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Biology, population dynamics and secondary production of *Tylos europaeus* (Isopoda, Tylidae) on the western coast of Portugal

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Abstract The biology, population dynamics, and production of *Tylos europaeus* were studied in two sandy beaches of the western coast of Portugal. At both sites, reproduction occurred seasonally, from April to July, with only one new cohort produced per year. Regarding population dynamics, cohort-splitting events were detected in males at the beginning of the reproduction period (April/May), resulting in two groups with distinct growth rates (fast-growing vs slow-growing males). Different biological characteristics were consequently detected in these two groups, namely regarding body size, lifespan, and contribution to the reproductive effort. Lifespan was estimated as approximately 3 years, for females and fast-growing males, and 4 years for slow-growing males. Cohort-splitting among males appeared as a possible strategy to cope with the highly male-biased sex ratios observed, which could lead to a strong male-male competition for mating. *T. europaeus* appeared as an annual species, with a univoltine life-cycle (one generation per year), and iteroparous females reproducing twice during their lifespan. Average growth production (P) was estimated at $0.082 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ AFDW (ash-free dry weight) and the average annual biomass (\bar{B}) (standing stock) at $0.052 \text{ g}\cdot\text{m}^{-2}$, resulting in a P/\bar{B} ratio of 1.58. These results produced baseline information for the construction of a population-dynamics model and highlighted the potential of this

species as an environmental quality-assessment bioindicator on sandy shores.

Introduction

Environmental quality decline of sandy-beach areas has been documented for many areas of the Atlantic (see for instance Peterson et al. 2000; Lercari and Defeo 2003), most often associated with socio-economic growth in coastal areas. Mechanisms responsible for the environmental quality decline under human-induced stress are complex and probably involve a combination of direct and indirect effects of changes in water and sand quality. For instance, tourism increase usually leads to changes in the sand beach areas and sometimes even in the dune system, which eventually leads to changes in the associated biological communities.

The development of ecological changes, taking place in sandy beaches under increasing human disturbance, is not well documented, partly because the early stages of the process are so gradual that they are usually not recognised until changes are well under way, and also because, for many locations, major changes occurred decades ago. However, an appreciation of such development is vital if remedial and restorative programmes for sand and dune areas are to be successful.

Isopods are important macrofaunal inhabitants in sandy beaches world-wide. Among them, the almost cosmopolitan oniscid semi-terrestrial genus *Tylos* is typical of the upper zones of sandy shores where back-beaches are adequate (Brown and McLachlan 1990). Several studies have been performed regarding, for instance, its zonation (e.g. Kensley 1974; Hayes 1977; Fallaci et al. 1996), burrowing behaviour (e.g. Brown and Trueman 1996), spatial distribution (Odendaal et al. 1999), and bioecology (e.g. Kensley 1974; Brown and Odendaal 1994 in Fallaci et al. 1996). However, the population dynamics and the role of this genus in the energy balance of beach

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ecosystems are still poorly understood. With the exception of the studies of Hammer et al. (1969) on the population dynamics of *Tylos punctatus* Holmes and Gay 1909, and of Hayes (1974) on the importance of this same species in the sand-beach energetics, focusing on two beaches in California, there are no other works on this topic available in the literature.

Along sandy beaches of the Mediterranean and Atlantic coasts of Europe, oniscid isopods and talitrid amphipods are common macrofaunal groups on the supralittoral and eulittoral zones (Brown and McLachlan 1990). Indeed, *T. europaeus* Arcangeli, 1938, together with the amphipods *Talitrus saltator* (Montagu, 1808) and *Talorchestia brito* Stebbing, 1891, represent the most abundant species in exposed sandy shores of the western coast of Portugal (S.C. Gonçalves, unpublished data), being also very well represented for instance on the French Atlantic coast (Colombini et al. 1996). Due to their ecological importance, *Tylos europaeus* might be used as a bioindicator of environmental quality in sandy shores, since oscillations in population dynamics, reproductive strategies and productivity might reflect environmental changes (e.g. human impacts). For instance, Paoletti and Hassall (1999) stated that terrestrial isopods of the family Oniscidae are appropriate organisms for assessing sustainability and can be used as bioindicators of heavy-metal contamination. Very few studies have been performed on the biology and ecology of *Tylos europaeus* (e.g. Giordani Soika 1954; Mead 1968, both in Fallaci et al. 1996; Kensley 1974), and most of the recent work centred on its surface activity (e.g. Colombini et al. 1996; Fallaci et al. 1996) and field orientation mechanisms (e.g. Ugolini et al. 1995). Following two recent studies on talitrid amphipods (Gonçalves et al. 2003; Marques et al. 2003), this work aims to fill the gap in knowledge of the biology, population dynamics and secondary production of *Tylos europaeus*, providing a tentative overview of its possible role in sandy-shore ecosystems, and simultaneously producing baseline information for the construction of a population dynamics model.

Materials and methods

Study sites and sampling programme

Sampling campaigns took place in two sandy beaches on the western coast of Portugal: Cabedelo and Quiaios, both located in the central region of Portugal, near Figueira da Foz (Fig. 1). The Quiaios study site (40°12'21'.N 8°53'48'.W) is located about 8 km north from Cape Mondego, while the Cabedelo study site (40°07'32'.N 8°51'49'.W) is located about 1 km south of the Mondego river mouth. Both beaches are relatively undisturbed, receiving a moderate number of summer visitors. According to the exposure rating scale proposed by McLachlan (1980), both beaches have a very exposed

