Functional response curves of avian molluscivores: high intake rates maintained even at low prey density

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ABSTRACT: Despite its low energy density, the blue mussel *Mytilus edulis* is a regular prey of various seaduck species. As a result, seaducks must ingest large quantities of mussels to meet their energy requirements. In this study, we modeled the functional response curve for a large avian molluscivore, the common eider *Somateria mollissima*, by measuring intake rates of captive individuals foraging in diving tanks under different mussel densities and at different attachment strengths. We estimated the mean maximum intake rate to be 45 prey min^{-1} (with a mean bottom time ± SD of 5.034 ± 3.793 s), which is relatively high compared to intake rates of other diving duck species and prey types. However, we found no significant effects of density and attachment strength on intake rates, indicating that eiders can maintain maximum intake rates even at low mussel densities. These results could explain the depletion of mussel beds sometimes observed in the wild, as well as the large negative impact that seaducks may have in aquaculture farms.

KEY WORDS: Seaduck · Blue mussel · Attachment strength · Prey depletion

INTRODUCTION

Natural variation in prey abundance has a pervasive influence on the foraging behavior of a predator, leading to consequences for both predator and prey. For example, prey density affects a predator's intake rate, which is described by the functional response. The most commonly applied functional response is the type II, whereby intake rate increases with prey density up to an asymptote where the individual is limited by handling time. At lower densities, predator intake rate is limited by the prey encounter rate, increasing the search time when prey is scarce (Stephens & Krebs 1986, Goss-Custard et al. 2006).

Predation pressure may in turn lead to prey depletion. According to the marginal value theorem, predators are expected to leave a patch and go to a new one when their intake rate drops below the average for all patches (Charnov 1976). Thus at some point, leaving the foraging patch is more beneficial than staying in, and this feedback mechanism can prevent complete depletion of a foraging habitat. However, this theoretical framework depends on the predator's intake rate decreasing with decreasing prey density. This phenomenon is expected to be particularly pronounced for scarce prey that is difficult to find or to catch (e.g. highly mobile, buried or cryptic prey; Gendron & Staddon 1983, Seitz et al. 2001). However, the extent to which this relationship holds true for abundant, highly detectable, and easily caught prey is unknown. Indeed, for such prey, the search and capture time should be negligible even at low densities, and have little or no impact on predator encounter rates. Hence, when foraging on this type of prey, a predator could cause complete prey depletion.

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To avoid energy shortfalls, predators that forage on low quality food have to maintain elevated intake rates. High density epibenthic organisms with low energy content, such as sea stars, urchins, or mussels, are often abundant on sea floors. These animals are generally attached or move slowly, and hence are easily found by aquatic predators. However, such prey has often developed passive protection against predation (e.g. shells, spines), making the handling or digestion of prey important processes for benthivorous predators. Among epibenthic organisms, Mytilidae are often abundant species in intertidal and subtidal zones of rocky coasts, and can occur in very high densities in large beds (up to 2.6 ha in the Mingan Archipelago in the northern Gulf of St. Lawrence, Quebec, Canada; Guillemette et al. 1996, Gosling 2003). Due to their high densities and broad distribution, mussels are important for many predators. Most predators (e.g. crabs, oystercatchers *Haematopus* spp., cichlids, sea stars) crush or open the shell to ingest only the flesh (Elner 1978, Hoogerhoud 1986). But some predatory birds, such as the red knot *Calidris canutus* and molluscivorous diving duck species (eiders, scoters *Melanitta* spp., longtailed duck *Clangula hyemalis*, goldeneyes *Bucephala* spp., scaups and other freshwater diving ducks *Aythya* spp.) ingest the mussel whole and crush it with their powerful gizzard (Guillemette 1994, De Leeuw 1999, Dekinga et al. 2001).

Most species of seaducks are benthivorous, and blue mussels are among their most consumed prey (Cottam 1939, Ouellet et al. 2013), for example composing up to 60% of the total diet of common eiders *Somateria mollissima* in the Wadden Sea (Perry et al. 2007, Laursen et al. 2009). As seaducks must dive to reach their prey and ingest their prey whole, large amounts of food are needed daily to achieve energy balance (Guillemette et al. 1992).

