

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

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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. *Pomatoschistus 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* hypothesis was raised, as the salinity incursion increased the piscivorous marine adventitious species in the downstream areas. *Pomatoschistus 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 conditions during the 3-year studied period.

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1. Introduction

The gobies *Pomatoschistus minutus* and *Pomatoschistus microps* are important inhabitants of lagoons, coastal areas and estuaries of the Atlantic and Mediterranean regions (Jaquet and Raffaelli, 1989; Arruda et al., 1993; Leitão et al., 2006). They are recognised 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 and Guelorget, 1998; Pampoulie et al., 2000). In fact, their great adaptability endows them with the potential capacity to successfully occupy different biotopes (Bouchereau and

Guelorget, 1998). Also, they are quite relevant in trophic webs as intermediate predators, being consumers of plankton, meio- and macro-benthos (Hesthagen, 1977; Doornbos and Twisk, 1987; Jaquet and Raffaelli, 1989; Salgado et al., 2004; Leitão et al., 2006), and prey of several larger fishes (Arruda et al., 1993) and birds (Doornbos, 1984). With regard to the structuring factors influencing their populations, combinations of temperature and salinity, which may constrain the development and survival of eggs and larvae (Fonds and Van Buurt, 1974; Hesthagen, 1977), food availability, sediment quality and suitable nest site availability seem determinant (Nellbring, 1993; Costa et al., 2002). 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

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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. Roessig et al., 2004; Sims et al., 2004; Cardoso et al., 2005). Taking into account the ecological importance of the *Pomatoschistus* species, their wide distribution and great plasticity, a better understanding of its life cycle and adaptations towards a changing ecosystem becomes relevant. The main goals of the present study were to understand the ability of each species to cope with environmental variations along a 3-year study period, thorough an analysis of the: (1) life cycle characteristics; (2) population spatial and temporal dynamics; and (3) secondary production.

2. Materials and methods

2.1. 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 km² area), with two arms (north and south) of distinct hydrologic characteristics. The north arm is deeper (5–10 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 6670 km² (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.

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 2 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).

2.2. 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 10–15 min duration per station. All fish caught were identified, from which *Pomatoschistus minutus* and *Pomatoschistus 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 at the bottom were measured. Algae

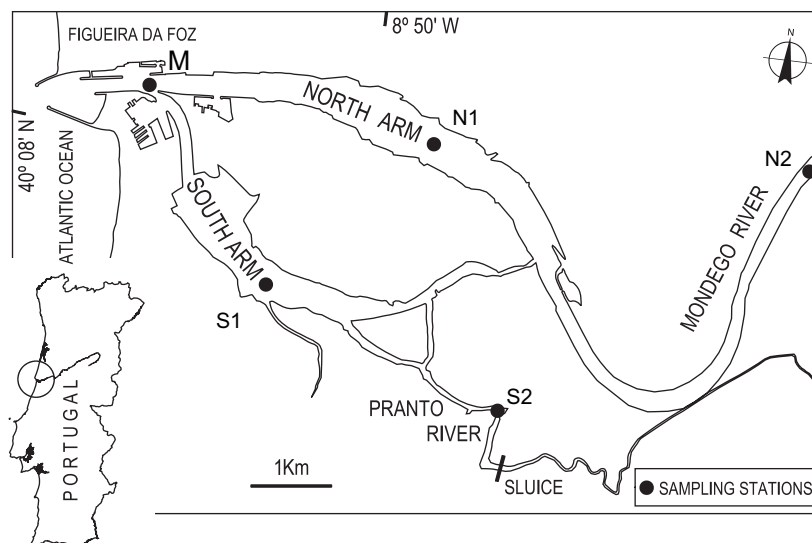


Fig. 1. Fish sampling stations on the Mondego estuary.

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.

