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7 **Does expansion of the introduced Manila clam *Ruditapes philippinarum***  
8 **cause competitive displacement of the European native clam *Ruditapes***  
9 ***decussatus*?**

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27

28 **Abstract**

29

30 In several estuaries or lagoons of Europe the introduced Manila clam *Ruditapes*  
31 *philippinarum* has supplanted the native grooved carpet shell clam *Ruditapes decussatus*  
32 by occupying almost entirely its ecological niche and relegating it to restricted areas.  
33 However, it is not clear if the nonindigenous clam is the direct responsible of this  
34 predominance patterns. Within this context, the main goal of the present study was to  
35 analyze the competitive interaction between the non indigenous Manila clam and the  
36 native carpet shell clam to determine whether this interaction could impact directly  
37 growth and mortality of the native clam populations. The effect of exposure to predators  
38 on both species was also examined. For this purpose, between May 2010 and May 2011 a  
39 field experiment was conducted on an intertidal area in the Bay of Santander (N Spain)  
40 where both species coexist without an extreme predominance of the introduced species.  
41 Relative density of clam species was manipulated in a randomized block experimental  
42 design. The results obtained show that (i) the increased density of Manila clam simulating  
43 species expansion scenario does not affect growth or mortality of the native clam; (ii) for  
44 densities of Manila clam substantially higher than observed in the field, predation plays  
45 an essential role in regulating both species populations, limiting their density increase.  
46 Moreover, Manila clam appears to be more negatively impacted by predation compared to  
47 the native clam. Overall, our results indicate that predation has a more significant effect  
48 on both populations when compared to competitive interaction.

49

50 **Keywords:** Competition, clams, nonindigenous, native, *Ruditapes decussatus*, *Ruditapes*  
51 *philippinarum*

52

### 53 **1. Introduction**

54 Biological invasions are natural and necessary for the persistence of life. However, the  
55 introduction and spread of invasive species has been identified as a major ecological  
56 threat in coastal marine communities (e.g. Cohen & Carlton 1998; Occhipinti-Amborgi,  
57 2001; Dawson et al., 2005; Claudet et al., 2010). This is the result of several mechanisms  
58 that can affect the native species such as predation, parasitism, herbivores, vectoring of  
59 pathogens, modification of critical habitat, hybridization, and competition (Simberloff,  
60 2000; Dudas et al., 2005; Occhipinti-Amborgi, 2007). The 1992 ‘Rio’ Convention on  
61 Biological Diversity included the problems caused by introduced species as a priority  
62 item (Mooney and Neville, 2000). Moreover, Elliot (2003) considered that introduced  
63 marine organisms can be treated in the same way as chemical pollutants and incites the  
64 use of the term biological pollution. Therefore, the invasion research and managers  
65 usually consider that nonindigenous origin of a species is relevant to predict and value  
66 their negative impacts (Kueffer and Hadorn, 2008). As a consequence, the use of the  
67 origin for judging a species is arguable since it could have close affinity to “xenophobia”  
68 or “racism” (e.g., Simberloff, 2003; Warren, 2007). Yet, coastal aliens could also play a  
69 beneficial role in ecosystem functioning and can result in a net gain of species (Sax and  
70 Gaines, 2003) and in an increase of biomass production (Minchin and Rossental, 2002;  
71 FAO, 2009). Nevertheless, a precautionary approach has been proposed for introduced or  
72 invasive species risk assessment, which assumes that an alien species is problematic until  
73 proven otherwise (Simberloff, 2005; Wittenberg and Cock, 2001).

74

75 In this context, pressure tends to increase on managers to minimize the impacts of  
76 nonindigenous species, and on scientists to provide control measures (Bax et al. 2001).

77 Consequently, the study of interactions between the nonindigenous and native marine  
78 species has become a focus of conservation biology in order to correct identify potentially  
79 injurious nonindigenous species. Moreover, research that contributes to gain insight into  
80 the effects of the interaction between introduced commercial species and native  
81 communities is of a particular significance from a socioeconomic point of view since it  
82 can affect positively or negatively the fisheries yield (e.g. Seijo et al., 1998; Reaser et al.,  
83 2007). In this regard, several species have been deliberately introduced for aquaculture  
84 purposes or in order to improve the fisheries yield: the oysters *Crassostrea gigas*,  
85 *C. ariakensis*, *C. rivularis*, and *Ostrea edulis* (Grizel and Héral, 1991; Langdon and  
86 Robinson, 1991; Mann, 1983), the hard clam *Mercenaria mercenaria* and the softshell  
87 clam *Mya arenaria* (Gollasch, 2006; Conde et al., 2010) and the Manila clam *Ruditapes*  
88 *philippinarum* (Breber, 1985). Moreover, the cultures of the Pacific cupped oyster  
89 *Crassostrea gigas* and Manila clam *Ruditapes philippinarum* were responsible for the  
90 introduction of the largest number (60) of non-native invertebrates and algae, often  
91 attached to packaging material, fouling the shell or parasitizing bivalve tissues (Mineur et  
92 al., 2007; Savini et al., 2010).

93

94 Largely due to overfishing and irregular yields of the European native grooved carpet  
95 shell clam, the confamilial Manila clam, native to the western Pacific Ocean (Scarlato,  
96 1981, Jensen et al., 2004), has been one of the most widely introduced species for  
97 aquaculture purposes in Europe. Moreover, Levings et al. (2002) described Manila clams  
98 as an ideal fishery species because of their large stock biomass, ease of capture, strong  
99 market demand, and rapid depuration of toxins accumulated from algal blooms. It was  
100 first introduced between 1972 and 1975 in France and later in England, Spain and Italy  
101 (Flassch and Leborgne, 1992; Humphreys, 2010). This species has shown a high

102 adaptability to various coastal environments and its sustainability for aquaculture (Laing  
103 and Child, 1996; Usero et al., 1997; Humphreys et al. 2007). Currently, it has become a  
104 natural population and one of the most commercially exploited bivalve molluscs along the  
105 European coast (i.e. Atlantic coast, Adriatic and Aegean seas) contributing more than  
106 90% to European yields of the two species (Gosling, 2003).

