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ORIGINAL PAPER

Predation impact of the notothenioid fish *Trematomus bernacchii* on the size structure of the scallop *Adamussium colbecki* in Terra Nova Bay (Ross Sea, Antarctica)

Ombretta Dell'Acqua[1] · Thomas Brey[2] · Marino Vacchi[3] · Mariachiara Chiantore[1]

Abstract Biotic interactions are particularly relevant in stable environments, such as the High Antarctic areas. Among them, predation has a key role in structuring community and population variables, including size-frequency distribution. This study aims to quantify the impact of predation by the notothenioid fish *Trematomus bernacchii* on the Antarctic scallop *Adamussium colbecki*-size distribution. We developed a model of this impact that estimates the size distribution of the preyed scallop population, taking into account for the predator-size distribution, sex structure, and daily consumption. Comparing this size distribution of the preyed *A. colbecki* with the living populations at Terra Nova Bay (Ross Sea, Antarctica), we were able to detect a relevant impact of fish predation. Fish-size frequency resulted to be the major factor shaping prey-size structure, with significant differences between predation by males and females. Our findings, given the key role of the two species in the littoral ecosystem of Terra Nova Bay (Antarctic Special Protected Area 161), fall into the framework of ecosystem management of High Antarctic coastal areas, particularly in the actual context of climate change, and increasing anthropogenic impact.

Introduction

Predation pressure exerted by fish can play a major role in structuring lower trophic levels through top–down regulation. Several studies revealed that fish predation, through direct consumption or altering interspecific interaction among their preys (Schoener 1993; Wootton 1993), can have profound effects on the surrounding community, affecting species richness, evenness, and composition (Webb and Mitsch 2001; Shears and Babcock 2002; Watzin et al. 2008; Peteiro et al. 2010; Winkelmann et al. 2011; Hammerschlag-Peyer et al. 2013). At the population level, fish predation can even alter size structure of their preys (Tegner and Levin 1983; Scheibling and Hamm 1991; Sala and Zabala 1996; Scheibling 1996; Craig et al. 2006; Nilsson 2010), with consequences on age structure or sex ratio with effects on reproductive output and recruitment of the prey (Ślusarczyk 1997; Svensson 1997).

Body size is known to play a crucial role in predation, since capture success, handling time, prey profitability, and vulnerability can be expressed as a function of the predator–prey-size ratio (Gill and Hart 1994; Juanes and Conover 1994; Scharf et al. 1998; Hartman 2000; Brose et al. 2006). Fish generally choose their prey into a specific size range to maximize the benefit/cost ratio, following the 'optimal foraging theory' (MacArthur and Pianka 1966; Schoener

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1979; Saito et al. 2004) and several works provided evidences for the existence of a positive predator–prey-size relationship (Lundvall et al. 1999; Scharf et al. 2000; Gill 2003; Floeter and Temming 2005). Moreover, Jacob et al. (2011) demonstrate the importance of body-size distribution for the robustness of a high Antarctic food web, whereas Mintenbeck et al. (2012) show that Antarctic fish feeding rates strongly depend on prey size.

Assessment of predator–prey interactions is a focal point in clarifying dynamics in those communities with outstanding trophic complexity, such as the Antarctic shelf communities (Jacob et al. 2006, 2011). One of these shelf areas is the Ross Sea, whose food webs are characterized by unique features, with relevance under ecological, social, and economic perspectives (Bradford-Grieve and Fenwick 2001; Fenwick and Bradford-Grieve 2002; Smith et al. 2007). This area is one of the most productive in the Southern Ocean and one of the few places in the world that still displays a complete food web, with a full community of top-level predators (Ainley 2002a; Ainley et al. 2007). With these characteristics, the Ross Sea offers rich opportunities for biological and ecological studies, also in the field of climate change. Great efforts have been made to depict the whole ensemble of trophic interactions, but these models still need implementation and links need to be explored in more detail (Ainley 2004; Smith et al. 2007; Pinkerton et al. 2010). One of these unexplored links between middle and lower levels is the role played by the fish *Trematomus bernacchii* predation upon the scallop *Adamussium colbecki*.

In the Ross Sea, along the Victoria Land coast, Terra Nova Bay is a huge bay (64 km long, 29.4 Km^2) that has been settled as Antarctic Special Protected Area (ASPA) 161 because of the ecological value and vulnerability of habitats and species. In the shelf waters of Terra Nova Bay, *T. bernacchii* is the most abundant fish (Vacchi et al. 1999), mostly living between 50 and 150 m. As a dominant species, it likely exerts an impact on other organisms through trophic interactions, feeding upon many invertebrate species. *T. bernacchii* feeds mostly on benthic preys: polychaetes, molluscs, isopods, amphipods, and algae, but it may also roam the water column, where it preys upon copepods, mysids, euphausiids, and fish (Vacchi et al. 1994; La Mesa et al. 2004a). The diet of *T. bernacchii* varies with location and season, making it a generalist feeder, and this high feeding plasticity enables this species to focus on the locally most abundant prey items (Kiest 1993; La Mesa et al. 2004a). In fact, at Terra Nova Bay, where *A. colbecki* is locally present in large assemblages (Chiantore et al. 2001), this scallop has the highest frequency of occurrence among *T. bernacchii* diet items (La Mesa et al. 2004a).

