Available online at www.sciencedirect.com
ScienceDirect

Estuarine, Coastal and Shelf Science 70 (2006) 85–97

ESTUARINE COASTAL AND SHELF SCIENCE
www.elsevier.com/locate/ecss

Ichthyoplankton dynamics in the Guadiana estuary and adjacent coastal area, South-East Portugal

Ana Faria*, Pedro Morais, M. Alexandra Chícharo

Centro de Ciências do Mar, Faculdade de Ciências do Mar e do Ambiente, Campus de Gambelas, Universidade do Algarve, 8005-139 Faro, Portugal

Received 23 January 2005; accepted 20 March 2006

Abstract

The species composition, abundance and distribution of the ichthyoplankton of the Guadiana estuary and adjacent coastal area were studied in relation to several environmental parameters. Sampling occurred during new moon Spring tides, at the ebb and flood, at nine stations, from March 2002 to February 2003. Temperature, salinity, dissolved inorganic macronutrients, seston and organic matter and chlorophyll *a* were determined at each station. A total of 22 and 34 fish eggs and larvae taxa were identified, respectively. The highest abundances were registered in the lower and middle part of the estuary, probably due to the presence of species that use the estuary as a preferential spawning ground, mainly *Pomatoschistus* spp. and *Engraulis encrasicolus sensu lato*. Temporal patterns of occurrence of ichthyoplankton allowed each species' spawning season to be determined. Two taxa dominated the ichthyoplanktonic community during spring and summer (*Pomatoschistus* spp. and *E. encrasicolus*), whereas *Sardina pilchardus* was particularly abundant during autumn and winter. The forcing variables responsible for community structure were chlorophyll *a* and seston for eggs, while temperature, salinity and nitrite explained the larval component. Comparisons of the results with previous ichthyoplankton studies of the Guadiana estuary conducted before the Alqueva dam was built also indicate that river flow has an important impact on the distribution and abundance of ichthyoplankton in the estuary.

Keywords: ichthyoplankton; spatial and temporal variation; environmental factors; Guadiana estuary; coastal zone; Alqueva dam

1. Introduction

Estuaries are unstable systems, generally having a limited number of species present. However, they may support high abundances of organisms due to their high productivity, providing important nursery areas where ichthyoplankton encounter suitable conditions for enhanced development (Moyle and Cech, 1996). Community level studies supply information on several aspects of species biology, allowing for the determination of spatial and temporal evolution of ichthyoplankton distribution (Stratoudakis et al., 2003), thus establishing preferred spawning grounds and seasons (Ishikawa et al., 2001). Moreover, it is also possible to identify factors that influence recruitment variability (Borja et al., 1998, 2002). Predation, food availability (Blaxter and Hunter, 1982; Leggett and Deblois, 1994) and environmental parameters have been pointed out as the main factors influencing ichthyoplankton dynamics. Among environmental parameters, temperature (e.g. Miranda et al., 1990; Blaxter, 1992), salinity (e.g. Loneragan et al., 1987; Whitfield, 1999) and river flow (e.g. Loneragan and Bunn, 1999; Whitfield and Harrison, 2003) are considered the most important variables affecting icthyoplankton communities in estuarine systems.

Several ichthyoplankton studies of limited temporal and/or spatial coverage have been carried out in the Guadiana estuary (SE Portugal) (Chícharo and Teodósio, 1991; Esteves et al., 2000; Chícharo et al., 2000). Chícharo and Teodósio (1991) and Chícharo et al. (2000) studied ichthyoplankton community composition, whereas Esteves et al. (2000) investigated factors influencing larval abundance and nutritional condition.

The Guadiana river basin has been strongly modified over the last decades, with numerous dams constructed that have

---

* Corresponding author.
E-mail address: afaria@ualg.pt (A. Faria).

0272-7714/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2006.05.032

considerably reduced river flow to the estuary. In February 2002, one month before the beginning of this study, the floodgates of the Alqueva dam were closed. This was the largest and most recent dam built in the Guadiana basin. The present study of the Guadiana estuary ichthyoplankton was based on sampling over an annual period and constitutes the first study conducted after the closure of Alqueva dam floodgates. This study is also the most comprehensive conducted in the Guadiana to date. It aims to provide a detailed characterization of the ichthyoplankton community and its spatio-temporal dynamics in the Guadiana estuary and adjacent coastal zone, an area that is poorly characterized. The main objectives are the following: (a) to identify and quantify the abundance of the ichthyoplankton in the estuary and adjacent coastal area; (b) to study the spatial and temporal distribution of ichthyoplankton in the estuary and adjacent coastal area; (c) to analyse the effects of the tides on the distribution of the ichthyoplankton in the estuary; (d) to identify the most important spawning grounds and seasons for locally abundant fish species; and (e) to evaluate the influence of environmental parameters on ichthyoplankton spatio-temporal dynamics.

2. Material and methods

2.1. Study site

This study took place in the Guadiana estuary, on the southern border of Portugal and Spain and in its adjacent coastal area. This estuary is approximately 70 km in length, with the lower 50 km constituting the southern border of Portugal and Spain (Iberian Peninsula, Europe) (Fig. 1a). It is a mesotidal estuary having an average depth of 6.5 m, occupying an area of 22 km^2, with tidal amplitudes that range from 1.3 to 3.5 m. The Guadiana river flow presents a marked variability between and within years, due to the influence of Mediterranean climate characteristics. The average annual rainfall fluctuates between 561 and 600 mm in the Portuguese basin, with considerable variation between years. This variability in rainfall is reflected in the Guadiana river flow, with average river flow oscillating between 8 and 63 m^3 s^{-1} during dry years, between 170 and 190 m^3 s^{-1} in typical years, and between 412 and 463 m^3 s^{-1} in wet years (Bettencourt et al., 2003).

2.2. Sampling strategy and field methodology

Eulerian sampling was carried out during new moon Spring tides at low and high tides, from March 2002 to February 2003 at nine stations: seven inside the estuary and two in the coastal area. Of the coastal stations, st. 1 was located in front of Praia de Santo António outside the direct influence of the estuarine outflow, whereas st. 2 was situated in the area where the river plume is formed (Fig. 1b). A boat equipped with an 80 hp engine was used for all sampling, except in February 2003 when a boat equipped with a 30 hp engine was used due to technical problems. Due to these technical problems, high tide sampling in January and February 2003 could not be carried out. Horizontal profiles of temperature and salinity were recorded with a Yellow Springs Instruments (YSI) 6600 probe. Sub-surface zooplankton trawls were carried out with a 250 μm net mesh, equipped with a flow meter (General Oceanics), and the collected samples were immediately preserved with buffered formaldehyde (4% final concentration). At the same depth as the zooplankton trawls, water samples were collected for the analysis of dissolved inorganic macronutrients (ammonium, nitrate, nitrite, orthophosphate and silicate), seston, suspended organic matter and chlorophyll *a*. Samples were cooled until laboratory processing (Kirkwood, 1996).

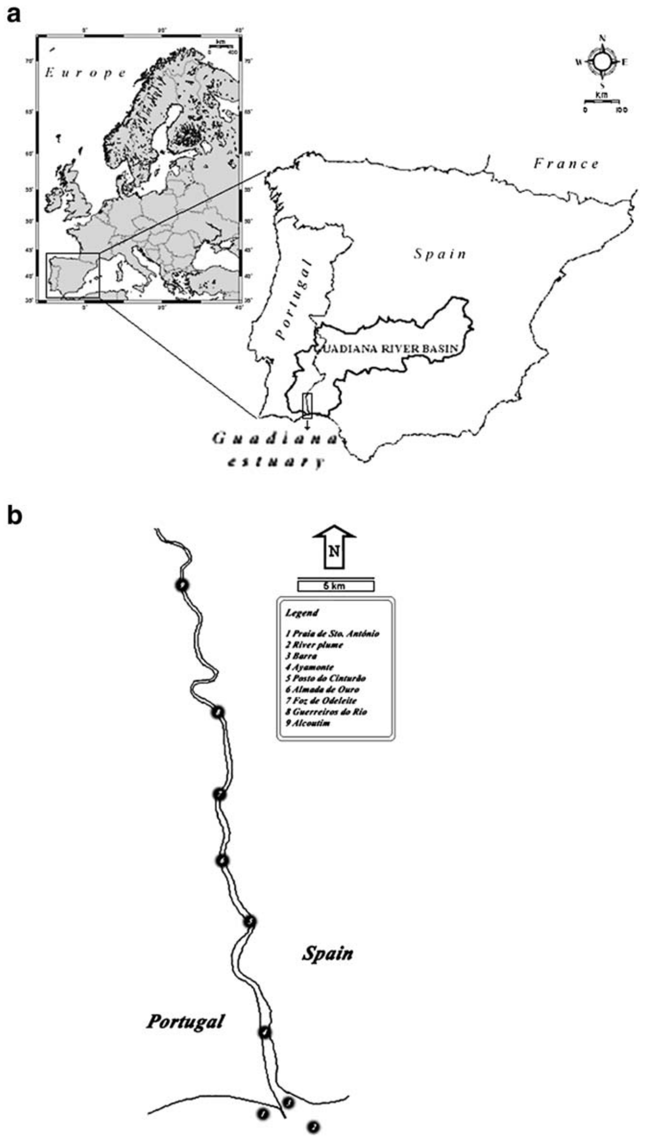

Fig. 1. Geographical context of the Guadiana estuary in the Iberian Peninsula (Europe) (a) and sampling stations localization along the estuary and in the adjacent coastal area (b). Stations 1 and 2 were considered coastal, stations 3 and 4 the lower estuary, stations 5 to 7 the middle estuary and stations 8 and 9 the upper estuary.

