Welcome arrivals?
The ecology and distribution of range-shifting gilthead seabream *Sparus aurata* in UK inshore waters

Submitted by Jen Lewis, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences in January 2020.

In collaboration with the Centre for Environment Fisheries and Aquaculture Science

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Thesis abstract

This thesis brings together information from three different techniques to provide novel information on the ecology of range-shifting gilthead seabream *Sparus aurata* in the Northeast Atlantic. My chapters take a systematic look at the ecology of *S. aurata* around the UK, to help explain the drivers that are facilitating the northwards range-shift. First, I use species distribution modelling to investigate the relative importance of temperature on the current distribution of *S. aurata*, and how it is likely to affect the species range in the future. I find that northern populations of *S. aurata* appear to be occupying a very different thermal niche to those in the native range, indicating that either a niche shift has occurred, or that northern populations consist primarily of non-reproducing adults. Although this distinction has important implications for successful management of the species, I also find that climate change is likely to result in a further northward shift by 2050. This climate-driven shift is likely to facilitate reproducing populations in the English Channel and the Celtic Sea, assuming that suitable nursery areas are available. Second, I use otolith microchemistry to identify whether multiple sources are contributing to *S. aurata* populations in the English Channel. Using a multi-element approach, I find evidence for three sources contributing to *S. aurata* populations in the Channel that have shared otolith chemistry, and that these are temporally stable. These sources could relate to environments that are either spatially or temporally-discrete. I also find that, although there appears to be some mixing after spawning, the three different sources do not contribute equally to populations in the Channel. This mixing could occur during larval dispersal or subsequent adult movement. The multi-element approach allows speculation as to where these sources could be and provides a basis for future research into identifying specific spawning locations. Finally, I use stable isotopes to investigate the potential consequences of increasing *S. aurata* populations on European seabass *Dicentrarchus labrax,* by examining the potential for resource competition between juveniles. I find that although both species appear to be feeding on similar prey, they also appear to have different realised niches within the study system. This apparent resource partitioning could indicate a negative competitive effect or a positive indirect effect through indirect mutualism. To my knowledge, this is the first in-depth study of *S. aurata* in UK waters. Therefore, this thesis provides useful information that can help inform future management measures and conservation of this target species.

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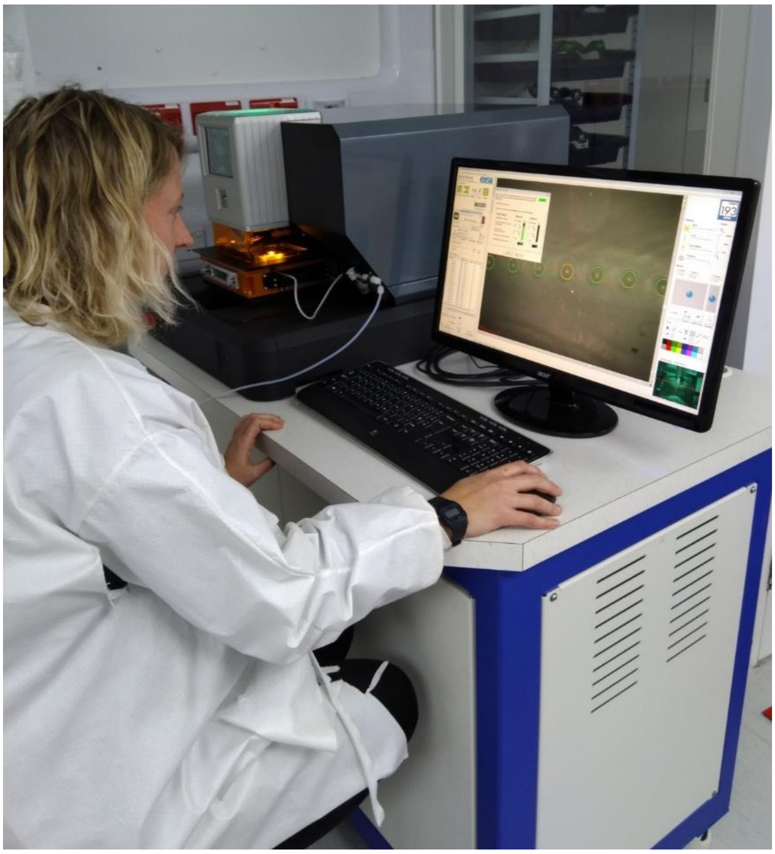

Author's Declaration

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Chapter 1

General introduction

1.1 Species distributions and range-shifts

Understanding the distribution of species across the globe is a fundamental part of ecology, and has been of interest to humans throughout our species history. Early human hunter-gatherers would have been acutely aware of the factors influencing where different plant and animal species would survive and reproduce (Lomolino, 2001). Spatial variation in these natural resources was likely one of the key drivers in the dispersal and colonisation of early humans across the world (Gamble, 1993; Irwin, 1992; Roebroeks, 2006). What these early humans were using to survive is a principle that we now call spatial autocorrelation, where environmental conditions are known to vary predictably over geographical gradients (Koenig, 1999). As a field of scientific study, we can trace this interest in species distributions, and their relationship with environmental conditions, as far back as Aristotle's 'natural state model'. Aristotle suggested a dynamic view of the earth to explain variation in life over space and time (Terrell, 2006). However, the more recent seminal works of Alfred Russel Wallace (A. R. Wallace, 1876) and Charles Darwin (Darwin, 1859) in the 1880s are the more commonly cited basis of what is now the modern field of 'biogeography', the study of relationships between geographic variation in biological diversity and the processes that have created them (Lomolino et al., 2017), or, why are species where they are, and not where they are not?

1.1.1 *Species distributions and fluctuating geographic conditions*

Species distributions are not static across space and time. The environmental conditions that dictate where a species can survive fluctuate spatially and temporally, from seconds to days, years, decades, and beyond (Gaston et al., 2009; Lehodey et al., 2006). For example, the distribution of marine species is linked to physical factors that vary spatially, particularly sea temperature, salinity, bathymetry and currents (Briggs, 1974; Dana, 1853; Ekman, 1953). Changes in species distributions, or 'species range-shifts', alter community interspecific interactions, such as competition (Svenning et al., 2014), predation (Zeidberg & Robison, 2007), parasitism (Ford & Smolowitz, 2007) and mutualism (Brooker et al., 2007), which can, in turn, have important implications for assemblage composition and ecosystem function (Dornelas et al., 2014). These range-shifts occur when a species tracks suitable environmental habitat through either a range expansion, contraction or relocation beyond its historical range

(Wallingford et al., 2020). Accumulating evidence demonstrates that many species range-shifts are currently occurring, in response to changes in biotic and abiotic factors (Chen et al., 2011; Hickling et al., 2006; Parmesan & Yohe, 2003; Pinsky et al., 2020). Therefore, understanding the extent of species current ranges and how and why they are shifting, is fundamental for successful conservation and management (Pinsky et al., 2018).

Species range boundaries can change at either the leading or trailing edge of their distribution. Leading-edge range expansions occur when species move into new regions that have favourable conditions. For example, over the previous 20-140 years, over half of all species have exhibited quantifiable changes in either their distribution or phenology, correlated with climate change (Chen et al., 2011; Parmesan & Yohe, 2003). On the other hand, trailing edge range contractions occur when a species becomes locally-extinct in part of its range. For example, the marine macroalga *Fucus vesiculosis* has recently undergone a range contraction of approximately 1250 km, a loss of around 23% of the species' range in the Northeast Atlantic (Assis et al., 2018a; Nicastro et al., 2013). The range contraction of *F. vesiculosis* is thought to be in response to warming sea temperatures and has negative consequences for the genetic diversity of the species. Trailing edge contractions are rarer than range expansions, however, this could be an artefact of it being harder to confirm that a species is no longer present in an area than if it has arrived in a new area. Anthropogenic climate change can explain a lot of the patterns observed in present-day species range-shifts. However, various other biotic and abiotic factors also affect species distributions.

1.2 Climate change as a driver of species range-shifts

The global climate is warming, with an observed linear trend of 0.85˚C between 1880-2012 (IPCC, 2014). Oceans are predicted to rise by 2-3˚C by the turn of the century (IPCC, 2014), a trend that is accelerating (Cheng et al., 2019). Climate change, whether anthropogenic or as part of a natural cycle, is thought to be the primary driver for patterns observed in present-day species range-shifts, from polar terrestrial to tropical marine environments (Chen et al., 2011; Parmesan & Yohe, 2003; Perry et al., 2005; Poloczanska et al., 2013; Thomas, 2010; Walther et al., 2002). Climate change has various effects, but changes in temperature appear to be the main driver for species range-shifts (Chen et al., 2011; Sunday et al., 2012). Temperature changes directly affect protein structure and cellular processes, such as metabolism (Clarke & Fraser, 2004).

The main evidence that range-shifts are due to climate change is that many species are showing highly significant, non-random general patterns of movement that correlate with the direction in which isotherms are moving (Chen et al., 2011). For example, terrestrial species are shifting their ranges to higher latitudes at a median rate of 16.9 kilometres per decade, and to higher altitudes at a rate of 11 metres a decade (Chen et al., 2011). In the marine environment, nearly two-thirds of species demonstrate a poleward shift in latitude, a shift in-depth, or both (Beare et al., 2004; Perry et al., 2005; Poloczanska et al., 2016; Rutterford et al., 2015). Climate velocity is the rate and direction in which isotherms move, and can explain some of the variation observed in species range-shifts that have not been in a poleward direction (Pinsky et al., 2020).

1.2.1 *Non-anthropogenic climate change evidence*

Species range-shifts as a response to a changing climate are not unprecedented (Fields et al., 1993). For example, climate warming led to the end-Permian mass extinction (approximately 252 million years ago (MYA)), that caused an estimated 95% of marine speices and 70% of terrestrial species to become extinct (Penn et al., 2018; Sahney & Benton, 2008). Species extinctions recorded during this time were clustered around taxa from higher latitudes, suggesting that they ran out of thermally suitable habitat (Penn et al., 2018). During the Late Ordovician (approximately 444 MYA), evidence suggests extreme climate cooling caused a mass extinction event (Finnegan et al., 2012). Species extinctions recorded during this time occurred globally but were clustered around taxa from lower latitudes, again suggesting that a lack of thermally suitable habitat was available for species to colonise. There is also evidence for species undergoing range expansions and contractions during the Quaternary period, in response to changes in temperature (Hewitt, 1996; Taberlet et al., 1998). During the Quaternary period, species extinctions were more common in northern populations in cooler times, and leading-edge range expansions in a poleward direction occurred in response to climate warming (Hewitt, 1996).

1.3 Sensitivity of marine species to climate change

Marine and terrestrial species exhibit similar response patterns to climate change. However, research suggests that in general, marine species are more responsive to warming than terrestrial species (Pinsky et al., 2019, 2020; Sorte et al., 2010; Sunday et al., 2012). Pinsky *et al.* (2019) used a global dataset to test how likely marine species were to become locally-extinct compared to terrestrial species. Extirpations were twice as common for marine species (56%) than terrestrial (27%) when species live near the upper thermal tolerance limits. Sunday et al. (2012) tested how well the observed latitudinal range limits of terrestrial and marine species match the areas that fall within their thermal tolerances. Terrestrial ectotherms do not fill their full potential latitudinal range, whereas the latitudinal ranges of marine ectotherms closely match their physiological limits (Sunday et al., 2012).

One way that terrestrial species can avoid warming temperatures is through taking refuge in locally variable habitats, making use of variation in microclimate (Maclean et al., 2015; Suggitt et al., 2018). Outside of the intertidal environment, thermal gradients in the ocean are generally weaker than they are on land (Burrows et al., 2011), and marine species are less likely than terrestrial to be able to access microclimate refuges. The daily and seasonal fluctuations in ocean temperature are also much smaller than those on land (Pinsky et al., 2020). This smaller amount of temperature variation has resulted in many marine species evolving narrower ranges of thermal tolerance over time, compared to terrestrial species (Sunday et al., 2011). For example, the thermal safety margins (upper and lower thermal tolerance limits) for marine species are around 80% as wide as margins for terrestrial species (Pinsky et al., 2019). The higher sensitivity of marine species to temperature change results in range contractions being more common in the ocean as on land (Pinsky et al., 2019).

Temperature in the sea is also tightly negatively correlated with dissolved oxygen availability (Pörtner & Knust, 2007). According to the oxygen- and capacity-limited thermal tolerance hypothesis, oxygen demand increases when a species is outside its thermal optimum (Pörtner, 2001). Warmer waters also increase metabolic rates, which in turn increase oxygen demand (Deutsch et al., 2015). Therefore, the combined effects of warming seas and a decrease in oxygen supply are likely to impact the ability of species to undergo a range-shift, in comparison to temperature alone.

1.3.1 *Dispersal capabilities of marine and terrestrial*

In general, marine species have dispersal capabilities far greater than terrestrial species (Kinlan & Gaines, 2003). Many marine species have a life cycle, including a pelagic larval stage, that can travel great distances on ocean currents before settling (Cowen et al., 2000; Gillanders et al., 2003). In terms of adult movement, buoyancy in water also reduces the amount of energy needed to swim the same distance as it would travel on land (Schmidt-Nielsen, 1972).

1.3.2 *Consequences of high sensitivity and dispersal ability*

The high physiological sensitivity of marine species to temperature and oxygen variation, combined with their strong ability to arrive at and colonise new areas (either as larvae or adults) suggest that range-shifts are a key way that marine species adapt to environmental change (Sunday et al., 2011). Marine species can respond faster and disperse over greater distances compared to terrestrial, but only if suitable habitat is available (Pinsky et al., 2019). Therefore, marine species that are living near the upper limits of thermal tolerance are vulnerable to local extirpation (Wiens, 2016), which could have consequences for ecosystem functioning and services (Luck et al., 2003; Pinsky et al., 2019).

1.3.3 *Climate change and phenology*

One way that changes in thermal habitat can affect species ranges is through changes in phenology, or the timing of seasonal life cycle events (G. Walther et al., 2002). The timing of these life events can have important implications for population success and colonisation of new areas. For example, in the English Channel, the timing of spring spawning in marine teleost fish is dependent on sea temperatures in the previous November and December, whereas for summer spawning fish it is dependent on March temperatures (Genner et al., 2010). Changes in phenology have important effects on ecosystem function and population success, as community members respond differently to environmental change (Edwards & Richardson, 2004). Decoupling of phenological relationships within a community can subsequently affect trophic interactions, food web dynamics and ecosystem function (Durant et al., 2007).

1.4 Species traits as predictors of range-shifts

Not all species can undergo a range-shift in response to a change in environment. Biotic characteristics and species traits can play an important role in determining a species range-shift capacity in response to environmental change (Burrows et al., 2011; Estrada et al., 2016, 2017; MacLean & Beissinger, 2017; Molinos et al., 2016; Sunday et al., 2015). Understanding the specific traits that facilitate or limit range-shifts can aid predictions and provide important information on species for which distribution data are limited.

1.4.1 *Terrestrial traits*

Estrada *et al.* (2016) reviewed the usefulness of species traits that affect the range-shift processes of emigration, movement, establishment and proliferation in terrestrial species. Ecological generalism had a positive effect in most studies, suggesting that species that can adapt to a variety of resources are likely to have high range-shift capacity. Species movement ability had a positive effect in fewer than half of the studies included in the review, suggesting that other processes could also have an important role. Species reproductive strategy only had a positive effect in a quarter of all cases studied, suggesting possible trade-offs with other traits, for example, competitive ability or persistence in unfavourable conditions (Estrada et al., 2016; Grime, 1977). The usefulness of species traits in range-shifts was also tested in European birds and mammals, by investigating the extent to which species fill climatically-suitable ranges (Estrada et al., 2017). Species traits related to establishment and proliferation processes significantly affected the ability of bird and mammal species to fill their ranges, with resource generalism (birds and mammals), early-reproduction (mammals), and high annual fecundity (birds) resulting in the greatest climatic range filling (Estrada et al., 2017).

1.4.2 *Marine traits*

Although not as well-studied, traits appear to have stronger predictive effects on range-shift capacity for marine species, compared to terrestrial (Luiz et al., 2012; Sunday et al., 2015). The sensitivity of marine species to environmental change and faster rate in which range-shifts occur in the marine environment (compared to terrestrial) allows relatively easy detection of shifts and gives greater analytical power for investigating interspecific variation (Sunday et al., 2015). As with terrestrial species, Sunday et al. (2015) found that resource generalism was a strong predictor of range-shift capacity, allowing species to find suitable resources in new locations. Movement ability, both through pelagic larval dispersal and adult movement, was also important, although directed movement by adults is a stronger predictive trait for species ranges (Brooker et al., 2007; Luiz et al., 2012; Sunday et al., 2015). The latitudinal range size of species also increases range-shift capacity, likely because a species with a larger latitudinal range will experience a broader range of environmental conditions, and will, therefore, have a greater capacity to colonise new areas (Hengeveld, 1994). Larger range sizes can also be associated with greater population abundance, and therefore propagule production, which could read to high range-shift capacity (Feary et al., 2014).

1.5 Non-climatic drivers of species range-shifts

1.5.1 *Changes in habitat and prey availability*

Interspecies variation in the direction and speed of range-shift capacity suggests that climate change is not the only driver of species range-shifts. For example, changes in habitat and prey availability can also affect species ranges. The urbanisation of terrestrial landscapes has resulted in a winter range expansion of more than 700 km by Anna’s hummingbird *Calypte anna* in North America (Greig et al., 2017). The successful range expansion of *C. anna* is primarily attributed to people providing supplementary food over winter, allowing the species to colonise cooler areas. Similarly, the Virginia opossum *Didelphis virginiana* has adapted to exploit human resources in urban environments that would not naturally be able to support populations (Kanda et al., 2009). The colonisation of new urban habitat is likely to continue, as *D. virginiana* populations from the occupied urban habitat locate new areas. The spread of invertebrate species in the marine environment has also been attributed to artificial hard structures, such as coastal defences or shipwrecks (Firth et al., 2015). Sessile species can colonise these structures, and if reproducing populations settle their larvae can disperse and settle outside their native range (Bishop et al., 2017). Another part of habitat suitability is prey availability. For a species to survive in an area, there must be enough prey to support the population. Therefore, changes in prey availability can also cause species range-shifts (Both, 2010; Durant et al., 2007). Artificial reef assemblages also provide an increase in prey that encourages predatory species to colonise the new habitat (Ross et al., 2016). Changes in prey availability can be an indirect effect of temperature causing either predator species range-shifts, changes in phenology (Genner et al., 2004), or another predator range-shift increasing demand on a prey source.

1.5.2 *Human exploitation and changes in abundance*

Human exploitation of species can also cause range-shifts. For example, hunters and fishers affect population densities by preferentially selecting the largest and oldest organisms (Darimont et al., 2009; Longhurst, 2006; Uusi-Heikkilä et al., 2015). Many species populations are spatially segregated by size (Ebenman & Persson, 1988), so this can result in range contractions if targeted individuals are at the edge of a species distribution (Fenburg & Roy, 2008). Fluctuations in population sizes can also result in species range-shifts. For example, marine fish species occupy inferior habitats when population numbers are high, moving out of these areas into the highest quality available if population densities decrease (MacCall, 1990; Quinn & Deriso, 1999).

1.5.3 *Adaptation and evolution*

The ability of a species to adjust its phenotype in response to environmental change is an important factor in range-shift capacity (A. Gonzalez et al., 2013; Reusch, 2014). The rate of anthropogenic climate change is imposing strong selective pressure on populations, forcing rapid adaptation or evolution to novel environments either through phenotypic plasticity or genetic adaptation (Gonzalez et al., 2013). The extent to which most species can do this is not known, and is logistically difficult to study, given that the genetic underpinnings of most traits are yet to be determined (Merilä & Hendry, 2014).

1.6 Impacts of marine species range-shifts

1.6.1 *Positive impacts*

Ability to colonise new habitats is beneficial for the survival of the range-shifting species, as it allows populations to move in response to environmental change (Hoegh-Guldberg et al., 2008). Species that run out of suitable habitat or are unable to colonise new areas are vulnerable to extinction (Thomas et al., 2004, 2006; Travis, 2003).

The arrival of new species can also benefit local economies. For example, billions of people worldwide rely on marine species for food, profits and employment (Costello et al., 2016). In terms of fisheries, commercial fishers often view range-expanding species as new exploitable resources that can potentially benefit the local economy. Anglers also enjoy catching new species, and recreational fisheries are valued for economic, cultural and social reasons (Elmer et al., 2017; Hyder et al., 2017; Townhill et al., 2019). However, range contractions of fished species distributions could also negatively impact fishing communities, depending on the flexibility of the fishing community to adapt to change in the species assemblage (L. A. Rogers et al., 2019).

1.6.2 *Negative impacts*

Introduced species have been shown to become invasive and have negative consequences across the globe (Ruiz et al., 1997; Williamson & Fitter, 1996). However, it is not yet clear whether range-shifting species have the same negative consequences (Simberloff et al., 2012; Sorte et al., 2010). Although range-expanding species are less likely to incur novel species interactions compared to introduced or invasive species, their arrival can still have negative biotic impacts on the recipient ecological communities (Sorte et al., 2010). One negative consequence of a species range-shift is predation on native species. For example, the Humboldt squid *Dosidicus gigas* has undergone a range expansion in the eastern North Pacific, linked to changes in oceanographic conditions and declines of other species that rely on similar prey (Zeidberg & Robison, 2007). The range expansion and increase in populations of *D. gigas* have resulted in a decline of Pacific hake *Merluccius productus,* an important commercial species that is a key prey source for *D. gigas* (Zeidberg & Robison, 2007). The spread of disease and parasites in response to environmental change is also a concern (Harvell et al., 1999). For example, in the 1990s, a warming episode correlated with outbreaks of the parasite *Perkinsus marinus* in the Eastern oyster *Crassostrea virginica* (Cook et al., 1998; Ford & Smolowitz, 2007). *P. marinus* had not been recorded previously in the region, and its range-shift caused disease outbreaks and mortality in oyster beds across a 500 km range in the northeastern United States (Ford & Smolowitz, 2007). In addition to predation and disease, negative impacts could include increased resource competition between range-shifting species and native species. For example, in the Northeast Atlantic, range-shifting warm-water kelp *Laminaria ochroleuca* populations are increasing and outcompeting native cold-water temperate species for habitat resource (Pessarrodona et al., 2019). The impacts of an increase in *L. ochroleuca* populations is already having ecosystem-wide affects, including supporting a greater diversity of invertebrates, despite being taxinomically-related and morphologically similar to cold-water species. In the Baltic Sea, range-expanding roach *Rutilus rutilus* has been shown to have high levels of trophic overlap with native flounder *Platichthys flesus* (Westerbom et al., 2018). Both *R. rutilus* and *P. flesus* have a similar diet, and competition for resource is high when prey sources are limited. However, it is also possible that population dynamics counteract negative competitive effects in certain cases, for example, indirect mutualism, where the arrival of a new predator reduces competition at lower trophic levels between prey sources, leading to positive effects on other prey sources and their predators (Dodson, 1970; Sanders & van Veen, 2012).

The consequences of range-shifting species can scale up to the whole ecosystem, altering community dynamics in new areas. For example, the range-shift of a tropical herbivorous fish in Eastern Australia, as a result of warming sea temperatures, has been linked to the destruction of kelp forests (Vergés et al., 2016). The destruction of kelp habitats commonly results in sea urchin barrens, which are characterised by low primary productivity and low food web complexity, relative to kelp communities (Filbee-Dexter & Scheibling, 2014).

Species range-shifts can also lead to social conflict, as a result of shifting natural resources. For example, shifting fisheries stocks can cause international conflict and governance disputes (K. A. Miller et al., 2013; Pinsky et al., 2018). Throughout the twentieth century, there were a series of confrontations between the United Kingdom and Iceland on fishing rights for Atlantic cod *Gadus morhua* in the North Atlantic (Engelhard et al., 2014; Mitchell, 1976). The outcome of these disputes resulted in British fishing communities losing access to rich fishing areas and hundreds of jobs being lost (Steinsson, 2016). A similar case occurred in 2007 when the Northeast Atlantic mackerel *Scomber scombrus* became rapidly more abundant in Atlantic waters. The increased resource availability of *S. scombrus* triggered conflict over the allocation of fishing quotas between the European Union, Norway, Iceland and the Faroe Islands (Spijkers & Boonstra, 2017). To determine effective ocean governance strategies, it is therefore essential to understand species range-shift dynamics (Pinsky et al., 2018)

1.7 Knowledge gaps

Although there are strong links between climate change and species range-shifts, there are other factors that can affect the success and speed of a species colonising a new area, and how far species can spread. Understanding the relative ability of a species to respond to different drivers, and subsequent impacts of species range-shifts are key to successful conservation and management. Key questions for investigating species' range-shifts are:

How important is temperature in defining a current and species range? This provides useful information on whether climate change is likely to cause future range-shifts.

What are the source and sink population dynamics of range-expanding species? Source populations occur in areas of good habitat quality, with sink populations occurring in a lower quality habitat that would not persist without immigration from source populations (Dias, 1996). Therefore, sink populations are likely to occur at the edge of species ranges, where the habitat is less optimal. A change from a sink to a source population can be an indication that a species is setting into a new part of its range (Kanda et al., 2009), as reproducing populations grow. Understanding these sink-source dynamics is especially important in species that are commercially exploited, such as marine fish. The distribution of source and sink populations has important implications for management at a national and international level (Pinsky et al., 2018).

What effects are range-expanding species having on receiving communities? The arrival of a new species can cause increased competition on shared resources. Changes in the composition and dynamics of species assembleges can also affect ecosytem function. Therefore, this information is essential for successful conservation.

1.8 Gilthead bream in the Northeast Atlantic as a study system

1.8.1 *Climate change and the Western English Channel*

The Western English Channel, in the Northwest Atlantic, is an ideal area to study the effect of climate warming on species range-shifts. The Northeast Atlantic is one of the fastest-warming ocean basins (A. J. Southward et al., 1995), with mean annual temperatures rising at a rate of 0.1-0.5˚C per decade (Dye et al., 2013), and coastal waters around the UK are expected to increase by over 3˚C by the end of the century (S. L. Hughes et al., 2017). Sea temperatures in the Channel have been rising since the 1980s, with a mean increase in 1˚C since 1990 (Alan J. Southward et al., 2004). This increase in temperature is a consequence of both anthropogenic climate change, and natural climate cycles such as the Atlantic multidecadal oscillation (Dye et al., 2013; Knight et al., 2006; McLean et al., 2019).

Over the past century, variations in species present in the Channel correlate with fluctuations in temperature (Hawkins et al., 2003). Compared to the present day, previous periods of relatively warm temperatures between 1920-50 increased the abundance of species typically associated with warmer water. In the 1960s, following a cooling period, cold-water species became more abundant (Hawkins et al., 2003). Current warming trends correlate with several ongoing northward range-shifts in marine species in the Northwest Atlantic (Rutterford et al., 2015; Simpson et al., 2011), for example, cod *Gadus morhua* (Drinkwater, 2005), the common sole *Solea solea* (Perry et al., 2005), European seabass *Dicentrarchus labrax* (Cardoso et al., 2015), Atlantic mackerel *Scomber scombrus* (Bruge et al., 2016) and copepod crustaceans (Beaugrand et al., 2002).

1.8.2 *Gilthead seabream*

Another species that has been undergoing an apparent range-shift in the Northeast Atlantic is the gilthead seabream *Sparus aurata,* a high value commercial and recreational target fish found throughout the Mediterranean and the Atlantic coasts of Spain, France and Portugal. Over recent decades *S. aurata* has started to appear more frequently in the Western English Channel and Celtic Sea (Craig et al., 2008; Davis, 1988; Fahy et al., 2005). In northern France, *S. aurata* landings increased from 11 to 146 tons between 2002 and 2014 (Avignon, 2017), and a similar pattern is observed in the UK (MMO, 2015). As *S. aurata* predominantly has a warm-temperate distribution, the primary reason for this range-shift is likely warming sea temperatures (Coscia et al., 2012).

Sparus aurata is a protandrous hermaphrodite with a pelagic life cycle that includes spatially-distinct spawning and nursery areas (Fig 1.1), connected by the pelagic larval stage that lasts between 50-100 days in the Mediterranean (Chaoui et al., 2006; Franchini et al., 2012; Lett et al., 2019; Morretti, 1999). In the spring, *S. aurata* larvae settle in coastal nursery areas, where the relatively warm shallow waters provide refuge from cooler waters and suitable prey over the summer months (Avignon, 2017; Tournois et al., 2017). For the first few years of life, *S. aurata* are generally dependent on these nursery areas for survival (Lasserre, 1976; Mercier et al., 2012; Morais et al., 2017; Tournois et al., 2017), although some individuals can grow to maturity in fully marine conditions (Mercier et al., 2012). Across *S. aurata's* range, mature fish demonstrate seasonal migrations, generally spending summer months in coastal waters, making the most of productive foraging areas. During the cooler winter months, adult fish move offshore into more suitable thermal habitat and spawning grounds (Avignon, 2017; Mercier et al., 2012).

Specific traits make *S. aurata* a prime candidate species for range-shifts. *Sparus aurata* are resource generalists, able to adapt their diet to available prey resources in newly colonised areas (Avignon, 2017; Avignon et al., 2017). For example, a study that investigated the diet of adult *S. aurata* from across the latitudinal range found significant differences between populations (Avignon et al., 2017). In some areas, like in the Bay of Biscay, there is evidence for *S. aurata* populations to have a relatively low level of dietary trophic diversity, whereas in Brittany (France) populations had high trophic diversity. Avignon *et al.* (2017) suggested that these diet variations are a response to differing levels of available prey species across the area of study. Range-shifting populations of *S. aurata* have also adapted to new environments by using estuaries as nursery areas, instead of the saline lagoons upon which Mediterranean juveniles depend for development (Avignon, 2017). Avignon (2017) used otolith microchemistry to investigate populations of *S. aurata* across its latitudinal range, from Bournemouth (UK) to the Mediterranean. The values observed for different element concentrations suggest that fish from all areas display evidence for seasonal migrations between coastal and marine environments, and the adaptive use of estuaries as nursery areas during the first year of life, in an area where lagoon habitat is generally absent. However, as yet the nursery areas and spawning grounds of northern populations of *S. aurata* have yet to be identified (Avignon, 2017).

