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UNIVERSIDADE D
COIMBRA

Sara Borges Lourenço

**LONG-TERM SHIFTS IN KEY FISH SPECIES
IN A TEMPERATE ESTUARY**

**Dissertation in MSc in Ecology, supervised by Dr Filipe Miguel Duarte
Martinho and Prof. Dr Miguel Ângelo do Carmo Pardal and presented to
the Department of Life Sciences, Faculty of Sciences and Technology of
the University of Coimbra**

June 2022

Coimbra Department of Life Sciences, Faculty of Sciences and
Technology of the University of Coimbra

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Statement of thesis contributions

I declare that this thesis was written and organized by me, and I confirm that it has not been previously submitted, in whole or in part, to obtain another academic degree. I confirm that the work described was done by me and by the co-authors, in the case of joint publications, as indicated in the chapter II. In these cases, my contribution is explicitly indicated below:

The work presented in chapter II, more specifically the sample collection, laboratorial work and data curation, was performed by several team members of the Marine Research Lab – Centre for Functional Ecology (CFE), of the University of Coimbra, and supervised by Dr. Filipe Martinho and Prof. Dr. Miguel Pardal. I wrote the first draft of the paper and incorporated later suggestions from other authors.

Declaração de contribuição da tese

Declaro que esta tese foi elaborada por mim e confirmo não ter sido previamente submetida, total ou parcialmente, para obtenção de outro grau académico. Confirmando que o trabalho descrito foi realizado por mim e pelos co-autores, no caso de publicações conjuntas, como indicado no capítulo II. Nestes casos, a minha contribuição está explicitamente indicada abaixo:

O trabalho apresentado no capítulo II, mais especificamente a recolha de amostras, trabalho laboratorial e processamento de dados, foi realizado por vários membros do Marine Research Lab – Centro de Ecologia Funcional (CFE), da Universidade de Coimbra, e supervisionados pelo Dr. Filipe Martinho e pelo Prof. Dr. Miguel Pardal. Escrevi a primeira versão do artigo e incorporei as posteriores sugestões de outros autores.

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Abstract

Understanding how climatic conditions affect the recruitment of key species in the long term is critical for fisheries management and, as a result, species and ecosystem conservation. This work aimed to analyse the variability of recruitment of five species: *Dicentrarchus labrax*, *Platichthys flesus*, *Solae solea*, *Pomatoschistus microps* and *Pomatoschistus minutus* in the Mondego estuary and to relate this variability to the dominant environmental factors within the estuary and in the adjacent coastal zone, during a period of 17 years (from 2003 to 2019). A dynamic factor analysis (DFA) showed three common trends in the data, associated with different habitat use patterns and life cycle of the five species (marine juvenile migrants vs estuarine residents). The best model included the three common trends and estuary water temperature and the Atlantic multidecadal oscillation (AMO) index lagged by 1 year, reinforcing the thermophilic nature of fish recruitment in coastal areas. Individual correlations also showed that these species are quite similar in their relationship with water temperature related variables, being favoured by a slight increase in temperature. However, a wide-ranging change in the AMO seems to have caused changes in the community between 2010 and 2012, causing a marked decrease in *P. flesus* and *S. solea* trends. This work demonstrates the importance of long-term studies on the recruitment of key species for more efficient conservation and management strategies, as species will react differently to climate change and at any time may adjust their response to changes in the surrounding environment.

Keywords: climate change, fish recruitment, fisheries management, nursery areas, dynamic factor analysis.

Resumo

Compreender como as condições climáticas afetam o recrutamento de espécies-chave de peixes a longo prazo é fundamental para a gestão das pescas e, conseqüentemente, para a conservação das espécies e dos ecossistemas. Este trabalho focou-se em analisar a variabilidade do recrutamento de cinco espécies: *Dicentrarchus labrax*, *Platichthys flesus*, *Solea solea*, *Pomatoschistus microps* e *Pomatoschistus minutus* no estuário do Mondego e relacionar esta variabilidade com os fatores ambientais dominantes dentro do estuário e na zona costeira adjacente, durante um período de 17 anos (de 2003 a 2019). O tratamento estatístico, *dynamic factor analysis* (DFA) mostrou três tendências comuns nos dados, associados aos diferentes padrões de utilização do habitat e ciclo de vida das cinco espécies (marinhos migrantes juvenis vs residentes estuarinos). O melhor modelo incluiu as três tendências comuns, a temperatura da água do estuário e a Oscilação Multidecadal do Atlântico (AMO) com 1 ano de desfasamento temporal. Correlações individuais mostraram também que estas espécies são bastante semelhantes na sua relação com variáveis relacionadas com a temperatura da água, sendo favorecidas por um ligeiro aumento da temperatura. No entanto, uma mudança de ampla amplitude no AMO parece ter provocado alterações na comunidade entre 2010 e 2012, provocando um decréscimo na tendência do *P. flesus* e *S. solea*. Este trabalho demonstra a importância de estudos a longo prazo sobre o recrutamento de espécies chave para uma conservação e gestão mais eficiente, uma vez que as espécies reagem de forma diferente às alterações climáticas e, a qualquer momento poderão ajustar a sua resposta às mudanças no ambiente circundante.

Palavras-chave: alterações climáticas, recrutamento de peixes, gestão de pescas, zonas de viveiro, dynamic factor analysis.

CHAPTER I – Introduction

1.1. Importance of estuarine ecosystems

1.2. Influence of environmental factors on fishes' life cycles

1.3. Study Species

1.3.1. *Dicentrarchus labrax*

1.3.2. *Platichthys flesus*

1.3.3. *Solea solea*

1.3.4. *Pomatoschistus microps* and *Pomatoschistus minutus*

1.4. Objectives

1.1. Importance of estuarine ecosystems

Estuaries are defined as transitional systems between the ocean and the river, providing a valuable supply of goods and services, and are among the most valuable and biologically productive ecosystems (Costanza et al. 1997, Beck et al. 2001). Consequently, estuaries are important for a wide range of species for a variety of reasons, which make them essential for the renewal of fish stocks and the conservation of fish species (Beck et al. 2001, Dahlgren et al. 2006). Not only do estuaries make important direct contributions to fisheries through partially or temporarily resident fish populations, but they also provide nursery areas for a diverse number of fish species that represent a significant amount of biomass exported for recreational and commercial harvesting in the inshore marine environment (Houde and Rutherford 1993, Lamberth and Turpie 2003, Dolbeth et al. 2010).

Nursery areas can be defined as habitats that support a high density of juveniles and contribute as much as possible to the growth of the adult population (Beck et al. 2001, Able 2005, Martinho 2020). These areas include a diversity of habitats, such as estuaries, which comprise several habitats types, like seagrass beds, mangroves, salt marshes, mudflats, or oyster reefs (França et al. 2009, Martinho 2020, Pessanha et al. 2021).

Several fish species use different habitats throughout their life cycle, including nursery areas. In these species, different stages of the cycle require different biotic and abiotic conditions and unfavourable conditions in a certain stage may lead to population decline, despite good conditions in the remaining life cycle (Able 2005, Wolfshaar et al. 2021). A good understanding of the life cycle stages in which different fish species use estuaries is necessary to understand the structure and function of these environments and manage the ecosystems and their faunas (Potter et al. 2013).

Several works have progressively built a proposal to characterize fish by the ways they use different habitats (Potter et al. 1990, Elliott and Dewailly 1995, Whitfield 1999, Franco et al. 2008). Elliott et al. (2007) and Potter et al. (2013) refined the concept by which the different life cycle categories of fishes use estuaries. To do this, fish species were grouped into four categories: marine, estuarine, diadromous, and freshwater. Each of these categories (i.e., guilds) contains several sub-groups that represent characteristics associated with spawning, feeding, and/or refuge sites, in some cases involving migratory movements between different ecosystems (Potter et al. 2013).

Marine estuarine-dependent and estuarine residents guilds (Fig. 1) represent the major part of the fish communities found in estuarine systems worldwide (Mathieson et al. 2000, Martinho et al. 2007b, Harrison and Whitfield 2008, Henriques et al. 2016, Lima et al. 2020). The first guild lies within the marine category and encompasses fish species that need the estuarine ecosystems for survival at a critical stage in their life cycle. These species usually spawn in coastal ecosystems and their larvae migrate to nursery areas inside the estuaries for the development of juveniles, which subsequently migrate back to the coast (Potter et al. 2013). The second guild belongs to the estuarine category and encompasses fish species that spend their entire life cycle within the estuarine environment (Potter et al. 2013).

