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FOOD SELECTION OF THE ANTARCTIC SEA STAR *ODONTASTER VALIDUS* (KOEHLER): LABORATORY EXPERIMENTS WITH FOOD QUALITY AND SIZE

ABSTRACT: According to Optimal Foraging Theory a consumer should select its diet in order to maximise net energy intake per unit of foraging time. Therefore, the Antarctic scavenging sea star *Odontaster validus* can be expected to choose food items of high profitability and ignore those of low profitability. Laboratory experiments with agar models of food items were performed to investigate the foraging behaviour and food selectivity of *O. validus*. Freshly caught sea stars were first fed with fish meat to minimize differences in their feeding status and then starved for 2 and 4 weeks. Sea stars were divided into three size groups (small – radius 1–3 cm, medium – radius 3–4 cm, large – radius 4–5.5 cm). Agar food items of different quality (low – 1.2 kJ, medium – 2.5 kJ, high – 4.1 kJ) and size (small – 8 cm³ and large – 64 cm³) were utilized in the experiments. Sea stars were individually presented with food items placed on the aquarium bottom, and their behaviour (number and type of investigated food items, time needed for final choice) was observed for 30 minutes. Starved individuals preferentially selected more profitable food items as is predicted by Optimal Foraging Theory. Choice of food item was probably mediated by contact chemoreception. Starvation time and sea star size had significant impact on selectivity. Mean number of food items of different quality investigated by sea stars starved for 2 weeks was higher than in sea stars starved for 4 weeks. Low quality food items were mostly chosen by small sea stars, and never

by large individuals starved for 2 weeks. Sea stars *O. validus* were also capable of distinguishing between small and large food items. Final choice made by sea stars presented with food items of differing size depended on their size with large and medium individuals choosing mostly large food items. Sea stars starved for 2 weeks chose higher proportion of large food items than individuals starved for 4 weeks. Such strategy in accordance with Optimal Foraging Theory allows for flexibility in *O. validus* feeding behaviour and enables this species to survive in harsh marine environment, where food resources accessible during the Antarctic winter are scarce and unpredictable in space and time.

KEY WORDS: food quality, Optimal Foraging Theory, scavengers, Antarctic, sea stars, *Odontaster validus*

1. INTRODUCTION

In natural environment organisms encounter different types of food items. According to the theory of optimal foraging, organisms choose their diet in order to maximise net energy intake and therefore should prefer food of higher energy content to those of lower quality (Pyke 1984, Perry and Pianka 1997). Such phenomenon was previously observed in species belonging to dif-

ferent marine invertebrates such as e.g. crabs *Carcinus maens* (Elner and Hughes 1978) and *Armases cinereum* (Buck *et al.* 2003), sea stars *Luidia clathrata* (McClintock and Lawrence 1985), *Leptasterias polaris* and *Asterias vulgaris* (Gaymer *et al.* 2001) or gastropods *Stramonita haemastoma* (Rilov *et al.* 2002).

In natural environment food selection is determined by numerous factors such as food quality (Elner and Hughes 1978, Beddingfield and McClintock 1993), food distribution and abundance (Gaymer *et al.* 2001, Wong and Barbeau 2005), handling costs (McClintock and Lawrence 1985, Barbeau and Scheibling 1994), environmental characteristics (Rilov *et al.* 2002, Buck *et al.* 2003), animal size (Tokeshi *et al.* 1989, Sommer *et al.* 1999), sex (Brousseau *et al.* 2001) or feeding status (Micheli 1995).

The present study examines foraging behaviour of an Antarctic benthic invertebrate, sea star *Odontaster validus* placed in different feeding situations. My objective was to investigate the effect of starvation time and body size on sea star foraging behaviour. Standardised food items were used to eliminate the effect of other differences except energy content and size. According to Optimal Foraging Theory a consumer should select its diet in order to maximise net energy intake per unit of foraging time (see reviews in Hughes 1980, Pyke 1984). Therefore, *O. validus* can be expected to choose food items of high profitability and ignore those of low profitability.

