DEPARTAMENTO DE CIÊNCIAS DA VIDA

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE DE COIMBRA

A decadal trend of juvenile European sea bass (*Dicentrarchus labrax*, L.) responses to climate patterns in the Mondego estuary, Portugal.

Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia, realizada sob a orientação científica do Professor Doutor Miguel Pardal (Universidade de Coimbra) e do Doutor Filipe Martinho (Universidade de Coimbra)

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2015

"Nenhum homem é uma ilha, isolado em si mesmo;

Todo o homem é um pedaço do Continente, uma parte da Terra Firme."

John Donne

"Se perderes a direcção da Lua
Olha a sombra que tens colada aos pés"

Excerto da letra de *"Senta-te aí "* do álbum *Rio Grande*

Para completar esta fascinante etapa, não só foi preciso o empenho, esforço e entreajuda de várias (grandes) pessoas para com o presente trabalho, como também a força, (boa) influência e apoio total de outras. Foram fundamentais para que tudo chegasse a bom porto. Como tal, nas próximas linhas quero expressar os meus mais cordiais e sentidos agradecimentos a todos aqueles que, como alguém uma vez disse, "participaram directa ou indirectamente no nascimento do meu filho", ou seja, na elaboração desta tese. Um grande bem-haja:

Ao Professor Dr. Miguel Pardal, meu orientador, por me ter aliciado e apresentado a um tema e grupo de trabalho tão interessantes e excepcionais, pelas palavras de incentivo e bons conselhos dados, assim como a disponibilidade prestada dentro do possível durante este período, apesar da sua atarefada actividade como director do Departamento de Ciências da Vida.

Ao Dr. Filipe Martinho, meu orientador e meu timoneiro nesta aventura. Não só é um intrépido camarada de inesquecíveis temporadas de pesca no estuário do Mondego mas também um exemplo de grande profissionalismo, dedicação ao seu trabalho e companheirismo. Acima de tudo, um bom amigo que me ajudou a entender que na prática da Ciência (e não só) "ver o que está na frente do próprio nariz requer um esforço constante", tal como dizia George Orwell.

Ao Centro de Ecologia Funcional, uma comunidade de cientistas e investigadores da qual me sinto orgulhoso de pertencer e onde conheci, com prazer, pessoas das mais variadas áreas e idades que me enriqueceram quer a nível científico, quer a nível pessoal. Sem dúvida, um local onde as suas instalações me permitiram aprender como trabalham ecólogos a sério.

Aos bravos investigadores e voluntários que participaram nas anteriores campanhas de pesca (triagens e identificações incluídas) e armazenaram toda a informação agora disponível nas bases de dados, desde o início das mesmas no IMAR até às mais recentes "zarpadas" do Darwin I. A todos eles e pelos frutos do seu trabalho, só posso dizer como Sir Isaac Newton: "se vi mais longe foi por estar de pé sobre ombros de gigantes."

Às minhas companheiras de luta Ana Vaz e Susana Pinheiro, porque três cabeças pensam melhor que uma e a minha, por vezes, dispersa-se para outras bandas. A sua curiosidade e cooperação, assim como boas gargalhadas, sempre ajudaram a que a triagem de uma amostra cheia de *Ulva lactuca, Carcinus maenas* (ainda) vivos, plástico e alguns *Pomatoschistus* sp. manhosos se tornasse num agradável passatempo.

À Marina Dolbeth, responsável por boa parte dos cálculos relativos à produção secundária (e não só) dos robalos do estuário do Mondego (entre outros organismos, sempre cheios de "productividade") e por estar sempre pronta a disponibilizar o seu conhecimento e experiência nesta matéria, apesar de a maior parte do tempo não ser possível o nosso contacto directo. Sem esta ajuda preciosa, bem que me podia "dedicar à pesca".

Ao Tiago Grilo, pela disponibilidade espontânea para com aqueles que com ele aprenderam a manusear o "moderníssimo" mas imprescindível *software* FiSAT II. De igual modo, pelo espírito de camaradagem que incentiva nos outros, pela paciência sobrenatural com que enfrenta todas as circunstâncias e pelo seu carácter lutador, justificando plenamente a máxima que diz que um homem que não se mede aos palmos.

A todos aqueles que conheci através da famosa sala 22 e a tornaram, provavelmente, no local de trabalho mais original e bem frequentado da UC. Aqui ficam as minhas palavras de apreço para a Ana Lígia Primo, a incansável "força da natureza" e *expert* "zooplanctónica"; Cláudia Mieiro, de sorriso contagiante, domina as experiências com peixes em aquário; Cristiano Gante, o rei dos momentos *nonsense* e um bom companheiro de Mestrado; Cristina Parodi, que vinda da Sardenha, foi sempre cooperativa e simpática com todos. Infelizmente, teve de voltar para solo italiano; Daniel Crespo, "bike enthusiast" e detentor duma capacidade de ingestão/digestão de almoços totalmente oposta à minha; Dániel Nyitrai, o companheiro "luso-magiar" dos finais de tarde da sala 22; Dina Gonçalves, apesar do pequeno convívio, alguém de quem recordo um bom coração; Elsa Rodrigues, sempre activa nas suas aventuras laboratoriais; Inês Pereira, sempre pronta a aprender um pouco mais e com uma paciência de santa para me aturar enquanto se faziam medições biométricas de peixe. Foi um grande prazer conhecê-la; Ivan Viegas, "aquaculturista" de semblante carregado mas sempre disponível para o próximo; a prestável, trabalhadora e bem-disposta Joana Baptista, a quem devo bons conselhos dados; Joana Falcão, a animadora oficial do laboratório, sempre pronta para pôr a malta num "*good mood*" e capaz de ultrapassar todo o tipo de obstáculos na vida; Joana Oliveira, investigadora alegre e culta, alguém com quem se pode contar; João Neves, o senhor Meixão, um grande compincha para todos os momentos, de trabalho e lazer; João Rito, especialista em metabolismo de peixes/aquacultura, permitiu-me trabalhar os bíceps e tríceps através do transporte de bidões com água salgada; João Rosa, reputado fotógrafo e parceiro de várias jornadas de faina sem o qual os lançamentos e recolhas da rede de arrasto seriam infernais; Mariaelena d'Ambrosio, que trata as medusas microscópicas por tu e nos dá a ouvir música (da boa) através da sua Virgin Radio; Margarida Nunes, por me proporcionar a experiência de ter assistido pela primeira vez a uma defesa de Doutoramento e que correu da melhor forma possível, diga-se de passagem; Marta Frazão, pela sua boa onda e disposição, apesar da quantidade "industrial" de plâncton que teve de exaustivamente analisar na sua

lupa laboratorial; Patrícia Cardoso, a imperatriz dos macrobentos, exemplar no empenho para com as suas experiências e com uma alegria formidável; Sara Leston, interessada pela presença de antibióticos na cadeia trófica marinha (mas mais interessante ainda é a sua badalada confecção de bolos caseiros); Sónia Cotrim, também *expert* "planctónica" e óptima colega de trabalho, que trata as dificuldades com a calma com que todos os problemas devem ser enfrentados. Para não falar na qualidade dos petiscos oferecidos, para as saídas de campo, pelo grupo feminino da sala 22, onde também se inclui. Tito Mendes, o "domador de *Carcinus*", colega e amigo de longa data que me incentivou a juntar-me à equipa de ecologia marinha do CFE. Um porreiraço, portanto. Se, por lapso meu, alguém ficou excluído desta dedicatória, sinta-se totalmente incluído.

À Dona Lina e à Dona Clara, pela eficácia com que tratam e "desinfectam" os materiais e locais que lhes compete, sem falar na boa disposição que despertam em todo o laboratório de cada vez que se apresentam no mesmo. Torna-se (quase) sempre um momento especialmente divertido.

Aos meus Amigos e colegas de Universidade, com enfoque naqueles que partilharam comigo uma Licenciatura em Biologia e muitos episódios dignos de guião de filme, a quem só posso desejar os maiores sucessos futuros e, se possível, a participação conjunta em novas temporadas de aventuras e episódios memoráveis.

À malta do atletismo da AAC, pela forma como fui integrado no grupo de treino e pelo que cresci como atleta e pessoa por causa do "coach" Ricardo Monteiro e de companheiros do melhor como Andreia Gomes, Bruno Abel Martins, Carolyn Müsse, Cristiana Cunha, Daniel Cravo, Erica Gomes, Francislaine Serra, Ivo Tavares, José Sá, Ricardo Gonçalves, entre outros atletas do melhor. *Mens sana in corpore sano*, é o nosso lema! Uma palavra ainda para a malta do remo da AAC, que também fez parte do meu percurso académico e me fez sentir o quão bom é ser-se desportista em *part-time*!

Ao Corto Maltese, ao Naruto Uzumaki e ao Gaston Lagaffe, heróis impagáveis da BD mundial e de quem sou devoto fã e leitor ávido. Quem melhor para me inspirar e mostrar que tudo na vida é possível e vale a pena? São bonecos desenhados, é verdade, mas até eles ficam parvos com as suas próprias histórias, onde tudo pode acontecer; um bocado à semelhança com a realidade.

Aos peixes e crustáceos recolhidos durante as campanhas no estuário, com destaque para os robalos *Dicentrarchus labrax*. Aprendi bastante com a sua "presença física" no campo e no laboratório. Sem a sua "contribuição prática" nestes dois anos e sem os resultados e as experiências por eles proporcionados, este trabalho não seria a mesma coisa, definitivamente.

À minha mãe Alexandra, ao meu pai José, ao meu "pequeno" grande irmão Francisco e ainda à Dona Maria das Dores, pois as palavras elogiosas não chegam para mostrar o quão grato estou por estar com eles, qual suporte e fonte de apoio ilimitado em tudo o que faço. Evidentemente, sem eles não estaria onde estou, faria o que faço e seria o que sou.

A toda a Família, com F grande, do lado dos Granja Bento e dos Antunes, dos avós aos tios e primos, passando por aqueles que já não estão cá. Por serem uma verdadeira dádiva e um factor de bem-estar, estabilização, diversão e união para qualquer um. Enfim, à famelga!

Ao meu Tio Jorge, cuja memória quero destacar nesta dedicatória. Apesar de já não o poder ver mais nos próximos tempos, sei que ele veria esta tese do sobrinho com muito bons olhos. E isso só pode ser motivo de orgulho para mim.

Estuarine systems support the life cycle stages of commercially important marine fish and are influenced by large and local-scale climatic patterns. Also, extreme events triggered by climate changes may influence the functioning of nursery grounds and recruitment for several fish species. In this study, performed in the Mondego estuary, Portugal, we used an 11-year database (2003-2013) for analyzing the variability in the population of a marine juvenile migrant fish, the European sea bass *Dicentrarchus labrax*, regarding changes in abundance, population structure, growth rates and secondary production and annual day of peak abundance. Higher densities and production occurred at the beginning of the study, but no differences in 0-group growth could be observed. In order to detect change points in both biological and climatic data, the cumulative sum (CUSUM) of the deviations from the mean for the 2003-2013 period were determined for each parameter. The relationship between large- and local-scale drivers and 0-group abundance, secondary production and day of peak abundance were evaluated using a Pearson correlation analysis of CUSUM of biological and environmental data, considering the correspondent yearly values and with a time-lag of 1 year. The North Atlantic Oscillation (NAO) index, sea surface temperature (SST) and their respective winter values were tested as large-scale factors, while river runoff, salinity and water temperature were considered as local climate patterns. River runoff was the significant factor explaining *D. labrax* 0-group abundances and the NAO and water temperature were also significant predictors considering the 1-year lag. Regarding *D. labrax* 0-group secondary production, salinity and water temperature were the significant predictors. The NAO with 1-year lag was also negatively correlated with the day of peak abundance. The observed variability regarding yearly trends in abundance of juvenile fish was mostly linked to local-scale climate patterns, which can influence habitat use patterns, whereas large-scale factors (NAO, SST) seem to operate at a wider time frame, as observed by the lag of 1-year on their influence on juvenile sea bass abundance.

Keywords: European sea bass; recruitment variability; climatic changes; Mondego estuary; large-scale patterns.

