

**Universidade do Algarve
Faculdade de Ciências do Mar e do Ambiente**

**ECOLOGY OF THE INVERTEBRATE MACROFAUNA OF A
RIA FORMOSA LAGOON SALT MARSH**

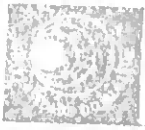
Ana Natália Domingues Dias

Ecology of the invertebrate
macrofauna of a Ria
Formosa lagoon - Dias.



**TESES
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**ECOLOGY OF THE INVERTEBRATE MACROFAUNA
OF A RIA FORMOSA LAGOON SALT MARSH**

**Dissertação apresentada à Faculdade de Ciências do Mar e do Ambiente da
Universidade do Algarve para obtenção do grau de Doutor em Ecologia**

Ana Natália Domingues Dias

FARO, 2003

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ABSTRACT

Populations of four terrestrial isopods (*Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii* and *Armadillidium album*) and three terrestrial amphipod species (*Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii*) were studied in a Ria Formosa salt marsh (South Portugal). Samples were taken 6-weeks intervals using pitfall traps and corers over a two year period. Samples were taken at the neap high tide level (NHTL), the mean high tide level (MHTL), and the spring high tide level (SHTL). The distributions of amphipods and isopods within the salt marsh showed a major overlap at the intermediate level (MHTL). At this level, great quantities of organic matter accumulate resulting from dead leaves of seagrasses, salt marsh plants and algae transported and deposited by the tides. Animals showed different microdistributions: *Orchestia* spp., *Porcellio*, *Halophiloscia* and *Armadillidium* were associated with wrack, while *Tylos* and *Talorchestia* were more abundant out of the debris. All these animals need saturated air or a humid substrate in their permanent habitats; the former species find suitable humidity conditions underneath the deposits while the latter can find it by excavating holes in the sediment. Distribution limits of peracarids according to the salt marsh tidal level appeared to be mediated by both abiotic environmental factors and biotic interactions.

During the present study marked demographic fluctuations were observed. The isopod *T. ponticus*, the dominant species of this assemblage, reached great densities in 1998 but suffered a decrease by 46% in the next year. Conversely, the remaining species increased their densities significantly in 1999 (76 to 98%). *Talorchestia deshayesii* population showed a decrease by 78% in 1999. Fluctuations in population density did not correlate with environmental factors, probably because these arthropods inhabit

well-buffered microhabitats in an environment without strong seasonality. Demographic alternations may be due to intra- and interspecific competition. The great overlap, although with different micro-distributions, of the sympatric species along the intertidal gradient suggests competitive interspecific interactions. Animals may be competing for high quality food. Potential mechanisms of avoiding competition deduced from the present data are discussed. Species-specific differences in nutritional requirements mediated by species-specific differences in digestive capabilities may reduce competition for food. In addition, character displacement in terms of size of the studied macrofauna species may allow the utilization of different food sources and maybe different micro-refuges. Coexisting species may also reduce competition between juveniles by displaying differential reproductive phenologies, as may be partially the case of the isopod assemblage in this study. Nevertheless, reproductive displacement in terms of phenology does not seem to be sufficient to explain coexistence of isopods and amphipods in this salt marsh. The effect of predation in these populations is unknown.

Annual production of isopods and amphipods was calculated by the increment summation method as 17.6 g ash free dry weight m^{-2} and 2.2 g ash free dry weight m^{-2} , respectively. It is speculated that these detritivores may contribute significantly to the re-mineralization of the organic matter in this salt marsh ecosystem.

RESUMO

As populações de quatro isópodes terrestres (*Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii* e *Armadillidium album*) e de três anfípodes terrestres (*Orchestia gammarellus*, *Orchestia mediterranea* e *Talorchestia deshayesii*) foram estudadas num sapal da Ria Formosa (Sul de Portugal). A amostragem foi efectuada durante dois anos, de seis em seis semanas utilizando armadilhas e “corers”. Foram recolhidas amostras no nível de maré-alta em marés mortas (NHTL), no nível médio de maré-alta (MHTL), e no nível de maré-alta em marés vivas (SHTL). A distribuição dos anfípodes e isópodes no sapal mostrou uma grande sobreposição no nível intermédio (MHTL). Neste nível existem grandes quantidades de matéria orgânica resultante de folhas mortas de fanerogâmicas marinhas e plantas do sapal bem como de algas transportadas e depositadas pelas marés. Os animais apresentaram micro-distribuições diferentes: *Orchestia* spp., *Porcellio*, *Halophiloscia* e *Armadillidium* estavam mais associadas com os depósitos de matéria orgânica enquanto que *Tylos* e *Talorchestia* foram mais abundantes no substrato sem depósitos. Todos estes animais precisam de ar saturado ou um substrato húmido nos seus habitats permanentes; o primeiro grupo de espécies encontra as condições de humidade adequadas debaixo dos depósitos enquanto que o último grupo encontra essas condições escavando buracos no sedimento. Os limites de distribuição dos peracarídeos de acordo com o nível de maré no sapal foram, aparentemente, mediados por factores abióticos ambientais e por interacções bióticas.

Durante o presente estudo observaram-se flutuações demográficas marcadas. O isópode *T. ponticus*, a espécie dominante desta comunidade, atingiu as maiores densidades em 1998 mas sofreu um decréscimo de 46% no ano seguinte. Contrariamente, as restantes espécies aumentaram significativamente as suas densidades

em 1999 (76 a 98%). A exceção foi *T. deshayesii* cuja população mostrou um decréscimo de 78% em 1999. As flutuações da densidade não estiveram correlacionadas com factores ambientais, provavelmente porque estes artrópodes habitam micro-habitats bem tamponizados, num ambiente sem grande sazonalidade. As alternâncias demográficas podem ser devidas a competição intra- e inter-específica. A grande sobreposição, embora com diferentes micro-distribuições, das espécies simpátricas ao longo do gradiente entre-marés sugerem interações inter-específicas de competição. Além disso, os animais podem estar a competir por um alimento de alta qualidade. Os potenciais mecanismos para evitar a competição deduzidos dos dados obtidos neste estudo foram discutidos. Diferenças específicas de cada espécie nos requisitos nutricionais mediados por diferenças específicas nas capacidades digestivas podem reduzir a competição por alimento. Para além disso, o desfasamento em termos de tamanho das espécies de macrofauna estudadas pode permitir a utilização de diferentes fontes de alimento e talvez micro-refúgios. As espécies coexistentes podem também reduzir a competição apresentando fenologias reprodutivas diferenciadas, como parece ter sido o caso da comunidade de isópodes neste estudo. No entanto, o desfasamento reprodutivo em termos de fenologia parece não ser suficiente para explicar a coexistência dos isópodes e dos anfípodes neste sapal. O efeito da predação é desconhecido.

A produção anual de isópodes e anfípodes foi calculada pelo método da soma de incrementos como 17.6 g peso seco livre de cinzas m^{-2} e 2.2 g peso seco livre de cinzas m^{-2} , respectivamente. Especula-se que estes detritívoros possam contribuir de forma significativa para a re-mineralização da matéria orgânica neste ecossistema de sapal.

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CHAPTER 1

General Introduction

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THE SALT MARSH ECOSYSTEM

What is a salt marsh?

Coastal salt marshes can be defined as areas that border saline water bodies and are vegetated by herbs, grasses or low shrubs which are subjected to periodic flooding as a result of fluctuations (tidal and non-tidal) in the level of the adjacent water body. Located in the interface between land and sea, salt marshes are characterised by features of the flora and fauna of both terrestrial and marine biotopes. In fact, salt marshes are best regarded as highly modified terrestrial ecosystems (Adam, 1990).

Marshes are sedimentary habitats that develop along low-energy coastal areas in mid and high latitudes worldwide (Chapman, 1992; Mitsch & Gosselink, 1993). They may occur in the shelter of sand spits, protected bays or in a lagoon behind a barrier island system and on open coasts if the adjacent sea is very shallow. The ideal locations for the formation of extensive salt marsh areas are river deltas associated with a coastal plain of very smooth slope (Chapman, 1976; Packham & Willis, 1997).

Tides are the dominant aspect of rapid and marked changes in the physical environment of a salt marsh. However, tides are regular and predictable, and thus, cannot be referred to as disturbances but rather act as stressors on intertidal organisms. Nevertheless, sudden climatic changes may exert unpredictable effects upon the tidal magnitude. The erosion caused by storms, rainfall and sediment displacement promoted by currents are some of the principal factors that tend to destabilise salt marshes. However, in most cases, salt marshes remain intact (Wiegert & Pomeroy, 1981) and are remarkably stable systems (Wiegert et al., 1981).

The importance of salt marshes

Salt marshes are generally acknowledged to be one of the most productive natural vascular plant communities on earth, exceeding the productivity of most agricultural crops systems (Odum, 1970; Chapman, 1992; Vernberg, 1993). The fate of the biomass of primary producers in salt marshes is controversial. Generally, consumption by herbivores is extremely limited (e.g., Jackson et al., 1985; Daehler & Strong, 1995; Packham & Willis, 1997; Pennings & Bertness, 2001), therefore most of the biomass of the marsh vegetation passes through the detritus pathway which includes a high variety of macro- and microorganisms (Duarte & Cebrián, 1996; Hemminga et al., 1996; Packham & Willis, 1997; Pennings & Bertness, 2001).

Teal (1962) was the first to suggest that salt marshes are organic matter exporters due to the excess of primary production which is not consumed in the system – “the outwelling hypothesis”. Since then a lot of authors have studied this topic but without conclusively supporting or rejecting the hypothesis. Odum (2000), reviewing numerous studies on this issue, concluded that enrichment of coastal waters by salt marshes strongly depends on the particular system studied and may not even exist in some areas. Levels of exportation are related to the level of productivity and extent of a salt marsh, the tidal magnitude and the geomorphology of the adjacent coastal environment. When export occurs, it does not necessarily occur in every tidal cycle, and it may be intermittent or even associated with great storms or major spring tides. Nevertheless, at each time a shoal of juvenile fishes visit the salt marsh during high tide to feed on detritus, microorganisms, macrofauna and algae, the salt marsh is exporting organisms and not organic matter or nutrients (Odum, 2000).

Teal & Howes (2000) reviewed published studies on the importance of salt marshes for fish production and have concluded that species in both the salt marsh and the surrounding estuarine environment at least partially depend upon salt marsh production for all or part of their nutrition. Furthermore, this wetland area functions as refuge for many larval and juvenile fishes probably due to the interaction between temperature, turbidity, and vegetation structure which restricts the penetration of predators (Deegan et al., 2000). Therefore, salt marshes are important for fisheries. Some species use this habitat as a nursery zone, while others, visiting from the adjacent estuary gain the energy they need from the salt marsh by horizontal fluxes of energy and nutrients from the salt marsh to the adjacent ecosystems through sequential consumption and nekton migration. In addition, salt marshes support the fisheries indirectly by exporting potential prey for carnivorous fish species that live in coastal waters (Deegan et al., 2000; Cicchetti & Diaz, 2000).

Furthermore, salt marshes are potentially large sinks for the excess carbon that is being produced by the burning of fossil fuels, and chemical processes in marsh sediments can reduce or limit the accumulation of nitrogen and sulphur by-products of human agriculture and industry (Pennings & Bertness, 2001).

Coastal marshes also buffer shorelines from flood and storm damage both by absorbing the energy of storms as they hit the land and by limiting storm-induced erosion by binding shoreline sediments. Salt marshes are also widely believed to enhance water quality and serve as sewage treatment systems (Pennings & Bertness, 2001).

Biotic composition of salt marshes

The lower intertidal part of a salt marsh is usually species-poor in terms of vascular plants. Often the lowest community forms a clear zone dominated by a single species, but there may occasionally be a coarse mosaic of communities with each community forming large patches dominated by a single species (Adam, 1990). In salt marshes all over the world, the most frequently dominant species belong to the genus *Spartina* (Wiegert et al., 1981). With increasing elevation, species diversity tends to increase. The extreme upper marsh, and the transition to terrestrial habitats, is a region of considerable environmental heterogeneity, strong environmental gradients and considerable temporal variability. This narrow zone supports a wide range of communities and a rich flora (Adam, 1990).

The productive plant populations of the salt marsh support abundant populations of animals (Montague et al., 1981). The salt marsh fauna can be subdivided in various ways: taxonomically, by ecological affinity (the salt marsh fauna includes groups with marine, freshwater and terrestrial affinities and evolutionary origins), trophically, by subhabitat occupied, or by residence status. Some animals are permanent residents in salt marshes; others are visitors, some seasonally (as are many migratory birds), some only at high tide, others only at low tide, some at particular stages in their life cycle, many only casually. For some visiting species, access to the salt marsh is essential, for others it may be important (or even essential) for particular populations but not essential for the species as a whole; for yet other species exploitation of salt marsh resources is opportunistic (Adam, 1990).

Salt marsh animals live in a particularly harsh intertidal habitat. They are species which exhibit structural, physiological and behavioural abilities to adapt to or to avoid a

wide range of salinity, temperature, humidity, inundation, desiccation and other environmental factors as the physical and chemical nature of the substrate (Kneib, 1984; Chapman, 1992). These parameters have both direct and indirect effects on the ability of animals to acquire food and shelter as well on the reproduction and care of the young. Few species possess tolerance limits wide enough to adapt to such variable conditions (Chapman, 1992).

Physical and biological conditions clearly exclude certain species from the salt marshes. Indeed, although population sizes of individual species are often large, diversity of species in the salt marsh is generally low. The most common groups of macrofauna include crustaceans, molluscs, insects, oligochaetes and polychaetes (Levin & Talley, 2000; Kreeger & Newell, 2000).

Saltmarshes differ from most terrestrial ecosystems in that, at least potentially, *in situ* production by plants is not the only major carbon and energy source for heterotrophs. An alternative supply is provided by material washed into the marsh by the tide (Adam, 1990). Although wrack may bring with it an associated fauna, major colonization is mainly from the shore on which it strands. The colonizers are a characteristic wrack fauna that utilizes the plant material as food and/or shelter. By their feeding activities and metabolism, or through their non-trophic activities such as movement through the substrate, the wrack animals assist in the microbial process of plant decay during which nutrients are mineralized and the wrack is converted either into refractory materials, living animal tissue, or excretory products (Averill, 1976; Lopez et al., 1977; Richardson & Morton, 1986; Hassall et al., 1987; Wildish, 1988; Zimmer et al., 2002). Wrack animals can also be preyed upon by other animals, including wrack invertebrates, fish, birds, and mammals (Wildish, 1988). These drift-litter beds may be important sites in the nutrient cycling processes of salt marshes and

fauna clearly play a major role in the processes which ultimately result in mineralization of the litter (Adam, 1990).

RATIONALE AND AIMS

As mentioned above, marshes are clearly important as they provide a variety of ecosystem services to humans, sheltering coasts from erosion, filtering sediments and nutrients from the water column, playing a significant role in the global cycling of carbon, nitrogen, and sulphur, and by supporting fisheries. Nonetheless, the loss of marsh acreage to human development can approach 80% in developed countries (Dreyer & Niering, 1995). Understanding how marsh communities function will be necessary to properly protect and restore them.

One of the biggest problems is that our understanding of marsh systems is based on a limited number of studies in an even more limited number of study systems. Most of the studies on the functioning of salt marsh ecosystems are centred in a very specific type of marsh: the *Spartina alterniflora* Loisel salt marsh of the East coast of US. Comparatively, few investigations have been done in other types of coastal marshes. Compared with North America very little attention has been paid to the study of biological and energetic processes in the European salt marshes (Adam, 1990; Chapman, 1992). Our understanding of geographic variation in pattern and process of European salt marshes is therefore less complete. Community-level studies of marsh systems are needed from different parts of the world and as coastal marshes continue to be destroyed and altered by anthropogenic impacts, our grasp of their community dynamics becomes more and more critical (Pennings & Bertness, 2001).

Conservation of these habitats begins with a thorough knowledge of the plant and animal species that occur there. Conservation of salt marshes require more information about the ecology and natural history of the resident faunal taxa which is essentially composed, according to Teal (1962), by isopods, amphipods, oligochaetes and other groups of fresh water or terrestrial origin e.g., arachnids and insects. Studies on the ecology of salt marsh macrofauna in European salt marshes are scarce and some focus on a single species or specific group (but see Nicol, 1935; Den Hartog, 1963; Amanieu, 1969; Fouillet, 1986 cited by Créach et al., 1997; Meyer et al., 1995; Sprung & Machado, 2000). In a preliminary study, Sprung & Machado (2000) found that a few peracarid species were both very abundant and dominant in a salt marsh of the Ria Formosa lagoon (South Portugal). These peracarids were amphipod and isopod species that accounted in most samples for more than 95% of the total individuals.

The Ria Formosa lagoon is the largest wetland area in southern Portugal and is an important ecosystem not only in an ecological but also in an economic context. Salt marshes occupy 40% of its intertidal area (Sprung et al., 2001).

- The present work aims to contribute to the so far limited knowledge on macrofaunal salt marsh residents, on their ecology, and ultimately on their roles in the ecosystem.
- In this context, the present study aims to analyse the distribution, population dynamics, life histories and secondary production of the peracarid species that inhabit a high intertidal salt marsh of the Ria Formosa lagoon.
- The relations between different species coexisting in the salt marsh habitat are analysed.

- Based on secondary production and biomass data of the studied species, estimations of the potential degradative impact of these faunal elements on the salt marsh ecosystem are made. The different species are treated in distinct chapters in this thesis.

The biology, population dynamics and production of the most abundant species of this macrofauna assemblage, the isopod *Tylos ponticus*, are investigated in Chapter 2. This subject has been presented as a first draft in a Master thesis (Dias, 2002). The second most abundant peracarid in the salt marsh is *Orchestia gammarellus*, which dominates the amphipod community. Its biology, population dynamics and secondary production are discussed in Chapter 3. Population dynamics and life history strategies used by the isopod assemblage to survive in the harsh salt marsh habitat are debated in Chapter 4. Distribution, population dynamics and relations between the different amphipod species are analysed in Chapter 5. The major results and conclusions obtained from the various chapters are integrated in Chapter 6.

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CHAPTER 2

Population dynamics and production of the isopod *Tylos ponticus* in a Ria Formosa salt marsh (South Portugal)

Dias, N. & M. Sprung, 2003. Population dynamics and production of the isopod *Tylos ponticus* in a Ria Formosa salt marsh (South Portugal). *Crustaceana Monographs*, 2: 133-149.

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INTRODUCTION

Salt marshes border shallow sheltered sediment coasts of temperate regions. They belong to the most productive natural sites of the world with net primary production rates in the order of magnitude of a well fertilized agricultural field (Vernberg, 1993). For the fate of this primary production exist controversial information, which may reflect regional differences. The problem is that primary production is frequently much higher than the degradative capacity of the elements of the salt marsh. In many cases the excess of organic matter is exported to the adjacent coastal areas (e.g., Valiela et al., 2000).

Generally, degradation by herbivorous activity is extremely limited (e.g., Jackson et al., 1985, but also Daehler & Strong, 1995). If degradation actually takes place in the marsh, it is mostly by the detritus pathway, which includes a high variety of macro- and microorganisms (Duarte & Cebrián, 1996; Hemminga et al., 1996; Bouchard et al., 1998).

Salt marshes are also physiologically difficult areas. Due to fluctuating physico-chemical factors, such as humidity, temperature and salinity, salt marshes are considered stressful habitats for most organisms. Only a restricted number of plant and animal species can cope with these conditions (Adam, 1990).

In the Ria Formosa lagoon salt marshes occupy 25 km² corresponding to 40% of the intertidal area (Sprung et al., 2001). The macrofauna of the salt marshes is dominated by amphipods and isopods. Species display a very particular distribution in a vertical profile (Sprung & Machado, 2000).

The isopod *Tylos ponticus* Grebnitzky, 1874 is the most abundant species close to the mean high tide level of the salt marshes. This species has been described mainly

from debris of coarse sandy beaches of the Mediterranean and the Black Sea, and Atlantic coast of northwestern Africa south to Dakar, Madeira and Canary islands (15° to 45° northern latitude) (Schmalfuss & Vergara, 2000). In the present paper we explore the life cycle strategy adopted by this isopod in the salt marsh environment. Our initial assumption has been that due to strong environmental fluctuations only *r*-strategists would propagate successfully, in particular species with a short life expectation, high fecundity and an extended reproductive period.

STUDY AREA

The Ria Formosa is a mesotidal lagoon separated from the ocean by a 55 km long barrier island system on the south coast of Portugal (Fig. 1). The salt marshes in this lagoon are of the dry coast type (Adam, 1990) with the vegetation consisting of *Spartina maritima* (Curtis) in the lower level, *Sarcocornia* spp. and *Atriplex portulacoides* (L.) in the intermediate region and *Suaeda vera* J. F. Gmelin, *Suaeda maritima* (L.), *Halimus atriplex* (L.) and *Limoniastrum monoptalum* (L.) Bss. in the upper zone.

MATERIALS AND METHODS

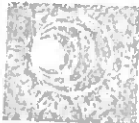
Temperature was registered daily by a minimum-maximum thermometer during the sampling period at a distance of 3 km from the study site. Precipitation data were obtained by the Direcção Regional da Agricultura do Algarve, which is nearly 7 km away from the site.

The animals were collected from the upper salt marsh every sixth week at neap tide between November 1997 and July 1999. Two different levels were sampled: (1) a lower stratum corresponding to the mean high tide level (MHTL) with deposits of *Zostera noltii* Hornem., *Spartina maritima* and some algae (mainly Ulvales); (2) an upper stratum corresponding to the spring high tide level (SHTL). Deposits in the upper stratum were less and consisted mainly of dry leaves and stems of plants of the salt marsh. Samples have been taken by two methods: (a) pit-fall traps filled with a very dilute formalin solution exposed for 4 nights (6 replicates); (b) sand cores of 113 cm² to a depth of 20 cm sieved with a 500 µm mesh on site (30 replicates).

The following characteristics were recorded for each specimen: body length, sex, presence and number of eggs/young, ash free dry weight. Ash free dry weight was obtained pooling 1 to 20 specimens of each size class (for each core or trap individually); they were dried for 2 days at 60°C and ashed for 3 h at 450°C. Aggregation was estimated by the variance-to-mean ratio (I_D) (Krebs, 1989). Cohorts were identified by size frequency analysis using the FISAT package (FAO-ICLARM Stock Assessment Tools). Relative growth rates were calculated from changes in mean length and weight of a cohort through time.

Annual mortality was assessed by the decrease of the abundance of each cohort, pooling all replicates. Age specific survivorship was calculated by the slope b of a regression of $\ln(n+1)$ (for a particular year class) versus time. An apparent increase in cohort abundance was treated as a lack of mortality. The annual mortality of a cohort (q_x) was given by the equation: $q_x = 1 - e^{b \times 365}$.

Secondary production was estimated by the increment summation method (Boysen Jensen, 1919) (a) and the removal summation method (b):



$$(a) P_{1,2} = \text{antilog} \left(\frac{\log n_1 + \log n_2}{2} \right) \times (\varpi_2 - \varpi_1)$$

$$(b) P_{1,2} = (n_1 - n_2) \times \text{antilog} \left(\frac{\log \varpi_2 + \log \varpi_1}{2} \right)$$

$P_{1,2}$: cohort production between sample date 1 and 2;

n_1, n_2 : abundance of the specimens of the cohort at date 1 and 2;

ϖ_1, ϖ_2 : mean weight of the specimens of the cohort at date 1 and 2.

Significance of the difference between two means was tested by a *t*-test (Zar, 1999).

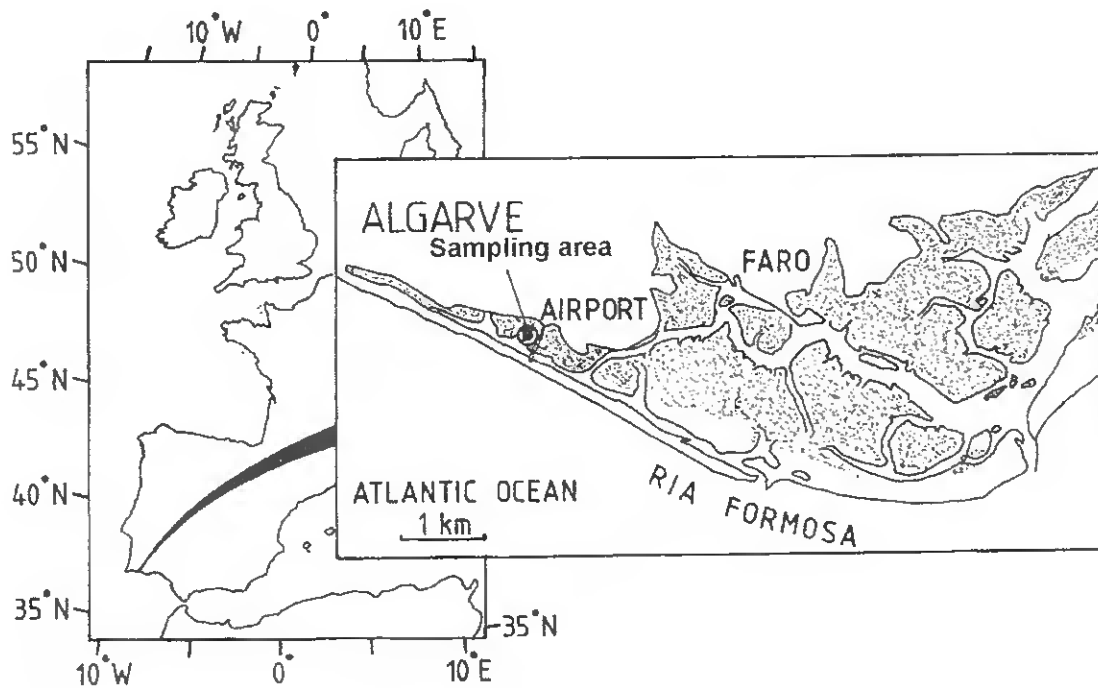


Fig. 1. Location of the study area.

RESULTS

Demography and distribution

The abundance of *Tylos ponticus* was correlated with air temperature (MHTL: $r = 0.79$, $P < 0.005$; SHTL: $r = 0.96$, $P < 0.001$). Precipitation had no apparent impact on the isopod abundance. Average density in the lower stratum was 3790 ind m⁻², varying between 788 and 8080 ind m⁻², with the highest values from June to November 1998. Density registered in November 1998 was nearly 4 times higher than in November 1997 indicating year to year variation. In the upper stratum density was significantly lower (t -test, $P < 0.05$) with an average of 2109 ind m⁻², ranging from 115 to 10387 ind m⁻², and a very pronounced peak in July 1998. In the following year there was no summer peak and density in July 1999 was 90 times lower than in the previous year. Rather the highest record in 1999 was in April (Fig. 2). Variance/mean ratio (I_D) at the MHTL was 3 to 124 (average 41) and at the SHTL 4 to 380 (average 62), which indicates a high aggregation in both cases.

Contrary to our expectation isopod density was higher where organic deposits were missing (Table 1). This could be proved by samples taken from sites (a) with deposits and (b) without deposits, but with a high number of holes in the sediment (probably by *Tylos*) (t -test, $P < 0.01$). This tendency was observed both at MHTL and SHTL.

Population structure was different at these two reference sites (Fig. 3). Juveniles (unsexed individuals - length < 4 mm) and non egg-carrying females were generally more abundant at the mean high tide level (t -test, $P < 0.05$), while egg-carrying females

and males were collected in greater densities at the spring high tide level (*t*-test, $P < 0.01$). However, mean length of the specimens was not significantly different between the intertidal levels (*t*-test, $P > 0.05$), which implies a high exchange rate of individuals.

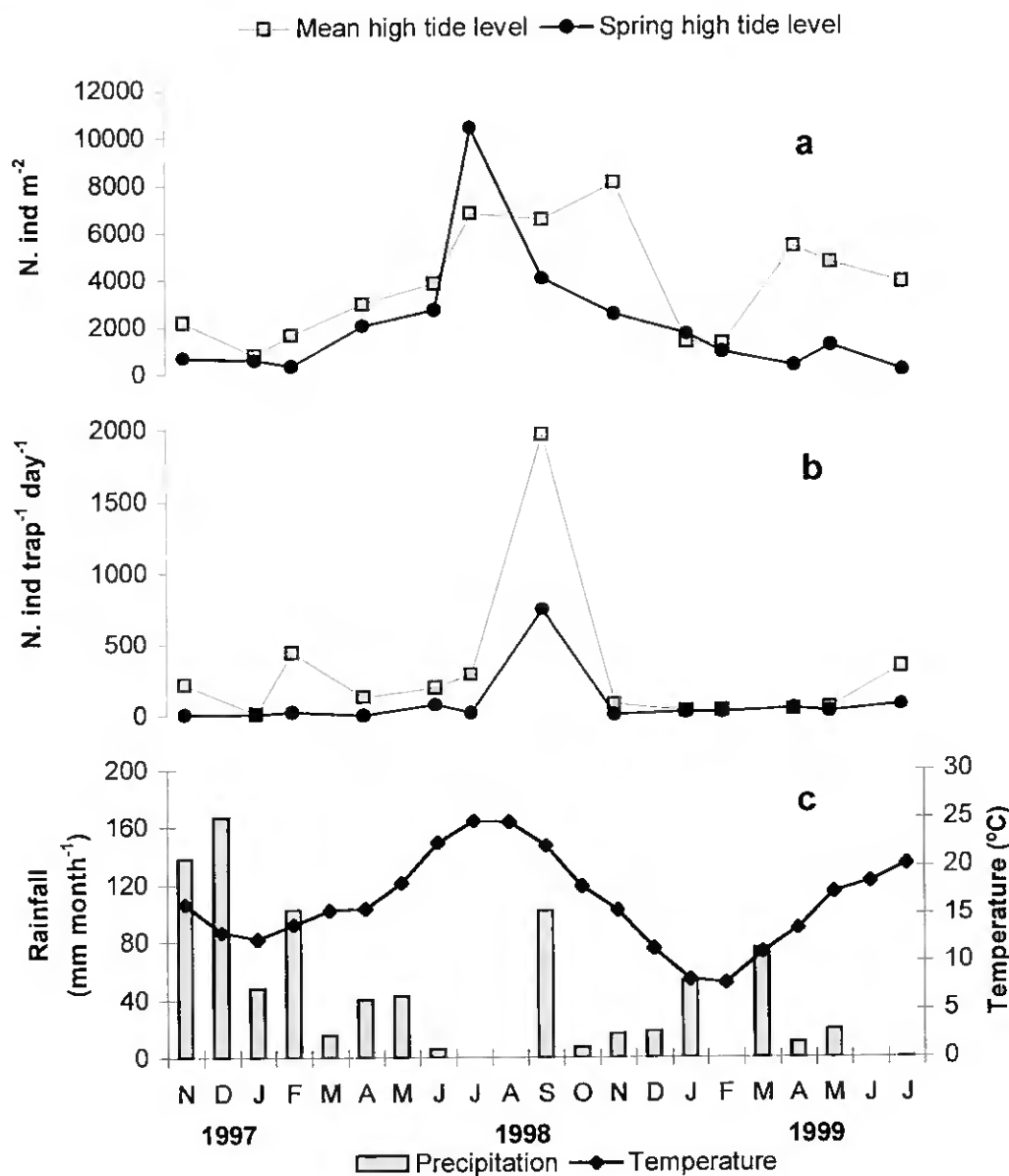


Fig. 2. a, Population mean density of *Tylos ponticus* Grebnitzky, 1874, at mean high tide and spring high tide levels (N. ind m⁻²); b, population activity at the sampling sites (N. ind per trap per day); c, temperature (°C) and rainfall (mm month⁻¹) registered during sampling in the study area.

