



## Season-dependent effects of ocean warming on the physiological performance of a native and a non-native sea anemone

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### ABSTRACT

The effects of ocean warming on the physiological performance of marine organisms have been widely studied. However, few studies have considered the relevance of seasonal acclimation to elevated temperatures and whether native and non-native species have similar tolerances to warming. We tested the hypotheses that the susceptibility to warming in two species of sea anemones from temperate latitudes is (i) higher in winter than in summer, and (ii) higher in the native than in the non-native species. Seasonal variability in the upper thermal tolerance limit of *Anthothoe chilensis* (native) and *Anemonia alicemartinae* (non-native) individuals from the northern-central coast of Chile was assessed in laboratory experiments during the austral winter 2015 and summer 2016. In line with our predictions, seawater warming (up to 16 °C above natural levels) significantly suppressed individual performance proxies such as survival and asexual reproduction (longitudinal fission) in the native species, but not in the non-native species. However, asexual reproduction in the non-native sea anemone was rare across warming treatments, and the native species showed a stronger capacity to detach from the substratum under adverse thermal conditions. Negative effects of warming on survival and fission were evident only in winter, when asexual reproduction is more intense in these taxa. Finally, water temperatures of 30 °C or more were lethal for both native and non-native sea anemones. These results show that the non-native species may have a broader thermal tolerance (in terms of survival) than the native taxonomically related species, but the latter displays behavioral adaptations to avoid adverse conditions of high temperatures. We suggest that knowledge about life history traits related to seasonal variations in water temperature and the invasion status of a species can help to predict its performance in a warming ocean.

### 1. Introduction

The magnitude and speed of ocean warming is challenging the adaptation and survival capacity of coastal organisms (Hoffmann and Sgrò 2011) and the consequences for benthic shallow water ecosystems are largely unpredictable. So far, most studies that focused on thermal tolerance in marine benthic ectotherms used annual averages as experimental temperatures (Boersma et al. 2016). Although these studies have significantly contributed to our understanding of the ecological consequences of climate change, they do not allow to answer the question how organisms from environments with a strong seasonality (e.g. temperate zones) respond to warming. This question gains special

relevance as ocean warming is predicted to be stronger in summer than winter in most oceanic areas of the world (Sen Gupta et al. 2015). As animals acclimate to seasonal temperature fluctuations, the effects of elevated seawater temperatures on their performance could depend on the season in which an experiment is conducted. Moreover, the effects of ocean warming could vary substantially between species with different thermal tolerance ranges. This could especially be the case in native and non-native species that evolved in different thermal environments, but share the same habitat after the non-native has been translocated to the home range of the native. Therefore, experiments on the thermal tolerance of ectotherms, which are repeated over the seasonal cycle and use native and non-native species, will increase our

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ability to accurately predict the ecological effects of ocean warming.

Thermal tolerance of ectothermic organisms from temperate regions can vary seasonally, because these organisms are physiologically acclimated to higher temperatures in summer and lower temperatures in winter (Hopkin et al. 2006; Campbell et al. 2010; Sunday et al. 2010; Durrant et al. 2012; Morley et al. 2012; Reiser et al. 2016; Horne et al. 2016). Furthermore, seasonal variability in temperature can induce changes in the behavior of some marine organisms (Moison et al. 2012; Godbold and Solan 2013; Pond et al. 2014). For example, in marine invertebrates and some marine vertebrates, locomotion or reaction to stimuli are reduced (or increased) at high temperatures (Kidawa et al. 2010; Moison et al. 2012; Kent and Ojanguren 2015). Vital processes, such as reproduction, can also be highly seasonal (Lombardi et al. 2006; Durrant et al. 2012), so that the effects of ocean warming on individual as well as on population performance can vary strongly between seasons. In several sea anemones, for instance, asexual reproduction (i.e. longitudinal fission) is more frequent during winter than during summer and its occurrence usually indicates a good health status (Johnson and Shick 1977; Mire 1998). Thus, a decrease in fission frequency as a consequence of temperature increase would be a symptom of physiological compromise in sea anemones and may have severe consequences for population persistence. Since asexual reproduction involves a large energy investment, winter should be the season of the year in which these organisms are most vulnerable to environmental stress (Snell 1986). Therefore, the adverse effects of ocean warming on the physiological performance of marine invertebrates can be stronger in winter than in summer.