The endemic scallop *A. colbecki* is one the best known and most studied Antarctic molluscs. Its circumpolar distribution is patchy, showing locally more or less dense populations. At Terra Nova Bay, *A. colbecki* reaches densities up to 60 ind/m^2 (Chiantore et al. 2001) and 100–120 gDW/m^2 biomass (Cattaneo-Vietti et al. 1997), totally covering the sea floor. Given its high density and biomass, *A. colbecki* is an important secondary producer in the Antarctic littoral system (Cattaneo-Vietti et al. 1997; Chiantore et al. 1998; Heilmayer et al. 2003), where it plays a fundamental role in the benthic–pelagic coupling by feeding on phytoplankton, sea-ice algae, benthic diatoms, foraminifera, and detritus (Chiantore et al. 1998). Moreover, this scallop acts as an ecosystem engineer, as its valves form a secondary substratum for epibiotic organisms (Cerrano et al. 2001, 2009). Due to its large size, long lifespan, and circumpolar distribution, *A. colbecki* has been involved in ecosystem management and conservation plans (Berkman and Nigro 1992; Berkman and Tipton-Everett 2001). Finally, CCAMLR included this scallop in its list of sentinel taxa used to identify Vulnerable Marine Ecosystems (VME), where benthic invertebrates with key attributes (such as to contribute to creation of complex three-dimensional structure and to be clustered in high densities) are utilized to identify areas particularly sensitive to commercial fishery (CCAMLR 2009a, b).

We reckon that a better understanding of the trophic interactions between these two key species is a precondition for the implementation of the Terra Nova Bay area management. The only information available on this trophic link comes from a previous work by Vacchi et al. (2000) that estimated a predator–prey-size linear relationship between *T. bernacchii* and *A. colbecki*, based on fishes' stomach contents. The innovative aspect of the present work relies on the application of this observed relationship to build a predictive probability model that estimates the preyed *A. colbecki* population-size distribution on the basis of the *T. bernacchii* population and its features (not taken into account in the previous work). This model aims at the description of the trophic relationship between these two species: (1) to verify the impact of fish predation on prey population-size structure and (2) to evaluate the relative importance of different fish population variables (size frequency, sex, and daily ration) in the predation effect.

Materials and methods

Study area: scallop and fish populations

Both fish and scallop sampling were performed in Terra Nova Bay (Victoria Land Coast, Ross Sea, Fig. 1). During austral summer 1990/91, over 650 T, *bernacchii* specimens have been collected by gill net sampling all around the Terra Nova Bay area. *A. colbecki* specimens were

Fig. 2 Linear regression between fish total length (TL) and preyed scallop shell length (SL); *thin lines* represent the limits of the predation range of any fish size along the best fit (*thick line*). Modified from Vacchi et al. (2000)
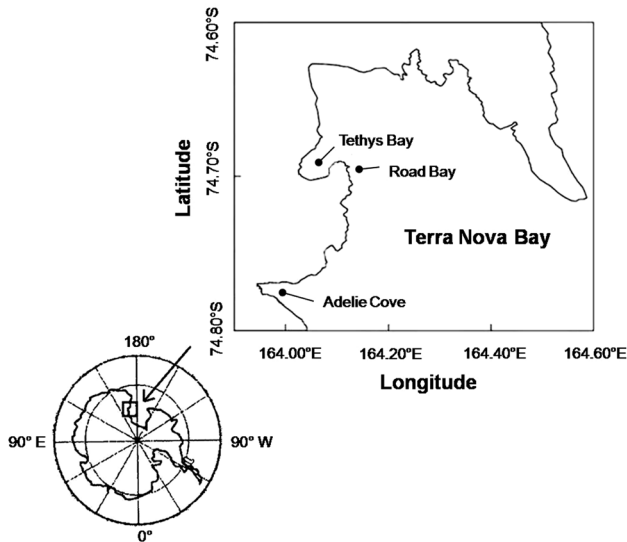
Fig. 1 Map of the regional context of study in Antarctic continent and detail of Terra Nova Bay area, showing the three *Adamussium colbecki* sampling sites (Road Bay, Tethys Bay and Adelie Cove). Edit from Ansell et al. (1998)

sampled during different austral summers at three different sites. The main sampling site was Road Bay (74°41.9′S and 164°07.5′E), where scallops were collected in 15 years, spanning from 1989/90 to 2012/13. In this small bay, close to the Italian Mario Zucchelli Station, the largest *Adamussium* beds can be found between 50 and 70 m (Cattaneo-Vietti et al. 1997; Chiantore et al. 2001). Two shorter data sets are from Tethys Bay and Adelie Cove (1998/99 to 2000/01, 2011/12, and 2012/13). In Tethys Bay (2 km North of Road Bay), *A. colbecki* density is up to 23 ind/m², while in Adelie Cove, it is up to 10 ind/m² (Chiantore et al. 2001).

Baseline prey–predator-size relationships

Vacchi et al. (2000) established a preliminary predator–prey-size relationship between *T. bernacchii* and preyed *A. colbecki*, using 59 fish stomach contents:

$$\mathrm{SL} = -27.406 + 0.279 \times \mathrm{TL} \quad R^2 = 0.417; p = 0.0009; n = 59 \tag{1}$$

where *SL* is *A. colbecki* shell length (mm) and *TL* is *T. bernacchii* total length (mm, Fig. 2). All the acronyms used in this work are reported in Table 1.

