case,  $1/n$  represents equal preference for all patches.

Prey densities on major foraging substrates were estimated by collecting samples ( $n = 10$  plants each type) in plastic bags underwater and counting the invertebrate prey items (methods in Schmitt & Holbrook 1984b). Selectivity of fish for the eight most common substrates and density of food items each contained were correlated using Spearman rank correlation.

**Response to Food Dispersion:** I first explored response to food dispersion in the laboratory with feeding choice experiments. This approach enabled me to use just one substrate type, the brown alga, *Zonaria farlowii* Setchell & Gardner, on which food density and dispersion were manipulated. The experiments compared selectivities for patch types containing equal amounts of food but with different dispersion patterns. Selectivities for patch types containing equal amounts of food but with different dispersion patterns could then be compared. After the response to dispersion was determined under laboratory conditions, foraging data from the field were analyzed to test whether fish responded to food dispersion under field conditions.

Young-of-year *Embiotoca jacksoni* (56-80 mm SL) were collected from the field with hand nets and maintained in large (5000 l) outdoor holding tanks. Natural food items were provided by presenting fish daily with the alga *Zonaria farlowii* (hereafter *Zonaria*) which supports abundant crustacean prey and is a favored foraging substrate (Schmitt & Holbrook 1984a, 1984b, 1985; Holbrook & Schmitt 1984).

The experiments were conducted in a circular outdoor tank (2 m diameter, 1 m deep, 2000 l) located under a sun screen to eliminate shadows. Light conditions were bright, as all

tests occurred between 1000 and 1400 hours. The tank bottom was divided in half by a thin polypropylene line and landscaped with a total of 300 (10 kg) freshly collected *Zonaria* plants. Crustacean prey can be removed from *Zonaria* plants by agitating them in sea water, and a washing technique was used to create patch types (tank halves) that had the same average densities of prey but which differed in dispersion. The same number and sizes of plants were placed in each tank half, but on one side prey were clumped (high among-plant variance) and on the other side prey were uniform. Treatments consisted of varying the mean density of food in the tank. Density and dispersion were estimated following each foraging bout by counting prey on 10 randomly selected plants per patch type per treatment. Sampling after the foraging bout ensured that the crustaceans had maintained the clumped patterns throughout the observation period. Prey depletion in each experiment was much less than 5-10%. A total of 11 prey densities was used, ranging from a low of < 4 items/gm algae (weighed damp) to a high of > 14/gm algae. The experimental range of values was similar to the natural range encountered in the field (see below).

The tank was freshly landscaped for each treatment and 10 randomly selected young-of-year black surfperch were added. Individual fish were not used in more than one treatment. Following a 10 min acclimation period, the foragers were observed for 20 consecutive 1 min intervals by 2 observers situated on opposite sides of the tank. In each interval and in each tank half, foraging effort (total number of bites taken) was recorded; at the end of every interval the distribution of fish on the two patches was determined. Previous experiments tested for and found no significant effects of tank position (Schmitt & Holbrook 1985). The time period of each trial (20 min) was sufficiently short to preclude depletion of prey or satiation of foragers (Schmitt & Holbrook 1985; Holbrook & Schmitt 1988b).

To determine if prey dispersion influenced choice of substrates under natural conditions, I compared selectivity of foraging fish for pairs of algal taxa with similar mean prey densities but different among-plant variabilities (dispersion) in prey level. A total of 22 pairs of substrates from three locations within 2 km of the Catalina Marine Science Center was analyzed. Selectivity was calculated for pairs of patches within each location. The patches ranged in mean prey densities from 4 to 16 items/gm algae.

Selectivity was determined by comparing use of the two patches by each local population of juvenile black surfperch with their relative availability using Manly's  $\alpha$ . In each location, use was documented by observing foraging young-of-year surfperch as described above. Availability of substrates and prey densities were determined as previously described.

For each pair of substrates at each location having similar estimated mean density of food, selectivity was calculated for the patch type having the greater variability in prey level among plants. Preference for the patch with the higher variance in prey was plotted against overall prey density for that pair. This procedure allowed comparison between field and laboratory results concerning the response of foragers to food dispersion as a function of food density.