2.3. Laboratory analysis

In the laboratory, ichthyoplankton was sorted from the zooplankton samples and identified to lowest possible taxa (Petersen, 1919; D'Ancona, 1931–1956; Fives, 1970, 1976;

Marinaro, 1971; Nichols, 1971, 1976; Demir, 1976; Russell, 1976; Garcia and Moyano, 1990; Lee, 1996; Ré, 1999).

In order to determine dissolved inorganic macronutrient levels, water samples were filtered through 0.45 μm pore cellulose acetate filters (MSI) and preserved frozen until being subjected to spectrophotometric analyses (Grasshoff et al., 1983; Kirkwood, 1996). Water samples collected for seston and suspended organic matter analysis were filtered through 0.7 μm pore filters (Whatman GF/F); filters were washed three times with distilled water and dried at 60 °C for seston determination. Subsequently, the sample was burned at 450 °C to allow organic matter determination (Greenberg et al., 1992). Finally, water samples collected for chlorophyll *a* determination were filtered through 0.7 μm pore filters (Whatman GF/F) without exceeding vacuum pressures of 100 mmHg, and the filters were kept frozen (−20 °C) until being subjected to fluorimetric analysis (Knap et al., 1996).

2.4. Data analysis

The analysis of river flow was based on data recorded at the Pulo do Lobo hydrometric station (code: 27L/01), located 85 km above the Guadiana estuary mouth. River flow data were made available by the "Instituto Nacional da Água" (INAG, 2004). Monthly average values of river flow were calculated for each sampling date from the daily average river flow observed since last sampling.

Non-parametric ANOSIM analysis and non-parametric multidimensional scaling (MDS) were used to examine seasonal and spatial patterns of icthyoplankton distribution and abundance according to five established factors: "Month" (month when sampling occurred); "Season" (spring = April, May and June 2002, summer = July, August and September 2002, autumn = October, November and December 2002, and winter = March 2002, January and February 2003); "Station" (from sampling st. 1 to sampling st. 9); "Studied Area" (coastal area = st. 1 and 2, lower estuary = st. 3 and 4, middle estuary = st. 5, 6 and 7, and upper estuary = st. 8 and 9); "Tide" (low and high). The similarity matrix constructed to perform these analyses was made after $\log(x + 1)$ data transformation and setting Euclidean distance as the similarity measure. ANOSIM analysis, which employs *R* statistics, was used to examine the existence of meaningful differences between the established groups for each considered factor (Clarke and Warwick, 2001). *R* values similar to 0 indicate small differences in the evolution pattern of the analysed parameters, in contrast to *R* values close to 1.

BIOENV analysis, which is comparable to a multiple regression analysis where all possible permutations of variables are examined, was performed to test the relationship between community composition and environmental variables. The analysis used the Spearman correlation coefficient, Euclidian distance as the similarity measure, and the base results were square root transformed. The ten variables used in the analysis were temperature (1), salinity (2), chlorophyll *a* (3), suspended organic matter (4), seston (5), ammonia (6), nitrates (7), nitrites (8), orthophosphates (9) and silicates (10). All multivariate techniques (ANOSIM, MDS and BIO-ENV) were applied using Primer 5.2.1 software (Primer-E Ltd.). Horizontal profiles of temperature, salinity, seston, suspended organic matter and chlorophyll *a* were constructed using Surfer 8.01 software (Golden Software Inc.), using kriging (linear variogram model) as the gridding method.

3. Results

3.1. Environmental parameters

River flow peaked from March 28 to April 15, 2002 (105.3 ± 179.8 $m^3 s^{-1}$), decreased abruptly the following month, and remained reduced until late November. Minimum flows of 3.9 ± 3.0 $m^3 s^{-1}$ were observed between June 12 and July 10, 2002 (Fig. 2a and b). The periods of February 27 to March 27, 2002, March 28 to April 15, 2002, December 5

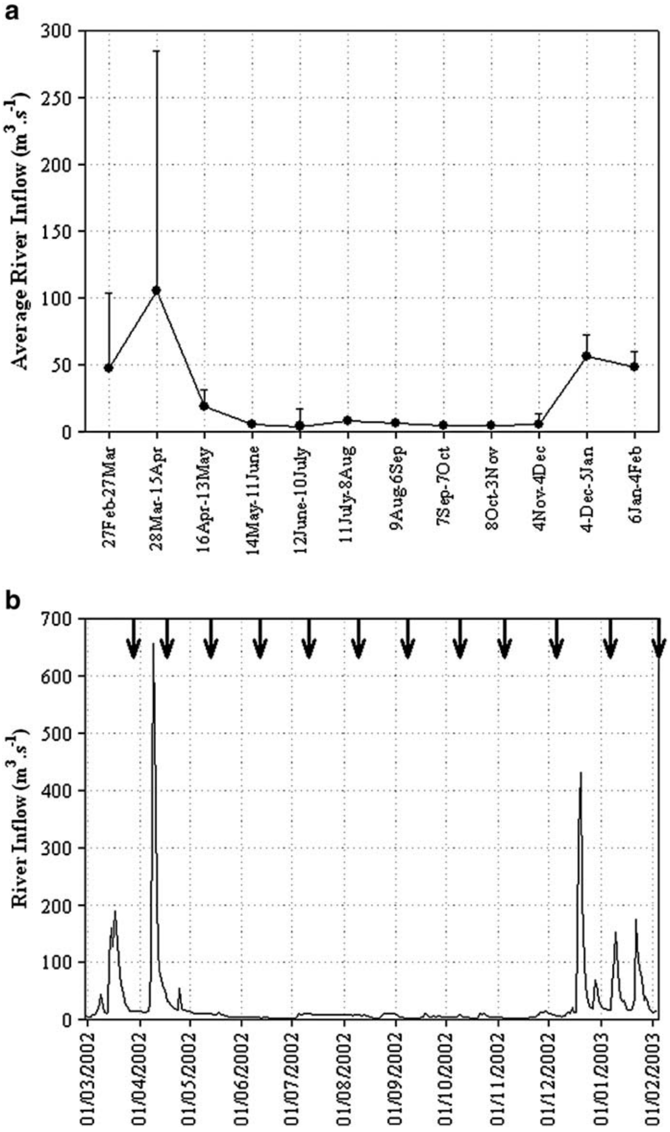

Fig. 2. Average river flow ($m^3 s^{-1}$) and respective standard deviation (a) and daily average river flow registered in Pulo do Lobo hydrometric station (b). Arrows at the top of the lower graph correspond to the sampling days.

to January 5, 2003 and January 6 to February 4, 2003 exhibited extreme river flow variability. The highest daily average river flow, 656.3 $m^3 s^{-1}$, was registered a few days before the April 2002 sampling (Fig. 2a and b).

Water temperature generally increased upstream, but in winter this tendency was inverted (Fig. 3a). Maximum water temperature (26.7 °C) was registered in August 2002 and the lowest (11.6 °C) in February 2003, both in the upper estuary.

Salinity increased towards the coastal area, ranging from 0.1 (st. 9) to 36.3 (st.1) (Fig. 3b). A pronounced decrease in salinity was detected in April 2002, coincident with the highest river flow registered (Fig. 2a and b). Saline intrusion was more pronounced from May to September 2002 and again from November to December 2002, periods of low river flow. Salinity decrease in October was coincident with increased rainfall.

Seston, suspended organic matter and chlorophyll *a* had an homogeneous spatial distribution pattern, increasing towards the upper estuary (Fig. 4a, b and c) during the periods of higher ichthyoplankton abundance, spring and summer. Seston concentration varied between 2.0 mg L^{-1} (July 2002) and 132.0 mg L^{-1} (July 2002) (Fig. 4a), whereas suspended organic matter ranged between 0.0 mg L^{-1} (July 2002) and 20.0 mg L^{-1} (November 2002) (Fig. 4b). Chlorophyll *a* concentration was highest in spring and summer, and varied between 0.3 μg L^{-1} (August, September and November 2002) and 12.3 μg L^{-1} (July 2002) (Fig. 4c).

According to the BIOENV analysis, chlorophyll *a*, seston and silicates were the best explanatory variables ($R = 0.452$) for defining the spatial and temporal evolution of the egg component of ichthyoplankton, while larval spatio-temporal dynamics were best explained by temperature, salinity and nitrites ($R = 0.265$).

3.2. Ichthyoplankton community characterization

Of the 22 classified taxa of fish eggs, only 6 were clearly identified to the genus or species level: *Belone belone* (Belonidae), *Arnoglossus* sp. (Bothidae), *Callionymus* sp. (Callionymidae), *Sardina pilchardus* (Clupeidae), *Engraulis encrasicolus sensu lato* (only *Engraulis encrasicolus* hereafter) (Engraulidae) and *Dicentrarchus* sp. (Moronidae). Two egg taxa were identified to the family level, Soleidae and Sparidae. The planktonic stages of *Belone belone*, *Arnoglossus* sp. and *Dicentrarchus* sp. were only captured during their egg stage.

