VÂNIA CATARINA VIEIRA BAPTISTA

# INFLUENCE OF OCEANOGRAPHY AND LARVAE BEHAVIOUR ON RECRUITMENT OF TEMPERATE FISHES: THE IMPORTANCE OF PHYSICS-BIOLOGY LINKS TO MANAGE FISHERIES AT A LOCAL SCALE

**UNIVERSIDADE DO ALGARVE**
Faculdade de Ciências e Tecnologia
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**Doutoramento em Ciências do Mar, da Terra e do Ambiente (ramo Ciências dos Mar, especialidade em Ecologia Marinha)**

**Trabalho efetuado sob orientação de:**
**Prof. Dra. Maria Alexandra Teodósio**
**Dr. Francisco Leitão**
**Prof. Dr. Eric Wolanski**

**UNIVERSIDADE DO ALGARVE**
Faculdade de Ciências e Tecnologia
2019

# DECLARATION OF AUTHORSHIP

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I declare to be the author of this work, which is original and unpublished. Authors and works consulted are duly cited in the text and are included in the list of references.

*Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.*

Vânia Catarina Vieira Baptista

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*“We all come from the sea, but we are not all of the sea. Those of us who are, we children of the tides, must return to it again and again, until the day we don't come back leaving only that which was touched along the way.”*

(Chasing Mavericks)

*Aos meus pais*

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# ABSTRACT

A central question in the ecology of fishing resources is understanding the mechanisms behind recruitment variability. This thesis aimed to analyse the factors responsible for recruitment variability of two economically relevant species, in Portugal, white seabream (*Diplodus sargus*) and two-banded seabream (*Diplodus vulgaris*). The temporal variability in sea surface temperature (SST) was studied over specific regions of the Portuguese coast, along the last decades. The effects of changes in environmental variables and fishing pressure on these resources were evaluated, using a multi-model approach. Swimming capabilities of fish larvae and their behavioural responses to environmental cues, potentially relevant for the selection of nursery areas and recruitment, were determined using Ria Formosa coastal lagoon and white seabream as a case study. The analysis of SST during the period 1980-2010 showed a generalized warming along the Portuguese coast, with region- and season-variable tendencies. The effects of environmental and fishing variability on the landings were species-specific, and also varied depending on region and season. The swimming ability of white seabream larvae, as well as their exploratory activity, increased during ontogeny. However, this species did not select any of the environmental stimuli tested. The exploratory behaviour of white seabream larvae presented consistent individual differences throughout ontogeny, indicating that the personality traits emerge early in their life cycle.The integration of these results into an individual-based model showed that both the location of spawning sites and directional swimming capabilities are important determinants of the ingress success of white seabream into a nursery area, as the Ria Formosa lagoon. Thus, the integration of region- and season-specific oceanographic and fishing processes, as well as fish larvae behaviour and dispersion modelling, and supported climate change scenarios, are required for improving the estimates of fish recruitment.

Keywords: dispersion; swimming performance; habitat choice; environmental variability; fisheries

# RESUMO

Uma questão central na ecologia dos recursos pesqueiros é compreender os mecanismos que causam variabilidade no recrutamento. Esta tese teve como objetivo analisar os fatores responsáveis pela variabilidade do recrutamento de espécies economicamente relevantes em Portugal, o sargo-legítimo (*Diplodus sargus*) e a safia (*Diplodus vulgaris*). A variabilidade na temperatura da superfície do mar (SST) foi estudada em regiões específicas da costa portuguesa nas últimas décadas. Os efeitos das alterações nas variáveis ambientais e da pescada nestes recursos foram avaliados, usando uma abordagem multimodelo. As capacidades natatórias das larvas de peixe e as suas respostas comportamentais às pistas ambientais, potencialmente relevantes para a seleção de zonas nursery e recrutamento, foram determinadas utilizando a Ria Formosa e o sargo-legítimo como estudo de caso. A análise da SST durante o período 1980-2010 mostrou um aquecimento generalizado ao longo da costa portuguesa, com tendências regionais e sazonais variáveis. Os efeitos da variabilidade ambiental e da pesca nos desembarques foram específicos para cada espécie, e também variaram dependendo da região e estação do ano. A capacidade natatória das larvas de sargo-legítimo, bem como a sua atividade exploratória, aumentou durante a ontogenia. No entanto, esta espécie não selecionou nenhum dos estímulos testados. O comportamento exploratório das larvas de sargo-legítimo apresentou diferenças individuais consistentes ao longo da ontogenia, indicando que os traços de personalidade aparecem cedo no seu ciclo de vida. A integração destes resultados num modelo individual mostrou que a localização dos locais de postura e a natação direcional são determinantes do sucesso do ingresso das larvas de sargo-legítimo numa zona de nursery, como a Ria Formosa. Assim, a integração dos processos oceanográficos e da pesca específicos para cada região e estação, bem como o comportamento das larvas de peixe e a modelação da dispersão, suportados pelos senários de alterações climáticas, são necessários para melhorar as estimativas de recrutamento de peixes.

Palavras-chave: dispersão; capacidade natatória; escolha de habitat; variabilidade ambiental; pescas

# RESUMO ALARGADO

As espécies de peixes de zonas costeiras temperadas têm uma história de vida bipartida: a postura ocorre no mar onde as larvas, eclodidas de ovos planctónicos, permanecem no ambiente pelágico durante semanas a meses antes de assentarem. Inicialmente os ovos e larvas são transportados passivamente dos locais de postura para as áreas de recrutamento (áreas de nursery costeiras: lagunas costeiras, estuários e áreas de costa rochosa) por processos oceanográficos costeiros.

Uma questão central na ecologia dos recursos pesqueiros é compreender as causas da variabilidade do recrutamento. Tem sido assumido que a sobrevivência e crescimento durante as fases larvar e juvenil são determinantes para a variabilidade espacial e temporal do recrutamento, que por sua vez afetam o tamanho e a dinâmica das populações locais. Esta variabilidade é também influenciada pela mortalidade devido às condições ambientais, fraca capacidade de alimentação e vulnerabilidade aos efeitos dos predadores, e pela interação dos processos físicos e biológicos relacionados com o transporte e retenção larvar. No entanto, a maioria dos fatores que determina o sucesso do recrutamento permanece pouco clara.

Por outro lado, os fatores ambientais têm sofrido alterações ao longo do tempo, como por exemplo, o aumento da temperatura da superfície do mar (SST) tem sido registado ao longo do século passado, bem como padrões do vento, chuvas e fluxos dos rios. No entanto, estas alterações ambientais no oceano não são homogéneas, e em conjunto com a atividade da pesca interagem de diferentes maneiras causando variabilidade nos recursos marinhos costeiros.

O desenvolvimento da acuidade sensorial e das capacidades natatórias das larvas de peixes costeiros, bem como as suas respostas às pistas das nurseries costeiras, são também essenciais para o sucesso do recrutamento. No entanto, a maioria dos estudos tem investigado estas capacidades comportamentais em larvas de peixes de recifes de coral, enquanto apenas alguns trabalhos têm estudado este tópico em larvas de peixes de regiões temperadas. A Hipótese da Acuidade Sensorial e Comportamental (SAAB) propõe que as larvas pelágicas de peixes de regiões temperadas também conseguem detetar pistas de áreas de nursery e ingressar nesses ecossistemas usando diversas estratégias ativas de natação.

Assim, o objetivo da presente tese foi avaliar os fatores responsáveis pela variabilidade do recrutamento de duas espécies de peixe com relevante valor económico em Portugal, o sargo-legítimo (*Diplodus sargus*; Linnaeus, 1758) e a safia (*Diplodus vulgaris*; Geoffroy Saint-Hilaire, 1817). Para este propósito estudou-se a variabilidade temporal e regional da SST ao longo das ultimas décadas na costa portuguesa; avaliaram-se os efeitos das alterações ambientais e da pressão da pesca nas capturas de sargo-legítimo e de safia ao longo da costa portuguesa; e determinaram-se as capacidades natatórias (velocidade crítica de natação – $U_{crit}$, e resistência) e o comportamento de resposta a pistas ambientais para a seleção de zonas nursery, ao longo do desenvolvimento, utilizando a Ria Formosa (sul de Portugal) e as larvas de sargo-legítimo como caso de estudo.

A análise da SST mostrou um aquecimento generalizado ao longo da costa portuguesa durante as últimas décadas (1980-2010), independentemente da fonte de dados utilizada. No entanto, o padrão de aquecimento não foi uniforme em todas as regiões: aproximadamente +0.1 °C década$^{-1}$ nas costas noroeste e sudoeste e +0.2°C década$^{-1}$ na costa sul. As taxas de incremento da SST também variaram sazonalmente, com os valores mais elevados registados na primavera e no verão (aproximadamente +0.4 °C década$^{-1}$). Esta variabilidade sazonal da SST é relevante para a dinâmica dos processos biológicos devido às diferenças na vulnerabilidade ao stress térmico entre espécies, que afeta o seu ciclo de vida, como por exemplo a postura, e desenvolvimento larval

Os efeitos da variabilidade ambiental e da pesca nas capturas de sargo-legítimo e de safia também variaram regionalmente e sazonalmente. Em ambas as espécies, o esforço de pesca não foi relacionado com as capturas, o que significa que a variabilidade das capturas foi induzida pela variabilidade ambiental e por fatores intrínsecos. Para o sargo-legítimo, os efeitos sazonais do outono, inverno e primavera foram relacionados com as captura nas costas noroeste, sudoeste e sul de Portugal, indicando um possível gradiente longitudinal costeiro. Enquanto que para a safia, as capturas foram relacionadas com o outono e o verão no noroeste, com o inverno no sudoeste e com o outono e inverno na costa sul. Embora algumas variáveis ambientais tenham a mesma relação com as capturas em ambas as espécies (por exemplo, o efeito positivo da magnitude do vento no outono), essas relações também foram específicas para cada espécie: a SST e o Índice de Oscilação do Atlântico Norte (NAO) tiveram efeitos negativos em ambas as espécies mas em diferentes estações e regiões; a componente do vento de leste e as descargas do rio foram apenas relacionados com as capturas de safia. Assim, cada uma das duas espécies estudadas no presente trabalho reage de maneira diferente à variabilidade ambiental.

Em relação à capacidade natatória, os resultados mostraram que as larvas de sargo-legítimo tornam-se nadadores mais competentes ao longo do desenvolvimento. A capacidade natatória das larvas aumentou de forma constante com a idade, alcançando os valores de $U_{crit}$ máximos aos 50 e 55 dias após a flexão (DPH; 23.0 cm $s^{-1}$); e a distância nadada nos testes de resistência mostrou um aumento abrupto dos 35 DPH (5.0 ± 6.0 km) para os 45 DPH (54.1 ± 22.1 km), com uma distancia máxima nadada de 86.5 km in 240.2 h. As larvas em pós-flexão de espécies de peixes temperados provaram ser melhores nadadoras que o esperado, com velocidades de natação várias vezes superiores ao seu comprimento do corpo por segundo e velocidades sustentadas superiores que as correntes típicas do seu ambiente natural, especialmente após os 35 DPH, nadando continuamente por dezenas de quilómetros durante várias horas ou dias, mesmo sem se alimentarem.

Contrariamente às nossas hipóteses, as larvas de sargo-legítimo não mostraram preferência por nenhum das pistas testadas (habitats da ria ou zonas costeiras rochosas, aumento da temperatura da água ou diminuição da salinidade da água). A atividade exploratória também aumentou ao longo do desenvolvimento e foi maior quando as larvas apresentaram comportamentos não responsivos ou inconclusivos, o que significa que as larvas podiam estar à procura de um estímulo diferente do que foi apresentado. Durante as fases iniciais do desenvolvimento, as larvas de sargo-legítimo exibiram uma variabilidade inter-individual altamente consistente nos seus comportamentos, o que indica que o aparecimento de traços de personalidade ocorre relativamente cedo na sua ontogenia.

Os resultados dos testes de capacidade natatória, da acuidade sensorial e traços de personalidade das larvas pós-flexão foram combinados num modelo de dispersão (individual based model – IBM) desenvolvido para a Ria Formosa e águas costeiras adjacentes, para quantificar o sucesso do ingresso das larvas de sargo-legítimo em função da distância e profundidade entre áreas de postura e a ria. Os dados demonstram que a localização dos locais de postura e a natação direcional são igualmente importantes no sucesso do ingresso das larvas de sargo-legítimo numa zona de nursery como a Ria Formosa. O sucesso do ingresso foi maior nos locais de postura localizados a 15.1-16.9 m de profundidade e quando as larvas em pós-flexão usaram a natação direcional. Neste cenário, as larvas ingressaram na lagoa usando correntes de maré (larvas em pré-flexão passivas) ou natação direcional (larvas em pós-flexão ativas). A natação direcional também impediu a exportação de larvas para a área costeira. Quando a postura ocorre longe da pluma olfativa de ervas marinhas as larvas são dispersadas para o oceano.

Concluindo, a gestão dos recursos marinhos deve considerar a combinação da regionalidade e sazonalidade dos processos oceanográficos e da pesca, bem como as capacidades natatórias, as respostas comportamentais às pistas ambientais e o potencial de dispersão das larvas de peixes temperadas através da modelação da dispersão larvar. Esta abordagem contribuirá para estimativas mais fiáveis do recrutamento, considerando também os cenários das alterações climáticas. Devido à diversidade de variáveis importantes para a variabilidade do recrutamento de espécies de peixes temperados, esta tese sugere a integração de todas essas fontes de variabilidade (por exemplo, fisiologia, biologia, comportamento, ambiente) numa framework de avaliação da vulnerabilidade dos stocks de pesca às alterações climáticas.

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ACF – Auto-Correlation Function

DFA – Dynamic Factor Analysis

DPH – Days Post-Hacting

EAI – Exploratory Activity Index

FE – Fishing Effort

GLS – Generalized Least Square

ICES – International Council for the Exploration of the Sea

ICOADS – International Comprehensive Ocean–Atmosphere Data Set

IPCC – Intergovernmental Panel on Climate Change

IXa – ICES area of Portugal

IXaCN – Northwestern coast of Portugal

IXaCS – Southwestern coast of Portugal

IXaS-Algarve – Southern coast of Portugal

KZ – Kolmogorov–Zurbenko filter

KZA – Kolmogorov–Zurbenko Adaptive filter

LPUE – Landings *per* Unit Effort

MAFA – Min/max Autocorrelation Factor Analysis

NAO – North Atlantic Oscillation index

PI – Preference Index

RD – River Discharges (dam$^3$)

RSI – Regime Shift Indicator test

SST – Sea Surface Temperature (°C)

Ucrit – Critical Swimming Speed

UPW – Upwelling index

UWIND – Easterly Wind component (m $s^{-1}$)

VWIND – Northerly Wind component (m $s^{-1}$)

WMAG – Wind Magnitude (m $s^{-1}$)

# CHAPTER 1

## General Introduction

# GENERAL INTRODUCTION

## 1.1 Mechanisms behind recruitment variability

Many fish species, including coastal species, have a bipartite life history (Radford et al., 2012). Spawning occurs at the sea, and the larvae, hatched from planktonic eggs, remain in the pelagic environment for weeks to months before recruiting to nursery habitats (Montgomery et al., 2001). Initially, eggs and larvae are passively transported from spawning sites to recruitment areas (Leis, 2006; Teodósio et al., 2016) by hydrodynamic processes, such as wind-driven transport, convergence by river fronts and internal waves, tidal currents, ocean currents, river plumes, surficial waves, upwelling or downwelling, and eddies (Montgomery et al., 2001; Hare et al., 2002; Parada et al., 2003). The variability of these oceanographic processes can be seasonal, interannual or stochastic (Blaber and Blaber, 1980; Whitfield, 1994; Gibson, 1997), leading to the transport of eggs and larvae at scales of few kilometres to hundreds of kilometres (Hare et al. 2002; Parada et al., 2003; Wolanski and Kingsford, 2014). Recruitment usually takes place in coastal nursery areas (i.e., coastal lagoons, estuaries and rocky shore areas) where high concentration of food resources and availability of refuge sites, increase survival and growth (Bradbury and Snelgrove, 2001; Barbosa and Chícharo, 2011; Chícharo et al. 2012).

A central question in the ecology of marine communities is understanding the mechanisms behind the recruitment variability (Hale et al., 2008). Survival and growth during the larval and juvenile phases have been assumed as crucial determinants of spatial and temporal variability in recruitment (Houde, 2008), in turn affecting the size and dynamics of local populations. Mortality is usually very high during the fish larval stages (Wolanski and Kingsford, 2014; Faillettaz et al., 2015), due to limiting environmental conditions, poor feeding ability and vulnerability to predators (Simpson et al., 2013; Jørgensen et al., 2014; Garrido et al., 2015), increasing with the duration of the larval stage (Paris et al., 2007). Recruitment variability is also influenced by the complex interactions of physical and biological processes

(Leis, 2010; Hale et al., 2008) that lead to larval transport and/or retention, and food web processes that sustain fish larvae (Santos et al., 2007). However, the specific relevance of the factors potentially determining recruitment success remains unclear (Hale et al., 2008; Faillettaz et al., 2015). For example, migration processes are still poorly understood (Boehlert and Mundy, 1988; James et al., 2008; Radford et al., 2012).

Over the last century, several hypotheses have been proposed to explain the variability in fish recruitment. The first hypothesis, "Critical Period" hypothesis, stated that, at the time of first feeding, food limitation may reduce larval survivor (Hjort, 1914). According to the "Aberrant Drift" hypothesis, recruitment variability is dictated by larvae dispersal by currents to unfavourable habitats (Hjort, 1926). The "Migration Triangle" hypothesis used distinct seasonal and ontogenetic migrations between feeding, spawning and nursery habitats (Harden-Jones, 1968). The "Match-Mismatch" hypothesis proposed that larval survival, and consequently recruitment, are a function of the timings of spawning, larval hatching and peak abundance of their prey (Cushing 1975, 1990). The "Stable Ocean" hypothesis suggested that the survival and recruitment of larvae would be improved when larvae and suitable prey are aggregated by transient vertical stratification of the water column, induced by the occurrence of calm periods in upwelling ecosystems (Lasker, 1978). The physical retention of eggs and larvae is critical for the recruitment success, according to "Stable Retention" (Iles and Sinclair, 1982) and "Member-Vagrant" hypotheses (Sinclair and Iles, 1989), and this stages could be lost from the population by transport into unfavourable areas. The "Predation" hypothesis stated that fish recruitment is controlled by predation (Bailey and Houde, 1989). The "Ocean Triads" hypothesis, a more integrative hypothesis, refer that recruitment variability depends on the combination of nutrient enrichment processes (upwelling, mixing, buoyant plumes), larval food concentration processes (convergence, frontal formation, water column stability), and larval retention processes (eddies, onshore flow) (Agostini and Bakun, 2002). The importance of larval retention for the completion life cycle of marine fishes was also advocated by Sinclair and Power (2015). To maximize recruitment it is important to minimize drift and transport, through the integration of different active processes, such as horizontal swimming capabilities and circadian vertical migrations, to maximize movement directly into the nursery habitats (Lough and Bolz, 1989) or areas with oceanographic characteristics benefiting retention and ingress (Sponaugle et al., 2002; Paris and Cowen, 2004; Secor et al., 2017).

## 1.2 Role of swimming and active habitat preferences

Beyond the initial passive phase (Leis, 2010), coral reef fish larvae are considered to have essential swimming and sensorial abilities for finding suitable coastal nursery habitats (Fisher et al., 2000; Leis, 2010; Wolanski and Kingsford, 2014; Atema et al., 2015). In contrast, temperate fish larvae have been described with limited swimming and sensorial abilities (Leis, 2010; Kashef et al., 2014; Silva et al., 2014). Yet, according to a recent hypothesis, the Sense Acuity And Behavioural (SAAB) hypothesis (Teodósio et al., 2016), the recruitment of temperate fish larvae is unlikely if based only on passive drift by water currents. Consequently, the development of sensorial acuity in temperate fish larvae, and their behavioural responses to nursery cues present in coastal areas, are essential for recruitment success. As the sensorial acuity and swimming capacity increase during ontogeny (Fisher et al., 2000; Gerlach et al., 2007; Faria et al. 2011a; Wolanski and Kingsford, 2014; Atema et al. 2015) larval behaviour for searching nursery habitats is expected to change during the larval development, using a hierarchy of sensorial cues to detect and ingress into nursery habitats (Teodósio et al., 2016). In offshore areas, away from nursery cues, the post-flexion temperate fish larvae are guided towards the coast by sun compass, earth's geomagnetic field, and innate swimming behaviour. In nearshore areas, these larvae can detect and follow nursery cues, including odour, sound and visual cues (Leis et al., 1996; Montgomery et al., 2006; Gerlach et al., 2007; Paris et al., 2013a; Faillettaz et al., 2015). After detecting nursery cues, temperate fish swim directly towards nursery habitats, using a set of swimming behaviours that vary according with cue intensity, combined with diel rhythms and feeding and predator avoidance strategies (Teodósio et al., 2016). Thus, the development of sensorial and swimming capabilities, that naturally interact with physical transport processes, has been linked to an active larval behaviour on dispersion and recruitment outcomes (Wolanski et al., 1997; Armsworth, 2001; Atema et al., 2002; Leis, 2006; Drake et al., 2011; Teodósio et al., 2016).

### 1.2.1 Larvae swimming capabilities

In general, pre-flexion larvae are poor swimmers (Leis, 2010), but due to the ontogenetic changes occurring during larval phase (e.g., development of fins, body musculature and skeleton ossification), and post-flexion larvae show improved swimming capabilities (Leis, 2006). However, there are exceptions: for example, of the Senegalese sole *Solea senegalensis*

(Kaup, 1858; Soleidae), pre-flexion larvae swim faster than post-flexion larvae, that quickly acquire a flat body to substrate adjustment (Faria et al., 2011b). Thus, it is important to consider morphological characteristics of larvae when comparing swimming performance across fish taxa.

The pelagic post-flexion fish larvae can be strong swimmers, with active horizontal and vertical capabilities (Leis et al., 1996; Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 2003). These larvae can swim horizontally at speeds greater than ambient currents, in a highly directional way, travelling long distances (Leis et al., 1996; Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 2003; Atema et al., 2015). Moreover, fish larvae can actively adjust their vertical position in the water column (Leis et al., 1996), allowing the active selection of appropriate currents to facilitate transport (Sponaugle et al., 2002; Paris and Cowen, 2004). As they can detect nursery habitats (Leis et al., 1996; Montgomery et al., 2001) through the development of sensorial abilities and maintaining their position there (Watt-Pringlea and Strydom, 2003), the development of swimming capabilities has been recognized as influencing larval dispersal (Stobutzki and Bellwood, 1997; Armsworth, 2001; Sponaugle et al., 2002; Atema et al., 2002; Leis, 2006; Drake et al., 2011) and settlement location (Wright et al., 2005). Swimming capabilities have also important consequences for fish’s ecological processes (Westcott and Graham, 2000), including in responses to predators, foraging abilities (Weins et al., 1995; Fisher, 2005; Jørgensen et al., 2014), conspecific interactions, and sensitivity to other biotic and abiotic conditions (Weins et al., 1995), influencing survival and recruitment of fish larvae (Cowen et al., 2000; Fisher, 2005; Leis, 2006).

In general, coral reef fish larvae have higher swimming capabilities than temperate and cold fish larvae. Most studies on swimming performance of fish larvae used tropical species, with high swimming speeds (e.g., Stobutzki and Bellwood, 1997; Fisher et al., 2000, 2005; Fisher, 2005; Leis et al., 2007), ranging from 5 to 100 cm $s^{-1}$ [3-46 Body length $s^{-1}$ (BL $s^{-1}$)] (Fisher et al., 2005; Leis, 2006). The good larval swimming performance was recently reported for temperate fish species (e.g., Koumoundouros et al., 2009; Faria et al., 2011b, 2014; Peck et al., 2012; Silva et al., 2015; see Table 2.1), varying between 0 and 33 cm $s^{-1}$ (0-15.7 BL $s^{-1}$; see Table 2.1). In addition, the maximum distance travelled by coral reef fish larvae evaluated in swimming endurance trials is 140.2 km (Leis and McCormick, 2002), higher than that registered for temperate species (80.9 km; see Table 2.1). Due to the reported influences of phylogeny, morphology (Leis and McCormick, 2002), fast development (Kashef et al., 2014) and environment (e.g., water temperature; Leis, 2010) on larval swimming capabilities, fish larvae are expected to swim more efficiently in warm-waters than in respected to temperate and cold-waters (Hunt von Herbing, 2002). Tropical fish larvae develop more rapidly than temperate and cold-water fish larvae, and exhibit different morphological characteristics, including body shape and muscle mass (Leis, 2006; Peck et al., 2012). Water temperature affects both the physiology of fish larvae (e.g., muscle contractility) and physical properties of seawater, the viscosity of water (Fuiman and Batty, 1997; Hunt von Herbing, 2002). As the seawater viscosity increases with decreasing temperature (Leis, 2006), most of the temperate and cold-water fish larvae swim in a more viscous environment (Reynolds number – Re < 300; Fuiman and Batty, 1997; Silva et al. 2014). This fact could partly explain their lower swimming speeds in comparison with warm-water fish larvae, that swim in a more inertial environment (Re < 300; Fuiman and Batty, 1997; Leis, 2006).

**Table 1.1.** Summary of reports on swimming performance (critical swimming speed – $U_{Crit}$, and swimming endurance) of temperate fish species, including size range. (na – data not available)

| **Order** | **Family** | **Species** | **Size range (mm)** | **$U_{crit}$ (cm s$^{-1}$)** | **Endurance (km)** | **Reference** |
|---|---|---|---|---|---|---|
| Anguiliformes | Anguilidae | *Anguilla rostrate* | 48.7-68.1 | 6.5-21.1 | na | Wuenschel and Able, 2008 |
| | Congridae | *Conger oceanicus* | 68.3-117.8 | 4.1-26.8 | na | Wuenschel and Able, 2008 |
| Atheriniformes | Atheriniidae | *Atherina presbyter* | 6.6-21.0 | 3.6-18.7 | na | Faria et al., 2014 |
| Clupeiformes | Clupeidae | *Sardina pilchardus* | 7.9-23.4 | 1.6-9.5 | na | Silva et al., 2014 |
| Gadiformes | Gadidae | *Gadus morhua* | Na | 1.2-9.7 | na | Guan et al., 2008 |
| Gobiesociformes | Gobiesocidae | *Lepadogaster lepadogaster* | 5.1-10.9 | 1.0-9.4 | na | Faria and Gonçalves, 2010 |
| | | *Lepadogaster purpurea* | 5.3-10.9 | 1.2-6.5 | na | Faria and Gonçalves, 2010 |
| Perciformes | Percichthyidae | *Macquaria novemaculeata* | 4.0-10.4 | 0-1.5 | 0-12.5 | Clark et al., 2005 |
| | | *Morone saxatilis* | 0.5-2.6 | 6.1-8.9 | na | Chick and Van Den Avyle, 2000 |
| | Sciaenidae | *Argyrosomus japonicus* | 3.0-14.0 | 4.0-16.6 | 0-22.4 | Clark et al., 2005 |
| | | *Scianops ocellatus* | 3.0-19.1 | 1.1-20.5 | na | Faria et al., 2009 |
| | Sparidae | *Acanthopagrus australis* | 4.9-11.1 | 2.0-27.0 | na | Clark et al., 2005 |
| | | *Diplodus capensis* | 8.9-16.0 | 2.8-35.2 | 0.2-32.4 | Pattrick and Strydom, 2009 |
| | | *Pagrus auratus* | 2.2-10.4 | 2.0-27.3 | 0-9.9 | Clark et al., 2005 |
| | | *Sarpa salpa* | 12.1-21.3 | 4.8-33.4 | 0.07-64.8 | Pattrick and Strydom, 2009 |
| | | *Sparus aurata* | 6.2-14.1 | 3.0-19.3 | 10.2-23.9 | Faria et al., 2011a |
| Pleuronectiformes | Solenidae | *Solea senegalensis* | 3.5-7.5 | 0.4-5.0 | na | Faria et al., 2011b |
| | Pleuronectidae | *Pleuronectes platessa* | 7.0-13.0 | 1.0-3.9 | na | Silva et al., 2015 |

### 1.2.2 Detection of environmental cues for habitat selection

In terms of recruitment, swimming capabilities are potentially useful only if larvae can detect environmental cues that guide them towards suitable settlement habitats (Doherty, 2006). Several studies have reported that fish larvae have an active participation in habitat choice. In respect to random allocation, any behaviour that guides individuals to select one habitat over another (Atema et al., 2002; Gerlach et al., 2007; Dixson et al., 2008), could be crucial for fish recruitment and could be mediated by the presence and interaction of multiple cues (Kingsford et al., 2002; Teodósio et al., 2016). Fish larvae use different senses to choose a suitable settlement habitat according to environmental characteristics/cues, such as odour (Atema et al., 2002, Gerlach et al., 2007, Dixson et al., 2008; Morais et al., 2017), sound (Montgomery et al., 2006; Leis et al., 2011) and vision (e.g., Whitfield, 1994; Faillettaz et al., 2015).

Although all these senses could contribute to habitat choice, olfaction has been recognised as the prevalent strategy for locating nursey habitats (Atema et al., 2002; Lecchini et al., 2005; Døving et al., 2006; Dixson et al., 2008; Morais et al., 2017). Fish larvae can feel odour cues over greater distances than any other environmental cue, and at very early developmental stages (Leis, 2010). In fact, fish larvae are capable to distinguish and follow several chemical stimuli present in water, derived from different substrate types (Carr, 1991), vegetation (Gerlach et al., 2007; Radford et al., 2012), presence of conspecifics (Døving et al., 2006), predators and prey (Lecchini et al., 2005), and use them for locate nursery habitats (Atema et al., 2002; Lecchini et al., 2005; Døving et al., 2006; Paris et al., 2013a). These odour cues are mixed and dispersed by oceanographic processes like waves, currents, and tides (Igulu et al., 2013), influencing the concentration and spatial gradients of chemical stimuli (Kingsford et al., 2002). For example, plumes generated by rivers, estuaries and lagoon habitats can be transported over tens of kilometres offshore by wind and ocean currents (Grimes and Kingsford, 1996; Atema et al., 2002).

Auditory capabilities (e.g., swim bladder, otoliths) are be useful for fish larvae to detect and follow nursery habitats (Montgomery et al., 2006; Radford et al., 2012; Lillis et al., 2014; Atema et al., 2015). The ability to detect sounds develops early in the larval phase, and increases during ontogeny (Leis, 2007). Fish larvae can discriminate between ecosystem soundscapes produced by the living animals, for example snapping shrimps, fish calls and grazing sea urchins (Simpson et al., 2013; Lillis et al., 2014; Atema et al., 2015), or by waves breaking along the coast (Montgomery et al., 2006; Simpson et al., 2013). However, the distance over which fish larvae can orientate to settlement habitats using auditory cues is considered small, around 1 km (Atema et al., 2015).

Fish larvae could also use vision to orientate themselves towards nursery habitats (Kingsford et al., 2002; Leis, 2006). Fish larvae have good visual abilities, improving during ontogeny (Lara, 2001; Atema et al., 2015). Visual cues, like water turbidity, bottom features, presence of conspecifics, and sun azimuth can be used by fish larvae to detect suitable nursery habitats and navigate, avoiding passive advection by currents (Whitfield, 1994; Leis, 2007; Atema et al., 2015; Faillettaz et al., 2015). However, the visual ability is limited to a close range, few tens of meters (Montgomery et al., 2001; Kingsford et al., 2002; Leis, 2007).

Other complementary environmental cues have been proposed as stimuli used by fish larvae to find suitable habitat, including Earth’s geomagnetic field, wave direction, pressure gradients and turbulence (Walker et al., 1992; Leis, 2007; Qin et al., 2015; Atema et al., 2015; O’Connor and Muheim, 2017). Further, several oceanographic variables have been proposed as important drivers that influence habitat choice, including current speed, turbidity, salinity, oxygen concentration, and temperature (Boehlert and Mundy, 1988; Whitfield, 1994; Gibson, 1997; Atema et al., 2002; Bos and Thiel, 2006; Angeletti et al., 2017). For example, water temperature gradients may influence the ingress of fish larvae into estuaries (Boehlert and Mundy, 1988) and may be an important triggering mechanism to stimulate the detection of odour cues by larvae (Atema et al., 2002). Reduction of salinity levels in nearshore areas provides a signal of the proximity to estuarine nursery habitats (Morais et al., 2007; Hale et al., 2008) due to drift from rivers and runoff (Sabates, 1990). Specific combinations of temperature and salinity are associated with water masses (Mann and Lazier, 1991), such as estuarine plumes characterized by vertical and horizontal gradients of salinity and temperature, providing potentially important environmental cues (Kingsford et al., 2002).

Thus, sensorial abilities of fish larvae in tandem with specific environmental properties, make the recruitment an active and behaviourally-mediated process (Boehlert and Mundy, 1988). Larvae may use multiple sensory cues to find nursery habitats and navigate towards them in order to settle and recruit (Kingsford et al., 2002; Hale et al., 2008; Huijbers et al., 2012; Igulu et al., 2013; Faillettaz et al., 2015; Teodósio et al., 2016). As these cues are variable, both in space and time (Huijbers et al., 2012), they can be used in a hierarchal way, depending on the concentration, gradients and distance from the source (Kingsford et al., 2002).

Despite the increasing interest over the past decades, most studies on use of environmental cues for habitat selection have been also conducted on coral reef fish larvae (e.g. Atema et al., 2002, 2015; Dixon et al., 2008; Gerlach et al., 2007; O'Connor et al., 2007; O'Connor and Muheim, 2017; Majoris et al., 2018). Coral and temperate fish species thrive under different environmental conditions, which can influence physiological traits and promote different behavioural responses (e.g., higher temperature stimulates growth and shorter pelagic duration for coral reef fishes; O'Connor et al., 2007). Coral reef fish larvae follow natal reef's characteristics "imprinted" during early development phases, due to egg development in reef areas (Dixson et al., 2008). However, temperate fish larvae swim to habitats never experienced before (Radford et al. 2012), due to egg development offshore, thus using an innate behaviour (Teodósio et al., 2016). Despite these differences, both coral and temperate fish larvae share common life history traits, relevant for ecological processes (Fonseca and Cabral, 2007). Thus, sensorial capabilities in coral-reef fish larvae must be useful to guide studies of temperate fish larvae (Teodósio et al., 2016).

For instance, post-flexion larvae of Cape stumpnose *Rhabdosargus holubi* (Steindachner, 1881; Sparidae) showed a preference for estuarine water instead of seawater control (James et al., 2008). Several studies demonstrated that the larvae of Australasian snapper *Pagrus auratus* (Forster, 1801; Sparidae) (Radford et al., 2012), red drum *Sciaenops ocellatus* (Linnaeus, 1766; Sciaenidae) (Havel and Fuiman, 2016), Australian bass *Macquaria novemaculeata* (Steindachner, 1866; Percichthyidae) and Japanese meagre *Argyrosomus japonicus* (Temminck & Schlegel, 1843; Sciaenidae) (O'Connor et al., 2017) swim towards nursery areas by following odour cues from seagrass habitats. Nevertheless, a recent study on the response of the gilt-head seabream *Sparus aurata* (Linnaeus, 1758; Sparidae) to nursery cues, showed that, even under starvation or a poor physiological condition, post-flexion larvae preferred rocky coastal water over lagoon water with seagrass cues (Morais et al., 2017). Post-larval European flounder *Pleuronectes flesus* (Linnaeus, 1758; Pleuronectinae) preferred water low salinity water (Bos and Thiel, 2006)). Moreover, damselfish *Chromis chromis* (Linnaeus, 1758; Pomacentridae), annular seabream *Diplodus annularis* (Linnaeus, 1758; Sparidae) and picarel *Spicara smaris* (Linnaeus, 1758; Sparidae) larvae were reported to use the sun position orienting themselves (Faillettaz et al., 2015).

The response of fish larvae to environmental cues depends on the ability to detect these signals, on swimming abilities to follow them (Boehlert and Mundy, 1988; Huijbers et al., 2012), and on individual behavioural characteristics that lead to decision making. Individual characteristics, like personality traits, can influence the reaction of individuals to environmental cues and, thus modulating a choice of habitat (Stamps, 2006). For example, bold individuals are related to a greater tendency to explore novel environments (Cote and Clobert, 2007). Individual variability in larval behaviour may also influence food acquisition and predator's avoidance (Biro et al., 2006). All these processes, potentially driven by behaviour, are important for understanding the dynamic of fish population, dispersal and recruitment (Nanninga and Berumen, 2014; Pasquet et al., 2016).

Past dispersal models have not included larval swimming and sensorial abilities, and considered oceanographic features as only determinants for larval dispersion and recruitment (e.g., Raimondi and Keough, 1990; Cowen et al., 2000; Gilg and Hilbish, 2003). However, for some species, more recent models of fish larvae dispersion have included biological traits like temperature-dependent development, requirement and availability of settlement habitat, mortality rates, transition between passive planktonic phase to a more active nektonic phase, diel or/and ontogenetic vertical migrations, horizontal swimming and sensorial abilities, and behavioural strategies (e.g., habitat selection and activity patterns) (e.g., Mullon et al., 2003; Fiksen et al., 2007; Gerlach et al., 2007; Paris et al., 2007, 2013b; Peck et al., 2009; Wolanski and Kingsford, 2014; Teodósio et al., 2016). However, just a few studies were conducted using temperate fish species (e.g., Mullon et al., 2003; Fiksen et al., 2007; Teodósio et al., 2016). Indeed, Lagrangian modelling studies of Teodósio et al. (2016) and Wolanski (2017) showed that the ingress of temperate fish larvae of Sparidae and Clupeidae (sardine *Sardina pilchardus*; Walbaum, 1792) into the Ria Formosa coastal lagoon (South of Portugal) is mediated by an active behaviour.

Thus, the study of behavioural responses and swimming capabilities of fish larvae, and their inclusion in dispersal models, is fundamental to understand recruitment variability, dispersion and connectivity of marine populations, being important tools for improving ecosystems conservation and fisheries management (Nanninga et al., 2014; Atema et al., 2015; O'Connor et al., 2017).

## 1.3 Impacts of environmental variability and changes on fish larvae, recruitment and fisheries

Historical records and recent ocean observations have revealed that oceans are changing (Roemich et al., 2012), with increasing sea surface temperature, rising sea level, altered precipitation regimes and wind patterns, and ocean acidification (Brander, 2007; IPCC, 2013). Observed and predicted changes indicate that the effects of climate change will be variable in magnitude and direction, across marine regions (Santos, 2006; IPCC, 2013).

Communities of marine fishes were considered naturally stable, and the majority of changes were usually attributed to human action. Only in recent decades, the variability of marine fish populations has been linked to climate variability (Morri and Bianchi, 2001). However, resolving the impact of climate and environmental variability on fish populations is complicated since climate variables influence multiple environmental factors which may, in turn, influence different processes, at different levels of biological organization (Lehodey et al., 2006; Ottersen et al., 2001) and at multiple intra-annual, inter-annual and decadal temporal scales, (Bertram et al., 2001; Brander, 2007; Lehodey et al., 2006). For instance, water temperature, winds, tidal currents and ocean circulation, upwelling, precipitation, river runoff, sea level, ice cover and glacial melt, frequency and intensity of storms and floods are known to directly affect the abundance and distribution of economically important fish species. However, these can also indirectly affect productivity, structure and composition of marine ecosystems, at both regional and oceanic scales (Planque and Frédou, 1999; Barange, 2002; Sponaugle et al., 2002; Harley et al., 2006; Boelens et al., 2005; Lehodey et al., 2006; Brander, 2007, 2010). Overall, both direct and indirect effects may change the growth, survival, reproduction and food supply of fish species, and inter-specific relationships, such as competition and predator-prey interactions (Ottersen et al., 2001; Perry et al., 2005).

As fish larvae have a narrower tolerance to environmental fluctuations than juveniles and adults, and are usually more sensitive and vulnerable to climate changes (Pörtner and Peck, 2010), the larval phase is a critical period that causes variability in marine fish production (Houde, 1997; Cushing, 1996). This reinforces the importance of high mortality rates observed during the early life stages on recruitment variability of most marine fish species (Santos et al., 2012) that are strongly affected by environmental processes described above.

It is assumed that water temperature is the most important environmental driver of the recruitment success of fish species (Peck et al., 2012). Water temperature has a direct impact on fish larvae, influencing metabolism, growth, developmental rates, stage duration and swimming performance (Houde, 1989; Sponaugle et al., 2002; Green and Fisher, 2004). Increasing ocean temperatures will generally reduce the duration of larval stages and consequently, their dispersal potentials (O'Connor et al., 2007; Munday et al., 2008). Higher larval growth due to the increase in water temperature will require more food availability or mortality rates could increase (Houde, 1989; Munday et al., 2008). Thus, as the appropriate timing for releasing fish larvae may be critical for the match or mismatch with prey availability (Cushing, 1969), the temperature may potentially alter these timings and consequently influence recruitment success (Genner et al., 2010). Moreover, increasing sea surface temperature could promote stratification in the upper mixed layers, reducing the encounters with food resources (Werner et al., 2007). However, it is important to note that some species may develop acclimation strategies or adaptation responses to changes in temperature across generations (Munday et al., 2008). Although these responses may not fully compensate the effects of temperature, they can mitigate the effects of ocean warming (Giménez, 2011). Additionally, some species exhibit a narrow temperature range for development, and phenology, outside of which mortality and abnormalities increase (Polo et al., 1991; Perry et al., 2005; Peck et al., 2012).

The increasing ocean temperatures and changing wind patterns (speed and direction) are projected to alter the speed and direction of currents, which will clearly impact the physical transport and dispersion of fish eggs and larvae, and ecosystems connectivity (Cowen and Sponaugle, 2009). Wind speed and direction also determine small-scale turbulence in the water column, affecting indirectly the feeding ability of larvae due to their influence on encounters between larval fish and their prey, thus affecting per capita feeding and larval growth (MacKenzie et al., 1994; Dower et al., 1997). Wind patterns may also influence larval distribution by creating or disrupting nearshore currents and areas of larval retention and increasing offshore advection (Sponaugle and Cowen, 1996). Alterations in strength and direction of wind influence the circulation and water mixture and disturb upwelling intensity in coastal regions, affecting the primary productivity and, eventually, the productivity of superior levels (Findlay and Allen, 2002; Rijnsdorp et al., 2009). In fact, upwelling events have been changing in the last years and are expected to continue to change in the future, with increasing of upwelling intensity, and associated increases in offshore advection (Bakun et al., 2015).

Increase in upwelling intensity could lead to increase hypoxic events and enlarge oxygen minimum zones, lower densities of food particles suitable for larval phases and, rising ocean acidity (Bakun et al., 2015).

Coastal areas are one of the most productive ecosystems in the world, playing a crucial role as nursery grounds for early life stages of economically important fish. Thus, the effects of sea level rising and habitat modifications on nursery areas will probably impact the larvae phases, altering the availability of nursery areas, as well as habitats for juveniles and adults (Cowen and Sponaugle, 2009). According with recent studies, the environmental cues used by fish larvae to locate nursery grounds are suffering significant changes due to climate change (e.g. Munday et al., 2009; Pecl et al., 2017; Rossi et al., 2018). For example, changing water temperatures and salinity patterns, two important cues to locate estuarine nursery habitats, were reported to affect not only the physiological processes, but also larval behaviour and habitat choice patterns (Pecl et al., 2017). Further, elevated $CO_2$, and ocean acidification were suggested to hamper the capacity of fish larvae to distinguish between ecologically important chemical cues (Munday et al., 2009), and  avoid functional environmental cues to become attracted to potentially deleterious cues (Munday et al., 2009; Rossi et al., 2018).

These climate-induced changes in early life stages of fish species may potentially affect the development of adult stocks and their availability for fisheries. Additionally, landings have been closely linked to climate dynamics (Lehodey et al., 2006) in the last years. The biodiversity loss and change in the demographic and geographic structures caused by excessive fishing pressure, increases the susceptibility of halieutic resources and marine ecosystems to environmental and climate changes (Planque et al. 2010). Moreover, as explained above, the environmental changes may reduce, or in some cases increase, the productivity of fisheries stocks through direct and indirect effects on production, survival and growth (Brander, 2007). Most of the major global fisheries have been reported to be affected by regional environmental variability (Brander, 2007), leading to a growing concern on the consequences of environmental changes for fisheries production (Brander, 2010). Climate change impacts are well documented for some fish species (e.g., Ottersen and Sundby, 1995; Daskalov, 1999; Planque and Frédou, 1999; Santos et al., 2001; Sirabella et al., 2001;  Sousa Reis et al., 2001; Borges et al., 2003; Fréon et al., 2005; Gröger and Fogarty, 2011; Leitão et al., 2014). For example, a significant relationship between environmental fluctuations (sea surface temperature, wind speed, stress and mixing, sea level, atmospheric pressure and river run-off) and the stock biomass of

European sprat *Sprattus sprattus* (Linnaeus, 1758; Clupeidae), whiting *Merlangius merlangus* (Linnaeus, 1758; Gadidae), European anchovy *Engraulis encrasicolus* (Linnaeus, 1758; Engraulidae) and Mediterranean horse mackerel *Trachurus mediterraneus* (Steindachner, 1868; Carangidae) in Black Sea was reported by Daskalov (1999). The stocks of Atlantic cod *Gadus morhua* (Linnaeus, 1758; Gadidae) in the North Atlantic were positively related with temperature for cold-water stocks and negatively related for stocks inhabiting relatively warm waters (Planque and Frédou, 1999). Sirabella et al. (2001) assert that a positive NAO phase with high sea temperature is unfavourable for *G. morhua* recruitment in the North Sea. A negative impact of winter upwelling events on recruitment of sardine and Atlantic horse mackerel *Trachurus trachurus* (Linnaeus, 1758; Carangidae) off Portugal was reported by Santos et al. (2001). Sousa Reis et al. (2001) concluded that the intense upwelling is associated to a decrease of sardine biomass in southwestern coast of Portugal. However, Chícharo et al. (2003) reported no adverse effects of upwelling events during winter on production and survival of sardine larvae in northwestern coast of Portugal due the presence of a stratified warm plume, high food production and retention. Borges et al. (2003) showed that sardine landings were lower when the frequency and intensity of northerly winds exceed a certain limit in winter off the Western coast of Portugal. Sousa Reis et al. (2001) also reported that the Atlantic bluefin tuna *Thunnus thynnus* (Linnaeus, 1758; Scombridae) dynamics seem to be related with NAO in the Northeastern Atlantic.

Despite the growing evidence of the relationship between environmental and climate changes and fisheries, the linkages between them have not yet been clearly demonstrated or integrated into sustainable fisheries management practices (Fréon et al., 2005). Nonetheless, improved knowledge regarding physiological, biological and ecological traits and the effect of environmental factors on fish population dynamics is required to understand recruitment variability. Thus, promote development of adaptive management practices for commercially important fish species, considering the projected future environmental changes.

## 1.4. Thesis objectives and structure

The main objective of the present thesis is to increase the knowledge of single and combined effects of changes in environmental drivers, fishing pressure, and habitat selection during larval phases on recruitment of temperate fish species.

The thesis includes an introductory chapter (Chapter 1), two main sections (Section I and Section II) and a chapter with concluding remarks (Chapter 8).

In **Chapter 1** (present chapter) the environmental drives of recruitment of fish larvae are reviewed: recruitment hypothesis developed over time; the recently discovered swimming and sensorial capabilities of fish larvae and the possible effects on larval dispersion and recruitment variability; and the effects of environmental and climate change and fishing pressure on the early life history of fish species and, consequently, on fisheries.

Section I addresses the environmental and climate changes occurring in Portuguese coast, and their effects on fisheries of temperate fish species. This section comprises three chapters which evaluate the variability of sea surface temperature (SST) (Chapter 2), an important factor for species life cycle; and the effects of diverse environmental changes and fishing pressure on artisanal fishing trends of two Sparidae species, *Diplodus sargus* (Linnaeus 1758) (Chapter 3) and two-banded seabream *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817) (Chapter 4) across different regions of the Portuguese coast (northwestern, southwestern and southern) with different fishing and oceanographic condition.

As the sea surface temperature (SST) has been identified as one of the most important environmental parameters for studies on climate change, the aim of **Chapter 2** is to analyse the variability of SST and evolution of regional trends, using a ca. 60 years' time series and the coastal oceanographic divisions established by the International Council for the Exploration of the Sea (ICES).This chapter describes region-specific annual, seasonal and monthly SST time series, and identifies the rates of SST increase and discontinuities (sudden shifts) in the time series with the goal of better understanding SST variability and the evolution of regional trends.

The objectives of the **Chapter 3** and **Chapter 4** are to determine the potential role of environmental factors and artisanal fishing pressure on the variability of white seabream and two-banded seabream landings, across different regions of Portuguese coast, using a multi-model approach. The effects of environmental change and fishing pressure are hypothesised to vary across Portuguese regions. The use of two species will allow determining if effects of these factors are species-specific.

Section II addresses the individual behavioural capabilities of temperate fish larvae, and their effects on dispersion and recruitment in coastal nursery areas. This section comprises three chapters (Chapter 5, Chapter 6 and Chapter 7) which evaluated swimming performance of temperate fish larvae, habitat and environmental selection, and the potential of these active behavioural strategies for controlling larval dispersion processes and, consequently, fish recruitment.

**Chapter 5** aims to determine the swimming performance of laboratory-reared white seabream larvae during ontogeny. For this purpose, laboratory experiments were used for measuring the critical swimming speed ($U_{crit}$) and the maximum distance travelled with swimming endurance throughout ontogeny (15 to 55 days post-hatching), and the effects of larvae physiological condition (nucleic acids and proteins quantification) are evaluated. Swimming abilities ($U_{crit}$ and distance swam in endurance test) of white seabream larvae are hypothesised to increase with development, body length and physiological conditions.

**Chapter 6** aims: (i) to detect consistent individual differences in behaviour in temperate pelagic fish larvae during ontogeny; (ii) test if and how these consistent behaviours relate to environmental changes (increase of water temperature and decrease of salinity); (iii) test if they affect the ability to choose nursery habitats by detecting different environmental cues. The central hypothesis is that fish larvae could detect and follow environmental cues for actively choosing suitable nursery habitats, and that this could be linked to personality traits.

**Chapter 7** aims to analyse the potential ingress of white seabream larvae into Ria Formosa lagoon and to evaluate the relevance of different behavioural processes behind the recruitment success. For this purpose, the directional swimming-advection-dispersion model developed by Teodósio et al. (2016) is used, and incorporates the swimming capabilities and habitat preferences obtained in previous chapters (Chapter 5 and Chapter 6). The results of this study are important to determine if white seabream larvae use directional swimming capabilities to ingress in this nursery habitat, or if they are just transported as passive particles by prevailing currents.

**Chapter 8** summarizes the major findings of this thesis. These findings are integrated in order to better understanding the causes (environment effects and larval behaviour) of recruitment variability in temperate fish species. Thus, providing important information for fisheries management and conservation in coastal areas, especially nursery habitats, with recommendations and future perspectives.

Chapters 2 to 7 are structured in a paper-style format, and were published or submitted for publication in indexed scientific journals. Therefore, each of these chapters constitutes a complete study and can be read independently of the others.

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# SECTION I

## Impacts of environmental variability and changes on fish larvae, recruitment and fisheries

# CHAPTER 2

## Sea surface temperature variability along the Portuguese coast since 1950

Baptista V, Silva PL, Relvas P, Teodósio MA, Leitão F (2018) Sea surface temperature variability along the Portuguese coast since 1950. International Journal of Climatology 38:1145-1160. doi:10.1002/joc.5231

# SEA SURFACE TEMPERATURE VARIABILITY ALONG THE PORTUGUESE COAST SINCE 1950

## Abstract

Overall an increase in sea surface temperature (SST) has been recorded over the last century. However, changes in SST are not homogeneous across the ocean. Most studies focus on the processes and mechanisms setting SST variability across broad scales and neglect changes occurring at a regional scale. So, this study aims to describe annual, seasonal and monthly time-series trends in SST along the Portuguese coast, compare trends among areas (northwest, southwest and south), quantify SST increase rates and SST time-series discontinuities. Time-series analyses showed that SST has the same annual and monthly trend regardless of the area and data sets used (ICOADS: 1950-2010; Satellite data: 1985-2010). SST increased in the three areas: +0.1 °C decade$^{-1}$ in northwestern and southwestern coasts (the same than global average), +0.2 °C decade$^{-1}$ in the southern coast. The higher monthly SST increment rates were observed in spring and summer (satellite data: +0.4 °C decade$^{-1}$ in June in northwestern; +0.4 °C decade$^{-1}$ in April in southwestern; +0.5 °C decade$^{-1}$ in June in southern). Discontinuities, that is, sudden shifts in time-series, were observed after 1987, 1995 and 1982-1983 in the northwestern, southwestern and southern areas, respectively. Overall, this study reinforces the hypothesis that SST varies regionally; so, studies assessing the impacts inherent to climate change along coastal areas, namely fisheries variability, ought to have this perspective into account.

**Keywords:** seasonal decomposition by Loess smoothing; dynamic factor analysis; regime shift indicator; Kolmogorov-Zurbenko filter; Kolmogorov-Zurbenko adaptive filter; fisheries variability; recruitment

## 2.1 Introduction

Historical records and actual ocean observations show that oceans are changing (Bindoff et al., 2007; Roemich et al., 2012) with increasing sea surface temperature (SST), rising sea level, altered precipitation regime and ocean acidification (IPCC, 2007). The Intergovernmental Panel on Climate Change (IPCC) has identified SST as one of the most important environmental parameters for studies on climate change (Houghton et al., 1996). Accurate predictions of global SST changes are critical for predicting climate change scenarios and to set adequate policies (Casey and Cornillon, 2001). Over the last several decades, it has been observed that SST depends on spatial and temporal scales, and trends shift between periods of time (Casey and Cornillon, 2001; Santos et al., 2011). Despite these differences, most studies conclude that over the last century, global SST has increased significantly and independently of specific data sets (Casey and Cornillon, 2001; Santos et al., 2011).

Recent climate change impacts and predictions of future impacts indicate that climate change is not homogeneous across oceans; therefore, their effects differ in magnitude and direction between regions (IPCC, 2001a, 2007; Santos, 2006). For example, increased SST is greater in the Northern hemisphere than in the southern hemisphere (Strong et al., 2000; Gómez-Gesteira et al., 2008), and the Atlantic Ocean is the primary contributor to global warming (Levitus et al., 2000; Strong et al., 2000). During the mid-1990s, multi-decadal warmth of the Atlantic and Indian Oceans have led to extreme warmth of the world’s oceans (Gómez-Gesteira et al., 2008). At a regional scale, the differences among areas are even more evident (Casey and Cornillon, 2001; Lemos and Pires, 2004; Santos et al., 2005; Gómez-Gesteira et al., 2008). The SST around Europe has increased faster than the global average (Gómez-Gesteira et al., 2011). However, the southern European regions are more vulnerable to climate change than other European regions (Santos, 2006). A rise in SST has also been observed in the Iberian Peninsula coast (southwestern Europe), namely, the Cantabrian Sea (northern coast), Galicia and the northwestern Portuguese coast (Gómez-Gesteira et al., 2008, 2011; Santos et al., 2011). However, local environmental variables (i.e. winds, ocean currents, thermocline depth, upwelling intensity and North Atlantic Oscillation) can cause more changes in regional SST than in global average trends (Gómez-Gesteira et al., 2008; Dogan et al., 2015a, 2015b). This phenomenon is particularly notable in such regions as the ocean off Atlantic Iberia coast, which is subject to strong interactions between the atmosphere and ocean. Northerly winds drive a seasonal coastal upwelling regime off western Iberia that intensifies during the peak summer months and is almost absent during winter (Relvas et al., 2007). Coastal upwelling drives the offshore displacement of warmer upper layer waters and its replacement by cold waters from the subsurface. The coastal upwelling process is highly sensitive to the wind pattern, the thermohaline structure of the water column and coastline and seabed configurations. Changes in these regional factors result in the adjustment of the upwelling pattern with consequences to the long-term variability of the regional SST and local modification of the global average SST trends. There is evidence that different mesoscale upwelling structures in the region experience different SST trends (Relvas et al., 2009).

