University of Reading

Modelling the northern stock of European Sea Bass (*Dicentrarchus labrax*): an individual based approach.

A thesis submitted for the degree of Doctor of Philosophy.

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Preface

This thesis includes one published manuscript (chapter Two).

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Chapter three has been prepared for submission as a journal article (currently prepared for submission to Ecological modelling).

Chapter four has been prepared for submission as a journal article and chapter five has been prepared as a TRACE article in support of the individual based model presented in chapter four (currently the MS is prepared for submission to Plos One and the TRACE as supplementary material).

Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Joseph W. Watson

Author contributions

For co-authored chapters, author contributions are as follows.

Chapter two: Joseph Watson, Kieran Hyder, Robin Boyd, Robert Thorpe, Marc Simon Weltersbach, Keno Ferter, Steven J. Cooke, Shovonlal Roy, and Richard Sibly made contributions as authors. JW led the writing of the manuscript. JW, KH, RS and RB contributed to the conception of the paper and design of the methodology. All authors contributed critically to the drafts and gave final approval for publication in Fish and Fisheries.

Chapter three: Joseph Watson, Angela Muench, Kieran Hyder, and Richard Sibly made contributions as authors. JW led the writing of the manuscript. All authors contributed to model development and gave critical comments on each draft of the manuscript. All authors gave permission for submission having seen the final draft.

Chapters four and five: Joseph Watson, Robin Boyd, Ritabrata Dutta, Georgios Vasdekis, Nicola Walker, Shovonlal Roy, Richard Everitt, Kieran Hyder, and Richard Sibly made contributions as authors. JW led the writing of the manuscript. All authors contributed to model development and gave critical comments on each draft of the manuscript. All authors gave permission for submission having seen the final draft.

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Abstract

Capture fisheries provide nutrition, jobs, and recreation across the world. However, the aquatic ecosystems in which they operate are under increasing pressures from climate change, fishing pressure and other anthropogenic stressors. It is the difficult role of fisheries management to consider all the needs of fisheries and threats to these aquatic resources and find an appropriate balance. In this thesis, I focus on what happens to individuals in capture fisheries and build a series of models to analyse both the fish and the fishers that catch them. I have specifically focused on the northern stock of the important commercially and recreationally targeted European sea bass (*Dicentrachus labrax*). By focusing on the individuals, I obtain mechanistic insights into different aspects of this fishery and make suggestions on how this could be used in future management.

Following the theme of the individual, I start by considering sublethal impacts of anthropogenic stressors on individual fish. Stressors caused by human activities can cause a range of sublethal impacts such as detrimental behavioural changes or injury that could result in reduced growth and reproduction. In chapter two I develop an energy budget approach to investigate how these sublethal stressors can influence life processes of fish. The method developed partitions impact into the initial energetic cost of attempts to escape from the stressor, followed by the energetic impacts of any injury or behavioural change, and their consequent effects on life processes. As a case study, I assess the sublethal effects of catch and release angling for the European sea bass. Chapter three moves on from fish and focuses on the fishing pressure caused by the fishers, where I analyse fisher decisions with the aim of gaining a mechanistic insight into fishing pressure. As in chapter two the study focuses on the northern UK stock of sea bass, specifically the under 10m fleet that target them. This study makes use of a vessel logbook scheme alongside environmental and economic data sets to investigate daily decisions made by commercial sea bass fishers. The primary result is the important effect of wave height on fisher behaviour, where I found that fewer vessels left UK ports during rough weather to go fishing and vessels that did were less successful. The findings from this study have implications for management as increases of extreme weather events during the key fishing seasons may impact on the ability of the small inshore vessels to land catch limits within allowed time periods, which may affect their profitability. In chapters four and five, consistent with the individual theme, I present a spatially explicit individual based model (IBM) of the northern stock of European sea bass. The IBM is developed from an existing IBM published by Walker et al., 2020. The key updates are the addition of a realistic energy budget driven by dynamic maps of phytoplankton density and the inclusion of all life stages. The energy budget additions now link population dynamics to environmental drivers which ultimately produce emergent population dynamics, including key fisheries management metrics. I present some encouraging fits to the ICES stock assessment data and suggest the IBM could be an additional tool in stock assessment.

This research can be used to inform future management of the northern stock of sea bass, especially in the context of spatial management. Future works should focus on using the IBM to test a range of management scenarios and responses to environmental change and has additional scope to add the findings from chapters two and three as sub models related to fisher behaviour and sublethal stressors. The approach developed for sea bass could be applied to other species and fisheries, which would allow spatial management measures to be tested more effectively.

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1 General introduction

This chapter begins by highlighting the general importance of capture fisheries and goes on to describe some of the diverse, direct and indirect threats, that global capture fisheries face. The highlighted threats include lethal effects, which add to fishing mortality, but also the more nuanced sublethal effects that reduce fish growth or reproduction resulting in a population level change. The importance of capture fisheries and the threats to it are complex and this chapter introduces the role of fisheries management whose task is to make sure fisheries are operating sustainably. After a brief overview of stock assessment methods, I outline some of their complexities and indicate where there may be room for improvement. In particular, stock assessment methods generally omit wider ecosystem drivers of important fisheries metrics, and typical single species stock assessment models do not consider spatial-temporal distribution of fish. Some assessments may benefit from considering the effects of fisher behaviour, and the impact of other anthropogenic stressors not directly related to fishing. The chapter then goes on to discuss how a focus on individuals, as is done throughout the thesis, may help complement current assessment models and overcome some identified shortfalls. The northern stock of sea bass is then introduced as a worthwhile case study that is used throughout the thesis, where I indicate its popularity as a commercial and recreational target and show how the declining stock has led to stringent harvest restrictions. The chapter then ends with a statement of aims and objectives and an outline of the thesis contents.

1.1 Value of capture fisheries

Fisheries around the world are endlessly diverse in both species targeted and the methods used. Initially global fisheries can be split into aquaculture and capture fisheries. In this thesis I focus on capture fisheries but it is important to note the increasing importance of the aquaculture sector which is estimated to equal capture fisheries by 2030 (Brander, 2007; Jennings *et al.*, 2016). We can further split capture fisheries into marine and fresh water which represent 87.4 % and 12.6 % of captures respectively (estimated for 2017-2019 [FAO, 2020][1]). The range and variety of capture methods for both marine and freshwater fisheries are highly diverse, ranging from small scale fish traps to technologically advanced factory trawlers. Many fishing methods involve a dedicated fishing vessel and there is estimated to be 4.56 million globally with ~82% of these motorised vessels measuring less than 12 meters in length (estimates for 2018, [FAO, 2020][1]). The fisheries industry is a major producer of food and employer, estimated to account for 17% of global animal protein consumption and employing around 40 million people including many woman especially in fish processing sector (estimates for protein 2017 and employment 2018 [FAO, 2020][1]). As well as providing food and employment, recreational fishing is also mass participatory sport with economic value and social benefits globally (Hyder *et al.*, 2018). Many of these benefits to capture fisheries (i.e., food, employment, and social benefits) are currently at risk from human activities such as overfishing, pollution and global warming. It is crucial that capture fisheries are managed successfully to preserve the benefits they currently provide.

1.2 Threats to fisheries

A rising human population is creating an ever-mounting pressure on the aquatic environment where more people need more food, and their activities create more disturbance. Climate change is arguably the biggest threat for marine and freshwater fisheries and is associated with a complex

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[1] Statistics in Section 1.1 are from FAO, 2020, FAO statistics rely on national reports, many of which are incomplete or have a significant amount of uncertainty.

combination of lethal and sublethal, direct and indirect consequences. Direct effects of climate change can act on fish physiology and behaviour which, in turn, can alter growth, reproductive capacity, mortality and distribution (Brander, 2007; Denechaud *et al.*, 2020) but these effects are often found alongside other indirect impacts. Climate change can cause indirect changes to the structure and composition of important fisheries ecosystems where altered temperatures, currents and salinity can cause shifting of aquatic organisms at different trophic levels. These changes can alter the ecosystem balance and consequently fishing opportunities (Brander, 2007; Pinsky, Selden and Kitchel, 2020). Alongside climate change, the activities associated with global development can have major consequences for fisheries. Like climate change, human activities can also be split into stressors that have direct and indirect, lethal and sublethal impacts on fisheries. The anthropogenic pressures that cause lethal consequences (e.g., pollution fish kills) are often easier to study than subtle but also important sublethal effects (e.g., effects on behaviour of noise pollution) for many of which the population level consequences are still unknown (Popper and Hastings, 2009; Slabbekoorn *et al.*, 2010; Hamilton *et al.*, 2016).

An obvious and serious threat to fisheries is overfishing, where advancements in fishing methods and technology have led to estimates of 34.2 % of marine fisheries being categorised as overfished (estimates for 2017 [FAO, 2020][1]). Fisheries are often size and species selective where fishers apply pressure and reduce the biomass of their target species, but also change their population age and size structure, with potential knock on effects through an ecosystems such as removal of key prey or predator species (Jennings and Kaiser, 1998; Brander, 2007). Different fishing methods have a range of unique unintended pressures on fisheries and the environment where more selective methods (e.g., hook and line) reduce levels of bycatch, discard and damage as other potentially less selective and more destructive methods such as trawls and seins (Dammannagoda, 2018). In addition to commercial fishing, recreational fishing can also have a significant contribution to fishing mortality (Radford *et al.*, 2018), and can inflict numerous sublethal impacts such as an injury or behaviour change as a result of catch and release angling (Bartholomew and Bohnsack, 2005; Lewin *et al.*, 2019). It is important to note that these threats to fisheries rarely appear in isolation and it is often the combination that makes fisheries vulnerable. For example a heavily fished population that is already under pressure will be more vulnerable to new anthropogenic stressors and climate change (Brander, 2007). The stresses that fisheries are under are recognised by global leaders, as is demonstrated by commitments to sustainable development goal 14.4; to end overfishing of marine fisheries (UN, 2020). However, the reality of enforcement of well-meaning mitigating legislation is extremely challenging especially as threats to fisheries continue to evolve, for example the effects of the COVID-19 pandemic on fisheries is still mostly unknown at the time of writing.

1.3 Stock assessment and fisheries management.

Capture fisheries are globally important but are under multiple threats (see sections 1.1 and 1.2) and it is the difficult task of fisheries management to balance the needs of consumers, fishers, and the environment. Fisheries managers use stock assessment models to assess the current stock state and the impacts of fishing mortality that it is subjected to. As with any model, there is some uncertainty with any estimations made, and a critical component of fisheries management is to understand and communicate this clearly to governments and regulators (Dankel, Vølstad and Aanes, 2016). Once the stock state is established and uncertainty is understood, then advice is provided to governments to set harvest limits using a range of regulatory methods (e.g., limiting total allowable catch, time and spatial catch limits, fishing gear restrictions).

To give complete advice for a stock assessment, fisheries management need four pieces of information. For a predetermined stock, mangers need to know how many fish are entering a fishery (recruitment), how fast they are growing (growth), how many die of natural causes (natural mortality) and how many are killed by fishers (fishing mortality). Fisheries scientists rarely have complete, long term data of these rates so use a variety of mathematical models fitted to available data to estimate missing information (Cadrin and Dickey-Collas, 2014). The data to which models are fitted can vary in availability, quality, and quantity, thus the type of models used depend on the circumstances with a bespoke solution developed for each stock. Basic catch data is taken from fishers targeting the stock, termed fisher dependent data and in some cases can be supplemented with more detailed data obtained from fisheries observers onboard fishing vessels or from fisher independent data from specific fisheries surveys. In data poor stocks, where the only data available is a time-series of catch records, fisheries managers are limited to using a catch only model upon which only crude advice can be given (ICES, 2012b). In stocks with more data available, such as age and size composition, it is possible to use more sophisticated statistical age structured models, and this is also possible in some data weak stocks with stock synthesis models (Methot and Wetzel, 2013). More sophisticated models can predict metrics such as age structure and population dynamics, and by estimating stock size and how it is being impacted by fishing mortality, managers can provide more complete advice (ICES, 2012b).

Fisheries management typically provide advice to governments on harvest for the following year for each fish stock, and in a single species stock assessment, each species is considered in isolation and species with multiple stocks are assumed to not interact (e.g., the Northern and Mediterranean Sea bass stocks). However, some species life history makes them more likely to be caught alongside other species and fisheries managers must consider these stocks as a mixed fishery (e.g., Mixed Fisheries Advice for the North Sea [WGMIXFISH-NS][2]). Mixed fishery stock assessments must consider the ecological interactions of species (e.g., predator prey interactions) and the technical interactions that lead to the fish ending up in the same net. An additional complication to stock assessments is when the species for assessment have a large spatial range and/or migrations that span international borders. These fisheries require international collaboration and decision-making to negotiate and advise on the allocation of harvest (e.g., The International Commission for the Conservation of Atlantic Tunas [ICCAT][3]).

1.4 Limitations to Stock assessment and fisheries management.

The majority of stock assessments are carried out with single species stock assessment models which are designed to use a range of fisheries dependent and independent data to assess the state of a fishery (see section 1.3). There are however some limitations to many single stock assessment models, namely a lack of spatial components, the omission of wider ecosystem effects and exclusion of fisher behaviour and/or any anthropogenic stressors beyond fishing.

It is well acknowledged that a combination of biological and physical ecosystem drivers influences fish populations and the key life processes of recruitment, growth, and natural mortality which stock assessments use to underpin harvest advice (Pepin, 1991; Mcbride *et al.*, 2015; Sibly *et al.*, 2015). The incorporation of wider ecosystem effects into fisheries management is acknowledged in increasing efforts towards ecosystem approach fisheries management (EAFM) and is mostly carried out through the use of ecosystem models to provide ecosystem context of single species assessments (Collie *et al.*, 2016). Examples include food web based models (e.g., OSMOSE [Shin and

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[2] https://www.ices.dk/community/groups/Pages/WGMIXFISH.aspx
[3] https://www.iccat.int/en/assess.html

Cury, 2001, 2004] and Ecopath with Ecosim [Polovina, 1984]) and multispecies oceanographic models (e.g., Atlantis [Fulton *et al.*, 2004]). Despite the efforts to include ecosystem models in management (Collie *et al.*, 2016), a recent worldwide review found that only 24 out of 1200 stocks reviewed incorporated ecosystem effects into their assessment (Skern-Mauritzen *et al.*, 2016). A further criticism of most stock assessments is the lack of consideration of any anthropogenic stressors other than commercial fishing pressure. In reality, fisheries are exposed to a raft of anthropogenic stressors (e.g., noise/chemical pollution and recreational fishing, for more details see section 1.2) many of which have the potential to influence population level effects on recruitment, growth, and mortality. These combined effects are becoming increasingly recognised as important with efforts towards Cumulative Effects Assessments (CEAs), however these are rarely incorporated into real-world management processes (Stelzenmüller *et al.*, 2018).

Single species stock assessments typically provide outputs of stock biomass, but most do not attempt to assess how the stock is distributed through both space and time within the year (Goethel, Quinn and Cadrin, 2011; Punt, 2019a). Stock assessments that are not spatially explicit are limited in their ability to assess the impacts of any spatial management measures such as where to place marine protected areas or in their ability to manage stocks of species that travel/migrate across international borders (Bailey *et al.*, 2013; Punt, 2019b). In addition to the spatial distribution of fish, single species models do not account for the spatial and temporal distribution of fishing pressure. To build models to account for this typically requires an understanding fisher behaviour defined as how fishers make decisions and react to bio-physical and socio-economic drivers (Andrews, Pittman and Armitage, 2020) and has been included in some ecosystem models (e.g., Atlantis [Fulton *et al.*, 2014]). It is important to note that the construction, parametrisation and validation of the complex ecosystem models that include the criticisms of single species assessment (i.e., spatially explicit fish and fisher distribution and the inclusion of wider ecosystem drivers) require a large amount of data and can create large uncertainties that are problematic with tactical management decisions (Hyder *et al.*, 2015; Collie *et al.*, 2016; Johnston *et al.*, 2019). Despite the data limitations of ecosystem models, attempts to understand how ecosystem drivers, fisher behaviour and anthropogenic stressors impact fish populations should where possible be included in fisheries assessments leading to potentially more complete advice.

1.5 The potential contributions of the individual approach

Fisheries are generally managed through single species stock assessment models (see section 1.3) many of which are limited by the lack of spatial components, the omission of wider ecosystem effects and non-incorporation of fisher behaviour and/or any anthropogenic stressors beyond fishing (see section 1.4). As mentioned in section 1.4, there are examples of ecosystem models that incorporate many of these omissions and are then used to provide ecosystem context to single species stock assessments (Collie *et al.*, 2016; Ward *et al.*, 2016). Ecosystem models populations can be split into species-based models, where populations are grouped by species that play a similar role within the ecosystem and size based models where species are grouped together by size regardless of species (Pethybridge *et al.*, 2019). In some ecosystem models populations are then further split into life stages and or age group where each subset is assumed to have the same characteristics i.e., all *age 1* fish of the same species will have the same body length and mass (Christensen, Walters and Pauly, 2005; Hyder *et al.*, 2015). However, the cases described above do not resolve the population to the individual and do not include intra cohort or life stage heterogeneity, which can limit the mechanistic capability of models in their support of fisheries management (Ward *et al.*, 2016). To include heterogeneous responses of individuals within groups, models must include traits that are adaptive to drivers of the fishery such as differing intra cohort growth rates that are influenced by

local food availability and/or sea temperatures. Models that include these adaptive traits can be considered more mechanistic with the potential to reveal emergent population dynamics that may otherwise be missed by models that are not resolved to the individual. Models that do this and split populations into discrete individuals are termed individual or agent-based models (IBM/ABM).

IBMs use a bottom-up approach and simulate a population of discrete individuals where a combination of individual state and environmental variables determine the behaviour of each individual (DeAngelis and Grimm, 2014). IBMs have been widely used in fisheries to study both the fish and the fishers of a fishery, and allow for heterogeneity of intracohort individuals such as fishers within the same fleet or fish within the same age class. By modelling the individuals mechanistically, the outputs from the model are emergent with realistic links to their original drivers. To provide a mechanistic link between environmental drivers and fish population, one widely accepted approach is to use energy budgets (Sibly *et al.*, 2013; Boyd, Walker, *et al.*, 2020). Here agents that represent fish ingest energy from the model environment (which can be inputted from remote sensing data [Boult *et al.*, 2018; Boyd *et al.*, 2020]), and then spend it on life processes including maintenance, growth, and reproduction. When conditions are suboptimal such as low abundance or high competition for resources in the model environment, individuals will differ in their vital rates. For example, individuals frequenting areas of reduced food abundance and cooler temperatures would grow and reproduce relatively slowly. In this way, the collective individual circumstances are all added together and the population dynamics that result are emergent from the drivers that caused the changes. Similarly when modelling fisher behaviour as part of an IBM (Jules Dreyfus-León, 1999; Millischer and Gascuel, 2006; Bastardie *et al.*, 2010) agents can represent fishing vessels and react individually to drivers of fisher behaviour such as weather, fuel price, or fish price, and the emergent total fleet response will have consequent impacts on fishing pressure.

The emergent outputs from the mechanistic process within an IBM make them a particularly useful approach to investigate fisheries response to novel environments such as climate change or new fisheries management measures. In reality, to construct, parametrise and validate IBMs requires huge amounts of data, and this complexity can lead to uncertainty which can make IBMs unsuitable tools for making tactical management decisions (Collie *et al.*, 2016; Johnston *et al.*, 2019). Here it is not suggested that IBMs will replace the current stock assessment models, but they may be useful as complementary tools allowing fishers management to provide more complete advice.

1.6 *Northern stock of Sea bass*

Sea bass are a generalist predator with a large geographical range and can be found from southern Norway to Northern Africa (Child, 1992; Pickett and Pawson, 1994). The sea bass in the northern stock on which we focus (North Sea, English Channel, Celtic Sea and Irish Sea) are relatively slow growing and long lived only maturing between 4-6 years (35-49cm) and have a maximum age of 30 years (Pickett and Pawson, 1994; Froese and Pauly, 2017). Sea bass are both highly eurythermic and euryhaline, these traits facilitate the complex life cycle and migratory behaviour seen in this stock (Pickett and Pawson, 1994). The life cycle begins with a pelagic larval stage lasting between 2 and 4 months as eggs, larvae and yolk-sac larvae drift from offshore spawning grounds to the UK coastline (Jennings and Ellis, 2015). During these younger life stages the youngest 0-groups remain in estuarine nursery areas and then move into deeper water as they grow (Pickett and Pawson, 1994). Young fish from 0-4 then tend to inhabit nursery areas in estuarine and nearshore environments before joining the mature population (Kelley, 1988). Once juvenile sea bass reach maturity they begin to undergo seasonal migrations between inshore summer feeding areas and offshore spawning grounds in the winter months (Pawson *et al.*, 2007). Seasonal migrations are triggered by

sea surface temperature (SST) changes (Pawson and Pickett, 1987) and sea bass move rapidly from costal feeding areas to offshore spawning grounds between October and December and begin returning around April - May to feed at the coast again (Pawson and Pickett, 1987; Pawson *et al.*, 2007). The timings of migrations vary interannually and between populations around the UK (Waldman, 1995) depending on annual SST. There is strong evidence that feeding areas are specific to local populations (Pawson *et al.*, 2008; Doyle *et al.*, 2017) and spawning generally occurs in the Celtic and southern North Seas between February and June. The geographic extent of spawning is thought to be bounded by a minimum temperature of 9°C meaning it can expand as the season progresses and in warmer years (Pickett and Pawson, 1994).

The UK commercial sea bass fishery has emerged in the last 50 years and was of little importance before 1970 (Pickett and Pawson, 1994). Growth through the 1970's and 1980's saw sea bass landings valued at £3-4 million by 1986, which accounted for a high proportion of the earnings of many inshore fishermen (Pawson, Pickett and Smith, 2005). Even from this short period of increased popularity, the increased exploitation was already contributing declining sea bass stocks (Pawson, Pickett and Smith, 2005). In 1990 the UK government responded to increasing evidence of the decline and implemented regulations to protect immature sea bass; a minimum landing size of 38cm, minimum mesh size and protected designated nursery areas from fishing pressure (Pawson, Kupschus and Pickett, 2007). The northern sea bass stock did then recover, attributed in part to the new implemented measures but also due to climate warming, known to be associated with good recruitment (Pawson, Pickett and Smith, 2005). Despite the new regulations the number of the vessels exploiting sea bass continued to increase (Pawson, Pickett and Smith, 2005) until 2010 when a drastic change saw stocks fall into a rapid decline (ICES, 2021). The decline continued for eight years and has since been attributed to a combination of weak year classes and fishing mortality (ICES, 2021). The decline led to the implication of emergency management measures in 2015 (ICES, 2021). The management measures included; a ban on pelagic trawling during spawning season; an increase in minimum landing size (increase from 36 to 42 cm), monthly quotas by gear type, recreational bag limits, closed fishing areas and a closed season February to March (Ares, 2016). The majority of vessels that now target sea bass in 2020 are under 10m, likely as a consequence of increased legislation. These vessels are limited to targeting sea bass with hook and line and landing a small amount of regulated bycatch from fixed gill nets, seins and trawls (GOV.UK, 2020). As well as an important commercial fishery, sea bass are a popular target for recreational anglers, who were responsible for around one quarter of total sea bass removals in 2012 (Radford *et al.*, 2018). Similar to commercial fishing, recreational targeting of sea bass has undergone changing restrictive legislation including: mandatory catch and release for periods of the year, minimum landing sizes (MLS), and bag limits that force anglers to release fish once there limit is achieved (GOV.UK, 2016, 2017, 2018, 2019, 2020).

The northern sea bass stock is assessed by the International Council for the Exploration of the Sea (ICES) using Stock Synthesis 3; an analytical Age- and length-based assessment model (ICES, 2019). SS3 includes: 1) a population dynamics model, which simulates growth, mortality, and recruitment; 2) an observation model which relates the population dynamics to available data; and 3) a statistical model which estimates parameters to maximise the goodness of fit between population model and data. To define the status of the stock, the assessment compares outputs from SS3 to maximum sustainable yield reference points (MSY, the largest long-term yield that can be taken without causing the stock to collapse) and keeping the stock within safe biological limits (termed precautionary reference points). Once the state of the stock is assessed, outputs from SS3 are used as a starting point to explore population effects of catch scenarios. From these, management can determine the catch advice for the following year (ICES, 2021). SS3 includes a "multi-area"

configuration, where a stock can be sub-divided into multiple geographical units (Methot and Wetzel, 2013) but this can be considered limited in its ability to model the outcome of any spatially explicit management measures (e.g., Sea bass fishery spatial closures in key of spawning areas [GOV.UK, 2020]).

1.7 Aims and objectives.

In this thesis, I focus on individuals in the hope of obtaining mechanistic insights into the fish and fishers of the northern stock of sea bass. This stock is a worthwhile and interesting case study because: 1) European sea bass (*Dicentrarchus Labrax*) is an important recreational and commercial target species in the UK; 2) The fishery has been in decline since 2010 and has been subject to a high level of regulation; and 3) The majority of commercial vessels that target sea bass in this stock are under 10m with potential vulnerability to environmental, economic, and legislative changes.

Specifically, I aim to:

1. Investigate the sublethal impacts of anthropogenic stressors on fish.
2. Assess fisher decisions and how these impact sea bass fishing pressure in the northern stock.
3. Develop an existing individual based model of the northern stock of sea bass to provide emergent spatially explicit population dynamics driven by remote-sensed data of phytoplankton abundance and sea surface temperature.

1.8 Thesis outline

Chapter one has outlined and introduced; capture fisheries, the role of fisheries management, some of the limitations to stock assessment methods and how an individual approach may be of benefit to addressing some of these limitations. This introductory chapter then introduced the northern stock of sea bass as a case study and stated the aims and objectives of this thesis, which is to use an individual approach to gain mechanistic understanding of the fish and the fishers of the northern sea bass fishery. From here I will outline and introduce the content of the remaining chapters two to six.

Chapter two uses an energy budget model to investigate the energetic impact of anthropogenic stressors on fish. Here I present a general method for using the population consequences of disturbance framework (PCoD) to investigate how stressors influence ecologically relevant life processes of fish. The developed method partitions impact into the initial energetic cost of attempts to escape from the stressor, followed by the energetic impacts of any injury or behavioural change, and their consequent effects on life processes. As a case study, the study assesses the sublethal effects of catch and release angling for the European sea bass. The energy budget model described is not intended to replace existing experimental approaches but does provide a simple way to account for sublethal impacts in assessment of the impact of a range of stressors and aid development of robust management approaches.

Chapter three moves on from fish and focuses on fishers to analyse fisher decisions and aims to gain a mechanistic understanding of fishing pressure. This chapter presents a methodology with which to identify the factors affecting fisher decisions and success as well as quantifying their effects. The method splits fisher behaviour into the decision of when to leave port, and the success of the fishing trip. To illustrate the method, I describe its application to the under 10-meter fleet targeting sea bass in the UK. The study documents the effects of wave height and shows with increasing wave height fewer vessels left port to go fishing. The study also reports on the effects of other factors and discusses the results in the context of management of sea bass and other small-scale inshore fisheries.

Chapters four and five maintain the theme of the individual and present a spatially explicit individual based model (IBM) which models population dynamics and simulates spatial distribution of the northern stock of European sea bass. In chapter four I present the model as a prepared manuscript and chapter five is a TRACE document which gives full technical model details. The model presented in chapters four and five is a major enhancement to an existing IBM of the northern stock of sea bass published by Walker *et al.*, 2020. The key updates are: 1) addition of a realistic energy budget driven by dynamic maps of phytoplankton density; and 2) inclusion of all life stages (i.e., pelagic stages, juvenile and mature fish). The new model retains the original model purpose of being spatially explicit and, with the energy budget additions, link population dynamics to the environmental drivers (sea surface temperature and phytoplankton density) which ultimately produce emergent fisheries management metrics: spawning stock biomass and both number and mass at age. The model is calibrated against data from the current stock assessment.

Chapter six discusses findings from the thesis, starting with a summary of findings obtained by my focus on individuals. Finally, the thesis ends with a discussion of some caveats and suggestions of how the work I have completed could be built upon.

2 Assessing the sublethal impacts of anthropogenic stressors on fish: An energy-budget approach.

2.1 Abstract

Fish are increasingly exposed to anthropogenic stressors from human developments and activities such as agriculture, urbanization, pollution and fishing. Lethal impacts of these stressors have been studied but the potential sublethal impacts, such as behavioural changes or reduced growth and reproduction, have often been overlooked. Unlike mortality, sublethal impacts are broad and difficult to quantify experimentally. As a result, sublethal impacts are often ignored in regulatory frameworks and management decisions. Building on established fish bioenergetic models we present a general method for using the population consequences of disturbance framework (PCoD) to investigate how stressors influence ecologically-relevant life processes of individual fish. We partition impact into the initial energetic cost of attempts to escape from the stressor, followed by the energetic impacts of any injury or behavioural change, and their consequent effects on life processes. As a case study, we assess the sublethal effects of catch and release angling for the European sea bass (*Dicentrachus labrax, Moronidae*), a popular target species for recreational fishers. The energy budget model described is not intended to replace existing experimental approaches but does provide a simple way to account for sublethal impacts in assessment of the impact of recreational fisheries and aid development of robust management approaches. There is potential to apply our energy budget approach to investigate a broad range of stressors and cumulative impacts for many fish species while also using individual-based models to estimate population level impacts.

2.2 Introduction

With a rising human population and increasing global development, there is a worldwide intensification in the production of food, energy and resources with manifold effects on biodiversity and the environment (Vitousek *et al.*, 1997). Aquatic ecosystems and their fish populations are under increasing pressure from stressors associated with these human activities (Gordon *et al.*, 2018; Reid *et al.*, 2019). The stressors that affect fish can be direct (e.g., exploitation via commercial and recreational fishing) and/or indirect (e.g., chemical pollution and anthropogenic noise), and consequences for fish range from mortality to more subtle sublethal effects on physiology or behaviour that impact fitness (Gordon *et al.*, 2018; Lewin *et al.*, 2019). Stressors can also interact in unpredictable and complex ways and may cause impacts that are greater than the sum of the individual stressors (Crain, Kroeker and Halpern, 2008).

Where possible, sublethal effects should be documented experimentally. Experimental studies investigating the effects of stressors on fish include: anthropogenic noise (Popper and Hastings, 2009); pollution (Hamilton *et al.*, 2016); climate (Cheung et al., 2012; Heath et al., 2012); commercial fishing (Cook *et al.*, 2019); and recreational fishing (Bartholomew and Bohnsack, 2005; Lewin *et al.*, 2019). Experimental approaches to investigate sublethal effects are mostly divided into containment, telemetry or mark-recapture studies (Ferter et al., 2015). Containment experiments keep live fish in a container, expose them to stressors, and observe their impacts. Containment gives direct access to all the study fish, but many species are not suited to be kept in cages (e.g., large or highly mobile and migratory species [Braun, Kaplan, Horodysky, & Llopiz, 2015; Horodysky, Cooke, Graves, & Brill, 2016]) and the effects of containment can obscure effects of the experimental stressor (Pollock and Pine, 2007). In telemetry studies, captured fish are tagged to record data on their behaviour after release (Pollock and Pine, 2007; Donaldson *et al.*, 2008) and often only fish in

good condition are tagged due to the cost of tags and ethics (Graves, Luckhurst and Prince, 2002; Brattey and Cadigan, 2004). Mark-recapture experiments are similar to telemetry but only use identification tags, requiring that the fish be recaptured, when its condition can be compared with the last time it was caught (Pollock and Pine, 2007). Both telemetry and mark-recapture have the advantage of taking place in the fish's natural environment but are often limited by difficulties tagging and following sufficient numbers of fish. In addition, stressor responses can be difficult to distinguish from the impacts of the surgery or tagging event (Pollock and Pine, 2007; Ferter *et al.*, 2015). So while experimental studies have made important contributions to our understanding of stressors, there are often major logistical limitations to what can be achieved, especially considering the broad range of sublethal impacts, in contrast to mortality effects where the individual either survives or dies. Despite the challenges, it is important to understand all stress effects including sublethal effects if we are to recognise and mitigate our impact on global fish populations.

A complementary approach to investigate sublethal effects from human stressors is to use modelling. One important approach is the population consequences of disturbance framework (PCoD) (National Research Council, 2005). This framework was originally developed for marine mammals, but is broadly applicable and appropriate for most fish species (National Research Council, 2005). The effects of stressors are first quantified on individuals, where effects depend on the severity and duration of exposure which generally varies between individuals within a population. Effects of exposure eventually affect fitness traits – survival, fecundity, and growth – and these in turn lead to effects on population dynamics. The success of this approach for marine mammals has been evaluated by Pirotta et al., 2018, who reviewed cases where the PCoD framework was used and the modelling methods that were available at each step from individual effects of stressor exposure through to population level impacts. Here we focus on the first stage of the PCoD framework, evaluating the sublethal effects of stressors on individual fish. Building on previous established bioenergetics modelling approaches (Beyers, Rice, & Clements, 1999; Beyers, Rice, Clements, & Henry, 1999; Beyers & Rice, 2002; Rice, 1990) we introduce a novel modelling approach that considers energy losses from both the initial escape and response to the stressors, not analysed in previous studies, and longer-term reduction in energy intake due to injuries or behavioural change. To do this, we employ widely-used fish energy budgets to calculate the effects of stressors on the fitness traits of growth and reproduction. The success of the energy budget approach derives from the similarities among fish in rates at which they can acquire energy from food and allocate it to vital processes. The same functional forms often well describe rates of energy uptake, maintenance (metabolism), growth and reproduction, and how they scale with body size and temperature (Peters, 1986; Clarke and Johnston, 1999; Sibly *et al.*, 2013). If information is known, or can be assumed, about behavioural responses to stressors, this can be incorporated into an energy budget model. For example, if an individual exhibits avoidance behaviour such that it does not feed, the resultant effects on growth and reproduction can be modelled using an energy budget. In this way, certain physiological and behavioural responses to stressors can be evaluated simultaneously. This is useful because it is nearly impossible to separate behaviour and physiology when studying wild fish in the field (Cooke *et al.*, 2014).

One example of a stressor with potentially appreciable sub-lethal effects is marine recreational fishing. Marine recreational fisheries are a high participation activity with large economic and social benefits, but can also have significant impact on fish stocks (Cooke and Cowx, 2004; Hyder *et al.*, 2018; Radford *et al.*, 2018). As a result, recreational fisheries need to be incorporated into fisheries assessment and management (Hyder *et al.*, 2018; Arlinghaus *et al.*, 2019). Catch and release (C&R) fishing is the process of capturing a fish with a hook and line, and then releasing the live fish back into the water assuming that the fish will survive (Arlinghaus *et al.*, 2007). C&R is an important tool

for the management of recreational fisheries (Policansky, 2002; Arlinghaus *et al.*, 2007). Global release rates have been estimated to be 60% in recreational fisheries, corresponding to about 30 billion released fish annually (Cooke and Cowx, 2004; Horodysky, Cooke and Brill, 2015). Release rates have also been shown to be high in the European marine recreational fishery and are driven by regulatory (e.g., bag limits) and voluntary (e.g., conservation ethic) processes (Ferter *et al.*, 2013). Hence, understanding the sublethal impacts of marine recreational fisheries is important for effective fisheries management. One good example is the European sea bass (*Dicentrachus labrax, Moronidae*). Sea bass are a valuable and important target species for commercial and recreational fisheries in Europe (Herfaut *et al.*, 2013; Vázquez *et al.*, 2014; Radford *et al.*, 2018) and assessments have shown a rapid decline in one important stock (northern sea bass) over the past decade attributed to a combination of poor recruitment and fishing mortality (ICES, 2018a). This has led to management measures since 2015 for both recreational and commercial fishers, including closed areas and seasons, an increase in the minimum landing size, and monthly bag and boat limits that all increase the numbers of fish being released (ICES, 2018a). Post-release mortality of recreationally caught sea bass is low (Lewin *et al.*, 2018) and has been included in the assessment of northern sea bass (ICES, 2018b). However, no attempt has been made to assess the sublethal effects of C&R as the impacts on reproduction and growth are difficult to measure, despite the large numbers of fish that are being released.

The challenges with assessing sublethal effects of stressors experimentally, the lack of comprehensive modelling approaches, the increasing number and magnitude of stressors, and management decisions increasing the number of fish released, all mean that new approaches are needed to ensure sustainable exploitation of fish stocks. Here we focus on the first stage of the PCoD framework, evaluating the sublethal effects of stressors on individuals. We introduce a modelling approach that uses energy budgets to calculate the effects of acute stressors on the fitness traits of growth and reproduction. We build on previous approaches and model the energetic costs of: 1) escaping the stressors effects and 2) longer-term reduction in energy intake due to injuries or behavioural change. Reduced feeding results in reduced energy available for growth and reproduction, and so reduced fitness which is estimated using the model. We illustrate the potential use of this general model through an application to C&R fishing for sea bass in the UK.

2.3 Methods

2.3.1 The energy budget model

An energy budget model was used to investigate the sublethal effects of anthropogenic stressors on individual fish. The energy budget model was implemented in R (version 3.4.3) (R Core Team, 2012). The total energetic cost of exposure to the stressor (C_T) is the sum of the energy required to escape from the stressor (C_E), for fish that attempt escape, and the energetic cost of injury or behavioural change caused by the stressor (C_I) (all units of energy are kJ):

$$C_T = C_E + C_I \qquad\qquad (1)$$

The energy used to escape the stressor (C_E) is dependent on the extent of swimming in excess of normal, the incurred oxygen debt, and the duration of escape. Assuming a fish swims at maximum speed to escape the stressor (see Discussion for further discussion of this assumption), then:

$$C_E = A_T(\delta R_\infty + O_\infty) \qquad\qquad (2)$$

where δ is duration of escape (seconds), R_∞ is the metabolic rate of the fish swimming at maximum speed (watts), and O_∞ is the cost of repaying the maximum post exercise oxygen debt (kJ). A_T adjusts for temperature using the Arrhenius function of absolute temperature T:

$$A_T = e^{-\left(\left[\frac{E_a}{K}\right]\left[\frac{1}{T} - \frac{1}{T_r}\right]\right)}$$

(3)

where E_a is activation energy (0.5eV [Gillooly et al., 2006]), K is the Boltzmann constant ($8.62*10^{-5}$ eV T^{-1}), and T_r is an arbitrary reference temperature. For background and justification of equations 3 and 5-8 see Sibly et al. (2013).

Injury or behavioural change due to exposure to the stressor will impact on energy uptake by reducing preference and/or ability to feed, causing changes to rate or quality of food acquisition, and a subsequent reduction in energy available for life processes. If Δ is the percentage loss in energy uptake due to injury or feeding impediment and E_i is the annual energy uptake by each fish, then:

$$C_I = \Delta E_i / 100$$

(4)

We define the sublethal impact of the stressor as the percentage reduction in maximum annual rate of growth or reproduction caused by the stressor. This is achieved by modelling the allocation of energy to different vital processes (i.e., maintenance, growth, and reproduction) and assessing the consequences for annual growth or reproduction relative to what can be achieved by a fish attaining maximum rates. After calculating the energy needed to cover maintenance, growth and reproduction (Eqn 5-8), the allocation of energy between different processes is complex (Sibly *et al.*, 2013). For simplicity, we take a worst-case approach, assuming the stressor acts solely on either growth or fecundity. So, when considering effects on growth, we assume fecundity has been prioritised and fecundity costs are the same as in an unstressed fish. But when considering effects on fecundity we assume growth is prioritised and growth costs are the same as in an unstressed fish. This allows computation of maximum sublethal effects on growth or reproduction without introducing assumptions about how energy is partitioned among the processes.

Maximum rates of ingestion, maintenance, growth and fecundity all depend on the size of the fish (Sibly *et al.*, 2013), taken here as size at the start of the year. The annual amount of energy that can be ingested each year (E_i) is:

$$E_i = \alpha M^{\frac{2}{3}} E_f \sigma A_T$$

(5)

where α is the mean voluntary food ingestion (g day^{-1} g$^{-2/3}$), M is the mass of the fish (g), E_f is the energy content of one gram of food (J) and σ is the feeding season length. The energy ingested is used to fuel maintenance, growth and reproduction, but may be reduced by anthropogenic stressors.

The annual cost of maintenance (C_M) is:

$$C_M = 2A_T S_a M^{0.79} \times 365$$

(6)

where S_a is a normalizing constant and is calculated from standard metabolic rate (SMR) data from respirometer experiments and a scaling factor of 0.79 is applied to mass for marine fish (Peters, 1986). *FMR* is obtained from *SMR* by multiplying by two (Peters, 1986) and the daily cost is multiplied by 365 to give the annual cost of maintenance. When the cost of maintenance has been paid then any remaining energy assimilated is allocated to growth and/or reproduction.

The maximum annual cost of growth (C_{G_∞}, kJ y^{-1}) is:

$$C_{G_\infty} = 3K_y A_T (M_\infty^{1/3} M^{2/3} - M) * 10.6$$

(7)

where K_y is the annual growth constant and M_∞ is maximum mass. Growth is modelled using the von Bertalanffy equation and the annual energy cost of growth is calculated by multiplying

maximum annual growth rate by the energetic cost of producing one gram of new flesh (10.6 kJg^{-1}; general value from Sibly et al., (2013).

The cost of producing a maximum amount of eggs for mature females ($C_{F\infty}$) is:

$$C_{F\infty} = E_i - C_{G_\infty} + C_M)$$

(8)

where we assume that all energy left over, after covering the cost of maintenance C_M and growth (C_{G_∞}), is available for fecundity.

Table 2-1. Parameter values used in equations 2-6 (see methods for details) and experimental details of the studies from which values are obtained for the European sea bass catch and release fishing case study. Experimental details; L= length (cm), M= mass (g), Θ = experimental temperature (oC), μ= mean, R= range. References: 1= Lanari, D'Agaro, & Ballestrazzi (2002), 2= Froese & Pauly (2018), 3= Pickett & Pawson (1994), 4 = Claireaux (2006), 5= Luna-Acosta, Lefrançois, Millot, Chatain, & Bégout (2011), 6= Jourdan-Pineau, Dupont-Prinet, Claireaux, & McKenzie (2010) 7= Zupa, Carbonara, Spedicato, & Lembo (2015), 8= Peixoto et al. (2016), 9= Pawson & Pickett (1987), 10= Sibly et al. (2013), 11= Cerdá, Carrillo, Zanuy, Ramos, & de la Higuera (1994), 12= Peters (1983), 13= CEFAS (2018) , 14= Wright, Metcalfe, Hetherington, & Wilson (2014), 15= Herskin & Steffensen (1998), 16= Chatelier, McKenzie, & Claireaux (2005), 17= Ozolina, Shiels, Ollivier, & Claireaux (2016), 18= YouTube videos.

Parameter	Value for sea bass	Reference	Experimental details
α Mean voluntary food ingestion	0.54 g day^{-1} g$^{-2/3}$	1	N= 8, L: μ= 37, R= 14-34; M: μ= 1023, R= 144-2749; Θ: R= 6-20
K_y Annual growth constant	0.09y^{-1}	2	N/A
M_∞ Maximum mass	10 kg	3	N/A
S_a Metabolic rate normalisation	0.12	4-8	N= 7, L: μ= 26, R= 14-34; M: μ= 217, R= 26-420; Θ: R= 7-20
φ Potential fecundity for mature female fish	0.3x10^6 eggs per kg of fish	9	N/A
E_e Energy to produce one gram of eggs	10.6 kJ	10	N/A
M_e Weight of one egg	0.96x10^{-3} grams	11	N/A
E_f Energy content of one gram of food	3.5*0.5 kJ*	12	N/A
F_s Number of feeding days	213 days (UK)	3, 13	N/A
R_∞ Metabolic rate swimming at max speed	17.8 - 21.6 watts ‡	4,5,14-16	N= 8, L: μ= 37, R= 14-34; M: μ= 1023, R= 144-2749; Θ: R= 6-20
SMR Standard metabolic rate	2.1 -21.7 watts ‡	4-8	N= 7, L: μ= 26, R= 14-34; M; μ= 217, R= 26-420; Θ: R= 7-20
O_∞ Cost of repaying the max EPOC**	kJ	17	N = 30, L: μ= 32 ± 1, R= 31–35; M; μ= = 520 ± 64 , R= 419–643; Θ: R= 11 ± 0.5°C
δ Duration of escape	10-289 seconds	18	N = 74 (videos available Nov/2017), L: R= 15-75 (estimated)

* assuming 50% of prey mass is flesh. ‡ Value range due to range of fish size. ** Excess post-exercise oxygen consumption.

2.3.2   Application to C&R angling for European sea bass

To investigate the sublethal impact of C&R angling on sea bass, the model was parameterised using data from the literature (Table 2-1). To ascertain the energetic demands of sea bass, data were compiled from studies in respirometers (for details see Table 2-1). Respirometer experiments recorded oxygen consumption which we convert in to watts (assuming $O^2 = 20$ Jml^{-1} [Peters, 1986]), the rates of energy use are then corrected from the experimental temperatures (Table 2-1) to the model reference temperature using the Arrhenius function (Eqn. 3). Sea bass are reported to feed less avidly in water below 10°C (Pickett and Pawson, 1994) so, for simplicity in the model, we assume individuals only feed and grow when sea surface temperature (SST) is 10°C or above. For UK waters this occurs for 213 days a year on average based on monthly SST from sites around the UK coast line from 1966-2012 (CEFAS, 2018) and the overall average SST for these days was 14°C. To show how the energy-budget approach can be applied to other locations we ran the model with the same sea bass parameters but with the ability to feed all year round and a mean SST of 20°C, representing recreational fishing of European sea bass in the Mediterranean.

