SIZE-DEPENDENT PREDATION BY OTTER *LUTRA LUTRA* ON SWAN MUSSELS *ANODONTA CYGNEA* (LINNAEUS 1758) – OBSERVATIONS AND RADIOTELEMETRY EXPERIMENT

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Abstract *Europe's increasing populations of medium-size predators pose a potential threat to freshwater mussels in some regions. Live mussels* (Anodonta cygnea) *collected from the bottom of Zalew Pińczowski reservoir (S Poland) did not differ in size from shells of individuals predated by otters, but the shells of predated individuals varied in size significantly less, suggesting that only the middle size class is predated. A similar size class was predated in a sample of live mussels equipped with radio transmitters and experimentally distributed near an otter den: 10% were eliminated within a month, indicating substantial predation pressure. Older mussels were not attacked or else the attacks were unsuccessful, suggesting that the otter cannot seriously threaten the reproductive-age part of the population, but predation on middle-size individuals might lead to ageing and eventual extinction of populations, especially small and isolated ones.*

Key words Anodonta cygnea, *size-selective predation*, *radio-tracking*, *otter* Lutra lutra

INTRODUCTION

Mammalian predators can cause significant mortality in mussels (Dillon, 2000). The list of species observed to predate on mussels includes the best-studied example of the muskrat *Ondatra zibethicus* (e.g. Neves & Odom, 1989; Diggins & Stewart, 2000) and scarce data on medium-size predators such as the river otters *Lutra lutra* (Veen, 1975) and N. American river otter *Lontra canadensis* (Stearns & Serfass, 2011) or the raccoon *Procyon lotor* (Gagnon *et al.*, 2004). The data on muskrat suggest that it can be an important mussel predator, especially dangerous to threatened species (Neves & Odom, 1989). Muskrats are both size-selective and species-selective feeders. From a large range of accessible mussel prey they choose those that maximize energy intake and minimize the handling cost: that is, large individuals of small species and small individuals of large species (Tyrrell & Hornbach, 1998), or species of middle size (Neves & Odom, 1989), or those of a specific cuboidal shape (Owen *et al.*, 2011). A similar prey-size optimizing pattern has been reported in studies of predation on single species: *Anodonta grandis* Say (Hanson, MacKay & Prepase, 1989) and *Margaritifera margaritifera* L. (Erickson, 2001). Of course, such optimal prey selection depends on what sort of prey is available at a given time and place. When the accessible clams (*Anodonta grandis*) were small, muskrats preyed on the larger ones (Convey, Hanson & MacKay, 1989); in another study the size range of accessible clams was much broader, and so was the range of prey size (Diggins & Stewart, 2000).

Muskrat predation is easy to study because muskrats make middens of the empty mussel shells after eating, which are easy to collect and analyze. Little is known of the impact of other mammal predators because they do not make middens, so their predation is much more difficult to investigate. The problem of other predators is becoming important because medium-sized mammalian predators are undergoing significant changes in their distribution throughout Europe. The muskrat has disappeared from large areas (e.g., in Poland – Brzeziński *et al.*, 2010), but the otter is quickly recovering throughout its range (Romanowski, 2006). Studies on the otter diet (e.g., Jędrzejewska *et al.*, 2001 for review; Lanszki, Szeles & Yoxon, 2009) usually do not indicate mussels as part of the diet, even in rivers well known for their abundant mussel populations (Brzeziński *et al.*, 2006), but unionid predation by this species has been reported (Veen, 1975; Kopij, 2011). In this study I used telemetry to determine whether otters prey on unionids and how the effect of their predation differs from well-described muskrat impacts. Telemetry is a technique only recently applied in malacology. I used it to accurately monitor the fate of a sample of clams exposed to otter predation and to compare those results from a fully controlled

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Figure 1 Evidence of otter attack on swan mussels: **A** shell edges showing clear bite marks; **B** bite marks on radio transmitter antenna; **C** mussel shell destroyed by otter, with transmitter antenna also showing bite marks at the base and end of the antenna.

experiment with data on predation based on shells collected near an otter's den.