**Feeding Mechanisms of Juvenile Black Surfperch:** Juvenile surfperch forage by visiting individual plants or small patches of turf and taking one or more bites before swimming to the next feeding location. The experiments and observations revealed that patch use by the foragers was not random; preference for types of substrates was influenced by both food density and dispersion. Higher preference for a given substrate type could result from the operation of several mechanisms, including: 1) higher visitation rate to food-rich patches; 2) higher probability of initiating feeding on a visited patch that has more food and 3) longer feeding bouts (more bites taken) on patches with high food levels. I

explored feeding patterns of individual fish in the laboratory and the field to determine which of these mechanisms was operating.

In a set of laboratory experiments, I provided individual foragers with an array of 9 *Zonaria* plants that varied in food density. In each replicate, I employed 3 prey densities: 25, 50 and 100% of ambient (field) density. Reductions were achieved by washing freshly collected plants in sea water; counts were made to verify food levels. An individual fish was observed feeding for 60 min. Analysis of the feeding data allowed me to test whether the density of food on plants influenced visitation rate, initiation of feeding, or lengths of feeding bouts. The experiment was repeated 9 times, using different foragers and new plant arrays for each replicate.

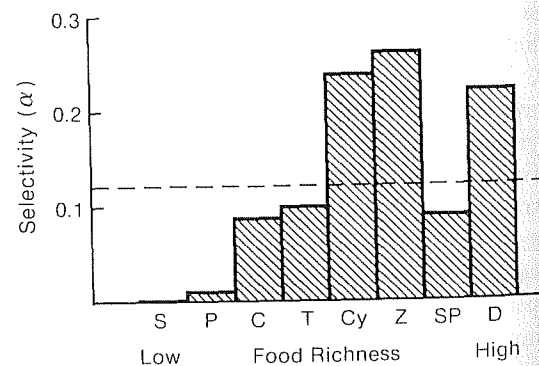
It was much more difficult to examine mechanisms of feeding in the field. The close spacing of algal plants precluded accurate determination of inspections of plants (unless a bite was taken). Therefore, field foraging data could not be used to explore whether density or dispersion of food influenced visitation or initiation of feeding. However, it was possible to determine if feeding bouts lasted longer (e.g., more bites taken) on substrates rich in food items than on types containing less food. Using the foraging data gathered in Big Fisherman Cove, the mean number of bites taken per plant visited was determined for each fish for the 6 foliose algae most frequently fed upon (*Colpomenia* sp., turf, *Cystoseira* sp., *Zonaria farlowii*, *Dictyopteris* sp., and *Sargassum palmeri*). Among-substrate differences in length of feeding bouts were tested by ANOVA. The two least-used feeding substrates, sand and *Phyllospadix torreyi*, had too few visits for analysis (3 and 1 respectively).

## Results

**Response to Food Density:** Observations of foragers in Big Fisherman Cove recorded 1,552 bites by 40 fish ( $\bar{x}$  bites/fish = 38.8,  $s = 14.3$ ) on 8 common substrates. Prey densities

were significantly different among substrates, ranging from less than 1 prey item/gm substrate to 8 items/gm substrate (Table 1). Fish selectively fed from substrates containing high food (Fig. 1). There was a significant positive correlation between preference rank and food density rank for substrates (Fig. 1).

**Response to Food Dispersion:** Laboratory tests revealed that the degree to which foraging effort was allocated between patches with high food dispersion and those with low dispersion varied with absolute prey density (Fig. 2). When overall prey levels were low, foragers selectively fed where food was relatively more clumped (high-variance patch). However, as food density increased, foragers devoted more foraging effort where food was more randomly distributed (low-variance patch). The negative relationship between mean food density and use of the high-variance patches was highly significant ( $r = -0.76$ ,  $t = 3.62$ ,  $P < 0.005$ ). The data demonstrate that patch choice was influenced by prey dispersion, with preference dependent on overall abundance of food.



**Figure 1.** Selectivity values (Manly's  $\alpha$ ) for foraging substrates of juvenile black surfperch at Big Fisherman Cove. Substrate types are arrayed in order of increasing prey density from left to right. The dashed line indicates the level of selectivity if all substrates were used at random. Spearman rank correlation between selectivity for a substrate and food richness,  $r = 0.75$ ,  $P < 0.05$ . S, sand; P, *Phyllospadix torreyi*; C, *Colpomenia* sp.; T, turf; Cy, *Cystoseira* sp.; Z, *Zonaria farlowii*; SP, *Sargassum palmeri*; D, *Dictyopteris* sp.

