Carcass feeding as a cryptic foraging mode in round goby *Neogobius melanostomus*

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Round gobies *Neogobius melanostomus* were observed readily consuming soft tissue from carcasses of larger fishes under both laboratory and field conditions. Consumption normally progressed in a typical sequence, starting with soft and easily accessible tissues such as the eyes, followed by puncture of the abdominal cavity, gut consumption and then muscle consumption. Carcass feeding has not previously been seen in *N. melanostomus* and has potential consequences for transfer of nutrients and contaminants.

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The perceived negative effects of invasive species are typically linked to their trophic ecology, with invaders often affecting ecosystems through predation, competition or other alterations to locally established trophic relationships (Farrell *et al.*, 2010). Within the Danube River basin, the invasive round goby *Neogobius melanostomus* (Pallas 1814) has been described as a predator with high dietary plasticity; it is considered to be a food generalist, although feeding mainly on benthic organisms such as crustaceans, insect larvae, molluscs and even small fishes (Polačik *et al.*, 2009; Števove & Kováč, 2013). The species is commonly regarded as showing a preference for zebra (quagga) mussels *Dreissena* spp. based on the large proportion found in their guts, laboratory experimentation and observations of morphological adaptation (Ghedotti *et al.*, 1995; Ray & Corkum, 1997). Diggins *et al.* (2002), however, suggested that *N. melanostomus* may prefer different prey. Hard shells of *Dreissena* spp. can cause an overestimation bias because they are easier to detect in the gut than soft prey (Barton *et al.*, 2005). In contrast, some soft prey items may remain underestimated during analysis.

It was hypothesized that the capability of *N. melanostomus* to feed on the sedentary, clump-occurring *Dreissena* spp. may have pre-adapted them to feed on soft tissues of larger fish carcasses. This foraging mode is likely to be difficult to identify during gut

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content examination as soft tissues ingested in this way will be quickly assimilated. In order to test the validity of this hypothesis, both laboratory and field tests based on the consumption of fish carcasses were performed.

Neogobius melanostomus for laboratory experiments were collected from the River Dyje near the town of Břeclav, Czech Republic (48° 44′ 12·70″; 16° 52′ 38·78″), in late September 2012 using a backpack electrofishing unit (Bednář; www.r-bednar.cz). All *N. melanostomus* were transported to the laboratory immediately after capture. The river stretch sampled (maximum depth 1 m) is artificially straightened, has a gravel bottom and banks strengthened with large stones. At present, the population density is *c.* 1·3 individuals m^{-2} (based on the electrofishing survey), making it the dominant fish species in the stretch. The native fish community is dominated by bleak *Alburnus alburnus* (L. 1758), supplemented by silver bream *Abramis bjoerkna* (L. 1758) and barbel *Barbus barbus* (L. 1758) (Adámek *et al.*, 2013).

Experimental *N. melanostomus* were kept in 200 l tanks for 7 days in order to acclimatize them and standardize their diet. Twice per day, the fish were offered frozen chironomid *Chironomus* sp. larvae with 15 min of *ad libitum* feeding. Uneaten food was subsequently siphoned away. Final feeding took place 12 h before the onset of the experiment.

A total of 90 *N. melanostomus* [43 males, 47 females; mean ± S.D. standard length $(L_S) = 89·5 ± 7·7$ mm] were used in the experiment. Experimental tanks (70 l) were equipped with a gravel substratum and three ceramic shelters. The water was maintained at a temperature of 16° C and constantly aerated. *Neogobius melanostomus* experienced a normal early October daylight regime (11L:13D).

Thirty experimental replicates took place, with three acclimatized *N. melanostomus* in each replicate introduced randomly into the experimental tank, together with the intact carcass of a cyprinid fish as a putative food source. Three similarly sized cyprinid species (each $n = 10$) were used; *A. bjoerkna* (mean ± S.D. $L_S = 107·5 ± 13·1$ mm), *A. alburnus* (113·9 ± 7·5 mm) and roach *Rutilus rutilus* (L. 1758) (106·9 ± 6·9 mm). No other food was provided during the experiment.

Neogobius melanostomus behaviour was recorded for 24 h at 2 h intervals, with experiments starting at 0800 hours. Degree and sequence of carcass consumption were recorded on a categorical basis; five distinct categories were identified in a pilot study. The five categories normally progressed in the following order: (1) consumption of one or both eyes, (2) attempting to gain access to the abdominal cavity from the ventral side of the carcass (as indicated by damaged scales or incomplete puncture), (3) a clear puncture into the abdominal cavity (guts still present), (4) guts consumed and abdominal cavity emptied and (5) consumption of muscle tissue.

Field experiments were also performed to test whether *N. melanostomus* were indeed attracted to and consumed fish carcasses in their natural habitat, thereby confirming that carcass consumption was not an artefact of the laboratory environment. The experiments were conducted at the same location as collection for the laboratory experiment in mid-October 2012, with 20 minnow traps (Douglas Net Company; www.douglasnets.com; length 45 cm, height 25 cm, aperture width 6·5 cm) placed along the shoreline. Trap depth was 0·6–0·7 m. Eleven traps were baited with a fresh *A. bjoerkna* carcass (140·0 ± 15·0 mm) and nine traps contained no bait. After 48 h exposure, the traps were checked and all *N. melanostomus* captured were counted and measured. Damage to the bait *A. bjoerkna* was evaluated using the same criteria as the laboratory experiment.

