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Irene Martins, Alex T. Ford, Teresa F. Fernandes. Intersexuality incidence, sex ratio fluctuations and intersex reproductive output as factors affecting the temporal variation of intersexed populations of the marine amphipod. *Marine Environmental Research*, 2009, 68 (4), pp.163. 10.1016/j.marenvres.2009.06.007 . hal-00505737

HAL Id: hal-00505737

<https://hal.science/hal-00505737>

Submitted on 26 Jul 2010

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Accepted Manuscript

Intersexuality incidence, sex ratio fluctuations and intersex reproductive output as factors affecting the temporal variation of intersexed populations of the marine amphipod *Echinogammarus marinus*

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PII: S0141-1136(09)00066-X

DOI: [10.1016/j.marenvres.2009.06.007](https://doi.org/10.1016/j.marenvres.2009.06.007)

Reference: MERE 3343

To appear in: *Marine Environmental Research*

Received Date: 14 February 2008

Revised Date: 17 March 2009

Accepted Date: 2 June 2009



Please cite this article as: Martins, I., Ford, A.T., Fernandes, T.F., Intersexuality incidence, sex ratio fluctuations and intersex reproductive output as factors affecting the temporal variation of intersexed populations of the marine amphipod *Echinogammarus marinus*, *Marine Environmental Research* (2009), doi: [10.1016/j.marenvres.2009.06.007](https://doi.org/10.1016/j.marenvres.2009.06.007)

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3 Intersexuality incidence, sex ratio fluctuations and intersex reproductive output as
4 factors affecting the temporal variation of intersexed populations of the marine
5 amphipod *Echinogammarus marinus*
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36 **Abstract**

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38 The occurrence of intersexuality in populations of the marine amphipod *Echinogammarus*
39 *marinus* has been related to several causes, including anthropogenic contamination,
40 microsporidian parasites and environmental sex determination (ESD). At the individual level, the
41 costs of intersexuality in *E. marinus* are reflected in reduced reproductive output of intersexes
42 compared to normal specimens. To understand the consequences of intersexuality at the
43 population level is essential to fully evaluate the impacts of intersexuality and other reproductive
44 disorders in nature. The aim of the present work is to simulate the density variation of real
45 populations of *E. marinus* with different intersexuality incidence, proportions of phenotypes and
46 intersex female reproductive rates. To achieve that, we have incorporated empirical data from
47 three intersexed populations of *E. marinus* into a population dynamic model. The original model
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1 was calibrated and validated for a stable population without intersexuality and sex ratio ~ 1 . In
2 the present version, the model includes an extra group, intersex females, but the total sum of
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4 flow rates from juveniles to adult groups was kept the same as in the original model to respect
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6 the previous validation. In these circumstances, results indicate that the male-biased population
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8 is very sensitive to intersexuality, even at low incidence levels, and exhibits significant density
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10 decrease through time if conditions do not change. On the contrary, the two *E. marinus*
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12 populations with a preponderance of female-biased sex ratios, low or moderate intersexuality
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14 incidence (up to an average value of 9% of the population) and with intersex reproductive rates
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16 corresponding to 80% the value of normal specimens, exhibit long-term persistence.
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19 The model is highly sensitive to adult female parameters (e.g. mortality), indicating that small
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21 variations on its values can significantly change population responses.
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24 Overall the present results suggest that, in spite the costs of intersexuality in *E. marinus*, the
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26 temporal variation of intersexed populations seems to depend on intersex incidence level, sex
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28 ratio fluctuations and reproductive output of intersexes. Simulations also suggest that other
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30 population processes (e.g. mortality rates of normal females) may play important roles in the
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32 maintenance of populations with intersexuality.
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41 Key-words: amphipod, intersexuality, reproductive disorders, reduced fitness, sex ratio,
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43 population-level effects, mathematical model
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49 **1. Introduction**

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51 Intersexuality is the occurrence, in dioecous species, of individuals that possess both male and
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53 female sexual characteristics (Kelly et al., 2004). The causes of intersexuality in Crustacea are
54
55 not yet fully understood but they seem to be due to different factors, such as chemical
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57 contamination (e.g. Takahashi et al., 2000; Olmstead and Leblanc, 2007), incomplete
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59 feminisation caused by microsporidian parasites (Kelly et al., 2002) or environmental sex
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determination (ESD) (Dunn et al., 1996, 2005). In a recent study carried out at distinct places in
relation to environmental quality, Ford et al. (2006) suggested that, at anthropogenic impacted
sites, the probable cause of intersexuality was parasitism, which seem to be enhanced by
pollution, while ESD was suggested as the possible cause of intersexuality at the reference
locations. Although the causes of intersexuality seem multi-factorial and complex to determine,
the decreased reproductive fitness of intersexes is a well-known consequence in several species
(Jobling et al., 2002; Kelly et al., 2004). Intersex individuals of *E. marinus* suffer from reduced
fecundity and fertility and mature at a larger size compared to normal specimens (Ford et al.,
2003; 2004b). It has also been suggested that the increased size and morphological abnormalities
of intersexes may result in reduced pairing success (Kelly et al., 2004; Ford et al., 2004). Thus,
accordingly to the sex allocation theory (Charnov, 1982), intersexes should be selected against,
which is somehow contradictory with the frequent finding of intersexes in some natural
populations (Ford and Glazier, 2008). This suggests that other processes are involved and
confirms our limited knowledge of the consequences of intersexuality and the underlying
processes.

