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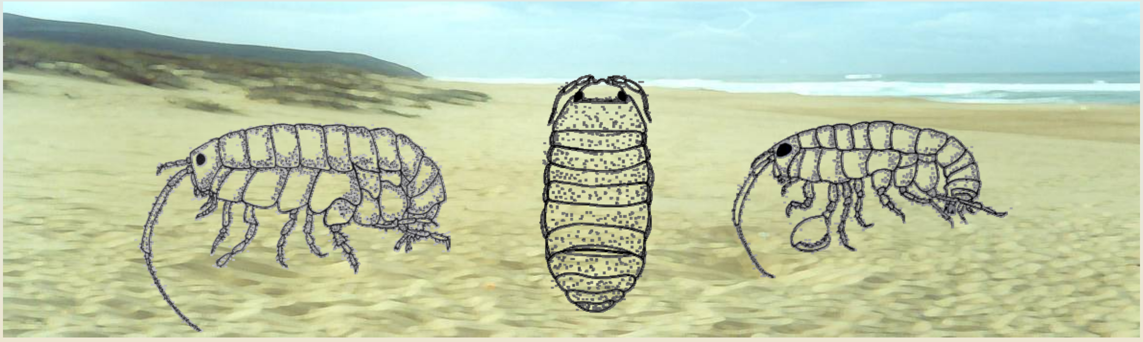

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Gonçalves SC, Marques JC, Pardal MA, Bouslama MF, El Gtari M, Charfi-Cheikhrouha F (2003). Comparison of *Talorchestia brito* (Amphipoda, Talitridae) biology, dynamics, and secondary production in Atlantic (Portugal) and Mediterranean (Tunisia) populations. *Estuarine, Coastal and Shelf Science,* 58: 901-916.

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Resumo

Os principais objectivos subjacentes ao presente trabalho são: a investigação e identificação de espécies chave na macrofauna de praias arenosas expostas da costa ocidental Portuguesa, o estudo da bioecologia destas populações e a avaliação da possibilidade deste conhecimento bioecológico desempenhar uma função na avaliação de mudanças globais. Para que esta avaliação seja efectuada numa escala mais ampla e atingindo um maior nível de compreensão, estudos bioecológicos comparativos entre populações Atlânticas (Portugal) e Mediterrânicas oriundas da Europa (Itália) e do norte de África (Tunísia) constituem também importantes objectivos, permitindo identificar e interpretar eventuais variações observadas na bioecologia.

Este trabalho será apresentado em quatro capítulos, incluindo um manuscrito submetido para publicação e três manuscritos já publicados em revistas científicas.

No início é apresentada uma breve introdução às praias arenosas e à sua relevância ecológica, aos seus problemas ambientais, nomeadamente associados com actividades humanas, e à sua investigação científica nas costas Atlânticas da Europa e Mediterrânicas da Europa e norte de África. A utilização potencial de populações macrofaunais abundantes, especialmente de crustáceos das famílias Talitridae e Tylidae, como espécies chave e indicadores de mudanças ambientais é primeiramente avançada, no contexto do crescente aumento de impactos humanos negativos nestes sistemas costeiros abundantes e sensíveis.

O primeiro capítulo analisa a estrutura das comunidades macrofaunais de duas praias expostas similares de Portugal, atendendo a densidades das comunidades, composição, espécies dominantes e diversidade, mas também distribuição horizontal dos organismos residentes entre as áreas supralitoral e intertidal. Foram também estudadas a influência da sazonalidade e as potenciais relações entre os dados biológicos e as variáveis ambientais. Os crustáceos Talitridae *Talitrus saltator* e *Talorchestia brito*, e Tylidae *Tylos europaeus* foram os animais mais abundantes nas duas praias analisadas, tendo sido identificados como espécies chave. Apesar da semelhança na exposição à ondulação de ambas as praias, as suas comunidades apresentam diferentes estruturas, nomeadamente no que diz respeito à contribuição relativa das espécies dominantes, mas também na densidade e composição das comunidades. Quanto às diferenças observadas, pensa-se que estas estarão principalmente relacionadas com diferenças no suplemento de detritos arrojados às praias (abundância e regularidade), juntamente com diferenças na granulometria do sedimento e na extensão da área intertidal.

O segundo capítulo é dedicado ao estudo comparativo da dinâmica populacional, biologia e produção secundária de *Talitrus saltator* em praias do Atlântico e do Mediterrâneo, investigando as adaptações desta espécie à vida em locais geograficamente distintos. Este animal revelou-se como sendo semianual, com fêmeas multíparas e exibindo um ciclo de vida bivoltino em todos os locais estudados. Algumas das suas características da história de vida (e.g. longevidade, período reprodutivo) apresentaram um padrão de variação latitudinal, enquanto outras variaram de forma distinta entre populações sugerindo adaptabilidade às condições ambientais locais (e.g. densidades, proporção sexual). Os valores de produção estimados foram, em geral, similares aos observados noutros talitridae.

No terceiro capítulo é apresentado um estudo comparativo da biologia, dinâmica populacional e produção secundária de *Talorchestia brito* entre populações Atlânticas e Mediterrânicas, estudo este que corresponde também ao primeiro estudo bioecológico completo desta espécie. Este talitridio revelou-se uma espécie semianual, com fêmeas multíparas e com um ciclo de vida bivoltino. Para a maior parte das características da história de vida (e.g. características morfométricas, longevidade, período reprodutivo) verificou-se uma variação geográfica, com a população Atlântica apresentando uma história de vida mais lenta. As proporções sexuais das populações analisadas não aparentam apresentar qualquer tipo de variação geográfica, sugerindo adaptabilidade a condições ambientais locais específicas. As estimativas de produção secundária foram semelhantes às observadas noutros Talitridae, mas menores que as observadas para as populações vizinhas de *T. saltator*. Porém, as proporções $P/\overline{B}$ e $E/\overline{B}$ entre ambas as espécies foram muito similares nos locais estudados.

O quarto capítulo foca a biologia, dinâmica populacional e produção secundária do isópode Tylidae *Tylos europaeus* na costa ocidental de Portugal, produzindo o primeiro estudo bioecológico completo para esta espécie. *Tylos europaeus* apresentou-se como um organismo anual, com fêmeas multíparas e um ciclo de vida univoltino. A reprodução ocorreu sazonalmente, apresentando uma duração curta, e apenas uma nova coorte foi recrutada por ano. Os animais apresentaram uma longevidade longa e, relativamente à dinâmica e estrutura populacional, foram detectados de forma consistente eventos de separação de coortes (*Cohort-splitting*) nos machos no início do período reprodutivo, dotando estes indivíduos de características biológicas distintas (tamanho corporal, longevidade, contribuição para o esforço reprodutivo da população). Sugeriu-se que estes eventos constituiriam uma possível estratégia que permitiria aos machos serem bem sucedidos em termos reprodutivos, apesar da escassez de fêmeas nestas populações, o que de outra forma conduziria certamente a uma forte competição entre machos por fêmeas. A produção secundária foi relativamente baixa, especialmente quando comparada com as razões $P/\overline{B}$ dos Talitridae residentes *T. saltator* e *T. brito*, consequência da história de vida lenta deste isópode.

Por fim é apresentada uma discussão geral acerca da importância dos crustáceos Talitridae e Tylidae como espécies chave em praias expostas de Portugal, e da sua relevância como indicadores do estado biológico das suas comunidades. A bioecologia local e comparativa das populações de espécies chave é discutida, revelando-se ainda uma grande plasticidade na ecologia destas populações ao longo de gradientes geográficos mas também às condições ambientais locais. A modelação da dinâmica populacional de espécies chave é discutida como uma ferramenta potencial na avaliação de mudanças ambientais em praias arenosas, apresentando-se neste contexto um exemplo concreto envolvendo uma das espécies chave estudadas no presente trabalho (*Talitrus saltator*). No que diz respeito aos resultados obtidos no presente estudo, o vasto conhecimento bioecológico produzido, e até mesmo o conhecimento produzido em termos de estrutura de comunidades, poderão ser considerados conhecimentos de referência no que diz respeito a praias expostas relativamente pouco perturbadas, utilizáveis no futuro como base de comparação. A grande quantidade de informação de base produzida em relação à bioecologia de espécies chave estabelece ainda um primeiro passo no sentido da construção, calibração e validação de modelos de dinâmica populacional, poderosas ferramentas na simulação e previsão de múltiplos cenários. O conhecimento produzido no presente trabalho poderá ser particularmente útil em futuras avaliações da integridade destes ecossistemas, no planeamento de cenários de gestão e em projectos de reabilitação destes ecossistemas, e torna-se especialmente relevante no contexto das rápidas mudanças globais que decorrem actualmente, a maioria das quais intimamente relacionada com as actividades humanas.

Abstract

In the present work, the main underlying goals are to investigate and to identify the existence of macrofaunal key species on exposed sandy beaches of the western coast of Portugal, to study the bio-ecology of these populations, and to evaluate the possibility of bio-ecological knowledge on key species populations presenting a role in global changes assessment. To accomplish this evaluation on a much wider and comprehensive scale, comparative bio-ecological studies between Atlantic (Portugal) and Mediterranean populations from Europe (Italy) and north Africa (Tunisia) are also important objectives that allow the identification and interpretation of the variations observed in bio-ecology.

This work will be presented in four specific chapters, including a manuscript submitted for publication and three manuscripts already published in scientific journals.

In the beginning, a brief introduction to sandy beaches and their ecological relevance, their environmental pressures, namely associated with human activities, and their scientific research on Atlantic and Mediterranean sandy coastlines of Europe and north Africa is presented. In the scope of the increasingly human detrimental impacts on these sensitive and abundant coastal systems, the potential use of local abundant macrofaunal populations, especially talitrid and tylid crustaceans, as key species and indicators of environmental change is firstly approached and hypothesized.

The first chapter analyses the macrofaunal community structure of two similar exposed beaches in Portugal, regarding communities' density, composition, dominant species and diversity, but also horizontal distribution of resident organisms between the supralittoral and intertidal areas. The influence of seasonality and the potential relationships between biological data and environmental variables was also studied. The crustacean talitrids *Talitrus saltator* and *Talorchestia brito*, and the tylid *Tylos europaeus* were the most abundant animals on both beaches and were identified as key species. Despite of the similarity in exposure to wave action of the beaches, their communities presented distinct structures, namely with regard to the relative contribution of the dominant species, but also in community density and composition. The differences observed are believed to be mainly explained by differences in detritus subsidies (abundance and regularity), combined with differences in sediment grain size and in the extent of the intertidal area at the study sites.

The second chapter is dedicated to the comparative study of *Talitrus saltator* population dynamics, biology and secondary production in Atlantic and Mediterranean beaches, investigating the adaptations of this species to life in geographically distinct locations. This animal was found to be semiannual, with iteroparous females, and exhibited a bivoltine life cycle at all study sites. Some life history features of *T. saltator* (e.g. life span, reproductive period) presented a latitudinal cline of variation, while others varied distinctly between populations suggesting adaptability to local environmental conditions (e.g. densities, sex ratio). Production values estimated were, in general, similar to the observed for other talitrids.

In the third chapter, a comparative study of the biology, dynamics and secondary production of *Talorchestia brito* is presented regarding Atlantic and Mediterranean populations, corresponding also to the first complete bio-ecological study on this species. This talitrid revealed itself as a semiannual species, with iteroparous females, and a bivoltine life cycle. Geographical variation was detected in most of the life history features (e.g. morphometrical characteristics, life span, reproductive period), with the Atlantic population presenting a slower life history. Population's sex ratios appeared not to fit in any kind of geographical variation, suggesting adaptability to specific local environmental conditions. Secondary production estimates were similar to those observed for other talitrids, but smaller than for the neighbouring populations of *T. saltator*. However, population turnovers between both species were very similar at the study sites.

The forth chapter focused the biology, population dynamics and secondary production of the tylid *Tylos europaeus* on the western coast of Portugal, producing, for the first time, a complete and comprehensive bio-ecological study on this species. *Tylos europaeus* turned out to be an annual species, with iteroparous females, and a univoltine life cycle. Reproduction was seasonal and short, and only one new cohort was recruited per year. The animals were long lived and, regarding population dynamics and structure, consistent cohort-splitting events were detected in males at the beginning of the reproductive period, endowing these individuals with distinct biological characteristics (body size, lifespan, contribution to the reproductive effort). These events were suggested to be a possible strategy to cope with the highly male-biased sex ratios observed, that otherwise could lead to strong male-male competition for mates. Secondary production attributes were rather low, especially when compared with the $P/\overline{B}$ ratios of the resident talitrids *T. saltator* and *T. brito*, a consequence of its slow life history.

At last, a general discussion about the importance of talitrid and tylid crustaceans as key species on exposed sandy beaches of Portugal, and their relevance as indicators of their biological communities' state are presented. Local and comparative bio-ecology of key species populations is discussed and a strong plasticity in population ecology features over geographical gradients and also to local characteristic environmental conditions was revealed. Modelling of key species population dynamics is discussed as a potential tool for environmental change assessment in sandy beaches and a specific example, involving one of the presently studied key species is presented (*Talitrus saltator*). Regarding the results achieved in this study, the wide knowledge produced on key species bio-ecology, and even the community structure knowledge, might be regarded as reference knowledge on relatively undisturbed exposed sandy beaches, useful in the future as a basis for comparison. Also, the large baseline information produced regarding key species bio-ecology establishes the first step towards the construction, calibration and validation of population dynamics models, powerful tools in simulation and prediction of multiple scenarios. The knowledge produced in the present work might be particularly useful in future ecosystem integrity assessments, planning of management scenarios and ecosystem restoration projects, and becomes especially relevant within the frame of the fast ongoing global changes of the present days, most of them closely related to human activities.

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Introduction

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INTRODUCTION

GENERAL INTRODUCTION

Sandy beaches as ecosystems – ecological relevance and environmental problems

Sandy beaches are the most abundant land/sea interface ecosystem worldwide, representing approximately ¾ of the worlds' coastlines (Bascom, 1980). They are harsh, dynamic and very complex environments, on which the interactions between sand, waves, winds and tides determines their instability. The ability to absorb wave energy, however, transforms sandy beaches in one of the most stable types of dynamic coastline (Brown and McLachlan, 1990).

Although variable in form, exposure and morphodynamic state, these ecosystems are in essence physically controlled. According to Brown and McLachlan (1990), wave energy is the driving force of most physical, chemical and biological processes in these environments. The ecology of sandy beaches and their surf zones is therefore closely linked with the physical conditions of the beach, and a strong relationship between beach type, regarding for instance exposure to wave action, and beach ecology exists (Short and Hesp, 1999).

Despite the difficulty of living on a sandy beach, these systems are not biological deserts. Beaches offer a series of diversified habitat possibilities (Short and Hesp, 1999) and may present a considerable diversity of organisms although their biomasses are in general low (Little, 2000). Besides supporting various local organisms in the sand and water column environments, they can also be used by transient organisms for different purposes. Sandy beaches and their surf zones are important nursery areas for diverse communities of juvenile fishes (Brown and McLachlan, 1990), some of which with economical importance (e.g. flatfishes), and its intertidal areas may even be used as spawning or nesting grounds by some vertebrates (see for instance Dugan *et al.*, 2000). Shorebirds, and even some land birds, may also use sandy beaches for roosting, nesting, chick rearing, and especially as foraging areas during their migrations or wintering and breeding seasons (e.g. Brown and McLachlan, 1990; Burger *et al.*, 1997; Dugan *et al.*, 2003; Hubbard and Dugan, 2003). However, overall, only a few species present abundant populations in sandy beaches, especially among macrofauna, and compared to other marine and littoral systems diversity is relatively low, which causes a high sensitivity to changes.

According to Brown and McLachlan (1990), sandy beaches are open marine systems that interact with several adjacent systems by exchanging materials using both seaward and landward boundaries. Besides this, there is also a clear interaction with the air environment. Moreover, the sandy beach ecosystem performs also other relevant ecological functions. Several authors recognise that sandy beaches are often important decomposing centres where decomposition of coastal debris takes place (e.g. Carter, 1988; Brown and McLachlan, 1990; Smith, 1996; Węslawski *et al.*, 2000a; Knox, 2001). This activity transforms sandy beaches in important sites for biogeochemical cycling, with the ability to supply offshore waters with nutrients, namely phosphates and nitrogen (Smith, 1996). Furthermore, some authors claim that the beach interstitial system functions as a biological filter that mineralizes organic materials and recycles nutrients to the sea (e.g. Brown and McLachlan, 1990), but also retains and processes pollutants (Węslawski *et al.*, 2000a).

Apart from their ecological relevance, sandy beaches also provide a series of direct goods and services to humans, in accordance to Constanza's *et al.* (1997) concepts. Some of the most obvious are for instance exploitation of living resources by fishing (fish and shellfish), extraction of sand and rare minerals, bait digging, or stranded seaweed harvesting. By absorbing large quantities of wave energy and since they are "normally" backed up by a dune system, sandy beaches also perform an important service in coastal protection against sand transport and natural hazards such as storms. Yet, recreation has been one of the most important services that sandy beaches have been providing to the human society in the latest centuries, and tourism is actually by far the most important sector of the beach-related economy (Węslawski *et al*., 2000a). For instance, in Portugal sandy beaches largely dominate the coastline, and tourism is one of the most important economical sectors, which represented 11% of the gross domestic product of the country in 2004 (Ministério da Economia e da Inovação, 2007). In this southern European country, sun-and-sand is actually one of the most important touristic products (e.g. Algarve).

Human populations have always been attracted to live near sandy beaches, because of their economical and aesthetical values with regard to natural resources, relaxation and leisure possibilities. As a matter of fact, the majority of the largest cities and ports of the world are located in coastal areas, as well as many industrial and tourist developments, and approximately 50% to 70% of the human population lives within 60 km of the coast, proportion that is actually increasing (Caffyn *et al*., 2002). These facts, as well as an enormous growth in beach tourism since the 1950s (Gormsen, 1997; Caffyn *et al*., 2002) and their associated facilities (e.g. resorts associated with domestic sewage and lifeguards areas), have introduced disturbance and negative impacts that may conduct to environmental degradation and quality decline.

Diverse human activities can pose direct detrimental impacts on sandy beach ecosystems, like for instance: i) construction of several kinds of structures (e.g. hotels, jetties, *promenades*, service areas); ii) removal and deposition of sand; iii) industrial and domestic sewage discharges; iv) organic pollution associated with oil-spill accidents; v) recreational activities that can produce several problems, such as intensive human trampling, deposition of litter and utilization of off-road motor vehicles on the beach and dunes. Sandy beaches are also subjected to other environmental problems, mostly related with human activities, which are threatening their environmental quality. These include an increase in beach erosion associated with an increase in storms occurrence and the rise in sea level due to global warming, and changes in the groundwater table within the beach and dune systems by depressing or elevating groundwater levels, which conduct to significant impacts on the beach face (erosion, deposition of sand) (Brown and McLachlan, 1990).

The natural and economical importance of sandy beaches, besides their important role on coastal ecology and dynamics, make the development and performance of proper management and protection strategies urgent. These strategies, however, will only be efficient if developed under correct ecological basis that ensure beaches ecosystems integrity. Therefore, assessing the complex ecology of sandy beaches must be a priority.

Atlantic and Mediterranean sandy coasts of Europe and north Africa as case studies

Most of the European coastline is fringed by the Atlantic Ocean. At the southernmost tip of the Iberian Peninsula, relatively cold surface Atlantic water flows to the Mediterranean basin and circulates over it, in an anticlockwise direction, returning to the ocean 80 to 100 years later (Turley, 1999; Pinet, 2003). The semi-enclosed waters of the Mediterranean Sea therefore bathe southern European shores, but also north Africa and south western Asia, linking the three continents.

Although connected by the narrow Strait of Gibraltar, these two water bodies present distinct properties which, combined with differences in climate, produce different environments in Atlantic and Mediterranean coasts of Europe and north Africa. Surface Mediterranean water is warmer and saltier than the Atlantic one, since the dominant climate of the Mediterranean region is hot and dry. In most of the Atlantic coast of Europe a wet milder climate of cold and rainy winters and short and cool summers is observed. Therefore, evaporation rates exceed precipitation and river discharges over the year in the Mediterranean (Pinet, 2003), warming and salting the sea due to the strong evaporative losses imposed by the continental climate (Bethoux *et al*., 1999). Also, tidal range is considerably distinct between north eastern Atlantic and Mediterranean coasts. In the Atlantic coastlines of Europe tides are mostly mesotidal (tidal range between 2 and 4 m), excepting a few macrotidal shores (Pinet, 2003), but in the Mediterranean tidal amplitudes are, in general, on the order of a few centimetres (Defant, 1961) and, therefore, clearly microtidal. Regarding nutrient supplies, Mediterranean surface waters are oligotrophic, especially in the eastern part of the basin (Turley, 1999; Turley *et al.* 2000, Bethoux *et al.*, 1999), and this low supply of nutrients keeps primary production equally low (figure 1), resulting in sparse biological populations (Pinet, 2003). This is not observed in the north Atlantic, where relatively nutrient enriched waters ensure seasonal increases in primary production (see for instance Nybakken, 2001; Pinet, 2003). Plus, between Atlantic and Mediterranean sandy beaches of Europe and north Africa, there are also considerable differences with regard to their latitudes and, consequently, on the local climates observed. Therefore, different environmental conditions are expected in Atlantic and Mediterranean sandy beaches, which may require different degrees of adaptation and plasticity from local populations of the same species.

Sandy beaches in Europe, especially in southern countries like Portugal, have been subjected to an increasingly human pressure associated with recreational activities and tourism in the last decades. This is also applied to the Mediterranean countries. Montanari (1995) stated that over 200 million tourists visit the region every year, 80% of which to European Union countries, and coined the Mediterranean region as the summer leisure space of Europe. Within this frame, sustainable management and protection plans for sandy beaches appear extremely important. The baseline research should in the first place aim to assess the biological or natural value of a given area, with a view to management, and include posterior eco-audits in order to monitor eventual changes in the biological value of the area and the sustainability of the management (Scapini, 2002). In this sense, the MECO project (Bases for the Integrated Sustainable Management of Mediterranean Sensitive Coastal Ecosystems), besides stimulating and promoting sandy beach research in Europe and north Africa in multidisciplinary fields, also produced an important output in the form of a manual with baseline information regarding research options for the integrated sustainable management of Mediterranean sandy beaches (Scapini, 2002 – editor).

Sandy beach ecology studies in European and north African coasts considerably increased, especially in the latest years. Several areas of study have been included namely macrofaunal community studies (e.g. Dexter, 1990; Bayed, 2003; Munilla and San Vicente, 2005; Rodil *et al.*, 2006), biology and population dynamics (e.g. Węslawski *et al.*, 2000b; Gonçalves, 2002; Colombini *et al.*, 2002; Marques *et al.*, 2003; Gonçalves *et al.*, 2003, 2005), behavioural studies (e.g. Scapini and Quochi, 1992; Mezzetti *et al.*, 1994; Fallaci *et al.*, 1999; Scapini *et al.*, 2002; Nardi *et al.*, 2003), and genetics (e.g. Bulnheim and Scholl, 1986; De Matthaeis *et al.*, 1998; Bulnheim and Schwenzer, 1999), many of which developed under the scope of the MECO project. Nevertheless, the number of sandy beach studies concerning ecology in these countries is still outnumbered by south American and south African investigations where there is a tradition on beach ecology research.

Recently, there has been a growing tendency on European sandy beach researchers to devote their effort towards integrated studies regarding the assessment of the impact that human activities pose on sandy beach organisms and environments, like for instance on the studies of Węslawski *et al.* (2000c), Tzatzanis *et al.* (2003), Malm *et al.* (2004), Junoy *et al.* (2005) and Gheskiere *et al.* (2006). In this sense, several authors also proposed different environmental monitoring methods based on distinct ecological tools, using for instance faunal organisms as indicators (e.g. Fialkowski *et al.*, 2000; Ketmaier *et al.*, 2003; Gheskiere *et al.*, 2005). In Portuguese sandy beaches, the ecology of these environments has been poorly studied, despite of representing approximately ¾ of Portugal's coastline. Excluding the recent studies of the Portuguese IMAR team, partners of the MECO project (Gonçalves, 2002; Marques *et al.*, 2003; Anastácio *et al.*, 2003;Gonçalves *et al.*, 2003, 2005; Gonçalves *et al. submitted*), very few studies were performed on Portuguese beaches (Dexter, 1988, 1990; Cunha and Ravara, 2003).

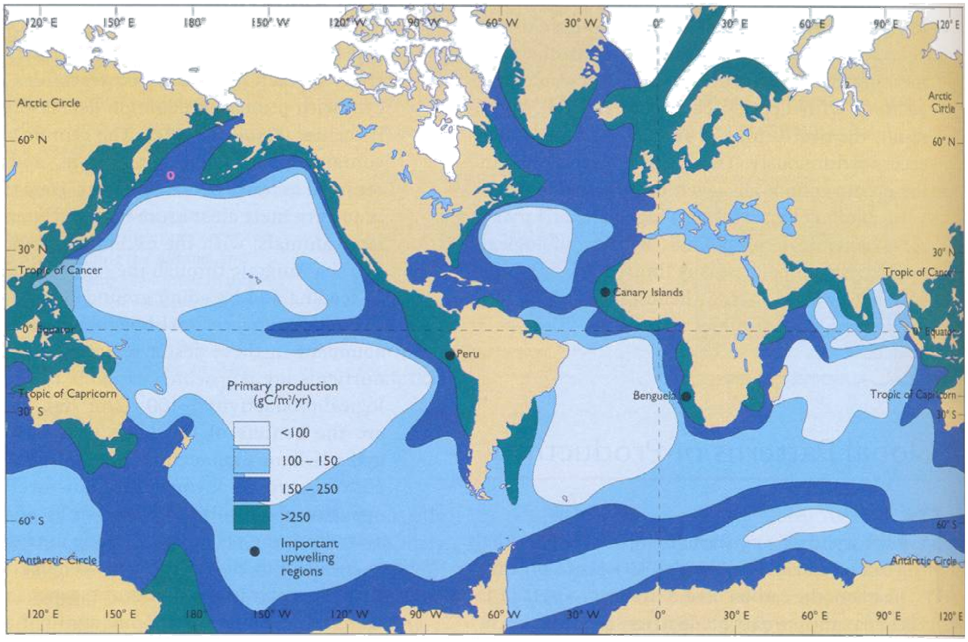

Figure 1. Global variation in primary production of surface waters of the world's oceans and seas (*In*: Pinet, 2003)

Therefore, it is very reasonable to say that there is a lot to do regarding Portuguese sandy beach ecology and, to a less extent, on other European and north African countries

The macrofaunal communities of exposed sandy beaches

On sandy beaches, the macrofaunal communities are usually dominated by crustaceans, molluscs and polychaetes, although several other groups may be represented (e.g. insects, nemerteans, anthozoans) (Brown and McLachlan, 1990). The relative proportion of these three groups is known to be variable according to the degree of exposure to wave action. Actually, Dexter (1983, 1990) demonstrated that crustaceans are the dominant group in exposed and more dynamic beaches, polychaetes are dominant in opposite conditions, and molluscs on intermediate exposure. The structure of these communities is strongly linked with the exposure to wave action (Dexter, 1990) and, in exposed sandy beaches where swash climate, wave energy and hydrodynamics are usually stronger, the environment is believed to be mostly physically controlled. In exposed conditions, animals with a high degree of mobility and a strong and quick burrowing ability, like the crustaceans, will therefore be better adapted to the local demanding environment (Brown and McLachlan, 1990) prevailing in these communities, while other taxa will be less abundant or even excluded. Common crustaceans in exposed sandy beaches include amphipods, isopods, crabs and callianassid shrimps (Knox, 2001).

The distribution of macrofaunal organisms in sandy beaches presents several peculiar features regarding spatial distribution by exhibiting patchiness, complex zonation patterns related with the tidal gradient, and fluctuations due to tidal and other types of migrations (Brown and McLachlan, 1990; Knox, 2001). Also, behavioural plasticity is an important feature for sandy beach macrofaunal survival, especially in exposed coasts, because their extreme dynamics requires from local populations a strong adaptability to the rapidly changing environment (Brown, 1996).

Numerous studies have focused on macrofaunal zonation patterns on the beach perpendicularly to the shoreline (e.g. Dahl, 1952; Salvat, 1964, 1966, 1967 *all in* Brown and McLachlan, 1990; McLachlan and Jaramillo, 1995). Zonation patterns in sandy beaches appear very complex since each species responds independently to the physical gradient and distributions vary on a daily basis

(Knox, 2001). However, McLachlan and Jaramillo (1995) reviewed the proposed zonation schemes to date and concluded that three zones could be identified by the presence of typical faunal organisms: (1) Supralittoral zone, inhabited by talitrid amphipods in temperate zones and by oxypodid crabs in the subtropics and tropics, as well as the isopod *Tylos* and insects (larvae and adults), especially in sandy beaches where macroalgal debris are common; (2) Littoral zone, inhabited by true intertidal species including cirolanid isopods, haustorid amphipods, callianassid shrimps, spionid and opheliid polychaetes and bivalves; (3) Sublittoral fringe, presenting a higher diversity including hippid and callianassid decapods, haustorid and oedicerotid amphipods, idoteid isopods, mysids, glycerid and nephtyid polychaetes and holothurians.

In sandy beaches, primary macroproducers suchs as macrophytes are usually absent due to substrate instability and wave action in intertidal areas, particularly on exposed beaches. Actually, beach and surf-zone flora consist of benthic microalgae on sands and phytoplankton on surf-zones, both often dominated by diatoms (Brown and McLachlan, 1990). On sheltered beaches, resident primary producers may contribute with some significance to local primary productivity, although the values involved are never high (0-50gC.m^{-2}.y^{-1}) (Brown and McLachlan, 1990). However, according to the same authors, in exposed conditions primary production on the beach is practically zero. The macrofaunal communities of exposed beaches must, therefore, rely on allochthonous food inputs, mainly in the form of stranded macrophytes and detritus (particulate organic matter) on a daily basis. These are brought ashore by tides, although they may also be blown by the winds from a terrestrial origin. This strong dependency on allochthonous food resources as already been demonstrated by some authors (e.g. Inglis, 1989; Dugan *et al*., 2003). Even though, it also occurs in less exposed conditions but always to a less extent and assuming a smaller importance. Wrack-associated macrofaunal organisms (i.e. scavengers) may therefore be the dominant functional group on macrofaunal communities of exposed beaches, overcoming filter feeders, usually dominant on sandy beaches (Brown and McLachlan, 1990).

Wrack-associated macrofauna, namely supralittoral amphipods, isopods and insects, are important wrack consumers that contribute significantly for wrack consumption and degradation (see for instance Inglis, 1989; Colombini *et al*., 2000). On the other hand, some macrofaunal organisms serve as prey for other macrofaunal members (for instance coleopterans and some crustaceans), and macrofaunal communities, as a whole, may serve as prey for top predators such as fishes or shorebirds (e.g. Hubbard and Dugan, 2003). However, with the exception of very sheltered beaches, macrofauna does not display trophic relationships with meiofaunal organisms living in sand interstices (Brown and McLachlan, 1990). Thus, macrofaunal communities play an important ecological role in sandy shore functioning by occupying a key-position in sandy beach food chains (Brown and McLachlan, 1990).

Local abundant populations as indicators

Sandy beaches are physically changing environments that change in a continuous fashion. These continuous changes become particularly important in exposed conditions. For each change induced in the system, local populations respond through adaptation, and behavioural plasticity is the most immediate and common adaptation to environmental change (Hazlett, 1988). According to Brown (1996), behavioural plasticity is a key factor in the survival and evolution of macrofauna of exposed sandy beaches since species must quickly adapt to the continuously changing circumstances. Integrated studies regarding the adaptative ability of sandy beach fauna will, therefore, allow the prediction of their responses to environmental changes in these systems (e.g. human activities).

Even though sandy beaches change rapidly, they can be regularly monitored using suitable approaches that must include the appropriate organisms in their bioassays (Wenner, 1988; Scapini and Morgan, 2002). Crustaceans constitute the most widespread and common invertebrates in all tidal levels of worldwide sandy beaches (Dexter, 1983; Brown and McLachlan, 1990; McLachlan and

Jaramillo, 1995), and especially in exposed ones. In the Mediterranean and Atlantic exposed beaches of Europe and north Africa, supralittoral talitrid amphipods and tylid isopods frequently present abundant populations (e.g. Colombini *et al.*, 1996, 2002, 2003; Scapini and Morgan, 2002; Rodil *et al.*, 2006; Gonçalves *et al.*, *submitted*). As already mentioned, these animals (figure 2) play important roles in the macrofaunal communities of exposed sandy beaches, but also in the ecosystem as a whole. Organisms with a relevant role on the equilibrium of the ecosystem are considered key species and, regarding management, are important indicators of sustainability (Scapini and Morgan, 2002). Removal or depletion of these organisms, as well as strong abnormal population' growths, can have profound effects in community structure and, therefore, on the ecosystems' equilibrium. Changes in the ecosystem will also be reflected in key species populations, since this is a dynamic equilibrium.

Although other common arthropods, like for instance abundant coleopteran populations, constitute key elements in sandy beach ecosystems and can be used in bioassays (e.g. Scapini and Morgan, 2002), crustaceans probably contain the greatest number of candidates to sandy beach indicators of environmental change (Wenner, 1988). They display the series of requirements, recognised by Philips (1980 *in* Wenner, 1988), that make them especially suitable candidates as bioindicators in sandy beach environments: (i) they often constitute very abundant populations; (ii) they can survive on environments with high levels of pollutants; (iii) they are easily sampled and sufficiently resistant to survive and maintain in the laboratory; (iv) their life spans are sufficiently long to allow the sampling and the accompaniment of more than one year class; (v) and, they generally present a reasonable size, which allows the extraction of tissues for analysis. Actually, some sandy beach crustaceans have already been proposed as ecological tools, for instance on the biomonitoring of trace metals (e.g. Rainbow *et al.*, 1998; Fialkowski *et al.*, 2000).

The study of key species at the population level is an adequate approach to the ecosystem when the aim is to assess the potential impact of induced environmental changes, namely regarding long term responses (Marques and Anastácio, 2002). Population dynamics and structure, reproductive strategies, growth rates, egg viability, parasite incidence, and other population biology associated features are particularly important and useful. Also, comparative studies regarding the dynamics of populations of the same species but inhabiting distinct beaches (different environmental conditions) may reflect variation in population biology, as a result of the adaptability of populations to the local environments (e.g. temperature, sand grain size, food resources). Based on these datasets, it is possible, for instance, to construct a model that can simulate the dynamics of a given population (Marques and Anastácio, 2002).

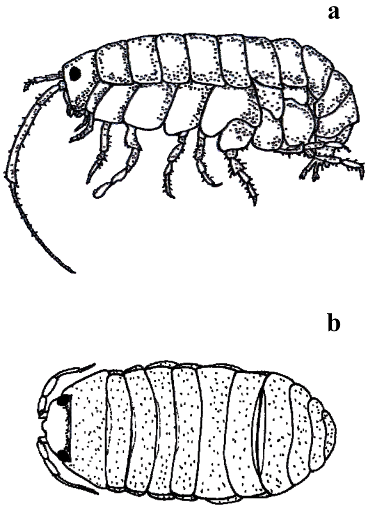

Figure 2. Drawings representing the Talitrid amphipod *Talitrus saltator* (a) and the Tylid isopod *Tylos europaeus* (b), common macrofaunal inhabitants of European and north African sandy beaches.

Outline of the major objectives

After considering the above mentioned, the present study aims to achieve three major underlying goals: to identify the key species in macrofaunal communities of exposed sandy beaches on western Portugal; to study the bio-ecology of these populations locally and comparatively with Mediterranean sandy beaches of Europe and north Africa; and to evaluate the possibility of applying the knowledge acquired on key species bio-ecology in global changes assessment. For these purposes, the following specific objectives are proposed:

a) To analyse and to compare the macrofaunal community structure of two exposed sandy beaches in the western coast of Portugal, especially regarding density and composition, in order to identify potential key species;
b) To investigate the role of seasonality and of several environmental factors on community structuring mechanisms;
c) To study the biology, population dynamics and productivity of the key species populations – the talitrid amphipods *Talitrus saltator* and *Talorchestia brito* and the tylid isopod *Tylos europaeus* – in the western coast of Portugal;
d) To assess the adaptation of talitrids to life in different sandy beaches by comparing the bioecology of Atlantic and Mediterranean populations;
e) To contribute with relevant knowledge by studying the bioecology of *Talorchestia brito* and *Tylos europaeus* for the first time;
f) To produce baseline information for future construction of population dynamics models of talitrids and tylids;
g) To analyse the possibility of using the key species bio-ecological information produced in global changes assessment;
h) Finally, to discuss a specific tool for environmental change assessment based on the bio-ecological information of one of the studied key species populations.

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CHAPTER 1:

Sandy beach macrofaunal communities on the western coast of Portugal – is there a steady structure under similar exposed conditions?

Sandy beach macrofaunal communities on the western coast of Portugal – Is there a steady structure under similar exposed conditions?

ABSTRACT

The structure of macrofaunal communities at two similar exposed sandy beaches on the western coast of Portugal were monitored for approximately 18 months by sampling all the beach area, from the shoreline to the base of the dunes. The beaches' physical environment, as well as supralittoral and intertidal community density and composition, seasonal variations and potential relationships between biological data and environmental parameters were studied. The two beaches had similar exposure to wave action, but differed in terms of sediment grain size, extent of the intertidal area, width of the surf-zone, and, principally, in terms of potential food availability in the form of allochtonous debris. Differences were observed with regard to the communities' structure, i. e. their density and composition, relative contribution of the dominant species and diversity. Seasonality, especially due to temperature variations, also had a strong influence on communities: controlling dominant species' density and promoting a differential utilization of the beach by several resident macrofaunal animals. The present study allows the identification of key species in exposed sandy beaches of western Portugal and demonstrates that a steady community structure does not persist in the similarly exposed conditions observed, which may be mainly explained as a response to distinct detritus subsidies, combined with differences in sediment grain size and extent of the intertidal area.