Table 1. *Tylos ponticus* Grebnitzky, 1874, mean density (n. ind core⁻¹) registered on sites with and without deposits of organic matter both at mean and spring high tide levels (MHTL and SHTL, respectively) (S. D. - standard deviation; n - number of samples).

| | MHTL | | | SHTL | | |
|------------------|--------------|-------|----|--------------|-------|----|
| | Mean density | S. D. | n | Mean density | S. D. | N |
| With deposits | 30.4 | 40.9 | 48 | 11.2 | 21.5 | 48 |
| Without deposits | 58.5 | 65.3 | 48 | 74.8 | 106.4 | 48 |

Activity

Animals were active during the whole year with a tendency of increasing activity from late spring to early fall with a maximum by the end of September (1962 ind trap⁻¹ day⁻¹ were caught at MHTL and 742 ind trap⁻¹ day⁻¹ at SHTL) (Fig. 2). Traps caught more specimens at the mean high tide level. However, a comparison of core and trap data revealed sex and age specific differences (Figs. 3, 4). Traps contained a higher male fraction in late spring and summer. In late September the most significant fraction caught by traps were animals > 4 mm body length (both males and females) and surprisingly not new recruits although they represented 65% of the specimens in the cores. Juvenile activity increased in late fall and in winter presenting a negative correlation with air temperature ($r = -0.57$, $P < 0.05$). Egg-carrying females were also active, especially during the beginning of the reproductive period (late spring) (Table 2). During summer their activity decreased and increased again in early fall. This is corroborated by a negative correlation between the activity of egg-carrying females

and temperature ($r = -0.92$, $P < 0.05$). For the entire population, however, no correlation was evident between the surface activity of isopods and the monthly rainfall ($r = 0.41$, $P > 0.05$) or air temperature ($r = 0.45$, $P > 0.05$).

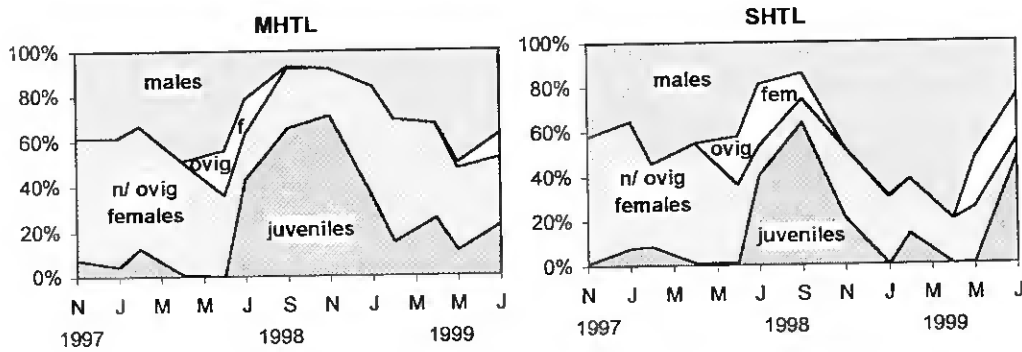


Fig. 3. *Tylos ponticus* Grebnitzky, 1874, percentage of non ovigerous females, ovigerous females, males and juveniles given in core samples taken at mean high tide level (MHTL) and spring high tide level (SHTL).

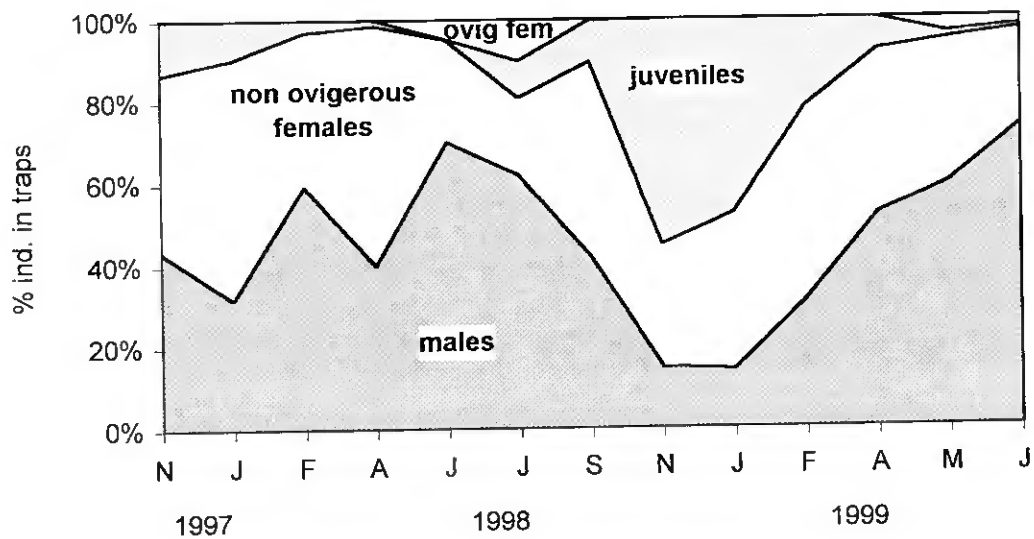


Fig. 4. *Tylos ponticus* Grebnitzky, 1874, activity of non ovigerous females, ovigerous females, males and juveniles.

Table 2. *Tylos ponticus* Grebnitzky, 1874, activity of egg-carrying females indicated by the ratio of their fraction in traps and in cores.

| | Egg-carrying females |
|-------------------|-------------------------|
| 4 June 1998 | 22.8 % |
| 29 July 1998 | 23.9 % |
| 25 September 1998 | 40.0 % |
| 23 May 1999 | 76.4 % |
| 24 July 1999 | 18.2 % |

Sex ratio

The percentage of females in the population was on an annual average 61% during the first year of sampling (November 1997 to November 1998). Dominance of females was more pronounced during summer and early fall (reproductive season), with a peak of 70% in late September. In 1999 (January to July) average percentage of females decreased to 48%. It must be stressed that this population is not infected by the feminizing bacterium *Wolbachia* (cf. Bouchon, pers. comm.). Analysis of sex ratio by age class showed that the population is female biased particularly in the younger age classes and this preponderance decreases progressively with older animals (Fig. 5).

Life history and growth

Cohort progression of males and females was different. Females had a life expectancy of approximately 3 years and reached up to 13 mm body length, while males lived up to 4 years and attained 14 mm body length (Fig. 6).

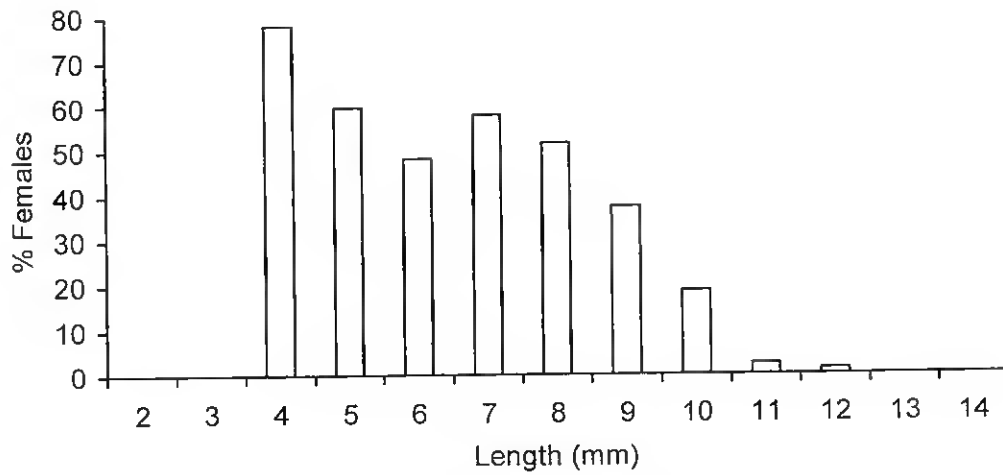


Fig. 5. *Tylos ponticus* Grebnitzky, 1874, percentage of females by size class, n = 5279.

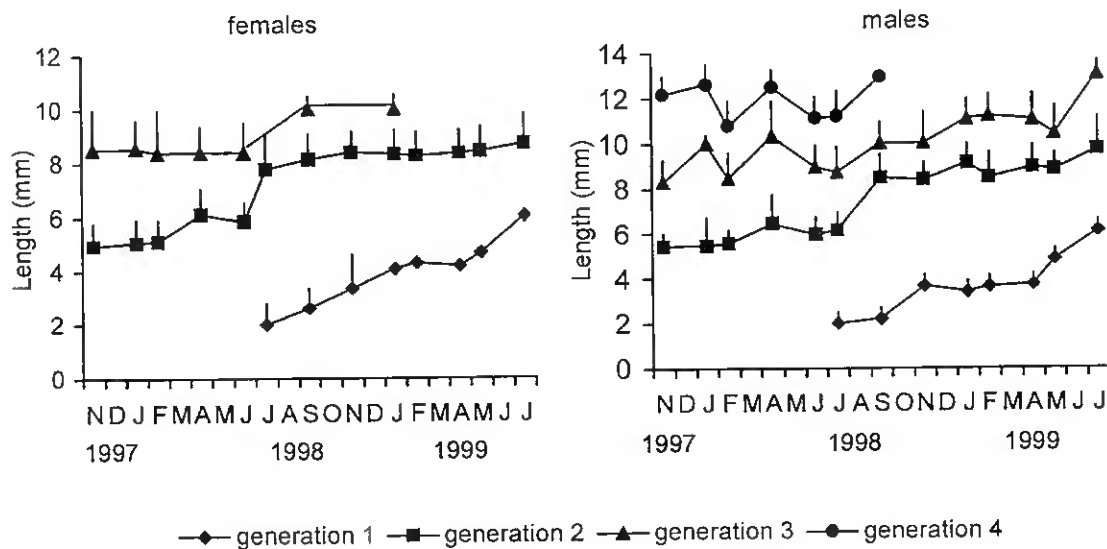


Fig. 6. *Tylos ponticus* Grebnitzky, 1874, cohort progression of females and males (• mean length, | standard deviation).

Juveniles were recruited at 2 mm length from July to November. Recruitment showed a peak in July with 3230 recruits per m² in 1998, but only 708 recruits m⁻² in 1999 (i.e., 4.5 times less). By the end of the recruitment season, in November, the new generation represented 64% of the population in 1998 in contrast to 6.6% in 1997.

Growth in length and weight was slow. As a tendency declined with age and was higher in males (Table 3). Body weight of females and males was not significantly different (*t*-test, $P > 0.05$). Weight at a specific length did not vary seasonally in both sexes (4 and 8 mm body length: ANOVA, $P > 0.05$).

Table 3. *Tylos ponticus* Grebnitzky, 1874, growth in length and weight of females and males for each year class.

| Year | Length increment (mm) | | Weight increment (%) | |
|------|-----------------------|-------|----------------------|-------|
| | Females | Males | Females | Males |
| 1 | 3.8 | 3.7 | 95.9 | 96.1 |
| 2 | 2.0 | 2.4 | 24.4 | 62.7 |
| 3 | 0.6 | 3.1 | 36.8 | 51.7 |
| 4 | | 0.4 | | 47.6 |

Reproduction

Ovigerous females were 5 and 11 mm long. This means that they potentially can reproduce after their first year. This is, however, only realized by a low fraction of animals (Table 4). The majority rather allocates energy into growth instead of reproduction thereby maximizing their individual fitness.

The breeding season extends from May to late September with the highest reproductive activity in mid summer (Table 5). However, contrary to this affirmation once an ovigerous female was found in January 1999. The number of eggs increases with female size and is given by the equation:

$$y = 4.02 x^{0.67}$$

n = 151; $r^2 = 0.40$

y: number of eggs

x: body ash free dry weight [mg]

Each female produced on average 11.9 eggs, with a range of 7 to 21. As to be concluded from their size, first ovigerous females caught in May and early June were 2-3 year old. In late July breeding females were 1, 2 and 3 year old and in late September only 1 year and 2 year old females were breeding. The highest fraction of offspring was produced by the 2 year old generation (Table 4).

Table 4. *Tylos ponticus* Grebnitzky, 1874, age specific fecundity.

| Year | % ovigerous females | Female fecundity | % eggs produced |
|------|---------------------|------------------|-----------------|
| 1 | 11.7 | 8 | 8 |
| 2 | 67.7 | 11 | 64.3 |
| 3 | 20.6 | 15.6 | 27.7 |

Table 5. *Tylos ponticus* Grebnitzky, 1874, reproductive activity indicated as the proportion of females carrying eggs.

| | Egg-carrying females |
|-------------------|----------------------|
| 4 June 1998 | 37 % |
| 29 July 1998 | 58 % |
| 25 September 1998 | 43 % |
| 23 May 1999 | 16 % |
| 24 July 1999 | 27 % |

Population structure

The population structure changed in a characteristic way during the sampling period (Fig. 7). During the first winter, generation 2 formed the bulk of the population. In spring and early summer the importance of generation 3 and 4 increased while the proportion of 2 year old individuals decreased. By midsummer generation 1 appeared and represented by November about 90% of the population. At this time recruitment ceased and a premature decline of generation 1 started, so that generation 2 became again the most important age class of the *T. ponticus* population in spring 1999.

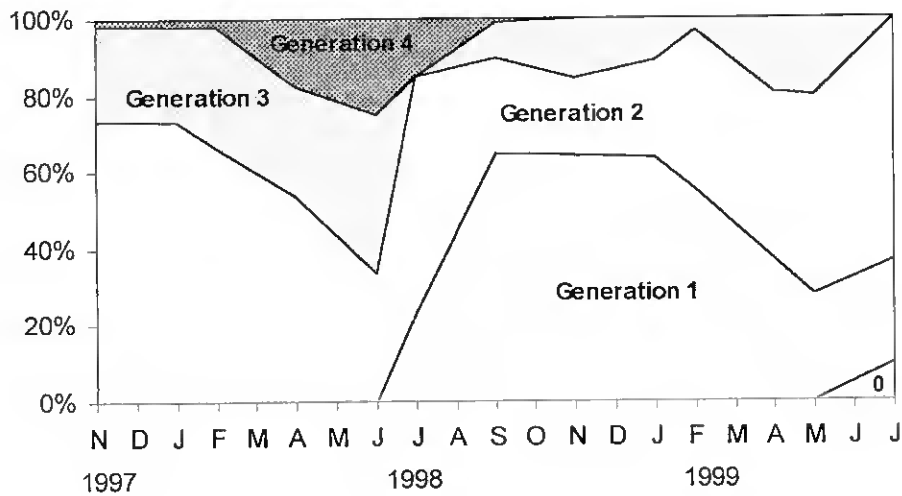


Fig. 7. *Tylos ponticus* Grebnitzky, 1874, variation in age structure. Age groups were classified as follows: generation 0 for individuals born in July 1999; generation 1 for those born in July 1998 < 1 year old; generation 2 for those 1-2 year old; generation 3 for those 2-3 year old and generation 4 for those 3-4 year old.

Mortality

During the first year of life, mortality in both sexes was not very different (78.4% in females and 82% in males). Analysis of juvenile mortality indicates that animals die mainly during the first months of life. No such figure could be indicated until November, because mortality was superimposed by recruitment. However, mortality during the 3 following months (November until February) shows nearly exactly the same reduction rate as during the whole first year of life.

During their second year of life the mortality of females was 25.3%, whereas males of the same age apparently did not decrease in number. This seems to be contradictory to an increase in the percentage of females in late September. At an age of 3 years all females and 46.2% of the males died. The male population did not survive the 4th year.

Secondary production

Secondary production obtained by the removal summation method was of 7.4 g ash free dry weight $m^{-2} year^{-1}$ and P/B ratio of 2.0. Using the increment summation method an annual production of 17.5 g ash free dry weight m^{-2} and a P/B ratio of 4.7 were calculated.

The highest biomass losses were in September. Biomass increment occurred during all seasons with a peak in January 1998 (Fig. 8).

Two year old specimens contributed most to the annual production calculated by both methods. It should be stressed that the production in September was due to cohort 2 and 4 and not to the recruits, as to be expected (Table 6).

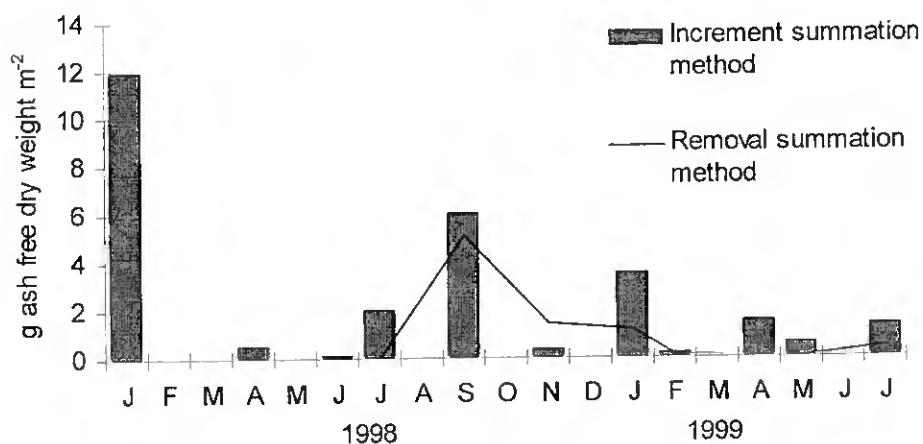


Fig. 8. *Tylos ponticus* Grebnitzky, 1874, secondary production calculated by the increment summation method and the removal summation method.

Table 6. *Tylos ponticus* Grebnitzky, 1874, secondary production.

| | Annual production (g ash free dry weight m ⁻²) Increment summation method | Annual production (g ash free dry weight m ⁻²) Removal summation method |
|------------------|---------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------|
| Generation 1 | 1.1 | 1.6 |
| Generation 2 | 8.3 | 2.2 |
| Generation 3 | 2.9 | 1.0 |
| Generation 4 | 5.2 | 2.6 |
| Total population | 17.5 | 7.4 |
| P/B | 4.7 | 2.0 |

DISCUSSION

Contrary to our initial assumption, despite the particularity of the salt marsh environment, most of the life history characteristics of *Tylos ponticus* are not that of an r -strategist. This does not mean automatically that it is a K -strategist. Rather the question is more subtle when the following aspects are considered.

Reproductive pattern

Age at first reproduction of *Tylos ponticus* is in general 2 years, however, a minor fraction of animals (11%) reproduces already after its first year of life. Hassall & Davis (1991) in a comparative analysis of 3 grassland isopods found a mean age at first reproduction between 13 and 25 months. *Tylos ponticus* attains sexual maturity late compared to these data, although it has the potential of some flexibility. Individual differences in breeding phenology can be interpreted simply as an adaptive strategy of the species (Zimmer & Kautz, 1997).

However, this can also be associated to another mechanism. According to Lawlor (1976) it is possible that some juveniles born earlier in the reproductive season grow slowly enough to attain the same size as the fastest growing juveniles born later in summer. The young produced earlier and exposed to the warmer summer would be sexually mature the following reproductive season in contrast to the young produced later in the season. Such a physiological mechanism incorporating the variance in growth rates and differential exposure to warm temperatures promoting gonadal development and maturity could account for the mixed strategy of reproduction among the intermediate size females in the breeding season.

In a compilation of data on number of eggs in the marsupium of different isopod species, Warburg (1987) quoted mean values between 3 and 124. In general, species with particularly low egg numbers are small in comparison to *T. ponticus*. Hence, its fecundity must be considered low. Female biased sex ratio can be a strategy to counterbalance this low fecundity.

During our first sampling year (November 1997 to November 1998) sex ratio remained female biased with an increase between June and September. An increase in female number at the beginning of the reproductive season has been reported by many authors for different isopod species, e.g., McQueen (1976), Hatchett (1947) and Dangerfield & Hassall (1994), but a percentage as high as 70% females by the end of the reproductive period has never been documented to our knowledge. On the contrary, several authors have observed that reproduction is a cause of female mortality (Geiser, 1934; Hatchett, 1947; Brody et al., 1983). Could males be more susceptible to death during the reproductive season? On the contrary, calculated annual mortality rates indicate higher mortality by females. Behavioural and activity differences, pointed out by McQueen (1976) can be excluded, because data are provided by cores and not by traps. Another possibility is that males burrow deeply in the substrate escaping from the sampling range. However, this seems to be doubtful, because males stay highly active during this period.

Mortality

Seasonal fluctuations in abundance in our study are not subject to catastrophic events, but rather to reproduction and possibly continuous predation. Natural isopod predators such as centipeds, beetles and arachnids (Sunderland & Sutton, 1980) coexist

with *Tylos ponticus*. However, their impact on this population is expected to be small, because their densities are extremely low (own unpubl. data).

One attribute of a *K*-strategist is that juvenile mortality is high compared to adult mortality. This applies clearly to *T. ponticus* in this study. A high quotient between juvenile and adult mortality would imply a high risk of extinction for the population in an unpredictable environment, which is not valid for this particular salt marsh.

Growth, life expectancy and body size

It is difficult to have an objective comparison to decide whether growth is slow, life expectancy is long and body size is large in order to be considered a *K*-strategist. This depends highly on characteristics of the specific animal group. In isopod terms an increment of about 3 mm in length per year is slow, life expectancy of 3 to 4 years is long and a maximum length of 14 mm is large although not extreme (Sutton et al., 1984; Hopkin, 1991).

Competitive ability

K-strategists are indicated to have a higher competitive ability than *r*-strategists. Our data do not provide direct information on this issue for *Tylos ponticus*, nevertheless indirect information may be discussed. Most cases of competition are due to limitation of space and food. In either case it is hard to imagine that this salt marsh environment would present any restrictions.

Some annual fluctuations in the density of *T. ponticus* population were observed during the study period. As these fluctuations did not mean a consistent decrease, but an increase as well, a local depletion of the population due to regular sampling can be

excluded. We speculate that there may be some alternation in isopod numbers between years such as pointed out by Al-Dabbagh & Block (1981) and Hassall & Dangerfield (1990) for a population of *Armadillidium vulgare* Latreille, 1802. Hassall & Dangerfield (1990) carried out experiments to explore which mechanisms control population density. They concluded that when a new recruit in one cohort is affected more strongly by an individual in the previous cohort than by other individuals in the same cohort, competition between them would not be reciprocated equally. As a consequence, in a year when the density of the older cohort was higher and that of recruits lower, growth and subsequently fecundity of the low density cohort would be depressed and the numbers in the following year cohort would remain low. Our data provide indication of the validity of this concept for *T. ponticus* for generation 1 and 2.

Another possibility for this annual fluctuation is interspecific competition. Hassall & Dangerfield (1989) demonstrated with populations of *Porcellio scaber* Latreille, 1804 and *A. vulgare* sharing the same niche, that an increase in the density of the *P. scaber* population had significant negative effects on the growth of young *A. vulgare*. As fecundity in isopods is generally determined by size, changes in growth rate caused by other species could be an important factor influencing the population dynamics of an isopod. Also Davis & Sutton (1978) observed that within an isopod community inhabiting a dune grassland, the total biomass was constant even if there were fluctuations in the relative abundance of each species. *Tylos ponticus* shares its environment with other isopods, *Halophiloscia couchii* (Kinahan, 1858), *Porcellio lamellatus* (Uljanin) Budde-Lund, 1885, *Armadillidium album* Dolfuss 1887 and talitrid amphipods, *Orchestia gammarellus* (Pallas 1766), *Orchestia mediterranea* Costa 1853, *Talorchestia deshayesii* (Audouin, 1826). Although each species occupies a characteristic level, they show a large overlap where they potentially may interact (Sprung & Machado, 2000).

Salt marsh primary production is large, and it is tempting to assume that animals in the salt marsh are not food limited. However, there is little experimental evidence to support or refute such an assumption (Montague et al., 1981). In concrete terms, annual net primary production of *Spartina maritima*, one of the most abundant plants in this salt marsh is 768 ash free dry weight m^{-2} (R. Santos & M. Sprung, unpubl. data). This is about 40 times higher than our production data for *T. ponticus*. However, to arrive to a more proper indication for a degradative potential, actual consumption rates are more informative. They can be extrapolated from the production rates, when the assimilation efficiency and respiration rates are known. For *Tylos punctatus* (Holmes & Gay, 1909), Hayes (1974) measured an assimilation efficiency of 64%, 34% of the assimilated fraction accounting for growth. If these data are also valid for *T. ponticus*, we can extrapolate a figure of about 80 g ash free dry weight $\text{m}^{-2} \text{year}^{-1}$ consumed. As such, the hypothesis cannot be totally rejected that *T. ponticus* may contribute significantly to the degradation of organic matter in the salt marsh examined.

However, the food actually available for the salt marsh animals is difficult to define. Much of the organic matter is refractory due to its mechanical or chemical accessibility or is buried in anaerobic soils. Montague et al. (1981) came to the conclusion that assimilable food is close to the threshold for long term survival of the animals in the salt marsh. In this particular case *T. ponticus* prefers algal deposits to *Zostera* or *Spartina*. This also refers to the other peracarid species, which share the same habitat, as well (own unpubl. obs.). *Spartina* and *Zostera* deposits are by far more abundant and continuously available, while the quantity of algal deposits is low and highly variable in space and time. Hence, it there may be competition if food quality is taken into consideration.

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CHAPTER 3

Population dynamics and production of the amphipod

***Orchestia gammarellus* (Talitridae) in a Ria Formosa salt marsh**

(southern Portugal)

N. Dias & M. Sprung, 2004. Population dynamics and production of the amphipod *Orchestia gammarellus* (Talitridae) in a Ria Formosa salt marsh (southern Portugal). Crustacena: 76 (9): 1123-1141.

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INTRODUCTION

The reproductive biology of *Orchestia gammarellus* (Pallas, 1766) has been studied by many authors in Western Europe, such as Charniaux-Cotton (1957), Amanieu (1969), Jones & Wigham (1993), Morritt & Stevenson (1993), and Persson (1999). Growth was examined in the Baltic Sea by Persson (1999). On the Mediterranean coast of Morocco, Aksissou & Elkaim (1994) studied the demography and population dynamics of the species. In more northern countries, *O. gammarellus* reproduces from March/April to September/October (Amanieu, 1969; Wildish, 1979; Moore & Francis, 1986; Jones & Wigham, 1993; Morritt & Stevenson, 1993) while in Morocco reproduction takes place between October and May with a resting period in February (Aksissou & Elkaim, 1994). This has its reflection on fecundity, growth rate, and longevity, and has shed a different light on the importance of environmental factors that condition the life cycle of *Orchestia*, such as temperature, day length, or humidity.

In the present paper, we examine the dynamics of a population of *O. gammarellus* in a salt marsh of the Ria Formosa lagoon on the Portuguese south coast, which is most close to the Moroccan population. *Orchestia gammarellus* is the most abundant amphipod living in this salt marsh and occurs along the upper marsh together with two other talitrids: *Orchestia mediterranea* A. Costa, 1857 and *Talorchestia deshayesii* (Audouin, 1826), and four isopods: *Tylos ponticus* Grebnitzky, 1874 (Tylidae), *Porcellio lamellatus* Budde-Lund, 1879 (Porcellionidae), *Halophiloscia couchii* (Kinahan, 1858) (Halophilosciidae) and *Armadillidium album* Dolfuss, 1887 (Armadillidiidae). We also estimated the secondary production of this amphipod, which has never been done before.

STUDY AREA

We worked in southern Portugal, in the Ria Formosa lagoon. The study site was located near the Faro Airport, off the causeway to Faro Beach (37°00'N 07°59'W). The Ria Formosa is a mesotidal lagoon separated from the ocean by a 55 km long barrier island system on the southern coast of Portugal (Algarve). The salt marshes in this lagoon are of the dry-coast type (Adam, 1990) with the vegetation consisting of *Spartina maritima* (Curtis) Fernald in the lower level, *Sarcocornia* spp. and *Atriplex portulacoides* L. in the intermediate region, and *Suaeda vera* J. F. Gmelin, *Suaeda maritima* (L.) Dumort, *Atriplex halimus* L., and *Limoniastrum monoptalum* (L.) Bss. in the upper zone. Salinity is about 36 psu all year round (Falcão & Vale, 1990).