Odontaster validus is a moderately sized, omnivorous sea star, common in most Antarctic benthic environments (Dearborn 1977, McClintock *et al.* 1988). It can utilize different kinds of food, acting as a scavenger, an active predator, a herbivore and a suspension feeder (Dayton *et al.* 1974, McClintock 1994). Its diet consists of detritus, carrion, feces, diatoms, algae, sponges, crustaceans, molluscs etc. (Dayton *et al.* 1974, Arnaud 1970, Dearborn 1977, McClintock *et al.* 1988). Data collected at Signy Island (South Orkney Islands, Antarctica) suggests that *O. validus* is feeding consistently only in summer, and starves for at least part of the winter (Stanwell-Smith and Clarke 1998). It is also reckoned to be one of the “keystone spe-

cies” regulating the abundance of other benthic invertebrates (Dayton *et al.* 1974).

2. MATERIAL AND METHODS

Odontaster validus specimens with a radius (measured from the centre of the disc to the tip of the longest arm) of 1.0–5.5 cm were collected by Scuba divers from Admiralty Bay (King George Island, South Shetlands, Antarctica). Animals were maintained in well-aerated tanks (*ca* 30 l each) at a temperature of 0.5°C and water salinity of 34.2–34.5 psu. For 10 days animals were fed *Notothenia* sp. meat to minimize differences in their feeding status and then starved for 2 or 4 weeks. No individual was tested more than once in three days and no animal was used for the same type of experiment more than once. Sea stars were divided in three size groups: small – radius 1–3 cm, medium – radius 3–4 cm, large – radius 4–5.5 cm. Each variant of the experiment was replicated 52–60 times. All tests were done at the temperature of 0.5°C and water salinity of 34.2–34.5 psu.

Two types of food items were utilized in the experiments. In the first experiment food items of different quality were used. They consisted of cubes ($2 \times 2 \times 2$ cm – 8 cm³) prepared by mixing agar with fresh fish meat in the concentration of 0 (pure agar), 15 (food item of low quality), 30 (food item of medium quality) and 50 g (food item of high quality) fish meat per 500 ml of agar. In the second experiment food items of different sizes were used. They consisted of agar cubes ($2 \times 2 \times 2$ cm – 8 cm³ – small food items and $4 \times 4 \times 4$ cm – 64 cm³ – large food items) prepared by mixing agar with fresh fish meat in the concentration of 50 g fish meat per 500 ml of agar. Assuming the caloric value of *Notothenia* sp. muscle meat as 5.16 kJ g⁻¹ FW (Kamler 2003, recalculated) the total energy content of food items used in the experiments can be estimated as:

- low quality food item – 1.2 kJ
- medium quality food item – 2.5 kJ
- high quality food item – 4.1 kJ
- small food item – 4.1 kJ
- large food item – 33.0 kJ

Taking into account the diversity of *O. validus* diet, ranging from low quality detritus to high quality prey meat, it can be assumed

that the proffered food items fall well within the natural food spectrum of this species.

Sea stars were individually presented with 8 food items of different quality (two of each quality type) or different size (four of each size). Food items were put on a bottom of a 40 x 50 x 15 cm aquarium, each item 10 cm from the aquarium centre in such a manner that similar food items were not put next to each other. Each sea star was placed in the aquarium centre and observed for 30 minutes. Number and type of food items investigated during each experiment, and time needed to make final choice were noted. In control experiments small stones were used in place of food items. Additional control observations were done on fed sea stars.

3. RESULTS

3.1. Impact of food item quality on *O. validus* selectivity

In control experiments with stones in place of food items behavioural differences were observed between fed and starved sea stars with more locomotoric activity displayed by starved individuals. Only 13% of sea stars starved for 2 weeks and 21% of sea stars starved for 4 weeks were sitting immobile on aquarium bottom for the whole 30

minutes of experiment in comparison with 30% of fed individuals.

Fed sea stars presented with food items were behaving in the same way as in control experiments, with 30% of individuals sitting immobile on aquarium bottom. No instances of feeding sea stars were observed.

No sea stars starved for 2 weeks presented with different quality food items were sitting immobile on aquarium bottom. All were moving about and investigating food items, and all but 10% of them began to feed. All non-feeding sea stars belonged to the largest individuals with the radius more than 4.6 cm.

All sea stars starved for 4 weeks presented with different quality food items were moving about and investigating food items. All except one big individual with a radius of 5.2 cm began to feed. Mean number of food items investigated by sea stars (all individuals pooled together) and time needed by them to make the final choice were significantly lower than in sea stars starved for 2 weeks (t-Student test, $P < 0.05$) (Table 1).