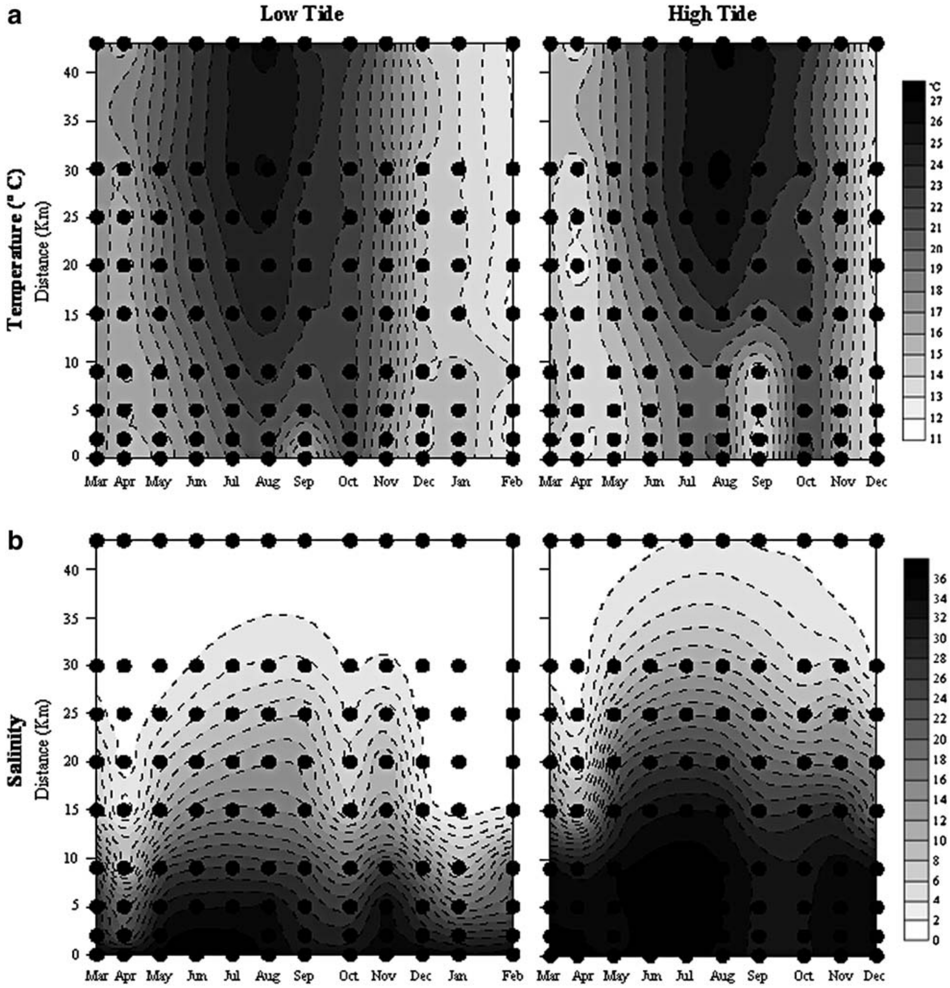

Fig. 3. Spatial and temporal evolution of surface temperature (°C) (a) and surface salinity (b) in the Guadiana estuary and adjacent coastal area, at low and high tides, from March 2002 until February 2003. Distance is measured in an upstream direction, starting at coastal station 1.

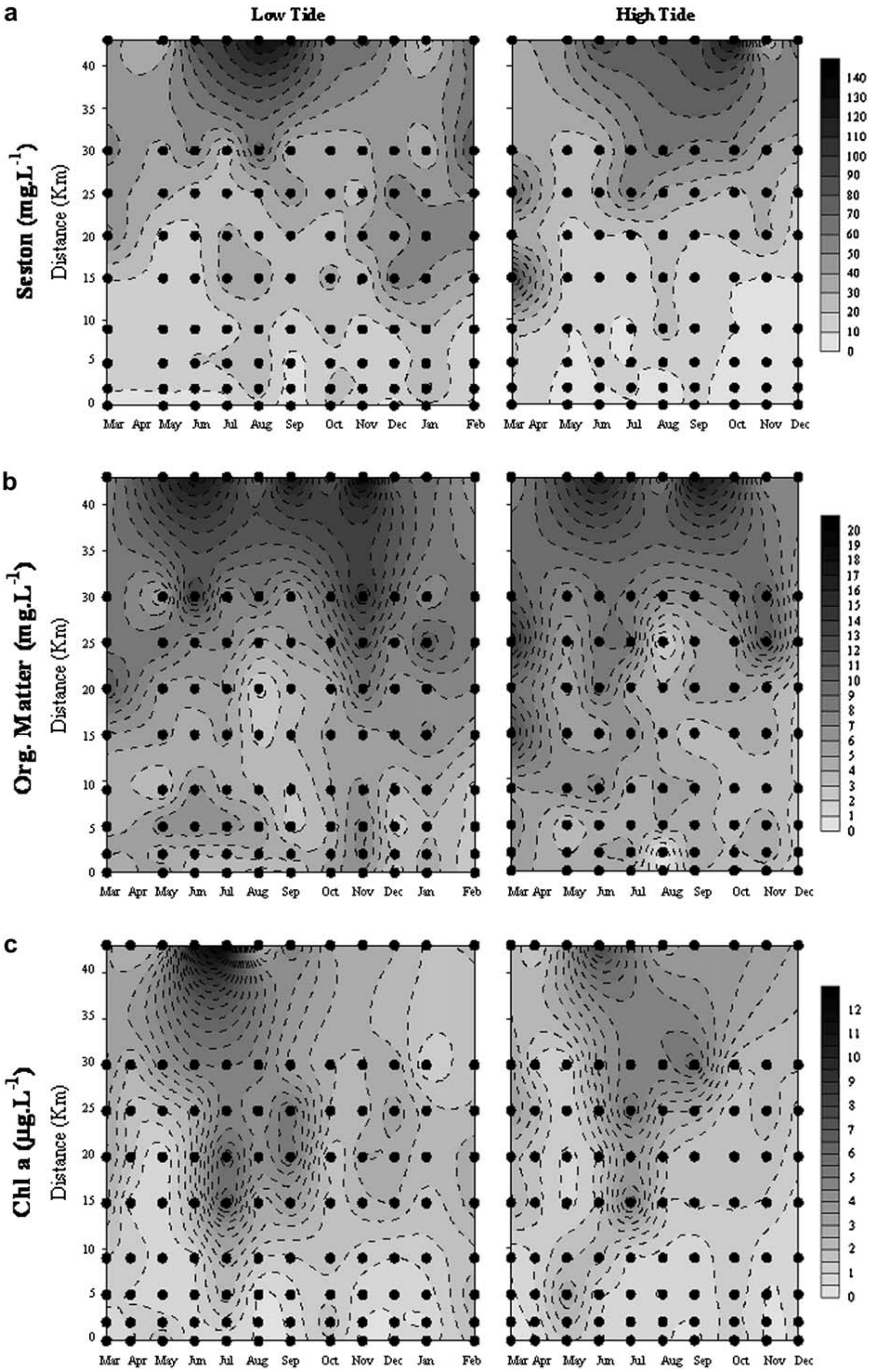

Fig. 4. Spatial and temporal evolution of surface seston (mg L^{-1}) (a), suspended organic matter (mg L^{-1}) (b), and surface chlorophyll *a* (µg L^{-1}) (c) in the Guadiana estuary and adjacent coastal area, at low and high tides, from March 2002 until February 2003. Distance is measured in an upstream direction, starting at coastal station 1.

A total of 34 larval species were identified, distributed in 13 different families. Twenty-eight taxa were identified to species, and 2 were identified to the genus level: *Callionymus* sp. and *Diplodus* spp. Six taxa were only identified to family level: Gobiidae (1), Soleidae (1) and Sparidae (4).

Most species were captured during spring and summer, with *Atherina* spp., *Parablennius gattorugine*, *Callionymus reticulatus*, *Symphodus melops*, *Symphodus bailloni*, *Solea lascaris*, *Solea senegalensis* and some Sparidae being the most abundant (Table 1). These species were preferentially distributed in the coastal area and lower estuary during spring and summer, although *Atherina* spp., *P. gattorugine* and *Parablennius pilicornis* were also collected at middle estuary stations (Table 2).

The species captured in winter were mainly present in the coastal area or in the lower estuary and included *Ammodytes*

Table 1
Seasonal occurrence of ichthyoplankton in the Guadiana estuary and adjacent coastal area form March 2002 to February 2003, with no distinction between low and high tide

Family	Species	Spring	Summer	Autumn	Winter
Blenniidae	*Coryphoblennius galerita*	X			
Callionymidae	*Callionymus* sp.	X			
Labridae	*Symphodus melops*	X			
Moronidae	*Dicentrarchus* sp.	X			
Soleidae	*Solea senegalensis*	X			
Syngnathidae	*Nerophis ophidion*	X			
Triglidae	*Trigla lyra*	X			
Atherinidae	*Atherina* spp.	X	X		
Blenniidae	*Parablennius gattorugine*	X	X		
Blenniidae	*Parablennius pilicornis*	X	X		
Bothidae	*Arnoglossus* sp.	X	X		
Callionymidae	*Callionymus reticulates*	X	X		
Engraulidae	*Engraulis encrasicolus*	X	X		
Gobiidae	*Gobius niger*	X	X		
	Pomatochistus mocrops	X	X		
	Pomatochistus minutus	X	X		
	Pomatochistus pictus	X	X		
Labridae	*Symphodus bailloni*	X	X		
Sparidae	*Diplodus* sp.	X	X		
Syngnathidae	*Syngnathus abaster*	X	X		
	Synagnathus acus	X	X		
Belonidae	*Belone belone*		X		
Mullidae	*Mullus surmuletus*		X		
Syngnathidae	*Hippocampus hippocampus*		X		
	Syngnathus typhle		X		
Clupeidae	*Sardina pilchardus*			X	X
Soleidae	*Monochirus hispidus*			X	X
Ammodytidae	*Ammodytes tobianus*				X
Soleidae	*Buglossidium luteum*				X
	Solea vulgaris				X
	Solea lascaris	X			X
Soleidade n.id.		X	X	X	X
Gobiidae n.id.		X	X		X
Sparidae n.id.		X	X	X	X
n.id.		X	X	X	X

Table 2
Spatial distribution of ichthyoplankton in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003, with no distinction between low and high tide