Os sistemas estuarinos albergam certas fases do ciclo de vida de peixes economicamente importantes, estando igualmente sob a influência de padrões climáticos de escala global e local. De facto, eventos climáticos extremos desencadeados por alterações climáticas podem afectar o funcionamento destes sistemas como zonas de viveiro e o recrutamento para várias espécies de peixes. Este estudo foi realizado no estuário do rio Mondego, Portugal, onde se usou uma base de dados de 11 anos (2003-2013) para analisar a variabilidade populacional de uma espécie de peixe migrante marinho, o robalo *Dicentrarchus labrax*, e assim observar diferenças na sua abundância, estrutura populacional, taxas de crescimento e produção secundária. Os valores de densidade e produção mais elevados ocorreram no período inicial do estudo, mas não se encontraram diferenças entre as taxas de crescimento do grupo 0+. Para detectar pontos de inflexão nos dados biológicos e climáticos, foram determinadas as somas cumulativas (CUSUM) dos desvios da média de cada parâmetro para o período de 2003-2013. As relações entre vectores de escala global e local e a abundância, produção secundária e dia do pico de abundância anual dos grupos 0+ de robalo foram avaliadas através de uma análise de correlação Pearson das CUSUM dos dados biológicos e ambientais, considerando os valores anuais correspondentes e do ano anterior. O índice da Oscilação do Atlântico Norte (NAO), temperatura da superfície do mar (SST) e respectivos valores foram testados como factores de escala global, enquanto o caudal de rio, salinidade e temperatura da água estuarina foram considerados padrões climáticos de escala local. O escoamento foi o factor significativamente relacionado com as abundâncias de *D. labrax* juvenis, mas também o índice NAO e a temperatura da água estuarina do ano anterior foram vectores significativos. Relativamente à produção secundária dos grupos 0+ de *D. labrax*, a salinidade e a temperatura de água estuarina foram os factores significativos. (O índice NAO respeitante ao ano anterior foi igualmente um parâmetro negativamente relacionado com os valores do dia anual de picos de abundância). A variabilidade observada nas dinâmicas anuais de abundância dos robalos juvenis foi maioritariamente associada a padrões climáticos de escala local, capazes de influenciar os padrões de uso de habitat. No que diz respeito a factores de escala global (NAO, SST), estes parecem actuar dentro de um prazo mais longo, tal como foi observado a sua influência na abundância de robalos juvenis a longo prazo.

Palavras-chave: Robalo; variações de recrutamento; alterações climáticas; estuário do Mondego; padrões de escala global.

CHAPTER 1

INTRODUCTION

Estuaries are transitional areas between river and sea waters and are essential ecosystems for the renewal of fisheries resources by providing important contributions to coastal fish stocks (Houde & Rutherford, 1993; Beck *et al*., 2001; Attrill & Power, 2002; McLusky & Elliott, 2004). These natural systems are also among the most productive and variable ecosystems on Earth (Nixon *et al.*, 1986; McLusky & Elliott, 2004; Able, 2005; Dolbeth *et al*., 2007a, 2008; Leitão *et al*., 2007), with low fish species diversity but high abundances of individual taxa (Whitfield, 1999; Baptista *et al*., 2010; Nyitrai *et al*., 2012). Estuarine waters sustain some life cycle stages of many commercially important marine and freshwater fish species (Houde & Rutherford, 1993; Elliott & Dewailly, 1995; Attrill & Power, 2002; Able, 2005), by displaying important environmental features such as migration pathways, shelter and nourishment areas (McLusky & Elliott, 2004; Dolbeth *et al*., 2008). Estuarine shallow waters also provide refuge from predators together with high productivity that enhance early stages growth (Beck *et al*., 2001; Able *et al*., 2013). Despite these characteristics showing benefits, both ecologically and economically, estuarine systems represent some of the most deteriorated ecosystems on the planet, due to human settlement since early ages (Edgar *et al*., 2000; Beck *et al.*, 2001; Dolbeth *et al*.,2007b). Finally, but not less important, estuarine systems supply significant nursery grounds for marine fish (e.g. Beck *et al.*, 2001; Cabral *et al*., 2007; Martinho *et al*., 2007a; Baptista *et al*., 2010; Freitas *et al.*,2012; Cardoso *et al.*, 2014).

Nursery habitats are a subset of juvenile habitats that make a greater than average overall contribution to adult population, having a greater level of productivity than other juvenile habitats (Beck *et al*., 2001; Gillanders *et al*., 2003; Dahlgren *et al*., 2006) and the former may be measured by density, growth and survival of juveniles and movement to adult habitats. Briefly, nurseries must be larval reservoirs, host juveniles that develop steady growth and survive long enough in order to emigrate to adult habitats and reproduce (Beck *et al.*, 2001; Able *et al.*, 2013). The nursery value of a habitat may vary annually due to temporal and

spatial larval supply to estuaries (Dahlgren *et al.*, 2006; Able *et al.*, 2013) and the same is applied for variations in recruitment patterns.

Recruitment variability of marine fish population is one of the most important issues in fisheries ecology (Rijnsdorp *et al.*, 2009). In fact, recruitment is considered to be an active process, in which fish larvae reach a particular developmental stage, and by receiving appropriate environmental cues, seek favorable nursery habitats (Jennings & Pawson, 1992). It is known that numerous factors contribute to recruitment variability (van der Veer *et al.*, 2000). Indeed, larvae and juvenile are influenced by two types of factors: density-dependent factors inside estuaries and density-independent factors outside estuaries (sea and coastal areas) (van der Veer *et al.*, 2000; Cabral *et al.*, 2007). Density-dependent factors may include food supply, predation, inter and intra competition and mortality (e.g. starvation), while wind and tidal circulation, currents, salinity and water temperature represent some density-independent factors. Recruitment of juvenile fish is heavily determined by density-independent factors in the larval stage (van der Veer *et al.*, 2000; Cabral *et al.*, 2007; Rijnsdorp *et al.*, 2009; Able *et al.*, 2014), due to adverse transport conditions, habitat degradation and climate change (Able *et al.*, 2014).

Concerning these aspects, long-term studies are important to analyze variability in fish populations related with changes in climate and provide a wider view of the fluctuations occurring during this period (Martinho *et al.*, 2009). Also, continuous long-term time series of biological data (>10 years) have been recognized as being extremely important for understanding the functioning of ecosystems (Attrill *et al.*, 1999). Considering that an increase in frequency and intensity of extreme weather events is also expected due to ongoing climate change (Collins *et al.*, 2013; IPCC, 2013; Nyitrai *et al.*, 2013; IPCC, 2014), their combination with continuous changes in the environment may lead to dynamical changes of estuarine systems, specifically on their nursery role (Allen & Baltz, 1997; Nyitrai *et al.*, 2013).

In this perspective, climatic changes are influencing climate patterns at large- and local-scales. For instance, the North Atlantic Oscillation (NAO) is considered the principal large-scale factor concerning changes in meteorological conditions in Europe and North America, influencing fish stocks, community composition, recruitment and fisheries (Attrill & Power, 2002; Stenseth *et al.*, 2002; Nyitrai *et al.*, 2013). At a local scale, the interaction between precipitation and river flow is important for larval migration into estuaries (Martinho *et al.*, 2009; Vinagre *et al.*, 2009a; Baptista *et al.*, 2010).

In this work, the chosen study species was the European sea bass *Dicentrarchus labrax* (Linnaeus, 1758) (Perciformes, Moronidae), a demersal euryhaline and eurythermic species of high commercial and recreational value in north-east Atlantic waters and in the Mediterranean Sea. Depending on its life cycle stage, it inhabits the open sea, coastal waters, lagoons, estuaries and occasionally rivers (Pickett & Pawson, 1994; Pickett *et al.*, 2004; Kottelat & Freyhof, 2007), and has a geographical distribution from Senegal to Norway, including the Mediterranean and the Black Sea (Cardoso *et al.*, 2014; FAO, 2015). Sea bass is an abundant species in the Portuguese coast, being characterized by marked seasonal abundance patterns within estuarine nurseries (Jennings *et al.*, 1991; Leitão *et al.*, 2007; Martinho *et al.*, 2007a; 2008). Depending on the specific location, *D. labrax* spawns mainly from January to June, at temperatures above 9°C, and larvae begins their estuarine colonization from April onwards in the Atlantic coastal waters (Jennings & Pawson, 1992; Pickett & Pawson, 1994; Kottelat & Freyhof, 2007; Martinho *et al.*, 2008). Previous studies showed that estuaries are significant sources for adult sea bass stocks (e.g. Lancaster *et al.*, 1998; Martinho *et al.*, 2007a; Vasconcelos *et al.*, 2008; Baptista *et al.*, 2010; Dolbeth *et al.*, 2010). In addition, and since it is an important commercial fish species, its fishery related activities may be adversely affected by temperature increase (Cabral & Costa, 2001; Vinagre *et al.*, 2009b), especially in the areas that are in the southern extent of their distribution (Almeida *et al.*, 2014). Still, long-term studies on sea bass abundance trends, as well as its relationship with environmental variability, are scarce

(e.g. Martinho *et al.*, 2009; Cardoso *et al.*, 2014), being necessary to further investigate how changes in climate drivers will influence these populations. Indeed, several authors have reported on the range extension and establishment of viable populations at more northern latitudes (such as the Norwegian coast, Baltic Sea and the Wadden Sea), as a result of warming of the ocean over the last 20 years (e.g. Brander *et al.*, 2003; Bagdonas *et al.*, 2011; Cardoso *et al.*, 2014).

Considering the previous statements, the aim of the present work was to assess the relationship between juvenile sea bass populations in the Mondego estuary (Portugal) and the climate patterns over a period of 11 years (2003-2013). The specific objectives were to: (1) analyze the variability in the densities, secondary production and day of peak abundance of juvenile *D. labrax* populations from 2003 to 2013; (2) assess sea bass population structure and determine the juvenile growth rates; (3) evaluate their relationship with climatic and environmental variations.

CHAPTER 2

MATERIALS AND METHODS

2.1 - Study site

The Mondego estuary, with an area of 8.6 km^2, is located in a warm temperate region characterized by a continental temperate climate (Pardal *et al.*, 2002) and lies on the western coast of continental Portugal (40°08'N, 8°50'W). In this small estuary, two arms (north and south) are separated approximately 7 km away from the coastline, joining again closely to the river mouth (Fig. 1). The north arm is the main navigation channel and the deeper one, with 5-10 m depth at high tide and a tidal range of 2-3 m, being constantly dredged to maintain its depth, so to preserve its frequent shipping activity. The south arm is shallower, with 2-4 m high tide, 1-3 m tidal range and is comprised about 75% of intertidal mudflats.

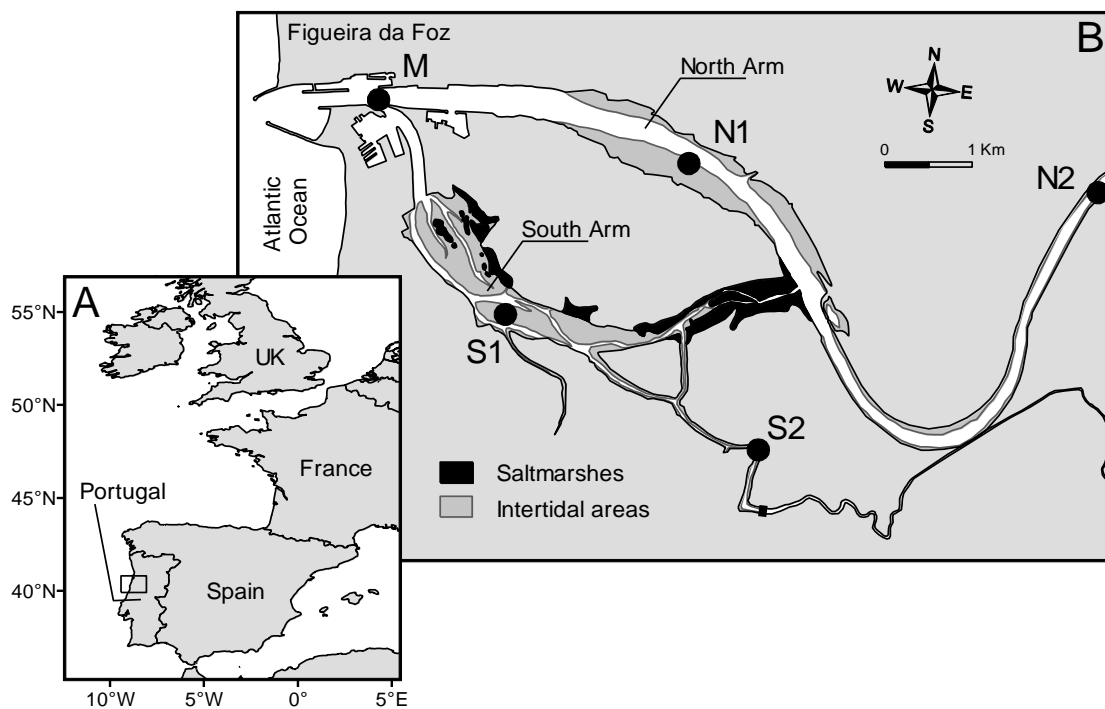**Figure 1.** Geographical location of the Mondego estuary (A) and of the five sampling stations (B), represented as black circles.

Freshwater flow occurs mainly in the north arm, due to the partial silting condition in the southern arm upstream areas. The south arm water circulation depends mostly on the tidal influx of seawater and on the freshwater input from the minor tributary Pranto river,

controlled by a sluice in accordance to the water needs from the surrounding rice fields of the Mondego agricultural valley. A connection between the two arms was enlarged in the year 2006, thus enabling a higher water circulation over the estuary's south arm.

2.2 - Sampling procedures and laboratory work

The sampling methodology employed to obtain data on the Mondego estuary sea bass population is briefly summarized here. Sampling was performed monthly from June 2003 until January 2007. After this period, bimonthly catches were performed until December 2013, with the exception of October and November 2008, September and November 2010 and March 2011, due to technical constraints and/or bad weather conditions. Five sampling stations (Fig. 1) were established for the fishing effort, which occurred during night time at high spring tides, using a 2-m beam trawl with one tickler chain and 5-mm stretched mesh size in the cod end. According to Able (1999), beam trawls are the most effective quantitative benthic samplers in deeper habitats (>1m). At each sampling station, three hauls were towed at the speed of two knots for an average of 3 minutes along the current, covering at least an area of 500m^2. Bottom-water physic-chemical parameters, such as temperature, salinity and dissolved oxygen were analyzed at each sampling station during fish sampling campaigns. Fish samples were transported to the laboratory, counted, sorted to species level and sea bass individuals were measured (TL, total length to nearest 1cm) and weighted (WW, wet weight, 0.01 g precision). Data from replicates collected at each station were averaged to form one monthly sample.

