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ORIGINAL ARTICLE

The role of the predator *Trophon geversianus* in an intertidal population of *Mytilus chilensis* in a rocky shore of the Beagle Channel, Tierra del Fuego, Argentina

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ABSTRACT

Predation influences changes in the abundance and the limits of spatial distribution of organisms on rocky shores. We quantified the effect of the predation pressure of the gastropod *Trophon geversianus* on the mytilid *Mytilus chilensis* in a rocky intertidal community of the Beagle Channel, Tierra del Fuego. We quantified the density of *T. geversianus* along with the density of *T. geversianus* preying on *M. chilensis* and examined the potential relationship between sizes of both *T. geversianus* and *M. chilensis*. Additionally, we carried out laboratory experiments to quantify the drilling and ingestion rates of *T. geversianus* on *M. chilensis* at different aerial exposure times. At mid intertidal levels, unlike at low intertidal levels, *T. geversianus* consumed more frequently the available size range of mussels. On average, sizes of predator and prey consumed were positively correlated. The drilling rate decreased with increasing time of aerial exposure. Additionally, permanently submerged predators invested less time consuming the same amount of food than individuals exposed for 4 out of 12 h (4/12 h). Predators exposed for 9/12 h invested less time and consumed less food than those exposed 4/12 h. Our results suggest that *T. geversianus* is an efficient predator of *M. chilensis*, due to both its high density and feeding rate. Our results suggest that the strong predation pressure of *T. geversianus* on *M. chilensis* prevents this key competitor from monopolizing space at the low level through controlling their abundance, and further limits their vertical distribution.

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Introduction

On a local scale, vertical zonation of intertidal communities is regulated by several physical and biological factors. As a general rule, abiotic stress imposes constraints in the upper levels, whereas biological interactions are more important in the lower zones (e.g. Dayton 1971; Connell 1972; Navarrete 1996; Harley 2007; Rius & McQuaid 2009). Among the latter, predation is one of the most relevant in structuring rocky intertidal communities, causing significant changes in the abundance and distribution of prey, size distribution, composition and diversity of species (e.g. Paine 1966; Menge 2000; see review by Robles & Desharnais 2002). In southern South America, knowledge of processes structuring the intertidal communities is largely different. On the Pacific coasts of Perú and Chile, mussels and barnacles are the main habitat-forming species (Navarrete & Castilla 1990, 2003; Tokeshi & Romero 1995), and can overgrow turf algae (Wieters 2005). North of 35°S, ascidians may

outcompete mussels or barnacles (Valdivia et al. 2005) and large kelps can recruit in and overgrow turf algae (Camus 1994). Post-settlement processes structure these communities including both biological interactions and local environmental factors, converging on a relatively common community structure (Caro et al. 2010). The spatial competitors, i.e. bivalves, may be controlled by predation, as for example the muricid gastropod *Concholepas concholepas* (Brugière, 1789), considered a keystone species preying upon the dominant bivalve *Perumytilus purpuratus* (Lamarck, 1819). The removal of gastropods (e.g. by commercial exploitation) changes the community to a dominance of bivalves (reviewed by Castilla 1999; Castilla et al. 2004). This top-down control holds for communities south to 32–33°S. Northerly, communities are regulated by the differential mussel recruitment caused by variation in the upwelling and subsequent larval supply (Navarrete et al. 2005). Moreover, local environmental conditions can also 'filter' the type of

species successfully establishing in an intertidal community, affecting the community structure (Valdivia et al. 2015). In contrast, the intertidal communities of the Atlantic coast are well described (Zaixso et al. 2015), but structuring mechanisms are poorly understood. Some Patagonian rocky intertidal communities on the Atlantic coast are mainly regulated by desiccation stress, driven by strong westerly winds (Bertness et al. 2006), competition for space, and physical disturbance (Calcagno et al. 2012; Gutiérrez et al. 2015). The Beagle Channel is a transitional area, connecting the Pacific and the Atlantic Ocean at the southern tip of South America and it is a typical site where faunas of both origins converge, particular processes may take place and thus its scientific relevance is evident (Arntz & Ríos 1999; Barnes 2005).

In the Beagle Channel, the rocky intertidal community of wave-exposed shores shows a vertical zonation with three conspicuous levels: the higher dominated by the acorn barnacle *Notochthamalus scabrosus* (Darwin, 1854), the mid level dominated by the bivalves *Mytilus chilensis* Hupé, 1854 and *Perumytilus purpuratus*, and the low level with *Notobalanus flosculus* (Darwin, 1854) and crustose coralline algae, with a few clumps of *M. chilensis* (Zaixso et al. 1978; Ojeda et al. 2014). The boundary between both the upper bivalve and the lower cirripede with coralline algae levels is rather sharp and abrupt. Below the low neap tide level bivalves become smaller and scarce. Preliminary experiments with exclusion cages at this low level demonstrated that large bivalves are highly predated by snails (Curelovich 2013). In the Beagle Channel, the only predator on intertidal bivalves is the snail *Trophon geversianus* (Pallas, 1774). This species shows a clear upper limit in its vertical distribution and is absent through all the intertidal mussel bed, only occurring up to the lower mid intertidal level (Curelovich 2013). *Trophon geversianus* is an abundant species of southern South America, with a very wide distribution extending on both the Atlantic coast, from 34°36'S to Cape Horn, and the Pacific coast, north to 42°S (Pastorino 2005). *Trophon geversianus* is a typical carnivorous gastropod of intertidal communities of the Magellan region (Ríos & Gerdes 1997; Ríos & Mutschke 1999) and the Beagle Channel (Gordillo 1991, 1994). *Trophon geversianus* is a trophically selective species with a marked preference for *M. chilensis*, probably as a result of both the high abundance of this species on sub-Antarctic rocky shores and its thin shell, which could reduce drilling, and consequently ingestion times (Gordillo & Amuchástegui 1998; Soto et al. 2004; Andrade & Ríos 2007). *Trophon geversianus* is also known to attack the other bivalves