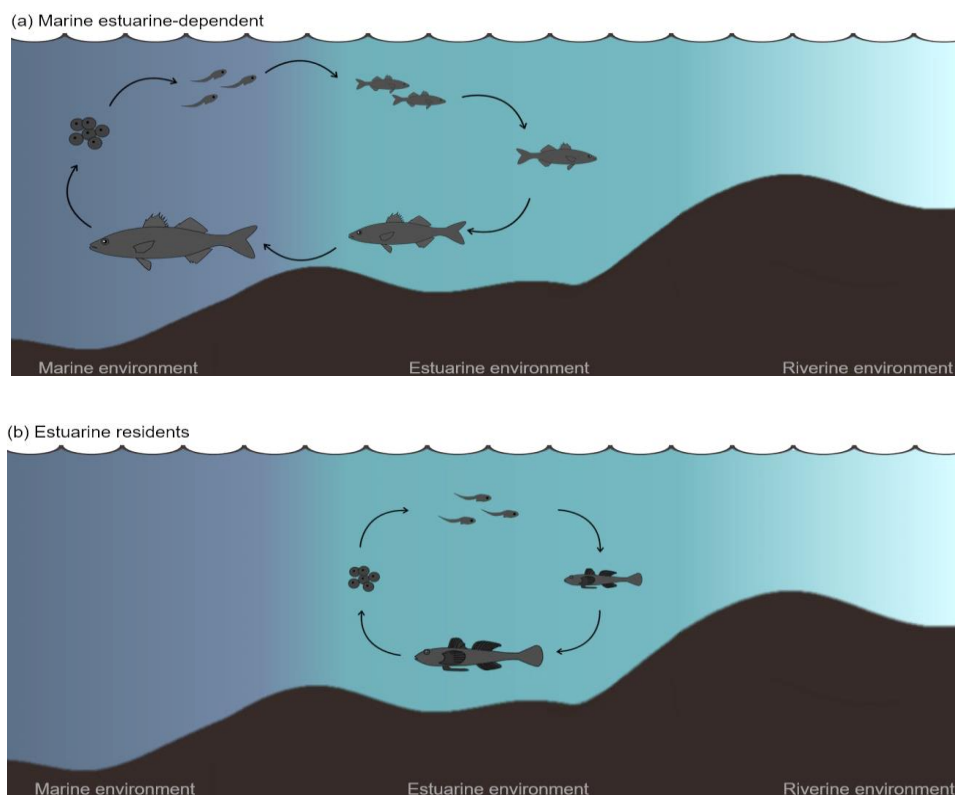


Figure 1. Life cycles categories using the estuarine usage functional group approach: (a) Marine estuarine-dependent; (b) Estuarine residents - Adapted from Potter et al. 2013.

For marine fish species whose transitions between life stages require changes in habitat use, connectivity between habitats is particularly important (Gillanders et al. 2003, Able 2005, Cowen and Sponaugle 2009). Functional, temporal and structural connectivity between coastal spawning grounds and nursery areas is a critical step in the recruitment of marine estuarine-dependent fishes as their larvae will die if they do not reach the nurseries to grow (Auffret et al. 2015, Wolfshaar et al. 2021).

The term recruitment refers to the transition of fishes to a new age class. Recruitment is used to identify the final number of individuals of a given age class that survived, such

as juveniles that have survived, will reach sexual maturity and join the adult population (van der Veer et al. 2000). The life cycle of fish is divided into different physical stages, in each mortality can be more density-dependent or more density-independent (Miller et al. 1991). Mortality in the eggs and larval stages is often considered density-independent because fish have less control over the habitats they occupy (Camp et al. 2020), being more affected by the surrounding environment and climate conditions (Martinho et al. 2009). Recruitment in the early life stages is therefore a decisive factor in the quantity of fish that survive to become larger spawning fish, determining the strength of the annual class (Rijnsdorp et al. 1992, van der Veer et al. 2000).

Recruitment variability has been used in fishery science as a tool for predicting the future success of a fishery or as a method for explaining variation in fish stocks (Attrill and Power 2002). Predicting future larval and juvenile fish performance scenarios in nurseries areas is necessary to enable adaptive management of fish stocks by taking life stage performance into account (Wolfshaar et al. 2011, 2021, Cabral et al. 2021). However, the complex response of recruitment at nursery grounds to climate change remains hard to be assessed (Wolfshaar et al. 2021).

1.2. Influence of environmental factors on fishes' life cycles

Climate strongly influences a variety of ecological processes at different levels of biological organization (Rijnsdorp et al. 2009) and, consequently affects different temporal and spatial patterns of populations and species abundance (Stenseth et al. 2005). Marine ecosystems go through changes from seasonal to centennial or longer over different time scales. Many of these scales are related to climatic and atmospheric processes, making these processes strong drivers of fluctuations in fish populations and fisheries (Lehodey et al. 2006). However, human-induced climate change has caused rapid alterations in ocean conditions faster than any natural change ever seen (Cheung et al. 2015), directly affecting marine and estuarine organisms and leading to species turnover and an increase in invasive species (Martinho et al. 2007b, Lacroix et al. 2018), strongly altering communities and ecosystems. Fish populations are particularly affected in larvae dispersion (Lacroix et al. 2013, Tanner et al. 2017), recruitment (van der Veer et al. 2000, Martinho et al. 2009) and connectivity (Gillanders et al. 2012, Wolfshaar et al. 2021) through changes in oceanic circulation and temperature.

Climate and its main characteristics have been recognized as key issues in the processes of estuary colonization, settlement and recruitment of both marine fish and

their larvae (Marchand 1991, Attrill and Power 2002, Martinho et al. 2009, Wolfshaar et al. 2021). Climate variability can be observed at various scales, either in atmospheric phenomena acting on a large scale or in regional and/or local weather patterns, which can have a more immediate effect on fish populations.

The North Atlantic Oscillation index (NAOi) is an irregular large-scale fluctuation of atmospheric pressure, and is calculated based on the difference in pressure at sea surface level between the Subtropical High (Azores, Portugal) and the Subpolar Low (Reykjavik, Iceland) (Hurrell J.W. 1995). The NAOi determines climate variability from the eastern seaboard of the United States to Siberia and from the Arctic to the subtropical Atlantic, mainly during winter (Hurrell J.W. 1995), and has been influencing several biological aspects in the long term, of which certain fish stocks (Attrill and Power 2002). The NAOi shifts between a positive and a negative phase. Both phases of the NAO are associated with large-scale changes in normal zonal and meridional heat and moisture transport patterns, which in turn result in changes in wind, temperature and precipitation patterns that often extend from the Gulf of Mexico to northern Europe (Stenseth et al. 2005). These environmental influences are most potentially affecting the most susceptible juveniles (Attrill and Power 2002, Sims et al. 2004, Martinho et al. 2009, Bento et al. 2016).

The Eastern Atlantic Pattern (EAP) is the second most important mode of low-frequency variability over the North Atlantic and appears as a major mode in all months (Barnston and Livezey, 1987). The EAP is structurally similar to the NAO and consists of a north-south dipole of anomaly centres that cover the North Atlantic from east to west (Barnston and Livezey, 1987). However, its centres of variability are south-eastward shifted and more zonally oriented compared to those of NAO (Barnston and Livezey, 1987). In addition to the NAO, the EAP plays an important role in modulating the geographic location of the North Atlantic action centres (upper Azores and lower Iceland) (Mellado-Cano et al. 2019). Temperature is mainly influenced by the NAO, however, the EAP can influence the magnitude and location of the pattern of these anomalies (Mellado-Cano et al. 2019). Precipitation, on the other hand, is more sensitive to the joint effect of EAP and NAO, but there are regions where EAP can reduce and even reverse the NAO-related precipitation signal (Mellado-Cano et al. 2019). There is a lack of research concerning the effects of EAP on ecological parameters, and although some studies have shown how it may have an impact on fish (Tanner et al. 2020, Pinto et al. 2021), there is still a lot to know about its effects on the estuary environment.

Another pattern of natural ocean-atmosphere variability in the North Atlantic is the Atlantic Multidecadal Oscillation (AMO) index. It is associated with long-lasting changes in sea surface temperature, with a period of 60 to 80 years (Gray et al. 2004). Studies show that patterns in pelagic fish densities in the English Channel and southern North Sea (McLean et al. 2018) and multidecadal spatial patterns in Arctic-Norway cod spawning areas (Sundby and Nakken 2008) may be associated with changes in the AMO index, which highlights its importance in studying long-term trends in fish communities (Buyse et al. 2022).

The Atlantic coast of the Iberian Peninsula is the northern limit of one of the eastern boundary upwelling systems (Canary Current Upwelling System). From late May/early June to late September/early October, equatorward winds prevail on the Atlantic coast of the Iberian Peninsula (Smyth et al. 2001). As such, the Iberian Atlantic coast is characterized by a persistent current with seasonal variations, which has effects on sea temperature and primary productivity (Peliz et al. 2002, Teles-Machado et al. 2016, Tanner et al. 2017). It is these winds that will induce upwelling along the Iberian margin of the continental shelf, which also causes Ekman transport of surface water (Huthnance 1995, Smyth et al. 2001). Ekman transport consists of water sinking in the ocean and upwelling in the rising of colder water to the surface to replace the warmer water that has sunk, creating a current with a spiral effect. These currents can substantially affect larval transport and migration to the estuaries, endangering their survival and, consequently affecting recruitment (Santos et al. 2007, Tanner et al. 2017).

Temperature affects different species physiologically being the dominant driver in species ecology and biogeography (Pinsky et al. 2013). Fish are ectoderms and are therefore particularly affected by water temperature, which is the environmental factor that most influences their growth (Morrongiello et al. 2014, Holt and Jørgensen 2015). Changes in water temperature not only affect growth but can also affect fishes' survival and reproduction (Holt and Jørgensen 2015), spawning (Lacroix et al. 2018, Vaz et al. 2019) and egg survival (Fonds and Buurt 1974, Vinagre et al. 2009b). Due to climate change, there has been an increase in both sea surface temperature (SST) and the temperature of estuarine waters. An average global temperature increase of 2-4°C is predicted by the end of this century, although there may be larger and more localized increases (Holt and Jørgensen 2015).

Species whose initial stages of the life cycle depend on different habitats become especially susceptible to temperature changes. With increasing temperature, the energy requirements of fish are expected to increase and there is a need for more food to

maintain the physiological functions (Donelson et al. 2010, Holt and Jørgensen 2015). However, changes in phytoplankton communities due to climate change will not be uniform, and in many locations, these communities may become less productive (Donelson et al. 2010). For instance, Cushing (1990) postulated the match/mismatch hypothesis, which relates the survival of fish larvae to the compatibility between the timing of larval occurrence and the production of their food. If food availability is reduced, larval survival and fish recruitment will be affected (Beaugrand et al. 2003).

