Growth and extremely high production of the non-indigenous invasive species *Corbicula fluminea* (Müller, 1774): Possible implications for ecosystem functioning

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ABSTRACT

The Asian clam *Corbicula fluminea* (Müller, 1774) is a major component of the River Minho estuary, almost completely dominating the benthic biomass. As part of a major study into the ecology of *C. fluminea*, benthic samples were collected monthly from January 2005 to August 2006. These data were then used to estimate the abundance, biomass, growth, and growth and elimination production of this non-indigenous invasive species. *Corbicula fluminea* growth was continuous throughout its life span. The annual 2005 growth production was estimated to be 463.778 g AFDW m⁻² year⁻¹, and the mean annual biomass was 160.651 g AFDW m⁻², resulting in a P/B ratio of 2.89 year⁻¹ and a turnover time of 126.4 days. In the light of these results, *C. fluminea* is a fundamental element in the River Minho estuary, possibly sequestering a large portion of the carbon available for benthic production and altering the ecosystem functioning. This species should be considered when modelling the nutrient cycles and energy flow in aquatic ecosystems.

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1. Introduction

The introduction of non-indigenous invasive species (NIS) in aquatic ecosystems has increased dramatically in recent decades (Cohen and Carlton, 1998; Ricciardi and Maclsaac, 2000; Light and Marchetti, 2007). Freshwater ecosystems are being extremely modified by human activities, resulting in a decline of the native species with a subsequent replacement and spread of NIS (Ricciardi and Rasmussen, 1999; Holeck et al., 2004). In addition, genetic, social and economic impacts provoked by these NIS are usually unpredictable and occasionally result in serious damage (Pimentel et al., 2000; Cox, 2004). Therefore, measuring and predicting the impact of NIS deserves attention so that managers and stakeholders can prioritize efforts to prevent invasion or control the impacts of the invader (Sakai et al., 2001; Sax et al., 2007). Special consideration should be given to invasive species that carry new attributes to ecosystems and species that dominate communities as virtual monocultures and thereby have the potential to disrupt ecosystem processes (Hall et al., 2006).

The Asian clam *Corbicula fluminea* (Müller, 1774) is recognized as one of the most important NIS in aquatic ecosystems (McMahon, 2002; Sousa et al., 2008b). In the last 80 years, species of the *Corbicula* genus have extended its range from Asia, Oceania and Africa to American and European ecosystems (Mouthon, 2001a,b; McMahon, 2002). Due to its invasive behaviour is essential to study the population structure in invaded ecosystems. Indeed, because of its abundance, this species may play a significant role in nutrient cycling and benthic-pelagic coupling which are potentially responsible for important ecological alterations (Sousa et al., 2008b). Consequently, this bivalve is the core of several studies carried out in European and American aquatic ecosystems dealing with biological invasions. However, this kind of information differs from ecosystem to ecosystem and it is essential to develop local studies, principally in areas with great abundance and biomass, such as River Minho estuary (Iberian Peninsula). In this estuary, *C. fluminea* was first recorded in October 1989 and in subsequent years the population underwent a massive expansion (Araujo et al., 1993). Nowadays, this species colonise all the middle and upper part of the estuary and reaching considerable abundance and biomass (e.g. some sites with an abundance and biomass of more...
than 4000 ind. m$^{-2}$ and 550 g AFDW m$^{-2}$, respectively) (Sousa et al., 2005, 2008a, 2008d, in press). The introduction of $C. fluminea$ to the River Minho estuary was most likely the result of human activities, as has occurred in other American and European ecosystems (McMahon, 2002). Secondary introduction from activities, as has occurred in other American and European source is improbable since the River Minho estuary is not subjected to water ballast discharges or aquaculture activities. Therefore, human activities such as the use of specimens as fish bait, transport of individuals as a curiosity and also the extensive capacities of this species to natural dispersion are probable vectors of introduction (McMahon, 2002; Sousa et al., 2008b).

The aims of this study were to estimate the abundance, biomass, growth, and growth and elimination production of $C. fluminea$ in the River Minho tidal freshwater wetlands (TFWs), describing the possible implications of these high values to the ecosystem functioning.

2. Materials and methods

2.1. Study area and sampling strategy

The River Minho estuary (Iberian Peninsula) extends for about 40 km with a tidal freshwater section of near 30 km. The characterization of this estuary with a particular emphasis on the macrozoobenthic assemblages existing along the estuarine gradient was previously described by Sousa et al. (2005, 2007b, in press).

Between January 2005 and August 2006 (always at the end of each month), quantitative monthly samples were carried out at three sites located in the River Minho TFWs, at high tide (Fig. 1). For each site, six replicates (one for sediment analysis and five for biological analysis) were gathered using a Van Veen grab with an area of 0.05 m$^2$.

