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Feeding intensity and daily mussel consumption of Rapa whelk (*Rapana venosa*) in the north-western Black Sea

by

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Abstract

Based on an experiment carried out in the north-western Black Sea (Snake Island), the feeding behavior of the Rapa whelk (*Rapana venosa* Valenciennes, 1846) was analyzed in relation to its size (N = 58; shell height: 30–90 mm). Mediterranean mussels (*Mytilus galloprovincialis* Lamarck, 1819) were placed in experimental cages with *R. venosa* to be used as food. It was found that the size of the prey was determined by the size of the predator. The mussels with a shell length of 20–40 mm were most affected by *R. venosa*. It was determined that the predator's contribution to the deposition of mussel shells in the bottom sediments is also associated with its size. Feeding intensity varies from 41 mg to 99 mg of the total mass of mussels per 1 g of the total mass of *R. venosa* per day, depending on the size of the predator. The daily consumption of mussel soft tissue varied from 0.189 g ind.$^{-1}$ per day^{-1} in small *R. venosa* specimens to 0.917 g ind.$^{-1}$ per day^{-1} in large predators. Regression equations were obtained between the length and mass of the mussels consumed (total mass, soft tissue mass and shell mass) and the shell height of the predator.

Key words: daily consumption, nutrition, invasive species, *Rapana venosa*, *Mytilus galloprovincialis*, Black Sea

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1. Introduction

One of the mass species of bivalve molluscs of the Black Sea is the Mediterranean mussel *Mytilus galloprovincialis* (Lamarck, 1819). Mass settlements of the species have a noticeable effect on the composition and structure of the benthic communities (Topaloglu & Kihara 1993; Çinar & Gonlugur-Demirci 2005; Çinar et al. 2008; Bondarev 2013; Revkov & Boltachova 2021). They serve as an additional substrate for fouling organisms and shelter for fish and other aquatic species (Gutiérrez et al. 2003; Varigin 2018). However, in recent decades, there has been a decreasing trend in the abundance of this mollusc and a significant reduction in the biomass of the extensive mussel assemblages that were previously located at depths of more than 10 m, ensuring the proper quality of the coastal waters (Zaika et al. 1990; Vorobyova et al. 2017; Snigirov et al. 2019). The degradation of mussel settlements is a result of the influence of a number of unfavorable factors (Shurova 1995, 2000, 2005; Shurova & Stadnichenko 2008; Kovaleva 2012; Bondarev 2013), the most significant of which are eutrophication of the marine environment, causing extensive kills of the benthic fauna; intensive fishing with bottom trawls, leading to the destruction of the bottom community; and active eating of mussels by the predatory, invasive Rapa whelk (Marinov 1990; Zaitsev & Mamaev 1997; Todorova & Konsulova 2000; Zaitsev 2000, 2008; Shurova 2013; Snigirev et al. 2013; Govorin 2019).

The Rapa whelk (*Rapana venosa* Vallenciennes, 1846) (Gastropoda: Muricidae) is an invasive species of the Black Sea malacofauna (Zolotarev 1996; Zaitsev & Öztürk 2001). Its native distribution includes the Sea of Japan, the Yellow Sea, the Bohai Sea and the East China Sea to Taiwan (Tsi et al. 1983). The first mention of the Rapa whelk in the Black Sea dates back to 1947 (Drapkin, 1953). This mollusc is the largest in the ecosystem of the Black Sea (Zaitsev & Öztürk 2001; Micu et al. 2008). Specimens of Rapa whelk up to 116.14 mm long have been found in the eastern Black Sea (Sağlam et al. 2015).

This large predatory gastropod later spread through the Marmara and Mediterranean Seas, being found in the Adriatic (Ghisotti 1974; Rinaldi 1985) and Aegean Seas (Koutsoubas & Voultsiadou-Koukoura 1991). Also, the Rapa whelk was discovered in the southern North Sea (Kerckhof et al. 2006), the Atlantic coast of Spain (Rolán et al. 2007), the Chesapeake Bay in North America (Harding & Mann 1999; Mann & Harding 2000) and in Samborombon Bay in South America (Pastorino et al. 2000).