In our case study, the escape from the stressor is the period during which a fish attempts to escape from the fishing rod, which is termed a fish fight. Fight durations are not generally recorded by recreational sea bass anglers, but videos of fights are placed on YouTube (https://www.youtube.com). We watched all videos (n = 74) publicly available in November 2017 and recorded the duration of fight (10-289 seconds) and the fish length (15-75 cm), estimated by comparison with length of the angler's forearm. For our case study, we use a range of fight durations of 0-300 seconds and the previously described method using equations 2-6 with the sea bass specific parameters (Table 2-1). It was not possible to distinguish from videos if the fish was fighting maximally for the whole fight duration, so we assume fighting for the total duration as a worst case scenario.

2.4   Results

Our results are presented for the case of C&R angling for European sea bass parameterised as in Table 2-1. To assess the sublethal effects of angling, we calculated the losses in energy, growth and fecundity that arise from an individual fish's efforts while fighting and from reduction in energy ingestion while feeding as a result of disturbance including injury. Losses are shown relative to the baseline of energy assimilated by an undisturbed fish which achieved maximum ingestion rate, and had sufficient energy to fulfil maximum growth (juvenile and mature fish) and fecundity (mature fish only) (see Methods for calculation details).

2.4.1   Local sensitivity analysis

The sensitivities of energy, growth and fecundity loss are shown in Table 2-2 as percentage change in output for a 10% change in the model parameters. These sensitivities are for a medium sized fish subject to intermediate levels of disturbance. Sensitivity differs between vital rates, the most sensitive parameters being associated with energy ingestion, which is expected as changes in energy inputs have direct effect on energy available for growth and reproduction. Sensitivities to 10% changes in the model parameters are generally less than or equal to 10% except for the sensitivity of fecundity loss, which is very high as a result of the way energy is allocated when calculating maximum rates: assimilated energy is allocated first to cover maintenance (C_M), and then growth (C_{G_∞}), only when these costs are paid is energy allocated to reproduction (Eqn 7 & 8). To see how sensitivities vary with fish size and levels of disturbance we ran the model with a large mature fish (Length = 70 cm) and a small immature fish (Length = 20 cm), in both severe (300 second fight, 45% reduction in feeding for 45 days) and minimal stress (30 second fight, 10% reduction in feeding for

10 days) scenarios (Supplementary Tables 2-3 & 2-4). Fecundity losses were higher for the large fish but lower for the small fish compared to the values shown in Table 2-2 for the medium fish scenario. Conversely, growth losses were higher for the small but lower for large fish compared to the values shown in Table 2-2 for medium fish scenario. The severity of stress had generally little effect on the small fish, but fecundity was negatively affected in the large fish scenario (Supplementary Tables 2-3 & 2-4).

Table 2-2. Sensitivities of energy, growth and fecundity loss of recreationally caught and released European sea bass to 10% changes in parameter values, presented as the % change in output averaged over an increase and decrease in the parameter value. Results are for a fish of middle size and a middle disturbance scenario (fish length = 42cm, escape duration = 200 seconds and a disturbance of 50% reduction of feeding for 20 days, see Supplementary Tables 3-3 and 3-4 for analyses of other cases).

Parameter	Energy		Growth		Fecundity	
	Escape	Dist[1]	Escape	Dist[1]	Escape	Dist[1]
Mean voluntary food ingestion (α)	10	10	0	7	49	59
Energy content of one gram of food (E_f)	10	10	0	67	49	59
Metabolic rate normalisation (S_a)	-	-	0	0	49	42
Maximum mass (M_∞)	-	-	6	10	3	4
Feeding season length (σ)	10	10	0	0	49	62
Annual growth constant (K_y)	-	-	10	17	6	7

[1]Disturbance

2.4.2 Effects on energy, growth, and fecundity loss

The effects of fight duration on individual energy, growth and fecundity losses are shown in Fig. 2-1 in relation to fish length. Losses increase with fight duration, as expected, but the effects of fish length are more nuanced. The energy cost of fish fights as a percentage of total annual ingested energy are very small. Smaller fish that are involved in a longer fight experience the most severe energy loss, but this only equates to a maximum of 1% loss of annual energy (Fig. 2-1A). Growth losses, shown in Fig. 2-1B, are calculated for juvenile and mature sea bass; in the latter we assume spawning occurs at its maximum rate. Growth losses are at most 3.5%, when a 60 cm fish is involved in a 300 second fish fight (Fig. 2-1B). For immature fish, growth loss reduces as the fish grow, but then increases after maturity at 42 cm as the fish is then assumed to produce eggs at maximum rate, and larger fish become increasingly affected (Fig. 2-1B). By contrast fecundity losses vary very little with fish length (Fig. 2-1C). The results in Fig. 2-1 relate to the worst-case scenario that a fish caught by an angler attempts to escape by burst swimming. We assume the fish is swimming away at maximum speed for the whole fight (see Discussion for justification of this assumption), though in reality a fish can only maintain maximum speed for a very short period due to physiological limitations (Horodysky, Cooke and Brill, 2015).

After the initial fight, injury or behavioural change may affect an individual fish's ability or preference to feed as a result of physical damage from fishing gear and/or air exposure whilst being caught (Siepker, Ostrand and Wahl, 2006). Losses in energy ingested, growth and fecundity are affected by both the duration and the level of reduction in feeding, as shown in Figs. 2-2 & 2-3 for mature female and juvenile sea bass, respectively. Over the parameter ranges investigated, energy losses for a mature bass could be as high as 60%, with consequent growth and fecundity losses up to 100% and 60%, respectively (Fig. 2). Individual juvenile sea bass show smaller energy and growth losses than adults, up to 30% and 50%, respectively (Fig. 2-3). Scenarios resulting in larger/longer reductions in feeding have as expected greater losses of energy, growth, and fecundity (Figs. 2-2 & 2-3).

The effects shown above are for fish living in UK waters, which are assumed to be able to feed for 213 days a year when the sea surface temperature is assumed to be 14°C. Fish in other areas may experience different conditions, but their effects can be readily calculated using our energy-budget analysis. Although the individual rates of ingestion, maintenance and growth increase with temperature, the relative effects of escape and disturbance (those shown in Figs, 2-1 – 2-3) would not change with temperature if the number of feeding days were kept constant. However number of feed days is likely to increase with average temperature. Sea bass in the Mediterranean, for example, are able to feed year round. If we assume sea surface temperatures there are 20°C and update the annual growth constant appropriate for Mediterranean temperatures (Ky = 0.03 [Froese & Pauly, 2018]), we find that all losses are reduced. Both growth and fecundity losses are less than for individuals in UK waters; fecundity losses 8 % as opposed to 28 % and growth losses 14 % as opposed to 48%. These figures are for a particular scenario of a 50 cm sea bass fighting for 150 seconds and experiencing injury that reduces its ability to feed by 50 % for 20 days, but we expect that losses will generally be lower where feeding conditions are better.
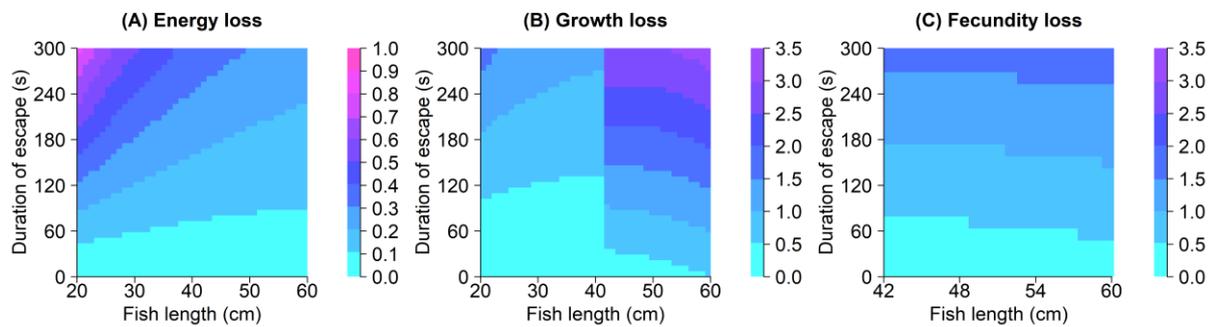
Figure 2-1. Effects of fish fights on growth and fecundity of recreationally caught and released European sea bass in relation to fish length and fight duration. Effects are shown as % loss of annual rates of A) Ingested energy B) growth and C) fecundity, relative to fish achieving maximum growth or fecundity, respectively. The scale of % loss is shown on the right.
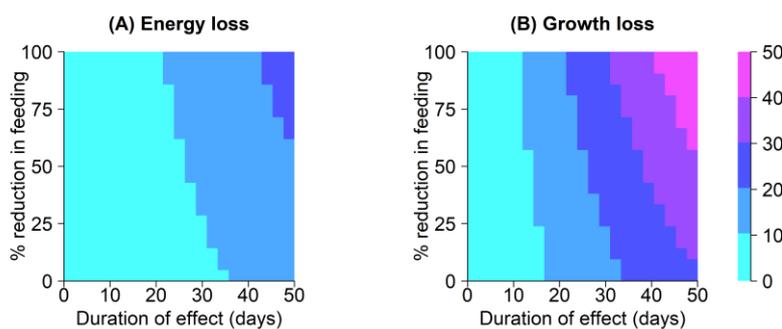
Figure 2-2. The effects of the duration and severity of capture/release effects, measured as % reduction in feeding, on energy intake, growth and fecundity of mature female European sea bass (42 cm). Effects are shown as % loss of annual rates of A) Ingested energy, B) growth and C) fecundity, relative to fish achieving maximum energy intake, growth or fecundity, respectively. The scale of % loss is shown on the right.
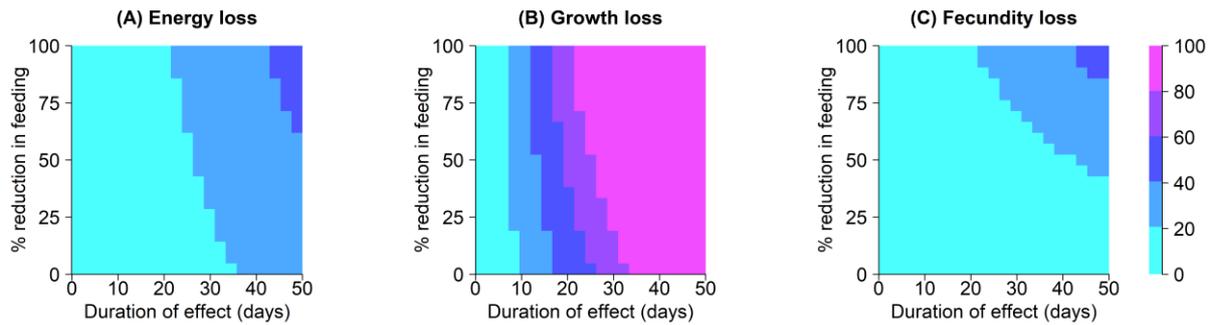
Figure 2-3.The effects of the duration and severity of capture/release effects on food intake, growth and fecundity of juvenile European sea bass (20 cm). Effects are shown as % loss of annual rates of A) Ingested energy and B) growth, relative to fish achieving maximum food intake and growth respectively. The scale of % loss is shown on the right.

2.5 Discussion

With increasing human populations, the impact of anthropogenic disturbances on the aquatic environment is growing (Vitousek *et al.*, 1997). Stressors to fish such as anthropogenic noise (Slabbekoorn *et al.*, 2010), fishing and pollutants (Kappel, 2005) can cause both lethal and sublethal impacts. The method introduced here uses energy budget models to investigate the often under-reported sublethal effects of stressors on growth, reproduction and ultimately fitness of fish. The models are not intended to replace existing experimental approaches, which are the method of choice, but to be used alongside when logistic constraints limit what can be achieved experimentally. For example, our method can be used as an initial step and can help identify needs for further analysis and experiments.

Unique to our method, over other bioenergetics stressor models (Beyers, Rice, & Clements, 1999; Beyers, Rice, Clements, et al., 1999;Beyers & Rice, 2002; Rice, 1990), is splitting the impact of the stressor into two parts. Firstly, assuming an escapable acute stressor, the fish may attempt to flee; this could include dodging an oil spill, avoiding anthropogenic noises or trying to break free from commercial or recreational fishing gear. The period for which fish swim to escape depends on many factors specific to individual stressors. For example, it may depend on the proximity of the fish to an oil spill, construction project or, in a fishing situation, how long gear is being pulled. In these situations, the fish is swimming at speed away from somewhere it does not want to be and is forced to spend energy that is subsequently unavailable for life processes. Some fish, however, freeze instead of attempting to escape, the metabolic implications of this would require similar analysis (Rupia *et al.*, 2016) but is not covered here. As well as escaping, the fish may suffer an injury or endure a change in behaviour due to the stressor. This could be an injury from commercial or recreational fishing gear (e.g., mouth damage from a hook), changed behaviour because of chemicals in the water, disturbance from marine construction or shipping noise. Such effects may impact an individual fish's ability and preference to feed, resulting in reduced ingested energy available for life processes. To show a broad range of possible impacts we display our results on heat maps that allow the simultaneous display of many individual scenarios shown as combinations of reduced ingestion rates and durations of effect (Figs. 2-1 – 2-3). Each combination of these is unique and equates to a loss of energy. When this loss is compared with the energy needed to achieve life processes it is possible to investigate the impact of the stressor in question.

To demonstrate the method in practice, we chose as a case study the European sea bass subject to the stress of recreational C&R fishing in the UK. In our worked example, the initial escape is the fish fight attempting to escape from recreational fishing gear. We show how the combination of fight duration and the size of fish affect the energetic cost of the fight and the subsequent impact on

growth and reproduction (Fig. 2-1). As described in methods, our analysis is worst case: when considering effects on growth, we assume fecundity has been prioritised and fecundity costs are the same as in an unstressed fish, but when considering effects on fecundity we assume growth is prioritised and growth costs are the same as in an unstressed fish.

The initial energetic cost of the fish fight is very small when compared to annual ingested energy, however this small amount of energy does show knock-on effects on both growth and fecundity (Fig. 2-1). In immature sea bass (< 42 cm) the pattern of growth loss mirrors that of energy loss and smaller immature sea bass are worse affected (Fig. 2-1B). This pattern switches at maturity, and larger sea bass are then more affected, because they pay the same fecundity costs as unstressed fish. Fecundity costs are greater in larger fish, leaving less energy available to fuel growth.

After the initial fight, the released fish may suffer injury or changed behaviour due to the capture event. This is analysed in Figs. 2-2 and 2-3 by looking at how injury or behavioural change can reduce ingestion and cause knock-on effects on individual growth and reproduction. Here the patterns of loss of growth/reproduction reflect those of energy loss. Effects on growth are greater than those on reproduction, and Fig. 2-2B shows that in extreme cases growth may cease altogether during the study year. Growth losses are more severe in adults than in immature fish (compare Figs. 2-2B and 2-3B) because adults are assumed to pay fecundity costs. We show how the energy-budget approach can be used to assess the effects of changing location by applying it to the Mediterranean, where we predict smaller losses for individual fish living in the warmer Mediterranean temperatures. As expected physiologically, ingestion, metabolic and growth rates all increase in warmer waters, but the number of feeding days increases too. More feeding days result in more energy being ingested, and because losses are calculated per annum, the net effect of the warmer temperatures is that losses are reduced. The model could be used in a similar way to test inter-annual temperature fluctuations or climate change driven sea temperature changes.

Our energy budget approach enables initial investigation of stressor effects on individual fish, but for many applications it will be important to consider how a stressor affects entire fish populations (with a notable exception of animal welfare studies where the focus is on individuals [Cooke & Sneddon, 2007; Davie & Kopf, 2006]). In our case study, a population analysis would require data on numbers and size distribution of sea bass being caught. Currently there is limited data on recreational fishing pressure, but relevant estimations may become possible as recreational fisheries become increasingly included in fisheries management (Radford *et al.*, 2018). More broadly for anthropogenic stressors, Pirotta et al., (2018) suggest that one way to approach population impacts is using individual based models (IBMs). IBMs use a bottom-up approach and simulate a population of discreet individuals where a combination of individual state and environmental variables change individual behaviour (DeAngelis and Grimm, 2014). In an IBM, each individual reacts to stressors uniquely depending on, among many other things, its energy reserves, life stage, size, and proximity to the stressor. The proportion of individuals within a population that are affected and the severity of these impacts on their life process determine the population level impacts of the stressor (Grimm and Railsback, 2005). The estimated effect of a stressor would be relevant in many cases of fisheries management. For example, stressor effects could change depending if in/out of a spawning season, or they may impact size-at-age with potential knock-on effects on time to reach maturity and fecundity. An IBM could also be used to test food-limited scenarios (Boyd *et al.*, 2018) when even mild impacts of the stressor may impact on the ingestion rate enough to show previously unforeseen emergent population-level effects. Gordon et al. (2018) identify scenarios in which individual fish may simultaneously experience combination of stressors. The use of an appropriate IBM in combination with our energy budget approach could be used to quantify the population impacts of multiple stressors varying in time and space.

2.5.1   Limitations and further research

Our method is broad and could, with appropriate consideration, be applied to a wide range of anthropogenic stressors and fish species. As in other bioenergetics models (e.g., Beyers & Rice, 2002), to apply this method to different stressors or species it is necessary to collect relevant values for duration of escape, if any, and re-parametrise equations 2-8 for the intended species (Table 2-1). If the ultimate aim is a predictive model then validation must be given thought, here we discuss some important considerations that would need to be addressed and some suggested experimental approaches that could provide validation data.

We are currently limited to investigating effects within one year and our method does not cover injuries or behaviour that extend beyond this. The model also does not allow for multiple stressor events within one year (i.e., if the same fish is caught and released multiple times) which has the potential to add up to substantial impact upon the individual. In addition, within the current model, catch-up growth is not considered where some species may be able to make up lost growth after one or more stressor events (i.e., compensatory growth; see example with largemouth bass (*Micropterus salmoides, Centrarchidae*) in Cline, Weidel, Kitchell, & Hodgson, 2012. However once embedded in a suitable IBM, heterogeneous responses to multiple events within one year or effects that extend beyond one year, including compensatory growth, could be studied.

For escape duration, our analysis assumes fish are swimming away from the stressor at maximum speed for the entire duration of escape and we assume that they incur a maximal oxygen debt. In reality there are physiological limitations which limit fish to short burst of maximum effort (Horodysky, Cooke and Brill, 2015). Furthermore for stressors that require fish to swim for long durations this may be an excessive estimation of used energy, so ours is a worst-case and a precautionary approach. One way to extend our precautionary approach and cover a non-escape response is to use burst swimming as an approximation of any increased metabolic rate due to the stressor stimuli. To better predict energetic costs and consequences beyond simple worst case scenarios, would require detailed information on swimming behaviour during stressor escape and/or any other metabolic changes. Data for this could be from tagging experiments to measure how long and fast fish swim (Graves, Horodysky and Latour, 2009; Brownscombe *et al.*, 2013; Horodysky, Cooke and Brill, 2015) and respirometer experiments for changes in metabolic rate (Rupia *et al.*, 2016).

There are also aspects of injury and behavioural changes after escape that are not accounted for in our model. Firstly, it may be important to consider the disease status of the study species/stock, as infected fish may suffer additional complications from anthropogenic stressors. For example striped bass in the USA that suffer from chronic diseases associated with *Mycobacterium spp.* (Gauthier *et al.*, 2008) have been shown to suffer reduced reproductive success (Gervasi *et al.*, 2019), growth rates (Latour *et al.*, 2012) and aerobic scope when exposed to hypoxic and warmer temperatures (Lapointe *et al.*, 2014). Furthermore, fish may suffer parasite or bacterial infections as a result of injuries or stress which could affect growth independently of feeding rate (Steeger *et al.*, 1994). Account must also be taken of variation in fish life histories. For example our model would underestimate the effect of disturbance on brood protecting species such as smallmouth and largemouth bass (*Micropterus dolomieu* and *Micropterus salmoides*) (Hanson *et al.*, 2007). When brood protecting species are subjected to C&R or other disturbances they are less able to defend their eggs (Suski *et al.*, 2003; Pinder *et al.*, 2017), and the increased risk of brood predation leaves a reproductive sublethal impact on top of the energy lost during disturbance. Finally, fish species may differ in their stress responses, from complete inhibition to increase of reproduction (Schreck, Contreras-Sanchez and Fitzpatrick, 2001; Lowerre-Barbieri, Vose and Whittington, 2003; Hall *et al.*, 2009). Such factors may vary the sub-lethal impacts of stress from those calculated using our exclusively energetics based approach.

2.6 Conclusions

We show a broadly applicable, complementary approach to field investigations that can be used to investigate sublethal impacts of a broad range of anthropogenic stressors on life processes of individual fish. Our approach builds on established bioenergetics approaches and provides a comprehensive energetics overview through from initial escape to longer term injury/behavioural changes. We demonstrate its application to C&R fishing of European sea bass and show impacts ranging from zero to losses of up to 100% growth and 62% fecundity. Validation of the model is out of the scope of this study but we suggest experimental approaches that could be used to gain potential data and parameters and extend the model utility. We further suggest using individual-based models to investigate combinations of multiple anthropogenic stressors that vary over time and space for more detailed analysis of population-level effects. Our comprehensive energy budget approach, embedded within an IBM, could indicate emergent population level effects for a broad range of anthropogenic stressors and cumulative impacts for many species and hence contribute to understanding and mitigating sublethal anthropogenic impacts on fish.

2.7 Acknowledgements

2.8 Supplementary tables

Table 2-3. Sensitivities of energy, growth and fecundity loss of recreationally caught and released European sea bass to 10% changes in parameter values, presented as the % change in output averaged over an increase and decrease in the parameter value. Results are for fish length = 70 cm in a severe (S) (300 second escape, 85% reduction in feeding for 45 days) and minimal (M) stress (30 second escape, 10% reduction in feeding for 10 days) scenario.

Parameter	Energy				Growth				Fecundity			
	Escape		Dist[1]		Escape		Dist[1]		Escape		Dist[1]	
	M	S	M	S	M	S	M	S	M	S	M	S
Mean voluntary food ingestion (α)	10	10	10	10	0	0	1	15	82	83	84	150
Energy content of one gram of food (E_f)	10	10	10	10	0	0	1	15	82	83	84	150
Metabolic rate normalisation (S_a)	-	-	-	-	0	0	0	0	67	68	69	150
Maximum mass (M_∞)	-	-	-	-	12	13	13	6	6	6	6	12
Feeding season length (σ)	10	10	10	12	0	0	0	0	82	83	84	183
Annual growth constant (K_y)	-	-	-	-	10	10	11	5	6	5	5	10

[1]Disturbance

Table 2-4. Sensitivities of energy, growth and fecundity loss of recreationally caught and released European sea bass to 10% changes in parameter values, presented as the % change in output averaged over an increase and decrease in the parameter value. Results are for fish length = 20 cm in a severe (S) (300 second escape, 85% reduction in feeding for 45 days) and minimal (M) stress (30 second escape, 10% reduction in feeding for 10 days) scenario.

Parameter	Energy				Growth			
	Escape		Dist[1]		Escape		Dist[1]	
	M	S	M	S	M	S	M	S
Mean voluntary food ingestion (α)	10	10	10	10	20	21	20	26
Energy content of one gram of food (E_f)	10	10	10	10	20	21	20	26
Metabolic rate normalisation (S_a)	-	-	-	-	10	11	10	16
Maximum mass (M_∞)	-	-	-	-	0	0	0	0
Feeding season length (σ)	10	10	10	12	20	21	21	32
Annual growth constant (K_y)	-	-	-	-	0	0	0	0

[1]Disturbance

3 Factors affecting fisher decisions: the case of the inshore fishery for European Sea bass (*Dicentrarchus labrax*)

3.1 Abstract

Fishery management relies on forecasts of fish abundance over time and space, on scales of months and kilometres. While much research has focussed on the drivers of fish populations, there has been less investigation of the decisions made day-to-day by fishers and their subsequent impact on fishing pressure. Studies that focus on the fisher decisions of smaller vessels may be particularly important due to the prevalence of smaller vessels in many fisheries and their potential vulnerability to bad weather and economic change. Here we outline a methodology with which to identify the factors affecting fisher decisions and success as well as quantifying their effects. We analyse first the decision of when to leave port, and then the success of the fishing trip. Fisher behaviour is here analysed in terms of the decisions taken by fishers in response to bio-physical and socio-economic changes and to illustrate our method, we describe its application to the under 10-meter fleet targeting sea bass in the UK. We document the effects of wave height and show with increasing wave height fewer vessels left port to go fishing. The decision to leave port was only substantially affected by time of high tide at one of the four ports investigated. We measured the success of fishing trips by the landings of sea bass (kg) per metre of vessel length. Fishing success was lower when wave height was greater and when fish price had increased relative to the previous trip. Fuel price was unimportant, but a large proportion of the variation in success was explained by variation between individual vessels, presumably due to variation in skipper ability or technical restrictions due to vessel characteristics. The results are discussed in the context of management of sea bass and other small-scale inshore fisheries.

3.2 Introduction

The global state of fish stocks is a cause for concern, and there is a need for increasingly effective fisheries management (Hilborn *et al.*, 2020). An area of management that has received less research attention is the human element of fisher behaviour (Wijermans *et al.*, 2020). As it is ultimately the fishers and not the fish that managers can directly influence, it is critical for successful management that fisher behaviour is taken into consideration (Branch *et al.*, 2006; Hilborn, 2007).

Fisher behaviour is analysed here in terms of the decisions taken by fishers in response to bio-physical and socio-economic changes, as recently reviewed by Andrews, Pittman and Armitage, 2020. Many of the studies (e.g., Wilen *et al.*, 2002; Salas and Gaertner, 2004; Branch *et al.*, 2006; Hilborn, 2007; Valcic, 2009) have sought to establish how management decisions affect the dynamics and distribution of fisher decisions and the subsequent pressure on the fishery. The drivers of fisher decisions are often complex and interlinked but can be coarsely categorised into environmental, economic, and legislative. Economic factors include fluctuations in fuel or fish price and their interaction through the market can have profound impacts on fisheries (Abernethy *et al.*, 2010), as can be seen for example in the changes of demand and supply during the COVID-19 pandemic (Bennett *et al.*, 2020). Profitability is often a balance of both environment and economic factors, but is also affected by legislation. Legislation can be broad and applied in a variety of ways, including restrictions on quota or fishing gears in addition to spatial or temporal closures, all of which can have major influence on fisher decisions (Fulton *et al.*, 2011; Abbott and Haynie, 2012).

Environmental drivers, such as weather and climate change including increasing storminess, have already been shown to affect fishing decisions and subsequent fishing pressure in some cases (Henry and Johnson, 2015; Shepperson *et al.*, 2016; Sainsbury *et al.*, 2018). Fisheries are likely to be exposed to a combination of pressures and the relevance and magnitude of fisher decisions may vary between different fisheries. Understanding of these relationships is increasingly recognised as an important component of fisheries management (Wijermans *et al.*, 2020).

The fishing method used to target catch is one obvious aspect of a fishery that will affect how different environmental, economic, and legislative pressures impact fisher decisions. Globally, fishing methods are extremely diverse, but often involve the use of a dedicated fishing vessel. These fishing vessels can range from small canoes up to factory trawler ships, and the decisions of fishers operating on vessels of different sizes may be affected by different predictors (Dorn, 2001; Thoya and Daw, 2019). Research into fisher behaviour is necessarily dependant on the data available. To gain detailed insight into spatial fishing pressure, studies that focus on European vessels longer than 12-meters can make use of data from Vessel Monitoring Systems (VMS) or Automatic Identification System (AIS) for vessels over 300 gross tonnes engaged in international voyages. However, for smaller vessels AIS is limited as it is voluntary (Shepperson *et al.*, 2018) and VMS is not required in European waters for these vessels. Smaller vessels are also potentially more vulnerable to environmental change (Sainsbury *et al.*, 2018; Young *et al.*, 2019) and importantly, despite their small size, small vessels make up a large percentage of global fisheries with 82% of recorded motorized fishing vessel lengths being less than 12 meters (FAO, 2020). It is therefore important to consider, for both small and larger fishing vessels, all available information in trying to understand fisher decisions and their impact on fishing pressure.

In this study, we focus on smaller vessels and use as a case study the UK under 10-meter fleet catching European sea bass (*Dicentrachus labrax, Moronidae*) in the North Sea, English Channel, Celtic Sea, Bristol Channel, and Irish Sea (Northern Stock, ICES 4b&c, 7a,d-h). Sea bass is a large, high value, slow growing and late maturing fish that until 2015 was not subject to catch restrictions. In the past decade, the northern stock size fell rapidly, which was attributed to a combination of poor year classes and fishing mortality (ICES, 2018a). The decline led to the implementation of emergency management measures in 2015 (ICES, 2019), and, since 2020, UK vessels have been limited to targeting sea bass with hook and line, and bycatch limits for fixed gill nets, seine nets, and trawls (GOV.UK, 2020). Sea bass continues to be an important species of the UK under 10-meter fleet as it is a high value species that can be harvested close to shore (Williams *et al.*, 2018).

In an attempt to gain insight into the complex decisions made by fishers using smaller fishing vessels, we analyse first the decision of when to leave port, and then the success of the fishing trip. To demonstrate our approach, we assess the impact of environmental and socio-economic drivers on under 10-meter fishery for sea bass. We collate data from a number of different sources which we use to predict when fishing trips occur and their success as measured by landings. Based on a linear regression approach, we assess the importance of different factors driving decisions to leave port and fishing success. The results are discussed in the context of management of sea bass and other small-scale inshore fisheries.

3.3 Methods

Our analysis has two components:

1. The decision to leave the port analysed here by a logistic model we term *Leave port*.

2. The success of the fishing trip analysed here by a linear regression model we term *Fisher success*.

Models are created for each of these processes independently. This is done by identifying possible predictors of fisher decisions and then attempting to obtain relevant data. The approach for this will vary extensively between fisheries, but to give an idea of how it can be done in practice, we illustrate our method below with a case study of the under 10m fleet of UK northern stock sea bass fishery.

3.3.1   Identifying possible predictors

Both fuel price and weather have been identified as explanatory variables in other fisher behaviour studies (e.g., Abernethy *et al.*, 2010; Shepperson *et al.*, 2016). Time of high water is a further environmental driver that is likely to affect the decision to leave port due to *a priori* understanding of logistical issues of low tides (e.g., navigating shallow water and ability to leave tidal moorings). To our knowledge daily tide cycles have not been included in fisher behaviour analyses until now, though Sharples *et al.* (2013) studied Celtic sea fishing activity in response to spring and neap tides and Poisson *et al.* (2010) assessed monthly tidal influence for a Réunion Island longline fishery. Inclusion of further possible fisheries behaviour predictors is necessarily constrained by the availability of data. In the case of the UK northern stock sea bass fishery, the best data source available to record when vessels leave port and their success are the Marine Management Organisation (MMO) logbooks, whose contents are described below. MMO logbooks contain information beyond a simple yes/no answer for leaving port, however we do not have any information on the reasoning when vessels have remained in port, so we cannot assess this in our case study leave port analysis. It was possible however to supplement logbook data with data from other sources, here in our case study we were able to obtain data on time of high water, wave height and fuel price (details shown below).

For the fishing success analysis, we defined the dependent variable, termed fisher success, as landings per metre of vessel length in order to standardise the outcome of fishing trips for differences in vessel size. For this analysis, we were able to use all the data in the MMO logbooks (in addition to our extra data sources) as predictors of fisher success, namely *wave height, tide*, *change in fish price, fuel price, month*, and *year*. One key recording from the MMO logbooks is fish price, however rather than use fish price directly we used the *change in fish price* since the previous fishing trip to account for potential changes in revenue and therewith profit (van Putten *et al.*, 2012). *Wave height*, to the nearest metre, was entered as a factor to capture any non-linear effects. Individual *vessel ID* and *port name* were entered as fixed effects to reveal associated unobserved effects of vessel and location. Yearly fixed effects capture the annual changes in fisheries legislation which might restrict harvest success. Vessel fixed effects captures skipper ability as well as capacity or technical restrictions due to vessel characteristics. We chose predictors from the logbook and other data sources on the assumption that they are likely predictors of fishing success and are of relevance to legislation and future management decisions (GOV.UK, 2016, 2017, 2018, 2019, 2020).

3.3.2 Obtaining data

In the case of the UK northern stock sea bass fishery, the main data source of when vessels leave port and their success are the MMO logbooks which incorporates sales notes for the under 10-meter vessels in similar format. In addition to recording the days on which named vessels left named ports, the logbooks record the weight of fish caught. These records were supplemented by data on wave height, time of high tide and fuel price. We analysed individual trip data for the years 2014-2018 for vessels of up to 10 meters in length for four study ports: Burry Port; Plymouth; West Mersea; and Weymouth (Fig. 3-1, Tables 3-1 and 3-2). The chosen ports represent the fishery spatially, each being chosen on the basis that it had the highest annual value landings of sea bass within its region (logbook data 2014 - 2018). Each study port had a fleet consisting of vessels with lengths over and under 10-meter, but sea bass fishing was more valuable to the under 10-meter vessels in all four ports (Table 3-1). We define vessels that are sea bass-targeting/impacting as those that recorded more than 10 trips with more than 10% landings by weight of sea bass. The resulting dataset contains 8,815 fishing trips between 2014 - 2018 (Table 3-2). The study ports differed in the number, size, and engine power of the vessels in their fleets, and the total landings of sea bass varied between ports with Weymouth catching the most sea bass (Table 3-2). Fishing gear also varied with more sea bass caught using hook and line than other fishing methods in all our study ports except West Mersea, where gill nets were favoured (Table 3-2).

We collated several environmental and socio-economic parameters for use in the analysis. Out of possible weather variables, we use *Wave height* to represent sea conditions due to availability of data and its convenience as a combination of wind speed, and direction. *Wave height* was taken from the UK strategic wave monitoring network WaveNet[4]. The closest Waverider buoys to our focus ports (Fig. 3-1) were used to calculate daily average *wave height*. The buoys are not always stationed directly outside our study ports but gave an adequate representation of the daily sea state for our purpose. To calculate *time of high tide,* we first obtained data on tidal movements, from the British Oceanographic Data Centre's (BODC) tide gauge archive[5]. The time of tide measurements were rounded to the nearest hour, we then checked in the first 12 hours (00:01 - 11:59) of each 24-hour period for the highest water and corresponding time, taking this as the first high tide of the day. We only used the first high tide time in our analysis as first and second tide times are closely correlated. Tide gauges are not all stationed directly outside our study ports (Fig. 3-1) but should give an adequate representative of tide state for our purpose.

To calculate *price change*, we extracted the mean daily price of sea bass for each port (£.kg^{-1}) from the MMO logbooks. We then subtracted the price received by the vessel on its previous trip. The resulting *price change* is either a positive or negative value indicating a price rise or drop, respectively. Data from February and March 2016 - 2018 were excluded because there was a ban on fishing for sea bass in these months (GOV.UK, 2016, 2017, 2018). To estimate *fuel price*, because daily fuel price at each port was not recorded, we used monthly red diesel prices[6] on the assumption that fishing vessels used untaxed diesel or other fuels (e.g., regular pump petrol) correlated to these prices.

All statistical analyses were carried out in R (version 3.6.1 [R Core Team, 2019]). Final estimations were derived by backwards stepwise regression (StepAICc MASS - Venables and Ripley, 2002) and a Likelihood ratio test (Step Stats - R Core Team, 2019). We checked for collinearity in model predictors using correlation matrixes and analysing variance inflation factor (VIF) scores.

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[4] Source: https://www.cefas.co.uk/data-and-publications/wavenet/ [last access: 02/02/2021]
[5] Source: https://www.bodc.ac.uk/data/hosted_data_systems/sea_level/uk_tide_gauge_network/ [last access: 02/02/2021]
[6] Source: https://www.gov.uk/government/statistical-data-sets/oil-and-petroleum-products-monthly-statistics [last access: 02/02/2021]
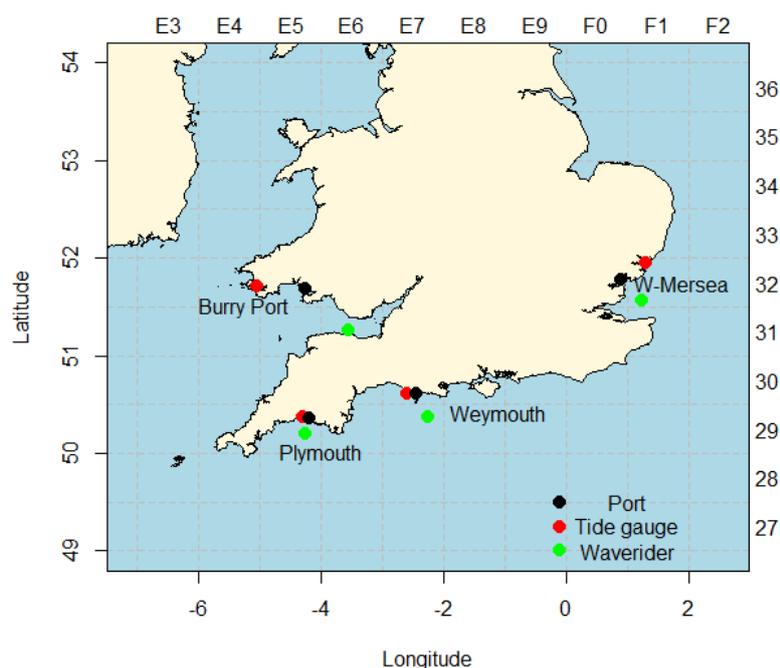
Figure 3-1. Map of study ports, and instruments from which data was taken. Black dots indicate the study port locations. Red dots and Green dots show the approximate location of tide gauges and waver rider buoys respectively.

Table 3-1. Descriptive statistics of the chosen ports from MMO landings data 2014-2018 (< 10 or > 10 indicated under & over 10-meter fleet respectively).

Port name	Total landings (t)		Sea bass Landings (t)		Sea bass % of total value of catch		Location in England & Wales
	<10	>10	<10	>10	<10	>10	
Burry Port	247	-	129	-	87	-	West
Plymouth	4207	47320	137	44.6	15	0.63	South-West
West Mersea	580	68	74	0.4	44	1.66	East
Weymouth	1891	6356	254	0.6	44	0.03	South

Table 3-2. Descriptive statistics of chosen vessels from MMO logbook scheme. *no. vessels* = number of vessels per port, *no. trips* = total number of fishing trips for all vessels in each port, *r.* = range, *m.* = mean, *GN* = Gill net, *HL* = Hook and line, *TRP* = Traps/Pots, *TRW* = Trawls).

Port name	no. vessels	no. trips	Vessel Length (m)		Vessel Power (hp)		Landings (t)	% caught by gear			
			r.	m.	r.	m.		GN	HL	TRP	TRW
Burry Port	42	2416	4.5 -10	5.7	15 - 170	58	97	36	64	0	0
Plymouth	46	3342	4.0 - 10	6.4	9 - 216	53	113	38	62	0.2	0.2
West Mersea	14	679	4.6 - 10	7.7	4 - 157	54	64	96	0.2	0.1	3.8
Weymouth	40	2378	4.3 - 10	7.5	4 - 158	103	200	11	89	0.1	0.8

3.4 Results

3.4.1 Leave port model

To assess the effects of factors affecting the decision of a fishing vessel to leave port, we used a binary logistic regression. The dependent variable was whether or not the vessel left port to go fishing, and the predictors were: *Wave height*, entered as a continuous variable, and *port* and *time of high tide*, entered as fixed factors. *Fuel price* was not included in the final model for reasons given in the discussion below. To identify any regional differences between ports, we included interaction terms *port*wave height* and *port*time of high tide*. It is not possible to use other information from the MMO logbook as predictors of whether a vessel leaves port as we only have data when vessels do leave, with unknowns when they do not.

P-values < 0.0005 for all predictors entered into the leave port model indicate that there is sufficient statistical evidence to reject the null hypothesis in favour of the alternative (Table 3 [null hypothesis = neither wave height, tide time or which port fishers are based have an effect on the vessel decision to leave port and go fishing]). In calm conditions (wave height less than a meter) most vessels left port, except from West Mersea where the proportion leaving port was lower (Fig. 3-2A). As wave height increased, fewer vessels left port to go fishing. Fewer than 25% left port when wave height exceeded 2 meters, and very few when wave height was over 3 meters (Fig. 3-2A). The effect of time of high tide is shown in Fig. 3-2B. The decision to leave port was little affected by time of high water except at Weymouth, where there was a distinct preference for later tides, between 6 a.m. and 11 a.m. (Fig. 3-2B).

3.4.2 Fisher success model

Fisher success is defined in this study as the natural logarithm of the landings of sea bass (kg) per metre of vessel length. We used a general linear model to assess the effects on fishing success of environmental and socio-economic variables. *Wave height* , *vessel identity* and *year* were entered as fixed factors and *change in fish price* was entered as a continuous variable. *Fuel price*, *time of high tide* and *month* were not included in the final model for reasons given in the discussion below. *Port* was also not included in this model as a result of a backwards stepwise regression used for model selection. P-values < 0.0005 for all predictors entered into the final regression model indicate that there is sufficient statistical evidence to reject the null hypothesis in favour of the alternative (Table 3-4 [null hypothesis = neither wave height, vessel ID, year of fishing trip or price of fish, effect the success of a fishing trip]). Fishing success was lower when wave height was greater (Fig. 3-3A) though note the large confidence intervals around fishing trips when wave height is above two meters. Fishing success is also shown to decrease when fish price had increased relative to the previous trip (Fig. 3-3B). Finally, a large proportion of the total sum of squares was explained by factors associated with individual vessel (*Vessel ID*, Table 3-4).
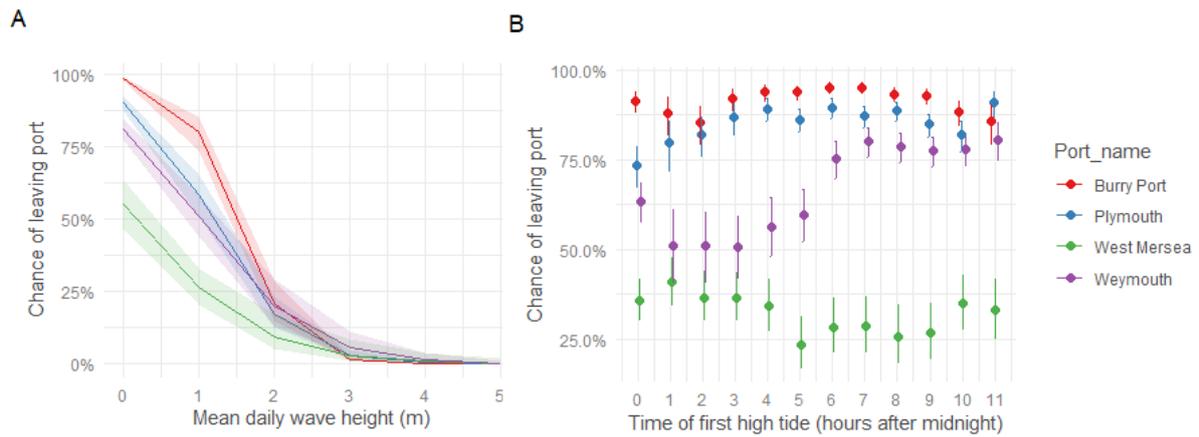
Figure 3-2. Predictors of whether a vessel will leave port from the binary logistic regression. A) mean significant wave height, B) time of first high tide. Bars and bands indicate confidence intervals. For both figures, colours are used to distinguish between ports where Red = Burry port, Blue = Plymouth, Green = West Mersea and Purple = Weymouth.
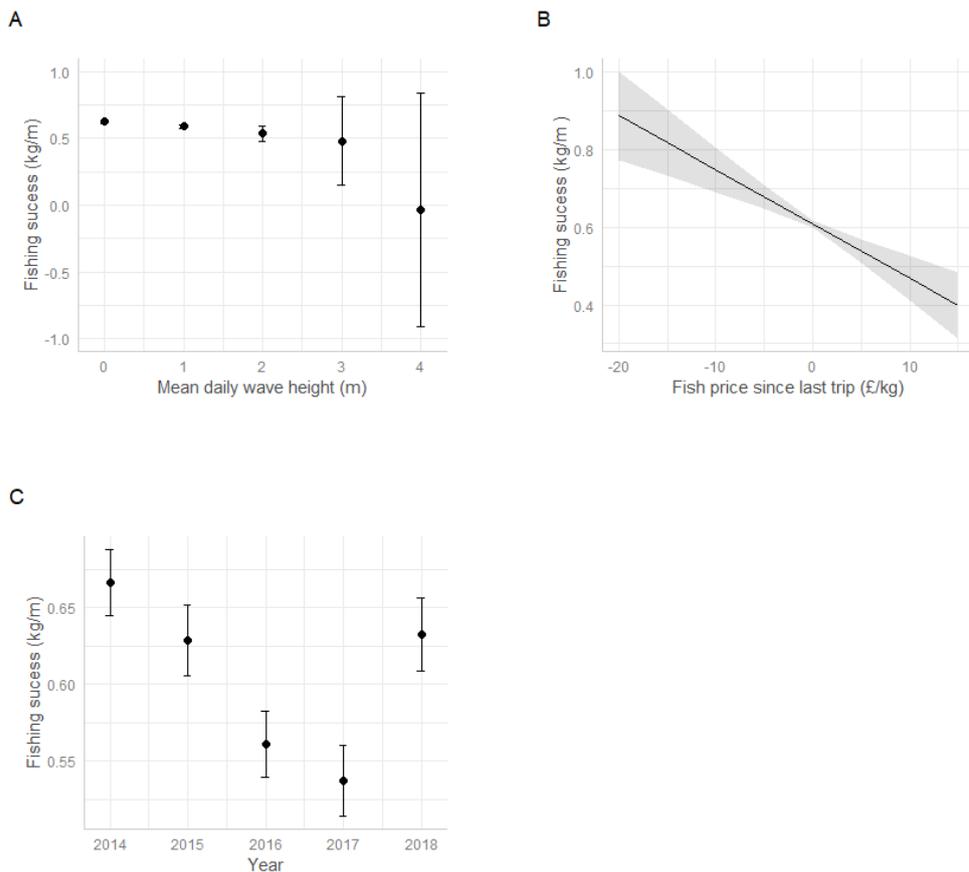
Figure 3-3. Effects of predictors on fishing success, from the regression analysis (Eqn. 2). A) Effect of mean daily wave height; B) Change in fish price from last trip; C) year the fishing trip took place. Bars and bands indicate confidence intervals.