The following abiotic parameters were measured in situ, close to the bottom using a multiparametrical sea gauge YSI 6820: temperature, total dissolved solids, redox potential, salinity, dissolved oxygen and pH. In addition, water samples were collected in the field in order to measure the concentration of nitrites, nitrates, ammonia, phosphates and hardness using a Palintest 270 standard photometer 7000. Finally, sediment samples were collected and analysed for granulometry and organic matter content following the procedure described in Sousa et al. (2007a).

Biological material was processed through a sieve with a mesh size of 500 μm and all individuals of $C. fluminea$ were measured with a vernier caliper. Length measurements were converted to estimates of individual biomass expressed as grams of ash free dry weight (AFDW). Thus, 24 individuals were dried to 60 °C for dry weight estimations every month and AFDW was obtained by ignition at 550 °C for 4 h following the procedure described in Sousa et al. (2006a).

2.2. Growth and production estimations

Growth rates were estimated following recognizable cohorts with size frequency distributions from the successive twenty monthly sample dates. Size-frequency analysis was carried out using the ANAMOD software package (Nogueira, 1992). The analysis reliability was always tested using the $\chi^2$ and the G test ($P=0.05$). Since growth rates were not constant throughout the year, empirical data were adjusted to a model that takes into account seasonal changes (Gaschütz et al., 1980), expressed as:

$$L_t = L_\infty \left\{ 1 - e^{-\left( \frac{kD(t-t_0)}{2} \right)^p \sin(2\pi(t-t_1))} \right\}^b$$

$L_t$: length of the organism at a given moment $t$; $L_\infty$: maximum possible length of the organism; $t$: given instant; $t_0$: instant when the organism would have a length equal to 0; $t_1$: time interval between growth start (when $t = 0$) and the first growth oscillation; growth is expressed by a sine curve which the period is 1 year; $k$: intrinsic growth rate; $C$: constant and the values can vary between 0 and 1; $D$: parameter that expresses metabolic deviations from the Von Bertalanffy rule.

Annual production estimates were based upon cohort recognition. Growth production ($P$) and elimination production ($E$) were calculated with a method derived from Allen (1971) with total values of $P$ and $E$ for the population of $C. fluminea$ expressed as:

$$P_t = \frac{N_{t+1} + N_{t}}{2} (W_{t+1} - W_t) \quad \text{for} \quad W_{t+1} > W_t$$

$$E_t = \frac{N_{t} + N_{t+1}}{2} (N_t + N_{t+1}) \quad \text{for} \quad N_t > N_{t+1}$$

$N$: density of the cohort in each sample date; $W$: mean individual biomass in each sample date; $t$ and $t + 1$: consecutive sample dates.

Total values of $P$ and $E$ for the population are expressed as:

$$P = \sum_{i=1}^{n} P_i$$

$$E = \sum_{i=1}^{n} E_i$$

$P_i$ and $E_i$ are the growth and elimination production of the cohort $i$. $P/B$ and $E/B$ ratios were also determined and $B$ (mean population biomass) is expressed as:

$$B = \sum_{i=1}^{n} N_i$$
\[ B = \frac{1}{T} \sum_{i=1}^{N} B_i t_i \]

\( T \): period of study; \( N \): number of successive cohorts in the period \( T \); \( B_i \): mean biomass of the cohort \( i \); \( t_i \): duration of the cohort \( i \).

### 3. Results

#### 3.1. Abiotic characterization

The abiotic characterization of all the River Minho TFWs is described in earlier studies (Sousa et al., 2005, 2008a, in press). In addition, the particular abiotic characterization of the three sites sampled in this study is in Sousa et al. (2008c). The abiotic data for each site are available on demand from the corresponding author.

#### 3.2. Abundance and biomass

The total monthly abundance and biomass per site from January 2005 to August 2006 are given in Figs. 2 and 3, respectively. The mean abundance for the 20 months of sampling was 521, 1320 and 680 ind. m\(^{-2}\) for the sites 1–3, respectively. The minimum abundance value occurred at site 3 in July 2005 with 92 ind. m\(^{-2}\). The higher mean abundance (ind. m\(^{-2}\)) at the 3 sites from January 2005 to August 2006 (the confidence bands represent standard deviations). The total monthly abundance and biomass per site from January 2005 to August 2006 are given in Figs. 2 and 3, respectively. The mean abundance for the 20 months of sampling was 521, 1320 and 680 ind. m\(^{-2}\) for the sites 1–3, respectively. The minimum abundance value occurred at site 3 in July 2005 with 92 ind. m\(^{-2}\). The higher mean abundance (ind. m\(^{-2}\)) at the 3 sites from January 2005 to August 2006 (the confidence bands represent standard deviations).