MATERIALS AND METHODS

Air temperature was registered daily by a minimum-maximum thermometer during the sampling period at a distance of 3 km from the study site. Precipitation values were obtained through the Direcção Regional da Agricultura do Algarve, which is nearly 7 km away from the site.

The animals were collected every sixth week at neap tide between November 1997 and July 1999. Three different levels were sampled: (1) a lower stratum corresponding to the neap high tide level (NHTL) dominated by *Sarcocornia* spp. and *Atriplex portulacoides*; (2) an intermediate stratum corresponding to the mean high tide level (MHTL) with deposits of *Zostera noltii* Hornem, *Spartina maritima*, and some algae (mainly Ulvales); (3) an upper stratum corresponding to the spring high tide level (SHTL). Deposits in the upper stratum were fewer and consisted mainly of dry leaves and stems of plants of the salt marsh. Samples have been taken by two methods: (a) pit-

fall traps filled with a very dilute formalin solution (0.01%) exposed for 96 h (3 replicates per level); (b) sand cores of 113 cm² to a depth of 20 cm sieved with a 500 µm mesh sieve on site (15 replicates per level).

The following characteristics were recorded for each specimen: body length, sex, presence and number of eggs or young, and ash-free dry weight (AFDW). Ash-free dry weight was obtained by pooling 1 to 20 specimens of each size class (for each core or trap individually). They were dried for 2 days at 60°C and ashed for 3 h at 450°C. Aggregation was estimated by the variance-to-mean ratio (I_D) (Krebs, 1989). Cohorts were identified by size frequency analysis for each sex by the Bhattacharya (1967) method using the FISAT software package (FAO-ICLARM Stock Assessment Tools) (core and trap data pooled). Sex could be distinguished in individuals larger than 6 mm body length but for the size frequency analysis individuals of smaller size classes were distributed by each sex according to their percentage in the population at each sampling date. Growth parameters of the non-seasonalized Von Bertalanffy growth curve (VBGF) were estimated using this routine:

$$L_t = L_\infty \{1 - e^{-K(t - t_0)}\}$$

where L_t is the length at age t , L_∞ is the asymptotic length, K is the intrinsic growth rate (curvature parameter) and t_0 is the computed age at length zero.

Growth curves of females and males were compared by an analysis of the residual sum of squares (RSS) following Zar (1999).

The overall growth performance was tested using “Munro’s phi prime test” (Pauly & Munro, 1984):

$$\phi' = 2 \log_{10} (L_\infty) + \log_{10} K$$

Mortality was assessed by the decrease in the abundance of all cohorts, pooling all replicates. Age specific survivorship was estimated as slope b of a regression of $\ln(n+1)$ versus time. The daily mortality of the population (q_x) was given by the equation:

$$q_x = 1 - e^b$$

Secondary production was estimated by the increment summation method (Boysen Jensen, 1919) (1) and the removal summation method (2):

$$(1) \quad P_{1,2} = \text{antilog} ((\log n_1 + \log n_2) / 2) \times (\varpi_2 - \varpi_1)$$

$$(2) \quad P_{1,2} = (n_1 - n_2) \times \text{antilog} ((\log \varpi_2 + \log \varpi_1) / 2)$$

$P_{1,2}$: cohort production between sample dates 1 and 2;

n_1, n_2 : abundance of the specimens of the cohort at dates 1 and 2;

ϖ_1, ϖ_2 : mean weight of the specimens of the cohort at dates 1 and 2.

Significance of the difference between two means was tested by t -test and between more than two data sets by ANOVA (Zar, 1999).

RESULTS

Distribution

The abundance of *Orchestia gammarellus* was highest at MHTL, with an average density of 700 ind m⁻². Densities in this level varied between 0 and 3690 ind m⁻², with the highest values being registered in spring 1999. At the lower level (NHTL) no individuals were caught with the corer. Average density at the upper level (SHTL) was 15 ind m⁻², with values ranging from 0 to 97 ind m⁻² (Fig. 1).

Density was not correlated with air temperature (MHTL: $r = -0.14$, $P > 0.05$; SHTL: $r = 0.18$, $P > 0.05$). Precipitation had no apparent impact on amphipod abundance (MHTL: $r = -0.29$, $P > 0.05$; SHTL: $r = 0.05$, $P > 0.05$). The variance/mean ratio (I_D) at the MHTL was 0.44 to 223 (average 41) and 0.66 to 5 (average 2) at the SHTL. This indicates in both cases that the population was aggregated.

Amphipod density was significantly higher where organic deposits were present (Table 1). This could be concluded from samples taken from sites (a) with deposits and (b) without deposits, but with a high number of holes in the sediment (probably dug by the isopod *Tylos ponticus*, and by *O. gammarellus* and the other talitrids). This tendency was observed both at MHTL and SHTL ($t = 19.62$ and $t = 5.78$; $P < 0.001$).

The structure of the population during the sampling period could be followed only at MHTL where 91% of the population was present (Fig. 2). On average, juveniles contributed 45%, non-ovigerous females 31%, males 23%, and ovigerous females 1% to the population. By comparing the composition of the population caught with cores and with traps, we found that males contributed to a higher fraction in traps than in cores ($t = 4.54$, $P < 0.01$) while for the non-ovigerous females the reverse situation occurred ($t = 3.04$, $P < 0.01$). Ovigerous females showed a higher proportion in traps than in

cores ($t = 2.85, P < 0.01$) and there were no differences for the juvenile fraction ($t = 0.72, P > 0.05$).

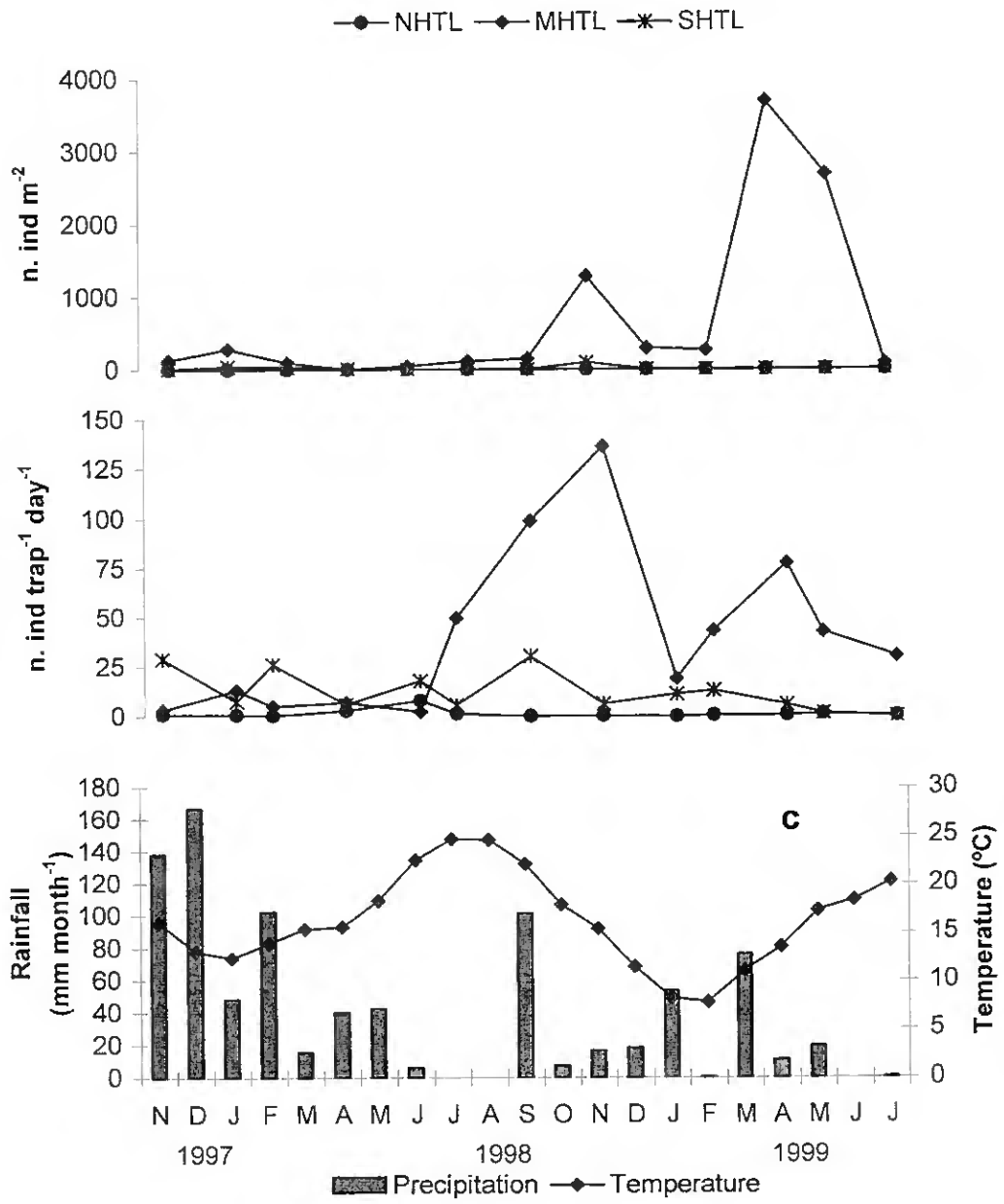


Fig. 1. *Orchestia gammarellus* (Pallas, 1766). a, population mean density at neap high tide level (NHTL), mean high tide level (MHTL), and spring high tide level (SHTL) (n. ind m⁻²); b, population activity at the sampling sites (n. ind trap⁻¹ day⁻¹); c, air temperature (°C) and rainfall (mm month⁻¹) registered during sampling in the study area.

Table 1. *Orchestia gammarellus* (Pallas, 1766), distribution of individuals in areas with deposits of organic matter and areas without deposits but presenting holes at mean high tide level (MHTL) and spring high tide level (SHTL); n = 85.

| | | Individuals per core | |
|------|------------------|----------------------|-------|
| | | Mean | S. D. |
| MHTL | With deposits | 18.20 | 50.19 |
| | Without deposits | 0.13 | 0.43 |
| SHTL | With deposits | 0.75 | 1.74 |
| | Without deposits | 0.25 | 0.44 |

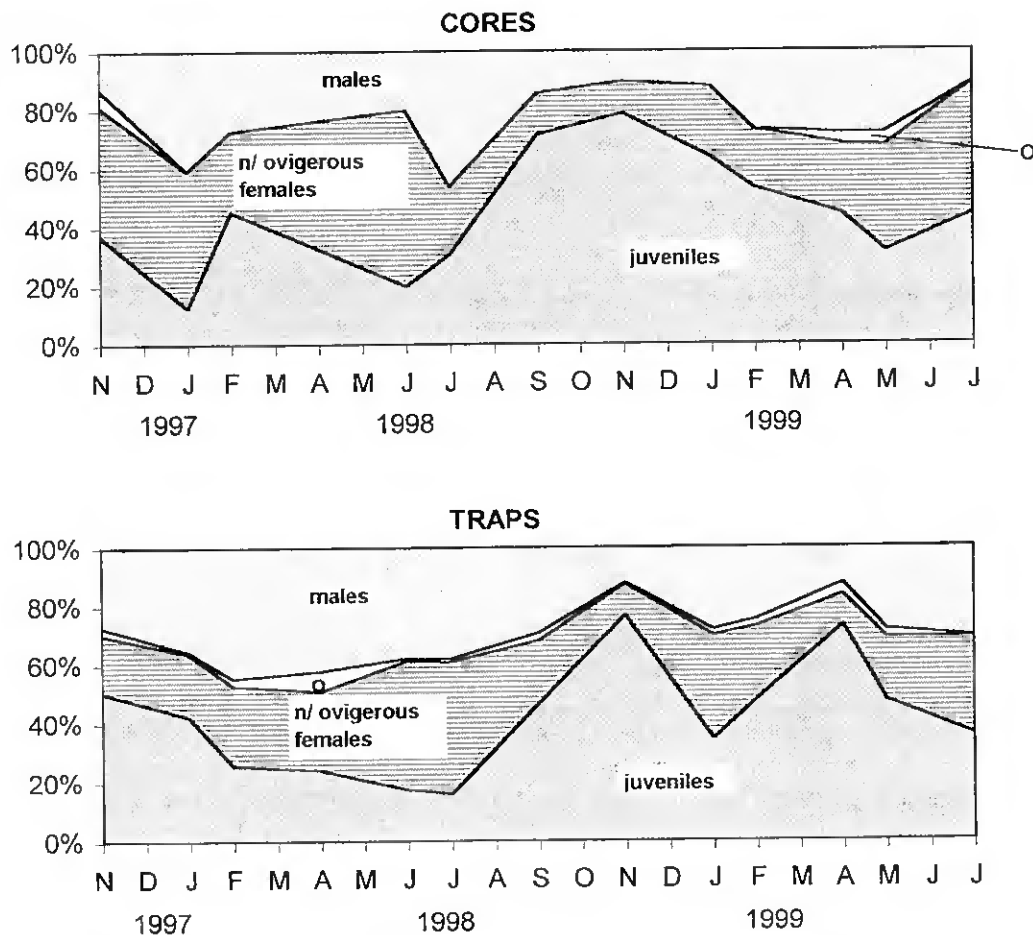


Fig. 2. *Orchestia gammarellus* (Pallas, 1766). Percentage of non-ovigerous females (n/ ovigerous females), ovigerous females (o), males, and juveniles given in samples taken at mean high tide level (MHTL) by the corer and traps.

The percentage of females in the population over 7 mm length was on average 58% (data from cores and traps pooled) (S. D. = 6; n = 5091). Analysis of sex ratio by age class showed that the population is female biased, particularly in the smaller age classes and this preponderance decreases progressively with larger animals (Fig. 3).

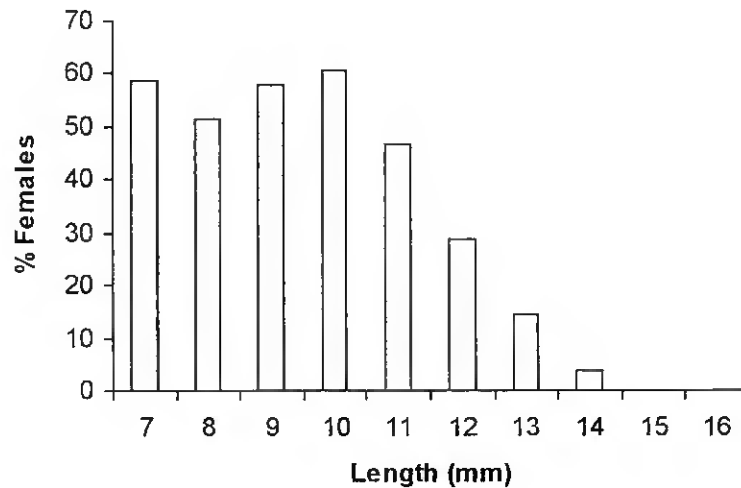


Fig. 3. *Orchestia gammarellus* (Pallas, 1766). Percentage of females by length class; data from cores and traps pooled, n = 5091.

Activity

Animals were active during the whole year, as can be concluded from pit-fall traps which collected animals in every level sampled. The highest values were registered in summer and fall 1998 and in spring 1999 at MHTL (Fig. 1). The activity of the animals was positively correlated with precipitation ($r = 0.81$, $P < 0.001$) at the upper level (SHTL) but no such correlation was found at the two remaining levels (NHTL: $r = -0.24$, $P > 0.05$; MHTL: $r = -0.21$, $P > 0.05$). Air temperature apparently has no influence on animal activity (NHTL: $r = 0.39$, $P > 0.05$; MHTL: $r = 0.13$, $P > 0.05$; SHTL: $r = 0.04$, $P > 0.05$).

Size, life span, growth, and mortality

Size-frequency distributions for each sex were analysed for recognizable cohorts (Figs. 4, 5). Females had a life expectancy of 8 to 11 months and reached up to 14 mm body length, while males lived from 8 to 12 months and attained a maximum body length of 16 mm. Outside of this sampling, a male with a body length of 17 mm was collected at the study site. Juveniles were recruited at 1 mm length throughout the year.

The Von Bertalanffy growth function was used and a growth curve was fitted for each sex (Fig. 6). No seasonality was observed in the growth of *Orchestia gammarellus*. The statistical comparison by RSS analysis showed that males and females have different growth curves ($F = -1171$, $P < 0.001$). The standard growth index ϕ' was higher in males (Table 2).

Mortality of *O. gammarellus* was calculated for both sexes pooled as 0.9% per day on average. Mortality rates were higher in spring/summer (1.8% day⁻¹) and lower in autumn/winter (0.5% day⁻¹).

Reproduction

Ovigerous females were found at every sampling date except in July 1999. Since reproductive activity was detected in July 1998, we assume there is no reproductive rest in this month. The highest reproductive activity rates were registered in April in both sampling years (Fig. 7). It must be noted that reproductive activity data were provided by traps and not by cores, because the latter method did not provide enough animals for data analysis.

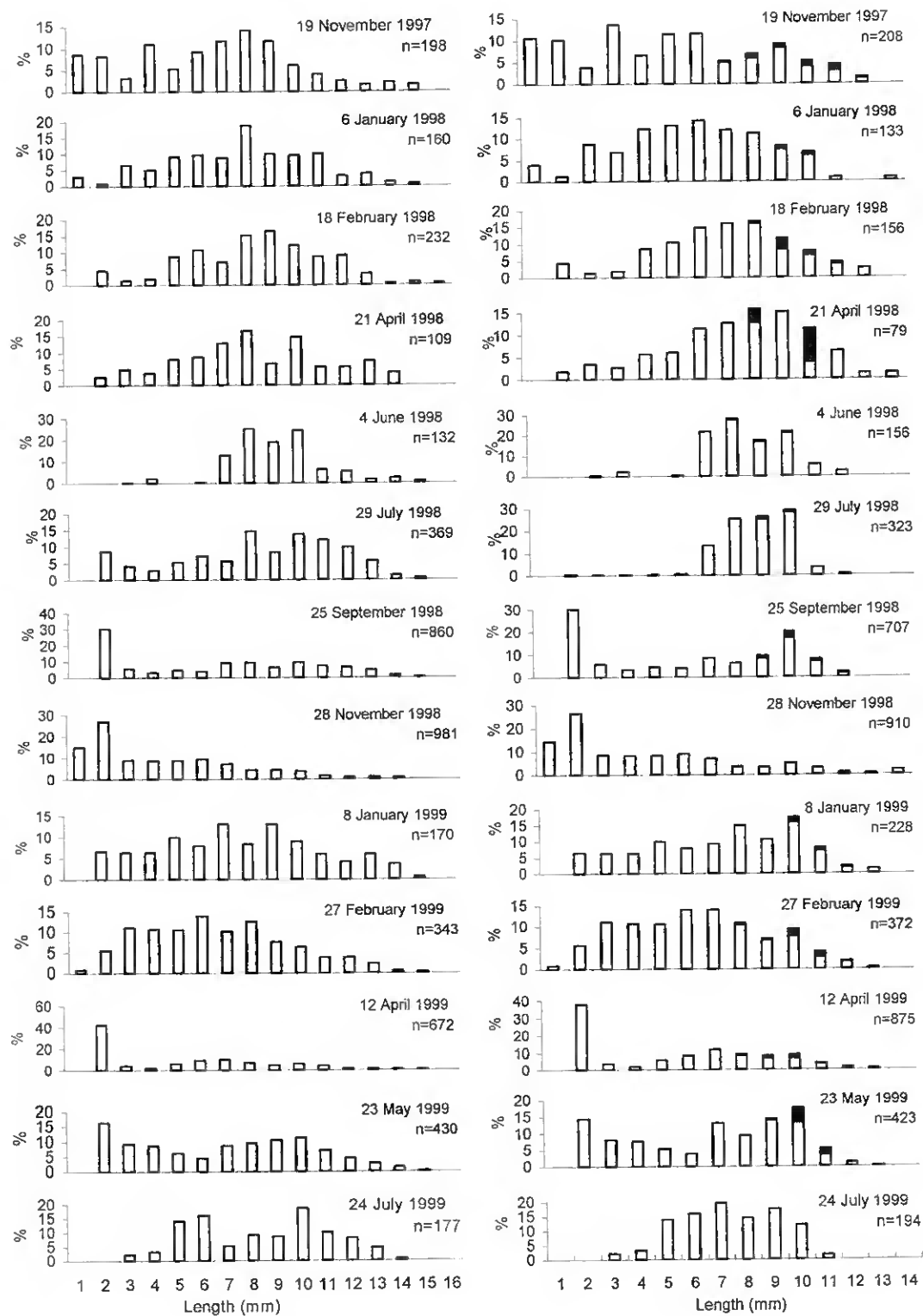


Fig. 4. *Orchestia gammarellus* (Pallas, 1766). Size-frequency distribution for each sex (filled areas correspond to ovigerous females); data of cores and traps pooled.

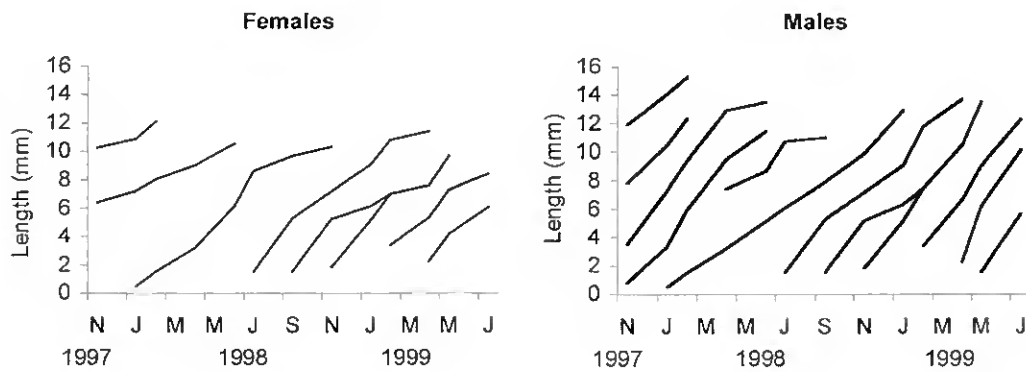


Fig. 5. *Orchestia gammarellus* (Pallas, 1766). Cohort progression of females and males.

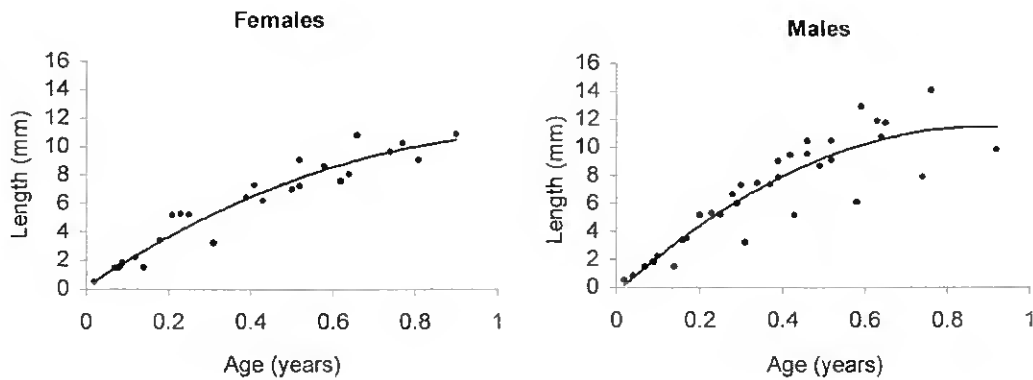


Fig. 6. *Orchestia gammarellus* (Pallas, 1766). Observed lengths at age and fitted non-seasonalized Von Bertalanffy growth function for females and males.

The minimum size of an ovigerous female was 8 mm and the maximum was 13 mm, whereas the average size observed was 10 mm. This means that the species potentially can reproduce after 6-7 months. Figure 7 shows the average size of ovigerous females along the sampling period. Older females are reproducing during winter, while the younger ones reproduce during spring.

Altogether, 169 broods were examined, but to estimate fecundity, the maximum number of eggs in each 1 mm size class was determined and used because eggs were easily lost from the brood pouch during sampling, sorting, and conservation. There was a significantly positive correlation between the length of the female and the number of

eggs ($r = 0.93$, $n = 5$, $P < 0.05$). The average number of eggs per female was 17 and the maximum number of eggs per female was 21.

Ovigerous females were collected in higher numbers at MHTL, just like rest of the population. This indicates that they are not segregated from the other components of the population.

Table 2. *Orchestia gammarellus* (Pallas, 1766), growth parameters determined by non-linear fitting of the Von Bertalanffy growth function (VBGF) for females and males; SE, approximate asymptotic standard error; L_{∞} , asymptotic length; K, intrinsic growth rate; t_0 , computed age at length zero; ϕ' , Munro's growth index; r^2 , coefficient of determination.

| Parameter | Females | | Males | |
|-------------------------|---------|--------|-------|--------|
| | Mean | (SE) | Mean | (SE) |
| L_{∞} (mm) | 14.19 | (2.96) | 13.62 | (2.29) |
| K (year ⁻¹) | 1.52 | (0.58) | 2.34 | (0.80) |
| t_0 (year) | 0.002 | (0.02) | 0.026 | (0.02) |
| ϕ' | 2.49 | (0.30) | 2.64 | (0.26) |
| r^2 | 0.93 | | 0.82 | |

Production estimates

Body weight of non-ovigerous females and males was not significantly different (7 mm: $t = 0.52$; 9 mm: $t = -0.41$; 11 mm: $t = -1.10$; $P > 0.05$). Weight at a specific length did not vary seasonally in both sexes (7, 9, and 11 mm body length: ANOVA: $F = 0.22$, $P = 0.8$). Thus, the entire data set was combined to provide a single regression expressed as:

$$W = 4.6 \cdot 10^{-6} \times L^{2.67}$$

$n = 989; r^2 = 0.89;$

W: ash-free dry body weight [g];

L: total body length [mm].

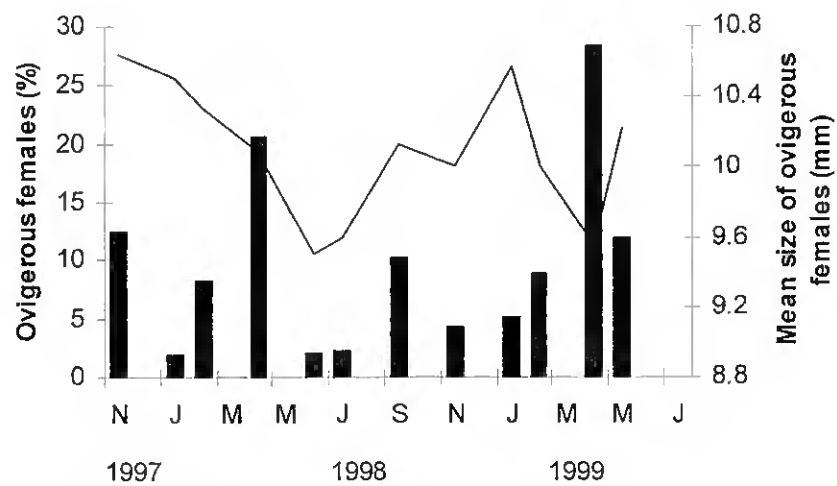


Fig. 7. *Orchestia gammarellus* (Pallas, 1766). Reproductive activity of the population given by the percentage of ovigerous females (bars) and mean size of ovigerous females along the year cycle (line).

Secondary production obtained by the removal summation method was 1.6 g AFDW $m^{-2} year^{-1}$ and the P/B ratio was 4.6. Using the increment summation method, an annual production of 1.4 g AFDW m^{-2} and a P/B ratio of 3.9 were calculated.

There was a very significant biomass increment in spring 1999 (April and May). Following this period, in July 1999 a pronounced peak in loss of biomass was registered (Fig. 8).

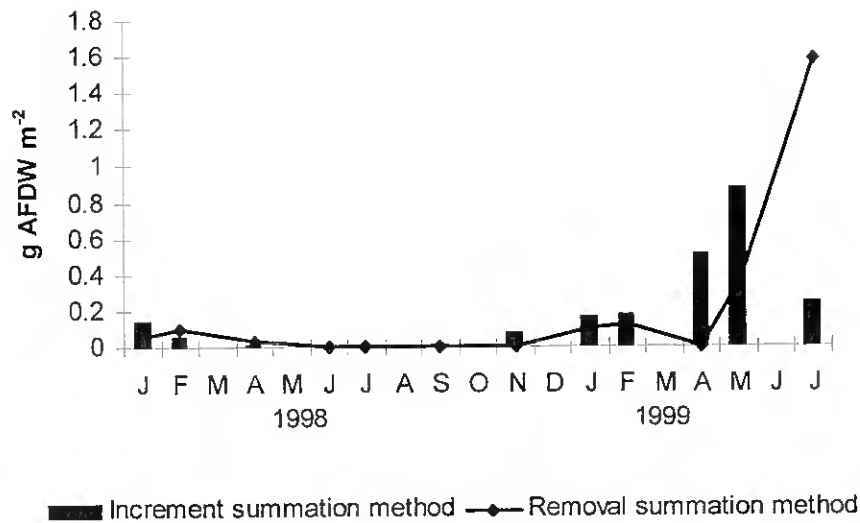


Fig. 8. *Orchestia gammarellus* (Pallas, 1766). Secondary production in ash-free dry weight (AFDW), calculated by the increment summation method and the removal summation method for the 6 week-intervals between sampling.

