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TITLE: Predicting the variation of *Echinogammarus marinus* populations from southernmost limits of distribution under global warming scenarios: Can sex-ratio make a difference?

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ABSTRACT

Critical to predicting how ecosystems will react to climate change is an understanding of environmental parameters constraining organisms distributions at their latitudinal extremes. The aims of this study were twofold, first, to predict the variation of amphipod populations of *Echinogammarus marinus* from the southernmost limit of its distribution under scenarios of global warming, and secondly to check if sex-ratio fluctuations - a mechanism frequently displayed by amphipods - might have impacts on the long-term variations of populations under climate disturbance conditions.

To achieve these aims, scenarios were run with a validated model of *Echinogammarus marinus* populations. Simulations were divided into two distinct phases, phase I, where the effects of climate change on amphipod populations were checked through three distinct scenarios: temperature increases (T), salinity fluctuations (S) and a combination of both (T-S), and phase II, where the previous scenarios were combined with realistic males to females proportions (R) in three other scenarios: T-R, S-R and T-S-R.

Results indicate that *Echinogammarus marinus* populations are highly sensitive to temperature rises ($>2^{\circ}\text{C}$) due to adverse effects on amphipod recruitment and growth.

Results from climate change scenarios coupled to sex-ratio fluctuations depend largely on the degree to female-bias within the population. Female biased populations seem able to cope with temperature rises of 2°C , particularly if conjugated with salinity increases, whereas male-biased populations were highly sensitive to any temperature and/or salinity variation, exhibiting long-term density decline. All simulations whereby temperature was increased of $+4^{\circ}\text{C}$ caused a continuous decline of *Echinogammarus marinus*. These results highlight the vulnerability of populations located at southernmost limits of distribution to global warming. In Europe, temperature increases

1 of 2°C may cause a withdrawal of 5° N of amphipod species located at southernmost
2 geographical borders. This is discussed in relation to *Echinogammarus marinus*
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4 distribution along the Atlantic coast.
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11 **KEYWORDS:** Amphipods; Southernmost limit; Climatic changes; Sex-ratio; Female-
12 biased; Resilience
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1. INTRODUCTION

1
2 In animal populations, sex-ratio - the proportion between males and females -
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4 can be either 1:1 or skewed towards males or females (Moore, 1981). Most species
5
6 show temporal and/or spatial variability in their sex-ratios (Wildish, 1997). Some of the
7
8 factors underlying differences in sex-ratios of populations include food availability,
9
10 sexually biased predation, time needed to associate with a female for successful mating,
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12 longevity between sexes, and parasitic factors (Appadoo & Myers, 2004). Sex-ratio
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14 variations may also be related to adaptive adjustments to environmental conditions
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16 (Paoletti & Cantarino, 2002).
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22 Amphipod populations often show sex-ratio fluctuations (Vlasblom, 1969),
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24 which appear to be regulated by environmental factors such as temperature and
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26 photoperiod (Lawrence & Soame, 2004; Dunn *et al.*, 2005). Salinity has also been
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28 referred as a factor capable of inducing sex-ratio changes on polychaete populations
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30 (Simonini & Prevedelli, 2003). This mechanism of environmental determination
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32 (Environmental Sex Determination - ESD) (Dunn *et al.*, 2005) seems to be an adaptive
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34 response that enables an individual to match its sex to its greatest expected future fitness
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36 (Charnov & Bull, 1977).
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41 In nature, *Echinogammarus marinus* populations with higher intersexuality
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43 incidence (i.e. a sexual abnormality which induces the occurrence, in dioecous species,
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45 of both male and female sexual characteristics in the same individuals - Kelly *et al.*,
46
47 2004), tend to be female-biased, which seems to be related with the amphipod's
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49 infection by microsporidian feminising parasites (Ford *et al.*, 2006). On the other hand,
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51 populations with female-biased sex ratios are less sensitive to increases on
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53 intersexuality incidence or decreases on the reproductive rate of intersexes (Martins *et*
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al. 2009), indicating that a selective advantage of female-biased populations may take place at high intersexuality levels (Ford *et al.*, 2003).

