Research Article
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Ecological features of two marine gastropod *Nucella heyseana* (Dunker, 1882) and *Ceratostoma burnettii* (Adams et Reeve, 1848)

Abstract

The article presents the results of the study of the population dynamics, spatial distribution, diet variability, food digestibility, growth rates and the impact of predatory gastropods *Nucella heyseana* (*N. heyseana*) and *Ceratostoma burnettii* (*C. burnettii*) on marine bivalves in Peter the Great Bay, Russia. The relationship between the size of *N. heyseana* and its prey, as well as its impact on the growth of surviving mollusks, is clarified. *N. heyseana* has a pelagic stage which allows it to populate artificial substrates and positively affect the cultivated Japanese scallop *Myzuhopecten yessoensis* by preferentially preying on *Mytilus trossulus*. *C. burnettii* does not have a pelagic stage, but by destroying trophic competitors of *M. yessoensis* on the sea floor, it also has a beneficial effect.

Keywords: predatory marine gastropods *N. heyseana* and *C. burnettii*, population dynamics, impact on bivalves

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Introduction

In the cultivation of the Japanese scallop *M. yessoensis* (Jay) and the Pacific mussel *M. trossulus* (Gould) in Minonosok Inlet of the Posyeta Bay (42º61`N, 130º86'E) and in Whale Inlet (43º06'N, 134º20'E) on artificial substrates, we have observed the role of the predatory gastropod *N. heyseana*. The empty shells of bivalve mollusks with characteristic drill holes 1-2mm across were observed. Artificial substrates, scallop collectors and cages, are located deep in water and the appearance of the *N. heyseana* in them can be explained by the presence of a pillaging stage in its development. However, most researchers of this field declare that *Nucella* (= *Purpura* = *Thais* = *Polytropa*) does not have a pelagic stage and that the juveniles emerging from the hatching capsules immediately begin to crawl.[1-4] The large impact of *N. heyseana* on *M. trossulus* in laboratory conditions,[5-8] and its capacity to switch from one prey species to another[2,9,10] requires more research of the *N. heyseana* ecology. The predator *C. burnettii* lives on the sea floor where *M. yessoensis* juveniles are sown and it is important to know how it impacts the cultured species. The present studies are devoted to understanding the population dynamics, feeding and larval development of *N. heyseana* and *C. burnettii*.

Material and methods

To research the population dynamics of *N. heyseana*, *M. yessoensis, M. trossulus* and *Asterias amurensis* (*A. amurensis*), the contents of scallop collectors of Japanese construction and of collector-cages containing cone-shaped polyethylene plates developed by us (Figures 1&2) were studied over 38 years (1977 – 2014) in Minonosok Inlet and in Klykova Inlet of Posyeta Bay (42º61'N, 130º85'E) (Figure 3).

Cage inhabitants were also studied one year after one-year-old *M. yessoensis* were settled in them. The same research was carried out for four years in Whale and Trinity Inlets (42º64'N, 131º11'E) (Figure 3). Scallop collectors that had overwintered at sea were processed in the following spring and a few were left for another year. The cages with *M. yessoensis* were kept in the sea for one year. In shallow bays they were lowered to a depth of 6-10m and in open areas up to 20m. In 1988-1990 the scallop collectors were placed in Minonosok Inlet serially - two garlands every other day from late May to early July. In September - November three collectors were removed from each garland, and all the mollusks and the *A. amurensis* were extracted. Live and dead individuals were counted. The counts were expressed per 1m^2. The height of the shells of 30–50 individuals of each species was measured from the crown to the ventral edge using a caliper with an accuracy of 0.1mm. From 1987 to 1996 the mollusks were weighed on a VLTK-500 scale with an accuracy of 0.01gr. The total body weight (W total, gr.), shell weight (W shell, gr.), soft body weight (W meat, gr.) and the dry mass of meat dried at 60º C to a constant weight (W dry meat, gr.). The meat weight of *M. trossulus* was determined according to.[11] The age of *N. heyseana* was determined by growth rings[12,13] and by the period the collectors/cages had been in the sea. The Bertalanffy equation was used as a linear growth model:

$$L_t = L_\infty [\,1 - e^{-k(t-t_0)}\,]$$

where L_t = the shell height (mm) at the age t (years),

L_∞ = the theoretical maximum shell length,

k = the constant characterizing the rate of deceleration growth,

t_0 = the age at which the shell length is zero.

The values of the parameters L_∞, k and t_0 of equation (1) were determined by the Walford method.[14] The life length D was found using the formula[15]

$$D = \frac{\ln L_\infty - \ln\,(L_\infty - L_{max})}{k}$$

where L_{max} = maximum shell size in the researched population. The food selectivity of *N. heyseana* was determined by,[2] and the diet range by the preference index α:[16,17]

$$\alpha_i = \frac{\ln[(n_{io} - r_i)/n_{io}]}{\sum_{j=1}^{m} \ln\left[{(n_{jo} - r_j)}/{n_{jo}}\right]} \qquad i=1,\ldots\ldots\ldots m$$

Where i = prey type,

n_{io} = a number of prey types i represented,

r_i = a number of prey types i consumed.

Figure 1 Collector-cage constructed of cones of diameter 300mm and height 100mm, 50mm apart.

Figure 2 A cone from a collector-cage.

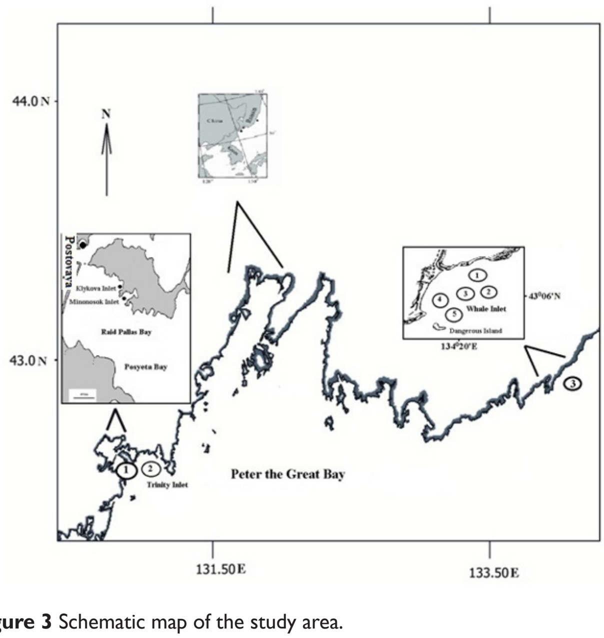

Figure 3 Schematic map of the study area.

