

Functional and energetic consequences of climate change on a predatory whelk



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ABSTRACT

The increasing rise in sea surface temperature caused by human activities currently represents the major threat to biodiversity and natural food webs. In this study we used the Lessepsian mussel *Brachidontes pharaonis*, one of the most recent invaders of the Mediterranean Sea, as a model to investigate the effect of a novel prey and a chronic increase in temperatures on functional parameters of local consumers, compared to the native mytilid species *Mytilaster minimus*. In particular we focused on the whelk *Stramonita haemastoma*, a widespread Mediterranean intertidal predator that actively preys on bivalves, barnacles and limpets, by studying the direct effects of such multiple stressors on feeding and growth rate, projected into a future climate change scenario (RCP8.5) relative to 2046–2065 with higher hypothesized temperatures of 2 °C. Gastropods showed a significantly higher feeding rate (ADFR) on *M. minimus* at high (6.45 ± 0.43) vs low temperatures (5.15 ± 0.33) compared to *B. pharaonis* (2.84 ± 0.37 vs 2.48 ± 0.27). Ingestion rate (ADIR), however, recorded higher values for *B. pharaonis* at high (1.71 ± 0.22) and low (1.49 ± 0.16) temperatures, compared to *M. minimus* (0.17 ± 0.01 vs 0.14 ± 0.01). Prey significantly influenced growth rate, condition index and the length-weight relationship (LWR) of whelks, while only ADFR seemed to be influenced by higher temperatures. In conclusion the extra amount of energy from the novel prey, together with temperature side effects, successfully influenced growth rates and reproductive events, positively affecting the global fitness of whelks.

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1. Introduction

Biotic interactions of local species are naturally shaped by environmental variability (Vasseur et al., 2007; Post, 2013). Seawater temperature, through the fundamental influence on metabolic machinery (Brown et al., 2004), plays a prominent role in driving functional and life history (LH) traits of most ectotherms, affecting their local persistence over time (*sensu* Sibly et al., 2012). Increasing temperature, as a consequence of future climate change (CC; IPCC, 2014), will probably determine cascading effects within natural communities, modifying current biodiversity (Gooding et al., 2009; Yamane and Gilman, 2009). Intertidal shores are harsh habitats with regard to temperature; the body temperatures of ectotherms can vary greatly according to daily tidal cycles and

seasonal weather conditions (Helmuth, 1998; Helmuth and Denny, 1999). Intertidal organisms are, for this reason, considered to live “on the edge” and thus CC is expected to modify the structure and species composition of those communities. CC may favour the spread of much more thermo-tolerant alien marine species, such as jellyfishes, bivalves and fishes by increasing the likelihood of reinforcing facilitation mechanisms (Southward et al., 1995; Stachowicz et al., 2002; Galil et al., 2015) or through the availability of empty niches in the invaded range (Hierro et al., 2005). Invasive species originated from the Red Sea (also called Lessepsian) and introduced to the Mediterranean Sea through the Suez Canal, are considerably more thermo-tolerant and better able to cope with highly changing thermal conditions than most Mediterranean species (Zerebecki and Sorte, 2011). Thus, when these species interact with local ecological equivalents, they will be advantaged by their major innate ability to survive under harsher conditions (Sarà et al., 2008). Invaders may then be able to replace native species in the local food webs (Simberloff et al., 2013) and