107

108 In several disturbed estuaries or lagoons of Europe as Arcachon Bay (France) or the  
109 lagoon of Venice (Italy), this species has supplanted the native clam *Ruditapes decussatus*  
110 by occupying almost entirely their ecological niche and relegating them to occupy very  
111 restricted areas (Aubby, 1993; Marin, 2003; Mistri, 2004; Caill-Milly et al., 2003, 2006).  
112 Occhipinti-Ambrogi (2007) stated that the success of the nonindigenous species after  
113 establishment is governed by two different filters: a local dispersal filter, mainly  
114 connected to invasion pressure (i.e. introduced repeatedly) and a habitat suitability filter  
115 (i.e. environmental and community filter), which determine a species to reach stage of  
116 invasion where it is widespread and dominant. However, this extreme dominance pattern  
117 of the introduced Manila clam has not yet been detected in other estuaries of Europe such  
118 as in Bahía de Santander, N Spain (Juanes et al., 2012), where both species are exploited  
119 regularly. In this estuary, regarding the relative presence, areas where (1) both species  
120 coexist, (2) nonindigenous species predominates and (3) the native species predominates  
121 were found (Juanes et al., 2012). Consequently, considering the differentiated stages of  
122 invasion of Manila clam in European estuaries and taking into account the absence of  
123 studies investigating the interaction with the native carpet shell clam or other biotic  
124 interactions, nowadays, the definition of this nonindigenous species as a direct threat for  
125 the European native clam is too daring.

126

127 Alien species can negatively affect native populations through interspecific competition,  
128 inter alia. Competition can regulate the distribution patterns and the abundance of  
129 intertidal communities if one species indirectly inhibits the growth of another species  
130 inhabiting the same area (Simberloff 2002). Inter-specific competition is, by definition, a  
131 negative interaction between two or more species that utilize the same limiting resource  
132 (Connell 1983). Resource competition, often measured through density-dependant  
133 reductions in growth or survival, has been observed in natural bivalve communities  
134 (Peterson 1985; Whitlatch et al. 1997). However, interspecific competition is relatively  
135 difficult to demonstrate unequivocally in invaded communities and, although only half the  
136 studies published have been experimental (Byers, 2009), they indicate that competition is  
137 important and common in marine invasions, so that it is necessary to take it into account.

138

139 Several authors have suggested that competition might be relatively unimportant in soft-  
140 bottom marine communities, since the habitat have a third dimension (i.e. sediment depth)  
141 and hence, it may not be as effective a structuring force as on hard bottom shores  
142 (Dayton, 1984; Peterson, 1991 and Wilson, 1991). Regarding the non native species  
143 Manila clam, few experimental studies have been designed to test directly whether  
144 resources of any sort are limiting to other infaunal bivalve species or whether competition  
145 for limited resources is an important process. Byers (2005) investigated the interaction  
146 between *Ruditapes philippinarum* and the native bivalve *Prothoaca staminea* and did not  
147 found direct effects of Manila clam on *Protothaca*. Lee (1996) also studied the interaction  
148 between Manila clam and *Anomalocardia squamosa* and did not find intense interaction  
149 effects. Similarly, Lum (2011) found a lack of competition between Manila clam and  
150 varnish clam (*Nuttallia obscurata*).

151

152 Despite the above, the assumption that an alien species is problematic until proven  
153 otherwise (Simberloff, 2005; Wittenberg and Cock, 2001) is a central tenant of  
154 conservation strategies. Therefore, it is essential to study the interaction between Manila  
155 clam and the European carpet shell clam in order to adopt appropriate management  
156 measures for the conservation and sustainable exploitation of these valuable marine  
157 resources. In recognition of both an increasing pressure on managers due to the detection  
158 of zones where the introduced Manila clam predominates (Juanes et al., 2012) and to the  
159 drastic declines of the native carpet shell clam occurred in other estuaries of Europe, a  
160 first experimental study was conducted in the Bay of Santander (N Spain) to examine the  
161 significance of the competition among these two congeneric species and to explore the  
162 impact of the nonindigenous Manila clam on the native carpet shell clam. Moreover, the  
163 role of predation in the regulation of the expansion of the nonindigenous species was  
164 explored. In order to achieve this goal, this study examines the effects of increasing  
165 density of Manila clam and predation on mortality and growth of both clam species.

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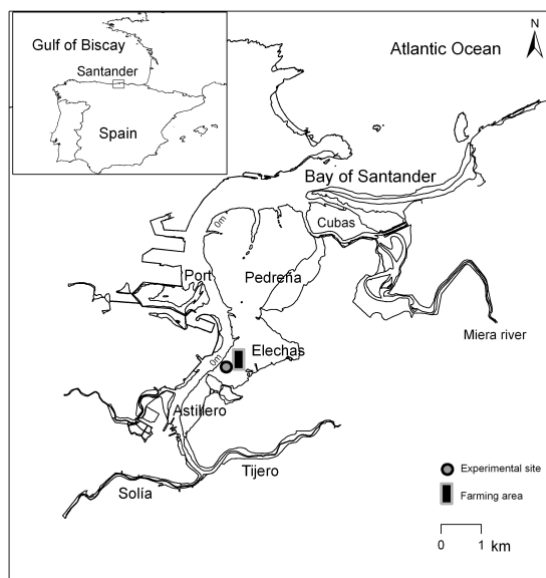
## 167 **2. Material and methods**

168

### 169 **2.1. Experimental site**

170 A field experiment was conducted between May 2010 and May 2011 in an intertidal area  
171 near the semiactive Manila clam farming zone in Bahía de Santander (Figure 1), the  
172 largest along the North coast of Spain (Gulf of Biscay) (2346 Ha). This estuary is  
173 classified as morphologically complex and dominated by intertidal areas and tidal  
174 dynamics (Galván et al., 2010). The experimental site was selected because: (i) it is on a  
175 large and open area containing populations of both Manila clam and grooved carpet shell  
176 clam, (ii) it is located approximately 1 km from the nearest public access, making it

177 effectively inaccessible to the general public and (iii) the experiment could be best  
 178 safeguarded by shell fishermen over its duration. The sediment on the experimental site  
 179 was composed by 25.3 % coarse, 51.2 % sand and 24.5 % silt, contained 3.74 % organic  
 180 matter which represents suitable conditions for both species (Bidegain et al., 2012).  
 181 Distribution and abundances of clam populations in the estuary obtained from Juanes et  
 182 al. (2012) were used to determine the experimental densities to simulate both natural  
 183 abundances and the effect of potential expansion of the nonindigenous species. Further  
 184 details of these estuaries and sand flats can be found elsewhere (e.g., Galván et al., 2010;  
 185 Puente et al., 2002).



