

# All's good in a famine? *Hydrobia ulvae* as a secondary prey for juveniles of Iceland moonsnails *Amauropsis islandica* at the White Sea sandflats

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*Many size-selective predators switch their diet during ontogeny. At the White Sea, the adult moonsnails Amauropsis islandica feed mostly on Macoma balthica clams. The diet of juveniles was largely unknown. We conducted a field survey and a caging experiment to find out if juvenile moonsnails can prey on Hydrobia ulvae, and whether they prefer this snail to their usual prey. Live molluscs and their intact or perforated shells were collected from 34 sediment cores. We exposed the single-prey cages with 50 Macoma (MP) or 50 Hydrobia (HP) together with five Amauropsis juveniles, as well as the cages where both prey species were in a 25:25 proportion (HMP). While live Hydrobia was more abundant in the natural assemblages, Amauropsis preferred Macoma, as indicated by proportions of perforated shells. The caging experiment produced similar results. Per capita Macoma consumption rate was significantly higher than Hydrobia consumption rate ( $6.4 \pm 0.5 \text{ mg day}^{-1} \text{ ind.}^{-1}$  vs.  $1.4 \pm 0.2 \text{ mg day}^{-1} \text{ ind.}^{-1}$  in MP and HP respectively). Prey consumption rates in the single-prey treatments were higher than in mixed-prey cages regardless of prey species. Different mechanisms explain this variation: for Hydrobia it is a consequence of the dietary shift, while for Macoma it reflects the 'floor' effect in HMP cages, where virtually all Macoma had been drilled by the end of exposure term. While Macoma is the preferable prey of young Amauropsis, Hydrobia can supplement the diet of juveniles when Macoma is scarce in certain locations.*

**Keywords:** caging experiments, ontogenetic diet shift, prey switching, boreholes, Naticidae, predator-prey interactions, *Amauropsis islandica*, *Hydrobia ulvae*, *Macoma balthica*, White Sea

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## INTRODUCTION

The diet of many predators can change during their life history, and the mechanism of such a shift is often linked to the relative size of predator and prey (Sullivan, 1988; Winemiller, 1989; Hughes *et al.*, 1992; Giaretta *et al.*, 1998). In most cases, the larger predators have a broader diet than smaller individuals of the same species (Shine *et al.*, 1998; Olabarria *et al.*, 2009). Predators can switch to a different kind of major prey (Hughes *et al.*, 1992; Clements & Rawlings, 2014) or narrow their diet during ontogeny (Aristov *et al.*, 2003; Moura *et al.*, 2008; Da Rosa *et al.*, 2011). We expect that the change in the population structure of predators (e.g. due to successful recruitment) can lead to the diet shift. For instance, juveniles may broaden their diet by including smaller suboptimal species when the availability of the major prey of appropriate size is low.

Moonsnails are size-selective predators (Edwards & Huebner, 1977; Kingsley-Smith *et al.*, 2003; Quijon *et al.*, 2007), widely known for their ability to drill the shells of

their prey (mainly bivalve molluscs) (Carriker, 1981; Huelsenken, 2011 and others). The drilled shells can provide information about the rations and occurrence of certain predator species (Vignali & Galleni, 1986; Kabat, 1990). There is evidence of voracious behaviour of moonsnails in the literature and they are believed to regulate the abundance of their prey (Wiltse, 1980).

The Iceland moonsnail *Amauropsis islandica* is a naticid that can dwell on the upper subtidal and lower intertidal flats of the White Sea. The feeding mode and the long-term changes in the intertidal populations of this predator had been monitored since 2001 at the Kandalaksha Natural State Reserve (Aristov, 2013). The programme revealed that the adult *Amauropsis* moonsnails feed on common intertidal bivalves, such as *Macoma balthica* (L., 1758), *Mya arenaria* (L., 1758) and *Mytilus edulis* L., 1758. Occasionally, *Littorina littorea* (L., 1758) gastropods and other littorinids supplement the diet. The preferred prey of adult *Amauropsis* is *Macoma balthica* (Aristov & Granovitch, 2011).