Thus assuming that i) under conditions of high disturbance, populations with the capability of adjusting their sex-ratios will presumably be favored and ii) *Echinogammarus marinus* populations are able to adjust their sex-ratio in response to environmental variables, the aim of this study was to test whether sex-ratio fluctuations may be a mechanism of persistence and resilience of macroinvertebrate populations against natural disturbances, namely, climatic changes. This was achieved through scenario forecasting through population dynamics models of *Echinogammarus marinus* populations.

2. MATERIAL AND METHODS

2.1. Data and the population dynamics model

At the Mondego estuary (western coast of Portugal, 40°08'N 8°50'W), *Echinogammarus marinus* (Amphipoda, Gammaridae) is an abundant species of the intertidal communities associated to the brown algae *Fucus vesiculosus* (Marques *et al.*, 1993), representing an important prey for upper trophic levels, namely, birds (Múrias *et al.*, 1996, 1997). Data from previous studies on productivity, growth, embryonic development and fecundity of *Echinogammarus marinus* (Maranhão *et al.*, 2001; Maranhão & Marques, 2003) were used to calibrate and validate a population dynamics model of the amphipod (Martins *et al.*, 2002).

For modelling purposes, the population was divided into four groups: juveniles, immature (non-reproductive) females, adult (reproductive) females and males (Fig. 1). Growth, maturation, mortality and recruitment regulate group density variation through time. Besides density, the model also calculates group weight variation throughout time according to a temperature-dependent modified von Bertalanffy model, which has been considered suitable to describe *E. marinus* growth (Marques, 1989; Marques *et al.*, 1991). The number of newly hatched juveniles was made dependent on female's size, temperature and salinity (Table 1) in accordance to experimental data (Maranhão & Marques, 2003). The initial model, designated hereafter as the base model, was run with temperature and salinity data sets, measured at the Mondego estuary, during the 90's (Fig. 2).

2.2. Scenario simulations

Scenario simulations were run in two distinct phases, phase I, that included variations in temperature and salinity according to expected variations caused by global

1 warming (IPCC, 2007) and phase II, which included the combined effects of
2 temperature and salinity variations, with different realistic proportions of sex-ratio.
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4 According to IPCC (2007), climate change predictions include variations in
5 temperature with expected increases of 2-4°C approximately, sea-level rise and extreme
6 weather events such as droughts and heavy precipitation, that may cause increases
7 and/or decreases in salinity due to changes in riverine freshwater input (Cayan &
8 Peterson, 1993; Justić *et al.*, 1996).
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10 Based on these predictions, during phase I, we have evaluated the effects of
11 temperature increases of 2 and 4°C, respectively, and of salinity fluctuations of \pm 5psu
12 on the variation of *E. marinus* populations, corresponding to scenarios T and S,
13 respectively. The simultaneous and combined effects of temperature and salinity
14 variations on *E. marinus* populations were also simulated (scenarios T-S)
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16 In phase II, the scenarios simulated during phase I were combined with different
17 values of sex-ratio, to assess if sex-ratio fluctuations could change the effects caused by
18 temperature and salinity variations. For this purpose, T-R and S-R scenarios were run
19 for the temperature and salinity effects combined with the sex-ratio fluctuations, along
20 with T-S-R scenarios, which included the combined effect of these three factors.
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22 Realistic sex-ratio fluctuations were achieved through controlled changes of the
23 fluxes $growth_{IF}$ and $growth_M$, allowing that the sum of the two fluxes was the same as in
24 the base model, which ensured that model validation was not affected.
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26 The initial values used in each simulation are shown in Table 2. Scenario
27 simulations run for approximately 11 years.
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3. RESULTS