Regional hydrology (precipitation, river flow) is also highly influential in coastal ecological processes. In years of extreme droughts and decreasing precipitation levels, freshwater is stored in dams located upstream, which leads to a decrease in the river flow and affects the salinity in the estuary and of the species that live there (Martinho et al. 2007b). Indeed, it is widely accepted that river plumes may play a key role in indicating the proximity of nursery areas to fish larvae (Marchand 1991, Martinho et al. 2009). In years of greater river drainage, these plumes will be larger and will therefore extend over a larger area within the coast where the larvae spawned, increasing the probability of being detected by the larvae, which will direct their movement towards the entrance of the estuaries (Vinagre et al. 2007, Martinho et al. 2009). Changes in precipitation and river flow will change the extension of these plumes, particularly affecting the recruitment of marine estuary-dependent species whose larvae need to find nursery grounds (Martinho et al. 2009, Tanner et al. 2017). In addition, precipitation directly impacts salinity. At low salinity levels, the floatability of pelagic eggs is reduced, which causes them to sink in less oxygen-rich waters where development is not possible (Florin and Höglund 2008). Increased salinity levels, on the other hand, can directly or indirectly affect fish communities within estuaries, due to the different physiological tolerances and habitat preferences of species and life stages or leading to an increase in marine species within the estuary (Cardoso et al. 2014, Baptista et al. 2015, Pessanha et al. 2021), which can increase predation on estuarine resident species (Dolbeth et al. 2007).

Long-term changes in marine ecosystems have been of increasing interest regarding ecological and management issues (van der Veer et al. 2011, Morrongiello et al. 2014, McCain et al. 2015, Pilotto et al. 2020). Indeed, long-term biological and climatic time series are important to understand ecosystem variability in response to climate change. This is particularly important in fish communities, given their social, cultural, ecological, and economical value. These long-term data series allow us to follow temporal patterns of fish abundance and to understand their responses to certain climatic effects (Henderson and Seaby 2005, van der Veer et al. 2015, Bueno-Pardo et al. 2020). In addition, long-term databases provide insight into the variability of fish communities, as

well as changes in the habitats they use (Baptista et al. 2015), all important matters in fisheries management. However, long-term and geographically wide datasets are rarely available (Martinho et al. 2007b, Buyse et al. 2022). Given their specificities, long-term datasets require the use of robust analytical methods to extract the dominant patterns against a background of natural variability. Dynamic factor analysis (DFA) is a method for modelling the response of multivariate time series in the presence of explanatory variables (Zuur et al. 2003) and has been used to study the effects of environmental factors on fish communities using long-term databases (Leitão et al. 2014, Bueno-Pardo et al. 2020, Buyse et al. 2022).

1.3. Study Species

This work will use five key species of the Mondego estuary (Portugal): *Dicentrarchus labrax*, *Platichthys flesus*, *Solea solea*, *Pomatoschistus microps* and *P. minutus*. These species were chosen not only because they are the most abundant species found in this estuary, but also because of their important economic and ecosystem value.

1.3.1 *Dicentrarchus labrax*

The European seabass, *Dicentrarchus labrax* (Linnaeus, 1758), is a demersal fish species that has a geographical distribution from Norway to Senegal, including the Mediterranean Sea and the Black Sea (Cardoso et al. 2014, Bento et al. 2016). Besides having considerable importance to the ecosystem as a keystone species and top predator (Maria et al. 2009), the European seabass also has great economic value all over Europe (Vinagre et al. 2009a, Cardoso et al. 2014).

This species has a typical marine estuarine-dependent life cycle, consisting of ontogenic migrations between ocean and estuarine environments as they mature, considering the stage of the life cycle in which they are (Pickett et al. 2004, Martinho et al. 2009). During the spawning season, which occurs in late winter/early spring in Portugal, from January to March, adult seabass aggregate in coastal areas to spawn (Martinho et al. 2007a, Vinagre et al. 2009a, Pinto et al. 2021). After the eggs hatch, larvae migrate to nursery areas carried by sea currents, where the juveniles spend the first years of their life (Martinho et al. 2007a, Cardoso et al. 2014). After reaching sexual maturity, which happens after approximately 4 to 5 years after entering the nursery areas, the mature fish migrate back to open ocean waters (Pickett et al. 2004, Bento et al. 2016).

In Portuguese estuaries, *D. labrax* populations exhibit seasonal patterns of abundance (Bento et al. 2016), related to the entry of juveniles into estuarine environments and the recruitment of mature juveniles back to the ocean, which highlights estuaries as important sources for adult seabass populations (Martinho et al. 2007a, Baptista et al. 2010). Additionally, it has also been reported a consistent effect of sea water temperature and the NAO on the interannual variability in hatch phenology of this species (Pinto et al. 2021).

1.3.2 *Platichthys flesus*

The European flounder, *Platichthys flesus* (Linnaeus, 1758), is an abundant epibenthic species in the northern European estuaries and coastal areas, whose geographic distribution ranges from Norway to Morocco, including the Mediterranean Sea (Freitas et al. 2009, Zucchetta et al. 2010). However, studies indicate that the central coastal areas of Portugal are the current southern limit for the distribution of the flounder (Cabral et al. 2007, Dolbeth et al. 2008). This species has a high commercial value in Europe, being one of the most commercially important flatfish in the Baltic Sea (Florin and Höglund 2008) and the only flatfish species commercially exploited in certain areas of Portugal, such as in the Minho River (Freitas et al. 2009).

The life cycle of *P. flesus* is a typically marine estuarine-dependent. In southern European coastal areas, spawning regularly takes place during winter, from December to February (Martinho et al. 2007a, 2013), as flounder's eggs are very sensitive to water temperature, with high mortality at temperatures above 12° C. (Cabral et al. 2007). After they spawn, the young metamorphosing fish migrate to estuaries, settling in the benthic beds of these nursery grounds (van der Veer et al. 1991, Martinho et al. 2013, Primo et al. 2021), which happens from May to August (Freitas et al. 2009). In *P. flesus*, larval settlement occurs simultaneously with metamorphosis. This process is preceded by a combination of short-distance passive transport and active swimming adjusted to tidal rhythms, resulting in more efficient transport of larvae from the coast to nursery areas (Martinho et al. 2013, Primo et al. 2013). The juveniles stay in the estuary to develop for about 2 years before migrating back to the sea (Martinho et al. 2007a).

The successful completion of their life cycle depends on nursery areas that provide favourable conditions for rapid growth, helping to increase the survival of the most vulnerable early life stages and the, consequently, the recruitment of adult populations that form the basis of many commercial fisheries (Martinho et al. 2007a, Freitas et al. 2009).

1.3.3 *Solea solea*

The common sole, *Solea solea* (Linnaeus, 1758), is a flatfish species of high commercial importance in Europe (Tanner et al. 2017), being one of the most valuable fish species in the southern North Sea (Lacroix et al. 2013) and a key component of the soft-bottom ecosystem (Lacroix et al. 2018). Sole's geographic distribution ranges from the North Atlantic to Senegal and the Mediterranean Sea (Vaz et al. 2019), having their southern distribution limit along the Senegalese coast (Queró et al. 1986).

As a marine estuarine-dependent species, *S. solea* exhibits ontogenic migrations throughout its life cycle (Rijnsdorp et al. 1992, Vaz et al. 2019), inhabiting different environments depending on the stage of the cycle. Sole spawn mainly in late winter and spring, from January to April on the Portuguese coast (Martinho et al. 2007a), as larval development is strongly influenced by seawater temperature (Rijnsdorp et al. 1992, Tanner et al. 2017). Sole is a batch spawner and adults release pelagic eggs in the water column (Houghton et al. 1985, Tanner et al. 2017). After hatching, larvae gain some swimming ability that assists them in their migration to the estuaries (Rijnsdorp et al. 1992, Vaz et al. 2019). During the transport, a metamorphosis occurs that will result in the change of the pelagic larvae to the benthic form (Marchand 1991, Tanner et al. 2017). Juveniles spend the next 2 years developing in the nursery areas before migrating back to the continental shelf (Cabral et al. 2007, Dolbeth et al. 2008).

Such as the other marine estuarine-dependent study species, not only is connectivity between habitats important for sole larvae to reach nursery grounds, but conditions within the estuary are also important for this species to complete its life cycle and, consequently, for recruitment of new adults to occur (Martinho et al. 2007a, Tanner et al. 2017).

1.3.4 *Pomatoschistus microps* and *Pomatoschistus minutus*

The common goby, *Pomatoschistus microps* (Krøyer, 1838), and the sand goby, *Pomatoschistus minutus* (Pallas, 1770), are ubiquitous and abundant species in most of Europe's estuaries (Nyitrai et al. 2013) and Mediterranean brackish lagoons (Pampoulie et al. 2000), being the most abundant Gobiidae species in Mondego estuary (Leitão et al. 2006). The geographic distribution of *P. microps* ranges from the Norwegian coast to the Gulf of Lion in the Mediterranean, and *P. minutus* occurs from the Norwegian coast to the western coast of the Black Sea (Salgado et al. 2004).

Both common and sand gobies are estuarine resident species, spending their entire cycle inside estuarine environments, with short life spans and distinct behavioural characteristics (Dolbeth et al. 2007, Nyitrai et al. 2013). These species play a valuable role in these ecosystems as intermediate predators of the food web, feeding on plankton, meio- and macro-benthos, and serving as prey for many other species of larger fish and birds (Leitão et al. 2006, Dolbeth et al. 2007).