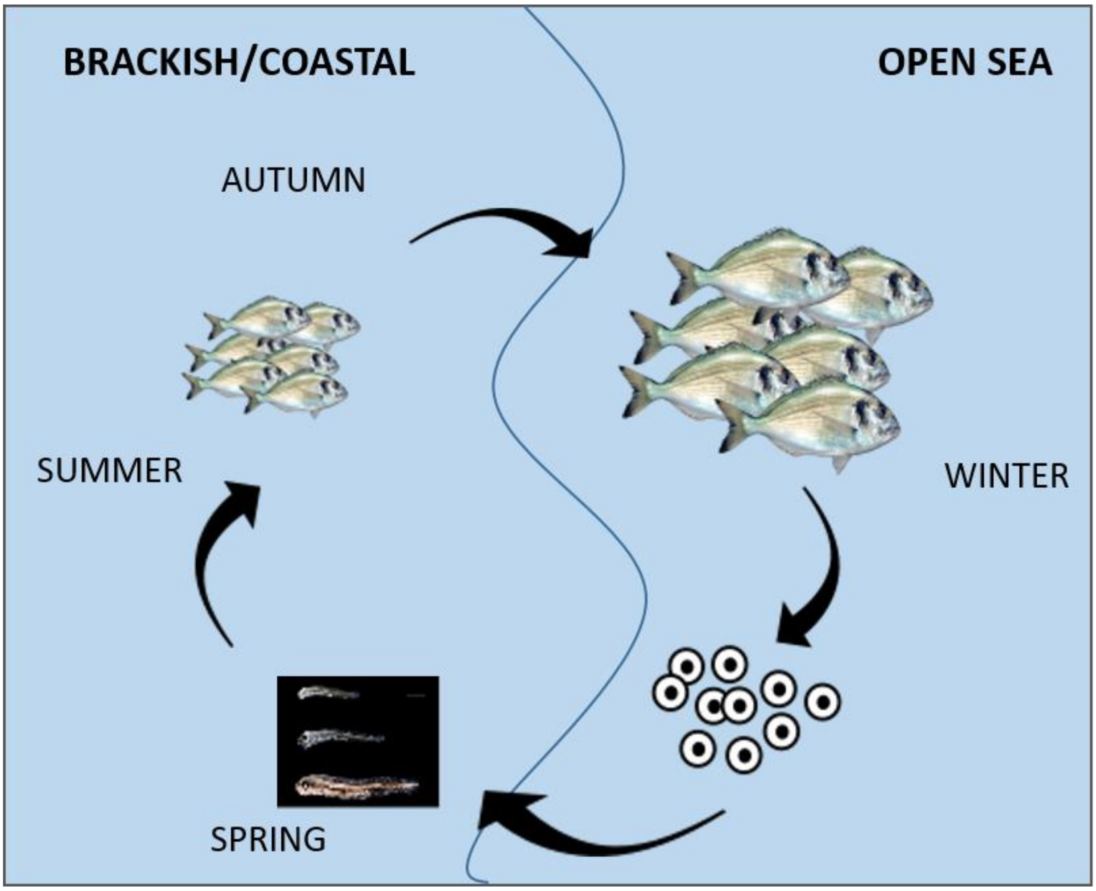


Figure 1.1 Life cycle of gilthead seabream *Sparus aurata* showing the pelagic larval phase and seasonal migrations between marine and coastal waters

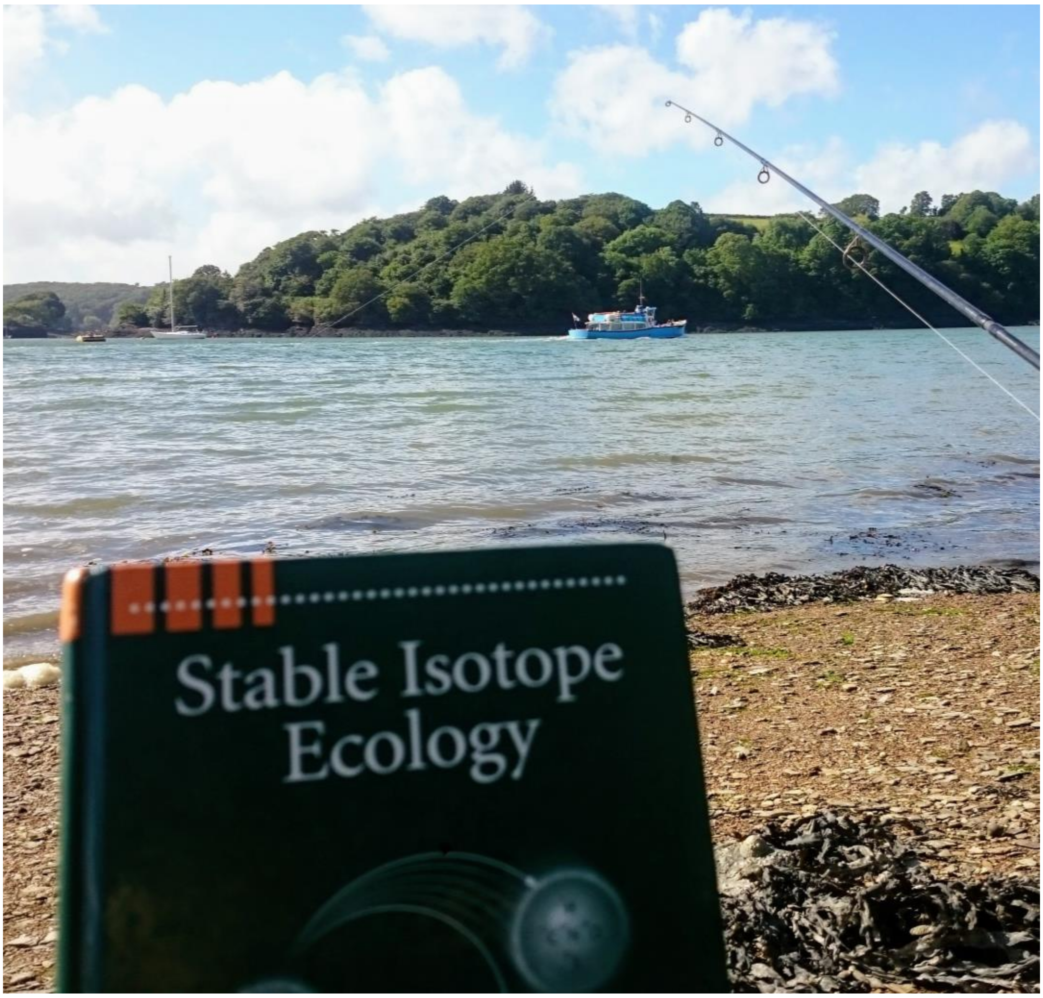
1.8.3 *Population structure*

Current knowledge of the stock structure of Atlantic *S. aurata* populations is limited. Findings from population genetics suggest there is significant spatial population structure within the Atlantic, with populations in the Celtic Sea of a relatively recent origin (Coscia et al., 2012). However, Coscia *et al.* (2012) only found evidence for spawning populations along the Atlantic coast of Spain, Portugal and France up to the Bay of Biscay. If accurate, this suggests that any populations in the English Channel and the Celtic Sea are likely to be more of a sink population rather than a source. A more recent study on the population genetics of *S aurata* found evidence for a relatively rapid population expansion for Irish and French populations, with shared alleles between populations from the Mediterranean to the Channel suggesting several waves of step-by-step colonisers from the south (Avignon, 2017). The observed general lack of population structure is reflective of a recent colonisation; however, Avignon (2017) did differentiate between the northernmost populations of *S aurata* and Mediterranean populations. This differentiation between north and south populations of *S. aurata* suggests limited mixing of individuals on a large spatial scale.

1.8.4 *Negative impacts*

While the arrival of a high-value commercial species has potential economic benefits, there are also possible negative consequences. For example, a recent rapid increase in *S. aurata* numbers in the Adriatic Sea, as a result of rising sea temperatures and fish farm escapees that have become specialised in feeding on bivalves (Glamuzina et al., 2014). This rapid increase in population caused the collapse of several local shellfish farms, which could be a cause for concern for UK shellfish aquaculture. Confirmed sightings of *S. aurata* have also been reported in the Gulf of California, far away from the natural range (Balart et al., 2009), thought to be as a result of aquaculture escapees colonising new areas. These reported colonisation events demonstrate *S. aurata’s* ability to inhabit new areas easily and warrant further study into the factors affecting range-shifts across the species range. The species traits, potential implications, and knowledge gaps make *S. aurata* an excellent species to use as a case study for range expansion in the Northeast Atlantic.


GILTHEAD
SEA BREAM
HOW TO CATCH THEM
FRANCISCO SUAY
TRANSLATED BY JOHN LANGRIDGE


Stable Isotope
Ecology

1.9 Thesis outline

I use gilthead bream *Sparus aurata* as a case study to address specific knowledge gaps for range-expanding species, in response to climate change and other drivers. I combine three different methods in an integrative approach, asking questions about *S. aurata's* current and future distribution, the likelihood of local source populations, and the potential impacts of a further range-shift on native species. I have prepared each chapter as a standalone manuscript, for future submission to journals.

In *Chapter 2,* I identify the thermal niche for both the native and expanded range of *S. aurata* using species distribution modelling. By modelling the thermal niche of the species, I am able to make inferences about the effect of temperature on the latitidunal distribution of *S. aurata,* and whether northern populations have undergone a niche shift as a result of climate change. I also project the distribution of *S. aurata* into the future under different climate change scenarios, to identify the liklihood of climate change causing a further range-shift.

In *Chapter 3,* I investigate whether there could be multiple sources contributing to northern populations of *S. aurata.* I use otolith microchemistry to identify groups of individual fish that have shared otoloith chemistry, for the section of the otolith relating to early larval life. I use a multi-element approach that allows me to make inferences about the potential environmental conditions experienced by these larvae, and the relative contributions of different sources to northern populations.

In *Chapter 4,* I explore how *S. aurata's* range-shift could affect a native species of fish (European seabass *Dicentrarchus labrax*) that occupies a similar ecological niche. I use a stable isotope approach to investigate the potential for resource partitioning between the two coexisting species, and whether the consequences of a further range-shift could be positive or negative.

As far as I am aware, this thesis is the first in-depth ecological exploration into the northwards expansion of *S. aurata* in UK waters. Therefore, this thesis provides useful information that can help inform future management measures and conservation of this target species.

Chapter 2

The influence of temperature on the present and predicted future geographic distribution of gilthead seabream *Sparus aurata*

2.1 Abstract

Species range-shifts can have economic and ecological consequences. Gilthead seabream *Sparus aurata* has been undergoing an apparent poleward range-shift in the Northeast Atlantic, with both commercial and recreational fisheries reporting increased catches around the UK, Irish and northern French coasts. Juveniles have also been captured in surveys around the UK and Ireland, suggesting that *S. aurata* could be reproducing further north than previously thought. The Northeast Atlantic is currently experiencing an increase in temperature, as a result of anthropogenic climate change. Temperature limits the spatial distribution of marine ectotherms, suggesting that climate change is likely to be a driver for the observed range-shift of *S. aurata.* With temperatures in the Northeast Atlantic predicted to continue increasing, a continued northward shift in *S. aurata* populations is likely. Here, we use species distribution modelling to investigate the relative influence of temperature on the native and expanded range of *S. aurata.* Our results suggest that winter temperatures are limiting the current northern distribution, likely inhibiting juvenile and larval survival. We also find that northern *S. aurata* populations are occupying a different thermal niche, compared to those in the native range. This observed difference could either indicate a niche shift, as a result of local adaptation, or that northern populations consist primarily of non-reproducing adults. Further work is needed to identify whether there is are latitudinal differences in thermal tolerance, or if there is evidence for spawning in northern *S. aurata* populations. Finally, we investigate the effect of future climate change on the distribution of *S. aurata*. We find evidence that a further northwards range expansion and southern range contraction is likely in all scenarios. This is likely to facilitate reproducing populations of *S. aurata* in Northeast Atlantic in the near future.

2.2 Introduction

Gilthead seabream *Sparus aurata* (Linnaeus 1758) has been undergoing an apparent range-shift into the English Channel and Celtic Sea (Coscia et al., 2012). Adults are being captured increasingly frequently by commercial and recreational fishers in the UK, Irish and northern French coasts. In northern France, *S. aurata* landings increased from 11 to 146 tons between 2002 and 2014 (Avignon, 2017), and we see a similar pattern in the UK (MMO, 2015). Reproducing *S. aurata* populations are primarily found in the Mediterranean but are also known to occur in the Atlantic as far north as the Bay of Biscay (Coscia et al., 2012). Recently settled juveniles (0-group fish) are present in surveys in the UK and Ireland since 1999 (Craig et al., 2008; Fahy et al., 2005), which could mean the species is breeding even further north than previously thought.

As well as being a valuable commercial target species, *S. aurata* is also of interest to recreational anglers. Recreational fisheries have economic, cultural and social value (Elmer et al., 2017). Recent regulations that limit recreational catches of European seabass *Dicentrarchus labrax* have encouraged sea anglers to identify other similar target species, such as *S. aurata* (Council Regulation (EU) 2019/124, 2019). There is already evidence for anglers targeting *S. aurata* in Ireland and south-west UK (Quigley, 2015), and the species is likely to be of significant benefit to the UK angling industry if populations continue to increase (Lawrence, 2005; Rees et al., 2010). However, there is also evidence for negative consequences when populations of *S. aurata* increase quickly in new areas. For example, in the Adriatic Sea, fast-growing populations have become specialised at feeding on bivalves and decimated mussel farms (Glamuzina et al., 2014). This is a potential concern for shellfish aquaculture industries in the English Channel (Avignon, 2017). Range-shifting species also potentially change the dynamics of food webs, resulting in increased competition for trophic or habitat resources (S. T. Ross, 1986; Sharma et al., 2007). For example, in the Baltic Sea, range-expanding roach *Rutilus rutilus* has been shown to have high levels of trophic overlap with native flounder *Platichthys flesus* (Westerbom et al., 2018), leading to competition when prey sources are limited. Regardless of whether the consequences are positive or negative, understanding the drivers and extent of *S. aurata’s* range expansion, and how it is likely to change in the future, is fundamental to the sustainable management of the species and the surrounding ecosystem.

2.2.1 *Climate change as a driver*

Climate change could be a driver for *S. aurata's* range expansion (Poloczanska et al., 2016). Many marine range expansions in the Northeast Atlantic are attributed to changes in temperature (Engelhard et al., 2014; Perry et al., 2005; Rutterford et al., 2015). Marine species are likely to shift their ranges as sea temperatures warm for multiple reasons. The geographic ranges of marine species tend to match closely with the species' physiological thermal limits (Sunday et al., 2012). Marine ectotherms, in particular, cannot regulate their temperature, so cannot persist in locations outside their thermal tolerances. Species with a long-lived pelagic larval stage also have high dispersal capabilities, which means they can rapidly colonise suitable areas outside of their native range (Pinsky et al., 2020). Species with strong adult swimming abilities can move more rapidly into newly available thermal habitats (Sunday et al., 2015). More generalist species that can be flexible on diet and habitat are also much more likely to thrive in new areas (Sunday et al., 2015).

2.2.2 *Species traits*

The life cycle, generalist traits and thermal tolerance of *S. aurata* make it a prime candidate for climate-driven range-shifts (Avignon et al., 2017; Early & Sax, 2014; Sunday et al., 2015) (Figure 1.1). *S. aurata* is a euryhaline sparid found in a variety of marine habitats. The species is tolerant to a wide range of salinities (Audouin, 1962) but its latitudinal distribution appears to be limited by thermal tolerance (Gallardo et al., 2003; Hattab et al., 2014; Heather et al., 2018; Ibarz et al., 2010). Adults are known to suffer from a condition known as "winter syndrome" at temperatures of 15˚C and below, which affects oxygen consumption, immune system, growth and metabolism, and temperatures below 5 ˚C are lethal to the species (Ibarz et al., 2010). Therefore, it is likely that winter temperature is limiting the species northern geographic range. There are also negative consequences from temperatures that are too high. Evidence suggests that the growth rate of individuals in the Mediterranean will be negatively affected by increased sea temperatures as a result of climate change (Heather et al., 2018). Under future climate scenarios projections in the Mediterranean, *S. aurata* is forecast to lose 17% of its range by 2050 and 57% by 2100 (Hattab et al., 2014); however, Hattab *et al.* (2014) only studied the Mediterranean area and did not investigate where climatically-suitable habitat may become available in the future. Sea temperatures in the Northeast Atlantic are increasing, due to climate change (Dye et al., 2013; IPCC, 2014; Alan J. Southward et al., 2004), so it is very possible that the species' northern range edge has expanded and will continue to do so.

2.2.3 *Local adaptation*

There is also a possibility that the observed range expansion is not yet a result of climate change. Evolutionary adaptation at the edge of species distributions can alter species' ecological niches, allowing settlement in new habitats that are initially poor for survival and reproduction (Kawecki, 2008). A study that investigated the population genetics of *S. aurata* from the Atlantic and the Celtic Sea found that populations in the Celtic Sea had an absence of unique haplotypes, suggest that they are of a relatively recent origin, likely colonised from further south (Coscia et al., 2012). A more recent study on the population genetics of *S aurata* observed also observed a general lack of population structure across Atlantic and Mediterranean populations, although there was some differentiation between the most northerly and most southerly populations sampled (Avignon, 2017). Coscia et al. (2012) did find evidence for higher haplotype and nucleotide diversity in the Irish populations, suggesting that there could be scope for local adaptation at the edge of *S. aurata's* range (Excoffier & Ray, 2008), potentially allowing the species to survive in novel habitats (Coscia et al., 2012). For there to be observable genetic differences in northerly populations of *S. aurata*, there has to be some form of selective pressure on populations, potentially from exposure to novel environments. Therefore, it is possible that the northerly populations of *S. aurata* have undergone a niche expansion, allowing them to inhabit areas that are different from their native niche.

2.2.4 *Effects of temperature*

To understand the role of climate change in *S. aurata's* current and future distribution, we need to examine the effects of temperature at key points during the species' annual life cycle. *Sparus aurata's* life cycle includes a pelagic larval stage, that that lasts between 50-100 days (Chaoui et al., 2006; Franchini et al., 2012; Lett et al., 2019; Morretti, 1999) (Figure 1.1). In the spring, *S. aurata* larvae settle in coastal nursery areas, where the relatively warm shallow waters provide refuge and suitable prey over the summer months. *S. aurata* spend the first few years of life dependent on these nursery areas for survival. Mature fish show seasonal migrations, generally spending summer months in coastal waters, making the most of productive foraging areas. During the cooler winter months, mature fish move offshore into more suitable thermal habitat and spawning grounds. Therefore, seasonal temperatures will have different effects on life stages. During the spring and summer months, temperatures need to be warm enough to facilitate the growth of juvenile fish that have settled in nursery habitats that year. Rates of feeding and growth in adults increase with temperature up to 25˚C (Hernández et al., 2003), resulting in higher lipid reserves for winter survival and the spawning season. Faster growth rates therefore result in higher winter survival rates, which increase population levels (T. J. Miller et al., 1988). Temperatures during the spawning period and early summer also need to be warm enough to facilitate larval dispersal and survival. Juvenile survival over the first winter of life is crucial for populations to grow, especially in new parts of a species range. Temperature over the winter months is particularly critical for early life stages (larvae and 0-group fish) that, unlike mature fish, cannot move into warmer water (Hurst, 2007). We expect both the summer and winter temperature to be important factors in the distribution of *S. aurata,* however the temperature throughout winter will facilitate or limit where the species can successfully reproduce, which will likely limit the latitudinal distribution of the species. Successful reproduction and dispersal in a new area is critical for a species to expand its range further (Hoffmann & Courchamp, 2016).

Here, we use species distribution models (SDMs) to investigate the role of climate change in the range expansion of *S. aurata.* SDMs use ecologically-relevant environmental variables to find statistical correlations with known species distributions (Araújo et al., 2019). We first create a SDM on *S. aurata's* native range, using a range of seasonal variables to establish the effect of temperature. We then use the native range SDM to identify whether *S. aurata* has expanded into areas that are climatically-similar to the native range. Based on these results, we take a closer look at the effects of seasonal temperature variables in *S.*

aurata's expanded range and ask whether there is evidence for seasonal temperature effects on specific life stages. Finally, we create a SDM on the current distribution of *S. aurata,* and predict the possible future distribution of the species, under different climate scenarios. We discuss the consequences of a further range-shift, based on these predictions.

2.3 Methods

2.3.1 *Species occurrence data*

We took records from the Global Biodiversity Information Facility (GBIF; http://gbif.org, accessed August 2019), the Environment Agency's National Fish Populations Database (NFPD; www.gov.uk/environment-agency, downloaded August 2019), primary literature (Abecasis & Erzini, 2008; Avignon, 2017; Craig et al., 2008; Fahy et al., 2005; Wheeler et al., 2004; Whitehead et al., 2006), angling reports (Quigley, 2015) and personally conducted surveys (Table 2.1). We used the R (R Core Team, 2019) package dismo (Hijmans et al., 2011) to download records from GBIF. We processed data to remove duplicated coordinates and those that fell on the land so were erroneous.

Table 2.1: Details of species records used in SDMs

Data source	No. records	Expanded/native	Date range	Method
GBIF	573	Both	1832-2019	Records from various sources (global)
Environment Agency	13	Expanded	2007-2018	Scientific surveys (UK)
Primary literature	15	Both	2008-2017	Scientific surveys (global)
Angling reports	18	Expanded	2001-2015	Angling observations (Ireland)
Personally conducted surveys	19	Expanded	2015-2018	Scientific surveys (South-west UK)

2.3.2 *Environmental data*

For SDMs, it is important only to include variables expected to affect the distribution of the species. If the SDMs include other variables, overfitting of models and under predicting species distributions is likely (Araújo & Guisan, 2006). Sea temperature has a direct influence on all life stages of *S. aurata*, with cooler winter temperatures being more critical for early life stages (Pankhurst & Munday, 2011). We selected variables derived from sea surface temperature (SST): MeanSST (annual average sea surface temperature), MaxSST (absolute maximum SST reached during the year), MinSST (absolute minimum SST reached during the year), SSTrange (the difference between min and max SST, as a proxy for seasonality), SpringSST (averaged across March, April May), SummerSST (averaged across June, July August), AutumnSST (averaged across September, October, November) and WinterSST (averaged across December, January, February). We downloaded all variables from Bio-Oracle (Assis et al., 2018b; Tyberghein et al., 2012) and MARSPEC (Sbrocco & Barber, 2013) at a spatial resolution of 5 arc-minutes using the R package sdmpredictors (Bosch et al., 2016). We selected climate change scenarios to represent conditions in 2040-2050 and 2090-2100, averaged from distinct atmosphere-ocean general circulation models provided by the Coupled Model Intercomparison Project (Assis et al., 2018b). We used two representative concentration scenarios. RCP45 (in which greenhouse gas levels stabilise), and RCP85 (a scenario of increasing emissions over time) (Moss et al., 2010). We obtained MeanSST, SSTrange, MinSST and MaxSST for each scenario and time period.

We considered other environmental data layers in addition to temperature, including salinity, bathymetry, distance to shore and habitat type. *S. aurata* can tolerate a wide range of salinities, from brackish to high saline lagoons (Audouin, 1962). The range of salinities in the environmental layers used were all within the reported tolerance for the species, so we did not expect salinity to add useful information to the model. We initially included bathymetry and distance to shore as variables, but they were always the most important variables in the model, potentially confounding the effects of temperature. We removed them for the following reasons: A lot of the observations we used in the model are angling records or shore-based surveys, and the underlying bathymetry of these points is not necessarily representative of the whole area inhabited by *S. aurata*. For this study, we are interested in the conditions of the environment affecting the distribution of *S. aurata*. In the Mediterranean, fishers capture *S. aurata* throughout inshore fishing districts (Mercier et al., 2012). Therefore, we clipped environmental data to the UK inshore fishing area (12 nautical miles) and removed bathymetry and distance to shore from the model to focus on the effect of temperature. *Sparus aurata* is found in a wide range of habitats and can feed on a wide range of prey, depending on what is available (Avignon et al., 2017). Therefore habitat type was not expected to affect the distribution.

2.3.3 *Species distribution models (SDMs)*

We modelled species distributions using the presence-background maximum entropy method Maxent (S. B. Phillips et al., 2006). Maxent takes a sample of background locations that it compares to the known presence observations, with the assumption that the species could feasibly be present anywhere within the landscape if conditions are suitable (Merow et al., 2013). For the reasons described above, we cropped environmental variables to the inshore environment (12 nautical miles), the area known to be used by *S. aurata* (Mercier et al., 2012).

For each SDM described below (unless otherwise stated), we randomly split the distribution data, using 80% of the species' occurrences to train the model. These models were then used to predict the remaining 20% of the data points. To evaluate how accurate these predictions were, we used the Area Under the Receiver Operator Curve (AUC) value, which is calculated from the model sensitivity (true positive rate, or number of correct presence predictions) and specificity (false positive rate, or number of correct absence predictions). Higher AUC values represent a better fitting model (with 0.5 being a random model, and 1 being a perfect fit). AUC values between 0.7 and 0.8 are often considered “fair” (Lawson et al., 2014).

Explanatory environmental variables that are correlated are not independent of each other, and including them in the same model can distort predictions (Dormann et al., 2013). We calculated pairwise Pearson's correlation coefficients for all environmental variables, and only included uncorrelated variables ($r<0.7$) in the same model. Where variables were correlated, multiple SDMs using different combinations of uncorrelated variables were run separately and then averaged in an ensemble model framework weighted by the AUC values (Araújo & New, 2007). We used Spearman's rank correlation coefficient for non-parametric data to test for correlation between the SDMs.

To identify the importance of each variable in the SDMs, we used the Maxent evaluation metric ‘percentage contribution’. Maxent calculates which variables contribute most to the SDM by removing each one in turn and calculating the resulting change in AUC, normalised to percentages. A large drop in AUC value indicates that the model depends heavily on the tested variable, and will therefore have a higher percentage contribution (S. B. Phillips et al., 2006).

2.3.4 *Comparing the native and expanded niche*

In order to identify how much suitable habitat *S. aurata* has colonised outside of its native range, we split the observations into “native range” and “expanded range”. The native range of a species can be hard to determine (Pereyra, 2019). For this study, we define the “native range” as within and south of the Bay of Biscay (45.5° North), which is where reproducing populations occur (Coscia et al., 2012). We define the “expanded range” as the English Channel and the Celtic Sea, where *S. aurata* has only been regularly recorded in the last 20 years, and there are no known reproducing populations (Figure 2.1) (Avignon, 2017; Coscia et al., 2012; Fahy et al., 2005). Comparing the thermal niche of the native and expanded range for *S. aurata* allows us to make inferences on whether a niche shift has occurred. A niche expansion occurs when a species is able to inhabit areas that fall outside of its native niche. A niche contraction has occured when a species is not found in areas that are expected to be suitable (based on the native range).

Question 1. Does temperature constrain the species native range?

We used observations from the native range (n = 558) to train and test the model (randomly split 80:20%) and clipped the model extent to include only background data from the native range. Due to high levels of correlation between all variables apart from SSTrange (Table S2.1), we ran seven model combinations with the following combinations of environmental variables; MeanSST & SSTrange; MaxSST & SSTrange; MinSST & SSTrange; SpringSST & SSTrange; SummerSST & SSTrange; AutumnSST & SSTrange; WinterSST & SSTrange. We combined the outputs from these models for presentation purposes in a weighted-means ensemble SDM, as described above (Araújo & New, 2007).

Question 2. Has S. aurata colonised areas in the expanded range that we would expect it to, given the thermal niche measured in the native range?

To understand whether *S. aurata* has undergone a niche shift, we used a different approach to train and test the model. We trained SDMs with the native range data (n= 558) and tested it with the expanded range data (n = 80). This allowed us to determine whether the conditions experienced by *S. aurata* in its native range enable predictions of its expanded range. To investigate the relationship between sensitivity and specificity, we imposed a 95% sensitivity threshold to convert continuous predictions of habitat suitability into binary presence/absence suitability (Liu et al., 2005). A 95% sensitivity threshold allowed us to be confident that the locations predicted suitable encompassed the variety of conditions experienced by *S. aurata* in the modelled range, whilst excluding outliers. We repeated the model combination and ensemble approach described in Q1.

Question 3. Is S. aurata occupying a specific thermal niche in the expanded range?

To determine the effect of the temperature variables on the expanded range distribution, we trained the SDMs with observations from the expanded range (n = 80) to train and test the model (randomly split 80:20%) and clipped the model extent to include only background data from the expanded range. Due to the low sample size of observations in the expanded range, we ran SDMs with each combination of environmental variables ten times (with a different training data each time) and calculated the mean AUC value and standard deviation (Table S2.2). We revised the approach described in Q1 and 2 to include different model combinations (MeanSST & SSTrange; MeanSST, SummerSST and WinterSST; MeanSST, MinSST and MaxSST) and used in the ensemble approach described in Q1 (Table S2.3.

2.3.5 *Future distribution*

Question 4. What will S. aurata's future distribution look like under future climate scenarios?

To assess the potential response of *S. aurata* to future climate change, we used observations from both the native and expanded range and present-day data to build SDMs and projected it to future climate conditions. We used two time points (2050 and 2100) and two emissions scenarios (RCP45 and RCP85, described above). We used the same approach described above to train and test the model, with the variable combinations: MeanSST & SSTrange; MaxSST & SSTrange; MinSST & SSTrange. We combined the outputs of each model in a weighted-means ensemble SDM. To quantify the direction of a range-shift, we calculated the centre of gravity for the present data model, and each climate scenario prediction for each time point.

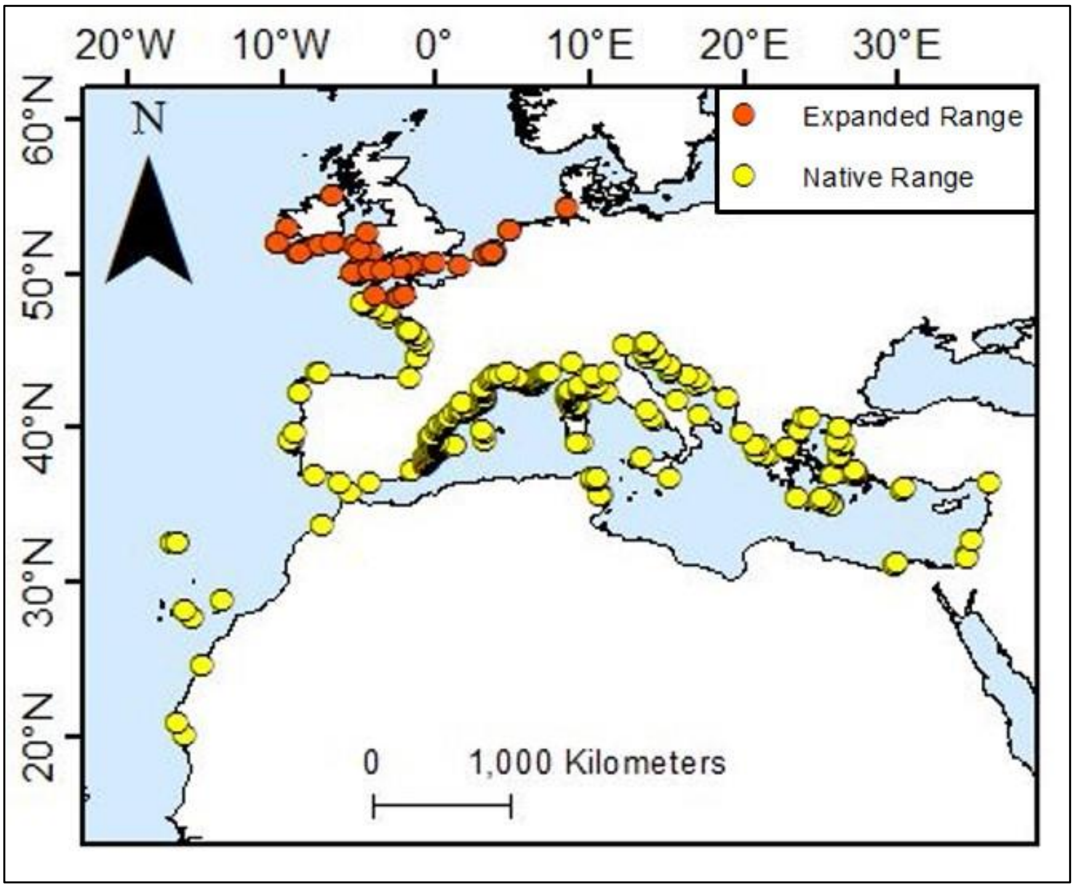


Figure 2.1 Observations of *S. aurata* used in the SDMs. Yellow circles indicate those used for the native range (n = 558), and red circles indicate those used for the expanded range (n = 80).