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Population dynamic models are suitable tools to incorporate individual fitness costs and assess
effects at the population level (Martins et al., 2002). This approach has been previously applied
to intersexed populations of *E. marinus* (Ford et al., 2007) and aimed to assess the effects of
varying levels of intersexuality and phenotypes on population response. Although this work was
important, as it was one of the first attempts to extrapolate individual-level effects to the
population-level, it relied on theoretical values of intersexuality incidence, normal and intersex
phenotypes proportions with a consequent narrow practical application.

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The aim of the present work is to simulate the density variation of real populations of *E. marinus*
with different intersexuality incidence, proportions of phenotypes and intersex female
reproductive rates. To achieve that, we have incorporated empirical data from three intersexed
populations of *E. marinus* into a population dynamic model. It is expected that results from this

1 type of approach will help us to understand the mid- to long-term consequences of intersexuality
2 in natural populations.
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6 7 **2. Materials and Methods**

8 9 *2.1. Model description*

10 The model used in this study is based on a previously calibrated and validated model for a
11 population of *E. marinus* with long-term stability, average sex ratio of 1 and without
12 intersexuality (Martins et al., 2002). The new version of the model incorporates intersex females
13 into the original structure of the model (Fig. 1) and accounts for phenotype variations (i.e.
14 proportion of normal males, normal females and intersex females) in accordance to values
15 obtained for three different Scottish populations between spring 2002 and spring 2003.
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26 Model state variables are juveniles, immature females, adult females, intersex females and
27 males in abundance (number of individuals m^{-2}). Intersex males were not included in the model
28 because 1) in the considered populations, intersex males correspond only to 3% of the population
29 and 2) empirical values of the costs of intersexuality in males are difficult to obtain.
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36 The model accounts for growth and mortality of all population groups and reproduction of
37 females. Due to lack of empirical data, the mortality rate of intersex females was considered
38 equal to the mortality rate of normal females.
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43 The weight of females is also accounted in the model because female reproduction rate depends
44 on their size. Female's weight is calculated on a dynamic way through the biomass calculation
45 module of the model (Martins et al., 2002), which follows a modified Von Bertalanffy (1957)
46 model and accounts for a temperature regulating factor (Table 1). At each sampling site, the
47 reproduction rate of intersex females was obtained in relation to the reproduction rate of normal
48 females, which was accounted in the model.
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2.2. Data sets

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2 Data sets used to extract the parameters to incorporate into the model were obtained between
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4 spring 2002 and spring 2003, at three sampling sites within the Firth of Forth (Scotland):
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6 Dunbar, Torry Bay and Inverkeithing Bay (Ford et al., 2006). Sex ratio was calculated as the
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8 number of males by the total number of females (normal and intersex females).
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11 The population of *E. marinus* at Dunbar exhibited the lowest incidence of intersex females
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13 corresponding to $5.4\% \pm 1.8$ (average \pm standard deviation) and, during the sampling period, this
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15 population was always male-biased, with normal females representing less than 41% of the
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17 population. As a consequence, this population exhibited the highest sex ratios, ranging from 1.1
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19 to 1.6 (Fig. 2). Intersex females presented, on average, 11.9% less reproductive output than
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21 normal females (extrapolated from Ford, 2004).
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25 *E. marinus* population at Torry Bay exhibited a proportion of intersex females corresponding to
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27 $7.2\% \pm 3$ of the population and the population was always female-biased, with sex ratios ranging
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29 between 0.29 and 0.84 (Fig. 2). Intersex females presented about 21.6% less reproductive output
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31 than normal females (extrapolated from Ford, 2004).
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35 The incidence of female intersexuality was the highest at Inverkeithing Bay, corresponding to
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37 $9.2\% \pm 5.2$ of the population and, except during winter, the population was always female-biased
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39 with a sex ratio variation between 0.32 and 1.19 (Fig. 2). Intersex females showed 19% less
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41 reproductive output than normal females (extrapolated from Ford, 2004).
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2.3. Re-calibration and sensitivity analysis

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51 In the original model, the flow units between population groups, corresponding to number of
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53 individuals $\text{m}^{-2} \text{d}^{-1}$, were calibrated in accordance to original empirical data (Maranhão et al.,
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55 2001; Maranhão and Marques, 2003). In the present version of the model, these parameters were
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57 re-calibrated until the proportion of phenotypes output by the model matched the observed
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59 proportion of phenotypes at each one of the three sampling sites (Table 2), corresponding to
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1 three different re-calibrations according to phenotype variation observed at Dunbar, Torry Bay
2 and Inverkeithing Bay, respectively.
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4 The present version of the model includes one extra state variable than the original version,
5 corresponding to intersex females. Consequently, this version also includes one extra flow
6 between groups corresponding to the flow of individuals from immature females to intersex
7 females (t_4 in Fig. 1). Nevertheless, to keep the balance of the present version in accordance to
8 the original validation, the total sum of flow rates between population groups was kept equal to
9 the original version of the model.
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18 Long-term scenarios (~ 5 years) of the three studied populations assumed that, for the entire
19 simulation period, the populations exhibited the same seasonal phenotype variation,
20 intersexuality incidence and reproductive rates as observed within the studied periods at Dunbar,
21 Torry Bay and Inverkeithing Bay. The variation of intersexuality incidence and sex ratio used to
22 force the model at the three simulated scenarios is shown in figure 3. These simulations were
23 hereafter designated as scenario D, T and I, respectively.
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33 The sensitivity of model responses to variations on intersex incidence, sex ratio fluctuations,
34 reproduction rate of intersex females and mortality rate of normal and intersex females was
35 assessed (Table 3).
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41 The model was written and run with Stella software version 7.0.3 (High Performance Systems,
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48 **3. Results**