Predation model

We built a model that describes the predation preferences of the fish in respect to the scallop size: this predation model estimates the probability for any *A. colbecki* size (SL) to be
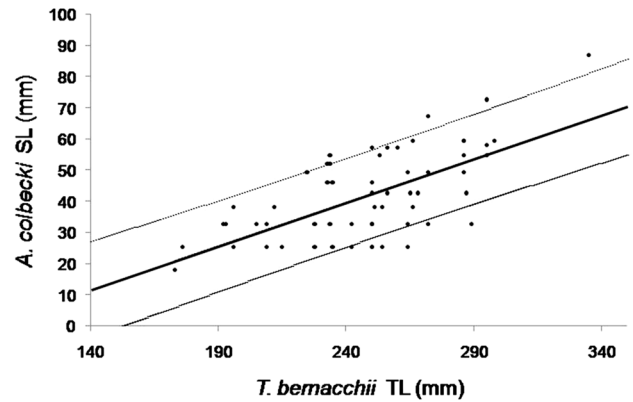
preyed by all the *T. bernacchii* sizes (TL), i.e., by the whole fish population. The population of *T. bernacchii* for this model was restricted to 140–350 mm TL, as fish <140 mm are very rare in samples collected in the depth range, where the large scallop beds are found (La Mesa et al. 1996). Consequently, juveniles of this species are supposed to have different feeding habits from adults. The 350 mm upper limit is close to the largest size observed in the area (335 mm, La Mesa et al. 1996; Vacchi et al. 2000; La Mesa and Vacchi 2001). The *A. colbecki*-size range was set to 1–100 mm SL. For both species, we used 1 mm size classes.

To build the model, we started to compute the predation-size range (PSR) that is the range of prey sizes consumed by any predator size. In fact, any fish size obviously does not feed on a single scallop size, but upon a range. According to other studies (see, for example, Boyce et al. 2015), computing this range corresponds to compute the prediction interval (PI; Eq. 2) of the regression 1, with a chosen probability. We have set 90% probability ($1 - \alpha = 0.90$). The PI is an interval associated with a random variable, yet to be observed, with a specified probability of the random variable lying within the interval. In our case, analyzing the stomach content of a *k*th fish size, we have 90% probability to find a scallop size belonging to the PI associated with that fish size. Thus, the PI corresponds to a range of prey sizes consumed by a specific predator size, and from now on, we will name it predation-size range of the *k*th fish TL (PSR$_k$):

$$\frac{1}{2}\left(\mathrm{PSR}_k\right) = \mathrm{SL}_k \pm t_{n-2,\frac{\alpha}{2}} \times \sqrt{S_e^2 \times \left(1 + \frac{1}{n} + \frac{\left(\mathrm{TL}_k - \mathrm{TL}_m\right)^2}{\sum_{i=1}^{n}\left(\mathrm{TL}_i - \mathrm{TL}_m\right)^2}\right)} \tag{2}$$

where PSR$_k$, centered on SL$_k$, defines the PSR$_k$ of each fish TL$_k$; SL$_k$ is any SL estimated with regression (1) for any

Table 1 Legend of the variables acronyms used in this study, in order of appearance

Acronym	Definition
TL	*T. bernacchii* total length, mm
TL_k	kth *T. bernacchii* total length, where $k \in [140, 350]$ mm
TL_m	*T. bernacchii* observed mean total length, mm
TL_i	*T. bernacchii* observed total length, mm
SL	*A. colbecki* shell length, mm
SL_k	*A. colbecki* estimated shell length by linear regression from Vacchi et al. (2000), mm
SL_i	ith *A. colbecki* shell length, where $i \in [1, 100]$ mm
PI	Prediction interval, the predictive range of a value on the best fit
PSR	Predation-size range (the range of scallop sizes consumed) for the kth fish size
PSR_k	Predation-size range referred to a specific fish TL_k
$\mathbb{P}(SL_i)_k$	Probability, for the ith scallop size in a kth predation range, to be preyed by the kth fish size (TL_k)
$\mathbb{P}_{SLi}$	Probability, for the ith scallop size, to be preyed by the whole range of fish size considered
$\mathbb{P}_{mode}$	Probability, for the scallop SL corresponding to the mode, to be consumed
PM	Predation model
PM_{SDp}	Predation model accounting for size distribution of the whole fish population
PM_{SDf}	Predation model accounting for size distribution of the female fish population
PM_{SDm}	Predation model accounting for size distribution of the male fish population
DFI	Daily food intake, i.e., daily amount of food consumed, g
DR	Daily food consumption expressed as percentage of body mass
BM	Body mass, g
BM_k	Body mass corresponding to the fish TL_k, g
BMF	Body mass factor: the relative contribute of a fish size on the mass of the whole population
BMF_k	Body mass factor for the kth fish size: the relative contribute of the kth fish size on the mass of the whole population
PM_{BMFp}	Predation model accounting for BMF, for the whole fish population
PM_{BMFf}	Predation model accounting for BMF, for the female fish population
PM_{BMFm}	Predation model accounting for BMF, for the male fish population
PM_p	Predation model accounting for both size distribution and body mass factor of the whole fish population
PM_f	Predation model accounting for both size distribution and body mass factor of the female fish population
PM_m	Predation model accounting for both size distribution and body mass factor of the male fish population

predator size (i.e., TL_k, where k is comprised between 140 and 350 mm); t is the Student's t-distribution; n is the number of observations (59); α is 0.10; Se^2 is the regression (1) variance; TL_m is the average observed fish size; and TL_i is the ith observed fish size.

To calculate the probability, for any scallop size in the population (SL_i), to be preyed by all fish sizes (i.e., the whole fish population), we added the probabilities $\mathbb{P}(SL_i)_k$ of each scallop SL_i to be preyed by each fish TL_k. In fact, any scallop SL_i can belong to more than one PSR_k, but accounting for different probability to be consumed, along with fish TL_k-size preference.

