



Does *Carcinus maenas* facilitate the invasion of *Xenostrobus securis*?

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ARTICLE INFO

Article history:

Received 4 March 2011

Received in revised form 27 May 2011

Accepted 31 May 2011

Available online 6 July 2011

Keywords:

Carcinus maenas

Climate change

Enemy release hypothesis

Feeding preference

Global warming

Invasion

Xenostrobus securis

ABSTRACT

Introduction of non-indigenous species can generate new trophic interactions that may facilitate or control their spread. The first recorded Atlantic population of the mytilid *Xenostrobus securis*, originally from New Zealand, offers an opportunity to examine how native predators may control the outcome of invasions. Laboratory experiments were done to evaluate the impact of the native crab, *Carcinus maenas*, on 2 species of mussels, *X. securis* and the native *Mytilus galloprovincialis*, at 3 different temperatures (15, 20 and 25 °C). In addition, we investigated handling time, breaking time and profitability for both species of mussel. We tested the hypotheses that (1) *C. maenas* exerts a greater predation pressure on the native mussel and (2) *C. maenas* increases its ingestion of the most profitable species of mussel at higher temperatures. The first hypothesis was supported because *C. maenas* consumed greater than twice as many native mussels as invasive ones at all temperatures. This greater consumption of *M. galloprovincialis* could be explained by its greater profitability and shorter handling and breaking time. These results are in concordance with the enemy release hypothesis suggesting that *C. maenas* might facilitate the invasion of *X. securis*. The consumer–prey relationship was not significantly affected by temperature although the number of *X. securis* ingested by *C. maenas* tended to decrease with increasing temperature, whereas the number of *M. galloprovincialis* consumed increased at the highest temperature. Results, therefore, suggest that global warming could enhance the facilitation of the invasion of *X. securis* due to its lower profitability and greater handling and breaking time.

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1. Introduction

Biological invasions are considered a major threat to biodiversity and the second most important cause of species extinction after habitat loss (Pejchar and Mooney, 2009). To be successful as invaders, non-indigenous species (NIS) have to complete several successive stages, beginning with their uptake and transfer from their native range to their release and establishment in a new area (Williamson, 2006). Thus, of all potential NIS only a few will successfully complete all the stages and proliferate in the introduced area (Williamson, 2006). In particular, once a NIS is introduced into a new region, the final outcome of the invasion depends both on the biological abilities of the NIS and its interaction with the environmental and biological conditions found at the host ecosystem (Lonsdale, 1999). Unfavourable environmental conditions may prevent the establishment of introduced species due to maladaptation (Lonsdale, 1999) but, when environmental conditions are tolerable, the recipient community may play a central role in the

invasion outcome. In marine habitats, most studies done on invader–recipient community relationships have focused their attention on the role of competitors and native diversity on the biotic resistance to NIS (e.g. Arenas et al., 2006; Stachowicz et al., 1999). Only recent studies have attempted to evaluate the role of herbivorous consumers on biological invasions in coastal systems (e.g. Britton-Simmons et al., 2011; Forslund et al., 2010; Vermeij et al., 2009). Few have evaluated the potential impact of predators on the success of NIS.

Two hypotheses involving consumer effects are widely cited as responsible for the success or failure of NIS when invading new areas. First, the enemy release hypothesis (ERH) proposes that an NIS may be favoured relative to native species due to the lack of specialised consumers or other enemies such as parasites or pathogens in the new area of distribution. Enemy release may also result from competitive release, as predation may disproportionately affect native competitors (Keane and Crawley, 2002). To date, most studies under the context of the ERH are limited to examining the effect of grazers, pathogens and parasites on terrestrial plants, where consumers generally show a high degree of species-specificity (Colautti et al., 2004). However, generalist consumers may also play an important role in ERH due to their potential greater impact on native species relative to NIS (Keane and Crawley, 2002). This is especially relevant in the marine environment where

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most consumers are generalists and specialists are uncommon (Thrush, 1999). Although the ERH cannot be the sole explanation of success for an invasion (Colautti et al., 2004), it has played an important role in the success of some invaders (reviewed in Keane and Crawley, 2002).