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2 According to results, the simulated temperature increases (phase I, scenarios T)
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4 cause a progressive decline of the density of *Echingammarus marinus* populations, with
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6 a more severe effect for temperature increases of 4°C (Fig. 3a). Simulated salinity
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8 changes (phase I, scenarios S) have an opposite effect on amphipod populations, whilst
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10 salinity decrease has a negative effect on the long-term variation of the population, a
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12 salinity increase of 5psu seems to favor the population, causing a gradual increase of
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14 density over time (Fig. 3b). However when salinity and temperature increases were
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16 combined (phase I, scenarios T-S), the positive effect of salinity was overlapped by
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18 temperature causing a population decline (Fig. 3c,d).
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24 During phase II simulations, all scenarios with male-biased populations presented a
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26 gradual decline over time (Fig. 4), whilst some scenarios with female-biased
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28 populations show some resistance to temperature and/or salinity variations (Fig. 4).
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30 However not even female-biased populations seem able to cope with temperature
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32 increases of 4°C or whenever a temperature increase of 2°C is conjugated with a salinity
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34 decrease of 5psu (Fig. 4b,d), exhibiting more or less abrupt decreases of density over
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36 time.
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4. DISCUSSION

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2 Results from this study indicate two levels of responses corresponding to phase I
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4 and phase II of scenario simulations, respectively. Phase I simulations suggest that
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6 *Echinogammarus marinus* populations will be negatively affected by temperature rise
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8 and by salinity decreases, with more severe effects for higher temperature increases.
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10 Whilst salinity increases alone would potentially benefit the amphipod population,
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12 which is in accordance with experimental data (Vlasbom & Bolier, 1971; Pinkster &
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14 Broodbaker, 1980), simultaneous increases of salinity and temperature seem to result on
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16 a gradual decrease of population density through time due to an apparent overlapping
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18 effect of temperature over salinity.
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24 Results from phase II suggest that male-biased populations of the amphipod
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26 *Echinogammarus marinus* are less resistant and resilient to temperature and salinity
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28 variations than female-biased populations. According to results, populations with a
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30 higher proportion of females can cope better both with temperature increases of 2°C
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32 alone or whenever conjugated with salinity increases of +5psu, exhibiting a gradual
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34 increase of density over time, which is related to enhanced recruitment rate of
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36 *Echinogammarus marinus* at higher salinities. However, even female-biased
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38 populations of the gammaridae seem unable to cope with temperature increases of 4°C,
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40 which is related to deviations from the optimum temperature range for growth and
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42 recruitment of *Echinogammarus marinus*. Previous works have found relationships
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44 between temperature and the duration of embryogenesis on *E. marinus*, whereby a
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46 decrease in the duration of the embryonic development was observed with a temperature
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48 increase from 5 to 10°C, reaching an optimum at 20°C, while the highest production of
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50 juveniles was recorded at 15°C (Vlasblom, 1969; Maranhão & Marques, 2003). On the
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52 other hand, for poikilotherm animals, a rise in temperature will necessarily cause an
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increase in metabolic rates, which can result in a decrease of the energy reserves of the animal and, thus, less energy available for growth and reproduction.

In the case of *E. marinus*, female-biased populations seem to be more persistent to less favorable conditions such as global warming (this study) or intersexuality (Martins *et al.*, 2009). Other species, such as some nematodes, exhibit male-biased populations when conditions are adverse (Snyder *et al.*, 2006). Again, this highlights the fact that sex-ratio adjustment by populations seems to be a mechanism by which those populations maintain their fitness.

Variations of *Echinogammarus marinus* populations under temperature increasing scenarios may be even more dramatic, if the overall increase of temperature throughout this century is greater than 4°C (up to 6.4°C), as predicted by the IPCC (2007) due to the growth of the global population and economy and the intensive consumption of fossil fuels persists.

Echinogammarus marinus populations reported in this study are located at the southernmost limit of the species distribution, the Mondego estuary (western coast of Portugal) (Maren, 1975a, 1975b; Marques & Bellan-Santini, 1993), where the nowadays average annual water temperature varies between 10 and 27°C (unpublished data from July 2011 to August 2012). Several global warming models and scenarios predict that, by the end of the 21st century, warming in Western Europe will range between 1.1 to 3.5°C (Meehl *et al.*, 2005). In these scenarios and according to our results, *E. marinus* populations from the Mondego estuary will be at considerable risk, particularly, if temperature varies $\geq 2^\circ\text{C}$. In these circumstances, the southernmost limit of the gammaridae may become restricted to further northern latitudes (45-51°N), which nowadays show lower water temperatures compared to the Mondego estuary (Noppe *et al.*, 2006; Glé *et al.*, 2008) but where, according to global warming models (Meehl *et al.*,