Table 3-3. Analysis of deviance table for the *Leave Port* model. The dependent variable was whether or not a vessel left port to go fishing.

Predictor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL			13286	15329	
Time of high tide (HT)	11	183	13275	15146	***
Port name (PN)	3	1307	13272	13839	***
Wave height (WH)	1	1826	13271	12014	***
HTxPN	33	210	13238	11803	***
WHxPN	3	82	13235	11721	***

*** < 0.0005
VIF range 1.09 – 1.46
Cragg-Uhler pseudo-R2= 0.35 for 51 df.

Table 3-4. Analysis of Variance table for the *Fisher Success* model. The dependent variable was landed weight of sea bass per meter of vessel.

Predictor	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Wave height (As factor)	4	11.09	2.7736	13.990	***
Change in fish price	1	4.97	4.9685	25.061	***
Year	4	16.83	4.2073	21.221	***
Vessel ID	138	693.20	5.0232	25.336	***
Residuals	8667	1718.32	0.1983		

*** < 0.0005
VIF range 1.01 – 2.69
R^2 = 0.30

3.5 Discussion

In this study, we demonstrate a general fisher behaviour modelling approach which analyses separately the decision to leave a fishing port and the impact of decisions on fishing trip success. When applying our method, it is important to note that each fishery will be unique in the data available and the predictors that significantly affect fisher decisions. We demonstrate our approach with a case study investigating the decisions of fishers in under 10-meter sea bass fishing vessels at four UK representative ports, aiming to identify how decisions are affected by socio-economic and environmental factors.

In both analyses we discarded some predictors because their estimated effects are *a priori* implausible, so including them could distort the analyses. Results including those variables are shown in Figs. 3-4 and 3-5. For both models we discarded *fuel price*, because increased fuel price was found to correlate with more trips and with more successful trips, which seem *a priori* implausible. Results including *fuel price* are shown in Fig. 3-4 and 3-5. For the Fisher Success model, we discarded *time of high tide* and *Month* from our analysis as we lack a sensible explanation of their effects. Tide time did not show consistent patterns hour-to-hour, unlike the Leave port model (compare Fig. 3-5A and Fig. 3-2B). Including the effect of month on fishing success suggests that December is the most profitable month to fish (Fig. 3-5C). This is unlikely to be a reliable result to include in the wider analysis as there are fewer fishing trips that occur in December compared to during peak fishing, from April to October (Pickett and Pawson, 1994). Hence, it is likely that the high profitability of December fishing is an artifact of incidental sea bass landings.

Our principal findings are that almost all vessels left port when wave height was below a meter, but less than a quarter when wave height exceeded 2 meters, and those that did then leave caught less (though note the large confidence intervals around the success of trips taken in over two meters wave height, likely due to a smaller sample of trips taken in these conditions [Fig. 3-3A]). Our finding that in rougher weather fewer vessels leave the port to go fishing (Fig. 3-2A) is in line with other studies of fisher behaviour (Shepperson et al., 2016; Sainsbury et al., 2018). Due to their small physical size the small vessels that make up the under 10-meter fleet have potential to be particularly vulnerable to rough weather. The port with the smallest mean vessel size is Bury Port (Table 3-2) and this is the port seemingly most impacted by wave height (Table 3-5), though note its distance from its Waverider buoy (Fig. 3-1).

Decisions to leave port were also affected by the time of high water. We describe the variation between ports, and present quantitative estimates of all effects. To our knowledge, there is only limited incorporation of environmental predictors other than weather variables in studies of fisher behaviours. Daily tidal state has not been included in any fisher behaviour study that we are aware of, though studies by Sharples et al. (2013) and Poisson et al. (2010) show results of fishers reacting differently throughout the monthly tide cycles depending on their target species. In our study, the vessels we have defined as targeting/impacting sea bass (see section 3.3.2 obtaining data) appear to have fishing decisions to leave port affected by the time of high water. However, the effects of daily tide cycle did differ between ports (Fig. 3-2B). Depth of water may limit the ability to leave or return to a tidal mooring, so leaving on an early tide may allow a fisher to stay out at sea and fish through two tide cycles rather than be limited to one. Early tides may also allow fishers more sociable hours and/or to fish in daylight. The preference for certain tide times could also be due to a perceived increased chance of catching sea bass and/or due to logistical preferences. Fishers may be attracted to certain tide times as changes in current velocity could carry the scent of bait further and also have a direct impact on feeding behaviour of fish (Stoner, 2004). Empirical studies of these effects are rare (Stoner, 2004), but grey literature in fishing magazines suggests sea bass have greater feeding activity during times of tidal movement, making them potentially profitable times to go fishing. A final consideration is the different effect tide can have on different fishing gears (Sharples et al., 2013). West Mersea was shown to have a different response to tidal effects than the other ports (Fig. 3-2B), contributing to this could be the prevalence there of using gill nets, which is different to the majority of vessels in other ports that used hook and line (Table 3-2).

The success of fishing trips, as measured by landed weight of sea bass per metre of vessel length, was generally greater in calmer seas (Fig. 3-3A). Fewer vessels go fishing in rougher weather (Fig. 3-2A) and the success of the vessels that do fish is reduced (Fig. 3-3A), reasons could include: not being able to fish the best/preferred fishing marks (Pet-Soede et al., 2001), being unable to deploy as much fishing gear (e.g., number of hooks), or because time spent at sea is reduced. Given the major effect of wave height on decision to leave port and fisher success, any change in storminess due to climate change (Sainsbury et al., 2018) could have implications for sea bass fishing pressure. Increased future storminess would result in more days when fishing is not possible and could result in significant changes to the spatial and temporal distribution of fishing pressure. In addition to changes in fisher behaviour, climate change has the potential to effect the distributions and reproductive biology of the sea bass that they target (Cheung et al., 2012; Heath et al., 2012). This combination of climate change effects on both sea bass and the fishers that target them could have compounding impact on the dynamics and distribution of future sea bass fishing pressure.

The success of fishing trips was also greater when the change in fish price, compared with the previous trip, was lower (Fig. 3-3B). Amongst other factors affecting success of catch, bad weather

may help explain this because prices are inflated when fewer fish are brought to market due to adverse fishing conditions such as bad weather (Graddy, 2006). Although the increase in storminess may impact when and where sea bass are landed, the economic outcome may have a limited net change. Fishing success varied between years, being greatest in 2014 (Fig. 3-3C). Fishing success varied substantially between vessels (Table 3-4), this is likely due to a variety of reasons including the effects of seasonality on individual trips but also variation in skipper experience and risk perception (Salas and Gaertner, 2004), sometimes termed the skipper effect (Thorlindsson, 1988). Although beyond the scope of this study, further insight into the skipper effect is often gained from semi-structured interviews and other survey techniques (Hill *et al.*, 2010; Zukowski *et al.*, 2011; Shepperson *et al.*, 2016).

We cover the top port per region for sea bass landings in the UK 2014-2018, and our logbook data covers at least 75% of the total trips per port (Tables 3-1 and 3-2). However, since our analysis shows ports react differently to environmental and socio-economic predictors, it is likely that other UK ports not included in this study may also differ. Furthermore, we know there is a 25 kg exemption from sales notes for landed sea bass, meaning that some landings of sea bass are unreported (Pawson *et al.*, 2007) and some discard mortality that cannot be captured, resulting in potential underestimation of fishing pressure and mortality. Nevertheless, we believe our study is a good starting point to indicate some of the mechanisms of fishing pressure responses between ports.

These findings have implications for the management of sea bass. Management is through technical measures that include catch limits (monthly, annual), closed seasons to protect spawning aggregations, and minimum size (GOV.UK, 2020). Increases of extreme weather events especially during the key fishing seasons may impact on the ability of under 10-meter inshore vessels to land catch limits within the allowed time periods. As these are time bound and there is no carryover, this will impact the potential revenue generated and therewith the profit. It may also be the case that as the stock expands northwards, due to warming sea temperatures, any seasonal closures may not protect spawning aggregations in all areas.

To further the use of our method for our case study and other fisheries, it would be useful to consider the spatial aspect of fisher behaviour. Spatial data is not necessary for estimating total pressure on the stock, but it is important when investigating the spatial concentration of fishing effort and the pressure of fishing near protected areas (McCluskey and Lewison, 2008). A promising line of future work would be to incorporate our fisher behaviour findings into an individual based model (IBM). IBMs use a bottom-up approach and simulate a population of discreet individuals where a combination of individual state and environmental variables change individual behaviour (DeAngelis and Grimm, 2014). IBMs have been used in fisheries research to study fish populations (Kühn *et al.*, 2008; Politikos, Huret and Petitgas, 2013; Boyd *et al.*, 2018; Boyd, Sibly, *et al.*, 2020; Walker *et al.*, 2020), but have also been used to study fisher behaviour (Jules Dreyfus-León, 1999; Millischer and Gascuel, 2006; Bastardie *et al.*, 2010; Bailey *et al.*, 2019; Lindkvist *et al.*, 2020). We suggest that incorporation of the fishing behaviour relationships we have found into a suitable IBM could be a useful management tool.

3.6 Conclusions

The primary findings from this study relate to the effect of wave height on the under 10-meter inshore vessels that target or impact sea bass around the UK. We found that fewer vessels left port during rough weather to go fishing and vessels that did were less successful. Fishers were also more

successful when fish price had decreased relative to the previous trip, due to supply/demand. The decision to leave port was only substantially affected by time of high tide at one of the four ports investigated. Fuel price was unimportant, but a large proportion of the variation in success was explained by variation between individual vessels, presumably due to variation in skipper ability or technical restrictions due to vessel characteristics. The findings from this study have implications for the management of sea bass fishing pressure as any increases of extreme weather events during the key fishing seasons may affect the ability of under 10-meter inshore vessels to land catch limits within the allowed time periods. As these are time bound and there is no carryover, this will impact the potential revenue generated and profit. We hope the methodology employed here will prove useful in future studies seeking to identify and quantify the effects of factors affecting fisher decisions and success.

3.7 Acknowledgements

3.8 Supplementary

Table 3-5. Coefficients for leaveport model Eqn. 1

Coefficients:	Estimates	Std. Error	Pr(>|z|)
(Intercept)	4.12009	0.21632	***
Time_F1	-0.35324	0.3136	
Time_F2	-0.59732	0.28589	*
Time_F3	0.10743	0.28563	
Time_F4	0.36582	0.2728	
Time_F5	0.35582	0.2538	
Time_F6	0.63745	0.25598	*
Time_F7	0.60632	0.25243	*
Time_F8	0.25861	0.24568	
Time_F9	0.2166	0.24688	
Time_F10	-0.338	0.24612	
Time_F11	-0.55768	0.2883	.
Port_namePlymouth	-1.867	0.2675	***
Port_nameWest Mersea	-3.91104	0.27867	***
Port_nameWeymouth	-2.6563	0.24813	***
mean_hs	-2.72693	0.10519	***
Time_F1:Port_namePlymouth	0.70653	0.41023	.
Time_F2:Port_namePlymouth	1.10812	0.37294	**
Time_F3:Port_namePlymouth	0.76895	0.3771	*
Time_F4:Port_namePlymouth	0.7316	0.35494	*
Time_F5:Port_namePlymouth	0.45929	0.32607	
Time_F6:Port_namePlymouth	0.48955	0.33135	
Time_F7:Port_namePlymouth	0.29396	0.32433	
Time_F8:Port_namePlymouth	0.77894	0.31797	*
Time_F9:Port_namePlymouth	0.48716	0.31605	
Time_F10:Port_namePlymouth	0.83087	0.32234	**
Time_F11:Port_namePlymouth	1.85447	0.39789	***
Time_F1:Port_nameWest Mersea	0.575	0.36751	
Time_F2:Port_nameWest Mersea	0.64275	0.347	.
Time_F3:Port_nameWest Mersea	-0.06729	0.34582	
Time_F4:Port_nameWest Mersea	-0.43089	0.34305	
Time_F5:Port_nameWest Mersea	-0.95588	0.351	**
Time_F6:Port_nameWest Mersea	-0.98164	0.3457	**
Time_F7:Port_nameWest Mersea	-0.93353	0.34348	**
Time_F8:Port_nameWest Mersea	-0.72119	0.34796	*

Time_F9:Port_nameWest Mersea	-0.63316	0.34232	.
Time_F10:Port_nameWest Mersea	0.31037	0.32386	
Time_F11:Port_nameWest Mersea	0.44027	0.36608	
Time_F1:Port_nameWeymouth	-0.13857	0.39052	
Time_F2:Port_nameWeymouth	0.09285	0.36526	
Time_F3:Port_nameWeymouth	-0.61662	0.35394	.
Time_F4:Port_nameWeymouth	-0.64804	0.33936	.
Time_F5:Port_nameWeymouth	-0.50917	0.31648	
Time_F6:Port_nameWeymouth	-0.0722	0.31454	
Time_F7:Port_nameWeymouth	0.23878	0.30617	
Time_F8:Port_nameWeymouth	0.50412	0.29658	.
Time_F9:Port_nameWeymouth	0.47708	0.29516	
Time_F10:Port_nameWeymouth	1.04772	0.29826	***
Time_F11:Port_nameWeymouth	1.42817	0.3559	***
Port_namePlymouth:mean_hs	0.81641	0.13656	***
Port_nameWest Mersea:mean_hs	1.4908	0.24574	***
Port_nameWeymouth:mean_hs	1.30149	0.17373	***
Observations	*13278*		
*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*			

Table 3-6. Coefficients for Success model Eqn. 2

Coefficients:	Estimates	Std. Error	Pr(>|z|)
(Intercept)	0.882048	0.111828	***
mean_hsr1	-0.035235	0.010603	***
mean_hsr2	-0.088608	0.029968	**
mean_hsr3	-0.143398	0.169473	
mean_hsr4	-0.663104	0.447051	
price_change	-0.013953	0.002884	***
vessel_id13	-0.234831	0.146437	
vessel_id16	-0.271115	0.115431	*
vessel_id21	-0.5056	0.12883	***
vessel_id43	-0.117583	0.157501	
vessel_id47	-0.417999	0.121167	***
vessel_id48	0.030674	0.151436	
vessel_id55	-0.029619	0.151365	
vessel_id56	-0.732218	0.145266	***
vessel_id59	-0.44641	0.148045	**
vessel_id63	-0.694191	0.174663	***
vessel_id68	-0.133228	0.192855	
vessel_id69	-0.838183	0.129204	***
vessel_id81	-0.954925	0.143791	***
vessel_id89	-0.443469	0.135121	**
vessel_id92	-0.694151	0.151387	***
vessel_id93	-0.829517	0.139788	***
vessel_id101	0.108991	0.135256	
vessel_id107	0.209084	0.120204	.
vessel_id119	-0.008595	0.117105	
vessel_id120	-0.255232	0.166542	
vessel_id121	0.142423	0.11793	
vessel_id132	-0.202831	0.138104	
vessel_id135	-0.633855	0.146704	***
vessel_id136	-0.199661	0.137845	
vessel_id160	-1.260379	0.157964	***
vessel_id162	-0.054863	0.128494	
vessel_id164	-0.114629	0.121475	
vessel_id171	0.137812	0.116195	
vessel_id178	-0.150051	0.125312	
vessel_id179	-0.01622	0.119351	
vessel_id183	-0.148641	0.117808	
vessel_id187	-0.341761	0.11535	**
vessel_id194	-0.802073	0.132871	***
vessel_id199	-0.509809	0.128694	***
vessel_id211	-0.167905	0.127416	
vessel_id212	-0.425032	0.192823	*
vessel_id215	-0.7002	0.135829	***
vessel_id219	-0.625107	0.185926	***
vessel_id222	-0.695224	0.185925	***
vessel_id231	-0.314065	0.174796	.
vessel_id237	-0.234348	0.116574	*
vessel_id240	-0.239747	0.118739	*
vessel_id243	-0.532558	0.146715	***
vessel_id260	-0.252448	0.136841	.
vessel_id265	0.131024	0.125388	
vessel_id278	0.051319	0.148712	
vessel_id282	-0.543862	0.157448	***
vessel_id286	-0.674815	0.11839	***
vessel_id290	-0.073338	0.117577	
vessel_id291	0.23684	0.17483	
vessel_id292	-0.123679	0.139664	
vessel_id298	-0.113263	0.193056	
vessel_id302	-0.275293	0.170517	
vessel_id306	0.349309	0.160319	*
vessel_id310	-0.567098	0.126361	***
vessel_id312	-0.019767	0.13892	
vessel_id321	-0.983429	0.163048	***
vessel_id325	-0.094321	0.13125	

Coefficients:	Estimates	Std. Error	Pr(>|z|)
vessel_id328	-0.354967	0.121113	**
vessel_id333	0.301551	0.12172	*
vessel_id337	0.75773	0.179884	***
vessel_id339	-0.259192	0.124293	*
vessel_id341	-0.291618	0.11924	*
vessel_id342	-0.22227	0.147914	
vessel_id345	-0.10561	0.130407	
vessel_id346	-0.559051	0.146604	***
vessel_id347	-0.263862	0.170088	
vessel_id348	-0.148419	0.134538	
vessel_id353	-0.164866	0.122626	
vessel_id354	-0.136339	0.118778	
vessel_id358	-0.49057	0.12889	***
vessel_id360	-0.002579	0.142594	
vessel_id361	0.038115	0.151151	
vessel_id364	0.371916	0.166827	*
vessel_id369	-0.686104	0.119703	***
vessel_id371	-0.288773	0.180844	
vessel_id372	0.093003	0.18618	
vessel_id377	-0.151009	0.117908	
vessel_id378	-0.444397	0.142968	**
vessel_id379	-0.454061	0.126557	***
vessel_id387	-0.575262	0.117643	***
vessel_id388	0.12595	0.125412	
vessel_id389	-0.182025	0.118785	
vessel_id390	0.209047	0.11406	.
vessel_id391	-0.393117	0.128177	**
vessel_id392	-0.390957	0.133125	**
vessel_id393	-0.854372	0.162977	***
vessel_id394	-0.193814	0.117747	.
vessel_id400	-0.998976	0.137153	***
vessel_id408	-0.016717	0.140533	
vessel_id410	0.054023	0.119785	
vessel_id411	-0.282638	0.115656	*
vessel_id412	-0.615609	0.116564	***
vessel_id414	-0.42587	0.11921	***
vessel_id415	-0.354622	0.132199	**
vessel_id416	-0.303555	0.142665	*
vessel_id418	-0.099567	0.119396	
vessel_id419	-0.619474	0.167004	***
vessel_id420	-0.400642	0.163519	*
vessel_id422	0.121783	0.119123	
vessel_id423	0.209912	0.115359	.
vessel_id427	-0.260952	0.120921	*
vessel_id428	0.003511	0.131043	
vessel_id430	-0.774729	0.193081	***
vessel_id431	0.077003	0.151233	
vessel_id434	-0.567203	0.133328	***
vessel_id435	-0.325312	0.135532	*
vessel_id438	-0.393286	0.174895	*
vessel_id443	-0.227639	0.127678	.
vessel_id445	-0.271582	0.151641	.
vessel_id448	-0.386843	0.119577	**
vessel_id449	-0.144921	0.114013	
vessel_id451	0.179578	0.115844	
vessel_id454	-0.172454	0.160786	
vessel_id457	-0.627976	0.123113	***
vessel_id458	-0.716978	0.146504	***
vessel_id460	-0.361209	0.135082	**
vessel_id461	-0.484931	0.185651	**
vessel_id464	0.197084	0.160108	
vessel_id466	0.016801	0.119696	
vessel_id467	-0.395992	0.130443	**
vessel_id469	-0.163483	0.115616	
vessel_id470	-0.368841	0.148173	*
vessel_id473	-0.773556	0.122655	***

Coefficients:	Estimates	Std. Error	Pr(>|z|)
vessel_id478	0.100286	0.116365	
vessel_id479	-0.150223	0.130906	
vessel_id481	-0.28821	0.170467	.
vessel_id483	-0.86852	0.166861	***
vessel_id487	0.20876	0.179988	
vessel_id488	-0.30349	0.12186	*
vessel_id493	-0.275667	0.123874	*
vessel_id494	-0.255734	0.129301	*
vessel_id495	-0.220427	0.127103	.
vessel_id497	-0.17912	0.126244	
vessel_id498	0.140055	0.193457	
vessel_id499	-0.022843	0.124846	
vessel_id500	-0.155012	0.139429	
vessel_id504	-0.258477	0.151908	.
year2015	-0.037601	0.015736	*
year2016	-0.105457	0.01594	***
year2017	-0.129264	0.016813	***
year2018	-0.033632	0.017329	.
Observations	8815		
*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*			
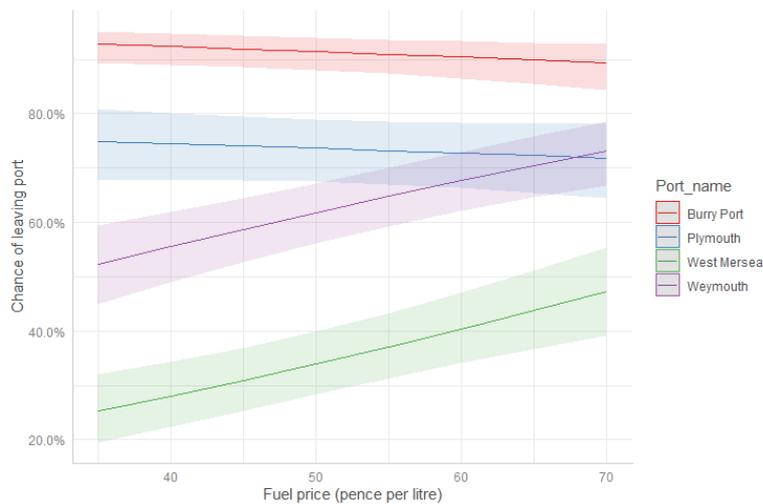
Figure 3-4. Prediction of whether a vessel will leave port with changes to fuel price (pence per litre of red diesel) from the binary logistic regression (Eqn. 1 + fuel price as a predictor).
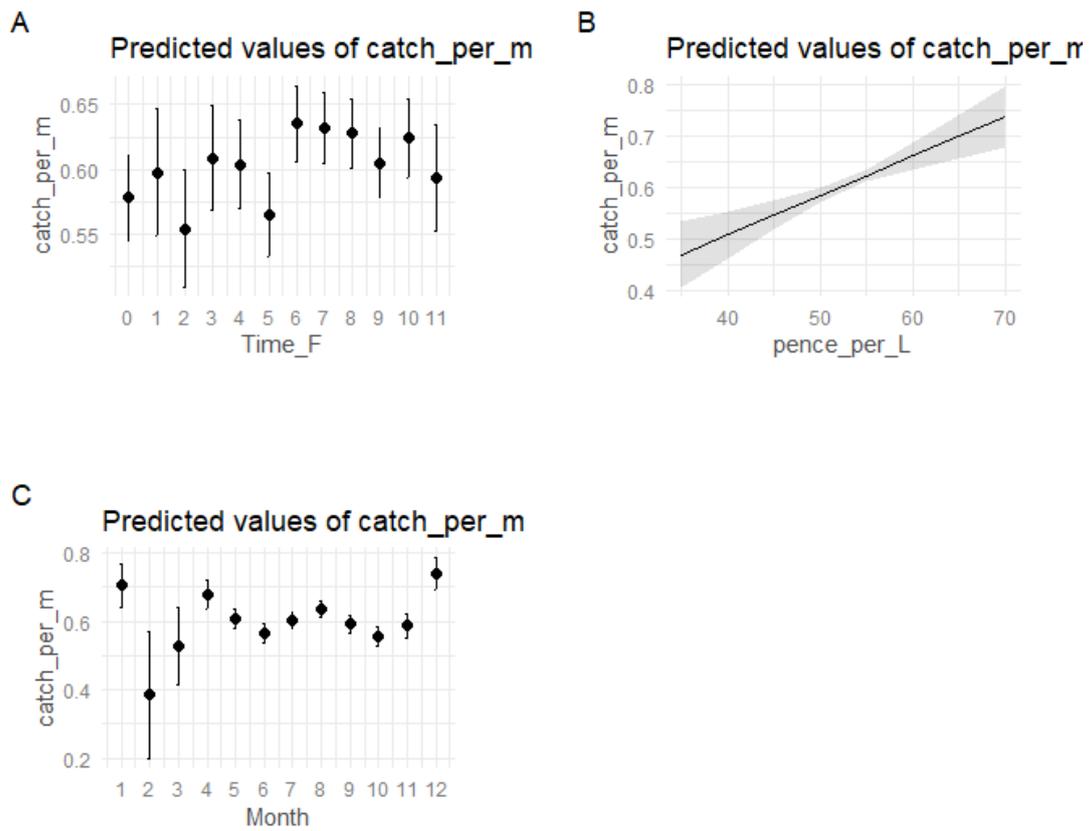
Figure 3-5. Predictors of fishing success, measured as landed weight per metre of vessel length, from the regression analysis (Eqn. 2 + time of high tide + fuel price and Month of fishing trip); A) time of high tide, B) fuel price, C) Month the fishing trip took place.

4 Incorporating environmental variability in a spatially-explicit individual-based model of European sea bass.

4.1 Abstract

The northern stock of European sea bass (*Dicentrarchus labrax*) is a large, high value, slow growing and late maturing fish that is an important target species for both commercial and recreational fisheries. Around the UK, scientific assessments have shown a rapid eight-year decline in spawning stock biomass since 2010 attributed to poor recruitment driven by environmental factors, and high fishing mortality. Management of the stock is informed by scientific assessments in which a population model is fitted to the available data and used to forecast the possible consequences of various catch options. However, the model currently used cannot represent the spatial distribution of the stock or any effects of environmental variability. Individual based models (IBMs) use agents to represent individual organisms that can interact with each other and their environment. The mechanistic nature of IBMs is often advantageous as a management tool for complex systems including fisheries. Here we add to an existing IBM to produce a spatio-temporally explicit IBM of the northern stock of sea bass in which individual fish respond to local food supply and sea surface temperature. All life stages (i.e., pelagic stages, juvenile and mature fish) are modelled and individual fish have their own realistic energy budgets driven by observed dynamic maps of phytoplankton density and sea surface temperature. The model is calibrated using Approximate Bayesian Computation (ABC). After calibration by ABC the model gives good fits to key population parameters including spawning stock biomass. The model provides a mechanistic link between observed local food supplies and sea surface temperatures and overall population dynamics. Alongside calibration plots, we show some spatial catch plots to demonstrate how the model uses the energy budget to predict spatial and temporal change in sea bass catch distribution in response to environmental variability. Our results show that the IBM is a promising approach that could be used to support stock assessment with the scope for testing a range of spatially and temporally explicit management scenarios in addition to testing stock responses to novel environmental changes.

4.2 Introduction

The European sea bass (*Dicentrarchus labrax*) has been an important target species for commercial and recreational fishers around the UK for more than 50 years, however after decades of exploitation and minimal regulation the stock began to rapidly decline in 2010 (Pickett and Pawson, 1994; ICES, 2021). The decline continued for eight years and was attributed to a combination of poor recruitment and fishing mortality which led to the implementation of emergency management measures in 2015 with continuing stringent harvest restrictions to present day (ICES, 2019, 2021). Sea bass are a slow growing, long lived, generalist predator with a complex life cycle that includes feeding and spawning migrations (Pickett and Pawson, 1994). A further complex component of the sea bass life cycle is the recruitment process (i.e., the surviving from egg through larval stages to a harvestable fish) which is particularly precarious and influenced by many drivers, the result of which can be observed as recruitment rates with high levels of interannual variation (Pickett and Pawson, 1994; ICES, 2021). These life history components make the building of assessment models for this stock particularly challenging.

The northern sea bass stock is assessed by the International Council for the Exploration of the Sea (ICES) using Stock Synthesis 3 (SS3); an analytical age - and length-based assessment model optimized for tactical management (ICES, 2019). SS3 includes: 1) a population dynamics model,

which represents growth, mortality, and recruitment; 2) an observation model which relates the population dynamics to available data; and 3) a statistical model which estimates parameters to maximise the goodness of fit between population model and data. While SS3 is well-suited for use in tactical management, there are important strategic questions which it cannot, and is not designed, to answer. First, SS3 can include only a crude representation of the spatial distribution of the stock using its "multi-area" configuration (Methot and Wetzel, 2013). For this reason it is limited in its ability to represent the effects of spatial management scenarios (e.g., sea bass fishery spatial closures in key of spawning areas [GOV.UK, 2020]). Second, SS3 does not represent the effects of environmental variability on the stock; for this reason it cannot make predictions about how the stock will develop against uncertain climate backdrops, or how climate uncertainty might interact with harvesting scenarios e.g., Boyd, Thorpe, et al., 2020.

Walker *et al.* (2020) developed an individual-based framework for European sea bass. IBMs such as Walker *et al.* (2020) are widely used to simulate the spatial distribution of fish populations (Watkins and Rose, 2017; Heinänen *et al.*, 2018; Boyd, Walker, *et al.*, 2020), as well as population size and structure (Politikos, Huret and Petitgas, 2015; Boyd, Walker, *et al.*, 2020; Bueno-Pardo *et al.*, 2020). In Walker *et al.* (2020) the stock's spatial distribution results from algorithms that govern the movements of the individuals, but the population dynamics component is that of SS3. The logical next step is to allow individuals to respond to observed local variation in key environmental drivers. To do so one must first identify important environmental drivers, and then incorporate sub-models that describe the ways in which the stock responds to these drivers.

Prey availability and temperature are two key environmental drivers that affect rates of growth and reproduction in sea bass and ultimately population dynamics (Pickett and Pawson, 1994). The effects of prey availability and temperature on fish are typically modelled using energy budgets (sometimes called bioenergetics). Our energy budget approach follows an established methodology (Sibly *et al.*, 2013) that has been used for a range of species and applications (Sibly *et al.*, 2013; Grimm *et al.*, 2014; van der Vaart *et al.*, 2015; Boult *et al.*, 2019; Boyd, Walker, *et al.*, 2020; Mintram *et al.*, 2020; Watson *et al.*, 2020). The energy budget models describe the acquisition of energy from food in the environment and its allocation to maintenance (metabolism), growth, reproduction, and energy storage. Rates of acquisition and expenditure depend on temperature and body size, and these can be modelled using established theoretical relationships. Recently, bioenergetics models have been implemented in IBMs which enables extrapolation of the individual-level effects of prey availability and temperature (e.g., on body size and reproductive output) to the population level. Here we use phytoplankton density, assessed through remote sensing, as an index of food supply, and we examine the implications for the sea bass population of individual fish having their own energy budgets. The energy budgets link population dynamics to environmental drivers and ultimately outputs the population metrics that are used in fisheries management.

In this study, we extend the model of Walker *et al.* (2020) incorporating a bioenergetics module to account for spatio-temporal variation in prey availability and temperature. Information on prey availability and temperature are derived from two satellite products: chlorophyll concentration, which we use as a proxy for prey availability (with additional assumptions about trophic delay); and sea surface temperature (SST). We estimate five parameters of the bioenergetics model by fitting the IBM to individual- and population-level outputs from the latest stock assessment. We show that the calibrated model matches the stock assessment outputs well, and we show some spatial outputs to demonstrate how the model links environmental drivers to spatial and temporal distribution of catch. Finally, we discuss the potential utility of our model for strategic management of the European sea bass stock.

4.3 Methods

4.3.1 Overview

Here we provide a summary description of the IBM. A full description following the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent based models (Grimm *et al.*, 2006, 2010, 2020) is provided in a TRACE (TRAnsparent and Comprehensive model Evaludation; Augusiak, Van den Brink, & Grimm, 2014; DeAngelis & Grimm, 2014; Schmolke, Thorbek, DeAngelis, & Grimm, 2010) document forming the supplementary material. The IBM is implemented in NETLOGO version 5.3.1 (Wilensky, 1999). All the codes and dataset used for this research, can be downloaded from https://github.com/eth-cscs/abcpy-models/tree/master/EcologicalScience/Bass. The model develops the approach of Walker *et al.* (2020) to include energy budgets for individual fish. The model environment is composed of a grid landscape of 36 x 38 patches (grid cells), representing the area from 9°E to 9°W and 48°N to 57.5°N (Fig. 4-1). The model uses dynamic patch variables of sea surface temperature (SST [shown in blue Fig. 4-1A]; a key driver of sea bass dynamics; Pickett & Pawson, 1994; TRACE Section 5.8.2 and 5.10.2), and now includes an additional patch variable of phytoplankton density (PHY[shown in orange Fig. 4-1B];, derived from chlorophyll concentration using an empirical conversion factor; see Discussion and TRACE Sections 5.8.2 , 5.10.3 for discussion of the role of PHY as a base of the marine food web and the basis for energy in our energy budget updates). The patches of the model environment are categorised depending on location within the environment (Fig. 4-1). Coastal patches are those within an ICES rectangle that intersects land and offshore patches are all remaining sea patches. Between February–May any offshore patches south of 54°N with an SST value between 9–15°C are assigned as spawning patches (Thompson and Harrop, 1987; Kelley, 1988; Beraud *et al.*, 2018). Nursery patches are those south of 54°N intersecting land; (Kelley, 1988; Beraud *et al.*, 2018). Patches are also assigned an ICES division (4.b, 4.c, 7.a, 7.d, 7.e or 7.fg see https://www.ices.dk/data/maps/Pages/ICES-statistical-rectangles.aspx) and region (North Sea, English Channel, Celtic Sea or Irish Sea). ICES divisions and regions are mutually exclusive while patch types are not, as all nursery patches are coastal, and all spawning patches are offshore (Fig. 4-1).

For simplicity, we assume the population is closed to migration outside the model domain. To keep model run times practical the sea bass population is modelled with super-individuals (hereafter termed individuals) each of which represents many fish with identical state variables (Scheffer *et al.*, 1995). Individuals are characterised by; the number of fish represented, age, life stage (see Figs. 4-1 and 4-2 and sub model *Transform*), length, weight (including structural mass, gonad mass and total mass), ingested energy, energy reserves, metabolic rate, location, swimming speed and daily direction changes, spawning trigger and counter, mortality rates (natural, commercial inshore/offshore fishing mortality and recreational-fishing mortality) and the division they have an affinity to feed in. Sea bass variables and processes are described further in Section *4.3.3* and full details can be found in the TRACE. After an initial spin up (1985-2004), the model runs in daily time steps from 1st of January 2004 to the 31st of December 2014, just prior to the implementation of emergency management measures in 2015 (ICES, 2021). In each time step, individuals follow six main processes, all constructed from several sub models: ingestion, metabolic rate, growth, reproduction, movement, and mortality. Fig. 4-2 provides a conceptual overview of the processes and sub models represented in the IBM. In the following sections we give an overview of these sub models, highlighting the new energy budget updates and directing the reader towards relevant supplementary materials (TRACE sections) for further details.

4.3.2 Initialization and spin up.

The model is initialised on 1st of January 1985 and runs with daily time steps for a 19-year spin-up period. Thereafter emergent results are collected from 1st of January 2004 until 31st of December 2014. During the spin up, Numbers-at-age data from the ICES stock assessment 2020 are used to base the initialized population and then each year new agents are introduced from estimates of numbers at age 0 also from the stock assessment. The remote sensing data for SST and PHY for 2004 is used on repeat for each year in the spin up as it was unavailable before this date (for full details of spin up see TRACE section 5.5).
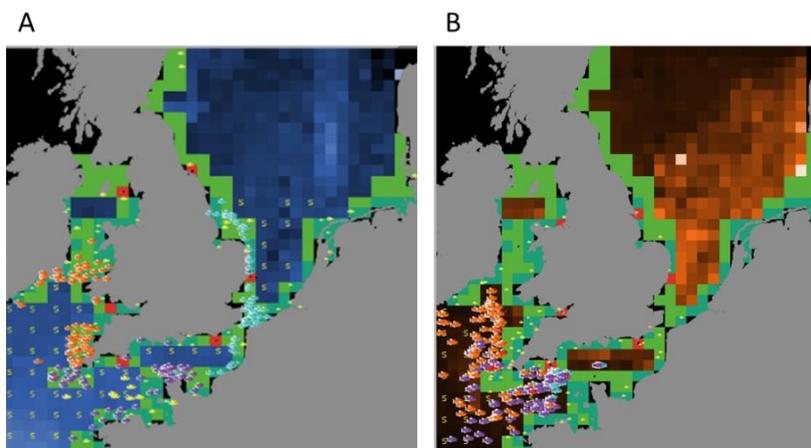
Figure 4-1. The model interface; Both sea surface temperature (SST) and phytoplankton concentration (PHY) can not be shown simultaneously in the model interface so here; A) shows offshore patches as blue with dark to light representing increasing SST (min and max potential values 0- 30°C), and B) shows offshore patches as orange with dark to light representing increasing PHY (min and max potential values 0-75 g/m^2). For both A) and B) coastal patches represented in green, nursery patches (also coastal) are turquoise. Targets that eggs and larval stages drift towards (depending on ICES division affinity) are represented by red patches. Agent colour represents life stage (white = eggs, black = ys-larvae and larvae, yellow = juvenile sea bass [not all life stages are shown here]). For mature sea bass colour shows the affinity to feeding ground. Spawning patches (which vary depending on time of year and environmental conditions) are shown with a yellow "S". These remote sensing data are updated every 8 days and agents perform all sub models each day (see section below 4.3.3).

4.3.3 Process overview and scheduling

An overview of the sub models is presented here but for complete detail we refer the reader to the relevant TRACE sections. The major addition to the model of Walker *et al.* (2020) are the energy budget processes and the sub models; *ingestion and assimilation*, *maintenance and reserves, growth,* and *reproduction.* The equations (1-5) that make up the energy budget approach follow an established methodology (Sibly *et al.*, 2013) that has subsequently been used for a range of species and applications (Sibly *et al.*, 2013; Grimm *et al.*, 2014; van der Vaart *et al.*, 2015; Boult *et al.*, 2019; Boyd, Walker, *et al.*, 2020; Mintram *et al.*, 2020; Watson *et al.*, 2020). The model proceeds through all sub models in daily time steps that reset every 365 days. The following sub models are executed in the order they are presented. Within each sub model, super-individuals and patches are processed in a random order as there are no interactions among agents (an overview can be seen in

Fig. 4-2). Agents age one day each time step and the cohort age is increased by one every 365 time steps.

Update-patches: New SST and PHY data is assigned to patches, and offshore patches update their spawning patch status (though note that SST and PHY data only changes every 8 days).

Natural mortality: The number of fish in each individual is discounted by its natural mortality rate. Any super-individuals reaching the age of 30 are removed from the simulation.

Ingestion and assimilation: All life stages calculate ingestion and assimilation except for eggs and egg- sac larvae as these early life stages rely on their own energy source rather than feeding (Pickett and Pawson, 1994). For the older life stages (larvae, juvenile and mature sea bass) the rates of ingestion and assimilation are dictated by size of the individual, energy available in the environment, temperature, and density dependence (i.e., intraspecific competition for food). The assimilated energy (E) is then the energy available for the remainder of the energy budget processes (i.e., growth, maintenance, and reproduction) and is calculated as:

$$E = \left(\left(\left(\left(Cmax * \left(\frac{PHY}{H+PHY}\right)\right) * M_t^{2/3}\right) * \left(i * \left(\frac{1}{M_{nm}^{\frac{2}{3}}}\right) * Ep\right)\right) * Ae\right) * Ah \tag{1}$$

where *Cmax* is the maximum consumption of food in relation to body size, *PHY* is the energy value of the patch, *H* is the half saturation constant, M_t is total mass, *i* is importance of conspecific density, M_{nm} is the sum of non-egg biomass in the same patch, *Ep* is the energy in phytoplankton and *Ae* is the product of assimilation efficiency (i.e., the proportion of energy that is absorbed from prey) and trophic delay (i.e., how long/how much energy from a phytoplankton bloom makes its way through the trophic levels to sea bass prey) and *Ah* is an Arrhenius function (for details see TRACE sections 5.7, 5.8.2, 5.10.3, and see Table. 4-1 for parameter values).

Maintenance and reserves: All life stages calculate metabolic rate and its energetic cost, except for eggs and egg- sac larvae. Metabolic rate is affected by body mass and temperature, and here we calculate field metabolic rate as twice the standard metabolic rate (Peters, 1986) and is calculated as *Mr* below:

$$Mr = \left(Ao * \left(M_t^{\frac{3}{4}} * 2\right)\right) * Ah \tag{2}$$

where *Ao* is a metabolic rate normalisation, M_t is total mass and *Ah* is an Arrhenius function. Once the energetic cost of maintenance/metabolic rate is established it is either paid for directly from assimilated energy or if this is insufficient (e.g., reduced feeding available in the winter) then energy reserves are added to assimilated energy and metabolic costs are taken from this (for details see TRACE sections 5.7 and see Table. 4-1 for parameter values).

Growth: All life stages except eggs calculate their total mass (mass of an individual including, if any, fat reserves and gonad mass):

$$M_t = \left(a * L^b\right) + \left(\left(\frac{Er}{El}\right) + Gm\right) \tag{3}$$

where *a* and *b* are Length-mass coefficient values (for details see TRACE Section 5.8.3), *Er* is how much energy is in reserves, *El* is the energy content of lipid and *Gm* is mass of gonads.

Next the maximum possible growth increment (Max_{Gr}) is calculated and here we assume individuals under 70 days have a constant maximum growth rate (for details see TRACE section 5.8.3) and those older are assumed to follow a von Bertalanffy growth curve:

$$Max_{Gr} = \begin{cases} Gl * Ah, & Age < 70 \; days \\ (L_{inf} - L) * (1 - exp(-k/365)) * Ah, & Age \geq 70 \; days \end{cases} \tag{4}$$

where *Gl* is the slope coefficient of a regression of larval length on age, L_{inf} is the asymptotic length of sea bass, *L* is fish length and *k* is the annual growth constant and *Ah* is an Arrhenius function. After calculating the theoretical maximum size increase, the energetic cost of this maximum increase is calculated. Eggs do not grow, instead they develop and transform into yolk-sac larvae which do not ingest energy and thus are assumed to have maximum energy available to grow maximally. However once egg-sac larvae have transformed to larvae they begin to ingest energy and here larvae, juvenile and mature sea bass only grow maximally if there is adequate assimilated energy and update length accordingly. If there is not enough assimilated energy, they will grow at a suboptimal growth rate (for details see TRACE section 5.8 and see Table. 4-1 for parameter values).

Calculate-speed: The swimming speed of each fish is calculated from its length and SST of the patch.

Transform: In our model update we include the full fish life cycle and use length-based definitions to distinguish between life stages. In the transform sub model if a super-individual meets the criteria (sufficient length; see Fig. 4-2) then it transforms to the next life stage. The life stages are egg; yolk-sac larvae; larvae; juvenile sea bass; and mature sea bass. When juveniles transition to mature sea bass, they set their coastal feeding ground affinity as the ICES division in which they are in at the time of exceeding this length requirement (this could be a different division to the original ICES division target they would have drifted towards when they were in pelagic stages, see TRACE section 5.8.7). Note that at the end of the first spawning migration there is an opportunity to change ICES division affinity which is altered with a probability that can be set by the model user.

Fishing-mortality: For fish that are over the minimum landing sizes the number of fish represented by each super individual is discounted by fishing mortality rates from the commercial offshore, commercial inshore and recreational fleets (data obtained from ICES stock assessment 2020).

Movement: Juvenile and mature movement sub models remain mostly unchanged from Walker et al., 2020. However, a major addition to the model is the full fish life cycle and the inclusion of life stages of eggs, yolk sac larvae and larvae. In our update we provide movement sub models for these pelagic life stages.

Spawn-migration: During the months October–May if SST is below the 9°C spawning trigger threshold then mature fish move towards offshore spawning grounds.

Feeding-migration: When spawning period is over at the end of May each mature fish moves back towards or within its assigned coastal feeding ground.

Local-movement: Each juvenile fish moves randomly within coastal patches. Juveniles less than 32cm (not yet classed as "adolescent") are further constrained to nursery coastal patches.

Larval stages drift: Each egg, yolk-sac larvae and larva move one patch closer to its assigned coastal feeding ground.

Reproduction: On the 17th of March mature sea bass calculate their potential fecundity and then the energy required to produce this number of eggs (Max_R):

$$Max_R \left(M_{str} * EG_{pw} \right) * EG_m * \left(E_f + F_s \right) \tag{5}$$

where M_{str} is Structural mass of sea bass (i.e., not including any fat reserves or gonad mass), EG_{pw} is number of eggs per kg of sea bass (Pickett and Pawson, 1994), EG_m is the weight of eggs, Ef is the energy in flesh and F_s is the cost of synthesising flesh. If there is enough energy to produce maximum potential fecundity, then the energy needed to do this is deducted from energy reserves and gonad mass and realised fecundity are set accordingly. However, if there is not enough energy to reach maximum fecundity then energy reserve is set to whatever is left after subtracting maintenance costs and gonad mass and realised fecundity is set to what is achievable with the limited resources. Once calculated for all mature sea bass, a random sample of 10 mature sea bass super-individuals spawn one super-individual which represents as many eggs as determined by total realised fecundity of the whole spawning stock divided by 10. The number of eggs is therefore based on the cumulative available energy reserves. With only 10 individuals spawning the number of super-individuals remains consistent for each cohort and 10 new super-individuals continue to represent the spatial aspect of the fishery (for details see TRACE sections 5.7, 5.8.7 and see Table. 5-1 for parameter values).

Table 4-1. Parameter values used in Energy budget equations.