present in these intertidal habitats, e.g. *Perumytilus purpuratus* and *Aulacomya atra* (Molina, 1782), but at a low frequency (Andrade & Ríos 2007).

Models of predator–prey dynamics predict that a predator selects its prey based on the profitability of the types of available prey (Kohn 1983; Hughes 1988). Profitability is expressed as the energy content of the prey divided by the units of time spent by the predator in searching for, dealing with and consuming it (Soto et al. 2004). Muricid gastropods, such as *T. geversianus*, are shell-boring species that excavate cylindrical or frustum-shaped drill-holes in its prey (Gordillo & Amuchástegui 1998; Gordillo & Archuby 2012) through a chemical/mechanical process by which the shell is softened by acid secretions and subsequently rasped using the radula (Carriker 1981). *Trophon geversianus* is the main drilling gastropod along all the Atlantic Patagonian coast, with drilling frequencies of 16% in the Beagle Channel (Martinelli et al. 2013). Thus, the duration of a gastropod attack on its prey includes the time necessary to gain entry into the shell, and to consume the tissue of the prey. Prey organisms have different defence strategies such as distribution in locations of difficult access, or a body size that prevents predation (Paine 1976; Robles et al. 1990; Yamada et al. 1998). Predatory gastropods are very sensitive to air exposure in daytime and changing temperatures during low tide (Menge 1978a), and because they move slowly and take a long time to handle a single prey item, these predators would avoid taking their prey far above the intertidal height where its physiological tolerance is compromised (Connell 1970; Menge 1978b). Consequently, prey organisms tend to be more abundant in areas less accessible to predators. Thus, predation on rocky shores can determine the lower intertidal distribution limits of both sessile and mobile invertebrates (Connell 1961; Paine 1966, 1971, 1974; Yamada & Boulding 1996; Rochette & Dill 2000).

The purpose of this study was to identify and quantify the effect of predation by *T. geversianus* on *M. chilensis* in a rocky intertidal community of the Beagle Channel, southern South America. Our first objective was to estimate the abundance and size–distribution patterns of *T. geversianus* at mid and low intertidal levels, with the hypotheses that both the abundance and sizes of this predator would be higher at low intertidal levels. Our second objective was to estimate the body size relationship of *T. geversianus*–*M. chilensis*, with the hypothesis that large gastropods consume large mussels. The third objective was to quantify the drilling and ingestion rates of *T. geversianus* on *M. chilensis* as a function of aerial exposure time under laboratory conditions, in

order to test the hypothesis that increasing the aerial exposure time would decrease both the drilling and ingestion rates.

Material and methods

Study site

The Beagle Channel is 200 km long and 4 km wide, oriented east–west, connecting the Pacific and Atlantic Oceans at the southern tip of South America (ca. 55°S). Prevailing winds are from the SW at an average speed of 31 km h⁻¹ (Bujalesky 2007). The channel offers a short fetch and waves are of short period (1–3 s), being small plunging breakers of 0.5 m (Bujalesky 2007). These features make the northern coast of the

Beagle Channel slightly to moderately exposed to the wave action. Tides are semidiurnal with an average tidal amplitude of 1.2 m, with maximum and minimum values of 2.20 m and 0.67 m during winter, for spring and neap tides, respectively (D’Onofrio et al. 1989). The present study was carried out on the coast of Ensenada Zaratiegui, Beagle Channel, Tierra del Fuego National Park, Argentina (54°51’S; 68°29’W) (Figure 1a). Average monthly air temperature ranges between -2.0°C and 14.7°C (Iturraspe et al. 1989), and average monthly seawater surface temperature ranges between 5.1°C (July) and 9.5°C (January) (Almendoz et al. 2011).

