

Characteristics of foraging in the soft-bottom benthic starfish *Luidia clathrata* (Echinodermata: Asteroidea): prey selectivity, switching behavior, functional responses and movement patterns

James B. McClintock* and John M. Lawrence

Department of Biology, University of South Florida, Tampa, FL 33620, USA

Summary. *Luidia clathrata* show a strong preference for the infaunal bivalve *Mulinia lateralis* in Tampa Bay, Florida. Quantitative and qualitative changes in diet occurred over a 7-month period. Individuals may shift from intraoral macrofaunal feeding to intra- and extraoral detrital feeding during periods of low macrofaunal availability. In the laboratory *L. clathrata* showed switching behavior, feeding disproportionately on the most abundant of two simultaneously presented food models. This switching mechanism may be related to either contact-chemoreceptive rejection of low-density food or enhanced distance-chemoreception of high density food. The use of standardized food models eliminated the possibility that handling time was important in switching behavior. Both fed and starved individuals showed functional responses to changes in prey density. However starved individuals ingested greater numbers of prey and spent more time foraging than did fed individuals. Switching and functional response behaviors may be important in promoting nutritional uptake and in causing density-dependent mortality of prey populations. Movement patterns of *L. clathrata* are directional in the absence of bivalve prey, but become non-directional once patches of prey are encountered. This allows individuals to remain in areas of high prey density. *Luidia clathrata* has characteristics of an optimal forager, where energy is maximized per unit feeding time.

Previous studies have indicated that the soft-bottom asteroid *Luidia clathrata* is chemoreceptive, has both extra- and intraoral modes of feeding, chooses particular sizes of prey, and can be conditioned to both photic and ingestive stimuli (see McClintock and Lawrence, 1981, 1982, 1984; McClintock et al. 1984, in press). These studies suggest that *L. clathrata* has characteristics of an "optimal" forager (sensu Emlen 1966; Schoener 1971). However, to better evaluate the feeding behavior of this asteroid within the context of optimization theory, a broader understanding of its foraging behavior is necessary. Additional factors which may lend insight into whether an organism is an "optimal" forager include choices of prey type, behavioral responses to changes in prey density and patterns of foraging

movements. An evaluation of these factors will permit a more thorough understanding of feeding behavior in *L. clathrata*, and ultimately, aid in predictions about the effect of this benthic predator on the ecology of prey populations.

Selectivity for different types of prey is considered an important component of optimal foraging models (Pulliam 1974; Charnov 1976). These models predict that an animal should choose the food or combination of foods which maximize food "value" (Emlen 1973). "Value" may be explained in terms of energy or nutrients gained per unit feeding time (Schoener 1971; Pyke et al. 1977), or, in an evolutionary context, in relation to differential reproductive success (Rapport 1980). Prey preferences may be related to relative availability, energy content, ease of handling, escape behaviors of prey and/or past feeding experience (Hughes 1980). Selection for prey may have important consequences on the nutrition of the predator, as well as the ecology and life-history characteristics of prey species.

Optimal diet choice models predict that only the abundance of better (higher energy yield per unit time) prey is important in prey choice decisions. These models assume that energy values of prey and ability to detect prey do not change as abundance changes. Estimations of the relation between total feeding time and total net energy yield suggest that an "optimal" feeder will increase feeding rate, or time spent feeding, with increased density of prey (Schoener 1971). This relationship between prey density and feeding rate has been well developed in the "functional response" models of Holling (1966). Prey switching theories (Murdoch 1969) are based on the assumption that animals can functionally respond to changes in relative prey density, while feeding disproportionately on the most abundant of two alternative prey species. Little information is available on switching or functional response behaviors of marine invertebrates. Switching behaviors and functional responses can have important consequences for individuals (e.g. nutrition and energetics), populations (e.g. density-dependent mortality) and communities (e.g. preventing competitive exclusion) (Murdoch and Oaten 1975).

Models of optimal foraging assume that predators should pattern their movement to coincide with the distribution of prey so as to maximize energetic intake per unit time spent foraging (Pyke et al. 1977; Hughes 1980). Efficient foragers are thought to choose a directional pattern of movement that minimizes the chances of recrossing its own path during a foraging bout (Cody 1971, 1974). Infor-

Offprint requests to: James McClintock

* Present address: Center for Marine Studies, University of California at Santa Cruz, Santa Cruz, CA 95064, USA

mation about foraging patterns of marine invertebrates can lend insight into aspects of their perception (e.g. chemoreception) and their potential trophic impact on differentially distributed invertebrate taxa.