**Table 1.** Food density on substrates. Given are the  $\bar{x}$  and SE (in parentheses) of food items (per gm damp weight substrate) ( $n = 10$  samples/substrate). Means not connected by a dashed line differ at  $P < 0.05$  by SNK test. The ANOVA table is presented below. Dic, *Dictyopteris* sp.; Sar, *Sargassum palmeri*; Zon, *Zonaria farlowii*; Cys, *Cystoseira* sp.; Col, *Colpomenia* sp.; Phy, *Phyllospadix torreyi*.

	Substrates						
	Dic	Sar	Zon	Cys	Turf	Col	Phy
	8.0 (1.1)	6.3 (0.7)	4.8 (0.8)	4.7 (0.5)	4.4 (0.5)	3.5 (0.6)	0.4 (0.1)
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ANOVA Table							
Source	df	MS	F	Significance			
Among substrates	6	55.56	13.48	$P < 0.0001$			
Error	63	4.12					

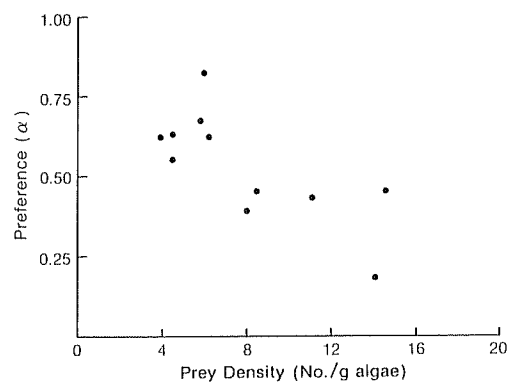
The relationship between prey density, prey dispersion, and patch choice was not the result of differences in overall foraging activity. Despite the variation in absolute food density among treatments, total feeding effort did not vary with food level ( $r = 0.05$ ,  $t = 0.16$ , NS;  $\bar{x}$  bites/forager/treatment = 13.3). Further, each bout was sufficiently short to exclude satiation as an explanation (Schmitt & Holbrook 1985). Thus, it appeared that overall search time by these foragers was relatively unaffected within the range of prey densities tested.

Analyses of foraging data from the field revealed that, for a given mean abundance, selectivity for patch types with more dispersed food decreased as a function of increasing food density (Fig. 3). The relationship between food density of substrate pairs and selectivity for the more variable member of each pair was negative and highly significant (Fig. 3;  $r = -0.57$ ,  $t = 3.13$ ,  $P < 0.005$ ). This response was comparable to that detected under controlled laboratory conditions (Fig. 2).

**Mechanisms Underlying Feeding:** To establish the mechanisms underlying allocation of foraging effort, foraging behavior of individual fish was examined. In the nine-plant arrays, the plants were spaced far enough apart that fish visits to plants, inspections, and bites were easy to determine. During the feeding trials, fish swam slowly through the arrays,

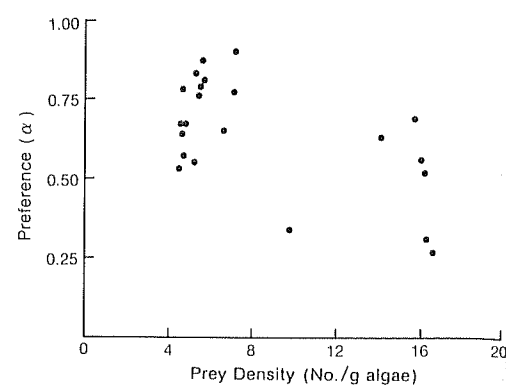
inspecting plants and taking bites from some of them.