Organisms with a wide thermal tolerance range have been suggested to have a greater capacity of colonizing and establishing in new environments and by this potentially become non-native species (Somero 2010; Sorte et al. 2010; Lenz et al. 2011; Kelley 2014; Tepolt and Somero 2014; Nagar and Shenkar 2016). In the case of marine sessile invertebrates, furthermore, non-natives could be favored over natives when ocean temperatures continue to increase, because the former often tolerate significantly higher temperatures than the latter (Stachowicz et al. 2002; Sorte et al. 2010; Zerebecki and Sorte 2011). For instance, heat stress during transport has been demonstrated to have the potential to enhance the survival of mussels in their non-native geographic ranges (Lenz et al. 2018); ocean warming and extended summer season have the potential to boost reproduction in non-native bivalves, zooplankton, amphipods, and mysids (Holopainen et al. 2016). To generate accurate predictions of invasion risk, a mandatory first step is to determine whether non-native species actually have a broader thermal tolerance than ecologically and functionally similar species native species.

For the northern-central coast of Chile (ca. 30°S), climate-change scenarios predict that sea surface temperatures (SST) will increase by ~2.5 °C to ~4 °C until the end of this century (2CO<sub>2</sub> and 4CO<sub>2</sub> simulation scenarios, respectively; Brochier et al. 2013; Oerder et al. 2015). In this area, the constant activity of an upwelling center locked to a large headland sustains a highly productive shore (Moraga et al. 2001; Rutllant & Montecino 2002). Ocean warming can pose a serious threat to the ecosystem services provided by this region, as shown elsewhere (e.g. southern California; Frölicher and Laufkötter 2018). Understanding the variations in the response of individual organisms to warming and how these responses relate to other climate change-related phenomena, such as species introduction, will improve our ability to predict how ocean warming can impact these productive ecosystems.

The objective of this study was to determine how ocean warming affects the thermal performance of a native and a non-native sea anemone species from the northern-central coast of Chile. Two hypotheses were tested: (i) since ectothermic organisms show seasonal acclimation, the effects of temperature increase on performance will be more pronounced in winter than in summer, and (ii) since non-native species often have a wider thermal tolerance range, the negative effect of warming on their performance will be less pronounced than in an

ecologically similar native species.

## 2. Material and methods

### 2.1. Study area and model organisms

The study was conducted in the region of Coquimbo (northern-central Chile), which is located in the transition zone between the Peruvian and Magellan biogeographical provinces (Fernandez et al. 2000; Camus 2001; Tapia et al. 2014). The average SST in this area is 14 °C in winter and 17.5 °C in summer (Torres et al. 1999; Tapia et al. 2009; Garreaud et al. 2011). HOBO (Onset) temperature loggers deployed in the study area (Fig. S1) showed that SST decreased from ~18 °C to ~14 °C between March and June 2015 (austral autumn). SST remained around 14 °C between June and mid-September (austral winter) to subsequently re-increase to values between ~16 °C and ~20 °C from October 2015 to February 2016 (austral summer). It should be noted that the experimental period coincided with a period of El Niño (El Niño Southern Oscillation, ENSO), so these temperatures may have been higher than during a period of La Niña. The salinity in coastal waters around Coquimbo is ~34 PSU (Moraga et al. 2001) and the study area is located north of Punta Lengua de Vaca (30.25°S), which is a highly productive upwelling zone (Moraga et al. 2001; Rutllant & Montecino 2002).

For this study, two species of common sea anemones from the northern-central coast of Chile were selected: the native *Anthothoe chilensis* and the non-native *Anemonia alicemartinae*. *Anthothoe chilensis* (Cnidaria, Anthozoa, Sagartiidae) inhabits the intertidal and the shallow rocky subtidal down to 60 m depth (Häussermann 2006.) The species is distributed in Chile between Arica (18°S) and the fjord region in the south (45°S; Häussermann 2006), but recent evidence suggests the existence of several cryptic species associated with four ecoregions (Spano et al. 2018). *Anthothoe chilensis* is a small anemone of about 2 cm in diameter, which is commonly found in wave-protected areas. This species forms well-defined patches of unisexual clones, which are the product of longitudinal fission, i.e. asexual reproduction (Excoffon et al. 1999). Two different types of phenotypic coloration have been observed for *A. chilensis*: one with mainly white lines and another with orange lines (Excoffon et al. 1997). Only anemones with orange lines were used in this study, because this phenotype is more abundant in the study area.

*Anemonia alicemartinae* (Cnidaria, Anthozoa, Actiniidae) is a medium-sized sea anemone (2 to 4 cm pedal disc diameter) and one of the most obvious species in rocky intertidal habitats in northern Chile due to its high abundance, its frequent occurrence in exposed places, and its bright red color (Häussermann and Försterra 2001). This anemone is considered a non-native species that presumably came from the coasts of southern Peru (Häussermann and Försterra 2001; Castilla et al. 2005; Canales-Aguirre et al. 2015) and that showed a substantial southward extension of its geographical range during the past 40 years (Castilla et al. 2005). *Anemonia alicemartinae* lives at depths of 0–16 m from 17°S to 37°S (Häussermann 2006; López et al. 2013; Canales-Aguirre et al. 2015). This species exhibits asexual reproduction through longitudinal fission, which can be evidenced by the presence of fission scars (López et al. 2013). Both species are typically associated, but *A. chilensis* occupies more shaded positions than *A. alicemartinae* (e.g. rock crevices; Häussermann and Försterra 2001).