The purposes of this study were to ascertain whether *Luidia clathrata* 1) selects specific prey in the field 2) shows "switching" behavior 3) functionally responds to changes in prey density and 4) forages in a directional manner.

Materials and methods

Study organism

The asteroid *Luidia clathrata* is found abundantly in sand or mud-sand bottom habitats from New Jersey to Brazil in 0–75 m water (Downey 1973). In contrast to other *Luidia* spp., which generally feed on echinoderms (Feder and Christensen 1966; Brun 1972; Penchaszadeh and Lera 1983), *L. clathrata* preys on a number of different taxa. *Luidia clathrata* ingests foraminiferans, nematodes, ostracods, gastropods, bivalves and crustaceans, in addition to sediment and detritus (Hulings and Hemlay 1963; Lawrence et al. 1974). *Luidia clathrata* shows foraging periodicity, alternating between periods of movement over, and burial beneath, the substratum (McClintock and Lawrence 1981). All individuals used in this study were collected in Old Tampa Bay, Florida (approximately 17°55'N, 83°35'W) in 3 m water.

Prey selection

Prey electivity was investigated by examining the gut contents of twenty *Luidia clathrata* (mean arm length (R) = 79 ± 20 mm) collected in April 1983. All starfish were collected by SCUBA and placed immediately into 20 × 15 cm plastic zip-lock bags to prevent loss of regurgitated stomach contents. Prey were identified to lowest taxon possible and the presence or absence of detrital material was noted. Faunal composition of the substrata was examined by removing 9 circular PVC cores (6 cm deep and 12 cm in diameter) from the collection site. Preliminary observations indicated that there was no significant ($P < 0.05$; Student's t test) difference between infaunal densities of 3 cores. Therefore 9 cores were adequate to evaluate accurately infauna availability. Substrata were washed through an 841- μ m sieve and the remaining material stained with rose Bengal to facilitate identification of macrofauna. Vanderploeg and Scavia's (1979) relativized electivity index was calculated to estimate the degree of faunal similarity between substrata and stomach samples. This index is defined as $E_i = (W_i - 1/n) / (W_i + 1/n)$; where $W_i = r_i / p_i / \sum r_i / p_i$, n = the number of kinds of food items, r_i and p_i = the proportions of foods i in the diet and the environment respectfully. Lechowicz (1982) concluded that this index was the best measure of prey electivity available. Seasonal variability in diet was investigated by examining gut contents of *Luidia clathrata* in June, August, September, October and December 1982, collected from the same site.

Prey-switching behavior

Luidia clathrata were collected in November 1982, and 24 individuals (mean $R = 70.3 \pm 1.0$ mm) were maintained individually in chambers (16 cm wide, 28 cm long, 40 cm

Table 1. Ratio of foods offered to two groups of *Luidia clathrata* over a 12-day period. Ratios were changed each three days

Day	1–3	4–6	7–9	10–12
Group 1 bivalve:shrimp	1:4	2:3	3:2	4:1
Group 2 shrimp:bivalve	4:1	3:2	2:3	1:4

deep) of subdivided aquariums with artificial seawater (25° C and 25 ppt). Food models were prepared using a modification of the methods of Klinger (1982). The flesh of the bivalve *Donax variabilis* and the shrimp *Panaeus duorarum* were homogenized and mixed with agar (1 g wet weight tissue/100 ml 5% agar). Models were disc shaped and measured 0.5 cm in diameter and 0.3 cm deep. *Luidia clathrata* shows no preference for equally abundant prey models made from the tissues of *D. variabilis* and *P. duorarum* (McClintock and Lawrence 1984). To facilitate identification, shrimp and bivalve models were prepared with carmine particles and Nile blue, respectively. Preliminary experiments indicated that neither agar nor dyes stimulated feeding behavior.

Switching experiments were based on a modification of the methods of Murdoch et al. (1975). Two groups of 12 starfish were presented with different densities of both food models over a 12-day period (Table 1). Individuals of both groups were offered 20 food models randomly scattered over the bottom of each experimental chamber. Starfish were allowed to feed for 5 min or until 20 food models were ingested. Only individuals which ingested at least 20 food models were considered in analyses. The type and number of food models ingested were recorded. Food-model densities were maintained by immediately replacing ingested models. To simulate high initial abundance of each prey species, each group of starfish was maintained on a diet of shrimp or bivalve for one week prior to experimentation. A student's t test was used to test for statistical significance.