2.3 - Acquisition of environmental data

River runoff values were obtained from the Portuguese Environment Agency (APA; http://snirh.apambiente.pt; 25.02.2015) station Açude Ponte Coimbra 12G/01AE, near the city of Coimbra and located 40 km upstream of the Mondego estuary.

The North Atlantic Oscillation (NAO) index (defined as the atmospheric pressure at sea level difference between Lisbon, Portugal, and Reykjavik, Iceland) data were supplied by NOAA - National Weather Service - Climate Prediction Centre (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based; 28.03.2015). Sea surface temperature (SST) data concerning the 1° Lat x 1° Long square in the Portuguese coast nearest to the Mondego estuary were acquired from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) online database (http://rda.ucar.edu/datasets/ds540.1/,Slutz *et al.*, 1985; 27.02.2015).

2.4 - Data analysis

Monthly density data (individuals per 1000 m^2) were determined by averaging the total number of individuals in relation to the five sampling stations and total sampled area. Mean annual densities were calculated by averaging the monthly data from each year, from January to December. Annual abundance peaks of 0- group sea bass were assessed by determining the sampling day of each year with the highest density values per month.

Population structure was determined by tracking recognizable cohorts from the successive sampling dates. Each spatial sample was aggregated and analyzed using the size-frequency distribution of the consecutive sampling dates, based on the modal progression analysis. Cohorts were determined using the FAO-ICLARM Stock Assessment Tools software (FISAT II, http://www.fao.org/fi/oldsite/statist/fisoft/fisat/index.htm). Bhattacharya's method was used at first to identify the location of the modes and then the estimated mean length for each age group was refined with the NORMSEP procedure, which separates normally distributed components of the size-frequency samples (Gayanilo Jr. *et al.*, 2005). This analysis provides the mean length, standard deviation, population sizes and the separation indices for the identified age groups. All fish larger than 250mm TL were excluded from further analyses,

due to low numbers and the corresponding difficulty in assigning correctly the respective cohort.

After identification of the cohorts, annual production was calculated using the cohort increment summation method (Winberg, 1971), according to:

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

where P_{cn} is the growth production (g WW 1000 m^{-2} year^{-1}) of cohort n; N is the density (ind 1000 m^{-2}), $\overline{w}$ is the mean individual weight (g WW), 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 included in the overall estimates and were assumed as zero production. Annual production was determined for each year, using the mean values from the month when estuarine colonization started until December.

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

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

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 determination of absolute growth rates (AGR, cm day^{-1}) for each 0-group cohort was performed according to:

$$AGR = \frac{L_{t_2} - L_{t_1}}{t_2 - t_1}$$

where L_{t2} and L_{t1} are the total length (TL) at time t_2 and t_1 respectively.

Detection of break points in biological and environmental parameters was computed by applying the cumulative sum (CUSUM) of the deviations from the mean of the 2003-2013 reference range. Steepness and sign of the slopes allow the observation of deviations of a

certain frame of time from the time-series mean value (Ibañez *et al.*, 1993; Marques *et al.*, 2014).

The relationships between the cumulative sums of 0-group sea bass densities, secondary production and day of peak abundance (response variables) with the environmental variables (explanatory variables) were analyzed with Pearson's correlation coefficient, using R software (R Development Core Team, 2013). The considered explanatory variables were divided in two distinct groups: large-scale factors and local-scale factors. In the first one, environmental variables included the North Atlantic Oscillation (NAO) index, sea surface temperature (SST) in the coastal area near the estuary, as well as their winter values regarded as isolated factors. In the second group, the included predictors were river (freshwater) runoff, salinity and mean estuarine water temperature. It was also tested a time-lag of one year between explanatory and response variables, in order to detect larger time scale patterns, an assumption based on the evidence that fish spawning, larval immigration and recruitment variability may be influenced by the previous environment history (Martinho *et al.*, 2009; Vinagre *et al.*, 2009a). All yearly environmental factors were obtained from January to December, with the exception of salinity and estuarine water temperature values, which were only considered from June to December, in order to better characterize the period of estuarine residency by 0-group sea bass. A significance level of 0.05 was used in all test procedures.

CHAPTER 3

RESULTS

3.1 - Environmental characterization

Average estuarine water temperature was in general higher than the SST in the adjacent coastal area, including SST winter values (mean values of 18°C, 17°C and 15°C, respectively) (Table 1). Average estuarine water temperature was lowest in 2004, whereas the highest value was observed in 2008. Overall SST was the lowest in 2013, while the highest value occurred in 2006 and considering only the winter periods of SST values, 2009 was the year that had the lowest average temperature, whereas 2007 was the year with the highest value in the study period (Table 1).

Table 1. Mean yearly environmental variables, with the respective standard deviation, for the Mondego estuary between 2003 and 2013: NAOw – North Atlantic Oscillation winter index; NAO – North Atlantic Oscillation index; SSTw – Sea surface temperature winter (°C); SST – Sea surface temperature (°C); Runoff – river runoff (dam^3); Salinity – mean estuarine salinity; Temperature – mean estuarine water temperature (°C). Salinity and Temperature data were obtained between June and December for each year.

Year	NAOw	NAO	SST (°C)	SSTw (°C)	Runoff (dam^3)	Salinity	Temperature (°C)
2003	-0.27 (±0.52)	0.03 (±0.43)	16.79 (±2.33)	15.07 (±1.01)	301003.17 (±389613.671)	20.90 (±1.52)	18.36 (±3.81)
2004	-0.07 (±0.77)	0.16 (±0.80)	16.93 (±2.65)	14.53 (±0.42)	99959.50 (±84989.513)	20.02 (±3.97)	16.57 (±4.92)
2005	-0.14 (±1.66)	-0.31 (±0.92)	16.91 (±2.24)	14.53 (±0.50)	47567.50 (±67509.506)	23.98 (±5.40)	17.45 (±4.01)
2006	-0.58 (±1.15)	-0.31 (±1.39)	17.67 (±2.54)	15.00 (±0.92)	221018.25 (±262223.712)	18.27 (±9.93)	18.59 (±3.00)
2007	0.26 (±1.05)	0.11 (±0.74)	16.77 (±1.64)	15.77 (±0.80)	105391.58 (±113157.267)	29.55 (±2.18)	16.58 (±2.43)
2008	0.21 (±0.37)	-0.45 (±0.93)	17.43 (±2.19)	15.70 (±0.56)	72911.17 (±79628.689)	30.37 (±0.35)	20.81 (±1.43)
2009	-0.27 (±0.31)	-0.32 (±1.12)	16.79 (±2.61)	13.60 (±1.22)	143870.58 (±190079.471)	27.82 (±5.97)	17.35 (±1.92)
2010	-1.93 (±0.57)	-1.29 (±0.71)	16.78 (±1.98)	15.10 (±1.39)	258797.50 (±283311.432)	24.98 (±3.02)	18.47 (±1.78)
2011	-0.69 (±1.14)	0.20 (±1.45)	17.39 (±2.02)	15.27 (±1.02)	96874.67 (±145174.745)	25.07 (±2.82)	17.62 (±3.89)
2012	1.02 (±0.92)	-0.53 (±1.02)	17.08 (±2.56)	15.30 (±1.15)	52688.17 (±58271.326)	26.89 (±4.50)	18.26 (±3.56)
2013	-0.77 (±0.99)	0.15 (±0.97)	16.74 (±2.20)	14.97 (±0.74)	214523.50 (±226502.965)	23.73 (±3.54)	18.75 (±3.79)

River runoff volume varied greatly along the years, going from the lowest value of 47567.50 dam^3 in 2005, reaching up until to the maximum value of 301003.17 dam^3 in 2003, with an average value of 146782.33 dam^3. When runoff values increased, salinity decreased and the opposite pattern occurred when runoff values, influenced by lower precipitation levels, diminished. Salinity had a mean value of 24.7 in the study period, varying from 20.0 in the year 2004 to 30.4 in 2008 (Table 1). The NAO index had an average value of 0.23 in the 11-year period and ranged from 0.03 to 1.29, while winter NAO index presented an average value of -0.29, ranging from -0.77 to 1.02 (Table 1).

3.2 - Population structure, abundance and growth rates

During the study period, the majority of sea bass population was constituted by 0 and I age groups, and only one cohort was produced per year (Fig. 2). Estuarine colonization by the new cohorts occurred mostly in June, but also often in May and July. Only one cohort, C8, started in August (2008, Fig. 2), which was also the latest month of *D. labrax* estuarine colonization in the entire study period. A total of 13 cohorts were identified. Considering cohorts C3, C4, C7, C11 and C12, a decrease in mean total length was observed during the autumn/early winter, beginning afterwards to increase in the spring/early summer months.
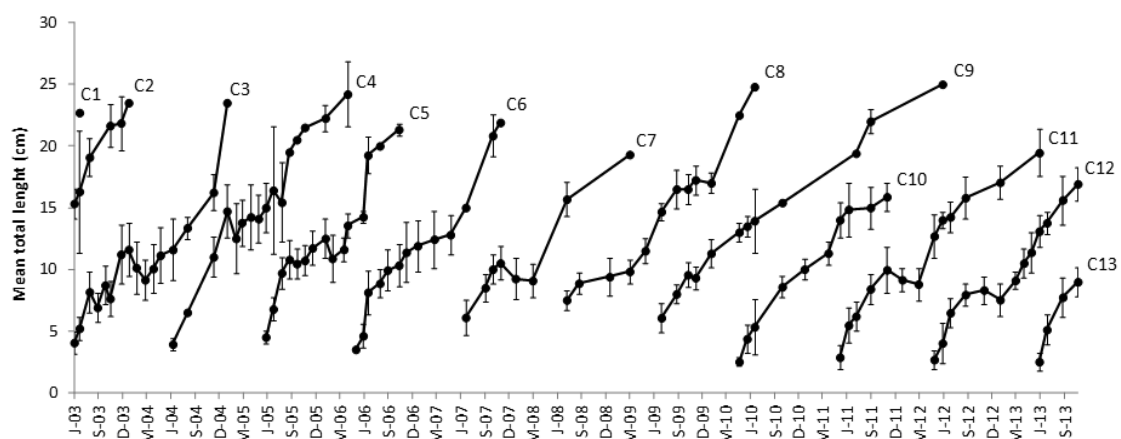

Figure 2. Mean total length of *Dicentrarchus labrax* population (± standard deviation) during the study period in the Mondego estuary, with indication of each yearly cohort (C).

D. labrax 0-group abundance was higher than I-group fish during all the study period with the exception of 2004, when I-group densities were higher in the Mondego estuary (Fig. 3). Only in 2008 and 2010 did the density values of the two groups occur in similar levels. Densities of 0-group sea bass were particularly high in 2003 and became lower and highly variable until 2013. In contrast, I-group densities presented constant values throughout the study period (Fig. 3).
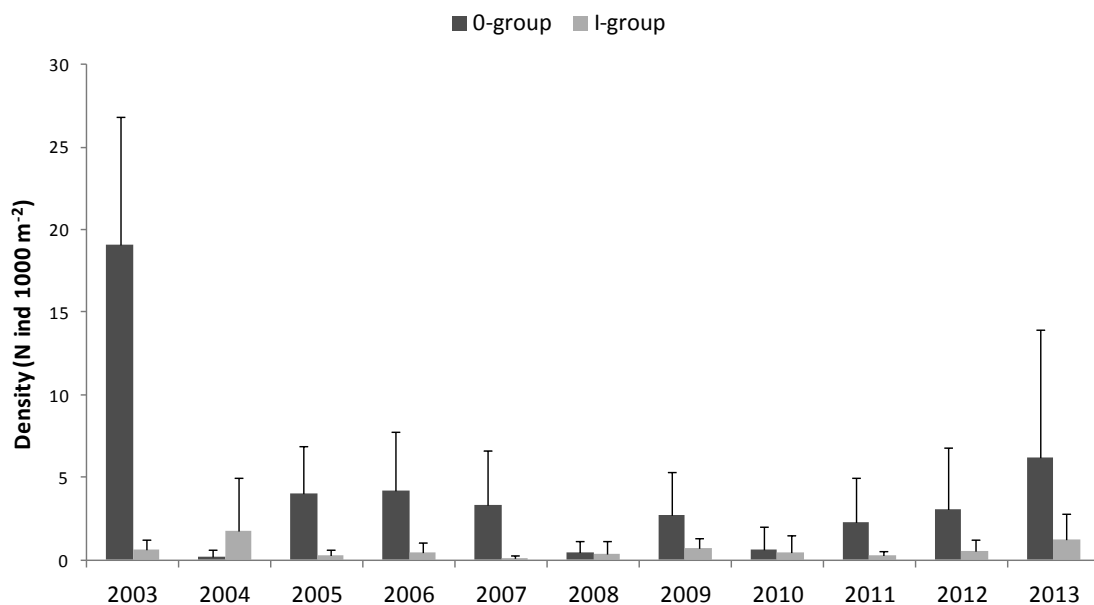

Figure 3. Mean annual density (± standard deviation) of *Dicentrarchus labrax* 0 and I-groups from 2003 to 2013. *Dicentrarchus labrax* density data was analyzed from the beginning of each cohort until the end of each year (December).