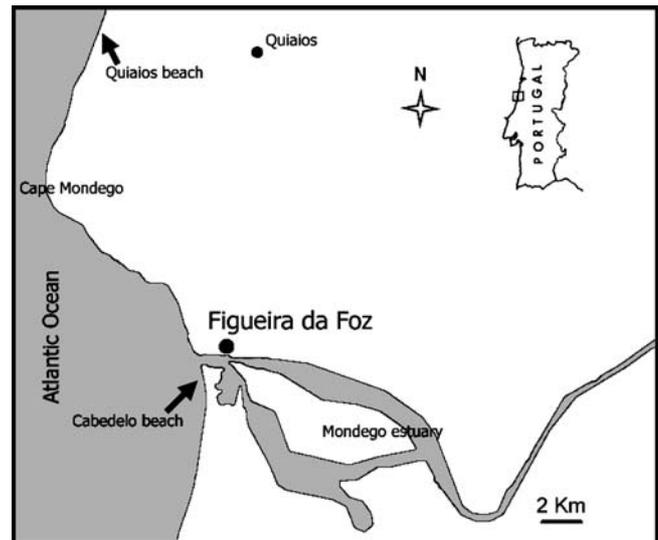


Fig. 1 Location of the two sampling stations (western coast of Portugal)

nature (exposure rates of 15 for Cabedelo and 16 for Quiaios). During storms, Cabedelo may be almost completely inundated, causing depositions of large amounts of drift wrack, mainly composed of macroalgae originating from rocky shores located north of the beach. For Quiaios, the input of beach debris is clearly more limited, since there are no rocky shores or other potential sources of debris near the study site. The main characteristics of these two sandy beaches are summarised in Table 1.

Quantitative samples (replicates of 0.25 m²) were taken fortnightly from the sandy-beach communities at both study sites. The sampling period lasted from January 1999 to June 2000 at Quiaios (18 months), and from March 1999 to June 2000 (15 months) at Cabedelo. The sampling programme followed the field-work protocol already described by Marques et al. (2003). Samples were taken at regular intervals along two transects from the shoreline to the base of the dunes (intertidal and supratidal areas), in order to account for differential horizontal distribution and to collect a suitable number of individuals necessary for statistical analysis (minimum of 100 individuals). The influence of environmental factors on both populations was investigated. For this purpose, debris quantity (potential food g.m⁻²), organic matter as ash-free dry weight (AFDW), and sediment moisture were determined according to the procedures described in Marques et al. (2003) (Table 1). Meteorological data were also obtained from the closest meteorological station, including average daily precipitation, maximum and minimum daily temperatures, visibility, cloudiness, wave height, wave period, and wind velocity.

Laboratory procedures

Individuals were counted and measured for their cephalic length (CL) to the nearest 0.013 mm. When

Table 1 Basic characteristics observed on the two sandy beaches used as sampling sites

Characteristic	Cabelo	Quiaios
Width of the eulittoral zone	60 m	100 m
Average slope	2.0%	1.8%
Tidal range	2–3.5 m	2–3.5 m
Extension of the intertidal area	Neap tides: 30 m Spring tides: 45 m	Neap tides: 50 m Spring tides: 75 m
Foredune height	2.5–3 m	2.5–3 m
Sediment granulometry (according to the Wentworth scale in Brown and McLachlan 1990)	Medium sand (0.250–0.500 mm)	Coarse sand (0.500–1.0 mm)
Average sediment moisture (%)	3.24 (± 1.22)	2.64 (± 0.95)
Average organic matter content in sediments (%)	0.15 (± 0.05)	0.19 (± 0.35)
Average detritus (g.m ⁻²)	9.15 (± 9.03)	2.02 (± 1.82)

necessary, total length (TL) was estimated from cephalic length, through the following equation:

$$TL = -1.28068 + 7.197359CL \quad (n = 163, r = 0.99) \quad (1)$$

Length-weight relationships were analysed for each season (spring, summer, autumn and winter). For this purpose, 150 to 200 randomly sampled specimens were weighted each time (AFDW, after combustion at 450°C for 3h). Since no seasonal differences were observed, the following estimated equation was used:

$$AFDW = 0.0013CL^{3.8165} \quad (n = 1418, r = 0.97) \quad (2)$$

After measuring, individuals were sexed, based on the presence of oostegites and/or broods in females (resting females and reproductive females), and the presence of copulatory appendages in males. Small individuals lacking these features were considered juveniles. Eggs and embryos were removed from the brood pouch of gravid females, classified (stages A, B and C), counted and measured. These data were then used to estimate fecundity, eggs and embryos dimensions, brood mortality and period necessary for embryonic development.

Data analysis

Multiple regression models were developed for each population, correlating abundance, sex ratio, percentage of reproductive females, mean individual fecundity and percentage of juveniles in the population with physico-chemical environmental factors. The models were fitted with data following the Stepwise Regression method using the MINITAB 12.2 software package.

According to a methodology previously utilised (Pardal et al. 2000; Gonçalves et al. 2003; Marques et al. 2003), field growth rates were estimated by tracking recognisable modal distributions in successive sample dates through size-frequency analysis, using the ANAMOD software package, in which the analysis consistency was tested using χ^2 and G -tests ($p=0.05$). The methodology was performed separately for males and females. Juveniles were combined to each sex, proportionally to the

average sex ratio observed in each sampling date. Field growth data were fitted to the Bertalanffy growth function (VBGF) with seasonal oscillation, according to a model proposed by Gaschütz and co-workers (1980), and previously applied with satisfactory results (e.g. Pardal et al. 2000; Achouri et al. 2003):

$$Lt = L\infty \left(1 - e^{-[KD(t-t_0)+C\left(\frac{KD}{2\pi}\right) \sin 2\pi(t-t_s)]} \right) \quad (3)$$

where Lt is the length of the organism at a given moment t , $L\infty$ the maximum possible length of the organism, t the given time instant, t_0 the instant in which the organism would have a length=0, t_s the time interval between the start of growth and the first growth oscillation, with growth being expressed by a sine curve with a period of 1 year, K the intrinsic growth rate, C a constant between 0 and 1, inherent to the species, and D a parameter expressing metabolic deviations from the Von Bertalanffy rule. In the present case, D was assumed as 1 since there is no information regarding the metabolism of *Tylos europaeus*.

Due to the complexity of the size-frequency analysis of the population, a size-frequency method to estimate secondary production was used, instead of a cohort-based one. The size-frequency method modified by Benke (1979) was chosen, expressed as:

$$P = a \left[\sum_{j=1}^{a-1} (\bar{N}_j - \bar{N}_{j+1}) \times \sqrt{(\bar{W}_j \times \bar{W}_{j+1})} \right] \left(\frac{365}{CPI} \right) \quad (4)$$

where \bar{N}_j is mean density in size class j (ind.m⁻²), \bar{W}_j is mean individual weight in size class j (mg AFDW), CPI is cohort production interval, which was considered in this species as equal to the lifespan, and j and $j+1$ are consecutive size classes ($j=1,2,\dots, a$).