2.3. Data analysis

The population structure of each species was defined by tracking recognisable cohorts from the successive sampling dates. Each spatial sample were pooled and analysed through size frequency distribution analysis of the successive sampling dates, in order to track recognisable 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:

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

where P_{cn} is the growth production ($\text{g WW m}^{-2} \text{y}^{-1}$) of cohort n ; N is the density (ind m^{-2}); \bar{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 (\bar{B}) was estimated according to:

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

where T is the period of study, which is always to 365 days (yearly cycles) as the mean annual biomass is being computed; Nc is the number of cohorts found in the study period; \bar{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 the 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 *Pomatoschistus* spp. 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).

3. Results

3.1. Environmental conditions

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 flow 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, in the estuary's mouth (station M) salinity presented typical values for marine water, except for the winter 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 values (Fig. 2B). The most upstream area (station N2) showed the lowest salinities, ranging between 0 and 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 high water temperatures were 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 – 26°C night temperature at S2 and N2). For the 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 the upstream (station M, annual means 9.6 – 10.8 mg l^{-1}) to the 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).

3.2. 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 *Pomatoschistus 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 *Pomatoschistus 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).

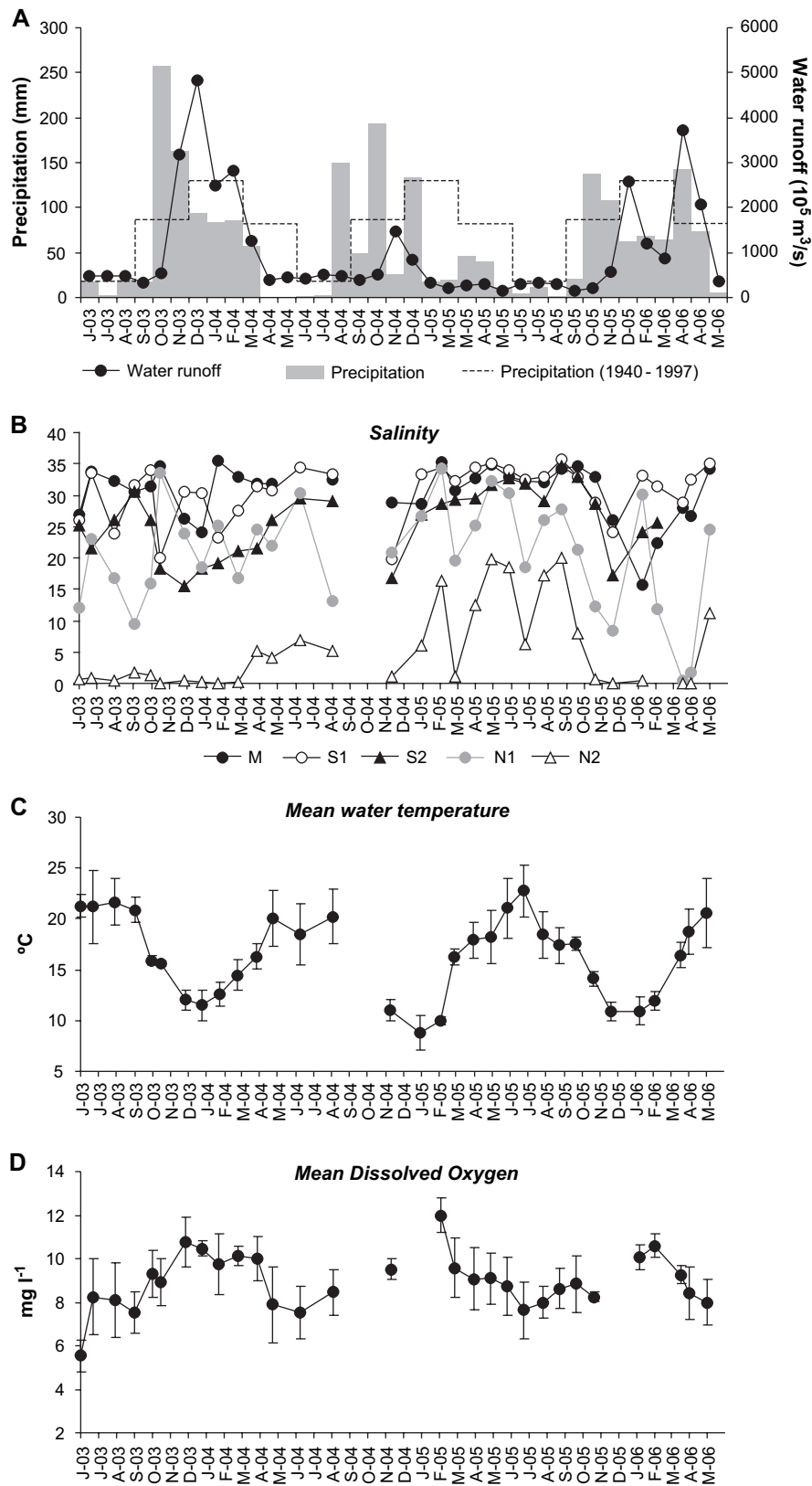


Fig. 2. Temporal variations of: (A) freshwater runoff of the Mondego estuary, precipitation during the study period and mean precipitation for central Portugal during the period of 1940–1997; (B) mean water temperature ± standard deviation; (C) salinity in the different sampling stations; and (D) mean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

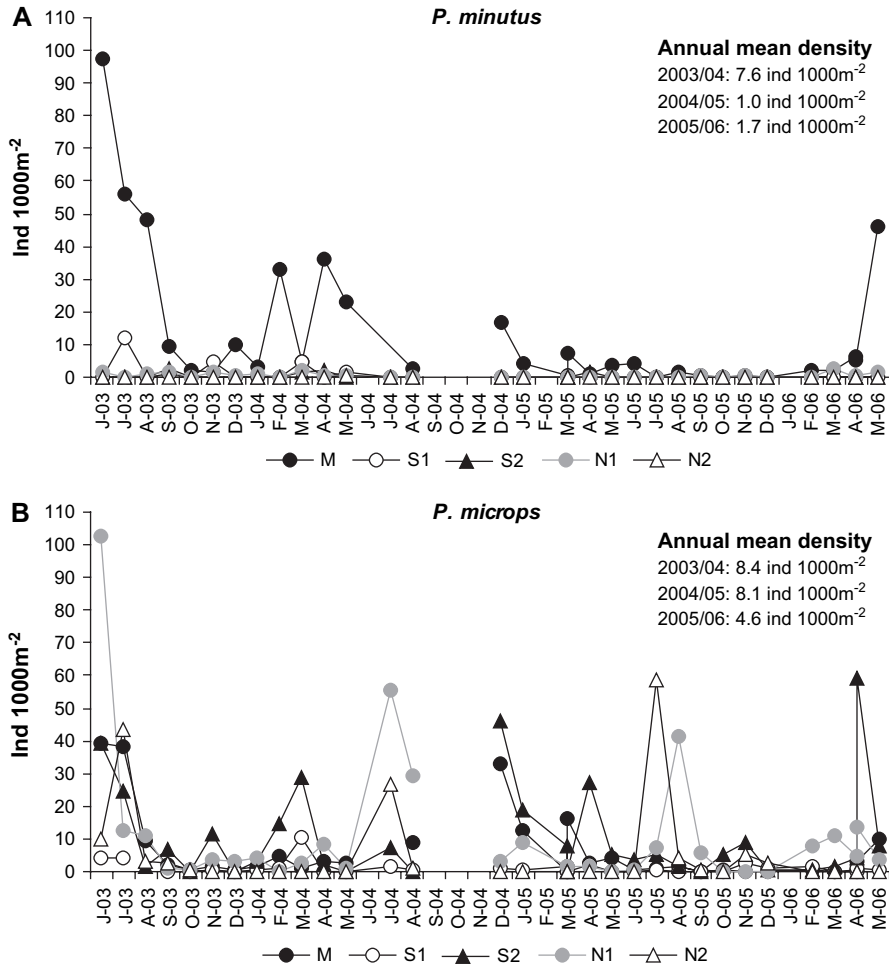


Fig. 3. Spatial and temporal distribution patterns for (A) *Pomatoschistus minutus*; and (B) *P. microps* in the Mondego estuary, with indication of the mean annual densities.