In relation to annual abundance peaks of 0-group sea bass, a general trend of the highest densities towards later days in each year was observed (Fig. 4). Most abundance peaks were observed in July and August (2004, 2008, 2009, 2011, 2012 and 2013). The latest abundance peak was observed on November 27th in 2007 and the earliest abundance peak value was on the 26th June in 2006 (Fig. 4).
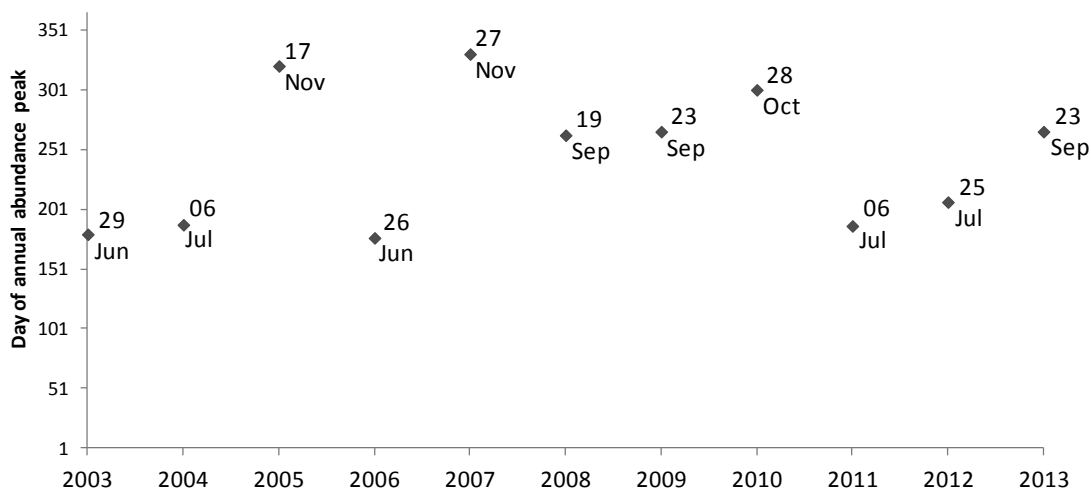
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Figure 4. Day of annual abundance peaks of 0-group *Dicentrarchus labrax*. Each year begins on the 1st January (1) and ends on the 31st December (365), except in the leap years of 2004, 2008 and 2012 (366 days).

No differences in mean annual growth rates were observed between sea bass cohorts (F=0.31; p>0.05) (Fig. 5). Mean growth rates were determined as 0.45 mm d^{-1} (± 0.23), with maximum values of 0.71 mm d^{-1} and minimum of 0.30 mm d^{-1}. Still, the highest growth rates for a 0-group cohort (until December) of 0.71 mm d^{-1} were observed in cohort C3 (2003).
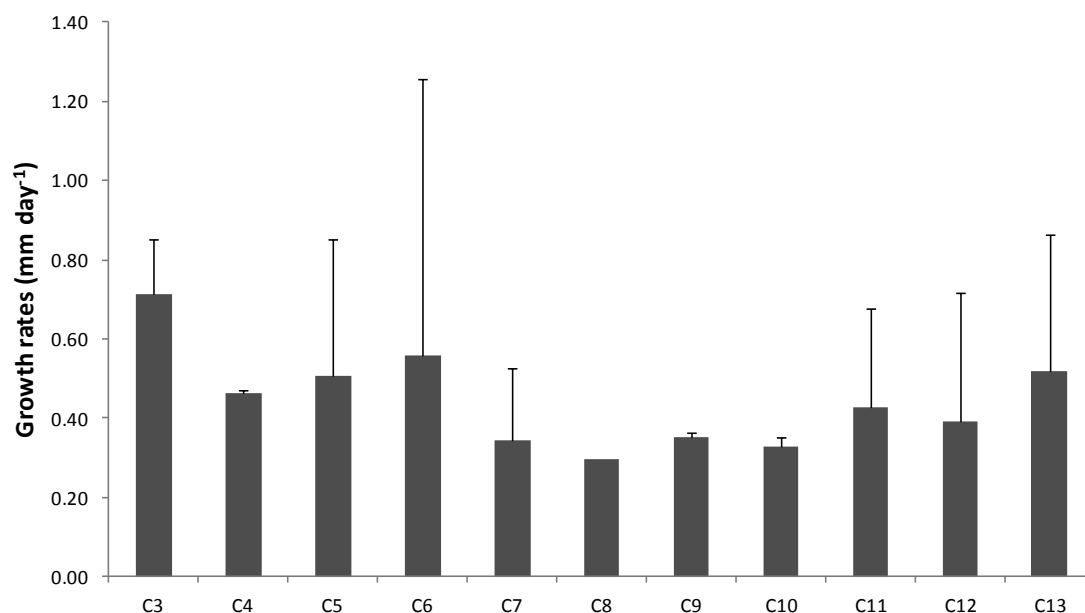

Figure 5. Mean annual growth rates (mm day^{-1}) of *Dicentrarchus labrax* 0-group cohorts (± standard deviation), determined from the beginning of each cohort until the end of the year (December).

3.3 - Production dynamics

Mean annual secondary production of 0-group *D. labrax* was relatively stable along the 11-year; an exception was in 2003, when the maximum value of 0.04 g WW 1000 m^{-2} year^{-1} was observed (Table 2). An increase in production values was observed since 2010. As for the mean annual secondary production in the total *D. labrax* population, a similar pattern was observed, with 0.42 g WW 1000 m^{-2} year^{-1} in 2003 as the maximum value observed. Concerning mean biomass, higher values were observed for 0-group cohorts in 2005, 2007 and 2013, while the highest value occurred in 2003 and the lowest in 2004. An increasing trend could be noticed between 2010 and 2013. For the total population, biomass values were more constant than for 0-group values only, although the 2003-2005 period had much higher numbers than the remnant following dates, reaching 0.10 and 0.12 g WW 1000 m^{-2} in these years.

Table 2. Secondary production values (g WW 1000 m^{-2} year^{-1}), mean biomass (g WW 1000 m^{-2}) and $P/\bar{B}$ ratios for 0-group cohorts and total population of *Dicentrarchus labrax*, the former being established for each year of the study period, since the beginning of each cohort until the last sample of the year (December), and the latter for the total population groups in each year, comprising yearly cohorts from one year to the next.

	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
0-group production (g WW 1000 m^{-2} year^{-1})											
	0.04	0.001	0.01	0.01	0.01	0.002	0.01	0.002	0.004	0.01	0.02
Total population production (g WW 1000 m^{-2} year^{-1})											
	0.42	0.21	0.13	0.14	0.06	0.11	0.08	0.07	0.07	0.09	–
0-group biomass (g WW 1000 m^{-2})											
	0.07	0.001	0.04	0.03	0.04	0.01	0.02	0.01	0.01	0.01	0.04
Total population biomass (g WW 1000 m^{-2})											
	0.10	0.12	0.04	0.03	0.03	0.04	0.05	0.01	0.03	0.03	–
0-group $P/\bar{B}$ (year^{-1})											
	0.66	0.40	0.34	0.35	0.21	0.29	0.35	0.32	0.40	0.39	0.52
Total population $P/\bar{B}$ (year^{-1})											
	4.39	1.81	3.12	4.00	1.94	2.61	1.55	5.55	2.19	3.08	–

In relation to secondary production and mean biomass of 0-group sea bass, 2003 was the year with the highest numbers, while regarding the total population of sea bass, the 2003-2005 period showed maximum values (Table 2). $P/\bar{B}$ ratios of 0-group cohorts were inconstant throughout the years, but showed a decreasing trend from 2003, year of maximum value of 0.66, to 2007, where it reached the lowest value. Thereafter, a relative increment in $P/\bar{B}$ values was noticed until 2013. Regarding $P/\bar{B}$ of the total population, maximum values were observed in 2003, 2006 and 2010, whereas 2004 and 2009 had the lowest values, thus showing an irregular pattern in the entire study period.

The determined mean total length and absolute growth rates maximum values at the end of fast growing season (late autumn and early winter), concerning 0-group sea bass from other geographical latitudes, were summarized using a latitude gradient in Table 3. It was also taken into account the most important abiotic factors responsible for the observed size and growth patterns in each study site. The presented data in this work was within the scope of values described for other temperate estuaries, although the Mondego maximum values for mean total length were lower compared to similar latitudinal estuaries in southwestern Europe (Table 3). A latitudinal trend was observed from the different geographical data included in Table 3, where sea bass populations from higher latitudes seemed to have lower mean total lengths at the end of fast growing season and absolute growth rate values than the southern latitudinal ones. Also, one of the most prevailing environmental factors in all study sites, concerning sea bass total length and growth rates, was water temperature (Table 3).

Table 3. Mean total length (mm) and absolute growth rate (AGR) (mm d^{-1}) maximum values of 0-group *Dicentrarchus labrax* at the end of fast growing season, according to geographical area, as well as the main environmental factors responsible for the observed habitat use and growth patterns; *Estimated values; †Estimated values based on length conversions by Aprahamian & Barr (1985); ‡Data only on females.

Geographical area	Total length (month)	AGR	Main environmental factors	Author(s)
The Netherlands Wadden Sea (52°56'N, 4°54'E)	50*	-	Depth; Prey availability; Salinity; Water temperature; Wind speed	Cardoso *et al.*, (2014)
Republic of Ireland Waterford Harbour (52°14'N, 6°57'W)	128† (November)	0.2†‡	Air and water temperature	Kennedy & Fitzmaurice (1972)
United Kingdom South Wales Coast (51°34'N, 3°53'W)	–	0.6	Water temperature	Jennings *et al*. (1991)
United Kingdom Severn Estuary (51°33'N, 2°45'W)	73† (November)	–	Water temperature	Claridge & Potter (1983)
United Kingdom Tamar Estuary (50°24'N, 4°12'W)	130 (November)	–	–	Hartley (1940)
France Vilaine and Loire Estuary (47°30'N, 2°30'W; 47°12'N, 2°15'W)	130 (November)	0.44	–	Desaunay *et al*. (1981)
France Thau Lagoon (43°25'N, 3°41'E)	174	–	–	Barnabé (1973)
Portugal Aveiro Lagoon (40°43'N, 8°40'W)	170 (December)	–	Water temperature	Gordo (1989)
Portugal Mondego Estuary (40°08'N, 8°50'W)	117 (December)	0.71	NAO; River runoff; Salinity; Water temperature	Present study; Martinho *et al*. (2009)
Portugal Tagus Estuary (38°46'N, 9°02'W)	173 (November)	1.53	Depth; Salinity; Water temperature	Cabral & Costa (2001)
Greece Messolonghi-Etoliko Lagoons (38°22'N, 21°22'E)	100* (December)	0.33*	Prey availability; Water temperature	Rogdakis *et al.* (2010)
Spain San Pedro Estuary and Bay of Cádiz (36°31'N, 6°14'W)	181	–	–	Arias (1980)
Morocco Atlantic Coast (32°15'N, 9°30'W)	190 (November)	0.83	–	Gravier (1961)
Egypt Alexandria Coast (31°16'N, 29°48'E)	192	0.66	Prey availability; Water temperature	Wassef & El Emary (1989)

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3.4 - Relation between environmental parameters and sea bass abundance

CUSUM analysis, by considering the cumulative sums of the deviations from the mean of the 2003-2013 reference range on both sea bass densities and environmental time-series data, showed different trends depending on the period of potential change (Fig. 6). Briefly, a positive slope in each time-series of the CUSUM figure indicates the time frame in which the considered parameter was higher than the time-series mean, and contrariwise when there is a negative slope. Thus, regarding *D. labrax* 0-group variables, juvenile densities exhibited an intense decline relative to the time-series mean until 2005, when their abundance started to rise slightly. Later in 2006, a small decrease was observed until 2008, followed by a stabilization between 2009 and 2011 and finally increased again until 2013 (Fig. 6 A). Concerning sea bass secondary production, CUSUM analysis showed a steep decrease until 2007, with a faint rise up to 2009, decreasing again in the next year and finally recovered slightly until 2013 (Fig. 6 B). In general, 0-group density and production presented similar variations from 2003 to 2013, showing a decline in the 2003-2007 period and afterwards, from 2010 to 2013, started to increase slightly (Fig. 6 A, B). Day of peak abundance of 0-group fish showed an inverse trend with density and production, with an increase until 2008, and then a decrease until 2012 (Fig. 6 C). Both periods of 2003 and 2013 showed similar values.