Results

Spatial distribution and abundance

During the whole sampling period, abundances were consistently higher at Quiaios than at Cabelo (Fig. 2). Despite differences in abundance, the seasonal variation

followed a similar pattern at the two stations, although Cabedelo data were approximately 1.5 months out of step: abundance reached the lowest values in winter, followed by an increase in early spring and a slight decrease by May/June. In summer, a strong peak was reached, first at Quiaios and then in Cabedelo, followed by a rapid decline in late summer and autumn (Fig. 2).

Stepwise multiple regression analysis revealed that population density (D) was positively correlated with temperature (T), at Cabedelo beach, according to the following regression model:

$$D = -6.87 + 1.31T \quad (r^2 = 0.551; p < 0.001)$$

The analysis of the Quiaios population did not reveal any significant statistical correlation.

Reproduction period, sex ratio and fecundity

The reproduction period took place from April to July, recognisable by the occurrence of reproductive females, and the appearance of new juvenile cohorts in the population (Figs. 3a,b, 4). Only one new cohort was detected during the sampling period (Fig. 5), suggesting the production of only one cohort per year. The appearance of reproductive females clearly preceded juveniles' recruitment, with a peak in the percentage of juveniles in the populations being attained between July and September (Fig. 3a,b).

Sex ratios (males/females) were significantly different in the two populations (paired t -test; $p < 0.05$) (Fig. 3c). However, both populations revealed similar annual patterns of variation and clearly male-biased sex ratios (average Quiaios 1.7:1; average Cabedelo 3.9:1). Short periods of female dominance were observed in Quiaios during the winter, at the beginning of 1999, and again by the end of summer and early autumn, in September/October of the same year.

The average fecundity for females carrying stage A embryos was 18.7 embryos/female, while for stage B carriers it was 16.3 embryos/female. Significant statistical correlations between the number of developing embryos (NE) in stages A and B within brood pouches and

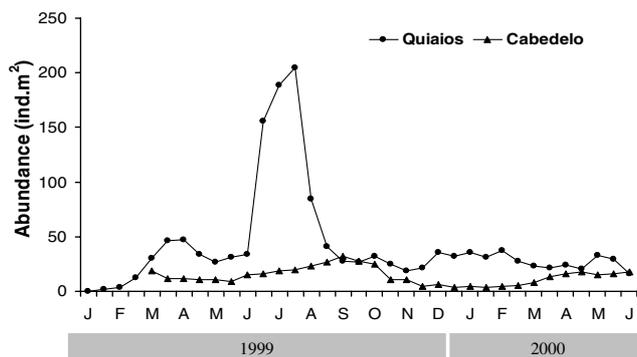


Fig. 2 Variation of *Tylos europaeus* population abundance on the western coast of Portugal

female cephalic length (CL) were found. The fitted regressions were expressed as:

$$\text{Stage A} \quad \text{NE} = 33.301\text{CL} - 33.24 \\ (170 \text{ females}; r^2 = 0.500)$$

$$\text{Stage B} \quad \text{NE} = 31.019\text{CL} - 29.52 \\ (44 \text{ females}; r^2 = 0.632)$$

According to the variability explained by these regressions, the equations might be considered reasonable predictors of the number of developing embryos.

Measurements of embryos (Table 2) showed that, during development, embryos increased their average diameter by 25.8% and their volume by 100.3%. Newly hatched juveniles (stage C) were 0.53 ± 0.07 mm CL, and therefore just slightly smaller than the minimum average CL of the newly born cohort recognised during the study period (Fig. 5). Embryos mortality between stages A and B was estimated as 13%. The embryonic develop-

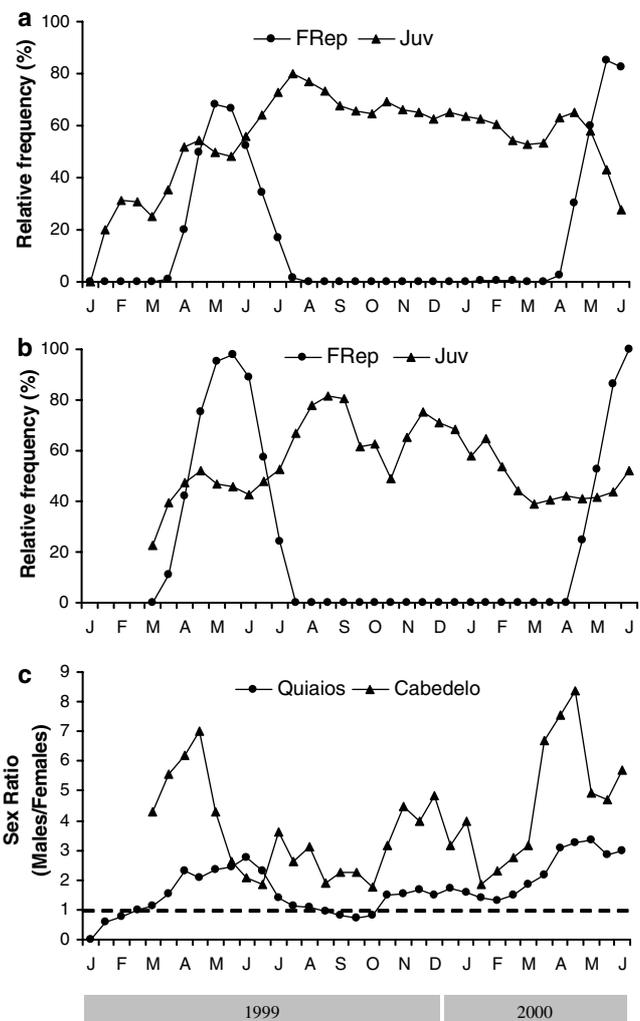


Fig. 3 Variation of biological features of *Tylos europaeus*. a Variation of reproductive females in the total female population, and of juveniles in the population, in Quiaios. b Variation of reproductive females in the total female population, and of juveniles in the population, in Cabedelo. c Variation of sex ratio in Quiaios and in Cabedelo

ment of *Tylos europaeus* was estimated at approximately 68 days ($SE \pm 4.95$), according to the temporal difference between the peaks of relative frequency of embryos in the first and the last stage (A and C).