A slight increase of SST can disrupt established physical and chemical dynamics and processes, fostering myriad changes in marine communities (Roessig et al., 2004). Thus, it is not surprising that current changes in SST are considered the most pervasive and severest drivers of change in coastal ecosystems worldwide (Halpern et al., 2008). For example, global climatic-driven SST changes lead to changes in primary production, such as a more than 6% decline in the global ocean's annual primary production since the 1980s (Gregg et al., 2003); redistribution of fish stocks and catch potential, with an increase of 30-70% in high-latitude regions and a decline of up to 40% in the tropics (Cheung et al., 2010); and an increased potential for successful biological invasions, for example, by *Bugula neritina*, *Schizoporella* sp., *Watersipora subtorquata*, *Botrylloides violaceus*, *Botryllus* sp., *Didemnum* sp. and *Diplosoma listerianum* in Bodega Bay (California; Sorte et al., 2010). All of these shifts have been studied across broad ocean region scales, while notably few studies have examined these changes at a more local scale, such as in the order of several hundred kilometres (Santos et al., 2001, 2007; Baptista and Leitão, 2014; Baptista et al., 2016 – Chapter 4 of the present Thesis; Leitão et al., 2016 – Chapter 3 of the present Thesis).

The Portuguese coast extends ca. 800 km on the western coast and ca. 200 km on the southern coast and it includes regions with distinct oceanographic and environmental characteristics, such as the Iberian Poleward Current, the Western Iberia Buoyant Plume (river effects), bathymetry, wind regimes and upwelling filaments (Cunha, 2001; Bettencourt et al., 2004; Santos et al., 2007). Moreover, the Portuguese coast is located in a biogeographical transition zone between temperate and subtropical waters and is one of the regions where SST has increased the most over the last century (IPCC, 2001a). These aspects can make Portuguese coastal species particularly vulnerable to climate change. There is a lack of standardization among SST studies regarding how the Iberian Peninsula areas are divided and this is challenging for aggregating results from different studies with specific questions. In our study, we aimed to analyse the SST time series over more than half a century using the coastal oceanographic divisions established by the International Council for the Exploration of the Sea (ICES) such that our results can be linked to biological data in the future. We ask: Has SST been increasing over the previous decades, and is this increase similar across regions? Are sudden SST shifts marked by higher SST increase rates than are yearly or semi-decadal increases? To answer these questions, we describe the annual, seasonal and monthly SST time series and identify the rates of SST increase and discontinuities (sudden shifts) in the SST time series with the goal of better understanding SST variability and the evolution of regional trends.

## 2.2 Methods

### 2.2.1 Study area

The Portuguese continental coast extends along the southwestern region of the Iberian Peninsula, and it can be divided into three regions based on oceanographic and biological features (Cunha, 2001; Bettencourt et al., 2004; Santos et al., 2007). The northwestern and southwestern coasts form the boundary between the temperate and subtropical regions of the Northeast Atlantic (Santos et al., 2001), while the southern Portuguese coast has a mixture of influences from the subtropical region of the Atlantic Ocean and Mediterranean Sea (Cunha, 2001; Bettencourt et al., 2004). Climatologically, the northwestern region has a temperate climate, while the other two regions have a Mediterranean climate. These three regions correspond to coastal areas already established by the International Council for the Exploration of the Sea (ICES), that is, the northwestern Portuguese coast is referred to as the IXaCN area, the southwestern Portuguese coast is the IXaCS area, and the southern Portuguese coast is the IXaS-Algarve area (Figure 2.1).

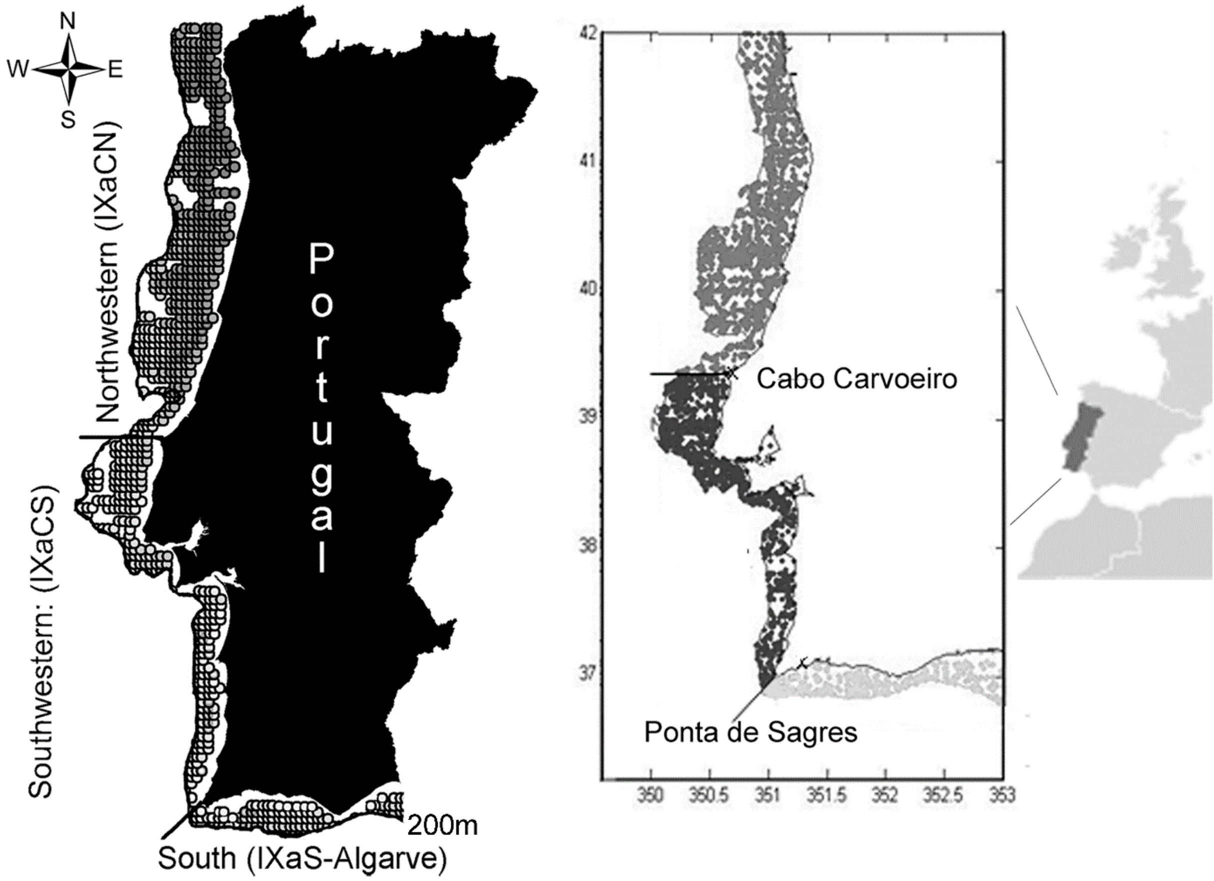

**Figure 2.1** Portuguese coast with different studied areas (northwestern and southwestern, representing the western coast; and southern coast) and information on satellite (left panel) and ICOADS (right panel) points used to extract average mean per area until 200m depth. The delimitation of the different areas of Portuguese coast was adapted accordingly oceanographic studies (Cunha, 2001; Bettencourt et al., 2004) and fisheries stocks division (ICES sub-division).

### 2.2.2 Data acquisition

Two independent data sets of nearshore SST were analysed: (1) a long-term data set consisting of the monthly mean SST data for the period 1950–2010 from the International Comprehensive Ocean–Atmosphere Data Set (hereafter referred to as the ICOADS data set) and (2) short-term data set consisting of the monthly mean SST data for the period 1985-2010 from the Modis-Aqua satellite (hereafter referred to as the Satellite data set).

The ICOADS data set was downloaded in a tabular format appropriate for statistical analyses. Monthly ICOADS data have been calculated as the monthly averages of climate records over grid cells of 1° × 1° boxes since 1950 for the world’s oceans. Grid cells covering the Portuguese continental coast were selected from the ICOADS data set (Figure 2.1). The number of retrieved samples and their location within a given grid cell varied monthly, while the time period of the data used from the ICOADS was longer, extending from 1950 to 2010 and with good representation over the coastal areas (Figure 2.1). Using these two sources of data, we could compare between recent SST observations and historical SST records from the past 60 years. Missing data (5 and 57months for the northwestern and southern coast, respectively) were estimated by two approaches: (1) mean replacement, which was used as much as possible, using the mean of the previous and subsequent years (N =28) and (2) linear regression replacement by using the results of linear regression between the ICOADS and Satellite data sets (N =34). Considering that the goal of our study is to follow SST trends, rather than evaluate data values, this data replacement (that does not occur at the beginning or end of the time-series) is not expected to affect trend analyses.

Satellite data are available on NASA Ocean Colour Giovanni website (http://gdata1.sci.gsfc.nasa.gov), which provides monthly summary imagery data with a spatial resolution of 4 km between 1985 and 2010. Satellite data of the Portuguese continental coast were obtained using Marine Geospatial Ecology Tools (MGET; Roberts et al., 2010). Data of the averages from each of the three ICES fishing areas were considered in this study (Figure 2.1). The satellite oceanographic data were obtained in raster format and conjugated into a tabular format. As such, the raster values contained within each polygon (divisions of the coast are shown in Figure 2.1) were averaged using the ‘isectpolyrst’ tool of the Geospatial Modelling Environment (GME; http://www.spatialecology.com/gme/isectpolyrst.htm).

### 2.2.3 Data analyses

Monthly, seasonal (winter – January to March; spring – April to June; summer – July to September and autumn – October to December) and yearly analyses of the data were conducted to describe the time-series trends. The yearly and half a decade ICOADS (1950-2010) time-series data were transformed into anomalies by subtracting the mean from the observed values. Regression analysis was used to describe the evolution of yearly ICOADS (1950-2010) and Satellite (1985-2010) SST time series along the years and the slope of the linear regression was used to evaluate warming rates.

The smoothed trends for the ICOADS (1950-2010) and Satellite (1985-2010) time series were obtained by means of seasonal decomposition with Loess smoothing (implemented in the software package Brodgar 2.5.1; http://www.brodgar.com). Cyclical and seasonal patterns were removed from the data using seasonal decomposition with Loess smoothing by decomposing a time series into a trend, a seasonal component and residual information. For the monthly time series, a smoother trend is fitted by considering that the yearly time series of all January data are smoothed; the same process is conducted for data of the other months. Hence, the method results in 12 smoothed monthly curves that will be subtracted from the original time series to estimate a long-term smoother trend and obtain a de-trended time series (Zuur et al., 2007).

Dynamic factor analysis (DFA) was used to explore the trends between data sets and regions. DFA is a multivariate time-series analysis method for estimating underlying common patterns (common trends) in a set of non-stationary time series (Zuur et al., 2003a, 2003b). Models with multiple common trends and noise were only considered because they allowed for the estimation of yearly and monthly common trends between the ICOADS and Satellite time series (only for matching the years 1985 to 2010) for the three areas of the study region (Northwestern, Southwestern and Southern coasts). Thus, six single-time series were initially introduced in the DFA model (two data sets × three fishing areas). LOESS monthly smoothed ICOADS and Satellite data were used for the DFA monthly trend analyses. The SST time-series data were standardized by subtracting the mean and dividing the result by its standard deviation (Zuur et al., 2003b). Models were fitted with a diagonal matrix, and the Akaike's information criterion (AIC) was used to compare between the models to determine the number of common trends needed to describe all of the time series (Zuur et al., 2003b). The DFA model with the lowest AIC value is indicative of the best model (Zuur et al., 2003a). Canonical correlations were used to analyse the relationship between the original time series and common trends. A canonical correlation that is higher than 0.5 signifies that the corresponding time series follows the pattern of the common trend (Zuur et al., 2007). In other words, if more than one time series is correlated with the common trend, then such time series are similar. Zuur et al. (2003a) provides a detailed statistical description of the dynamic factor analysis. For this analysis, DFA was conducted with the software package Brodgar 2.5.1.

When the statistical parameters of a process do not change over time, the process may be defined as stationary (Challis and Kitney, 1991). Estimating the correlation between non-stationary variables can result in spurious dependencies and erroneous conclusions regarding the development of SST trends. Therefore, if a given variable has a deterministic trend, a trend-adjusted series should be used, such as by DFA, to cope with intra-annual non-stationary data, such as the SST data (as shown in Table 1.A1). Consequently, a preliminary analysis of stationarity was based on the graphs of the annual and monthly observed time series, as well as by the auto-correlation function (ACF) analysis, which relates the correlation of time observations separated by different time periods (Zuur et al., 2007). The ACF analysis (conducted with the software package Brodgar 2.5.1) was also applied to the SST ICOADS (1950-2010) time series to investigate the underlying periodicity that is useful for the Regime Shift Indicator test, the Kolmogorov–Zurbenko (KZ) filter and the Kolmogorov–Zurbenko adaptive (KZA) filter.

Trends and transitions in the yearly SST ICOADS (1950-2010) time series long-term data were investigated using the Regime Shift Indicator test (RSI; Rodionov, 2004). This test is based on sequential t-test analyses of intra-annual data that can signal the possibility of a regime shift (Rodionov, 2004). Therefore, we tested the homogeneity and normality of the time-series using R-software package 'gvlma'. The distribution was normal for all time series ($p<0.01$). Homogeneity was also observed for all time series. The sequential algorithm focuses in detecting periods of change in the mean values of the respective time series, enabling early detection of a regime shift and subsequent monitoring of changes in magnitude over time (Rodionov, 2004, 2005). The RSI test provides flexibility by allowing for the customization of several parameters (target significance level, cut-off length, Huber weight parameter) to detect shifts with meaningful environmental implications. Details on the RSI calculation are provided by Rodionov (2004, 2005, 2006), Rodionov and Overland (2005), and the Bering Climate website (http://www.beringclimate.noaa.gov), where a version of the algorithm is available as an Excel software Add-In. The parameters were set through a series of attempts to obtain a model that detects periods with meaningful shifts; models were re-tested, and the data were explored to search for better statistical fitness (for all areas a significance level of 0.1 was selected, comprising 10% of smooth yearly data; a cut-off of 10 was used for the Southwestern and Southern coasts, and a cut-off of 20 was used for the Northwestern coast; Huber's weight parameter of 3 was used for outliers).

The KZ and KZA filters were used to investigate trends and detect abrupt discontinuities in yearly and monthly SST ICOADS time series (1950-2010). The KZ filter was used to classify various phenomena in the time series as short-term, seasonal, and long-term variations (Zurbenko et al., 1996). The KZ filter is a low-pass filter produced through repeated iterations of a moving average; it can remove high frequency variations from a time series (Galanis et al., 2011). This filter provides a good separation of frequencies and does not require special treatment for time series with missing data (Rao and Zurbenko, 1994). The filter smooths out abrupt discontinuities (Zurbenko et al., 1996), and it can be used to detect environmental data trends (Jongh et al., 2006). The KZ filter has been described in detailed by Rao and Zurbenko (1994). In contrast, the KZA filter has been applied to detect abrupt discontinuities throughout a time series (in the presence of seasonal patterns and trends) without modifying the changes that occur slowly over time (Zurbenko et al., 1996; González et al., 2013). The KZA filter is a modification of the KZ filter (Zurbenko et al., 1996) and a low-pass filter. The adaptive filter depends on an iterative moving average that separates seasonal and high-frequency variations from long-term variations of the original time series but dampens sharp breaks. Discontinuities are detected with the low-frequency component (González et al., 2013). The KZA filter does not require a specific model of the time series, which is a typical advantage of a nonparametric approach (Yang and Zurbenko, 2010a, 2010b). The KZA filter is primarily used to detect discontinuities in long-term meteorological series and in SST and sea level data (González et al., 2013). For our analyses, a lag of 11, 10 and 12 years (size of the window) were used for the northwestern, southwestern and southern coasts, respectively, after re-testing several models with different smooth/window sizes and considering the auto-correlation function (ACF) as a preliminary analysis. Analyses of the KZ and KZA filters were conducted with R-software 3.0.2 ('kza' and 'kzft' packages).

## 2.3. Results

### 2.3.1. Inter-annual variability of SST

The dynamic factor analysis showed that ICOADS and Satellite data sets have the same annual trend (i.e. one common trend describes all ICOADS and Satellite single trends), regardless of the area (Figures 2.2a, Appendix 2.A1). Therefore, ICOADS annual data were preferentially used for long-term regime shifts. Nevertheless, SST of the ICOADS data set are usually lower than that of the Satellite data set, except for the northwestern coast, where both data sets display the same trends. The auto-correlation function analysis (Table 2.A1) showed an autocorrelation of yearly data in the northwestern, southwestern and southern coasts for lags of 3 and 7, 2, 7 and 9 and 1-8 years, respectively. The yearly SST time series is non-stationary, as there is no systematic autocorrelation of SST in previous and subsequent years.

Oscillations in SST monthly values were observed over the years (Figure 2.2a). The SST monthly values (LOEES) increased above the mean values over the last several decades (1980-2010), specifically in the southwestern (16.7±0.3 °C) and southern (17.7±0.4 °C) coasts (Figure 2.2a). Monthly average annual SST has an evident seasonal cycle for both data sets and regions, with minimum values being registered between January and March (13.6-14.1 °C) and maximum values being registered between July and September (20.8-21.6 °C) (Figure 2.2b).

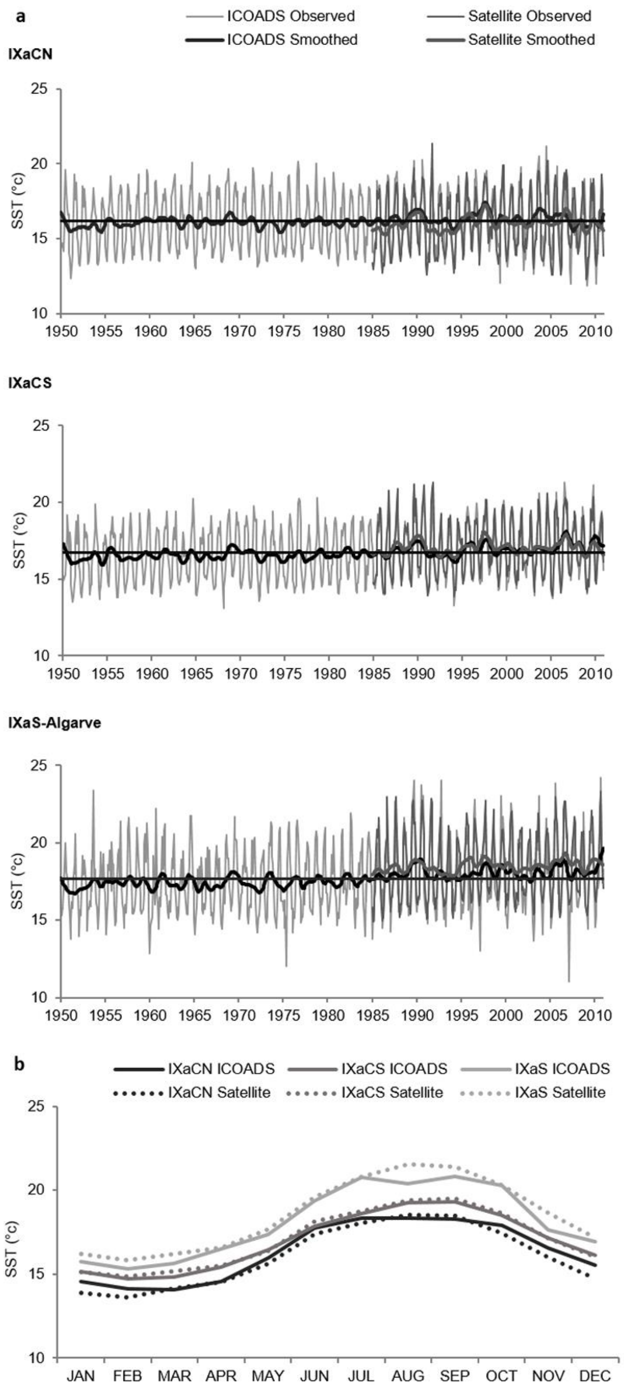

**Figure 2.2** (a) Observed and smoothed (LOESS) ICOADS (1950-2010) and Satellite (1985-2010) monthly sea surface temperature (SST) average values for Portuguese coastal areas (northwestern – IXaCN, southwestern – IXaCS and southern – IXaS-Algarve); (b) annual SST cycle for the observed ICOADS and Satellite data for Portuguese coastal areas (northwestern – IXaCN, southwestern – IXaCS and southern – IXaS-Algarve), average for the period 1985-2010.

Yearly SST increased linearly across the areas independent of the data source (Figure 2.3a). In the southwestern and southern coasts, the yearly SST mean surpassed general SST mean (mean of all years of the time series) after 1995 (16.7±0.3 °C) and 1986 (17.7±0.4 °C), respectively (Figure 2.3a). A similar pattern was evident in the half-a-decade mean SST values that showed positive anomalies (increase of SST above the mean of the time series: 16.2±0.2 °C in northwestern coast, 16.7±0.3 °C in southwestern coast and 17.7±0.4 °C in southern coast) after the mid-1980s (Table 2.1; Figure 2.3b). Overall, the maximum half-a-decade SST values increased above the mean maximum temperature (16.6±0.4 °C in the northwestern coast, 17.1±0.4 °C in southwestern coast and 18.18±0.47 °C in southern coast) after 1985–1989 and regardless of the coastal area (Table 2.11). The minimum semi-decadal SST values also increased above the mean minimum values (15.8±0.3 °C) after 1970–1974 (15.8-16.3 °C) for the northwestern coast, except for 2005-2009 (15.5 °C; Table 2.1). The minimum half-a-decade SST values also increased above the mean minimum values in the southwestern (16.4±0.3 °C) and southern coasts (17.3±0.4 ∘C) after 1990–1994 (16.8-16.9 °C) and 1975–1979 (17.3-17.8 °C), respectively (Table 2.1).

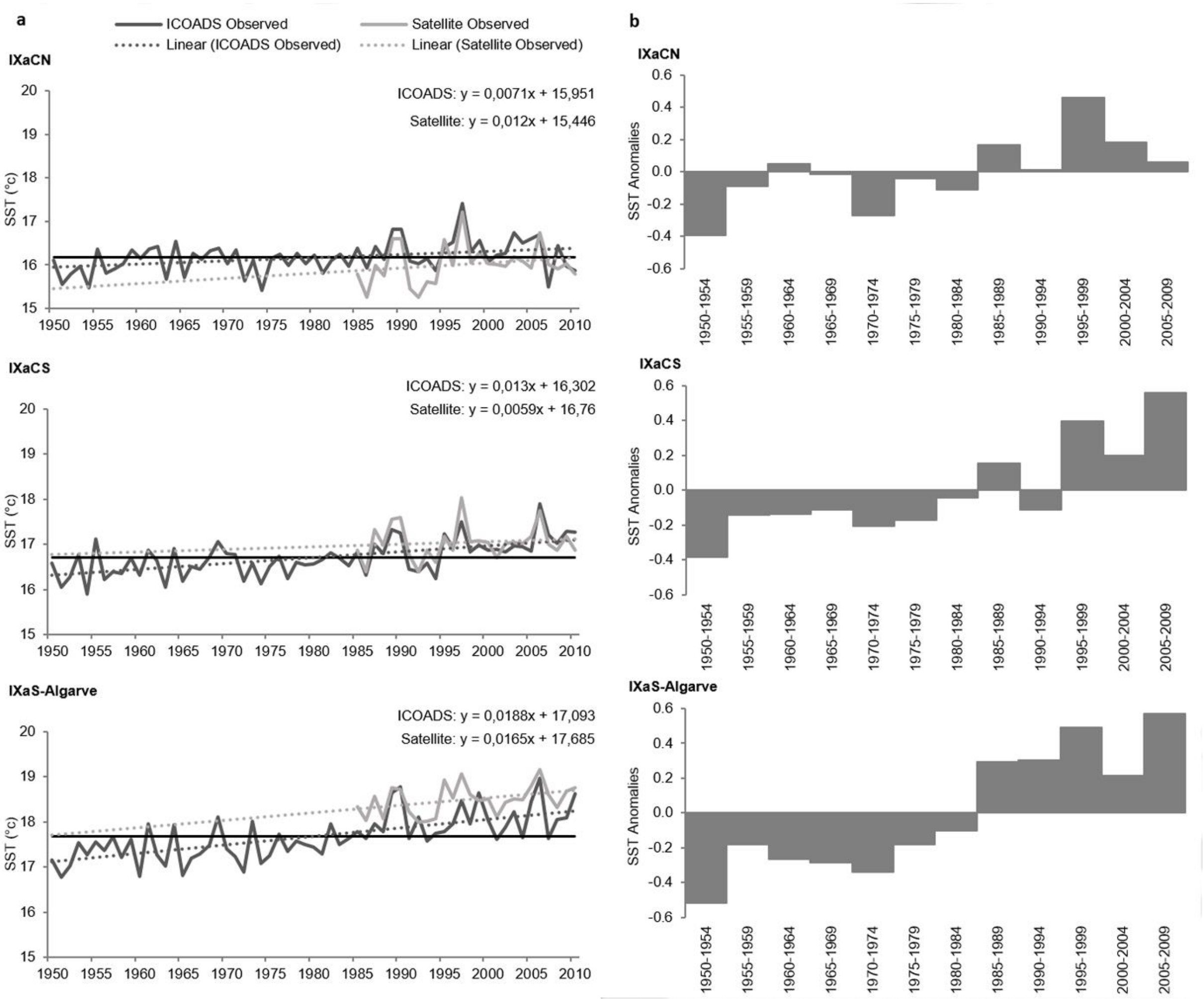

**Figure 2.3** (a) Observed ICOADS (1950-2010) and Satellite (1985-2010) annual mean sea surface temperature (SST) values for Portuguese coastal areas with corresponding adjusted linear regression lines (the horizontal black line represent the average yearly value for ICOADS data); (b) half a decade SST anomalies based on ICOADS data for Portuguese coastal areas (northwestern – IXaCN, southwestern – IXaCS and southern – IXaS-Algarve).

**Table 2.1** Mean, maximum and minimum half a decade sea surface temperature (SST) values based on ICOADS data (1950-2010) for Portuguese coastal areas (northwestern – IXaCN, southwestern – IXaCS and southern – IXaS-Algarve).

| | **IXaCN** | | | **IXaCS** | | | **IXaS- Algarve** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Years** | **Mean** | **Max** | **Min** | **Mean** | **Max** | **Min** | **Mean** | **Max** | **Min** |
| **1950-1954** | 15.78 (±0.27) | 16.12 | 15.47 | 16.31 (±0.37) | 16.77 | 15.89 | 17.14 (±0.29) | 17.53 | 16.76 |
| **1955-1959** | 16.09 (±0.25) | 16.36 | 15.81 | 16.55 (±0.36) | 17.11 | 16.21 | 17.48 (±0.19) | 17.66 | 17.21 |
| **1960-1964** | 16.23 (±0.34) | 16.53 | 15.67 | 16.56 (±0.37) | 16.91 | 16.05 | 17.40 (±0.53) | 17.94 | 16.79 |
| **1965-1969** | 16.16 (±0.27) | 16.39 | 15.71 | 16.58 (±0.33) | 17.06 | 16.17 | 17.38 (±0.48) | 18.11 | 16.81 |
| **1970-1974** | 15.90 (±0.38) | 16.35 | 15.42 | 16.49 (±0.32) | 16.80 | 16.12 | 17.32 (±0.43) | 18.02 | 16.89 |
| **1975-1979** | 16.13 (±0.12) | 16.26 | 15.99 | 16.52 (±0.18) | 16.73 | 16.23 | 17.48 (±0.19) | 17.73 | 17.25 |
| **1980-1984** | 16.07 (±0.18) | 16.24 | 15.81 | 16.65 (±0.12) | 16.82 | 16.52 | 17.56 (±0.25) | 17.96 | 17.29 |
| **1985-1989** | 16.34 (±0.34) | 16.83 | 15.94 | 16.85 (±0.36) | 17.32 | 16.32 | 17.95 (±0.40) | 18.63 | 17.62 |
| **1990-1994** | 16.19 (±0.36) | 16.81 | 15.87 | 16.58 (±0.40) | 17.26 | 16.24 | 17.97 (±0.50) | 18.78 | 17.57 |
| **1995-1999** | 16.63 (±0.44) | 17.40 | 16.31 | 17.09 (±0.27) | 17.49 | 16.83 | 18.15 (±0.37) | 18.63 | 17.77 |
| **2000-2004** | 16.36 (±0.26) | 16.74 | 16.08 | 16.90 (±0.05) | 16.96 | 16.83 | 17.88 (±0.25) | 18.22 | 17.62 |
| **2005-2009** | 16.24 (±0.51) | 16.71 | 15.49 | 17.26 (±0.39) | 17.89 | 16.85 | 18.23 (±0.50) | 18.96 | 17.62 |
| **Mean** | 16.18 (±0.22) | 16.56 (±0.36) | 15.80 (±0.26) | 16.70 (±0.27) | 17.09 (±0.35) | 16.36 (±0.33) | 17.66 (±0.36) | 18.18 (±0.47) | 17.27 (±0.38) |

The annual average data did not show differences among the long-term SST linear adjusted trends (ICOADS) and short-term SST linear adjusted trends (Satellite) (Table 2.2; Figure 2.3a) and among regions with the exception of the southern coast, where the SST increment rate (+0.2 °C decade$^{-1}$) was greater than for the western coast (northwestern and southwestern coasts; +0.1 °C decade$^{-1}$).

**Table 2.2** Slope values of linear regression lines for ICOADS (1950-2010) and Satellite (1985-2010) annual, monthly and seasonal sea surface temperature (SST) data for Portuguese coastal areas (northwestern – IXaCN, southwestern – IXaCS and southern – IXaS-Algarve).

| | **SATELLITE: 1985-2010** | | | **ICOADS: 1950-2010** | | |
|---|---|---|---|---|---|---|
| | **IXaCN** | **IXaCS** | **IXaS** | **IXaCN** | **IXaCS** | **IXaS** |
| **Annual** | 0.012 | 0.006 | 0.017* | 0.007* | 0.013* | 0.019* |
| **January** | -0.010 | -0.003 | 0.017 | 0.012 | 0.013* | 0.012* |
| **February** | 0.004 | 0.006 | 0.026 | 0.009* | 0.010* | 0.002 |
| **March** | 0.005 | 0.019 | 0.007 | 0.001 | 0.008 | 0.005 |
| **April** | 0.036 | 0.036 | 0.035 | 0.001 | 0.011 | 0.019* |
| **May** | 0.032 | 0.012 | 0.019 | 0.009 | 0.011 | 0.010 |
| **June** | 0.044 | 0.030 | 0.045 | 0.019 | 0.016 | 0.028* |
| **July** | 0.012 | -0.005 | -0.010* | 0.004* | 0.012* | 0.039* |
| **August** | <0.000* | -0.008 | 0.018 | -0.001 | 0.026* | 0.038* |
| **September** | 0.010 | -0.033* | -0.003 | -0.001 | 0.022* | 0.027* |
| **October** | 0.037 | 0.022 | 0.029 | 0.008 | 0.007 | 0.033* |
| **November** | -0.001 | 0.002 | 0.015 | 0.011* | 0.009 | 0.003 |
| **December** | -0.026 | -0.008* | <0.000 | 0.013 | 0.014* | 0.008 |
| **Winter** | -0.0003 | 0.007 | 0.017 | 0.008 | 0.010* | 0.007 |
| **Spring** | 0.037 | 0.026 | 0.033 | 0.009 | 0.013 | 0.019* |
| **Summer** | 0.007* | -0.015 | 0.002 | 0.001 | 0.020* | 0.035* |
| **Autumn** | 0.003 | 0.005 | 0.015 | 0.011 | 0.010 | 0.015* |

No outliers were highlighted by the sudden shifts yearly analyses [regime shift index (RSI)] for any area, demonstrating that the model parameters were well-selected regarding Huber's weight. The lack of outliers is supported by the exploratory graphical analyses that do not show anomalous SST yearly values in the time series by area (Figure 2.4a). Generally, the observed yearly time-series trends agree with the estimated RSI trends (Figure 2.4a). The RSI detected SST changes in all areas. In the northwestern coast, yearly sudden shifts analyses showed an increase in SST mean values (from 16.1 to 16.4 °C; RSI = 0.58) in 1987 and a decrease (from 16.4 to 15.9 °C; RSI= -3.87) after 2007 (Table 2.3; Figure 2.4a). In the southwestern coast, yearly sudden shifts analyses showed an increase in SST mean values in 1995 (from 16.6 to 17.0 °C; RSI = 0.58) and 2006 (from 17.0 to 17.3 °C; RSI = 1.79) (Table 2.3; Figure 2.4a). In the southern coast, yearly sudden shifts analyses showed an increase in SST mean values in 1982 (from 17.4 to 18.0 °C; RSI = 0.70) and 2010 (from 18.0 to 18.6 °C; RSI = 0.84) (Table 2.3; Figure 2.4a).

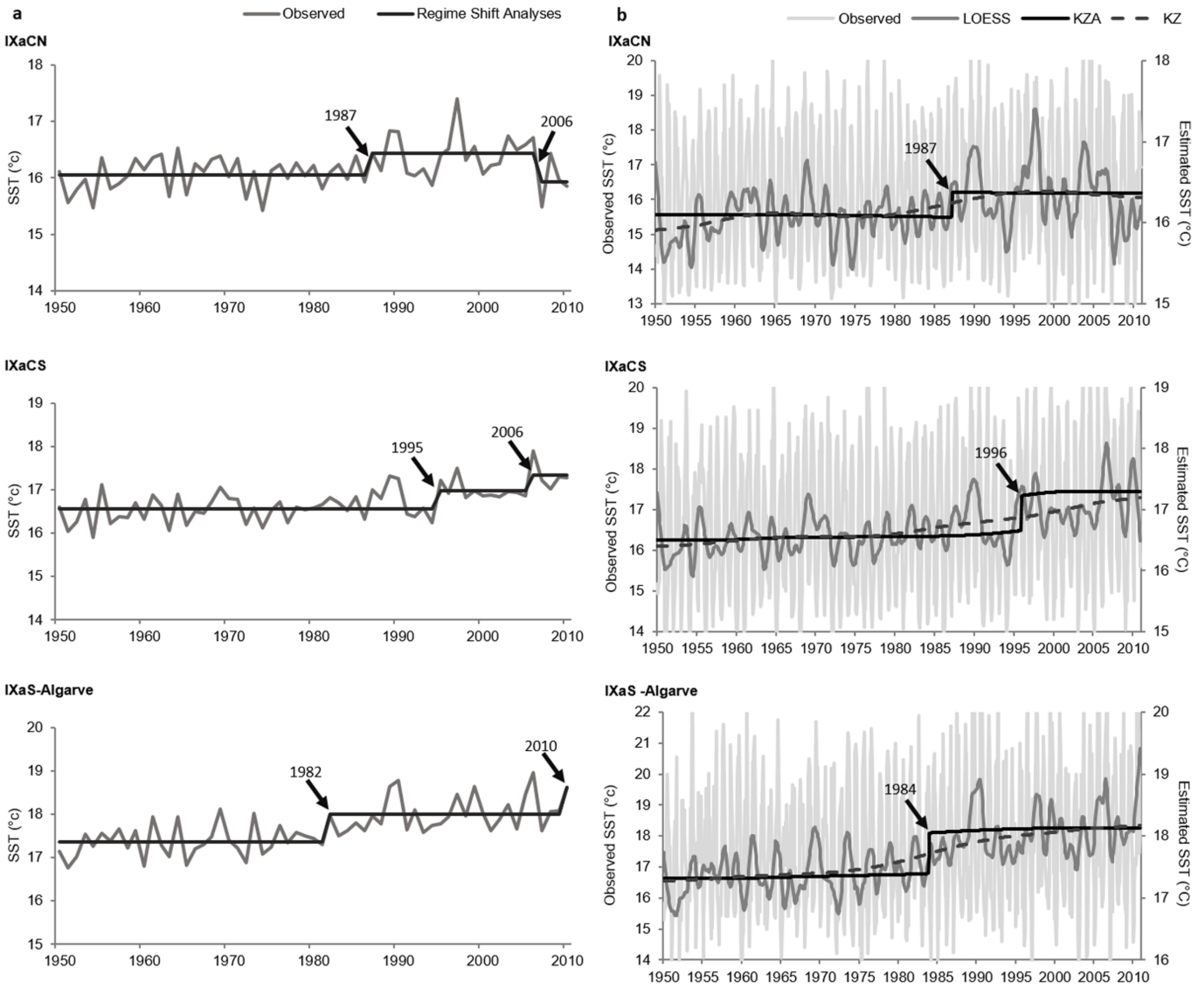

**Figure 2.4** (a) Observed and estimated (Regime Shift Indicator – RSI) of yearly ICOADS sea surface temperature (SST) values for Portuguese coastal areas (northwestern – IXaCN, southwestern – IXaCS and southern – IXaS-Algarve). The model was calculated based on Significance level of 0.1, cut-off length of 10 and Huber parameter of three for northwestern (IXaCN) and southwestern (IXaCS) and Significance level of 0.1, cut-off length of 20 and Huber parameter of three for southern coast (IXaS-Algarve). (b) Observed and estimated (LOESS values and Kolmogorov-Zurbenko and Kolmogorov-Zurbenko Adaptive filters values) of monthly ICOADS SST values for Portuguese coastal areas. The model was calculated based on 132, 120 and 144 months for northwestern, southwestern and southern coasts.

**Table 2.3** Regime Shift Indicator (RSI) and confidence level of the difference between the mean values of the neighbouring regimes based on the Student's two-tailed t-test with unequal variance (Conf) values based on sea surface temperature (SST) ICOADS data (1950-2010) for Portuguese coastal areas (northwestern – IXaCN, southwestern – IXaCS and southern – IXaS-Algarve). The model was calculated based on Significance level of 0.1, cut-off length of 10 and Huber parameter of 3 for northwestern and southwestern coasts and Significance level of 0.1, cut-off length of 20 and Huber parameter of 3 for southern coast.

| | **IXaCN** | | **IXaCS** | | **IXaS-Algarve** | |
|---|---|---|---|---|---|---|
| **Years** | **RSI** | **Conf** | **RSI** | **Conf** | **RSI** | **Conf** |
| **1982** | 0 | - | 0 | - | 0.698 | < 0,000 |
| **1987** | 0.577 | 0.000 | 0 | - | 0 | - |
| **1995** | 0 | - | 0.576 | < 0,000 | 0 | - |
| **2006** | 0 | - | 1.787 | 0.068 | 0 | - |
| **2007** | -3.873 | 0.078 | 0 | - | 0 | - |
| **2010** | 0 | - | 0 | - | 0.843 | - |

The KZA filter detected discontinuities in the SST time series in the northwestern, southwestern and southern coasts followed by an increase of SST values in 1987 (from 16.1 to 16.4 °C), 1995 (from 16.7 to 17.2 °C) and 1983 (from 17.4 to 17.7 °C), respectively (Figure 2.4b). The RSI and KZA filter analyses were consistent with yearly and monthly SST sudden shifts.

### 2.3.2. Seasonal variability of SST

The dynamic factor analyses of individual monthly SST showed that one common trend described ICOADS and Satellite single trends in all areas. Generally, monthly SST time series were similar among regions, regardless of the data sets (Figure 2.A1). In addition, the high variability found in yearly anomalies of monthly SST values over the years show that the data are non-stationary (Figure 2.5). A linear annual increase in SST monthly values was observed for both ICOADS and Satellite data sets, independent of the area (Figure 2.6). However, there are several exceptions. In the northwestern coast, the SST linear trend declined along time for both data sets in August (when higher SST average monthly values were recorded at 18.5 °C) (Figure 2.6a). Moreover, SST trends also showed linear opposite tendencies among the two data sets: (1) the ICOADS data set showed a yearly decrease in September, while the Satellite data set showed a yearly increase and (2) an increase in SST annual values was recorded for the ICOADS data set in January, November and December, while an SST decrease was observed in the Satellite data set. In the southwestern coast, SST annual values decreased linearly in January, summer (July, August and September) and December, as shown by the Satellite data set (Figure 2.6b). On the southern coast, SST annual values decreased linearly in July, September and December, as shown by the Satellite data set (Figure 2.6c).

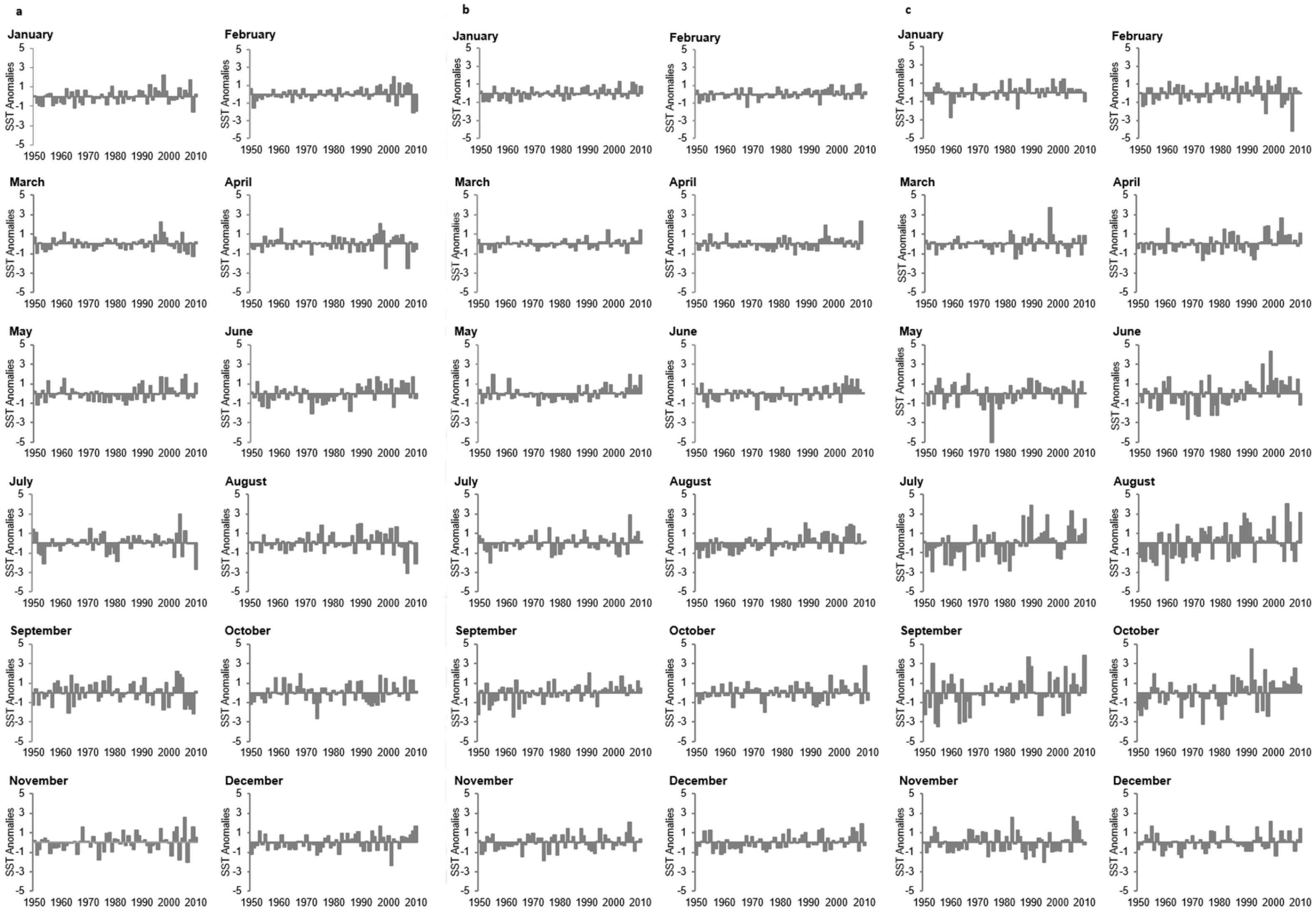

**Figure 2.5** Yearly monthly ICOADS (1950-2010) sea surface temperature (SST) anomalies for Portuguese coastal areas: (a) northwestern (IXaCN), (b) southwestern (IXaCS) and (c) southern (IXaS-Algarve) coasts.

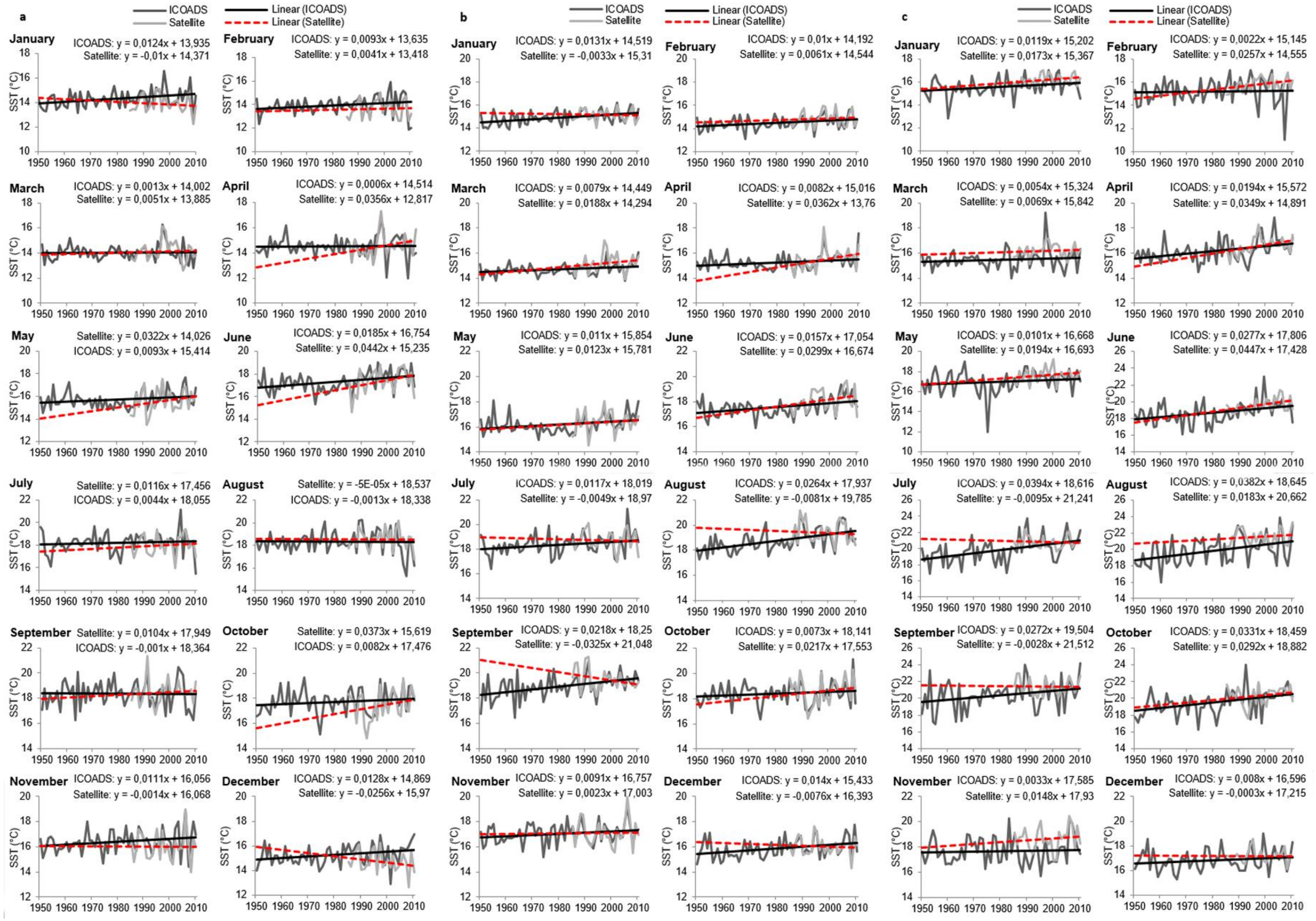

**Figure 2.6** Observed ICOADS (1950–2010) and Satellite (1985-2010) monthly sea surface temperature (SST) mean values for Portuguese coastal areas: (a) northwestern (IXaCN), (b) southwestern (IXaCS) and (c) southern coasts (IXaS), with corresponding adjusted linear regression lines.

Overall, the ICOADS data set reveals that SST increased at a higher rate in autumn (+0.1 °C decade$^{-1}$ for the northwestern coast) and summer (+0.2 °C decade$^{-1}$ for the southwestern coast and +0.4 °C decade$^{-1}$ for the southern coast), while short-term data reveal that SST increased at a higher rate in spring, regardless of the area (Table 2.2). Monthly data analyses showed differences among the long-term SST (ICOADS) and short-term SST (Satellite) linear adjusted trends (Table 2.2; Figure 2.6). For the northwestern, southwestern and southern coasts, the monthly SST ICOADS values increased at a higher linear rate in June (+0.2 °C decade$^{-1}$), August (+0.3 °C decade$^{-1}$) and July (+0.4 °C decade$^{-1}$), respectively. A decrease of the SST ICOADS values occurred at higher rate in the northwestern coast in August and September (-0.01 °C decade$^{-1}$). The monthly SST Satellite values in the northwestern, southwestern and southern coasts increased at a higher linear rate in June (+0.4 °C decade$^{-1}$), April (+0.4 °C decade$^{-1}$) and June (+0.5 °C decade$^{-1}$), respectively. The SST Satellite values decreased at a higher linear rate in the northwestern, southwestern and southern coasts in December (-0.3 °C decade$^{-1}$), September (-0.3 °C decade$^{-1}$) and July (-0.1 °C decade$^{-1}$).

## 2.4. Discussion

The two data sets presented here differ in relation to the time-series period (ICOADS: 1950-2010; Satellite: 1985-2010) and SST values; however, the trends in the data sets were similar with respect to the year. In this study, the trend analysis was privileged, and differences between data set observations (observed values) are beyond the scope of this study. Overall, according to an annual or monthly time frame, and the ICOADS or Satellite data sets, SST has increased along the Portuguese coast over the last several decades (1980-2010). However, the warming pattern is not uniform across space; there is a north–south increasing gradient along the coast.

### 2.4.1. Inter-annual variability of SST

The two methods (RSI and KZA filter analyses) used to detect discontinuities in the SST time series had similar results regarding the period when both yearly and monthly SST sudden shifts occurred, that is, 1987, 1995 and 1982-1983 on the northwestern, southwestern and southern coasts, respectively. On the western coast of Iberian Peninsula, Santos et al. (2011) observed three warming-cooling periods: a warming period in 1920-1950 (before our study period), a cooling period in 1950-1974, and another warming period in 1974-2008 that was more intense that the previous one. Thus, in accordance with Santos et al. (2011), the early years of our study correspond to a cooling period of SST along the Portuguese coast, and discontinuities of the SST time-series are observed in the second and more intense warming period. In a global context, Nerem et al. (1999) and Levitus et al. (2000) observed a peak in global SST during the mid-1990s. The sudden shift analyses enable better understanding of SST dynamics by revealing periods when sudden shifts of SST occurred. Such shift periods were characterized with an increase in SST several times higher than inter-annual or decadal increment rates. For instance, in the northwestern, southwestern and southern coasts, SST increased after 1987, 1995 and 1982 more than 0.5 °C in 1 year. These temperature increases are considerably higher than those ever recorded for annual or decadal SST increment rates.

The intensity of SST variability differed between areas, with the annual SST increment rate being twice as great in the southern coast (+0.2 °C decade$^{-1}$) than in the western areas (northwestern and southwestern coasts; approximately +0.1 °C decade$^{-1}$). Differences in the warming patterns along a small latitudinal gradient (ca. 800 km) were also recorded in the Bay of Biscay, where the SST increment rate was greater in the southeastern (+0.6 °C decade$^{-1}$) section of the bay than in the northeastern (+0.1 °Cdecade$^{-1}$) part (Planque et al., 2003).

Differences in SST variability across the areas were also detected by the auto-correlation function analyses, which showed that the SST time series in the northwestern and southwestern coasts do not correlate for more than two consecutive lags, while the southern coast was auto-correlated during the first 9 years. Such findings reveal more stability in SST patterns across years for the southern coast than for the western coast (northwestern and southwestern). This finding means that in the northwestern and southwestern coasts, the effects of climate change and SST regional warming can be difficult to forecast due to high inter-annual variability, which is in opposition to the Southern coast. Regional differences along the Portuguese coast are due to differences in wind regimes, ocean currents, thermocline depth, cloudiness, upwelling intensity (Fiúza, 1983; Sánchez and Relvas, 2003; Gómez-Gesteira et al., 2008), and orientation and exposure of the Portuguese coast (Fiúza et al., 1982). For instance, based on remote sensing SST data, Relvas et al. (2009) found contrasting warming rates between coastal and offshore waters in the southern part of the western Iberia but not for the northern part. Differences in the warming trends at the regional scale (or mesoscale) may arise from a variety of physical factors. Stratification of the water column and the pycnocline depth strongly affect the depth from which the subsurface water upwells, influencing the SST during upwelling events. Additionally, wind intensity along with the wind stress curl drives the offshore extent of cold upwelled water at the surface. The coastline configuration and presence of prominent capes define the regions of intensified upwelling and the formation of upwelling filaments, creating regions with altered SST variability. Regional differences in SST variability were also observed in the Black Sea (1982-2000), where a more intense warming was found in the deep eastern part (+1.1 °C decade$^{-1}$) of the sea than in the western part (+0.8 °C decade$^{-1}$), and this phenomenon is associated with the sea's local characteristics and circulation (Ginzburg et al., 2004).