Individuals of both species were collected from two low-intertidal areas in Bahía La Herradura, Coquimbo (29.98°S and 71.36°W) during low tide and daylight hours. The individuals were transported while still attached to mid-sized (ca. 15 cm in diameter) rocks to the facilities of the Universidad Católica del Norte, Campus Guayacán, located in the same bay. Once in the wet laboratory, each individual was carefully removed from the stone with the aid of a small paint scraper and a thin plastic thread. One individual was retrieved from each rock to avoid using clones as replicates in the experiment.

## 2.2. Experimental design

The experimental design comprised the factors “species” (2 levels) and “temperature” (5 levels), with 10 replicates per treatment combination. The temperature levels were as follows: (a) a control that corresponded to the seasonal average SST in the study area (14 °C in winter, and 18 °C in summer), (b) average + 4 °C, (c) average + 8 °C, (d) average + 12 °C, and (e) average + 16 °C. Thus, the temperatures were 14 °C, 18 °C, 22 °C, 26 °C, and 30 °C for winter, and 18 °C, 22 °C, 26 °C, 30 °C, and 34 °C for summer.

The experiment was conducted in plastic tanks of 50 cm × 30 cm × 20 cm in length, width, and height, respectively. Each tank was maintained with running filtered seawater and air supply, and was coated with polystyrene for better temperature insulation. In each tank, we deployed twenty 250-ml plastic containers, each of one was assigned to one individual sea anemone (ten of each species in total). According to this setup, 100 individuals of sea anemones were used in the experiment, i.e. 50 individuals of the native and 50 of the non-native species. The containers received the treated seawater from the respectively tank. In each container, water variables, such as pH, oxygen, and salinity were checked every fourth day by a multi-parameter Multi 3430 WTW with the respective sensor. To check the concentration of nitrogen compounds, i.e. NH<sub>3</sub>, NH<sub>4</sub>, and NO<sub>2</sub> in the water, TETRA brand tests were used every fourth day. The study animals were fed ad libitum once daily in the morning with 3 ml of a self-cultivated solution of *Artemia salina* (~600–700 nauplii/ml). In the afternoon, we discharged the whole volume of water of the experimental units manually, making sure that the sea anemone would not fall out of its container. Afterwards we refilled each container with the treated seawater from its respective tank.

Once the sea anemones were placed individually in the experimental containers, we monitored their performance (survival and behavior) under the laboratory conditions for two days. After that period, water temperatures in the aquaria were gradually raised by increasing them by 2 °C per day. We started with the treatment level that had the highest temperature increase. In this way, it was ensured that all treatment levels reached their specific target temperatures on the same day, which was considered the “initial day” of the experiment and the experiment lasted for 21 days thereafter. Water temperature in each tank was increased by titanium heaters (Schego, USA), and monitored and fine-tuned by HOBBY Biotherm Pro regulators. The running seawater connection ensured a slow-pace refilling of the tanks in order to readjust the water to the target temperature and to avoid drastic temperature declines.

The experiment was repeated during three periods: from June 8 to July 4, 2015 (austral late autumn - early winter); from August 18 to September 16, 2015 (austral late winter); and from January 7 to February 5, 2016 (austral summer)—the three experiments are referred to as early winter, late winter, and summer, respectively. For each period, we collected (and acclimated) new individuals from the field to assure independency between experiments.

The rationale of conducting separate early and late winter experiment is that demographic processes, such as asexual reproduction, can be more frequent in sea anemones during winter (see for example for Sebens 1982, Lin et al. 1992, and Billingham and Ayre 1997 for *Anthopleura elegantissima*, *A. dixoniana*, and *Anthothoe albocincta*, respectively). In addition, the early- and late-winter experiments represented different environmental conditions within one season: SST showed a marked decrease (by ca. 2 °C) from May to June (right before the start of the early-winter experiment) and then re-increased by a similar amount from August to September (during the late-winter experiment). This indicates that the organisms used in the two experiments were acclimatized to different thermal conditions. This is because the sea anemones for the early-winter experiment were collected after they experienced a decrease in temperature, while those for the late-winter experiment experienced cooler and more stable conditions for three

months before and during the experiment (Fig. S1 in the supplementary material; see also Section 2.1 above).