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consequently, local native consumers may count on a larger selection of prey. Nonetheless, local consumers, for their part, will also have to cope with increasing temperatures due to CC. However, although the effect of temperature is essentially pervasive (Gillooly et al., 2001), there is still little research to investigate the crossed effect between an alien prey and the increasing temperature on feeding behaviour (e.g. prey preference and consumption rate) of a local consumer apart from a single study dealing with the planktonic food webs (Seifert et al., 2014). According to theory (e.g. Arrhenius law; Kooijman, 2010; Sarà et al., 2014), increasing temperature should be particularly effective in enhancing the consumption rates in ectotherms (Sibly et al., 2012; Seifert et al., 2014). As a consequence, it is possible that an altered scheme of consumption dynamics of an abundant local predator has important local implications for the destabilization of the entire community equilibria (Vasseur and McCann, 2005; Seifert et al., 2014). Consumers are widely believed as able to adapt their feeding behaviour, and in particular the quality and quantity of food consumed in order to adjust their energy intake as a response to a varying environment (Tylianakis et al., 2008; Kordas et al., 2011; Kaspari et al., 2012). Ecologists use the term “plasticity” to describe this ability of organisms to modify their feeding behaviour, with compensatory feeding patterns, e.g. increased predation or ingestion rate to compensate for low quality resources or stressful conditions (Duarte et al., 2015). The same kind of plasticity can also be observed when consumers maximize consumption of high quality resources (Jacobsen and Sandjensen, 1994; Falkenberg et al., 2013) at the same time satisfying their energetic requirements and enhancing the individual fitness as suggested by classical ecological theory (Optimal Foraging Theory; Pyke, 1984). Here, we designed an experimental set-up to test if a widespread intertidal carnivorous gastropod, *Stramonita haemastoma*, when fed with an invasive bivalve, *Brachidontes pharaonis* (Sarà et al., 2000, 2003) under constant increased temperature of a few degrees (IPCC, 2014; RCP8.5 scenario relative to 2046–2065), will show any difference in the individual fitness with respect to when it fed with the native ecological equivalent prey, the bivalve *Mytilaster minimus*. Thus, we investigated whether (i) functional traits, such as those involved in feeding processes (i.e. predation and ingestion) were modified, and (ii) if any repercussions on life history (LH) traits, such as growth and fecundity, were evident. *Brachidontes* and *Mytilaster* (and *Stramonita*) represent a perfect model for this study: the former is one of the first time invaders (Pallary, 1912; Sarà et al., 2000, 2003), forms dense clusters on lower mid-littoral and subtidal rocks where *Stramonita* lives and spreads to the Western Basin (Sarà et al., 2013; Porporato et al. accepted, 2017). If present, it out-competes *M. minimus* (Safriel et al., 1980) that usually, in the absence of the alien species, proliferates and represents one of the most frequent items in the *Stramonita* diet (Safriel et al., 1980). Results from the present experiment comprise an important tool to evaluate the species colonization process and predict future spread, but will also be useful when assessing the potential expansion of Lessepsian species under higher temperatures and salinity conditions in the Mediterranean Sea, as a result of current global warming, where Lessepsian species would have a distinct advantage over native species (Sarà et al., 2008).

2. Materials and methods

Specimens of *S. haemastoma* were collected alive at low tide during the month of June 2014 from the intertidal shores near San Vito Lo Capo and the natural reserve of Monte Cofano (Castelluzzo, TP) (LAT: 38° 6'23.42"N; LONG: 12°42'17.84"E), where the mussels *B. pharaonis* and *M. minimus* were both present, although with different densities. As in surveys conducted along 100-m transects,

whelks were relatively abundant in this site with a density of ~0.56 ind./m² (Giacoletti et al., 2016), while *M. minimus* reached densities of ~19,753.3 ± 9445 ind./m² (G. Sarà, unpublished data), and *B. pharaonis* showed an occasional distribution. Whelks were brought back to the Experimental Aquaculture Facility at IAMC-CNR in Messina, and acclimated at room temperature (20–22 °C) and seawater salinity (37–38), and starved for one week to reduce stress generated by manipulation and transport (Garton and Stickle, 1980), before being transferred to experimental tanks (1350 L). The first tank (Tank A) was equipped with a 1500 W electric heater in order to maintain a higher temperature of 2 °C than the second tank (Tank B), which received water at ambient temperature. Water from each tank (A, B) was distributed into 16 1 L plastic compartments, divided in two groups of 8, each containing a single whelk. Natural variation of temperatures due to the open water flow were continuously monitored through the use of temperature data loggers (model: iButton G1, prec. ± 1 °C, res. ± 0.5 °C, <http://www.alphamach.com>). Each group of whelks was fed for the first 7 days with *B. pharaonis* or *M. minimus*, respectively, in order to allow whelks to experience handling with their prey (Rovero et al., 1999). After this last period of adaptation, animals were starved for another week prior to the start of the experiment: this step allowed for hunger levels to be standardized (Garton and Stickle, 1980). No drill mortality was detected during the experiment.

2.1. Prey-size selection

Size-classes for each prey species (*M. minimus* and *B. pharaonis*) used during the experiment were determined through a preliminary prey-choice test, following the experimental design proposed by Underwood and Clarke (2005). In practice, we tested 36 specimens of *S. haemastoma* of the same size, and acclimated as above. In the first experiment two size-classes of *M. minimus* (5–10 mm and >10 mm) were offered simultaneously, without replacement, to each single whelk in their respective 1-L plastic compartment. The experiment was replicated twice. In the second experiment, four size-classes of *B. pharaonis* (10–15, 15–20, 20–25 and 25–30 mm) were offered simultaneously to each single whelk, with the same experimental setting. These prey class-sizes were chosen as they corresponded to the most common sizes observed in the field where the whelks were observed feeding (unpubl. obs.). Each experiment was replicated twice. Attacks were considered to start when the prey was put in the arena, and ended as soon as specimens of *S. haemastoma* had made their choice. To meet the independence criterion (*sensu* Underwood, 1997), each whelk was used only once, and later they were killed by gentle freezing.