In the last 4 years, the number of young *Amauropsis* snails in our surveys has increased (Aristov, 2013), and the number of small *Macoma* has dropped below the level that could support the juvenile predators. This made us assume that the small moonsnails consume other prey besides clams. The sizes of the other known potential victims generally lay

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outside the size range accessible to the juvenile predators, and the identity of the prey that can supplement the diet of juvenile *Amauropsis* was yet to be revealed. Among the other molluscs inhabiting the White Sea sandflats, only the mudsnail *Hydrobia ulvae* (Pennant, 1777) is small enough for juvenile moon snails. In addition, it was very abundant at the site throughout the monitoring period (Aristov, 2013). We conducted a survey of the sandflat molluscan assemblages and caging experiments to assess the role of *H. ulvae* in the diet of *A. islandica* juveniles and to compare it with *M. balthica* as a prey.

## MATERIALS AND METHODS

### Study area

Both the survey of molluscan assemblages and caging experiment were held in July – early August 2014 at the sandflats of the Youzhnaya inlet (67°00' N 32°34' E, Ryashkov island, Severny archipelago, Kandalaksha State Nature Reserve, Figure 1).

Youzhnaya inlet is the sheltered shallow bight at the south of Ryashkov island, where the tidal amplitude is about 1.8 m. A stream flows into the head of the bight and fresh water runs over the tidal flat during ebb. The tidal sediments consist of fine and coarse sand with a trace of clay. There is no distinct intertidal-subtidal boundary marked by a ridge of boulders; large boulders (up to 1.7 m high) are scattered across the low intertidal zone of the inlet. A dense population of the lugworm *Arenicola marina* (L., 1758) dwells within the lower zone, together with common intertidal species such as *Macoma balthica*, *Hydrobia ulvae*, *Microspio theeli* (Söderström, 1920) (Aristov, 2013).

### Survey of natural molluscan assemblages

In July 2014, we collected *Hydrobia ulvae* from 20 cores sampled with a  $4 \times 10^{-3} \text{ m}^2$  tube corer and sieved on a 0.5 mm mesh, *Macoma balthica* from 14 cores with an area

of  $3 \times 10^{-2} \text{ m}^2$  and *Amauropsis islandica* from 14 cores with an area of  $2.5 \times 10^{-1} \text{ m}^2$  that were sieved on a 1 mm mesh. To ensure compatibility of the abundance estimates from different sieving methods, all *Hydrobia* snails smaller than 1 mm in width were excluded from the subsequent analyses. We counted live *A. islandica*, *H. ulvae* and *M. balthica* specimens and empty shells of the two latter species – intact and perforated. Only unarticulated bivalve shells were collected. We measured the width of *Amauropsis* and *Hydrobia*, and the length of *Macoma* shells with a microscope micrometer. The live molluscs (except *Amauropsis*) were wet weighted using spring balances with 0.001 g accuracy.

### Caging experiments

To assess *A. islandica* feeding rates on both types of prey (*H. ulvae* and *M. balthica*) and possible species-selectivity in feeding, we set up a caging experiment. We encaged five *Amauropsis* snails with different prey: *Hydrobia* (HP, 4 replicates times 50 ind.), *Macoma* (MP, 4 replicates times 50 ind.), and *Macoma* together with *Hydrobia* (HMP, 8 replicates, 25 ind. of each species). As a control, we separately exposed *Hydrobia* (HC, 3 replicates times 50 ind.), and *Macoma* (MC, 3 replicates times 50 ind.). The cages were exposed for 16 days (19 – 3 August 2014). The number of molluscs in the cages was chosen so that the total density of prey in the cages was equal. The sizes of prey were selected so that the total weight of soft tissues, estimated using a previously established relationship (Poloskin, 1995), was similar between the species within a cage. Before the experiment, on 16–19 July 2014, we collected 80 ind. of *Amauropsis islandica* 5–6 mm in height, 550 ind. of *Hydrobia ulvae* 1.7–2.5 mm in width and 550 ind. of *Macoma balthica* 3–5.5 mm in length.

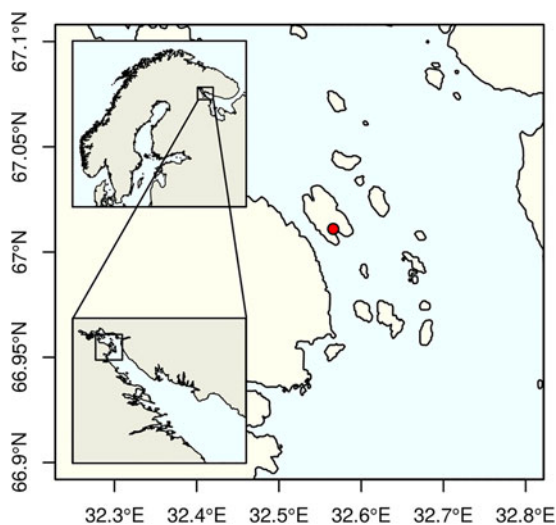
The 22 cages, made of plastic boxes (10 × 10 × 10 cm, 1 L) and screened with 1 mm capron mesh, were filled with a 5 cm layer of sand. Predators and prey were added, and the cages were placed in one block at the intertidal sandflat in the Youzhnaya inlet near the chart datum. The cages belonging to different treatments were arranged checkerwise within the block.

