Population dynamics of *Cyathura carinata* (Isopoda) in a eutrophic temperate estuary

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**Abstract**

From January 1993 to September 1995, *Cyathura carinata* was a target species of a monitoring programme carried in the Mondego Estuary (Portugal). Being one of the key species of the intertidal mud flats, this isopod was found to be most abundant in a eutrophic area, where seasonal macroalgal blooms usually occur. Its density decreased towards downstream areas, where some *Zostera noltii* beds exist. At the Mondego Estuary, the present work stated that *C. carinata*: (a) had a 2-year life span, even though, 80–90% of the individuals died when 1 year old, revealing a strong post-reproduction mortality; (b) produced a single cohort per year; (c) showed continuous growth (with lower rates during winter); (d) evidenced protogynous hermaphroditism and (e) presented a high growth production and a low turnover ratio. A latitudinal gradient reflected in the life features of *C. carinata* was described.

Except for the life span and the frequency of reproduction, which are generally valid for all populations, *C. carinata* from the Mondego Estuary fitted the characteristics of other populations from the south of Europe. The effects of macroalgal blooms were assessed. *Cyathura carinata* seemed to temporarily benefit from the presence of macroalgae, due to higher energy resources and more efficient protection against predators. In a long term, algal blooms had negative consequences. It was particularly evident on the recruitment success, which had repercussions in population abundance, and on the secondary production. Therefore, repeated events of algal blooms embracing the distribution areas of *C. carinata* represent a threat to this species in eutrophic estuaries.

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**Keywords:** *Cyathura carinata*; eutrophication; isopod; macroalgal bloom; population dynamics; secondary production

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**1. Introduction**

Similar to other coastal systems worldwide (Everett, 1994; Norkko and Bonsdorff, 1996a,b; McMahon and Walker, 1998; Beukema et al., 1999; Norkko et al., 2000; Wooldridge and Callahan, 2000; Sfriso et al., 2001), the Mondego Estuary has been undergoing a eutrophication process (Marques et al., 1997, 2003; Martins et al., 1997, 2001; Pardal et al., 2000, 2004; Cardoso et al., 2002; 2004; Dolbeth et al., 2003). Apart from supporting several industries, this small temperate intertidal estuarine system (1600 ha) receives an agricultural run-off from 15000 ha of cultivated land (mostly rice and corn fields), upstream of its location. During the last 2 decades, there has been a seasonal proliferation of opportunistic green macroalgal species (e.g. *Ulva* sp.), parallel to a severe reduction of *Zostera noltii* beds, the richest habitats concerning productivity and biodiversity (Marques et al., 1997; Martins et al., 2001; Dolbeth et al., 2003; Cardoso et al., 2004).

*Cyathura carinata* (Kroyer, 1847) is an estuarine tubicolous isopod, widely distributed along the Atlantic coasts of Europe (Cléret, 1960; Legrand and Juchault, 1963; Amanieu, 1969; Bamber, 1985; Köhn and Sammour, 1990; Sola and Arzubialde, 1993; Marques et al., 1994), Baltic (Muus, 1967; Jażdżewski, 1969;
Wägele, 1979; Ólafsson and Persson, 1986) and Mediterranean Seas (Argano, 1979). Previous studies about the macrobenthic community structure in the Mondego Estuary revealed C. carinata as one of the most abundant species, both in terms of density and biomass. Thus, the population dynamics of this isopod was studied during a 1-year period (Marques et al., 1994) and a population dynamics model was elaborated (Martins et al., 1997). The main objective of the present work is to follow the evolution of C. carinata's population in relation to the eutrophication processes occurring in the estuary. Also, it is intended to gather all the information about this species, most of it published until the middle 1980s, and compare it with the few recent publications. So, a long monitoring programme of 32 months was carried out, in order to: (a) clarify some of the questions raised by different authors, especially those that caused divergence of opinions, such as life span, recruitment frequency and evidence of protogenous hermaphroditism (a process by which some females sex reverse into males); (b) to evaluate the effects of macroalgal blooms on population dynamics, biology and production and (c) to assess if eutrophication processes may endanger the presence of this species in affected estuaries.

