Macrozoobenthic and Fish Production of the Mondego Estuary

Anthropogenic and Climate Variability Impact

Marina Paula Dolbeth Henriques da Silva

Universidade de Coimbra
2007

MACROZOOBENTHIC and FISH PRODUCTION of the MONDEGO ESTUARY

Anthropogenic and Climate Variability Impact

Doctoral dissertation in Biology (Scientific area of Ecology) presented to the University of Coimbra

Dissertação apresentada à Universidade de Coimbra para obtenção do grau de Doutor em Biologia (especialidade Ecologia)

Marina Paula Dolbeth Henriques da Silva

Universidade de Coimbra
2007

This thesis was supported by:

FCT - Portuguese Foundation for Science and Technology, through a PhD grant attributed to M Dolbeth (SFRH/BD/14112/2003)

IMAR – Institute of Marine Research
Department of Zoology, FCT, University of Coimbra

This thesis is based on the following manuscripts:

Dolbeth M, Lillebø AI, Cardoso PG, Ferreira SM, Pardal MA (2005) Annual production of estuarine fauna in different environmental conditions: an evaluation of the estimation methods. J Exp Mar Biol Ecol 326: 115-127;

Dolbeth M, Cardoso PG, Ferreira SM, Verdelhos T, Raffaelli D, Pardal MA (2007) Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period. Mar Pollut Bull 54: 576 - 585;

Dolbeth M, Martinho F, Leitão R, Cabral H, Pardal MA (2007) Strategies of *Pomatoschistus minutus* and *Pomatoschistus microps* to cope with environmental instability. Estuar Coast Shelf Sci 74: 263 – 273;

Dolbeth M, Nielsen SN, Martinho F, Cabral H, Pardal MA (2007) Modelling the life cycle, population and biomass dynamics of two Gobiidae fish species. Submitted to Ecol Model;

Dolbeth M, Martinho F, Leitão R, Cabral H, Pardal MA (2007) Feeding patterns of a temperate estuarine fish community: detecting major links within trophic levels. Submitted to J Fish Biol;

Dolbeth M, Martinho F, Viegas I, Cabral H, Pardal MA (2007) Estuarine production of resident and nursery fish species: conditioning by drought events? Submitted to Estuar Coast Shelf Sci.

CONTENTS

GENERAL INTRODUCTION

CHAPTER I

Secondary production of estuarine macrobenthic invertebrate communities

CHAPTER II

Population dynamics of *Pomatoschistus minutus* and *Pomatoschistus microps*

CHAPTER III

Links between macroinvertebrates and fish

CHAPTER IV

Estuarine fish production

GENERAL DISCUSSION AND CONCLUSIONS

ABSTRACT

The major aim of the present thesis was to estimate the macrozoobenthic intertidal community and the dominant fish community production of the Mondego estuary. Such estimates allowed to assess the ecological integrity of the estuary, under anthropogenic and climate variability stress, and infer on the links between macrobenthos and fish. The thesis core was divided into four main chapters, focusing on: 1) the estuarine macrozoobenthic community production, where it was presented an overview of the main impacts occurring in the Mondego estuary over a ten-year study period, namely eutrophication and flood effects; 2) the population dynamics, regarding density, biomass and production, of *Pomatoschistus minutus* and *Pomatoschistus microps*, through an analysis of the real population dynamics (field study) and by the development of an ecological model to simulate that dynamics; 3) the links between macroinvertebrates and fish, by studying the fish diets; and 4) the estuarine production of resident and marine juveniles fish species using the estuary as nursery grounds (nursery species).

In chapter I, empirical estimation methods were tested to be used for the computation of the macrozoobenthic community production. For this purpose, five estuarine species were used, each with a different life histories and abundances. Two areas, with contrasting anthropogenic activities impact, were tested. Brey (2001) version 4-04 produced the most satisfactory estimates, being considered the best methodology. Then, the assessment of the macrozoobenthic community production of the south arm of Mondego estuary over a ten-year study period - 1993 to 2002, enabled to evaluate the impact of macroalgal blooms and *Zostera noltii* decline, resulting from eutrophication. The success of a restoration programme implemented in 1998 could also be monitored. Before the mitigation measures of 1998, the *Z. noltii* beds declined gradually. In parallel, species richness, mean biomass and production of the macrozoobenthic community also decreased. After the management measures, the seagrass bed seemed to recover, along with a substantial increase in the mean biomass and production of the community for the whole intertidal area of the south arm of the Mondego estuary. Nevertheless, during this period, the occurrence of strong flood events (2001) induced a drastic reduction of the macrozoobenthic annual production. This study showed that the resilience of the macroinvertebrate populations may have been lowered by a prior disturbance history (eutrophication) and consequent interactions of multiple stressors.

In chapter II, the population dynamics of *P. minutus* and *P. microps* was assessed from June 2003 to May 2006, in order to understand the ability of these species to withstand environmental variability, particularly during extreme climate events. Increasing drought conditions were observed, starting with a normal hydrological year in 2003 and attaining a severe drought in 2005. This resulted in low freshwater discharges mainly in 2005. Occasionally, abnormal high water temperatures were observed. During the drought year, non-expressive recruitments and the quick disappearance of the parental cohort were observed for *P. minutus*. This translated into a clear decrease in the fish density and production. For *P. microps*, the correspondent decrease was not so pronounced. No direct effects were attributable to the salinity and temperatures variations. Yet, the hypothesis of higher predation pressure on *P. minutus* was raised since the higher salinity incursion in the estuary increased the piscivorous marine adventitious species. These were more often in the downstream areas, where *P. minutus* distributed. *Pomatoschistus microps* benefited from a wider temperature and salinity range tolerance, allowing the species to occupy different estuarine areas. Therefore, *P. microps* seemed more adapted to withstand the environmental variability during the study period. Subsequently, an ecological model to simulate the population dynamics of the *Pomatoschistus* spp. studied previously, regarding density and biomass, was developed having as baseline the three-year field study mentioned above. The model comprised two sub-models: 1) an individual growth; and 2) a population dynamics (density) of juveniles and adults. These two sub-models were then coupled to form a cohort model (density and biomass). The cohorts were grouped, and again coupled according to the fish recruitments, to simulate their population. Results predicted by the model were in agreement with the field results. This approach also allowed to formulate hypotheses regarding possible restriction effects of the drought on the fish population development.

The diet of 14 species from the fish community was assessed in chapter III. The most important prey were invertebrates with several polychaetes (*Nephtys* spp., Capitellidae, Spionidae, Eunicidae), *Corophium* spp. and *Crangon crangon* among the dominant ones. *Pomatoschistus* spp. were the most preyed fish and calanoid copepods (mainly *Acartia* spp.) were the most preyed plankton species. Several fish species showed a tendency for a specialized diet. Yet, almost all fish also showed some degree of opportunistic behaviour, as they preyed on other food resources. High diet overlap was found between some fish species but exploitative competition for food resources could not be concluded.

Finally, in chapter IV, the production of the resident (*P. minutus* and *P. microps*) and nursery species (*Dicentrarchus labrax*, *Platichthys flesus*, *Solea solea*) was assessed from June 2003 to May 2006. These species comprised about 70% of all the fish community, both in numbers and biomass. In general, production was lower in the Mondego estuary, compared to other systems, which was probably due to its small area. Production decreased in the drought year, especially for *D. labrax, P. minutus and P. flesus*. Again, no direct effects could be attributable to the salinity and temperature variations and to the low freshwater discharges (resulting from the drought and high temperatures). Yet, these were pointed as the probable major reasons for the decreased production: directly due to the tolerances of each species and indirectly thorough a potential higher predation pressure. A significant reduction of the potential estuarine production to be exported for coastal areas by nursery species was also estimated for drought conditions.

RESUMO

A presente tese teve como principal objectivo estimar a produção da comunidade macrozoobentónica intertidal e a produção da comunidade ictiológica dominante do estuário do Mondego. Por sua vez este estudo visou compreender os efeitos de impactos antropogénicos e de origem climática no estuário, e inferir acerca das relações entre os invertebrados macrobentónicos e os peixes em estudo. Com efeito, a estrutura da tese compreendeu quatro capítulos principais em que foram estudados 1) a produção estuarina da comunidade macrozoobentónica intertidal, em que foi apresentado um historial dos principais impactos no estuário do Mondego ao longo de dez anos de estudo, nomeadamente os efeitos da eutrofização e efeitos de cheias; 2) a dinâmica populacional, no que respeita a densidade, biomassa e produção, de *Pomatoschistus minutus* e *Pomatoschistus microps*, através de uma análise da dinâmica real da população (dados de campo) e através de um modelo ecológico desenvolvido para simular a referida dinâmica; 3) a relação entre os macroinvertebrados e os peixes, através da análise das dietas dos peixes; 4) a produção estuarina das espécies de peixes residentes e dos juvenis marinhos utilizando o estuário como área de viveiro.

No capítulo I, foram testados métodos empíricos de produção, para serem utilizados no cálculo da produção da comunidade macrozoobentónica. Cinco espécies estuarinas foram utilizadas para o efeito, com diferentes histórias de vida e representatividade (abundâncias) no estuário, em duas áreas com condições ambientais contrastantes no que respeita ao impacto de actividades humanas. O método de Brey (2001) versão 4-04 produziu os resultados mais satisfatórios, sendo considerado o melhor método alternativo. Seguiu-se o cálculo da produção da comunidade macrobentónica intertidal do braço Sul do estuário, no período de 10 anos - 1993 a 2002, permitindo avaliar o impacto dos *blooms* macroalgais e consequente declínio da macrófita *Zostera noltii*, bem como monitorizar o sucesso de um programa de recuperação ambiental implementado em 1998. Antes das medidas de mitigação de 1998, em paralelo com o declínio dos bancos de *Z. noltii*, a riqueza específica, biomassa média e a produção decresceram acentuadamente. Após as medidas de gestão, os bancos de *Z. noltii* pareceram recuperar gradualmente, concomitante com aumentos consideráveis na biomassa média e produção da comunidade macrobentónica em toda a área intertidal do braço sul do estuário do Mondego. No entanto, durante este período, a ocorrência de fortes cheias (em 2001) induziu a uma redução drástica da produção anual. Este estudo mostrou que a resiliência das populações de macroinvertebrados poderá ter sido comprometida pelo efeito da perturbação anterior no estuário (eutrofização) e consequente interacção de múltiplos agentes de stress.

No capítulo II, a dinâmica populacional de *P. minutus* e *P. microps* foi estudada de Junho 2003 a Maio 2006, de forma a perceber como estas espécies reagem à variabilidade ambiental, em particular a efeitos climáticos extremos. Neste período, situações de seca foram graduais, começando com um ano hidrológico normal em 2003, até atingir a condição de seca extrema em 2005, resultando numa diminuição do fluxo fluvial. Ocasionalmente, foram observadas temperaturas anormais elevadas da água. Durante o ano de seca os recrutamentos de *P. minutus* foram pouco expressivos e a coorte parental desapareceu rapidamente, traduzindo-se num decréscimo da densidade e produção. Para *P. microps* este decréscimo não foi muito pronunciado. Não foi possível concluir um efeito directo das variações de salinidade e temperatura para os decréscimos observados. Contudo foi sugerida a hipótese do aumento de predação em *P. minutus*, dado que a maior incursão salina no estuário conduziu a um aumento de espécies de peixes marinhos adventícios piscívoros a jusante, onde *P. minutus* se distribui mais frequentemente. *Pomatoschistus microps* beneficiou de uma maior tolerância a variações na salinidade e temperatura, permitindo-lhe ocupar diferentes áreas no estuário, e desta forma pareceu melhor adaptado para lidar com as variações ambientais. Posteriormente foi desenvolvido um modelo ecológico para as mesmas espécies, com intuito de simular a dinâmica populacional (densidade e biomassa) de ambas. Para tal, foi utilizado como base, para obtenção dos parâmetros necessários ao modelo, o estudo de campo no período de três anos referido anteriormente. O modelo compreendeu duas fases/sub-modelos: 1) o de crescimento individual; e 2) dinâmica populacional (densidade) de juvenis e adultos. Estes sub-modelos foram agrupados para formarem o modelo de uma coorte (densidade e biomassa). As coortes foram então agrupadas e organizados de acordo com os recrutamentos de cada espécie, de forma a simular a população dos peixes em estudo. Os valores simulados pelo modelo foram concordantes com os valores reais de densidade e biomassa, obtidos no estudo de campo. Este procedimento permitiu igualmente constituir hipóteses no que respeita a possíveis condicionantes no desenvolvimento dos peixes em estudo, com particular relevância aos efeitos da seca extrema.

A dieta de 14 espécies de peixe foi analisada no capítulo III. Entre as presas mais importantes constavam macroinvertebrados, nomeadamente vários poliquetas (*Nephtys* spp., Capitellidae, Spionidae e Eunicidae), *Corophium* spp. e *Crangon crangon*. Os peixes mais predados foram *Pomatoschistus* spp., e os copépodes calanoides as principais espécies presas de plâncton. Vários peixes demonstraram alguma tendência para uma dieta especializada. No entanto, quase todos demonstraram algum oportunismo alimentar, dado se alimentarem, ocasionalmente ou frequentemente, doutros recursos disponíveis no sistema. Foi observada uma elevada sobreposição alimentar entre algumas espécies de peixe, mas não foi possível concluir a existência de competição por recursos alimentares.

Finalmente, no capítulo IV, a produção dos peixes residentes (*P. minutus* e *P. microps*) e dos peixes marinhos utilizando o estuário como viveiro (*Dicentrarchus labrax*, *Platichthys flesus* e *Solea solea)* foi avaliada, no período de Junho 2003 a Maio 2006. Estas espécies compreenderam cerca de 70% da comunidade ictiológica, no que respeita a densidade e biomassa. No geral, a produção do estuário do Mondego foi menor que noutros sistemas, sendo associada à área relativamente pequena do estuário. A produção decresceu no ano da seca, especialmente evidente para *D. labrax*, *P. minutus* e *P. flesus*. Não foi possível provar que estes efeitos se deviam às variações da temperatura e salinidade, e ao baixo fluxo fluvial (resultantes da seca e altas temperaturas). No entanto, estes constituíram a base para as hipóteses sugeridas para o decréscimo na produção: efeito directo, devido às tolerâncias de cada espécie e efeito indirecto através de um possível aumento da predação. Relativamente ao potencial de produção a ser exportado do estuário para zonas costeiras pelas espécies marinhas juvenis também se verificou uma diminuição durante as condições de seca.

GENERAL INTRODUCTION

Estuarine ecosystem, its production and major threats

Estuaries and coastal lagoons are among the most productive natural ecosystems in the world (Kennish 2002, McLusky & Elliott 2004, Gamito et al. 2005, Dolbeth et al. 2007). This high production lies in their high primary production and because they act as detritus traps for the abundant autochthonous and allochthonous material (Elliott et al. 2002, Akin & Winemiller 2006, Svensson et al. 2007). Thus, a plentiful supply of food resources is available for the estuarine inhabitants, either for direct or indirect consumption (throughout the steps of the food chain) (Elliott et al. 2002, McLusky & Elliott 2004, Gamito et al. 2005).

Allied to the abundant food availability is the high diversity of habitats, allowing shelter and protection, which are considered as primary attractions for invertebrate (Cardoso et al. 2004, Dolbeth et al. 2007, Ferreira et al. 2007), fish (Haedrich 1983, Beck et al. 2001, Elliott et al. 2002, Cabral et al. 2007, Leitão et al. 2007, Martinho et al. 2007) and bird (Lopes et al. 2006) species. These invertebrate, fish and bird species may use the estuary during their complete life cycle or at least in part of it for a rapid growth and development, as nursery grounds, as migratory routes or simply as food supplier (for the resident, migratory and/or occasional species) (McLusky & Elliott 2004, Gamito et al. 2005).

Although estuaries are biologically challenging, as inhabitants are exposed to great physiological stress, they are focal points around which many coastal communities develop and grow (McLusky & Elliott 2004, Svensson et al. 2007). Fisheries, agriculture and other industries prosper in and around estuarine ecosystems, forming a large economic resource from those communities and the ecosystem itself (Kennish 2002, Svensson et al. 2007, Vasconcelos et al. 2007). Additionally, estuaries have several other goods and services critical to the society, besides providing food. These include: decomposition and nutrient cycling, flux regulation of water and pollutants, protection against natural hazards, recreation and tourism, among others (Costanza et al. 1997, Kennish 2002, McLusky & Elliott 2004, Martinez et al. 2007). Thus, estuaries are also considered among the most economic valuable aquatic ecosystems (Costanza et al. 1997, Martinez et al. 2007). A great part of human population is attracted to live on estuarine shores and coastal areas and this human concentration has placed these environments under increasing human pressure (Martinez et al. 2007). Consequently, a wide array of human impacts may be expected, colliding with the ecological function of estuaries and threatening their long term integrity (Kennish 2002, McLusky & Elliott 2004, Martinez et al. 2007, Vasconcelos et al. 2007). In fact, reports on eutrophication and habitat loss are frequent worldwide (Kennish 2002, Cardoso et al. 2004, 2007, Dolbeth et al 2005, 2007, Lillebø et al. 2007), along with the over exploitation of the estuarine natural resources (McLusky & Elliott 2004, Vasconcelos et al. 2007). These have been considered as major threats to estuarine and coastal ecosystems (McLusky & Elliott 2004, Martinez et al. 2007).

Also, the increasing rate of climate variability, hypothesized to be a direct consequence of global climate change, has been focusing scientists' attention on how this change may affect the biota and the ecological functions of several ecosystems (Roessig et al. 2004, Emmerson et al. 2005, Meynecke et al. 2006, Marques et al. 2007). Estuaries are particularly sensitive to environmental parameters. The interacting effects of numerous global changes, including rising temperatures, altered precipitation patterns, nutrient cycling changes, and species loss, are assumed to affect greatly the structure and functioning (such as the productivity and stability of the food webs) of the estuarine system (Emmerson et al. 2005). So, besides the severe anthropogenic and inherent natural stress, estuaries and their inhabitants will have to deal with increased climate variations occurrence.

Understanding the estuarine environment

A major challenge for ecologists is the understanding of the ecosystem dynamics and function under natural, climate and anthropogenic impacts. Biodiversity, stability and natural productivity are considered as three major aspects of an ecosystem (Begon et al. 1996). Several studies have been focusing on these aspects when trying to assess the estuaries ecological integrity. In fact, due to the increasing human pressure on aquatic ecosystems several countries have been developing criteria and tools in order to evaluate their ecological status. The aim of this evaluation is to implement future measures to improve the water physicochemical and ecological status (e.g. European Union Water Framework Directive, European Marine Strategy, Convention for the Protection of the Marine Environment of the North-East Atlantic, among others) (Lillebø et al. 2007, Teixeira et al. 2007).

Several methods (or combination of methods) have been proposed to assess the ecological status. In general, they define the threshold regarding a reference condition (ecological and physicochemical properties) considered to be in high quality status and analyze the deviation to that threshold (Lillebø et al. 2007, Teixeira et al. 2007). The structure cannot be apart from the function and, recently, more attention has been given to whether an "estuary is still functioning as an estuary" after a disturbance (Elliott & Quintino 2007). Hence, methods to study structural and functional symptoms are being recommended (Elliott & Quintino 2007).

One approach to study the ecosystem function may be through the analysis of the different components contributing to production and how this production may be influenced by external factors. This information may provide considerable insight on the actual ecological integrity of the studied ecosystem. The production integrates the influence of numerous biotic variables and environmental conditions affecting individual growth and population mortality (Cusson & Bourget 2005, Dolbeth et al. 2005). Some studies have tried to assess anthropogenic or climate impacts on the ecosystem, through the study of the macroinvertebrate population or community production (Brey 2001, Cusson & Bourget 2005, Dolbeth et al. 2005, 2007, Ferreira et al. 2007). Since the fish and shellfish harvested, from marine ecosystems, depend on the production of lower trophic levels, production studies can also be used to infer on the carrying capacity for those resources (Cowley & Whitfield 2002, McLusky & Elliott 2004). In order to understand this, it is also important to know the fish and shellfish prey. Some prey, although highly productive, may not be accessible or preferred by the higher trophic levels (Elliott et al. 2002, McLusky & Elliott 2004).

Regarding fish production, studies have been focusing in predicting potential yields for fishery species (Cowley & Whitfield 2002). Yet, the potential of fish production for evaluating stress is higher, especially when assessing resident species or species spending an important part of the life cycle in the estuarine systems (i.e., marine dependent species). These are directly linked to higher trophic levels, or may constitute itself a significant amount of biomass exported for coastal recreational and commercial fisheries (Houde & Rutherford 1993, Cowley & Whitfield 2002). This knowledge may be also useful for ecosystem modelling (energy budget) studies (Costa et al. 2002, Cowley & Whitfield 2002).

Secondary production estimation

Secondary production studies are extremely time-demanding (Cowley & Whitfield 2002, Dolbeth et al. 2005). Although extremely useful as a quantification of the ecosystem dynamics, this measure cannot be used as a quick tool to evaluate the quality status of a system.

In order to achieve confident and reliable estimates of production for invertebrate and fish sufficient sampling time (at least 1 year) and high sampling effort is needed, making the study expensive (Costa et al. 2002, Cowley & Whitfield 2002, Cusson et al. 2006). The classical techniques are broadly classified as cohort-based (Allen curve, increment summation, removal summation, instantaneous-growth) and size-based (size frequency, mass-specific growth rate and mass-specific mortality rate) (Cusson et al. 2006). The cohort-based methods have been assumed to provide the best estimates of production, and they are widely used in several studies with invertebrate (Brey 2001, Cusson & Bourget 2005, Dolbeth et al. 2005, 2007, Ferreira et al. 2007) and fish (Costa et al. 2002, Cowley & Whitfield 2002). Following each species population and biomass dynamics is required in these studies. Cohorts must be recognized and followed (when there is synchronic development), so that a survivorship curve (density against individual biomass) may be defined. The different cohort methods are simply different ways of quantifying the area within the survivorship curve of the each cohort (Crisp 1984). The production of the population will be the sum of each of the cohorts' production along the study time period (Crisp 1984). The estimation of community secondary production for invertebrate or fish is laborious task. Very often the available data is not sufficient to apply the classical methods of production. This happens when: 1) there are no cohorts or age determination is not possible (size-based methods may be applied, although they are also time demanding); 2) the species have occasional occurrence in the system (Dolbeth et al. 2005). For fish, this task may be even more difficult since their populations are very dynamic due to fluctuating levels of recruitment and migration (Costa et al. 2002, Cowley & Whitfield 2002).

In order to find an easier, quicker and reliable way to estimate secondary production, some authors have tried to establish methods based on empirical relationships. For invertebrates, several equations were proposed, relating the production or the $P/\overline{B}$ ratio to the population or/and environment parameters (Brey 2001, Dolbeth et al. 2005). The $P/\overline{B}$ ratio corresponds to annual production divided by the annual mean biomass, and constitutes a measure of the species turnover rate (Brey 2001, Dolbeth et al. 2005). Some equations were also proposed for fish (Edgar & Shaw 1995). Some works with estuarine fish have considered a $P/\overline{B}$ ratio varying within 2.5 and 2.75 representative of fish general $P/\overline{B}$ ratios, and production has been computed from these ratios and the measured biomass (Hostens & Hamerlynk 1994, Costa et al. 2002). Although empirical methods constitute an easier way to estimate secondary production, results have to be interpreted with caution, as they will provide only a mean result. High deviations from the real production may be observed with empirical estimates, especially for single species production (Cusson & Bourget 2005, Dolbeth et al. 2005).

The study system: the Mondego estuary

The field work of the present thesis was done in the Mondego estuary (Portugal), located in a warm temperate region, on the Atlantic coast of Portugal (40°08'N, 8°50'W), near to Figueira da Foz city. It is a small estuary (3.4 km^2 area), with two arms (north and south) of distinct hydrologic characteristics, separated by the Murraceira island (Fig. 1). The north arm is deeper (4-10 m during high tide, tidal range 1-3 m) and constitutes the main navigation channel and the location of the Figueira da Foz harbour. The main freshwater inputs to the north arm are from the Mondego river (Fig. 1). The south arm is shallower (2-4 m during high tide, tidal range 1-3 m) and characterized by large areas of exposed intertidal flats during low tide (about 75% of total area). Water circulation in the south arm mostly depends on the tides and on the freshwater input from the Pranto river (Fig. 1), as the upstream areas are almost silted up, with only a small connection with north arm. The downstream areas of the south arm exhibit *Spartina maritima* marshes and *Zostera noltii* beds (Fig. 1).

Studies carried out in the Mondego estuary, in the last 15 years, have provided a large database and a comprehensive information background. These include studies related to the structure or/and functioning of the system, regarding their nutrient dynamics (Lillebø et al. 2005, 2007 and references therein), sedimentary dynamics, parasite populations (Ferreira et al. 2007 and references therein), primary producers (Cardoso et al. 2004, Martins et al. 2007 and references therein), plankton community (Marques et al. 2007 and references therein), intertidal and subtidal macroinvertebrate populations and community (Cardoso et al. 2004, 2007, Dolbeth et al. 2007, Ferreira et al. 2007, Teixeira et al. 2007, and references therein), fish populations and community (Leitão et al. 2007, Martinho et al. 2007 and references therein), bird populations (Lopes et al. 2006 and references therein), as well as the relation within them (Marques et al. 2003, Silva-Santos et al. 2006, Patrício & Marques 2006 and references therein).

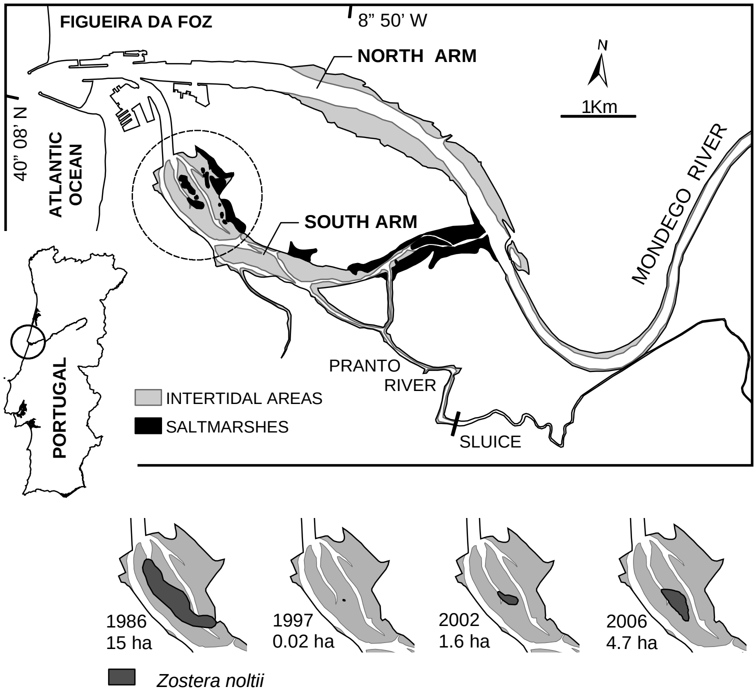


Fig. 1 The Mondego estuary, with indication of intertidal area, salt marshes and the seagrass bed (*Zostera noltii*) evolution in the south arm since 1986 until 2006.

Anthropogenic pressures

The Mondego estuary has a high regional value for man, sustaining several industries (mostly cellulose and paper related industries), aquacultures (several old salt-ponds transformed into semi-intensive aquacultures), some traditional salt extraction, the location of the mercantile harbour of Figueira da Foz city and a marina (Ribeiro 2002). There is also an increasing human pressure in the area, with more than 60 000 habitants in Figueira da Foz city (Ribeiro 2002). Upstream the estuary, in the Lower Mondego valley, there are agriculture fields (more than 15 000 ha of cultivated land), producing mainly rice (Lillebø et al. 2005). Several interventions were made along the river bed and the Mondego valley in order to improve irrigation efficiency of the agriculture fields and for the water supplies of the cellulose industries. They included construction of channels, regularization of margins (to reduce flooding of the fields), construction of dams to regulate the water level inside the fields and intensification of land use (Ribeiro 2002, Cardoso et al. 2007). Additionally, the Mondego estuary is also affected by resource exploitation, mainly through fishing directed to some fish species, such as eel and lamprey, as well as illegal capture of juvenile eel (glass eel), sea bass, flounder and sole (Martinho 2005), and the capture of cockles and clams (Cardoso et al. 2007).

These anthropogenic activities have been the cause of high environmental pressure on the estuary, due to physical disturbance, due to the high input of nutrients from agricultural fields and aquacultures, and due to the pollutants input from the domestic and industrial discharges (Ribeiro 2002, Lillebø et al. 2005, Cardoso et al. 2007). Accordingly, the main disturbance sources on the two arms of the estuary can be summarized into:

1) Constant dredging and shipping in the north arm, causing the physical disturbance of the bottoms, with the re-suspension of sediments and pollutants;

2) Raw sewage disposal and high nutrient inputs from agricultural and fish farms in the upstream areas of the south arm.

In fact, until the end of 1998, the south arm of the Mondego estuary was almost silted up in the upstream areas. Water circulation was mainly dependent on tides and on the freshwater input from the Pranto river. This was artificially controlled by a sluice, according to the rice fields irrigation needs in the Lower Mondego valley. The occasional freshwater flow to the estuary caused the high input of nutrients and high water residence time (about 5-7 days) (Lillebø et al. 2005). Consequently, since the 80's, clear eutrophication symptoms were observed. The downstream areas maintained *S. maritima* marshes and the *Z. noltii* bed, but in the inner parts of the estuary the seagrass bed completely disappeared and blooms of the opportunistic macroalgae *Ulva* spp. were common (Lillebø et al. 2005, Cardoso et al., 2007, Dolbeth et al. 2007, Ferreira et al. 2007). The occurrence of macroalgae blooms were pointed out as one of the major reason for *Z. noltii* decline, which was reduced from 15 ha in 1986 to 0.02 ha in 1997 (Fig. 1) (Cardoso et al. 2007, Dolbeth et al. 2007).

Restoration process of Mondego's South Arm

In 1998/99, mitigation measures were taken in order to restore the original seagrass bed of the south arm (Lillebø et al. 2005, Cardoso et al. 2007, Dolbeth et al. 2007). These included the reduction of nutrient loading and the water residence time (from 5-7 days to 1 day) through:

1) reduction of Pranto river sluice opening (most of the nutrient enriched freshwater was then diverted through the north arm by another sluice located more upstream);

2) improving the hydraulic regime, by enlarging the upstream connection between the two arms and allowing water to flow from the north arm at high tide conditions (Lillebø et al. 2005, Cardoso et al. 2007).

These measures seemed to have some success. Nutrient loading was significantly reduced and no further macroalgal blooms were recorded (Lillebø et al. 2005, Cardoso et al. 2007, Ferreira et al. 2007). In addition, *Z. noltii* is gradually recovering, both in biomass and extent (4.7 ha in 2006, Fig. 1), starting to re-colonize the upstream areas (personal observation). The biomass and production of the macrozoobenthic community also increased, together with a slight increase in biodiversity (Cardoso et al. 2007, Dolbeth et al. 2007). The Polychaeta *Alkmaria romijni* and *Capitella capitata*, considered as indicators of nutrient enrichment and pollution of estuarine systems, gradually declined (Cardoso et al. 2007).

Climate as a forcing function

The understanding of how climate change will affect the planet is a key issue worldwide and lately more attention has been given to the global ecological change. There is a clear increased rate of scientific reports (Intergovernmental Panel on Climate Change - IPCC reports) and papers (e.g. current contents will produce over 7 500 references under the "global climate change" theme search) on the subject. The scientific data has even been transposed to several didactic documentaries to general public (e.g. "Inconvenient Truth", by Al Gore). This is a clear sign that at least a part of the society is concerned with this human generated problem. In fact, climate warming is unequivocal, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and global mean sea level rise (Alley et al. 2007 from IPCC report).

In these last years several differences in the climate of Portugal have been recorded when compared to the general climate patterns for last century (IM - Portuguese Weather Institute http://web.meteo.pt/pt/clima/clima.jsp, INAG - Portuguese Water Institute http://snirh.inag.pt). Although this cannot be proven to be a consequence of global climate change, the occurrence of these events mostly in the last decade suggests that such climate patterns are not a normal cycle. In fact, six of the last twelve years ranked among the warmest and driest years for the last 100 years (IM). There was high variability in precipitation regime, with active hydrological cycles of heavy precipitation events and

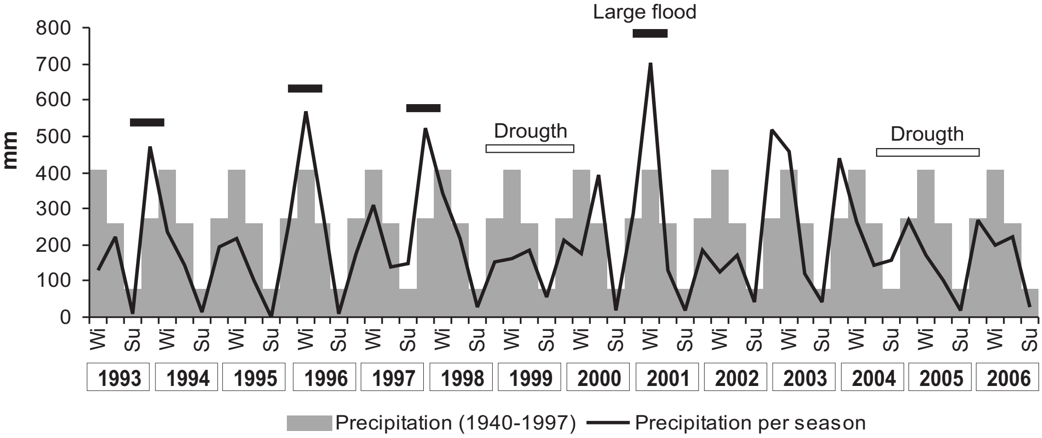


Fig. 2 Seasonal values of precipitation from 1993 to 2006, with indication of the mean values for the period of 1940 to 1997.

drastic shifts to very low levels in precipitation (Fig. 2). Along the study period, from 1993 to 2006, the winter 2000/01 reached unprecedented high values of precipitation, especially for the central Portugal (2000/01: 1802.1 mm against a mean annual value for 1940 to 1997: 1030.6 mm, Fig. 2), causing one of the largest floods of the century. It was followed by the gradual occurrence of a drought, starting in 2004 and attaining a severe drought in 2005 (2005: 486.1 mm against the mean annual of 1030.6 mm, Fig. 1). Additionally, a clear increase of mean air temperature has been recorded and several episodes of exceptional high air temperatures (heat waves) were also registered, mainly in 2003 (IM).

REFERENCES

Alley R, Berntsen T, Bindoff NL, Chen Z, Chidthaisong A, Friedlingstein P, Gregory J, Hegerl G, Heimann M, Hewitson B, Hoskins B, Joos F, Jouzel J, Kattsov V, Lohmann U, Manning M, Matsuno T, Molina M, Nicholls N, Overpeck J, Qin D, Raga G, Ramaswamy V, Ren J, Rusticucci M, Solomon S, Somerville R, Stocker TF, Stott P, Stouffer RJ, Whetton P, Wood RA, Wratt D (2007) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change, p 21.

Akin S, Winemiller KO (2006) Seasonal variation in food web composition and structure in a temperate tidal estuary. Estuar Coast 29 (4): 552–567.

Beck MW, Heck KL, Able JrKW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51: 633–641.

Begon M, Harper JL, Towsend CR (1996) Ecology. Individuals, populations and communities. 3rd Edition. Blackwell Science, p 1068.

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. *http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html* Alfred Wegener Institute for Polar and Marine Research, Germany.

Cabral NH, Vasconcelos RP, Vinagre C, França S, Fonseca V, Maia A, Reis-Santos P, Lopes M, Ruano M, Campos J, Freitas V, Santos P, Costa MJ (2007) Relative importance of estuarine flatfish nurseries along the Portuguese coast. J Sea Res 57: 209–217.

Cardoso PG, Pardal MA, Lillebø AI, Ferreira SM, Raffaelli D, Marques JC (2004) Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. J Exp Mar Biol Ecol 302: 233–248.

Cardoso PG, Bankovic M, Raffaelli D, Pardal MA (2007) Polychaete assemblages as indicators of habitat recovery in a temperate estuary under eutrophication. Estuar Coast Shelf Sci 71: 301–308.

Costa MJ, Cabral HN, Drake P, Economou AN, Fernandez-Delgado C, Gordo L, Marchand J, Thiel R (2002) Recruitment and production of commercial species in estuaries. In: Elliot M, Hemingway K (Eds) Fishes in estuaries. Blackwell Science, Bodmin, United Kingdom, p 54–123.

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Naeem S, Limburg K, Paruelo J, O'Neill RV, Raskin R, Sutton P, ven den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387: 253–60.

Cowley PD, Whitfield AK (2002) Biomass and production estimates of a fish community in a small South African estuary. J Fish Biol 61: 74–89.

Crisp DJ (1984) Energy flow measurements. In: Holme NA, McIntyre AD (Eds). Methods for the study of marine benthos. 2nd Edition. Blackwell Scientific Publications, Norfolk, USA, p 284–372.

Cusson M, Bourget E (2005) Global patterns of macroinvertebrate production in marine benthic habitats. Mar Ecol Prog Ser 297: 1–14.

Cusson M, Plante JF, Genest C (2006) Effect of different sampling designs and methods on the estimation of secondary production: a simulation. Limnol Oceanogr: Methods 4: 38–48.

Dolbeth M, Lillebø AI, Cardoso PG, Ferreira SM, Pardal MA (2005) Annual production of estuarine fauna in different environmental conditions: an evaluation of the estimation methods. J Exp Mar Biol Ecol 326: 115–127.

Dolbeth M, Cardoso PG, Ferreira SM, Verdelhos T, Raffaelli D, Pardal MA (2007) Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a ten-year period. Mar Pollut Bull 54: 576–585.

Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish assemblages in southern Australia I. Species richness, size-structure and production of fishes in Western Port, Victoria. J Exp Mar Biol Ecol 194: 53–81.

Elliott M, Hemingway KL, Costello MJ, Duhamel S, Hostens K, Labropoulou M, Marshall S, Winkler H (2002) Links between fish and other trophic levels. In: Elliot M, Hemingway K (Eds) Fishes in estuaries. Blackwell Science, Bodmin, United Kingdom, p 124–216.

Elliott M, Quintino V (2007) The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar Pollut Bull 54: 640–645.

Emmerson M, Bezemer M, Hunter MD, Jones TH (2005) Global change alters the stability of food webs. Glob Chang Biol 11: 490–501.

Ferreira SM, Brandão A, Baeta A, Neto JM, Lillebø AI, Marques JC, Jensen KT, Pardal MA (2007) Effects of restoration management on the estuarine isopod *Cyathura carinata*: mediation by trematodes and habitat change. Mar Biol 151:109–118.

Gamito S, Gilabert J, Diego CM, Pérez-Ruzafa A (2005) Effects of changing environmental conditions on lagoon ecology. In: Gönenç IE, Wofflin J (Eds) Coastal lagoons: ecosystem processes and modelling for sustainable use and development. CRC Press, Boca Raton, USA, p 193–229.

Haedrich RL (1983) Estuarine fishes. In: Ketchum B (Ed) Ecosystems of the world: estuaries and enclosed seas. Elsevier, Amsterdam, The Netherlands, p 183–207.

Hostens K, Hamerlynck O (1994) The motile epifauna of the soft bottoms in the subtidal Oosterschelde estuary: structure, function and impact of storm-surge barrier. Hydrobiologia 282/283: 479–496.

Houde ED, Rutherford ES (1993) Recent trends in estuarine fisheries: prediction of fish production and yield. Estuaries 16:161-176.

Kennish MJ (2002) Environmental threats and environmental futures of estuaries. Environ Conserv 29: 78–107.

Leitão R, Martinho F, Cabral HN, Neto JM, Jorge I, Pardal MA (2007) The fish assemblage of the Mondego estuary: composition, structure and trends over the past two decades. Hydrobiologia 587: 269–279.

Lillebø AI, Neto JM, Martins I, Verdelhos T, Leston S, Cardoso PG, Ferreira SM Marques JC, Pardal MA (2005) Management of a shallow temperate estuary to control eutrophication: The effect of hydrodynamics on the system's nutrient loading. Estuar Coast Shelf Sci 65: 697–707.

Lillebø AI, Teixeira H, Pardal MA, Marques JC (2007) Applying quality status criteria to a temperate estuary before and after the mitigation measures to reduce eutrophication symptoms. Estuar Coast Shelf Sci 72: 177–187.

Lopes RJ, Pardal MA, Múrias, T, Cabral JA, Marques JC (2006) Influence of macroalgal mats on abundance and distribution of dunlin Calidris alpina in estuaries: a long-term approach. Mar Ecol Prog Ser 323: 11–20.

Martinho FMD (2005) O estuário do Mondego como viveiro para a ictiofauna: Ecologia dos juvenis de *Dicentrarchus labrax*, *Platichthys flesus* e *Solea solea*. MSc thesis, University of Coimbra, p 66.

Martinho F, Leitão R, Viegas I, Dolbeth M, Neto JM, Cabral HN, Pardal MA (2007) The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. Estuar Coast Shelf Sci doi:10.1016/j.ecss.2007.05.040.

Martins I, Lopes RJ, Lillebø AI, Neto JM, Pardal MA, Ferreira JG, Marques JC (2007) Significant variations in the productivity of green macroalgae in a mesotidal estuary: Implications to the nutrient loading of the system and the adjacent coastal area. Mar Pollut Bull 54: 678–690

Martínez ML, Intralawan A, Vázquez G, Pérez-Maqueo O, Sutton P, Landgrave R (2007) The coasts of our world: ecological, economic and social importance. Ecol Econ 63: 254–272.

Marques JC, Nielsen SN, Pardal MA, Jørgensen SE (2003) Impact of eutrophication and river management within a framework of ecosystem theories. Ecol Model 166: 147–168.

Marques SC, Martinho F, Azeiteiro UM, Pardal MA (2007) Climate variability and planktonic communities: the effect of an extreme event (severe drought) in a southern European estuary. Estuar Coast Shelf Sci 73: 725–734.

McLusky DS, Elliott M (2004) The estuarine ecossystem. ecology, threats and management. 3rd Edition. Oxford, University Press, United Kigdom, p 213.

Meynecke JO, Lee SY, Duke NC, Warnken J (2006) Effect of rainfall as a component of climate change on estuarine fish production in Queensland, Australia. Estuar Coast Shelf Sci 69: 491–504

Patrício J, Marques JC (2006) Mass balanced models of the food web in three areas along a gradient of eutrophication symptoms in the south arm of the Mondego estuary (Portugal). Ecol Model 197: 21 – 34.

Ribeiro JLGS (2002) Conflicts in the Mondego estuary: sustainability of natural resources and of traditional land use. Littoral 2002, The Changing Coast. EUROCOAST / EUCC, Porto – Portugal Ed. EUROCOAST – Portugal, ISBN 972–8558–09–0.

Roessig JM, Christa MW, Joseph JrJC, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. Rev Fish Biol Fish 14: 251 – 275.

Silva-Santos P, Pardal MA, Lopes RJ, Múrias T, Cabral JA (2006) A Stochastic Dynamic Methodology (SDM) to the modelling of trophic interactions, with a focus on estuarine eutrophication scenarios. Ecol Indicat 6: 394 – 408.

Svensson CJ, Hyndes GA, Lavery PS (2007) Food web analysis in two permanently open temperate estuaries: Consequences of saltmarsh loss? Mar Environ Res 64: 286-304.

Teixeira H, Salas F, Borja Á, Neto JM, Marques JC (2007) A benthic perspective in assessing the ecological status of estuaries: the case of the Mondego estuary (Portugal). Ecol Indicat doi:10.1016/j.ecolind.2007.02.008.

Vasconcelos RP, Reis-Santos P, Fonseca V, Maia A, Ruano M, França S, Vinagre C, Costa MJ, Cabral H (2007) Assessing anthropogenic pressures on estuarine fish nurseries along the Portuguese coast: a multi-metric index and conceptual approach. Sci Total Environ 374: 199 – 215.

GENERAL AIM AND THESIS OUTLINE

The anthropogenic impacts and climate variations occurring in the Mondego estuary (as presented in the general introduction) have triggered the thesis major aim: to quantify those impacts on the overall energy/biomass of the system. Accordingly, the thesis core is structured into four chapters, comprising six papers. Essentially, there are three main questions to be answered, that constitute the specific aims of the thesis:

- What is the macrozoobenthos and fish production of the Mondego estuary?
- How is the macrozoobenthos and fish production influenced by anthropogenic and climate factors?
- How the macrozoobenthic production relates with the fish production? (possible fluxes of biomass/energy)

At the end of the thesis, a summarizing discussion with main conclusions is presented, where a general overview and integration of the four chapters are provided.

Chapter I

The first chapter deals with the macrozoobenthic community secondary production. In order to compute the whole community production, empirical methods have to be used. The first paper, "Annual production of estuarine fauna in different environmental conditions: an evaluation of the estimation methods", has the major objective to find the best empirical method to estimate secondary production in marine macroinvertebrate populations. The production estimated by the different empirical methods is evaluated for different *taxa* (with different life history strategies) and different environmental scenarios. Estimates computed by a cohort method were used as benchmark for the comparisons with the estimates of the empirical methods.

After defining the best empirical method, the macrozoobenthic community production is estimated, using a cohort method for dominant species and empirical methods for the remaining ones. One of the aims of "*Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a ten-year period*" is to provide the background history of Mondego estuary, regarding their anthropogenic and natural impacts. Changes at ecosystem level are studied through the exploration of the intertidal macrobenthic production over a ten-year period (from 1993 to 2002). During this time period the system suffered from eutrophication (with the decrease of the *Z. noltii* bed) and experienced extreme weather-related events (large flood). Additionally, this study aims to assess the effectiveness of the restoration plan implemented by the end of 1998. Besides the regional relevance, this study has also a global importance, considering that eutrophication is a worldwide problem affecting coastal areas and there is an increasing occurrence of climate extremes.

Macrobenthos are important food resources for several upper trophic levels in the food web. Changes in their production will affect other estuarine inhabitants, such as fish and birds. This perspective has triggered the development of the following chapters of the thesis, focusing on fish dynamics, production and possible interconnections with the macrobenthos production.

Chapter II

The second chapter focuses essentially on the population dynamics and biomass production of two resident fish species: *Pomatoschistus minutus* and *Pomatoschistus microps*. These gobies are among the most abundant in the Mondego estuary and on several other European estuaries. Besides being dominant species, these fish are also intermediates in the estuarine food web, being an important link between invertebrates and other fish. A detailed analysis of the fish dynamics and production will allow an overview of the potential external impacts on the ecosystem during a time period not assessed by the previous chapter, i.e., from 2003 to 2006.

"*Strategies of Pomatoschistus minutus and Pomatoschistus microps to cope with environmental instability*", has the aim to assess the strategies of both species to cope with changing environment within a three-year period (2003-2006). Particular importance was given to the effects of the drought occurred in 2004 and 2005 on the fish development, through an analysis of life history and population dynamics. Additionally, it aims to reveal if one species is dominant towards the other and if this relation changes along the study period.

One fundamental aspect when trying to estimate secondary production is to follow the density and individual biomass of the population through time within an ecosystem. This aspect constitutes the major goal of "*Modelling the life cycle, population and biomass dynamics of two Gobiidae fish species*", where the main idea is to build a model, using *Stella* programming language, to simulate the fish population and biomass dynamics. The target species were *P. minutus* and *P. microps*, whose baseline information for the model development has been studied in the previous paper. Comparing the real data with the modelled one will also enable to set hypotheses, regarding the potential restrictions to the population development.

Chapter III

The intertidal macrobenthos and the gobies *P. minutus* and *P. microps* are important in the estuarine food web, in particular for other fish. Yet, interconnections with each other and other fish are not known. In chapter III the actual link between the macrobenthos and fish is studied. Objectives of "*Feeding patterns of a temperate estuarine fish community: detecting major links within trophic levels*" are to identify the major prey of the fish community (at least of the most abundant fish) and infer on the basal resource of the Mondego estuary. Additional objectives include the understanding of fish feeding strategies and to infer on the potential competition for food resources. A simplified estuarine fish food web will also be set. This chapter may clarify if the main productive invertebrate species are actually preyed or not.

Chapter IV

Finally, chapter IV deals with the production of the most abundant fish of the Mondego estuary, i.e., the resident species and the marine juvenile species using the estuary as nursery area. "*Estuarine production of resident and nursery fish species: conditioning by drought events?*" aims to reveal the productive potential of the estuary for the fish resources during 2003-2006, giving particular focus to the potential production exports from the marine juveniles to coastal stocks. Furthermore, the study is conducted in order to understand how an extreme drought can affect the fish production. By analysing anthropogenic impacts in the Mondego estuary throughout the last decades (habitat loss and decrease in macroinvertebrate production) hypotheses will also be suggested regarding their influence on the fish production.

CHAPTER I

Secondary production of estuarine macrobenthic invertebrate communities

Annual production of estuarine fauna in different environmental conditions: An evaluation of the estimation methods

Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a ten-year period

Annual production of estuarine fauna in different environmental conditions: an evaluation of the estimation methods

Abstract Secondary production is one of the most comprehensive measurements of ecosystem health. Production of five estuarine species, with different life history and abundance in the ecosystem, was estimated for 2 consecutive years at a *Zostera noltii* bed and sand-muddy area, with contrasted environmental conditions. Calculations were performed using different estimation methods, commonly cited in secondary production studies. Annual production estimated by cohort increment summation varied between 43.3 and 209.2 g AFDW m^{-2} y^{-1}. All the other methods were compared with the results obtained from this methodology to evaluate each method's performance. In general, satisfactory results were obtained with Brey (2001) [Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. *http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html.* Alfred Wegener Institute for Polar and Marine Research, Germany] version 4-04 (deviations that ranged between -4 to +10%). The responses of the other empirical methods were more variable, depending on the species characteristics. Therefore, the optimal selection of an empirical method in secondary production studies depends on the species considered and on the quality of the parameters required for the application of the method. Brey (2001) [Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook.Version 01.2. *http://www.awibremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html.* Alfred Wegener Institute for Polar and Marine Research, Germany] version 4-04 was considered the best methodology. For the less representative species the simple sum of biomass increments from one sampling date to the next may be an easy and valid option.

Keywords Cohort increment summation, Empirical methods, Eutrophication, Macrobenthic production

INTRODUCTION

Somatic production of macrozoobenthic populations is an important parameter for the study of ecosystem dynamics. It is a quantitative measure of population function in the ecosystem, being often used to assess environmental stress, rational management of biological resources, energy flow, organic matter cycling and food web interactions (Waters & Crawford 1973, Cushman et al. 1978, Benke 1984, 1993, Crisp 1984; Morin et al. 1987, Tumbiolo & Downing 1994). Moreover, it may acquire economic importance, when related with fish and shellfish yield (Waters & Crawford 1973, Crisp 1984, Brey 1990a).

For long time, methods based on the recognition of cohorts have been considered to provide accurate evaluation of secondary production (Waters & Crawford 1973, Cushman et al. 1978, Benke 1993, Sprung 1993, Medernach 1999, Brey 2001).

Whenever cohorts are not recognizable, size frequency and mass specific growth rate methods have been applied (Benke 1984, Brey 2001). Nevertheless, estimations made by these methods are time consuming and often data are not available (Brey 1990a, Sprung 1993, 1994, Medernach 1999, Dolbeth et al. 2003).

In order to find an easier yet reliable way to estimate secondary production, many authors have tried to establish methods based on empirical relationships (Robertson 1979, Banse & Mosher 1980, Schwinghamer et al. 1986, Brey 1990a, Morin and Bourassa 1992, Benke 1993, Sprung 1993, Tumbiolo & Downing 1994, Brey 2001). These methods are based on good correlations found between population (e.g. life span, maximum individual weight, mean individual weight, mean biomass) or environment (e.g. temperature, depth) characteristics and secondary production or $P/\overline{B}$ ratio (Medernach 1999, Brey 2001). Still, estimates obtained by these methods must be analysed cautiously, as they may be misleading in certain cases (Sprung 1993, Morin 1997, Medernach 1999, Brey 2001, Mistri et al. 2001).

In the present study, secondary production was estimated and compared using cohort increment summation and empirical methods for five species whose lifestyles are representative of *taxa* generally found in intertidal flats. First, the secondary production was estimated by cohort increment summation and computed in order to: a) provide reference values of the species production in different habitats, b) understand the production variations in the different habitats and environments; second, secondary production was estimated by empirical methods in order to: c) understand the performance of each empirical method for different species and habitats, d) find the best alternative methodology to estimate secondary macrobenthic production in temperate estuaries.

MATERIALS AND METHODS

Study site and sampling

The Mondego estuary (Portugal) is located in a warm temperate region (40°08'N, 8°50'W) and has two arms. Anthropogenic activities in the estuary have been the cause of high environmental pressure, which has resulted in persistent eutrophication over the past two decades. The downstream areas of the south arm still remain relatively unchanged, exhibiting *Zostera noltii* meadows, whereas in the inner parts, the seagrass community has completely disappeared and *Ulva* spp. blooms have been observed (Lillebø et al. 1999, Pardal et al. 2000, 2004, Cardoso et al. 2002, 2004, Dolbeth et al. 2003, Ferreira et al. 2004).

Sampling occurred fortnightly from February 1993 to June 1994 and monthly until February 1995, at low tide in the Mondego estuary south arm. Two sites were considered: a) non-eutrophic area, *Zostera noltii* bed and b) eutrophic area, a sand-flat where an *Ulva* spp. bloom occurred in the spring 1993, followed by the algal crash in July 1993. On each sampling occasion, 6 to 10 cores (141 cm^2) were taken to a depth of 20 cm. Samples were washed in 500 µm mesh sieve bags. At the laboratory, the biological material was separated and preserved in a 4% buffered formalin solution. In the present study, five intertidal benthic species were used: a) *Hydrobia ulvae* (Gastropoda), dominant species at the *Zostera* bed, b) *Cyathura carinata* (Isopoda), dominant species at the eutrophic area, c) *Scrobicularia plana* (Bivalvia), more abundant at the eutrophic area and d) *Ampithoe valida* and *Melita palmata* (Amphipoda), less abundant species in both areas. All individuals were counted, measured and their ash-free dry weight (AFDW) assessed after combustion for 8 h at 450°C. Together, these species account for 80 – 90% of the total macrobenthic production in the Mondego estuary (Dolbeth et al. 2003).