2.2. Growth rates and fecundity

The experiment involved 48 medium size (30–40 mm) individuals of *S. haemastoma*, and lasted for 135 days, from July 2nd to November 19th, 2014, in order to evaluate the influence of prey and temperature on the growth rate of our model predator. As before detailed, water from each experimental fiberglass tanks was distributed in two groups of 8 whelks, and each group was fed with a different diet. The first diet (D1) consisted of a fixed daily density (n = 12) of the indigenous mussel *M. minimus*, while the second diet (D2) involved the same density of the Lessepsian mussel *B. pharaonis*. Each day consumed items were replaced, in order to maintain a constant density of the prey, allowing the whelks to feed *ad libitum*. Specimens of *S. haemastoma* were weighed and measured every two weeks, by taking five different variables (Fig. 1): total weight (TW), shell length (SL), shell width (SW), aperture height (AH), and aperture width (AW) (Clau et al., 2002),

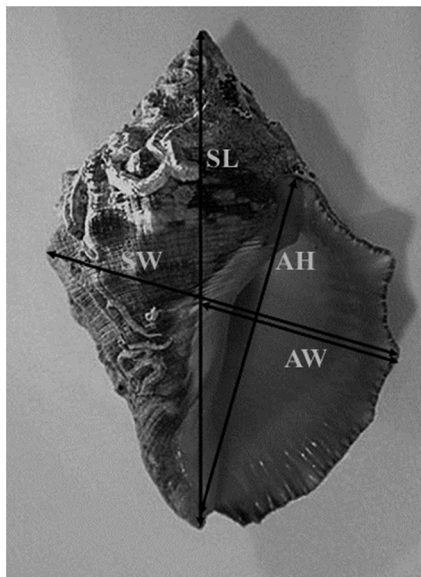


Fig. 1. Morphometric variables of *Stramonita haemastoma*: shell length (SL), shell width (SW), aperture height (AH), aperture width (AW).

in order to determine growth throughout the experimental period. Four whelks for each group (total = 16) were initially sacrificed in order to investigate the flesh organic content at the beginning of the experimental period.

The biomass of whelks exposed under two different temperatures and fed with two different diets was compared by estimating the individual dry weight (oven 95 °C for 24 h) and the ash content (muffle furnace at 450 °C for 4 h) of tissue to determine the Ash Free Dry Weight (AFDW) to the nearest 0.001 g. The Condition Index (CI) of whelks was estimated as: $CI = \left(\frac{FDW}{SDW} \right) * 100$ (Davenport and Chen, 1987), where FDW is the flesh dry weight, and SDW is the shell dry weight. The relationship (LWR) between shell length (SL) and total weight (TW) was calculated, as reported by Merella et al. (1997), in order to better estimate the growth rate of whelks through the comparison of the allometric regression slopes (b). Such a descriptor is powerful in capturing also the slightest differences in growth performance of marine invertebrates (sensu Gould, 1966). Fecundity and timing were estimated through simple daily visualization and here, unfortunately, no estimates of number of eggs or amount in grams are reported. Accordingly, whelks from both tanks were daily inspected, during the whole reproductive period, in order to annotate the presence or absence of released egg capsules. The proportion of individuals with eggs is used, in this study, as a proxy for fecundity.

2.3. Predation rates of whelks

Individual feeding rates of whelks was determined in single 1-L plastic compartment, as suggested by other authors (Palmer, 1983; Garton and Stickle, 1980). Prey of uniform length (*M. minimus* of ~10 mm; *B. pharaonis* of 15–20 mm) was selected to remove size as a variable within the experimental design. Feeding rates were determined by daily removing and counting the number of consumed prey from the fixed density ($n = 12$) for both *M. minimus* and *B. pharaonis*, constantly maintained through the experiment. The daily ingestion rate was determined by estimating the average prey tissue from $n = 100$ mussels of same size, and multiplying it for the predation rate. The predation rate was measured as the average daily feeding rate (ADFR, prey per drill/day; Garton and

Stickle, 1980) and the ingestion rate as the average daily ingestion rate of tissue (ADIR, g of tissue per drill/day) during the 20-day experiment. The determination of ADFR and ADIR was the first part of the experiment, and took place after the acclimation and conditioning period, with daily measurement for 20 consecutive days on the same 48 experimental whelks, in order to compare potential differences between treatments (temperature and diet). After that whelks were left feeding *ad libitum* with their respective prey, in order to calculate the growth rate.

2.4. Statistical analysis

In order to test for significant differences in predation, ingestion, and growth rates, ANOVA were performed using feeding or morphometric variables as fixed factors, with two levels of temperatures (T Low: seawater ambient temperature and T High: seawater ambient temperature + 2 °C). When significant differences were detected, the Student-Newman-Keuls (SNK) post-hoc pair wise comparisons of means were used (Underwood, 1997). Cochran's test was used prior to ANOVA to test the assumption of homogeneity of variances (Underwood, 1997). Pearson χ^2 test was used to test significant differences in temperatures, and data from prey size experiments (Darmaillacq et al., 2006). In order to test for significant differences in the condition index of whelks, a Permutational Multivariate Analysis of Variance (PERMANOVA) was used, considering time (initial - final), temperature (low - high), prey (*Brachidontes* – *Mytilaster*) as a fixed factor (2 levels). The Euclidean similarity measure was used, and all p-values were calculated using 9999 permutations of the residuals under a reduced model (Anderson, 2001).