TABLE I. Summary of binomial generalized linear model (GLM) (numbers 1–4) and Cox proportional hazard (number 5) modelling, showing sample-size corrected Akaike information criterion (AIC_c) for the full (saturated) model and final model [model with minimum AIC_c from all models (*i.e.* all possible predictor combinations)], predictors in the final model and their significance (*P*), % of variability explained by the final model (% exp) and sample size (*n*). The full model always consisted of the following predictors: *Neogobius melanostomus* standard length (L_S), carcass type, carcass L_S and carcass type × carcass L_S interaction

Model number	Response variable	AIC_c full	AIC_c final	Predictor	*P*	% exp	*n*
1	Abdominal cavity punctured	39·2	34·7	–	–	–	30
2	Muscle tissue consumed	46·9	38·5	Carcass type	<0·05	10·9	30
3	Eye consumption	57·8	40·3	–	–	–	30
4	Dorsal muscle consumption	31·3	19·9	Carcass type	<0·01	32·6	20
5	Time to abdominal penetration	137·3	130·2	Carcass type	<0·05	13·3	30

Generalized linear models (GLMs; binomial distribution; Zuur *et al.*, 2009) and the Cox proportional hazard model (PHM; Therneau & Grambsch, 2000) were used to determine the effect of different predictors (see Table I) on the response variables [GLMs: prey state after 24 h, PHM: time until penetration of the abdominal cavity (right censored variable)]. In order to stress the differences observed between soft-bodied *A. alburnus* and hard-bodied *A. bjoerkna* and *R. rutilus*, data for the latter were pooled. GLMs (quasipoisson distribution) and *t*-tests were used to compare number and size, respectively, of *N. melanostomus* caught in baited and unbaited traps.

In the laboratory, *N. melanostomus* readily consumed carcasses of larger cyprinids. Each experimental carcass was at least partly consumed, progressing at least to abdominal penetration in 76·7%, and up to muscle consumption in 66·7%, of replicates. Carcass consumption normally progressed in a typical sequence (Fig. 1). *Neogobius melanostomus* first consumed soft and easily accessible tissues such as the eyes [Fig. 1(a)]. In 75% of replicates progressing up to muscle consumption, carcass consumption followed three characteristic steps: (1) puncture of the abdominal cavity on the ventral side [Fig. 1(a)], (2) consumption of the guts [Fig. 1(b)] and (3) consumption of muscle tissue [Fig. 1(c)]. In the remaining 25% of replicates, *N. melanostomus* attempted to gain access to the abdominal cavity through the dorsal side. There was no evidence that *N. melanostomus* were able to eat through larger bones such as ribs.

Size of carcass and size of *N. melanostomus* had no influence on any of the variables studied, although carcass type did (Table I). Access to the abdominal cavity was significantly faster in *A. alburnus* compared to the relatively firmer-bodied *R. rutilus* and *A. bjoerkna* group (hazard ratio = 0·39; Table I). *Neogobius melanostomus* also consumed muscle tissue from *A. alburnus* more frequently (90% incidence) than from *A. bjoerkna* and *R. rutilus* (55% incidence; Table I).
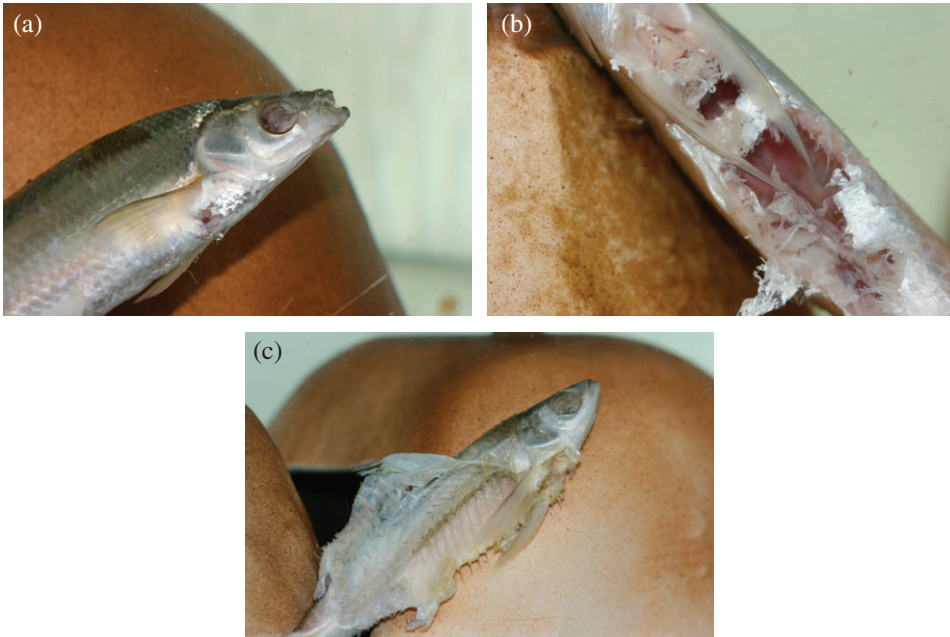
FIG. 1. An example of a typical sequence of actions and steps during carcass consumption by a *Neogobius melanostomus*. The process starts with (a) consumption of the eyes and penetration of the abdominal cavity on the ventral side, followed by (b) consumption of the gut and then (c) muscle tissue.