Parameter	Description	Value	Reference
a	Length-mass coefficient (for details see TRACE Section 5.8.3).	1.296×10^{-5} *0.95	(Pickett and Pawson, 1994; ICES, 2012a)
b	Length mass scaling exponent.	2.969	(ICES, 2012a)
A_o	Normalizing constant for relationship between Metabolic rate and fish size.	0.1227808	(Claireaux, 2006; Jourdan-Pineau et al., 2010; Luna-Acosta et al., 2011; Zupa et al., 2015; Peixoto et al., 2016)
A_e	Efficiency of energy from phytoplankton to fish.	1.64×10^{-3}	Parameterised with ABC
C_{max}	Max ingestion.	0.54 grams per gram of fish	(Lanari, D'Agaro and Ballestrazzi, 2002)
E_f	Energy content of flesh.	7 kJ g^{-1}	(Peters, 1986)
EG_m	Sea bass egg mass.	0.96×10^{-3} g	(Cerdá et al., 1994)
EG_{pw}	Potential egg production per gram of sea bass.	375,000	(Pickett and Pawson, 1994)
E_l	Energy content of lipid.	39.3 kJ g^{-1}	(Schmidt-Nielsen, 2013)
E_p	Energy content of phytoplankton.	6.02 kJ g^{-1}	(Annis et al., 2011)
F_s	Energy to synthesise flesh.	3.6 kJ g^{-1}	(Sibly and Calow, 1986; Sibly et al., 2013)
GL	Larval stages growth coefficient.	0.02485 cm d^{-1}	(Jennings, Jennings and Pawson, 1992; Regner and Dulčić, 1994)
H	Half saturation constant	4.87×10^{-1}	Parameterised with ABC
I	Importance of density on ingestion.	$5.14 \times 10^{+13}$	Parameterised with ABC
K	Annual growth rate coefficient.	0.096699	(ICES, 2012a)
L_{inf}	Asymptotic length.	84.55 cm	(ICES, 2012a)
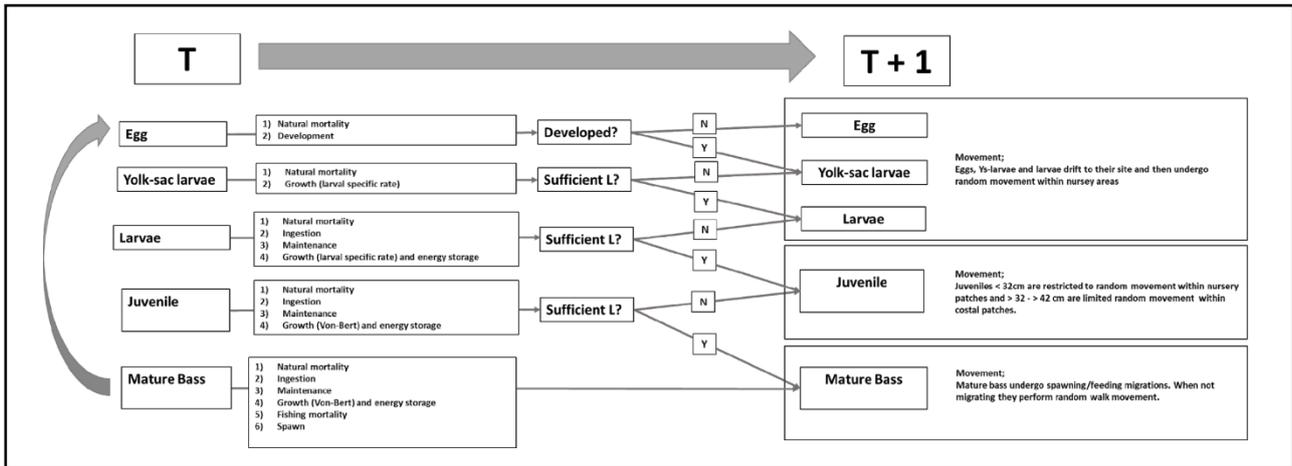
Figure 4-2. Model overview showing for each life stage the processes occurring on day T that may result in transformation to the next life stage at the end of the day. For each life stage (egg, yolk-sac larvae, larvae, juvenile, and mature sea bass) the sub models are indicated in the order of model execution. Eggs transform to the next life stage after a specified time and from then on transformation is length based. Overviews of movement sub models are given on the right.

4.3.4 Model calibration

The model contains 25 parameters, and the values were where possible taken from literature (see TRACE section 5.5 and Table 5-2). Where absolute values of these parameters could not be directly taken from the literature, we used a version of Approximate Bayesian Computation (ABC) called Simulated Annealing ABC (Albert, Künsch and Scheidegger, 2015) as implemented in the Python library ABCpy (Dutta *et al.*, 2017) to fit 5 parameters to calibrate the model. The five calibrated parameters were: *H*; half saturation constant, *AM*: adult natural mortality, *AE*; absorbed energy, *PM*: pelagic mortality, *I*; importance of density dependence. This method is highly parallelizable, making it an excellent algorithm for use by high-performance computers. ABC began by randomly drawing values of *H*, *AM*, *AE*, *Pm* and *I* from uniform prior distributions (for full details of priors see TRACE section 5.9.4) and ran the IBM with these parameter values. Subsequent runs were guided according to how well the outputs of previous runs fitted data as indicated by the sum of the weighted Euclidean distance between the model outputs and data. The data used for parameter calibration was from the sea bass stock assessment model (stock synthesis 3, SS3). SS3 outputs for SSB and numbers at age are estimated annually, however mass at age is simply taken as the stock assessment parameters of the von Bertalanffy model. It is necessary to include mass at age in the calibration to get a realistic population size structure, and in the absence of real data this is the best available guide. The estimated posterior means for all five parameters and 95% credible intervals are shown in Table 4-2 together with the prior distributions used. The estimated correlation matrix between parameters is shown in Table 4-3 and the values shown suggest medium to weak correlations between these five model parameters, with a maximum of -0.47 between parameters *PM* and *AM*.

To quantify the uncertainty in predictions that results from uncertainty in the five calibrated parameters, we ran a posterior predictive check by drawing 111 parameter samples from the inferred approximate posterior distribution and simulating 111 data sets, each using a different

parameter sample. From these we obtained posterior predictive inter-quartile ranges, and these are shown in Figs. 4-3 – 4-5 to indicate the uncertainty in predictions.

Table 4-2. Values for priors, posterior mean and 95% credible intervals for parameters obtained by ABCpy. H: half saturation constant, AM: adult natural mortality; AE: absorbed energy, PM: pelagic mortality, I: importance of density dependence. For rationale for choice of priors see TRACE section 5.9.4

Parameter	Priors	Posterior mean	95% credible intervals
H	$2.5 \times 10^{-1}, 7.5 \times 10^{-1}$	4.87×10^{-1}	3.04×10^{-1}, 7.26×10^{-1}
AM	$2.8 \times 10^{-4}, 5.9 \times 10^{-4}$	4.71×10^{-4}	3.43×10^{-4}, 5.87×10^{-4}
Ae	$0.0, 3 \times 10^{-3}$	1.64×10^{-3}	2.51×10^{-4}, 2.88×10^{-3}
PM	$4.5 \times 10^{-2}, 1.35 \times 10^{-1}$	8.01×10^{-2}	5.76×10^{-2}, 1.02×10^{-1}
I	$2.5 \times 10^{+13}, 7.5 \times 10^{+13}$	$5.14 \times 10^{+13}$	$2.72 \times 10^{+13}$, $7.39 \times 10^{+13}$

Table 4-3. Estimated correlation matrix between the parameters shown in Table 4-2.

-	AM	Ae	PM	I
H	0.19	-0.04	0.06	0.02
AM		-0.04	-0.47	-0.05
Ae			0.35	0.17
PM				0.13

4.3.5   Sensitivity analysis

The sensitivities of model outputs for SSB and numbers/mass at age are shown in Table 4-4 as percentage change in output for a 10% decrease/increase in model parameters. The model remains robust against most parameters with most sensitivities less than 10%. The model was most sensitive to changes in length weight parameter (b_g). For the full table of sensitivities of number and mass at age see TRACE section 5.12.

Table 4-4. Sensitivities of SSB, mean mass at age, and numbers at age, to changes in parameter values. Results are presented as % change in output for a 10% decrease/increase in parameter value relative to values in Table 4-1 or, for the five fitted parameters, the posterior means shown in Table 4-2. For mass and numbers at age we show the range of values for brevity, for full table see TRACE section 5.12 and Table 5-6.

Parameter	Value	Output Variable					
		SSB		Mass at age		Numbers at age	
		Decrease	Increase	Decrease	Increase	Decrease	Increase
linf	84.55	-9.56	0.79	-21.9,0.8	-12.0,25.7	-2.1,7.5	-10.5,3.6
K	0.096699	-1.68	10.52	-20.5,2.7	-4.8,21.5	-2.7,12.3	-2.5,11.6
t0	-0.73	-7.60	-1.53	-16.3,2.0	-14.1,2.7	-1.8,17.1	-2.0,6.6
Ea	0.5	1.71	-0.45	-10.1,4.0	-9.9,2.8	-1.8,10.8	-2.2,2.0
EaS	0.1903656	10.13	-0.67	-10.8,4.7	-10.0,7.6	-2.5,7.7	-1.7,3.2
Cmax	0.54	4.12	6.53	-9.4,7.5	-5.3,6.4	-2.0,13.5	-1.9,10.2
ep	6.02	-1.27	2.18	-9.8,5.6	-10.8,5.1	-1.6,3.7	-3.0,19.4
A0	0.1227808	7.09	-2.12	-7.2,9.9	-6.5,3.1	-1.2,10.1	-2.6,7.9
Ef	7	-11.62	-8.11	-9.3,3.8	-11.6,7.4	-2.3,11.6	-2.3,8.5
El	39.3	4.52	-6.25	-8.3,3.5	-13.4,2.3	-2.4,2.4	-2.5,14.3
Ls	14.7	-10.30	0.55	-17.8,5.5	-8.9,2.6	-2.4,9.3	-2.6,8.1
Fs	3.6	-1.50	0.12	-12.3,2.3	-7.5,3.8	-1.8,14.5	-1.8,11.3
egg_mass	0.00096	5.58	4.29	-16.7,5.9	-8.7,3.4	-1.5,21.8	-3.4,2.0
a_g	1.23×10^{-5}	-5.00	10.66	-17.8,-7.2	2.9,16.0	-1.6,6.7	-2.1,20.4
b_g	2.969	-61.27	152.43	-72.9,-45.0	29.8,265.7	-57.5,5.3	-1.2,5.8
eggs_per_bass	375000	-0.06	-4.45	-11.4,9.4	-22.0,3.9	-1.7,10.5	-2.1,13.9
Gl	0.02485	3.66	-0.78	-7.8,7.7	-11.2,3.9	-28.2,17.6	-2.1,51.8
H	4.46×10^{-1}	0.67	6.65	-5.3,6.1	-5.8,7.4	-2.7,9.7	-3.3,11.7
AM	4.91×10^{-4}	-0.89	3.49	-8.9,5.0	-6.8,6.4	-0.7,8.9	-3.3,6.8
AE	1.57×10^{-3}	1.52	6.78	-17.5,2.7	-8.4,4.7	-3.4,19.0	-1.8,10.6
PM	8.42×10^{-2}	1.18	-1.46	-7.4,3.7	-7.5,4.4	-1.3,71.9	-37.1,2.7
I	5.20×10^{13}	2.75	5.49	-7.2,4.3	-10.8,4.8	-2.7,2.4	-3.6,5.6

4.4 Results

To assess the model fits to data, we compare the IBM outputs for SSB and numbers/mass at age with outputs from stock synthesis 3 from 2004 to 2014 (ICES, 2019), as shown in Figs. 4-3 – 4-5. In these figures the black points represent the 'data', i.e., outputs from stock synthesis 3, and the solid red lines/dots are IBM outputs using posterior medians. Uncertainty about these outputs is indicated by ribbons representing posterior predictive inter-quartile ranges.

SSB is the total mass of all fish that are mature (>42cm). The fit of SSB is shown in Fig. 4-3. The IBM captures the shape of the data well and follows the decline in SSB from 2010 suggested by the SS3 data. Mass-at-age predictions are assessed by reference to the von Bertalanffy growth curve assumed by SS3 (Fig. 4-4), which assumes no variation year-to-year. The model slightly overpredicts mass for ages 0 to 4, and underpredicts mass after age 7. The fit of numbers-at-age predictions are shown in Fig. 4-5. Model fits to the SS3 data are good for ages 5 and above, and reasonably good for all ages. In addition to the calibration plots (Figs, 4-3, 4-4 and 4-5) we show some spatial model outputs in Figure 4-6. Here we show the total catch (see sub model *Calculate-catch* Trace section 5.7) for each patch for each year (2004-2014). In general, costal patches (see Fig. 4-1 for distribution of model coastal patches) are where the greatest mass of sea bass are predicted to be caught, however there are interannual variations. For example the model predicts there is a greater mass of sea bass caught in the Irish sea in 2007 than in all other years shown (Fig 4-6).
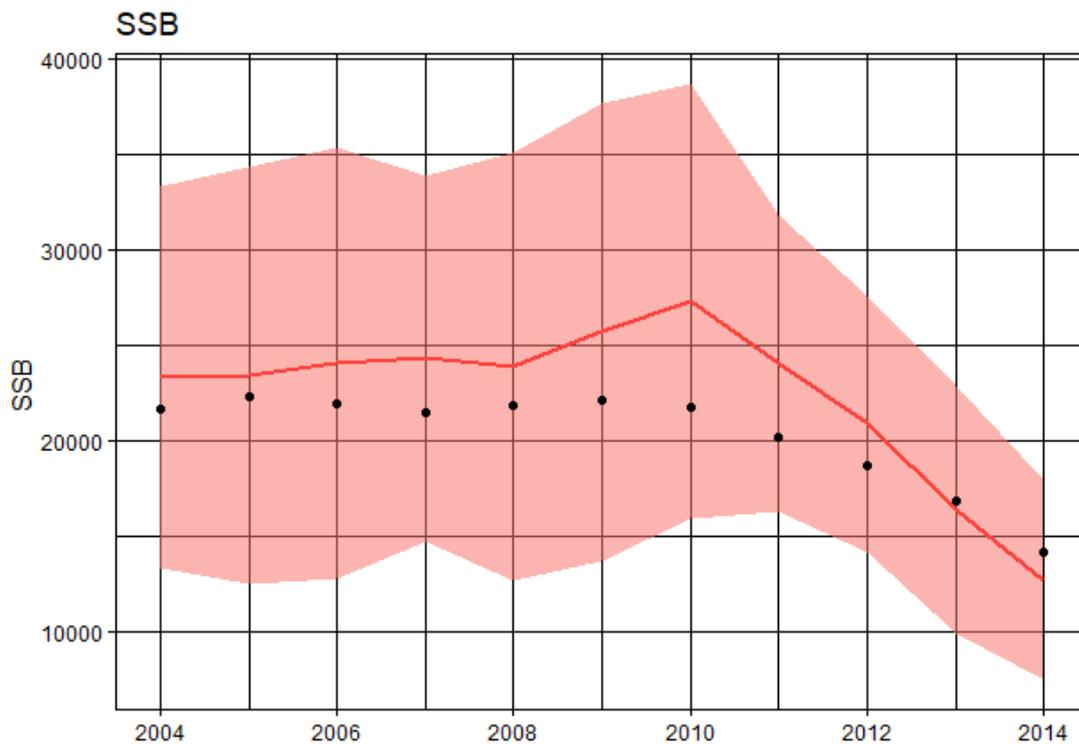
Figure 4-3. Model calibration for Spawning Stock Biomass (SSB) for years 2004-2014. Black dots represent the outputs of SS3; solid red line is IBM output using posterior medians; ribbon represents interquartile range.
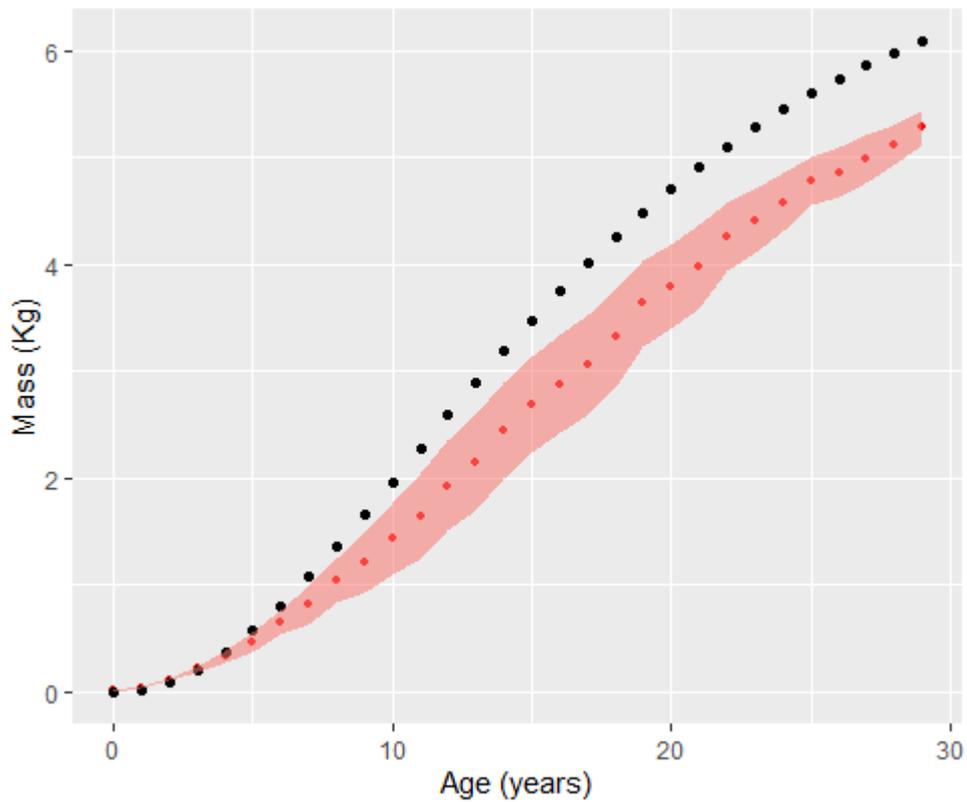
Figure 4-4. Model calibration for individual average masses (kg) over years 2004-2014 of 30 age classes. Black dots represent the Bertalanffy growth curve used by SS3; red dots are the IBM outputs using posterior medians; ribbon represents interquartile range (which is calculated for each age as the average of the yearly interquartile ranges). For model fits of each of the 30 age classes for years 2004-2014 see TRACE section 5.11.
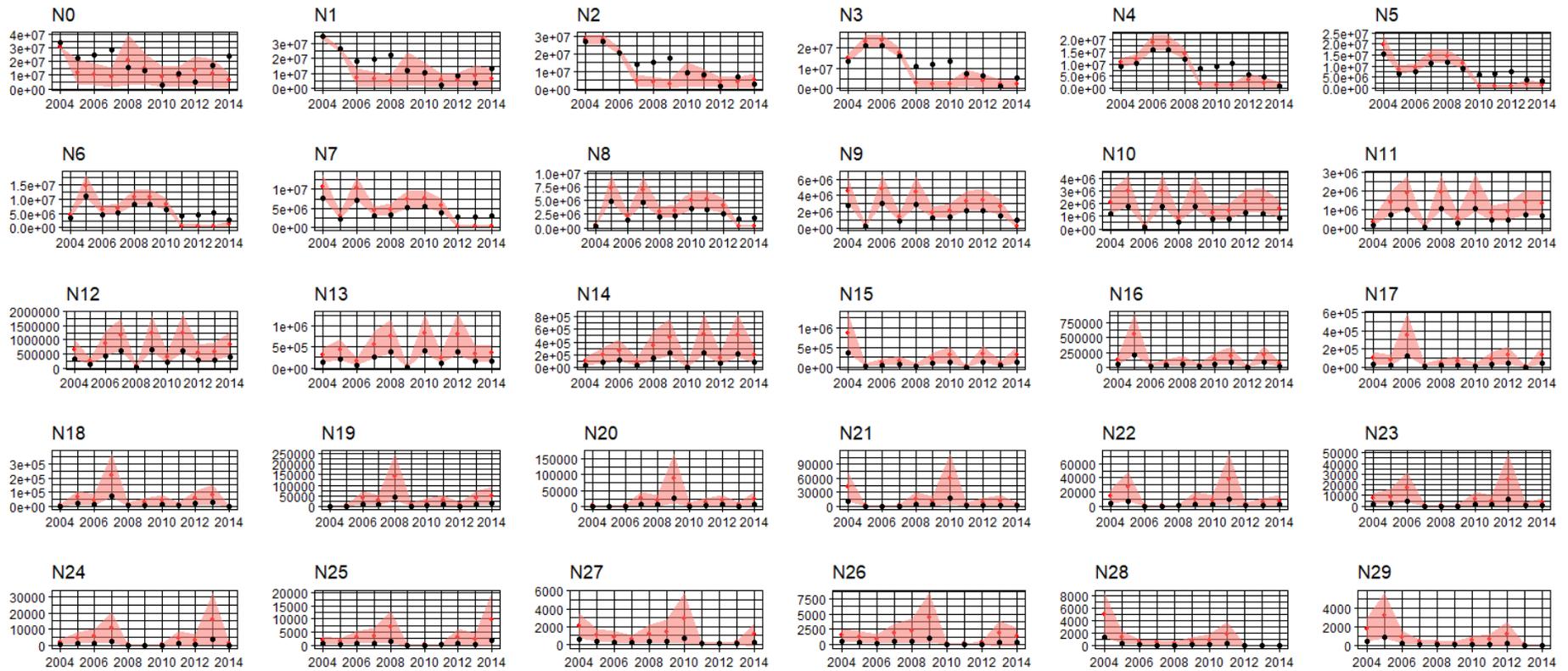
Figure 4-5. Model calibration for numbers in 30 age classes for years 2004-2014. N0 = number at age 0, N1 = number at age 1, etc. Black dots represent the outputs of SS3; red dots are the IBM outputs using posterior medians; ribbon represents interquartile range.
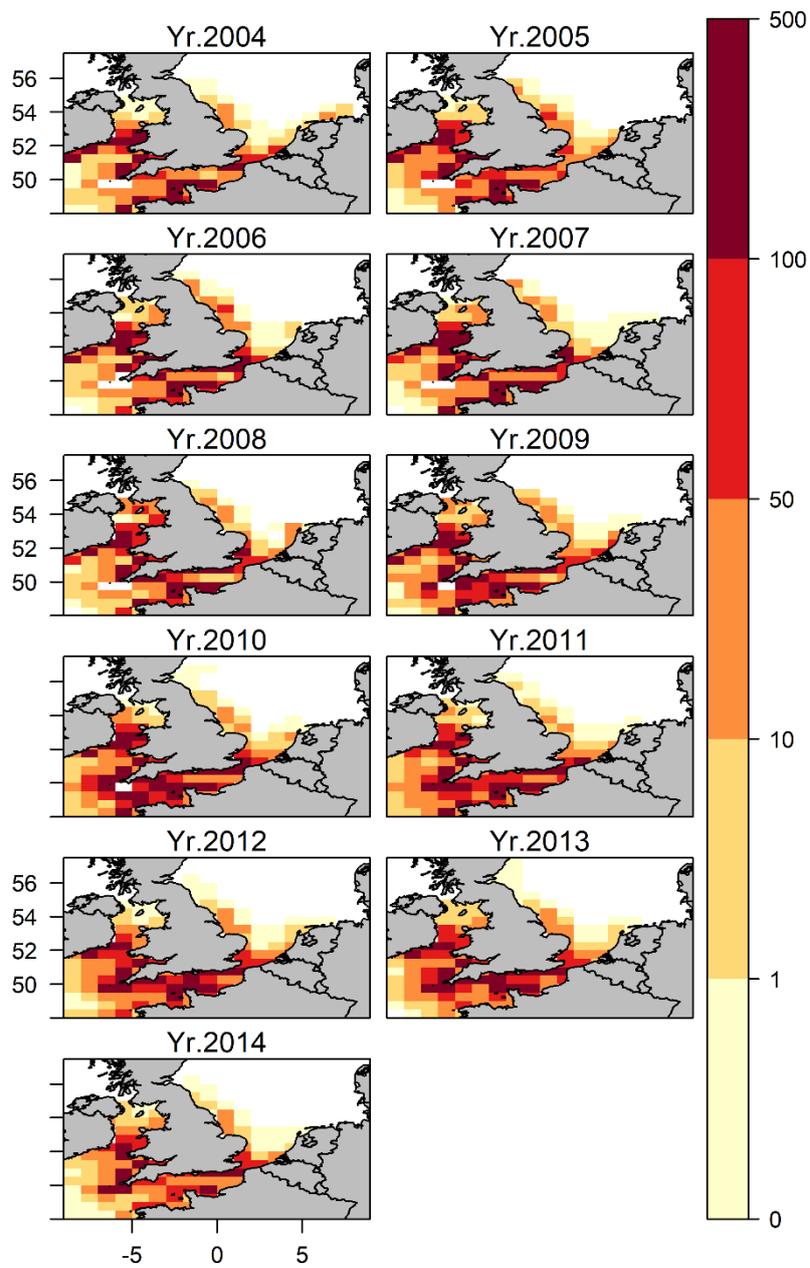
Figure 4-6 Total catch per patch per year (2014-2015) Catch is recorded in tonnes ranging from 0 catch to 500 tonnes and indicated by colour (light yellow = low catch and dark red = high catch).

4.5 Discussion

Here we present a spatially explicit individual based model of the northern stock of sea bass which has been calibrated and assessed for goodness of fit against stock synthesis 3 outputs of SSB and the numbers and individual masses of 30 age classes. The model builds on Walker *et al.* (2020), but our addition of individual energy budgets driven by phytoplankton density provides a mechanistic link between environmental drivers and fish populations. Here we also present spatial outputs of annual catch to demonstrate how the energy budget creates a mechanistic link between changes in environmental drivers and predictions of temporal and spatial distribution of sea bass catch. The energy budget approach follows established methods (Boyd, Walker, *et al.*, 2020; Mintram *et al.*, 2020; Watson *et al.*, 2020) however it is important to note that our model is intended for use by fisheries managers to complement, not replace, current stock assessment approaches using SS3.

A key assumption in our model is that local food density available to sea bass can be represented by observed phytoplankton density. Sea bass are generalist predators, and their diet is opportunistic, so it is difficult to predict what they will be eating at any particular time (Pickett and Pawson, 1994). Their food choices could in principle be derived from a model of local ecosystems, but this would require many unobservable parameters (i.e., what, when and where sea bass are eating and the associated uncertainly). We therefore chose instead to make use of remote sensing data of phytoplankton blooms which constitute the base of the marine food web. There are a number of key necessary assumptions required when attempting to estimate how much of the energy present in phytoplankton is feasibly available to sea bass. Our first assumption is that areas of high phytoplankton density are favourable to all trophic levels i.e., will correlate with high densities of species that directly consume phytoplankton and consequently will be attractive to species that prey upon these secondary consumers and a continuation of this pattern up the food chain. We also assume that there is likely a delay (which we term *trophic delay*) in time from a large amount of energy being present in the form of phytoplankton till it is available to sea bass as a range of prey (i.e., an increase in biomass of prey species through individual growth or reproduction). A final assumption is that energy is lost at each trophic interaction and many species in the marine environment (including much of sea bass prey) are highly mobile and may move around seeking energy in the form of their preferred prey. In this model we cumulate these important assumptions and bypasses these complexities by using a single parameter *absorbed energy* to indicate how much of the phytoplankton ends up in the fish. Here this combines all the unknowns of how-much/how-long energy takes to become available from phytoplankton to bass prey. Our approach can be considered justified by the good fits to the data seen in Figs, 4-3, 4-4 and 4-5.

Methods of calibrating and evaluating complex models have advanced considerably in recent years. Here we used Simulated Annealing ABC (SABC [Albert, Künsch and Scheidegger, 2015]) to calibrate five model parameters (adult and pelagic mortality rates, absorbed energy and two density dependences) that would otherwise be extremely difficult to estimate. SABC is much faster and more accurate than rejection ABC methods (Dutta *et al.*, 2017) which have previously been used to calibrate similar IBMs (e.g., Boult et al., 2018; Boyd, Walker, et al., 2020; van der Vaart et al., 2015).

The model outputs we have presented give insight into how different aspects of the model are working. Spawning stock biomass (SSB, Fig. 4-3) is the size of the mature stock, which is the basis for setting legislative targets to manage the stock. We see good fits for SSB across the simulation period. We also see good fits to body weights-at-age (Fig. 4-4) which suggests that both the numbers and sizes of the individuals are reasonable. The numbers and masses in each age class are discussed below.

The numbers in each age class are shown in Fig. 4-5. Assessing numbers at age rather than total abundance is necessary to avoid the more numerous younger fish dominating the model fits. Overall, the dynamic model age structure shown in Fig. 4-5 is a good fit against the SS3 data, although some of the goodness of fit may stem from what happens in the spin up period. Cohorts born in the spin up period are read in from ICES numbers at age data, and their numbers thereafter are only affected by two model parameters, natural mortality (*AM*) and fishing mortality.

The N0 panel shown in Figure 4-5 represents the number of fish that are age 0 and no longer in the pelagic stage (defined in our model as an individual with age < 1 and Length > 1.4 cm [Beraud *et al.*, 2018]). Predicted N0 fits SS3 data well in some years but in others there are significant discrepancies. Discrepancies may arise from lack of realism in our model, but may also arise from errors in the SS3 'data'. The SS3 estimates of the N0 are outputs of a population-dynamics model described in the Introduction, and subject to some uncertainty. So the discrepancies between our predictions and the SS3 data do not necessarily mean our predictions are wrong. N0 (i.e., the number of N0 individuals) in our model is an emergent property driven by the number of mature fish and their spawning success, which depends on the condition of the parents (Mcbride *et al.*, 2015), and early survival. Larger fish with higher fat reserves can produce more eggs (i.e., have higher potential fecundity) than smaller fish, so the more mature fish there are in the simulation, the greater their collective realised fecundity. If the mature fish have had access to abundant energy, there is more left to produce eggs after the necessary allocation to maintenance and growth. It is important to note that the model does not cover quality of eggs though there is some evidence that fish that have had access to better nutrition may also be able to produce higher quality eggs, which may increase larval survival and stock recruitment (Cerdá *et al.*, 1994; Chatzifotis *et al.*, 2011). In the model presented the amount of energy to produce eggs is also influenced by temperature, since individuals in warmer sea temperatures are able to ingest more energy, grow faster and have higher levels of reserves from which to produce eggs. The other major contributor to the N0 output is pelagic natural mortality rate. The daily pelagic mortality rate 8.01×10^{-2} is far greater than that of the adult mortality parameter in our model 4.71×10^{-4}, so there is a substantial payoff to growing faster to escape the pelagic phase earlier. In this way the number of larvae that make it through to be juvenile fish (i.e., classified as N0) is dependent on their growth rate, which in turn depends on food availability, temperature, and the density of competitors.

The masses of the individuals in each age class are presented in Fig. 4-4. Although the models provide fairly good fits for younger fish, the masses of older fish are underpredicted. Discrepancies between our predictions and the SS3 data do not necessarily mean our predictions are wrong, because the SS3 'data' are simply outputs of a fitted von Bertalanffy growth curve (ICES, 2021). Discrepancies may also arise as a result of the spin-up process. During spin up we read in the numbers at age 0 estimates from SS3 as is done in the spawning sub models of Walker *et al.* (2020), but afterwards spawning is determined by the fishes' energy budgets, and the two methods differ in when spawning takes place. The result is that the IBM age 0 cohort consists of older and larger fish than in the SS3 data. As the cohort ages it continues heavier for a few years, and this may explain the overpredictions of mass for M0 – M4 in the first few years of the simulations (see Figure 5-17 in TRACE section 5.11). The underpredictions of masses of older fish are harder to explain but may result from some lack of realism in our representation of energy budgets. In our model an individual's mass depends on its history of ingesting energy, and this in turn depends on the energy available in the environment, competition from other fish and sea surface temperature and this is what the *AE* and *I* parameters hoped to capture. In excess of structural mass individuals have the potential to put on weight as fat reserves. High reserves result from abundant energy, high SST

and/or low competition, and eventually allow mature individuals to spawn. These processes result in fluctuations in fat reserves that the SS3 assessment does not capture.

There are many potential fisheries management applications for the IBM we present here. The original model published by Walker *et al.*, 2020 was designed to complement the SS3 stock assessment and to test spatial management scenarios, and the updated model here still retains that utility (though note movement sub model limitations discussed below). We demonstrate some of the spatial and temporal utility in Figure 4-6 where results show predictions of interannual variation in the distribution of sea bass catch. Our energy budget additions and the subsequent emergent population dynamics that are driven by the environmental drivers make the model a good tool to study a range of climate impacts on the stock. Using different climate projections the energy budget could capture the effect of temperature on life processes of ingestion, metabolic rate, growth and sea bass recruitment (known to be heavily influenced by temperature [Pawson, Pickett and Smith, 2005]) and the subsequent impacts of the stock could be analysed. Another advantage of the full fish life cycle and closed energy budget additions is that changes in condition or number of the spawning stock will have consequences on the following year's recruitment. This closed loop facilitates testing of a range of existing and new management measures for recreational and commercial fishing (e.g., spatial, and temporal closures, changes to total allowable catch/minimum landing size, bag limits etc.).

The model is built in a modular fashion making additions or changes to further the model utility achievable. One promising line of work is to add other dynamic maps of anthropogenic stressors to the model environment. For example, the addition of a soundscape map to which the individuals would suffer sublethal effects through reduced ingestion and the knock-on effects through the energy budget (Watson *et al.*, 2020) would give rise to emergent population effects of anthropogenic noise (a similar approach was done for porpoise in a study by Nabe-Nielsen *et al.*, 2014). In addition, there is scope to update fishing pressure which is currently read in from ICES data to a more mechanistic sub model. Sea bass are mostly targeted by the under 10m fleet in the UK (Williams *et al.*, 2018) and the small vessels are often most vulnerable to bad weather (Sainsbury *et al.*, 2018; Young *et al.*, 2019). An updated fishing pressure sub model that responded mechanistically to environmental and socio-economic pressures would further develop the model utility to fisheries management (e.g., [Dreyfus-León, 1999; Millischer and Gascuel, 2006; Bastardie *et al.*, 2010; Bailey *et al.*, 2019; Lindkvist *et al.*, 2020]).

We believe that the IBM we present here is a useful tool in its current form, however there are some caveats and further opportunities for improvement. Firstly, a general critique of individual/agent based models is the large amount of data that they require for model parameterisation, calibration, and validation (Johnston *et al.*, 2019). To calibrate and asses the fits of the model, we use outputs from the sea bass SS3 assessment model. The SS3 model takes all the available data from surveys and literature to assess the state of the stock (ICES, 2021) and outputs modelled 'data', so we are fitting the IBM model outputs to another model's outputs. This is suboptimal but in the absence of the extensive long-term field data on individuals, outputs from SS3 remain the best calibration option and the limited availability of calibration data may also explain why the credible intervals remain wide for the five parameters fitted with ABC (Table 4-2). Further detailed spatial distribution data would also be required to truly validate the spatial and temporal explicit predictions by the model (shown in Fig 4-6). Another limitation is the movement sub model which remains unchanged from Walker *et al.*, 2020. Walker *et al.*, 2020 outline how modern tagging methods (Quayle *et al.*, 2009; O'Neill *et al.*, 2018; de Pontual *et al.*, 2019) could provide data on which a mechanistic movement sub model could be built and added to further the spatial utility of the model. To conclude we hope that fisheries managers may find the spatial, mechanistic, and emergent merits of this IBM a useful

complementary tool to SS3 with scope for further development to aid the sustainable management of northern sea bass stock.

4.6 Acknowledgements

5 "TRAnsparent and Comprehensive model Evauldation" (TRACE) document for a spatially explicit individual-based model of the northern stock of European sea bass *Dicentrarchus labrax*.

This is a TRACE document ("TRAnsparent and Comprehensive model Evaludation") which provides supporting evidence that our model presented in this thesis was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

Schmolke A, Thorbek P, DeAngelis DL, Grimm V. 2010. Ecological modelling supporting environmental decision making: a strategy for the future. *Trends in Ecology and Evolution* 25: 479-486.

and uses the updated standard terminology and document structure in:

Grimm V, Augusiak J, Focks A, Frank B, Gabsi F, Johnston ASA, Liu C, Martin BT, Meli M, Radchuk V, Thorbek P, Railsback SF. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling* 280:129-139.

and

Augusiak J, Van den Brink PJ, Grimm V. 2014. Merging validation and evaluation of ecological models to 'evaludation': a review of terminology and a practical approach. *Ecological Modelling* 280:117-128.

5.1 Problem formulation

This TRACE element provides supporting information on: The decision-making context in which the model will be used; the types of model clients or stakeholders addressed; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

5.1.1 Summary:

A spatially explicit individual-based model (IBM) was developed to simulate the population dynamics and geographical distribution of the northern sea bass stock. Life processes are driven by energy budget equations from sea surface temperature and phytoplankton density remote sensing inputs. Assumptions regarding movement relate to past observations.

The model is designed to model population dynamics and simulate spatial distribution of the European sea bass (*Dicentrarchus labrax)* in ICES divisions' 4.b–c, 7.a and 7.d–h. Sea bass are a large, slow growing, late maturing, high value fish that is exploited by both commercial and recreational fisheries (Pickett and Pawson, 1994). Scientific assessments for the UK have shown a rapid decline in spawning stock biomass for eight years since 2010 which has been attributed to poor recruitment (driven by environmental factors) and high fishing mortality. The decline led to the implementation of emergency management measures in 2015, and has resulted in significant reductions in the harvest (ICES, 2021).

The model described here builds upon the model of Walker et al. (2020). Walker et al. (2020) used the ICES stock assessment as a basis for the population dynamics. In our update, population dynamics are now emergent from the model, based on an energy budget. The energy budget is driven from remote sensing environmental data (sea surface temperatures [SST] and phytoplankton density [PHY]). In this way, environmental changes are linked to life processes and ultimately population dynamics. With emergent population dynamics, there is scope for model predictions in novel environmental conditions whilst improving reliability of predictions for management strategies for the spawning stock. The model output, spawning stock biomass (SSB), is an important metric of stock status currently used by scientists to provide advice on fishing opportunities for the stock. We focused on statistics related to SSB to evaluate the impact of management strategies on stock status. The IBM could also be used to assess other aspects of performance such as yield maximisation, risk reduction, and Total Allowable Catch (TAC) stability. In addition, the model could act as a tool to test the impact of:

- Behaviours of commercial and recreational fishers.

- Management approaches that limit catch and/or effort.

- Environmental/anthropogenic stressors (e.g., anthropogenic noise, catch and release fishing injuries etc.).

The scope for a broad range of testing applications means stakeholders for this model include scientists and organisations advising on fishing opportunities for sea bass as well as decision makers.

The spatial component of the IBM retains the hardwired movement of Walker et al., 2020. However, the model remains a useful tool to complement the stock assessment through enhanced predictions of management scenarios and testing spatial strategies, which are not possible with a population-based assessment model. Important future additions to the model are steps to further elucidate the mechanisms underlying sea bass movement. This is suggested to be done with new mechanistic

migration sub models that allow for spatial predictions in novel environmental conditions and improve reliability of predictions for strategies relating to the spawning stock.

5.2 Model description

This TRACE element provides supporting information on: The model and provides a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex sub models it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

5.2.1 Summary

Here, we provide an ODD (Overview, Design concepts and Details) description of the individual-based model for sea bass (Grimm *et al.*, 2006, 2010, 2020)**.**

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm *et al.*, 2006, 2010, 2020). The model was implemented in NetLogo 5.3.1 (Wilensky, 1999), a free software platform for implementing individual-based models.

Purpose and patterns

The purpose of the model is to simulate the population dynamics and spatial distribution of the European sea bass (*Dicentrarchus labrax*) in the North Sea, Channel, Celtic & Irish seas (ICES divisions' 4.b–c, 7.a and 7.d–h). Using the emergent population dynamics, there is scope to use the model as a tool to test differing fisher behaviours (both commercial and recreational), management approaches (both catch limiting and spatial) and the impacts of environmental/anthropogenic sublethal stressors (e.g., anthropogenic noise, catch and release fishing injuries etc.).

Entities, state variables and scales

The model has two types of entity: sea bass super-individuals and square patches which represent the local environment. Super-individuals (hereafter termed individuals) comprise many sea bass with identical state variables, and were employed to reduce run times while dealing with the large number of fish in the stock (Scheffer *et al.*, 1995). Sea bass super-individuals are characterised by the variables: age (years), the number of fish represented, life stage (egg, yolk-sac larvae [ys-larvae], larvae, juvenile or mature [adult]), length (cm), weight (including structural mass, gonad mass and total mass [kg]), ingested energy, energy reserves, metabolic rate, location, swimming speed and daily direction changes, spawning trigger and counter, mortality rates (natural, commercial inshore/offshore fishing mortality and recreational-fishing mortality) and the division they have an affinity to feed in (site fidelity; 4.b, 4.c, 7.a, 7.d, 7.e or 7.fg). The temporal extent spans from 1st of January 2004 to 31st of December 2015 and the model proceeds in discrete daily time-steps.
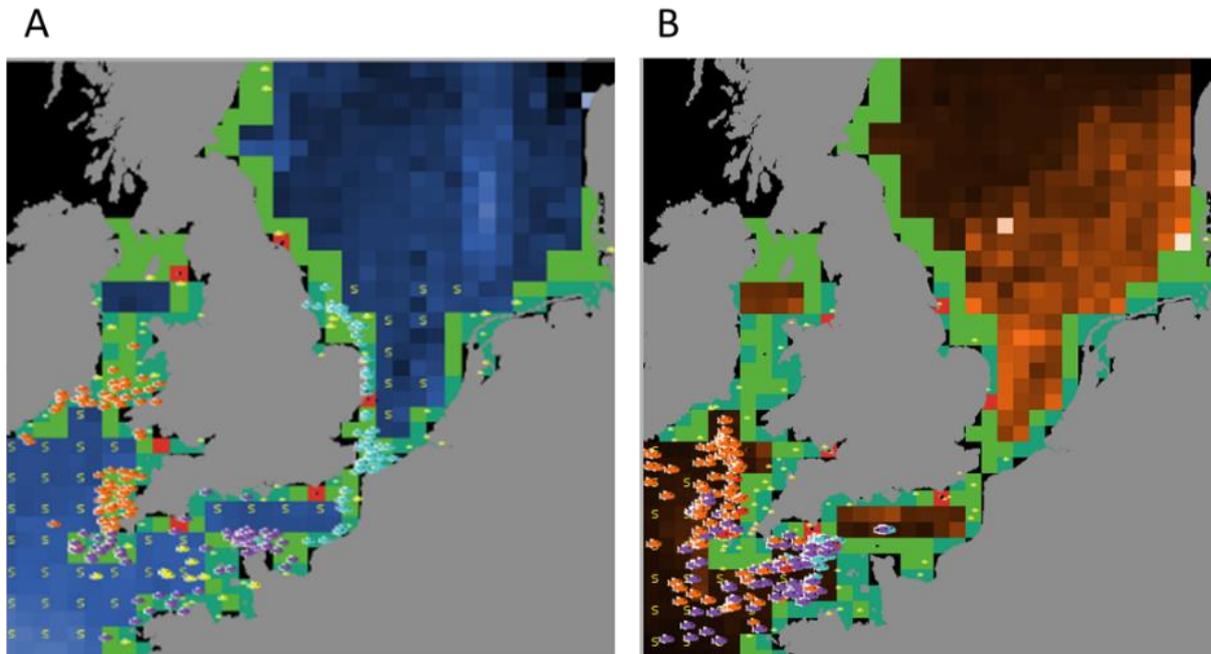
Figure 5-1. The model interface; Both sea surface temperature (SST) and phytoplankton concentration (PHY) can not be shown simultaneously in the model interface so here; A) shows offshore patches as blue with dark to light representing increasing SST (0- 30ºC), and B) shows offshore patches as orange with dark to light representing increasing PHY (0-75 g/m^2). For both A) and B) coastal patches represented in green, nursery patches (also coastal) are turquoise. Targets that eggs and larval stages drift towards (depending on ICES division affinity) are represented by red patches. Agent colour represents life stage (white = eggs, black = ys-larvae and larvae, yellow = juvenile sea bass [not all life stages are shown here]). For mature sea bass colour shows the affinity to feeding ground. Spawning patches (which vary depending on time of year and environmental conditions) are shown with a yellow "S". These remote sensing data are updated every 8 days and agents perform all sub models each day (see section below 4.3.3).

The patches make up a grid landscape of 36 x 38 patches representing the area from 9° east to 9° west and 48° to 57.5° north (Fig. 5-1). Sea patches are characterised by dynamic variables sea surface temperature (SST °C) (shown in blue for demonstration purposes in Fig. 5-1A) and phytoplankton density (shown in orange for demonstration purposes in Fig. 5-1B). The patches also have variables for area type (sea, coastal, offshore, spawning and nursery; see TRACE section 5.5), ICES division (4.b, 4.c, 7.a, 7.d, 7.e, or 7.fg) and spawning region (North Sea, Celtic Sea, Channel or Irish Sea). Each patch is approximately 30 x 30 km, although this distance varies by latitude due to the Earth's spheroid shape (29.9 x 27.8 km north of the domain, 37.2 x 27.8 km south of the domain). The model runs in discrete daily time steps (assuming 365 days in a year) from 2004 to 2015 (excluding a spin up from 1985 – 2004; see TRACE Section 5.5). This time span covers 10 years of assessment period to a point when management measures were introduced.

Table 5-1. Key state variables for the model entities.