DISCUSSION AND CONCLUSIONS

Interspecific competition

Competitive interaction and density control within the benthos is likely to be a result of the interplay of competition for food and space (Lopez et al., 1977). Interspecific competition may occur where the distribution of different species of shore hoppers overlaps, for example *Orchestia gammarellus* and *Orchestia mediterranea* (cf. Charniaux-Cotton, 1957; Den Hartog, 1963), *Orchestia cavimana* Heller, 1865 and *O. gammarellus*, *Orchestia aestuarensis* Wildish, 1987 and *O. mediterranea* (cf. Den Hartog, 1963; Wildish, 1987), and *O. gammarellus* and *Orchestia platensis*

Krøyer, 1845 (cf. Dahl, 1946). The latter species was introduced in the Baltic Sea in the 19th century, and, by possessing a higher reproductive potential, has ousted *O. gammarellus*. The nature of the interactions between these species pairs is unknown (Wildish, 1988).

Although salt marsh primary production is large, we cannot presume that its inhabitants are not food limited. Indeed, there is not enough evidence to support or refute this assumption (Montague et al., 1981). The food actually available for the salt marsh fauna is difficult to define, because much of the organic matter is refractory due to its mechanical or chemical inaccessibility, or is buried in anaerobic soils. According to Montague et al. (1981) assimilable food is close to the threshold for long term survival of the salt marsh macrofauna.

In the present salt marsh, the amphipods *O. mediterranea* and *Talorchestia deshayesii* apparently do not offer competition to *O. gammarellus* because of their lower density (own unpubl. data). *Porcellio lamellatus*, *Halophiloscia couchii*, and *Armadillidium album*, isopods sharing the same habitat, are also weak competitors for the same reason (own unpubl. data). However, there is a potential competitor: *Tylos ponticus*. This isopod is the most abundant species of the macrofauna in the upper marsh and, like *O. gammarellus*, also digs holes in the sediment to hide during the day. Using data of Dias & Sprung (2003) we can compare abundance in the most critical period (April to July) of 1998 with 1999. We observed that in 1999 the density of *T. ponticus* suffered a 46% decrease, while *O. gammarellus* density increased by 98%. Feeding preference experiments (own unpubl. data) revealed that both species prefer to eat algae (e.g., Ulvales) rather than *Zostera* or *Spartina*. While *Zostera* and *Spartina* deposits are always present in high amounts, algal deposits are irregularly present in space and time. We speculate that *O. gammarellus* and *T. ponticus* may be competing

for high quality food and for space. Obviously, more data would be needed to confirm this hypothesis.

Growth and life cycle

The lower growth rates of females in relation to males were also observed in *Pseudorchestoidea brasiliensis* (Dana, 1853) (cf. Cardoso & Veloso, 1996) and in *Talitrus saltator* (Montagu, 1808) (cf. Williams, 1978). According to Cardoso & Veloso (1996) this must be related to a greater investment of energy in reproduction (production and maintenance of eggs and embryos), since the females do not undergo ecdysis during the period of incubation, making it difficult for them to continue to grow at the same pace as males. In contrast, O'Hanlon & Bolger (1997) concluded higher growth rates in females of the amphipod *Arcitalitrus dorrieni* Hunt, 1925 on the basis of their larger size.

Two populations of *Orchestia gammarellus* living on the Swedish coast present an annual life cycle with most females being semelparous (Persson, 1999). Males live for 12 months and the life expectancy of females is 12-15 months. However, other authors have described *O. gammarellus* as a semi-annual and iteroparous amphipod with a life expectancy of 6 to 9 months (e.g., Dahl, 1946; Wildish, 1979; Moore & Francis, 1986; Aksissou & Elkaim, 1994).

In the present study, males had a maximum life expectancy of 8-12 months, a bit longer than females, which could live for 8-11 months. In *O. gammarellus*, hatchlings are released from the marsupium 33-36 days after laying the eggs (cultured at 15°C; Morritt & Spicer, 1996, 1999). The average period between the release of the post-marsupial juveniles and the appearance of the second brood was 11.0 ± 0.8 days in *O. gammarellus* females that were subject to an artificial initiation of breeding two

months after the end of their natural breeding season (September) (cultured at 15°C; Morrill & Stevenson, 1993). Hence, we may expect that females in the present population are not semelparous but can potentially produce up to 3 broods, because they commence reproduction when they are 6-7 months old. The number of broods can even be higher than this, as elevated temperatures result in a significant reduction in development time in *O. gammarellus* (cf. Magniette & Ginsburger-Vogel, 1982) and at our study site the average temperature remained above 21°C from May to October. On the other hand, the low percentage of ovigerous females in the population indicates that this reproductive potential is not fully exploited.

Reproduction

Many reports show that in northern countries *Orchestia gammarellus* reproduces from March/April to September/October (Amanieu, 1969; Wildish, 1979; Moore & Francis, 1986; Jones & Wigham, 1993; Morrill & Stevenson, 1993) while in a southern country such as Morocco, reproduction extends from October to May with a sexual resting period in February (Aksissou & Elkaim, 1994). At our study site, breeding activity was registered throughout the yearly cycle.

Temperature is the critical factor controlling reproduction in *O. gammarellus* according to Stevenson & Morrill (1993). The only argument against is the result from Williamson (1951), who could not induce reproduction in individuals collected after the end of the reproductive period (October) by merely raising temperature. However, Charniaux-Cotton (1957) maintained a group of *O. gammarellus* breeding continuously in culture at 24°C for more than one year. Our results indicate that temperature must override day length in inducing reproduction, because we observed breeding activity all along the yearly cycle.

According to Morritt & Stevenson (1993), reproduction starts when maximum air temperature reaches 10°C. In our study area the maximum air temperature was always above this value. Thus, differences with the northern populations are easily explained by temperature. This cannot be valid for the difference with the Moroccan population, because of the geographic proximity and similarity of climate. Average temperature was 16°C at both localities. The main difference is in terms of salinity, which in the Ria Formosa lagoon is 36 psu while in Lake Smir it varies from 0.3 to 24 psu. However, salinity was found to be insignificant for the initiation of the breeding cycle of *O. gammarellus* in the experiments of Morritt & Stevenson (1993). On the other hand, substrate humidity may play an important role here, because the reproductive rest in Morocco occurs during the dry season. In the salt marsh, tides prevent permanent desiccation of the substrate, in contrast to Lake Smir. Thus, it seems that in addition to temperature, humidity is also an important factor controlling reproductive activity, as already suggested by Aksissou & Elkaim (1994).

Sexual maturation experiments with *O. gammarellus* were carried out by many authors who obtained different results: e.g., at an age of 2-2.5 months at 15°C (Williamson, 1951); 3-4 months at 24°C (Charniaux-Cotton, 1957); 105 days at 18°C (Wildish, 1972); and 3 months at 20°C (Zerbib, 1980). Field data collected at Great Cumbrae Island (U.K.) by Moore & Francis (1986) suggest that eggs laid in mid-May and hatching in mid-June could have developed through to mature adults by August to September. In this study, amphipods took 6-7 months to be sexually mature at 16°C average temperature. In Morocco, with the same temperature, individuals took approximately 4 months to reach sexual maturity. It should be noted, however, that this variation may be attributed to the different ambient conditions to which different populations were exposed. Furthermore, it must be considered that salt marshes are physiologically difficult areas, due to fluctuating physico-chemical factors such as

humidity, temperature, and salinity.

Average fecundity in a population of *O. gammarellus* in the U.K. studied by Wildish (1979) was 19.1 eggs per female at 18 mm maximum body length. Persson (1999) obtained a figure of 14.0 and 15.5 eggs per female at mean sizes of 11.8 and 12.4 mm, respectively, in two populations in the Baltic coast of Sweden, where maximum body length of females was 16.5 mm. In Morocco, Aksissou & Elkaim (1994) observed a fecundity of 15.1 for females with 12.25 mm average body length and a maximum body length of 17 mm. In this study, reproductive females with a mean size of 10 mm produced an average of 17 eggs each and the maximum length of the females was 14 mm. This means a relatively higher fecundity in this population and invalidates the suggestion of Aksissou & Elkaim (1994) that temperature was the cause for the lower fecundity they obtained in Lake Smir. A decrease in mean size of reproductive females in summer versus winter populations of amphipods has been previously noted also in other studies (Steele & Steele, 1969; Dexter, 1971; Nelson, 1980), where it has been attributed to high temperature, shortage in food supply, and predation.

Production

Annual production of *Orchestia gammarellus* is higher than the estimate for the beach talitrid, *Pseudorchestia brasiliensis* (0.33-0.36 g AFDW m⁻² y⁻¹; Cardoso & Veloso, 1996), about the same as estimated for the salt marsh talitrid, *Uhlorchestia spartinophila* Bousfield & Heard, 1986 (0.77-1.44 g AFDW m⁻² y⁻¹; Covi & Kneib, 1995), but much lower than the production of the beach amphipod, *Talorchestia margaritae* (Stephensen, 1948) (660.39 g DW m⁻² y⁻¹; Venables, 1981).

The high production of the latter species must be related to the extraordinary abundance of this population (5692 to 39047 ind m⁻²) subject to low mortality (Venables, 1981).

According to Ansell et al. (1978) the ratio between annual production and mean biomass (P/B) should provide a convenient index for comparison of the potential production of different species, populations, and communities. The P/B ratio calculated for *O. gammarellus* is higher than that recorded for amphipods with longer life-spans, e.g., *Talorchestia capensis* (Dana, 1853) (2.25; Van Sensus & McLachlan, 1986), *Pseudorchestia brasiliensis* (2.16-2.30; Cardoso & Veloso, 1996), and *Arcitalitrus dorrieni* (2.41-3.01; O'Hanlon & Bolger, 1997), but it is much lower than in amphipods with shorter life-spans, e.g., *Ulorchestia spartinophila* (15.4-17.3; Covi & Kneib, 1995) or *Talorchestia margaritae* (29.2; Venables, 1981). Indeed, the P/B ratio was correlated by Wildish (1984) with the life-span of amphipods by the following equation:

$$\text{Log}_{10} \text{P/B} = 0.66 - 1.10 (\text{log}_{10} \text{life-span})$$

where the life-span is indicated in years. If the maximum estimated life-span for *O. gammarellus* of 12 months (1 year) is inserted into the above equation, the resulting P/B ratio will be 4.6. This is exactly the value calculated by the removal summation method in this study, and not much different from the one calculated by the increment summation method (3.9). If we use the minimum estimated life-span of 8 months (0.66 years), we will obtain a P/B ratio of 5.8, a bit higher than the actual results.

Life history

Although the studied salt marsh is a remarkably stable ecosystem, most of the life history characteristics found here for *Orchestia gammarellus* are those of an

r-strategist as summarized by Pianka (1970) for ephemeral or unpredictable habitats. Curiously, we found, in the same marsh, many characteristics for the isopod *Tylos ponticus* that point in the opposite direction (Dias & Sprung, 2003) and classify *Tylos* as a *K*-strategist. For example, the life expectancy of *O. gammarellus* is less than 1 year, in contrast to *T. ponticus*, in which it is 3 to 4 years; the onset of reproduction is at 6 months in contrast to 12 months for *T. ponticus*; reproduction is mostly continuous in contrast to being restricted to summer months; mortality rate is high at all stages, while it slows down considerably in adults of *T. ponticus* and levels out strong oscillations in density. How are two opposing strategies compatible with the long term survival in the same habitat? The habitat should favour either one or the other type of life strategy.

There are many possible explanations, but no definite answer. Hence, we can speculate that minor differences in height in the tidal zone imply profound changes in the predictability of the habitat, e.g., whether inundation is regular (caused by tides) or irregular (caused by storm events). Another explanation is that differences in life history may be linked to different strategies of exploiting the habitat. In concrete terms, the animals may show different activity peaks during a day-night cycle, the micro-habitat may be different, e.g., being more associated with plant cover or not, or preferences in the diet may be distinct. The last point to raise is that the *r/K* continuum may be an oversimplification of the demands of a habitat. A second gradient pointing in another direction may be superimposed and hence limit its explanatory value (as discussed by Grime, 1979; Begon et al., 1990; McCann & Shuter, 1997).

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CHAPTER 4

Distribution, population dynamics and life histories of terrestrial isopods in a salt marsh of the Ria Formosa lagoon (southern Portugal)

N. Dias & M. Sprung. Distribution, population dynamics and life histories of terrestrial isopods in a salt marsh of the Ria Formosa lagoon (southern Portugal). In preparation.

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INTRODUCTION

Isopods have intensively colonized the upper fringe of a salt marsh of the Ria Formosa lagoon (southern Portugal). Four species of sympatric terrestrial Oniscidea isopods can be found: *Tylos ponticus* Grebnitzky, 1874 (Tylidae), *Porcellio lamellatus* (Uljanin) Budde-Lund, 1885 (Porcellionidae), *Halophiloscia couchii* (Kinahan, 1858) (Halophilosciidae) and *Armadillidium album* Dolfuss, 1887 (Armadillidiidae). Isopods are originally marine species animals. Representatives of these 4 families show morphological and physiological adaptations and modifications that make them independent of the aquatic environment to a different degree.

Porcellionidae and Armadillidiidae encompass fully terrestrial species that have adapted to terrestrial habitats away from the sea coast and can survive periodic desiccation of their environment (Schmalfuss, 1998). This is possible due to a number of adaptations, e.g., changes in the cuticle reducing transpiration, two to five pairs of pleopodal lungs, together with other qualities like shortening of the antennal flagellum (Schmalfuss, 1989, 1998; Hopkin, 1991; Erhard, 1998). Tylidae, in contrast, still have an open water conducting system (Schmalfuss, 1998), which only permits a limited capture of water droplets from the environment. On the other hand, Halophilosciidae is the only family lacking lungs (Schmalfuss, 1998). Consequently, species of these two families are exclusively restricted to coastal marine supra-littoral habitats, while *Armadillidium album* and *Porcellio lamellatus* have secondarily returned to marine littoral habitats.

Animals living in salt marshes have to cope with many physical and chemical constraints such as fluctuations in salinity, temperature, oxygen, inundation and other factors such as the physical and chemical nature of the substrate (Chapman, 1992). For this reason salt marshes are considered stressful environments. However, this stress is

predictable as it depends mostly on the tides. At the same time salt marshes are extremely productive with large amounts of organic matter accumulated, especially in the upper fringe. Debris of marine plants (e.g., *Zostera noltii* Hornem) and green algae (e.g., Ulvales) from the surrounding intertidal and subtidal region are deposited next to dead leaves from the salt marsh plants (e.g., *Spartina maritima* (Curtis) Fernald).

In this paper we examine how these systematically different isopod species achieve to survive in this habitat. In particular we analyse their population dynamics, life histories and secondary production. Provided the salt marsh environment is sufficiently stable in space and time we will expect that they can only coexist by spatial segregation, segregation of food sources or different attributes of their life strategies.

MATERIALS AND METHODS

Study area

The study area was in a salt marsh system bordering the Ria Formosa, a mesotidal lagoon on the southern coast of Portugal separated from the Atlantic ocean by a 55 km long barrier island system. The salt marshes in this lagoon are of the dry coast type (Adam, 1990) with the vegetation consisting predominantly of *Spartina maritima* in the lower level, *Sarcocornia* spp. and *Atriplex portulacoides* L. in the intermediate region and *Suaeda vera* J. F. Gmelin, *Suaeda maritima* (L.) Dumort, *Atriplex halimus* L. and *Limoniastrum monoptalum* (L.) Bss. in the upper zone. Water salinity is approximately 36 psu all year round (Falcão & Vale, 1990).

Meteorological data

Air temperature was recorded daily, by a minimum-maximum thermometer, during the sampling period at a distance of 3 km from the study site. Precipitation data were obtained from the Direcção Regional da Agricultura do Algarve, which is 7 km away from the site. Evaporation was registered daily using an evaporimeter tank located 3 km away from the study site.

Sampling methods

The animals were collected every sixth week at neap tide between November 1997 and July 1999. Three different levels were sampled: (1) a lower stratum with compact mud at the surface, corresponding to the neap high tide level (NHTL) dominated by *Sarcocornia* spp. and *Atriplex portulacoides*; (2) an intermediate stratum with sandy soil and deposits of *Zostera noltii*, *Spartina maritima* and some algae (mainly Ulvales), which corresponds to the mean high tide level (MHTL); (3) an upper stratum with sandy soil, corresponding to the spring high tide level (SHTL). Litter and wrack deposits in the upper stratum were rare and consisted mainly of dry leaves and stems of salt marsh plants. Samples were taken by two methods: (a) pit-fall traps (plastic flasks with 16 cm height \times 6 cm diameter) filled with a very diluted formalin solution (0.01 %) exposed for 96 h (3 replicates per level, randomly); (b) cores of 113 cm² to a depth of 20 cm and sieved with a 500 μ m mesh on site (15 replicates per level, randomly).

The following characteristics were recorded for each specimen: body length (1 mm size class), sex, presence and number of eggs/young, ash free dry weight (AFDW). Ash free dry weight was obtained pooling 1 to 20 specimens of each size

class for each core or trap which were dried for 2 days at 60°C and ashed for 3 h at 450°C.

Breeding season is defined here as the time from the first appearance of ovigerous females to the time of the last appearance of eggs/young in the marsupium. Reproductive activity is indicated by the percentage of females carrying eggs/young in the brood pouch.

Sediment analysis

The sediment was characterized at each sampling level (NHTL, MHTL, and SHTL) and 3 different strata: depth range of: 0-6 cm, 6-12 cm and 12-20 cm. The physical parameters assessed were: mean grain size; percentage of silt and clay in the sediment determined by the moments method (Friedman & Sanders, 1978); sediment water content, obtained by drying the sediment samples at 60°C during 48 h; sediment organic matter content, obtained by drying the sediment for 48 h at 60°C and ashing it for 3 h at 450°C.

Statistic analysis

Cohorts were identified by size frequency analysis using the Bhattacharya (1967) method in the FISAT soft ware package (FAO-ICLARM Stock Assessment Tools).

Annual mortality was estimated as the decrease of the abundance of each cohort, pooling all replicates. Age specific survivorship for each cohort was calculated by the slope b of the regression $\ln(n+1)$ versus time (Krebs, 1998). An apparent increase in cohort abundance was treated as a lack of mortality. The annual mortality of a cohort

(q_x) was given by the equation:

$$q_x = 1 - e^{b \times 365}$$

Secondary production was estimated by (1) the increment summation method (Boysen Jensen, 1919) and (2) the removal summation method:

$$(1) P_{1,2} = \text{antilog} ((\log n_1 + \log n_2) / 2) \times (\varpi_2 - \varpi_1)$$

$$(2) P_{1,2} = (n_1 - n_2) \times \text{antilog} ((\log \varpi_2 + \log \varpi_1) / 2)$$

where

$P_{1,2}$: represents cohort production between sample time 1 and 2;

n_1, n_2 : represents the abundance of specimens of the cohort at time 1 and 2;

ϖ_1, ϖ_2 : represents the mean weight of the specimens of the cohort at time 1 and 2.

Variance/mean ratio (I_D) was calculated to investigate the type of dispersion (Krebs, 1998).

RESULTS

Distribution

Two different types of data were collected: quantitative which indicate density (by cores) and qualitative which measure activity (by traps). Although cores provide reliable quantitative data to assess abundances of populations, pit-fall traps give us a broader idea of the distribution and the relative abundance of each species on the

sampling area because traps were exposed for four days and therefore they were able to collect a much higher number of species and specimens.

Tylos ponticus always contributed to more than 90% of the total captured specimens in each level regardless of whether traps or cores are considered (Fig. 1). However, *T. ponticus* density was extremely low at the lower level (NHTL). At this level *T. ponticus* was only caught in cores in April and June 1998 and in January 1999 (but see below). The upper layer of the substrate at this site is quite different from the other levels as it is composed of medium grain sand with a higher amount of organic matter and higher percentage of clay and silt (Table 1) which make it compact and very difficult to penetrate.

Halophiloscia couchii was more abundant than *Porcellio lamellatus* at the lower and intermediate levels. Contrary, at the upper level *P. lamellatus* was 13 times more abundant than *H. couchii*. *Armadillidium album* represented only a small fraction of the isopod community and next to *T. ponticus* was the only species that showed a higher fraction in cores than in traps, indicating the low vagility of the species.

Armadillidium album and *T. ponticus* showed very similar distributions with 35-36% of their populations at the SHTL and 64-65% at the NHTL (Fig. 2). *Porcellio lamellatus* showed a preference for the intermediate substrate where it maintained 77% of its population and 23% at the upper substrate. *Halophiloscia couchii* was the more intertidal species: 2% of the total captured individuals were found at the upper level, the same percentage of specimens was detected at the lower level with 96% of the population located in the intermediate level.

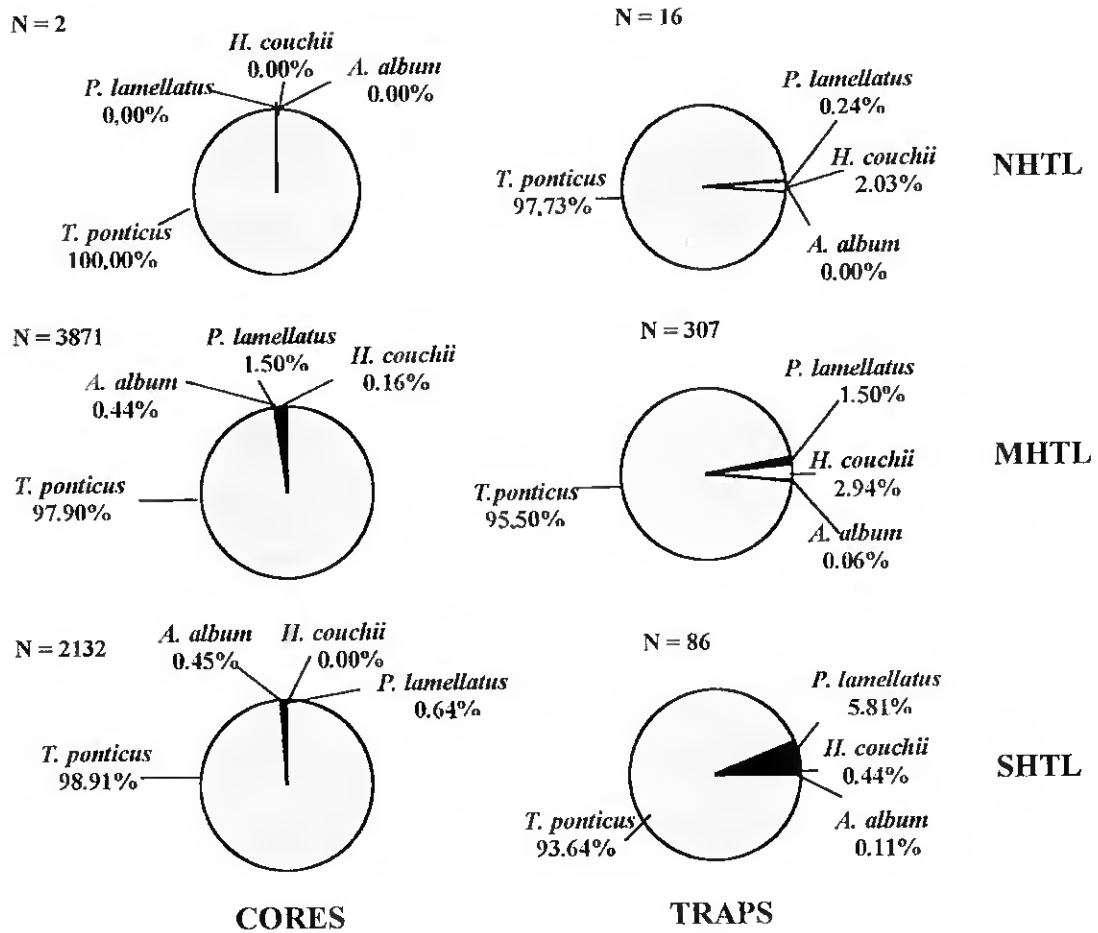


Fig. 1. Relative abundance of the study species caught using both corers and pitfall traps at NHTL (neap high tide level), MHTL (mean high tide level) and SHTL (spring high tide level). N indicates near densities m^{-2} for cores and the near numbers traps $^{-1}$ day $^{-1}$ for pitfall traps over the entire sampling period.

To investigate the relation of the isopods with the deposits of organic matter samples were taken from sites (a) with deposits and (b) without deposits, but with a high number of holes in the sediment. Results showed that *Tylos* was the only species whose distribution was not correlated with the organic deposits (Table 2). *Halophiloscia couchii* was only captured in cores once (in organic deposits) but this species is always found in association with deposits (N. Dias, unpubl. obs.).

Table 1. Physical characteristics of the sediment at the three sampling levels (NHTL, MHTL and SHTL) (data shown as mean values).

| Tidal Level | Depth (cm) | Water content (%) | Grain size (mm) | Organic matter (%) | Clay and silt (%) | Textural group |
|-------------|------------|-------------------|-----------------|--------------------|-------------------|----------------|
| NHTL | 0-6 | | 0.30 | 10.53 | 32.84 | Medium |
| | 6-12 | 13.70 * | 0.50 | 1.18 | 19.30 | Coarse |
| | 12-20 | | 0.62 | 0.41 | 13.40 | Coarse |
| MHTL | 0-6 | | 0.57 | 2.00 | 0.15 | Coarse |
| | 6-12 | 7.34 * | 0.48 | 0.57 | 10.08 | Medium |
| | 12-20 | | 0.60 | 0.38 | 12.99 | Coarse |
| SHTL | 0-6 | | 0.55 | 0.96 | 0.72 | Coarse |
| | 6-12 | 5.14 * | 0.59 | 1.93 | 0.68 | Coarse |
| | 12-20 | | 0.55 | 1.35 | 0.32 | Coarse |

* Data obtained for the entire 20 cm sediment profile in June 2001.

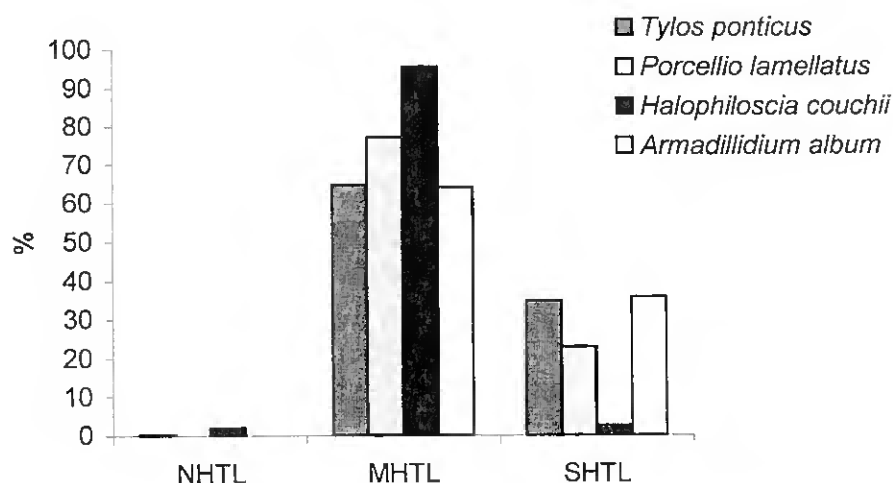


Fig. 2. Distribution of *Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii* and *Armadillidium album* in the sampling area: NHTL (neap high tide level), MHTL (mean high tide level) and SHTL (spring high tide level). Data are presented as mean percent of the total number for each species captured both by cores and traps.

Generally, all species were highly aggregated. For *T. ponticus* I_D varied from 3 to 124 (average 41) at MHTL and 4 to 380 (average 62) at SHTL. For *P. lamellatus* I_D was 1 to 12 (average 6) at MHTL and 1 to 10 (average 4) at SHTL. *Halophiloscia couchii* showed an I_D of 9 in May 1999 (the only capture with cores). Finally, *A. album* presented an I_D of 1 to 11 (average 4) at MHTL and of 1 to 11 (average 6) at SHTL.

Table 2. Mean density (n. ind core⁻¹) of *Tylos ponticus*, *Porcellio lamellatus* and *Armadillidium album* collected in sites with and without deposits of organic matter (S. D. - standard deviation; n - number of samples).

| Substrate | <i>Tylos ponticus</i> | | | <i>Porcellio lamellatus</i> | | | <i>Armadillidium album</i> | | |
|------------------|-----------------------|-------|----|-----------------------------|-------|----|----------------------------|-------|----|
| | Mean | S. D. | n | Mean | S. D. | N | Mean | S. D. | n |
| With deposits | 18 | 33 | 90 | 1 | 4 | 45 | 1 | 3 | 25 |
| Without deposits | 53 | 77 | 90 | 0 | 0 | 45 | 0.08 | 0.2 | 25 |

Abundance

Density of *Tylos ponticus* varied from 0 to 9 ind m⁻² at NHTL, 788 to 8080 ind m⁻² at MHTL and from 115 to 10387 ind m⁻² at SHTL. Demographic peaks occurred in July (SHTL) and in November 1998 (MHTL). In the following year the density peak decreased dramatically and occurred in April (Fig. 3).

Porcellio lamellatus was never captured in cores at the lower level. At the intermediate level the density ranged from 0 to 283 ind m⁻² and at the higher level varied from 0 to 89 ind m⁻². Highest densities were observed in April and May 1999 at MHTL.

Halophiloscia couchii was only captured in cores in May 1999 at MHTL, when the average density was 79 ind m⁻².

Average density of *Armadillidium album* was higher at the intermediate level (25 ind m⁻²) than at the upper tidal level (4 ind m⁻²). The highest numbers were recorded in November 1998 at SHTL and in May 1999 at MHTL.

Correlations between the isopod density and meteorological conditions were insignificant except for a positive correlation between *T. ponticus* density and temperature (NHTL: $r = 0.79$, $P < 0.005$; SHTL: $r = 0.96$, $P < 0.001$).