Cumulative sums of environment variability indicated that the NAO and NAO winter indices showed similar patterns, characterized by one slight decrease from 2005 to 2006 and a major negative slope from 2008 to 2010 and to 2011 for the NAO time-series and the NAO winter time-series, respectively, after which an increase occurred until 2012 (Fig. 6 D and F). Yearly and winter SST also experienced similar strong decrease in the 2008-2010 period and both had, after a slight decrease, increasing values from 2004 until 2006 for SST and from 2005 to 2008 for SST winter values (Fig. 6 H and J). Only in the global SST time-series was observed again a strong downward change from 2012 to 2013.
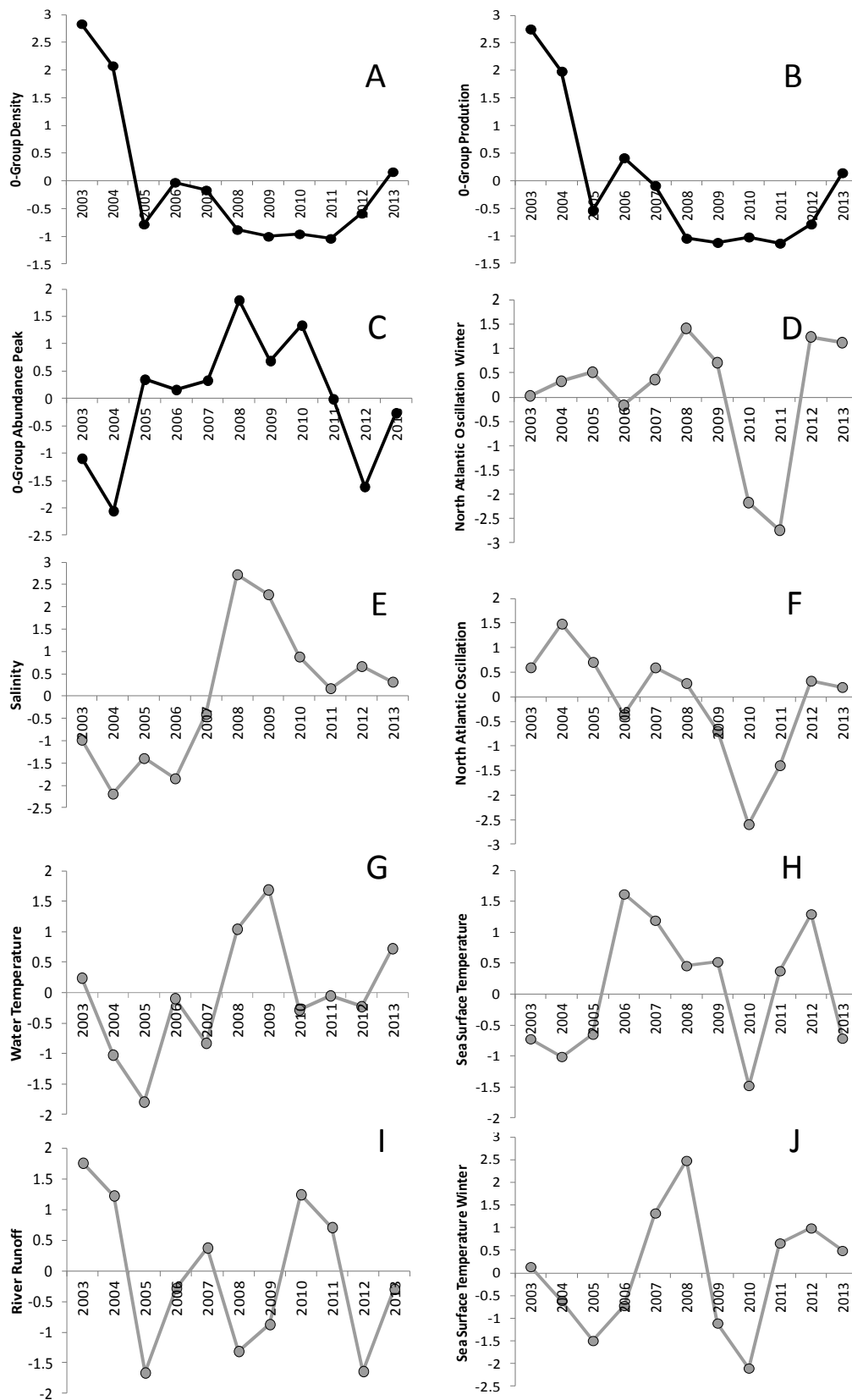
Figure 6. Cumulative sums of mean yearly biological variables (black circles): 0-Group Density (A), 0-Group Production (B) and 0-Group Day of Peak Abundance (C); and environmental parameters (gray circles): North Atlantic Oscillation Winter index (D), Salinity (E), North Atlantic Oscillation index (F), Water Temperature (G), Sea Surface Temperature (H), River Runoff (I) and Sea Surface Temperature Winter (J); data from 2003-2013.

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The cumulative sums of salinity and water temperature were similar in the period of 2006-2008 and 2005-2009, respectively, with major positive slopes during these periods (Fig. 6 E and G). River runoff expressed the highest variability in the CUSUM time-series analysis (Fig. 6 I), with clear contrast with break points in the 2006-2010 period of certain variables, such as NAO, NAO winter and SST (Fig. 6).

The Pearson correlation analysis between the cumulative sums of 0-group abundance, secondary production and day of peak abundance, and the environmental parameters showed a significant influence of environmental drivers on the biological responses, considering both corresponding year and 1 year time lag datasets (Table 4). Regarding large-scale factors, the NAO lagged by one year was the only significant factor, explaining *D. labrax* 0-group abundance (r=0.68), secondary production (r=0.71) and day of peak abundance (r=-0.63) (Table 4).

Table 4. Pearson correlation (r) values between the cumulative sums of 0-group densities (N ind 1000 m^{-2}), secondary production (g WW 1000 m^{-2} $year^{-1}$) and day of annual abundance peak, including the respective one year lag data, and the environmental parameters: NAOw – NAO winter index, NAO – NAO index, SST – Sea surface temperature (°C), SSTw – Winter sea surface temperature (°C), Runoff – River runoff (dam^3), Salinity – Average estuarine salinity, and Temperature – Average estuarine water temperature (°C). Salinity and Temperature data were obtained between June and December for each year. Significant r values are highlighted in italic bold (p<0.05).

	Large-scale factors				Local-scale factors		
	NAOw	NAO	SST	SSTw	Runoff	Salinity	Temperature
0-group density	0.16	0.56	-0.34	-0.01	*0.61*	-0.59	-0.15
0-group secondary production	0.15	0.57	-0.30	-0.06	0.59	*-0.67*	-0.21
0-group day of peak abundance	-0.16	-0.55	0.05	0.00	-0.25	0.60	0.32
0-group density (1 year lag)	0.24	*0.68*	-0.44	-0.20	0.07	-0.59	*-0.64*
0-group secondary production (1 year lag)	0.24	*0.71*	-0.34	-0.15	0.09	-0.62	*-0.67*
0-group day of peak abundance (1 year lag)	-0.42	*-0.63*	0.42	0.07	0.19	0.54	0.58

Concerning local-scale factors, river runoff was the significant predictor explaining sea bass 0-group abundance over the study period (r=0.61), whereas salinity explained 0-group production with a time-lag of one year (r=-0.67). Average estuarine water temperature lagged by one year was the only significant factor elucidating 0-group densities (r=-0.64) and secondary production (r=-0.67) (Table 4).

CHAPTER 4

DISCUSSION

4.1 - Abundance, growth and production – influence of environmental conditions

The present work focused on analyzing a decadal trend in estuarine habitat use patterns by juvenile European sea bass in a temperate nursery ground, and their relationships with changes in climate patterns. Variance in the abundance patterns of juvenile sea bass in estuaries and inshore coastlines have been observed in many European estuarine and coastal areas (Kennedy & Fitzmaurice, 1972; Aprahamian & Barr, 1985; Henderson & Corps, 1997; Martinho *et al*., 2007a, 2009; Dolbeth *et al.*, 2010; Cardoso *et al.*, 2014), showing great year-to-year variability. Focusing on single species responses, and particularly considering large time scales, allows for the identification of the critical factors responsible for shaping the patterns of community change (Genner *et al*., 2004), particularly under a climate change scenario.

Abundance of juveniles varied greatly between 2003 and 2013, and 0-group fish were always found in higher densities than I-group, with the exception of 2004, when 0-group densities were particularly low. The presence of a majority of 0-group fish indicates that the estuary has been functioning as an effective nursery ground for this species in the long-term. Such high interannual variability in 0-group sea bass has been reported elsewhere (e.g. Cabral *et al.*, 2001; Cardoso *et al.*, 2014), as well as for other marine species that use estuaries as nursery grounds (van der Veer *et al.*, 2000, 2015; Cabral *et al.*, 2007; Hermant *et al.*, 2010; Martinho *et al.*, 2010; Nyitrai *et al.*, 2013). In fact, fish densities and year-class strength can be highly variable even in neighboring estuaries, as demonstrated by Dolbeth *et al.* (2010) and Vasconcelos *et al.* (2010). According to several authors, year-class strength in sea bass is mostly determined by growth conditions and overwintering survival ability of 0-group fish, considering the combined effects of both density-independent (abiotic) and density-dependent (biotic) factors (Pawson, 1992; Martinho *et al.*, 2009; Cardoso *et al.*, 2014) on which cannibalism by 1 and 2-group towards 0-group age classes can also be an important contribution for the variability in *D. labrax* recruitment (Henderson & Corps, 1997). Also, the previous years to estuarine colonization by juveniles in the Mondego estuary, i.e. regarding

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their egg and larvae phase, could have been characterized by variations in the hydrodynamic circulation and high rates of mortality, thus critically affecting post-larvae and 0-group *D. labrax* abundance, and respective cohort survival (Allen & Baltz, 1997; van der Veer *et al.*, 2000).

CUSUM analysis revealed a positive correlation between sea bass abundance and river runoff values, indicating that years with high levels of 0-group densities, such as 2003 and 2013, were characterized by elevated freshwater discharges, which are closely related to abundant precipitation regimes. In fact, high precipitation and river runoff play an important role in recruitment strength of marine juvenile migrant fish, such as sea bass, by expanding the river plumes into the coastal areas and thus providing particular cues that larvae take advantage of for their estuarine colonization (Boesch & Turner, 1984; Martinho *et al.*, 2007b, 2009, 2010; Dolbeth *et al.*, 2008; Baptista *et al.*, 2010; Nyitrai *et al.*, 2012; Le Pape & Bonhommeau, 2013). Added to these factors, wind speed and direction, tidal movements and ocean currents have also been recognized as major density-independent factors concerning estuarine settlement by marine fish by influencing larval transport towards coastal areas (Jennings & Pawson, 1992; Henderson & Seaby, 2005; Martinho *et al.*, 2009; Vinagre *et al.*, 2009a), hence shaping density patterns.

Assessing secondary production is a way of measuring ecosystem functioning, and may reveal further insights into ecosystem change when combined with long-term datasets (Dolbeth *et al.*, 2011). Despite that determining secondary production in marine fish can be difficult due to possible bias in determining effective population sizes and their changes (Cowley & Whitefield, 2002), estimating changes in marine fish production provide additional information than that obtained from other static measures such as density or biomass (Dolbeth *et al.*, 2012). Annual secondary production patterns were similar to the variations in abundance of 0-group fish, and values for the whole population were within the reported range in previous surveys in the Mondego estuary by Dolbeth *et al.* 2010. For 0-group fish,

secondary production and $P/\bar{B}$ values were rather low, given that low biomass of the smaller sized individuals.

Higher production values for both 0-group and total population occurred in the first year of the study, which were linked to high river runoff and precipitation values, and lower salinities. In fact, salinity is a key controlling factor for estuarine organisms with high seasonal patterns (Aprahamian & Barr, 1985; Attrill *et al.*, 1999; Saillant *et al.*, 2003; Martinho *et al.*, 2009; Dolbeth *et al.*, 2010), such as juvenile *D. labrax*. Years with lower salinities were coincident with higher production values, evidenced by the strong negative correlation between the CUSUM of these two variables. This was observed at the beginning and at the end of the study period, as well as a contrasting effect, elucidated in the particular dry year of 2005, already reported in previous studies in this area (Martinho *et al.*, 2007b; Dolbeth *et al.*, 2008; Baptista *et al.*, 2010; Nyitrai *et al.*, 2013). In juvenile sea bass, secondary production increased in response to an increment in nutrient availability and in primary production (Houde & Rutherford, 1993; Costa *et al.*, 2002; Dolbeth *et al.*, 2007a; Vinagre *et al.*, 2009a), which are known to provide better growth conditions to estuarine fish (Martinho *et al.*, 2007b; Dolbeth *et al.*, 2008; Vinagre *et al.*, 2009a,b; Baptista *et al.*, 2010; Nyitrai *et al.*, 2013). As also observed by Dolbeth *et al.* (2010), the relationship between salinity and fish production might not be uniquely a direct one, related also with changes in food availability, larval immigration or competition for food and space, due to different river flow regimes.