After the exposure, the content of the cages was sieved through the 1-mm mesh. The molluscs and their shells – intact and perforated – were counted and measured using a microscope micrometer or vernier calipers. During the experiment, we found that small *H. ulvae* individuals crept into all cages from outside. Consequently, we used only the data on *Hydrobia* larger than 1.5 mm in width.

### Statistical methods

We used parametric descriptive statistics: the estimates of all means are reported with standard errors. The pairwise comparisons between the means were made with Welch's t-test which allows for unequal within-group variances. We compared the proportions of drilled shells between species using  $\chi^2$ -test (Agresti & Franklin, 2013).

The biomass of the two types of prey consumed in each cage of the experiment was reconstructed using previously fitted equations. For *Hydrobia* we used the equation  $W = 2.90 L^{1.53}$ , where  $W$  is wet weight of *Hydrobia* in mg, and  $L$  is the width of the last whorl in mm. The regression was obtained for 83 *H. ulvae* from the same location. Despite its poor support ( $R^2 = 0.46$ ), the average differences between the



**Fig. 1.** The study area. The dot marks the Youzhnaya inlet at the Ryashkov island (Kandalaksha Bay, the White Sea), where the field survey and caging experiment were carried out.

observed and predicted biomass of the live *Hydrobia* did not exceed  $7 \pm 2\%$ . We deduced the biomass of *Macoma* using the equation  $W = 0.16 L^{2.96}$ , where  $W$  is the wet weight in mg, and  $L$  is the shell length in mm (Maximovich *et al.*, 1993). The average differences between the observed and predicted biomass of the live *Macoma* were  $8 \pm 3\%$ .

We estimated the total per capita prey consumption as the biomass of each type of prey consumed in a cage per number of predators, which survived until the end of exposure. We compared the per capita prey consumption of each prey species between single-prey and mixed-prey treatments (HP vs. HMP treatments for *H. ulvae* and MP vs. HMP treatments for *M. balthica*) using the analysis of covariance (Quinn & Keough, 2002). In each of the two models, we controlled for the predator size using an average shell length of *Amauropsis* in a cage as a covariate. The residuals of both models were checked for normality using quantile plots, and for the variance heterogeneity using Breusch–Pagan test (Breusch & Pagan, 1979). The assumptions were met for the model of *H. ulvae* consumption. The variance heterogeneity for the model of *M. balthica* consumption was successfully corrected by  $\log_{10}$ -transformation of the response variable. As both models contained only two treatments, the differences between the levels were evaluated using the coefficients of the fitted models that were t-tested for significance. The differences between the treatments in the model of the per capita consumption of *M. balthica*, where the predictor was  $\log_{10}$ -transformed, were transformed back to the original scale.

All calculations were performed using R 3.1.0 (R Core Team, 2014) in RStudio (RStudio, 2014). We used *car* and *lme4* packages for diagnostics of regression assumptions (Zeileis & Hothorn, 2002; Fox & Weisberg, 2011) and *ggplot2* to produce the figures (Wickham, 2009; Chang, 2012).

## RESULTS

### Natural molluscan assemblages

The total density of *Amauropsis islandica* at the study site around the caging area was  $21.1 \pm 5.6 \text{ ind. m}^{-2}$ . About 14% ( $2.9 \pm 1.5 \text{ ind. m}^{-2}$ ) were juvenile snails with shell height less than 6 mm. The average density and biomass of *Macoma balthica* was lower than in the case of *Hydrobia ulvae* (Figure 2). Despite this, *Amauropsis* snails fed mostly on *Macoma*, as indicated by the higher perforated/intact ratio than for *Hydrobia ulvae* (4.69 vs. 1.26,  $\chi^2$ -test,  $P < 0.01$ ). Still, *Hydrobia* supplemented the diet of the predator.