49 Results indicate that *E. marinus* populations with male-biased sex ratios, average intersexuality
50 incidence of 5.4% and a reproductive output rate of intersexes 12% lower than that of normal
51 specimens show a significant decrease throughout time (Fig. 4). On the contrary, *E. marinus*
52 populations with intersexuality incidence between 7.2-9.2%, a reproductive output
53 corresponding to ~ 80% the value of normal specimens and with a preponderance of female-
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biased sex ratios show long-term persistence and with a tendency for population density increase (Fig. 4). As expected, predictions change if conditions differ. For example, in the case of scenario D, population density shows a more stable tendency, if sex ratio presents stronger seasonal fluctuations with periods where the population is female-biased (Fig. 5A). On the contrary, *E. marinus* population at scenario T starts gradually decreasing if intersexuality incidence increases to 19% or intersex reproductive output decreases to 54% the rate of normal specimens (Fig. 5B). In scenario I, *E. marinus* density starts decreasing when intersexuality reaches 15% of the population or intersex reproductive output decreases to 34% the rate of normal specimens (Fig. 5C). *E. marinus* population at scenario I is more sensitive to variations on intersexuality incidence and reproduction rate of intersexes than population at scenario T because the population at scenario T is more strongly female-biased.

Sensitivity analysis indicates that the model is very sensitive to juvenile- and normal female-related parameters. For instance, at scenario D, if normal female mortality decreases to 10% of the basic run value, the population density increases in the long-term even with male biased sex ratios (Fig. 6).

4. Discussion

In this work, we have used parameters obtained from real populations of *E. marinus* and incorporated them into a previously validated model, thus, the present results must be interpreted as the immediate effects of intersexuality on stable *E. marinus* populations without intersexuality and with average sex ratio ~ 1 .

According to results, *E. marinus* populations with male-biased sex-ratios are quite sensitive to female intersexuality, even at low incidence levels, unless certain processes take place (e.g. decreased mortality rate of females), which would compensate for the lower number of females compared to males. Recently, Ford and Glazier (2008) reported a population of freshwater amphipods (*Gammarus minus*) with male-biased sex ratios and intersexuality. Population

1 mechanisms that allow the maintenance of populations with such unusual characteristics are still
2 unknown, but previous reports confirm the viability and stability of these populations for
3 decades (Miller and Buikema, 1976; Buikema et al., 1980), thus, it seems that male-biased sex
4 ratios and intersexuality may co-exist in viable populations.
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9 The present results also indicate that sex ratio fluctuations, which cause the population to be
10 female-biased during certain periods of the year, can counteract the decreasing tendency
11 observed in the population at scenario D. It is well known that environmental parameters, such as
12 temperature and photoperiod can control the sex ratio in some species of amphipods (Watt and
13 Adams, 1993; Naylor et al., 1998; Dunn et al., 2005). In the case of *E. marinus* populations
14 monthly and yearly sex ratio fluctuations are frequently observed (Vlasblom, 1969). This
15 indicates that, at least in certain periods, sex ratio variation can favour females in amphipod
16 populations.
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29 The present results also indicate that intersexed female-biased populations of *E. marinus* are
30 viable and can even exhibit an increasing density tendency for moderate intersex incidence
31 (<14%) and if the reproduction rate of intersex females is not considerably lower than that of
32 normal females (not lower than 54%). According to results, more strongly female-biased
33 populations are less sensitive to increases on intersexuality incidence or decreases on the
34 reproduction rate of intersexes. In general, intersex populations of *E. marinus* tend to be female-
35 biased, which seems to be caused by microsporidian parasites that can be simultaneously the
36 cause of intersexuality and female-biased sex ratios in certain populations (Ford et al., 2006).
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48 It is expected that, above a certain threshold, sex ratio distortion leads to population extinction.
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51 In cases of female-biased populations, if males become too rare to maintain the population
52 through reproduction, the populations will collapse (Hatcher et al., 1999). In the future, it would
53 be useful to determine the minimum male to female ratio which allows viable populations of *E.*
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marines and include it in population models.

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Besides sex ratio, the reproduction rate of intersex females is another process affecting the maintenance of intersexed populations. If the output rate of intersex females is much lower than that of normal females, then the populations will be more sensitive to intersexuality even if the sex ratio remains female-biased. Apparently, in some species, intersex females do not present a lower fecundity rate than normal females (Ladewig et al., 2007). However, this is not the case of *E. marinus*, where the reproductive rate of intersexed females is significantly lower than the rate of normal females (20% on average), particularly, in more polluted and impacted sites (Ford et al., 2003; 2004b). Thus, although a general cause-effect between pollution and intersexuality has not been established (Ford et al., 2006), intersexed populations of *E. marinus* from polluted sites may be at a higher risk due to lower reproduction rates of both of normal and intersex females among other factors (Ford et al., 2003).

The present simulations corroborate, in general, the simulations of our previous theoretical approach (Ford et al., 2007) but they have brought more understanding to, at least, some of the underlying processes which seem to occur in intersexed populations and to regulate their variation.