#### 3.3. Growth and production

Size-frequency distributions were analysed for recognizable cohorts (Fig. 4). In the 20-months of sampling, the presence of 18 different cohorts was observed. The biggest clam gathered had a length of 41.83 mm.

Growth rates were estimated using the mean size of the recognizable cohorts identified. Growth was continuous throughout the life cycle and life span may vary between 24 and 36 months. A mathematical growth model including seasonal adjustment was used on data derived from the recognizable cohort 5 + cohort 11 (Fig. 5). The growth parameters were: \( L_\infty = 49.8 \text{mm} \) and \( k = 0.68 \text{year}^{-1} \).

Monthly growth production ranged from 12.272 to 77.514 with a mean value of 41.100 g AFDW m\(^{-2}\) year\(^{-1}\) and a turnover time of 126.4 days. The annual 2005 elimination production was 855.219 g AFDW m\(^{-2}\) year\(^{-1}\), resulting in a \( E/B \) ratio of 5.32 year\(^{-1}\).

### 4. Discussion

#### 4.1. Biotic characterization

The bivalve \( C. \) fluminea was always present in the three sampled sites and the population abundance and biomass showed spatial and temporal variations. In an earlier study, it was found that the abundance and biomass of this NIS in this estuarine ecosystem are well correlated with the abiotic factors, principally redox potential, nutrients, hardness, organic matter and sediment characteristics (Sousa et al., 2008a). Therefore, the abundance and biomass differences in the three sites may also result from the different abiotic conditions. The abundance and biomass of \( C. \) fluminea in these three sites were not significantly different from other sites already surveyed in this estuary (for a comparison see Sousa et al., 2005, in press). However, such persistence of high abundance (principally of adult specimens) and biomass for several years after the introduction is not common (Phelps, 1994). Mean abundance is usually much lower, especially if large scale sampling as opposed to specific patches is carried out (Mouthon, 2001a,b; Mouthon and Parghentanian, 2004; Sousa et al., 2006a,b). Indeed, this species can achieve high abundance and biomass in the first years of an invasion but then generally undergo a decline (Phelps, 1994). In the River Minho, the \( C. \) fluminea population has persisted in the ecosystem in high abundance and biomass for more than 15 years and there is no sign of decline (Sousa et al., 2005, 2007b, 2008a, 2008d, in press).

In the River Minho estuary, \( C. \) fluminea growth is continuous throughout its life cycle and its life span seems to vary between 24 and 36 months, which is similar to other populations worldwide (Mouthon and Parghentanian, 2004). However, there are exceptions to this; some populations have shorter (Aldridge and McMahon, 1978; Hornbach, 1992) or longer (Cataldo and Boltovskoy, 1999; Mouthon, 2001a,b) life spans. These differences are probably related to latitude, temperature, and available food resources. In this study the estimation of the life span was made indirect since during the 20 months of sampling we were not able to follow a cohort from the beginning until the end. In addition,
a clear recruitment period was not found. This situation was not caused by sampling error because in the same samples we found little juveniles from the bivalve Pisidium amnicum (Sousa et al., 2008c). A possible explanation is that C. fluminea juveniles settle in sites not surveyed in this study, possibly in intertidal or very shallow areas with submerged vegetation, and after that migrate to deeper sites. Alternatively, the recruitment sites may be located in upstream areas and the clams migrate downstream after a time. Due to great river discharge, the migration of C. fluminea inside the estuarine area is possible, even for adults. These uncertainties do not allow us to estimate an accurate life span and also create some problems for the estimation of the growth rates due to the absence of small juveniles.

