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RESEARCH PAPER

Foraging Behaviors of a Predatory Snail (*Hexaplex trunculus*) in Group-Attacking

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Abstract

The behavior of a group of predators may have effects which cannot be predicted using data from a solitarily observed predator however in many experimental studies on the aspects of predation, one predator at a time have been examined. In the present study consumption rates of *H. trunculus* were tested with experimental setups that allow communal feeding, and some reassessments were attempted to be made on the foraging capabilities of this species, which can be used in ecology and aquaculture studies alike. Furthermore, the influence of predator hunger level was evaluated in an auxiliary experiment. Experiments were designed as two equal periods. The prey species *Mytilus galloprovincialis* were offered to the snails in four size groups. Consumption rates of *H. trunculus* were found to be highly consistent between the first and the second period and were about 0.09 mussel snail^{-1} day^{-1}; higher than previous reports. In the hunger level experiment which had a shorter experimental duration, consumption rates were quite high in the beginning and were decreased drastically after the first period as expected. Consumed prey sizes did not differ between main and hunger level experiments; therefore, snails did not make a particular size selection caused by their hunger level.

Introduction

Muricid gastropods may have a strong effect on the population dynamics of benthic communities; the impact of their predation may cause major changes on diversity and abundance of their prey (Menge, 1976; Carriker, 1981; Morton, 2004, 2008; Kosyan, 2016). *Hexaplex trunculus* (Linnaeus, 1758) is one of the most widespread and common members of family Muricidae in Mediterranean region (Rilov, Benayahu, & Gasith 2004; Morton, Peharda, & Harperet, 2007); *H. trunculus* is a generalist opportunistic predator, can forage on a wide variety of prey (Morton *et al.*, 2007) and is a heavy consumer of valuable and cultivated bivalve species like *Ostrea edulis* and *Mytilus galloprovincialis* (Peharda &Morton, 2006). Moreover *H. trunculus* is a commercial marine food and the primary source of the ancient dye Tyrian purple (Cooksey, 2001; Lahbib, Abidli, & Trigui El Menif, 2011; Zarai, Balti, Mejdoub, Gargouri, & Sayari, 2012).

Due to its ecological importance as a generalist predator species, its impact on cultivated bivalves and its economic importance, many aspects related to *H. trunculus* were previously studied, for example: reproduction and larval development (Lahbib *et al.*, 2011; Güler & Lök, 2014), aquaculture and stock management (González-Tizón, Fernández-Moreno, Vasconcelos, & Martínez-Lage, 2008; Lahbib, Abidli, & Trigui El Menif, 2010), morphology and population dynamics (Marzouk, Chenuil, Blel, & Saïd, 2016; Vasconcelos, Barroso, & Gasparet, 2016; Elhasni *et al.*,

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2017), food processing (Zarai *et al*., 2012), bioaccumulation and imposex (Anastasiou, Chatzinikolaou, Mandalakis, & Arvanitidis, 2016; Lahbib, Mleiki, & Trigui El Menifet, 2016; Cacciatore *et al*., 2018), Tyrian purple dye (Vasileiadou, Karapanagiotis, & Zotouet, 2016), as well as behavioral feeding mechanism (Rilov *et al*., 2004; Peharda & Morton, 2006; Morton *et al*., 2007; Sawyer, Zuschin, Riedel, & Stachowitsch, 2009; Güler & Lök, 2016). *H. trunculus* mostly accesses its preys flesh by drilling and/or chipping and can consume a broad size range of its bivalve prey; leaving abandoned shells after a few predation steps (Peharda & Morton, 2006).