Overall, the present results indicate that the survivorship of intersexed populations of *E. marinus* will not depend only on the incidence level of intersexuality but instead it seems to be regulated by a set of different factors, whereby the incidence of intersexuality, sex ratio and reproduction rate of intersexes seem to play important roles.

In highlighting the sensitivity of amphipod populations to changes in sex ratios, fecundity and the incidence of intersexuality, the model also emphasises the potential effect changes in the climate and that of pollutants could have on population dynamics with plasticity in their sex determination. The speed that populations respond genetically may ultimately dictate how populations can adapt to anthropogenic changes in their environment.

Acknowledgements

This work was funded by CRUP – The Board of Rectors from Portuguese Universities, by the British Council within the Treaty of Windsor Anglo-Portuguese Joint Research Programme (AI-B/05), IMAR – The Institute of Marine Research, Coimbra Interdisciplinary Centre and by Napier University, UK.

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Figure 1- Simplified conceptual diagram of the model. The model has 5 state variables: *Juveniles, males, immature females, adult females* and *intersex females* expressed as individuals m^{-2} (ind m^{-2}). $m_{1,2,3,4,5}$ - mortality rates; $t_{1,2,3,4}$ - flow rates of individuals between groups; ra - reproduction rate of adult females; ri - reproduction rate of intersex females. Rate units correspond to ind $m^{-2} d^{-1}$. The dash line indicates that ri is calculated as a proportion of ra according to Ford (2004). Temperature and salinity are the forcing functions that regulate reproduction and growth (not shown).

Figure 2- Observed variation of intersexuality incidence (A) and sex ratio (B) of *Echinogammarus marinus* populations at study sites: Dunbar (●), Torry Bay (○) and Inverkeithing Bay (▼) during Spring and Summer 2002, Winter and Spring 2003.

Figure 3- Imposed variation of intersexuality incidence (A) and sex ratio (B) at scenario D (solid), T (dotted) and I (dash)

Figure 4- Long-term variation of *Echinogammarus marinus* density (ind m^{-2}) at scenario D (solid), T (dotted) and I (dash)

Figure 5- Long-term variation of *Echinogammarus marinus* density (ind m^{-2}) at the three scenarios under different conditions. A- Scenario D with sex ratio fluctuations (solid line), population density (dash line), B- Scenario T with higher intersexuality (solid line) or low reproduction output of intersexes (dash line), C- Scenario I with higher intersexuality (solid line) or low reproduction output of intersexes (dash line).

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Figure 6- Long-term variation of *Echinogammarus marinus* density at scenario D (**dash line**) with male biased sex ratios (**solid line**) and lower mortality rate of normal adult females. In these circumstances, the population exhibits long-term stability.

