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INVESTIGATION OF TROPHIC INTERACTIONS BETWEEN INTERTIDAL PREDATORS AND THEIR PREY: FOCUS ON GASTROPODS OF GENUS NUCELLA

The aim of this study was the investigation of trophic interactions in intertidal food webs with focus on trophic links between rocky intertidal predators of genus Nucella and their prey (mussels and barnacles). Foraging strategy of naturally feeding dogwhelL· was observed in the field. The pattern that dogwhelks tended to prey mostly on Mytilus californianus rather than on Mytilus trossulus and barnacles was clearly seen. Complete diet records were obtained for 16 dogwhelL· fed on Mytilus trossulus in the laboratory experiment. The results indicated preferential consumption of larger mussels regardless the individual weight of a whelk. Correlation between growth in shell and body mass with number of mussels consumed turned to be questionable. ä

Introduction

In order to understand the trophic links between rocky intertidal predators and their prey (*Nucella* spp., mussels and barnacles respectively) this study was carried out. The goal of this study was to examine the feeding behavior of individuals in a population of marine snails both in lab and in the field (Boiler Bay and Strawberry Hill study sites).

Whelks are ubiquitous gastropod predators in mid-low zones of rocky intertidal communities around the world, where they can have from negligible to extreme effects on their prey. The *Nucella* whelk and other members of its genus have been shown to be important predators in rocky coastal areas of Great Britain [5, 15], New England [9, 10] and the northeast Pacific [4, 6, 7].

On the wave-exposed coast of Oregon the whelks *Nucella ostrina* and *Nucella canaliculata* are found in dense aggregations in the low zone, below the mussel beds of the California mussel *Mytilus califomianus* in patches among the mussels in the mid-zone [13]. These *Nucella* species have similar activity patterns, remarkably similar preferences for prey species and prey sizes [18], approximately the same prey consumption rates, and similar effects on mussel prey in the lower intertidal zone of the Oregon coast [17]. Although predation by both species is restricted to small prey sizes (whelks cannot handle large prey) [7, 18], they can have important effects on mussel and barnacle populations [5, 7, 16, 17].

Dogwhelks take from several hours to more than a day to handle each prey item. The shells of eaten prey remains attached to the rock for many days. Dogwhelks search for prey only during tidal immersion, when they move net distances of up to about 0.2 m [9]. Individual dogwhelks may be expected to differ in their foraging activities [20]. Activity and the process of predation by *Nucella* species were observed in the field. After selecting its prey, *Nucella* normally drills trough the shell, inserts its proboscis, and rasps out the soft body parts with the radula. Observations made at both low and high tides indicate that the snails are most active when submerged; they remain relatively inactive after exposure to air at low tide [20]. If an animal is feeding at the time of a receding tide, it continues to grip its prey while exposed to air. The predator's proboscis is usually not extended into the prey during low tide, but the snail remains in the feeding position until it is submerged again. Snail remains with the same individual prey from hours to days, depending on size and species of the prey.

Growth in shell and body mass, measured at the beginning and end of the field experiment, proved to be correlated with consumption of mussels (energy intake), which in turn varied among individual snails.

Methods

Study sites: *Nucella* field feeding data were collected at our study sites: Boiler Bay (BB) (44° 15' N, 124°03' W) on April 22, 2002 and Strawberry Hill (SH) (44° 15' N, 124°07' W) on April 23, 2002. Two sites are separated by 83 km on the central coast of Oregon, USA [12, 13]. Both sites include broad rocky benches with a range of wave exposures. These intertidal communities are typical of rocky shores assemblages in the Pacific Northwest, with the exception of the differences in relative dominances of seaweeds, sessile invertebrates, and invertebrate consumers [14]. Zonation patterns are clear at both sites, but there are differences in community structure, particularly in the low zone. At BB algae dominate the low zone and bare space is scarce, the low zone at SH exposed is dominated by filter feeders (mostly barnacles and mussels) and bare rock space [17].

Nucella feeding behavior was observed at wave-exposed areas at each site. At SH the wave-exposed area was a series of irregular outcrops and benches broken up by large pools and surge channels. This area was directly exposed to breaking waves [19]. Bench at BB ran perpendicular from the shore out into the ocean. Nucella feeding was examined at the wave-exposed area of the bench.