Family	Species	Coastal area	Low estuary	Mid estuary	High estuary
Ammodytidae	*Ammodytes tobianus*	X			
Mullidae	*Mullus surmuletus*	X			
Soleidae	*Solea vulgaris*	X			
	Monochirus hispidus	X			
Synganthidae	*Syngnathus typhle*	X			
Blenniidae	*Corphyoblennius galerita*	X	X		
Callionymidae	*Callionymus reticulates*	X	X		
	Callionymus sp.	X	X		
Clupeidae	*Sardina pilchardus*	X	X		
Labridae	*Symphodus bailloni*	X	X		
Soleidae	*Solea lascaris*	X	X		
	Solea senegalensis	X	X		
Soleidae	*Buglossidium luteum*		X		
Syngnathidae	*Nerophis ophidion*		X		
	Symphodus melops		X		
Triglidae	*Trigla lyra*		X		
Atherinidae	*Atherina* spp.	X	X	X	
Blenniiae	*Parablennius gattorugine*	X	X	X	
	Parablennius pilicornis	X	X	X	
Bothidae	*Arnoglossus* sp.	X	X	X	
Moronidae	*Dicentrarchus* sp.	X	X	X	
Sparidae	*Diplodus* sp.	X	X	X	
Belonidae	*Belone belone*			X	
Syngnathidae	*Hippocampus hippocampus*			X	
Engraulidae	*Engraulis encrasicolus*	X	X	X	X
Gobiidae	*Gobius niger*	X	X	X	X
	Pomatochistus minutus	X	X	X	X
	Pomatochistus microps	X	X	X	X
	Pomatochistus pictus	X	X	X	X
Syngnathidae	*Syngnathus abaster*		X	X	X
	Syngnathus acus		X	X	X
Soleidade n.id.		X	X	X	
Gobiidae n.id.		X	X	X	X
Sparidae n.id.		X	X	X	
n.id.		X	X	X	

tobianus and some Soleidae, such as *Buglossidium luteum*, *Monochirus hispidus* and *Solea vulgaris* (Tables 1 and 2). *Sardina pilchardus* was also collected mainly during autumn and winter and at downstream stations (Tables 1 and 2).

Egg and larval abundance were higher in the coastal area and in the lower estuary during spring and summer, with maximums of 2122 eggs 100 m^{-3} and 285 larvae 100 m^{-3} in June 2002 (Figs. 5 and 6). In upstream stations, highest ichthyoplankton abundance was observed during June and July 2002. Increasing ichthyoplankton abundance coincided with an increase in water temperature (Fig. 3a) and a decrease in river flow (Fig. 2a and b). Ichthyoplankton abundance decreased in autumn and winter, except in November in downstream stations (Fig. 5), coinciding with *Sardina pilchardus* spawning (Fig. 9).

Engraulis encrasicolus was the dominant species in the egg component, accounting for 50% of all the eggs sampled. In general, more eggs of *E. encrasicolus* were caught during low tide than in high tide. Although present in the whole estuary and adjacent coastal area, their presence was higher in the lower and middle estuary, mainly in March, May and June 2002, with a maximum abundance of 2106 eggs 100 m^{-3} in June 2002, and a strong evidence of tidal transport was clearly observed. In April 2002, a sharp decrease in abundance (Fig. 7) coincided with the maximum river flow (105.3 ± 179.81 $m^3\ s^{-1}$) (Fig. 2).

Engraulis encrasicolus larvae represented 22% of the total captured larvae. From May to September 2002, it was one of the species with the highest contribution to upstream larval assemblages; however, it was most abundant in the middle estuary. The highest abundance (218 larvae 100 m^{-3}) was registered during June 2002, when the species comprised more than

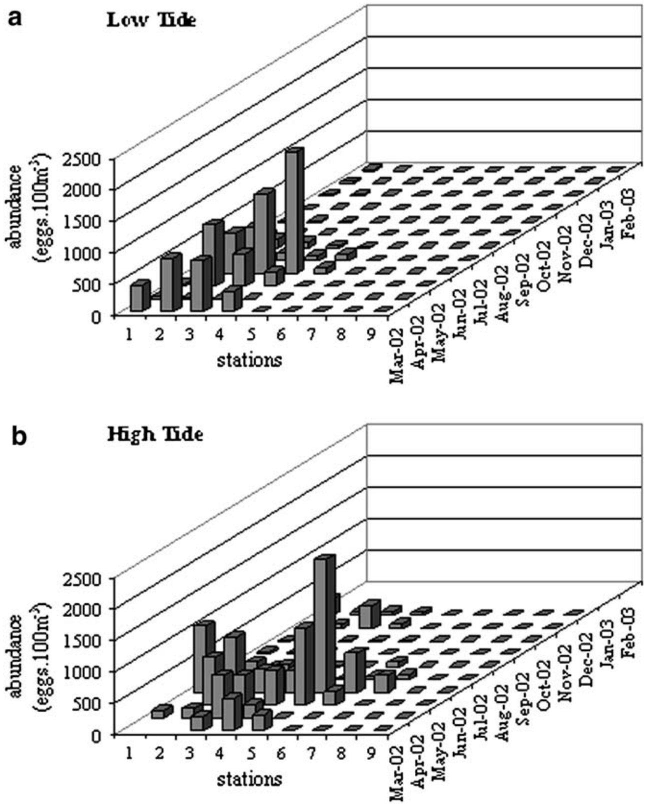

Fig. 5. Spatial and temporal evolution of total egg abundance (eggs 100 m^{-3}), captured in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003, at low tide (a) and high tide (b).

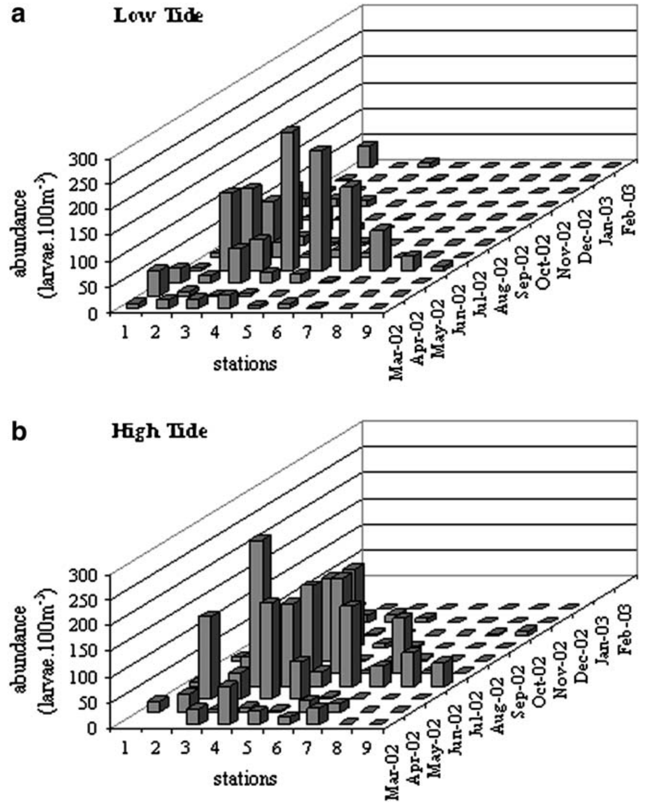

Fig. 6. Spatial and temporal evolution of total larval abundance (larvae 100 m^{-3}), captured in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003, at low tide (a) and high tide (b).

90% of total larval abundance, whereas in winter it was very scarce (Fig. 8).

Sardina pilchardus eggs represented only 3.4% of all eggs, however they were relatively abundant during winter and spring in downstream stations (Fig. 9). A maximum abundance of 255 eggs 100 m^{-3} was registered in November 2002. Unlike *Engraulis encrasicolus* eggs, the presence of *S. pilchardus* eggs was always higher during the high tide than in the low tide (Fig. 9).

Sardina pilchardus was not very abundant, comprising only 1.2% of the total of captured larvae. It was present mainly in the coastal area and lower estuary (Fig. 10). Although collected in autumn and winter, its abundance was highest in June 2002 (16 larvae 100 m^{-3}).

Gobiidae dominated the larval abundance, constituting 65% of the captures; the most abundant genus was *Pomatoschistus*. Gobiid species were present during all months, with maximum abundances in summer. Although distributed throughout the estuary and adjacent coastal area, their presence was reduced in the upper estuary (Fig. 11).

The ANOSIM analysis revealed that ‘‘Studied Area’’ and ‘‘Season’’ were the most important factors structuring the ichthyoplankton community. The egg component in the coastal area and lower estuary were similar to one another ($R = 0.058$; $p = 1.2$), as were the middle and upper estuary ($R = 0.099$; $p = 23.4$). A seasonal approach revealed that the egg community was most similar during winter and spring ($R = 0.094$; $p = 3.9$), in contrast with autumn vs. summer ($R = 0.586$; $p = 0.1$) and autumn vs. spring ($R = 0.412$; $p = 0.1$). For larvae, the analysis revealed that the most similar study areas were the coastal area and lower estuary ($R = 0.006$; $p = 32.9$), just as determined for the eggs. Seasonally, the closest groups were spring and summer ($R = 0.04$; $p = 2.4$), while the most distant were autumn vs. summer ($R = 0.463$; $p = 0.1$) and autumn vs. spring ($R = 0.436$; $p = 0.1$) (Table 3). These findings are easily observed in the MDS analysis (Fig. 12).