1 2005), the water temperature will rise to values similar to nowadays southern Europe.
2 This is in accordance with other works, where the northward movement of marine
3 species driven by global warming has been predicted along European coast lines
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5 (Philippart *et al.*, 2011).
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9 In conclusion, the present work predicts that *Echinogammarus marinus* populations
10 will be adversely affected by temperature rise. Due to this, by the end of the 21st century
11 if global warming is $\geq 2^{\circ}\text{C}$, the southernmost limit of *E. marinus* may be displaced
12 about 5°N compared to nowadays. Additionally, our results suggest that populations
13 able to adjust their sex-ratios may be more resilient to climatic changes. In the case of *E.*
14 *marinus*, female-biased populations seem to be more resistant to temperature rise than
15 male-biased populations. Nevertheless, if males become too rare to fertilize the
16 available females, the population will collapse (Hatcher *et al.*, 1999). Thus, even
17 female-biased populations of *E. marinus* may only subsist up to certain thresholds of
18 sexual bias and temperature rise.
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6. ACKNOWLEDGEMENTS

The authors are indebted to all colleagues from IMAR – The Institute of Marine Research, Marine and Environmental Research Centre, who assisted in field and laboratory work.

The present study was carried using financial support from R&D research projects 3M-RECITAL (LTER/BIA-BEC/0019/2009), INPACTAR PTDC/MAR/111537/2009), and CIÊNCIA 2007 (FCT, QREN,COMPETE). It was also subsidized by the European Social Fund and MCTES national funds, through the POPH (*Human Potential Operational Programme*) – NSRF (*National Strategic Reference Framework–4.4.*)

7. FIGURE CAPTIONS

Figure 1 – Conceptual diagram of the model. The state variables represent the density (ind.m⁻²) and the weight (mg) of the population groups: *Juveniles*, *Immature Females*, *Adult Females* and *Males*. Mortality rates of population groups (ind.m⁻².days⁻¹): *mort_J* – Juvenile mortality, *mort_{IF}* – Immature Female mortality, *mort_{AF}* – Adult Female mortality and *mort_M* – Male mortality. Flow rates of individuals (ind.m⁻².days⁻¹): *growth_{IF}* rate of transfer from Juveniles to Immature Females, *growth_M* – rate of transfer from Juveniles to Males, *maturation* – rate of transfer from Immature Females to Adult Females. *Recruitment* – reproduction rate of Adult Females (ind.m⁻².days⁻¹). *Temperature* and *Salinity* are the forcing functions that regulate reproduction and growth (°C and psu, respectively) (see Martins *et al.*, 2002 for details).

Figure 2 – Initial values of the Temperature (a), Salinity (b) and Sex-ratio (c) used in each scenario. (a) - Temperature variation throughout time used in: base model (solid line) which were achieved using data obtained by Maranhão *et al.*, (2001); scenario for temperature increases of 2°C (dashed line) and 4°C (dotted line) which were obtained by inflation / deflation of the initial values used in the base model (+2°C and +4°C respectively). (b) – Salinity variation throughout time used in: base model (solid line) which were achieved using data obtained by Maranhão *et al.* (2001); scenario for salinity increases of 5psu (dashed line) and decreases of 5psu (dotted line); which were obtained by inflation/deflation of the initial values used in the base model (+5psu and -5psu, respectively). (c) – Sex-ratio fluctuations throughout time used in: base model (solid line) sex-ratio=1; scenarios for female-biased (sex-ratio<1; dashed line) and