To compute $\mathbb{P}(SL_i)_k$, we assumed capture probability by predator TL_k to be normally distributed within the PSR_k, i.e., with maximum probability at $SL_i = SL_k$, following approach suggested by similar studies (Pearre 1986; Cowan et al. 1996; Lundvall et al. 1999; Craig

et al. 2006). Accordingly, we calculated the standard deviation σ_k for each PSR_k:

$$\sigma_k = \frac{SL_{max} - SL_k}{Z_{0.95}} = \frac{SL_{min} - SL_k}{Z_{0.05}} \tag{3}$$

where σ_k is PSR_k standard deviation; SL_{max} and SL_{min} are the PSR_k upper and lower limits, respectively; and SL_k is the PSR_k mean (or centre). Using discrete intervals, we then computed the probability for each scallop SL_i in a PSR_k, to be consumed by that predator TL_k:

$$\mathbb{P}(SL_i)_k = \mathbb{P}(SL_i + 0.5 \text{ mm})_k - \mathbb{P}(SL_i - 0.5 \text{ mm})_k \tag{4}$$

where $\mathbb{P}(SL_i)_k$ is the probability, for any *A. colbecki* SL_i (where i is comprised between 1 and 100 mm) occurring in the PSR_k, to be preyed by the *T. bernacchii* TL_k.

Finally, we calculated the probability, for any scallop SL_i to be preyed by the whole fish-size range that is the sum of the probabilities to be preyed by each fish TL_k:

$$P_{SL_i} = \sum_{(k=140)}^{350} P(SL_i)_k \quad i \in [1, 100] \text{ mm.} \tag{5}$$

Standardizing this sum on a total of 100% (that is $\mathbb{P} = 1$), we were able to build the distribution of probability, for *A. colbecki* population (1–100 mm), to be preyed by the whole *T. bernacchii* population (140–350 mm). This basic predation model (PM) did not take into account any *T. bernacchii* population variable, but only the assumption of normality of probability to be captured by the predator.

We used this basic predation model (PM) to explore the relative effect of two predator population variables on the trophic impact: the size distribution (specifically from the Terra Nova Bay population) and daily food intake of *T. bernacchii*; both have been calculated for the whole population and the two sexes separately. The more a fish size occurs in the population, the larger is the probability of capture for the prey sizes it feeds upon. We multiplied each $\mathbb{P}(SL_i)_k$, in Eq. 4, for TL_k frequency, after checking for the normality of the whole population (and of males and females separately)-size distribution. The PM is a probability function, which is a frequency as well, so there was no need for conversion. We obtained three models: predation model built with the size distribution of the whole fish population (PM$_{SDp}$), of females (PM$_{SDf}$) and males (PM$_{SDm}$) separately.

The second predation variable we considered is the predator feeding amount. This is usually expressed as daily food intake (DFI) that is computed using daily ration (DR), which is a percentage of body mass (BM; see Maynou and Cartes 1998, for references). The more a predator eats, the higher is the probability of capture for the prey sizes it feeds upon. No specific study on *T. bernacchii* DR is available, but some studies on other notothenioids DR (Kock 1992; Coggan 1997; Bushula et al. 2005) do not report ontogenetic patterns, except for differences between juveniles and adults (Olaso et al. 2004). As *T. bernacchii* specimens here considered were all adults, we assumed a constant DR for our fish sizes. That means that daily food intake is positively linearly correlated with BM:

$$DFI = DR\,(\%) \times BM\,(g) \tag{6}$$

where DFI is the daily food intake in grams, DR is the daily ration, and BM is fish body mass in grams. So far, the only variable affecting the DFI and the impact on preys is BM. We then estimated the BM for every fish TL re-analyzing the correlation between *T. bernacchii* TL and BM from the original data (La Mesa et al. 1996) and we provided the following regressions for the whole population (8), for males (9) and females (10) separately:

$$BM = 10^{-6} \times TL^{3.454} \quad R2 = 0.948; \; p < 0.0001; \quad n = 654 \tag{7}$$

$$BM = 10^{-6} \times TL^{3.421} \quad R2 = 0.902; \; p < 0.0009; \quad n = 208 \tag{8}$$

$$BM = 10^{-6} \times TL^{3.418} \quad R2 = 0.933; \; p < 0.0009; \quad n = 417. \tag{9}$$

This approach would have not been possible if different fish sizes (and, thus, different BM) had different diet preferences, but La Mesa et al. (1996) reported no differences in the frequency of occurrence of *A. colbecki* in the diet, for the considered *T. bernacchii* population, nor between males and females. With constant DR and diet preferences, the probability of impact on any *A. colbecki* size depends only on *T. bernacchii* BM. To take this variable into account in the PM, we needed a non-dimensional factor. We standardized the BM of each TL_k (BM_k) on the total mass of the fish population to obtain a factor (body mass factor—BMF), which takes into account the BM in the impact on prey:

$$BMF_k = \frac{BM_k}{\sum_{k=140}^{350} BM_k} \times 100 \tag{10}$$

where BMF_k is the relative impact (depending only on BM) that any *T. bernacchii* TL_k has, compared to any other TL_k, on the *A. colbecki* sizes in its PSR_k. We multiplied BMF_k for the $\mathbb{P}(SL_i)_k$ in Eq. 4, as we did for fish-size frequency, obtaining other three models: Predation Model built with the BMF of the whole fish population (PM$_{BMFp}$), of females (PM$_{BMFf}$) and males (PM$_{BMFm}$).