Secondary production

Secondary production was estimated by the increment summation method (*Cohort*, Table 1), after recognition of the cohorts following the procedure of Lillebø et al. (1999), Pardal et al. (2000, 2002), Cardoso et al. (2002), Ferreira et al. (2004), Verdelhos et al. (2005). All cohorts were recognized through size–frequency distribution analysis of successive sampling dates, performed with ANAMOD software (Nogueira 1992). The production estimates of *S. plana* were made for individuals larger than 4 mm. These results (*Cohort*) were used as a reference to be compared with the estimates of the empirical methods.

Six empirical methods, commonly used in secondary production studies, were selected for estimate comparisons. The sum of biomass from one sampling date to next (*Inc Sum*) was also considered. All methods equations and symbols used in the text are presented in Table 1. The data required for the application of the empirical methods are presented in Table 2. Life spans (Table 2) were referred in Cardoso et al. (2002), Pardal et al. (2000, 2002), Ferreira et al. (2004) and Verdelhos et al. (2005).

Table 1 Methods used for the computation of secondary production, with reference to the method symbol and equation units.

Method	Equation	Symbol	Units
Cohort method			
Increment summation Winberg (1971)	$P = \sum_{t=0}^{T-1} \left(\frac{N_t + N_{t+1}}{2} \right) \times \left(\overline{w}_{t+1} - \overline{w}_t \right)$	*Cohort*	N, ind m^{-2}; $\overline{w}$, g AFDWm^{-2}
Empirical methods			
Robertson (1979)	$\mathit{log}\, P / \overline{B} = 0.66 - 0.726\, \mathit{log}\, L$	*Robert*	L, years
Shwinghamer et al. (1986)	$P / \overline{B} = 0.525 \overline{w}^{-0.304}$	*Schw*	$\overline{B}$ and $\overline{w}$, Kcal m^{-2}; Δt, days
Sprung (1993)	$P_{\Delta t} = \left(\frac{P / \overline{B}_{spec}}{365} / \overline{w}^{-0.25} \right) \times \overline{w}_{\Delta t}^{-0.25} \times \overline{B}_{\Delta t} \times \Delta t$	*Sprung 1, 2*	$\overline{w}$ and w_{ind}, g AFDW m^{-2};Δt, days
Morin & Bourassa (1992)	$\mathit{log}\, P = -0.75 + 1.01 \mathit{log}\, \overline{B} - 0.34\, \mathit{log}\, \overline{w} + 0.037 \times \overline{T}$	*M&B*	$\overline{B}$ and w, g DW m^{-2}; T, °C
Tumbiolo & Downing (1994)	$\mathit{log}\, P = 0.18 + 0.97\, \mathit{log}\, \overline{B} - 0.22\, \mathit{log}\, w + 0.04 \overline{T} - 0.014 \overline{T}\, \mathit{log}(D + 1)$	*T&D*	$\overline{B}$, g DW m^{-2} ; w_m, mg DW m^{-2} T, °C; D, m; Δt, days
Brey (2001)	$\log P / \overline{B} = 7.947 - 2.294 \log w - 2409.856 \times \left(1 / \left(T + 273 \right) \right) + 0.168 \times (1 / D) + + 0.194\, SubT + 0.180\, InEpi + 0.277\, MoEpi + 0.174\, Taxon\, 1 - 0.188\, Taxon\, 2 + + 0.33\, Taxon\, 3 - 0.062\, Habitat\, 1 + 582.851 \times (\log w \times (1 / (T + 273))$	*Brey 4-04*	w, kJ m^{-2}; T, °C; D, m
"Simple increment summation"	Sum of the increases in biomass from one sampling date to the next (application of the equation cohort, without the recognition of cohorts)	*Inc Sum*	N, ind m^{-2}; $\overline{w}$, g AFDWm^{-2}

P, production; $\overline{B}$, mean biomass; N, mean density; $\overline{w}$, mean individual body weight; w_m, maximum individual body weight; t, t+1, consecutive sampling dates (t = 1, 2, …n); Δt, difference between sampling dates; $P/\overline{B}_{spec}$, estimate of the typical $P/\overline{B}$ of the species; L, lifespan; T, mean bottom water temperature; D, mean depth; SubT, subtidal (SubT=1) or intertidal (SubT=0); InFau, infauna (InFau=1) or epifauna (InFau=0); MoEpi, motile epifauna (MoEpi =1) or not (MoEpi =0); Taxon1, Annelida or Crustacea (Taxon1=1) or other taxon (Taxon1=0); Taxon2, if Echinodermata (Taxon2=1) or other taxon (Taxon2=0); Taxon3, if Insecta (Taxon3=1) or other taxon (Taxon3=0); Habitat1, lake (Habitat1=1) or other habitat (Habitat1=0).

Table 2 Data used for the application of the empirical methods. $\overline{B}$, mean biomass; $\overline{w}$, mean body weight; w_m, maximum individual body weight; $P/\overline{B}_{spec}$, estimate of the typical $P/\overline{B}$ of the species; L, lifespan; T, mean bottom temperature.

	H. ulvae	***C. carinata***	***S. plana***	***A. valida***	***M. palmata***
General					
w_{max} (mg DW m^{-2})	96.9	67.0	6870.9	4.1	6.1
L (months)	16 to 20	23 to 24	62	7 to 9	4 to 7
$P/\overline{B}_{spec}$ 2	3.37	2.64	2.53	3.92	3.28
DW	16.104×AFDW-1.084	1.2003×AFDW-0.00004	18.054×AFDW-0.0031	1.0976×AFDW-0.0000008	1.1623×AFDW-0.000003
AFDW	0.0589×DW+0.00986	0.8258×DW+0.00004	0.0546×DW+0.0003	0.8258×DW+0.00004	0.826×DW+0.000005
Zostera 1993					
$\overline{B}$ (g AFDW m^{-2})	56.0	0.0862	2.19	0.964	0.0606
$\overline{w}$ (g AFDW m^{-2})	0.000982	0.00203	0.0474	0.000396	0.000238
$P/\overline{B}_{spec}$ 1	2.07	3.61	2.39	4.86	5.87
T (°C)	17.7	17.7	17.7	17.7	17.7
Zostera 1994					
$\overline{B}$ (g AFDW m^{-2})	67.1	1.12	2.01	0.0733	0.219
$\overline{w}$ (g AFDW m^{-2})	0.000865	0.00710	0.00732	0.000346	0.000206
$P/\overline{B}_{spec}$ 1	2.73	3.61	0.42	4.18	3.78
T (°C)	19.7	19.7	19.7	19.7	19.7
Eutrophic 1993					
$\overline{B}$ (g AFDW m^{-2})	9.49	7.22	10.3	0.123	0.0864
$\overline{w}$ (g AFDW m^{-2})	0.000225	0.00400	0.0840	0.000192	0.000125
$P/\overline{B}_{spec}$ 1	4.82	3.53	1.34	3.65	5.80
T (°C)	21.5	21.5	21.5	21.5	21.5
Eutrophic 1994					
$\overline{B}$ (g AFDW m^{-2})	1.78	9.60	4.04	0.00144	0.00802
$\overline{w}$ (g AFDW m^{-2})	0.000199	0.00488	0.0415	0.0000682	0.0000311
$P/\overline{B}_{spec}$ 1	4.52	2.98	0.12	8.88	3.67
T (°C)	20.0	20.0	20.0	20.0	20.0

For the application of Sprung (1993) method, an alternative equation was used (following previous instructions from the author). Two $P/\overline{B}_{spec}$ were tested: one calculated from the *Cohort* results, named as $P/\overline{B}_{spec}$ 1 (*Sprung 1*); and the other estimated as the mean of $P/\overline{B}$ ratios found in literature, for the same species in other temperate regions and similar environments, named as $P/\overline{B}_{spec}$ 2 (*Sprung 2*). In Tumbiolo & Downing (1994) method (*T&D*), a 0 m depth was considered, according to the suggestion of the authors for intertidal species. The estimates obtained by Brey's (2001) model were done using the model version 4-04 available on his computation spreadsheet (*Brey 4-04*).

Final results were all converted to g AFDW m^{-2} y^{-1}. In *Schw* the conversion used was: 1 g AFDW = 5.6 Kcal (Winberg 1971). In *Brey 4-04*, the conversions used were: *H. ulvae*, 1 g AFDW = 23.04 kJ; C. *carinata*, *A. valida*, *M. palmata*, 1 g AFDW = 22.74 kJ; *S. plana*, 1 g AFDW = 22.79 kJ (Brey 2001).

For each method, 20 annual estimates (5 species x 2 areas x 2 years) were obtained. The quality and patterns of deviation of each empirical method were checked by a linear regression model II, Major Axis Regression method (Sokal & Rohlf 1981), of the empirical method estimates versus cohort increment summation estimates, i.e., *Empirical_method* = a + b * *Cohort_method*, for n = 20. Model II regression was applied as both variables are subjected to error (Sokal & Rohlf 1981). The H_0 was of no deviation between *Cohort* and empirical method occurs when simultaneously the intercept = 0 and slope = 1, which was tested with a Dent and Blackie test, using F-test with 2 and (n–2) degrees of freedom (Tedeschi 2004).

RESULTS

Annual community production

Annual production was always highest in the *Zostera* bed (Fig. 1, Table 3). In 1993, the *Zostera* bed showed lower production, followed by a substantial increase in 1994. For the eutrophic area, production was higher in 1993 (macroalgal bloom year), but decreasing considerably (almost half) in the following year (Fig. 1, 2, Table 3).

The most consistent estimates of annual production were obtained with *Brey 4-04*, with good results for both areas and years (deviations lower than 10%, Fig. 1). The linear regression resulted in a slope close to 1 and intercept close to 0 (Fig. 3), yet, the Dent and Blackie test generated significant differences (F = 21.1, $p \leq 0.05$), mainly due to the small mean square error (MSE = 11) obtained with this method. The other empirical methods

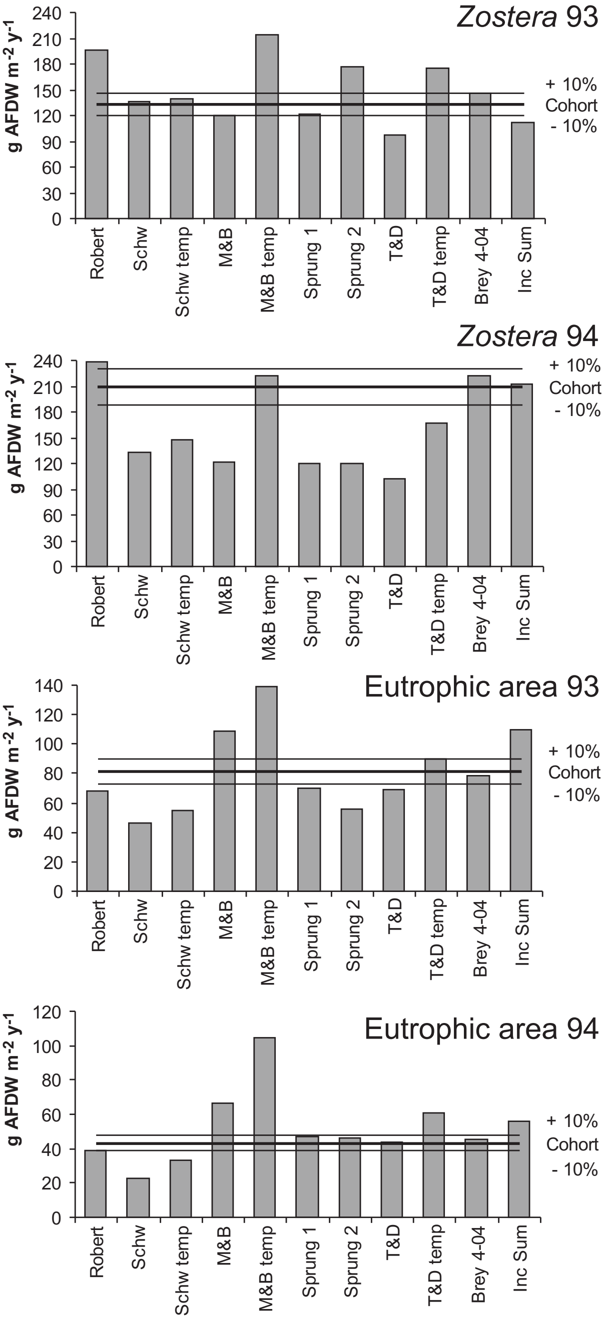


Fig. 1 Annual production estimates of the five species community, with indication of the 10% of deviation to the cohort increment summation estimates.

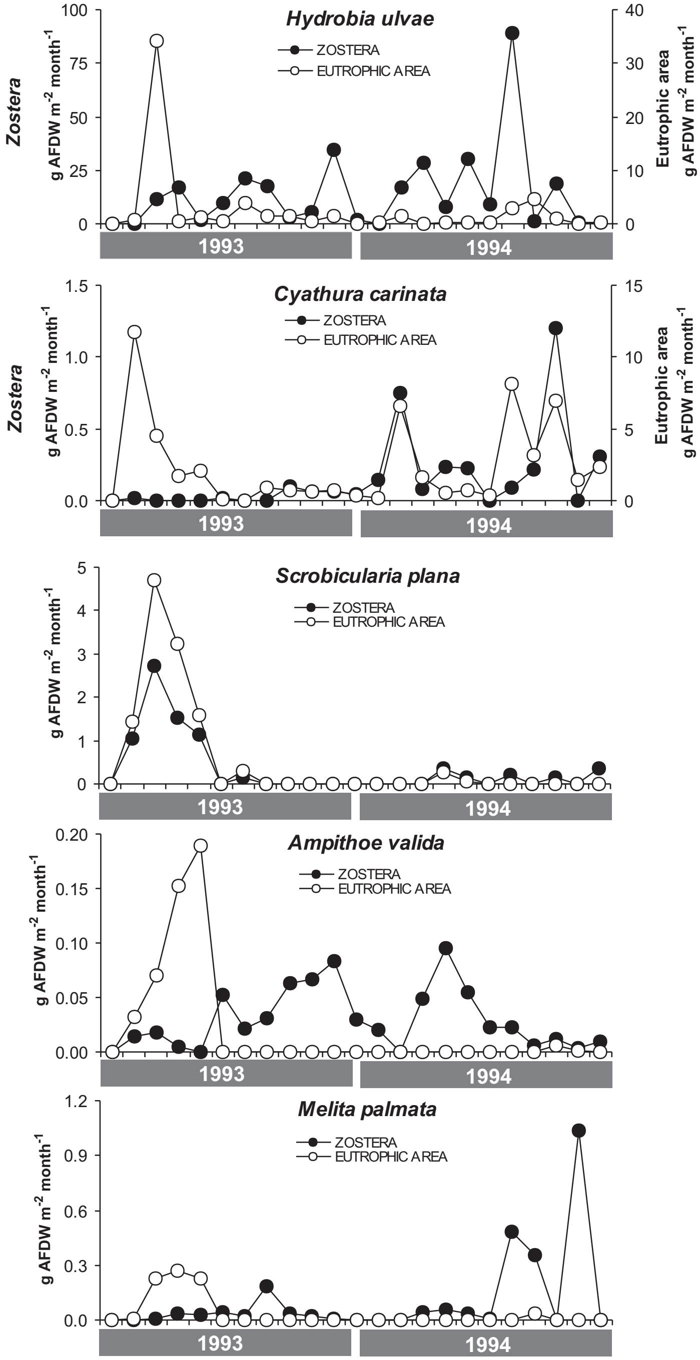


Fig. 2 Monthly variation of the secondary production estimated by the cohort increment summation method, for each species and both areas.

presented more variable responses. *Sprung 1* estimates were comparatively good for annual production with deviations near 10%, but quite high for the *Zostera* bed in 1994 (-43%, Fig. 1), and regression line parameters were significantly different from 1 and 0 (Fig. 3; F = 11.6, $p \leq 0.05$). Also, higher deviations could be reached with *Sprung 2* (Fig. 1). Its regression line parameters differed from 1 and 0, along with a low determination coefficient ($R^2 = 0.78$, Fig. 3), yet no significant differences were found (F = 1.1, $p > 0.05$), mainly due to the high mean square error (MSE = 455), increasing its tolerance (Tedeschi 2004). *Robert* produced estimates with deviations also close to 10%, with the exception of the *Zostera* bed in 1993 (+49%, Fig. 1). The estimates provided by *Inc Sum* were reasonable for the *Zostera* bed, but over-estimated for the eutrophic area (Fig. 1). In general, *Schw* and *T&D* produced under-estimations and *M&B* showed a tendency for over-estimation (Fig. 1). These three last methods showed the highest deviations among the empirical methods tested (Fig. 1). Dent and Blackie test proved significant differences in the slopes and intercepts ($p > 0.05$) for *Robert* (F = 16.7; MSE = 151), *Schw* (F = 6.8; MSE = 137), *M&B* (F = 6.5; MSE = 174) and *T&D* (F = 20.6; MSE = 75). *Inc Sum* had a slope near 1 but a relatively high intercept (Fig. 3), although no significant differences were found (F = 0.5, $p > 0.05$; MSE = 159), and yet again the mean square error was quite high (Tedeschi 2004).

Schw, *M&B* and *Inc Sum* methods gave better results for the *Zostera* bed than for the eutrophic area, which production was hugely over-estimated with *M&B* and under-estimated with the other two methods (Fig. 1, Table 3). Instead, *Robert*, *Sprung 2* and *T&D* produced better estimates for the eutrophic area (Table 3). Nevertheless, for almost all methodologies in study, the estimates for the *Zostera* bed in 1994 could reach very high deviations.

Different species production

With the exception of C. *carinata* (dominant in the eutrophic area), all species had higher production in the *Zostera* bed (Fig. 2, Table 3). *H. ulvae* always attained the higher production, with exception of the eutrophic area in 1994, when C. *carinata* production was higher (Fig. 2, Table 3). In 1994, production increased substantially in the *Zostera* bed for *H. ulvae*, *C. carinata* and *A. valida*, decreasing for *S. plana* and *M. palmata* (Fig. 2, Table 3). By contrast, in the eutrophic area, all species showed an initial increase in production during the spring of 1993, followed by a considerable decrease in late summer (Fig. 2),

Table 3 Annual production estimates for the different species, by the different methods.

	H. ulvae	***C. carinata***	***S. plana***	***A. valida***	***M. palmata***	**Total**
***Zostera* 93**						
Cohort	**124.9**	**0.4**	**6.6**	**0.4**	**0.4**	**132.6**
Robert	192.2	0.2	3.0	0.6	0.6	196.7
Schw	134.4	0.2	1.7	0.3	0.2	136.8
Schw temp	137.2	0.2	1.6	0.3	0.2	139.5
M&B	114.4	1.9	1.8	1.1	1.1	120.3
M&B temp	209.2	0.4	1.9	1.2	1.0	213.7
Sprung 1	115.4	0.3	5.1	0.5	0.3	121.6
Sprung 2	171.3	0.2	5.4	0.39	0.2	177.5
T&D	93.9	0.3	2.2	0.6	0.3	97.2
T&D temp	172.2	0.2	2.2	0.6	0.5	175.8
Brey 4-04	144.0	0.3	1.5	0.0	0.4	146.1
Inc Sum	101.6	0.5	10.2	0.2	0.2	112.6
***Zostera* 94**						
Cohort	**202.5**	**3.2**	**1.2**	**2.0**	**0.3**	**209.2**
Robert	230.2	3.1	2.8	0.4	1.6	238.2
Schw	127.9	1.5	2.8	0.2	0.8	133.1
Schw temp	133.2	10.0	3.1	0.2	1.0	147.6
M&B	108.2	3.9	4.0	1.0	4.3	121.5
M&B temp	200.8	7.4	5.9	1.1	6.5	221.6
Sprung 1	113.8	3.4	1.0	0.2	1.7	120.1
Sprung 2	109.1	3.3	5.9	0.3	1.0	119.5
T&D	94.0	4.0	2.3	0.5	1.4	102.3
T&D temp	153.7	4.6	4.1	0.5	3.4	166.4
Brey 4-04	215.1	2.8	2.7	0.0	1.6	222.2
Inc Sum	200.3	2.9	7.8	0.2	0.5	211.8
Eutrophic area 93						
Cohort	**45.4**	**23.7**	**11.2**	**0.4**	**0.7**	**81.6**
Robert	32.6	20.3	14.1	0.8	0.7	68.5
Schw	27.3	11.7	6.6	0.4	0.4	46.3
Schw temp	36.3	11.0	6.6	0.4	0.3	54.7
M&B	47.6	43.0	12.0	2.4	3.5	108.5
M&B temp	78.2	44.1	12.2	2.2	2.5	139.2
Sprung 1	42.7	23.8	2.9	0.4	0.4	70.2
Sprung 2	31.8	18.0	5.5	0.4	0.2	55.9
T&D	25.2	28.1	13.6	1.1	0.7	71.2
T&D temp	42.9	27.3	17.1	1.1	1.3	89.6
Brey 4-04	47.1	22.4	6.8	1.0	0.8	78.0
Inc Sum	29.9	25.4	53.3	0.5	0.5	109.6
Eutrophic area 94						
Cohort	**10.9**	**32.0**	**0.4**	**0.0**	**0.0**	**43.3**
Robert	6.1	26.9	5.5	0.0	0.1	38.7
Schw	5.2	14.4	3.1	0.0	0.0	22.7
Schw temp	12.3	18.3	2.7	0.0	0.0	33.3
M&B	11.7	50.7	4.1	0.0	0.2	66.8
M&B temp	24.2	75.0	4.9	0.0	0.1	104.1
Sprung 1	11.9	34.8	0.3	0.0	0.0	47.1
Sprung 2	8.9	29.7	7.4	0.0	0.0	46.0
T&D	5.2	33.2	4.9	0.0	0.1	43.3
T&D temp	12.0	42.9	5.9	0.0	0.0	60.8
Brey 4-04	10.6	31.5	3.6	0.0	0.1	45.9
Inc Sum	2.5	30.3	22.8	0.0	0.1	55.6

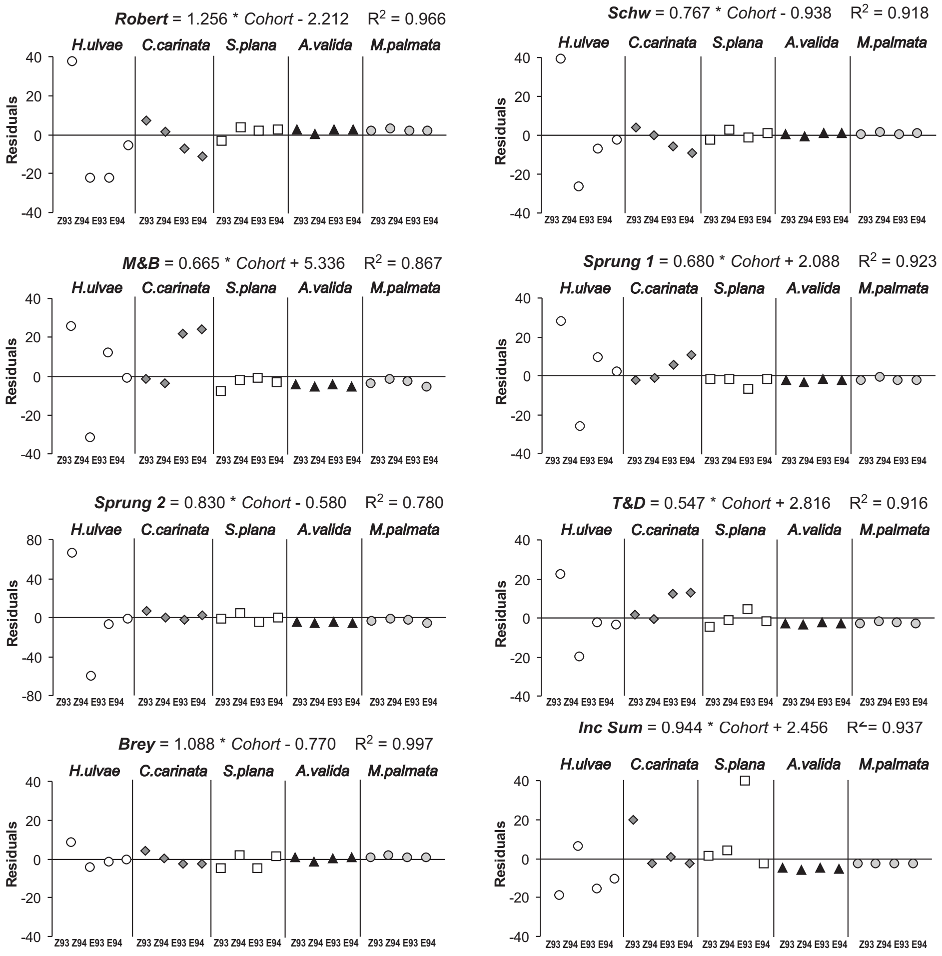


Fig. 3 Residuals from the linear regression model II analysis of *Cohort* method versus empirical method provided for the 20 annual estimates (five species × 2 areas × 2 years), with indication of the regression line parameters.

varying along with the macroalgal biomass dynamics. In this area, the production values remained low during the rest of the study period, with the exception of *C. carinata* (Fig. 2).

None of the methods responded well for all species analyzed. Nevertheless, *Brey 4-04* and *Sprung 1* can be pointed as providing the most consistent results for annual production (Table 3), with generally low residuals, exception for *H. ulvae* in *Zostera* under *Sprung 1* (Fig. 3). Yet, for the less abundant species (*A. valida* and *M. palmata*), deviations could be considerable high, mainly due to very low production values (e.g. deviations of 492 to 530%, Table 3).

With the other methods the responses were highly variable (Table 3). In general, for all methods, higher residuals were obtained for the most representative species, especially *H. ulvae* in *Zostera* and eutrophic area 1993, followed by *C. carinata* in the eutrophic area and *Zostera* 1993, and by *S. plana* especially with *Inc Sum* (Fig. 3). Lower residuals were observed for the less abundant species, *A. valida* and *M. palmata*. Yet, M&B showed high residuals for these species (Fig. 3), associated with the over-estimated productions (Table 3).

Scrobicularia plana was the species with the worst results, with deviations that could reach more than 1000% in the eutrophic area, due to the low production absolute value (Table 3). In general, *Sprung* and *Schw temp* gave under-estimations, while *M&B*, *T&D* and *Inc Sum* largely over-estimated production. This last method showed quite high residuals in the eutrophic area (Fig. 3).

DISCUSSION

Methodological comparisons

Production estimated by the increment summation method was always highest in the *Zostera* bed. Species seemed to take advantage of the seagrass coverage, either by food or protection, to enhance their production (Edgar et al. 1994, Sprung 1994, Heck et al. 1995, Cardoso et al. 2002, 2004, Dolbeth et al. 2003, Verdelhos et al. 2005). Nevertheless, all species showed adaptive behavioural patterns, related to resource availability and habitat heterogeneity during the macroalgal bloom, with a rapid increase in secondary production at the eutrophic area. After the macroalgal crash, production decreased dramatically, emphasizing the instability of the eutrophic area. The macroalgal blooms temporarily benefited the ecosystem, but never replaced the production associated to the seagrasses, as concluded also by Norkko et al. (2000), Cardoso et al. (2002, 2004), Dolbeth et al. (2003), Ferreira et al. (2004) and Verdelhos et al. (2005). Also, several differences in the pattern of variation in production were found at species level, mainly due to life cycle characteristics such as voltinism, life spans, or to different abundances in the areas considered (each species will be discussed below). All these natural (e.g. *Zostera*) or environmentally constrained (eutrophic area) adaptations to the ecosystem may bias estimations of secondary production by empirical methods at community and more obviously at species level. Nevertheless, a good model for estimating secondary production must be applicable to a broad set of conditions. In the present study, there was an attempt to understand the different empirical methods performance, regarding different habitats, catastrophic events (macroalgal bloom) and different species' voltinism, life span and abundances.

Calculation methods such as those based on cohort increment or removal summation, Allen's curve, instantaneous growth, and the size frequency methods have been previously studied and compared (Waters & Crawford 1973, Cushman et al. 1978, Wildish & Peer 1981, Benke 1984, Giberson & Galloway 1985, Morin et al. 1987). In general, cohort methods were considered as providing similar and more accurate estimates (although with instantaneous growth estimates could be slightly more biased [Cushman et al. 1978, Morin et al. 1987]), whereas size frequency methods have been pointed out to over estimate production (Waters & Crawford 1973, Cushman et al. 1978, Wildish & Peer 1981, Benke 1984). Also, cohort increment summation is often used in secondary production studies (Brey 1990a, b, Benke 1993, Sprung 1994, Mistri et al. 2001, Dolbeth et al. 2003), which justifies its use as a benchmark. Yet, the method assumes that the population growth is perfectly synchronous, meaning that a good estimate will depend on how well the growth or the survivorship curve approximates the real one (Benke, 1984, Morin et al. 1987). In the present study, it was not possible to provide confidence limits to the cohort increment summation estimates, using the bootstrapping technique (Morin et al. 1987, Brey 1990b), due to the large number of multicohort species involved in the calculations (in two different areas and two years). Anyway, assuming those estimates as accurate, a deviation limit lower than a 10% was assumed to be representative of a good estimate provided by an empirical method, along with the slope and intercept of a linear regression line between the cohort and the empirical methods not significantly different from 1 and 0 respectively.

Results suggested *Brey 4-04* as a good alternative methodology. Nevertheless, the good results for the intertidal species were obtained without computing a value for depth, meaning 0 m, according to the suggestion of Tumbiolo & Downing (1994) for intertidal species. The model is also very easy to apply.

After *Brey 4-04*, *Sprung* was the method that gave better responses, yet some important differences could be found, mainly at species level (discussed below), producing different slopes and intercepts. The results strongly depend on the $P/\overline{B}_{spec}$ achieved, as seen by the different responses of the two versions of the method. $P/\overline{B}_{spec}$ 1 (*Sprung 1*) is the best ratio for the species studied, as it was achieved by a cohort method and reflects the ecosystem dynamics for the period of time considered. Accordingly, estimates were better with *Sprung 1* than with *Sprung 2* (which is the most available form of application of the method).

Robert produced consistent results for the annual productions, in agreement with the findings of Medernach (1999). Yet, this method depends on the correct evaluation of the species life span, which makes it difficult to apply.

Inc Sum assumes that all data represent a single cohort. Negative production is considered zero. This procedure is very easy to apply. Nevertheless, the estimated production may change very drastically as a function of yearly dynamics, as real dynamics of production may not be obtained, since the development of a population is not followed. This means that the results will depend on the species life cycle, as error will certainly increase with species' voltinism and life span.

As a tendency, *Schw* and *T&D* produced under-estimations (very clear with Schw, due slope and intercept in the regression analyze lower than 1 and 0). In accordance, the study of Mistri et al. (2001) also provided underestimates for *Schw*. With regard to *T&D*, some factors were not taken into account, which probably would increase the method's performance. As example, data on molluscs, used for the equation, did not take into account the shell, which represents an important part of secondary production (Bachelet 1982).

Huge over-estimations were obtained with *M&B*. This model was developed using production data of freshwater invertebrates, whose $P/\overline{B}$ ratios can be higher than those from the marine and estuarine invertebrates. This leads in general to higher productions (Mourin & Bourassa 1992). Facing the present results, this method may not be advisable for marine or estuarine species, as it has already been applied in other studies (Cartes & Sorbe 1999).

Systematic considerations

All empirical methods worked better if used for the sum of the species, which has been recommended by some authors (Brey 1990a). Anyway, it is important to understand how estimates varied among species life cycles and abundances within the sampling areas, so that potential deviations to the *Cohort* estimates may be known.

Hydrobia ulvae is a dominant species in the *Zostera* bed. It has four recruitments per year (Lillebø et al. 1999, Cardoso et al. 2002). At the *Zostera* bed, this species maximizes its reproduction and growth, which is translated into high *Cohort* productions with high natural variations. In contrast, the eutrophic area was an alternative habitat, especially during the macroalgal bloom, where this species showed an opportunistic behaviour, related with food resources (Cardoso et al. 2002). In accordance, almost all methods showed high residuals for this species in the *Zostera*, which were especially high with *Sprung*, *Schw* and *M&B* methods. In contrast, better annual production and lower residuals were observed in the eutrophic area, as the effects of voltinism are not so visible and production was low during the whole year. *Brey 4-04* produced the best estimates for this species.

Cyathura carinata is a dominant species in the eutrophic area and consequently it was in this area that the highest *Cohort* production was obtained. The production of *C. carinata* increased substantially during the macroalgal bloom, but decreased soon after, being more stable in 1994. At the *Zostera* bed, its production was relatively low and was related with high parasite pressure in the *Zostera*, which inhibits reproduction and turns population more erratic (Jensen et al. 2004). This species has only one cohort per year (Ferreira et al. 2004). Accordingly, with the exception of *M&B* and *Schw*, all methods seemed to provide reasonable estimates, with deviations between 0 and 20%. *Inc Sum*, along with *Brey 4-04*, showed the best response to production variation and annual estimates of *C. carinata*, yet residuals were high in *Zostera* 1993.

Scrobicularia plana is a long-lived species, which has one single cohort per year (Verdelhos et al. 2005). Production was relatively low, with the highest values in the eutrophic area in 1993, during the algal bloom, but decreasing afterwards. Yet, the potential production can be much higher, as seen by Dolbeth et al. (2003), due to the fact that juveniles (< 4 mm) were not used for the estimates. Anyway, the long-term effects of macroalgae on the production were harmful, as seen by Verdelhos et al. (2005). The worst estimates of the empirical methods were obtained for this slow-growing species, with comparatively high individual biomass. High deviations were obtained, especially with *Inc Sum* with high residuals, followed by *M&B* and the remaining methods. Even *Brey 4-04* produced high deviations, especially for the *Zostera* bed and the eutrophic area in 1994, where production was very low.

Both *Ampithoe valida* and *Melita palmata* had very low productions in both areas. This reflects in a higher possibility of deviations if the secondary production is analysed for each single species, as it deals with very low absolute values. Accordingly, almost all methods showed high deviations, especially *M&B*. Yet, the effect of these high deviations is lessened when species are pooled for the computation of community production, as seen by the low residuals values of these two species, especially for *Sprung* and *Schw*. So, whenever in community production studies low abundant and rare species appear, the optimal empirical method should be the easiest one to apply, as the estimates have more or less the same degree of variation and the sum of all less representative species may smooth deviations.

CONCLUSIONS

Empirical production methods are effective for the synthesis of data and as predictive tools, when cohort, size frequency methods or mass growth methods are not applicable. The empirical methods that took into account population and environmental parameters performed more satisfactorily if used for a sum of species. Also, species life history and abundance in the study area are quite important for the choice of method. Within a community, biased production estimates of empirical methods potentially increase if the community is dominated by single species, especially if these are fast-growing and multicohort species. In fact, if *H. ulvae* estimates were eliminated from the regression analysis the slopes and intercepts would be much closer to the reference values (1 and 0), meaning closer empirical estimates to the cohort increment summation estimates (e.g. *Sprung 1* = 1.045 *Cohort* – 0.746, R^2=0.95, for n = 16). Among empirical methods, Brey (2001) version 4-04 method was considered the best alternative methodology. Sprung (1993) method can also provide reasonable results. Yet, $P/\overline{B}$ ratios of all species in a community can be difficult to obtain, especially for less abundant and rare species. In these cases, the sum of biomass increases from consecutive sampling dates (*Inc Sum*) may be applied.

REFERENCES

Bachelet G (1982) Quelques problèmes liés à l'estimation de la production secondaire. Cas des bivalves *Macoma balthica* et *Scrobicularia plana*. Oceanol Acta 4: 421–431.

Banse K, Mosher S (1980) Adult body mass and annual production/biomass relationships of field populations. Ecol Monogr 50 (3): 355–379.

Benke AC (1984) Secondary production of aquatic insects. In: Resh VH, Rosenberg DM (Eds) Ecology of aquatic insects. Praeger, New York, USA, p 289–322.

Benke AC (1993) Concepts and patters of invertebrate production in running waters. Verh Internat Verein Limnol 25: 15–38.

Brey T (1990a) Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. Meeresforsch 32: 329–343.

Brey T (1990b) Confidence limits for secondary production estimates: application of the bootstrap to the increment summation method. Mar Biol 106: 503–508.

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html Alfred Wegener Institute for Polar and Marine Research, Germany.

Cardoso PG, Lillebø AI, Pardal MA, Ferreira SM, Marques JC (2002) The effects of different primary producers on *Hydrobia ulvae* population dynamics: a case study in a temperate intertidal estuary. J Exp Mar Biol Ecol 277: 173–195.

Cardoso PG, Pardal MA, Lillebø AI, Ferreira SM, Raffaelli D, Marques JC (2004) Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. J Exp Mar Biol Ecol 302: 233–248.

Cartes JE, Sorbe JC (1999) Estimating secondary production in bathyal suprabenthic peracarid crustaceans form the Catalan Sea slope (western Mediterranean, 391-1255 m). J Exp Mar Biol Ecol 239: 195–210.

Crisp DJ (1984) Energy flow measurements. In: Holme NA, McIntyre AD (Eds) Methods for the study of marine benthos. 2nd Edition. Blackwell Scientific Publications, Norfolk, USA, p 284–372.

Cushman RM, Shugart HH, Hildebrandt SG, Elwood JW (1978) The effect of growth curve and sampling regime on instantaneous-growth, removal-summation, and Hynes/Hamilton estimates of aquatic insect production: a computer simulation. Limnol Oceanogr 23: 184–189.

Dolbeth M, Pardal MA, Lillebø AI, Azeiteiro UM, Marques JC (2003) Short and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. Mar Biol 143: 1229–1238.

Edgar GJ, Shaw C, Watson GF, Hammond LS (1994) Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. J Exp Mar Biol Ecol 176: 201–226.

Ferreira SM, Pardal MA, Lillebø AI, Cardoso PG, Marques JC (2004) Population dynamics of *Cyathura carinata* (Isopoda) in a eutrophic temperate estuary. Estuar Coast Shelf Sci 61: 669–677.

Giberson DJ, Galloway TD (1985) Life history and production of *Ephoron album* (Say) (Ephemeroptera: Polymitarcidae) in the Valley River, Manitoba. Can J Zool 63: 1668–1674.

Heck KL, Able KW, Roman CT, Fahay MP (1995) Composition, abundance, biomass, and production of macrofauna in a new england estuary - comparisons among eelgrass beds and other nursery habitats. Estuaries 18: 379–389.

Jensen KT, Ferreira SM, Pardal MA (2004). Trematodes in a *Cyathura carinata*_population from a temperate intertidal estuary: infection patterns and impact on host. J Mar Biol Ass UK 84: 1151–1158.

Lillebø AI, Pardal MA, Marques JC (1999) Population structure, dynamics and production of *Hydrobia ulvae* (Pennant) (Mollusca: Prosobranchia) along an eutrophication gradient in the Mondego estuary (Portugal). Acta Oecol 20: 289–304.

Medernach LGA (1999) Comparaison de méthodes d'évaluation de la production secondaire d'une population de l'annélide polychète *Ditrupa arietina* (O.F. Muller). Oceanol Acta 22: 337–352.

Mistri M, Fano EA, Rossi R (2001) Macrofaunal secondary production in a lagoon of the Po River Delta: an evaluation of estimation methods. Ital J Zool 68: 147–151.

Morin A (1997) Empirical models predicting population abundance and productivity in lotic systems. J N Am Benthol Soc 16: 319–337.

Morin A, Bourassa N (1992) Modèles empiriques de la production annuelle et du rapport P/B d'invertébrés benthiques d'eau courante. Can J Fish Aquat Sci 49: 532–539.

Morin A, Mousseau TA, Roff DA (1987) Accuracy and precision of secondary production estimates. Limnol Oceanog 32: 1342–1352.

Nogueira AJA (1992) ANAMOD – Extracção dos componentes modais de distribuições de frequência de variáveis biométricas. Trabalho de síntese apresentado para prestação de provas de aptidão pedagógica e capacidade científica. University of Coimbra, Portugal, p 67.

Norkko A, Bonsdorff E, Norkko A (2000) Drifting algal mats as an alternative habitat for benthic invertebrates: species specific responses to a transient resource. J Exp Mar Biol Ecol 248: 79–104.

Pardal MA, Marques JC, Metelo I, Lillebø AI, Flindt MR (2000) Impact of eutrophication on the life cycle, population dynamics and production of *Ampithoe valida* (Amphipoda) along an estuarine spatial gradient (Mondego estuary, Portugal). Mar Ecol Prog Ser 196: 207–219.

Pardal MA, Marques JC, Metelo I, Lillebø AI, Flindt MR (2002) Impact of eutrophication on amphipods *Melita palmata* and *Ampithoe valida* in the Mondego estuary. In: Pardal MA, Marques JC, Graça M (Eds) Aquatic ecology of the Mondego River basin. Global importance of local experience. Imprensa da Universidade, Coimbra, Portugal, p 457–472.

Pardal MA, Cardoso PG, Sousa JP, Marques JC, Raffaelli D (2004) Assessing environmental quality: a novel approach. Mar Ecol Prog Ser 267: 1–8.

Robertson AI (1979) The relationship between annual production: biomass ratios and life spans for marine macrobenthos. Oecologia 38: 193–202.

Schwinghamer P, Hargrave B, Peer D, Hawkins CM (1986) Partioning of production and respiration among size groups of organisms in an intertidal benthic community. Mar Ecol Prog Ser 31: 131–142.

Sokal RR, Rohlf FJ (1981) Biometry. The principles and practice of statistics in biological research. 2nd Edition. Freeman and Company, New York, USA, p 859.

Sprung M (1993) Estimating macrobenthinc secondary production from body weight and biomass: a field test in a non-boreal intertidal habitat. Mar Ecol Prog Ser 100: 103–109.

Sprung M (1994) Macrobenthic secondary production in the intertidal zone of ria formosa - a lagoon in southern Portugal. Est. Coast Shelf Sci 38: 539–558.

Tedeschi LO (2004) Assessment of the adequacy of mathematical models. Department of Animal Science. Cornell University, Ithaca, NY 14850, USA. Available on *http://www.cncps.cornell.edu/modeval/modeval web.htm*.

Tumbiolo ML, Downing J (1994) An empirical model for the prediction of secondary production in marine benthic invertebrate populations. Mar Ecol Prog Ser 114: 165–174.

Verdelhos T, Neto JM, Marques JC, Pardal MA (2005) The effect of eutrophication and coastal management on the bivalve *Scrobicularia plana*. Estuar Coast Shelf Sci 63: 261–268.

Waters TF, Crawford GW (1973) Annual production of a stream mayfly population: a comparison of methods. Limnol Oceanogr 18: 286–296.

Wildish DJ, Peer D (1981) Methods for estimating secondary production in marine Amphipoda. Can J Fish Aquat Sci 38: 1019–1026.

Winberg GG (1971) Methods for the estimation of production of aquatic animals. Academic Press Inc, London, United Kingdom, p 175.

Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a ten-year period

Abstract For some decades, the Mondego estuary has been under severe ecological stress, mainly caused by eutrophication. The most visible effect was the occurrence of macroalgal blooms and the concomitant decrease of the area occupied by *Zostera noltii* beds. Since the end of 1998, mitigation measures were implemented in the estuary to promote the recovery of the seagrass beds and the entire surrounding environment. The present study offers a unique opportunity to evaluate the impact of disturbance and the success of the initial recovery process (before and after implementation of the management measures), over a ten-year period, having secondary production as the descriptor. Before the implementation of the mitigation measures, in parallel with the decrease of the *Z. noltii* beds, species richness, mean biomass and production also decreased, lowering the carrying capacity of the whole Mondego's south arm. Yet, after the introduction of management measures, the seagrass bed seemed to recover. Consequently, the biomass and production also increased substantially, for the whole intertidal area. Nevertheless, even after the mitigation measures implementation, natural-induced stressors, such as strong flood events induced a drastic reduction of annual production, not seen before the implementation of those measures. This shows that the resilience of the populations may have been lowered by a prior disturbance history (eutrophication) and consequent interactions of multiple stressors.

Keywords Macrobenthic production, Disturbance, Mitigation measures, Recovery

INTRODUCTION

Estuaries are among the most productive natural ecosystems (Kennish 2002, Dolbeth et al. 2003, Paerl 2006). Their importance is recognized worldwide, for providing essential ecological functions (decomposition, nutrient cycling, and flux regulation of water, particles and pollutants) and services, such as habitat, protection, food for migratory and resident species, shoreline protection, fisheries resources, navigation routes and harbours, and recreational purposes (Kennish 2002, Paerl 2006). As transitional areas between land and sea, most estuaries and coastal lagoons receive large amounts of nutrients and pollutants derived from urban, agricultural and industrial effluents (Lillebø et al. 2005, Paerl 2006). Due to the shallow depth and relatively weak exchange with the open sea, these systems are particularly vulnerable to eutrophication, recognized as a major problem worldwide (Kennish 2002, Marques et al. 2003, Pardal et al. 2004, Lillebø et al. 2005, Munkes 2005, Powers et al. 2005). In addition, global warming and sea-level rise will have important consequences for aquatic ecosystems (Short & Neckles 1999, Simas et al. 2001, Lawrence & Soame 2004, Beukema & Dekker 2005). A major challenge for ecologists is the understanding of the ecosystem functioning and dynamics in the face of natural, anthropogenically-induced and extreme climate variability. One approach to this is through an analysis of the different components of the system contributing to production, widely used to assess the ecological integrity of ecosystems, including anthropogenic effects or climate change effects (Brey 2001, Dolbeth et al. 2003, Cusson & Bourget 2005, Polte et al. 2005). Here, changes are described in the macrobenthic secondary production of the Mondego estuary, Portugal, over a ten-year period, during which the system has undergone significant eutrophication and more recently has experienced extreme weather-related events. The impacts of these stressors on the population dynamics of key species have been described elsewhere (Pardal et al. 2000, Cardoso et al. 2004a, 2005, Ferreira et al. 2004, Verdelhos et al. 2005). At the end of 1998, a management plan was implemented to restore the estuary, which included measures to improve water transparency, decrease nutrient loading and the physical protection of the seagrass bed (Lillebø et al. 2005, Martins et al. 2005). In the present paper, we assess the impact of these stressors and the effectiveness of the mitigation programme at the ecosystem-level through an exploration of the changes in macrobenthic secondary production.

MATERIALS AND METHODS

Study area

The Mondego estuary (Portugal) is located in a warm temperate region, on the Atlantic coast of Portugal (40°08'N, 8°50'W). It is a small estuary of 3.4 km^2, comprising two arms, north and south, separated by an island (Fig. 1). The north arm is deeper (4-10 m during high tide, tidal range 1-3 m), highly hydrodynamic and provides the main navigation channel and the location of the Figueira da Foz harbour. The south arm is shallower (2-4 m during high tide, tidal range 1-3 m) and is characterized by large areas of exposed intertidal flats during low tide. Anthropogenic activities in the estuary led to an ongoing process of eutrophication since the end of the 1980's, mainly in the south arm. The downstream areas of the south arm still remain relatively unchanged, with *Spartina maritima* marshes and a *Zostera noltii* meadow, but in the inner parts the seagrass community has completely disappeared and blooms of the opportunistic macroalgae *Ulva* spp. were common. The macroalgae *Ulva* spp. blooms consist in the rapid growth and accumulation of biomass of these species, due to the combination of the nutrient surplus with low hydrodynamics and high salinity (Martins et al. 2005).

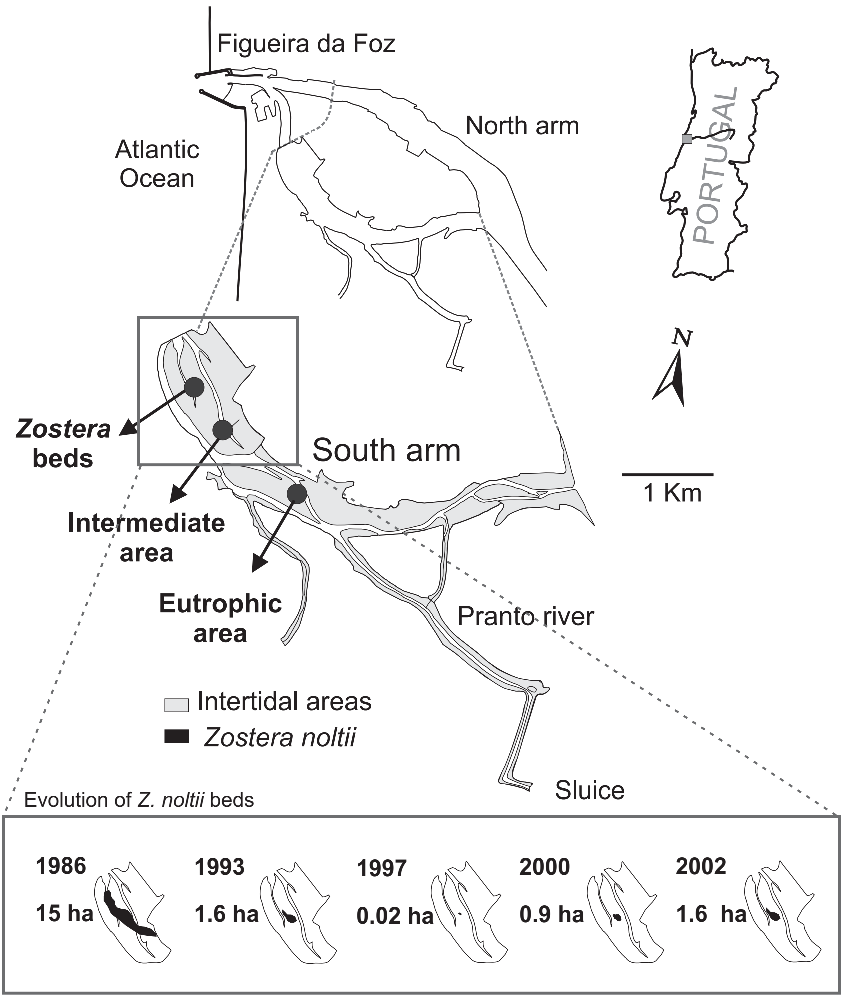


Fig. 1 Location of the Mondego estuary showing sampling stations. Expanded area maps show evolution of the *Zostera noltii* bed's area and cover, since 1986.

Until the end of 1998 this sub-system was almost silted up in the upstream areas. Water circulation was therefore mainly dependent on tides and on the freshwater input from the Pranto river (Fig. 1), artificially controlled by a sluice, according to rice field irrigation needs in the lower Mondego valley (Pardal et al. 2004, Cardoso et al. 2005, Lillebø et al. 2005).

This sub-system is recently and gradually recovering from the effects of eutrophication after the implementation of mitigation measures in 1998 which improved water transparency and decreased nutrient loading (Cardoso et al. 2005, Lillebø et al. 2005).

These included: 1) the re-establishment of the south arm riverhead connection, improving freshwater circulation; 2) nutrient loading reduction, essentially ammonia (Lillebø et al. 2005); 3) seagrass bed protection from human disturbance; and 4) public education of the ecological importance of intertidal vegetation for health and related socio-economic activities of the estuary.

In these last years several differences in the climate of Portugal have been recorded when compared to the general climate patterns for period 1931-1990. There was a clear increase of mean air temperature (from 1931 to 2005: + 0.15°C per decade) and a high variability in precipitation (INAG - Portuguese Water Institute, http://snirh.inag.pt/ and IM - Portuguese Weather Institute, http://web.meteo.pt/pt/clima/clima.jsp). For instance, during the winter of 2000/01 precipitation reached unprecedented high values, especially for central Portugal (2000/01: 1802.1 mm against a mean annual value for 1940 to 1997: 1030.6 mm), causing a large flood.

Sampling and biological material processing

Samples were taken during low tide in three areas representing different environments along the eutrophication gradient: 1) the seagrass bed, characterized by muddy sediments covered with *Z. noltii*, higher organic matter content (mean 6.2% ± 1.76), and higher water-flow velocity (1.2 – 1.4 m s^{-1}) compared to the other two areas; 2) an intermediate area, characterized by muddy sediments and some roots of *Z. noltii*, with physical-chemical conditions similar to those of previous area; 3) a eutrophic area, characterized by sandy sediments, which has not supported rooted macrophytes for more than 15 years, lower organic matter content (mean 3.0% ± 1.14), lower water flows (0.8 – 1.2 m s^{-1}), and which has been regularly covered seasonally by green macroalgae (Fig. 1). The sampling technique described by Dexter (1983) for intertidal sandy beaches was adapted for the Mondego estuary intertidal soft sediments. So, ten (during the first 18 months) to six sediment cores (141 cm^2 core sectional area) were randomly taken to a depth of 20 cm, by using a manual corer. Samples were collected in the morning, during low tide, fortnightly for the first 18 months, monthly thereafter. For the results section, data were merged to present only the seasonal variations. Each sample was sieved through a 500 μm mesh using estuarine water, organisms identified to the species level, counted and measured. Plant material was sorted and separated into green algae and *Z. noltii*. For both faunal and plant material the ash-free dry weight (AFDW) was assessed, after combustion for 8 h at 450°C (shells of molluscs included).