1 male-biased population (sex-ratio>1; dotted line) which were obtained by increasing in
2 0.001 the initial value, used in the base model, of the parameters $growth_{IF}$ and $growth_M$,
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4 respectively.
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9 **Figure 3 – Scenario T, S, and T-S.** (a) – Long-term variation of *E. marinus* total
10 density (ind.m⁻²) under base model conditions (solid line), temperature increase of 2°C
11 (dashed line) and temperature increase of 4°C (dotted line). (b) – Long Long-term
12 variation of *E. marinus* total density (ind.m⁻²) under base model conditions (solid line),
13 salinity increase of 5psu (dashed line) and salinity decrease of 5psu (dotted line). (c) –
14 Long-term variation of *E. marinus* total density (ind.m⁻²) under conditions of
15 temperature increases of 2°C, combined with variations in salinity: base model
16 conditions (solid line), temperature increase of 2°C and salinity increase of 5psu (dashed
17 line) and temperature increase of 2°C and salinity decrease of 5psu (dotted line). (d) –
18 Long-term variation of *E. marinus* total density (ind.m⁻²) under conditions of
19 temperature increases of 4°C, combined with variations in salinity: base model
20 conditions (solid line), temperature increase of 4°C and salinity increase of 5psu (dashed
21 line) and temperature increase of 4°C and salinity decrease of 5psu (dotted line).
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44 **Figure 4 – Scenario T-S-R.** Long-term variation of *E. marinus* total density (ind.m⁻²) at
45 four scenarios under different conditions of temperature, salinity and sex-ratio. (a) –
46 Temperature increases of 2°C and salinity increase of 5psu combined with variations in
47 sex-ratio: sex-ratio=1, temperature increase of 2°C and salinity increase of 5psu (solid
48 line), male-biased (sex-ratio>1), temperature increase of 2°C and salinity increase of
49 5psu (dashed line) and female-biased (sex-ratio<1), temperature increase of 2°C and
50 salinity increase of 5psu (dotted line). (b) – Temperature increases of 2°C and salinity
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1 decrease of 5psu combined with variations in sex-ratio: sex-ratio=1, temperature
2 increase of 2°C and salinity decrease of 5psu (solid line), male-biased (sex-ratio>1),
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4 temperature increase of 2°C and salinity decrease of 5psu (dashed line) and female-
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6 biased (sex-ratio<1), temperature increase of 2°C and salinity decrease of 5psu (dotted
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8 line). (c) – Temperature increases of 4°C and salinity increase of 5psu combined with
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10 variations in sex-ratio: sex-ratio=1 , temperature increase of 4°C and salinity increase of
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12 5psu (solid line), male-biased (sex-ratio>1), temperature increase of 4°C and salinity
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14 increase of 5psu (dashed line) and female-biased (sex-ratio<1), temperature increase of
15
16 4°C and salinity increase of 5psu (dotted line). (d) – Temperature increases of 4°C and
17
18 salinity decrease of 5psu combined with variations in sex-ratio: sex-ratio=1, temperature
19
20 increase of 4°C and salinity decrease of 5psu (solid line), male-biased (sex-ratio>1),
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22 temperature increase of 4°C and salinity decrease of 5psu (dashed line) and female-
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24 biased (sex-ratio<1), temperature increase of 4°C and salinity decrease of 5psu (dotted
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Table 1

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Table 1

$\frac{\partial J}{\partial t} = recruitment - mort_j - growth_{IF} - growth_M$	Variation of juvenile density per unit of time
$\frac{\partial IF}{\partial t} = growth_{IF} - mort_{IF} - maturation$	Variation of young female density per unit of time
$\frac{\partial M}{\partial t} = growth_M - mort_M$	Variation of male density per unit of time
$\frac{\partial AF}{\partial t} = maturation - mort_{AF}$	Variation of adult female density per unit of time
$mort_{j,IF,AF,M} = mort_{j,IF,AF,M} \times Density_{j,IF,AF,M}$	Mortality rate of population groups as a function of density
$recruitment = NBJ \times f(S) \times f(T) \times 0.0291 \times AF$	Number of newly hatched juveniles (NBJ) from adult females per unit of time
$AvW = \frac{W_{i-1} + W_i}{2}$	Average weight of population groups
$W_i = W_{i-1} + f(T) \times days_{i-1,i} \times (h + W_{i-1}^{2/3} - k \times W_{i-1})$	Weight of <i>E. marinus</i> at the end of population group i
$DW = 1,592924 \times CL^{3,94344}$	Regression between dry weight and cephalic length
$NBJ = 0 \text{ for salinity } \leq 4$ $NBJ = -70.3 + 62.8 \times CL_{AF} \text{ for temperature } < 15$ $NBJ = -50.4 + 44.8 \times CL_{AF} \text{ for temperature } \geq 15 \text{ and } < 23$ $NBJ = -11.7 + 12.2 \times CL_{AF} \text{ for temperature } \geq 23$	Significant regression (p<0.05) between the number of newly hatched juveniles and females cephalic length and dependency of NBJ on salinity and temperature
$f(T) = \left(\frac{T}{T_{opt}}\right)^{2.5} \times e^{\left(1 - \left(\frac{T}{T_{opt}}\right)^{2.5}\right)}$ for $T < T_{opt}$ $f(T) = 1 - \left(\frac{T - T_{opt}}{T_{max} - T_{opt}}\right)^2$ for $T \geq T_{opt}$	Effect of temperature on recruitment
$f(S) = 0 \text{ else } f(S) = 1 \text{ for salinity } = 4 \text{ or salinity } < 4$	Effect of salinity on recruitment