The remarkable high euryhaline features of the European sea bass have been recognized in several studies (Pickett & Pawson, 1994; Rogdakis *et al.*, 2010; Tine *et al.*, 2014). In fact, Tine *et al.* (2014) recently sequenced the genome of *D. labrax* and pointed out that it contains the largest set of functional aquaporins in vertebrates, membrane proteins involved in osmoregulation, as well as the highest number of gene copies associated to ion and water regulation among totally sequenced teleost fish, highlighting the resilience of sea bass to the typical salinity variations of estuarine systems. Even though, years of particular high salinity

levels (a consequence of small river drainage values), such as 2008, showed some of the lowest values of 0-group abundances and $P/\bar{B}$ ratios in the entire 11-year period.

Temperature is considered as another key abiotic variable by influencing abundance and fitness along a fish life cycle (Magnuson *et al.*, 1979; Henderson & Corps, 1997; Attrill & Power, 2004). As poikilothermic species, *D. labrax* is vulnerable to water temperature variations and these may affect fish metabolism, growth and reproduction (Almeida *et al.*, 2014), thus acting directly in fish thermal ecological niches (Magnuson *et al*., 1979; Cardoso *et al.*, 2014). In this work, variations in water temperature explained the changes in abundance of 0-group sea bass significantly with a time-lag of one year, implicating a strong influence of this local-scale driver in this species within the Mondego estuary (Table 4). This assumption is corroborated by the CUSUM analysis, where a negative correlation between average estuarine water temperature and *D. labrax* 0-group abundance and secondary production was found, considering one year lag between the independent and response variables. In marine organisms, high water temperatures trigger various responses, such as an increase in metabolic maintenance costs, inhibition of feeding behavior and lower investment in growth (Pickett & Pawson 1994; Henderson & Corps, 1997; Able *et al.*, 2014). In addition, higher water temperatures also lead to fluctuations in food availability, thus influencing predator/prey interactions (Brett, 1979; Tulp *et al.*, 2008; Cardoso *et al.*, 2014). Therefore, temperature-driven effects may indirectly affect, even in a long-term perspective, the nursery habitat use patterns by juvenile sea bass, as well as their growth and survival rates. In fact, water temperature has been shown to influence significantly the early life stages of *D. labrax* (see Table 3).

Concerning annual abundance peaks, higher estuarine water temperature, especially in the driest years, coincided with later abundance peaks, occurring mostly in late summer/early autumn, when temperatures began to fall. Nonetheless, relations between temperature and juvenile abundance are not linear , considering that temperature affects

organisms' physiology, fitness and survival with distinct intensity, spatial and temporal variations (Attrill & Power, 2004; Nyitrai *et al.*, 2013; Able *et al.*, 2014).

Based on the present work and published literature, a latitudinal pattern was observed along the Atlantic and Mediterranean coasts regarding several early-life history characteristics, in which higher mean total length at the end of the growing season and growth rates occurred at lower latitudes, and decreased as latitude increased. Such observations were considered by some authors, to whom temperature and photoperiod influences the onset and duration of spawning, growth rates and life-span (Gravier, 1961; Kennedy & Fitzmaurice, 1972; Arias, 1980; Wassef & El Emary, 1989; Jennings & Pawson, 1992; Vinagre *et al.*, 2009b; Morrongiello *et al.*, 2014). In more detail, spawning of adult sea bass started earlier at lower latitudes, from October in the Bay of Cadiz (Arias, 1980) to April in the Irish coast (Kennedy & Fitzmaurice, 1968). Additionally, the onset of spawning is not solely triggered by an increase in water temperature, related with gonadal maturation, but rather with photoperiod (see Vinagre *et al.*, 2009b). According to the previous authors, spawning will occur when fish are subjected to a suitable day duration, given that temperature conditions are within favorable limits, whose maximum value for sea bass has been determined as 17°C (Devauchelle & Coves, 1988).

The estimated growth rates of *D. labrax* 0-group cohorts, with a mean total value of 0.45 mm d^{-1} and maximum value of 0.71 mm d^{-1} were within the range values observed in other northeast Atlantic and Mediterranean estuaries and coasts (see Table 3). However, the present data can be slightly underestimated, as the growth values from the 0-group cohorts were only considered between the onset of estuarine colonization and December of each year. The mean total length of 0-group sea bass from the Mondego estuary was lower in the end of fast growing season when compared to other close-by estuarine nurseries, such as the Aveiro lagoon (Gordo, 1989) and Tagus estuary (Cabral & Costa, 2001). This pattern had already been demonstrated by Martinho *et al.*, 2008, and was confirmed its long-term occurrence. According to the previous authors, these results suggest that growth conditions in the

Mondego estuary might be sub-optimal for this species given its relatively small area, leading to a smaller overwintering size. This might also induce an earlier migration to the neighboring coastal areas by the largest specimens in the autumn, given by the decrease in the mean length of some 0-group cohorts (Fig. 2). Despite this, the Mondego estuary remains as one important supplier of juvenile fish for the coastal sea bass stocks, as determined by otolith microchemistry (Vasconcelos *et al.*, 2008). In addition, long-term differences in growth among year-classes have also been attributed to the influence of environmental conditions experienced by fish as juveniles, which can have more significant and prolonged effects in population productivity than density-dependent growth responses (Morrongiello *et al.*, 2014).

4.2 - Influence of large-scale climatic patterns on sea bass populations

One environmental predictor that stood out as a having a significant influence in the variations of 0-group sea bass densities, secondary production and annual abundance peaks was the North Atlantic Oscillation (given by the NAO Index - NAOI), considering a time-frame of one year lag. Various authors have assessed the direct and indirect effects of the NAO climatic phenomenon on both large-scale (Attrill & Power, 2002; Stenseth *et al.*, 2002; Martinho *et al.*, 2009; Nyitrai *et al.*, 2013) and local-scale climate patterns (Attrill & Power, 2002; Henriques *et al.*, 2007; Martinho *et al.*, 2009, 2012; van der Veer *et al.*, 2015), as well as on the biological components of marine ecosystems   (Attrill & Power, 2002; Stenseth *et al.*, 2002; Henriques *et al.*, 2007; Vinagre *et al.*, 2009a; Nyitrai *et al.*, 2013). Briefly, a positive NAOI phase is characterized by dry winter weather in southern Europe and mild and wet winter weather in northern Europe, while a negative NAOI phase has roughly the opposite conditions (Stenseth *et al.*, 2002).

The NAOI showed a positively relationship with 0-group sea bass densities and secondary production, and also a negative relationship with the day of annual abundance peaks. These relationships show how large-scale factors affect local climate patterns and

consequently fish assemblages over an extended period of time (Henriques *et al.*, 2007; Vinagre *et al.*, 2009a; Nyitrai *et al.*, 2013), and supports other studies where a positive relationship between the NAOI and *D. labrax* abundance, growth and recruitment was demonstrated in the Thames estuary (UK) (e.g. Attrill & Power, 2002) , at least during warm and positive NAOI years.

The temperature differential between estuarine and marine waters, boosted by the NAO influence on climatic variability, is in the basis of facultative exploitation of optimal thermal habitats by commercially important fish species (Attrill & Power, 2002). According to this study, increases in the population size of southern species in the Thames estuary, such as sea bass, during warm, high NAOI years is consistent with an opportunistic use of available thermal habitat. Also, it was observed that minimum and average winter temperatures are lower in the Thames estuarine waters than in the North Sea during years of high NAOI, and vice-versa. Considering the Portuguese coast, the NAO has been indicated as a key element in influencing SST, wind and current patterns and precipitation cycles (Lancaster *et al.*, 1998; Stenseth *et al.*, 2002; Henriques *et al.*, 2007), which are density-independent factors that determine the strength and direction of sea bass larvae transport towards estuaries and coasts. These factors, combined with the positive effects of river runoff in estuarine migration of fish larvae, as a promoter of a higher extension of river plumes towards coastal areas, are being influenced by global climate changes and will probably affect sea bass populations in an indirect way (Stenseth *et al.*, 2002; Vinagre *et al.*, 2009a). Precipitation, for instance, is expected to decrease in the Portuguese territory in the future, thus decreasing river drainage and river plumes that are essential for *D. labrax* larvae estuarine colonization (Zhang *et al.*, 1997; Vinagre *et al.*, 2009a) , as well as for other commercially important estuarine-dependent species (e.g. Boesch & Turner, 1984; Martinho *et al.*, 2009; Baptista *et al.*, 2010; Nyitrai *et al.*, 2012; Pasquaud *et al.*, 2012; Le Pape & Bonhommeau, 2013).

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On the other hand, the annual days of 0-group peak abundance was negatively correlated with the NAO of the previous year, contrary to 0-group densities and secondary production. In more detail, in years under a negative NAO phase, abundance peaks were observed later in the autumn season, particularly in November of 2005 and 2007. Despite that negative NAO conditions are characterized by wet and warm winters in southern Europe, stochastic episodes of climate extremes might occur, overriding the general climate patterns at a local scale. This seems to be the case of the 2005 and 2007 cohorts, which were the ones whose abundance peak was observed later in the season, matching also the occurrence of two extreme low precipitation periods which, as previously referred, are also determinant for the recruitment success of sea bass populations (Zhang *et al.*, 1997; Martinho *et al.*, 2009; Vinagre *et al.*, 2009a; Baptista *et al.*, 2010; Nyitrai *et al.*, 2012, 2013). Hence, NAO positive years seem to favor an earlier colonization of estuarine nurseries, which in turn will benefit local populations by providing a wider window of opportunity for growth, allowing attaining a better overwintering condition for juveniles.

Sea surface temperature was not significantly correlated with sea bass biological variables, which might be due to estuaries behaving as thermal buffers, by providing protection to juvenile fish species against harsher marine conditions and hence 0-group *D. labrax* may not be affected directly by oceanic conditions (Attrill & Power, 2002). Another reason may be the geographic localization of the Portuguese coast, which lies in the mid-range of sea bass distribution in the northeastern Atlantic Ocean. In fact, Vinagre *et al.*, 2009b reported that the water temperatures during the spawning season are well within the range of thermal tolerance for this species, so it is expected that only sudden and high intensity changes in water temperature will trigger measurable changes in growth and survival of juvenile sea bass. However, this is not the case of their northern limit populations, where increments in SST due to global climatic variability, are prompting increases in the population size and impelling a northwards shift towards higher latitudes, such as in the Wadden Sea

(Cardoso *et al.*, 2014), east and southeast coast of England (Henderson & Corps, 1997; Attrill & Power, 2002; Pawson *et al.*, 2007), west coast of Norway (Brander *et al.*, 2003) and the Baltic Sea (Bagdonas *et al.*, 2011). These phenomena are not exclusive to *D. labrax* populations, and are being reported for various marine and estuarine fish in the Atlantic inshore waters (Brander *et al.*, 2003; Perry *et al.*, 2005; Henriques *et al.*, 2007; Rijnsdorp *et al.*, 2009; Hermant *et al.*, 2010; Martinho *et al.*, 2010; Schaffler *et al.*, 2013; Able *et al.*, 2014).

It was clear that estuarine usage by juvenile fish, and particularly *D. labrax*, is considered a climate-dependent behavior (Attrill & Power, 2002). As extreme weather events are predicted to increase in future years (IPCC, 2014), including droughts, floods and heat waves, along with changes in the trends of large-scale climatic patterns that encompass NAO and SST variations, it is expected that sea bass abundances, production and growth will be affected, at least in an indirect way. NAOI values showed an overall decreasing trend in the last years of the study period, indicating a transition from a positive to a negative phase, as it was already noticed by some authors (e.g. Martinho *et al.*, 2012; Nyitrai *et al.*, 2013) and implicating variations in the dynamic responses of *D. labrax* and other marine juvenile migrant fish not only in the Mondego estuary, but at a more broad scale. Despite that the observed variations in SST are not expected to affect directly 0-group sea bass along the Portuguese coast, at northern European latitudes, ocean warming seems to be an important vector for increasing abundance and expansion of this species (Henderson & Corps, 1997; Brander *et al.*, 2003; Vinagre *et al.*, 2009b; Cardoso *et al.*, 2014). This assumption emphasizes the significant contributions of long-term studies as tools to the analysis of recruitment, habitat use patterns and variations in fish populations (Martinho *et al.*, 2009; Rijnsdorp *et al.*, 2009) in a climate change scenario, given that the nursery role of some estuarine areas might be affected by the combined interaction of food and thermal constraints (Freitas *et al*, 2012).

4.3 - Conclusions

This study elucidated how the 0-group populations of European sea bass *Dicentrarchus labrax* in estuaries are controlled by variations in both large-scale and local-scale climatic patterns, whose effects are observed in the abundance, production and on the process of nursery habitat colonization. Also, *D. labrax* nursery habitat use trends provided a good insight on how environmental changes, concerning global climatic changes, can significantly affect fish assemblages, and to a further extent, the structure and functioning of estuarine and marine ecosystems.

<u>References</u>

Able, K. W. (1999). Measures of Juvenile Fish Habitat Quality: Examples from a National Estuarine Research Reserve. In *American Fisheries Society Symposium* (Vol. 22, pp. 134–147).