The size ranges of the perforated shells of the two prey species mostly overlapped (Figure 3). The minimal height of the drilled *Hydrobia* shells (range 1–2.4 mm) was smaller than the length of the smallest drilled *Macoma* shells (range 1.5–12.8 mm). The prey sizes later selected for experiments were potentially accessible for moon snails, as indicated by the size structure of the drilled shells.

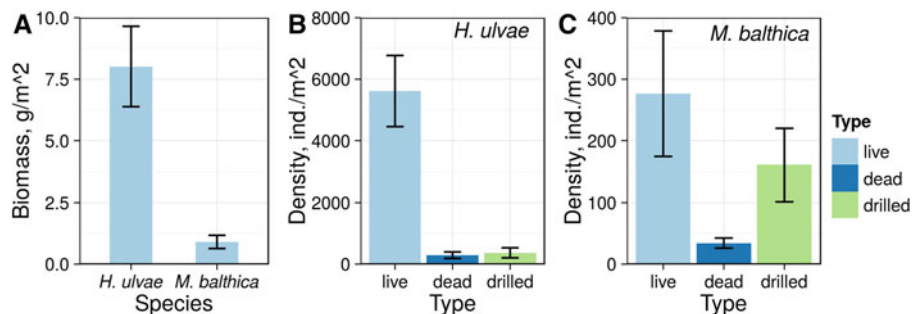


Fig. 2. Abundance of the two prey species *Hydrobia ulvae* and *Macoma balthica* and their empty shells in the natural assemblage: (A) average biomass of live mollusks; (B, C) average density of live mollusks and their empty shells (intact and perforated) for *Hydrobia* and *Macoma* respectively. Error bars are  $\pm 1$  SE.

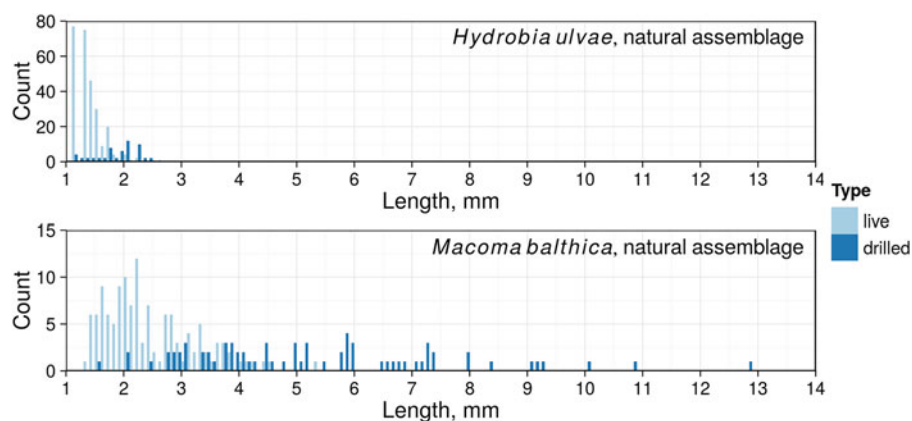
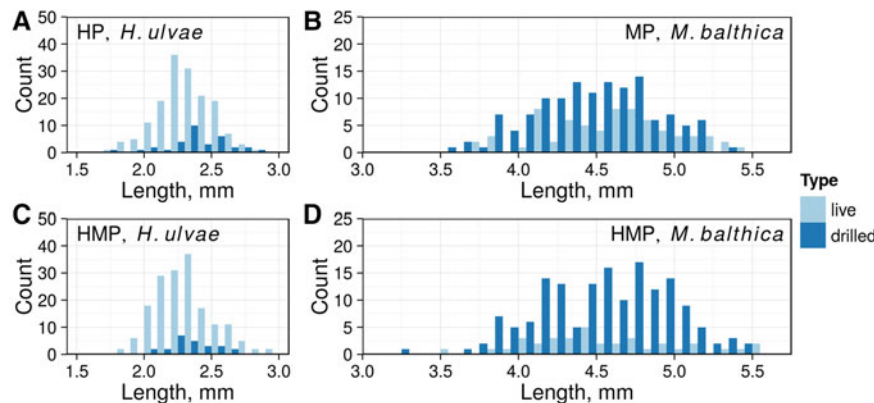


Fig. 3. The size distribution of drilled shells of *Macoma balthica* and *Hydrobia ulvae* in the natural assemblage.



**Fig. 4.** The size distribution of perforated shells of *Macoma balthica* and *Hydrobia ulvae* in the caging experiment. (A) *Hydrobia* as a single prey in HP treatment; (B) *Macoma* as a single prey in MP treatment; (C, D) *Hydrobia* and *Macoma* together in HMP treatment.