Materials and Methods

The study was done at the south bank of Zalew Pińczowski Reservoir. It is a semi-natural old river bed left after river regulation work, partly altered to form the Reservoir (50°31'33''N, 20°31'13''E; *ca* 10 ha; modal depth *ca* 1.5 m; maximum depth 3 m; highly eutrophic – chlorophyll *a* 103.9±24.1 μg/dm^3). The south bank, left in its natural state, is completely devoid of trees and bushes. It has a narrow strip of *Phalaris arundinacea*, *Glyceria maxima* and *Carex gracilis* along the bank, then a zone of *Hydrocharis morsus-ranae* and *Ceratophyllum demersum* extending to 3 m from the bank, then at 3–6 m from the bank there are sparse stems of *Potamogeton* sp.

Zalew Pińczowski reservoir is inhabited by a large population of swan mussels *Anodonta cygnea* (*ca* 50,000 individuals in the late 1990s; Zając, 2003). Most of the living mussels occur within 10 m of the bank. The bottom sediments were sampled in 1998 (15 August to 3 September). Samples were taken using a dredge rake 38.5 cm wide with nylon netting (3 mm mesh) on a depth gradient along 10 cross-sectional transects, each 10 m long, along the south bank at 50 m intervals. All the bottom sediment was taken to 20 cm depth from an area of 0.385 m^2 and then sieved, with the mussels retained in the rake netting. Their shell length, width and height were measured to the nearest 0.1 mm with a vernier caliper and they were aged by counting growth rings, which are very clear in this species.

Muskrats occurred at Zalew Pińczowski reservoir until the mid 1990s, when they suddenly disappeared and never recovered; otters were always there and have remained. At Zalew Pińczowski reservoir an otter was observed during foraging and its den was located on the south bank in 1999. The area near the otter den was carefully checked for the presence of mussel shells within a 10 m radius. Mussel shells showing clear traces of predation (Fig. 1a) were collected. Only fresh shells lying on the surface of the mud were collected, identified to species and measured. The strong relation between shell length and other shell dimensions made it possible to determine the length of partly destroyed shells. That relation is expressed in these regression equations: length=27.8+2.34 (width), R^2=0.94; n=224, F > 3000, P << 0.001; or length=-6.8+1.97 (height), R^2=0.95; F > 4000, n=227, P << 0.001.

In 2002 a sample plot was set up near the otter den. Within a 20×22 m area the bottom profile was measured with a meter stick every 20 cm along the depth gradient and every 50 cm along the bank, after which a model of the area was created using GIS. All the mussels from the bottom of the western half of the sample plot were removed. A 42-mussel sample was taken: 14 in the second year of life, 14 that were 3–4 years old, and 14 older than 5 years. Each swan mussel was fitted with a radio transmitter (LTM, 1.4 g, Titley Electronics, sealed with plastic to waterproof it and to decrease weight; Fig. 1b,c) and marked with a code written on the shell with a oil marker. Then the sample of radio-fitted swan mussels was distributed at the nodes of a grid of 1 m squares (7 September 2002). The grid ran 6 m along the bank and 7 m into the water in the western half of the sample plot. All age classes were represented in each row running along the same depth profile; they were not ordered by age along the row but rather placed randomly. Two

Table 1 Results of radio-tracking marked mussels Lost mussels: due to transmitter fault (t) or death of mussel (d)

	Primary plot			Control plot	
Date	N traced	N predated	N lost ind.	N traced	N predated
2002-09-07	42	0		19	0
2002-09-12	42	0		19	0
2002-09-13	39	2	1t	19	1
2002-09-18	38	1		18	0
2002-09-19	38	0		18	0
2002-09-21	38	0		18	0
2002-10-01	36	0	2d	18	0
2002-10-03	36	0		18	0
2002-10-08	35	1		18	0