The results showing a linear increase of SST on the Portuguese coast differed from results found in other parts of the world. For example, in the Black Sea, the increment rate of SST was about +0.9 °C decade-$^{1}$ in 1982-2000 (Ginzburg et al., 2004), which is nine times greater than values found for the western Portuguese coast. These discrepancies are related to oceanographic conditions. For example, the Black Sea is a semi-enclosed basin with restricted water exchange with the open sea (Ginzburg et al., 2004); therefore, any changes in the environment are intensified. In contrast, the Portuguese coast is exposed to the open sea (Fiúza et al., 1982). In a global context, Casey and Cornillon (2001) showed a warming trend of SST of +0.1 °C decade$^{-1}$ in 1960-1990. Lemos and Pires (2004) and Sousa Reis et al. (2006) also found a warming trend of close to +0.1 °C decade$^{-1}$ in western Portugal during 1941-2000. However, several researchers registered values twice as high as those found in our study; increased temperatures of +0.2 °C decade$^{-1}$ between 1985 and 2005 were recorded in the western part of the Iberian Peninsula (Gómez-Gesteira et al., 2008); +0.2 °C decade$^{-1}$ between 1974 and 2010 were recorded in the northwest of the Iberian Peninsula (Gómez-Gesteira et al., 2011); and +0.2 °C decade$^{-1}$ between 1974 and 2007 were recorded in the Bay of Biscay (deCastro et al., 2009). The discrepancies found between studies are likely due to the different time periods analysed, data sets used, and geographical delimitations considered in each study. Some authors have also found discrepancies and apparent contradictory results regarding the increase (Dickson et al., 1988; Bakun, 1990; Schwing and Mendelssohn, 1997; Santos et al., 2005; McGregor et al., 2007, Demarcq, 2009; Narayan et al., 2010; Miranda et al., 2013) or decrease (Lavin et al., 2000; Lemos and Pires, 2004; Lemos and Sansó, 2006; Alvarez et al., 2008; Barton et al., 2013) of the upwelling intensity in the region and worldwide. Therefore, if we consider a large spatial scale, such as from the Bay of Biscay (North Iberian Peninsula: Planque et al., 2003; Gómez-Gesteira et al., 2008, 2011; deCastro et al., 2009) to Algarve (South Iberian Peninsula: Present findings: Sousa Reis et al., 2001; Lemos and Pires, 2004), there is no homogeneous latitudinal gradient response in the SST increase rates. Overall, higher SST increase rates were found in the northern and southern Iberian Peninsula, while the lowest increment rates for SST were recorded in the western Iberian Peninsula. Future studies, however, should use the same spatial and temporal scales to enable standardized comparisons; these standards should be based on oceanographic regimes, climatic patterns and fisheries management. Therefore, we propose that the ICES divisions for stock assessment be used in future studies because it considers regional oceanographic characteristics (Cunha, 2001; Santos et al., 2001; Bettencourt et al., 2004) that can be matched with long-term biological data.

### 2.4.2. Seasonal variability of SST

The monthly analyses denoted a general increasing SST time series, with certain discrepancies being linked to the data sets and areas. In general, these discrepancies are more evident in the spring and summer months. For example, along the northwestern coast, in August (when higher SST values were recorded), the SST time series declined across time, which was contrary to the southwestern and southern coasts. The northwestern coast is a transition zone with a particular type of oceanographic regime (Gómez-Gesteira et al., 2011). Therefore, monthly SST analyses showed that coastal warming is not constant during the year and for some months; cooling of the coastal waters were observed, and the response is not spatially uniform.

Monthly SST increment rates are usually lower for long-term data (ICOADS) than for short-term data (Satellite), suggesting that regional warming has intensified since 1980. However, the monthly increment rates of SST varied along the coast and between data sets; greater increments occurred in the spring and summer (ca. +0.4 °C decade$^{-1}$). This seasonal pattern was observed in the Black Sea, where the greatest increments were registered in the spring and summer (ca. +0.7 °C decade$^{-1}$), and the lowest increments were registered in winter (+0.2 °C decade$^{-1}$) (Ginzburg et al., 2004). These results are contrary to those observed by Planque et al. (2003), who observed more pronounced increments during the winter (ca. +0.1 °C decade$^{-1}$) in Bay of Biscay between 1901 and 2000. In the northwestern Portuguese coast, higher SST increment rates occurred in June (+0.4 °C decade$^{-1}$ for Satellite data and +0.2 °C decade$^{-1}$ for ICOADS data), while in the southwestern and southern coasts, higher SST increment rates varied between data sets. In the southwestern coast, the higher increment rate was observed during April (+0.4 °C decade$^{-1}$ for Satellite data) and August (+0.3 °C decade$^{-1}$ for ICOADS data), while in the Southern coast, it was observed during June (+0.5 °C decade$^{-1}$

for Satellite data) and July (+0.4 °C decade$^{-1}$ for ICOADS data). In general, the monthly SST increment rates were similar to those found in the northwestern Iberia Peninsula (+0.4 °C decade$^{-1}$ in spring and +0.3 °C decade$^{-1}$ in summer) (Gómez-Gesteira et al., 2011). Moreover, in these seasons/months, the SST increment rates were higher than rates found for annual SST data (approximately +0.1 °C decade$^{-1}$ in the northwestern and southwestern coasts, and +0.2 °C decade$^{-1}$ in the southern coast).

The seasonality of the SST changes is relevant for biological dynamic processes due to species differences in thermal stress vulnerability, which affects their life cycle (Pörtner and Farrell, 2008). Seasonal variability along the year, such as the SST variation from winter to summer, triggers biological activity and decisive change (e.g. spawning, larvae development and recruitment). Thus, the timing and magnitude of warming during spring and summer (the period when most species reproduce and spawn) on the Portuguese coast over the last decades have an important effect on marine biota (Bertram et al., 2001). For instance, changes in the timing of seasonal increasing of SST are likely to increase phenological changes in species (Bradshaw and Holzapfel, 2008). These SST changes can have broader ecological implications due to the cascade effect across trophic webs (Sydeman et al., 2006; Pincebourde et al., 2008). For example, phytoplankton, zooplankton and benthic communities (Colebrook, 1982; Tunberg and Nelson, 1998), which belong to lower trophic levels, can be responsible for fluctuations in higher trophic levels and, consequently, in fisheries (Vinagre et al., 2006).

Many recent studies have focused on the impacts of SST on recruitment of Portuguese commercial species. According to Martinho et al. (2010), flatfish species, which have a more northern temperate affinity (*Platichthys flesus* and *Scophthalmus rhombus*), are highly affected by increased SST, while species with a more southern affinity (*Dicologlossa hexophthalma* and *Pegusa lascaris*) can benefit from SST increase. Higher SST favours the catch of *Sepia officinalis* and *Engraulis encrasicolus* on the southern coast during autumn but has negative effects on catch of *S. officinalis* on the Western coast during summer (Ullah et al., 2012). Increased SST benefits *Spisula solida* catches on the northwestern coast and negatively affects *S. solida* catches on the southern coast, particularly during the spawning season (Baptista and Leitão, 2014). *Diplodus sargus* catch rates were negatively affected by increased SST during autumn, winter and spring in northwestern, southwestern and southern coasts, respectively (Leitão et al., 2016 – Chapter 3 of the present Thesis). *Diplodus vulgaris* catch rates were negatively associated with winter SST on the southwestern coast (Baptista et al., 2016 – Chapter 4 of the present Thesis). Landings of *Sardina pilchardus* and *Trachurus trachurus* was negatively correlated with SST and landings of *Scomber colias* were positively correlated with SST (Teixeira et al., 2016). Teixeira et al. (2014) showed that increased SST affected landings significantly; landings of temperate species decreased, while landings of subtropical/tropical species increased.

### 2.4.3. Comparison with future scenarios

Changes of the global climate are expected (Santos and Miranda, 2006), and Portugal is likely to face rapid alterations in SST that are more significant than the global mean alterations rate (IPCC, 2001b). According to simulations of the HadRM3 model for the Portuguese coast (region independent), SST will increase between 1 and 2 °C, depending on the scenarios tested (B2 and A2), until the end of the 21st century (2071-2100; Sousa Reis et al., 2001). These scenarios concur with our calculations of SST annual and decadal increment rate, as well with other studies (Sousa Reis et al., 2001; Lemos and Pires, 2004; Gómez-Gesteira et al., 2008, 2011; deCastro et al., 2009). This fact supports the hypothesis that future SST would increase at the same incremental rate as in the past half-century (1950–2010). Earth system model scenarios, however, consider the combustion of fossil fuels, which has increased exponentially over the past 200 years, raising the atmospheric concentrations of carbon dioxide (NOAA, 2013). This increase is expected to cause global environmental changes with noticeable increases in SST (Meehl et al., 2007). Thus, it is difficult to understand how SST increase rates in past decades are similar to those predicted for the end of the 21st century, if the global combustion of fossil fuels is expected to increase in coming years. Caution is therefore urged when conducting global model analyses because there are many sources of uncertainty that propagate during the transfer of information from global to regional scales during downscaling exercises (García-Bustamante et al., 2012).

## 2.5 Conclusion

A generalized warming of SST was observed along the Portuguese coast during the last decades (1980–2010), and sudden SST increase (more than 0.5 °C) occurred after 1987, 1995 and 1982-1983 in the northwestern, southwestern and southern coasts, respectively. The SST annual increment rate varied along latitude with a lower increment in the northwestern and southwestern coasts than in the southern coast. The SST monthly analyses had discrepancies along the coast and according to the data set used, with the short-term data (Satellite) showing the higher increment rates than long-term data (ICOADS). Generally, the highest monthly SST increment rates occurred in spring and summer: (1) northwestern coast in June (+0.4 °C decade$^{-1}$ for Satellite data and +0.2 °C decade$^{-1}$ for ICOADS data); (2) southwestern coast in April (+0.4 °C decade$^{-1}$ for Satellite data) and August (+0.3 °C decade$^{-1}$ for ICOADS data) and (3) southern coast in June (+0.5 °C decade$^{-1}$ for Satellite data) and July (+0.4 °C decade$^{-1}$ for ICOADS data). This study reinforces the notion of a general increase of SST along the Portuguese coast since 1980, mainly in spring and summer. Finally, we urge the scientific community studying for instance fish recruitment, especially small pelagic fish (e.g. sardine) to focus also on studies dealing with regional and seasonal variability of SST. This strategy will allow to evaluate and manage the risks associated with climate change at a regional scale, which are far more realistic for a given region than global scenarios.

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## 2.8 Appendix

**Table 2.A1** Akaike's information criterion (AIC) and canonical correlation values for dynamic factor analysis (DFA) models with one common trend tested for the period between 1985 and 2010 with: six (regions and data sets), three (regions) and two (data sets) variables for yearly monthly sea surface temperature (SST) values, and six (regions and data sets) variables for monthly SST values, for Portuguese coastal areas (northwestern – IXaCN, southwestern – IXaCS and southern – IXaS-Algarve), based on a diagonal matrix.

| | **AIC Values** | **ICOADS IXaCN** | **ICOADS IXaCS** | **ICOADS IXaS** | **Satellite IXaCN** | **Satellite IXaCS** | **Satellite IXaS** |
|---|---|---|---|---|---|---|---|
| **All** | 2591.830 | 0.704 | 0.849 | 0.596 | 0.909 | 1.000 | 0.853 |
| **IXaCN** | 453.116 | 0.730 | - | - | 1.000 | - | - |
| **IXaCS** | 321.450 | - | 0.849 | - | - | 1.000 | - |
| **IXaS** | 618.018 | - | - | 0.626 | - | - | 1.000 |
| **ICOADS** | 1381.925 | 0.496 | 1.000 | 0.571 | - | - | - |
| **Satellite** | 659.269 | - | - | - | 0.909 | 1.000 | 0.853 |
| **January** | 413.833 | 0.717 | 0.850 | 0.288 | 0.888 | 0.894 | 0.851 |
| **February** | 363.256 | 0.541 | 0.909 | -0.116 | 0.979 | 0.973 | 0.862 |
| **March** | 366.736 | 0.444 | 0.700 | 0.656 | 0.926 | 0.998 | 0.881 |
| **April** | 346.048 | 0.568 | 0.935 | 0.696 | 0.914 | 0.980 | 0.909 |
| **May** | 376.091 | 0.793 | 0.812 | 0.510 | 0.951 | 0.977 | 0.804 |
| **June** | 400.117 | 0.787 | 0.761 | 0.429 | 0.922 | 0.941 | 0.728 |
| **July** | 431.132 | 0.435 | 0.645 | 0.496 | 0.794 | 0.954 | 0.790 |
| **August** | 422.274 | 0.496 | 0.824 | 0.374 | 0.760 | 0.995 | 0.558 |
| **September** | 417.750 | 0.529 | 0.847 | 0.496 | 0.915 | 0.929 | 0.678 |
| **October** | 352.223 | 0.769 | 0.910 | 0.071 | 0.914 | 0.989 | 0.904 |
| **November** | 353.602 | 0.516 | 0.890 | 0.243 | 0.920 | 1.000 | 0.863 |
| **December** | 405.385 | 0.421 | 0.860 | 0.354 | 0.912 | 0.988 | 0.718 |

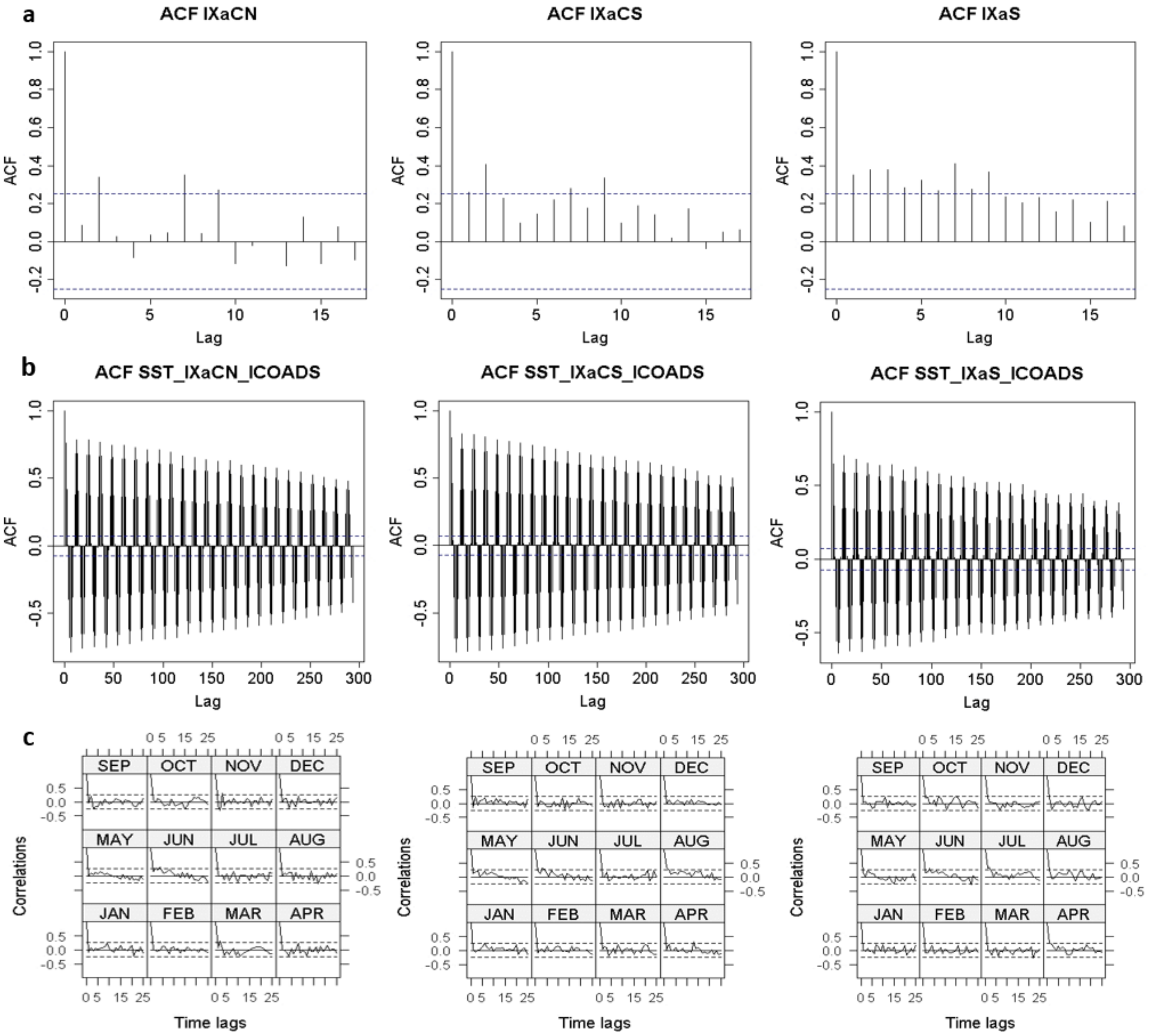

**Figure 2.A1** Autocorrelation function analyses (ACF) based on sea surface temperature ICOADS data (1950-2010) for Portuguese coastal areas (northwestern – IXaCN, southwestern – IXaCS and southern – IXaS-Algarve) for: (a) yearly data; (b) monthly data and (c) each month data.

# CHAPTER 3

## The role of environmental and fisheries multi-controls in white seabream (*Diplodus sargus*) artisanal fisheries in Portuguese coast

Leitão F, Baptista V, Teodósio MA, Samantha Jane Hughes SJ, Vieira V, Chícharo L (2016) The role of environmental and fisheries multi-controls in white seabream (*Diplodus sargus*) artisanal fisheries in Portuguese coast. Regional Environmental Change 16:163–176. doi:10.1007/s10113-014-0726-5

# THE ROLE OF ENVIRONMENTAL AND FISHERIES MULTI-CONTROLS IN WHITE SEABREAM (*DIPLODUS SARGUS*) ARTISANAL FISHERIES IN PORTUGUESE COAST

## Abstract

Evaluating the effects of fishing and environmental factors on fish populations are fundamental tenets of fisheries science. In this study, we assess associations between environmental variables (sea surface temperature; North Atlantic Oscillation index; upwelling; wind magnitude; westerly winds; northerly winds; river discharge) and fishing variables (fishing effort) in *Diplodus sagus* catch rates accounting for regional analyses (northwestern coast; southwestern coast and Algarve – southern coast). Different time series models for data fitting (multi-model approach) were used. The models were lagged, according to species fishing recruitment age based on the hypothesis that fisheries catches depend on larvae recruitment and survivorship. *D. sargus* catch rates across areas were unrelated to fishing effort but correlated to environmental variables, with seasonal events explaining much of the variability in trends. On the northwestern coast, the catch rates were mainly set by sea surface temperature (SST) and wind magnitude; however, southwestern coast catch rates were set by NAO winter. On the southern coast, only one statistical model (SST, upwelling and westerly winds) associated spring conditions with *D. sargus* catch rates. The multi-model approach revealed autumn, winter and spring seasonal effects to be related with northwestern, southwestern and Algarve coastal catch rates, respectively, indicating a possible coastal longitudinal gradient related with given periods of spawning and larval availability. The metadata analysis yielded different results from the regional analyses. In summary, marine resource management should take regional environment characteristics and variability into account when determining sustainable catch rates in given areas for species with high habitat site fidelity.

**Keywords:** Fish-environment relationships; Portuguese coast; Regional analyses; Min/max autocorrelation factor analysis; Dynamic factor analyses; Generalize least squares

## 3.1 Introduction

Community structure varies in space and time in response to a complex array of physical and biological factors. The extent to which these different factors influence ecosystem function is one of the fundamental issues of ecosystem ecology and coastal fisheries. Environmental change such as sea temperature, upwelling, wind and currents can affect productivity at both regional- and large-scale areas (Planque and Frédou, 1999; Baptista et al., 2014; Baptista and Leitão, 2014). In recent decades, major attention has been given to climate drivers that affect the life cycle of small fish such as pelagic species (Santos et al., 2001; Fréon et al., 2005; Lehodey et al., 2006; Ullah et al., 2012). More recently, fisheries studies have highlighted environmental effects on other commercial groups such as demersal long-lived species (Ottersen and Sundby, 1995; Planque and Frédou, 1999; Solow, 2002; Gröger and Fogarty, 2011), cephalopods (Zuur and Pierce, 2004; Ullah et al., 2012), bivalves (Baptista et al., 2014; Baptista and Leitaão, 2014) and crustaceans (Herraiz et al., 2009).

Coastal areas are some of the most productive ecosystems in the world, with a crucial role as nursery grounds for the immature phases of economically important fish such as sparids as well as invertebrate species. Seabreams (Sparidae), namely the genus *Diplodus*, are found in coastal waters worldwide and sustain important recreational and commercial fisheries (Fischer et al., 1987). *Diplodus sargus* (Linnaeus 1758) is an abundant species, found on the continental shelf and in the lagoons and estuaries of the Portuguese coast (Gonçalves, 2000; Gomes et al., 2001; Sousa et al., 2005; Ribeiro et al., 2006). This species occurs across a wide variety of marine habitats ranging from rocky to sand bottoms and at depths ranging from 0 to 50 m, although they tend to be more common in coastal areas less than 150 m deep (Abecasis et al., 2008) and are mostly fished at depths of approximately 30 m (Erzini et al., 1996).

Both *D. sargus* and *Diplodus vulgaris* contribute greatly to the total fish abundance (in number) in southern European rocky infralittoral zones, representing up to 56 % of total abundance in the northwestern Mediterranean Sea (García-Rubíes, 1997). These two species account for 40 % of overall resident artificial reef fish assemblages and 20 % of the overall artificial reef fish assemblage at 20 m depth (Leitaão et al., 2008) along the Algarve coast of southern Portugal. *D. sargus* has pelagic larval stages; young recruits concentrate mainly in near shore coastal areas on rocky bottoms and coastal lagoons (Monteiro et al., 1990). Subadult and adults move toward deeper waters in response to ontogenic changes in habitat choice (García-Rubíes and Macpherson, 1995; Harmelin-Vivien et al., 1995). *D. sargus* has high site fidelity and is categorized as a resident rocky areas species (Santos et al., 2005; Leitão et al., 2007, 2009).

The Portuguese coastal fishing fleet is divided into inshore (local or artisanal), coastal and long-distance fleets along the coast (Figure 3.1). The local/artisanal fishery is of considerable socioeconomic importance for the local population which has increased along the coast over the last decades. The fishing effort of the multi-gear fleet on many fisheries resources is very intense, involving large numbers of fishermen. In Portugal, *D. sargus* is mainly caught by the multi-gear (artisanal) fishing sector. National data bases (Direção-Geral de Recursos Naturais, Segurança e Serviços Marítimos; DGRM) between 1989 and 2009 reveal that multi-gear fishing contributed to 57 % of the overall species landings on average (73 %of fishing effort, units: fishing days.boats), followed by trawling (19 %) and seine netting (24 %). In certain areas such as the southern-southwestern coast of Portugal, hook and line multi-gear fleet fisheries can directly target Sparidae species (Erzini et al., 2001). In southern Algarve coast, multi-gear fishing account for 78 % of the total landings while in northwestern and southwester 66 and 43 % (Source: DGRM data between 1989 and 2009). *D. sargus* is a highly prized species that reaches high prices at auction (7, 5 and 10 € kg$^{-1}$ average, minimum and maximum auction price between 1989 and 2009: Source DGRM). In the multi-gear sector, this species is not normally discarded, therefore landings can be assumed as directly proportional to catches based on this sector while in other sectors (seine and trawl) the species is accidently caught, although in low percentages (Fernandes et al., 2007; Gonçalves et al., 2008).

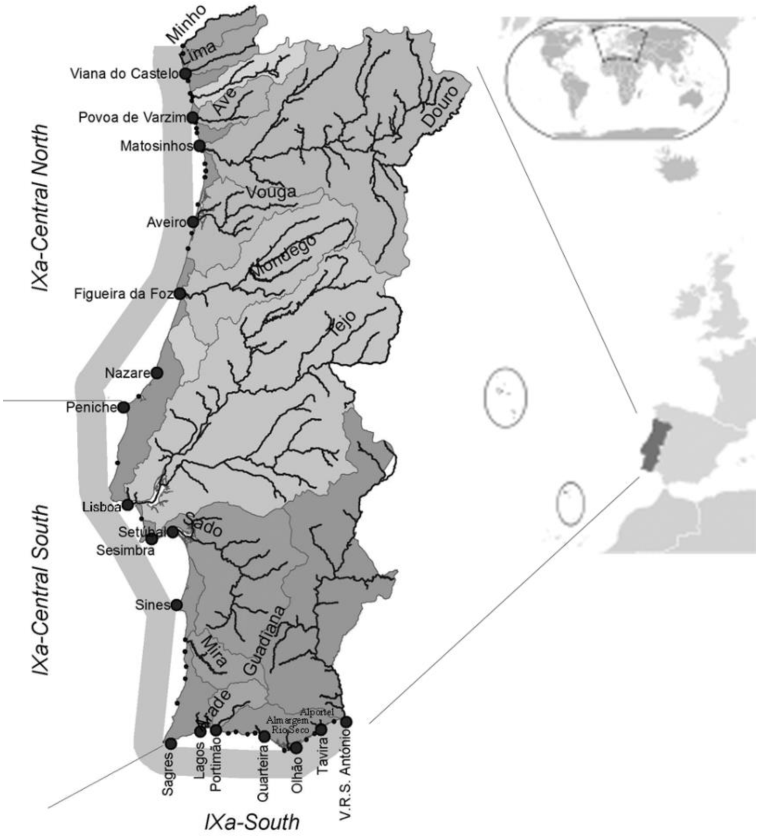

**Figure 3.1** Location of the rivers and ports of Portuguese coastal study areas: northwestern (IXaCN) southwestern (IXaCS) and southern (IXaS-Algarve).

The theory of ‘Ocean triads’ (processes of enrichment, concentration and transport/retention of larvae) has been a source of important discussions on environmental effects on fish recruitment (Santos et al., 2007). However, understanding the processes that influence recruitment is a fundamental objective of fisheries biology. Recruitment of small pelagic and most marine fish (Cushing, 1996) is highly variable with no clear links with parental stock abundance levels (spawning stock biomass). This is because of high and variable mortality rates during the early life stages (among other factors) that are thought to be strongly affected by environmental processes (Santos et al., 2012). Environmental controls of recruitment have been an important component of fisheries research for at least a century (Helland-Hansen and Nansen, 1909; Hjort, 1914) resulting in the development of many hypotheses that are still actively discussed in the environment-fisheries literature (Lasker, 1975; Cury and Roy, 1989).

Evidence that environmental factors (hydrological and oceanographic) cause long-term, large-scale variability in fish stocks is growing although it is mistaken to assume that the effects of fishing are less important. These associations have not yet been clearly demonstrated or integrated into sustainable coastal fisheries management (Fréon et al., 2005). Hypotheses underlying sets of representative models can be used to make inferences about dominant factors controlling fisheries (Loots et al., 2011). A multi-inference model theoretic approach can be used to determine environment-fisheries links and evaluate model ‘‘predictive’’ capabilities, rather than data fitting performances (Johnson and Omland, 2004). Studies on climate effects on benthopelagic species such as sparids are scarce. This study seeks to determine the potential role of climate factors and artisanal fisheries pressure on *D. sargus* catch rates, across different regions of the coast (different fishing and oceanographic regimes), using a multi-model approach, that can provide important information for fisheries managers.

## 3.2 Materials and methods

### 3.2.1 Study area

The effect of climatic variability and fishing on *D. sargus* catch rates was evaluated across three biogeographic areas situated off the Portuguese coast, namely the northwestern, southwestern and southern Atlantic coast of Portugal (Figure 3.1). Each of these areas has distinct oceanographic regimes (Cunha 2001; Bettencourt et al. 2004). The three areas match the International Council for the Exploration of the Sea (ICES): IXa subdivision area for Portugal and are hereafter designated as northwestern coast (IXaCN), southwestern coast (IXaCS) and Algarve southern coast (IXaS-Algarve).

### 3.2.2 Acquisition of environmental and fisheries data

Landing and fishing effort data for the artisanal fleet (responsible for most landings across the regions) for the period 1989–2009 where obtained from the Direção-Geral de Recursos Naturais, Segurança e Serviços Marítimos (DGRM). The database includes information on fisheries practices such as monthly effort (number of fishing days.boats and/or fishing events) and monthly landings per boat per month. Fishing data were then amalgamated into annual periods. Landings per unit effort (LPUE or catch rates) were used as a proxy for fish biomass production (abundance index proxy). LPUE (response variable) were estimated by dividing total annual landings by fishing effort (FE; fishing days.boats) (LPUE units: kg per fishing days.boats). The aggregations for spawning for this species in late winter/beginning of spring are well known by the recreational fishermen (anglers) in same locals of IXaCS and IXaS-Algarve coast. In these areas, recreational fisheries catches for the species can reach meaningful values regarding commercial fisheries: Forty-four percentage of the total catches by number and 48 % by mass (Veiga et al., 2010). However, this study is on commercial fisheries only and does not include the recreational fisheries data which is unreported (Leitão et al., 2014a).

The annual and seasonal mean sea surface temperature (SST; °C), annual and seasonal upwelling index (UPW), and yearly and seasonal u-wind and v-wind components were used as oceanographic explanatory variables. Geostrophic wind in satellite data is broken into its two horizontal components: The ‘‘u’’ component (UWIND; m $s^{-1}$) represents the east–west wind components while the ‘‘v’’ component (VWIND; m $s^{-1}$) represents north–south winds. SST data were obtained from summary imagery data obtained from Modis-Aqua 4 km satellite available on the NASA Ocean Color Giovanni website, (http://gdata1.sci.gsfc.nasa.gov). The upwelling index was obtained from Pacific Fisheries and Environmental Laboratory website (www.pfeg.noaa.gov). Wind components (u- and v-) were obtained from NASA Jet Propulsion Laboratory California Institute of Technology – Physical Oceanography Distributed Active Archive Centre (PODAAC; http://podaac.jpl.nasa.gov/dataset/CCMP_MEASURES_ATLAS_L4_OW_L3_5A_MONTHLY_WIND_VECTORS_FLK?ids=&values=) (Atlas et al., 2011). Wind magnitude (WMAG; m $s^{-1}$) [WMAG: $SQRT(u^2 + v^2)$] was modelled using u- and v-wind components. Coastal oceanographic data were used to derive a range of depths from Mean High Water Line to 200 m (Figure 3.1), in order to compensate a lack of some near shore satellite data (cloud effect). Therefore, SST, UPW, WMAG, UWIND and VWIND data are averaged means for the geographical area.

Yearly river discharge data (RD; $dm^3$) from January to December was used to test the effect of hydrology on catch rates. RD comprised cumulative monthly contribution (discharges volumes in cubic decametres, $dam^3$), of the principal Portuguese rivers or Basins (Figure 3.1), including (1) northwestern coast: Cávado, Lima, Douro, Vouga, Mondego, (2) southwestern coast: Tejo, Sado, Mira and (3) Algarve southern coast: Guadiana river and minor inputs from three smaller river systems (Seco, Alportel and Almargem). The monthly hydroclimatic date series of freshwater discharged into coastal areas were downloaded from Agência Nacional do Ambiente (APA online data base, SNIRH: http://snirh.pt/). All data were collected from the same hydrological stations located nearest the shore.

The North Atlantic Oscillation [NAO and NAO winter (December-March)] indices were used as climatic explanatory variables (http://www.cgd.ucar.edu/jhurrell/nao.html, last accessed 2010; Hurrell, 1995). NAO indices are the difference between sea level atmospheric pressure located at the Azores and Iceland, respectively. These phenomena influence precipitation, temperature and wind regimes over most of the northwestern Europe (Witbaard et al., 2005).

### 3.2.3 Time series analyses

We used catch rates (LPUE) as the response variable for statistical purposes while effort and environmental variables were the explanatory variables. We assumed that fishing recruitment variability would be largely determined by survival during the larval stages. Hypotheses can be postulated that link larval fish survival (affecting recruitment into the fisheries) with environmental and fishing conditions during the larval stage. Therefore, the hypothesis applied in this study is that larvae recruitment is influenced by regional environmental and fisheries factors that affect larval mortality rate and recruitment to the fishery and consequently short-term catch rates. *D. sargus*, a long-lived species that can live for up to 25 years, commonly reaches maturity at 2-year old (Erzini et al., 1996, 2001, 2003; Morato et al., 2003). The adult stage becomes available to the fishery when individuals reach the minimum landing size of 15 cm, a proxy of the age of first maturity. Environmental variables lags of 2 years were applied for the analyses, since *D. Sargus* recruitment to fishery occurs in the 2nd year class. The analysis is based on the assumption that landings per unit effort are directly proportional to biomass (catch rate as biomass proxy) and that landings are directly proportional to catches. This is the case for *D. sargus* for multi-gear sector: Direct proportionality with catches is assumed since this species is residually discarded due to their high commercial value. Fishing effort can also affect spawning biomass (adults) and recruitment in subsequent years. To accommodate this effect, environmental data and FE (number of fishing days.boats) were manipulated using a 2-year time lag to reflect temporal change. We also included FE in the models as an explanatory variable after collinearity between catch rate and FE was tested with pair plots and was found to be absent (collinearity between catch rate and FE: IXaCN = 0.01; IXaCS = 0.64; IXaS-Algarve = 0.14; Total = 0.21).

We hypothesized that the larval survival rates would vary according to seasonal environmental marine conditions. We considered winter (January-March), spring (April-June), summer (July-September) and autumn (October-December) seasons. Finally, we assumed that *D. sargus* fisheries are affected by distinct environmental conditions on the coast; therefore, separate models were produced for each region, to each explanatory variable. Nevertheless, data were also evaluated taking into consideration all Portuguese area (ICES IXa) (metadata analyses or total area). For metadata analyses, fishing data and RD were pooled (cumulative contribution) while other environmental data (e.g., SST) was averaged across areas.

A complementary multi-model results approach was used including min/max autocorrelation factor analysis (MAFA), dynamic factor analysis (DFA) and generalized least squares (GLS) models. Since different analyses might give different results, a selection criterion was adopted to identify variables with a higher probability of explaining changes in LPUE. The best candidate variables were model-based and probability was defined according to the number of models that identified the same explanatory variable. This simple selection criterion allows classification of variables with either a high (the variable is highlighted in more than one model) or low probability of influencing catch rate.

Prior to the analyses, all data series were tested for normality (Quantile-Quantile plots – QQ-plots) and collinearity (pair plots) following Zuur et al. (2010). In the case of both yearly *D. sargus* catch rates and explanatory variables, no transformation was applied. First, we computed simple models and tested for the significance of the relationship without accounting for more than one variable. Whenever more than one variable was identified, we tested the significance of the relationship (in DFA and GLS analyses, see below), accounting for combining fisheries and environmental data series by surrogate testing. Since collinearity occurred between yearly northerly wind (VWIND) and wind magnitude (WMAG), these variables were not combined in the same models whenever they were both found to be statistically significant. Both response and explanatory variables were standardized before running the models as advised by Zuur et al. (2003a, b). The standardization method used for converting data into the same dimensional scale was normalization that consist in centring all variables around zero ($Xi = (Y\ I - \hat{Y})/\sigma y$), where $\hat{Y}$ is the sample mean, $Yi$ the value of the $i^{th}$ sample and $\sigma y$ the sample standard deviation. All statistical analyses were made using Brodgar software package that uses R version 3.0.1 (http://www.brodgar.com).

### 3.2.3.1 Min/max autocorrelation factor analysis (MAFA)

MAFA is a type of principal component analysis (PCA) for short time series that can be used to extract common behaviour trends of the original time series and for smoothing. A set of orthogonal linear combinations of the original time series (MAFs) of decreasing smoothness, measured by lag-one autocorrelation, are constructed (Solow, 1994). The MAFA axes represent autocorrelation with lag 1; the first MAFA axis represents the main trend in the data, while the others represent the other less important trends (Solow, 1994). Cross correlations between MAFA axes and explanatory variables can also be estimated, allowing significant relationships between trends and explanatory variables to be identified (Erzin, 2005; Zuur et al., 2007). The MAFA analyses that best fitted to the available data (providing the data availability for the species) considered only a single MAFA trend (autocorrelation time lag 1 year) for each region.

### 3.2.3.2 Dynamic factor analysis (DFA)

Trend analyses of the effect of environmental and fishing variables on catches rates of *D. sargus* were carried out for each region using dynamic factor analysis (DFA). DFA is a multivariate technique used for non-stationary time series analysis to estimate underlying common patterns, evaluates interactions between response variables (LPUE) and determines the effects of explanatory variables (environmental and fisheries variables) on response variables (Zuur et al., 2003a, 2007). A separate DFA univariate time series model/analysis was used for each region in order to account for the different environmental conditions and spatial independence (Ullah et al., 2012; Baptista et al., 2014; Baptista and Leitão, 2014; Leitão et al., 2014b). Models were fitted with a diagonal covariance matrix, and the Akaike Information Criterion (AIC) was used to compare models. The t values resulting from estimation of regression parameters were used to indicate either a positive or negative relationship between explanatory variables and response variable (t values with an absolute value greater than 3 indicate a strong relationship among variables).

### 3.2.3.3 Generalized least square (GLS)

Generalized least squares (GLS) is an extended linear mixed-effect modelling method where errors are can be correlated and/or have unequal variance (Pinheiro and Bates, 2000; Lloret et al., 2001). Several GLS models were applied without autocorrelation and with an autoregressive process imposed on the error components allowing errors to have unequal variance (Zuur et al., 2007). Thus, errors were specified to follow an autoregressive process of degree 1 that was determined using the partial autocorrelation function and the goodness of fit of an auto-regressive moving average (ARMA) model. This approach can be used for most regular spaced datasets (Zuur et al., 2007), assuming that autocorrelation is highest between consecutive years. Therefore, the GLS models with and without different autocorrelation structures were compared using the lowest AIC as decision criterion; only the best GLS models are presented. An important criterion into consider is whether the decrease in AIC is large enough to proceed with discarding the simple linear regression model in favour of a more complex GLS model. If the difference in AIC values of two models is smaller than 2, general statistical consensus dictates using the simpler linear model (Zuur et al., 2007). A significance level of $p < 0.05$ was used for the explanatory variables. The type of the relationship in GLS between the explanatory and response variables is evaluated by the sign (? or -) of the slope.

## 3.3 Results

The SST revealed similar yearly trend variations among study regions (northwestern, southwestern and southern coast of Portugal), peaking in 1989-1990, 1995, 1997 and 2006 (Figure 3.2a). The SST was colder in the northwestern and southwestern regions than in the southern region (Table 3.1). The NAO index declined markedly until 1996 (Figure 3.2b) and then varied although values below the mean became more frequent.

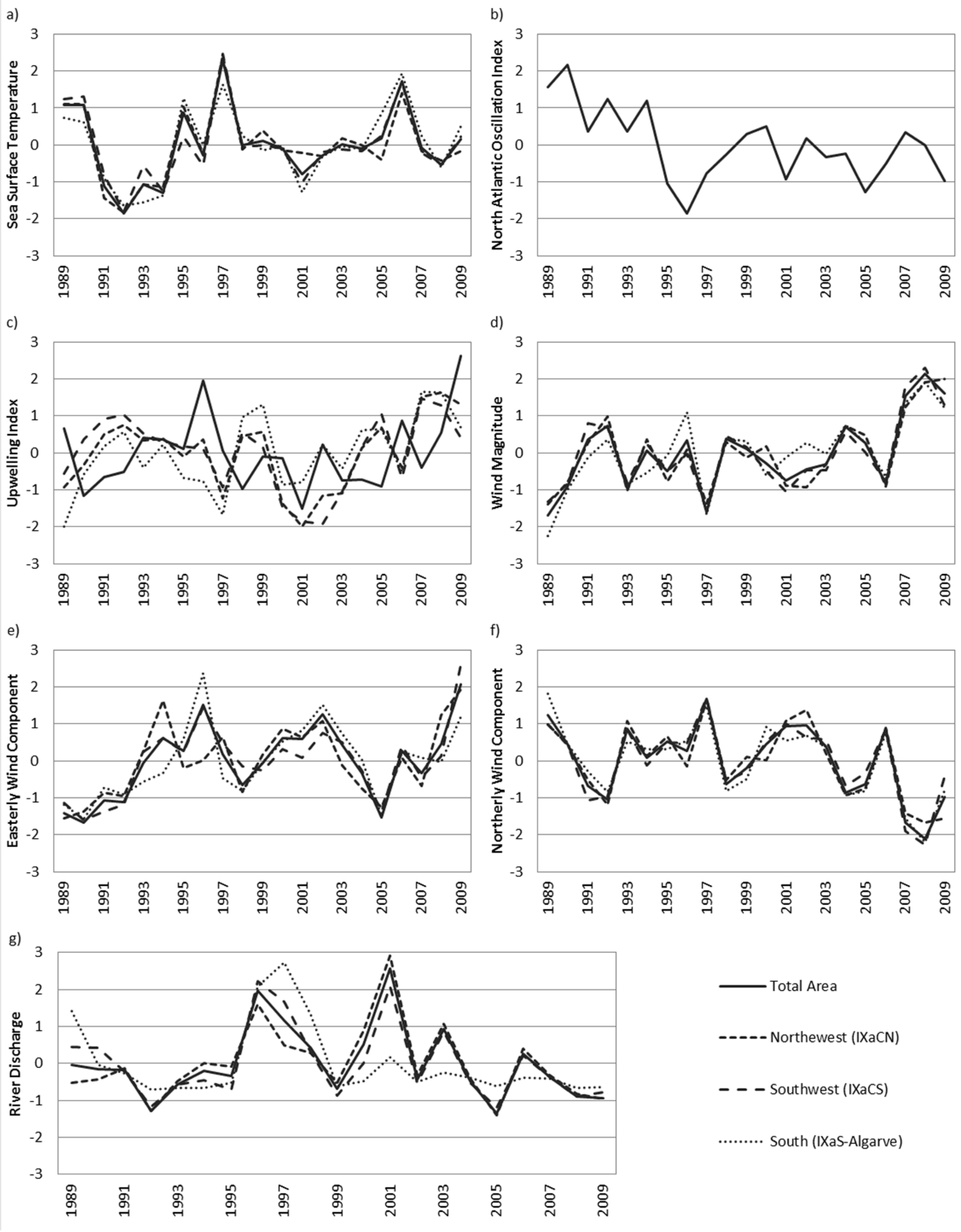

**Figure 3.2** Standardized time series of the yearly environmental variables, during the period 1987–2007 (for time series models the variables were lagged two years, therefore the data match the fisheries period 1989–2009) in the northwestern (IXaCN), southwestern (IXaCS) and southern (IXaS-Algarve) regions, and total area (IXa) of Portugal: sea surface temperature (a), North Atlantic Oscillation index (b), upwelling index (c), wind magnitude (d), easterly wind component (e), northerly wind component (f) and river discharge (g).

**Table 3.1** Means and standard deviation of annual and seasonal (winter, spring, summer and autumn) environmental variables, and total river discharge values, during the period 1987-2007 (for time series models the variables were lagged two years, therefore the data match the fisheries period 1989–2009) in the northwestern (IXaCN), southwestern (IXaCS) and southern (IXaS-Algarve) regions, and total area (IXa) of Portugal.

| **Variables** | **Total Area (Ixa)** | | **Northwest (IXaCN)** | | **Southwest (IXaCS)** | | **South (IXaS-Algarve)** | |
|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| **SST** | | | | | | | | |
| **Annual** | 17.20 | 0.37 | 16.02 | 0.46 | 17.04 | 0.38 | 18.51 | 0.33 |
| **Winter** | 15.10 | 0.55 | 14.11 | 0.66 | 15.05 | 0.61 | 16.18 | 0.45 |
| **Spring** | 16.88 | 0.57 | 15.88 | 0.71 | 16.68 | 0.61 | 17.98 | 0.48 |
| **Summer** | 19.60 | 0.61 | 18.53 | 0.64 | 19.15 | 0.68 | 21.04 | 0.70 |
| **Autumn** | 17.25 | 0.80 | 15.86 | 0.94 | 17.06 | 0.83 | 18.82 | 0.75 |
| **NAO** | | | | | | | | |
| **Annual** | 0.30 | 0.62 | 0.30 | 0.62 | 0.30 | 0.62 | 0.30 | 0.62 |
| **Winter** | 1.01 | 1.70 | 1.01 | 1.70 | 1.01 | 1.70 | 1.01 | 1.70 |
| **UPW** | | | | | | | | |
| **Annual** | 4.17 | 8.74 | -4.66 | 17.80 | 13.20 | 9.80 | -0.48 | 7.72 |
| **Winter** | -16.23 | 21.74 | -25.70 | 40.47 | -4.24 | 22.65 | -13.62 | 25.58 |
| **Spring** | 18.43 | 10.72 | 26.39 | 15.69 | 29.91 | 17.12 | 12.02 | 9.87 |
| **Summer** | 35.84 | 9.47 | 43.01 | 12.38 | 49.46 | 14.26 | 8.69 | 7.12 |
| **Autumn** | -28.14 | 25.69 | -48.60 | 53.20 | -21.86 | 30.62 | -3.29 | 28.14 |
| **WMAG** | | | | | | | | |
| **Annual** | 3.03 | 0.52 | 2.87 | 0.60 | 3.71 | 0.56 | 2.45 | 0.46 |
| **Winter** | 2.45 | 0.64 | 1.93 | 0.93 | 3.11 | 0.88 | 2.48 | 0.54 |
| **Spring** | 3.93 | 0.71 | 3.83 | 0.80 | 5.02 | 0.88 | 3.56 | 0.65 |
| **Summer** | 4.60 | 0.53 | 4.46 | 0.70 | 5.34 | 0.65 | 3.75 | 0.58 |
| **Autumn** | 2.48 | 0.97 | 2.69 | 1.03 | 2.78 | 1.29 | 2.25 | 0.82 |
| **UWIND** | | | | | | | | |
| **Annual** | 1.14 | 0.43 | 1.02 | 0.43 | 1.28 | 0.46 | 0.94 | 0.54 |
| **Winter** | -0.05 | 1.35 | 0.69 | 1.14 | 0.27 | 1.35 | -0.83 | 1.74 |
| **Spring** | 2.07 | 0.57 | 1.72 | 0.65 | 2.00 | 0.57 | 2.19 | 0.66 |
| **Summer** | 1.70 | 0.33 | 1.35 | 0.36 | 1.81 | 0.29 | 2.02 | 0.58 |
| **Autumn** | 0.19 | 1.32 | 0.18 | 1.29 | 0.29 | 1.43 | 0.20 | 1.49 |
| **VWIND** | | | | | | | | |
| **Annual** | -2.61 | 0.55 | -2.52 | 0.64 | -3.21 | 0.60 | -2.06 | 0.46 |
| **Winter** | -2.14 | 0.95 | -1.25 | 1.27 | -2.91 | 1.07 | -1.90 | 0.74 |
| **Spring** | -3.63 | 0.88 | -3.55 | 1.10 | -4.45 | 1.04 | -2.64 | 0.68 |
| **Summer** | -4.23 | 0.58 | -4.41 | 0.76 | -5.05 | 0.71 | -3.21 | 0.55 |
| **Autumn** | -1.77 | 1.62 | -1.87 | 2.17 | -2.13 | 1.67 | -1.53 | 1.23 |
| **RD** | | | | | | | | |
| **Annual** | 42461.43 | 20461.42 | 27050.41 | 13363.74 | 6999.66 | 6348.43 | 1134.55 | 2417.12 |
| **Winter** | 17782.92 | 16792.25 | 10799.63 | 11327.00 | 1772.88 | 4797.06 | 339.79 | 1592.59 |
| **Spring** | 7631.91 | 3428.82 | 5443.01 | 2945.85 | 1092.84 | 633.51 | 140.97 | 135.77 |
| **Summer** | 3760.61 | 1127.49 | 2775.88 | 760.97 | 777.55 | 485.12 | 74.64 | 58.58 |
| **Autumn** | 13285.99 | 8973.27 | 6480.82 | 5486.53 | 2059.98 | 3039.32 | 317.86 | 1363.22 |

The UPW index revealed differing trends among study regions and marked oscillations over time (Figure 3.2c). The northwestern and southwestern regions had higher UPW index values in 1992, 1999-2000, 2005 and 2007-2008. In the southern region, UPW index values peaked in 1996 and 2009. Along the Portuguese coast, UPW was predominant in the spring and summer, particularly in the northwest region (Table 3.1).

The WMAG showed a similar pattern among study regions, oscillating around the mean value and peaking in 2008 (Figure 3.2d). The WMAG was strongest on the southwestern coast (Table 3.1). Seasonal WMAG varied considerably across the study areas with increasingly weaker seasonal oscillations in the southern. WMAG tended to be stronger in the spring and summer. The easterly wind (UWIND) component showed an increasing trend oscillating around the mean (Figure 3.2e). Values greater than the mean of UWIND (positive anomalies) were found in 1993-1997, 1998-2004 and 2006-2009. The northerly wind component (VWIND) trend oscillated around the mean over time, with values falling below the mean from 2004 reached the lowest values recorded for all-time series after 2006 (Figure 3.2f).

Northwestern and southwestern RD presented similar trends, oscillating around the mean with positive peaks in 1996 and 2001 (Figure 3.2g). RD peaked in 1989 and 1997 in the southern region. Maximum RD volumes occurred during the winter and lowest RD volumes in the summer, independent of region (Table 3.1). RD was far higher in the northwestern region regardless of season, followed by the southwestern and the southern, respectively. RD values were significantly lower in the southern region compared to the other regions.

Standardized FE for *D. sargus* had similar pattern among different study regions (Figure 3.3). FE remained at a steady state until 2004 and then increase markedly until 2009.

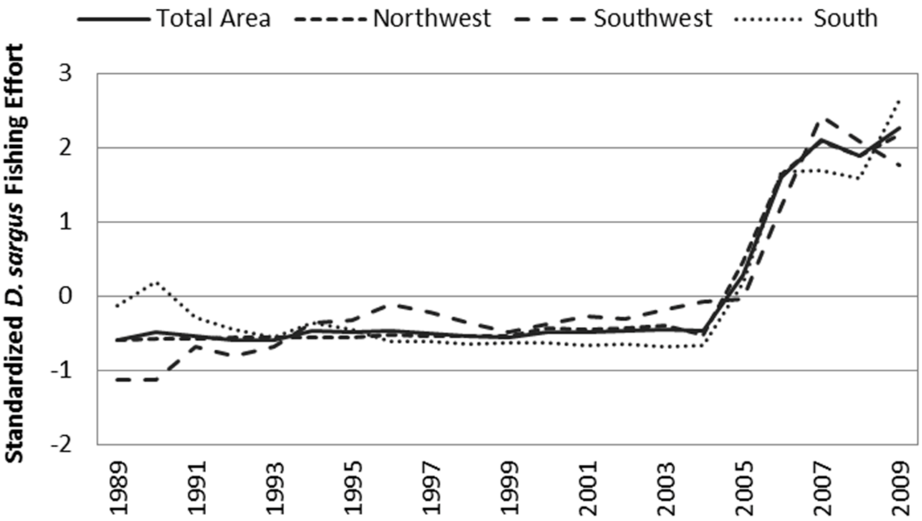

**Figure 3.3** Standardized yearly fishing effort (number of fishing days and boats) for *Diplodus sargus* during the period 1989-2009 in the northwestern (IXaCN), southwestern (IXaCS) and southern (IXaS-Algarve) regions, and total area (IXa) of Portugal.

Catch rate trends of *D. sargus* varied among the three regions (Figure 3.4). For total area, the LPUE trend increased rapidly, with peaks in 1994 and 1998, followed by a drastic decrease in 1999 and then a gentle increase (Figure 3.4). In the northwestern region, the catch rate trend increased until 1998, then decreased and remained close to the mean value (Figure 3.4). For the southwestern region, the catch rate showed an increasing trend with values increasing from below the average after 2002 (Figure 3.4). In the southern region, the catch rate was oscillatory. Standardized oscillation values varied between -1 and 1, indicating a low oscillation range and a steady state across time, except 1995, when the LPUE value peaked (Figure 3.4).

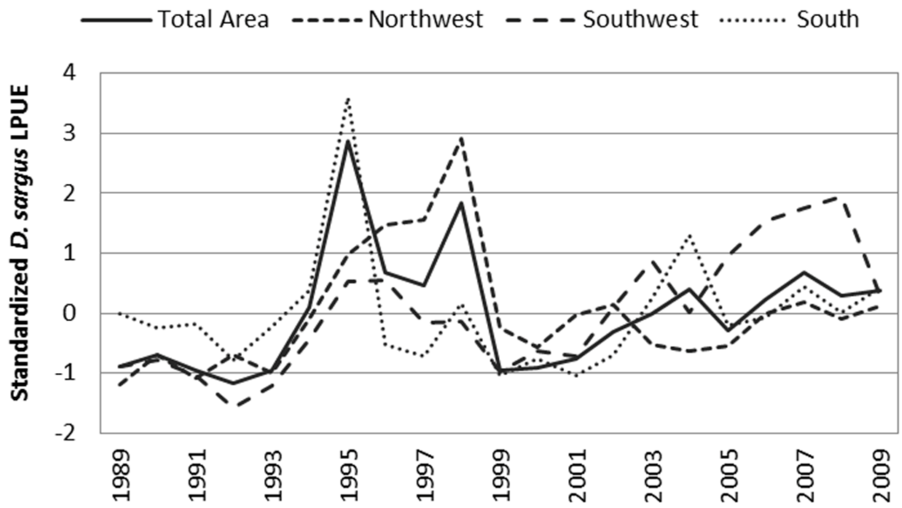

**Figure 3.4** Standardized *Diplodus sargus* LPUE between 1989 and 2009 in the northwestern (IXaCN), southwestern (IXaCS) and southern (IXaS-Algarve) regions, and total area (IXa) of Portugal.

Explanatory variables selected as significant in more than one model have a high probability of influencing *D. sargus* recruitment (Table 3.2). Summarized results of explanatory variables related with *D. sargus* catch rates for each region and statistical approach (MAFA, DFA and GLS) are given in Table 3.2 (and Appendix 3.A).

**Table 3.2** Summary of results of relationship between Diplodus sargus LPUE and explanatory (fishing and environmental) variables for min/max autocorrelation factor analysis (MAFA), dynamic factor analysis (DFA) and generalized least square (GLS) methods in the northwestern (IXaCN), southwestern (IXaCS) and southern (IXaS-Algarve) regions, and total area (IXa) of Portugal.

| | **Explanatory variables** | **MAFA** | **DFA** | **GLS** | **Probability** |
|---|---|---|---|---|---|
| **Total Area (IXa)** | SST Annual | n.s. | **sig. (-)** | n.s. | Low |
| | SST Summer | **sig. (-)** | **sig. (-)** | **sig. (-)** | High |
| | UPW Annual | n.s. | **sig. (+)** | n.s. | Low |
| | UPW Autumn | n.s. | **sig. (+)** | n.s. | Low |
| | WMAG Annual | n.s. | **sig. (+)** | n.s. | Low |
| | WMAG Summer | n.s. | **sig. (+)** | n.s. | Low |
| | UWIND Annual | **sig. (+)** | **sig. (+)** | **sig. (+)** | High |
| | UWIND Spring | n.s. | **sig. (+)** | n.s. | Low |
| | UWIND Summer | n.s. | **sig. (+)** | n.s. | Low |
| | UWIND Autumn | n.s. | **sig. (+)** | n.s. | Low |
| | VWIND Summer | n.s. | **sig. (-)** | **sig. (-)** | High |
| | RIVER Summer | n.s. | **sig. (-)** | n.s. | Low |
| **Northwestern (IXaCN)** | SST Autumn | n.s. | **sig. (-)** | **sig. (-)** | High |
| | WMAG Spring | n.s. | n.s. | **sig. (-)** | Low |
| | WMAG Autumn | n.s. | **sig. (+)** | **sig. (+)** | High |
| **Southwestern (IXaCS)** | EFFORT | **sig. (+)** | n.s. | n.s. | Low |
| | SST Winter | n.s. | **sig. (-)** | n.s. | Low |
| | NAO Annual | n.s. | n.s. | **sig. (-)** | Low |
| | NAO Winter | n.s. | **sig. (-)** | **sig. (-)** | High |
| | UWIND Annual | n.s. | **sig. (+)** | n.s. | Low |
| | UWIND Spring | n.s. | n.s. | **sig. (+)** | Low |
| | UWIND Summer | **sig. (+)** | n.s. | n.s. | Low |
| | RIVER Summer | n.s. | n.s. | **sig. (+)** | Low |
| **Southern (IXaS-Algarve)** | SST Annual | n.s. | **sig. (-)** | n.s. | Low |
| | SST Spring | n.s. | **sig. (-)** | n.s. | Low |
| | UPW Spring | n.s. | **sig. (+)** | n.s. | Low |
| | UWIND Spring | n.s. | **sig. (+)** | n.s. | Low |

The MAFA model results showed no significant results in the northwestern region. DFA and GLS results revealed a negative association between catch rate and autumn SST and a positive association with autumn WMAG. The spring WMAG was also negatively associated with catch rate in the GLS model. For this reason, the autumn SST (negative) and autumn WMAG (positive) were the environmental variables with a high probability of affecting *D. sargus* catch rate.