The second hypothesis linking consumers and invasions is the biotic resistance theory (BR). It suggests that native consumers could prevent NIS proliferation (Elton, 1958). However, studies testing BR on the marine realm have not been conclusive. Trowbridge (1995) found that grazing by native consumers on the invasive green alga *Codium fragile* ssp. *fragile* did not affect the spread and proliferation of this NIS, while other studies found that native consumers were able to limit the abundance and distribution of NIS (Byers, 2002; deRivera et al., 2005; Reusch, 1998).

Although both hypotheses are often framed as competing, it is more likely that invader–consumer interactions play out differently in different places and times. The intensity and strength of the consumer–prey relationship are indeed modulated by physical characteristics of habitat and/or environmental factors (Byers, 2002; Dudas et al., 2005; Yamane and Gilman, 2009). Interactions among environmental stressors including biological invasions have been often predicted (Walther et al., 2009), thus future increases in temperature due to climate warming (IPCC, 2007) could accelerate or reduce invasion success if new environmental conditions affect native consumers–NIS relationships. In particular, temperature increases the consumer's energetic demand and reduces time needed for digestion. With increasing temperature, increased rates of consumption and capture probability and decreased handling time by vertebrate and invertebrate consumers could be expected (Bergman, 1987; Gresens et al., 1982; McCoull et al., 1998; Yamane and Gilman, 2009). However, our understanding of how temperature mediates predator–prey interactions and foraging behaviour is limited and mostly missing in the context of biological invasions.

The recent introduction of the black-pygmy mussel *Xenostrobus securis* (Lamarck, 1819) into the Iberian Atlantic shores provides the chance to study the interaction of the major generalist predator in European estuaries the crab *Carcinus maenas* (Linnaeus), with this introduced species and the native mussel *Mytilus galloprovincialis* (Lamarck). *X. securis* is endemic to the brackish waters of New-Zealand and Australia, but since the early 90s it has been reported as a NIS in Italian coastal lagoons, the Po River delta, French Mediterranean lagoons and in Japanese waters (Pascual et al., 2010). Moreover, populations of *X. securis* have been recently reported in the inner part of the Ría de Vigo (Spain) (García et al., 2007), the first observed Atlantic population of this species. The introduced *X. securis* and native *M. galloprovincialis* belong to the same functional group, as both are sessile suspension feeders and can form extensive beds of individuals attached to substratum by byssus. Since it was first reported in the Ría de Vigo (García et al., 2007), the population of *X. securis* has spread, displacing the native *M. galloprovincialis* in the inner part of the ría (authors' personal observation), becoming a potential threat to the intensive mussel culture of this area. However, studies about the ecological impact of this NIS remain scarce and more information is needed to properly evaluate the real risk of this introduction.

In the present study, laboratory feeding experiments were carried out at different temperatures in order to test hypotheses related to consumer–prey relationships. Firstly, we tested if *C. maenas* exerts a greater predation pressure on the native mussel *M. galloprovincialis*. Secondly, we tested the hypothesis that *C. maenas* increases the ingestion of the most profitable species of mussel at higher temperatures. Predation pressure of *C. maenas* on the two species of mussels was evaluated using two approaches: 1) the behavioural preference of *C. maenas* for native and invasive mussels and 2) the number of native and invasive mussels consumed by *C. maenas* at three different temperatures.

This study provides valuable information about the role of *C. maenas* on the biological resistance or enemy release of *X. securis* in this new colonised area under different conditions of temperature.

2. Materials and methods

2.1. Collection and storage of animals

Laboratory experiments were performed at the Laboratory of Coastal Biodiversity in Porto (Portugal) from February to April 2010. The introduced *X. securis* belongs to the family Mytilidae, and thus, we selected *M. galloprovincialis*, the only native mytilid that serves as a similar prey, for this experiment. *C. maenas* was chosen as a native consumer because it is the major benthic generalist predator in estuarine areas (Chaves et al., 2010) and mytilids are an important component of its diet (Cunningham and Hughes, 1984; Mascaro and Seed, 2000). Adult *C. maenas* (4.5–5.7 cm carapace width) were collected using a baited drop net in the Cavado Estuary (41°31'39.01" N, 8°46'52.12"W) (Portugal). Only undamaged female crabs were used in the experiments to avoid possible morphological or sexual differences in predatory behaviour. Intertidal *M. galloprovincialis* and *X. securis* (3–4 cm shell length) were collected by hand at the mouth of the Douro Estuary (41°09'18.11"N, 8°40'50.36"W) (Portugal) and in the inner part of the Ría de Vigo (42°20'43.64"N, 8°36'25.12"W) (Spain), respectively. After collection, mussels were examined, epizotic organisms removed from the shells, and damaged mussels discarded.