The differences between both winter experiments were statistically tested by means of Pearson chi-square analyses on mortality and fission rates (see details in Sections 2.3 and 2.4, below). The models included the factors presence or absence of “mortality” or “fission”, “temperature”, “species”, and “timing” of the experiment (i.e. early or late winter). The results showed a statistically significant interaction between the experimental factors and timing, indicating that the responses of both variables to warming significantly varied between early and late winter ( $\chi^2_{25} = 54.74$ ,  $P < 0.001$  for mortality;  $\chi^2_{25} = 57.78$ ,  $P < 0.001$  for fission rate).

## 2.3. Response variables

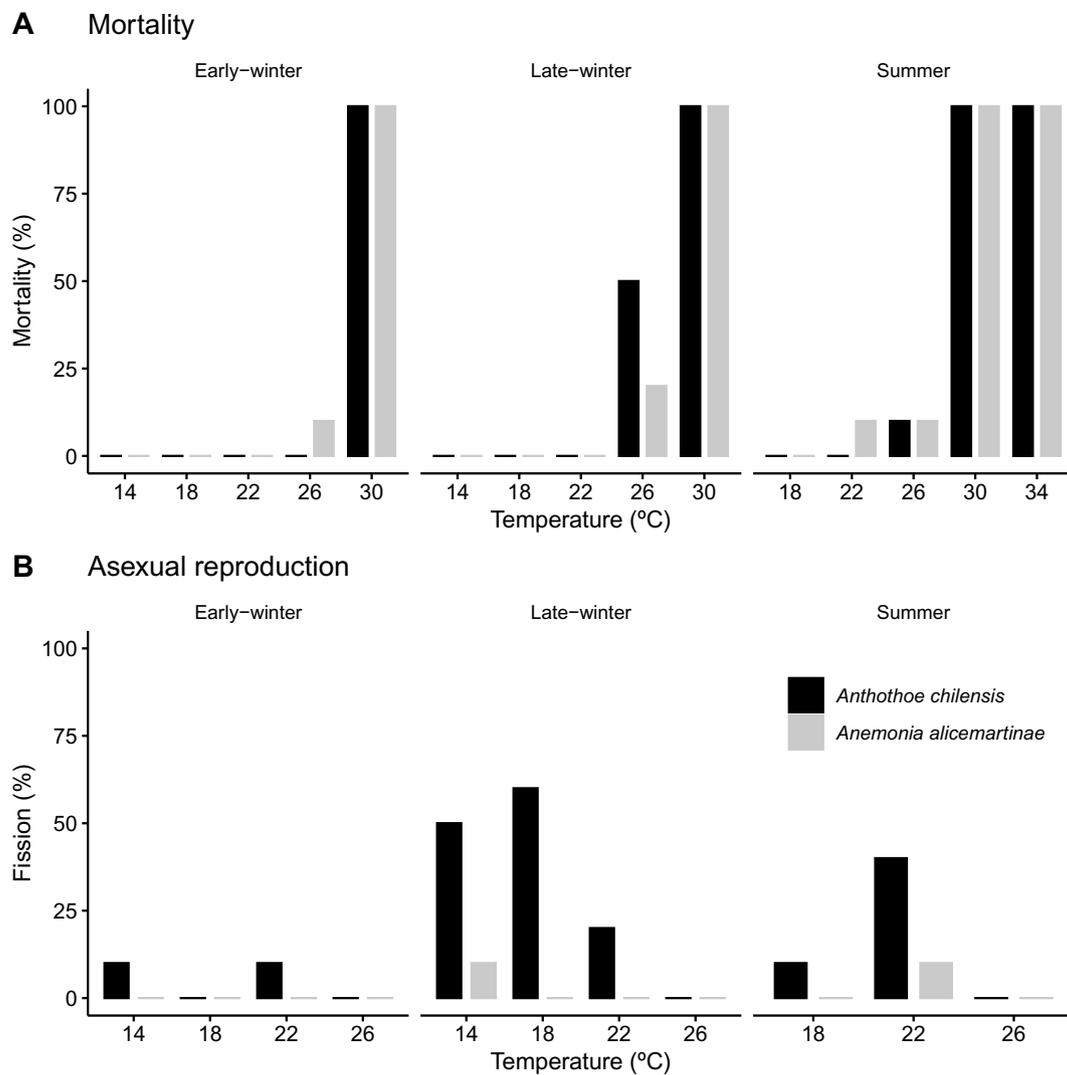
All test individuals were observed daily to assess survival, frequency of fission, and detachment rate. The main signs of death were a rapid decrease in body size, formation of mucus rings around the body, detachment, low or no tentacle activity, no response of the body to chemical (food) and mechanical (touch) stimuli, and the appearance of a reddish milky tone in the water inside the container. Detachment from the substratum occurred if an individual started to float after having been gently touched with a plastic pipette. Detachment rate for each individual was estimated as the number of detachment events standardized by the number of days of the experiment (21 days). Sea anemones show diverse asexual reproduction strategies (Chia 1976; Hand and Uhlinger 1992; Bocharova and Kozevich 2011), with longitudinal fission being reported for both of our test species. Only longitudinal fission events were considered and were recorded daily as present or absent.