186  
 187 **Figure 1** - Bay of Santander. The grey circle represents the location of the experimental  
 188 site.

189

## 190 2.2. Clam collection and laboratory procedures

191 All clams used in this experiment were collected from the same zone in the bay, near the  
 192 experimental site, to reduce the effects of potential genetic variability. As allometric  
 193 relationships of studied species are slightly different (Bald and Borja, 2001,2004; Caill-



194 Milly et al., 2003,2006; Bradbury et al., 2005), the selected adult clams sizes were higher  
195 ( $36.8 \pm 2.8$  mm) for *R. decussatus* than for *R. philippinarum* ( $33.5 \pm 3.0$  mm), in order to  
196 have similar biomass for both species in treatments containing the same density. Bivalves  
197 were transported to the laboratory in a tank filled with sea water, and maintained at field  
198 temperature ( $16.5^{\circ}\text{C}$ ) in order to minimize physical and/or chemical stress. In the  
199 laboratory, they were dried, measured (maximum length) and marked with a nail polish.  
200 Marked clams were transported again to the field and were allocated to the experimental  
201 units. One year after the start of the experiment, individuals collected in each enclosure  
202 were measured and counted to determine growth and mortality of clams. Additionally,  
203 mortality source was examined (1) periodically, during the year when dead individuals or  
204 cracked shells were found during enclosure nets maintenance and (2) meticulously, at the  
205 end of the experiment when enclosures were excavated. For the clams that were recovered  
206 with the identification markings, from both covered and uncovered enclosures, it was  
207 discerned the source of mortality (i.e. cracked shells=predation; empty valves intact and  
208 blackened=anoxia or disease, unrecovered clams also assumed dead by a predator).

209

### 210 **2.3. Experimental design**

211 A factorial experiment was designed with two fixed factors, relative density of clam  
212 species and predation, to examine their effect on growth and mortality of both clams.  
213 Relative density factor includes three levels as follows: (1) *R. decussatus* (*RD*) or *R.*  
214 *philippinarum* (*RP*) monoespecific, including 10 individuals (2) Coexistence, with 10  
215 individuals of *RD* + 10 individuals of *RP* and (3) predominance of Manila clam, including  
216 10 individuals of *RD* and 20 individuals of *RP*. Whilst, predation includes two levels:  
217 exposure (uncovered) and no exposure (covered) to predation. Therefore, the experiment  
218 examined a total of eight treatments. Density levels were selected to simulate (i) zones

219 containing only one species at natural densities, (ii) zones where both species coexist in  
220 moderate but higher density levels (augmented by ~ 50 %) than quantified in the field  
221 surveys and (iii) zones where *R. philippinarum* predominate (augmented x 4 natural  
222 densities observed in the field). The latter two levels, but in particular the Manila clam  
223 predominance scenario, simulated the effect of potential expansion of the nonindigenous  
224 population in the bay due to a hypothetical situation where it forms widespread and  
225 dominant populations in the whole Bay after repetitive and intense introductions (see  
226 invasive stages, Occhipinti-Amborgi, 2007).

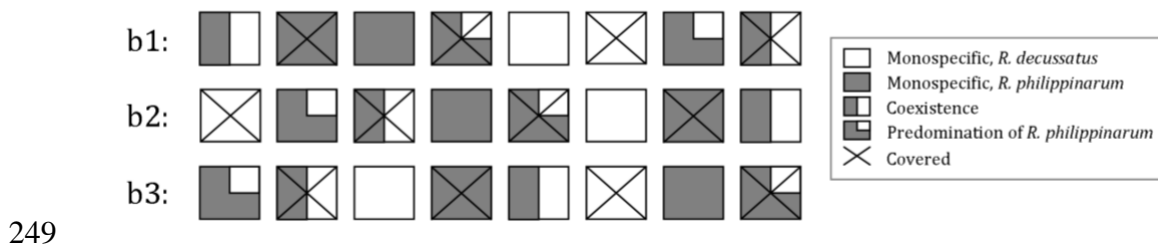
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228 The experiment was laid out in a randomized block design where the treatments were  
229 replicated in three blocks for a total of 24 plots (Figure 2). Assuming that species follow  
230 the Lotka-Volterra equations three replicas are sufficient to determine if two species  
231 compete (Tilman, 1987). Blocks were spaced 10 cm apart to also ensure homogeneity of  
232 environmental conditions between them. Although treatments were placed randomly  
233 regarding density treatments, a covered and uncovered treatments were systematically  
234 interspersed to reduce potential biases from predators (i.e. crabs) foraging in uncovered  
235 enclosures and spilling over onto an adjacent uncovered enclosure (Figure 2).

236

237 The treatments were examined in plots consisting of nylon net enclosures (0.25 m<sup>2</sup>,  
238 height=15 cm), located along a tidal height contour of ~ 1 m above MLLW. For exposure  
239 to predator treatments, enclosures were both laterally and top covered with 8.0 mm mesh  
240 size nylon net. Enclosures were inserted in to the substrate beyond typical maximum  
241 burial depths (~ 2 - 12 cm) for these species (Vilela, 1950; Lee, 1996; Gosling, 2003) to  
242 avoid lateral migrations of clams out of the experimental plot. Top nets tried to exclude  
243 predators (e.g. fish, crabs and birds) from the enclosure. For no exposure treatments

244 enclosures were not top covered. Prior to initiating the experiment the sediment below  
 245 each enclosure was sieved to remove predators and clams. The area was refilled and  
 246 clams were placed on the surface until buried in the sand. Top nylon nets of enclosures  
 247 were cleaned every two-three weeks to keep the mesh free of algae and other fouling  
 248 organisms.