Table 1 - Main equations of the model. *J* – Juveniles (Individuals m⁻²); *IF* –Immature Females (Individuals m⁻²); *AF* –Adult Females (Individuals m⁻²) and *M* – Males

(Individuals m^{-2}). AvW – average dry weight (mg), W_{i-1} – dry weight at the beginning of the population group i (mg), W_i – dry weight at the end of the population group i (mg), $days_{i-1,i}$ – average duration of a certain population group (days), h – anabolism parameter, k – catabolism parameter, DW – ash free dry weight (mg AFDW), CL – cephalic length (mm), T – temperature ($^{\circ}C$), T_{op} – optimum temperature for growth, T_{max} – maximum temperature at which growth ceases, S – salinity (psu) (for a better explanation of the biomass calculation module see Martins *et al.*, 2002).

Table 2

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Table 2

Parameter (symbol)	Description	Units	Base Model	T Scenario		S Scenario		R Scenario	
				+2°C	+4°C	+5psu	- 5psu	Female Biased	Male Biased
J Init	Initial density of juveniles	Individuals m ⁻²	72/experimental						
W _{J Init}	Initial Weight of juveniles	mg	0.065369/experimental						
Days _J	Juveniles duration	days	60/experimental						
mort _J	Juveniles mortality	per day	0.05/experimental						
growth _{IF}	Rate of transfer from juveniles to immature females	per day	0.0085/calibration				0.0095 calibration	0.0075 calibration	
growth _M	Rate of transfer from juveniles to males	per day	0.009/calibration				0.008 calibration	0.01 calibration	
M Init	Initial density of males	Individuals m ⁻²	18/experimental						
Days _M	Males duration	days	500/experimental, calibration						
Mort _M	Males mortality	per day	0.024/experimental, calibration						
IF Init	Initial density of	Individuals m ⁻²	16/experimental						

Table 2 – Mains symbols, description, units, initial values used in each scenario and estimation method of parameters.

Figure 1
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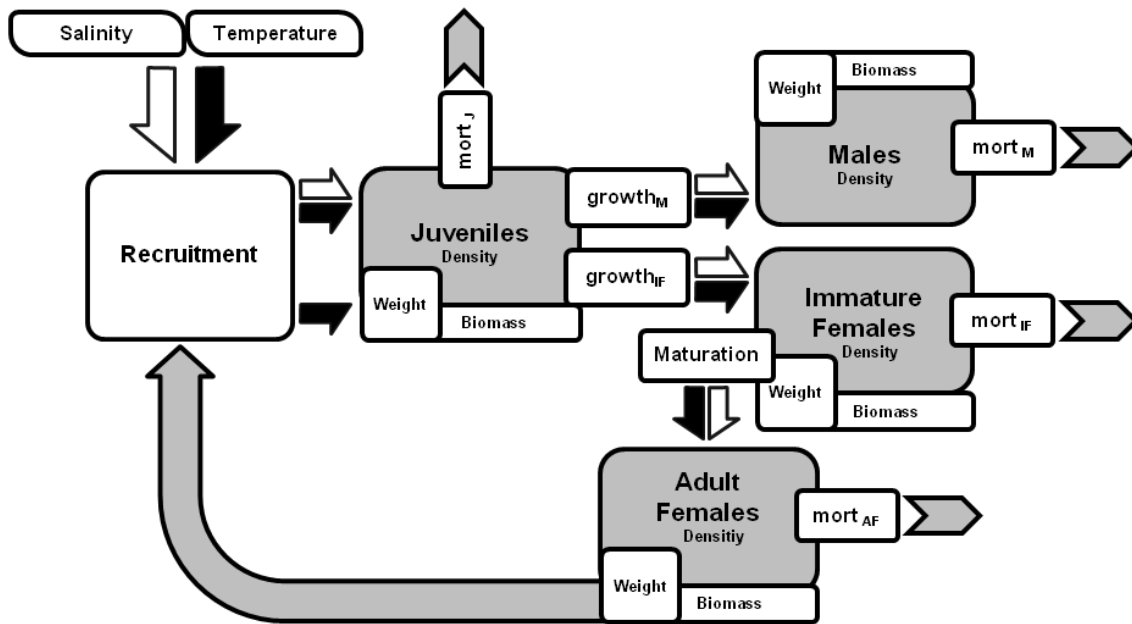