In the laboratory, crabs were maintained in individual plastic containers (20 L) filled to a depth of 10 cm with aerated water (salinity 22 psu) in a walk-in CT chamber (Fitoclima 13000E). Water in the containers was replaced every 3 days. Containers were maintained under constant photoperiod (12 h light:12 h dark) and temperatures (15 °C, 20 °C, or 25 °C) during both the acclimation period and experimental tests. The lower experimental temperature (15 °C) corresponds to mean changes of temperature recorded at 10 m depth in the Ría de Vigo in April and May between 2006 and 2010 (14.93 °C ± 0.38 °C, www.metogalicia.es). In this area 20 °C is the maximum common temperature of superficial water observed at the end of summer (www.metogalicia.es). Finally, the elevated temperature (a further increase of 5 °C to 25 °C) was intended to simulate the ongoing increase in global sea temperature with an expected additional warming ranging from 1.4 to 5.8 °C (IPCC, 2007).

Mussels of each species were maintained in separate containers in the same conditions as described above for crabs, and were fed with a 10 mL of a concentrate culture of *Isochrysis galbana* every 2 days. Crabs were first starved for 48 h to standardise hunger levels. Afterwards, they were fed with the flesh of the native and invasive mussels for a further 48 h to ensure that all crabs recognised both species as prey and to avoid bias due to the crab's previous experience (Cunningham and Hughes, 1984). Finally, crabs were starved for a further 48 h prior to the start of the experiment.

2.2. Predation experiments

Experiments were performed in a walk-in CT chamber (Fitoclima 13000E). A single predator was placed in individual plastic container (n = 30) under constant photoperiod, temperature and salinity conditions, as outlined in the acclimation process. To test for prey preference, we used the experimental design proposed by Underwood and Clarke (2005). This design with choice and non-choice treatments considers prey preference when a predator exercises a non-random behaviour in the consumption of prey when presented with individuals of the two prey species, avoiding bias due to differences in handling time. Prior to the experiments, pilot feeding trials (n = 10) were performed to determine (a) the size range of each mussel species that crabs could successfully consume, and (b) the number of mussels that must be offered to crabs to avoid the total depletion of each prey type.

Crabs were offered a single type of prey of the native or the invasive mussel (10 prey per container) in the non-choice treatment or both types of prey simultaneously (5 native and 5 invasive prey per container) in the choice treatment. The total number of replicates per

treatment was 10. Containers were randomly distributed in the walk-in chamber to minimise the effect of location on crab responses. Tests ran for 48 h and at the end of this time the number of mussels of each species ingested by *C. maenas* was counted. Experiments were done at three different temperatures (15, 20 and 25 °C). Different crabs and mussels were used in each trial to ensure the independence of data.

2.3. Handling time and breaking time experiments

To study the time needed by *C. maenas* to consume each species of mussel, a handling time experiment was done at 20 °C. Individual *C. maenas* were maintained as indicated above and starved for 4 days to ensure that acquired predatory skills were lost (Cunningham and Hughes, 1984). Thereafter, 20 crabs were placed individually into plastic containers and offered either one individual native or one individual invasive mussel ($n=10$). Both crab and mussel sizes were similar to those used in the previous experiments. To calculate handling and breaking time, animals were recorded using a webcam (Microsoft® LifeCam 3.0) until they entirely consumed the mussel. Handling time and breaking time were calculated in seconds using the recorded videos. Handling time was evaluated as the period from the first contact of the crab with the mussel until the meal was completed and the empty shell abandoned. Breaking time was evaluated as the interval from the first contact of the crab with the mussel to the first bite of flesh (Dudas et al., 2005).