Four different-sized *N. heyseana* were individually fed *M. trossulus* of mixed sizes. A prey size preference histogram was constructed by categorizing the numbers of live and dead *M. trossulus* in four size classes for each predator.

For the aquarium studies of predatory preference, 108 two-year *M. trossulus* were placed with 16 *N. heyseana* in December 1996. In spring of 1997, three two-year-old *M. trossulus* were placed with nine *N. heyseana* in an aquarium with a bowl of sludge. Over the subsequent two years, the food supply was replenished with more *M. trossulus* taken from the collectors. Each aquarium had a volume of 140liters and the water there was changed every other day. The aeration in the aquariums was constant.

In early June 1997, *C. burnettii* (Figure 4) were collected in the Minonosok Inlet of Posyeta Bay at a water surface temperature of 10º C and placed in an aquarium where *N. heyseana* had previously been kept. They were given the same food as the *N. heyseana* that had been transplanted into another aquarium.

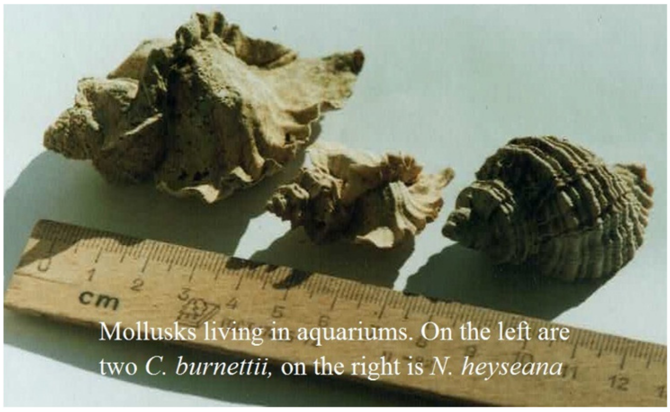

Figure 4 Samples of predatory mollusks grown in aquariums.

Every day after spawning, one capsule of *N. heyseana* and *C. burnettii* was removed from the clutch and the embryonic development of the larvae was observed under MBS-9 and "Docuval" microscopes. The young emerging from the clutch were photographed using a micro-photon trap. To study the feeding activity of *N. heyseana* young, four cylinders with diameter of 5cm, floating at the water surface, were placed in the aquarium; the bottom was covered with a nylon sieve with a mesh size of 200μm. Each cylinder contained about 40 juvenile *N. heyseana*. A small *M. trossulus* (up to 7mm in valve height) was placed in one of the cylinders. A one-year-old gastropod *Epheria turrita* was placed in another cylinder, and in the other two, juvenile *N. heyseana* were placed with either empty capsules or without capsules. The experiment lasted for five months - until the *N. heyseana* had all died.

To feed the bivalves, a microalgae culture was added to the aquarium, and all dead mollusks were removed and examined at water changes. The height and thickness of the shell at the drilling site, the diameter of the hole and its location, as well as the number of holes were measured. The mass of dead *M. trossulus* was determined according to the previously established methods.

The values of salinity and surface water temperature, wind speed and direction, sea level and precipitation in Posyeta Bay in June 1977-2014 were obtained from the weather station in the Posyeta village (42°39' N, 130°48' E). Statistical analysis was carried out using the STATISTICA 6 program[18] and tested at the level of $\alpha = 0.05$.

Results

Results of observations in natural conditions

On natural substrates, *N. heyseana* is found in the parts of bays and coves with most surf. These are typically rocky capes where other predatory invertebrates cannot survive because they are dislodged by wave action. *N. heyseana* has a smoother shell and is able to live above sea level. *N. heyseana* are found where the water is colder compared to the shallow, well-warmed Bays, where the thermophilic *C. burnettii* is more common. In these Bays the larvae of *N. heyseana* do not settle on collectors but the adult *N. heyseana* can easily be found on the capes bordering Minonosok, Klykova, Postovaya (42º65'N, 130º80'E), Reid Pallada (42º59'N, 130º84'E), Trinity Inlet of Posyeta Bay and in the cold-water Kit Bay (Figure 3). In Minonosok Inlet, *N. heyseana* settles below the littorina habitat, on flat stones populated with potential food, and *C. burnettii* lives on a rock submerged to a depth of 1.5 - 2m.

Table 1 reports the distribution statistics of the annual abundance of *M. yessoensis, M. trossulus, A. amurensis and N. heyseana* between 1977 and 2014 in scallop collectors in Posyeta Bay. The key character of these data is the non-normality and irregularity of the counts with years of high abundance typically followed by years of low abundance. Also, the species are not in phase so that all the correlations are low.

Table 1 Distribution statistics of the annual abundance of *M. yessoensis, M. trossulus, A. amurensis and N. heyseana* between 1977 and 2014 in scallop collectors in Posyeta Bay

	M. yessoensis	*M. trossulus*	*A. amurensis*	*N. heyseana*
Mean	492	802	2.0	0.021
Range	14:2083	8:3344	0:25 (9 zeros)	0.0:0.6 (27 zeros)
Standard Deviation	439.25	830.	4.30	0.055
Skewness	1.73	1.36	4.33	2.81
Kurtosis	3.09	1.05	18.87	5.93
Correlations	1.0			
M. trossulus	0.212	1.0		
A. amurensis	0.158	0.129	1.0	
N. heyseana	0.129	0.277	-0.095	1.0

Despite the abundance of mariculture plantations in Minonosok Bay, it is difficult to find live *M. trossulus* on the sea floor due to their poor resilience. They are sometimes found under the plantations on fallen artificial substrates and near the pier where mollusks in scallop collectors are sorted. On the sea floor *N. heyseana* has competitors: several species of starfish, gastropods, sea urchins, fish and birds which quickly eat *M. trossulus.* In the littoral zone, *M. trossulus* die in winter due to the sea level falling and the abrasive ice effect. In summer the supply of prey for *N. heyseana* runs out resulting in some cannibalism and mass death. At the end of October 1986, we found 19 dead *N. heyseana* on the 5-meter shore at Cape Lowland (42º60'N, 130º87'E) and five of them had holes evidently from cannibalism.