Functional response of fed and starved individuals

Eighty *Luidia clathrata* (mean $R = 75.6$ mm) were collected in June 1983 and maintained in artificial seawater (25° C and 25 ppt). Individuals were divided into two equal groups; a fed group which received a maintenance diet (1.88 g wet wt of the bivalve *Donax variabilis*/starfish/week) (see Diehl and Lawrence 1979) and a starved group which received no food over a seven-week period.

Feeding and foraging responses to changes in prey density were investigated in both fed and starved groups by presenting individuals with one of three densities of *Donax variabilis* (0.5, 5.0 and 50/m²). Ten *Luidia clathrata* were tested at each density for both starved and fed groups. Prey-density experiments were conducted in a 1 × 1.5 m seawater-table containing a 3-cm layer of fine sand. *Luidia clathrata* and *D. variabilis* were introduced randomly into the seawater-table, and prey densities were maintained throughout each experiment by immediately replacing each ingested bivalve. Starfish were dyed with Nile blue to permit identification. Both the number of prey ingested and the time spent actively foraging was recorded for each starfish.

Foraging time began upon the introduction of an individual into the seawater-table and terminated upon burial in the substratum. Times of digestion were examined in similarly sized *Luidia clathrata* from both starved and fed groups ($n=10$ for each group). Digestion time was considered the amount of time from ingestion of a single *D. variabilis* (2-cm length) to ejection of the bivalve shell through the oral opening. A Student's *t* test was used to test for statistical significance.

Foraging movements

Foraging movements of *Luidia clathrata* were investigated at 0.5 m depth in Old Tampa Bay. To facilitate observations of individuals a 3×3 m enclosure was constructed of $\frac{1}{2}$ inch PVC pipe fitted with a 1×1 cm wire mesh. The enclosure was divided into 9 one-m square sections to form a 3×3 grid using a fine nylon line. This enclosure was placed onto substratum of relatively uniform composition. All macrofauna were removed from within the enclosed area. *Luidia clathrata* were collected using SCUBA immediately prior to the experiment.

Movement patterns of *Luidia clathrata* were investigated by simultaneously introducing five individuals into the enclosure and recording their paths over a 30-min period. Individuals were dyed with Nile blue and then randomly placed within the enclosure. In one experiment individual movement patterns were observed within the enclosure in the absence of food. In a second experiment, different densities of the bivalve *Donax variabilis* were spread evenly within randomly chosen 1 m^2 sections of the enclosure. Frozen bivalves were positioned 1 to 2 mm below the surface of the substratum. Densities of prey increased exponentially from 4 to 256 prey/ m^2 . In both experiments the magnitude and direction of displacement were recorded for each individual. Frequency distributions of angular deviations were analyzed for their conformance to uniformity using the Rayleigh test (Zar 1974).

Results

Prey selection

Luidia clathrata ingested numerous taxa of prey in the field and showed strong selectivity for the bivalve *Mulinia lateralis* (Table 2). Mean numbers ± 1 S.E. of *M. lateralis* ingested and in sediment cores were $19.2 \pm 3.5/L. clathrata$ and $2.9 \pm 0.9/\text{core}$ (678 cm^3 sediment) respectively. The *Mulinia lateralis* ingested were relatively small (mean length ± 1 S.E. = 3.8 ± 0.1 mm; $n=227$). No selectivity was found for the other 13 invertebrate taxa observed in substrata or stomach contents. Of the 50 *L. clathrata* examined for seasonal composition of diet, 49 (98%) contained food. Bivalves were consistently the most abundant prey item found in the stomachs of *L. clathrata* (Table 3). Mean percent frequency ± 1 S.E. of bivalves from stomach samples of individual starfish over the seven month sampling period was 79 ± 8 . Gastropods, polychaetes, turbellarians, amphipods, and decapods occurred less consistently and in significantly ($P < 0.05$; chi-square analysis) lower numbers than bivalves. Mean numbers of prey/starfish varied greatly between sampling periods (Table 4). An inverse correlation ($r = -0.92$) between the mean number of prey/starfish and the percent frequency of individuals with detrital material in their stomachs was found (Fig. 1).