Secondary production

For *Hydrobia ulvae* (Gastropoda), *Cyathura carinata* (Isopoda), *Ampithoe valida,* and *Melita palmata* (Amphipoda), secondary production was estimated by the increment summation method, after definition of cohorts through size–frequency distribution analysis of successive sampling dates and using ANAMOD software (after Pardal et al. 2000, Ferreira et al. 2004, Cardoso et al. 2005, Dolbeth et al. 2005, Verdelhos et al. 2005), according to:

$$P_{cn} = \sum_{t=0}^{T-1} \left(\frac{N_t + N_{t+1}}{2} \right) \times \left(\overline{w}_{t+1} - \overline{w}_t \right) \qquad \text{equation 1}$$

where P_{cn} is the growth production of cohort n, N is the density (ind m^{-2}), $\overline{w}$ is the mean individual weight (g WW m^{-2}), and t and t+1, consecutive sampling dates. Population production estimates correspond to the sum of P_{cn} (each cohort production):

$$P = \sum_{n=1}^{N} P_{cn} \qquad \text{equation 2}$$

The mean annual biomass ($\overline{B}$) was estimated according to:

$$\overline{B} = \left(\frac{1}{T} \right) \times \sum_{n=1}^{N} \left(\overline{B}_{cn} t \right) \qquad \text{equation 3}$$

where T is the period of study (yearly cycles, 365 days), N is the number of successive cohorts in the study period, $\overline{B}_{cn}$ is the mean biomass of cohort n, and t is the duration of the cohort n.

Brey (2001) method version 4-04 (worksheet provided in Brey 2001, www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.htm) was used as an alternative empirical method for secondary production estimation (after Cusson & Bourget 2005 and Dolbeth et al. 2005) for other representative species - *Carcinus maenas, Crangon crangon* (Decapoda), *Capitella capitata, Hediste diversicolor*, *Heteromastus filiformis* (Polychaeta), *Cerastoderma edule, Scrobicularia plana* (Bivalvia), *Haminoea hydatis* and *Littorina littorea* (Gastropoda). The weight-to-energy ratios needed for the application of the empirical method are also provided in Brey (2001). For the species with lower densities and biomasses, production was estimated by summing the increases in biomasses from one sampling date to the other, using the cohort increment summation equation (equation 1), but without following the cohorts.

Mean biomass and $P/\overline{B}$ ratios (annual production divided by the annual mean biomass) were also computed for the main species. The $P/\overline{B}$ ratio is the turnover rate of a species' biomass, meaning the amount of time it takes to replace the biomass of its population (McLusky 1989, Cusson & Bourget 2005). It is closely related to the species' life span and affected by life history characteristics and potentially also by environmental factors (in a indirect way), being a clear indication of the ecological performance of a population (McLusky 1989, Cusson & Bourget 2005). Long lived species will have lower $P/\overline{B}$ than short lived species (McLusky 1989).

Each species production was then cumulated into community production. Biomass and production within the community is represented essentially by detritivores (Dolbeth et al. 2003, Cardoso et al. 2004a).

Multivariate analysis

The production distribution within the macrobenthic community at different sites in different years was investigated using multivariate techniques provided by the PRIMER software (version 5.2.6, PRIMER-E Ltd), in order to investigate if there were spatial and temporal differences in the production of each area, before and after the mitigation periods. Similarity relationships of the production results were determined by Bray-Curtis coefficient, after square-root-transformation of the raw data. Square-root-transformation of the data was used in order to scale down the scores of the very productive species (Clarke & Warwick 2001). Non-metric multidimensional scaling (MDS) analysis was performed afterwards, from which similar groups were defined. One way ANOSIM tests (Clarke & Warwick 2001) were used to test for differences between groups. For each group, a Similarity Percentages-species contributions (SIMPER) was used to determine which species' production contributed most to the differences among the groups.

RESULTS

Climate - Precipitation

In the Mondego estuary there was a clear seasonal pattern of rainfall over the ten-year period, with the highest precipitation values in the winter (Fig. 2A). Yet, taking into consideration the mean precipitation regime for central Portugal during the period of 1940-1997 (winter: 418 mm, spring: 265 mm, summer: 62 mm, autumn: 285 mm, INAG - http://snirh.inag.pt) some above-mean precipitation was evident (Fig. 2A). The hydrological years of 1993/94 (autumn: 593 mm) and 1995/96 (winter: 670 mm) were

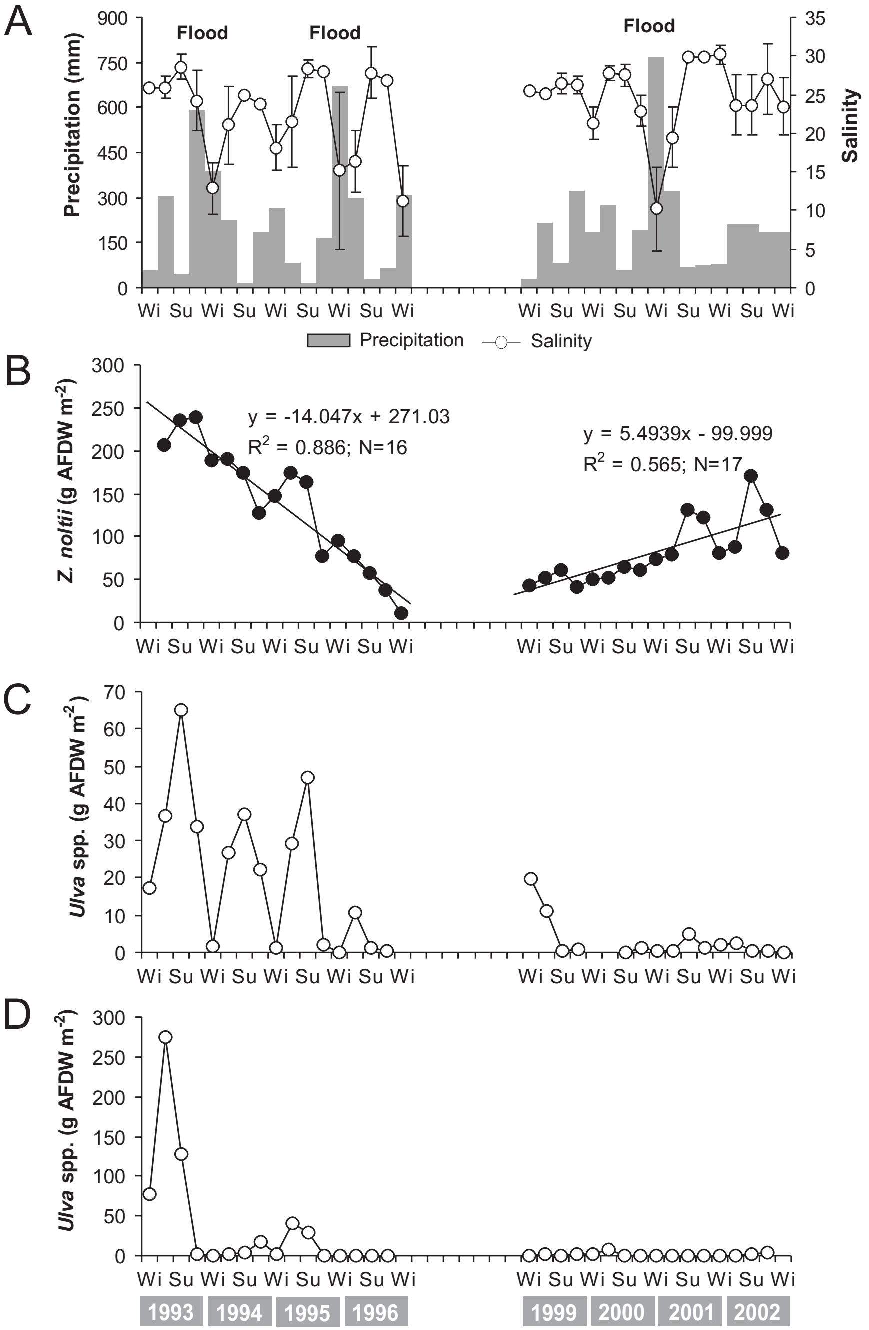


Fig. 2 Seasonal long-term variation in: (A) mean salinity and precipitation in all three areas, (B) seagrass biomass in the *Zostera noltii* beds, (C) macroalgal biomass in the intermediate area, (D) macroalgal biomass in the eutrophic area.

atypical, suffering floods, and 2000/01 was even more atypical, with severe flooding occurring (winter: 767 mm) (INAG - http://snirh.inag.pt).

The seasonal pattern of rainfall and the flooding reflected the seasonal and inter-annual variation of salinity in the south arm. During periods of intense rainfall, salinity declined dramatically (Fig. 2A), occasionally reaching < 5 (Feb 96, Jan 97 and Jan 01). Also, during these times of high rainfall there was an extensive opening of the Pranto river sluice, further contributing to the salinity decline (Lillebø et al. 2005).

Seagrass and macroalgal biomass

There was a clear seasonal pattern of the seagrass biomass over the study period with higher biomass in spring/summer and lower in autumn/winter. However, seagrass biomass showed a significant decline over the pre-mitigation period, from 1993 to 1997 (Fig. 2B, $R^2 = 0.89$). After the mitigation measures were introduced in 1998, there seems to be a gradual recovery of the seagrass bed (Fig. 2B, $R^2 = 0.56$). Significant differences were observed when comparing the pre-mitigation with the post-mitigation period (Student's t-test, $t_{[16, 17]} = 2.88$, $p < 0.05$).

In the intermediate area, the biomass of green algae showed a characteristic seasonal pattern until 1997, with lower values during winter, following the decrease of salinity (Fig. 2A), and increasing in spring and summer (Fig. 2C). In the eutrophic area, there was a spring bloom in 1993 (maximum biomass of 415 g AFDW m^{-2} / 508 g DW m^{-2} in April 1993), followed by a crash in early summer (Fig. 2D). In 1995, algal biomass again reached high values, but not enough to be considered a spring bloom (maximum biomass of 111 g AFDW m^{-2} / 142 g AFDW m^{-2} in April 1995) (Fig. 2D). Several studies on macroalgal blooms and mats have reported algae biomass in these periods ranging from 425 to 625 g DW m^{-2} (Pihl et al., 1996), comparable to the reported values for the Mondego estuary bloom. In both intermediate and eutrophic areas, differences were evident in algal biomass between the pre- and post-mitigation periods. Macroalgal blooms in the eutrophic area and some macroalgae in the intermediate area were present in the pre-mitigation period, particularly during dry years, but blooms were never recorded after the post-mitigation measures (Fig. 2C, D).

Macrobenthic community

Species richness, abundance and biomass

A total of 80 different taxa were recorded over the ten-year period. In general, the number of species, mean biomass and abundance were higher in the *Z. noltii* beds compared to the other two areas (Fig. 3).

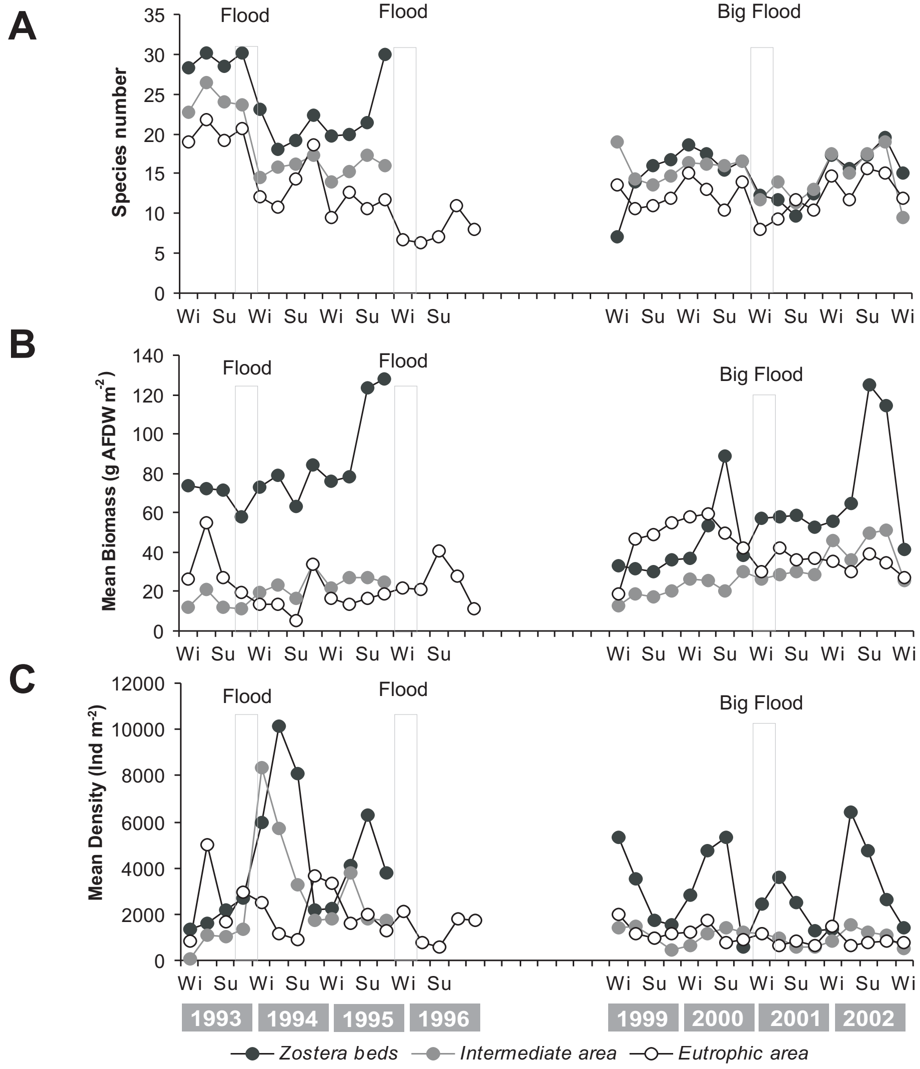


Fig. 3 Seasonal long-term variation of: (A) species richness, (B) mean biomass, and (C) mean density, for the *Zostera noltii* beds, intermediate and eutrophic areas.

In the pre-mitigation period, there was a clear decrease in the number of species for the intermediate and eutrophic areas, which was more pronounced after the floods (Fig. 3A). In the *Z. noltii* beds, there was a pronounced decrease after the 1993/94 flood, followed by an increase until the end 1995 (Fig. 3A). Yet, the species number was much lower at the beginning of the post-mitigation, suggesting a considerable decrease after 1995 (Fig. 3A). With the recovery process, in the post-mitigation period there was a tendency for the species number increase, but the values seen in 1993 were not attained again. The post-mitigation increase was interrupted in 2000/01 following major floods, continuing afterwards, a pattern seen in all three areas (Fig. 3A).

For the pre-mitigation period, in both *Z. noltii* and eutrophic areas there was a decrease in biomass between 1993 and 1994, followed by a slight increase until 1995 (more pronounced in the eutrophic area), and in the eutrophic area biomass decreased again after the summer of 1996. In the post-mitigation period, with the recovery process, mean biomass was low at the start but increased until the 2000/01 flooding and continued afterwards until the end of 2002 (Fig. 3B). For the intermediate area, biomass tended to increase throughout the study period. Mean densities showed a clear seasonal pattern in both *Z. noltii* and intermediate areas, with higher values in spring and summer throughout the study period.

In the eutrophic area mean density and biomass were high during spring 1993 and winter/spring 1995 (Fig. 3C). Those periods matched with the periods of higher macroalgal biomass (Fig. 2D). In the remaining period (after 1995) the values appeared to maintain a relatively stability.

Secondary production

Total production

In general, higher annual production and mean biomass values were recorded in the *Z. noltii* beds than in the other two areas (Table 1), except in 1999 at the beginning of the post-mitigation period (Table 1). Both the *Z. noltii* beds and intermediate area production was greatest in 1994 and 2002. In these years, the area covered with *Z. noltii* was practically the same (1.4% of the intertidal area, Table 1). For the eutrophic area, production were highest in 1993 (Table 1) when a macroalgal bloom occurred (Fig. 2D). Production was lowest in 1999, when *Z. noltii* cover and biomass were least (Fig. 2B), for both intermediate area and *Z. noltii* beds (Table 1). After the mitigation measures, the

Table 1 Macrobenthic community production estimates (P: g AFDW m^{-2} y^{-1}) and mean biomass (between brackets, $\bar{B}$: g AFDW m^{-2}) for each habitat and mean estimate for the south arm intertidal area (without *Spartina* and *Scirpus* marshes) of the Mondego estuary, taking into account the area of each habitat relative to the whole intertidal area.

Year	*Z. noltii* beds	**Intermediate area** (muddy)	**Eutrophic area** (sand-muddy)	**South Arm's intertidal area**	
1993	P: 148.0 ($\bar{B}$: 75.1)	P: 30.7 ($\bar{B}$: 20.1)	P: 89.3 ($\bar{B}$: 31.4)	1.4% *Z. noltii*, 84.9% muddy, 13.7% sand-muddy, Macroalgal bloom	P: 40.4 ($\bar{B}$: 26.9)
1994	P: 222.9 ($\bar{B}$: 84.6)	P: 60.3 ($\bar{B}$: 23.4)	P: 45.8 ($\bar{B}$: 15.8)	1.1% *Z. noltii*, 85.2% muddy, 13.7% sand-muddy	P: 60.1 ($\bar{B}$: 23.3)
1995	P: 137.9 ($\bar{B}$: 105.8)	P: 48.8 ($\bar{B}$: 30.1)	P: 32.8 ($\bar{B}$: 19.7)	0.72% *Z. noltii*, 85.6% muddy, 13.7% sand-muddy Small macroalgal bloom	P: 47.3 ($\bar{B}$: 29.5)
1996	-	-	P: 30.3 ($\bar{B}$: 25.8)	-	-
1997	-	-	-	0.013% *Z. noltii*, 86.3% muddy, 13.7% sand-muddy	-
1998	***Mitigation measures***				
1999	P: 45.9 ($\bar{B}$: 34.9)	P: 27.7 ($\bar{B}$: 20.9)	P: 57.0 ($\bar{B}$: 45.0)	0.019% *Z. noltii*, 86.0% muddy, 13.7% sand-muddy	P: 28.1 ($\bar{B}$: 24.2)
2000	P: 121.3 ($\bar{B}$: 60.1)	P: 35.5 ($\bar{B}$: 37.5)	P: 60.6 ($\bar{B}$: 62.3)	0.57% *Z. noltii*, 85.7% muddy, 13.7% sand-muddy	P: 39.5 ($\bar{B}$: 41.0)
2001	P: 88.4 ($\bar{B}$: 54.4)	P: 34.4 ($\bar{B}$: 29.2)	P: 51.7 ($\bar{B}$: 37.8)	1.0% *Z. noltii*, 85.3% muddy, 13.7% sand-muddy	P: 37.3 ($\bar{B}$: 30.7)
2002	P: 199.5 ($\bar{B}$: 94.8)	P: 55.9 ($\bar{B}$: 48.4)	P: 58.2 ($\bar{B}$: 35.0)	1.4% *Z. noltii*, 84.9% muddy, 13.7% sand-muddy	P: 58.3 ($\bar{B}$: 47.2)

production increased gradually, with a decrease in 2001, following the highest flood event.

Contrasting areas

The MDS analysis was performed only for the most contrasting environments, *Z. noltii* beds (least disturbed) and the eutrophic area (most disturbed). The intermediate area is still undergoing change (Marques et al. 2003). The MDS analysis revealed that the areas were indeed distinct in terms of their production characteristics (AB versus CD, ANOSIM test: R = 0. 888 to p = 0.001) and that there were also important differences pre- and post-mitigation (A versus B and C versus D, ANOSIM test: R = 0.859 to p = 0.001) (Fig. 4, Table 2). SIMPER analysis showed that in the *Z. noltii* beds in the pre-mitigation period, at least nine species were necessary to explain 80% (simper cut-off) of the group similarity, yet *H. ulvae* accounted for the higher contribution. After the mitigation measures only five species were needed to explain 80% (simper cut-off), with *H. ulvae, S. plana* and *H. diversicolor* as major species (Table 2). In the eutrophic area only four to five species were necessary, before and after mitigation measures implementation, to explain between 86 - 87% of the similarity. Of these species, *S. plana*, *C. carinata H. ulvae* and *H. diversicolor* were consistently identified and their contribution was more evenly distributed (Table 2).

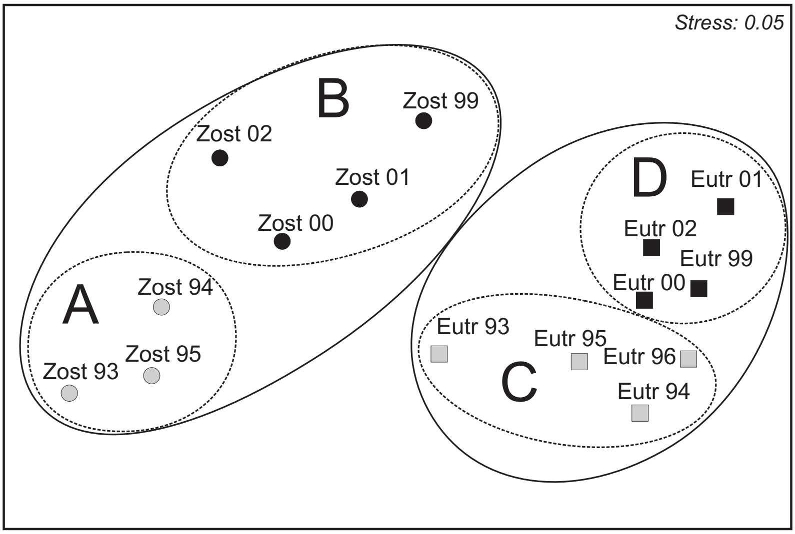


Fig. 4 Two-dimensional non metric multidimensional scaling (MDS) ordination plot of macrobenthic community production for the *Zostera noltii* bed (ZOST, circles) and the eutrophic area (EUTR, squares). Grey symbols, before mitigation measures, black symbols, after mitigation measures, A, B, C, D, spatial aggregation of the different groups, defined in the MDS.

Main species

Hydrobia ulvae was the dominant species within the *Z. noltii* beds. In some of the years, the production of this species alone represented a major part of the total annual community production (e.g. 1993, 1994, 1995 and 2002 Table 1, Table 3). This species also contributed to production in the eutrophic area in the pre-mitigation period (Table 3). The $P/\overline{B}$ ratio of *H. ulvae* was much higher in the eutrophic area (between 2.7 and 4.8) than in the *Z. noltii* beds (between 1.3 and 3.0).

Table 2 MDS formed groups for the *Zostera noltii* and eutrophic areas' production, with indication each group similarities (%) and the most representative species (%) contributing for the similarity within the group, determined with SIMPER analysis.

Group	**A**	**B**	**C**	**D**
Site and year	*Z. noltii* bed 93 - 95	*Z. noltii* bed 99 - 02	Eutrophic area 93 - 95	Eutrophic area 96, 99 - 02
Group mean similarity (%)	78.42	73.88	75.54	83.13
Main Species (after each species the % of contribution for the similarity within the group)	*H. ulvae* - 44.7 *C. edule* - 7.6 *S. plana* - 7.1 *L. littorea* - 5.0 *H. filiformis* - 4.4 *C. maenas* – 3.9 *M. palmata* – 3.4 *C. carinata* – 3.2 *A. valida* – 2.1	*H. ulvae* – 39.9 *S. plana* – 19.3 *H. diversicolor* – 11.8 *C. carinata* – 7.0 *C. maenas* – 4.7	*C. carinata* - 34.1 *H. ulvae* - 22.4 *S. plana* - 21.1 *H. diversicolor* - 8.2	*S. plana* - 37.6 *C. carinata* - 28.9 *H. ulvae* - 10.4 *H. diversicolor* - 10.1

The production of *S. plana* was higher in the eutrophic area, showing a significant increase after the introduction of mitigation measures accompanied by the increase of mean annual biomass (Table 3). The $P/\overline{B}$ ratios for this species also decreased in this period. Like *H. ulvae*, in 2001 after the extreme flood, there was a decrease in *S. plana* production, which increased again in the following year (Table 3).

Cyathura carinata production was also higher in the eutrophic area, but after the mitigation measures, it increased in the *Z. noltii* beds, although never reaching the production values of the eutrophic area (Table 3). The $P/\overline{B}$ ratios were in general higher in *Z. noltii* beds.

Production by *H. diversicolor* started slightly greater in the eutrophic area. After mitigation measures, it increased for both areas, but remained higher in the *Z. noltii* beds, especially over the last two years of the study, 2001 and 2002 (Table 3).

DISCUSSION

Previous studies on the Mondego estuary have shown that the system is highly productive (Dolbeth et al. 2003), in line with other systems elsewhere (see for example, Sprung 1994, Heck et al. 1995). The present study confirms the high estuarine production of the Mondego estuary and demonstrates that seagrass beds are more productive and

Table 3 Annual production (P: g AFDW m^{-2} y^{-1}), mean biomass ($\overline{B}$: g AFDW m^{-2}) and P/$\overline{B}$ ratios (P/$\overline{B}$: y^{-1}) estimates for the main species for the *Zostera noltii* and eutrophic areas.

	H. ulvae			***S. plana***			***C. carinata***			***H. diversicolor***		
Year	P	$\overline{B}$	P/$\overline{B}$	P	$\overline{B}$	P/$\overline{B}$	P	$\overline{B}$	P/$\overline{B}$	P	$\overline{B}$	P/$\overline{B}$
***Z. noltii* bed**												
1993	122.6	59.2	2.1	3.0	3.4	0.9	0.4	0.1	4.6	0.2	0.1	2.0
1994	204.3	74.1	2.8	2.9	1.6	1.8	3.2	1.1	2.9	0.9	0.7	1.3
1995	110.5	82.1	1.3	3.5	2.7	1.3	3.8	1.3	3.0	0.5	0.4	1.3
1999	26.8	11.3	2.4	10.8	15.8	0.7	0.9	0.4	2.4	3.4	3.1	1.1
2000	95.4	32.0	3.0	13.9	17.0	0.8	3.4	1.7	2.0	2.9	2.1	1.4
2001	62.0	30.3	2.0	9.6	14.9	0.6	3.6	1.7	2.2	10.8	6.5	1.7
2002	167.1	65.7	2.5	12.7	16.6	0.8	1.4	0.6	2.2	10.3	7.4	1.4
Eutrophic area												
1993	45.3	9.4	4.8	18.4	11.6	1.6	19.8	6.9	2.9	1.0	0.5	2.0
1994	10.9	2.4	4.5	6.7	4.2	1.6	29.2	8.6	3.4	0.7	0.4	1.8
1995	8.6	3.6	2.4	6.6	6.3	1.0	14.8	8.8	1.7	1.5	1.0	1.5
1996	3.1	1.0	3.1	8.7	14.4	0.6	16.4	8.5	1.9	1.6	1.4	1.1
1999	3.2	1.1	2.9	34.1	33.6	1.0	17.5	11.2	1.6	1.1	0.8	1.4
2000	8.3	2.0	4.1	34.8	36.8	0.9	14.8	9.9	1.5	1.9	1.0	1.9
2001	1.3	0.5	2.7	24.6	25.5	1.0	15.7	7.9	2.0	5.6	2.9	1.9
2002	4.5	1.2	3.6	24.7	20.9	1.2	21.6	7.9	2.7	5.8	2.9	2.0

support higher species richness than bare muddy/sandy areas, as seen also by Sprung (1994) and Heck et al. (1995). Seagrass beds provide essential processes and services, such as nutrient cycling, detritial production and export, sediment stabilization and optimal habitat for growth, survival and reproduction for a variety of fish and invertebrate species (Heck et al. 2003, Cunha et al. 2005, Polte et al. 2005), which have been pointed out as the major reasons for the importance of the habitat. Yet, seagrass beds are in decline around the world (Short & Neckles 1999, De Jonge & de Jong 2002, Charpentier et al. 2005, Munkes 2005). As shown here for the Mondego, such decline will lead to a reduction of both species richness and production of the whole estuary. The need for active restoration programs becomes urgently required worldwide (De Jonge & de Jong 2002, Cardoso et al. 2004b, Pardal et al. 2004, Lillebø et al. 2005, Martins et al. 2005, Munkes 2005), and especially for the Mondego estuary, since there is evidence that the *Z.*

noltii beds and eutrophic area are alternate stable states in the system between which it is difficult to shift without major intervention (Cardoso et al. 2004a). Eutrophication symptoms and impacts on the biological communities were pointed out as major reasons for the decline of the *Z. noltii* beds and for the restructure of living biota (Dolbeth et al. 2003, Marques et al. 2003, Pardal et al. 2004, Cardoso et al. 2004a, 2005, Verdelhos et al. 2005). For the Mondego, a shift from seagrass beds to areas covered by green macroalgae (eutrophic areas) seemed to occur. Natural disturbances appeared not to be the main factor triggering the observed changes, as seen in Cunha et al. (2005), with exception for 2000/01, when the big flood occurred. This shift clearly represents a loss of the ecological integrity of the whole estuary (Marques et al. 2003). Within this ten-year period, the Mondego has experienced several extremes of biological, chemical and physical stress (Cardoso et al. 2005, Lillebø et al. 2005). The macroalgal bloom observed in 1993 in the eutrophic area stimulated a pulse of production. Macroalgae may function as temporary habitats for macrofauna (Salovius et al. 2005), but their benefits are quite short-lived, as the long-term effects necessarily imply a loss of the estuarine production (Dolbeth et al. 2003). Additionally, the extreme salinity fluctuations, induced by floods, seemed also to have an impact on the plant and faunal communities. Estuaries are defined by salinity change over tidal cycles, but floods (of varying intensity, frequency, and duration) can alter salinity regimes dramatically to the detriment of the benthic communities (Ritter et al. 2005). With future climate change, more extreme fluctuations in salinity are expected, which in turn will affect both plant (Short & Neckles [1999] review for seagrass) and faunal communities (Lawrence & Soame 2004). Ecosystems such as the Mondego estuary will have to deal with the effect of multiple stressors, which may act synergistically to considerable lower the resilience and resistance of the populations to disturbance (Adams 2005, Cardoso et al. 2005).

There is evidence that the implementation of the mitigation measures in the Mondego estuary at the end of 1998 have been effective, regarding the water and environment quality improvement in the south arm. Nutrient loading was significantly reduced and no further macroalgal blooms were recorded (Cardoso et al. 2005, Lillebø et al. 2005). In addition, *Z. noltii* is gradually recovering, both in biomass and extent, and at the present is even starting to re-colonize the intermediate area (personal observation). With respect to the macrobenthic community recovery, all areas showed an increase in mean biomass, production and species richness from the low values achieved at the beginning of the post-mitigation period in 1999. This translated into an increase of the mean estuarine biomass and production for the whole south arm of the estuary. Nevertheless, the numbers of species have not yet attained former levels. The initial recovery response of the macroinvertebrate community appears to be with an increase in total biomass or energy, to which the opportunistic species mainly contributed, but not in complexity. This was particularly clear for the years following disturbance events, such as the macroalgal bloom followed by a crash in 1993, and the extreme flood in 2000/01. Kennish (2002) provides, for a hypothetical whole estuary, the mean macrobenthos production approaching 50 g AFDW m^{-2} yr^{-1} and the mean biomass up to 25 g AFDW m^{-2}. These values correspond to the ones estimated for the whole Mondego's south arm, yet following the disturbances in 1994 and 2002, the estuarine production clearly exceeded the 50 g AFDW m^{-2} yr^{-1}, and in the post mitigation period the mean biomass was also exceeded. This seems the system response to the maximization of the available resources, which takes place through a more efficient species composition (Marques et al. 2003). Especially in 1994, the production values are higher, but not the mean biomass values (higher $P/\overline{B}$ ratio of the community), suggesting a higher turnover of the community.

The most opportunistic species (r-strategists), such as *H. ulvae*, seemed to prevail with the major production after disturbance periods. *Hydrobia ulvae* was clearly the dominant producer in the *Z. noltii* beds, with lower $P/\overline{B}$ ratios in this area, as it presents structured populations with all age classes, while in the eutrophic area the population is dominated by juveniles (unstable population with higher turnover rates) (Cardoso et al. 2005). This species alone, contributed to the major part of all *Z. noltii* beds production (more than 80%) before the mitigation measures and then again in 2002. However, in the latest years of the study, there is some evidence of succession from r-strategists towards K-strategists species. *Scrobicularia plana*, typically a slow growing species, increased considerably in the estuary after the mitigation measures, especially in the eutrophic area, probably responsible by the increase of the estuarine mean biomass in the estuary. $P/\overline{B}$ ratios were lower in the post-mitigation period, suggesting higher stability of the population, and agreeing with the typical values of about 1.0 for longer-living molluscs (McLusky 1989). Consistent with the successional paradigm, *H. diversicolor*, which is also a longer-lived and larger-bodied species, increased its production mainly at the end of study in 2001 and 2002. The increase in these species has contributed to the general increase in the mean estuarine biomass during the post mitigation period. *Cyathura carinata* maintained its dominance in the eutrophic area, where it is tolerant to macroalgal blooms and floods (Ferreira et al. 2007). Also, there is the possibility of higher parasite pressure in the *Z. noltii* area, inhibiting *C. carinata* reproduction and making the population more erratic, which might also explain the lower production in the area and the higher $P/\overline{B}$ ratios registered, especially in the pre-mitigation period (Ferreira et al. 2007).

To interpret the present results, the prior disturbance history of a site has also to be taken into account. Thus, after the flood of 1993/94, production and species richness appeared to recover quicker when compared to the recover after the flood of 2000/01. In fact, by the time of the extreme flood in 2000/01, the species richness was much lower and this may have compromised the recovery process, consistent with current thinking on system resilience provided by biodiversity (Loreau et al. 2002, Marques et al. 2003, Raffaelli et al. 2003). If biodiversity is severely reduced by one stressor, then the effects of subsequent ones may be much greater than imagined. When considered alone, both *Z. noltii* beds and the eutrophic area responded to disturbance in similar ways, but at different rates. Thus, the *Z. noltii* beds were able to reduce production during a disturbance and almost double it afterwards, while the eutrophic area production only showed a slow tendency to increase production. *Zostera noltii* beds are considered to represent the original more pristine conditions of the estuary (Marques et al. 2003), whereas the eutrophic area represents the loss of ecological integrity. Actually, in the beginning of the 1980s, the *Z. noltii* beds covered a large fraction of the intertidal area, extending to the upstream section of the south arm, where is located the eutrophic area (Marques et al. 2003). At the present time, the *Z. noltii* beds are recovering but the eutrophic area restoration is still far away from a habitat similar to the *Z. noltii* beds. Quite recently, some very small patches of *Z. noltii* are appearing in the eutrophic area (personal observation), but the plant recovery is not fully taking place. As a simple bare sandy/muddy habitat, the eutrophic area appears less variable over time. Potentially this area may be reaching a new steady state community for bare sand/mud, which is consistent with the increase of the K-strategists species (e.g. *S. plana*) in this area.

ACKNOWLEDGMENTS

The authors are indebted to all colleagues from IMAR-Coimbra that participated in field and laboratory work.

REFERENCES

Adams SM (2005) Assessing cause and effect of multiple stressors on marine systems. Mar Pollut Bull 51: 649–657.

Beukema JJ, Dekker R (2005) Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Mar Ecol Prog Ser 287: 149–167.

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html Alfred Wegener Institute for Polar and Marine Research, Germany.

Cardoso PG, Pardal MA, Lillebø AI, Ferreira SM, Raffaelli D, Marques JC (2004a) Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. J Exp Mar Biol Ecol 302: 233–248.

Cardoso PG, Pardal MA, Raffaelli D, Baeta A, Marques JC (2004b) Macroinvertebrate response to different species of macroalgal mats and the role of disturbance history. J Exp Mar Biol Ecol 308: 207–220.

Cardoso PG, Brandão A, Pardal MA, Raffaelli D, Marques JC (2005) Resilience of *Hydrobia ulvae* populations to anthropogenic and natural disturbances. Mar Ecol Prog Ser 289: 191–199.

Charpentier A, Grillas P, Lescuyer F, Coulet E, Auby I (2005) Spatio-temporal dynamics of a *Zostera noltii* dominated community over a period of fluctuating salinity in a shallow lagoon, Southern France. Estuar Coast Shelf Sci 64: 307–315.

Clarke KR, Warwick RM (2001) Change in Marine Communities. An Approach to Statistical Analysis and interpretation, 2nd edition. Primer-E, Plymouth, United Kingdom.

Cunha AH, Santos RP, Gaspar AP, Bairros MF (2005) Seagrass landscape-scale changes in response to disturbance created by the dynamics of barrier-islands: A case from Ria Formosa (Southern Portugal). Estuar Coast Shelf Sci 64: 636 – 644.

Cusson M, Bourget E (2005) Global patterns of macroinvertebrate production in marine benthic habitats. Mar Ecol Prog Ser 297: 1–14.

De Jonge VN, de Jong DJ (2002) Ecological restoration in coastal areas in the Netherlands: concepts, dilemmas and some examples. Hydrobiologia 478: 7–28.

Dexter DM (1983) Community structure of intertidal sandy beaches in new South, Australia. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. Dr W Junk W Publishers, The Hague, The Netherlands, p 461–472.

Dolbeth M, Pardal MA, Lillebø AI, Azeiteiro UM, Marques JC (2003) Short and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. Mar Biol 143: 1229–1238.

Dolbeth M, Lillebø AI, Cardoso PG, Ferreira SM, Pardal MA (2005) Annual production of estuarine fauna in different environmental conditions: An evaluation of the estimation methods. J Exp Mar Biol Ecol 326: 115–127.

Ferreira SM, Pardal MA, Lillebø AI, Cardoso PG, Marques JC (2004) Population dynamics of *Cyathura carinata* (Isopoda) in a eutrophic temperate estuary. Estuar Coast Shelf Sci 61: 669–677.

Ferreira SM, Brandão A, Baeta A, Neto JM, Lillebø AI, Marques JC, Jensen KT, Pardal MA (2007) Effects of restoration management on the estuarine isopod *Cyathura carinata*: mediation by trematodes and habitat change. Mar Biol 151:109–118.

Heck KL, Able KW, Roman CT, Fahay MP (1995) Composition, abundance, biomass, and production of macrofauna in a new england estuary - comparisons among eelgrass beds and other nursery habitats. Estuaries 18 (2): 379–389.

Heck KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 25: 123–136.

Kennish MJ (2002) Environmental threats and environmental futures of estuaries. Environ Conserv 29: 78–107.

Lawrence AJ, Soame JM (2004) The effects of climate change on the reproduction of coastal invertebrates. Ibis 146: 29–39

Lillebø AI, Neto JM, Martins I, Verdelhos T, Leston S, Cardoso PG, Ferreira SM Marques JC, Pardal MA (2005) Management of a shallow temperate estuary to control eutrophication: The effect of hydrodynamics on the system's nutrient loading. Estuar Coast Shelf Sci 65: 697–707.

Loreau M, Dowining A, Emmerson M, Gonzalez A, Hughes J, Inchausti P, Joshi J, Norberg J, Sala O (2002) A new look at the relationship between diversity and stability. In: Loreau M, Naeem S, Inchausti P (Eds) Biodiversity and Ecosystem Functioning. Oxford University Press, Oxford, United Kingdom, p 79–91.

Marques JC, Nielsen SN, Pardal MA, Jørgensen SE (2003) Impact of eutrophication and river management within a framework of ecosystem theories. Ecol Model 166: 147–168.

Martins I, Neto JM, Fontes MG, Marques JC, Pardal MA (2005) Seasonal variation in short-term survival of *Zostera noltii* transplants in a declining meadow in Portugal. Aquat Bot 82: 132–142.

McLusky DS (1989) The estuarine ecosystem. 2nd Edition Chapman and Hall, New York, USA, p 215.

Munkes B (2005) Eutrophication, phase shift, the delay and the potential return in the Greifswalder Bodden, Baltic Sea. Aquat Sci 67: 372–381.

Paerl HW (2006) Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: interactive effects of human and climatic perturbations. Ecol Eng 26: 40–54.

Pardal MA, Marques JC, Metelo I, Lillebø A, Flindt MR (2000) Impact of eutrophication on the life cycle, population dynamics and production of *Amphitoe valida* (Amphipoda) along an estuarine spatial gradient (Mondego Estuary, Portugal). Mar Ecol Prog Ser 196: 207–219.

Pardal MA, Cardoso PG, Sousa JP, Marques JC, Raffaelli D (2004) Assessing environmental quality: a novel approach. Mar Ecol Prog Ser 267: 1–8.

Pihl L, Magnusson G, Isaksson I, Wallentinus I (1996) Distribution and growth dynamics of ephemeral macroalgae in shallow bays on the swedish west coast. J Sea Resear 35: 169–180.

Polte P, Schanz A, Asmus H (2005) The contribution of seagrass beds (*Zostera noltii*) to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea. Mar Biol 147: 813–822.

Powers SP, Peterson CH, Christian RR, Sullivan E, Powers MJ, Bishop MJ, Buzzelli CP (2005) Effects of eutrophication on bottom habitat and prey resources of demersal fishes. Mar Ecol Prog Ser 302: 233–243.

Raffaelli D, Emmerson M, Solan M, Biles C, Paterson D (2003) Biodiversity and ecosystem processes in shallow coastal waters: an experimental approach. J Sea Res 49: 133–141.

Ritter C, Montagna PA, Applebaum S, (2005) Short-term succession dynamics of macrobenthos in a salinity-stressed estuary. J Exp Mar Biol Ecol 323: 57–69.

Salovius S, Nyqvist M, Bonsdorff E (2005) Life in the fast lane: macrobenthos use temporary drifting algal habitats. J Sea Res 53: 169–180.

Short FT, Neckles HA (1999) The effects of global climate change on seagrasses. Aquat Bot 63: 169–196.

Simas T, Nunes JP, Ferreira JG (2001) Effects of global climate change on coastal salt marshes. Ecol Model 139: 1–15.

Sprung M (1994) Macrobenthic Secondary Production en the Intertidal Zone of Ria Formosa - a lagoon in Southern Portugal. Estuar Coast Shelf Sci 38: 539–558.

Verdelhos T, Neto JM, Marques JC, Pardal MA (2005) The effect of eutrophication and coastal management on the bivalve *Scrobicularia plana*. Estuar Coast Shelf Sci 63: 261–26.

CHAPTER II

Population dynamics of *Pomatoschistus minutus* and *Pomatoschistus* microps

Strategies of Pomatoschistus minutus and Pomatoschistus microps to cope with environmental instability

Modelling the life cycle, population and biomass dynamics of two Gobiidae fish species

Strategies of *Pomatoschistus minutus* and *Pomatoschistus microps* to cope with environmental instability

Abstract The populations of *Pomatoschistus minutus* and *Pomatoschistus microps* were studied from June 2003 to May 2006 in the Mondego estuary, in order to understand the ability of these species to withstand environmental variability. During this period a severe drought occurred (2005), with consequent lower freshwater runoff and higher salinity incursion into the estuary. Occasional abnormal high water temperatures were observed in 2003 and 2005. The fish populations were sampled monthly along an estuarine gradient, from which population density, structure, growth and biomass production was assessed. *P. minutus* distributed mainly at the most saline downstream area, while *P. microps* distributed within the whole estuary, in accordance to the salinity and temperature tolerances for the species. A clear decrease in density and production was observed for *P. minutus* in the dry year, with non-expressive recruitments and the quick disappearance of the parental cohort. For *P. microps*, the decrease was not so pronounced. No direct effects were attributable to the salinity and temperatures variations (resulting from the drought and high temperatures). Yet, higher predation pressure on *P. minutus* was a hypothesis raised, as the salinity incursion increased the piscivorous marine adventitious species in the downstream areas. *P. microps* benefited from a wider temperature and salinity range tolerance, allowing the species to occupy different areas in the estuary and by this seemed better able to cope with the environmental variability during the three-year studied period.

Keywords Gobiidae, Life cycle, Population dynamics, Secondary production, Environmental variability

INTRODUCTION

The gobies *Pomatoschistus minutus* and *Pomatoschistus microps* are important inhabitants of lagoons, coastal areas and estuaries of the Atlantic and Mediterranean regions (Jaquet & Raffaelli 1989, Arruda et al. 1993, Leitão et al. 2006). They are recognized by their plasticity towards environmental perturbations (Pampoulie et al. 2000), mainly through variations in the reproductive effort (number and duration of spawning) and egg size (Bouchereau et al. 1991, Bouchereau & Guelorget 1998, Pampoulie et al. 2000). In fact, their great adaptability endows them with the potential capacity to successfully occupy different biotopes (Bouchereau & Guelorget 1998). Also, they are quite relevant in trophic webs as intermediate predators, being consumers of plankton, meio- and macro-benthos (Hesthagen 1977, Doornbos & Twisk 1987, Jaquet & Raffaelli 1989, Salgado et al. 2004, Leitão et al. 2006), and prey of several larger fishes (Arruda et al. 1993) and birds (Doornbos 1984). Temperature and salinity, which may constrain the development and survival of fish eggs and larvae (Fonds & van Buurt

1974, Hesthagen 1977), food availability, sediment quality and suitable nest site availability (Nellbring 1993, Costa et al. 2002) seem to be the structuring factors of fish populations. Changes in these conditions are quite usual in estuarine ecosystems due to natural and anthropogenic induced variations (Maes et al. 2004). Estuaries are mainly located in human-populated areas and therefore may be exposed to high variability due to anthropogenic effects, such as eutrophication, that has been recognized as a major problem in several estuaries worldwide (Marques et al. 2003, Lillebø et al. 2005, Powers et al. 2005, Paerl 2006, Dolbeth et al. 2007). Parallel to the anthropogenic induced stress, the climate variations may also have important consequences on aquatic ecosystems (Roessig et al. 2004). All together, this high variability will exacerbate the natural variations and constrain the life cycle characteristics and population dynamics of the estuarine inhabitants (e.g. Sims et al. 2004, Roessig et al. 2004, Cardoso et al. 2005). Taking into account the ecological importance of the *P. minutus and P. microps*, their wide distribution and great plasticity, a better understanding of their life cycle and adaptations towards a changing ecosystem becomes relevant. The main goals of the present study were to understand the ability of *P. minutus* and *P. microps* to cope with environmental variations along a three-year study period, thorough an analysis of the 1) life cycle characteristics, 2) population spatial and temporal dynamics and 3) secondary production.

MATERIALS AND METHODS

Study area

The Mondego estuary (Portugal) is located in a warm temperate region, on the Atlantic coast of Portugal (40°08'N, 8°50'W) (Fig. 1). It is a small estuary (3.4 km^2 area), with two arms (north and south) of distinct hydrologic characteristics. The north arm is deeper (4-10 m during high tide, tidal range 1-3 m) and constitutes the main navigation channel and the location of the Figueira da Foz harbour. The main freshwater inputs to the north arm are from Mondego river (Fig. 1), with 227 km extension and draining a hydrological basin of approximately 6 670 km^2 (Marques et al. 2002). The south arm is shallower (2-4 m during high tide, tidal range 1-3 m), characterized by large areas of exposed intertidal flats during low tide (about 75% of total area). Water circulation in the south arm mostly depends on the tides and on the freshwater input from the Pranto river (Fig. 1), as the upstream areas are almost silted up, with only a small connection with north arm. The Pranto river is controlled by a sluice according to the water needs in the rice fields of Mondego valley.

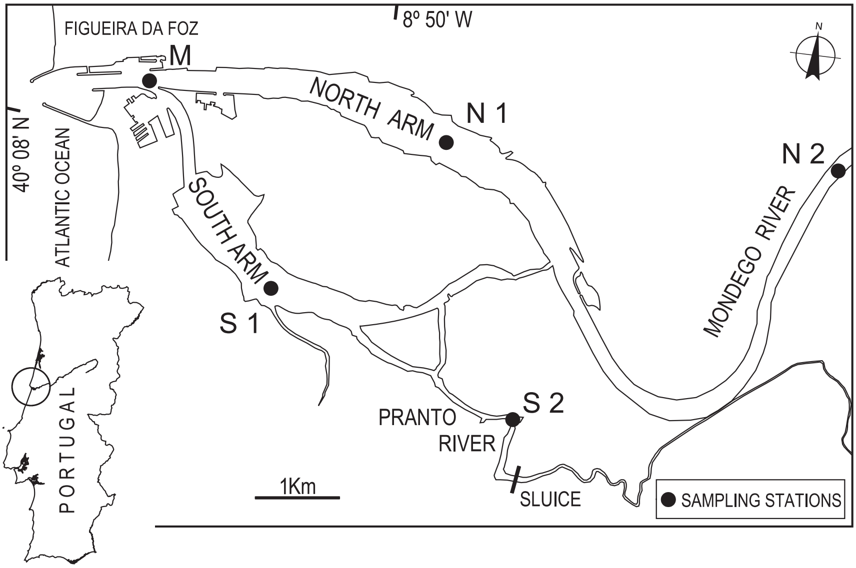


Fig. 1 Location of the Mondego estuary, with indication of the sampling stations.

The main disturbance sources on the Mondego estuary are 1) the dredging and shipping in the north arm and 2) the raw sewage disposal and high nutrient inputs from agricultural and fish farms in the upstream areas of the south arm. In the past two decades, clear symptoms of eutrophication were observed in the south arm, with the occurrence of macroalgae blooms and seagrass decline. In 1998/1999, mitigation measures were taken to reduced the nutrient loading and the system seems to be gradually recovering (for further details see Cardoso et al. 2005, Lillebø et al. 2005, Dolbeth et al. 2007).

Sampling procedures

From June 2003 to June 2006 fish were collected monthly, using a 2 m beam trawl, with one tickler chain and 5 mm stretched mesh size in the cod end. Sampling was carried out during the night, at the ebbing tide of spring tides, in five stations (M, S1, S2, N1, N2, Fig. 1): M - at 1.5 km from the estuary's mouth, 8.7 ± 1.2 m deep, area subjected to constant dredging; S1 - located upstream a *Zostera noltii* bed, 2.3 ± 0.4 m deep; S2 - near Pranto river sluices, which control the main freshwater flow from Pranto river to the south arm, 2.4 ± 1.0 m deep; N1 – with regular freshwater flow, 5.5 ± 0.5 m deep; N2 -

most upstream area, with lower saline influence and permanent freshwater flow (from the Mondego river), 4.5 ± 0.3 m deep. Each survey consisted of three hauls, at each sampling station, in a total of 10 to 15 min duration per station. All fish caught were identified, from which *P. minutus* and *P. microps* were measured (total length, with 1 mm precision) and weighted (wet weight – WW, with 0.001 g precision). In each sampling station, water temperature, salinity, pH and dissolved oxygen were measured at the bottom. Algae collected together with fish in beam trawl samples were also weighed (WW). Each season (summer, autumn, winter and spring), sediment samples were collected using a Van Veen grab, in order to determine granulometry.

Data analysis

The population structure of each species was defined by tracking recognizable cohorts from the successive sampling dates. Each spatial sample was pooled and analysed through size frequency distribution analysis of the successive sampling dates, in order to track recognizable cohorts. The cohorts were determined with ANAMOD software package (Nogueira, 1992), which provides the modes and their standard deviation, and checks the reliability of the estimated parameters.

After recognition of the cohorts, the annual production was estimated by the cohort increment summation method (Winberg 1971), according to:

$$P_{cn} = \sum_{t=0}^{T-1} \left(\frac{N_t + N_{t+1}}{2} \right) \times \left(\overline{w}_{t+1} - \overline{w}_t \right)$$

where P_{cn} is the growth production (g WW m^{-2} y^{-1}) of cohort n, N is the density (ind m^{-2}), $\overline{w}$ is the mean individual weight (g WW m^{-2}), and t and t+1, consecutive sampling dates. Population production estimates correspond to the sum of each cohort production (P_{cn}).

The mean annual biomass ($\overline{B}$) was estimated according to:

$$\overline{B} = \left(\frac{1}{T} \right) \times \sum_{n=1}^{Nc} \left(\overline{B}_{cn} t_{cn} \right)$$

where T is the period of study, which is always 365 days (yearly cycles) as the mean annual biomass is being computed, Nc is the number of cohorts found in the study period, $\overline{B}_{cn}$ is the mean biomass (g WW m^{-2}) of cohort n, t_{cn} is the time period of the cohort n (days), from the first appearance of individuals until they disappeared.

The relationships between fish densities and environmental variables were investigated using a canonical correspondence analysis (CCA), performed with CANOCO software (version 4.5) (Ter Braak 1988). The population was divided into juveniles and adults, according to the minimal length of the last maturation stage found for each species. Each juvenile and adult *P. minutus* and *P. microps* densities were averaged per sampling area (station M, S1, S2, N1, N2) and season (summer, autumn, winter, spring). CCA allows the assessment of the relative importance of the environmental variables to the distribution patterns of the species (Ter Braak 1988). After defining the most important variables according to the CCA analyses, correlations with the species density were analysed individually by performing Spearman Rank Correlation test, using Statistica software (version 6.0).