4. Discussion

4.1. Ichthyoplankton and its temporal and spatial abundance and distribution

In the present study 38 species were identified, whereas 24 and 11 taxa were identified in the Guadiana estuary by Chícharo and Teodósio (1991) and Chícharo et al. (2000), respectively. This can be attributed to the longer sampling period and larger studied area of the present study. *Ammodytes tobianus*, *Callionymus reticulatus*, *Coryphoblennius galerita*, *Gobius niger*, *Monochirus hispidus*, *Mullus surmuletus*, *Nerophis ophidion*, *Parablennius pilicornis*, *Pomatoschistus microps*, *Pomatoschistus minutus*, *Pomatoschistus pictus*, *Solea vulgaris*, *Symphodus bailloni*, *Symphodus melops* and *Trigla lyra* were registered in the present work but were absent in the

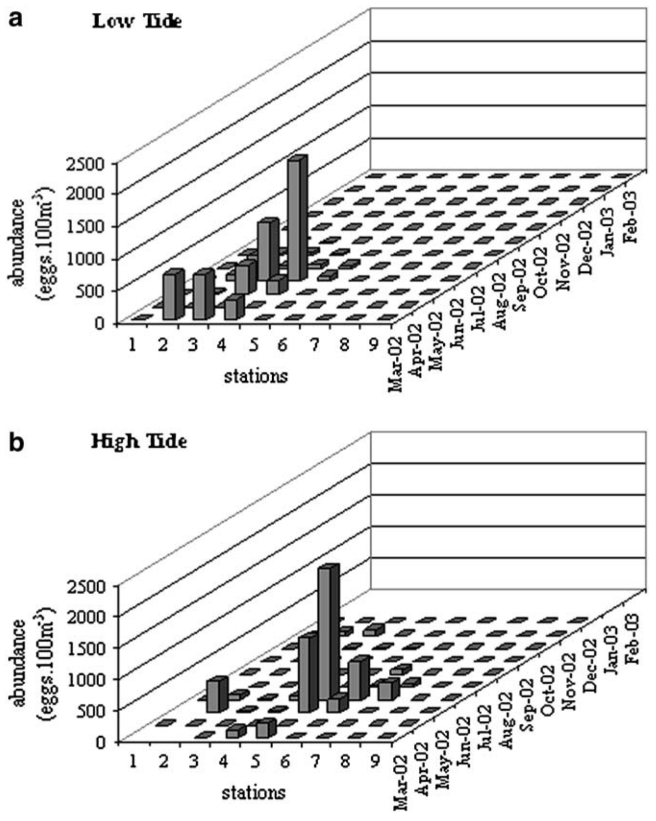

Fig. 7. Spatial and temporal evolution of *Engraulis encrasicolus* egg abundance (eggs 100 m^{-3}), captured in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003, at low tide (a) and high tide (b).

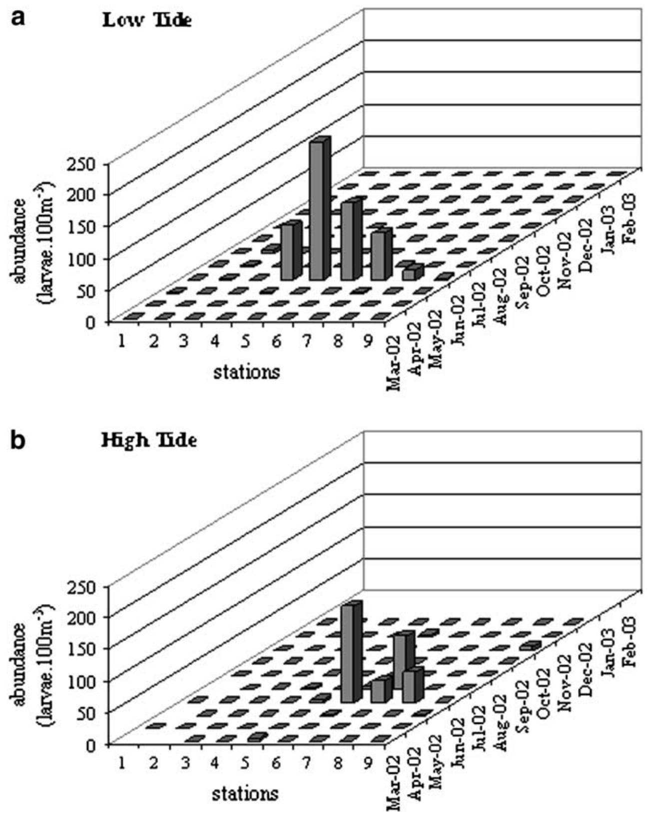

Fig. 8. Spatial and temporal evolution of *Engraulis encrasicolus* larval abundance (larvae 100 m^{-3}), captured in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003, at low tide (a) and high tide (b).

study of Chícharo and Teodósio (1991); however, these authors caught other species that were not collected in this study (*Blennius ocellaris*, *Dicentrarchus labrax*, *Diplodus sargus*, *Echiichthys vipera*, *Hyperoplus* sp., *Labrus bergylta*, *Lipophrys pholis* and *Sparus aurata*).

The majority of taxa displayed substantial seasonal variations in abundance, being essentially captured during late spring and early summer, periods of high zooplanktonic productivity along the Portuguese coast (Cunha, 1993) and in its estuaries (Cabeçadas et al., 1999). Although June and July 2002 had the highest ichthyoplankton abundances, a significant decrease from one month to the other was observed which may be explained by increased jellyfish abundance in July. Jellyfish are known to be important of fish larvae predators and are considered important zooplanktonic community regulators in several ecosystems (Frank and Leggett, 1985; Schneider and Behrends, 1994). The summertime decrease in ichthyoplankton might also be linked with the end of species' spawning periods and not just to predation impact.

Ichthyoplankton abundance in the lower and middle estuary was generally greater than in the coastal area, once the majority of species use the estuary as a preferential spawning ground, namely *Pomatoschistus* spp. and *Engraulis encrasicolus* (Ré, 1991). Furthermore, larval retention mechanisms in these estuarine areas may allow the larvae to continue to benefit from the favourable conditions that it provides.

One of the more pronounced differences between the present study and Chícharo and Teodósio (1991) was the relative abundance of *Engraulis encrasicolus*. We captured almost 4 and 3 times fewer eggs and larvae of *E. encrasicolus*, respectively. This may be due to the fact that 6 days prior to April 2002 sampling, an exceptional increase in river flow was registered, from 26 $m^3 s^{-1}$ to 656 $m^3 s^{-1}$. River flow of only 14 $m^3 s^{-1}$ was registered in April 1988 (Chícharo and Teodósio, 1991), so it is reasonable to hypothesize that the high river flow registered in April 2002 may have been responsible reduced larval abundance, by promoting the advection of the larval stages away from the estuary and into the coastal area. Riverflow quantity and timing are critical components of the ecological integrity of river systems. However, current management approaches often fail to recognize that the integrity of flowing water systems depends largely on their natural dynamic character (Poff et al., 1997).

The decrease in abundance of *Engraulis encrasicolus* coincided with an increase in that of *Pomatoschistus* spp. Chícharo and Teodósio (1991) reported approximately 1.5 times more Gobiidae larvae than Engraulidae, whereas in the present study this proportion doubled. A decrease in estuarine productivity might explain the reduced abundance of *E. encrasicolus* in comparison with *Pomatoschistus* spp., given that the latter species possesses benthonic eggs and larvae that are more highly developed and less dependent on the available food upon hatching, unlike *E. encrasicolus* larvae that emerge from

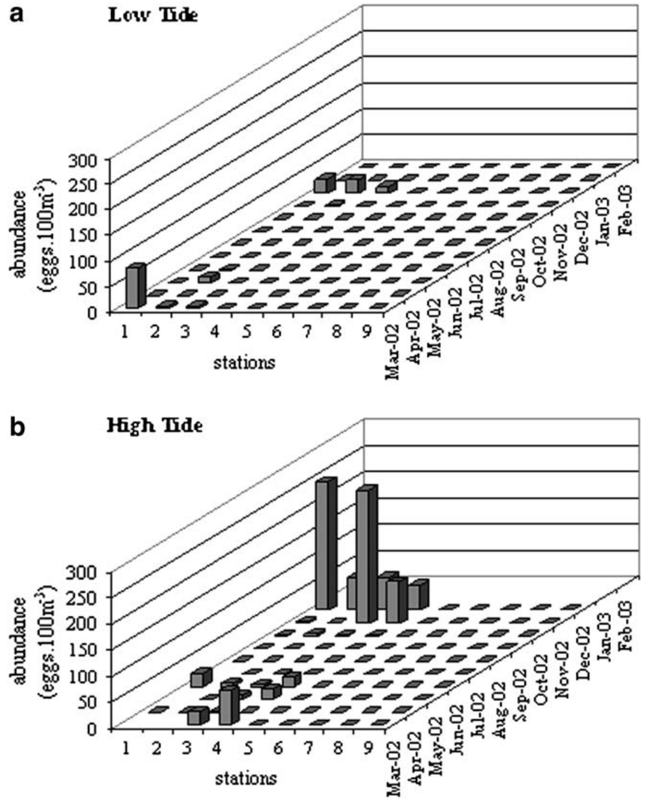

Fig. 9. Spatial and temporal evolution of *Sardina pilchardus* egg abundance (eggs 100 m^{-3}), captured in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003, at low tide (a) and high tide (b).