Population structure, cohort-splitting and field growth rates

Four cohorts (C1', C2, C3, C4) were identified in the males group at the first date suitable for analysis (23/03/99), while in the females group, only three cohorts were detected (C2, C3, C4) (Figs. 4, 5). According to the pattern achieved, females from the C1 cohort presumably died the previous year to the study.

Only one new distribution, C5, corresponding to a new recruitment, was detected (χ^2 and G -tests not significant; $p \geq 0.05$). Therefore, the population produced only one new cohort during 1999, which was detected from the samples collected on 2 July. A similar observation was not repeated in the next year, since the sampling campaigns were concluded in June 2000, most probably slightly before a new recruitment, according to the pattern observed.

The size-frequency analysis of the males group revealed some peculiar features. Slightly before completing 3 years (April/May of each year studied), males born in the same reproductive period originated two different speed growing groups: a fast-growing group, called C2' and C3', and a slow-growing group called C1', C2' and C3' (Fig. 5). This phenomenon has already been observed in several arthropods, namely in isopods (e.g. Grundy and Sutton 1989; Zimmer and Kautz 1997), and has been called cohort-splitting by Sunderland et al. (1976) when they observed it in a field population of the isopod *Philoscia muscorum* Scopoli, 1763. These two groups presented different biological characteristics, namely in body size, lifespan, growth rates and contribution to reproduction. At the time of their disappearance, males C2' presented a maximum average CL of 2.19 mm (14.45 mm TL), while C3' were generally larger, presenting 2.27 mm CL (15.05 mm TL). No statistically significant differences were observed between the proportions of individuals belonging to each one of these groups (fast-growing vs slow-growing from the same original cohort) (paired t -test; $p \geq 0.05$). For the females group, no division was apparent. In both groups, growth rates were clearly higher in mid-spring and during summer, decreasing significantly in autumn and winter (Figs. 5, 6). Since no cohort could be followed from birth to disappearance, lifespans were estimated by combining the size at birth and first growth stages of the new cohort recognised in 1999 (C5) with the observable development through time of all the other cohorts identified (the so-called "composed" cohort). Females appeared to live approximately 3 years (36 months), while fast-growing males (C2' cohorts) lived the same as females, and slow-growing males (C3' cohorts) appeared to live 1 more year (48 months).

Three growth models—females, fast-growing males (C2') and slow-growing males (C3')—were obtained (Fig. 6). According to the models: (a) growth was approximately constant during life stages; (b) the period required by females to reach sexual maturity was 55–59 weeks; (c) the period necessary for male sexual differentiation was estimated as 18–19 weeks for C2' males, and 22–25 weeks for C3' males (Table 3). Therefore, sexual differentiation tended to occur much earlier in males than in females, and approximately 1 month earlier in fast-growing males when compared to slow-growing males.

Life-cycle

The recruitment pattern of *Tylos europaeus* was constructed (Fig. 7), and probable parental relations among cohorts were identified. Regarding females, cohorts C2 and C3 were responsible for the appearance of the cohort born in July 1999, while females C3 and C4 must have been the contributors during the reproductive period of the year 2000 (Figs. 4, 7). Nevertheless, as already explained, the population could not be followed long enough to observe the occurrence of recruitment in 2000. Thus, females became reproductive in their second spring (1.75 years; e.g. C4), contributing to the reproductive effort of the population in 2 consecutive years. After their second reproductive season, females died. Regarding males, although cohorts C3 and C4, in 1999 and 2000 respectively, might have been able to reproduce with females of their cohorts, they were probably out-competed by older males with larger body sizes: males C1', C2' and C2' in 1999, and males C2', C3' and C3' in 2000.