For the southwestern coast of Portugal, the MAFA analyses showed that yearly FE and summer UWIND were positively related with catch rate. The winter SST, NAO winter index and yearly UWIND were related with catch rate in the DFA model; the former two variables had a negative relationship with catch rate while the latter was positively related with catch rate. Yearly and winter NAO indexes were negatively related with catch rate in GLS results, while spring UW and summer RD shared a positive relationship with catch rate. The NAO winter index was the only environmental variable with a high probability of affecting *D. sargus* catch rate.

Only DFA results identified variables associated with LPUE in the southern region. This model revealed a negative relationship between yearly and spring SST and LPUE while spring UPW and UWIND had a positive relationship. Thus, all tested significant environmental variables had a low probability of affecting *D. sargus* catch rate in the southern regions.

For metadata analyses (Total IXa coast), the MAFA results showed that the summer SST was negatively related to *D. sargus* LPUE but positively related with the annual UWIND component. The DFA model had a negative relationship for yearly and summer SST, summer VWIND wind component and summer RD with LPUE while positive relationship for yearly and autumn UPW, yearly and summer WMAG wind magnitude and yearly, spring, summer and autumn UWIND. In GLS, summer VWIND was negatively related with LPUE and the yearly UWIND positively related with LPUE. Overall, the environmental variables with a high probability of influencing on *D. sargus* LPUE were summer SST (positive), yearly UWIND (negative) and summer VWIND (positive).

## 3.4 Discussion

Several factors affect survival of fish eggs and larvae, such as offshore winds that induce upwelling phenomena that transport eggs and larvae away from areas where they have a better chance of survival (e.g., Guisande et al., 2001; Landaeta and Castro. 2002), predation (Bailey and Houde 1989), water temperatures outside the survival range (Rijnsdorp et al. 1995) and shortage of food (Cushing 1972; Houde 1987). Very few studies have addressed the role of fishing and environment effects on sparids, namely *D. sargus* fisheries (catch rates as a proxy of biomass index). FE remained in a relatively steady state until it began to increase in 2004, although this did not match an increase in catch rate. FE did not appear to be related to catch rate trends in any of the study areas. In most areas, except the Sagres area in the southwestern region which has a hook and line fishery (Erzini et al., 1996, 1997, 1998, 2001, 2003), the fishery is not exclusively targeted on *D. sargus*. Given that *D. sargus* inhabits rocky coastal areas, this habitat preference might also reduce vulnerability to certain types of artisanal gears, such as trammel and gill nets (which not set in rocky areas due to the higher risk of gear loss and damage), that make up most of the artisanal fleet landings. However, results showed the effect of climate on catch rates varied between regions and that seasonal events were often caused short-term variation in catch rates.

### 3.4.1 Northwestern coast (IXaCN)

*D. sargus* spawning occurs within an optimal range of 15-17 °C, with the onset and duration of the spawning season being influenced by sea water temperatures. As latitude decreases in the northern and southern hemispheres, the spawning season of *D. sargus* populations starts earlier and is more prolonged (Morato et al., 2003 and references therein).

According to Morato et al. (2003), the optimal range of SST in the northwestern, southwestern and Algarve occurred in autumn, winter and spring (Table 3.1). Thus, peaks in *D. sargus* spawning events differ across the regions, a phenomenon already recorded for other commercial species along the Portuguese coast (Gonçalves, 2000; Stratoudakis et al., 2007). There are few studies on species spawning in northwestern Portugal. However, changes in SST in the northwestern can affect gametogenic activity by creating favourable conditions for early spawning in the autumn, compared to the southwestern and southern. The spawning season of *D. vulgaris*, a similar species that breeds from to autumn to winter, was found to vary inter-annually (Gonçalves, 2000; Mouine et al., 2012) as a function of SST and the number of hours of direct sunlight, since the onset and duration of the spawning season is negatively correlated with these environmental parameters (Gonçalves, 2000).

SST can affect larval survival since higher temperatures enhance larval growth rates and reduce the time interval between spawning and benthic settlement phases (Morato et al., 2003; Mouine et al., 2007; Vinagre et al., 2009). Since the eggs of *D. sargus* are spawned on the coast, larvae must be transported toward estuarine nurseries and shallow rocky coastal waters where *D. sargus* normally occurs (Harmelin-Vivien et al., 1995; Abecasis et al., 2009; Vinagre et al., 2009). This phase between spawning and successful arrival in the nursery areas is crucial for recruitment because high mortality rates can occur (Houde, 1987). Thus, regional seasonal SST variations can affect recruitment into the fishery in different ways such as the timing of spawning/reproduction and larval availability. We found that autumn SST was negatively related with *D. sargus* catch rates with a 2-year time lag (the age fish recruit into the fishery as adults). In coastal areas the decrease of SST was related with UPW events (Santos et al., 2001) that are usually weak in autumn compared to other seasons, where UPW events bringing rich nutrient waters are essentially required for larvae feeding. Although upwelling is more frequent between March and September, winds that favour this phenomenon are a recurrent feature on the Portuguese coast that can also occur in winter (Huthnance et al., 2002). Strong upwelling events, caused by north–south alongshore winds, can lead to offshore Ekman transport of surface water that can transport eggs and larvae away from the coastal nurseries, resulting in high mortality rates (Santos et al., 2001; Borges et al., 2003). This effect has not observed, providing the results found between SST and *D. sargus* catch rate in autumn when moderate upwelling conditions prevail.

The WMAG was positively related with species catch rates in autumn in northwestern coast. Wind strength is low during both the winter and autumn compared to the spring and summer seasons (Table 3.1). However, increase in wind strength and direction (south–north predominant winds in this period), strongly affects coastal drift currents (Moita, 1986; Melo, 1989; Vila-Concejo et al., 2003) which are essential for food supply (Fernández et al., 1993; Santos et al., 2012) and larval transport and retention (Jager, 2001; Vinagre et al., 2009), factors that influence larval settlement and growth. Wind strength also affects dispersal of river plumes, an important factor that influences the destination of larvae in rich estuarine waters (Tanaka, 1985; Vinagre et al., 2007) as well as their retention in sheltered coastal areas (Borges et al., 2007). In the northwestern coast, drift currents (indirect wind effect) tend to run parallel to the shore to depths of up to 40 m (Martinho, 2006). Thus, when the autumn spawning season takes place (Gonçalves, 2000; Mouine et al., 2012) an increase of WMAG can benefit *D. sargus* recruitment. Eggs are spawned on the coast and larvae undergo a complex transport process toward estuarine nurseries and rocky coastal areas that are crucial for successful recruitment (Houde, 1987; Borges et al., 2007; Vinagre et al., 2009). In summary, upwelling has two major effects on fish recruitment: One is to trigger a productivity boom which is good for the larvae survivorship and the second is to transport the larvae away from the shore which could be negative to survival rates. The timing of each upwelling and spawning event is crucial for the balance of the effects.

### 3.4.2 Southwestern coast (IXaCS)

Reproduction of *D. sargus* occurs mainly in winter and spring on the southwestern coast (Erzini et al., 2001). These periods were identified in single model analyses as being seasonally associated with catch rates. However, the multi-model approach only indicated NAO winter being strongly associated with catch rate. However, it is known that SST is highly correlated with NAO (Witbaard et al., 2005). The surface waters along the Portuguese shore are dominated by the Canary current, which brings a regular supply of cold water from the north (Bischof et al., 2003). In years, when the NAO is positive, the Canary current persists throughout all seasons. When the winter NAO is negative and strong, south and southwest winds predominate and the Canary current may be temporarily replaced by a poleward flow (Frouin et al., 1990) affecting temporal patterns of fish variation observed in Portuguese coast (Henriques et al., 2007). It is important to emphasize that the NAO index operates indirectly and at a broader spatial scale than the other environmental variables considered in this study. Environmental factors affected by NAO such as SST, wind velocity and wind strength, precipitation, water circulation and stratification patterns are expected to directly influence recruitment and growth (Witbaard et al., 2005), metabolic rates (Ottersen et al., 2001) and food availability (Carroll et al., 2009). During the positive NAO phase north winds predominate (Borges et al., 2003; Lehodey et al., 2006), causing cold dry weather in the Mediterranean regions, while the negative phase is characterized by warmer temperatures and increased precipitation (Lehodey et al., 2006). For *D. sargus* the NAO winter (spawning season; Erzini et al., 2001) indexes were negatively related to LPUE trends, i.e., years with a predominant NAO winter negative phase, warmer temperatures and wet conditions are favourable to species recruitment. Differences in the sensitivity of different species and populations to NAO winter are related to species biology. Ecological responses to NAO comprise changes in timing of reproduction, population dynamics, abundance, distribution and interspecific relationships such competition and predator–prey interactions (Ottersen et al., 2001; Baptista et al., 2014). Although the NAO exerts an effect at a higher spatial scale, it only influences the recruitment and catch rate of *D. sagus* in southwestern coast. These finding shows that local effects can be driven by large-scale effects and that catch rate variability depends on a combined set of local/regional phenomena.

### 3.4.3 Southern coast, Algarve (IXaS-Algarve)

The multi-model approach did not identify any single particular variable as being more probable to affect catch rates. Compared to other regions, the eastern coast of the Algarve has the lowest level of rocky habitat availability. Sandy bottom habitats comprise a large part of the fishing grounds, especially in leeward region. For this reason, the deployment of artificial reefs has been considered essential to provide suitable habitats for *D. sargus* assemblages (Leitão et al., 2009). Moreover, southern coastal lagoons and estuaries systems have also been identified as important larvae recruitment areas (Monteiro et al., 1990; Veiga et al., 2006). *D. sargus* larval abundance (in final larval stage development) and settlement density occur preferentially in shallow rocky areas and lagoons where *D. sargus* is considered a resident species due to high site fidelity (Harmelin-Vivien et al., 1995; Macpherson, 1998; Vigliola and Harmelin-Vivien, 2001; Abecasis et al., 2009; Leitão et al., 2009; Vinagre et al. 2009). Studies showing strong habitat selective preferences by *Diplodus* spp. (Ross, 1986) indicated that fish assemblage food segregation was the most important resource partitioned by species rather than habitat, space or time. Thus, egg and larval survival in shallow waters and nursery areas (lagoons, estuaries) depend less on offshore oceanographic condition and more on inshore local causes (river flow; Vinagre et al., 2009, 2010) such as the lack of suitable habitat for larvae. In fact, in the southern area, LPUE was characterized by smooth trend in variability despite the fact that conditions for the fishery all year round generally allow higher number of fishing days than in western regions.

## 3.5 Conclusions

Metadata analyses revealed that total results (analyses for the coastal population) differed across the three study regions and emphasise the importance of stock analyses at sub-area or sub-stock levels (e.g., mackerel in IXa (e.g., ICES 2011). Little is known about the general population and sub-populations of *D. sargus* along the Portuguese coast (IXa division). Nevertheless, by ignoring subdivision analyses, only partial knowledge on resource status will be gained. For example, early stage larval recruitment is determined by regional climatic variability, therefore it is not expected that that SST in northwestern areas affects larval survivorship in south Algarve. Metadata containing the cumulative LPUE contribution of each area and its relationship with explanatory variables are sensitive to the effects of group-averaged data. For instance, a metadata approach erroneously indicates that the summer SST correlates with stock catch rates (a period of low spawning activity) when in fact summer SST did not show any such correlation within any area. Thus, stock assessment of species with high habitat fidelity should be based on regional analyses. For such species, the regional analysis can be considered conservative, because mobility tends to break up any spatial pattern (García-Charton and Péres-Ruzafa, 2001). Taking this concept into consideration plus the fact that habitat is conservative over time habitat associated species can be a good indicator for regional analyses environmental and fisheries studies. The multi-model approach across areas revealed autumn, spring and summer environmental effects to be related with northwestern, southwestern and Algarve coast catch rates. This appears to indicate a longitudinal gradient related with spawning and larvae availability and regional environmental condition effects over species early life stages. These regional differences result in different biological responses of *D. sargus* life cycle processes. The magnitude of these impacts is determined by the ‘‘timing’’ of interactions between specific stages of the life cycle and local environmental conditions. According to the regional circulation models, the evolution of climate may differ from region to region along the Portuguese mainland, resulting in heterogeneous responses of some stocks (Sousa Reis et al., 2006). Since environmental variables fluctuate over time, management of marine resources should take into account regional environment characteristics in order to develop suitable management measures based on yearly sustainable catch rates at regional scale. However, considering the potential values of fish caught in same areas of the IXaCS and IXaS-Algarve, recreational fisheries should also be included in fisheries-environmental research management in the future.

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## 3.8 Appendix

**Table 3.A1** Detailed model results of all model approaches (MAFA, DFA and GLS), including all explanatory variables related to D. sargus LPUE in the northwestern (IXaCN), southwestern (IXaCS) and southern (IXaS-Algarve), regions and total area (IXa) of Portugal

| | **Total Area (Ixa)** | | | | | | | **Northwest (IXaCN)** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **MAFA** | **DFA** | | **GLS** | | | | **MAFA** | **DFA** | | **GLS** | | | |
| **Variables** | **values** | **AIC** | **t** | **AR process** | **AIC** | **p** | **slop** | **values** | **AIC** | **t** | **AR process** | **AIC** | **P** | **slop** |
| | (0.44) | (65.65) | | | | | | (0.44) | (56.58) | | | | | |
| **Effort** | 0.15 | 66.08 | 0.71 | no AR | 66.49 | 0.51 | 0.15 | 0.09 | 58.56 | 0.83 | no AR | 66.93 | 0.92 | 0.02 |
| **SST** | | | | | | | | | | | | | | |
| **Annual** | -0.34 | **64.04** | **-1.65** | no AR | 64.65 | 0.14 | -0.34 | -0.09 | 56.93 | -4.01 | ARMA(1,0) | 58.42 | 0.43 | -0.14 |
| **Winter** | -0.11 | 66.30 | -0.53 | no AR | 66.68 | 0.62 | -0.11 | 0.02 | 58.58 | -0.20 | ARMA(1,0) | 59.00 | 0.34 | 0.20 |
| **Spring** | 0.05 | 67.62 | 0.25 | no AR | 66.88 | 0.81 | 0.05 | 0.23 | 58.47 | 1.99 | ARMA(1,0) | 60.41 | 0.89 | -0.02 |
| **Summer** | **-0.51** | **60.28** | **-2.72** | **no AR** | **61.24** | **0.02** | **-0.51** | -0.29 | 57.22 | -3.99 | ARMA(1,0) | 60.91 | 0.23 | -0.17 |
| **Autumn** | -0.22 | 65.51 | -1.78 | ARMA(1,0) | 63.33 | 0.54 | 0.17 | -0.18 | **56.09** | **-4.53** | **ARMA(1,0)** | **57.84** | **0.03** | **-0.28** |
| **NAO** | | | | | | | | | | | | | | |
| **Annual** | -0.22 | 66.29 | -1.44 | ARMA(1,0) | 63.91 | 0.06 | -0.16 | -0.21 | 58.44 | -1.98 | ARMA(1,0) | 61.31 | 0.90 | -0.01 |
| **Winter** | -0.15 | 66.78 | -0.98 | no AR | 66.47 | 0.50 | -0.16 | -0.08 | 58.06 | -0.86 | ARMA(1,0) | 65.59 | 0.46 | -0.20 |
| **UPW** | | | | | | | | | | | | | | |
| **Annual** | 0.26 | **65.04** | **1.27** | no AR | 65.55 | 0.25 | 0.26 | 0.22 | 56.93 | 4.06 | ARMA(1,0) | 60.39 | 0.25 | 0.23 |
| **Winter** | 0.10 | 66.36 | 0.47 | no AR | 66.74 | 0.66 | 0.10 | 0.16 | 58.07 | 2.19 | ARMA(1,0) | 61.77 | 0.95 | 0.01 |
| **Spring** | -0.09 | 66.41 | -0.40 | no AR | 66.79 | 0.71 | -0.09 | -0.21 | 58.30 | -2.31 | ARMA(1,0) | 62.41 | 0.98 | -0.01 |
| **Summer** | 0.20 | 67.28 | 1.13 | no AR | 66.18 | 0.39 | 0.20 | 0.27 | 58.56 | 2.26 | ARMA(1,0) | 54.92 | 0.15 | 0.21 |
| **Autumn** | 0.23 | **65.45** | **1.08** | ARMA(1,0) | 63.91 | 0.15 | 0.42 | 0.18 | 57.38 | 3.11 | ARMA(1,0) | 61.16 | 0.27 | 0.16 |
| **WMAG** | | | | | | | | | | | | | | |
| **Annual** | 0.23 | **65.33** | **1.11** | no AR | 65.86 | 0.31 | 0.23 | 0.25 | 57.11 | 3.15 | ARMA(1,0) | 60.40 | 0.16 | 0.20 |
| **Winter** | 0.03 | 67.64 | 0.18 | no AR | 66.92 | 0.91 | 0.03 | 0.14 | 56.84 | 2.01 | ARMA(1,0) | 58.42 | 0.97 | -0.01 |
| **Spring** | -0.10 | 67.59 | -0.56 | no AR | 66.76 | 0.68 | -0.10 | -0.26 | 57.74 | -2.75 | **ARMA(1,0)** | **56.06** | **0.04** | **-0.33** |
| **Summer** | 0.40 | **62.89** | **2.01** | no AR | 63.61 | 0.07 | 0.40 | 0.20 | 57.55 | 2.95 | ARMA(1,0) | 59.47 | 0.16 | 0.31 |
| **Autumn** | 0.18 | 66.83 | 1.18 | ARMA(1,0) | 64.70 | 0.32 | 0.19 | 0.36 | **56.33** | **3.60** | **ARMA(1,0)** | **58.01** | **0.00** | **0.29** |
| **UWIND** | | | | | | | | | | | | | | |
| **Annual** | **0.45** | **61.72** | **2.34** | **no AR** | **62.55** | **0.04** | **0.45** | 0.43 | 57.79 | 4.11 | ARMA(1,0) | 61.40 | 0.08 | 0.22 |
| **Winter** | 0.03 | 67.65 | 0.18 | no AR | 66.91 | 0.89 | 0.03 | -0.05 | 58.45 | 0.05 | ARMA(1,0) | 60.94 | 0.28 | 0.21 |
| **Spring** | 0.18 | **63.63** | **1.93** | ARMA(1,0) | 64.38 | 0.09 | 0.27 | -0.05 | 57.91 | 2.93 | ARMA(1,0) | 61.13 | 0.20 | 0.20 |
| **Summer** | 0.41 | **62.68** | **2.08** | no AR | 63.41 | 0.06 | 0.41 | 0.30 | 58.24 | 2.60 | no AR | 66.21 | 0.40 | 0.19 |
| **Autumn** | 0.22 | **65.45** | **1.08** | no AR | 65.92 | 0.32 | 0.23 | 0.31 | 58.45 | 2.60 | ARMA(1,0) | 64.37 | 0.44 | 0.25 |
| **VWIND** | | | | | | | | | | | | | | |
| **Annual** | -0.08 | 67.52 | -0.37 | no AR | 66.83 | 0.75 | 0.83 | -0.12 | 57.53 | -1.91 | ARMA(1,0) | 60.58 | 0.18 | -0.19 |
| **Winter** | 0.18 | 65.86 | 1.57 | no AR | 66.29 | 0.43 | 0.18 | -0.07 | 58.49 | -1.03 | ARMA(1,0) | 62.07 | 0.58 | -0.12 |
| **Spring** | 0.20 | 66.44 | 1.30 | no AR | 66.14 | 0.38 | 0.20 | 0.23 | 57.85 | 2.56 | ARMA(1,0) | 59.43 | 0.10 | 0.33 |
| **Summer** | -0.30 | **64.65** | **-1.42** | **ARMA(1,0)** | **69.25** | **0.00** | **-0.07** | -0.15 | 57.85 | -2.47 | ARMA(1,0) | 60.89 | 0.34 | -0.18 |
| **Autumn** | -0.18 | 67.28 | -1.05 | no AR | 66.34 | 0.45 | -0.18 | -0.18 | 57.27 | -4.00 | ARMA(1,0) | 62.23 | 0.26 | -0.20 |
| **RD** | | | | | | | | | | | | | | |
| **Annual** | -0.11 | 66.33 | -0.50 | no AR | 66.71 | 0.64 | -0.11 | 0.08 | 58.37 | 0.62 | ARMA(1,0) | 64.26 | 0.23 | 0.21 |
| **Winter** | -0.00 | 67.57 | -0.01 | no AR | 66.93 | 0.99 | -0.00 | 0.10 | 58.36 | 0.95 | ARMA(1,0) | 63.88 | 0.86 | 0.04 |
| **Spring** | -0.15 | 66.09 | -0.70 | no AR | 66.50 | 0.51 | -0.15 | 0.04 | 58.18 | 0.16 | ARMA(1,0) | 60.42 | 0.12 | 0.24 |
| **Summer** | -0.21 | **65.62** | **-0.99** | no AR | 66.07 | 0.36 | -0.21 | 0.00 | 57.49 | 0.63 | ARMA(1,0) | 61.18 | 0.28 | 0.13 |
| **Autumn** | -0.15 | 66.11 | -0.69 | no AR | 66.52 | 0.52 | -0.15 | -0.03 | 58.39 | -0.68 | ARMA(1,0) | 61.10 | 0.84 | 0.04 |

**Table 3.A1** (cont.) Detailed model results of all model approaches (MAFA, DFA and GLS), including all explanatory variables related to D. sargus LPUE in the northwestern (IXaCN), southwestern (IXaCS) and southern (IXaS-Algarve), regions and total area (IXa) of Portugal

| | **Southwest (IXaCS)** | | | | | | | **South (IXaS-Algarve)** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Variables** | **MAFA values** (0.44) | **DFA AIC** (49.10) | **t** | **GLS AR process** | **AIC** | **p** | **slop** | **MAFA values** (0.44) | **DFA AIC** (64.57) | **t** | **GLS AR process** | **AIC** | **P** | **Slop** |
| **Effort** | **0.54** | 50.36 | -1.70 | ARMA(1,0) | 46.33 | 0.44 | 0.16 | 0.03 | 66.55 | 0.14 | no AR | 66.92 | 0.90 | 0.04 |
| **SST** | | | | | | | | | | | | | | |
| **Annual** | -0.19 | 49.57 | -2.35 | ARMA(1,0) | 51.48 | 0.43 | -0.09 | -0.41 | **62.81** | **-2.04** | no AR | 63.53 | 0.07 | -0.41 |
| **Winter** | -0.43 | **46.43** | **-7.30** | ARMA(1,0) | 47.66 | 0.13 | -0.19 | -0.09 | 66.39 | -0.43 | no AR | 66.77 | 0.69 | -0.09 |
| **Spring** | 0.16 | 50.99 | -0.32 | ARMA(1,0) | 52.10 | 0.87 | 0.02 | -0.32 | **64.28** | **-1.56** | no AR | 64.86 | 0.16 | -0.32 |
| **Summer** | -0.27 | 50.48 | -1.73 | ARMA(1,0) | 50.29 | 0.56 | -0.06 | -0.22 | 65.52 | -1.04 | no AR | 65.99 | 0.34 | -0.22 |
| **Autumn** | 0.07 | 51.13 | -0.90 | no AR | 66.75 | 0.67 | 0.10 | -0.26 | 65.10 | -1.24 | no AR | 65.61 | 0.26 | -0.26 |
| **NAO** | | | | | | | | | | | | | | |
| **Annual** | -0.34 | 49.18 | -2.66 | **ARMA(1,0)** | **49.27** | **0.01** | **-0.26** | -0.02 | 66.56 | -0.09 | no AR | 66.93 | 0.93 | -0.02 |
| **Winter** | -0.39 | **46.11** | **-3.14** | **ARMA(1,0)** | **47.43** | **0.04** | **-0.11** | -0.01 | 66.57 | -0.06 | no AR | 66.93 | 0.96 | -0.01 |
| **UPW** | | | | | | | | | | | | | | |
| **Annual** | 0.25 | 50.38 | -1.54 | ARMA(1,0) | 41.85 | 0.73 | -0.05 | 0.16 | 66.00 | 0.76 | no AR | 66.42 | 0.48 | 0.16 |
| **Winter** | 0.11 | 50.48 | -1.26 | ARMA(1,0) | 50.06 | 0.29 | -0.15 | -0.07 | 66.45 | -0.34 | no AR | 66.83 | 0.75 | -0.07 |
| **Spring** | 0.09 | 49.53 | -2.78 | ARMA(1,0) | 50.29 | 0.30 | -0.14 | 0.34 | **64.07** | **1.64** | no AR | 64.67 | 0.14 | 0.34 |
| **Summer** | 0.28 | 51.09 | -0.29 | ARMA(1,0) | 43.26 | 0.58 | 0.09 | 0.18 | 65.84 | 0.87 | no AR | 66.27 | 0.42 | 0.18 |
| **Autumn** | 0.06 | 51.46 | 0.43 | ARMA(1,0) | 50.78 | 0.53 | -0.09 | 0.05 | 66.51 | 0.25 | no AR | 66.88 | 0.82 | 0.05 |
| **WMAG** | | | | | | | | | | | | | | |
| **Annual** | 0.20 | 50.10 | -2.17 | ARMA(1,0) | 47.22 | 0.54 | -0.08 | 0.07 | 66.46 | 0.34 | no AR | 66.83 | 0.75 | 0.07 |
| **Winter** | 0.20 | 50.38 | 2.51 | ARMA(1,0) | 52.01 | 0.87 | 0.02 | 0.02 | 66.56 | 0.09 | no AR | 66.93 | 0.94 | 0.02 |
| **Spring** | -0.03 | 49.57 | -3.29 | ARMA(1,0) | 47.93 | 0.16 | -0.17 | 0.27 | 65.02 | 1.28 | no AR | 65.53 | 0.24 | 0.27 |
| **Summer** | 0.13 | 50.04 | 1.99 | ARMA(1,0) | 46.10 | 0.63 | 0.11 | 0.13 | 66.19 | 0.62 | no AR | 66.59 | 0.56 | 0.13 |
| **Autumn** | -0.00 | 49.60 | -4.03 | ARMA(1,0) | 50.81 | 0.59 | -0.08 | 0.03 | 66.56 | 0.13 | no AR | 66.92 | 0.91 | 0.03 |
| **UWIND** | | | | | | | | | | | | | | |
| **Annual** | 0.39 | **48.91** | **2.63** | ARMA(1,0) | 47.62 | 0.09 | 0.29 | 0.09 | 66.40 | 0.42 | no AR | 66.78 | 0.70 | 0.09 |
| **Winter** | 0.19 | 49.46 | 2.03 | ARMA(1,0) | 48.41 | 0.10 | 0.25 | -0.11 | 66.32 | -0.51 | no AR | 66.71 | 0.64 | -0.11 |
| **Spring** | 0.10 | 50.90 | 0.19 | **ARMA(1,0)** | **50.10** | **0.00** | **0.09** | 0.34 | **63.94** | **1.68** | no AR | 64.56 | 0.13 | 0.34 |
| **Summer** | **0.52** | 50.37 | 1.64 | ARMA(1,0) | 50.27 | 0.27 | 0.17 | 0.13 | 66.20 | 0.61 | no AR | 66.60 | 0.57 | 0.13 |
| **Autumn** | 0.03 | 50.94 | -0.72 | ARMA(1,0) | 49.96 | 0.88 | -0.02 | 0.02 | 66.56 | 0.09 | no AR | 66.93 | 0.94 | 0.02 |
| **VWIND** | | | | | | | | | | | | | | |
| **Annual** | -0.11 | 49.82 | 2.54 | ARMA(1,0) | 46.48 | 0.33 | 0.13 | -0.02 | 66.56 | -0.10 | no AR | 66.93 | 0.93 | -0.02 |
| **Winter** | 0.00 | 50.15 | 1.39 | ARMA(1,0) | 53.56 | 0.16 | 0.24 | 0.22 | 65.55 | 1.03 | no AR | 66.01 | 0.34 | 0.22 |
| **Spring** | 0.03 | 49.54 | 3.24 | ARMA(1,0) | 49.75 | 0.23 | 0.16 | -0.01 | 66.57 | -0.05 | ARMA(1,0) | 63.38 | 0.22 | 0.23 |
| **Summer** | -0.05 | 50.16 | -1.90 | ARMA(1,0) | 46.42 | 0.93 | 0.02 | -0.09 | 66.39 | -0.43 | no AR | 66.77 | 0.69 | -0.09 |
| **Autumn** | -0.09 | 51.03 | 0.41 | ARMA(1,0) | 45.44 | 0.39 | 0.13 | -0.14 | 66.18 | -0.63 | no AR | 66.58 | 0.56 | -0.14 |
| **RD** | | | | | | | | | | | | | | |
| **Annual** | -0.14 | 49.87 | 1.42 | ARMA(1,0) | 49.53 | 0.12 | 0.18 | -0.29 | 64.75 | -1.38 | no AR | 65.29 | 0.21 | -0.29 |
| **Winter** | -0.05 | 49.75 | 1.69 | ARMA(1,0) | 51.73 | 0.93 | -0.02 | -0.24 | 65.28 | -1.16 | no AR | 65.77 | 0.28 | -0.24 |
| **Spring** | -0.09 | 50.48 | 1.39 | ARMA(1,0) | 51.25 | 0.29 | 0.11 | -0.20 | 65.74 | -0.93 | no AR | 66.18 | 0.39 | -0.20 |
| **Summer** | -0.23 | 51.01 | 0.80 | **ARMA(1,0)** | **50.74** | **0.00** | **0.04** | -0.21 | 65.60 | -1.00 | no AR | 66.05 | 0.35 | -0.21 |
| **Autumn** | -0.13 | 51.18 | 0.26 | ARMA(1,0) | 52.35 | 0.77 | 0.03 | -0.19 | 65.84 | -0.87 | no AR | 66.27 | 0.42 | -0.19 |

# CHAPTER 4

## The influence of environmental factors and fishing pressure on catch rates of *Diplodus vulgaris*

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# THE INFLUENCE OF ENVIRONMENTAL FACTORS AND FISHING PRESSURE ON CATCH RATES OF *DIPLODUS VULGARIS*

## Abstract

The variability of coastal marine resources has been linked to environmental variability but the impacts of artisanal nearshore fishing activity and environmental factors interact in different ways. Time series, Min/Max Autocorrelation Factor, Generalised Least Squares and Dynamic Factor Analyses models were applied to examine the role of environmental factors (SST, NAO Index, Upwelling Index,Wind Magnitude, Easterly Wind Component, Northerly Wind Component, Coastal River Discharges) and fisheries effort on commercial catch rates of *Diplodus vulgaris* in the northwestern, southwestern and southern Portuguese coast. Environmental factors were found to affect short-term variations of catch rates with a time lag of 2 years, according to the regions and seasons. In the northwestern, autumn wind magnitude and summer river discharges were positively correlated with *D. vulgaris* catch rates. In the southwestern, *D. vulgaris* catch rates were negatively associated with variations in winter sea surface temperature. In the southern, catch rates were positively associated with yearly westerly wind component and yearly, winter and autumn river discharges whilst negatively associated with the North Atlantic Oscillation (NAO) Index. These results indicate that both large-scale climatic patterns and local hydrological factors can have an influential role in determining the abundance of *D. vulgaris* stocks. Fishery assessment should therefore incorporate information on ecosystem and environmental effects to help managers to make informed decisions on how to best regulate coastal fisheries.

**Keywords:** fish-environment relationships; environmental variability; Portuguese coast (ICES IXa); regional analyses; multi-model inference

## 4.1 Introduction

Fisheries activity and fish population dynamics are closely linked to climate dynamics and weather patterns (Lehodey et al., 2006). Resolving the impact of climate changes on fish populations is however complicated because climatic variables influence multiple environmental factors which may, in turn, influence different processes at different levels of biological organisation (Lehodey et al., 2006; Ottersen et al., 2001). For instance, temperature, salinity, upwelling, winds, tidal currents and oceanic circulation, precipitation and river runoff and nutrients are known to influence productivity, abundance and distribution of fishing stocks at both regional and oceanic scales (e.g. Baptista et al., 2014; Baptista and Leitão, 2014; Brander, 2007, 2010; Borges et al., 2003; Erzini, 2005; Lehodey et al., 2006; Planque and Frédou, 1999; Santos et al., 2001). All of these parameters have been implicated on changes in timing of reproduction, population dynamics, abundance, distribution and inter-specific relationships such as competition and predator–prey interactions (Ottersen et al., 2001). However, the impacts of fishing activity and climate variability interact in different ways. The direct effects include alterations in abundance and distribution of exploited species (Brander, 2007, 2010; Lehodey et al., 2006). The indirect effects relate to changes in productivity, structure and composition of marine ecosystems (Brander, 2007, 2010). Therefore, the environmental changes may reduce, or in some cases improve, the productivity of fisheries stocks since they influence production, survival, growth and offspring (Brander, 2007). According to Cushing (1996), the larval period is a major cause of variability in marine fish production. Houde (1987) analysed the impact of variations in life-stage duration or mortality from the egg, larval and juvenile stages and concluded that for most species the larval stages have the greatest influence in regulating year-class size. This reinforces the importance of larval survival in the dynamics of recruitment.

Studies linking environmental variability to fisheries have been based on a wide range of fishing biological ‘indicators’ including recruitment (Solow, 2002), spawning stock biomass (Gröger and Fogarty, 2011), landings (Erzini, 2005) and catch rates data (Baptista et al., 2014). Over recent decades, many studies have increased our understanding of the impacts of environmental factors on commercial fisheries, including those of pelagic fishes (Lehodey et al., 2006; Santos et al., 2001; Ullah et al., 2012), demersal fishes (Gröger and Fogarty, 2011; Planque and Frédou, 1999; Solow, 2002), cephalopods (Ullah et al., 2012), bivalves (Baptista et al., 2014; Baptista and Leitão, 2014) and crustaceans (Herraiz et al., 2009). However, most studies are limited to specific geographical areas and do not evaluate in detail the combined impact of climatic factors on fisheries variability (Ullah et al., 2012).

*Diplodus vulgaris* (Sparidae), the two-banded sea bream (Geoffroy Saint-Hilaire 1817), have distribution in the Mediterranean areas and along the eastern Atlantic coast from France to Senegal, including the Madeira, the Azores and the Canaries Archipelagos (Bauchot and Hureau, 1986). Owing to the intense exploitation in the Mediterranean Sea, a variety of management tools have been adopted to maintain the sustainability of the fishery such as daily bag limitations or gear restrictions, a minimum legal size of 180 mm (Morales- Nin et al., 2010). This euryhaline species inhabits rocky and sandy bottoms to a maximum depth of 160 m (Gonçalves et al., 2003). The Portuguese continental shelf is the northern distribution limit for nursery areas (Vinagre et al., 2010) because this species does not tolerate temperatures lower than 15 °C. *D. vulgaris* is particularly sensitive to alterations in temperature during the initial stages of the life cycle with adults spawning near the coast and the larvae migrating to nursery and shallow coastal areas to continue their development (Vinagre et al., 2009). However, *D. vulgaris* is a rocky associated resident species (Leitão et al., 2009), remaining in a specific area if favourable habitat conditions for growth and survival are found (Harmelin-Vivien et al., 1995). Success of recruitment in *Diplodus* spp. has been mostly attributed to specific requirements of early juveniles for settlement and on the availability of suitable habitats, which is known to determine population structure and dynamics (Harmelin-Vivien et al., 1995).

Despite progress in understanding the complex processes involved in the variability of fish stocks, especially at short and medium time scales, our ability to predict abundance and catches is limited (Fréon et al., 1993). The published literature and experience in the fisheries-environmental relationship sciences can be used to help formulate a set of a priori candidate models (Burnham and Anderson, 1998). Several time series models can be used for analysing yearly or monthly fisheries data (for review see: Keyl and Wolff, 2008). Most of them allow smoothing of non-stationary data such as fisheries data (Zuur et al., 2003a, b, 2007). Other examples of commonly used techniques include forecasting statistics (surplus production models, Fréon et al., 1993; autoregressive moving average, Lloret et al., 2001) or model fitness [dynamic factorial analyses, min/max autocorrelation factor analyses and generalized linear models (Lloret et al., 2001)]. Most studies exploring the relationships between environmental and fisheries variability use single model analyses (Zuur et al., 2003a) and only a few use complementary or multi-model approaches (Baptista et al., 2014; Erzini, 2005; Lloret et al., 2001). Although the use of complementary approaches (several statistics models) is common practice in ecological studies (Zuur et al., 2007), these routines have not been used in time series analyses of fisheries data (Loots et al. 2011; Planque et al., 2011). The use of multiple modelling techniques can be regarded as a more accurate measure of the strength of the relationships between these types of datasets (Baptista et al., 2014; Erzini, 2005; Leitão et al., 2014a; Zuur et al., 2007).

The Portuguese coast has experienced substantial changes in climatic events impacting on ocean circulation, namely increasing sea surface temperatures (Relvas et al., 2009), changing wind patterns (Baptista et al., 2014), intensification of upwelling (Relvas et al., 2009) and frequency of negative and positive phases of the North Atlantic Oscillation (NAO) Index (Hurrell, 1995). Climate change projections indicate that these modifications could have significant impacts on fishing grounds in this biogeographical area (Relvas et al., 2009). Therefore, it is anticipated that the population dynamics of many species is likely to respond to these pressures in the near future (Santos and Miranda, 2006; Teixeira et al., 2014), particularly along the coastal region off western and southern Portugal (IPCC, 2001).

*D. vulgaris* is a valuable commercial species in the context of the inshore fisheries around the coast of Portugal. Most fishing vessels operating from ports in this area are fibreglass open deck boats <7 m long which use a variety of fishing gears (Gonçalves and Erzini, 2000; Gonçalves et al., 2003), such as gill and trammel nets, hooks and longline, traps and pots (Leitão et al., 2014b) to capture a combination of species generally fishing out to 3 to 6 miles from the coast. From1989 to 2009, multi-gear fishing contributed to 65 % of the total landings on average and 83 % of the fishing effort (fishing days boats$^{-1}$), followed by seine netting (26 % of the fishing effort) and demersal trawling (9 % of the fishing effort). In 2011, 395.8 tonnes of this species were landed in Portuguese ports (DGRM, 2012). *D. vulgaris* is a moderately priced species that can reach high prices at auction (3 € kg$^{-1}$ on average from 1989 to 2009; Source: DGRM).

Over the past decades, landings of seabreams into Portuguese ports have steadily decreased (Gonçalves et al., 2003). However, to date, *D. vulgaris* has not been subject to national quota or total allowable catches (ICES, 2010). The justification is that research, assessment and management have traditionally focused on fisheries with the greatest landings and revenues such as the sardine fishery which is data rich and has available funds and expertise required to complete stock assessments and provide state-of-the-art advice to managers. Improved knowledge of the effect of environmental factors on *D. vulgaris* population dynamics is required to help inform options for management of this socially and economically important species. The predicted increases in coastal water temperatures associated with global climate changes can affect both the abundance and distribution of *D. vulgaris* (Vinagre et al., 2010). This study addresses this knowledge gap by exploring the relationships between environmental factors and catch rates of *D. vulgaris* across areas with distinct hydrographic conditions.

## 4.2 Material and Methods

### 4.2.1 Study Area

The shoreline of the Portuguese mainland extends on the western coast of the Iberian Peninsula. Three different biogeographical areas, with distinct oceanographic regimes (Cunha, 2001), are found in this portion of the European coast: the northwestern and the southwestern coasts, which represent subtropical eastern boundaries of the North Atlantic Ocean (Santos et al., 2001) and the southern coast which shares characteristics of the Atlantic Ocean and the more saline and warm waters of the Mediterranean Sea (Cunha, 2001) typically characterised by Mediterranean climate (Figure 4.1).

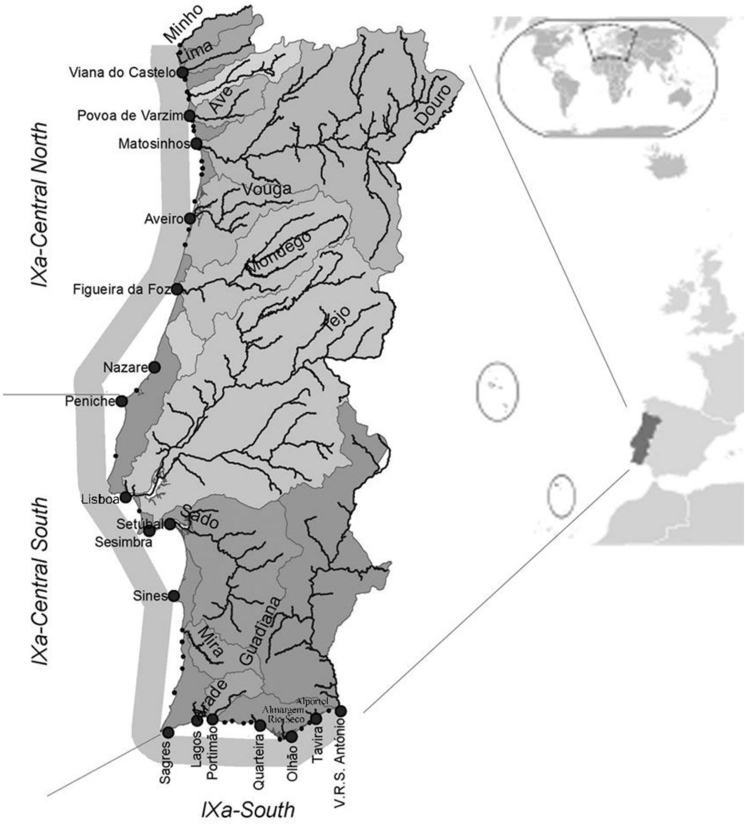

**Figure 4.1** Location of the main fishing commercial ports and freshwater inputs to the three geographical regions on the coast of Portugal: northwestern, southwestern and southern.

### 4.2.2 Environmental and Fisheries Data Sources

A database of fishing activity for the period 1989-2009 was obtained from Direção-Geral de Recursos Naturais, Segurança e Serviços Marítimos (DGRM). The database contains information on fisheries practices such as fishing effort (FE – number of fishing days) and monthly landings per boat per month. For the purposes of this study, landing and fishing effort data were concatenated into annual and seasonal time periods. Yearly landings per unit effort (LPUE), estimated by dividing total annual landings by the FE (LPUE units: kilogrammes per fishing day), were used as a proxy for yearly fish biomass production (abundance index proxy). In particular, multi-gear fishing accounts for 68 % of the total landings on the southern coast and 61 and 54 % of the total landings on the northwestern and southwestern coasts, respectively (Source: DGRM data between 1989 and 2009).

Annual and seasonal mean sea surface temperature (SST), annual and seasonal upwelling index (UPW) and annual and seasonal u- and v wind measurements were used as oceanographic variables. SST data were obtained from Modis-Aqua 4Km satellite imagery available from the NASA Ocean Color Giovanni website (http://gdata1.sci.gsfc.nasa.gov). The upwelling index data were obtained from the Pacific Fisheries and Environmental Laboratory website (www.pfeg.noaa.gov). Geostrophic wind data were obtained from PODAAC (http://podaac.jpl.nasa.gov/dataset/CCMP_MEASURES_ATLAS_L4_OW_L3_5A_MONTHLY_WIND_VECTORS_FLK?ids=&values=) (Atlas et al., 2011). These data were split into two horizontal components: the ‘u’ component (UWIND), which represents the east–west component of the wind; and the ‘v’ component (VWIND), which represents the north–south component. Wind magnitude [*WMAG: SQRT*$(u^2 + v^2)$] was modelled using u- and v- wind components. Due to the lack of satellite data (cloud effect) in some nearshore areas, the spatial coverage of the analyses included the range of depths from mean high water line to 200 m (Figure 4.1). SST, UPW, WMAG, UWIND and VWIND data were averaged for each geographical area (the Northwest, Southwest and South of Portugal).

Monthly information on river discharge (RD) was used for testing the effect of freshwater inputs on catch rates of *D. vulgaris* to account for the known association of this species with estuarine systems (Vinagre et al., 2009). The yearly data (January-December) consisted in the cumulative monthly contribution (discharges volumes in cubic decametres, $dam^3$), of the main Portuguese rivers or Basins (Figure 4.1), including: (i) Cávado, Lima, Douro, Vouga and Mondego for the northwestern coast; (ii) Tejo, Sado and Mira for the southwestern coast; and (iii) rivers Guadiana, Seco, Rio Arado, Ribeira de Quarteira, Alportel and Almargem for the Algarve southern coast. Monthly flow measurement data for gauging stations located in the proximity of the mouth of these rivers were obtained from the Agência Nacional do Ambiente hydrological database (APA, SNIRH: http://snirh.pt/).

The NAO (North Atlantic Oscillation) and NAO winter (December-March) indices were used as climatic variables (http://www.cgd.ucar.edu/jhurrell/nao.html, last accessed 2010; Hurrell, 1995). The NAO index is the difference between sea level atmospheric pressure in the Azores and Iceland and largely regulates rainfall, temperature and wind regimes over most of northwestern Europe (Hurrell, 1995).

### 4.2.3 Time Series Analyses (Statistical Models)

For the purposes of statistical modelling, landing per unit effort (LPUE) was considered the response variable whereas fishing effort and environmental variables were the response explanatory variables.

The variability of fishing recruitment was considered to be largely determined by survival during the larval and juvenile stages. Therefore, it was assumed that larval fish survival is linked to environmental factors. The hypothesis of this study was that the recruitment and thus survival of fish larvae (fishing recruitment) and catch rates of *D. vulgaris* off the Portuguese coast is influenced by environmental and fisheries factors. This species commonly reaches sexual maturity in the second year (Gonçalves and Erzini, 2000) and can live up to 14 years (Gonçalves et al., 2003). Most fish are caught during adult stages (Erzini et al., 2003). Since most commercially caught *D. vulgaris* belongs to the 2-year class, a time lag of 2 years was considered when selecting the environmental datasets for statistical modelling. The methodology used in this study implies that landings are directly proportional to catches. This is the case for *D. vulgaris* for multi-gear sector were direct proportionality with catches can be assumed as this species is not discarded, mainly due to their high commercial value. Therefore, it can be assumed that there are positive relationships between LPUE (LPUE biomass proxy) and biomass. Fishing effort can also affect adult spawning biomass and recruitment in the following years. To accommodate this effect, environmental and FE data were adjusted with a 2-year time lag to accommodate these temporal changes. It was decided to include fishing effort (FE) in the models tested as an explanatory variable since no collinearity between LPUE and FE were observed after pair-plots analyses (collinearity between *D. vulgaris* LPUE and FE; northwestern = 0.41, southwestern = 0.39, southern = 0.01).

In this study, it was hypothesised that the survival rate of *D. vulgaris* larvae would vary according to regional environmental conditions off the coast of Portugal. Therefore, separate regional models were produced thus allowing for spatial independency. In these models, seasons were considered as follows: winter (January to March), spring (April to June), summer (July to September) and autumn (October to December).

A multi-model approach was used including min/max autocorrelation factor analysis (MAFA), dynamic factor analysis (DFA) and generalised least squares (GLS). Since different time series analyses could reveal different results regarding the effect of explanatory variables in catch rates, a selection criterion was adopted aiming to discriminate the variables with higher probability of explaining changes in LPUE. The best candidate variables were model-based, and probability was defined according to the number of models that highlighted the same explanatory variable. This selection criterion allows classifying the variables with high (the variable is highlighted in more than one model) or low probability of affecting LPUE. Hypotheses underlying the selected set of models highlighting a variable can thus be inferred to represent the dominant controls of an explanatory variable (climatic driver) over fisheries time series data (Leitão et al., 2014a; Loots et al., 2011).

All data were tested for normality (quantile-quantile Plots – QQ-plots) and collinearity (pair-plots) (Zuur et al., 2010). After QQ-plots analyses, no transformation was applied to yearly LPUE and explanatory variables. The results of exploratory analysis over explanatory variables (pair-plots) revealed collinearity between yearly northerly wind (VWIND) and wind magnitude (WMAG). Therefore, these variables were used separately in the models. Simple models were firstly tested for significance of the relationship without accounting for more than one variable. In situations where more than one variable was highlighted (i.e. belonging to the same data set: seasonal or annual), the significance of the relationship was tested by accounting for combined fisheries and environmental data series using surrogate testing. All statistical analyses were carried out using Brodgar software package (http://www.brodgar.com).

#### 4.2.3.1 Min/Max Autocorrelation Factor Analysis

Min/max autocorrelation factor analysis (MAFA) is similar to principal component analysis (PCA) and gives axes. These axes are derived in such a way that the first axis has the highest autocorrelation with a time lag of 1 year which is typically associated with a smooth trend. MAFA extracts the main trends in the time series, and the first MAFA axis is considered the most important underlying pattern or index function in the multivariate time series dataset (Solow, 1994). A set of orthogonal linear combinations of the original time series (MAFs) of decreasing smoothness as measured by lag-one autocorrelation are constructed (Solow, 1994). Cross correlations between MAFA axes and explanatory variables can also be estimated, allowing significant relationships between trends and explanatory variables to be identified (Erzini, 2005; Zuur et al., 2007). Therefore, given the type of fishery that targets single species with corresponding fishing effort information, the MAFA analyses considered only a single MAFA trend (autocorrelation time lag 1 year) for each species using Brodgar software package (http://www.brodgar.com). Both response and explanatory variables were standardised before running the MAFA models as advised by Zuur et al. (2003a, b). The standardisation method used for converting data into the same dimensional scale was normalisation that consist in centering all variables around zero ($Xi=(Yi - \hat{Y})/\sigma y$), where $\hat{Y}$ is the sample mean, $Yi$ the value of the $i^{th}$ sample and $\sigma y$ the sample standard deviation.

### 4.2.3.2 Dynamic Factor Analysis

Trend analyses of the effect of environmental and fishing variables on catch rates of *D. vulgaris* were carried out independently for each geographical area by means of dynamic factor analysis (DFA). This multivariate technique is often used for non-stationary time series analysis to estimate underlying common patterns, evaluate interactions between response variables (ex. LPUE) and determine the effects of explanatory variables (ex. environmental and fisheries variables) on response variables (Zuur et al., 2003a, 2007). A separate DFA univariate time series model/analysis was used for each region to account for the different environmental conditions and spatial independence among regions (Baptista et al., 2014; Baptista and Leitão, 2014; Ullah et al., 2012). Models were fitted with a diagonal covariance matrix, and the Akaike's information criterion (AIC) was used to compare models. The *t* values resulting from estimation of regression parameters were considered as an indication of either a positive or negative relationship between variables and response variables (*t* values with an absolute value greater than 3 indicate a strong relationship among variables). Both response and explanatory variables were standardised before running the DFA models as advised by Zuur et al. (2003a, b). The standardisation method used was the same as for MAFA.

### 4.2.3.3 Generalised Least Square

Generalised least square (GLS) is an extended linear mixed effect model in which errors are allowed to be correlated and/or have unequal variance (Lloret et al., 2001; Pinheiro and Bates, 2000). Several GLS models were applied without autocorrelation and with an autoregressive process imposed on the error components to allow unequal variance of the errors (Zuur et al., 2007). Errors were specified to follow an autoregressive process (assuming that the autocorrelation is highest between following years) of degree 1 or p which was determined using the partial autocorrelation function and the goodness of fit of an ARMA model. Therefore, GLS models with and without different autocorrelation structures were tested and compared (only better models are presented). The best fitting models were selected on the basis of the lowest AIC coefficients. The question then becomes whether the decrease in AIC is enough to discard the simple linear regression model in favour of a more complex GLS model. The simpler model was selected whenever the difference in AIC coefficients between two models was smaller than 2. Models were considered significant at the 95 % level of confidence. Positive and negative slopes are denoted as (+) or (−), respectively.

## 4.3 Results

The SST was lower in the northwestern and southwestern regions than in the southern region (Table 4.1). The SST had similar yearly trend variations among study regions (northwestern, southwestern and southern coast of Portugal) peaking in 1989-1990, 1995, 1997 and 2006 (Figure 4.2a).