Key words: Exposed sandy beaches, macrofaunal community structure, species composition, seasonality, key species, detritus subsidies, Redundancy Analysis.

INTRODUCTION

Sandy beaches are important dynamic coastal systems that border most of the shores worldwide. They are natural interfaces between sea and land, capable of absorbing large quantities of incoming wave and wind energy, despite of their relative fragility as ecosystems (Brown and McLachlan, 1990). Moreover, the human use of sandy shores is quickly increasing (*e.g.* construction of engineering structures and recreational facilities) at the expense of environmental quality (*e.g.* Węslawski *et al.,* 2000; Lercari and Defeo, 2003; Gheskiere *et al.,* 2005).

Although apparently devoid of life to the untrained eye, sandy beaches support several macrofaunal and meiofaunal populations, some of which are often very abundant. Macrofaunal communities of these systems are normally dominated by Crustaceans, Molluscs and Polychaetes, especially in the intertidal area, with different relative abundances according to the local exposure to wave action (Dexter, 1983, 1990). Insects are common inhabitants at the upper reaches of the shore and the dunes (Brown and McLachlan, 1990), associated with wrack and algal deposits stranded by tides and/or blown overland by the wind from a terrestrial origin.

Several recent studies have focused on macrofaunal communities of sandy beaches. Studies like those by Dexter (1983, 1990), McLachlan and Jaramillo (1995), Dugan *et al.* (2003) and Rodil *et al.* (2006) have analysed these communities' structure, at distinct levels, and in terms of zonation patterns, while the impact of human activities on communities' composition and structure has been assessed for instance in Lercari and Defeo (2003), Junoy *et al.* (2005) and Veloso *et al.* (2006).

Dexter (1990) has pointed out that macrofaunal community structure is strongly influenced by exposure to wave action, and McLachlan and Jaramillo (1995) noted that general patterns found in sandy beach macrofauna exhibit a negative correlation between species richness, exposure rating and grain size. Thus, a harsh and dynamic environment, mainly physically controlled, is expected in exposed sandy beaches. Exposed sandy beach communities will therefore have different compositions and distinct structures in comparison to more sheltered conditions, as demonstrated for instance by McLachlan *et al.* (1993) and Rodil and Lastra (2004). However, studies on macrofaunal communities, especially towards the exposed extreme of the gradient of exposure to wave action and of an intermediate morphodynamic nature, are not available for Portuguese sandy beaches. The exceptions are Dexter's studies (1988, 1990), the first describing the intertidal fauna of Portugal, and the second analysing the effect of exposure and seasonality on the community structure of semi-exposed to very protected beaches. More recently, Cunha and Ravara (2003) have also studied the macrofaunal zonation on a dissipative estuarine beach, based on a snapshot sampling event towards the end of spring. Thus, comprehensive and temporally extended studies on exposed and intermediate sandy beach macrofaunal communities of Portugal, covering all the beach area from the low tide watermark to the base of the dunes, are needed. In this study macrofaunal communities of two similarly exposed sandy beaches on the western coast of Portugal are analysed and compared from a structural point of view, focusing on density, composition, diversity and horizontal distribution between the supralittoral and intertidal areas. The structural analysis of these communities is also relevant regarding the identification of key species in these environments. Additionally, taking advantage of a relatively long sampling program, the role of seasonality and of several other environmental parameters on community structuring mechanisms is also examined.

MATERIALS AND METHODS

Study Sites

Two sandy beaches – Cabedelo and Quiaios – on the western coast of the Iberian Peninsula and located in the central region of Portugal (figure 1) were selected as study sites. The Cabedelo sandy beach (40º07'32'' N 8º51'49'' W) is 1 km south of the Mondego river mouth, in the vicinity of its estuarine environment, while Quiaios beach (40º12'21'' N 8º53'48'' W) is further north approximately 8 km north from Cabo Mondego. These beaches are separated by a 28 km stretch of coast. In general Quiaios and Cabedelo are relatively undisturbed beaches, receiving a moderate number of summer visitors. Cabedelo has probably been subjected to increasingly higher human pressure than Quiaios in the past few years, since it is closer to the town of Figueira da Foz, an important tourist centre where sandy beaches are the main attraction. These are exposed beaches, which present relatively similar conditions of exposure to wave action (see Beaches Physical Environment section). Regarding the morphodynamic state both study sites are considered intermediate beaches. Tides in the western Portuguese coast are semidiurnal and mesotidal, with a tidal range between 2 and 3.5 m.

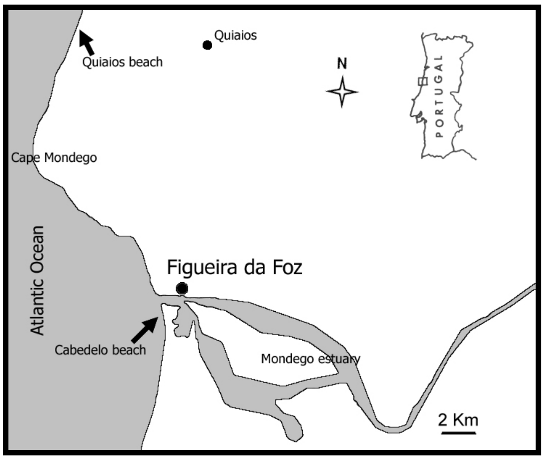

Figure 1. Location of the sandy beaches used as study sites: Cabedelo and Quiaios (western coast of Portugal).

During storms, Cabedelo may be almost completely submerged, causing depositions of large amounts of drift wrack, mainly composed of macroalgae from rocky shores located north of the beach and possibly also from the Mondego estuarine system. The input of drift wrack at Quiaios is clearly more limited, since there are no rocky shores or other potential sources of debris nearby. The exposed nature of both beaches meant that no vegetation was found on the supralittoral areas of these study sites. Supplementary characteristics of these two sandy beaches are provided in table 1.

Sampling Procedures

The sandy beach macrofaunal communities were sampled fortnightly, during low neap-tides, from January 1999 to June 2000 at Quiaios (18 months), and from March 1999 to June 2000 (16 months) at Cabedelo. Samples were taken on the supralittoral and intertidal areas, at regular intervals along two transects arranged from the low tide water mark to the base of the dunes. This sampling procedure was able to account for differential horizontal distribution of the macrofauna during the year. Sampling was performed using a woodsquare of $0.25m^2$ and removing the first 20 cm of the sand surface layer. The sand was sieved through a 1 mm mesh and the animals collected were then separated in the laboratory and preserved in 70% alcohol, after fixation in 4% formalin. Sediment grain size composition was determined from seasonal samples to check for significant differences, and classified according to the Wentworth scale described in Brown and McLachlan (1990).

A set of physicochemical parameters were measured over the study period to account for possible relationships between the macrofaunal communities and their environment. Debris quantity (potential food $g.m^{-2}$), organic matter in the sediment (AFDW), and sediment moisture content were determined according to the procedures described in Marques *et al.* (2003). Meteorological data were also obtained from the nearest meteorological stations (Coimbra

Table 1. Basic characteristics observed in the two sandy beaches used as study sites. For quantitative characteristics, averages ± standard deviations for the period of study are given.

Characteristic	Cabedelo	Quiaios
Width of the beach (m)	60	100
Average slope (%)	2.0	1.8
Extension of the intertidal area (m)	Neap tides: 30 Spring tides: 45	Neap tides: 50 Spring tides: 75
Foredune height (m)	2.5 – 3	2.5 – 3
Sediment granulometry (mm)	Medium sand (0.250 – 0.500)	Coarse sand (0.500 – 1.0)
Sediment moisture (%)	3.24 (±1.22)	2.64 (±0.95)
Supralittoral	2.53 (±1.44)	2.08 (±1.30)
Intertidal	4.11 (±1.88)	3.07 (±0.88)
Organic matter content (%)	0.15 (±0.05)	0.19 (±0.35)
Supralittoral	0.13 (±0.03)	0.19 (±0.35)
Intertidal	0.15 (±0.04)	0.21 (±0.38)
Detritus ($g.m^{-2}$)	9.15 (±9.03)	2.02 (±1.82)
Supralittoral	15.94 (±14.67)	3.63 (±3.76)
Intertidal	1.18 (±1.75)	0.63 (±0.91)
Temperature (ºC)	15.65 (±4.77)	15.02 (±4.91)
Precipitation (mm)	2.41 (±5.63)	2.36 (±5.49)
Cloudiness	4.06 (±2.67)	3.97 (±2.68)
Visibility	6.05 (±1.05)	6.11 (±1.03)
Wave height (m)	0.05 (±0.32)	0.06 (±0.33)
Wave period (s)	0.11 (±0.65)	0.12 (±0.65)
Wind velocity ($m.s^{-1}$)	3.92 (±2.98)	4.05 (±3.03)

for temperature and precipitation and Figueira da Foz harbour for the other parameters): precipitation, atmospheric temperatures, visibility, cloudiness, wave height, wave period, and wind velocity.

Data Analysis

All the animals collected (marine, semi-terrestrial and terrestrial) were considered in the study. Density (individuals/m^2) was calculated for each site and analysed for all the sampling period and for each season. Supralittoral and intertidal areas were compared with regard to density, horizontal distribution and species composition. Animals with a frequency of occurrence higher than 10% of the complete period of sampling were considered resident species. Diversity trends were also analysed using the number of species as a measure of species richness and Shannon-Wiener's *H'* as a measure of heterogeneity.

Potential relationships between the density of resident species and environmental parameters were explored using multivariate techniques performed with the statistical software package CANOCO 4.0 for windows (ter Braak and Šmilauer, 1998). For both data sets, all the biological data were square-root transformed in the analysis and there was no down-weighting of rare species. The environmental parameters tested as explanatory variables in the subsequent multivariate analyses were: debris quantity, organic matter of sediment, sediment moisture content, precipitation, atmospheric temperature, visibility, cloudiness, wind velocity, wave period and wave height. All these were previously checked for normality, using the MINITAB 12.2 software package, and transformed whenever necessary.

The multivariate analysis technique used was selected following a sequence of procedures. Biological data matrixes were initially subjected to a Detrended Correspondence Analysis (DCA), with detrending by segments, to measure the gradient lengths. This procedure makes it possible to decide whether a linear species response-based or a unimodal species response-based ordination method should be used. In all cases, the gradient length of the first axis obtained was less than 3.0, suggesting that an analysis based on linear species response should be used. The constrained ordination method used, therefore, was Redundancy Analyses (RDA). The forward selection procedure was used with a Monte Carlo Permutation Test (999 permutations) to determine which environmental variables were significant ($p < 0.05$) and explained the largest amount of variation in each biological data set. The significance of the reduced RDA models finally obtained was also assessed using Monte Carlo Permutation Tests ($p < 0.05$ after 999 permutations).

RESULTS

Beaches' Physical Environment

Quiaios beach is considerably wider than Cabedelo, and has a smaller average slope (table 1). The seasonal variation of sediment grain size composition was not significant ($p<0.05$). According to the Wentworth scale described in Brown and McLachlan (1990), Cabedelo has predominantly medium sand grains, while in Quiaios the sediment is classified as coarse (table 1). Considering the other parameters in McLachlan's (1980) rating scheme for assessing the degree of exposure in sandy beaches, Quiaios is classified as a very exposed beach (exposure rate: 16) and Cabedelo as exposed (exposure rate: 15). Besides differences in granulometry, Cabedelo presents a moderate surf zone and in Quiaios waves break almost entirely on the beach. The two beaches can thus be considered relatively similar regarding exposure to wave action.

Intertidal areas presented higher moisture contents than the supralittoral ones (table 1). At Quiaios, the average organic matter content of the sand was higher than at Cabedelo. At both beaches, supralittoral areas presented slightly less organic content than the intertidal ones. Regarding average detritus, Cabedelo had a much higher input (4.5 times more). Detritus was much more abundant in the supralittoral areas of both beaches.

Communities' Structure

On both beaches, the communities' structure was dominated by arthropods, and of these crustaceans were the most abundant macrofaunal group (table 2) (94.5% at Cabedelo and 97.0% at Quiaios), followed by insects (5.3% at Cabedelo and 2.4% at Quiaios). Other

Table 2. Community structure in Cabedelo and Quiaios beaches based in selected species. Avg – average; SD – standard deviation; Occu. (%) – Percentage of occurrence; Avg % contrib. – Average percentual contribution; unidt. – unidentified; abs. – absent.

	Cabedelo				**Quiaios**			
	Density (ind.m^{-2})		Occu. (%)	Avg % contrib.	Density (ind.m^{-2})		Occu. (%)	Avg % contrib.
	Avg	SD			Avg	SD		
Crustacea								
Talitrus saltator	67.08	50.90	100	69.52	4.48	4.01	100	6.22
Tylos europaeus	14.66	11.07	100	15.19	47.50	77.07	100	65.95
Talorchestia brito	7.69	7.57	97	7.97	17.65	15.52	100	24.50
Gastrosaccus sanctus	1.13	4.26	23	1.17	abs.	-	0	-
Eurydice naylori	0.38	0.70	48	0.39	0.00	0.04	<10	0.01
Pontocrates arenarius	0.13	0.31	19	0.13	0.00	0.02	<10	0.00
Armadillidium album	0.07	0.13	26	0.07	0.22	0.49	29	0.31
Other Crustacea	0.01	0.06	10	0.01	0.01	-	<10	0.02
Total Crustacea				**94.45**				**97.01**
Insecta								
Coleoptera								
Scarabaeidae larvae	0.51	1.09	45	0.53	0.04	0.09	26	0.06
Elateridae larvae	0.41	0.54	58	0.43	0.16	0.28	43	0.22
Unidt. larvae *a*	abs.	-	0	-	0.06	0.18	17	0.08
Unidt. larvae *b*	abs.	-	0	-	0.02	0.06	14	0.03
Phaleria acuminata	0.49	0.67	61	0.50	0.18	0.36	46	0.25
Gonioctena olivacea	abs.	-	0	-	0.03	0.10	14	0.05
Callicnemis latreillei	0.13	0.28	26	0.13	abs.	-	0	-
Aegiala arenaria	0.12	0.23	32	0.13	abs.	-	0	-
Olisthopus rotundatus	0.04	0.13	13	0.04	0.01	0.04	6	0.01
Saprinus sp.	0.03	0.09	13	0.03	abs.	-	0	-
Tenebrionidae unidt. species 1	0.02	0.06	10	0.02	0.02	0.07	14	0.03
Psammodius porcicollis	0.01	0.04	7	0.01	0.02	0.06	14	0.03
Other Coleoptera	0.39	-	< 10	0.41	0.16	-	<10	0.22
Sub-total				2.23				0.98
Diptera								
Cyclorrhapha larvae	1.29	1.33	16	1.33	0.01	0.04	9	0.02
Unidt. larvae	0.03	0.03	13	0.03	0.04	0.16	9	0.06
Other diptera	0.70	-	< 10	0.73	0.71	-	<10	0.98
Sub-total				2.09				1.06
Hemiptera	0.63	-	< 10	0.65	0.10	-	<10	0.14
Hymenoptera	0.27	-	< 10	0.29	0.06	-	<10	0.09
Mecoptera	abs.	-	0	-	0.05	-	<10	0.08
Lepidoptera	abs.	-	0	-	0.01	-	<10	0.01
Total Insecta				**5.26**				**2.36**
Other Arthropoda	0.16	-	< 10	0.17	0.04	-	<10	0.04
Mollusca								
Cochlicella barbara	abs.	-	0	-	0.03	0.07	14	0.04
Other Mollusca	0.10	-	< 10	0.10	0.1	-	<10	0.14
Annelida								
Enchytraeidae unidt. species	0.02	0.08	<10	0.02	0.08	0.37	14	0.11
Other Annelida	0.00	-	< 10	0.00	0.16	-	<10	0.21
Nemertea	abs.	-	0	-	0.06	-	<10	0.09
Total	**96.50**	**60.25**		**100**	**72.02**	**85.00**		**100**

groups of arthropods, along with molluscs, annelids and nemerteans, had only residual contributions (< 1%), and most of them were quite rare.

Amphipods and isopods were the most abundant crustaceans but were differently represented in the two beaches (figure 2) with, an average of 77.6% of amphipods and 15.7% of isopods at Cabedelo, and 66.3% of isopods and 30.7% of amphipods at Quiaios.

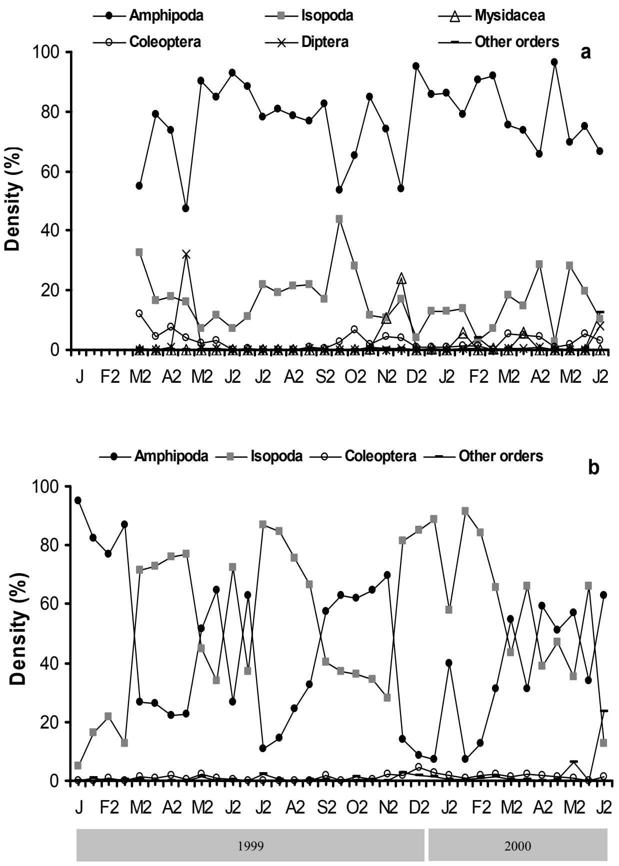

Figure 2. Relative contribution of the different orders observed in the studied sandy beach communities at the western coast of Portugal. (a) – Cabedelo; (b) – Quiaios.

The best represented insect groups were the Coleoptera and the Diptera (especially larvae) (table 2, and figure 2) with similar proportions in both beaches. Amphipod dominance at Cabedelo was very consistent (figure 2a), and isopods were the second most abundant group. Despite the general dominance of isopods, the structure was far more changeable at Quiaios (figure 2b). Amphipods became dominant in the winter of 1999 and in most autumn months, and in the spring of 2000 the two groups presented similar proportions.

Overall, 123 species were recorded at Cabedelo, and 103 species at Quiaios. Insects were by far the most diverse group (105 species in Cabedelo and 78 species in Quiaios). Crustaceans, although highly abundant, were found in only 8 species at Cabedelo and 9 at Quiaios. In general, the average number of species and the values for the Shannon-Wiener index (table 3) were higher at Cabedelo, but many of the species identified were rare (73% at Cabedelo and 58% at Quiaios), especially insect species. Only a small number of the communities consisted of resident species – 16 species at Cabedelo and 14 species at Quiaios (table 2). This included crustaceans (especially talitrid amphipods and isopods), coleopterans (especially tenebrionids and scarabids, besides different kinds of larvae), dipterans larvae, the terrestrial mollusc *Cochlicella barbara* (Linnaeus, 1758) and an unidentified Enchytraeidae annelid. Arachnids, although found frequently, were not considered as resident since they are natural sandy beach invaders and do not actually live there (Brown and McLachlan, 1990).

Despite their obvious similarities regarding the general composition of the resident fauna, some differences were observed between the communities. Species like the mysid *Gastrosaccus sanctus* (Van Beneden, 1861) and the coleopterans *Callicnemis latreillei* Castelnau, 1832, *Aegiala arenaria* Fabricius, 1787 and *Saprinus* sp. occurred only at Cabedelo, while the coleopterans *Gonioctena olivacea* Forster, 1771, larvae *a* and *b*, and the mollusc *C. barbara*, although resident in Quiaios, were never observed at Cabedelo. *Eurydice naylori* Jones & Pierpoint, 1997, *Psammodius porcicollis* Reitter, 1892 and some diptera larvae, for instance, although present at both beaches, could only be considered as resident at one of them (see table 2 for other examples).

The amphipods *Talitrus saltator* (Montagu, 1808) and *Talorchestia brito* Stebbing, 1891, and the isopod *Tylos europaeus* Arcangeli, 1938 were the most abundant animals found at both communities (table 2; figure 3b and 3c). At Cabedelo, *T. saltator* was dominant (70% of the community's total density), followed by *T. europaeus* and *T. brito*, while at Quiaios, *T. europaeus* was the most abundant species (66% of the total density), followed by *T. brito* and, in much smaller numbers, *T. saltator*.

Considering the whole communities, the average total density (figure 3a) was higher at Cabedelo beach, and it also showed smaller variations over the study period (26.8 to 255.1 ind.m^{-2} at Cabedelo compared with 4.6 to 510.6 ind.m^{-2} at Quiaios). But, minimum and maximum density was always recorded, respectively, in January (winter) and July (summer) at both beaches. This clearly

Table 3. Comparative analysis of diversity indexes in the macrofaunal communities of Cabedelo and Quiaios sandy beaches. Seasonal and average values ± standard deviations for the study periods are given. Spri – spring; Sum – summer; Aut – autumn; Win – winter.

	Cabedelo					**Quiaios**				
	Spri	Sum	Aut	Win	Study period	Spri	Sum	Aut	Win	Study period
Number of species	16	5	10	9	11 (±12.4)	12	6	7	9	9 (±7.8)
Diversity, *H'*	1.54	0.93	1.58	1.34	1.38 (±0.56)	1.41	1.11	1.16	1.16	1.24 (±0.35)

Table 4. Comparative structure of supralittoral and intertidal communities at Cabedelo and Quiaios sandy beaches. Unidt. – unidentified; abs – absent; n.r. – not resident; spc. – species.

	Cabedelo				**Quiaios**			
	Average density (ind.m^{-2})		**Average contribution**		**Average density (ind.m^{-2})**		**Average contribution**	
Resident animals	**Supral.**	**Inter.**	**Supral.**	**Inter.**	**Supral.**	**Inter.**	**Supral.**	**Inter.**
Talitrus saltator	49.63	68.58	63.0%	73.6%	2.33	5.14	5.8%	7.7%
Talorchestia brito	2.33	11.62	3.0%	12.5%	2.22	25.63	5.5%	38.2%
Pontocrates arenarius	abs.	0.27	-	0.3%	abs.	n.r.	-	-
Tylos europaeus	20.90	9.60	26.6%	10.3%	34.43	36.25	85.0%	54.1%
Armadillidium album	0.13	abs.	0.2%	-	0.38	abs.	0.9%	-
Eurydice naylori	0.08	0.67	0.1%	0.7%	abs.	n.r.	-	-
Gastrosaccus sanctus	abs.	2.44	-	2.6%	abs.	abs.	-	-
Phaleria acuminata	1.05	n.r.	1.3%	-	0.43	n.r.	1.0%	-
Tenebrionidae unidt. spc.1	n.r.	n.r.	-	-	0.04	abs.	0.1%	-
Callicnemis latreillei	0.26	abs.	0.3%	-	abs.	abs.	-	-
Psammodius porcicollis	n.r.	abs.	-	-	0.03	n.r.	0.1%	-
Aegiala arenaria	0.27	abs.	0.3%	-	abs.	abs.	-	-
Saprinus sp.	0.09	abs.	0.1%	-	abs.	abs.	-	-
Elateridae larvae	0.85	n.r.	1.1%	-	0.29	n.r.	0.7%	-
Scarabaeidae larvae	0.92	n.r.	1.2%	-	0.21	abs.	0.5%	-
Coleoptera unidt. larvae a	abs.	abs.	-	-	0.09	abs.	0.2%	-
Coleoptera unidt. larvae b	abs.	abs.	-	-	0.05	abs.	0.1%	-
Diptera unidt. larvae spa	0.06	abs.	0.1%	-	n.r.	n.r.	-	-
Cyclorrhapha larvae	2.14	abs.	2.7%	-	n.r.	n.r.	-	-
Cochlicella barbara	abs.	abs.	-	-	0.04	abs.	0.1%	-
	Supralittoral		**Intertidal**		**Supralittoral**		**Intertidal**	
Total mean density (ind.m^{-2})	79.5 (± 58.9)		96.2 (± 99.9)		41.1 (± 46.9)		68.8 (± 90.9)	
Total number of species	44		90		40		77	
Mean number of species	7.6 (± 4.2)		6.5 (± 12.7)		6.0 (± 4.4)		5.3 (± 7.9)	
Mean density of the resident community (ind.m^{-2})	71.1 (± 60.4)		93.4 (± 93.7)		38.2 (± 46.1)		67.2 (± 88.9)	
Number of resident species	13		6		12		3	
Minimum density	Spring (May)		Winter (December)		Summer (July)		Winter (January)	
Maximum density	Summer (Septem.)		Spring (May)		Winter (February)		Summer (July)	

reflected the patterns of variation of the dominant species, *T. saltator* at Cabedelo and *T. europaeus* and *T. brito* at Quiaios (figure 3).

Supralittoral *vs* Intertidal Areas

The two horizontal areas revealed differences in terms of species composition, namely regarding the resident fauna (table 4).

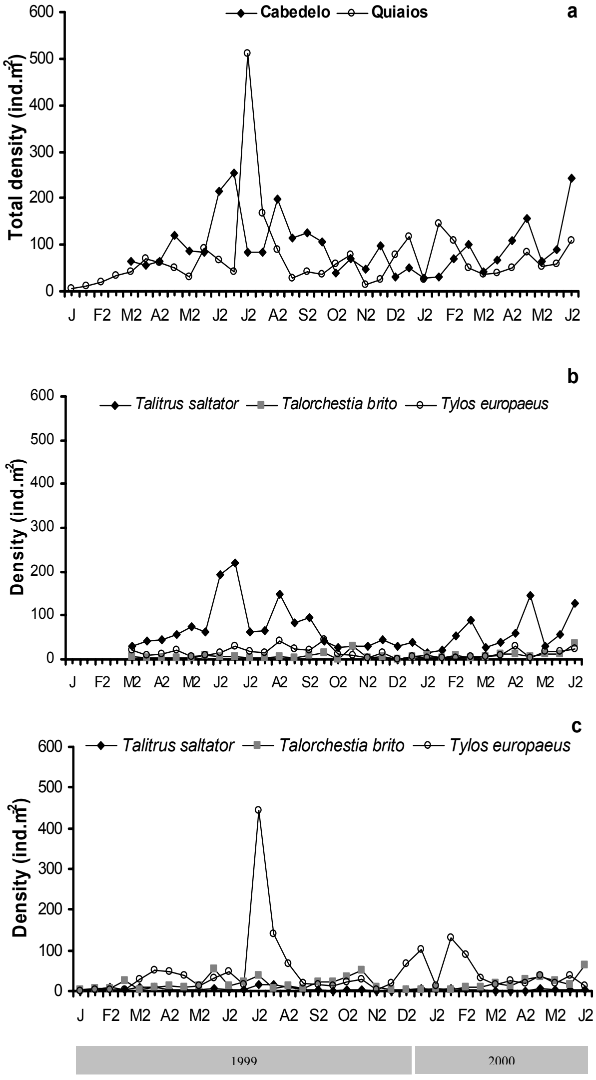

Figure 3. Variation of community density on the western coast of Portugal. (a) Variation of total density in each community during the study period; (b) Variation of population density in the dominant species at Cabedelo during the study period; (c) Variation of population density in the dominant species at Quiaios during the study period.

For instance, the isopod *Armadillidium album* Dollfus, 1887, and the coleopterans *Callicnemis latreillei*, *Aegiala arenaria*, as well as some unidentified coleopteran larvae and the mollusc *Cochlicella barbara* were only found in the supralittoral areas. Other resident insect larvae (coleoptera and diptera), the coleopterans *Phaleria acuminata* (Küster, 1852), *Psammodius porcicollis* and the unidentified tenebrionid species exhibited a stronger supralittoral affinity, while the isopod *E. naylori* was mainly found in the intertidal area. The amphipod *Pontocrates arenarius* and the mysid *Gastrosaccus sanctus* were exclusively observed in the lower intertidal area. Regarding the three dominant species, *T. saltator* was the most abundant organism in both the supralittoral and intertidal areas at Cabedelo, *T. europaeus* showed clear supralittoral affinity, and *T. brito* attained their highest density in the intertidal area (table 4).

Despite the fact that average total communities' density was consistently higher in the intertidal areas (table 4), some interesting seasonal patterns of variation were observed at each study site (figure 4). Density is higher in the intertidal area by the end of spring and during summer, becoming approximately similar at both areas in early autumn. From the end of this season and during winter, densities show an increase in the supralittoral and decrease in the intertidal zones. This reflects a variation in the horizontal

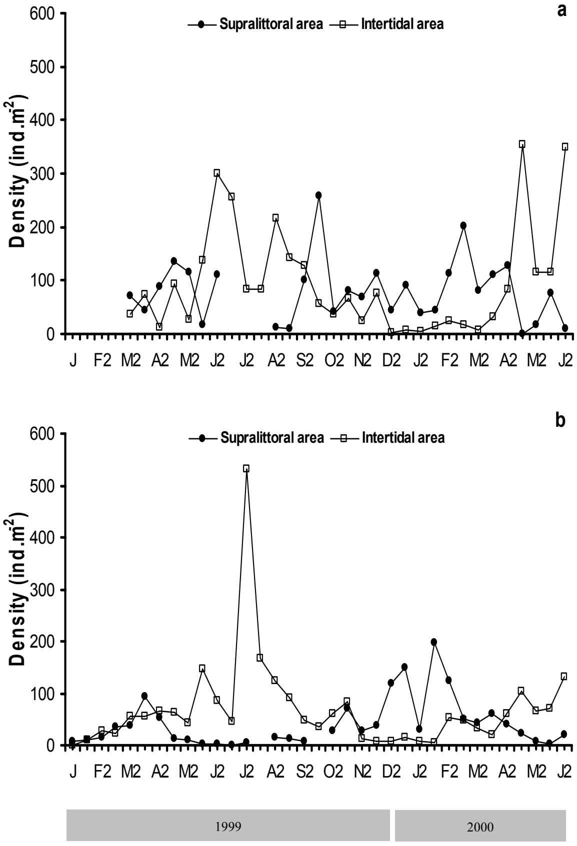

Figure 4. Variation of total density in the supralittoral and intertidal areas of each study site between January 1999 and June 2000. (a) – Cabedelo; (b) – Quiaios.

distribution of dominant macrofaunal species over the year (see also the next section).

The total number of species observed in the intertidal areas was almost twice the number of species collected in the supralittoral zone (table 4), but only a small proportion of these animals (30% in the supralittoral, 7% in the intertidal at Cabedelo; 30% in the supralittoral, 4% in the intertidal at Quiaios) were residents. Actually, 86% of the species found in the intertidal at Cabedelo and 74% at Quiaios, mostly insects, were rare. Also, the supralittoral resident fauna is much more diverse than the intertidal one in both beaches (table 4).

Seasons and Communities Structure

Densities increase in spring and peak in summer, decreasing by autumn and attain the lowest values in winter (figure 3a), showing a similar pattern at both beaches. For simplification, the influence of seasonality on the resident macrofauna was assessed considering only the species presenting an average proportion in the community >1%. The other organisms were pooled into higher taxonomical groups (orders or classes). In both communities, *T. saltator* and *T. europaeus* densities peaked in summer (figure 5), but *T. brito* presented highest densities during summer and autumn months of 1999, and in spring 2000. *Gastrosaccus sanctus* was present only in autumn 1999 and during the winter and spring months of 2000, attaining a maximum mean density in the autumn (figure 5a). Crustaceans, like *A. album* and *P. arenarius*, and insects, like *C. latreillei* and *A. arenaria* were only seasonally present in these beaches. The number of species was higher in spring and attained the lowest values during summer at both beaches (table 3). On the other hand, although Shannon-Wiener's *H'* also reached the lowest values in summer in both communities, the highest values were attained in different seasons – autumn for Cabedelo and spring for Quiaios.

The variation of dominant species' density in the supralittoral and intertidal areas of the beaches (not shown for simplification), as well as the periods of maximum and minimum density of the whole communities (table 4), confirm the occurrence of seasonal movements of abundant macrofaunal organisms in both beaches.

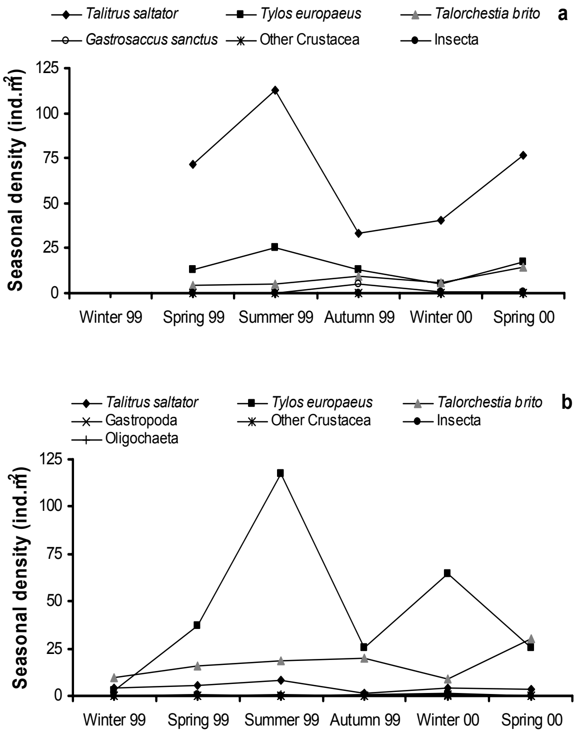

Figure 5. Variation of communities' seasonal density in the western coast of Portugal between January 1999 and June 2000. (a) – Comparison of the seasonal density between resident organisms at Cabedelo community; (b) – Comparison of the seasonal density between resident organisms at Quiaios community.

Influence of Environmental Variables on the Communities' Structure

Different environmental variables were considered significant (Monte Carlo Permutation Test, $p < 0.05$, after 999 permutations) regarding the Cabedelo and Quiaios resident communities after forward selection procedures applied to Redundancy Analysis (RDA), resulting in distinct ordination diagrams for each community studied (figure 6).

Only temperature had a significant contribution ($p = 0.001$) in explaining the variance of the faunal data at Cabedelo, and since only one variable was selected in the RDA, the first axis is constrained to this variable, while the remaining axes are unconstrained. The eigenvalue of the first axis obtained was 0.24 and the eigenvalue of the second was 0.36. The two first RDA axes thus account for 60% of the cumulative variance observed in faunal data. The second axis concerns the residual variance in the data,

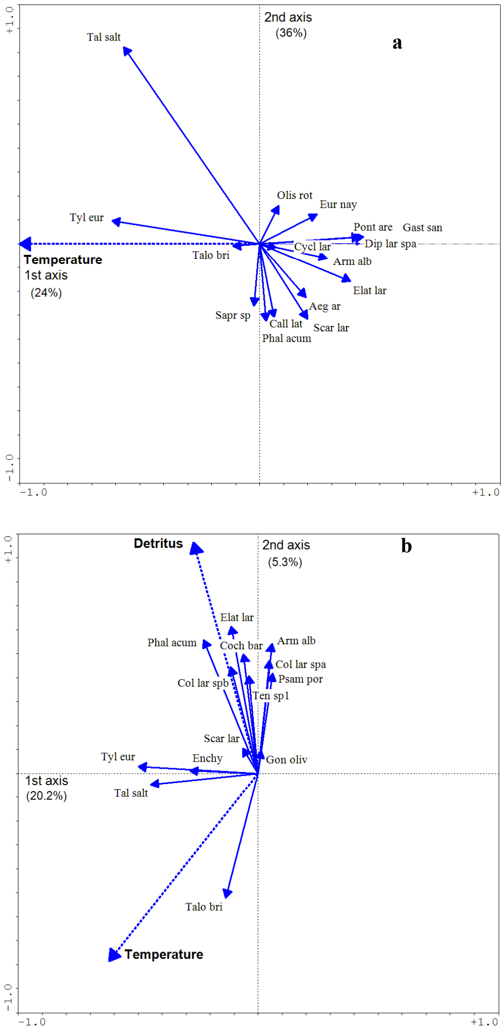

Figure 6. RDA ordination diagrams of macrofaunal communities data and environmental parameters at Cabedelo and Quiaios sandy beaches (western coast of Portugal). (a) – RDA ordination diagram of resident community data and environmental parameters at Cabedelo beach; (b) – RDA ordination diagram of resident community data and environmental parameters at Quiaios beach. Tyl eur – *Tylos europaeus*; Tal salt – *Talitrus saltator*; Talo bri – *Talorchestia brito*; Eur nay – *Eurydice naylori*; Pont are – *Pontocrates arenarius*; Gast san – *Gastrosaccus sanctus*; Arm alb – *Armadillidium album*; Dip lar – Diptera unidentified larvae; Cycl lar – Cyclorrhapha larvae; Olis rot – *Olisthopus rotundatus*; Aeg ar – *Aegiala arenaria*; Call lat – *Callicnemis latreillei*; Phal acum – *Phaleria acuminata*; Psam por – *Psammodius porcicollis*; Gon oliv – *Gonioctena olivacea*; Sapr sp – *Saprinus* sp.; Ten sp1 – Tenebrionidae unidentified species 1; Elat lar – Elateridae larvae; Scar lar – Scarabaeidae larvae; Col lar spa – Coleoptera unidentified larvae species a; Col lar spb – Coleoptera unidentified larvae especies b; Enchy – Enchytraeidae unidentified species; Coch bar – *Cochlicella Barbara*.

however, explained by a hypothetical environmental variable, which, according to the reduced RDA model obtained has more influence than temperature. The significance of the final RDA, using temperature as the explanatory variable, was also significantly assessed using the Monte Carlo Permutation Test (p = 0.002, F-ratio: 8.80, after 999 permutations). The corresponding ordination diagram (figure 6a) showed that *T. europaeus* was strongly and positively influenced by temperature. The crustaceans *P. arenarius*, *G. sanctus*, *E. naylori* and *A. album*, as well as most of the insect larvae (diptera, and especially the coleopterans elateridae) responded negatively to temperature, increasing their density from left to right along the first axis. *Talitrus saltator* and *O. rotundatus* were positively influenced by the second ordination axis, and the talitrid presented the highest fit. The remaining coleopterans formed an isolated group exhibiting a negative relationship with the second axis. Density variation of *T. brito* and Cyclorrhapha larvae were not explained by the ordination diagram.