Table 2. Frequency (%) and electivity coefficients for macroinvertebrates in substratum samples of nine circular cores (12 cm diameter; 6 cm deep) and stomach contents of twenty *Luidia clathrata* collected in Tampa Bay in April, 1983. Electivity coefficients are based on percent frequencies of invertebrate taxa

Taxon	Frequency (%)		Vanderploeg and Scavia's relativized electivity index
	sub-stratum	stomach contents	
Mollusca			
Gastropoda			
<i>Acteocina caniculata</i>	10	—	—
Bivalvia			
<i>Mulinia lateralis</i>	21	97	0.76
<i>Ensis minor</i>	7	1	-0.04
<i>Semele</i> sp.	5	—	—
Annelida			
Polychaeta			
<i>Glycera americana</i>	5	—	—
<i>Pectinaria gouldii</i>	8	1	-0.04
<i>Clymenella mucosa</i>	6	—	—
Platyhelminthes			
Polycladida	—	0.5	—
Arthropoda			
Crustacea			
Ostracoda	9	—	—
Isopoda			
<i>Erichsonella</i> sp.	—	0.5	—
<i>Edotea montosa</i>	3	0.5	-0.04
Amphipoda			
<i>Ampelisca verrilli</i>	21	0.5	-0.05
<i>Rudilemboides naglei</i>	5	—	—
Malacostraca			
Cumacea			
<i>Cyclaspis</i> sp.	5	—	—

Prey-switching behavior

Starfish in the laboratory ingested significantly ($P < 0.05$) lower and higher frequencies of shrimp models than expected at correspondingly low (0.2 shrimp: 0.8 bivalve, days 1 to 3) and high (0.8 shrimp: 0.2 bivalve, days 10 to 12) proportions of availability (Fig. 2). Mean percentages of prey models ingested by starfish offered 20 and 80 percent shrimp on days 1 to 3 and 10 to 12 were 14.5 (S.E. = 1.4, $n=34$) and 83.4 (S.E. = 1.0, $n=35$) respectively. Numbers of starfish in group 2 ingesting at least twenty food models were relatively low (Fig. 3). However 100% of these starfish ingested significantly ($P < 0.05$) lower or higher frequencies of bivalve models than expected at correspondingly low (0.2 bivalve: 0.8 shrimp, days 1 to 3) and high (0.8 bivalve: 0.2 shrimp, days 10 to 12) proportions of availability.

Functional response of fed and starved individuals

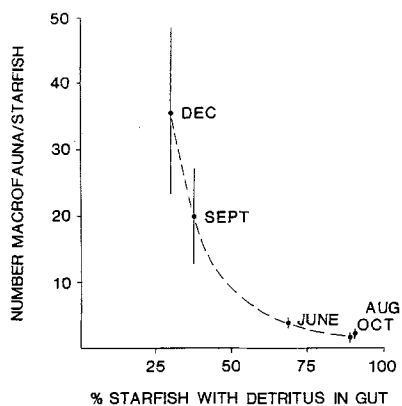
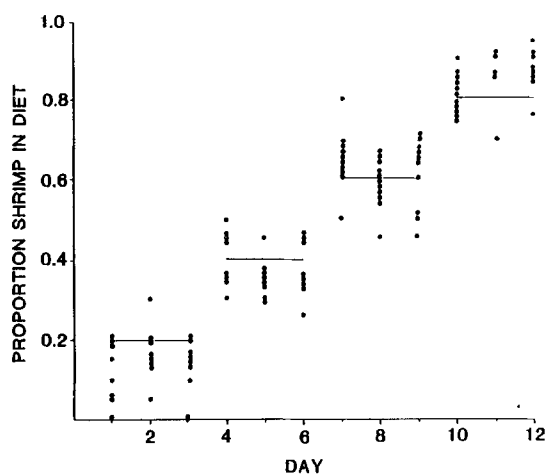
Luidia clathrata showed a functional response to changes in relative prey density. Foraging time of fed individuals increased significantly ($P < 0.01$) for all three densities of prey (Fig. 4). Starved individuals showed a significant ($P <$

Table 3. Frequency (%) of macroinvertebrates in stomach contents of *Luidia clathrata* collected in Old Tampa Bay from June to December, 1983

Stomach item	Collection period					
	June (n=9)	August (n=10)	September (n=11)	October (n=10)	December (n=10)	Means \pm 1 S.E. (n=5)
Bivalves	54	76	99	73	92	79 \pm 8
Gastropods	10	0	1	9	2	4 \pm 2
Polychaetes	11	8	0	9	0	6 \pm 2
Turbellarians	11	0	0	0	0	2 \pm 2
Amphipods	4	8	0	0	0	2 \pm 1
Decapods	10	8	0	0	5	5 \pm 2
Ostracods	0	0	0	0	0.5	0.1 \pm 0.1
Isopods	0	0	0	0	0.5	0.1 \pm 0.1