2.4 Results

2.4.1 *Q1. Does temperature constrain the species native range?*

AUC values for all native models are between 0.7-0.8, which we consider ‘fair’ (Table S2.2). Individual model predictions included in the ensemble SDM are displayed in supplementary information (Figure S2.4, S2.5). All SDMs included in the ensemble were highly correlated (Spearman’s correlation >0.7), suggesting that all model combinations had a similar effect on the predicted distribution of *S. aurata*. SSTrange had the highest percentage contribution in all model combinations, apart from when combined with SummerSST and MaxSST (Figure S2.8).

2.4.2 *Q2. Has S. aurata colonised areas in the expanded range that we would expect it to, given the thermal niche measured in the native range?*

We found very low AUC scores of between 0.22 and 0.29 for all combinations of variables (Table S2.2), which means that the SDMs performed worse than a random model (0.5) when using the native range to predict the expanded range of *S. aurata*. To identify the relative sensitivity and specificity for the SDMs, we imposed a 95% sensitivity threshold (Table S2.2). This threshold had to be set very low (0.01-0.05) to encompass 95% of the expanded range data, resulting in poor specificity for all models. Conditions occupied in the expanded range are different from the native range (Figure 2.2, Figure S2.6). All SDMs included in the ensemble were highly correlated (Spearman’s correlation >0.7, Figure S2.1), suggesting that all model combinations had a similar effect on the predicted distribution of *S. aurata*.

2.4.3 *Q3. Is S. aurata occupying a specific climatic niche in the expanded range?*

All mean AUC values for the models were > 0.8 (±0.3 sd) (Table S2.3). Each variable combination produced very well-fitting models and were all included in the ensemble SDM (Figure 2.2, Figure S2.7). MeanSST was the highest percentage contributing variable (>80%) in all models (Figure S2.8). In the model including WinterSST and SummerSST, winter temperature was slightly more important than summer. In the model with MaxSST and MinSST, the maximum temperature was more important than the minimum. All SDMs included in the ensemble were highly correlated (Spearman’s correlation >0.7), suggesting that all model combinations had a similar effect on the predicted distribution of *S. aurata*.

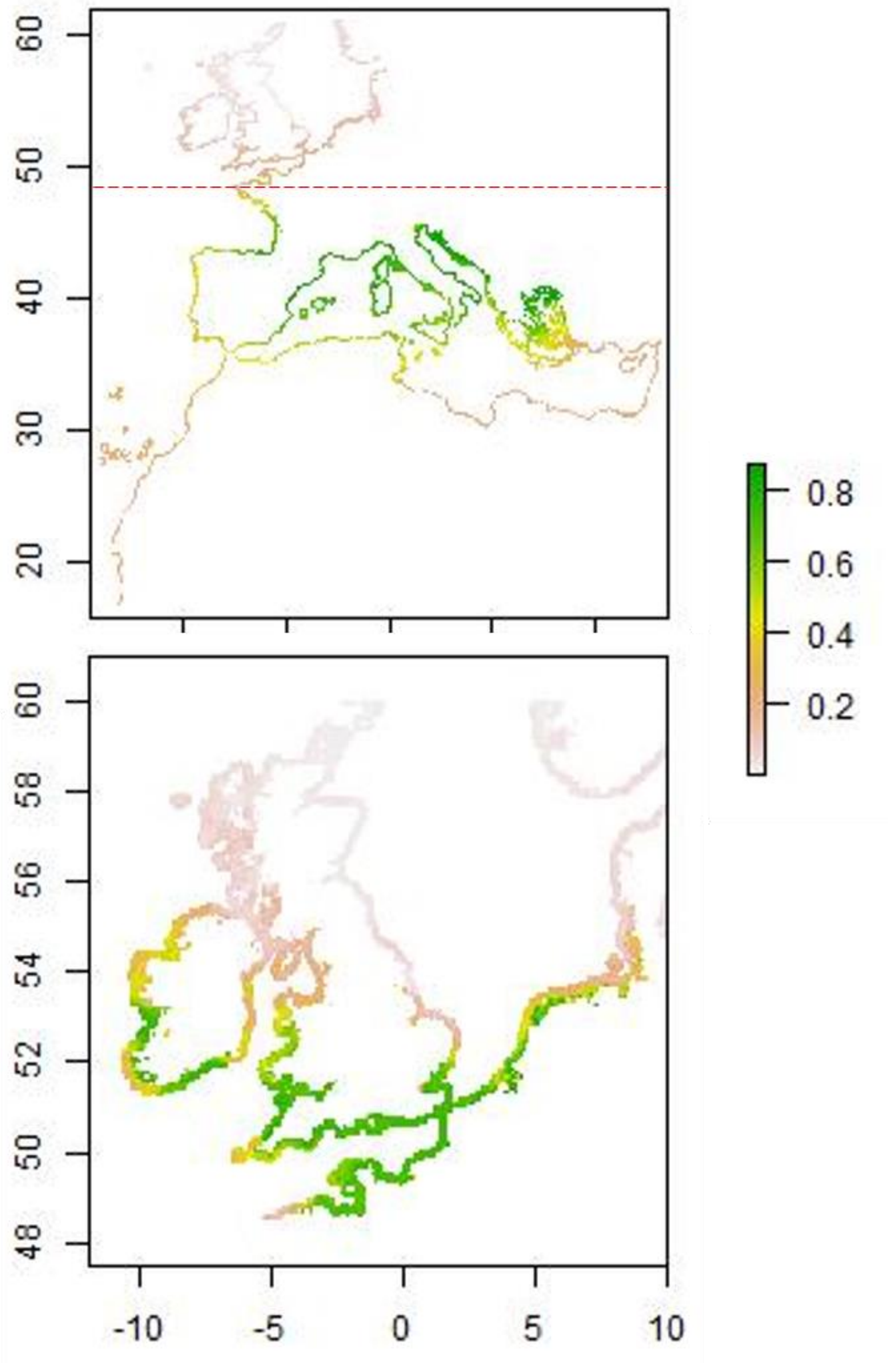


Figure 2.2 Forecasted suitability index for *S. aurata*. Top: Ensemble SDM constructed with data from the native range and used to predict suitability in both the expanded range and the native range (Question 1 and 2). Native range below red dashed line, expanded range above. Bottom: Ensemble SDM constructed with data from the expanded range.

2.4.4 *Q4. What will S. aurata's future distribution look like under future climate scenarios?*

In all climate scenarios, a shift in the centre of gravity (COG) of the areas predicted suitable demonstrates a poleward shift in *S. aurata's* potential range (Figure 2.3, 2.4). The average latitudinal COG for present day conditions was ˚N42.6 (±0.5 sd). In 2050, this rose to ˚N44.5 (±0.6 sd) in the low emission scenario and ˚N44.7 (±0.8 sd) in the high emission scenario. In 2100, the low emission scenario latitudinal COG was ˚N44.9 (±0.6 sd), similar to 2050. This rose to ˚N48.5 (±1.65 sd) for the high emission scenario.

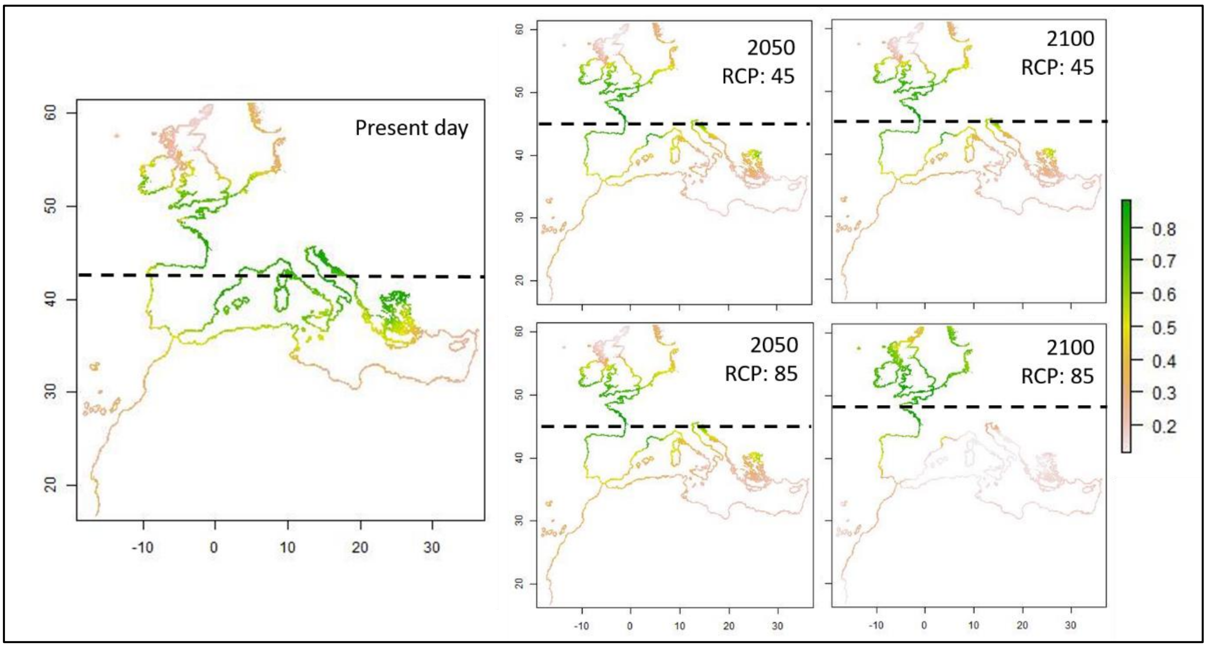


Figure 2.3. Forecasted suitability index for *S. aurata* in future climate scenarios. Ensemble SDM constructed from all model variable combinations. Dashed line shows average COG for each model.

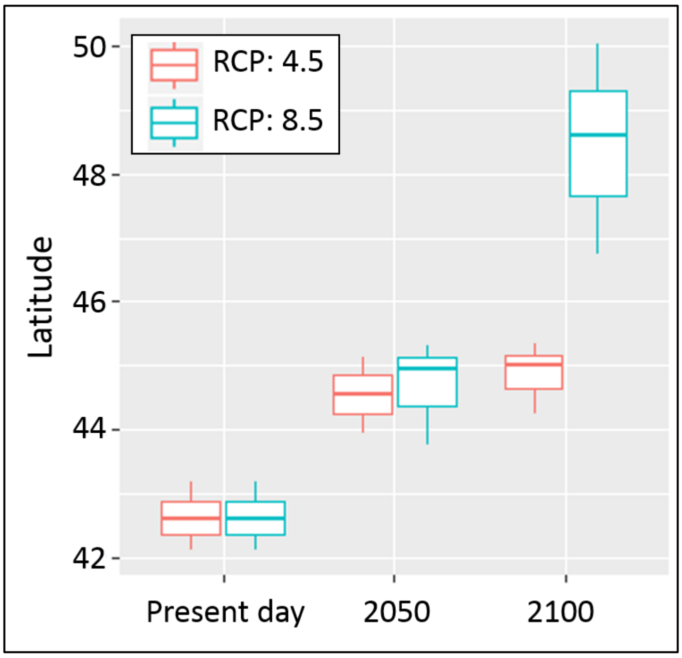


Figure 2.4 Latitudinal shifts in the centre of gravity over time for different climate scenarios. Boxes represent the latitudinal variation for each model variable combination used in each ensemble SDM. Whiskers show the minimum and maximum values, and the horizontal line represents the median value.

2.5 Discussion

Here, we use ensemble SDM models to investigate the influence of temperature on the current distribution of *S. aurata.* Our results suggest that temperature constrains the latitudinal distribution, and this is primarily due to winter temperatures. We also find that range-expanding populations of *S. aurata* are surviving in a very different thermal niche to those in the native range. Finally, our results suggest that future climate change will result in a significant further poleward expansion and contraction in the species range, with thermal conditions becoming more suitable in the north and less suitable in the south. We discuss the implications of these results for the conservation and management of *S. aurata.*

2.5.1 *Native range niche*

Q1. Does temperature constrain the species native range?

The temperature variables used predict the native distribution with a high level of accuracy, supporting the hypothesis that thermal habitat constrains the latitudinal distribution of *S. aurata* (Table S2.2). This strong predictive ability justified investigating the impacts of future climate change on the distribution of *S. aurata*. In model combinations, we found that the variable SSTrange contributed less than the annual mean, minimum or winter SST (Figure S2.8), suggesting that cooler temperatures are likely to be limiting the distribution of the species, regardless of seasonality. For the variable combinations that included summer and maximum SST, SST range has a higher percentage contribution to the model (Figure S2.8), which indicates that seasonality is important in the native range, possibly facilitating the seasonal life cycle of *S. aurata*.

Q2. Has S. aurata colonised areas in the expanded range that we would expect it to, given the thermal niche measured in the native range?

If *S. aurata's* observed range expansion is a direct result of climate change, observations in the expanded range should reflect the thermal habitat experienced in the native range. We saw the expanded range restricted to a much narrower thermal niche than predicted by the native range, with *S. aurata* now occurring in climatically-unexpected areas. There are a number of explanations for this that we discuss below: 1) *Sparus aurata* may not have yet colonised its thermal niche; 2) Populations of *S. aurata* in the expanded range may be primarily sink, rather than source, populations; 3) A niche shift has occurred in the expanded range, potentially as a result of local adaptation.

2.5.2 *Niche filling*

Sparus aurata may not yet have fully colonised its thermal niche (Estrada et al., 2016). One explanation for this could be that non-climatic range determining variables (such as biotic interactions) correlate with the temperature variables used to predict species native ranges, and that these non-climatic variables correlate with climatic conditions (Early & Keith, 2019; Early & Sax, 2014). If the combination of climatic and non-climatic variables is different in a species' new range, using SDMs with only climatic variables to characterise the native niche will give the impression that the species new range is outside its native climate niche. However, there is evidence that marine ectotherms with high dispersal capability are likely to fill thermally-suitable habitat, and that temperature is the primary driver for many marine species distributions (Chen et al., 2011; Sunday et al., 2012). Sunday et al. (2012) tested how well the observed latitudinal range limits of terrestrial and marine species match the areas that fall within their thermal tolerances. The latitudinal ranges of marine ectotherms are generally well correlated with isotherms within the seascape (Sunday et al., 2012), due to a combination of narrow thermal tolerances, and high dispersal ability (either through larval dispersal or adult movement).

The traits of *S. aurata* suggest that non-climatic drivers are likely to have less of an effect than temperature. *Sparus aurata* has a long-lived pelagic life stage and adults can swim long distances, suggesting dispersal is not likely to be a limiting factor for the species to arrive at climatically-suitable areas. For example, a restocking program around the Southwest Spanish coast showed that adult fish travelled over 120 kilometres away from the release location (Sánchez-Lamadrid, 2002). We also observed outliers in the expanded range data for *S. aurata* (Figure 2.1), which supports the idea of adult migrants swimming into new areas to find new suitable habitat (Sunday et al., 2015). *Sparus aurata* is an ecological generalist, occupying a range of habitats and able to consume a diverse selection of invertebrate prey, depending on what is available (Avignon et al., 2017). Therefore, biotic interactions are less likely to affect the distribution of *S. aurata,* compared to species with more specialist ecological requirements. Given the ability to access new areas and the ecological generalism of *S. aurata*, we would expect *S. aurata* to have fully colonised its climatic niche.

One potential limiting factor to a further *S. aurata* range-shift, could be lack of suitable nursery areas for juveniles. In the native range, *S. aurata* rely on saline lagoons as nursery areas, a habitat that is not as readily available in the expanded range (Barnes, 1989). The lack of lagoon habitat may be limiting the northern distribution; however, Avignon (2017) found evidence from otolith microchemistry to suggest that northern populations of *S. aurata* can use estuaries, instead of lagoons, as nursery areas. Understanding whether these estuaries offer the same quality of nursery area to *S. aurata* would be a useful avenue of future research, for example by comparing size, body condition, growth rate and food sources for juveniles between different nursery areas (Isnard et al., 2015). Understanding the effectiveness of estuaries as nursery areas for *S. aurata* would provide useful information on whether the lack of lagoon habitat will limit further range-shift.

2.5.3 *Source sink population dynamics*

There is also the explanation that northern populations of *S. aurata* are still primarily sink, rather than source populations. Adult *S. aurata* are mobile and can move out of thermally-stressful conditions, into more favourable conditions, whereas juveniles and larvae cannot. We built the SDMs on observations of adult and juvenile individuals, but information about the reproductive capability of these individuals is not known. Therefore, the temperature variation in the expanded range may be warm enough for adult *S. aurata* to survive, but not to facilitate successful spawning populations. Sink populations occur in areas of lower habitat quality when larvae arrive from source populations, and do not persist without immigration from source populations (Dias, 1996). In 2012, Coscia *et al.* only found evidence for reproducing populations as far north as the Bay of Biscay, and the long pelagic larval life stage of *S. aurata* could mean that juveniles recruiting into northern nursery areas come from spawning populations further south (Chaoui et al., 2006; Franchini et al., 2012; Lett et al., 2019; Morretti, 1999). If northern *S. aurata* populations are still primarily sink populations, it is likely that larval dispersal capability is currently a barrier to further northern range expansion.

2.5.4 *Niche shifts and local adaptation*

Another explanation for the differences in thermal niche observed between the native and expanded range could be local adaptation (Kawecki, 2008), either through phenotypic plasticity or genetic adaptation (Valladares et al., 2014). For example, one study that investigated the phenotypic plasticity of juvenile *S. aurata* found that individuals were able to modify their phenotype in response to different temperatures (Loizides et al., 2014). Interspecific variation across a species range can result in subpopulations, that may respond very differently to climate change (Chardon et al., 2019). For example, Chardon et al. (2019) constructed multiple SDMs for the arctic-alpine cushion plant *Silene acaulis* across the species global distribution. Intraspecific SDMs were considerably more accurate than a species-level SDM, suggesting locally-adapted populations have different climatic niches. Therefore, it is possible that there are multiple sub-populations of *S. aurata* across its distribution that have adapted to local conditions.

Studies into the population genetics of *S. aurata* across its distribution provide some evidence for genetic adaptation in northern populations (Avignon, 2017; Coscia et al., 2012). For example, both Coscia et al. (2012) and Avignon (2017) found evidence for genetic diversion between northern *S. aurata* populations and all other populations studied. At the leading edge of a species range-shift, there is strong selective pressure on the population, favouring individuals with longer dispersal capabilities (Travis et al., 2010). Selection of these individuals can allow rapid adaptation or evolution to novel environments through the process of ‘allele surfing’, where genetic mutations ‘surf‘ to higher frequencies and spatial extent (Excoffier & Ray, 2008). Therefore, the strong divergence signal detected by Coscia et al*.* (2012) and Avignon (2017) could be a result of adaptation at the leading edge of *S. aurata’s* range. One way to test this hypothesis would be to gather molecular evidence from populations of *S. aurata* over a latitudinal gradient. Determining the relative amount of change in gene sequence to adapt proteins to warmer temperatures would give an indication of the rate of adaptive evolution at different latitudes (Somero, 2010).

2.5.5 *Expanded range niche*

Q3. Is S. aurata occupying a specific climatic niche in the expanded range?

The temperature variables used predict the expanded distribution with a high level of accuracy (Table S2.3). We found the mean SST had the highest percentage contribution to the SDMs in all model combinations (Figure S2.8), again supporting the hypothesis that thermal habitat constrains the latitudinal distribution of *S. aurata*. In the model combination for mean, winter and summer SST, winter temperature had a slightly higher percentage contribution compared to summer, whereas in the model with mean, max and min SST, the maximum temperature had a higher percentage contribution than the minimum. The greater importance of winter temperature compared to the minimum temperature suggests that it is the sustained colder temperatures during winter limiting the species current distribution in the expanded range, rather than the absolute minimum temperature. This could provide further support for the hypothesis that conditions in the expanded range are less favourable for juvenile survival through the winter, and that northern *S. aurata* are not successfully reproducing.

The thermal tolerance of northern populations of *S. aurata* is not known. In the western English Channel, sea surface temperatures rarely rise above 10˚C in the winter months. In the east of the English Channel, it is common for temperatures to drop below 5˚C (Figure 3.1, Sbrocco and Barber, 2013), which is the reported lower lethal limit for the populations of *S, aurata* in the native range (Ibarz et al., 2010; Polo et al., 1991). For populations in *S. aurata's* native range, the optimal temperature for embryonic development is 16-24˚C (Polo et al., 1991), and negative effects of cold temperature are reported for *S. aurata* adults when temperatures are 15˚C or below (Ibarz et al., 2010). The thermal conditions experienced by northern populations of *S. aurata* during the spawning season are below and at the lower end of this thermal tolerance (Figure 3.1). One explanation for the observed *S. aurata* populations in the expanded range, is that they have undergone a niche shift, locally adapting to inhabit a climatically-cooler niche in the expanded range. Again, research into the thermal tolerance of *S. aurata* over a latitudinal gradient is likely to provide useful information to interpret these results further.

2.5.6 *Future distribution*

Q4. What will S. aurata's future distribution look like under future climate scenarios?

We found a poleward shift in the predicted distribution for *S. aurata* in both climate scenarios over time (Figure 2.3, 2.4). Both scenarios showed a similar northwards shift in 2050, but predictions for RCP85 (increasing emissions over time) in 2100 were much higher than RCP45 (in which greenhouse gas levels stabilise) (Figure 2.3, 2.4). Our results for the native and expanded range niche suggest that winter conditions are currently limiting the latitudinal distribution of *S. aurata* spawning populations. The predictions from SDMs under different climate scenario suggest that regardless of this, it is only a matter of time before thermally-suitable spawning habitat becomes available in areas like the English Channel and Celtic Sea, facilitating further range expansion of *S. aurata*. An example of a species that has successfully undergone a poleward population shift is the Atlantic croaker *Micropogonias undulatas.* The expansion of *M, undulatas* has been linked to sequentially warmer winter temperatures, allowing cold-sensitive juveniles to survive and establish populations further north than the historical range (Hare & Able, 2007).

AquaMaps an online tool that uses a general standardised modelling approach to make large scale predictions of marine species (Kesner-Reyes et al., 2019). For all species, the model uses the variables depth, water temperature, salinity, primary productivity and association with sea ice or coastal areas in combination with species records from online databases (such as GBIF). Models are produced for the current range and for the year 2050 under the RCP8.5 emissions scenario. The AquaMaps model output for *S. aurata* has similarities to our model for 2050 under the RCP8.5 scenario, however the loss of suitable habitat in the Mediterranean is not predicted to the same extent. Our findings demonstrate the importance of selecting specific parameters to predict the response of a species to climate change. Our SDMs predict a range contraction in the southern part of *S. aurata's* range in response to the climate scenarios, suggesting that much of the Mediterranean will become unsuitable habitat, even in the short-term low emissions scenario (Figure 2.3). Our results support the findings of Hattab *et al.* (2014), who predicted a range loss of 17% by 2050 and 57% by 2100 under a low emissions scenario. The increase in sea temperature in the southern part of

S. aurata's range is likely to negatively affect growth (Heather et al., 2018; Madeira et al., 2016). An increase in temperature is also likely to cause a decrease in dissolved oxygen availability in seawater (Pörtner & Knust, 2007). According to the 'oxygen- and capacity-limited thermal tolerance hypothesis', oxygen demand increases when a species is outside its thermal optimum (Pörtner, 2001). Metabolic rates also rise in warmer waters, which in turn increase oxygen demand (Deutsch et al., 2015). Although we did not include oxygen in our SDM, the combined effects of warming seas and a decrease in oxygen supply are likely to be the cause of this predicted range contraction, rather than temperature alone.

2.6 Conclusion

We found evidence that temperature is limiting the latitudinal range of *S. aurata* in both the native and expanded range. Our results suggest that winter temperatures are limiting the current northern distribution, likely by affecting the reproductive success of adults and overwinter survival of newly recruited juveniles and larvae. We also found evidence that *S. aurata* populations are inhabiting a different thermal niche in the expanded range, compared to the native range. Our findings are inconclusive, but this is could either be evidence of a niche shift through local adaptation, or that populations in the expanded range currently consist of primarily non-reproducing adults. An increase in *S. aurata* populations in its expanded range, as a result of future climate change, will have economic and ecological consequences. Therefore, identifying how far north *S. aurata* is already successfully spawning, and whether the northern population is already acting as a source, is a key area to focus on for future research.

Regardless of whether local adaptation has occurred, we find that with climate change, conditions will become more thermally-suitable for *S. aurata* in the Northeast Atlantic. In theory, this increase in suitability will facilitate reproducing populations of *S. aurata* in the English Channel and the Celtic Sea. If *S. aurata* is able to locally-adapt to novel thermal habitat at the leading range edge, this poleward shift could occur at a greater rate than predicted by climate change scenarios.

2.7 Supplementary information

Table S2.1 Pairwise Pearson's correlation coefficient matrix for variables in the native range (top), entire range (middle) and expanded range (bottom). Highly correlated variables (>0.7) shown in green, uncorrelated variables (<0.7) in red

	Mean SST	SST Range	Max SST	Min SST	Spring SST	Summer SST	Autumn SST	Winter SST
Mean SST	1.00	0.07	0.77	0.78	0.90	0.78	0.97	0.78
SST Range	0.07	1.00	0.64	-0.57	-0.30	0.64	0.16	-0.54
Max SST	0.77	0.64	1.00	0.22	0.46	0.99	0.81	0.24
Min SST	0.78	-0.57	0.22	1.00	0.92	0.23	0.69	0.98
Spring SST	0.90	-0.30	0.46	0.92	1.00	0.49	0.84	0.93
Summer SST	0.78	0.64	0.99	0.23	0.49	1.00	0.82	0.26
Autumn SST	0.97	0.16	0.81	0.69	0.84	0.82	1.00	0.72
Winter SST	0.78	-0.54	0.24	0.98	0.93	0.26	0.72	1.00

	Mean SST	SST Range	Max SST	Min SST	Spring SST	Summer SST	Autumn SST	Winter SST
Mean SST	1.00	0.11	0.93	0.94	0.98	0.94	0.98	0.93
SST Range	0.11	1.00	0.46	-0.24	-0.02	0.42	0.17	-0.21
Max SST	0.93	0.46	1.00	0.75	0.86	0.99	0.93	0.76
Min SST	0.94	-0.24	0.75	1.00	0.96	0.77	0.90	0.98
Spring SST	0.98	-0.02	0.86	0.96	1.00	0.89	0.96	0.97
Summer SST	0.94	0.42	0.99	0.77	0.89	1.00	0.95	0.79
Autumn SST	0.98	0.17	0.93	0.90	0.96	0.95	1.00	0.92
Winter SST	0.93	-0.21	0.76	0.98	0.97	0.79	0.92	1.00

	Mean SST	SST Range	Max SST	Min SST	Spring SST	Summer SST	Autumn SST	Winter SST
Mean SST	1.00	-0.12	0.33	0.57	0.84	0.45	0.83	0.49
SST Range	-0.12	1.00	0.88	-0.88	-0.46	0.78	0.04	-0.85
Max SST	0.33	0.88	1.00	-0.55	-0.06	0.94	0.41	-0.57
Min SST	0.57	-0.88	-0.55	1.00	0.76	-0.43	0.35	0.93
Spring SST	0.84	-0.46	-0.06	0.76	1.00	0.10	0.65	0.77
Summer SST	0.45	0.78	0.94	-0.43	0.10	1.00	0.53	-0.47
Autumn SST	0.83	0.04	0.41	0.35	0.65	0.53	1.00	0.37
Winter SST	0.49	-0.85	-0.57	0.93	0.77	-0.47	0.37	1.00

Table S2.2 AUC values for the native range model (top) and AUC values and 95% sensitivity thresholds for the model testing the native range model with the expanded range data (bottom)

Model	**AUC**
Mean SST & SST Range	0.72
Max SST & SST Range	0.73
Min SST & SST Range	0.71
Spring SST & SST Range	0.71
Summer SST & SST Range	0.72
Autumn SST & SST Range	0.75
Winter SST & SST Range	0.75

Model	**AUC**	**95% sensitivity threshold**
Mean SST & SST Range	0.25	0.01
Max SST & SST Range	0.27	0.05
Min SST & SST Range	0.29	0.05
Spring SST & SST Range	0.22	0.01
Summer SST & SST Range	0.24	0.04
Autumn SST & SST Range	0.28	0.03
Winter SST & SST Range	0.27	0.01

Table S2.3 Mean AUC values and standard deviation for the expanded range model (10 x model runs)

Model	**Mean**	**SD**
Mean SST & SST Range	0.84	0.031774
Mean, Summer and Winter SST	0.86	0.031494
Mean, Min and Max SST	0.82	0.027625