N. heyseana became more common on the sea floor and then first appeared on artificial substrates 6years after the start of industrial cultivation of the mussel *M. trossulus* in 1979 in the Minonosok Inlet. However, their presence in collectors was erratic and they were not found in 27 of the 38years reviewed (Table 1). They were present in five of the years (1979-1989) of industrial cultivation of *M. trossulus.*

The density of *N. heyseana* on the sea floor was steadily increasing and by the summer of 1996 reached 2,200ind./m^2 with biomass up to 6.9kg/m^2. However, on artificial substrates, the density of *N. heyseana* did not exceed 0.6ind./m^2 (Table 1). They settled in scallop collectors that were submerged in the sea from May 25 to June 8 and were found at depths of 0-17m, but mainly at 6-8m.

The influence of weather measurements taken in June over 38years on the abundance of 4 species was examined in by multiple regression on the square root scale, including interactions of the more significant variables. F statistics showed that the abundance of *M. yessoensis* strongly depends on wind strength and precipitation (P<0.001), while the abundance of *M. trossulus* was not significantly dependent on climatic factors or the presence of predators *N. heyseana* and *A. amurensis*. The abundance of *A. amurensis* strongly depends on precipitation and solar activity in Wolf numbers (P<0.01), and only wind speed significantly affects the abundance of *N. heyseana*.

After the abandonment of *M. trossulus* cultivation in Minonosok Inlet in 1989, the abundance of *M. trossulus* began to decline, and by 1991 *N. heyseana* was not found in collectors. However, in 1994, an attempt was made to cultivate *M. trossulus* in Minonosok Inlet again, and by June 1996 the abundance of *N. heyseana* returned to high values on the sea floor, and its juveniles began to appear in marine plantations overgrown with *M. trossulus*. At the Voevoda Inlet Marine Farm (43º 00 N, 131º78 E) where *M. trossulus* has been cultivated for many years, the abundance of *N. heyseana* in collectors in 2024 reached 1.0ind./m^2.

In a study of 8 scallop collectors with an *N. heyseana* predator, *M. yessoensis* and varying populations of *M. trossulus,* there is a strong preference for *N. heyseana* to eat *M. trossulus* but the numbers eaten vary greatly (Figure 5). Zero values for *M. yessoensis* indicate 100% survival of this mollusk.

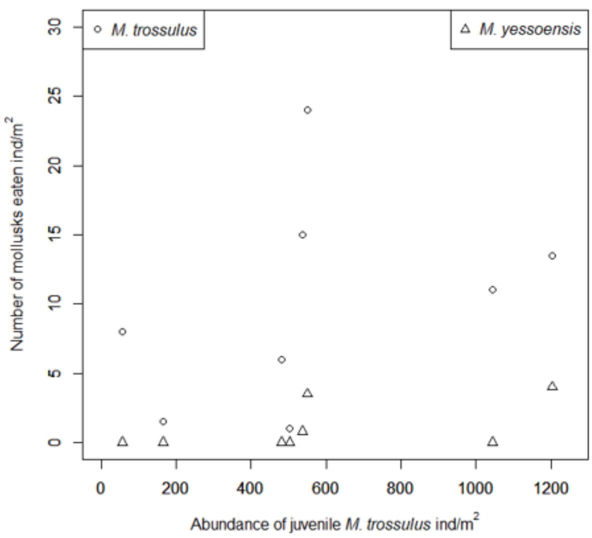

Figure 5 Interannual variability in the abundance of *M. trossulus* and *M. yessoensis* preyed on by a *N. heyseana*, relative to the total abundance of *M. trossulus* in collectors.

The number of *M. yessoensis* eaten also depends on their abundance. In the harvest year of 1988, the settling of *M. yessoensis* larvae in the collector - cages at Klykova Inlet was 1025ind./m^2, and the death rate from one *N. heyseana* over 14months was 0.24%. However, in the non-harvest year of 1989, the settling of *M. yessoensis* larvae in the collector - cages at Klykova Inlet was 300ind./m^2, and the death rate from *N. heyseana* over a 14.5months was 0%.

Citation: Gabaev DD, Kolotukhina NK, Gilmour AR. Ecological features of two marine gastropod *Nucella heyseana* (Dunker, 1882) and *Ceratostoma burnettii* (Adams et Reeve, 1848). *J Aquac Mar Biol. 2025;14(3):117‒126. DOI: 10.15406/jamb.2025.14.00424*

From the same study of 8 scallop collectors as Figure 5, Figure 6 shows the size of *M. yessoensis* and *M. trossulus* eaten by a single *N. heyseana* indexed by the size of the predator. The standard deviation around these means is about 8 but the actual numbers eaten are unknown. There appears to be a tendency for larger *N. heyseana* to eat larger prey and one large *M. yessoensis* was overcome by a large *N. heyseana*.