Mean number of different quality food items investigated by sea stars starved for 2 weeks depended on sea star size (ANOVA $F_{(N=51,2)} = 7.44$, $P < 0.05$) with large individuals investigating significantly more food items than small and medium ones (RIR Tukey test, $P < 0.05$) (Table 1). Time needed

Table 1. Number of food items (mean values for all items of different quality pooled together) investigated by sea stars *O. validus* during 30 minutes of the experiment and time needed by them to make final choice. Food item size: $2 \times 2 \times 2$ cm (8 cm^3). Food item quality: low – 1.2 kJ, medium – 2.5 kJ, high – 4.1 kJ. Sea star size: small – radius 1–3 cm, medium – radius 3–4 cm, large – radius 4–5.5 cm. Means sharing the same letter are not significantly different ($P > 0.05$).

Feeding status	Sea star size	n	No of food items investigated by one individual		Time needed to make a final choice (min)	
			mean	SD	mean	SD
Starved 2 weeks	small	16	1.9 ^a	0.77	15.5 ^a	6.13
	medium	16	2.2 ^a	0.98	9.1 ^b	3.31
	large	22	3.3 ^b	1.52	9.9 ^b	5.30
	all	54	2.6	1.33	11.3	5.7
Starved 4 weeks	small	12	1.4 ^a	0.51	6.5 ^a	3.00
	medium	22	1.5 ^a	0.74	5.7 ^a	2.97
	large	25	2.32 ^b	1.11	5.6 ^a	3.19
	all	59	1.8	0.97	5.8	3.04

Table 2. Percentage of sea stars *O. validus* feeding on food items of different quality. Sea star size: small – radius 1–3 cm, medium – radius 3–4 cm, large – radius 4–5.5 cm. Food item size: $2 \times 2 \times 2$ cm (8 cm^3). Food item quality: low – 1.2 kJ, medium – 2.5 kJ, high – 4.1 kJ. The distribution 1:1:1 (each food item except pure agar is chosen with the same frequency) was used as the expected value to calculate χ^2 value in each experiment. A $P < 0.05$ was considered significant and marked with an asterisk (*).

Feeding status	Sea star size	n	Food item quality				χ^2
			pure agar	low	medium	high	
Starved 2 weeks	small	16	–	3	11	2	9.2*
	medium	16	–	1	6	9	6.2*
	large	22	–	0	4	18	24.5*
	all	54	–	4	21	29	18.1*
Starved 4 weeks	small	12	–	5	5	2	1.5
	medium	22	–	5	11	6	2.8
	large	25	–	4	11	10	3.5
	all	59	–	14	27	18	4.5

by sea stars starved for 2 weeks to make the final choice also depended on sea star size (ANOVA $F_{(N=51,2)} = 7.93$, $P < 0.05$) with large and medium individuals needing less time than small ones (RIR Tukey test, $P < 0.05$) (Table 1). Mean number of different quality food items investigated by sea stars starved for 4 weeks also depended on sea star size (ANOVA $F_{(N=56,2)} = 7.11$, $P < 0.05$) with large individuals investigating significantly more food items than small and medium ones (RIR Tukey test, $P < 0.05$) (Table 1). Time needed by sea stars starved for 4 weeks to make the final choice did not depend on sea star size (ANOVA $F_{(N=55,2)} = 0.34$, $P = 0.712$).

Mean numbers of different quality food items investigated by medium and large sea stars starved for 2 weeks were significantly higher than in sea stars of same size but starved for 4 weeks (t-Student test, $P < 0.05$) (Table 1). For every size group time needed to make the final choice was significantly lower in sea stars starved for 4 weeks than in individuals starved for 2 weeks (t-Student test, $P < 0.05$) (Table 1).

In any variant of the experiment with food items of different quality no sea star began to feed on food item consisting of pure agar (Table 2). Final choice made by sea stars depended on their size and starvation time, with large sea stars choosing more high quality food items than medium and small ones,

and sea stars of any size starved for 2 weeks choosing more high quality food than same size individuals starved for 4 weeks. Low quality food items were mostly chosen by small sea stars, and never by large individuals starved for 2 weeks (Table 2). The difference between observed and expected (1:1:1, each food item except pure agar is chosen with the same frequency) final choice was statistically significant only for sea stars starved for 2 weeks.