2.4. Mussel profitability

To quantify the profit obtained by crabs consuming each species of mussel, the available soft tissue (flesh) per unit of handling time was calculated (Elnor and Hughes, 1978). To determine the relationship between shell length and flesh weight, mussels were measured to the nearest 0.01 cm using callipers and the flesh removed from the shell by cutting the adductor muscle. The flesh was dried at 50 °C for 48 h and its dry weight determined to the nearest 0.01 g. The length and flesh dry weight relationship was evaluated using linear regression analysis ($y=0.077x-0.133$ $R^2=0.621$ for *M. galloprovincialis*; $y=0.104x-0.219$ $R^2=0.537$ for *X. securis*). Then flesh dry weight of the mussels used in the handling time experiments was thus estimated. Profitability was calculated as the net energy intake (flesh dry weight) per unit of handling time (Dudas et al., 2005).

2.5. Data analyses

Data on feeding preferences were analysed separately for each temperature by χ^2 test. A total of 30 comparisons were made (10 at each temperature) and individual test consisted of similar sized crabs (Stallings, 2010). The number of each species of mussel consumed in the non-choice treatments (expected values) were compared with the number of each species of mussel consumed in the choice treatment (calculated values). Corrections proposed by Underwood and Clarke (2005) were applied to decrease the probability of Type I error.

A two-way ANOVA was used to evaluate the effect of temperature on the number of ingested individuals of both species of mussel. For this analysis, only the non-choice treatments were considered. Species of mussel (fixed; 2 levels) and temperature (fixed; 3 levels) were considered as orthogonal factors.

Finally, one-way ANOVA was used to analyse possible differences between species of mussel on handling time, breaking time and mussel profitability. Species of mussel (fixed; 2 levels) was the only factor considered.

Prior to the ANOVA, data were examined for homogeneity of variances using the Cochran's test. Data transformation was not needed to achieve homogeneity of variances, except for mussel profitability data for which data were Ln (x)-transformed.

3. Results

3.1. Predation experiments

C. maenas consumed both the native (*M. galloprovincialis*) and the invasive (*X. securis*) mussels but, on average, crabs consumed more *M. galloprovincialis* than *X. securis* across all choice and temperature combinations (Fig. 1). Comparisons where χ^2 values could be calculated showed that *C. maenas* did not show preference sensu Underwood and Clarke (2005) for either the native or the invasive species of mussel under the three different temperatures (Table 1). This means that the proportion of each species of mussel consumed by *C. maenas* when they were presented alone was not significantly different from the proportion of the same species consumed when they were offered simultaneously. However, one out of the 10 comparisons conducted at 15 °C produced a significant χ^2 value. This was due to the only choice treatment where the crab consumed more *X. securis* than *M. galloprovincialis*.

There were, however, significant differences in the number of native and invasive mussels consumed by *C. maenas* (Table 2). *C. maenas* consumed more than twice as many *M. galloprovincialis* than *X. securis* (Fig. 2) at all studied temperatures. Even though the crab did not show