As a common and useful (often necessary) way to investigate the feeding mechanism or consumption rates, “one chamber per one predator” experimental setup is frequently used for predatory gastropods (e.g. Savini & Occhipinti-Ambrogi, 2006; Das, Chattopadhyay, & Chattopadhyay, 2015; Hu *et al*., 2016), as well as other benthic predatory organisms such as sea stars (e.g. Güler & Lök, 2015) and so on. However, multiple predators may have unexpected effects which cannot be predicted using data from a solitarily observed predator (Sih, Englund, & Wooster, 1998; Chattopadhyay & Baumiller, 2007). In the example of *H. trunculus*, Peharda and Morton (2006) reported feeding characteristics and feeding rates preying on Mediterranean mussel (*Mytilus galloprovincialis*) in their detailed study, using “one chamber per one predator” experimental setups (however they also reported group foraging behavior for this species from field and laboratory observations). And in a recent study, communal feeding and group attacking events were reported for juvenile phase of *H. trunculus* (Güler & Lök, 2016). Consequently, additional research on communal feeding became necessary to obtain more knowledge on the foraging behaviors of *H. trunculus*. Furthermore, studies pointed out group foraging behavior in drilling predator-prey systems are limited. In an example on the naticids, Hutchings and Herbert (2013) investigated the effects of communal feeding and competition on the frequency of incomplete drill holes. On the Muricids, Chattopadhyay and Baumiller (2007) focused on the drilling behavior again. According to Brown and Alexander (1994) group foraging may have only small benefits to another muricid *Stramonita haemastoma*. In the present study some aspects of foraging behaviors of *H. trunculus* were tested with experimental setups that allow communal feeding, and some reassessments were attempted to be made on the foraging capabilities of this well studied species, which can be used in ecology and aquaculture studies alike.

As shown in previous studies with predatory gastropods, the behaviors observed during the predation event such as the attack type, attack place, prey type or prey size selection can be dependent on some basic tactics (Hughes & Dunkin, 1984; Ansell & Morton, 1987). And generally, these tactics are associated with the predictions of the optimal foraging theory (Hughes, 1980; Pyke, 1984). In relation to the adaptations of this theory, effects of the predators hunger level may play an important role in the whole predation event (Hughes &Dunkin, 1984; Perry, 1987; Croy & Hughes, 1991; Das *et al*., 2015). In the present study, the effects of hunger level on the consumption rates and prey size selection of the predators were evaluated as well as the other aspects.

In the experiments, Mediterranean mussel (*Mytilus galloprovincialis*) was used as the prey species. *M. galloprovincialis* was considered as a suitable prey species for this kind of study with *H. trunculus*. Using this species as prey provides ease of comparison with the previous studies and more importantly, beside its key role in benthic communities, *M. galloprovincialis* is a valuable bivalve species and widely cultivated in Mediterranean area (Neofitou *et al*., 2014; Irisarri, Cubillo, Fernández-Reiriz, & Labarta, 2015) and *H. trunculus* is considered its pest in some culture areas (Peharda & Morton, 2006).

Materials and Methods

Adult *H. trunculus* individuals (hereafter snails) were collected from the Urla seashore (Izmir, Turkey; Figure 1), and taken to the laboratories of the Fisheries Faculty, Ege University in Urla. Snails were stocked in 500 L indoor tanks with running seawater and aeration. Throughout the adaptation period (approximately 3 months) they were fed ad libitum with live bivalves and fresh fish meat. Prey species, *M. galloprovincialis* (hereafter mussels), used in the study were collected from shores of Izmir Bay (Turkey; Figure 1) then transported to the laboratories. After classification as four size categories according to their SL (S1: 30–35 mm, S2: 40–45 mm, S3: 50–55 mm and S4: 60–65 mm) mussels were placed in 500 L indoor stock tanks with running seawater and aeration. Average wet flesh weights of the mussels were obtained by extracting and weighing the flesh of 10 representative mussels for each size class before each experimental phase. These values were used to calculate feeding amounts of the snails.