Due to its tolerance to wide fluctuations in temperature, salinity and oxygen concentration (Chukhchin 1984; Zolotarev 1996; Harding & Mann 1999; Mann & Harding 2000, 2003), reproductive ecology with multiple egg-capsule deposition and long-term larval development (Chukhchin 1970; Chung et al. 2002; Uyan & Aral 2003, Mann et al. 2006; Saglam & Düzgüneş 2007, Saglam et al. 2009), adaptive morphological differentiation (Kos'yan 2013; Bondarev 2015 Morhun et al. 2021) and biochemical features (Alakrinskaya 1989; Ershova et al. 2018), this gastropod is a successful invader of marine coastal/brackish ecosystems (Harding et al. 2007).

The main reason for the successful invasion of the Rapa whelk in the Black Sea is the absence of natural enemies such as predatory sea stars and octopuses, which control the abundance of this snail in its native range (Chukhchin 1984; Zolotarev 1996). Also, the lack of significant competitors has a positive effect on the Rapa whelk population. Thus, the main food competitors of this snail in the Black Sea are bivalve-eating fishes, e.g. the round goby (*Neogobius melanostomus* Pallas, 1814), whose diet comprises 95% mussels (Snigirev et al. 2013, 2016; Zamorov et al. 2022).

The predator has a significant ecological impact on the populations of bivalves in the Black Sea. The Rapa whelk uses various molluscs as food: *Mytilus galloprovincialis*, *Chamelea gallina* (L., 1758), *Anadara kagoshimensis* (Bruguière, 1789), *Ruditapes philippinarum* (Adams & Reeve, 1850) and *Donacilla cornea* (Poli, 1795), *Cardium* spp., *Pecten* spp., as well as gastropods such as *Patella* spp. and *Tritia* spp. and crustaceans (Chukhchin 1984; Zolotarev 1996; Kos'yan 2013).

An additional aspect of the influence of *R. venosa* on marine ecosystems is the replenishment of the bottom sediments with mineral components contained in the shells of destroyed molluscs (Norling 2015; Kosyan et al. 2012; Kosyan 2018). After the molluscs' death, their shells become elements of thanatocenosis – subfossil groups in modern bottom and coastal deposits (Kidwell & Bosence 1991; Kidwell 2002; Lockwood & Work 2006; Tsolakos et al. 2021). Bottom thanatocenoses are constantly replenished with dead mollusc shells from their alive communities, particularly as a result of the damaging effect of predators (Alexander & Dietl 2003; Martinelli 2022). After destruction, the shells turn into separate crystals of calcium carbonate (calcites and aragonites) (Foote et al. 2015; Brom & Szopa 2016). Once decomposed, the mineral components of the shells, the remainder of the bottom or coastal sediments, become elements of other ecological systems, passing from the biosphere to the lithosphere (Behrensmeyer et al.

2000; Zolotarev & Stadnichenko 2021). However, the potential increase in the shell substance of the mussel due to the feeding activity of the Rapa whelk in the Black Sea has not been analysed.

The feeding behavior of the Rapa whelk has been analysed by many authors, in both native and invasive ranges. Previous studies have been conducted to determine the predator's food preferences among different bivalve species (Harding & Mann 1999; Savini & Occhipinti-Ambrogi 2006; Hu et al. 2016); consumption rates; frequency of food intake and gastric emptying (Savini et al. 2002; Seyhan et al. 2003); and the dynamics of predator feeding behavior, depending on the size of the prey and/or predator in laboratory conditions (Giberto 2011; Lanfranconi 2013; Saglam & Düzgünes 2014; Hu et al. 2016).

Experimental studies in the natural habitat of the north-western Black Sea revealed a dependence between the intensity of nutrition and the sex of *R. venosa* (Kurakin & Govorin 2011), and determined the morphological and phenotypic differences between the shells of mussels that were offered as feed and those consumed by the predator (Stadnichenko & Kurakin 2014). The study of the consumption rates of Rapa whelk in the natural environment showed that this predatory mollusc most actively consumes mussels 30 to 40 mm in length (40.2 ± 3.2%) (Govorin 2019). These data on the feeding behavior are typical of snails with a shell size of 64 to 84 mm. To evaluate the predatory affect on the mussel beds, it is necessary to check the daily consumption of the Rapa whelk, differentiating the individuals by size.