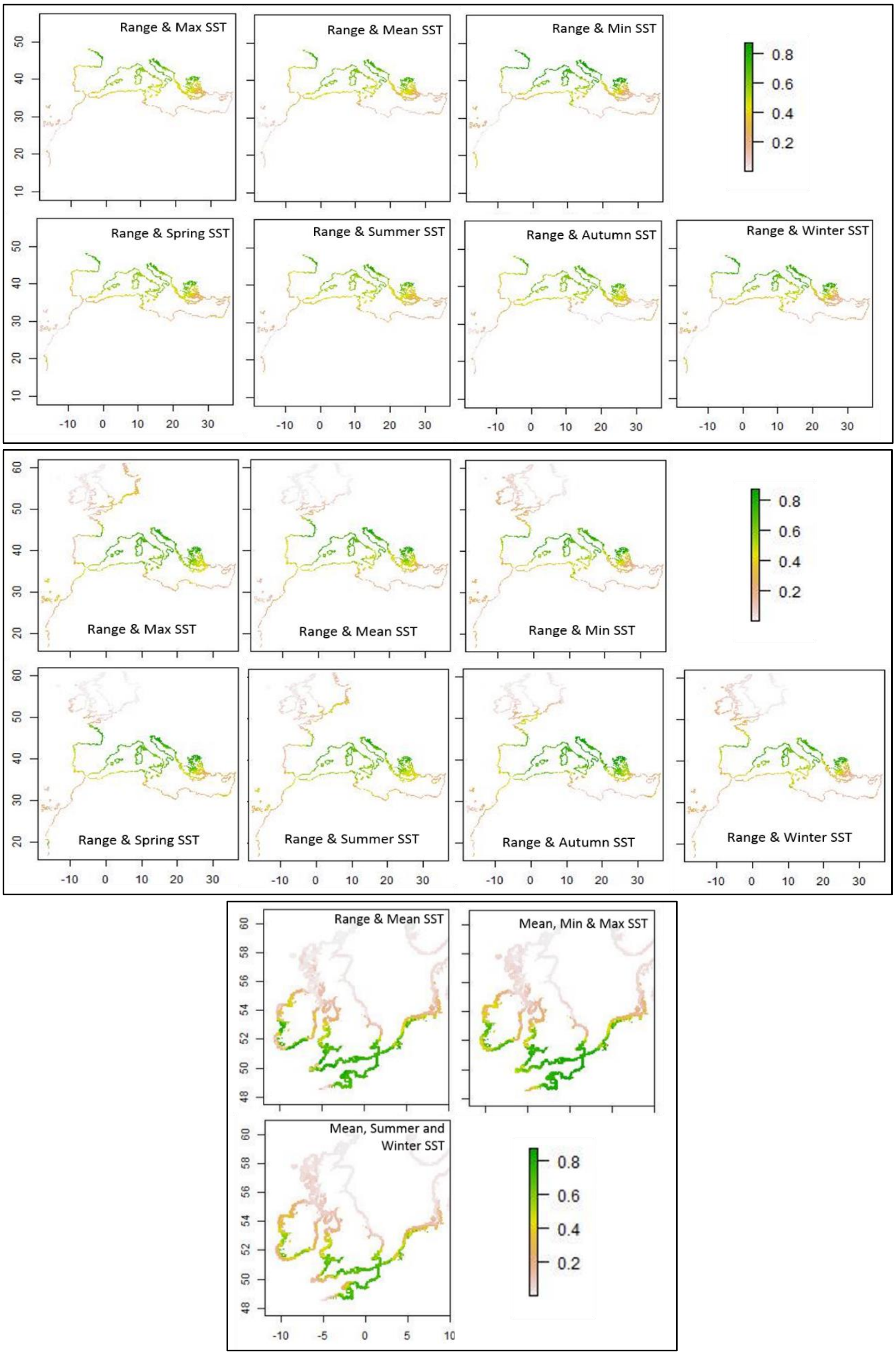


Figure S2.4 SDM models used in ensemble SDMs for native range (top), current distribution, with suitability in the expanded range predicted by the native range (middle) and expanded range (bottom)

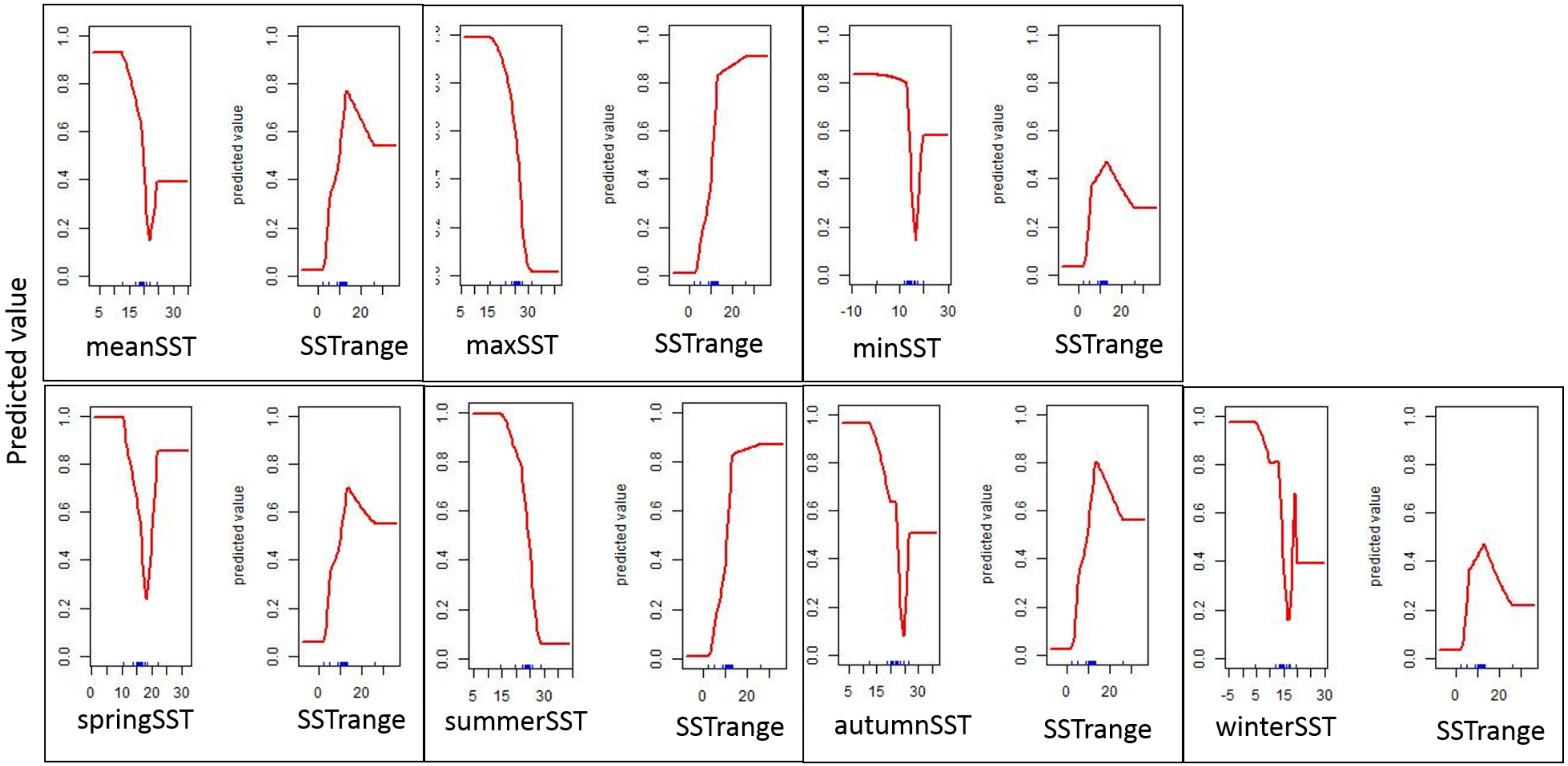


Figure S2.5 Response curves for the SDMs trained and tested on native data. Red line shows how the suitability of the model prediction changes in relation to each model variable

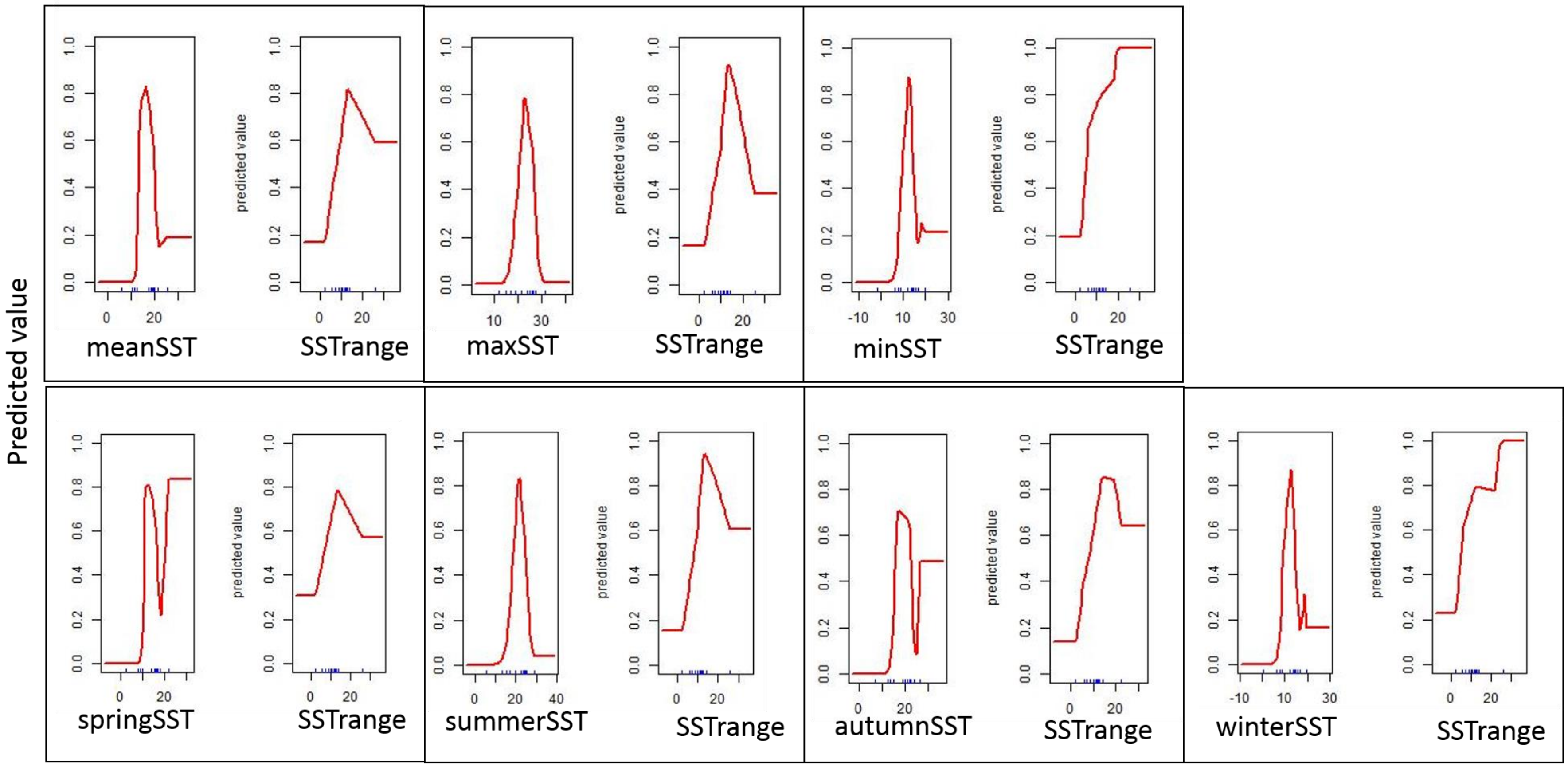


Figure S2.6 Response curves for the SDMs trained on native range and tested on expanded range data. Red line shows how the suitability of the model prediction changes in relation to each model variable

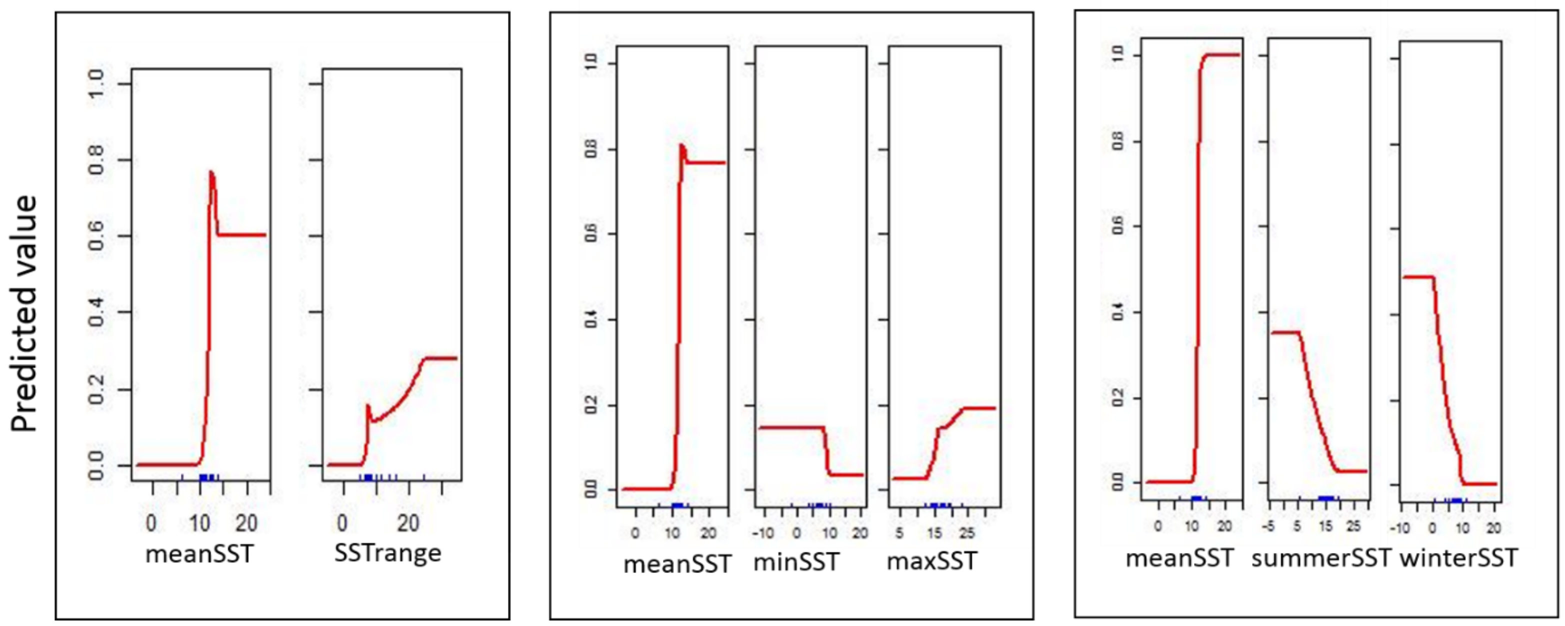


Figure S2.7 Response curves for the SDMs trained and tested on expanded range data. Red line shows how the suitability of the model prediction changes in relation to each model variable

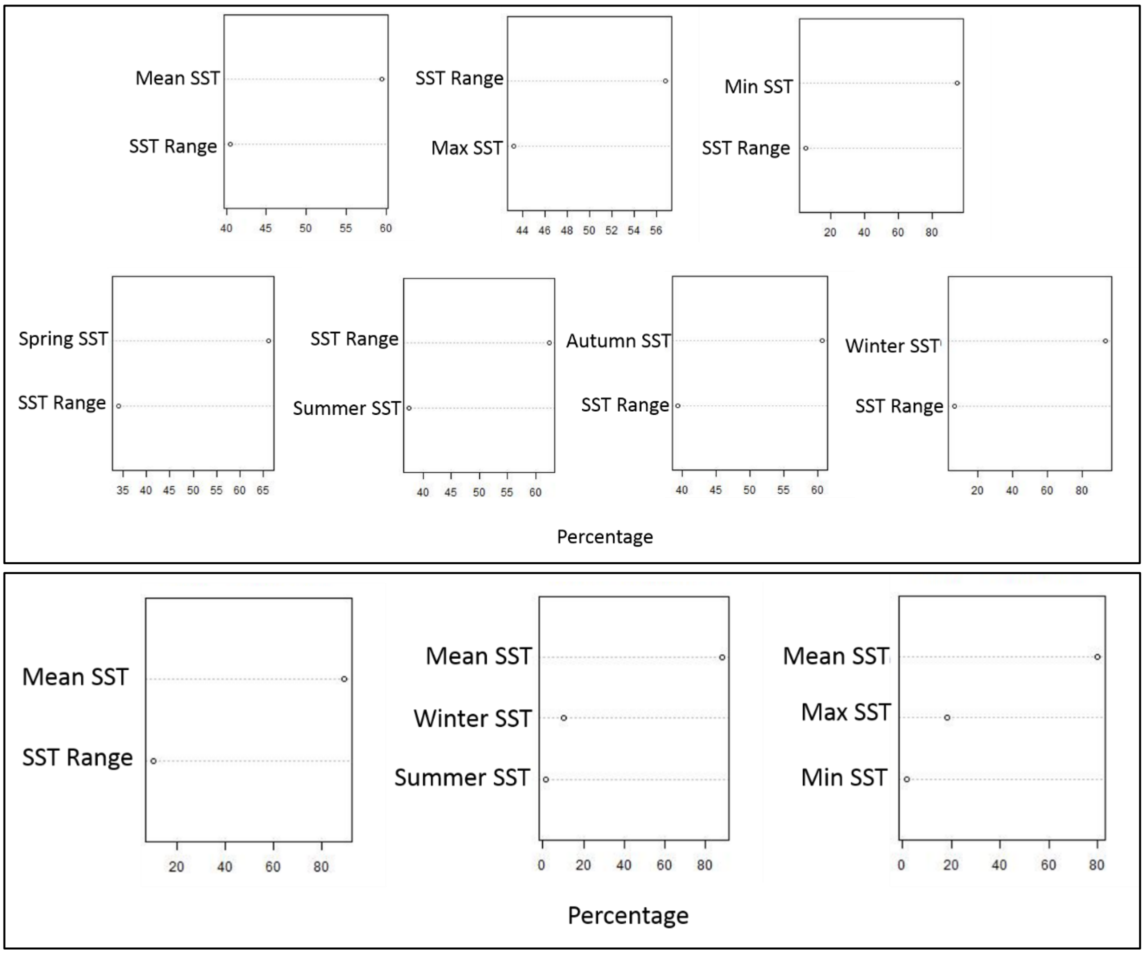


Figure S2.8 Importance of variables in the native range models (top) and expanded range models (bottom)

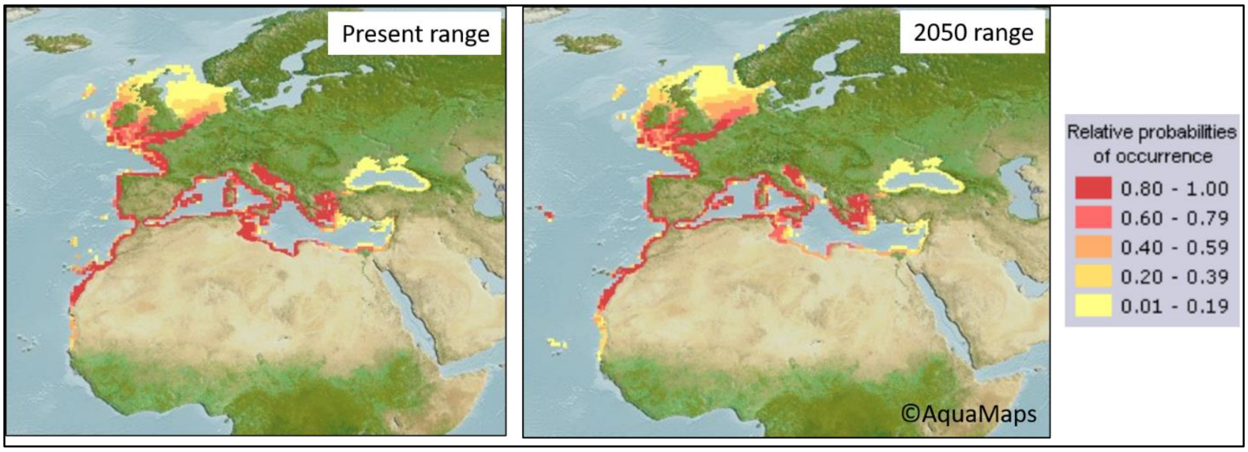
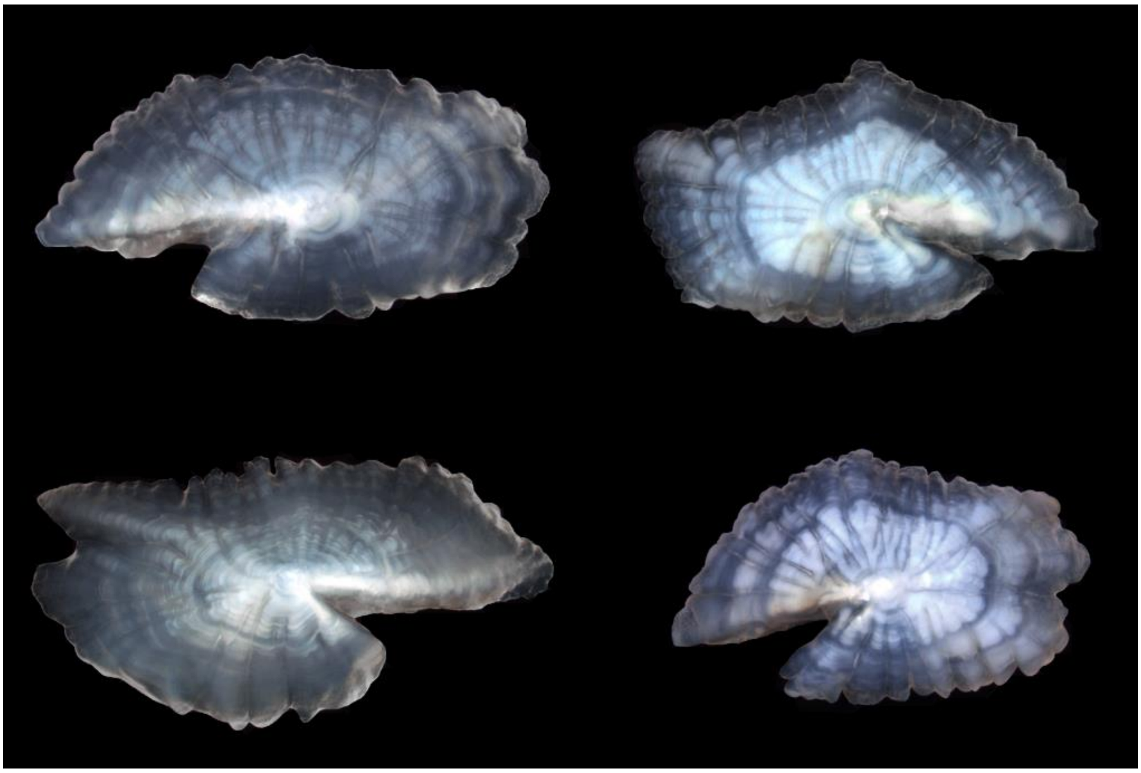


Figure S2.9 AquaMaps modelled distribution of *S. aurata* range based on the parameters depth, water temperature, salinity, primary productivity and association with sea ice or coastal areas

Chapter 3

Can otolith microchemistry provide evidence for source populations at the edge of *Sparus aurata'*s range?



3.1 Abstract

Many marine species have life cycles dependant on a pelagic larval stage that can connect spatially-distinct populations. Understanding the movement of larvae between populations has important implications for population stock structure, and the ability of a population to act as a source. Gilthead bream *Sparus aurata* is a high value target species, currently undergoing a poleward range-shift into the English Channel and Celtic Sea. Knowledge of the stock structure of *S. aurata* in the Northeast Atlantic is limited, but recent research suggests genetic differentiation between northern populations and those further south. For there to be observable genetic differences in northerly populations of *S. aurata*, some form of local adaptation is likely to have occurred, potentially allowing more thermally-tolerant individuals to spawn successfully in cooler northern waters. We use otolith microchemistry to provide tentative evidence that multiple sources are contributing to *S. aurata* populations in the English Channel, and that these could be occurring at higher latitudes than previously thought. The source populations we identify are temporally stable across multiple *S. aurata* cohorts, and represent either spatially or temporally-discrete areas. We also find different levels of contribution from the identified sources, to two sites in the English Channel that are 200 kilometres apart, however there is also evidence for source population mixing between the sites. This mixing could occur during larval dispersal or subsequent adult movement. Our findings provide the basis for further research into the location of sources that are contributing to northern *S. aurata* populations. *S. aurata* is an attractive target fish to both the commercial and recreational fishing industry, and sustainable management of this species should be carried out at the appropriate level to protect source populations.

3.2 Introduction

3.2.1 *Fish stocks*

Determining the structure of fish stocks is a complex, but a fundamental component of sustainable fisheries management (Begg & Waldman, 1999). Many marine fish species have a life cycle that includes spatially-distinct spawning and nursery areas, connected by a pelagic larval stage (Cowen et al., 2000; Gillanders et al., 2003). Ocean hydrodynamics and the duration of the larval stage influence larval dispersal and resulting connectivity between spawning and nursery areas (Beraud et al., 2017; Cowen et al., 2000). Therefore, the degree of larval dispersal defines the degree of mixing between spatially-distinct populations (Beer et al., 2011; Mercier et al., 2012).

The spatial origin of larvae that recruit to nursery areas has important implications for population structure. A spawning population that produces larval recruits is considered a source population (Crowder et al., 2000). Larvae from source populations can recruit to nursery areas that are both close to and spatially-distinct from the spawning grounds. Sink populations rely on larval recruits from source populations and cannot sustain local populations on their own (Dias, 1996). Therefore, this process can maintain spatially-distinct populations, even when the individuals that make up this population are not spawning successfully (Dias, 1996). When larvae only recruit to areas proximal to the spawning grounds, demographically-closed populations can also occur. The distribution of source and sink populations generally varies across species ranges, with populations often being maintained by a mixture of these source-sink dynamics (Guo et al., 2005).

Understanding the balance of these population dynamics is important for successful species management, as it affects how well local populations buffer against decreases in abundance following exploitation, disease or pollution events, and environmental change (Hart & Reynolds, 2002). For example, limiting fishing within a source population has a positive impact on all populations that rely on larval recruits from that source (Crowder et al., 2000; Seijo & Caddy, 2008). It is even more important to understand the balance of source and sink populations for species that are expanding their range into new areas. Localised spawning and recruitment at the edge of a species range is an indication that a species has settled into a new area, and is capable of further range expansion (Estrada et al., 2016; Hoffmann & Courchamp, 2016).

3.2.2 *Gilthead seabream populations*

Many species of marine fish have shown poleward shifts in response to sea temperature change (Perry et al., 2005). One of these is the gilthead seabream *Sparus aurata*, with an apparent recent range expansion into the English Channel and Celtic Sea (Craig et al., 2008; Fahy et al., 2005). Recently recruited juveniles (0-group fish) have appeared in surveys in the UK, and Ireland since 1999 (Craig et al., 2008; Fahy et al., 2005), which could mean *S. aurata* is reproducing at the northern edge of its range. Current knowledge of the stock structure of Atlantic *S. aurata* populations is limited. Findings from population genetics in 2012, only found evidence for substantial spawning populations of *S. aurata* along the Atlantic coast of Spain, Portugal and France up to the Bay of Biscay (Coscia et al., 2012). If still accurate, this suggests that populations in the English Channel and the Celtic Sea are sink populations rather than source ones, with larvae arriving from source populations further south.

In Chapter 2, we investigated the differences in the thermal niche between the native and the expanded range. Our results show that northern populations of *S. aurata* are occupying a very different thermal niche compared to those in the native range. The thermal conditions experienced by northern populations of *S. aurata* are not likely to facilitate successful spawning unless they have undergone local adaptation and are more thermally-tolerant. A recent study on the population genetics of *S aurata* found differentiation between the northernmost populations of *S aurata* and Mediterranean populations, suggesting limited mixing of individuals on a large spatial scale (Avignon, 2017). Avignon (2017) also found evidence for a relatively rapid population expansion for Irish and French populations, with shared alleles between populations from the Mediterranean to the Channel suggesting several waves of step-by-step colonisers from the south. For there to be observable genetic differences in northerly populations of *S. aurata*, there is likely to be some form of selective pressure on populations from exposure to novel environments. Therefore, the northerly populations of *S. aurata* may have undergone a niche expansion through local adaptation, allowing them to successfully spawn in areas that are different from their native niche. Successful source populations in northern waters would have important implications for successful management of *S. aurata* and are, therefore, a key knowledge gap that requires further research.

3.2.3 *Otoliths as natural markers*

One way to investigate the source and sink dynamics of fish stocks is through the use of natural markers, such as otoliths (Arkhipkin et al., 2009; Barbee & Swearer, 2007; Campana et al., 1994; Patterson et al., 2004; T. A. Rogers et al., 2019). Otoliths are paired calcified structures located in the inner ear of teleost fishes (Panfili et al., 2006). Otoliths develop through the deposition of a calcium carbonate matrix via the haemolymph, into which other elements are incorporated from the surrounding seawater in trace levels (Campana, 1999). Otoliths grow throughout the life of the fish, exhibiting annual and daily growth rings (Panfili et al., 2006), and are metabolically inert, permanently retaining any material deposited within the otolith structure over the life of the individual fish (Campana, 1999; Campana & Neilson, 1985).

Due to the relationship between fish age and otolith growth, it is possible to determine the otolith chemistry for specific periods of an individual’s life. The incorporation of elements into the otolith matrix is complex but primarily influenced by environmental conditions that the fish experience or physiological processes (A. Darnaude & Hunter, 2018; A. M. Darnaude et al., 2014; Elsdon & Gillanders, 2003, 2004; Izzo et al., 2018; Anna M. Sturrock et al., 2015). Although the relationship between otolith chemistry and the environment is complex, the occurrence and periodicity of chemical patterns are informative, irrespective of whether we understand what causes them. Otoliths can successfully discriminate between fish stocks (Campana et al., 1994, 2000; Tanner et al., 2016), natal origins (Arkhipkin et al., 2009; Barbee & Swearer, 2007; Patterson et al., 2004; T. A. Rogers et al., 2019) and nursery areas (Gillanders & Kingsford, 2000; Marriott et al., 2016; Schilling et al., 2018; Tournois et al., 2017). Therefore, otoliths can provide a way to investigate ontogenetic differences in environmental experience encountered by individual fish (Campana et al., 2000; Marriott et al., 2016; A. M. Sturrock et al., 2012; Tanner et al., 2016).

Sparus aurata are batch spawners and produce eggs throughout the spawning season (Figure 1.1). Information from the Northeast Atlantic is scarce, but in the Mediterranean, this occurs primarily over winter between January and April (Lasserre, 1976; Lett et al., 2019; Mercier et al., 2012). Due to this long spawning season, individuals have the potential for higher growth rates if spawned at the beginning of the season compared to at the end. Physical conditions can also vary spatially and temporally across the range of *S. aurata* during the spawning season, so larvae are exposed to a variety of different environments during early development, depending on when and where they were spawned (Figure 3.1). Therefore, larvae spawned at the same time of year in the same area are likely to experience similar environmental conditions. Identifying similarities and differences between the environmental conditions individual larvae experience during very early life can indicate how many different source populations are contributing to fish populations.

Here, we use otolith microchemistry to investigate the origin of *S. aurata* individuals that recruit to sites in the English Channel. We specifically use multi-element signals in the part of the otolith corresponding to the very early stage of an individual’s life to investigate the hypothesis that there are multiple (potentially localised) spawning populations contributing to populations in the Channel, rather than a single mixed population acting as a source.