3. Results

Different temperatures were significantly ($\chi^2 = 29.5$, $df = 140$, $p < 0.05$) maintained through the 135 day experimental period (Fig. 2). Mean temperatures recorded through the whole experimental period were 24.65 ± 1.65 for Tank A and 22.64 ± 1.76 for Tank B.

3.1. Prey-size selection

S. haemastoma showed a greater and significant preference for

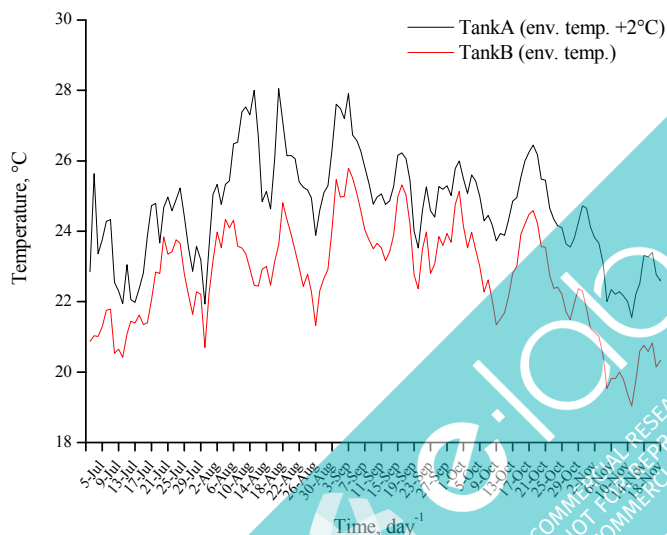


Fig. 2. Temperatures of tanks (A, B), continuously monitored through an electronic submersible data logger, for the whole length of the experiment (135 days).

the >10 mm class size of *M. minimus* ($\chi^2 = 12.1$, $df = 68$, $p < 0.05$), and for the 15–20 mm specimens of *B. pharaonis*, although not

statistically significant ($\chi^2 = 1.81$, $df = 68$, $p > 0.05$), (Fig. 3). Around 11% of whelks fed with *B. pharaonis* and 22% of specimens fed with *M. minimus* manifested no feeding or other activity, with a closed operculum.

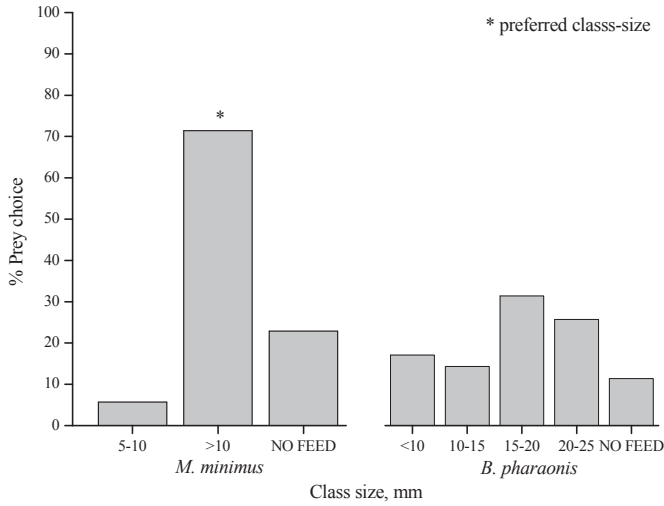


Fig. 3. Prey-size experiment, % prey choice on two different sizes of *M. minimus*, and on four different sizes of *B. pharaonis* (Preferred classes are indicated by *).

3.2. Growth rates and fecundity

Shell length (SL), aperture height (AH) and aperture width (AW) were not significantly influenced by *Brachidontes* at T High (SNKs; Fig. 4; Table 1). Condition index (CI) of whelks was derived from dry weight (DW) of flesh and shell, and resulted significantly influenced by time (PERMANOVA $p < 0.001$) and diet (PERMANOVA $p < 0.01$), while temperature revealed no significant effect (PERMANOVA $p > 0.05$; Table 2).