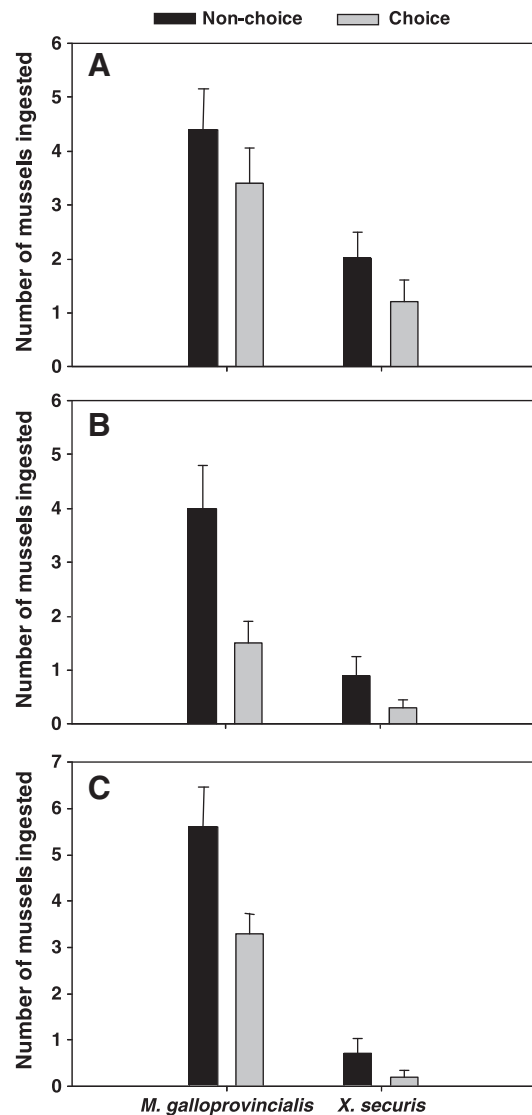


Fig. 1. Mean number (+SE) of *Mytilus galloprovincialis* and *Xenostrobus securis* ingested by *Carcinus maenas* in the choice and non-choice treatments of feeding preference experiments at 15 °C (A), 20 °C (B) and 25 °C (C).

Table 1

Test for prey preference by *Carcinus maenas* for either *Mytilus galloprovincialis* or *Xenostrobus securis* performed at 15, 20 and 25 °C. Observed (Obs) and null (Exp) values are given. m1 is the number of *M. galloprovincialis* eaten in stage 1, m2 is the number of *X. securis* eaten in stage 1, n1 is the number of *M. galloprovincialis* eaten in stage 2 and n2 is the number of *X. securis* eaten in stage 2.

Temperature	Test	Obs m1	Obs m2	Obs n1	Obs n2	Exp m1	Exp m2	Exp n1	Exp n2	X ²	p
15 °C	1	0	5	0	0	0.00	5.00	0.00	–	–	–
	2	4	3	5	1	4.54	2.24	4.02	1.98	1.18	>0.05
	3	2	1	2	2	1.74	1.27	2.31	1.69	0.21	>0.05
	4	6	3	5	2	6.09	2.84	4.77	2.23	0.05	>0.05
	5	5	3	5	4	4.81	3.25	5.37	3.63	0.11	>0.05
	6	5	2	3	2	4.80	2.29	3.38	1.62	0.20	>0.05
	7	3	1	5	0	3.38	0.44	4.42	0.58	1.45	>0.05
	8	4	2	5	0	4.54	1.12	4.01	0.99	2.13	>0.05
	9	8	0	4	0	8.00	0.00	4.00	0.00	0.00	–
	10	7	0	0	1	6.71	0.82	0.89	0.11	9.12	<0.005
20 °C	1	4	1	1	0	4.10	0.84	0.83	0.17	0.24	>0.05
	2	4	0	0	0	4.00	0.00	0.00	0.00	–	–
	3	7	0	0	0	7.00	0.00	0.00	0.00	–	–
	4	6	2	3	0	6.20	1.56	2.39	0.60	0.92	>0.05
	5	0	0	0	0	–	–	–	–	–	–
	6	6	0	2	1	5.70	0.65	2.69	0.31	2.48	>0.05
	7	2	1	3	0	2.40	0.50	2.48	0.52	1.23	>0.05
	8	6	0	2	1	5.70	0.65	2.69	0.31	2.48	>0.05
	9	0	2	3	1	0.97	1.04	1.93	2.07	3.21	>0.05
	10	5	3	1	0	5.17	2.75	0.65	0.35	0.57	>0.05
25 °C	1	10	0	4	0	–	–	–	–	–	–
	2	9	2	5	0	9.06	1.42	4.32	0.68	1.06	>0.05
	3	5	0	4	1	4.72	0.50	4.52	0.48	1.19	>0.05
	4	8	3	5	0	8.19	2.18	3.95	1.05	1.75	>0.05
	5	3	1	2	0	3.23	0.68	1.65	0.35	0.61	>0.05
	6	4	0	3	0	4.00	0	3.00	0.00	–	–
	7	6	0	3	1	5.73	0.59	3.63	0.37	1.82	>0.05
	8	2	0	4	0	2.00	0	4.00	0.00	–	–
	9	6	0	1	0	6.00	0.00	1.00	0.00	0.00	–
	10	3	1	2	0	3.23	0.68	1.65	0.35	0.61	>0.05

preference for any species of mussel, it consumed more native mussels than invasive ones.