RESULTS

Environmental conditions

During the study period, precipitation had some unusual variations when compared to the mean precipitation regime for central Portugal observed during the period of 1940-1997 (annual precipitation values of 1030 mm, INAG - http://snirh.inag.pt) (Fig. 2A). All years had lower annual precipitation values when compared to the 1940-1997 mean, especially in 2004 and 2005. The lowest annual precipitation was observed in 2005 (486.1 mm), with below–mean precipitation periods quite evident, being considered a very dry year (extreme drought). The freshwater runoff also evidenced a severe reduction in 2005, with values considerably lower than the ones observed in 2003 and 2006 (Fig. 2A). Consequently, salinity also showed high variations throughout the study period (Fig. 2B). Spatially, salinity presented typical values for marine water in the estuary's mouth (station M), except for the winter of 2006 (Fig. 2B). In general, higher salinities were recorded in the south arm (stations S1 and S2) than in the north arm (N1 and N2) (Fig. 2B). Station S1 showed similar values to the ones recorded in the estuary's mouth (M), while stations S2 and N1 presented typical brackish water salinity values (Fig. 2B). The most upstream area (station N2) showed the lowest salinities, ranging between 0 – 2 (Fig. 2B). Yet, in 2005, abnormal high salinities were observed (14.0 ± 6.46 from February 05 to September 05, Fig. 2B), due to low precipitation and low freshwater runoff (extreme drought, Fig. 2A) and the high water temperatures recorded in that period (Fig. 2C). In fact, the water temperature showed the typical variation usually found in temperate estuarine systems. Yet, in July 2003 and July 2005 higher temperatures were observed when compared to the same period in 2004 (Fig. 2C), with the highest values recorded in the upstream sampling stations (24°C to 26°C night temperature at S2 and N2). For the

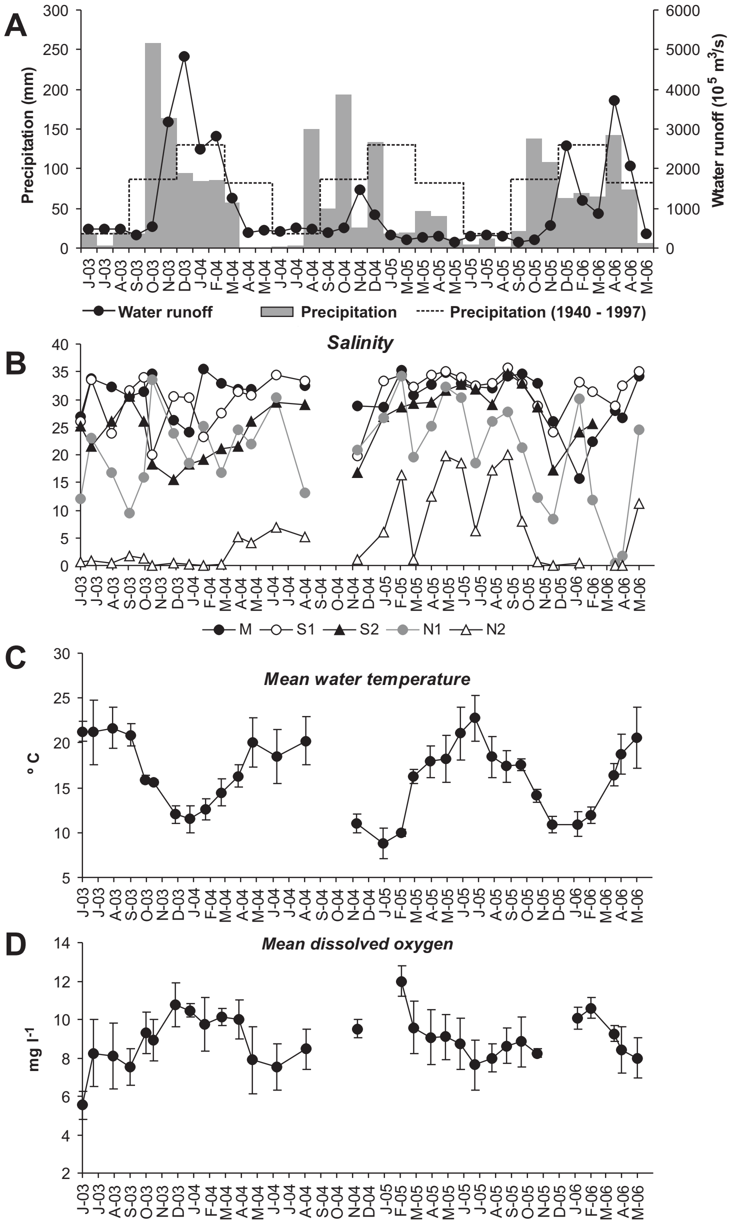


Fig. 2 Temporal variations of A) freshwater runoff and precipitation of the Mondego estuary, during the study period, and mean precipitation for central Portugal during the period of 1940-1997, B) salinity in the different sampling stations, C) mean water temperature ± standard deviation, D) mean dissolved oxygen ± standard deviation of the whole Mondego estuary.

whole estuary, the lowest values of mean dissolved oxygen were recorded in the spring and summer (Fig. 2D), following the highest temperatures (Fig. 2C). These values increased from upstream (station M, annual means 9.6-10.8 mg l^{-1}) to downstream areas (station N2, annual means 8.2-8.5 mg l^{-1}). pH values were relatively stable throughout the study period and sampling areas (8.0 ± 0.25).

Population spatial and temporal dynamics

For both species, the highest densities were observed in Jun-Aug 2003 (summer), after which similar values were never attained again (Fig 3). For *P. minutus*, there were some density increases in Feb-May and Dec 2004 and Apr-May 2006. Nevertheless there seemed to be a decreasing trend throughout the study period, especially in 2005 where values were comparatively very low (Fig. 3A). Regarding *P. microps*, the higher density increases occurred in the winter, spring and early summer in all years (Fig. 3B). No pronounced decrease in density was observed in 2005 during the extreme drought (Fig. 3B).

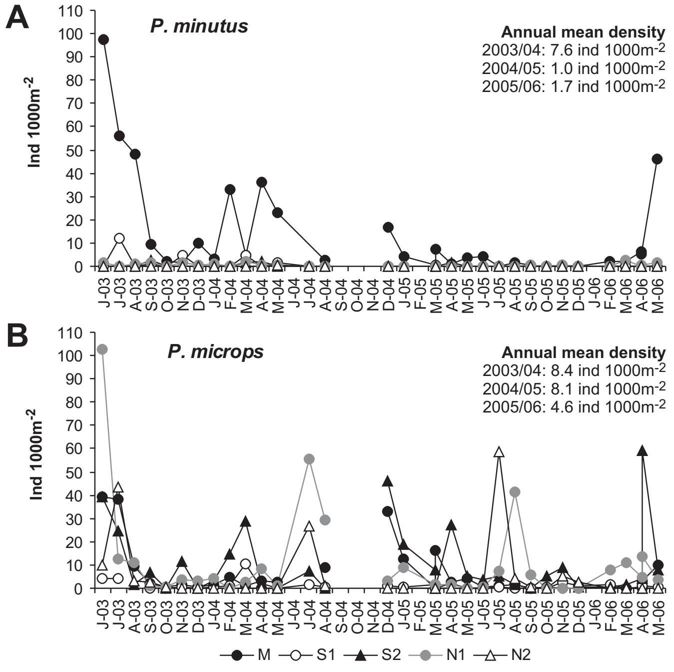


Fig. 3 Spatial and temporal distribution patterns for A) *Pomatoschistus minutus*, and B) *P. minutus* in the Mondego estuary, with indication of the mean annual densities.

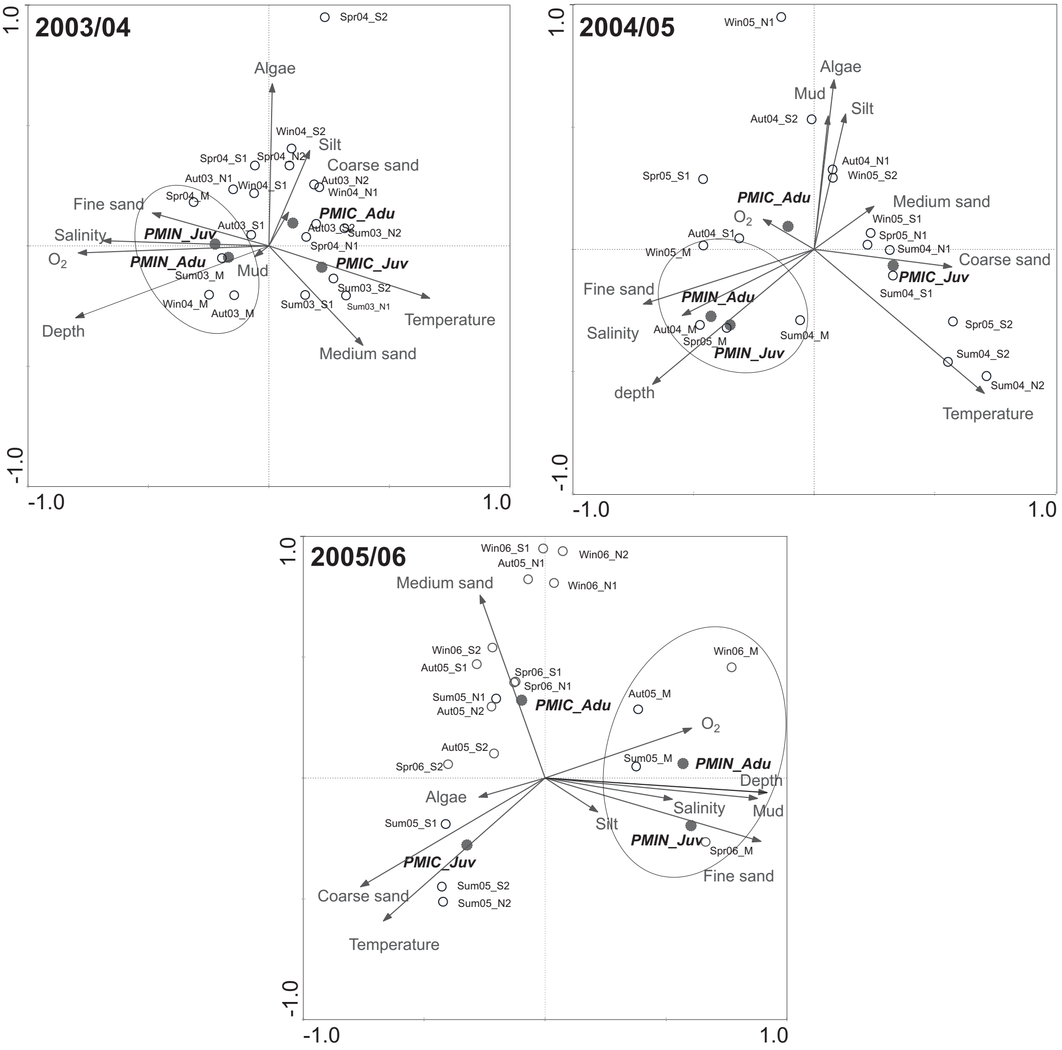


Fig. 4 Canonical Correspondence Analysis (CCA) ordination diagram relative to the fish density data for the three-year study period. Gray circles, both *Pomatoschistus* spp. juveniles and adults densities; open circles, stations positions within the ordination space; vector lines, relationship of significant environmental variables to the ordination axis, whose length is proportional to their relative significance. *PMIN_Juv*, *P. minutus* juveniles; *PMIN_Adu*, *P. minutus* adults; *PMIC_Juv*, *P. microps* juveniles; *PMIC_Juv*, *P. microps* adults.

Comparing both species, *P. microps* attained higher densities than *P. minutus* (Fig. 3). In 2004/05, *P. minutus* had the lowest annual mean density (1.0 ind m^{-2}), while *P. microps* only showed a marked decrease for 2005/06 (4.6 ind m^{-2}), during the 3-year study period (Fig. 3). With regard to the spatial distribution, *P. minutus* occurred mainly at the estuary's mouth (station M, Fig. 3A), with juveniles and adults occupying the same area (Fig. 4). *P. microps* occurred throughout the estuary, with slightly higher densities in the north arm of the estuary. Yet, the highest densities were observed at both sampling stations S2 and N1 (Fig. 3B, Fig. 4), typically brackish water environments. *Pomatoschistus minutus* occurred only once in the most upstream area (with very low density), where *P. microps* attained high densities, especially in the hot summers of 2003 and 2005 (Fig. 3B).

With regard to the environmental parameters most influencing fish distribution, temperature, salinity and depth seemed the most important for all years (Fig. 4). Algae, fine sands and dissolved oxygen also presented a high relevance in certain years (algae for 2003-2005, fine sand for 2004-2006 and dissolved oxygen in 2003/04 and 2005/06, Fig. 4). The first two axes of the CCA analysis accounted for at least 78% of the total variability in all the years. For both *P. minutus* juveniles and adults, significant positive correlations were found with depth for all years (except for adults in 2003/04) and with salinity in 2003/04 (Table 1). For *P. microps*, temperature was the only variable that had a significant (positive) correlation with juveniles in all years and the adults' density in 2003/04 (Table 1).

Table 1 Spearman rank correlation coefficients between fish mean density and environmental factors for the three years (n = 12 for 2003/04 and 2005/06, and n = 8 for 2004/05); ns, none significant, * significant at $p \leq 0.05$.

	P. minutus			***P. microps***		
	2003/04	2004/05	2005/06	2003/04	2004/05	2005/06
Juveniles						
Temp.	- 0.03 ns	-0.17 ns	- 0.00 ns	**0.50** *	**0.49** *	**0.75** *
Salinity	**0.63** *	0.06 ns	0.16 ns	0.07 ns	-0.09 ns	-0.11 ns
Depth	**0.59** *	**0.47** *	**0.59** *	-0.11 ns	- 0.07 ns	-0.05 ns
Adults						
Temp.	- 0.01 ns	-0.10 ns	-0.14 ns	**0.45** *	-0.19 ns	0.15 ns
Salinity	**0.80** *	0.22 ns	0.20 ns	0.08 ns	0.28 ns	-0.14 ns
Depth	0.44 ns	**0.58** *	**0.72** *	0.09 ns	0.30 ns	0.17 ns

Population structure and growth

Both *Pomatoschistus* spp. seemed to have discontinuous reproduction (Fig. 5). For *P. minutus* two recruitments were recorded per year, in April (spring) and November (late autumn) (Fig. 5A). Nevertheless, the April recruits of 2003 and 2005 (cohorts 3 and 7 respectively), with 4.0 - 5.0 cm, were missing from October to February (Fig. 5A). The November cohort 5 finished earlier than the others, with the largest individuals with 4.7 cm (Fig. 5A). In 2005, individuals were scarce, nevertheless it seemed to appear a new cohort in August (cohort 8), not seen in the other years (Fig 5A). New recruits of the November cohort of 2005 did not appear (Fig. 5A). Yet, the presence of two new length classes in April 2006 suggests that the older class could belong to the new November 2005 recruits and these were included in the November recruitments (cohort 9, Fig. 5A). The mean growth of the cohorts belonging to each recruitment was determined (April: C1, C3, C5, C7, C8, C10; November: C2, C4, C6, C9). In general, the April recruits showed higher growth rate than the November recruits (Fig 5B). The exception occurred from day 180 to 300, corresponding to summer months for the November recruits with higher growth rate, and winter months for April recruits (Fig. 5B). Life span varied between 18 and 19 months (Fig 5A, B).

For *P. microps* it seemed to exist three recruitment periods: January, April and June (Fig. 5C). The population consisted mainly of young individuals, with one year old individuals representing only a small fraction of the overall population. In 2005, there were no new recruits from the January cohort, nevertheless these seemed to appear short after, in April (cohort 12, Fig. 5C). The mean growth rate of both April recruits (C1, C4, C7, C10, C13) and January recruits (C3, C6, C9, C12) was higher than the June recruits (C2, C5, C8, C11) (Fig. 5D). Life span varied between 15 and 17 months (Fig. 5C, D).

Production

Annual production and mean biomass estimates showed a clear decreasing trend along the study period for *P. minutus*, while for *P. microps* similar values were obtained for all years (Table 2, 3). The lowest production values were obtained in 2005/06 (Table 2). When comparing both species, production values were considerably higher for *P. minutus* than for *P. microps*, especially in 2003/04. Mean annual biomass was also highest for *P. minutus*, except for 2005/06 (Table 2). For *P. microps*, $P/\overline{B}$ ratios were similar throughout the study period, with the lowest value in 2004/05 (Table 3). For *P. minutus* the highest

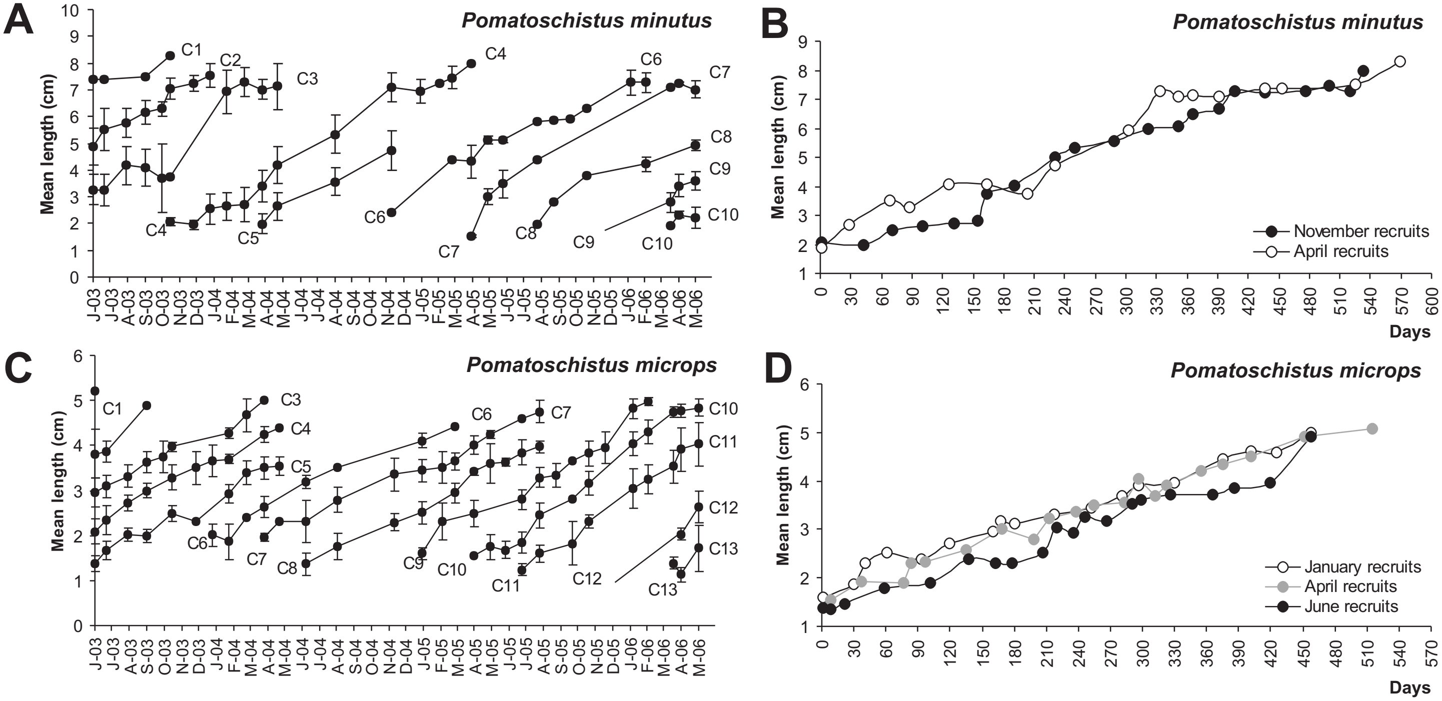


Fig. 5 Linear growth of the cohorts, mean length class measure ± standard deviation, with indication of the appearance of the first individual for each cohort (A, C) and mean linear growth of each recruitment (B, D) for *Pomatoschistus minutus* and *P. microps*.

$P/\overline{B}$ ratios were registered in 2003/04 and 2004/05 (Table 3), years with the highest temperatures in the spring and early summer.

DISCUSSION

Life cycle general considerations

Differences in the recruitments were found for both *Pomatoschistus* spp. in the Mondego estuary when compared to other Atlantic (Healey 1972, Fonds 1973, Hesthagen 1977, Arruda et al. 1993, Bouchereau & Guelorget 1998) and Mediterranean regions (Bouchereau et al. 1990, Bouchereau & Guelorget 1998), which may be related with the temperature. This relationship was clear for *P. minutus*, as the high temperatures observed in the summer might have delayed one recruitment to the autumn, due to the temperature boundaries for the eggs and larval development of *P. minutus*, determined experimentally to vary between 10 and 20°C (Fonds & van Buurt 1974). Also, winter reproductive migrations to sea seem to occur in the Mondego estuary, as suggested before (Leitão et al. 2006), and similarly to other studies (Bouchereau et al. 1990, 1991, Pampoulie et al. 1999). In fact, sexually mature individuals with 4.0 to 5.0 cm disappeared from November to February in 2003 and 2005 and new cohorts appeared in the following April, reinforcing the reproductive migration hypothesis, at least for the parental cohorts of April recruits. For the parental cohort of November recruits there were no clear evidences of migration.

Recruitment seemed discontinuous for *P. microps*, in January (contrarily to the February recruitment found by Leitão et al., 2006), April and June. Yet, the warm summers and the high productivity of the Mondego estuary (Dolbeth et al. 2007), also allows the hypothesis of a continuous breeding season from January to June, as suggested by Healey (1972), Fouda & Miller (1981), Bouchereau et al. (1991), Bouchereau & Guelorget (1998) and Pampoulie (2001), who claim a long breeding season for the species. In fact, Mazzoldi & Rasotto (2001) suggested that in highly productive habitats with warm summers, long breeding season of short living species (such as *P. microps*) can give rise to more than one spawning peak in the breeding period, which may be the case of *P. microps* in the Mondego estuary.

The spring recruits of *P. minutus* had higher mean growth rates, probably due to temperature, as also seen by Arruda et al. (1993) and Bouchereau & Guelorget (1998). Yet, for *P. microps* this difference was not pronounced when comparing the winter (January) and spring (April and June) recruits. Contrarily to expected, the June cohorts, subjected to higher temperatures in the cohort beginning, showed lower growth rates than the January cohorts, and the April cohorts appeared to have a higher life span than the January ones. According to the maximum body lengths found in the field data, the life span was estimated to be 18-19 months for *P. minutus*, and 15-17 months for *P. microps*. These estimates were higher compared to the ones obtained for the Mediterranean region (12-16 months for *P. minutus* and 12-14 months for *P. microps*, Bouchereau & Guelorget 1998), and shorter than the North Atlantic regions ones (20-24 months for *P. minutus* and 19-23 months for *P. microps*, Fonds 1973, Hesthagen 1977, Fouda & Miller 1981, Bouchereau & Guelorget 1998). The differences found may be related with the reproductive strategy (date and duration), the age at first maturity and the growth rates, associated with warmer climate of the Mondego estuary, as proposed by Bouchereau & Guelorget (1998), Pampouile et al. (1999) for the Mediterranean species.

Species spatial dynamics

Pomatoschistus minutus and *P. microps* have high diet overlap (Magnhagen & Wiederholm 1982, Salgado et al. 2004, Leitão et al. 2006), but seem to select habitats differently when in sympatry. In general, *P. microps* can reduce its area in benefit of *P. minutus* (Magnhagen & Wiederholm 1982, Costa et al. 2002). In the Mondego estuary, these species seemed to occupy different areas, with *P. minutus* occurring more frequently at most marine and deeper areas (downstream), while *P. microps* occurred more at the inner areas, with typical brackish water characteristics. These distribution areas also agree with the temperature and salinity preferences of each species (Fonds and van Buurt 1974, von Oertzen 1984), and for *P. minutus* may also be related with the preference for deeper waters to spawn, as claimed by Nellbring (1993). According to Attrill and Power (2004), similar species (taxonomically or functionally) may use distinct thermal spaces to minimise competition between them, which may be the present case. In the Mondego estuary,

Table 2 Mean density, growth production and turnover rate ($P/\overline{B}$ ratio) estimates for *Pomatoschistus minutus*. * References *in* Costa et al. (2002). Conversions to ash free dry weight (ADFW) according to: g wet weight (WW) / g AFDW = 1/0.251; kJoules (kJ) / g AFDW = 25.57 (Brey 2001).

Location	**Study Period**	**Mean density (Ind m^{-2})**	**Production**	**Production with converted units (g AFDW m^{-2} yr^{-1})**	**$P/\overline{B}$ (y^{-1})**	**Sampling gear**	**Production method**	**Reference**
P. minutus								
Gullmarsvik, Sweden	1977/78	0.6 – 2.6	0.1 – 0.2 g AFDW m^{-2} yr^{-1}	0.1 – 0.2	-	Drop trap	Cohort Increment summation	Phil & Rosenberg 1982
Gullmar Fjord Sweden	1976 1977	-	2 4 kJ m^{-2} y^{-1}	0.07821 0.15643	-	-	-	Evans 1984
Grevelingen estuary, Netherlands	1980 1981	-	0+ group: 1.06 0+ group: 0.14 g AFDW m^{-2} yr^{-1}	1.06 0.14	- -	Beam trawl	Instantaneous growth	Doornbos & Twisk 1987
Baltic Sea, Germany	1987 1988	-	0+ group: 0.012, 1+ group: 0.0001 0+ group: 0.126 g WW m^{-2} y^{-1}	0.00301 0.00003 0.03163	-	-	-	Thiel 1990*
North Sea, Netherlands	1988	-	0.02 g AFDW m^{-2} yr^{-1}	0.02		-	-	Hostens and Hamerlynck 1994*
Wadden Sea, Germany	1992	-	0.05 g AFDW m^{-2} yr^{-1}	0.05	2.2	-	-	Del Norte Campos 1995*
Mondego estuary, Portugal	2003/04 2004/05 2005/06	0.008 0.001 0.002	0.0167 0.0039 0.0017 g WW m^{-2} yr^{-1}	0.0042 0.0010 0.0004	3.32 2.12 1.30	Beam trawl	Cohort Increment summation	Present study

Table 3 Mean density, growth production and turnover rate (P/$\overline{B}$ ratio) estimates for *Pomatoschistus microps*. * References *in* Costa et al. (2002). Conversions to ash free dry weight (ADFW) according to: g wet weight (WW) / g AFDW = 1/0.251; kJoules (kJ) / g AFDW = 25.57 (Brey 2001).

Location	**Study Period**	**Mean density (Ind m^{-2})**	**Production**	**Production with converted units (g AFDW m^{-2} yr^{-1})**	**P/$\overline{B}$ (y^{-1})**	**Sampling gear**	**Production method**	**Reference**
P. microps								
Skagerrak-Gull: Gullmarsvik, Sand: Sandvik, Sweden	1977/78 1978/79	10.7 – 15.1 0.6 - 0.8 12.0 - 25.0	0.4 - 0.6 Gull. 0.3 - 0.4 Sand. 0.01 – 0.04 Gull. g AFDW m^{-2} yr^{-1}	0.4 - 0.6 0.3 - 0.4 0.01 – 0.04	- -	Drop trap	Cohort Increment summation	Phil & Rosenberg 1982
Grevelingen estuary, Netherlands	1981	-	0+ group: 0.81 g AFDW m^{-2} yr^{-1}	0.81	-	Beam trawl	Instantaneous growth	Doornbos & Twisk 1987
Baltic Sea, Germany	1987 1988	-	0+ group: 0.043 1+ group: 0.031 0+ group: 0.062 1+ group: 0.004 g WW m^{-2} yr^{-1}	0.0108 0.0078 0.0156 0.0010	-	-	-	Thiel 1990*
Wadden Sea, Germany	1991 1992	-	0.108 - 0.146 0.068 - 0.220 g AFDW m^{-2} yr^{-1}	0.108 - 0.146 0.068 - 0.220	4.5 to 5.4 2.52 to 4.49	-	-	Del Norte Campos 1995*
Sylt-Rømø Bight, Germany	July to September 2003	2.3 – 10.7 (seagrass) 0.3 – 2.0 (sand)	0.204 ±15 (seagrass) 0.010 ± 2 (sand) g AFDW m^{-2} month^{-1}	-	-	Portable Drop trap	Cohort Increment summation	Polte et al. 2005
Mondego estuary, Portugal	2003/04 2004/05 2005/06	0.008 0.008 0.005	0.0036 0.0030 0.0030 g WW m^{-2} yr^{-1}	0.0009 0.0008 0.0007	2.73 2.38 3.13	Beam trawl	Cohort Increment summation	Present study

P. microps distributed in areas with higher temperatures and the density was positively correlated with temperature. Also, when densities were plotted against temperature for both species, *P. microps* density seemed to follow the seasonal variation of temperature (Fig. 6), although recruitment also occurred in the winter.

Besides temperature, salinity also played an important role in the distribution and abundance patterns of both *Pomatoschistus* spp., as observed also by Pampouile et al. (2001) and Leitão et al (2006), probably due to its effects on the egg development (Fonds and van Buurt 1974). *Pomatoschistus microps* supports a wider range of salinities than *P. minutus* (salinities within 5-35 and 5-15 for maximum egg survival and maximum larval size respectively for *P. microps*; and salinities within 15-35 for egg survival and maximum larval size at 35 for *P. minutus*). These range tolerances explained the distribution of *P. microps* within all estuary, while *P. minutus* occurred mainly at the estuary mouth and was correlated positively with salinity in the 2003/04. Therefore, *P. microps* may take advantage in dispersing to other estuarine areas, as it is more tolerant to salinity and temperature variations. With this behaviour, *P. microps* may also take advantage of the presence of alternative food sources, such as *Corophium* spp., highly abundant in the upstream areas (Leitão et al. 2006).

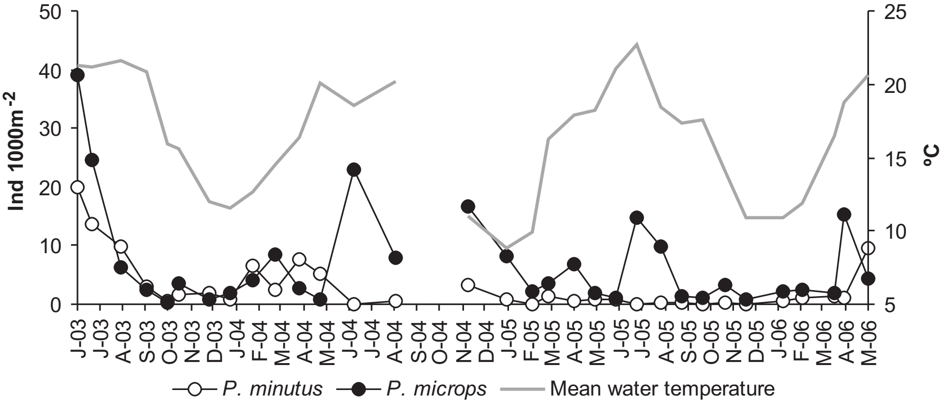


Fig. 6 Temporal variations of *Pomatoschistus minutus* and *Pomatoschistus microps* densities (Ind 1000m^{-2}), and mean water temperature (°C) for the whole Mondego estuary.

Species temporal dynamics and production

For *P. minutus* a clear decrease in density (especially evident in 2005) and production was observed along the study period. Several hypotheses may be causing such decrease:

a) mortality or migration to sea (Fonds and Veldhuis 1973, Hesthagen 1977, 1979, von Oertzen 1984) as suggested by the complete disappearance of cohort 5 after the reproductive period; b) behavioural differences; or c) inter-annual variability in the recruitment's success, as suggested by Pampoulie et al. (2000), Attrill and Power (2004) and Maes et al. (2004). In fact, the scarcity of individuals in 2005 suggests a non-expressive recruitment, although the April recruitment seemed to occur in two periods (April and August 2005), which may also be an adaptation to the environmental conditions. Fonds and van Buurt (1974) found experimentally that *P. minutus* eggs do not survive at 25°C. High water temperatures were observed in the estuary in the spring and early summer of 2003 and 2005 (higher in the inner areas of the estuary). Yet, density was high in 2003/04, excluding a clear temperature effect on the fish population in 2005. An important factor was the occurrence of the extreme drought in 2005, which although not changing considerably the fish community of the Mondego estuary, induced a gradual replacement of freshwater by marine adventitious species (Martinho et al. 2007). These piscivorous species benefited from a higher salinity incursion, distributing in the same areas of *P. minutus*, which might have caused a higher predation pressure on the species, increasing mortality and weakening the subsequent recruitment. Migration or population development in the sea after the reproductive period might have also occurred, but the predation pressure is potentially also high. For *P. microps* no clear decrease in density and production was observed during the extreme drought year. This species supports a wider range of temperature and salinity variations, which seems an advantage towards *P. minutus*, as it may disperse within the inner estuarine areas, potentially not subjected to such predation and with more alternative habitats and food resources. Also advantageous is the potentially longer breeding season and several spawning periods for *P. microps*, which maximizes the surviving changes.

The estuarine production of *P. minutus* was higher than for *P. microps* in 2003/04 and 2004/05, although with lower mean density. This is probably related with their life cycle characteristics, as *P. minutus* can attain higher biomass and a slight higher growth rate than *P. microps*.

Secondary production studies of *P. minutus* and *P. microps* are dated and in literature, values were only found for North-Atlantic coastal areas (Table 2). Nevertheless, the estimates for the Mondego estuary were lower than the ones found in the North-Atlantic (Table 2), when it would be expected production increases with decreasing latitudes (Cowley and Whitfield, 2002). Both *Pomatoschistus* spp. densities seemed also lower, comparing with Pihl and Rosenberg's (1982) results (Table 2). The catch efficiency of the sampling gear (beam trawl) used in the present study has been widely assumed to be 30% (Hemingway & Elliott 2002), but even if the density and production values were multiplied by a factor (3.3333) they would still be lower. Besides possible inaccuracies in determining population sizes and their changes, fish production estimates are subjected to other sources of error: different effects of mortality, emigration and immigration to the estuary (Costa et al. 2002, Cowley & Whitfield 2002), different growth rates along the life cycle, as seen by Fouda & Miller (1981) for *P. microps*, and different methods to estimate production (Costa et al. 2002). In the present study, the estimated production refers only to the population inhabiting the estuary. These estimates are certainly affected by migration, hypothesized to occur for *P. minutus*, and by the high variability of the abiotic and potentially biotic conditions (e.g. predation). The anthropogenic impacts that occurred in the last decades in the Mondego estuary are also relevant. Accordingly, the estuary might have lost part of its production potential for these species, explaining the differences found with other studies elsewhere. As an example, the fish production of *P. microps* is potentially much higher in eelgrass beds than in bare sand (Table 2; Polte et al. 2005) and the Mondego estuary seagrass beds were considerably reduced in the early 90's in the south arm, loosing part of its production potential (Dolbeth et al. 2007). Presently, the seagrass beds are recovering (Cardoso et al. 2005), allowing more alternative habitats and potentially increasing invertebrate production in the following years (Dolbeth et al. 2007), which may translate into higher fish productions.

ACKNOWLEDGEMENTS

The authors are indebted to Daniel Crespo, Heliana Teixeira, Ivan Viegas, João Miguel Neto, Rui Margalho and Tiago Verdelhos who helped in field work.

REFERENCES

Arruda LM, Azevedo JN, Neto AI (1993) Abundance, age-structure and growth, and reproduction of Gobies (Pisces, Gobidae) in the Ria de Aveiro Lagoon (Portugal). Estuar Coast Shelf Sci 37: 509–523.

Attrill MJ, Power M (2004) Partitioning of temperature resources amongst an estuarine fish assemblage. Estuar Coast Shelf Sci 61: 725–738.

Bouchereau JL, Guelorget O (1998) Comparison of three Gobidae (Teleostei) life history strategies over their geographical range. Oceanologica Acta 24: 503 – 517.

Bouchereau JL, Quignard JP, Tosmasini JA, Joyeux JC, Capape C (1990) Cycle sexuel, condition, fécondité et ponte de *Pomatoschistus minutus* (Pallas, 1770) (Gobiidæ) du golfe du Lion, France. Cybium 14: 251–267.

Bouchereau JL, Quignard JP, Joyeux JC, Tosmasini JA (1991) Stratégies et tactiques de reproduction de *Pomatoschistus microps* (Krøyer, 1838) et de *Pomatoschistus minutus* (Pallas, 1770) (Pisces, Gobiidæ) dans le golfe du Lion. Nids, déterminisme de la sédentarité et de la migration. Cybium 15: 315–346.

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. *http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html* Alfred Wegener Institute for Polar and Marine Research, Germany.

Cardoso PG, Brandão A, Pardal MA, Raffaelli D, Marques JC (2005) Resilience of *Hydrobia ulvae* populations to anthropogenic and natural disturbances. Mar Ecol Prog Ser 289: 191–199.

Costa MJ, Cabral HN, Drake P, Economou AN, Fernandez-Delgado C, Gordo L, Marchand J, Thiel R (2002) Recruitment and production of commercial species in estuaries. In: Elliot M, Hemingway K (Eds) Fishes in estuaries. Blackwell Science, Bodmin, United Kingdom, p 54–123.

Cowley PD, Whitfield AK (2002) Biomass and production estimates of a fish community in a small South African estuary. J Fish Biol 61: 74–89.

Dolbeth M, Cardoso PG, Ferreira SM, Verdelhos T, Raffaelli D, Pardal MA (2007) Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a ten-year period. Mar Pollut Bull 54: 576–585.

Doornbos G (1984) Piscivorous birds on the saline Lake Grevelingen, The Netherlands: abundance, prey selection and annual food consumption. Netherlands J Sea Resear 18: 457–479.

Doornbos G, Twisk F (1987) Density, growth and annual food consumption of gobiid fish in the saline Lake Grevelingen, The Netherlands. Neth J Sea Resear 21: 45–74.

Evans S (1984) Energy budgets and predation impact dominant epibenthic carnivores on a shallow soft bottom community at the swedish west coast. Estuar Coast Shelf Sci 18: 651–672.

Fonds M (1973) Sand gobies in the Dutch Wadden Sea (*Pomatoschistus*, Gobiidae, Pisces). Neth J Sea Resear 6: 417–478.

Fonds M, Veldhuis C (1973) The oxygen consumption of four *Pomatoschistus* species (Pisces, Gobiidae) in relation to water temperature. Neth J Sea Resear 7: 376–386.

Fonds M, van Buurt G (1974) The influence of temperate and salinity on development and survival of goby eggs (Pisces, Gobiidae). Hydrobiol Bull 8: 110–116.

Fouda MM, Miller PJ (1981) Age and growth of the common goby, *Pomatoschistus microps* on the south coast of England. Estuar Coast Shelf Sci 12: 121–129.

Jaquet N, Raffaelli D (1989) The ecological importance of the sand goby *Pomatoschistus minutus* (Pallas). J Exp Mar Biol Ecol 128: 147–156.

Healey MC (1972) On the population ecology of the common goby in the Ythan estuary. J Nat Hist 6: 133–145.

Hemingway KL, Elliott M (2002) Field methods. In: Elliot M, Hemingway K (Eds) Fishes in estuaries. Blackwell Science, Bodmin, United Kingdom, p 410–509.

Hesthagen IH (1977) Migrations, breeding and growth in *Pomatoschistus minutus* (Pallas) (Pisces, Gobiidle) in Oslofjorden, Norway. Sarsia 63: 17–26.

Hesthagen IH (1979) Temperature and avoidance in the sand goby, *Pomatoschistus minutus* (Pallas), collected at different seasons. Environ Biol Fish 4: 369–377.

Leitão R, Martinho F, Neto JM, Cabral H, Marques JC, Pardal MA (2006) Feeding ecology, population structure and distribution of *Pomatoschistus microps* (Krøyer, 1838) and *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. Estuar Coast Shelf Sci 66: 231–239.

Lillebø AI, Neto JM, Martins I, Verdelhos T, Leston S, Cardoso PG, Ferreira SM Marques JC, Pardal MA (2005) Management of a shallow temperate estuary to control eutrophication: The effect of hydrodynamics on the system's nutrient loading. Estuar Coast Shelf Sci 65: 697–707.

Maes J, Van Damme S, Meire P, Ollevier F (2004) Statistical modelling of seasonal and environmental influences on the population dynamics of an estuarine fish community. Mar Biol 145: 1033–1042.

Magnhagen C, Wiederholm AM (1982) Habitat and food preferences of *Pomatoschistus minutus* and *P. microps* (Gobiidae) when alone and when together: an experimental study. Oikos 39: 152–156.

Marques JC, Graça MAS, Pardal MA (2002) Introducing the Mondego River basin. In: Pardal MA, Marques JC, Graça MAS (Eds) Global importance of local experience. Universidade de Coimbra, Coimbra, Portugal, p 7–12.

Marques JC, Nielsen SN, Pardal MA, Jørgensen SE (2003) Impact of eutrophication and river management within a framework of ecosystem theories. Ecol Model 166: 147–168.

Martinho F, Leitão R, Viegas I, Dolbeth M, Neto J, Cabral HN, Pardal MA (2007) The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. Estuar Coast Shelf Sci doi:10.1016/j.ecss.2007.05.040.

Mazzoldi C, Rasotto MB (2001) Extended breeding season in the marbled goby, *Pomatoschistus marmoratus* (Teleostei: Gobiidae), in the Venetian Lagoon. Environ Biol Fish 61: 175–183.

Nellbring S (1993) Spawning of two *Pomatoschistus* species (Gobiidae) in relation to nets availability and depth: a field experiment. Neth J Sea Resear 31: 173–179.

Nogueira AJA (1992) ANAMOD – Extracção dos componentes modais de distribuições de frequência de variáveis biométricas. Trabalho de síntese apresentado para prestação de provas de aptidão pedagógica e capacidade científica. University of Coimbra, Portugal, p 67.

Paerl HW (2006) Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: Interactive effects of human and climatic perturbations Ecol Eng 26: 40–54.

Pampoulie C (2001) Demographic structure and life history traits of the common goby *Pomatoschistus microps* (Teleostei, Gobidae) in a Mediterranean coastal lagoon (Rhône River delta, France). Acta Oecol 22: 253–257.

Pampoulie C, Rosecchi E, Bouchereau JL, Crivelli AJ (1999) Life history traits of *Pomatoschistus minutus* (Teleostei, Pisces) in the Rhône Delta, France. J Fish Biol 55: 892–896.

Pampoulie C, Bouchereau JL, Rosecchi E, Poizat G, Crivelli AJ (2000) Annual variations in the reproductive traits of *Pomatoschistus microps* in a Mediterranean lagoon undergoing environmental changes: evidence of phenotypic plasticity. J Fish Biol 57: 1441–1452.

Phil L, Rosenberg R (1982) Production, abundance and biomass of motile epibenthic marine fauna in shallow waters western Sweden. J Exp Mar Biol Ecol 57, 273–301.

Polte P, Schanz A, Asmus H (2005) The contribution of seagrass beds (*Zostera noltii*) to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea. Mar Biol 147: 813–822.

Powers SP, Peterson CH, Christian RR, Sullivan E, Powers MJ, Bishop MJ, Buzzelli CP (2005) Effects of eutrophication on bottom habitat and prey resources of demersal fishes. Mar Ecol Prog Ser 302: 233–243.

Roessig JM, Christa MW, Joseph JCJr, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. Rev Fish Biol Fish 14: 251–275.

Salgado JP, Cabral HN, Costa MJ (2004) Feeding ecology of the gobies *Pomatoschistus minutus* (Pallas, 1770) and *Pomatoschistus microps* (Krøyer, 1838) in the upper Tagus estuary, Portugal. Scient Mar 68: 425–434.

Sims DW, Wearmouth VJ, Genner MJ, Southward AJ, Hawkins SJ (2004). Low temperature-driven early spawning migration of a temperate marine fish. J Anim Ecol 73: 333–341.

Ter Braak CJF (1988) CANOCO – a fortran program for canonical community ordination by partial detrended canonical correspondence analysis, principal components and redundancy analysis. Agricultural and Mathematical Group, Wageningen, The Netherlands.

von Oertzen JA (1984) Influence of steady-state and fluctuating salinities on the oxygen consumption and activity of some brackish water shrimps and fishes. J Exp Mar Biol Ecol 80: 29–46.

Winberg GG (1971) Methods for the estimation of production of aquatic animals. Academic Press Inc, London, United Kingdom, p 175.

Modelling the life cycle, population and biomass dynamics of two Gobiidae fish species

Abstract A model to simulate the population and biomass dynamics was developed for *Pomatoschistus minutus* and *Pomatoschistus microps*, the sand and the common gobies. These are among the most abundant species in the fish community of European estuarine systems. In the Mondego estuary (Portugal) they were collected along a three-year study period and both presented discontinuous recruitment and short life spans. The model design comprised two sub-models: one with the individual growth and another with a class structured (juveniles and adults) population dynamics, which were then coupled to form a cohort density and biomass model. For the population and biomass dynamics several cohort models were joined, according to the life history of each species. The parameters needed for the model were based: 1) on the life history characteristics (recruitment periods, maturity and maximum weight); and 2) on the population properties (birth, growth, mortality rates) of each species. These parameters were computed or calibrated from the three-year field study period. The results on density and biomass dynamics predicted by the model were compared with the values observed in the field and were consistent. This simple approach to simulate the fish dynamics was useful as it revealed some of system's properties. It also allowed to formulate new hypotheses for its understanding, such as the effect of potential limitations to the population development. No forcing functions were yet added to the model but were discussed for future model improvements.

Keywords Modelling, Stella, Gobiidae, Population dynamics, Growth

INTRODUCTION

Several studies in ecology have addressed the life cycle and population dynamics of invertebrate and fish species inhabiting different ecosystems (Pampoulie 2001, Baeta et al. 2005, Cardoso et al. 2005, Leitão et al. 2006, Dolbeth et al. 2007a). Besides being a fundamental aspect of ecology itself, this knowledge may 1) provide important economic value when commercial species are studied or 2) be crucial for the management and conservation of ecosystems, in particular if key species are considered. In fact, a helpful tool for an effective management and conservation of the biological resources would be the ability to predict its fluctuations in abundance and biomass production caused by anthropogenic or natural environmental stressors (Jørgensen & Bendoricchio 2001, Franco et al. 2006, Patrício & Marques 2006, Silva-Santos et al. 2006). In this perspective, ecological modelling may be considered as a synthesis of the ecological knowledge of the ecosystem, or component, with regard to a given problem (Jørgensen & Bendoricchio 2001, Patrício & Marques 2006). Models have limitations error ranges and can be complex. Yet, they are powerful tools for surveying complex systems and forecasting their potential impacts (Jørgensen & Bendoricchio 2001).

Fish are important components of aquatic ecosystems and their commercial value often turns them into preferential study targets. Some forecast models on fish dynamics have been developed, mainly for fisheries management purposes (Needle 2002, Rose 2005, Bardos et al. 2006, Klanjšček & Legović 2007). Models commonly used in fisheries are surplus-production, age-structured and size-structured models, with the age-structured ones among the most widely used (Rose 2005, Klanjšček & Legović 2007). More recently, fish individual based models are becoming more usual. These models focus on the physiological requirements of the fish growth (Bryant et al. 1995, Hallam et al. 2000, Neill et al. 2004, Rose 2005) and may consider other aspects, such as space (Anneville et al. 1998), intra and interspecific interactions (van Nes et al. 2002, Persson & Roos 2006). However, the prediction of population dynamics in natural systems is difficult due to the multitude of physiological, biotic and environmental processes that influence each individual in the population (Hallam et al. 2000, Rose and Cowan 2000, van Nes et al. 2002, Rose 2005).

For the present study, a different approach is proposed: to develop a generic model for fish that synthesizes its life cycle and population dynamics based on simple population properties. The model conceptualization focused on the population structure, using density and biomass, according to the individual growth rate and population mortality rate (estimated using field data). Physiological requirements, space and potential biotic interactions addressed in other fish models were not taken into account. This is a simple approach to model fish population dynamics but it enables to set hypotheses regarding potential restrictions to the population development, through comparisons of the real data and modelled one. The model can also be used for other species, with changes in the parameter values required for input. In the future, different variables limititing the fish dynamics could also be included and studied. Two gobiid fish species, *Pomatoschistus minutus* and *P. microps*, were chosen as target species, since they are important estuarine inhabitants and occur in high abundance in several Atlantic and Mediterranean coastal regions (Bouchereau & Guelorget 1998, Pampoulie et al. 1999, Pampoulie 2001, Leitão et al. 2006). These Gobiidae fish are also important intermediates on the estuarine food web (Doornbos & Twisk 1987; Leitão et al. 2006). Hence, the ability to predict fluctuations in their population would be quite advantageous to understand potential consequences on the food webs and the dynamics of the ecosystem.

DATA FOR MODEL CALIBRATION

Study area and sampling procedures

Sampling occurred in the Mondego estuary, located in a warm temperate region, on the Atlantic coast of central Portugal (40°08'N, 8°50'W). It is a small estuary of 3.4 km^2, comprising two arms, north and south, separated by an island (Fig. 1). From June 2003 until May 2006 fish were collected monthly, using a 2 m beam trawl, with one tickler chain and 5 mm stretched mesh size in the cod end. Sampling was carried out during the night, at the ebbing tide of spring tides, in five sampling stations (Fig. 1): M - at 1.5 km from the sea (estuary's mouth), 8.7 ± 1.2 m deep, an area subjected to constant dredging; S1 - in the south arm, located upstream a *Zostera noltii* bed, 2.3 ± 0.4 m deep; S2 – in the south arm, near the Pranto river, a small tributary of the Mondego river, whose freshwater flow is controlled by sluices according to the water needs of rice field crops of the Mondego valley, 2.4 ± 1.0 m deep; N1 – in the north arm, with regular freshwater flow, 5.5 ± 0.5 m deep; N2 - in the north arm at the most upstream area, with lower saline influence and permanent freshwater flow (from Mondego river), 4.5 ± 0.3 m deep. Each survey consisted of three hauls, at each sampling station, in a total of 10 to 15 min per station. Fish captured were frozen and afterwards identified in laboratory, from which *P. minutus* and *P. microps* were measured (total length) and weigh (wet weight - WW). The data

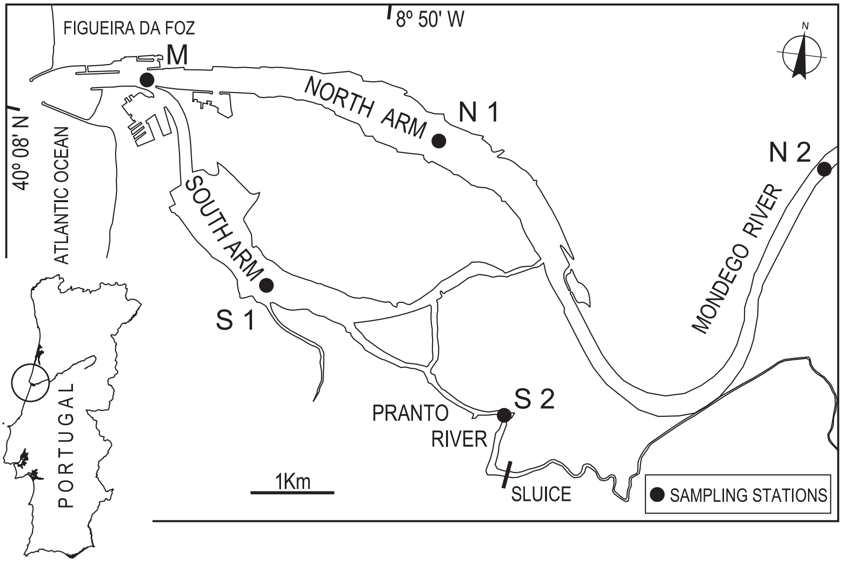


Fig. 1 The location of Mondego estuary, with indication of the sampling stations.

from the 5 sampling stations were pooled to provide the mean abundance and mean biomass for the estuary and from which the population structure was studied, to provide knowledge for the development of the model's structure and parameters.

Both *P. minutus* and *P. microps* were among the most abundant species in the fish community of the Mondego estuary (Leitão et al. 2006, Martinho et al. 2007). The life cycle, population dynamics, biomass and secondary production of the fish species used in the present study for the model development and calibration was first assessed in Dolbeth et al. (2007a). During the three-year study period, 2003 and 2006 were considered as normal hydrological years, while 2004 was considered dry and 2005 as extremely dry, with consequent lower water runoff and higher salinity incursion in the estuary. In the early summer of both 2003 and 2005, high abnormal air temperatures were registered, concomitant with high water temperatures, mainly in the inner parts of the estuary.

Fish population structure and cohorts origin

Pomatoschistus minutus had recruitments in April and November, with an estimated life span of 18 months, while *P. microps* had recruitments in January, April and June, with an estimated life span varying between 16 to 18 months (Leitão et al. 2006, Dolbeth et al. 2007a). According to the length and age at first maturity, the origin of the cohorts was set up (Fig. 2). For *P. minutus* ovigerous females were found in higher percentage in February-March and July-August, with the minimal length of the last maturation stage of 44 mm (mean weight of 0.5349 g WW, Table 1), corresponding to an age of 9.3 and 9.4 months (as each recruitment had a slightly different growth rate). These values are in agreement with the maturity ages found in Mediterranean regions (10 months and 40 mm length, Bouchereau et al. 1991, Bouchereau & Guelorget 1998, Pampoulie et al. 1999), whose temperature ranges were similar to the ones found in the Mondego estuary. Thus, *P. minutus* of 9-10 months age were assumed to be sexually mature and capable of spawning. This means that for *P. minutus* April and November recruits are only able to generate new recruitments one year later, since before they are not sexually mature (< 10 months old, Fig. 2A).