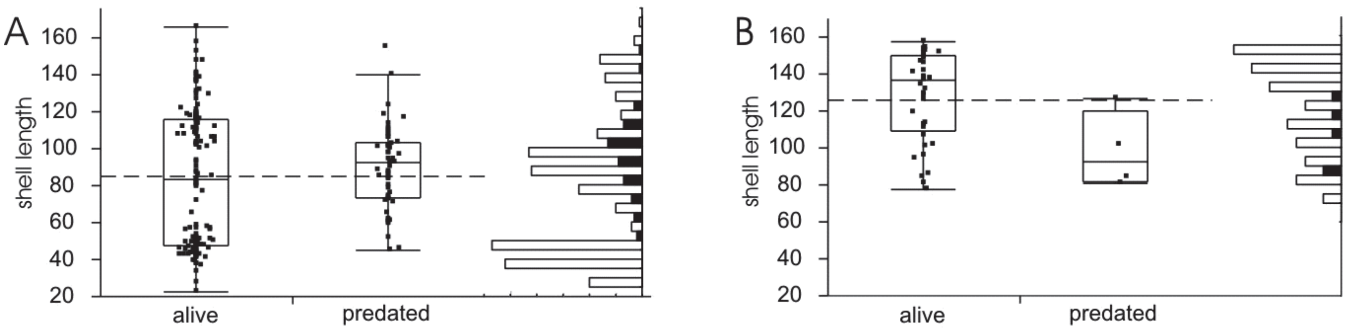

Figure 2 Shell length (means, SE and SD) of mussels not predated versus those predated by an otter at Zalew Pińczowski reservoir: **A** mussels from transects (live) vs shells collected near otter den (predated), with corresponding shell length histograms; **B** mussels not predated vs otter-predated during radiotelemetry experiment, with corresponding shell length histograms; dashed line indicates whole sample mean.

additional transects were made in the eastern part of the sample plot and parallel to the other ones, 8 m and 10 m from the boundary of the western half of the plot. Each swan mussel more than a year old (and thus able to carry a transmitter) found along these two transects was fitted with a transmitter and put back exactly where it was found (n=19).

During the following days the mussels were tracked with a radio receiver using a wand antenna (Table 1). Each individual was located precisely by signal strength, and its position was finally determined with maximum accuracy by touching the wand antenna to the transmitter antenna, generating a loud buzzing sound. After 1 October when temperatures dropped, some individuals were pulled out of the sediments during the surveys in order to check whether they are still active (moving, burrowing). On 8 October 2002 they were located for the last time, collected and inspected in detail.

RESULTS

The sample of live mussels collected in 1998 along the transects (n=140) did not differ in shell length from the sample of predated mussels collected near the den (n=51; Kruskal-Wallis test: H=1.41, P=0.23; Fig. 2a). However, analysis of histograms showed that the shell length distribution differed greatly between live and predated mussels (χ^2=224, df=14, P<0.0001). The size variance of the predated ones was significantly lower (SD=22.6, n=51) than that of the live ones collected along the transects (SD=36.4, n=140; Bartlett test: F=14.06, df=1, P=0.0002).

In 2002, during the radiotelemetry experiment (Tab. 1), the otter attacked 4 (*ca* 10%) of the 42 transmitter-fitted mussels in the sample plot, and 1 (5%) of 19 mussels on the two other transects (8% in total). One tagged mussel with signs of attack on its shell was found inside the otter's den together with a fish with bite marks (body length *ca* 25 cm). Analysis of the shell lengths of radio-tracked individuals from the sample plot showed that the attacked mussels (n=4) were significantly shorter than those not attacked (Fig. 2b; n=38; Kruskal-Wallis test: H=4.87, df=1, P=0.027). Their other shell dimensions were also smaller (mean±SD; Kruskal-Wallis test for height: live 66.5±11.3 mm vs predated 52±8.7 mm, H=4.78, P=0.029; and for width: live 40.1±11.2 mm vs predated 27.8±7.9 mm, H=4.41, P=0.036). In Fig. 2, note that the mean shell length of attacked individuals is practically the same in the sample collected at the den as in the sample of radio-tracked mussels. An unsuccessful attack on one very large mussel (shell length 147 mm) was recorded in the final check (8 October): there were toothmarks on the antenna and transmitter but the mussel was alive, buried in sediment and functioning normally.