Finally, we put fish-size distribution and BMF together and we ran three overall PM: for the whole fish population (PM$_p$), for females (PM$_f$) and males (PM$_m$). We compared these last three size distributions of modeled preyed *A. colbecki* population generated by the PM with the size distribution of the living scallop populations sampled throughout the years at Road Bay, Tethys Bay and Adelie Cove. To remove the fluctuations between years and obtain a more representative long-term 'average' population, a multiyear-size-frequency distribution of the living *A. colbecki* populations was generated for each site. We, first, converted each sample-size distribution into percentage values (i.e., *N* per sample = 100%), and subsequently, we pooled all these distributions from the different years, obtaining a pluriannual average distribution for each of the three sites.
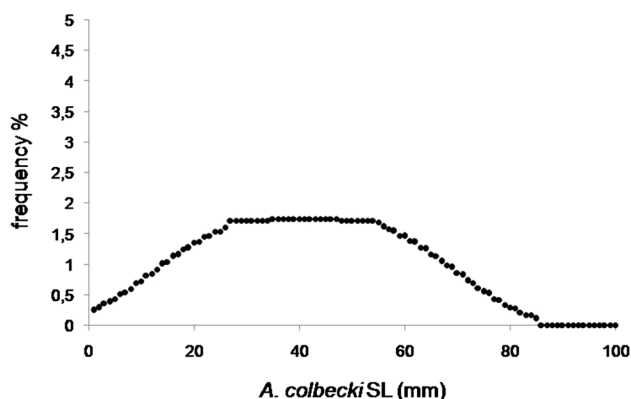
Results

Trematomus bernacchii males, females, and total populations were normally distributed (Shapiro–Wilk test, $p = 0.9981$ for all three), and females and males resulted to be different populations in terms of size structure (Welch's test, $p = 0.0009$). Means and standard deviations were

Table 2 Statistic indexes (mean, mode, standard deviation, and skewness) of all the predation models ran in this work

	Mean	SD	Mode	SK
Basic PM	41.338	32.496	38	0.102
PMSDp	38.121	42.810	38	0.762
PMSDf	42.268	48.658	42	0.797
PMSDm	30.629	41.266	31	1.026
PMBMFp	53.461	54.688	55	0.612
PMBMFf	53.369	54.482	55	0.609
PMBMFm	53.377	54.499	55	0.609
PMp	43.110	48.608	43	0.765
PMf	46.310	53.660	48	0.800
PMm	32.764	44.049	34	1.019

All measures are in millimeters

Fig. 4 Predation model built by taking into account for the predator-size distribution of whole population (*filled circles*), females (*empty circles*), and males (*triangles*). *SL* scallop shell length
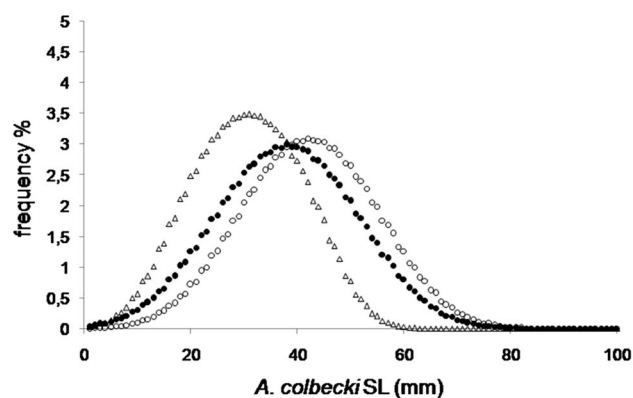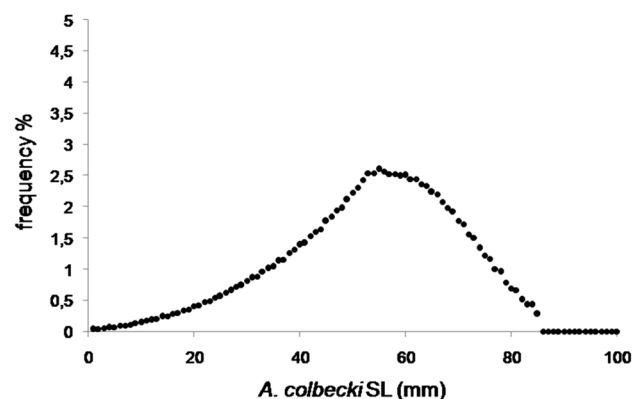

Fig. 3 Basic predation models built on the predator–prey-size relationship, (without considering predator-size distribution nor predator body mass factor). *SL* scallop shell length

Fig. 5 Predation model built by taking into account predator body mass factor. Note that it is impossible to distinguish among the impact from the different predator populations (whole, female, and male). *SL* scallop shell length

234 ± 36.465 for the whole population, 249 ± 33.514 for females, and 208 ± 21.922 for males.

The charts of the different predation models display, on x-axis, the consumed *A. colbecki* size (SL, from 1 to 100 mm) and, on y-axis, the probability to be preyed by the fish population, whether it is whole, female or male. All PM parameters are summarized in Table 2.

Basic PM (Fig. 3) comes from the assumption of normality of probability of capture into each predation-size range; this has been possible as predator–prey-size regression (Eq. 1) errors showed normality distribution (Mann–Whitney $p = 0.3758$). Basic PM does not consider any predator variable and depicts the predation impact in case that all fish sizes occur with the same frequency and eat exactly the same food amount.

$PM_{SDp,m,f}$ are built taking into account fish-size-frequency distribution in Terra Nova Bay (Fig. 4). Differences are detected between PM_{SDp} and PM_{SDm} (Kolmogorov–Smirnof test, $p = 0.0004$) and between PM_{SDm} and

PM_{SDf} (Kolmogorov–Smirnof test, $p < 0.0001$). We can see that predation by fish mostly affects the scallop medium sizes, even if with differences among the three population (see Table 2).

PM_{BMFs}, built by taking into account BMF, are shown in Fig. 5; they are substantially overlapped as the three functions; binding TL and BM are almost identical. Kolmogorov–Smirnof test gives $p = 1$, indicating that they are the same population. The distribution shape strongly reflects the power–law relationship between fish body mass and length: the consumption amount raises with the same power–law; thus, the impact does not vary constantly along fish-size range. The distribution is strongly left skewed, and the predation is concentrated around the scallop size of 56 mm.

