Discriminating Eaters: Sea Stars Asterias rubens L. Feed Preferably on Mytilus trossulus Gould in Mixed Stocks of Mytilus trossulus and Mytilus edulis L.

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Abstract. Sea stars *Asterias rubens* are important natural enemies of the blue mussel *Mytilus* in the North Atlantic. We asked whether these predators distinguish between the cryptic species *M. edulis* and *M. trossulus* that occur sympatrically in the White Sea. In mixed experimental stocks, the odds of being eaten by sea stars were about four times greater for *M. trossulus*. We also showed that *A. rubens* preferred smaller mussels to larger ones, irrespective of their species affinity. Our findings support earlier indirect observations showing that sea stars recognize *M. trossulus* as a more preferable prey than *M. edulis*. Dramatic differences in the vulnerability to sea star predation may explain the segregation of habitats between the two mussel species in contact zones; *M. tross*

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Abbreviations: a, distance from the umbo to the anterior boundary of the prismatic layer under the ligament nympha; l, distance from the umbo to the posterior boundary of the ligament; L, shell length; PMTL, probability of a mussel being *Mytilus trossulus*-like; PSU, practical salinity unit.

Online enhancement: supplementary appendix.

sulus usually tends to occupy habitats where the sea star predators are scarce.

Introduction

Blue mussels (*Mytilus* spp.), well-known ecosystem engineers, are an important component of coastal communities (Seed and Suchanek, 1992; Buschbaum *et al.*, 2009). The structure and dynamics of their populations are, in many respects, a function of biological interactions between mussels and coexisting organisms (Tsuchiya and Nishihira, 1985, 1986; Dittmann, 1990; Khaitov, 2013). A powerful biological factor affecting the structure of the mussel community is the impact of organisms feeding on mussels, such as seabirds, crabs, dog whelks, and sea stars (Seed and Suchanek, 1992 and references therein). These predators, which regulate mussel abundance, are considered keystone species in the system (Menge *et al.*, 1994).

The struggle for survival between invertebrate predators and their prey in mussel beds is regulated by very delicate mechanisms. Invertebrate predators feeding on mussels can be attracted by their waterborne cues (Gagnon *et al.*, 2003; Lowen *et al.*, 2013; Zimmer *et al.*, 2016, 2017) or repelled by signals from their epibionts (Auker et al., 2014). Predators may also shift their efforts from mussels overgrown by epibionts to clean ones, based on tactile sensations (Auker et al., 2014), or from large (and thus more energetically valuable) mussels to smaller ones, because attack on the latter incurs a lower risk of damage to the predator by the valves of the resisting mollusc (Hummel et al., 2011). On the other hand, mussels under pressure from predation exhibit defense reactions reflected in morphological, physiological, and ethological changes, such as an increased mass of the adductor muscles, thicker shells, strengthened byssus attachments, consolidation in aggregations, and even immobilization of predators by byssus (Davenport et al., 1996; Reimer and Tedengren, 1997; Leonard et al., 1999). These mechanisms are likely to depend on the genetic constitution of interacting species as well as on phenotypic responses (Hersch-Green et al., 2011). This implies, among other things, that studies of musselpredator interactions may be significantly complicated by the cryptic taxonomic diversity of Mytilus.

The M. edulis species complex in the Northern Hemisphere consists of three closely related species: M. edulis Linnaeus, 1758, M. galloprovincialis Lamarck, 1819, and M. trossulus Gould, 1850 (Koehn, 1991; Seed, 1992). These species coexist and interbreed in many areas. For instance, M. edulis and M. trossulus occur along both coasts of the North Atlantic (Riginos and Cunningham, 2005; Väinölä and Strelkov, 2011; Katolikova et al., 2016 and references therein). For decades, comparative ecological studies of sympatric mussels were complicated by a virtual absence of credible, distinctive morphological characters. They had to be routinely identified based on molecular genetic methods (McDonald et al., 1991; Riginos and Cunningham, 2005), which are expensive and time-consuming. In particular, these methodological problems stood in the way of answering an important question: Should studies of mussel interaction with predators take into account the cryptic taxonomic diversity of these molluscs?

The first hint about the importance of the taxonomic diversity of mussels in prey-predator interactions emerged in pioneer experiments with *M. trossulus* from the Baltic Sea acclimated in the North Sea and with *M. edulis* from the North Sea (Kautsky *et al.*, 1990). *Asterias rubens* sea stars that were offered a mixture of Baltic and North Sea mussels preferably attacked *M. trossulus* (Kautsky *et al.*, 1990). The sea stars needed a much shorter handling time to open the shells of the Baltic mussels than the shells of their North Sea counterparts (Norberg and Tedengren, 1995).