Able, K. W. (2005). A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. *Estuarine, Coastal and Shelf Science*, *64*(1 SPEC. ISS.), 5–17. http://doi.org/10.1016/j.ecss.2005.02.002

Able, K. W., Wuenschel, M. J., Grothues, T. M., Vasslides, J. M., & Rowe, P. M. (2013). Do surf zones in New Jersey provide "nursery" habitat for southern fishes? *Environmental Biology of Fishes*, *96*(5), 661–675. http://doi.org/10.1007/s10641-012-0056-8

Able, K. W., Grothues, T. M., Morson, J. M., & Coleman, K. E. (2014). Temporal variation in winter flounder recruitment at the southern margin of their range: is the decline due to increasing temperatures? *ICES Journal of Marine Science*, *71*(8), 2186–2197. http://doi.org/10.1093/icesjms/fsu094

Allen, R. L., & Baltz, D. M. (1997). Distribution and microhabitat use by flatfishes in a Louisiana estuary. *Environmental Biology of Fishes*, *50*(1), 85–103. http://doi.org/10.1023/A:1007398517163

Almeida, J. R., Gravato, C., & Guilhermino, L. (2014). Effects of Temperature in Juvenile Seabass (Dicentrarchus labrax L.) Biomarker Responses and Behaviour: Implications for Environmental Monitoring. *Estuaries and Coasts*, 1–11. http://doi.org/10.1007/s12237-014-9792-7

Aprahamian, M. W., & Barr, C. D. (1985). The Growth, Abundance and Diet of O-Group Sea Bass, Dicentrarchus Labrax, From the Severn Estuary. *Journal of the Marine Biological Association of the United Kingdom*, *65*(01), 169. http://doi.org/10.1017/S0025315400060884

Arias, A. M. (1980). Crescimiento, regimen alimentario y reproduccion de la dourada (Sparus aurata L.) y del robalo (Dicentrarchus labrax L.) en los esteros de Cádiz. *Inv. Pesq.*, *44*(1), 59–83.

Attrill, M. J., & Power, M. (2002). Climatic influence on a marine fish assemblage. *Nature*, *417*(1999), 275–278. http://doi.org/10.1038/417275a

Attrill, M. J., & Power, M. (2004). Partitioning of temperature resources amongst an estuarine fish assemblage. *Estuarine, Coastal and Shelf Science*, *61*, 725–738. http://doi.org/10.1016/j.ecss.2004.07.010

Attrill, M. J., Power, M., & Thomas, R. M. (1999). Modelling estuarine Crustacea population fluctuations in response to physico-chemical trends. *Marine Ecology Progress Series*, *178*, 89–99. http://doi.org/10.3354/meps178089

Bagdonas, K., Nika, N., Bristow, G., Jankauskiene, R., Salyte, a., & Kontautas, a. (2011). First record of Dicentrarchus labrax (Linnaeus, 1758) from the southeastern Baltic Sea (Lithuania). *Journal of Applied Ichthyology*, *27*, 1390–1391. http://doi.org/10.1111/j.1439-0426.2011.01817.x

Baptista, J., Martinho, F., Dolbeth, M., Viegas, I., Cabral, H., & Pardal, M. (2010). Effects of freshwater flow on the fish assemblage of the mondego estuary (Portugal): Comparison between drought and non-drought years. *Marine and Freshwater Research*, *61*, 490–501. http://doi.org/10.1071/MF09174

Barnabé, G. (1973). Étude morphologique du loup Dicentrarchus labrax L. de la région de Sète. *Atlantic*, *37*(3), 397–410.

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., & Eggleston, D. B. (2001). The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. *Bioscience*, *51*(8), 633–641.

Boesch, D. F., & Turner, R. E. (1984). Dependence of Fishery Species on Salt Marshes: The Role of Food and Refuge. *Estuaries*, *7*(4), 460. http://doi.org/10.2307/1351627

Brander, K. M., Blom, M. F., Borges, M. ., Erzini, K., Henderson, G., MacKenzie, B. R., … Toresen, R. (2003). Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature? *ICES Marine Science Symposia*, *219*, 261–270.

Brett, J. R. (1979). Environmental Factors and Growth. *Fish physiology*, *8*, 599-675. New York: Academic Press.

Cabral, H., & Costa, M. J. (2001). Abundance, feeding ecology and growth of 0-group sea bass, Dicentrarchus labrax, within the nursery areas of the Tagus estuary. *Journal of the Marine Biological Association of the UK*, *81*, 679–682. http://doi.org/doi:10.1017/S0025315401004362

Cabral, H. N., Costa, M. J., & Salgado, J. P. (2001). Does the Tagus estuary fish community reflect environmental changes? *Climate Research*, *18*(1991), 119–126. http://doi.org/10.3354/cr018119

Cabral, H. N., Vasconcelos, R., Vinagre, C., França, S., Fonseca, V., Maia, A., … Costa, M. J. (2007). Relative importance of estuarine flatfish nurseries along the Portuguese coast. *Journal of Sea Research*, *57*, 209–217. http://doi.org/10.1016/j.seares.2006.08.007

Cardoso, J. F. M. F., Freitas, V., Quilez, I., Jouta, J., Witte, J. I., & Van Der Veer, H. W. (2014). The European sea bass Dicentrarchus labrax in the Dutch Wadden Sea: from visitor to resident species. *Journal of the Marine Biological Association of the United Kingdom*, 1–12. http://doi.org/10.1017/S0025315414001714

Claridge, P. N., & Potter, I. C. (1983). Movements, abundance, age composition and growth of bass, Dicentrarchus labrax, in the Severn Estuary and inner Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom*, *63*(04), 871–879. http://doi.org/10.1017/S0025315400071289

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W.J. Gutowski, T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A. J. Weaver and M. Wehner (2013). Long-term Climate Change: Projections, Commitments and Irreversibility. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1029 –1136, doi:10.1017/CBO9781107415324.024.

Costa, M. J.; Cabral, H. N.; Drake, P.; Economou, A. N.; Fernandez- Delgado, C.; Gordo, L.; Marchand, J.; Thiel, R. (2002): Recruitment and production of commercial species in estuaries. In: *Fishes in estuaries*. M. Elliott, K. Hemingway (Eds.). Blackwell Science, UK, pp. 54–123.

Cowley, P. D., & Whitefield, A. K. (2002). Biomass and production estimates of a fish community in a small South African estuary. *Journal of Fish Biology*, *61*, 74–89. http://doi.org/10.1111/j.1095-8649.2002.tb01763.x

Dahlgren, C. P., Kellison, G. T., Adams, A. J., Gillanders, B. M., Kendall, M. S., Layman, C. a., … Serafy, J. E. (2006). Marine nurseries and effective juvenile habitats: Concepts and applications. *Marine Ecology Progress Series*, *312*(Shulman 1985), 291–295. http://doi.org/10.3354/meps312291

Desaunay, Y., Perodou, J.-B., & Beillois, P. (1981). Étude des nurseries de poissons du littoral de la Loire-Atlantique. *Science et Pêche*, (319), 23.

Devauchelle, N., & Coves, D. (1988). Sea bass (Dicentrarchus labrax) reproduction in captivity: gametogenesis and spawning. *Aquatic Living Resources*, *1*(4), 215–222. http://doi.org/10.1051/alr:1988021

Dolbeth, M., Cardoso, P. G., Ferreira, S. M., Verdelhos, T., Raffaelli, D., & Pardal, M. a. (2007a). Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period. *Marine Pollution Bulletin*, *54*(5), 576–585. http://doi.org/10.1016/j.marpolbul.2006.12.005

Dolbeth, M., Martinho, F., Leitão, R., Cabral, H., & Pardal, M. a. (2007b). Strategies of Pomatoschistus minutus and Pomatoschistus microps to cope with environmental instability. *Estuarine, Coastal and Shelf Science*, *74*, 263–273. http://doi.org/10.1016/j.ecss.2007.04.016

Dolbeth, M., Martinho, F., Viegas, I., Cabral, H., & Pardal, M. a. (2008). Estuarine production of resident and nursery fish species: Conditioning by drought events? *Estuarine, Coastal and Shelf Science*, *78*, 51–60. http://doi.org/10.1016/j.ecss.2007.11.021

Dolbeth, M., Martinho, F., Freitas, V., Costa-Dias, Ś., Campos, J., & Pardal, M. Â. (2010). Multi-year comparisons of fish recruitment, growth and production in two drought-affected Iberian estuaries. *Marine and Freshwater Research*, *61*(Brey 2001), 1399–1415. http://doi.org/10.1071/MF10002

Dolbeth, M., Cardoso, P. G., Grilo, T. F., Bordalo, M. D., Raffaelli, D., & Pardal, M. a. (2011). Long-term changes in the production by estuarine macrobenthos affected by multiple stressors. *Estuarine, Coastal and Shelf Science*, *92*(1), 10–18. http://doi.org/10.1016/j.ecss.2010.12.006

Dolbeth, M., Cusson, M., Sousa, R., Pardal, M. a., & Prairie, Y. T. (2012). Secondary production as a tool for better understanding of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*, 1230–1253. http://doi.org/10.1139/f2012-050

Edgar, G. J., Barrett, N. S., Graddon, D. J., & Last, P. R. (2000). The conservation significance of estuaries: A classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. *Biological Conservation*, *92*(3), 383–397. http://doi.org/10.1016/S0006-3207(99)00111-1

Elliott, M., & Dewailly, F. (1995). The structure and composition of european estuarine fish assemblages. *Netherlands Journal of Aquatic Ecology*, *29*, 397–417.

FAO. (2015). *Species Fact Sheets: Dicentrarchus labrax (Linnaeus, 1758)* (Vol. 9). Available at http://www.fao.org/fishery/species/2291/en. [accessed 9 April 2015]

Freitas, V., Kooijman, S. a L. M., & Van Der Veer, H. W. (2012). Latitudinal trends in habitat quality of shallow-water flatfish nurseries. *Marine Ecology Progress Series*, *471*, 203–214. http://doi.org/10.3354/meps10025

Gayanilo Jr., F. C., Sparre, P., & Pauly, D. (2005). *FAO-ICLARM stock assessment tools II (FiSAT II). Revised version. User's guide.* Rome: FAO Computerized Information Series (Fisheries). No. 8. Revised Version. Food and Agriculture Organisation, Rome.

Genner, M. J., Sims, D. W., Wearmouth, V. J., Southall, E. J., Southward, A. J., Henderson, P. a, & Hawkins, S. J. (2004). Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1539), 655–661. http://doi.org/10.1098/rspb.2003.2651

Gillanders, B. M., Able, K. W., Brown, J. a., Eggleston, D. B., & Sheridan, P. F. (2003). Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: An important component of nurseries. *Marine Ecology Progress Series*, *247*, 281–295. http://doi.org/10.3354/meps247281

Gordo, L. S. (1989). Age, growth and sexuality of sea bass, Dicentrarchus labrax (Linnaeus, 1758) (Perciformes, Moronidae) from Aveiro lagoon, Portugal. *Sci. Mar.*, *53*(1), 121–126.

Gravier, R. (1961). Les bars (loups) du Maroc Atlantique: Morone labrax (Linné) et Morone punctata (Bloch). *Revue Des Travaux de l'Institut Des Pêches Maritimes*, *25*(3), 281–292.

Hartley, P. H. T. (1940). The Saltash tuck-net fishery and the ecology of some estuarine fishes. *Journal of the Marine Biological Association of the United Kingdom*, *XXIV*, 1–68. Retrieved from http://sabella.mba.ac.uk/1147/

Henderson, P. A., & Corps, M. (1997). The role of temperature and cannibalism in interannual recruitment variation of bass in British waters. *Journal of Fish Biology*, *50*, 280–295. http://doi.org/10.1111/j.1095-8649.1997.tb01359.x

Henderson, P. A., & Seaby, R. M. (2005). The role of climate in determining the temporal variation in abundance, recruitment and growth of sole Solea solea in the Bristol Channel. *Journal of the Marine Biological Association of the UK*, *85*(1), 197–204. http://doi.org/10.1017/S0025315405011069h

Henriques, M., Gonçalves, E. J., & Almada, V. C. (2007). Rapid shifts in a marine fish assemblage follow fluctuations in winter sea conditions. *Marine Ecology Progress Series*, *340*, 259–270. http://doi.org/10.3354/meps340259

Hermant, M., Lobry, J., Bonhommeau, S., Poulard, J. C., & Le Pape, O. (2010). Impact of warming on abundance and occurrence of flatfish populations in the Bay of Biscay (France). *Journal of Sea Research*, *64*(1-2), 45–53. http://doi.org/10.1016/j.seares.2009.07.001

Houde, E. D., & Rutherford, E. S. (1993). Recent Trends in Estuarine Fisheries : Predictions of Fish Production and Yield, *16*(2), 161–176.

Ibañez, F., Fromentin, J. M., & Castel, J. (1993). Application de la méthode des sommes cumulées à l'analyse des séries chronologiques en océanographie. *Comptes rendus de l'Académie des sciences. Série 3, Sciences de la vie*, *316*(8), 745–748. Retrieved from http://cat.inist.fr/?aModele=afficheN&cpsidt=4880317

Intergovernmental Panel on Climate Change. (2013): Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp, doi:10.1017/CBO9781107415324. Available at http://www.ipcc.ch/report/ar5/ [accessed 23 March 2015].

Intergovernmental Panel on Climate Change. (2014): Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp. Available at http://www.ipcc.ch/report/ar5/ [accessed 23 March 2015].