The rocky coast of Ensenada Zaratiegui is representative of the northern shore of the Beagle Channel (Zaixso et al. 1978) and shows a species zonation

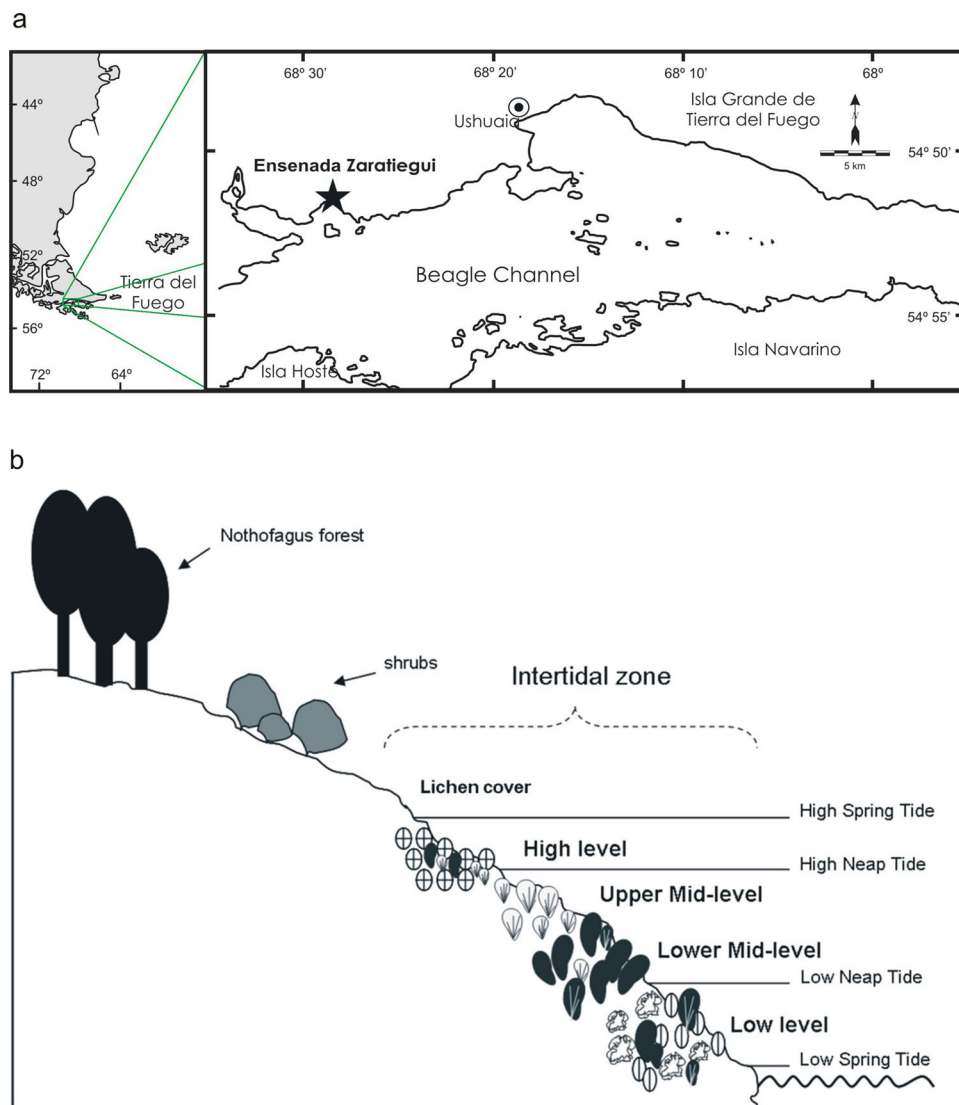


Figure 1. (a) The study site at the Beagle Channel, in Tierra del Fuego National Park, Argentina. (b) Profile of the coastline of Ensenada Zaratiegui, Tierra del Fuego, Argentina. Intertidal zonation pattern is shown. (⊕) *Notochthamalus scabrosus*, (⊖) *Perumytilus purpuratus*, (●) *Mytilus chilensis*, (◐) *Aulacomya atra*, (◑) *Notobalanus flosculus*, (⊗) coralline algae.

pattern. Mytilid bivalves form a band in the mid intertidal level, with *Perumytilus purpuratus* dominating the upper portion (hereafter 'upper-mid level'), while *Mytilus chilensis* covers the lower portion (hereafter 'lower-mid level'). There is an overlapping zone in between where both species are layered, with *M. chilensis* generally occupying the top layer and *P. purpuratus* placed beneath. *Aulacomya atra* occurs at low densities in the lower-mid level. The high intertidal level, which is dominated by barnacles (*Chthamalus* sp.), some individuals of *P. purpuratus* and *M. chilensis* are present mainly in crevices, and individual sizes are much smaller than those in lower intertidal areas. In the low intertidal level, which is dominated by barnacles (*Notobalanus* sp.) and crustose coralline algae, small groups of *M. chilensis* and *A. atra* of varying sizes are observed (Figure 1b). *Trophon geversianus* is abundant at the lower-mid and low intertidal levels. There is no other predatory snail inhabiting this rocky shore.

Density and size distribution of *Trophon geversianus*

To quantify the natural density and size distribution of *Trophon geversianus* at mid and low intertidal levels (above or below ca. 0.35 m of chart datum, respectively), we took 30 samples with a randomly placed 0.25 × 0.25 m quadrat (total area = 0.063 m²) at each level, in September 2008. In each quadrat all *T. geversianus* were counted. At the high level no samples were taken because *T. geversianus* was absent.

For an assessment of size–frequency distributions, the maximum shell length (SL), from the tip of the spire to the end of the siphonal canal, was measured to the nearest 0.1 mm using a digital Vernier calliper. Densities were expressed as the number of individuals per square metre.