3.2. Impact of size of food item on *O. validus* selectivity

No sea stars starved for 2 weeks presented with food items of different size were sitting immobile on aquarium bottom. All were moving about and investigating food items, and all but 13% of them began to feed. All non-feeding sea stars belonged to the largest individuals with the radius more than 4.8 cm.

All sea stars starved for 4 weeks presented with food items of different size were moving about and investigating food items. All except one big individual with a radius of 5.2 cm began to feed. Mean number of food items investigated by sea stars (all individuals pooled together) and time needed by them to make the final choice were significantly lower than in sea stars starved for 2 weeks (t-Student test, $P < 0.05$) (Table 3).

Mean number of food items of different size investigated by sea stars starved for 2 weeks depended on sea star size (ANOVA $F_{(N=49,2)} = 25.24, P < 0.05$) with large and medium individuals investigating significantly more food items than small ones, and large ones investigating more food items than medium ones (RIR Tukey test, $P < 0.05$) (Table 3). There were no statistically significant differences between times needed by large, medium and small sea stars starved for 2 weeks to make the final choice (ANOVA $F_{(N=49,2)} = 2.06, P = 0.139$) (Table 3).

Mean number of food items of different size investigated by sea stars starved for 4 weeks depended on sea star size (ANOVA $F_{(N=57,2)} = 11.66, P < 0.05$) with large individuals investigating significantly more food items than medium and small ones (RIR Tukey test, $P < 0.05$) (Table 3).

Time needed to make the final choice was significantly higher in small sea stars starved for 4 weeks than in medium and large ones, and it was also significantly higher in medium sea stars than in large ones (ANOVA $F_{(N=57,2)} = 18.15, P < 0.05$) (RIR Tukey test, $P < 0.05$) (Table 3).

Mean number of food items of different size investigated by small, medium and large sea stars starved for 2 weeks were significant-

ly higher than in sea stars of same size but starved for 4 weeks (t-Student test, $P < 0.05$) (Table 3). Time needed to make the final choice was significantly lower in large sea stars starved for 4 weeks than in individuals of the same size starved for 2 weeks (t-Student test, $P < 0.05$) (Table 3).

Final choice made by sea stars presented with food items of differing size depended on their size with large and medium individuals choosing mostly large food items (Table 4). Sea stars starved for 2 weeks chose higher proportion of large food items than individuals starved for 4 weeks (Table 4). The difference between observed and expected (1:1, each food item is chosen with the same frequency) final choice was statistically significant only for large sea stars, irrespective of the starvation period.

No statistically significant differences were found between mean number of food items of different quality and different size investigated by sea stars starved for 2 weeks (t-Student test, $P < 0.05$) or 4 weeks (t-Student test, $P < 0.05$). Small and large sea stars starved for 2 weeks spent significantly more time investigating food items when presented with items of different quality than with food items of different size (t-Student test, $P < 0.05$).

Table 3. Number of food items (mean values for all items of different size pooled together) investigated by sea stars *O. validus* during 30 minutes of the experiment and time needed by them to make final choice. Sea star size: small – radius 1–3 cm, medium – radius 3–4 cm, large – radius 4–5.5 cm. Food item size: small – $2 \times 2 \times 2$ cm (8 cm^3), large – $4 \times 4 \times 4$ cm (64 cm^3). Means sharing the same letter are not significantly different ($P > 0.05$).

Feeding status	Sea star size	n	No of food items investigated by one individual		Time needed to make a final choice (min)	
			mean	SD	mean	SD
Starved 2 weeks	small	17	1.7 ^a	0.68	8.5 ^a	2.16
	medium	18	2.8 ^b	0.98	7.5 ^a	2.35
	large	17	4.2 ^c	1.29	7.2 ^a	1.39
	all	52	2.9	1.42	7.7	2.06
Starved 4 weeks	small	13	1.1 ^a	0.27	8.6 ^a	2.35
	medium	18	1.4 ^a	0.61	6.5 ^b	1.41
	large	29	2.1 ^b	0.87	5.1 ^c	1.62
	all	60	1.7	0.83	6.3	2.20

Table 4. Number of sea stars *O. validus* feeding on food items of different size. Sea star size: small – radius 1–3 cm, medium – radius 3–4 cm, large – radius 4–5.5 cm. Food item size: small – $2 \times 2 \times 2$ cm (8 cm^3), large – $4 \times 4 \times 4$ cm (64 cm^3). The distribution 1:1 (each food item is chosen with the same frequency) was used as the expected value to calculate χ^2 value in each experiment. $P < 0.05$ was considered significant and marked with an asterix (*).