**Table 4.1** Yearly and seasonal means and standard deviations (SD) for environmental variables tested in the models for the period 1989-2009 in three geographical regions (northwestern, southwestern and southern) on the coast of Portugal.

| Variables | Northwestern | | Southwestern | | Southern | |
|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD |
| **SST Annual** | 16.02 | 0.46 | 17.04 | 0.38 | 18.51 | 0.33 |
| **SST Winter** | 14.11 | 0.66 | 15.05 | 0.61 | 16.18 | 0.45 |
| **SST Spring** | 15.88 | 0.71 | 16.68 | 0.61 | 17.98 | 0.48 |
| **SST Summer** | 18.53 | 0.64 | 19.15 | 0.68 | 21.04 | 0.70 |
| **SST Autumn** | 15.86 | 0.94 | 17.06 | 0.83 | 18.82 | 0.75 |
| **NAO** | 0.30 | 0.62 | 0.30 | 0.62 | 0.30 | 0.62 |
| **NAO Winter** | 1.01 | 1.70 | 1.01 | 1.70 | 1.01 | 1.70 |
| **UPW Annual** | -4.66 | 17.80 | 13.20 | 9.80 | -0.48 | 7.72 |
| **UPW Winter** | -25.70 | 40.47 | -4.24 | 22.65 | -13.62 | 25.58 |
| **UPW Spring** | 26.39 | 15.69 | 29.91 | 17.12 | 12.02 | 9.87 |
| **UPW Summer** | 43.01 | 12.38 | 49.46 | 14.26 | 8.69 | 7.12 |
| **UPW Autumn** | -48.60 | 53.20 | -21.86 | 30.62 | -3.29 | 28.14 |
| **WMAG Annual** | 2.87 | 0.60 | 3.71 | 0.56 | 2.45 | 0.46 |
| **WMAG Winter** | 1.93 | 0.93 | 3.11 | 0.88 | 2.48 | 0.54 |
| **WMAG Spring** | 3.83 | 0.80 | 5.02 | 0.88 | 3.56 | 0.65 |
| **WMAG Summer** | 4.46 | 0.70 | 5.34 | 0.65 | 3.75 | 0.58 |
| **WMAG Autumn** | 2.69 | 1.03 | 2.78 | 1.29 | 2.25 | 0.82 |
| **UWIND Annual** | 1.02 | 0.43 | 1.28 | 0.46 | 0.94 | 0.54 |
| **UWIND Winter** | 0.69 | 1.14 | 0.27 | 1.35 | -0.83 | 1.74 |
| **UWIND Spring** | 1.72 | 0.65 | 2.00 | 0.57 | 2.19 | 0.66 |
| **UWIND Summer** | 1.35 | 0.36 | 1.81 | 0.29 | 2.02 | 0.58 |
| **UWIND Autumn** | 0.18 | 1.29 | 0.29 | 1.43 | 0.20 | 1.49 |
| **VWIND Annual** | -2.52 | 0.64 | -3.21 | 0.60 | -2.06 | 0.46 |
| **VWIND Winter** | -1.25 | 1.27 | -2.91 | 1.07 | -1.90 | 0.74 |
| **VWIND Spring** | -3.55 | 1.10 | -4.45 | 1.04 | -2.64 | 0.68 |
| **VWIND Summer** | -4.41 | 0.76 | -5.05 | 0.71 | -3.21 | 0.55 |
| **VWIND Autumn** | -1.87 | 2.17 | -2.13 | 1.67 | -1.53 | 1.23 |
| **RD Annual** | 27050.41 | 13363.74 | 6999.66 | 6348.43 | 1134.55 | 2417.12 |
| **RD Winter** | 10799.63 | 11327.00 | 1772.88 | 4797.06 | 339.79 | 1592.59 |
| **RD Spring** | 5443.01 | 2945.85 | 1092.84 | 633.51 | 140.97 | 135.77 |
| **RD Summer** | 2775.88 | 760.97 | 777.55 | 485.12 | 74.64 | 58.58 |
| **RD Autumn** | 6480.82 | 5486.53 | 2059.98 | 3039.32 | 317.86 | 1363.22 |

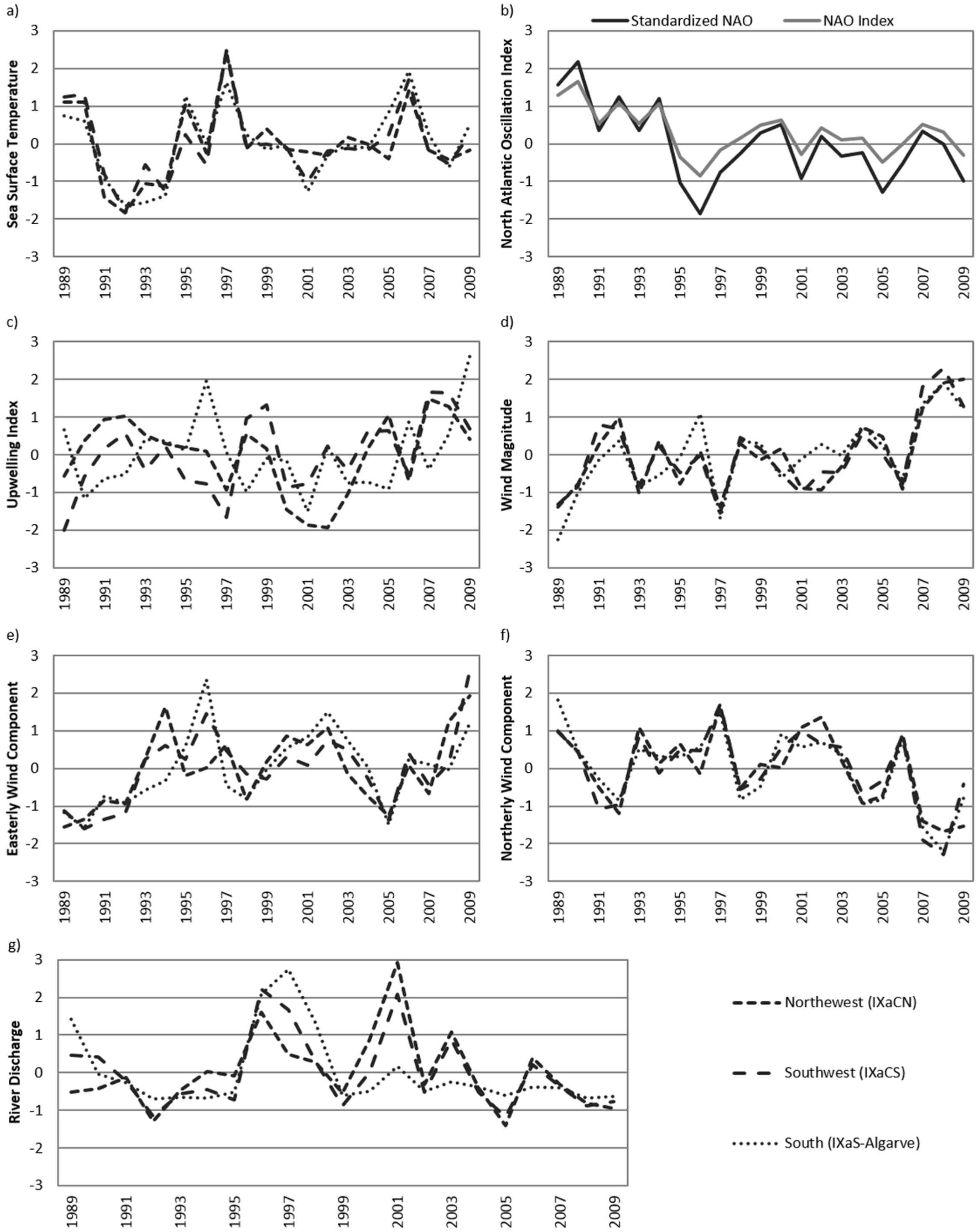

**Figure 4.2** Standardised time series of the yearly environmental variables during the period 1989-2009 in the three geographical regions on the coast of Portugal (northwestern, southwestern and southern): sea surface temperature (a), North Atlantic Oscillation Index (b), Upwelling Index (c), wind magnitude (d), easterly wind component (e), northerly wind component (f) and river discharge (g).

During the time period relevant to this study, the NAO index remained generally negative. This index decreased markedly until 1996 (Figure 4.2b), varying considerably below the mean value thereafter.

On the Portuguese coast, UPW index was predominant in the spring and summer, particularly in the northwestern and southwestern regions (Table 4.1). The UPW showed different trends between regions, with substantial variation over time (Figure 4.2c). The northwestern and southwestern regions had higher values of this index in 1992, 1999-2000, 2005 and 2007-2008 whereas in the southern UPW peaked in 1996 and 2009.

The WMAG showed a similar pattern among study regions, varying around the mean level and peaking in 2008 (Figure 4.2d). WMAG varied considerably in the study areas with less pronounced seasonal variations in the southern. The average WMAG was strongest in the southwestern (Table 4.1). WMAG was stronger in the spring and summer. The easterly wind (UWIND) component values varied around the mean level (Figure 4.2e). Values above the mean for this parameter (positive anomalies) were detected in 1993-1997, 1998-2004 and 2006-2009. Variations in UWIND levels were similar among study areas after 1998 when compared to the period from 1989 to 1997. The northerly wind component (VWIND) trend varied around the mean but declined since 2004 below the mean; after 2006, reached the lowest values recorded for all-time series (Figure 4.2f).

Irrespective of the geographical regions considered, the higher RD volumes were detected in the winter and the smaller volumes in the summer (Table 4.1). Overall, RD volumes were significantly higher in the northwestern region than in the southwestern and the southern regions. Temporal trends in RD volumes were similar in the northwestern and southwestern regions, peaking in 1996 and 2001 (Figure 4.2g). In the southern, RD volumes peaked in 1989 and 1997.

Standardised FE for *D. vulgaris* showed high variability over the period of study. In addition, variations in this parameter showed different patterns between the three geographical regions (Figure 4.3). In the northwestern, FE showed a positive peak in 1990 varying above the mean level until 2001 and decreasing until 2009. The lowest LPUE values over the study period occurred during the period 2004 (Figure 4.4). In the southwestern, a gradual increase was observed until 1998, decreasing thereafter to low levels in 2001; LPUE increased from 2001 to 2007. On the southern coast, LPUE peaked in 1990 and 2003-2004. Standardised FE values were below average in the three regions after the period 2005-2006.

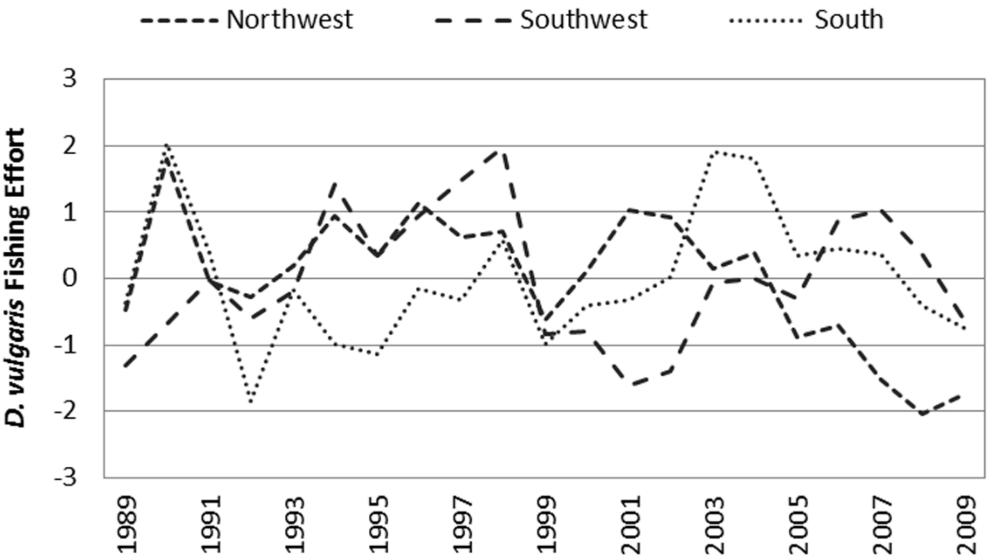

**Figure 4.3** Standardised yearly fishing effort (number of fishing days and boats) for *Diplodus vulgaris* from 1989 to 2009 in three geographical regions (northwestern, southwestern and southern) on the coast of Portugal.

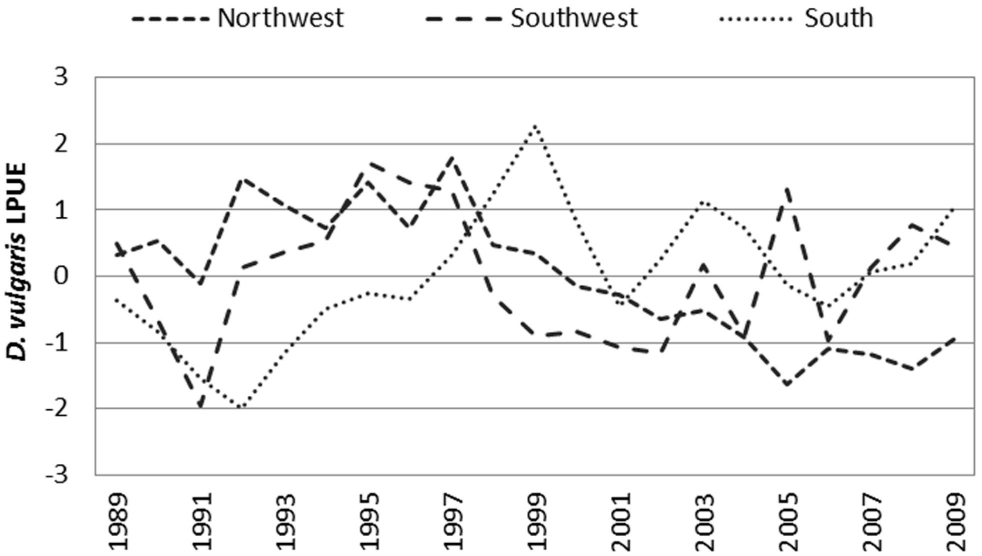

**Figure 4.4** Standardised *Diplodus vulgaris* landings per unit effort (LPUE) from 1989 to 2009 in three geographical regions on the coast of Portugal (northwestern, southwestern and southern).

In the northwest, the LPUE values increased until 1997, decreasing and remaining below average after 1999. In the southwest, the LPUE reached the lowest values in 1991 peaking in 1995 and declining afterwards until 2002, oscillating onwards. In the south, the LPUE levels increased above the mean after 1996 peaking in 1999, keeping close to, or slightly above, the mean level thereafter.

The results of the relationships between *D. vulgaris* LPUE and explanatory (fishing and environmental) variables for MAFA, DFA and GLS models in the three geographical regions are summarised in Table 4.2. Detailed results of these models are shown in Appendix 4.A1.

**Table 4.2** Summary results of the relationships between *Diplodus vulgaris* landings per unit effort (LPUE) and explanatory (fishing and environmental) variables in three geographical regions on the coast of Portugal (northwestern, southwestern and southern) using min/max autocorrelation factor analysis (MAFA), dynamic factor analysis (DFA) and generalised least square (GLS) modelling techniques.

| | **Explanatory variables** | **MAFA** | **DFA** | **GLS** | **Probability** |
|---|---|---|---|---|---|
| **Northwestern** | WMAG Autumn | n.s. | **sig. (+)** | **sig. (+)** | High |
| | RD Summer | n.s. | **sig. (+)** | **sig. (+)** | High |
| **Southwestern** | EFFORT | n.s. | **sig. (+)** | n.s. | Low |
| | SST Annual | n.s. | **sig. (-)** | n.s. | Low |
| | SST Winter | **sig. (-)** | **sig. (-)** | **sig. (-)** | High |
| | UPW Spring | n.s. | **sig. (-)** | n.s. | Low |
| | UPW Summer | n.s. | **sig. (-)** | n.s. | Low |
| | WMAG Winter | n.s. | **sig. (+)** | n.s. | Low |
| | UWIND Summer | n.s. | **sig. (+)** | n.s. | Low |
| | RD Annual | n.s. | **sig. (-)** | n.s. | Low |
| | RD Summer | n.s. | **sig. (-)** | n.s. | Low |
| | RD Autumn | n.s. | **sig. (-)** | n.s. | Low |
| **Southern** | SST Winter | **sig. (+)** | n.s. | n.s. | Low |
| | SST Spring | **sig. (+)** | n.s. | n.s. | Low |
| | NAO Annual | **sig. (-)** | **sig. (-)** | n.s. | High |
| | NAO Winter | n.s. | n.s. | **sig. (-)** | Low |
| | UWIND Annual | **sig. (+)** | n.s. | **sig. (+)** | High |
| | UWIND Spring | n.s. | **sig. (+)** | n.s. | Low |
| | UWIND Autumn | n.s. | n.s. | **sig. (+)** | Low |
| | RD Annual | n.s. | **sig. (+)** | **sig. (+)** | High |
| | RD Winter | **sig. (+)** | **sig. (+)** | n.s. | High |
| | RD Autumn | n.s. | **sig. (+)** | **sig. (+)** | High |

On the northwestern coast, *D. vulgaris* catch rates were positively associated with autumn WMAG and summer RD as indicated by GLS and DFA models.

On the southwestern coast, MAFA, DFA and GLS revealed that LPUE was negatively associated with winter SST. DFA models also showed that FE, winter WMAG and summer UWIND were positively associated with LPUE whereas yearly SST, spring and summer UPW and yearly, summer and autumn RD were positively associated with LPUE. Overall, winter SST was the environmental variable most likely associated with *D. vulgaris* LPUE.

On the south coast, MAFA analyses showed that winter and spring SST, yearly UWIND and winter RD were positively associated with LPUE whereas yearly NAO index was negatively associated with LPUE. DFA models showed that the yearly NAO index was negatively associated with LPUE whereas spring UWIND and yearly, winter and autumn RD were positively associated with LPUE. The GLS model indicated that the NAO winter index was negatively associated with LPUE whereas yearly and autumn UWIND and RD showed a positive relationship with LPUE. In the autumn, the yearly NAO index (negative), the yearly UWIND (positive) and yearly, winter and autumn RD (positive) were the environmental variables most likely associated with *D. vulgaris* LPUE.

## 4.4 Discussion

The survival of fish species during egg and larval stages (the underlying assumption of catch rates variability in the present study) are affected by several factors, such as the offshore winds, that induce upwelling and transport larvae offshore where development to adult stages is less likely to occur (e.g. Landaeta and Castro, 2002), predation (Bailey and Houde, 1989), water temperatures outside the range for survival and shortage of food (Cushing, 1996; Houde, 1987). Very few studies have however investigated the role of fishing practices and environmental parameters on sparids, particularly *Diplodus* species. To our knowledge, this study is the first showing that environmental factors have greater effect than fishing factors on *D. vulgaris* catch rates. The results showed also that the effects of environment on catch rates varied regionally, with seasonal events playing major role on short-term variations of catch rates of this species. The role of a selection of environmental parameters on the fishery of *D. vulgaris* on three geographical areas is discussed below.

### 4.4.1 Northwestern coast

On the Portuguese coast, the spawning activity of *D. vulgaris* occurs mainly during the autumn-winter period (Gonçalves and Erzini, 2000; Gonçalves et al., 2003). In the northwestern coast, a positive relationship was found between WMAG and catch rates of this species in the autumn. The wind magnitude is lower in the autumn and winter than in the spring and summer (Table 4.1). During the autumn, increased wind strength can strongly affect coastal drift currents (Moita, 1986) which are essential for increasing food supply for larvae (Fernández et al., 1993) and promoting retention/settlement of larvae in nearshore benthic environments (Borges et al., 2007; Vinagre et al., 2009). The early stages of development of *D. vulgaris* from juvenile stages take place in sheltered shallow coastal areas (Borges et al., 2007). Therefore, the arrival of early juvenile fish to benthic nursery areas is critical in determining the success of recruitment of these juveniles into adult populations because high mortality can occur during this process (Houde, 1987). Wind strength also affects the dispersion of freshwater plumes which is another important factor driving mobilisation of larvae in shallow estuarine environments (Tanaka, 1985). In addition to wind strength, the GLS model indicates that RD also affects *D. vulgaris* catch rates in the summer on the northwestern coast. The extended onset in the spawning season of this species is large (Gonçalves et al., 2003) and larvae, although in low numbers, can also be found in the summer (Borges et al., 2007). Larvae mortality is expected to be higher when larvae availability in the water column is higher (spawning season). However, the results indicate that larvae recruitment out of the peak of the spawning period also affects catch rates, such as in the summer when RD are positively associated with catch rates. RD is generally lower in the summer. However, peak discharges during this season can also promote the establishment of nursery areas thus enhancing larvae survival and recruitment over short periods of time (Vinagre et al., 2009). This highlights the importance of studies focused on evaluating the role of environmental factors driving the biological peak of reproduction of *D. vulgaris*.

### 4.4.2 Southwestern coast

Although the spawning season of *D. vulgaris* occurs mainly in the autumn-winter period, there are year on year variations associated with changes in SST (Gonçalves et al., 2003) because this parameter can determine the commencement and duration of the spawning. The effect of SST on spawning (larvae availability) is also shown in this study. The winter SST was the environmental variable most likely correlated with LPUE. In the Southwest coast, the decrease in SST from about 17 °C in the autumn to 15 °C in the winter (Table 4.1) is an environmental trigger for the beginning of spawning activity. At present, the mechanisms driving recruitment during the winter are not known. There is also insufficient knowledge on the factors influencing high catch rates over short timescales. In this study, we found that winter SST is negatively correlated with catch rates. This indicates that changes in SST affect the fishery and that this could be due to winter SST anomalies affecting the duration of the spawning activity as suggested by Gonçalves et al. (2003) and therefore the abundance of larvae production during this period.

### 4.3.2 Southern coast

The multi-model approach indicated that the NAO index is correlated with LPUE. During the positive NAO phase, winds from the northern sector predominate on the Portuguese coast (Borges et al., 2003; Lehodey et al., 2006), causing cold and dry weather in the South Portuguese regions. During periods of strong negative NAO, the coast is predominantly influenced by winds from the south and southwest sectors, leading to warmer temperatures and increased precipitation (Lehodey et al., 2006). This study shows that the NAO index is negatively correlated with *D. vulgaris* LPUE. Periods of predominantly negative NAO index, warmer temperatures and wet weather conditions are associated with years of good recruitment of this species. The partial contribution of each of these parameters to recruitment success is however complex because the NAO index operates indirectly and affects a high number of environmental factors, including SST, wind velocity and strength, precipitation and water circulation and stratification patterns which are expected to influence recruitment and growth, metabolic rates and food availability (Ottersen et al., 2001).

As mentioned above, precipitation increases when the NAO index is negative which in turn increases the amount of freshwater volumes (RD) discharged to the coast. During the study period, NAO index remained predominantly negative. On the southern coast, RD was positively associated with *D. vulgaris* LPUE during the autumn, winter and yearly mean. These seasons represent the beginning of the spawning period when adults are more dependent upon food abundance and availability of appropriate habitat conditions. RD is clearly an important process increasing inputs of organic matter to the coast and therefore increasing food abundance for larvae, juveniles and adults living on the coast (Cushing, 1996; Lloret et al., 2001).

The southern coast of Portugal is affected directly by upwelling under locally favourable, westerly winds which blow only occasionally. In contrast, downwelling occurs when the easterly winds are prevalent (Fiúza, 1983). In fact, for this region, UWIND (east–west direction component, representing the downwelling process) was positively correlated with *D. vulgaris* LPUE. The most likely explanation for this association is the influence of UWIND on coastal drift currents (Moita, 1986) which favour retention of fish larvae in inshore areas (Vinagre et al., 2009). It should be noted that over most of the southern coast bottom sediments are mostly composed of sand which are not favourable habitats for the early development of this species (Leitão et al., 2009). Therefore, UWIND helps to maintain larvae in nursery areas (estuaries and lagoons are essential for species larvae recruitment success; Vinagre et al., 2009, 2010) near the coast which otherwise would be transported to offshore areas and consequently reduce catch rates due to higher mortality and low recruitment as reported for other species with pelagic larval life cycles (Borges et al., 2003; Cury and Roy, 1989; Ullah et al., 2012).

## 4.5 Conclusions

A multi-model approach was used to describe the relationships between catch rates and environment and fisheries variables in three geographical areas of the Atlantic Iberian coast. Whilst environmental variables were found to be correlated with catch rates, no association was found between FE and LPUE. This can be explained by the fact that sparids inhabit rocky coastal areas (Gonçalves et al., 2003), and these decreases vulnerability to the artisanal gears (trammel and gill nets) used by the fishing fleet in Portuguese waters. However, hook and lines are used in areas on the South coast (Sagres) where the fishery is targeted to several Sparidae species including *D. vulgaris* (Erzini et al., 2003).

For fish species that spawn offshore and recruit inshore, the transport of eggs and larvae from spawning areas to nursery areas constitutes a critical process in its life cycle (Parrish et al., 1981). Results show that *D. vulgaris* is affected by oceanographic and climatic conditions (as can be expected because nearshore coastal areas are affected by offshore large-scale drivers) which impact on the development of reproductive strategies of fish communities in response to the most crucial factors regulating reproductive success (Bakun, 1985). Sparid settlement areas are situated at locations sheltered from the prevailing winds, usually bounded by promontories beyond which the coast is unprotected and exposed to wave action (García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). Planes and Lenfant (2002) hypothesised that

*D. sargus* in general have extremely large variance in individual reproductive success, owing to high fecundity and unpredictable chance matching of reproduction with oceanographic conditions permitting maturation, fertilisation, larval development and recruitment. Therefore, it would be useful also to introduce some recruitment hypothesis discussed in the fish ecology literature to explain short-term variability of *D. vulgaris* catch rates (a time lag of 2 years was used to settle hypothesis on recruitment). For instance, phenological processes such as match-mismatch (Cushing, 1996), mesoscale features, optimal environmental window (Cury and Roy, 1989) or the Stable Ocean Hypothesis (Lasker, 1978) advocate that stable physical and biological ocean conditions, such as the flow of currents and food availability, are important to the survival of young fish larvae and their future recruitment. Moreover, ‘Ocean triads’ (Agostini and Bakun, 2002) that defined that larvae’s fate might depend on: (a) enrichment processes – upwelling, mixing] and buoyant plumes; (b) concentration processes – convergence, frontal formation and water column stability; (c) retention processes within, or drift towards, appropriate habitats – water circulation, wind and these stochastic physical processes determine success recruitment, namely because the retention of larvae in more productive habitats very closed to the shore (suitable habitats near the coast or nursery areas such as lagoons which hydrology depends on coastal water changes cycle) may explain some of the results found in this study.

In summary, results from this study show that the influence of environmental factors on *D. vulgaris* catch rates varies between regions and seasons. Therefore, overall wind strength and river discharges were identified as good proxies to explain catch rate variability. These environmental variables are potentially important factors driving survival of larvae and recruitment of *D. vulgaris*. The general pattern found in the relationships across the three areas is consistent with the spawning season, highlighting the importance of seasonal environmental variability on the abundance of commercial stocks. However, it should be noted that seasonal events that are not temporally coincident with the peak of spawning also affect catch rates. Therefore, it is essential to consider this information when designing monitoring programmes targeted at sparids. The differences in the strength and significance of the relationships obtained between regions reveal local impacts on commercial catch rates of *D. vulgaris*. Therefore, consideration must be given to the biological sensitivity of this species to local environmental variability when developing and adopting future fishery management plans.

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## 4.8 Appendix

**Table 4.A1** Detailed results from MAFA, DFA and GLS modelling approaches used in the study, including explanatory variables related to *D. vulgaris* LPUE in three geographical regions (northwestern, southwestern and southern) on the coast of Portugal.

| | Northwestern | | | | | | | Southwestern | | | | | | | Southern | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Variables** | **MAFA values** (0.44) | **DFA AIC** (39.63) | **T** | **GLS AR process** | **AIC** | **p** | **slop** | **MAFA values** (0.44) | **DFA AIC** (66.35) | **T** | **GLS AR process** | **AIC** | **p** | **Slop** | **MAFA values** (0.44) | **DFA AIC** (54.20) | **t** | **GLS AR process** | **AIC** | **p** | **Slop** |
| **EFFORT** | 0.42 | 39.93 | 4.15 | ARMA(1,0) | 47.21 | 0.17 | 0.21 | 0.24 | **65.38** | **1.11** | no AR | 65.85 | 0.30 | 0.24 | -0.25 | 55.61 | -1.20 | ARMA(1,0) | 53.78 | 0.20 | -0.25 |
| **SST** | | | | | | | | | | | | | | | | | | | | | |
| **Annual** | -0.15 | 41.56 | -1.15 | ARMA(1,0) | 48.92 | 0.93 | 0.01 | -0.30 | **64.56** | **-1.46** | no AR | 65.11 | 0.18 | -0.30 | 0.24 | 56.21 | -0.06 | ARMA(1,0) | 57.32 | 0.12 | 0.189 |
| **Winter** | 0.18 | 40.67 | 2.08 | ARMA(1,0) | 47.91 | 0.82 | 0.03 | **-0.48** | **61.03** | **-2.53** | **no AR** | **61.92** | **0.03** | **-0.48** | **0.47** | 56.27 | 0.50 | ARMA(1,0) | 55.83 | 0.73 | 0.048 |
| **Spring** | -0.14 | 41.61 | -0.83 | ARMA(1,0) | 44.50 | 0.42 | 0.07 | -0.03 | 68.33 | -0.14 | no AR | 66.92 | 0.91 | -0.03 | **0.44** | 56.20 | -0.21 | ARMA(1,0) | 58.27 | 0.15 | 0.18 |
| **Summer** | -0.23 | 41.54 | -2.28 | ARMA(1,0) | 50.30 | 0.78 | 0.03 | -0.10 | 66.37 | -0.45 | no AR | 66.76 | 0.68 | -0.10 | -0.30 | 56.28 | -0.33 | ARMA(1,0) | 55.97 | 0.83 | -0.03 |
| **Autumn** | -0.16 | 41.62 | -1.51 | ARMA(1,0) | 49.79 | 0.88 | -0.02 | -0.14 | 67.77 | -0.87 | no AR | 66.56 | 0.54 | -0.14 | 0.17 | 56.73 | 0.07 | ARMA(1,0) | 55.64 | 0.90 | 0.02 |
| **NAO** | | | | | | | | | | | | | | | | | | | | | |
| **Annual** | 0.22 | 41.51 | 1.63 | ARMA(1,0) | 44.83 | 0.98 | 0.00 | -0.10 | 67.02 | -0.79 | no AR | 66.74 | 0.66 | -0.10 | **-0.60** | **51.91** | **-5.06** | **ARMA(1,0)** | **49.41** | **0.00** | **-0.47** |
| **Winter** | 0.37 | 40.98 | 3.47 | ARMA(1,0) | 49.33 | 0.79 | -0.03 | -0.05 | 67.70 | -0.38 | no AR | 66.89 | 0.83 | -0.05 | -0.42 | 55.85 | -0.94 | **ARMA(1,0)** | **56.00** | **0.01** | **-0.30** |
| **UPW** | | | | | | | | | | | | | | | | | | | | | |
| **Annual** | 0.34 | 39.89 | 3.69 | ARMA(1,0) | 47.14 | 0.35 | 0.15 | 0.09 | 68.35 | 0.53 | no AR | 66.79 | 0.71 | 0.09 | 0.12 | 56.16 | -0.21 | ARMA(1,0) | 57.82 | 0.62 | 0.07 |
| **Winter** | 0.15 | 41.59 | 1.24 | ARMA(1,0) | 49.74 | 0.65 | -0.06 | 0.07 | 67.31 | 0.38 | no AR | 66.85 | 0.78 | 0.07 | -0.02 | 56.56 | -0.05 | ARMA(1,0) | 55.85 | 0.40 | -0.16 |
| **Spring** | 0.07 | 40.19 | 1.08 | ARMA(1,0) | 49.85 | 0.40 | 0.09 | -0.17 | **65.97** | **-0.79** | no AR | 66.39 | 0.47 | -0.17 | 0.12 | 55.97 | 0.93 | ARMA(1,0) | 59.26 | 0.12 | -0.16 |
| **Summer** | 0.06 | 41.58 | 0.94 | ARMA(1,0) | 46.41 | 0.94 | 0.00 | -0.19 | **65.77** | **-0.91** | no AR | 66.21 | 0.40 | -0.19 | 0.33 | 55.82 | -1.05 | ARMA(1,0) | 55.49 | 0.77 | -0.06 |
| **Autumn** | 0.32 | 39.93 | 3.48 | ARMA(1,0) | 47.87 | 0.47 | 0.11 | 0.28 | 66.80 | 1.82 | no AR | 65.39 | 0.22 | 0.28 | -0.01 | 56.59 | -0.15 | ARMA(1,0) | 56.66 | 0.86 | 0.02 |
| **WMAG** | | | | | | | | | | | | | | | | | | | | | |
| **Annual** | -0.19 | 41.58 | -1.31 | ARMA(1,0) | 46.40 | 0.12 | -0.21 | 0.10 | 68.14 | 0.61 | no AR | 66.76 | 0.68 | 0.10 | 0.29 | 55.98 | -0.92 | no AR | 65.31 | 0.21 | 0.29 |
| **Winter** | 0.00 | 41.62 | -0.18 | no AR | 66.92 | 0.92 | -0.02 | 0.24 | **65.32** | **1.14** | no AR | 65.80 | 0.29 | 0.24 | 0.07 | 54.96 | 1.60 | ARMA(1,0) | 54.98 | 0.25 | 0.13 |
| **Spring** | -0.04 | 41.43 | -0.14 | ARMA(1,0) | 50.43 | 0.81 | -0.03 | -0.01 | 68.30 | -0.05 | no AR | 66.93 | 0.97 | -0.01 | 0.09 | 54.95 | 1.72 | ARMA(1,0) | 60.85 | 0.92 | 0.01 |
| **Summer** | 0.13 | 41.48 | 1.14 | ARMA(1,0) | 47.22 | 0.13 | -0.24 | 0.15 | 68.34 | 0.90 | no AR | 66.49 | 0.51 | 0.15 | 0.33 | 55.89 | -0.98 | ARMA(1,0) | 62.73 | 0.92 | 0.03 |
| **Autumn** | -0.32 | 41.20 | -1.88 | **ARMA(1,0)** | **45.24** | **0.00** | **0.10** | -0.19 | 67.54 | -1.15 | no AR | 66.26 | 0.42 | -0.19 | 0.42 | 54.56 | 1.82 | ARMA(1,0) | 56.98 | 0.33 | 0.13 |

**Table 4.A1**(cont.) Detailed results from MAFA, DFA and GLS modelling approaches used in the study, including explanatory variables related to *D. vulgaris* LPUE in three geographical regions (northwestern, southwestern and southern) on the coast of Portugal.

| | **Northwestern** | | | | | | | **Southwestern** | | | | | | | **Southern** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **MAFA** | **DFA** | | **GLS** | | | | **MAFA** | **DFA** | | **GLS** | | | | **MAFA** | **DFA** | | **GLS** | | | |
| **Variables** | **values** | **AIC** | **T** | **AR** | **AIC** | **p** | **slop** | **values** | **AIC** | **T** | **AR** | **AIC** | **p** | **Slop** | **values** | **AIC** | **t** | **AR** | **AIC** | **p** | **Slop** |
| | (0.44) | (39.63) | | **process** | | | | (0.44) | (66.35) | | **process** | | | | (0.44) | (54.20) | | **process** | | | |
| **UWIND** | | | | | | | | | | | | | | | | | | | | | |
| **Annual** | -0.05 | 41.63 | 0.158 | no AR | 66.86 | 0.79 | -0.06 | 0.13 | 67.62 | 0.82 | no AR | 66.60 | 0.57 | 0.13 | **0.57** | 56.01 | 0.29 | ARMA(1,0) | 55.90 | 0.76 | 0.06 |
| **Winter** | 0.01 | 41.62 | -0.15 | ARMA(1,0) | 44.35 | 0.47 | -0.07 | 0.19 | 66.88 | 1.29 | no AR | 66.22 | 0.40 | 0.19 | 0.19 | 56.26 | -0.16 | ARMA(1,0) | 54.13 | 0.94 | 0.01 |
| **Spring** | -0.01 | 41.32 | -0.06 | ARMA(1,0) | 45.58 | 0.35 | 0.12 | 0.00 | 68.27 | 0.02 | no AR | 66.93 | 0.99 | -0.00 | 0.31 | **53.48** | **2.84** | ARMA(1,0) | 57.15 | 0.10 | 0.31 |
| **Summer** | -0.25 | 41.53 | -1.63 | ARMA(1,0) | 45.74 | 0.36 | -0.14 | 0.13 | **66.21** | **0.61** | no AR | 66.60 | 0.57 | 0.13 | 0.32 | 55.07 | -1.44 | ARMA(1,0) | 57.50 | 0.45 | -0.16 |
| **Autumn** | 0.06 | 41.52 | 0.90 | ARMA(1,0) | 43.48 | 0.27 | 0.11 | -0.07 | 678.00 | -0.45 | no AR | 66.84 | 0.77 | -0.07 | 0.249 | 56.14 | 0.19 | **ARMA(1,0)** | **57.66** | **0.02** | **0.20** |
| **VWIND** | | | | | | | | | | | | | | | | | | | | | |
| **Annual** | 0.16 | 41.58 | 1.15 | ARMA(1,0) | 46.90 | 0.31 | 0.16 | -0.06 | 68.05 | -0.36 | no AR | 66.87 | 0.80 | -0.06 | -0.02 | 55.57 | 1.26 | no AR | 66.93 | 0.94 | -0.02 |
| **Winter** | 0.15 | 40.59 | 1.80 | ARMA(1,0) | 43.68 | 0.33 | 0.10 | -0.08 | 68.35 | -0.45 | no AR | 66.82 | 0.74 | -0.08 | 0.32 | 55.11 | 1.72 | ARMA(1,0) | 56.34 | 0.13 | 0.24 |
| **Spring** | 0.14 | 41.61 | 1.21 | ARMA(1,0) | 43.30 | 0.35 | 0.08 | 0.03 | 68.22 | 0.19 | no AR | 66.92 | 0.90 | 0.03 | 0.10 | 56.21 | -0.26 | ARMA(1,0) | 55.72 | 0.68 | 0.06 |
| **Summer** | -0.17 | 41.56 | -1.41 | ARMA(1,0) | 47.83 | 0.20 | 0.18 | -0.14 | 68.34 | -0.85 | no AR | 66.53 | 0.53 | -0.14 | -0.17 | 56.19 | 0.25 | ARMA(1,0) | 56.14 | 0.15 | 0.12 |
| **Autumn** | 0.05 | 41.31 | -0.07 | ARMA(1,0) | 45.66 | 0.70 | -0.03 | -0.02 | 68.35 | -0.14 | no AR | 66.93 | 0.92 | -0.02 | -0.18 | 56.22 | 0.59 | ARMA(1,0) | 55.70 | 0.68 | 0.06 |
| **RD** | | | | | | | | | | | | | | | | | | | | | |
| **Annual** | -0.13 | 41.48 | -1.12 | ARMA(1,0) | 48.59 | 0.64 | -0.06 | -0.19 | **65.79** | **-0.90** | no AR | 66.23 | 0.41 | -0.19 | 0.40 | **48.58** | **4.94** | **ARMA(1,0)** | **48.58** | **0.01** | **0.44** |
| **Winter** | -0.01 | 41.44 | 0.23 | ARMA(1,0) | 49.36 | 0.99 | 0.00 | -0.05 | 67.96 | -0.28 | no AR | 66.89 | 0.84 | -0.05 | **0.50** | **52.13** | **5.77** | ARMA(1,0) | 49.57 | 0.08 | 0.34 |
| **Spring** | -0.09 | 40.98 | -1.06 | ARMA(1,0) | 43.92 | 0.27 | -0.11 | 0.01 | 67.45 | 0.16 | no AR | 66.93 | 0.95 | 0.01 | -0.07 | 56.45 | -0.14 | ARMA(1,0) | 56.01 | 0.46 | 0.07 |
| **Summer** | -0.15 | 41.49 | -1.34 | **ARMA(1,0)** | **46.22** | **0.00** | **0.05** | -0.22 | **65.52** | **-1.04** | no AR | 65.98 | 0.33 | -0.22 | 0.09 | 56.47 | 0.36 | ARMA(1,0) | 55.35 | 0.78 | 0.05 |
| **Autumn** | -0.21 | 39.85 | -2.42 | ARMA(1,0) | 49.57 | 0.35 | -0.12 | -0.28 | **64.83** | **-1.35** | no AR | 65.36 | 0.22 | -0.28 | 0.12 | **54.15** | **2.26** | **ARMA(1,0)** | **54.19** | **0.03** | **0.42** |

# SECTION II

## Recruitment, swimming capabilities and habitat selection in temperate fish larvae

# CHAPTER 5

## Swimming abilities of temperate pelagic fish larvae prove that they may control their dispersion in coastal areas

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# SWIMMING ABILITIES OF TEMPERATE PELAGIC FISH LARVAE PROVE THAT THEY MAY CONTROL THEIR DISPERSION IN COASTAL AREAS

## Abstract

The Sense Acuity and Behavioural (SAAB) Hypothesis proposes that the swimming capabilities of temperate fish larvae and their sense acuity triggers behavioural responses which allow these larvae to find and swim towards nursery areas present along with coastal areas, which are crucial for their successful recruitment. The development of these swimming capabilities and behaviours that interact with physical transport processes has been recognized as influencing larval dispersion outcomes. Despite the recent work done about swimming performance of fish larvae, little is known about how horizontal swimming capabilities varies along ontogeny on Sparidae larvae. The swimming capability of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae along ontogeny, and their relationship with their physiological condition were studied. Thus, critical swimming speed ($U_{crit}$) and the distance swam (km) during endurance tests were determined for fish larvae with 15, 25, 35, 45 and 55 days post-hatching (DPH) and their physiological condition was assessed by analysing their RNA and DNA contents, and protein content. Results showed that white seabream larvae became more competent swimmers along the ontogeny: $U_{crit}$ increased from 1.1 cm $s^{-1}$ (15 DPH) and 23 cm $s^{-1}$ (5o and 55 DPH); and the distance swam by larvae in the endurance experiments increased from 0.01 km (15 DPH) to 86.5 km (45 DPH). This finding supports one of the premises of the SAAB hypothesis that proposes that fish larvae emerging from pelagic eggs can influence their transport and distribution in coastal areas due to their swimming capabilities. These results should be considered in individual-based models of the larval transport which can be crucial to understand population dynamics and connectivity, and for management and conservation of fish stocks.

**Keywords**: fish larvae; recruitment; dispersion, swimming capacity, $U_{crit}$, endurance

## 5.1 Introduction

Temperate fish species that spawn at sea and where the larvae remain in the pelagic environment for weeks or months before they settle, must rely on currents, tides, and weather events (Montgomery et al., 2001) have their eggs and larvae advected from spawning sites (Roberts, 1997), either to coastal nursery areas (i.e., coastal lagoons, estuaries, and rocky shore areas) or they become lost at sea (Teodósio et al., 2016). It has been recognized that this passive stage is short and is greatly influenced by biological and physical processes (Leis, 2010). Since fish larvae develop swimming capabilities that may exceed typical coastal currents and possess sensorial abilities that may help larvae finding coastal nursery habitats (Fisher et al., 2000; Leis, 2010; Wolanski and Kingsford, 2014; Atema et al., 2015; Teodósio et al., 2016).

According to the Sense Acuity And Behavioural (SAAB) hypothesis (Teodósio et al., 2016), if larvae drift passively through water currents the recruitment of temperate fish larvae is unlikely and thus the sense acuity of temperate fish larvae and their behavioural responses to nursery cues presented in coastal areas (e.g., odour, sound, visual and geomagnetic cues) are crucial for recruitment success. As the sensorial acuity and swimming capacity increase along ontogeny (Fisher et al., 2000; Leis, 2006; Wolanski and Kingsford, 2014; Atema et al., 2015; Teodósio et al., 2016), according to SAAB hypothesis, it is expected that larval sensorial cues to detect and navigate to nursery areas change hierarchy during the larval development (Teodósio et al., 2016). Thus, in offshore areas, the post-flexion temperate fish larvae are guided towards the coast by sun compass orientation, earth's geomagnetic field, and by an innate behaviour; when they are in coastal areas, they are able to detect and follow nursery cues through olfaction, audition and vision (Leis et al., 1996; Wright et al., 2005; Montgomery et al., 2006; Mouritsen et al., 2013; Paris et al., 2013; Faillettaz et al., 2015; Teodósio et al., 2016). After finding nursery cues, temperate fish larvae orientate their swimming directly to nursery habitats (Leis et al., 1996; Atema et al., 2002; Kingsford et al. 2002; Wolanski and Kingsford, 2014; Teodósio et al., 2016) and maintain their position there (Watt-Pringle and Strydom, 2003) using distinct swimming behaviours which vary according to the cues concentration and are conciliated with diel rhythms (Teodósio et al., 2016). Thus, the development of swimming capabilities and behaviours that interact with physical transport processes has been recognized as having influence on larval dispersion outcomes (Stobutzki and Bellwood, 1997; Wolanski et al., 1997; Armsworth, 2001; Sponaugle et al., 2002; Atema et al., 2002; Leis, 2006; Drake et al., 2011) and settlement location (Wright et al., 2005).

The post-flexion larvae of some fish species are strong swimmers displaying active horizontal and vertical capabilities (Leis et al., 1996; Leis and Carson-Ewart, 2003; Stobutzki and Bellwood, 1997). Some of these fish larvae can swim horizontally at speeds greater than ambient currents, in a highly directional way and at long distances (Leis et al., 1996; Leis and Carson-Ewart, 2003; Stobutzki and Bellwood, 1997; Atema et al., 2015). Fish larvae can also adjust their vertical position (Leis et al., 1996), which allows for the active selection of currents that facilitate their transport (Sponaugle et al., 2002; Paris and Cowen, 2004), and search for a nursery habitat. These swimming capabilities also have significant consequences for several ecological processes (Westcott and Graham, 2000), such as the response of larvae to predators, foraging abilities (Weins et al., 1995; Fisher, 2005; Leis, 2006; Jørgensen et al., 2014), interaction with conspecifics, and biotic and abiotic conditions experienced (Weins et al., 1995). Understanding the mechanisms that influence larval dispersal and fish population dynamics is essential to the management of marine fish populations (Kashef et al., 2014).

Most studies on the swimming performance of fish larvae have been performed on wild tropical species (Stobutzki and Bellwood, 1994, 1997; Fisher et al., 2000, 2005; Fisher, 2005; Leis et al., 2007, 2009), while fewer studies were done on temperate species (Koumoundouros et al., 2009; Faria et al., 2011b, 2014; Peck et al., 2012; Silva et al., 2015). So, little is known about how horizontal swimming capabilities of temperate fish larvae affect retention in nursery areas along ontogeny (Leis, 2010).

Therefore, we aim to determine the swimming capacity of laboratory-reared white seabream *Diplodus sargus* (Linnaeus, 1758) (Pisces: Sparidae) larvae along the ontogeny. For this propose, we conducted laboratory experiments measuring the critical swimming speed ($U_{crit}$) and the maximum distance swum during swimming endurance trial done throughout ontogeny (15 to 55 days post-hatching). The effect of their physiological condition (nucleic acids and proteins quantification) on swimming capacity was also evaluated. We hypothesized that swimming abilities of white seabream larvae increase along ontogeny, with increased body length, and physiological conditions, which may allow larvae to orientate towards a nursery habitat.

## 5.2 Material and methods

### 5.2.1 Model species

The *Diplodus* genus sustains important commercial and recreational fisheries along the Portuguese coast, as the white seabream *Diplodus sargus* (Linnaeus, 1758) (Pisces: Sparidae) (Erzini et al., 1999; Veiga et al., 2010). The white seabream is a demersal fish present along the Northeastern Atlantic and the Mediterranean Sea (Pajuelo and Lorenzo, 2002), being abundant along the Portuguese coast over the continental shelf (Leitão et al., 2007; Abecasis et al., 2013), lagoons (Ribeiro et al., 2006), and estuaries (Faria et al., 2006). This species is generally more abundant from shore to 50 m depth (Harmelin-Vivien et al., 1995; Lloret and Planes. 2003), inhabiting coastal rocky reefs, sandy bottoms and seagrass beds (Pajuelo and Lorenzo, 2002). White seabream adults spawn in coastal areas (Faria et al., 2006; Leitão et al., 2007) and eggs and larvae can be dispersed by marine currents (Di Franco et al., 2012) before reaching favourable habitats for recruitment, like sandy-rocky bottoms (Garcia-Rubies and Marcpherson, 1995; Harmelin-Vivien et al., 1995), coastal lagoons (Monteiro et al., 1990) and estuaries (Faria et al., 2006; Gonçalves et al., 2015).

### 5.2.2 Overview of the experimental design

Experiments were conducted in a temperature-controlled room and quiet conditions, at the Aquaculture Research Station (EPPO) of the Portuguese Institute for the Ocean and Atmosphere (IPMA) in Olhão (Portugal) during 2016. White seabream larvae were obtained from natural spawns of wild broodstocks held at EPPO. Exogenous feeding started at 3 DPH at the onset of the mouth opening (Ortiz-Delgado et al., 2003). Larvae were fed *ad libitum* with rotifers *Brachionus* sp. (Pallas, 1766) for the first 14 DPH, with rotifers, branchiops *Artemia* spp. (Leach, 1819) nauplii, and dry feed (Caviar from BernAqua) from 15 to 21 days post-hatching (DPH), and then only with a dry feed of increasing granule size as development progressed.

The swimming capacity of white seabream larvae was tested with critical swimming speed ($U_{crit}$) and swimming endurance experiments performed in nine occasions along ontogeny (15, 20, 25, 30, 35, 40, 45, 50, and 55 DPH) (Table 5.1).

Locomotory behaviour observations were done to evaluate the activity of larvae, through a series of Modal Action Patterns (MAPs) observations. Subsequently, larvae were placed in liquid nitrogen and then stored at -80 ºC for biochemical analysis (nucleic and protein analysis). Photographs of larvae were taken under a stereoscope (Leica 58APO, coupled with a camera Leica MC170 HC) to measure the total length (TL; ±0.01 mm) using Image J software (version 1.50i). Then, larvae were freeze-dried and weighed (±1 µg dry weight – DW) on an electronic microbalance (Sartorius M5P). These larvae were used posteriorly for biochemical analyses.

**Table 5.1** Number of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae used in locomotory behaviour experiments: Critical swimming speed ($U_{Crit}$), Endurance (water flow speed is shown), Modal Action Patterns (MAPs); at nine occasions along ontogeny – 15, 20, 25, 30, 35, 40, 45, 50, and 55 days post-hatching (DPH).

| **Experiment** | 15 DPH | 20 DPH | 25 DPH | 30 DPH | 35 DPH | 40 DPH | 45 DPH | 50 DPH | 55 DPH |
|---|---|---|---|---|---|---|---|---|---|
| **$U_{Crit}$** | 15 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
| **Endurance**<br>flow speed (cm s$^{-1}$) | 8<br>1.5 | - | 8<br>5.0 | - | 8<br>6.0 | - | 8<br>10.0 | - | - |
| **MAPs** | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |

### 5.2.2.1 Critical swimming speed ($U_{crit}$)

The critical swimming speed ($U_{crit}$, cm s$^{-1}$) of white seabream larvae was assessed in a multilane swimming chamber, following the design of Stobutzki and Bellwood (1994, 1997) and later adapted by Faria et al. (2009). The chamber was made of transparent Perspex® comprising six parallel swimming lanes (30 mm wide, 50 mm high, 180 mm long) (Figure 5.1). Plastic flow diffusers (∅ - 5 mm; 40 mm long) were placed after the intake water valve to uniformize flow in the different lanes. And two mesh bands were installed in both ends of each lane of the chamber to retain larvae. For details about swimming chamber characteristics see Faria et al. (2009).

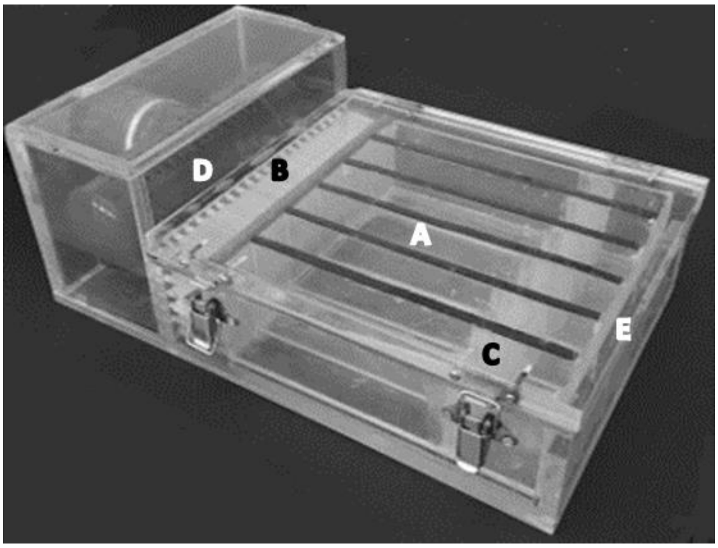

**Figure 5.1** Swimming chamber used in critical swimming speed and swimming endurance experiments of white seabream Diplodus sargus (Linnaeus, 1758) larvae (based on Stobutzki and Bellwood [18, 30], and adapted by Faria et al. [53]). The chamber comprise six parallel swimming lanes (A) with the following dimensions 180 × 30 × 50 mm (L × W × H) two sets of plastic flow diffusers (B) (∅ - 5 mm; 40 mm L) placed to uniformize flow in the different lanes, two mesh bands installed in both ends of each lane of the chamber to retain larvae (C), (D) correspond to water intake and (E) correspond to the water outlet.

Larvae were randomly selected from the holding tank and transferred to a swimming chamber lane. Each larva was tested individually and allowed to acclimate for 5 min at a flow speed of 1 cm $s^{-1}$. Individuals with stress symptoms observed during the acclimation period were replaced by another larva. After the acclimation period, $U_{Crit}$ measurement was carried increasing current velocity by approximately 1 cm $s^{-1}$ every 2 min until larvae were unable to swim against the current for 2 min. The maximum flow speed tested was 22 cm $s^{-1}$. $U_{crit}$ was calculated following equation 1 (Brett, 1964):

$$U_{crit} = U + (t/t_i \times U_i) \text{ (Equation 1)}$$

where U is the second last velocity increment that a larva could maintain, $U_i$ is the velocity increment (1 cm $s^{-1}$), t is the time swam in the final velocity increment, and $t_i$ is the time interval for each speed velocity (2 min). Larvae were not fed during the swimming experiments to avoid any effect on swimming performance.

### 5.2.2.2 Swimming Endurance

Swimming endurance measures time that larvae swim at a constant speed until exhaustion (Pattrick and Strydom, 2009; Faria et al., 2011a). The multilane swimming chamber used to calculate critical swimming speed ($U_{crit}$) was also used in this test. Swimming endurance was performed at ages 15, 25, 35, and 45 DPH for eight larvae in each day (n = 32; Table 5.1). A single larva was randomly collected from the holding tank and placed in a speed-lane to acclimatize for 5 minutes at 1 cm $s^{-1}$. Individuals showing symptoms of stress during the acclimation period were removed and replaced. After the acclimatization period, water velocity was increased rapidly up to a ~50% of the maximum $U_{crit}$ reached for each age (Faria et al., 2011a) (Table 5.1). Larvae were video recorded with a KONIG SAS-IPCAM110B camera during the entire experiment to determine the fatigue time (i.e., until larva stopped swimming and got trapped in the retaining mesh). Swimming duration and flow speed were used to calculate the distance swam by each larva (Faria et al., 2011a). Larvae were not fed during endurance experiments to avoid the effect of feeding on swimming performance.

### 5.2.2.3 Locomotory behavioural observations

Modal action patterns (MAPs) were assessed to categorized white seabream larvae behaviour (Barlow, 1968; Silva et al., 2014), namely: locomotory movements (*swimming* – forward movement of the larva through the water column; *pause-swimming* - short-pulse movements of the larva in the water column), and undirected movements (*pause* – larva was motionless and stationary in the water column; *sink* – larva was motionless and sank to the bottom). Ten larvae were tested at each one of the nine experiment-days along ontogeny (15, 20, 25, 30, 35, 40, 45, 50, and 55 DPH), in a total of 90 larvae (Table 5.1). Larvae behaviour were tested in a 500-ml glass beaker with *ad-libidum* food for 1-minute interval.