Body size relationships of available versus consumed prey and of predator versus prey

To determine two size relationships, the first between available and consumed *Mytilus chilensis*, and the second between *T. geversianus* and *M. chilensis* consumed, we took 10 samples. In this case, we used a modified quadrat consisting of a rectangle of 0.10 × 0.60 m at the mid level because *T. geversianus* is distributed on the lower limit of the mussel bed forming a band (no more than 15 cm wide); thus, a square quadrat would have underestimated the density of the gastropods preying on mussels. We sampled 10 randomly placed quadrats. In each

quadrat we registered the sizes of all mussels without drilling marks and also those of all mussels paired with *T. geversianus* (only mussels that were being drilled or eaten by the predator at the time of sampling were considered, in order to ensure that *T. geversianus* was actually feeding). We also measured the size of *T. geversianus* in these predator–prey pairings. We calculated the instantaneous predation proportion as the ratio between the density of snails attached on and drilling mussels and the density of *M. chilensis* at each of both studied intertidal levels.

Drilling and ingestion rates by *Trophon geversianus* on *Mytilus chilensis* as a function of aerial exposure time

As we did not observe any gastropod preying at higher intertidal levels during the experimental period, we decided to examine the effect of the exposure to air on drilling rate, drilling and ingestion time and amount of meat consumed, under laboratory conditions. Individuals of *T. geversianus* and *M. chilensis* were collected from the intertidal zone of Ensenada Zaratiegui, Beagle Channel, and immediately transferred to aquaria in the Centro Austral de Investigaciones Científicas (CADIC).

Gastropods between 33 and 46 mm (mean length 40.33 ± 3.23 mm) were collected on 30 September 2010. Taking into account that *T. geversianus* takes approximately 9–10 days to drill and consume one mussel prey (Gordillo & Amuchástegui 1998), we starved the organisms for 14 days at 6°C to standardize fast levels. During this period, we did not observe any gastropod killed by cannibalism (but see Cumplido et al. 2011; Gordillo 2013). Mussels between 43 and 58 mm (mean length 47.99 ± 3.44 mm) were collected two days before the beginning of the experiment. Individuals were measured to the nearest 0.1 mm using a digital Vernier calliper. The experiment was conducted in individual 1 l aquaria with standing, aerated seawater at 6°C, placed into a cool chamber. Previously, predators and prey organisms were placed together in 20 l plastic containers with standing, aerated seawater at 6°C, in order to allow pairing between gastropods and mussels, i.e. the gastropod started to prey on the mussel. Six 20 l containers with 10 predators and 20 prey organisms each were used to get 45 pairs. Once the gastropod–prey pair was established, if the predator crawled away from the mussel prey, the pair was discarded and a new one chosen. We achieved a total of 45 pairs after 3 h. Each pair was then transferred to an individual 1 l aquarium. The 45 pairs were randomly selected and assigned to one of the nine

possible combinations of three experiments with different duration and three times of exposure to air: 0/12 which was the permanently submerged as a control, 4/12 and 9/12 h. This pattern of exposure to air and immersion per treatment was repeated twice a day because in the area the tidal regime is semidiurnal, i.e. total hours of emersion per day per treatment: 0/24, 8/24 and 18/24. Exposure to air or immersion of the snail–mussel pairs were performed manually by siphoning or adding water to the aquaria according to the regime established for each treatment. The durations of the three experiments were: 2 and 5 days, and a third time spanned the number of days until the gastropods crawled away from the mussel prey, i.e. *T. geversianus* had finished eating. Water for the control treatment was renewed every 2 days. Treatments for each experiment were replicated five times. The photoperiod throughout the experiment was 8:16 h light:dark. All the experiments extended for a maximum of 14 days.

We quantified the drilling rate, drilling and ingestion time and meat consumed. To estimate the drilling rate after 2 and 5 days the depth of the drilling mark was measured with a Nikon Eclipse Ti microscope by focusing on the top edge and the bottom of the borehole and recording the distance in micrometres.

In the experiment in which the gastropods finished drilling and consuming the mussels, both the number of days since the beginning of the experiment (drilling and ingestion time) and the remnants of mussel tissue without valves (most mussels were not totally consumed) were registered. For this, mussels were placed in boiling water for a few seconds to open the valves and the remaining soft tissues were blotted to remove excess water before weighing. At the beginning of the experiment we chose pairs of snail–mussel from the 20 l containers and hence we could not know in advance which mussel would be chosen by each gastropod; therefore, we estimated the entire mussel weight for each individual consumed indirectly. For this, we performed a linear regression with the entire tissue weight data from 50 mussels ranged in size from 42 to 58 mm. We obtained the amount of meat consumed from the difference between entire and remnant tissue weights for each mussel.