Before the beginning of the experiments mussels were placed in plastic perforated cases with equal numbers in stock tanks where they remained for about three or four days to complete the byssal attachment process. Snails to be used in the main experiment were transferred to a 1500 L indoor experiment tank with running seawater and aeration. Sizes of the snails were measured between 55–70 mm SL (n=39) during the experimental period. Experiment began with the placement of 4 plastic cases filled with the mussels, on the bottom of the experiment tank. There were 15 mussels of each size group in each plastic case; total 240 mussels (Figure 2). Experiment was ended in 42

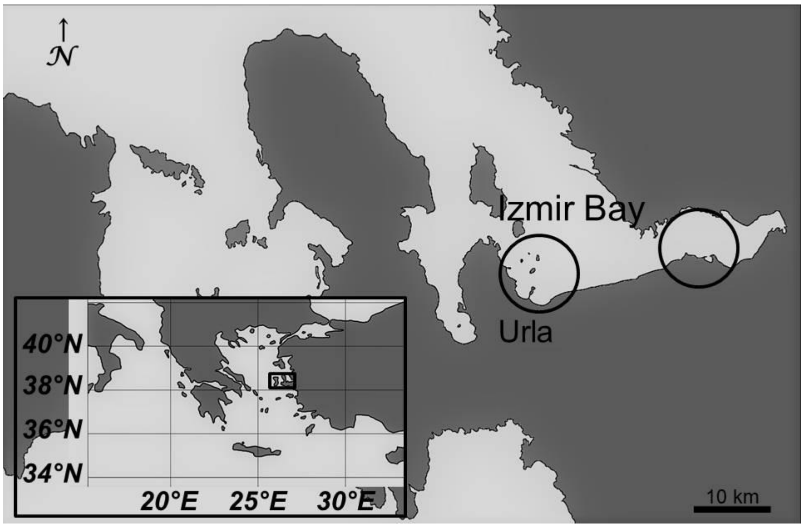

Figure 1. The map of İzmir Bay (Turkey) where the predator (left circle) and prey specimens (right circle) were collected.

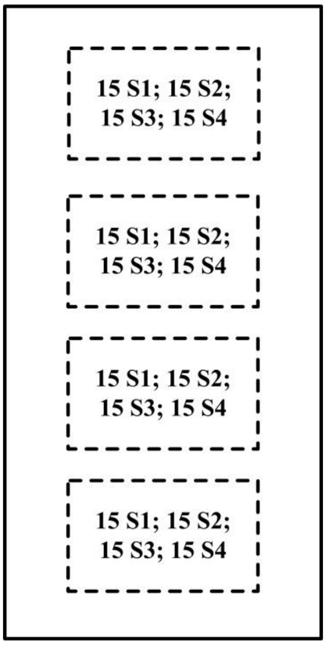

Figure 2. Schematic diagram of the experimental setup and numbers of the mussel per case according to the size groups, S1: 30–35 mm, S2: 40–45 mm, S3: 50–55 mm and S4: 60–65 mm sized mussels.

days and the setups were examined as two periods (21+21 days). Consumed mussels were replaced with similar-sized live mussels; the initial mussel number was maintained as much as possible. After the end of the first period (21 days after beginning), plastic cases were replaced with 4 new cases identical to the initial cases. Setup was monitored continuously and contents of the cases were counted to find consumption rate (simply mortality of the prey, Figure 3a, 3b). Throughout the experiments water temperatures were measured between 23–28 C°.

In the predator hunger level experiment snails were placed in a 1500 L indoor tank, again with running seawater and aeration. Water temperatures were measured between 24–27 C° during the experimental period. In the experiment 34 snails with sizes of 55 to 70 mm were used as predator and mussels used as prey. Four size classes of mussels were used again in the plastic cases same as the main experiment. Before the experiments individuals were starved for 25 days. Some snails died or were wounded by cannibalism during the starving period and were not included in the experiment; there was no obvious reduction in the flesh of the dead snails. Experiment took 8 days and the setup was examined as two periods. In the beginning of the experiments snails were assumed to be starved and in the beginning of the second period were assumed to be full. At the end of the first period