Biomass estimates of the isopods during the sampling period (summarized over all sites), based on size class data, are shown in Fig. 4. *Tylos* had the greatest biomass followed by *Porcellio*, *Armadillidium* and *Halophiloscia*. As with the density, biomass of *Tylos* decreased in 1999 while the other isopod species increased in biomass during the same period.

Activity

As the most abundant species, *Tylos ponticus* also showed the highest rates of activity at all sampling levels (Fig. 3). Activity peaks occurred in September 1998: 147 ind trap⁻¹ day⁻¹ at NHTL; 1962 ind trap⁻¹ day⁻¹ at MHTL; 742 ind trap⁻¹ day⁻¹ at SHTL.

Of the other species studied, *Halophiloscia couchii* was the more active at the lower and intermediate level while *Porcellio lamellatus* dominated pit-fall captures in the upper level. Activity peaks were very variable. In the case of *H. couchii* activity was more pronounced during late fall, except at the lower level where animals were more active during the summer.

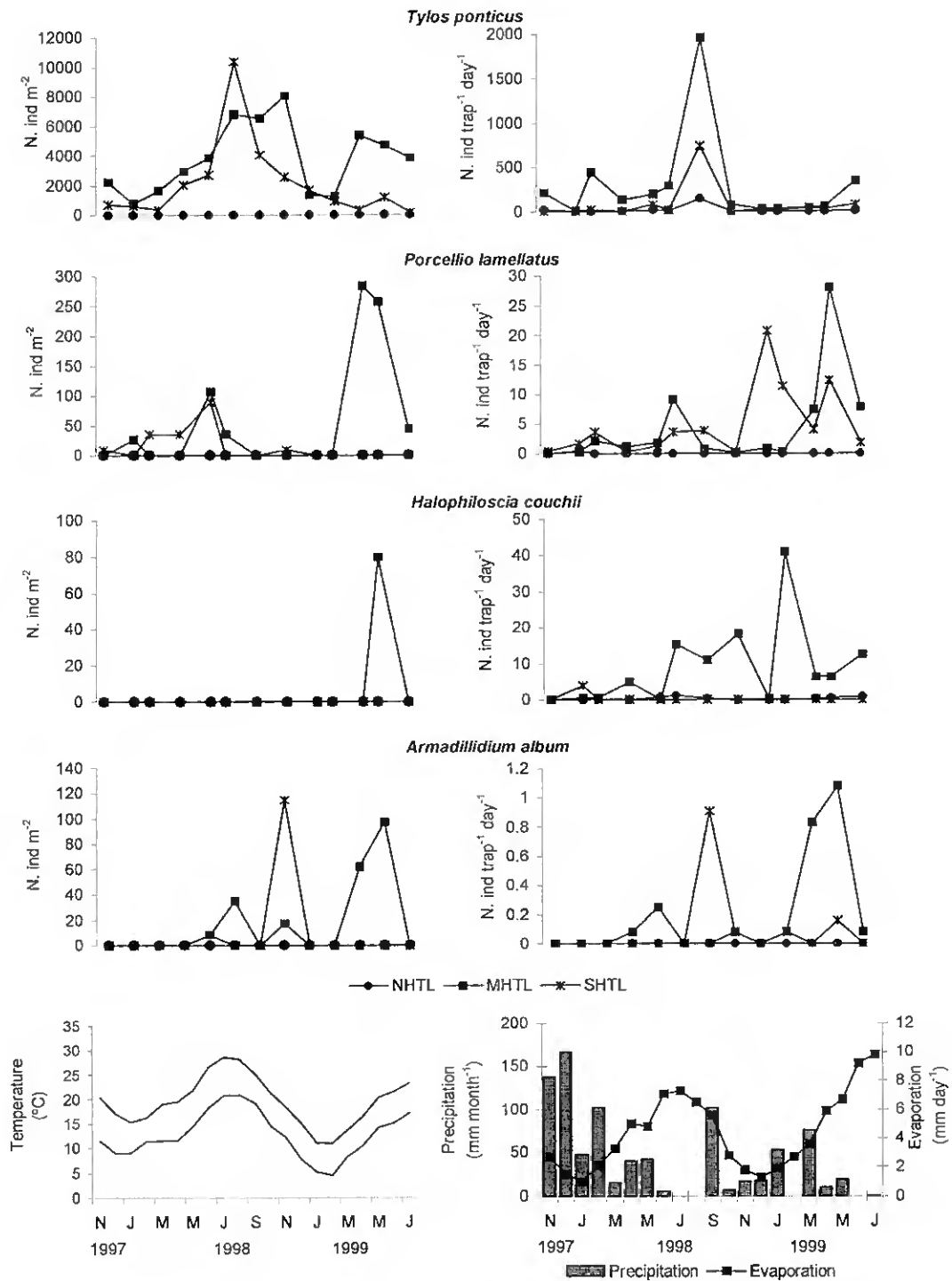


Fig. 3. Density and activity of the isopods *Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii* and *Armadillidium album* at each sampling level during the study period (NHTL - neap high tide level; MHTL - mean high tide level; SHTL - spring high tide level). Also shown are the maximum and minimum air temperatures, evaporation rates and precipitation.

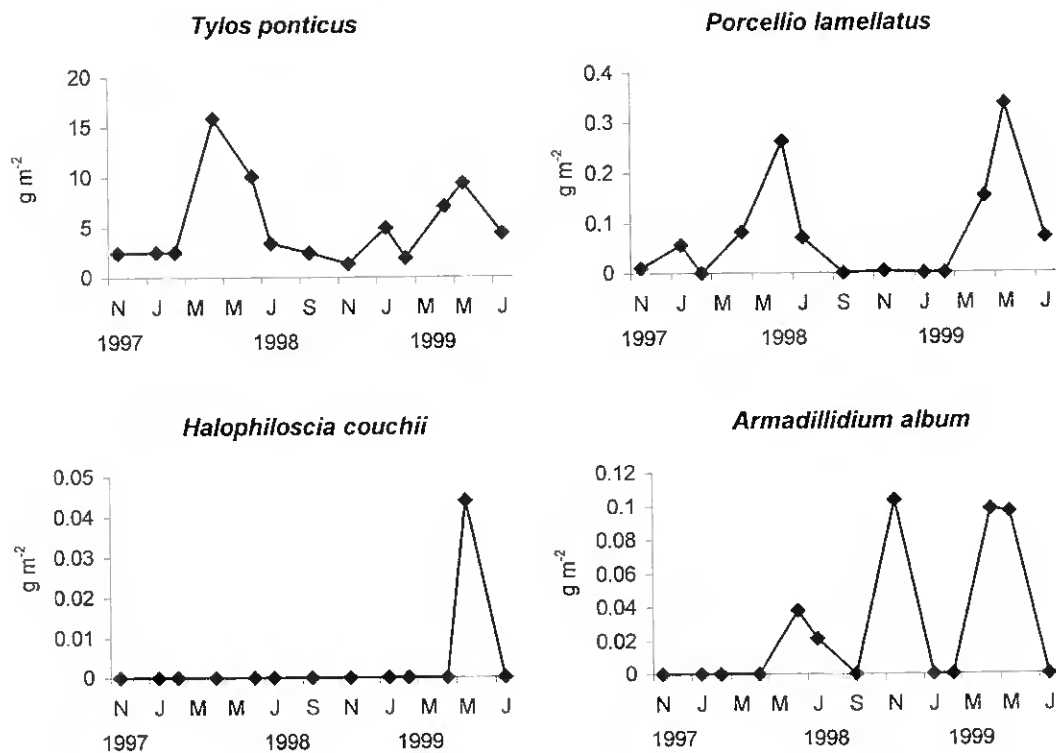


Fig. 4. Biomass of the isopods ($\text{g ash free dry weight m}^{-2}$) in the salt marsh during the study period.

Porcellio lamellatus was captured by traps only once at NHTL (January 1998) and at MHTL the highest activity rates occurred during late spring 1999 in contrast to winter 1999 at the SHTL level. *Armadillidium album* was the least active isopod. Activity peaks were very subtle and occurred during late spring 1999 at MHTL ($1 \text{ ind trap}^{-1} \text{ day}^{-1}$) and early fall 1998 at SHTL ($0.9 \text{ ind trap}^{-1} \text{ day}^{-1}$).

Activity of *Tylos* and *Porcellio* was not significantly correlated with abiotic parameters. However, activity of *Halophiloscia* at NHTL was positively correlated with temperature ($r = 0.82, P < 0.001$) and evaporation ($r = 0.84, P < 0.001$). Activity of *Armadillidium* was positively correlated with precipitation at SHTL ($r = 0.80, P < 0.001$).

Life history of *Tylos ponticus*

This analysis is based on 18238 specimens of *T. ponticus*. Average individual growth in length was 3.7 mm in the first year, progressively decreasing to 0.5 mm by the fourth year (Fig. 5). Maximum length of females was 13 mm and of males 14 mm. Sex could be distinguished in individuals larger than 3 mm body length. On average, females made up 56% (S. D. = 8) of the adult population. Maximum life expectancy was 3 years for the females and 4 years for the males. Females with 4 mm body length were heavier than males of the same size ($t = -3.60$, $P < 0.001$), however the body weight of males and females with 8 mm total length was not significantly different ($t = -0.06$, $P > 0.05$). Weight at a specific length did not vary seasonally in both sexes (4 and 8 mm body length: ♀ - ANOVA: $F = 0.29$, $P = 0.74$; ♂ - ANOVA: $F = 0.27$, $P = 0.76$). The length/weight relationships for both sexes are given in Table 3.

The reproductive period extended from May to September/October. Fecundity was low (11.9 eggs per female, varying from 7 to 21) and positively correlated with the size of breeding females (data of the relation between egg number and ovigerous female weight are given in Table 4). Peak reproductive activity in both years occurred in July (Fig. 6a). According to our estimated size-age relation, females can start reproduction when 1 year old, however most reproduced when they reached their second year. The fraction of smaller ovigerous females increased towards the end of the reproductive season (Fig. 6b). Neonate juveniles belonged to the 2-mm size class and were found from July to November, mostly at the intermediate level (MHTL). Mortality was high in juveniles (86%) but low during the adult life (2nd year of life: females 25% per year, males 0% per year; 3rd year of life: males 46% per year). More details of the life history of this isopod are given by Dias (2002) and Dias & Sprung (2003).

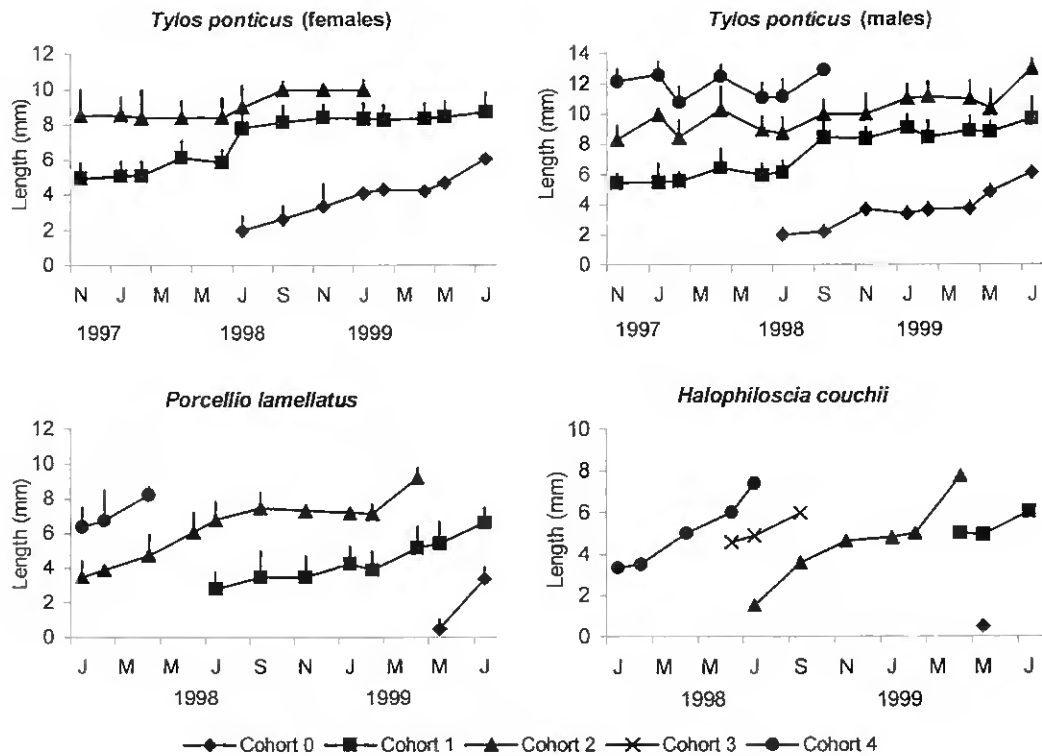


Fig. 5. Mean length of the isopods *Tylos ponticus* (females and males), *Porcellio lamellatus* and *Halophiloscia couchii* over the study period showing the cohort progression. Error bars indicate one standard deviation.

Life history of *Porcellio lamellatus*

The results below were obtained based on 1401 specimens. The largest female observed measured 11 mm body length, the largest male 14 mm. Analysis of cohorts indicated that *P. lamellatus* lives on average for 2 years (Fig. 5). Average growth in length was of 4.4 mm during the first year and 4.5 mm during the second year of life. Sex could be distinguished in individuals larger than 2 mm. The mean percentage of females in the population during the sampling period was 48% (S. D. = 9). Weight at a specific length did not vary seasonally in both sexes (4, 6 and 8 mm body length: ANOVA: ♀ - $F = 0.38$, $P > 0.24$; ♂ - $F = 0.05$, $P > 0.02$). In 4 and 6 mm size classes males had lower body weight than females (4 mm: $t = -2.52$, $P < 0.025$;

6 mm: $t = -18.95$, $P < 0.005$). However, the body weight of males and females with 8 mm total length was not significantly different ($t = -0.58$, $P > 0.05$). The length/weight relation for both sexes is given in Table 3.

Table 3. Regressions for the length/weight relationships for the study species using the equation: $W = a \times L^b$, where W = ash free dry weight (g), L = length (mm) and a and b are constants (r^2 = coefficient of determination; n = number of estimates).

| | a | b | r^2 | n |
|------------------------------|----------------------|------|-------|------|
| <i>Tylos ponticus</i> | $1.85 \cdot 10^{-5}$ | 2.51 | 0.89 | 1174 |
| Females | | | | |
| <i>Tylos ponticus</i> | $1.59 \cdot 10^{-5}$ | 2.62 | 0.89 | 1224 |
| Males | | | | |
| <i>Porcellio lamellatus</i> | $1.74 \cdot 10^{-5}$ | 2.46 | 0.78 | 129 |
| Females | | | | |
| <i>Porcellio lamellatus</i> | $1.65 \cdot 10^{-5}$ | 2.42 | 0.82 | 162 |
| Males | | | | |
| <i>Halophiloscia couchii</i> | $1.14 \cdot 10^{-5}$ | 2.34 | 0.74 | 118 |
| Females | | | | |
| <i>Halophiloscia couchii</i> | $1.03 \cdot 10^{-5}$ | 2.38 | 0.68 | 93 |
| Males | | | | |
| <i>Armadillidium album</i> | $3.67 \cdot 10^{-5}$ | 2.15 | 0.57 | 21 |

Breeding animals were observed from March to September/October. The highest reproductive activity rate (90%) occurred in June 1998. One month later there was a drastic reduction in the percentage of females carrying broods followed by another increase in late September. This suggests that two laying periods may exist. Curiously, during the following year reproductive activity was much reduced (Fig. 6a). Ovigerous females measured 5 mm to 9 mm in total length. This implies that *P. lamellatus* can

reproduce after their first year. Females with 6 and 7 mm body length formed the bulk of the ovigerous population (68%). Mean size of ovigerous females over the breeding season is given in Fig. 6b. Average fecundity was 14.2 eggs per female, with a range of 9 to 37. The relationship between egg number and female size is given in Table 4. New born individuals recruited with 1 mm body length from May to November and evenly distributed between the intermediate and the upper intertidal levels.

Life history of *Halophiloscia couchii*

Traps and cores caught 1047 individuals of *H. couchii* during the sampling period. *Halophiloscia* was the fastest growing isopod of this assemblage, with a life expectancy of 1 year (Fig. 5). Sex could be differentiated in individuals larger than 2 mm total length. Average percentage of females in the population during the sampling period was 58% (S. D. = 18). Analyses of the possible contamination of this population with the feminizing bacteria *Wolbachia* were positive (D. Bouchon, pers. communication). Maximum length reached by females was 11 mm and by males 9 mm.

Weight of females and males did not change significantly during the year cycle (4, 6 and 8 mm body length: ANOVA: ♀ - $F = 0.23$, $P = 0.87$; ♂ - $F = 0.16$, $P = 0.91$). Females of 4 mm body length were heavier than males of the same size ($t = 4.55$, $P < 0.0005$) even though in larger animals the differences in weight of both sexes were not significant (6 mm: $t = -0.12$, $P > 0.05$; 8 mm: $t = 1.66$, $P > 0.05$). Hence two regressions for females and males were developed separately (Table 3).

Ovigerous females ranged from 5 to 8 mm body length. According to our estimated size-age relation it appears that individuals took 9 to 11 months to reach maturity. Average fecundity was 14.4 eggs per female, varying from 6 to 32. Breeding activity commenced in March and extended to September/October. In 1998, although

663 individuals were caught, reproductive activity was only detected in late September. However, in the following year ovigerous females were found in April, May and July (Fig. 6a). Mean length of ovigerous females over the breeding season is shown in Fig. 6b. As for the other isopod species, fecundity was correlated with female size (see Table 4). Juveniles recruited with 1 mm total length from May to November. Young were found exclusively at MHTL (mean high tide level).

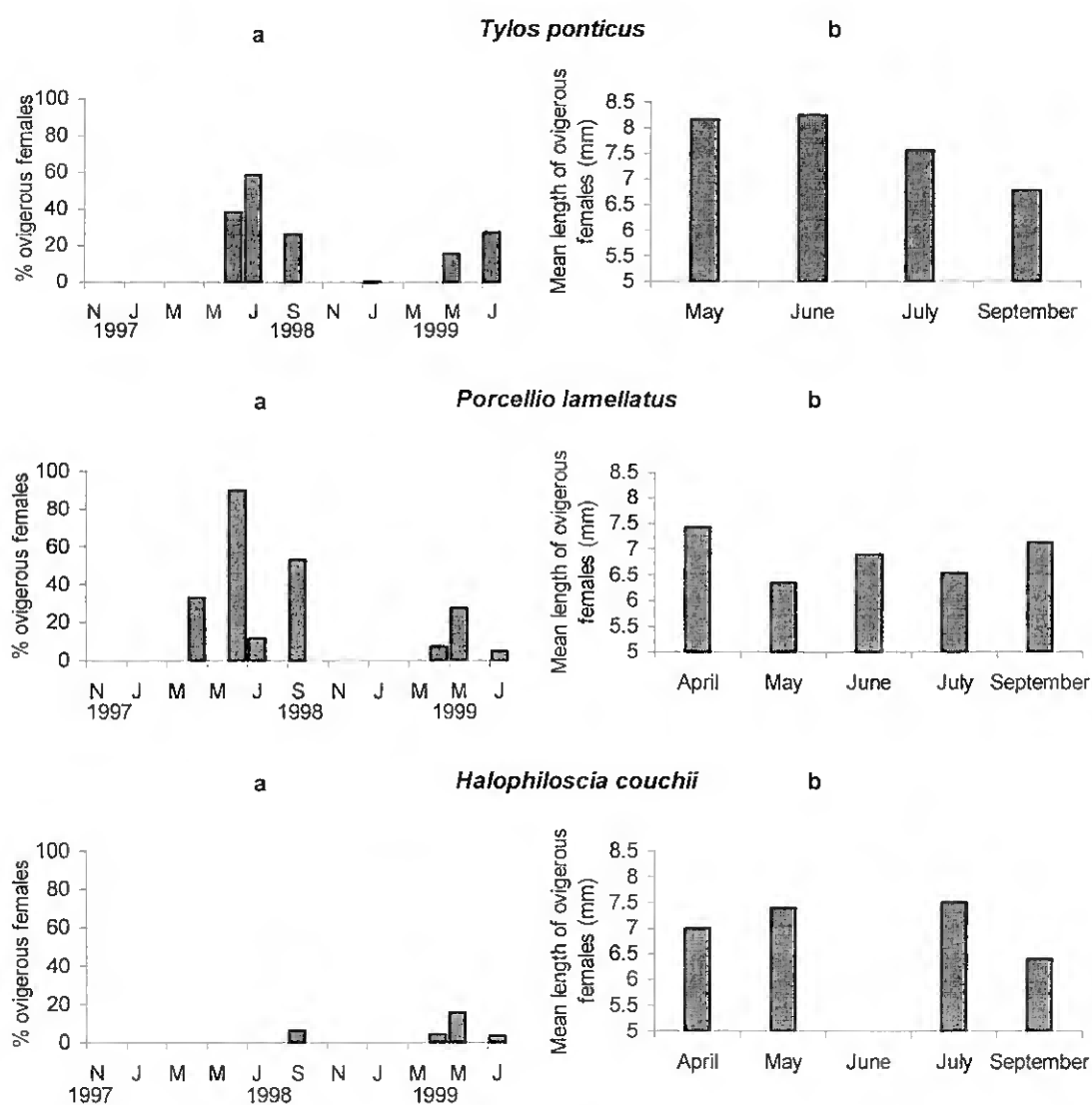


Fig. 6. *Tylos ponticus*, *Porcellio lamellatus* and *Halophiloscia couchii*. Figure showing the percentage of ovigerous females during the breeding season (a) and changes of mean length of ovigerous females during the breeding season (b).

Table 4. Regression parameters relating the ash free dry weight of ovigerous females to the number of eggs for each isopod species. The values given are for the following equation: $F = a \times W^b$; where F = fecundity (number of eggs per female); W = ash free dry weight (mg) and a and b are constants (r^2 = coefficient of determination; n = number of estimates).

| | a | b | r^2 | n |
|------------------------------|-------|------|-------|-----|
| <i>Tylos ponticus</i> | 4.02 | 0.67 | 0.40 | 151 |
| <i>Porcellio lamellatus</i> | 10.28 | 0.49 | 0.49 | 88 |
| <i>Halophiloscia couchii</i> | 11.16 | 0.73 | 0.29 | 15 |
| <i>Armadillidium album</i> | 7.62 | 0.36 | 0.65 | 16 |

Life history of *Armadillidium album*

Only 84 individuals were caught during the sampling period. For this reason it was impossible to assess its growth, lifespan and sex ratio. Sex could be differentiated in individuals larger than 2 mm. Maximum observed length was 7 mm both in females and males. Weight can be obtained by the expression shown in Table 3.

Breeding activity extended, presumably, from May to July as concluded from observations in May 1999 (14 ovigerous females out of 18 animals) and July 1998 (all 4 animals caught were ovigerous females). Ovigerous females ranged from 4 to 6 mm in body length, however most were of intermediate size (4 mm: 35%; 5 mm: 59%; 6 mm: 6%). Average fecundity was 7.5 eggs per female, varying from 4 to 11. As in other isopods, larger females carried a higher number of eggs in their marsupium (Table 4). No recruits were found during the sampling period.

Main life history traits of the isopods *Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii* and *Armadillidium album* are summarized in Table 5.

Table 5. Life history traits of the isopods *Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii* and *Armadillidium album*.

| | <i>Tylos ponticus</i> | <i>Porcellio lamellatus</i> | <i>Halophiloscia couchii</i> | <i>Armadillidium album</i> |
|-----------------------------------------|-----------------------|-----------------------------|------------------------------|----------------------------|
| Life span (years) | 4 | 2 | 1 | 2* |
| Maximum size | | | | |
| Length (mm) | 14 | 14 | 11 | 7 |
| Weight (mg AFDW) | 15.8 | 9.6 | 3 | 2.5 |
| % females | 56 | 48 | 58 | ? |
| Mean age at first reproduction (months) | 24 | 12 | 9 | 12* |
| Mean size of breeding females | | | | |
| Length (mm) | 8 | 7 | 7 | 5 |
| Weight (mg AFDW) | 3.6 | 1.8 | 1.0 | 1.1 |
| N. of broods in lifetime of individuals | 2-3 | 2-4? | 1 | 2* |
| Breeding season | May-Sep/Oct | March-Sep/Oct | March-Sep/Oct | May-July |
| Fecundity (n. eggs/female) | 11.9 | 14.2 | 14.3 | 7.5 |
| Size of recruits | | | | |
| Length (mm) | 2 | 1 | 1 | 1* |
| Weight (mg AFDW) | 0.186 | 0.018 | ? | ? |

* source: Vader & Wolf (1988).

Secondary production

Production of *Tylos ponticus* was 292 times higher than the production of *Porcellio lamellatus* (Table 6). This difference is not a direct reflection of their abundances, as the average density of *T. ponticus* was only 6 times higher than *P. lamellatus*. Generally, peaks of production did not coincide (Fig. 7). Major increases in increment rates in *T. ponticus* occurred in January and September 1998 while in the case of *P. lamellatus* they occurred in June 1998 and April 1999. Biomass removal rates were more pronounced in September 1998 in the case of *T. ponticus* and in July 1998, 1999 for *P. lamellatus*. Secondary production could not be estimated for *H. couchii* due to lack of density data. The extremely low number of captured individuals of *A. album* made the calculation of its production impossible.

Table 6. Annual secondary production estimates for *Tylos ponticus* and *Porcellio lamellatus* using both the increment and removal summation methods (P/B = Production/Biomass ratio).

| | Annual production (g ash free weight m ⁻²) | | Annual production (g ash free weight m ⁻²) | |
|-----------------------------|-----------------------------------------------------------|-----------|-----------------------------------------------------------|-----------|
| | Increment summation method | | Removal summation method | |
| <i>Tylos ponticus</i> | 17.51 | P/B: 4.67 | 7.36 | P/B: 1.96 |
| <i>Porcellio lamellatus</i> | 0.06 | P/B: 2.46 | 0.05 | P/B: 1.87 |

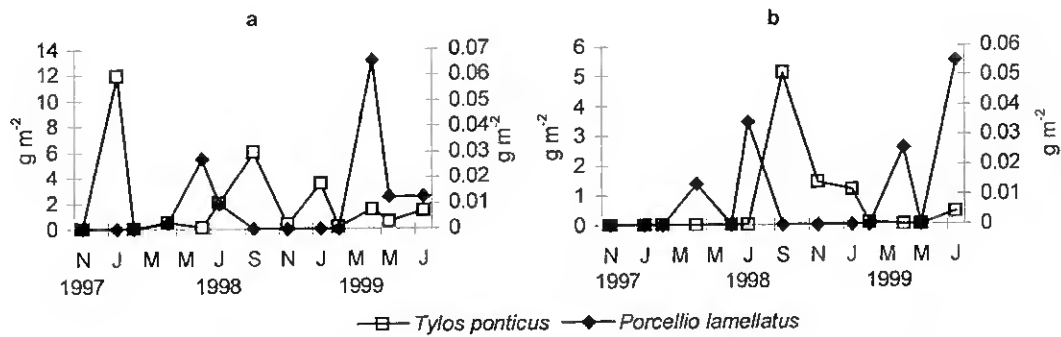


Fig. 7. Secondary production estimates (g ash free weight m⁻²) over the study period for *Tylos ponticus* and *Porcellio lamellatus* as determined by (a) the increment summation method and (b) the removal summation method. The left axis with a higher scale is for *T. ponticus* and the right axis with the smaller scale is for *P. lamellatus*.

DISCUSSION

Distribution

A common feature of terrestrial isopods is that several species often coexist within a small area (Davis & Sutton, 1977; Warburg et al., 1984). In many cases species can coexist by spatial separation within a habitat. In the present study, isopod species showed a great overlap in the intermediate level (Fig. 2). During the day there was some vertical separation as *Tylos ponticus* and *Armadillidium album* dig holes and bury themselves in the sand. Interference between these two species may be prevented by their different distribution, *A. album* being associated with organic deposits while *T. ponticus* is more abundant in the substrate free of wrack. However, it is also common, during daylight, to find many individuals of *T. ponticus* hidden within and underneath the deposits (N. Dias, unpubl. observations).

Low abundance of isopods at NHTL was apparently caused by the physical characteristics of the substrate. *Armadillidium album* was never found at this level and

Porcellio lamellatus was only captured there once. Therefore, these two are clearly supra-littoral species.

Tylos ponticus dominated at each level showing that it is the best adapted to the salt marsh conditions. *Armadillidium album* was the rarest species. Horizontal separation of *H. couchii* and *P. lamellatus* is possibly related to physiological differences. *Halophiloscia couchii* is less adapted to cope with desiccation (cf. Schmalzfuss, 1998) and dominated in the more humid levels (NHTL and MHTL). Conversely, *P. lamellatus* is better equipped to withstand drier environments (cf. Schmalzfuss, 1998) and it was more abundant than *H. couchii* at the upper level. It must be stressed that the abundance of all isopods was greatest at MHTL. This is most probably related to the presence of organic deposits as they not only provide food for these animals but also protect them against radiation, desiccation and predation.

Thus, the isopod species studied herein live in sympatry in the salt marsh, exhibiting partial overlap in their spatial distributions. When there is usually more than one species present in the same place at the same time, there is a potential for interspecific competition which could be either by exploitation or by interference. But competition alone may not fully explain the dramatic population fluctuations that were observed during this study. The possible causes of these changes in isopod demography will be discussed.