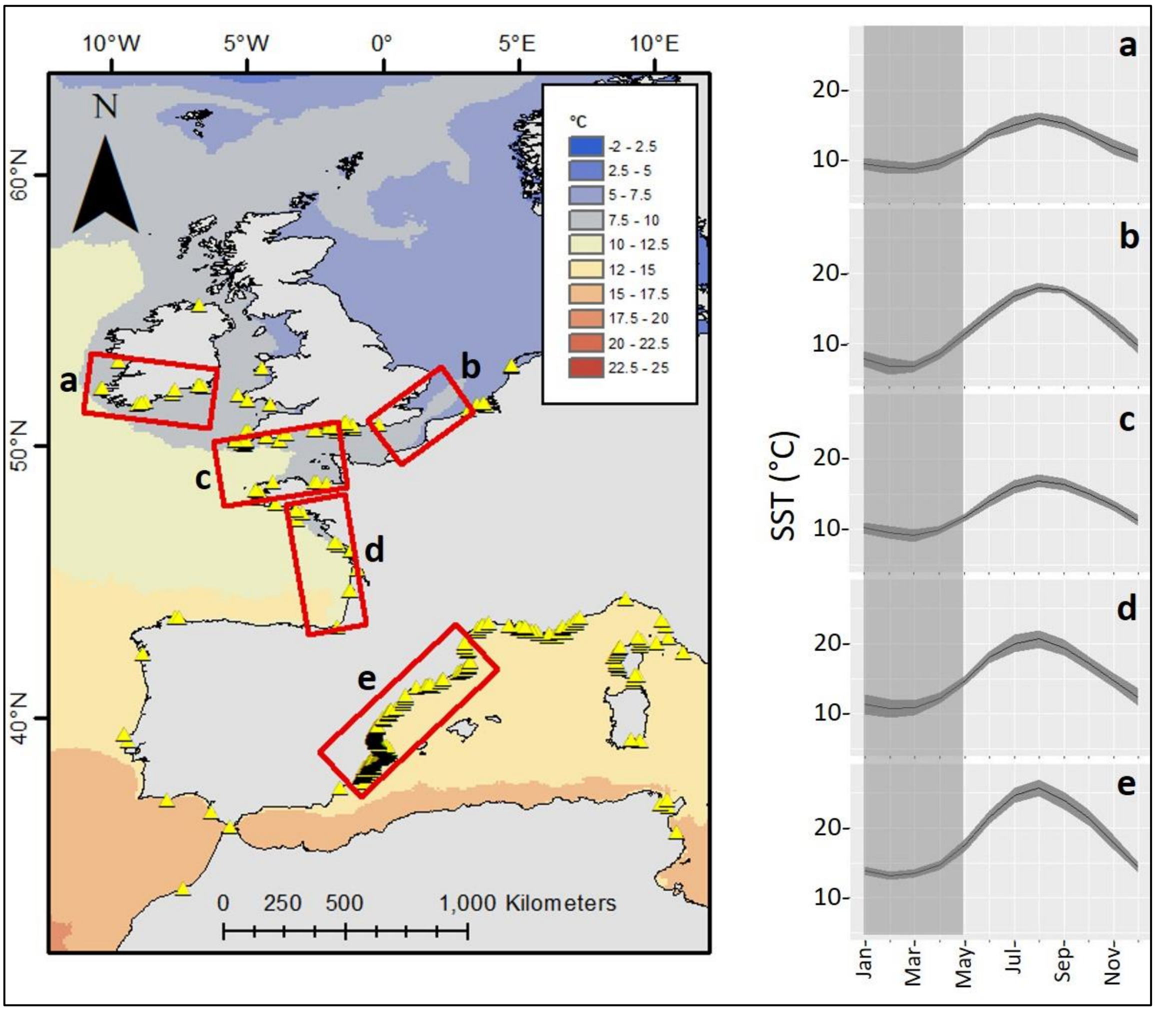


Figure 3.1 Spawning season (Jan-April) sea surface temperature (SST) in the Northeast Atlantic and Western Mediterranean (left) for present-day conditions (2000-2014) based on monthly averages. Time series (right) display the monthly average SST (± SD) for example regions (red boxes). The shaded area in the right-hand panel represents the spawning season (identified from Mediterranean spawning populations). Known observations of *S. aurata* are shown by yellow triangles (SST data from Aqua-MODIS; http://oceancolor.gsfc.nasa.gov/, see Chapter 2 for observation data).

3.3 Methods

3.3.1 *Sample collection*

We obtained adult and juvenile specimens of *S. aurata* (n=86) from two sites in the English Channel (Figure 3.2) either opportunistically from anglers or from small fish surveys between May 2014 and September 2017. We had approval from the University of Exeter Ethics Committee for sampling from surveys (2016/1449). Both sampling locations are near to nursery habitats where 0-group *S. aurata* have been captured in multiple years, suggesting that adult fish in these localities could have spawned nearby (Fahy et al., 2005). To identify the spawning cohort of each fish, we used the capture year minus the age of the individual (identified from annual otolith growth rings).

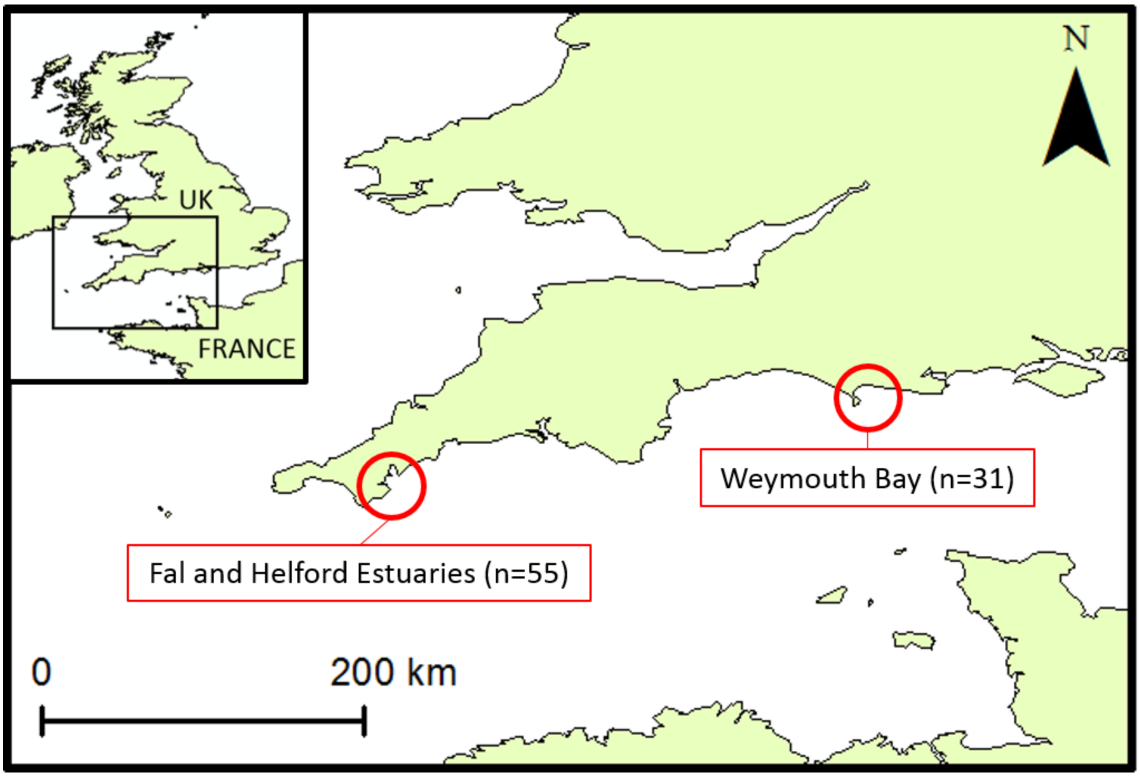


Figure 3.2 Location of the samples used in this study. The number of samples included for each location.

3.3.2 *Otolith processing*

To minimise contamination of samples, we extracted the otoliths with plastic forceps, cleaned with ultrapure water and used a plastic brush to remove any remaining tissue. We placed samples in a sonication bath for five minutes, then dried them under a positive pressure laminar flow hood and stored specimens in 1ml plastic Eppendorf tubes. We had no reason to expect differential elemental composition between the right and left otoliths, but chose the right otolith where possible for consistency (Campana et al., 1994). We embedded otoliths in epoxy resin (Araldite 2020) in silicon moulds and placed them in a drying oven to harden. We sectioned the otoliths transversely with a diamond-edged low-speed saw and polished the resulting sections to within ~15µm of the core with increasingly fine silicon carbide discs (Grit-800, 1200 and 2400), using ultrapure water between each polishing to remove surface contamination. We mounted the sections onto glass slides with a thermal adhesive, before placing them in a sonication bath once more for five minutes. Finally, we triple-rinsed the samples with ultrapure water, dried under a laminar flow hood and stored in individual sealed plastic bags until further analysis.

3.3.3 *Trace element analysis*

We used laser ablation inductively-coupled plasma mass spectrometry (LA-ICPMS) to measure otolith elemental composition. We conducted all analyses at the School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, Southampton (UK), using a New Wave NWR193 laser ablation system coupled to a Thermo Fisher Scientific ELEMENT XR (Table S3.1). We placed the mounted sections inside a sealed chamber and viewed remotely through an image analysis system to guide the laser sampling. To measure the variation in elemental chemistry across the otolith, we programmed the laser to continuously ablate along a predefined transect path from the core to the dorsal edge (Figure 3.3). Before each analysis, we conducted pre-ablation runs over each path (70 µm at 100µm s^{-1}) to remove possible surface contamination. The ICP-MS continuously scanned for selected isotopes (resolution optimised for each element) throughout the laser transect using Mode ‘2’. We conducted preliminary work screening a number of elements in *S. aurata* otoliths. Based on this, we chose the following elements that were consistently present in high enough levels for subsequent analysis: ^{7}Li, ^{86}Sr, ^{136}Ba, ^{138}Ba and^{139}La were measured in low resolution, and ^{24}Mg, ^{31}P, ^{55}Mn, ^{43}Ca, ^{44}Ca, in medium resolution. We also scanned for ^{83}Kr (to correct ^{86}Sr) and ^{140}Ce (to correct ^{138}Ba). We used a multi-element approach to compare between water bodies as this has shown to have more discriminatory power than using single elements (Leakey et al., 2009; Marriott et al., 2016; Mercier et al., 2012; T. A. Rogers et al., 2019; Thorrold et al., 1997b; Tournois et al., 2013).

To convert the raw data from counts per second (cps) to element concentrations (expressed as µg g^{-1}), we used the R package ELEMENTR (Sirot et al., 2017). Following blank subtraction, we calibrated the data using National Institute of Standards and Technology (NIST) 610, 612 and 614 glass standards and the USGS MACS-3 synthetic calcium carbonate standard. We analysed the standards (10 times each) at the beginning and end of each analytical session, and after every ~ ten samples to correct for machine drift (which was negligible). We calculated the limits of detection for each element using three times the standard deviation of the gas blank average values. Out of the elements scanned for, ^{138}Ba, ^{7}Li, ^{24}Mg, ^{55}Mn, ^{31}P and ^{86}Sr, all had >25% measurements above the limits of detection within the transect and included in our subsequent analyses. To control for variation in the amount of material ablated from the otolith, we used ^{44}Ca as an internal standard, with an assumed concentration of 38.8% (Yoshinaga et al., 2000). All data are normalised to calcium and presented as µg g^{-1}.

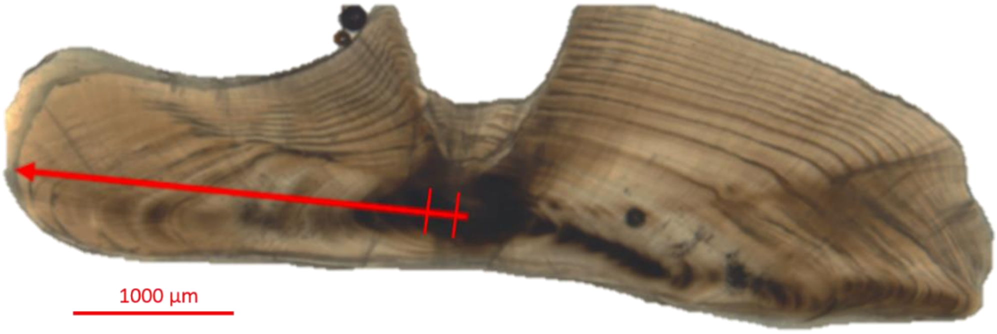


Figure 3.3 Laser transect path from the core to the edge of otolith along the dorsal axis. Approximate location of the early life section used for element chemistry shown on the transect. Age: 12 years, size: 48cm (fork length). Captured in the Helford estuary in 2015.

3.3.4 *Data analysis*

To characterise the spawning environments experienced by individual fish, we used elemental data from the part of the otolith representing the first ~two weeks of larval life (50-150µm from the core, Figure 3.3). To avoid bias from the maternal egg, we did not use data from the core area (0-50µm) (Elsdon et al., 2008; Hegg et al., 2019). For each individual, we took the mean concentration for each element and performed a principal components analysis (PCA) on the data using the R package FactoMineR (Le et al., 2008). We then used agglomerative hierarchal clustering (Wards method) on the PCA results to identify groups of individuals that shared similar otolith chemical concentrations, cutting the dendrogram to attain the optimal number of clusters based on the FactoMineR package algorithm (Le et al., 2008). To identify whether capture location affected cluster assignment we used Pearson's chi-squared test. To identify whether cohort affected cluster assignment we used Fisher's exact test, due to the small number of expected frequencies in each cell (Table S3.2).

We used a combination of multivariate and univariate statistical techniques to look at the differences between single and multi-element otolith concentrations on cluster assignment, with the assumptions for normality met following $\log_{10}$ transformation of the data for the six retained elements (Kolmogorov-Smirnov test). We used a MANOVA (Pillai's trace statistic) to investigate the effect of the multi-elemental data (continuous dependent variables) on cluster assignment (categorical independent variable) and a summary of the MANOVA to investigate which elements had significant effects on cluster assignment. Where we found a significant effect from an element in the MANOVA summary, we used a separate 1-way ANOVA for each element (the continuous dependent variable) with the assigned cluster as the categorical independent variable. We followed this with Tukey's HSD *post-hoc* test to identify how the element concentrations differed between clusters.

We also investigated whether there were differences in growth rates over the first year of life, between the different clusters. We used distance from the core to the start of the first annual increment (µm), as otolith growth is a proxy for fish length in *S. aurata* (Avignon, 2017). We used the imaging software NIS-Elements to measure the otolith sections. To investigate differences in growth rate between clusters, we used a 1-way ANOVA with the otolith measurement being the continuous dependent variable and the categorical independent variable being cluster. We used Tukey’s HSD *post-hoc* tests to identify significant differences between the clusters. We conducted all analysis for this study using R version 3.6.0 (R Core Team, 2019).

3.4 Results

3.4.1 *PCA and clustering*

We retained the first three principal components (PC) of the PCA that explained 62% of the variation in the data for subsequent analysis (Figure 3.4, S3.1). The primary contributing elements to PC1 are Sr (38.7%), Mg (26.3%) and Li (17.2%). The primary contributing elements to PC2 are P (33.9%) and Li (31.9%). Mn (65%) is the primary element contributing to PC3 (Figure S3.1). The hierarchical clustering on the three PCs identified three groups with different chemical signatures (Figure S3.2). We found no relationship between cohort and cluster assignment (Fisher's p=0.248), and a significant relationship between the capture location and cluster assignment (Pearson's: X-squared = 6.092, df = 2, p = 0.048) (Table S3.2).

We found significant differences between the multi-elemental concentrations between the clusters (MANOVA: $F_{2,36}$ = 13.917, p = < 0.001), with significant effects found for four out of six elements (Sr, Mg, P and Mn) on cluster assignment (Table 3.1). In addition to this, we found significant differences in single element concentrations (Sr, Mg, P and Mn) between the clusters from the ANOVA results (Table 3.2). From the pairwise comparisons between clusters, we found Sr and Mn were significantly different for all comparisons (Table 3.2). Mg was significantly different in two out of three pairwise comparisons (Table 3.2). P had the most variability and was only significantly different in one pairwise comparison (Table 3.2). We found that cluster 1 had the lowest concentrations of Sr and Mn and elevated concentrations of Mg and P compared to the other clusters (Figure 3.5). Cluster 2 had higher levels of Sr than cluster 1, and elevated concentrations of Mg, P and Mn. Cluster 3 had the highest Sr levels, but relatively low levels of Mg, P and Mn (Figure 3.5).

3.4.2 *Growth rates*

We found significant differences in otolith growth rate in the first year between fish in the different clusters (ANOVA: $F_{2,82}$ = 7.847, p < 0.001) (Figure 3.6). Individuals in cluster 3 had significantly lower growth rates than those in clusters 1 (p = 0.002) and 2 (p = 0.001) (Figure 3.6).

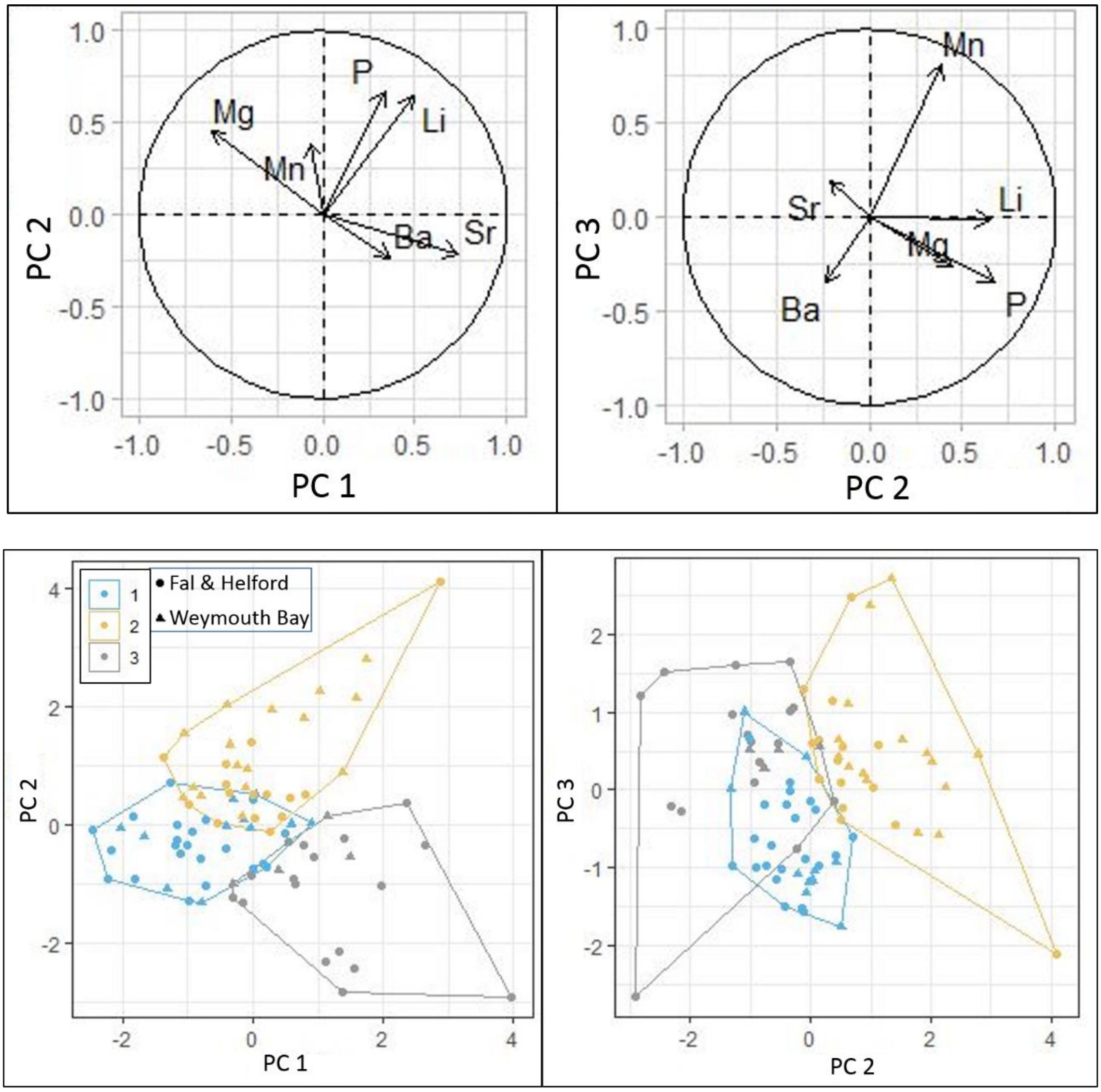


Figure 3.4 Variables factor maps from the PCA (top) showing how each element affected the PC axes. Allocation of individual *S. aurata* to the identified clusters (bottom). Left-hand plots show principal components 1 and 2, and the right-hand plots show 2 and 3. Colours show cluster identity, and shape denotes the place of capture. Cluster 1 contained 34 individuals (Fal & Helford: 23, Weymouth Bay 11). Cluster 2 contained 31 individuals (Fal & Helford: 15, Weymouth Bay: 16). Cluster 3 contained 21 individuals (Fal & Helford: 17, Weymouth Bay: 4)

Table 3.1 MANOVA results for comparisons of mean element concentrations from the part of otolith representing the first two weeks of life between the three identified clusters. Significant results in bold.

Element	$F_{2,36}$ =	*P*-value
Sr	9.2145	**<0.001**
Ba	2.6192	>0.050
Mg	14.395	**<0.001**
P	5.929	**0.010**
Li	0.4105	>0.050
Mn	22.928	**<0.001**

Table 3.2 ANOVA results for comparisons of mean element concentrations between the three identified clusters, for the four elements that were found significant in the MANOVA (Sr, Mg, P and Mn). Results of Tukey's *post-hoc* tests shown with significant results in bold.

Element	$F_{2,82}$ =	Pairwise comparison	*P*-value
Sr	25.92	1-2	**0.020**
		1-3	**<0.001**
		2-3	**<0.001**
Mg	27.77	1-2	>0.050
		1-3	**<0.001**
		2-3	**<0.001**
P	6.48	1-2	>0.050
		1-3	>0.050
		2-3	**0.002**
Mn	16.97	1-2	**<0.001**
		1-3	**0.030**
		2-3	**0.020**

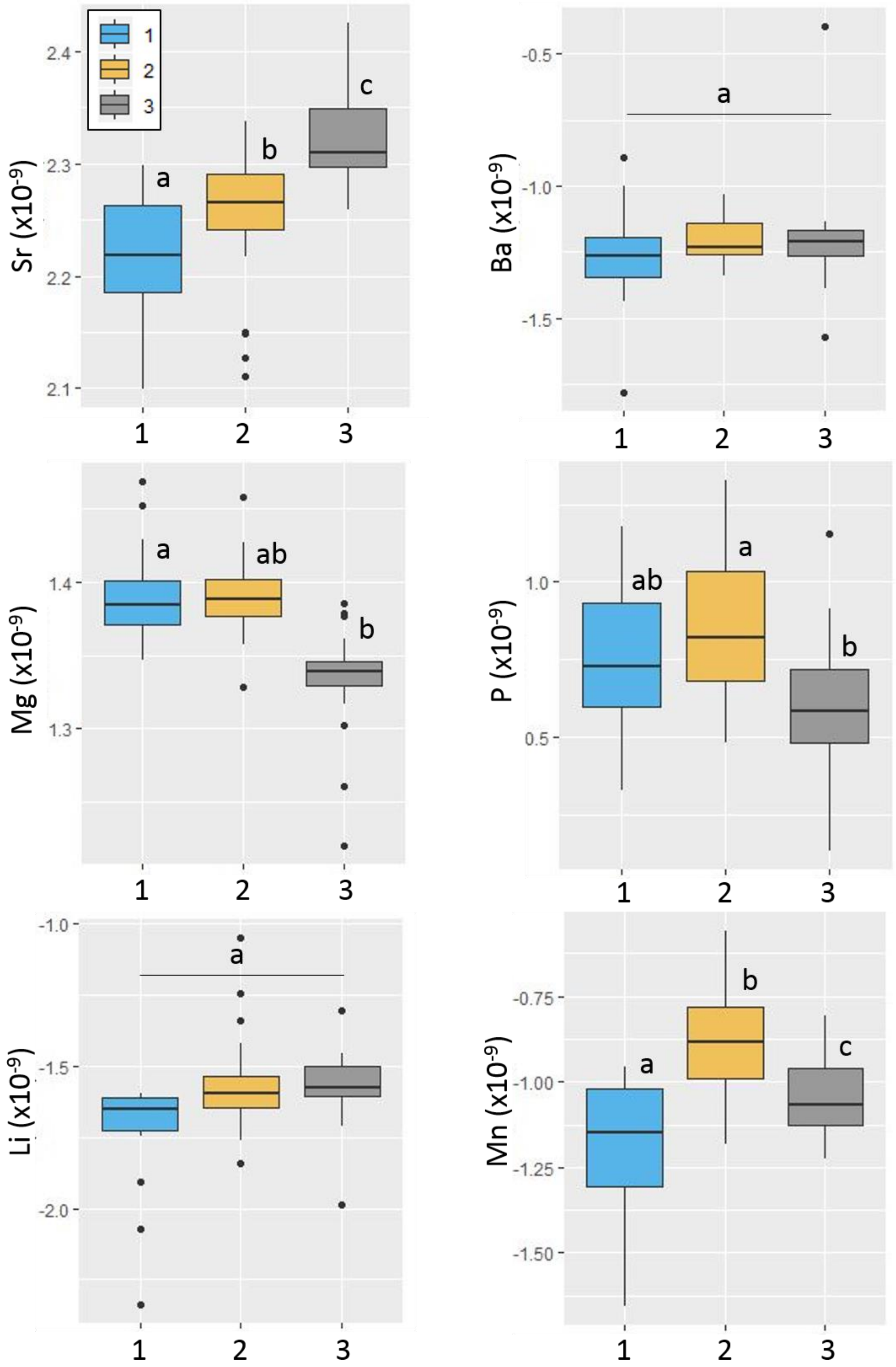


Figure 3.5 Differences in elemental concentrations (µg g^{-1}) between the three clusters. Letters denote significant differences (p=<0.05) from an ANOVA with Tukey HSD *post-hoc* pairwise comparisons.

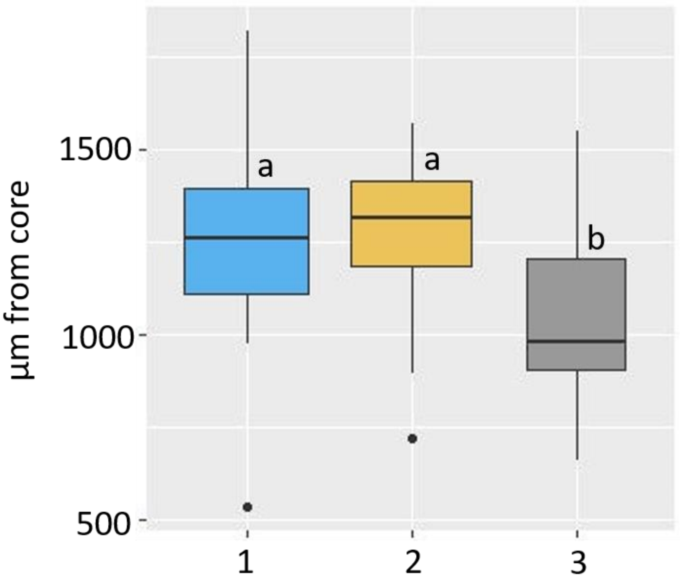


Figure 3.6 Differences in otolith growth rate (as a proxy for fish growth) at the end of the first year of life between the three clusters. Box width relative to individuals in each cluster. Letters denote significant differences (p=<0.05).

3.5 Discussion

We investigated whether *S. aurata* captured at the northernmost edge of their distribution recruit either from a single or from multiple source populations. The otolith microchemistry approach that we applied provides evidence for the environmental conditions experienced by *S. aurata* larvae during larval life. Otolith elemental concentrations can also be affected by many other factors, for example, in response to diet and intrinsic factors. By using the same part of the otolith in each individual, we have controlled for the influence of physiology (e.g. larval metamorphosis) between individuals. We also avoided using data from the core, to avoid bias from the maternal egg signal (Hegg et al., 2019).

We used multi-elemental signals near otolith cores to identify three different groups that were relatively temporally stable over multiple cohorts of fish. These identified groups of shared similar otolith chemistry could either represent spatially different spawning locations, or temporal differences across the spawning season. Our results also suggest some population structure at the northern edge of *S. aurata*'s range, with the relative contributions of each identified source differing between the sampling sites.

3.5.1 *Spatial vs temporal influences on otolith chemistry*

Our results suggest that northern-caught *S. aurata* early-stage larvae experience multiple environmental conditions, and do not all originate from the same place at the same time. Due to the long duration of *S. aurata*'s spawning season, observed differences in otolith elemental composition could represent either spatial or temporal differences in seawater environmental characteristics (Campana, 1999; Thorrold et al., 1997a). The oceanographic conditions of potential source populations vary considerably spatially and temporally (Figure 3.1). In the Bay of Biscay, there are also two rivers (the Gironde and Loire) that have high levels of runoff during the winter, which will impact the temperature, salinity and elemental composition of coastal waters during that time (Kelly-Gerreyn et al., 2006; Puillat et al., 2004).

The multi-element approach to analysing otolith chemistry we applied has more discriminatory power than using single elements (Leakey et al., 2009; Marriott et al., 2016; Mercier et al., 2012; T. A. Rogers et al., 2019; Thorrold et al., 1997b;

Tournois et al., 2013). However, the uptake of each of these elements into the otolith can be affected differentially by environmental and physiological influences. Hard acid elements (e.g. Sr, Ba and Mn) have similar ionic radii to Ca, substituting easily for Ca within the otolith material (Elsdon & Gillanders, 2003; A. M. Sturrock et al., 2012; B. D. Walther & Thorrold, 2006). Sr generally has a positive relationship with salinity and is often used for discriminating between marine and freshwater environments (Elsdon & Gillanders, 2006; Gillanders, 2005; Martin & Thorrold, 2005; B. D. Walther & Limburg, 2012). Sea temperature can also have a negative relationship with Sr in temperate marine species (Elsdon & Gillanders, 2002, 2004; Secor & Rooker, 2000). For example, Avignon (2017) successfully used Sr to infer movement of *S. aurata* individuals between marine and estuarine environments in the Northeast Atlantic, with higher Sr values observed in fish occupying marine environments. Therefore, the significantly higher values for Sr we observe in cluster three are likely to represent cooler, more saline water that has less coastal influence compared to the other clusters. This signal could represent areas in the Bay of Biscay that are less influenced by river outflows earlier in the spawning season, or cooler areas further north (Figure 3.1). Clusters one and two had lower concentrations of Sr, suggesting that they represent warmer, potentially less saline water. For example, towards the end of the spawning season in the Bay of Biscay, temperatures are likely to be warmer but still influenced by freshwater runoff from the Gironde and the Loire (Figure 3.1).

Although also a hard acid element, Mg is important in various biological processes. For example, Mg is positively correlated with growth and metabolic rate (Limburg et al., 2018; Martin & Thorrold, 2005; Weiner, 2008). Therefore, changes in Mg are less likely to be a direct environmental signal, although physiologically-induced changes in otolith chemistry can also be an indirect response to spatial or temporal changes in environmental conditions (Limburg et al., 2018; Anna M. Sturrock et al., 2015). Mn is often used as a discriminatory element in marine and coastal studies and can have both a negative (Limburg & Casini, 2018; J. A. Miller, 2009) and positive (Marohn et al., 2011) relationship with temperature. Higher Mn levels are also associated with hypoxic conditions (Limburg & Casini, 2018).