By destroying the food webs in the Black Sea ecosystem, the Rapa whelk significantly affects the stocks of commercially important fish species (Snigirev et al. 2013; Janssen et al. 2014; Zamorov et al. 2022). On the other hand, this invasive snail has commercial importance in the Black Sea, showing good socioeconomic status and prospects for long-term exploitation (Janssen et al. 2014). Therefore, this study aims to quantify, under controlled experimental conditions in the north-western Black Sea, the consumption rate of mussels by *R. venosa*, as well as the mass of shell material deposited in the bottom sediments, depending on the size of the predator.

2. Materials and methods

2.1. Size and mass characteristics of *Rapana venosa*

In the experiment, 58 specimens of *R. venosa* with shell heights ranging from 34.5 to 85.1 mm were used, since this size range represents a predator in the native habitat of the island. To study the dependence of the feeding behavior of a predator on its size, gastropods were divided into four groups according to the height of the shell (maximum distance from the crown to the lower border of the mouth) (Morhun et al. 2021). The size differentiation was carried out underwater in the animal's natural environment in order to avoid stressful loads on the predator, which could affect its feeding activity. Between 10 and 20 *R. venosa* specimens were placed in each cage, covering the entire size range of the predator living in the area. The characteristics of the size groups of Rapa whelk in the experimental cages are set out in Table 1. The placement of the experimental cages with Rapa whelk and mussels at a depth of 8.7 m in the coastal waters of Snake Island is shown in Figure 1.

2.2. Size and mass characteristics of the Mediterranean mussel *Mytilus galloprovincialis*

To allow free choice of prey, samples from the natural mussel settlements ranging between 2.6 and 62.8 mm in length were placed in the cages with *R. venosa* according to the maximum abundance and diversity of sizes of prey in the mussel habitat of the Snake Island near-shores. In all cages, mussels of the 20–30 mm size class and with an average total weight of 2.52 g predominated. The average length of

Table 1

Morphometric characteristics of *Rapana venosa* used in experimental cages (Snake Island, north-western Black Sea, Ukraine)

N	Size class, mm	n	Shell height (*SH*), mm		Total mass (W_R), g	
			min. – max	*SH* means ± SE	min. – max	W_R means ± SE
1	30–40	20	34.5–44.7	40.7* ± 0.56	6.17–13.69	10.19 ± 0.44
2	41–50	18	42.1–50.4	46.48 ± 0.51	14.15–25.48	18.46 ± 0.77
3	60–70	10	61.3–67.0	64.44 ± 0.64	41.93–63.20	53.13 ± 2.28
4	80–90	10	80.6–85.1	83.46 ± 0.43	100.33–136.31	118.33 ± 3.69

N – cage number; n – number of Rapa whelk in the cage (ind.); SE – standard error; * – the maximum size of the predator group of 30–40 mm was exceeded due to its growth over the course of the experiment, as size fixation was carried out at the end of the experiment.

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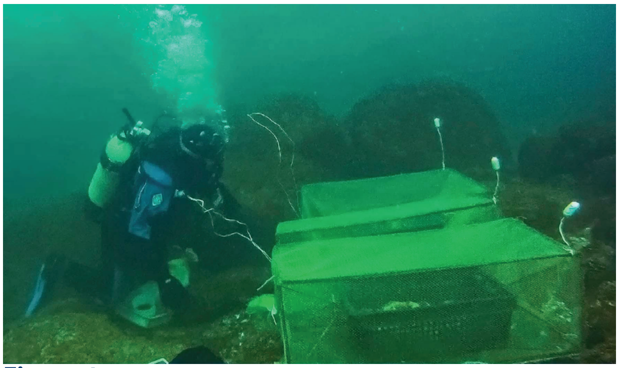

Figure 1

Placement of the experimental cages with Rapa whelks and mussels in the coastal waters of the Snake Island (photo by A.P. Kurakin)

mussels varied from 24.85 mm in Cage No. 1, with small Rapa whelks, to 28.49 mm in Cage No. 4, with large predators. The size and mass characteristics of the mussels in the experimental cages are given in Table 2. A total of 2267 mussels were used in the experiment. To determine the natural mortality of mussels in this habitat, a control cage with mussels was additionally installed.