State variable	Description	Details
Individuals		
Age	Non integer age of egg/larvae/fish.	years
Assimilation-energy	The energy that ends up assimilated by each individual fish within the super-individual.	kJ
Breed	Life stage of agent; Egg, yolk-sac larvae, larvae, juvenile or mature sea bass.	NA
Cohort	Integer age of year class.	years
Development	The number of days remaining before an egg hatches. Based on embryo-duration.	Days
Embryo-duration	The time for an egg to hatch. This is currently fixed at 5 days (range of 3-7.5 days in [Beraud et al., 2018]).	Days
Energy-reserve	The amount of energy a fish has stored based on the difference between ingested and expended energy.	kJ
Energy-reserve-max	The maximum amount of energy a fish can store, based on size.	kJ
ER	The energy reserve left after the energetic cost of maintenance is taken out.	kJ
Fci	Commercial inshore fishing mortality. Per day (fishing pressure limited to 214 days per year).	Daily
Fco	Commercial offshore fishing mortality. Per day (fishing pressure limited to 151 days per year).	Daily
Fri	Recreational offshore fishing mortality. Per day (fishing pressure is 365 days a year).	Daily
Func-response	Holling type II functional response adjusts ingestion rate based on phytoplankton density.	NA
Gonad-mass	Mass of gonads is calculated from the energy that went into producing eggs.	kg
Growth-costs	The energetic cost of adding new length and mass to larvae and fish.	kJ

Growth-rate	The realised amount of length added in a day if there is insufficient energy to grow maximally.	(cm)
Ingestion-rate	The maximum ingestion rate a fish can achieve; based on size, temperature, availability of food, and conspecific density.	grams per day
IVbt	Affinity to division IVb. *	True or 0 for no affinity
IVct	Affinity to division IVc. *	True or 0 for no affinity
L	Length of egg, larvae or fish.	cm
Maintenance-energy	10% of energy reserves at the beginning of spawning is saved for maintenance costs while fasting on the spawning grounds.	kJ
Max-growth-rate	Maximum daily growth increment is calculated for different life stages. Mature and juvenile sea bass growth rate is calculated with the von Bertalanffy equation. Young life stages are calculated with the Gompertz growth equation.	cm
Max-R	The energetic costs of synthesising potential fecundity.	kJ
Migrating	A Boolean switch that prevents super-individuals "moving locally" if true.	True or 0 if False
MR	Metabolic rate equals SMR x2 (Peters, 1986) and is based on size and SST.	kJ
Number	Number of individual fish the super-individual represents.	Number
Potential-fecundity	The maximum potential number of eggs that can be produced based on size of fish.	Number
R	Movement repeats. Steps per day. This limits how far agents travel in one direction before turning.	Number
Realised-fecundity	Number of eggs that are produced from energy available.	Number
Spawn-count	Time in spawning ground.	days
Spawn-trigger	Migration switch.	0 = feeding; 1 = spawning
Speed	Swimming speed.	Patches per day
Standard-L	Standard length, the measure of head to base of tail fork.	cm

Std-mass	standard mass = mass as calculated from length using aL^b (see Table 5-2).	kg
Structural-mass	Structural mass is total mass minus lipid energy reserve and gonad mass.	kg
Total-mass	Total mass is the total of; structural, lipid energy reserve and gonad mass.	kg
VIIat	Affinity to division VIIa. *	True or 0 for no affinity
VIIdt	Affinity to division VIId. *	True or 0 for no affinity
VIIet	Affinity to division VIIe. *	True or 0 for no affinity
VIIfgt	Affinity to division VIIfg. *	True or 0 for no affinity
W	Body mass.	kg
Patches		
ArrS	Arrhenius multiplier calculated with specific parameters when calculating swimming speed.	
PHY	Phytoplankton density value from remote sensing.	gm^2
Processed	For use in set up patches as a check that the distance from target patch is only calculated once.	True or 0
Spawn-patches	Marker for spawning patches, depending on time of year and SST.	True or 0 (dynamic)
SST	Sea surface temperature from remote sensing.	°C

*Affinity is the assigned ICES division that agents are given.

5.3 Process overview and scheduling

The model proceeds in daily time steps, resetting ticks every 365 days. The following sub models are executed in the order they are presented below. Within each sub model, super-individuals and patches are processed in a random order as there are no interactions among agents (an overview can be seen in Fig. 5-2).

Sea check: Make sure super-individuals are in the sea, if not they move back to the sea and then continue with processes.

Update-patches: New SST and PHY data are assigned to patches, the Arrhenius rates for each patch recalculated (required to calculate speed), and offshore patches update their spawning patch status. Note this sub model is ran every tick but remote sensing data is only updated every 8 days due to limitations of the data

Calculate-catch: The catch taken by fishing fleets is calculated for each sea patch.

Natural mortality: the number of fish in each individual is discounted by its natural mortality rate. Any super-individuals reaching the age of 30 or with less than one individual fish continue to represent a decimal number of fish.

Calc ingestion *larvae, juvenile and mature sea bass only*: Calculates the energy ingested from mass, energy available, temperature and density dependence.

Calc assimilation *larvae, juvenile and mature sea bass only*: Calculates the energy assimilated and available for life processes.

Calc maintenance *larvae, juvenile and mature sea bass only*: The energy used for maintenance, adjusted by Arrhenius. Paid for either from assimilated energy or, if insufficient available food, paid from reserves.

Calc-growth: The maximum daily growth rate is calculated. Agents under 70 days have a constant maximum growth rate (see TRACE section 5.8.3) for fish older than 70 days we use a von Bertalanffy curve. The maximum daily growth rate depends on fish length and SST.

Grow: Each fish increases its length as a fraction of the maximum growth increment, calculated above, dependent on SST and available energy.

Calc-total-mass: The mass of each fish is calculated from its length, with the addition of the mass of energy reserves and gonad mass.

Calculate-speed: The swimming speed of each fish is calculated from its length and SST of the patch.

Calculate-r: The number of 'steps' taken by each fish is calculated from its swimming speed.

Transform: If a super-individual meets the criteria (sufficient length; see Fig. 5-2) then it transforms to the next life stage. The life stages are egg; yolk-sac larvae; larvae; juvenile; and mature. When juveniles graduate to mature sea bass (Length > 42 cm) they set their coastal feeding ground affinity as the ICES division in which they are in at the time of ticking over this length requirement (this could be a different division to the original ICES division target they would have drifted towards when they were in pelagic stages, see TRACE 5.8.7). Note that at the end of the first spawning migration there is an opportunity to change ICES division affinity which is altered with a probability defined by the site-fidelity slider on the model interface (GUI).

Fishing-mortality: The number of individuals each super individual represents is discounted by fishing mortality rates from the commercial offshore, commercial inshore and recreational fleets (data obtained from ICES stock assessment 2020).

Spawn-migration: If (ticks >= 274) or (ticks < 152) each mature sea bass with spawn-trigger equal to 1 moves towards offshore spawning grounds. This action can only be executed between ticks 274–151 corresponding to the months October–May.

Feeding-migration: Each mature sea bass with spawn-trigger equal to 0 moves towards or within its assigned coastal feeding ground.

Local-movement: Each juvenile sea bass moves randomly within coastal patches. Juveniles less than 32cm (not yet classed as "adolescent") are further constrained to nursery coastal patches.

Drift eggs: Each egg moves one patch closer to its assigned coastal feeding ground.

Drift_ys-larvae: Each yolk-sac larva moves one patch closer to its assigned coastal feeding ground.

Drift_larvae: Each larva moves one patch closer to its assigned coastal feeding ground.

Age: Agents age a day each tick. The cohort age is increased by one at the end of tick 365.

Spawn: On the 60th tick every year (17th of March) 10 mature sea bass super-individuals spawn, producing as many eggs as determined by total realised fecundity of the whole spawning stock (the number of eggs is based on cumulative available energy reserves and fish size, see TRACE section 5.8.7).

Calc-egg-development: Eggs get one day older per tick until they hatch in correspondence with the embryo-duration.

Temperature effects

Throughout the model, temperature affects life processes via its effect on energy budgets. This is accomplished using the Arrhenius function. Biological rates increase exponentially with absolute temperature according to an Arrhenius function, A_T, as:

$$A_T = e^{-\left(\left[\frac{E_a}{boltz}\right]\left[\frac{1}{T} - \frac{1}{Tref}\right]\right)}$$

(3)

where E_a is activation energy, *boltz* is the Boltzmann constant, T is absolute temperature and *Tref* is a reference temperature for the energy budget. The parameters used are different for calculating speed (see TRACE section 5.7 *calc speed*), where we use a specific activation energy (*EaS* = 0.1903656) and reference temperature (*TrefS* = 6°C) (see TRACE section 5.8.4). For ease of understanding we write out the Arrhenius function where used throughout the document.
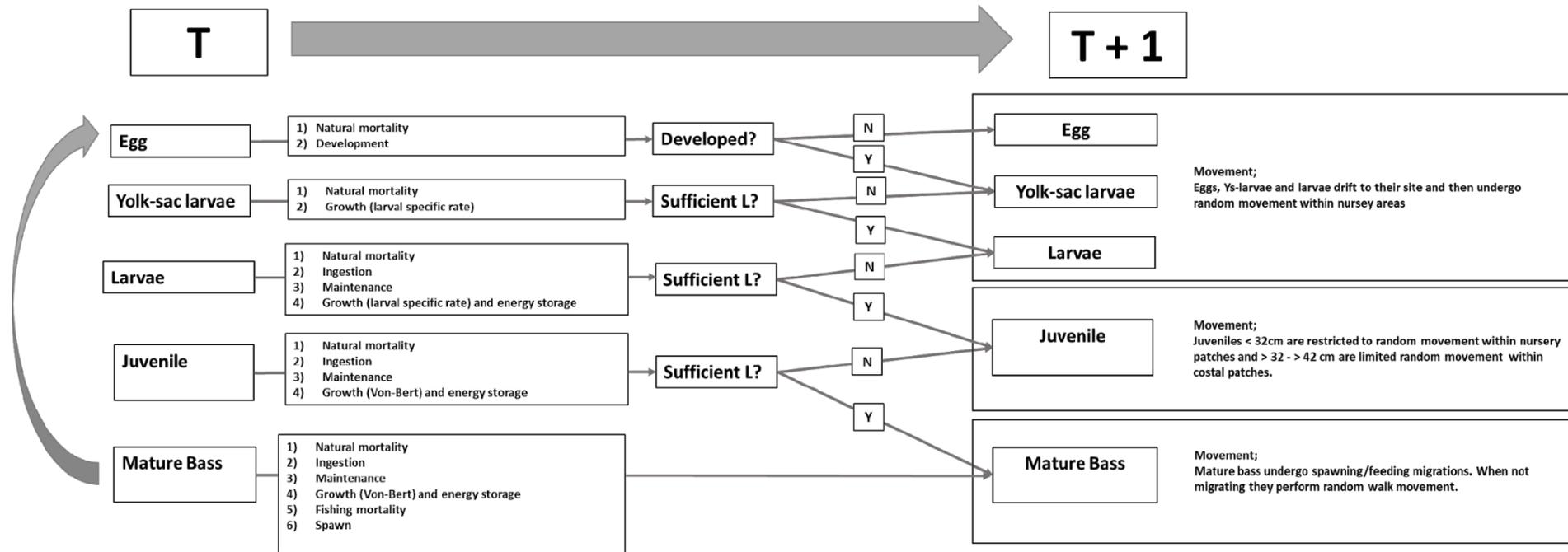
Figure 5-2. Model overview; Each life stage (egg, yolk-sac larvae, larvae, juvenile and mature sea bass) is outlined with the sub models applicable to each stage are presented in the order of model execution. To transform to the next life stage, eggs develop after a specified time and from then on transformation is length based. Each life stage gives details about their movement sub models. After spawning the egg super-individuals then start the processes from the beginning again.

5.4 Design concepts

Basic principles: We aim to model the population dynamics and simulate spatial distribution of European sea bass in ICES divisions' 4.b–c, 7.a and 7.d–h. Life processes are driven by energy budget equations driven by sea surface temperature (SST) and phytoplankton density (PHY) remote sensing inputs to give emergent population dynamics. The spatial aspect of the model is not fully emergent and relies on assumptions relating to past observations. The visualisation of the large-scale migrations known to be undertaken by sea bass each year is not possible with a population model (for example the stock synthesis 3 model used for sea bass stock assessment) but is essential for simulating the spatial distribution of sea bass.

Emergence: The model's primary result – population dynamics – emerge from; the numbers at age 0, growth and mortality of sea bass.

Growth follows a fixed relationship adjusted by the effects of temperature and energy available.

Numbers at age 0 is dependent on energy ingested that is stored and then used to produce eggs as well as the environmental conditions that eggs and larvae experience.

Migrating adults follow a set of empirical rules triggered by an environmental cue while non-migrating adults and juvenile sea bass move randomly within an area type.

Adaptation: The movement and migratory behaviour of mature fish is an adaptive trait. The departure time and arrival in offshore spawning grounds is influenced by SST, while cessation of spawning is imposed after a fixed number of days.

All processes that are influenced by SST and energy availability are adaptive including ingestion, growth, spawning and numbers at age 0.

As the factors affecting navigation are otherwise unknown, fish follow a set of empirical rules that reproduce observed migratory patterns. Super individuals may choose to switch assigned feeding area after spawning; however, because the mechanisms of site fidelity are unknown, new allocations are assigned randomly with fixed probability defined by the *site-fidelity* slider on the model interface. Site fidelity was fixed at 100% in the current study.

Sensing: Individuals are assumed to know their length, location and the type of patch currently occupied so that they can apply the correct migratory rules. Mature sea bass are assumed to sense temperature so they may successfully arrive in suitable spawning grounds. The model does not include *interaction* among sea bass or environmental patches.

Stochasticity: The main uses of stochasticity are to: (1) distribute and age super-individuals when they enter the model at initialisation; (2) simulate the movement and site fidelity of sea bass; (3) assign super-individuals to ICES division at initialisation; and (4) the random component of the movement sub models.

Collectives: Beyond the distinction of the different life stages (egg, yolk-sac larvae, larvae, juvenile or mature sea bass) there is no social grouping between the super-individuals. Using super-individuals to represent multiple individual fish could be representative of shoaling behaviour (e.g., Shin & Cury, 2001) although its introduction was for computational feasibility and reducing run times.

Observation: For model testing, the spatial distribution and migration patterns of the super-individuals were observed. The population variables spawning stock biomass (SSB), numbers at age and mass at age are recorded on the 1st of January (tick 1) and compared to ICES stock assessment values.

5.5 Initialisation

The model starts with a spin-up initiated in 1985 and then the model begins on 1st of January 2004 and continues till 2015. During the 19 years of spin up, we use the 2004 SST and PHY remote sensing data and read in yearly numbers-at-age data from the ICES stock assessment 2020. The spin up allows individual energy rates to settle before running the model for the years used for calibration and assessment of fits (2004-2015). The relevant SST and PHY data is loaded and assigned to patches within a shapefile of the UK and surrounding countries (Figs.5-1A and 5-1B). Patches with an SST value within the stock area (ICES divisions' 4.b–c, 7.a and 7.d–h) are set as sea patches. ICES rectangles (sets of four sea patches) intersecting land and patches (14, 34), (18, 24), (20, 20), and (16, 6) are set as coastal patches (green patches in Figs. 5-1A and 5-1B), and all other sea patches are set as offshore (blue patches see Fig. 5-1A). Coastal patches whose midpoint intersect land are assumed mostly land and set as non-sea patches, except for patches (28, 21), (15, 10), (13, 10) and (5, 22). Individual coastal patches intersecting land south of 54°N (y coordinate < 24) are assigned as nursery patches. The patches that eggs, ys-larvae and larvae drift towards are termed Target patches (shown as red patches in Fig. 5-1 and used for ease of coding). We calculate how far away each patch is from each target patch for use in sub models Drift_eggs/ys_larvae/larvae (see TRACE 5.7 for details of sub models). All coastal patches are assigned to an ICES division (4.b, 4.c, 7.a, 7.d, 7.e or 7.fg) and all offshore patches south of 54° N to a spawning region (IS – Irish Sea, CS – Celtic Sea, C – Channel or NS – North Sea). Both sea surface temperature (SST) and phytoplankton concentration (PHY) cannot be shown simultaneously in the model interface so for demonstration purposes Fig.5-1B shows offshore patches as orange with dark to light representing increasing PHY.

Numbers-at-age data from the ICES stock assessment 2020 are used in spin up. 10 super-individuals are created per cohort, with the number of fish represented by an individual taken as the stock assessment numbers-at-age estimated for the year divided by 10. Juvenile super-individuals are distributed randomly amongst nursery patches if less than four years of age, and amongst all coastal patches if four to six years of age. Mature super-individuals are distributed randomly in pre-spawning areas (ICES divisions' 7.e–g) with *spawn-trigger* set equal to 1. Each mature individual is assigned a random ICES division (4.b, 4.c, 7.a, 7.d, 7.e, or 7.fg) for which it has an affinity to feed.

Initial *cohort* age of super-individuals is taken as the whole number stock assessment age, but actual *age* is incremented by a random number between 222 and 314 days to reflect mid-year spawning. From that *length* is calculated from the von Bertalanffy growth equation:

$$L_t = L_\infty \left(1 - e^{-K[t-t_0]}\right)$$

where L_∞ is the asymptotic length, K the growth rate coefficient and t_0 the hypothetical age at length 0 (Table 5-2). Note these calculations are at initialisation only, once running there are different processes for deciding ICES division affinity and growth of larval stages which use a different growth model (see TRACE sections 5.7 and 5.8.7).

Remaining energy budget variables starting values calculated and initialised as follows;

Calculate structural mass;

Structural-mass = a * (L ^ (b))

where *L* (cm) is the length and *a* and *b* are Length-mass coefficient values taken from the ICES stock assessment (Table 5-2) (parameter *a* is adjusted to account for the original values being used to calculate total mass, for details see TRACE section 5.8.3).

Calculate maximum energy reserve;

energy-reserve-max = ((Structural-mass * 0.01) * El)

where *El* is the energy content of lipid (Table 5-2).

Calculate energy reserve;

energy-reserve = (energy-reserve-max * 0.5)

Calculate total mass;

Total-mass = (structural-mass + (energy-reserve / El))

where *El* is the energy content of lipid (Table 5-2).

Calculate maintenance (the energy put aside to pay for maintenance during spawning);

Maintenance-energy = (energy-reserve * 0.1)

Calculate potential fecundity (number of eggs that could theoretically be produced by a fish that size);

Potential-fecundity = (std-mass / 1000) * (eggs_per_bass)

Calculate potential fecundity (the energy required to produce the potential fecundity);

Max-R = (potential-fecundity * egg-mass * (Ef + Fs))

where *Ef* is the energy content of flesh and *Fs* is the energy to synthesise flesh (Table 5-2).

Calculate-speed; See sub model Calc-speed.

Calculate-r; See sub model calc-r.

Table 5-2. Parameter values used in the model.

Parameter	Description	Value	Reference
A	Aspect ratio of the caudal fin.	1.76	(Froese and Pauly, 2017)
a	Length-mass coefficient (for details see TRACE Section 5.8.3).	1.296×10^{-5} * 0.95	(Pickett and Pawson, 1994; ICES, 2012a)
b	Length mass scaling exponent.	2.969	(ICES, 2012a)
A0	Normalizing constant for relationship between Metabolic rate and fish size.	0.1227808	(Claireaux,2006; Jourdan-Pineau *et al.*, 2010; Luna-Acosta *et al.*, 2011; Zupa *et al.*, 2015; Peixoto *et al.*, 2016)

AE	**Efficiency of energy from phytoplankton to fish.**	**1.64×10^{-3}**	*
boltz	Boltzmann constant.	$8.62\ 10 \times 10^{-5}$ eV K^{-1}	
Cmax	Max ingestion.	0.54 grams per gram of fish	(Lanari, D'Agaro and Ballestrazzi, 2002)
Ea	Activation energy.	0.5 eV	(Gillooly *et al.*, 2006)
EaS	Activation energy for speed Arrhenius function.	3.05×10^{-20} J	(Claireaux, 2006)
Ef	Energy content of flesh.	7 kJ g^{-1}	(Peters, 1986)
egg-mass	Sea bass egg mass.	0.96×10^{-3} g	(Cerdá *et al.*, 1994)
Eggs_per_bass	Potential egg production per gram of sea bass.	375,000	(Pickett and Pawson, 1994) (reference states between 1/4 and 1/2 a million eggs per kg of sea bass)
El	Energy content of lipid.	39.3 kJ g^{-1}	(Schmidt-Nielsen, 2013)
ep	Energy content of phytoplankton.	6.02 kJ g^{-1}	(Annis *et al.*, 2011)
Fs	Energy to synthesise flesh.	3.6 kJ g^{-1}	(Sibly and Calow, 1986; Sibly *et al.*, 2013)
GL	Larval stages growth coefficient.	0.02485 cm d^{-1}	Jennings, Jennings and Pawson, 1992; Regner and Dulčić, 1994)
H	**Half saturation constant.**	**4.87×10^{-1}**	*
I	**Importance of density on ingestion.**	**$5.14 \times 10^{+13}$**	*
k	Annual growth rate coefficient.	0.096699	(ICES, 2012a)
L$^{\infty}$	Asymptotic length.	84.55 cm	(ICES, 2012a)
Ls	Energy to synthesise lipid.	14.7 kJ	(Pullar and Webster, 1977)
AM	**Natural mortality rate juvenile and mature sea bass.**	**4.71×10^{-4}**	*
PM	**Natural mortality rate eggs, ys-larvae and larvae.**	**8.01×10^{-2}**	*

ncohort	Number in each super-individual.	10	
T$_0$	Age at length 0.	-0.73 years	(ICES, 2012a)
TrefS	Reference temperature at which swimming speed at the length used in the paper coincides with that from the model.	6 °C	(Claireaux, 2006)
Tref	Reference temperature for the energy budget.	285.15 K (12°C)	

*parameters in bold are calibrated with ABC see TRACE section 5.9 for calibration details.

5.6 Input data

Numbers-at-age, used to initialise the model and introduce recruits at setup come from the 2020 stock assessment. Environmental inputs comprise dynamic maps of chlorophyll-a concentration and SST. The satellite remote-sensing data were taken from NASA's ocean colour portal in NetCDF format (NASA, 2017; NASA OBPG, 2017). Processing of the satellite data included: 1) cropping to the model extent (Fig. 5-1); 2) estimating missing values using linear temporal interpolation (e.g., NAs for a cell in one time period become the average of the last prior period with a value, and next subsequent period with a value); 3) fill in any further gaps with the annual average; 4) re-sampling the spatial resolution from 9km x 9km to 30km x 30km; and 5) convert chlorophyll to plankton biomass; Chlorophyll-a was converted to carbon mass using a C:Chl-a ratio of 75. Then, a wet mass:C ratio of 10 was used to obtain phytoplankton biomass (g wet mass m^{-2}) (Link *et al.*, 2006). This gives phytoplankton biomass (g m^{-2}) = chl-a (mg m^{-2}) x 0.75 and 6) re-project on to lambert azimuthal equal area projection.

5.7 Sub models

The following sections provide full detail on how model processes are simulated. The equations in Netlogo code are shown in blue.

Seacheck: Super-individuals check if the patch they are on is sea if not then move to the closest sea patch within a radius of 2 patches before continuing processes.

Update-patches: Sea patches are assigned new SST data each tick. Between ticks 32–151 any offshore patches south of 54°N with a SST value between 9–15°C are set as *spawn-patches*.

Natural-mortality: The number of sea bass within each individual is discounted with a mortality constant.

Eggs, yolk-sac larvae and larvae have a greater mortality rate than older life stages. The quicker they grow through to a juvenile sea bass the higher the number of age 0 for that year. The growth of these is influenced by energy available [PHY] and sea surface temperature [SST].

We update the number of individuals each super-individual represents each tick with;

number * exp (- PM)

Here *number* is the number of eggs, egg-sac larvae or larvae that the super-individual represents. *PM* is the daily natural mortality rate for these young life stages. The actual value of *PM* is unknown so is calibrated with ABC see TRACE section 5.8.9.

Juvenile and adult sea bass experience less mortality than egg, yolk-sac larvae and larvae life stages and we update the number of super-individuals each super-individual represents each tick with;

number * exp (- AM)

Here *number* is the number of individual fish the super individual represents and *AM* is the adult daily natural mortality rate calibrated with ABC see TRACE section 5.9 for details. Finally, in addition to daily natural mortality, any super-individuals reaching the age of 30 are removed from the simulation. If the super-individual represents less than one fish then they become decimal. This is required to keep the number of super-individuals per cohort constant and avoid any erroneous knock-on distribution bias whilst making sure there is not misleading excess biomass.

Calculate-catch: Each patch calculates the catch, C_t, in tonnes taken by commercial and recreational fishing fleets during that time-step and adds it to a running total, resetting annually.

$$C_t = C_{t+1} + \frac{1}{1000} \sum_{a=0}^{30} \quad w \left(\frac{\sum_f \quad F_{a,f}}{\sum_f \quad F_{a,f} + M} \right) N_t \left(1 - e^{-(M + \sum_f \quad F_{a,f})} \right)$$

where Nt is the number of fish occupying the patch in time step t, Fa,f is the fishing mortality on cohort age; a, by fishing fleets; f (f = commercial inshore and recreational if the patch is coastal and commercial offshore if the patch is offshore; see TRACE section 5.8.9), M is natural mortality (see TRACE 5.7 *Natural-mortality*) and w is the mass of individual fish (see TRACE 5.7 *calc total mass*).

Fishing-mortality: The number of sea bass within each individual is discounted exponentially by fishing mortality *F*, partitioned and applied daily. Partial fishing mortality estimates by age and metier derived from the ICES stock assessment outputs (ICES, 2018c) were aggregated to give fishing mortality rates for three broad fishing fleets (see Trace section 5.8.9): commercial inshore (*FCi*), commercial offshore (*FCo*) and recreational (*FRi*). Fishing mortality is distributed by area type such that the commercial inshore and recreational fishing mortality rates are applied only to fish occupying coastal patches and the commercial offshore fishing mortality rate is applied only to fish occupying offshore patches. The annual commercial fishing mortality rates were raised inversely proportional to the amount of days spent fishing, where the commercial offshore fleet is assumed to operate for 151 days between November and April (ICES, 2012a) and the commercial inshore fleet for 214 days during the remainder of the year (giving raising factors ~2.4 and ~1.7 respectively). Recreational fishing is assumed to occur all year and hence no raising factor is applied. The total *F* applied to super-individuals is then the sum of the fishing mortality from relevant fleets.

Catches taken by commercial fleets (commercial inshore and offshore) are summed across. Once the specified quota has been reached (if set), fishing mortality is switched off until the running total is reset according to the time-scale specified.

Minimum conservation reference sizes (MCRS) for the commercial and recreational fleets can be specified via the com-net-hole-size and angler-min-size sliders on the models GUI. If set > 0 fishing mortality from the commercial and recreational fleets will apply only to the fish exceeding the specified lengths, which can be set up to 60cm / 80cm for the commercial / recreational fleets respectively. It is important to mention that any post-release/discard mortality is not included in the model.

Calc ingestion: The first life stages (Eggs and egg-sac larvae) do not feed until they transform into larvae. We calculate an ingestion rate for each life stage that is based on the energy available, the size of the larvae/fish and SST.

For larvae ingestion:

Func-response = (PHY / (H + PHY))

ifelse (any? other turtles-here)

[ingestion-rate = (Cmax * exp((- Ea / Boltz) * ((1 / (SST + 273.15)) - (1 / Tref))) * func-response * (total-mass ^ (2 / 3))) * (I * (1 / ((mass_near_me ^ 2 / 3)))))]

[ingestion-rate = (Cmax * exp((- Ea / Boltz) * ((1 / (SST + 273.15)) - (1 / Tref))) * func-response * (total-mass ^ (2 / 3))) * (I * (1 / ((total-mass ^ 2 / 3) * number))))]

where *PHY* is the energy value of the patch, *H* is the half saturation constant, *Cmax* is the max consumption of food in relation to body size, *I* is the importance of density, *mass_near_me* is the sum of biomass of all larvae, juvenile and mature sea bass in the same patch. The remainder of the equation components relate to the Arrhenius function (Table 5-2).

For the older life stages, juvenile and adult ingestion was previously restricted to only feeding over 9°C SST, but this was subsequently relaxed during the process of bug testing and manually fitting parameters. Previous to this relaxation many fish were starving to death. We assume it unlikely a starving fish will refuse to eat if food was available, even in cold water. Instead we reduce the feeding temperature threshold ensuring fish will feed until SST is less than 5°C.

Func-response = (PHY / (H + PHY))

ifelse (any? other turtles-here)

[ingestion-rate = (Cmax * exp((- Ea / Boltz) * ((1 / (SST + 273.15)) - (1 / Tref))) * func-response * (total-mass ^ (2 / 3))) * (I * (1 / ((mass_near_me ^ 2 / 3)))))]

[ingestion-rate = (Cmax * exp((- Ea / Boltz) * ((1 / (SST + 273.15)) - (1 / Tref))) * func-response * (total-mass ^ (2 / 3))) * (I * (1 / ((total-mass ^ 2 / 3) * number))))]

where *PHY* is the energy value of the patch, *H* is the half saturation constant, *Cmax* is the max consumption of food in relation to body size, *I* is the importance of density *mass_near_me* is sum of biomass of all larvae, juvenile and mature sea bass in the same patch. The remainder of the equation components relate to the Arrhenius function (Table 5-2).

Calc assimilation: We calculate the proportion of ingested energy available for energy budget processes (e.g., growth, maintenance and reproduction);

Assimilation-energy = ((Ingestion-rate * ep) * AE)

Ingestion rate is calculated as above and influenced by available food (PHY), fish size, SST and the density of agents competing for the same food. *ep* is the energy in phytoplankton and *absorbed-energy* is the percentage of ingested energy that becomes available to the budget. *AE* is the product of assimilation efficiency (i.e., the proportion of energy that is absorbed from prey) and trophic delay (i.e., how long/how much energy from a phytoplankton bloom makes its way through the trophic levels to sea bass prey). For more details see TRACE section 5.10.3.

Calc maintenance: We calculate the field metabolic rate as twice the standard metabolic rate (Peters, 1986) with;

MR = (A0 * (total-mass ^ (0.75)) * 2) * exp ((- Ea / boltz) * ((1 / (SST + 273.15)) - (1 / Tref)))

where *Ao* is a metabolic rate normalisation. Maintenance energy is influenced by both mass and SST with Arrhenius (Table 5-2).

Once we have calculated the cost of maintenance we check if it can be covered by the assimilated energy. If assimilated energy is sufficient to cover maintenance, we subtract this cost from the assimilated energy. If there is not enough assimilated energy (e.g., reduced feeding available in the winter) then energy reserves are added to assimilated energy and then metabolic costs are taken from this:

If there is sufficient assimilated energy to cover metabolic rate then;

Assimilation-energy = assimilation-energy - MR

Otherwise if there is insufficient assimilated energy to cover metabolic rate then pay out of reserves;

Energy-reserve = (energy-reserve + assimilation-energy) – MR

We then set assimilation energy to 0 as it has all been used.

Note that here we check that this does not create a negative energy reserve, if it does we force the individual set energy reserves as 0.

Calc total mass: The structural mass (without reserves and gonad mass) of each fish is calculated from its length following the standard allometric equation:

Structural-mass = a L ^b

Where *a* and *b* are Length-mass coefficient values were taken from the ICES stock assessment (Table 5-2). Note ICES *a* and *b* coefficients are for calculating total mass (which includes energy reserves mass and gonad mass), to adjust this we adjust parameter *a*, reducing it by 5% for details see TRACE Section 5.8.3.

To calculate the total mass (sum of structural, fat and gonad mass) we check if there are energy reserves then calculate the total mass of all reserves and gonads. If energy reserve is greater than 0 then:

Total-mass = structural-mass + (energy-reserve / El) + gonad-mass

where *El* is the energy content of lipid (Table 5-2).

However, if there are no energy reserves then:

Total-mass = structural-mass + gonad-mass

Calc growth: Calculate max daily growth rate. Agents under 70 days have a constant maximum growth rate (see TRACE section 5.8.3):

Max-growth-rate = GL * exp((- Ea / boltz) * ((1 / (SST + 273.15)) - (1 / Tref)))

where *GL* = 0.02485 and is the slope coefficient of a regression of larval length on age (see TRACE section 5.8.3). The remainder of the equation components relate to the Arrhenius function (Table 5-2).

Fish older than 70 days year are assumed to follow a von Bertalanffy growth curve:

Max-growth-rate = (linf - L) * (1 - exp(- k / 365)) * exp((- Ea / boltz) * ((1 / (SST + 273.15)) - (1 / Tref)))

where, *linf* is the asymptotic length of sea bass, *L* is fish length and *k* is the annual growth constant, divided by 365 to get daily growth. The remainder of the equation components account for the effects of temperature using the Arrhenius function (Table 5-2).

Now the max daily growth increment has been calculated we can apply this to agents.

We calculate what the potential new fish length could be and how much this will cost in energy.

Possible-L = (L + max-growth-rate)

Growth-costs = ((((a * (possible-L ^ b)) - structural-mass)) * (Fs + Ef))

where *L* is fish length, *a* and *b* are Length-mass coefficient values, *Fs* is the energy content of flesh and *Ef* the costs of synthesising flesh (Table 5-2).

Eggs; eggs do not grow, instead they develop (described later) and then transform into yolk-sac larvae.

Ys-larvae; yolk-sac larvae do not ingest energy and are nourished by the yolk sac thus are assumed to have maximum energy available to grow maximally;

Growth-rate = max-growth-rate

L = L + max-growth-rate

Structural-mass = a * (L ^ (b))

Total-mass = structural-mass

Larvae; once the egg-sac larvae have transformed to larvae they begin to ingest energy. We first check if there is adequate assimilated energy to grow maximally and update length accordingly (note this is a different measure of length specifically for calculating swimming speed). From the new length the new structural mass is calculated and because larvae do not store lipid their structural mass is equal to their total mass.

If larvae are assimilating enough energy then they grow maximally:

L = L + max-growth-rate

Structural-mass = a * (L ^ b)

Total-mass = structural-mass

Assimilation-energy = assimilation-energy - growth-costs

If larvae don't assimilate enough energy they then grow sub-maximally:

Growth-rate = (max-growth-rate / growth-costs) * assimilation-energy

L= L + growth-rate

Structural-mass = a * (L ^ (b))

Assimilation-energy = 0

Juvenile and mature sea bass have to ingest energy so their growth will depend on the energy they have available.

If assimilated energy on a particular day is enough to cover growth then they will grow maximally. Juvenile and mature sea bass allocate energy equally to growth in length and to fat reserves;

if (Assimilation-energy * 0.5) >= growth-costs

After checking available energy, sea bass with enough energy grow maximally;

L = L + max-growth-rate

Structural-mass = a * (L ^b)

Assimilation-energy = assimilation-energy - growth-costs

Calc-storage

If the sea bass don't have enough energy they grow at a suboptimal growth rate.

Growth-rate = (max-growth-rate / growth-costs) * (assimilation-energy * 0.5)

L = L + growth-rate

Structural-mass = a * (L ^ b)

Assimilation-energy = assimilation-energy * 0.5

Calc-storage

where *L* is length and *a*, *b* are Length-mass coefficient values were taken from the ICES stock assessment (Table 5-2). For both scenarios total mass is calculated later, after they have stored lipid a procedure *calc-storage* is called that converts remaining energy to lipid stores and accounts for the cost of synthesis.

Calc speed: The sustained swimming speed of each fish is calculated from its length and adjusted by the Arrhenius factor for the occupied patch to account for the effects of temperature on the chemical processes that contribute to swimming speed:

$$S = (10^{-0.828+0.6196(L_t)+0.3478(A)}) * K_s$$

$$k_s = e^{\frac{EaS}{K}\left(\frac{1}{T}-\frac{1}{TrefS}\right)}$$

where A is the aspect ratio of the caudal fin (Froese & Pauly, 2017; Table 5-2). Note that the Arrhenius parameters are different for speed specific Arrhenius equations see table 5-2, and TRACE section 5.7 *update patches*. Values in kilometres per hour were converted to patches per day assuming 12 swimming hours spent per day in patches of 30 x 30 km.

Calculate-r: The speed of each fish is divided by a movement repeat variable r with fish moving r times per day. r is chosen as the smallest integer such that fish travel no more than 0.25 patches before changing direction. This allows fish to change direction whilst moving the correct distance and was introduced to reduce overlap with land.

Transform: If a super-individual meets the criteria (sufficient length [see Fig. 5-2]) then it will transform to the next life stage and the necessary energy budget variables values will be calculated.

Eggs into yolk-sac larvae; after a development period of 5 days (a study by a Beraud et al., 2018 gave a range of 3 - 7.5 days):

Std-mass = 0.001

Energy-reserve-max = 0

Energy-reserve = energy-reserve-max

Larval-production = larval - production + number

Yolk-sac larvae into larvae: larvae do not store energy, they feed continuously to grow:

L >= 0.35 (study by Beraud et al., 2018 gives a range of 1.5 - 5.5mm)

structural-mass = a * (L ^ b)

energy-reserve-max ((structural-mass * 0.01) * El)

Energy-reserve = energy-reserve-max

Larvae into juvenile sea bass:

L >= 1.425 (study by Beraud et al., 2018 gives a range of 10.5-18mm)

structural-mass = a * L ^ (b)

energy-reserve-max ((structural-mass * 0.01) * El)

Energy-reserve = energy-reserve-max * 0.5

Juvenile sea bass into mature sea bass:

L >= 42

Male and female sea bass mature at different rates which vary regionally within the stock (Pickett and Pawson, 1994). However for simplicity and to ensure the model remains precautionary with outputs of SSB we use the larger but generally accepted maturity length as 42cm for all adult sea bass (Pickett and Pawson, 1994), note 42cm is also the minimum landing size for sea bass in northern stock legislation since 2015 [ICES, 2021]). When juveniles graduate to mature sea bass (Length > 42 cm) they set their coastal feeding ground affinity as the ICES division in which they are in at the time of ticking over this length requirement (this could be a different division to the original ICES division target they would have drifted towards when they were in pelagic stages, see TRACE section 5.8.7. At the end of the first spawning migration there is an opportunity to change ICES division affinity which is altered with a probability defined by the site-fidelity slider on the GUI.

Spawn-migration: This sub model is executed between ticks 274–151 corresponding to the months October–May. Between ticks 274–90, corresponding to the months October–March, any mature super-individuals not currently performing a spawning migration (spawn-trigger = 0) on a patch that either neighbours a spawning patch or is less than 9°C switches its spawning trigger to 1 (Fig. 5-3). All super-individuals with spawn-trigger equal to 1 take r steps of distance S/r (see TRACE section 5.7 *calculate-speed* and *calculate-r*) according to the hierarchy presented in Fig. 5-4.

Once a mature individual reaches a spawning patch its spawn-count increments by 1 each tick. When the spawn counter reaches 60 (indicating the agent has spent 60 ticks/days cumulatively on a spawning patch) or the end of the spawning period is reached (tick 152 corresponding to the 1st of June) both spawning trigger and counter are set to zero, and the individual no longer executes spawn-migration but defaults to feeding-migration (see TRACE section 5.7 *feeding-migration*). Before ending a spawning migration, each individual changes its affinity to a new coastal feeding area with fixed probability set by the site-fidelity slider on the model's interface. Each new assignment is

random with equal probability between the six coastal feeding areas. Site fidelity was fixed at 100% in the reported results.
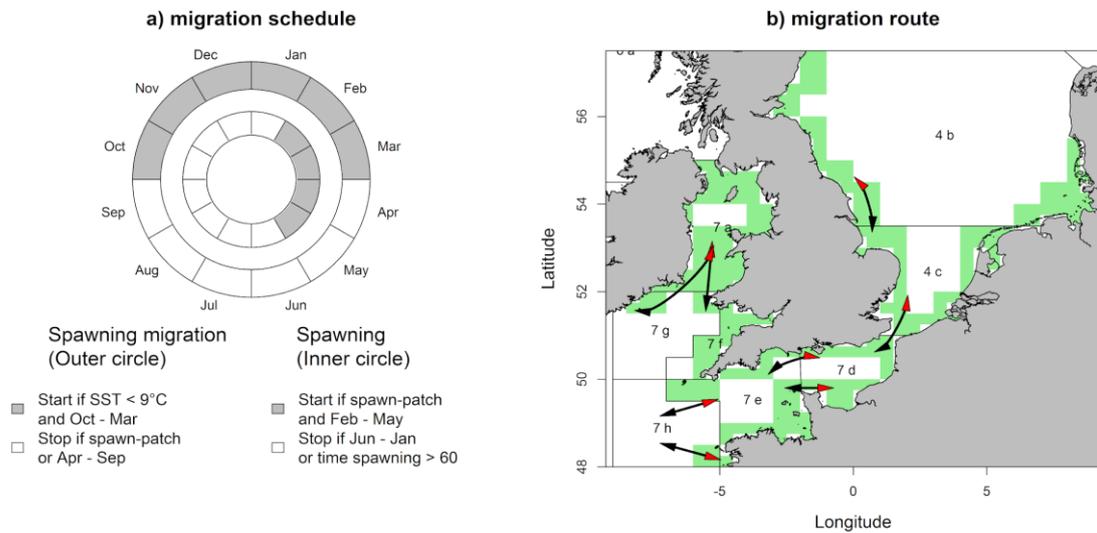
Figure 5-3. (a) Schedule for spawning migrations. Outer circle: migration to (pre-) spawning areas is triggered by sea surface temperature and can take place between October and March. Inner circle: spawning takes place within offshore spawning patches in February–May. b) Migrations of mature super-individuals follow the hypotheses of Pawson et al. (1987, 2007). Arrows show movement around the coast to and from the Channel and Celtic Sea with black arrow heads representing the spawning migration and red arrow heads the feeding migration.
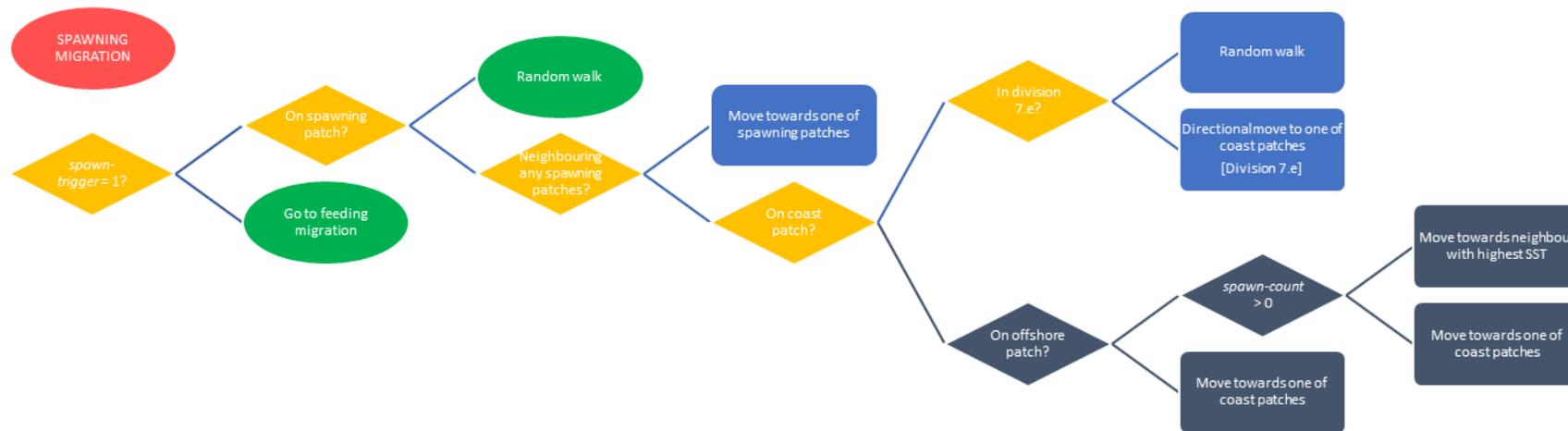
Figure 5-4. Decision hierarchy for the spawning migration. Diamonds represent decisions, green circles terminators and rectangles processes. Upward links are followed when the answer to a decision is 'yes' and downward links when the answer is 'no'. The hierarchy moves mature super-individuals towards offshore spawning patches where they are assumed to have reached their destination and move randomly (green 'Random walk' terminator). Blue processes show the action to take for a repeat in the current time-step, after which the hierarchy is followed from the beginning for the next repeat or time-step. Division 7.e. is a reported pre-spawning area; hence super-individuals take directed steps towards 7.e via coast patches, and then move randomly until spawning patches start to appear (see TRACE section 5.7 *update-patches*). The grey nodes represent troubleshooting decisions and actions. Given that migrations take place along the coast, any occupied offshore patch should be a spawning patch. If it is not then either (1) the offshore patch lost its spawning status during a update-patches, in which case the individual searches for a new spawning patch by moving to the offshore neighbour with the highest SST; or (2) the individual moved off the coast (either onto an offshore patch or land), as a consequence of allowing super-individuals to travel across square patches at any angle. In either of these two cases the individual is moved towards a neighbouring coastal patch.
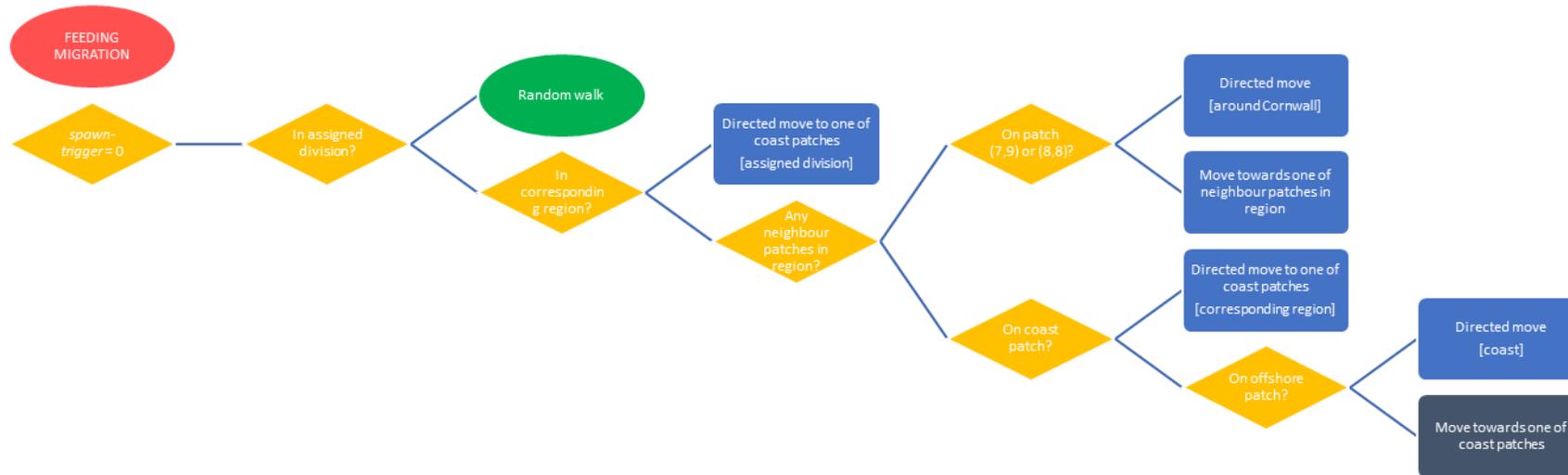
Figure 5-5. Decision hierarchy for the feeding migration. Diamonds represent decisions, green circles terminators and rectangles processes. Upward links are followed when the answer to a decision is 'yes' and downward links when the answer is 'no'. The hierarchy moves mature individuals towards their assigned feeding divisions where they are assumed to have reached their destination and move randomly (green 'Random walk' terminator). Blue processes show the action to take for a repeat in the current time-step, after which the hierarchy is followed from the beginning for the next repeat or time-step. The square brackets indicate the immediate target which, assuming the individual starts the feeding migration offshore following spawning, broadly follows (1) move to the coast, (2) move to the correct region and (3) move to assigned division. Additional rules are in place to move individuals around, rather than over, Cornwall. The grey node represents a troubleshooting action for individuals that move onto land as a result of individuals traveling across square patches at any angle. In this event the individual is moved towards a neighbouring coastal patch.