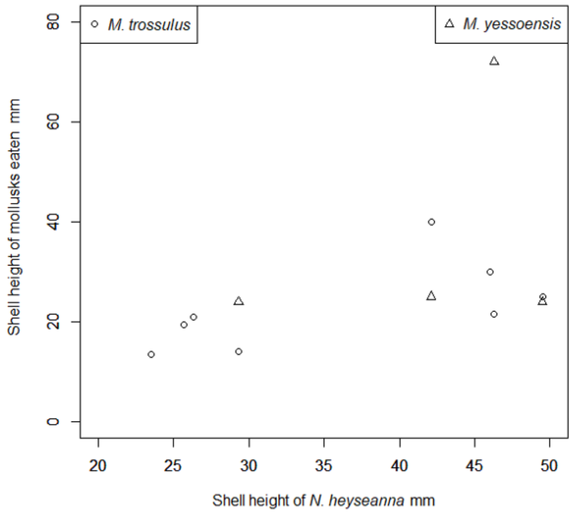

Figure 6 Mean sizes of prey eaten by different sized *N. heyseana*.

This is supported by classifying 2140 individual *M. trossulus* by the diameter of holes in with the height of their shells in aquariums (Figure 7). The standard deviation of shell height was about 5 and larger *M. trossulus* had larger holes.

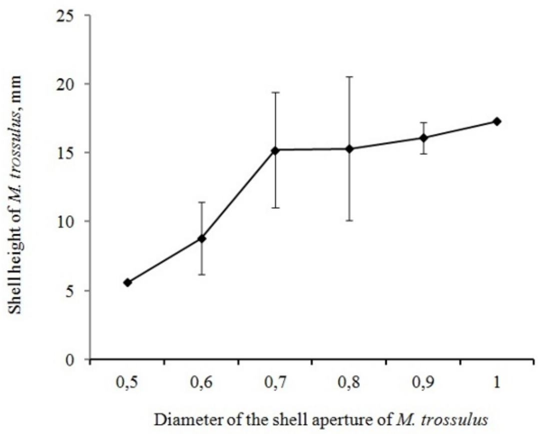

Figure 7 Relationship between the size of *M. trossulus* and the diameter of the hole in the shell from *N. heyseana*

The correlation coefficient between the size of the shell of *M. trossulus* and the diameter of the hole from *N. heyseana* is 0.555 at $p = 0.061$. At the same time, comparison of the size of surviving *M. trossulus* in collectors with and without predators sometimes contradicts this pattern. In the presence of predators, surviving *M. trossulus* sometimes reach larger sizes than without predators due to decreased intraspecific competition (Figure 8).

In the summer of 1996, an overwintered population of *M. trossulus* was discovered in the offset zone of Trinity Inlet, which *N. heyseana* fed on. The holes on the shell were more often located at the junction of the winter and spring growth zones. The dead (eaten) *M. trossulus* were significantly larger than the live ones with shell lengths of 19.80 ± 0.57mm and 16.19 ± 1.06mm, respectively, $t = 3.29$; $p = 0.002$.

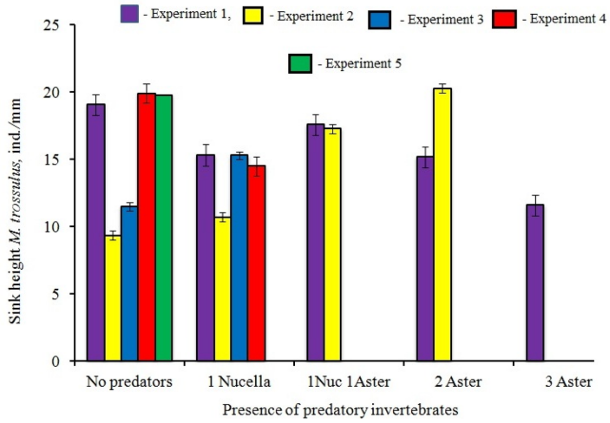

Figure 8 Shell height of *M. trossulus* survivors with different abundance of predators in the collectors.

In November 2001, many juvenile oysters of *Magallana* (=*Crassostrea*) (*M. gigas*), which *N. heyseana* fed on, were found on the littoral of the Minonosok Inlet. The average diameter of the drill holes was 0.853 ± 0.142mm and the surviving *(M. gigas)* had a shorter shell length compared to the dead ones (10.41 ± 0.36mm and 11.07 ± 0.41mm, respectively, $t = 1.21$; $p = 0.23$). The holes from *N. heyseana* were mainly near the umbo (45.16%) and in the area of the closure muscle (32.26%).

A study of the food preferences of four *N. heyseana* individuals of different sizes shows considerable variability but no obvious pattern in the preference for large or small *M. trossulus* prey (Figure 9).

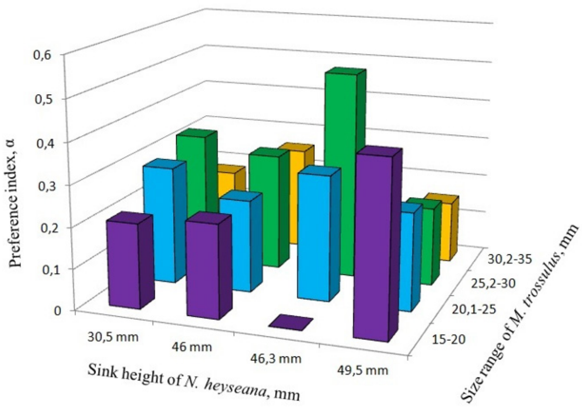

Figure 9 Ranking of *M. trossulus* eaten by four *N. heyseana*.

A study of the proportion of *M. trossulus* eaten by a single *N. heyseana* in 8 scallop collectors showed all *M. trossulus* were eaten in 5 of the collectors and the proportion eaten in the other 3 ranged from 40% to 95%. The proportion eaten was not related to the proportion of other scallops present which ranged from 3.7% to 76.7 %. However, whensettling in collector cages divided by plates into areas of 0.1m^3, and having destroyed *M. trossulus* there, *N. heyseana* were forced to switch to *M. yessoensis*. If the year turned out to be fruitful for young scallops *Ch. farreri*, they switched to it, despite its shells with spines.

A comparison of the contents of collectors with and without *N. heyseana* showed that in collectors with a predator, as a rule, there were two more species of bivalves. These are mainly *Ch. farreri* and *M. senchousia.* In collectors without *N. heyseana*, the death of all *M.*

yessoensis and *Ch. farreri* was sometimes observed already in late summer.