Fish visited plants randomly within the arrays (Fig. 4). There was no difference in proportion of visits made to the three prey-richest and three prey-poorest plants in the array (Fig. 4; paired  $t$  test,  $t = 1.78$ , 8 df, NS). This pattern suggested that at least when all plants looked alike (same size and species), close inspection by the forager was required to determine whether a plant was a potential feeding location. By contrast, once a fish had visited (inspected) a plant, food density did influence initiation of feeding. Visits to prey-rich plants in the arrays resulted in bites significantly more often than visits to the prey-poor plants in the array ( $t = 2.07$ , 8 df,  $P < 0.05$ , one-tailed). As a result, a significantly greater proportion of bites was taken from plants containing more prey (Fig. 4). Once feeding was initiated on any given plant, prey density did not influence the total number of bites taken during a bout. Overall, fish averaged few bites during a feeding visit (prey-richest:  $\bar{x} = 1.7$  bites/visit; prey-poorest:  $\bar{x} = 1.6$  bites/visit). Together, the data indicated that plants in the arrays containing different amounts of prey were visited more or less at random. The tendency of an individual to begin to feed, but not the length of a feeding bout, was dependent on prey density.



**Figure 2.** Allocation of foraging effort to the more variable patch during laboratory experiments. Preference (Manly's  $\alpha$ ) for the tank half containing more clumped prey is plotted against overall prey density (number prey items/gm algae). Spearman rank correlation between food density and use of the high variance (clumped prey) patch,  $r = -0.76$ ,  $P < 0.005$ .

Analysis of the field foraging data corroborated the laboratory finding that number of bites taken in a foraging bout was not associated with food density. I compared the mean number of bites per visit to a plant for the six most commonly visited foliose algae. The foragers averaged just over 1 bite per visit (Table 2). The number of bites per visit on *Zonaria*, a substrate that was rich in prey, was significantly higher than the rest of the substrates. However, there were no differences in bites per visit among the other substrates, despite great differences in prey density. These results mirrored the laboratory finding that



**Figure 3.** Selectivity for foraging substrates in the field. Plotted is selectivity (Manly's  $\alpha$ ) for the more variable taxon of pairs of algal species having equal prey density. The prey density of each pair of algae is indicated on the x axis. Random substrate use would be  $\alpha = 0.5$ . Spearman rank correlation between food density of substrate pairs and selectivity for the more variable member of the pair,  $r = -0.57$ ,  $P < 0.005$ .

prey density did not greatly influence number of bites taken during feeding visits.

### Discussion

Mobile foragers are often selective in their use of available patches of food. A large body of patch selection theory has been developed based on the notion that patch quality is linked with food reward (MacArthur & Pianka 1966; Pyke 1984). Fitness of individual foragers is assumed to be maximized by selectively feeding in patches yielding the greatest net food return per unit time spent foraging. The food reward

**Table 2.** Number of bites taken per feeding visit on 6 algal substrates. The  $\bar{x}$  and SD (in parentheses) are given. Means not connected by the dashed line differ at  $P < 0.05$  by Duncan Multiple Range Test. The ANOVA table is given below. Turf,  $n = 36$ ; Sar, *Sargassum palmeri*,  $n = 35$ ; Cys, *Cystoseira* sp.,  $n = 31$ ; Col, *Colpomenia* sp.,  $n = 11$ ; Dic, *Dictyopteris* sp.,  $n = 40$ ; Zon, *Zonaria farlowii*,  $n = 40$ .

Substrates						
Turf	Sar	Cys	Col	Dic	Zon	
1.1	1.2	1.2	1.2	1.3	1.5	
(0.14)	(0.27)	(0.30)	(0.60)	(0.32)	(0.43)	
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ANOVA Table						
Source	df	MS	F	Significance		
Among Substrates	5	0.87	7.69	$P < 0.001$		
Error	187	0.11				