Feeding-migration: This sub model is executed by mature individuals not on a spawning migration (spawn-trigger = 0). All individuals with spawn-trigger equal to 0 take r steps of distance S/r (see TRACE section 5.7 *calculate-speed* and *calculate-r*) according to the hierarchy in Fig. 5-5.

Local-movement: All juvenile individuals follow a random walk process, taking r steps of distance S/r (see TRACE section 5.*7 calculate-speed* and *calculate-r*) in random directions. Juveniles that move off coastal patches turn 180° to move back to their last position on a coastal patch. Juveniles with length less than 32 cm are further constrained to nursery coastal patches.

Drift eggs: If the egg is on the target patch associated with is assigned affinity, then it moves at random around its target area. If not on the target patch it moves to the next patch with one less target distance, thus moving one patch closer to the target every tick. *

Drift_ys-larvae: If the ys-larvae is on the target patch associated with is assigned affinity then it moves at random around its target area. If not on target patch move to the next patch with one less target distance. Thus moving one patch closer to target every tick. Once reached the target patch the ys-larvae undergoes random movement restricted to nursery patches. *

Drift larvae: If the larvae is on the target patch associated with is assigned affinity then it moves at random around its target area. If not on target patch move to the next patch with one less target distance. Thus moving one patch closer to target every tick. Once reached the target patch the larvae undergoes random movement restricted to nursery patches. *

* It is important to note that we use ICES affinity as a convenient way of ensuring new cohorts are split spatially across the model domain, and there is no evidence to our knowledge that larval stages inherit their affinity from their parents. Instead, once transformed through the life stages, a newly mature sea bass is leaving the coast for its first spawning migration, its fidelity is set to the ICES areas it is leaving. Thus is more in-keeping with evidence from tagging studies reviewed by Pawson, Brown, Leballeur, & Pickett, 2008 (for more details see TRACE section 5.8.7).

Spawning: Initiate spawning on the 60th tick which is the 17th of March (picked as the middle of the spawning period). We first calculate potential fecundity and then the energy required to produce this number of eggs (*Max-R*) for all mature sea bass. We allow for maintenance costs whilst spawning by setting aside 10% of reserves:

Potential-fecundity = (std-mass / 1000) * (Eggs_per_bass)

Max-R = (potential-fecundity * (egg-mass * (Ef + Fs)))

Maintenance-energy = energy-reserve * 0.1

where we assume a female sea bass can produce 375,000 eggs per kg of sea bass (Pickett & Pawson, 1994 state between 0.25 and 0.5 million per kg). *Ef* is the energy in flesh and *Fs* is the cost of synthesising flesh (Table 5-2).

If there is enough energy to produce max fecundity, then the energy needed to produce the max number of eggs is taken from the energy reserve and we set the gonad mass and realised fecundity accordingly:

(Energy-reserve - maintenance-energy) >= max-R

Energy-reserve = energy-reserve - max-R

Gonad-mass = (max-R / (Ef + Fs))

Realised-fecundity = potential-fecundity

However, if there is not enough energy for max fecundity then energy reserve is set to whatever is left after subtracting maintenance costs. We then set the gonad mass and realised fecundity to what is achievable with the limited resources:

ER = energy-reserve - maintenance-energy

Gonad-mass = (ER) / (Ef + Fs)

Realised-fecundity = (ER / (max-R)) * potential-fecundity

where *Ef* is the energy in flesh and *Fs* is the cost of synthesising flesh (Table 5-2).

Once we have calculated how many eggs can be produced, we ask 10 mature super-individuals to spawn the total realised fecundity of the total SSB (all mature sea bass). We choose 10 to keep the number of super-individuals consistent for each cohort (see TRACE section 5.8.7). We split the 10 new super-individuals to represent the spatial aspect of the fishery (see TRACE section 5.8.7).

5.8 Data evaluation

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

5.8.1 Summary

The population dynamics component of the IBM is emergent from the energy budget equations, while parameters and inputs were derived from the literature or public databases. The movement sub model was based on hypotheses drawn from tagging studies.

5.8.2 Environmental inputs

SST and PHY: Environmental inputs comprise dynamic maps of chlorophyll-a concentration, and sea surface temperature. The satellite remote-sensing data were taken from NASA's ocean colour portal in NetCDF format (NASA, 2017; NASA OBPG, 2017). Processing of the satellite data included: 1) cropping to the model extent (Fig. 5-1), 2) estimating missing values using linear temporal interpolation (e.g., NAs for a cell in one time period become the average of the last prior period with a value, and next subsequent period with a value), 3) fill in any further gaps with the annual average, 4) re-sampling the spatial resolution from 9km x 9km to 30km x 30km, 5) convert chlorophyll to plankton biomass. Chlorophyll-a was converted to carbon mass using a C:Chl-a ratio of 75, then, a wet mass:C ratio of 10 was used to obtain phytoplankton biomass (g wet mass m^{-2}) (Link et al., 2006). This gives phytoplankton biomass (g m^{-2}) = chl-a (mg m^{-2}) x 0.75 and 6) re-project on to lambert azimuthal equal area projection.

5.8.3 Growth

Juvenile and mature sea bass von Bertalanffy L_∞, k: L_∞ is the maximum length a sea bass can reach, and *K* is annual growth constant. The IBM uses the same von Bertalanffy growth parameter values as used in the stock assessment (Table 5-2). These parameter values were estimated from data derived from sampling of UK fishery catches around England and Wales as well as from trawl surveys of young sea bass in the Solent and Thames estuary, and consisted of over 90,000 fish sampled and

aged between 1985–2011. All ageing was done from scales and the growth curve was fit in Excel solver using non-linear minimization. Standard deviations of length-at-age are also provided in (Armstrong and Walmsley, 2012).

Length weight growth parameters a, b: Length weight parameters *a* and *b*, (used to convert calculated lengths from growth equations into estimates of mass are sourced from ICES, 2012). These parameters are originally used to calculate total mass from fish length, thus include the mass of gonads and fat reserves. In this model we require estimates of structural mass (the minimum weight of fish without gonad or fat reserve mass). To allow for this we have taken average figures of energy reserve mass (~1% of body weight [Pickett and Pawson, 1994]) and gonad somatic index (~4% of body weight [Pickett and Pawson, 1994]), to inform a reduction in parameter *a* by 5%.

Early life: We used sea bass larvae growth experimental data from Regner and Dulčić, 1994 to set the maximum growth rate during the first 70 days of growth after hatching (Fig. 5-6). 70 days is also consistent with other studies of length of the pelagic stages of sea bass (Jennings and Ellis, 2015; Beraud *et al.*, 2018). For the first 70 days we calculate that larva grow at a constant rate which is affected by temperature. At the reference temperature of 14°C this is 0.02485 cm/d (also consistent with daily growth value of 0.2mm in Jennings, Jennings and Pawson, 1992) We test the effect of extremes of observed SST on maximum growth rate. The highest observed SST (30°C) results in a greater maximum growth rate (0.07216844 cm/d) when compared to growth in the lowest observed SST (0°C, maximum growth = 0.008824422 cm/d).
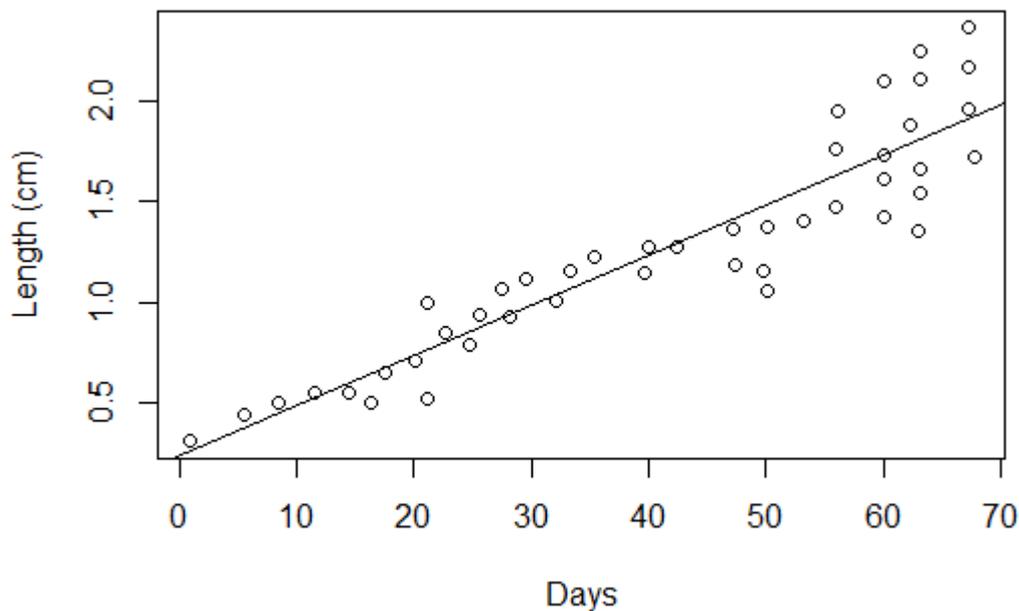
Figure 5-6. Digitised larvae growth data from (Regner and Dulčić, 1994). The solid line represents the regression from which we use the slope coefficient (0.02485 cm/d) to represent maximum growth rate.

Reference temperature: This is the temperature used in the Arrhenius functions throughout the model (except for the use with calc-speed). 12°C was chosen as the reference temperature following Walker et al., 2020.
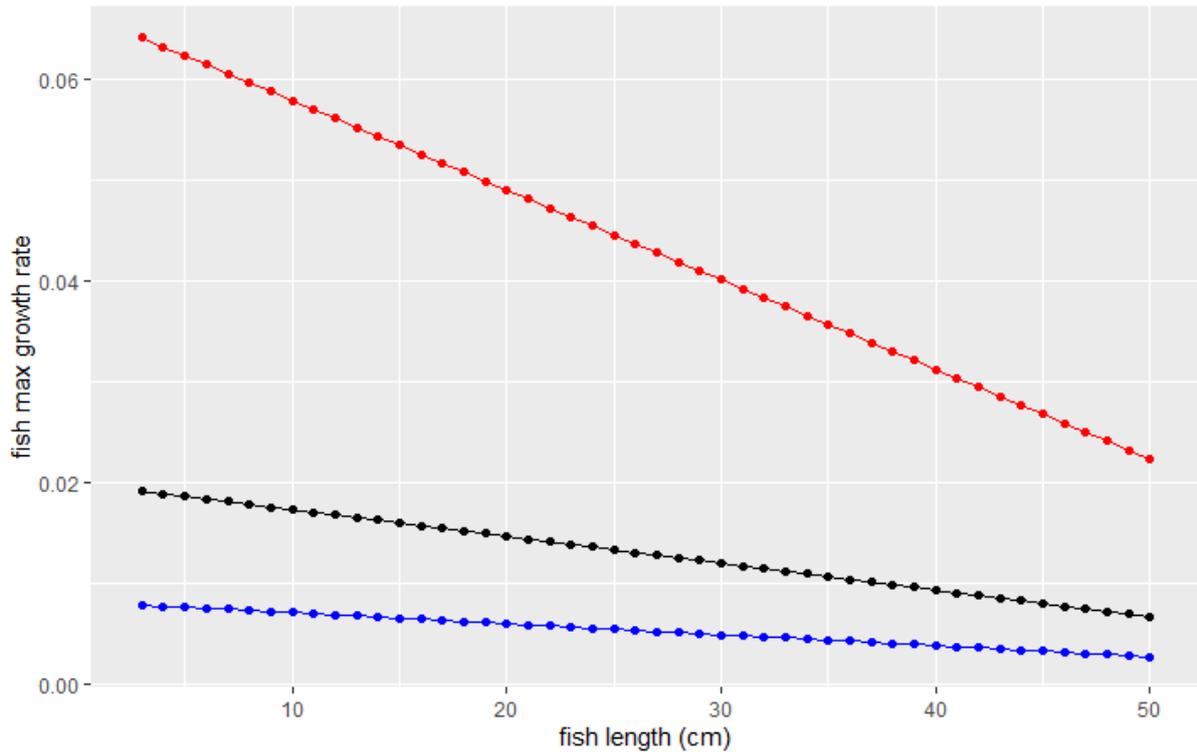
Figure 5-7. Juvenile and mature max daily growth rate using the von Bertalanffy growth equation for European sea bass. Red, black, and blue shows the extremes obtained if larvae were to continuously inhabit a patch at the highest (30°C), reference (14°c) or lowest (0°C) observed SST.

5.8.4 Swimming

Aspect ratio of the caudal fin A: The value of 1.76 was obtained from FishBase (Swim type) based on the value reported in a doctoral thesis (FishBase Ref No. 12676).

Activation energy E_S: The activation energy used in the Arrhenius equation used when calculating speed (see TRACE section 5.7 *calculate-speed*). The temperature dependences of biological processes are known to vary with activity levels, reducing as activity levels increase (Bennett, 1985). This is why the activation energy for sea bass swimming fast is lower than the activation energy for sea bass at other times (Claireaux, 2006). The activation energy value used is 0.1903656 following (Walker *et al.*, 2020).

Reference temperature T_S: The reference temperature used in the Arrhenius equation used when calculating speed (see TRACE section 5.7 *calculate-speed*) The reference temperature value used as 6°C following rational in Walker *et al.*, 2020. Fig. 5-8 illustrates the potential effects of the Arrhenius multiplier on swimming speeds in the IBM.
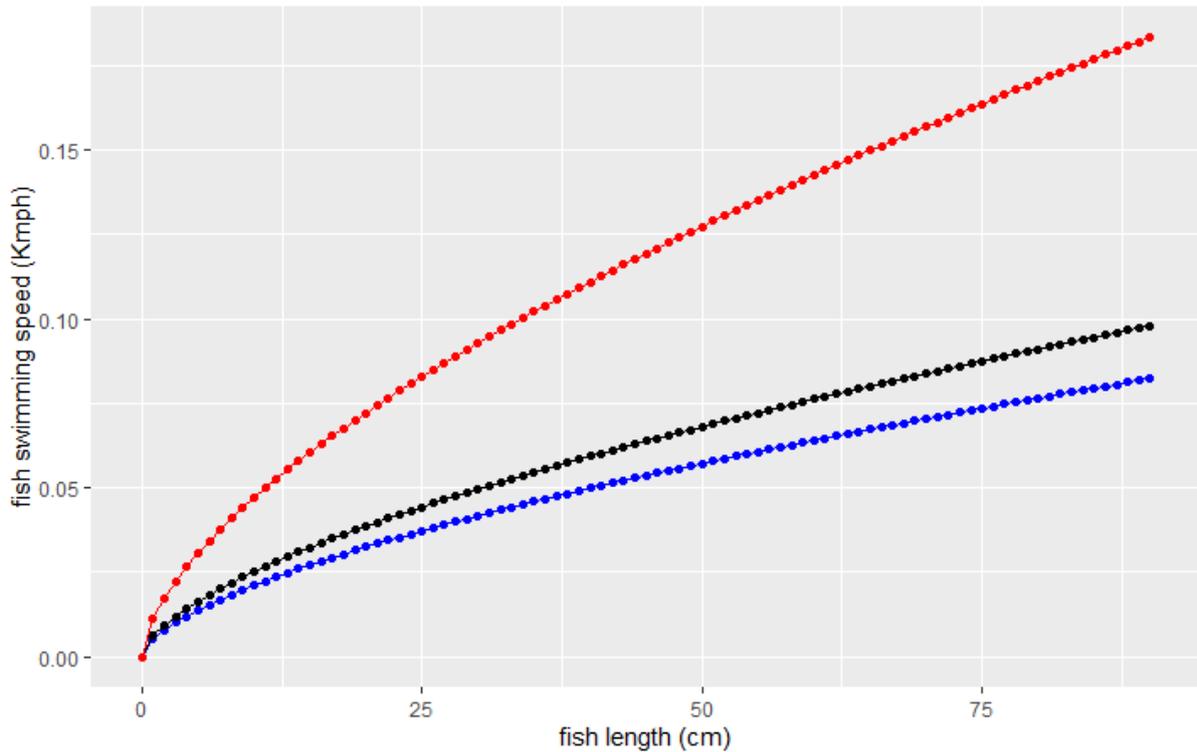
Figure 5-8. The deterministic swimming speed of European sea bass (kilometres per hour) at the reference temperature of 6°C (black curve). red, and blue which show the extremes obtained if larvae were to continuously inhabit a patch at the highest (30°C), or lowest (0°C) observed SST.

Time spent swimming: 12 hours was chosen arbitrarily in the absence of further information.

Movement repeats: Fish move r times per day where r is the smallest integer is such that fish travel no more than 0.25 patches before changing direction. With no movement repeats ($r = 1$) fish sometimes overlap with land, while restricting movement to 0.1 patches before enforcing a direction change can prevent fish from reaching feeding grounds and results in tighter grouping at the divisional boundaries, particularly for fish with an affinity to feed in division 4.

5.8.5   Ingestion

Cmax: *Cmax* is the maximum ingestion rate in grams of food per day per gram of fish. Currently *Cmax* is set as Cmax = 0.54 grams per day per gram of fish. This value is used in Watson *et al.*, 2020 which was based on extrapolation from data in Lanari, D'Agaro and Ballestrazzi, 2002. Lanari, D'Agaro and Ballestrazzi, 2002 used sea bass specimens weighing 60 - 250 grams but we assume this *Cmax* is appropriate for all agents in the model that feed (i.e., larvae, juvenile and mature fish).
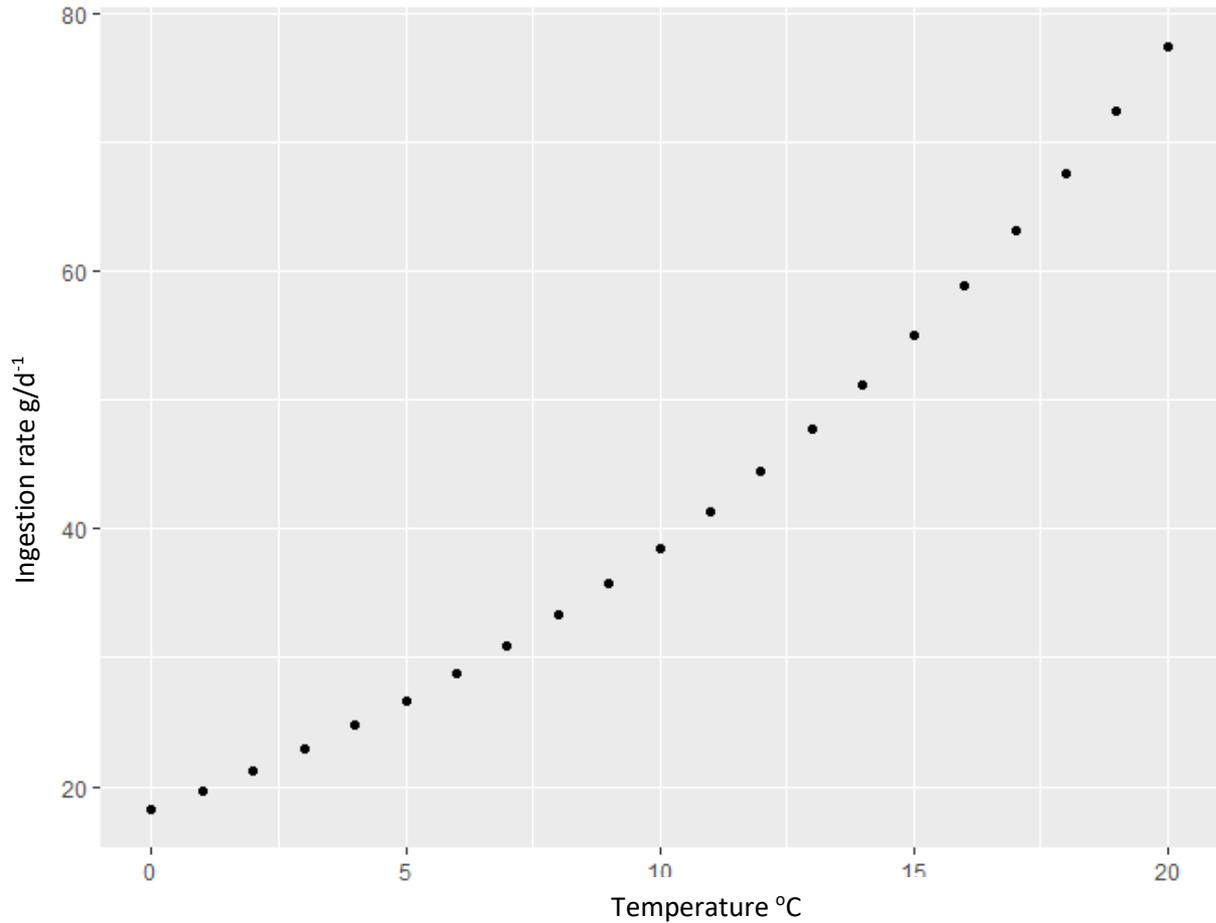
Figure 5-9. Temperature effect on ingestion rate (PHY = 2, h = 0.5, fish length = 42cm).

Half saturation constant (*H*): Half saturation constant is the resource availability at which half of the maximum intake is reached. We show how *H* affects ingestion rate in Fig. 5-10. This parameter is calibrated with ABC (see TRACE section 5.9)
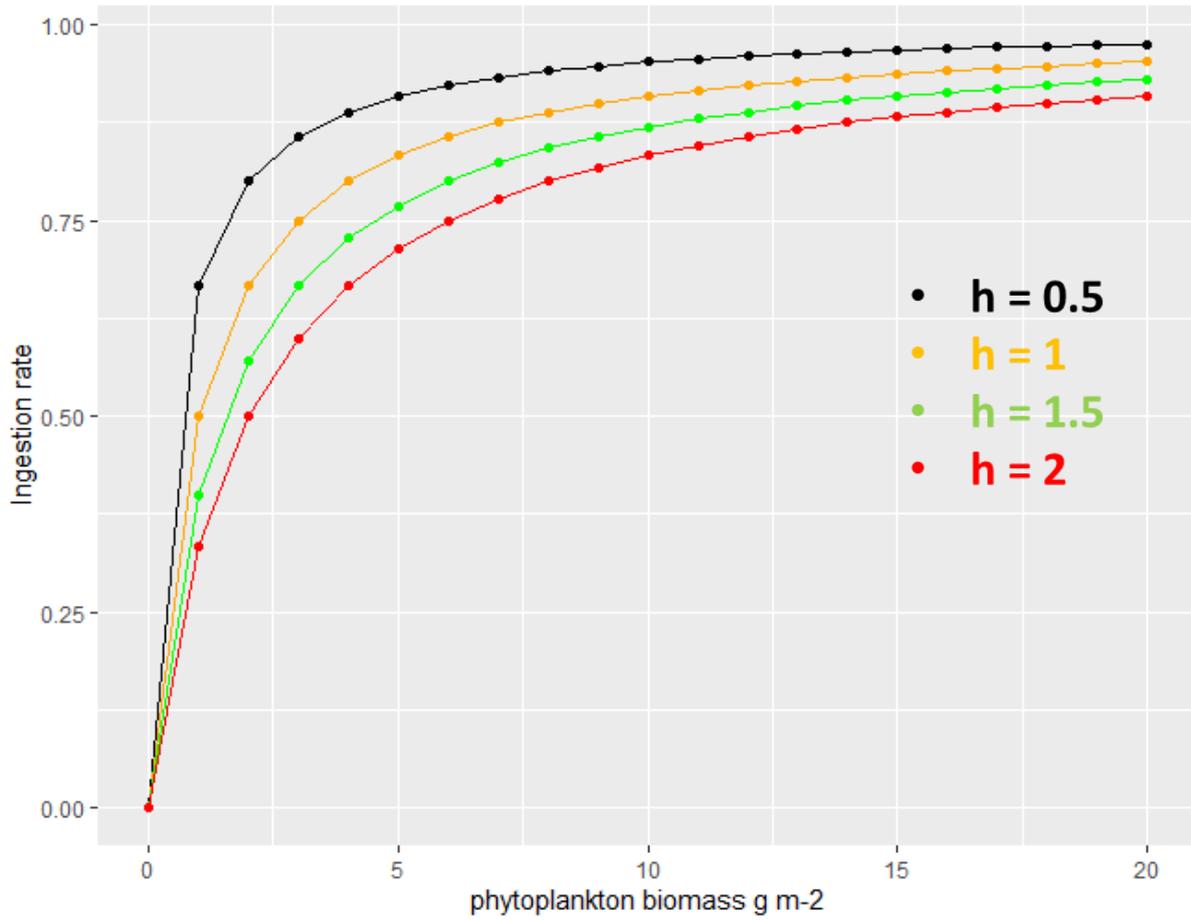
Figure 5-10. Ingestion rate as a function of phytoplankton biomass with half saturation constant values 0.5 (black), 1 (yellow), 1.5 (green) and 2 (red).

Absorbed energy (*AE*): Absorbed energy is the fraction of energy in the environment (phytoplankton [PHY]) that is ingested and assimilated for use in life processes. To keep parameters to a minimum we combined the correlated parameters assimilation efficiency (which was set at 0.95 for mackerel in Boyd *et al.*, 2020) and a trophic delay term. Trophic delay is needed as sea bass do not directly access the energy being read into the model in the form of PHY remote sensing data. The sea bass will only access a fraction of this due to inefficiencies as energy is passed through the trophic levels to the broad range of sea bass prey. This parameter is calibrated with ABC (see TRACE section 5.9)

Density dependence importance (*I*): Importance of density dependence is necessary to give a consequence of having an inflated population, for example a profitable area to feed becomes less optimal as the number of individuals there increases. This parameter is calibrated with ABC (see TRACE section 5.9).

5.8.6   Maintenance

Maintenance is assumed to be the same cost all year round and is assumed to be twice Standard Metabolic Rate to take account of activity in the field (Peters, 1986).

Normalizing constant (*Ao*): *Ao* is the scaling coefficient between fish size and metabolic rate. We use the mean scale coefficient (*Ao* = 0.1227808) between fish size and metabolic rate from data used in Watson *et al.*, 2020 (Fig. 5-11).
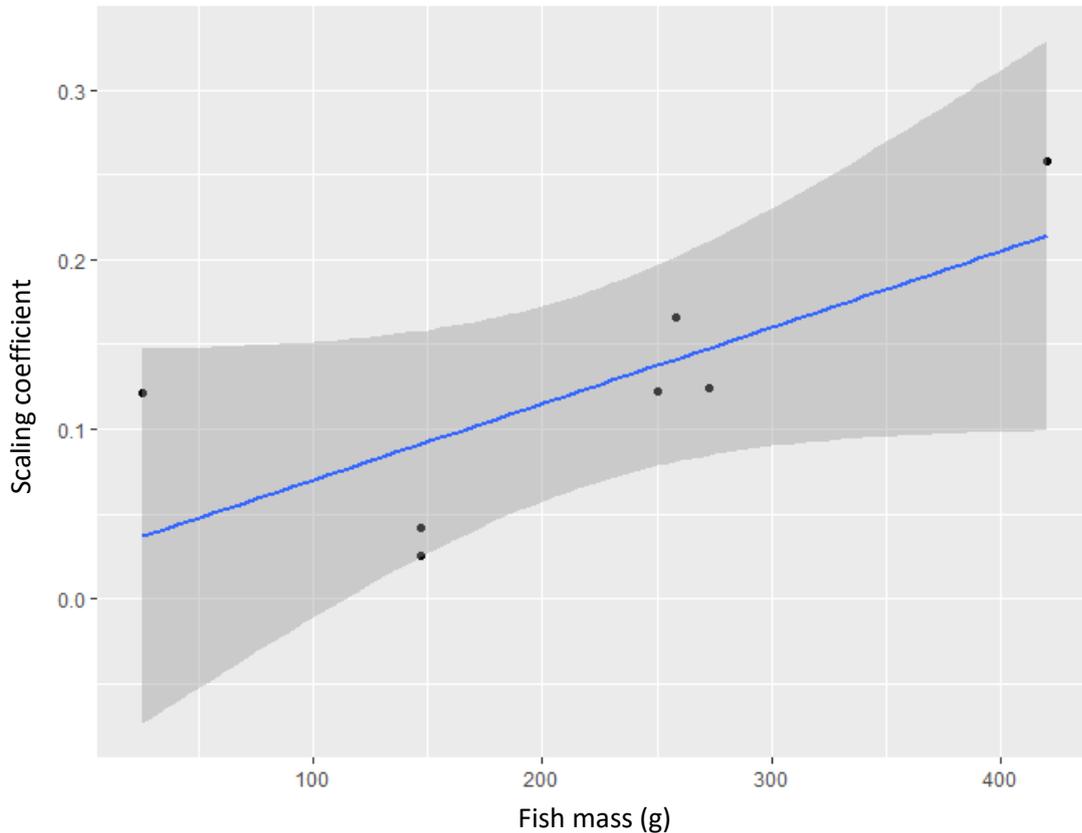
Figure 5-11. The scale coefficient between fish mass and metabolic rate.

5.8.7 Spawning

Numbers eggs per sea bass: Pickett and Pawson, 1994 give a range of ¼ to ½ a million eggs per kg of sea bass so we use a value of 0.33×10^6 eggs per kg of sea bass.

Representative spawning super-individuals: We maintain 10 super-individuals per cohort throughout the model simulation by introducing 10 new super-individuals each year. To ensure the new cohort are spatially representative we split the new 10 into; 3 super-individuals with affinity to Celtic/Irish Sea (VIIfg and VIIa), 5 with affinity to the Channel (VIId and VIIe) and 2 with affinity to the North Sea (IVb and IVc). We have based this distribution on (Walker *et al.*, 2020).

Although this fixes the number of super-individuals, note that each super individual can represent many fish. So, although there are only two super-individuals in the North Sea, they could in theory still represent more fish than the whole Channel if necessary. In this way we still can adequately spatially represent the fishery.

It is important to note that we use ICES affinity as a convenient way of ensuring new cohorts are split spatially across the model domain, and there is no evidence to our knowledge that larval stages inherit their affinity from their parents. Instead, once transformed through the life stages, a newly mature sea bass that is leaving the coast for its first spawning migration sets its fidelity to the ICES area it is leaving. Thus is more in-keeping with evidence from tagging studies reviewed by (Pawson *et al.*, 2008).
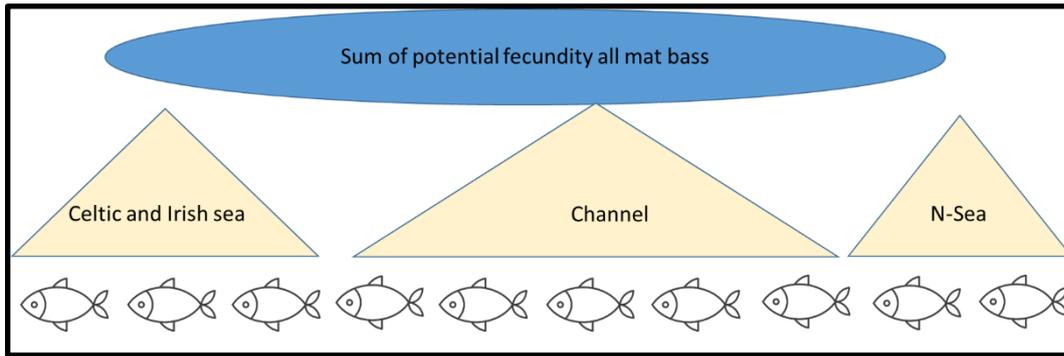
Figure 5-12. Schematic showing how we represent the total spawning potential of all mature sea bass with a new cohort consisting of 10 super-individuals split between the three main areas in the fishery.

5.8.8   Natural mortality

Early life mortality (*PM*): *PM* is the young life stages daily natural mortality rate. Young life stage (eggs, egg-sac larvae and larvae) are exposed to a much higher mortality rate than juvenile and mature sea bass. Early life mortality can be impacted by a multitude of factors including: SST, predation and weather, making it complex to model explicitly. Instead, *PM* is calibrated with ABC see TRACE section 5.9

Juvenile and mature mortality (*AM*): For juvenile and mature sea bass we do not follow the ICES assessment and *AM* is calibrated with ABC see TRACE section 5.9.

5.8.9   Fishing mortality

Fishing mortalities were taken as those estimated by the stock assessment (ICES, 2018c). Catch data for six fishing fleets (1. UK bottom trawls and nets; 2. UK lines; 3. UK midwater pair trawls; 4. French fleets (combined); 5. Other (other countries and UK fleets combined) and 6. Recreational fisheries) are taken as input to the SS3 assessment, and fishing mortalities estimated to match the observed catch (Methot and Wetzel, 2013).

For the purposes of the IBM, fishing mortality was partitioned among the fleets modelled within SS3 by proportion of catch:

$$F_{a,y,f} = \frac{C_{a,y,f}}{\sum_f C_{a,y,f}} F_{a,y}$$

where $F_{a,y}$ is fishing mortality-at-age estimated by the assessment and $C_{a,y,f}$ catch-at-age by fleet f. Fishing mortalities for fleets 1–5 (UKOTB_Nets, Lines, UKMWT, French and Other) were summed to give overall commercial fishing mortality-at-age while fleet 6 (RecFish) gave recreational fishing mortality-at-age.

5.8.10 Numbers-at-age

Numbers-at-age data were used to set up the initial population of sea bass and introduce recruits into the IBM for the first year from the stock assessment. Thereafter the numbers at age are emergent from the energy budget equations and discounted by the appropriate fishing mortality.

5.8.11 Movement

Movements and migrations follow the Pawson et al. (1987) hypothesis. This hypothesis is based on data for 5959 tagged sea bass, with a follow-on exercise for 4959 sea bass confirming the validity of the hypothesis 20 years later (Pawson *et al.*, 2007).
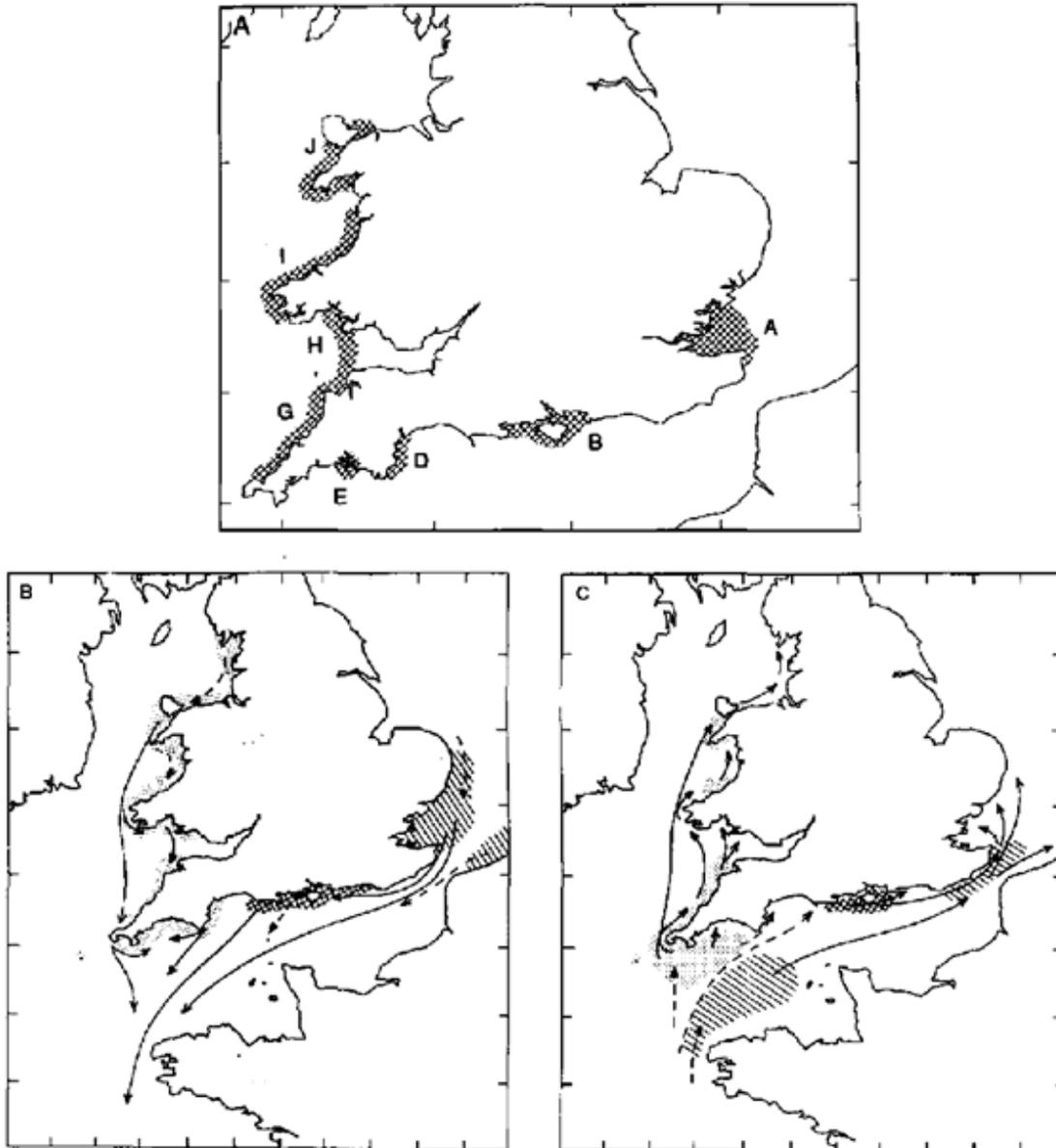
The typical distribution ranges of the tagged bass in populations around England and Wales. (A) Juveniles throughout the year. (B) Adults in summer and their postulated autumn movements. (C) Adults in winter and their postulated spring movements.

Figure 5-13. Hypothesised distribution and movements of sea bass. Figure from (Kelley and Pickett, 1987).

5.9 Calibrating parameters

The model contains 25 parameters, and the values were where possible taken from literature (see TRACE section 5.5 and Table 5-2). Where absolute values of these parameters could not be directly taken from the literature, we used a Bayesian analysis to fit five parameters to calibrate the model. The five calibrated parameters were: *H*; half saturation constant, *AM*: adult natural mortality, *AE*; absorbed energy, *PM*: pelagic mortality, *I*; importance of density dependence. We assigned a prior distribution to these five parameters, which was later updated to a posterior distribution, influenced by the observed data. Our goal to simulate from the posterior is made difficult by the complexity of the model which makes the likelihood function not analytically available and hard to compute. In this section we describe the technique used to overcome this problem.

5.9.1   Approximate Bayesian Computation (ABC)

In settings where the likelihood function is intractable, ABC allows us to perform approximate statistical inference by drawing samples from an approximation of the posterior distribution of parameters. In a fundamental rejection ABC scheme, a parameter value is simulated from the prior distribution and given this value, fake observations y_0 are generated, which are then compared to the actual observations y, using some predefined discrepancy function d(y_0,y). Based on this discrepancy function, the parameter value is only accepted if d(y_0,y) is less than some predetermined threshold ε. This procedure is repeated multiple times until we have a reasonable number of acceptances, which are then distributed approximately like the posterior. The problem with this method is that it typically needs a lot of runs and model evaluations before it generates a reasonable number of samples. This is due to the vast number of rejected samples which are wasted.

A different approach is, instead of explicitly rejecting and wasting the samples that generated fake data distant from the true observations, to store them but give them a very low weight. In contrast, the samples that led to fake data close to the actual observations are given a larger weight, which also depends on the threshold ε. This ε threshold measures the distance between the actual posterior and the approximate posterior and in an ideal setting would be set equal to zero. Instead of fixing ε, one could try to decrease it as the algorithm is running, in such a way that it takes into account the current outputs of the algorithm. This adapted decrease of ε, may allow the algorithm to sample values very close to the posterior. The algorithm we use to calibrate the five parameters was constructed to incorporate this idea and is called Simulated Annealing ABC (SBAC) (Albert, Künsch and Scheidegger, 2015). This algorithm has been seen to sample values from the posterior distribution faster and has the additional advantage of being highly parallelisable. One can see a run of this algorithm as the evolution of a set of particles that move almost independently of each. This allows SABC to be implemented within a High Performance Computing (HPC) framework with multiple cores.

In order to implement SABC for the inference of the parameters of this model with the help of High Performance Computing, we used the Python library ABCPy (Dutta *et al.*, 2017). We used 4 nodes of Orac Server with 28-core each (Lenovo NeXtScale nx360 M5 servers with 2 x Intel Xeon E5-2680 v4 (Broadwell) 2.4 GHz 14-core processors) maintained by the Scientific Computing Research Technology Platform of the University of Warwick. The algorithm ran for 10 iterations which took approximately 2 hours. All the tuning parameters of the algorithm were set to the default values specified in ABCPy. Overall, 111 samples were generated approximately from the posterior. The quantities needed to run SABC, i.e., the discrepancy measure between the observed and fake data,

the prior distribution of parameters and the perturbation kernel to explore the parameter space, are described next.

5.9.2 Observed Data and Discrepancy Function

The data used for parameter calibration was from the sea bass stock assessment model (stock synthesis 3, SS3). SS3 outputs for SSB and numbers at age are estimated annually, however mass at age is simply taken as the stock assessment parameters of the von Bertalanffy model. It is necessary to include mass at age in the calibration to get a realistic population size structure, and in the absence of real data this is the best available guide. As a summary statistic in order to run SABC, we use the whole data set, i.e., Spawning Stock Biomass (SSB), mass and numbers at ages.

Here we define the discrepancy function used to decide the weight we assign to every parameter. We recall that the larger the distance between the fake observations and the actual one, the less we weigh the parameter value that generated those fake observations. If we write $y=(SSB\_1,...,SSB\_{11},N\_{1,1},...,N\_{11,30}, M\_{1,1},...,M\_{11,30})$ for the actual observations (where SSB_i is the SSB at year i and $N\_{i,j}$ and $M\_{i,j}$ the numbers and the mass at year i of the j age group) and respectively y^0 for a fake observation then we use the discrepancy function d defined as

$$d(y, y^0) = \left(\sum_{i=1}^{11} 1000 * \ (SSB_i - SSB_i^0)^2 + 1/30 * \sum_{j=1}^{30}(N_{i,j} - N^0_{i,j})^2 + (M_{i,j} - M^0_{i,j})^2\right)^{1/2}.$$

Note that we consider all the components of the data, i.e., SSB for all 11 different years and number and mass for all 11 different years and 30 different ages. For each component of the fake data, we consider its difference from the component of the actual data, we square it and we sum over all components. However, each component has a different weight, more precisely we add a weight of 1000 to the SSB components and 1/30 to the numbers and masses. This means that we prioritise the fake SSB to be close to the actual one for a parameter to be accepted.

5.9.3 Perturbation Kernel

To explore the parameter space of the five fitted parameters, we consider a five-dimensional truncated multivariate Gaussian distribution as the perturbation kernel. The truncation range is the support of the prior distributions (see next subsection). SABC inference scheme centres the perturbation kernel at the sample it is perturbing and updates the variance-covariance matrix of the perturbation kernel based on the samples learned from the previous step.

5.9.4 Prior Distribution

As a prior distribution we set all five parameters to be uniform distributions independent of each other. Here we describe the reasoning behind the prior values used in the ABC approach to calibrate our unknown IBM parameters (*H*: half saturation constant, *AM*: adult natural mortality, *AE*: absorbed energy, *PM*: pelagic mortality, *I*: importance of density dependence). We began by running the model extensively in a process we term "manual parametrisation" where we adjusted parameter values on the model interface in an attempt to get fairly good fits to the SS3 data. In the absence of other data or knowledge, to give a starting point for priors, we have used half and double (50% and 150%) the values revealed by our manual parametrisation. We have then updated priors wherever sensible after insight from multiple rounds of rejection ABC.

H: half saturation constant

Best value from manual parametrisation was 0.5.

Initial Priors 0.25 and 10.75 (double/half). were updated and final priors were set at 0.25 and 0.75 These updates were after rounds of rejection ABC that revealed no good parameter values at the upper end of the parameter space.