M. trossulus were more numerous in scallop collectors than on the sea floor, so after 2.5years of life, the shell height of *N. heyseana* was generally higher than that of its bottom-dwelling relatives (Figure 10).

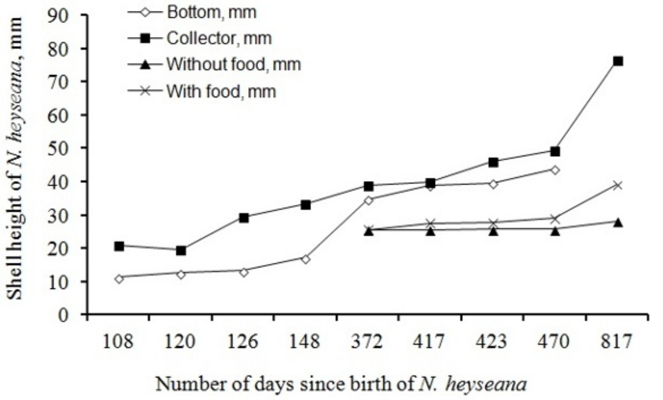

Figure 10 Shell height of four *N. heyseana* in different habitats.

In the littoral of the middle part of the Primorsky Territory (Whale Inlet), *M. trossulus* is easy to find; predatory sea stars *A. amurensis* and *Distolasterias nippon* do not occur there. Due to the abundance of food and lower temperatures, which lengthen their life span, *N. heyseana* have been found with a shell height of 78mm there and of 77mm in the Minonosok Inlet collectors.

The calculation of the eaten mass of *M. trossulus* and the weight gain of *N. heyseana* on artificial substrates allowed us to establish that the digestibility of its food in the collector - cage is 63.6%, and in the cage with a scallop - 50.3%. In the collector, to increase the diameter of the “trunk” by 0.1 mm, the *N. heyseana* had to eat an average of 3 *M. trossulus* specimens.

Results of keeping predators in an aquarium

In a large sample of *M. trossulus* (n = 2140), no clear relationship was found between *N. heyseana* aperture diameter and *M. trossulus* shell size (r = 0.0902; p = 0.000), as there was a negative relationship between shell thickness at the drilling site and hole diameter in *M. trossulus* (r = - 0.060; p = 0.005), suggesting that large *N. heyseana* most often drilled into the thin-walled vertebral or ventral part of the shell (24.9 and 20.8%, respectively) (Figure 11).

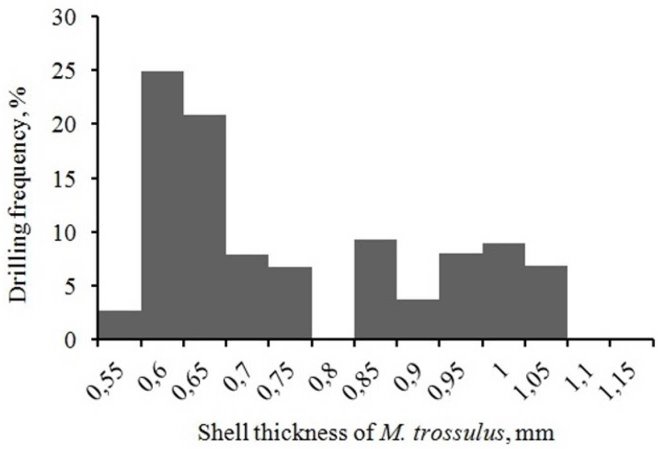

Figure 11 Selectivity of *N. heyseana* of the shell thickness of *M. trossulus*.

However, the preference of *N. heyseana* for large *M. trossulus* is supported by the fact that a highly significant relationship was found between the size of *M. trossulus* and the number of holes on its shell obtained from several *N. heyseana* (r = 0.974; p = 0.000) (Figure 12).

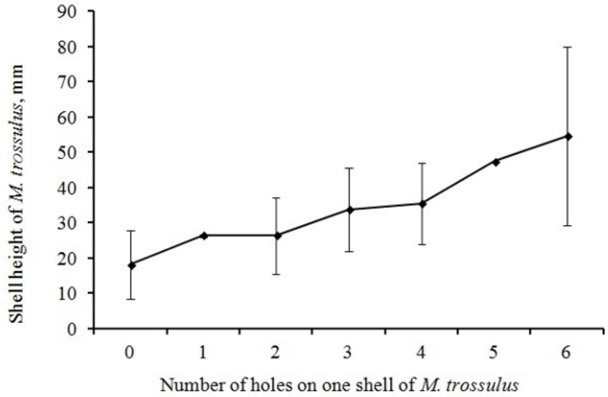

Figure 12 Number of holes per shell of *M. trossulus* as a function of their shell size.

Incomplete holes (0.33%) were found in 7 *M. trossulus* specimens out of 2140, and they were located in the thick part of the shell, which were larger (L = 26.1 $\pm$ 5.6mm) than those drilled to the end (L = 21.8 $\pm$ 0.2mm).

Without food, *N. heyseana* had cases of death, cannibalism and carrion feeding, and sometimes drilling began inside the deceased *M. trossulus.* Those that were buried in the aquarium mud (possibly feeding on detritus) survived better. They did not grow for 9months, but after the introduction of *M. trossulus*, compensatory growth was observed. However, their growth rate lagged behind that of individuals living in the natural environment (Figure 10).

N. heyseana sensed the appearance of food at a distance; 10-12hours after the introduction of *M. trossulus*, *N. heyseana* was found on them, having travelled 65cm. The prey also senses the presence of predators, as the scattered *M. trossulus* has already formed a group (druse) when the *N. heyseana* approached. Because of this, predators drilled holes in the unprotected part of the shell and almost half of the holes (47.7%) were made at the vertebral edge.

The feeding activity of *N. heyseana* is greatest in March (from 0.38 to 0.50 individuals/day) and then decreases, with a slight rise at the end of April to 0.23 individual day (Figure 13).