Finally, Fig. 6 shows the $PM_{p,f,m}$ built with both predator-size frequency and BMF. PM_m is different from
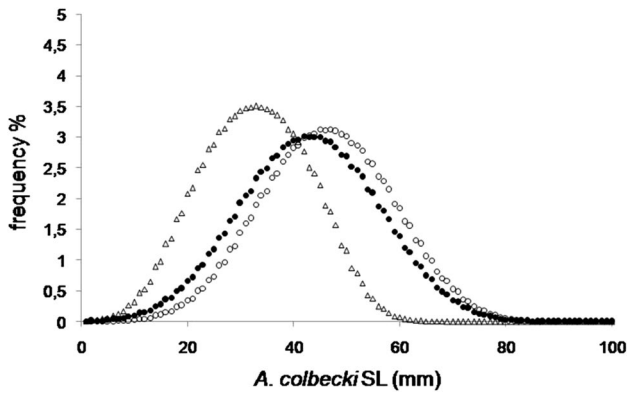
Fig. 6 Predation model built by taking into account for predator-size distribution and BMF of predator whole population (*filled circles*), females (*empty circles*), and males (*triangles*). *SL* scallop shell length

PM_p and from PM_f as well (Kolmogorov–Smirnof test, $p < 0.0001$ for both). In the comprehensive model considering the whole fish population, the greatest impact is around scallop SL of 43 mm.

P values, despite non being significant, indicate that PM_{SD} is more similar to PM than PM_{BMF}. The BMF effect results in a slight shift of the mode rightwards with respect to size distribution. Given the high sensitivity of the K–S test, we also tried Mann–Whitney test and it confirmed all the above results from K–S.

Comparison of 'preyed' vs. 'living' population-size distribution

We compared PM_p with the average *A. colbecki*-size distribution coming from Road Bay, Tethys Bay, and Adelie Cove. The Road Bay average-size distribution displayed a distinct gap in the middle-size range, and our PM_p is almost specular (Fig. 7a). The sizes with the highest probability to be consumed are the ones with the lowest frequency in the sampled population. As the consumption probability slows down towards the tails, the frequency rises almost in mirror image at the two sides of the gap.

The comparison between PM_p with the average-size distribution from Tethys Bay (Fig. 7b) indicates a similar
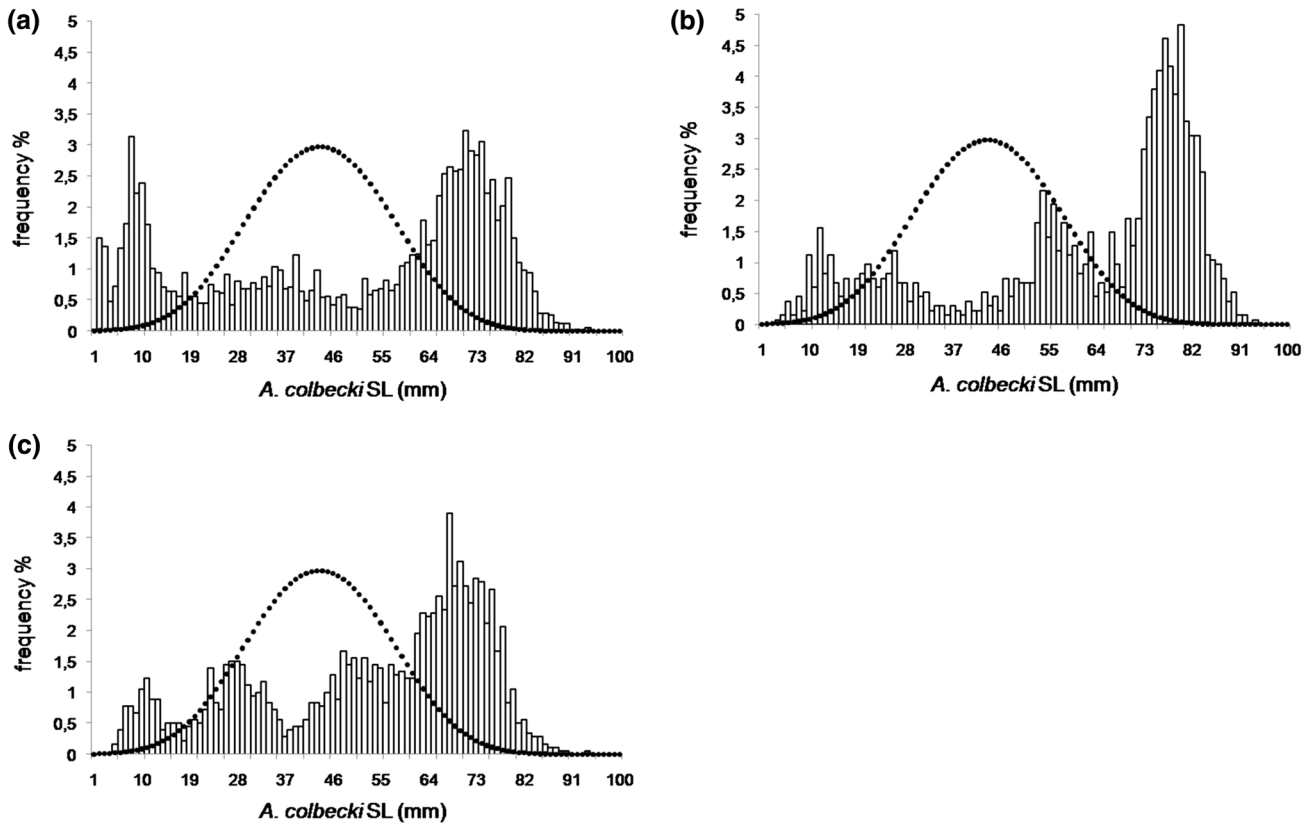