Similar interactions were recorded in experiments with *A. rubens* and mussels from eastern Canada (Lowen *et al.*, 2013). In that study, *M. edulis* and *M. trossulus* from local populations were kept in two-chamber cages that were inaccessible to the sea stars. Each chamber contained mussels of one species. The sea stars exhibited an attack stance in response to the chamber with *M. trossulus* more frequently than to the chamber with *M. edulis*. In their turn, the mussels under attack

showed decreased shell growth, increased growth of adductor muscle, and increased attachment strength. Defense reactions were generally weaker in *M. trossulus* than in *M. edulis* (Lowen *et al.*, 2013). Similar species-specific differences in predatorinduced plasticity were also reported for the Baltic and North Sea mussels (Reimer and Harms-Ringdahl, 2001).

In the experiments of Lowen et al. (2013), M. trossulus and M. edulis were taken from local populations, and it was clear there were no serious doubts that differences in the defense reactions were species-specific. However, in the transplantation experiments (Kautsky et al., 1990; Norberg and Tedengren, 1995; Reimer and Harms-Ringdahl, 2001) mussels were taken from different geographical populations. Even though acclimated to the North Sea, the Baltic M. trossulus mussels might have had thinner shells and other maladaptive features because they had spent their early life in the brackish-water, predator-free environment. This means that one cannot distinguish with certainty the effect of species (*i.e.*, evolutionary) divergence and that of phenotypic plasticity to the local environment. In addition, in Lowen et al. (2013) the sea stars were not allowed to attack the mussels. Equal amounts of sizestandardized M. edulis and M. trossulus were offered to the sea stars in all previous studies (Kautsky et al., 1990; Norberg and Tedengren, 1995). However, A. rubens, as a generalist predator (Anger et al., 1977), is unlikely to make an unequivocal choice between M. trossulus and M. edulis in natural communities. We may expect some difference only in the probability of attacks on the two mussel species. Finally, sea stars are known to have a preference for smaller mussels (Hummel et al., 2011), and sympatric populations of cryptic mussel species may be quite different in size structure (Elliott et al., 2008; Katolikova et al., 2016). Therefore, ideally, predator choice analysis should include the factor of mussel size.

In our study of the interactions between A. rubens and the two mussel species in the White Sea, we designed the experiments with the aim of assessing mussel-predator interactions more directly. The Kandalaksha Bay in the White Sea, where our study was conducted, is a mussel-rich area, with mussel biomass in the beds approaching dozens of kilograms per square meter (Lukanin, 1985). In contrast to most other boreal seas, there are no intertidal crabs and no dog whelks in the White Sea (Derjugin, 1928). The only invertebrate predator of mussels is the sea star A. rubens, which consumes, by some estimates, 30%-40% of adult mussels in the populations annually (Beer, 1980). Thus, the mussel-predator system is much simpler in the White Sea than in areas where mussels encounter multiple predators and are forced to develop complex adaptations against them (cf., Freeman et al., 2009).

At the top of the Kandalaksha Bay, *M. edulis*, *M. trossulus*, and their hybrids occur sympatrically, mostly in the same habitats. The frequency of hybrids in mixed populations is about 18% (Katolikova *et al.*, 2016). *Mytilus trossulus* and *M. edulis* in the White Sea can be distinguished with a high

accuracy on the basis of a simple morphological trait, "dark strip under the ligament," which was confirmed by genotyping (Katolikova *et al.*, 2016). Eighty percent of *M. trossulus* in the White Sea possess an underdeveloped nacre with a distinct "dark strip" of a prismatic layer under the ligament nympha, whereas 97% of *M. edulis* lack this stripe. Hybrids cannot be distinguished from purebreds but usually morphologically resemble the species whose genes dominate in their genotypes (Katolikova *et al.*, 2016). The use of shell morphology for the identification of *M. edulis* and *M. trossulus* greatly facilitates the processing of large amounts of material needed for ecological investigations. It proves especially helpful in studies of *Mytilus-Asterias* interactions because sea stars usually leave behind clean mussel shells without any soft tissues for genotyping (VK and AM, pers. obs.).

The aim of our study was to find out directly whether the sea stars *A. rubens* prefer one mussel species to another when feeding on mixed stocks of *M. trossulus* and *M. edulis*, taking into account the variability of mussel size structure.