### 5.2.2.4 Physiological condition

The concentration of nucleic acids (RNA, DNA) were quantified for each fish larva using a microplate fluorescent assay (Wagner et al. 1998; Caldarone et al. 2001). The extraction nucleic acids from larvae involved a mechanical (sonication: 3 pulses 50 A during 1 min) and a chemical homogenization (cold sarcosyl Tris-EDTA extraction buffer) of tissues, addition of Gel Red (GR) (a nucleic acid fluorochrome dye), and subsequent fluorescence-photometric measurements. Fluorescence was measured on a microplate reader (Biotek synergy HT model SIAFRTD) with an excitation wavelength of 365 nm and an emission wavelength of 590 nm. Following the first scan (total fluorescence of RNA and DNA), ribonuclease A (Type-II A) solution was added to each well, and the concentration of DNA was calculated directly from the standard curve. The RNA fluorescence was calculated subtracting the DNA fluorescence (second scan) from total fluorescence (first scan). Concentrations were determined by running standard curves of DNA-GR and RNA-GR every day with known concentrations of λ-phagus DNA (0.25 $\mu g\ \mu l^{-1}$) and 16S−23S *E. coli* RNA (4 $\mu g\ \mu l^{-1}$) (Roche). The average ratio of DNA and RNA slopes (average ± SD) was 3.56 ± 0.59. The RNA/DNA ratios were standardized (sRD) using DNA and RNA slope ratios and the reference slope ratio of 2.4 (Caldarone et al., 2006).

Aliquots of the bicinchoninic acid protein assay were used for protein quantification (Smith et al., 1985). The extraction procedure consisted in using a sarcosyl solution for the nucleic acids extraction with a copper sulfate:bicinchoninic acid (1:50) as protein reagent. Protein concentration (µg protein $mg^{-1}$ dry weight) was quantified through a standard curve using bovine serum albumin P-0914 (SIGMA). The absorbance was measured at 562 nm after incubation at 37 °C for 30 min on a microplate reader (Biotek synergy HT model SIAFRTD).

The physiological condition of larvae was estimated with nucleic acid- and protein-derived indices, namely: RNA (µ $mg^{-1}$ DW), DNA (µ $mg^{-1}$ DW), sRD (standardized RNA/DNA ratios), resRNA (residual-based index from RNA content), and proteins (µg $larva^{-1}$). The residual-based index from RNA was used to remove the allometric size effect and derived from the residuals of a global regression of ln(RNA + 1 on ln(DW)) (Chícharo et al., 1998; Silva et al., 2014). The effect of size on these indices was tested with a linear model.

### 5.2.3 Data analyses

Linear regression analyses were performed to analyse the relations between white seabream swimming $U_{crit}$ and distance swam during endurance tests with a set of independent variables, namely: a) days post-hatching – DPH, b) total length – TL, mm, c) RNA, µg $mg^{-1}$ DW; d) DNA, µg $mg^{-1}$ DW, e) sRD; f) resRNA; g) µg protein $larva^{-1}$. The model with the highest $r^2$ value was chosen. The potential of independent variables to explain the variability of $U_{crit}$ and distance swam during endurance tests was conducted with a covariance (ANCOVA) analyses. All statistical analyses were done in R (version 3.5.2). Data are presented as mean ± standard deviation (SD).

## 5.3 Results

The swimming performance of white seabream larvae was tested in 175 individuals, 143 were tested for critical swimming speed ($U_{crit}$) and 32 for endurance trials. There is an exponential length-weight relationship for the larvae tested in these experiments (Figure 5.2a, Table 5.2). The total length of white seabream larvae increased along ontogeny, varying between 1.3 and 29.5 mm between 15 and 55 DPH (Figure 5.2b, Table 5.2).

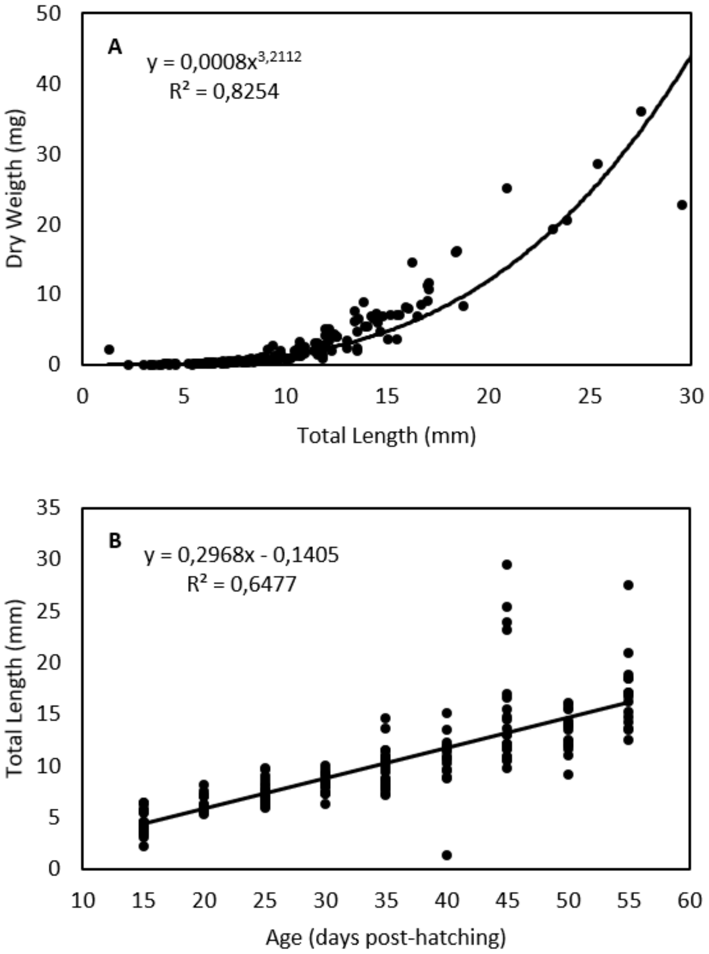

**Figure 5.2** Relationships between total length (mm) and dry weight (mg) (N = 175) (a), and between age (days post-hatching) and total length (mm) (N = 175) (b) for white seabream *Diplodus sargus* (Linnaeus, 1758) larvae tested for swimming capabilities along ontogeny (15, 20, 25, 30, 35, 40, 45, 50, and 55 days post-hatching).

**Table 5.2** Mean and standard deviation values of critical swimming speed (U$_{crit}$), swam distance in the endurance experiment, total length (TL), dry weight (DW), nucleic acid concentrations (RNA, DNA), sRD (standardized RNA:DNA ratio), resRNA (RNA residuals), and protein concentration (Proteins) for seabream *Diplodus sargus* (Linnaeus, 1758) larvae across ages (DPH – days post-hatching). N is the number of larvae used in each age. (*analytical parameters refer to the last day of swimming endurance; the period of the test in these two ages varied between 1 and 10 days).

| **U$_{crit}$** | **N** | **TL** (mm) | **DW** (mg) | **U$_{crit}$** (cm s$^{-1}$) | **RNA** ($\mu$ mg$^{-1}$ DW) | **DNA** ($\mu$ mg$^{-1}$ DW) | **sRD** | **resRNA** | **Proteins** ($\mu$ larva$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| 15 DPH | 15 | 3.9 ± 0.8 | 0.1 ± 0.0 | 1.9 ± 0.7 | 33.7 ± 25.6 | 42.3 ± 28.8 | 0.4 ± 0.2 | -0.4 ± 0.8 | 302.7 ± 195.3 |
| 20 DPH | 16 | 6.4 ± 0.9 | 0.2 ± 0.1 | 5.4 ± 1.3 | 27.4 ± 10.9 | 39.4 ± 15.0 | 0.5 ± 0.2 | 0.0 ± 0.7 | 566.7 ± 238.6 |
| 25 DPH | 16 | 6.8 ± 0.7 | 0.4 ± 0.2 | 5.4 ± 1.8 | 24.6 ± 8.6 | 36.3 ± 11.7 | 0.5 ± 0.1 | 0.1 ± 0.4 | 524.2 ± 206.2 |
| 30 DPH | 16 | 8.3 ± 1.0 | 0.5 ± 0.2 | 4.5 ± 1.1 | 22.6 ± 6.9 | 28.1 ± 7.4 | 0.6 ± 0.2 | 0.2 ± 0.3 | 410.4 ± 147.9 |
| 35 DPH | 16 | 8.6 ± 1.1 | 0.7 ± 0.4 | 7.6 ± 2.7 | 20.1 ± 6.0 | 25.0 ± 7.7 | 0.6 ± 0.2 | 0.1 ± 0.3 | 413.4 ± 244.8 |
| 40 DPH | 16 | 10.5 ± 3.0 | 1.6 ± 0.7 | 11.3 ± 4.0 | 17.4 ± 5.0 | 23.3 ± 6.1 | 0.5 ± 0.1 | 0.3 ± 0.2 | 279.2 ± 154.4 |
| 45 DPH | 16 | 12.0 ± 1.9 | 2.6 ± 1.6 | 14.1 ± 5.3 | 13.5 ± 4.7 | 17.9 ± 5.7 | 0.5 ± 0.1 | 0.1 ± 0.3 | 619.6 ± 500.2 |
| 50 DPH | 16 | 13.3 ± 2.0 | 5.6 ± 2.1 | 19.6 ± 5.3 | 7.4 ± 2.8 | 16.3 ± 3.9 | 0.3 ± 0.1 | -0.3 ± 0.3 | 1168.6 ± 492.4 |
| 55 DPH | 16 | 17.0 ± 3.6 | 12.1 ± 8.4 | 22.0 ± 3.19 | 6.0 ± 2.0 | 12.0 ± 1.7 | 0.4 ± 0.1 | -0.2 ± 0.3 | 1890.4 ± 1221.2 |

| **Endurance** | **N** | **TL** (mm) | **DW** (mg) | **Distance** (km) | **RNA** ($\mu$ mg$^{-1}$ DW) | **DNA** ($\mu$ mg$^{-1}$ DW) | **sRD** | **res RNA** | **Proteins** ($\mu$ larvae$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| 15 DPH | 8 | 5.8 ± 0.6 | 0.1 ± 0.1 | 0.1 ± 0.1 | 25.3 ± 9.5 | 44.5 ± 22.7 | 0.4 ± 0.1 | 0.0 ± 0.5 | 831.0 ± 46.4 |
| 25 DPH | 8 | 8.3 ± 1.2 | 0.9 ± 0.4 | 1.0 ± 0.4 | 19.5 ± 4.5 | 30.4 ± 8.2 | 0.5 ± 0.2 | 0.1 ± 0.2 | 566.2 ± 111.0 |
| 35 DPH* | 8 | 11.6 ± 1.7 | 3.2 ± 2.0 | 5.0 ± 6.0 | 12.8 ± 3.0 | 22.3 ± 3.3 | 0.4 ± 0.1 | -0.1 ± 0.2 | 1516.4 ± 1255.8 |
| 45 DPH* | 8 | 20.3 ± 6.1 | 15.0 ± 8.9 | 54.1 ± 22.1 | 12.5 ± 4.6 | 21.1 ± 5.5 | 0.4 ± 0.1 | 0.1 ± 0.4 | 2293.6 ± 1127.7 |

The $U_{crit}$ increased throughout ontogeny from 1.9 ± 0.7 cm $s^{-1}$ at 15 DPH up to 21.9 ± 3.2 cm $s^{-1}$ at 55 DPH (Figure 5.3, Table 5.2). $U_{crit}$ ranged from 1.1 cm $s^{-1}$ at 15 DPH and 23.0 cm $s^{-1}$ at 50 and 55 DPH, which corresponds to 2.0 to 25.1 body lengths (bl) $s^{-1}$, respectively. $U_{crit}$ variability was best explained by age ($p< 0.001$) (Figure 5.3, Table 5.3).

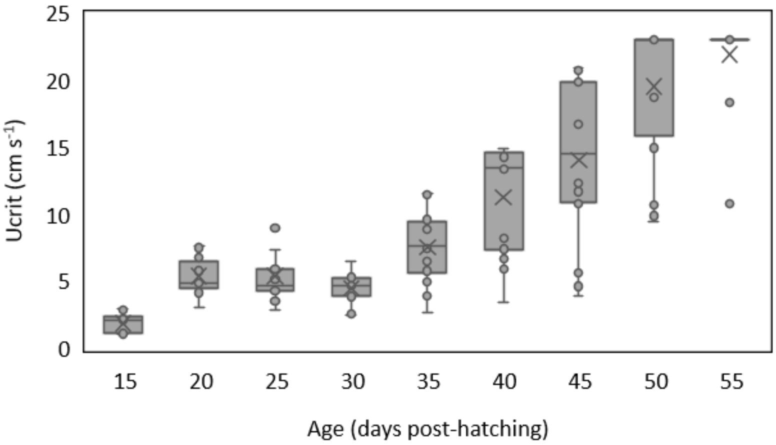

**Figure 5.3** Variation of critical swimming speed ($U_{crit}$; cm $s^{-1}$) for white seabream *Diplodus sargus* (Linnaeus, 1758) larvae along ontogeny (15, 20, 25, 30, 35, 40, 45, 50, and 55 days post-hatching). The lines inside the boxes represent the median, × represents the mean, the lower and upper box limits represent the 25th and the 75th percentiles, whiskers represent the standard deviation, while dots represent the outliers.

The distance swam by larvae in the endurance tests increased along ontogeny (Figure 5.4). The total length of larvae explained the variation of distance swam during the endurance experiments ($p< 0.001$; Table 5.3). White seabream larvae swam an average distance of 0.1± 0.1) km at 15 DPH (minimum distance at 15 DPH – 0.01 km) and 54.1 ± 22.1 km at 45 DPH (maximum distance at 45 DPH – 86.5 km) (Figure 5.4, Table 5.2). Larvae swam for 1.3 ± 0.9 h at 15 DPH and 150.1 ± 61.3 h at 45 DPH, and ranged from 0.3 h (15 DPH) to 240.2 h (45 DPH). It can be observed a high increment at age 35 and a larger one at 45 DPH.

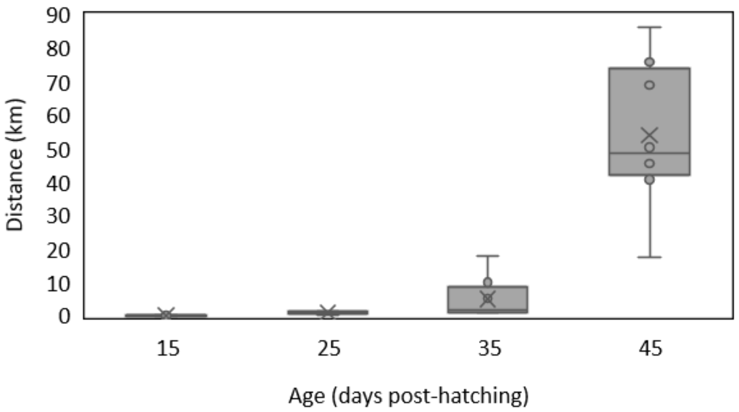

**Figure 5.4** Distance (km) swam by white seabream *Diplodus sargus* (Linnaeus, 1758) larvae during endurance swimming experiments at 15, 25, 35, and 45 days post-hatching. The lines inside the boxes represent the median, × represents the mean, the lower and upper box limits represent the 25th and the 75th percentiles, whiskers represent the standard deviation, while dots represent the outliers.

The concentration of nucleic acids (RNA, DNA) and sRD of white seabream larvae decreased with age and with swimming performance ($U_{crit}$, distance swam during endurance experiments), but the opposite trend was observed for the resRNA index and protein concentration (Figure 5.5, Table 5.2). However, no condition indexes explained the swimming performance variability (Figure 5.5, Table 5.3).

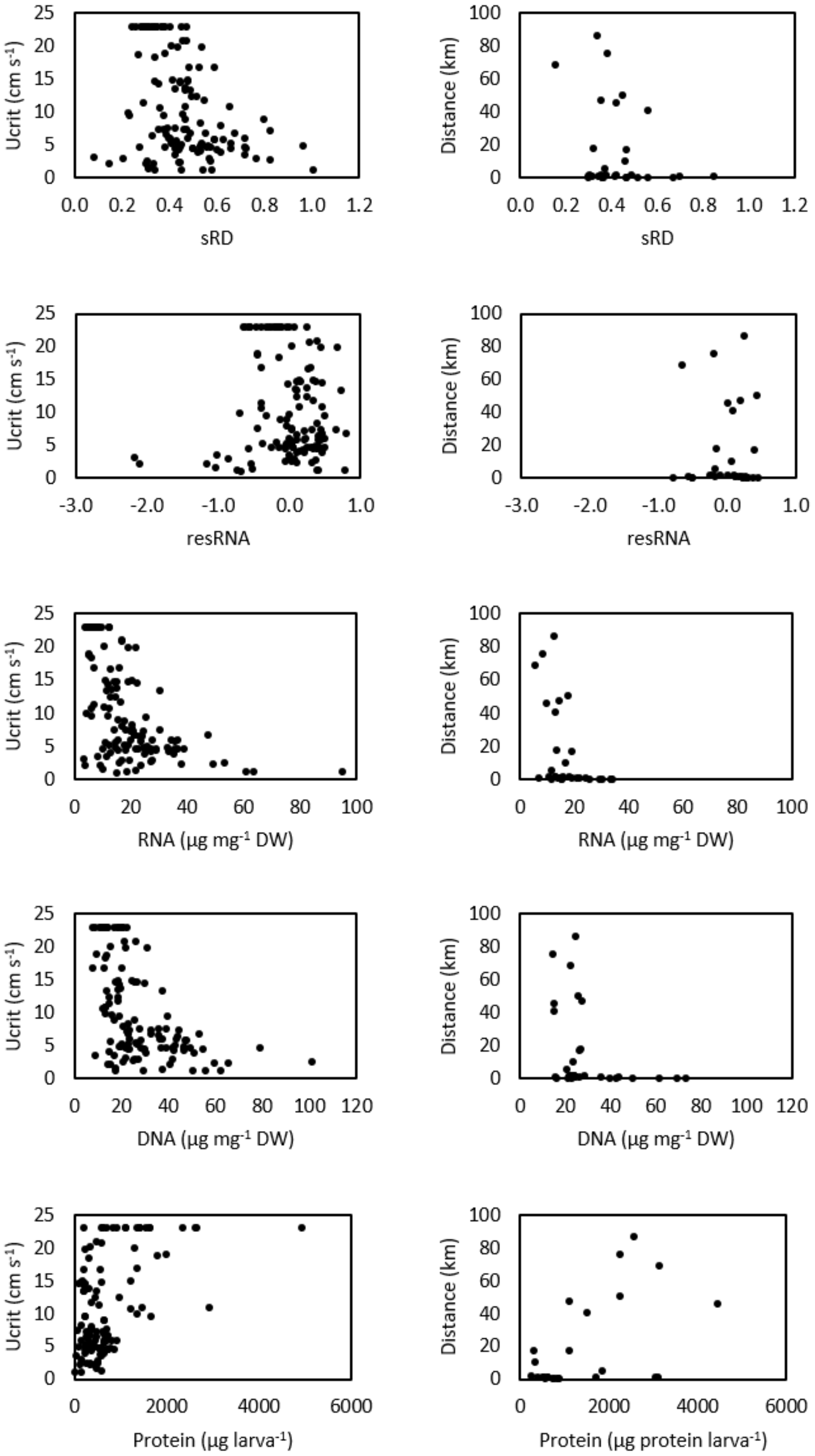

**Figure 5.5** Relation between critical swimming speed ($U_{crit}$, cm $s^{-1}$) (left panels) and distance (km) swam during endurance experiments (right panels) with condition indexes (RNA, µg RNA $mg^{-1}$ DW; DNA, µg DNA $mg^{-1}$ DW; sRD, standardized RNA:DNA ratio; resRNA, residuals of RNA; concentration of proteins, µg protein $larva^{-1}$) for white seabream *Diplodus sargus* (Linnaeus, 1758) larvae tested along ontogeny (15, 20, 25, 30, 35, 40, 45, 50, and 55 days post-hatching (DPH) for $U_{crit}$ experiments, at 15, 25, 35, and 45 DPH for endurance experiments). An increase in sRD and resRNA indexes corresponds to the better nutritional condition.

**Table 5.3** Linear regression analysis between white seabream *Diplodus sargus* (Linnaeus, 1758) larvae age (DPH – days post-hatching), total length (TL, mm), dry weight (DW, mg), nucleic acid concentrations (RNA, µg RNA $mg^{-1}$ DW; DNA, µg DNA $mg^{-1}$ DW; sRD, standardized RNA:DNA ratio; and resRNA, residuals of RNA), and proteins concentrations (µg protein $larva^{-1}$) and critical swimming speed ($U_{crit}$, cm $s^{-1}$) and distance (km) swam during the endurance experiment.

| **Variables** | **Linear equation** | **$R^2$** | **p** |
|---|---|---|---|
| **$U_{crit}$** | | | |
| $U_{crit}$ vs. DPH | y = 0.490x - 6.980 | 0.729 | <0.001 |
| $U_{crit}$ vs. TL | y = 1.392x - 3.226 | 0.625 | <0.001 |
| $U_{crit}$ vs. RNA | y = -0.321x + 16.378 | 0.326 | <0.001 |
| $U_{crit}$ vs. DNA | y = -2.069x + 17.410 | 0.288 | <0.001 |
| $U_{crit}$ vs. sRD | y = -17.047x + 18.337 | 0.159 | <0.001 |
| $U_{crit}$ vs. resRNA | y = -1.521x + 10.251 | 0.009 | 0.262 |
| $U_{crit}$ vs. Proteins | y = 0.005x + 6.776 | 0.235 | <0.001 |
| **Endurance** | | | |
| Distance vs. DPH | y = 0.388x + 13.151 | 0.550 | <0.001 |
| Distance vs. TL | y = 3.619x - 26.527 | 0.820 | <0.001 |
| Distance vs. RNA | y = -1.461x + 40.631 | 0.201 | 0.010 |
| Distance vs. DNA | y = -0.560x + 31.593 | 0.112 | 0.061 |
| Distance vs. sRD | y = -46.060x + 34.420 | 0.060 | 0.176 |
| Distance vs. resRNA | y = -0.048x + 15.034 | <0.000 | 0.997 |
| Distance vs. Proteins | y = 0.014x - 0.483 | 0.309 | 0.003 |

The Modal Action Patterns (MAPs) did not show a clear trend along the ontogeny of white seabream larvae for the time spent swimming, in pause-swimming and sink (Table 5.4). However, the time larvae spent in pause behaviour increased at ages 40 (31 ± 0), 45 (39 ± 7), 50 (20 ± 19), and 55 DPH (44 ± 18). The time spent in pause-swimming mode was more prolonged than in any other locomotory behaviours.

**Table 5.4** Mean and standard deviation that white seabream *Diplodus sargus* (Linnaeus, 1758) larvae spent doing each Modal Action Pattern behaviour (swimming, pause-swimming, pause and sink) along ontogeny (DPH – days post-hatching).

| Age (DPH) | Swimming (s) | Pause-swimming (s) | Pause (s) | Sink (s) |
|---|---|---|---|---|
| 15 | 38 ± 24 | 52 ± 14 | - | - |
| 20 | 35 ± 19 | 29 ± 14 | - | - |
| 25 | 32 ± 19 | 35 ± 13 | - | - |
| 30 | 59 ± 1 | 2 ± 0 | 4 ± 0 | 2 ± 1 |
| 35 | 38 ± 19 | 19 ± 15 | - | - |
| 40 | 50 ± 17 | 9 ± 4 | 31 ± 0 | 7 ± 3 |
| 45 | 48 ± 20 | 24 ± 19 | 39 ± 7 | 3 ± 0 |
| 50 | 35 ± 22 | 31 ± 20 | 20 ± 19 | 5 ± 3 |
| 55 | 20 ± 21 | 41 ± 21 | 44 ± 18 | 5 ± 2 |

## 5.4 Discussion

This study reinforced the Sense Acuity And Behavioural (SAAB) hypothesis (Teodósio et al., 2016), since white seabream post-flexion larvae, a temperate pelagic fish larvae hatching from pelagic eggs, swim fast and are strong enough to control their destiny in normal oceanographic conditions to allow them to ingress into coastal nursery areas. White seabream larvae were able to swim 86.5 km in 240.2 h (i.e., ten straight days) between 45 and 55 DPH. Thus, there is already enough data published to affirm that the notion that all fish larvae are, per definition, planktonic-wonderer organisms is incorrect.

### 5.4.1 Swimming performance of temperate fish larvae

The swimming abilities of white seabream larvae just before metamorphosis and settlement allow us to understand their dispersion potential. Indeed, larvae became more competent along ontogeny, as revealed by the $U_{crit}$ and endurance experiments, as found for fish species belonging to many other families [Acanthuridae, Chaetodontidae, Lethrinidae, Monocanthidae, Nemipteridae, Pomacanthidae (Stobutzki and Bellwood, 1997), Apogonidae, Pomacentridae (Stobutzki and Bellwood, 1997; Fisher et al., 2000), Clupeidae (Silva et al.

2014), Ephippidae, Serranidae (Leis et al., 2009), Gobiesocidae (Faria and Gonçalves, 2010), Lutjanidae (Stobutzki and Bellwood, 1997; Leis et al., 2009), Percichthydae (Clark et al., 2005), Sciaenidae (Clark et al., 2005; Faria et al, 2011a), Sparidae (Clark et al., 2005; Faria et al, 2011a; Pattrick and Strydom, 2009)]. Other than for a few exceptions [e.g., Senegalese sole *Solea senegalensis* (Kaup, 1858; Soleidae); Faria et al., 2011b], this is possible owing to development of musculature and morphological structures associated with increased swimming capabilities (Leis, 2006).

Despite that pre-flexion temperate fish larvae are usually poor swimmers (Miller et al., 1988; Silva et al., 2014), as we observed for the white seabream ($U_{crit}$ = 1.1 cm $s^{-1}$ at 15 DPH) and as reported for other species [e.g., sardine *Sardina pilchardus* (Walbaum, 1792) (Silva et al., 2014); rockfish *Sebastes* spp. (Cuvier, 1829) (Kashef et al., 2014)], these larvae are much better swimmers than once expected, since their swimming speeds exceed several times their body length per second (Clark et al., 2005; Faria et al., 2009, 2011a, 2014; Silva et al., 2014; this study). The $U_{crit}$ range we measured for the white seabream (1.1-23.0 cm $s^{-1}$, 2.0-27.2 bl $s^{-1}$) is within those ranges observed for other Sparidae larvae but higher than for non-perciform temperate species (Table 5.5).

**Table 5.5** Summary of reports on swimming performance (critical swimming speed – $U_{Crit}$, and swimming endurance) of temperate fish species, including size range. (na – data not available).

| **Order** | **Family** | **Species** | **Size** (mm) | **$U_{crit}$** ($cm\ s^{-1}$) | **$U_{crit}$** ($bl\ s^{-1}$) | **Endurance** (km) | **Reference** |
|---|---|---|---|---|---|---|---|
| Atheriniformes | Atheriniidae | *Atherina presbyter* | 6.6-21.0 | 3.6-18.7 | 5.2-17.6 | na | Faria et al., 2014 |
| Clupeiformes | Clupeidae | *Sardina pilchardus* | 7.9-23.4 | 1.6-9.5 | 1.8-6.9 | na | Silva et al., 2014 |
| Gadiformes | Gadidae | *Gadus morhua* | na | 1.2-9.7 | 2.2-6.9 | na | Guan et al., 2008 |
| Gobiesociformes | Gobiesocidae | *Lepadogaster lepadogaster* | 5.1-10.9 | 1.0-9.4 | 1.5-9.6 | na | Faria and Gonçalves, 2010 |
| | | *Lepadogaster purpurea* | 5.3-10.9 | 1.2-6.5 | 2.1-6.8 | na | Faria and Gonçalves, 2010 |
| Perciformes | Percichthyidae | *Macquaria novemaculeata* | 4.0-10.4 | 0-1.5 | na | 0-12.5 | Clark et al., 2005 |
| | Sciaenidae | *Argyrosomus japonicus* | 3.0-14.0 | 4.0-16.6 | na | 0-22.4 | Clark et al., 2005 |
| | | *Scianops ocellatus* | 3.0-19.1 | 1.1-20.5 | na | na | Faria et al., 2009 |
| | Sparidae | *Acanthopagrus australis* | 4.9-11.1 | 2.0-27.0 | na | na | Clark et al., 2005 |
| | | *Diplodus capensis* | 8.9-16.0 | 2.8-35.2 | max 26.1 | 0.2-32.4 | Pattrick and Strydom, 2009 |
| | | *Pagrus auratus* | 2.2-10.4 | 2.0-27.3 | na | 4.0-9.9 | Clark et al., 2005 |
| | | *Sarpa salpa* | 12.1-21.3 | 4.8-33.4 | max 15.7 | 0.1-64.8 | Pattrick and Strydom, 2009 |
| | | *Sparus aurata* | 6.2-14.1 | 3.0-19.3 | 4.5-20.9 | 10.2-23.9 | Faria et al., 2011a |
| Pleuronectiformes | Solenidae | *Solea senegalensis* | 3.5-7.5 | 0.4-5.0 | 0.2-11.9 | na | Faria et al., 2011b |
| | Pleuronectidae | *Pleuronectes platessa* | 7.0-13.0 | 1.0-3.9 | 1.3-3.5 | na | Silva et al., 2015 |

The distance swam by white seabream larvae in the endurance experiments also increased along ontogeny (0.01 km at 15 DPH to 86.5 km at 45 DPH), as observed for other temperate fish larvae (Trnski, 2002; Pattrick Strydom, 2009). Contrary to $U_{crit}$ that increased steadily with development, the swimming endurance of white seabream larvae increased abruptly, more than 10 times, from 35 DPH (5.0 ± 6.0 km) to 45 DPH (54.1 ± 22.1 km). This is likely to the fact that endurance swimming develops later than $U_{crit}$ (Fisher et al., 2000; Clark et al., 2005). Physiological changes during ontogeny (Fisher et al., 2000), like availability of energy reserves, increased growth (Leis and McCormick 2002), development of musculature (Leis, 2006) and fins (Atema et al., 2015) and the have been proposed to increase fish larvae capacity for sustained swimming.

The average distance travelled in endurance results for white seabream larvae at 45 DPH (54.1 ± 22.1 km at a speed of 10.0 cm $s^{-1}$) were greater than the maximum recorded for other Sparidae larvae (see Table 5.5). We tested white seabream larvae endurance without providing food or rest, even though one larva swam 86.5 km during 240.2 h. So, if they were fed during the experiment to at least replenish their energy, then their swimming endurance could have been unlimited (Leis and Clark, 2005; Nilsson et al., 2007). This fact even supports further the SAAB hypothesis which mentions that temperate fish larvae have the swimming capabilities to swim towards nursery habitats if they can detect the cues emanated from such ecosystems (Teodósio et al., 2016).

Flexion and post-flexion white seabream larvae can be deterred from reaching nursery areas if oceanographic conditions are not favourable. However, their sustained speeds are higher than the typical currents in their natural habitat (4-10 cm $s^{-1}$ in Portuguese coast; Sánchez et al., 2006; Zuo et al., 2007), especially after 35 DPH. In fact, hydrodynamic models of fish larval transport suggest that larvae only require modest swimming speeds (1-10 cm $s^{-1}$) to be able to control their dispersion (Wolanski et al., 1997). Furthermore, fish larvae can regulate their vertical position at which the currents are favourable to horizontal swimming (Paris and Cowen, 2004; Fisher, 2005; Leis et al., 2006; Kashef et al., 2014). Thus, from a biophysical modelling perspective, white seabream larvae cannot be seen as passive particles as they are capable of active behaviours, combining vertical and horizontal swimming. Such behaviour can strongly influence their transport and distribution in the wild, controlling dispersal patterns or to prevent advection offshore.

Due to the wide range of larval lengths observed at specific age (coefficient variation, CV= 0.68) the total length was the better predictor of swimming performance in white seabream than age in distance swum in swimming endurance; contrarily to observed in $U_{crit}$, that had lower variability in larval lengths at the same age (CV = 0.16). This inter-individual variability of white seabream larvae is a consequence of survival of slow growers in laboratory conditions due to the absence of predators (Silva et al., 2014) and low inter-individual competition. In wild, most of the fish larvae face high mortality rates until settlement (Houde, 1987; Cushing, 1990). Despite the effect of size on swimming performance, it was expected that other factors influenced swimming performance, such as larval condition (Leis and McCormick, 2002).

### 5.4.2 Swimming performance and physiological condition

Nucleic acids derived indices (RNA, DNA, sRD) decreased with larval development (size and age), and consequently with swimming performance ($U_{crit}$ and endurance). This is a common phenomenon (Faria et al., 2011a, 2011b; Silva et al., 2014), since growth depended on the increase of cell size (hypertrophy) which reduces the concentration of nucleic acids by tissue portion (Olivar et al., 2009). So, we used the RNA residual-based index and protein content to circumvent the effect of growth (Chícharo et al., 1998). These two indices increased along ontogeny, as described for other species (e.g., Senegalese sole *Solea senegalensis* Kaup, 1858; Silva et al., 2015). The increase of protein content is associated with an increase of body mass and growth due to changes in the rates of protein synthesis and/or degradation, or to changes in protein retention (Houlihan et al., 1993). The protein content of white seabream larvae was the index that better explained the variability of their swimming performance. However, no physiological condition indices were significantly correlated with the swimming capabilities ($U_{crit}$ and endurance) of white seabream larvae. This fact might have occurred because all the larvae were tested under the same optimal feeding conditions.

### 5.4.3 Climate change and the swimming abilities of temperate fish larvae

White seabream larvae, and most other temperate fish larvae, have lower swimming abilities than tropical fish larvae. The swimming speeds of pre-settlement coral reef larvae range from 5 to 100 cm $s^{-1}$ (3-46 LB $s^{-1}$; Fisher et al., 2005; Leis, 2006) and swimming endurance range between 3.1 to 140.2 km, with some species swimming up 288.5 h (Leis and McCormick, 2002). Several factors may explain these differences, as warmer water temperature and thus larvae swim in a less viscous environment (Fuiman and Batty, 1997; Leis, 2006); however, phylogenetic and morphological differences at early stages of development – tropical reef larvae are more developed and develop faster than temperate fish larvae which allow them to swim faster and longer at the same age (Leis and McCormick, 2002; Leis, 2006; Peck et al., 2012; Kashef et al., 2014).

Water temperature has a direct impact on fish larvae, influencing metabolism, growth, developmental rates, stage duration and swimming performance (Houde, 1989; Sponaugle et al., 2002; Green and Fisher, 2004). Therefore, in a context of climate change, white seabream larvae could eventually benefit from increased sea surface temperature along the Portuguese coast (increase of 1 to 2 °C until the end of the century; Sousa Reis et al., 2001), which would accelerate larval development and improve muscle contractibility and swimming performance (Fuiman and Batty, 1997; Hunt von Herbing, 2002). The distance between the spawning grounds and nursery areas could be reduced due to the improved swimming performance in a warmer environment (Munday et al., 2008). However, this would also imply an increase in energetic expenditure, leading, for example, to more time spending on foraging (Houde, 1989; O’Connor et al., 2007; Munday et al., 2008). This crucial metabolic regulation might dictate the collapse of populations if larvae are unable to balance the energy spend on thermal regulation and on all other activities that could promote their survival and growth. Thus, intrinsic factors responsible for variability of larval survival recruitment interact with the effects of currents on dispersal patterns (Munday et al., 2008) making difficult to predict the effects of increased water temperature in larval swimming performance in the natural environment.

## 5.5 Conclusions

The swimming behaviour of white seabream larvae indicates that flexion and post-flexion stages can swim faster than the typical coastal currents, allowing them to reach and be retained in coastal nursery areas, and therefore optimize recruitment. The swimming performance of white seabream larvae and their sensorial abilities to detect cues involved in directional swimming, support the SAAB hypothesis. Nonetheless, future studies should consider the putative differences between wild and laboratory-reared larvae. It is critical to test the swimming capacity of larvae at different temperature setups to predict the impact of climate change on the chances of fish larvae to swim towards nursery areas while balancing increased metabolic activity due to energy expenditure on thermal regulation. The results shown on this study will feed individual-based models of the larval transport which can be crucial to understand population dynamics and connectivity along with coastal ecosystems, ultimately with repercussions on the management and conservation of fish stocks.

## 5.6 Ethics statement

CCMAR facilities and their staff are certified to house and conduct experiments with live animals ("group-1" license by the Veterinary General Directorate, Ministry of Agriculture, Rural Development and Fisheries of Portugal) in accordance with the three "R" policy and national and European legislation.

## 5.7 Acknowledgements

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# CHAPTER 6

## Do consistent individual differences in temperate and pelagic fish larval behaviour affect recruitment in nursery habitats?

Baptista V, Carere C, Morais P, Cruz J, Cerveira I, Castanho S, Ribeiro L, Pousão-Ferreira P, Leitão F, Teodósio MA. Do consistent individual differences in temperate and pelagic fish larval behaviour affect recruitment in nursery habitats? Submitted to Behavioral Ecology and Sociobiology

# Do consistent individual differences in temperate and pelagic fish larval behaviour affect recruitment in nursery habitats?

## Abstract

Individual animals across all taxa differ consistently in behaviour, i.e., they show personality traits. This inter-individual variability has significant ecological and evolutionary consequences, since it affects a range of population-level processes. Here, we focus on the selection and recruitment of nursery habitats in temperate fish larvae. A recent hypothesis (Sense Acuity and Behavioural Hypothesis), proposed that fish larvae could detect and follow environmental cues to actively choose suitable nursery habitats. We empirically tested this hypothesis questioning if this non-random, active process occurs and if it could be linked to personality traits. Individual larvae of the white seabream *Diplodus sargus* (Linnaeus, 1758; Pisces: Sparidae) were tested repeatedly at different ages in a two-channel choice-chamber apparatus exposing them to a flow with water from different nursery habitats (coastal and lagoon), and different temperatures or different salinity and recording exploratory activity and preference in the different conditions. Most larvae changed behaviour across ontogeny, but they were also significantly consistent in their behaviour, revealing strong individuality, yet no significant preference for the presented stimuli emerged. Exploratory activity was higher when larvae showed unresponsive or inconclusive behaviours, meaning that the larvae may seek a stimulus different from the one that we were offering. Individual behavioural consistency could influence the process of searching for suitable nursery habitats and, consequently, dispersion and connectivity of white seabream population. Characterizing the behaviour of temperate pelagic marine fish larvae may shed light on fish recruitment variability, on larval dispersion models and possibly on effects of climate change on fish population distribution and connectivity.

**Keywords:** fish larvae; personality; recruitment; environmental cues; habitat choice

## 6.1 Introduction

Many fish species, such as coastal temperate fish species, have a bipartite life history (Radford et al., 2012): spawning occurs at the sea where the larvae hatch from planktonic eggs and spend time in the pelagic environment, subjected to currents effects before they recruit (Leis, 2006; Teodósio et al., 2016). Recruitment occurs in coastal nursery areas (i.e., coastal lagoons, estuaries, and rocky shore areas) where survival and growth are possible thanks to the availability of food resources and protection from predators (Bradbury and Snelgrove, 2001; Barbosa and Chícharo, 2011; Chícharo et al. 2012; Teodósio et al., 2016).

The survival and growth during the larval and juvenile phases are crucial for spatial and temporal recruitment variability (Houde, 2008; Teodósio et al., 2017), which affect the size and dynamics of local populations. Recruitment variability is influenced by the complex interaction of physical and biological processes related to larval transport and retention (Hale et al., 2008), and with the food web processes that sustain fish larvae (Santos et al., 2007). However, this important migration process is still poorly understood (James et al., 2008; Radford et al., 2012).

Several hypotheses have been proposed to explain the variability in fish recruitment, as the Critical Period (Hjort, 1914), Match-Mismatch (Cushing 1975, 1990), Stable Ocean (Lasker, 1978), Member-Vagrant (Sinclair and Iles, 1989), referring, in general, that fish larvae disperse passively at the mercy of oceanographic factors, such as ocean currents, tides, or weather events (Thorrold et al., 1994; Sponaugle and Cowen, 1997; Montgomery et al., 2001). This concept was improved in the Ocean Triads hypothesis (Agostini and Bakun, 2002), highlighting the importance of nutrient enrichment and food concentration for retention or drift toward suitable habitats. However, all these hypotheses assume a passive and stochastic drift of larvae, without any active role of the individual larvae in the migration from spawning grounds to nursery ecosystems and the ability to find and swim toward them.

Recently, Teodósio et al. (2016) proposed the Sense Acuity And Behavioural (SAAB) hypothesis, stating that the recruitment of temperate fish larvae is unlikely if the larvae drift passively through water currents, and that sense acuity of temperate fish larvae and their behavioural responses to nursery cues in coastal areas are essential for recruitment success. As the sensorial acuity and swimming capacity increase during ontogeny (Fisher et al., 2000; Gerlach et al., 2007; Teodósio et al., 2016; Chapter 5 of present Thesis), it is expected that larval behaviour to search nursery habitats differentiates during the larval development using a hierarchy of sensorial cues to detect and navigate to these areas (Teodósio et al., 2016). Thus, in offshore areas, the post-flexion temperate fish larvae would be initially guided towards the coast by sun compass, earth's geomagnetic field, and by an innate swimming behaviour when they are away from any nursery cue. In nearshore areas, they would be able to detect and follow nursery cues (odour, sound, visual) (Montgomery et al., 2006; Gerlach et al., 2007; Faillettaz et al., 2015; Teodósio et al., 2016) and swim towards specific nursery habitats using distinct swimming behaviours, which vary according to the cues concentration, diel rhythms, feeding and predator avoidance strategies (Teodósio et al., 2016).

Thus, habitat choice – any behaviour that leads individuals to prefer and spend more time in one habitat than in another respect to random allocation (Atema et al., 2002; Dixson et al., 2008; Gerlach et al., 2007) – could be crucial for fish recruitment and could be mediated by the presence and interaction of multiple cues (Kingsford et al., 2002; Teodósio et al., 2016). Fish larvae use different senses to choose a suitable settlement habitat according to water characteristics/cues, such as odour (Atema et al., 2002, Gerlach et al., 2007, Dixson et al., 2008; Morais et al., 2017), vision (Whitfield, 1994; Faillettaz et al., 2015) sound (Montgomery et al., 2006; Leis et al., 2011; Staaterman et al., 2014) and magnetism (Qin et al., 2015). Although all these senses contribute to habitat choice, olfaction has been recognized as the prevalent cue for locating nursery habitats (Atema et al., 2002; Lecchini et al., 2005b; Døving et al., 2006; Dixson et al., 2008). Fish larvae are capable of distinguishing and following several chemical stimuli (e.g., type of substrate, vegetation, conspecifics, predators, prey) present in water (Lecchini et al., 2005b; Døving et al., 2006; Gerlach et al., 2007; Radford et al., 2012). On the other hand, oceanographic factors such as current speed, turbidity, salinity, oxygen concentrations, and temperature (Boehlert and Mundy, 1988; Whitfield, 1994; Gibson, 1997; Atema et al., 2002; Boss and Thiel, 2006; Angeletti et al., 2017) also influence habitat choice. Recently, there are evidences that these cues are changing due to global climatic changes (Munday et al., 2009; Pecl et al., 2017; Rossi et al., 2018; Gouraguine et al., 2019), affecting settlement behaviour and recruitment of fish larvae (O'Connor et al., 2015). For example, changes in water temperature and salinity were reported to affect the behaviour and habitat choice patterns, in addition to critical physiological processes (Pecl et al., 2017).

Despite the increase of studies on larval settlement strategies over the past decades, most have been conducted on the use of environmental cues for habitat selection by coral-reef fish larvae (e.g. Atema et al., 2002; Dixon et al., 2008; Gerlach et al., 2007) and just a few studies suggested that they could play a role in the recruitment of temperate fish larvae (James et al., 2008; Randford et al., 2012; Havel and Fuiman, 2016; Morais et al., 2017).

The recruitment may be an active and behaviourally mediated process (Boehlert and Mundy, 1988). Individual animals across many taxa, including fish, differ consistently in behaviour, i.e., they show personality traits (e.g., Briffa and Weiss, 2010; Carere and Maestripieri, 2013). This inter-individual variability, which can be seen as a behavioural polymorphism, has significant ecological and evolutionary consequences, since it affects a range of population-level processes. More recently, empirical and theoretical work has suggested that personality traits can influence all phases of dispersal processes (departure, transience, settlement), and consequently spatial patterns of populations (Cote et al., 2010; Nanninga and Berumen, 2014; Canestrelli et al., 2016). However, studies on fish personality traits have been mostly focused on juveniles (Biro et al., 2010; Wilson et al., 2011; Castanehira et al., 2013, 2016) or adults (Bell and Stamps, 2004; Biro et al., 2004, 2006; Wilson et al., 2011), with few exceptions in fish larvae (Sundström et al., 2004; Budaev and Andrew, 2009; Pasquet et al., 2016). Sundström et al. (2004) found that, in brown trout *Salmo trutta* (Salmonidae) (Linnaeus, 1758), bolder individuals were more likely to become dominant. Budaev and Andrew (2009) showed that the development of eggs and larvae of zebrafish *Danio rerio* (Cyprinidae) (Hamilton, 1822) in darkness increased shyness and reduced behavioural asymmetries in response to predators and Pasquet et al. (2016) showed that Northern pike *Esox Lucius* (Esocidae) (Linnaeus, 1758) larvae could be ranked along a gradient of boldness-shyness. The small size and the fragility of fish larvae with consequent technical difficulties for proper behavioural testing could explain the low number of studies so far (Pasquet et al., 2016). However, individual variation in larval behaviour may be essential to understand the dispersal and recruitment dynamics of fish populations (Nanninga and Berumen, 2014; Pasquet et al., 2016) due to its influence on food acquisition, predator's avoidance (Biro et al., 2006; Stamps, 2007), and consequently on habitat selection (Stamps, 2006; Stamps and Groothuis, 2010).

Under this general framework, we hypothesized that fish larvae could detect and follow environmental cues to actively choose suitable nursery habitats (Teodósio et al., 2016) and that this could be linked to personality traits. Thus, we aimed to (i) detect consistent individual differences in behaviour in temperate pelagic fish larvae across ontogeny; (ii) test if and how these consistent behaviours relate to environmental changes (increase of water temperature and decrease of salinity); (iii) test if they affect the ability to choose nursery habitats by detecting different environmental cues;

## 6.2 Material and methods

### 6.2.1 Model species

The white seabream *Diplodus sargus* (Linnaeus 1758) is a demersal fish distributed in the Northeast Atlantic Ocean and Mediterranean Sea (Pajuelo and Lorenzo, 2002). This species inhabits coastal rocky reefs, sandy bottoms, and seagrass beds at depths down to about 150 m (Pajuelo and Lorenzo, 2002) but is generally more abundant from the shore to 50 m depth in the Northeast Atlantic and Mediterranean (Harmelin-Vivien et al., 1995). White seabream is abundant in the Portuguese coast, on the continental shelf (Leitão et al., 2007), lagoons, and estuaries (Vinagre et al., 2010), and it sustains important recreational and commercial fisheries (Erzini et al., 1999; Veiga et al., 2010).

White seabream adults spawn in coastal areas from March to June (Morato et al., 2003; Faria et al., 2006), producing pelagic eggs that hatch after 3 days (Di Franco and Guidetti, 2011), and larvae spend up to 4 weeks in the pelagic environment (González-Wangüemert et al., 2010). During the pelagic phase, eggs and larvae can disperse 100-200 km through marine currents, before reaching favourable habitats for recruitment (Di Franco et al., 2012). Settlement takes place at shallow depths (0-2 m) on sandy-rocky bottoms (Harmelin-Vivien et al., 1995), coastal lagoons (Monteiro et al., 1990), and estuaries (Gonçalves et al., 2015; Faria et al., 2006). They remain in these habitats for about a year (Planes et al., 1999), after that, in response to ontogenetic changes in habitat choice, they move toward deeper habitats to recruit into the adult population (Harmelin-Vivien et al., 1995). Thus, as many of Sparidae, white seabream behaves as cyclic migrants, migrating to nursery habitats after metamorphosis and spending the early stages of life in these environments (Pajuelo and Lorenzo, 2004).

### 6.2.2 Animals and housing conditions

White seabream larvae were obtained from natural spawns of wild broodstocks established at the Aquaculture Research Station (EPPO) of the Portuguese Institute for the Ocean and Atmosphere (IPMA) in Olhão (Portugal). Larvae (21 DPH – days post-hatching) were collected 24 hours before the beginning of the experiment at the EPPO (Table 6.1) and kept on a 20 L tank at a quiet and temperature-controlled room where the experiments were conducted (CCMAR facilities, University of Algarve).

**Table 6.1** Timeline of housing and choice-chamber test for white seabream *Diplodus sargus* (Linnaeus, 1758) larvae.

| DPH | Procedure | Age Group |
|---|---|---|
| 21 | Collected and housing | - |
| 22 | Individual housing and acclimatization | Age 1 |
| 23 | Test I and Test II | |
| 24 | Test I and Test II | |
| 25 | Test III and Test IV | |
| 26 | Test III and Test IV | |
| 32 | Individual housing and acclimatization | Age 2 |
| 33 | Test I and Test II | |
| 34 | Test I and Test II | |
| 35 | Test III and Test IV | |
| 36 | Test III and Test IV | |
| 42 | Individual housing and acclimatization | Age 3 |
| 43 | Test I and Test II | |
| 44 | Test I and Test II | |
| 45 | Test III and Test IV | |
| 46 | Test III and Test IV | |
| 52 | Individual housing and acclimatization | Age 4 |
| 53 | Test I and Test II | |
| 54 | Test I and Test II | |
| 55 | Test III and Test IV | |
| 56 | Test III and Test IV | |

Forty larvae were randomly selected from the tank and individually housed in breeding containers (10×10×10 cm) in two tanks (each containing 110 L) with water from the Ria Formosa lagoon (Ramalhete Station, Portugal, 37º00’21.13’’ N, 7º58’02.39’’ W; R from now onwards; see Table 6.2). During all experiments, the water temperature was kept similar in both tanks, at 19.4 (±1.2) °C. Whenever possible, the same individual larvae were tested throughout all ages and conditions. Because of normal larval mortality during the experiment, the dead larvae were replaced by new larvae at ages 2 and 3 to maintain a sample size of 40, which led to a total 93 larvae used (see Table 6.3). All larvae were tested on the same day for each of the four tests.

**Table 6.2** Water conditions experienced in housing and choice-chamber testes for white seabream *Diplodus sargus* (Linnaeus, 1758) larvae.

| **Procedure** | | **Water Conditions/Stimuli** | **Code** |
|---|---|---|---|
| Housing Standard Individual Conditions | | Ria Formosa lagoon – Ramalhete | R |
| Test I | Control | Housing water | R |
| | Stimulus | Lagoon habitat - Ria Formosa main channel | L |
| Test II | Control | Housing water | R |
| | Stimulus | Coastal habitat – Olhos de Água rocky shore beach | C |
| Test III | Control | Housing water | R |
| | Stimulus | Housing water with an increase of 4 °C | R+4C |
| Test IV | Control | Housing water | R |
| | Stimulus | Housing water with a decrease of 10 in salinity | R-10 |

**Table 6.3** Number of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae tested across ontogeny in each binary test. The number of replaced larvae is in brackets.

| **Stimulus** | **Age 1** | | | **Age 2** | | | **Age 3** | | | **Age 4** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Day 0** | **Day 1** | **Day 2** | **Day 0** | **Day 1** | **Day 2** | **Day 0** | **Day 1** | **Day 2** | **Day 0** | **Day 1** | **Day 2** |
| Acclimatization | 40 | - | - | 40<br>(27) | - | - | 40<br>(26) | - | - | 29 | - | - |
| Test I | - | 38 | 35 | - | 40 | 34 | - | 38 | 34 | - | 28 | 26 |
| Test II | - | 38 | 36 | - | 40 | 37 | - | 37 | 35 | - | 29 | 27 |
| Test III | - | 26 | 24 | - | 28 | 25 | - | 32 | 31 | - | 25 | 25 |
| Test IV | - | 24 | 24 | - | 30 | 23 | - | 31 | 31 | - | 25 | 25 |

The larvae's mouth opens at 3 DPH (Ortiz-Delgado et al., 2003) when they start the exogenous feeding. Larvae were fed *ad libitum* with rotifers *Brachionus* sp. (Pallas, 1766) for the first 14 DPH, with rotifers, branchiops *Artemia* spp. (Leach, 1819) nauplii, and dry feed (Caviar from BernAqua) from 15 to 21 DPH, with *Artemia* spp. nauplii and dry feed until 37 DPH, and towards just with dry feed which granule size increased as development progressed. This diet is ideal for development and growth of white seabream larvae (Pousão-Ferreira, 2005); however, intrinsic factors can lead to variability in physiological condition within the same diet (Faria et al., 2011).

### 6.2.3 Design and experimental set-up

White seabream larvae underwent one series of tests at each of four ages (Age 1 – 22-26 DPH, Age 2 – 32-36 DPH, Age 3 – 42-46 DPH, and Age 4 – 52-56 DPH; see Table 6.1). At each age, a series consisted of four tests performed on four consecutive days, preceded by an acclimatization day where the behaviours were also recorded. In each test, the subject was exposed to two different water conditions: typical nursery odour cues (Test I and Test II) or changes in physical water conditions (Test III and Test IV; see Tables 6.1 and 6.2). In Test I, larvae were subjected to control water (R) and water from the main channel of Ria Formosa lagoon (Portugal, 37º00'11.17''N, 7º59'09.17''W) with the presence of dwarf eelgrass *Zostera noltii* (Hornemann, 1832). In Test II, the larvae were subjected to the control water (R) and water from a coastal habitat (C) collected in tide pools of a rocky shore beach (Olhos de Água beach, Portugal, 37º05′21.57″N, 8º11′27.56″W). In Test III, we used the control water (R) at housing temperature and the same water with an increase of 4 ºC in temperature (R+4C), that represents the tendency of the rise in sea surface temperature in last decades (1950-2010) during spring in the Portuguese coast (Baptista et al., 2018 – Chapter 2 of the present Thesis). In Test IV, we used control water (R) at housing salinity (36) and the same water diluted to reach a salinity of 26 (R-10) that represents the proximity to estuarine conditions in the southern Portuguese coast (Morais, 2007). The experimental water used in the tests was collected in each site in the day before tests, during the ebb tide, stored at ambient conditions before use, avoiding temperature differences between water sources.

Each test series started with the individual housing and acclimatization of larvae to the chamber environment using control water (same water used in housing; see Tables 6.1 and 6.2). At each given age, each test was repeated on the following day for testing short-term repeatability (Table 6.1).

The behavioural responses of white seabream larvae to different environmental conditions (odour cues and water physical properties) were evaluated using a two-channel choice-chamber apparatus (Figure 6.1) based on the one designed by Gerlach et al. (2007). The choice-chamber was made with plexiglass [20 × 4 × 2.5 cm (L × W × H)] and had two frontal water inlets and a rear water outlet. The flow rate in each choice lane was 20 ml min$^{-1}$ for larvae at Age 1 and 60 ml min$^{-1}$ for older larvae (Ages 2, Age 3 and Age 4). With these flows, larvae swam freely between chamber areas. In each test, a single larva was gently taken from the breeding container with a transparent plastic spoon, placed in the centre of the choice-chamber, and left 300 seconds undisturbed to habituate to the flow and to the water sources (odour or physical cues, pre-test). At the end of this pre-test phase, the larva behaviours were observed for 120 seconds (Trial 1). During the next 120 seconds, the water sources positions were switched to control for possible side preferences not associated with odour cues. After that, the procedure was repeated: 300 seconds for pre-test, followed by 120 seconds for behavioural observation (Trial 2).