ACCEPTED MANUSCRIPT

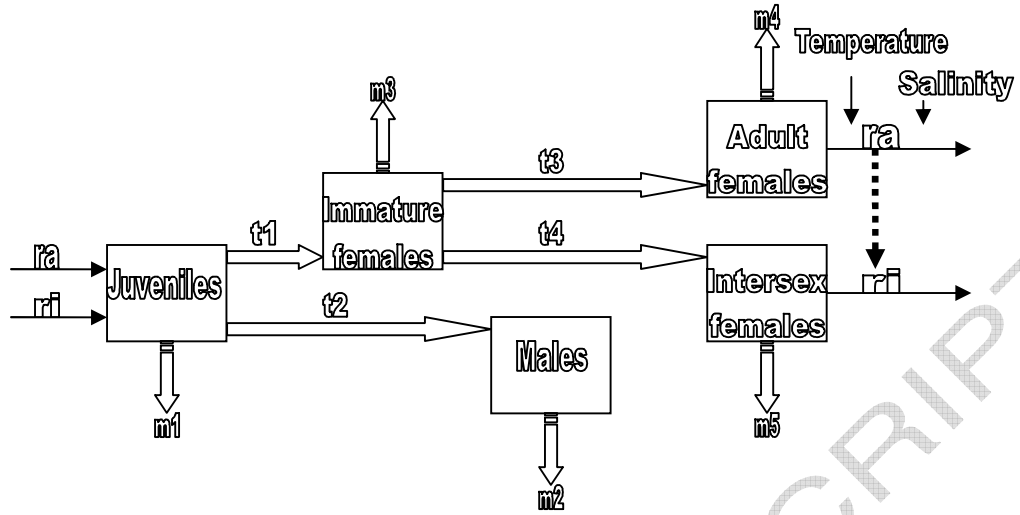


Figure 1

Figure 2

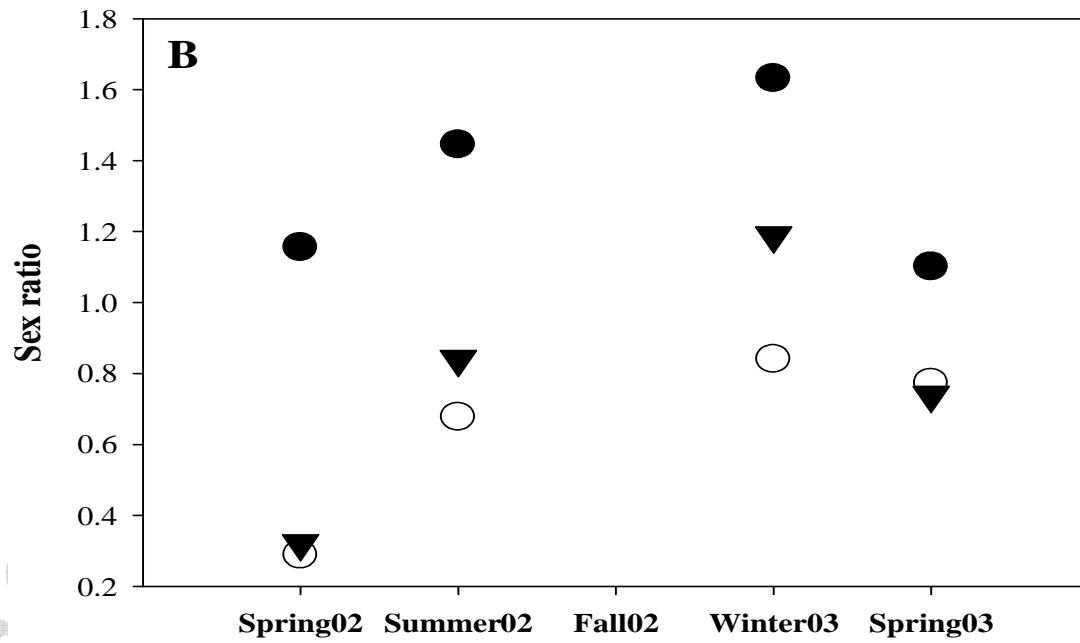
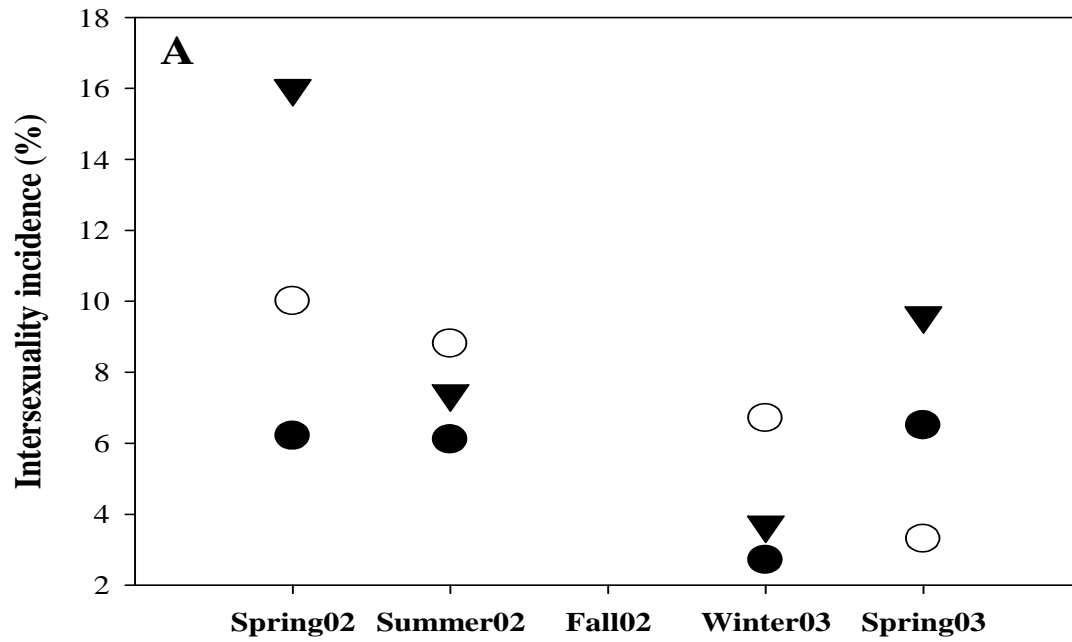