## 2.4. Statistical analysis

For each dependent variable, separate analyses were run for each experiment. This approach allowed us to compare the effects of experimental treatments (i.e. main effects of the factors “temperature” and “species” and their interaction) between seasons (prediction i), and to test the effect of invasion status (i.e. the factor “species”) separately for each season (prediction ii).

Separate Pearson chi-square analyses were used to test for interactive effects of temperature and species on survival and fission frequency. For each variable, three-way tables with the following three factors were used: presence or absence of “mortality” or “fission”, “temperature” (four or five levels depending on the season of the year), and “species” (*A. chilensis* or *A. alicemartinae*). The testing procedure compares the frequency distribution of mortality or fission events, respectively, with a hypothetical distribution that indicates no interaction among the three variables. Following Bishop et al. (1975) and Sokal and Rohlf (1995), we used for each experiment the Likelihood Ratio to test a series of hierarchical models in order to find the best model with significant interaction terms. When significant interactions were found, paired post-hoc comparisons were made for each species separately (Sokal and Rohlf 1995). In these tests, frequency distributions of the control groups (14 °C or 18 °C) were compared with the other temperature levels.

Effects of “temperature” and “species” on the detachment rate per individual were investigated using a Generalized Linear Model (GLM) with Poisson error distribution. Residual vs. fitted value plots were used to assess heterogeneity of variances. The “treatment” contrast, in which a reference group (i.e. control) is contrasted against all other groups in the design, was used to estimate effect coefficients. Since a logarithmic link function was used, the effects were interpreted as exponential functions of the coefficients estimated by the models. These coefficients indicate multiplicative effects in the case of “species” and slopes in the case of “temperature”. Temperature by species interactive effects were evidenced by statistically significant differences between species-



**Fig. 1.** Mortality (A) and asexual reproduction (B) in *Anthothoe chilensis* (dark grey bars) and *Anemonia alicemartinae* (light grey bars) at different water temperatures in the experiments conducted in early winter, late winter, and summer (n = 10 replicates per temperature). The values are expressed as the percentage of individuals that died (A) or performed longitudinal fission (B) in each experiment and temperature treatment. 14 °C treatment was included only in early winter and late winter, and 34 °C only in summer. Fission was not analyzed in the 30 °C and 34 °C treatments due to 100% mortality.

specific slopes of temperature.

All analyses were performed in the R statistical v. 3.5.2 programming environment. The base and ggplot2 R-packages were used (Wickham 2016; R Core Team 2018).

### 3. Results

#### 3.1. Survival

Survival among sea anemones of both species was generally high in all experiments and at all temperature levels. Exceptions were the 30 °C level in all experiments and the 34 °C level in the summer experiment. In these groups, all individuals died during the acclimation period or during the first days of the experiment.

In the early-winter experiment, all *A. chilensis* individuals that survived the acclimation period (see previous paragraph) survived until the end of the experiment (Fig. 1A), while 10% of the individuals of *A. alicemartinae* that were subjected to 26 °C died. No mortality was observed at the other temperature levels (Fig. 1A). According to these small differences in survival between the two species, no significant interaction was observed between “temperature” and “species” (Table 1).

**Table 1**

Summary of three independent chi-square analyses (one per season) for the survival of *Anthothoe chilensis* and *Anemonia alicemartinae* under the influence of different water temperatures. “Species” (i.e. *A. chilensis* and *A. alicemartinae*), “temperature”, and “mortality rate” were included in each model.

Experiment	X <sup>2</sup>	DF	P
Early winter	7.09	10	0.717
Late winter	28.70	10	0.001
Summer	3.16	7	0.870

DF = degrees of freedom.

In the experiment conducted in late winter, 50% of the individuals of the native species and 20% of the non-native sea anemones died when they were exposed to 26 °C, while the individuals at the other temperature levels again showed no mortality (Fig. 1A). We observed a statistically significant interaction between “species” and “temperature” for the frequency of mortality events (Table 1). The post-hoc test showed significant differences in survival rates between 14 °C and 26 °C for the native but not for the non-native species (Table 2).

In Summer, there was one mortality event among the native sea anemones that were exposed to 26 °C and two mortality events in the non-

**Table 2**

Chi-square analyses on the frequency of survival events in late winter, after a significant interaction have been observed between the factors “species” (*Anthothoe chilensis* and *Anemonia alicemartinae*) and “temperature”.