Statistical analyses

The Statistica 6.0 software was used to carry out the analyses. The effect of the intertidal level (mid and low) on the density of *T. geversianus* was analysed by a Student's *t*-test. Both relationships of predator–prey and available–consumed prey size were analysed by

means of the Pearson's product–moment correlation coefficient. For the latter relationship, the number of mussels available vs. consumed for each size range were compared. The effects of aerial exposure time on the drilling rate ($\mu\text{m h}^{-1}$), drilling and ingestion time (h) and tissue consumed (g) were analysed with respective one-way ANOVAs followed by Tukey's post-hoc comparisons (Sokal & Rohlf 1995). In order to meet the assumptions for normality and homogeneity of variance, the Lilliefords and Bartlett tests were performed, respectively.

Results

Density and size distribution of *Trochus geversianus*

In November 2008, gastropod density was significantly higher at the low intertidal level (mean \pm sd: $99.1 \pm 118.5 \text{ m}^{-2}$) than at the mid intertidal level ($24.5 \pm 23.7 \text{ m}^{-2}$) (Student's *t* = 3.37, *P* < 0.01). The mean sizes of *T. geversianus* at the mid and low intertidal levels were $28.8 \pm 8.1 \text{ mm}$ and $27.56 \pm 6 \text{ mm SL}$, respectively. The size–frequency distribution of *T. geversianus* at the mid and low intertidal levels shows that the most common sizes at both intertidal levels ranged from 20 to 35 mm SL (Figure 2a). The sizes > 40 mm SL were better represented at the mid intertidal level (Figure 2a). Mussel density was $1125 \pm 38 \text{ m}^{-2}$ at the fringe of lower-mid level and $3395 \pm 62 \text{ m}^{-2}$ at the patches with mussels at the low level. The predation proportion was different between levels (Student's *t*: 4.3, *P* < 0.01): 7.8% ($\pm 5.7\%$) and 0.06 (± 0.04) at the mid and the low intertidal levels, respectively.

Body size relationships of available–consumed prey and predator–prey

At the lower-mid intertidal level the size frequency distribution of *Mytilus chilensis* available was bimodal, with a first modal group representing recruits (< 5 mm SL) and the second representing individuals of 45–50 mm SL (Figure 3a). At the low intertidal level, mussels were smaller than those at the lower-mid intertidal level (15–20 mm SL) (Figure 3b).

The size–frequency distributions of *M. chilensis* available and consumed at the lower-mid intertidal level showed that *T. geversianus* preferably consumed most mussels in the range of 40–50 mm SL (Figure 3a). In addition, sizes of prey available and consumed at this level correlated positively (*r* = 0.798, *P* < 0.01). At the low level, *T. geversianus* consumed *M. chilensis* >

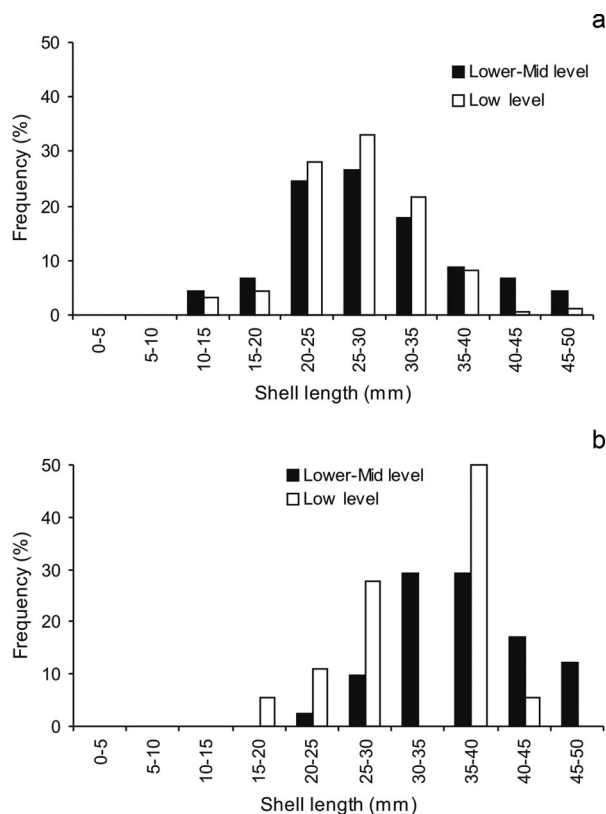


Figure 2. Size–frequency distribution of (a) *Trophon geversianus* at the lower-mid ($n=45$) and low intertidal ($n=161$) levels, in September 2008; (b) *Trophon geversianus* preying on *Mytilus chilensis* at the lower-mid ($n=41$) and low ($n=18$) intertidal levels.

20 mm SL, whereas the most abundant size range of the available prey was 10–20 mm SL (Figure 3b). Furthermore, no correlation was observed between sizes of prey available and consumed ($r=0.107$, $P=0.783$).

At the lower-mid and low intertidal levels the size range of *T. geversianus* preying on mussels ranged from 20 to 50 mm SL (mean value 36.88 ± 5.97 mm SL) and 15 to 45 mm SL (mean value 32.4 ± 6.02 mm SL), respectively, the 25–40 mm SL being the more frequent sizes for both intertidal levels (Figure 2b). Interestingly, the frequency of smaller snails (< 35 mm SL) preying on mussels (Figure 2b) was lower than the large proportion of these sizes observed in both intertidal zones (see Figure 2a). Size frequencies varied between levels with *T. geversianus* > 40 mm SL being more frequent at the lower-mid level compared to low level, and individuals < 40 mm SL being more frequent at the low level compared to lower-mid level (Figure 2b).