Due to the abundance and availability of mussels, we assume that the search time of seaducks for mussels, once a mussel bed is found, is very low, leading us to hypothesize that maximum intake rates may be maintained even at low densities. Also, since mussels are attached to their substrate, the ability of seaducks to detach each mussel could affect handling time of this prey. Thus, we also predict that the attachment strength of mussels could have an impact on intake rates, leading to different functional response curves for mussel attached or unattached to the substrate. To test these hypotheses, we conducted experiments in captivity to study underwater seaduck foraging behavior, which is very difficult to do in the field. Moreover, captive conditions allowed for better control of factors such as water depth and temperature, and prey size, density and attachment strength.

MATERIALS AND METHODS

Hand-raised, captive common eiders *Somateria mollissima*, 3 females and 2 males, were used for this experiment. Their mean mass (±SD) during this experiment was 1671 ± 129 g. They had been kept since February 2012 at the Maurice Lamontagne Institute (MLI), Fisheries and Oceans Canada, in an isolated room with 2 fiberglass tanks supplied with filtered sea water from the St. Lawrence Estuary, and had been previously used for other foraging experiments (Varennes et al. 2013, authors' unpubl. data). Water temperature and salinity in tanks followed natural variation in the Estuary (approximate temperature range: −1.3 to 11.9°C; approximate salinity range: 23.8 to 29.9‰). Full-spectrum artificial light followed the natural photoperiod, and room temperature was maintained between 15 and 19°C. Each tank had a pool (4 m wide × 6 m long × 1.3 m deep) and a loafing platform (1 × 4 m) covered by rubber and plastic mesh mats. One tank was a holding tank where birds were kept when they were not involved in an experiment. Birds had ad libitum access to pelleted food and fresh water, as well as some live mussels thrown daily onto the bottom of the tank to stimulate diving behavior. The other tank, the experimental tank, was equipped with 2 above-water video cameras and 1 underwater video camera to record underwater foraging behaviors. Each bird was generally kept for 2 to 3 d in the experimental tank for this experiment.

The intertidal mussels used in this experiment were harvested at low tide during fall 2012 in the intertidal zone at Metis Point on the South shore of the Saint Lawrence Estuary (Quebec, Canada), 12.7 km east of the MLI. Mussels were then stocked in small tanks supplied with raw sea water from the Estuary, until the experiment was conducted from March to May 2013.

During each experimental session, a known number of mussels was presented to the bird on a single slate tile (25 × 25 cm). Eight densities were tested (Table 1) with 2 tiles per density, one tile with mussels naturally attached to the tiles and the other with mussels unattached. Naturally attached mussels were put on the tile in raw sea water at least 1 wk before the experiment (Lee et al. 1990). We did not measure mussel attachment during this experiment, but attachment strength measurements on similar tiles and similar experimental conditions have been

Table 1. Densities (number of mussels *Mytilus edulis* per tile and equivalent number of mussels m^{-2}) presented to 5 captive common eiders. For each density, one tile had attached mussels and the other had unattached mussels

Density level	Mussel per tile	Density per m^2
1	10	160
2	15	240
3	22	352
4	44	704
5	100	1600
6	180	2880
7	281	4496
8	350	5600

done elsewhere (unpubl. data). In these measurements, mussels of different sizes were put together on similar tiles and attachment strength was randomly recorded every 2 d for 35 d, using a dynamometer fixed on a tripod allowing for vertical pulling (Lachance et al. 2008). According to these measurements, attachment strength of intertidal mussels of 15 to 25 mm ranged from 0.20 to 3.00 N (with n = 186).

All mussels used in the experiment had a shell length of 15 to 25 mm. Each of the 5 birds was presented with all mussel treatments, for a total of 16 tiles per bird. Treatment order was determined randomly.

All experimental sessions were done with 1 bird at a time in the experimental tank to measure individual intake rates. However, to reduce stress and encourage the bird to dive, a female-like decoy duck was placed on the surface of the experimental tank with the tested bird. The tested bird was put in the experimental tank at least one day before the experiment. It had ad libitum access to food and fresh water during this habituation period. Pelleted food was removed about 12 h before the start of each experimental session, to motivate the bird to dive during the experiment. Tiles were placed in a wooden tray (0.6 m wide × 1.1 m long × 7.6 cm deep) and put at the bottom of the tank with a pulley system. Birds were accustomed to the set-up and procedure before the experiment. All experimental session durations were adjusted to avoid excessive decrease in abundance (more than 10 to 20 %) from original prey densities. Moreover, the number of experimental sessions each day was adjusted to prevent bird satiation. The experimental protocol was approved by the Canadian Council on Animal Care (CPA-38-09-70-R2). At the end of a session, tiles were recovered and remaining mussels were counted. The number of mussels eaten for each density was then estimated by subtracting the number of remaining mussels from the initial number of mussels.