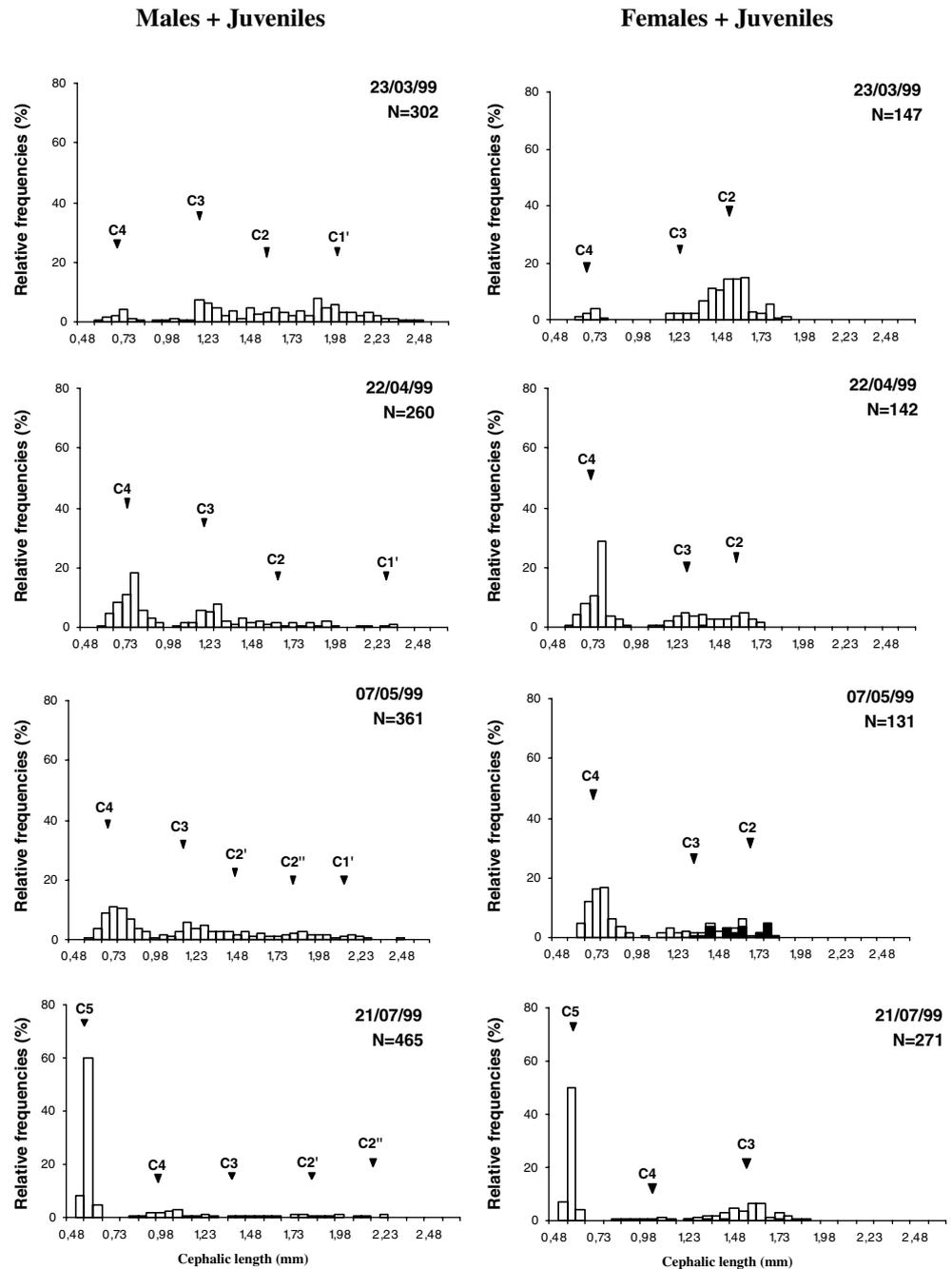
Production estimates

Length-weight relationships were used in production estimates. Growth production (P) was estimated at $0.093 \text{ g.m}^{-2}.\text{yr}^{-1}$ AFDW for the individuals with a lifespan of 3 years, and $0.07 \text{ g.m}^{-2}.\text{yr}^{-1}$ AFDW for individuals with a 4 year lifespan. The average growth production of *Tylos europaeus* was $0.082 \text{ g.m}^{-2}.\text{yr}^{-1}$ AFDW, and the average annual biomass (\bar{B}) (standing stock) was 0.052 g.m^{-2} , resulting in a P/\bar{B} ratio of 1.58 (Table 3).

Discussion and conclusions

Population abundances were consistently higher at Quiaios, during the whole study period. Differences in the sediment granulometry between the two sandy beaches (Table 1) might be the cause. According to Kensley (1974), *Tylos europaeus* avoids beaches of fine sand and river mouths, inhabiting instead crevices, rocks or coarse-sand beaches. Nevertheless, the seasonal varia-

Fig. 4 Size-frequency distribution of *Tylos europaeus* on the western coast of Portugal. Sampling dates are indicated (*N* number of measured individuals). Arrowheads indicate average cephalic length of the numbered cohorts. Black areas indicate reproductive females