## Caging experiments

In the caging experiment, perforated prey shells were found only in the cages with *Amauropsis*. The distribution of drilled and undrilled shells revealed that the moonsnails were able to consume *M. balthica* and *H. ulvae* of the sizes offered (Figure 4). The range of the drilled shells did not change between treatments, indicating that we effectively controlled for the predator size selectivity.

Almost all mortality of *H. ulvae* and *M. balthica* in the cages with *Amauropsis* was caused by predation. A total of 8 mud snails (2%) and 2 clams (<1%) died due to other reasons. Such a low level of natural mortality during the experiment indicated good caging conditions.

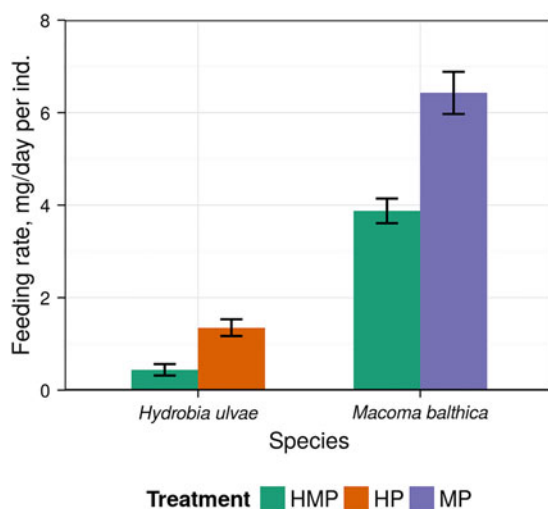
The feeding rates of *Amauropsis islandica* juveniles in the cages with *Hydrobia ulvae* only ( $1.4 \pm 0.2$  mg day<sup>-1</sup> ind.<sup>-1</sup>) were significantly lower than in the cages with *Macoma balthica* ( $6.4 \pm 0.5$  mg day<sup>-1</sup> ind.<sup>-1</sup>, t-test,  $t_{3,92} = 10.36$ ,  $P < 0.01$ ; Figure 5).

We compared the total per capita consumption of *H. ulvae* and *M. balthica* between the treatments where they were offered separately and together. The average shell length of *Amauropsis* in the cage that was used as a covariate affected

the prey consumption in neither of the two models. Since initially all the moonsnails were of the same size, the absence of the predator size effect means that either the predator growth did not depend on prey consumption, or the 16-day exposure was too short to register the effect on shell growth.

The consumption of *Hydrobia* significantly differed between the treatments where *Hydrobia* was alone and where it was mixed with *Macoma* ( $F_{1,9} = 16.13$ ,  $P < 0.01$ ). As predicted by the model, each predator in the HP treatment consumed during the exposure period on average  $15.0 \pm 3.7$  mg of *Hydrobia* more than in the HMP (t-test of the linear model coefficient,  $t_9 = 4.02$ ,  $P < 0.01$ ). The proportion of *Hydrobia* consumed did not exceed 30% in both treatments. *Amauropsis* juveniles consumed 0–29% of *Hydrobia* in the mixed treatment ( $12.3 \pm 3.5\%$ ) and 12–25% when *Hydrobia* was offered alone ( $16.5 \pm 2.9\%$ ).

The log<sub>10</sub>-transformed total per capita consumption of *Macoma* also significantly differed between treatments where *Macoma* was alone and where it was accompanied by *Hydrobia* ( $F_{1,9} = 16.21$ ,  $P < 0.01$ ). The predicted consumption of *Macoma* in the treatment where it was alone was  $1.6 \pm 0.2$  times higher (back-transformed scale) than when it was mixed with *Hydrobia* as an alternative prey (t-test of the linear model coefficient,  $t_9 = 4.03$ ,  $P < 0.01$ ) (Figure 5). In some cages of the mixed treatment the predators consumed almost all available *Macoma*, presumably because the total starting amount of *Macoma* in the mixed treatment was too low. By the end of the experiment, from 50 to 100% ( $81 \pm 7\%$ ) of *Macoma* had been eaten. At the same time, in the treatment where *Macoma* was offered as a single prey, only 56–71% ( $65 \pm 3\%$ ) of clams had been drilled by the end of the exposure period.



**Fig. 5.** Average feeding rates of *Amauropsis islandica* in the caging experiment in the treatments where *Hydrobia ulvae* (HP) or *Macoma balthica* (MP) were offered alone, or together (HMP). Error bars are  $\pm 1$  SE.