2. Materials and methods

2.1. Study site and field programme

The south arm of the Mondego Estuary (Fig. 1) is a shallow water system (2–4 m deep in high tide, with a tidal range of 1–3 m), where Zostera noltii beds covered most part of the intertidal areas more than 3 decades ago. Three different study locations were established along a spatial gradient, according to different eutrophication symptoms (Fig. 1). (a) The eutrophic area, a sandy mudflat in the inner parts of the estuary, from where Z. noltii disappeared without trace more than 25 years ago and where seasonal green macroalgal blooms occur (Ulva sp.). This site is characterised by higher total inorganic nitrogen concentrations of the water (30–50 µmol N l⁻¹) and lower salinity values (15.0–25.0), water-flow velocities (0.8–1.2 m s⁻¹) and organic matter content of the sediment (3.7 ± 1.0%, mean ± S.D.). (b) The intermediate area, located in the middle section, is a mudflat that had Z. noltii coverage until 5 years prior to this study, where some rhizomes could be found still. Its physical–chemical conditions are relatively similar to the third area. (c) The Z. noltii beds, located downstream, correspond to a relatively non-eutrophic area. This site is characterised by lower total inorganic nitrogen concentrations of the water (15–30 µmol N l⁻¹) and higher salinity values (20.0–30.0), water-flow velocities (1.2–1.4 m s⁻¹) and organic matter content of the sediment (6.8 ± 1.0%, mean ± S.D.) (Martins et al., 2001).

Sampling was carried out from January 1993 to September 1995. Random samples were collected fortnightly in the first 18 months and monthly thereafter. For every sampling date, at each station, temperature, salinity, pH and dissolved oxygen were measured in situ, in low water pools. At each study area, 6–10 cores (13.5 cm diameter) were taken to a depth of 15 cm, washed over a 0.5 mm mesh sieve and preserved in 4% buffered formalin. Later, animals were separated and kept in 70% ethanol. Sorted plant material from all the cores (Chlorophyceae and Zostera noltii leaves and rhizomes) was dried during 48 h at 60 °C and weighed. Afterwards, the ash free dry weight (AFDW) was determined by loss on ignition (8 h at 450 °C).

2.2. Laboratory procedures

Cyathura carinata individuals were counted, measured for cephalic length and sexed, according to previous literature (Cléret, 1960; Bamber, 1985; Ólafsson and Persson, 1986; Marques et al., 1994). Total body length (mm) and biomass (g of AFDW) of each individual were determined from cephalic length using regression models (total body length = 0.745133 + 9.01010 × cephalic length, \( r^2 = 0.968521 \), \( N = 115 \) and biomass = 0.0190549 × cephalic length\(^2 \), \( r^2 = 0.964352 \), \( N = 800 \)) established by Marques et al. (1994).

Embryos were removed from gravid females, counted, measured and classified in 3 developmental stages, according to literature (Jazdewski, 1969; Bamber, 1985; Ólafsson and Persson, 1986; Marques et al., 1994): (a) stage A, corresponding to oval homogeneous embryos, recently laid; (b) stage B, referring to elongated embryos, sometimes with pereiopods and antennae already identifiable; and (c) stage C, indicating newly
hatched juveniles still inside the brood pouch of the female.

2.3. Statistical analysis

Multiple regression models were developed to relate the variation of *Cyathura carinata* density, biomass and abundance of juveniles with physical–chemical factors and vegetation biomass. The variables were subjected to suitable transformations, when necessary, to fulfil required assumptions of homocedasticity and normality of the data (Zar, 1996). The *C. carinata* population structure was defined by tracking recognisable cohorts from successive sampling dates through size–frequency distribution analysis, performed by ANAMOD software, based on the probability paper method (Cassie, 1954). Reliability was checked by application of $\chi^2$ and $G$ tests ($P = 0.05$).

The equation of Gaschütz et al. (1980) was used to express field growth rates because it takes into account seasonal variations. It is expressed as: $L_t = L_\infty(1 - \exp(-(kD(t-t_0) + C(kD/2\pi)\sin 2\pi(t-t_0)))1/D$, where $L_t$ is the length of the organism at a given moment $t$; $L_\infty$ the maximum possible length of the organism; $t_0$ the instant when the organism would have a length equal to 0; $t_s$ the time interval between the start of growth (when $t = 0$) and the first growth oscillation, being growth expressed by a sine curve with a 1-year period; $k$ the intrinsic growth rate; $C$ the parameter in which the values can range from 0 to 1, depending on the species; and $D$ the parameter that expresses metabolic deviations from the von Bertalanffy’s 2/3 rule.