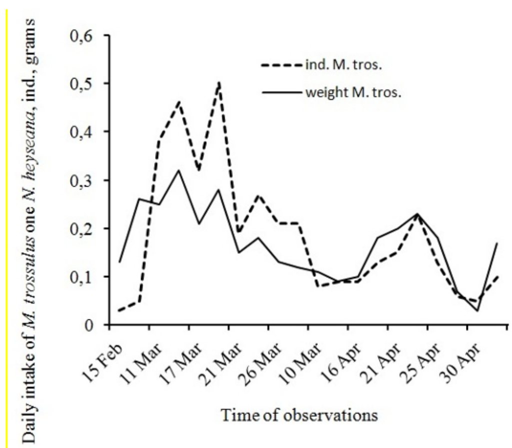

Figure 13 Daily consumption of *M. trossulus* by *N. heyseana* (individuals and grams).

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In this case, the digestibility of food reached 65.5%. The average consumption intensity is 0.28 individuals/day. Consequently, per year one adult *N. heyseana* eats about 102 *M. trossulus* in an aquarium. Unlike *N. heyseana*, the maximum feeding activity of *C. burnettii* was observed in September - 0.18 individual day and decreased in October and February to 0.024 and 0.049 individual/day, respectively (Figure 14).

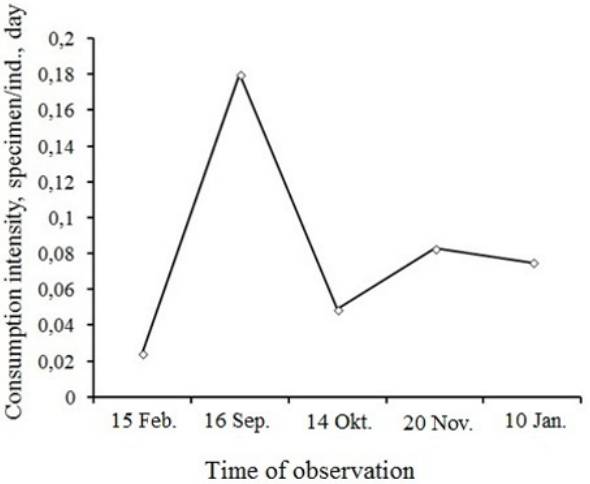


Figure 14 *Arca boucardi* consumption of one *C. burnettii* per day.

The feeding preferences of the two predators can be seen in the Table 2.

Table 2 Food spectrum of *N. heyseana* and *C. burnettii*

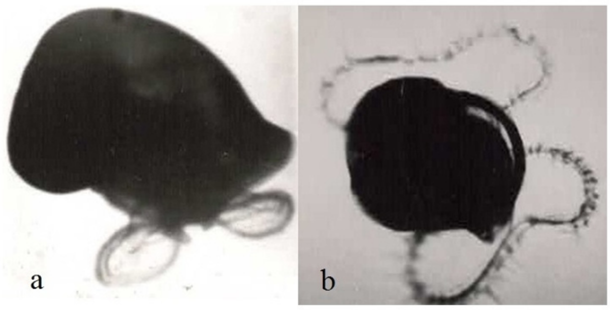
Foods	*N. heyseana*	Eaten, ind.	*C. burnettii*	Eaten, ind.
Mytilus trossulus	+	97.0	-	0
Musculista senhousia	+	1.0	-	0
Tegula rustica	+	1.0	-	0
Littorina spp.	+	2.0	-	0
Epheria turrita	+			
Crenomytilus grayanus	+	31.0	-	0
Crassostrea gigas	+	3.0	-	0
Cannibalism	+	5.0	-	0
Detritophagy	+		+	
Mizuhopecten yessoensis	-	0	+	2.0
Chlamys farreri	+	0	+	1.0
Modiolus kurilensis	-	0	+	4.0
Arca boucardi	-	0	+	117.0
Septifer keenae	-	0	+	5.0
Glycymeris yessoensis	-	0	+	1.0
Foods	*N. heyseana*	Eaten, ind.	*C. burnettii*	Eaten, ind.
Mytilus trossulus	+	97.0	-	0
Musculista senhousia	+	1.0	-	0
Tegula rustica	+	1.0	-	0
Littorina spp.	+	2.0	-	0
Epheria turrita	+			

Table 2Continued...

Crenomytilus grayanus	+	31.0	-	0
Crassostrea gigas	+	3.0	-	0
Cannibalism	+	5.0	-	0
Detritophagy	+		+	
Mizuhopecten yessoensis	-	0	+	2.0
Chlamys farreri	+	0	+	1.0
Modiolus kurilensis	-	0	+	4.0
Arca boucardi	-	0	+	117.0
Septifer keenae	-	0	+	5.0
Glycymeris yessoensis	-	0	+	1.0

Note: + sign means eaten species, - sign means untouched species

At a temperature of 13°C, N. heyseana began deposited capsules in mid-December and the laying completed in the surface layer of the aquarium on February 17, subsequently turned out to be the largest. During the day, the individual interrupted spawning, crawled away, copulated with another individual and returned back. 108 spindle-shaped capsules 8-13 mm high with 25-60 eggs were laid. Their development lasted 35 days and during this time, 14-30 eggs of feeders were eaten in each capsule and 11-30 larvae entered the water. They swam inside the capsule and immediately after exiting it, then crawled, and later released the sail and began to swim again. Other individuals, after leaving the capsule, were attached to the surface of the water with the sole of their foot for several hours. The duration of the pelagic period was influenced by the temperature of the water. At 8°C, it lasted about a day, and at room temperature it was just 4 hours. However, even a month after settling on the substrate, the N. heyseana larvae is able to float to the surface of the water and stay in the water for about a day. During this time, the surface current can carry it some distance while it seeks a suitable place to live.