The density of *T. geversianus* preying on *M. chilensis* at the lower-mid level was more than two times higher than that at the low level (68.3 ± 2.28 vs. 30.4 ± 14.01 m^{-2}).

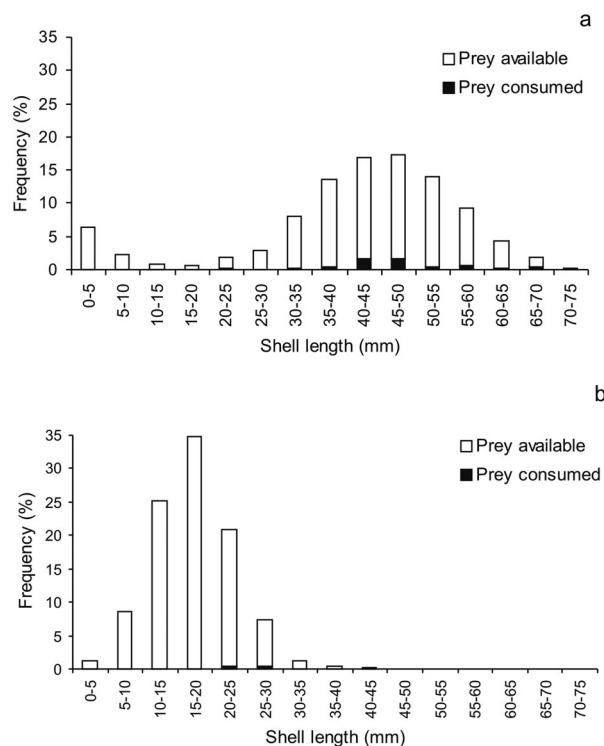


Figure 3. Size–frequency distribution of *Mytilus chilensis* available and consumed by *Trophon geversianus* at the lower-mid and low intertidal levels. (a) Lower-mid level, available $n=644$, consumed $n=40$; (b) low level, available $n=2055$, consumed $n=18$.

A significant correlation ($r=0.320$, $P<0.05$) between sizes of *T. geversianus* and *M. chilensis* consumed was observed (Figure 4). This shows that, on average, *T. geversianus* individuals preferably prey on mussel sizes according to their own body size, i.e. large *T. geversianus* prey on large mytilids. Our results show that, at the mid level, the average density of *T. geversianus* and *M. chilensis* is 68 and 1000 individual m^{-2} , respectively. If *T. geversianus* consumes at least one mussel per individual per month, we estimate

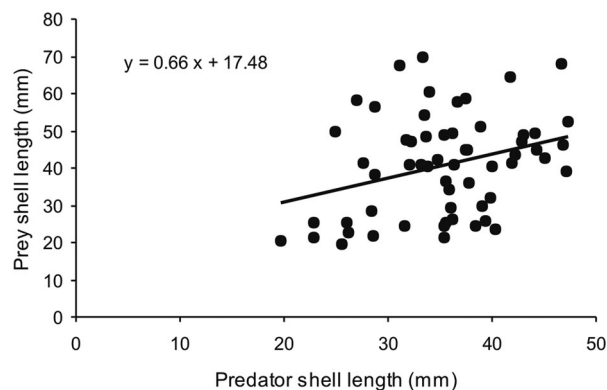


Figure 4. Relationship between the sizes of *Trophon geversianus* and *Mytilus chilensis* consumed, $y = 0.66x + 17.48$.

that the minimum amount of *M. chilensis* predated per month by *T. geversianus* will reach 7.5% of the population. This fact, coupled with the low recruitment observed of *M. chilensis* (Curelovich 2013), makes *T. geversianus* a predator of great impact in those sub-Antarctic rocky intertidals where this snail is abundant.

Drilling and ingestion rates on *Mytilus chilensis* by *Trophon geversianus* as a function of aerial exposure time

The drilling rate ($\mu\text{m h}^{-1}$) at different aerial exposure times for the 2 day treatment decreased with increasing exposure to air. Particularly, the drilling rate in the 9/12 h air exposure treatment was significantly lower compared to the control (0/12 h air exposure) (ANOVA $F_{2,12} = 4.29$, $P < 0.05$, Tukey's comparisons, $P < 0.05$; Figure 5). In the 5 day treatment, in the 0/12, 4/12 and 9/12 h air exposure treatment, the percentage of mussels' valves completely perforated was 60%, 100% and 79%, respectively. Finally, in those replicates where the gastropod finished consuming mussel, the quantity of consumed meat was similar in both the control (0/12 h) and 4/12 h treatments (1.37 ± 0.62 and 1.35 ± 0.04 , respectively) (ANOVA $F_{2,12} = 1.18$, $P = 0.34$; Figure 6). The average handling (drilling and ingestion) time was shorter in the control experiment (individuals permanently submerged, 185.4 (7.4 days) ± 35 h) than in the 4/12 h treatment (234.4 (9.4 days) ± 52.7 h), although no statistical differences were found. In the 9/12 h treatment, *Trophon geversianus* used less time in handling of prey (212.6 (8.6 days) ± 1.8 h) than in the 4/12 h treatment, but the consumption of prey was lower (Figure 6). No statistical differences were found (ANOVA $F_{2,12} = 3.16$, $P = 0.079$).