Annual production estimates were based upon cohort recognition. The values of $P$ for the population followed the procedures and techniques used by Pardal et al. (2000), Cardoso et al. (2002) and Dolbeth et al. (2003), expressed as: $P = \sum_{n=1}^{N} P_c$, where $P_c$ is the growth production of a cohort $n$. The mean population biomass $B$ was calculated as: $B = (1/T) \sum_{n=1}^{N} B_n$, where $T$ is the period of study; $N$ the number of cohorts in the period $T$; $B_n$ the mean biomass of the cohort $n$ and $t$ the duration of that same cohort.

3. Results

3.1. Macroalgae and macrophyte biomass

Based on the green macroalgal biomass at the eutrophic area (Fig. 2a), there were differences between the spring periods from the 3 sampled years. During the first 6 months of 1993, there was a biomass increase, characteristic of a spring bloom (reaching 452 ± 118 g m⁻² AFDW, mean ± S.E.), followed by its sudden disappearance in late June (algal crash). In contrast, no algal development was observed in 1994.

The following year was an intermediate situation, in which the macroalgal biomass reached 111 ± 55 g m⁻² AFDW (mean ± S.E.). Along the south arm of the estuary, green macroalgae were especially abundant in the eutrophic area, decreasing towards *Zostera noltii* beds. The intermediate area (Fig. 2b) showed proportionally small abundance of green macroalgae, during the 3 consecutive years. In the downstream area, *Z. noltii* biomass gradually decreased throughout the entire period (Fig. 2c). Even so, it was possible to discern a seasonal pattern, in which the total biomass depended mostly on the growth of leaves during spring and summer, with rhizome biomass becoming dominant during autumn and winter.

3.2. Spatial distribution and abundance

*Cyathura carinata* densities varied spatially, being most abundant at the eutrophic area (1851 ± 169 ind. m⁻², mean ± S.E.) (Fig. 2a). The annual variation pattern was...
very regular. Maximum values were always achieved during autumn, declining continuously until late spring. Inter-annual differences mostly concerned autumn maxima of each year. In 1993 and 1995, when macroalgae occurred, the maxima densities (respectively 3759 ± 319 and 3475 ± 884 ind. m\(^{-2}\), mean ± S.E.) were lower than in 1994 (5518 ± 470 ind. m\(^{-2}\), mean ± S.E.), when there was no algal development. Moreover, the initial density of 1993 (3397 ± 202 ind. m\(^{-2}\), mean ± S.E.) was very close to the autumnal maximum of that year, when the population was already in decline, according to the density pattern.

The intermediate (Fig. 2b) and downstream (Fig. 2c) areas recorded lower densities (172 ± 24 and 172 ± 34 ind. m\(^{-2}\), mean ± S.E., respectively). Indeed, Cyathura carinata was totally absent from Zostera noltii beds in the beginning of 1993. Nevertheless, density increased almost constantly throughout the study period, reaching the highest value of 851 ± 255 ind. m\(^{-2}\) (mean ± S.E.) in June 1995.

3.3. Population structure, growth and life span

Size–frequency polymodal distributions were analysed for recognisable cohorts (Fig. 3), taking only into account data from the eutrophic area (in fact, the methodology used could not be applied to the data sets from the other two areas, due to low abundances). It was possible to recognise 5 cohorts and establish that the population recruits only once a year (Fig. 4a). This observation is supported by the appearance of newly born cohorts, respectively C\(_1\), C\(_2\) and C\(_5\), around June each year. Therefore, it seems reasonable to assume that cohorts C\(_1\) and C\(_2\) resulted from recruitments that took place in 1991 and 1992. The population life span was estimated at 23 ± 1 months. Nevertheless, it is important to note that all cohorts suffered severe density reduction of 80–90% in the summer when the isopods completed 1 year of life (Fig. 4b). Such decreases coincided with recruitment periods and seemed to portray a strong post-reproduction mortality. Therefore, only 10–20% of the individuals may in fact reach the estimated life span of approximately 2 years.