Materials and Methods

Mussels and sea stars for experiments

Mussels ranging in size from 15 to 39 mm shell length were collected from three intertidal populations situated on Oleny Island (population 1: 67.106288 N, 32.322558 E), on Ryazhkov Island (population 2: 67.006814 N, 32.578677 E), and in the Voronya Inlet (population 3: 66.928005 N, 32.491266 E) (Fig. 1). These three localities are generally characterized by regular semidiurnal tides and salinities common in the Kandalaksha Bay: 21–22 PSU (practical salinity unit) (Sukhotin and Berger, 2013; Katolikova *et al.*, 2016). At low tide, population 1 experiences a minor freshening from the Niva River (VK, pers. obs.). The three populations have been recently studied genetically (Katolikova *et al.*, 2016). *Mytilus trossulus* Gould, 1850 dominated the Oleny Island samples, while *M*.

edulis Linnaeus, 1759 dominated in the Voronya Inlet and Rhyazhkov Island samples (Katolikova *et al.*, 2016). Therefore, we used population 1 as a source of *M. trossulus* and population 2 (in 2015) and population 3 (in 2016) as sources of *M. edulis*.

Mussels collected from each population were kept separately in fishing net cages attached to a floating mooring for one week prior to the experiments, which were conducted at the Biological Station of the Kandalaksha State Nature Reserve on Ryazhkov Island (67.007874 N, 32.574808 E, Fig. 1; environmental conditions as in sampling localities). Sea stars *Asterias rubens* Linnaeus, 1758 of medium size (radius: 40–110 mm) were collected by snorkeling, from a depth of 0–2 m near the Biological Station. They were starved for 2–5 days before the experiments because waterborne signals from previously consumed prey might have affected the behavior of mussels (see Griffiths and Richardson, 2006).

Experimental design

Experiments were conducted in August 2015 and 2016 (Table 1) on an intertidal sand flat at the Biological Station. Plastic containers (length: 38 cm, width: 20 cm, height: 14 cm) were buried in sediment along the shoreline to a depth of three-quarters of their height at a distance of about 1 m from each other. The top of each container was covered with a plastic net (mesh size: 1 mm) to allow free water exchange while preventing the animals from escaping. The tops of the containers were exposed to air for about 1.5–2 h at every low tide, and containers were always filled with water. The air temperature during the experiments ranged from 11.5 °C to 17.8 °C (in 2015) and from 6.7 °C to 17.9 °C (in 2016).

We conducted five experiments with equivalent designs, differing by the number of containers used, the number of mussels per container, and duration (see Table 1 for details). Half of the mussels (selected randomly) placed in each container were from population 1; the other half came from population 2 (in



Figure 1. Map of (a) the White Sea and (b) top of the Kandalaksha Bay. Numbered circles indicate mussel populations sampled; the star indicates the place where experiments were conducted.

Table 1	
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Summary of experiments

	2015			2016	
Experiment ID	Exp1	Exp2	Exp3	Exp4	Exp5
No. of containers for modeling data set	5	7	8	10	10
No. of containers for testing data set	4	1	1	2	2
No. of mussels per container	70	24	24	30	30
Mussel size range (mm)	15-39	14–38	15-37	17-30	20-31
No. of sea stars per container	2	2	2	2	2
Duration of experiment (days)	4	4	4	2	2

Shown are year of experiment, number of containers in modeling and testing data sets, mussel abundance per container and size range, sea star abundance, and experiment duration. Exp, experiment.

2015) or population 3 (in 2016). At the start of each experiment mussels were put into the containers and left for 24 hours to allow them to attach by byssus. After that, unattached mussels were removed (3% of all experimental mussels), and two randomly selected sea stars were placed into each container. The density of the sea stars in the containers was close to the maximal density observed at the experimental site (27 individuals per square meter, VK and AM, unpubl. data). We examined the containers for the presence of empty mussel shells at each low tide (i.e., twice per day). The empty shells found were carefully removed. After the end of the experiment, all surviving mussels were opened, and their soft tissues were removed. All the sea stars were weighed. The mussel shells were individually marked and used for morphological analysis (see Mussel morphometry, below). In 2016 the experiments were shortened to two days because in 2015 we observed that the sea stars had largely ceased eating mussels by this time.

Mussel morphometry

Three morphological parameters (Fig. 2) were measured on the right valve of the shell of each mussel, using electronic callipers or a microscope eyepiece micrometer, to the nearest 0.1 mm: the shell length (*L*), the distance from the umbo to the posterior boundary of the ligament (*l*), and the distance from the umbo to the anterior boundary of the prismatic layer under the ligament nympha (*a*). The degree of expression of the morphological trait "dark strip under the ligament" (Katolikova *et al.*, 2016) was assessed for each individual by calculating the *Z*-index (Z = a/l). The quantitative interpretation of *Z* was used in further statistical analysis, along with the qualitative interpretation. Following Katolikova *et al.* (2016) we divided all mussels into two morphotypes. Mussels with Z = 0 (*i.e.*, with an unbroken "dark strip") were classified as the T-morphotype (characteristic of 80% of *M. trossulus*), whereas other specimens (Z > 0) were classified as the Emorphotype (characteristic of 97% of *M. edulis*) (Katolikova *et al.*, 2016).