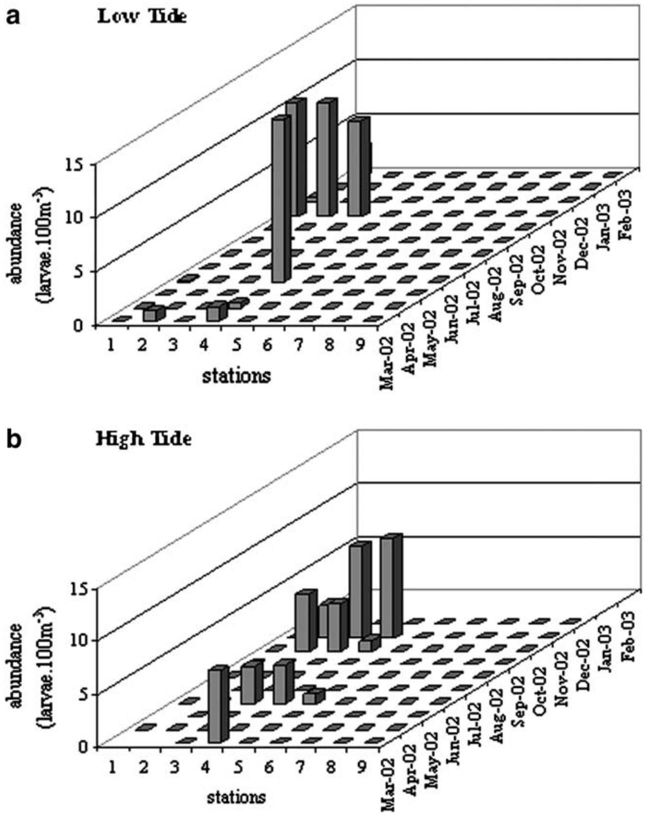

Fig. 10. Spatial and temporal evolution of *Sardina pilchardus* larval abundance (larvae 100 m^{-3}), captured in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003, at low tide (a) and high tide (b).

pelagic eggs and are planktitrophic. Alterations in the amount of river flow into the estuary and adjacent coastal areas affect the concentration of nutrients, with consequences for the primary productivity and associated trophic chains (Wolanski et al., 2004). The Aswan High dam (Nile river, Egypt) is a classic example; after its construction the load of nutrients exported to the coastal area decreased more than 90%, leading to the collapse of fishing activity in the coastal area (Nixon, 2003, 2004).

Of the total fish larvae captured in the present study, 70% were from benthonic eggs; in the Mondego estuary (West Portugal) they represented up to 90% of the larvae (Ribeiro and Gonçalves, 1993), thus reflecting the success of this spawning strategy in estuaries. Nevertheless, in the Rio de la Plata estuary (North Argentina) most larvae hatch from pelagic eggs, accounting for 75% and 94% of total species number and abundance, respectively (Berasategui et al., 2004). Thus, the concept that pelagic eggs and their larvae have reduced contributions to estuarine ichthyoplanktonic communities should not be generalized (Haedrich, 1983). Truly, it is fundamental to consider that the physiography of the two estuaries is completely different. The Rio de la Plata is funnel shaped and 230 km wide at the mouth (Guerrero et al., 1997), unlike the Guadiana which has a channel shape and a maximum width of 0.55 km (Rodrigues da Costa, 1980). The Guadiana estuary should be compared with estuaries of similar size and shape, since these characteristics are highly variable and can have a decisive influence on the biological dynamics (Barnes, 1974).

4.2. Identification of the most important spawning grounds and seasons

Generally, the collected species represented two distinct groups: estuarine and coastal spawners, whose larval stages remain preferentially inside the estuary or in the coastal zone/low estuary, respectively. Most taxa were marine species, rather than true estuarine species (e.g. *Pomatoschistus* spp.). On the one hand, this is due to the high physiological stress that these organisms are submitted to and to the fact that estuaries are relatively recent systems from an evolutionary perspective; not enough time has elapsed for the emergence of more species adapted to the unique conditions of these ecosystems (McLusky, 1989).

Although marine ichthyoplankton constituted most of the taxa observed in the present study, the greatest fraction was represented by relatively few individuals and their presence can be explained by tidal passive transport. Usually, more species were caught in the low estuary during the high tide presumably due to the advection of marine species into the system, thus increasing the species diversity of this area.

Differences in the relative densities of *Sardina pilchardus* and *Engraulis encrasicolus* eggs allowed us to conclude that the spawning grounds of these species are different. *Sardina*

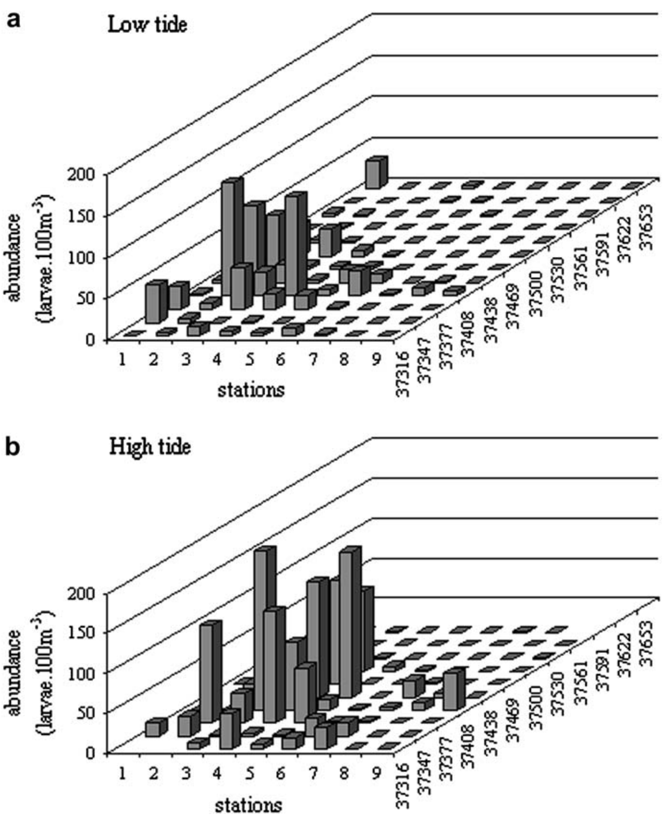

Fig. 11. Spatial and temporal evolution of *Pomatoschistus* spp. larvae abundance (larvae 100 m^{-3}), captured in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003, at low tide (a) and high tide (b).

Table 3
ANOSIM analysis of the factors Study area (A) and Season (B) determined for the fish eggs and larvae captured in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003

Groups	Eggs	Larvae
	R (*p*)	*R* (*p*)
(A)	Global *R*: 0.237, *p*: 0.1	Global *R*: 0.148, *p*: 0.1
Coastal area, low estuary	0.058 (1.2)	0.006 (32.9)
Coastal area, middle estuary	0.455 (0.1)	0.123 (0.1)
Coastal area, high estuary	0.492 (0.1)	0.334 (0.1)
Low estuary, middle estuary	0.225 (0.1)	0.109 (0.1)
Low estuary, high estuary	0.365 (0.4)	0.419 (0.1)
Middle estuary, high estuary	0.099 (23.4)	0.282 (0.1)
(B)	Global *R*: 0.305, *p*: 0.1	Global *R*: 0.22, *p*: 0.1
Winter, Spring	0.094 (3.9)	3.9
Winter, Summer	0.209 (0.1)	0.1
Winter, Autumn	0.251 (0.1)	0.1
Spring, Summer	0.234 (0.1)	0.1
Spring, Autumn	0.412 (0.1)	0.1
Summer, Autumn	0.586 (0.1)	0.1

pilchardus spawning occurs preferentially in the coastal area, while *E. encrasicolus* spawns somewhere between the lower and middle estuary, as observed in the Tagus (Ré, 1986a,b) and Mira estuaries (West Portugal) (Ré and Gonçalves, 1993). *Pomatoschistus* spp. have benthonic spawning and are truly estuarine species, as indicated by the high abundances of larvae in the middle and upper estuary.

Besides using different regions of the estuary and the coastal area, spawning season may also differ among species. The spatial preferences of organisms within estuaries and their adjacent coastal areas are intrinsically related to the salinity gradient (Cyrus and Blaber, 1992; Thiel et al., 1995), whereas spawning seasons are dictated by temperature evolution. In fact, temperature is related to the adult reproductive cycle and spawning (Holmes and Henderson, 1990; Palomera, 1992). The larvae and eggs of some species were captured during all (*Pomatoschistus* spp.) or most of the year (*Engraulis encrasicolus*), while others appeared during a restricted period. Thus, two main spawning periods, spring/summer and autumn/winter, were identified according to species presence and abundance. The spring/summer spawners were *Arnoglossus* sp., *Atherina* spp., *Belone belone*, *Callionymus reticulatus*, *Callionymus* sp., *Coryphoblennius galerita*, *Dicentrarchus* sp., *Diplodus* spp., *E. encrasicolus*, *Gobius niger*, *Hippocampus hippocampus*, *Mullus surmuletus*, *Nerophis ophidion*, *Parablennius gattorugine*, *Parablennius pilicornis*, *Pomatoschistus microps*, *Pomatoschistus minutus*, *Pomatoschistus pictus*, *Solea senegalensis*, Sparidae, *Symphodus bailloni*, *Symphodus melops*, *Syngnathus abaster*, *Syngnathus acus Syngnathus typhle* and *Trigla lyra*, while *Ammodytes tobianus*, *Buglossidium luteum*, *Monochirus hispidus*, *Sardina pilchardus*, *Solea lascaris* and *Solea vulgaris* were classified as autumn/winter spawners.

In addition to temperature and salinity (Blaxter, 1992; Motos et al., 1996), several other parameters such as seston (Cyrus and Blaber, 1992; North and Houde, 2003), suspended organic matter, chlorophyll *a* and river flow (Loneragan and Bunn, 1999; Whitfield and Harrison, 2003) decisively affect spatial organization of estuarine communities (Jaureguizar et al., 2004). The start of most species' reproduction periods coincide with periods of greater food availability, thereby ensuring greater larval development success and explaining the link between spawning dynamics and chlorophyll *a* and seston concentrations.