Feeding status	Sea star size	n	Food item size		χ^2
			large	small	
Starved 2 weeks	small	17	8	9	0.6
	medium	18	13	5	3.6
	large	17	17	0	17.0*
	all	52	38	14	11.1*
Starved 4 weeks	small	13	7	6	0.8
	medium	18	11	7	0.9
	large	29	23	6	10.0*
	all	60	41	19	8.1*

4. DISCUSSION

Data presented in this paper shows that the Antarctic sea stars *O. validus* are selective consumers consistently selecting food items of higher quality (higher energy content), as is predicted by the theory of optimal foraging.

Selective feeding by sea stars was previously documented by several authors (McClintock and Lawrence 1985, Tokeshi *et al.* 1989, Beddingfield and McClintock 1993, Sommer *et al.* 1999, Gaymer *et al.* 2001, Saier 2001, Wong and Barbeau 2005). Sea star *Luidia clathrata* (Say) actively selected bivalves *Mulinia lateralis* (Say) because of its high energy content, accessibility and lack of escape capabilities (McClintock and Lawrence 1985). Sea star *Astropecten articulatus* (Say) used contact chemoreception to select small, easy to manipulate prey of higher nutrient and energy value (Beddingfield and McClintock 1993). Wong and Barbeau (2005) established that sea stars *Asterias vulgaris* (Verrill) actively selected prey based on prey energy content and escape probabilities. Sea stars *Asterias vulgaris* (Saier 2001) preferred subtidal mussels with clean shells above ones covered with barnacles. Author speculated that sea star tube feet

adhered more efficiently to clean shells decreasing handling costs (Saier 2001).

Choice of appropriate food item in our experiments was probably mediated by contact chemoreception. Before choosing one of the food items sea stars *O. validus* moved from one item to another, touching them with tube feet which are the main site of chemosensory cells. Same behaviour was observed in sea stars *Luidia clathrata* (McClintock and Lawrence 1985) or predatory marine snails *Acanthina spirata* (de Blainville) and *Thais emarginata* (Deshayes) (Murdoch 1969). Shore crabs *Carcinus maenas* (Linnaeus) selected mussels of optimal size by manipulating them with their chela and mouthparts (Elner and Hughes 1978, Jubb *et al.* 1983). Some sea stars such as *Astropecten articulatus* (Beddingfield and McClintock 1993) and *Asterias forbesi* (Desor) (Doering 1981) were observed to evaluate the size of infaunal bivalves by touching and manipulating them.

My data showed that nutritional state of *O. validus* individuals was an important factor influencing their food selectivity. Much of previous observations on marine invertebrates food selectivity were done in natural environment where it was impossible to control animal feeding status (e.g. Tokeshi *et al.*

1989, Moore and Wong 1995, Kelaher *et al.* 2003, Gaymer *et al.* 2004). In the laboratory experiments such control is easily done. In previously published work experimental invertebrates (different species of crabs or sea stars) were starved for periods ranging from 1 day to 7 weeks (McClintock and Lawrence 1985, Sommer *et al.* 1999, Brousseau *et al.* 2001, Gaymer *et al.* 2001, Saier 2001, Rilov *et al.* 2002, Saito *et al.* 2004, Wong and Barbeau 2005) but there is only scarce data on changes in selectivity between fed and starved animals. McClintock and Lawrence (1985) established that sea stars *Luidia clathrata* starved for 7 weeks ingested greater number of prey and spent more time foraging than did fed individuals. Micheli (1995) observed that the blue crabs showed preference for smaller individuals of the hard clam *Mercenaria mercenaria* (Schumacher), with hungrier crabs being less selective than the less hungry ones.