AM: Adult natural mortality

Final priors set at 2.8×10^{-4} and 5.9×10^{-4}

We set these priors based on an online app (http://barefootecologist.com.au/shiny_m) which estimates the value of *AM* from a range of life-history based methods. The priors are the highest and lowest values given.

AE: absorbed energy

Best value from manual parametrisation was 1×10^{-3}

Initial Priors set at 5×10^{-1} and 2×10^{-2} (double/half) and based on assumption ~10% efficiency at each trophic level and the assumption that sea bass are around trophic level 3. Initial priors were then updated and finally set at 0, 3×10^{-3} after rounds of rejection ABC that revealed uncertainty at both the upper and lower bound.

PM: pelagic mortality

Best value from manual parametrisation was 3.71×10^{-2}

Initial Priors set at 1.86×10^{-2} and 7.42×10^{-2} (double and half) were then updated to 4.5×10^{-2}, 1.35×10^{-1}. These updates were after rounds of rejection ABC that showed that poor fits were obtained outside this range.

I: importance of density dependence

Best value from manual parametrisation was 5×10^{13}

Initial Priors set at 2.5×10^{13} and 1×10^{14} (double and half) then updated to 2.5×10^{13}, 7.5×10^{13}. These updates were after rounds of rejection ABC that showed that poor fits were obtained outside this range.

5.9.5   Posterior Shape

The mean of the posterior (or the mode) can serve as a particular value estimate of the parameter. The estimated posterior mean for all five parameters and 95% credible intervals are shown in Table 5-3 together with the prior distributions used. The estimated correlation matrix between parameters is shown in Table 5-4: the values shown suggest medium to weak correlations between these five model parameters, with a maximum of -0.47 between parameters *PM* and *AM*. Finally, Figure 5-14 presents the estimated probability density functions (PDFs) of the marginal distributions for each one of the five fitted parameters. For every pair of these five parameters, the figure also presents their estimated joint marginal PDF by showing their contours. Each contour line indicates the area of the space where the joint PDF has the same value, and this value is presented next to the contour plot (Fig. 5-14).

Table 5-3. Values for priors, posterior mean and 95% credible intervals from ABCpy runs for parameters *H*; half saturation constant, *AM*: adult natural mortality, *AE*; absorbed energy, *PM*: pelagic mortality, *I*; importance of density dependence. For rationale for choice of priors see TRACE section 5.9.4.

Parameter	Priors	Posterior mean	95% credible intervals
H	$2.5 \times 10^{-1}, 7.5 \times 10^{-1}$	4.87×10^{-1}	3.04×10^{-1}, 7.26×10^{-1}
AM	$2.8 \times 10^{-4}, 5.9 \times 10^{-4}$	4.71×10^{-4}	3.43×10^{-4}, 5.87×10^{-4}
Ae	$0.0, 3 \times 10^{-3}$	1.64×10^{-3}	2.51×10^{-4}, 2.88×10^{-3}
PM	$4.5 \times 10^{-2}, 1.35 \times 10^{-1}$	8.01×10^{-2}	5.76×10^{-2}, 1.02×10^{-1}
I	$2.5 \times 10^{+13}, 7.5 \times 10^{+13}$	$5.14 \times 10^{+13}$	$2.72 \times 10^{+13}$, $7.39 \times 10^{+13}$

Table 5-4. Estimated correlation matrix between the parameters shown in Table 5-2.

-	AM	Ae	PM	I
H	0.19	-0.04	0.06	0.02
AM		-0.04	-0.47	-0.05
Ae			0.35	0.17
PM				0.13
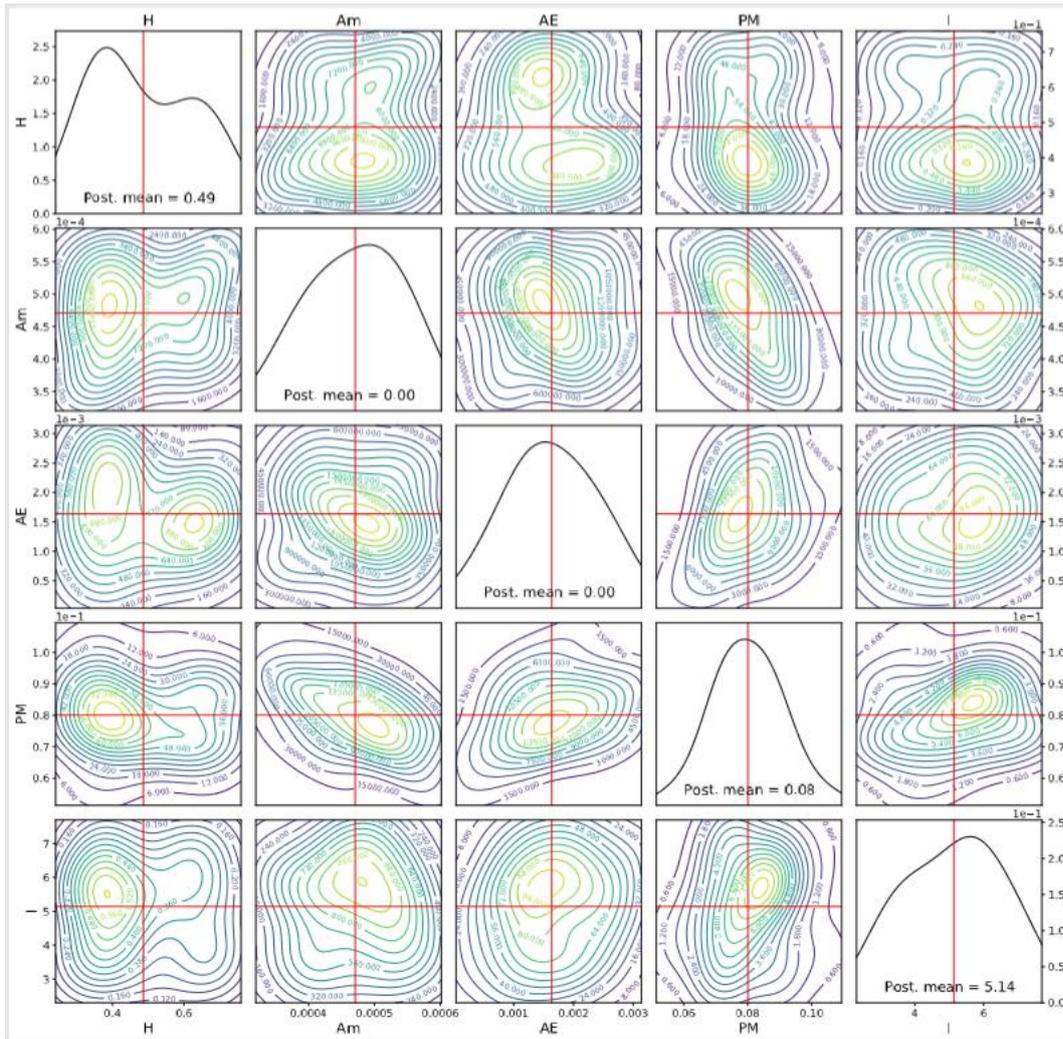
Figure 5-14. Estimated joint posterior distributions and posterior means (red lines) of the five fitted parameters *H*, *Am*, *AE* and *I*, where each of the diagonal and off-diagonal panels show correspondingly the probability density functions (PDF) of the univariate and bivariate marginal posterior distributions. For example, the second panel in the top row shows the contour plot of the marginal posterior PDF of *Am* and *H*, indicating areas of the space where their joint PDF takes specific values, presented next to the contour plots.

5.10 Conceptual model evaluation

This TRACE element provides supporting information on: The simplifying assumptions underlying a model's design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

5.10.1 Summary

Here we provide rationale for our choice of temperature as a forcing variable and phytoplankton density as an energy input. We provide justification for our use and handling of super-individuals, life stages and describe the trade-offs associated with increasing the number of super-individuals in the IBM. We describe how we approached fishing pressure and finally summarise how observations and hypotheses in the literature have informed our movement sub models.

5.10.2 Temperature as a forcing variable

Temperature is a key driver of sea bass dynamics influencing several processes:

Spawning and numbers at age 0: Sea temperature influences distribution of the spawning population and the growth of eggs and larval stages. Larvae that grow faster are quicker to graduate to the lower mortality rate inflicted on the juvenile and adult/mature life stages. This means that faster growth in response to warmer SSTs will influence numbers at age 0 (Pawson, 1992). To test this we show a positive relationship between SST on spawning patches from the model and the numbers at age 0/SSB from ICES stock assessment figures for the years 1985.- 2017 (Fig. 5-15 and Table 5-5). Eggs are rarely found in SST of less than 8.5–9°C or above 15°C leading to the belief that spawning is bound by the 9°C isotherm (Thompson and Harrop, 1987; Pickett and Pawson, 1994), and this governs where spawning patches appear in the IBM (see TRACE section 5.2).

Growth: Water temperature affects growth of sea bass (Pickett and Pawson, 1994) and is modelled through use of an Arrhenius multiplier.

Movement: Swimming speed is positively correlated with temperature (Pickett and Pawson, 1994; Claireaux, 2006) and modelled through use of an Arrhenius multiplier. Temperature also provides an important cue to initiate spawning migrations (Kelley and Pickett, 1987; Pickett and Pawson, 1994) reflected in our migration sub models (TRACE section 5.7).

Ingestion: Water temperature affects ingestion rates of larvae , juvenile and mature sea bass (Pickett and Pawson, 1994) and is modelled through use of an Arrhenius multiplier.

Modelling this complex phenomenon to calculate how much energy and how long it will take to get from a phytoplankton bloom to a sea bass is beyond the scope of this model and requires too many complex assumptions which we term trophic delay. *Trophic delay* is highly correlated with *assimilation efficiency* and so are combined as a single parameter termed *Absorbed energy (AE)*. *AE* is calibrated with ABC, for more details see TRACE section 5.9.

5.10.4 Super-individuals

Super-individuals comprise many sea bass with identical state variables and were employed to make simulation of the large population of European sea bass computationally feasible.

Grimm & Railsback (2005) list three approaches to handle the relationship between the number of super-individuals in an IBM and number of individuals per super-individual as population size decreases due to mortality:

1) Assume that mortality reduces the number of individuals per super-individual while the number of super-individuals remains constant.

2) Assume that mortality reduces the number of individuals per super-individual, but combine super-individuals as needed to keep the number of individuals relatively constant.

3) Assume that an entire super-individual either lives or dies.

Our approach is most similar to option 1, in that we fix the number of super-individuals per cohort and divide the population numbers-at-age accordingly (Shin and Cury, 2001). This option reduces spatial artefacts by keeping the total number of super-individuals relatively constant and allows application of mortality in a way that is compatible with the stock assessment.

The fixed number of super-individuals chosen per cohort introduces a trade-off between spatial distributions, longevity and model run times: more super-individuals allow for more variability and better spatial age-structure, but the lower number of super-individuals within super-individuals may lead to truncation of cohorts before the maximum age of 30 years. Conversely, having fewer super-individuals containing more individual fish better preserves the overall age structure of the population and reduces model run times but may result in patchy age distributions at the divisional level.

5.10.5 Life stages

After the young life stages (eggs, ys-larvae, larvae) have drifted back to the coastline (see TRACE section 5.7 *drift_x sub models*) juvenile and adult/mature sea bass are the two life stages represented in the IBM. Juvenile and adult/mature sea bass are the two life stages which broadly relate to the two distinct movement patterns described in the literature (Kelley and Pickett, 1987; Pickett and Pawson, 1994; Pawson *et al.*, 2007): (1) juvenile residency in nursery grounds and coastal areas and (2) large scale migrations between spawning and feeding grounds upon reaching maturity. Our choice of maturity of fish greater than 42 cm is consistent with observations in which maturity is based on length rather than age (Pickett and Pawson, 1994).

5.10.6 Fishing fleets

Although sea bass are caught by a variety of gears, commercial fisheries operating in the northern management unit are considered to have two distinct components catching different subsets of the population throughout their life and migration-cycles (ICES, 2012a):

1) Offshore fisheries on pre-spawning and spawning sea bass, predominantly by pelagic trawlers from France and the UK, operating during November to April.

2) Small-scale inshore fisheries catching immature sea bass and mature sea bass returning to coastal areas following spawning. These fisheries include many small (10m and under) vessels employing a variety of gears and often take sea bass as by-catch with other species.

Sea bass are also a popular target for recreational fishing in European waters.

5.10.7 Movement and migrations

Although the mechanisms informing sea bass navigation are largely unknown, our empirical movement sub models were constructed to incorporate observations and hypotheses reported in the literature:

Egg, egg-sac larvae and larvae movement: The mechanism by which early life stages return to the coast after offshore spawning is understood to be driven by a complex combination of wind, currents and sea temperatures alongside some active vertical movement of larvae to utilize currents (Beraud *et al.*, 2018). These enable the pelagic stages (eggs, yolk sac larvae and larvae) to reach nursery areas around the coast of the UK, made up of estuaries, harbours, backwaters, creeks and shallow bays (Pickett and Pawson, 1994). It is not feasible to explicitly model this movement, instead for model simplicity the pelagic life stages drift the most direct route back to their target site. This is the forced distribution that ensures that each new 10 super individuals follow a spatial distribution as set out by (Walker *et al.*, 2020) for more details see TRACE section 5.8.7.

Juvenile movement: The local movement of juveniles within the IBM is consistent with observations that juveniles remain within nursery grounds for the first few years of life and disperse primarily during the adolescent phase (Pickett and Pawson, 1994; Pickett, Kelley and Pawson, 2004).

Spawning cues: Movement to pre-spawning and offshore spawning grounds takes place as the water cools between October and December, when mature females seek water warmer than 9°C (Kelley and Pickett, 1987; Pickett and Pawson, 1994), but may be delayed and take place over shorter distances during warmer winters. This is captured by using temperature as a trigger for the spawning migration: most mature sea bass will depart between October and December but some will depart later in warmer years, which allows for spawning in the North and Irish Seas as spawning patches start appearing there. Triggering spawning migrations by appearance of spawning patches also encourages movement from the coastal Channel (divisions 7.de) to offshore in warmer years when patches there do not always drop below the 9°C temperature threshold. Use of a temperature-based cue also allows spawning to extend into April–May as super-individuals with a later departure complete their spawning cycle. Currently 10 mature sea bass spawn only once on the 60th tick (17th of March) assuming they are on a spawning patch. These 10 sea bass are representative of the entire SSB. We currently have only one spawning event (60th tick) for modelling simplicity, however we appreciate that there is evidence of sea bass as a fractional spawner (spawning 3-4 batches [Mayer, Shackley and Witthames, 1990]).

Cessation of spawning: Feeding migrations don't appear to be triggered by an environmental cue, but occur when fish are spent at the end of spawning (Pawson *et al.*, 2007). This is modelled with a 60-day spawning period once a mature fish locates a spawning patch, after which it is assumed spent and defaults to the feeding migration. Assumption of 60 days in spawning grounds was chosen for modelling reasons to prevent fish performing more than one spawning migration per year while

ensuring that fish begin feeding migrations in the months April and May (Kelley and Pickett, 1987; Pawson *et al.*, 2007).

Migrations: Our empirical rules consist of choosing a suitable neighbouring patch based on destination direction and patch type, ensuring direct movement along the coast (Pickett and Pawson, 1994) when migrating between spawning and feeding grounds.

Site fidelity: Sea bass have a high affinity for coastal feeding grounds (Kelley and Pickett, 1987; Pawson *et al.*, 2008), but the reason for this and its extent is unclear. Hence the probability that fish change affinity to a feeding area can be specified via the *site-fidelity?* Slider on the model's GUI. Site fidelity was fixed at 100% in the current study.

5.11 Implementation verification

This TRACE element provides supporting information on: (1) whether the computer code implementing the model has been thoroughly tested for programming errors, (2) whether the implemented model performs as indicated by the model description, and (3) how the software has been designed and documented to provide necessary usability tools (interfaces, automation of experiments, etc.) and to facilitate future installation, modification, and maintenance.

5.11.1 Summary

A series of techniques were employed to test and debug the model code and check that it performs according to the ODD specification. These checks included syntax checking, visual testing, print and error statements, spot tests with agent monitors, test procedures and programs, independent reimplementation and testing of sub models in R.

The original model on which this model has developed from had extensive bug checking adding to the confidence in model behaviour (Walker *et al.*, 2020). In addition to the bug testing on the original model we have performed a range of checks to ensure the model is behaving as expected. The NetLogo syntax checker and GUI interface was used to test and debug the code throughout all stages of model development. In the new model updates we add dynamic maps of chlorophyll remote sensing data. To check this is working correctly we visually checked the dynamic maps by representing the data as colours and plots in the model GUI. We performed extensive testing of energy budget sub models both through spot checks of individual agents and by re-coding the sub model in R and testing the outputs with a range of values. The model outputs we fit of number and mass at age also add to confidence in model performance allowing obscure results to be spotted and cohorts to be followed through the simulation. The model is coded in a modular fashion making it feasible for sub models to be updated by new users however modifications of the model will require knowledge of NetLogo. The model has been implemented in NetLogo version 5.3.1 (Wilensky, 1999), a free software platform. The developers of NetLogo provide transition guides to new versions of NetLogo and keep old versions available for download.

5.11.2 Model output verification

This TRACE element provides supporting information on: (1) how well model output matches observations.

 Summary: Here we compare model output to ICES SS3 stock assessment data.
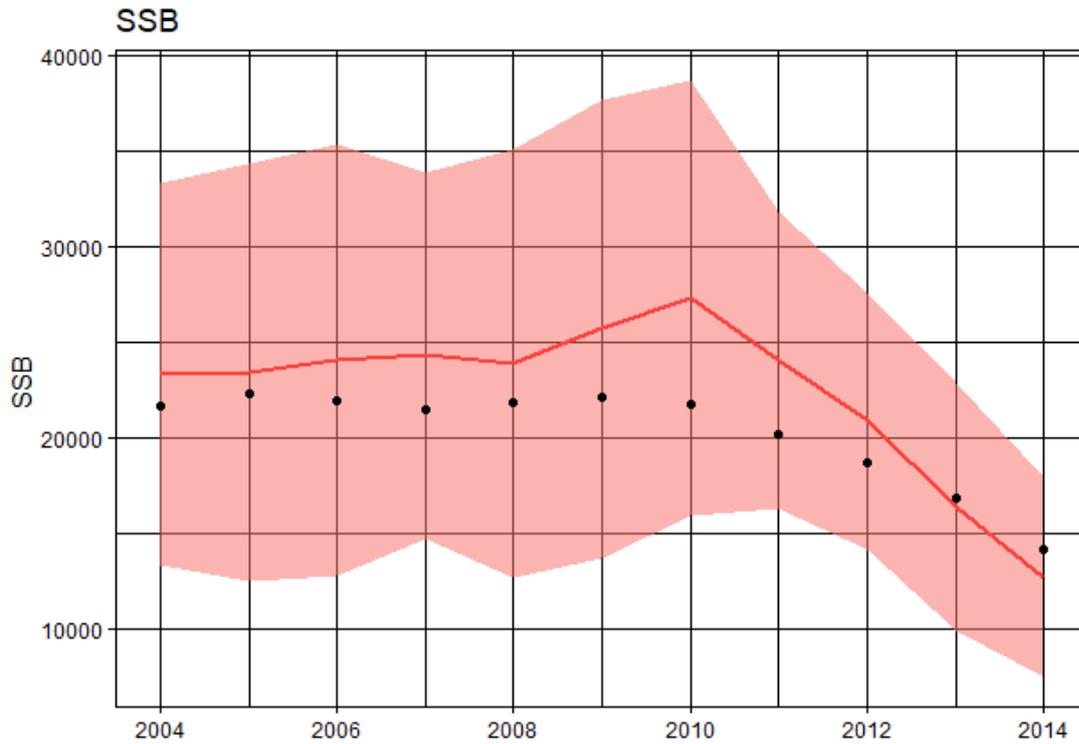
Figure 5-16. Model callibration for Spawning Stock Biomass (SSB) for years 2004-2014. Spawning stock biomass is shown here as the cumulative mass of all individuals over 42cm in length as the threshold for being classed as a mature sea bass. Black dots represent the outputs of SS3; red dots are the IBM outputs using posterior medians; ribbon represents interquartile range.
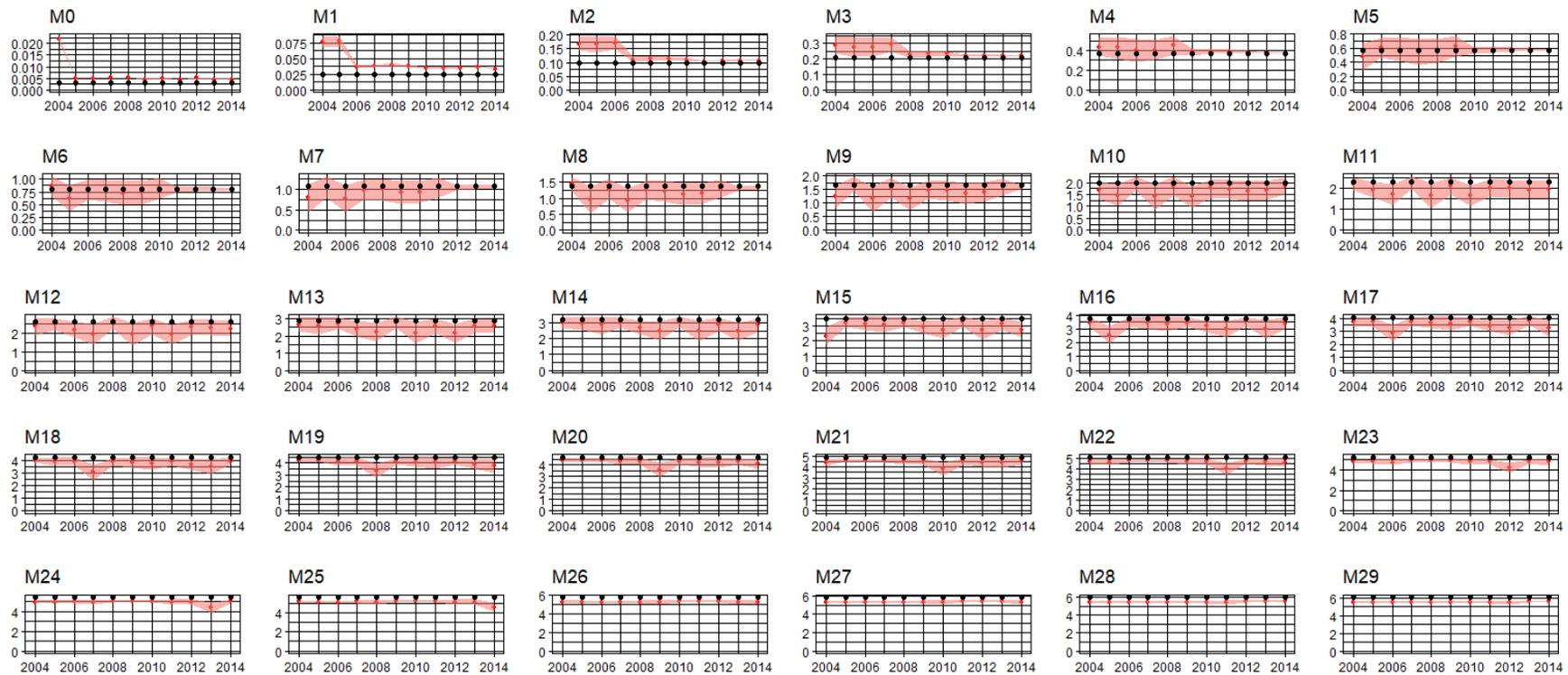
Figure 5-17. Model calibration for mean mass (kg) of 30 age classes for years 2004-2014. M0 = mass at age 0, from then on M1 = mass at age 1, M2 = mass at age 2 etc. Black dots represent the outputs of SS3 (note these are based on as von Bertalanffy growth curve and are fixed so do not change year to year); red dots are the IBM outputs using posterior medians; ribbon represents interquartile range.
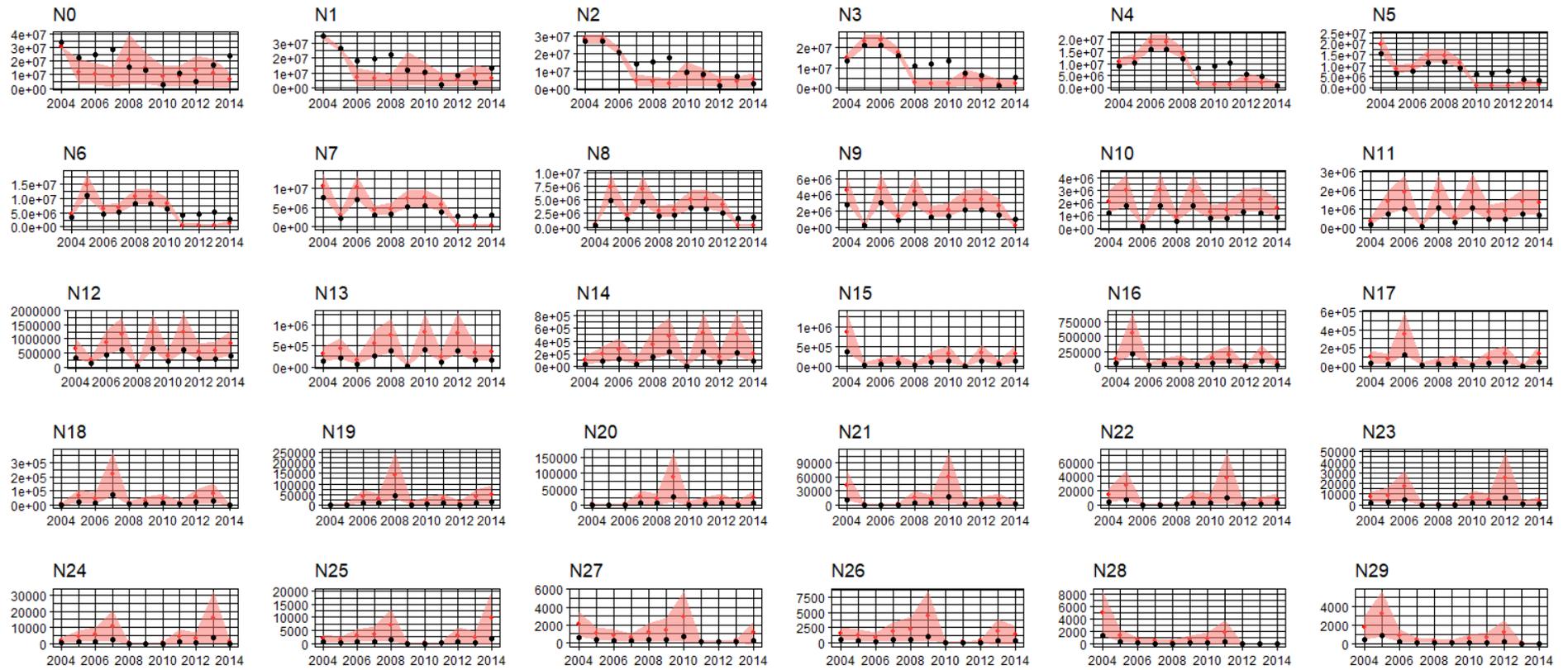
Figure 5-18. Model callibration for numbers of 30 age classes for years 2004-2014. Numbers in each age class, N0 = number at age 0, N1 = number at age 1, etc. Black dots represent the outputs of SS3; red dots are the IBM outputs using posterior medians; ribbon represents interquartile range.

5.12 Model analysis

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

5.12.1 Summary:

The sensitivities of model outputs for SSB, mass at age and numbers at age are shown below as percentage change in output for a 10% increase and decrease in the model parameters. One parameter was tested at a time whilst keeping all other parameters at their base value. To keep run times achievable we repeat the test five times for each parameter and after the spin up (1985-2003) we take the results after one year of energy budget simulations (1st tick of 2005). A full table of results can be seen below in Table 5-6. The model is robust to most parameters with most sensitivities reported at less than 10% change in output for a 10% change in parameter value. The model is most sensitive to changes in length weight parameter (*b_g*). The parameters that are calibrated with ABC, Half saturation constant, Adult mortality and Absorbed energy, Pelagic mortality and Importance of density dependence (*H*, *AM*, *AE, PM, I*) are relatively robust with the majority of output changes less than 10%, though note the output of N0 high sensitivity to PM.

Table 5-6. Sensitivities of SSB, mean mass at age, and numbers at age, to 10% changes in parameter values. Results are presented as the change in relative output to a 10% decrease/increase in parameter value.

Parameter	Value	SSB.dec	SSB.inc	M0.dec.	M0.inc	M1.dec.	M1.inc	M2.dec.	M2.inc	M3.dec.	M3.inc	M4.dec.	M4.inc	M5.dec.	M5.inc	…
linf	84.55	-9.6	0.8	-21.9	25.7	-12.9	13.2	-7.9	1.2	-13.4	-10.3	-4.5	-2.8	-12.2	-7.3	…
K	0.096699	-1.7	10.5	-20.5	21.5	-10.2	4.1	-9.0	4.4	-0.3	5.5	-9.8	2.5	-12.4	-1.9	…
t0	-0.73	-7.6	-1.5	-1.2	-0.7	-0.7	-0.9	-9.6	2.7	-8.5	-3.6	-6.9	1.2	-10.3	-14.1	…
Ea	0.5	1.7	-0.4	-4.0	2.8	-5.5	1.3	-3.0	-0.6	-0.9	-7.5	2.4	-9.9	-1.9	-2.7	…
EaS	0.1903656	10.1	-0.7	-2.0	-2.1	-5.4	-0.6	2.2	7.6	0.4	4.5	2.8	-2.7	-10.8	-6.4	…
Cmax	0.54	4.1	6.5	-1.2	-0.7	-2.7	2.9	-1.4	5.0	-0.8	-2.2	-0.2	6.4	-7.2	-5.3	…
ep	6.02	-1.3	2.2	-1.6	-0.1	-1.2	1.9	5.6	4.9	1.6	-9.3	1.2	-10.8	-5.4	2.5	…
A0	0.1227808	7.1	-2.1	-0.7	-0.3	-2.8	-4.2	3.6	-1.7	-3.7	-6.5	2.5	-5.3	-7.0	-1.3	…
Ef	7	-11.6	-8.1	0.2	-0.8	-1.7	-3.2	0.6	-1.1	-7.1	7.4	-2.2	-6.4	-8.9	-4.8	…
El	39.3	4.5	-6.3	-0.3	-1.3	-4.0	-0.9	-5.3	-3.9	-1.3	-5.4	-0.7	2.0	-8.3	-13.4	…
Ls	14.7	-10.3	0.5	-0.6	-0.1	-0.4	-0.5	1.2	2.6	-3.6	-8.9	-3.3	-6.8	-13.6	-5.7	…
Fs	3.6	-1.5	0.1	-0.2	0.0	-1.3	-5.4	-2.4	-5.9	-7.7	-2.0	-5.2	-0.4	-12.3	2.6	…
egg_mass	0.00096	5.6	4.3	-0.2	-1.0	-5.0	1.6	1.1	3.4	-16.7	-8.7	-2.0	-1.3	2.1	-6.7	…
a_g	0.000012312	-5.0	10.7	-9.7	7.2	-8.0	3.6	-12.9	2.9	-16.1	4.5	-9.3	5.1	-16.1	4.3	…
b_g	2.969	-61.3	152.4	-45.0	29.8	-56.0	80.8	-58.3	98.6	-61.5	73.2	-61.0	119.8	-65.8	130.2	…
eggs_per_bass	375000	-0.1	-4.5	-1.1	-0.9	-0.2	-2.4	-1.4	-5.9	-7.2	-4.1	1.9	0.4	-11.4	-5.6	…
GI	0.02485	3.7	-0.8	-5.3	3.0	-1.7	-4.1	-4.4	-2.7	-6.1	-11.2	-0.5	-4.9	-7.8	-7.6	…
H	4.46E-01	0.7	6.7	0.5	-2.1	-0.2	-5.8	1.8	-2.6	2.9	-3.1	0.2	-4.9	-5.3	-5.0	…
AM	4.91E-04	-0.9	3.5	0.2	-0.7	-2.3	0.7	0.8	3.4	-0.5	6.4	-1.9	-1.4	-7.5	2.5	…
AE	1.57E-03	1.5	6.8	0.3	-1.5	-4.2	-2.4	1.0	-0.3	0.1	0.0	2.7	-4.7	-3.9	-8.4	…
PM	8.42E-02	1.2	-1.5	-0.3	0.6	-0.7	-1.5	-2.3	-1.5	3.7	2.8	-2.3	-2.1	-3.2	0.2	…
I	5.20E+13	2.8	5.5	-1.8	0.0	-5.9	0.1	0.0	-6.1	-3.2	-10.8	-4.4	-4.6	-7.2	-6.9	…

Parameter	Value	M6.dec.	M6.inc	M7.dec.	M7.inc	M8.dec.	M8.inc	M9.dec.	M9.inc	M10.dec.	M10.inc	M11.dec.	M11.inc	M12.dec.	M12.inc	...
linf	84.55	-1.9	-11.2	-4.2	-12.0	-10.5	0.8	-4.0	1.2	-4.6	3.2	-5.3	3.4	-3.4	5.0	...
K	0.096699	-8.6	10.6	-10.7	-1.1	-10.0	3.9	-6.2	-0.8	0.5	-0.1	-7.5	1.8	-6.2	1.6	...
t0	-0.73	0.1	-9.2	-16.3	-2.6	-7.1	-11.0	0.2	-9.5	-3.7	-1.2	-0.4	-5.1	-1.7	0.8	...
Ea	0.5	3.9	-6.3	-6.6	-4.5	-10.1	-4.0	3.4	0.0	-2.4	2.8	2.8	-0.9	3.4	1.7	...
EaS	0.1903656	4.7	4.3	-1.8	-10.0	3.6	-7.7	0.0	1.2	2.3	0.9	0.2	-2.6	3.3	-1.4	...
Cmax	0.54	7.5	0.6	-0.1	-2.0	-9.4	-4.8	-5.2	-0.6	-4.9	3.8	2.4	1.2	-0.3	2.9	...
ep	6.02	-0.4	0.8	-9.8	-3.0	3.8	-3.3	-2.1	-0.6	-1.4	-3.1	1.9	5.1	1.3	1.4	...
A0	0.1227808	9.9	-0.3	1.1	-4.0	-7.2	-5.2	1.1	0.2	0.4	-0.7	-0.5	0.5	0.4	0.4	...
Ef	7	0.9	-2.9	-3.3	-4.7	-9.3	-11.6	1.9	-2.7	-8.4	-9.1	-9.0	2.0	0.9	1.6	...
El	39.3	-1.9	-1.7	-3.3	-3.3	-5.3	-9.9	2.4	-2.3	1.4	-8.2	0.4	-1.5	1.0	1.3	...
Ls	14.7	0.6	-0.8	-0.1	-3.2	-17.8	-3.6	-5.2	0.3	-0.2	1.1	0.5	-0.6	0.5	-1.3	...
Fs	3.6	-0.6	3.5	-6.8	-7.5	-9.8	-7.1	-0.6	0.0	-7.5	2.9	0.2	0.4	0.2	-0.4	...
egg_mass	0.00096	-8.0	-4.0	-2.0	-6.3	0.2	-2.2	-0.1	-0.3	5.9	2.7	-1.6	1.4	-1.5	2.0	...
a_g	0.000012312	-7.2	16.0	-11.9	3.5	-17.8	9.6	-8.7	9.6	-10.9	11.7	-11.5	10.4	-8.0	10.9	...
b_g	2.969	-64.5	145.3	-66.9	134.5	-66.6	177.9	-68.2	182.1	-66.0	174.0	-69.2	196.8	-69.8	219.8	...
eggs_per_bass	375000	9.4	-11.2	-2.7	-4.7	-0.7	-22.0	0.5	0.6	5.2	-0.4	-1.4	3.9	-0.7	1.8	...
Gl	0.02485	7.7	-6.9	-1.3	-7.4	-1.6	-9.9	-0.4	-0.2	2.6	1.3	1.8	0.9	-1.4	0.7	...
H	4.46E-01	6.1	7.4	-2.0	-2.2	0.1	-2.4	-1.0	-0.8	-3.3	2.1	-1.8	2.5	0.3	-0.6	...
AM	4.91E-04	-2.4	4.6	-6.3	-0.7	-6.6	-2.6	-2.6	1.4	-1.9	-6.8	5.0	5.6	1.1	2.1	...
AE	1.57E-03	2.4	4.7	-3.9	-3.7	-13.3	2.0	-6.0	0.0	-17.5	1.8	-3.9	3.6	1.4	1.2	...
PM	8.42E-02	-4.7	-2.5	-4.0	-7.5	-5.4	-5.1	-5.2	1.4	-3.8	0.4	-7.4	3.2	1.2	1.7	...
I	5.20E+13	2.4	4.8	-3.3	-7.1	-0.9	-2.1	0.9	-0.6	3.3	1.9	2.8	1.5	0.8	-0.4	...

Parameter	Value	M13.dec.	M13.inc	M14.dec.	M14.inc	M15.dec.	M15.inc	M16.dec.	M16.inc.	M17.dec.	M17.inc	M18.dec.	M18.inc	M19.dec.	M19.inc	…
linf	84.55	-1.8	5.7	0.8	4.5	-3.3	3.8	-1.7	-5.6	-1.2	3.0	-2.9	2.8	-1.4	4.2	…
K	0.096699	0.8	-2.0	2.7	3.1	-0.6	1.6	-12.4	-4.8	2.2	2.5	0.6	-0.1	1.0	1.7	…
t0	-0.73	-7.1	2.0	0.0	-0.1	-4.9	-1.4	-8.9	-1.2	1.3	1.3	-0.1	0.2	2.0	1.9	…
Ea	0.5	1.4	2.2	4.0	1.6	-0.4	-1.9	0.8	-1.2	1.8	0.9	0.5	-0.5	1.1	1.6	…
EaS	0.1903656	2.2	-4.4	4.0	3.5	-0.4	-0.3	-2.1	-1.1	2.9	1.4	1.1	1.1	1.4	1.8	…
Cmax	0.54	-0.6	2.6	2.7	3.0	0.2	0.6	-0.3	-0.1	0.8	2.0	0.0	0.5	1.1	2.1	…
ep	6.02	-1.6	1.0	2.0	3.0	-0.1	-0.8	-0.3	-2.7	0.8	1.6	0.3	0.0	0.9	1.2	…
A0	0.1227808	0.5	0.5	3.8	3.1	-0.2	0.4	-1.9	-3.7	0.9	-2.9	0.0	0.1	1.3	2.1	…
Ef	7	3.6	1.8	3.8	2.1	-0.3	1.0	-1.7	-0.3	1.8	1.7	-0.6	0.6	1.0	2.1	…
El	39.3	1.2	-6.3	3.5	2.3	-1.2	-0.7	2.0	-4.9	1.1	0.3	0.6	0.7	1.2	1.8	…
Ls	14.7	2.8	2.0	5.5	-1.7	-1.7	-0.2	-5.4	-3.9	0.5	-1.5	0.6	-0.6	1.1	1.9	…
Fs	3.6	-2.6	0.3	1.2	3.8	-0.7	-2.7	-7.7	-2.4	-0.7	-1.4	1.0	0.8	2.3	0.4	…
egg_mass	0.00096	0.9	-0.4	3.5	3.0	0.0	-0.5	-2.0	-0.2	1.4	0.6	0.3	-0.1	1.3	1.6	…
a_g	0.000012312	-9.7	11.6	-8.9	12.9	-12.3	11.0	-11.1	5.6	-9.8	11.0	-9.7	9.2	-8.5	11.1	…
b_g	2.969	-70.2	225.1	-70.4	242.8	-70.9	241.2	-70.8	211.2	-70.9	248.2	-71.4	250.0	-71.3	252.8	…
eggs_per_bass	375000	-2.5	-0.9	2.1	3.8	-1.0	0.2	-3.8	0.4	2.8	0.5	0.4	0.1	1.8	1.7	…
Gl	0.02485	0.6	2.0	2.6	3.9	0.7	-0.1	-6.6	-2.5	1.1	0.5	-1.5	1.3	1.0	1.8	…
H	4.46E-01	1.9	0.2	-0.2	2.8	-0.8	-1.1	-2.6	-5.4	1.9	1.4	0.1	-0.8	1.4	1.1	…
AM	4.91E-04	-0.7	-0.7	-0.2	4.2	-0.2	0.1	-8.9	1.2	-2.6	0.4	2.6	0.7	2.2	1.5	…
AE	1.57E-03	-6.3	0.8	-2.1	3.1	-0.1	0.8	-1.4	-4.0	0.3	1.3	0.1	0.0	1.6	1.5	…
PM	8.42E-02	1.8	3.4	2.2	4.4	-2.2	-2.3	-1.1	-2.7	1.5	-0.3	-0.3	-1.3	1.1	0.9	…
I	5.20E+13	-1.4	-1.3	4.3	4.6	0.2	1.4	-0.8	0.5	0.7	2.6	0.5	-0.4	1.5	1.5	…

Parameter	Value	M20.dec.	M20.inc	M21.dec.	M21.inc	M22.dec.	M22.inc	M23.dec.	M23.inc	M24.dec.	M24.inc	M25.dec.	M25.inc	M26.dec.	M26.inc	...
linf	84.55	-4.1	3.2	-2.1	2.9	-2.6	3.3	-3.7	2.5	-3.5	2.4	-3.0	4.0	-3.2	3.3	...
K	0.096699	0.2	1.1	0.5	0.8	0.2	1.0	0.1	0.5	-0.3	0.5	0.8	1.5	-0.7	0.7	...
t0	-0.73	0.2	0.2	0.3	0.6	0.9	0.1	-0.5	0.3	-0.4	0.5	0.7	0.9	0.2	0.8	...
Ea	0.5	-0.4	0.6	0.0	1.0	0.1	1.0	-0.8	0.4	-0.5	-0.2	1.2	1.0	0.7	0.5	...
EaS	0.1903656	-0.4	0.3	0.5	0.9	0.4	0.4	0.4	0.0	0.1	-0.3	1.1	0.8	0.6	1.4	...
Cmax	0.54	0.2	0.1	-0.3	0.1	0.2	-0.2	-0.4	-0.3	-0.8	-0.8	0.3	1.3	0.9	0.8	...
ep	6.02	-0.7	0.4	0.2	0.1	-0.5	0.0	-0.9	-0.1	-0.4	-1.2	0.0	0.1	-0.5	0.9	...
A0	0.1227808	-0.3	0.5	0.7	0.8	0.4	0.8	-0.2	0.1	-0.5	-1.1	0.2	1.7	-0.1	0.5	...
Ef	7	-0.3	0.2	0.7	0.6	0.7	0.3	-1.6	0.2	-0.4	-0.4	0.5	0.8	0.9	0.6	...
El	39.3	-0.8	-0.1	-0.1	0.9	0.4	0.1	-0.4	-0.2	0.1	-0.7	0.4	0.4	0.4	0.8	...
Ls	14.7	-0.9	0.2	-1.0	0.9	0.8	0.6	-0.7	0.1	0.8	-0.5	1.1	1.5	0.7	1.1	...
Fs	3.6	0.4	-0.8	1.7	0.6	-0.1	0.1	0.0	-0.8	-0.9	-0.3	1.0	0.5	0.5	0.7	...
egg_mass	0.00096	-0.1	-0.2	1.0	0.3	0.7	0.4	0.2	-0.3	-0.7	-1.5	1.1	1.1	1.6	1.2	...
a_g	0.000012312	-9.4	9.2	-10.1	10.2	-9.2	9.8	-10.0	10.0	-11.2	8.7	-9.9	10.5	-9.7	10.4	...
b_g	2.969	-72.1	255.3	-71.9	255.7	-72.1	257.9	-72.2	258.4	-72.5	254.9	-72.4	262.4	-72.3	262.5	...
eggs_per_bass	375000	-1.4	-0.8	0.2	-0.3	0.5	0.4	-0.2	-0.5	-0.3	-0.4	1.2	1.0	1.3	0.7	...
Gl	0.02485	0.9	0.7	-0.1	0.3	0.8	0.7	-0.2	-0.7	-0.1	-0.9	0.7	1.6	0.8	1.5	...
H	4.46E-01	-0.4	0.0	-0.3	-0.5	0.5	0.7	-0.2	-0.9	-0.1	-0.2	0.5	0.6	0.8	0.5	...
AM	4.91E-04	0.1	-0.3	1.2	-0.2	0.1	0.3	0.3	0.0	0.5	-1.8	1.0	0.2	0.6	0.2	...
AE	1.57E-03	0.5	0.3	0.9	0.7	1.3	0.9	-0.4	-0.4	-0.3	-0.6	0.9	0.3	0.8	0.7	...
PM	8.42E-02	-0.2	-0.4	1.0	-0.9	1.2	-0.6	-1.4	-1.2	-0.2	-0.3	1.3	0.1	0.9	0.7	...
I	5.20E+13	-0.3	0.0	0.2	1.1	0.2	1.2	-0.2	-0.7	-0.8	-0.4	0.3	0.8	0.9	0.3	...