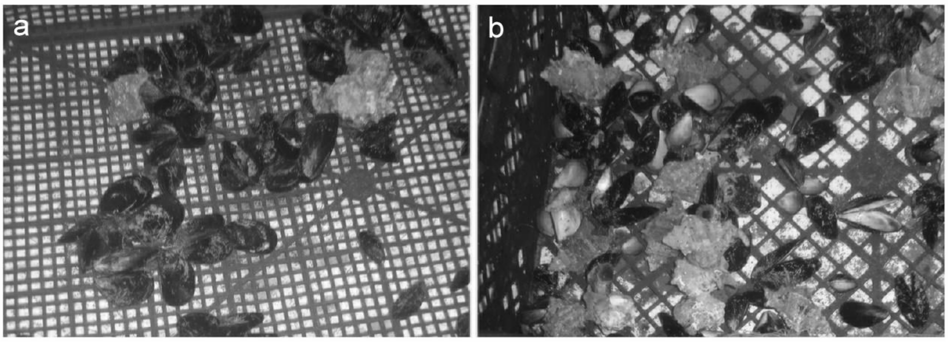

Figure 3. Representative photographs on a predation event from another experiment which has a similar setup; (a) attacking and (b) abandonment of the empty valves of the prey after consumption.

(4 days) contents of the four plastic cases were counted and replaced with 4 new cases identical to the initial cases, and at the end of the experiment counted again. Results of the first four days of the first period of the main experiment and results of the first period of the hunger level experiment on prey sizes were compared with Mann-Whitney U test to find the effect of the hunger level on the sizes of prey eaten.

Results

At the end of the main experiment, snails consumed 143 mussels (73, first period; 70, second period) regardless of the prey size; this is equivalent to a consumption rate of 0.087 mussel snail^{-1} day^{-1}(Figure 4); 0.089 mussel snail^{-1} day^{-1}for the first period and 0.085 mussel snail^{-1} day^{-1}for the second period. At the same time snails consumed 0.15 g mussel wet flesh snail^{-1} day^{-1} during the experiment period; 0.14 g snail^{-1} day^{-1} in the first period and 0.16 g snail^{-1} day^{-1} in the second period (Figure 5). The most consumed mussel sizes were S1 and S2 in the first period while S2 and S3 in the second period (Figure 6). When the wet flesh weights of the mussels are considered, the most consumed mussel size was S3 throughout the entire experiment (Figure 7).

Group attacks were observed frequently in both main and the hunger level experiments and the numbers of the snails in the groups varied continuously. In the first period of the predator hunger level experiment, snails consumed 0.32 mussel snail^{-1} day^{-1} and in the second period 0.04 mussel snail^{-1} day^{-1} (Figure 4). On average, snails consumed 0.33 g mussel wet flesh snail^{-1} day^{-1}in the hunger level experiment (Figure 5) and the most preferred mussel size class was S2 during the entire hunger level experiment (S1=27, S2=33, S3=23, S4=17%). Additionally consumed prey sizes did not differ between main and hunger level experiments ($P>0.1$).

Discussion

Consumption rates of *H. trunculus* preying on *M. galloprovincialis* were found to be highly consistent between the first and the second period of the main experiment. But when compared with the previous studies, the rates seem quite high. Peharda and Morton (2006) calculated that an adult *H. trunculus* (55 mm SL) consumes 12.7 (up to 18) mussels (*M. galloprovincialis*, 50 mm SL) per year. According to results of the main experiments at the present study, an adult snail with a bit larger size can consume ~32 mussels per year; roughly 2 times higher. Several explanations can be made to explain this difference: First, in the present study predators were larger and prey sizes were varied; it is a clear explanation for a difference. However, although the prey sizes were varied in the present study, the mean prey sizes were similar between two studies and predator sizes were not different enough to make a statement by itself to explain such differences between the two studies. Secondly, this result may be a function of communal feeding; group attacks were observed frequently in the experiments. It has been reported before that the benefits of collective consumption are limited for another muricid *Stramonita haemastoma* (Brown & Alexander, 1994) and again for a muricid *Nucella lapillus* Hughes and Dunkin (1984) pointed out the competitive effects of another predator and observed that the other predators or “interlopers” lengthen the pre-consumption inspection and handling times. Another approach, Dietl, Herbert and Vermeij (2004) and Dietl and Herbert (2005) argued that competition may cause changes in the attack type of the predatory snails. Güler and Lök (2016) pointed out dislocation of the snail on its prey due to group-attacking which can cause unsuccessful predation attempts. However, in the same study multiple attacks (and signatures of successful multiple attacks) were frequently observed and mentioned as useful (probably) for the predators. Additionally for *S. haemastoma* again Brown and Richardson (1987) reported that snails feeding in groups had greater consumption rates. So, high consumption rates observed in the present study with *H. trunculus* may set an example of effectiveness of group foraging. Thirdly, water temperatures may have been a factor: Temperature may effect the physiology