Validation of the Z-index as a taxonomic marker

The Z-index was validated as a taxonomic marker based on two types of genetic data. Katolikova et al. (2016) analyzed the distribution of the Z-index and the frequencies of the T- and E-morphotypes among three genotypic groups of mussels (M. edulis, M. trossulus, and their hybrids) and showed a high correlation between the Z-index and the genetic status of the mussel. In this study we confirmed the power of morphological identification of species-specific genotypes using an independent data set, a sample of mussels from a mixed population in the Chupa Inlet (66.270043 N, 33.070512 E; material was sampled in 2015) genotyped by the polymerase chain reaction (PCR)-based nuclear marker ME15/16 (Inoue et al., 1995). This locus, considered to be diagnostic for the blue mussel species, is widely used for its identification in ecological surveys (e.g., Elliott et al., 2008; Brooks and Farmen, 2013).

We also re-analyzed the data set from Katolikova *et al.* (2016): 1048 mussels with known multilocus allozyme genotypes and Z-indexes. Instead of considering three genetic groups—*M. edulis, M. trossulus,* and hybrids (which morphologically and ecologically resemble the species whose genes dominate their genotypes; Katolikova *et al.*, 2016)—we classified the mussels into two groups: mussels with genotypes dominated by *M. trossulus* genes (hereafter *M. trossulus*-like mussels) and mussels with genotypes dominated by *M. edulis* genes (hereafter *M. edulis*-like mussels).

Based on these data, we developed a logistic regression model predicting the probability of a mussel being *M. trossulus*-like (PMTL) as a function of the *Z*-index. This function was used to calculate PMTL values for the mussels from the experiments.

Statistical analysis of experimental data

All the containers pooled from 2015 and 2016 (n = 50) were randomly divided into two groups. The first group (modeling data set, 40 containers, Table 1) was used for regression modeling. The second group (testing data set, 10 containers, Table 1) was used for checking the quality of the model's prediction. Using the functions of the statistical programming language R (R Core Team, 2016), we applied the following statistical treatments to the first group.

We calculated the proportion of the T-morphotype among mussels placed in each container and analyzed the frequency distribution of this value. This proportion was analyzed in the same way for the eaten mussels and the survived mussels separately. The distribution of these values was visualized by



Figure 2. Morphological features of experimental mussels. (a) Morphological traits used for assessment of mussel size (length, *L*) and calculation of the *Z*-index, where *a* is the distance from the umbo to the anterior boundary of the prismatic layer under the ligament nympha and *l* is the distance from the umbo to the posterior boundary of the ligament. The *Z*-index is calculated as *a*/*l*. (Inset) Scanning electron microscopic picture showing the boundary between the nacreous layer and the prismatic layer, structurally reflected as a seam. (b) Frequency distribution of the *Z*-index for all experimental mussels. Black bars indicate eaten mussels; gray bars indicate survived mussels. (c–e) Box-whisker plots reflecting frequency distributions of the proportion of T-morphotypes across containers in different experiments. (c) Mussels initially placed into containers; (d) survived mussels; (e) eaten mussels. The horizontal lines in plots reflect medians; the boxes indicate the upper and lower quartiles; the whiskers reflect 1.5 times the interquartile range; points out of whisker fences are outliers.

means of box-whisker plots, using the functions from the ggplot2 package (Wickham, 2009).

The logistic mixed-effect model (Zuur *et al.*, 2009) was constructed to predict the probability of a mussel being eaten as a function of a number of predictors. The dependent variable was coded as 1 for eaten mussels and 0 for survived mussels. We considered Z-index, *L*, year of experiment, and all interactions between these factors as predictors in the fixed part of the full model. The full model also included three covariates: the initial number of mussels in the container, the proportion of T-morphotypes, and the total weight of sea stars in a container. "Experiment" and "Container" nested into "Experiment" were considered random factors in the model, which was constructed as a random-intercept model. The model parameters were assessed with the glmer() function from the package "lme4" (Bates *et al.*, 2015). After the en-

tire model was constructed, it was simplified using the backward selection protocol (Zuur *et al.*, 2009) with the function drop1() from the package "stats" (R Core Team, 2016). The validity of the final model was visually checked by analysis of residual plots. No evidence of overdispersion was found in the model.