P. microps is generally smaller than *P. minutus*, reaching about 6 cm (Nyitrai et al. 2013). It is an annual species that lives for about 12 to 14 months in the Mediterranean Sea (Pampoulie et al. 2000) but can live 19 to 26 months in northern Europe (Bouchereau and Guelorget 1998), and between 15 to 17 in Portugal, namely in the Mondego estuary (Dolbeth et al. 2010, Nyitrai et al. 2013). In southern Atlantic European systems, its reproductive season is estimated to last between December and April (Arruda et al. 1993, Leitão et al. 2006), but is longer in northern estuaries (Healey 1972), with the ability to spawn several times during its reproductive season (Leitão et al. 2006). The common goby spawns preferentially at temperatures between 15°C and 20°C and the temperature seems to be the main factor influencing this process, with higher egg survival at 20°C (Fonds and Buurt 1974).

P. minutus grows up to 8 cm (Nyitrai et al. 2013) and lives for about 16 to 20 months (Leitão et al. 2006). It is able of spending its entire life cycle within estuarine environments, however, adults and juveniles may perform migrations to shore in search of food or to avoid predation (Healey 1972, Leitão et al. 2006, Nyitrai et al. 2013). The reproductive season of the sand goby occurs from February to August/September in the Mondego estuary, and consists of two peaks (Leitão et al. 2006). However, it can occur from three to five months, beginning in spring through summer, in other Atlantic estuaries and coastal lagoons (Healey 1971). The sand goby is not adapted to high temperatures, contrary to the common goby. The eggs of *P. minutus* have higher survival rates at 10°C and do not survive at temperatures above 25°C (Fonds and Buurt 1974).

Both goby species are recognized for their plasticity towards climatic conditions (Pampoulie et al. 2000), varying the number and duration of spawning and egg size in the case of environmental variability (Pampoulie et al. 2000, Dolbeth et al. 2007). In fact, their great adaptability allows them to occupy different biotopes, however, temperature and salinity may limit the development and survival of their eggs and larvae (Fonds and Buurt 1974, Pampoulie et al. 1999, Dolbeth et al. 2007). *P. microps* tolerates a wider range of temperature and salinity variations, which may be an advantage over *P. minutus*

(Dolbeth et al. 2007). Because of this, in some estuaries like the Mondego, *P. microps* is usually more abundant than *P. minutus* (Dolbeth et al. 2007, Nyitrai et al. 2013).

1.4. Objectives

Understanding how climatic factors impact the recruitment of key species in the long-term is fundamental for fisheries management and consequent conservation of fish species and ecosystems. Therefore, the main objectives of this work are:

1. To analyse the variability of recruitment of *Dicentrarchus labrax*, *Platichthys flesus*, *Solea solea*, *Pomatoschistus microps* and *Pomatoschistus minutus* in the Mondego estuary, by investigating the changes in 0-group abundance from 2003 to 2019.

2. To relate the recruitment variability of the five study species with the dominant environmental factors within the estuary and in the adjacent coastal zone, to determine possible climate change-induced impacts.

CHAPTER II - Materials & Methods

2.1. Study area

2.2. Sample acquisition & processing

2.3. Environmental data acquisition

2.4. Data analysis

2.4.1. Biological and environmental data

2.4.2. Dynamic factor analysis

2.4.3. Individual trends

2.1. Study area

The Mondego River estuary is a small intertidal system, located on the Atlantic coast of Portugal (Fig. 2) and is characterized by a continental temperate climate. About 7 km from the coast, the estuary is divided into two arms, the north arm and the south arm, joining again near the river mouth.

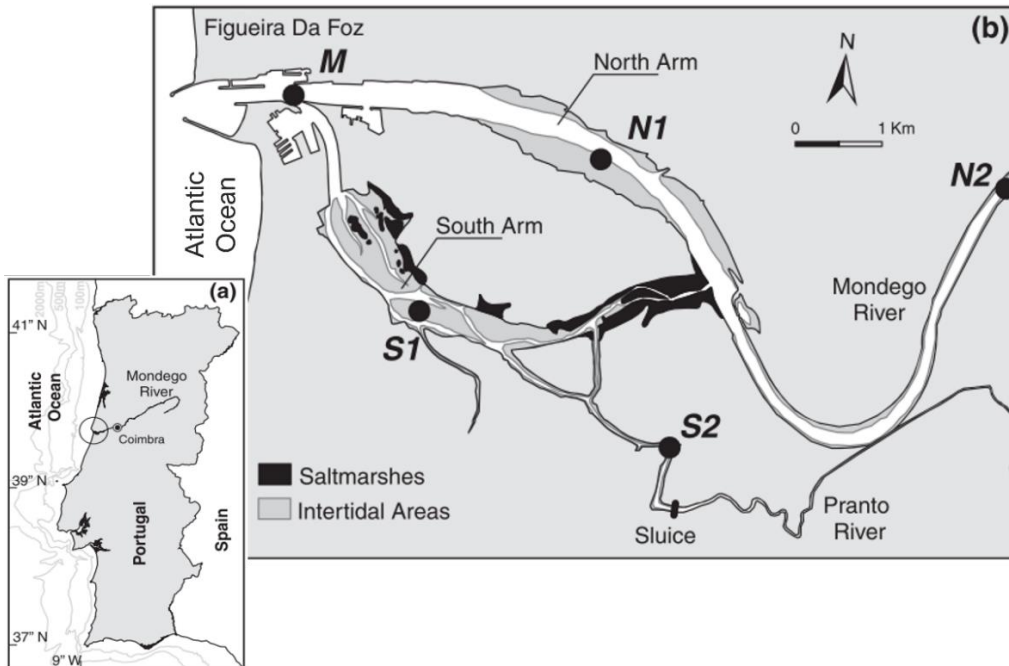


Figure 2. The geographical location of the Mondego estuary (a) and five sampling stations (b). M is the station located closest to the river mouth. S1 is in the southern arm of the Mondego, S2 is in the Pranto River, which in turn influences the southern arm of the Mondego River. N1 is in the northern arm and N2 in the upper arm of the Mondego estuary.

The north arm receives most of the freshwater input from the Mondego River and is, therefore, deeper, reaching depths of 5 to 10 meters during high tide, with a tidal range of 2 to 3 meters, being the main navigation channel (Martinho et al. 2007b, Nyitrai et al. 2013). Water circulation in the south arm depends mainly on the tidal influx of seawater and small freshwater input from the Pranto River, reaching depths of 2 to 4 meters during high tides (Martinho et al. 2007b). In this arm, about 75% of the total area are intertidal mudflats, while in the north arm they represent less than 10% (Martinho et al. 2007b).

2.2. Sample acquisition & processing

Sampling was done monthly from June 2003 to October 2019, excluding some months due to technical constraints or adverse weather conditions, on five different sampling stations (Fig. 2) to guarantee the representation of the whole estuary.

Fishing was performed at night during high tide, so the fish could not see the net and escape. At each station, three replicates were performed with a 2 m beam trawl with one tickler chain and 5 mm mesh size cod-end and at a speed of two knots, for an average duration of three minutes, covering at least 500 m². While fishing, bottom water was analysed for temperature and salinity. In the laboratory, all individuals were identified and the total length (TL) in centimetres and wet weight (WW) in grams were measured. Sample collection, laboratorial work and data curation was performed by several team members of the Marine Research Lab – Centre for Functional Ecology (CFE), of the University of Coimbra, and supervised by Filipe Martinho and Miguel Pardal.

Since recruitment in fish early life stages determines the strength of year class (Rijnsdorp et al. 1992, van der Veer et al. 2000), in this work we only used data on the 0-group to analyse the density variations of newly hatched fish in each year, and thus to study recruitment in the early life stages. To obtain 0-group fish data, seabass, sole and flounder individuals with a TL less than 12 cm were selected, since previous studies indicated that this is the average size for these species at the end of the first year (Martinho et al. 2008, Dolbeth et al. 2010). Similarly, for the common goby, were only selected individuals with a TL smaller than 3.5 cm and the sand goby with a TL smaller than 4.5 cm, based also on previous studies that reported this to be the average length of individuals at the end of the first year (Dolbeth et al. 2007, Nyitrai et al. 2013).

2.3. Environmental data acquisition

The mean monthly values of all environmental variables were obtained from different online sources from 2001 to 2019 to assess their effect on the 0-group density of each species over the years. The effect of some environmental variables was tested with a temporal lag, being necessary to obtain the values up to 2 years before the database of biological variables.

The North Atlantic Oscillation index (NAOi) is established by the difference in the surface sea-level pressure between the Subtropical High (Azores, Portugal) and the

Subpolar Low (Reykjavik, Iceland), and is known for affecting parameters such as temperature and precipitation, being linked to ocean productivity and, consequently, having a potentially influential role in fish recruitment (Attrill and Power 2002). NAOi monthly values were obtained from NOAA - National Weather Service - Climate Prediction Centre (<https://www.ncdc.noaa.gov/teleconnections/nao/>; accessed in June 2021).

The Eastern Atlantic Pattern (EAP) is the second most influential atmospheric pattern in the North Atlantic. Despite being a similar pattern to NAO, its centre of activity is located more to the southeast of the North Atlantic, behaving differently from NAO, but also being a potential factor influencing recruitment (Barnston and Livezey 1987). All data corresponding to EAP was obtained from NOAA - National Weather Service - Climate Prediction Centre (ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/ea_index.tim; accessed in June 2021).

The Atlantic Multidecadal Oscillation (AMO) index shows importance as a potential predictor of fish abundance behaviour when studying long-term trends in fish communities (Buyse et al. 2022) since it is a series of long-term changes in the sea temperature in the North Atlantic Ocean. AMO index values were obtained from NOAA - National Weather Service - Climate Prediction Centre (<https://psl.noaa.gov/data/correlation/amon.us.long.data>; accessed in June 2021).

Upwelling causes a short-term, seasonal and interannual variability in currents, temperature, and primary productivity, which may have a significant impact on larval transport and consequently recruitment success (Santos et al. 2007, Tanner et al. 2017). The Upwelling index (UI) was obtained in $m^3 \cdot s^{-1} \cdot km^{-1}$ from the Spanish Oceanographic Institute (<http://www.indicedeafloramiento.ieo.es/interactivo.html>; Figueira da Foz FNMO station; accessed on in October of 2021).