Only one of the mussels on the additional transects was attacked. When both sources of data are pooled the results also show significant differences between live mussels (n=55) and predated ones (n=5; Kruskal-Wallis test: H=4.35; df=1, P=0.037). There was no significant difference in predation frequency between the mussels distributed experimentally in the sample plot and those from the other two transects (Fisher exact test: $P > 0.99$).

Discussion

The condition of the mussel remnants found in this study shows that the otter actively opened the shell by biting the outer edge and breaking it piece by piece. After removing usually one of the valves it consumed the soft body tissues. The otter bypassed the many young mussels and the very old ones; those of intermediate size were the ones predated most intensively (Fig. 2).

Among the artificially distributed radio-tracked mussels, representing only larger size classes (the smallest ones could not carry the device), the predated individuals showed the same distribution of size; it is striking that the mean values for length of predated shell are the same for the sample of shells collected near the den and the sample from the telemetry experiment. This means that the otter's ability to predate mussels is fairly restricted – it prefers to eat middle-size individuals, which are still thin-shelled but large enough to supply a good portion of food. The youngest swan mussels are most abundant (Zajac, 2003) but to my knowledge it has never been determined whether otters consume them. It would be difficult technically: they could be consumed whole, in which case the stomach content would have to be analyzed, or their shells could be broken into small undetectable pieces. In my experience it is exceedingly hard to detect very small swan mussels by observing the bottom; an otter would face the same problem. The time needed to find, manipulate and open a young mussel shell would increase the cost/benefit ratio of consuming such prey, and eating them whole might injure the gastrointestinal tract. The young mussels were very abundant, but an otter would have to eat a great number of them to obtain substantial nourishment, and this would be reflected in the prey size distribution as an increase in the number of prey with decreasing size; in fact, only middle-size mussels were consumed (Fig. 2). At the other end of the size scale, the largest mussels can survive an attack unharmed, making them unprofitable as well. In avoiding large mussels, whose stronger shell needs greater force to break, the otter may also be avoiding the risk of tooth damage.

Such a trade-off between handling time and energy content has already been proposed for muskrat (Tyrrell & Hornbach, 1998; Zahner-Meike & Hanson, 2001). The size-specific predation pattern I found for otter closely resembles the pattern observed for muskrat (for various mussel species – Tyrrell & Hornbach, 1998; Neves & Odom, 1989; for *Anodonta grandis* – Hanson *et al.*, 1989 and *Margaritifera margaritifera* – Erickson, 2001), suggesting that the two species adopt the same prey selection rules.

How can otters affect mussel populations? Ten percent of the ones I distributed near the den were eliminated within about a month, suggesting that otters can exploit a substantial proportion of a population. My sample of radio-tracked individuals was small, however, and reflected the predation behavior of only one animal. In a large swan mussel population inhabiting a large water body the otters cannot plunder the whole area, so the old mussels, though far fewer than the young ones, will reproduce safely for long periods. Populations in small water bodies should be more threatened (Strayer, 2008); there, otters can reduce the number of middle-size mussels, ultimately leading to population ageing and extinction. *Anodonta cygnea* is threatened with extinction in Poland, mostly due to river regulation (Zając, 2002; Zając, 2005). In regulated or artificial water bodies, with their simpler channel relief and less abundant immersed vegetation, otters should be expected to detect mussels more easily than at natural sites; such an interaction needs further study. Radiotelemetry and other related techniques provide a new methodological tool for this kind of research, enabling the researcher to fully monitor the subsequent fate of a prey sample exposed to predation.

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