Discussion

In our intertidal study area, *Trophon geversianus* occurs mostly at the lower fringe of the mussel bed (lower-mid level), and at the low intertidal level, at high densities and with a wide range of body size (10–50 mm). The observed size range was similar to that found in the intertidal of the Straits of Magellan, although density was much lower than in the Beagle Channel for the same time of year (Andrade et al. 2009). However, in the subtidal at 3–15 m depth of the eastern Straits of Magellan, *T. geversianus* density is lower and between 0.5 and 16.2 m^{-2} (González et al. 2007). In the Beagle Channel, the density of *T. geversianus* was higher at the low than at the mid level. The low intertidal level, which is rarely uncovered by water, is the most

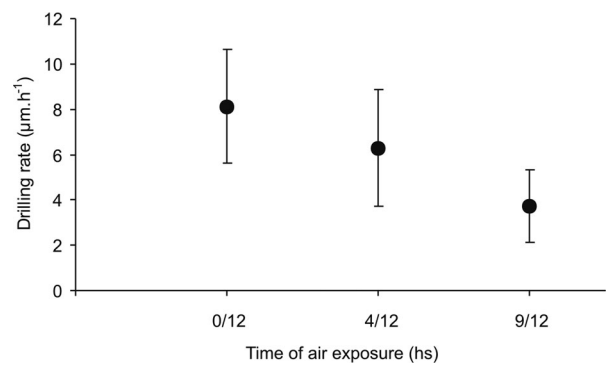


Figure 5. Drilling rate ($\mu\text{m h}^{-1}$) of *Trophon geversianus* on *Mytilus chilensis* as a function of aerial exposure after 2 days from the beginning of the experiment.

favourable environment for the growth and survival of this species, as follows. The lower fringe of the mussel bed is exposed, at most, for 4 h only during the extreme spring tides during the solstices. The relatively calm wave regime of the study area makes it unlikely that the upper levels are submerged by the action of strong waves or splash. These physical features likely constrain the activity of *T. geversianus* upwards because air exposure kills snails, for example at the upper part of the mussel bed, i.e. about 1 m above chart datum (Curelovich 2013). Moreover, longer periods of air exposure make predation less efficient (Figures 5 and 6). In our experiment, drilling time and feeding activity was less at the longest time of exposure (9 h), because drill-holes were not completed nor were the mussels fully consumed. Apparently, for *T. geversianus* the upper boundary of predation is physical stress and the mid intertidal level provides a refuge for mussels from the snail predation (Connell 1975 and see Robles & Desharrais 2002 for a general review).

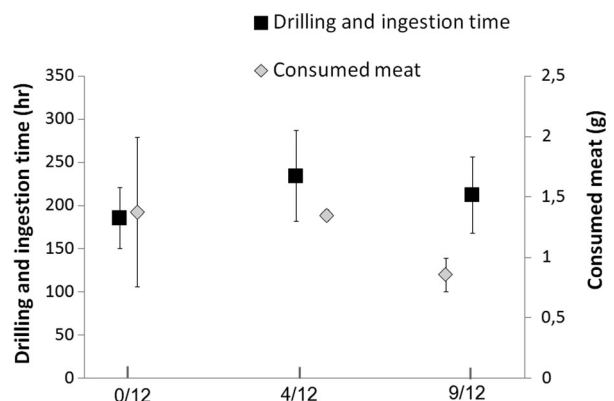


Figure 6. Drilling and ingestion time (h) and consumed mussel meat (g) for *Trophon geversianus* on *Mytilus chilensis* after the gastropod finished eating, i.e. when predator crawled away from prey.

Nevertheless, for *T. geversianus*, knowledge about the physiological tolerance to desiccation combined with temperature is still needed.

The density of *T. geversianus* preying on *M. chilensis* was higher at the mid level compared to the low level, and this could be due to both the higher density and larger sizes of prey at the mid level. Moreover, at the mid level *T. geversianus* preferably consumed the most common sizes of *M. chilensis* > 20 mm SL, which compares to the 17 mm SL reported in a preference experiment (Gordillo & Archuby 2012). Hence, approximately 17–20 mm SL is likely to be the minimum body size suitable to invest in drilling time. At the low level, *T. geversianus* preferably consumed the least common sizes of *M. chilensis* probably due to the large number of small-sized prey individuals (between 10 and 25 mm) present at this level. This was also observed in laboratory and field experiments in Tierra del Fuego, where *T. geversianus* and other intertidal gastropod species showed size-selectivity when preying on the least commonly occurring intertidal bivalves (*Perumytilus purpuratus* and *Aulacomya atra*) (Gordillo & Archuby 2012). Additionally, our results suggest that there would be a tendency of *T. geversianus* to consume prey sizes according to their own body size, i.e. large gastropods prey on large mussels. This positive relationship between predator and prey sizes agrees with previous results (Gordillo & Amuchástegui 1998; Andrade & Ríos 2007) for the same species. Although the most frequent size range of *T. geversianus* (25–40 mm SL) preying on *M. chilensis* in the intertidal zone of Ensenada Zaratiegui was the same for both mid and low intertidal levels, smaller individuals of *T. geversianus* (between 15 and 20 mm SL) were more frequently observed preying on *M. chilensis* at the low level, while those between 40 and 50 mm SL were more frequently observed preying at the lower-mid level, where mussels are larger. This could show a preference of the predators for more profitable sizes of *M. chilensis*, being the larger mussels preferred by larger gastropods (e.g. Palmer 1984; Serra et al. 1997).