The goodness of fit for the final model was assessed by means of marginal and conditional pseudo- R^2 (Nakagawa and Schielzeth, 2013), using the function r.squaredGLMM() from the package "MuMIn" (Bartoń, 2017). The marginal pseudo- R^2 describes the goodness of fit when only fixed factors are taken into account, whereas the conditional pseudo- R^2 assesses the goodness of fit when both fixed and random factors are considered.

Coefficients from the fixed part of the final model were used to predict the probability of being eaten for mussels from the testing data set. We calculated the probability predicted by the model for actually eaten mussels and for survived mussels. The frequency distribution of the predicted probabilities was visualized by box-whisker plots, using the functions from the ggplot2 package (Wickham, 2009).

Finally, we constructed a regression model, the structure of which was analogous to that of the final model described above but which included as a predictor the values of PMTL instead of the Z-index. This model was intended to predict the probability of mussels being eaten as a function of their PMTL. We developed this model to assess directly the differences in the ratio of the odds of being eaten for *M. trossulus*-like and *M. edulis*-like mussels.

Results

The frequency distribution of the Z-index for mussels used in the experiments was bimodal (Fig. 2b). The first peak was associated with Z = 0 and the second with Z = 1. The mussels with 0 < Z < 0.4 were extremely rare. Thus, two distinct morphotypes, the T-morphotype (Z = 0) and the Emorphotype (Z > 0) (Katolikova *et al.*, 2016), could be easily recognized among the experimental mussels (Fig. 2b). However, analysis of the genetic data showed a high probability of identifying as M. trossulus a mussel with a Z-index in the range of 0 < Z < 0.6. Hence, from the statistical point of view, the continuous expression of a morphological trait allows a better discrimination of M. edulis- and M. trossulus-like mussels than the discrete (E-morphotype vs. T-morphotype) expression (see appendix, available online). Based on this result, we assumed that a discrete classification of mussels into two morphotypes had to be supported by an assessment in terms of a continuous Z-index.

In total, the sea stars consumed 312 mussels out of 1755. The proportion of eaten mussels varied across individual containers (0%-42%) and experiments (12%-29%). The range and the median values of the proportion of T-morphotypes among mussels initially placed into boxes, among survived mussels, and among eaten ones were 23%-58% and 40%, 17%–64% and 36%, and 14%–100% and 67%, respectively. In all five experiments, the mean proportion of T-morphotypes among eaten mussels was higher than among survived mussels (Fig. 2). The full logistic regression model describing the probability of being eaten as a function of all predictors included (Akaike information criterion [AIC] = 1152) was significantly improved by backward selection. This procedure allowed us to delete the interaction terms as well as year, number of initially placed mussels, initial proportion of T-morphotypes, and total weight of sea stars. Thus, the final model (AIC = 1144.8) included only two main terms in the fixed part: Z-index and L. The removal of year from the model meant that the model parameters were independent of the year or, in other words, that the results were reproducible. The removal of the initial proportion of T-morphotypes meant that the probability of being

Table 2

Parameters of the model describing the probability of being eaten as a function of the Z-index (Z) and mussel shell length (L)

Estimate	SE	Z-value	P-value
-1.267	0.1725	-7.343	< 0.0001
-0.1089 1.813	0.0180 0.4639	-6.044 3.909	<0.0001 <0.0001
	Estimate -1.267 -0.1089 1.813	Estimate SE -1.267 0.1725 -0.1089 0.0180 1.813 0.4639	Estimate SE Z-value -1.267 0.1725 -7.343 -0.1089 0.0180 -6.044 1.813 0.4639 3.909

Shown are parameters from the fixed part of the model. All estimations of the parameters are given in logit scale. SE, standard error.

eaten did not significantly depend on the proportion of morphotypes in the range investigated (23%-58%). The removal of all interaction terms meant that the Z-index and L were independent parameters influencing predator choice.

The parameters of the final model are presented in Table 2. The goodness of fit in terms of the marginal pseudo- R^2 (*i.e.*, fixed factors only) and the conditional pseudo- R^2 (*i.e.*, both fixed and random effects included) was near 0.14 and 0.16, respectively. Therefore, the variation associated with random factors (conditions of particular experiments or experimental containers) did not considerably influence predator choice. To visualize the fitted model, we constructed Figure 3, where the abscissa reflects the Z-index of a mussel, and the ordinate reflects its probability of being eaten. Since the model includes shell size as the second predictor, we provided three logistic curves, constructed for middle-sized, small, and large mussels (shell length equal to first and third quartiles of size distribution). A clear pattern could be seen: mussels with a lower Z-index value and smaller mussels had a higher probability of being eaten (also note negative slopes in Table 2). We applied the final model to mussels from the testing data set to predict the probability of their being eaten. Z-index values and measures of L of individual mussels were used as predictors in the calculation. The frequency distribution of the calculated values (Fig. 4) showed a clear divergence between eaten mussels and survived mussels. The probabilities predicted for the former were, on average, greater (median value: (0.26) than those predicted for the latter (median value: (0.15)). Thus, the model tested on the data set not included in the regression analysis revealed an expected difference in the probability of being eaten between consumed mussels and surviving mussels. Analogously, the data from the testing data set followed the pattern predicted by the linear model (Fig. 3, open dots). This indicated that the parameters of the final regression model reflected realistic values.