Temperature (p = 0.036) and detritus (p = 0.011) were selected as explanatory variables regarding the Quiaios resident fauna. In this model, the first two axes of the RDA account for only 26% of the cumulative variance observed in the species data (figure 6b). The final RDA using these two explanatory variables was significant (Monte Carlo Permutation Test, p = 0.004, F-ratio: 5.48, for the test of significance of all canonical axes, after 999 permutations). The crustacean *T. brito* is strong and positively influenced by temperature (figure 6b), and negatively related to the quantity of detritus. The other two dominant crustaceans and the annelid are negatively related to the first ordination axis. Many species were positively related to the quantity of detritus, but the coleopterans *Phaleria acuminata* and elateridae larvae had the strongest fit with this axis. The crustacean *A. album*, and the coleopterans *P. porcicollis*, and the unidentified larvae *a*, formed a distinct group, positively related to the second axis and with quantity of detritus. Variations in density of *G. olivacea* and Scarabid larvae were not explained by the ordination diagram.

DISCUSSION

Overall, the physical environment of the two study sites can be considered relatively similar. Apart from differences observed in the extension of the intertidal area, sediment grain size, surf-zone width and detritus supplies, the general characteristics of both beaches can be considered identical, as demonstrated by the proximity of the scores obtained with the McLachlan's (1980) rating scheme. Nevertheless, several differences were observed with regard to community structure and composition.

The communities studied were strongly dominated by crustaceans (amphipods and isopods), a common feature in exposed sandy beaches, as demonstrated by Dexter (1983, 1990) along a gradient of exposure to wave action. Although molluscs and polychaetes are important components in sandy beach communities, insects (especially Coleoptera and Diptera) represented a much higher contribution in these communities, with the second being both the most abundant group and the most diverse one. Besides the studies on stranded wrack macrofaunal communities of sandy beaches (*e.g.* Inglis, 1989; Colombini *et al*., 2000; Jędrzejczak, 2002; Dugan *et al*., 2003; Jaramillo *et al*., 2006), little relevance is given to insects since the intertidal macrofauna is usually the focus of attention. However, most of the allochtonous food resources stranded by tides are consumed by scavengers (*e.g.* amphipods, isopods and insects) in the supralittoral areas, which have proven to be especially important in exposed sandy beaches. Sampling the beach all along its distance across, allowed a more accurate analysis of the macrofaunal communities and demonstrated that insects also have an important place in their structure, especially in the supralittoral area, where the relative importance of resident insects in the community's composition increases (from 3.2% to 7.1% at Cabedelo; from 0.8% to 2.8% at Quiaios).

A large number of species was observed in this study, in both beaches. However, the number of species in the communities' composition has certainly been overestimated since a large proportion of the insect species were recorded on a single occasion (June 2000). This suggests that a foreign insect invasion from the dunes, or from the terrestrial environment behind the beach, took place in a passive (blown by the winds) or active way (attracted to the wrack), as previously suggested by Brown and McLachlan (1990). Considering only the resident macrofauna, the number of species is equivalent to those observed by Rodil and Lastra (2004), when only frequently found organisms were considered, in similarly exposed beaches of northern Spain. The difference in species numbers between the Cabedelo and Quiaios communities, and the higher diversity at Cabedelo, may be easily explained by differences in grain size and food availability. In fact, a negative correlation between species richness and exposure to wave action and grain size has been generally accepted for sandy beaches (McLachlan and Jaramillo, 1995; McLachlan and Dorvlo, 2005). The harsher conditions observed in Quiaios, and its poorer conditions in terms of food inputs have probably contributed to exclude some of the species.

A stable structure dominated by amphipods (mainly talitrids) was observed at Cabedelo while in the Quiaios community the structure was highly variable, with amphipods and isopods seasonally replacing each other in the lead. Abundant species are exactly the same in both communities, but different species are driving the main changes observed in their structure. *Talitrus saltator* is the dominant organism in Cabedelo and is responsible for the fluctuations observed in total community density. At Quiaios, community dominance is seasonally shared by *Tylos europaeus* and *Talorchestia brito*. Amphipods are dominant in winter 1999 and autumn months because *T. brito* is the densest population in these periods, while in the other seasons the isopod *T. europaeus* is present in higher densities. These three crustaceans are the driving forces at different levels of the macrofaunal community structure of the sandy beaches on the western coast of Portugal. Talitrids and tylids may well have similar roles in other exposed sandy shores of Europe and even north Africa. Furthermore, as dominant species that form abundant populations on exposed sandy shores, these animals constitute key species in these environments and may be used as indicators of environmental quality. However, before they can be used in this way, their population dynamics, reproductive strategies and productivity must be known, as already achieved by Marques *et al.* (2003), and Gonçalves *et al.* (2003; 2005).

Why is the relative dominance of the three key species so distinct in the Cabedelo and Quiaios communities? The differences observed are believed to be mainly related to the different feeding habits and habitat preferences of the dominant species. The talitrids *T. saltator* and *T. brito* are sympatric species that frequently inhabit the same exposed beaches, but have distinct habitat preferences regarding their optimum zone on the beach – *T. brito* occupies the intertidal zone, taking advantage of the extended intertidal area of Quiaios beach, while *T. saltator* prefers the supralittoral. Also, according to Lagardère (1966), *T. saltator* as a preference for finer sands, condition observed at Cabedelo beach. Moreover, although both can be considered scavengers *sensu lato*, *T. brito* is more of an herbivore which feeds on the interstitial flora of the sediment (Lagardère, 1966), and is therefore less dependent on detritus subsidies. In this scope, the coarsest nature of Quiaios sands may even be an advantage, by promoting the development of a richer and more abundant interstitial flora. Of course, biological interactions between these two species, namely competition, must not be excluded. Concerning the supralittoral crustacean *T. europaeus,* a clear preference for coarse-sand beaches, avoiding fine sediments which make their locomotion more difficult (Kensley, 1974), explains the higher population densities recorded in Quiaios. This tylid is known to be an important decomposer of stranded wrack (Kensley, 1974; Brown and McLachlan, 1990), but these animals were frequently observed associated with embryo dunes vegetation at Quiaios, namely with *Otanthus maritimus* (personal observations). This suggests that *T. europaeus* possibly also feeds directly on living plants, as an alternative food resource when detritus are limited. However a competitive possibility with *T. saltator* due to a considerable niche overlapping between both species should not be discarded.

Resident macrofaunal composition was similar to other Atlantic and Mediterranean sandy beaches of Europe, especially regarding semi-terrestrial and marine organisms (*e.g.* Lagardère, 1966; Dexter, 1988, 1990; Rodil *et al*., 2006). Abundant populations of the talitrids *T. saltator* and *T. brito*, and the tylid *T. europaeus* are also a common feature on these coasts. Their abundance was observed throughout the beach, although they are normally reported as abundant species only in supralittoral areas (see for instance Lagardère, 1966; Rodil *et al*., 2006). Despite the similarity between the communities in terms of composition, some resident species observed were exclusive to only one of the beaches, such as the benthoplanktonic mysid *G. sanctus*, most probably because there is an adequate surf-zone area at Cabedelo. Differences in scavenger insect fauna were also observed, i.e. the coleopterans *Saprinus* sp., *A. arenaria* and *C. latreillei*, exclusive to Cabedelo. As proposed by Dugan *et al.* (2003) for exposed beaches of southern California, this suggests that wrack subsidies on exposed sandy beaches can increase species richness, especially regarding insects.

Total mean densities recorded are equivalent to the observed values for other sandy beaches having similar conditions (*e.g.* Rodil and Lastra, 2004; Rodil *et al*., 2006) but naturally smaller than the ones reported by Dexter (1990) in semi-exposed to protected beaches of southern Portugal. It is not surprising that higher mean densities are recorded at Cabedelo than at Quiaios since, regarding food availability (quantity and regularity under the form of allochtonous debris), Cabedelo is a more favourable environment, and the dominant species have scavenger feeding habits.

Supralittoral and intertidal zones of sandy beaches present distinct and characteristic macrofaunal forms. In western Portugal, the macrofaunal composition also reflects the typical patterns observed in sandy beaches: air-breathing crustaceans, like talitrid*s* in temperate latitudes and tylids*,* as well as insects, in the supralittoral zones (although talitrids and tylids were also frequently found in the intertidal areas); aquatic breathers such as cirolanid isopods in the littoral zone (Brown and McLachlan, 1990). The intertidal impoverishment recorded (only crustaceans were resident), although a common feature of exposed sandy shores (Brown and McLachlan, 1990), is not frequent in other studies on similar beaches (*e.g.*

Bayed, 2003; Rodil *et al*., 2006). In general, our data confirm that *T. europaeus* is most representative of the supralittoral and *T. brito* of the intertidal. *Talitrus saltator* was more abundant and shared a greater contribution in the intertidal areas of both beaches, contrasting with other studies where it is frequently referred to as exclusive to the supralittoral areas (see for instance Rodil *et al.* 2006). However, community studies are often based on snapshot sampling events, masking possible seasonal movements of the macrofauna on the beach that, according to Brown and McLachlan (1990), are frequent.

Macrofaunal densities were higher in the intertidal zone, most probably because there is a more favourable microclimatic environment here. Higher moisture content and lower sediment temperatures can prevent problems like excessive transpiration rates and desiccation. But, submersion and dragging by waves and winds may pose enormous threats. Talitrids and *T. europaeus* exhibit several behavioural adaptations that allow them to establish tidal migrations on the beach, stay in their optimal ecophysiological zones and display zonal recovery mechanisms if accidentally displaced from their optimum zones (*e.g.* Ugolini *et al*., 1995; Fallaci *et al*., 1999).

Seasonal patterns of density variation observed in the abundant species are associated with their particular population dynamics (see Marques *et al*., 2003 for *T. saltator*, Gonçalves *et al*., 2003 for *T. brito* and Gonçalves *et al*., 2005 for *T. europaeus*). Differences observed between *T. europaeus* and *T. brito* population dynamics, especially the timing of recruitments and average population densities, explain the seasonal variation in community structure dominance at Quiaios between isopods and amphipods. Seasons also have a clear influence on the population dynamics and bio-ecology of the abundant species in these Portuguese beaches. This is particularly evident through the positive correlations between population density and temperature found in earlier studies on these populations (Marques *et al*., 2003; Gonçalves *et al*., 2003, 2005), but it is also revealed in the significant relationships observed with multivariate methods in the present study. However, several authors also indicate the photoperiod as an important reproduction regulating factor in talitrids (*e.g.* Williams, 1978) and oniscid isopods like *Tylos* (*e.g.* Souty-Grosset *et al*., 1991), although this was not evaluated in this work.

Several resident organisms were only seasonally observed. The seasonal disappearance of terrestrial insects (*e.g. C. latreillei* and *A. arenaria*) during the extreme seasons (summer and winter) may be a way of avoiding extreme environmental conditions on the beach, namely severe storms and extreme temperatures, while for marine crustaceans (*e.g. G. sanctus*) it may prevent dragging by winter storms. Temporal trends observed in the seasonal analysis of diversity indexes also support seasonal changes in the utilization of the beach by the macrofauna, since the highest values in species number and diversity (*H'*) were always attained in moderate seasons, and the lowest in extreme ones.

Seasonal differences in the horizontal distribution of talitrids and of *T. europaeus* on the beach were recorded in the present study. Population densities increased in the intertidal areas in the warm seasons, while in the supralittoral increases were recorded in the coldest seasons. Previous studies (Gonçalves 2002; Marques *et al*., 2003; Gonçalves *et al*., 2003, 2005) also suggested that the low winter densities observed in these populations may be a consequence of a partial movement of these animals to the dunes, or even a displacement in their burrowing depth, as they burrow deeper into the sand. Similar seasonal fluctuations in horizontal distribution have been reported by Lagardère (1966) for *T. brito* and *T. europaeus* in France and by Williams (1995) for *T. saltator* in United Kingdom, and for other talitrids (*e.g.* Tsubokura *et al*., 1997). Seasonal movements along the beach may avoid potential situations of desiccative stress and extreme temperatures, by burrowing in the beach zones where sand moisture content and sediment temperature create a more favourable microhabitat, thus enabling these animals to survive in such dynamic and severe environments (Williams, 1995; Tsubokura *et al*., 1997).

Redundancy analyses showed that temperature has a positive influence on the dominant crustaceans *T. brito* and *T. europaeus*, confirming previous results. This was not observed for *T. saltator*, however, despite the positive results in another study

(Marques *et al*., 2003). The negative influence of temperature on the seasonally resident crustaceans' *P. arenarius*, *G. sanctus*, *A. album* and *E. naylori,* and also on several insect larvae, was expected. These results reinforce the relevance of seasons in controlling population densities and beach utilization by several organisms, shaping the structure and composition of these communities.

In Cabedelo, many resident organisms were distinctly related to the second ordination axis, which had a higher influence than temperature in species data, producing two assemblages of species. *Talitrus saltator* and *Olisthopus rotundatus* were positively influenced by this hypothetical environmental variable, while all the resident scavenger coleopterans were negatively influenced. A combination of the variables detritus quantity and relative moisture content of detritus (fresh weight) appears to be a plausible explanation for these results. All these species are directly or indirectly (in the case of the predator *O. rotundatus*) associated with wrack deposits on sandy beaches. Several authors (*e.g.* Inglis, 1989; Colombini *et al*., 2000; Jędrzejczak, 2002) have demonstrated that wrack-associated macrofauna colonize detritus in succession, invading the debris at different times according to their metabolic and trophic needs. Talitrid amphipods are primary colonizers of recently stranded fresh debris (*e.g.* Colombini *et al*., 2000; Jaramillo *et al*., 2006), and invasion by coleopteran predator species often coincides with amphipod and isopod colonization (*e.g.* Colombini *et al*., 2000; Jędrzejczak, 2002). Furthermore, Jaramillo *et al.* (2006) reported that the scavenger tenebrionid *Phalerisida maculata* Kulzer on Chilean sand beaches was more abundant on old dry wrack deposits. Based on these evidences, the negative influence of the second ordination axis observed on the coleopteran scavengers' assemblage, including, for instance, one tenebrionid, might be related to a preference to consume older and drier debris. Therefore, although detritus quantity was assessed (dry weight form), freshness and aging of the debris was not qualified in this study and it might be an important explanatory variable regarding wrack-associated macrofaunal abundances.

Besides temperature, the quantity of detritus was also selected as an explanatory variable at Quiaios, and several scavenger species were positively related to it. Since in this beach the input of debris is more irregular over time and more limited, these conditions may lead to a more obvious and clear reflection in scavenger density and occurrence data at the community level, making the relationship clearer. The two distinct macrofaunal assemblages associated with the first and second ordination axes for this resident community are unclear and difficult to interpret, suggesting that other environmental variables should be tested in the future (*e.g.* sediment temperature).

On the whole, this study demonstrates that these similarly exposed sandy beaches on the western coast of Portugal present several differences regarding community structure and composition, relative contribution of the abundant species, total densities and diversity. The absence of a steady structure is believed to be mainly associated with relevant differences in detritus subsidies and, to a lesser extent, with differences in sand grain size and extent of the intertidal area. Seasons influence relevantly these communities by shaping various community and population features differentially throughout the year, as the significant relationships with temperature demonstrated. Wrack deposits are believed to play an extremely important role in exposed sandy beaches where macrofaunal communities are dominated by supralittoral wrack-associated fauna and, they may overlap with the physical characteristics of the beach, as demonstrated by Dugan *et al.* (2003). This work further demonstrates that supralittoral macrofaunal organisms, especially talitrid and tylid crustaceans, play a relevant role in the structure of exposed sandy beach communities and should be considered key elements and potential indicators in future management options for these environments. However, the role of detritus subsidies, and especially the functioning of macrofaunal communities, should be investigated more deeply in the future.

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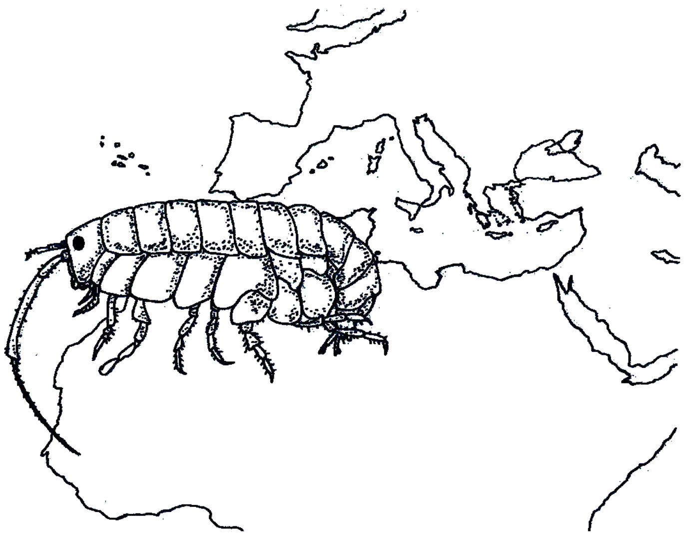
CHAPTER 2:

Comparison of *Talitrus saltator* (Amphipoda, Talitridae) biology, dynamics, and secondary production in Atlantic (Portugal) and Mediterranean (Italy and Tunisia) populations



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ABSTRACT

Talitrus saltator biology, population dynamics, and production were studied at three sandy beaches: Lavos, on the Western Coast of Portugal, Collelungo, on the Italian Coast of the Thyrrenean Sea, and Zouara, on the Northern Coast of Tunisia. Densities were higher at Lavos than at Collelungo and Zouara. Reproduction took place from March to late September at Lavos, early April to late September at Collelungo, and from late February to early November at Zouara. The average sex ratio was favourable to males at Lavos and Collelungo, and to females at Zouara. Based on data from Lavos, the population abundance was positively correlated with temperature, while the percentage of juveniles in the population was positively correlated with temperature and sediment moisture. Adult individuals from the Atlantic population were larger than the Mediterranean ones, while newborn individuals from the Mediterranean were slightly larger than Atlantic ones. Life span was estimated at 7 to 11 months at Lavos, 6 to 9 months at Collelungo, and 6 to 8 months at Zouara. Cohorts born at the beginning of the reproductive period tend to have shorter lives than the ones born later in the season, with longer life spans by crosseing the winter to breed in the next year. The minimum period necessary for sexual differentiation after birth occurred earlier in the Italian males and later in the Tunisian ones, while in females it occurred earlier and with the same age in Mediterranean populations. The period necessary for female's sexual maturation was longer in the Atlantic population. At the studied sites *Talitrus saltator* appeared as a semiannual species, with iteroparous females producing at least two broods per year, and exhibited a bivoltine life cycle. Growth production (*P*) was estimated at 0.74 g.m^{-2}.y^{-1} AFDW at Lavos, 0.12 g.m^{-2}.y^{-1} AFDW at Collelungo, and 0.61 g.m^{-2}.y^{-1} AFDW at Zouara. Elimination production (*E*) was estimated at 1.40 g.m^{-2}.y^{-1} AFDW at Lavos, 0.20 g.m^{-2}.y^{-1} AFDW at Collelungo, and 1.11 g.m^{-2}.y^{-1} AFDW at Zouara. The average annual biomass ($\overline{B}$) (standing stock), was estimated at 0.13 g.m^{-2} at Lavos, 0.014 g.m^{-2} at Collelungo, and 0.084 g.m^{-2} at Zouara, resulting in $P/\overline{B}$ ratios of 5.7 at Lavos, 8.2 at Collelungo, and 7.3 at Zouara, and $E/\overline{B}$ ratios of 10.8 at Lavos, 14.4 at Collelungo, and 13.1 at Zouara. The present results, combined with information from literature, revealed a geographic variation in *Talitrus saltator* populations with regard to their morphological characteristics, growth rates, life spans, and life cycles.

Key words: *Talitrus saltator*, biology, population dynamics, Atlantic, Mediterranean, Geographical variation.

INTRODUCTION

The littoral zone of sandy beaches constitutes a harsh environment, and the animal communities living at the interface between land and sea have evolved eco-physiologically (see for instance Morrit and Spicer, 1982) and behaviourally to cope with the environmental constraints of this changing habitat. However, in recent times, human impact has severely threatened the sand littoral ecosystems, stressing the need to investigate the extent to which organisms can adapt to environmental and human induced changes, foreseeing a sustainable use of beach environments. In fact, biological responses to environmental changes are complex, since different phenotypes may result from modification of gene expression, and the genome may also change through natural selection (Hoffman and Parsons, 1991). It is therefore important to evaluate the adaptation of local populations to such changes and the degree of natural variation between and within populations appears as a useful indicator (Hazlett, 1988).

Talitrid amphipods constitute one of the predominant arthropod groups in sandy beach fauna, exhibiting a dynamic equilibrium with environment. Due to their ecological importance, talitrids have been studied worldwide from different points of view. For example, a large number of papers have been published on talitrid behaviour, behavioural plasticity, and genetic determination of different behaviours (for instance Gerard *et al*., 1993; Scapini *et al*., 1993; Scapini, 1997) while factors influencing their spatial distribution and oriented movements in sandy beaches have also been studied to a great extent (for instance Borgioli *et al*., 1999; Scapini *et al*., 1989; 1995; 1999 a; Scapini and Fasinella, 1990; Scapini and Quochi, 1992). With regard to biodiversity, namely along the European coasts, talitrid populations have been compared genetically to assess inter-specific and intra-specific variation (De Matthaeis *et al*., 1995). Finally, in terms of applied research, a number of papers have been produced on trace metals (Cu, Zn, Fe, Cd, Pb, Mn, and Ni) concentrations and bioaccumulation by talitrids and on their role in biomonitoring (see for instance Rainbow *et al*., 1989; Weeks, 1992; Fialkowski *et al*., 2000).

Population size, reproductive strategies, and potential for dispersal between habitats are usually considered to reflect evolutionary fitness. Likewise, it may be assumed that different beaches offer different food resources, and that local populations would vary with regard to feeding habits (e.g. Pennings *et al*., 2000), efficiency in using the available energy, productivity, and reproductive capacity. Nevertheless, there are no comprehensive studies of strand-line talitrids in this respect, and the contribution of this group to the energy of beach ecosystems is still poorly understood. In fact, there are few studies on the reproductive biology and population dynamics of talitrids (Williamson, 1951a; Palluault, 1954; Hartog, 1963; Williams, 1978; Van Senus, 1988; Marsden, 1991a; Jones and Wigham, 1993; Persson, 1999), and even less on secondary production (e. g. Van Senus and McLachlan, 1986; Cardoso and Veloso, 1996).

Talitrids comprise species such as the sandhopper *Talitrus saltator,* widely distributed along the Mediterranean and European sandy coasts, and generally abundant where it occurs. A previous study by Williams (1978) provided an elegant approach to studies on the annual pattern of reproduction of this species in Northern Europe (British Islands). The underlying objective of this paper was to investigate the adaptation of *Talitrus saltator* to life in sand beaches, and simultaneously to provide data necessary for the development of a population dynamics model (Anastácio *et al*., 2003). For this purpose, a comparative study of Atlantic and Mediterranean populations was carried out, focusing on their biology, population dynamics, and productivity.

MATERIALS AND METHODS

Study sites

To allow comparisons between Atlantic and Mediterranean populations, three different sets of data were provided by sampling campaigns carried out at three sandy beaches: Lavos, on the Western Coast of Portugal, Collelungo, on the Italian Coast of the Thyrrenean Sea, and Zouara, on the Northern Coast of Tunisia (figure 1).

The Lavos sandy beach, located on the central region of Portugal, is approximately 25 Km long, between the mouth of the Mondego River and the Ervedeira coastal lagoon, close to Pedrógão, a small village. It is a relatively undisturbed beach, which receives a moderate number of summer visitors. The site chosen for the study, called Cabedelo (40º07’32’’ N 8º51’49’’ W), was located at about 1 km south from the Mondego river mouth and is an exposed beach (exposure rate = 15). The eulittoral zone was about 60 m in width, with an average slope of 2 %. Tidal range varies approximately between 2 and 3.5 m, and consequently the extension of the intertidal area ranges from approximately 30 m, on neap tides, to 45 m in width, on spring tides. During storms, the beach may be almost completely inundated, which causes the deposition of large masses of drift wrack, mainly macroalgae from rocky shores located to the north. The sediment was classified as medium sand, with a mean grain size between 0.250 and 0.500 mm (Wentworth scale)

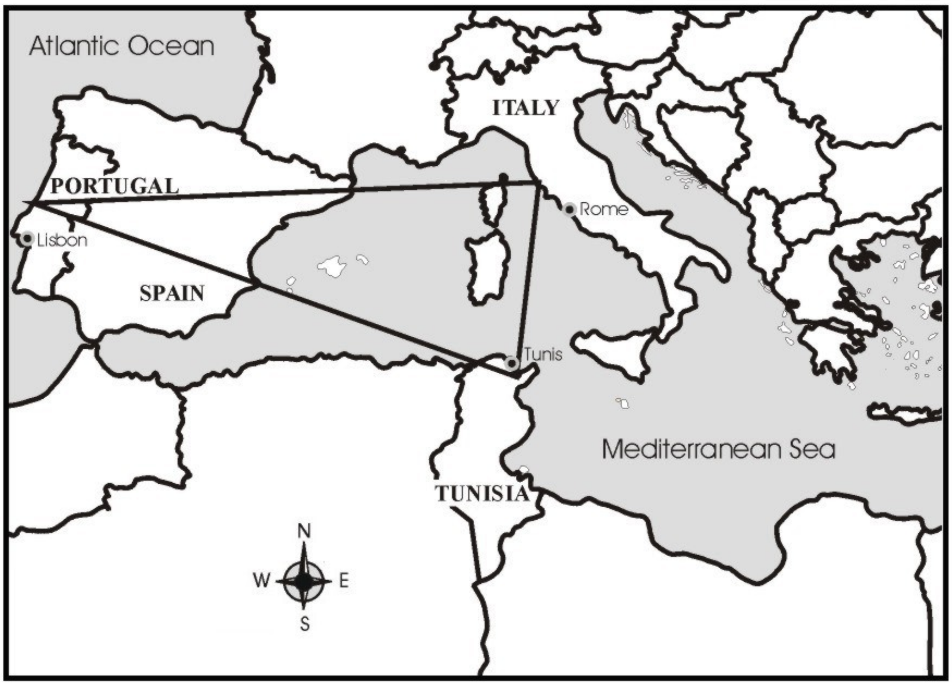

Figure 1. Location of the study sites at Lavos (Atlantic, Western Coast of Portugal), Collelungo (Thyrrenean Sea, Italy), and Zouara (Mediterranean Sea, Northern Coast of Tunisia).

(Brown and McLachlan, 1990).

No vegetation was found in the supralittoral area. The foredune was approximately 2.5 to 3 m in height, presenting a vegetation cover dominated by a single species, *Ammophila arenaria*, while in the secondary dune we also found *Euphorbia paralias* and *Cakile maritima* as species of major importance.

The Collelungo sandy beach, located in the Southern part of Tuscany, is about 7 Km long, between the Ombrone River and the beginning of the rocky shores east - south east of the Uccellina mountains. It constitutes a well-preserved sandy beach ecosystem, belonging to the Regional Park of Maremma. However in the past 25 years the coastline profile has been modified a great deal in relation to the decrease of sediment transportation of the Ombrone River. This has caused beach erosion at the mouth of the river and accretion at Collelungo (42°37’55”N 11°04’57”E), the site where the study was carried out.

Collelungo is an exposed beach (exposure rate = 12), presenting a wide eulittoral (average width about 40 m) with no vegetation. In relation to its slight slope (1%) this area was subjected to heavy inundation during sea storms that caused stranding of an abundant quantity of the phanerogama plant *Cymodocea nodosa* and of driftwood. The sediment mean grain size ranged between 0.250 and 0.500 mm, corresponding also to medium sand (Wentworth scale). Mean tidal excursions were from 20 to 30 cm at neap and spring tides respectively. The supralittoral was characterised by typical pioneer plants such as *Ammophila arenaria, Cakile maritime* and *Euphorbia paralias.* The dune was 3 m in height and presented a vegetation cover mainly composed of *Ammophila arenaria* and *Euphorbia paralias.* Retrodunal areas were characterised by Mediterranean maquis and pine wood vegetation planted a few centuries ago.

The Zouara beach-dune system, located in the northern coast of Tunisia, extends for about 25 Km, between Tabarka and Cap Negro. The system is interrupted at several points by the mouths of several oueds, El Kebir, Bouterfess, Berkoukech and Zouara (the most important one). The catchments are of Oued Zouara discharges into the sea at Zouara beach, a well-developed beach backed up by high coastal dunes. In the last two years, this beach dune system has undergone severe human impact due to the construction of a dam across the Oued, which seriously affected the equilibrium of the local coastal line. The dune vegetation from Tabarka to Cap Negro includes many species typical of this harsh environment, even if some (e.g. *Cakile maritima*) were rare. The dominant species in the dune were *Ammophila arenaria, Eryngium maritimum and Euphorbia paralias*, whereas annual dominant species were *Cutandia divaricata, Silene succulenta* and *Polygonum maritimum*.

The site chosen for the study (37°0'41"N 08°53'26"E) was located at 3 km west from the mouth of Oued (River) Zouara, constituting a very exposed beach (exposure rate = 16). The eulittoral zone was about 50 m in width, with an average slope of 3 %. The first dune belt was about 20 m in height. Mean tidal excursions ranged from 10 to 20 cm at neap and spring tides respectively, and therefore tides were frequently hidden by local wave action. Beach debris was limited. The sediment was mainly medium sand, with a mean grain size ranging from 0.250 and 0.500 mm (Wentworth scale).

All the three sites correspond to relatively undisturbed beaches. Nevertheless, in the case of Zouara, there are development plans for the whole area, which may alter substantially the present scenario in the near future, with a probable increase of human pressure over the beach and the dunes. The preparation of management scenarios appears therefore as a priority, and the use of *Talitrus saltator* as indicator species to assess the impact of human activities on the beach communities may constitute a useful tool.

Sampling programme

At the three study sites, quantitative samples were taken from the sandy beach communities, which consisted mainly of arthropod populations. The sampling period at Lavos (Atlantic, Western coast of Portugal) lasted 16 months, from March 1999 to June 2000, while at Collelungo (Western coast of Italy) it lasted from February 1999 to January 2000, and at Zouara (North-Western coast of Tunisia) from December 1998 to December 1999. Although samples were not taken exactly coincidentally, there was a significant overlap of activities at the three sites. The study period was longer at Lavos in order to obtain a larger data set necessary for further modelling development.

Samples were expressed as a function of the sampled area, always trying to collect at least 100 specimens of *Talitrus saltator* (Amphipoda), considered as the minimum suitable number for modal analysis of the population structure. Three teams participated in the sampling effort, and the field methodologies were previously inter-calibrated through reciprocal visits to the different sites.

Samples were taken at regular intervals along two transects from the shoreline to the base of the dune. No quantitative samples were carried out in the dune because it was considered that it would cause too much physical disturbance. This sampling strategy allowed simultaneously to account for differential vertical distribution and to collect the minimum of individuals necessary for statistical analysis. Sampling occurred every 15 days, during the neap tides, and, when possible, rainy days were avoided because precipitation usually causes animal dispersion.

Each replicate was obtained using a metal or wood-square of 0.25 m^2 to bound the sampling area. Using a small scoop, the first 20 cm of the sand surface layer, where the organisms would most probably be found, was removed. The sand was sieved through 1 mm mesh size bags, which retained all individuals of *Talitrus saltator*, including newly hatched juveniles. Animals and the largest sand fraction were retained in the sieve, kept alive in plastic bags, until separated in the laboratory where the animals were preserved in 70% alcohol.

To investigate the influence of physicochemical factors on the *Talitrus saltator* population at Lavos, for each replicate, before sieving the sand, all superficial debris were collected, sieved through a 2 mm mesh size, and dry weighted in the laboratory (potential food /$mg.m^{-2}$). Sediment samples were frozen at -18^o C and kept for a period no longer than 2 months before analysis of organic matter content. The organic matter of the sediments was determined as ash free dry weight (AFDW) after combustion at 550^o C during 12 h. Sediment samples were also taken, kept in plastic bags, and immediately analysed at the laboratory to estimate sediment moisture, which was given by the difference between the initial weight of sediment samples and its dry weight after 24 h at 60° C.

Meteorological data during the study period were obtained from the closest meteorological station. These included average daily precipitation, visibility, cloudiness, wave height, wave period, and wind velocity, and maximum and minimum daily temperatures.

Laboratory procedures

The goal was to obtain quantitative data on the main biological features, field growth rates, and productivity of the populations of *Talitrus saltator* at the three study sites, allowing the further calibration of growth models and the development of a population dynamics model.

Field samples were processed at three laboratories: in Portugal (Coimbra), Italy (Florence), and Tunisia (Tunis). At each laboratory, individuals collected were measured for the cephalic length using binocular microscopes equipped with micrometrical ocular lens, calibrated with objective micrometers. When necessary, total length (TL) was estimated from cephalic length (CL) through the following estimated linear equations:

$$TL = -1.74516 + 10{,}88863CL$$ for the Lavos population

$$TL = 0.515093 + 8.82335CL$$ for the Collelungo population

$$TL = 0.186381 + 9.12423CL$$ for the Zouara population

After measured, individuals were sexed (males, females, or juveniles) based on the presence of copulatory appendages in the males, and presence of oostegites, with or without setae, in the females. Females with setae were considered as mature, meaning that it would carry eggs soon, or that they had just been released. In the absence of any secondary sexual dimorphic features individuals were considered juveniles. Specimens were therefore classified as: a) males, b) resting females, c) gravid females or d) juveniles. The gravid females group included both females carrying eggs and females bearing setae on the oostegites.

Embryos were removed from the brood pouch of gravid females and counted. The average diameter was determined taking into account the length, width, and depth, and eggs were classified, using a simplified version of Williams (1978) proposal:

Stage A – eggs approximately round in shape, although showing internally different aspects of cell division;
Stage B – eggs oval, embryo comma-shape and showing the initial segmentation of head and limb rudiments, dorsal organ with maximum size;
Stage C - eggs oval, head and limb rudiments clearly visible, appearance of optic rudiment, regression of dorsal organ;
Stage D – eggs oval, head clearly defined, appearance of pigmented eye, limb development completes;
Stage E – hatched juveniles retained in the brood pouch.

However, due to handling, gravid females dropped an undetermined number of embryos from brood pouches, so that any significant statistical analysis regarding brood mortality was impossible.

It was assumed that the relationships between length and weight of the individuals could vary through the year. Thus, for each season, 150 to 200 specimens, randomly sampled, were weighed (ash free dry weight, after combustion at 450° C during 3 h) with a 10^{-5} mg precision. However seasonal differences were not significant. Smaller juveniles could not be weighed individually, and were pooled in groups consisting of specimens of approximately the same size. Data on cephalic length (CL) and weight (AFDW) were then used to determine the following equations:

$$AFDW = 0.00261025CL^{3.79929}$$ for the Lavos population

$$AFDW = 0.0023215CL^{2.87104}$$ for the Collelungo population

$$AFDW = 0.0024378CL^{2{,}85113}$$ for the Zouara population

Data analysis

The spatial distribution of the studied populations was analysed using the index $I = S^2/\overline{X}$, where S^2 is the variance of densities estimated per replicate, expressed as a function of the sampled area, and $\overline{X}$ is the mean density (Elliot, 1977).

Multiple regression models based on data from Lavos (Atlantic) were developed, correlating density, sex ratio, percentage of gravid females, and percentage of juveniles in the population with physicochemical environmental factors. The fitted regression models were expressed as:

$$Y' = a + b_1X_1 + b_2X_2 + \ldots + b_KX_k$$

Where Y' is the value of a given dependent variable (*e.g.* density) predicted by the equation, and X_1, $X_2 \ldots X_k$ are independent variables (e.g. salinity). The solutions are the estimate of the regression coefficients a, b_1, $b_2 \ldots b_k$. The significance of the fitted regressions was tested through analysis of variance (F), using additionally the t test for the regression coefficients. The models were fitted with data following the Stepwise Forward Analysis method performed by the Statgraphics 4.0 statistical package.

Field growth rates were estimated by tracking recognizable modal distributions in the population using size-frequency of distributions (0.04 mm length classes) from successive sample dates, following a methodology previously described (Marques and Nogueira, 1991; Marques *et al.*, 1994; Pardal *et al.*, 2000). Modal distributions are assumed to result from pulses in recruitment, conventionally referred to as cohorts. Size frequency analysis was carried out using the probability paper method (Harding, 1949), as performed by Cassie (1954; 1963). The reliability of the method was tested employing both the χ^2 and G tests ($p \leq 0.05$). Computations were performed using the ANAMOD software (Nogueira, 1992).

Field growth rates were expressed using the Von Bertalanffy's model (Bertalanffy, 1957):

$$Lt = L\infty(1 - e^{-k(t-to)})$$

Where:

Lt - length of the organism at a given moment t;

L∞ - maximum possible length of the organism;

t - given instant;

t_o - instant in which the organism would have a length = 0;

k - intrinsic growth rate;

Production estimates were based upon cohort's recognition, taking into account growth production (*P*) and elimination production (*E*). Production was estimated by growth and elimination methods as derived by Allen (1971). Approximate values of *P* and *E* for each cohort during a given time interval may be expressed as:

$$P = \frac{(N_t + N_{t+1})}{2} * (\overline{W}_{t+1} - \overline{W}_t)$$

$$\text{for } \overline{W}_{t+1} > \overline{W}_t$$

$$E = \frac{(\overline{W}_t + \overline{W}_{t+1})}{2} * (N_t - N_{t+1})$$

$$\text{for } N_t > N_{t+1}$$

N - density of the cohort at each sample date;

$\overline{W}$ - mean individual biomass in each sample date;

t and t+1 - consecutive sample dates;

Total values of *P* and *E* for each cohort are expressed as:

$$P = \sum_{t=0}^{t=n} \frac{(N_t + N_{t+1})}{2} \Delta\overline{W}$$

$$E = \sum_{t=0}^{t=n} \frac{(\overline{W}_t + \overline{W}_{t+1})}{2} \Delta N$$

Total values of *P* and *E* for the population are expressed as:

$$P = \sum_{n=1}^{N} P_{cn} \text{ and } E = \sum_{n=1}^{N} Ecn$$

Where:

P_{cn} and E_{cn} are the growth and elimination production of cohort *n*.

