Estuarine, Coastal and Shelf Science 94 (2011) 89–92

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Small is profitable: No support for the optimal foraging theory in sea stars *Asterias rubens* foraging on the blue edible mussel *Mytilus edulis*

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ARTICLE INFO

Article history:
Received 26 May 2010
Accepted 27 May 2011
Available online 7 June 2011

Keywords:
sea stars
Asterias
mussels
Mytilus
predation
size preference
cafeteria trial

ABSTRACT

Doubt has been shed recently on the most popular optimal foraging theory stating that predators should maximize prey profitability, i.e., select that prey item that contains the highest energy content per handling time. We hypothesized that sea stars do not forage on blue mussels according to the classical optimal foraging theory but are actively avoiding damage that may be caused by e.g. capture of foraging on too-strong mussel shells, hence the sea stars will have a stronger preference for mussels that are smaller than the most profitable ones. Here we present experimental evidence of the sea star *Asterias rubens* as a predator that indeed chooses much smaller blue mussels *Mytilus edulis* to forage on than the most profitable ones. Hence this study does not support the optimal foraging theory. There may be other constraints involved in foraging than just optimizing energy intake, for example predators may also be concerned with preventing potential loss or damage of their foraging instruments.

1. Introduction

The most popular version of the optimal foraging theory states that predators, when offered the choice between two different prey types, should choose the one that has the highest profitability, which is defined as the energy content per unit handling time (Emlen, 1966; MacArthur and Pianka, 1966). The classical example of such energy yield maximizer is the shore crab, *Carcinus maenas* foraging on the blue edible mussel *Mytilus edulis* (Elner and Hughes, 1978). Smallegange and van der Meer (2003) have recently shed some doubt on this textbook example as they showed that there are other constraints involved. Foraging shore crabs avoid the risk of damaging their claws by eating mussels that are suboptimal from a profitability perspective. A similar phenomenon is observed in oystercatchers (*Haemotopus ostralegus*) feeding on cockles (*Cerastoderma edule*) who risk damaging their bills when trying to open bigger, more profitable, cockles (Johnstone and Norris, 2000).

Here we present another example of a predator that might be more concerned about avoiding damage than about maximizing profitability. *Asterias rubens*, the most common sea star of the Wadden Sea, is an extra-oral feeder that has the ability to feed on protected prey with an outer shell, such as the blue mussel *M. edulis*, by penetration of the stomach between the shell and the soft parts of the prey (Lavoie, 1956; Jangoux, 1982). They do so by attaching their tube-feet with suckers to the shell and pull the two shell parts from each other. The space needed between the two valves is only 0.2 mm. The mussel then undergoes extra-oral digestion. Handling of mussels by the sea star may take a considerable time, i.e. approximately 12 h (Wong and Barbeau, 2005) and one can imagine that profitability plays an important role in the predators' prey choice. It is, however, also easy to imagine that when a sea star inserts its stomach into a large mussel, with powerful adductor muscles (Norberg and Tedengren, 1995), that the risk exists that the mussel closes its valves resulting in damage to the stomach (Anderson, 1965).

Our experiments focused on the predation of *M. edulis* by *A. rubens*, investigated over a range of mussel and sea star sizes. The profitability of all size classes of mussels for all size classes of sea stars was measured by determining the energy content and the handling time. Following this, the preference for a certain mussel size was determined. According to the classical optimal foraging theory, the preferred mussel size should be the same as the most profitable mussel size. In this study we tested the hypothesis that in case sea stars foraging on blue mussels do not obey the classical optimal foraging theory, but are also actively avoiding damage, the sea stars will have a stronger preference for mussels that are smaller than the most profitable ones.

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doi:10.1016/j.ecss.2011.05.028

2. Materials & methods

2.1. Collecting animals

Mussels were collected from an intertidal site at Den Helder, the Netherlands, in September and October 2007. The sampling site and the coverage with mussels resemble intertidal areas as can be found everywhere along the coast of Europe and in other temperate areas. The mussels covered a size range as large as possible. They were cleaned from fouling organisms, such as barnacles and epigrowth. Shell length was measured using digital calipers and each animal was assigned to one of five size classes: 3–11 mm, 14–22 mm, 25–33 mm, 36–44 mm, and 47–55 mm, hereafter referred to as size classes 7, 18, 29, 40 and 51. The size classes were not continuous, we kept gaps between the size classes (e.g. 11–14 mm, 22–25 mm, etc.) in order to prevent difficulties in assigning mussels to a certain size class. The mussels were marked using different permanent colours for different size classes.

Sea stars were sampled using a 1 m bottom dredge in the Wadden Sea near musselbeds between Robbenzand and Timmekesplaat at coordinates 53°4'N, 4°57'E. The largest diameter, which is the distance between the tips of the two longest arms, was measured using a ruler. Each animal was assigned to one of three size classes: 5–9 cm, 10–14 cm, and 15–19 cm, hereafter referred to as small, medium and large.