The cohort C\(_3\) field data were used to calibrate a growth model (Fig. 4c). Growth was found to be continuous, although its rate varied with size (age) and temperature (season), being higher at early life stages and during spring and summer.

3.4. Life cycle

Cyathura carinata exhibited protogynous hermaphroditism, with males being present only between February and August (Fig. 5a). A continuous decrease of the sex ratio was noted throughout the study period, from 0.32 in 1993 to 0.16 in 1995. Approximately one month and a half after the appearance of males, the first ovigerous females were detected, being found from March to September, with a peak around June (Fig. 5b). The juveniles’ percentage variation confirmed that the population produced a single generation per year (Fig. 5b). Multiple regression analysis corroborated that the percentage of juveniles was correlated negatively to green macroalgal biomass and positively to water temperature during all the 32 months: arcsine√juvenile%/100 = −0.272 − 0.0446 ln (green macroalga + 1) + 0.0303 temperature (N = 46; \(R^2 = 57.10\%\)).

Consistently, embryos at different developmental stages could be found once a year, during spring and summer (Fig. 5c). Based on the time interval between the peaks of embryos in stages A and C, the embryonic development was estimated to last about 45 days. Most ovigerous females were found with total or partially empty brood pouches. This accounts for most of the inconsistencies observed in the sequence of embryo stages. Preservation in formaldehyde led to an embryo loss, especially of those from the last stage, which are already able to survive on their own. Consequently, very few embryos (C) were observed and no reliable fecundity data could be presented.

3.5. Production

Annual and spring (February to June) productions were estimated to assess the effect of the presence/absence of macroalgae. The annual growth production (\(P\)) (Table 1) was higher in 1994, when no algae occurred. The respective spring period (9.81 g m\(^{-2}\) 4 months\(^{-1}\)) represented approximately 1/3, suggesting that the production rate was regular during that year. On the other hand, the spring of 1993 (20.14 g m\(^{-2}\) 4 months\(^{-1}\)) represented more than 50% of the annual estimation.

The mean annual population biomass (\(\bar{B}\)) was also higher in the absence of macroalgae (Table 1). Nevertheless, the population biomass estimated during the macroalgal bloom in 1993 (13.58 g m\(^{-2}\)) was much higher than the annual average, while in 1994 (5.54 g m\(^{-2}\)) it was approximately half. With regard to \(P/\bar{B}\) ratio (Table 1), no major differences were found between the 2 years or between the respective spring periods (1.48 in 1993 and 1.77 in 1994).

4. Discussion

4.1. Spatial distribution and abundance

A regular seasonal density pattern was observed in the eutrophic area, consistent with other European populations (Legrand and Juchault, 1963; Muus, 1967;
Cyathura carinata showed a spatial variation, with the population decreasing from inner areas towards the Zostera noltii beds. There are references relating the presence of C. carinata in Zostera sp. and other macrophytes beds (Bamber, 1985; Sola and Arzubialde, 1993; Ölafsson and Persson, 1986). Therefore, the explanation for the low abundance initially recorded in the Z. noltii beds and subsequent increase remains unknown. Processes related with (a) the specific habitat selection by crustaceans, (b) the Z. noltii decline due to eutrophication, with consequent increase of habitat similarity with the eutrophic area, and (c) parasite pressure (Jensen et al., in press) may be some possible mechanisms that could explain the observed pattern.

4.2. Population structure, growth and life span

Cyathura carinata generated a single cohort per year, and not two consecutive ones that rapidly become merged, as stated by Marques et al. (1994). However, reproduction is extended through all summer, which may have allowed distinguishing two different intensity periods in that particular year. The approximately 2 years life span at the Mondego Estuary agrees with most observations in other populations (Legrand and
Juchault, 1963; Muus, 1967; Bamber 1985; Ölafsson and Persson, 1986; Sola and Arzubialde, 1993). Only the ones from Puck Bay (Jazdzewski, 1969), Kiel Canal (Wa¨ gele, 1979), Wismar Bight (Ko¨ hn and Sammour, 1990) and Kingsnorth (Bamber, 1985) appeared to live 3 years. Nevertheless, as in the populations from Arcachon (Amanieu, 1969) and Bidasoa (Sola and Arzubialde, 1993), a strong reduction of 80–90% of the individuals took place at the end of the first year of life (in the beginning of each summer), which apparently corresponds to post-reproduction mortality (Table 1).