Field survey design: Horizontal transects were established along the lower edge of the mussel beds (where whelks are most common). Every effort was made to observe the snails and their prey with minimal disturbance. Every whelk found was first identified. If it was sitting on or close to a barnacle or mussel, the shell was gently tilted away from the anterior end until proboscis could be seen. If proboscis wasn't seen, we checked the spots where the snail's mouth was against the prey and looked for holes, pits, or if it was over the edge of a mussel shell or a barnacle operculum, a notch. If no holes or pits or notches were found, the snail wasn't feeding. Shell length of each snail was measured and recorded. Prey species were also identified and recorded in data book. All data were analyzed in Microsoft Exel. Graphs were constructed using Chart Wizard Microsoft Exel.

Lab experiment design: Specimens of *Nucella canaliculata* were collected at Yachats, OR and transported to the laboratory. While in the laboratory, dogwhelks were kept in tanks in recirculatory seawater at 12 °C. Shell length of 16 snails (from apex to siphonal canal tip) was measured with the ruler to the nearest 1 mm. Snails were measured and weighted at the beginning and end of the experiment. After all measurement were done, specimens were placed two per each of eight plastic containers with holes and mesh screens to allow water flow while keeping whelks inside. The prey cohorts were placed in the containers with predators: 25 small (< 2 cm) and 25 large (> 2 cm) *Mytilus trossulus.* Snails were serviced daily for eight days. Mussels eaten were counted and replaced. Appropriate records were made (number and sizes of mussels eaten). Two control containers were also maintained (C1 and C2) with 25 'small' and 25 'large' mussels, but no predators in order to check the assumption that all mortality of mussels is due to predation. Control containers were maintained the same way as treatments, mussels were counted and any mussels that had died were removed and replaced with the same size new individual.

The experiment was terminated after 8 days on 1 May 2002.

Results

Field observations: The data obtained suggest that more snails of species *Nucella ostrina* than those of species *Nucella canaliculata* were observed feeding in the field (~60 % vs. ~50 % at SH and ~70 % vs. 5 % at BB) (Figure 1). The graph also shows that predation of *Nucella ostrina* was more intense at BB and predation of *Nucella canaliculata* at SH.

Figure 2 shows that whelks of species *Nucella ostrina* were observed feeding mostly on *Mytilus californianus* (> 20 %) and less on *Mytilus trossulus* (5 %) and barnacles (2–4 %).

Figure 3 shows that *Nucella canaliculata* were also observed feeding mostly on *Mytilus californianus* (20 % at SH and 50 % at BB) and less on *Mytilus trossulus* (5 %) and barnacles (3 %).

Lab experiment: Complete diet records were obtained for 16 dogwhelks in the lab experiment. The total number of mussels (*Mytilus trossulus*) eaten by individuals is presented in Figure 4. The pattern that 'small' whelks tend to eat less mussels and 'larger' whelks tend to eat more mussels (except the largest whelk) can be observed.

In Figure 5 one can see how many large vs. small mussels were eaten by individuals in each container.

Figure 6 shows the pattern of preferential consumption of large mussels regardless the weight of the snails.

Figure 7 shows the comparison of the weight obtained at the beginning of the experiment vs. end weight (average weight of two individuals in container). One can clearly see that in each container