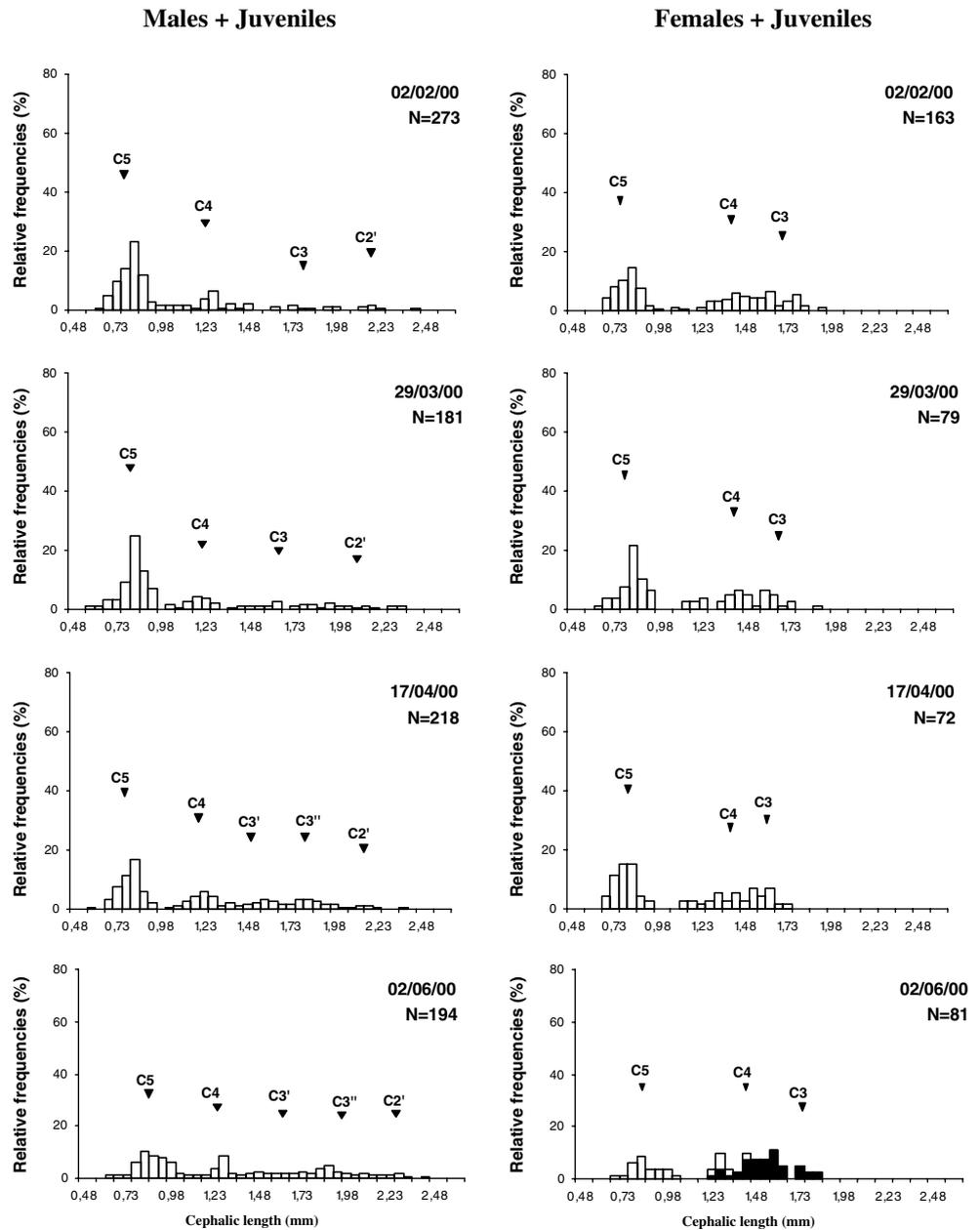


tion of abundance followed a similar pattern in Quiaios and Cabedelo. The strong peak reached in summer is a natural consequence of recruitment, while the rapid decline observed in autumn results from the death of older individuals after reproductive effort. The lowest values reached during winter (more evident in Cabedelo) may suggest that, similarly to talitrids, *Tylos europaeus* have the capability of changing their horizontal and vertical distributions as a response to harsh environmental conditions (see, for instance, Williams 1995; Gonçalves et al. 2003; Marques et al. 2003; for similar discussions, Fallaci et al. 1996 for changes in the annual static zonation of *Tylos europaeus*). The decrease in

density may be a result of migration from the beach to the dunes or a displacement of the burrow zone to deeper layers of the sediment, up to a metre or more (Brown and Trueman 1996), where generally a more stable microclimatic environment is achieved during this season. The increase of the population in early spring reflects, most probably, a return to the normal horizontal and vertical patterns of distribution of the population due to more favourable environmental conditions.

The positive correlation between population density and temperature, found at Cabedelo, is not unexpected. According to several authors (Mocquard et al. 1980,

Fig. 4 (Contd.)



1984; Juchault et al. 1982; Souty-Grosset et al. 1991, all in Caubet 1998), reproduction of oniscids is often seasonal and is associated with combined oscillations in temperature and photoperiod.

In oniscid isopods, reproduction often occurs once a year followed by a long period of female sexual rest, as for instance in *Tylos granulatus* (Kensley 1974) and *P. muscorum* (Sunderland et al. 1976). In the present study, *Tylos europaeus* was found to reproduce from April to July, and only one new distribution was detected (July), suggesting the production of only one cohort per year.

Female-biased sex ratios appear to be an extremely common feature among oniscids, as observed for instance in *Porcellio laevis* (Kight et al. 2001) and *Porcellionides pruinosus* Brandt, 1833 (Achouri et al. 2003).

Infections by the endocyttoplasmic *Wolbachia* bacterium (trans-ovarially transmitted parasite) have been shown to be the main cause of this sex-ratio distortion in several oniscids (Juchault et al. 1993, 1994; Rigaud et al. 1997, all in Marcadé et al. 1999). However, contrary to these oniscids, *Tylos europaeus* presented a clearly male-biased sex ratio. A non-homogeneous distribution of the two sexes between the beach and the dunes, as suggested by Gonçalves et al. (2003) for the amphipod *Talorchestia brito*, may occasionally explain the difference observed. Fallaci et al. (1996) observed that juveniles, females and males of a Tyrrhenian population of *Tylos europaeus* were zoned, respectively, in three successive bands from the sea towards the land. In the present study, the pattern found might be distinct, with females burrowing in the dunes (sampling in the dunes was not performed),

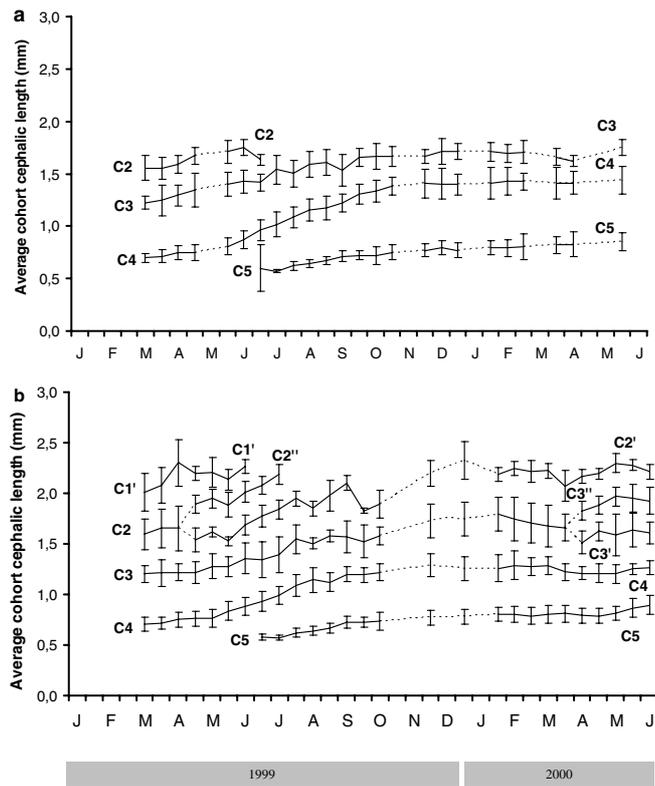


Fig. 5 Estimated growth and life span (field growth data) of *Tylos europaeus* cohorts (average cephalic length \pm standard deviation) on the western coast of Portugal. *Broken lines* indicate probable cohort evolution through time. **a** Females + juveniles group. **b** Males + juveniles group

since contrary to the population studied by Fallaci et al. (1996), significant tidal fluctuations are present in Atlantic beaches.

Despite the average sex ratio observed, in Quiaios, during 1999, females became occasionally dominant in mid-winter and again in late summer/early autumn. Differential mortality of males, particularly after the reproduction period, might be the cause, since highly male-biased sex ratios often lead to strong competition for mates. However, there is some uncertainty in this hypothesis, since a temporal delay between the two events (reproduction period/sex ratio inversion) arises from the observations.

In several arthropod populations, as for instance in the oniscid isopods *Philoscia muscorum* (Sunderland et al. 1976) and *Porcellio scaber* Latreille, 1804 (Zimmer and Kautz 1997), cohort-splitting appears to be a rele-

vant structuring mechanism of the dynamics and life-history of these populations. Indeed, in the present study, fast-growing and slow-growing males presented distinct biological features (e.g. lifespan, total length and contribution to reproduction) as a consequence of their diverse growth rates.