250 **Figure 2** –Layout for the randomized block design (b1, b2, b3) to examine the effect of  
 251 increasing density of *R. philippinarum* and predation in growth and mortality of both  
 252 species. Covered and uncovered treatments were systematically interspersed within each  
 253 block.

254

255 Additional plots were added in order to demonstrate the absence of effects of both  
 256 enclosures and disturbance of the sediment on clam responses. For this purpose, three  
 257 replicates for each effect analysis were located ~ 1m from the experimental array. On the  
 258 one hand, for the enclosures effect analysis, the sediment was sieved from an area of 0.50  
 259 m<sup>2</sup>, to remove predators and clams as it was done in the original experiment. Then the  
 260 area was refilled and 20 measured and marked individuals of each species were placed in  
 261 three replicates until buried. No enclosures were placed above them. This density of  
 262 clams was selected to mirror the coexistence density treatment of uncovered enclosures;  
 263 although a higher number of clams (x 2) were added on a larger area (x 2). This difference  
 264 was assumed in order to recover individuals at the end of the experiment, considering that  
 265 in absence of enclosures a certain lateral migration of clams could be expected. On the

266 other hand, for the disturbance effect analysis, 10 marked individuals of each species  
267 were added to areas of 0.25 m<sup>2</sup> where no marks of infaunal organisms (e.g. sand crabs,  
268 polychaetes, clams, razor clams) were detected. Thus, without disturbing the sediment,  
269 clams were placed on the surface, and we waited until sure that they were buried in the  
270 sand. Then the enclosures with top nylon net were inserted above.

271

#### 272 **2.4. Data analysis**

273 Growth and mortality response variables were examined at the end of the experiment (1  
274 year). For this purpose, clams were recovered from enclosures, and then counted and  
275 measured. The difference between the initial maximum length size and the final size of  
276 individuals was used to estimate growth for each species and for each treatment.

277 Mortality was estimated as the proportion of dead individuals in each treatment. Growth  
278 and mortality distributions normality was checked for statistical analyses. Additionally,  
279 the proportion of dead individuals corresponding to each mortality source (i.e. predation  
280 or anoxia or disease) was estimated in order to know the role of predation. Normality of  
281 the growth and mortality distributions was checked for statistical analyses. Then, two-  
282 way ANOVA was used to examine the effect of relative density and predation (fixed  
283 factors) on the response variables and, additionally, to test the effect of interaction  
284 between the two factors. In addition, t-Test was applied to analyze differences in growth  
285 and mortality between species.

286

287 In order to demonstrate the absence of both enclosures and disturbed sediment on growth  
288 and mortality, a one way ANOVA test was used. First, to analyze the effect of the  
289 enclosure, growth and mortality were compared between individuals placed in uncovered  
290 enclosures and individuals placed in patches with no enclosure. Second, to examine the

291 effect of the sediment disturbance, response variables were compared between individuals  
 292 placed in covered enclosures with disturbed sediment and individuals placed in covered  
 293 enclosures with untouched sediment.

294

### 295 3. Results

#### 296 3.1. Density effect on growth and mortality of clams

297 Increasing the density of *R. philippinarum* had no effect on the growth of either species  
 298 (Table 1). The nonindigenous species grew significantly more than the native *R.*

299 *decussatus* ( $t = -12.9$ ,  $df = 126$ ,  $p < 0.0001$ ). Whilst *R. philippinarum* grew 5.7 mm ( $\pm 1.6$   
 300 SD), *R. decussatus* grew 2.4 mm ( $\pm 1.1$  SD)(Fig. 3a, Covered). Moreover, *R.*

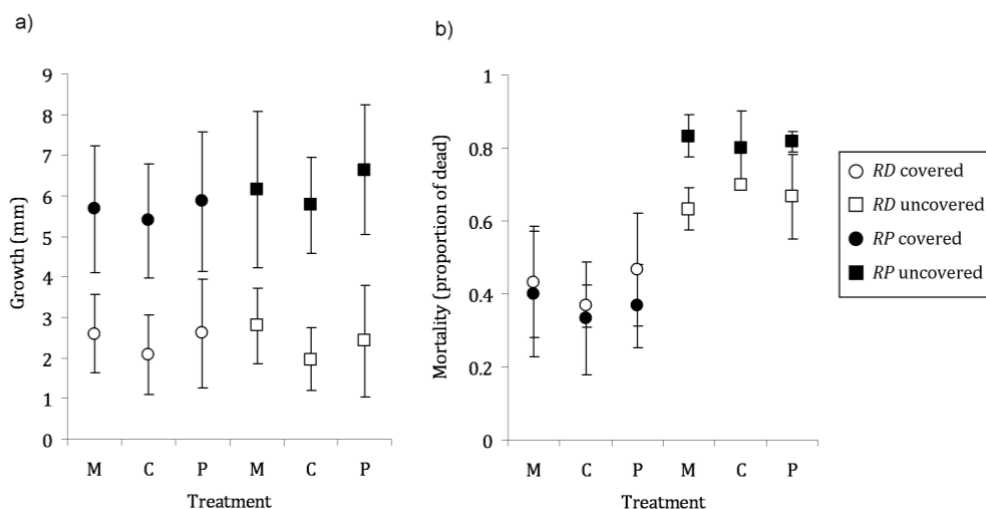
301 *philippinarum* density also had no effect on the mortality of none of the species (Table 1).