Comparing the secondary production results obtained in this study with values gathered in freshwater ecosystems in which total invertebrate (or a high fraction of production) was estimated, we can observe that C. fluminea production in the years 2005 and 2006 can be considered to be extremely elevated for freshwater species (for comparisons see Benke (1993) and references therein) (Fig. 8). In addition, the values obtained in this study correspond to single species estimation and not to the total secondary production as the majority of the other studies. Given these values there are two fundamental questions: 1) how does the ecosystem supports such elevated levels of C. fluminea abundance and biomass? and 2) what is the fate of this production? To answer the first question it is fundamental to know the extent of the primary production based on phytoplankton, C. fluminea consumption rates and whether this abundant population may be able to control primary production as already observed in populations from temperate waters (Phelps, 1994). The River Minho estuary is oligotrophic and has a low residence time (no more than 36 h). Since the primary production based on phytoplankton is therefore probably far too low to support the C. fluminea population, this NIS may use additional food sources such as organic matter contained in the sediments which are rich in macroalgal detritus, submerged vegetation detritus, and bacteria, among others (Hakenkamp and Palmer, 1999). In relation to the C. fluminea consumption rates, several authors agree that this bivalve has one of the greatest filtration rates worldwide which also results in high assimilation rates (McMahon, 2002 and references therein). Given the abundance and biomass present in the River Minho TFWs it is possible that this NIS control the primary production and has extreme importance in benthic processes. For the second question, several uncertainties exist about the possible predators that could exploit the high abundance and biomass present in this estuary. According to an earlier study, C. fluminea is responsible for almost 98% of the macrozoobenthic biomass along the total estuarine gradient (Sousa et al., in press). In theory, several species of birds, fishes and mammals could consume these clams. Indeed, stomach content analyses done in some fish species present in this estuarine ecosystem show that C. fluminea is consumed by Platichthys flesus.
and Cobitis paludica (Dias, unpublished data). However, the large abundance and biomass of C. fluminea does not seem to be fully exploited by the higher trophic levels and a great part goes directly to the detritus food-web. For example, in the summer of 2005, due to specific abiotic conditions (e.g., high temperatures, low dissolved oxygen, low redox potential, low flow conditions), significant C. fluminea mortality occurred and a great portion of biomass went directly to the sediments (Sousa et al., 2005, 2007b, 2008a, in press). Secondly, in the River Minho TFWs (the 16 sites surveyed in Sousa et al. (2008a) was 99.1 g AFDW m⁻². However, in 2006 and 2007 this biomass was substantially higher with mean values for all the 16 sites of 121.4 and 161.0 g AFDW m⁻², respectively. Since high C. fluminea production was driven by high biomass, the estimates for 2005 appear to be conservative compared with greater biomass of 2006 and 2007.

4.2. Ecological significance

The ecological role of C. fluminea in the River Minho estuary is defined by its position in the food-web, by the amount of energy flowing through this invasive population and the possible changes in ecosystem functioning which occurred after its introduction. Since C. fluminea is a filter and pedal feeder, it represents a direct link between pelagic primary production and higher trophic levels. Therefore, given the abundance, biomass and production of this NIS in the River Minho TFWs, C. fluminea can be regarded as a fundamental species in this estuarine ecosystem. A before–after control–impact is impossible to perform in order to quantify the C. fluminea invasion effects in the River Minho TFWs due to a lack of both pre-invasion data and suitable reference sites (Hall et al., 2006). Indeed, there were no pre-invasion quantitative (only qualitative) data on invertebrate assemblages or primary production from which to estimate the impact of C. fluminea. Additionally, and since places located in the estuary are already colonised by this clam (Sousa et al., 2005, 2007b, 2008a, in press) potential control sites are only available in the tributaries which have completely different environmental and ecological conditions. Despite these limitations, we suggest that the impact has been large for several reasons: 1) the vast majority of benthic invertebrate abundance and biomass was constituted by C. fluminea (Sousa et al., 2007b, in press); 2) production was extremely high for freshwater ecosystems and can only be comparable to that of dominant taxa in highly

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The invasion of Corbicula fluminea has caused changes in ecosystem processes and community structure. (Nichols et al., 1990; Kimmerer et al., 1994; Caraco et al., 2008). The dominance shown by some invasive species may be an indicator of ecological impact within and between trophic levels (Hall et al., 2006). Corbicula fluminea may affect ecosystem functioning via the additional secondary production estimated for each C. fluminea cohort.

![Fig. 7. Relationships between biomass and annual growth (\(\uparrow\)) and elimination (\(\downarrow\)) production estimated for each C. fluminea cohort.](image)

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References


5. Conclusion

A proper estimation of impact of invasions is fundamental, as many NIS have negligible consequences while others will require management actions if they strongly affect ecosystem processes or economic interests (Hall et al., 2006).

Corbicula fluminea dominated the abundance, biomass and secondary production in River Minho TFWs and the same is potentially true for several worldwide aquatic ecosystems. They had among the highest secondary production values ever measured for a species colonising a freshwater ecosystem, and this situation may be responsible for changes in the benthic assemblages and/or in the ecosystem functioning. The mechanism behind its ecological dominance may be higher competitiveness, either because they are better at exploiting resources or because its abundance is so high that they interfere with the capacity of native invertebrates to acquire resources (Byers, 2000; Hall et al., 2006). In addition, this species has an r-strategy life cycle (e.g. short life span, early maturity, rapid growth and high fecundity) which can be an advantage in ecosystems subject to periodical disturbances. In fact, in this estuary C. fluminea rapidly recovered from the impacts caused by the 2005 heatwave but the native bivalves almost disappeared.

We conclude that C. fluminea is a fundamental element in the River Minho estuary and this species should be considered when modelling the nutrient cycles and energy flow in aquatic ecosystems. Preventing the spread and future introductions of C. fluminea into aquatic ecosystems should be a conservation priority.