Minimum and maximum limits for our tested densities were set by experimental restrictions. The maximum limit was set by the maximum number of mussels that could fit on a single tile, without stacking too many mussels and creating oxygen depletion problems for the covered mussels in the clump. The minimum limit was set by the need to avoid total ingestion of all mussels so that ingestion rates could be estimated correctly. This minimum density was 10 mussels per tile (equivalent to 160 mussels m^{-2}). Moreover, our tested densities corresponded to the range normally found in the intertidal zone (É. Varennes pers. obs., Cusson & Bourget 2005, Kirk et al. 2007), which generally range between 1000 and 30 000 mussels m^{-2} and rarely fall below 300 mussels m^{-2}.

All experimental sessions were analyzed by the same observer (É. Varennes) with the behavioral recording software JWatcher V1.0. A foraging cycle in seaducks is composed of a feeding bout separated by a long resting period (Guillemette et al. 1992). Each feeding bout corresponds to a succession of dives for which the duration is the sum of the travel time, bottom time, and a short pause before resuming diving (Guillemette et al. 1992). Our camera installation allowed us to record, for each experimental session, the travel time, bottom time (inside and outside the tile), and surface time between dives and between feeding bouts. For our analysis of ingestion rates, we used the bottom time spent on the tile, corresponding to the duration of time birds spent actually ingesting prey.

Intake rates, i.e. the number of mussels ingested per minute of bottom time (IR, no. min^{-1}), were analyzed using 2 methods. In the first method, IR were expressed according to prey density (DENSITY, no. m^{-2}) with the Michaelis-Menten equation:

$$\text{IR} = a \times \text{DENSITY} / (b + \text{DENSITY})$$

where a corresponds to the maximum intake rate (asymptote) and b, the search time coefficient corresponding to the intake rate at $a/2$ (Lovvorn & Gillingham 1996). Coefficients a and b were calculated with non-least square estimation (function nlsList in the nlme package in R; Pinheiro et al. 2013).

In the second method, intake rates were log transformed and compared between mussel densities and attachment conditions with repeated measures AN-COVA including bird identity as a random factor. All statistical analyses were performed with R v.2.15.0 (R Development Core Team 2013). All p-values were considered significant at the α = 0.05 level. Conditions of normality and homogeneity of variance were tested graphically and with the Shapiro-Wilk normality test and Bartlett's test of homogeneity of variances.

RESULTS

For the general foraging behavior, mean dive duration ± SD was 7.6 ± 4.9 s, with a mean descent time of 1.2 ± 0.67 s, a mean ascent time of 1.4 ± 0.8 s, and a mean bottom time ± SD of 5.0 ± 3.8 s. The mean surface pause duration was 5.7 ± 7.9 min, but, because we did not record the duration of each surface pause, this value was estimated by dividing the total surface duration in each experimental session by the number of dives. The mean maximum intake rate was 45 ± 21 mussels min^{-1} bottom time (corresponding to 0.75 ± 0.36 mussels s^{-1} bottom time).

We estimated the *a* and *b* coefficients by fitting intake rates to the Michaelis-Menten equation for attached or non-attached mussels (Fig. 1). The *a* coefficient estimates were significant, but that was not the case for the *b* coefficient estimates.

Intake rates did not vary significantly with prey density ($F_{1,72} = 1.115$, p = 0.295), mussel attachment ($F_{1,72} = 0.019$, p = 0.892), or their interaction ($F_{1,72} = 0.193$, p = 0.662).

DISCUSSION

We established functional response curves for common eiders (large benthivorous seaducks) foraging on attached and non-attached mussels at varying densities. We did not find any effect of density or attachment on eider intake rates. The absence of density effect confirmed our hypothesis that intake rates of seaducks foraging on highly detectable and accessible mussels may not decrease appreciably with prey depletion. Moreover, results indicate that attachment strength of mussels does not seem to affect seaduck intake rates.