302 Both species showed similar mean values of mortality 0.42 ( $\pm 0.12$  SD) for *R. decussatus*  
 303 and 0.37 ( $\pm 0.13$  SD) for *R. philippinarum* ( $t = 0.93$ ,  $df = 16$ ,  $p < 0.36$ ) (Fig. 3b, Covered).

304 Similar specific growth patterns and absence of density effects, on both growth and

305 mortality of both species, were also observed on uncovered plots (Figure 3ab,

306 Uncovered).



307

308 **Figure 3** - Growth (a) and mortality (b) of *Ruditapes decussatus* (RD) and *Ruditapes*  
 309 *philippinarum* (RP) (mean  $\pm$  SD (error bars)) during the experiment (1 year) for three  
 310 density treatments in covered and uncovered plots: monoespecific (M), (2) coexistence  
 311 (C), and (3) predominance of Manila clam (P).  
 312

	df	F	p
<b><i>R. decussatus</i></b>			
Growth			
Density	2	1.24	0.30
Predation	1	0.15	0.70
Density x Predation	2	0.16	0.85
Mortality			
Density	2	0.47	0.65
Predation	1	27.66	0.0001
Density x Predation	2	0.35	0.71
<b><i>R. philippinarum</i></b>			
Growth			
Density	2	0.57	0.58
Predation	1	3.58	0.06
Density x Predation	2	0.05	0.95
Mortality			
Density	2	0.15	0.86
Predation	1	85.76	0.0001
Density x Predation	2	0.03	0.97

313  
 314

315 **Table 1** - Effects of varying relative density of *R. philippinarum* and *R. decussatus* and  
 316 predator exposure on the mortality and shell growth of both species. Differences were  
 317 considered statistically significant at  $p \leq 0.01$ .

318

319 **3.2. Predator exposure effects and source of mortality**

320 Predator exposure affected *R. decussatus* and *R. philippinarum* differently (Fig. 3b,  
321 Uncovered). Whilst mortality did not show differences between species in enclosures  
322 protected from predators, it was significantly higher for *R. philippinarum* than for *R.*  
323 *decussatus* in uncovered enclosures ( $t = -4.8$ ,  $df = 16$ ,  $p = 0.0002$ ). This augment in  
324 percentage of dead individuals was considerably higher for *R. philippinarum* (from 37%  
325 to 82 %) than for *R. decussatus* (from 42% to 67 %) on average, considering together all  
326 density treatments (Figure 3b). Moreover, exposure to predators had no significant effect  
327 on the growth of none of the two species (Table 1). The growth for no top plots was 6.4  
328 mm ( $\pm 1.5$  SD) for *R. philippinarum* and 2.5 mm ( $\pm 1.0$  SD) for *R. decussatus*. Finally,  
329 interaction effects between predation and density were not detected in any of the two  
330 response variables for none of the species (Table 1).

331

332 Regarding the source of mortality, in covered enclosures few clams were cracked by  
333 predators or missing so that only a low percentage of *R. decussatus* (10 %) and *R.*  
334 *philippinarum* (16 %) died due to predation. However, in uncovered enclosures 55% of *R.*  
335 *decussatus* mortality was attributed to crab, fish and other macropredators, compared to a  
336 considerably higher 73 % for *R. philippinarum* (Table 2). Mortality due to anoxia (empty  
337 and blackened shells) was higher for *R. decussatus* (75 % of undamaged shells) than for  
338 *R. philippinarum* (43 % of undamaged shells).

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Species, treatment	Status of shells (mortality source)		
	Undamaged shells (e.g. anoxia, disease or starvation)	Cracked shells (definitely predator killed)	Missing clams (probably predator killed)
<i>R. decussatus</i> , Covered	34	2	2
<i>R. decussatus</i> , Uncovered	27	8	25
<i>R. philippinarum</i> , Covered	37	4	3
<i>R. philippinarum</i> , Uncovered	26	11	60

347

348

349 **Table 2** - Status of shells of experimental clams and the mortality source discerned following Byers

350 (2005). Initial number of clams was 90 for *R. decussatus* and 120 for *R. philippinarum*.

351  
352

### 353 3.3. Effect of enclosures and sediment disturbance

354 None of the species exhibit significant differences between no enclosure and enclosed

355 uncovered plots neither for growth (*R. decussatus*,  $F = 3.5$ ,  $df = 1$ ,  $p = 0.07$ , *R.*

356 *philippinarum*:  $F = 0.12$ ,  $df = 1$ ,  $p = 0.74$ ) (Fig. 4a) nor for mortality (*R. decussatus*,  $F =$

357  $1.0$ ,  $df = 1$ ,  $p = 0.37$ , *R. philippinarum*:  $F = 0.8$ ,  $df = 1$ ,  $p = 0.42$ ) (Fig. 4b). The effect of

358 the disturbance was examined comparing response variables for both species between

359 covered enclosures with disturbed sediment and covered enclosures with untouched

360 sediment free of infaunal invertebrates marks. The 1-way ANOVA test did not show

361 significant differences in any species neither in growth (*R. decussatus*,  $F = 0.5$ ,  $df = 1$ ,  $p =$

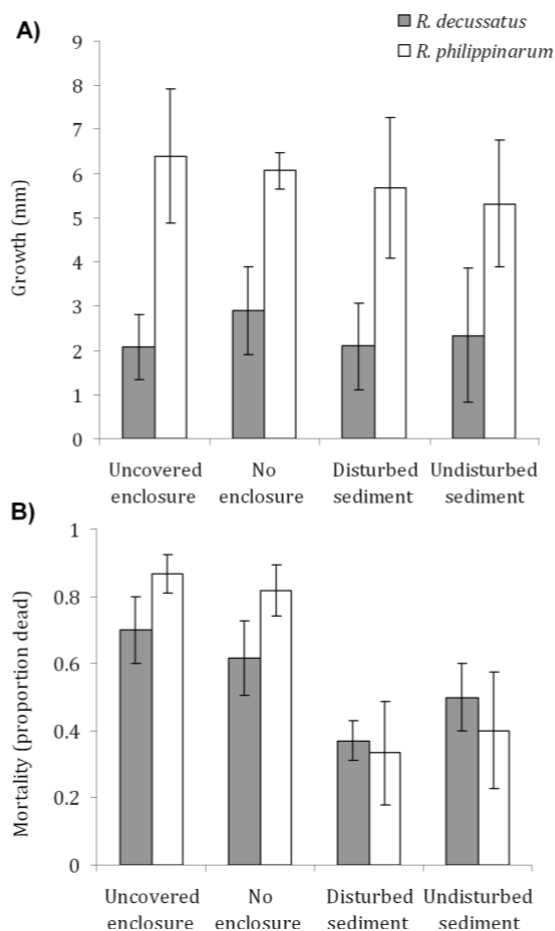
362  $0.48$ , *R. philippinarum*:  $F = 0.02$ ,  $df = 1$ ,  $p = 0.89$ ) (Fig. 4a) nor in mortality (*R.*