$P/\overline{B}$ and $E/\overline{B}$ ratios were determined, with $\overline{B}$ (mean population biomass) being expressed as:

$$\overline{B} = (1/T)\sum_{n=1}^{N} \overline{B}_n t$$

Where:
T - period of study;
N - number of successive cohorts in the period T;
$\overline{B}$ n - mean biomass of cohort n;
t - duration of cohort n.

RESULTS

Spatial distribution and density

Talitrus saltator exhibited a consistent pattern of aggregated distribution at the three study sites, the spatial distribution always being higher than 1 (Elliot, 1977). Despite seasonal variations, densities were consistently higher at Lavos beach, in the Atlantic, than at Collelungo and Zouara in the Mediterranean (figure 2).

Despite differences in density, the pattern of seasonal variation appears to be very similar at Lavos and Collelungo: the lowest densities in late winter, a rapid increase from early spring to June/July, when the maximum is attained, a slight decrease, followed immediately by a second, although smaller, peak in late August, and a gradual decrease from late summer until the next winter (figure 2). The pattern of variation is very different at Zouara. Highest densities in the beach were observed during winter, followed by a clear decrease in numbers of *Talitrus saltator*, which sometimes almost completely disappeared from the beach (figure 2).

Period of reproduction and sex ratio

The period of reproduction is indicated by the occurrence of gravid females (figure 3), consisting of both ovigerous and mature females, and the appearance of new juvenile cohorts in the population (figure 3 and figures 5 to 7).

The appearance of ovigerous females roughly preceded juvenile recruitment, but there was no synchronization between the females regarding the state of embryonic development, as eggs in all stages occurred at each sampling date. Eggs average diameter increased ± 43% from stage A to stage D, corresponding to an increase of ±192% in volume, which is relatively similar to the value of 240% recorded by Williams (1978).

The period of reproduction was therefore equivalent in the populations studied on the Atlantic coast of Portugal and in Italy, but clearly longer in North Africa. At Lavos, reproduction took place: a) from March to late September, with new cohorts being detected in March, April, May, June, July, and one late in early September. The breeding season was similar at Collelungo, from early April to late September, with new cohorts recognized in early April, May, June, July, August, and September. At Zouara however, breeding occurred from late February to early November, with new cohorts in February, April, June, in the period between July and October, and finally in November.

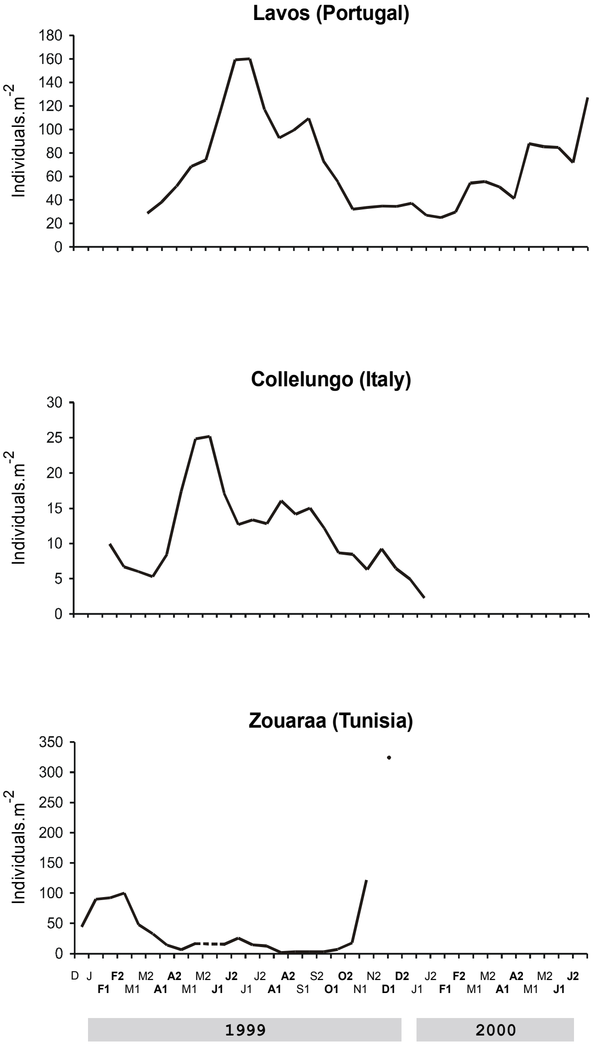

Figure 2. Variation of *Talitrus saltator* population density (ind.m^{-2}) at the three study sites.

Five or six new groups were produced at Lavos, taking into account that cohort 5, consisting of very small animals was detected at the first sampling date. Six were evident at

Zouara, while eight new cohorts could be recognized in the Collelungo population. Therefore, despite differences regarding the reproduction period between the North African population and the other two, the reproductive output was more or less equivalent. Additionally, an equivalent pattern was observed at Lavos and Collelungo regarding the variation of the percentage of juveniles in the population (figure 3). An initial peak of recruitment occurred in spring, followed by a slacking in early summer, and a new maximum in August and September, just before the winter pause. At Zouara there is a strong suggestion that the same might have occurred (figure 3), but the available data does not allow to recognize the pattern clearly.

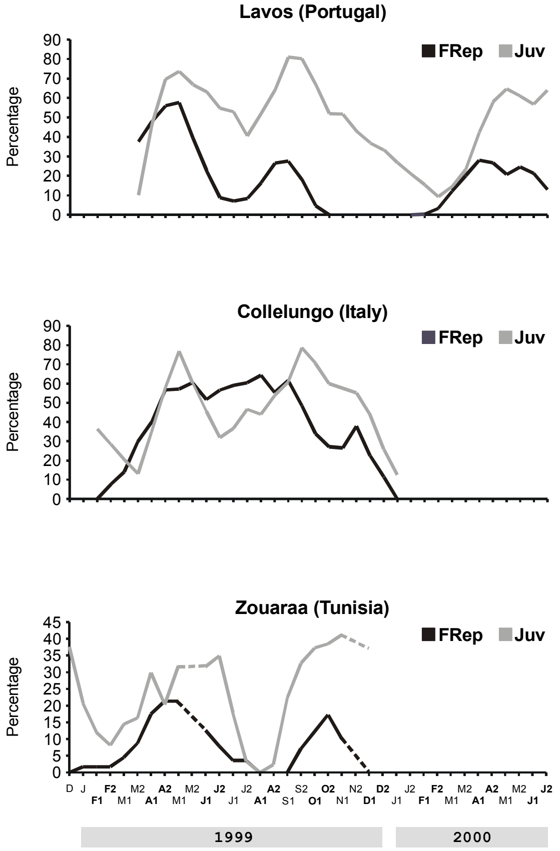

Figure 3. Percentages of gravid females of *Talitrus saltator*, relative to the total female population, and of juveniles, relative to the whole population, at the three study sites.

With regard to the sex ratio, there is a clear difference between Lavos and Collelungo, on one hand, and Zouara, on the other (figure 4). At Lavos and Collelungo, the sex ratio was almost always favourable to males (average 1.2:1 and 1.04:1 respectively), except briefly during spring, at both sites, during the summer (July/August), at Lavos, and in autumn at Collelungo. At Zouara the opposite was oserved, with a dominance of females in the population (0.54:1), except in early December 1999. This difference will be discussed below.

Influence of environmental factors on the population structure

Data regarding the average values and range of variation of physico-chemical factors at Lavos during the whole study period are summarized in table 1. The entire data sets regarding the biological variables (density, biomass, sex ratio, percentage of gravid females, and percentage of juveniles in the population) and physicochemical factors determined at each sample date were used to establish multiple regression models (stepwise approach).

As might be expected, the population density (D) was positively correlated with temperature (T), as well as the population biomass (B). Moreover, the percentage of juveniles in the population (PJ) was positively correlated with temperature (T) and sediment moisture (SM). The following regression models describe these relations:

$$Ln\ (1+D) = 2.59 + 0.0987T$$
$$(r^2 = 0.593;\ p = 0.0000)$$

$$B = 0{,}0482 + 0.00570T$$
$$(r^2 = 0.19;\ p = 0.009)$$

$$PJ = -57.9 + 3.72T + 34.1\ Ln\ (1 + SM)$$
$$(r^2 = 0.49;\ p = 0.000 \text{ for temperature and } p = 0.003 \text{ for sediment moisture}).$$

The positive correlations between density (D) or biomass (B) and temperature (T) may be interpreted as a cause-and-effect relation, with temperature favouring recruitment and, consequently, the increase in density and biomass. As expected, biomass and population density were also significantly correlated (r^2 = 0.67, for 30 observations).

The significant positive correlation between the percentage of juveniles in the population (PJ) and temperature (T) appears obviously to be a function of recruitment, which took place in spring and summer, the

Table 1. Average (A) daily values and standard deviation (SD) of physicochemical factors at Lavos beach (Western Coast of Portugal) regarding the period from March 1999 to June 2000.

	A	SD
Temperature (ºC)	15.65	4.77
Precipitation (mm)	2.41	5.63
Sediment moisture (%)	3.24	1.22
Organic matter content (%)	0.15	0.05
Detritus (g.m^{-2})	9.15	9.03
Wind velocity (m.s^{-1})	3.92	2.98
Cloudiness	4.06	2.67
Visibility	6.05	1.05
Wave height (m)	0.05	0.32
Wave period (s)	0.11	0.65

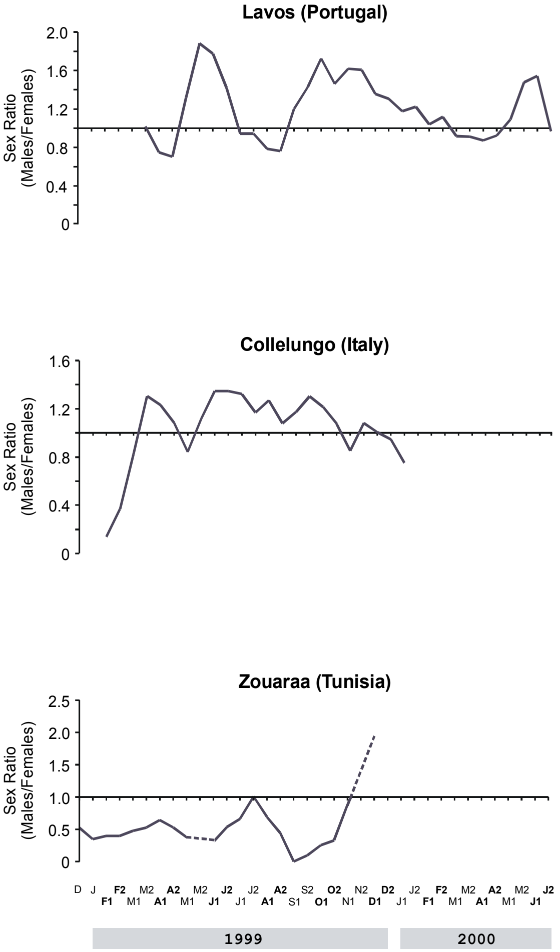

Figure 4. Variation of *Talitrus saltator* sex ratio (males/females) at the three study sites.

warmest months in the year, while the positive correlation with sediment moisture basically expresses a non uniform distribution of juveniles in the beach, with younger individuals, which are probably more sensitive to dehydration, concentrating closer to the water line.

Field growth rates and life span

Size-frequency polymodal distributions were analysed for recognizable cohorts (figures 5 to 7). At Lavos, five cohorts (1, 2, 3, 4, and 5) could be identified from data from the first sampling date (24/03/99) (figure 5). From modal analysis, eight new distributions, presumably corresponding to new recruitments, were clearly identified (figure 5) (χ^2 and G tests not significant; p≤ 0.05) during a study period of 18 months, respectively on 7 of April (6), 10 of May (7), 17 of June (8), 21 of July (9), and 3 of September (10), in 1999, and again on 17 of March (11), 29 of March (12), and 19 of May (13), in 2000.

At Collelungo, three cohorts (1, 2, and 3) were recognized at the first sampling date (09/02/99) (figure 6), and eight new cohorts were detected and tracked during the next 12 months, which was the duration of the study period in Italy, respectively on 8 of April (4), 7 of May (5), 7 of June (6), 6 of July (7), 20 of July (8), 3 of August (9), 3 of September (10), and 17 of September 1999 (11) (figure 6). From results of modal analysis, the number of new recruitments in the Italian population is higher than in the Atlantic population during the same period. Therefore, although cohort recognition was still possible, the Italian population approximated more closely to continuous breeding during the reproductive period.

Finally, at Zouara, four cohorts (1, 2, 3, and 4) were recognized at the first sampling date (02/12/98), and six new distributions were identified during a study period of 12 months, respectively on 20 of February (5), 29 of April (6), 2 of June (7), during the period between 21 of July and 2 of October (8 and 9), and 10 of November 1999 (11) (figure 7).

Size of cohorts at the moment of detection (minimal size) varied as a function of study sites (figure 8). At Lavos, the minimum average cephalic length (CL) of new cohorts ranged from 0.49 to 0.55 mm (3.59 to 4.26 mm TL - total length), while the maximum average cephalic length attained ranged from 1.48 to 1.78 mm CL (14.37 to 17.64 mm TL). At Collelungo, the minimum average cephalic length (CL) ranged from 0.38 to 0.45 mm (3.86 to 4.48 mm TL), and the maximum

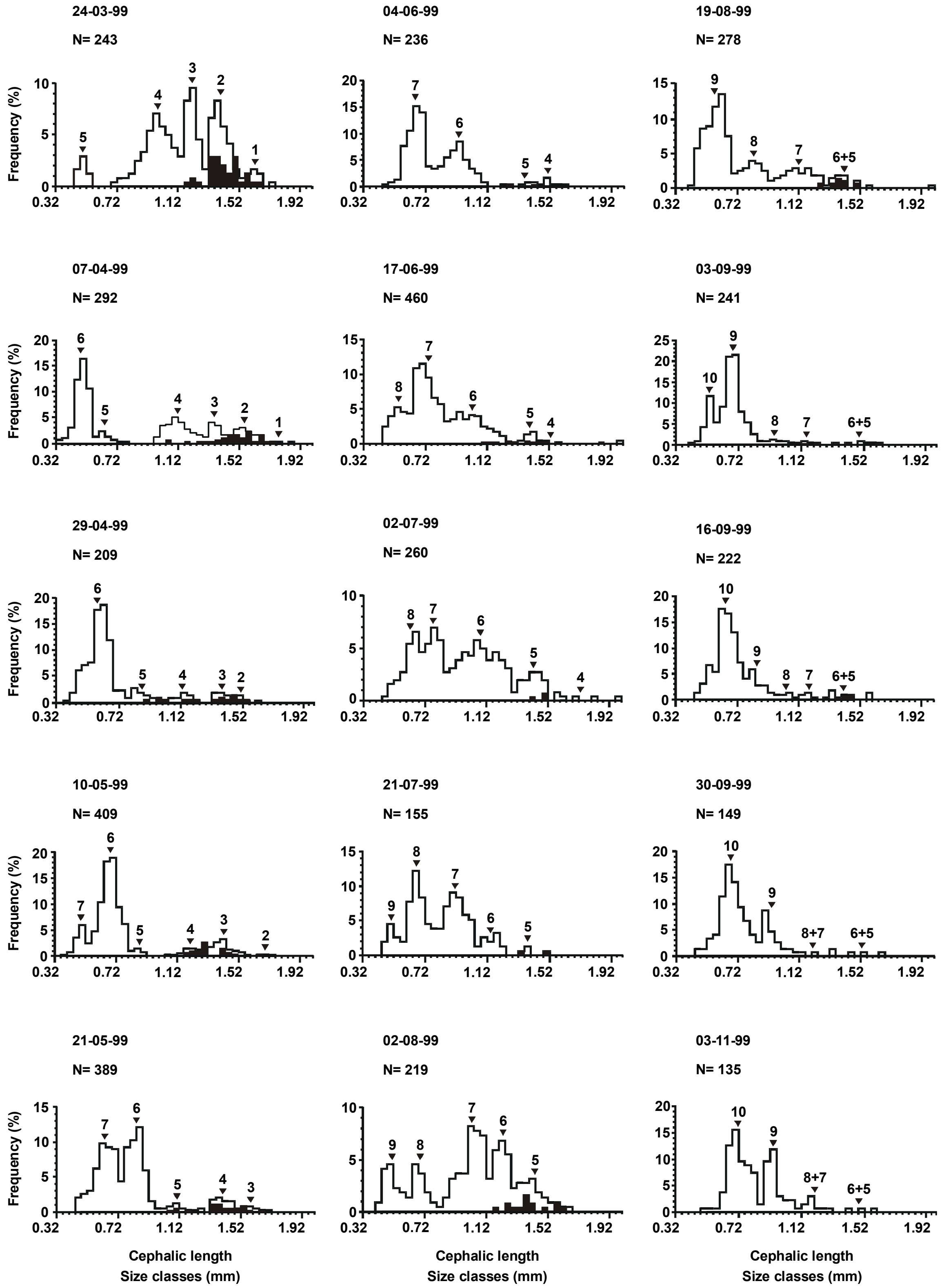

Figure 5. Size-frequency distribution of *Talitrus saltator* at Lavos (Portugal) from 24 of March 1999 to 16 June 2000. Sampling dates are indicated. N = number of measured individuals. Arrowheads indicate average cephalic length of the numbered cohorts or groups of cohorts. Black areas indicate gravid females.

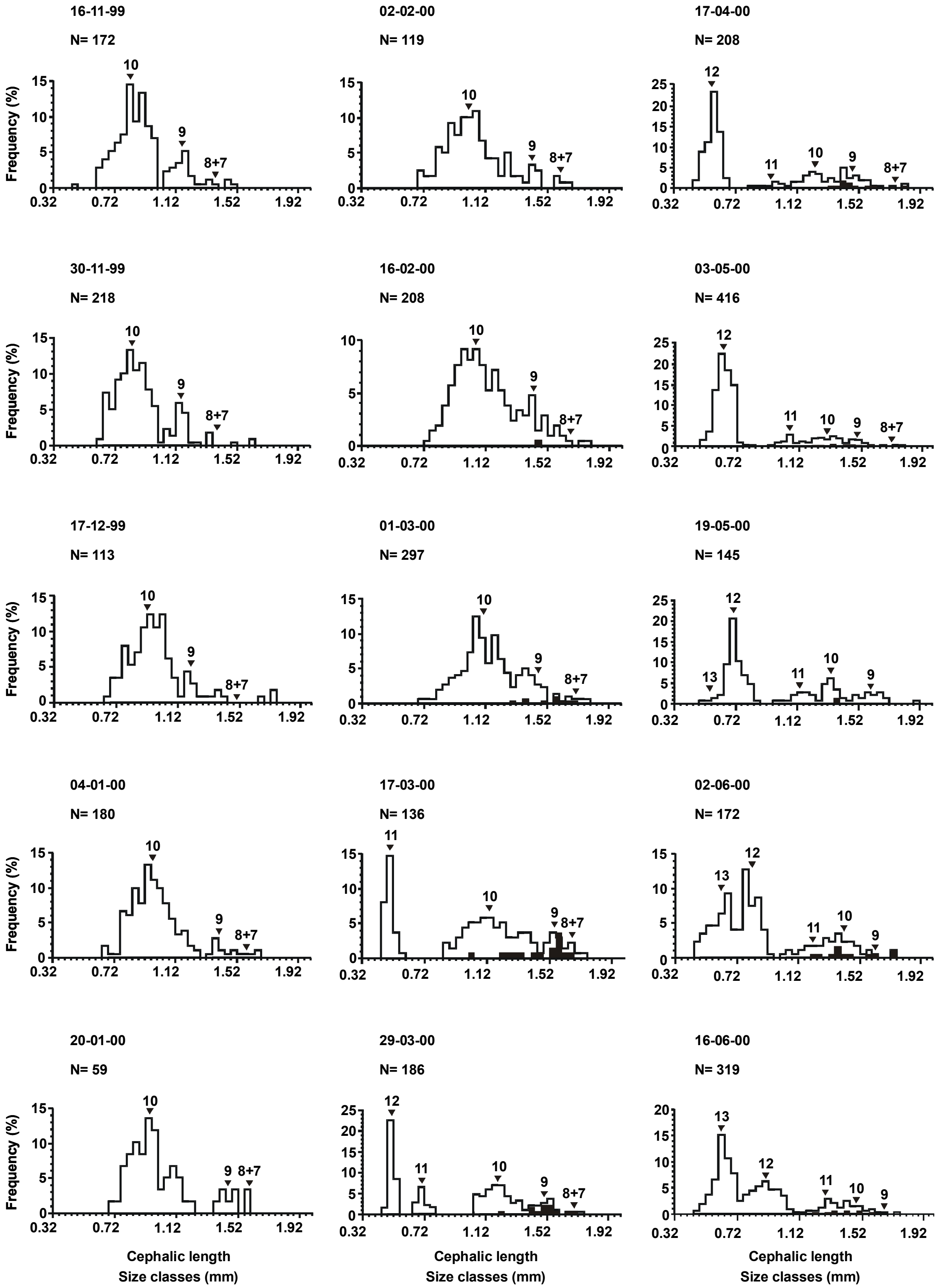

Figure 5 (continued)

values ranged from 1.23 to 1.38 mm CL (11.36 to 12.69 mm TL). Finally, at Zouara, the minimum average cephalic length (CL) ranged between 0.41 and 0.57 mm (3.92 to 5.39 mm TL), and the maximum ranged from 1.34 to 1.72 mm CL (12.41 to 15.88 mm TL).

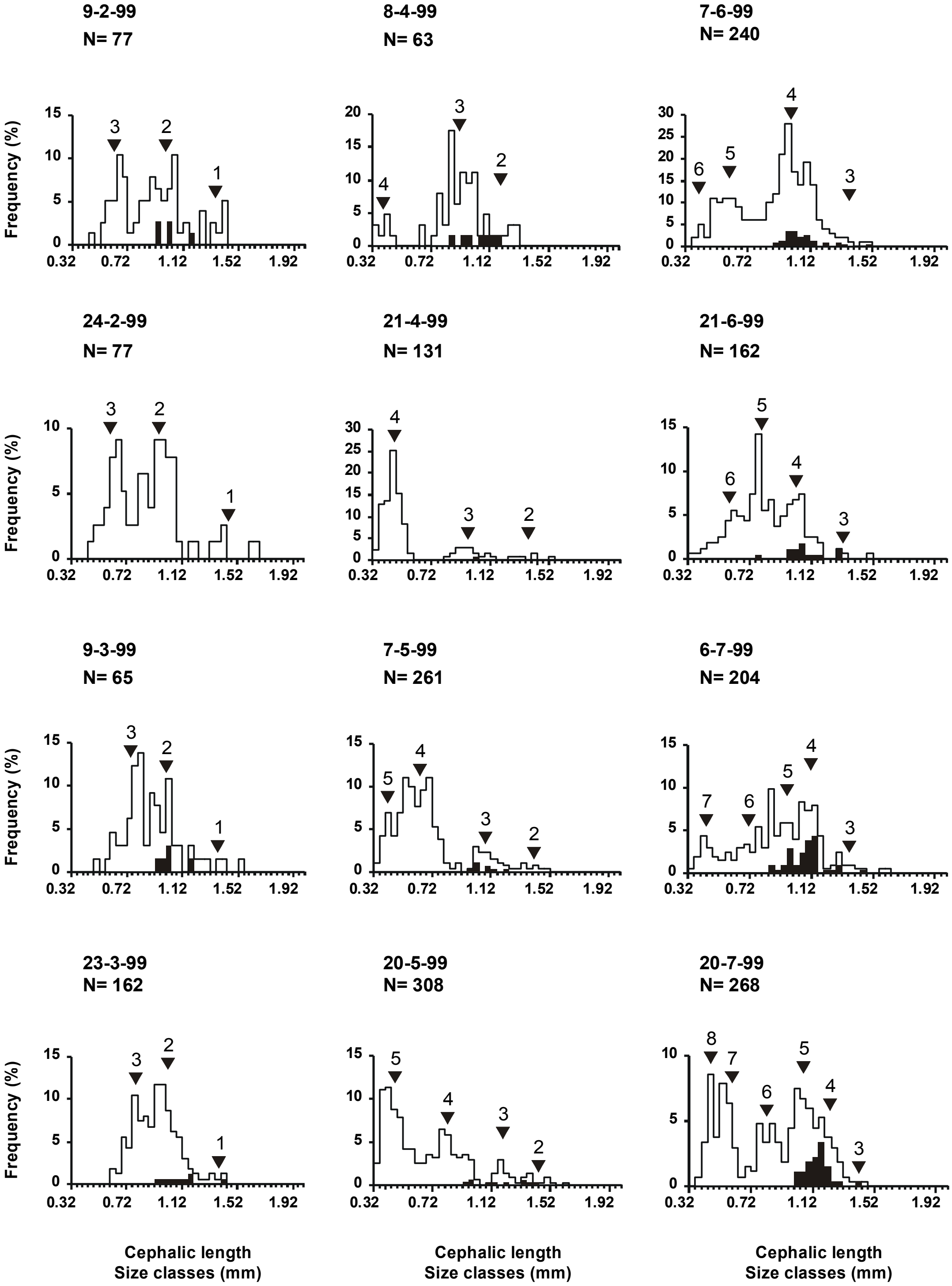

Figure 6. Size-frequency distribution of *Talitrus saltator* at Collelungo (Italy) from 9 of February to 12 of December 1999.

On average, the population presenting the largest adults was that from Lavos (Atlantic), while the smallest individuals came from the Collelungo population (Italy), with individuals from the Zouara population (Tunisia) ranging in the middle. Nevertheless, taking into account the equations relating data on cephalic length and total length given above, newborn individuals from the two Mediterranean populations appeared slightly larger in total length than the ones from the Atlantic population. Growth was found to be continuous across the life span of *Talitrus saltator*, although

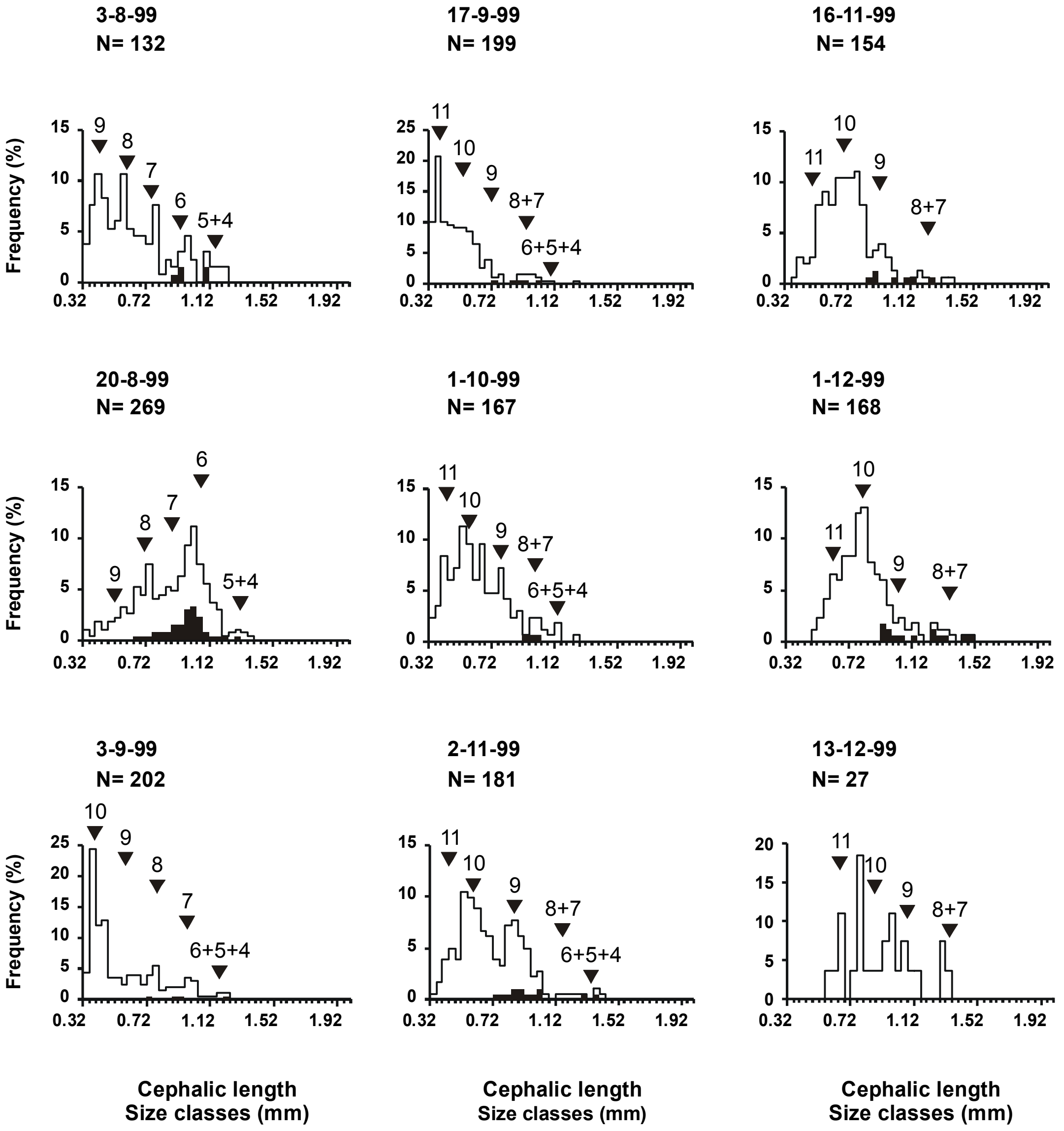

Figure 6 (continued)

growth rates varied with size and temperature. Growth rates were faster in the early phases, and appeared to be higher during spring and summer (figure 8). This pattern was recognizable at Lavos and Collelungo, although it was less clear at Zouara. Taking into consideration growth rates and the disappearance of cohorts, life span was estimated at 7 to 11 months at Lavos, 6 to 9 months at Collelungo, and 6 to 8 months at Zouara (table 2). As a general pattern, at the three sites, cohorts born at the beginning of the reproductive period tend to have shorter lives than those born later in the season. The longer life spans were observed in cohorts that over-wintered and bred in the next reproductive period (figure 8).

Growth data sets from the three sites were used to calibrate the growth model proposed by Von Bertalanffy (1957), providing a different set of parameters in each case. Growth data fitted the model well, with faster growth rates in the early phases (figure 9). Based on the model, the minimum period necessary for male sexual differentiation after birth was estimated at ± 4 weeks at Lavos, ± 3 weeks at Collelungo, and ± 4.5 weeks at Zouara. Regarding females sexual differentiation, the same period was estimated at ± 6 weeks at Lavos, and ± 5 weeks at Collelungo, and Zouara. Finally, the period necessary for female sexual maturation after birth was estimated at ± 10 weeks at Lavos, and ± 8 weeks at Collelungo and Zouara (table

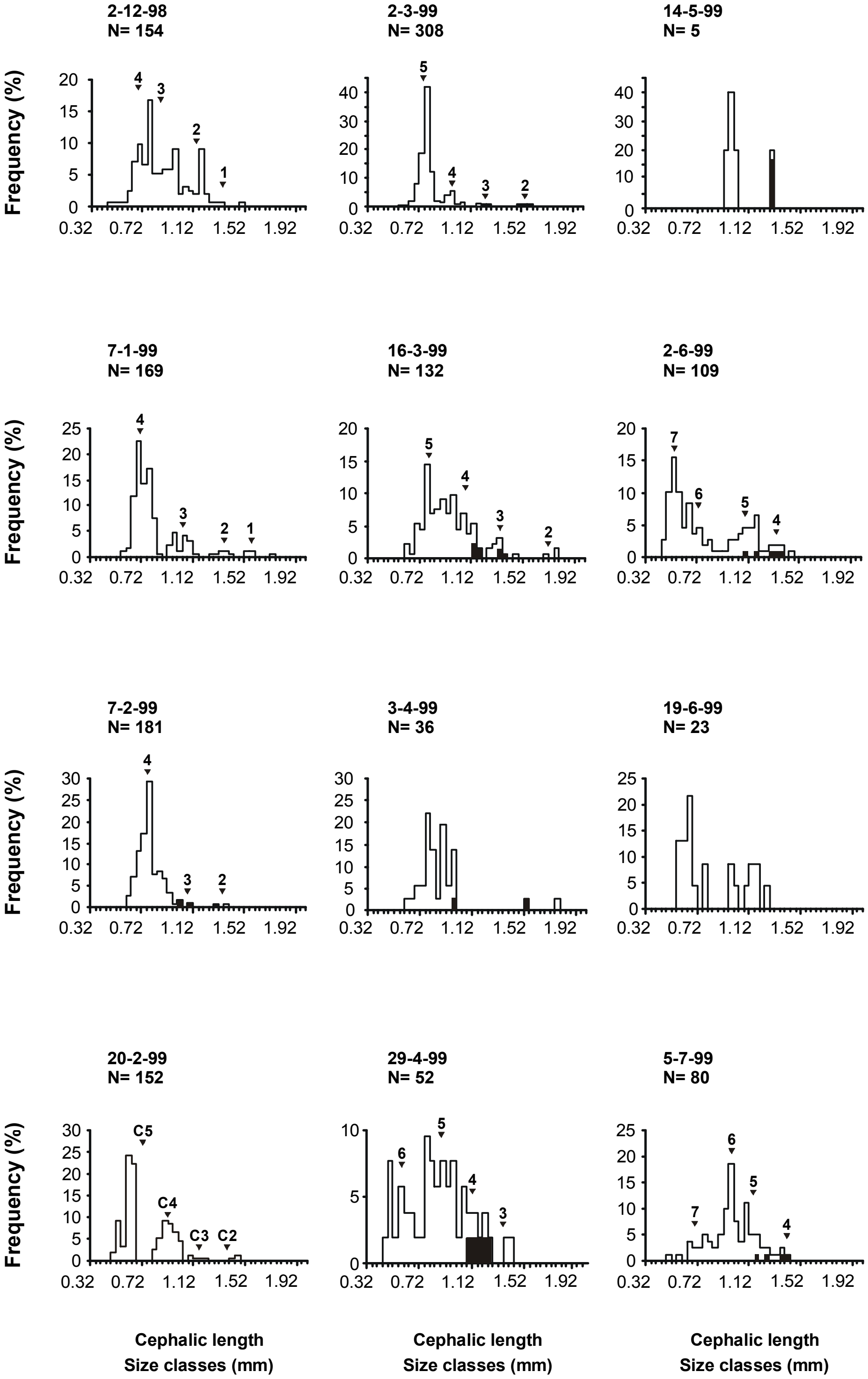

Figure 7. Size-frequency distribution of *Talitrus saltator* at Zouara (Tunisia) from 2 of December 1998 to 6 of December 1999.

2). Sexual differentiation tends, therefore, to occur earlier in males than in females. Moreover, although the output from the model calibrated with data from Zouara provided some unexpected results regarding male sexual differentiation, there is a suggestion, at least in females, that sexual differentiation occurs later after birth in Atlantic populations in comparison to the Mediterranean.

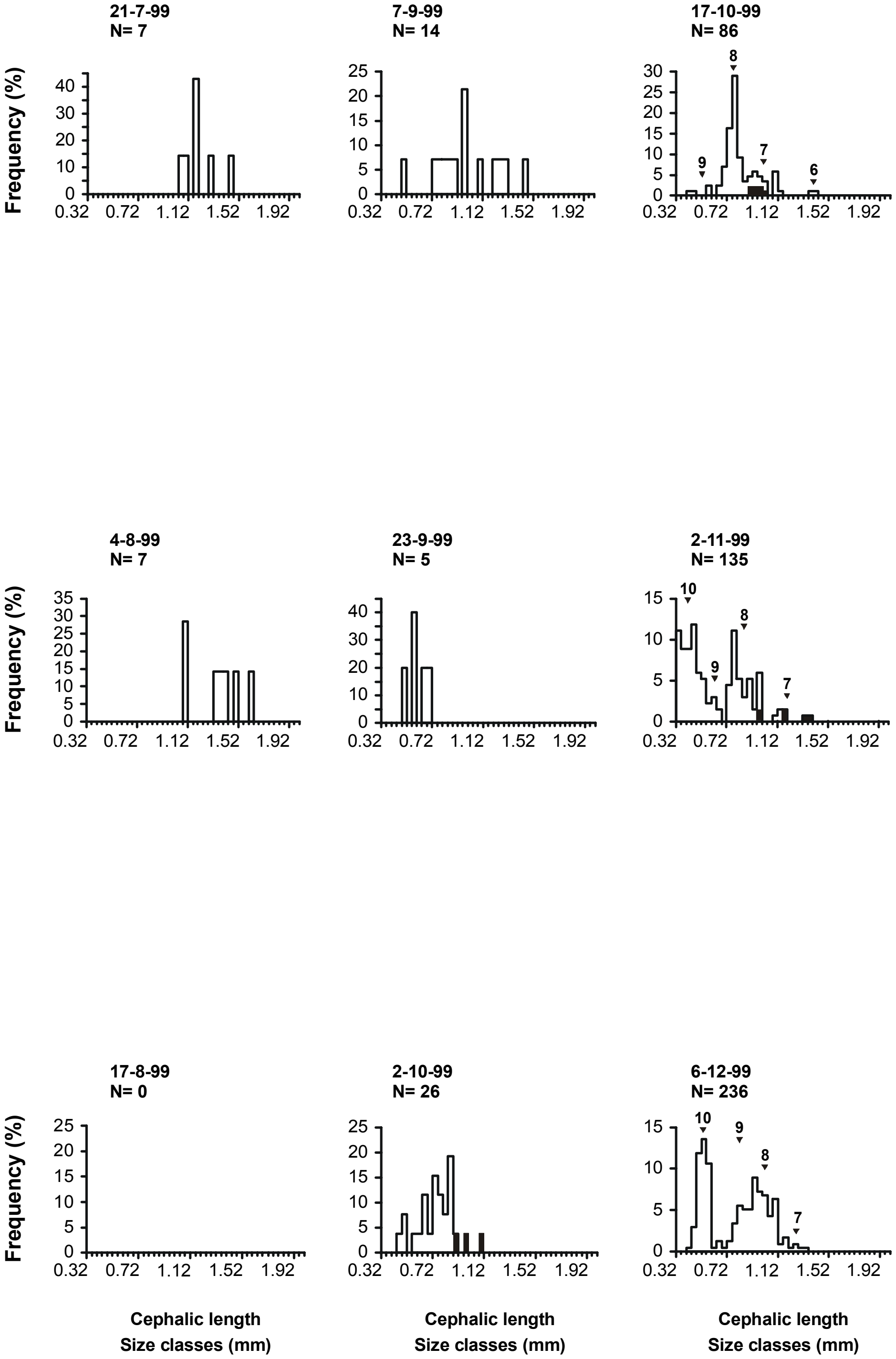

Figure 7 (continued)

Life cycle

Size-frequency analysis (figures 5 to 7) allowed to determine the cohorts to which males and gravid females belonged, and thus to assess their contributions to recruitment. Parental relations between existing cohorts and new ones that came out in the population during the study period could therefore be interpreted, permitting the comparison of the three studied populations with regard to life cycle characteristics (figure 10).