Jennings, S., Lancaster, J. E., Ryland, J. S., & Shackley, S. E. (1991). The Age Structure and Growth Dynamics of Young-of-the-year Bass, Dicentrarchus labrax, Populations. *Journal of the Marine Biological Association of the United Kingdom*, *71*, 799–810. http://doi.org/10.1017/S0025315400053467

Jennings, S., & Pawson, M. G. (1992). The origin and recruitment of bass, Dicentrarchus labrax, larvae to nursery areas. *Journal of the Marine Biological Association of the United Kingdom*, *72*(01), 199–212. http://doi.org/10.1017/S0025315400048888

Kennedy, M., & Fitzmaurice, P. (1968). Occurence of eggs of bass Dicentrarchus labrax on the southern coasts of Ireland. *Journal of the Marine Biological Association of the United Kingdom*, *48*, 585–592. Retrieved from http://sabella.mba.ac.uk/2503/

Kennedy, M., & Fitzmaurice, P. (1972). The biology of the bass, Dicentrarchus labrax, in irish waters. *Journal of the Marine Biological …*, *52*, 557–597. http://doi.org/doi:10.1017/S0025315400021597

Kottelat M. and Freyhof J. (2007) *Handbook of European freshwater fishes*. Kottelat, Cornol, Switzerland and Freyhof, Berlin, Germany.

Lancaster, J. E., Pawson, P. E., Pickett, G. D., & Jennings, J. (1998). The Impact of the "Sea Empress" Oil Spill on Seabass Recruitment. *Marine Pollution Bulletin*, *36*(9), 677–688. http://doi.org/10.1051/alr:2004029

Le Pape, O., & Bonhommeau, S. (2013). The food limitation hypothesis for juvenile marine fish. *Fish and Fisheries*, 1–26. http://doi.org/10.1111/faf.12063

Leitão, R., Martinho, F., Cabral, H. N., Neto, J. M., Jorge, I., & Pardal, M. a. (2007). The fish assemblage of the Mondego estuary: Composition, structure and trends over the past two decades. *Hydrobiologia*, *587*, 269–279. http://doi.org/10.1007/s10750-007-0688-4

Magnuson, J. J., Crowder, L. B., & Medvick, P. A. (1979). Temperature as an Ecological Resource. *American Zoologist*, *19*, 331–343. http://doi.org/10.1086/280210

Marques, S. C., Primo, A. L., Martinho, F., Azeiteiro, U. M., & Pardal, M. Â. (2014). Shifts in estuarine zooplankton variability following extreme climate events: A comparison between drought and regular years. *Marine Ecology Progress Series*, *499*, 65–76. http://doi.org/10.3354/meps10635

Martinho, F., Leitão, R., Neto, J. M., Cabral, H. N., Marques, J. C., & Pardal, M. a. (2007a). The use of nursery areas by juvenile fish in a temperate estuary, Portugal. *Hydrobiologia*, *587*, 281–290. http://doi.org/10.1007/s10750-007-0689-3

Martinho, F., Leitão, R., Viegas, I., Dolbeth, M., Neto, J. M., Cabral, H. N., & Pardal, M. a. (2007b). The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. *Estuarine, Coastal and Shelf Science*, *75*, 537–546. http://doi.org/10.1016/j.ecss.2007.05.040

Martinho, F., Leitão, R., Neto, J. M., Cabral, H., Lagardère, F., & Pardal, M. a. (2008). Estuarine colonization, population structure and nursery functioning for 0-group sea bass (Dicentrarchus labrax), flounder (Platichthys flesus) and sole (Solea solea) in a mesotidal temperate estuary. *Journal of Applied Ichthyology*, *24*, 229–237. http://doi.org/10.1111/j.1439-0426.2007.01049.x

Martinho, F., Dolbeth, M., Viegas, I., Teixeira, C. M., Cabral, H. N., & Pardal, M. a. (2009). Environmental effects on the recruitment variability of nursery species. *Estuarine, Coastal and Shelf Science*, *83*, 460–468. http://doi.org/10.1016/j.ecss.2009.04.024

Martinho, F., Dolbeth, M., Viegas, I., Baptista, J., Cabral, H. N., & Pardal, M. a. (2010). Does the flatfish community of the Mondego estuary (Portugal) reflect environmental changes? *Journal of Applied Ichthyology*, *26*, 843–852. http://doi.org/10.1111/j.1439-0426.2010.01486.x

Martinho, F., Cabral, H. N., Azeiteiro, U. M., & Pardal, M. a. (2012). Estuarine nurseries for marine fish: Connecting recruitment variability with sustainable fisheries management. *Management of Environmental Quality: An International Journal*, *23*, 414–433. http://doi.org/10.1108/14777831211232236

McLusky, D. S., & Elliott, M. (2004). *The Estuarine Ecosystem: Ecology, Threats, and Management* (3rd Editio). Oxford University Press. http://doi.org/10.1093/ISBN

Morrongiello, J. R., Walsh, C. T., Gray, C. a., Stocks, J. R., & Crook, D. a. (2014). Environmental change drives long-term recruitment and growth variation in an estuarine fish. *Global Change Biology*, *20*(6), 1844–1860. http://doi.org/10.1111/gcb.12545

Nixon, S. W., Oviatt, C. a., Frithsen, J., & Sullivan, B. (1986). Nutrients and the Productivity of Estuarine and Coastal Marine Ecosystems. *Journal of the Limnological Society of Southern Africa*, *12*(1-2), 43–71. http://doi.org/10.1080/03779688.1986.9639398

Nyitrai, D., Martinho, F., Dolbeth, M., Baptista, J., & Pardal, M. a. (2012). Trends in estuarine fish assemblages facing different environmental conditions: Combining diversity with functional attributes. *Aquatic Ecology*, *46*(2), 201–214. http://doi.org/10.1007/s10452-012-9392-1

Nyitrai, D., Martinho, F., Dolbeth, M., Rito, J., & Pardal, M. a. (2013). Effects of local and large-scale climate patterns on estuarine resident fishes: The example of Pomatoschistus microps and Pomatoschistus minutus. *Estuarine, Coastal and Shelf Science*, *135*, 260–268. http://doi.org/10.1016/j.ecss.2013.10.030

Pardal, M. A., Marques, J.C., & Graça M. A. (2002) *Aquatic Ecology of the Mondego River Basin Global Importance of Local Experience*. Coimbra, Imprensa da Universidade de Coimbra.

Pasquaud, S., Béguer, M., Larsen, M. H., Chaalali, A., Cabral, H., & Lobry, J. (2012). Increase of marine juvenile fish abundances in the middle Gironde estuary related to warmer and more saline waters, due to global changes. *Estuarine, Coastal and Shelf Science*, *104-105*, 46–53. http://doi.org/10.1016/j.ecss.2012.03.021

Pawson, M. G. (1992). Climatic influences on the spawning success, growth and recruitment of Bass (Dicentrarcus Labrax) in British Waters. In *ICES Marine Science Symposia* (Vol. 195, pp. 388–392).

Pawson, M. G., Pickett, G. D., Leballeur, J., Brown, M., & Fritsch, M. (2007). Migrations, fishery interactions, and management units of sea bass (Dicentrarchus labrax) in Northwest Europe. *ICES Journal of Marine Science*, *64*, 332–345. http://doi.org/10.1093/icesjms/fsl035

Perry, a L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, *308*(June), 1912–1915. http://doi.org/10.1126/science.1111322

Pickett, G. D. & Pawson, M. G. (1994) *Sea Bass. Biology, Exploitation and Conservation* (1st edition). London: Chapman & Hall, Fish and Fisheries Series Vol. 12.

Pickett, G. D., Kelley, D. F., & Pawson, M. G. (2004). The patterns of recruitment of sea bass, Dicentrarchus labrax L. from nursery areas in England and Wales and implications for fisheries management. *Fisheries Research*, *68*, 329–342. http://doi.org/10.1016/j.fishres.2003.11.013

R Development Core Team. (2013). *R : A Language and Environment for Statistical Computing* (3.0.1 ed., Vol. 1). R Foundation for Statistical Computing. http://doi.org/10.1007/978-3-540-74686-7

Rijnsdorp, A. D., Peck, M. a., Engelhard, G. H., Möllmann, C., & Pinnegar, J. K. (2009). Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*, *66*(7), 1570–1583. http://doi.org/10.1093/icesjms/fsp056

Rogdakis, Y., Ramfos, A., Koukou, K., Dimitriou, E., & Katselis, G. (2010). Feeding habits and trophic level of sea bass (Dicentrarchus labrax) in the Messolonghi-Etoliko lagoons complex (Western Greece). *Journal of Biological Research-Thessaloniki*, *13*, 13–26.

Saillant, E., Fostier, A., Haffray, P., Menu, B., & Chatain, B. (2003). Saline preferendum for the European sea bass, Dicentrarchus labrax, larvae and juveniles: Effect of salinity on early development and sex determination. *Journal of Experimental Marine Biology and Ecology*, *287*, 103–117. http://doi.org/10.1016/S0022-0981(02)00502-6

Schaffler, J. J., Montfrans, J. Van, Jones, C. M., & Orth, R. J. (2013). Fish Species Distribution in Seagrass Habitats of Chesapeake Bay are Structured by Abiotic and Biotic Factors. *Marine and Coastal Fisheries*, *5*(1), 114–124. http://doi.org/10.1080/19425120.2013.804013

Slutz, R. J., Lubker, S. J., Hiscox, J. D., Woodruff, S. D., Jenne, R. L., Joseph, D. H., … Elms, J. D. (1985). Comprehensive Ocean Atmosphere Data Set. Release 1.

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S., & Lima, M. (2002). Ecological effects of climate fluctuations. *Science*, *297*(5585), 1292–1296. http://doi.org/10.1126/science.1071281

Tine, M., Kuhl, H., Gagnaire, P.-A., Louro, B., Desmarais, E., Martins, R. S. T., … Reinhardt, R. (2014). European sea bass genome and its variation provide insights into adaptation to euryhalinity and speciation. *Nature Communications*, *5*(May), 5770. http://doi.org/10.1038/ncomms6770

Tulp, I., Bolle, L. J., & Rijnsdorp, A. D. (2008). Signals from the shallows: In search of common patterns in long-term trends in Dutch estuarine and coastal fish. *Journal of Sea Research*, *60*, 54–73. http://doi.org/10.1016/j.seares.2008.04.004

Van der Veer, H. W., Berghahn, R., Miller, J. M., & Rijnsdorp, a. (2000). Recruitment in flatfish, with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia. *ICES Journal of Marine Science*, *57*(2), 202–215. http://doi.org/10.1006/jmsc.1999.0523

Van der Veer, H. W., Dapper, R., Henderson, P. A., Jung, A. S., Philippart, C. J. M., Witte, J. I., & Zuur, A. F. (2015). Changes over 50 years in fish fauna of a temperate coastal sea: Degradation of trophic structure and nursery function. *Estuarine, Coastal and Shelf Science*, *155*, 156–166. http://doi.org/10.1016/j.ecss.2014.12.041

Vasconcelos, R. P., Reis-Santos, P., Tanner, S., Maia, A., Latkoczy, C., Günther, D., … Cabral, H. (2008). Evidence of estuarine nursery origin of five coastal fish species along the Portuguese coast through otolith elemental fingerprints. *Estuarine, Coastal and Shelf Science*, *79*, 317–327. http://doi.org/10.1016/j.ecss.2008.04.006

Vasconcelos, R. P., Reis-Santos, P., Maia, a., Fonseca, V., França, S., Wouters, N., … Cabral, H. N. (2010). Nursery use patterns of commercially important marine fish species in estuarine systems along the Portuguese coast. *Estuarine, Coastal and Shelf Science*, *86*, 613–624. http://doi.org/10.1016/j.ecss.2009.11.029

Vinagre, C., Santos, F. D., Cabral, H. N., & Costa, M. J. (2009a). Impact of climate and hydrology on juvenile fish recruitment towards estuarine nursery grounds in the context of climate change. *Estuarine, Coastal and Shelf Science*, *85*(3), 479–486. http://doi.org/10.1016/j.ecss.2009.09.013

Vinagre, C., Ferreira, T., Matos, L., Costa, M. J., & Cabral, H. N. (2009b). Latitudinal gradients in growth and spawning of sea bass, Dicentrarchus labrax, and their relationship with temperature and photoperiod. *Estuarine, Coastal and Shelf Science*, *81*(3), 375–380. http://doi.org/10.1016/j.ecss.2008.11.015

Wassef, E., & El Emary, H. (1989). Contribution to the biology of bass, Dicentrarchus labrax L. in the Egyptian Mediterranean waters off Alexandria. *Cybium*, *13*(4), 327–345. Retrieved from http://cat.inist.fr/?aModele=afficheN&cpsidt=6844662

Whitfield, A. K. (1999). Ichthyofaunal assemblages in estuaries: A South African case study. *Reviews in Fish Biology and Fisheries*, *9*(2), 151–186. http://doi.org/10.1023/A:1008994405375

Winberg, G.G., (1971). *Methods for the Estimation of Production of Aquatic Animals*. Academic Press, London, p. 175.

Zhang, X., Wang, X. L., & Corte-Real, J. (1997). On the relationships between daily circulation patterns and precipitation in Portugal. *Journal of Geophysical Research*, *102*(D12), 13495–13507. http://doi.org/10.1029/97JD01012

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