363 *decussatus*,  $F = 4.0$ ,  $df = 1$ ,  $p = 0.12$ , *R. philippinarum*:  $F = 0.25$ ,  $df = 1$ ,  $p = 0.64$ ) (Fig.

364 4b).



365



366

367 **Figure 4** - Growth (a) and mortality rate (b) of *Ruditapes decussatus* and *Ruditapes*  
 368 *philippinarum* during the field experiment (1 year) in (i) coexistence treatments;  
 369 “Uncovered enclosures” (no top enclosures with disturbed sediment) and “Disturbed  
 370 sediment” (covered enclosures with disturbed sediment) and (ii) in their respective  
 371 “controls”; “No enclosure” to examine effect of enclosure (treatment with no enclosure  
 372 and disturbed sediment) and “Undisturbed sediment” to examine effect of sediment  
 373 disturbance (treatment with covered enclosure and undisturbed sediment).

374

#### 375 **4. Discussion**

376 The results of this study were necessary for two reasons: first, to test for the effects of  
 377 varying density of the introduced nonindigenous species *Ruditapes philippinarum* on

378 growth and mortality of the native clam *Ruditapes decussatus*; and second, to explore the  
379 effect of predation in the regulation of both populations, with a particular emphasis on the  
380 nonindigenous species. For this purpose, the experimental study conducted in the Bay of  
381 Santander simulates a scenario of Manila clam expansion, where it would form a  
382 widespread and dominant population. Results suggest that, for this potential scenario, the  
383 nonindigenous clam cannot be defined as an ecological threat regarding competitive  
384 interaction and predation has an important effect on the regulation of the expansion of this  
385 species.

386

387 The highest density of the introduced species examined (i.e. x 4 natural density observed  
388 in the field by Juanes et al., 2012) experiencing no density mitigation by predators  
389 (covered enclosures), directly affected neither the growth nor the mortality of the  
390 confamilial native carpet shell clam. In fact, no differences were observed in response  
391 variables of outplanted Manila or carpet shell clams regardless of the density treatments  
392 examined (i.e. monoespecific, coexistence and predominance of manila clam). As  
393 density-dependant studies are suitable to estimate resource competition between two  
394 species (e.g. Peterson 1985, Whitlatch et al. 1997; Byers, 2009 and reference therein) the  
395 results suggest that clam densities tested in this study did not result in interspecific  
396 competition. Results obtained in uncovered plots regarding density effects were similar to  
397 those found in covered enclosures, yet they should be taken with caution since density  
398 they experienced a high density mitigation effect due to predation exposure.

399

400 Enclosures can modify microenvironmental conditions (Underwood, 1985) and have an  
401 effect on results. However, the enclosures and the sediment disturbance did not show any  
402 substantial effects on response variables studied for none of the species. Byers (2005) also

403 found that the effect of enclosures on mortality and growth of two bivalves were not  
404 significant. Although this conclusion permits to extrapolate the results and estimate  
405 natural life history properties, some caution should be taken interpreting these results. On  
406 the one hand, considering that the experimental site was located near a Manila clam  
407 culture area, the location could be affecting the growth rates and survival of clams in the  
408 neighbour zones (Nizzoli et al., 2005) since high densities of cultivated bivalves are  
409 generally considered as “sinks” of oxygen and particulate organic matter (Richard et al.,  
410 2007a,b) and hence, may cause a food shortage and be attractors of macropredators. In  
411 this experiment this potential effect was assumed to be similar for different treatments and  
412 not intense since observed growth rate for both species was similar to other authors’  
413 findings (e.g., Urrutia et al., 1999; Cannas, 2010). On the other hand, the effects of  
414 enclosure and sediment disturbance on reproduction or meat content were not estimated  
415 and may give additional insight on the short-term dynamics related to food availability.  
416

417 Competition between both species at Manila clam relatively high densities, simulating a  
418 predominance scenario, may not be an essential factor regulating the distribution and  
419 abundance of the native species. This is in good agreement with previous studies where  
420 there is no evidence that Manila clam has negative effects on native or alien species  
421 neither at natural densities (Breber, 2002, Juanes et al., 2012) nor at higher densities than  
422 observed in nature where, similarly, a lack of competition between bivalve species has  
423 been observed. Black and Peterson (1988) manipulated the densities of large suspension  
424 feeding bivalves in three Western Australian sites to test their effect on the density and  
425 diversity of smaller bivalves and other invertebrates. The bivalves had no significant  
426 effect on small bivalves, gastropods, polychaetes, amphipods, other taxa, and all taxa  
427 combined, despite maximum treatment densities were x 2 the natural densities. Byers

428 (2005) examined the effects of Manila clam densities on the growth, mortality, and  
429 fecundity of the native littleneck clam, *P. staminea* and found that at densities 50% higher  
430 than natural ones (up to ~200 clams / m<sup>2</sup>) the Manila clam had no effect on the native  
431 littleneck clam or on itself. Similarly, Lum (2011) did not observe differences in the  
432 growth rates of *R. philippinarum* and *N. obscurata* regardless of the relative densities of  
433 each species (intra-specific competition) or the density of the other species (inter-specific  
434 competition), even when clam densities doubled natural densities observed in preliminary  
435 surveys. Despite using densities larger than natural ones, these authors suggested that the  
436 experimental densities used were still not large enough to reach the critical level to trigger  
437 competition. Black and Peterson (1988) point out that their one year duration experiment  
438 may have been insufficient to permit the small infauna to colonize densely enough for  
439 competition to occur. The present experimental study could have a similar result because  
440 of densities (80 Manila clam individuals/ m<sup>2</sup>) insufficient to produce competition.  
441 However, densities were well above the average found in the Bay of Santander (i.e. 4  
442 times the natural densities of Manila clam found under ambient conditions) and  
443 considered as sufficient to simulate a scenario of potential expansion of the  
444 nonindigenous species.