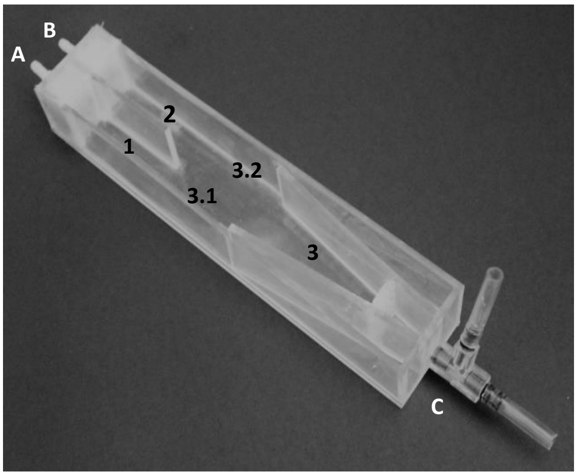

**Figure 6.1** Choice-chamber used in preference tests of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae to different odour cues (based on the designed by Gerlach et al., 2007). The dimensions of the chamber are 20 × 4 × 2.5 cm (L × W × H) (A) and (B) correspond to water intake, (C) correspond to the water outlet, areas (1) and (2) are choice lanes, areas (3), (3.1) and (3.2) are considered unresponsive areas [area (3.1) is more influenced by source (A), while area (3.2) is more influenced by source (B)].

All phases were recorded with a GoPro HERO4 Silver Edition Adventure and later analysed with BORIS (Behavioral Observation Research Interactive Software; Friard and Gamba, 2016) v 4.1.1 by one single observer (VB).

### 6.2.4 Data collection – Behavioural observations

We recorded the position of larvae in the choice-chamber (stimulus 1, stimulus 2 or unresponsive areas; Figure 6.1) throughout the observation period (120 seconds) in each trial.

We used the Preference Index (PI) developed by Morais et al. (2017) to express the preference of white seabream larvae to different water odour cues. Importantly, this index considers the unresponsive (time spent in unresponsive areas) and inconclusive behaviours (when the larvae spent equal time in each choice area), overlooked in most of the habitat choice studies (e.g., Atema et al., 2002; Gerlach et al., 2007; James et al., 2008; Radford et al., 2012). The Preference Index (PI) was calculated using Equation 6.1,

$$\boldsymbol{PI} = [(\sum t_{CW} - \sum t_{SW}) \times T^{-1}] \times (1 - \sum t_{UNR} \times T^{-1}) \text{ (Equation 6.1)}$$

where T is the sum of both trials' duration (240 seconds), $\sum t_{CW}$ is the total time that larva spent in control area, $\sum t_{SW}$ is the total time that larva spent in the situmlus area, and $\sum t_{UNR}$ is the total time that larvae spent in the unresponsive area in both trials. PI varies between -1 (preference for control water during the entire trial) and +1 (preference for stimulus water during the entire trial), while 0 indicates that larvae had an unresponsive behaviour (without following an odour cue).

We measured exploration as the total number of areas of the choice-chamber visited by a larva (maximum of five areas; see Figure 6.1), and activity as the number of crossings between areas of the chamber. We combined these two measurements in an Exploratory Activity Index (EAI) expressed by Equation 6.2:

$$\boldsymbol{EAI} = \frac{NA}{NAmax} \times \frac{NC}{NCmax} \quad \text{(Equation 6.2)}$$

where NA is the number of areas of the chamber visited by a larva (exploration), $NA_{max}$ the number of areas available in the chamber (five areas: 1, 2, 3.1, 3.2, and 3; see Figure 6.1), NC is the number crossings (activity), and $NC_{max}$ the number of movements done by the larva who changed the most between chamber areas during the entire test. EAI varies between 0 (low exploratory activity) and 1 (high exploratory activity).

### 6.2.5 Data analysis

We used Chi-square tests (data not shown) to detect the differences in the response of each larva to odour cues between trials. Larvae with the same response in both trials were analysed adding the observations from each trial (240 seconds in total). On the other hand, the larvae that showed different responses in each trial were considered inconclusive in the response to the odour cues and excluded from the analyses (Morais et al., 2017).

Since the assumptions of ANOVA were not satisfied for our dataset, we used the Kruskal-Wallis rank sum test to investigate the behavioural responses of white seabream larvae between each test including their repetition on the following day. No differences were observed between each test and its repetition (*p*-values > 0.05), so we averaged the two test days for the following analysis.

The differences in absolute frequencies between ages (Age 1, Age 2, Age 3, Age 4) in different stimuli (Test I, Test II, Test III, Test IV), and between stimuli in different ages were also analysed with Chi-square tests.

Spearman's correlation was used to test the correlations between different behavioural measurements (activity, exploration, and EAI). Since there was a significant positive correlation between indices (Appendix 6.A1), we decided to only use the EAI data in subsequent analyses.

We also used the Kruskal-Wallis rank sum test to investigate the behavioural responses (PI and EAI) of larvae to odour cues for each test along ontogeny (Age 1, Age2, Age 3 and Age 4). The post-hoc Holm-Sidak test was used to test the significance of differences between each factor level.

We used the Friedman rank sum test to analyse the presence of differences between EAI and the PI. The significance of differences between each factor level were tested using the Conover post-hoc multiple comparison test.

Individual-based repeatability (RICC) across ages and tests was calculated by linear mixed-effects models (LMM) with individual identity as a random factor.

The analyses were conducted using the open source software R (versions 3.5.2) and R Studio (1.1.463), except the Pearson's correlations and individual-based repeatability that were conducted using StatView 5.0 (Abacus Concepts, USA) and SPSS 23.0, respectively. Data are presented as mean ± standard error (SE) and statistical significance threshold was set at $\alpha = 0.05$.

## 6.3 Results

The response of white seabream larvae to different habitat conditions increased until Age 3 (up to 21.4%), then decreased at Age 4 (down to 4.0%) (Figure 6.2). Larvae tended to prefer lagoon water in during Age 1 (6.8%), and control water during Ages 2 (6.9%) and 3 (12.8%) (Figure 6.2A). For the remaining tested habitat conditions, larvae did not change the source preference along ontogeny, preferring control water to coastal water (6.7-12.5%) (Figure 6.2B), lower water temperature (0-14.3%) (Figure 6.2C) and higher water salinity (2.0-9.3%)

(Figure 6.2D). The higher preference for control water occurred at Age 2 for the decrease of water salinity (9.3%) (Figure 6.2D), at Age 3 when tested with lagoon water (12.8%) (Figure 6.2A) and increase of water temperature (14.3%) (Figure 6.2C), and at Age 3 and Age 4 when tested with coastal water (12.5%; Figure 6.2B). Unresponsive behaviour decreased along ontogeny in all tested habitats (Test I – lagoon cue test: 67.8-54.3%; and Test II – rocky cue test: 58.5-50.4) and increased in the reduced salinity test (Test IV: 56.3-60-3%) (Figure 6.2). The higher percentage of the unresponsive behaviour was found at Age 2 in Tests I (lagoon cue test: 67.8%) (Figure 6.2A) and Test II (rocky cue test: 58.5%) (Figure 6.2B), at Age 3 in Test III (increased temperature test: 60.3%;) (Figure 6.2C), and at Age 1 in Test IV (reduced salinity test: 70.8%;) (Figure 6.2D). Generally, the inconclusive behaviour decreased until Age 3 (from 34.5±6.1 to 21.0±2.2) and then increased at Age 4 in all tests (Figure 6.2). This behaviour accounts for those larvae without a clear preference for any chamber areas. Significant differences were found in absolute frequencies between Age 2 and Age 4 for Test I ($\chi^2$ test, p= 0.042) and between Age 3 and Age 4 for Test IV ($\chi^2$ test, p< 0.0001) (Table 6.4). Within ages we also found significant differences between Test II and Test IV for Age 1 ($\chi^2$ test, $p = 0.026$), Age 2 ($\chi^2$ test, $p = 0.040$) and Age 4 ($\chi^2$ test, $p = 0.020$), and between Test II and Test IV for Age 4 ($\chi^2$ test, $p = 0.012$) (Table 6.4).

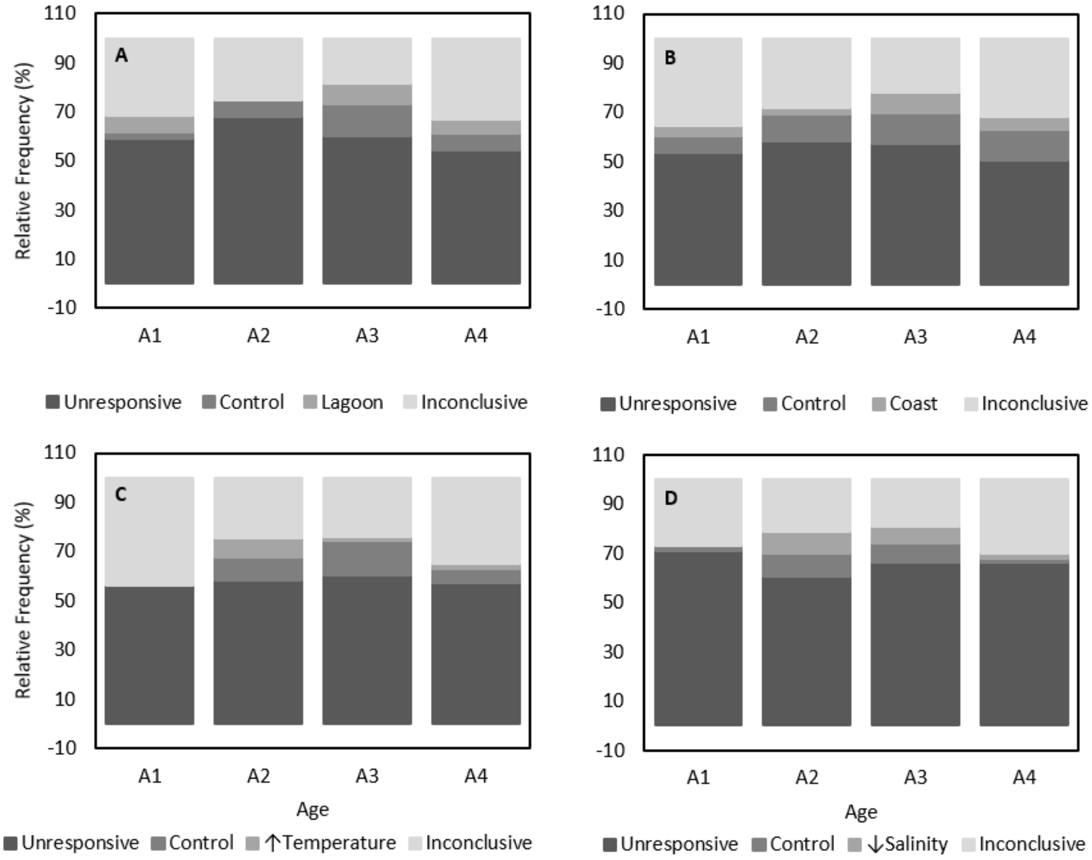

**Figure 6.2** Preference of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae for different habitat conditions (A- lagoon water, Test I; B- coastal water, Tests II; C- increase of 4 °C in water temperature, Test III; D- decrease of 10 units of water salinity, Test IV) in choice-chamber experiments along ontogeny (A1- Age 1, A2- Age 2, A3- Age 3, A4- Age 4).

**Table 6.4** Chi-square test results on the absolute frequency of behaviours exhibited by white seabream *Diplodus sargus* (Linnaeus, 1758) larvae (unresponsive, preference for control water, preference for stimulus water, and inconclusive behaviour) in choice-chamber experiment trials for each test (Test I- lagoon habitat, Test II- coastal habitat, Test III- increase of temperature, Test IV- decrease of salinity) and along ontogeny (Age 1, Age2, Age 3, Age4). Significant differences are highlighted in bold.

| Comparisons | *p* | Comparisons | *P* |
|---|---|---|---|
| *Test I* | | *Age 1* | |
| Age1 vs. Age2 | 0.799 | Test I vs. Test II | 0.926 |
| Age1 vs. Age3 | 0.149 | Test I vs. Test III | 0.257 |
| Age1 vs. Age4 | 0.125 | Test I vs. Test IV | 0.110 |
| Age2 vs. Age3 | 0.386 | Test II vs. Test III | 0.402 |
| Age2 vs. Age4 | **0.042** | Test II vs. Test IV | **0.026** |
| Age3 vs. Age4 | 0.160 | Test III vs. Test IV | 0.302 |
| *Test II* | | *Age 2* | |
| Age1 vs. Age2 | 0.636 | Test I vs. Test II | 0.790 |
| Age1 vs. Age3 | 0.259 | Test I vs. Test III | 0.066 |
| Age1 vs. Age4 | 0.201 | Test I vs. Test IV | 0.049 |
| Age2 vs. Age3 | 0.635 | Test II vs. Test III | 0.066 |
| Age2 vs. Age4 | 0.111 | Test II vs. Test IV | **0.040** |
| Age3 vs. Age4 | 0.332 | Test III vs. Test IV | 0.986 |
| *Test III* | | *Age 3* | |
| Age1 vs. Age2 | 0.353 | Test I vs. Test II | 0.961 |
| Age1 vs. Age3 | 0.400 | Test I vs. Test III | 0.227 |
| Age1 vs. Age4 | 0.927 | Test I vs. Test IV | 0.896 |
| Age2 vs. Age3 | 0.446 | Test II vs. Test III | 0.246 |
| Age2 vs. Age4 | 0.488 | Test II vs. Test IV | 0.749 |
| Age3 vs. Age4 | 0.054 | Test III vs. Test IV | 0.793 |
| *Test IV* | | *Age 4* | |
| Age1 vs. Age2 | 0.780 | Test I vs. Test II | 0.840 |
| Age1 vs. Age3 | 0.279 | Test I vs. Test III | 0.220 |
| Age1 vs. Age4 | 0.985 | Test I vs. Test IV | **0.020** |
| Age2 vs. Age3 | 0.458 | Test II vs. Test III | 0.083 |
| Age2 vs. Age4 | 0.182 | Test II vs. Test IV | **0.012** |
| Age3 vs. Age4 | **0.000** | Test III vs. Test IV | 0.851 |

White seabream larvae preferred control water in most of the tests and ages as shown by the Preference Index (PI), which varied between 0.00 ± 0.00 (Age 1 in Test III and Test IV) and 0.10 ± 0.26 (Age 3 in Test III), with a minimum of -1.00 and a maximum of 1.00 (Figure 6.3). There were significative differences in PI between ages only in Test I (Kruskal-Wallis chi-squared = 12.0053, df = 3, $p$ = 0.01), and through *post-hoc* test we verified that the only significant difference was observed between Age 1 and Age 2 ($p$ = 0.016) (Table 6.5).

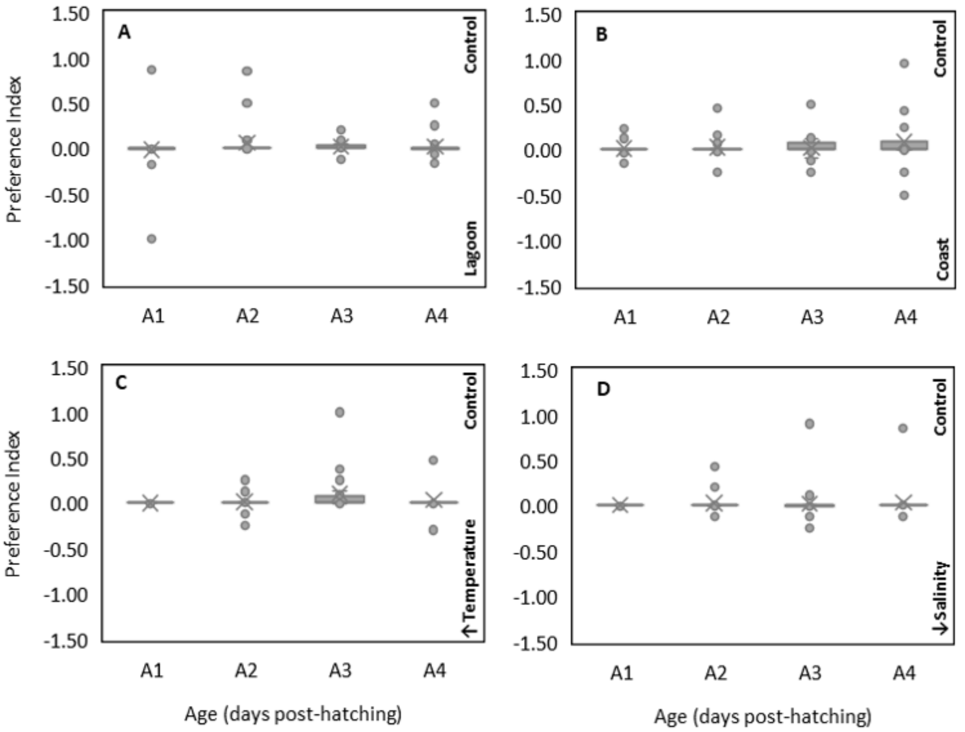

**Figure 6.3** Preference Index of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae in choice-chamber experiment trials for each test (Test I- lagoon habitat, Test II- coastal habitat, Test III- increase of temperature, Test IV- decrease of salinity) and along ontogeny (Age 1, Age2, Age 3, Age4). Negative values of this index indicate a preference for stimulus water, while positive values indicate a preference for control water. The mean is represented by across, the line inside the boxes represent the median, and full circles represent the outliers.

**Table 6.5** The post-hoc Holm-Sidak test for multiple comparations of Preference and Exploratory Activity Indexes of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae in each test (Test I- lagoon habitat, Test II- coastal habitat, Test III- increase of temperature, Test IV- decrease of salinity) and along ontogeny (Age 1, Age2, Age 3, Age 4). Significant differences are highlighted in bold.

| **Comparisons** | **Z** | **Unadjusted *p*** | **Adjusted *p*** | **Comparisons** | **Z** | **Unadjusted *P*** | **Adjusted *p*** |
|---|---|---|---|---|---|---|---|
| *Preference Index: Test I* | | | | *Activity Index: Test I* | | | |
| Age1 vs. Age2 | **-2.999** | **0.003** | **0.016** | Age1 vs. Age2 | 0.759 | 0.448 | 0.695 |
| Age1 vs. Age3 | -2.453 | 0.014 | 0.069 | Age1 vs. Age3 | -0.324 | 0.746 | 0.746 |
| Age1 vs. Age4 | -0.451 | 0.652 | 0.652 | Age1 vs. Age4 | -1.954 | 0.051 | 0.229 |
| Age2 vs. Age3 | 0.485 | 0.628 | 0.861 | Age2 vs. Age3 | -1.074 | 0.283 | 0.631 |
| Age2 vs. Age4 | 2.178 | 0.029 | 0.113 | Age2 vs. Age4 | -2.631 | 0.009 | 0.050 |
| Age3 vs. Age4 | 1.717 | 0.086 | 0.237 | Age3 vs. Age4 | -1.646 | 0.100 | 0.343 |
| *Preference Index: Test II* | | | | *Activity Index: Test II* | | | |
| Age1 vs. Age2 | -0.034 | 0.973 | 0.973 | Age1 vs. Age2 | 0.682 | 0.496 | 0.745 |
| Age1 vs. Age3 | -0.257 | 0.798 | 0.992 | Age1 vs. Age3 | 1.095 | 0.273 | 0.721 |
| Age1 vs. Age4 | -1.170 | 0.242 | 0.810 | Age1 vs. Age4 | -0.872 | 0.383 | 0.765 |
| Age2 vs. Age3 | -0.228 | 0.829 | 0.968 | Age2 vs. Age3 | 0.437 | 0.662 | 0.662 |
| Age2 vs. Age4 | -1.160 | 0.246 | 0.756 | Age2 vs. Age4 | -1.527 | 0.127 | 0.492 |
| Age3 vs. Age4 | -0.929 | 0.353 | 0.824 | Age3 vs. Age4 | -1.900 | 0.057 | 0.299 |
| *Preference Index: Test III* | | | | *Activity Index: Test III* | | | |
| Age1 vs. Age2 | 0.025 | 0.980 | 0.980 | Age1 vs. Age2 | -0.651 | 0.515 | 0.886 |
| Age1 vs. Age3 | -0.887 | 0.375 | 0.847 | Age1 vs. Age3 | -0.550 | 0.582 | 0.825 |
| Age1 vs. Age4 | 0.322 | 0.747 | 0.984 | Age1 vs. Age4 | **-2.635** | **0.008** | **0.049** |
| Age2 vs. Age3 | -0.938 | 0.348 | 0.882 | Age2 vs. Age3 | 0.138 | 0.889 | 0.889 |
| Age2 vs. Age4 | 0.304 | 0.761 | 0.943 | Age2 vs. Age4 | -2.050 | 0.040 | 0.152 |
| Age3 vs. Age4 | 1.221 | 0.222 | 0.778 | Age3 vs. Age4 | -2.289 | 0.022 | 0.106 |
| *Preference Index: Test IV* | | | | *Activity Index: Test IV* | | | |
| Age1 vs. Age2 | 1.292 | 0.196 | 0.583 | Age1 vs. Age2 | 0.920 | 0.358 | 0.83 |
| Age1 vs. Age3 | 1.620 | 0.105 | 0.486 | Age1 vs. Age3 | 0.411 | 0.681 | 0.681 |
| Age1 vs. Age4 | 0.213 | 0.832 | 0.832 | Age1 vs. Age4 | -0.485 | 0.627 | 0.861 |
| Age2 vs. Age3 | 0.340 | 0.734 | 0.929 | Age2 vs. Age3 | -0.551 | 0.581 | 0.927 |
| Age2 vs. Age4 | -1.083 | 0.279 | 0.625 | Age2 vs. Age4 | -1.446 | 0.148 | 0.618 |
| Age3 vs. Age4 | -1.414 | 0.157 | 0.575 | Age3 vs. Age4 | -0.934 | 0.350 | 0.884 |

In general, the exploratory activity index (EAI) increased along ontogeny (from Age 1 to Age 4) independently of the habitat conditions (Test I – lagoon cue test, to Test IV – reduced salinity test, (Figure 6.4). There were significant differences between ages only in Test III (increased temperature test: Kruskal-Wallis chi-squared = 8.1385, df = 3, p = 0.04), and particularly between Age 1 and Age 4 (*p* = 0.049) (Table 6.5).

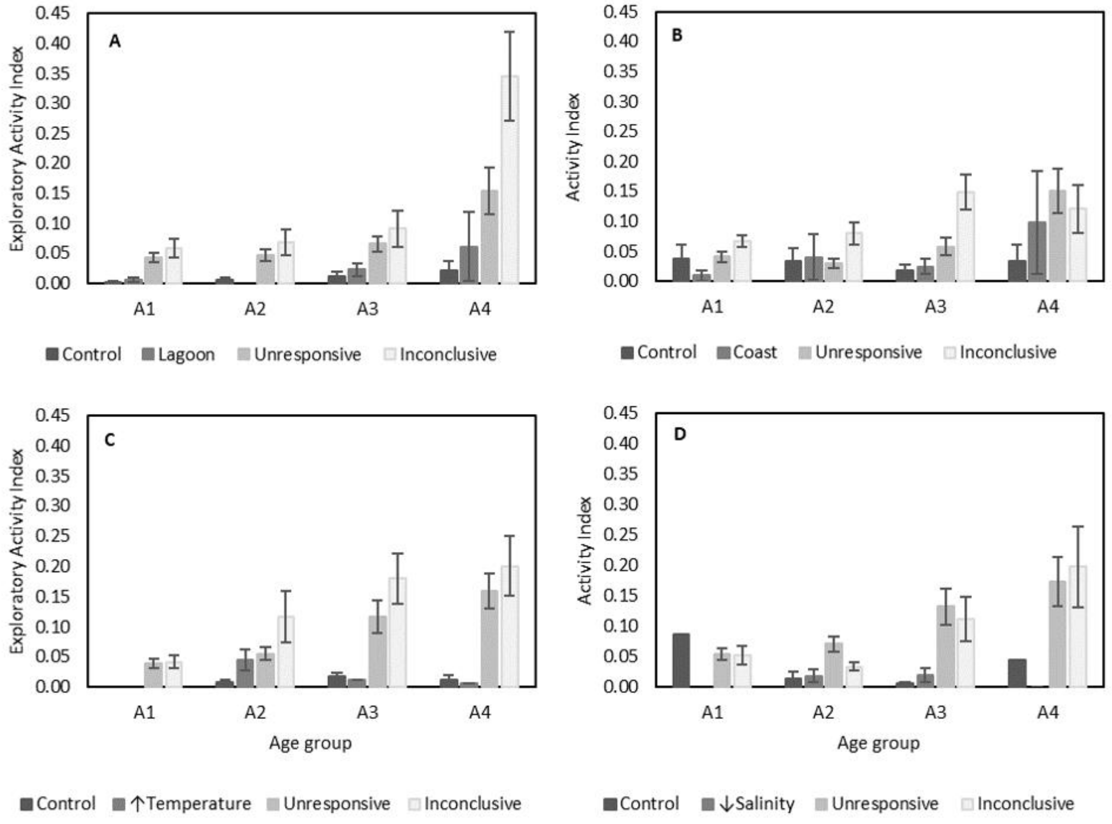

**Figure 6.4** Average Exploratory Activity Index (EAI) exhibited by white seabream *Diplodus sargus* (Linnaeus, 1758) larvae in choice-chamber experiments separated by different behaviours (control water preference, stimulus water preference, unresponsive or inconclusive behaviour) in different habitat conditions (A- Test I, lagoon habitat; B- Test II, coastal habitat; C- Test III, increase of temperature; D- Test IV, decrease of salinity) and across ontogeny (Age 1, Age2, Age 3, Age 4).

The significant repeatabilities observed indicated that *D. sargus* larvae showed consistent individual differences across ages and tests (Tables 6.6-6.8). Significant short-term repeatabilities of EAI were verified in all ages across tests, increasing along ontogeny (Table 6.6). The same was verified for long-term repeatability (Age 1 vs. Age 2, Age 2 vs. Age 3, Age 3 vs. Age 4) across tests (Table 6.7). Longer-term significant repeatabilities occurred in comparisons of Age 2 with Age 3 (Test I, Test II, Test IV) and of Age 3 with Age 4 (Acclimatisation, Test II, Test III and Test IV) (Table 6.8). As for the PI, significant short-term repeatability occurred in Age 2 (Table 6.6) and in the comparison of Age 2 with Age 3 across ages (Table 6.7), and specifically in Test II (Table 6.8).

**Table 6.6** Descriptive measures of Exploratory Activity and Preference Indices exhibited by white seabream *Diplodus sargus* (Linnaeus, 1758) across tests performed in choice-chamber experiments (Acclimatisation, Test I, Test II, Tests III, Test IV) across ontogeny (Age 1, Age2, Age 3, Age 4). Legend: mean ± standard error (SE), coefficient of variation (CV), individual-based repeatability ($R_{IOC}$) with 95% confidence intervals (CI), significance (p). Significant results are highlighted in bold.

| **Behavioural variable** | **N** | **Mean ± SE** | **CV** | **$R_{ICC}$** | **CI** | ***p*** |
|---|---|---|---|---|---|---|
| *Exploratory Activity Index* | | | | | | |
| Age 1 | 24 | 0.049 ± 0.004 | 0.838 | **0.556** | **[0.197, 0.785]** | **0.003** |
| Age 2 | 28 | 0.052 ± 0.005 | 1.218 | **0.759** | **[0.583, 0.876]** | **0.000** |
| Age 3 | 31 | 0.096 ± 0.010 | 1.310 | **0.859** | **[0.761, 0.924]** | **0.000** |
| Age 4 | 25 | 0.159 ± 0.018 | 1.234 | **0.938** | **[0.888, 0.969]** | **0.000** |
| *Preference Index* | | | | | | |
| Age 1 | 24 | -0.009 ± 0.011 | -12.715 | 0.150 | [0.539, 0.588] | 0.286 |
| Age 2 | 28 | 0.021 ± 0.010 | 5.472 | **0.448** | **[0.042, 0.751]** | **0.017** |
| Age 3 | 31 | 0.038 ± 0.012 | 3.830 | 0.170 | [0.403, 0.555] | 0.239 |
| Age 4 | 25 | 0.038 ± 0.018 | 5.271 | 0.095 | [0.620, 0.554] | 0.353 |

**Table 6.7** Descriptive measures of Exploratory Activity and Preference Indices exhibited by white seabream *Diplodus sargus* (Linnaeus, 1758) across tests performed in choice-chamber experiments (Acclimatisation, Test I, Test II, Tests III, Test IV) for each age-combination (Age 1 to Age 4). Legend: mean ± standard error (SE), coefficient of variance (CV), individual-based repeatability ($R_{IOC}$) with 95% confidence intervals (CI), significance (p). Only comparisons with N higher than ten are shown. Significant results are highlighted in bold.

| **Behavioural variable** | **N** | **Mean ± SE** | **CV** | **$R_{IOC}$** | **CI** | ***p*** |
|---|---|---|---|---|---|---|
| *Exploratory Activity Index* | | | | | | |
| Age 1 vs. Age 2 | 10 | 0.059 ± 0.007 | 1.168 | **0.683** | **[0.278, 0.907]** | **0.003** |
| Age 2 vs. Age 3 | 10 | 0.052 ± 0.008 | 1.609 | **0.837** | **[0.630, 0.952]** | **0.000** |
| Age 3 vs. Age 4 | 25 | 0.128 ± 0.011 | 1.32 | **0.935** | **[0.889, 0.967]** | **0.000** |
| *Preference Index* | | | | | | |
| Age 1 vs. Age 2 | 10 | 0.001 ± 0.011 | 157.737 | -0.324 | [-2.013, 0.613] | 0.658 |
| Age 2 vs. Age 3 | 10 | 0.050 ± 0.014 | 2.808 | **0.703** | **[0.324, 0.913]** | **0.002** |
| Age 3 vs. Age 4 | 25 | 0.039 ± 0.011 | 4.497 | 0.020 | [-0.672, 0.504] | 0.441 |

**Table 6.8** Measures of Exploratory Activity and Preference Indices exhibited by white seabream *Diplodus sargus* (Linnaeus, 1758) within each test performed in choice-chamber experiments (Acclimatisation, Test I, Test II, Tests III, Test IV) for each age-combination (Age 1 to Age 4). Legend: mean ± standard error (SE), coefficient of variance (CV), individual-based repeatability ($R_{IOC}$) with 95% confidence intervals (CI), significance (p). Only comparisons with N higher than ten are shown. Significant results are highlighted in bold.

| Behavioural variable | N | Mean ± SE | CV | $R_{IOC}$ | CI | p |
|---|---|---|---|---|---|---|
| *Exploratory Activity Index* | | | | | | |
| Aclim: Age 1 vs. Age 2 | 13 | 0.046 ± 0.013 | 1.423 | 0.341 | [-1.159, 0.799] | 0.240 |
| Aclim: Age 2 vs. Age 3 | 14 | 0.041 ± 0.013 | 1.669 | 0.006 | [-2.098, 0.681] | 0.496 |
| Aclim: Age 3 vs. Age 4 | 29 | 0.126 ± 0.023 | 1.374 | **0.515** | **[-0.033, 0.772]** | **0.030** |
| Test I: Age 1 vs. Age 2 | 13 | 0.072 ± 0.017 | 1.224 | 0.433 | [-0.858, 0.827] | 0.169 |
| Test I: Age 2 vs. Age 3 | 12 | 0.035 ± 0.009 | 1.252 | **0.781** | **[0.240, 0.937]** | **0.009** |
| Test I: Age 3 vs. Age 4 | 28 | 0.130 ± 0.025 | 1.446 | 0.439 | [-0.212, 0.740] | 0.070 |
| Test II: Age 1 vs. Age 2 | 13 | 0.062 ± 0.010 | 0.860 | -0.189 | [-2.898, 0.637] | 0.616 |
| Test II: Age 2 vs. Age 3 | 13 | 0.048 ± 0.012 | 1.311 | **0.722** | **[0.089, 0.915]** | **0.018** |
| Test II: Age 3 vs. Age 4 | 29 | 0.101 ± 0.017 | 1.258 | **0.634** | **[0.221, 0.828]** | **0.005** |
| Test III: Age 1 vs. Age 2 | 10 | 0.053 ± 0.010 | 0.866 | -0.417 | [-4.704, 0.648] | 0.694 |
| Test III: Age 2 vs. Age 3 | 10 | 0.065 ± 0.025 | 1.717 | 0.575 | [-0.710, 0.895] | 0.109 |
| Test III: Age 3 vs. Age 4 | 25 | 0.143 ± 0.027 | 1.355 | **0.754** | **[0.441, 0.891]** | **0.001** |
| Test IV: Age 1 vs. Age 2 | 10 | 0.061 ± 0.023 | 1.645 | 0.233 | [-2.087, 0.810] | 0.349 |
| Test IV: Age 2 vs. Age 3 | 10 | 0.067 ± 0.022 | 1.447 | **0.771** | **[0.078, 0.943]** | **0.019** |
| Test IV: Age 3 vs. Age 4 | 26 | 0.137 ± 0.021 | 1.118 | **0.807** | **[0.569, 0.913]** | **0.000** |
| *Preference Index* | | | | | | |
| Aclim: Age 1 vs. Age 2 | 13 | -0.053 ± 0.042 | -4.053 | -0.385 | [-3.540, 0.577] | 0.709 |
| Aclim: Age 2 vs. Age 3 | 14 | 0.020 ± 0.015 | 3.828 | 0.533 | [-0.455, 0.850] | 0.092 |
| Aclim: Age 3 vs. Age 4 | 29 | 0.056 ± 0.029 | 3.954 | -0.030 | [-1.193, 0.517] | 0.530 |
| Test I: Age 1 vs. Age 2 | 13 | 0.002 ± 0.023 | -74.139 | -0.129 | [-2.702, 0.655] | 0.582 |
| Test I: Age 2 vs. Age 3 | 12 | 0.028 ± 0.023 | 4.057 | -0.085 | [-2.770, 0.688] | 0.553 |
| Test I: Age 3 vs. Age 4 | 28 | 0.007 ± 0.015 | 16.085 | -0.582 | [-2.302, 0.293] | 0.862 |
| Test II: Age 1 vs. Age 2 | 13 | -0.003 ± 0.028 | -43.653 | -6.516 | [-23.631, -1.293] | 0.999 |
| Test II: Age 2 vs. Age 3 | 13 | 0.050 ± 0.024 | 2.451 | **0.857** | **[0.532, 0.956]** | **0.001** |
| Test II: Age 3 vs. Age 4 | 29 | 0.068 ± 0.026 | 2.891 | 0.394 | [-0.291, 0.715] | 0.096 |
| Test III: Age 1 vs. Age 2 | 10 | 0.024 ± 0.018 | 3.409 | 0.043 | [-2.854, 0.762] | 0.475 |
| Test III: Age 2 vs. Age 3 | 10 | 0.098 ± 0.046 | 2.083 | -0.297 | [-4.220, 0.678] | 0.647 |
| Test III: Age 3 vs. Age 4 | 26 | 0.043 ± 0.021 | 3.567 | 0.139 | [-0.920, 0.614] | 0.355 |
| Test IV: Age 1 vs. Age 2 | 10 | -0.007 ± 0.010 | -6.321 | 0.208 | [-2.190, 0.803] | 0.367 |
| Test IV: Age 2 vs. Age 3 | 10 | 0.035 ± 0.031 | 3.996 | 0.647 | [-0.423, 0.912] | 0.069 |
| Test IV: Age 3 vs. Age 4 | 25 | 0.016 ± 0.019 | 8.371 | -0.196 | [-1.714, 0.473] | 0.668 |

In the four tests, larvae with unresponsive or inconclusive behaviours showed higher values of exploratory activity index than larvae with a preference for control water or stimulus water, except for Age 1 in Test IV, where the larvae with a preference for control water showed higher EAI (Figure 6.4). There were significative differences in EAI between ages in Test I (Friedman chi-squared = 9.0, df = 3, *p* = 0.029), and between tests in Age 3 (Friedman chi-squared = 10.2, df = 3, *p* = 0.017) and Age 4 (Friedman chi-squared = 9.9, df = 3, *p* = 0.019). Trough Conover post-hoc test we verified that the significant differences were observed between preference for control water and inconclusive behaviour and between preference for control water and unresponsive behaviour in Test I (Table 6.9). Significant differences were also observed between preference for control water and inconclusive and unresponsive behaviours, and between preference for stimulus water and inconclusive and unresponsive behaviours during Ages 3 and 4 (Table 6.9).

**Table 6.9** The post-hoc Conover test for multiple comparations of Exploratory Activity Index of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae considering their responses obtained in Preference Index (R- preference for control water, S- preference for stimulus water, U- unresponsive behaviour, I- inconclusive behaviour) in each test (Test I- lagoon habitat, Test II- coastal habitat, Test III- increase of temperature, Test IV- decrease of salinity) along ontogeny (Age 1, Age2, Age 3, Age4). Significative are highlighted in bold.

| | **p** | | **p** | | **p** | | **P** |
|---|---|---|---|---|---|---|---|
| *Test I* | | *Test II* | | *Test III* | | *Test IV* | |
| R vs. I | **0.002** | R vs. I | 0.058 | R vs. I | 0.740 | R vs. I | 1.000 |
| R vs. S | 0.060 | R vs. S | 0.607 | R vs. S | 1.000 | R vs. S | 1.000 |
| R vs. U | **0.034** | R vs. U | 0.409 | R vs. U | 1.000 | R vs. U | 0.810 |
| S vs. I | 0.102 | S vs. I | 0.157 | S vs. I | 0.740 | S vs. I | 1.000 |
| U vs. I | 0.153 | U vs. I | 0.539 | U vs. I | 1.000 | U vs. I | 1.000 |
| S vs. U | 0.629 | S vs. U | 0.607 | S vs. U | 1.000 | S vs. U | 1.000 |
| *Age 1* | | *Age 2* | | *Age 3* | | *Age 4* | |
| R vs. I | 1.000 | R vs. I | 0.077 | R vs. I | **0.001** | R vs. I | **0.004** |
| R vs. S | 1.000 | R vs. S | 0.345 | R vs. S | 0.504 | R vs. S | 1.000 |
| R vs. U | 1.000 | R vs. U | 0.478 | R vs. U | **0.004** | R vs. U | **0.013** |
| S vs. I | 1.000 | S vs. I | 0.658 | S vs. I | **0.004** | S vs. I | **0.004** |
| U vs. I | 1.000 | U vs. I | 0.606 | U vs. I | 0.504 | U vs. I | 0.572 |
| S vs. U | 1.000 | S vs. U | 0.739 | S vs. U | **0.015** | S vs. U | **0.013** |

## 6.4 Discussion

The major finding of this study was that during early phases of ontogeny, white seabream *Diplodus sargus* larvae exhibited a highly consistent inter-individual variability in behaviours across age and tests, suggesting a strong individuality. This previously unsuspected individual consistency highlights the need of consideration of the possible consequences of this individuality, especially when inferring about larval dispersal processes and selection of settlement areas to recruit.

### 6.4.1 Response to habitat and environmental cues

In general, white seabream larvae did not show a clear preference for any stimuli, contrary to the expectation that they would prefer lagoon and coastal habitats, which are used as nursery habitats across southern Europe (Monteiro et al., 1990; Faria et al., 2006; Gonçalves et al., 2015; Garcia-Rubies and Marcpherson, 1995; Harmelin-Vivien et al., 1995). Despite this lack of preference, we observed statistical differences for the Preference Index between Age 1 and Age 2 in Test I (lagoon cue test). At Age 1 (around 25 DPH), some larvae preferred Ria Formosa lagoon water collected in a main and open channel with seagrass beds and with high water exchange levels. Some studies reported that temperate post-flexion fish larvae could detect and swim towards odour cues from nursery habitats with seagrass beds( (e.g., silver seabream *Pagrus auratus* (Sparidae) (Forster, 1801) (Radford et al., 2012); red drum *Sciaenops ocellatus* (Sciaenidae) (Linnaeus, 1766) (Havel and Fuiman, 2016); Japanese meagre Australian bass *Macquaria novemaculeata* (Percichthyidae) (Steindachner, 1866); *Argyrosomus japonicus* (Sciaenidae) (Temminck & Schlegel, 1843) (O'Connor et al., 2017)). However, other studies found that most post-flexion gilthead seabream *Sparus aurata* (Sparidae) Linnaeus, 1758 larvae preferred rocky coastal water over Ria Formosa lagoon water with seagrass cues – even though the predominance of unresponsive behaviour was remarkable (Morais et al., 2017), as it was in this study. Gilthead seabream larvae also had a weak reaction to seagrass cues in the Mediterranean Sea (Díaz-Gil et al., 2017). However, some species seem to ignore odour cues in detriment of another sensory stimulus. For example, linesnout goby *Elacatinus lori* (Gobiidae) (Colin, 2002) post-flexion larvae, a coral reef species, select sponge habitats using visual rather that odour cues (Majoris et al., 2018), similarly to other coral reef species (Lecchini et al. 2005a, 2014; Igulu et al., 2011).

Regarding environmental and climatic changes, salinity and temperature variability are known to influence the recruitment of fish larvae into nurseries areas (Maynou et al., 2014; Baptista et al., 2016 – Chapter 4 of the present Thesis; Leitão et al., 2016 – Chapter 3 of the present Thesis; Pecl et al., 2017) due to their effects on behaviour, physiology, distribution and migration (Bertram et al., 2001; Hunt von Herbing, 2002; Pecl et al., 2017). Lower salinity plumes signal the presence of rivers along with coastal areas (Sabates, 1990), while depth salinity and temperature variability could indicate the direction of currents and water sources that could be used as environmental cues (Hughes, 1969). However, the present results did not indicate any clear preference by increase of temperature or reduced salinity compared to control. This could mean that in the case of white seabream, larvae reach the estuaries through other cues, and the differences in temperature may not be enough to serve as a habitat cue. Another important point is that in the flume-chamber the different tested temperatures mixes and could provide a water with favourable temperature in unresponsive areas (see Figure 6.1).

The unresponsive (no preference by stimulus or control areas) and inconclusive behaviours showed by most post-flexion larvae could mean that their olfactory stimulus must be complemented with other stimuli, as ecosystem soundscapes [e.g., living animals (Simpson et al., 2005; Lillis et al., 2014; Atema et al., 2015), waves breaking on the coast (Montgomery et al., 2006)], visual cues (e.g., water turbidity, bottom features, object detection such as conspecifics) (Whitfield, 1994; Atema et al. 2015), magnetism (Crisp, 1974; Qin et al., 2015), pressure gradients (Burke et al., 1995), or oceanic currents (Crisp, 1974).

Although there was no clear preference for an habitat or environmental cue, we observed that white seabream larvae showed responsive behaviour (preference for control or stimulus water) for different habitat cues (Test I – lagoon cue test, and Test II – rocky cue test) at Age 3 and environmental conditions (Test III – increased temperature test, and Test IV – reduced salinity test) at Age 2. These observations could be related to the timing when different sensorial organs develop during ontogeny. A hypothesis may be that white seabream larvae can detect differences in water temperature and salinity early in development, while chemoreception of odour cues occurs later. Indeed, the SAAB hypothesis assumes that the ability to detect cues increases with ontogeny, and the response to cues increases with increasing swimming capabilities (Teodósio et al., 2016). For example, a fish of the same family only responded to nursery odour cues during the post-flexion stage (Morais et al., 2017). Another interesting point is that the critical swimming speed and swimming endurance of white seabream larvae increase considerably at ages 2 and 3 (Chapter 5 of present Thesis).

Although the exploratory activity increased with age in all tests, only the test with different temperatures (Test III) induced significant differences between ages. Temperature increase has been related to increased activity in some fish species (Biro et al., 2007, 2010; Pasquet et al. 2016), either due to feeding behaviours (Theodorou et al., 2012; Reynisson and Ólafsdóttir, 2018) or typical effects upon the metabolism of ectothermic animals (O'Connor et al., 2007; Biro and Stamps, 2010). Thus, the increase and fluctuations of water temperature and changes in salinity in coastal areas must be framed in a context of environmental and climatic changes, which may alter the responses of white seabream to nursery habitat cues in the near future.

In future studies, we should strive to introduce more complex experimental designs when testing chemical, visual, and sound cues along ontogeny (e.g., offshore water cues; presence/absence of conspecifics, prey, and predators), either for wild or laboratory-reared larvae (Díaz-Gil et al., 2017; Morais et al., 2017). Finally, personality traits must be analyzed in such experiments (i.e., activity and exploration) simultaneously to more traditional metrics (i.e., time spent following each cue).

### 6.4.2 Individual behavioural consistency

White seabream larvae showed consistent behaviours when subject to different environmental stimuli through time indicating the emergence of personality traits early in their development. These finding confirms the few existing studies that showed consistent individual behavioural differences in brown trout (Sundström et al., 2004), zebrafish (Budaev and Andrew, 2009), and Northern pike larvae (Pasquet et al., 2016). Gilthead seabream also show consistent personality traits at least during the juvenile phase (Castanheira et al., 2016).

We found relatively high coefficients of repeatability (0.51 ± 0.29), above those reported in other studies (0.37) is the average reported in the meta-analysis made by Bell et al. (2009) which includes both vertebrates and invertebrates). However, behavioural consistency varies among individuals (Bell et al., 2009). For example, proactive individuals display behaviours that are more repeatable than reactive individuals (Marchetti and Drent, 2000; Carere et al., 2005). So, we cannot assume that all individuals respond consistently to environmental stimuli. Short-term repeatability of exploratory activity increased with ontogeny, with higher values recorded at Age 4. The same tendency was observed for long-term repeatability.

Bell et al. (2009) showed that the repeatability is significantly greater than 0 for a large range of taxa and behaviours, but not all behaviours can be repeatable (Bell et al., 2009). Indeed, we observed that repeatability was not verified in all ages and tests, which implies that personality traits vary depending on the situation (e.g., when the exploratory activity of white seabream was evaluated separately in each test and for habitat preference). Individual habitat preference was only consistent at Age 2, and when Age 2 was compared with Age 3, and in one test (Test II – rocky cue test). In a marine invertebrate species (European common cuttlefish *Sepia officinalis* Linnaeus, 1758), it was found that some variables showed relatively high repeatability, while other variables showed little or no repeatability (Zoratto et al., 2018). Environmental conditions are one of many factors underlying trait stability, so it is difficult to identify the causes of this variation and why some behaviours are more repeatable than others (Bell et al., 2009).

Personality traits may have implications in the response of individuals to ecological challenges and increasing settlement into a suitable habitat (Wolf and Weissing, 2012; Canestrelli et al., 2016). Activity and exploration behaviours may affect dispersal in all developmental stages (Cote et al., 2010). Proactive individuals (i.e., more active, exploratory, and bold) have more propensity to take risks (Koolhaas et al., 1999; Coppens et al., 2010; Hall et al., 2015) and consequently more ability to acquire food and avoid predators that are determinants for growth, survival and dispersal (Dall and Griffith, 2014; Cote et al., 2010; Jørgensen et al., 2013; Nanninga et al. 2014). This strong influence of personality traits on dispersal strategies has been reported to affect the direction and distance of larval dispersion (Sundelöf and Jonsson, 2012).

Currently, the influence of individual behavioural consistency of white seabream larvae on dispersal, or any other temperate fish larvae hatching from pelagic eggs, remains unknown. Nonetheless, the increase in exploratory activity across ontogeny may diminish random dispersion of white seabream larvae.

## 6.5 Conclusions

Contrary to our hypotheses, white seabream larvae did not show a preference for either lagoon or rocky shore habitats, neither towards increased water temperature or decreased water salinity. However, they increased exploratory activity during ontogeny. Importantly, we demonstrated for the first time that personality traits of a temperate fish larvae hatched from pelagic eggs are present early in the development, with high short-term repeatability in exploratory activity index, independently of the presented stimulus. We also observed that the exploratory activity was higher when larvae showed unresponsive or inconclusive behaviours, meaning that the larvae are possibly trying to find stimulus different from those that were offered. Thus, personality traits could influence the process of searching for suitable nursery habitats and, consequently, dispersion and connectivity of white seabream populations. Ultimately, characterizing the behaviour of temperate pelagic marine fish larvae and understanding active habitat selection may increase our understanding of recruitment variability, refine larval dispersal models, and add to the body of knowledge on the effects of environmental and global changes and habitat degradation on fish distribution.

## 6.6 Ethics statement

The experiments were conducted in accordance with the Guidelines of the European Union Council (86/609/EU) and Portuguese legislation for the use of laboratory animals. CCMAR facilities and their staff are certified to house and conduct experiments with live animals (“group-1” license by the Veterinary General Directorate, Ministry of Agriculture, Rural Development and Fisheries of Portugal) in accordance with the three “R” policy and national and European legislation.