Comparison	<i>A. chilensis</i>			<i>A. alicemartinae</i>		
	X <sup>2</sup>	DF	P	X <sup>2</sup>	DF	P
14 °C–18 °C	< 0.01	1	0.99	< 0.01	1	> 0.990
14 °C–22 °C	0.87	1	0.34	< 0.01	1	> 0.990
14 °C–26 °C	4.26	1	0.03	< 0.01	1	> 0.990

native species at 22 °C and at 26 °C, respectively (Fig. 1A). No significant effects of “temperature” or “species” emerged (Table 1).

### 3.2. Fission frequency

Longitudinal fission was more recurrent in the native than in the non-native species and the largest number of fission events was observed in late winter.

In early winter, two fission events occurred among the individuals of the native species, one in the group subjected to 14 °C and another in the group subjected to 22 °C, but none among the non-native sea anemones (Fig. 1B). No significant differences between species or the temperature levels were observed (Table 3).

During late winter, a substantial increase in fission events was observed in the native sea anemones, particularly at the lower temperatures (14 °C and 18 °C). *Anthothoe chilensis* exhibited 13 fission events, which comprised 50%, 60%, and 20% of the individuals in the groups exposed to 14 °C, 18 °C, and 22 °C, respectively (Fig. 1B). The non-native species reached a fission rate of only 10% and this was the case at 14 °C (Fig. 1A). In this season, “temperature” and “species” had a significant interactive effect on fission rates (Table 3). This was due to differences between the groups of the native *A. chilensis* that were exposed to 14 °C and 26 °C (Table 4).

In summer and in the native species, 10% and 40% of the individuals exposed to 18 °C and 22 °C, respectively, showed longitudinal fission (Fig. 1B), while the non-native sea anemones exhibited a fission rate of 10% at 22 °C (Fig. 1B). No fission events were observed in the group of anemones that were kept at 26 °C (Fig. 1B). Accordingly, no significant effects of “species” or “temperature” on fission rates were observed in summer (Table 3).

### 3.3. Detachment rate

A total of 38 detachment events were observed throughout the three experiments, of which nine occurred in early winter, six in late winter, and 23 in summer. The native species displayed the highest number of events in summer, particularly at 26 °C (Fig. 2). Only during Summer, a statistical interaction between “temperature” and “species” was observed (Table 5). In this season, the influence of temperature on detachment rates was about 2.5 times stronger in the native species than in the non-native species (Table 5).

**Table 3**

Summary of three independent chi-square analyses (one per season) for the fission rates of *Anthothoe chilensis* and *Anemonia alicemartinae* under the influence of different water temperature. “Species” (*A. chilensis* and *A. alicemartinae*), “temperature”, and “fission rates” were included in each model.

Experiment	X <sup>2</sup>	DF	P
Early winter	6.15	10	0.802
Late winter	28.80	10	0.001
Summer	13.30	7	0.064

DF = degrees of freedom.

**Table 4**

Chi-square analyses after significant associations between “species” (*Anthothoe chilensis* and *Anemonia alicemartinae*) and “temperature” on fission rates in late winter.

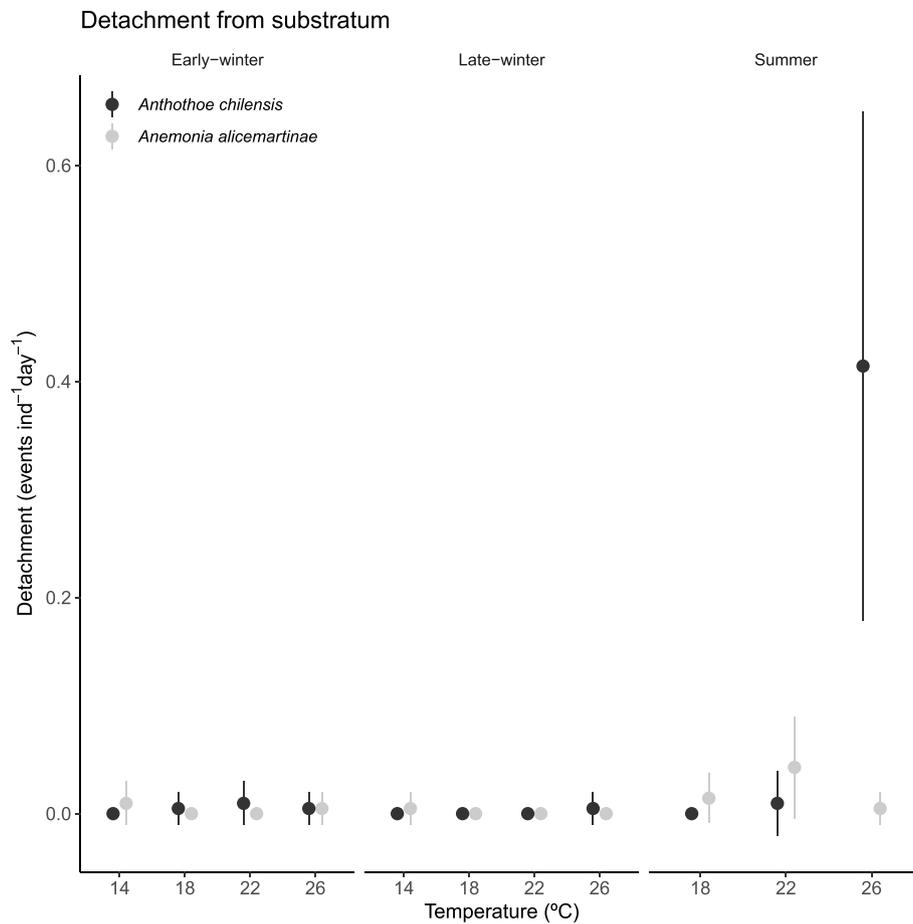
Comparison	<i>A. chilensis</i>			<i>A. alicemartinae</i>		
	X <sup>2</sup>	Df	P	X <sup>2</sup>	Df	P
14 °C–18 °C	< 0.01	1	0.99	< 0.01	1	> 0.990
14 °C–22 °C	0.87	1	0.34	< 0.01	1	> 0.990
14 °C–26 °C	4.26	1	0.03	< 0.01	1	> 0.990