Larvae after quit capsule. a - *S. burnettii* , b - *N. heyseana*

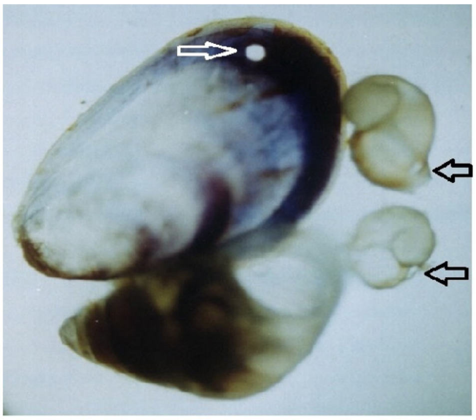
The larvae came out of the capsules (Figure 15) with a small supply of yolk which sustained them for a while. However, on the fourth day, the larvae have drilled the shells of almost one- year-old *M. trossulus* and some were eating them.

Cannibalism was observed in cylinders without food, and up to 5 shell holes were found in the dead *N. heyseana* and *Epheria turrita (E. turrita)* (Figure 16).

In a cylinder, thanks to the abundance of food, *N. heyseana* grew quickly and in a month overtook the one-year-old *E. turrita* in shell height (3.5 and 3.0mm, respectively).

Using our observations of the daily consumption of *N. heyseana* and determining the average meat weight of recently settled *M.*

trossulus larvae, we found that one young *N, heyseana* is able to eat 5.6 *M. trossulus* per day. Therefore, in five months, by the time the contents of the collectors are examined, the *N. heyseana* could eat 840 *M. trossulus* larvae. These calculations are consistent with the actual difference in the abundance of juvenile *M. trossulus* in collectors with and without *N. heyseana*. The average shortage of *M. trossulus* in collectors with *N. heyseana* is 805 specimens. As *M. trossulus* increase in size, their mortality decreases and some larger *N. heyseana* switch to smaller prey (Figure 9).



Prey of *N. heyseana* larvae: *M. trossulus*, *E. turrita* and *N. heyseana*. Arrows point to shell holes

Unlike *N. heyseana*, *C. burnettii* began spawning in late December. Two females laid 124 capsules 10–14 mm high, held together by a common base. The total number of eggs per capsule varied from 100 to 600, but only 6–18 larvae hatched from the capsules. The remaining eggs were eaten by the embryos during development. At a temperature of 15.5ºC, the development of larvae took 60 days. By the time they emerged from the capsules, the veligers had lost their sail and began crawling with the help of a well-developed leg. The young emerged with a supply of nutrients and did not attack the mollusks offered for 15 days. They did not engage in cannibalism.

The predatory preference of *N. heyseana* for *M. trossulus* is favorable for *M. yessoensis* production because *M. trossulus* is its competitor. *C. burnettii*, which actively consumes food competitors of *M. yessoensis* on the sea floor, is suitable for improving the trophic conditions of *M. yessoensis* juveniles sown on the sea floor. These data allow us to recommend the joint cultivation of *M. yessoensis* with *N. heyseana* on artificial substrates, and *C. burnettii* on the sea floor.

Discussion

Marine gastropods are considered a prime subject for the study of many general biological problems.[12] In the 60s, no significant populations of *N. heyseana* were found in Posyeta Bay.[3,19,20] The predators reached the highest density in the southern Kuril Islands of 33-150ind./m^2 with a biomass of 7-90g/m^2.[21]

The absence of *N. heyseana* in the shallow bays of the Posyeta Bay is due to the high summer water temperature (about 30°C), since the southern boundary of the related species *N. lapillus* is limited to below a temperature of 19ºC.[1]

With an increase in cultivation of *M. yessoensis* and *M. trossulus* in the Minonosok Inlet, the abundance of *N. heyseana* on the sea floor increased to 2,200ind./m^2, and the biomass to 6.9kg/m^2.[22] The cultivation of *M. trossulus* contributes to the colonization of coastal communities by its larvae, which increases the fertility of *N. heyseana*, because an abundance of food provides high energy reserves.[23] The number of predators is proportional to the density of the prey settlement and the area of its accumulation,[9] and the dynamics of the number of consumers is strictly related to the limiting factor – food.[24]

The food presence seems to have an impact on the vertical distribution of *N. heyseana*, since in the 60s predators were found from the middle and lower horizons of the littoral and littoral baths to a depth of 1m.[3] According to our observations with the increase of marine plantations in the Posyeta Bay, *N. heyseana* began to occur in scallop collectors placed in the open Raid Pallada Bay (Posyeta Bay) to a depth of 17m.

The calculations using the formula of[25] showed that at 15ºC *M. trossulus* larvae are in the plankton for 27 days. A correlation analysis conducted with the 38-year dynamics of the population of *N. heyseana* and the climatic factors have shown that the wind speed in June has a significant positive effect on its reproduction ($r = 0.476$; $p = 0.002$). During their pelagic development, mainly south-eastern winds blow in the Posyeta Bay and the larvae can be carried away from the Minonosok Inlet over long distances. In this case, the larvae of *N. heyseana*, which had been in the plankton for about 4 hours, by the time they reached metamorphosis could have lost the food supply coming from the plantations in Minonosok Inlet, if not for the mechanism of their return to their parents by the deep countercurrent.[26] Most of the late larvae have negative phototaxis and descend into the lower horizons overnight,[27] being carried with the bottom stream to the shore[28] where they find their prey.

The larvae of the planktotrophic *M. trossulus* have a negative impact on the community of small phytoflagellates in the Vostok Bay,[29] which is typical for planktophages.[30] *M. trossulus* begins to spawn earlier than *A. amurensis*, which has a planktotrophic larva.[31] The area of plantations in Minonosok Inlet is not less than in Vostok Bay, therefore, the early finding of *M. trossulus* larvae in plankton and their eating of phytoplankton is probably one of the main factors that reduced the abundance of *A. amurensis* juveniles in scallop collectors by an order of magnitude in 1979 – 1989.[32]

During the period of high trophic load on diatoms caused by the joint cultivation of *M. yessoensis* and *M. trossulus* in the Minonosok Inlet, the abundance of *A. amurensis* juveniles in collectors decreased, and *N. heyseana*, which has a stock of yolk and does not need phytoplankton, increased from 1977 to 1995 (Table 1). The ability to feed on older prey allows *N. heyseana* to lag behind by a year their main food source, *M. trossulus*, and the relative abundance of prey-predator numbers acquires a classic appearance.[33-35] However, the juveniles of *A. amurensis* cannot overpower one-year-old *M. yessoensis*, so their relative abundance patterns coincide.[36,37]

In *A. amurensis* larvae, a preferred colonization of collectors with a larger number of mollusks was found.[37] According to literature data, chemotaxis is well known in gastropods when larvae are choosing a substrate.[13] Probably, it is also present in *N. heyseana*, since the abundance of *M. yessoensis* in collectors with *N. heyseana* was higher than without it (on average 856 and 796 individuals accordingly).