Figure 1. Nucella canaliculata

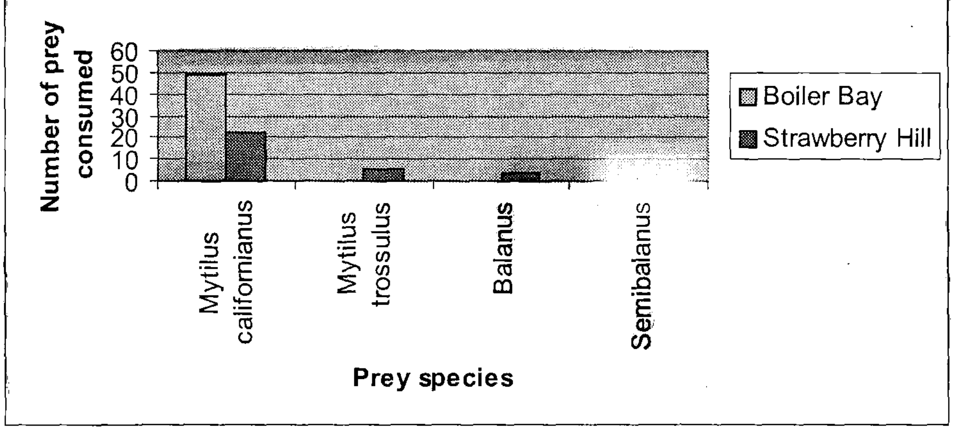


Figure 2. Nucella ostrina

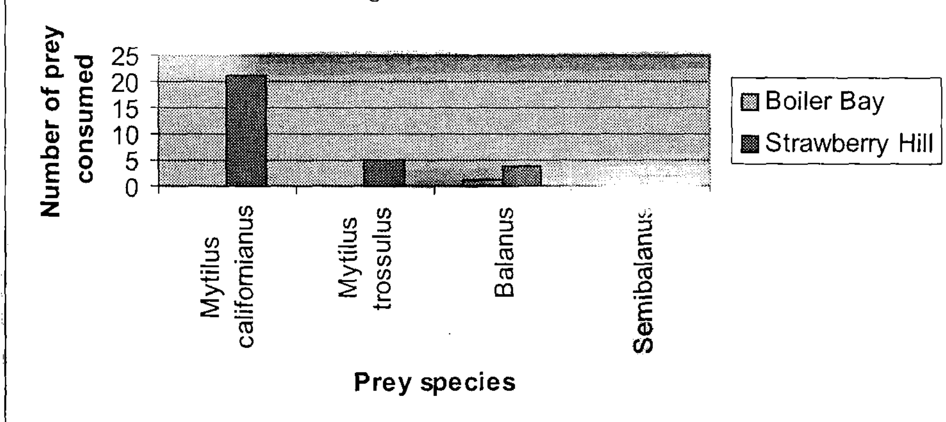


Figure 3. Persent observed feeding

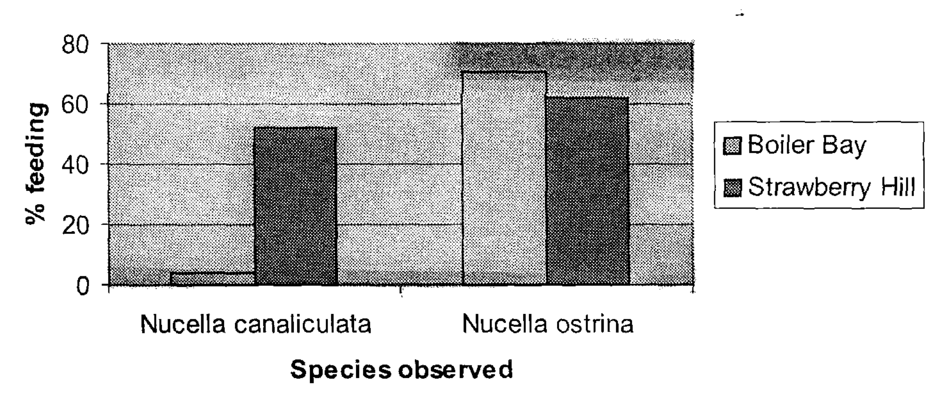


Figure 4. Number of mussels eaten (8 days)

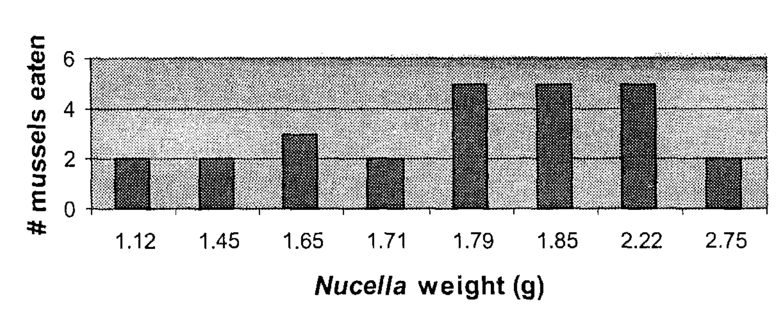
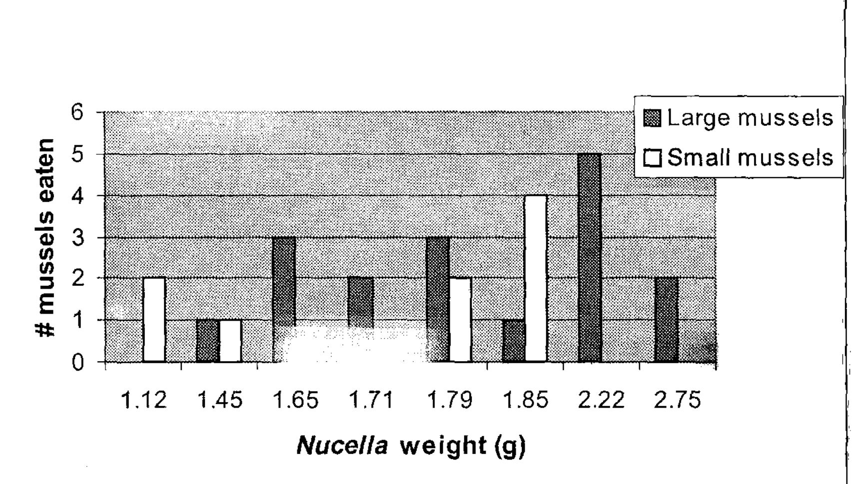