The L-W relationship of whelks at the end of the experimental period revealed higher allometric b values for the whelks that fed on *B. pharaonis* at both temperatures (T High 2.62 ± 0.32 ; T Low 2.43 ± 0.38), while lower values were recorded when feeding on *M. minimus* at T Low (2.34 ± 0.41), and in particular at T High (1.76 ± 0.92). Comparing the different growth rates of SL (Fig. 5), whelks showed a tendency to slow down shell growth during the reproductive period up to the month of August, whereafter SL increased again. The delta (δ) shell length has been calculated as

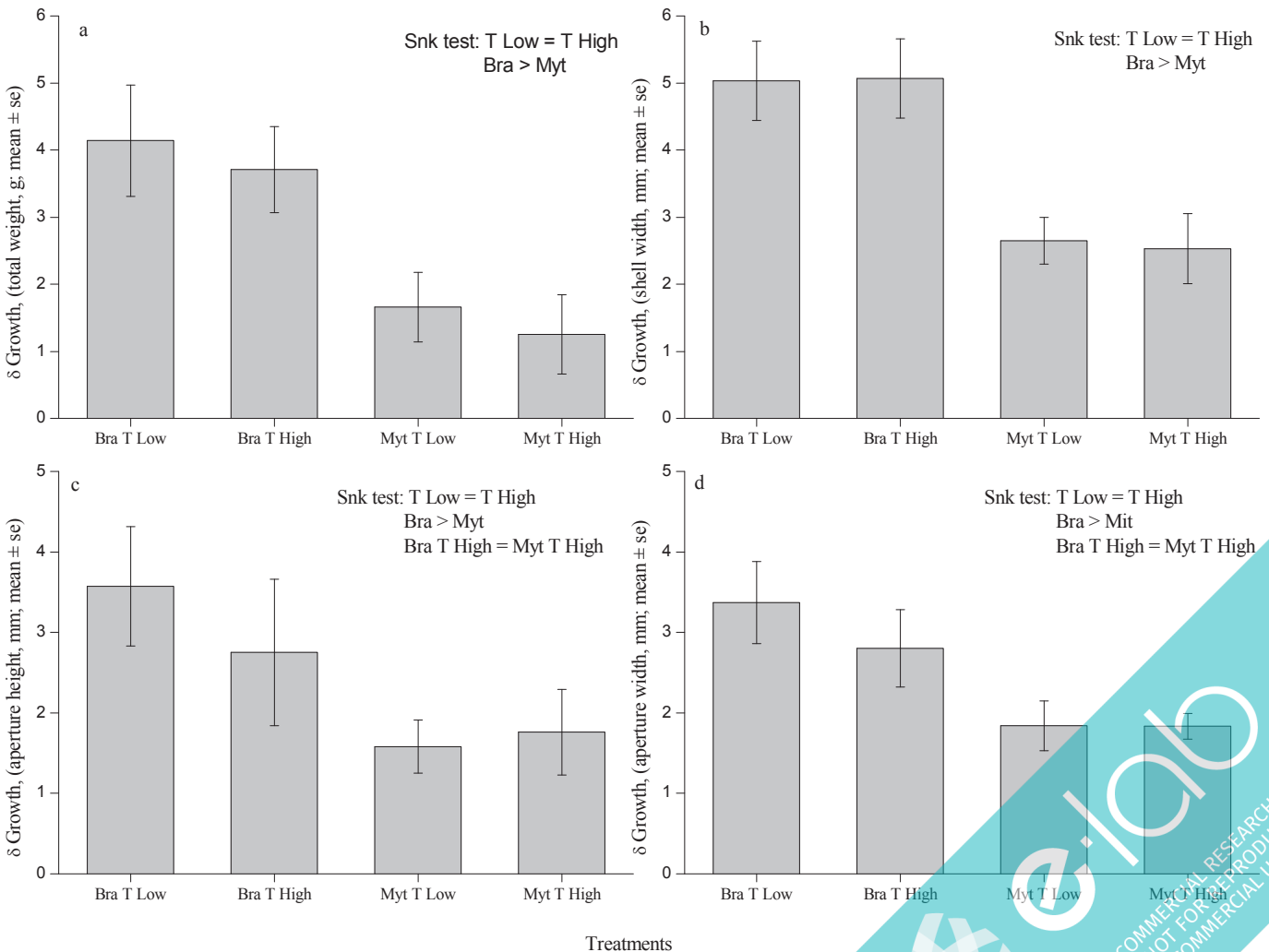


Fig. 4. (a-b-c-d) Growth rates of *S. haemastoma* analysed between treatments. Compared variables are from left to right, and from top to bottom: (a) total weight (TW), (b) shell width (SW), (c) aperture height (AH), (d) aperture width (AW).

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Table 1

ANOVA on morphometric variables of *S. haemastoma* feeding on two different prey species at different temperatures (* = $p < 0.05$; ** $p < 0.01$; *** = $p < 0.001$; ns = non-significant difference). TW = Total weight, SL = Shell length, SW = Shell width, AH = Aperture Height, AW = Aperture width.

	df	TW (g)			SL (mm)			SW (mm)		
		MS	F	p	MS	F	p	MS	F	p
Temp	1	1.41	0.41	ns	5.94	1.02	ns	0.014	0.01	ns
Prey	1	48.81	14.23	***	63.53	10.89	**	48.44	22.48	***
Temp*Prey	1	0.0024	0.00	ns	1.16	0.2	ns	0.047	0.02	ns
Residuals	28	3.43			5.83			2.15		

	df	AH (mm)			AW (mm)		
		MS	F	p	MS	F	p
Temp	1	0.81	0.23	ns	0.67	0.55	ns
Prey	1	17.85	5.02	*	12.5	10.38	**
Temp*Prey	1	1.99	0.56	ns	0.63	0.52	ns
Residuals	28	3.55			1.2		

the relative average growth rate (in mm) for each period by subtracting two consecutive time intervals (e.g. T1–T0; T2–T1; T3–T2, etc.) of experimental whelks.