In the field experiment, *N. melanostomus* were caught significantly more often in baited [mean 4·64 individuals, C.I.; (estimated by GLM) $= 3·04 - 6·72$] than in unbaited traps (mean 0·89 individuals, C.I. $= 0·27 - 2·09$; GLM, $F_{1,18} = 13·00$, $P < 0·01$). Trapped *N. melanostomus* fed on the bait *A. bjoerkna* and consumption progressed to muscle consumption in 72·7% of the traps. *Neogobius melanostomus* captured in the baited traps were significantly larger than those in unbaited traps [t-test, $t_{57} = 2·95$, $P < 0·01$; mean $\pm$ S.D. $L_S = 86·4 \pm 9·8$ (baited) and $74·6 \pm 14·5$ (unbaited)].

The capability of *N. melanostomus* to consume carcasses of larger fishes was demonstrated both in the laboratory and under natural conditions, with each experimental carcass at least partly consumed. Furthermore, baited traps attracted significantly more *N. melanostomus* than unbaited traps, documenting the attractiveness of fish carcasses to *N. melanostomus*.

Facultative necrophagy on carcasses larger than the necrophage is a relatively rare phenomenon in fishes and has so far been documented only in a small number of species (Helfman & Clark, 1986; Witte, 1999). It is known if *N. melanostomus* is able to detect a range of olfactory cues (Yavno & Corkum, 2011) but it is plausible that it can respond to odours released from a fish carcass. Although there are potential costs to feeding exclusively on carcasses, *e.g.* extended searching and handling time, these can be traded-off against a lack of active prey avoidance and increased energy intake. Soft fish tissues have no ballast component and represent a high quality food resource that is more profitable than low energy density invertebrate prey, such as molluscs (Ruetz *et al.*, 2009).

Fish carcasses may represent a seasonally abundant food resource across ecosystems as many fish species suffer increased mortality at certain times of the year, *e.g.* following spawning (P. Jurajda, pers. obs.). The tendency of *N. melanostomus* to feed on carcasses may also vary within a single population. For example, Ng *et al.* (2008) found that some *N. melanostomus* in Lake Michigan had a higher estimated trophic level than their predator, smallmouth bass *Micropterus dolomieu* Lacépède 1802. These individuals were hypothesized to feed on fish eggs, but carcass feeding may have also contributed to the elevated trophic position. It is likely, therefore, that carcass consumption may only be an occasional, but wholly natural, mode of nutrition for *N. melanostomus*.

The characteristic, repeated sequence of steps in carcass consumption points to the existence of an inherent behavioural adaptation. In the majority of replicates, *N. melanostomus* correctly identified the spot where the abdominal cavity was unprotected by rib bones and hence could be easily penetrated (see Video S1, Supporting Information). Notably, carcass consumption corresponded in many aspects to the way in which *N. melanostomus* prey on *Dreissena spp.*, *i.e.* an attached mussel is removed from the substratum by the *N. melanostomus* taking a firm grasp with its jaws and jerking its body and head repeatedly in order to break the attachment by the byssal threads (Ghedotti *et al.*, 1995; Morano, 2007). *Neogobius melanostomus* used the same technique to remove large scales and tear away flesh from the carcass (Supporting Information, Video 1).

Alburnus alburnus, with its relatively soft body and loose scales, was consumed at a faster rate than *R. rutilus* or *A. bjoerkna*. Access to the profitable soft tissues in this case may be limited by *N. melanostomus*' ability to break through the scale armour. Since size of carcass did not increase the time required to gain access to the muscle tissue or guts, it may be that the larger and more firmly attached scales of *R. rutilus* and *A. bjoerkna* increased handling time. For the same reason, *N. melanostomus* avoid larger *Dreissena* spp. due to their increased handling costs (Djuricich & Janssen, 2001). In the case of carcass consumption, however, other scavengers, such as necrophagous crayfish or crabs, may facilitate access by penetrating through the scales (Willman *et al.*, 1994).

Confirmation of *N. melanostomus* carcass feeding suggests that they may ecologically function not only as predators, but also as scavengers. Notably, this additional trophic pathway can position *N. melanostomus* closer to the top of the food chain with consequences for the transfer and accumulation of contaminants (Hogan *et al.*, 2007).

Supporting Information

Supporting Information may be found in the online version of this paper:
Video S1. Round goby gaining *Neogobius melanostomus* access to abdominal cavity of a roach *Rutilus rutilus*

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