Figure 5. Number of mussels eaten: large vs. small mussels



snails gained weight (about 0.1–0.3 g) during the length of the experiment.

Figure 8 shows my attempt to find a correlation between the number of mussels eaten and the net weight gained. My hypothesis that the more mussels are eaten the more net weight should be gained wasn't supported. Net weight gained turned not to be a function of whether snails ate more or less mussels.

Figure 9 shows comparison between number and sizes of Mytilus trossulus eaten by whelks in each container and net weight gained as measured at the end of the experiment.

Figure 6. Preferences in mussel consumption

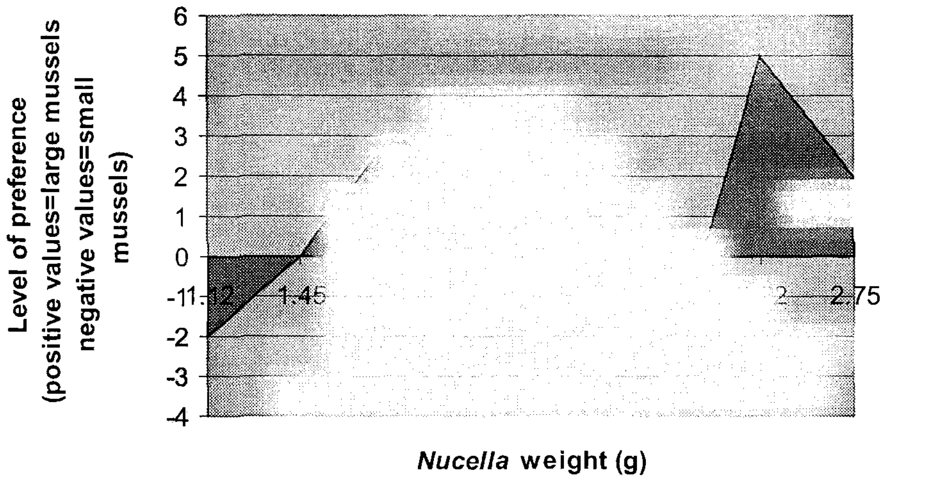


Figure 7. Start weight vs. End weight of *Nucella canaliculata*

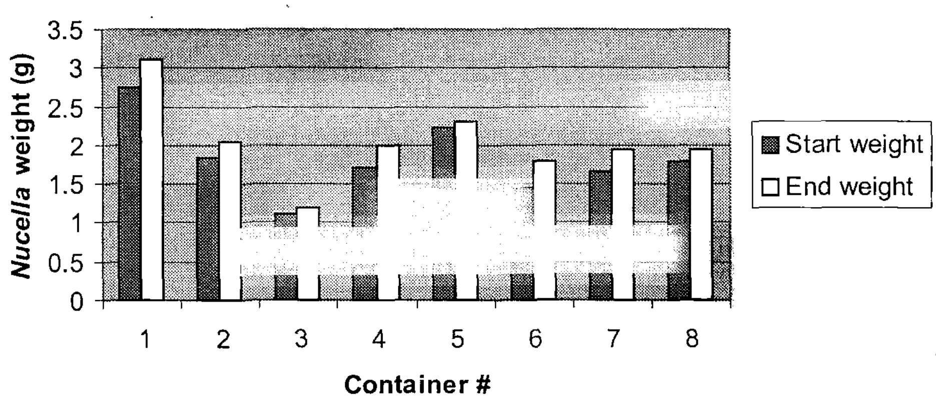
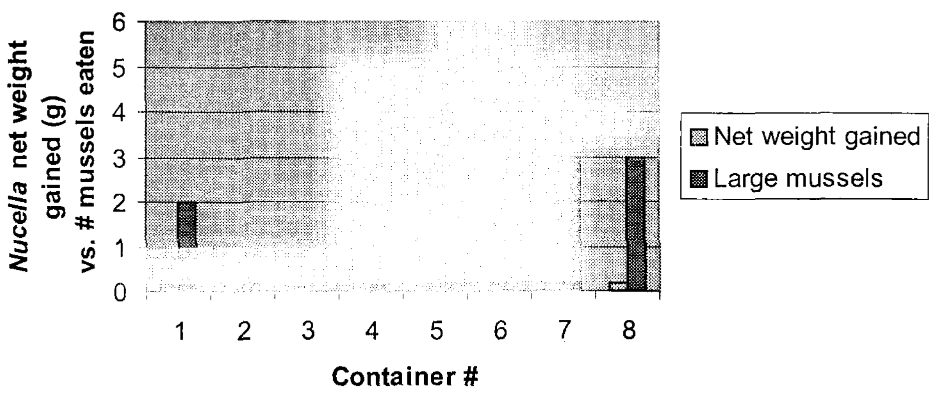
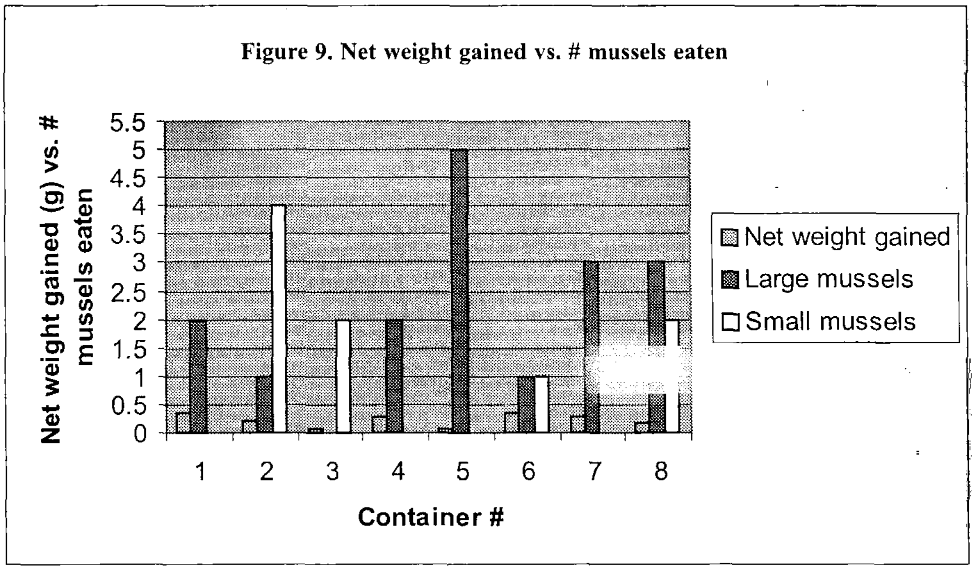


Figure 8. Comparison between # mussels eaten & *Nucella* net weight gained





Discussion

Field observations: SH and BB study sites are inhabited by several species of carnivorous snails. Of those species, *Nucella ostrina* occurred in the highest densities at both sites (personal observations), followed by *Nucella canaliculata*. Prey species eaten at the two sites were the mussels *Mytilus californianus* and *Mytilus trossulus* and the barnacles *Balanus glandula* and *Semibalanus cariosus*. Of those prey species only *Balanus glandula* and *Mytilus californianus* were eaten at BB. All species of mussels and barnacles were eaten by both *Nucella ostrina* and *Nucella canaliculata* at SH. I suppose this pattern is due to invertebrates' domination at SH and the fact that they are relatively scarce at BB, hence observed to be eaten less. However, study of Lani West [20] demonstrated that differences between individual snail diets are not necessarily linked to the relative abundance of prey than an individual contacts as it moves across rock surfaces. Hughes and Dunkin [9] also report that diet preferences of *Nucella* in laboratory choice experiments were not changed by short-term fluctuations in relative abundance of prey species. In Washington State Palmer [18] found that *Nucella ostrina* (= *emarginata*) and *Nucella canaliculata* did not simply eat whatever potential prey they happened across, nor did snails choose prey in proportion to the relative abundance found in their surroundings.