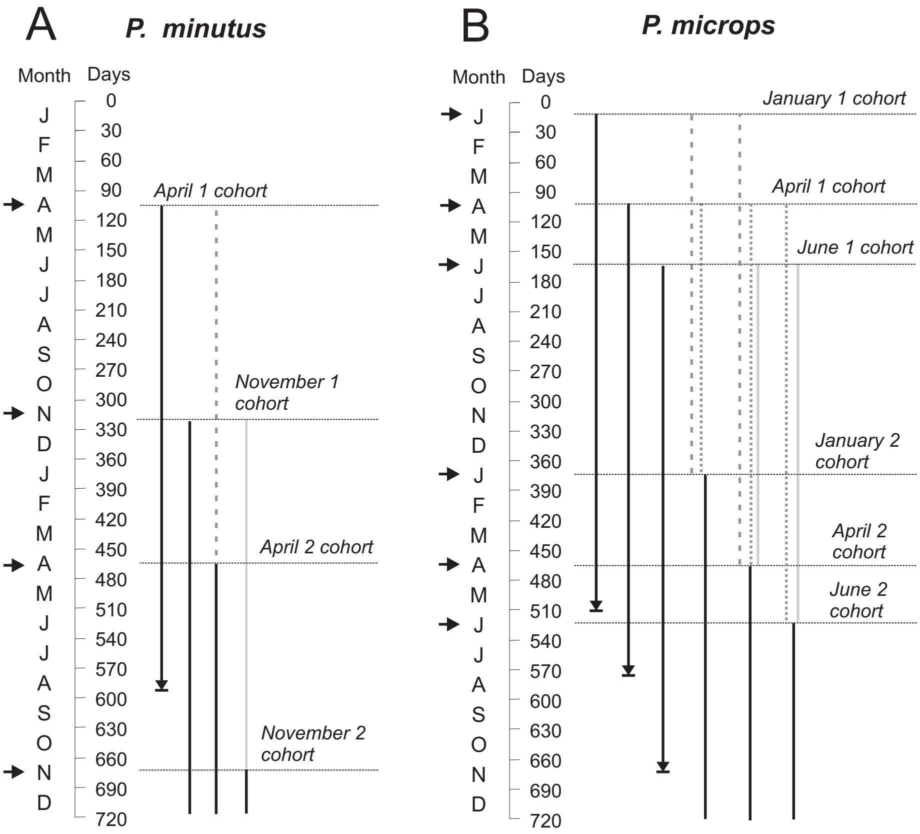


Fig 2. Origin (month and day) of the cohorts belonging to the different recruitment time in a 720 days period for A) *Pomatoschistus minutus* and B) *P. microps.*

For *P. microps* ovigerous females were found in higher percentage in March-April, August and December, with the minimal length of the last maturation stage of 28 mm (mean weight of 0.1389 g WW, Table 1), corresponding to an age of 6.7 months (January and April recruitments) and 7.2 months (June recruitment). In Mediterranean regions, *P. microps* are sexually mature at 4-5 months old, whereas in the Atlantic maturation begins at 8-12 months old (Bouchereau et al. 1991, Bouchereau & Guelorget 1998). It has also been reported that each cohort is able to spawn several times. In fact, for the Mediterranean region, spawning seems to occur in two time periods: 1) one soon after birth (4-5 months), during few weeks, and 2) another in the following year during the whole reproduction period (Bouchereau et al. 1991, Bouchereau & Guelorget 1998,

Table 1 State variables, parameters and equations used in the model, with respective values when applicable, and brief description of each component. Jan: January recruitment; Apr: April recruitment; Jun: June recruitment; Nov: November recruitment; WW: fish wet weight; * after calibration.

Type	Symbol	Value/Equation	Units	Description
St variable	NJuveniles	Modelled	Ind 1000m^{-2}	Juveniles densities
St variable	NAdults	Modelled	Ind 1000m^{-2}	Adults densities
St variable	W	Modelled	g WW	Individual weight
Parameter	Eggs	Several constant values*	-	Calibrated according to the fish density
Parameter	INIT W	*P. minutus*: Nov = 0.0425; Apr = 0.0317; *P. microps*: Jan = 0.0111; Apr = 0.0194; Jun = 0.0115	g WW	Initial weight W$_0$
Parameter	MatW	*P. minutus*: 0.5349 *P. microps*: 0.1389	g WW	Weight at maturity
Parameter	MaxW	*P. minutus*: 4.938 *P. microps*: 1.812	g WW	Maximum weight
Parameter	r	*P. minutus*: Nov = 0.009; Apr = 0.0105; *P. microps*: Jan = 0.0089; Apr = 0.0088; Jun = 0.0098	day^{-1}	Growth rate
Parameter	zAdu	*P. minutus*: 0.001* *P. microps*: 0.003*	day^{-1}	Adults mortality rate
Parameter	zJuv	*P. minutus*: 0.002* *P. microps:* 0.0041*	day^{-1}	Juveniles mortality rate
Parameter	Recruitment time	*P.minutus*: Apr (day 91, 451), Nov (day 331, 691); *P.microps*: Jan (day 1, 361) , Apr (day 91, 451), Jun (day 151, 511)	day	days when recruitment occurs
Parameter	Timenew	720	days	Time function
Parameter	Juv to Adu	If W > MatW then 1 else 0	-	Allows G after MatW
Parameter	Mort	if W > MaxW then W/dt else 0	-	Allows Growth until MaxW
Equation	Recruitment	NAdults*Eggs*Recruitment time	Ind 1000m^{-2}	Recruitment: entry of new individuals to the population
Equation	NMortality Juveniles	zJuv *NJuveniles	Ind 1000m^{-2}	Population natural mortality of juveniles
Equation	G	Juv to Adu *NJuveniles	Ind 1000m^{-2}	Transfer of juveniles to adults
Equation	NMortality Adults	IF W > MaxW THEN NAdults/dt ELSE zAdu*NAdults	Ind 1000m^{-2}	Population natural mortality of adults
Equation	WGrowth	r*W	g day^{-1}	Individual growth
Equation	START growth W	Recruitment time*INIT W	g WW	Starting growth value
Equation	WMortality	W * Mort	-	Death the individual

Pampoulie 2001). For the Mondego estuary, the same strategy was assumed for *P. microps* population, whose individuals may be able to spawn more than once during their life span. *P. microps* with 7 months (0.1389 g WW) were assumed to be sexually mature and capable of spawn. Accordingly, all recruits were considered to generate new recruitments one year after they were born, which will be the major egg's contribution for the new recruitment. Another recruitment will occur before or after the major recruitment, in agreement with the defined maturity weight and life span (Fig. 2B), but with a low egg contribution. April recruits will contribute for three recruitments during their life span (17 months), while January and June recruits will contribute for two recruitments during their life span (17 months, Fig. 2B).

Growth rates

The growth of both species appeared to be linear, with some seasonal differences, such as higher growth rate in summer and lower in winter periods (Dolbeth et al. 2007a), usual in temperate climates (Jørgensen & Bendoricchio 2001). To simplify the model it was considered a mean growth rate, diluting the slight seasonal variations. The fish lengths (L, cm) were transformed into individual wet weight (WW, g) - *P. minutus*: WW = 0.0036 × $L^{3.3755}$ and *P. microps*: WW = 0.004 × $L^{3.4456}$. Unlimited resources and exponential growth were assumed, because this was the simplest growth function (equation 1, after Gamito 1998):

$$w_t = w_0 e^{rt} \qquad (1)$$

where w_t is the individual weight at time t, w_0 is the in initial weight, r the growth rate, t is the time interval between w_t and w_0. These growth rates (*r*) were estimated using the mean values of the cohorts belonging to each recruitment (e.g. for *P. minutus* November recruitment, r computed using the mean values from cohorts 3, 6 and 9).

MODEL DESCRIPTION AND EQUATIONS

The model development in Stella® 8.1 software comprised three steps: 1) the model of each cohort individual growth – *individual growth sub-model* (Fig. 3); 2) the model of each cohort population dynamics, coupled with the individual growth as regulator – *cohort population growth sub-model* (Fig. 3); and 3) the model with the recruitment cohorts coupled for each species, according to the recruitment patterns described previously – *fish population growth model* (Fig. 4, Appendix 1). This procedure was done for each species separately. The symbol meaning and values used for the model are expressed in Tables 1.

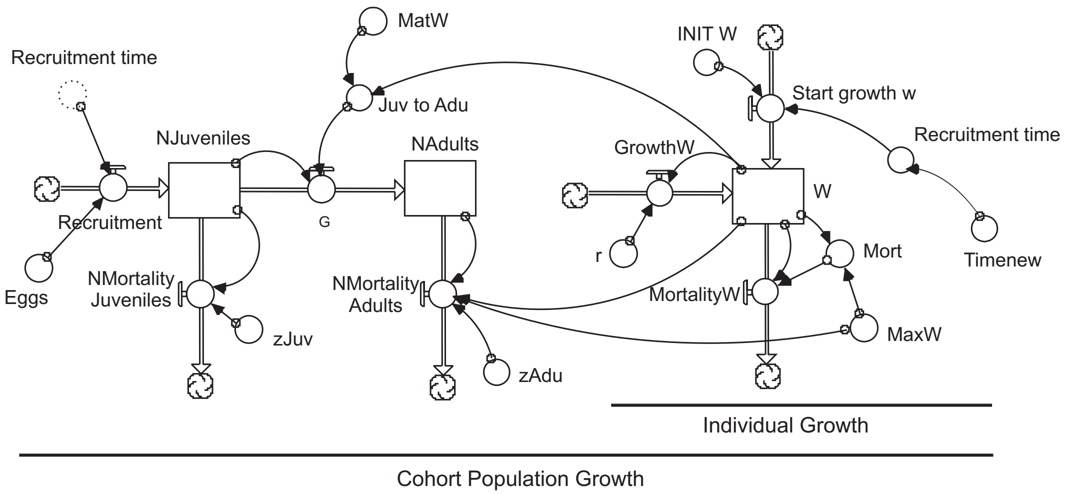


Fig. 3 Stella diagram of the population growth model for one cohort, indicating the coupling between the individual growth sub-model coupled to the population dynamics sub-model. Model symbols and explanation in Table 1.

The model equations are described for one cohort – cohort x:

1. Individual growth

In the individual growth sub-model, individuals start to grow with an initial weight (INIT W), according to the growth rate (r), until they achieve a maximum weight (MaxW) (Fig. 3). The MaxW works as growth limit, after which growth stops. For the cohort x, the growth of each individual will be a function of two processes, the individual growth and mortality that only occurs when the maximum weight is achieved (equation 2):

$$\frac{dW_x}{dt} = \mathrm{GrowthW}_x - \mathrm{MortalityW}_x \qquad (2)$$

where the GrowthW$_x$ is described as a simple exponential function of r$_x$ and the individual biomass/weight (W$_x$) of the cohort x (equation 2.1):

$$\mathrm{GrowthW}_x = r_x * W_x \qquad (2.1)$$

The MortalityW$_x$ the cohort x is defined here by the maximum weight (MaxW$_x$) found in the population, after which no more growth occurs (equation 2.2):

$$\mathrm{MortalityW}_x = \begin{cases} 0 \\ W_x \quad \text{if } W_x > \mathrm{MaxW}_x \end{cases} \qquad (2.2)$$

2. Population dynamics

In the population dynamics sub-model the increase in the number of individuals was regulated according to the individual weight growth (Fig. 3). The fish population was subdivided into juveniles and adults, each one constituting a state variable (Fig. 3). Juvenile population of the cohort x (*NJuveniles*$_x$) is described by the processes recruitment and the juvenile mortality (equation 3):

$$\frac{dNJuveniles_x}{dt} = Recruitment_x - NMortalityJuveniles_x - Maturation_x \qquad (3)$$

Recruitment corresponds to the contribution of the adult density to the entry of new individuals for the overall fish population, i.e., to new cohorts. So, it is described by the number of eggs (Eggs$_x$) multiplied by adult density (NAdults$_x$), originating a new cohort. As reproduction is discrete (Dolbeth et al. 2007a), and it occurred only in certain time periods within the year, recruitment will only occur in the defined recruitment time (equation 3.1):

$$Recruitment_x = \begin{cases} 0 \\ NAdults_x * Eggs_x \quad \text{if start\_day} < \text{Recruitment time} < \text{end\_day} \end{cases} \qquad (3.1)$$

For the present model, recruitment time starts at start_day and finishes at end_day. These recruitment time periods changed for each species, in agreement to the ones defined by the field study (Dolbeth et al. 2007a) (see later).

The juvenile mortality is described as a simple exponential function of the juvenile density and the juvenile mortality rate (z$_x$) (equation 3.2):

$$NMortalityJuveniles_x = zJuv_x * NJuveniles_x \qquad (3.2)$$

All juveniles turn into adults after achieving the maturity weight (MatW$_x$) that controls the maturation process (equation 3.3) of the cohort x:

$$Maturation_x = \begin{cases} 0 \\ NJuveniles_x \quad \text{if } W_x > MatW_x \end{cases} \qquad (3.3)$$

The maturity weight was defined according to the field data, considering the minimal length and weight at which ovigerous females were found with the maximal maturation stage (Table 1). These values were also in accordance to the ones found in literature for both species (see above, section Population structure and cohorts' origin).

The adult population of cohort x is defined by processes maturation and mortality (equation 4):

$$\frac{dNAdults_x}{dt} = Maturation_x - NMortalityAdults_x \qquad (4)$$

Adult mortality is described as a simple exponential function of NAdults$_x$ and adult mortality rate (zAdu$_x$). This process is regulated according to the MaxW$_x$, after which the whole population dies and defines the life span of the cohorts from each recruitment (equation 4.1):

$$NMortalityAdults_x = \begin{cases} zAdu_x * NAdults_x \\ NAdults_x \quad \text{if } W_x = MaxW_x \end{cases} \qquad (4.1)$$

Maturation in described in equation 3.3.

A rough estimate of the mortality rates for juveniles and adults was computed with field data, according to equation 5 (after Jørgensen & Bendoricchio 2001):

$$N_t = N_0 e^{-zt} \qquad (5)$$

where N_t is final density, N_0 is the initial density, z the mortality rate, t is the time interval between N_t and N_0. For this computation, the mean values of all cohorts were used. The estimated mortality rates had a high degree of uncertainty but these values were used for the first model simulations. Then they were tested with the sensitivity analysis (later in the text).

For each species, recruitments in a two-year period (720 days) were joined – several cohort population sub-models - by coupling the adult density from a previous cohort to the recruitment of a new cohort (NAdults coupled to Recruitment, e.g. for *P. minutus* population in Figure 4). During two-year period, two year × two recruitments were considered for *P. minutus* (recruitments in April and November: Apr 1, Nov 1, Apr 2, Nov 2) (Fig. 4); and two year × three recruitments were considered for *P. microps* (recruitments in January, April and June: Jan 1, Apr 1, Jun 1, Jan 2, Apr 2, Jun 2) (Appendix I). The recruitment times presented in equation 3.1 varied for each species. For *P. minutus* recruitment time varied: Apr 1, between day 91 and day 95; Nov 1, between day 335 and day 339; Apr 2, between day 451 and day 455; Nov 2, between day 691 and day 695. For P. microps: Jan 1, between day 1 and day 5; Apr 1, between day 91 and day 95; Jun 1, between day 151 and day 155; Jan 2, between day 361 and day 365; Apr 2, between day 451 and day 455; Jun 2, between day 511 and day 515.

In summary, the processes that regulate the number of individuals over time are: a) individual growth, determining the number of individuals transferred from juveniles to adults; b) death, describing the number of individuals subtracted to both juveniles and adults by mortality; and c) recruitment, which describes the input of new juveniles (Fig. 5). In addition to the population dynamics, the model also includes the biomass dynamics by multiplying the individual weight by the density of each group.

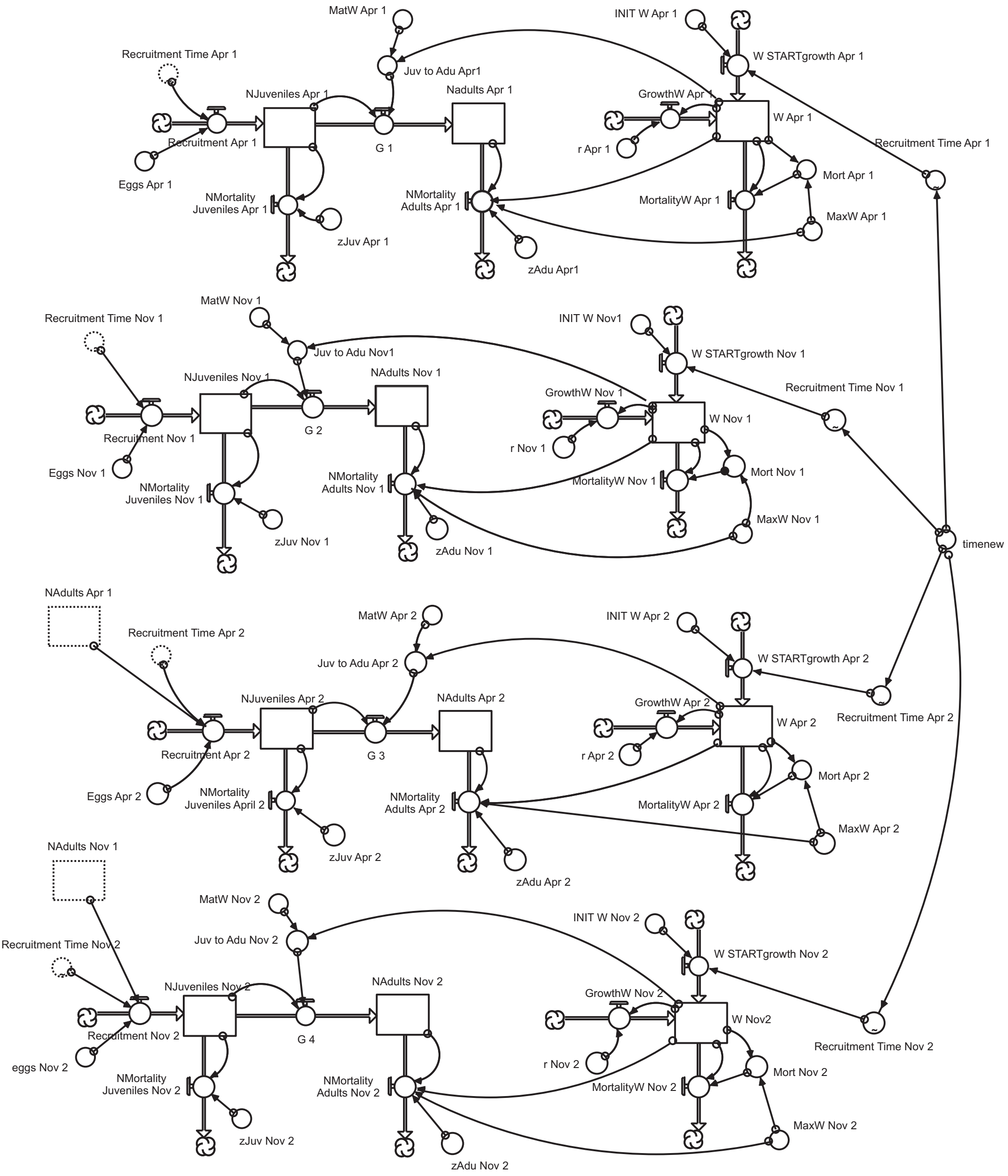


Fig. 4 Stella diagram of the population growth model for *P. minutus* population, indicating the coupling between cohorts (2 year * 2 recruitments). Model symbols and explanation in Table 1.

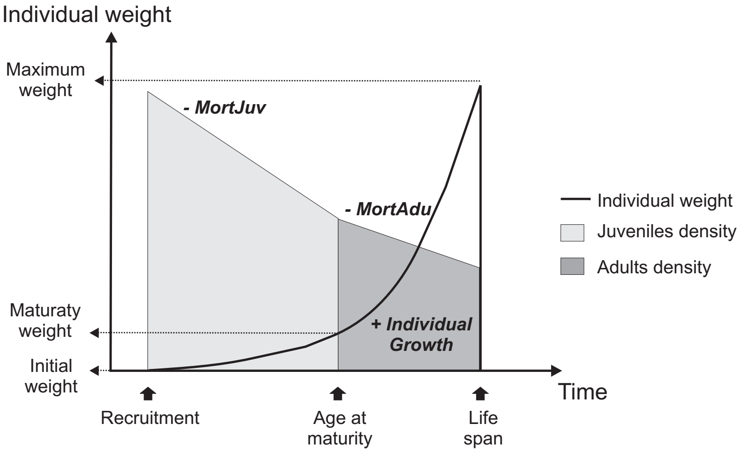


Fig. 5 General expected model output regarding individual growth, juveniles and adults density dynamics for 1 cohort.

MODEL SIMULATIONS, VERIFICATION AND SENSITIVITY ANALYSES

All model simulations were compared with the field data for the same sampling dates and in agreement with the observed number of cohorts for *P. minutus* and *P. microps* populations. In the three-year field study, 10 cohorts were observed for *P. minutus* population and 13 cohorts were observed for *P. microps* (Dolbeth et al. 2007a). To compare the field data with the model simulations the model was run during 4.5 years, in order to have 10 and 13 model cohorts for each species respectively. Model values were registered monthly starting at day 537 (corresponding to 26 June 2003, the first field sampling date) until day 1 587 (correspondent to 29 May 2006, the last field sampling date). The number of eggs that the adults provide for the next cohort was achieved by the trial and error method, according to the mean density of the fish during a three-year period field study. It was considered that similar recruitments would start growing with the same number of individuals, independently of the year. The different field data recruitments were compared in order to find the different density proportions occurred within recruitments, and the density proportions comparing the juvenile and the adult populations. November and April mean density recruitments were proportionally similar for *P. minutus*, whereas for *P. microps* the April recruitment had higher density than the January (- 40%) and the June recruitments (- 50%). Juvenile mean densities were higher than the adult ones (≈ - 60%) for both species.

A sensitivity analysis was performed to the model, in order to provide a measure of the parameter's sensitivities and an additional knowledge of the model properties. The sensitivity of each parameter was measured according to equation 5 (after Jørgensen & Bendoricchio 2001):

$$S = \left[\partial x / x\right] / \left[\partial P / P\right] \qquad (5)$$

where S is the sensitivity, x is the state variable and P the parameter. A variation of ± 10 % was considered as suitable to detect the most sensitive parameters.

After a first quantitative sensitivity analysis, the parameters whose values had a higher impact on the growth model were detected. The most sensitive parameters were the mortality rates of juveniles and adults, eggs for both species, and the growth rates for *P. microps*. According to the results obtained by Dolbeth et al. (2007a), it was considered high degree of confidence in the growth rates estimates. So, a new calibration of the model was done but this time by changing the eggs and the mortality rates, taking into consideration the three-year period field mean density and biomass. After this new calibration, a new sensitivity analyses was performed for each species (Tables 2 and 3).

The deviation between model values and field data were checked by a linear regression model II, Major Axis Regression method (Sokal & Rohlf 1981), of the model simulated versus field values for each year (n= 12, 8, 12). Model II regression was applied as both variables are subjected to error (Sokal & Rohlf 1981). The H_0 was of no deviation between Field and Model values occurs when simultaneously the intercept = 0 and slope = 1. This H_0 was tested with a Dent and Blackie test, i.e., an *F*-test with 2 and (n-2) degrees of freedom (Tedeschi 2006). This *F*-test calculation is considered to be only valid for deterministic models, as the slope should not be expected to be unity when using stochastic (or probabilistic) models (Tedeschi 2006).

RESULTS

Pomatoschistus minutus simulations

In a two-year period, the first April cohort is completed, meaning that individuals born in April (after day 90, Fig. 2A, Fig. 6) lived their whole life span. Two new born cohorts started in November and in April one year after (starting at day 331 and 451 respectively, Fig 2A, Fig. 6). The juvenile density started high and afterwards was subjected to a high mortality rate. After achieving the maturity weight the remaining juveniles became adults, until achieving the maximum weight (Fig. 6). The model simulations, i.e., the individual weight, juvenile and adult density simulations, were consistent through time, starting in each recruitment time. At day 1 590, six cohorts (at least one per each of the recruitments) were completed and another three cohorts were

Table 2 Sensitivity analyses for juvenile (NJuveniles) and adult (NAdults) densities and individual weight (W) state variables of *Pomatoschistus minutus* to ± 10% in the model parameters. Apr 1, Nov 1, Apr 2, Nov 2: 1st and 2nd April and November recruitments respectively.

			STATE VARIABLES											
			NJuveniles Apr 1	NAdults Apr 1	W Apr 1	NJuveniles Nov 1	NAdults Nov 1	W Nov 1	NJuveniles Apr 2	NAdults Apr 2	W Apr 2	NJuveniles Nov 2	NAdults Nov 2	W Nov 2
PARAMETERS	**Eggs**	Apr 1	1.00	1.00	0	1.00	1.00	0	0	0	0	0	0	0
		Apr 2	0	0	-0.54	-0.25	0	0	0	0	0	0	0	0
		Nov 1	0	0	0	0	0	0	1.00	1.00	0	1.00	1.00	0
		Nov 2	0	0	0	0	0	0	0	0	0	1.00	1.00	0
	Initial weigth	Apr 1	-0.24	0.19	0.00	0.10	0.10	0	0	0	0	0	0	0
		Apr 2	0	0	0	-0.27	0.42	0.41	0	0	0	0	0	0
		Nov 1	0	0	0	0	0	0	-0.28	0.22	-0.01	0.11	0.11	0
		Nov 2	0	0	0	0	0	0	0	0	0	-0.17	0.22	0.02
	Maturity weigth	Apr 1	0.24	-0.60	0	-0.10	-0.10	0	0	0	0	0	0	0
		Apr 2	0	0	0	0.27	-0.64	0	0	0	0	0	0	0
		Nov 1	0	0	0	0	0	0	0.29	-0.62	0	-0.11	-0.11	0
		Nov 2	0	0	0	0	0	0	0	0	0	0.17	-0.62	0
	Maximum weigth	Apr 1	0	0.41	1.00	0	0	0	0	0	0	0	0	0
		Apr 2	0	0	0	0	0.22	0.59	0	0	0	0	0	0
		Nov 1	0	0	0	0	0	0	0	0.4	1.01	0	0	0
		Nov 2	0	0	0	0	0	0	0	0	0	0	0.4	0.96
	Growth rate	Apr 1	-0.67	-0.36	-1.00	0.27	0.27	0	0	0	0	0	0	0
		Apr 2	0	0	0	-0.75	0.58	0.67	0	0	0	0	0	0
		Nov 1	0	0	0	0	0	0	-0.74	-0.11	-0.5	0.28	0.28	0
		Nov 2	0	0	0	0	0	0	0	0	0	-0.42	-0.32	-0.91
	Adults mortality rate	Apr 1	0	-0.10	0	-0.09	-0.09	0	0	0	0	0	0	0
		Apr 2	0	0	0	0	-0.09	0	0	0	0	0	0	0
		Nov 1	0	0	0	0	0	0	0	-0.12	0	-0.07	-0.07	0
		Nov 2	0	0	0	0	0	0	0	0	0	0	-0.12	0
	Juveniles mortality rate	Apr 1	-0.22	-0.54	0	-0.54	-0.54	0	0	0	0	0	0	0
		Apr 2	0	0	0	-0.25	-0.54	0	0	0	0	0	0	0
		Nov 1	0	0	0	0	0	0	-0.26	-0.57	0	-0.57	-0.57	0
		Nov 2	0	0	0	0	0	0	0	0	0	-0.23	-0.57	0

Table 3 Sensitivity analyses for juvenile (NJuveniles) and adult (NAdults) densities and individual weight (W) state variables of *Pomatoschistus microps* to ± 10% in the model parameters. Jan1, Apr 1, Jun 1, Jan 2, Apr 2, Jun 2: 1st and 2nd January, April and June recruitments respectively.

			STATE VARIABLES																	
			NJuveniles Jan 1	NAdults Jan 1	W Jan 1	NJuveniles Apr 1	NAdults Apr 1	W Apr 1	NJuveniles Jun 1	NAdults Jun 1	W Jun 1	NJuveniles Jan 2	NAdults Jan 2	W Jan 2	NJuveniles Apr 2	NAdults Apr 2	W Apr 2	NJuveniles Jun 2	NAdults Jun 2	W Jun 2
PARAMETERS	**Eggs**	Jan 1	1.00	1.00	0	0	0	0	0	0	0	0.69	0.69	0	0.08	0.08	0	0	0	0
		Jan 2 I	0	0	0	0	0	0	0	0	0	0.31	0.31	0	0	0	0	0	0	0
		Jan 2 II	0	0	0	0	0	0	0	0	0	0.69	0.69	0	0	0	0	0	0	0
		Apr 1	0	0	0	1.00	1.00	0	0	0	0	0.31	0.31	0	0.79	0.79	0	0.27	0.27	0
		Apr 2 I	0	0	0	0	0	0	0	0	0	0	0	0	0.12	0.12	0	0	0	0
		Apr 2 II	0	0	0	0	0	0	0	0	0	0	0	0	0.79	0.79	0	0	0	0
		Apr 2 III	0	0	0	0	0	0	0	0	0	0	0	0	0.08	0.08	0	0	0	0
		Jun 1	0	0	0	0	0	0	1.00	1.00	0	0	0	0	0.12	0.12	0	0.73	0.73	0
		Jun 2 I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-0.73	-0.73	0
		Jun 2 II	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.27	0.27	0
	Initial weigth	Jan 1	-0.16	0.47	0.00	0	0	0	0	0	0	0.09	0.09	0	0.01	0.01	0	0	0	0
		Jan 2	0	0	0	0	0	0	0	0	0	-0.21	0.63	0.34	0	0	0	0	0	0
		Apr 1	0	0	0	-0.26	0.46	-0.00806	0	0	0	0.04	0.04	0	0.10	0.10	0	0.03	0.03	0
		Apr 2	0	0	0	0	0	0	0	0	0	0	0	0	-0.31	0.64	0.30	0	0	0
		Jun 1	0	0	0	0	0	0	-0.23	0.42	-0.01	0	0	0	0.01	0.01	0	0.08	0.08	0
		Jun 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-0.23	0.69	0.17
	Maturity weigth	Jan 1	0.16	-0.72	0	0	0	0	0	0	0	-0.09	-0.09	0	-0.01	-0.01	0	0	0	0
		Jan 2	0	0	0	0	0	0	0	0	0	0	-0.77	0	0	0	0	0.21	0	0
		Apr 1	0	0	0	0.27	-0.71	0	0	0	0	-0.04	-0.04	0	-0.10	-0.10	0	-0.03	-0.03	0
		Apr 2	0	0	0	0	0	0	0	0	0	0	0	0	0.31	-0.79	0	0	0	0
		Jun 1	0	0	0	0	0	0	0.23	-0.68	0	0	0	0	-0.01	-0.01	0	-0.08	-0.08	0
		Jun 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.23	-0.87	0
	Maximum weigth	Jan 1	0	0.24	1.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Jan 2	0	0	0	0	0	0	0	0	0	0	0.13	0.66	0	0	0	0	0	0
		Apr 1	0	0	0	0	0.25	1.01	0	0	0	0	0	0	0	0	0	0	0	0
		Apr 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0.14	0.70	0	0	0
		Jun 1	0	0	0	0	0	0	0	0.26	1.01	0	0	0	0	0	0	0	0	0
		Jun 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.17	0.83
	Growth rate	Jan 1	-0.40	0.56	-1.00	0	0	0	0	0	0	0.22	0.22	0	0.03	0.03	0	0	0	0
		Jan 2	0	0	0	0	0	0	0	0	0	-0.52	1.27	0.44	0	0	0	0	0	0
		Apr 1	0	0	0	-0.52	0.28	-1.00	0	0	0	0.08	0.08	0	0.19	0.19	0	0.07	0.07	0
		Apr 2	0	0	0	0	0	0	0	0	0	0	0	0	-0.61	0.92	0.07	0	0	0
		Jun 1	0	0	0	0	0	0	-0.57	0.38	-1.01	0	0	0	0.03	0.03	0	0.20	0.20	0
		Jun 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-0.57	1.29	-0.38
	Adults mortality rate	Jan 1	0	-0.38	0	0	0	0	0	0	0	-0.15	-0.15	0	-0.04	-0.04	0	0	0	0
		Jan 2	0	0	0	0	0	0	0	0	0	0	-0.34	0	0	0	0	0	0	0
		Apr 1	0	0	0	0	-0.37	0	0	0	0	-0.05	-0.05	0	-0.33	-0.33	0	-0.16	-0.16	0
		Apr 2	0	0	0	0	0	0	0	0	0	0	0	0	0	-0.32	0	0	0	0
		Jun 1	0	0	0	0	0	0	0	-0.34	0	0	0	0	-0.02	-0.02	0	-0.23	-0.23	0
		Jun 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-0.28	0
	Juveniles mortality rate	Jan 1	-0.43	-1.18	0	0	0	0	0	0	0	-0.82	-0.82	0	-0.10	-0.10	0	0	0	0
		Jan 2	0	0	0	0	0	0	0	0	0	-0.48	0	0	0	0	0	0	-1.18	0
		Apr 1	0	0	0	-0.34	-0.91	0	0	0	0	-0.28	-0.28	0	-0.72	-0.72	0	-0.25	-0.25	0
		Apr 2	0	0	0	0	0	0	0	0	0	0	0	0	-0.39	-0.91	0	0	0	0
		Jun 1	0	0	0	0	0	0	-0.43	-1.04	0	0	0	0	-0.13	-0.13	0	-0.76	-0.76	0
		Jun 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-0.43	-1.04	0

were developing (Fig. 6). If both recruitments attained the maximal weight, correspondent to the largest fish found in the field, with 85 mm - 4.938 g WW, the model life span would vary between 15.8 months for April recruits and 17.4 months for the November recruits.

The model simulated some of the population density variation patterns found in the field data (Fig. 7A). The highest increases and decreases in the density were detected by the model estimates, yet with a lower mean value, meaning that the natural oscillations of the field density values are buffered in the model estimates (Fig. 7A). This is also clear for the annual estimates, where differences were high, especially for 2003/04 and 2004/05 (Table 4). The Dent and Blackie regression tests proved significant differences between field and model data (Table 4). Similar model performance was obtained for the biomass simulations (Fig. 7B). However, model biomass variations (especially the biomass increases) were not completely simultaneous with the field data ones (Fig. 7B) and the Dent and Blackie regressions showed significant differences between field and models values (Table 4). Considering the mean annual biomass values, predicted and field values were more similar and no significant differences were found (Table 4). The inter-annual variability of model results was more pronounced with the density than with the biomass values (Table 4).

The most sensitive parameters were the number of eggs for the juveniles and adults densities of all recruitments (Table 2). The maximum weight and growth showed also higher sensitivities for the individual weight (Table 2).

Recruitment graphs showed that the first field cohorts of *P. minutus* had higher densities than the last ones, when compared to the model simulated density, computed with the three-year study period mean (Fig 8). This was very clear with cohorts 2 and 3 (C2 and C3), whose densities were considerably higher (Fig 8). For the remaining cohorts, the field densities decreased progressively. The field C4 mean values were to the model means; C5 had a higher density in the beginning, but the cohort was not completed throughout its possible life span; and C6, C7, C8 and C9 field densities were clearly lower than the model (Fig. 8). During the three-year study period, *P. minutus* had 10 cohorts (Dolbeth et al. 2007a) but for the purpose of this study only the major cohorts are presented (Fig. 8).

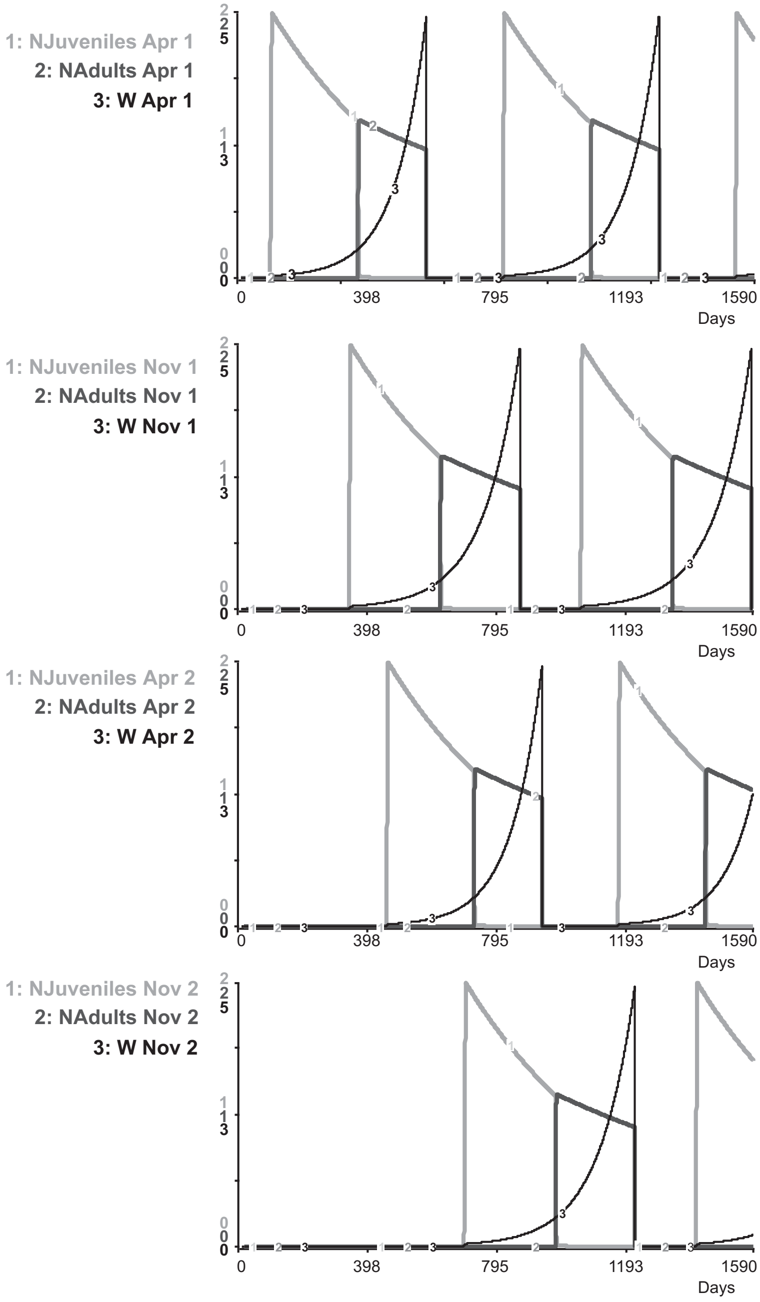


Fig. 6 Daily variation of the individual growth (g WW), juveniles and adults densities (ind m^{-2}) for cohorts of *Pomatoschistus minutus* starting each April and November in 1 590 days period (Apr 1, Nov 1, Apr 2, Nov 2: 1st and 2nd April and November recruitments respectively).

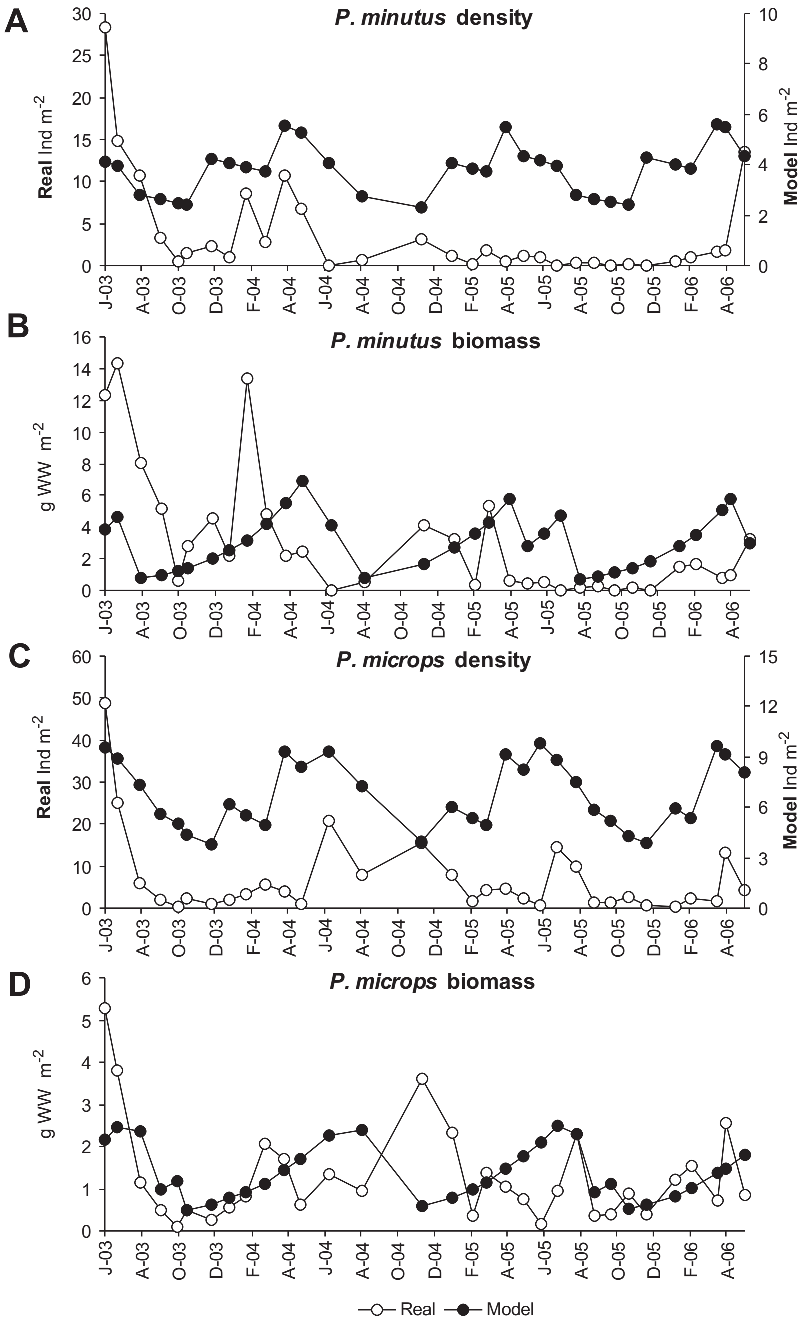


Fig. 7 Monthly variations of the field values and the model simulated values for population density and mean biomass of (A, B) *Pomatoschistus minutus* (C, D) *Pomatoschistus microps.*

Table 4 Annual and three-year study period mean values of density and biomass for the field data and the model simulations of *Pomatoschistus minutus* and *Pomatoschistus microps*, with indication of the linear regression model II (Reduced Major Axis method) coefficients (b, slope; a, intercept) between model simulated and field values, and the Dent and Blackie tests (*F*-test) applied to the coefficients; ns, none significant differences; * $p \leq 0.05$.

		Field data	Model	Regression coefficients and F-test
P. minutus	***Mean population density*** (Ind 1000m^{-2})			
	2003/04	7.6 ± 7.7	3.8 ± 1.0	b: 7.8, a: -21.7, F = 18.4 *
	2004/05	1.0 ± 1.0	3.8 ± 0.9	b: 1.0, a: -2.9, F = 6.8 *
	2005/06	1.7 ± 3.6	3.8 ± 1.0	b: 3.5, a: -11.9, F = 25.3 *
	All years	3.8 ± 6.0	3.8 ± 1.0	
	Mean population biomass (g WW 1000m^{-2})			
	2003/04	6.07 ± 4.60	3.08 ± 1.88	b: 2.4, a: 1.4, F = 0.15 ns
	2004/05	1.81 ± 1.94	3.22 ± 1.48	b: 1.4, a: -2.4, F = 1.41 ns
	2005/06	0.78 ± 0.92	2.86 ± 1.64	b: 0.6, a: -0.8, F = 2.6 ns
	All years	3.02 ± 3.86	3.03 ± 1.71	
P. microps	***Mean population density*** (Ind 1000m^{-2})			
	2003/04	8.4 ± 13.7	6.6 ± 1.9	b: 7.0 a: -37.9, F = 33.0 *
	2004/05	8.1 ± 6.3	6.8 ± 1.9	b: 3.3, a: -14.5, F = 4.4 ns
	2005/06	4.4 ± 4.8	6.9 ± 2.0	b: 2.4, a: 12.1, F = 20.5 *
	All years	6.9 ± 9.6	6.8 ± 2.0	
	Mean population biomass (g WW 1000m^{-2})			
	2003/04	1.45 ± 1.52	1.35 ± 0.65	b: 2.3, a: -1.7, F = 6.78 *
	2004/05	1.47 ± 0.97	1.43 ± 0.63	b: 1.5, a: -0.7, F = 0.28 ns
	2005/06	1.03 ± 0.73	1.38 ± 0.64	b: 1.2, a: -0.6, F = 1.48 ns
	All years	1.30 ± 1.16	1.38 ± 0.64	

Pomatoschistus microps simulations

In a two-year period the first cohorts of January, April and June recruitments are completed (started after day 1, 91 and 151 respectively, Fig. 2B). The model output for the daily individual growth, juveniles and adults density was identical to the one with the *P. minutus* (Fig. 6) but this species has 6 cohorts, starting every January, April and June (graphs are not shown here). Juvenile density started high and was subjected to higher mortality than *P. minutus* juveniles (Table 1), so a high proportion of *P. microps* population was composed by juveniles. The largest fish in the field samples had 59 mm, 1.812 g WW. If all recruitments attained the maximal weight found in the field samples, model life span would vary between 19.1, 16.7 and 16.9 months for January, April and June recruitments respectively.

The model performance with *P. microps* was similar to *P. minutus*. In general, density variation patterns were reproduced by the model simulation, but with lower mean values (Fig. 7C). For the biomass, only some variations were reproduced and these were not completely simultaneous with the field data variations (Fig. 7D). Yet, no significant differences between the biomass simulated and field annual values were found, with exception for *P. microps* in 2003/04 (Dent and Blackie *F*-tests, Table 4).

The model simulations buffered the field data natural variations for density and biomass (Fig. 7C, D), so differences were found in their annual estimates, as the model produced similar mean annual values for all three years (Table 4). However, the differences with *P. microps* annual estimates were not as pronounced as they were with *P. minutus*, for both density and biomass estimates (Table 4).

Among the most sensitive parameters in the new sensitivity analysis were the growth rates, especially the January one for all state variables, i.e., individual weight, juvenile density and adult density (Table 3). The juvenile mortality rate and the number of eggs, especially the first recruitments of January (Jan 1) and June (Jun 1), for juvenile and adult densities, showed also high sensitivity (Table 3).

Regarding the recruitment strength analysis, the first field cohorts of *P. microps* had higher densities than the last ones, especially C3, C4, C5 and C7 (Fig. 8). Comparing with the model simulations for these cohorts, C3, C4, C5 and C7, simulated values were considerably lower the field density results (Fig 8). For the last cohorts (C8, C9, C10, C11), the model simulated and the field values were similar, if the mean of field values is considered (Fig. 8). Several cohorts were not completed through their possible life span (C3, C4, C5, C6, C8, C9), with the most evident case with C6, which had clearly a lower field density and finished 7 months before the maximum expected life span, when compared to the simulated values (Fig. 8). During the three year period, *P. microps* had 13 cohorts, but for the purpose of this study only 10 cohorts, the ones comprised the maximum life span, were presented.

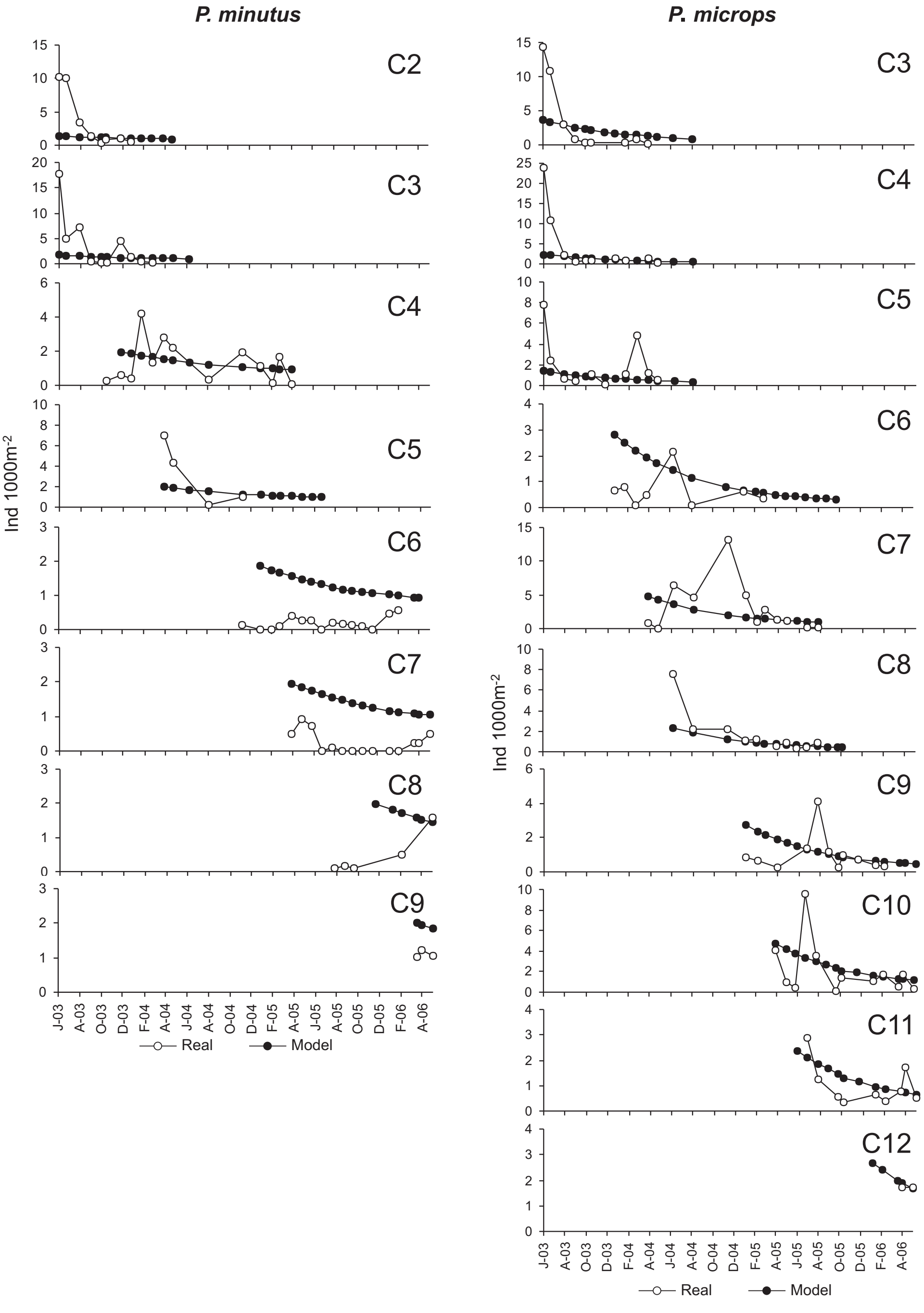


Fig. 8 Recruitment strength (density) of the major cohorts (C) for *Pomatoschistus minutus* and *Pomatoschistus microps*, field data (white symbols) versus model simulated data (black symbols) for each cohort.

DISCUSSION

Model scope

Ecological modelling has been increasingly used in ecology as an instrument to understand the ecosystem properties and as tool for management and conservation of natural resources (Jørgensen & Bendoricchio 2001, Franco et al. 2006, Silva-Santos et al. 2006). The present model revealed useful in the sense that: 1) it allowed the survey of complex systems, such as the fish population dynamics; 2) it revealed the system's properties and allowed the setting of new hypotheses for its understanding, such as the effect of potential restrictions of the population development; and 3) it revealed the model weakness and clarified its research priorities. These will be discussed in the following sections.

Surveying complex systems

The model developed simulates a simplified life cycle and the population structure, generally addressed in population ecology studies (e.g. Doornbos and Twisk 1987, Pampoulie et al. 1999, Pampouile 2001, Leitão et al. 2006, Dolbeth et al. 2007a). It provides the density and biomass values that would be expected if all cohorts from the fish recruitments could develop without limitations. Physiological aspects were considered to be included on the parameters used in the model, which were computed or determined through calibration according to a three-year study field data. Also, the model presented a framework for short-lived populations (and non target fishing species), with discontinuous reproduction, and it could be adapted to other species with small changes in the parameters. Different scenarios could be added and tested by the inclusion of the functions most influencing the fish development. The present approach agrees with the physiologically structured models approach, as it focused on the link between individual growth and population growth (Bryant et al. 1995, Persson & De Roos 2006), but it does not account for the explicit physiological aspects of the individual growth.

The results were consistent with the expectations, both for the individual and population density and biomass growth. Similar simulated life spans were obtained, although slightly higher for *P. microps* (especially in the January recruitment) than *P. minutus*, when the expected would be a lower life expectancy. This may be related with the defined maximum weight for *P. microps*. It was assumed that all cohorts could achieve the largest/heaviest individual found in the field. Yet, only two individuals were found with the maximum length and these were not accounted for the growth rate computation, as the cohort to which they belonged could not be ascertain confidently.

The model simulated density and biomass variation patterns along time (increase/decrease) showed a close agreement with the life history traits of each fish, in particular with the recruitment, which is expected as model was developed using, in part, field data. Some differences were found, probably due to the influence of strong external factors. The natural dynamics of the fish population (density and biomass) along the study period was quite variable, as it was seen by the different recruitment strengths in the different three years (Dolbeth et al. 2007a), assumed to be equal by the model. This variability in the recruitment strength was potentially caused by differences in the temperature and salinity regimes (Fonds & van Buurt 1974, von Oertzen 1984), also associated to differences in the river flow (Costa et al. 2007), and by density-dependent processes on the growth and survival, such as different predation pressure and competition (Rose & Cowan Jr 2000, Anderson 2001, Rose 2005, Bardos et al. 2006), or for *P. minutus* by migration for reproduction (Bouchereau & Guerlorget 1998; Pampouile et al. 1999; Leitão et al. 2006). Nevertheless, the present modelling approach still allows to set hypotheses regarding the fish development (see below).