Cohorts born early in the reproductive period, *i.e.* spring, at Lavos and Collelungo, and late winter/early spring at Zouara, will in principle still reproduce in the same season, but will live less and, most probably will not survive the winter. On the other hand, cohorts born later in the reproductive period, i.e.

Table 2. Comparison of *Talitrus saltator* population's characteristics at different sites with regard to biology, life cycle, and production, based on data produced in the present study and from Williams (1978) *.
** - Estimated according to Wildish (1984; 1988 *in* O'Hanlon and Bolger, 1997).

Characteristic	Isle of Man (U.K.) Atlantic *	Lavos (Portugal) Atlantic	Collelungo (Italy) Mediterranean	Zouara (Tunisia) Mediterranean
Reproductive period	May to late August	March to September	April to September	February to October
Average sex ratio (♂/♀)	0.69:1	1.2:1	1.04:1	0.54:1
Age of males at sexual differentiation	12 to 16 weeks	± 4 weeks	± 3 weeks	± 4.5 weeks
Age of females sexual differentiation	12 to 16 weeks	± 6 weeks	± 5 weeks	± 5 weeks
Age of females at sexual maturation	-	± 10 weeks	± 8 weeks	± 8 weeks
Life span	18 to 21 months	7 to 11 months	6 to 9 months	6 to 8 months
Recruitment pattern	Univoltine	Bivoltine	Bivoltine	Bivoltine
Growth production (*P*)	-	0.74 $g.m^{-2}.y^{-1}$	0.115 $g.m^{-2}.y^{-1}$	0.61 $g.m^{-2}.y^{-1}$
Elimination production (*E*)	-	1.40 $g.m^{-2}.y^{-1}$	0.20 $g.m^{-2}.y^{-1}$	1.11 $g.m^{-2}.y^{-1}$
Average annual biomass (*B*)	-	0.13 $g.m^{-2}$	0.014 $g.m^{-2}$	0.084 $g.m^{-2}$
P/B	2.47 to 2.93 **	5.7	8.2	7.3
E/B	-	10.8	14.4	13.1

summer or early autumn, will live longer, going through winter, becoming sexually active and breeding only in the next reproductive period. Despite differences between the three study sites, this constitutes a consistent pattern. Therefore, all the studied populations produced two generations within the same reproductive period. Moreover, taking into account the probable parental relations between existing cohorts and new ones (figure 10), it appears that females from each cohort breed at least twice.

At the studied sites *Talitrus saltator* is a semiannual species, with iteroparous females appearing to produce at least two broods per year, and has a bivoltine life cycle, since the populations produce two generations per year (table 2).

Production Estimates

Length-weight relationships previously established were used in production estimates (see methods). Growth production (*P*) was estimated at 0.74 $g.m^{-2}.y^{-1}$ AFDW at Lavos, 0.12 $g.m^{-2}.y^{-1}$ AFDW at Collelungo, and 0.61 $g.m^{-2}.y^{-1}$ AFDW at Zouara, which for talitrids is approximately equivalent respectively to 17.7 $KJ.m^{-2}.y^{-1}$, 2.8 $KJ.m^{-2}.y^{-1}$, and 14.3 $KJ.m^{-2}.y^{-1}$ (Jørgensen *et al.*, 1991). Elimination production (*E*) was estimated at 1.40 $g.m^{-2}.y^{-1}$ AFDW (33.5 $KJ.m^{-2}.y^{-1}$) at Lavos, 0.20 $g.m^{-2}.y^{-1}$ AFDW (4.8 $KJ.m^{-2}.y^{-1}$) at Collelungo, and 1.11 $g.m^{-2}.y^{-1}$ AFDW (26.6 $KJ.m^{-2}.y^{-1}$) at Zouara (table 2). The average annual biomass ($\overline{B}$) (standing stock), was estimated at 0.13 $g.m^{-2}$ at Lavos, 0.014 $g.m^{-2}$ at Collelungo, and 0.084 $g.m^{-2}$ at Zouara, resulting on $P/\overline{B}$ ratios of 5.7 at Lavos, 8.2 at Collelungo, and 7.3 at Zouara, and $E/\overline{B}$ ratios of 10.8 at Lavos, 14.4 at Collelungo, and 13.1 at Zouara (table 2).

The analysis of the temporal variation of growth and elimination productions at the three study sites (figure 11) shows, at Lavos and Collelungo, that the highest values of growth production (*P*) were observed during spring and summer, as one should expect. At Zouara, however, the highest values were recorded in late winter and early spring, becoming extremely low throughout the summer. As for elimination production (*E*), at Lavos and Collelungo values increased during

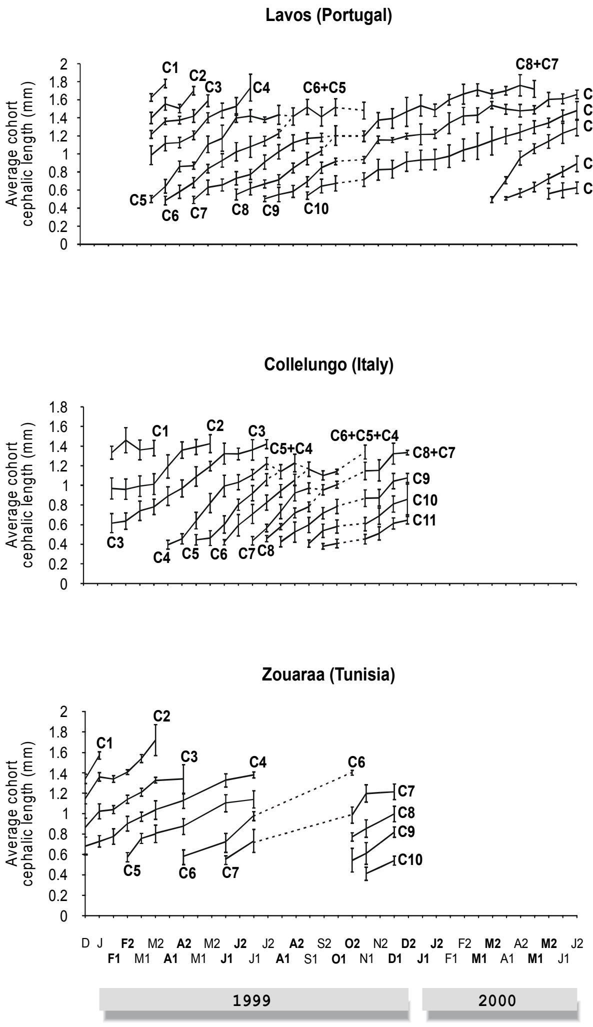

Figure 8. Estimated growth and life span (field growth data) of *Talitrus saltator* cohorts or groups of cohorts (average cephalic length ± standard deviation) at the three study sites. Broken lines indicate probable cohort merging or cohort evolution through time.

spring and summer periods, but were also augmented during winter, while at Zouara there was a clear peak from January to April, and again a small increase in autumn.

DISCUSSION

Talitrus saltator showed a pattern of aggregated distribution at all the three sites. Talitrids are usually associated with freshly deposited wrack (Marsden, 1991b), which was also confirmed with regard to *Talitrus saltator*. This patchiness is evident at small spatial scales, e. g. of the order of ¼ m^{-2}, but becomes diluted at larger scales, since no significant correlation was found between population density and drift material biomass when the whole set of replicates collected each date was accounted for. This is consistent with observations on *Talorchestia quoyana* in New Zealand, where no connection was found between density and kelp biomass, although spatial distribution was dependent on the availability of drift wrack (Marsden, 1991a; b).

Population densities were consistently higher at Lavos, in comparison with the two Mediterranean beaches. If, as in other talitrids (Pennings *et al*., 2000) the feeding preferences of *Talitrus saltator* at the three sites are basically similar, and if the debris has a similar value as food, the most probable explanation for the observed differences in density is the availability of drift wrack. In the Mediterranean, wrack supply to beaches depends on storms, while in the Atlantic coasts the tides may provide more regular supply, twice each day.

The pattern of variation of population density was very similar at Lavos and Collelungo, and clearly different at Zouara. Present results suggest that differences observed could be explained by a major displacement of *Talitrus saltator* from the beach to the dunes during the hotter months, while *Talorchestia brito*, a sympatric species at Lavos and Zouara, would tend to move from the dunes to the beach. Such interpretation would be consistent with results from other authors regarding burrowing and surface migration as behavioural responses to variations in temperature and sand moisture (Tsubokura *et al*., 1997; Morritt, 1998). Besides, it would also be supported by the fact that *Talorchestia brito* reaches the highest densities in the beach precisely during spring and summer, suggesting a combination of inter-specific competition and behavioural plasticity. However, there is not a sound explanation for the observed variation of population density, and there is an apparent contradiction with the observations reported by Charfi-Cheikhrouha *et al*. (2000), which suggested that *Talitrus saltator* tends to migrate from the dune to the shoreline in spring.

Spatial and temporal behavioural plasticity between the sympatric species *Talitrus saltator* and *Talorchestia brito* in relation to air humidity, sand temperature and moisture, atmospheric pressure, and tidal elevation was

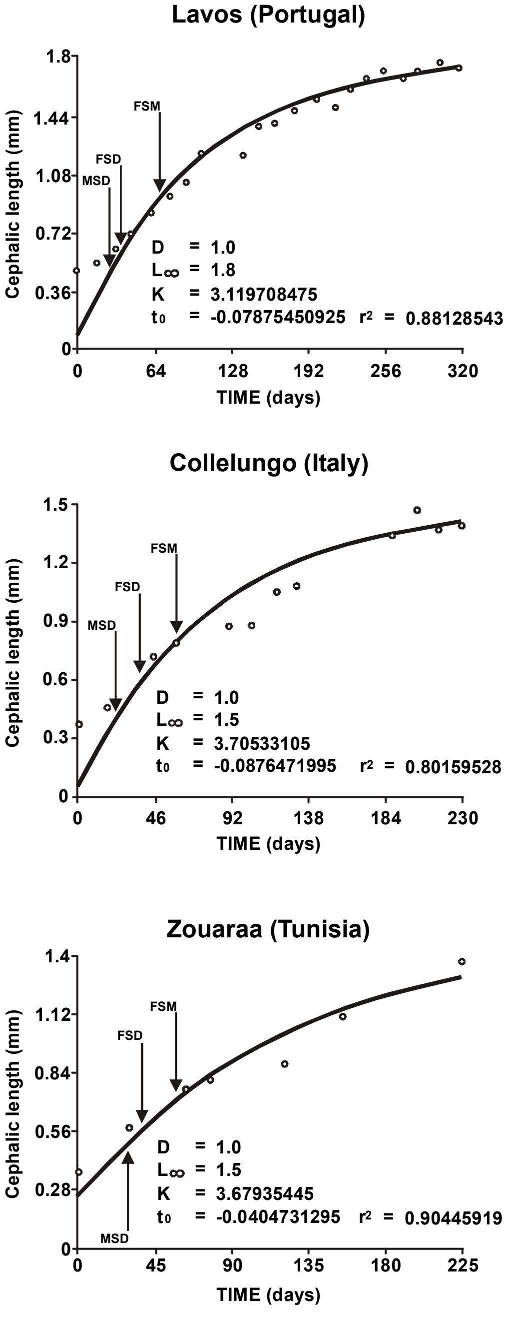

Figure 9. Individual growth model (Bertalanffy, 1957) of *Talitrus saltator* at the three study sites. The models were calibrated with field growth data from cohorts or groups of cohorts (plotted points). Model parameters are given; r^2 = correlation between predicted and observed values. MSD – male's sexual differentiation; FSD – female's sexual differentiation; FSM – female's sexual maturation.

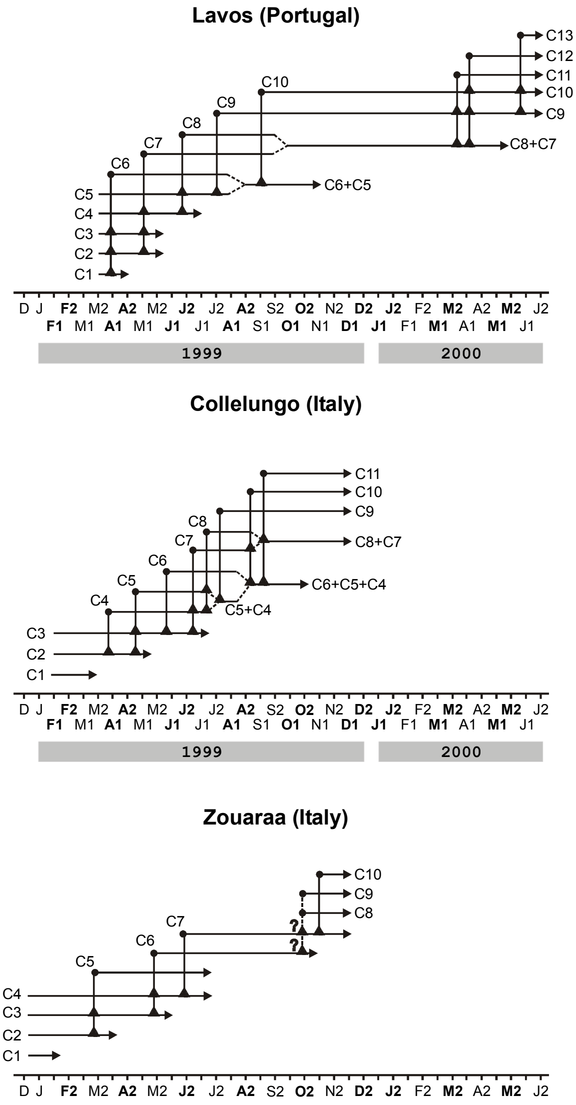

Figure 10. Analysis of the recruitment pattern of *Talitrus saltator* at the three study sites. The horizontal arrows represent the period during which each cohort was followed during the study period, starting in the solid circles. The assumed contributions of each cohort or group of cohorts are indicated (triangles).

observed in French Atlantic beaches (Fallaci *et al.*, 1999), and at the Zouara beach (Colombini *et al.*, 2002; Scapini *et al.*, 2002). The role of vertical separation in the litter as a factor avoiding inter-specific competition between *Talitrus* and *Orchestia* species from Tasmania has also been described (Richardson and Devitt, 1984; Richardson, 1993). Ecophysiological responses in regulating the talitrids spatial distribution and inter-specific competition are of obvious importance (Morrit and Spicer, 1999). For instance, species that lose more water through the gills have more constraints in terms of their spatial distribution on sandy beaches, being limited to areas of relatively higher humidity. This is illustrated

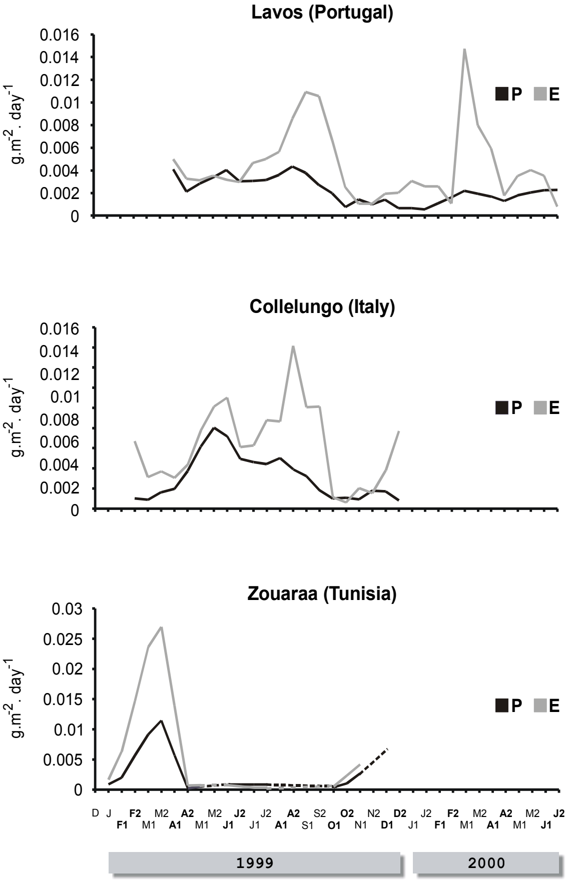

Figure 11. Analysis of the temporal variation of growth (*P*) and elimination (*E*) productions at the three study sites.

by the spatial competition between *Talorchestia quoyana* and *Transorchestia chiliensis* from New Zealand (Marsden, 1991 c), and the difference in distribution between *Talitrus saltator* and *Talorchestia brito* may be similarly explained. On the other hand, the role of burrowing and surface migration as behavioural responses to variations in temperature and sand moisture as been described for *Trinorchestia trinitatis* from Japan (Tsubokura *et al*., 1997), and some authors are of the opinion that behavioural adaptations to potentially desiccating conditions are more important than physiological mechanisms to reduce water loss (e. g. Hazlett, 1988). The fact that *Talitrus saltator* is almost the only talitrid species at Lavos and Collelungo (approximately 90% of the individuals collected), while at Zouara it occurs together with the sympatric *Talorchestia brito*, supports the suggestion that a combination of inter-specific competition and behavioural plasticity constitutes the most probable explanation for differences observed in the distribution of population abundance.

Recruitment took place from March and early April to late September at Lavos and Collelungo respectively, and from late February to early November at Zouara, corresponding to the longer reproductive period at the southern most study site. In the British Isles, farther to the north, *Talitrus saltator* reproduction occurs from May to late August (Williams, 1978). These two data sets represent the only available information on the annual patterns of reproduction of *Talitrus saltator*. A geographical pattern of variation emerges, with shorter recruitment periods in the north and longer in the south, which points towards temperature and photoperiod as major factors controlling gonadal maturation and the duration of the reproductive period (c.f. Williamson, 1951b; Bregazzi and Naylor, 1972). In this regard, data on *Talitrus saltator* are fully consistent with the pattern of geographical variation known among other talitrid species. For instance, *Orchestia gammarellus* reproduces from May to September, in the Baltic (Persson, 1999; 2001), and from April to August in South-Western British Islands (Cornwall) (Jones and Wigham, 1993). Closer to the equator, talitrids tend to reproduce through the year, e.g. *Pseudorchestoidea brasiliensis*, in Brazil (Rio de Janeiro) (Cardoso and Veloso, 1996), or *Talorchestia quoyana*, in New Zealand (Marsden, 1991b). Present results with *Talitrus saltator* reinforce the idea that large-scale distribution patterns do not correspond to fixed species physiology, as already suggested by Kevin and Spicer (1998) for *Orchestia gammarellus*.

During most of the study period, the sex ratio was favourable to males at Lavos and Collelungo, with male's proportion in the population decreasing just before the stronger recruitment periods. This might eventually be explained by wearing out of males in relation to reproductive activity, namely pre-copula, or perhaps by the displacement of females from the dunes to the beach. This second possibility is speculative, since no direct evidence of changes in zonation was ever found between males and females, although Marchetti and Scapini (2003) observed differences in orientation between males and females at

Zouara. This contrasts with the observed at Zouara where, with the exception of December 1999, females were dominant in the population. A sex ratio favourable to females appears to be the most common situation among talitrid populations, *e.g.* in *Orchestia gammarellus* (Jones and Wigham, 1993: Persson, 1999), *Peudorchestoidea brasiliensis* (Cardoso and Veloso, 1996), or *Talitrus saltator* (Williams, 1978). Thus, the reason for this sex-ratio is unclear. In sandy beach/dune systems, a non-homogenous distribution of the two sexes between the beach and the dunes might occasionally explain the differences observed. Parasitic infestation by *Paramarteilia orchestiae*, a trans-ovarilly transmitted parasite, has also been identified as a possible cause of sex ratio deviations towards male dominance in *Orchestia gammarellus*, *Orchestia mediterranea*, and *Orchestia aestuarensis* from European Atlantic and Mediterranean coasts (Ginsburger-Vogel and Magniette-Margault, 1981; Ginsburger-Vogel, 1989; 1991), but there happens to be no such study on *Talitrus saltator*. It is an interesting possibility but at the present stage, these results are insufficient to allow answering this question, and further research would be necessary to approach it.

The population density, expressed both as ind.m^{-2} and biomass.m^{-2} positively correlated with temperature. Regarding juveniles, a positive correlation was also found with sediment moisture, suggesting that younger individuals are probably more sensitive to dehydration, and concentrate closer to the water line. No other significant correlations were found between population features and environmental factors, but it is often extremely difficult to establish statistically significant links between population dynamics and environmental controls from field data (see for instance Marsden, 1991b).

Based on field data, there is always a relative uncertainty regarding the size of cohorts at the moment of detection due to sampling periodicity. Also newborn individuals may remain in the brood pouch, where the osmotic environment is under maternal control for variable periods, depending on the external conditions (Morritt and Spicer, 1999). Despite possible bias, field growth rates were estimated from cohort recognition and tracking. The results show that the population presenting the largest adults, both in terms of weight and body length was the one from the Atlantic, while the smallest individuals came from Italy, with individuals from the Tunisian population ranging in the middle. Morphological differences between Mediterranean and Atlantic populations of *Talitrus saltator* have been observed before (Scapini *et al*., 1999b), but it was then hypothesized that such differences would not correspond to a geographic cline, depending instead on local ecological features.

The life span estimations, as well as the minimum periods necessary for sexual differentiation and for female's sexual maturation after birth (table 2), were very different from observations on *Talitrus saltator* carried out in the British Isles (Cornwall), using approximately the same methodologies. There, life span was estimated at 21 months for males and 18 months for females, while sexual differentiation occurred 3 or 4 months after birth (Williams, 1978). Present results are nevertheless closer to life span estimations obtained for other talitrid species: 12 months for *Orchestia gammarellus* in the British Isles (Jones and Wigham, 1993), 6 to 8 months for *Orchestia meditterranea*, *Orchestia montagui*, and *Orchestia platensis* in the Mediterranean (Louis, 1974), 13 months for *Talorchestia quoyana* in New Zealand (Marsden, 1991a), or 12 to 21 months for *Pseudorchestoidea brasiliensis* in Brazil (Cardoso and Veloso, 1996). Life span among talitrids appears therefore to be extremely variable.

As a whole, these results, when combined with the ones from Williams (1978) and Scapini *et al*. (1999b), suggest that there might be a geographic cline variation in *Talitrus saltator* populations, with adult size and life span decreasing from Northern European populations towards the Mediterranean ones.

Regarding the life cycle characteristics, the three studied populations of *Talitrus saltator* produced two generations within the same reproductive period, and apparently females from each cohort breed at least twice. This typically characterizes bivoltin life cycles, involving iteroparous females (table 2), which contrasts with the univoltin life cycle observed farther to the North, in the British Isles (Williams, 1978). The same plasticity was found in the life cycles from talitrid species - for instance *Orchestia gammarellus* may vary from bivoltin, in the Baltic (Persson, 1999) to multivoltin in a sewage treatment works in Britain (Jones and Wigham, 1993) – and appears to be a common feature among amphipods that may eventually play a role in speciation processes (see Wildish, 1982).

With regard to growth production, higher values found in spring and summer at Lavos and Collelungo (table 2) are probably related to increased temperature and metabolism, and also for sure with more available food sources in the beaches. At Zouara, nevertheless, the extremely low values of both growth and elimination productions found through late spring and summer had certainly to do with the decrease of population density in the beach above discussed.

Increased elimination production is usually related with higher mortality rates, and this explanation is in a certain extent consistent with observations carried out at Lavos and Collelungo. In fact, higher mortalities of older, and therefore larger, individuals are expected to occur after reproductive efforts (spring and summer), and also as a response to more extreme conditions during winter. However, once again, population movements from the beach to the dunes may predictably contribute to an artificial increase of elimination production estimations, which may hide the real picture.

Values of growth and elimination production estimated in the present study (table 2) could not be directly compared with other results, since production estimations for *Talitrus saltator* are absent in the literature. A few estimations could nevertheless be found for other talitrid species: $P = 2.9$ to 7.2 g.m^{-2}.y^{-1} for *Talorchestia capensis* (DW) (Van Senus and McLachlan, 1986), approximately equivalent to 51.5 to 127.9 KJ.m^{-2}.y^{-1} (Jørgensen *et al*., 1991), with a $P/\overline{B}$ ratio of 2.25.y^{-1}, and $P = 0.3$ g.m^{-2}.y^{-1} AFDW (7.2 KJ.m^{-2}.y^{-1}) for *Pseudorchestoidea brasiliensis*, with a $P/\overline{B}$ ratio of 2.16 to 2.3.y^{-1} (Cardoso and Veloso, 1996).

The production values estimated in the present work are of the same magnitude of values found by Cardoso and Veloso (1996) in Brasilian sandy beaches, but are inferior to those estimated by Van Senus and McLachlan (1986) in South Africa. Differences observed do not appear to have any special meaning, and it is not recognisable any emergent pattern. Plausibly, different beaches simply offer different food resources, which must reflect on talitrids feeding habits and productivity. It is nevertheless worthy to note that at all the three sites studied $P/\overline{B}$ and $E/\overline{B}$ ratios founf for *T. saltator* were much higher than those found for *Talorchestia capensis*, and *Pseudorchestoidea brasiliensis*. It became therefore worthy to assess if these estimations are theoretically consistent.

Wildish (1984; 1988 *in* O'Hanlon and Bolger, 1997) proposed a general equation for amphipods, which relates growth production, biomass and life span (expressed in years), allowing to estimate $P/\overline{B}$ ratios from life span:

$$\log_{10} P{:}\overline{B} = 0.66 - 1.10\ (\log_{10} \textit{life span})$$

Applying this equation to life spans estimated for the three studied populations, the resulting $P/\overline{B}$ ratios are fully consistent with the field estimations. Moreover, for a life span of 18 to 21 months (Williams, 1978), the resulting $P/\overline{B}$ ratio will be 2.47 to 2.93, corresponding to approximately ½ of the annual turnover in the Lavos population, which again suggests a geographical cline.

At a local scale, from the conservation and management viewpoints, information on dominant species production and $P/\overline{B}$ ratios might be very useful to assess short and long term consequences of human actions, like for instance nourishment or bulldozing to increase primary dunes on beaches affected by coastal erosion (Petersen *et al*., 2000). As a whole, results from studies on talitrids reinforce the need to reserve the full range of translittoral habitats, as already suggested by Richardson *et al*. (1997), which will not necessarily be achieved by establishing reserve boundaries on the basis of vegetation associations.

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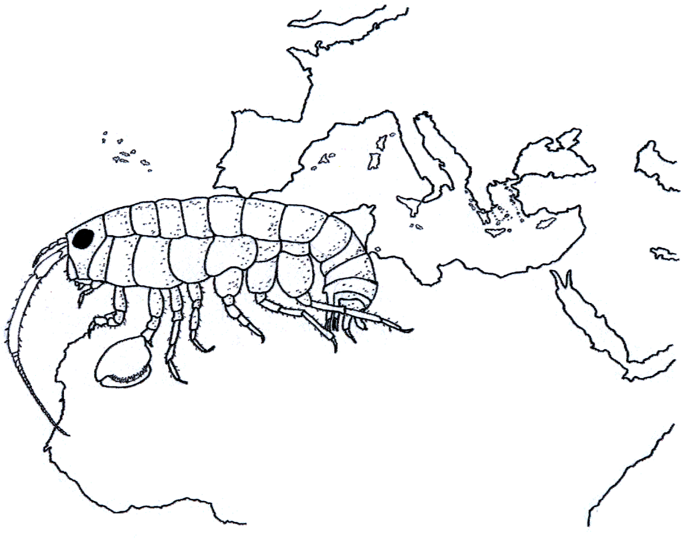
CHAPTER 3:

Comparison of *Talorchestia brito* (Amphipoda, Talitridae) biology, dynamics, and secondary production in Atlantic (Portugal) and Mediterranean (Tunisia) populations



Comparison of *Talorchestia brito* (Amphipoda, Talitridae) biology, dynamics, and secondary production in Atlantic (Portugal) and Mediterranean (Tunisia) populations

ABSTRACT

The biology, population dynamics, and production of *Talorchestia brito* was studied at two sandy beaches located on the Atlantic (Portugal) and on the Mediterranean (Tunisia) coasts. The seasonal variation in abundance and overall densities were similar in both populations. Reproduction occurred from February to September in the Atlantic, and from March to early November in the Mediterranean. Based on data from the Atlantic population, both abundance and the proportion of reproductive females were positively correlated with temperature, while the proportion of juveniles in the population was positively correlated with temperature and sediment moisture. In average, individuals from the Atlantic were larger and presented longer life spans than Mediterranean inhabitants. *Talorchestia brito* showed to be a semiannual species, with iteroparous females producing two broods per year, and a bivoltine life cycle. Growth production (P) was estimated at 0.19 $g.m^{-2}.y^{-1}$ AFDW (4.3 $KJ.m^{-2}.y^{-1}$) in the Atlantic population, and 0.217 $g.m^{-2}.y^{-1}$ AFDW (4.9 $KJ.m^{-2}.y^{-1}$) in the Mediterranean one. Elimination production (E) was estimated at 0.35 $g.m^{-2}.y^{-1}$ AFDW (7.9 $KJ.m^{-2}.y^{-1}$) in the Atlantic, and 0.28 $g.m^{-2}.y^{-1}$ AFDW (6.3 $KJ.m^{-2}.y^{-1}$) in the Mediterranean. The average annual biomass ($\overline{B}$) (standing stock), was estimated at 0.032 $g.m^{-2}$ in the Atlantic beach, and 0.029 $g.m^{-2}$ in the Mediterranean, resulting respectively in $P/\overline{B}$ ratios of 5.9 and 7.5 and $E/\overline{B}$ ratios of 10.9 and 9.6. Like other talitrids, *Talorchestia brito* exhibited geographic variation in morphometrical characteristics, sex ratio, growth rates, life span, and reproduction period, with the Atlantic population presenting a slower life history.

Key words: *Talorchestia brito*, biology, population dynamics, geographical variation, Atlantic, Mediterranean, sandy beaches.

INTRODUCTION

Talitrid amphipods constitute one of the dominant groups in sandy beach fauna (Dahl, 1945; 1952; McLachlan and Jaramillo, 1995), exhibiting a dynamic equilibrium with a changing environment. Talitrids' ecological relevance has justified worldwide studies, for instance with regard to their behavioural plasticity (e.g. Scapini *et al.*, 1993; 1995; Scapini and Fasinella, 1990; Mezzetti *et al.*, 1994), to the factors influencing their spatial distribution and oriented movements in sandy beaches (e.g. Borgioli *et al.*, 1999; Scapini *et al.*, 1999; Scapini and Quochi, 1992), their behavioural strategies (e.g. Fallaci *et al.*, 1999), genetic comparisons between populations (De Matthaeis *et al.*, 1995; Bulnheim and Schwenzer, 1999), bioaccumulation by talitrids and their role in biomonitoring (e.g. Rainbow *et al.*, 1989; Moore *et al.*, 1991; Fialkowski *et al.*, 2000).

Talitrids' reproductive strategies and their contribution to the energy balance in beach ecosystems are, however, still poorly understood. There are few studies on talitrids population biology (e.g. David, 1936; Palluault, 1954; Williams, 1978; Elkaïm *et al.*, 1985; Van Senus, 1988; Wildish, 1988; Marsden, 1991a; Jones and Wigham, 1993; Persson, 1999), and even less on their secondary production (e.g. Van Senus and McLachlan, 1986; Cardoso and Veloso, 1996; O'Hanlon and Bolger, 1997; Marques *et al.*, 2003). Moreover, most of these studies refer to different species at different sites, and very few really compare the life-history features of the same species on geographically distinct beaches. Since different beaches offer diverse environmental conditions (e.g. temperatures, food resources, humidity, exposure to predators, substrate characteristics, exposure to waves and tidal excursions), different biological features are to be expected, as illustrated by a recent study on *Talitrus saltator* (Marques *et al*., 2003).

The sandhopper *Talorchestia brito* is widely distributed along the European Atlantic coast and on Western Mediterranean, occurring on more or less exposed beaches, often sympatrically with *Talitrus saltator*. With the exception of some short notes on its ecology (Lagardère, 1966; Vader, 1970), there were no studies on *Talorchestia brito*'s biology, population dynamics and secondary production. In the present work these issues are analysed through a comparative study of two populations, one from the Atlantic and the other from the Mediterranean.

MATERIALS AND METHODS

Study Sites

Two sets of data were provided by samples collected at two very exposed sandy beaches: Quiaios (40º12'21'' N 8º53'48'' W), on the Western Coast of Portugal (Atlantic) and Zouara (37°0'41"N 08°53'26"E), on the North-Western Coast of Tunisia (Mediterranean) (figure 1). Both study sites are relatively undisturbed beaches where the input of beach debris was limited. The main differences between the two study sites are summarised in table 1. More extensive details regarding the characteristics of these two beaches, including the identification of existing and potential human impacts and pressures are provided in a previous paper (Marques *et al*., 2003).

Sampling Programme

Quantitative samples were taken from the sandy beach communities at the two study sites. The sampling period lasted from January 1999 to June 2000, at Quiaios (Atlantic), and from December 1998 to December 1999 at Zouara (Mediterranean), respectively 18 and 12 months. Although logistic constraints did not allow sampling exactly at the same time, there was a significant time overlap of field work at the two sites. The study period was longer at Quiaios in order to obtain a larger data set, which was considered necessary for further modelling development. Two teams (Tunisian and Portuguese) were involved in the sampling effort, and the field methodologies were previously inter-calibrated through reciprocal visits to both sites. The sampling programme followed the field work protocol already described by Marques *et al*. (2003).

The influence of environmental factors on the *Talorchestia brito* population was investigated at Quiaios. For this purpose, debris quantity (potential food g.m^{-2}), organic matter of the sediment as ash free dry weight (AFDW) and sediment moisture were determined according to the procedures described in Marques *et al.* (2003), Meteorological data during the study period were obtained from the nearest weather station, including average daily precipitation, maximum and minimum daily temperatures, visibility, cloudiness, wave height, wave period, and wind velocity.

Laboratory Procedures

Field samples were processed at two laboratories in Portugal (Coimbra) and Tunisia (Tunis), respectively. The laboratory procedures used for the biometric and biological analysis, namely cephalic length (CL) measurements, individuals sexing, and classification of embryos are described in Marques *et al.* (2003). When necessary, total length (TL) was estimated from cephalic length (CL) through the following equations:

$$TL = -3.22705 + 13.02842CL$$

n = 164, $r^2 = 0.93$ for the Quiaios population

$$TL = -0.62306 + 9.49091CL$$

n = 148, $r^2 = 0.89$ for the Zouara population

The quantitative nature of the field sampling procedure together with animals' manipulation caused gravid (mature) females to drop an undetermined number of embryos from brood pouches, which made any further significant statistical analysis unrealistic regarding broods mortality and egg dimensions.

The relationships between length and weight of the individuals were analysed each season (spring, summer, autumn, and winter). For this purpose 150-200 randomly sampled specimens were weighed each time (AFDW, after combustion at 450^{o} C during 3 h) with a

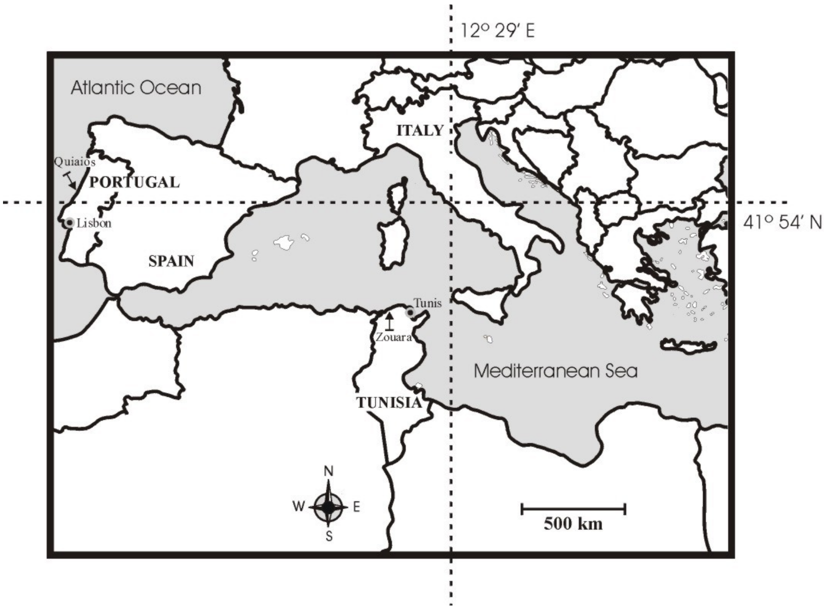


Figure 1. Location of the two sampling stations: Quiaios (Atlantic, Western Coast of Portugal) and Zouara (North Western Coast of Tunisia).