Since we assessed the slope for the Z-index as -1.27 (Table 2), we could state that when the Z-index increased from 0 (T-morphotype) to 1 (E-morphotype), the ratio of the odds of being eaten changed by a factor of 0.28 ($e^{-1.27}$). Therefore, it was 3.6 (0.27^{-1}) times higher for mussels with Z = 0 than for mussels with Z = 1.



Figure 3. Probability of being eaten as a function of mussel *Z*-index and size (visualization of the final model). The abscissa reflects the *Z*-index of a mussel, while the ordinate is its probability of being eaten. Logistic curves represent the predictions of being eaten for mussels of a median shell size (thick line, marked M), small mussels with a shell size equal to the first quartile of the size distribution (thin line, S), and large mussels with a shell size equal to the third quartile of the size distribution (thin line, L). The dots represent the proportion of eaten mussels in groups of individuals with different *Z*-indexes (filled dots indicate the modeling data set; open dots indicate the testing data set). For this, experimental mussels from each set were ordered by the range of their *Z*-indexes, and the range was split into 10 groups of equal size; the proportion of eaten mussels and the mean *Z*-index were estimated for each group.

The independent genetic data sets analyzed contained statistical associations between the Z-index and the mussel genotype at the ME15/16 locus and at allozyme loci (see appendix, available online). Mussels with an allele characteristic of *M. edulis* at ME15/16 mostly had high Z-values, while mussels with an allele characteristic of *M. trossulus* had low values. Similarly, *M. edulis*-like mussels identified by allozymes mostly had a Z-value close to 1, while *M. trossulus*-like mussels had a value close to 0. In total, 96% of *M. edulis*-like mussels had E-morphotypes (*i.e.*, Z > 0), while 74% of *M. trossulus*-like mussels had T-morphotypes (Z = 0). The dependence of PMTL on the Z-index is described by the formula

$$PMTL = \frac{e^{1.67 - 5.54Z}}{1 + e^{1.67 - 5.54Z}}$$

where e is the base of the natural logarithm and Z is the Z-index. (See appendix, available online for more details.)

Using this formula, we recalculated the Z-index of each mussel from the experiments into PMTL. To assess the association between the probability of a mussel being eaten and its PMTL, we constructed a random intercept mixed-effect regression model. The probability of being eaten was a dependent variable, while PMTL and mussel length (L) were predictors (Experiment and Container nested into Experiment were random factors). The parameters of the model estimated (Table 3) revealed a positive slope for PMTL as a predictor. It

meant that the ratio of the odds of being attacked by sea stars for *M. trossulus*-like mussels (PMTL close to 1) was $e^{1.4} = 4.1$ times higher than for *M. edulis*-like mussels (PMTL close to 0).

Discussion

In this study we provide the first direct evidence that *Asterias rubens* can discriminate between sympatric *Mytilus* species in the White Sea. While many researchers have tried to determine whether *M. edulis* or *M. trossulus* is more susceptible to predation by *A. rubens* (Lowen *et al.*, 2013, see also below), to our knowledge no experiments involving sea stars feeding on mussels from sympatric populations have been performed before. In part, this was due to the fact that cryptic *Mytilus* species are difficult to identify without genotyping.

In our comparative study, we identified cryptic taxa by a morphological rather than a genetic criterion. To be entirely confident about identification, we additionally tested and found a good congruence between the trait under consideration (expressed as the Z-index) and the "taxonomic" molecular marker ME15/16. Using a more reliable multilocus data set from Katolikova *et al.* (2016), we also estimated the efficiency of the identification of *M. edulis*- and *M. trossulus*-like mussels by the Z-index. In terms of the qualitative Z-index (broken *vs.* unbroken dark strip under the ligament), as much as 96% of *M. edulis*-like mussels had E-morphotypes, while 74% of *M. trossulus*-like mussels had T-morphotypes. The precision was even better in terms of the quantitative Z-index (see appendix, available online).