There is limited understanding on the uptake of Li into the otolith matrix, but it can also have a positive relationship with salinity and temperature (Hicks et al., 2010; Milton & Chenery, 2001; Anna M. Sturrock et al., 2014). Explanations for concentrations of P in the otolith matrix are rare, but it could be an indicator of variations in ambient water concentrations (Fengqin et al., 2011).

3.5.2 *Location of source populations*

Ocean hydrodynamics that can affect larval dispersal in and around the Bay of Biscay are complex (Ayata et al., 2010; Puillat et al., 2004), but it is feasible that at least some of the northern recruits come from spawning events in the Bay of Biscay. A previous study that investigated water transport from two river outflows in the Bay of Biscay (the Loire and Gironde) found that the transport of these waters into the Western English Channel was likely to be a common occurrence during winter (Kelly-Gerreyn et al., 2006), coinciding with the spawning season of *S. aurata*. Another study that used a coupled bio-physical individual-based model to investigate invertebrate larval connectivity between the Bay of Biscay and the English Channel found evidence for connectivity under certain conditions, including a late winter/early spring spawning event and long larval duration (4 weeks) (Ayata et al., 2010). *Sparus aurata* has a reported pelagic larval duration of between 45-100 days in the Mediterranean (Lett et al., 2019), which is therefore likely to be long enough to facilitate dispersal between the Bay of Biscay and sites in the English Channel.

To determine the exact locations of source populations is beyond the scope of this paper; however, we can interpret the differences in element concentrations observed between the identified clusters with caution:

Cluster one

Cluster one had the lowest concentrations of Sr, Li and Mn and high concentrations of Mg. The negative relationship between Sr and Li with temperature and the positive relationship between Sr and salinity could indicate that this represents warmer, less saline water. In the Bay of Biscay, the water temperature over the spawning season varies from 10-15˚C (Figure 3.1). There are also two large freshwater riverine outputs (the Loire and the Gironde) affecting salinity levels in the Bay of Biscay that are greatest during the winter, over the spawning season (Kelly-Gerreyn et al., 2006). The higher concentrations of Mg observed could represent a higher growth rate by individuals in cluster one (Martin & Thorrold, 2005), which would be facilitated by higher temperatures. Individuals in clusters one and two were also significantly larger than cluster three by the end of the first year of life, which also supports higher growth rates (Figure 3.6). Further research into the relative growth rates of the larval and juvenile portion of the otolith is needed to explore this hypothesis further (Isnard et al., 2015).

Cluster two

Cluster two had higher concentrations of Sr compared to cluster one, similar concentrations of Mg and Li, and the highest concentrations of Mn. The elevated Sr concentrations observed in cluster two compared to cluster one could indicate cooler, more saline water. Cluster two could represent a source population further north, or earlier in the spawning season compared to cluster one. The concentration of Mn concentrations from terrestrial origins decreases with both depth and distance from the coast (Benchetrit et al., 2017; Bruland & Lohan, 2003). Mn has previously been used to discriminate between marine and coastally influenced waters (Forrester & Swearer, 2002; Leakey et al., 2009; Moore & Simpfendorfer, 2014). Therefore, this higher level of Mn observed in cluster two could also represent a source population exposed to higher levels of river runoff. For example, adult *S. aurata* captured in the Bay of Biscay showed high levels of otolith Mn, suggested to be an influence from proximity to the river Gironde (Avignon, 2017).

Cluster three

Cluster three had the highest concentrations of Sr, lowest concentrations of Mg and medium concentrations of Mn compared to clusters one and two. Higher Sr concentrations could be indicative of a lower temperature and higher salinity. We only observed a small number of individuals captured from Weymouth Bay in cluster three (Figure 3.4), which could provide evidence for cluster three representing a later spawning event. The duration of *S. aurata's* spawning season

(Jan-April) combined with the pelagic larval stage duration (45-100 days) means that there could be a difference of up to four months between larval recruitment after spawning. Weymouth Bay is 200km east of the Fal and Helford Estuaries, so larvae travelling from the northern Bay of Biscay, or the Western Channel would likely take longer to reach nursery areas, resulting in a shorter feeding season. Individuals in cluster three were also significantly smaller than the other clusters (Figure 3.6). If individuals from cluster three represent a more northern source population, they are likely only to be able to spawn successfully towards the end of the season when temperatures reach an acceptable upper threshold. For example, there is only a small area in the western English Channel, where temperatures are above 10˚C during the spawning season (Figure 3.1). The findings of Avignon (2017) support this hypothesis, where northern *S. aurata* adults had the highest levels of Sr. Again, further research into the relative growth rates of the larval and juvenile portion of the otolith is needed to explore this hypothesis further (Isnard et al., 2015).

3.5.3 *Connectivity and contribution of source populations to each capture site*

We found that the capture location had a significant effect on the cluster assignment, suggesting that there was some differentiation between the source populations contributing to each site (Figure 3.4). The Fal and Helford Estuaries and Weymouth Bay are approximately 200km apart (Figure 3.2). If all northern caught fish came from the same source population, we would expect to see no significant difference in element concentrations between the capture locations. The observed differences suggest that there is an element of structuring between the two capture locations and that they could rely on different source populations for larval recruits. However, we also found fish from both sites in all three clusters, providing evidence for mixing after spawning. Mixing could occur either during the larval dispersal phase or from subsequent adult movement. One way of investigating this hypothesis would be to analyse the otolith signature of newly recruited 0-group fish in different nursery areas. This signature would potentially identify multi-element signatures for specific nursery areas. Analysing the nursery signature, along with the part of the otolith representing the source population, would provide evidence for when population mixing occurred, as well as identifying the relative contributions of source populations to different nursery areas.

3.5.4 *Further considerations*

In Chapter 2, we suggest that local adaptation at the northern edge of *S. aurata's* range could be facilitating source populations of *S. aurata* further north than previously thought. Local adaptation to marginal habitats is only possible with the establishment of locally-spawning populations (Kawecki, 2008). If local adaptation has occurred, there are likely to be source populations further north than previously suggested, possibly in the Western English Channel where temperatures towards the end of the spawning season could facilitate larval survival (Donelson et al., 2019; Sorte et al., 2011). Identifying the potential routes between adult spawning grounds and nursery areas would provide useful information to further interpret the levels of connectivity between the Bay of Biscay and more northerly nursery areas. For example, through the development of an individual-based model coupled with hydrodynamics to track particles, specific to *S. aurata* larval characteristics (Beraud et al., 2017).

3.6 Conclusion

We provide tentative evidence that multiple sources are contributing to *S. aurata* populations in the English Channel, and that these could be occurring at higher latitudes than previously thought. Although we found some differences, we also found evidence for a high level of mixing of the sources between two sites that are 200 kilometres apart. This mixing could occur during larval dispersal or subsequent adult movement. Understanding the balance of source/sink population dynamics is important for successful fisheries management, especially for species that are expanding their range into new areas. *S. aurata* is an attractive target fish to both the commercial and recreational fishing industry, and sustainable management of this species should be carried out at the appropriate level to protect source populations.

3.7 Supplementary information

Table S3.1 LA-ICPMS analytical details

New Wave NWR 193 Laser Ablation System	
Sample chamber	TwoVol2 Cell with Teflon transfer tubing and quartz mixing cell
He carrier gas	650ml/min
N_2 additional gas	6ml/min
Spot size	35µm
Raster rate	5 µm/sec
Laser Power	60%
Repetition rate	7hz
Analysis time	3-12 minutes (depending on otolith size)
Thermo Fisher Scientific ELEMENT XR	
Using Jet Interface pump, Jet sample cone (Ni), 'X' skimmer cone (Ni)	
Ar cool gas	15l/min
Ar auxiliary gas	0.8l/min
Ar sample gas	0.6-0.7l/min
Acquisition	'Speed' mode

Table S3.2 Details of the number of individuals from each cohort (left) and region (right) assigned to each cluster

Cohort	**Cluster**			**Total**
	1	**2**	**3**	
2007	2	1	0	**3**
2008	2	1	0	**3**
2011	1	0	1	**2**
2012	1	1	0	**2**
2013	1	2	0	**3**
2014	10	6	2	**18**
2015	9	10	4	**23**
2016	7	9	9	**25**
2017	1	1	5	**7**
Total	**34**	**31**	**21**	

Region	**Cluster**			**Total**
	1	**2**	**3**	
FalHelford	23	15	17	**54**
Portland	11	16	4	**31**
Total	**34**	**31**	**21**	

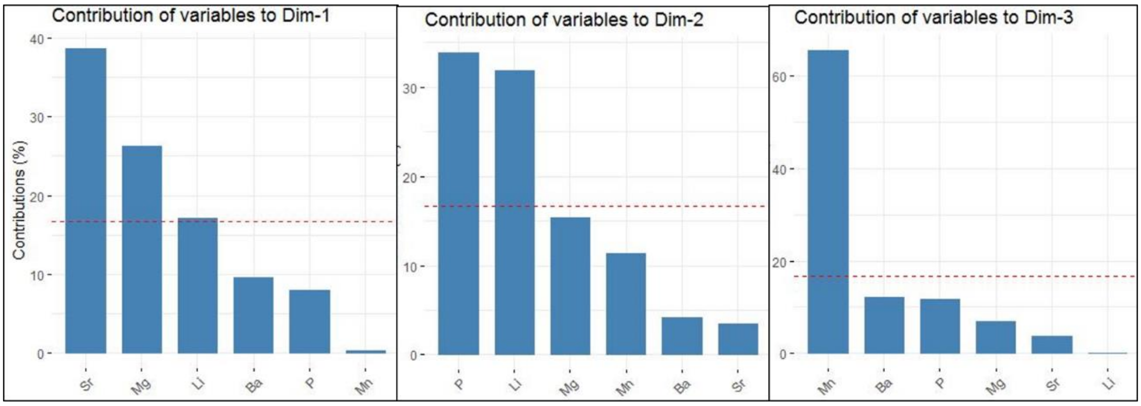


Figure S3.1 Contribution of different elements to the first three principal components. The red line indicates the percentage where each element would contribute equally to the principal component (16.7%)

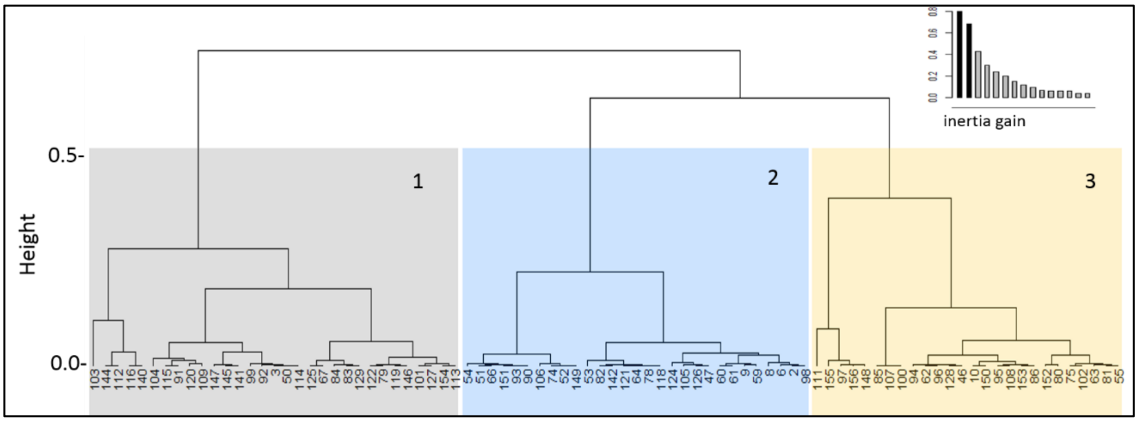


Figure S3.2 Hierarchical clustering dendrogram showing inertia gain at different levels

Chapter 4

Potential resource competition between coexisting juvenile gilthead seabream *Sparus aurata* and European seabass *Dicentrarchus labrax*

4.1 Abstract

Changes in species distribution can affect resource competition between species that occupy similar ecological niches. Gilthead seabream *Sparus aurata* has undergone a recent poleward range expansion into the English Channel and the Celtic Sea, a pattern that is likely to continue with future climate warming. *Sparus aurata* has a similar life history and occupies a similar ecological niche to European seabass *Dicentrarchus labrax,* populations which are currently in steep decline in the Northeast Atlantic. Juveniles of *S. aurata* and *D. labrax* have similar diets and are likely to experience resource competition when inhabiting the same areas. Therefore, an increase in *S. aurata* population levels, as a result of further range expansion, could result in niche competition with *D. labrax.* Here, we use stable isotope techniques to quantify the relative isotopic niche widths and overlap of each species at the northern range edge of *S. aurata.* We find contrasting patterns between the isotopic niche widths of *S. aurata* and *D. labrax*, with *S. aurata's* starting relatively wide and decreasing with age, and *D. labrax* showing the opposite pattern. Our results suggest that although both species are coexisting within the same habitat and feed on similar prey sources, they have different realised ecological niches within our study system. The observed resource partitioning between *S. aurata* and *D. labrax* may indicate interspecific competition. However, further work is needed to identify whether the presence of *S. aurata* is having a negative competitive effect or a positive indirect effect (through indirect mutualism) on *D. labrax* populations. To our knowledge, this is the first study to examine potential resource competition between the two study species as a consequence of a *S. aurata* range expansion.

4.2 Introduction

Changes in species distribution can affect resource competition between species (Gilman et al., 2010). Over recent years, gilthead seabream *Sparus aurata* (Linnaeus 1758) has been captured more frequently at the northern edge of its range (Craig et al., 2008; Fahy et al., 2005). This observed range-shift is bringing more individuals into the area, potentially competing for resources with species that are already there. In Chapter 2, we applied bioclimatic envelope models to known observations of *S. aurata* and projected the distribution into the future under different climate change scenarios. Under both scenarios, the range showed a poleward shift over time, suggesting *S. aurata* is likely to become more abundant in the English Channel, the Celtic Sea, and possibly the North Sea. Therefore it is essential to understand the ecology of *S. aurata* at the northern edge of its range and identify possible impacts on native species.

4.2.1 *Gilthead seabream and European seabass*

Sparus aurata occupies a similar fundamental niche to the native European seabass *Dicentrarchus labrax*. Both *S. aurata* and *D. labrax* are coastal euryhaline species that exploit a range of marine and estuarine environments. Mature individuals of both species spawn in the open sea over winter/early spring, and larvae remain pelagic for approximately three months at sea before settling in nursery areas, such as estuaries or lagoons (Beraud et al., 2017; Jennings & Pawson, 1992; Mercier et al., 2012; Pawson et al., 2007) (Figure 1.1). Most juvenile *D. labrax* and *S. aurata* individuals spend the first few years of life within these nursery areas, dependent on the productive intertidal habitats (Mercier et al., 2012; Pickett & Pawson, 1994). *D. labrax* population levels are currently in such steep decline that recommended catch recommendations have dropped considerably in recent years (ICES, 2015; UK Government, 2015). In the UK, ‘Bass Nursery Areas’ are designated in areas known to be important for juvenile bass, where fishing is restricted for all or part of the year (MAFF, 1990). The decline in *D. labrax* stocks is likely to be linked to increased fishing pressure and high juvenile mortality as a result of recent winter conditions (Ares, 2016). Although the coexistence of *D. labrax* and *S. aurata* is not novel in other areas of their range, the range-shift of *S. aurata* in the Northeast Atlantic could result in increased resource competition with *D. labrax*, a species already in decline, especially if *S. aurata* populations continue to increase and move poleward (as predicted in Chapter 2).

As an opportunistic generalist, the diet of *S. aurata* varies geographically and relies on invertebrates as a major prey source (Avignon et al., 2017). The diet of juvenile individuals primarily consists of small crustaceans (shrimp, prawns, crabs, isopods, amphipods), bivalves, gastropods and polychaetes (Fahy et al., 2005; Tancioni et al., 2003). Juvenile *D. labrax* has a very similar diet (Fonseca et al., 2011; Kelley, 1987; Martinho et al., 2008; Pinnegar, 2014). There is evidence that both species vary their diet geographically, depending on the variety of different prey sources available in the area (Avignon et al., 2017; Cardoso et al., 2015; Fonseca et al., 2011; Laffaille et al., 2001; Schattenhofer et al., 2009). The diet of both species diversifies and also diverges to some extent with age with *S. aurata* consuming a wider range of molluscs (mussels, scallops, chitons), larger crustaceans, coralline algae and the occasional fish (Avignon et al., 2017; Hadj et al., 2013; Mariani et al., 2002; Tancioni et al., 2003). Adult *D. labrax* forage at generally higher trophic levels than juveniles, with fish and crustaceans being the primary dietary components (Kelley, 1987). Therefore, the most potential for resource competition between the two species is likely to occur at the juvenile stage (Ferrari & Chieregato, 1981). As far as we are aware, this potential for competition between juvenile *S. aurata* and *D. labrax,* as a consequence of the range expansion, has not been studied before.

4.2.2 *Stable isotopes*

One way to understand the extent of resource competition between the two species is to identify trophic overlap in areas where they both coexist (S. T. Ross, 1986; Sánchez-Hernández et al., 2017). Observational and molecular methods of diet analysis are useful here but also have limitations. Such techniques only offer a snapshot in time of the diet. Hard-to-digest prey is often overestimated, and soft-bodied items are hard or impossible to identify and quantify (Lamb et al., 2019). An alternative and complementary method, given prior knowledge of dietary items, is the use of stable isotope analysis. Stable isotope ratios (expressed as δ-values) are incorporated into tissues of organisms, relative to the values in prey sources (Parnell et al., 2013; D. L. Phillips et al., 2014).

Therefore by analysing stable isotope ratios of consumer tissues, it is possible to get information about the longer-term importance of different diet resources. For example, the cell turnover rate of muscle tissue in fish represents 49-107 days (Buchheister & Latour, 2010). Stable isotope techniques are especially useful for species that are challenging to observe for extended periods in the field, such as marine fish (J. G. Gonzalez et al., 2019; Inger et al., 2010; Polačik et al., 2014). Stable isotope values can also be affected by factors other than diets, such as body condition, size and metabolic rate, but are widely accepted to be of ecological origin (Jackson et al., 2011). $\delta^{15}N$ can be used to estimate trophic position because the $\delta^{15}N$ value of a consumer generally increases by 3-4‰ relative to its prey source, a process known as fractionation (Minagawa & Wada, 1984; Peterson & Fry, 1987; Post, 2002). $\delta^{13}C$ values are more conservative as carbon moves through food webs, and can, therefore, provide information on different sources of carbon consumed by primary consumers. For example, in the marine environment, there are $\delta^{13}C$ differences between benthic primary production, and pelagic primary production (France, 1995). However, both $\delta^{13}C$ and $\delta^{15}N$ are also affected by environmental and anthropogenic influences and can vary spatially and temporally, for example along an estuarine – coastal gradient (Cambiè et al., 2016; Connolly et al., 2013; A. M. Darnaude et al., 2004; Panfili et al., 2015). Therefore understanding the background variation within a system is essential before making inferences about the isotopic information obtained from consumer tissues. Long-lived invertebrates that feed on primary producers are the best models to understand this background variation (Post, 2002). Therefore, by sampling both grazing gastropods and filter feeders across the area of interest, it is possible to obtain site-specific baseline information on the relative amount of $\delta^{13}C$ derived from both benthic and pelagic sources of primary production, and the background levels of $\delta^{15}N$ within the system (Cabana & Rasmussen, 1996). Known background levels make it possible to make inferences, based on the observed stable isotope ratios in consumer tissues.

Variation in isotopic niche space characterises intra and inter-individual variation, and is commonly used as a proxy for a species realised ecological niche (J. G. Gonzalez et al., 2019; Jackson et al., 2011; Newsome et al., 2007). Comparing isotopic niche widths between species also provides information on the amount of potential for resource competition (Bearhop et al., 2004; J. G. Gonzalez et al., 2019; Jackson et al., 2011; Newsome et al., 2007). Here, we first quantify and compare the relative isotopic niche widths and overlap of juvenile *S. aurata* and *D. labrax* using Bayesian standard ellipses areas (Jackson et al., 2011) and use Layman's isotopic niche metrics to quantify the differences in niche widths (Layman & Post, 2007). We then use a Bayesian mixing model framework to quantify the relative proportions of known prey sources in the diet of *S. aurata* and *D. labrax,* based on consumer tissue isotopic variation (Stock et al., 2018). To our knowledge, this is the first study to examine potential resource competition between the two species as a consequence of a *S. aurata* range expansion.

4.3 Methods

4.3.1 *Consumer and prey samples*

We sampled juvenile *S. aurata* and *D. labrax* from the Fal and Helford Estuaries (designated Bass Nursery Areas (MAFF, 1990)), between August 2016 and August 2018 (Figure 4.1, Table S4.1). For prey sources, we used Gastropods, Bivalves, Malacostraca and Polychaetes (known common prey sources for both species) from across the Fal and Helford Estuaries (Table S4.2). We conducted all lethal fish sampling under Schedule 1 of the Animals [scientific procedures] Act, 1986. Before the study commenced, we obtained authorisations from Cornwall IFCA, Natural England and the Marine Management Organisation. We also had approval from the University of Exeter Ethics Committee for this study 2016/1449.

4.3.2 *Stable isotope analysis*

To sample consumer tissue, we took small plugs of white muscle from below the dorsal fin. We removed skin and bones to avoid isotopic disparity from inorganic carbon. To sample prey sources, we sampled tissue from the foot of grazing gastropods and the adductor muscle from filter-feeding bivalves. For Malacostraca samples, we took muscle tissue and for Polychaete samples, we used the whole organism. We freeze dried all tissue samples for 24 hours, and then sealed and stored at room temperature until subsequent analysis. After homogenisation with a pestle and mortar, we weighed 0.7±0.1 mg into tin capsules using a Mettler-Toledo MX5 balance with a precision of 0.001 mg. We analysed all samples for $\delta^{13}C$ and $\delta^{15}N$ values at NERC Life Sciences Mass Spectrometry Facility, SUERC, using an Elementar Vario Pyrocube (Hanau, Germany) coupled to an IsoPrime (now Elementar) VisION Mass Spectrometer (Cheadle, UK). The internal reference materials (mean ± SD) were GEL (gelatin solution, $\delta^{13}C$= -20.09 ± 0.19‰, $\delta^{15}N$= 5.59 ± 0.12‰), ALAGEL (alanine-gelatine solution spiked with 13C-alanine, $\delta^{13}C$= -8.69 ± 0.17, $\delta^{15}N$= 2.22 ± 0.08‰), and GLYGEL (glycine-gelatine solution, $\delta^{13}C$= -38.35 ± 0.13‰, $\delta^{15}N$= 23.19 ± 0.22‰), each dried for two hours at 70°C. We used four USGS 40 glutamic acid standards (Coplen et al., 2006; Qi et al., 2003) as independent checks of accuracy.

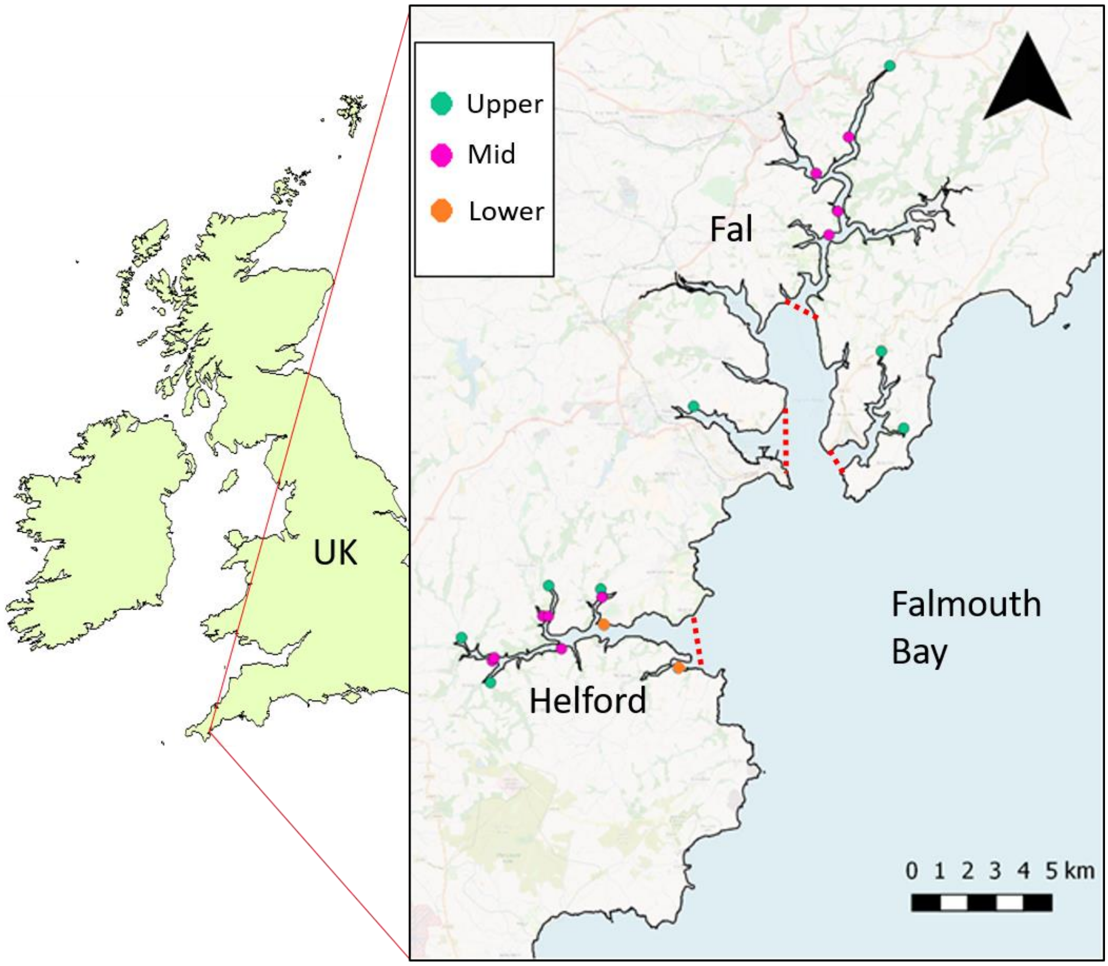


Figure 4.1 Map showing the Fal and Helford estuaries. Points show prey source sample locations. Consumer samples of both species were captured from the same areas as prey samples, within the areas indicated by red dashed lines

4.3.3 *Baselines*

To obtain an integrated long-term average of primary producer $\delta^{13}C$ and $\delta^{15}N$ values across the local area, we sampled tissue from the foot of grazing gastropods and the adductor muscle from filter-feeding bivalves. We collected gastropods (n = 56) and bivalves (n = 58) from across the Fal and Helford Estuaries (50°7'N, 5°3'W) between August 2016 – August 2018 (Table S4.2). Both the Fal and Helford that consist of predominantly marine habitats, as they receive very low freshwater input. From the baseline data, we can make inferences about the trophic level at which each fish species is feeding, with an assumed diet-tissue fractionation rate ($\delta^{15}N$) of 3.4‰ between trophic levels (Cabana & Rasmussen, 1996). $\delta^{13}C$ has a relatively low fractionation rate as it moves through trophic levels, so any observed changes in $\delta^{13}C$ represent information on the amount of basal energy derived from either benthic or pelagic sources. To investigate the differences in isotope values between benthic and pelagic prey sources, we fitted a multiple linear regression model. We fitted separate models for $\delta^{13}C$ and $\delta^{15}N$ (continuous dependent variables) with the categorical independent variable being the energy source (benthic or pelagic).

To help interpret the results, we also investigated how much spatial isotopic variation there was across prey source sample locations. We used a 1-way ANOVA for each isotope (the continuous dependent variable) with the sample location (upper, mid, lower estuary) as the categorical independent variable. We followed this with Tukey's HSD *post-hoc* test to identify how the isotopic values differed spatially. We conducted all analysis for this study using R version 3.6.0 (R Core Team, 2019).

4.3.4 *Lipid extractions*

Lipid concentrations vary seasonally and between individuals (Gallagher et al., 1989; Perkins et al., 2013). Tissues that are high in lipid are also depleted in $\delta^{13}C$, relative to proteinaceous tissues. Therefore it is a requirement to remove excess lipids from consumer tissue to get the true dietary $\delta^{13}C$ value (DeNiro & Epstein, 1977; Perkins et al., 2013; Post et al., 2007; Skinner et al., 2016). Lipids contain little nitrogen so theoretically have minimal effects on $\delta^{15}N$ values (Sweeting et al., 2006); however, the process of chemical lipid extraction can affect the values of $\delta^{15}N$. To identify whether there were excess lipids in the consumer samples, we conducted lipid extraction on a subset of ten samples of muscle (five for each species) using 2:1 Chloroform:Methanol wash. We used the Wilcoxon matched-pairs test for nonparametric data and found significant differences for both species ($V=55$, $p=0.002$). Untreated muscle samples were depleted in $\delta^{13}C$ by a mean of -0.83‰ (range -2.28 to -0.32‰). Therefore, to avoid running samples twice (once for $\delta^{15}N$ before lipid extraction treatment and then again for $\delta^{13}C$ after lipid treatment), we applied a mathematical correction to all of the untreated consumer samples to correct the $\delta^{13}C$ values. We used the recognised method from Post et al. (2007), which assumes that in aquatic organisms, there is a strong relationship between the carbon-to-nitrogen (C:N) and percentage lipid:

$$\delta^{13}C_{\text{normalised}} = \delta^{13}C_{\text{untreated}} - 3.32 + 0.99 \times C{:}N$$

Lipid extraction is not deemed necessary for invertebrate prey samples. The whole organism (including lipids) is available to the consumer as a prey source and is therefore reflected in the tissue of the consumer (Perkins et al., 2013).

4.3.5 *Quantifying isotopic niche space*

We used multivariate Bayesian standard ellipse areas (SEAc) to compare and quantify the isotopic niche space used by different age groups of *S. aurata* and *D. labrax* using the R package SIBER (Jackson et al., 2011). This method takes into account sampling error and other sources of uncertainty and allows us to make robust statistical comparisons. Isotopic niche area and overlap ($‰^2$) were estimated based on 100 000 posterior draws of the SEAc using Markov chain Monte Carlo (MCMC) simulation. We kept the default (uninformative) priors and used the default setting for the standard ellipse size, drawn on the core (approximately 40%) of the data (Jackson et al., 2011). We calculated the overlap of SEAc as a proportion of the non-overlapping area (a completely overlapping ellipse is equal to one, and a non-overlapping ellipse is equal to zero). To quantify differences between each species isotopic niche, we also calculated Layman's metrics based on the SEAc for each group, including the range of $\delta^{15}N$ as an indicator of prey trophic level diversity and the range of $\delta^{13}C$ as an indicator of diversity in basal energy sources (Layman & Post, 2007).