Outside,[38,39] many publications have noted the desire of predators to optimize their nutrition by selecting the largest prey[5,6,40,41] and the rate of consumption depends on the size of the predator.[42] However, the size selection by the predator can lead to depletion of the main age class of the prey.[43,44] By eating large individuals, *N. heyseana* and *A. amurensis* reduce the total number of *M. trossulus* and its growth rate increases (Figure 8) along with the survival rate of the surviving individuals.[22] Susceptibility to predation decreases with the thickening of the shell[45] as well an increase in the size of the prey.[46]

Having reached a height of 40 mm, *M. trossulus* becomes largely invulnerable,[41] however, *N. heyseana* does eat large prey, up to 59 mm.

The intensity of *Nycella* predation largely depends on temperature and increases before spawning,[23,40,47] as confirmed by our aquarium observations. In winter, the nutritional requirement of one individual of *N. heyseana* did not exceed 0.05 *M. trossulus* per day, but before spawning it increased to 0.50 individuals per day (Figure 13).

In predatory gastropods, the assimilation efficiency is higher than in herbivores and it ranges from 60 to 90%,[13] and in *N. lapillus* it reaches 66%.[40] We obtained similar values for *N. heyseana* on artificial substrates and in an aquarium (63.6 and 65.5%, respectively).

The effectiveness of gastropods as predators depends on the surf strength of waves and drainage.[47-50] Perhaps, therefore, the growth rate and the life duration *N. heyseana* in collectors exceeds that of those living on the sea floor,[22] and the compensatory growth observed in many animals[51] is also observed in *N. heyseana* in the aquarium (Figure 10). The larvae of cultured mollusks settling to the sea floor increase the abundance of food for *N. heyseana* there and they reach 44mm in shell height, and the largest individual of *N. heyseana* in the 60s reached 38mm at the bottom.[3] The fertility of *N. heyseana* has also increased, as their abundance at the bottom has increased.

The ability of large *N. lapillus* individuals to push apart the flaps of *Mytilus edulis*[9] and even use drugs[41] somewhat conceals their predatory role, since there are no holes on the empty flaps. Perhaps, therefore, the observed preference of some large *N. heyseana* for the small *M. trossulus* (Figure 9) arose from the fact that some of the large *M. trossulus* deaths (13%) were misclassified as natural causes because no drill holes were found.

During the feeding process, predators can switch from their favorite food to an energetically more profitable one, and the preferred prey species has a chance to preserve the population.[2,10] However, the littoral *M. trossulus* are doomed to complete destruction due to the hydrology of the area.[6,7] According to observations in Trinity Inlet, by the end of June, we found only 50 *M. trossulus* of spawning two-year age. The cape where they survived was characterised by strong surf.

In littoral biocenosis, mussels are often a competitive dominant and they are the preferred food of starfish,[52] *Tais* and *Nucella*[8,48] which increases the species diversity of the community. A slight increase in the number of bivalve species with *N. heyseana* in scallop collectors was also detected in our experiments. In part, this smooths out the negative impact of mariculture plantations on the species richness of benthic communities.[53]

Global warming has a positive effect on the reproduction of *M. trossulus,* since we found in the Posyeta Bay a small positive correlation coefficient ($r = 0.24$; $p = 0.155$) between annual changes of water temperature in June over 38 years and the abundance of its juveniles in scallop collectors. As a result of an increase in the abundance of food, the fertility of *N. heyseana* will increase. *N. heyseana* and its juveniles will begin to populate scallop collectors and cages again, which will have a positive effect on the production performance of *M. yessoensis* by suppressing *M. trossulus.* At the end of the fifth month of life of *M. yessoensis* in collectors, their survival and size were higher with *N. heyseana.*[22] In the case of *N. heyseana* settling into cages with one-year-old scallops, the predator, having eaten 102 specimens of *M. trossulus* in a year, can eat two-year-old *M. yessoensis* (shell height 73mm). However, the survival rate of the remaining *M. yessoensis*, their size, weight of soft tissues and the muscle turned out to be higher than that of those living in a cage with two *A. amurensis* and especially without predators.[22]

The publications on the absence of a pelagic larva in the genus *Nucella (Thais)* contradict the data of[54] on the pelagic larva in *T. haemastoma* in the tropical Atlantic Ocean and in *T. emarginata* at the California coast. The presence of a pelagic larvae in *N. heyseana*, which lives on artificial substrates, as well as the presence of other gastropods on such substrates: *Boreotrophon candelabrum* and *Mitrella burchardi* suggest a pelagic stage in them. At least *M. lunata* has it cited by[54]

Conclusion

Protected by law due to its rarity, *C. burnettii* commonly destroys bivalves that are trophic competitors of cultivated *M. yessoensis*. Therefore, the presence of this species under plantations improves the living conditions of the juvenile *M. yessoensis* sown on the bottom. The results of our experiments showed the negative impact of the Pacific mussel *M. trossulus* on the production of cultivated *M. yessoensis* and the preferred consumption of *M. trossulus* by a predator – *N. heyseana* allows us to recommend it as a biological defense against competitors of *M. yessoensis.*

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Some of the work reported in this paper was done before 2000 and the data used to generate some of the figures is no longer available.

Conflicts of interest

We declare that there is no conflict of interest of any kind.

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