Intake rates in our experiment increased very rapidly at what we consider low densities, probably reaching the asymptote at densities lower than 160 mussels m^{-2}. This minimum tested density is lower than densities of Mytilidae normally found in intertidal, infralittoral, and subtidal zones, or in aquaculture sites (Guillemette et al. 1996, Hamilton et al. 1999, Cusson & Bourget 2005, Kirk et al. 2007). Moreover, this minimal density is close to minimal densities of benthic prey tested in other studies on functional responses of birds. Indeed, even though De Leeuw (1999) established functional responses for very low benthic prey densities (equivalent to 5 prey m^{-2}), other studies used comparative minimal densities (50 to 200 prey m^{-2}; Richman & Lovvorn 2003, Goss-Custard et al. 2006, Beauchamp 2009). Thus, seaducks should be able to maintain their maximum intake rate in all blue mussel habitats they are known to forage in, and prey depletion should not affect their intake rates, at least for densities above our 160 mussels m^{-2} minimum limit. This result might explain the ability of common eiders or other seaducks to largely deplete prey patches composed of mussels or other easily detectable prey (Guillemette et al. 1996). For instance, Guillemette & Larsen (2002) estimated the biomass of bivalves *Spisula* sp. at the beginning and end of winter, as well as predation rates. They

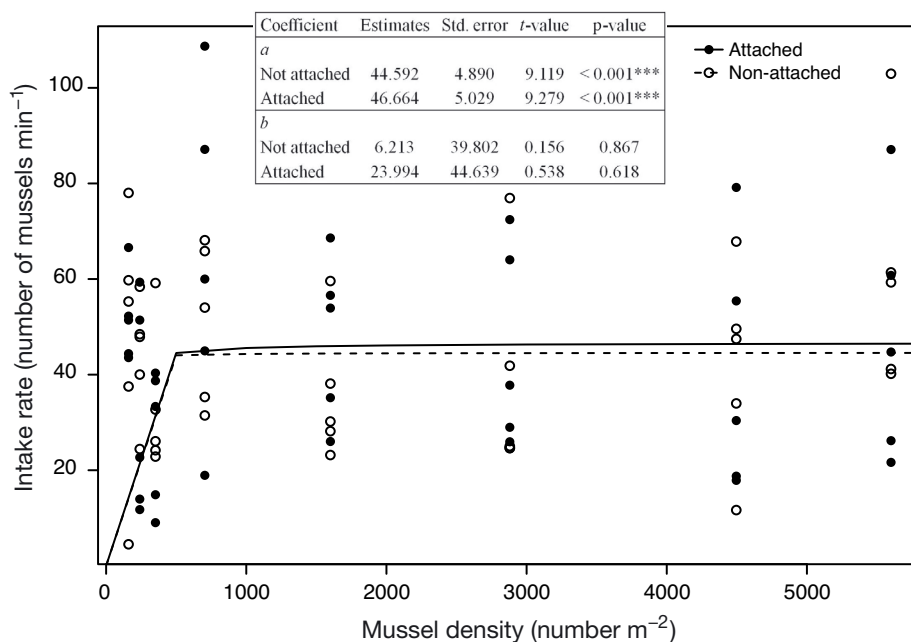| Coefficient	Estimates	Std. error	*t*-value	p-value
a				
Not attached	44.592	4.890	9.119	<0.001***
Attached	46.664	5.029	9.279	<0.001***
b				
Not attached	6.213	39.802	0.156	0.867
Attached	23.994	44.639	0.538	0.618

Fig. 1. Intake rates (number of mussels *Mytilus edulis* ingested per minute bottom time) of 5 captive common eiders *Somateria mollissima* according to prey densities (number of mussels m^{-2}) when mussels are attached to the tile or non-attached. The inset table shows statistical results (estimates, standard errors, *t*-values and p-values) of the Michaelis-Menten fit for the maximum intake rate (*a*) and the search time coefficient (*b*) in both attachment conditions. Curves are plotted using estimates from the table

found that common eiders were capable of completely depleting *Spisula* although they could not eliminate the role of other predators. Similarly, in the field and in experiments, seaducks are able to completely deplete mussels on collector ropes in mussel farms (authors' unpubl. data), leading to critical depredation problems for aquaculture in several countries (Ross & Furness 2000).