Comparing both species, *Pomatoschistus microps* attained higher densities than *Pomatoschistus minutus* (Fig. 3). In 2004/05, *P. minutus* had the lowest annual mean density (1.0 ind 1000 m⁻²), while *P. microps* only showed a marked decrease for 2005/06 (4.6 ind 1000 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). *Pomatoschistus 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 (Figs. 3B and 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 *Pomatoschistus 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 *Pomatoschistus 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).

3.3. Population structure and growth

Both *Pomatoschistus* species seem to have discontinuous reproduction (Fig. 5). For *Pomatoschistus 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 larger individual measuring 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, yet the presence of the two new length classes in April 2006 suggests that the older class could belong to it and so this was included in the November recruitments (cohort 9, Fig. 5A). The mean

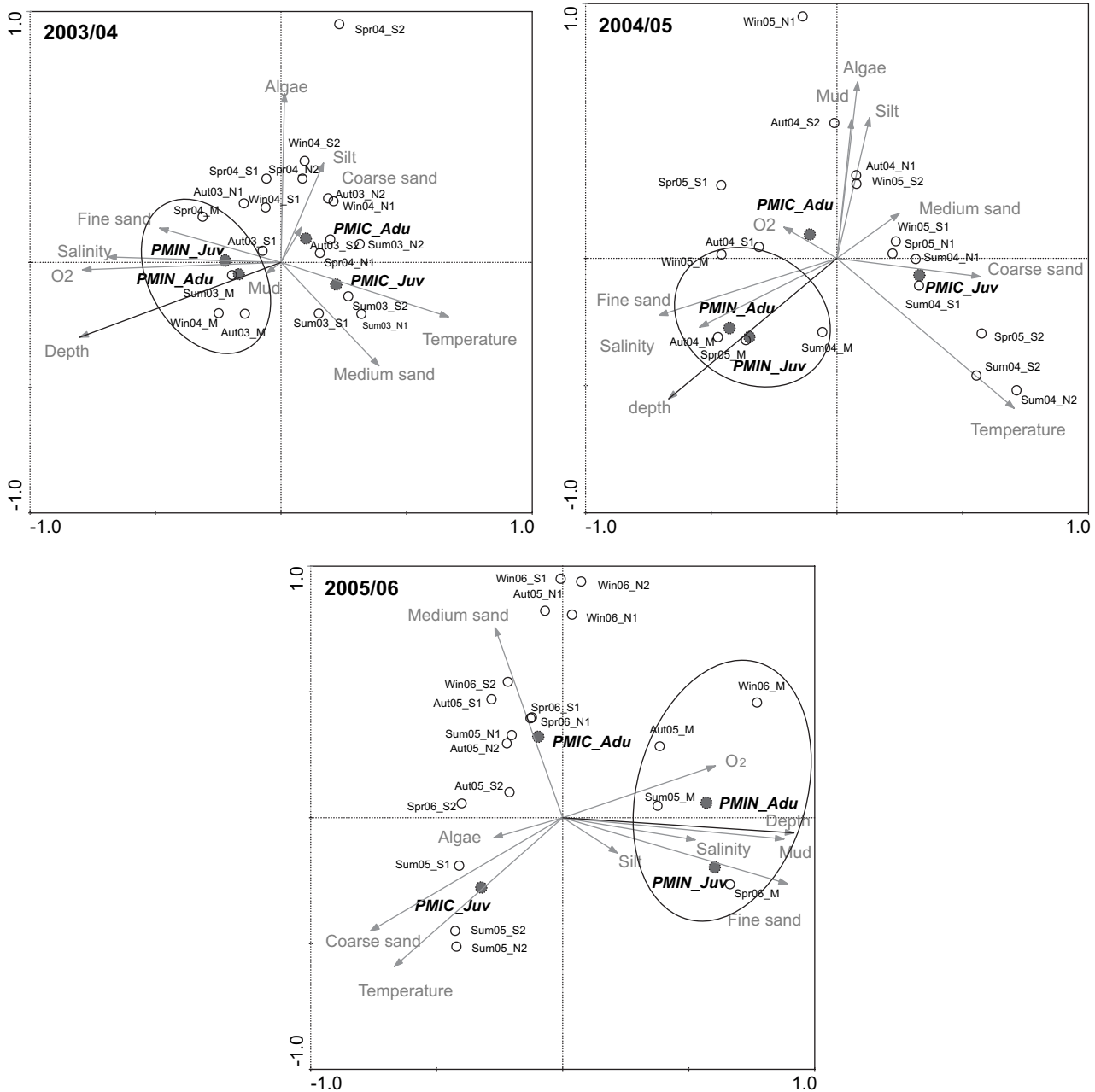


Fig. 4. CCA ordination diagram relative to the fish density data for the 3-year study period. Gray circles, *Pomatoschistus* spp. juveniles and adults densities; open circles, stations positions within the ordination space; vector lines, relationship of significant environmental variables to the ordination axis, whose length is proportional to their relative significance.

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 recruiters showed higher growth rate than the November recruiters (Fig. 5B). The exception occurred from day 180 to 300, corresponding to summer months for the November recruiters with higher growth rate, and winter months for April recruiters (Fig. 5B). Life span varied between 18 and 19 months (Fig. 5A,B).

For *Pomatoschistus microps* it seems 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, yet these seem to appear short after, in April (cohort 12, Fig. 5C). The mean growth rate of both April recruiters (C1, C4, C7, C10, C13) and January recruiters (C3, C6, C9, C12) was higher than the June recruiters (C2, C5, C8, C11) (Fig. 5D). Life span varied between 15 and 17 months (Fig. 5C,D).