Growth was also consistent with the rates of populations at the south of Europe (Amanieu, 1969; Bamber, 1985; Sola and Arzubialde, 1993; Marques et al., 1994), reducing during the coldest months of the year, but without ever ceasing as in the northern populations (Jazdzewski, 1969; Wa¨ gele, 1979; Ölafsson and Persson, 1986; Ko¨ hn and Sammour, 1990) (Table 1).

4.3. Life cycle

Like in other European populations (Legrand and Juchault, 1963; Jazdzewski, 1969; Wa¨ gele, 1979; Bamber, 1985; Sola and Arzubialde, 1993), protogynous hermaphroditism was observed. Males were usually larger individuals (the mean total length of the 100 biggest males was 10.7 mm against only 7.9 mm in reproductive females). Based on the fact that males appear one and a half months before ovigerous females and that most individuals were able to reproduce in their first year of
### Table 1
Summary of biological features from several *Cyathura carinata* populations, ordered from north to south (symbology: “–” absence of information, “av” average, “max” maximum, “min” minimum, “prot. herm.” protogynous hermaphroditism and “C” cohort)

<table>
<thead>
<tr>
<th>Reference</th>
<th>Study site</th>
<th>Density (ind. m$^{-2}$)</th>
<th>Life span (months)</th>
<th>Recruitment period</th>
<th>Males</th>
<th>Gravid females</th>
<th>Sex ratio</th>
<th>Prot. herm.</th>
<th>Embryogenic development (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Muus, 1967</td>
<td>Several sites in Denmark</td>
<td>Av: 200–400, max: 3000</td>
<td>24</td>
<td>July to ?</td>
<td>–</td>
<td>–</td>
<td>1.46</td>
<td>No</td>
<td>21–28</td>
</tr>
<tr>
<td>Ólafsson and Persson, 1986</td>
<td>South-west Sweden</td>
<td>Min: 437; max: 4253</td>
<td>24</td>
<td>July to August</td>
<td>June to July</td>
<td>June to July</td>
<td>1.18</td>
<td>Yes</td>
<td>28–35 (21, in lab.)</td>
</tr>
<tr>
<td>Jazdzewski, 1969</td>
<td>Gdansk Gulf, Poland</td>
<td>–</td>
<td>24–36</td>
<td>August to September</td>
<td>June to September</td>
<td>July to September</td>
<td>1.18</td>
<td>Yes</td>
<td>28–35</td>
</tr>
<tr>
<td>Wägelle, 1979</td>
<td>Kiel Canal, Germany</td>
<td>–</td>
<td>36</td>
<td>July to September</td>
<td>May to July</td>
<td>June to September</td>
<td>1</td>
<td>Yes</td>
<td>21–28</td>
</tr>
<tr>
<td>Köhn and Sammour, 1990</td>
<td>Wismar Bight, Germany</td>
<td>Max: 1200</td>
<td>36</td>
<td>June to July</td>
<td>January to July</td>
<td>May to August</td>
<td>–</td>
<td>Yes</td>
<td>–</td>
</tr>
<tr>
<td>Bamber, 1985</td>
<td>Kingsnorth, U.K.</td>
<td>Av: 538, max: 4040</td>
<td>36</td>
<td>May to August</td>
<td>March to August</td>
<td>March to September</td>
<td>0.33</td>
<td>Yes</td>
<td>–</td>
</tr>
<tr>
<td>Cléret, 1959, Cléret, 1960</td>
<td>Several sites in France</td>
<td>–</td>
<td>24</td>
<td>June to September</td>
<td>March to September</td>
<td>–</td>
<td>–</td>
<td>0.57</td>
<td>–</td>
</tr>
<tr>
<td>Legrand and Juchault, 1963</td>
<td>Arcachon, France</td>
<td>–</td>
<td>12</td>
<td>June to August</td>
<td>April to August</td>
<td>April to September</td>
<td>0.65</td>
<td>±60</td>
<td>–</td>
</tr>
<tr>
<td>Sola and Arzubialde, 1993</td>
<td>Bidasoa, Spain</td>
<td>167.7 ± 93.2 (in decline)</td>
<td>24</td>
<td>July to September</td>
<td>February to August</td>
<td>April to September</td>
<td>0.37</td>
<td>Yes</td>
<td>–</td>
</tr>
<tr>
<td>Marques et al., 1994</td>
<td>Mondego, Portugal</td>
<td>Min: 200, max: 1050</td>
<td>18–22</td>
<td>July to September</td>
<td>March to September</td>
<td>April to September</td>
<td>0.22</td>
<td>Yes</td>
<td>32</td>
</tr>
<tr>
<td>Present work</td>
<td>Mondego, Portugal</td>
<td>Min: 291, max: 3759</td>
<td>23 ± 1</td>
<td>May to August</td>
<td>February to August</td>
<td>March to September</td>
<td>0.33</td>
<td>Yes</td>
<td>45</td>
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<td></td>
<td>Min: 601, max: 5518</td>
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<td></td>
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<td></td>
<td>0.27</td>
<td>Yes</td>
<td>45</td>
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<td></td>
<td>Min: 556, max: 3475</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td>0.17</td>
<td>–</td>
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</table>