Table 4. Frequency (%) of ingested detritus and numbers of ingested prey in stomach contents of *Luidia clathrata* collected in Old Tampa Bay from June to December, 1983. Sizes of *L. clathrata*, water temperature, and time of collection are also shown

	Collection period				
	June (n=9)	August (n=10)	September (n=11)	October (n=10)	December (n=10)
Number of prey/individual ($\bar{x} \pm 1$ S.E.)	4.0 \pm 1.7	2.0 \pm 0.5	19.7 \pm 6.7	1.8 \pm 0.4	35.6 \pm 12.8
Radius of <i>L. clathrata</i> (cm, $\bar{x} \pm 1$ S.E.)	7.6 \pm 0.1	7.2 \pm 2.5	6.9 \pm 1.8	7.7 \pm 2.5	7.1 \pm 2.5
Frequency of individuals containing detritus in stomach (%)	67	90	36	90	30
Time of collection	1100	1130	1100	1600	1100
Temperature ($^{\circ}$ C)	29	31	30	25	24

**Fig. 1.** Relationship between the percent *Luidia clathrata* with detritus in their gut and the mean number \pm 1 S.D. of macrofauna/starfish. Each point represents a different month of sampling and a minimum of nine *L. clathrata***Fig. 2.** Switching in *Luidia clathrata* offered different proportions of shrimp and bivalve models. Each point represents the diet of one starfish on a given day. The horizontal lines indicate the proportion of shrimp models available for each three-day period

0.01) increase in foraging time when prey density was increased from 0.5 to 5.0 bivalves/m². Starved individuals spent significantly ($P < 0.01$) greater amounts of time foraging than fed individuals at densities of 0.5 and 5.0 bivalves/m². There was no significant difference in the amount of time spent foraging by either starved or fed individuals offered 50 bivalves/m².

The number of bivalves ingested by both fed and starved

individuals increased significantly ($P < 0.01$) over all three densities of prey (Fig. 5). Starved individuals ingested significantly ($P < 0.01$) greater numbers of bivalves than fed individuals at densities of 0.5 and 5.0 bivalves/m². There was no significant difference in the number of bivalves ingested by either fed or starved individuals offered 50 bivalves/m².

Ninety-percent of the fed individuals offered low prey

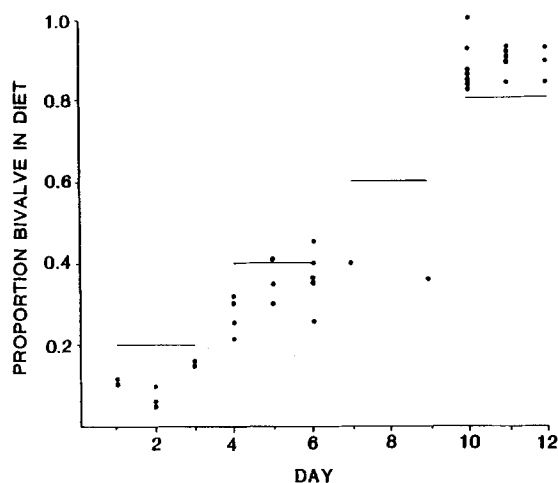


Fig. 3. Switching in *Luidia clathrata* offered different proportions of bivalve and shrimp models. Each point represents the diet of one starfish on a given day. The horizontal lines indicate the proportion of bivalve models available for each three-day period

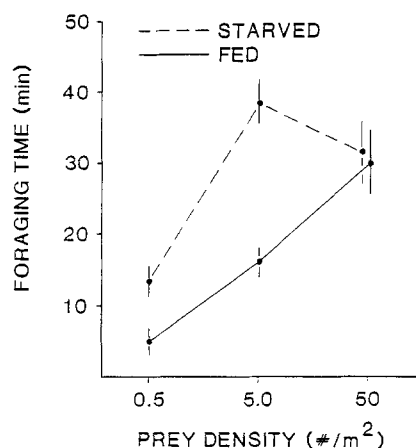


Fig. 4. Foraging times of fed (solid line) and starved (dashed line) *Luidia clathrata* with different densities of *Donax variabilis* available for ingestion. Means ± 1 S.E. are given. ($n = 10$)