To determine the number of *M. galloprovincialis* mussels consumed by the predator *R. venosa* in the coastal waters of Snake Island from 9 to 26 August 2012, four mesh cages measuring 100 × 50 × 30 cm were placed at a depth of 8.7 m. The experiment was prepared and carried out in the natural marine environment using diving methods. All molluscs – both prey and predators – were selected from the same native habitat where the experimental studies were subsequently carried out. The temperature (22.81 ± 0.078°C) and salinity (16.03 ± 0.26) of the seawater were uniform during the study period throughout the thickness, fluctuating over the exposure time within insignificant limits. The duration of the experiment was 17 days.

After the exposure was completed, all molluscs were removed from four cages – the live rapa whelks and the shells of the eaten mussels. The shell height (*SH*, mm) measured using a vernier caliper to within 0.1 mm, and the total mass (W_R, g) are presented in Table 1. Whelks were measured from the tip of apex to the end of the siphonal canal (Morhun et al. 2021). In live mussels, the shell length (*L*, mm), the total mass ($W_{M.gall}$, g), the soft tissue mass (*Ww*, g) and the shell mass (*Wst*, g) were measured. The molluscs were weighed using

Table 2

Morphometric characteristics of the Mediterranean mussels (*Mytilus galloprovincialis*) used in the experimental cages (Snake Island, north-western Black Sea, Ukraine)

N	n	Length (*L*), mm		Total mass (W_{mussel}), g	
		min.–max	*L* means ± SE	min.–max	W_{mussel} means ± SE
1	468	2.6–62.8	24.85 ± 0.41	0.002–22.67	2.09 ± 0.106
2	666	5.3–60.0	24.96 ± 0.33	0.017–19.85	2.07 ± 0.091
3	573	5.1–53.3	26.60 ± 0.40	0.015–14.05	2.55 ± 0.114
4	560	6.2–60.5	28.49 ± 0.49	0.026–20.34	3.378 ± 0.153

N – cage number; n – number of mussels in cage (ind.); SE – standard error

2.3. Experimental layout

For the experimental layouts we chose the coastal waters of Snake (Zmiiny) Island, located in the western Black Sea (45°15′08.2″N; 30°12′09.8″E) (Figure 2). The island coasts are characterised by rock cliffs with rocky bottom off-shores, with established mussel beds and a stable rapa whelk population. The parts of the island and its adjacent shelf (232 hectares) are a part of the National Zoological Protected Area 'Snake Island' (IBA code 088) (Snigirev et al. 2013). The study area was chosen based on the minimal anthropogenic impact on the bottom community, the relatively low pollution, the lack of mass catch and the high populations of both species of molluscs (Snigirev et al. 2019).

Figure 2

Location of the experimental site near Snake Island, north-western Black Sea (45°15′08.2″N; 30°12′09.8″E) an AXIS AD 500 electronic balance with an accuracy of 0.001 g.

The measurements of the mass and length of the live mussels were analyzed to identify the relationship between their linear and weight indicators in order to estimate the mass of the mussels eliminated by the predators: ln $Y = a + b$ ln L, where Y is one of the characteristics of the mass of the mussel shell, L is the shell length and a and b are allometric coefficients determined from empirical data (Shurova 2013).

As a quantitative indicator of the feeding activity of *R. venosa*, feeding intensity (*FI*, mg g^{-1} per day^{-1}) was calculated for each predator size group as a ratio of the total mass (shell + tissue) of mussels consumed to the total mass of the predator per day (Kurakin & Govorin 2011). The daily ration (*DR*, g ind^{-1} per day^{-1}) was determined as the mass of soft tissue of mussels consumed by each individual per day (Kurakin & Govorin 2011). The amount of shells transferred by the predator to the bottom sediments (M_{SM}, g ind^{-1} per day^{-1}) in the course of feeding was calculated, taking into account the number of prey and the shell mass of mussels consumed by each Rapa whelk per day.