3.4. Production

Annual production and mean biomass estimates showed a clear decreasing trend along the study period for *Pomatoschistus minutus*, while for *Pomatoschistus microps* similar

Table 1

Spearman rank correlation coefficients between fish mean densities and environmental factors for the 3 years ($n = 12$ for 2003/04 and 2005/06, and $n = 8$ for 2004/05). NS, non-significant. *Significant at $p < 0.05$

	<i>P. minutus</i>			<i>P. microps</i>		
	2003/04	2004/05	2005/06	2003/04	2004/05	2005/06
<i>Juveniles</i>						
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
<i>Adults</i>						
Temp.	-0.01 NS	-0.10 NS	-0.14 NS	0.45*	-0.19 NS	0.15 NS
Salinity	0.80*	0.22NS	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

values were obtained for all years (Table 2). The lowest production values were obtained in 2005/06 (Table 2). When comparing both species, production values were considerably higher for *P. minutus*, especially in 2003/04. Mean annual biomass was also higher for *P. minutus*, except for 2005/06 (Table 2). For *P. microps*, P/\bar{B} ratios were similar throughout the study period, with the lowest value in 2004/05, while for *P. minutus* higher P/\bar{B} ratios were registered in 2003/04 and 2004/05 (Table 2), years with higher temperatures in the spring and early summer, compared to the others.

4. Discussion

4.1. Life cycle general considerations

Differences in the recruitments were found for both *Pomatoschistus* species in the Mondego estuary when compared to

other Atlantic (Healey, 1972; Fonds, 1973; Hesthagen, 1977; Arruda et al., 1993; Bouchereau and Guelorget, 1998) and Mediterranean regions (Bouchereau et al., 1990; Bouchereau and Guelorget, 1998), which may be related with the temperature. This was clear for *Pomatoschistus 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 and 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 4.0–5.0 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