Interspecific competition

Porcellio lamellatus, *Halophiloscia couchii* and *Armadillidium album* numbers were lower in 1998 but increased in spring 1999. Conversely, *Tylos ponticus*, the most abundant isopod, showed great density peaks in summer 1998, but during the following year the peaks were less pronounced. Density was 4 times lower in July 1999 and mean

density for the period of steep density increase (April to July) in 1999 was half that in 1998. For *Tylos*, the other species are likely to be weak competitors as indicated by their much lower densities (70 to 380 times less). However, there are also amphipods cohabiting with the isopods in the salt marsh, these being: *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii*. They are more abundant at the intermediate level as well, *O. gammarellus* and *O. mediterranea* being associated with the debris and *T. deshayesii* burying in the substrate free of wrack (Dias et al., unpubl. data). Density levels of *O. gammarellus* (700 ind m⁻², on average; Dias & Sprung, 2004) suggest that it may compete with *T. ponticus*. In fact, in 1999 the density of *O. gammarellus* increased 98% (Dias & Sprung, 2004) while *T. ponticus* decreased 46%.

This may be a result of interspecific competition, similar to descriptions of populations of *Armadillidium vulgare* Latreille, 1802 and *Porcellio scaber* Latreille, 1804 in grasslands of England (Hassall & Dangerfield, 1989). The latter authors have found that when the density of the *P. scaber* population increased, a strong and significant negative effect was observed on the growth of young *A. vulgare*. As fecundity is a function of size in isopods (e.g., Paris & Pitelka, 1962; Sutton et al., 1984; Hassall & Dangerfield, 1990; Warburg & Cohen, 1993), changes in growth rate caused by other species could be an important factor influencing the population dynamics of these crustaceans (Hassall & Dangerfield, 1989).

Accordingly, Davis & Sutton (1978) made a comparative study in dune grassland isopods and observed that although the relative abundance of isopod species may change in a community, total isopod biomass remains relatively constant. Comparing the period of steep density increase of the salt marsh peracarid species (April to July) we found that isopod community biomass showed a small change, being 27% lower in 1999 in comparison to the preceding year. According to

Hassall & Dangerfield (1989), the constancy in biomass could be explained if the whole community is limited by interspecific competition for high quality food. High quality food could be in this case algae of the family Ulvales which are the preferred plant detritus of all isopods of this salt marsh (N. Dias, unpubl. data). Algal deposits are not as abundant as seagrass and salt marsh plant deposits along the mean high tide level (MHTL), and are irregular in space and time. However, animals may utilize the same available food resource in different ways, e.g., consuming distinct parts or different decomposition stages of the wrack or just feeding on microorganisms colonizing the litter (c.f. Lopez et al., 1977; Koop et al., 1982; Zimmer & Topp, 2000; Zimmer et al., 2002). This has already been observed by Zimmer & Topp (2000) who found that the sympatric isopods *Porcellio scaber* and *Oniscus asellus* Linnaeus, 1758 may partly avoid competition for food by species-specific differences in nutritional requirements.

Intraspecific competition

Intraspecific competition may be also one cause for fluctuations in the density of isopod populations. Dangerfield (1989) showed that for *P. scaber* and *A. vulgare* interference between conspecifics was very important and that the presence of the other species affected growth to the same extent as a similar number of conspecifics. This author found prominent effects of crowding in *A. vulgare*, such as reduced growth with the consequent reduction of fecundity and offspring size.

Furthermore, summer recruits that comprise the bulk of the population at the beginning of winter may be highly variable from year to year due to a combination of (1) availability of high quality food; (2) female growth; (3) adult survivorship; (4) juvenile survivorship; and (5) the spring age/size structure of the population

(Lawlor, 1976b). The year to year variation in recruitment may be further amplified by the intense winter density-dependent mortality resulting in major population fluctuations (Lawlor, 1976b).

It is possible then, that the elevated numbers of *T. ponticus* in 1998 generated intraspecific competition which reduced its population in the following year.

Breeding phenology

To avoid competition, coexisting species may develop differential reproductive phenologies. One consequence of sympatry might be a change in the reproductive biology of an organism to favour reduced age at first reproduction and higher reproductive effort during the early stages of the breeding season (Sibly & Callow, 1986). In the present study *Tylos* and *Porcellio* were, potentially, iteroparous while *Halophiloscia* was semelparous (see Table 5). The mean size of breeding females was higher in *Tylos* which is, in part, a consequence of later initiation to reproductive activity (2 years for *Tylos* and 1 year or less for the other species) and in another part due to the greater size and the slower growth of *Tylos*. As fecundity is directly correlated with size in isopods it should be expected that larger females will produce higher number of eggs. However, the inverse situation occurred. Instead of investing energy in higher number of offspring *Tylos* used their resources to produce larger offspring. Newly released young of *Tylos* were the largest. According to Lawlor (1976a), largest young at the time of the release show higher growth increases. Larger size in isopods means higher fecundity. Smaller individuals and slower growth imply higher susceptibility to physical-chemical factors. Female fitness is ultimately determined by two factors: (1) the number of offspring produced, and (2) the

subsequent fitness of those offspring. The fitness of the offspring depends on both their survival to maturity and their own fecundity (Lawlor, 1976a).

Dangerfield (1989) found that there was a benefit for individuals in mixed cultures of *P. scaber* and *A. vulgare* with both exhibiting shorter pre-reproductive periods, particularly in *A. vulgare*. In this study, *P. lamellatus* and *H. couchii* started recruitment 2 months before *Tylos*. This life history strategy may avoid interspecific competition of juveniles, simultaneously extending the growing period of new recruits and leading to greater sizes at first reproduction. However, juveniles of *P. lamellatus* and *H. couchii* still may possibly interfere. Recruits of *P. lamellatus* are evenly distributed between the intermediate and the upper intertidal levels while newly released offspring of *H. couchii* are restricted to MHTL. This partial spatial separation together with the low densities of the two species may possibly prevent major competition among their offspring. *Armadillidium album* had the shortest reproductive season. Data from Vader & Wolf (1988) confirm that this isopod has a short breeding activity extending from May to July. In conclusion, there appears to be three breeding strategies: (1) *H. couchii* and *P. lamellatus* exhibiting an extended breeding season (7 to 8 months) starting early in the season (in March), (2) *T. ponticus* starting breeding later (in May) with reproduction lasting for 5 to 6 months and (3) *A. album* which breeds during a short period of 3 months (May to July). A very similar phenological phenomenon has been described by Zimmer & Brauckmann (1997) and Zimmer (2003) for an isopod community living in a flood-plain forest in the south western Germany. Nevertheless, it should be noted that the different reproductive strategies may not be related to competition but may be rather due to flexibility in reproductive allocation of the species (but see Dangerfield & Telford, 1995).

Abiotic constraints

Annual fluctuations may also be due to environmental variability. According to Warburg et al. (1984) oscillations of isopod populations are probably related mainly to climatic factors such as air humidity, rainfall, soil humidity and temperature. Temperature regulates growth rates, reproduction and survival and these parameters determine population density, as found by McQueen (1976) for *Porcellio spinicornis* Say, 1818. Analyzing the period of steep density increase of the studied isopods (April to July) for the two years, we found that in 1999 average temperature was 3°C lower, precipitation was 14 mm month⁻¹ less and evaporation was 2 mm day⁻¹ higher. Furthermore, we can speculate that lower winter temperatures may have stopped growth and prevented gonad maturation. Comparing the winter temperatures of 97/98 and 98/99 we found that mean temperatures were on average 3°C lower during the winter of 98/99. However, we consider that these are slight climatic changes that had no influence on the demography of the isopods.

Another hypothesis is that the population fluctuations of the terrestrial isopods in this study may be due to disturbance in the ecosystem. A disturbance is any relatively discrete event in time that removes organisms or otherwise disrupts the community by influencing the availability of space or food resources, or by changing the physical environment (Begon et al., 1996). Although this salt marsh is remarkably stable, there are some occasional disturbances such as extreme spring tides caused by storms and variable inputs of organic deposits, namely the very patchily distributed green algae which are the preferred food of the isopods. These stochastic events are not very frequent but may alter the physical conditions of the environment in terms of humidity, shelter and food quality.

The basic idea of the **intermediate disturbance hypothesis** of Connell (1978) is that disturbance maintains diversity by preventing competitively dominant species from excluding others. Diversity is thought to be maximized by disturbances of intermediate frequency and intensity. Intense or frequent disturbances disrupt the community leading to reduced diversity through the loss of species that are particularly sensitive to disturbance (Krebs, 1994; Begon et al., 1996; Morin, 1999). Disturbance may then be, the reason for the coexistence of the 3 sympatric isopod species in the upper salt marsh. *Tylos*, the dominant species, buries in the sand so is relatively safe from extreme spring tides but is still exposed to disturbance induced variability in organic matter inputs, particularly the preferred food: green algae.

Predation

Most communities are probably organized by a mixture of forces – competition, predation, disturbance and recruitment – although their relative importance may vary systematically, with competition and predation figuring more prominently in communities where recruitment levels are high and in less disturbed environments (Begon et al., 1996). This is probably the case for the present community although we believe that predation may not be significant, i.e. possibly it has no influence on the population dynamics of these species. Sunderland & Sutton (1980) found that predation by centipedes, coleoptera and arachnids reduced the sub-adult population of the isopods *Armadillidium vulgare* and *Philoscia muscorum* Scopoli, 1763 by a minimum of 21%. In the study area there is also the same type of predators but their densities are so low (N. Dias, unpubl. data) that they lead us to speculate that their impact on the isopod populations is very small. Other potential predators visiting the study area are fishes and birds but their influence in the isopod populations is uncertain.

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CHAPTER 5

Coexistence of sympatric talitrid amphipods in a salt marsh of the Ria Formosa lagoon (southern Portugal)

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INTRODUCTION

Amphipods are important decomposers of organic matter in a variety of coastal systems ranging from sandy beaches to salt marshes (Averill, 1976; Lopez et al., 1977; Griffiths & Stenton-Dozey, 1981; Inglis, 1989; Marsden, 1991a; Marques & Nogueira, 1991). In intertidal systems, the amphipod fauna is dominated by a single family, the Talitridae (superfamily Talitroidea), which alone contains truly terrestrial species (obligate land-dwellers) that are thought to have used salt marshes and/or estuaries as a route to colonization of the land (Wildish, 1988; Richardson & Swain, 2000).

Three talitrid amphipods inhabit a high intertidal salt marsh of the Ria Formosa lagoon (Algarve, southern Portugal): *Orchestia gammarellus* (Pallas 1766), *Orchestia mediterranea mediterranea* Costa 1853 and *Talorchestia deshayesii* (Audouin, 1826). Living above the neap high tide level, they are numerically important members of the macroinvertebrate community in the salt marsh together with some terrestrial isopods (Isopoda: Oniscidea), *Tylos ponticus* Grebnitzky 1874 (Tylidae), *Porcellio lamellatus* (Uljanin) Budde-Lund 1879 (Porcellionidae), *Halophiloscia couchii* (Kinahan, 1858) (Halophilosciidae) and *Armadillidium album* Dolfuss 1887 (Armadillidiidae), all of them being involved in decomposition of salt marsh detritus and algal wrack (Sprung & Machado, 2000; N. Dias & M. Sprung, unpubl. obs.).

This study was done in the Ria Formosa lagoon, the largest wetland on the southern coast of Portugal. Studies on the ecology and biology of amphipod communities living in European salt marshes are rare (but see Den Hartog, 1963; Amanieu, 1969; Fouillet, 1986 cited by Créach et al., 1997; Sprung & Machado, 2000). Thus, the aim of this study is to analyze the distribution and population dynamics of the

sympatric amphipods *O. gammarellus*, *O. mediterranea* and *T. deshayesii*. For this, the amphipod community of the Ria Formosa salt marsh was sampled during two years, and population dynamics as well as relations between different species coexisting in the salt marsh habitat were analyzed.

MATERIALS AND METHODS

Study area

The Ria Formosa is a mesotidal lagoon separated from the Atlantic ocean by a 55 km long barrier island system on the south coast of Portugal (Algarve). The salt marshes in this lagoon are of the dry coast type (Adam, 1990) with the vegetation consisting of *Spartina maritima* (Curtis) Fernald in the lower level, *Sarcocornia* spp. and *Atriplex portulacoides* L. in the intermediate intertidal zone, and *Suaeda vera* J. F. Gmelin, *Suaeda maritima* (L.) Dumort, *Atriplex halimus* L. and *Limoniastrum monoptalum* (L.) Bss. in the upper intertidal zone. Water salinity is about 36 psu throughout the year (Falcão & Vale, 1990).

Study species

The beachflea *Orchestia gammarellus* usually occupies a fully saturated (> 95% R. H.) environment in the supralittoral, whether it be in strand-line wrack or under dense salt marsh grass swards (Morritt, 1998). It is distributed over a wide geographical area from Norway and South-West Iceland in the North to the

Mediterranean Sea, the Canary Islands and the Black Sea in the South. It also occurs on the Atlantic coast of Canada and northern USA (Moore & Francis, 1986).

Orchestia mediterranea lives under stones around mean high water neap tide level, but also occurs frequently in salt marshes (Den Hartog, 1963). Because *O. mediterranea* migrates on the shore so that its diurnal refuge is only covered by each recent tide, it is a true eulittoral species. This species shows an upshore migration as tides change from neap to spring and a downshore migration as tides change from spring to neap (Wildish, 1988). It is a Mediterranean-Atlantic species reaching its northern distribution limit in the Irish Sea and southern part of the North Sea, while its southern limit is in the Mediterranean Sea (Den Hartog, 1963; Lincoln, 1979).

The sandhopper *Talorchestia deshayesii* inhabits sand beaches and occurs in non-tidal areas (Mediterranean and Baltic coasts) near the waterline as well as in areas with wide tidal ranges (e.g., British Atlantic coasts) at the base of the dune above high tide marks. It is distributed along the European coasts from southern Scandinavia to the Mediterranean Sea (Nardi et al., 2000).

Meteorological data

Air temperature was registered daily by a minimum-maximum thermometer during the sampling period at a distance of 3 km from the study site. Precipitation data were obtained by the Direcção Regional da Agricultura do Algarve, which is about 7 km away from the site. Evaporation was registered daily using an evaporimeter tank located 3 km away from the study site.

Sampling methods

Amphipods were sampled every six weeks during neap tide periods from November 1997 to July 1999 using two methods: (a) core samples of 113 cm² taken to a depth of 20 cm and sieved using a 500 µm mesh sieve (45 replicates/date); (b) pit-fall traps (plastic flasks with 16 cm height × 6 cm diameter) filled with a dilute formalin solution (0.01 %) exposed for 96 h (9 replicates/date).

Samples were collected at three different tidal levels: (1) low intertidal zone with a compact mud surface, corresponding to the neap high tide level (NHTL), and dominated by *Sarcocornia* spp. and *Atriplex portulacoides*; (2) intermediate intertidal zone with sandy soil, corresponding to the mean high tide level (MHTL), with detrital deposits of *Zostera noltii* Hornem, *Spartina maritima* and some algae (mainly Ulvales); and (3) high intertidal zone with sandy soil, corresponding to the spring high tide level (SHTL). Litter and wrack deposits in the upper stratum were rare and consisted mainly of dry leaves and stems of salt marsh plants. At each intertidal level, the small-scale distribution of the amphipods was assessed by taking samples from two microhabitats: (1) substrate with deposits of organic matter and (2) substrate without deposits, but with a high number of holes in the sediment (probably dug by the isopod *Tylos ponticus* and by talitrids).

For each amphipod specimen, we determined (1) length of extended body, measured from the anterior edge of the cephalon to the telson (assigned to 1-mm size classes), (2) sex, (3) presence and number of eggs/young, (4) ash free dry weight (AFDW). Ash free dry weight was obtained by pooling up to 20 specimens of each size class (for each core or trap individually), drying them for 2 days at 60°C, and ashing them for 3 h at 450°C.

Reproductive activity is defined here as the presence of females carrying eggs or juveniles in the marsupium. To estimate (maximum) fecundity, the maximum number of eggs in each size class was determined, because the loss of eggs from the brood pouches during sampling, sorting and conservation would result in underestimation of fecundity.

Sediment analysis

The sediment was characterized at each sampling level (NH TL, MH TL, and SH TL) and at 3 different depths (0-6 cm, 6-12 cm and 12-20 cm). We measured (1) mean grain size and percentage of silt and clay using the moments method (Friedman & Sanders, 1978); (2) sediment water content by drying samples at 60°C for 48 h; (3) sediment organic matter content, obtained by ashing dried sediments for 3 h at 450°C.

Statistic analysis

Cohorts of amphipods were identified by size frequency analysis with the Bhattacharya (1967) method using the FISAT package (FAO-ICLARM Stock Assessment Tools) (core and trap data pooled). Sex could be distinguished in individuals larger than 6 mm (*Orchestia gammarellus*) and 5 mm (*Orchestia mediterranea* and *Talorchestia deshayesii*) body length; individuals of smaller size classes were distributed by sex according to the sex ratio in the larger size classes (Dias & Sprung, 2004). Growth parameters and the non-seasonalized Von Bertalanffy growth curve (VBGF) were estimated using the same routine:

$$L_t = L_\infty \{1 - e^{-K(t-t_0)}\}$$

where L_t is the length at age t , L_∞ is the asymptotic length, K is the intrinsic growth rate (curvature parameter) and t_0 is the computed age at length zero. Although this method does not account for individual intra- (cf. for isopods, Sunderland et al., 1976; Zimmer & Kautz, 1997) or inter-cohort differences in growth rates (e.g., Powell et al., 1996), the estimation of age based on size is commonly used in studies on amphipod populations (e.g., Cederwall & Jermakovs, 1999).

The overall growth performance was tested using the “Munro’s phi prime test” (Pauly & Munro, 1984):

$$\phi' = 2 \log_{10} (L_\infty) + \log_{10} K$$

Cohort mortality was estimated based on changes in abundance within every cohort, pooling all replicates. Age-specific survivorship was calculated by the slope b of a regression of $\ln(n+1)$ versus time (Krebs, 1998). The daily mortality of the population (q_x) was given by the equation:

$$q_x = 1 - e^b$$

Secondary production was estimated by (1) the increment summation method (Boysen Jensen, 1919) and (2) the removal summation method:

$$(1) P_{1,2} = \text{antilog} ((\log n_1 + \log n_2) / 2) \times (\varpi_2 - \varpi_1)$$

$$(2) P_{1,2} = \text{antilog} ((\log \varpi_2 + \log \varpi_1) / 2) \times (n_1 - n_2)$$

$P_{1,2}$: cohort production between sample dates 1 and 2;

n_1, n_2 : abundance of the specimens of the cohort at dates 1 and 2;

ϖ_1, ϖ_2 : mean weight of the specimens of the cohort at dates 1 and 2.

Variance/mean ratio (I_D) was calculated to investigate the type of dispersion (Krebs, 1998).

Differences between two means were tested for significance by means of *t*-tests and between more than two means by ANOVA. When variances were different, the Mann-Whitney test was used (Zar, 1999).

RESULTS

Distribution, abundance and activity

Orchestia gammarellus was the most abundant amphipod at the high intertidal salt marsh, followed by *Orchestia mediterranea*; *Talorchestia deshayesii* had the lowest abundance. Almost all *O. gammarellus* (96%) and *O. mediterranea* (92%) were captured at the intermediate level (MHTL). At higher and lower intertidal levels, the populations of *O. gammarellus* and *O. mediterranea* showed opposite distributions, the upper level (SHTL) being colonized more densely by the former species, the lower level (NHTL) being colonized more densely by the latter species (Fig. 1). The distribution of *T. deshayesii* was quite different with equally divided populations between MHTL (51%) and SHTL (49%) (Fig. 1).

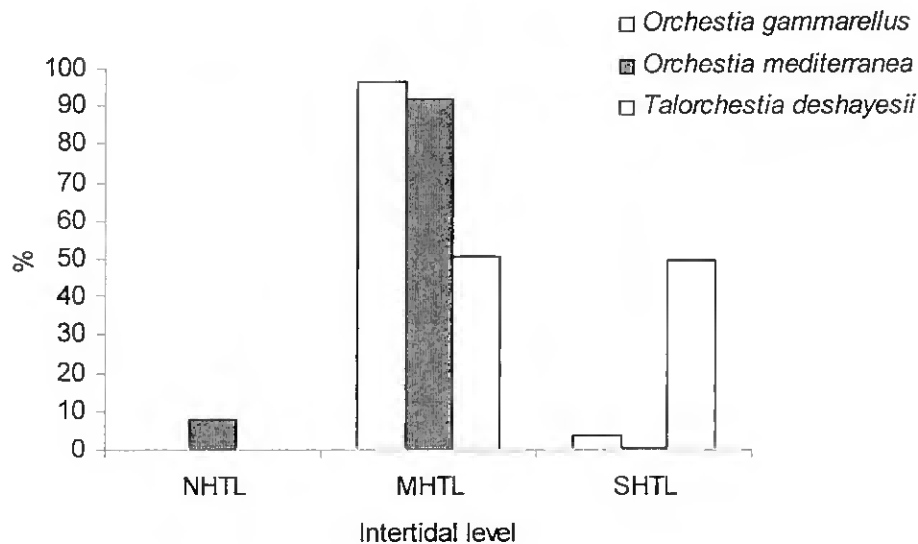


Fig. 1. Distribution of *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii* along the intertidal gradient (NHTL - neap high tide level, MHTL - mean high tide level, SHTL - spring high tide level). Data are presented as mean percent of the total number for each amphipod species.

At the lower level, no *O. gammarellus* or *T. deshayesii* and only one individual of *O. mediterranea* were caught with the corer. Substrate characteristics may be the reason for the scarcity of amphipods in this level (see Table 1). At MHTL, the average densities of *O. gammarellus*, *O. mediterranea* and *T. deshayesii* were 700 ind m⁻² (0 to 3690 ind m⁻²), 91 ind m⁻² (0 to 628 ind m⁻²) and 44 ind m⁻² (0 to 150 ind m⁻²), respectively. Average densities at the upper level were 15 ind m⁻² (0 to 97 ind m⁻²) for *O. gammarellus* and 42 ind m⁻² (0 to 195 ind m⁻²) for *T. deshayesii*, while *O. mediterranea* was never captured at this level with the corer. Density peaks of *O. gammarellus* and *O. mediterranea* occurred during spring 1999, while *T. deshayesii* was found in highest densities in February 1998 (SHTL) and in June 1998 (MHTL) (Fig. 2).

Table 1. Physical characteristics of the sediment at the three sampling sites (NHTL, MHTL and SHTL).

| Tidal Level | Depth (cm) | Water content (%) | Grain size (mm) | Organic matter (%) | Clay and silt (%) | Textural group |
|-------------|------------|-------------------|-----------------|--------------------|-------------------|----------------|
| NHTL | 0-6 | | 0.30 | 10.53 | 32.84 | Medium |
| | 6-12 | 13.7 * | 0.50 | 1.18 | 19.30 | Coarse |
| | 12-20 | | 0.62 | 0.41 | 13.40 | Coarse |
| MHTL | 0-6 | | 0.57 | 2.00 | 0.15 | Coarse |
| | 6-12 | 7.34 * | 0.48 | 0.57 | 10.08 | Medium |
| | 12-20 | | 0.60 | 0.38 | 12.99 | Coarse |
| SHTL | 0-6 | | 0.55 | 0.96 | 0.72 | Coarse |
| | 6-12 | 5.14 * | 0.59 | 1.93 | 0.68 | Coarse |
| | 12-20 | | 0.55 | 1.35 | 0.32 | Coarse |

* Data obtained for the entire 20 cm sediment profile in June 2001.

Biomass of all three species fluctuated dramatically over time. During the spring of 1999, the biomass of *O. gammarellus* and *O. mediterranea* increased 17- and 15-times, respectively, when compared with the same period in 1998. By contrast, the biomass of *T. deshayesii* decreased eight-fold in the early summer 1999 (Fig. 3).

To assess the dispersion of the three populations the variance/mean ratio (I_D) was calculated for each sampled level (Table 2). All three amphipods were generally strongly aggregated. At the intermediate level *O. gammarellus* was the most aggregated species, I_D was 41 on average. At SHTL the most aggregated amphipod was *T. deshayesii* that kept the same level of aggregation both at SHTL and MHTL, I_D was on average 4.

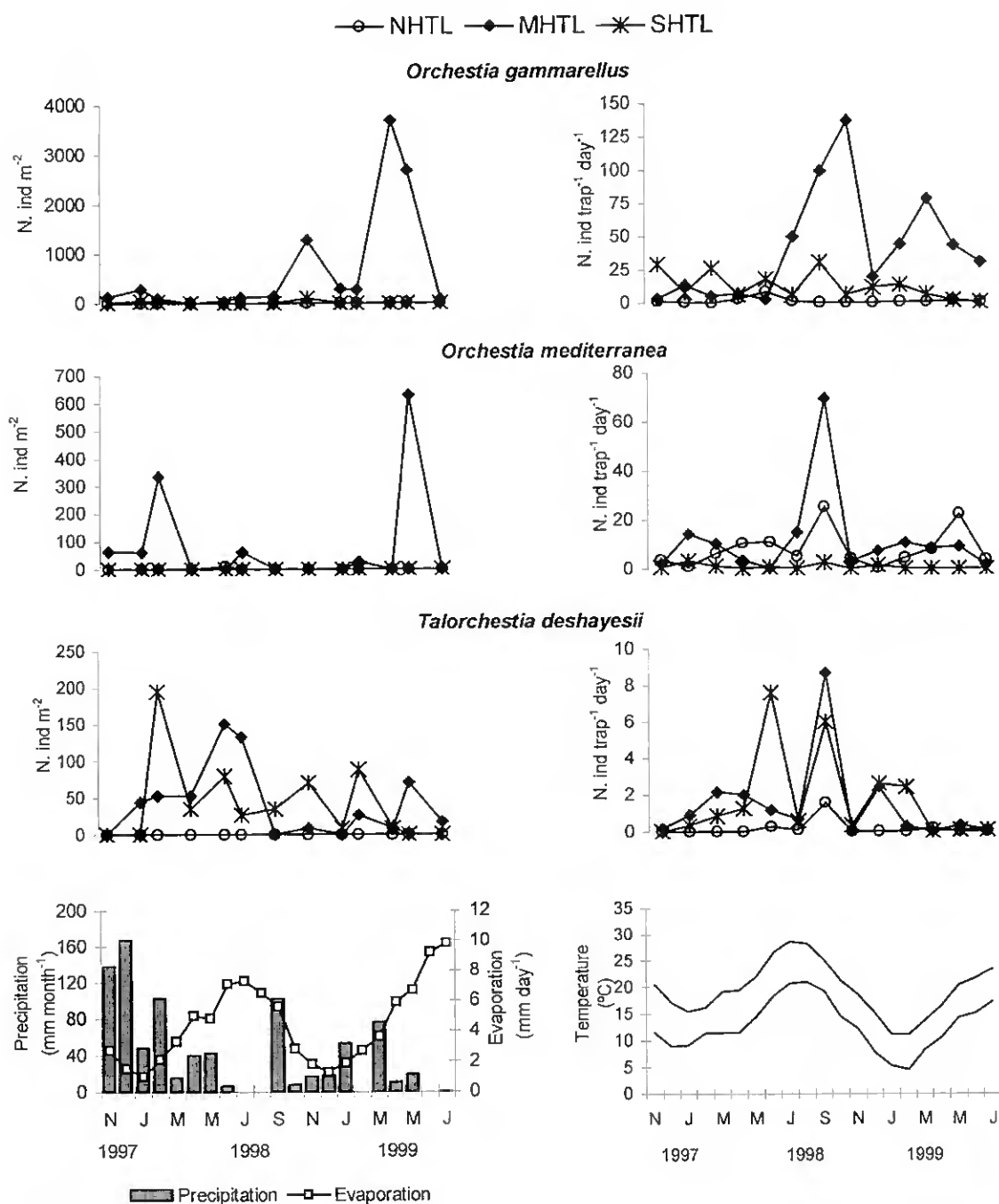


Fig. 2. Density (left: cores) and activity (right: pitfall traps) of the amphipods *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii* at each sampling level during the study period (NHTL - neap high tide level; MHTL - mean high tide level; SHTL - spring high tide level). Also shown are maximum and minimum air temperatures, evaporation rates and precipitation.

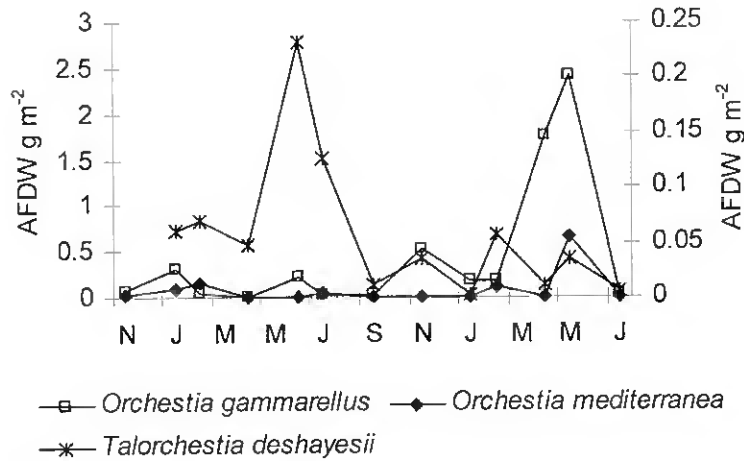


Fig. 3. Biomass of salt marsh amphipods (g ash free dry mass m⁻²) during the study period. The left axis with a higher scale is for *Orchestia gammarellus* and *Orchestia mediterranea*, while the right axis with the smaller scale is for *Talorchestia deshayesii*.