2.4. Statistical analysis

Linear regression analysis between the linear and non-linear parameters (i.e. length/mass relationships) was performed using the statistical package Statgraph Plus 5.0; the data were log10-transformed to normalise/homogenise any variances. Individual characteristics of the mussels and *R. venosa* (shell measurements, total mass, body mass and shell mass) were determined with one-way analysis of variance (ANOVA). The results are presented as means ± standard error (SE) and the significance level used in the tests was $p < 0.05$ (Lakin 1986).

3. Results

Allometric equations were calculated based on the measurements of the length and weight of live mussels. The coefficients of these equations are presented in Table 3. These ratios were used to calculate the mass of mussels consumed during the experiment based on shell length. At the beginning of the experiment, the dominant mussel size across all cages was 20–30 mm and 2.52 ± 0.06 g. The average length of the mussels across the cages varied from 24.85 ± 0.41 mm (Cage No. 1, small species) to 28.49 ± 0.45 mm (Cage No. 4, large species), as seen in Table 2.

The four predator groups in the experiment, differentiated by shell height (30–40 mm, 40–50 mm, 60–70 mm and 80–90 mm), differed in the number and size of the mussels eaten. The smallest mussels, with a shell length from 0.1 to 10 mm, were food for only the group of small molluscs, 30–40 mm in size. Mussels 20–30 mm long became the dominant food class for predators up to 70 mm high (Table 4). It is likely that for *R. venosa*, the consumption of mussels with a length of 20–30 mm is the most optimal in terms of the ratio of energy spent on their prey and received by the predator in the process of feeding. For small Rapa whelks, the number of consumed mussels with a length of 20–30 mm was 21.37% of the total number of offered mussels; those in the second size category (40–50 mm) consumed 13.51% of the offered mussels with a length of 20–30 mm. The Rapa whelks with a height of 60–70 mm and 80–90 mm consumed 9.95% and 5% of mussels of this size class from the total number available in the cages. Thus, with an increase in the predator's size, the proportion of mussels 20–30 mm long in its diet decreases, while those with a length of 30–50 mm make up more of the diet.

The size groups of the predator differed in preferences as to the length of mussels consumed

Table 3

Regression coefficients of the size/mass ratio for mussels near Snake Island, based on feeding experiments in the north-western Black Sea

Regression	Parameters		SE *a*	SE *b*	R^2 (%)
	a	*b*			
$\ln W = a + b\ln L$	–8.955	2.917	0.093	0.027	99.8
$\ln W_w = a + b\ln L$	–10.588	2.905	0.180	0.050	99.3
$\ln W_{st} = a + b\ln L$	–9.345	2.782	0.119	0.034	99.7

L – shell length (mm); W – total mass (shell + tissue; g); W_w – wet tissue mass (g); W_{st} – shell mass (g); a and b – parameters of the equation; R^2– coefficient of determination; SE – standard error

Table 4

Quantity (in %) of mussels consumed, by shell size

Mussels shell length (mm)		Shell height of *Rapana venosa* (mm)			
		30–40	41–50	60–70	80–90
0–10		5.7	–	–	–
10–20		10.76	10.20	6.57	3.73
20–30		**63.29**	**61.22**	**41.61**	20.90
30–40		14.56	19.73	**32.85**	**31.34**
40–50		5.06	6.12	14.60	**32.09**
50–60		0.63	2.72	4.38	11.94
Number of mussels	eaten	158	147	137	134
	total	468	666	573	560

L – shell length (mm); W – total mass (shell + tissue; g); W_w – wet tissue mass (g); W_{st} – shell mass (g); a and b – parameters of the equation; R^2– coefficient of determination; SE – standard error

($p < 0.0001$). For the gastropods with a shell height of 30–40 mm, the average prey length was 25.58 mm, which increased with the size of the predator, reaching 38.12 mm in the 80–90 mm group (Table 5).

The total mass of mussels eaten varied widely, from 0.002 to 19.440 g; the average values were higher for small and large gastropods, varying from 2.169 g to 6.225 g, respectively ($p < 0.0001$). The average weight of the consumed mussel soft tissue varied from 0.407 g in the group of small gastropods (Cage No. 1) to 1.165 g in the largest group in the experiment (Cage No. 4).