Sea Surface Temperature (SST) has been increasing worldwide due to climate change (Holt and Jørgensen 2015). Water temperature is known to affect a diversity of factors in fish's life cycles (Cabral et al. 2001, Vinagre et al. 2009b, Vaz et al. 2019), compromising the survival of the initial stages and, therefore, fish recruitment. SST values (°C) were obtained from Copernicus Marine Environment Monitoring Service (CMEMS; <https://marine.copernicus.eu>; accessed in June 2021).

Precipitation influences river flow and, consequently, the formation of river plumes that extend into the ocean. These plumes are important in the migration process of marine fish larvae to the estuary, as they indicate the proximity of nursery grounds

(Marchand 1991, Martinho et al. 2009). The smaller the plumes are, the less likely larvae are to head for the nursery grounds, risking their survival (Martinho et al. 2009, Tanner et al. 2017), which tends to result in worse recruitment and thereby less abundance of 0-group fish. Precipitation values (mm) were obtained from the Portuguese Sea and Atmosphere Institute (IPMA; <https://www.ipma.pt/>; accessed in June 2021) and the river flow values ($\text{m}^3.\text{s}^{-1}$) from the National Water Resources Information System (SNIRH; <https://snirh.apambiente.pt/>; accessed in June 2021).

2.4. Data analysis

2.4.1. Biological and environmental data

Monthly abundance data (number of individuals per 1000 m^{-2}) were obtained for each species by dividing the number of individuals collected in all sampling stations in each month by the total area covered in the respective month. Abundance data was then log-transformed to stabilize the variance and was subsequently standardized by subtracting the mean and dividing by the standard deviation, which removes seasonality and consequently reduces the error associated with it, since these species have seasonal peak abundances in the estuary. For temperature and salinity measured during sampling, all five stations were averaged for each month. All environmental variables were also standardized by subtracting the mean and dividing by the standard deviation, to approximate the different scales between variables and to obtain unitless (without units) results, making it easier to interpret them.

Multi-collinearity of the environmental variables was tested through pair-plots and Spearman correlation coefficients. High collinearity was found for SST and AMO ($r = 0.52$), SST and precipitation ($r = -0.44$), SST and estuary water temperature ($r = 0.78$), precipitation and estuary water temperature ($r = -0.61$), precipitation and salinity ($r = -0.48$), upwelling index and precipitation ($r = 0.71$), upwelling index and estuary water temperature ($r = 0.51$) and upwelling index and chlorophyll a ($r = 0.53$). Thus, it was decided to include only the variables of NAO, EAP, AMO, salinity and estuarine water temperature variables in further analyses as they better explained the variations in fish communities according to initial analyses and that did not correlate among each other. All environmental variables were also examined with time lags of one and two years to investigate potential lagged responses of biological variables. All data operations were performed in R software (R Core Team, 2021).

2.4.2. Dynamic factor analysis

Dynamic factor analysis (DFA) is a dimension-reduction technique specially designed for multivariate non-stationary time series analysis (Zuur et al. 2003). DFA allows to estimate common trends, evaluate interactions between response variables (fish abundance) and determine the effects of explanatory variables (environmental variables) on the former (Zuur et al. 2003, Bueno-Pardo et al. 2020).

The response time series were modelled in terms of a linear combination of 1 to 3 common trends, explanatory variables, a level parameter, and a noise component. The common trends, which are independent of one another, represent the underlying common patterns of variation along time (Bueno-Pardo et al. 2020). In DFA it is possible to select the number of common trends and explanatory variables to include in the models. The models used comprised all the possible combinations of 1, 2 or 3 common trends, 1 or 2 explanatory variables and a diagonal and unequal error covariance matrix. The best models were selected by Akaike's information criterion (AIC), along with a stepwise approach to identify the best set of explanatory variables (Zuur et al. 2003, Buyse et al. 2022). Models with the lowest AICc (AIC corrected for small sample size) were considered drivers of the variability of the response variables (Bueno-Pardo et al. 2020). Factor loadings were used to identify the relative importance of a common trend to a particular fish species and which species are related to the same common trend. A cut-off level for loadings of 0.2 is commonly used to establish whether a species is associated with a given trend, and species with values below this level do not contribute as much to the trend as those above (Zuur et al. 2003, Buyse et al. 2022). Still, this value can be attenuated or just considered the most positive values as the strongest relationship of each variable to a particular trend (Goethel et al. 2019). The analyses were conducted using the *MARSS* package (Holmes and Ward 2011) version 2.8, in R software.

2.4.3. Individual trends

While common trends provide insight into general temporal trends in fish communities, time series analysis of each separate species enables the identification of significant increases or decreases for each species (Buyse et al. 2022). To explore whether trends in individual species could be linked to certain environmental variables,

Spearman rank-order correlation tests were performed for each species and environmental factors standardized time series. As temperature proved to be an important factor in the previous analyses, SST was also included here, as the correlations are individual and there would be no collinearity conflict with the remaining variables. All environmental variables were also examined with time lags of one and two years to look for potential lagged responses of biological variables, A value of 0.4 was used as threshold to define a strong relationship. The analyses were conducted using the *corrplot* package (Wei and Simko, 2021), in R software.

CHAPTER III – Results

3.1. Biological and environmental data

3.2. Analysis of common trends

3.3. Individual species trends

3.1. Biological and environmental data

There were clear seasonal variations in the density of all 0-group fish in the Mondego estuary during the study period, with higher numbers of juveniles in spring/summer (Fig. 3). The abundance peak of *D. labrax* was observed in 2003 with 30 individuals per 1000 m⁻² and the closest density to that was in 2013 and 2017, with nearly 20 individuals per 1000 m⁻². The density of 0-group *P. flesus* was very low during the early years, but increased since 2011, with peaks in 2008, 2012 and 2019 of approximately 16, 19 and 34 individuals per 1000 m⁻², respectively. *Solea solea* reached lower densities during the study years, and like the European flounder, 0-group densities increased over time, with the highest peak in 2017, with about 17 individuals per 1000m², and about 14 individuals per 1000 m⁻² the next year.



Figure 3. Annual variation in density (number of individuals per 1000m²) of the 5 study species from 2003 to 2019

Regarding the estuarine resident species, in addition to seasonal variation, *P. microps* had an increasing tendency in abundance, with several peaks in 2018 of about 34, 38 and 50 individuals per 1000 m⁻² and a large peak in 2019 of over 100 individuals per 1000 m⁻². On the other hand, *P. minutus* showed a decreasing tendency, with density

peaks of 32 and 33 in 2010 and 2012, but currently with 1, 2 or even no individuals per 1000 m⁻² since 2016.

Seasonal variation was also noticeable on the main environmental drivers (Fig. 4). The NAO index alternated between positive and negative phases throughout the years but had a long negative phase between early 2010 and mid-2011, which ended with its highest positive peak (2.48). In mid-2015 it had its negative peak (-3.18) and from 2016 its negative phases have been less negative and shorter.

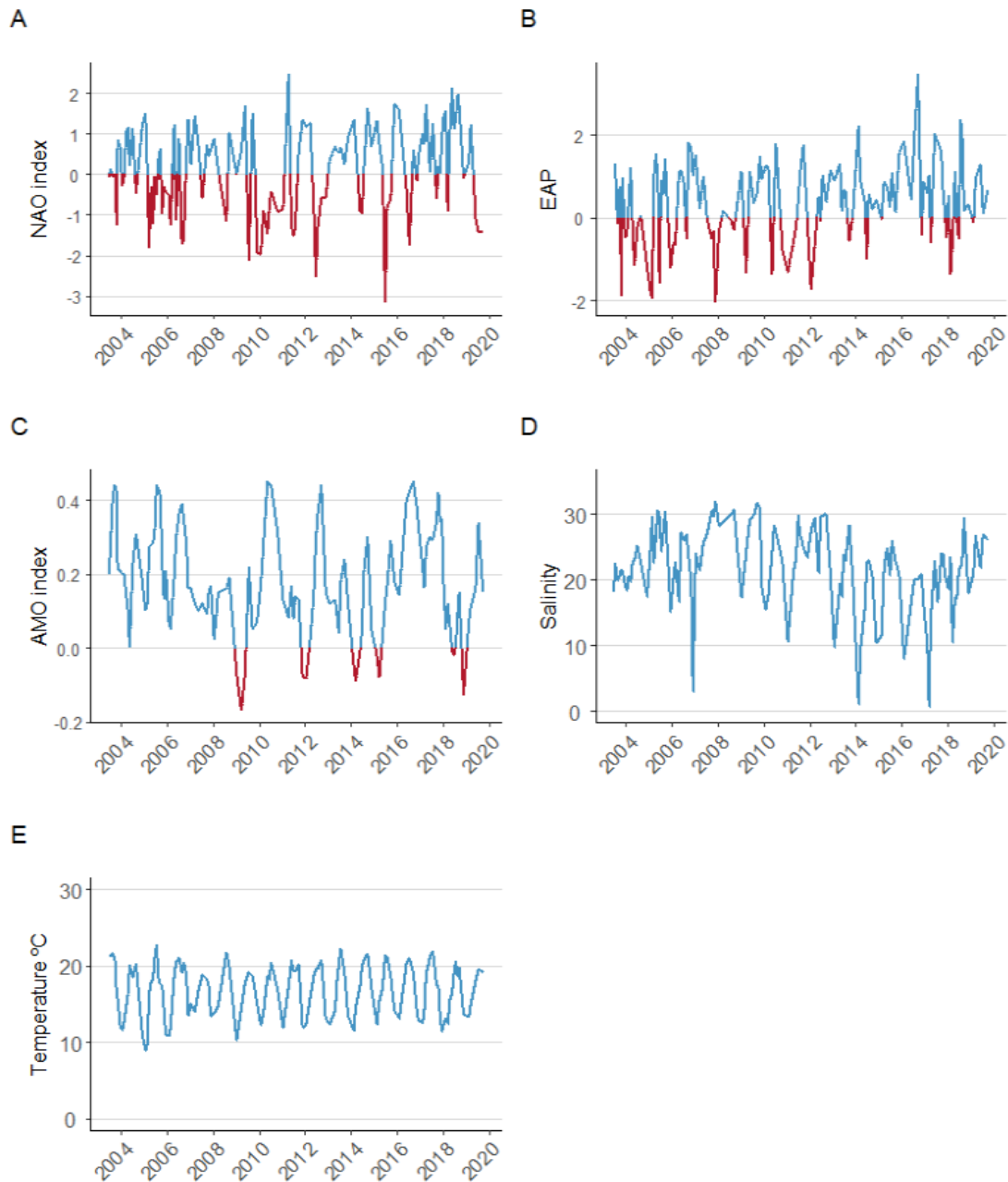


Figure 4. Variation of the five environmental variables from 2003 to 2019: North Atlantic Oscillation index (A), Eastern Atlantic Pattern (B), Atlantic Multidecadal Oscillation (C), estuarine salinity (D) and estuarine water temperature (E).