Various causes have been shown as plausible explanations for cohort-splitting, but it has been stressed that field studies are insufficient to evaluate them, and extensive laboratory studies are needed to clarify the causes (Grundy and Sutton 1989). Nevertheless, in the present study, a careful analysis of the data provides some clues that point to a possible explanation. Contrary to most studies, the split of individuals in *Tylos europaeus* was only detectable in males. Thus, male cohort-splitting might be an adaptative strategy to cope with the highly male-biased sex ratio observed. Sex ratio is an important determinant of the intensity of sexual selection (Manning 1980), and if females are scarce, male-male competition for mates will also be much more severe. Slowing up the growth to achieve larger body sizes might be an efficient strategy to out-compete smaller males and maximise the access to females. Moreover, this feature gives slow-growing males the opportunity to increase their reproductive success by reproducing once more, in the following year, when fast-growing males, born in the same breeding season, have already died.

Temperature appears to have an important role in growth rates, since clearly higher rates were achieved in spring and summer, and the two cohort-splitting events observed (1999, 2000) also occurred in middle spring (April/May). Similar results were observed in the field population of *Philoscia muscorum* in the United Kingdom, with the split occurring by the end of May (Sunderland et al. 1976). Grundy and Sutton (1989), in laboratory investigations with this same species, showed that populations maintained in constant laboratory conditions did not develop the split, while populations outside or with simulated seasonal changes in temperature and day length in the laboratory presented a definitive split into two distinct growth-rate groups.

In the present study, longevity of approximately 3–4 years was estimated. These observations are similar to the lifespan estimated for a German population of *Porcellio scaber*—2.5–3 years (Zimmer and Kautz 1997). It should be noted that the occurrence of the cohort-splitting phenomenon increases the longevity of slow-growing males by 1 year, while females and fast-growing males present a 3-year lifespan.

Table 2 Average diameter and average volume of embryos in developmental stages A and B of *Tylos europaeus*, and average cephalic length of embryos in stage C

	Average diameter (mm)	Standard deviation	Estimated volume (mm ³)	Size of sample (<i>n</i>)
Stage A embryos	0.90	0.05	0.39	58
Stage B embryos	1.13	0.08	0.78	53
Stage C embryos	Average cephalic length 0.53	0.07		4

Fig. 6 Individual growth models (Gaschütz et al. 1980) of *Tylos europaeus* on the western coast of Portugal. **a** Females group. **b** Fast-growing males group ($C' : \cdot$). **c** Slow-growing males group (C). The models were calibrated with field-growth data from cohorts (plotted points). Day 0 coincides with the month of July (moment of detection of the new cohort). Model parameters are given: r^2 = correlation between predicted and observed values (see Materials and methods for details)

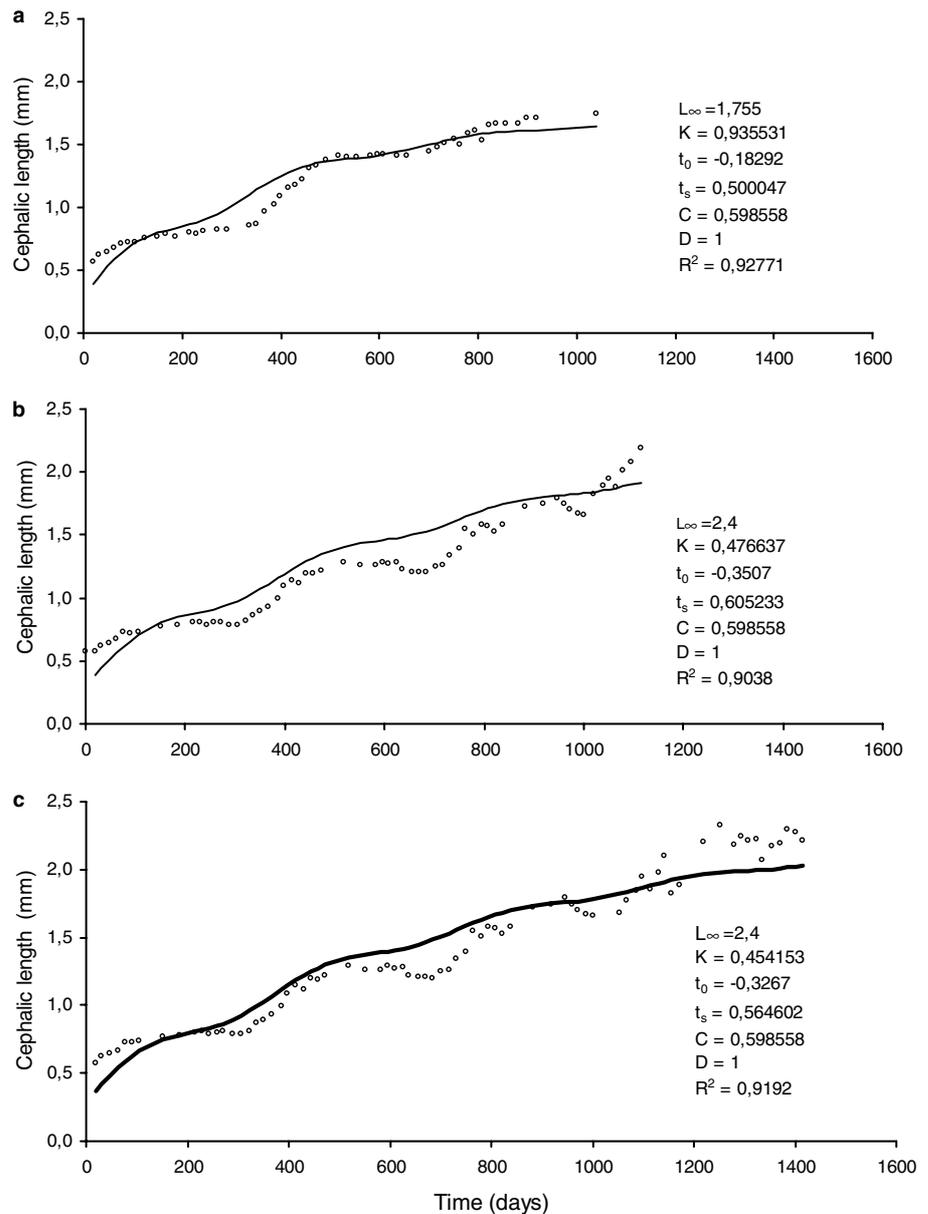


Table 3 Summary of *Tylos europaeus* population's characteristics in the western coast of Portugal with regard to biology, life-cycle, and production (based on data produced in the present study) (CL cephalic length)