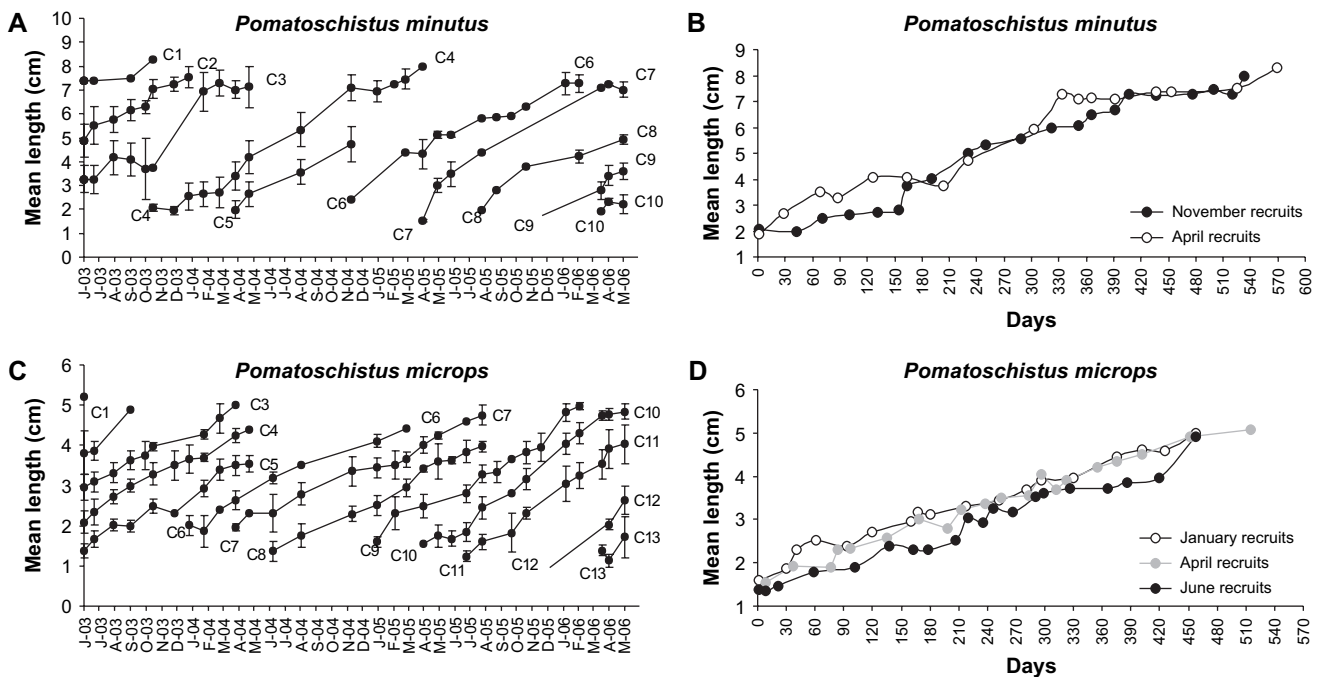


Fig. 5. Linear growth of the cohorts, mean length class measure \pm standard deviation, with indication of the appearance of the first individual for each cohort (A, C) and mean linear growth of each recruitment (B, D) for *Pomatoschistus minutus* and *P. microps*.

Table 2
Growth production, mean density and P/\bar{B} ratio (y^{-1}) estimates. Conversions to AFDW according to: g WW/g AFDW = 1/0.251; kJ/g AFDW = 25.57 (Brey, 2001). (A) *Pomatoschistus minutus*; and (B) *P. microps*. *References in Costa et al. (2002)

Location	Study period	Mean abundance (Ind m^{-2})	Production	Production: units converted (g AFDW $m^{-2} yr^{-1}$)	P/\bar{B} (y^{-1})	Sampling gear	Production method	Reference
(A) <i>P. minutus</i>								
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 and 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 and 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
(B) <i>P. microps</i>								
Skagerrak-Gull: Gullmarsvik, 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 and Rosenberg, 1982
Grevelingen estuary, Netherlands	1981	–	0+ group: 0.81 g AFDW $m^{-2} yr^{-1}$	0.81	–	Beam trawl	Instantaneous growth	Doornbos and 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	4.5–5.4 2.52–4.49	–	–	Del Norte Campos, 1995*
Sylt-Rømø Bight, Germany	Jul–Sep 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

cohorts of April recruiters. For the parental cohort of November recruiters there were no clear evidences of migration.

Recruitment seemed discontinuous for *Pomatoschistus 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 and Miller (1981), Bouchereau et al. (1991) Bouchereau and Guelorget (1998) and Pampoulie (2001), who claim a long breeding season for the species. In fact, Mazzoldi and 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 peaks in the breeding period, which may be the case of *P. microps* in the Mondego estuary.