Revealing system properties and setting up research priorities

The model results may provide some insight on the impacts on the ecosystem. The model simulated the ideal (and equalitarian) development of the population, as the parameters were computed or calibrated from a three-year field mean and it was assumed that growth and mortality would not vary significantly through time. Comparing the ideal with the real values, hypotheses may be raised that help understanding the ecosystem properties. The recruitment strength analyses exemplified this. The first cohorts, occurring in 2003 (from parental cohorts of 2002 and 2003), had field values clearly above-mean for both fish species. The remaining cohorts (mainly the ones starting in 2004 and 2005) had quite below-mean values for *P. minutus* and similar mean values for *P. microps*. This translated into markedly low density in 2005 for *P. minutus*, and slightly lower density in 2005 than in 2003/04 for *P. microps*. Hypotheses may be suggested for the different strength in recruitments, which highlights the future model research priorities, as simulations do not reproduce the real recruitment strength. During the three-year period, important climate variability occurred in Portugal, with the occurrence of an extreme drought in 2005 and higher salinity incursion in the estuary (Dolbeth et al. 2007a, Martinho et al. 2007). Although no direct effects of the temperature and salinity on both the *Pomatoschistus* spp. density and biomass could be confirmed (Dolbeth et al. 2007a), these were pointed out as major reasons for the differences found in the population dynamics. It was suggested the piscivorous marine adventitious species increased in the estuary (Martinho et al. 2007), which could have increased predation pressure on the gobiids, mainly on *P. minutus* (Dolbeth et al. 2007a). In fact, predation would be an important external function influencing the mortality rates. In natural ecosystems, predation is considered as the dominant source of the fish natural mortality (Lorenzen 1996). This was probably high for both *Pomatoschistus* spp., as they are dominant preys of several other trophic levels from the trophic webs (Doornbos & Twisk 1987). It has also been suggested that after a good recruitment, such as the one of 2003, the consequent high prey density may induce higher predator pressure (Andersen 2001). Besides, other studies revealed temperature and salinity as important factors for both *P. minutus* and *P. microps* eggs and larval development (Fonds & van Buurt 1974, von Oertzen 1984). This relation has been investigated experimentally, with results showing that *P. minutus* was less tolerant to temperature and salinity variations than *P. microps* (Fonds & van Buurt 1974, von Oertzen 1984). Field data study showed that *P. minutus* recruitment occurring in the drought year was weaker (Dolbeth et al. 2007a and present results). Therefore, temperature and salinity will be determinant for both gobiid species, especially on the recruitment strength and to the parameter “eggs” of the model. In future model developments, temperature and salinity should be included as functions influencing the fish population. The possibility of *P. minutus* migrations (Pampouile et al. 1999, Leitão et al. 2006) and the possibility of food limitation, as growth strongly depends upon food availability (Persson & Roos 2006) should also be considered.

CONCLUSIONS

The main aim to set up a simple procedure to simulate the population and biomass growth was accomplished. This is one of the most important aspects of the model: being able to simulate both density and biomass of a fish population in a consistent way. In order to make it simple, some assumptions were considered, namely that the input model parameters, obtained as a mean of a three-year study period field data or by calibration, would be representative of the population’s properties. Nevertheless, important inter-annual variability occurred, especially evident in growth and mortality rates, essentially due to the different temperature and salinity regimes, increased predation, competition and migration. The inclusion of forcing functions, working as natural limits for population growth, could probably improve the model performance. However, it would be a major constrain to distinguish among the most important factors, since estuarine systems are naturally highly dynamic. The present approach presented some advantages towards other fish models due to its simplicity, whose parameters can be easily obtained, and it revealed some of the ecosystem properties. It also allows the setting of new hypotheses for the ecosystem understanding, such as the effect of the potential restrictions on the fish population development.

ACKNOWLEDGEMENTS

The authors are indebted to Daniel Crespo, Heliana Teixeira, Ivan Viegas, João Miguel Neto and Tiago Verdelhos who helped in field work.

REFERENCES

Anderson TW (2001) Predator responses, prey refuges, and density-dependent mortality of marine fish. Ecology 82: 245–257.

Anneville O, Cury P, Le Page C, Treuil JP (1998) Modelling fish spatial dynamics and local density-dependence relationships: detection of patterns at a global scale. Aquat Living Resour 11: 305–314.

Baeta A, Cabral HN, Neto JM, Marques JC, Pardal MA (2005) Biology, population dynamics and secondary production of the green crab *Carcinus maenas* (L.) in a temperate estuary. Estuar Coast Shelf Sci 65: 43–52.

Bardos DC, Dayb RW, Lawsonb NT, Linacre NA (2006) Dynamical response to fishing varies with compensatory mechanism: An abalone population model. Ecol Model 192: 523–542.

Bouchereau JL, Quignard JP, Joyeux JC, Tosmasini JA (1991) Stratégies et tactiques de reproduction de *Pomatoschistus microps* (Krøyer, 1838) et de *Pomatoschistus minutus* (Pallas, 1770) (Pisces, Gobiidæ) dans le golfe du Lion. Nids, déterminisme de la sédentarité et de la migration. Cybium 15: 315–346.

Bouchereau JL, Guelorget O (1998) Comparison of three Gobidae (Teleostei) life history strategies over their geographical range. Oceanol Acta 24: 503–517.

Bryant AD, Health MR, Broekhuizen N, Ollason JG, Gurney WSC, Greenstreet SPR (1995) Modelling the predation, growth and population dynamics of fish within spatially-resolved shelf sea ecosystem model. Neth J Sea Res 33: 407–421.

Cardoso PG, Brandão A, Pardal MA, Raffaelli D, Marques JC (2005) Resilience of *Hydrobia ulvae* populations to anthropogenic and natural disturbances. Mar Ecol Prog Ser 289: 191–199.

Costa MJ, Vasconcelos R, Costa JL, Cabral HN (2007) River flow influence on the fish community of the Tagus estuary (Portugal). Hydrobiologia 587: 113–123.

Dolbeth M, Martinho F, Leitão R, Cabral H, Pardal MA (2007a) Strategies of *Pomatoschistus minutus* and *Pomatoschistus microps* to cope with environmental instability. Estuar Coast Shelf Sci 74: 263–273.

Doornbos G, Twisk F (1987) Density, growth and annual food consumption of gobiid fish in the saline Lake Grevelingen, The Netherlands. Neth J Sea Resear 21: 45–74.

Franco AR, Ferreira JG, Nobre AM (2006) Development of a growth model for penaeid shrimp. Aquaculture 259: 268–277.

Fonds M, van Buurt G (1974) The influence of temperate and salinity on development and survival of goby eggs (Pisces, Gobiidae). Hydrobiol Bull 8: 110–116.

Gamito S (1998) Growth models and their use in ecological modelling: an application to a fish population. Ecol Model 113: 83–94.

Hallam TG, Lassiter RR, Henson SM (2000) Modelling fish population dynamics. Nonlinear Anal 40: 227–250.

Jørgensen SE, Bendoricchio G (2001) Fundamentals of Ecological Modelling. 3rd Edition. Elsevier, Oxford, United Kingdom, p 530.

Klanjšček J, Legović T (2007) Is anchovy (*Engraulis encrasicolus*, L.) overfished in the Adriatic Sea? Ecol. Model. 201, 312–316.

Leitão R, Martinho F, Neto JM, Cabral H, Marques JC, Pardal MA (2006) Feeding ecology, population structure and distribution of *Pomatoschistus microps* (Krøyer, 1838) and *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. Estuar Coast Shelf Sci 66: 231–239.

Lorenzen K (1996) The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J Fish Biol 49: 627–647.

Martinho F, Leitão R, Viegas I, Dolbeth M, Neto JM, Cabral HN, Pardal MA (2007) The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. Estuar Coast Shelf Sci doi:10.1016/j.ecss.2007.05.040.

Needle CL (2002) Recruitment models: diagnosis and prognosis. Rev Fish Biol Fish 11: 95–111.

Neill WH, Brandes TS, Burke BJ, Craig SR, DiMichele LV, Duchon K, Edwards RE, Fontaine LP, Gatlin DM, Hutchins C, Miller JM, Ponwith BJ, Stahl CJ, Tomasso JR, Vega RR (2004) Ecophys.Fish: A simulation model of fish growth in time-varying environmental regimes. Rev Fish Sci 12: 233–288.

Pampoulie C (2001) Demographic structure and life history traits of the common goby *Pomatoschistus microps* (Teleostei, Gobidae) in a Mediterranean coastal lagoon (Rhône River delta, France). Acta Oecol 22: 253–257.

Pampoulie C, Rosecchi E, Bouchereau JL, Crivelli AJ (1999) Life history traits of *Pomatoschistus minutus* (Teleostei, Pisces) in the Rhône Delta, France. J Fish Biol 55: 892–896.

Patrício J, Marques JC (2006) Mass balanced models of the food web in three areas along a gradient of eutrophication symptoms in the south arm of the Mondego estuary (Portugal). Ecol Model 197: 21–34.

Persson L, De Roos AM (2006) Food-dependent individual growth and population dynamics in fishes. J Fish Biol 69: 1–20.

Rose KA (2005) Lack of relationship between simulated fish population responses and their life history traits: inadequate models, incorrect analysis, or site-specific factors? Can J Fish Aquat Sci 62: 886–902.

Rose KA, Cowan JrJH (2000) Predicting fish population dynamics: compensation and the importance of site-specific considerations. Environ Sci Pol 3: S433–S443.

Silva-Santos P, Pardal MA, Lopes RJ, Múrias T, Cabral JA (2006) A Stochastic Dynamic Methodology (SDM) to the modelling of trophic interactions, with a focus on estuarine eutrophication scenarios. Ecol Indicat 6: 394–408.

Sokal RR, Rohlf FJ (1981) Biometry. The principles and practice of statistics in biological research, 2nd Ed. Freeman and Company, New York, USA, p 859.

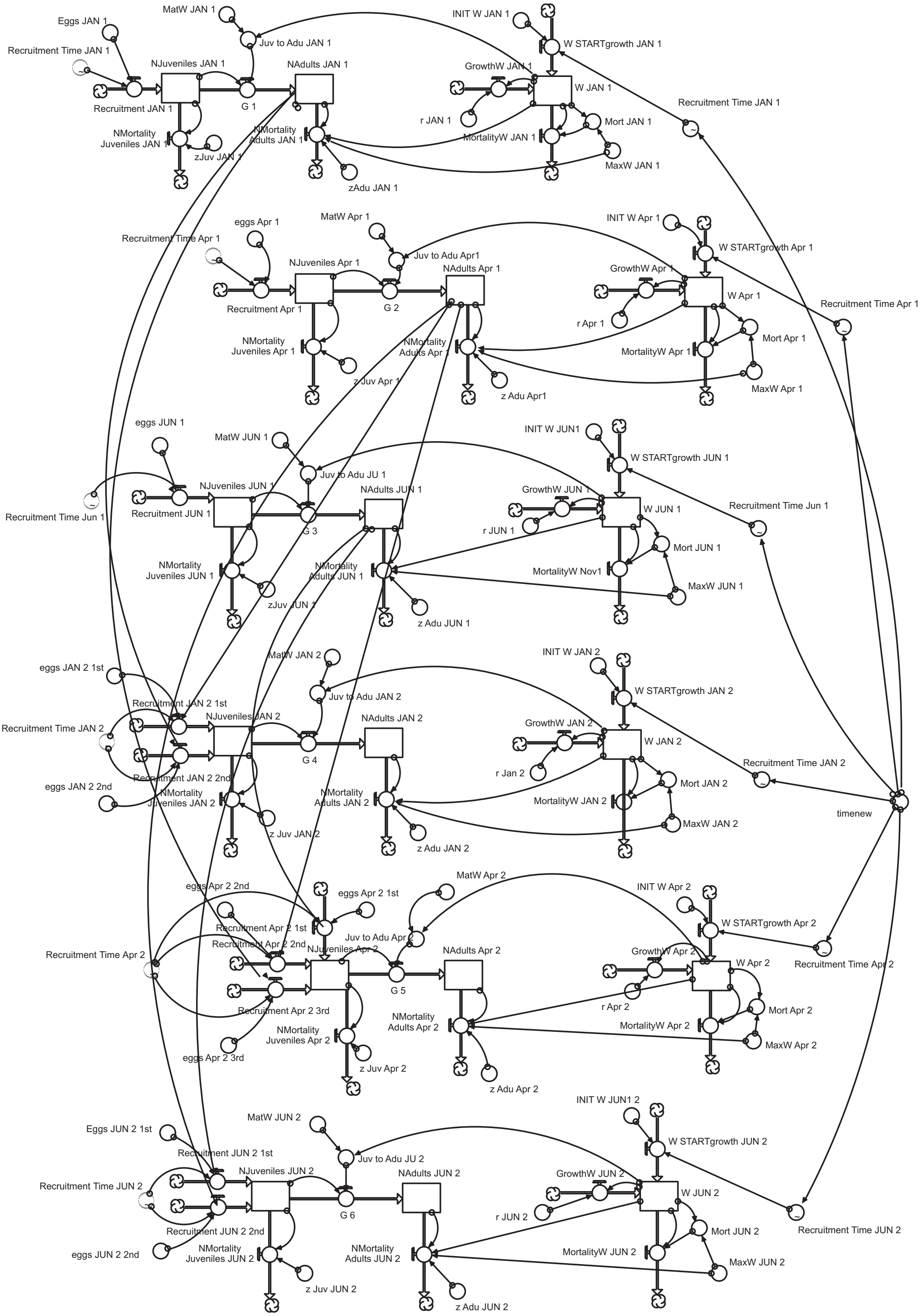
Tedeschi LO (2006) Assessment of the adequacy of mathematical models. Agric Syst 89: 225–247.

van Nes EH, Lammens EHRR, Scheffer M (2002) PISCATOR, an individual-based model to analyze the dynamics of lake fish communities Ecol Model 152: 261–278.

von Oertzen JA (1984) Influence of steady-state and fluctuating salinities on the oxygen consumption and activity of some brackish water shrimps and fishes. J Exp Mar Biol Ecol 80: 29–46.

APPENDIX I

Stella diagram of the population growth model for *Pomatoschistus microps* population, indicating the coupling between cohorts (two years * three recruitments). Model symbols and explanation in Table 1.


MatW JAN 1
Eggs JAN 1
Recruitment Time JAN 1
Juv to Adu JAN 1
NJuveniles JAN 1
NAdults JAN 1
Recruitment JAN 1
G 1
NMortality Juveniles JAN 1
NMortality Adults JAN 1
zJuv JAN 1
zAdu JAN 1
INIT W JAN 1
W STARTgrowth JAN 1
GrowthW JAN 1
W JAN 1
r JAN 1
Mort JAN 1
MortalityW JAN 1
MaxW JAN 1
Recruitment Time JAN 1
MatW Apr 1
eggs Apr 1
Recruitment Time Apr 1
Juv to Adu Apr1
NJuveniles Apr 1
NAdults Apr 1
Recruitment Apr 1
G 2
NMortality Juveniles Apr 1
NMortality Adults Apr 1
z Juv Apr 1
z Adu Apr1
INIT W Apr 1
W STARTgrowth Apr 1
GrowthW Apr 1
W Apr 1
r Apr 1
Mort Apr 1
MortalityW Apr 1
MaxW Apr 1
Recruitment Time Apr 1
eggs JUN 1
MatW JUN 1
Juv to Adu JU 1
NJuveniles JUN 1
NAdults JUN 1
Recruitment JUN 1
Recruitment Time Jun 1
G 3
NMortality Juveniles JUN 1
NMortality Adults JUN 1
zJuv JUN 1
z Adu JUN 1
INIT W JUN1
W STARTgrowth JUN 1
GrowthW JUN 1
W JUN 1
r JUN 1
Mort JUN 1
MortalityW Nov1
MaxW JUN 1
Recruitment Time Jun 1
eggs JAN 2 1st
MatW JAN 2
Juv to Adu JAN 2
Recruitment JAN 2 1st
Recruitment Time JAN 2
NJuveniles JAN 2
NAdults JAN 2
G 4
Recruitment JAN 2 2nd
eggs JAN 2 2nd
NMortality Juveniles JAN 2
NMortality Adults JAN 2
z Juv JAN 2
z Adu JAN 2
INIT W JAN 2
W STARTgrowth JAN 2
GrowthW JAN 2
W JAN 2
r Jan 2
Mort JAN 2
MortalityW JAN 2
MaxW JAN 2
Recruitment Time JAN 2
timenew
eggs Apr 2 2nd
eggs Apr 2 1st
MatW Apr 2
Recruitment Apr 2 1st
Recruitment Apr 2 2nd
Juv to Adu Apr 2
NJuveniles Apr 2
NAdults Apr 2
Recruitment Time Apr 2
G 5
Recruitment Apr 2 3rd
NMortality Juveniles Apr 2
NMortality Adults Apr 2
eggs Apr 2 3rd
z Juv Apr 2
z Adu Apr 2
INIT W Apr 2
W STARTgrowth Apr 2
GrowthW Apr 2
W Apr 2
Recruitment Time Apr 2
r Apr 2
Mort Apr 2
MortalityW Apr 2
MaxW Apr 2
MatW JUN 2
Eggs JUN 2 1st
Juv to Adu JU 2
Recruitment JUN 2 1st
NJuveniles JUN 2
NAdults JUN 2
Recruitment Time JUN 2
G 6
Recruitment JUN 2 2nd
eggs JUN 2 2nd
NMortality Juveniles JUN 2
NMortality Adults JUN 2
z Juv JUN 2
z Adu JUN 2
INIT W JUN1 2
W STARTgrowth JUN 2
GrowthW JUN 2
W JUN 2
r JUN 2
Mort JUN 2
MortalityW JUN 2
MaxW JUN 2
Recruitment Time JUN 2

CHAPTER III

Links between macroinvertebrates and fish

Feeding patterns of a temperate estuarine fish community: detecting major links within trophic levels

Feeding patterns of a temperate estuarine fish community: detecting major links within trophic levels

Abstract The diet of the 14 most abundant fish species of the Mondego estuary, Portugal, was studied, using fish caught between June 2003 and May 2006. The stomach contents were analysed for the prey identification, counting and weighting. According to prey importance in diets three main feeding guilds were identified: 1) zooplanktonic and detritus feeders; 2) invertebrate feeders; and 3) invertebrate and fish feeders. Besides these main feeding guilds, some fish also presented fractions of algae in their stomach contents. The most abundant preyed items were macroinvertebrates, with several polychaetes (*Nephtys* spp., Capitellidae, Spionidae, Eunicidae), *Corophium* spp. and *Crangon crangon* among the dominant prey. *Pomatoschistus* spp. were the most preyed fish and calanoid copepods (mainly *Acartia* spp.) the most consumed plankton species. Several fish species showed a tendency for a specialized diet. However, almost all fishes also showed some degree of opportunistic feeding, by feeding on other food resources. High diet overlap was found between some fish species, yet exploitative competition could not be concluded.

Keywords Fish community, Feeding ecology, Diet overlap, Macrobenthos, Mondego estuary

INTRODUCTION

Estuaries are among the most productive ecosystems on earth (Gamito et al. 2003, McLusky & Elliott 2004, Dolbeth et al. 2007a). This high productivity and the diversity of available habitats and protection to predators have been identified as primary attractive for the high abundance of fishes in estuaries (Whitfield 1999, Elliott et al. 2002, McLusky & Elliott 2004, Able 2005, Akin & Winemiller 2006). For this reason, estuarine environments often function as nursery grounds, being essential for the reproduction of many coastal fishes, where survival, development and growth are potentially optimized (Elliott & Dewailly 1995, McLusky & Elliott 2004, Able 2005, Martinho et al. 2007a, Svensson et al. 2007).

The high production of estuarine systems lies in the fact that they act as detritus traps for both autochthonous and allochthonous material (mostly amorphous organic matter associated with autotrophic or heterotrophic organisms or debris) (Akin & Winemiller 2006, Svensson et al. 2007). Thus, estuaries provide abundant food resources for plankton (Svensson et al. 2007), benthic invertebrate (filter- and deposit-feeding) and detritivorous fish species (Whitfield 1999). The potentially high availability of phytoplankton (especially in estuaries which receive regular inputs of freshwater), benthic microalgae and macroalgae is also important as basal resources for fish (Hall & Raffaelli 1991, Akin &

Winemiller 2006), either for direct feeding (Horta et al. 2004) or for the feeding of intermediate predators of the trophic chain (Elliott et al. 2002, Marques et al. 2006). The availability of a food type is expected to show fluctuations over time especially due to environmental changes (Whitfield 1999), to episodes that modify predator-prey interactions, to behavioural patterns avoiding predation and to disturbance (Robertson 1984, Eriksson et al. 2005). The main factors determining the feeding will include: 1) abiotic factors, as environment controls the prey production and limits predator abundances; and 2) biological factors, with fish choosing the prey and determining its abundance in the environment, and by predator levels which compete for the prey (Gorman & Raffaelli 1993, Elliott et al. 2002, Eriksson et al. 2005).

Estuaries have a vital role for the development of several fishes. In this perspective, is important to know the trophic relations between fish and their potential prey, as well as within the fish community itself. This information will enhance the understanding of the ecosystem structure, functioning and the potential carrying capacity of the estuary for fish production. Also, the concept of food web as summary of resource-consumer interactions helps to assess the population dynamics of its different components (Hall & Raffaelli 1991, Akin & Winemiller 2006). The present study was developed to describe the feeding ecology of the main fish species of the Mondego estuary, in particular aimed to: 1) describe and examine the feeding patterns (diet, strategy) of single species; 2) identify the main preyed items of the Mondego estuary, and therefore infer on the main fluxes of biomass/energy; 3) identify potential competition for food resources within the fish community based on the diet statistics; and 4) to set a generalized food web for the main fish species of the Mondego estuary.

MATERIALS AND METHODS

Study area

The Mondego estuary (Portugal) is located in a warm temperate region, on the Atlantic coast of Portugal (40°08'N, 8°50'W) (Fig. 1). It is a small estuary (3.4 km^2 area), with two arms (north and south) of distinct hydrologic characteristics. The north arm is deeper (4-10 m during high tide, tidal range 1-3 m) and constitutes the main navigation channel and the location of the Figueira da Foz harbour. Besides the severe changes imposed by the construction of the harbour facilities, constant dredging and shipping occurs in this sub-system, causing physical disturbance of the bottoms. The main freshwater

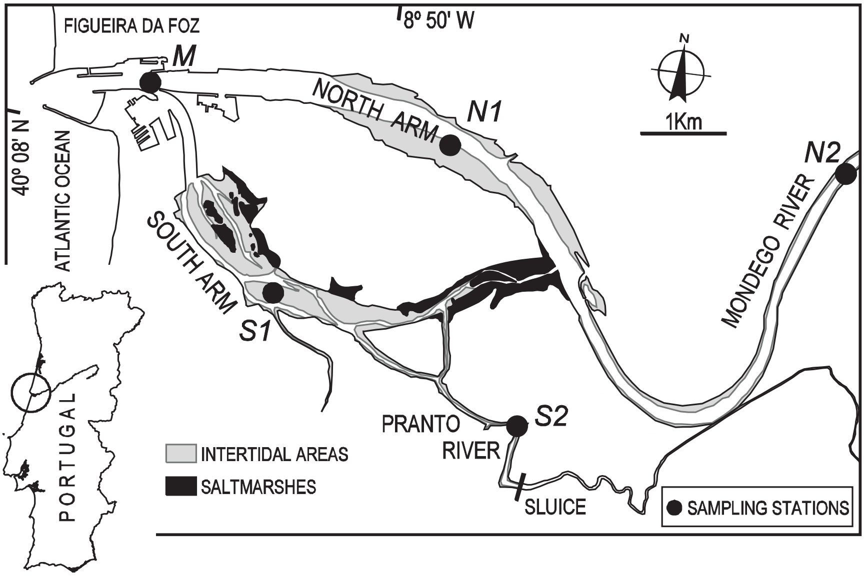


Fig. 1 The Mondego estuary, with indication of the sampling stations, intertidal area and saltmarshes.

inputs to the north arm are from Mondego river. The south arm is shallower (2-4 m during high tide, tidal range 1-3 m), characterized by large areas of exposed intertidal flats during low tide (about 75% of total area). The downstream areas of the south arm are relatively unchanged, with *Spartina maritima* marshes and a *Zostera noltii* meadow, but in the inner parts the seagrass community has completely disappeared, mainly due to severe eutrophication problems occurring in the past (detailed description in Cardoso et al. 2004, Dolbeth et al. 2007a). Water circulation in the south arm mostly depends on the tides and on the freshwater input from the Pranto river, as the upstream areas are almost silted up, with only a small connection with north arm. The Pranto river is controlled by a sluice according to the water needs in the rice fields of Mondego valley. In the south arm, about 75% of the total area consists of intertidal mudflats, while in the north arm they stand for less than 10%.

Fish community considerations and sampling procedures

The fish community of the Mondego estuary has been studied since 2003, with a monthly periodicity (e.g. Leitão et al. 2006, Dolbeth et al. 2007b, Martinho et al. 2007a, b). The dominant species are the estuarine residents *Pomatoschistus minutus, P. microps* and the species using the estuary as nursery, such as *Dicentrarchus labrax, Platichthys flesus* and *Solea solea* (Martinho et al. 2007a, b), whose information on the diets already exists (Leitão et al. 2006, Martinho, unpublished data). Fish were collected in the Mondego estuary from June 2003 until May 2006 using 2 techniques: 1) a 2 m beam trawl, equipped with one tickler chain and 5 mm stretched mesh size in the cod end, during a three year study period, with a monthly periodicity; 2) an otter trawl, during 2003/04, with a seasonal periodicity. All surveys occurred during the night, at the ebbing tide of spring tides, in five sampling stations with the beam trawl (M, S1, S2, N1, N2, Fig. 1) and in 2 sampling stations with the otter trawl (M, N1, Fig. 1).

For the present study, 14 fish species were analysed belonging to different ecological guilds (Table 1). These comprised the most abundant species, whose stomachs were removed and contents preserved in 4% buffered formalin for later identification. Data relative to fewer than 20 fish or to fish with a very different length or weight within the collected were not further analyzed. All prey were identified to the species level whenever possible, counted and their wet weight (g WW) assessed.

Additionally, the subtidal macrobenthic assemblage was also sampled in the same fish sampling areas (Fig. 1), with a seasonal periodicity and using a Van Veen grab. Samples were washed in a 1 mm sieve bags and were subsequently sieved, identified to the possible lowest *taxon* and counted. Detailed information on the macrobenthic subtidal community will be provided by INAG – Portuguese Water Institute, http://snirh.inag.pt. Information of the zooplankton availability within the estuary is provided in Marques et al. (2006).

Data analysis

Diet characterization was based solely on the stomach contents to avoid overestimation of prey with exoskeletons or other hard structures. The feeding activity was evaluated by the vacuity index, defined as the percent of empty stomachs (Hyslop 1980). Univariate and multivariate techniques were used to describe the feeding ecology of the fish community (multi-species analyses) (after Hyslop 1980, Marshall & Elliott, 1997). For a simpler presentation of the results, prey data was organized into major taxonomic groups: Amphipoda, Mysidae, Isopoda, Decapoda, Copepoda, Ostrocoda, Bivalvia, Polychaeta, Teleostei, plant material and Others (composed by non identified items and less abundant taxa prey such as Gastropoda, Scaphopoda, Cumacea, Echinodermata, Insecta, Nemertea). The groups Nematoda, Digenea and the species *Paragnathia formica*

Table 1 Fish species considered in the study, with indication of the ecological guild, the number of stomachs analysed (N), the vacuity index and the mean density in the Mondego estuary during the three-year study period.

Species	Ecological guild	N	Vacuity %	Mean density (Ind 1000m^{-2})
Anguilla anguilla	Catadromous	49	14	0.633 ± 0.94
Atherina boyeri	Estuarine resident	40	13	0.789 ± 1.29
Callionymus lyra	Marine adventitious	46	59	0.148 ± 0.27
Chelidonichthys lucerna	Marine juvenile	41	2	0.120 ± 0.26
Ciliata mustela	Marine juvenile	18	6	0.129 ± 0.21
Dicentrarchus labrax	Nursery	324	14	7.507 ± 7.93
Liza ramada	Catadromous	21	19	0.250 ± 0.58
Mullus surmuletus	Marine juvenile	35	40	0.104 ± 0.17
Platichthys flesus	Nursery	204	25	1.501 ± 1.64
Pomatoschistus microps	Estuarine resident	103	21	8.155 ± 11.58
Pomatoschistus minutus	Estuarine resident	100	17	3.685 ± 6.04
Scophthalmus rhombus	Marine juvenile	40	10	0.050 ± 0.07
Solea solea	Nursery	304	34	1.663 ± 1.42
Trisopterus luscus	Marine adventitious	41	5	0.102 ± 0.24

(Isopoda), were also found in some stomach contents, but were removed for the subsequent analyzes, since they are fish parasites and not prey.

The relative importance of each prey item was expressed as percent of numerical abundance (N_I, numerical index), occurrence (O_I, occurrence index, accounted relatively to the total number of stomach with prey) and weight (G_I, gravimetrical index) (Hyslop 1980, Marshall & Elliott 1997) of the food items in stomachs. The dietary coefficient (Q_I), defined as $Q_I = N_I \times G_I$, was also computed (after Leitão et al. 2006). This method considers both the weight and the number of ingested prey, classifying them into dominant ($Q_I \geq 200$), secondary ($200 < Q_I \geq 20$) or unimportant ($Q_I < 20$). This coefficient was also computed for each prey species separately, in order to detect the dominant prey species/taxon.

Interspecific diet overlap was evaluated by Schoener's Index (S_I) (Linton et al. 1981):

$$S_I = 1 - 0.5\left(\sum_{i=1}^{n} \left| p_{i_A} - p_{i_B} \right|\right)$$

where p_{iA} and p_{iB} are the numerical frequencies of item *i* on the diet of species *A* and *B*, respectively. Both N_I and G_I were used to compute this index. There are no critical levels for this index, yet several studies have considered that values higher than 0.6 should be regarded as biologically significant (Linton et al. 1981, Warburton & Blaber 1992, Leitão et al. 2006, Vinagre et al. 2006). The diet similarities within the fish community were also analysed through similarity relationships, determined by the Bray-Curtis coefficient of the Q_I index performed with the main prey taxa for all fish species. Subsequently, a CLUSTER analysis was performed. The Shannon-Wiener diversity and the Pielou evenness indexes were also computed to provide a measure of the niche breadth (after Marshall & Elliott 1997). These indexes were computed using the abundances of each of the main taxa prey occurring in the fish stomach. These analyses were performed with PRIMER software package (version 5.2.6, PRIMER-E Ltd).

The distribution of the fish species and main macrobenthic prey items within the estuary was investigated using a correspondence analysis (CA), performed with CANOCO software (version 4.5) (Ter Braak 1988).

RESULTS

General patterns

At least 79 different taxa of prey were identified in the diet of the 14 fish species analysed in the present study. The vacuity index (for all species caught at night) was in general low, with exception of three species (*C. lyra*, *M. surmuletus* and *S. solea*), whose value reached more than 30% (Table 1). The graphical disposition of the numerical, gravimetrical and occurrence indexes (respectively N_I, G_I and O_I) enabled to clarify diet patterns for each species and also to detect some general patterns for the community: 1) dominant prey taxa, as the most preyed taxa will have high values of all indexes; 2) fish feeding strategy, as a single dominant taxa in diet will have indexes values near 100%, indicating a more specialized diet; and the indexes values for displayed in a cluster near the centre will mean a more generalist diet; and 3) diet complexity, as it is possible to have a general idea of the diet breadth, by analyzing the number of prey taxa displayed in the graph (Fig. 2). Accordingly, the main preyed taxa for the whole community were Amphipoda, Copepoda, Decapoda and Polychaeta (Fig. 2). *Atherina boyeri, P. flesus, A. anguilla, L. ramada, P. minutus,* C. *lucerna, S. solea* and *S. rhombus* seemed to be specialized feeders (Fig. 2). The other species of the fish community appeared to be generalist feeders, with no clear preference for single taxa in their diets (Fig. 2). This was particularly evident for *M. surmuletus*, *T. luscus*, *D. labrax* and *P. microps* (Fig. 2).

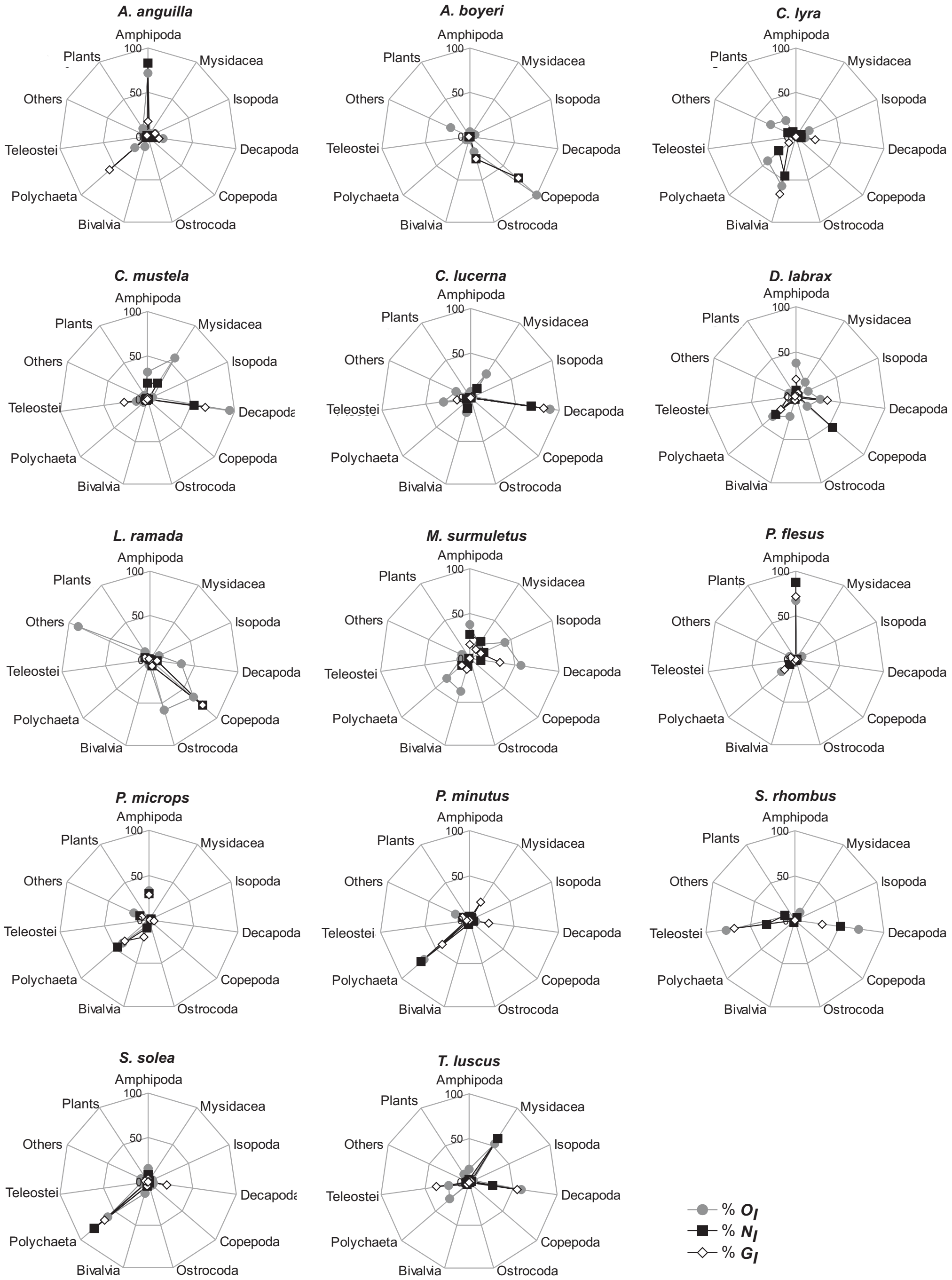

A. anguilla
A. boyeri
C. lyra
C. mustela
C. lucerna
D. labrax
L. ramada
M. surmuletus
P. flesus
P. microps
P. minutus
S. rhombus
S. solea
T. luscus
Amphipoda
Mysidacea
Isopoda
Decapoda
Copepoda
Ostrocoda
Bivalvia
Polychaeta
Teleostei
Others
Plants
100
50
0
% O_I
% N_I
% G_I

Fig. 2 Numerical (%N_I), gravimetrical (%G_I) and occurrence (%O_I) indices for the main species of the Mondego estuary.

Description of the diet of single species

Both *A. anguilla* and *P. flesus* fed preferentially on Amphipoda (Fig. 2), especially on *Corophium* spp. according to the Q_I index (Table 2, Q_I higher than 1 400). For *P. flesus* Amphipoda (*Corophium* spp.) was highly dominant in the diet, as all N_I, G_I and O_I showed high percentages (Fig. 2). For *A. anguilla* Polychaeta had also an important contribution in weight (high G_I, Fig. 2), with Eunicidae polychaetes as important secondary prey (Table 2). The tendency for a specialized diet of these species (Fig. 2) was also confirmed by the low evenness (J') and diversity (H') found for both species' diet (Table 2).

The diet of *A. boyeri* and *L. ramada* was mainly composed by Copepoda. All *A. boyeri* analysed had Copepoda in their stomach contents. Evenness was considerably low for *A. boyeri*, mainly due to the dominance of Copepoda (Table 2). Although no clear dominance of a single Copepoda species could be proved (most individuals could not be accurately identified), Cyclopinidae individuals appeared in slightly higher proportions. For *L. ramada*, the O_I for the group "Others" was considerably high, mainly due to the presence of detritus (assigned as "Others") in several stomachs, together with other prey. *Acartia* sp. (Copepoda) was a dominant prey of *L. ramada* (Table 2) and Ostrocoda had also a fairly presence, but in lower numbers (Fig. 2). *D. labrax* also showed high N_I of Copepoda, yet this group did not occur in all stomachs (low O_I, Fig. 2).

Solea solea and *P. minutus* had high abundance of Polychaeta in their diets (Fig. 2). In fact, the dominance of Polychaeta in the diet of *S. solea* was quite evident, with *Nephtys* spp. as dominant prey and other Polychaeta species as secondary prey (Table 2). This tendency was complemented by the low diversity and evenness observed for *S. solea* (Table 2). For *P. minutus*, Mysidae and *Crangon crangon* (Decapoda) had also an important contribution in weight (Fig. 2, Table 2). For *D. labrax* and *P. microps,* the group Polychaeta, in particular the capitellids, had also an important contribution in their diets (Fig. 2, Table 2). Yet, both species showed a more generalist feeding behaviour, with other items also contributing considerably for their diets, e.g. *Corophium* spp. (Table 2).

Ciliata mustela, *C. lucerna*, *T. luscus* and *S. rhombus* had at least two common items in their diets, varying in dominance: the group Decapoda, with a prevalence of *Crangon crangon*, and Teleostei (Fig. 2, Table 2). For *C. lucerna* the dominance of *Crangon crangon* was clear (high values N_I, G_I and O_I), while for *C. mustela* and *T. luscus*, *Carcinus maenas* was also an important prey among Decapoda species (Table 2). Mysidae also had a considerable occurrence, especially in *T. luscus* (Fig. 2, Table 2). In terms of weight (G_I), an important contribution was also observed for Teleostei (Fig. 2) for *T. luscus*. The highest percentages in both weight and occurrence of Teleostei were found in *S. rhombus* (Fig. 2).

Table 2 Niche breadth (J', Shannon and Wiener diversity index; H', Pielou evenness index), and dominant and secondary prey, according to the dietary coefficient (Q_I).

Fish	Niche breadth*	Dominant prey	Secondary prey
A. boyeri	H' = 0.7, J' = 0.4	Copepoda ni	-
L. ramada	H' = 0.8, J' = 0.4	*Acartia* sp.	Ostrocoda ni
D. labrax	H' = 1.2, J' = 0.6	Capitellidae ni Copepoda ni	*Corophium* spp. *Crangon crangon*
S. solea	H' = 0.8, J' = 0.4	*Nephtys* spp.	Capitellidae ni Polychaeta ni Spionidae ni
P. microps	H' = 1.4, J' = 0.8	Polychaeta ni *Corophium* spp.	*Scrobicularia plana* Capitellidae ni Spionidae ni Crustacea ni
P. minutus	H' = 1.1, J' = 0.5	Polychaeta ni	Mysidae ni *Crangon crangon* Capitellidae ni
A. anguilla	H' = 0.7, J' = 0.3	*Corophium* spp.	Eunicidae ni *Carcinus maenas* *Idotea* sp.
P. flesus	H' = 0.5, J' = 0.2	*Corophium* spp.	Spionidae ni
T. luscus	H' = 1.2, J' = 0.5	*Crangon crangon*	*Carcinus maenas* Mysidae sp_1 Teleostei ni
C. mustela	H' = 1.3, J' = 0.6	*Crangon crangon* *Carcinus maenas*	*Pomatoschistus microps*
C. lucerna	H' = 1.0, J' = 0.5	*Crangon crangon*	Teleostei ni
S. rhombus	H' = 1.2, J' = 0.7	*Pomatoschistus* sp. Other Teleostei *Crangon crangon*	-
M. surmuletus	H' = 1.8, J' = 0.9	*Crangon crangon* *Sphaeroma* sp. *Gastrosaccus spinifer* *Gammarus* spp. *Scrobicularia plana*	Amphipoda ni *Melita palmata* *Cyathura carinata*
C. lyra	H' = 1.4, J' = 0.8	*Parvicardium ovale* *Scrobicularia plana* Polychaeta ni	*Portumnus latipes*

In fact, Teleostei was only considered as a dominant prey for *S. rhombus*, with *Pomatoschistus* spp. as an important preyed fish (Table 2).

Mullus surmuletus was the species with the most generalist feeding behaviour and with the most diverse diet (Fig. 2), also seen by the highest diversity and evenness indexes (Table 2). Among the preferential prey were Decapoda, Amphipoda, Isopoda, Polychaeta and Bivalvia (Fig. 2), with at least five different species considered as dominant prey according to the Q_I (Table 2). Similarly, C. *lyra* had a diverse diet (high J' and H', Table 2), though the group Bivalvia evidenced as a preferential preyed taxa, occurring in about 60% of the stomachs analysed (Fig. 2). Within Bivalvia, *Parvicardium ovale* and *Scrobicularia plana* were the most frequent species (Table 2).

Multi-species comparisons - diet overlap

At least five groups of fishes were discriminated according to the similarities in their diets, regarding the main prey (Fig. 3). These diet similarities highlighted the diet overlap and potential competition for food resources within the fish community. In general, the groups of species formed in the cluster analysis also showed high Schoener index (S_I) (Table 3). *Atherina boyeri* and *L. ramada* showed a high diet similarity (86% similarity) and were clearly separated from the other fish (group I, Fig. 3). The S_I for these species was high with both N_I and G_I (Table 3), reinforcing the diet overlap between the species. *Dicentrarchus labrax* also showed high S_I with *L. ramada*, but only for the S_I computed with the N_I (Table 3).

Chelidonichthys lucerna, C. *mustela, T. luscus,* and *S. rhombus* also had high similarity in the diet (group II, Fig. 3). T. luscus and *S. rhombus* shared about 75% of dominant prey (Fig. 3) and had high S_I values for both N_I and G_I (Table 3). Regarding S_I, comparisons within the other pairs of species, both C. *mustela* (with S_I computed with N_I and G_I) and *T. luscus* (S_I computed with G_I) showed high overlap with the other two remaining fish (Table 3). Additionally, C. *mustela* also showed high numerical S_I with *M. surmuletus*, being the species with the highest number of S_I values above 0.6, i.e. biologically significant (Table 3). C. *lucerna* had a high S_I in weight with *S. rhombus* (Table 3).

Platichthys flesus and A. anguilla shared similar food resources (group III, Fig. 3), but the S_I was only high with the N_I (Table 3).

Solea solea, P. minutus, P. microps, and *D. labrax* also showed similarities in food preferences (group IV, Fig. 3). Nevertheless, only *S. solea* had a high S_I with the other

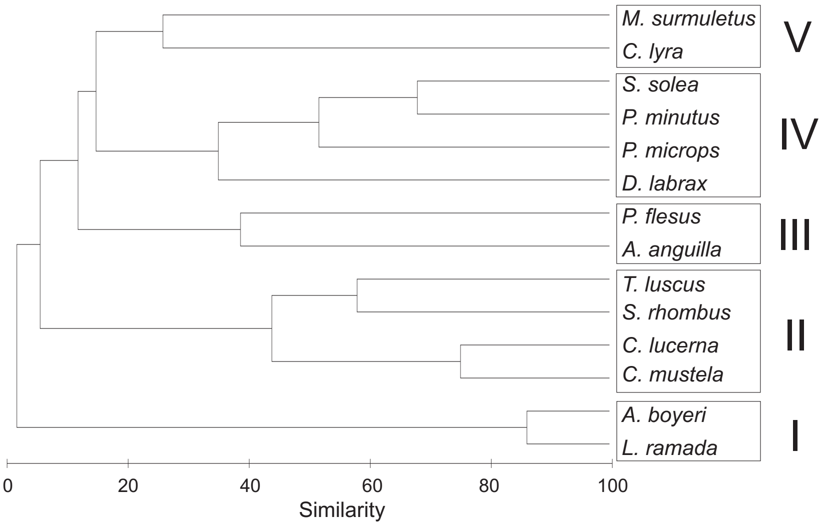


Fig. 3 Dendrogram with dietary similarities within the fish community of the Mondego estuary, determined with Bray-Curtis similarities of the dietary coefficient (Q_I), computed with the main taxa prey.

species, for N_I or G_I, and *P. minutus* and *P. microps* with each other for the N_I (Table 3). Additionally, *A. anguilla* (a species of other group) showed high S_I values, computed with the G_I, with *P. microps, P. minutus* and *S. solea* (Table 3), probably due to the relatively high G_I of Polychaeta in *A. anguilla* diet (Fig. 2).

The last group of species, C. *lyra* and *M. surmuletus*, showed a similarity of about 25% (Fig. 3), mainly due to the presence of Bivalvia as a dominant prey in both fishes (Table 2). Yet, the diet of these fishes was highly diversified, leading to the observed low similarity (Fig. 2, Table 3). For these species only the S_I computed with the N_I was high (Table 3).

Fish and macrobenthic community distribution within the estuary

The different fish species in study distributed differently within the estuary, in accordance with CA results (Fig. 4). *Callionymus lyra*, *C. lucerna*, *T. luscus* and *P. minutus* occurred together and were always associated to the mouth of the estuary (M, Fig. 4A). In general, *D. labrax*, *L. ramada* and *A. boyeri* were associated to the most upstream area of south arm (S2, Fig. 4A). *Platichthys flesus* and *A. anguilla* were associated with the north arm of the estuary, especially to its most upstream area (N2, Fig. 4A). The remaining species distributed in several areas within the estuary, showing no clear preference for

Table 3 Schoener index estimated based on the numerical percentage index N_I (below -) and on the gravimetric percentage index G_I (above -); in bold values equal or above 0.6.

	A. anguilla	*A. boyeri*	*C. lyra*	*C. mustela*	*D. labrax*	*L. ramada*	*M. surmuletus*	*P. flesus*	*P. microps*	*P. minutus*	*S. rhombus*	*S. solea*	*C. lucerna*	*T. luscus*
A. anguilla	-	0.0	0.2	0.2	0.5	0.1	0.4	0.4	**0.6**	**0.6**	0.1	**0.8**	0.1	0.2
A. boyeri	0.0	-	0.0	0.0	0.1	**0.8**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C. lyra	0.1	0.0	-	0.3	0.4	0.1	**0.6**	0.2	0.4	0.3	0.2	0.4	0.2	0.3
C. mustela	0.3	0.0	0.1	-	0.5	0.1	0.4	0.1	0.1	0.3	**0.6**	0.3	**0.8**	**0.9**
D. labrax	0.1	0.5	0.3	0.1	-	0.2	**0.6**	0.4	0.5	0.5	0.4	**0.6**	0.5	0.5
L. ramada	0.1	**0.8**	0.2	0.1	**0.6**	-	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1
M. surmuletus	0.4	0.0	0.4	**0.6**	0.3	0.1	-	0.2	0.4	0.5	0.3	0.4	0.3	0.4
P. flesus	**0.9**	0.0	0.1	0.2	0.2	0.0	0.3	-	0.5	0.3	0.0	0.3	0.0	0.1
P. microps	0.3	0.0	0.5	0.2	0.5	0.1	0.5	0.4	-	0.5	0.1	0.5	0.1	0.1
P. minutus	0.2	0.0	0.4	0.2	0.4	0.1	0.3	0.2	**0.7**	-	0.3	**0.7**	0.3	0.3
S. rhombus	0.1	0.0	0.2	**0.6**	0.1	0.2	0.2	0.0	0.2	0.2	-	0.2	0.5	**0.7**
S. solea	0.2	0.0	0.3	0.1	0.5	0.1	0.3	0.2	**0.6**	**0.9**	0.1	-	0.2	0.3
C. lucerna	0.1	0.0	0.2	**0.7**	0.1	0.1	0.4	0.0	0.1	0.2	**0.6**	0.1	-	**0.7**
T. luscus	0.2	0.0	0.1	**0.6**	0.1	0.1	0.5	0.1	0.1	0.2	0.3	0.1	0.4	-

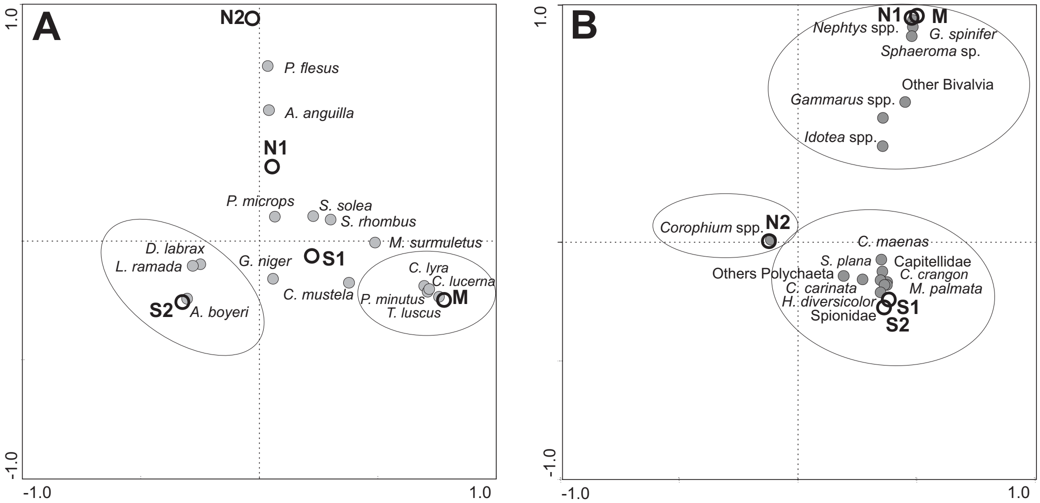


Fig. 4 Correspondence analysis of the A) fishes density and B) main macrobenthic prey, according to Q_I.

one area (Fig. 4A). In fact, *C. mustela* distributed mainly within M and S1 stations, *M. surmuletus, S. rhombus* and *S. solea* mainly within M and N1, and *P. microps* within N1 and S1 (Fig. 4A). The cumulative percentage variation of the species data, explained by the first 2 axes was 89%.

The distribution of the most predated macrobenthic items, according to their Q_I for each fish species, was also analysed with the CA. The clearest pattern was observed for *Corophium* spp. associated to the most upstream area (N2, Fig. 4B). The remaining areas were associated in pairs, sharing a similar group of species: species that distributed both in the estuary mouth and downstream the north arm (M and N1); and another group of species in the south arm (S1, S2, Fig. 4B). *Nephtys* spp., *G. spinifer* and *Sphaeroma* sp. occurred together and were clearly associated to M and N1, while *Idotea* spp., *Gammarus* spp. and other Bivalvia were also associated to those areas, but seemed to occur alone (Fig. 4B). The remaining species seemed to occur together and were associated to the south arm (Fig. 4B). The cumulative percentage variation of the species data, explained by the first 2 axes was 82%.

DISCUSSION

General considerations

Among the 14 fish species analysed, 8 showed a more specialized feeding strategy (*A. anguilla, A. boyeri, L. ramada*, *P. flesus*, *P. minutus*, *C. lucerna*, *S. solea,* and *S. rhombus*), while the others seemed more generalist feeders (*C. lyra, C. mustela, D. labrax, M. surmuletus, P. microps,* and *T. luscus*). Among the 8 specialized feeders, 3 pairs of species showed great diet and niche overlap, suggesting the possibility of interspecific competition. For the Mondego estuary, different categories of feeding guilds, according to main food resource, could be distinguished: 1) *C. lyra*, *M. surmuletus*, *P. microps*, *P. minutus*, *S. solea*, *P. flesus,* and *A. anguilla* were mainly feeding on invertebrates, both infauna and epifauna and therefore classified as invertebrate feeders (I) (although *A. anguilla*, *S. solea*, *P. flesus,* and *P. minutus* could also feed, on a small fraction of other fish, and thus be considered invertebrate and fish feeders); 2) *T. luscus, C. lucerna, S rhombus,* and *C. mustela* were feeding on both invertebrate and other fish, therefore classified as invertebrate and fish feeders; 3) *A. boyeri* and *L. ramada* fed essentially on zooplankton, therefore classified as plankton feeders, although *A. boyeri* could also feed on a small fraction of invertebrates, and *L. ramada* also on detritus, invertebrates and microalgae; and 4) *D. labrax*, besides eating invertebrates also fed on plankton, and therefore it was considered as plankton and invertebrate feeder. Slight differences were found regarding the classification of Elliott & Dewailly (1995) for the same species, which may be related with the ontogeny of the captured fish (Warburton & Blaber 1992, Hamper et al. 2005, Akin & Winemiller 2006), since most of the *S. solea, P. flesus* and *D. labrax* individuals were mainly young individuals (less than 1 year old). For the entire community, the dominance of invertebrate and invertebrate/fish feeding guilds is in agreement with the dietary preferences of typical European systems (Elliott & Dewailly 1995, Mathieson et al. 2000).

Potential competition for food resources

It is difficult to assess whether the fish distribution and composition in an estuary is determined primarily by physical aspects or by biological ones, such as resource partitioning and predation (Thorman & Widerholm 1986, Elliott et al. 2002). It has been argued that in unstable environments such as estuaries, the unpredictability of the abiotic factors keeps the living populations below their carrying capacity for food, therefore excluding competition (Thorman & Widerholm 1986). For the Mondego estuary competition could not be concluded, although several species showed some degree of diet overlap. The estuary seems highly productive, at least its south arm (Dolbeth et al. 2003, 2007a), yet, this study did not assess whether the consumption by fish was much lower than the food production in order to exclude competition (Edgar & Shaw 1995). Also, not all the most productive invertebrates were intensively consumed by fish (e.g. *H. ulvae*, Dolbeth et al. 2003, 2007a) and prey availability may be also reduced due to behavioural patterns (e.g. burrowing, Robertson 1984, Eriksson et al. 2005). C*rangon crangon* was one of the most preyed items, whose production compared to other systems has been considered low (Viegas et al. 2007), which could lead to competition among fishes for this resource. However, predation is probably high, judging by the piscivorous fish found in the present study and by the potential high predation pressure found at larvae/juveniles stages of several fishes by crabs (Baeta et al. 2005), shrimps and other fish (Vinagre et al. 2006), which may reduce the competition within the species (Evans 1983).