Fig. 7 Comparison between the modeled size distribution of preyed scallops (*filled circles*) with the pooled pluriannual population-size structure (*bars*) at Road Bay (**a**) from 1989 to 2013, Tethys Bay (**b**), 5 years: from 1998 to 2001 plus 2011/12 and 2012/13, and Adelie Cove (**c**), the same years as Tethys Bay. The predation model here shown is the one of the whole fish population that takes into account for both fish-size distribution and body mass factor. *SL* scallop shell length

relationship compared to that in Road Bay (although less clear), whereas the one with Adelie Cove appears to be quite different (Fig. 7c), providing clue for additional drivers shaping the prey population structure.

Discussion

We built a predation model (PM) that describes the distribution of probability for any *A. colbecki* size to be removed from the population because of *T. bernacchii* predation only. How much is this modeled preyed-size-frequency distribution complementary with the natural 'living' scallop population? i.e., if and how much does *T. bernacchii* predation affect *A. colbecki* population-size structure? The most important finding of this model is that predation pressure exerted by *T. bernacchii* mostly regards *A. colbecki* medium sizes (see Table 2), particularly on the mode of 43 mm. The relevant role of the fish in shaping prey-size structure is confirmed by the gap in living population centered on the same medium-sized specimens.

Basically, the new findings of this work, compared to the previous one (Vacchi et al. 2000), come from the probability statistical approach. Compared to the linear relationship alone, which is some kind of static, providing a mean prey size for any predator size, the computation of the predation-size range allowed to model the 'susceptibility (in terms of probability) to predation' of any scallop size in relation to any fish size and, as a consequence, to the whole predator population. Basically, a linear relationship is an observation, while a probability model is a prediction. Based on this approach, we were able to build a predator–prey relationship which can be tuned on potential changes in the fish population structure.

The predator–prey-size relationship, which our model relies on, is based on 59 observations and accounts for an increasing error with increasing *T. bernacchii* size. With more data, we would have had a greater goodness of fit, and consequently, we could have computed a smaller prediction interval for the scallop size on the best fit (i.e., a smaller predation range for any fish size) and/or a lower error. This would have given us more chance to detect differences between the different PMs, and in addition, our model would have been more accurate.

Both predator variables have substantial weight in determining trophic impact: normality of the *T. bernacchii*-size distribution drives the shape of the impact, while the BMF is responsible for the most impacted prey sizes (BMF moves mode rightwards, as larger fish eat more, thus have greater impact on prey sizes they feed upon). A major shortcoming could be that no specific DR for *T. bernacchii*, nor ontogenetic or sex-related differences are available in the literature. Flores et al. (2004) found that DR increases

along size for the notothenioid *Champsocephalus gunnari*; if this would be the case also for *T. bernacchii*, the overall PM would have been more left skewed. The overall effect of fish population on scallop one is more driven by the females, being more abundant (sex ratio 2:1, La Mesa et al. 2004a) and larger in size compared to males (consequently, eating more and larger prey items).

The low predation pressure on very small scallops (1 and 2 year juveniles) can be explained by the fact that they are probably not attractive for the fish sizes here considered. In fact, *T. bernacchii* has two main foraging behaviors. As a hunt and peck predator (Kiest 1993), it swims on the bottom seeking for its prey. In this way, smaller sizes do not maximize the benefits/costs ratio, as costs represent time and energy spent for seeking. However, *T. bernacchii* is also an ambush predator (Kiest 1993), relying on its lateral line organ, given that the fish does not show a good visual ability (Pankhurst and Montgomery 1989). Only movements above a certain threshold are likely to be detected by this organ (Carton and Montgomery 2002), and this could be a limit in detecting very small scallops as they perform smaller and weaker swimming bursts (Cattaneo-Vietti et al. 1997; Ansell et al. 1998). No scallops shorter than 19 mm SL were found in fish stomachs, so we could hypothesize that this size represents the lower threshold length, under which scallops become negligibly valuable in terms of "gain and effort" for the *T. bernacchii* sizes present in the population. Male fishes are probably the only ones responsible for the predation on this scallop size (see Table 2). Very small scallops could be attractive for very small fishes, but these latter are actually very few because of the size distribution and, in addition, exert little predation pressure because of the very limited food amount required. We can appreciate these size-related effects by looking at the differences between the basic PM and PM_{SD} and the basic PM and PM_{BMF}.

As far as the larger (adults) *Adamussium* specimens, the low predation pressure seems mostly due to the normality of the *T. bernacchii*-size distribution (which leads to a low abundance of larger fish) and the ability of adult *A. colbecki* to escape predation by swimming (Ansell et al. 1998). We can take 70 mm as upper threshold of consumed scallop size, as this size has the same probability to be consumed than 19 mm (the lower threshold), that is, they mirror in respect to the mode (see PM_p, Figs. 6, 7). Moreover, only 1 scallop over 70 mm has been found in *T. bernacchii* guts; larger scallop is probably too big to be handled even by the largest *T. bernacchii* available in the fish population.