The Eastern Atlantic pattern (EAP) started with a negative phase between 2004 and 2005 and from then on alternated between positive and negative phases over the years, with a negative phase that reached a value of -2.07 at the end of 2007. Since the end of 2014 it has been more positive, with very short negative phases. Its positive peak was in September of 2009 (value of 3.48).

The Atlantic Multidecadal Oscillation (AMO) was highly variable but mostly positive, with values up to 0.5 in several years. In 2009 it had its first negative phase in the study period, which was also its negative peak (-0.17).

Within the estuary, high salinity was observed particularly between 2003 and 2006, with values between 20 and 30, associated with extreme drought conditions (IPMA 2003, 2004, 2005, 2006). Its lowest peaks were associated with heavy precipitation in late 2006, early 2014, and early 2017. In the remaining years, estuarine salinity remained between average values of 10 and 30.

The estuarine water temperature showed a clear seasonal variation, increasing in the summer months and decreasing in the winter months. This variation was relatively stable and ranged from about 10 to 22°C. However, since 2009, the minimum winter temperatures are getting warmer, with the lowest value being 13.3 °C in 2019.

3.2. Analysis of common trends

Among all the models provided by the DFA (Table 1), the model with the lowest AICc (1250.65) was the one considering three common trends plus the effect of the estuary water temperature and the 1 year lagged AMO. The next model, considering three common trends plus the effect of estuarine water temperature had an AICc of 1252.9. Despite that this model considers fewer explanatory variables, and since there are more than 2 AICc units between both models, it was considered the first one as the best available one.

Table 1. Best five dynamic factor analysis models with the lowest AICc (AIC corrected for small sample size) with a diagonal and unequal matrix R.

Common Trends	Explanatory Variables	AICc
3	Estuary water temperature + AMO with 1 year time lag	1250.648
3	Estuary water temperature	1252.891
3	Estuary water temperature + AMO with 2 years time lag	1254.458
3	Estuary water temperature + NAO	1254.592
3	Estuary water temperature + AMO	1256.717

The first common trend identified showed a decreasing pattern at the beginning of the time series (Fig. 5), with a slight increase during 2005. Its minimum was from mid-2010 to late 2012 and increased afterwards, with a slight decrease in 2017-18. The second trend found, with a smoother shape, is contrary to the first. It decreased until mid-2005 and increased thereafter, reaching its maximum between 2011 and 2012. In late 2012, it declined again until the end of the time series.

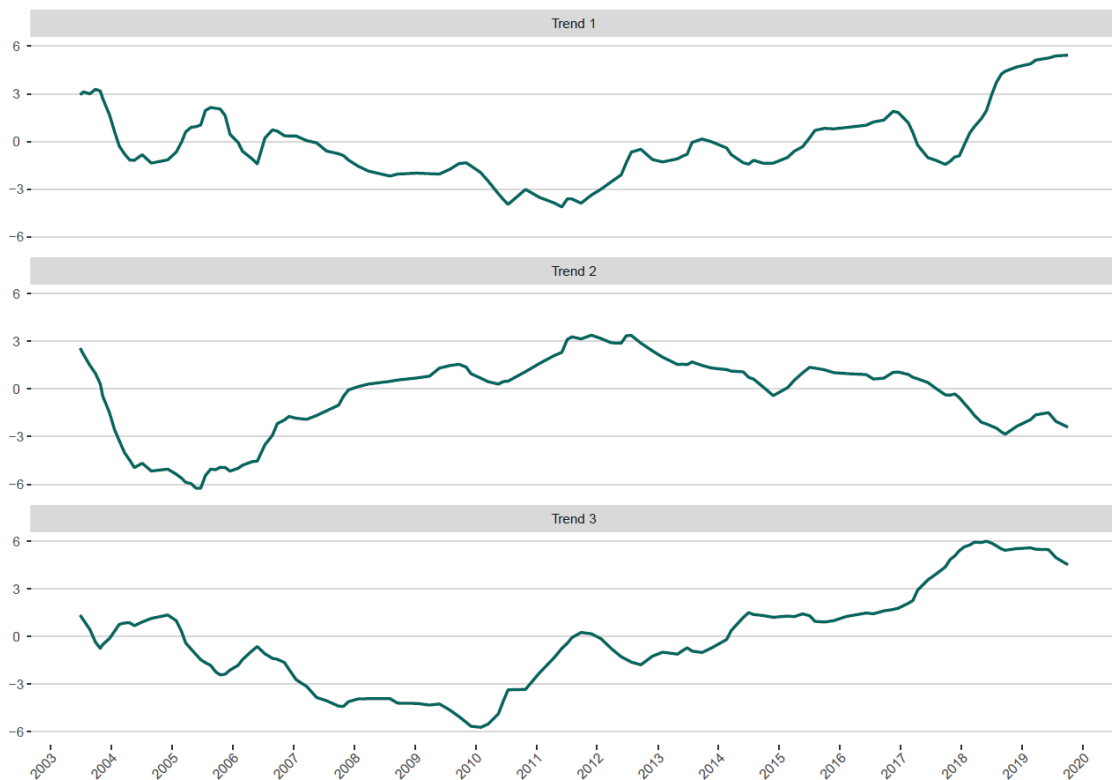


Figure 5. Common trends identified by the model containing three common trends and a diagonal and unequal matrix. Common trends are unitless.

The third trend identified was less variable than the first one but followed a similar pattern. Indeed, this trend started with a slight decrease similarly to the first, from 2003 to 2010, when it reached its minimum, and increasing again until 2019. In contrast with the first trend that had a small decrease between 2017 and 2018, the third trend had its maximum in 2018 and started to decrease slightly. Interestingly, 2012 was an inflexion point for both trends 1 and 2, while the most marked inflexion in trend 3 was observed in 2010.

The factor loadings indicate the relationship between common trend and each species (Table 2). *D. labrax* is highly related to the first trend (0.40), the *P. flesus* and *S. solea* positively related to the second trend (0.13 and 0.16, respectively), *P. microps* is negatively related to trend 1 (-0.21), and positively with trend 3 (0.17), and *P. minutus* is positively related with trend 3 (0.17).

Table 2. Factor loadings for each species and the three common trends. Higher correlations are highlighted in bold.

Species	Trend 1	Trend 2	Trend 3
<i>D. labrax</i>	0.40	0.22	-0.13
<i>P. flesus</i>	0.02	0.13	0.02
<i>S. solea</i>	0.02	0.16	0.02
<i>P. microps</i>	-0.06	0.03	0.17
<i>P. minutus</i>	-0.21	0.03	0.17

3.3. Individual species trends

Individual species trends also showed quite some variability along the time series, with only *P. microps* showing a clear increasing trend, especially since 2009 (Fig. 6). Except for *D. labrax*, individual models for each species showed a similar pattern to the trend they were most related to. In *P. flesus* and *S. solea* it was noticeable a decreasing pattern in the beginning of the time series with an increasing afterwards 2006 and ending with a decrease again, like in the second common trend. Gobies' fitted values showed a decreasing in the beginning, followed by an increasing pattern and ending with a slight decrease (more evident in *P. minutus*), similarly to the third trend. Additionally, it was also noted a predicted seasonal variability in every species.