<table>
<thead>
<tr>
<th>Reference</th>
<th>Sexual maturity (mm)</th>
<th>Reproductive individuals (%)</th>
<th>Total length (mm)</th>
<th>Growth</th>
<th>$P$ (g m$^{-2}$ year$^{-1}$)</th>
<th>$\overline{T}$ (g m$^{-2}$)</th>
<th>$P/\overline{T}$ (1 year)</th>
</tr>
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<tbody>
<tr>
<td>Muus, 1967</td>
<td>–</td>
<td>–</td>
<td>? to 14</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Ólafsson and Persson, 1986</td>
<td>–</td>
<td>100 (2nd year)</td>
<td>1.25–12.5</td>
<td>Ceases in winter</td>
<td>C$<em>{1980}$: 2.045, C$</em>{1981}$: 1.577</td>
<td>0.598, 0.393</td>
<td>3.42, 4.02 (2 years; WW; 1 mm sieve)</td>
</tr>
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<td>Jazdzewski, 1969</td>
<td>7</td>
<td>57.30 (1st year)</td>
<td>2–14.5</td>
<td>Ceases in winter</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Wägelle, 1979</td>
<td>7</td>
<td>48.90 (1st year)</td>
<td>2–16</td>
<td>Ceases in winter</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Köhn and Sammour, 1990</td>
<td>8.5–11</td>
<td>–</td>
<td>2.2–16</td>
<td>Ceases in winter</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Bamber, 1985</td>
<td>7.5</td>
<td>92.50 (1st year)</td>
<td>2.5–18.7</td>
<td>Continuous in winter, ceases in reproduction</td>
<td>0.750</td>
<td>–</td>
<td>–</td>
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<td>Cléret, 1959, Cléret, 1960</td>
<td>7</td>
<td>–</td>
<td>3–14</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<td>Legrand and Juchault, 1963</td>
<td>–</td>
<td>–</td>
<td>3–13.5</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Amanieu, 1969</td>
<td>6.5</td>
<td>89.1 (1st year)</td>
<td>–</td>
<td>Slows down in winter, ceases in reproduction</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Sola and Arzubialde, 1993</td>
<td>8</td>
<td>80–85 (1st year)</td>
<td>1.27–14.7</td>
<td>Continuous in winter, ceases in reproduction</td>
<td>0.628</td>
<td>0.184</td>
<td>3.42</td>
</tr>
<tr>
<td>Marques et al., 1994</td>
<td>8.13 ± 1.65</td>
<td>–</td>
<td>? to 14.8</td>
<td>Continuous, slows down in winter</td>
<td>5.7–9.9</td>
<td>2.7–6.0</td>
<td>1.65–2.03</td>
</tr>
<tr>
<td>Present work</td>
<td>5.14 ± 1.44</td>
<td>90</td>
<td>2.29–14.26</td>
<td>Continuous, slows down in winter</td>
<td>23.88</td>
<td>6.76</td>
<td>3.53</td>
</tr>
<tr>
<td>1994</td>
<td>80</td>
<td></td>
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<td></td>
<td>31.95</td>
<td>10.70</td>
<td>2.99</td>
</tr>
<tr>
<td>1995</td>
<td>90</td>
<td></td>
<td></td>
<td></td>
<td>(1st year)</td>
<td>(AFDW; 0.5 mm sieve)</td>
<td>–</td>
</tr>
</tbody>
</table>
life, the sexual maturity of this isopod was estimated in 8–
10 months. Since the northern populations grow slower,
sexual maturity is reached later. This might be the reason
why these populations show fewer individuals (or none at
all) reproducing on the first year (Jazdewski, 1969;
Wagle, 1979; Bamber, 1985). In the case of a population
located on southwest Sweden (Olafo¨sson and Persson,
1986), this scenario was so extreme that the authors
rejected the hypothesis of protogynous hermaphrodit-
ism, based on the fact that organisms only reached sexual
maturity at their second (and last) year of life.