Measures of seston can be used to determine estuarine turbidity maximum (ETM) location (Herman and Heip, 1999). The ETM is commonly located in the middle estuary, near Foz de Odeleite (st. 7) (Chícharo et al., 2001). However, seston maximum values in this study were determined in the upper estuary, near Alcoutim (st. 9). Although the position of ETM varies seasonally and at short time scales due to variations in freshwater input and wind forcing (North and Houde, 2001), this indicates that the ETM was displaced upstream likely due to the reduced flow imposed during filling of the Alqueva reservoir. ETM has been identified as an important nursery area in several estuaries, such as the St. Lawrence (Winkler et al., 2003) and Chesapeake Bay (North and

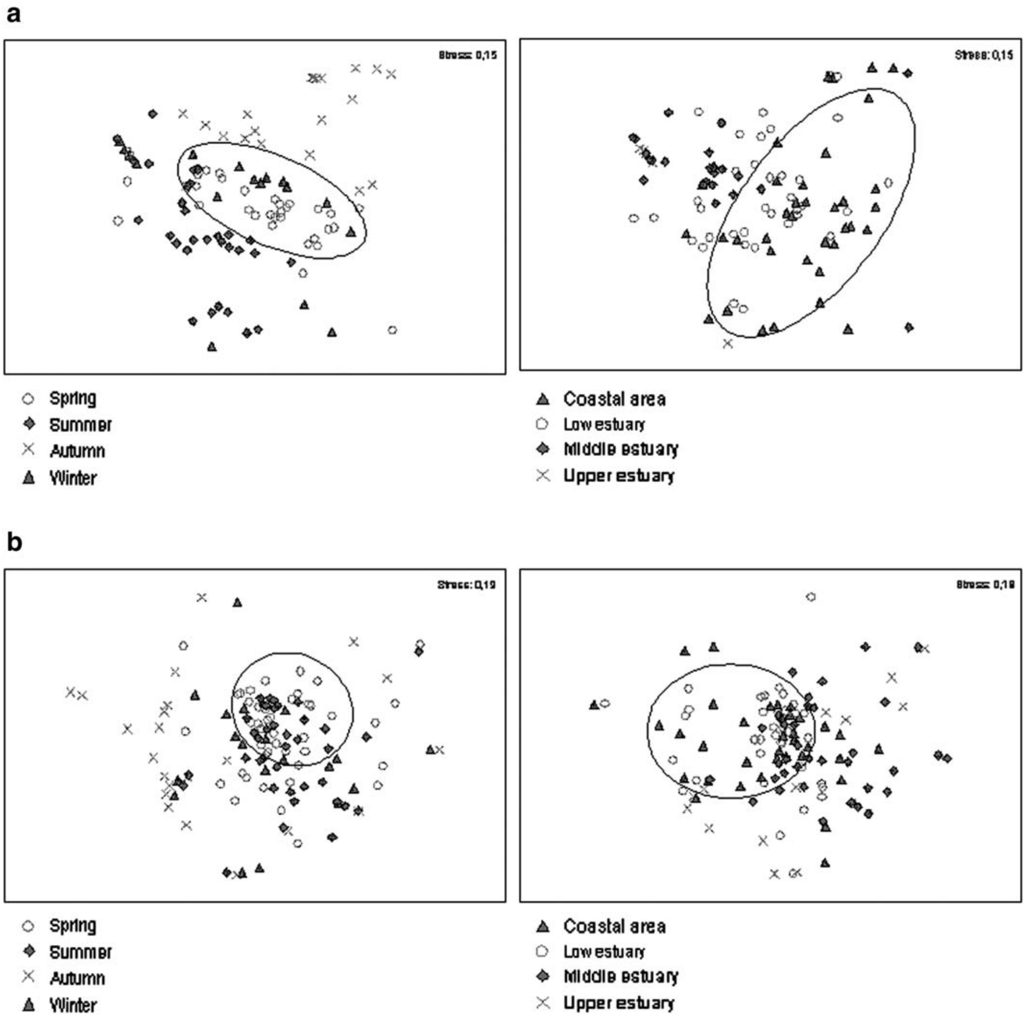

Fig. 12. Non-metric multidimensional scaling (MDS) plots of ichthyoplanktonic community, eggs (a) and larvae (b), in different seasons and study areas of Guadiana estuary. (MDS) plots based on triangular matrices of Bray-Curtis similarities using log(1 + x) transformed species abundance data.

Houde, 2003), either by providing protection from predators (Cyrus and Blaber, 1987) or due to high productivity levels (Roman et al., 2001). However, in this study, ichthyoplankton diversity and abundance was low in the ETM. Several hypothesis may explain the low observed diversity: (a) the high turbidity might constitute a feeding impediment for some species since larvae are visual predators (Houde, 1982); (b) larvae collected in this region were larger and many might have avoided the net, and (c) larvae in the ETM might have occupied deeper depths during the day than elsewhere, due to their more advanced development, which enabled them to regulate their position in the water column. The reduced abundance of eggs collected for some species characteristic of the ETM can in part be explained because they are benthonic spawners. Besides these hypotheses, annual differences in freshwater flow alter the physical and biological characteristics of the ETM region, thus affecting retention and productivity (North and Houde, 2001). This way we cannot put aside the hypothesis that the ETM zone does not constitute an important nursery area in the Guadiana estuary, as observed elsewhere.

5. Conclusions

It seems clear that river inflow played a major role in structuring the ichthyoplankton community in the Guadiana estuary and adjacent coastal area from March 2002 to February 2003. Persistent reduced inflow conditions can lead to degraded estuarine environments and loss of important nursery habitats. Moreover, sudden increase in river flow may cause the advection of fish eggs out of the system, compromising future recruitment, mainly of those species with reduced reproduction periods. Thus, it seems reasonable that the most effective way to maintain ecosystem integrity would be to follow a water management regime that mimics the natural inflow regime, reducing by as much as possible the time elapsed between the peak in precipitation and river flow.

Based on our findings new dilemmas arose that urge to be resolved. There is a clear constraint on current methodological sampling devices and strategies. Introducing different methodologies, such as light traps, will permit the collection of broader size range of larvae and facilitate the study of larval retention strategies. Deeper insight into the importance of creeks as nursery areas is needed. But above all, it is crucial to establish a permanent monitoring program in the Guadiana estuary to assess the influence of long term river inflow variations on the ecosystem.

Acknowledgements

This work was funded by the project "Effect of river flow changes on the icthyofauna communities in Douro, Tejo and Guadiana estuaries and in its adjacent coastal areas. Ecological and socioeconomical predictions" (FCT/P/MAR/15263/1999), by the Ph.D. scholarship granted to Pedro Morais ("*Engraulis encrasicolus* population dynamics in the Guadiana estuary and in the adjacent coastal area"—SFRH/BD/5187/2001), and by the Project "Impact of fishing with clam dredge on the ecosystem. Interdiction area for fishing. Instruments for environmental and fishing administration" (MGS/42319/2001). The authors would like to acknowledge Mr Antero Fernandes and Luís Cristóvão for their invaluable help and support during field work, Rita Borges for her help with fish larvae identification, André Neves for his contribution in the innumerable laboratorial analyses, Isabel Marques for her input in ichthyoplankton sorting and Tim Loher for the intensive revision on the earlier drafts of this paper. The manuscript also benefited from the comments and suggestions of two anonymous reviewers.

References

Barnes, R.S.K., 1974. Estuarine Biology. The Institute of Biology's Studies in Biology, No. 49. Edward Arnold, London, 73 pp.

Berasategui, A.D., Acha, E.M., Araoz, N.C.F., 2004. Spatial patterns of ichthyoplankton assemblages in the Río de la Plata Estuary (Argentina—Uruguay). Estuarine, Coastal and Shelf Science 60, 599—610.

Bettencourt, A., Gomes, V., Dias, J.A., Ferreira, G., Silva, M.C., Costa, L., 2003. Estuários Portugueses. Instituto da Água, Lisboa, 300 pp.

Blaxter, J.H.S., 1992. The effect of temperature on larval fishes. Netherlands Journal of Zoology 42 (2—3), 336—357.

Blaxter, J.H.S., Hunter, J.R., 1982. The biology of clupeoid fishes. Advances in Marine Biology 20, 1—223.

Borja, A., Uriarte, A., Egana, J., Motos, L., Valencia, V., 1998. Relationships between anchovy (*Engraulis encrasicolus*) recruitment and environment in the Bay of Biscay (1967—1996). Fisheries Oceanography 7 (3/4), 375—380.

Borja, A., Uriarte, A., Egana, J., 2002. Environmental factors and recruitment of mackerel, *Scomber scombrus* L. 1758, along the north-east Atlantic coasts of Europe. Fisheries Oceanography 11 (2), 116—127.

Cabeçadas, G., Nogueira, M., Brogueira, M.J., 1999. Nutrient dynamics and productivity in three European estuaries. Marine Pollution Bulletin 38 (12), 1092—1096.

Chícharo, L., Teodósio, M.A., 1991. Contribuição para o estudo do Ictioplâncton do estuário do Guadiana. Revista de Biologia da Universidade de Aveiro 4, 277—286.

Chícharo, L., Chícharo, A., Amaral, A., Condinho, S., Dias, S., Morais, P., Pinto, G., 2000. Valorização dos recursos pesqueiros do estuário do Guadiana. Relatório Final do Projecto. Acção de Valorização do Baixo Guadiana. ODIANA, 111 pp.

Chícharo, M.A., Chícharo, L.M., Galvão, H., Barbosa, A., Marques, M.H., Andrade, J.P., Esteves, E., Miguel, C., Gouveias, I., 2001. Status of the Guadiana estuary (south Portugal) during 1996—1998: An ecohydrological approach. Aquatic Ecosystem Health and Management Society 4, 73—89.

Clarke, K.R., Warwick, R.M., 2001. Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation, second ed. Primer-e, Plymouth, UK, 160 pp.

Cunha, M.E., 1993. Variabilidade estacional do zooplâncton na plataforma continental portuguesa. Boletim UCA Universidade do Algarve 1, 229—241.

Cyrus, D.P., Blaber, S.J.M., 1987. The influence of turbidity on juvenile marine fishes in estuaries. Part 2. Laboratory studies, comparisons with field data and conclusions. Journal of Experimental Marine Biology and Ecology 109, 71—91.

Cyrus, D.P., Blaber, S.J.M., 1992. Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. Estuarine, Coastal and Shelf Science 35, 545—563.