10^{-5} mg precision, following the same approach described in Marques *et al.* (2003). Four significantly different (analysis of variance; $p<0.05$) seasonal equations were estimated (table 2).

Data Analysis

The spatial distribution of the studied populations was analysed using the index $I = S^2/\overline{X}$ according to Elliot (1977). Multiple regression models were developed based on data from Quiaios (Atlantic), correlating density, sex ratio, percentage of gravid females, and percentage of juveniles in the population with physicochemical environmental factors. As in a previous study (Marques *et al.*, 2003), the models were fitted with data following the Stepwise Regression method using the MINITAB 12.2 software package.

Field growth rates were estimated by tracking modal distributions recognisable in successive sample dates through size-frequency analysis, following a methodology successfully used before (Marques *et al.*, 1994, 2003; Lillebø *et al.*, 1999; Pardal *et al.*, 2000). Modal distributions are in this case assumed to result from pulses in recruitment, conventionally referred to as cohorts. Computations were performed using the ANAMOD software (Nogueira, 1992), based on the probability paper method (Harding, 1949), as performed by Cassie (1954; 1963). The reliability of the method was tested employing both the χ^2 and G tests ($p \leq 0.05$).

Field growth data were fitted to the Von Bertalanffy's growth model (Bertalanffy, 1957), and previously applied with satisfactory results (e.g. Marques *et al*, 2003):

$$Lt = L\infty\,(1 - e^{-K\,(t-t0)})$$

Where:
Lt - length of the organism at a given moment t;
L∞ - maximum possible length of the organism;
t - given time instant;
t_o - instant in which the organism would have a length = 0;
K - intrinsic growth rate.

Growth (P) and elimination (E) productions, as well as $P/\overline{B}$ and $E/\overline{B}$ ratios, were estimated based upon cohort recognition, according to a method derived by Allen (1971) and fully described in a previous paper (Marques *et al.*, 2003).

RESULTS

Spatial Distribution and Density

The two studied populations presented contagious spatial distribution, corresponding to values of *I* always higher than 1 (Elliot, 1977). At both sites a greater number of individuals were concentrated in the intertidal zone, almost always just below high water mark, occupying a more restricted and seaward area than the sympatric species

Table 1. Differences observed between the two sandy beaches used as sampling sites.

Characteristic	Quiaios (Atlantic)	Zouara (Mediterranean)
Width of the beach (m)	100	50
Average slope (%)	1.8	3
Tidal range (m)	2 - 3.5	0.1 - 0.2
Extension of the intertidal area (m)	Neap tides: 50 Spring tides: 75	Tides frequently hidden by local wave action
Other (m)	Foredune height: 2.5 – 3	First dune belt height: 20 m

Table 2. Estimated seasonal length and weight equations for *Talorchestia brito* at the two sampling sites.

	Atlantic	Mediterranean
Winter	$AFDW = 0.003256\ CL^{3.98217}$	$AFDW = 0.003365\ CL^{3.97211}$
Spring	$AFDW = 0.002658\ CL^{4.18694}$	$AFDW = 0.002762\ CL^{4.15690}$
Summer	$AFDW = 0.002323\ CL^{3.92355}$	$AFDW = 0.002434\ CL^{3.8835}$
Autumn	$AFDW = 0.00412\ CL^{4.94227}$	$AFDW = 0.00423\ CL^{4.90232}$

Talitrus saltator, also present.

The seasonal variation in density followed a similar pattern at the two study sites: densities always reached the lowest values in winter, followed by a rapid increase from early spring up to a maximum in May/June. Then a slight decrease occurred during the summer, followed by a second peak in October/November, even stronger than the first one at Zouara, and a gradual decrease from late autumn until the next winter (figure 2).

Period of Reproduction and Sex Ratio

The occurrence of reproductive females (figure 3A - B), consisting of both gravid and mature females, and the appearance of new juvenile cohorts in the population (figure 3A - B and figures 4 for some examples) allowed identification of the reproductive period. Recruitment took place from February to September at Quiaios, with new cohorts being recognised in February, April, June, July, August and September. In Tunisia, the reproductive period was longer, from March to early November, with new cohorts detected in March, April, July, August, September and November (figure 5).

The percentage of juveniles in the population (figure 3A, B) showed a seasonal pattern of variation at Quiaios, with a first peak in late spring, followed by a small decrease in early summer, a second and strongest peak in August and September, another short dropping in early autumn, and a last peak in October and November, just before winter. Although reproduction started in early February, the strongest breeding took place from late spring to early autumn, which is consistent with the variation in the proportion of reproductive females (figure 3A). At Zouara, although data suggest that recruitment was stronger during summer, the percentage of juveniles in the population does now show any clear pattern of variation (figure 3B).

Sex ratios (males/females) were clearly different in the two populations (figure 3C, D). While in Quiaios the sex ratio was clearly male biased (average 1.2:1), except for a short time in spring (April/May) and autumn (September/October), in Zouara the population was clearly dominated by females (average 0.453:1), except in middle spring (April/May).

Influence of Environmental Factors on the Population Structure

Multiple regression models were established using complete data sets on the biological variables (population density, population biomass, sex ratio, percentage of juveniles in the population, percentage of

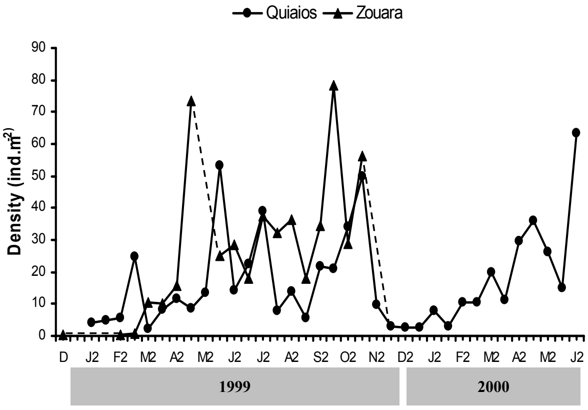


Figure 2. Variation of *Talorchestia brito* population density in the Atlantic (western coast of Portugal, Quiaios beach) and in the Mediterranean (north western coast of Tunisia, Zouara beach). Sampling periodicity took place every 15 days. Broken lines indicate probable density evolution when data were insufficient.

reproductive females over the total female population) and physicochemical factors determined at each sampling date in Quiaios. The average values and range of variation of physicochemical factors in Quiaios during the 18 months study period are summarised in table 3.

Stepwise multiple regression analysis revealed that population density (*D*) and the proportion of reproductive females (*PFrep*) were positively correlated with temperature (*T*). Moreover, the percentage of juveniles in the population (*PJ*) was positively correlated with temperature (*T*) and sediment moisture (*SM*). The following regression models describe these relationships:

$$ln\ (1+D) = 1.22 + 0.101\ T$$
$$(r^2 = 0.4;\ p = 0.000)$$

$$PFrep = -13.8 + 1.72\ T$$
$$(r^2 = 0.495;\ p = 0.000)$$

$$PJ = -24.6 + 2.60\ T + 4.79\ SM$$
$$(r^2 = 0.51;\ p = 0.000 \text{ for temperature and } p = 0.022 \text{ for sediment moisture}).$$

Field Growth Rates and Life Span

Size-frequency polymodal distributions were analysed for recognizable cohorts (figures 4, for some examples). Three cohorts (C1, C2, and C3) were identified in Quiaios at the first sampling date (21/01/99) (figure 4), and 10 new cohorts, presumably corresponding to new recruitments, were further identified during the 18 months study period (figure 5A) (χ^2 and G tests not significant; p ≥ 0.05). The population therefore produced 6 new cohorts in Quiaios during 1999 (C4, C5, C6, C7, C8, C9), recruiting between February and September, and 4 other new ones from February to June 2000 (C10, C11, C12, and C13, respectively), which confirmed the recruitment pattern.

At Zouara, the total duration of the study period was only 12 months. Four cohorts (C1, C2, C3, and C4) were recognised at the first sampling for which enough individuals were collected to perform modal analysis (16/03/99). Taking into account the average cephalic length at the moment of detection, cohort C4 was assumed as new born. Additionally, 6 new distributions were detected in the next 9 months (figure 4). The Zouara population produced therefore 7 new cohorts during 1999 (C4, C5, C6, C7, C8, C9, C10), recruiting between March and November (figure 5B). As expected, comparing the two populations, the rhythm of recruitment was higher in the Mediterranean.

Table 3. Average (A) values and standard deviation (SD) of physicochemical factors at Quiaios beach (Western Coast of Portugal) regarding the period from January 1999 to June 2000.

	A	SD
Temperature (ºC)	15.02	4.91
Precipitation (mm)	2.36	5.49
Sediment moisture (%)	2.64	0.95
Organic matter content in sediments (%)	0.19	0.35
Detritus (g.m^{-2})	2.02	1.82
Wind velocity (m.s^{-1})	4.05	3.03
Cloudiness	3.97	2.68
Visibility	6.11	1.03
Wave height (m)	0.06	0.33
Wave period (s)	0.12	0.65

Minimum and maximum average size of cohorts, respectively, at the moment of detection and of disappearance, varied as a function of study sites (figure 5). At Quiaios,

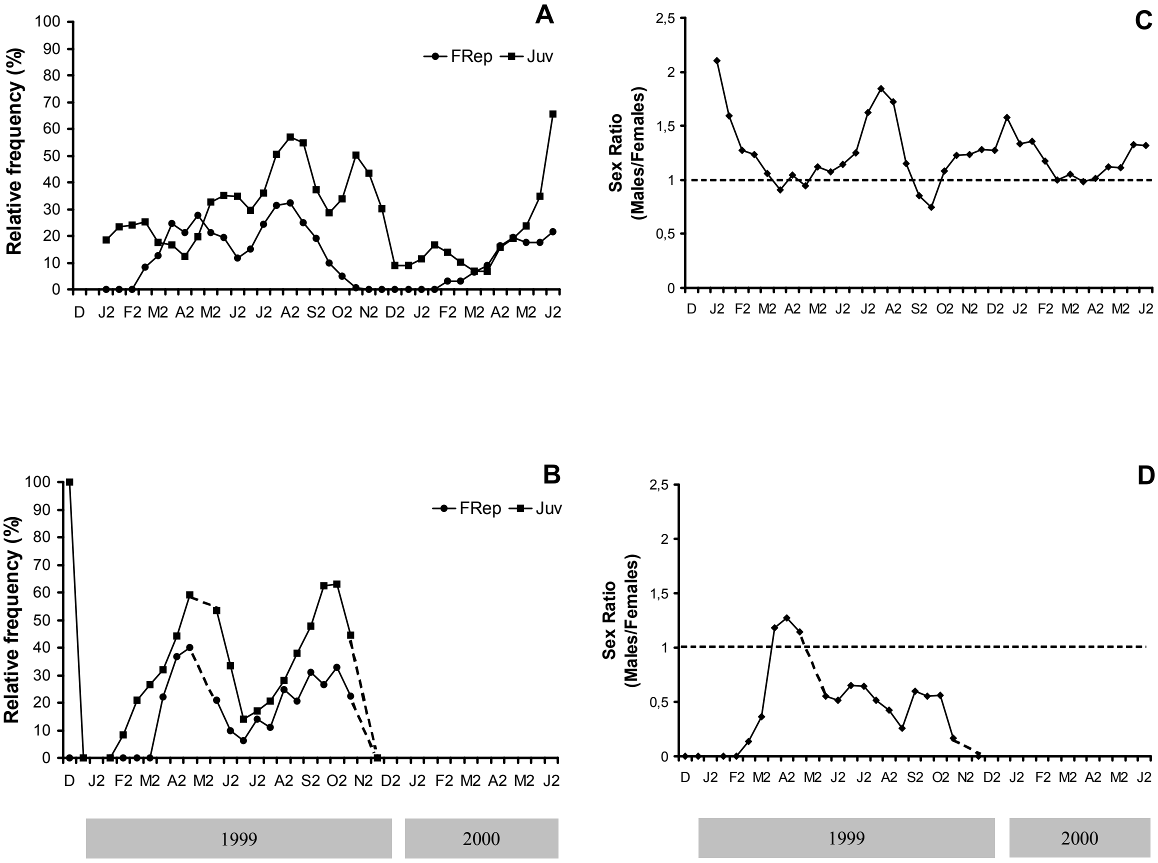


Figure 3. Variation of biological features of *Talorchestia brito*. (A) Variation of gravid females in the total female population, and of juveniles in the population, in the Atlantic; (B) Variation of gravid females in the total female population, and of juveniles in the population, in the Mediterranean; (C) Variation of sex ratio in the Atlantic; (D) Variation of sex ratio in the Mediterranean. Broken lines indicate probable evolution when data were insufficient.

the minimum average cephalic length (CL) of new cohorts ranged from 0.46 (spring) to 0.6914 mm (late winter) (2.77 - 5.78 mm TL), while the maximum average CL ranged from 1.1826 to 1.52 mm (12.18 - 16.58 mm TL). At Zouara, the minimum ranged from 0.4193 to 0.5023 mm CL (3.36 - 4.14 mm TL), and the maximum from 1.1242 to 1.36 mm CL (10.05 - 12.28 mm TL). The Atlantic population therefore presented the largest newborn and the largest adult individuals, which is consistent with the known variation of Gammaridea life history patterns as a function of latitude (Wildish, 1982, 1988; Sainte-Marie, 1991).

Growth was continuous throughout life but growth rates varied as a function of size and temperature, being higher during early life stages, and apparently also during spring and summer (figure 5). This was a recognizable pattern at Quiaios, but less clear at Zouara. Life spans were estimated at 6 (spring or summer cohorts) to 9 (autumn or winter cohorts) months for the Atlantic population and 5 (spring or summer cohorts) to 8 (autumn or winter cohorts) months for the Mediterranean one (table 4). Therefore, as a pattern, cohorts born in the beginning of the reproductive period showed a tendency to have shorter lives, while cohorts born near the end of the reproductive period over-wintered and bred in the next breeding season (figure 5), exhibiting longer life spans.

Growth data sets from the two sites were used to calibrate the growth model, providing a different set of parameters in each case (figure 6). According to the model: a) growth was faster in the early life stage phases (figure 6); b) the minimum period necessary for male sexual differentiation after birth was estimated at approximately 5 weeks in Quiaios and 4 weeks in Zouara; c) the period required by females to attain sexual differentiation after birth was estimated at approximately 7 weeks

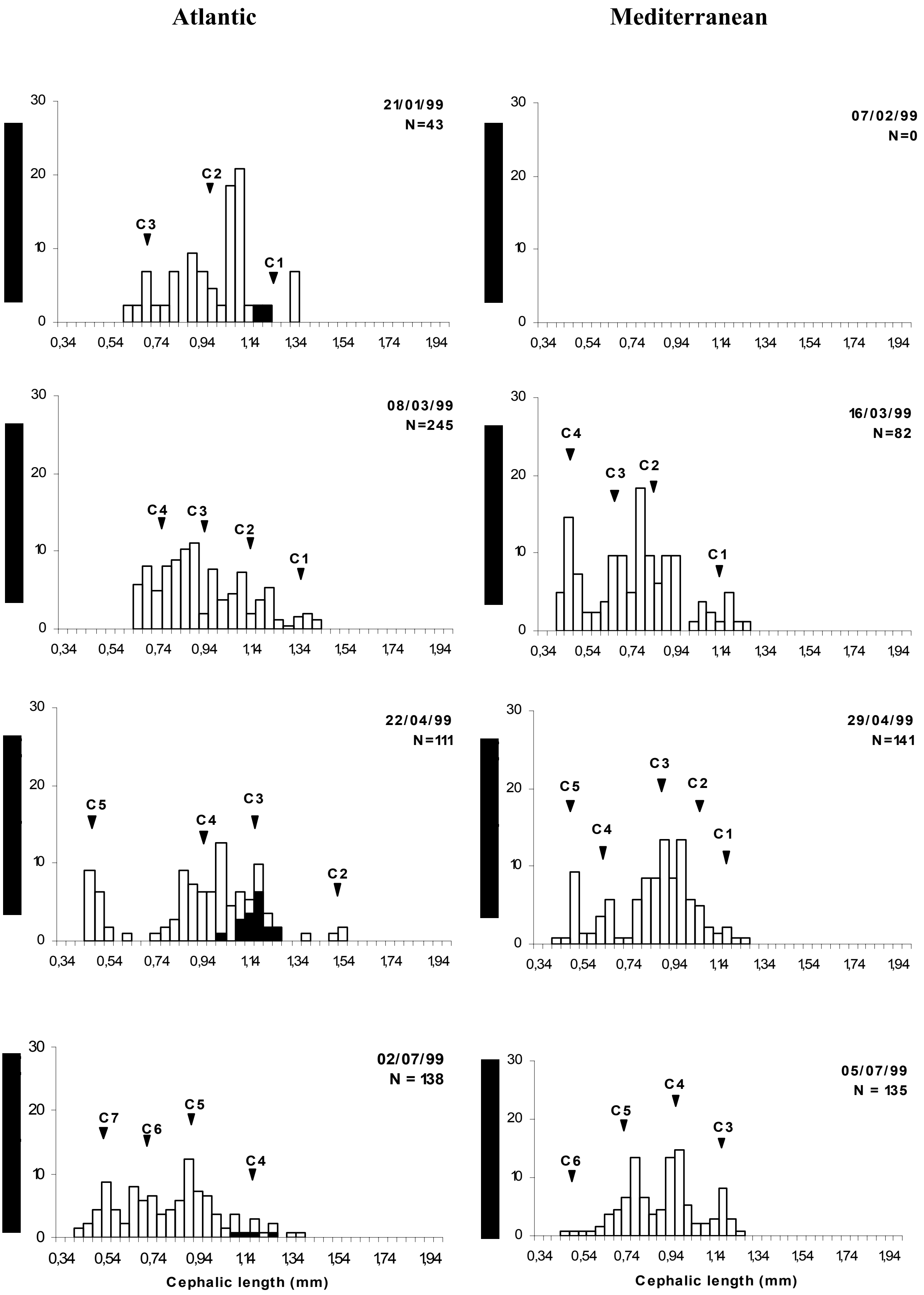


Figure 4. Size-frequency distribution of *Talorchestia brito* at the Atlantic (Quiaios) and at the Mediterranean (Zouara). Sampling dates are indicated. N = number of measured individuals. Arrowheads indicate average cephalic length of the numbered cohorts. Black areas indicate gravid females.

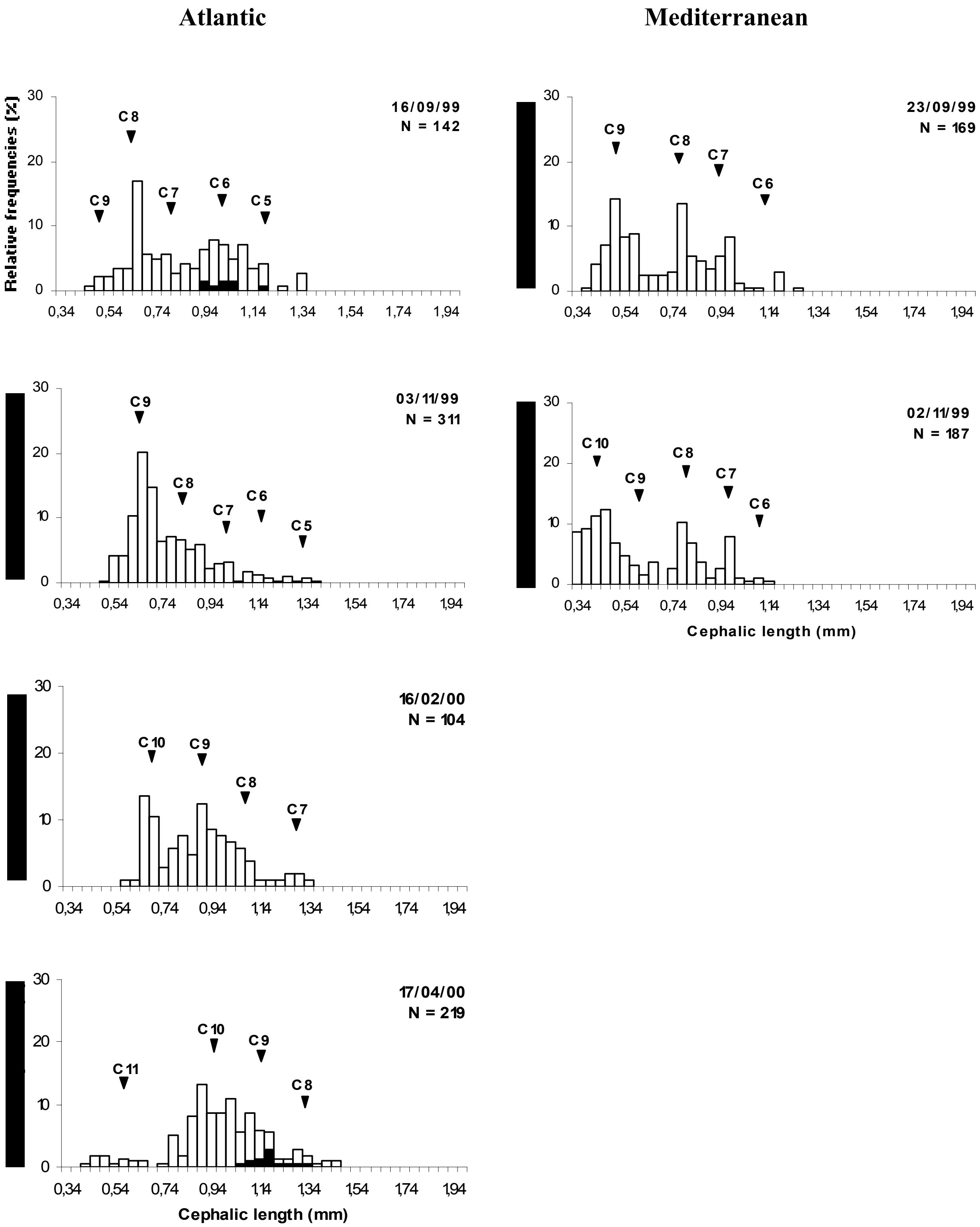


Figure 4 (continued)

in Quiaios, and 5 weeks at Zouara; d) the period necessary for female sexual maturation after birth was estimated at approximately 15 weeks in Quiaios and 10 weeks at Zouara (table 4). Sexual differentiation therefore tended to occur earlier in males than in females. Female

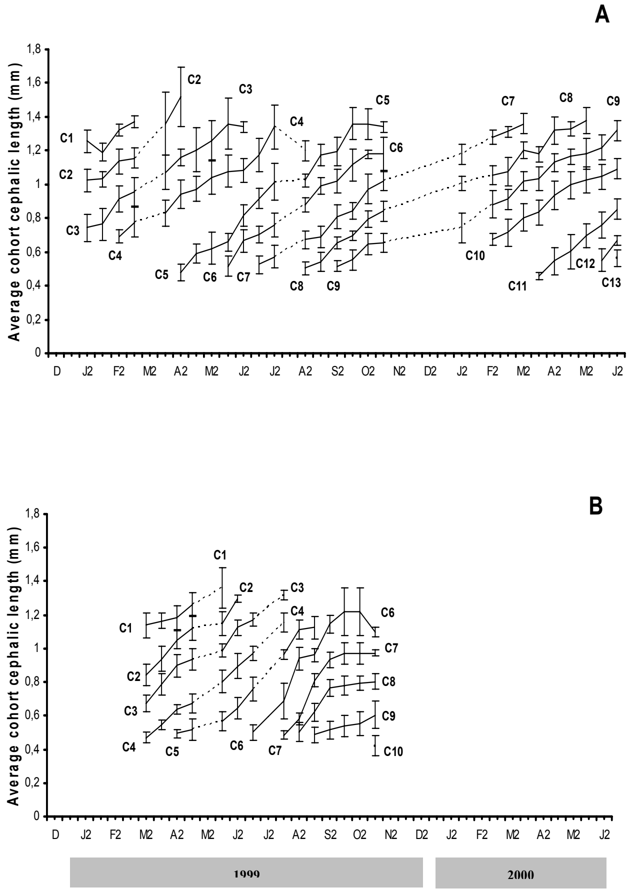


Figure 5. Estimated growth and life span (field growth data) of *Talorchestia brito* cohorts (average cephalic length ± standard deviation) at the two study sites. Broken lines indicate probable cohort evolution through time. (A) Atlantic, western coast of Portugal (Quiaios); (B) Mediterranean, north western coast of Tunisia (Zouara).

sexual maturation moreover occurred earlier in the Mediterranean population than in the Atlantic one.

Life Cycle

Size-frequency analysis (figure 4) allowed determination of the cohorts to which males and reproductive females belonged. The analyses of probable parental relations between the existing cohorts and the new ones recruited during the study period also allowed comparison of the life cycle characteristics of the two populations (figure 7).

As a pattern, cohorts born in the beginning of the reproductive period, i.e. late winter (Quiaios) and spring (Quiaios and Zouara), reproduced in the same season, exhibiting shorter life spans and most probably not surviving the winter. On the contrary, cohorts born later in the breeding season, i.e. summer and autumn, lived longer, over wintering, becoming sexually active, and breeding only in the next spring. Both populations appeared to produce two generations within the same reproductive period. Females from each cohort breed apparently twice a year (figure 7). At both sites, therefore, *Talorchestia brito* (a) behaves like a semiannual species, with iteroparous females producing two broods per year and (b) exhibits a bivoltine life cycle, with populations producing two generations per year (table 4).

Table 4. Comparison of *Talorchestia brito* population's characteristics at the study sites with regard to biology, life cycle, and production, based on data produced in the present study.

Characteristic	Quiaios (Portugal) Atlantic	Zouara (Tunisia) Mediterranean
Reproductive period	February – September	March – November
Average sex ratio (♂/♀)	1.2:1	0.453:1
Age of males at sexual differentiation	± 5 weeks	± 4 weeks
Age of females sexual differentiation	± 7 weeks	± 5 weeks
Age of females at sexual maturation	± 15 weeks	± 10 weeks
Life span	6 to 9 months	5 to 8 months
Recruitment pattern	Bivoltine	Bivoltine
Growth production (*P*)	$0.19\ g.m^{-2}.y^{-1}$	$0.217\ g.m^{-2}.y^{-1}$
Elimination production (*E*)	$0.35\ g.m^{-2}.y^{-1}$	$0.278\ g.m^{-2}.y^{-1}$
Average annual biomass (*B*)	$0.032\ g.m^{-2}$	$0.029\ g.m^{-2}$
P/B	5.9	7.5
E/B	10.9	9.6

Production Estimates

Length-weight relationships were used in production estimates. Growth production (*P*) was estimated at $0.19\ g.m^{-2}.y^{-1}$ AFDW in Quiaios, and $0.217\ g.m^{-2}.y^{-1}$ AFDW in Zouara, which for talitrids is approximately equivalent to 4.3 KJ.m^{-2}.y^{-1}, and 4.9 KJ.m^{-2}.y^{-1} respectively (Jørgensen *et al.*, 1991). Elimination production (*E*) was estimated at 0.35 g.m^{-2}.y^{-1} AFDW (7.9 KJ.m^{-2}.y^{-1}) in Quiaios, and 0.28 g.m^{-2}.y^{-1} AFDW (6.3 KJ.m^{-2}.y^{-1}) in Zouara (table 4). The average annual biomass ($\overline{B}$) (standing stock), was estimated at 0.032 g.m^{-2} in Quiaios, and 0.029 g.m^{-2} in Zouara, resulting respectively in $P/\overline{B}$ ratios of 5.9 and 7.5 and $E/\overline{B}$ ratios of 10.9 and 9.6 (table 4).

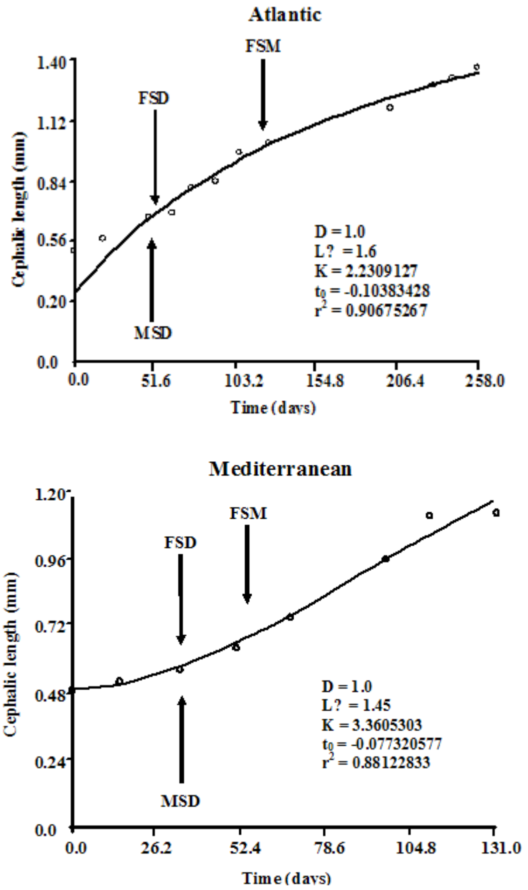


Figure 6. Individual growth model (Bertalanffy, 1957) of *Talorchestia brito* at the two study sites. The models were calibrated with field growth data from cohorts (plotted points). Model parameters are given; r^2 = correlation between predicted and observed values (see methods for details). MSD – male's sexual differentiation; FSD – female's sexual differentiation; FSM – female's sexual maturation.

Growth and elimination productions were analysed with regard to their temporal variation (figure 8). In Quiaios, growth production (*P*) was higher in autumn, while in Zouara it was roughly constant throughout the year. Variations in elimination production (*E*) were much stronger, with the highest values from spring to autumn in Quiaios, and during autumn in Zouara. A consistent comparison of the temporal patterns of variation nevertheless became difficult due to the lack of a bigger data set concerning the Zouara population.

DISCUSSION

Talorchestia brito showed an aggregated pattern of distribution. Since it feeds mainly on the interstitial flora (Vader, 1970) such patchy distribution may be related to the distribution of the stranded surf zone diatoms, as proposed by Colombini *et al.* (2002). The restricted diet of this species may also explain why, despite differences in the range of tidal excursions between the Atlantic and Mediterranean coasts, densities in Quiaios and Zouara populations were similar.

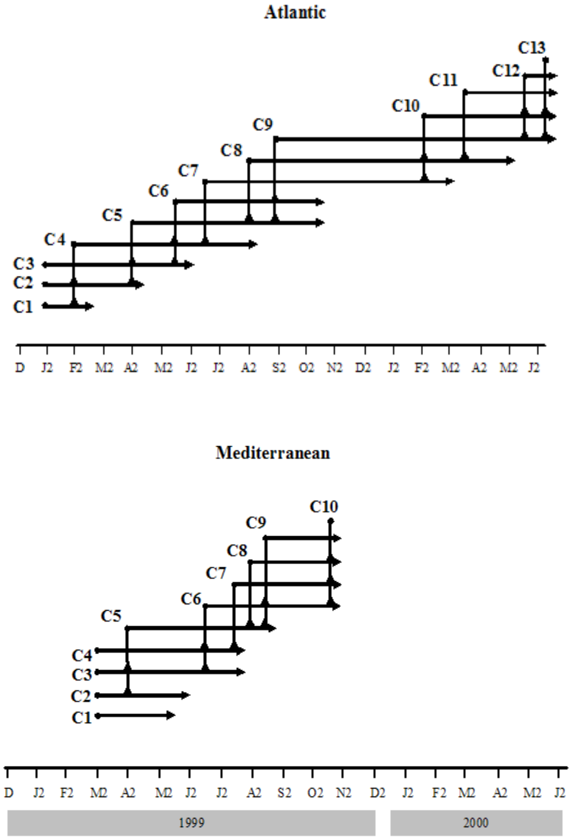


Figure 7. Analysis of the recruitment pattern of *Talorchestia brito* at the two study sites. The horizontal arrows represent the period during which each cohort was followed during the study period, starting in the solid circles. The assumed contributions of each cohort is indicated (triangles).

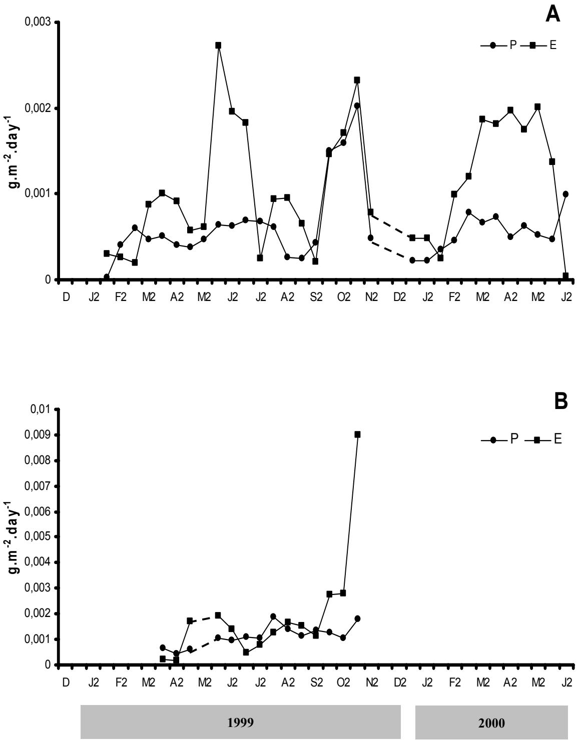


Figure 8. Temporal variation of growth (*P*) and elimination (*E*) productions at the two study sites. (A) Atlantic, western coast of Portugal (Quiaios); (B) Mediterranean, north western coast of Tunisia (Zouara). Broken lines indicate probable evolution when data were insufficient due to sampling constraints.

The seasonal variation in density followed a comparable pattern in Quiaios and Zouara. This reflects a similar population dynamics, despite differences in life history traits. In fact, the increase in density in spring, summer and early autumn is a natural consequence of recruitment, while the general decrease observed in late autumn results from the death of older individuals after the breeding season. Minimum densities during winter obviously suggest that alongshore and sediment depth distributions vary as a response to environmental constraints (Williams, 1995; Tsubokura *et al*., 1997; Morritt, 1998). Nevertheless, the extremely drastic reduction of the population in Zouara during the winter may be apparent, and two alternative explanations could be considered: a) a mass migration from the beach to the dunes, completely changing the horizontal distribution, as suggested by Marques *et al.* (2003) and b) a displacement of the burrow zone into deeper layers where a more stable microclimatic habitat is achieved (Tsubokura *et al.,* 1997), as observed in populations from SW France (Lagardère, 1966).

Talorchestia brito showed a more restricted and seaward distribution in comparison with *Talitrus saltator*'s, which is consistent with previous observations on the French Atlantic coast (Fallaci *et al*., 1999) and in Zouara (Colombini *et al*., 2002; Scapini *et al*., 2002). As suggested by these authors, this may reflect the presence of specific mechanisms of spatial and temporal behavioural plasticity between these sympatric species in relation to distinct trophic and microclimatic needs, possibly to avoid inter-specific competition. For instance, smaller body sizes and higher transpiration rates of several talitrid species, in comparison with *Talitrus saltator*, may indicate lower desiccation tolerances, which could restrict their spatial distribution to areas of relatively higher moisture content (Morritt, 1987). Together with the differences in feeding preferences (Vader, 1970; Williams, 1978; Morritt, 1987) and migratory behaviour (Fallaci *et al*., 1999), this could explain differences in spatial distribution between *T. saltator* and *T. brito* (this study and Marques *et al*., 2003).

In the present study, the reproductive period was somewhat longer in Tunisia. In Netherlands, *Talorchestia brito* reproduces from June to September (Vader, 1970), and in SW France from March to October (Lagardère, 1966). Although these four data sets represent to our knowledge the only available information on this species annual pattern of reproduction, a clear geographical pattern of variation emerges from their analysis. Recruitment periods are shorter at the northern most part of *T. brito* European distribution, becoming longer as a function of a decrease in latitude. The combined seasonal changes in temperature and photoperiod may therefore act as major controlling factors regarding gonadal maturation and duration of reproductive period, as proposed for the sympatric species *Talitrus saltator* (e.g. Bregazzi and Naylor, 1972). The fact that the same pattern has been observed in other talitrid species reinforces this hypothesis. For instance, *Orchestia mediterranea* reproduces from April to October, in Great Britain, March to November in France, and throughout the year in the Morocco coast (Elkaïm *et al*., 1985), and *T. saltator*, reproduces from May to September in the British Isles (Williams, 1978), from early March to late September in Portugal (Atlantic) and Italy (Mediterranean), and from late February to early November in Tunisia (Mediterranean) (Marques *et al*., 2003). Therefore, as argued by Gaston and Spicer (1998) regarding *Orchestia gammarellus*, it appears that large-scale distribution patterns do not correspond to "fixed" species physiology, and that ecologists should proceed with caution when attempting to make generalisations about the physiology of a species based on studies of a single population.

Deviations from the hypothetical Mendelian sex ratio (1:1) are a common feature among other amphipods, and thus not surprising in talitrids. A female biased sex ratio appears to be the most common situation among talitrids, as observed in *Pseudorchestia brasiliensis* (Cardoso and Veloso, 1996), *Orchestia gammarellus* (Jones and Wigham, 1993; Persson, 1999), *Talitrus saltator* (Williams, 1978) or *Talorchestia capensis* (Van Senus, 1988). The sex ratio in the Zouara population, with the exception of April/May, fits in this patterm, but in Quiaios, during most of the study period, males were dominant in the population. The same was observed in Portuguese and Italian populations of *T. saltator* (Marques *et al*., 2003), but reasons for male biased sex ratios remain unclear. A non-homogeneous distribution of the two sexes between the beach and the dunes may occasionally explain the differences observed. Sex ratio deviations towards male dominance have also been observed in Atlantic and Mediterranean populations of *O. gammarellus*, *O. mediterranea*, and *Orchestia aestuarensis*, and parasitic infestations *by Paramarteilia orchestiae* (trans-ovarily transmitted parasite) were then indicated as a possible cause (Ginsburger-Vogel and Magniette-Margault, 1981; Ginsburger-Vogel, 1989; 1991). This might be also an interesting hypothesis, but was not investigated.