## 4. Discussion

In this study, survival and asexual reproduction rates of two sea anemones (*Anthothoe chilensis* and *Anemonia alicemartinae*) were affected by temperature increase, while the size of this effect depended on the invasion status of the study species. Furthermore, significant effects of warming on these two response variables emerged only during the late winter experiments. Hence, we showed that the effects of ocean warming on two aspects of animal performance were dependent on the season of the year and were stronger in the native than in the non-native species (*A. chilensis* and *A. alicemartinae*, respectively). In contrast to this, warming had a stronger and positive effect on the detachment rate of the native than of the non-native species, and in this case the effect was observed only during summer (Summer). In the following, we discuss the role of seasonal acclimatization in maintaining the performance (survival, fission, and detachment rates) of *A. chilensis* and *A. alicemartinae* under conditions of ocean warming.

The fact that negative effects of increased temperature on the survival of the native species emerged only in late winter could be an indication that being acclimatized to low temperatures could compromise this species when water temperatures increase. Similar results have been found for other species. For example, Hamdoun et al. (2003) demonstrated that the thermal tolerance limit of the Japanese oyster *Magallana gigas* is lower in winter than in summer, with a difference in the limit between both seasons of 2–3 °C. Similarly, Morley et al. (2012) showed that the lethal temperature limits of the starfish *Odontaster validus* and the bivalve *Laternula elliptica* are also lower in winter than in summer. A similar case was reported for the mussel *Mytilus edulis*, whose upper thermal tolerance limit also varied with season (Jones et al. 2009), and the same has been observed in crustaceans (Hopkin et al. 2006). Likewise, seasonality mediates the effects of seawater warming on the ability of *M. galloprovincialis* individuals to cope with chemical pollution in the Mediterranean (Nardi et al. 2018). These seasonal differences in thermal tolerance and performance are possible due to the expression of different forms of HSP70 proteins (Chapple et al. 1998; Encomio and Chu 2005), although recent evidence suggests that season-dependent biochemical processes can prevent the variations in HSP70 protein expression (see Madeira et al. 2016 for an example in the intertidal shrimp *Palaemon elegans*). Other studies have shown that the effect of increasing SST in different periods of the year can vary between populations of the same species. For example, the populations of the barnacle *Pollicipes elegans* on the Pacific coast of Mexico show higher mortality rates in response to warming in summer than in winter, while those on the coast of Peru show no such seasonal differences (Crickenberger et al. 2015). Thus, seasonal acclimatization should be considered relevant when assessing the thermal tolerance of marine sessile invertebrates (e.g. Conover 1992; Storch et al. 2009).

In our study, the native species displayed more fission events than the non-native. Due to the low frequency of fission events, however, these differences were statistically significant only during late winter. In this period of the year, individuals of the native species showed the highest numbers of fission events at 14 °C and 18 °C, suggesting that these temperatures favor asexual reproduction. Since asexual reproduction is common in sea anemones and indicates healthy



**Fig. 2.** Detachment in *Anthothoe chilensis* and *Anemonia alicemartinae* at different water temperatures in early winter, late winter, and summer. Symbols indicate means and the error bars standard deviation (n = 10 replicates per temperature). 14 °C treatment was not included in the summer experiment.