Figure 2
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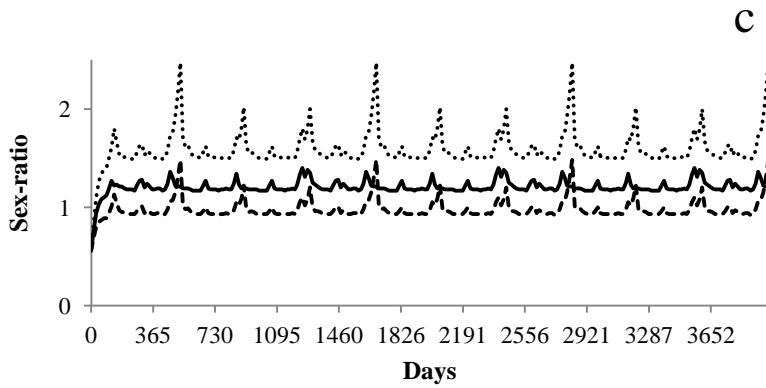
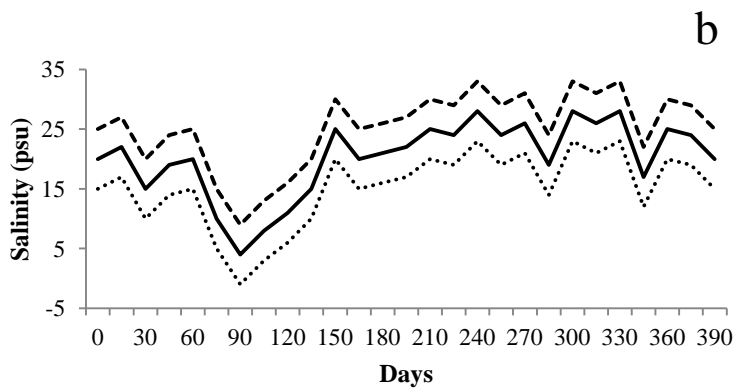
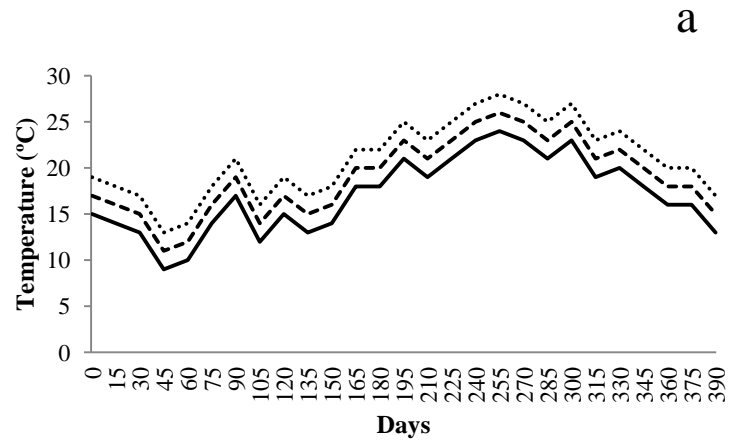