Dogwhelks tended to take larger numbers of prey in 'mussel' diets than in 'barnacle' diets (Figures 2 and 3).

Another pattern observed at the field was that the distribution of whelks over space was not homogenous. Some areas within the study site had more whelks, while in others whelks were scarce. However, high frequencies of whelks were not necessarily areas with higher densities. The effect of this spatial variation in frequency and density of whelk *Nucella* could also affect our results.

Although we have quantified in some detail the diets of naturally feeding dogwhelks, we know little of the behavioral decisions that underlie the observed diets. Prey are distributed in a complex spatial pattern on the shore, while predators are likely to have highly variable perceptions of encounter rates and handling times, depending on their history of prior encounters.

Lab experiment: From our observations of *Nucella* feeding in the lab we couldn't come up with any hypothesis about its preferences in prey diet (mussels vs. barnacles or *Mytilus californianus* vs. *Mytilus trossulus*) because all whelks were fed on *Mytilus trossulus*. What we could observe was the pattern illustrated by Figure 6 that shows that during the lab experiment whelks showed the highest rate of consumption of 'large' (> 2 cm) mussels of species *Mytilus trossulus* (positive values at the upper part of the graph). Dogwhelks preferentially consumed larger mussels regardless their own weight. On the graph (Figure 6) one can see that both 'small' and 'large' whelks ate more larger size mussels than small ones. I assume that large mussels were often preferred because they assimilated more efficiently and promote maximal growth of whelks. *Nucella* in containers #1, 4, and 7 ate only large mussels and as the result gained most weight at the end of the experiment. Unexpectedly, individuals in container #5 that ate only large mussels, moreover they consumed the largest number of those – 5 prey items per

8 days (Figure 5), didn't show any significant changes in weight at the end of the experiment (Figure 9).

Possible explanation for this pattern could be the fact that growth characteristics of *Nucella* depend upon the state of maturity, phenotype and environment. Young animals and sub-adults tend to accumulate shell and body mass faster than adults, and males may grow at a different rate from females [8].

The great individual variation in prey consumption rates among whelks seems to indicate that their behavior may depend upon the internal state of the predator. Dogwhelks exhibit bouts of feeding and resting when provided with mussels in the lab [1]. The post-ingestive pause is thought to be associated with digestion of the previous meal.

Stress may also affect foraging activity of *Nucella*. Individuals could avoid feeding during periods associated with changes in environmental conditions while in the lab.

The results we got are also not very reliable because of the lack of data, short duration of the experiment and limited number of treatments. Human factor also plays an important role. The experiment was monitored by different people, some of them probably couldn't identify the holes drilled by whelks, because of its small size and byssal threads that covered mussel shells and thus could hide the signs of foraging activity. We also had a couple mussels died in the control containers (without predators), thus we can assume that mussels could die regardless predation by whelks.

All the factors mentioned above lead to the conclusion that in order to better understand trophic interactions between rocky intertidal predator *Nucella* and mussels, more studies need to be done. The results we obtained during the experiment should be the stimulus for further investigations and discoveries.

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ДОСЛІДЖЕННЯ ТРОФІЧНИХ СТОСУНКІВ ТИПУ «ХИЖАК-ЖЕРТВА» НА ПРИКЛАДІ МОЛЮСКІВ РОДУ *NUCELLA*

У статті наведено результати дослідження, проведеного з метою вивчення трофічних зв 'язків типу «хижак—жертва» на прикладі молюсків та ракоподібних припливно-відпливної зони Північно-західного узбережжя Тихого океану (штат Орегон, США). У ході польових спостережень досліджено харчову поведінку черевоногих молюсків роду Nucella безпосередньо в їхньому життєвому середовищі. Спостерігалася чітка тенденція до переважання «мідієвої» дієти над дієтою з ракоподібних та до вибіркового поїдання особин виду Mytilus californianus більшістю морських равликів досліджуваних популяцій. Харчову поведінку 16 особин Nucella було досліджено в лабораторному експерименті, у ході якого визначилася тенденція до переваленого поїдання більших за розмірами мідій (умовно «великих»), незалежно від індивідуальної маси хижака. Залежність приросту біомаси та розміру черепашки Nucella від кількості спожитих мідій виявилась недостовірною.

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