**Table 5**

Poisson GLM estimated effects of temperature on the number of detachments from the substratum of *Anthothoe chilensis* and *Anemonia alicemartinae* during the autumn, winter, and summer experiment.

Season	Factor	Estimate	p
Early winter	Temperature	0.09	0.45
	Species	0.03	0.29
	Interaction	1.23	0.21
Late winter	Temperature	0.01	0.99
	Species	< 0.01	0.99
	Interaction	1.00	0.99
Summer	Temperature	0.94	0.49
	Species	< 0.01	< 0.01
	Interaction	2.49	< 0.01

The adjusted proportional difference between species (“species”), the adjusted slope of the regression line between the number of detachments and temperature (“temperature”), and the difference in slopes between species (i.e. the interaction) are provided.

individuals (Johnson and Shick 1977; Chia 1976; Hand and Uhlinger 1992; Mire 1998; Bocharova and Kozevich 2011), a decrease in fission frequency as a consequence of temperature increase should be considered as a symptom of physiological compromise (Snell 1986). Sea-water temperature, as a factor that varies seasonally in most temperate regions, has a significant influence on the frequency of fission in several species of cnidarians and porifera (Minasian and Mariscal 1979; Sebens 1980). For example, other sea anemones like *Heteractis magnifica* (Hoolbrook and Schmitt 2005), *Anthopleura elegantissima* (Sebens 1980; Sebens 1982), and *A. dixoniana* (Lin et al. 1992) reproduce asexually

more frequently in winter than in other periods of the year. Sponges occurring in the Mediterranean, like *Mycale contarenii* and *Tethya citrina*, also have their period of asexual reproduction in winter (Coma et al. 2000). Furthermore, the jellyfish *Aurelia aurita* reproduces asexually during winter and reduces this activity when it is exposed to elevated temperatures (Purcell et al. 2012). Consequently, ocean warming during winter should change the demographic dynamics of *A. chilensis*, and very likely also of other marine invertebrates, because it impairs asexual reproduction.

Mortality and asexual reproduction events in the native species were both more frequent in late winter than in early winter (June–July) and summer. Is there perhaps a relationship between mortality and asexual reproduction, which could become stronger in the course of ocean warming? Possibly yes, since the energy loss that results from longitudinal fission (Rosell 1993) may aggravate the effects of stress caused by warming. Both stressors together could therefore have impaired the survival of *A. chilensis* in our study during late winter. Similarly, the octocoral *Paramuricea clavata* is more vulnerable to elevated water temperatures during its reproductive period (Arizmendi-Mejía et al. 2015). In contrast to *A. chilensis*, warming had a small effect on survival and no effect on the asexual reproduction rates in the non-native *A. alicemartinae*. While the first observation suggests that *A. alicemartinae* is more robust than *A. chilensis*, the second could simply be due to the fact that *A. alicemartinae* exhibited lower fission rates than *A. chilensis*.

In this study, the effect of warming on the detachment rate was 2.5 times stronger in the native than the non-native species. Contrary to what was observed for mortality and asexual reproduction rates, however, this difference occurred during summer. This could be explained

by an evading behavior of *A. chilensis*, which may have evolved to avoid high temperatures that occur in summer. Such a behavior has been described for other sea anemones, such as *M. senile* (Wahl 1985a, 1985b) and *Sagartia troglodytes* (Riemann-Zörneck 1998), which tend to detach under adverse conditions. Furthermore, this could also represent a mechanism of dispersal as it has already been described for *A. alicemartinae*, which actively detaches from the substratum by inflating the pedal disk (López et al. 2013). If harsh environmental conditions trigger sea anemone detachment, then the question arises why we did not observe this behavior as a response to warming in winter? Possibly, the higher frequency of fission did not allow *A. chilensis* individuals to allocate energy to detaching. Something similar is known from the jellyfish *A. aurita*, which allocates most of its energy to asexual reproduction during winter, which even reduces somatic growth (Ishii and Bamstedt 1998). Indeed, seawater temperatures above 27 °C, which represent a summer heatwave scenario, notably reduce survival probability and impair the life cycle of *A. aurita* in the North Sea (Chi et al. 2019).

## 5. Conclusion

Our results show that the non-native sea anemone has a broader thermal tolerance, in terms of survival, than the native species. In addition, the frequent asexual reproduction of the native species was impaired by warming, which may compromise population growth in a scenario of ocean warming. Yet, the non-native sea anemone showed only few events of asexual reproduction, and the individuals of the native species showed a higher capacity to actively detach from the substratum during adverse abiotic conditions. These results suggest that, while the non-native species may be more resistant to thermal stress than the native species, the latter displayed behavioral adaptations that may aid the individuals to move to areas where less adverse abiotic conditions prevail.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2019.151229>.

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