Figure 4. Box-whisker plot reflecting the distribution of probabilities of being eaten for mussels from the testing data set. Notches (triangular notches in the box plots) that do not overlap indicate significantly different medians.

Parameters of the model describing the probability of being eaten as a function of the probability of being identified as Mytilus trossulus-like mussel (PMTL) and shell length (L)

	Estimate	SE	Z-value	P-value
PMTL	1.3963	0.1939	7.201	< 0.0001
L	-0.1089	0.0180	-6.044	< 0.0001
(Intercept)	0.6208	0.4591	1.352	0.176

Shown are parameters from the fixed part of the model. All estimations of the parameters are given in logit scale. SE, standard error.

A limitation of the morphological method is that hybrids could not be distinguished. They were categorized together with purebreds of the species whose genes dominated in their genotypes. We think, however, that this did not significantly affect our comparisons for the following reasons. (1) Earlygeneration hybrids were not numerous in the populations sampled (about 20%, Katolikova *et al.*, 2016). (2) It is assumed that hybrids do not demonstrate transgressive (*i.e.*, unique) ecological phenotypes but resemble the species whose genes dominate in their genotypes (Katolikova *et al.*, 2016).

According to our results, in mixed stocks of M. edulis and M. trossulus the odds of being eaten by A. rubens were about four times higher for *M. trossulus*-like mussels than for *M.* edulis-like mussels. The predator choice did not depend on the proportion of species in the mixed stock. However, we can state this only for the range studied (23%-58% of Tmorphotypes, i.e., about 19%-47% of M. trossulus-like mussels), while in nature the proportion of *M. trossulus*-like mussels varies in broader limits. We also found that predator choice depended on prey size. The sea stars more readily consumed smaller mussels, irrespective of their species affinity. In the range of mussel sizes studied (length: 15-39 mm), the odds of being eaten were approximately nine times higher for the smallest mussels than for the largest ones (taking the Z-index as the mean, see coefficients in Table 2). Bearing in mind that M. trossulus is, on average, smaller than M. edulis in the White Sea (20% in shell length, Katolikova et al., 2016), we may expect the predation pressure on this species in mixed populations to be even more than four times greater than on M. edulis.

As shown in comparative studies of *M. edulis* and *M. trossulus* from other geographic contact zones, *M. trossulus* has thinner and more flexible shells (which are easier for the predator to open) (Kautsky *et al.*, 1990; Mallet and Carver, 1995; Beaumont *et al.*, 2008; Penney *et al.*, 2008) and is less inclined to form aggregations (while consolidation into tight clumps complicates predation) (Liu *et al.*, 2011). In addition, plastic defense reactions in the presence of sea stars, such as an increase in the growth of the adductor muscle and the strength of attachment, are weaker in *M. trossulus* (Lowen

et al., 2013). To note, an underdevelopment of the nacreous layer under the ligament observed in most M. trossulus individuals in the White Sea (the character used for species identification in our study) can in itself indicate the fragility of their shells, because the nacreous shell layer is mechanically the strongest one (Currey and Taylor, 1974). Moreover, as shown in the elegant experiments of Lowen et al. (2013), sea stars identify *M. trossulus* as a more desirable prey by its smell (waterborne chemical cues). These observations indicate that M. trossulus is generally less well defended against sea stars and so, apparently, is more attractive to these predators than is M. edulis. It is not clear whether the "attractiveness" of *M. trossulus* to sea stars is associated with its higher energetic quality. While Penney et al. (2008) demonstrated that *M. trossulus* typically has a lower flesh weight than *M*. edulis of the same size at Newfoundland aquaculture sites, Beaumont et al. (2008) found no clear differences between species at Scottish aquaculture sites. At present there are no clear data on energetic content to consider M. trossulus as a more energetically valuable prey species. Unfortunately, no comparative studies on these two species have been conducted in the White Sea.

The preference for smaller mussels shown by the sea stars in our experiments may be explained in two ways. (1) We used relatively small sea stars in our experiments. *Asterias* stars may be twice as large in the White Sea (VK, pers. obs.). Smaller sea stars are known to choose smaller mussels (Gooding and Harley, 2015). (2) Sea stars indeed prefer to consume smaller mussels, because an attack on smaller prey entails a lesser risk of damage to their soft stomach (Hummel *et al.*, 2011).