Although sex ratio was predominantly male biased in Quiaios, females became dominant just before the peak of breeding activity in April/May and September/October. This might be related with reproductive activity, males copulating and dying quickly after ecdysis as observed in some *Ampelisca* species (e.g. Hastings, 1981; Carrasco and Arcos, 1984), or perhaps with a horizontal or vertical displacement of males. For instance, Williams (1995) found differences in the summer burrowing depth pattern of males and non gravid females versus gravid females of *T. saltator*. Nevertheless, so far, no evidence of changes in zonation between sexes was found in *Talorchestia brito*.

Population density and the proportion of reproductive females were positively correlated with temperature, which appears therefore to play an important role in controlling breeding activity and recruitment. Changes in photoperiod might also be a factor of major influence, although this was not studied. The positive correlation found between the proportion of juveniles in the samples and sediment moisture suggests that, like in other talitrids, these are probably more sensitive to dehydration, hence concentrating closer to the recent high water mark (Morritt, 1987). No other significant correlations were found between population features and environmental factors, which is not surprising since it is often extremely difficult to establish significant statistical links between population dynamics and environmental controls from field data (e.g. Marsden, 1991b).

The largest individuals were found in the Atlantic population, both in terms of weight and body length. This agrees with Bergmann's law (Fonseca *et al*., 2000), which states that individuals of higher latitude populations have larger maximum sizes than their counterparts of lower latitudes, suggesting the existence of a geographical temperature cline in body size.

Talorchestia brito's lifespan has not been estimated before. It was found that the Atlantic population lived longer (6 to 9 months at Quiaios) than the Mediterranean one (5 to 8 months at Zouara), which fits the pattern known from other talitrids: 7 to 11 months in Portugal and 6 to 8 months in Zouara for *Talitrus saltator* populations (Marques *et al*., 2003), 5 to 9 months for a Moroccan population of *Orchestia mediterranea* (Elkaïm *et al*., 1985), 12 months for *O. gammarellus* in the British Isles (Jones and Wigham, 1993), and 6 to 8 months for *O. mediterranea*, *O. montagui* and *Platorchestia platensis* in the Mediterranean (Louis, 1974).

In both populations, male sexual differentiation after birth occurred earlier than in females (table 4). Sexual differentiation of both males and females occurred later in Quiaios as compared to Zouara, respectively, 1 week for males and 2 weeks for females. It was estimated that females reached sexual maturity 5 weeks earlier at Zouara. As in *T. saltator* (Marques *et al*., 2003), sexual differentiation and female sexual maturation after birth appear to take place earlier in Mediterranean populations in comparison to the Atlantic ones. Although there are no data available for northern European populations, this supports the existence of a cline variation, with adult size and lifespan increasing with latitude.

Both populations produced two generations per year, and apparently females from each cohort breed twice a year, which corresponds to a bivoltine life cycle, with iteroparous females (table 4). On the other hand, northern European populations of *T. brito* present a much shorter reproductive season (from June to September) (Vader, 1970) than in Portugal and Tunisia, which suggests that other life cycle characteristics, namely voltinism, may also change as a function of latitude. Such kind of plasticity has in fact been observed in other talitrids – *Talitrus saltator* may vary from univoltine, in the British Isles (Williams, 1978) to bivoltine in Portugal, Italy and Tunisia (Marques *et al*., 2003) – and appears to be a common feature among amphipods (see Wildish, 1982; Sainte-Marie, 1991).

Higher values in growth production (P) are usually related to increased temperature and metabolism, and also with more abundant food resources. In our case, P values were higher in autumn in both locations, although in Zouara such increase was rather modest. Peaks in density (figure 2) and in the percentage of juveniles in the population (figure 3A and B) may probably explain these results. The highest values in elimination production (E) were reached from spring to autumn in Quiaios, and during autumn in Zouara, which is probably related to higher mortality rates involving older individuals after the reproductive effort, and juveniles as a response to winter nearness. Nevertheless, to a certain extent, seasonal changes in horizontal and vertical distributions may have hidden the real situation.

No other estimations of *Talorchestia brito* production are known, but the present results can be compared with other Talitrid species. Present estimations are of the same magnitude of values found by Cardoso and Veloso (1996) in Brazilian sandy beaches for *Pseudorchestoidea brasiliensis*, but are lower than those estimated for *Talitrus saltator* in the same beaches (Marques *et al*., 2003), and for *Talorchestia capensis* in South Africa (Van Senus and McLachlan, 1986). Differences observed are especially relevant in the case of comparisons with *T. saltator*, since the overall methodology used (Marques *et al*., 2003) was the same, thus eliminating possible bias related with different methods of estimation. Results suggest diverse trophic needs and feeding habits reflecting on productivity as plausible causes. In fact, *T. brito* is known to feed mainly on Cyanophyceae and Diatomeae from the interstitial flora (Vader, 1970) and surf zone, while *T. saltator* feeds mainly on decomposing kelp and wrack stranded by waves and tides (Williams, 1978; Morritt, 1987).

Very similar $P/\overline{B}$ and $E/\overline{B}$ ratios were found for *Talorchestia brito* and *Talitrus saltator* (Marques *et al*., 2003) in both study sites, although the standing stock biomass was significantly lower in the case of *T. brito*, and much higher than that found for *Talorchestia capensis* by Van Senus and McLachlan (1986), and for *P. brasiliensis* by Cardoso and Veloso (1996). It was considered therefore useful to assess as to what extent these estimations were theoretically consistent. Wildish (1984) proposed a general equation for amphipods, which relates growth production, biomass and life span (expressed in years), allowing the ability to estimate $P/\overline{B}$ ratios from life span:

$$\log_{10} P{:}\,\overline{B} = 0.66 - 1.10\ (\log_{10} \textit{life span})$$

Applying this equation to life spans estimated for the two studied populations, the resulting $P/\overline{B}$ ratio intervals show reasonable agreement with the field estimations.

As a whole, differences observed between *Talorchestia brito* Atlantic and

Mediterranean populations, namely regarding morphometrical characteristics, reproduction periods, life spans, and growth rates, illustrate the existence of a geographical variation, with the Atlantic population presenting a slower life history.

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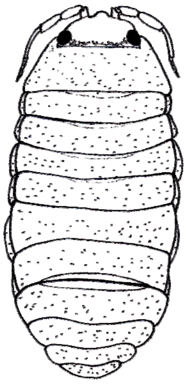
CHAPTER 4:

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



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

ABSTRACT

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

Key words: *Tylos europaeus*, biology, population dynamics, cohort-splitting, secondary production.

INTRODUCTION

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

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

Isopods are important macrofaunal inhabitants in sandy beaches world-wide. Among them, the almost cosmopolitan oniscid semi-terrestrial genus *Tylos* is typical of the upper zones of sandy shores where back-beaches are adequate (Brown and McLachlan, 1990). Several studies have been performed regarding for instance its zonation (e.g. Kensley, 1974; Hayes, 1977; Fallaci *et al.*, 1996), burrowing behaviour (e.g. Brown and Trueman, 1996), spatial distribution (Odendaal *et al.*, 1999), and bio-ecology (e.g. Kensley, 1974; Brown and Odendaal, 1994 in Fallaci *et al.*, 1996). However, the population dynamics and the role of this genus in the energy balance of beach ecosystems are still poorly understood. With the exception of the studies of Hammer *et al.* (1969) on the population dynamics of *Tylos punctatus*

Holmes and Gay 1909, and of Hayes (1974) on the importance of this same species in the sand-beach energetics, focusing on two beaches in California, there are no other works on this topic available in the literature.

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

MATERIALS AND METHODS

Study Sites and sampling programme

Sampling campaigns took place in two sandy beaches on the western coast of Portugal: Cabedelo and Quiaios, both located on the central region of Portugal, near Figueira da Foz. The Quiaios study site (40º12’21’’ N 8º53’48’’ W) is located about 8 km north from Cape Mondego, while the Cabedelo study site (40º07’32’’ N 8º51’49’’ W) is located at about 1 Km south of the Mondego river mouth. Both beaches are relatively undisturbed, receiving a moderate number of summer visitors. According to the exposure rating scale proposed by McLachlan (1980) both beaches have an exposed nature (exposure rates of 15 for Cabedelo and 16 for Quiaios). During storms, Cabedelo may be almost completely inundated, causing depositions of large amounts of drift wrack, mainly composed of macroalgae coming from rocky shores located north from the beach. Regarding Quiaios, the input of beach debris is clearly more limited, since there are no rocky shores or other potential sources of debris near the study site. The main characteristics of these two sandy beaches are summarised in table 1.

Quantitative samples (replicates of 0.25 m^2) were taken fortnightly from the sandy beach communities at both study sites. The sampling period lasted from January 1999 to June 2000 at Quiaios (18 months), and from March 1999 to June 2000 (16 months) at Cabedelo. The sampling programme followed the field work protocol already described by Marques *et al.* (2003). Samples were taken at regular intervals along two transects from the shoreline to the base of the dunes (intertidal and supralittoral areas), in order to account for differential horizontal distribution and to collect a suitable number of individuals necessary for statistical analysis (minimum of 100 individuals). The influence of environmental factors on both populations was investigated. For this purpose, debris quantity (potential food $g.m^{-2}$), organic matter of the sediment as ash free dry weight (AFDW) and sediment moisture were determined according to the procedures described in Marques *et al.* (2003) (table 1). Meteorological data were also obtained from the closest meteorological station, including average daily precipitation, maximum and minimum daily temperatures, visibility, cloudiness, wave height, wave period, and wind velocity.

Laboratory Procedures

Individuals were counted and measured for their cephalic length (CL) to the nearest 0.013 mm. When necessary, total length (TL) was estimated from cephalic length, through the following equation:

$$TL = -1.28068 + 7.197359CL$$
$$(n = 163, r^2 = 0.99)$$

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

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

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

Data Analysis

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

According to a methodology previously utilised (Pardal *et al.*, 2000; Marques *et al.*, 2003; Gonçalves *et al.*, 2003), field growth rates were estimated by tracking recognisable modal distributions in successive sample dates through size-frequency analysis, using the ANAMOD software package (Nogueira, 1992), in which the analysis consistency was tested using the χ^2 and G-tests ($p = 0.05$). The methodology was performed separately for males and females. Juveniles were combined to each sex, proportionally to the average sex ratio observed in each sampling date. Field growth data were fitted to the Bertalanffy growth function (VBGF) with seasonal oscillation, according to a model proposed by Gaschütz and co-workers (1980), and previously applied with satisfactory results (e.g. Pardal *et al.*, 2000; Achouri *et al.*, 2003):

$$Lt = L\infty\left(1 - e^{-\left[KD(t-t0)+C\left(\frac{KD}{2\pi}\right)\sin 2\pi(t-ts)\right]}\right)$$

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

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

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

where $\overline{N}_j$ – mean density in size class j (ind.m^{-2}); $\overline{W}_j$ - mean individual weight in size class j (mg AFDW); CPI – cohort production interval, which was considered in this species as equal to the life span; j and j+1 – consecutive size classes (j = 1,2,..., a).

RESULTS

Spatial Distribution and Density

During all the sampling period, densities were consistently higher at Quiaios than at Cabedelo (figure 1). Despite differences in density, the seasonal variation followed a similar pattern at the two stations, although Cabedelo data were approximately 1.5 months out of step: density reached the lowest values in winter, followed by an increase in early

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

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

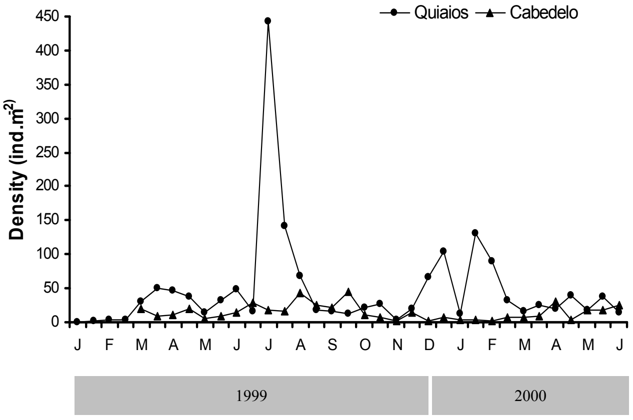


Figure 1. Variation of *Tylos europaeus* population density in the western coast of Portugal.

spring and a slight decrease by May/June. In summer, a strong peak was reached, first at Quiaios and then in Cabedelo, followed by a rapid decline in late summer and autumn (figure 1).

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

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

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

Reproduction Period, Sex Ratio and Fecundity

The reproduction period took place from April to July, recognisable by the occurrence of reproductive females, and the appearance of new juvenile cohorts in the population (figures 2a, b and 3). Only one new cohort was detected during the sampling period (figure 4), suggesting the production of only one cohort per year. The appearance of reproductive females clearly preceded juveniles' recruitment, with a peak in the percentage of juveniles in the populations being attained between July and September (figures 2a, b).

Sex ratios (males/females) were significantly different in the two populations (paired t test; $p<0.05$) (figure 2c). However, both populations revealed similar annual patterns of variation and clearly male biased sex ratios (average Quiaios 1.7:1; average Cabedelo 3.9:1). Short periods of female dominance were observed in Quiaios during the winter, in the beginning of 1999, and again by the end of summer and early autumn, in September/October of the same year.

The average fecundity for females carrying stage A embryos was 18.7 embryos/female, while for stage B carriers was 16.3 embryos/female. Significant statistical correlations between the number of developing embryos (NE) in stages A and B within brood pouches and female cephalic length (CL) were found. The fitted regressions were expressed as:

Stage A $NE = 33.301CL - 33.24$

(170 females; $r^2 = 0.500$)

Stage B $NE = 31.019CL - 29.52$
(44 females; $r^2 = 0.632$)

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

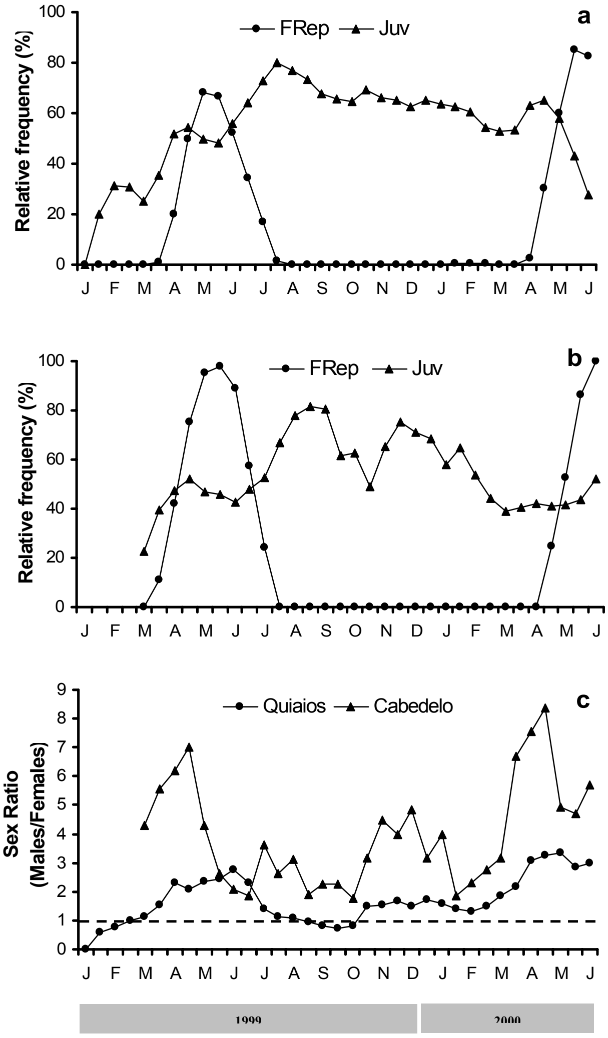


Figure 2. Variation of biological features of *Tylos europaeus*. (**a**) Variation of reproductive females in the total female population, and of juveniles in the population, in Quiaios; (**b**) Variation of reproductive females in the total female population, and of juveniles in the population, in Cabedelo; (**c**) Variation of sex ratio in Quiaios and in Cabedelo

Measurements of embryos (table 2) showed that during development embryos increased its average diameter by 25.8% and their volume 100.3%. Newly hatched juveniles (stage C) were 0.53 ± 0.07 mm CL, therefore just slightly smaller than the minimum average CL of the newly born cohort recognised during the study period (figure 4). Embryos mortality between stages A and B was estimated as 13%. The embryonic development of *Tylos europaeus* was estimated at approximately 68 days (SE ± 4.95), according to the temporal difference between the peaks of relative frequency of embryos in the first and in the last stage (A and C).

Population Structure, Cohort-Splitting and Field Growth Rates

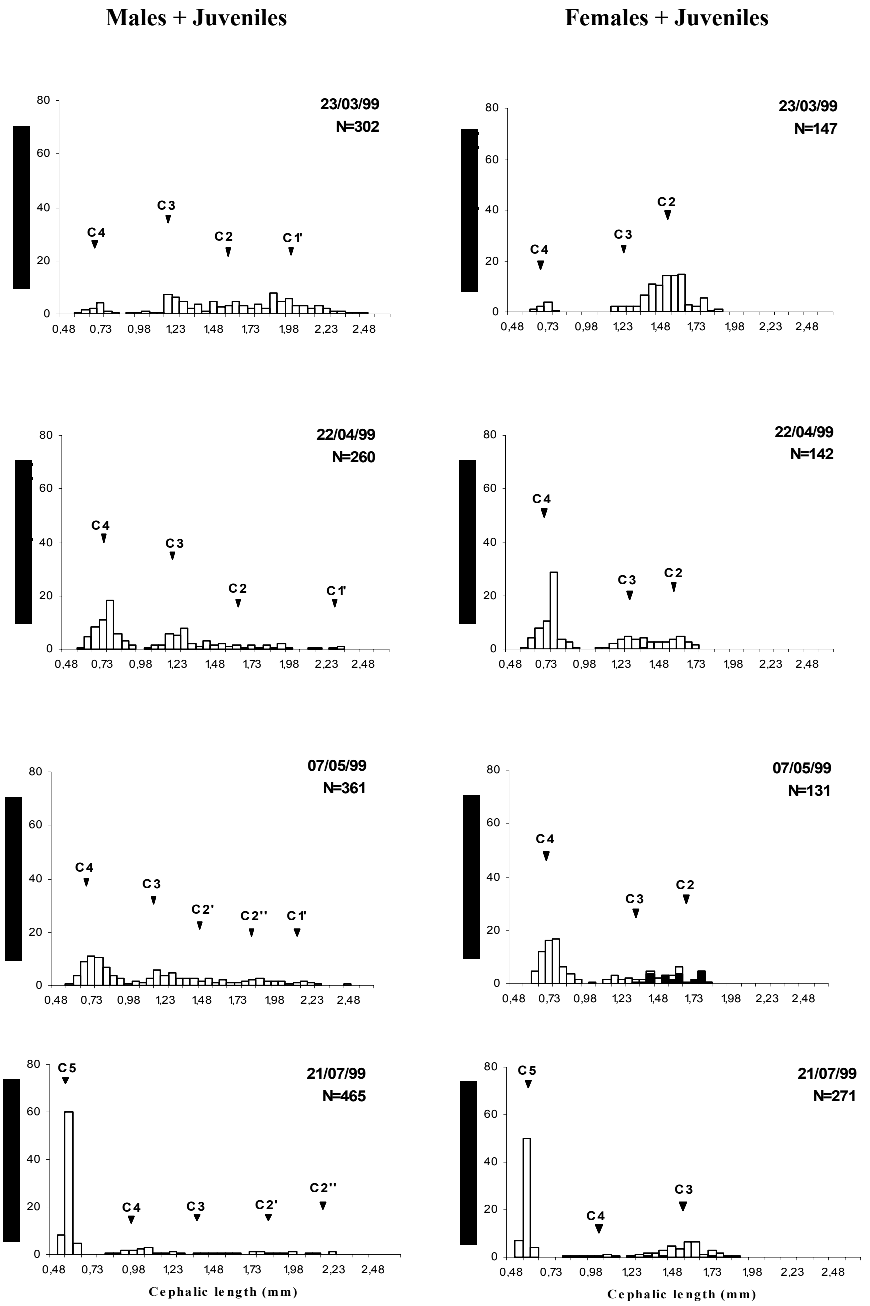
Four cohorts (C1', C2, C3 and C4) were identified in the males group at the first date suitable for analysis (23/03/99), while in the females group only three cohorts were detected (C2, C3 and C4) (figures 3 and 4). According to the pattern observed females from the C1 cohort presumably died the previous year before the study.

Only one new distribution, C5, corresponding to a new recruitment, was detected (χ^2 and G tests not significant; $p \geq 0.05$). Therefore, the population produced only 1 new cohort during 1999, which was detected from the samples collected on 2 of July. A similar observation was not repeated in the next year, since the sampling campaigns were concluded in June 2000, most probably slightly before a new recruitment, according to the pattern observed.

The size-frequency analysis of the males group revealed some peculiar features. Slightly before completing 3 years (April/May of each year studied), males born in the same reproductive period originated two different speed growing groups: fast growing groups which will be called C2'' and C3'', and slow growing groups called C1', C2' and C3' (figure 4). This phenomenon has already been observed in several arthropods, namely in isopods (e.g. Grundy and Sutton, 1989; Zimmer and Kautz, 1997) and has been called cohort-splitting by Sunderland *et al.* (1976) when they observed it in a field population of the isopod *Philoscia muscorum* Scopoli, 1763. These two groups presented different biological characteristics, namely in body size, life span, growth rates and contribution to reproduction. At the time of their disappearance, males C'' presented a maximum average CL of 2.19 mm (14.45 mm TL), while C' were generally larger presenting

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

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


Males + Juveniles

Females + Juveniles

Figure 3. Size-frequency distribution of *Tylos europaeus* in the Western coast of Portugal. Sampling dates are indicated. N = number of measured individuals. Arrowheads indicate average cephalic length of the numbered cohorts. Black areas indicate reproductive females.

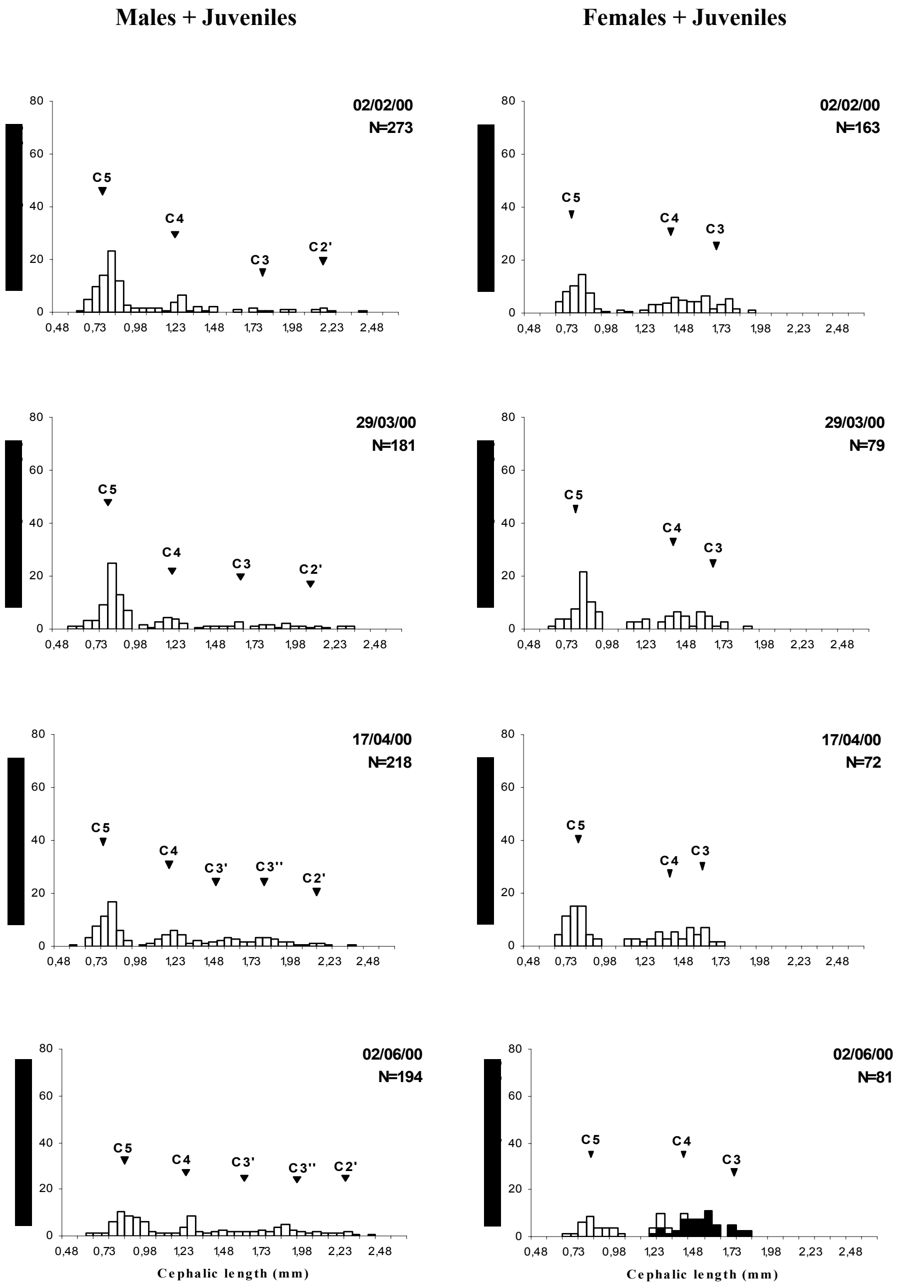


Figure 3 (Continued)

2.27 mm CL (15.05 mm TL). No statistically significant differences were observed between the proportions of individuals belonging to each one of these groups (fast growing *versus* slow growing from the same original cohort) (paired t test; $p \geq 0.05$). Regarding the females group, no division was apparent. In both groups growth rates were clearly higher in mid spring and during summer, decreasing considerably in autumn and winter (figures 4 and 5). Since no cohort could be followed from birth to disappearance, life spans were estimated by combining the size at birth and first growth stages of the new cohort recognised in 1999 (C5) with the observable development through time of all the other cohorts identified (the so called "composed cohort"). Females appeared to live approximately 3 years (36 months), while fast growing males (C'' cohorts) lived the same as females and slow growing males (C' cohorts) appear to live one more year (48 months).

Three growth models – females, fast growing males (C'') and slow growing males (C') – were obtained (figure 6). According to the models: a) growth was approximately constant during life stages; b) to reach sexual

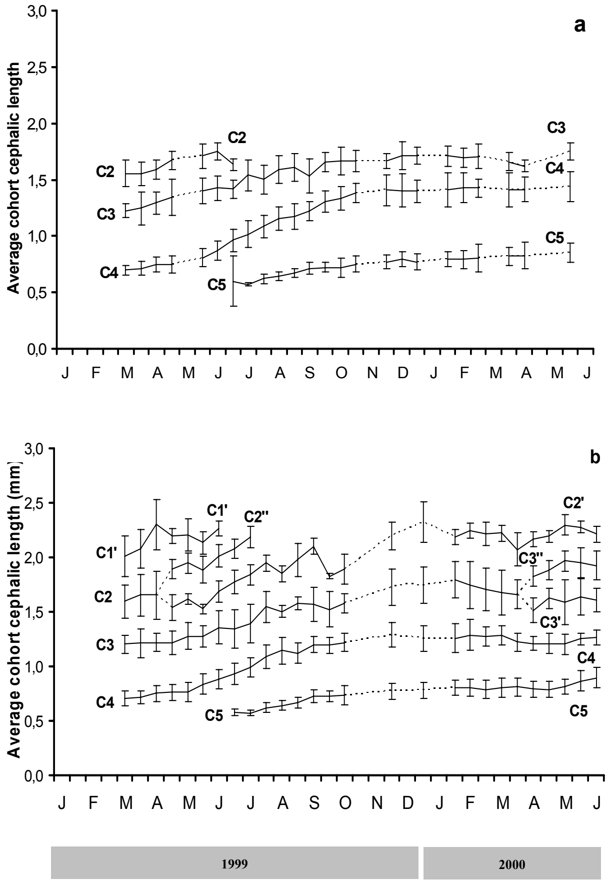


Figure 4. Estimated growth and life span (field growth data) of *Tylos europaeus* cohorts (average cephalic length ± standard deviation) at the western coast of Portugal. Broken lines indicate probable cohort evolution through time. (**a**) Females + juveniles group; (**b**) Males + juveniles group.

maturity females required 55 to 59 weeks; c) the period necessary for male sexual differentiation was estimated in 18 to 19 weeks for C'' males, and 22 to 25 weeks for C' males (table 3). Therefore, sexual differentiation tended to occur much earlier in males than in females, and approximately one month earlier in fast growing males when compared to slow growing males.

Life Cycle

The recruitment pattern of *Tylos europaeus* was constructed (figure 6), and probable parental relations among cohorts were identified. Regarding females, cohorts C2 and C3 were responsible for the appearance of the cohort born in July 1999, while females C3 and C4 must have been the contributors during the reproductive period of the year 2000 (figures 5 and 6). Nevertheless, as already explained, the population could not be followed long enough to observe the occurrence of recruitment in 2000. Females became reproductive on their second spring (1.75 years; e.g. C4) contributing to the reproductive effort of the population in two consecutive years. After their second reproductive season, females died. Regarding males, although cohorts C3 and C4, in 1999 and 2000 respectively, might have been in conditions to reproduce with females of their cohorts, they were probably out-competed by older males with larger body sizes: males C1', C2'' and C2' in 1999; and males C2', C3'' and C3' in 2000.

Production Estimates

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

DISCUSSION

Population densities were consistently higher at Quiaios, during the whole study period. Differences in the sediment granulometry between the two sandy beaches (table 1) might be the cause. According to Kensley (1974), *T. europaeus* avoids beaches of fine sand and river mouths, inhabiting instead crevices, rocks or coarse sand beaches. Nevertheless, the seasonal variation of density followed a similar pattern in Quiaios and Cabedelo. The strong peak reached in summer is a natural consequence of recruitment, while the rapid decline observed in autumn results from the death of older individuals after reproductive effort. The lowest values reached during Winter (more evident in Cabedelo) may suggest that, similarly to talitrids, *T. europaeus* has the capability of changing their horizontal and vertical distributions as a response to harsh environmental conditions (see for instance Williams, 1995; Gonçalves *et al.,* 2003; and Marques *et al.,* 2003; for similar discussions, Fallaci *et al.,* 1996 for changes in the annual static zonation of *T. europaeus*).

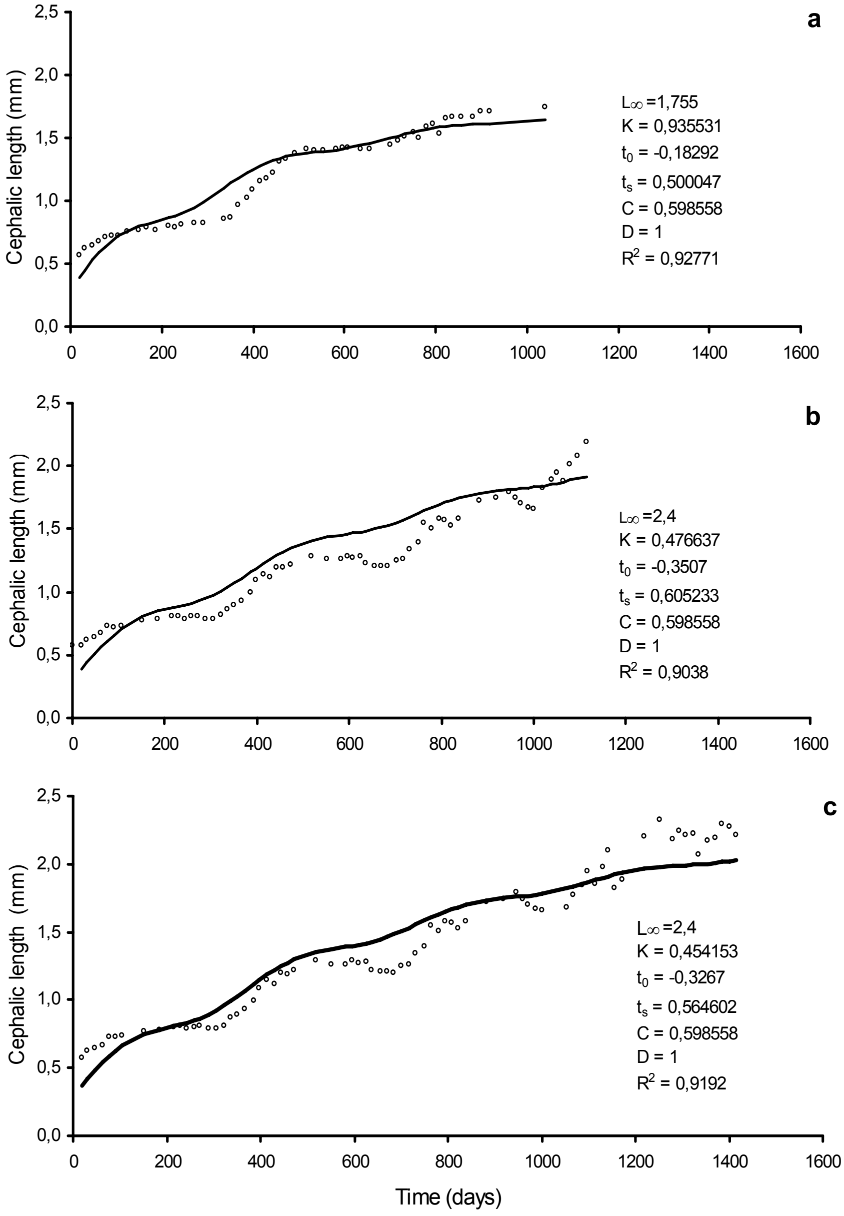


Figure 5. Individual growth models (Gaschütz *et al.,* 1980) of *Tylos europaeus* on the western coast of Portugal. (**a**) Females group; (**b**) Fast growing males group (C''); (**c**) Slow growing males group (C'). The models were calibrated with field growth data from cohorts (plotted points). Day 0 coincides with the month July (moment of detection of the new cohort). Model parameters are given; r^2 = correlation between predicted and observed values (see methods for details).

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

The positive correlation between population density and temperature, found at Cabedelo, is not unexpected. According to several authors (Mocquard *et al.,* 1980; Juchault *et al.,* 1982; Mocquard *et al.,* 1984; *all in* Caubet 1998) reproduction of Oniscids is often seasonal and is associated with combined oscillations in temperature and photoperiod.

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

Female biased sex ratios appear to be an extremely common feature among oniscids, as

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

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

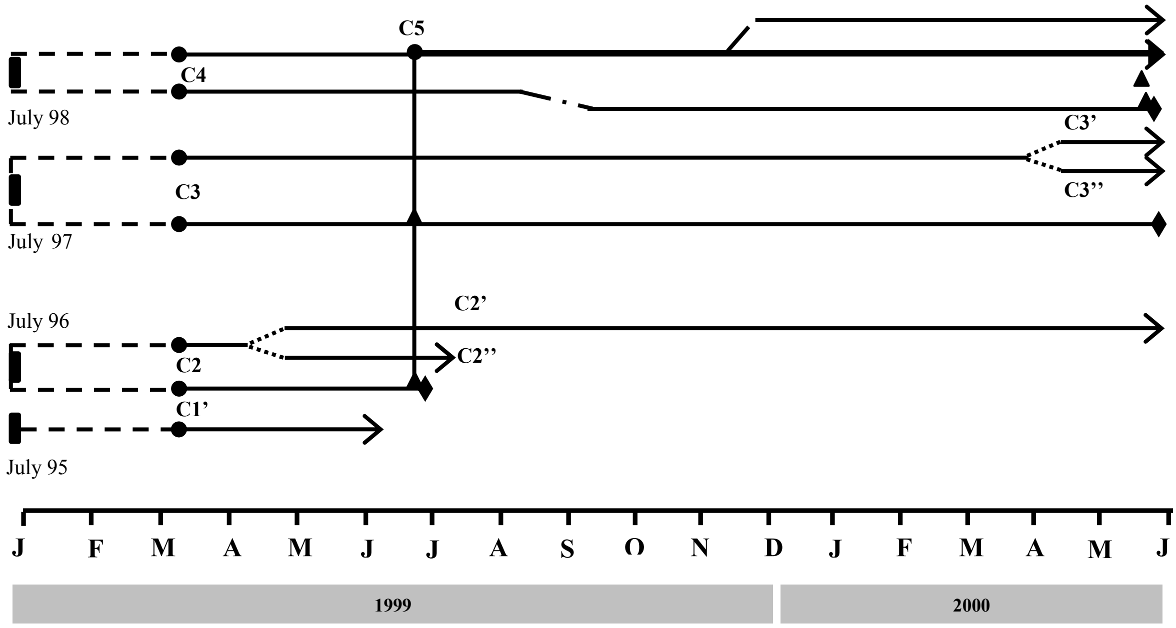


Figure 6. Analysis of the recruitment pattern of *Tylos europaeus* at the western coast of Portugal. The horizontal arrows represent the period during which each cohort was followed during the study period, starting in the solid circles. The assumed contribution of each cohort is indicated (*triangles*). (*arrow*) Males; (*arrow + diamond*) Females; (*filled arrowhead*) Juveniles; (*dashed line*) Probable cohort appearance (the probable month and year of appearance are given); (*dotted line*) Probable cohort-splitting; (*dashed/dotted line*) Probable average sexual differentiation.

observed for instance in *Porcellio laevis* (Kight *et al.,* 2001) and *Porcellionides pruinosus* Brandt, 1833 (Achouri *et al.,* 2003). Infections by the endocytoplasmatic *Wolbachia* bacterium (trans-ovarily transmited parasit) have been pointed out as the main cause of this sex ratio distortion in several oniscids (Juchault *et al.,* 1993; Juchault *et al.,* 1994; Rigaud *et al.,* 1997 *all in* Marcadé *et al.,* 1999). However, contrarily to the previously exposed, *T. europaeus* presented a clearly male biased sex ratio. A non-homogeneous distribution of the two sexes between the beach and the dunes, as suggested by Gonçalves *et al.* (2003) for the amphipod *Talorchestia brito*, may occasionally explain the difference observed. Fallaci *et al.* (1996) observed that juveniles, females and males of a Tyrrhenian population of *T. europaeus* were zoned, respectively, in three successive bands from the sea towards the land. In the present case, the pattern found might be distinct, with females burrowing in the dunes (sampling in the dunes was not performed), since contrarily to the population studied by Fallaci *et al.* (1996) significant tidal fluctuations are present in Atlantic beaches.