The predator's contribution to the deposition of mussel shells in the bottom sediments depended on its size ($p < 0.0001$). In the process of eating the soft tissues of the prey, one individual of small gastropods (30–40 mm) added 0.428 g of mussel shells to the bottom soil per day; with a height of the predator of 80–90 mm, the mass of shells deposited on the bottom increased to 1.995 g (Table 5).

Feeding intensity (*FI*), represented by the ratio between the total mass of the mussels consumed and the total mass of the predator, was highest for the small Rapa whelks, amounting to 99 mg of mussels per 1 g of *R. venosa* per day. As the size of the predator increased, this indicator decreased, amounting to 41 mg of mussel weight per 1 g for the largest *R. venosa* in the experiment (Table 5; Fig. 3). Thus, small animals are more vulnerable to a shortage of food, since the growth process requires more energy than with large predators.

The daily ration (*DR*) of mussel soft tissue ingested by a single predator varied with its size, increasing from 0.189 g in small animals to 0.917 g in large *R. venosa* (Table 5). The dependence of the Rapa whelk's daily consumption (*DR*) on the height of its shell (*SH*) is determined by the following regression equation:

$$DR = 0.017 \times SH - 0.537 \qquad (R^2 = 99.7;\ SE = 0.024),$$

where R^2 is the coefficient of determination and SE is the standard error of the equation, which shows the error of the *DR* values calculated from the dependence.

According to the results of the experiment, the regression equations between the height of the predator's shell (*SH*) and the average total mass W_{mussel}, average mass of soft tissue Ww_{mussel} and average shell length L_{mussel} of the mussel as well as between the average mass of the soft tissue Ww_{mussel} consumed and the average total mass of the predator were as follows:

$$W_{mussel} = 0.091 \times SH - 1.617 \qquad (R^2 = 96.3;\ SE = 0.422),$$

$$Ww_{mussel} = 0.017 \times SH - 0.301 \qquad (R^2 = 96.3;\ SE = 0.079),$$

$$L_{mussel} = 14.520 + 0.278 \times SH \qquad (R^2 = 98.3;\ SE = 0.854),$$

$$Ww_{mussel} = 0.007 \times W_R + 0.358 \qquad (R^2 = 99.4;\ SE = 0.032),$$

The resulting regression equations make it possible to take into account the maximum damage exerted by the predators on the mussel population in accordance with their size. A regression equation was obtained to calculate the mass of mussel shells released into the bottom sediments (M_{SM}, g) by an individual predator during feeding:

Table 5

Size and mass characteristics of the Mediterranean mussel (*Mytilus galloprovincialis*) consumed in experiment (Snake Island, north-western Black Sea, Ukraine

Parameters		Shell height (*SH*) *Rapana venosa*, mm			
		30–40	40–50	60–70	80–90
L_{mussel}, mm	min.–max m ± SE	2.6–52.5 25.58 ± 0.69	12.3–58.3 28.20 ± 0.68	14.1–51.9 31.62 ± 0.75	17.9–59.6 38.12 ± 0.84
$W_{M.gal}$, g	min.–max m ± SE	0.002–13.43 2.169 ± 0.169	0.194–18.237 2.764 ± 0.234	0.29–12.991 3.731 ± 0.257	0.582 –19.440 6.225 ± 0.350
$Ww_{M.gal}$, g	min.–max m ± SE	0.001–2.509 0.407 ± 0.031	0.037–3.402 0.518 ± 0.043	0.055–2.427 0.699 ± 0.048	0.110–3.627 1.165 ± 0.065
$Ws_{M.gal}$, g	min.–max m ± SE	0.001–5.321 0.920 ± 0.06	0.094–7.123 1.16 ± 0.092	0.137–5.154 1.549 ± 0.102	0.267–7.573 2.531 ± 0.137
Mussel shell mass (M_{SM}), g ind^{-1} per day $^{-1}$		0.428	0.557	1.248	1.995
Feeding intensity (*FI*), mg g^{-1}per day^{-1}		99	72	57	41
Daily ration (*DR*), g ind^{-1} per day $^{-1}$		0.189	0.249	0.563	0.917

m – mean parameters; SE – standard error; W_{mussel}–whole animal mass (g); W W_{mussel}–wet tissue mass; W_s – shell mass (g); L_{mussel},–average shell length (mm)

$M_{SM} = 0.037 \times SH - 1.135$ ($R^2 = 99.7$; SE = 0.047),

where *SH* is the height of Rapa whelk in mm.