While in previous investigations the importance of taxonomical differences between coexisting mussel species was only outlined, our observation that *M. trossulus*-like mussels are selectively preyed upon in mixed stocks of *M. trossulus* and *M. edulis* in the White Sea is in accord with the results of earlier experiments with Baltic and North Sea mussels. In those experiments, sea stars preferably attacked Baltic *M. trossulus* and opened their shells more quickly than those of North Sea *M. edulis* (Kautsky *et al.*, 1990; Reimer and Harms-Ringdahl, 2001). Our observation also agrees with one made in eastern Canada that *A. rubens* is more attracted by waterborne cues from *M. trossulus* than from *M. edulis* (Lowen *et al.*, 2013).

To note, the history of coexistence (and thus of coevolution) of Asterias and the two mussel species seems to have been quite different in the White Sea, the western Atlantic, and the Baltic Sea. In the western Atlantic, *M. edulis* and *M. trossulus* have probably coexisted with each other and with sea stars for millennia (Rawson and Harper, 2009). The history of mussel populations in the White Sea is not well known, but the present consensus is that *M. edulis* is a native species, while *M. trossulus* was introduced by marine traffic during the middle of the twentieth century (Väinölä and Strelkov, 2011), that is, a few dozen *A. rubens* and *Mytilus* generations ago. In the Baltic Sea, the distribution areas of *M. trossulus* and *A. rubens* have minimal overlap because of their strikingly different salinity preferences (Casties *et al.*, 2015, see also below; Stuckas *et al.*, 2017). In transplantation experiments (Kautsky *et al.*, 1990; Reimer and Harms-Ringdahl, 2001), *M. trossulus* was a completely unfamiliar prey for *A. rubens* because the sea stars were taken from the *M. trossulus*-free North Sea. Nevertheless, in all experiments *M. trossulus* was a universally preferable prey.

The consistency of results across different studies indicates that the differences in the vulnerability of *M. edulis* and *M. trossulus* to predation by *A. rubens* are species-specific traits rather than traits associated with particular geographic regions or populations. Taking into account the global importance of sea stars as mussel predators (Nauen, 1978; Beer, 1980; Seed and Suchanek, 1992), we could expect that their selective predation would affect the demography and habitat distribution of *M. edulis* and *M. trossulus* in different contact zones.

Studies of M. edulis and M. trossulus in different contact zones have invariably depicted their habitat segregation at a local and/or regional scale. In the Baltic Sea, M. edulis dominates in areas with high salinity, while M. trossulus keeps to areas with low salinity (Riginos and Cunningham, 2005; Stuckas et al., 2017). In the western Atlantic, M. trossulus tends to occupy exposed shores, while M. edulis is confined to sheltered bays (Innes and Bates, 1999). In northern Scotland, M. trossulus invades en mass artificial structures such as marina pontoons and, especially, ropes of suspended aquaculture, but the species is rare in natural intertidal habitats (Dias et al., 2009). Along the northern coasts of Scandinavia and Russia, M. trossulus is mainly found in anthropogenically polluted harbor areas, both saline and permanently freshened (Väinölä and Strelkov, 2011; Katolikova et al., 2016). In addition, in the White Sea, M. trossulus predominates on fucoid algal substrates, while M. edulis tends to live directly on the bottom (Katolikova et al., 2016).

Why these two species show such inconsistent patterns of habitat segregation in different zones is a long-standing issue (e.g., Riginos and Cunningham, 2005; Katolikova et al., 2016). What stands out, however, is that M. trossulus is always more abundant in the areas where Asterias sea stars are scarce or absent. In the Baltic Sea, these are areas with a salinity under 12 ppt (Stuckas et al., 2017), which is the lower tolerance limit of Asterias (Casties et al., 2015). In the western Atlantic, these are exposed shores, where sea stars as well as other predators are likely to be dislodged by waves (Reimer and Tedengren, 1997; Gagnon et al., 2003; St-Pierre and Gagnon, 2015). The preference of M. trossulus for polluted harbors may be due to the limited abundance of sea stars there, as the latter are more sensitive to pollution than mussels (Canty et al., 2009). Thalli of intertidal fucoids rising above the bottom at high tide and floating substrates such as ropes of suspended aquaculture may grant the mussels a refuge against crawling benthic predators (Dias *et al.*, 2009; Katolikova *et al.*, 2016).

We hypothesize that *Asterias* and probably other invertebrate predators such as intertidal crabs and dog whelks govern the habitat distribution of *M. trossulus* and *M. edulis* everywhere in their contact zones. While we know less about the relationships between sympatric mussels and predators other than sea stars, indirect evidence indicates that *M. trossulus*, with its thinner and more flexible shells, should be less resistant than *M. edulis* to the crushing claws of crabs (Lowen *et al.*, 2013), the drilling radulae of dog whelks (Sherker *et al.*, 2017), and, presumably, the powerful bills of oystercatchers (Le Rossignol *et al.*, 2011).

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