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

In several arthropod populations, as for instance in the oniscid isopods *Philoscia muscorum* (Sunderland *et al.,* 1976) and *Porcellio scaber* Latreille, 1804 (Zimmer and Kautz, 1997), cohort-splitting appears to be a relevant structuring mechanism of the dynamics and life history of these populations. Indeed, in the present study, fast growing and slow growing males presented distinct biological features (e.g. lifespan, total length and contribution to reproduction) as a consequence of their different growth rates.

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

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

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

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

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

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

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DISCUSSION

GENERAL DISCUSSION

Talitrids and Tylids – key species in exposed sandy beaches of western Portugal

Since intertidal sediments are not stable enough to allow the construction of stable burrows, intertidal fauna in exposed conditions is usually impoverished and supralittoral organisms may prevail in these communities (Brown and McLachlan, 1990). In the present study, a supralittoral enrichment regarding species richness and frequency of occurrence of the resident organisms was observed, contrary to other studies with similar beaches (e.g. Bayed, 2003; Rodil *et al*., 2006). Crustaceans were the most abundant organisms of the resident fauna and insects, namely coleopterans and dipterans, were the second most abundant group, exceeding molluscs and polychaetes that were only residual contributors. The supralittoral fauna of temperate exposed beaches is usually represented by talitrid amphipods, and oniscid isopods (e.g. Dexter, 1988; Brown and McLachlan, 1990; Colombini *et al*., 1996; Rodil *et al*., 2006) but also by several insects. In the western coast of Portugal, talitrid amphipods and tylid isopods (suborder Oniscidea) represented the structural bulk of both the supralittoral and intertidal communities, but coleopteran (adults and larvae) and dipteran (only larvae) insects also assumed some importance in the supralittoral.

Despite the general similarity in the physical environments regarding exposure to wave action (see chapter 1), macrofaunal community structure at Cabedelo and Quiaios beaches was distinct. A stable structure was observed over time at Cabedelo, but at Quiaios, community structure was far more variable and seasonally dominated by different crustacean species (Gonçalves *et al*., *submitted*). Yet, three species constitute the ecological dominants of both communities studied: the talitrids *Talitrus saltator* and *Talorchestia brito* and the tylid *Tylos europaeus*. However, different species are responsible for the differences observed in community structure: the fluctuations observed in community density at Cabedelo are mainly related with *T. saltator*' population oscillations, the most abundant animal of this community, while *T. europaeus* and *T. brito* shared seasonally the community's dominance at Quiaios. Differences observed in community structure between Cabedelo and Quiaios beaches must be related with differences in habitat preferences and feeding habits of the ecological dominants. Although these sandy beaches are similar regarding exposure, there are clear differences of food availability (detritus supplies), sand grain size and extent of the intertidal area (chapter 1). However, biological interactions between the 3 species must not be excluded since the talitrids are sympatric species that co-occur in both beaches, and there is a considerable niche overlapping between *T. saltator* and the isopod *T. europaeus*.

Abundant, widespread organisms present an important role on community structure because they give support to the community, just like the columns of a building (Piraino *et al*., 2002) and, generally, play a relevant role on the equilibrium of the ecosystem, constituting key elements. In the exposed sandy beaches of western Portugal, the abundant talitrids *Talitrus saltator* and *Talorchestia brito*, as well as the tylid *Tylos europaeus* constitute key species that support the structure of these communities. Also, they are geographically widespread organisms that inhabit the sandy beaches of Atlantic and Mediterranean coasts of Europe and north Africa (Dahl, 1952 *in* Williams, 1978; Colombini *et al*., 1996; Rodil *et al*., 2006). Therefore, these animals may have similar structural roles in other communities and must also be regarded as key species in similarly exposed conditions. Moreover, talitrids and tylids are reported as common crustacean families living in the supralittoral zone of temperate beaches (McLachlan and Jaramillo, 1995) where they often are abundant (e.g. Rodil *et al*., 2006). Thus, even if the intertidal fauna is more diverse and abundant than the supralittoral one, due to different degrees of beach exposure, these animals may still present a key role in supralittoral communities. Key species can be used as tools regarding management because they are important indicators of sustainability (Scapini and Morgan, 2002) and of their biological communities' state, and may also help in ecosystem integrity assessment.

Sandy beaches are sensitive coastal ecosystems, frequently subjected to strong human disturbances. The sandy beaches studied in the western coast of Portugal, however, are both relatively undisturbed systems, receiving a moderate number of summer visitors and, in general, a small degree of human disturbance. Although they are not pristine ecosystems, the knowledge on community structure produced in this study might be used as a reference attribute regarding an ecological equilibrium state of these ecosystems. Reference attributes are very useful because they may function as a basis for further comparison, for instance in ecosystem integrity assessment studies. Moreover, they may also be used in management planning and assessment, or even in ecosystem restoration programs. In fact, community structural attributes (e.g. dominant species, abundances, species number) have been commonly used in ecosystem assessments and are easily visualised (Bain *et al.*, 2000). However, since ecosystem structure and function are profoundly linked, some authors claim that both types of attributes should be employed in ecosystem integrity assessment, especially after implementing restoration programs (Mayer and Galatowitsch, 2001; Mayer *et al.*, 2004). Furthermore, the potential of this knowledge as a reference study is large because, although these are similarly exposed beaches, differences in sand granulometry, extent of the intertidal area and, especially, food availability as detritus supplies, appear to be crucial in the structuring of these communities. Therefore, similarity in exposure does not mean similar community structure, and demonstrates that exposed beach communities are not only controlled by the physical environment, with detritus subsidies playing a very important role (Gonçalves *et al.*, *submitted*). The relevance of detritus subsidies in sandy beach macrofaunal communities has also been demonstrated by Dugan *et al.* (2003) and Jaramillo *et al.* (2006) for upper shore wrack-associated arthropods in Californian and Chilean sandy beaches, respectively. The knowledge produced becomes especially relevant because both beaches studied in the western coast of Portugal, namely Cabedelo, appear to be increasingly developing their touristic and recreational appeal, and might be subjected to a considerable human pressure in the near future.

Local and comparative bio-ecology of Atlantic and Mediterranean key species populations – potential role in global change assessment

In the western coast of Portugal, the sympatric talitrids *Talitrus saltator* and *Talorchestia brito* present several similar bio-ecological features at the population level. Both are semiannual species, with a bivoltine life cycle and iteroparous females, although *T. saltator*'s females may produce as far as 3 broods per year instead of only 2 (Marques *et al.*, 2003; Gonçalves *et al.*, 2003). Also, both species present similarly male biased sex ratios and produce a total of 6 new cohorts per year. With regard to secondary production parameters, despite *T. saltator* presenting, on average, 4 times higher values in average annual biomass ($\overline{B}$), growth production (*P*) and elimination production (*E*) than *T. brito*, both species present very similar secondary production ratios (see Marques *et al.*, 2003 and Gonçalves *et al.*, 2003). The 4 times higher values in the production related attributes are associated primarily with the difference in average population densities, 4 times smaller in *T. brito*. These consistently distinct population densities between both species may be related with the differences in trophic needs and feeding habits of the talitrids (Gonçalves *et al.*, 2003) – overall methodologies of estimation were the same and reproductive outputs are similar.

These talitrids also present some distinct bio-ecological features that allow them to coexist sympatrically in Portuguese beaches and reduce inter-specific competition. These include: (1) differences in the extension of the reproduction period, which begins one month earlier for *T. brito*; (2) differences in the timing of the recruitments – new recruitments are more frequent in the summer and more spaced in the earlier reproductive period in *T. brito*, while in *T.saltator* recruitments occur regularly between spring and summer; (3) differences in the seasonal patterns of density variation – *T. saltator* attains high densities in spring and especially in summer, and low densities in autumn; *T. brito* attains the highest densities in summer and especially in autumn, and the lowest ones in winter; (4) distinct optimum zones on the beach and distinct feeding habits (see chapter 1); (5) differences in lifespan (*T. saltator* lives on average 1.5 months longer) and of average size and weight (*T. saltator* is a larger and heavier talitrid – more robust).

The tylid *Tylos europaeus* was found to be an annual species, with an univoltine life cycle and iteroparous females that produced only 2 broods during their lifespan (Gonçalves *et al*., 2005). Reproduction period is short and only one new cohort is recruited per year, contrarily to talitrids. This animal presents a slow life history, evident in its slow reproductive cycle, very long life spans, and slow growth rates (see Gonçalves *et al*., 2005). This slow life history is also reflected in population' production attributes, chiefly in production turnovers which are much smaller compared to talitrids. Population structure and dynamics of the tylid are much more complex than the structure of talitrid populations, due to a very consistent phenomenon of cohort-splitting in males at the beginning of the reproductive period (Gonçalves *et al*., 2005).

Biological features of *T. europaeus*, not dependent on size-frequency analysis, were analysed separately for each population dataset (Quiaios *versus* Cabedelo) and a few differences were observed, such as: (1) a much higher average population density at Quiaios beach due to differences in sand grain size (see Gonçalves *et al*., 2005 and Gonçalves *et al*., *submitted*). Also, the considerable niche overlap between this species and *T. saltator* are propitious conditions for competitive interactions between these animals, contributing to the smaller population density of *T. europaeus* at Cabedelo (Gonçalves *et al.*, *submitted*), where *T. saltator* is competitively stronger; (2) although both populations present clearly male biased sex-ratios, males dominance is more pronounced at Cabedelo (see Gonçalves *et al*., 2005). Density variation of both populations revealed a seasonal pattern, very similar to the observed in *T. saltator*. Population densities of the 3 key species studied in Portugal were positively correlated with temperature (Gonçalves *et al*., 2003, 2005; Marques *et al*., 2003).

With the exception of a few recent studies performed in the American continent (Defeo and Cardoso, 2002; Cardoso and Defeo, 2003, 2004) and in the presently analysed European and north African Atlantic and Mediterranean coasts (Gonçalves *et al*., 2003; Marques *et al.,* 2003), large scale population studies in sandy beach macrofaunal organisms are rare. Few studies have investigated how these animals respond to geographical variations in the environment and if these variations are reflected in life history traits and population dynamics producing, for instance, latitudinal patterns. The bio-ecological comparisons between talitrid populations of Atlantic (Portugal) and Mediterranean (Italy, Tunisia) sandy beaches presented by Gonçalves *et al*. (2003) and Marques *et al.* (2003) were performed in exposed and relatively undisturbed beaches, narrowing down possible variations in bio-ecology related to different types of exposure to wave action (sheltered *versus* exposed, for instance) and different degrees of human disturbance. Environmental differences between the beaches studied are mostly related with their distinct geographical origins (e.g. temperature, precipitation) and with the different nature of the water bodies that bathe them (e.g. tidal range, salinity). However, in some cases, local differences in the beaches physical environment may also be relevant (e.g. detritus supplies, exposure rate, sand grain size).

According to a review of Defeo and McLachlan (2005), macroscale variations in life history of sandy beach animals were detected in the first place in cirolanid isopods, namely regarding reproduction (Fish, 1970; Jones, 1970 *all in* Defeo and McLachlan, 2005). Recently, Cardoso and Defeo (2004) detected consistent geographical patterns of variation in the population features of the cirolanid *Excirolana braziliensis* from temperate to tropical beaches in the Atlantic and Pacific coasts of America. These included decreases in individual sizes and growth rates, a linear decrease in lifespan and increasing natural mortality, all with decreasing latitude. Clear geographical patterns were also detected in the population dynamics and life history of the south American mole crab *Emerita brasiliensis*, including a decrease in the female size at maturity, a shift from seasonal to continuous reproduction and recruitment, a decrease of individual weight at size, a linear decrease in lifespan and an asymptotic increase in natural mortality with the decrease of latitude (Defeo and Cardoso, 2002).

The talitrid populations analysed in the present study have also revealed geographical variation patterns in bio-ecology, suggesting a latitudinal cline for some life history traits. Both talitrids presented shorter lifespans, earlier female sexual differentiation and maturation, and larger reproduction periods from Atlantic to Mediterranean coasts (Gonçalves *et al*., 2003; Marques *et al*., 2003). Combining *T. saltator*' datasets with the results produced by Williams (1978) in United Kingdom, latitudinal clines observed in the extension of the reproductive period, age of females sexual maturation and lifespan are reinforced, and two new clines arise with regard to life cycle and recruitment pattern. Datasets concerning *T. brito* can be combined with results from Atlantic populations studied in France (Lagardère, 1966) and Netherlands (Vader, 1970). This analysis emphasizes the latitudinal pattern of shorter reproductive periods in northernmost locations and also suggests that other life cycle characteristics, namely voltinism, might also change with latitude (Gonçalves *et al*., 2003). Population studies on *T. brito* also revealed a higher number of recruitments per year, an earlier age of sexual differentiation in males and a smaller adult size and weight in the Mediterranean (Gonçalves *et al*., 2003), suggesting a latitudinal variation in these features.

Most of the macroscale variations observed in life history traits of talitrids reported by Marques *et al.* (2003) and Gonçalves *et al.* (2003) are in agreement with the trends observed in *Excirolana braziliensis* (Cardoso and Defeo, 2004) and *Emerita brasiliensis* (Defeo and Cardoso, 2002) in American beaches, and confirm the strong plasticity of sandy beach macrofauna over latitudinal gradients, as suggested by Cardoso and Defeo (2004). The latitudinal trends observed between the Atlantic and the Mediterranean talitrids are believed to be mostly related with macroscale variations in temperature over latitude, but also with other associated environmental variables such as the photoperiod. In fact, positive correlations between both population densities and proportion of juveniles, and temperature as a predictor were observed in the Portuguese populations (Gonçalves *et al.*, 2003; Marques *et al.*, 2003), but also between proportion of reproductive females and temperature for *T. brito* (Gonçalves *et al*., 2003), demonstrating the link between temperature and biological features in these talitrids.

Some of the population dynamics and life history features of talitrids revealed differences between Atlantic and Mediterranean beaches which can be related with local environmental conditions, including variations in the physical environment, but also in their biotic environment (e.g. competitive interactions). These included higher population densities of *T. saltator* in the Atlantic beach, related with a higher availability of detritus supplies, regularly stranded in Cabedelo by tides (twice a day), and a distinct seasonal pattern of density variation for the Tunisian population as compared to Portuguese and Italian talitrids which had similar patterns (Marques *et al*., 2003). In fact, the Tunisian population presented an exactly opposed pattern, with higher densities in winter months and lowest densities in summer, almost disappearing from the beach. The Zouara' results suggest that *T. saltator* may be changing its horizontal distribution by migrating from the beach to the dunes (Marques *et al*., 2003), or its vertical distribution by burrowing deeper in the sand to depths higher than the 20 cm of sampling, during the hottest months of the year, preventing excessive transpiration rates and consequent desiccation stress. These behaviours were already observed in this species during winter to avoid extremely low temperatures (see for instance Lagardère, 1966; Williams, 1980 *in* Williams, 1995), but also in other talitrids during summer (e.g. Tsubokura *et al*., 1997). Also, Scapini *et al.* (1992) have suggested a general decrease of the locomotor activity of *T. saltator* during August, when extremely high sand temperatures were recorded in a Mediterranean beach. Marques *et al.* (2003) also suggest that the pattern observed at Zouara may result of combined effects between behavioural plasticity (burrowing and surface migration), and inter-specific competition with the sympatric talitrid *T. brito*. However, another possibility may be related with the strong dependency of *T. saltator* upon detritus supplies as the only feeding items. Lagardère (1966) reported that the annual density variation and behaviour of this amphipod on the beach was profoundly influenced by the seasonal deposition of wrack debris in the French coast, but not in the case of *T. brito*. Highest *T. saltator*' densities were coincident with the seasonal abundance of detritus supplies, and the opposite was observed when debris were seasonally absent, with the population concentrating on the dunes (Lagardère, 1966). Detritus supplies are generally limited in abundance at Zouara, contrarily to Collelungo (Italy) where, although limited in time, detritus are often abundant when present (Marques *et al*., 2003). However, the prevalence of storms during winter months may conduct to a similar effect to the one reported by Lagardère (1966) in France, and eventually to a displacement of the population from the dunes to the beach to feed upon the stranded debris.

For both talitrids similar differences in the proportion of sexes were observed, with Portuguese and Italian populations presenting a consistent dominance of males over females, contrarily to the observed in Tunisian populations (Gonçalves *et al*., 2003; Marques *et al*., 2003). In the majority of talitrids (e.g. Van Senus, 1988; Cardoso and Veloso, 1996; Persson, 1999) female biased sex ratios are a common feature. According to Marques *et al.* (2003) and Gonçalves *et al.* (2003), male biased sex ratios observed in Portuguese and Italian populations may be related with: (1) a differential distribution of the sexes between the beach and the dunes; (2) parasitic infestations capable of deviating population sex ratios towards males, similar to the ones reported for several talitrid species of the genus *Orchestia* in Atlantic and Mediterranean populations (Ginsburger-Vogel and Magniette-Mergault, 1981; Ginsburger-Vogel, 1989; 1991). However, none of these hypothesis as yet been demonstrated for these two species.

The Italian population of *T. saltator* presented some remarkable and unexpected features. Italian adults were smaller in size and weight, young males became sexually differentiated at an earlier age and the population produced 2 additional recruitments per year when compared to the other two studied populations (see Marques *et al.*, 2003). Combined with the higher productivity turnovers observed in Italy, these data suggest that the Italian talitrids present faster metabolism and faster growth rates, possibly related with some peculiar local ecological features (e.g. temperatures, food abundance), in spite of a generally lower population density. Furthermore, excluding the productivity turnovers of the Italian population from the analysis performed in Marques *et al.* (2003), a geographical cline of variation in these attributes is evident, with the populations' turnovers decreasing as a function of latitude.

The present scenario of global changes is fast and appears to be mostly related with human activities. Besides global climate change, this scenario includes for instance the increase in human population, the concentration of human populations in coastal areas, an increasing land use and a general unbridled increase in natural resources exploitation. Global changes are, therefore, responsible for an increasing detrimental impact in ecosystems and, especially, in the fragile and sensitive littoral systems because of an increasing demand of human populations for coastal areas, where social and economic opportunities prosper. Tourism and associated recreational activities, which have been rapidly increasing in the last years, also place additional pressures in littoral systems, although often in a seasonal basis, contributing to the progressive degradation of the environmental quality of these areas.

Ecosystems integrity of pristine or low impacted coastal areas must be known and comprehended to establish reference states of ecologically balanced ecosystems, and ecological indicators (e.g. population level, community structure and/or function levels) developed, if global changes in ecosystems are to be assessed, and management or even restoration projects are to be implemented. Sandy beaches perform a series of important ecological roles and also provide to humans multiple services and goods. Moreover, because of the increasing demand for these sensitive coastal ecosystems, mainly associated with recreational and touristic activities, the production of knowledge that might fulfil or provide clues regarding the above mentioned needs is extremely important, especially because sandy beaches are still among the most neglected coastal ecosystems with regard to scientific research.

Key species population bio-ecology is often a useful tool if the aim is to use them as indicators of environmental quality and assess potential impacts of induced environmental disturbances in the ecosystem. For this purposes, population dynamics and structure, reproductive strategies, productivity and turnovers of key species populations must be known. For instance, oscillations in the reproductive strategies or in the population dynamics of a given species may reflect the occurrence of a specific environmental change. The low disturbed nature of the exposed sandy beaches analysed in the present study and their moderate number of summer visitors is reflected in all hierarchical levels of the ecosystem, namely in populations bio-ecology and communities structural and functional attributes. Knowledge of key species populations' bio-ecology may, therefore, function as reference attributes that will allow further ecosystem integrity assessment in similar or even in these same beaches, after environmental disturbances take place, like for instance caused by human activities.

From the knowledge produced in the present study (Marques *et al*., 2003; Gonçalves *et al*., 2003, 2005, *submitted*) some *a priori* examples of variations in population bio-ecology induced by environmental disturbances, with anthropogenic origin, can be derived and predicted. For instance, considering an exposed beach similar to Cabedelo with regard to food availability and sand grain size, significant decreases in population densities of *T. saltator* and *T. europaeus*, bellow the average reference values here presented, will produce serious effects in population ecology. Depending on the nature of the disturbance, changes in population dynamics and in the reproductive strategies may take place, as a response to increased population mortality rates. Consequently, if the disturbance is reflected in population bio-ecology, secondary production attributes and population turnovers will also denunciate the disturbance, deviating from reference attributes. Community structure will also change and the relative dominances of both these key species and the resident community densities may decrease. Since macrofaunal animals play a key role in the centre of sandy beach food chains (Brown and McLachlan, 1990), decreases in top predators such as birds and fishes, and in invertebrate macrofaunal predators (e.g. coleopterans) may also be expected, and decreases in the consumption rates of stranded wrack deposits are highly probable. Ecosystems' processes, structure and function will also be disturbed, changing into a modified state distinct of the initial one.

Several manmade disturbances may conduct to such a chain of events and jeopardize beaches ecological states. For instance, increases in touristic and recreational activities on beaches produce several kinds of impacts which, consequently, may increase natural mortality rates of key species populations, and possibly also of other macrofaunal organisms. In fact, Węslawski *et al.* (2000) considers the increase in touristic activity as one of the main causes for the sharp decline of *T. saltator* occurrence and its markedly lower population densities observed in the Baltic coast of Poland between the early 1960's and 1996.

Intense human trampling and, also, mechanical trampling by off-road vehicles, used for instance in recreational activities, can pose damage in these animals, destroying their burrows or even fatally crush them. A comparative study with urbanized and protected beaches in Rio de Janeiro (Brazil) performed by Veloso *et al.* (2006), indicates that the talitrid *Pseudorchestoidea brasiliensis* is more vulnerable to trampling than other local macrofaunal organisms, and that this vulnerability may even result in the complete disappearance of these animals in stretches of beach heavily trampled. According to Da Silva (2002), human occupation densities recorded in the intertidal area of several Portuguese sandy beaches in August (1998 and 1999) corresponds to 1/3 of the observed values in the upper beach (supralittoral). Beach facilities were also concentrated in this area (Da Silva, 2002), so these observations demonstrate that trampling may be much more intense precisely in the supralittoral habitats. Moreover, a study on South Africa revealed that there was a linear direct relation between the number of supralittoral isopods *Tylos capensis* damaged by off-road vehicles and the intensity of vehicle presence, with 10% of animals damaged by approximately 17 vehicle passes, although they burrow themselves in average 25 cm bellow sand surface (van der Merwe and van der Merwe, 1991 *in* Stephenson, 1999). Although studies in this regard are not yet available for *T. brito*, these animals will certainly be similarly vulnerable to these kinds of physical impacts because, despite its intertidal affinity, this talitrid is less robust, presents slower movements and apparently a less efficient jumping behaviour than *T. saltator* (Fallaci *et al*., 1999), making it less resistant and a slower escaper if disturbed.

Beach grooming with heavy mechanical equipment is another touristic and recreational associated activity that can result in density decreases of the key species, but also of other wrack-associated animals like for instance insects (e.g. Dugan *et al*., 2003). Grooming to remove stranded wrack and human debris is a common activity in sandy beaches of touristic and populated regions (Llewellyn and Shackley, 1996), that takes place mainly in the upper reaches of the beach (the strandline), in order to enhance beach attractiveness to tourists and improve the recreational qualities of the beach. These include, for instance, decreasing the organic contents of the sand, brightening the shore and increasing sand stability to walking by visitors (Malm *et al*., 2004). However, beach grooming with heavy machinery, on a regular basis or even only seasonally, can pose several problems to macrofaunal animals, especially to wrack-associated taxa. The physical impact that heavy machines introduce in the sand environment, where these animals are burrowed during the day, is known to cause a decrease or even disappearance of these macrofauna, but also of some of their predators such as wading birds (Brown and McLachlan, 1990; Llewellyn and Shackley, 1996). Besides the obvious negative effects of removing regularly large quantities of fresh debris used as food by wrack-associated macrofauna, several of these animals also often use the debris as foraging habitat or even as refuge from predators during the day (Brown and McLachlan, 1990; Colombini *et al*., 2000; personal observations). For instance, Dugan *et al.* (2003) in a study performed in 15 exposed sandy beaches of southern California demonstrated that significant decreases in species richness, abundance and biomass of wrack-associated animals were observed on groomed beaches, and grooming also appeared to introduce impacts on communities' composition and trophic structure. Therefore, Dugan *et al.* (2003) proposed that areas of natural ungroomed beaches should be preserved and interspred with groomed areas as a coastal management approach for sandy beaches. This approach is similar to the one of Węslawski *et al.* (2000), who proposed a concentration of tourist facilities in sandy beach areas separated by stretches of undisturbed coast, as a conservation option to avoid further declines in sandhoppers occurrence in the Polish Baltic coast. These kinds of options become particularly relevant for talitrids and tylids because these animals have reduced dispersal capabilities (they lack drifting larval stages) and, therefore, recolonization of beach impacted areas is a very difficult task.

The construction of touristic, recreational and some urban associated facilities is known to be frequently responsible for coastal dune degradation and destruction, and common for instance on highly developed and touristic European coasts. This kind of impact disturbs coastal dune biota, and jeopardizes some of the important ecological services that the beach/dune system provides. Furthermore, coastal dune degradation and destruction may also disturb sandy beach macrofauna, especially supralittoral organisms that, like talitrids, perform seasonal movements on the beach/dune system using the dunes for overwintering or even to avoid extreme high temperatures in summer (e.g. Lagardère, 1966; Tsubokura *et al*., 1996; Marques *et al*., 2003). This kind of activity was also proposed to interfere with the movements of other sandy beach animals between the beach and the dune, such as in the widespread burrowing ghost crabs in Australian beaches (Barros, 2001). Besides these examples of human impacts, mostly related with the increasing demand for sandy beaches as touristic and recreational targets, several others with potential to induce changes of macrofaunal sandy beach populations could be also mentioned. These may include, for instance, climatic changes (e.g. abnormal temperatures, changes in storm occurrence and intensity – Węslawski *et al*., 2000), beach erosion, beach nourishment (e.g. Peterson *et al*., 2000) and human harvesting (e.g. Defeo and de Alava, 1995).

The comparative bio-ecology of talitrid populations in Atlantic and Mediterranean sandy beaches, and of the two Portuguese populations of *T. europaeus*, revealed the strong plasticity of macrofaunal populations to local environments and over geographical gradients. Temperature, and possibly also other latitude related environmental variables, food availability, sand grain size and competitive interactions are believed to be the major causes of the bio-ecological variation observed between these populations. From this baseline knowledge, future variations in bio-ecology induced by environmental disturbances and not matching the present ones, may be more easily identified and related with their possible causes. Thus, knowledge on key species bio-ecology of low impacted sandy beaches may play a relevant role in coastal management, conservation and restoration, and function as reference attributes useful in ecosystem integrity assessment, and planning of management scenarios and restoration projects. Key species may be used as biological indicators to assess global changes impacts derived from human activities.

The Mediterranean beach of Zouara (Tunisia) is a particularly good example of the usefulness of this knowledge. Although it was a relatively undisturbed ecosystem by the time the present studies took place, the region was afterwards subjected to infrastructural development. This included the construction of a dam relatively close to the coast, which was reported to have affected the beach and fore-dune zone due to transformations in sediment dynamics and in the hydrological regime of the area (Cassar *et al.*, 2002). Furthermore, Cassar *et al.* (2002) report that, due to these transformations, Zouara beach is extremely vulnerable to human impacts, especially a development of this area for touristic and recreational activities. There is also an increasing touristic and recreational demand for the Portuguese western sandy coastline, which may result in increased human impacts on these sensitive ecosystems. Therefore, regular monitoring of key species populations may assume a very important role in human impact and ecosystem integrity assessment, alerting for important structural and functional changes that might occur at the community or even at the ecosystem levels.

Modelling local populations as a potential tool for environmental change assessment

Ecological modelling assumes a great importance in scientific research as a way of exploring and understanding the ecological systems and processes under modelling, and their regulation by the physical and biotic environments. It is also a very important simulation and prediction tool, increasingly used for management and assessment purposes, but also in conservation biology. In fact, conservation biology, ecological management and assessment options, nowadays, often rely on population dynamics (e.g. Anastácio *et al.*, 1999; Martins *et al.*, 2002; Morales *et al.*, 2006; Rushton *et al.*, 2006) and communities' dynamics modelling (e.g. Gertseva *et al.*, 2004).

The construction of population dynamics models, that can comprehensively and correctly simulate the dynamics of a given population, is a powerful tool that allows the simulation of multiple scenarios that might reflect potential changes in environmental conditions, induced or not by human activities. The simulation of distinct scenarios forecasts how the population will respond to the environmental change introduced in the modelling process, and which population parameters will change and to what extent. By building a population dynamics model of a key species, indicator of a given biological community, the response of the system to a given change may be anticipated (Marques and Anastácio, 2002). Furthermore, despite of the complex and time consuming process of model development, a calibrated and ideally validated model, once obtained, is a very quick simulation tool, which is especially relevant when contrasted with the global changes occurring at a fast rate at the present time.

Population dynamics models for the sandy beach macrofaunal key species *Talitrus saltator*, *Talorchetia brito*, and *Tylos europaeus* holds large potential as practical and dynamic tools in integrated coastal management and planning of these sensitive and abundant ecosystems. Moreover, according to Anastácio *et al.* (2003) these models may also be used to understand or mitigate the impacts that environmental changes, driven for instance by human activities, pose upon the modelled population.

Anastácio *et al.* (2003) developed a population dynamics model of the talitrid key species *Talitrus saltator*, and used the field data of the Portuguese population studied by Marques *et al.* (2003) and Gonçalves (2002) for model calibration and replicative validation purposes. Constructed with Stella simulation software and based upon differential equations, the model used the age class as its basic unit. During model development five different model versions, with distinct modes of recruitment that could fit the data, were tested (see Anastácio *et al*., 2003). The simplest model version, version (e), included causality and provided the best statistical results and the most realistic mortality rates, a very important parameter for model stability. This version (similarly to version (d)) considers the reproduction dependent on temperature and photoperiod, and occurring on a semi-lunar basis. Moreover, this model version was considered replicatively validated, as well as version (b). Thus, version (e) was the model version elected by the authors as the most realistic one and statistically plausible.

Sensitivity analysis performed on the model revealed that the abundance (IST, ind.m^{-1}) of *T. saltator* is highly affected by changes in the recruitment mechanism, namely in minimum recruitment day length, minimum temperature at recruitment and the period between recruitments (Anastácio *et al*., 2003). The abundance was also most sensitive to the initial number of individuals in the age class 5 (approximately 4 months of age), and least sensitive to the initial number in the age class 9 (approximately 8 months of age) (Anastácio *et al*., 2003). Also, due to the high summer temperatures, an arrest in recruitment had to be introduced in the model in order to replicate the dynamics of the real population. Similarly to the studies of Gonçalves (2002), Marques *et al.* (2003) and, Gonçalves *et al.* (2003) on the related species *T. brito*, Anastácio *et al*. (2003) highlights the need for further studies regarding the factors that influence the timing of reproduction and recruitment, since this was a clear gap revealed during the development process of the model. At the present stage the model is replicatevely validated, but it is necessary to test its predictive validity (Rykiel, 1996) i.e. to determine if it is able to make correct predictions under different scenarios. The Mediterranean population datasets produced by Marques *et al.* (2003) regarding *T. saltator*' bio-ecology may be used in such way and, if the predictive validity of the model is confirmed, a more robust modelling tool will be achieved (Anastácio *et al*., 2003).

Based on the above mentioned example, the large bio-ecological knowledge produced in the studies of Gonçalves *et al.* (2003, 2005) also provides important baseline information that might be used in the construction, calibration and validation of population dynamics models of the other sandy beach key species: the talitrid *T. brito* and the tylid *T. europaeus*. However, regarding *T. europaeus*, since there is no comparative Mediterranean population information available, another year of study in the same location, or in another nearby or even geographically distant population is necessary for predictive validity testing. With population dynamics models of beach macrofaunal key species the following scenarios may, for instance, be simulated: (1) significant decreases in food availability in the form of detritus supplies (naturally or artificially induced by human actions); (2) significant increases or decreases in temperature; (3) significant increases in human trampling. These simulations will allow the prediction of the populations' responses and, using these responses, changes in the communities may be anticipated and preventive management or mitigation actions implemented. Thus, modelling local populations of key species must be regarded as an important tool for environmental change assessment in sandy beaches, and even in other littoral systems provided that the necessary adjustments are performed.

Concluding remarks and subjects for further investigation

In exposed sandy beaches, distinct macrofaunal community structures may be expected caused mainly by local differences in food availability (detritus supplies), sand grain size and eventually also in the width of the intertidal area, despite of similarities in the beaches exposure rate. Macrofaunal species present distinct habitat preferences and feeding habits, but biotic interactions, such as inter-specific competition, and seasonality may also play a relevant role in community structuring mechanisms, as demonstrated in the western coast of Portugal. Nevertheless, talitrid and tylid crustaceans are ecological dominants in either case, and must be regarded as key species in Portuguese sandy beach communities, as well as indicators of the ecological state of the macrofaunal communities. Moreover, since these animals are widespread and abundant in Atlantic and Mediterranean sandy beaches of Europe and north Africa, they may certainly hold similar structural roles at these coasts and, even if these roles are restricted only to the supralittoral communities, they should also be considered key species in such conditions. Due to the relatively undisturbed nature of the studied beaches (for instance regarding human impacts), this work might be considered a reference study for the structure of macrofaunal communities of exposed beaches, suitable for comparison in ecosystem integrity assessment and coastal management, or even conservation studies. Furthermore, development of ecological indicators for sandy beach ecological assessment based on community structure attributes (e.g. abundances, dominant species) or on functional attributes (e.g. biomass production, decomposition) appear as a promising subject for further investigation.

Several bio-ecological features of talitrid populations presented large latitudinal patterns of variation, while a few others were related with local conditions of the physical and biotic environments of each beach. All these findings confirm previous statements that sandy beach macrofaunal crustaceans present a strong plasticity in population ecology features, adapting their bio-ecology over geographical gradients and to local characteristic environmental conditions. Notwithstanding, some bio-ecological aspects of these populations need further investigation, if a better understanding of some population mechanisms and features is to be achieved: (1) the seasonal movements along the beach/dune system, as well as possible seasonal displacements in their vertical distribution (depth of burrowing) in Atlantic and Mediterranean populations should be analysed to clarify which strategies are adopted and by which species; (2) burrowing zonation patterns of both sexes, between the beach and the dunes, should be studied in the 3 species to determine if the biased sex ratios observed are related with a differential distribution of the sexes in the beach/dune system; (3) the incidence of parasites should also be approached in the 3 species, and their consequences determined, in Atlantic and Mediterranean populations. In talitrids, parasites may even be the agents promoting the male biased sex ratios observed; (4) a local study at Collelungo (Italy) to clarify the links between the environmental conditions and the population features of *T. saltator* should be performed since this population revealed peculiar features that could be explained only by hypothesis; (5) the importance of temperature and photoperiod on reproduction and recruitment mechanisms should be profoundly studied in the 3 species, namely with laboratory studies; (6) distinct geographical populations of *T. europaeus* should be studied to determine if in this species life history traits also change over latitudinal gradients and/or with other local sources of variation. The prevalence of cohort-splitting events as a structuring mechanism in these populations should also be analysed; (7) cohort-splitting events in *T. europaeus* should be further studied to test the explanatory hypothesis proposed. Laboratory experiments are therefore necessary.

Knowledge on key species bio-ecology of relatively undisturbed sandy beaches might function as reference attributes that can be used as indicators of environmental quality in ecosystem integrity assessment, after the occurrence of environmental disturbances, induced or not by human activities. Induced disturbances are reflected in key species bio-ecology features and, consequently, community structure and function, as well as ecosystem' structure, function and even processes, may also be disturbed and deviated from the initial states. In the scope of the fast environmental global changes of the present time, sandy beach reference knowledge might assume important roles in coastal management and protection, implementation of restoration projects in already disturbed systems, and ecosystem integrity assessment. The significant increase in touristic and recreational activities in sandy beach areas and of their associated facilities and activities (e.g.

beach grooming, trampling of different sources) on the beach/dune system have been considered as one of the major threats to sandy beach integrity. These increases are very realistic in European sandy beaches and, especially, in the very disturbed sandy coasts of the Mediterranean. In this context, regular monitoring programs on key species populations should be implemented, and conservation and management options like the ones proposed by Węslawski *et al.* (2000) and Dugan *et al.* (2003) should be rapidly adopted, if macrofaunal communities and ecosystems' integrity are to be preserved.

Modelling key species population dynamics assumes a crucial relevance as a quick (once constructed, calibrated and validated) and dynamic tool that may assist in environmental change assessment and coastal management planning in sandy beaches. These models allow the simulation of multiple scenarios and the prediction of the modelled populations' responses and, consequently, the anticipation of the communities' or even the ecosystems' responses to the disturbance or to the management option. Therefore, the development of calibrated and validated models for *Talorchestia brito* and *Tylos europaeus*, as well as the predictive validation testing of the model developed for *Talitrus saltator* (Anastácio *et al*., 2003) should be considered priorities in further investigation.

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