Most fishes seemed to distribute primarily in accordance to their salinity preferences (Martinho et al. 2007b), with the search for a specific food resource probably a secondary aspect as fish showed some degree of opportunism in their feeding strategies. However, in some occasions, the avoidance for competition, combined with higher tolerance to environmental changes, may have prevailed. Although *P. microps* and *P. minutus* fed on the same resources (with high diet overlap), they distributed in different estuarine areas, probably excluding competition, as also studied in more detailed by Leitão et al. (2006) and Dolbeth et al. (2007b). *Solea solea* also showed high diet overlap with the former species, but again distributed in different estuarine areas. Also, it has been argued that juvenile flatfishes consume the most abundant food resources in an opportunistic way, which strongly reduces the potential for competition in highly productive systems such as estuarine habitats (Cabral et al. 2007).

Other groups of fishes in the community shared the same food resources (Fig. 5), having a high diet and niche overlap, as they distributed in similar areas. Nevertheless, one of the fish could have a wider diet breadth, excluding to some extent the possibility of competition for food resources. Such pattern occurred with *A. boyeri* and *L. ramada*, feeding essentially on calanoid copepods and distributing in the south arm, near the Pranto river. Their distribution areas agreed with the food resource availability, since a major part of zooplankton within the estuary is concentrated in those areas (Marques et al. 2006). Yet, *L. ramada* presented wider diet breadth, feeding also in algae and detritus. *Dicentrarchus labrax* was also found preferentially near the Pranto river, but fed only occasionally on Copepoda (more intensive feeding with the youngest individuals, Warburton & Blaber 1992, Hampell et al. 2005) and present a wider diet range (Fig. 5). *Anguilla anguilla* and *P. flesus* fed preferentially on *Corophium* spp. (Fig. 5), retaining high diet overlap. In agreement, strong niche overlap was also observed, as the fishes distributed intensively in the areas of the highest concentration of *Corophium* spp. populations, i.e., the most upstream area of the estuary. Yet, *A. anguilla* could also feed intensely on polychaetes.

According to the results of the subtidal macrobenthic community sampled with the Van Veen grab, *C. crangon* was associated to inner areas of estuary. A detailed study on the *C. crangon* population, sampled with the beam trawl, showed that the greatest abundances of this species were concentrated at the mouth of the estuary (Viegas et al., 2007). In agreement, the highest densities of *T. luscus, C. lucerna, S. rhombus,* and *C. mustela,* all feeding on *C. crangon* (Fig. 5), were also found at the estuary mouth and showed some degree of food overlap. Yet, all species also fed on other items, showing some degree of opportunism in the feeding strategy (Fig. 5).

Simplified Food Web

Most of the feeding resources used by the fish community were components of the macrobenthic community, followed by zooplankton and other fish (Fig. 5). According to the main prey, the contribution of the highly productive intertidal areas of the Mondego estuary (Dolbeth et al. 2003, 2007a) is probably large, as also hypothesised for other estuaries (Gorman & Raffaelli 1993, Moreira et al. 1992, Cabral 2000, Elliott et al. 2002, Vinagre et al. 2006), combining the contribution of both bare mudflats and saltmarshes (Hampell et al. 2005). In the Mondego estuary, the intertidal areas may contribute for the food webs either by generating food resources (several polychaetes, molluscs, among others), or by feeding other intermediate levels in the trophic web, such as *C. maenas* (Baeta et al. 2006), *C. crangon* and *Nephtys* spp. (Elliott et al. 2002, McLusky & Elliott 2004).

A great part of the biomass/energy produced by the intertidal benthos arises via the detritus food chains, as detritivores are among the dominant productive trophic group, with a smaller contribution from the grazing generated food chains (Dolbeth et al. 2003, Cardoso et al. 2004, Patrício & Marques 2006). In agreement, several of the main prey of the subtidal community are deposit feeders, such as the highly abundant *Corophium* spp. (McLusky & Elliott 2004). These patterns are agree with the ones found in several estuarine food webs, which are chiefly initiated by detritus energy sources (and attached bacteria) available constantly throughout the year, and to a lower extent by

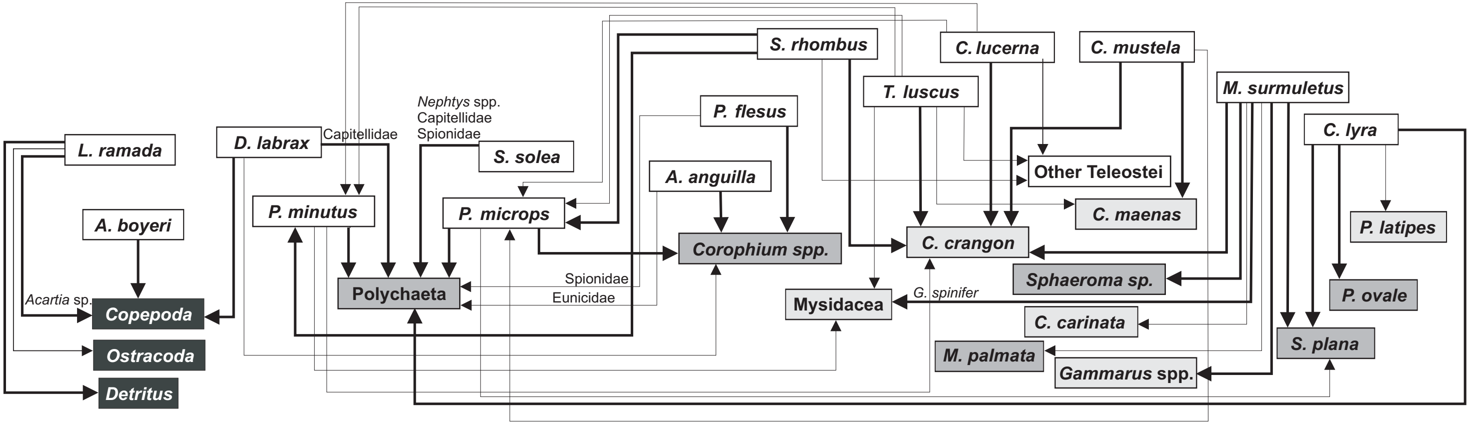


Fig. 5 Generalised food web of the main fish species of the Mondego estuary. Thick arrows, dominant prey; thin arrows, secondary prey according to Q_I; light grey prey boxes, carnivores and omnivores (*Nephtys* spp. and Eunicidae belonging to this group); dark grey prey boxes, detritivores and herbivores.

phytoplankton, benthic algae or macroalgae energy sources (seasonally and spatially variable) (Whitfield 1999, Mathieson et al. 2000, Elliott et al. 2002, Akin & Winemiller 2006, Svensson et al. 2007). Benthos, zooplankton, micronekton or even detritivorous fish follow in the food chains as the secondary trophic levels (Whitfield 1999, Elliott et al. 2002).

Similarly to other food webs (e.g. Humber, Cádiz and Tagus estuaries, Elliott et al. 2002; Ria Formosa, Gamito et al. 2003, Guadina, Sá et al. 2006), some general characteristics were also observed in the Mondego estuary's simplified food web: 1) fishes had some degree of opportunism in feeding; 2) certain prey played a central role in supporting the estuarine fishes. In fact, although some fish seemed to prefer a certain food item, they could also feed on other prey, reflecting opportunist behaviour (Fig. 5). These findings were similar to the ones of Elliott et al. (2002) and Gamito et al. (2003), who also conclude a generalist feeding behaviour of several estuarine fishes. In addition, some species that seemed to have a more specialized diet, such as *L. ramada* and *A. anguilla*, also fed significantly on other items besides their dominant prey (Fig. 5). Regarding the prey playing a central role in supporting the estuarine fishes, the present study revealed Polychaeta (e.g. *Nephtys* spp., Capitellidae, Spionidae, Eunicidae), *Corophium* spp., C*rangon crangon* and *Pomatoschistus* spp. as the most important. These prey were feeding the most abundant fish species of the Mondego estuary or assigned as dominant prey in several fishes (Fig. 5), similarly to other estuarine systems (Moreira et al. 1992, Hampel et al. 2005, Sá et al. 2006). The loss of these key species could therefore have important implications for the conservation of the estuary. The group Copepoda was important for the planktonic fish (and for the youngest fish). The main prey species may differ from other trophic web studies (e.g. gammarids and mysids for the Humber estuary), yet almost all are preponderant in stating the key role of epi-benthic crustaceans as an important link between benthos and fish (Edgar & Shaw 1995, Whitfield 1999, Elliott et al. 2002, Gamito et al. 2003, Sá et al. 2006). For the Mondego estuary, infaunal prey such as polychaetes had also a great importance, as they were dominant prey for the most abundant species in the Mondego estuary (i.e, *D. labrax, S. solea, P. minutus* and *P. microps*, Martinho et al. 2007b). Yet, these were not key prey in other food webs (e.g. Gamito et al. 2003).

Relatively few trophic paths (short chains) seem to occur in the fish community of the Mondego estuary (Fig. 5) (even when added the basal resources such as detritus, phytoplankton), similarly to the findings of Whitfield (1999). However, the wide range of possible interconnections within prey and predators (Fig. 5), reflecting some degree of opportunistic feeding, is probably a fundamental aspect allowing survival in the estuarine environment, as also claimed by Warburton & Blaber (1992), Elliott et al. (2002) and Gamito et al. (2003).

ACKNOWLEDGEMENTS

The authors are indebted to all colleagues who assisted in field work, to Daniel Nyitsai for his help in the laboratory work and to Sónia Cotrim for her help with the identification of zooplankton.

REFERENCES

Able KW (2005) A re-examination of fish estuarine dependence: Evidence for connectivity between estuarine and ocean habitats. Estuar Coast Shelf Sci 64: 5–17.

Akin S, Winemiller KO (2006) Seasonal variation in food web composition and structure in a temperate tidal estuary. Estuar Coast 29 (4): 552–567.

Baeta A, Cabral HN, Neto JM, Marques JC, Pardal MA (2005) Biology, population dynamics and secondary production of the green crab *Carcinus maenas* (L.) in a temperate estuary. Estuar Coast Shelf Sci 65: 43–52

Baeta A, Cabral HN, Marques JC, Pardal MA (2006) Feeding ecology of the green crab, *Carcinus maenas* (L. 1758) in a temperate estuary, Portugal. Crustaceana 79: 1181–1193

Cabral H (2000) Comparative feeding ecology of sympatric *Solea solea* and *S. senegalensis*, within the nursery areas of the Tagus estuary, Portugal. J Fish Biol 57: 1550–1562.

Cabral NH, Vasconcelos RP, Vinagre C, França S, Fonseca V, Maia A, Reis-Santos P, Lopes M, Ruano M, Campos J, Freitas V, Santos P, Costa MJ (2007) Relative importance of estuarine flatfish nurseries along the Portuguese coast. J Sea Resear 57: 209–217.

Cardoso PG, Pardal MA, Lillebø AI, Ferreira SM, Raffaelli D, Marques JC (2004) Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. J Exp Mar Biol Ecol 302: 233–248

Dolbeth M, Pardal MA, Lillebø AI, Azeiteiro UM, Marques JC (2003) Short and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. Mar Biol 143: 1229–1238.

Dolbeth M, Cardoso PG, Ferreira SM, Verdelhos T, Raffaelli D, Pardal MA (2007a) Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a ten-year period. Mar Pollut Bull 54: 576–585.

Dolbeth M, Martinho F, Leitão R, Cabral H, Pardal MA (2007b) Strategies of *Pomatoschistus minutus* and *Pomatoschistus microps* to cope with environmental instability. Estuar Coast Shelf Sci 74: 263–273.

Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow water fish assemblages in southern Australia. II. Diets of fishes and trophic relationships between fish and benthos at Western Port, Victoria. J Exp Mar Biol Ecol 194: 83–106.

Elliott M, Dewailly F (1995) The structure and components of European estuarine fish assemblages. Neth J Aquat Ecol 29: 397–417.

Elliott M, Hemingway KL, Costello MJ, Duhamel S, Hostens K, Labropoulou M, Marshall S, Winkler H (2002) Links between fish and other trophic levels. In: Elliot M, Hemingway K (Eds) Fishes in estuaries. Blackwell Science, Bodmin, United Kingdom, p 124–216.

Eriksson SP, Wennhage H, Norkko J, Norkko A (2005) Episodic disturbance events modify predator-prey interactions in soft sediments. Estuar Coast Shelf Sci 64: 289–294.

Evans S (1983) Production, predation and food niche segregation in a marine shallow soft-bottom community. Mar Ecol Prog Ser 10: 147–157.

Gamito S, Pires A, Pita C, Erzini K (2003) Food availability and the feeding ecology of ichthyofauna of a Ria Formosa (south Portugal) water reservoir. Estuaries 26: 938–948.

Gorman ML, Raffaelli D (1993) Classic sites - The Ythan estuary. The Biologist 40: 10–13.

Hall SJ, Raffaelli D (1991) Food-web patterns: lessons from a species rich web. J Anim Ecol 60: 823–842.

Hampel H, Cattrijsse A, Elliott M (2005) Feeding habits of young predatory fishes in marsh creeks situated along the salinity gradient of the Schelde estuary, Belgium and The Netherlands. Helgol Mar Res 59: 151–162

Horta M, Costa MJ, Cabral H (2004) Spatial and trophic niche overlap between *Diplodus bellottii* and *Diplodus vulgaris* in the Tagus estuary, Portugal. J Mar Biol Ass UK 84: 837–842

Hyslop EJ (1980) Stomach contents analysis: a review of methods and their application. J Fish Biol 17: 415–429.

Leitão R, Martinho F, Neto JM, Cabral H, Marques JC, Pardal MA (2006) Feeding ecology, population structure and distribution of *Pomatoschistus microps* (Krøyer, 1838) and *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. Estuar Coast Shelf Sci 66: 231–239.

Linton RL, Davies RW, Wrona FJ (1981) Resource utilization indices; an assessment. J Anim Ecol 50: 283–293.

Marques SC, Azeiteiro UM, Marques JC, Neto JM, Pardal MA (2006) Zooplankton and ichthyoplankton communities in a temperate estuary: spatial and temporal patterns. J Plankton Res 28: 297–312.

Marshall S, Elliott M (1997) A comparison of univariate and multivariate numerical and graphical techniques for determining inter- and intraspecific feeding relationships in estuarine fish. J Fish Biol 51: 526–545.

Martinho F, Leitão R, Neto J, Cabral HN, Marques JC, Pardal MA (2007a) The use of nursery areas by juvenile fish in a temperate estuary, Portugal. Hydrobiologia 587: 281–290.

Martinho F, Leitão R, Viegas I, Dolbeth M, Neto JM, Cabral HN, Pardal MA (2007b) The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. Estuar Coast Shelf Sci doi:10.1016/j.ecss.2007.05.040.

Mathieson S, Cattrijsse A, Costa MJ, Drake P, Elliott M, Gardner J, Marchand J (2000) Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. Mar Ecol Prog Ser 204: 225–242.

Moreira F, Assis CA, Almeida PR, Costa JL, Costa MJ (1992) Trophic relationships in the community of the upper tagus estuary (Portugal): a preliminary approach. Estuar Coast Shelf Sci 34: 617–623.

McLusky DS, Elliott M (2004) The estuarine ecossystem. Ecology, threats and management. 3rd Edition. Oxford, University Press, United Kigdom, p 213.

Patrício, J., Marques, J.C., 2006. Mass balanced models of the food web in three areas along a gradient of eutrophication symptoms in the south arm of the Mondego estuary (Portugal). Ecol Model 197: 21–34.

Robertson AI (1984) Trophic Interactions between the fish fauna and macrobenthos of an eelgrass community in Western Port, Victoria. Aquat Bot 18: 135–153.

Sá R, Bexiga C, Veiga P, Vieira L, Erzini K (2006) Feeding ecology and trophic relationships of fish species in the lower Guadiana River Estuary and Castro Marim and Vila Real de Santo António Salt Marsh. Estuar Coast Shelf Sci 70: 19–26.

Svensson CJ, Hyndes GA, Lavery PS (2007) Food web analysis in two permanently open temperate estuaries: Consequences of saltmarsh loss? Mar Environ Res 64: 286-304.

Ter Braak CJF (1988) CANOCO – a Fortran Program for Canonical Community Ordination by Partial Detrended Canonical Correspondence Analysis, Principal Components and Redundancy Analysis. Agricultural and Mathematical Group, Wageningen, The Netherlands.

Thorman S, Widerholm AM (1986) Food, habitat and time niches in a coastal fish species assemblage in a brackish water bay in the Bothnian Sea, Sweden. J Exp Mar Biol Ecol 95: 67–86.

Viegas I, Martinho F, Neto JM, Pardal MA (2007) Population dynamics, distribution and secondary production of the brown shrimp C*rangon crangon* (L.) in a southern European estuary – latitudinal variations. Scient Mar 71: 451–460.

Vinagre C, França S, Cabral HN (2006) Diel and semi-lunar patterns in the use of an intertidal mudflat by juveniles of Senegal sole, *Solea senegalensis*. Estuar Coast Shelf Sci 69: 246-254.

Warburton K, Blaber SJM (1992) Patterns of recruitment and resource use in a shallow-water fish assemblage in moreton Bay, Queensland. Mar Ecol Prog Ser 90: 113–126.

Whitfield AK (1999) Ichthyofaunal assemblages in estuaries: a South African case study. Rev Fish Biol Fish 9: 151–186.

CHAPTER IV

Estuarine fish production

Estuarine production of resident and nursery fish species: conditioning by drought events?

Estuarine production of resident and nursery fish species: conditioning by drought events?

Abstract The production of resident (*Pomatoschistus minutus* and *Pomatoschistus microps*) and marine juvenile fish species using the Mondego estuary (central Portugal) as nursery grounds (*Dicentrarchus labrax*, *Platichthys flesus*, *Solea solea*), was assessed in order to: 1) understand the potential of the estuary for fish production; 2) know the production of nursery fish species likely to be exported to the coastal stocks; and 3) how anthropogenic and natural stress could influence the estimated production. Sampling occurred from June 2003 to May 2006 and together the studied species comprised around 70% of all the fish community numbers and biomass. Increasing drought conditions were observed, starting by a normal hydrological year in 2003 until attaining a severe drought in 2005, which resulted in low river discharges. Additionally, high water temperatures were observed. The secondary production was estimated using the increment summation method, after recognition of the cohorts. Production was in general lower in the Mondego estuary when compared to other systems, which was associated to the estuary's small area. *Dicentrarchus labrax* was among the most productive species. Production decreased in the drought year for all species, especially evident for *D. labrax, P. minutus and P. flesus*. No direct effects could be attributable to the salinity and temperature variations and to the low freshwater discharges (resulting from the drought and high temperatures), yet these were pointed as probable major reasons for the decreased production. A significant reduction was also concluded for the potential production to be exported for coastal areas by the nursery species in the drought conditions.

Keywords Fish production, Resident species, Nursery species, Drought, Mondego estuary

INTRODUCTION

Estuarine systems are extremely valuable for many marine fish species of the continental shelf, by providing important nursery grounds (Cabral et al. 2007, Martinho et al. 2007a, Nicolas et al. 2007), as well as for several other fishes, such as the resident ones, spending their complete life cycle within the estuary (Elliott & Dewailly 1995, Dolbeth et al. 2007a). Frequently, these two ecological fish guilds (marine juvenile and resident) represent the major part of the fish community found in estuarine systems (Elliott & Dewailly 1995, Martinho et al. 2007b). The juvenile growth and survival of the marine species, hence recruitment into adult populations, and the maintenance of the resident species within the estuarine ecosystem are greatly determined by its environmental quality, regarding both anthropogenic stress and natural variability (Nicolas et al. 2007). The availability of essential habitats (such as seagrasses and saltmarshes), providing protection from predators, and their great production, providing abundant food supplies, are considered as major determinants for fishes in estuaries (Beck et al. 2001, Cabral et al. 2007, Martinho et al. 2007a). Several of the marine juvenile fishes that occur in estuaries are commercially important, hence estuaries may be considered as essential ecosystems for the renewal of fisheries resources, acquiring also a direct relevant economic value for mankind (Houde & Rutherford 1993, Cowley & Whitfield 2002, Able 2005, Nicolas et al. 2007). Regarding resident species, their role as intermediates in the estuarine food web turns them crucial for the overall dynamics and functioning of the estuarine system (Leitão et al. 2006, Dolbeth et al. 2007a). Yet, estuarine areas are highly affected by human activities such as habitat reclamation, water quality impoverishment and fishing activities (Cabral et al. 2007, Vasconcelos et al. 2007) and are known by their high natural environmental variability (Maes et al. 2004, Elliott & Quintino 2007). In this perspective, understanding the potential of estuarine areas for these fishes production and the influence of external environmental or anthropogenic impacts on that production becomes quite relevant. This information may be useful as a tool to support protection measures and ensure resource sustainability, or for the study of the overall estuarine ecological integrity. In fact, production estimates integrate the influence of numerous biotic variables and environmental conditions affecting individual growth and population mortality (Cusson & Bourget 2005, Dolbeth et al. 2005). Therefore, production studies have been used to assess the impacts of natural and anthropogenic stressors (Cardoso et al. 2005, Dolbeth et al. 2005, 2007b), in ecosystem modelling studies (energy budgets and flows, Patrício & Marques 2006, Gamito & Erzini 2005), and for fish assemblages have been used more frequently to assess the potential yields for fishery species (Houde & Rutherford 1993, Wilson 2002, Pombo et al. 2007).

The present study aims to estimate the secondary production of the resident and marine juvenile fish species of the Mondego estuary (central Portugal). More specifically, it aims to understand: 1) the productive potential of the estuary for the fish resources, and ultimately for other consumers; 2) the production potential to be exported by the marine juveniles to the coastal stocks (infer on the production produced in the estuary transferred to the coastal areas); and 3) how anthropogenic and natural stress influence the production estimates.

MATERIALS AND METHODS

Study area

The Mondego estuary (Portugal) is located in a warm temperate region, on the Atlantic coast of Portugal (40°08'N, 8°50'W) (Fig. 1). It is a small estuary (3.4 km^2 area), with two arms (north and south) of distinct hydrologic characteristics. The north arm is deeper (4-10 m during high tide, tidal range 1-3 m), it is a main navigation channel and is the location of the Figueira da Foz harbour. Besides the severe changes imposed by the construction of harbour facilities, constant dredging and shipping occurs in this area, causing physical disturbance of the bottom. The main freshwater input to the north arm is from the Mondego river. The south arm is shallower (2-4 m during high tide, tidal range 1-3 m), characterized by large areas of exposed intertidal flats during low tide (about 75% of total area). Water circulation in the south arm mostly depends on the tides and on the freshwater input from the Pranto river (Fig. 1), as the upstream areas are almost silted up, with only a small connection with north arm. The Pranto river is controlled by a sluice according to the water needs in the rice fields of Mondego valley. The downstream areas of the south arm are relatively unchanged, with *Spartina maritima* marshes and a *Zostera*

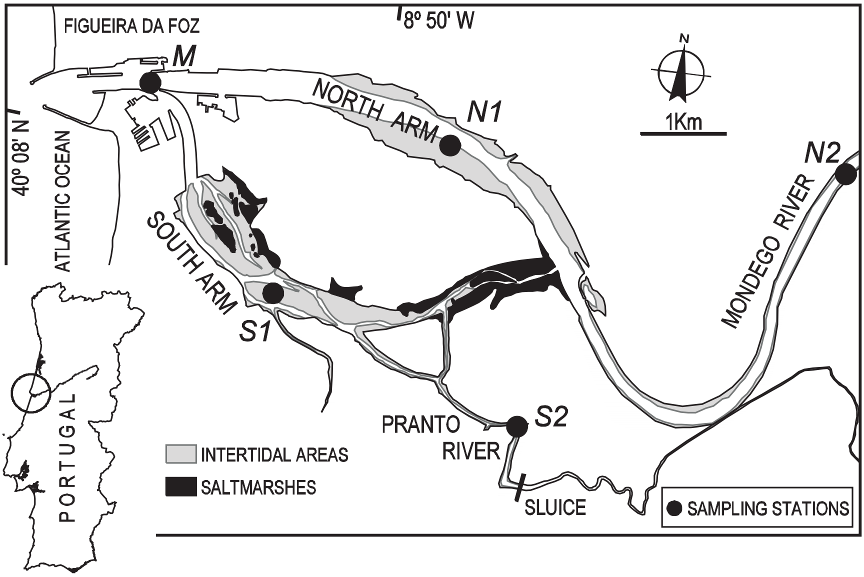


Fig. 1 The Mondego estuary, with indication of the sampling stations, intertidal area and saltmarshes.

noltii meadow, but in the inner parts the seagrass community has completely disappeared, mainly due to severe eutrophication problems occurring in the past. In 1998/1999 mitigation measures were taken to reduce the nutrient loading and the system seems to be gradually recovering (for further details see Cardoso et al. 2005, Dolbeth et al. 2007b).

Sampling procedures

From June 2003 to May 2006 fish were collected monthly, using a 2 m beam trawl, with one tickler chain and 5 mm stretched mesh size in the cod end. Sampling was carried out during the night, at the ebbing tide of spring tides, in five stations (M, S1, S2, N1, N2, Fig. 1): M - at 1.5 km from the estuary's mouth, 8.7 ± 1.2 m deep, area subjected to constant dredging; S1 - located upstream a *Z. noltii* bed, 2.3 ± 0.4 m deep; S2 - near the Pranto river sluices, which controls the main freshwater flow from Pranto river to the south arm, 2.4 ± 1.0 m deep; N1 – with regular freshwater flow, 5.5 ± 0.5 m deep; N2 - most upstream area, with lower saline influence and permanent freshwater flow from the Mondego river, 4.5 ± 0.3 m deep. Each survey consisted of three hauls, at each sampling station, in a total of 10 to 15 min duration per station. All fish caught were identified, measured (total length, with 1 mm precision) and weighted (wet weight – WW, with 0.001 g precision). A detailed description of the community structure is provided in Martinho et al. (2007b). Due to the amount of data required for the production estimates, only the most abundant fish species, along the surveyed period, were used in the present study, i.e. the marine juveniles using the estuary as nursery grounds – nursery species, *Dicentrarchus labrax*, *Platichthys flesus*, *Solea solea* and the residents *Pomatoschistus minutus* and *P. microps*, which live in the estuary throughout their life cycle (nursery and resident ecological guilds, adapted from Elliott & Dewailly 1995, and according to Martinho et al. 2007b).

In each sampling station, hydrological data was registered and bottom water parameters were measured. Precipitation values were acquired in the Casal do Rato 13D/04UG station, from INAG – Portuguese Water Institute (available in www.snirh.inag.pt),. Freshwater runoff was acquired from INAG station Açude Ponte Coimbra 12G/01A, near the city of Coimbra (located 40 km upstream).

Secondary production

The population structure of each species was defined by tracking recognizable cohorts from the successive sampling dates. Spatial samples were pooled together and analyzed through size frequency distribution of successive sampling dates. For *D. labrax, P. flesus and S. solea* the cohorts were determined using FAOICLARM Stock Assessment Tools (FiSAT software, provided in http://www.fao.org/fi/statist/fisoft/fisat/index.htm). For *P. minutus* and *P. microps*, as the class interval for the length frequency analyses was lower than 0.25 cm, ANAMOD software package was used, which provided the modes and their standard deviation, and checked the reliability of the estimated parameters. This analysis is described in Dolbeth et al. (2007a).

After recognition of the cohorts, the annual production was estimated by the cohort increment summation method (Winberg 1971), according to:

$$P_{cn} = \sum_{t=0}^{T-1} \left(\frac{N_t + N_{t+1}}{2} \right) \times \left(\overline{w}_{t+1} - \overline{w}_t \right)$$

where P_{cn} is the growth production (g WW m^{-2} y^{-1}) of cohort n; N is the density (ind m^{-2}); $\overline{w}$ is the mean individual weight (g WW m^{-2}); and t and t+1, consecutive sampling dates. Population production estimates correspond to the sum of each cohort production (P_{cn}). Negative production values were not accounted for the overall fish estimates, which were regarded as no production.

The mean annual biomass ($\overline{B}$) was estimated according to:

$$\overline{B} = \left(\frac{1}{T} \right) \times \sum_{n=1}^{Nc} \left(\overline{B}_{cn} t_{cn} \right)$$

where T is the period of study, which is always 365 days (yearly cycles) as the mean annual biomass is being computed; Nc is the number of cohorts found in the study period; $\overline{B}_{cn}$ is the mean biomass (g WW m^{-2}) of cohort n; t_{cn} is the time period of the cohort n (days), from the first appearance of individuals until they disappeared.

RESULTS

Environmental background

From June 2003 to May 2006, precipitation showed unusual variations when compared to the mean precipitation regime for central Portugal observed during the period of 1940-1997 (annual precipitation values of 1030 mm, INAG - http://snirh.inag.pt) (Fig. 2A). All years had lower annual precipitation values when compared to the 1940-1997 mean, especially in 2004 and 2005, considered as dry

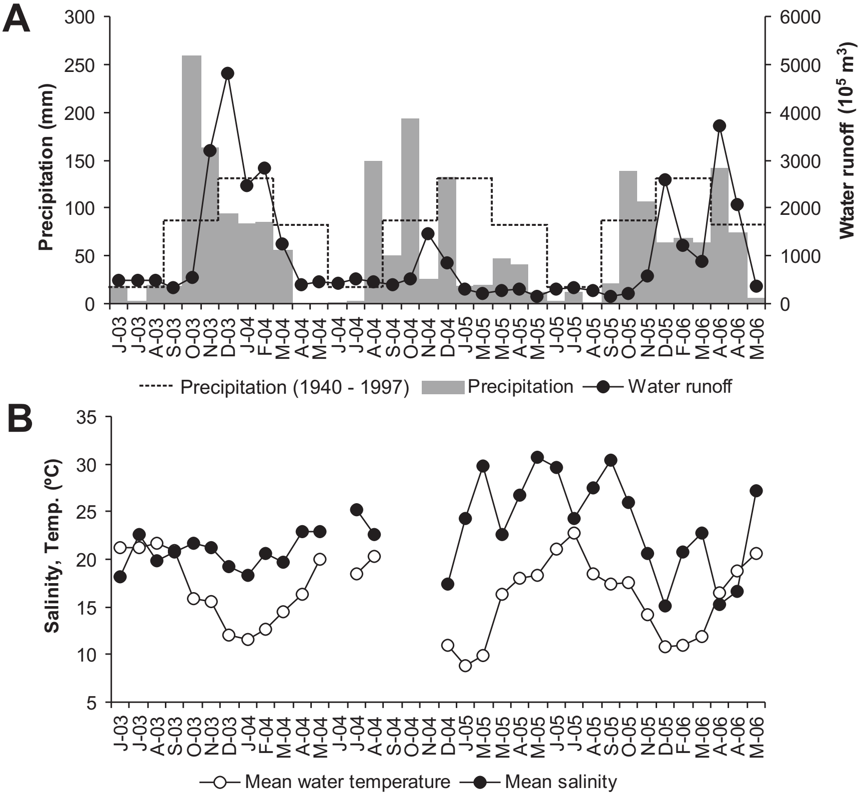


Fig. 2 Temporal variations of A) precipitation during the study period and mean precipitation for central Portugal during the period of 1940-1997 and freshwater runoff to the Mondego estuary; B) mean estuarine water temperature and mean estuarine salinity of the whole Mondego estuary.

years. The lowest annual precipitation was observed in 2005 (486.1 mm), with below–mean precipitation periods quite evident - extreme drought. The freshwater flow had a severe reduction in 2005, with values considerably lower than the ones observed in 2003 and 2006 (Fig. 2A). Consequently, the mean estuarine salinity was highly variable, with the highest mean estuarine values observed in 2005 (Fig. 2B). Detailed information on the salinity variations in the different sampling stations (including salinity anomalies) is reported in Marques et al. (2007). Water temperature showed variations usually found in temperate systems. In July 2003 and July 2005 higher temperatures were observed when compared to the same period in 2004 (Fig. 2B). More information on the environmental and hydrological parameters (e.g. dissolved oxygen, pH, water transparency, chlorophyll *a*) is reported in Dolbeth et al. (2007a) and Marques et al. (2007).

Fish density, biomass and production

Mean annual density, biomass and production of the community estimates showed a clear decreasing trend along the study period for the fish species in study, with the highest values observed in 2003/04, almost two-fold the values occurring in 2005/06 (Table 1). For each species alone, this tendency was maintained for the mean density values, yet both *P. flesus* and *S. solea* had higher production values in 2004/05 than in the other years (Table 1). *Pomatoschistus microps* maintained similar values of mean biomass and production throughout the three-year study period (Table 1). Comparing all species, the highest production values, highest mean density and biomass were observed for *D. labrax* (except for the mean biomass in 2005/06). *Solea solea* was the second most productive species, with the highest production obtained in 2004/05 (Table 1). The resident species *P. minutus* and *P. microps* had the lowest mean biomass values and the lowest production estimates (Table 1). In fact, *P. microps* was the least productive species, although it attained high densities (Table 1). The $P/\overline{B}$ ratios ranged from 1.3 (for *P. minutus*) to 3.9 (for *S. solea*), with no clear tendency variation (Table 1). *Pomatoschistus microps* was the only species that maintained similar $P/\overline{B}$ ratios through the three-year study period (Table 1).

The trend of the annual production values was clarified with the study of production tendency along the three-year study period (Fig. 3). The highest production peaks were observed for *D. labrax* in 2003 and later by the end of 2004 and beginning of 2005, while the production in 2005/06 was lower (Fig. 3A). For *S. solea* the highest peaks were observed by the end of 2004 and in 2005, yet after these peaks there was a drastic decrease in production (Fig. 3C). *Platichthys flesus* was the least productive species of the nursery species. Its production maintained similar values throughout the study period, with exception of May 2004 and from June to December 2005, where production decreased considerably (Fig. 3B). The production of the resident species was at least three-fold lower than the nursery species one. *Pomatoschistus minutus* showed the highest increases of production in 2003/04, decreasing afterwards to considerably lower values from 2005 until the end of the study period (Fig. 3D). *Pomatoschistus microps* had the highest production values in 2003 and in the winter of 2004/05 (Fig. 3E).

Table 1 Annual mean density (Ind m^{-2}), mean biomass (g WW m^{-2}), production (g WW $m^{-2}y^{-1}$) and $P/\overline{B}$ ratios for each species and the fish community in study. Between brackets production values after correction for the catch efficiency of the beam trawl (3.333).

	D. labrax	*P. flesus*	*S. solea*	*P. minutus*	*P. microps*	All
Density (Ind m^{-2})						
2003/06	0.0150	0.0025	0.0024	0.0076	0.0088	0.036
2004/05	0.0031	0.0017	0.0012	0.0011	0.0083	0.015
2005/06	0.0029	0.0005	0.0013	0.0017	0.0046	0.011
Biomass (g WW m^{-2})						
2003/06	0.10	0.05	0.07	0.005	0.0013	0.22
2004/05	0.08	0.05	0.06	0.002	0.0013	0.19
2005/06	0.04	0.02	0.09	0.001	0.0010	0.15
Production (g WW m^{-2} y^{-1})						
2003/06	0.44 *(1.47)*	0.11 *(0.38)*	0.19 *(0.65)*	0.017 *(0.056)*	0.0036 *(0.012)*	0.77 *(2.57)*
2004/05	0.20 *(0.67)*	0.13 *(0.42)*	0.24 *(0.78)*	0.004 *(0.012)*	0.0030 *(0.011)*	0.57 *(1.91)*
2005/06	0.14 (0.48)	0.07 *(0.22)*	0.19 (0.63)	0.002 (0.005)	0.0030 *(0.010)*	0.39 *(1.31)*
$P/\overline{B}$ (y^{-1})						
2003/06	4.3	2.3	3.0	3.3	2.7	3.5
2004/05	2.5	2.8	3.9	2.1	2.4	3.1
2005/06	3.2	3.6	2.1	1.3	2.9	2.6

Recruitment and potential production for exportation of nursery fish species

For *D. labrax* recruitment occurred systematically in June of all years (Fig. 4A). Individuals stayed in the estuary until at least 18-19 months (see cohorts C2, C3 and C4), disappearing afterwards by the end of January to February, with 20-25 cm (Fig. 4A). After this period, only few and larger individuals were found, suggesting an occasional return to the estuary (between 2 and 3 years old, Fig. 4A). Comparing the mean annual production of cohorts C3 and C4, the only ones whose complete development in the estuary could be followed, C3 showed a noticeably higher production than C4 (Fig. 4A). The lack of a significant part of the other cohorts (only the larger individuals in C2 and only the juveniles in C5) does not enable to have a comparable measure of their productive potential and exportation (Fig. 4A). This procedure was followed for the other species (Fig. 4). Yet, the mean monthly production for the same selected time period

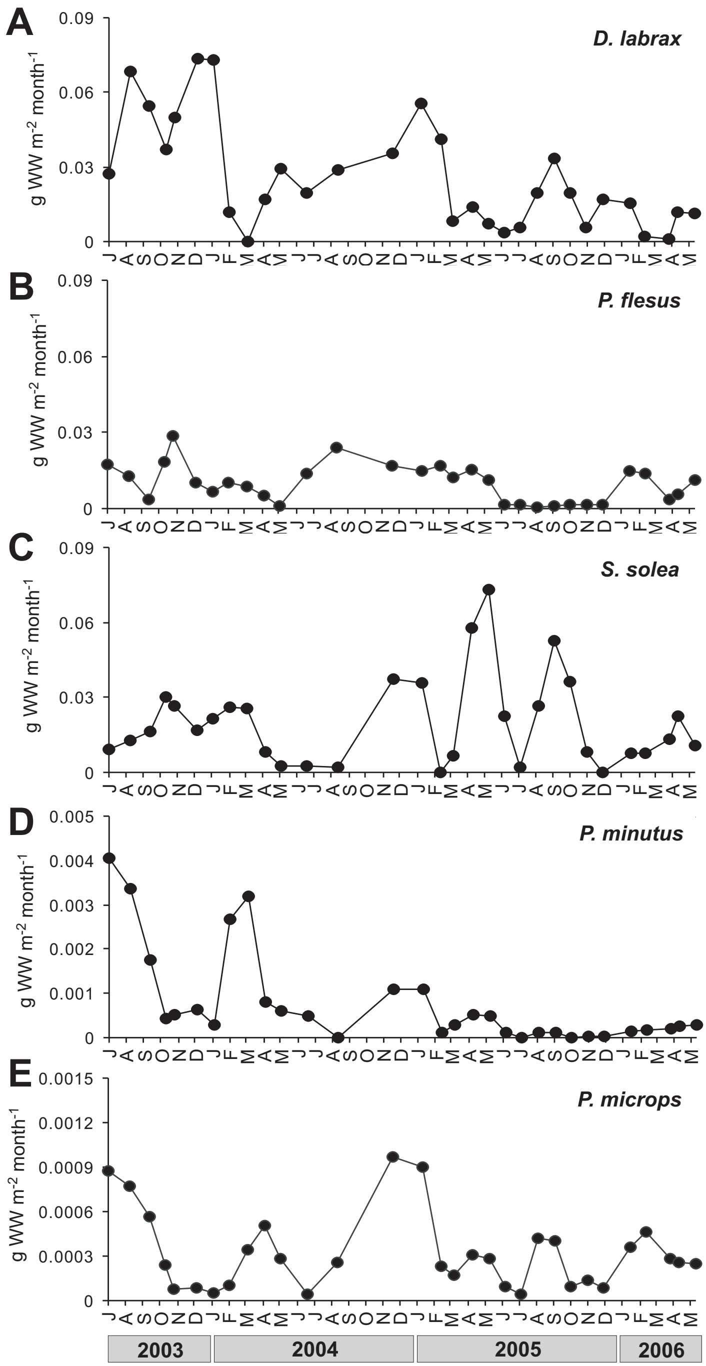


Fig. 3 Monthly variation of production along the three-year study period for: A) *Dicentrarchus labrax*, B) *Platichthys flesus*, C) *Solea solea*, D) *Pomatoschistus minutus*, and E) *Pomatoschistus microps*.

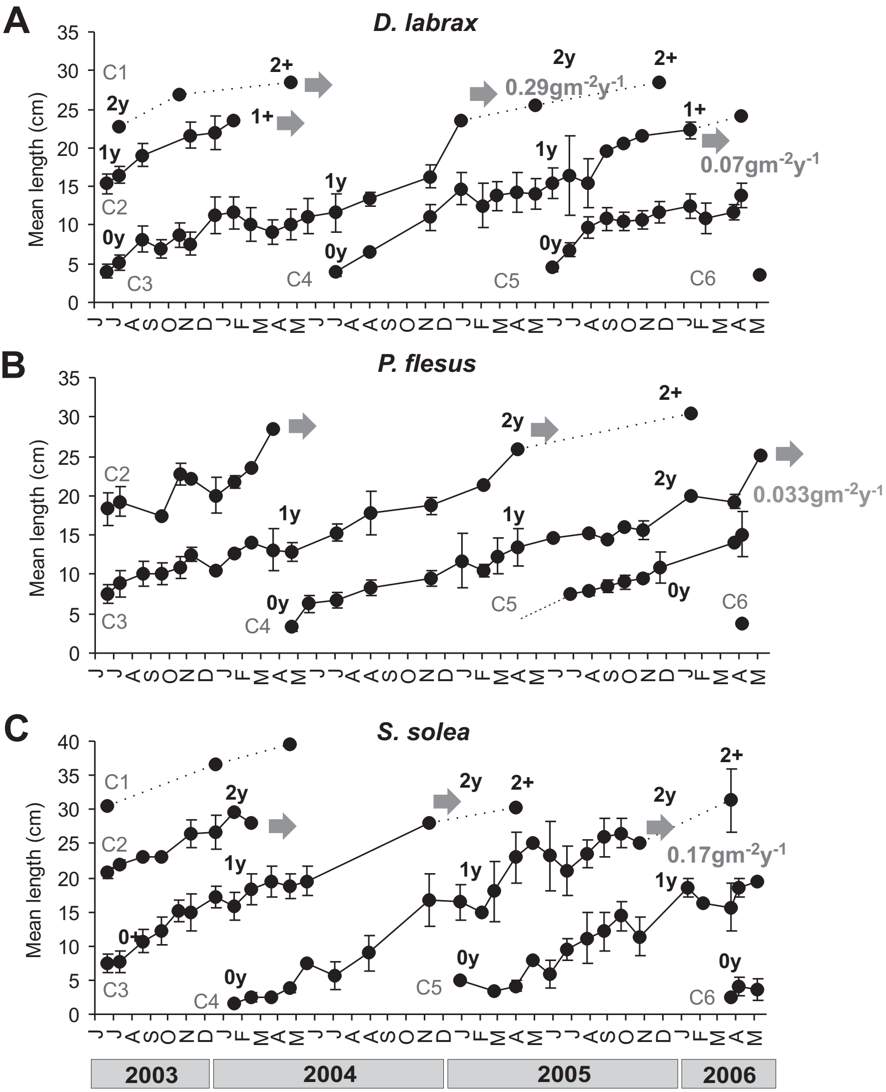


Fig. 4 Linear growth of the nursery species (*Dicentrarchus labrax*, *Platichthys flesus* and *Solea solea*), with indication of production of the seawards migrating individuals for a selected length interval and time period.

and similar length class interval was also estimated (Table 2). With this procedure comparisons could be made regarding the production potential of three consecutive recruitments, based on the youngest individuals (Table 2). For *D. labrax*, there was a clear decrease over the three-year study period, with the highest production obtained for the

Table 2 Monthly production of the selected lengths and time interval for the three consecutive cohorts of the nursery species (*Dicentrarchus labrax*, *Platichthys flesus* and *Solea solea*).

	Cohort	Recruitment	Length interval (cm)	Time interval (months)	Production per month (g WW m^{-2} month^{-1})
D. labrax	3	2003	4 to 12	10	0.031
	4	2004	4 to 14	10	0.007
	5	2005	5 to 14	10	0.009
P. flesus	3	2003	8 to 14	9	0.006
	4	2004	7 to 14	9	0.005
	5	2005	7 to 14	9	0.001
S. solea	3	2003	7 to 20	10	0.015
	4	2004	6 to 23	10	0.014
	5	2005	6 to 19	10	0.006

recruits of 2003, followed by considerably lower production for the recruits of 2004 and 2005 (Table 2).

For *P. flesus* and *S. solea* the recruitment period was not as clear as for *D. labrax*. *Platichthys flesus* recruitment seemed to occur in April (clear in 2004 and 2006). With the present data, this April recruitment was not evident in 2003 and 2005, as in 2003 there was no data before June, and in 2005 the new cohort only appeared in July (C3 and C5 respectively, Fig. 4). It is difficult to ascertain if the recruitment of April was delayed to June/July or if no juveniles were caught in April/May 2005. However, individuals caught in July 2003 and 2005 were larger than 6 cm, which was the same length of the July 2004 individuals (Fig. 4). *Platichthys flesus* individuals stayed at least two years in the estuary, migrating around April-May (Fig. 4B). Larger individuals showed only occasional occurrence and completely disappeared before achieving three years (Fig. 4B). Only C4 could be followed throughout its complete estuarine lifespan (Fig. 4B). For *P. flesus* the production of 2003 and 2004 recruits was similar, but it decreased considerably with the recruits of 2005 (Table 2).

Regarding *S. solea*, recruitment seemed to occur in January (Fig. 4). Yet, in 2006 recruitment was clearly delayed to April (C6), as extremely small size length classes appeared only in April (Fig. 4). Similarly to the other species, *S. solea* individuals seemed to leave the estuary before attaining two years old, with approximately 20 months and around 25 cm, by November-December (Fig. 4C). Older individuals returned to the estuary occasionally (C3 and C4, Fig. 4C). Only C4 could be followed throughout its complete estuarine lifespan (Fig. 4C). Similarly to *P. flesus*, the production of *S. solea* recruits of 2003 and 2004 was similar and decreased considerably with the recruits of 2005 (Table 2).

Comparing the production assessed for the partial cohorts of all species, the highest values were observed for *D. labrax* recruits of 2003, followed the recruits of *S. solea* of 2003 and 2004 (Table). The lowest partial cohorts' production was obtained for *P. flesus* recruits (Table 2).

DISCUSSION

Fish production general considerations

A high effort is required to estimate the secondary production of estuarine inhabitants, making it difficult for certain habitats and several species (Elliott 2002, Dolbeth et al. 2005). Most accurate estimates are provided with both a short time interval relative to the population dynamics of the studied species and with a large population size (Elliott 2002), in order to correctly assess the growth or the mortality. This bears problems when trying to estimate the production of estuarine fish, since these populations are very dynamic due to fluctuating levels of recruitment and migration (Costa et al. 2002, Cowley & Whitfield 2002, Pombo et al. 2007). In fact, several fishes have only an occasional occurrence in the estuary, while others migrate according to age and hydrological environment (Elliott & Dewailly 1995, Costa et al. 2002), conditioning a correct assessment of their population dynamics. Therefore, the present study dealt with the production estimation for the most abundant fish species of the Mondego estuary. These comprised more than 75% of all fish community density for the studied years (Martinho et al. 2007b) and about 56% of the community biomass (unpublished data). Estimates were representative of the nursery species production (100% of density and biomass), and of the resident species production (88% of density and 63% of the biomass) potential within the estuary.

Negative production values were not accounted for the production estimates. In fish populations, these negative productions have been associated to possible migration and/or size selective mortality (Costa et al. 2002, Pombo et al. 2007). The studied species are supposed to spend their life cycle (resident) or their early life stages (nursery) in the estuary (Elliott & Dewailly 1995), therefore the negative values were not considered for the annual production estimates evaluation, as these could lead to an underestimation of the estuarine production.

Resident and marine juvenile species production

In general, the production of the resident and the marine juvenile species of the Mondego estuary seemed lower when compared to other estuarine systems, even after correcting the production estimates for the catch efficiency of the sampling gear (beam trawl, 30% according to Hemingway & Elliott 2002) (Table 3). As a result, the expectation that production would increase with decreasing latitudes (Cowley & Whitfield 2002) seemed not to be fulfilled, similarly to the findings of Pombo et al. (2007), though this relationship occurred with the macrozoobenthic intertidal community production (Dolbeth et al. 2007b). There are several possible sources of error when assessing the fish production (more detailed in Costa et al. 2002 and Cowley & Whitfield 2002), which turns difficult to compare with other estimates elsewhere. Nevertheless, hypotheses related with environmental pressures within the estuary or its relatively low area (Table 3) may be suggested. It is also possible that an important part of the fish production was not accounted, as the fish inhabiting the seagrass and saltmarsh areas of the Mondego estuary were not correctly assessed. These are known as important nursery areas, providing both food and shelter for several small fishes (Beck et al. 2001, Costa et al. 2001, Cabral et al. 2007), and where fish production can be considerably higher compared to unvegetated areas (Edgar and Shaw 1995). Also, the relative low density and biomass of the marine species, hence production, may be attributed to the small size and small opening of the Mondego estuary, which may limit the entrance of marine species (Martinho et al. 2007b). However, in some occasions, the nursery species production of the Mondego overcame the estimates from other estuaries and coastal lagoons (Table 3).

For the Mondego estuary, the annual production of the nursery species was higher than the production of the residents ones, contrarily to Pombo et al. (2007), where *Atherina boyeri*, a pelagic resident species (not easily caught by the beam trawl used in the present study), had a high production in the estuary. In general, the resident species attained higher densities (especially *P. microps* in 2004-2006) but these coupled with considerably low biomasses, resulted in lower productions. Among the nursery species, *D. labrax* was the most productive. Similar production values were obtained in the Ria the Aveiro, also in Portugal (0.02 - 0.66 g WW $m^{-2}y^{-1}$, Pombo et al. 2007), yet few data, for comparative purposes, exists on the sea bass production in natural conditions elsewhere (Costa et al. 2002). The production seemed to decrease after the migration period, hypothesized to occur between January/February, which agrees with downstream dispersion of the older individuals occurring in the winter and early spring (Leitão et al.

Table 3 Comparison of production estimates in European estuaries for resident and nursery species (flatfishes and seabass), with indication of the number of species contributing for each group.* Original units in ash free dry weight – ADFW – were converted to WW (WW-AFDW: 0.251, Brey 2001); between brackets production after correction for the catch efficiency of the sampling gear.

Location	**Area**	**Study Period**	**Sampling gear**	**Production estimation method**	**Nursery species production** g WW m^{-2} y^{-1}	**Resident species production** g WW m^{-2} y^{-1}	**Reference**
Skagerrak (Gullmarsvik), Sweden	15 km^2	1978 - 1979	Drop trap	Cohort Increment summation	1.16 – 1.27 * 1 sp	0.40 – 2-63 * 2 spp	Pihl & Rosenberg 1982
Forth estuary, Scotland	84 km^2	1982 -1985	Beam trawl	Instantaneous growth	1.15 - 1.88 3 spp	-	Elliott & Taylor 1989
Oosterschelde estuary, Netherlands	351 km^2	1987/88	Beam trawl	Empirical: $P/\overline{B} = 2.5$	2.01 – 29.40 * 4 spp	0.39 – 2.39 * 4 spp	Hostens & Hamerlynck 1994
Ria de Aveiro, Portugal	47 km^2	1999 - 2000	"Chincha", traditional beach-seine net	Instantaneous growth	0.015 (0.02) - 0.596 (0.66) 1sp	0.160 (0.178) - 0.107 (0.119) 2 spp	Pombo et al. 2007
Mondego estuary, Portugal	3.4 km^2	2003 - 2006	Beam trawl	Cohort Increment summation	0.39 (1.30) -0.75 (2.51) 3 spp	0.005 (0.015) - 0.020 (0.068) 2 spp	Present study

2007, Martinho et al. 2007a). For *P. flesus,* production decreases after the migration period was not so clear. Annual production was lower than the one observed for the Forth estuary (around 1.3 g WW $m^{-2}y^{-1}$, Elliott & Taylor 1989) where the species behaves as resident (Elliott & Dewailly, 1995), but similar for other systems elsewhere (0.07 for the Elbe and 0.16 g WW $m^{-2}y^{-1}$ for the Oosterschelde estuaries, Costa et al. 2002). Although, it was not conclude a preference of this species for colder waters (within a range of 11 to 26ºC), the north and central coast of Portugal (i.e., Mondego estuary) appears to be the southern limit for the distribution of *P. flesus* (Cabral et al. 2007). Also, the decrease in more southern areas (e.g. Tagus estuary) has been associated to increases in water temperature (Cabral et al. 2001), which also occurred in the Mondego estuary and could explain the lower productions obtained. *Solea solea* maintained a similar production throughout the study period and similar values to other systems elsewhere (0.02 for the Irish Sea, Costa et al. 2002, and 0.24 g WW $m^{-2}y^{-1}$ for Osterschelde estuary, Hostens & Hamerlynck 1994). *Pomatoschistus minutus* showed a considerable decrease in production in the drought year of 2005 contrarily to *P. microps*, which is more tolerant to higher temperatures (Fonds & van Buurt 1974).

Implications of anthropogenic and natural impacts

Important anthropogenic impacts have been occurring in the Mondego estuary that, to certain extent, might have compromised the fish production. Within these anthropogenic impacts affecting the fish community, bank reclamation (due to port activities and agriculture), fishing and eutrophication, with consequent reduction of the seagrass (more details in Cardoso et al. 2005, Dolbeth et al. 2007b), were considered as major impact sources (Martinho et al. 2007b, Vasconcelos et al. 2007). Although there are no fish production estimates from the past, it is quite plausible that the production might have decreased, both due to a decrease of alternative habitats (Martinho et al. 2007a, Vasconcelos et al. 2007) and due to the overall decrease in the macrobenthic production (Dolbeth et al. 2007b). The decrease in the macrobenthic production means a decrease in the food availability, as the studied species feed intensively on the macrobenthos (namely polychaetes and small crustaceans, Leitão et al. 2006 and Dolbeth et al. unpublished data). Actually, trends of the fish community over the last two decades showed lower fish diversity at the present time, as a result the impoverishment of the environmental quality of the Mondego estuary (Leitão et al. 2007). Presently, seagrass beds are recovering (Cardoso et al. 2005), allowing more alternative habitats and potentially increasing invertebrate production in the following years (Dolbeth et al. 2007b), which may translate into higher fish productions.