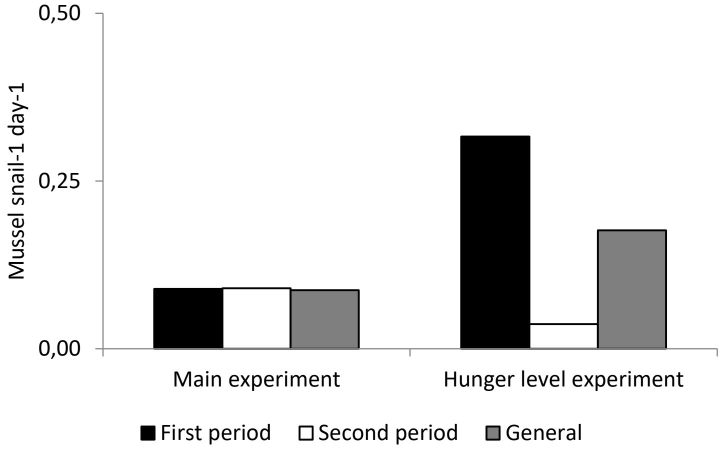

Figure 4. Daily consumption rates of *H. trunculus* feeding on *M. galloprovincialis*, regardless of the prey size.

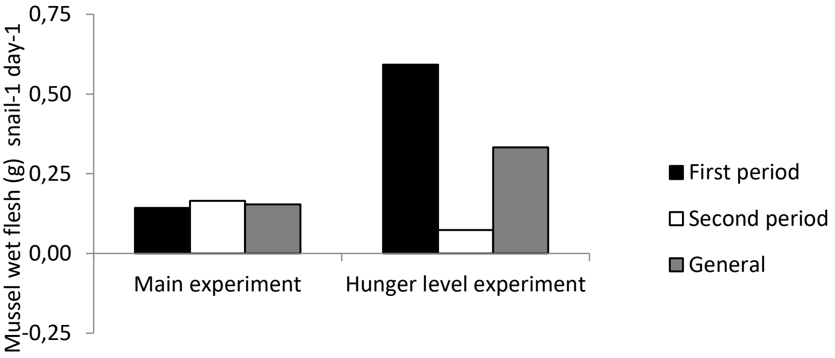

Figure 5. Daily consumption rates of *H. trunculus* as wet flesh weight (g), feeding on *M. galloprovincialis*.

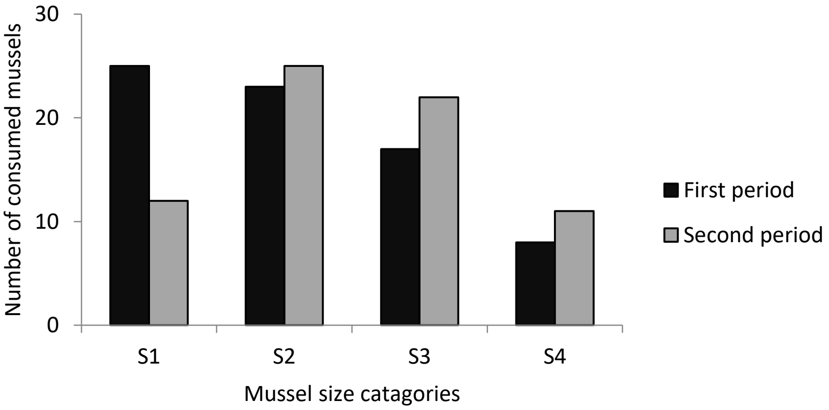

Figure 6. Numbers of consumed mussels from different size categories (S1: 30–35 mm, S2: 40–45 mm, S3: 50–55 mm and S4: 60–65 mm) by *H. trunculus* during the first and the second periods.