The spring recruiters of *Pomatoschistus minutus* had higher mean growth rates, probably due to temperature, as also seen by Arruda et al. (1993) and Bouchereau and Guelorget (1998). Yet, for *Pomatoschistus microps* this difference was not pronounced when comparing the winter (January) and spring (April and June) recruiters. 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 in 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 and Guelorget, 1998), while 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 and Miller, 1981; Bouchereau and Guelorget, 1998). The differences found may be related with the reproductive strategy (date and duration), the age at first maturity and the growth rates, as also proposed by Bouchereau and Guelorget (1998), Pampoulie et al. (1999), which is probably also associated with the temperature regime of the Mondego estuary.

4.2. Species spatial dynamics

Pomatoschistus minutus and *Pomatoschistus microps* have high diet overlap (Magnhagen and 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 and Wiederholm, 1982; Costa et al., 2002). In the Mondego estuary, these species seem 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, *P. microps* distributed in areas with higher temperatures and the density was positively correlated with temperature. Also, when plotted the densities of both species with temperature, *P. microps* density seemed to follow the seasonal variation of temperature (Fig. 6), although recruitment also occurred in the winter. Besides temperature, salinity also plays an important role in the distribution and abundance patterns, as observed by Pampoulie 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* (maximum egg survival at 5–35 with maximum larval size at 5–15, against 15–35 with maximum larval size at 35, for each species respectively), explaining that while *P. microps* distributed within all estuary, *P. minutus* occurred mainly at the estuary mouth, correlated positively with salinity in the 2003/04. So, *P. microps* may take advantage in dispersing to other estuarine areas, as it is more tolerant to salinity and temperature variations, and also due to the presence of alternative food sources, such as *Corophium* spp., highly abundant in the upstream areas (Leitão et al., 2006).

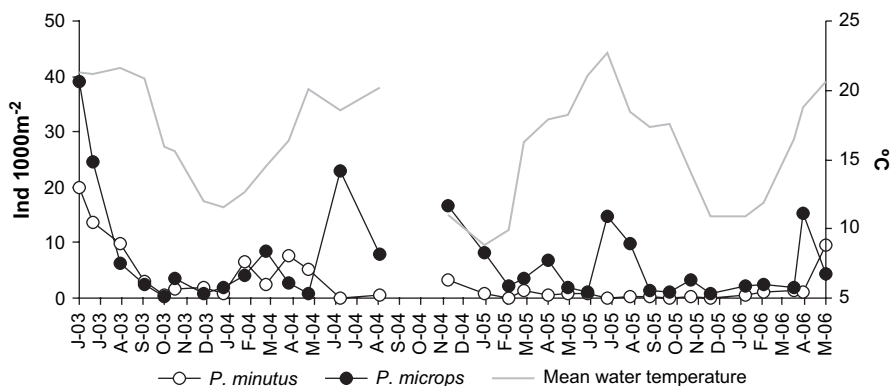


Fig. 6. Temporal variations of *P. minutus* and *P. microps* densities, and mean water temperature for the whole Mondego estuary.

4.3. Species temporal dynamics and production

For *Pomatoschistus minutus* a clear decrease in density (especially evident in 2005) and production was observed. Several hypotheses may be causing the 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 environment 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 (unpublished results). 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 *Pomatoschistus 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 *Pomatoschistus minutus* was higher than for *Pomatoschistus microps* in 2003/04 and 2004/05, although with lower mean density. This is probably related with the life cycle characteristics, as *P. minutus* can attain higher biomass and slight higher growth rate than *P. microps*.

Secondary production studies of these *Pomatoschistus* species are a bit dated and in literature, values were only found for North-Atlantic coastal areas (Table 2). Nevertheless, the estimates for the Mondego estuary were lower (Table 2), when it would be expected production increases with decreasing latitudes (Cowley and Whitfield, 2002). *Pomatoschistus* spp. densities seemed also lower, comparing with Phil 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 and 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 and Whitfield, 2002), different growth rates along the life cycle, as seen by Fouda and Miller (1981) for *Pomatoschistus 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 *Pomatoschistus 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.

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