Overall, every morphometric variable was significantly influenced by the prey consumed: TW ($p < 0.001$), SL ($p < 0.01$), SW ($p < 0.001$), AH ($p < 0.05$), AW ($p < 0.01$), while they were not affected by the different temperatures (ANOVA $p > 0.05$; Table 1; Figs. 4 and 5). Lastly, approx. 38% of the whelks feeding on *B. pharaonis* at normal temperature, and 50% at high temperatures, released egg capsules during the whole reproductive period, while no whelks that fed on the native prey completed the reproductive event (i.e. no eggs were produced). Under the higher temperature treatment, whelks produced eggs approx. 7 ± 3 days before those at ambient temperature.

3.3. Predation rates of whelks

The feeding experiments showed that temperature significantly affected the average daily feeding rates (ADFR) (ANOVA $p < 0.05$; Table 3). Significantly different ADFR resulted also on the two different prey species (ANOVA $p < 0.001$; Table 3).

SNK test showed a significantly higher ADFR on *M. minimus* at T High compared to T Low, while the ADFR on *B. pharaonis* was not significantly different between the two temperatures (Fig. 6a). The ADFR always resulted higher on *M. minimus* compared to *B. pharaonis* (Table 3). A non-significant effect of temperature (ANOVA $p > 0.05$; Table 3) was detected on the average daily ingestion rate (ADIR), but prey elicited significant differences in ADIR (ANOVA $p < 0.001$; Fig. 6b; Table 3). A significantly higher ADIR was evidenced when *Stramonita* fed on *B. pharaonis* compared to *M. minimus* in both tanks (A-B) (Table 3).

Table 2

(PERM)ANOVA table of result and group analysis for the Condition Index (C.I.) of *S. haemastoma* of tank A (env. temp. +2 °C) and tank B (env. temp.). (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant). T0 = Start of experimental period; Tf = End of experimental period; Bp = *B. pharaonis*; Mt = *M. minimus*.

Source	df	MS	Pseudo-F	P(perm)	Unique perms	Groups	t	P(perm)	Unique perms
Time	1	144.14	27.742	***	9821	T0, Tf	5.2671	***	9842
Temperature	1	0.2306	0.04438	ns	9847	Bp, Mt	3.1558	**	9846
Prey	1	51.745	9.9589	**	9822				
Time*Temp	1	1.4081	0.271	ns	9855				
Time*Prey	1	1.5876	0.30555	ns	9822				
Temp*Prey	1	0.0818	0.01574	ns	9831				
Time*Temp*Prey	1	0.0299	0.005771	ns	9812				
Residuals	38	5.1958							

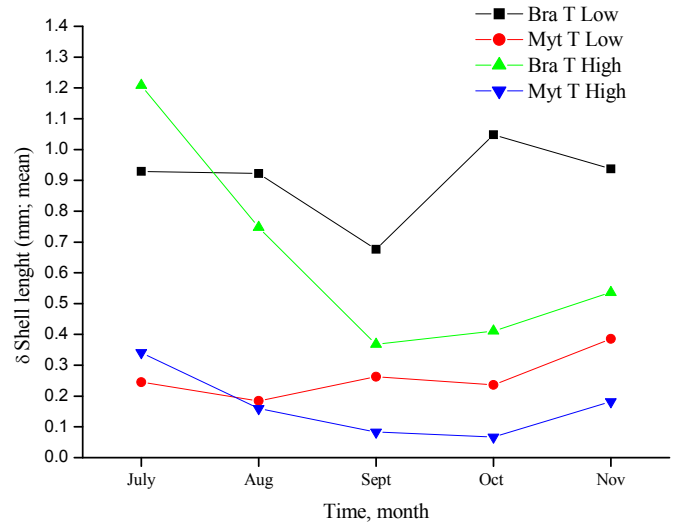


Fig. 5. Growth rates of *S. haemastoma* expressed in terms of $\bar{\delta}$ shell length (SL) during the whole experimental period (135 days), compared between treatments.