Characteristic	Western coast of Portugal
Reproductive period	April to July
Average sex ratio	1.7:1 (Quiaios population) 3.9:1 (Cabedelo population)
Size of largest males (mm)	2.45 $CL \pm 0.041$
Size of smallest males (mm)	0.76 $CL \pm 0.014$
Age of males at sexual differentiation (weeks)	22–25 for the slow-growing groups (C) 18–19 for the fast-growing groups ($C' : \cdot$)
Size of largest females (mm)	1.90 $CL \pm 0.037$
Size of smallest females (mm)	1.24 $CL \pm 0.026$
Age of females at sexual differentiation (weeks)	55–59
Size of smallest reproductive females (mm)	1.25 $CL \pm 0.027$
Age of females sexual maturation (weeks)	55–59
Life span	3–4 years
Recruitment pattern	1 generation·year ⁻¹
Average net production (P)	0.082 $g \cdot m^{-2} \cdot yr^{-1}$
Average annual biomass (B)	0.052 $g \cdot m^{-2}$
P/B	1.58

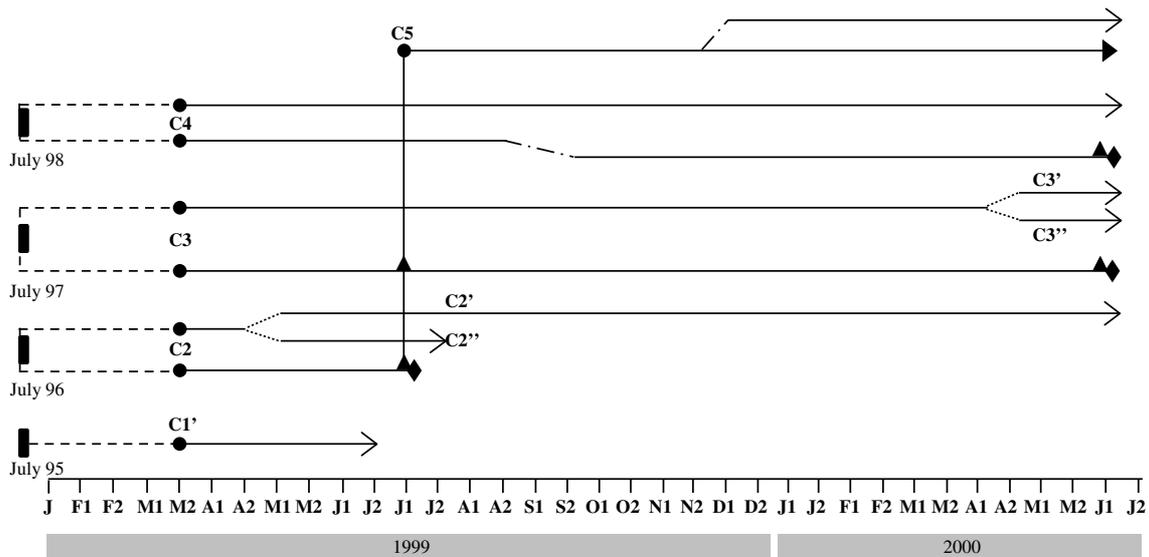


Fig. 7 Analysis of the recruitment pattern of *Tylos europaeus* on the western coast of Portugal. The horizontal arrows represent the period during which each cohort was followed during the study period, starting in the filled circles. The assumed contribution of each cohort is indicated (triangles). (arrow) Males; (arrow + diamond) females; (filled arrowhead) juveniles; (dashed line) probable cohort appearance (the probable month and year of appearance are given); (dotted line) probable cohort-splitting; (dashed/dotted line) probable average sexual differentiation

According to the present results, the life cycle of *Tylos europaeus* on the western coast of Portugal may be characterised as follows: (a) an annual species, with females producing only one brood per year; (b) iteroparous females, which reproduce twice during their lifespan; (c) a univoltine life-cycle, with only one generation per year. These features are not surprising since terrestrial isopods present, in general, slow reproductive cycles, with only one or two periods of breeding activity per season (Kensley 1972; Sunderland et al. 1976) and, among isopods, *Tylos* are known to be relatively slow breeders (Kensley 1972). The present study is unique in terms of population dynamics and reproductive biology of *Tylos europaeus*, which makes impossible any comparison and analysis of possible variations in these features among populations with distinct geographic origins.

As a natural consequence of its slow life-history, growth production and standing stock of *Tylos europaeus* were rather low. Likewise, population turnover is also small, especially when compared with P/\bar{B} ratios of the other abundant resident macrofauna of the two studied beaches, namely talitrid amphipods, *Talitrus saltator* and *Talorchestia brito*, characterised by rapid life-histories (semiannual and bivoltine species) and high population turnovers (Gonçalves et al. 2003; Marques et al. 2003). Nevertheless, *Tylos* are known to be important decomposers of the stranded wrack brought ashore by tides on beaches worldwide (e.g. Hayes 1974; Kensley 1974; Brown and McLachlan 1990), representing an important role in the energy flow of sandy beaches.

The present work contributes with relevant knowledge on the biology, population dynamics and secondary production of *Tylos europaeus*, where an interesting cohort-splitting phenomenon emerges as a possible strategy to cope with a highly male-biased sex ratio. At the local scale, from the conservation and management viewpoints, information on dominant-species production and P/\bar{B} ratios might be very useful to assess short- and long-term consequences of human actions like, for instance, nourishment or bulldozing to increase primary dunes on beaches affected by coastal erosion. As a whole, results from studies on this oniscid reinforce the need to reserve the full range of translittoral habitats (Richardson et al. 1997), which will not necessarily be achieved by establishing reserve boundaries on the basis of vegetation associations. Moreover, the knowledge and data achieved in this study are essential for the construction of a population-dynamics model, an important simulation/prediction tool under multiple scenarios, which will allow a better understanding of how environmental changes in the quality of sandy shores affect the associated biological communities.

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