On the basis of their experiments on invertebrate reaction to food odours Zimmer-Faust (1987) and Steele *et al.* (1999) concluded that animals possessing considerable energetic reserves (or living in food-rich environment) were more selective in their foraging strategy than starved individuals. In consequence, they would actively seek out large, high quality food particles (or prey), whereas starved individuals (or individuals living in food-poor environment) would be content with smaller, lower quality food.

My experiments showed that sea stars *O. validus*, like *Astropecten articulatus* (Beddingfield and McClintock 1993) and *Asterias forbesi* (Doering 1981), were capable of distinguishing between small and large food items. Large *O. validus* were ignoring small food items and actively selecting large ones. Each encountered food item was evaluated, and if it was of an unsatisfactory size sea stars continued their search.

Size selection of potential prey or food particles was previously observed in several species of marine invertebrates (Tokeshi *et al.* 1989, Juanes 1992, Beddingfield and McClintock 1993, Seed and Hughes 1995, Sommer *et al.* 1999, Brousseau *et al.* 2001, Gaymer *et al.* 2001, 2004). In theory, larger prey (or larger food particle) means more energy gained by the consumer, but it

may also require higher costs (e.g. searching, handling, digestion). Therefore, these additional costs may outweigh high energy gain associated with larger food items. Gaymer *et al.* (2001) observed that sea stars *Leptasterias polaris* (Müller and Troschel) and *Asterias vulgaris* (Linnaeus) consumed mussels *Mytilus edulis* (Linnaeus) according to their availability, reducing the costs of searching for prey of preferred size. Brousseau *et al.* (2001) observed that crabs *Hemigrapsus sanguineus* (De Haan) preferred smaller mussels which was probably related to the size and biomechanics of the predator's chelae. Similar constraints (lack of capacity for extraoral digestion) limited the maximal size of prey that could be ingested by sea stars *Astropecten articulatus* (McClintock and Lawrence 1981). Stomach everting and extraoral digestion typical for *O. validus* mean that this species may be limited only by the costs of food searching. Optimal diet model predicts that as predators grow, they will eat larger prey (Hughes 1980, Juanes 1992). Behaviour of *O. validus* in my experiments was consistent with this theory, with large individuals consistently choosing large food items. Similar observations were also done on other sea stars such as *Asterias rubens* (Linnaeus) (Sommer *et al.* 1999) or *Heliaster helianthus* (Lamarck) (Tokeshi *et al.* 1989).

My experiments showed that *O. validus* size was an important factor modifying the impact of starvation time on food selectivity. Starvation impact (measured as loss of food selectivity) was less visible in large *O. validus*. Small sea stars starved for 4 weeks began to feed on the first encountered food item, whereas large ones invested time and energy in searching for food items of high quality or large size. Small size can be a factor restricting animal capabilities. Small individuals have smaller energetical reserves and higher locomotory costs. They are also moving slower and therefore need more time to search for food. Such constraints can cause differences in a way an animal function in its environment, making it more prone to conserve energy. Previous work done on the same species showed that metabolic rate of small, starved for 4 week *O. validus* was more sensitive to chemical stimuli than of large individuals, with small sea stars reacting even

to low signal concentration (Kidawa 2005). Therefore, it can be assumed that small *O. validus* were more susceptible to starvation and, in consequence, prone to be less selective in food choice.

The major factors shaping Antarctic benthic ecosystems are extremely low but stable temperatures and intense seasonality of food (Clarke 1983, 1988). The majority of autotrophic production takes place as a pulse during austral summer (Clarke and Leakey 1996). For the remaining part of the year the water column is essentially devoid of potential food supply that can reach benthic communities. In consequence, these organisms cease feeding or switch to other food sources (carrion, seal feces, discarded prey remains), which was the cause of the periodic intensification of both intra- and interspecific competition (Arnaud 1970). Food resources accessible to necrophagous species are probable unpredictable in space and time, making scavenging opportunities relatively rare. Flexibility of foraging strategies can be especially important for species living in an environment of such limited and unpredictable food resources. Such flexibility was observed in *O. validus*. Individuals with considerable energy reserves functioned as highly selective foragers, more hungry ones, especially small ones, were conserving energy, and in consequence they were feeding on the first encountered food item. Such strategy enables *O. validus* to survive in harsh Antarctic marine environment.

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