4. Discussion

The modification of phenology (Duarte, 2007) and reproductive failure (Helmuth et al., 2014; Montalto et al., 2014, 2016) are the two most important repercussions of temperature change in a context of CC claimed to have a strong effect on the persistence of local populations over time. Here, we showed that *S. haemastoma* consumption rates of two different bivalves were affected by increased temperature. This is consistent with what has already been shown by other authors when whelks fed on oyster spat (*C. virginica*; Garton and Stickle, 1980). On the contrary, temperature did not directly influence growth rate: the ~ 2 °C higher temperature condition based on a projected future climate change scenario (IPCC, 2014; Paris COP21) was not sufficient (or not maintained for sufficient time) to significantly affect the growth rates of our whelks. However, this result may be consistent with the theory that assumes ectotherms follow the Von Bertalanffy growth function (VBGF), where the asymptotic length in VBGF does not strictly depend on body temperature (Kooijman, 2010). This supports the concepts that ectotherms such as gastropods and bivalves, living under different body temperature conditions (as our experimental animals did), should not record significant deviations from natural common patterns (as those at ambient temperature did) in reaching the maximum/asymptotic size. In contrast, theory would suggest that the maximum body size of an individual is dependent on energy allocated to growth and maintenance requirements, and that it is directly dependent on food characteristics (i.e. quality and density). Such a fact will have consequences on the approaching

Table 3

Reported values and ANOVA table of results of: Average Daily Feeding Rate (ADFR) and Average Daily Ingestion Rate (ADIR) of *S. haemastoma* on two different prey species (*B. pharaonis* and *M. minimus*) at two different temperatures (environmental; env. + 2 °C) (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant).

VALUES			ADFR		ADIR		ANOVA	ADFR				ADIR			
Tank	Temp	Prey	mean	s.e.	mean	s.e.		df	MS	F	p	df	MS	F	p
A	High	Bra	2.84	0.37	1.71	0.22	Temp.	1	5.57	5.58	*	1	0.25	2.72	ns
A	High	Myt	6.45	0.43	0.17	0.01	Prey	1	78.91	79.09	**	1	41.67	454.99	***
B	Low	Bra	2.48	0.27	1.49	0.16	tempXprey	1	1.73	1.74	ns	1	0.025	0.27	ns
B	Low	Myt	5.15	0.33	0.14	0.01	Residuals	28	0.997			28	0.091		

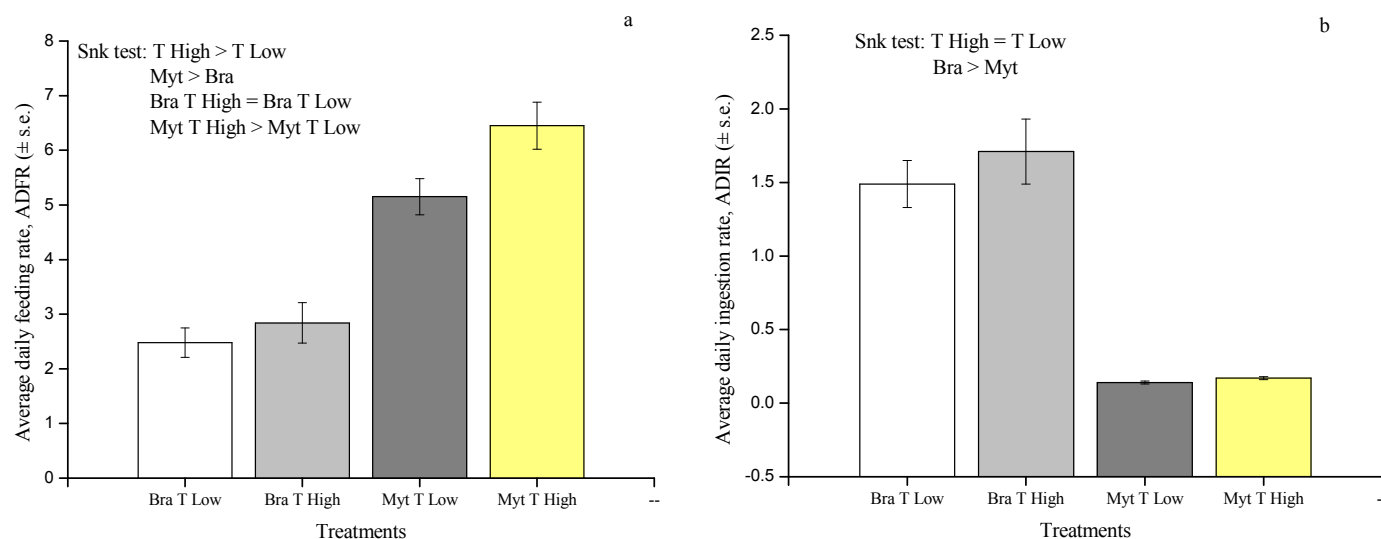


Fig. 6. (a–b) Predation rate experiment on two prey species with different temperatures: (a) Average daily feeding rate (ADFR); (b) average daily ingestion rate (ADIR).