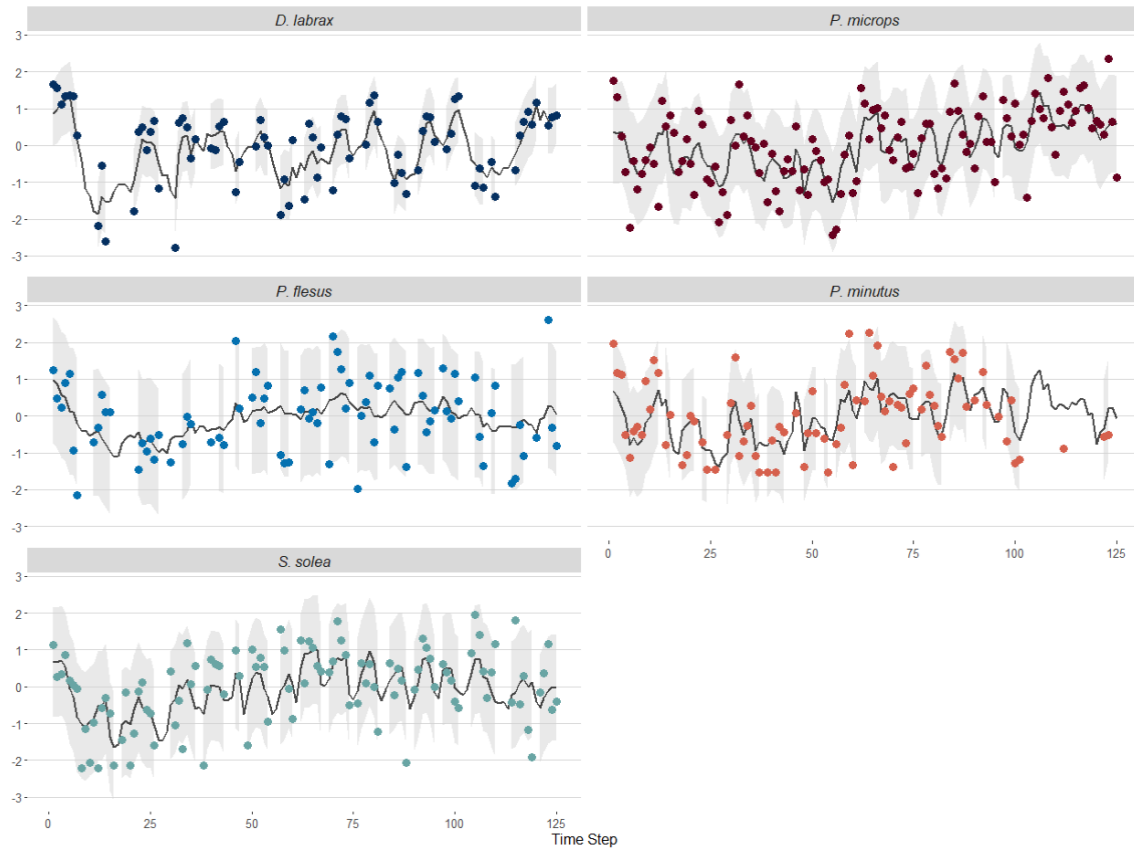


Figure 6. Fitted values obtained by the DFA model including three common trends and a diagonal and unequal matrix R for each study species. The black lines represent the fitted values, the dots represent the observed standardised values, and the grey polygons represent the confidence intervals. Time step corresponds to the 125 months of the study, 1 corresponding to June of 2003, 55 to February of 2010 and 125 corresponding to October of 2019 (Annex 1). Fitted values are unitless.

The 5 species were quite similar in their relationship with water temperature, which was the variable that influenced fish density the most (Table 3). All species density was favoured by increasing estuary water temperature, SST and AMO when considering the corresponding year, 1 and 2-year time lags. Although AMO does not seem to have an influence as strong on the individual species as it does on the community itself. Except for *S. solea*, marine species density had stronger correlation with SST than with estuary water temperature (Table 3). *P. microps* was positively correlated with estuarine water temperature, while *P. minutus* did not present any significant correlation with the environmental variables.

Table 3. Spearman rank correlation coefficients between species and the used environmental variables. Only significant correlations ($p < 0.05$) are shown in this table, and values above 0.4 are highlighted in bold.

	<i>D. labrax</i>	<i>P. flesus</i>	<i>S. solea</i>	<i>P. microps</i>	<i>P. minutus</i>
NAO	-0.22	-0.25			-0.21
EAP					
AMO	0.34	0.23	0.26		
SST	0.72	0.56	0.52	0.26	
Temperature	0.48	0.47	0.6	0.4	0.29
Salinity	0.26		0.26		
NAO 1-year time lag			-0.26		-0.24
EAP 1-year time lag	0.24			0.2	
AMO 1-year time lag	0.26		0.24	0.33	
SST 1-year time lag	0.69	0.49	0.51	0.22	
NAO 2-year time lag		-0.27	-0.26		-0.2
EAP 2-year time lag					
AMO 2-year time lag	0.42		0.29		
SST 2-year time lag	0.69	0.53	0.55	0.26	0.24

CHAPTER IV - Discussion

4.1. Temperature and AMO as key drivers in fish populations

4.2. Final considerations

A critical step in marine ecosystem conservation is to understand how climatic conditions affect the recruitment of key species over time. Such specific long-term studies are not very common, yet they will allow for better and more localized fisheries management. This is the first study on the recruitment of juveniles of key fish species (*Dicentrarchus labrax*, *Platichthys flesus*, *Solea solea*, *Pomatoschistus microps* and *Pomatoschistus minutus*) in the Portuguese coast that uses such a long database (17 years). Common trends and individual species densities were studied using a combination of multivariate (dynamic factor analysis) and univariate methods (Spearman rank correlation). We observed different patterns between *D. labrax*, a demersal species, *P. flesus* and *S. solea*, epibenthic species, and *P. microps* and *P. minutus*, estuarine residents, related with changes in water temperature, particularly the estuarine water temperature, and in the AMO with 1 year time lag.

4.1. Temperature and AMO as key drivers in fish populations

DFA outputs indicated that the best model included 3 common trends for the 5 species with the added effect of water temperature and the AMO lagged by 1 year. *D. labrax*, a marine and demersal species, is associated with trend 1; *P. flesus* and *S. solea*, epibenthic marine flatfishes, are both associated with trend 2; and both gobies, which are estuarine residents with a shorter life cycle, are associated with trend 3. The common trends show how populations respond to the environmental parameters included in the model, and each common trend should be linked to a set of response variables that share a characteristic (Zuur et al. 2003). In this case, the factor loadings relate species that use different environments and have different life cycles to each one of the three common trends.

Temperature and AMO with 1 year time lag were included in the models as the most important explanatory variables defining the 3 common trends, meaning that they are the ones with the most influence on the 0-group densities of the studied species. Temperature has been described as a crucial factor in fish life cycles, including spawning period and the timing of colonization of estuaries (Amara et al. 2000, Martinho et al. 2013), egg survival and development (Greve et al. 2005, Tsoukali et al. 2016), metamorphosis time (Hutchinson and Hawkins 2004), and even growth (Vinagre et al. 2009a, Drinkwater et al. 2010). Water temperature related explanatory variables (estuary water temperature and SST) are the result of the combination of several environmental factors, such as currents, seasonal variations and long-term climate oscillations

(Cannaby and Husrevoglu 2009, Buyse et al. 2022) and are therefore accurate descriptors of the rates and dynamics governing ecosystems.

The AMO can be seen as an additional water-temperature related variable, as it is measured from the oscillation of the North Atlantic SST over a large temporal and spatial scale. The AMO index is estimated to have a 60-80 year period (Gray et al. 2004), where higher AMO index values are associated with higher SST. The effect of AMO on fish dynamics has also been found to be significant on larger temporal scales (Auber et al. 2015, Bueno-Pardo et al. 2017, Buyse et al. 2022), affecting the species in different ways according to oceanographic regions in the North Atlantic. The fact that the best model considers a 1-year-lagged AMO points to a direct relationship between the increase of fish populations and the SST trend over the previous years. This result can be obtained from a positive effect of the SST trend on the survival and/or reproduction of the adult populations or other mechanisms by which SST trends could promote an increase of the fish densities at the Mondego estuary. Furthermore, AMO cycles may cause geographical shifts in some species (Alheit et al. 2014) as response as the change of the SST, causing changes in migrations (Auber et al. 2015) and spawning habitats (Sundby and Nakken 2008), leading to an increase in abundances in particular locations. In general, we could infer those warmer years are linked to higher recruitment and consequently higher fish densities, with this effect being visible one or two years later. Nevertheless, the AMO is a long-term natural oscillating climate index that is currently approaching its maximum warming value and subsequently starting to decline. In a future cooling phase, the trends in fish density may slow down or even invert their direction (Buyse et al. 2022).

None of the models with the lowest AICc nor the individual correlations included EAP, being a variable with very little or no influence on the recruitment of the study species. Although there are some studies where this variable played an important role in fish communities (Tanner et al. 2020, Pinto et al. 2021), here it appears to be less relevant than temperature and AMO. Salinity was also not included in any of the best models. This variable most likely has a smaller spatial and temporal impact on the system and the species living there. Although salinity has already been determined as an important factor within estuaries in different regions, including the Mondego estuary (Freitas et al. 2009, Martinho et al. 2009, Cardoso et al. 2014, Lima et al. 2020), it does not appear to have a long-term effect as evident as water temperature on the recruitment of these species. The negative relationship found between the species' individual densities and the NAO index, even though it was not a strong one, also points towards a positive influence of warmer and rainy years on the fish species at the Mondego estuary, since

higher NAO values are associated with low precipitation and temperature in southern and central Europe.

Ecosystems can reorganize themselves, but preserve the same function, structure, and identity when affected by natural and anthropogenic changes (Walker et al. 2004). However, in some circumstances, the ecosystem can be altered in ways that its structure and function its changed (Scheffer et al. 2001). This transition can be described as a regime shift. Regime shifts are defined as changes of high amplitude and low frequency, are usually suddenly observed in species abundance and community composition, and are observed at various trophic levels (McKinnell et al. 2001, Szalaj et al. 2021). In the North Atlantic, two regime shifts have already been identified: one in the mid-90s (Auber et al. 2015, Perälä et al. 2020) and one coinciding with our study period, in mid-2010 (Meyer-Gutbrod et al. 2021), including in the Portuguese continental shelf (Szalaj et al. 2021). Changes in species abundance and community composition are part of the new regime (Szalaj et al. 2021). This change was most likely caused by an external factor, like environmental forces, including the increase in temperature and AMO. Indeed, the mid-1990s shift its believed to be linked to the change of AMO from a cold phase to a warm phase (Alheit et al. 2014, Auber et al. 2015).