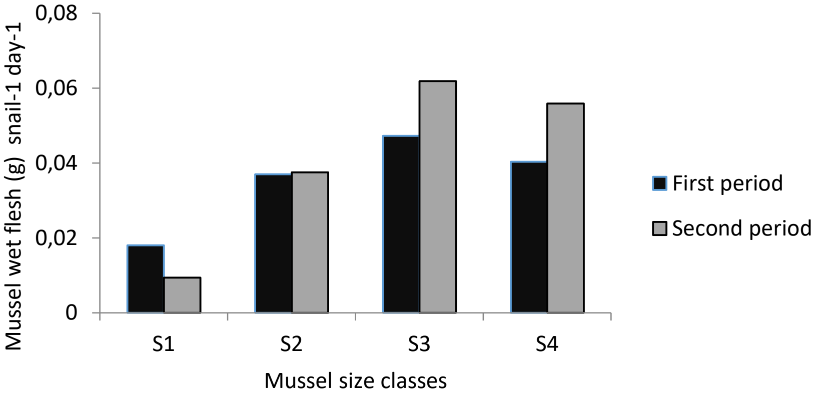

Figure 7. Daily consumption rates of *H. trunculus* feeding on *M. galloprovincialis* as wet flesh weight (g).

of ectothermic animals including gastropods (Yee & Murray, 2004) and present study was probably conducted in higher water temperatures. Miller (2013) reported the reducing effect of the rise in temperature on prey handling time and ingestion time in a muricid snail *N. lapillus*. Probably all three explanations can be considered as logical. Anyway, *H. trunculus* is a predatory gastropod whose presence in the field of bivalve culture areas must be considered (Peharda &Morton, 2006; Morton *et al*., 2007) and according the results of the present study foraging capacities and consumption rates of *H. trunculus*can be re-evaluated with regard to bivalve production aspects as well as ecological perspective.

In previous studies researchers pointed out the wide range feeding capacity of *Hexaplex trunculus*. According to Sawyer *et al*. (2009) there is no size refuge for *Mytilus galloprovincialis* from attack by adult *H. trunculus* in the field. Peharda and Morton (2006) documented that the adults of *H. trunculus* can consume a broad size range of mussels (20-65 mm shell length). Güler and Lök (2016) reported similar results with the juveniles (post larval form of *H. trunculus* up to SL of 15 mm); although they showed preference for particular mussel size classes according to the predator sizes. The results of the present study are compatible with previous studies; snails could forage a broad size range of mussels. Additionally consumed prey sizes did not differ between main and hunger level experiments. This result can be considered as compatible with both reports of Peharda and Morton (2006) that indicate non selective behavior of this species preying on mussels and assumptions of Elner and Hughes (1978) that predict on non-elective consumption of a hungry predator. The abundance and accessibility of the prey were similar for all 4 size groups in the both experimental setups and snails did not make a particular size selection caused by their hunger level. Hungry predators are more likely to forage on first prey encountered than to assess the prey profitability (Elner & Hughes, 1978; Kaiser, Westhead, Hughes, & Gibson, 1992) and can be less selective; and it was documented before for naticids (Das *et al*., 2015) and muricids (Perry, 1987) that prey selectivity decreases with hunger. Results of the present study were not incompatible with those findings.

The extraordinary consumption rates in the hunger level experiment can be considered a remarkable effect of long starvation and short experimental times. It was documented before that starved muricids (*N. lapillus*) are more motivated than the fed ones (Vadas, Burrows, & Hughes, 1994) and long starvation periods before an experiment may cause overfeeding at the first encounter with the prey (Morton, 2008; Giberto, Schiariti, & Bremec, 2011; M. Güler personal observation). Additionally high feeding rates in the hunger level experiment may relate to high water temperatures and communal feeding, again; group attacks were observed intensely during the hunger level experiment too. Consumption rates drastically decreased after the first period in the hunger level trial. Similar results on muricids were reported before, for example Hughes and Dunkin (1984) reported becoming idle for a variable number of days after a successful consumption for *N. lapillus*. It shows the importance of the hunger level of the predator on consumption stability.

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