Despite the lack of significant differences (i.e. no significant effects of Temperature or Temperature × Species interaction, Table 2), there is a trend that the number of native and invasive mussels ingested by *C. maenas* increased and decreased respectively with temperature (Fig. 2).

3.2. Handling time, breaking time and profitability

The greater consumption of *M. galloprovincialis* by *C. maenas* could be explained by differences in handling time, breaking time, and/or profitability provided by the native or the invasive mussels. *C. maenas* spent significantly more time eating individuals of *X. securis* than individuals of *M. galloprovincialis* ($F_{1, 18} = 6.5$, $p < 0.02$; Fig. 3A). Crabs also spent more time opening the shells of *X. securis* than those of *M. galloprovincialis* ($F_{1, 18} = 7.37$, $p < 0.02$; Fig. 3B). Finally, individuals of *M. galloprovincialis* presented significantly greater profitability than individuals of *X. securis* ($F_{1, 18} = 6.57$, $p < 0.02$; Fig. 3C).

4. Discussion

The influence of predators in shaping the structure of intertidal communities has been largely studied (Menge, 2000; Thrush, 1999). In the context of biological invasions, an increasing number of studies have focused their attention on the role of predators controlling the success of introduced species (e.g. Dudas et al., 2005; López et al., 2010; Shinen et al., 2009), but facilitation of invasion by native consumers has been scarcely reported (but see Simoncini and Miller, 2007). Here, we investigated the preference and consumption of two species of mussel by the predator *C. maenas* and how this consumption could shift depending on temperature. Results partially supported at least the initial hypotheses. Firstly, *C. maenas* showed a greater predation

pressure on the native mussel *M. galloprovincialis*. Secondly, temperature did not significantly affect the consumption of mussels by *C. maenas*, but there was an opposite trend in the consumption of native and invasive mussels with increasing temperature.

Preference implies that the consumer shows an active behavioural choice between the offered preys (Stallings, 2010). Thus, preference experiments are useful to isolate the behaviour of choice separating process from patterns observed in nature (Singer, 2000). This study has not detected a preference (sensu Underwood and Clarke, 2005) of *C. maenas* for either of the two species of mussel, although it consumed at least twice as many native mussels than invasive ones. As *C. maenas* did not show an active behavioural choice between the two mussel species, the greater consumption of the native mussel supports the first hypothesis of this study. Thus, *C. maenas* exerts a greater predation pressure on the native prey *M. galloprovincialis* than on the invasive species *X. securis*. The precise reasons for such higher consumption are not clear, although a greater profitability and shorter breaking and handling time might be some causal factors. Diverse morphological and ecological characteristics of bivalves have been interpreted as having been evolved to minimise the risk of predation. Indeed, several studies have reported that decapod crustaceans that include bivalves in their diet selectively forage depending on the morphological characteristics of their prey (see Sanchez-Salazar et al., 1987).

Although the two mussel species share similar ecological functions, they differ significantly in the morphology of their shells. In fact, *X. securis* has a subcylindrical shell with ventral arcuate margin and almost terminal umbones (see Garcí et al., 2007) whereas *M. galloprovincialis* has an oval, subtriangular shell, with prominent umbones, pointed and slightly curved ventrally (see List, 1902). These differences could affect their relative vulnerability to predation by crabs (Dudas et al., 2005; Mascaró and Seed, 2000), thus allowing *M. galloprovincialis* to be broken and consumed more quickly than *X. securis*, making it more profitable to *C. maenas*.

Table 2

Results of ANOVA on the prey consumption by *Carcinus maenas*. Species of mussel and temperature were fixed factors.

Cochran's test		C = 0.305 p > 0.05		
Source of variation	df	MS	F	P
Species	1	180.267	44.69	<0.001
Temperature	2	3.516	0.87	>0.4
Species × temperature	2	8.3167	2.06	>0.1
RES	54	4.0333		
Total	59			

Additionally, Pascual et al. (2010) found that *X. securis* collected at the Ría de Vigo shows less parasites than the native mussel *M. galloprovincialis*. The fact that *X. securis* experiences an ecological release from parasites and predators might facilitate its invasion. These findings are, therefore, in agreement with the ERH which states that generalist predators will have a greater impact on the native species than on the NIS (Keane and Crawley, 2002). But to date, most studies dealing with the ERH have been focused on invasive plants in terrestrial habitats (Colautti et al., 2004).