445

446 Most favoured areas of Venice Lagoon hold densities ~ 1000 individuals / m<sup>2</sup> (Breber  
447 2002) whilst in Arcachon Bay the maximum density is around ~ 45 individuals / m<sup>2</sup>  
448 (Caill-Milly et al., 2006). Hence, the competition between the two species may not be the  
449 main reason for the drastic reductions of the native clam occurred in Arcachon Bay. In the  
450 case of the Lagoon of Venice the densities of Manila clam could have been large enough  
451 to reach the critical level to trigger competition and drastically impact the native species.  
452 However, other factors can be responsible of these reductions, such as the biogeochemical

453 cycles altered by the farming of *R. philippinarum* (Bartoli et al., 2001) or invasions by  
454 parasites that can caused long lasting or even irreversible consequences (Harvell et al.,  
455 2002), as in case of *Bonamia ostreae*, a disease of the European native oyster *Ostrea*  
456 *edulis*, which caused severe decline in their populations and, as a consequence,  
457 destruction of native oyster bed ecosystems (Wolff and Reise, 2002). Complementary  
458 possible hypotheses have been pointed out to explain the reduction of native species  
459 occurred, such as the failure of non specific management measures (e.g. identical  
460 minimum capture size) adopted during years or decades, leading to an overexploitation of  
461 the native species (Juanes et al., 2012) which has some biological disadvantages such as  
462 slower growth and less tolerant or resistant species (Spencer, 1991; Mistri, 2004 and  
463 references therein).

464

465 Furthermore, the small scale at which we studied the density effects (0.25 m<sup>2</sup>) makes us  
466 cautious with respect to the interpretation and extrapolation results regarding density  
467 effects, since large areas with high densities of suspension feeding bivalves are needed for  
468 food depletion from the water (Peterson and Black, 1987; Kamermans, 1993). In this  
469 respect, Kamermans (1993) found an effect of 10 m<sup>2</sup> mussel beds on cockle growth while  
470 no effect could be detected on smaller plots (Kamermans et al., 1992). This indicates that  
471 our initial results should be taken with care and that future studies should explore the  
472 possibility that density effects might be present by using larger experimental plots or  
473 conducting the experiments in proximity of areas (or even better within) with much  
474 higher densities (see for example Thrush et al., 1997).

475

476 However, on the other hand, three-dimensionality of infaunal species habitat (Peterson,  
477 1979; Wilson, 1991), different or alternative feeding modes or food sources (Peterson

478 1982; Kamermans et al. 1992), filter feeding and vulnerability to predators (i.e. burial  
479 depth) (Peterson and Andre 1980; Byers, 2009) are considered to play important roles  
480 making direct interference competition ineffective at relatively high densities. Regarding  
481 food sources, Bodoy & Plante-Cuny (1984) found that the growth rate of *R. decussatus* is  
482 mainly related to the primary production of the water column, whilst Page and Lastra  
483 (2003) in their study about diet of intertidal bivalves with stable isotopes proposed that  
484 this species use primarily resuspended microbenthos during periods of low phytoplankton  
485 concentration, but phytoplankton increases in relative dietary importance during bloom  
486 events. Meanwhile, also using stable isotopes, Watanabe, et al. (2009) found that *R.*  
487 *philippinarum* seems to feed mainly on particulated organic matter resuspended from the  
488 sediment (i.e. detritus and microphytobenthos).

489

490 Both species are filter feeders of a food resource that is frequently replenished (i.e., with  
491 tidal cycle and resuspension due to currents) and whose supply is often decoupled from  
492 consumptive pressure by resident organisms. Moreover, burial depth of *R. decussatus* (~  
493 10-12 cm) is considerably higher than that of *R. philippinarum* (~ 2-4 cm) (Vilella, 1950;  
494 Lee, 1996; Gosling 2003). This difference in burial depth is essential in order to interpret  
495 the differences in growth and mortality between species observed in this experiment  
496 which in turns are consistent with current knowledge.

497

498 Growth of *R. philippinarum* during the experiment (1 year) was ~ 6 mm regardless of the  
499 exposure to predators. For *R. decussatus* it was considerably lower, ~ 2.5 mm. As  
500 commented above, these differences are in line with findings of several authors for the  
501 large clams (~ 35 mm) used in this study (e.g. Spencer et al., 1991; Solidoro et al., 2000;  
502 Urrutia et al., 1999; Cannas, 2010). The energetic efficiency of feeding with a siphon