Thus, based on the experimental conditions, which were as close as possible to natural conditions, the daily mussel diet (*DR*) per individual of *R. venosa* in the north-western Black Sea was determined. For the size class of 30–40 mm, with an average shell height (*SH*) of 40.7 mm, *DR* corresponded to 1.008 g of the total mass of *M. galloprovincialis* or 0.189 g of mussel meat per day. For the size class of 40–50 mm, with an average height (*SH*) of 46.5 mm, *DR* corresponded to 1.328 g of the total mass of *M. galloprovincialis* or 0.211 g of mussel meat per day. For the size class of 60–70 mm, with an average height (*SH*) of 64.4 mm, *DR* corresponded to 3.001 g of the total mass of *M. galloprovincialis* or 0.563 g of mussel meat per day. For the size class of 80–90 mm, with an average height (*SH*) of 83.5 mm, *DR* corresponded to 4.907 g of the total mass of *M. galloprovincialis* or 0.917 g of mussel meat per day.

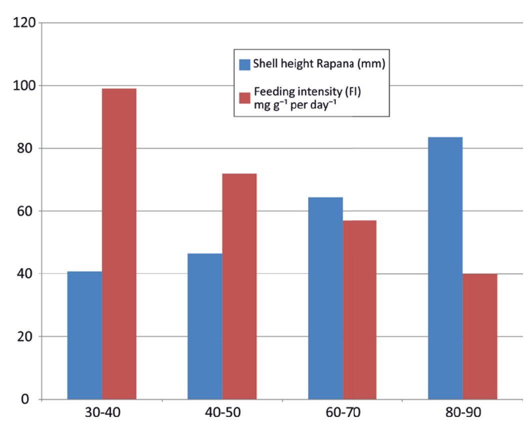

Figure 3

Dependence of the feeding intensity on the shell height of *Rapana venosa* in the experiment

4. Discussion

In this field study experiment in the coastal waters of Snake Island in the north-western Black Sea, we estimated the feeding intensity and daily consumption of Rapa whelks (*R. venosa*) among four size groups and their preference for mussel size. These field experiments were done on the Black Sea Rapa whelk population for the first time. Similar studies have been conducted on the invasive Rapa whelk populations from the Southern Atlantic (Argentina) and the Adriatic Sea (Italy) (Savini & Occhipinti-Ambrogi 2006; Giberto et al. 2011). In the previous study, for the Rapa whelk of the Adriatic Sea, an average consumption of 1.2 g of bivalve mollusc meat per day was experimentally determined (Savini & Occhipinti-Ambrogi 2006); however, the *R. venosa* in Italian waters were larger (99–110 mm) than those in our study (83.5 mm). Thus, the value of the indicator representing consumption (0.917 g of mussel meat per predator per day) was comparable to the dependencies described earlier.

Giberto et al. (2011) reported that a Rapa whelk with a shell width of 70 mm maintained at a temperature of 20°C and a salinity of 23 PSU ate 0.68 g of mussel tissue (wet weight) per day per individual in the Rio de la Plata estuary and adjacent marine coasts, between Uruguay and Argentina. The daily consumption rate (*DR*) of mussels by *R. venosa* for a snail with a 70-mm shell was 0.65 g ind^{-1} per day^{-1}, according to the equation justified in this article. This demonstrates the similarity of feeding behaviour in different environmental conditions in a given situation of temperature and salinity. In the coastal waters of Snake Island, in the north-western Black Sea, the salinity of the bottom layer varies from 11.8 to 20.1 PSU (Snigirev et al. 2016); during these experimental studies it was 16.03 ± 0.26 PSU. Thus, the differences in environmental parameters in terms of temperature (20 vs 23°C) and salinity (23 vs 16 PSU) during experiments carried out in laboratory conditions and the native habitat did not affect the daily consumption of Rapa whelk.