Recent works have studied the ERH on marine environments and most of them were focused on parasites (Torchin et al., 2001, 2002, 2003) or grazers (Cacabelos et al., 2010; Forslund et al., 2010; Strong et al., 2009; Vermeij et al., 2009). To our knowledge, the present study and the one by Simoncini and Miller (2007) are the only studies that found a smaller vulnerability of invasive species to generalist consumers in marine environments. When generalist consumers are considered, the relationship between the NIS and native consumers will depend basically on the biological traits of the NIS (Verhoeven et al., 2009). Here the lower profitability and greater breaking and handling times of *X. securis* compared to the native mussel could lead the native consumer to exert a greater predation pressure on the native mussel. Nevertheless, this initial ecological release could only be a temporary circumstance, as predatory skills and preference may change over space and time (Britton-Simmons et al., 2011).

Different prey types are able to induce changes in the behaviour and morphology of predators. For example, *C. maenas* exposed to different prey types showed a morphological response to improve prey handling after only two moults (Edgell and Rochette, 2009). On the other hand, many consumers seem to need a time lag to actively ingest introduced species (Britton-Simmons et al., 2011; López et al., 2010; Reusch, 1998). The mechanism responsible for this shift could be related to the relative abundance of the NIS. Changes in the abundance of prey could modify the probability of encounter resulting in shifts in the feeding behaviour

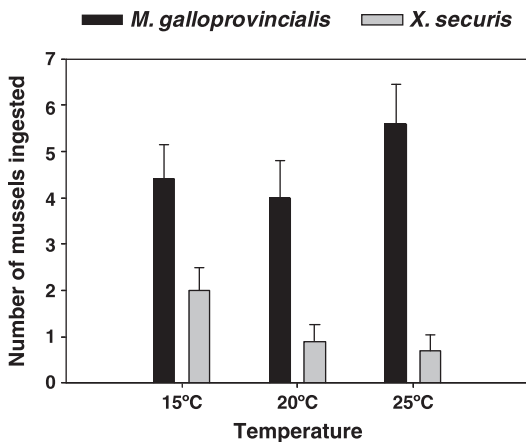


Fig. 2. Mean frequency (+SE) of predation by *Carcinus maenas* on the native *Mytilus galloprovincialis* and the invasive *Xenostrobus securis* at different temperatures in the laboratory.

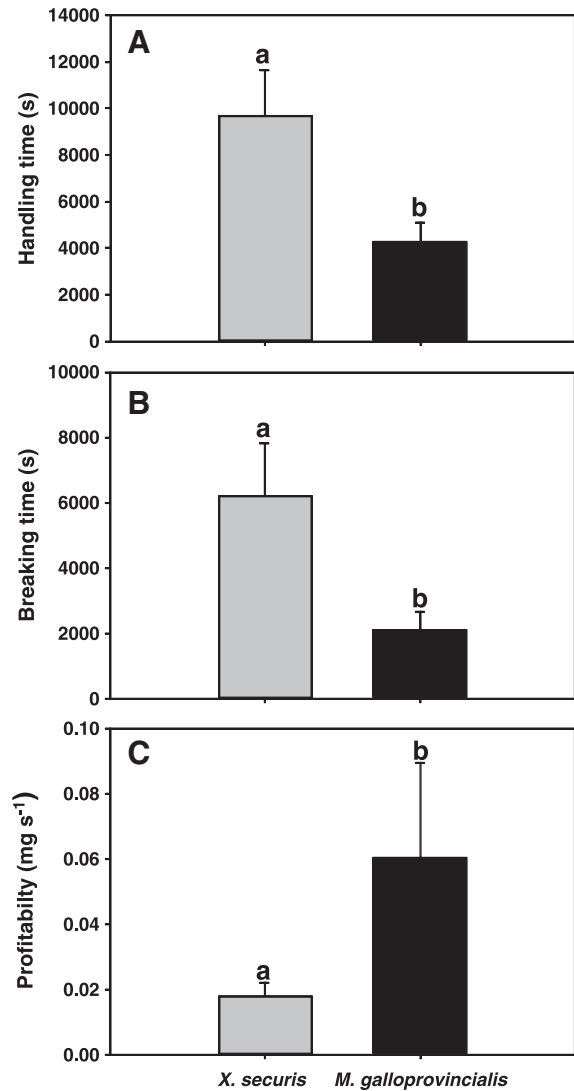


Fig. 3. Mean values (+SE) of: handling time (A); breaking time (B) and profitability (C) for *Xenostrobus securis* and *Mytilus galloprovincialis*. Different letters indicate significant differences between species of mussel ($p < 0.05$).