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## 6.9 Appendix

**Table 6.A1** Spearman's correlation coefficients between behavioural measurements: activity (ACT), exploration (EXP) and Exploratory Activity Index (EAI), for white seabream *Diplodus sargus* (Linnaeus, 1758) in each test (T1- lagoon habitat, T2- coastal habitat, T3- increased temperature and T4- reduced salinity), at Age 1, Age 2, Age 3 and Age 4. (* and ** corresponding to correlation significant at the 0.05 and 0.01 level, respectively).

| | **ACT Acl** | **ACT T1** | **ACT T2** | **ACT T3** | **ACT T4** | **EXP Acl** | **EXP T1** | **EXP T2** | **EXP T3** | **EXP T4** | **EAI Acl** | **EAI T1** | **EAI T2** | **EAI T3** | **EAI T4** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Age 1** | | | | | | | | | | | | | | | |
| ACT Acl | 1.000 | | | | | | | | | | | | | | |
| ACT T1 | 0.104 | 1.000 | | | | | | | | | | | | | |
| ACT T2 | 0.276 | 0.385* | 1.000 | | | | | | | | | | | | |
| ACT T3 | 0.517** | 0.464* | 0.485* | 1.000 | | | | | | | | | | | |
| ACT T4 | 0.316 | 0.094 | 0.368 | 0.331 | 1.000 | | | | | | | | | | |
| EXP Acl | 0.543** | 0.251 | 0.032 | 0.343 | 0.181 | 1.000 | | | | | | | | | |
| EXP T1 | 0.018 | 0.672** | 0.058 | 0.277 | 0.208 | 0.039 | 1.000 | | | | | | | | |
| EXP T2 | 0.136 | 0.007 | 0.543** | -0.057 | 0.425* | 0.018 | -0.035 | 1.000 | | | | | | | |
| EXP T3 | 0.465* | 0.111 | 0.147 | 0.736** | 0.316 | 0.210 | 0.325 | -0.079 | 1.000 | | | | | | |
| EXP T4 | 0.356 | -0.351 | 0.119 | 0.055 | 0.553** | 0.193 | -0.038 | 0.364 | 0.236 | 1.000 | | | | | |
| EAI Acl | 0.933** | 0.182 | 0.236 | 0.531** | 0.306 | 0.771** | -0.004 | 0.085 | 0.429* | 0.365 | 1.000 | | | | |
| EAI T1 | 0.078 | 0.980** | 0.304 | 0.448* | 0.096 | 0.214 | 0.757** | -0.034 | 0.123 | -0.339 | 0.138 | 1.000 | | | |
| EAI T2 | 0.296 | 0.337* | 0.970** | 0.410* | 0.475* | 0.032 | 0.102 | 0.689** | 0.144 | 0.245 | 0.241 | 0.266 | 1.000 | | |
| EAI T3 | 0.287 | 0.045 | 0.273 | 0.285 | 0.974** | 0.143 | 0.211 | 0.424* | 0.315 | 0.587** | 0.259 | 0.060 | 0.386 | 1.000 | |
| EAI T4 | 0.497** | 0.383 | 0.470* | 0.979** | 0.359 | 0.330 | 0.283 | -0.043 | 0.805** | 0.124 | 0.509** | 0.379 | 0.415* | 0.322 | 1.000 |
| **Age 2** | | | | | | | | | | | | | | | |
| ACT Acl | 1.000 | | | | | | | | | | | | | | |
| ACT T1 | 0.316* | 1.000 | | | | | | | | | | | | | |
| ACT T2 | 0.194 | 0.595** | 1.000 | | | | | | | | | | | | |
| ACT T3 | 0.116 | 0.523** | 0.461* | 1.000 | | | | | | | | | | | |
| ACT T4 | -0.138 | 0.342 | 0.345 | 0.790** | 1.000 | | | | | | | | | | |
| EXP Acl | 0.713** | 0.148 | 0.134 | 0.117 | -0.034 | 1.000 | | | | | | | | | |
| EXP T1 | 0.290 | 0.703** | 0.337* | 0.519** | 0.228 | 0.046 | 1.000 | | | | | | | | |
| EXP T2 | 0.163 | 0.452** | 0.692** | 0.353 | 0.153 | 0.044 | 0.411** | 1.000 | | | | | | | |
| EXP T3 | 0.126 | 0.375* | 0.455* | 0.585** | 0.552** | 0.148 | 0.491** | 0.298 | 1.000 | | | | | | |
| EXP T4 | -0.021 | 0.194 | 0.067 | 0.316 | 0.541** | 0.066 | 0.097 | -0.096 | 0.451* | 1.000 | | | | | |
| EAI Acl | 0.989** | 0.295 | 0.197 | 0.128 | -0.104 | 0.792** | 0.242 | 0.141 | 0.139 | -0.002 | 1.000 | | | | |
| EAI T1 | 0.305 | 0.991** | 0.592** | 0.534** | 0.344 | 0.114 | 0.757** | 0.466** | 0.387* | 0.217 | 0.277 | 1.000 | | | |
| EAI T2 | 0.175 | 0.589** | 0.976** | 0.401* | 0.314 | 0.105 | 0.351* | 0.789** | 0.367 | 0.032 | 0.172 | 0.593** | 1.000 | | |
| EAI T3 | -0.125 | 0.393* | 0.334 | 0.759** | 0.984** | -0.016 | 0.230 | 0.132 | 0.547** | 0.643** | -0.089 | 0.395* | 0.305 | 1.000 | |
| EAI T4 | 0.104 | 0.542** | 0.475* | 0.985** | 0.822** | 0.149 | 0.517** | 0.358 | 0.646** | 0.373 | 0.124 | 0.550** | 0.413* | 0.799** | 1.000 |

**Table 6.A1**(cont.) Spearman's correlation coefficients between behavioural measurements: activity (ACT), exploration (EXP) and Exploratory Activity Index (EAI), for white seabream *Diplodus sargus* (Linnaeus, 1758) in each test (T1- lagoon habitat, T2- coastal habitat, T3- increased temperature and T4- reduced salinity), at Age 1, Age 2, Age 3 and Age 4. (* and ** corresponding to correlation significant at the 0.05 and 0.01 level, respectively).

| | **ACT Acl** | **ACT T1** | **ACT T2** | **ACT T3** | **ACT T4** | **EXP Acl** | **EXP T1** | **EXP T2** | **EXP T3** | **EXP T4** | **EAI Acl** | **EAI T1** | EAI T2 | EAI T3 | EAI T4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Age 3** | | | | | | | | | | | | | | | |
| ACT Acl | 1.000 | | | | | | | | | | | | | | |
| ACT T1 | 0.487** | 1.000 | | | | | | | | | | | | | |
| ACT T2 | 0.533** | 0.540** | 1.000 | | | | | | | | | | | | |
| ACT T3 | 0.501** | 0.522** | 0.768** | 1.000 | | | | | | | | | | | |
| ACT T4 | 0.441* | 0.740** | 0.619** | 0.715** | 1.000 | | | | | | | | | | |
| EXP Acl | 0.676** | 0.493** | 0.444** | 0.408* | 0.315 | 1.000 | | | | | | | | | |
| EXP T1 | 0.055 | 0.613** | 0.278 | 0.257 | 0.518** | 0.231 | 1.000 | | | | | | | | |
| EXP T2 | 0.229 | 0.342* | 0.688** | 0.451** | 0.376* | 0.419** | 0.519** | 1.000 | | | | | | | |
| EXP T3 | 0.251 | 0.478** | 0.461** | 0.660** | 0.481** | 0.370* | 0.467** | 0.410* | 1.000 | | | | | | |
| EXP T4 | 0.135 | 0.387* | 0.377* | 0.439* | 0.781** | 0.081 | 0.468** | 0.381* | 0.376* | 1.000 | | | | | |
| EAI Acl | 0.972** | 0.500** | 0.544** | 0.481** | 0.423* | 0.802** | 0.092 | 0.276 | 0.293 | 0.121 | 1.000 | | | | |
| EAI T1 | 0.469** | 0.985** | 0.533** | 0.510** | 0.737** | 0.485** | 0.672** | 0.370* | 0.516** | 0.432* | 0.484** | 1.000 | | | |
| EAI T2 | 0.514** | 0.545** | 0.983** | 0.745** | 0.642** | 0.426** | 0.330* | 0.749** | 0.463** | 0.434* | 0.526** | 0.548** | 1.000 | | |
| EAI T3 | 0.418* | 0.711** | 0.602** | 0.692** | 0.992** | 0.282 | 0.495** | 0.360* | 0.480** | 0.829** | 0.397* | 0.709** | 0.620** | 1.000 | |
| EAI T4 | 0.506** | 0.530** | 0.785** | 0.988** | 0.706** | 0.387* | 0.270 | 0.440* | 0.678** | 0.440* | 0.479** | 0.527** | 0.766** | 0.683** | 1.000 |
| **Age 4** | | | | | | | | | | | | | | | |
| ACT Acl | 1.000 | | | | | | | | | | | | | | |
| ACT T1 | 0.658** | 1.000 | | | | | | | | | | | | | |
| ACT T2 | 0.742** | 0.640** | 1.000 | | | | | | | | | | | | |
| ACT T3 | 0.717** | 0.876** | 0.800** | 1.000 | | | | | | | | | | | |
| ACT T4 | 0.690** | 0.687** | 0.775** | 0.816** | 1.000 | | | | | | | | | | |
| EXP Acl | 0.665** | 0.453* | 0.551** | 0.608** | 0.550** | 1.000 | | | | | | | | | |
| EXP T1 | 0.578** | 0.747** | 0.542** | 0.618** | 0.571** | 0.458* | 1.000 | | | | | | | | |
| EXP T2 | 0.495** | 0.496** | 0.760** | 0.746** | 0.732** | 0.681** | 0.457* | 1.000 | | | | | | | |
| EXP T3 | -0.039 | 0.143 | 0.225 | 0.258 | 0.068 | 0.106 | 0.460* | 0.424* | 1.000 | | | | | | |
| EXP T4 | 0.354 | 0.431* | 0.501* | 0.618** | 0.687** | 0.466* | 0.550** | 0.715** | 0.476* | 1.000 | | | | | |
| EAI Acl | 0.987** | 0.668** | 0.737** | 0.737** | 0.705** | 0.756** | 0.586** | 0.544** | -0.028 | 0.397* | 1.000 | | | | |
| EAI T1 | 0.659** | 0.985** | 0.623** | 0.860** | 0.696** | 0.452* | 0.797** | 0.503** | 0.148 | 0.468* | 0.668** | 1.000 | | | |
| EAI T2 | 0.723** | 0.643** | 0.991** | 0.791** | 0.746** | 0.578** | 0.533** | 0.789** | 0.250 | 0.487* | 0.726** | 0.622** | 1.000 | | |
| EAI T3 | 0.663** | 0.700** | 0.765** | 0.842** | 0.984** | 0.556** | 0.617** | 0.754** | 0.142 | 0.762** | 0.683** | 0.717** | 0.734** | 1.000 | |
| EAI T4 | 0.698** | 0.867** | 0.801** | 0.991** | 0.812** | 0.588** | 0.662** | 0.769** | 0.345 | 0.655** | 0.716** | 0.855** | 0.790** | 0.846** | 1.000 |

# CHAPTER 7

## Modelling the ingress of a temperate fish larva into a nursery coastal lagoon

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# MODELLING THE INGRESS OF A TEMPERATE FISH LARVA INTO A NURSERY COASTAL LAGOON

## Abstract

The development of sensorial acuity and swimming capabilities of coastal fish larvae, as well as their responses to coastal nursery cues, are essential for recruitment success. However, most studies delved into the response of coral reef fish larvae to environmental cues and recruitment into nursery areas, while only a few committed to study this topic with fish species from temperate regions. The Sense Acuity and Behavioural (SAAB) Hypothesis proposes that temperate region fish larvae hatching from pelagic eggs are also able to sense nursery cues and ingress into these ecosystems by using several active swimming strategies. Thus, we aimed to test the SAAB hypothesis by studying the ingress of a temperate fish larvae – white seabream *Diplodus sargus* (Linnaeus, 1758) – into a coastal nursery area, the Ria Formosa lagoon. We combined the results from sensory acuity tests, swimming capability trials, and personality traits of post-flexion larvae with a directional swimming-advection-dispersion model developed for the Ria Formosa lagoon and the adjacent coastal water, to quantify the success of ingress of white seabream in function of the distance and depth between spawning grounds and the lagoon. Data demonstrated that the location of spawning sites and directional swimming capabilities are equally important on the ingress success of white seabream into the Ria Formosa lagoon. Recruitment was higher when spawning sites are located at 15.1-16.9 m deep and when post-flexion larvae use their directional swimming capabilities. In this scenario, the larvae ingressed into the lagoon using tidal currents (passive pre-flexion larvae) or directional swimming capabilities (active post-flexion larvae). The directional swimming capabilities also prevented larval export into the coastal area. When spawning occurs away from the seagrass smell plume, either close to the shore or offshore, larvae are advected into the ocean. These results were valid when the eastward mean current prevails, which represents half of the spawning season. There are no data when westward mean currents prevail, so other recruitment patterns may occur.

Finally, this study demonstrates the relevance of combining fish larvae behaviour and oceanography processes in modelling the dispersion of larvae and to estimate fish recruitment.

**Keywords**: fish larvae; directional swimming; smell plume; individual-based models

## 7.1 Introduction

The causes of recruitment variability are a central question in the ecology of marine communities (Hale et al., 2008). Several hypotheses try explaining fish recruitment variability, as the critical period hypothesis (Hjort, 1914), the aberrant drift hypothesis (Hjort, 1926), the migration triangle hypothesis (Harden-Jones, 1968), the match-mismatch hypothesis (Cushing, 1975; 1990), the stable ocean hypothesis (Lasker, 1978), the stable retention hypothesis (Iles and Sinclair, 1982), the predation hypothesis (Bailey and Houde, 1989), the member/vagrant hypothesis (Sinclair and Iles, 1989), and the ocean triads hypothesis (Agostini and Bakun, 2002). The latter proposes that the variability of year-class in a population depends on enrichment processes (upwelling, mixing, buoyant plumes), concentration processes (convergence, frontal formation, water column stability), and retention processes (eddies, onshore flow) (Agostini and Bakun, 2002). Sinclair and Power (2015) referred the importance of larval retention for the life-cycle closure of a marine fish, in which the selection of spawning location is important to minimize drift and transport during early stages. Thus, it is necessary for the larvae to minimize drift and transport to maximize recruitment, using different active mechanisms to reach nursery areas, by combining horizontal swimming capabilities with circadian vertical migrations to maximize movement directly to nursery ecosystems (Lough and Bolz, 1989) or to areas with hydrodynamic features that favor retention and ingress (Kingsford and Suthers, 1994; Sponaugle et al., 2002; Paris and Cowen, 2004; Secor et al., 2017). All hypothesis stated before, considered that fish larvae spawned in coastal areas reached nursery habitats through a passive way depending on oceanographic processes, such as ocean currents, tides, or weather events (Kingsford et al., 1991; Thorrold et al., 1994; Montgomery et al., 2001; Simpson et al., 2013). Actually, it has been emphasized that fish larvae have swimming capabilities that can exceed typical mean currents and sensorial abilities essential to orient their swimming so as find suitable coastal nursery habitats (Fisher et al., 2000; Leis, 2010; Atema et al., 2015; Teodósio et al., 2016).

A recent hypothesis, the Sense Acuity and Behavioural (SAAB) hypothesis (Teodósio et al., 2016), state that the development of sensorial acuity in temperate fish larvae and their responses to coastal nursery cues (e.g., odour, sound, visual, geomagnetic) are essential for recruitment success. Thus, along with the development of sensorial and swimming capabilities and the interaction with physical transport processes, it has been recognized that fish larvae can control, or at least influence, their dispersion and recruitment (Wolanski et al., 1997; Armsworth et al., 2001; Leis, 2006; Drake et al., 2011; Wolanski and Kingsford, 2014; Teodósio et al., 2016; Wolanski, 2017).

Until recently, larval dispersal models did not include the swimming behaviour of larvae (Raimondi and Keough, 1990; Cowen et al., 2000, 2007; Gilg and Hilbish, 2003). However, since the implementation of Individual-Based Models (IBM's), fish larvae's swimming behaviour began to be included in tandem with larvae's biological traits to orient swimming and coastal oceanographic patterns, which allows inferring dispersion and transport of eggs and larvae, and to identify recruitment habitats (Cowen et al., 2000, 2006; Montgomery et al., 2001; Fiksen et al., 2007; Paris et al., 2007; Peck et al., 2009; Ospina-Alvarez et al., 2015). Biological traits like temperature-dependent development, availability of settlement habitats, mortality rates, transition between passive planktonic phase to more active nektonic phase, diel or/and ontogenetic vertical migrations, horizontal swimming and sensorial abilities, and behavioural strategies such as habitat selection and activity patterns have been included in some marine fish larval IBM's (Cowen et al., 2000, 2006; Mullon et al., 2003; Fiksen et al., 2007; Paris et al., 2007; 2013; Peck et al., 2009; Teodósio et al., 2016).

Despite the interest in including larval behaviour and swimming capabilities on larval dispersal models, most studies were conducted for coral fish species (Armsworth et al., 2001; Gerlach et al., 2007; Paris et al., 2007, 2013; Peck et al., 2009; Wolanski and Kingsford, 2014). Recently, Teodósio et al. (2016) and Wolanski (2017) simulated the ingress of Sparidae and Clupeidae (*Sardina pilchardus*) larvae into the Ria Formosa Lagoon (southern of Portugal), respectively, known as an essential nursery area for many fish species (Andrade, 1990; Ribeiro et al., 2006; Abecasis et al., 2009; Chícharo et al., 2012).

Thus, our study aimed to quantify the ingress of white seabream *Diplodus sargus* (Linnaeus 1758) larvae into the Ria Formosa Lagoon under different oceanographic conditions and from various possible spawning sites. So, we merged the directional swimming-advection-dispersion model developed by Teodósio et al. (2016) for the Ria Formosa Lagoon with the swimming capabilities, habitat preferences, and personality traits determined for white seabream larvae (Chapters 5 and 6 of the present Thesis).

## 7.2 Material and methods

### 7.2.1 Model species

The white seabream *Diplodus sargus* (Linnaeus 1758) is a temperate demersal fish that inhabits coastal rocky reefs, sandy bottoms and seagrass beds (Pajuelo and Lorenzo, 2002). It is abundant in inshore areas down to 50 m deep in the Northeast Atlantic Ocean and Mediterranean Sea (Harmelin-Vivien et al., 1995). White seabream is an abundant species along the Portuguese coast, sustaining important recreational and commercial fisheries (Erzini et al., 1999; Veiga et al., 2010). As many Sparidae species, white seabream behave as cyclic migrants, migrating to nursery habitats after metamorphosis and spending the early stages of life in these environments (Pajuelo and Lorenzo, 2004). Off southern Portugal, adults spawn in coastal areas (Faria et al., 2006), pelagic eggs hatch after three days (Di Franco and Guidetti, 2011), and larvae can spend up to 3-4 weeks in the pelagic environment (Di Franco et al., 2011). Eggs and larvae are dispersed by ocean currents (Di Franco et al., 2012), and as the swimming and sensory capabilities develop along ontogeny, larvae use directional swimming to follow environmental nursey cues (Chapters 5 and 6 of the present Thesis) before reaching suitable settlement habitats. These habitats are shallow (0-2 m deep) sandy-rocky bottoms (Harmelin-Vivien et al., 1995) in coastal lagoons (Vinagre et al., 2010) and estuaries (Faria et al., 2006; Vinagre et al., 2010; Gonçalves et al., 2015). White seabream remain in these habitats for about a year (Planes et al., 1999) and move toward deeper habitats to recruit into the adult population (Harmelin-Vivien et al., 1995).

### 7.2.2 Study area

The Ria Formosa is a shallow and mesotidal coastal lagoon on the south coast of Portugal occupying an area of ~170 km$^2$ (Newton and Mudge, 2003) (Figure 7.1). The lagoon is protected from the Atlantic Ocean by a system of multi-inlet sand-barrier islands. The average depth is less than 3 m, with 14% of the lagoon surface permanently submerged. The water volume exchanged during each tide is around 50-75% due to a strong tidal influence (Águas, 1986; Falcão and Vale, 1990). The freshwater input is reduced and coincides with short periods of winter runoff (Falcão and Vale, 1990; Newton and Mudge, 2003). All these characteristics combined with the extensive seagrass meadows, salt marshes, and intertidal areas (Andrade, 1990; Cabaço et al., 2012; Cabaço and Santos, 2014) make the Ria Formosa Lagoon a highly productive ecosystem (Falcão and Vale, 1990) and an important nursery habitat for white seabream in southern Portugal (Ribeiro et al., 2006; Abecasis et al., 2009).

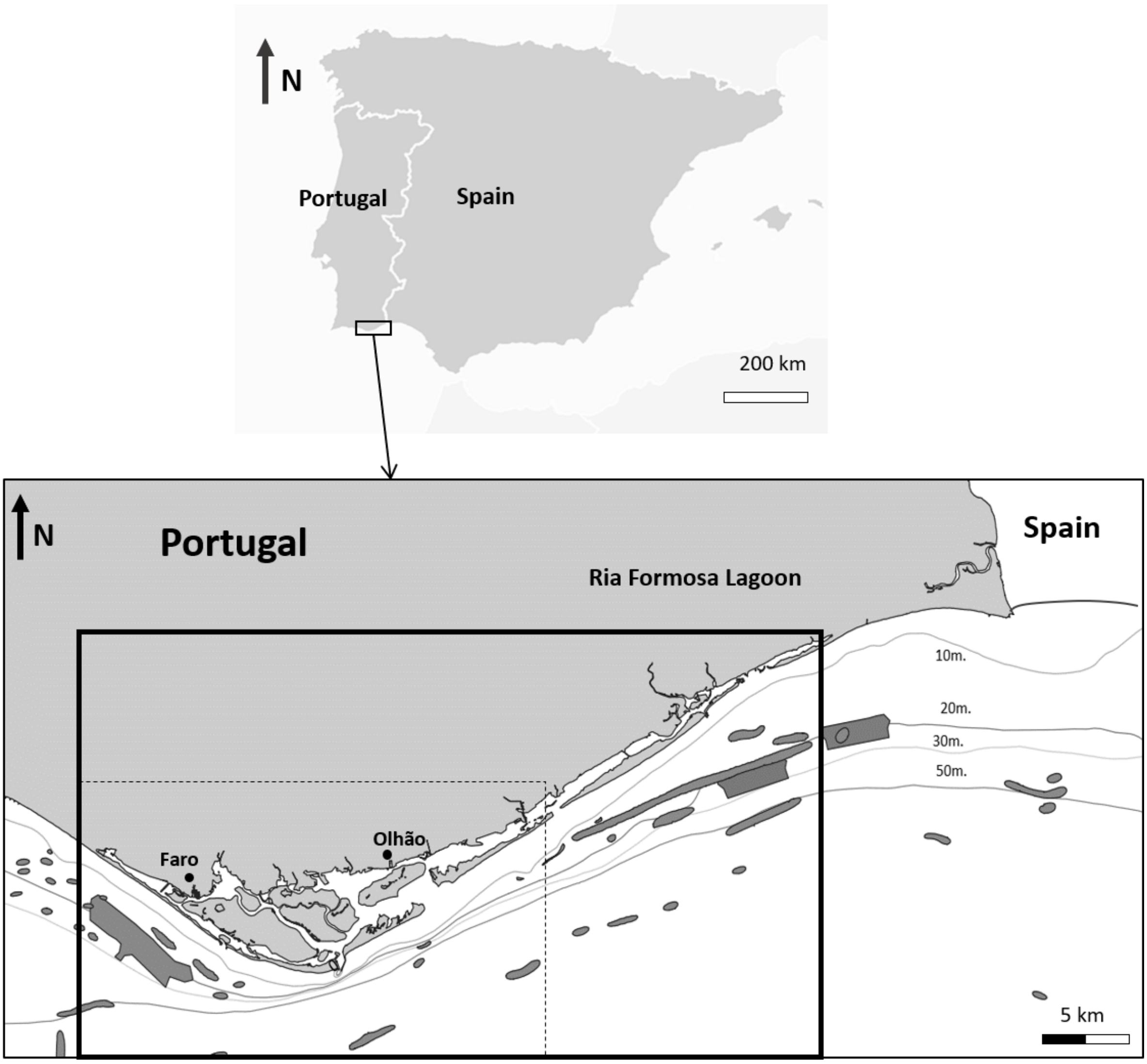

**Figure 7.1** Bathymetry of spawning sites (dark spots) adjacent to the Ria Formosa lagoon off southeastern Portugal. The thick line represents the model domain used in the present study and the thin dashed line represents the model domain used by Teodósio et al. (2016).

### 7.2.3 Model

The importance of directional swimming abilities on the ingress of white seabream larvae into Ria Formosa lagoon was assessed by using a finite-difference, directional swimming-advection-dispersion model developed by Teodósio et al. (2016). This two-dimensional Lagrangian model was developed for the lagoon and adjacent coastal areas (Teodósio et al., 2016) and incorporates the sensory and swimming capabilities of white seabream larvae reported by Baptista et al. (Chapters 5 and 6 of the present Thesis) to quantify the importance of the lagoon odour cue on their recruitment into the lagoon (Wolanski, 2017). The model mesh size was 50 m, the depth was limited to 30 m in coastal waters, and the model domain included the whole lagoon and adjacent coastal area (Figure 7.1). The Teodósio et al. (2016) model domain was extended 15 km eastward to incorporate the entire lagoon. The model used currents measured in September 2006 provided by Flavio Martins (CIMA, University of Algarve) with dominant eastward mean currents, and it was forced at the open oceanic boundaries by the tides, winds and mean sea level slope west to east. The predicted smell seagrass plume emanating from the lagoon to the adjacent coastal area is shown in Figure 7.2.

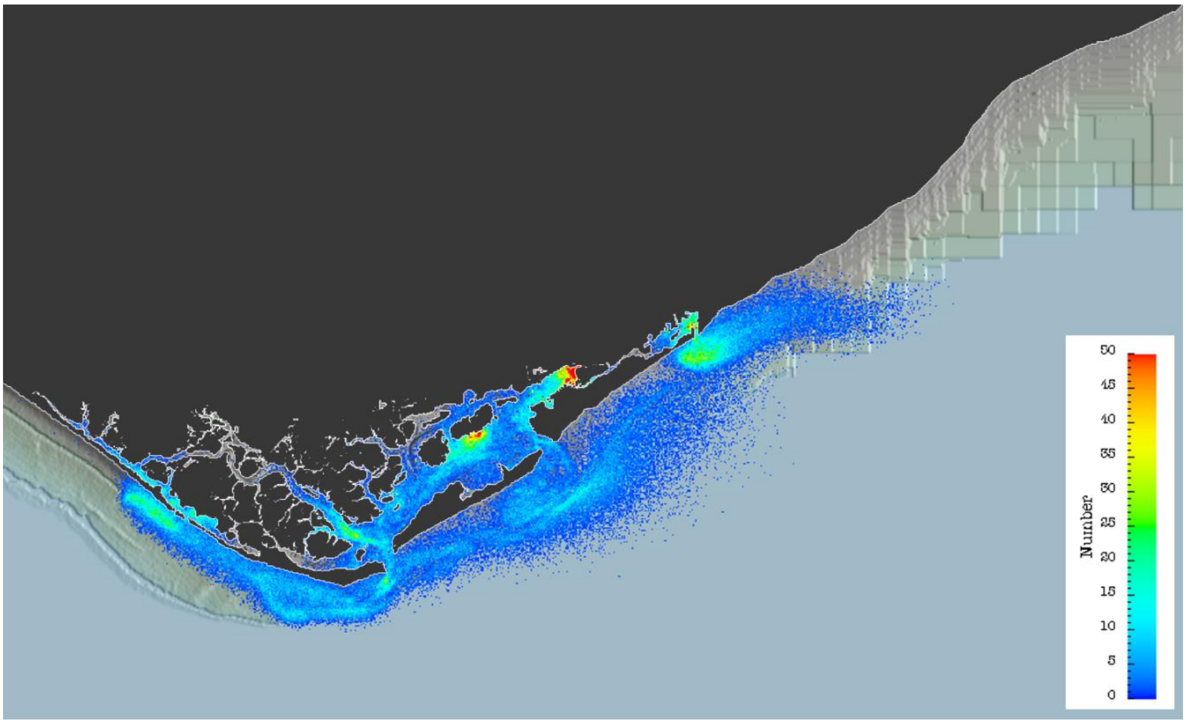

**Figure 7.2** Predicted smell seagrass plume emanating from the Ria Formosa Lagoon to the adjacent coastal area. The colour bar indicates the intensity of the smell plume in the adjacent coastal area.

The advection velocity of post-flexion larvae was calculated as the vectorial sum of water velocity and the larval swimming velocity, and the dispersion was calculated using a Markov diffusion process based on horizontal turbulent diffusion coefficient $K_x$ equal to 0.1 $m^2$ $s^{-1}$ following Okubo (1976). As the spawning of white seabream larvae takes place offshore, the pre-flexion larvae were positioned offshore the lagoon, modelled as passive particles moved by the oceanographic currents and diffused by turbulent mixing. After the period of passive transport, the fate of the post-flexion larvae was determined by two scenarios run separately: 1) the post-flexion larvae remained passive; and 2) the post-flexion larvae used directional swimming to follow the lagoon chemical cue gradient, starting with a critical swimming speed ($U_{crit}$) of 0 m $s^{-1}$ at day 17 and increasing linearly reaching a constant velocity of 0.05 m $s^{-1}$ at day 25, the simulations were run until day 26. These swimming parameters were derived from our laboratory experiments (Chapters 5 and 6 of the present Thesis). The spawning sites are located at depths between 10 to 60 m (Figure 7.1) as determined by the species biology and subtract type (Leitão et al. 2007). Three scenarios were hypothesized considering the depth of spawning location: a) the spawning takes place at lower deeps (e.g., 10 m deep) and near the coast; b) location of spawning grounds at medium depth (e.g., 16 m deep) near the smell plume; and c) spawning occurs at higher depth (e.g., 50 m deep) and far from the smell plume. The success of ingress into the lagoon was calculated for the 22 simulations (11 depth positions off the coast × 2 swimming capabilities – i.e., with or without), as the number of larvae entering the lagoon divided by the number of eggs release at the beginning of simulations.

### 7.2.4 Altimetry

Altimetry-derived surface currents around Portugal were obtained from NOAA-OSCAR to estimate the variability of the oceanographic currents, with the spatial and temporal resolution of the data was 1/3 degree and 5 days respectively, for the whole of the year 2010.

## 7.3 Results

Three scenarios of larval ingress into the lagoon were tested with our IBM, by varying the location of spawning according to depth (Figure 7.1). The first scenario showed that larvae spawned at depths between 10 and 15 m were advected away from the spawning sites and when they reached the post-flexion stage with swimming capacities, they were located far eastward from the smell plume of Ria Formosa. At these depths, we also observed that some larval ingress into the lagoon was possible; it started quickly after spawning just by passive advection through the tidal currents.

In the second scenario, with spawning occurring between 15.1 and 16.9 m deep, we observed that: i) the highest number of larvae were dispersed eastward away from the smell plume of Ria Formosa; ii) some larvae also ingressed into the lagoon by passive advection through the tidal currents; and iii) some larvae ingressed into the lagoon using directional swimming capacity when they were in the smell plume. An example of the differences in the number of larvae trapped in Ria Formosa lagoon with and without directional swimming capabilities was presented in Figure 7.3. At pre-flexion stage, the ingress of larvae in the lagoon was due to tidal currents; most of these larvae were later exported by tidal diffusion. At that stage the number of larvae recruited whether passive or active was nearly identical, the small differences were due to diffusion processes. Passive dispersion lasted until day 17 when the larvae started swimming; the swimming speed increased linearly until 0.05 m $s^{-1}$ at day 25. Figure 7.3 shows that the swimming larvae were able to remain in the lagoon and thus recruit, while additional larvae ingressed from offshore using directional swimming. On day 26 the increment rate of larval ingress into the lagoon was 30% larger through directional swimming than through a passive way, showing that behaviours have an important role in the self-recruitment process.

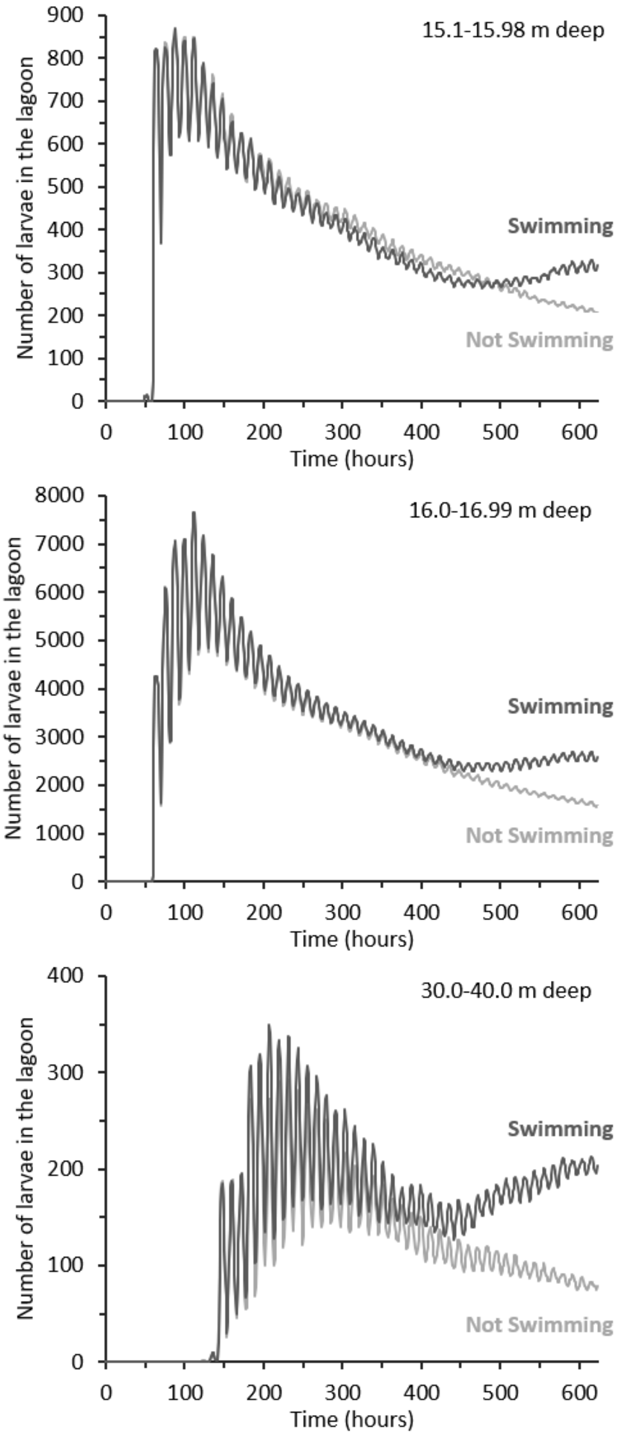

**Figure 7.3** Number of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae trapped in the Ria Formosa lagoon (southern Portugal) along 624 h (26 days) of simulation for larvae with and without swimming capabilities and spawning locations at 15.1-15.98 m deep, 16.0-16.99 m deep and 30.0-40.0 m deep (the other eight spawning locations were not present because the ingress into the lagoon was zero or near zero).

The ingress success of post-flexion larvae in Ria Formosa lagoon was higher when larvae had directional swimming capabilities (Figure 7.4). The ingress success of post-flexion larvae with directional swimming capabilities (2.0-3.4% for all spawning sites at 15.1-16.99 m deep) was higher than success of ingress for post-flexion larvae without swimming capabilities (1.3-2.0% for these spawning sites at 15.1-16.99 m deep). The success of ingress in the lagoon was higher for the spawning sites between 15.1 and 16.99 m deep (2.0-3.4%), decreasing to lower values in depths of 30-40 m (0.2%). In the remaining locations, before 15.1 m and after 40 m deep, the ingress success was zero.

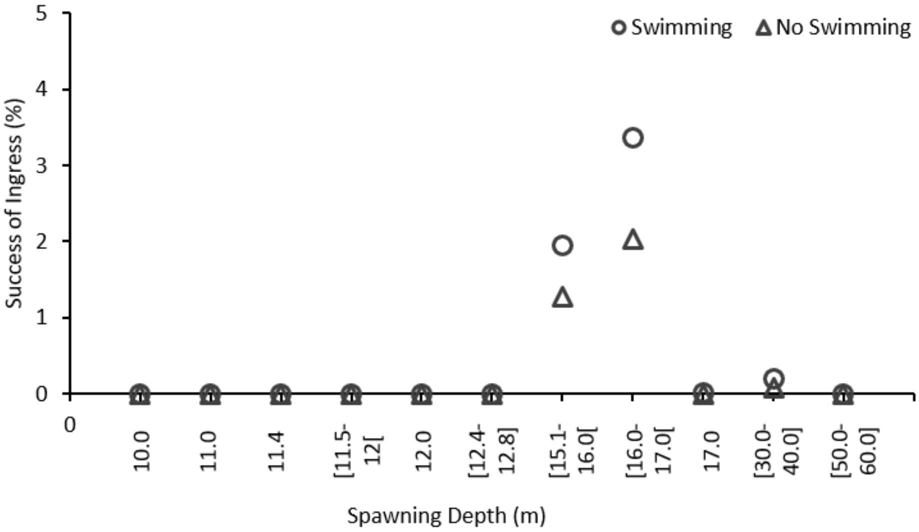

**Figure 7.4** Ingress success (%) of white seabream *Diplodus sargus* (Linnaeys, 1758) larvae into the Ria Formosa lagoon (South Portugal) according to the offshore depth of the spawning site, and depending if post-flexion larvae swam actively towards the smell cue gradient originated from the lagoon (○) or not (△).

In the third scenario, with spawning sites at 50-60 m deep, no larvae were advected into the lagoon by tidal currents, nor through they reached the lagoon's smell plume to induce active swimming towards the lagoon (Figure 7.4).

## 7.4 Discussion

The location of white seabream spawning grounds off the Ria Formosa lagoon, in tandem with the sensorial and swimming capabilities of larvae, are essential to maximizing the ingress of larvae into the lagoon, as well as to prevent their advection from the nursery (Figure 7.5). This IBM was parameterized with data obtained for white seabream (Chapters 5 and 6 of the present Thesis), and it corroborates the general framework proposed by the Sense And Acuity Behavioural (SAAB) hypothesis (Teodósio et al., 2016). We also found support to propose the use of future improved versions our IBM to refine the management of the artificial rocky reefs placed off the Ria Formosa lagoon, as well as along the entire Algarve coast.

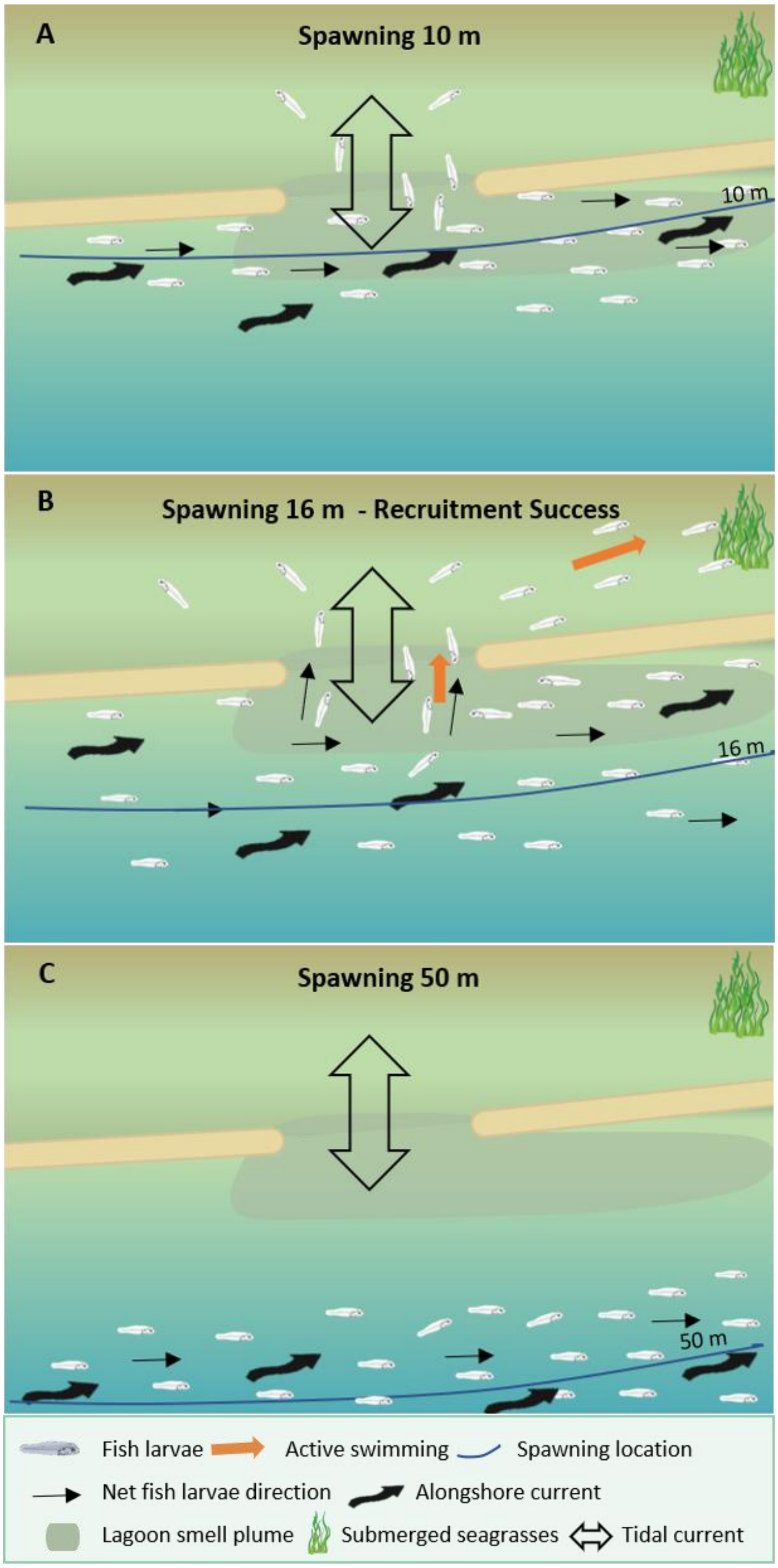

**Figure 7.5** Scenarios for ingress success of white seabream *Diplodus sargus* larvae in the Ria Formosa Lagoon (southern Portugal) taking into account the spawning location: (A) spawning occurring at 10 m deep; (B) spawning occurring at 16 m deep resulting in success of ingress; (C) spawning occurring at 50 m deep.

### 7.4.1 The relevance of spawning ground location and fish larvae directional swimming

The location of fish spawning grounds in coastal areas is essential for the recruitment of species that use estuaries and lagoons as nursery areas (Sinclair, 1988; Tanaka et al., 1989; Jenkins et al., 1996). The same is valid for the white seabream population spawning off the Ria Formosa lagoon in southern Portugal (Figure 7.5). There are cases when recruitment decreases with increasing distance towards the nursery area (Cowen et al., 2000, 2006; Buston et al., 2011). However, we found that white seabream larvae that spawned nearshore (10-15 m deep) and close to the lagoon's inlets were advected eastwards and away from the smell plume due to local oceanographic features, before larvae acquired active swimming strategies (Figure 7.5A). Notwithstanding, a few pre-flexion larvae ingressed passively into the lagoon with the tidal currents. Other forcing factors can advect larvae into coastal nursery areas, for example wind-driven transport (Werner et al., 1997; Schieler et al., 2014), buoyancy-driven flows (Werner et al., 1997; Bakun, 2006), internal waves, surface waves (Gawarkiewicz et al., 2007; Schieler et al., 2014), turbulence (Gawarkiewicz et al., 2007; Scotti and Pineda, 2007), but our model did not test these.

The highest ingress rates were observed for larvae whose spawning grounds lay between 15.1 m and 16.9 m deep and caused both by passive transport and directional swimming along the lagoon's odour plume (Figure 7.5B). This information is critical to optimize the management of the artificial reefs placed off the Ria Formosa lagoon since the 1990s (Leitão et al., 2007). The ingress success of spawning sites located at bathymetries deeper than 17 m is extremely reduced (< 0.2 %). At these locations, dispersion processes advect eggs and pre-flexion larvae eastwards along the coast or offshore away from the lagoon and their odour plume, while disabling directional swimming into the lagoon when larvae acquire swimming capabilities (Figure 7.5C).

Once again it is demonstrated that larval behaviour minimized the advection caused by oceanographic processes, while maximizing their retention in nearshore areas and inside the Ria Formosa lagoon (Kingsford et al., 2002; Pineda et al., 2007; Hamilton et al., 2008). Retention within the lagoon was possible because of the ability of larvae to swim against the net currents, and not their capacity to swim against the tidal currents since larvae have smaller swimming speeds than the peak tidal currents in the channels (Chapter 5 of the present Thesis; Dias et al., 2009).

Pioneering work on pelagic fish larvae personality traits showed that larvae might exhibit a consistent habitat preference through ontogeny (Chapter 6 of the present Thesis). The white seabream can use an array of ecosystems as a nursery, placing this species in a competitive advantage compared to other species that need to use estuarine ecosystems as nurseries. For example, only 7% of post-flexion larvae choose the Ria Formosa lagoon as their nursery. However, this behavioural plasticity might be enough to buffer environmental and biological mismatch across the habitats used by the white seabream and thus increase population and even metapopulation resilience.

### 7.4.2 Improving IBMs to refine fisheries management and marine protected areas (MPAs)

Our IBM showed that most larvae failed to ingress into the Ria Formosa lagoon. However, this is not a synonym that white seabream larvae were unable to find a nursery area and recruit. First, there are other adjacent coastal ecosystems located eastwards from the Ria Formosa lagoon (predominant direction to where larvae were transported) that may serve as a nursery area (Drake and Arias, 1991; Faria et al., 2006; Martín-López et al., 2011) which larvae can find by following an array of environmental cues (see Teodósio et al., 2016 for a review). Second, the shallow sandy-rocky habitats presented along the coast can also serve as nursery areas for the white seabream and other Sparidae (Harmelin-Vivien et al., 1995).

The facts mentioned above demonstrate that our IBM can be improved. First, because this IBM only considers the oceanographic conditions observed in September 2016, when the dominant mean current was headed eastward and that prevailed during the second half of the year. However, transient oceanic eddies generating stagnation conditions and westward longshore currents off the Ria Formosa lagoon (not shown). Variable oceanographic conditions can also occur during the spawning season. For example, during the spawning season of white seabream from March to June; Morato et al., 2003), westward mean currents prevailed for 55 days during the beginning white seabream spawning season in 2010, (Figure 7.6A), while mean eastward currents prevailed afterwards for 65 days (Figure 7.6B). Thus, extrapolations made from this work must take into consideration the oceanographic conditions used in our IBM. Undoubtedly, variable oceanographic conditions are one of the critical aspects we aim to improve in future versions of this IBM.

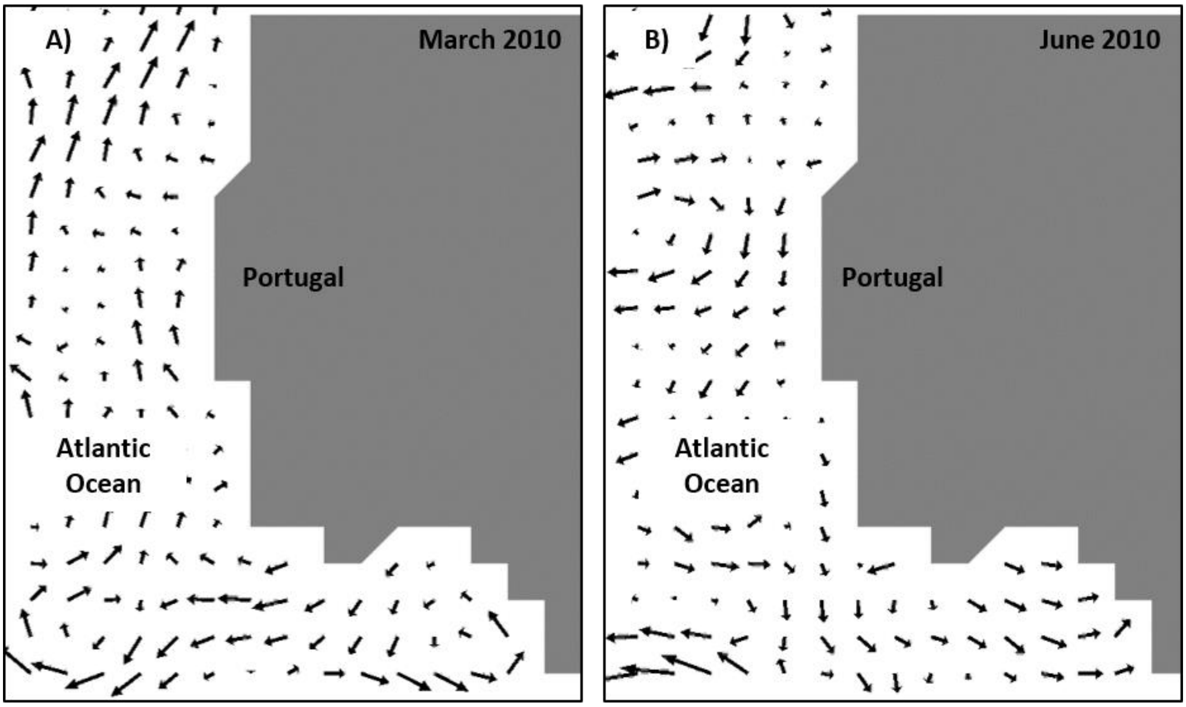

**Figure 7.6** Altimetry-derived surface currents along the southwestern coast of the Iberian Peninsula during the 2010 spawning season of white seabream *Diplodus sargus* (Linnaeus, 1758) which usually occurs from March till June (Morato et al., 2003). Image retrieved using data obtained from NOAA-OSCAR.

Our IBM will also need to improve its spatial resolution by incorporating 3D processes and even to extend its horizontal domain. Restrictions on the horizontal domain disable the inclusion of other relevant nursery ecosystems to where larvae could have ingressed into, while vertical restrictions of the model domain and mesh size disable the capture of short-resolution physical processes that may enhance the retention of larvae in a given area. Finally, this comprehensive approach can be essential to understand how fish larval dispersion and metapopulation connectivity vary in face environmental and climatic changes.

Once we improve our IBM by incorporating variable oceanographic conditions and its spatial resolution, but also other biological traits, we might be able to provide this IBM to fishery stakeholders to used it as a management tool to refine the management of white seabream fisheries (e.g., fishing areas, restriction habitat closures, location of artificial rocky reefs), as well as of other important fisheries in southern Portugal (e.g., sardines, mackerel, horse mackerel) (Leitão et al. 2014; Teixeira et al., 2016). Finally, IBMs used as part of an array of management tools of MPA and MPA networks ought to incorporate fish larvae behavioural traits since it influences the overall outcome of these models, and eventually of management decisions.

## 7.5 Conclusion

The ingress of white seabream larvae into the Ria Formosa lagoon largely depends on the location of the spawning grounds off the lagoon, particularly on their depth and distance from the smell plume and the lagoon mouths. Their ingress success also depends on the sensorial and swimming capabilities that minimize the advection by oceanographic processes, maximizing their retention in nearshore areas and inside the Ria Formosa lagoon. Thus, the highest ingress rates were observed for larvae with spawning grounds located between 15.1 m and 16.9 m deep and caused both by passive transport and directional swimming along the lagoon’s odour plume. The present study proposes the use of future improved versions our IBM to understand the effects of environmental and climatic changes on fish larval dispersion, to refine the management of the artificial rocky reefs and MPAs and improve fisheries management.

## 7.6 Acknowledgements

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# CHAPTER 8

# General Conclusion and Final Remarks

# GENERAL CONCLUSION AND FINAL REMARKS

The results obtained in this thesis increased our knowledge on the response of temperate fish species to recruitment variability (using two Sparidae species from the Portuguese coast as biological models) by studying their response to environmental and fishing variability and behavioural ecology, swimming performance, and dispersion potential.

Several parts of this thesis were already presented to the scientific community through the publication of research articles in peer-reviewed scientific journals and oral and poster presentations in international conferences.

In this chapter, I present a general conclusion drawn from this thesis, as well as final remarks, recommendations, and launch the basis for future works.

## 8.1 General conclusions

The impact of climate change on marine ecosystems, their species, and fishery resources are under active debate. Nevertheless, most of the information is based on forecasted global models. So, it is necessary to analyse real data from different regions where different impacts are also mentioned. Using observation data, the analysis of the sea surface temperature (SST) (Chapter 2) showed a generalized warming trend of SST along the Portuguese coast during the last decades (1980-2010). However, the warming pattern is not uniform across latitudes, and a north-south increasing gradient was observed: approximately +0.1 °C decade$^{-1}$ in the northwestern and southwestern coasts and +0.2 °C decade$^{-1}$ in the southern coast. The increment of SST rates also varied seasonally, with the highest values registered in spring and summer (approximately +0.4 °C decade$^{-1}$). This seasonal SST variability is relevant for dynamic biological processes due to species differences in thermal stress vulnerability, which affects the species life cycle (Pörtner and Farrell, 2008), such as spawning and larvae development. Thus, recruitment of fish species, a key parameter in fisheries management, is expected to be directly affected by the increase of SST.

The multi-model approach to investigate the variability of white seabream (*Diplodus sargus*) (Chapter 3) and two-banded seabream (*Diplodus vulgaris*) catch rates (Chapter 4) revealed that catch rates was not related with fishing effort was but rather to environmental variability and intrinsic factors. For white seabream, the autumn, winter, and spring seasonal effects were associated with catch rates in northwestern, southwestern and southern coasts of Portugal, respectively, indicating a possible coastal longitudinal gradient. For the two-banded seabream, the catch rates were related with autumn and summer conditions in the northwestern coast, winter in the southwestern coast, and autumn and winter conditions in the southern coast. Although some environmental variables had the same relationship with catch rates for both species (the positive effect of wind magnitude in autumn), these relations were also species-specific: SST and the North Atlantic Oscillation Index showed adverse consequences for both species but during different seasons and for distinct regions; eastward wind component and river discharges were positively related with the two-banded seabream. Thus, each of these two species reacted in a different way to environmental variability.

The physiological condition and behaviour of temperate marine fish larvae were studied to increase our insights about some of the causes behind the recruitment variability (Chapter 5). Results showed that for white seabream larvae, the development of body morphology (e.g., flexion of the notochord, development of fins) lead to increased swimming abilities during ontogeny: 1) maximum $U_{crit}$ = 23.0 cm $s^{-1}$ at 50 and 55 days post-hatching – DPH; 2) the distance swum in the endurance test increased abruptly from 35 DPH (5.0 ± 6.0 km) to 45 DPH (54.1 ± 22.1 km), with a record of distance swum of 86.5 km in 240.2 h. These data confirm that post-flexion larvae of temperate fish species are better swimmers than once thought. The swimming performance of white seabream larvae suggests that they can influence their transport and distribution in coastal areas due to their swimming capabilities, which can lead them to actively explore coastal habitats or to prevent offshore dispersion.

The most significant finding of Chapter 6 was that during early ontogeny, white seabream larvae exhibit a highly consistent inter-individual behaviour variability (personality traits) across age and tests. Contrary to our hypotheses, white seabream larvae did not show a preference for either lagoon or rocky shore habitats, neither towards increased water temperature or decreased water salinity. Despite this lack of choice, we observed statistical differences for the Preference Index between Age 1 (~25 DPH) and Age 2 (~35 DPH) in the lagoon cue test. At Age 1, some larvae preferred the Ria Formosa lagoon water (from a main and open channel with seagrass beds and with high water exchange levels). Exploratory activity was higher when larvae showed unresponsive or inconclusive behaviours, meaning that larvae may seek a stimulus different from the one offered. Thus, personality traits could influence the process of searching for suitable nursery habitats and, consequently, dispersion and connectivity of white seabream populations.

The integration of swimming capabilities (Chapter 5) and behavioural responses to environmental cues (Chapter 6) into an individual-based model (IBM) (Chapter 7) showed that the location of white seabream spawning grounds off the Ria Formosa lagoon, in tandem with the sensorial and swimming capabilities of larvae, are essential to maximizing the ingress of larvae into the lagoon. Thus, the highest ingress rates were observed for larvae with spawning grounds located between 15 m and 17 m deep and caused both by passive transport and directional swimming along the lagoon’s odour plume. The behaviour of larvae minimizes the advection caused by oceanographic processes while it maximizes their retention in nearshore areas and inside the Ria Formosa lagoon due to the ability of larvae to swim against the net currents. This evidence corroborates the general framework proposed by the Sense And Acuity Behavioural (SAAB) hypothesis (Teodósio et al., 2016).

## 8.2 Final remarks, recommendations, and future perspectives

The increment rates of SST along the Portuguese coast presented in Chapter 2 agree with the HadRM3 model simulations for the same area (region independent) by the end of the 21st century (2071-2100) (Santos and Miranda, 2006). It is not expected that the future SST increase at the same incremental rate as during 1950–2010, so caution is needed when comparing past trends and future predictions.

This thesis emphasizes the importance of stock analyses at sub-area or sub-stock levels (Chapters 3 and 4). According to regional circulation models, the evolution of climate may differ between regions along the Portuguese coast (as shown for SST variability in Chapter 2), resulting in mixed responses by some stocks (Sousa Reis et al., 2006). It was also demonstrated that seasonal events explain much of the variability in both white seabream and two-banded seabream catch trends. The magnitude of these impacts is determined by the ‘‘timing’’ of interactions between early life cycle stages and local environmental conditions. Thus, suitable marine fishery policies must consider that seasonal and regional environmental characteristics act differently upon different species. This strategy will allow fishery managers to evaluate and manage the risks associated with climate change at a regional scale, which is far more realistic for a given region than if based on global scenarios. Future studies should use the same spatial and temporal scales to enable standardized comparisons, in which they should be based on oceanographic regimes, climatic patterns, and fisheries management (Chapters 2, 3, and 4). Therefore, the ICES (International Council for the Exploration of the Sea) divisions for stock assessment should be used since it considers regional oceanographic characteristics that match with long-term biological data.

Characterizing the swimming abilities (Chapter 5), behaviour and active habitat selection of temperate pelagic marine fish larvae (Chapter 6) may increase our knowledge of recruitment variability and dispersion potential. Since behaviour differs between wild and laboratory-reared larvae, future studies should also investigate wild larvae. It is also essential to test larval swimming capacity at different temperature setups because temperature may affect the distribution and production of marine species, as well as to modulate their response to environmental cues signalling nursery habitats. In habitat preference tests, new research efforts should strive to introduce more complex experimental designs when testing chemical, visual, and sound cues along ontogeny (e.g., offshore water cues; presence/absence of conspecifics, prey, and predators). Still, preference and personality traits must be analysed in such experiments (i.e., activity and exploration) simultaneously to more traditional metrics (i.e., time spent following each cue). Ultimately, characterizing the behaviour of temperate pelagic marine fish larvae and understanding active habitat selection may increase our understanding of recruitment variability, refine larval dispersal models, and add to the body of knowledge on the effects of environmental changes and habitat degradation on fish distribution.

The Individual-Based Model (IBM) developed on Chapter 7 incorporated the swimming capabilities (Chapter 5) and behavioural responses of white seabream larvae to environmental cues (Chapter 6) which demonstrated the importance of directional swimming capabilities on the recruitment of temperate fish species. The incorporation of variable oceanographic conditions is critical to improving future versions of this IBM, as well as the incorporation of

3D processes – to capture short-resolution physical processes that may enhance the retention of larvae in a given area – and to extend the horizontal domain to include adjacent nursery ecosystems. This comprehensive approach will deepen our knowledge of how fish larval dispersion and metapopulation connectivity varies under environmental changes, and provide fishery stakeholders with more robust tools to improve the management of white seabream fisheries (e.g., fishing areas, restriction habitat closures, location of artificial rocky reefs), or of other important fisheries. Finally, this IBMs could be adapted to other locations and be used as part of an array of management tools of MPA and MPA networks.

The expected changes in physical oceanographic conditions (e.g., increase SST, upwelling intensity), wind regimes, and river runoff induced by climate changes could affect the recruitment success of temperate fish species in different ways. It can increase the productivity of some species and a decrease of other species. Thus, due to the diversity of factors causing recruitment variability in temperate fish species, the present thesis suggests the integration of all these sources of variability (e.g., physiology, biology, behaviour, environment) to the assess the vulnerability of fish stocks to climate change. Since vulnerability is a function of exposure, sensitivity, and adaptive capacity (IPCC, 2001), this approach must include species-specific data (Welch et al., 2014). Exposed indicators must incorporate environmental variables predicted to change and that influence a particular species (Chapters 2, 3, and 4). Sensitivity and adaptive capacity indicators can be provided by physiology, behaviour, or ecology data. Sensitivity is focused on species life history traits that can affect the abundance, distribution, and phenology, including the capacity for larval dispersal (Chapters 5, 6, and 7).

In conclusion, the future management strategies of fishery resources must be species-specific and incorporate both fishing pressure and the variability of relevant environmental factors along a species life cycle at different spatial and temporal contexts, as well as species' behavioural characteristics, in the context of global and regional environmental and climatic changes.

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