The sea stars were kept under controlled conditions in large aquaria with continuously running seawater and aeration. The water in the aquaria was kept at a temperature of 16 °C, the average water temperature of the Wadden Sea at the time of sampling. The aquaria were checked on a daily basis and any dead sea stars were removed immediately. The sea stars were starved for one week prior to the start of the experiments in order to standardize hunger levels. Each sea star was used only once and after finishing the experiments was returned to the sea. All experiments were carried out in a climate room. The air and water temperature were kept constant at 16 °C, and the photoperiod was kept constant at a 12 h dim-light, 12 h dark cycle for the prey size selection experiment. For the handling time experiment the dim-light was constantly turned on, because the video cameras needed light to record the handling of the sea stars.

2.2. Prey profitability

To assess the prey profitability for each mussel size class the energy content and handling time by sea stars were measured.

2.2.1. Mussel energy content

The energy content of the mussels was determined by the ash free dry weight (ADW). Fifty mussels, 10 of each size class, were opened and the tissue was removed. This was then dried at 60 °C for 4 days, weighed, combusted at 540 °C for 5 h and weighed again to give the ADW. The shell length (*L*) of the mussels was measured to 0.1 mm using digital callipers. Then the shell length was plotted against the ash free dry weight (*ADW*) to produce an energy content curve based on shell length. The curve followed the allometric relationship (LaBarbera, 1989):

$$ADW = a \times L^b$$

The scaling coefficient *a* and the scaling exponent *b* were estimated using ADW and shell length logarithmic regressions:

$$\log ADW = \log a + b \log L$$

2.2.2. Handling time

The handling time of a sea star is defined as the time that passes between encountering of the mussel by a sea star, and the releasing of the empty shell. During a pilot experiment the required number of observations in order to arrive at a coefficient of variation of 5% variation was determined, being 20 observations per sea star size class. During the experiment the sea stars were kept in plastic aquaria 18 cm wide, 19 cm high and 33 cm deep. The handling was recorded on video camera using time lapse recording. Every 5 min, 2 s of handling was recorded. The handling time can thus be examined at 5 min accuracy.

The handling time was determined using 20 sea stars of the same size class per mussel size class. The sea stars were each fed with one mussel of one size class at a time. This means that in total 300 sea stars were fed 300 mussels. For standardization of the mussel size, all mussels were of approximately the same size, respectively 7 mm, 18 mm, 29 mm, 40 mm and 51 mm. The experiments were terminated after 3 days, due to practical restrictions of our video equipment; the videos were examined and the handling time of each individual sea star was noted. Since the observation of handling time was restricted to 3 days and profitability is ash free dry weight divided by handling time, the calculated profitability is a maximum estimate.

2.3. Prey size selection

To determine the sea star preference for a certain mussel size a cafeteria trial experiment was used. The cafeteria trial is a multiple choice feeding experiment in which all food types are simultaneously offered to a group of consumers (Roa, 1992). In this experiment six aquaria were used per sea star size class. An aquarium contained a total of five sea stars, and 20 mussels of each of the five size classes. A control aquarium with a hundred mussels, without sea stars, was included to compensate for the natural death of mussels.

The sea stars were left to forage on the mussels for twelve days given that in twelve days, approximately half of the prey items were eaten. Afterwards the empty shells were collected, counted and measured using digital callipers. Also the empty shells in the control aquarium were collected, counted and measured.

To determine if there was any preference, a preference value was defined as:

$$\text{Preference value} = \frac{n_7 \times 1 + n_{18} \times 2 + n_{29} \times 3 + n_{40} \times 4 + n_{51} \times 5}{n_7 + n_{18} + n_{29} + n_{40} + n_{51}}$$

Where n_7, n_{18}, n_{29}, n_{40}, n_{51} are the numbers of mussels eaten per mussel size class, 7 being mussel size class 7, 18 being mussel size class 18, etc. The value of no preference is found when $n_7 = n_{18} = n_{29} = n_{40} = n_{51}$. For reasons of convenience, but without loss of generality, the numbers 1–5 are taken instead of the original values 7, 18, 29, 40 and 51. A one sample *t*-test was used with a null hypothesis of a preference value equal to 3. The normality was examined with visual inspection of normal probability plots. When using this test it has, however, to be taken into account that a preference for size class 29 will also yield a value near 3 – a graphical analysis was then used.

3. Results

3.1. Prey profitability

The ash free dry weight of the mussels followed an allometric relationship (Fig. 1;$ADW = 1.43 \times 10^{-6} L^{3.4262}$; $n = 50$, $r^2 = 0.76$, $p = 4.03 \times 10^{-7}$). The energy content of mussels thus increases exponentially with their length.