Figure 3

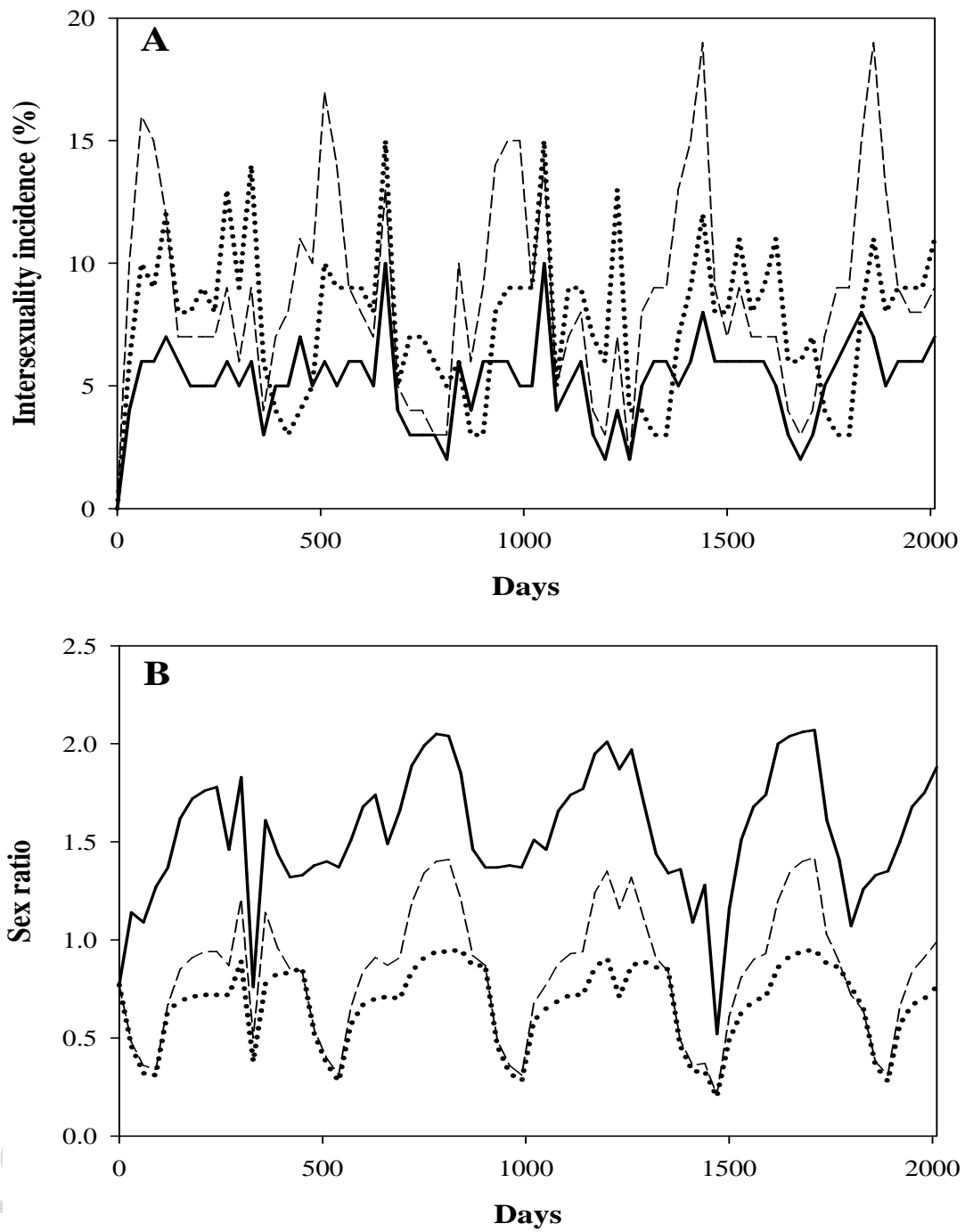


Figure 4

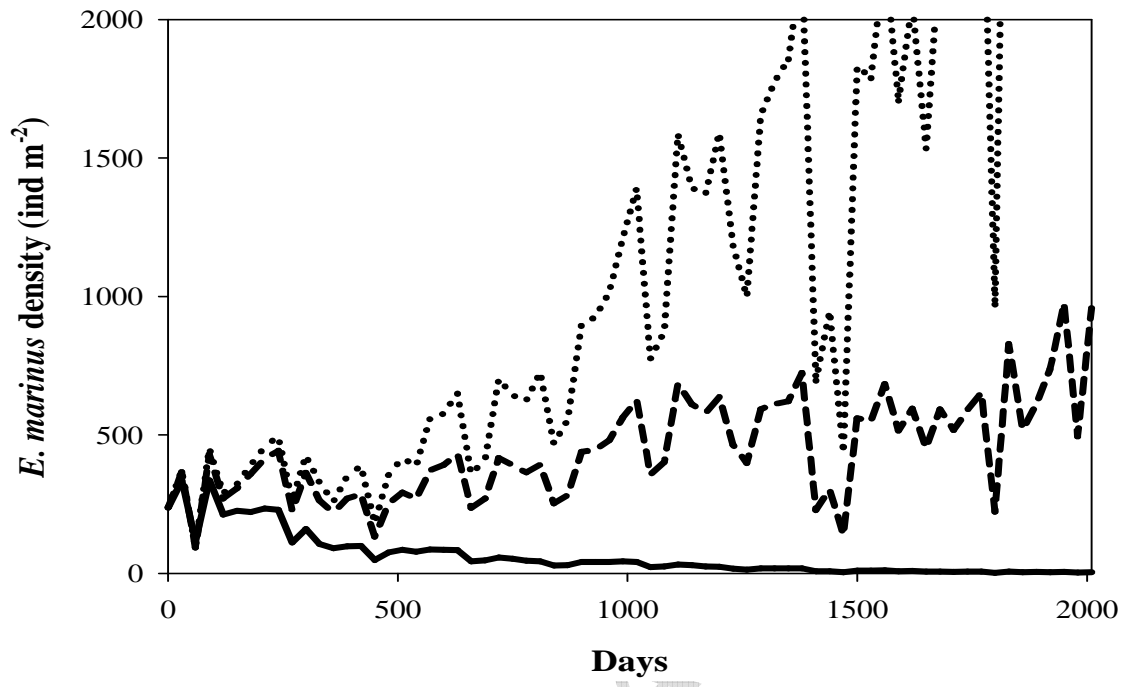


Figure 5

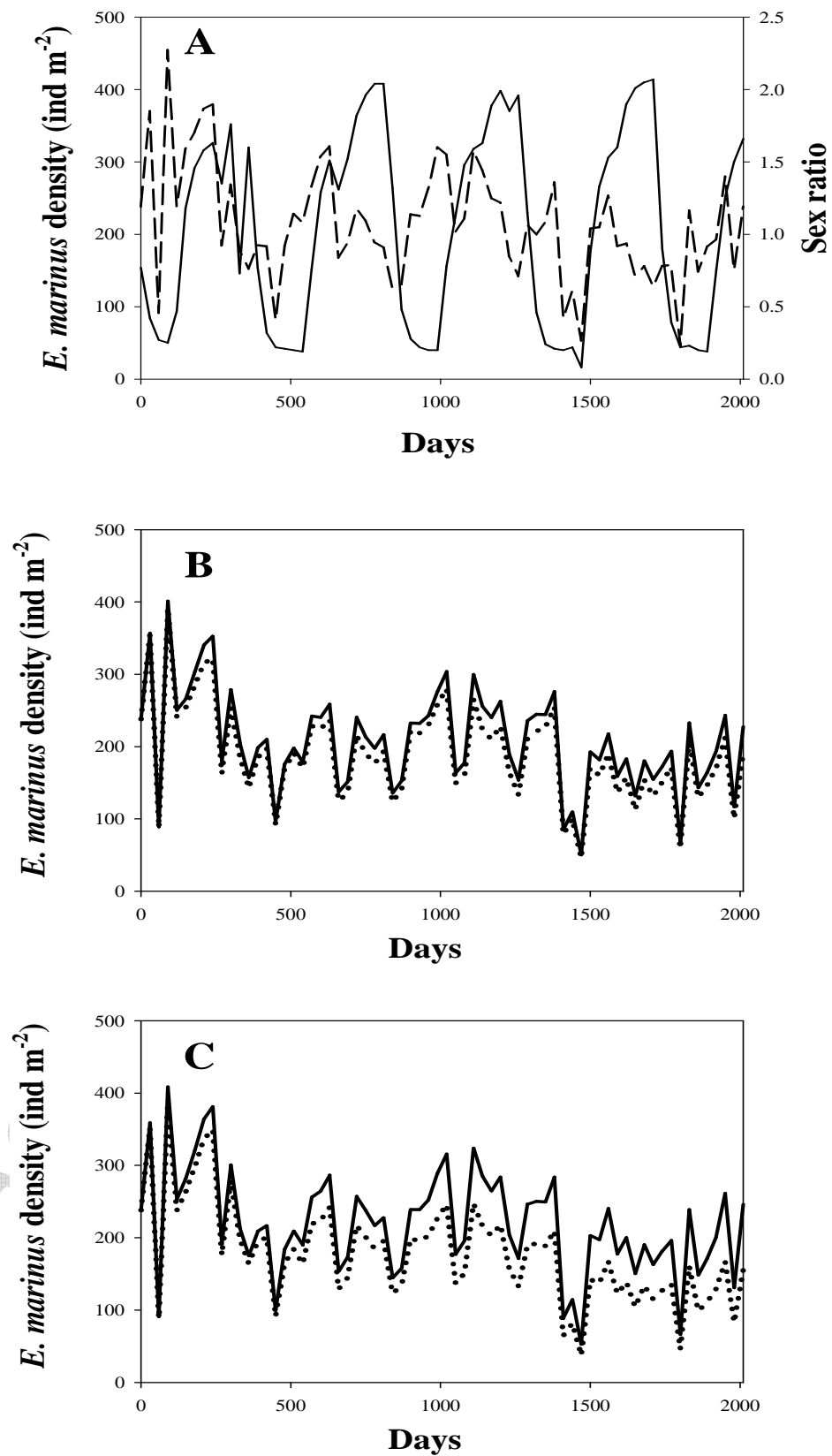


Figure 6

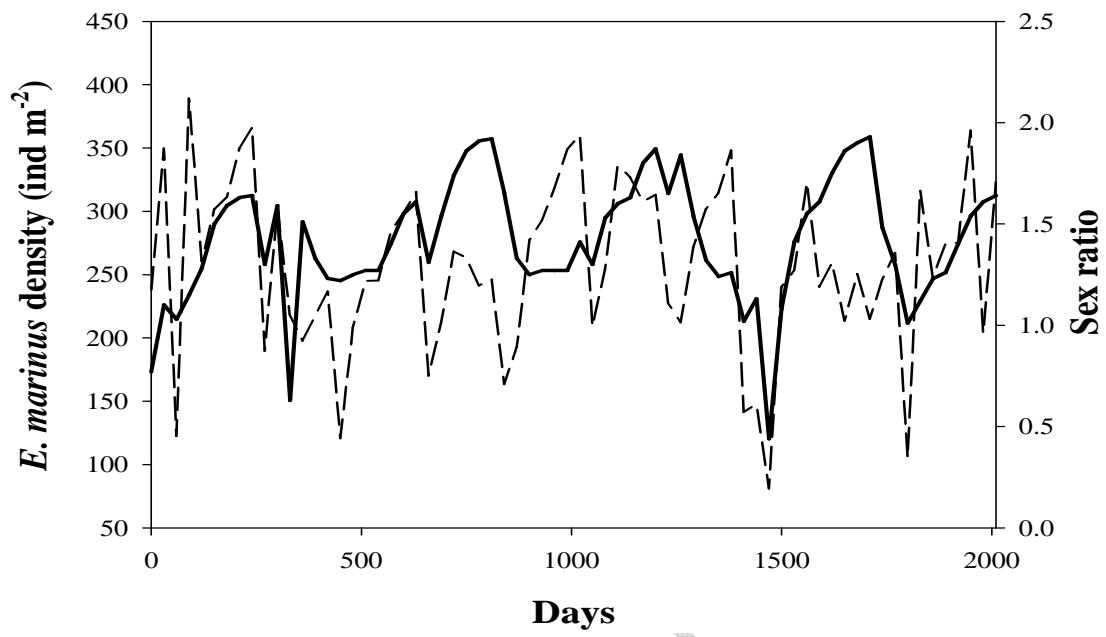


Table 1- Main equations of the model. Juv- juveniles, FIm- immature females, FA- adult females, FInt- intersex females, Male- males, R- recruitment, mort- mortality, t- transfer of individuals from one population group to the next, AvW- average weight, W_{i-1} - weight at the beginning of the population group i, W_i - weight at the end of population group i, $days_{i-1,i}$ - average duration of a certain population group, W- weight, CL- cephalic length, h- anabolism parameter, k- catabolism parameter, f(T)- temperature factor, t- time (for a better explanation of the biomass calculation module see Martins et al., 2002).