Parameter	Value	M27.dec.	M27.inc.	M28.dec.	M28.inc.	M29.dec.	M29.inc.	N0.dec.	N0.inc	N1.dec.	N1.inc	N2.dec.	N2.inc	...
linf	84.55	-2.8	3.5	-2.7	2.4	-2.5	3.7	7.5	-10.5	0.0	0.0	0.0	0.0	...
K	0.096699	-0.7	0.5	-0.8	-0.2	0.2	0.6	0.0	6.8	0.0	0.0	0.0	0.0	...
t0	-0.73	-0.4	0.4	-1.2	-0.5	-0.1	0.2	-1.8	6.6	0.0	0.0	0.0	0.0	...
Ea	0.5	0.2	0.3	-0.7	-0.2	-0.3	0.2	10.8	0.3	0.0	0.0	0.0	0.0	...
EaS	0.1903656	0.0	0.0	-0.5	0.1	0.4	0.3	7.7	0.8	0.0	0.0	0.0	0.0	...
Cmax	0.54	-0.3	0.4	-0.4	-0.4	0.5	0.1	13.5	10.2	0.0	0.0	0.0	0.0	...
ep	6.02	0.4	0.1	-0.4	-0.5	-0.4	0.0	3.7	19.4	0.0	0.0	0.0	0.0	...
A0	0.1227808	-0.5	0.2	0.4	0.1	0.1	0.0	10.1	7.9	0.0	0.0	0.0	0.0	...
Ef	7	-0.2	0.0	-0.5	-0.4	0.2	0.2	11.6	-0.5	0.0	0.0	0.0	0.0	...
El	39.3	-1.1	0.0	-0.1	0.1	0.7	0.0	-1.9	14.3	0.0	0.0	0.0	0.0	...
Ls	14.7	0.1	-0.5	-0.2	0.3	0.1	0.3	0.6	4.3	0.0	0.0	0.0	0.0	...
Fs	3.6	0.5	0.3	-0.5	-0.3	0.1	0.5	14.5	11.3	0.0	0.0	0.0	0.0	...
egg_mass	0.00096	0.0	-0.8	0.3	-0.5	0.9	0.9	21.8	-3.4	0.0	0.0	0.0	0.0	...
a_g	0.000012312	-9.9	10.1	-9.7	9.4	-10.3	10.4	6.7	20.4	0.0	0.0	0.0	0.0	...
b_g	2.969	-72.7	262.6	-72.9	260.9	-72.7	265.7	-57.5	5.8	0.0	0.0	0.0	0.0	...
eggs_per_bass	375000	0.4	-0.1	-0.2	0.1	0.5	0.5	6.4	13.9	0.0	0.0	0.0	0.0	...
Gl	0.02485	-0.2	-0.1	-0.3	-0.3	0.4	-0.3	-28.2	51.8	0.0	0.0	0.0	0.0	...
H	4.46E-01	-0.2	0.0	-0.3	-0.3	1.0	0.7	9.6	11.7	0.0	0.0	0.0	0.0	...
AM	4.91E-04	0.6	-0.4	-0.4	-0.1	0.4	0.4	8.9	-2.0	1.7	-1.7	1.7	-1.7	...
AE	1.57E-03	-0.2	0.2	-0.5	-0.1	0.5	0.3	-3.4	10.6	0.0	0.0	0.0	0.0	...
PM	8.42E-02	0.4	0.1	-0.4	-0.3	0.3	0.7	71.9	-37.1	0.0	0.0	0.0	0.0	...
I	5.20E+13	0.0	-0.2	-0.5	-0.6	0.3	0.4	-1.6	-0.9	0.0	0.0	0.0	0.0	...

Parameter	Value	N3.dec.	N3.inc	N4.dec.	N4.inc	N5.dec.	N5.inc	N6.dec.	N6.inc	N7.dec.	N7.inc	N8.dec.	N8.inc	N9.dec.	N9.inc	...
linf	84.55	0.0	0.1	0.0	0.3	0.0	-0.3	-2.1	-1.9	0.4	-0.5	3.9	-0.7	-0.6	-1.3	...
K	0.096699	-0.1	-0.1	-0.1	-0.3	0.1	-0.9	0.6	-0.7	0.7	0.2	-0.8	1.1	-2.7	-1.0	...
t0	-0.73	0.0	0.1	-0.2	-0.2	0.0	-0.7	-1.0	-1.9	1.9	-0.5	2.9	-1.9	-0.7	-0.8	...
Ea	0.5	0.0	0.1	0.0	-0.4	-0.6	-0.8	-1.5	-1.1	-0.3	-0.3	2.8	-1.4	-1.7	-1.0	...
EaS	0.1903656	0.0	0.0	0.0	-0.3	-0.9	0.0	-0.5	0.6	-0.2	0.6	0.6	-0.2	-0.5	-1.1	...
Cmax	0.54	0.1	0.0	-0.2	0.0	0.0	-0.6	-1.8	-1.3	0.9	0.0	1.2	3.0	4.6	-1.6	...
ep	6.02	0.0	0.0	-0.2	-0.2	1.1	0.0	-1.4	-1.5	1.5	0.6	1.1	0.8	-1.3	0.4	...
A0	0.1227808	0.0	0.0	-0.3	0.1	0.2	0.6	-0.9	-0.6	-0.7	0.2	-0.9	0.9	-1.0	-1.1	...
Ef	7	-0.1	0.0	0.0	0.2	0.0	-0.2	-0.9	-0.1	1.3	0.1	4.0	-1.0	-1.2	-2.1	...
El	39.3	-0.1	0.1	-0.3	-0.3	-0.7	0.1	-0.6	-0.2	0.9	-0.7	0.8	4.5	-1.5	-1.8	...
Ls	14.7	0.1	0.2	-0.1	-0.3	-0.5	-0.4	1.3	-0.5	-0.1	1.2	-2.4	0.0	-1.4	-0.9	...
Fs	3.6	-0.1	0.0	0.0	-0.4	-0.3	-0.1	-1.8	-0.3	0.1	-0.7	2.3	1.4	-1.8	-0.7	...
egg_mass	0.00096	0.0	0.0	0.2	-0.3	0.1	-0.3	-0.7	-1.1	1.3	0.4	-0.2	-0.6	-0.9	-1.0	...
a_g	0.000012312	0.0	0.1	-0.1	-0.2	0.3	-0.2	-1.3	-2.1	0.1	-0.4	6.0	1.1	-1.6	-0.7	...
b_g	2.969	0.1	0.0	-0.3	-0.4	-0.1	-0.8	-2.2	-1.2	-0.3	-0.2	5.3	-0.2	0.0	-0.6	...
eggs_per_bass	375000	0.1	0.1	0.4	-0.3	-0.3	-0.6	-0.7	-0.4	0.1	1.0	0.4	-0.7	-1.7	-1.3	...
Gl	0.02485	0.0	-0.1	-0.3	-0.2	0.4	-0.6	-1.7	-0.7	0.7	-0.9	-0.3	-1.6	-0.7	-0.2	...
H	4.46E-01	-0.1	0.0	-0.1	0.0	0.1	0.1	-1.2	-1.9	-0.7	-0.2	3.4	2.1	-0.7	-1.0	...
AM	4.91E-04	1.7	-1.8	1.4	-2.1	1.1	-2.1	1.2	-2.2	1.4	-1.1	4.5	0.6	-0.1	-2.7	...
AE	1.57E-03	0.0	0.0	0.0	-0.3	0.3	-0.7	-1.0	-1.7	-0.4	-0.2	3.3	1.6	-1.6	-1.0	...
PM	8.42E-02	0.1	0.0	-0.3	0.0	-1.0	1.0	-0.9	-1.4	-0.3	-1.0	-0.4	0.1	-1.3	-1.1	...
I	5.20E+13	-0.1	0.0	0.0	-0.2	-0.6	0.0	1.7	-1.6	0.1	-0.1	2.4	3.4	-0.2	-0.9	...

Parameter	Value	N10.dec.	N10.inc	N11.dec.	N11.inc	N12.dec.	N12.inc	N13.dec.	N13.inc	N14.dec.	N14.inc	N15.dec.	N15.inc	N16.dec.	N16.inc.	...
linf	84.55	0.9	2.0	0.5	1.2	-0.6	-1.4	-1.2	-1.1	-2.0	0.2	0.3	1.1	0.3	-2.4	...
K	0.096699	0.5	4.6	10.5	0.5	12.3	1.8	-0.6	2.0	-1.1	-2.0	0.8	0.7	8.9	11.6	...
t0	-0.73	0.8	0.9	-0.1	0.3	-0.3	-0.2	17.1	-2.0	-1.4	-0.7	0.5	1.5	10.6	-1.2	...
Ea	0.5	5.4	1.8	3.4	-0.1	-1.6	-0.6	-1.8	-2.0	0.2	-2.2	0.5	0.8	0.2	-0.1	...
EaS	0.1903656	0.1	0.1	-0.2	-0.7	1.3	-0.1	-1.0	-1.5	-0.3	-0.1	-0.9	1.1	0.7	3.2	...
Cmax	0.54	2.2	0.5	1.6	0.2	0.1	-0.9	-2.0	-1.3	-0.3	-0.5	0.2	0.8	0.3	-0.3	...
ep	6.02	0.4	1.6	1.5	2.0	-0.4	-0.7	-1.6	2.4	-1.4	-1.1	0.5	0.1	0.4	3.4	...
A0	0.1227808	4.9	-1.2	3.3	0.8	-1.1	-1.1	-0.9	-1.4	-1.2	-2.0	2.4	0.9	0.8	0.6	...
Ef	7	-1.1	8.5	5.3	-0.9	-0.3	-0.8	-1.0	-0.3	-0.5	-0.8	0.1	-1.6	-2.3	-1.5	...
El	39.3	0.5	-2.2	-0.6	-0.2	0.8	1.2	-0.4	2.7	-0.7	-1.0	0.8	2.6	-2.4	2.7	...
Ls	14.7	3.3	4.0	-0.5	0.8	-0.6	0.2	-1.5	-0.5	-1.8	-0.6	0.6	0.5	9.3	4.7	...
Fs	3.6	-0.8	1.4	0.0	1.9	1.3	1.2	5.8	-1.6	0.8	-1.1	1.0	0.9	5.8	-1.2	...
egg_mass	0.00096	2.4	1.4	2.6	1.8	1.0	-0.5	-0.8	-2.0	-1.4	-0.4	1.9	0.9	-1.0	1.0	...
a_g	0.000012312	2.1	-1.5	0.3	-0.3	-0.8	-0.8	2.8	-0.8	-1.4	0.0	-1.0	0.0	2.3	-0.7	...
b_g	2.969	0.6	-1.0	2.4	-0.8	-0.4	1.3	-0.9	0.1	1.0	0.2	-0.2	2.4	-0.4	3.5	...
eggs_per_bass	375000	0.6	0.0	3.6	0.5	2.8	-0.7	-0.4	-0.9	-1.6	-1.7	0.3	-0.3	10.5	-2.1	...
Gl	0.02485	9.6	1.1	0.0	0.1	-0.2	-0.8	-0.2	-0.7	0.6	-2.1	0.8	2.2	17.6	-1.2	...
H	4.46E-01	6.4	0.6	-0.6	0.2	-0.4	0.2	-1.5	-0.7	6.6	-1.6	0.5	0.5	9.7	-3.3	...
AM	4.91E-04	0.1	6.8	1.1	-0.8	1.9	-2.5	-0.1	-3.1	-0.7	-1.9	0.5	0.2	1.2	-2.6	...
AE	1.57E-03	9.2	1.7	12.1	2.6	0.0	-0.3	15.3	3.2	19.0	-1.8	0.2	1.2	-2.3	0.7	...
PM	8.42E-02	2.5	0.4	12.2	1.2	0.2	0.9	-1.2	-1.1	-0.6	-1.1	0.9	0.9	-1.0	-2.2	...
I	5.20E+13	-0.4	1.3	0.4	1.4	-0.5	-0.5	-1.1	0.2	-0.5	-1.1	0.8	0.1	-0.7	5.6	...

Parameter	Value	N17.dec.	N17.inc	N18.dec.	N18.inc	N19.dec.	N19.inc	N20.dec.	N20.inc	N21.dec.	N21.inc	N22.dec.	N22.inc	N23.dec.	N23.inc	...
linf	84.55	-0.4	-0.2	1.9	1.3	-0.4	-1.0	0.7	-0.1	2.3	-0.1	0.6	3.6	0.0	-0.9	...
K	0.096699	-0.3	-1.0	0.2	0.2	-1.3	-0.1	-0.1	1.0	-0.6	-0.3	-0.2	0.3	-0.5	-0.3	...
t0	-0.73	0.9	-1.3	1.1	0.1	0.4	1.5	-0.1	0.3	3.0	0.5	1.7	-0.2	-0.2	-0.2	...
Ea	0.5	-1.6	-0.8	1.3	0.9	-0.7	-0.1	-0.2	-0.2	-0.3	1.4	0.9	2.0	0.2	0.1	...
EaS	0.1903656	-0.3	-1.0	1.3	0.8	-0.5	-0.1	0.6	-1.0	2.0	1.6	2.0	1.5	-1.4	-1.6	...
Cmax	0.54	0.6	1.2	1.4	0.1	2.1	-0.6	0.0	-0.8	-0.1	1.7	1.5	2.0	-0.4	0.2	...
ep	6.02	-0.1	-0.8	-1.1	-1.4	-1.0	-1.0	-1.5	-0.5	0.7	1.0	2.0	1.5	-0.9	-3.0	...
A0	0.1227808	-1.1	-0.8	0.5	0.8	0.3	-0.4	-0.5	0.0	-0.2	0.9	0.9	0.8	-1.2	-0.6	...
Ef	7	-0.8	-1.9	0.2	0.6	-0.4	0.4	-0.1	0.4	2.7	-0.4	1.2	-0.2	-1.2	-0.6	...
El	39.3	-1.1	-2.5	1.2	-1.4	-2.2	0.5	0.6	-0.3	0.4	-0.5	2.4	1.3	0.3	-0.8	...
Ls	14.7	0.1	8.1	-0.1	0.3	-0.8	1.9	-0.8	0.7	-0.7	0.4	0.7	1.5	-0.4	-2.6	...
Fs	3.6	-1.0	-0.1	0.1	1.2	0.1	1.0	-0.4	1.6	0.5	0.5	1.8	1.6	-0.2	-1.8	...
egg_mass	0.00096	-1.5	-1.9	0.0	1.4	-0.6	-0.5	-0.2	-1.0	1.3	0.2	1.1	1.2	0.6	-0.8	...
a_g	0.000012312	-0.3	-1.1	-1.1	-0.3	1.0	-1.5	-0.1	-0.7	0.5	1.5	1.4	2.4	0.0	0.0	...
b_g	2.969	-0.8	-0.8	0.2	0.6	1.9	-0.2	-0.3	-0.3	1.5	1.3	0.3	1.1	1.2	-0.5	...
eggs_per_bass	375000	-0.1	-1.2	1.5	1.8	-0.6	-0.1	-0.1	-0.8	-0.3	-0.9	1.1	-0.1	-1.2	-0.7	...
GI	0.02485	0.6	-2.1	8.3	0.0	0.4	0.1	0.9	0.6	0.8	0.8	1.3	0.5	-2.3	-1.7	...
H	4.46E-01	-0.9	-1.0	0.6	2.3	-1.0	0.8	-0.1	0.7	0.8	0.7	1.5	1.1	-1.5	-0.7	...
AM	4.91E-04	0.6	-3.0	2.7	-0.7	0.6	-2.5	3.3	-2.2	3.0	-1.4	4.4	-0.2	0.9	-3.3	...
AE	1.57E-03	-1.5	-0.1	0.7	-0.3	-0.8	0.2	0.9	0.1	1.0	0.9	2.3	2.9	-1.8	0.5	...
PM	8.42E-02	-0.4	-0.6	-0.2	0.2	1.1	1.0	-1.1	-0.4	0.3	-1.2	2.1	1.1	-0.4	-0.9	...
I	5.20E+13	-1.8	-0.9	1.1	0.6	-1.8	0.2	-1.0	-0.5	0.5	1.2	1.0	1.2	0.6	-3.6	...

Parameter	Value	N24.dec.	N24.inc	N25.dec.	N25.inc	N26.dec.	N26.inc	N27.dec.	N27.inc	N28.dec.	N28.inc.	N29.dec.	N29.inc.
linf	84.55	-1.3	-0.5	1.2	1.8	1.1	0.1	0.5	1.3	-1.6	-2.5	-0.4	0.3
K	0.096699	0.1	-1.6	2.1	1.5	-0.2	-0.1	-0.6	0.9	-2.1	-2.5	-0.7	-0.6
t0	-0.73	-0.5	0.9	1.1	0.2	0.6	-0.4	0.0	0.6	-1.4	-1.5	0.3	-1.8
Ea	0.5	-0.8	-0.5	2.0	1.8	0.7	-0.4	0.8	0.4	-0.8	-2.0	-0.7	-1.4
EaS	0.1903656	-0.3	0.6	1.6	1.6	-0.1	2.3	0.2	-0.6	-2.5	-1.7	0.4	-0.4
Cmax	0.54	-0.6	-1.9	-0.3	0.3	0.1	0.5	1.8	1.1	-0.4	-0.8	1.8	0.0
ep	6.02	-1.2	-1.0	-0.1	2.4	0.0	0.4	-0.1	0.4	-1.4	-1.9	0.0	0.2
A0	0.1227808	-0.7	-1.0	1.5	2.2	-0.6	2.1	0.1	1.9	-1.1	-2.6	0.0	-0.1
Ef	7	-0.6	-1.0	1.1	2.0	0.8	0.4	0.5	-0.1	-1.9	-2.3	-0.5	-0.9
El	39.3	-0.8	-2.2	0.4	0.7	0.7	0.5	1.1	0.6	-0.8	-0.6	-0.4	-0.3
Ls	14.7	-2.0	-2.4	0.3	1.2	2.0	1.6	0.7	-0.2	-1.8	-1.7	-0.8	0.1
Fs	3.6	-1.6	-0.9	1.3	0.6	-0.3	1.3	0.4	0.8	-1.2	-0.8	-0.3	-1.1
egg_mass	0.00096	-0.6	-0.7	1.6	2.0	2.5	1.2	1.5	-0.7	-0.9	-1.9	0.7	0.4
a_g	0.000012312	-0.1	-1.6	2.0	1.0	-0.4	1.2	0.8	1.4	-1.2	-1.8	-1.0	-0.5
b_g	2.969	-0.4	-0.7	1.4	1.9	1.3	1.7	0.2	0.4	-1.3	-0.8	-0.7	-0.6
eggs_per_bass	375000	-0.4	0.4	2.2	1.2	1.3	0.9	1.1	0.7	-1.4	0.0	0.4	0.3
Gl	0.02485	-1.0	-0.3	2.4	2.2	0.2	-0.1	1.0	0.1	-1.5	-1.5	0.1	-0.5
H	4.46E-01	-0.6	-1.9	1.4	1.5	0.6	0.9	1.8	1.3	-2.7	-2.4	0.3	-0.5
AM	4.91E-04	2.6	-2.2	3.2	-1.4	3.4	0.0	4.3	-2.0	0.0	-3.2	1.6	-2.0
AE	1.57E-03	-0.4	-1.8	0.5	1.6	1.3	2.0	0.0	0.5	-1.7	0.1	-1.9	-0.8
PM	8.42E-02	-0.9	-0.3	2.1	0.5	1.1	2.7	1.8	0.1	-1.2	-0.9	0.7	-0.2
I	5.20E+13	0.2	-1.0	2.3	1.5	1.1	0.0	0.5	1.2	-2.7	-0.3	-0.3	-1.1

5.13 Model output corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

5.13.1 Summary

Tests from the original model by (Walker *et al.*, 2020) on the Spatial patterns of the IBM remain the same. In addition to these we compare estimations of egg production for the stock and maturity at age outputs from SS3.

The IBM shows reasonable correlation between potential fecundity and predicted egg production in SS3 (Fig. 5-19). Here the IBM output is the total combined potential egg production of the spawning stock, which is a function of the number and size of the individuals. When we compare realized fecundity with the egg predictions from SS3 we see poor fits (Fig. 5-20). Here realized fecundity is a function of number, size, and condition of the individuals and one explanation for the poor fits may be that the data from the stock assessment we use for calibration and assessment of fits does not consider condition of individuals. An additional explanation for the poor fits may be an over estimation of the cost of producing eggs. We show a similar pattern to age at maturity in IBM outputs vs SS3 (Fig. 5-21). Walker et al., 2020 compared IBM spatial outputs to catch data from the Scientific, Technical and Economic Committee for Fisheries (STECF) and showed reasonable correlation with some trends to overestimate catch in the Celtic and Irish Seas and underestimate catch in the North Sea. We did not re-run the spatial tests done by Walker *et al.*, 2020 as the movement sub models for migration remain mostly unchanged (see TRACE sections 5.7 and 5.8.11 for more details on movement sub models).

Figure 5-19. Combined potential fecundity IBM outputs vs number of egg predictions from the SS3 stock assessment output for years 2004-2014. Black = SS3, Red = IBM outputs.

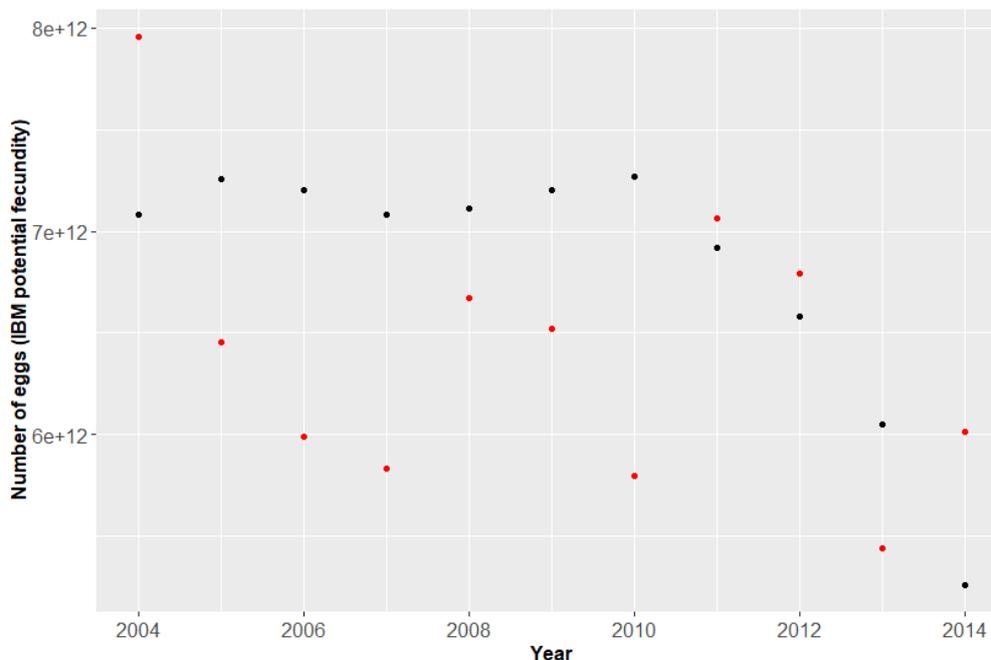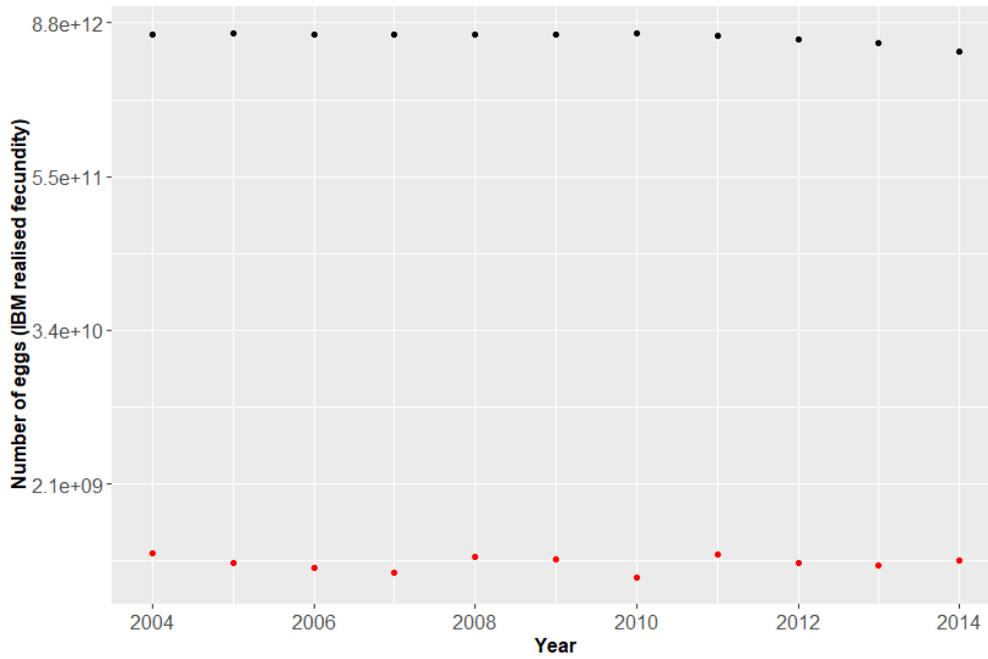**Figure 5-20. Combined realized fecundity IBM outputs vs number of egg predictions from the SS3 stock assessment output for years 2004-2014. Black = SS3, Red = IBM outputs.**
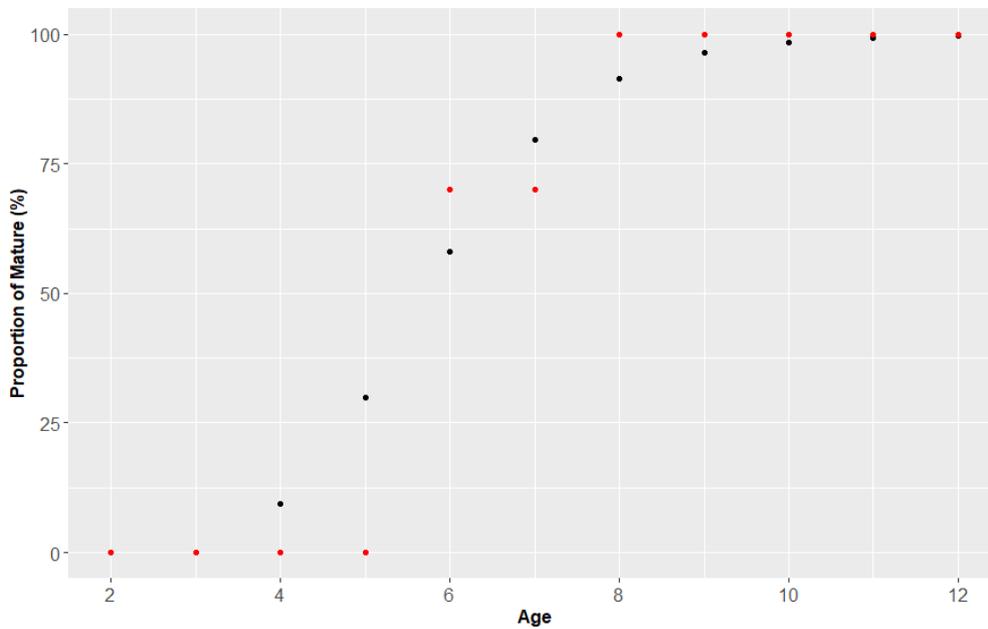

Figure 5-21. Percentage of each age class (2- 12 years of age) that are mature (>42 cm L) IBM outputs vs proportion mature predictions from the SS3 stock assessment. Black = SS3, Red = IBM outputs.

6 General discussion

In this final chapter, I give a detailed overview of the thesis and highlight the potential implications for management from my work. I then go on to discuss some caveats and consider possible future developments.

6.1 Thesis overview

Throughout this thesis I have focussed on the individual with the aim of gaining mechanistic insight into the fish and fishers of the northern stock of sea bass. Chapters two, three and four are written as journal articles and chapter five is a technical document (TRACE) in support of the IBM presented in chapter four.

Chapter two shows a broadly applicable modelling approach to investigate sublethal impacts of a broad range of anthropogenic stressors on the life processes of individual fish. The approach developed is built on established bioenergetics methods and provides a comprehensive energetics overview through from initial escape to longer term injury/behavioural changes. Unique to this method, over other bioenergetics stressor models, is splitting the impact of the stressor into two parts. Firstly, assuming an escapable acute stressor, the fish may attempt to flee; this could include dodging an oil spill, avoiding anthropogenic noises, or trying to break free from commercial or recreational fishing gear. The period for which fish swim to escape depends on many factors specific to individual stressors. For example, it may depend on the proximity of the fish to an oil spill, construction project or, in a fishing situation, how long gear is being pulled. In these situations, the fish is swimming at speed away from somewhere it does not want to be and is forced to spend energy that is subsequently unavailable for life processes. As well as escaping, the fish may suffer an injury or endure a change in behaviour due to the stressor. This could be an injury from commercial/recreational fishing gear (e.g., mouth damage from a hook) or changed behaviour from a range of anthropogenic stressors e.g., chemical pollution and/or noise pollution from construction and shipping. Such effects may impact an individual fish's ability and preference to feed, resulting in reduced ingested energy available for life processes. To show a broad range of possible impacts, results are presented using heat maps that allow the simultaneous display of many combinations of reduced ingestion rates and durations of effect. Each combination of these is unique and equates to a loss of energy. When this loss is compared with the energy needed to achieve life processes it is possible to investigate the overall impact of the stressor in question.

The study uses catch and release fishing (C&R) of European sea bass as a case study for the modelling approach developed in chapter two. C&R fishing is the process of capturing a fish with a hook and line, and then releasing the live fish back into the water presumably unharmed (Arlinghaus *et al.*, 2007). C&R is widely used as part of enforced legislation either exclusively or as part of other capture regulations. For example, recreational targeting of sea bass in the UK has undergone changing restrictive legislation including mandatory catch and release for periods of the year, minimum landing sizes and bag limits that force anglers to release fish once their limit is achieved (GOV.UK, 2016, 2017, 2018, 2019, 2020). C&R fishing is also practiced as a voluntary act for example in the UK there is a long tradition of C&R (Lewin *et al.*, 2018). Although C&R is generally used with the assumption that the returned fish are unharmed it is now understood that there is often a percentage of released fish that suffer post release mortality in addition to a range of sublethal impacts (Cooke and Cowx, 2004). The results from the study in chapter two show potential impacts of catch and release angling on a single sea bass. Most outcomes where quite minor but did range from zero to losses of up to 100% growth and 62% fecundity, and although these results are not

validated this may be a good starting point to review potential effects and to establish the relevance of possible experimental investigation. I go on to suggest that the energy budget approach could be used within an IBM (such as the model presented in chapters four and five). Here an IBM could help indicate emergent population level effects for a broad range of anthropogenic stressors and cumulative impacts for many species and hence contribute to understanding and mitigating sublethal anthropogenic impacts on fish.

Chapter three moves on from fish, and focuses on the factors influencing fisher decisions of the UK under 10m fleet that target sea bass. Here results and deductions are shown from the analysis of fishing logbooks alongside environmental and socio-economic datasets. It is well appreciated that fisher decisions are influenced by complex socio-economic factors (Ota and Just, 2008) and that small vessels can be particularly vulnerable to environmental change (Sainsbury *et al.*, 2018). In fisher behaviour studies involving larger vessels, automatic information or vessel monitoring systems (AIS and VMS) are often used to provide high resolution fisher behaviour data (Lee, South and Jennings, 2010). The number of vessels that use AIS and VMS is increasing by 10-30% annually (estimated between 2014-2017 [FAO 2020][1]) and provides scope for more detailed analysis of fisher behaviour in further studies. Unfortunately, the vessels in the study fleet of under 10m vessels analysed in chapter three have yet to adopt these measures. Instead, the study relies on fishing vessel logbook data with environmental and socio-economic data to investigate fisher behaviour. The method presented splits fisher behaviour into two components, firstly the decision to leave the port, analysed with a logistic model, and then the success of the fishing trip, analysed with a linear regression model. To assess the predictors of whether a vessel leaves harbour I chose a range of predictors to enter into the model namely *wave height*, *fuel price* and *time of first high tide*. The chosen predictors were believed to be key predictors of fisher behaviour and both fuel price and weather had been highlighted in other fisher behaviour studies (e.g., Abernethy *et al.*, 2010; Shepperson *et al.*, 2016). To then assess if any of our predictors had a significant effect on fishing success, I used the same predictors (*wave height, tide,* and *fuel price)* in addition to *change in fish price, month,* and *year*. The predictors chosen from the logbook are assumed to be key predictors of fishing success and of relevance to legislation and future management decisions (GOV.UK, 2016, 2017, 2018, 2019, 2020).

At the start of my fisher behaviour analysis, I incorporated as many feasible and relevant predictors as possible within the limitations of data availability. However, a large proportion were inconsequential to fishing decisions or had an unexplained effect. The main finding were that weather had a large influence on fisher behaviour. Results showed that in calm conditions (wave heights less than one meter) most vessels left port, but fewer than 25% left port when wave height exceeded two meters, and those that did leave then caught less. Another notable result was the impact of tide on these fisher decisions. The decision to leave port was affected by the time of high water, but effects differed between ports. There is likely a range of explanations for the impact of tidal state; for example depth of water may limit the ability to leave or return to a tidal mooring, so leaving on an early tide may allow a fisher to stay out at sea and fish through two tide cycles rather than be limited to one. Another possible explanation is that early tides allow fishers more sociable hours and/or to fish in daylight. The preference for certain tide times could also be due to a perceived increased chance of catching sea bass and/or due to logistical preferences. Fishers may be attracted to certain tide times as changes in current velocity could carry the scent of bait further and also have a direct impact on feeding behaviour of fish (Stoner, 2004). Empirical studies of these effects are rare (Stoner, 2004) but grey literature in fishing magazines suggests sea bass have greater feeding activity during times of tidal movement, making them potentially profitable times to go fishing. A final consideration is the different effect tide can have on different fishing gears (Sharples

et al., 2013). West Mersea was shown to have a different response to tidal effects than the other ports, contributing to this could be the prevalence of using gill nets, which is different to most vessels in other ports that choose hook and line. Findings from chapter three have some implications for the management of sea bass and other small-scale inshore fisheries. Management for sea bass is through technical measures that include catch limits (monthly, annual), closed seasons to protect spawning aggregations, and minimum size (42cm). Increases of extreme weather events especially during the key fishing seasons may impact on the ability of under 10-meter inshore vessels to land catch limits within the allowed time periods. As these are time bound and there is no carryover, this could impact the potential revenue generated and the profitability of fishers.

Chapters four and five present a spatially explicit individual based model (IBM), which models population dynamics and simulates spatial distribution of the northern stock of sea bass in ICES divisions' 4.b–c, 7.a and 7.d–h. In chapter four, I present the IBM as a journal article and then go on to give full technical details in chapter five in a TRACE document. The model presented is a major enhancement to an existing IBM of the northern stock of sea bass published by Walker et al., 2020. The key updates are: 1) addition of a realistic energy budget driven by dynamic maps of phytoplankton density; and 2) inclusion of all life stages (i.e., pelagic stages, juvenile and mature fish). The energy budget approach in the IBM presented uses the approach developed in chapter two and both are based on an established method (Sibly *et al.*, 2013) that has been used for a range of species and applications (e.g., Sibly *et al.*, 2013; Boult *et al.*, 2019; Boyd, Walker, *et al.*, 2020). The basis of the energy budget is that organisms absorb energy which they spend upon life processes including maintenance, growth, and reproduction. Organisms prioritise energy allocation in the order of maintenance, growth reproduction and any excess energy is stored until the reserves are full. If there is insufficient energy, then the organism can 'pay' for growth and reproduction from reserve energy until depleted, at this critical point all energy is then retained for essential maintenance (Sibly *et al.*, 2013). The IBM benefits from dynamic maps (sourced from remote sensing data) of sea surface temperature (SST) and chlorophyll concentration which act as a proxy for phytoplankton biomass and ultimately represent food availability. Individuals respond to their local food availability and SST according to their energy budgets and give rise to the emergent population dynamics model outputs.

The IBM outputs are important metrics of stock status currently used by scientists to provide advice on fishing opportunities for the stock. The model is assessed for goodness of fit with a comparison of outputs (numbers and mass at age, spawning stock biomass) to those from the current ICES assessment (stock synthesis 3 [Methot and Wetzel, 2013]). I present some encouraging fits to the ICES stock assessment data and suggest that this IBM could be a promising complementary stock assessment tool. The mechanistic and modular nature of IBMs are recognised in fisheries and are a well-established tool to study both fish populations (Kühn *et al.*, 2008; Politikos, Huret and Petitgas, 2013; Boyd *et al.*, 2018), and fisher behaviour (Jules Dreyfus-León, 1999; Millischer and Gascuel, 2006; Bastardie *et al.*, 2010; Bailey *et al.*, 2019; Lindkvist *et al.*, 2020). Here I suggest that there is scope to use the sea bass IBM to test a range of management scenarios and responses to environmental change as well as the potential to add in some of the sublethal stressor and fisher behaviour findings in chapters two and three.

6.2 Caveats and future work

Throughout this thesis I have focused on the individual fish and fishers of the northern European sea bass and by using an individual-based approach I have attempted to gain insights into some of the important mechanisms of this fishery. A common limitation and caveat through all work completed

as part of this thesis is a shortage of data: this is a widely recognised constraint with many forms of mechanistic and individual-based analysis (Johnston *et al.*, 2019). Results from all three models presented in chapters two, three, and four would be more robust with more data. Nevertheless, despite data limitations, the chapters are a step towards the original thesis aims. Throughout the remainder of this chapter, I will highlight some specific caveats to my work and identify some promising future directions for the models developed in this thesis.

The energy budget modelling approach in chapter two is broad and could, with appropriate consideration, be applied to a wide range of anthropogenic stressors and fish species. As in other bioenergetics models (e.g., Beyers and Rice, 2002), to apply this method to different stressors or species it is necessary to collect relevant values for duration of escape, if any, and re-parametrise the energy budget equations for the intended species. Websites such as FishBase (Froese and Pauly, 2018) are a useful starting point for many life history parameters; however understanding the range of escape durations and injury/behaviour severity would ideally be grounded in experimental or field work. For example more detailed information on swimming behaviour during stressor escape could be learned from tagging experiments, to measure how long and fast fish swim (Graves, Horodysky and Latour, 2009; Brownscombe *et al.*, 2013; Braun *et al.*, 2015) and respirometer experiments could be used to investigate changes in metabolic rate (Wright *et al.*, 2014; Rupia *et al.*, 2016). The end user of this modelling approach would be required to consider the appropriate caveats for their own study species. Considerations include disease status of the study species/stock, as infected fish may suffer additional complications from anthropogenic stressors (Steeger *et al.*, 1994; Gauthier *et al.*, 2008; Latour *et al.*, 2012; Lapointe *et al.*, 2014; Gervasi *et al.*, 2019), and it may also be necessary to take into account complications with unique life history, e.g., brood protecting species (Suski *et al.*, 2003; Hanson *et al.*, 2007; Pinder *et al.*, 2017). To combat any of these issues it is important to consider any further information/experimental data available and make sure to add in these effects or to be aware of the impacts they may have on any conclusions taken. Users may be able to borrow some parameters from similar species or make assumptions about responses to similar stressors in the literature, however more detailed experimental data would be required if the aim was to validate the model.

A promising future line of work is to use the energy budget model within the IBM presented in chapters four and five. An IBM could be used to investigate sublethal impacts that last beyond one year, (e.g., long term injury's or behaviour changes) as well as account for any catch-up growth where some species may be able to make up lost growth after a stressor event (e.g., compensatory growth [Cline *et al.*, 2012]). By taking advantage of the modular structure of the IBM it is possible to make a range of additions to further its utility. For example, with the addition of a dynamic map of noise, it may be possible to investigate the emergent population effects of anthropogenic noise pollution similar to work completed on harbour porpoise by Nabe-Nielsen *et al.*, 2014.

Chapter three focuses on fisher behaviour with the principal result from the study being the large influence of weather and, to a lesser extent tide, on fisher behaviour. However, aside from weather and tide, a large proportion of the variables tested were inconsequential to fishing decisions or had an unexplained effect, with a notable result being that fishing decisions varied substantially between vessels. The heterogeneity between vessels is likely due to a variety of reasons including the effects of seasonality on individual trips but also variation in skipper experience and risk perception (Salas and Gaertner, 2004), sometimes termed the skipper effect (Thorlindsson, 1988). Further insight into the skipper effect is often gained from semi-structured interviews (SSI) and other survey techniques (Hill *et al.*, 2010; Zukowski *et al.*, 2011; Shepperson *et al.*, 2016). A worthy extension to the work completed in chapter three would be to carry SSI to compliment the findings from the data.

SSIs are commonly used in social science (Leavy, 2014) and also within fisheries research (Hill *et al.*, 2010; Zukowski, Curtis and Watts, 2011). This interview technique is designed to make use of the knowledge that can be gained through dialogue and strikes a balance between flexibility, to allow the interviewer to follow up on important points, and structure to guide the conversation towards the desired information (Leavy, 2014). There are many ways to analyse the outcomes of SSI (e.g., thematic analysis or hypothesis testing tables [Robson, 2011; Zukowski, Curtis and Watts, 2011]) that would make an interesting extension to the work completed in chapter three. A further interesting extension to chapter three's fisher behaviour work would be the inclusion of any VMS data that becomes available in the future (FAO, 2020). The main reason for using logbooks is the lack of opportunity to use VMS/AIS which is not used by the smaller vessels that target sea bass. Although this may become possible in the future (FAO, 2020) and would facilitate more detailed analysis of vessel movements and fisher behaviour (Shepperson *et al.*, 2018). However, without interviews or VMS data I believe our study is a good starting point to indicate some of the mechanisms of fishing pressure responses to a range of drivers. An attractive next step would be to add fisher behaviour sub models to the IBM. Here it might be possible to have a mechanistic link between some of the important fisher behaviour drivers and the fishing pressure they inflict on the sea bass stock (e.g., the spatial concentration of fishing effort and the pressure of fishing near protected areas [McCluskey and Lewison, 2008]).

Chapters four and five present a spatially explicit IBM of the northern stock of sea bass. The IBM provides emergent outputs of SSB, numbers and mass at age and is built in a modular fashion. Throughout the construction, parametrisation and validation of the IBM it is necessary to make a series of assumptions and simplifications. However, to reduce the number of assumptions and to reduce uncertainty around model outputs would require large amounts of data which is one of the main limitations of IBMs (Johnston *et al.*, 2019). One sub model that could be substantially improved in the IBM presented is movement. Here the timings of fish migrations within the model are influenced by SST but the actual movement sub model is hardwired with the empirical rules set for movement and migration from the hypothesis of Pawson and Pickett, 1987; Pawson *et al.*, 2007. Future updates might be to use modern tagging studies (Quayle *et al.*, 2009; O'Neill *et al.*, 2018; de Pontual *et al.*, 2019) that could provide data on which a mechanistic movement sub model could be built and added to further the spatial utility of the model. As mentioned, there is scope to capitalize on the modular nature of the IBM and include both a mechanistic fisher behaviour sub model and responses to some different anthropogenic stressors. Despite the limitations I believe that the modelling assumptions are sensible, and the model developed produces good fits against the available calibration data from the current stock assessment (SS3). With or without these additions there is a scope to use the IBM for a range of scenario testing including management measurements (e.g., spatial/temporal closures, changes to total allowable catch or landing size limits) and reactions to both ecosystem drivers (e.g., changes associated with climate change) and anthropogenic stressors (e.g., sublethal responses to chemical/noise pollution and/or catch and release angling).

6.3 Impact of the research

The work in this thesis has focussed on the northern stock of sea bass and has resulted in some new applications. Firstly, the energy budget model developed in chapter two has been discussed in its application to recreational fisheries at the ICES recreational fishing working group (WGRFS) and this same approach has also been adopted in an ongoing project with University of Exeter. Working with Exeter we are using the energy budget approach (from chapter two) to add in responses to the stresses of anthropogenic noise (e.g., wind farms and shipping) in the sea bass IBM (from chapters four and five). For this project the IBM has been updated with: 1) a dynamic noise map added to the

model environment; 2) modifiers have been added to the energy budget equations. With these additions the ingestion rate of individuals within the model can respond to the noise map, these then cause knock on changes to vital rates through the energy budget and give rise to emergent population changes. This project is ongoing and not yet complete but is a good example of how the sea bass IBM can be/is being used to test different stressors and scenarios for the stock.

An important application of the models built in this thesis is the identification of gaps in data sets relevant to sea bass. Here, I will give some short examples from each chapter which highlight where future research focus could improve the data available for this stock. The work in chapter two highlighted the need for more experimental work towards the realised impact of interruption of ingestion due to sublethal injuries of behavioural changes. Results from real experiments would allow the testing/validation of some of the hypothesis scenarios in this study (e.g., the realised reduction in feeding efficiency after a hook injury). Moving on to chapter three the study showed how the lack of AIS/VMS usage of the small vessels that target sea bass make analysing fisher behaviour much harder. This could be used as potential evidence for a legislative change that would encourage these small vessels to use these tracking technologies and improve understanding of fisher behaviour. Finally, when developing and calibrating the IBM in chapters four and five I found data gaps which led assumptions and decisions with knock on consequences to model uncertainty. The assumptions made because of these gaps are discussed in TRACE section 5.10 (examples include; better migration data, site fidelity, connectivity between spawning and nursery areas and spatial patterns of fishing mortality) but any endeavours towards filling them could help reduce model uncertainty and increase utility of the IBM and other models. The IBM approach has been presented to the stock assessors for sea bass within the ICES Working Group for Celtic Sea Ecoregion, and opportunities for incorporation of the outputs in the broader advice discussed.

6.4 Concluding remarks

Capture fisheries provide nutrition, jobs, and recreation across the world but are experiencing an increasing range of pressures and stressors. It is the difficult role of fisheries management to consider all the needs and threats of these aquatic resources and find an appropriate balance between stakeholders. In this thesis I have taken an individual-based approach to build a series of models of capture fisheries that analyse both the fish and the fishers of the northern stock of European sea bass. Specifically, I have: 1) developed an energy budget model to investigate the energetic impact of anthropogenic stressors on fish; 2) used statistical models to investigate fisher behaviour; and 3) developed a spatially explicit individual-based model with emergent population dynamics. The main limitation throughout the work completed is a lack of data, which has limited the strength of many of the conclusions made throughout the thesis. However, this could also be considered a benefit of these modelling exercises, by highlighting where there are data shortages that could be targeted in the future. Despite the limitations of lack of data, the work presented makes a promising case for developing the individual-based approach in modelling fisheries. The individual and mechanistic approaches presented and discussed throughout this thesis are suggested to be a useful complementary approach to current stock assessment models and could contribute to the successful management of the northern stock of sea bass amongst other important fish stocks.

7   References

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