## DISCUSSION

Our results confirm that juvenile naticids can feed on prey uncommon for adults. Under natural conditions *Amauropsis islandica* moonsnails were able to prey upon *Hydrobia ulvae* mudsnails, although they mostly consumed their usual prey – *Macoma balthica* clams. The size distribution of shells suggested that *Hydrobia* were consumed by smaller moonsnails, and the caging experiment confirmed that the juvenile moonsnails were able to feed on the mudsnails.



The juveniles of predatory gastropods can sometimes consume different items compared with adults. For example, young muricids can attack spirorbid polychaetes (Palmer, 1988), some naticids can prey upon gastropods (Berry, 1982), while the juveniles of other moonsnails are able to perforate the tests of Foraminifera (Saidova & Beklemishev, 1953). During ontogeny the diet of predators either narrows (Moura *et al.*, 2008) or, more often, broadens (for review see Wilson, 1975). In any case, smaller prey items can be displaced by larger ones as the size-selective predators grow and new types of prey become accessible (Da Rosa *et al.*, 2011). The possible reason for such displacement is an unprofitable gain/spent energy ratio. For example, the diet of the growing muricids typically changes from the less energetically favourable barnacles to bivalves (Hughes *et al.*, 1992). Similar size-related diet shifts happen in other consumers (for review see Werner & Gilliam, 1984).

*Amauropsis islandica* is a size-selective predator like other naticids (Edwards & Huebner, 1977). When *Macoma* is scarce, *Amauropsis* can benefit from the ability to feed on abundant, but apparently less desirable, *Hydrobia* snails. Prey switching during ontogeny has been reported recently (Clements & Rawlings, 2014) for another naticid species, *Lunatia heros* (Say, 1822). The ability to diversify food sources is also important for other size-selective predators, especially when primary prey supply is unstable.

The conclusion about the non-random diet of *Amauropsis* juveniles was based on the proportion of drilled to intact prey shells – a common tool used to describe naticid feeding (Vignali & Galleni, 1986; Artemieva *et al.*, 2004). However, the method may give biased estimates because of the different dissolution rates of damaged and intact shells, or because of the species-specific rate of shell fragmentation, dissolution and removal by waves. The former was unlikely to affect the results, because there is evidence that disintegration rates of perforated and intact shells are similar (e.g. Dudley & Vermeij, 1978). Even if the damaged shells dissolved faster, we could only have underestimated the importance of *Hydrobia*. The latter source of bias could hardly alter the proportion of perforated shells among empty shells and thus was unlikely to affect the conclusions.

Unfortunately, we could not adequately assess the prey selection by *Amauropsis* juveniles, because of the high consumption of *Macoma* in the mixed-prey treatment. We believe that it indicated the ‘floor effect’ – the situation when almost all measurements come from the lower end of the range (Ruxton & Colegrave, 2006). The potential level of *Macoma* consumption may be underestimated, because too few clams were offered initially. In contrast, no ‘floor effect’ was observed for *Hydrobia*. The consumption of *Hydrobia* could even be overestimated. The density of live *Macoma* in the mixed-prey treatment dropped by the end of experiment, so the starving moonsnails, who failed to find the clam, could become more inclined to feed on the second-best prey.

Although *Amauropsis* juveniles are able to consume *H. ulvae*, small *Macoma* remains the preferred prey of young and adult predators. It is possible that the density of the adult moonsnails may be indirectly regulated by predation of juveniles on *Macoma*, as predicted for other predator-prey systems (Osman & Whitlatch, 2004; De Roos *et al.*, 2008). On the other hand, the ability to feed on *Hydrobia* can help the young predators to survive the periods of primary prey shortage, until new clams migrate from the other biotopes

(Hiddink, 2003) or other usual prey species become accessible for growing predators.

We have shown that *Amauropsis* juveniles can consume different prey than adults. Other naticids may also be able to switch diet in a similar fashion. At least one of the other four White Sea naticids (Golikov, 1987) – *Cryptonatica affinis* (Gmelin, 1791) – also occurs in the intertidal, where it feeds on mussels *Mytilus edulis* (Alyakrinskaya, 2002). It is possible that the juvenile *Cryptonatica* also may broaden their diet and include other small prey when the mussels of appropriate size are scarce. The similar ontogenetic diet shift may be predicted for any other size-selective generalist predator in the habitat where very few prey species are available or abundant.

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