Estuaries are exposed to severe of anthropogenic and inherent natural stress, hence it is difficult to distinguish among their impacts (Elliott & Quintino 2007). Even though, the fish community composition, as well as the population dynamics of single species, seems to be strongly affected by density independent factors, such as temperature, salinity, wind regime, tides (among others) in several estuarine systems (Marshal & Elliott 1998, Powers et al. 2000, Costa et al. 2002, Maes et al. 2004, Akin et al. 2005). Regarding climate variability impacts on the Mondego estuary within the study period, the gradual occurrence of a drought (starting by a normal hydrological year in 2003 and attaining a severe drought in 2005), high water temperatures and low freshwater discharges seemed the most relevant episodes. Accordingly, the production showed a clear decrease during the drought year of 2005, with the highest decreases observed for *D. labrax* and *P. minutus*. It is difficult to ascertain the main factors for this decrease (in agreement to the "Estuarine Quality Paradox", Elliott & Quintino 2007), yet experimental studies have revealed the limiting effect of high temperatures and salinity variations on eggs and larval development of *P. minutus* and *P. microps* (Fonds & van Buurt 1974) and of *P. flesus* (Cabral et al. 2007). *Solea solea* seems more tolerant to variations in temperature and salinity (Fonds 1975). Some studies have also showed a positive influence of moderate river discharges for an overall increase in primary production of estuarine systems (Houde & Rutherford 1993, Costa et al. 2002, Costa et al. 2007, Vinagre et al. 2007), with consequent impacts on the production of the other trophic levels. Additionally, river drainage has been positively associated with marine juvenile densities, due to the existence of chemical cues used by their larvae for movement orientation into the estuary (Costa et al. 2007, Vinagre et al. 2007). Drought and the consequent decrease in river discharge will lower both the primary production and the chemical cues reaching coastal waters, less detectable by larvae. These relationships between fish abundance and freshwater flow may be quite different according to species (Costa et al. 2007), and several studies have showed an increase in the fish community density in dry years (Costa et al. 2007). Yet, others showed that the recruitment of the marine species could be reduced (Costa et al. 2002), as well as the overall density of the resident species (Martinho et al. 2007b). Altogether, these studies highlight the hypothesis that salinity, temperature and river discharge variations may be major driving forces acting in the recruitment success and population development of the studied species, due to high natural mortality. This change in the environmental conditions might have increased the predation pressure by piscivorous fishes (mostly marine adventitious species) whose abundance increased in the estuary (Martinho et al. 2007b), or induced seawards migration, as also suggested by Dolbeth et al. (2007a) for the resident species.

Ultimately, the decrease in the fish production may have important consequences for the adult stocks of the marine species (see below) and for the estuarine food web, as the resident species are dominant prey of several other fishes (Dolbeth et al. unpublished data).

Exportation of commercially important fish species

For several marine spawning fishes, recruitment is followed by an estuarine residence phase during the early life cycle, and then emigration back to coastal areas. In the North Atlantic, the most abundant and commercially important flatfishes present similar life history patterns, with spawning occurring in the continental shelf, egg and larval migration towards coastal areas, through passive and active processes, and concentration in estuarine and/or shallow marine areas for feeding and protection (Cabral et al. 2007, Martinho et al. 2007a). The emigration back to the coastal areas will transfer large amounts of energy, which was accumulated in the estuary (Cowley & Whitfield 2002, Gillanders et al. 2003). In fact, in several locations, a fraction higher than 50% of the fisheries harvests are estuarine or estuarine-dependent in at least some life stages (Houde & Rutherford 1993, Able 2005). In this perspective, estuaries are crucial for the overall development of several fish populations and what happens in the estuarine system may compromise the coastal stocks and ultimately the fisheries, with important socio-economic impacts. In the present study, a direct measurement and comparison of each recruitment production contribution to exportation was not possible, as not all the cohorts could be followed completely. It is also difficult to evaluate the actual connectivity of this estuarine production to the coastal area (Gillanders et al. 2003, Able 2005, Gillanders 2005). Nevertheless, at least part of the cohort from consecutive recruitments, occurring in different hydrological years (i.e., with gradual drought effect) could be assessed and their consequent potential production for exportation evaluated and compared. For the three nursery species in study, the lowest production was observed when the recruitment occurred in 2005, the extreme drought year. This reduction in production (and potential reduction of emigrating fish) could influence the biodiversity and stability of the neighbouring inshore coastal or shelf ecosystems (Cowley & Whitfield 2002). Ultimately, this could affect the economy, due to the high commercial value of the studied species.

ACKNOWLEDGEMENTS

The authors are indebted to Daniel Crespo, Heliana Teixeira, Ivan Viegas, João Miguel Neto and Tiago Verdelhos who helped in field work.

REFERENCES

Able KW (2005) A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. Estuar Coast Shelf Sci 64: 5–17.

Akin S, Buhan E, Winemiller KO, Yilmaz H (2005) Fish assemblage structure of Koycegiz lagoon estuary, Turkey: spatial and temporal distribution patterns in relation to environmental variation. Estuar Coast Shelf Sci 64: 671–684.

Beck MW, Heck KL, Able Jr KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51: 633–641.

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html Alfred Wegener Institute for Polar and Marine Research, Germany.

Cabral HN, Costa MJ, Salgado JP (2001) Does the Tagus fish community reflect environmental changes? Climate Res 18: 119–126

Cabral NH, Vasconcelos RP, Vinagre C, França S, Fonseca V, Maia A, Reis-Santos P, Lopes M, Ruano M, Campos J, Freitas V, Santos P, Costa MJ (2007) Relative importance of estuarine flatfish nurseries along the Portuguese coast. J Sea Resear 57: 209–217.

Cardoso PG, Brandão A, Pardal MA, Raffaelli D, Marques JC (2005) Resilience of *Hydrobia ulvae* populations to anthropogenic and natural disturbances. Mar Ecol Prog Ser 289: 191–199.

Costa MJ, Catarino F, Bettencourt A (2001) The role of salt marshes in the Mira estuary (Portugal). Wet Ecol Managt 9: 121–134.

Costa MJ, Cabral HN, Drake P, Economou AN, Fernandez-Delgado C, Gordo L, Marchand J, Thiel R (2002) Recruitment and production of commercial species in estuaries. In: Elliot M, Hemingway K (Eds). Fishes in estuaries. Blackwell Science, Bodmin, United Kingdom, p 54–123.

Costa MJ, Vasconcelos R, Costa JL, Cabral HN (2007) River flow influence on the fish community of the Tagus estuary (Portugal). Hydrobiologia 587:113–123.

Cowley PD, Whitfield AK (2002) Biomass and production estimates of a fish community in a small South African estuary. J Fish Biol 61: 74–89.

Cusson M, Bourget E (2005) Global patterns of macroinvertebrate production in marine benthic habitats. Mar Ecol Prog Ser 297: 1–14.

Dolbeth M, Lillebø AI, Cardoso PG, Ferreira SM, Pardal MA (2005) Annual production of estuarine fauna in different environmental conditions: an evaluation of the estimation methods. J Exp Mar Biol Ecol 326: 115–127.

Dolbeth M, Martinho F, Leitão R, Cabral H, Pardal MA (2007a) Strategies of *Pomatoschistus minutus* and *Pomatoschistus microps* to cope with environmental instability. Estuar Coast Shelf Sci 74: 263–273.

Dolbeth M, Cardoso PG, Ferreira SM, Verdelhos T, Raffaelli D, Pardal MA (2007b) Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a ten-year period. Mar Pollut Bull 54: 576–585.

Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish assemblages in southern Australia I. Species richness, size-structure and production of fishes in Western Port, Victoria. J Exp Mar Biol Ecol 194: 53–81.

Elliott M (2002) An overview of the status, study and management of fishes in estuaries. In: Elliot M, Hemingway K (Eds) Fishes in estuaries. Blackwell Science, Bodmin, United Kingdom, p 556–575.

Elliott M, Taylor CJL (1989) The structure and functioning of an estuarine/marine fish community in the Forth Estuary, Scotland. Proceedings of the 21st. European Marine Biology Symposium. Polish Academy of Sciences and Institute of Oceanology Gdansk, Gdansk, p 227–240.

Elliott M, Dewailly F (1995) The structure and components of European estuarine fish assemblages. Neth J Aquat Ecol 29: 397–417.

Elliott M, Quintino V (2007) The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar Pollut Bull 54: 640–645.

Fonds M, van Buurt VG (1974) The influence of temperate and salinity on development and survival of goby eggs (Pisces, Gobiidae). Hydrobiol Bull 8: 110–116.

Fonds M (1975) The influence of temperature and salinity on the growth of young sole *Solea solea* L. 10th European Symposium on marine Biology, Ostend, Belgium, p 17–23.

Gamito S, Erzini K (2005) Trophic food web and ecosystem attributes of a water reservoir of the Ria Formosa (south Portugal). Ecol Model 181: 509–520.

Gillanders BM (2005) Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. Estuar Coast Shelf Sci 64: 47–57.

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar Ecol Prog Ser 247: 281–295.

Hemingway KL, Elliott M (2002) Field methods. In: Elliot M, Hemingway K (Eds) Fishes in estuaries. Blackwell Science, Bodmin, United Kingdom, p 410–509.

Houde ED, Rutherford ES (1993) Recent trends in estuarine fisheries: prediction of fish production and yield. Estuaries 16:161–176.

Hostens K, Hamerlynck O (1994) The motile epifauna of the soft bottoms in the subtidal Oosterschelde estuary: structure, function and impact of storm-surge barrier. Hydrobiologia 282/283: 479–496.

Leitão R, Martinho F, Neto JM, Cabral H, Marques JC, Pardal MA (2006) Feeding ecology, population structure and distribution of *Pomatoschistus microps* (Krøyer, 1838) and *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. Estuar Coast Shelf Sci 66: 231–239.

Leitão R, Martinho F, Cabral HN, Neto JM, Jorge I, Pardal MA (2007) The fish assemblage of the Mondego estuary: composition, structure and trends over the past two decades. Hydrobiologia 587: 269–279.

Lillebø AI, Neto JM, Martins I, Verdelhos T, Leston S, Cardoso PG, Ferreira SM Marques JC, Pardal MA (2005) Management of a shallow temperate estuary to control eutrophication: The effect of hydrodynamics on the system's nutrient loading. Estuar Coast Shelf Sci 65: 697–707.

Maes J, Van Damme S, Meire P, Ollevier F (2004) Statistical modelling of seasonal and environmental influences on the population dynamics of an estuarine fish community. Mar Biol 145: 1033–1042.

Marques SC, Martinho F, Azeiteiro UM, Pardal MA (2007) Climate variability and planktonic communities: The effect of an extreme event (severe drought) in a southern European estuary. Estuar Coast Shelf Sci 73: 725–734.

Martinho F, Leitão R, Neto J, Cabral HN, Marques JC, Pardal MA (2007a) The use of nursery areas by juvenile fish in a temperate estuary, Portugal. Hydrobiologia 587: 281–290.

Martinho F, Leitão R, Viegas I, Dolbeth M, Neto JM, Cabral HN, Pardal MA (2007b) The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. Estuar Coast Shelf Sci doi:10.1016/j.ecss.2007.05.040

Marshall S, Elliott M (1998) Environmental influences on the fish assemblage of the Humber estuary, UK. Estuar Coast Shelf Sci 46: 175–184.

Nicolas D, Le Loch F, Désaunay Y, Hamon D, Blanchet A, Le Pape O (2007) Relationships between benthic macrofauna and habitat suitability for juvenile common sole (*Solea solea*, L.) in the Vilaine estuary (Bay of Biscay, France) nursery ground. Estuar Coast Shelf Sci 73: 639–650.

Pombo L, Rebelo JE, Elliott M (2007) The structure, diversity and somatic production of the fish community in an estuarine coastal lagoon, Ria de Aveiro (Portugal). Hydrobiologia, 587: 253–268.

Patrício J, Marques JC (2006) Mass balanced models of the food web in three areas along a gradient of eutrophication symptoms in the south arm of the Mondego estuary (Portugal). Ecol Model 197: 21–34.

Phil L, Rosenberg R (1982) Production, abundance and biomass of motile epibenthic marine fauna in shallow waters western Sweden. J Exp Mar Biol Ecol 57, 273–301.

Powers M, Attrill MJ, Thomas RM (2000) Environmental factors and interactions affecting the temporal abundance of juvenile flatfish in the Thames Estuary. J Sea Resear 43: 135–149

Vasconcelos RP, Reis-Santos P, Fonseca V, Maia A, Ruano M, França S, Vinagre C, Costa MJ, Cabral H (2007) Assessing anthropogenic pressures on estuarine fish nurseries along the Portuguese coast: a multi-metric index and conceptual approach. Sci Total Environ 374: 199–215.

Vinagre C, Costa MJ, Cabral HN (2007) Impact of climate and hydrodynamics on sole larval immigration towards the Tagus estuary, Portugal. Estuar Coast Shelf Sci doi:10.1016/j.ecss.2007.05.035

Wilson JG (2002) Productivity, fisheries and aquaculture in temperate estuaries. Estuar Coast Shelf Sci 55: 953–967.

Winberg GG (1971) Methods for the estimation of production of aquatic animals. Academic Press Inc, London, United Kingdom, p 175.

GENERAL DISCUSSION AND CONCLUSIONS

Macrozoobenthic and fish production

Methodological considerations

The potential of secondary production studies as tools for the ecosystem understanding is huge, as they represent a measure of their inhabitants' fitness (Brey 2001, Dolbeth et al. 2003, 2005, Cusson & Bourget 2005, Cusson et al. 2006). It is important to correctly evaluate the production to avoid misinterpretations of the ecosystem.

Empirical methods to estimate production are valuable tools, when the classical cohort-based and size frequency-based methods are not applicable, or simply because they are a quicker and easier way to obtain production estimates (Cusson & Bourget 2005, Dolbeth et al. 2005, Cusson et al. 2006). Empirical methods allow:

1) the generation of hypotheses;

2) comparisons between communities from different sites or habitats;

3) may help to assess community production, for the species with limited field data, for rare species or those with unknown dynamics;

(Brey 2001, Cusson & Bourget 2005, Dolbeth et al. 2005).

Nevertheless, results must be interpreted carefully, as estimates may be quite deviated from the real production (Brey 2001, Dolbeth et al. 2005). The present study showed that different empirical methods have different performances, depending mainly on the species characteristics (voltinism, life span, mean individual weight). These results are in accordance with Cusson & Bourget (2005), who found a higher predictability of production estimates by the biotic variables. All methods showed better results when used for a sum of species, rather than a single one. The associated mean residual error of the sum of the species may be lower than the one for each species alone. In agreement, within a community, empirical production estimates will probably be more biased if the community is largely dominated by single species. So, when computing the community production, the best approach is to use the classical and more reliable methods for the dominant species and empirical methods for the remaining ones (Dolbeth et al. 2005, Chapter I). Using this procedure, a good compromise of time versus confident estimates may be achieved.

For the computation of the intertidal macrobenthic community production of the Mondego estuary south arm (Dolbeth et al. 2007a, Chapter I), cohort increment summation method was used for dominant species (Cardoso et al. 2005, Dolbeth et al. 2005, Ferreira et al. 2007). Among empirical methods, Brey (2001) version 4-04 method gave the best results, in agreement to Cusson & Bourget (2005), and was considered the best alternative. This method was then used for other representative species within the community (in agreement to Dolbeth et al. 2003). For the less abundant and rare species, the sum of biomass increases from consecutive sampling dates, appeared as the easiest and most effective procedure. For such rare species the associated error will be small, considering their importance in the community (Dolbeth et al. 2005, Chapter I), which according to Dolbeth et al. (2003) represented less than 6% of the production.

Regarding fish production, two aspects have to be considered:

1) it is generally easier to determine the fish age and therefore to recognize cohorts, in order to apply cohort estimating methods;

2) fish are highly mobile and estuaries must be regarded as open systems for fish.

In fact, in estuarine ecosystems, the fish community is composed by several ecological guilds. This means that some fish use the estuary through their whole life cycle (residents), others use it during a part of it (e.g. marine juveniles), and others use it only occasionally (marine or freshwater stragglers and migrants) (Elliott & Dewailly 1995, Whitfield 1999). It is difficult to have the needed data to correctly follow the growth with such dynamic populations (Costa et al. 2002, Cowley & Whitfield 2002, Chapter II, IV). Therefore, few data exists on the biological production of estuarine fish assemblage (Costa et al. 2002).

Estuarine production estimates

The intertidal macrobenthic community production of the south arm of the Mondego estuary was considerably high, when compared to other similar systems (Dolbeth et al. 2003). A warmer climate might have triggered the differences found, as growth and reproduction are stimulated (Cardoso et al. 2002, Cusson & Bourget 2005). In fact, the invertebrate production and $P/\overline{B}$ ratio estimates suggest an increase from high to mid-latitudinal zones, in agreement to the general trends concluded by Cusson & Bourget (2005). Yet, this seemed not to occur with fish production estimates, as suggested by Cowley & Whitefield (2002). The production of the resident and of the marine juvenile fish, using the estuary as nursery grounds (nursery species), was in general lower in the Mondego estuary, when compared, for example, to the Skagerrak (Gullmarsvik) in Sweden (Pihl & Rosenberg 1982) and the Oosterschelde estuary in the Netherlands (Hostens & Hamerlynck 1994). At least for the resident species, *P. minutus* and *P. microps*, an intermediate life span and body mass between the ones determined for Mediterranean and the Atlantic regions was found (Fouda & Miller 1981, Bouchereau & Guelorget 1998, Pampouile et al. 1999, Pampouile 2001), in agreement with the intermediate temperature regime of the Mondego estuary (Dolbeth et al. 2007b, Chapter II). In the study of Cusson & Bourget (2005) for marine invertebrates, production and $P/\overline{B}$ ratios were negatively affected by life span and body mass. Proportionally, larger and older individuals use more energy for respiration than for growth, explaining the $P/\overline{B}$ ratios and production decrease with age and body mass. Transporting the same logic for fish, it would be expected at least higher productions in the Mondego estuary than in the North Atlantic regions, which did not occurred. However, in Ria de Aveiro, a larger coastal lagoon also in Portugal (same latitudinal range), production values for *P. microps* were higher (Pombo et al. 2007), which may indicate that the lower production obtained in the Mondego estuary may be related with its small area.

A great part of the invertebrate production was due to the large contribution of *Zostera noltii* areas. Several studies have reported on the ecological importance of seagrass beds, mostly as shelter and feeding areas, sustaining high diversity and production of invertebrate (Heck et al. 1995, Dolbeth et al. 2003, 2007a) and fish species (Edgar & Shaw 1995, Beck et al. 2001, Heck et al. 2003, Polte et al. 2005, Cabral et al. 2007, Martinho et al. 2007a). The present study confirmed this trend for the invertebrate community, as the highest species diversity and production was obtained for the seagrass bed (Dolbeth et al. 2007a, Chapter I). Yet, the fish community and production was not accurately assessed in the seagrass bed, which might also partially explain the lower estuarine production estimates obtained for the Mondego estuary. In fact, several studies have concluded high abundances and production of fish in vegetated areas (Edgar & Shaw 1995), especially for resident species such as *P. minutus* and *P. microps* (Polte et al. 2005). Again, it is important to considerer the relatively small area and small opening of the Mondego estuary that may limit the marine species entrance, as also suggested by Martinho et al. (2007b).

Although the analysed fish community production seemed low, there was an important contribution from the marine juvenile using the estuary as nursery grounds in the Mondego estuary: *Dicentrarchus labrax*, *Platichthys flesus* and *Solea solea*. In some occasions, their production overcame the estimates from other estuaries and coastal lagoons (compared to Elliott & Taylor 1989 and Pombo et al. 2007). This highlights the importance of the Mondego estuary as a nursery ground for these marine species, as also suggested by

Martinho (2007a). Despite its relative small area, the estuary role in sustaining coastal fisheries stocks may be significant (Chapter IV).

Anthropogenic, natural and climate variability impacts

Estuaries are considered as naturally stressed environments (McLusky & Elliott 2004). Yet, several organisms, during their whole or partial life cycle, find in estuarine areas good grounds to grow and develop (Kennish 2002, McLusky & Elliott 2004, Elliott & Quintino 2007). Estuarine inhabitants are resilient towards natural stressors, being well adapt to the high spatial and temporal variability characteristics of the system (McLusky & Elliott 2004, Elliott & Quintino 2007). Nevertheless, the high productivity associated to these systems, along with several other goods and services (Kennish 2002, McLusky & Elliott 2004, Martínez et al. 2007), have been attracting great part of human population to live on the estuarine shores, placing these systems under huge human pressure. Severe anthropogenic stress is a general problem in several estuarine systems worldwide, with eutrophication, habitat loss and overexploitation of resources among the major threats (Kennish 2002, McLusky & Elliott 2004). Adding to these anthropogenic sources of stress, climate extremes (which indirectly may be considered resultant from human action) are being more frequent (Adams 2005, Alley et al. 2007, Marques et al. 2007). So, estuarine inhabitants have been considered resilient towards natural stress; but are they resilient towards several other sources of stress? Evidences sustain that they are not, judging by the increase need of restoration programs (De Jonge & de Jong 2002, Cardoso et al. 2005, Lillebø et al. 2005, Munkes 2005) and implementation of directives to restore the system to its good ecological status (Lillebø et al. 2007, Teixeira et al. 2007).

The present work is supported by a long-term database, from 1993 until 2006. This database enabled the study at least two major impacts occurring in this system, anthropogenic and climatic ones:

1) eutrophication and habitat loss;
2) weather extremes: large floods and prolonged droughts.

Additionally, following a restoration programme, the initial recovery of the system was also monitored.

In the south arm of the Mondego estuary, eutrophication and its effects may be regarded as one of the major reasons for the *Z. noltii* beds decline. Eutrophication is a worldwide phenomena, with effects changing according to the intrinsic characteristics of the aquatic system and climate (Kennish 2002, Marques et al. 2003, Pardal et al. 2004, Lillebø et al. 2005, Munkes 2005, Powers et al. 2005). One of the consequences of eutrophication is the replacement of primary producers, mostly from the slow growing rooted plants (seagrass) to the fast and opportunist macroalgae (Dolbeth et al. 2003, Marques et al. 2003, Pardal et al. 2004, Lillebø et al. 2005). This also occurred in the Mondego estuary. As evidenced by the present study, the seagrass beds are among the most productive of the whole estuarine system (Dolbeth et al. 2003, 2007a). Their reduction induced an overall decrease in the macrobenthic intertidal community production for the whole estuary. In fact, the lowest macrobenthic estuarine production was registered when the seagrass beds had the lowest area and extent.

No data exist for the fish community production before the mitigation measures but the hypothesis of the production decrease is reasonable. Part of the food resources used by fish is provided from the studied intertidal areas, whose production decreased, and which are also important habitats for fish. Also, trends of the fish community comparing the two time periods, 1990/91 and 2003/04, showed lower fish diversity at the present time, as a result of Mondego estuary environmental quality impoverishment (Leitão et al. 2007).

Following the implementation of the mitigation measures at the end of 1998, there were evidences that these have been effective (Lillebø et al. 2005, Cardoso et al. 2007, Dolbeth et al. 2007a):

1) no further macroalgal blooms were recorded;
2) *Z. noltii* is gradually recovering, both in biomass and extent;
3) macrobenthic community mean biomass, production and species richness increased, compared to the low values achieved at the beginning of the post-mitigation period in 1999;
4) K-strategists species (e.g. *S. plana*) are increasing their production, concomitant with a decrease of opportunist species (such as *Alkmaria romijni* and *Capitella capitata*, Cardoso et al. 2007).

Compliant with the recovery process was the reappearance of fish species associated to seagrass beds, such as *Symphodus bailloni* (Martinho et al. 2007b).

More important than dealing with the anthropogenic impacts alone is their combination with other sources of stress. For the Mondego estuary, during the study period, the most impacting factors were the occurrence of severe floods and droughts. Ecosystems are being subjected more frequently with multiple stressors, which may act synergistically to lower the natural resilience of the estuarine populations to disturbance (Raffaelli et al. 2003, Adams 2005, Cardoso et al 2005). The present study has showed this multiple stressors effects for the macrobenthic community, with macroalgal blooms and gradual seagrass decline occurring simultaneously with the natural cycles of floods. The prior disturbance history of the area, due to the overall effects of eutrophication, seemed to be an impairing factor for the resilience of the macrobenthic populations towards the floods (Dolbeth et al. 2007a, Chapter I). The recover of the macrobenthic community after the floods seemed to take longer in the post mitigation period, as the system had already suffered from other disturbance sources. This ecosystem response was thought to be linked to the biodiversity lost, because the species richness was much lower by the time of the extreme flood in 2000/01, which might have compromised the recovery process. In fact, several authors believe that system resilience may be provided by biodiversity (Loreau et al. 2002, Marques et al. 2003, Raffaelli et al. 2003). If biodiversity is severely reduced by one stressor, the effects of subsequent ones may be much greater than imagined (Loreau et al. 2002, Marques et al. 2003, Raffaelli et al. 2003), especially if the functional biodiversity is lost, as suggested by Elliott & Quintino (2007). The impact of these multiple stressors could not be assessed for the fish community.

The present study database enabled to monitor other important limitations, such as the drought effects on the fish community. Fish are highly motile populations, so the way to cope with climate variability is quite different from invertebrates, as they can migrate in order to escape adversity (McLusky & Elliott 2004). As a general trend, the production and the recruitment strength of the resident and nursery species decreased in parallel with the increasing drought, from 2004 until in 2005. This was especially evident for *D. labrax, P. minutus* and *P. flesus*. The dynamics of fish populations may be governed by several density-independent (salinity, temperature, oxygen, turbidity, among others) and dependent factors (competition, predation, among others). So, it is difficult to ascertain the main drives behind the observed results. No direct effects could be attributable to the salinity and temperature variations and to the low freshwater discharges, resulting from the drought and high temperatures. Nevertheless, these two factors were hypothesized as probable reasons for the decreased production, both directly and indirectly:

1) Due to the temperature and salinity range tolerances of the studied species (Von Westernhagen1970, Fonds & van Buurt 1974, Fonds 1975, von Oertzen 1984). These tolerance ranges might have induce to mortality or migration to more stable areas, or to a lower recruitment strength (for e.g. for *P. minutus,* whose recruitment was clearly weaker, as also tested by the model results, Chapter II);

2) Due to an increased predation pressure from the piscivorous marine adventitious species which increased in the downstream areas (Martinho et al 2007b), resulting from a higher salinity incursion in the estuary.

A clearer view on the fish dynamics allowed detecting other aspects that could clarify why some species seemed more affected than others by the environmental variability. For example, *P. microps* did not seem strongly affected by the drought (Dolbeth et al. 2007b). This species benefited from a wider temperature and salinity range tolerance (Fonds & Buurt 1974, von Oertzen 1984), which allows it to occupy different areas within the estuary. This behaviour enabled *P. microps* to take advantage from other alternative food resources (Leitão et al. 2006, Dolbeth et al. 2007b) and to better cope with the climate variability during the three-year study. Although no competition for food could be concluded, a high diet overlap was found between *P. microps* and *P. minutus*. Attrill & Power (2004) suggested that similar species might use distinct thermal spaces to minimize potential competition between them, which might have happen with *P. microps* and *P. minutus*.

Links between macrobenthos and fish

The high intertidal macrobenthic community production of the Mondego estuary suggests abundant food resources for the other trophic levels. Nevertheless, it is important to bear in mind:

1) if this production is actually accessible to the higher trophic levels;
2) if the species contributing to the overall production are among the preferential prey.

Basically, the main issue is to assess if the production is consumed and transformed into other sources of biomass, such as fishes and birds.

With regard to fish feeding resources, several studies have showed the importance of the intertidal areas (combining bare mudflats, seagrass and saltmarshes, Hampel et al. 2005) as food providers (Cabral 2000, Elliott et al. 2002, McLusky & Elliott 2004, Vinagre et al. 2006). The diets of the main fish species of the Mondego estuary suggested an important contribution of the intertidal invertebrate production. In fact, among the preferential prey of *P. minutus, P. microps*, *D. labrax* and *Callionymus lyra* were several species whose abundance was high on the intertidal mudflats, such as several polychaetes (e.g. Capitellidae, Spionidae), *S. plana*, among others (Cardoso et al. 2007, Dolbeth et al. 2007a). Furthermore, this intertidal production may also be important for intermediate levels in the fish trophic chains, as suggested for *P. minutus* and *P. microps* (Chapter III), *C. maenas* (Baeta et al. 2006), *Crangon crangon* and *Nephtys* spp. (Elliott et al. 2002, McLusky & Elliott 2004), important prey of *Chelidonichthys lucerna*, *Ciliata mustela*, *Scophthalmus rhombus, Trisopterus luscus,* among others (Chapter III).

Several of the major prey were most abundant in the north arm (such as *Corophium* spp.), at subtidal areas (such as *C. crangon, Nephtys* spp.) or in the water column (calanoid copepods), whose production was not assessed. However, a counterbalance with the main intertidal productive species of the south arm (for the period of 1993-2002) becomes pertinent as an exercise. *Hydrobia ulvae, C. carinata, S. plana* and *Hediste diversicolor* were the main productive species of the Mondego estuary south arm (Dolbeth et al. 2007a). The fish diets showed that *S. plana* and eventually *H. diversicolor* (several items were non identified Polychaeta) were among preferential prey of some fishes (e.g. *P. microps, S. solea, C. lyra*). *C. carinata* was also important prey for the generalist feeder *Mullus surmuletus*. *H. ulvae*, whose production was high especially after disturbance periods (Dolbeth et al. 2003, 2007a), was not heavily consumed by the fish community (chapter III). So, for fish, the recovery of the environmental quality of the estuary is most valuable especially due to the production increase of their preferred prey items, such as *S. plana* and *H. diversicolor*. The production of these prey clearly increased after the mitigation measures (Dolbeth et al. 2007a).

One of the key prey of the fish species analysed was *C. crangon*. Its production was assessed by Viegas et al. (2007), who found lower values comparatively to other European systems. A considerable decrease was also observed in the dry year of 2004/05 (Viegas et al. 2007). There were no means of direct relating this production with the fish production, as no consumption studies were performed. Yet, hypotheses could be raised on the potential for the competition between fish feeding mainly on this resource, especially on the dry year. However, practically all fish showed some degree of opportunistic feeding, by feeding on other food resources.

As a final remark, detritus seemed to be a basal resource of the fish food web, similarly to other estuarine fish food webs (Whitfield 1999, Mathieson et al. 2000, Elliott et al. 2002, Akin & Winemiller 2006, Svensson et al. 2007). Still, recent studies suggest that the contribution of microphytobenthos may be also of considerable importance for the Mondego estuary (Baeta, unpublished data).

Conclusions

The present study showed that the Mondego estuary is highly productive, especially the macrozoobenthic community. The highest productive habitats were the seagrass beds. This macrozoobenthic production is transformed into other resources, such as fish, which have several invertebrate prey. Yet, estuarine areas are also heavily used by man, which may inflict severe change at the ecosystem level. This was clear with the study of the eutrophication effects and consequent macroalgal blooms and seagrass bed decline. These events resulted in a production decrease, compromising the overall integrity of the whole estuary. In addition, climate variability (such as occurrence of floods and droughts) is another important stressor (of increasing frequency), impairing the health and fitness of resident biota. Climate extremes acted as a multiple stressors for the macrobenthic community and also severely affected the recruitment strength and production of marine juvenile and resident estuarine fish species. The production of all these fish seemed reduced by the extreme drought associated effects. Important consequences may occur for the adult stocks of the marine species and for the estuarine food web, as the resident species are dominant prey of several other fishes. Nevertheless, estuaries can be considered as relatively resilient. There seemed to be a gradual recovery of the estuary, after the mitigation measures implementation. This ecosystem response highlights the need of such restoration programmes to improve the environmental quality in other estuarine systems with similar problems.

REFERENCES

Adams SM (2005) Assessing cause and effect of multiple stressors on marine systems. Mar Pollut Bull 51: 649–657.

Akin S, Winemiller KO (2006) Seasonal variation in food web composition and structure in a temperate tidal estuary. Estuar Coast 29: 552–567.

Alley R, Berntsen T, Bindoff NL, Chen Z, Chidthaisong A, Friedlingstein P, Gregory J, Hegerl G, Heimann M, Hewitson B, Hoskins B, Joos F, Jouzel J, Kattsov V, Lohmann U, Manning M, Matsuno T, Molina M, Nicholls N, Overpeck J, Qin D, Raga G, Ramaswamy V, Ren J, Rusticucci M, Solomon S, Somerville R, Stocker TF, Stott P, Stouffer RJ, Whetton P, Wood RA, Wratt D (2007) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change, p 21.

Attrill MJ, Power M (2004) Partitioning of temperature resources amongst an estuarine fish assemblage. Estuar Coast Shelf Sci 61: 725–738.

Baeta A, Cabral HN, Marques JC, Pardal MA (2006) Feeding ecology of the green crab, *Carcinus maenas* (L. 1758) in a temperate estuary, Portugal. Crustaceana 79: 1181–1193.

Beck MW, Heck KL, Able JrKW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51: 633–641.

Bouchereau JL, Guelorget O (1998) Comparison of three Gobidae (Teleostei) life history strategies over their geographical range. Oceanol Acta 24: 503–517.

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html Alfred Wegener Institute for Polar and Marine Research, Germany.

Cabral H (2000) Comparative feeding ecology of sympatric *Solea solea* and *S. senegalensis*, within the nursery areas of the Tagus estuary, Portugal. J Fish Biol 57: 1550–1562.

Cabral NH, Vasconcelos RP, Vinagre C, França S, Fonseca V, Maia A, Reis-Santos P, Lopes M, Ruano M, Campos J, Freitas V, Santos P, Costa MJ (2007) Relative importance of estuarine flatfish nurseries along the Portuguese coast. J Sea Resear 57: 209–217.

Cardoso PG, Lillebø AI, Pardal MA, Ferreira SM, Marques JC (2002) The effects of different primary producers on *Hydrobia ulvae* population dynamics: a case study in a temperate intertidal estuary. J Exp Mar Biol Ecol 277: 173–195.

Cardoso PG, Brandão A, Pardal MA, Raffaelli D, Marques JC (2005) Resilience of *Hydrobia ulvae* populations to anthropogenic and natural disturbances. Mar Ecol Prog Ser 289: 191–199.

Cardoso PG, Bankovic M, Raffaelli D, Pardal MA (2007) Polychaete assemblages as indicators of habitat recovery in a temperate estuary under eutrophication. Estuar Coast Shelf Sci 71: 301–308.

Costa MJ, Cabral HN, Drake P, Economou AN, Fernandez-Delgado C, Gordo L, Marchand J, Thiel R (2002) Recruitment and production of commercial species in estuaries. In: Elliot M, Hemingway K (Eds) Fishes in Estuaries. Blackwell Science, Bodmin, United Kingdom, p 54–123.

Cowley PD, Whitfield AK (2002) Biomass and production estimates of a fish community in a small South African estuary. J Fish Biol 61: 74–89.

Cusson M, Bourget E (2005) Global patterns of macroinvertebrate production in marine benthic habitats. Mar Ecol Prog Ser 297: 1–14.

Cusson M, Plante JF, Genest C (2006) Effect of different sampling designs and methods on the estimation of secondary production: A simulation. Limnol Oceanogr: Methods 4: 38–48.

De Jonge VN, de Jong DJ (2002) Ecological restoration in coastal areas in the Netherlands: concepts, dilemmas and some examples. Hydrobiologia 478: 7–28.

Dolbeth M, Pardal MA, Lillebø AI, Azeiteiro UM, Marques JC (2003) Short and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. Mar Biol 143: 1229–1238.

Dolbeth M, Lillebø AI, Cardoso PG, Ferreira SM, Pardal MA (2005) Annual production of estuarine fauna in different environmental conditions: an evaluation of the estimation methods. J Exp Mar Biol Ecol 326: 115–127.

Dolbeth M, Cardoso PG, Ferreira SM, Verdelhos T, Raffaelli D, Pardal MA (2007a) Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a ten-year period. Mar Pollut Bull 54: 576–585.

Dolbeth M, Martinho F, Leitão R, Cabral H, Pardal MA (2007b) Strategies of *Pomatoschistus minutus* and *Pomatoschistus microps* to cope with environmental instability. Estuar Coast Shelf Sci 74: 263–273.

Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish assemblages in southern Australia I. Species richness, size-structure and production of fishes in Western Port, Victoria. J Exp Mar Biol Ecol 194: 53–81.

Elliott M, Taylor CJL (1989) The structure and functioning of an estuarine/marine fish community in the Forth Estuary, Scotland. Proceedings of the 21st. European Marine Biology Symposium. Polish Academy of Sciences and Institute of Oceanology Gdansk, Gdansk, p 227–240.

Elliott M, Dewailly F (1995) The structure and components of European estuarine fish assemblages. Neth J Aquat Ecol 29: 397–417.

Elliott M, Quintino V (2007) The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar Pollut Bull 54: 640–645.

Elliott M, Hemingway KL, Costello MJ, Duhamel S, Hostens K, Labropoulou M, Marshall S, Winkler H (2002) Links between fish and other trophic levels. In: Elliot M, Hemingway K. (Eds). Fishes in estuaries. Blackwell Science, Bodmin, United Kingdom, p 124–216.

Ferreira SM, Brandão A, Baeta A, Neto JM, Lillebø AI, Marques JC, Jensen KT, Pardal MA (2007) Effects of restoration management on the estuarine isopod *Cyathura carinata*: mediation by trematodes and habitat change. Mar Biol 151:109–118.

Fonds M, Buurt VG (1974) The influence of temperate and salinity on development and survival of goby eggs (Pisces, Gobiidae). Hydrobiol Bull 8: 110–116.

Fonds M (1975) The influence of temperature and salinity on the growth of young sole *Solea solea* L. 10th European Symposium on marine Biology, Ostend, Belgium, p 17–23.

Fouda MM, Miller PJ (1981) Age and growth of the common goby, *Pomatoschistus microps* on the south coast of England. Estuar Coast Shelf Sci 12: 121–129.

Hampel H, Cattrijsse A, Elliott M (2005) Feeding habits of young predatory fishes in marsh creeks situated along the salinity gradient of the Schelde estuary, Belgium and The Netherlands. Helgol Mar Res 59: 151–162.

Heck KL, Able KW, Roman CT, Fahay MP (1995) Composition, abundance, biomass, and production of macrofauna in a new england estuary - comparisons among eelgrass beds and other nursery habitats. Estuaries 18: 379–389.

Heck KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 25: 123–136.

Hostens K, Hamerlynck O (1994) The motile epifauna of the soft bottoms in the subtidal Oosterschelde estuary: structure, function and impact of storm-surge barrier. Hydrobiologia 282/283: 479–496.

Kennish MJ (2002) Environmental threats and environmental futures of estuaries. Environ Conserv 29: 78–107.

Leitão R, Martinho F, Neto JM, Cabral H, Marques JC, Pardal MA (2006) Feeding ecology, population structure and distribution of *Pomatoschistus microps* (Krøyer, 1838) and *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. Estuar Coast Shelf Sci 66: 231–239.

Lillebø AI, Neto JM, Martins I, Verdelhos T, Leston S, Cardoso PG, Ferreira SM Marques JC, Pardal MA (2005) Management of a shallow temperate estuary to control eutrophication: The effect of hydrodynamics on the system's nutrient loading. Estuar Coast Shelf Sci 65: 697–707.

Lillebø AI, Teixeira H, Pardal MA, Marques JC (2007) Applying quality status criteria to a temperate estuary before and after the mitigation measures to reduce eutrophication symptoms. Estuar Coast Shelf Sci 72: 177–187.

Lopes RJ, Pardal MA, Múrias, T, Cabral JA, Marques JC (2006) Influence of macroalgal mats on abundance and distribution of dunlin Calidris alpina in estuaries: a long-term approach. Mar Ecol Prog Ser 323: 11–20.

Loreau M, Dowining A, Emmerson M, Gonzalez A, Hughes J, Inchausti P, Joshi J, Norberg J, Sala O (2002) A new look at the relationship between diversity and stability. In: Loreau M, Naeem S, Inchausti P (Eds) Biodiversity and ecosystem functioning. Oxford University Press, Oxford, United Kingdom, p 79–91.

Martinho F, Leitão R, Neto J, Cabral HN, Marques JC, Pardal MA (2007a) The use of nursery areas by juvenile fish in a temperate estuary, Portugal. Hydrobiologia 587: 281–290.

Martinho F, Leitão R, Viegas I, Dolbeth M, Neto J, Cabral HN, Pardal MA (2007b) The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. Estuar Coast Shelf Sci doi:10.1016/j.ecss.2007.05.040.

Marques JC, Nielsen SN, Pardal MA, Jørgensen SE (2003) Impact of eutrophication and river management within a framework of ecosystem theories. Ecol Model 166: 147–168.

Marques SC, Martinho F, Azeiteiro UM, Pardal MA (2007) Climate variability and planktonic communities: The effect of an extreme event (severe drought) in a southern European estuary. Estuar Coast Shelf Sci 73: 725–734.

Martínez ML, Intralawan A., Vázquez G., Pérez-Maqueo O, Sutton P, Landgrave R (2007) The coasts of our world: ecological, economic and social importance. Ecol Econ 63: 254-272.

Mathieson S, Cattrijsse A, Costa MJ, Drake P, Elliott M, Gardner J, Marchand J, (2000) Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. Mar Ecol Prog Ser 204: 225–242.

McLusky DS, Elliott M (2004) The estuarine ecossystem. Ecology, threats and management. 3rd Edition. Oxford, University Press, United Kingdom, p 213.

Munkes B (2005) Eutrophication, phase shift, the delay and the potential return in the Greifswalder Bodden, Baltic Sea. Aquat Sci 67: 372–381.

Pampoulie C (2001) Demographic structure and life history traits of the common goby *Pomatoschistus microps* (Teleostei, Gobidae) in a Mediterranean coastal lagoon (Rhône River delta, France). Acta Oecol 22: 253–257.

Pampoulie C, Rosecchi E, Bouchereau JL, Crivelli AJ (1999) Life history traits of *Pomatoschistus minutus* (Teleostei, Pisces) in the Rhône Delta, France. J Fish Biol 55: 892–896.

Pardal MA, Cardoso PG, Sousa JP, Marques JC, Raffaelli D (2004) Assessing environmental quality: a novel approach. Mar Ecol Prog Ser 267: 1–8.

Phil L, Rosenberg R (1982) Production, abundance and biomass of motile epibenthic marine fauna in shallow waters western Sweden. J Exp Mar Biol Ecol 57: 273–301.

Polte P, Schanz A, Asmus H (2005) The contribution of seagrass beds (*Zostera noltii*) to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea. Mar Biol 147: 813–822.

Pombo L, Rebelo JE, Elliott M (2007) The structure, diversity and somatic production of the fish community in an estuarine coastal lagoon, Ria de Aveiro (Portugal). Hydrobiologia, 587: 253–268.

Powers SP, Peterson CH, Christian RR, Sullivan E, Powers MJ, Bishop MJ, Buzzelli CP (2005) Effects of eutrophication on bottom habitat and prey resources of demersal fishes. Mar Ecol Prog Ser 302: 233–243.

Raffaelli D, Emmerson M, Solan M, Biles C, Paterson D (2003) Biodiversity and ecosystem processes in shallow coastal waters: an experimental approach. J Sea Res 49: 133–141.

Svensson CJ, Hyndes GA, Lavery PS (2007) Food web analysis in two permanently open temperate estuaries: Consequences of saltmarsh loss? Mar Environ Res 64: 286-304.

Teixeira H, Salas F, Borja Á, Neto JM, Marques JC (2007) A benthic perspective in assessing the ecological status of estuaries: the case of the Mondego estuary (Portugal). Ecol Indicat doi:10.1016/j.ecolind.2007.02.008.

Viegas I, Martinho F, Neto JM, Pardal MA (2007) Population dynamics, distribution and secondary production of the brown shrimp *Crangon crangon* (L.) in a southern European estuary – latitudinal variations. Scient Mar 71: 451–460.

Vinagre C, França S, Cabral HN (2006) Diel and semi-lunar patterns in the use of an intertidal mudflat by juveniles of senegal sole, *Solea senegalensis*. Estuar Coast Shelf Sci 69: 246-254.

von Oertzen JA (1984) Influence of steady-state and fluctuating salinities on the oxygen consumption and activity of some brackish water shrimps and fishes. J Exp Mar Biol Ecol 80: 29–46.

Von Westernhagen H (1970) Erbrütung der Eier von Dorsch (*Gadus morhua* L.), Flunder (*Pleuronectes flesus* L.) und Scholle (*Pleuronectes platessa* L.) unter kombinierten Temperatur-und Salzgehaltbedingungen. Helgol Wiss Meeresunters 21: 21–102.

Whitfield AK (1999) Ichthyofaunal assemblages in estuaries: a South African case study. Rev Fish Biol Fish 9: 151–186.

FUTURE PERSPECTIVES

In this section, potential research lines that became pertinent during the conception of the present thesis are provided. These are structured into the following investigation lines:

Long term studies

Long term studies are important for the understanding of complex and slow processes in dynamic systems such as estuaries. In fact, many ecological investigations need such data to understand the functioning of these systems and address their management and conservation needs. This thesis presented an overview of the long term studies potential to understand several complex phenomena. Short-term and long-term stress effects could be evaluated, as well as the complex interaction of multiple stressors impact on the system. The continuation of the macrozoobenthic community and fish community database seems a logic path to follow, so that other processes may be monitored, which seems to be of particular relevance to the Mondego estuary:

1) continue to monitor the success of the restoration programme;
2) study the effects of climate variations, or other rare events, on the system.

Besides being essential in ecology, these studies may also provide a way of identifying and managing important societal issues (such as an integrated and sustainable estuarine use by man).

Modelling climate change

The fish model presented in the thesis aimed at reproducing the fish population dynamics, using a simple approach. Several aspects were left behind, inclusively the forcing functions that could greatly improve the performance of the model. The proper forcing functions could allow predicting the fish dynamics towards a changing environment. The increasing rate of climate extremes will impose stress in the fish population and communities (Roessig et al. 2004, Meynecke et al. 2006) and investigated in the chapters II and IV of the present thesis. In fact, salinity and temperature variations are assumed to occur more frequently due to increases in average global temperature and changing patterns of precipitation (Alley et al. 2007, IPCC report). Therefore, a tool that enables to predict the impacts of change must be regarded as most valuable, especially towards a scenario of climate change. Therefore, the next step for the model is the inclusion of relevant forcing functions, to simulate different climate pressure scenarios. For *P. minutus* and *P. microps*, the target species of the model, the most striking forcing functions are probably temperature and salinity (as seen in chapter II). Several other processes and outputs (e.g. predation, migration), relevant for the fish population dynamics, should be included. However including temperature and salinity could provide an important insight on the possible consequences for the fish development.

Consumption studies – actual fluxes of biomass/energy

The answer to the question "How the macrobenthic production relates with the fish production?" was not fully achieved. It was not possible to quantify fluxes of biomass/energy within macrobenthos and fish. Also, only hypotheses could be suggested regarding competition between the fish retaining high diet overlap. These aspects could be overcome if the resource consumption was assessed. In fact, the trophic interactions, i.e., the actual transfer of biomass/energy from one trophic unit (prey) to another one (predator), could be properly assessed combining the diet analysis (assessed in chapter III) with consumption studies.

Seagrass habitats for fish production

Seagrass beds are essential habitats for several organisms, maintaining high levels of production. This aspect was concluded for the macrozoobenthic community (chapter I) and hypothesized to be important for fish. In fact, other studies report these areas as preferential nursery grounds for some fish (Heck et al. 2003). Nevertheless, their potential is not known for the Mondego estuary. The need to know the actual contribution of seagrass beds for fish production becomes pertinent. With this approach, a better understanding on the carrying capacity of the estuary for fish may be achieved, along with additional knowledge on the importance of this habitat, so that correct management measures can be taken.

REFERENCES

Alley R, Berntsen T, Bindoff NL, Chen Z, Chidthaisong A, Friedlingstein P, Gregory J, Hegerl G, Heimann M, Hewitson B, Hoskins B, Joos F, Jouzel J, Kattsov V, Lohmann U, Manning M, Matsuno T, Molina M, Nicholls N, Overpeck J, Qin D, Raga G, Ramaswamy V, Ren J, Rusticucci M, Solomon S, Somerville R, Stocker TF, Stott P, Stouffer RJ, Whetton P, Wood RA, Wratt D (2007) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change, p 21.

Heck KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 25: 123–136.

Meynecke JO, Lee SY, Duke NC, Warnken J (2006) Effect of rainfall as a component of climate change on estuarine fish production in Queensland, Australia. Estuar Coast Shelf Sci 69: 491–504.

Roessig JM, Christa MW, Joseph JCJr, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. Rev Fish Biol Fish 14: 251–275.

AGRADECIMENTOS/ACKNOWLEDGEMENTS

Este documento está quase a findar e curiosamente ainda não abandonei a questão "produção". De facto, o que acabo de vos apresentar representa uma quantificação de algo (ou muitos algos), ou seja uma produção. Produção esta sujeita a variações externas, nomeadamente ao estímulo e ao acreditar de várias pessoas que tornaram a regra válida de que "não há produções negativas"! É a elas a quem dirijo o meu sincero obrigada!

Começo então por referir as pessoas mais directamente envolvidas neste trabalho:

Foi um privilégio trabalhar com os meus orientadores, ambos são um exemplo para mim! Obrigada por estarem presentes neste passo importante da minha vida!

Ao Professor Miguel Pardal, meu orientador! Agradeço precisamente por ser um orientador no sentido mais genuíno da palavra, pela confiança, constante incentivo e apoio ao longo de anos de trabalho em conjunto. Mas sobretudo deixo um obrigada por estar atento, e dar aquela palavra amiga quando é preciso!

Ao Professor Henrique Cabral, meu co-orientador! Agradeço o estímulo científico, a disponibilidade para orientar e os conselhos que muito valorizaram o presente trabalho. O seu profissionalismo e a serenidade com que aborda as questões mais complexas serão sempre um marco para mim!

Ao Professor João Carlos Marques, pelo seu apoio científico e logístico, há já alguns anos de trabalho no IMAR Coimbra.

To Søren Nielsen! For introducing me into a new "research world", for the precious advises and, I should also say, for the patience! Thanks for the friendly way he receive me in Copenhagen (and the lovely Portuguese lunch).

Ao Filipe Martinho, companheiro de trabalho e amigo! Pela discussão das "dúvidas científicas", pela prontidão com que abarcou a resolução dos meus inúmeros apelos. Pois bem, "*Muito obrigada é o que te desejo!*"

A todos os restantes co-autores dos trabalhos apresentados na tese, pelo seu contributo para esta produção: Patrícia Cardoso, Susana Ferreira, Ana Isabel Liliebø, Ricardo Leitão, Dave Raffaelli, Tiago Verdelhos e Ivan Viegas.

A todos os colegas que participaram nas saídas de campo, a quem já fui agradecendo nos vários capítulos desta tese.

À Matildinha pela copiosa e paciente tarefa de ler a ultima versão desta tese, mas também pelo incentivo e amizade!

Na anterior tarefa incluo o André, pela sua ajuda na fase finalíssima desta tese!

Ao Júlio Dolbeth, por ter tornado este documento numa peça única para coleccionadores de arte contemporânea, ao contribuir com a capa da presente tese!

À Gabi, pelo seu entusiasmo e sua preocupação com o meu bem estar!, pelos seus emails amigos!

A todos colegas e amigos que conheci no IMAR – Coimbra, que tornaram e tornam o dia-a-dia mais alegre. Obrigada João Neto, Cláudia, Joana, Arantza, Lui Malgalho, kalangas João e Filipe, Nelson, Júnior, Pileco, Alexandra, Elsa, Irene, Daniel, Ricardo, Isabel, Sara, Margarida, Rute, "Sónias", Helena, ... e todos os restantes elementos desta grande equipa, e aqueles já mencionados anteriormente!

Em especial, a todos os estiveram pela "sala do alunos", aquando os meus momentos de *abstracção* (?!)...

Para último, deixo obrigada às pessoas que mais cuidaram da minha "saúde mental" ao longo da desta produção. Convosco o saldo só poderia ser positivo!

Aos amigos, aqueles que estiveram nos bons e nos menos bons momentos!

Às minhas queridas manjericões Adriana e Lilita, que tão prontamente me delegaram para a categoria de rosa... mas cabemos na mesma jarra, né? (kkkk)!, à companheira Maria João, ao Mário e *Lolinhas*, por me acolherem na sua casa!, aos espinhenses Mena, Du e Peter, por estarem presentes há já "mais de década"!, à Fuensanta, Emerson, e mais recentemente Patrick, pelo enorme carinho!, à Su!, pois também vai constando uma década!, À restante malta que conheci por Aveiro, Coimbra, Espinho!

Also thanks to Olmo and Hannah, for letting me stay at the cosiest place of Copenhagen!, to Niels, for his help in my first days at a foreign country! Thanks to -J- and to all the nice people I've have met during my stay in Copenhagen!

Ao Andrézinho, pelo seu empenho no meu sorrir!

À minha família!

Aos meus pais, António e Lina, e mais uma vez ao meu mano, Jú! Vocês são a minha estrutura! A minha fonte "energias renováveis" e motivo grande de incentivo e inspiração! O meu (e)terno obrigada!