The low sex ratio values observed in the Mondego
Estuary may have some ecological significance, suggest-
ing male’s capability to inseminate several females
(Bamber, 1985). Nonetheless, the observed decline of
sex ratio from 1/3 in 1993 to approximately less than 1/5
in 1995 may endanger population reproduction capacity
and species continuity.

The presence of green macroalgae apparently fav-
oured the abundance of ovigerous females, probably
due to better shelter and more food resources (Everett,
1994; Raffielli et al., 1998; Norkko et al., 2000; Pardal
et al., 2000; Cardoso et al., 2002). Yet, it affected
negatively the recruitment of juveniles. Macroalgae
might promote juvenile dispersion to adjacent areas
and/or induce differential mortality, as a result of the
effects induced by their presence (e.g. decrease of
dissolved oxygen, entrapment on the algae matrix,
etc.). Also, the possibility of embryo loss, when females
are subjected to environmental stress, cannot be
excluded. The most evident negative impact of green
macroalgae on Cyathura carinata was the decrease in
recruitment success. In opposition to Martins et al.
(1997), who suggested lower survival rates due to the
coincident occurrence of events (post-reproduction
mortality and the algal crash), cyathurans seem to be
rather tolerant to hypoxia conditions (Burbank and
Burbank, 1979; personal observation). This tolerance
may explain the fact that C. carinata was comparatively
less affected by the algal crash than other macro-
invertebrates at the Mondego Estuary (Pardal et al.,
2000, 2004; Cardoso et al., 2002, 2004; Dolbeth et al.,
2003).

4.4. Production

Growth production and mean population biomass of
Cyathura carinata increased during the development of
green macroalgae, which was evident from the values
estimated for spring periods. Still, if the presence of
macroalgae appeared to represent an immediate benefit
for the population, in their absence, production values
seemed to be more constant and well balanced through-
out the year. Overall, growth production at the eutro-
phic area was comparatively much higher than values
estimated for other populations (Table 1).

5. Conclusions

In general, the comparison of several Cyathura
carinata populations (Table 1) points to the conclusion
that there is a latitudinal gradient reflected in the
biological features of the species. This gradient, from
north to south of Europe, can be described as follows:
(a) clinal variation towards continuous growth during
dlife; (b) earlier sexual maturity in southern latitudes,
anticipation of the recruitment period and evidence of
protogynous hermaphroditism; (c) increase in the pro-
portion of individuals able to reproduce after complet-
ing 1-year, with consequent post-reproduction mortality
reducing the number of isopods capable of achieving the
estimated life span; (d) decrease in the sex ratio (males/
females), and (e) shorter life span (controversial
characteristic according to Olafo¨sson and Persson’s
(1986) results that all populations have a life span no
longer than 2 years). Still, all presented univoltine life
cycles, with a single generation each year. The pop-
ulation of the Mondego Estuary follows all these
southern characteristics.

Facing the threat of eutrophication, macroalgal
blooms do have negative effects over Cyathura carinata,
especially on its reproductive success and secondary
production. Still, C. carinata is a resilient species. There-
fore, a single isolated bloom does not represent a severe
threat. However, in the absence of a reproducing popu-
lation nearby eutrophic areas, repeated events will
endanger the species and ultimately, will lead to its
eradication from affected estuaries.

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