Table 2. Dispersion index I_D (variance/mean) for *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii*.

| | <i>O. gammarellus</i> | | <i>O. mediterranea</i> | | <i>T. deshayesii</i> | |
|------|-----------------------|-----------|------------------------|----------|----------------------|--------|
| | Average | range | Average | range | Average | range |
| MHTL | 41 | 0.4 - 223 | 6 | 0.2 - 33 | 4 | 1 - 11 |
| SHTL | 2 | 0.7 - 5 | - | - | 4 | 1 - 8 |

Our data on small-scale distribution of the amphipods (Table 3) indicate that *O. gammarellus* (Mann-Whitney test: $Z = 4.66$, $P < 0.0005$) and *O. mediterranea* (Mann-Whitney test: $Z = 3.67$, $P < 0.0005$) are closely associated with detrital deposits, while *T. deshayesii* ($t = 9.48$, $P < 0.0005$) is more abundant at wrack-free sites.

All amphipod species were active throughout the year (Fig. 2). In coincidence with its high densities (as determined with cores), *O. gammarellus* was the species most frequently captured in pitfall traps. For this species, activity was greatest at MHTL with an average of 41 ind trap⁻¹ day⁻¹ and moderate at SHTL where mean activity was 12 ind trap⁻¹ day⁻¹. *Orchestia gammarellus* became increasingly active in November 1998 and April 1999. By contrast, *O. mediterranea* exhibited highest activity (as deduced from captured numbers in pitfall traps) during September 1998. At MHTL, average activity was 12 ind trap⁻¹ day⁻¹, and at NHTL average activity was 8 ind trap⁻¹ day⁻¹. Alike density, *T. deshayesii* activity was balanced between MHTL and SHTL, but generally very low (2 ind trap⁻¹ day⁻¹), with peaks in June 1998 at SHTL and September 1998 at MHTL.

Table 3. Mean density (ind core⁻¹) of *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii* registered on sites with and without deposits of organic matter (S. D. - standard deviation; n - number of samples).

| Substrate | <i>O. gammarellus</i> | | | <i>O. mediterranea</i> | | | <i>T. deshayesii</i> | | |
|------------------|-----------------------|-------|----|------------------------|-------|----|----------------------|-------|----|
| | Mean | S. D. | n | Mean | S. D. | n | Mean | S. D. | n |
| With deposits | 18 | 50 | 55 | 2 | 3 | 25 | 3 | 2 | 95 |
| Without deposits | 0.1 | 0.4 | 55 | 0.2 | 0.4 | 25 | 6 | 2 | 95 |

Generally, density and activity of amphipods were independent of abiotic parameters such as air temperature, evaporation and precipitation (Tables 4, 5), except for *O. gammarellus* with its density being negatively correlated with evaporation at the

upper intertidal level ($r = -0.56$, $P < 0.05$) and its activity being positively correlated with precipitation at the lower intertidal level ($r = 0.81$, $P < 0.05$).

Table 4. Correlation coefficients between amphipod density and environmental parameters (temperature, evaporation and precipitation). Significant correlation coefficients are given in bold.

| Density | <i>O. gammarellus</i> | | <i>O. mediterranea</i> | | | <i>T. deshayesii</i> | |
|---------------|-----------------------|--------------|------------------------|--|--|----------------------|-------|
| | MHTL | SHTL | MHTL | | | MHTL | SHTL |
| Temperature | -0.14 | 0.18 | 0.08 | | | 0.45 | 0.17 |
| Evaporation | 0.13 | -0.56 | 0.04 | | | 0.40 | -0.29 |
| Precipitation | -0.29 | 0.05 | 0.09 | | | -0.41 | -0.15 |

Table 5. Correlation coefficients between amphipod activity and environmental parameters (temperature, evaporation and precipitation). Significant correlation coefficients are given in bold.

| Activity | <i>O. gammarellus</i> | | | <i>O. mediterranea</i> | | | <i>T. deshayesii</i> | | |
|---------------|-----------------------|-------|-------|------------------------|------|-------|----------------------|--------|------|
| | NHTL | MHTL | SHTL | NHTL | MHTL | SHTL | NHTL | MHTL | SHTL |
| Temperature | 0.39 | 0.13 | 0.04 | 0.46 | 0.28 | -0.06 | 0.37 | 0.15 | 0.25 |
| Evaporation | 0.32 | 0.01 | -0.33 | 0.40 | 0.04 | -0.41 | 0.19 | -0.008 | 0.15 |
| Precipitation | 0.81 | -0.24 | -0.21 | 0.12 | 0.36 | 0.52 | 0.33 | 0.48 | 0.03 |

Population structure

Due to the low numbers of *Orchestia mediterranea* and *Talorchestia deshayesii* captured in cores, our core data only allow for analyzing *Orchestia gammarellus*

populations at MHTL. For the other species, we will use pitfall trap data instead, although population structure may be represented insufficiently by these data, due to stage-specific (e.g., juveniles or ovigerous females) differences in activity.

The population of *O. gammarellus* was constituted on average by 45% juveniles (unsexed animals < 7 mm), 31% non-ovigerous females, 23% males and 1% ovigerous females. Juveniles were the dominant fraction of the population from September 1998 until April 1999 (Fig. 4). The percentage of females in the adult population was on average 58% (S. D. = 6; n = 5091) (Fig. 5).

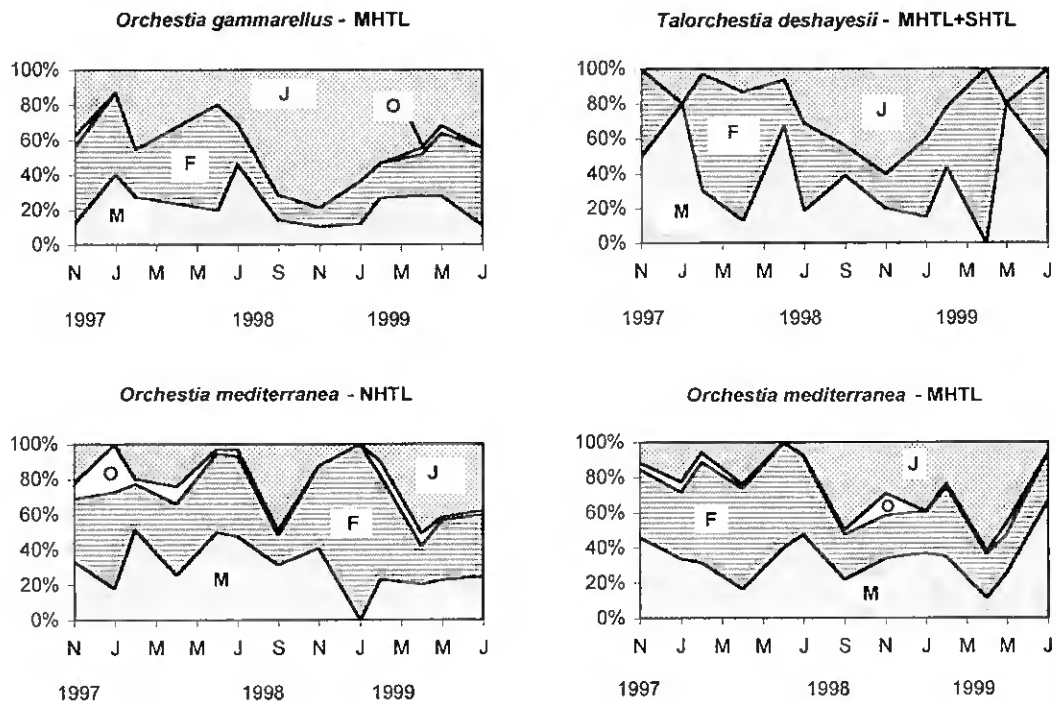


Fig. 4. Population structure of *Orchestia gammarellus* at the mean high tide level (MHTL) (data from cores), of *Talorchestia deshayesii* at the mean and spring high tide levels (data from traps) and of *Orchestia mediterranea* for the neap and mean high tide levels separately (data from traps) (J – juveniles; F – non-ovigerous females; M – males; O – ovigerous females).

The population of *O. mediterranea* was composed on average by 26% juveniles (unsexed animals < 6mm), 36% non-ovigerous females, 34% males and 4% ovigerous females. Population structure differed between NHTL and MHTL. The fraction of juveniles ($t = 2.24$, $P < 0.05$) and of males ($t = 3.17$, $P < 0.05$) was greater at the intermediate intertidal level, while the proportion of non-ovigerous females ($t = 3.25$, $P < 0.05$) and of ovigerous females ($t = 4.13$, $P < 0.05$) was higher at the lower intertidal level (Fig. 4). Sex ratio was slightly female biased ($54 \pm 7\%$; $n = 2129$) (Fig. 5).

The population of *T. deshayesii* was dominated by adults except in November 1998, when juveniles (unsexed specimens < 6 mm) constituted 60% of the population. On average, males accounted for 39%, non-ovigerous females for 41%, and juveniles for 20% of the population (Fig. 4); we only found two ovigerous females of this species (see below). There is not enough data to compare the population structure at MHTL and SHTL. Sex ratio could not be assessed for every sampling date, but the available data indicate an even sex ratio (51% females; Fig. 5).

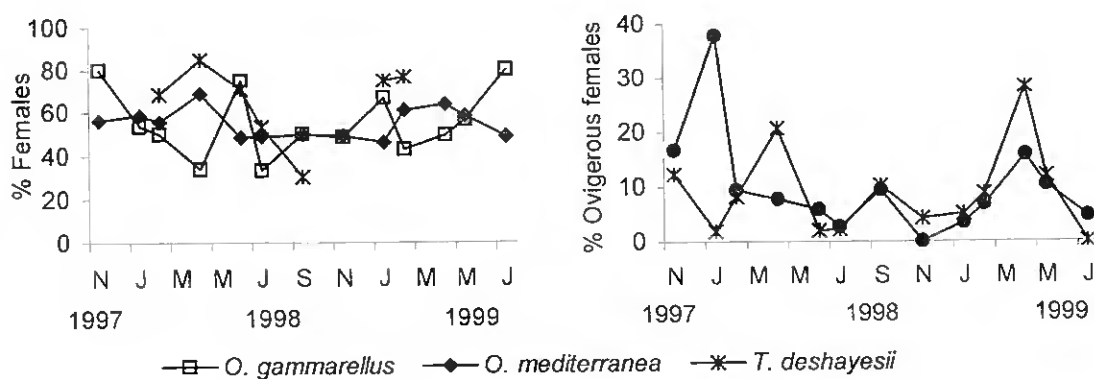
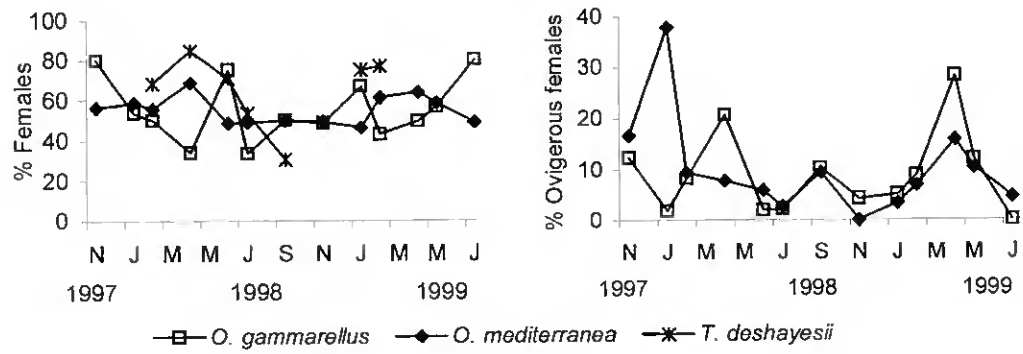


Fig. 5. Sex ratio of *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii* as deduced from the percentage of females, and reproductive activity of these species as indicated by the percentage of ovigerous females over the year cycle.

ERRATA

Figure number 5 of Chapter 5, page number 122, should be substituted by the following figure:



Life histories

Orchestia gammarellus

A total of 9597 specimens of *O. gammarellus* was measured and sexed. Females and males attained a maximum of 14 mm and 16 mm body length, respectively. Size-frequency distributions of each sex were analyzed for recognizable cohorts (Fig. 6). Longevity was estimated as 8 to 11 months for females and 8 to 12 months for males. Growth was estimated for each sex separately (Fig. 7), revealing that males and females had different growth curves ($F = -1171$, $P < 0.001$); the standard growth index ϕ' was higher in males indicating that they have a faster growth (Table 6). Daily mortality of *O. gammarellus* was on average 0.9 % (both sexes pooled), being higher in spring/summer (1.8 % day⁻¹) than in autumn/winter (0.5 % day⁻¹).

Ovigerous females were always present throughout the year except in July 1999. Because reproductive activity was observed in July of the previous year, we assume that reproduction occurs year-round. The percentage of the females that were ovigerous was relatively low, being on average 9%. Highest rates of breeding activity were detected in April 1998 and April 1999 (21% and 28%, respectively) (Fig. 5). According to the size of ovigerous females (8 to 13 mm, 10 mm on average), they appear to reach maturity at the age of 6-7 months. Mean brood size was 17 ± 4 , with a range of 11-21 eggs. There was a significant positive correlation between the length of the female and the number of eggs ($r = 0.93$, $n = 5$, $P < 0.05$). Neonate juveniles belonged to the 1-mm size class.

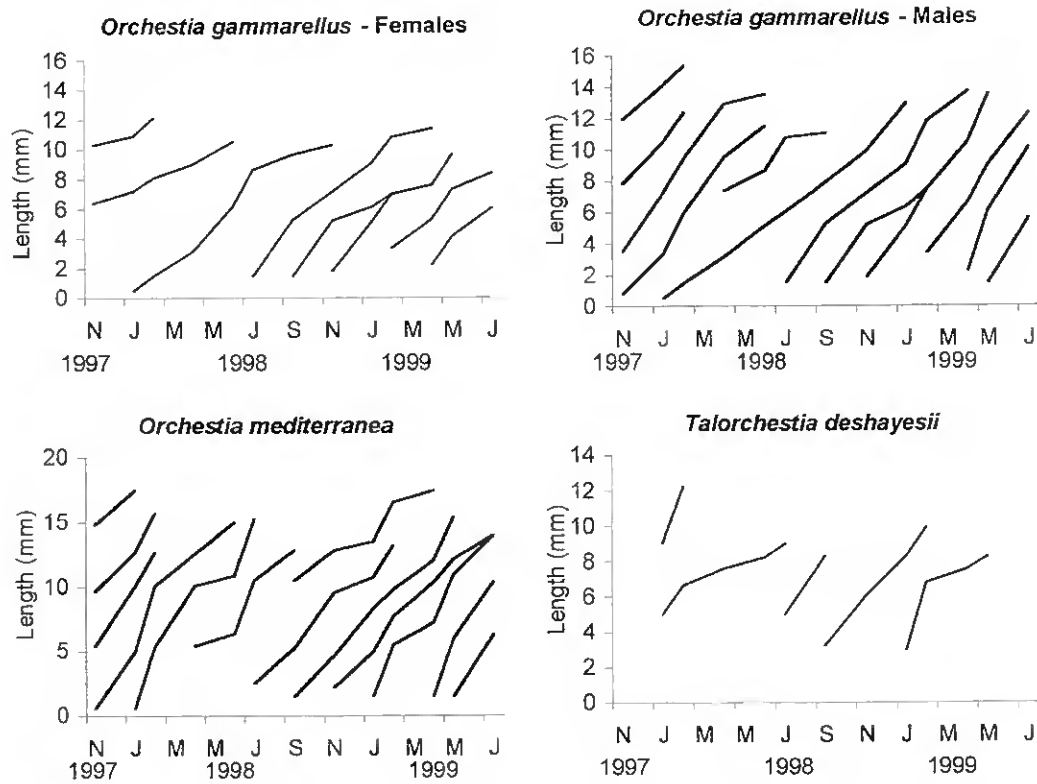


Fig. 6. Mean length of *Orchestia gammarellus* (females and males), *Orchestia mediterranea* and *Talorchestia deshayesii* over the study period showing cohort progression.

Orchestia mediterranea

A total of 3418 individuals of *O. mediterranea* were examined. Females attained 26 mm body length, while males reached 20 mm. Cohort analysis (Fig. 6) indicate that the longevity of this talitrid is 8 to 12 months (both sexes pooled). According to the Von Bertalanffy growth function (Fig. 7), the standard growth index ϕ' was 2.8 (Table 6). Mortality of *O. mediterranea* was on average 0.7% per day (both sexes pooled). It was not possible to investigate effects of season and size on mortality.

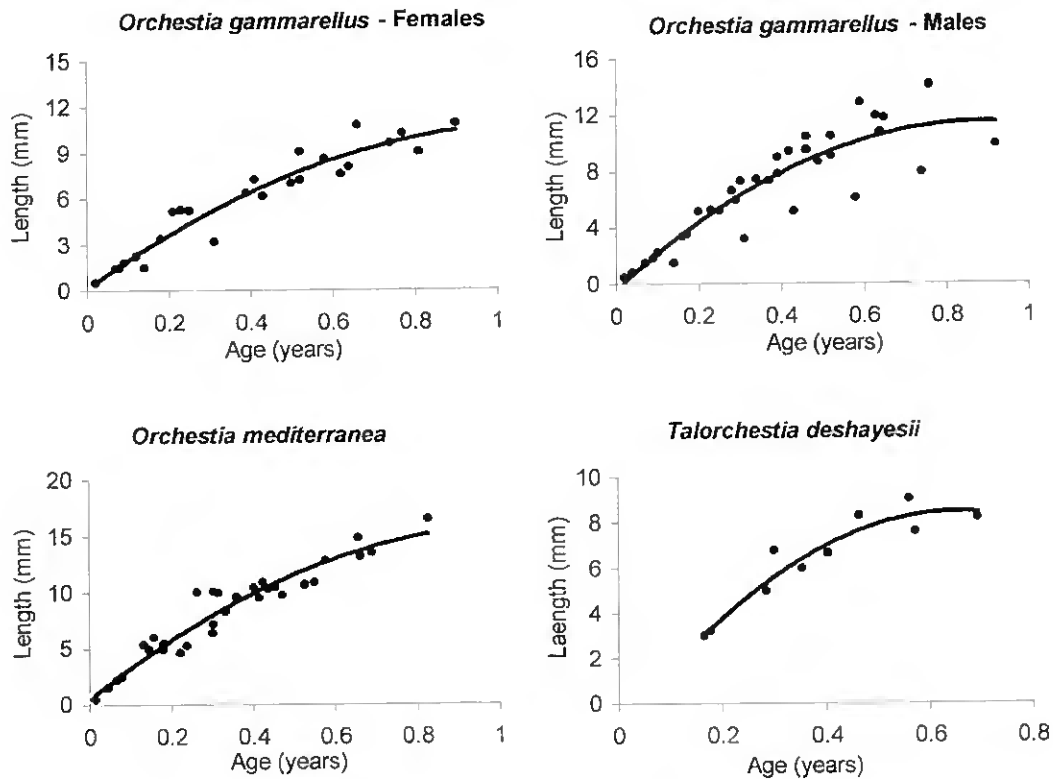


Fig. 7. Observed lengths at particular age and fitted non-seasonalized Von Bertalanffy growth function for *Orchestia gammarellus* (females and males), *Orchestia mediterranea* and *Talorchestia deshayesii*.

Brooding *O. mediterranea* were recorded at every sampling date except in November 1998. Because reproductive activity was observed in November 1997, we assume that reproduction occurs year-round. The percentage of females carrying eggs/juveniles averaged 10% with peaks in November 1997 (17%) and January 1998 (38%). In January 1999, in contrast, the rate of reproductive activity was one of the lowest during the sampling period (Fig. 5). The minimum size of ovigerous females was 7 mm and the maximum was 17 mm with an average of 11 mm. According to our estimated size-age relation, females, thus, would attain maturity at the age of 3 months, but would mostly reproduce when they are 5-6 months old. The mean number of eggs per brood was 18 ± 8 (8-30) eggs. The number of eggs (fecundity) was positively

correlated with female weight [$F = 7.43 W^{0.52}$, $r^2 = 0.48$, $n = 29$; $F =$ fecundity, $W =$ ash free dry weight (AFDW, mg)]. Neonate juveniles belonged to the 1-mm size class.

Talorchestia deshayesii

For the study of the life cycle of *T. deshayesii*, 624 specimens were analyzed. Maximum observed size of females and males was 10 mm and 11 mm, respectively. Distinct cohorts were identified through size-frequency distribution analysis (Fig. 6). By following cohorts, we estimated a longevity of 5 to 11 months, with a growth curve as shown in Fig. 7. The standard growth index ϕ' was 2.6 (Table 6).

Table 6. Growth parameters determined by non-linear fitting of the non-seasonalized Von Bertalanffy growth function (VBGF) for *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii*; SE: approximate asymptotic standard error; ϕ' : Munro's growth index; r^2 : coefficient of determination.

| Parameter | <i>O. gammarellus</i> | | <i>O. gammarellus</i> | | <i>O. mediterranea</i> | | <i>T. deshayesii</i> | |
|-------------------------|-----------------------|--------|-----------------------|--------|------------------------|--------|----------------------|--------|
| | Females | | Males | | | | | |
| | Mean | (SE) | Mean | (SE) | Mean | (SE) | Mean | (SE) |
| L_{∞} (mm) | 14 | (3) | 14 | (2) | 21 | (3) | 9 | (1) |
| K (year ⁻¹) | 1.5 | (0.6) | 2.3 | (0.8) | 1.5 | (0.4) | 4 | (2) |
| t_0 (year) | 0.002 | (0.03) | 0.03 | (0.02) | -0.009 | (0.02) | 0.08 | (0.04) |
| ϕ' | 2.5 | (0.3) | 2.6 | (0.3) | 2.8 | (0.3) | 2.6 | (0.2) |
| r^2 | 0.93 | | 0.83 | | 0.95 | | 0.90 | |

Only two ovigerous females were found during the entire sampling period. These females had a body length of 8 mm and were caught in April 1998 at SHTL.

Females had 1 and 2 eggs respectively in their brood pouches; we consider this an artifact of sampling, because neonate juveniles were regularly found throughout the year, belonging to the 1-mm size class.

Daily mortality of *T. deshayesii* was 0.2% (both sexes pooled). Due to too few data, it was impossible to investigate effects of season and size on mortality.

Size-weight relationship

Body weight of *O. gammarellus* females and males of a particular size (Table 7) was not significantly different from each other (7 mm: $t = 0.52$; 9 mm: $t = -0.41$; 11 mm: $t = -1.10$; $P > 0.05$). Further, weight at a particular length did not vary seasonally in either sex (7, 8, 9, 10 mm body length: ANOVA: $F_{\text{females}} = 1.12$, $P = 0.37$; $F_{\text{males}} = 0.65$, $P = 0.55$).

In *O. mediterranea*, size-corrected body mass of females and males (Table 7) was not significantly different from each other in smaller individuals (e.g., 7 mm: $t = -1.09$; 9 mm: $t = 0.63$; $P > 0.05$), but larger females were heavier than males of the same size (e.g., 11 mm: $t = 2.32$; 14 mm: $t = 3.58$; 17 mm: $t = 3.98$; $P < 0.05$). Weight at a particular length did not vary seasonally in either sex (7, 9, 11, 14, 17 mm body length: ANOVA: $F_{\text{females}} = 0.47$, $P = 0.7$; $F_{\text{males}} = 0.75$, $P = 0.52$).

In *T. deshayesii* body weight of similar-sized females and males (Table 7) did not differ from each other (e.g., 7 mm: $t = 0.1$; 9 mm: $t = 1.93$; $P > 0.05$) nor did the size-corrected weight of both sexes differ throughout the year (6, 8 mm: ANOVA: $F_{\text{females}} = 0.51$, $P = 0.67$; $F_{\text{males}} = 0.47$, $P = 0.70$).

Table 7. Regressions for the length/weight relationship: $W = a \times L^b$, W - ash free dry weight (g), L - length (mm), a, b - constants; r^2 - coefficient of determination; n - number of estimates.

| | a | b | r^2 | n |
|------------------------|----------------------|------|-------|-----|
| <i>O. gammarellus</i> | $5.25 \cdot 10^{-6}$ | 2.63 | 0.66 | 310 |
| Females | | | | |
| <i>O. gammarellus</i> | $3.93 \cdot 10^{-6}$ | 2.75 | 0.81 | 387 |
| Males | | | | |
| <i>O. mediterranea</i> | $3.07 \cdot 10^{-6}$ | 2.79 | 0.80 | 265 |
| Females | | | | |
| <i>O. mediterranea</i> | $4.63 \cdot 10^{-6}$ | 2.59 | 0.79 | 313 |
| Males | | | | |
| <i>T. deshayesii</i> | $4.64 \cdot 10^{-6}$ | 2.78 | 0.61 | 115 |
| Females | | | | |
| <i>T. deshayesii</i> | $1.36 \cdot 10^{-5}$ | 2.28 | 0.53 | 91 |
| Males | | | | |

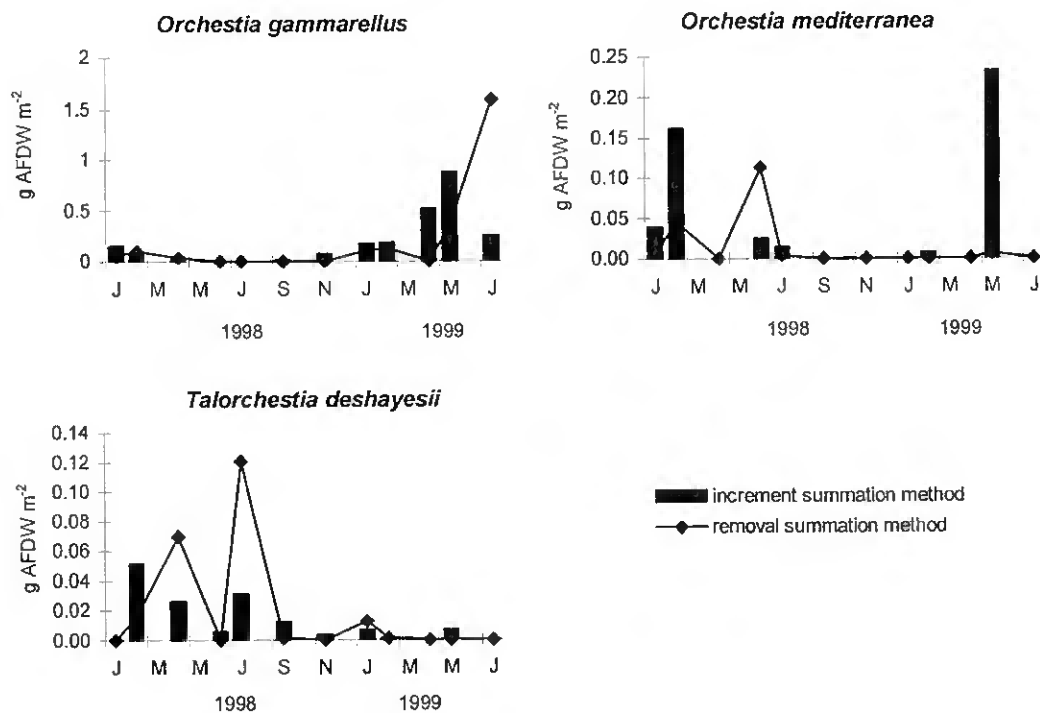
Secondary production

Secondary production of *Orchestia gammarellus* was the highest, being four times the production of *Orchestia mediterranea* and eight times the production of *Talorchestia deshayesii* (Table 8).

The population of *O. gammarellus* exhibited highest biomass increments in April and May 1999, while for *O. mediterranea* peaks of biomass production occurred in February 1998 and May 1999; for *T. deshayesii*, biomass gain was highest in February 1998. The most significant losses of biomass were observed during spring and summer (Fig. 8).

Table 8: Secondary production estimates for *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii*.

| | Annual production (g ash free weight m ⁻²) | | Annual production (g ash free weight m ⁻²) | |
|------------------------|-----------------------------------------------------------|-----------|-----------------------------------------------------------|-----------|
| | Increment summation method | | Removal summation method | |
| <i>O. gammarellus</i> | 1.62 | P/B: 4.62 | 1.36 | P/B: 3.87 |
| <i>O. mediterranea</i> | 0.37 | P/B: 5.09 | 0.15 | P/B: 2.04 |
| <i>T. deshayesii</i> | 0.21 | P/B: 4.96 | 0.12 | P/B: 2.75 |

**Fig. 8.** Secondary production estimates (g ash free weight m⁻²) over the study period for *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii* as determined by the increment summation method and the removal summation method.

DISCUSSION

Distribution and population patterns

The distributions of *Orchestia gammarellus* and *Orchestia mediterranea* within the Ria Formosa salt marsh overlap almost completely in the intermediate intertidal (Fig. 1). Only 4% of the former and 8% of the latter colonize the higher and lower intertidal zone, respectively. While *O. gammarellus* obviously has the physiological and ecological capabilities to inhabit the supralittoral (Wildish, 1988), *O. mediterranea* was classified by Wildish (1988) as an eulittoral species, being capable of inhabiting the low intertidal zone and withstanding prolonged inundation. Accordingly, Den Hartog (1963) observed that *O. mediterranea* colonized lower intertidal areas than *O. gammarellus* in Dutch salt marshes. This author suggested that the lower part of its vertical range may function as refuges for *O. mediterranea*, being able to penetrate into the territory of *O. gammarellus* when ecological circumstances are favourable. On the other hand, *O. gammarellus* may be excluded from the lower intertidal either by abiotic constraints (e.g., inundation) or by *O. mediterranea* being competitively superior under these circumstances. Even without competitive displacement, *O. mediterranea* extends downward to spots never occupied by *O. gammarellus* (Den Hartog, 1963), indicating that *O. mediterranea* tolerates a higher degree of moisture than *O. gammarellus*. When the degree of moisture is optimal for *O. mediterranea*, this species may be a fervent competitor, driving out *O. gammarellus*, which may be the case in low intertidal salt marshes (Den Hartog, 1963).