The absence of a negative effect of decreasing prey densities on intake rates has also been found in other prey–predator systems: diving greater scaup foraging on zebra mussels (De Leeuw 1999), various shorebirds eating macro-invertebrates (Goss-Custard et al. 2006), and geese foraging on grass (Durant et al. 2003, Van Der Graaf et al. 2006). In all these examples, prey was abundant and easily accessible, supporting the hypothesis that intake rates of predators foraging on highly detectable and accessible prey does not decrease easily with prey density, allowing large prey depletion. In contrast, decreasing prey densities had a negative effect on intake rates of lesser scaup and white-winged scoters foraging on clams buried at different depths, showing the impact of searching on predators' intake rates at low prey densities when prey is less accessible (Richman & Lovvorn 2003).

We did not find any effect of attached versus non-attached mussel on the eiders' intake rates, whatever the density, as found in some other studies (Draulans 1982, De Leeuw 1999). De Leeuw (1999) observed no difference in apparent intake rates of tufted ducks foraging on 'moderate clumps' and 'unattached mussels', but there was a significant difference for scaups. Moreover, apparent intake rates did decrease at strong mussel attachment for both duck species (De Leeuw 1999). Depending on mussel size, reproductive condition or environmental factors, mussel attachment strength may range from 1 to 20 N (Kirk et al. 2007). In our experimental set up, we measured maximal mussel attachment strength no higher than 3 N. This low attachment strength may be explained either by the small size of mussels used (20 mm), or experimental conditions that did not properly recreate environmental conditions leading to stronger mussel attachment.

Maximum intake rate in our experiment was about 45 mussels min^{-1} bottom time. This value is consistent with measurements or estimates of intake rates of diving ducks foraging on mussels in other studies (Guillemette 1994, De Leeuw 1999). For example, De Leeuw (1999) measured maximum intake rates of 27 g mussel wet mass min^{-1} for scaup and 21 g mussel wet mass min^{-1} for tufted ducks.

Taking 0.644 g as the total wet mass of an intertidal mussel of 15 to 25 mm (authors' unpubl. data); we found a similar maximum intake rate of 28 g wet mass min^{-1}.

Intake rates of diving ducks foraging on mussels may vary with mussel size due to different handling times for different sizes. For example, tufted ducks handled large freshwater mussels individually, often manipulating prey at the surface, while small mussels were rapidly ingested by suction-feeding (De Leeuw & Van Eerden 1992). In our experiment, small mussels were ingested mainly underwater, with little handling at the surface. These different feeding modes can lead to large differences in intake rates depending on mussel size. In our experiment, we used mussels of about 20 mm length because it is the size generally found to be preferred by eiders (Bustnes & Erikstad 1990, Guillemette et al. 1996, Bustnes 1998). However, some other studies have shown a preference of eiders for larger mussels (Hamilton et al. 1999, Nehls 2001). Interestingly, Hamilton et al. (1999) showed that prey size selection of eiders changed throughout the year, with a general preference for small mussels (10 to 20 mm), except in winter when larger mussels were preferred (30 to 40 mm). Thus, further studies are needed to differentiate intake rates of eiders for different mussel sizes and to better understand size preference variations in seaducks.

Having shown that seaducks can maintain high intake rates at densities that are low for mussel habitats, we can speculate on how quickly a flock can deplete a hypothetical intertidal habitat using intake rates measured in controlled conditions. It would take about 3.5 d (with 6 h spent feeding per day) for a flock of 100 eiders to deplete a 2 ha mussel bed with a density of 300 mussels m^{-2}. Likewise, it would take a little less than 1 wk (6 d with 6 h spent feeding per day) for a flock of 2000 eiders to deplete the same surface area (2 ha) at a density of 10000 mussels m^{-2}. Thus, it would not take much time for a typical flock of 100 to 2000 eiders (Guillemette et al. 1993) to deplete a mussel habitat at the intake rates found in this experiment.

Hypothetically, large depletion coupled with rapid regeneration of mussel populations might help to equalize and maintain foraging habitats with small preferred prey, and thus reduce seaducks' search time. Hence, instead of creating a shortfall, large mussel depletion by seaducks might have quite the opposite effect by ensuring a replenished foraging habitat of mostly highly suitable small prey in time for the next visit.

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