The effect of the environmental variables studied on species densities was consistent across years, with all five species having a similar response to all variables even with temporal lags, especially with the variables related to water temperature. However, there was a clearly observable change in both individual and common trends between 2010 and 2012. Coincidentally, between 2009 and 2011 the AMO recorded the most negative value during the study period, with a drastic increase to its positive peak. Between one and two years later the direction of the common trends reversed. This supports the idea that the shift that occurred in 2010 may have been caused by changes in the AMO, namely the sudden increase from a small negative phase to a large positive phase, which may have led to a quick increase in SST. The fact that the AMO strongly acts on the Mondego estuary fish species with a time lag of one year may thus explain the reversal of the trends' direction one to two years later. In these years, the winter temperature of the estuarine water started to increase year by year, which may have amplified this shift inside the nursery area.

Our results suggest that this alteration in AMO allied with changes in estuarine water temperature was beneficial for the species associated with the first and third trends, *D. labrax* and both *Pomatoschistus* species, respectively, but not so much for the species associated with the second trend: *P. flesus* and *S. solea*. Although these flatfishes are

positively correlated with AMO individually, this correlation is not strong and within the community this change has negatively affected them. This might be linked to either direct effects of the increase in AMO or indirect relationships such as increase in predation or decrease of food availability, associated with shifts in the habitat of different fish species (Alheit et al. 2014, Auber et al. 2015) or changes in plankton abundance and distribution due to temperature changes (Hays et al. 2005). Based on ocean modelling simulations, Cabral et al. (2021) observed that the recruitment of different species, including *D. labrax*, was highest in warm years, in contrast with *P. flesus* that recorded no recruitment on the southern Iberian coast during warm years, which supports the decrease in trend 2. In fact, the rising of SST has been described as the most probable cause of this species' decrease in the Tagus estuary (Cabral et al. 2001). In the Mondego estuary fish community, recruitment of *S. solea* did not seem to benefit from this change either. In this sense, abrupt changes in the AMO seem to affect the community of key epibenthic species in the estuary, which may be due to a myriad of factors, one of them being the effect that changes in SST may have on spawning, egg survival, pelagic stage duration and metamorphosis of these species (Hutchinson and Hawkins 2004, Vinagre et al. 2008, Primo et al. 2021). For instance, in species such as the European flounder and the common sole, the age and size at the metamorphosis phase is a critical determinant of recruitment success (Chambers and Leggett 1992, Geffen et al. 2007, Primo et al. 2021). Changes in water temperature does not appear to have a direct influence on metamorphosis, but rather on the time it takes to reach this stage (Hutchinson and Hawkins 2004). Variations in seawater temperature can therefore alter the age and size at which larvae begin metamorphosis, compromising the recruitment and consequently decreasing fish densities in the next years.

D. labrax populations were positively affected by higher water temperature, also in agreement with (Cabral et al. 2021). Indeed, growth rates and juvenile recruitment of European seabass have already been demonstrated to be faster at higher temperatures (Vinagre et al. 2009a). Thus, an increase in SST caused by the rapid rise of AMO and consequent increase of estuarine water temperature may have favored growth of both juveniles and adults, and therefore contributing to increased recruitment in subsequent years. Warmer winter temperatures are also considered to induce *D. labrax* to extend their stay in the nursery areas during summer (Pawson et al. 2007). As a result, a warming climate may lengthen juveniles' stay in the estuary and/or provide ideal winter conditions (Cardoso et al. 2014), resulting in increased recruitment and, as a result, a higher number of adults reproducing, followed by a higher number of juveniles in succeeding years. Since a recent study indicated that early life phenology of *D. labrax* is

also regulated by water temperature (Pinto et al., 2021), a better understanding of the mechanisms in seabass life history and recruitment will surely contribute to a better development of stock management and protection measures.

Since both goby species are highly adaptable to changing environmental conditions (Pampoulie et al. 2000), it is natural that this environmental shift was less adverse to them. Still, this variation in water temperature may benefit the survival of adults of both species, with increased recruitment in the next years. In the Mondego estuary, a positive relationship between temperature and the abundance of *P. microps* has already been found, whose juvenile abundance is higher in areas with higher temperatures (Leitão et al. 2006, Dolbeth et al. 2007). The common goby's reproductive season presents a climatic gradient, with temperature being the key controlling factor: populations in the colder North Atlantic have a shorter reproductive season and those in warmer Mediterranean lagoons have a longer reproductive season (Bouchereau and Guelorget 1998). Additionally, *P. microps* can spawn multiple times throughout the course of the reproductive season (Miller 1984, Leitão et al. 2006). This slight temperature increase may lead to a longer breeding season for the common goby, allowing for greater spawning and egg survival, increasing recruitment, and contributing for the abrupt increase in the third trend. In contrast, *P. minutus* had a weak positive correlation with temperature. The reproduction of the sand goby in the Mondego estuary has two peaks, one in late winter and the other in late summer, and the difference between these two peaks may be linked to the high temperatures in the Mondego estuary in the spring and summer (Leitão et al. 2006). The slight increase in temperature may somewhat influence the timing of these recruitment peaks, which can favor higher abundance of this species. However, *P. minutus* is not so well adapted to high temperatures like *P. microps* (Fonds and Buurt 1974), and a continuous increase in water temperature can reach a point where it becomes harmful by compromising reproduction, egg and juvenile survival and/or growth.

In fact, fish individual growth takes place within a narrow thermal range that varies throughout developmental stages and even between populations of the same species; this occurs since a specific temperature range is required for a sufficient supply of oxygen (Pörtner 2001). When temperature increases exceed the species' range, aerobic performance is compromised, bringing consequences for growth, reproduction and motor performance (Drinkwater et al. 2010), as well as jeopardizing several other factors in the life cycles of fish, such as egg survival and development (Tsoukali et al. 2016). Thus, a slight increase in temperature within the thermal range to an optimal temperature can be beneficial for a population, which seems to be the case of all our species

individually. However, in a context of climate change it is expected that the temperature will continue to increase and at any time the temperature range for each species can be outpaced, compromising species recruitment and prevalence, and consequently affecting the marine ecosystems' functioning and the goods and services provided by them. Still, responses to environmental changes may differ between species, trophic levels, and geographical locations (Poloczanska et al. 2016, Tsoukali et al. 2016).

4.2. Final considerations

This study demonstrates the thermophilic nature of the fish species evaluated due to their strong relationships with the temperature-related environmental variables. Even though estuarine water temperature has remained relatively constant between 2003 and 2019, with only minimal changes, we showed that a slight increase in temperature favours the recruitment of these key species in the Portuguese coast. However, if the temperature continues to increase, which is likely in the context of climate change, these trends could quickly change, and fish could start to be negatively affected. Our results also show a major shift in the abundance of the Mondego estuary key fish species between 2010 and 2012, most probably as a response to a regime shift cause by changes in large-scale climate factors. Indeed, the DFA allowed unravelling how different species within a community respond to environmental changes and is therefore scalable to many other sites and biological communities. As such, with increasing pressures in marine and estuarine systems, the periodicity and intensity of regime shifts are expected to increase, altering the local communities and ecosystems.

Altogether, this work demonstrates the usefulness and importance of long-term databases in the study of fish recruitment in response to major climate drivers, as well as understanding which environmental factors exert the most pressure on the system. Indeed, analysing the long-term variability of the recruitment of key species in specific regions is fundamental in fisheries management and ecosystem conservation, which enables recording how different species respond to large and local-scale environmental factors.

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Annexes

Annex 1: Correspondence between time step (Fig. 6) and the respective year and month.

Time step	Year	Month	Time step	Year	Month	Time step	Year	Month
1	2003	6	43	2007	11	85	2014	6
2	2003	7	44	2008	1	86	2014	7
3	2003	8	45	2008	3	87	2014	9
4	2003	9	46	2008	8	88	2014	11
5	2003	10	47	2008	9	89	2015	2
6	2003	11	48	2009	1	90	2015	4
7	2003	12	49	2009	3	91	2015	5
8	2004	1	50	2009	5	92	2015	7
9	2004	2	51	2009	7	93	2015	8
10	2004	3	52	2009	9	94	2015	9
11	2004	4	53	2009	11	95	2015	11
12	2004	5	54	2009	12	96	2016	2
13	2004	7	55	2010	2	97	2016	6
14	2004	8	56	2010	3	98	2016	7
15	2004	12	57	2010	5	99	2016	9
16	2005	1	58	2010	6	100	2016	11
17	2005	2	59	2010	7	101	2016	12
18	2005	3	60	2010	10	102	2017	2
19	2005	4	61	2011	1	103	2017	3
20	2005	5	62	2011	4	104	2017	4
21	2005	6	63	2011	6	105	2017	6
22	2005	7	64	2011	7	106	2017	7
23	2005	8	65	2011	8	107	2017	9
24	2005	9	66	2011	9	108	2017	10
25	2005	10	67	2011	11	109	2017	11
26	2005	11	68	2012	1	110	2017	12
27	2005	12	69	2012	3	111	2018	1
28	2006	2	70	2012	5	112	2018	2
29	2006	3	71	2012	6	113	2018	3
30	2006	4	72	2012	7	114	2018	4
31	2006	5	73	2012	9	115	2018	5
32	2006	7	74	2012	11	116	2018	6
33	2006	8	75	2013	1	117	2018	7
34	2006	9	76	2013	4	118	2018	8
35	2006	11	77	2013	5	119	2018	9
36	2006	12	78	2013	6	120	2018	11
37	2007	1	79	2013	7	121	2019	2
38	2007	3	80	2013	9	122	2019	3
39	2007	5	81	2013	11	123	2019	6
40	2007	7	82	2014	2	124	2019	7
41	2007	9	83	2014	3	125	2019	10
42	2007	10	84	2014	5			