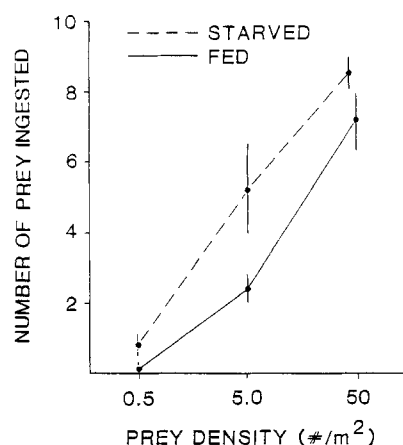


Fig. 5. Numbers of prey ingested by fed (solid line) and starved (dashed line) *Luidia clathrata* with different densities of *Donax variabilis* available for ingestion. Means ± 1 S.E. are given. ($n = 10$)

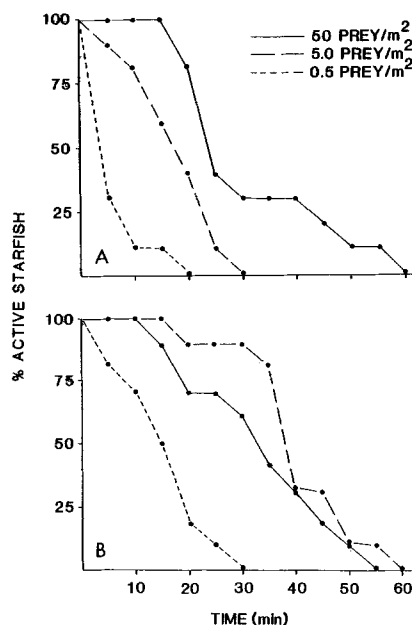


Fig. 6. Percent active individuals of fed (A) and starved (B) *Luidia clathrata* offered different densities of *Donax variabilis*. Dotted lines represent individuals offered 0.5 prey/m²; dashed lines represent individuals offered 5.0 prey/m²; solid lines represent individuals offered 50 prey/m². ($n = 10$)

densities (0.5 prey/m²) buried within 10 min (Fig. 6A). Fed individuals presented with intermediate (5.0 prey/m²) and high (50 prey/m²) densities of prey showed a sharp decline in percent active individuals between 15 and 30 min. However some individuals exposed to high levels of prey density (50 prey/m²) remained active up to one h. Ninety-percent of the starved individuals offered low prey densities (0.5 prey/m²) buried within 25 min (Fig. 6B). Starved individuals presented with intermediate (5.0 prey/m²) and high (50 prey/m²) densities of prey showed a sharp decline in percent active individuals between 55 and 60 min.

Mean times of digestion ± 1 S.D. of fed and starved *Luidia clathrata* offered a single *Donax variabilis* were 9 h 29 min ± 19 min and 6 h 30 min ± 2 h 16 min respectively. Starved individuals showed a greater variability in times of digestion and required significantly ($P < 0.05$) less time to digest prey than fed individuals.

Foraging movements

Patterns of movement in *Luidia clathrata* are influenced by prey availability. In the absence of prey *L. clathrata* showed highly directional movement as indicated by a significantly ($P < 0.05$) non-uniform distribution of angular deviations in direction (Fig. 7A). Angular deviations of less than 60 degrees occurred in 61 percent of the total number of observed changes in direction ($n = 28$). Mean total distance ± 1 S.E. traveled by individuals over the 30-min period was 3.05 ± 0.45 m. There was no pattern of directional orientation, as two individuals moved SE; another N; and the other two, NW.

In the presence of prey, *Luidia clathrata* showed less directional movement as indicated by the significantly ($P < 0.05$) uniform distribution of angular deviations in direction (Fig. 7B). Angular deviations of less than 60 degrees oc-