Figure 3
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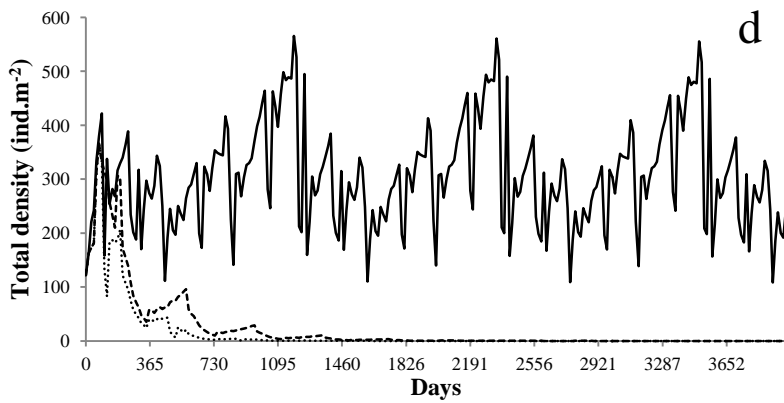
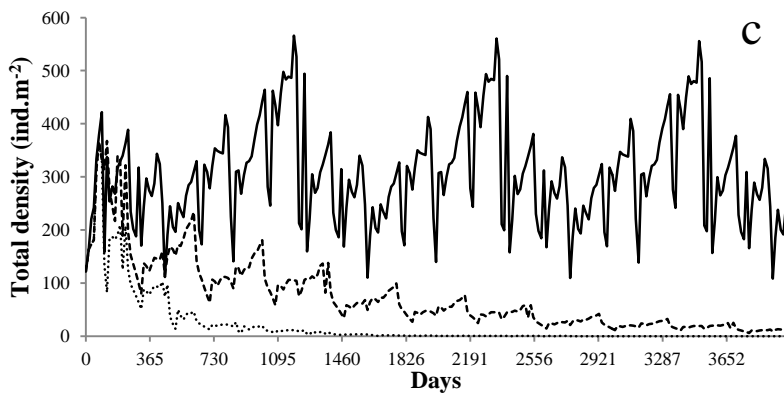
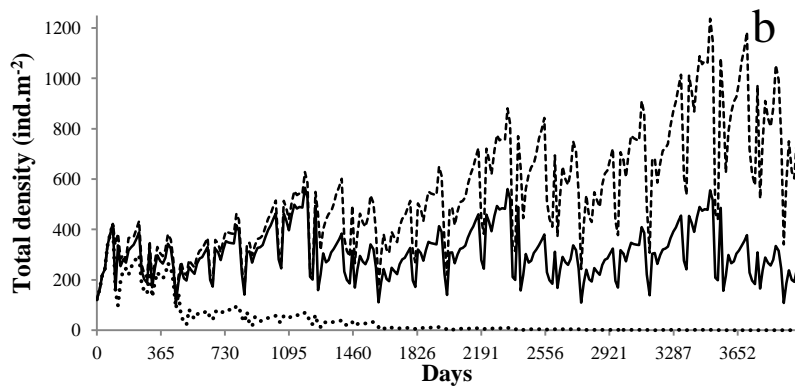
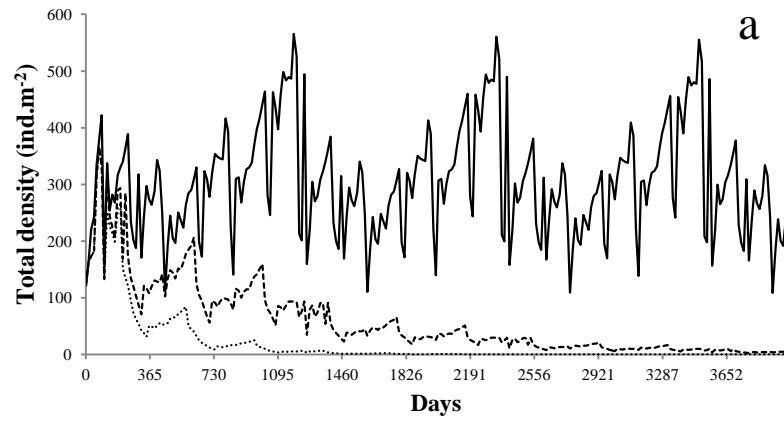


Figure 4
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