4.3.6 *Estimating proportions of prey in the diet*

To identify isotopically-discrete prey sources, we used the same modelling approach described for baseline data to investigate the difference between prey source isotope values, with the prey source as the categorical independent variable. We used stable isotope mixing models to estimate the proportion of isotopically-discrete prey sources in the diet of *S. aurata* and *D. labrax.* We used MixSIAR, a Bayesian mixed-effects framework that allows for individual variation by including the individuals as a random effect (Stock et al., 2018). Within the MixSIAR package, we conducted MCMC simulations by running three replicate chains, each with 1000,000 draws, removing the first 500,000 iterations as burn-in. We used uninformative (generalist) priors because although common prey items for each fish species are known, they are not quantified within this study system. We used MixSIAR to produce a range of solutions to the mixing model, to which we then assigned credibility intervals. We fitted mixing models using individual consumer stable isotope $\delta^{13}C$ and $\delta^{15}N$ values, the mean ± SD isotopic variation of prey sources and the trophic discrimination factors estimated by Post (2002) and Minagawa and Wada (1984) of $\delta^{13}C = 0.39 \pm 1.3$ SD and $\delta^{15}N = 3.4 \pm 0.98$ SD. Trophic discrimination is the amount of fractionation that occurs to the isotope values between trophic levels and is one of the biggest sources of uncertainty when using mixing models as it can be affected by multiple factors (DeNiro & Epstein, 1977). The discriminatory power of the mixing model decreases with the number of sources, especially when there are not large isotopic differences between the sources (D. L. Phillips et al., 2014). After inspecting the raw data, we combined prey sources into the three isotopically-discrete groups to give the model greater power. We included primary grazers (e.g. gastropods), primary filter feeders (e.g. bivalves), and secondary consumers (e.g. scavenging Malacostraca and polychaetes).

4.4 Results

4.4.1 *Baselines*

We found significant differences between the benthic and pelagic energy sources for both $\delta^{13}C$ and $\delta^{15}N$ values in the baseline data (Figure 4.2a). Benthic sources are significantly more enriched than pelagic in $\delta^{13}C$ (LM: $F_{1,112} = 168.36$, $p<0.001$, $R^2=0.59$) and $\delta^{15}N$ (LM: $F_{1,112} = 54.74$, $p<0.001$, $R^2=0.32$).

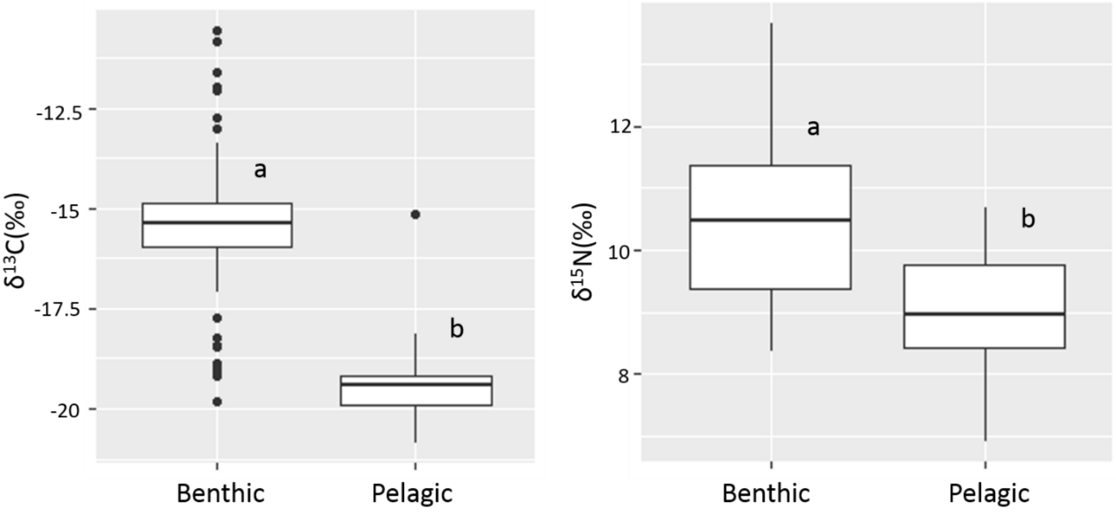


Figure 4.2a Variation in baseline data for benthic and pelagic sources of $\delta^{13}C$ (left) and $\delta^{15}N$ (right). Boxes represent the interquartile range. Whiskers show the minimum, and maximum values (excluding outliers) and the horizontal line represents the median value. Box width scaled to represent the number of samples included in each group. Data identified by different letters are statistically different

We found significant spatial differences for both $\delta^{13}C$ and $\delta^{15}N$ values (Figure 4.2b). Samples from the upper estuary were significantly depleted in $\delta^{13}C$ compared to samples from the mid and lower estuary (ANOVA: $F_{2,244} = 22.98$, $p < 0.001$). Samples from the lower estuary were significantly depleted in $\delta^{15}N$ compared to samples from the mid and upper estuary (ANOVA: $F_{2,244} = 18.07$, $p < 0.001$).

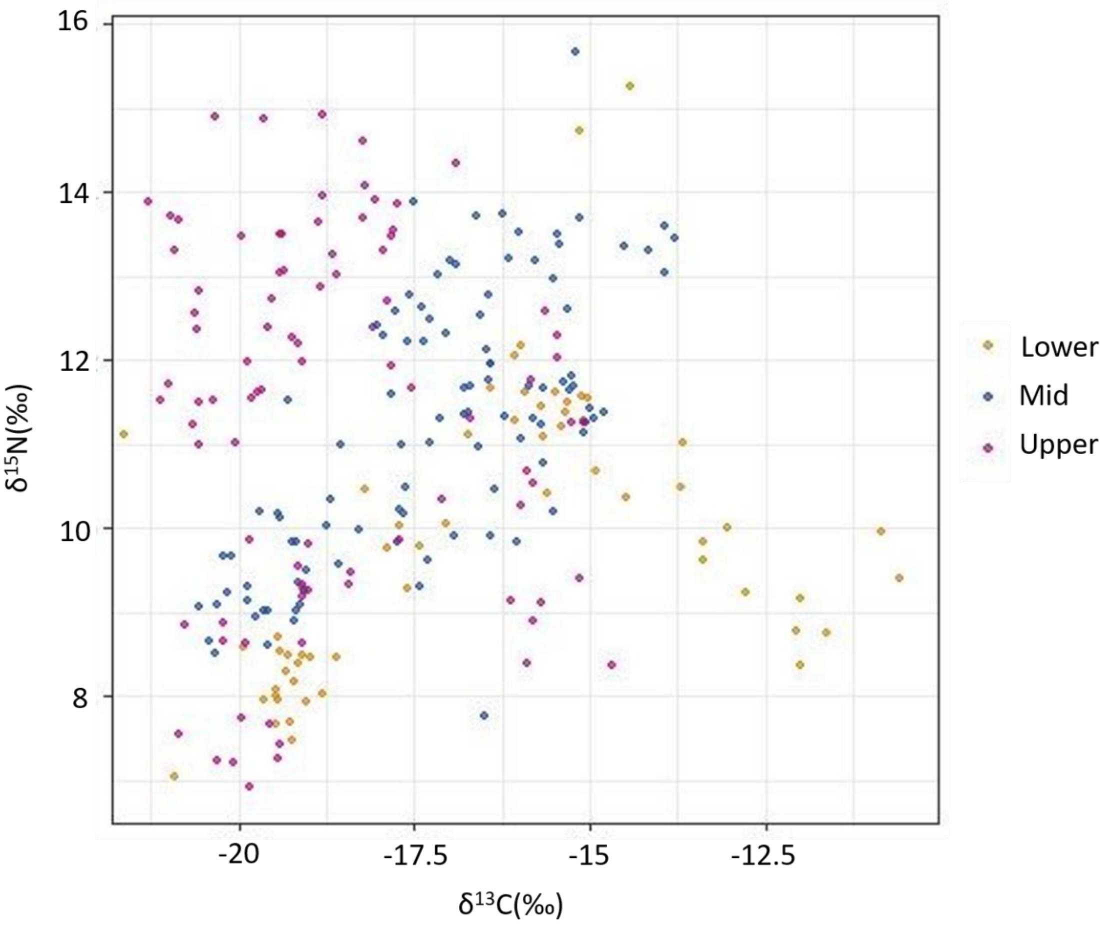


Figure 4.2b δ^{13}C - δ^{15}N bi-plot of prey sources coloured by sample location within the estuaries. Lower estuary sites in yellow, mid estuary sites in blue and upper estuary sites in blue

4.4.2 *Isotopically-discrete prey sources*

We grouped the prey sources into primary grazers (gastropods), primary filter feeders (bivalves) and secondary scavengers (polychaetes and Malacostraca). We found significant differences between the isotopic compositions of the prey sources for both $\delta^{13}C$ and $\delta^{15}N$ (Figure 4.3). Primary filter feeders (mean -19.44 ± 0.83 SD) and secondary scavengers (mean -17.44 ± 1.64 SD) were both significantly depleted in $\delta^{13}C$ compared to primary grazers (mean -15.43 ± 2.13 SD), and secondary scavengers were enriched in $\delta^{13}C$ compared to primary filter feeders (LM: $F_{1,336}$=85.483, p<0.001, R^2=0.33). Primary grazers (mean 10.37 ± 1.08 SD) and primary filter feeders (mean 9.96 ± 0.97 SD) were both significantly depleted in $\delta^{15}N$ compared to secondary consumers (mean 12.33 ± 1.15 SD) (LM: $F_{1,336}$=244.94, p<0.001, R^2=0.59). Primary grazers had enriched $\delta^{15}N$ compared to primary filter feeders.

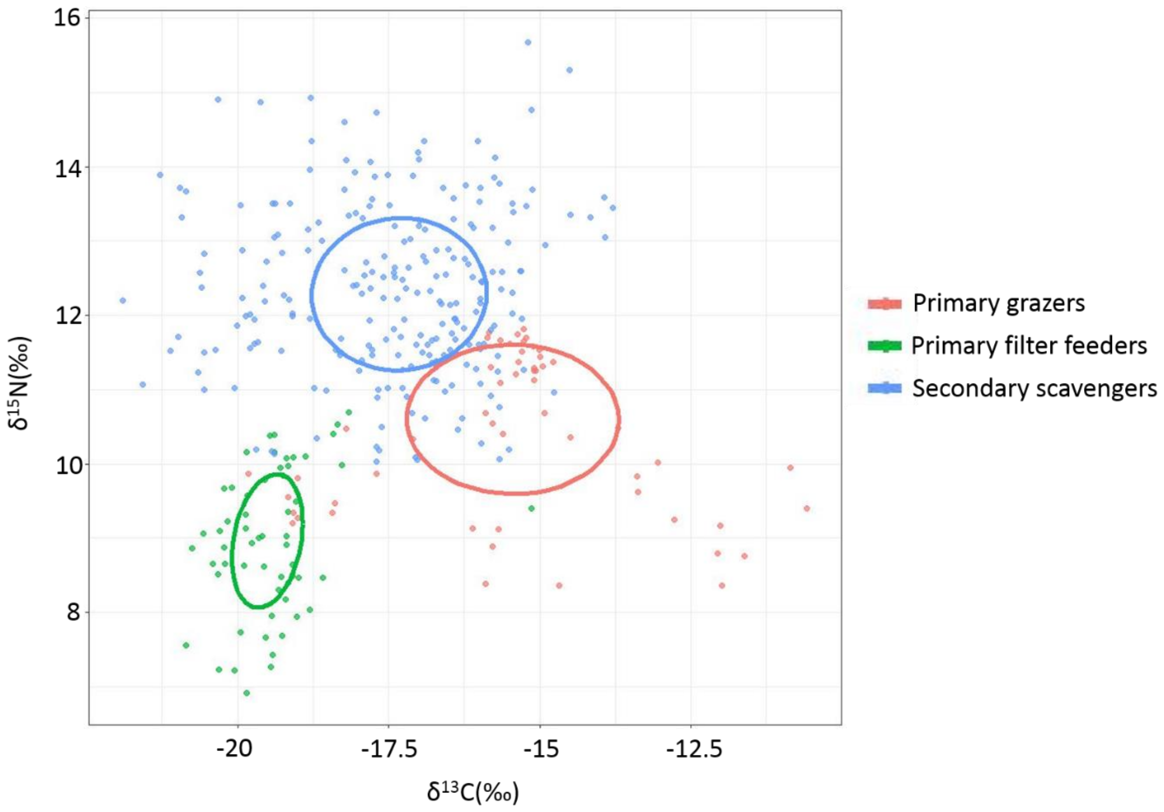


Figure 4.3 $\delta^{13}C$ - $\delta^{15}N$ bi-plot of prey sources used in the mixing model. Primary grazers in red, primary filter feeders in green and secondary scavengers in blue. Ellipses scaled to cover the core data (approximately 40% the data).

4.4.3 *Quantifying isotopic niche space*

We used the isotopic values from *S. aurata* and *D. labrax* muscle to estimate the isotopic niche width. When looking at the standard ellipse areas (SEAc) for all age groups combined, both *S. aurata* and *D. labrax* had a similar-sized isotopic niche (2.88 and 2.90 respectively) (Table 4.1). *D. labrax* had a slightly higher range for δ^{15}N (3.44‰) compared to *S. aurata* (3.28‰). *S. aurata* had a higher range for δ^{13}C (7.64‰) compared to *D. labrax* (5.67‰). Breaking this down into age groups (Table 4.1), the isotopic niche width (SEAc) for *S. aurata* decreases with age from 3.16 to 1.17. For *D. labrax*, the width of the niche increases with age, from 1.17 to 3.39. *S. aurata* had the highest δ^{15}N range aged 0 (3.1‰) that decreased in years 1 and 2. The δ^{15}N range for *D. labrax* increased with age from 0.3 to 5.67‰.

The proportion of overlap in shared isotopic niche space (SEAc) between the two species over all age groups was 0.14. The largest overlap between the age groups was between *S. aurata* and *D. labrax* 1-groups at 0.22, followed by *S. aurata* 0-group and *D. labrax* 1-group (0.16) (Figure 4.4, Table 4.2).

Table 4.1 Isotopic niche width (SEAc) and metrics for *S. aurata* and *D. labrax* between different age groups

	S. aurata				***D. labrax***			
	All age groups	**0**	**1**	**2**	**All age groups**	**0**	**1**	**2**
SEAc	2.88	3.16	1.6	1.17	2.90	0.14	0.67	3.39
δ^{15}N range (‰)	3.28	3.1	1.17	1.52	3.44	0.3	1.17	3.44
δ^{13}C range (‰)	7.64	7.15	3.04	2.97	5.67	0.75	1.15	5.67

Table 4.2. Overlap of SEAc as a proportion of the non-overlapping area between *S. aurata* and *D. labrax* for each age group

		S. aurata		
	Age	**0**	**1**	**2**
D. labrax	**0**	0.04	0.09	0.00
	1	0.16	0.22	0.00
	2	0.05	0.03	0.00

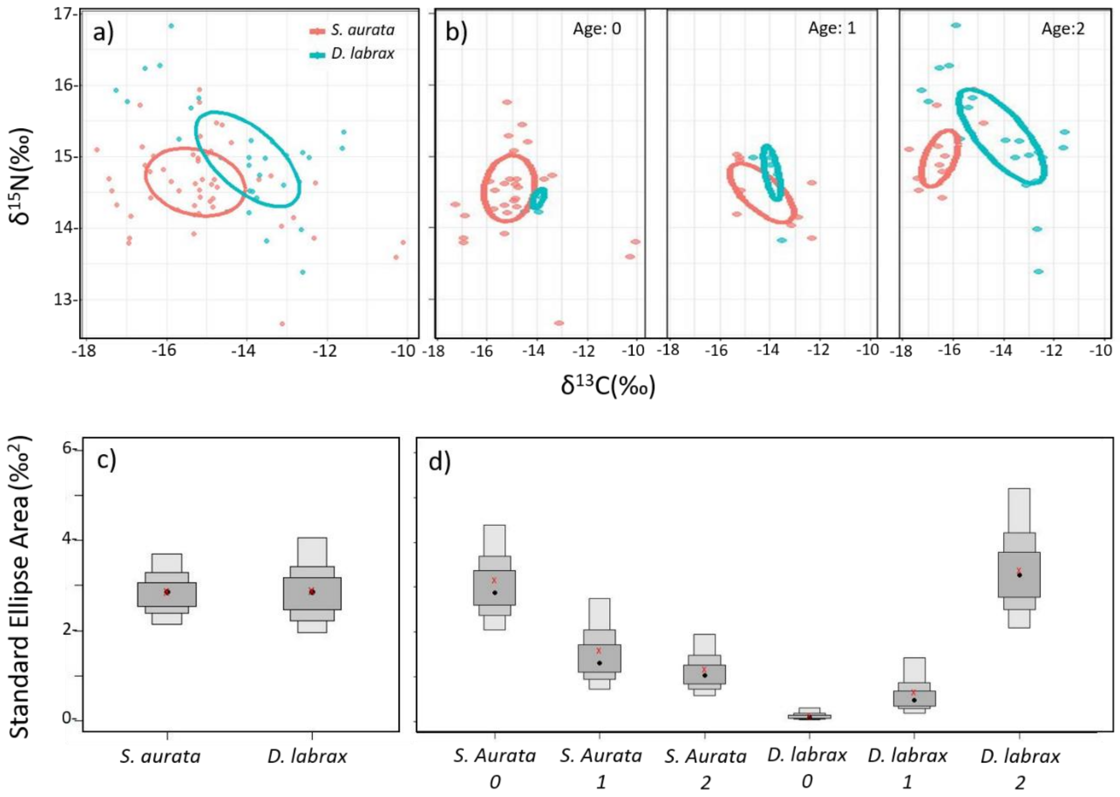


Figure 4.4 Standard ellipse areas (SEAc) over the core of the data (40%) to show relative isotopic niche for *S. aurata* and *D. labrax* (a) all individuals and (b) split by age group. SIBER density plots showing the Bayesian estimates of standard ellipse areas (SEAb) to show niche width for *S. aurata* and *D. labrax* (c) all individuals and (d) split by age group. Black dots represent the mode value of SEAb, and the red crosses represent the mode of the SEAc. The shading represents the 50, 75 and 95% credible intervals.

4.4.4 *Estimating proportions of prey in the diet*

We used the isotopic values from *S. aurata* and *D. labrax* muscle in the MixSIAR mixing model to estimate the contribution of different prey sources to long-term consumer diet. The mixing model shows that primary filter feeders are not an important prey source for either species during the first three years of life, with an estimated 2% overall median contribution to *S. aurata* diet and 1% for *D. labrax* (Figure 4.5, Table S4.3). We also found that primary grazers are the most important prey source for both species in the first two years of life, and that secondary scavengers become more important for both species in year three (Figure 4.5, Table S4.3). Primary grazers make up 56-85% of the diet for *S.*

aurata in the first year of life, falling to 22-53% by year three (Figure 4.5, Table S4.3). The mixing model results show more variation for *D. labrax* compared to *S. aurata.* Primary grazers make up 49-98% of the diet in year one, falling to 16-87% in year three. Secondary scavengers become more important for both species with age (Figure 4.5, Table S4.3), making up 14-42% of the diet for *S. aurata* in the first year of life, rising to 47-76% in the third year of life. For *D. labrax*, secondary scavengers make up 2-50% in the first year of life, rising to 13-84% in the third year of life.

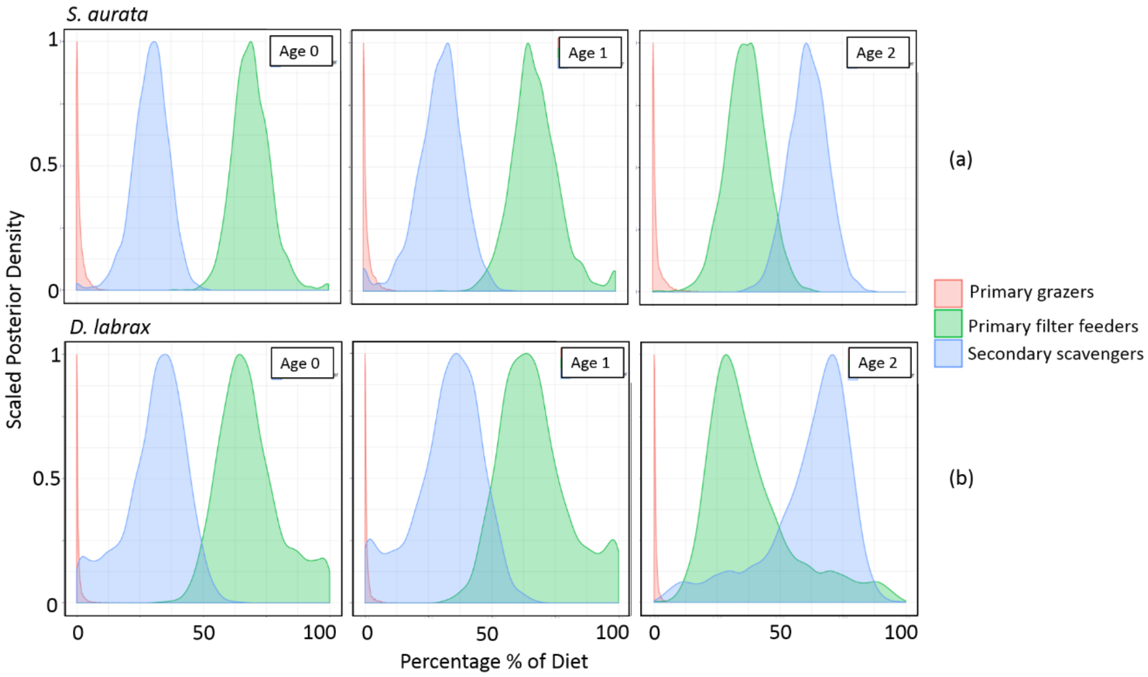


Figure 4.5 MixSIAR posterior density plot of (a) *S. aurata* and (b) *D. labrax* diet at different ages to show the proportions of sources that make up the overall diet. Median and 95% credible intervals shown in Table S4.3

4.5 Discussion

Here, we present findings on the potential for resource competition between *S. aurata* and *D. labrax.* First, we demonstrate that there are ontogenetic size differences in the isotopic niche width between the two species. The isotopic niche for *S. aurata* started relatively large in 0-group fish and decreased with age, whereas we see the opposite pattern for *D. labrax.* Secondly, we present evidence for niche differentiation between the two species. Finally, we show that despite these observed differences, both species rely on isotopically similar prey sources during the first three years of life. We discuss these results and their implications for conservation and management.

4.5.1 *Isotopic niche widths*

We found clear differences between the isotopic niche widths of *S. aurata* and *D. labrax*, across the first three years of life. Variation in isotopic niche space characterises intra and inter-individual variation, and is commonly used as a proxy for the realised ecological niche (J. G. Gonzalez et al., 2019; Jackson et al., 2011; Newsome et al., 2007). Our results suggest that although both species are coexisting in the study area, they have different realised ecological niches within our study system. Species realised ecological niches are influenced by various local biotic and abiotic factors and are therefore often much smaller than their fundamental niche (McGill et al., 2006). Although not solely influenced by diet, $\delta^{13}C$ and $\delta^{15}N$ ratios in consumer tissues are often tightly correlated to trophic sources (Fry, 1988). Variation in the isotopic niche space can, therefore, also provide useful information on the trophic niche of individuals (Jackson et al., 2011; Peterson & Fry, 1987).

Our results showing opposing patterns in isotopic niche widths between the species suggest that there is a level of trophic partitioning between the two species in our study system. 0-group *S. aurata* can forage for a wider range of prey sources compared to 0-group *D. labrax.* In contrast to this, the older 2-group *D. labrax* forage on a higher diversity of prey sources compared to 2-group *S. aurata.* The morphological differences in oral characteristics between *S. aurata* and *D. labrax* could explain this difference in trophic niche. *S. aurata* have strong specialised oral cavities for breaking down hard bodied prey that are developed from a young age (Elgendy et al., 2016) and could facilitate foraging on a wide range of prey. In general, studies that have investigated the feeding habits of *S. aurata* have found the species to have quite a wide niche, able to adapt its diet according to what is available but they can also become specialised in some areas (Avignon et al., 2017; Ferrari & Chieregato, 1981; Hadj et al., 2013; Pita et al., 2002). One study looking at two adjacent lagoons in the Mediterranean found that populations in one lagoon specialised on bivalves and *Carcinus sp.*, whereas in the adjacent lagoon they had a more heterogeneous diet, related to the composition of the benthic community (Mariani et al., 2002; Tancioni et al., 2003). In contrast to *S. aurata*, *D. labrax* have relatively weak teeth, unable to break down larger prey items in the same way. Mouth size is also likely to be a limiting factor for *D. labrax*, enabling a higher diversity of prey to be consumed as it gets larger with age (El-Bakary, 2011). One study that investigated the diet of *D. labrax* in a lagoon complex in Greece found a similar pattern to our results, showing an increase in prey diversity with age (Rogdakis et al., 2010). However there is also evidence for alternative patterns. For example, Fonesca et al.(2011) studied juvenile *D. labrax* within a managed realignment site and found that 1-group *D. labrax* specialised on only one prey species, whereas 0-group *D. labrax* had a varied diet. Most studies investigating the feeding habits of juvenile bass have found that they too are opportunistic and feed on a variety of different prey sources depending on what is available in the area, sometimes becoming more specialised (Cardoso et al., 2015; Fonseca et al., 2011; Laffaille et al., 2001; Rogdakis et al., 2010; Schattenhofer et al., 2009).

4.5.2 *Trophic implications*

Although we found a large range of $\delta^{13}C$ values in both 0-group *S. aurata* and 2-group *D. labrax,* the actual values observed for both suggest that $\delta^{13}C$ is still primarily assimilated from prey that derive their energy from benthic energy sources. Prey reliant on pelagic energy sources (such as primary filter feeders) might not be that important for either species during the first three years of life in our study system. Our results from the Bayesian mixing models support this, showing low estimated proportions of primary filter feeders in the diet of either species, across all age groups studied. Filter feeding bivalves are a known prey item for both *S. aurata* and *D. labrax* in other areas, especially for *S. aurata,* where there is evidence for populations specialising on bivalves and decimating mussel farms in the Adriatic Sea (Glamuzina et al., 2014). Bivalves are abundant in the Fal and Helford area and we expected them to be a more important prey resource. An abundance of other more desirable prey sources within the study system could explain this lack of evidence for primary filter feeders in the diet of both fish. In general, consumers are likely to preferentially select prey that has a high energy content, with minimal handling time (Hart & Reynolds, 2002). Therefore, it is likely that both *S. aurata* and *D. labrax* would chose softer-bodied prey such as polychaetes and small crustaceans over hard shelled molluscs. It is possible that bivalves could become more a more important diet resource if populations of *S. aurata* continue to increase, which could represent a problem for the growing shellfish industry (Avignon, 2017; Glamuzina et al., 2014).

The larger $\delta^{15}N$ values observed in 0-group *S. aurata* and 2-group *D. labrax* suggest that they feed on a higher diversity of prey species, including those from higher trophic levels like secondary consumers. Our results from the mixing models support this but also do not show clear differences between the proportions of secondary consumers in the diet of each species. Considering the clear differences found in isotopic niche width between the species; any trophic resource partitioning must be occurring at a finer scale that can be identified by the prey source data in the present study. We found a lot of isotopic variation in Malacostraca and polychaete samples (Figure 4.4), which led us to combine them into one prey source. Still, there are likely to be differences in the species consumed by *S. aurata* and *D. labrax* within this prey source. For example, the 0-group bass had a very small isotopic niche width that is likely to relate to specific secondary consumer species. A wider sampling strategy that took into account the seasonality and size of prey sources could help differentiate these further, and identify where differences in diet were at a finer level. Stomach content analysis could also provide further information here; however this technique is still likely to overestimate the importance of items that are harder to digest (Brush et al., 2012). Another explanation for the enriched $\delta^{15}N$ values observed in 2-group *D. labrax* is that they could be foraging at higher trophic levels than sampled, for example, on fish (Kelley, 1987). These were not included as a prey source in the mixing model but would raise $\delta^{15}N$ values in consumer tissue

(Peterson & Fry, 1987). We also found that prey sources from the mid and upper estuary were more enriched in $\delta^{15}N$, therefore it is possible that 0-group *S. aurata* and 2-group *D. labrax* are foraging preferentially further up the estuaries (Figure 4.2b). Juvenile *D. labrax* are believed to stay within nursery areas for the first few years of life (Kelley, 2002; Pawson et al., 2007), whereas *S. aurata* are known to undergo seasonal migrations into coastal waters after the first summer (Mercier et al., 2012). Therefore, our results may provide further evidence for the reliance of juvenile *D. labrax* on estuarine nursery areas.

Given the similarities in diet and ability of both species to forage for a wide range of available prey, we would expect to see similar-sized isotopic niche widths between the species that captured in the same location. One interpretation of the dissimilar niche widths is that this trophic resource partitioning has occurred as a result of interspecific competition between the coexisting species (Levine, 1976). One study that investigated the feeding behaviour of *S. aurata* found evidence for aggressive interactions while feeding that resulted in a dominance hierarchy and trophic partitioning between size groups (Goldan et al., 2003). It is possible that within the local study system, the presence of *S. aurata* has forced the 0 and 1-group *D. labrax* into a relatively small isotopic niche.

However, an alternative interpretation of the observed differences in isotopic niche width and limited overlap is that both species are preferentially feeding on different prey items within the area. We know that both *S. aurata* and *D. labrax* can feed on a wide variety of prey, so there may be no negative consequence of competition between them. Trophic separation is understood to be more important than habitat separation in fish assemblages, allowing species with similar fundamental niche requirements to coexist within their separate realised niche (S. T. Ross, 1986). Partitioning similar prey sources between the species could also have a positive indirect effect on the populations of both *S. aurata* and *D. labrax* through indirect mutualism (Levine, 1976). Consumers that reduce prey density, also reduce competition at lower trophic levels between prey sources, leading to positive effects on other prey sources and their consumers (Dodson, 1970; Sanders & van Veen, 2012). A much wider sampling strategy, investigating the relative isotopic niche widths of *S. aurata* and *D. labrax* in similar habitats where they are found both coexisting and separately would be required to investigate these hypotheses further. Another way of investigating this would be to experimentally removal *S. aurata* and see how it affected the isotopic niche width of *D. labrax* (Paine, 1971). However, this would have to be done within a mesocosm-based framework, as it would be very difficult to do at an estuary level.

4.5.3 *Further considerations*

We used the isotopic values from *S. aurata* and *D. labrax* muscle tissue in the present study. Muscle has a turnover rate of 49-107 days (Buchheister & Latour, 2010), allowing us to estimate long-term foraging habits for each species and age group. Different tissues also have different cell turnover rates. For example, liver has been shown to represent diet over 10-20 days (Buchheister & Latour, 2010). Therefore, the use of other consumer tissues could provide information on the longer-term stability of these results, allowing us to investigate whether all individuals within the groups are following the same resource partitioning strategy (Bearhop et al., 2004). The individuals that make up a population define the width of a realised ecological niche, and can this can vary widely among species and within populations (Bolnick et al., 2003). A variety of physiological, behavioural and ecological processes can all affect the individual variation, and there may be a degree of specialisation within the age groups that have broad isotopic niche widths. For example, a recent study using stable isotope analysis found that juvenile seabass can form trophic-generalist populations, made up of individual specialists (Cobain et al., 2019). This degree of specialism within a group has important implications, as it can affect a population’s ability to adapt to new environments (Bolnick et al., 2003).