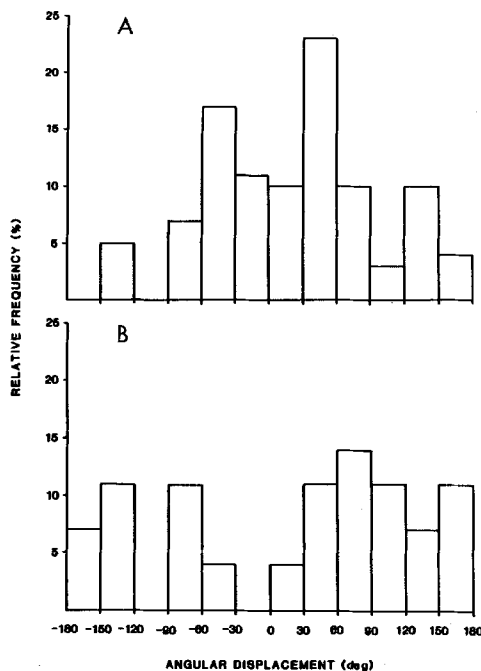


Fig. 7. A Distribution of changes in direction of five *Luidia clathrata* introduced into a 3 × 3 m enclosure and followed over a 30 min period ($n=28$). B Distribution of changes in direction of five *L. clathrata* introduced into a 3 × 3 m enclosure containing different densities of the bivalve *Donax variabilis* and followed over a 30 min period ($n=30$). An angle of 0 means no change in direction. A clockwise change in direction was considered positive, counter-clockwise negative.

occurred in only 29 percent of the total number of observed changes in direction ($n=30$). Individuals encountering a patch of the bivalve *Donax variabilis* typically responded by increasing both the number and the amplitude of changes in direction. Individuals responded to different densities of bivalve prey; four of the five individuals moved from low to high density prey areas. Three of these individuals ended the 30-min movement period within the highest prey quadrats (128 and 256 prey/m²). Mean total distance ± 1 S.E. traveled by individuals over a 30-min period was 2.82 ± 0.48 m. There was no pattern of directional orientation, as the five individuals moved N, NW, S, NE, and SW respectively.

Discussion

Luidia clathrata is a selective feeder on bivalves in Tampa Bay, specifically *Mulinia lateralis*. Seasonal analyses of stomach contents indicated that *M. lateralis* consistently dominated the diet of this starfish. Low frequencies of amphipods and decapods in starfish stomachs may be related to high prey mobility, while the absence of polychaetes may reflect behavioral avoidance of predation (withdrawal into tubes) or a high rate of digestion. *Luidia clathrata* ingested higher proportions of the smaller specimens of *M. lateralis*.

When offered equal numbers and amounts of different sizes of bivalve models, *Luidia clathrata* chose the smaller (McClintock and Lawrence 1981). McClintock and Lawrence showed that choice of small bivalves by *L. clathrata* facilitates maximization of energy intake per unit foraging

effort, as they ingested more food per unit time. In the field, *Luidia clathrata* may feed disproportionately on *Mulinia lateralis* due to this bivalve's small size, accessibility, energy content and/or nutrient composition relative to other prey species; this remains to be investigated. The only other prey species to occur in such high abundance was the amphipod *Ampelisca verrilli* which probably escapes predation via locomotion.

The frequency of detrital ingestion is inversely related to the number of macrofaunal prey items per starfish suggesting detrital feeding may supplement nutritive requirements during periods of low macrofaunal availability. Detritus may be the primary source of nutrients during extraoral feeding in *Luidia clathrata* (McClintock et al. 1983). Other *Luidia* spp. ingest sediments and detrital material (Hulings and Hemlay 1963; Carey 1972).

Optimal diet choice models assume that the ability of a predator to detect prey does not change as prey abundance changes. The results of this study suggest that this assumption is inappropriate in the case of switching behavior in *Luidia clathrata*. Switching behavior may be related to either contact-chemoreceptive rejection of low-density food or enhanced distance chemo-location of high density food. *Luidia clathrata* encountered low-density food models with their tube feet, moving across these models towards more distant high-density food models. However, *L. clathrata* never completely ignored low-density food models, in some instances choosing to ingest these models. The marine snails *Acanthina spirata* and *Thais emarginata* show similar behaviors (Murdoch 1969). These snails move over prey at random, "handling" many individuals before choosing one to ingest. Murdoch terms this a "variable rejection rate" dependent upon previous feeding experience. *Luidia clathrata* showed similar variable rejection rates. The use of artificial prey models eliminated the possibility that ability to handle prey is a factor in the preference demonstrated. Ingestive conditioning in *L. clathrata* (McClintock and Lawrence 1984) may be related to an olfactory search image. Olfactory search-images have been suggested to be important in ingestive conditioning behavior of other asteroids (*Pisaster ochraceus*, Landenberger 1968; *Acanthaster planci*, Collins 1974; Huxley 1976; Ormond et al. 1976). *Luidia clathrata* show distance chemoreception to animal tissues (*Donax variabilis* and *Panaeus duorarum*) (McClintock and Lawrence 1984).