Other works on fish predation preferences found a similar dome-shaped function of prey vulnerability with respect to prey size (Lundvall et al. 1999; Craig et al. 2006; Staudinger and Juanes 2010). Encounter rate is generally assumed to be a positive function of prey size, as the preys

become more detectable and more profitable, whereas capture success is assumed to be negatively related to prey size because of the increasing difficult in handling large preys: the resulting vulnerability curve is typically a convex (dome-shaped) function. The basic PM is dome shaped as the assumption of normality of capture into predation-size range (Claessen et al. 2002); if the maximum vulnerability would have been towards lower (or upper) limits of PSR, the PM would have been more right (or left) skewed.

It is very likely that there are further significant predator variables in addition to size frequency and daily consumption to be taken into account. For instance, individual behavior and preferences, periodicity in feeding (Kondo et al. 1990), and time of reproduction and spawning (which could lead to a greater daily feeding demand), may affect predation patterns, too. Yet, the variables used here can be considered constant over the years in which we investigated. Indeed, the *T. bernacchii* sampling performed in austral summer 1990/91 is the largest and most standardized sampling ever performed in the Terra Nova Bay area. Moreover, there is no reason for us to assume either a relevant shift in the fish-size structure or changes in diet niche through time.

In Road Bay, we can observe a heavy role of predation by *T. bernacchii* in structuring *A. colbecki* population-size structure. Selective predation has a substantial weight in shaping-size distribution of the scallop. Our model very well falls into the low of the scallop population-size-frequency distribution. The most impacted sizes are those with the lower frequency of occurrence in the living population; as the impact declines towards the sides, the frequency of the small and large-sized scallops rises. These findings provide robust evidence that *T. bernacchii* predation is a factor mostly affecting scallop population-size distribution in Road Bay. In addition, some invertebrate are reported to prey upon *A. colbecki*, such as the sea star *Odontaster validus* and the gastropod *Neobuccinum eatoni*, but no data are available on their rate of consumption. Yet, our results suggest that *T. bernacchii* has the major role in shaping the scallop-size structure. Moreover, no other fishes are reported to consume *A. colbecki* in a significant way (Naito and Iwami 1982; Vacchi et al. 2000). Obviously, other factors may affect *A. colbecki*-size distribution, such as intermittent recruitment (Berkman et al. 1991; Chiantore et al. 2002), occurrence of low salinity lenses to which only large and swimming capable individuals can escape (Stockton 1984), and possibly other still unknown variables, among which hydrographical drivers, such as episodic El Nino events. All these drivers can be responsible for differences across sites and times. In fact, while Tethys Bay shows a similar pattern, although less clear, in Adelie Cove, predation impact does not seem to be the main driver affecting *A. colbecki* population structure. This

'V'-shaped bay is set apart from the open sea by a 12–15 m deep sill, which forms a barrier to in- and outflows (Povero et al. 2001) and favours the persistence of fine sediments enriched in organic matter. Here, the scallop density is very low (max 10 ind/m^2). As *T. bernacchii* feeds on the most abundant prey item; herein, the fish probably shifts its diet to other items. This could also explain the lower strength of the pattern found in Tethys Bay: even if the scallop density here is greater than in Adelie Cove, it is quite low compared to Road Bay.

Other works in the literature show how predation can cause a bimodal prey population-size structure. Tegner and Dayton (1981) reported a bimodal-size-frequency distribution in the red sea urchin *Strongylocentrotus franciscanus* populations, caused by predation from spiny lobsters and sheephead. Juveniles (up to 40 mm) are protected by the spine canopies of adults, while urchins of medium size (50–80 mm) are very vulnerable to predators and large adults (>90 mm) to attain a partial refuge in size. Tegner and Levin (1983) confirmed their hypothesis on the role of predators in shaping prey population-size structure with laboratory studies. No specific patterns were found in other areas without predators, where *S. franciscanus* displayed various size distribution patterns, due to other factors, such as food availability and settlement and survival of juveniles (see Kato and Schroeter 1985, for references), as seems to be the case for Adelie Cove. Scheibling (1996) found a bimodal-size distribution, with prominent juvenile and adult modes and fewer intermediate-sized individuals in *Strongylocentrotus droebachiensis*, too.

Prey-size selectivity can affect preys population structure beyond their size distribution, with consequences on population dynamics and reproduction, as well as individual life history (Ślusarczyk 1997; Svensson 1997; Claessen et al. 2002). Heilmayer et al. (2003) found that *A. colbecki* reaches maturity at 8–9 year (around 45–65 mm length). Our model indicates that *T. bernacchii* feeds most intensely on *A. colbecki* of about 43 mm, i.e., on scallops that are just about to enter the reproductive phase. Accordingly, the fish may exert a major control on the scallop reproductive potential and thus on the population growth, similar to the predator control of population size in sea urchins (Scheibling and Hamm 1991). As *A. colbecki* is a key species and an ecosystem engineer in the Terra Nova Bay littoral, we can assume that relevant community attributes could be affected by the population dynamics of the scallop.

There is an increasing recognition that the High Antarctic area is a unique evolutionary site for fishes, and this has implications for the food web. Despite the increasing field studies, our knowledge about trophic web in the Ross Sea still needs to be elucidated, particularly in regard to middle trophic levels (Ainley 2002a; Pinkerton et al. 2010) and notothenioids are part of this research frame (La Mesa

et al. 2004b). Knowledge and predictive potential of the model developed in this study provide a potential tool to assess fish predation effects on a key benthic species in a predictive perspective which can be modulated to encompass variability in space and time in the fish population structure. Such knowledge should be used by the management authorities and advisory bodies to help develop management strategies. This is particularly true for some areas such as Terra Nova Bay that has been declared ASPA 161 in 2003 and still needs implementation in managing and protection, especially in the current climate change scenario, under which functional responses of Antarctic trophic web and ecosystem functions are still unclear (Trathan and Agnew 2010).

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