$\frac{dJuv}{dt} = r_A + r_I - m_1 - t_1 - t_2$	Variation of juvenile density per unit of time
$\frac{dF Im}{dt} = t_1 - m_3 - t_3 - t_4$	Variation of immature female density per unit of time
$\frac{dMale}{dt} = t_2 - m_2$	Variation of male density per unit of time
$\frac{dFA}{dt} = t_3 - m_4$	Variation of adult female density per unit of time
$\frac{dFInt}{dt} = t_4 - m_{5t}$	Variation of intersex female density per unit of time
$AvW = \frac{W_{i-1} + W_i}{2}$	Average weight of population groups
$W_i = W_{i-1} + f(T) \times days_{i-1,i} \times (h \times W_{i-1}^{2/3} - k \times W_{i-1})$	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
$f(T) = \left(\frac{T}{T_{opt}}\right)^{2.5} \times e^{\left(1 - \left(\frac{T}{T_{opt}}\right)^{2.5}\right)}$ for $T < T_{opt}$ $f(T) = 1 - \left(\frac{T - T_{opt}}{T_{max} - T_{opt}}\right)^2$ for $T \geq T_{max}$	Temperature –dependency function for growth

<p>$NBJ = 0$ for salinity ≤ 4</p> <p>$NBJ = -70.3 + 62.8 \times CL_{FA}$ for temp. < 15</p> <p>$NBJ = -50.4 + 44.8 \times CL_{FA}$ for temp. ≥ 15 and < 23</p> <p>$NBJ = -11.7 + 12.2 \times CL_{FA}$ for temp. ≥ 23</p>	<p>Number of new-born juveniles as a function of salinity, temperature and normal adult female's cephalic length</p>
<p>$r_a = NBJ \times 0.0291 \times FA$</p>	<p>Reproduction rate of adult females</p>
<p>$r_i = NBJ \times 0.025637 \times FInt$ for Dunbar</p> <p>$r_i = NBJ \times 0.022814 \times FInt$ for Torry</p> <p>$r_i = NBJ \times 0.023629 \times FInt$ for Inverkeithing</p>	<p>Reproduction rate of intersex females at the three sites calculated according to a % of decrease relatively to 0.0291</p>
<p>$m_i = m_i \times D_i$</p>	<p>Mortality rate of spopulation groups $_i$ as a function of density</p>

Table 2 – Observed and simulated phenotype variation (%) for *E. marinus* populations at the three studied sites and during the study periods. Observed values were obtained by Ford et al. (2006). Simulated values were obtained after re-calibration of the model (see text for explanation).

Sites/season	Phenotypes	Observed	Simulated
Dunbar – Spring 2002	male	53.6	53.6
	normal female	40.2	40.3
	intersex female	6.2	6.1
Summer 2002	male	59.1	59.1
	normal female	34.8	34.9
	intersex female	6.1	6.1
Winter 2002/03	male	62	62.1
	normal female	35.3	35.3
	intersex female	2.7	2.7
Spring 2003	male	52.4	52.2
	normal female	41.1	41.3
	intersex female	6.5	6.5
Torry Bay – Spring 2002	male	22.4	22.2
	normal female	67.7	67.8
	intersex female	10	10.0
Summer 2002	male	40.3	40.3
	normal female	50.7	50.9
	intersex female	8.8	8.8
Winter 2002/03	male	45.7	45.8
	normal female	47.7	47.7
	intersex female	6.7	6.5
Spring 2003	male	43.6	43.6
	normal female	53.1	53.1
	intersex female	3.3	3.3
Inverkeithing Bay – Spring 2002	male	24.3	23.9
	normal female	59.7	60.1
	intersex female	16	16.1
Summer 2002	male	45.7	45.9
	normal female	47	46.8
	intersex female	7.4	7.4
Winter 2002/03	male	54.3	54.4
	normal female	42	41.9
	intersex female	3.7	3.7
Spring 2003	male	42.5	42.5
	normal female	47.9	47.9
	intersex female	9.6	9.6

Table 3 – Sensitivity (*sensu* Jørgensen, 1994) of the population density to $\pm 10\%$ variations on mortality parameters at the three considered scenarios. m1- juvenile mortality, m2- male mortality, m3- immature female mortality, m4- adult female mortality and m5- intersex female mortality.

Parameter	Variation	Sensitivity Scenario D	Sensitivity Scenario T	Sensitivity Scenario I
m1	+10%	-2.2	-3.2	-3.0
	-10%	+2.0	+2.8	+2.7
m2	+10%	-0.2	-0.1	-0.1
	-10%	+0.3	+0.1	+0.2
m3	+10%	-1.2	-1.5	-1.5
	-10%	+1.2	+1.4	+1.4
m4	+10%	-1.9	-2.7	-2.3
	-10%	+1.8	+2.3	+2.1
m5	+10%	-0.6	-0.7	-0.8
	-10%	+0.7	+0.7	+0.9