4.6 Conclusion

We have discussed the results from our study concerning the trophic ecology of *S. aurata* and *D. labrax*, but isotope values in tissue are also affected by other factors. For example, values can vary in response to body condition, size, metabolic rate, sex, physiology, spatially and temporally (Gorokhova, 2018; Jackson et al., 2011). It was beyond the scope of this study to investigate the effect of these. Still, we incorporate the seasonal and temporal variation within the study system by sampling consumers and prey over three years. We also use a method that allowed us to make robust statistical comparisons by taking into account sampling error and other sources of uncertainty such as small sample sizes (Jackson et al., 2011).

Our results show that although both *S. aurata* and *D. labrax* are coexisting within the same habitat and can forage for similar prey, they have different realised ecological niches within the Fal and Helford Estuaries. The ability of juvenile *S. aurata* to forage for a wide range of prey is likely to be one of the traits enabling the range expansion. Trophic partitioning appears to be occurring between *S. aurata* and *D. labrax*, potentially as a result of interspecific competition. However, further work is needed to identify whether the presence of *S. aurata* is having a negative competitive effect or a positive indirect effect on *D. labrax* populations. Modelling estuary population dynamics across multiple trophic levels may provide further information that would be useful for the management of these two commercial species.

4.7 Supplementary information

Table S4.1 Details of consumer samples collected for stable isotope analysis

Species	**Age**	2016		2017			2018		**Total**
		Aug	Sept	May	Jul	Aug	Jun	Aug	
S. aurata	**0**	9	9		6	2	1	2	29
	1	-	-	5	1	-	4	-	10
	2	-	-	1	8	-	-	-	9
D. labrax	**0**	-	-	-	2	-	3	-	5
	1	-	-	4	-	-	1	-	5
	2	-	-	-	13	-	7	-	20

Table S4.2 Details of prey sources collected for stable isotope analysis

Prey source	**2016**	**2017**			**2018**			**Total**
	Aug	**May**	**Aug**	**Sep**	**May**	**June**	**Aug**	
Bivalvia	30	-	14	-	-	11	3	58
Gastropoda	35	-	-	-	10	10	-	55
Malacostraca	10	5	13	13	3	16	1	61
Polychaeta	36	-	54	26	13	17	19	165

Table S4.3 Median and 90% credible intervals showing the contribution of different prey sources to the % diet of *S. aurata* and *D. labrax* (a) at different ages (b)

(a)

Species	Prey source	2.5%	Median %	97.5%
S. aurata	**Bivalve**	0%	2%	42%
	Gastropod	12%	54%	83%
	Secondary scavenger	10%	42%	78%
D. labrax	**Bivalve**	0%	1%	44%
	Gastropod	11%	52%	94%
	Secondary scavenger	3%	45%	82%

(b)

Species	Age	Prey source	2.5%	Median %	97.5%
S. aurata	**0**	**Bivalve**	0%	1%	6%
		Gastropod	56%	69%	85%
		Secondary scavenger	14%	30%	42%
	1	**Bivalve**	0%	1%	7%
		Gastropod	51%	67%	90%
		Secondary scavenger	8%	31%	46%
	2	**Bivalve**	0%	1%	8%
		Gastropod	22%	37%	53%
		Secondary scavenger	47%	62%	76%
D. labrax	**0**	**Bivalve**	0%	0%	5%
		Gastropod	49%	66%	98%
		Secondary scavenger	2%	33%	50%
	1	**Bivalve**	0%	0%	4%
		Gastropod	45%	65%	99%
		Secondary scavenger	1%	34%	54%
	2	**Bivalve**	0%	0%	3%
		Gastropod	16%	34%	87%
		Secondary scavenger	13%	66%	84%

Chapter 5

General discussion

5.1 Thesis context

Species distributions are not static, as the biotic and abiotic conditions that dictate where species can survive fluctuate spatially and temporally. Understanding the drivers that affect species distributions is fundamental to successful conservation and management. Climate change, specifically global warming, is a key driver for species distributions, with many species showing highly significant, non-random general patterns of movement that correlate with increases in temperature (Chen et al., 2011). This predictable pattern of changing species distributions occurs in both terrestrial and marine environments; however, marine species appear to be more responsive to warming, with the latitudinal ranges closely matching physiological limits (Sunday et al., 2012). Climate change has had and will continue to have, significant impacts on the marine environment (Pinsky et al., 2019, 2020; Poloczanska et al., 2016). The Northeast Atlantic is one of the fastest-warming ocean basins (A. J. Southward et al., 1995), with temperatures rising at a rate of 0.1-0.5˚C per decade (Dye et al., 2013). Coastal waters around the UK are expected to increase by over 3˚C by the end of the century (S. L. Hughes et al., 2017), making it an ideal study system for the effect of climate warming on species distributions. Gilthead seabream *Sparus aurata* has been undergoing a poleward range expansion, into the English Channel and the Celtic Sea. The arrival of *S. aurata* has both positive and negative potential economic and ecological consequences. Therefore, a better understanding of the ecology of northern populations, and the ability to predict how the distribution of this new population is likely to change in the future, is key to inform any future management.

5.2 Synopsis of the results

This thesis is the first in-depth ecological exploration of *S. aurata* in UK waters, investigating the drivers and consequences of a poleward range-shift in the Northeast Atlantic. I have applied a range of methodologies and techniques to address different aspects of *S. aurata*'s ecology at the current northern limit of its range Figure 5.1.

In Chapter 2, I explored the fundamental role that temperature plays in driving the distribution of native and on the native and expanded range of *S. aurata*. Through modelling these ranges, I found that temperature predicted the known distribution of *S. aurata* with a high level of accuracy, supporting the hypothesis that *S. aurata* is likely to be responsive to warming, under current climate change projections. I found that winter temperatures are likely to be an important limiting factor on the northern latitudinal distribution of the species. This limit is likely due to cooler temperatures in northern areas impacting on the juvenile and larval fish, causing raised levels of mortality, and limiting the dispersal ability of the species (Hare & Able, 2007). I also found that, although temperature seems to be a strong predictor for distributions in both the native and expanded range of *S. aurata,* the northern populations occupy a very different thermal niche to those in the native niche (known source populations). This apparent difference in the thermal niche could be for several reasons. It may be that northern populations are sink populations (Dias, 1996), consisting primarily of non-reproducing adult early colonists. Adult fish are significantly more mobile than juveniles and larvae, and are therefore able to relocate to more suitable habitat during the cooler months (Hare & Able, 2007). There is also the explanation that northern populations of *S. aurata* have undergone a niche shift, and have become more locally-adapted to temperatures outside the native niche. Previous research into the population genetics of *S. aurata* populations across the latitudinal range finds evidence for a stepwise northward colonisation (Avignon, 2017; Coscia et al., 2012), which supports the possibility of local adaptation, the possibility of which is explored in more depth in Chapter 3. Given the effectiveness of temperature at predicting the native and expanded range of *S. aurata,* I also use two different climate scenarios to predict how the distribution may change in the future. Assuming there are no other biotic or abiotic limiting factors, a continued northward range expansion into

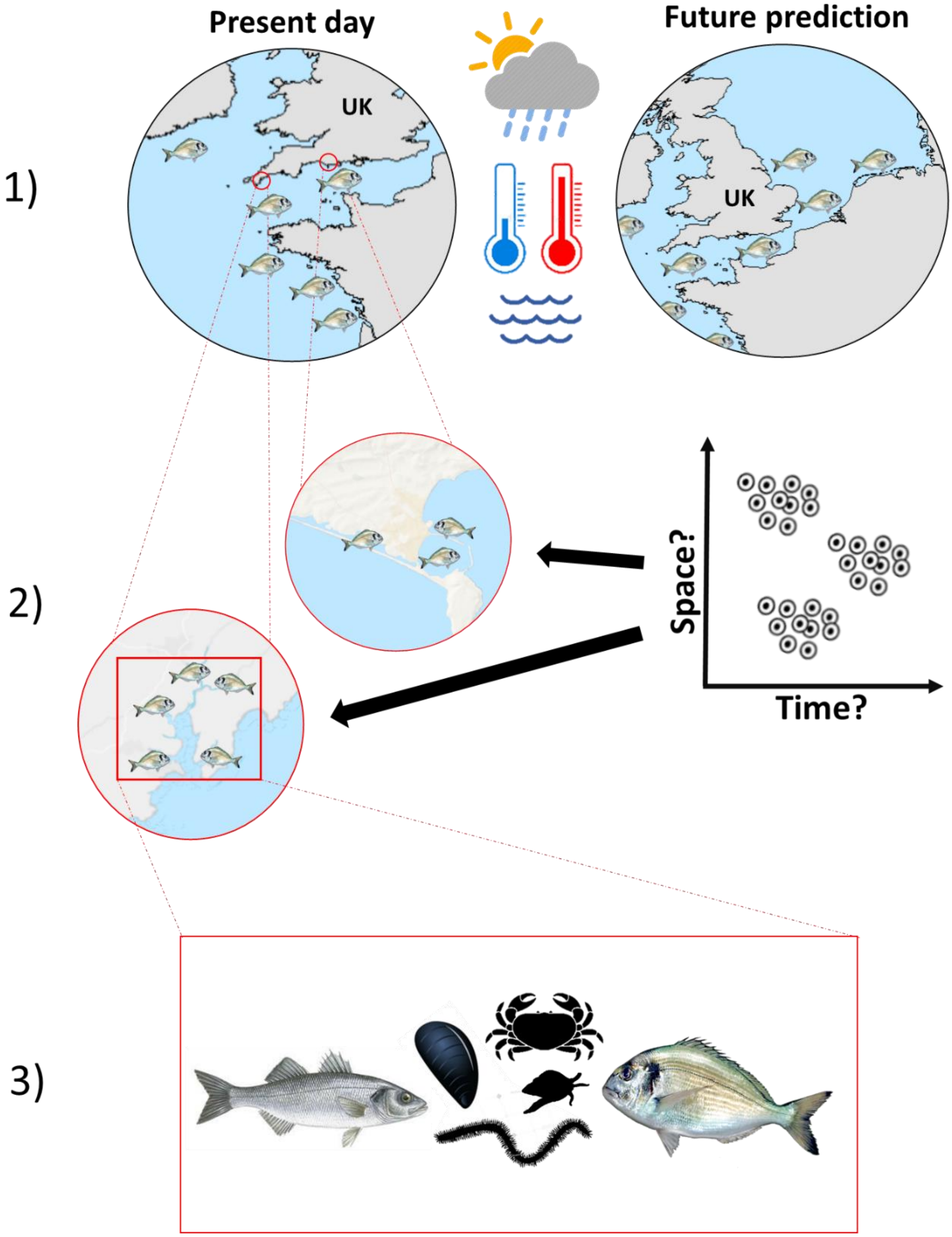


Figure 5.1 Conceptual model of the thesis results. 1) The predicted northward pattern of range expansion of *S. aurata* in response to climate change. 2) Three sources contributing to juvenile populations in nursery areas on the south coast of the UK, separated either spatially or temporally. 3) *S. aurata* and *D. labrax* juveniles are both found together in these nursery areas and have a similar diet. Increasing populations of *S. aurata* has potential competitive effects

the Channel and the Celtic Sea and a southern range contraction is predicted, resulting in much of the Mediterranean becoming unsuitable habitat by 2050. The increase in the suitability of northern habitat is likely to facilitate reproducing populations of *S. aurata* in the English Channel and the Celtic Sea, regardless of whether or not northern populations are currently acting as a source.

In Chapter 3, I use otolith microchemistry to try and identify whether *S. aurata* populations in the English Channel recruit from one or more sources. I use a multi-element approach to identify three temporally stable sources that have shared otolith chemistry, based on the portion of the otolith accreted during early larval life. I use known information about the environmental and physiological drivers of element uptake into otoliths, to infer information about the different environments the elemental concentrations might represent. I find that, although mixing appears to occur after spawning, the three different sources identified do not contribute equally to the Channel populations. Although methodological limitations mean that it has not been possible to identify specific spawning locations at this time, my findings provide the basis for future research to identify source spawning grounds and to determine the relative contribution of each to the different nursery areas.

In Chapter 4, I investigate the potential consequence of an increase in *S. aurata* populations for a potential competitor, the European seabass *Dicentrarchus labrax.* Juveniles of both species occupy a similar ecological niche and have similar prey sources*.* Populations of *D. labrax* are currently in steep decline in the Northeast Atlantic (ICES, 2016), and there is a concern that the arrival of a new species could result in increased competition for resources. I use stable isotopes to infer information about resource overlap between the two species during their first three years of life. Clear differences between the relative ecological niche widths between the species were identified. *Sparus aurata* demonstrated an ecological niche which was initially wide, which diminished with age, while *D. labrax* exhibited the opposite pattern. Although both species seem to be feeding on similar prey, there is evidence for potential resource partitioning between the species. While the presence of *S. aurata* could be having a negative effect on *D. labrax* through interspecific competition therefore, the corollary is that the presence of *S. aurata* may also provide indirect beneficial effects on *D. labrax* populations through indirect mutualism.

5.2.1 Novel findings

This thesis provides a snapshot of what the current range of *S. aurata* looks like, how it might change in the future, and explores potential impacts of the range shift (Figure 5.1). Through the use of species distribution modelling, I investigated the relative importance of different temperature variables to the current and predicted future range of *S. aurata,* in response to forecasted climate change. Previous studies have modelled *S. aurata's* range using either generic predictor variables (Kesner-Reyes et al., 2019), or left out the northern part of the range expansion in future predictions and focused on the projected decline in suitable thermal habitat in the Mediterranean (Hattab et al., 2014). My species distribution model for *S. aurata's* current expanded range shows for the first time that individuals at the northern edge of the range are existing in a very different thermal niche to the native range, implying that either a thermal niche shift has occurred, or that northern populations consist primarily of non-reproducing adults.

If northern populations of *S. aurata* are not currently reproducing, as Chapter 2 indicates is possible, this has important implications. It is key to understand the dynamics of source populations to inform future management, as sink populations are not able to sustain themselves without immigration from source populations (Dias, 1996). In Chapter 3, I identified three sources of fish that have shared otolith chemistry by analysing the section of otolith relating to the first ~two weeks of larval life. Although it was beyond the scope of my thesis to establish whether these indicated spatial or temporal differences, I did find that there were individuals from all three identified groups present in samples from both the Fal and Helford estuaries and Weymouth Bay. This implies a level of population mixing in the English Channel (either during larval settlement or subsequent adult movement) that could act as a buffer against exploitation, disease or pollution events that affect source populations (Hart & Reynolds, 2002) and invites further research questions in this area. A recent study by Avignon (2017) also investigated otolith microchemistry in mature *S. aurata* from northern France and the UK. Avignon (2017) performed a principal component analysis on chemistry data from individual otolith core samples to try to identify whether the chemistry was related to capture location. No differentiation was found between samples, but no subsequent analysis was carried out to determine if there were shared chemical signatures between individuals, independent of capture location. It is possible that an extra analysis step would identify groups of individuals with shared chemistry, similar to the results of Chapter 3. Another explanation for the lack of observed grouping could be because the core area of the otolith gives the maternal signal (Hegg et al., 2019), rather than the natal source, demonstrating the importance of using the appropriate section of the otolith for the research question. Apart from Avignon (2017), this is the first time to my knowledge that otolith microchemistry data has been obtained from *S. aurata* at the northern edge of its range. My data can be used for future research, in conjunction with molecular data from the same individuals, to further investigate hypotheses about *S. aurata* population structure across the species range. As *S. aurata's* range continues to shift, in response to climate change, new sources are also likely to develop as new suitable spawning habitat becomes available. Chapter 3 provides a framework for assessing future changes in source populations that contribute to northern populations of *S. aurata* and for identifying numbers of source populations in other teleost species.

I have shown that the three sources of *S. aurata* populations identified in Chapter 3 are all recruiting into multiple estuaries on the south coast of the UK, where they are sharing nursery areas with native species and potentially causing increased competition for common resources. In Chapter 4 I find little evidence for resource competition between *S. aurata* and *D. labrax*, although they do appear to be feeding on similar prey sources. It is feasible that over the next few years, if populations do increase as a result of further climate change (Chapter 2), the level of competition could increase as demand for common prey sources grows.

5.3 Relevance of results for future research

Species range-shifts have, and will continue to have, significant impacts on the marine environment and the ecology of the species that live there. Through the use of different techniques, I have provided novel information on the ecology of *S. aurata* at the northern edge of its range. Inevitably the research has generated more questions than it has been possible to answer. I will now summarise how my findings suggest some key research areas that would be useful to further our knowledge of range-shifting *S. aurata,* and range-shifting species in general.

A key question arising through the results generated from Chapters 2 and 3 is whether northern populations of *S. aurata* have become locally-adapted. Adaptation has important implications for whether *S. aurata* is successfully spawning at the northern limit of its current distribution. If *S. aurata* populations continue to increase (as predicted in Chapter 2), both commercial and recreational fishers are likely to target them increasingly. One way to investigate the potential for local adaptation would be to investigate differences in thermal tolerance across *S. aurata's* current range, possibly in combination with molecular markers that could identify amino acids related to thermal tolerance (Somero, 2010). Identifying latitudinal differences in thermal tolerance would provide useful insight into the potential for local spawning source populations of *S. aurata*. The use of modern high-throughput molecular sequencing techniques (e.g. recently developed SNPs) would also provide useful information on the fine-scale population structure of *S. aurata* across its latitudinal range (García-Fernández et al., 2018). The use of molecular techniques was beyond the scope of this thesis, however I obtained samples for this purpose and it would be a feasible area to continue research into northern populations of *S. aurata*.

Otoliths offer further scope for investigating the relative contribution of source populations to nursery areas, and also the relative importance of nursery areas to the wider population. Quantifying the movement of larvae between their natal origin, nursery areas, and their subsequent success as functioning adults is one of the greatest challenges in fisheries science. These movements determine whether a population can self-recruit, or if it forms part of a larger meta-population made up of multiple sources. However, to use otoliths for this purpose successfully, sampling larvae from the location of source populations and juveniles from nursery areas is required. Sampling from the source population allows characterisation of the source signature, which can then be compared with juveniles that have recruited into nursery areas. Since the location of source populations is not currently known, I could not obtain samples for this purpose for this thesis. It is possible that this will be feasible in the future, if further research is conducted into where *S. aurata* spawning grounds are located. Identifying the location of source populations is a major challenge in fisheries science. For example, even in well-studied populations of *S. aurata* that in the Mediterranean the origin of source populations remains a knowledge gap (Lett et al., 2019). Combined with further understanding of adult movements and the degree of philopatry, the use of individual-based models, coupled with hydrodynamics, would allow further understanding as to where *S. aurata* could be spawning in the northeast Atlantic. Models like this are already developed for *Dicentrarchus labrax* so this would be a relatively easy avenue of research in the future.

By catching the same cohorts in subsequent years within the same nursery areas, it is also possible to compare information from the otoliths to estimate the importance of different nursery areas to the wider population. Due to time constraints and the logistics of setting up a new research project in a new area, I did not obtain enough samples of recently recruited juveniles in nursery areas from successive years to identify the relative importance of different nursery areas. Populations of *S. aurata* are still relatively low, but it is likely that as juvenile populations increase this will be a feasible and useful avenue of research in the near future. Otoliths are also useful in the study of adult migrations, a technique that has been successfully used for this species in both the Northeast Atlantic (Avignon, 2017) and the Mediterranean (Mercier et al., 2012).

Range-shifting species are likely to have community-level effects. Using stable isotope analysis of muscle tissue, I found evidence for resource partitioning between *S. aurata* and *D. labrax* juveniles (Chapter 4). Through the use of other tissues, stable isotopes have the potential to provide information on the trophic history of fish, allowing interpretation of any change in diet over time and also the degree of individual specialisation (Cobain et al., 2019). For example, eye lenses consist of metabolically inert layers of tissue that represent the isotopic history of the individual (Quaeck-Davies et al., 2018; A. A. Wallace et al., 2014). Although working with eye lenses was beyond the scope of this thesis, I obtained eye lens samples from both species. This would be a feasible area for further research to explore the interaction of northern populations of *S. aurata* with *D. labrax* in more depth.

Another way to investigate the interaction between juveniles of *S. aurata* and *D. labrax* further would be through the use of an acoustic array tagging program within a nursery area. Quantifying habitat use over a longer temporal scale would potentially provide further information as to how the observed resource partitioning was occurring. Acoustic tags have been successfully used to investigate the movement of *S. aurata* populations between nursery areas and the sea in the Mediterranean (Abecasis & Erzini, 2008). Although I planned to do this as part of my thesis, I was unable to catch enough samples in the array location so the project could not go ahead (Figure 5.1). If we see the predicted increase in population levels of *S. aurata* in the northern part of the range, it is likely to become easier to obtain samples for a tagging project in the future. Further research into the estuary-wide population dynamics, possibly modelling interactions across multiple trophic levels will also provide further information that would be useful for the management of these two commercial species.

Previous studies have suggested that there is a concern for shellfish aquaculture from increasing *S. aurata* populations becoming specialised to feed on bivalves. In the Adriatic, rapidly increasing populations are attributed to the collapse of mussel farms (Glamuzina et al., 2014), and this could also be a potential concern for French and future UK shellfish aquaculture (Avignon, 2017). I did not find evidence that bivalves were a major prey source for *S. aurata* (Chapter 4), even though they appeared to be abundant in the local area. There are several mussel farms in the Western English Channel (e.g. Offshore Shellfish Ltd, a rope cultured mussel farm currently being built off the coast of Lyme Bay, Devon, UK), and this could become an issue with a further increase in *S. aurata* population levels.

One key part of *S. aurata's* ecology that I was unable to address within the scope of this thesis is that it is a sequential hermaphrodite, maturing first as a male, and then as a female. The size and age at which this occurs vary across *S. aurata's* current range, dependant on factors such as temperature (Shen & Wang, 2014).

For example, in the Melllah lagoon in Algeria, juveniles mature as males from around 22cm, and then females become dominant in size classes over ~50cm (Chaoui et al., 2006). In the Bardawil lagoon in Egypt, males mature at ~20 cm and females at 22 cm (Ahmed, 2011). This information has important implications for future management of the species, and a more thorough study into the age and size structure of northern populations would be a useful avenue of future research. As a recreational target species, the larger fish are more highly prized, which could result in the removal of important big old fat fecund female fish (BOFFFFs), which can have a high contribution to population growth (Hixon et al., 2014). Although it would not provide information on the age at which *S. aurata* matures as male and female, the use of scales would be a useful, non-invasive technique to identify the size and age structure of northern populations, possibly through a network of anglers collecting samples.

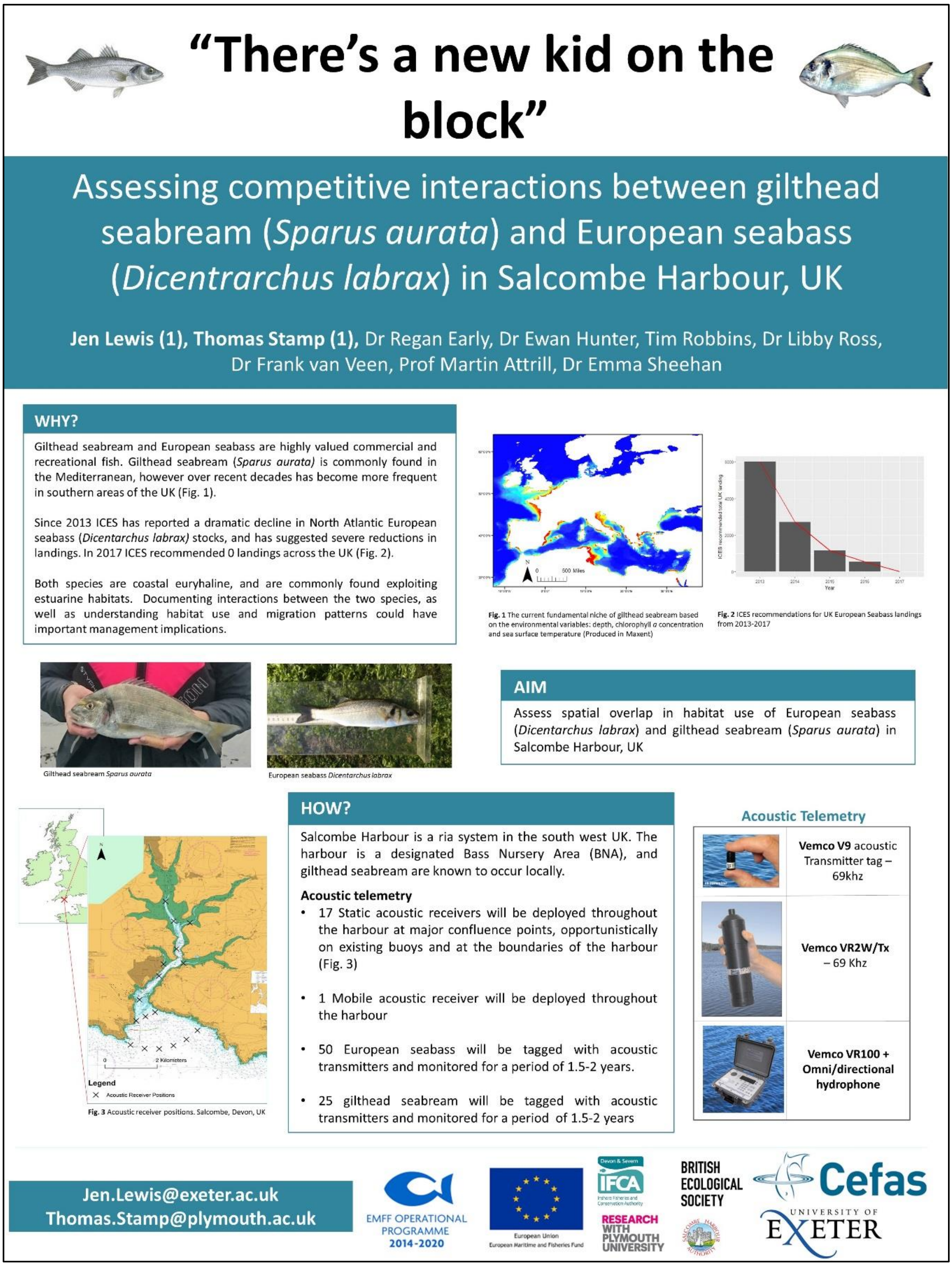
5.3.1 Research priorities for the next 5-10 years

Identifying whether northern populations of *S. aurata* are successfully reproducing, along with the size and age at which this occurs for each sex, is a key area for future research. To identify the sex and fecundity of individuals, gonad histology across size classes needs to be observed. Previous studies have successfully identified this information for *S. aurata* in other areas (e.g. Bruslea-Sicard & Fourcault, 1997), however the size and age at which these stages occur varies spatially and depends on environmental factors such as temperature (Shen & Wang, 2014; Tobin & Wright, 2011). The ability to collect large enough numbers of representative samples was the limiting factor for me to include this within my thesis. Most of the samples I obtained from surveys could not be sexed due to the age of the fish and the fact that gonads had not yet developed. Samples from mature fish were provided by anglers who had already gutted the fish before donating samples. It is possible that setting up a network of recreational and commercial fishers who target *S. aurata* could facilitate sample collection of gonads for this purpose. If populations do increase in the future, as predicted in Chapter 2, *S. aurata* is likely to become more of a commercial target species. Therefore, attaining enough samples for this purpose should be possible within the next decade. Obtaining this information is fundamental to understand the reproductive status of northern populations and could also be used to recommend a minimum landing size limit for recreational and commercial fishers to conserve stocks.

5.4 Concluding remarks

I have used *S. aurata* as a case study to explore the effect of climate change range-shifts and discussed the implications on recipient ecological communities. This thesis provides new insight into the drivers of range-shifts in a temperate marine fish while highlighting the complexities of range expansion. I suggest the need for further research into the population structure of this important species, to ensure sustainable exploitation from recreational and commercial fisheries. A greater understanding of this target fish will benefit sea-anglers and fishers, the coastal tourism sector and conservationists managing the long-term sustainability of inshore fisheries.

5.5 Supplementary material



“There’s a new kid on the block”

Assessing competitive interactions between gilthead seabream (*Sparus aurata*) and European seabass (*Dicentrarchus labrax*) in Salcombe Harbour, UK

Jen Lewis (1), Thomas Stamp (1), Dr Regan Early, Dr Ewan Hunter, Tim Robbins, Dr Libby Ross, Dr Frank van Veen, Prof Martin Attrill, Dr Emma Sheehan

WHY?

Gilthead seabream and European seabass are highly valued commercial and recreational fish. Gilthead seabream (*Sparus aurata*) is commonly found in the Mediterranean, however over recent decades has become more frequent in southern areas of the UK (Fig. 1).

Since 2013 ICES has reported a dramatic decline in North Atlantic European seabass (*Dicentarchus labrax)* stocks, and has suggested severe reductions in landings. In 2017 ICES recommended 0 landings across the UK (Fig. 2).

Both species are coastal euryhaline, and are commonly found exploiting estuarine habitats. Documenting interactions between the two species, as well as understanding habitat use and migration patterns could have important management implications.

Fig. 1 The current fundamental niche of gilthead seabream based on the environmental variables: depth, chlorophyll *a* concentration and sea surface temperature (Produced in Maxent)

Fig. 2 ICES recommendations for UK European Seabass landings from 2013-2017

Gilthead seabream *Sparus aurata*

European seabass *Dicentarchus labrax*

AIM

Assess spatial overlap in habitat use of European seabass (*Dicentarchus labrax*) and gilthead seabream (*Sparus aurata*) in Salcombe Harbour, UK

Fig. 3 Acoustic receiver positions. Salcombe, Devon, UK

HOW?

Salcombe Harbour is a ria system in the south west UK. The harbour is a designated Bass Nursery Area (BNA), and gilthead seabream are known to occur locally.

Acoustic telemetry

- 17 Static acoustic receivers will be deployed throughout the harbour at major confluence points, opportunistically on existing buoys and at the boundaries of the harbour (Fig. 3)
- 1 Mobile acoustic receiver will be deployed throughout the harbour
- 50 European seabass will be tagged with acoustic transmitters and monitored for a period of 1.5-2 years.
- 25 gilthead seabream will be tagged with acoustic transmitters and monitored for a period of 1.5-2 years

Acoustic Telemetry

Vemco V9 acoustic Transmitter tag – 69khz

Vemco VR2W/Tx – 69 Khz

Vemco VR100 + Omni/directional hydrophone

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Figure S5.1 Poster for a study investigating the interactions between *S. aurata* and *D. labrax* that was unable to go ahead

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