D'Ancona, U., 1931—1956. Uova, larve e stadi giovanili di Teleostei. Fauna Flora Golfo Napoli, Monografia 38 (1—4). Edizione della Statione Zoologica di Napoli, 1064 pp.

Demir, N., 1976. Callionymidae of the northeastern Atlantic. Fiches d'Identification du Zooplankton 148, 1—5.

Esteves, E., Pina, T., Chícharo, M.A., Andrade, J.P., 2000. The distribution of estuarine fish larvae: nutritional condition and co-occurrence with predators and prey. Acta Oecologica 21 (3), 161—173.

Fives, J.M., 1970. Blenniidae of the North Atlantic. Fiches d'Identification du Zooplankton 3, 1—4.

Fives, J.M., 1976. Labridae of the eastern North Atlantic. Fiches d'Identification du Zooplankton 149, 1—7.

Frank, K.T., Leggett, W.C., 1985. Reciprocal oscillations in densities of larval fish and potencial predators: a reflection of present or past predation. Conseil International pour l'Exploration de la Mer 42, 1841—11849.

Garcia, A., Moyano, P., 1990. Estados juveniles de la ictiofauna en los caños de las salinas de la Bahia de Cadiz. Instituto de Ciências Marinas de Andalucia (CSIC), Cadiz, 163 pp.

Grasshoff, K., Ehrhardt, M., Kremling, K., 1983. Methods of Seawater Analysis, second ed. Verlag Chemie, Kiel, 419 pp.

Greenberg, A.E., Clesceri, L.S., Anton, A.D., 1992. Standard Methods for the Examination of Water and Wastewater, 18th ed. APHA, Washington.

Guerrero, R.A., Acha, E.M., Framinan, M.B., Lasta, C.A., 1997. Physical oceanography of the Rio de la Plata Estuary, Argentina. Continental Shelf Research 17 (7), 727—742.

Haedrich, R.L., 1983. Estuarine fishes. In: Ketchum, B.H. (Ed.), Ecosystems of the World Estuaries and Enclosed Seas, 26, pp. 183—207.

Herman, P.M.J., Heip, C.H.R., 1999. Biogeochemistry of the Maximum Turbidity Zone of Estuaries (MATURE): some conclusions. Journal of Marine Systems 11, 89—104.

Holmes, R.H.A., Henderson, P.A., 1990. High fish recruitment in the Severn Estuary: the effect of a warm year. Journal of Fish Biology 36, 961—963.

Houde, E.D., 1982. Micro and Fine Scale Biology. Fish Ecology—A Recruitment Experiment, pp. 97—122.

INAG (Instituto Nacional da Água), 2004. http://www.inag.pt.

Ishikawa, S., Suzuki, K., Inagaki, T., Watanabe, S., Kimura, Y., Okamura, A., Otake, T., Mochioka, N., Lee, T.W., Friche, H., Tsukamoto, K., 2001. Spawning time and place of the Japanese eel *Anguilla japonica* in the North Equatorial Current of the western North Pacific Ocean. Fisheries Science 67, 1097—1103.

Jaureguizar, A.J., Menni, R., Guerrero, R., Lasta, C., 2004. Environmental factors structuring fish communities of the Rio de la Plata estuary. Fisheries Research 66, 195—211.

Kirkwood, D., 1996. Nutrients: Practical Notes on their Determination in Sea Water. ICES, Copenhagen, 25 pp.

Knap, A.H., Michaels, A.T., Close, A., Ducklow, H., Dickson, A. (Eds), 1996. Protocol for the Joint Global Ocean Flux Study (JGOFS) Core measurements, JGOFS Report No. 19, Reprint of the IOC Manuals and Guides No. 29, UNESCO 1994.

Lee, J.Y., 1996. Ouefs et larves planctoniques de poissons. Revue des Travaux de l'Institut des Pêches Maritimes 2—3, 171—208.

Leggett, W.C., Deblois, E., 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherlands Journal of Sea Research 32 (2), 119—134.

Loneragan, N.R., Bunn, S.E., 1999. River flows and estuarine ecosystems: implications for coastal fisheries from a review and a case study of the Logan River, Southeast Queensland. Australian Journal of Ecology 24, 431–440.

Loneragan, N.R., Potter, I.C., Lenanton, R.G.J., Caputi, N., 1987. Influence of environmental variables on the fish fauna of the deeper waters of a large Australian estuary. Marine Biology 94, 631–641.

Marinaro, J.-Y., 1971. Contribution à l'étude des œufs et larves pélagiques de poissons méditerranéens. V. Oeufs pélagiques de la Baie d'Alger. Pelagos 3 (1), 1–118.

McLusky, 1989. The Estuarine Ecosystem, second ed. Blackie and Son, 215 pp.

Miranda, A., Cal, R.M., Iglesias, J., 1990. Effect of temperature on the development of eggs and larvae of sardine *Sardina pilchardus* Walbaum in captivity. Journal of Experimental Marine Biology and Ecology 140, 69–77.

Motos, L., Uriarte, A., Valencia, V., 1996. The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus* L.). Scientia Marina 60 (2), 117–140.

Moyle, P.B., Cech, J.J., 1996. Fishes: An Introduction to Ichthyology, third ed. Prentice Hall, Upper Saddle River, NJ, 590 pp.

Nichols, J.H., 1971. Pleuronectidae. Fiches d'Identification du Zooplankton 4–6, 1–18.

Nichols, J.H., 1976. Soleidae of the Eastern North Atlantic. Fiches d'Identification du Zooplankton 150–151, 1–10.

Nixon, S.W., 2003. Replacing the Nile: are anthropogenic nutrients providing the fertility once brought to the Mediterranean by a Great River? Ambio 32 (1), 30–39.

Nixon, S.W., 2004. The artificial Nile. American Scientist 92, 158–165.

North, E.W., Houde, E.D., 2001. Retention of white perch and striped bass larvae: biological-physical interactions in Chesapeake turbidity maximum. Estuaries 24, 756–769.

North, E.W., Houde, E.D., 2003. Linking ETM physics, zooplankton prey, and fish early-life histories to striped bass *Morone staxatilis* and white perch *M. americana* recruitment. Marine Ecological Progress Series 260, 219–236.

Palomera, I., 1992. Spawning of anchovy *Engraulis encrasicolus* in the Northwestern Mediterranean relative to hydrographic features in the region. Marine Ecological Progress Series 79, 215–223.

Petersen, C.G.J., 1919. Our gobies (Gobiidae). From the egg to the adult stages. Reports of the Danish Biological Station 26, 45–66.

Poff, N., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The Natural Flow Regime—A paradigm for river conservation and restoration. BioScience 47 (11), 769–784.

Ré, P., 1986a. Ecologia da postura e fase planctónica de *Sardina pilchardus* (Walbaum, 1792) na região central da costa Portuguesa. Boletim da Sociedade Portuguesa de Ciências Naturais 23, 5–81.

Ré, P., 1986b. Ecologia da postura e fase planctónica de *Engraulis encrasicolus* (Linnaeus, 1758) no estuário do Tejo. Publicações do Instituto de Zoologia "Dr. Augusto Nobre" 196, 45 pp.

Ré, P., 1991. Ecologia do ictioplâncton estuarino: estuários do Tejo e do Mira. Revista de Biologia da Universidade de Aveiro 4, 245–252.

Ré, P., 1999. Ictioplâncton estuarino da Península Ibérica (Guia de identificação dos ovos e estados larvares planctónicos). Câmara Municipal de Cascais, Cascais, 163 pp.

Ré, P., Gonçalves, E., 1993. Ecologia da fase planctónica da anchova (*Engraulis encrasicolus*) no estuário do rio Mira. Resultados de 8 anos de estudo (1985/1992). Boletim UCA, UCTRA, Universidade do Algarve 1, 527–542.

Ribeiro, R., Gonçalves, F., 1993. Padrões espacio-temporais na diversidade da comunidade larvar de teleósteos no estuário do Mondego. Boletim Uca 1, 490–506.

Rodrigues da Costa, A.B., 1980. A navegabilidade do rio Guadiana. Anais do Clube Militar Naval 110, 661–682.

Roman, M.R., Holliday, D.V., Sandford, L.P., 2001. Temporal and spatial patterns of zooplankton in the Chesapeake Bay turbidity maximum. Marine Ecology Progress Series 213, 215–227.

Russell, F.S., 1976. The Eggs and Planktonic Stages of British Marine Fishes. Academic Press, London, 524 pp.

Schneider, G., Behrends, G., 1994. Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. ICES Journal of Marine Science 51, 359–367.

Stratoudakis, Y., Bernal, M., Borchers, D., Borges, F., 2003. Changes in the distribution of sardine eggs and larvae off Portugal, 1985–2000. Fishery Oceanography 12 (1), 49–60.

Thiel, R., Sepúlveda, A., Kafemann, R., Nellen, W., 1995. Environmental factors as forces structuring the fish community of the Elbe Estuary. Journal of Fish Biology 46, 47–69.

Whitfield, A.K., 1999. Ichthyofaunal assemblages in estuaries: a south African study. Reviews in Fish Biology and Fisheries 9, 151–186.

Whitfield, A.K., Harrison, T.D., 2003. River flow and fish abundance in a South African estuary. Journal of Fish Biology 62, 1467–1472.

Winkler, G., Dodson, J.J., Bertrand, N., Thivierge, D., Vincent, W.F., 2003. Trophic coupling across the St. Lawrence River estuarine transition zone. Marine Ecology Progress Series 251, 59–73.

Wolanski, E., Boorman, L.A., Chicharo, L., Langlois-Salious, E., Lara, R., Plater, A.J., Uncles, R.J., Zalewski, M., 2004. Ecohydrology as a new tool for sustainable management of estuaries and coastal waters. Wetlands Ecology and Management 12 (4), 235–276.