The predation frequency of *T. geversianus* on *M. chilensis* in the intertidal community of the Beagle Channel was significant, so we suggest that this predator is responsible for the main mortality of *M. chilensis* in the study area. This predation frequency seems to be site-variable because in locations 8 km apart in the Beagle Channel, drilling frequency, used as a proxy of predation (Gordillo & Archuby 2012), doubled (16%) in our reported predation frequency and this was probably due to different shore features (Menge et al. 1994). The low densities and small sizes

of *M. chilensis* observed at the low tide level could be the result of the strong predation pressure by *T. geversianus* that would be affecting the abundance and size structure of prey, as observed in other intertidal communities with gastropod predators (Castilla & Durán 1985; Navarrete 1996). In the intertidal of Ensenada Zaratiegui, there is no other snail species preying on mussels, and other organisms, like starfishes *Anasterias* sp. and birds, occur in a very low frequency (authors' personal observations, 2007). *Trophon geversianus* seems to be a candidate for a keystone species on the rocky shore of the Beagle Channel, but rather in the narrow strip of < 0.4 m in vertical width of the lower intertidal/upper subtidal. However, so far there are not enough results to definitely sustain such a statement. They exert such an important predation pressure that at this level only mussels of small size (< 20 mm SL) occur, probably because they are less preferred (Gordillo & Archuby 2012). This high predation was suggested by a preliminary experiment with cages, in which mussel mortality by *T. geversianus* at the upper subtidal tripled that of the lower mid intertidal (Curelovich 2013). On the other hand, the ratio of mussel:trophon densities in the Magellan subtidal is similar to our reported predation frequency (González et al. 2007). However, these mussel beds have size–frequency distributions, with individuals of 30–60 mm SL and densities of 18–420 mussels m⁻², that are lower than our density from the intertidal (also see Curelovich 2013). Nonetheless, a proper exclusion experiment is needed to assert the role of keystone species for *T. geversianus* in the subtidal rather than in the intertidal.

The abundance of *T. geversianus* in the lower mid intertidal may contradict the concept of keystone species as 'is one whose effect is disproportionately large relative to its abundance' (Power et al. 1996). In well-known systems, predator density is in the order of 1–10 m⁻² for autochthonous systems (e.g. Castilla & Duran 1985; Menge et al. 1994). However, in *T. geversianus*, the time of manipulation is long and therefore the large effect on the community would be accomplished by having larger numbers of predators. All studies coincide in that the time of consumption is long: experimentally mussels are consumed in a range of 7–10 days (our study; Gordillo & Amuchástegui 1998; Andrade & Ríos 2007; Gordillo & Archuby 2012). The longest consumption rate of 12.4 days per mussel was reported for an in-situ experiment in the Straits of Magellan (González et al. 2007).

Considering the fact that *T. geversianus* needs several days to drill and consume a single individual mussel, and that gastropods exposed to air for longer

periods during the feeding process appear to be less efficient in food intake, we propose that this predator selects individuals of *M. chilensis* at sites that are exposed to air for only a few hours a day and a few times in the year, avoiding areas that are exposed to air for longer periods. Because desiccation is one of the most important sources of mortality for many species of intertidal gastropods and other organisms (reviewed by MacMahon 1990), the absence of *T. geversianus* at higher intertidal levels could be due to the incompatibility between environmental conditions and the physiological demands of this species. For example, on the Atlantic shore of Tierra del Fuego there are no predators on the mussel beds, probably due to the desiccation by the strong westerlies (Calcagno et al. 2012). Lack of adaptations for the thriving upper levels of the intertidal can be water loss due to desiccation or the inability of retaining water (Sokolova & Pörtner 2001). Moreover, because drilling implies an active movement of the radula, the capacity of aerobic metabolism of the snail could be constrained by the time of aerial exposure (e.g. Simpfendorfer et al. 1995), which also adds additional limitations to their anaerobic metabolism (Sokolova & Pörtner 2001).

Trophon geversianus seems to be an efficient predator of *M. chilensis* in the community studied, due to both its high density and feeding rate. We postulate that the strong predation pressure of *T. geversianus* on *M. chilensis*, mainly at the low level, prevents this key competitor in monopolizing space, thus allowing less-competitive species, i.e. barnacles and coralline algae, to establish and survive. Accordingly, studies aimed at evaluating the direct and indirect effects of predation on *M. chilensis* exerted by other species are needed for a better understanding of this sub-Antarctic community organization.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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