Menge (1972) found that the asteroid *Leptasterias hexactis* increased foraging intensity with increased availability of prey. He suggested that the functional response of asteroids is great as a result of their ability to feed on many prey items during a single foraging bout. *Luidia clathrata* responded to increased densities of *Donax variabilis* by increasing both the time spent foraging and the number of prey ingested. Increased foraging time was generally positively correlated with increased prey location and ingestion, especially at the lower prey densities.

The basis of the ability for *Luidia clathrata* to increase its foraging with increased density of food may be related to chemoreception. As the density of *Donax variabilis* was increased, so was the concentration of chemical stimulants. The initiation and maintenance of foraging behavior may require a "threshold" level of chemical stimulation. At prey densities of 0.5 prey/m² this threshold level may not have been attained as only individuals randomly positioned in close proximity (10 to 20 cm) to prey were stimulated to

feed. However when prey density was increased to 5.0 and 50 prey/m², individuals increased their foraging (time spent active, numbers of prey ingested). At the highest density (50 prey/m²) individuals frequently moved directly from prey to prey, reflecting their ability to sense distant prey. The dose-dependent feeding response of *L. clathrata* to the amino-acids L-cysteine, L-glutamic acid, and L-isoleucine supports this threshold hypothesis (McClintock et al. in press).

Nutritive condition has a pronounced effect on foraging in *Luidia clathrata*. Starved individuals spent more time foraging and ingested greater numbers of prey than fed individuals at low and intermediate densities of prey. Hunger may decrease the threshold of chemical stimulation necessary to initiate and maintain foraging behaviors. Ernsting (1977) suggested that thresholds for feeding activities lie at different levels of hunger in the beetle *Notophilus biquattatus*. He suggested that hunger-dependent activity may depend on a hunger threshold below which active foraging ceases. The lack of significant differences in time spent foraging or numbers of prey ingested by fed and starved *L. clathrata* at the highest prey density suggests that the "cost" of foraging was relatively low and individuals became satiated.

Time required to digest a single prey (*Donax variabilis*) decreased following starvation in *Luidia clathrata*. This may indicate a change in the physiological state of the organism (i.e. production or release of digestive enzymes). *Luidia clathrata* accumulates secretory granules within the pyloric caeca when starved (Klinger, pers. comm.). Ultimately, this may facilitate a greater turnover of ingested prey, by allowing more time for active foraging. Starved individuals did show greater levels of activity than fed individuals.

The general foraging path of *Luidia clathrata* is directional. However, once prey are encountered the frequency and amplitude of changes in direction increase resulting in an individual remaining in an area of high prey density. *Luidia clathrata* generally moved from areas of low to high prey-density, indicating an ability to detect distant prey. Chemical detection of distant prey may provide the necessary stimulus to increase the frequency and magnitude of changes in direction of movement.

Other asteroids show similar patterns of foraging. *Astropecten aranciaceus* travel in a significantly more directional manner outside, rather than within, artificial prey-patches of the bivalve *Cerastoderma edule* (Jost 1982). Jost suggested that this type of foraging pattern allows *A. aranciaceus* to obtain maximum energetic profit (number of bivalves) per unit foraging time and thus conforms to predictions of optimal foraging theory. The foraging path of the microphagous grazing asteroid *Oreaster reticulatus* is highly directional (Scheibling 1981). This asteroid differs markedly from *Astropecten* spp. in its feeding method, grazing on substrata containing a relatively uniform distribution of its particulate food source. This foraging strategy optimizes energetic return per unit effort as a directional pattern decreases the chances of regrazing of substrata and extends the foraging range. Highly directional patterns of foraging movements in *L. clathrata*, in the absence of macrofaunal prey, could provide an efficient mechanism for extraoral feeding on more uniformly distributed detrital material (see McClintock et al. 1983).

In summary, *Luidia clathrata* shows many behavioral characteristics of an "optimal" forager. This can be attrib-

uted to a generally carnivorous diet in which energy is the basic unit to be maximized. There are some characteristics of foraging (e.g. switching behavior) in *L. clathrata* which do not agree with optimal foraging models under certain assumptions. However *L. clathrata* appears to forage optimally within its perceptual constraints. It is evident that feeding behaviors in *L. clathrata* are adapted to respond to changes in the abundance and distribution of benthic macroinvertebrate prey.

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