of predators (Fairweather, 1988). In the inner part of the Ría de Vigo, *X. securis* has out-competed and excluded *M. galloprovincialis* (authors' personal observation), becoming the only available mussel prey in this area. Thus, dominance of *X. securis* could lead *C. maenas* to prey on *X. securis*, shifting from initial enemy release to biological resistance in the future. However, in the present study *C. maenas* consumed less *X. securis* than *M. galloprovincialis* in the non-choice treatment where each prey was presented alone. Moreover, in some of the choice treatments crabs did not consume any invasive mussel, even when all the available native mussels had been consumed (Table 1).

Although results did not show significant effects of temperature in the consumption of *M. galloprovincialis* or *X. securis*, there was a trend to a greater consumption of the former one and a lower consumption of the latter one at the highest temperature. Such relationships have been reported in some other studies (Sanchez-Salazar et al., 1987; Wallace, 1973). The fact that these patterns were not significant may be explained by the large variability among replicates. Large variability within treatment can increase the probability of type II error i.e. retention of the null hypothesis when it is false (Underwood, 1981). Another possibility is that the ANOVA analysis was not able to detect these small but, probably biologically important, changes in consumption related to temperature (Underwood, 1981). Temperature is a key

factor controlling physiology and behaviour of organisms (Newell and Branch, 1980; Yamane and Gilman, 2009). For example, changes in temperature may increase metabolic activity (Sanchez-Salazar et al., 1987; Wallace, 1973) and thus decrease the time needed for digestion and handling of prey. Not only could the metabolism of predators be enhanced by temperatures, but so could be the metabolism of prey. In addition, temperature may affect predator–prey interactions, although the direction and magnitude of these effects are very variable (Pincebourde et al., 2008; Sanford, 2002; Yamane and Gilman, 2009).

In conclusion, results indicated that *X. securis* suffered a lower predation pressure than did *M. galloprovincialis*. This greater consumption of the native mussel agrees with the predictions of the ERH and thus invasion of *X. securis* might be indirectly facilitated by predatory behaviour of *C. maenas*. Results also suggest that increased temperature could enhance this facilitation and favour the mussel's spread due to its lower profitability and associated greater handling and breaking times. In a global warming scenario *C. maenas* could increase the consumption of native mussels and reduce the consumption of *X. securis* and therefore, facilitate its spread. Although results of experimental work should always be interpreted with caution, the present findings have important implications for our understanding of invaded communities.

Future research should be focused on long time studies in the field that help to clarify if this ecological release is permanent or if it may shift to biological resistance due to different mechanisms such as plasticity of the predator or changes in the relative abundance of native and invasive prey. Moreover, crabs could learn how to consume the invasive mussel.

This is particularly relevant since this Atlantic population of the black-pygmy mussel is located in an area with an intense commercial culture of *M. galloprovincialis* (around 270,000 tonnes of mussels per year are produced in Galicia). Part of this production comes from the estuarine part of the ría where both species of mussel are present and *C. maenas* is abundant. In the Galician rías mussels are cultured on rafts so, the facilitation by crabs will not be possible on cultured mussels. However, the rapid increase of *X. securis* on the area could increase the recruitment of this species on the rafts where they could compete with the native mussel.

Acknowledgments

Financial support comes from the project “The AXA Marine Aliens and Climate Change Project” and P. Veiga is the beneficiary of a financial contribution from the AXA Research Fund. Authors thank Dr. E. Cacabelos for valuable comments and help on the data analyses and R. Vieira for her help on crabs and mussel collection. We are also grateful to two anonymous referees, whose helpful comments and suggestions improved the manuscript. [ST]

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