velocity to the VBG asymptotic size. Thus, the time needed to reach maturity (if the amount of energy is sufficiently larger than that necessary for somatic and reproductive maintenance) will be influenced. In indeterminate growing ectotherms, maximum length is directly linked to the absolute reproductive output (i.e. Darwinian fitness), and then food quality and quantity may become main determinants of fitness of our investigated species. That growth rate can be directly linked with food value and density has been shown in many studies (Walne, 1963; Verity and Villareal, 1986; Kawamura et al., 1998), in particular when food is supplied *ad libitum* under experimental conditions. The diet relied on by the Lessepsian species promoted the most rapid growth and achievement of egg production, while growth of whelks relying on the indigenous *M. minimus* was slower and the energy ingested was not sufficient to reach reproduction; temperature did not influence these processes. Although a previous study showed a similar energetic value of flesh for g^{-1} for the two prey species (Giacoletti et al., 2016), the differences in the amount of edible tissue per individual were, on average, of such a magnitude to promote the Lessepsian mussel as the most profitable prey with respect to the native bivalve. All whelk morphometric variables measured here followed the same increasing pattern as they were significantly influenced by the prey eaten rather than temperature. The overall beneficial effect of the alien species diet on whelk performance is also testified by the condition index (CI). CI estimates were higher in specimens that actively fed on the alien rather than the native species, although a significant influence of temperature was not always evident. The analysis of allometric coefficients (b) further corroborated this, even though it revealed a kind of masked effect of the higher temperature treatment on mass-length ratios, not previously captured by other growth descriptors. Further research

is needed to investigate this phenomenon, which could be inconsistent with what has been previously observed and with theory. Most whelks fed with *B. pharaonis* (38% and 50% at normal temperature and high temperature, respectively) released egg capsules. In contrast, not surprisingly, whelks fed with the native species showed a massive reproductive failure (100% of individuals never produced eggs). At both temperatures, it appeared that whelks, particularly those who fed upon the Lessepsian mussels, started to divert energy from structure allocation (shell and flesh) towards reproduction as the temperature approximated to that of the reproduction threshold (~21–22 °C). This agrees with recent bioenergetics (e.g. Kooijman, 2010; Sarà et al., 2014) as also seen in other gastropods *Littorina keenae* (Chow, 1987). Reproductive failure was evident in those whelks fed on the natives and this was likely due to the lower food value of that species, which might be assumed to be sub-optimal (*sensu* Krebs and Davies, 1997) in the diet of our whelks. Consequently, in sites with no Lessepsian bivalves, whelks in nature probably prey on more than one species, selecting each time the more profitable item, using a strategy of trophic integration to outstrip the intrinsic energetic limitations of a diet based exclusively on *M. minimus*. While bioenergetic theory reports that size at the maturity is fixed (Kooijman, 2010), current research shows that prey promoting more rapid growth may be able to induce an anticipation of the age at the first reproduction: the more optimal the prey, the quicker the first maturity size is reached. In addition, a better diet should influence the so-called maternal effect that in whelks may comprise more and larger egg capsules (not measured in this study, but see Palmer, 1983). Our results are consistent with this theory as the whelks we studied, under a higher temperature relying on the alien species, anticipated a number of days the beginning of egg production and with the

observation on the planktonic larval duration time in fish and invertebrates. The planktonic larval duration time was shorter in the case of increasing temperature affecting the dispersal distance and optimal trophic conditions for the young stage (Duarte, 2007; O'Connor et al., 2007). Increased temperatures produced a similar effect in our whelks that may be subjected to similar effects influencing the ability of local populations to assure the best trophic conditions for new juveniles (O'Connor et al., 2007) with direct implications for population structure and then local diversity.

5. Concluding remarks

Our experiments allowed us to investigate how a novel prey may result as optimal in the diet of a predator, and even if through a borderline descriptor (allometric slopes) increased temperature showed a side effect in only a few months of exposure. Such observations should further raise awareness on the possible role of multiple stressors (here alien vs. increasing temperature; Vye et al., 2015) in reinforcing the effect of increasing temperature on life history traits of marine invertebrates. This means that a possible climate change scenario involving the warming of sea surface temperatures by $\sim 2^\circ\text{C}$ (IPCC, 2014), and the presence of a richer diet represented by an alien species, may alter the natural common temporal schemes of physiological processes and biotic interactions (Blois et al., 2013). In this context, the food acquisition process may represent a key point allowing the organismal energetic balance (Kooijman, 2010). Overall, the alien species, *B. pharaonis*, provided an extra amount of energy compared to the native mussel, *M. minimus*, at the same time promoting the fastest growth and release of egg capsules during the whelk's reproductive period, while none of the individuals feeding on *M. minimus* did the same. Altogether, these results appear to demonstrate that *M. minimus* will not be able to satisfy energetic requirements of whelks in a global climate change scenario, while the alien species will be.

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