503 decreases with burial depth (Zaklan and Ydenberg, 1997) and it explains, at least  
504 partially, why the more deeply burrowing *R. decussatus* does not grow as fast as *R.*  
505 *philippinarum*. With a shallower burial depth Manila clam can filter particles more  
506 quickly and invests less in the development of its siphons compared to a deeper  
507 burrowing clam with a longer siphon. One of the important reasons to introduce the  
508 nonindigenous Manila clam worldwide for aquaculture purposes was precisely its fast  
509 growth together with the important commercial value (Laing and Child, 1996; Usero et  
510 al., 1997). The resulting growth was not significantly different for any species between  
511 covered and uncovered enclosures. This result is in contradiction to the studies of  
512 sublethal effects of predators on clams which confirmed generally that predator presence  
513 significantly decreases clam growth (e.g. Irlandi and Peterson, 1991; Nakaoka, 2000).  
514  
515 Because of its high vulnerability to predation, it seems that high densities or dramatic  
516 expansion of the nonindigenous Manila clam might rarely occur in estuaries with a high  
517 exposure to macropredators such as the Bay of Santander. Recent findings by Bidegain et  
518 al. (2013) suggest that the habitat suitability for this species in the Bay of Santander is  
519 also essential in regulating its potential expansion. During the year of the study, each time  
520 top nylon nets of enclosures were cleaned (i.e. every two-three weeks) the presence of  
521 gulls, oystercatchers and crabs around the experimental area was detected at low tides. A  
522 considerable abundance of fishes (e.g., gill-head breams, sting rays and mullets),  
523 searching for food in the sediment, was also observed during rising tide (Bidegain pers.  
524 Obser.). These observations and the results of the predator's exposure experiment are  
525 compatible with previous studies where predation on Manila clam was considered to be  
526 strong and a great variety of macropredators were described: moonsnails (*Euspira lewisi*),  
527 sea stars (*Pisaster spp.*), a variety of birds, e.g. diving ducks (*Aythya affinis*), gulls

528 (Family Laridae), crows (Family Corvidae), oystercatchers, (e.g. *Haematopus ostralegus*  
529 *ostralegus*), scoters (Family Anatidae) (Toba et al., 1992; Gillespie et al., 2001; Caldow et  
530 al., 2007), *Cancer sp.* crabs (Gillespie et al., 2001; Byers, 2005, Lum, 2011) and bottom  
531 fish such as rays (Peterson, 1982, Jamieson et al., 2001). These authors also described the  
532 important role of predation on regulation of the nonindigenous species expansion.

533

534 The high vulnerability of infaunal species to predation is related with the burial depth  
535 since clam survival increases with increasing burial depth (Zaklan and Ydenberg, 1997).  
536 When clams were exposed to predators the mortality was considerably higher for Manila  
537 clam than for carpet shell clam (87 % and 67 % respectively). For *R. decussatus*, 55% of  
538 this mortality was attributed to crab, fish and other macropredators, whilst, for *R.*  
539 *philippinarum*, 73 % of the mortality was attributed to this cause. This higher  
540 vulnerability to predation of Manila clam compared with the native carpet shell clam  
541 agrees with the hypothesis of the authors mentioned above, since the typical burial depths  
542 are considerably different between species. Although, the burial depth was not measured  
543 meticulously, we noticed that at the end of the experiment, in most cases, the carpet shell  
544 clam was found relatively deeper in the sediment than Manila clam. Thus, predators may  
545 mitigate high *R. philippinarum* density preying on them more than on *R. decussatus*,  
546 presumably because crabs, birds and fish excavate the shallowly burrowing Manila clam  
547 more easily (Seitz et al., 2001). However, while deeper burial depth increases *R.*  
548 *decussatus* protection from predators and humans, it also exposes clams to a more anoxic  
549 environment (Byers, 2005). In fact, this species exhibited greater mortality indicative of  
550 anoxia (i.e. undamaged, blackened shells) than *R. philippinarum*.

551

552



553

554 **5. Conclusions**

555 To our knowledge this is the first study that has attempted to investigate competitive  
556 interaction between these species. The results suggest that neither the current distribution  
557 of populations (i.e. coexistence) nor a potential spread of the Manila clam in the Bay of  
558 Santander can be defined as an ecological threat for the native carpet shell clam regarding  
559 the experimental densities. Moreover, predation plays an important role in regulating both  
560 species populations, but more drastically the expansion of the nonindigenous species and,  
561 hence, high densities of this clam species are not expected in this estuary. When  
562 extrapolating our experimental densities to other estuaries of Europe, it seems that the  
563 competitive interaction between these species is not always the main reason of the drastic  
564 decrease of the native clam since our expansion scenario densities were higher than those  
565 observed in field (e.g. Bay of Arcachon). However, this finding should be taken with  
566 caution and it should be recognised that before generalizing from small to estuary scale  
567 we should explore competitive mechanisms operating at larger scales. The strength of  
568 competitive interactions may be linked to abiotic and biotic processes operating over  
569 different scales (Schneider, 1994; Thrush et al., 1997), and in fact in other environments  
570 changes in density effects have already been shown to be a function of scale (Kamermans  
571 et al., 1992; Kamermans, 1993). Moreover, additional experimentation in other estuaries  
572 is essential and research including early recruiters and juveniles will help to determine the  
573 importance of competition in this more critical life phase.

574

575 Conservation strategies of one of the most appreciated resource in many estuaries of  
576 Europe, the native carpet shell *Ruditapes decussatus*, requires several quantitative  
577 challenges including that of competitive interaction. However, these strategies might be

578 more focused on aspects other than the potential direct impact of Manila clam, although a  
579 dramatic increase in density as it occurred in Venice Lagoon should be avoided. For this  
580 purpose, care should be taken in seeding of the nonindigenous species in culture zones i.e.  
581 control of pressure of introductions (Carlton, 1996; Lawrence and Cordell, 2010) and  
582 specific fishery management measures should be adopted considering the differences in  
583 life history attributes.

584

585 With the appropriate conservation and management measures adopted, the nonindigenous  
586 species could have beneficial aspects, including (i) enhance of biodiversity and (ii)  
587 positive socioeconomic impacts. Moreover, Manila clam could have the potential to be  
588 also of considerable benefit to several shorebird populations and other macropredators as  
589 suggested by Mieszkowska et al. (2006) and Caldow et al. (2007), since it is more readily  
590 consumed due to its shallower burial depth. As a consequence, predation on the native  
591 clam may actually decrease. However, this food source could in turn increase predators'  
592 abundance and influence nearshore community structure. Thus, since natural systems are  
593 highly dynamic and governed by complex nonlinear interactions, conservation measures  
594 and strategies may also be re-evaluated over the years to cope with the changes resulting  
595 from species' spatio-temporal population dynamics.

596

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604

605

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