Based on the laboratory studies, a high intake rate relative to body weight (up to 12%) for small (<60 mm) and medium (60–90 mm) gastropods was established; in large gastropods (>90 mm) this decreased to 5% (Giberto et al. 2011). Under the conditions of the north-western Black Sea, the rate of consumption of mussels in relation to the mass of *R. venosa* had a similar feature: it decreased with the increasing size of the predator, ranging from 10% in small predators with a height of 30–40 mm to 4% in the size group of 80–90 mm. Thus, the most gluttonous was the *R. venosa* with a shell height of 30–40 mm; the required amount of food decreased by a factor of 2.4 for the maximum size of *R. venosa* for the given water area. This must be taken into account for measures aimed at preserving and restoring natural settlements of mussels and when establishing additional solid artificial substrates and organising mussel farms. In terms of preferred prey size, veined whelks consume more intermediate than large or small bivalves. As with our study, a size preference of 20–30 mm was previously reported among the prey of various bivalve species (Savini & Occhipinti-Ambrogi 2006; Lanfranconi 2013). Thus, the preferences in the amount of prey do not differ in the regions invaded by the predatory gastropod.

Minor differences in daily consumption reported in studies on the feeding behavior of the Rapa whelk in different marine areas are the result of differences in the size of the gastropods used in the experiments, the types of prey and differences in temperature, salinity and other factors not accounted for.

The mussel habitats in the north-western Black Sea experience the maximum damaging effect from *R. venosa* due to the destruction of the most productive and stress-resistant molluscs with a length of 20–40 mm, which are the population core of this species of bivalve molluscs in the ecosystem. In all the experimental cages, the average length of the mussels eaten by the predator was greater than the average length of the mussels offered for food.

For the ecosystem of the eastern part of the Black Sea, laboratory studies have previously determined that *R. venosa* specimens weighing 50 g consumed an average of 0.17–0.30 g of mussel meat per day (Seyhan et al. 2003). Under natural conditions of the north-western Black Sea, higher rates were determined: for Rapa whelks weighing 50 g, the daily ration was 0.492 g of mussel meat, which may be the result of the abundance and free choice of prey.

Previously, experimental studies in the north-western Black Sea revealed a decrease in the number of mussels in the settlements, depending on the size of the Rapa whelk population – from 33 to 79 ind. day^{-1} m^{-2} – and the feeding intensity of *R. venosa* in the height range of 62 to 84 mm – one mussel with a length of 36.3 ± 1.5 mm and a total weight of 3.9 ± 0.2 g per day (Kurakin & Govorin 2011). The dependence between the average total mass of mussels W_{mussel} and the height of the predator's shell (*SH*) calculated in our study confirms the previously substantiated indicators and allows us to calculate the nutritional needs of the predator population in a wide size range (from 34 to 85 mm) for the ecosystem of the north-western Black Sea.

States of marine and terrestrial beach communities and dynamics of beach are in strong and complicated interconnections, because changes in the composition and abundance of bivalves are among the underestimated reasons for degradation of the Black Sea beaches (Shadrin et al. 2012). The dependence between the size of the Rapa whelk and the mass of mussel shells released during its feeding, revealed during the experiment, allows us to predict the formation of bottom and coastal sediments in coastal areas where there are numerous mussel settlements. This data will be useful for predicting changes in the coastline.

The quantitative parameters of the feeding behaviour and feeding intensity of *R. venosa* found in the study correspond to the consumption rate determined for other water areas and expand the range of their use in accordance with the size of the predator. The data on the feeding behaviour of *R. venosa* contribute to the understanding the role that this invasive gastropod plays in and the ecological impact it has on the Black Sea ecosystem. Using the information regarding the abundance and size breakdown of *R. venosa* on the solid substrate of the north-western Black Sea, it is possible to calculate the practical damage caused to the settlements of *M. galloprovincialis* mussels by this predator.

Reasonable quantitative indicators of the feeding activity of the Rapa whelk should be used as initial information for the management and conservation of the natural resources of mussels, as well as for reasonable rationing of the predator's catch in the Black Sea.

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