The upper distribution limit of *O. gammarellus* may be determined either by physical stress (e.g., desiccation or heat) or by the existence of *T. deshayesii* that

inhabits the intermediate and the high intertidal salt marsh equally well (Fig. 1), in turn, probably being limited by abiotic environmental factors higher up the salt marsh and by competition further down the intertidal. Several examples have been documented that illustrate the distribution of salt marsh inhabitants being limited by physical stress on one side (i.e., seaward for terrestrial species, landward for aquatic species) and by competition on the other side. However, transplantation experiments in Kneib's (1982) investigation suggested that the influence of physical factors alone could explain the distribution of the amphipod *Orchestia grillus* Latreille Ln Bose, 1802 in a Sapelo Island marsh.

Still, the three sympatric talitrids we studied exhibit a marked partial overlap in their spatial distribution, being truly syntopic in the intermediate intertidal (Fig. 1). Since resources (e.g., space or nutrients) are limited in a given habitat, coexisting species are expected to compete for these resources. The "principle of competitive exclusion" (Hardin, 1960; Armstrong & McGehee, 1980) predicts that the strongest competitor will eventually outcompete its inferiors. However, species-specific differences in ecological requirements and/or temporal and spatial variability of the environment ("intermediate disturbance") have been proposed to allow for coexistence of species within an ecological guild (Begon et al., 1996, for intermediate disturbance). Coexisting species, thus, cannot have identical requirements, but will only partially compete for a limited number of resources (cf. Zimmer, 2003, for isopods). Further, coexistence is possible if intraspecific competition exceeds interspecific competition (e.g., Volterra, 1931; Lotka, 1932). Under these conditions, intraspecific competition as well as reproduction and mortality will cause fluctuations (long-term, e.g., annual) and oscillations (short-term) in population density. Fluctuations in species abundance make the coexistence of (partially) competing species possible (e.g., Levins, 1979;

Armstrong & McGehee, 1980; Huisman & Weissing, 1999). We will discuss possible mechanisms of competition avoidance in turn.

Small-scale spatial distribution

Talitrids are highly susceptible to water loss and possess well-developed hygrokinetic responses, resulting in preferential aggregation in damper parts of humidity gradients (Morritt, 1998). In a salt marsh, thigmotaxis is also of great value, since the habitat is heterogeneous, and it would be advantageous for an amphipod to stay in close contact with the vegetation cover or detrital deposits rather than open mud (Morritt, 1998; but see Wildish, 1988 for *T. deshayesii*). These are probably the reasons why we found more than 90% of *O. gammarellus* and *O. mediterranea* under detrital deposits at the mean high tide level (MHTL). Wildish (1988) classified *O. gammarellus* and *O. mediterranea* as wrack-dwelling. *T. deshayesii*, in contrast, is not associated with the debris because it finds suitable humidity conditions burrowing in the sand at the intermediate and upper tidal levels (Wildish, 1988).

Interspecific interference

Orchestia gammarellus was the most abundant species of the amphipod community in the Ria Formosa salt marsh throughout our study, but population densities of amphipods exhibited marked fluctuations. However, temperature, precipitation and evaporation did essentially not differ between 1998 and 1999, and density maxima of the three species never coincided so that no common abiotic factor appears to be responsible here. Rather, interspecific displacement appears to be the

consequence of competitive interactions (but see above), or population fluctuations may be the result of predation.

According to our sampling-based estimates, mortality was lowest in *T. deshayesii* and highest in *O. gammarellus*, despite the opposite picture in terms of population density. Amphipods can kill each other through inter- or intra-specific fighting (Friend & Richardson, 1977). Van Dolah (1978) observed adult males of the aquatic *Gammarus palustris* Bousfield, 1969 grappling in an apparent fight, but in crowding experiments with this species he observed that space limitations did not induce aggressive behaviour. Rather, avoidance was the general response, with many amphipods clinging to the side of the high-density chambers. Predation is thought to affect the populations of amphipods, and a wide range of natural predators of talitrids has been recognized including invertebrates, fish, birds and mammals. According to Bowers (1964) and Wildish (1982) birds represent the most important group of amphipod predators. Although predators generally feed on a wide range of prey, some beetles are specialized on preying upon shore hoppers, like the staphylinid *Thinopinus pictus* Le Conte, 1852 (Richards, 1983; Wildish, 1988), and intertidal crabs prey upon wrack-dwelling amphipods at high tide (T. Lewis, M. Mews, D. Jelinski & M. Zimmer, unpubl. obs.). Van Dolah (1978) found that predation by a fish, a mud crab and a shrimp was the regulating factor of a population of *Gammarus palustris* living in a salt marsh at Chesapeake Bay (USA). According to Nelson (1979), predation may determine the relative abundance in a community of different amphipod species, seasonal changes in species diversity by selectively removing certain species, and – to some degree – the spatial distribution of amphipod abundance and diversity.

Talorchestia deshayesii is the smallest and fastest (N. Dias, unpubl. obs.) species of the amphipod community in the Ria Formosa salt marsh rendering it a

difficult prey to catch. Contrary, *O. mediterranea* is the largest amphipod of this assemblage making it a more valuable prey. On the other hand, *O. gammarellus* is the most abundant amphipod in the Ria Formosa salt marsh, therefore the most probable to encounter and capture with a low energetic cost for predators (in terms of foraging effort). Although several potential predators of talitrids live in the Ria Formosa salt marsh or visit it periodically, the extent to which predation plays a role in the control of the *Orchestia* populations is difficult to ascertain. In Barkley Sound (Vancouver Island, B.C., Canada), predation pressure by staphylinid beetles and crabs appears to be too weak to control populations of wrack- (e.g., *Traskorchestia traskiana* (Stimpson, 1857)) or sand-dwelling (e.g., *Megalorchestia pugettensis* Dana, 1853) amphipods that appear in high densities of several thousands per m² on sand and pebble beaches (T. Lewis, L. Neame, M. Mews, D. Jelinski & M. Zimmer, unpubl. data).

Besides amphipods there are four sympatric species of terrestrial isopods living in this saltmarsh, *Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii* and *Armadillidium album* (e.g., Sprung & Machado, 2000; N. Dias & M. Sprung, unpubl. data), being abundant at the intermediate intertidal level (MHTL). *Porcellio lamellatus*, *H. couchii* and *A. album* are directly associated with organic deposits, while *T. ponticus* is not (N. Dias & M. Sprung, unpubl. data). Although not all mentioned crustaceans use the debris as a refuge, all of them use it as food source. Furthermore, all the species prefer feeding on green algae, mainly Ulvales (N. Dias, unpubl. data). Most abundant organic deposits at the mean high tide level are *Zostera* and *Spartina* litter; green algae are less abundant, not always available and usually clumped. Thus, animals could be competing for high quality food.

Tylos ponticus is the most abundant isopod and its density was on average 16- and 2-times the density of *O. gammarellus* during 1998 and 1999, respectively

(Dias, 2002; Dias & Sprung, 2003). During the period of steep density increase of these two species (April to May/June) in 1999 there was a decrease of 46% in the density of *T. ponticus* and an increase of 98% in *O. gammarellus*. Although these changes in population density may well be just inherent fluctuations that would occur even in the absence of competitors, it is interesting to speculate on potential competitive interactions between syntopic detritivores. Possibly, *T. ponticus* maintained *O. gammarellus* at low densities during 1998. Apparently, this eased the interspecific competition between amphipods, and *T. deshayesii* clearly benefited from it. For the same reason, *O. mediterranea* may have competed better with *O. gammarellus* during 1998 although its densities were low. However in the next year, during spring, possibly as a result of intra- and interspecific competition, *T. ponticus* suffered a reduction in population density (Dias, 2002; Dias & Sprung, 2003) to which *O. gammarellus* responded with increased reproductive activity and a massive increase in density. At the same time the population size of *O. mediterranea* increased by 90%, while the numbers of its potential competitor, *T. deshayesii*, decreased by 76%.

Reproductive strategies

Both reproducing earlier in the breeding season and reducing age of sexual maturity may be important strategies to avoid direct competition between the juveniles of sympatric species (Sibly & Callow, 1986). Further, reproductive output (number and size of offspring) may affect the competitive ability of a species. For example, Dahl (1946) documented that *Orchestia platensis* Kröyer, 1845, an invasive species in North Western Europe, was apparently replacing *O. gammarellus* in parts of its range, probably due to its superior reproductive potential. Graça et al. (1994) found that a

population of the freshwater amphipod *Gammarus pulex* (Linnaeus, 1758) had a shorter and less intensive reproductive period in sympatry with the isopod *Asellus aquaticus* (Linnaeus, 1758) than in an allopatric population.

Both *O. gammarellus* and *O. mediterranea* reproduced throughout the yearly cycle; average percentage of ovigerous females ($t = -1.1$, $P > 0.05$) and fecundity (egg number) ($t = -0.5$, $P > 0.05$) of the two species were not significantly different, although slightly more elevated in *O. mediterranea*. In 1998, the reproductive peak of *O. mediterranea* was higher and earlier (38% in January) than the breeding peak of *O. gammarellus* (21% in April). During 1999, both peaks occurred in April, and the percentage of ovigerous females of *O. gammarellus* (28%) was almost twofold that of *O. mediterranea* (16%), indicating that these species do not exhibit stable species-specific reproductive patterns in response to sympatry, but rather show annual variations in reproduction. Similarly, neonates of both species were of roughly the same size.

As we deduced from cohort analyses, females of *O. mediterranea* were mature earlier in their life than *O. gammarellus* females. While in the former species most of the females involved in reproduction were 5 to 6 months old, in the latter the majority of females breeding were 8 to 11 months old. This difference may be due to different growth rates, since Munro's growth index (ϕ') was slightly but significantly higher in *O. mediterranea* (2.8 ± 0.3 , pooled for both sexes) than in *O. gammarellus* (2.5 ± 0.3 , for females) ($t = 3.85$, $P < 0.05$). Wildish (1979) found as well higher growth rates in *O. mediterranea* than in *O. gammarellus* in the Medway estuary. The mean size of ovigerous females did not differ between the species in the present study, indicating that *O. mediterranea* reached the same size in about half the time. Fast growth has the advantage of shortening the juvenile phase at which amphipods are subject to high

mortality as demonstrated by Louis (1977) for *O. mediterranea*. Marsden (1991b) also observed a high mortality in juveniles of *Talorchestia quoyana* (Milne-Edwards). Elkaim et al. (1985) proposed that early developmental stages are particularly sensitive to climatic conditions especially to low temperatures. Apparently, high temperatures, on the other hand, would increase the risk of desiccation in young amphipods which have a higher rate of area/volume than adults. Thus, *O. mediterranea* seems to have evolved other mechanisms that increase fitness (here: higher number and survival of offspring) than *O. gammarellus*, but data available so far are contradictory in terms of how this corresponds to interspecific competition.

Female-biased sex ratio will result in increased total reproductive output of a population (cf. Wildish, 1979) and is used by some sexual parasites (such as the protozoan *Paramarteilia*) to increase their transmission rates to the next generation. The population of *O. gammarellus* was the more female-biased (58%), while that of *O. mediterranea* was only slightly female biased (54% of females), and in *T. deshayesii* both sexes were found in even quantities (51% of females). Biased sex ratio could be a consequence of differential representation of the sexes in the production of offspring that could be caused by a polygenic determinism (*Gammarus pulex*, Anders, 1957) or by feminizing parasites such as the protozoan *Paramarteilia orchestiae* (*O. gammarellus*, Ginsburger & Desportes, 1979a, b), sex-specifically differential mortality such as male-killing by some sexual parasites (*Drosophila*, Williamson & Poulson, 1979). No such data are available for the present populations of amphipods.

Beyond sex ratio, we cannot infer more about the reproductive strategy of *T. deshayesii*, because we only captured two ovigerous females during the sampling period. In the Bay of Bou Ismael (Algeria) Louis (1980) has observed reproductive

activity of *T. deshayesii* from the early March to late November. Breeding activity was highest in late May and late September and lowest in late June. Sexual maturity was attained at an age of 3-4 months, and average fecundity was 4-7 eggs per female (Louis, 1980). Ovigerous females of *T. deshayesii* seem to seek a distinct micro-habitat where they possibly maintain a low activity during the incubation of their eggs. We assume them to hide under the shrubs in the upper tidal level, possibly explaining why we did not capture them with the corer nor with the pitfall traps. In many other amphipods, it was found that females are separated from the rest of the population, e.g., *Talorchestia megalophthalma* Bate, 1862 and *Talorchestia longicornis* Sau., 1818 (I. Marsden, unpublished obs.), *Talorchestia capensis* (Dana, 1853) (Van Senus & McLachlan, 1985), *Talorchestia quoyana* (Marsden, 1991b), and *Talitrus saltator* Montagu, 1808 (Williams, 1983a). Ovigerous females of the sand-dwelling *Orchestia corniculata* Stout, 1913 burrow deeper than their conspecifics (Craig, 1973).

Differences in size

Differences in body sizes of coexisting species may reduce competition through the utilization of different resources ("character displacement"). Studying five species of Haustoriidae at Sapelo Island, USA, Croker (1967) found that species sharing the same environment differed in size more strongly than those living in different habitats. Hutchinson (1951, 1959, in Sameoto, 1969) determined the size ratio in coexisting species as varying between 1.1 and 1.4 (with a mean of 1.3). Sameoto (1969) found this size difference in two intertidal sand-burrowing amphipods living in a salt marsh creek at Cape Cod (USA). In the present study, the body size ratio varied between 1.4 and 2.6

for females and between 1.5 and 1.8 for males, indicating that interspecific differences in size are large enough to avoid direct competition for food. Reduced competition for food has been proposed as mechanism allowing for coexistence of isopods in salt marshes on Sapelo Island (USA) (Zimmer et al., 2002).

Differences in food utilization

Intraspecific competition for food between older age classes and juveniles acts as an important process causing abundance changes in Baltic Sea populations of the deposit-feeding amphipod *Monoporeia affinis* (Lindström, 1855). Competitive mechanisms are primarily exploitative and/or interference for food (Wenngren & Ólafsson, 2002). Intraspecific competition for food is likely to occur in the talitrids studied herein, but the alternation of population densities and the decrease and increase of the reproductive activity of *O. mediterranea* and *O. gammarellus*, respectively, suggest that interspecific competition for food may be more relevant in this amphipod community.

Interspecific competition intensity can be reduced by specialization in terms of resource utilization (Menge & Sutherland, 1976). Species-specific differences in nutritional requirements mediated by species-specific differences in digestive capabilities may function in avoiding competition for food (Zimmer, 2003, for isopods). Crustacean detritivores in the salt marsh may, thus, differentially utilize the debris, consuming distinct parts or different decomposition stages of the wrack and some may just feed on microorganisms colonizing the litter (Lopez et al., 1977; Koop et al., 1982; Zimmer & Topp, 2000; Zimmer et al., 2002). Detailed studies on the amphipod species

studied herein are needed to decide upon species-specific food utilization in these salt marsh detritivores.

Conclusions

According to their distribution within the intertidal zone of the Ria Formosa salt marsh, talitrid amphipods are potential competitors at the intermediate intertidal elevation. Distribution limits appear to be mediated by both abiotic environmental factors and biotic interactions. *Orchestia mediterranea* may be constrained abiotically at its upper distribution limit, while the same may be true for *Orchestia gammarellus* at its lower limit. The upper limit of the latter species appears to be controlled by both environmental constraints and the occurrence of *Talorchestia deshayesii*. Effect of predation is unknown.

At the intermediate intertidal level, small-scale segregation appears to prevent interference competition between the *Orchestia* spp. and *T. deshayesii*, but the former share the same micro-habitat. Further, detritivorous salt marsh isopods potentially compete with the amphipods studied herein for space and food at MHTL, the sand-dwelling *Tylos ponticus* possibly interfering with *T. deshayesii*, while *Porcellio lamellatus*, *Halophiloscia couchii* and *Armadillidium album* are similar to the *Orchestia* spp. in that they spend most of their time underneath detrital deposits. Too little is known about the biology of any of these salt marsh detritivores to unambiguously decide upon mechanisms to avoid competition.

Reproductive displacement in terms of phenology does not seem to be sufficiently stable to explain coexistence alone. However, character displacement in terms of size apparently allows for utilizing different food sources and maybe different micro-refuges. Further field and laboratory studies should focus on differential

utilization of resources and differences between sympatric and allopatric populations that could be interpreted in terms of character displacement to reduce or even avoid interspecific competition within the guild of detritivores in the Ria Formosa salt marsh.

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CHAPTER 6

General Conclusions

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SYNOPSIS

The community of the invertebrate macrofauna permanently inhabiting the high intertidal zone of a Ria Formosa lagoon salt marsh has been studied. This community is composed by terrestrial peracarid species. The most abundant species in the high marsh are crustaceans from the Order Isopoda (Suborder Oniscidea), *Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii* and *Armadillidium album*, and from the Order Amphipoda (Suborder Gammaridea), *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii*. The population dynamics, life histories and relations between the different species were debated in the present work.

DISTRIBUTION PATTERNS

The distribution of amphipods and isopods within the Ria Formosa salt marsh showed a major overlap in the intermediate intertidal (MHTL). More than 90% of the populations of the amphipods *Orchestia* spp. were found at the mean high tide level (MHTL), 50% of the population of the amphipod *Talorchestia*, 65%, 77%, 96% and 64% of the populations of the isopods *Tylos*, *Porcellio*, *Halophiloscia* and *Armadillidium*, respectively. Thus, intra-guild competition is likely to occur within this area but small-scale segregation might prevent interference to some extent.

Indeed, some species showed different microdistributions, *Orchestia* spp., *Porcellio*, *Halophiloscia* and *Armadillidium* being directly associated with the wrack. Talitrid amphipods are highly susceptible to water loss and possess well-developed hygrokinetic responses (Morritt, 1998). Furthermore, thigmotaxis is also of great value, since salt marshes are heterogeneous habitats and it is advantageous for an amphipod to

stay in close contact with the vegetation cover or detrital deposits rather than open mud (Morritt, 1998). Isopods, too, need saturated air or a humid substrate in their permanent habitats (Edney, 1954). According to Warburg et al. (1984) both distribution and abundance of isopods seem to be controlled in great extent by humidity. Conversely, *Talorchestia* and *Tylos* were more abundant out of the debris because they are sand-dwellers and find suitable humidity conditions excavating holes in the sediment at the intermediate and higher levels. Thus, it seems that interference is more likely to occur between *Orchestia* spp., *Porcellio*, *Halophiloscia* and *Armadillidium* underneath the debris while *Talorchestia* and *Tylos* are potential competitors in the substrate free of wrack.

The lower intertidal level (NHTL) was the least occupied by these macrofauna species. This is probably due to abiotic constraints, such as the nature of the substrate (compact mud surface) and the higher degree of inundation. It seems that *Halophiloscia couchii* and *Orchestia mediterranea* are the best equipped to withstand a higher degree of inundation/humidity, once only they had a part of their populations in this level, albeit very small (2 and 8%, respectively). Biotic factors might be also preventing some species from colonizing this level. *Orchestia gammarellus* may be excluded from the lower intertidal by *O. mediterranea* because the latter species is competitively superior under these circumstances (Den Hartog, 1963).

The upper limit of the distribution of some of these species also appeared to be controlled by both environmental and biotic constraints. The upper intertidal level (SHTL) is the driest and sand burrowers are better adapted to colonize it. Indeed, significant fractions of the populations of *Talorchestia*, *Armadillidium* and *Tylos* were found at this level (50, 36 and 35%, respectively). On average, 23% of the captured *Porcellio* inhabited the zone around SHTL because this species can stand drier

environments (Schmalfuss, 1998). In turn, *O. mediterranea* and *H. couchii* were almost absent at this area because they are not physiological adapted to such dry conditions (Wildish, 1988; Schmalfuss, 1998). In turn, *O. gammarellus* is a supra-littoral species (Wildish, 1988), but possibly it might be excluded by *Talorchestia* and *Tylos*.

In conclusion, distribution limits of peracarids in the salt marsh appeared to be mediated by both abiotic environmental factors and biotic interactions.

POPULATION FLUCTUATIONS

Since resources (e.g., space or nutrients) are limited in a given habitat, coexisting species are expected to compete for these resources. The "principle of competitive exclusion" (Hardin, 1960; Armstrong & McGehee, 1980) predicts that the strongest competitor will eventually outcompete its inferiors. However, species-specific differences in ecological requirements and/or environment disturbances allow for species coexistence (Begon et al., 1996, for intermediate disturbance). Further, coexistence is possible if intraspecific competition exceeds interspecific competition (e.g., Volterra, 1931; Lotka, 1932). Under these conditions, intraspecific competition as well as reproduction and mortality will cause fluctuations (long-term, e.g., annual) and oscillations (short-term) in population density. Fluctuations in species abundance make the coexistence of (partially) competing species possible (e.g., Levins, 1979; Armstrong & McGehee, 1980; Huisman & Weissing, 1999).

During the present study, marked demographic fluctuations of isopods and amphipods were observed. The isopod *Tylos*, the dominant species of this assemblage, reached greatest densities during 1998, when a density as high as 10400 ind m⁻² was recorded. However, in the next year its population suffered a decrease by 46%. On the

other hand, the amphipod *O. gammarellus*, which is the second most abundant peracarid in the salt marsh, increased its numbers by 98% during 1999. Similarly, the isopod *Porcellio* increased its density by 76% and the abundance of *O. mediterranea* was 90% higher in 1999 than in 1998. *Talorchestia* suffered the reverse process, its abundance decreasing by 78%. For *H. couchii* and *A. album* was not possible analyse these trends due to insufficient density data.

Such demographic alternations may be due to intra- and interspecific competition. Extremely elevated numbers of *T. ponticus* in 1998 might have generated strong intraspecific competition, e.g., between adults and juveniles (Hassall & Dangerfield, 1990; Wenngren & Ólafsson, 2002) or among juveniles (Hatchett, 1947; Lawlor, 1976), leading to a population reduction in the following year. Possibly, the decrease of *Tylos* population offered the opportunity to other peracarids to increase their densities as happened with *Orchestia* spp. and *Porcellio*. *Talorchestia* is a particular case. It seems that *T. ponticus*, maintaining *O. gammarellus* at low density during 1998, has relaxed interspecific competition within the amphipod assemblage and *T. deshayesii* clearly benefited from it.

The whole community might be competing for space and for high quality food. High quality food could in this case be Ulvales which is the preferred plant detritus of all peracarids in this salt marsh (N. Dias, unpubl. data). Algal deposits are not as abundant as seagrass and salt marsh plant deposits along the mean high tide level (MHTL) and are found irregularly in space and time. However, species-specific differences in nutritional requirements mediated by species-specific differences in digestive capabilities may avoid competition for food (Zimmer, 2003, for isopods). Crustacean detritivores in the salt marsh may, thus, make a differential use of the debris, consuming distinct parts or different decomposition stages of the wrack and some may

just feed on microorganisms colonizing the litter (Lopez et al., 1977; Koop et al., 1982; Zimmer & Topp, 2000; Zimmer et al., 2002).

Another strategy that coexisting species can use to avoid competition is differential reproductive phenology. One consequence of sympatry might be a change in the reproductive biology of an organism to favour reduced age at first reproduction and higher reproductive effort during the early stages of the breeding season (Sibly & Callow, 1986). Within the isopod assemblage there appeared to exist three breeding strategies: (1) *Halophiloscia* and *Porcellio* exhibiting an extended breeding season (7 to 8 months) starting early in the season (already in March), (2) *Tylos* starting breeding later (in May) with reproduction lasting for 5 to 6 months and (3) *Armadillidium* which breeds during a short period of 3 months (May to July). The mean size of breeding females was significantly higher in *Tylos* which is a consequence of later initiation to reproductive activity (2 years for *Tylos* and 1 year or less for the other species). As fecundity is directly correlated with size in isopods (Paris & Pitelka, 1962; Sutton et al., 1984; Hassall & Dangerfield, 1990; Warburg & Cohen, 1993) it should be expected that *Tylos*, with larger females, would produce higher number of eggs. However, instead of investing energy in higher number of offspring, *Tylos* produced larger young. Nevertheless, it should be noted that the different reproductive strategies may not be related to competition but may be rather due to flexibility in reproductive allocation of the species (but see Dangerfield & Telford, 1995).

In the amphipods, reproductive strategies can only be analysed for *Orchestia* spp., because insufficient data on the reproductive biology of *Talorchestia* were available. Both *O. gammarellus* and *O. mediterranea* reproduced throughout the yearly cycle. These species do not exhibit stable species-specific reproductive patterns in response to sympatry, but rather show annual variations in reproduction. Similarly,

neonates of both species were of roughly the same size. *Orchestia mediterranea* seems to have evolved other mechanisms that increase fitness (here: higher number and survival of offspring) than *O. gammarellus*, but data available so far are contradictory in terms of how this corresponds to interspecific competition. In conclusion, reproductive displacement in terms of phenology does not seem to be sufficiently stable to explain coexistence of amphipods.

Character displacement in terms of size apparently allows for utilizing different food sources and maybe different micro-refuges. In the present study, the body size ratio between the several amphipod species ranged from 1.4 and 2.6, while in isopods it varied from 1.6 to 6.3 which indicates that interspecific differences in size are large enough to avoid direct competition for food according to Hutchinson (1951, 1959, in Sameoto, 1969). Reduced competition for food has been proposed as a mechanism allowing for coexistence of isopods in salt marshes on Sapelo Island (USA) (Zimmer, 2003).

Annual fluctuations may also be due to environmental variability. According to Warburg et al. (1984), oscillations of isopod populations are probably related mainly to climatic factors such as air humidity, rainfall, soil humidity and temperature. However, in this study temperature, precipitation and evaporation did not differ significantly between 1998 and 1999.

Predation is thought to affect the populations of amphipods, and a wide range of natural predators of talitrids has been recognized including invertebrates, fish, birds and mammals (Wildish, 1988). Predation may also significantly reduce isopod populations. Main isopod predators are centipedes, beetles and spiders (Sunderland & Sutton, 1980). In the study area, such potential predators exist, but their effect on this peracarid community is unknown.

CONTRIBUTION TO DECOMPOSITION PROCESSES

Feeding by detritivores accelerates the decomposition of plant material not only by the mechanical action of fragmenting tissue but, also by spreading microorganisms or by maintaining the surface microbial community in a youthful state (Inglis, 1989). According to Hassall et al. (1987) and Richardson & Morton (1986), the most important contribution these macrodecomposers make to the decomposition of organic deposits may be in physically transporting it to more humid microsites lower in the profile. By foraging in surface litter layers, usually at night, and then transporting and depositing 80% or more of what they have eaten as faeces in their sheltered resting sites, they may make a contribution to litter disappearance (Hassall et al., 1987).

The bulk of the organic matter deposited in the intermediate intertidal level of the studied salt marsh consists of dead leaves of *Spartina maritima* and *Zostera noltii*. *Spartina maritima* is the most abundant plant in the salt marsh and has a primary production of 768 g AFDW m⁻² year⁻¹ (R. Santos & M. Sprung, unpubl. data). *Zostera noltii* is the most abundant seagrass of the Ria Formosa lagoon and it is estimated that about 95% of its production stays inside the lagoon (R. Santos, unpubl. data). Its leaves are transported by the tides to the salt marsh and accumulate next to *Spartina* leaves at the mean high tide level (MHTL). The production of *Z. noltii* in the Ria Formosa lagoon has been estimated by González (2000) as 2300 g AFDW m⁻² year⁻¹.

To estimate the impact of the amphipods and isopods in the degradation of organic matter of the studied salt marsh we need to use data from literature, both consuming rates and energy budgets calculated for other species. Lopez (1976) measured consumption rates of the amphipod *Orchestia grillus* on *Spartina alterniflora* to be 362 times higher than its growth production. Extrapolations from other species

imply a more efficient energy conversion, consumption being 53 times the secondary production in *Talorchestia capensis* (Muir, 1977 cited by Griffiths et al., 1983) and 37 times in *Arcitalitrus dorrieni* (O'Hanlon & Bolger, 1998). Assuming these data are also valid for *Orchestia gammarellus*, *Orchestia mediterranea* and *Talorchestia deshayesii* we arrive at a potential consumption rate of the amphipod assemblage in the range of 11 to 100% of the assumed primary production of *Spartina* and 4 to 35% of *Zostera* production.

For the isopods we will use data from Zimmer et al. (2002) for the consuming rates of the salt marsh isopods *Littorophiloscia vitata* (Say, 1818), *Porcellionides virgatus* (Budde-Lund, 1885) and *Venezillo parvus* (Budde-Lund, 1885) on the salt marsh plant *Juncus roemerianus* Scheele. The authors obtained consumption rates for these isopods ranging from 0.08 to 0.25 mg DW mg⁻¹ day⁻¹. Extrapolating such consumption rates for the isopods studied herein (*Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii* and *Armadillidium album*) results in an estimate of 255 to 790 g DW m⁻² year⁻¹ consumed. As such, this isopod assemblage may potentially degrade 23 to 75% of the *Spartina* and 8 to 26% of the *Zostera* production primary production.

These estimates of the potential contribution to the degradation of the *Zostera* are underestimates because these peracarids occupy the intertidal area of the salt marsh which is approximated double the area of the *Zostera* beds in the Ria Formosa lagoon (Fidalgo, 1996).

The present work revealed the necessity of further studies to increase understanding of the role that this macrofauna guild plays in the salt marsh, studies on consumption rates, assimilation efficiency and species-specific food utilization in these salt marsh detritivores being particularly important. Also, too little is known about the biological interactions between the studied species and which mechanisms they use to

avoid competition. Further field and laboratory studies should focus on differential utilization of resources and differences between sympatric and allopatric populations that could be interpreted in terms of character displacement to reduce or even avoid interspecific competition within the guild of detritivores in the Ria Formosa salt marsh.

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