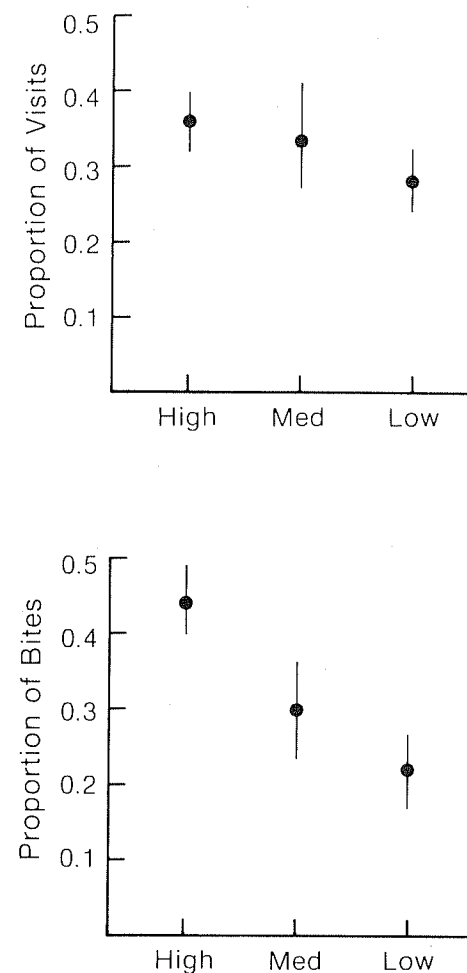
of a particular patch type has two components: 1) abundance of various prey items and 2) "energetic value" (e.g., energy gain/foraging cost) to the forager of those items (Werner & Hall 1974; Elner & Hughes 1978; Werner *et al.* 1983a, 1983b; Bence 1986). In the surfperch system, the energetic value of food items is similar among patches, because the same taxa of food occur on different patches. In this situation the abundance of items on a patch type is frequently used as a measure of quality.

It is well established that many kinds of foragers can discriminate among patches and selectively feed from those with the highest food levels. Previous work revealed this pattern to be true of juvenile black surfperch, in that they consistently rank substrate types by average prey density, with the richest substrates being the most highly preferred (Schmitt & Holbrook 1985). This strong response accounts for the overall pattern of substrate preference displayed by juvenile black surfperch (Fig. 1; Holbrook & Schmitt 1984, 1988b; Schmitt & Holbrook 1984a, 1984b, 1985).

The data presented here indicate that within-substrate variation in prey levels is also a component influencing patch selection. Under laboratory conditions, juvenile surfperch responded to differences in dispersion patterns of prey. Preference for the more variable patch type (where prey were more clumped) decreased with increasing food density (Fig. 2). A similar response to prey variability was detected when the field foraging data were analyzed (Fig. 3). The discovery of a detectable response to food dispersion in field populations was a surprising result, since the conditions under which surfperch forage in nature are complicated by several factors that could easily obscure subtle patterns of feeding behavior. At Santa Catalina Island, numerous substrate types (8 rather than 2) occur in shallow reef areas, and food levels differ in mean as well as in variability. Further, substrates are intermingled on a small spatial scale, such that a forager has simultaneous access to a variety of patch types. The structure of patches differs,

which can alter the ability of the fish to harvest food and confer differing degrees of protection to the surfperch from their predators (Schmitt & Holbrook 1985). Foragers are thus simultaneously confronted by a variety of substrates and factors that might influence their use.

The response to food abundance and variability by juvenile black surfperch appears to be a simple consequence of its foraging



**Figure 4.** Feeding activity by individual foragers on high ranked ( $n = 3$  plants, prey-rich), medium ranked ( $n = 3$  plants), and low ranked ( $n = 3$  plants, prey-poor) plants in the arrays of 9 *Zonaria* plants. Shown are the mean ( $\pm 1$  SE) proportions of visits to and bites taken from plant groups ( $n = 9$  replicates).

tactics. During the plant choice experiments, the probability that a bite would be taken on a plant depended on its prey density. If prey level was sufficiently low, the plant still would be inspected, but a bite would be unlikely to occur. Thus, when two patch types have low mean prey but differ in dispersion, most plants visited would contain too few prey and would not be fed upon, and bites would be concentrated on plants containing the highest prey levels. Overall, these plants would tend to belong to the more variable patch type. As overall prey densities of the two patch types increased, only the most prey-poor plants in the environment would fail to elicit a feeding response. These would belong to the more variable patch type. Feeding at higher prey densities would thus be concentrated on the less variable patch type. This foraging strategy, if used across an appropriate range of prey densities, yields a behavior that is consistent with the patterns of response to prey mean and variability described above.

#### Acknowledgments

I thank R. Ambrose, J. Bence, T. Hughes, M. Keough, R. Schmitt, and S. Walde for critical discussions and comments on the manuscript. J. Crisp, M.M. Perez, and J. Jolly assisted in the field and laboratory. Financial support was provided by the National Science Foundation (OCE-8314832, OCE-8614148). R. Given and A. Muscat, as well as the staff of the Catalina Marine Science Center, provided gracious hospitality and logistic support.

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Contribution No. 133 of the Catalina Marine Science Center.