



Developing dynamic energy budget (DEB) models for small pelagic fishes in the Southern Benguela.

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Thesis presented in fulfilment of the degree of Doctor of Philosophy in the department of Biological Sciences, Faculty of Science, University of Cape Town, South Africa.

May 2021

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The financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at are those of the author and are not necessarily to be attributed to the NRF.

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Date: 6 May 2021

Location: Pinelands, Cape Town, South Africa

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Acknowledgements

Many people have helped in the completion of this thesis in one way or another.

Financial support for this project was provided by the SEACChange Project of the South African Network for Coastal and Oceanic Research, funded by the Branch: Fisheries, and the National Research Foundation. The financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at are those of the author and are not necessarily to be attributed to the NRF.

I need to acknowledge and thank my supervisors Associate Professor Coleen Moloney and Dr. Carl van der Lingen for their organisation, proof reading, encouragement, and abundant support during this thesis. Thanks to Coleen for all the help with the model and to Carl, for organising the survey data from 2012 to 2016 from DFFE for the parameters and general ground truthing of the model. It has been a long road and I would not have been able to do it without your guidance. Special thanks to the now Department of Forestry, Fisheries and the Environment (formerly the Department of Agriculture, Forestry and Fisheries (DAFF) and Department of Environment, Forestry and Fisheries (DEFF)) for supplying the survey data.

To my parents Martin and Grea Wessels, who have supported me through this journey both financially and emotionally, thank you. Thank you for giving me a chance to follow my dreams and for always encouraging me.

Last but not least, to my husband, Hendrik Groenewald, thank you for being my rock through this long journey. For all your help with computer technical issues, setting up backups for the data and just being a sounding board, thank you.

Abstract

Dynamic energy budget models are useful for describing energy flow in individual organisms as functions of their state (*e.g.*, age, size, and energetic reserves) and environment (*e.g.*, food and temperature). Anchovy (*Engraulis encrasicolus*), redeye round herring (*Etrumeus whiteheadi*) and sardine (*Sardinops sagax*) are short-lived fish species co-occurring in the Southern Benguela upwelling system, where they experience marked environmental variability. This study developed full life cycle dynamic energy budget models of these species in the Southern Benguela, which could be compared to the same or similar species in other ecosystems and investigated trade-offs between temperature and feeding conditions in influencing the growth and reproductive outputs of the three species. The key hypothesis was that there would be niche differences among bioenergetic factors for the three species that allow them to co-occur. Models were created and calibrated using published information and survey data (recruitment, biomass, weight-at-length) from 2012-2016. Best visual fit values were estimated for five parameters, using von Bertalanffy growth models and length-weight relationships of each species. Results indicated that redeye round herring invested less than anchovy and sardine in reproductive storage capacity (larger maintenance ratio) and had lower assimilation rates. Sardine had higher structural growth costs than anchovy and redeye round herring. Larval redeye round herring took longer to reach metamorphosis than anchovy and sardine. In all three species, decreased growth rates of larvae in cool waters were mitigated by increased growth from good food availability. Good feeding condition associated with cooler temperatures halved the time spent as recruits in all three species. Thus, increased growth rates from good food availability outweighed decreased growth rates from cool temperatures and resulted in higher egg batch production in adults. Comparisons of Southern Benguela anchovy and sardine to similar species in other ecosystems showed differences in core parameters between regions because of the influence of environmental inputs and species differences, indicating that model parameters may not be species-specific or transferable between ecosystems. Differential responses of small pelagic fish species to environmental factors help in understanding the variable population dynamics of these species and can help predict the impacts of climate change.

Keywords: dynamic energy budget, DEB, anchovy, redeye round herring, sardine

List of Acronyms and Abbreviations

abj	a-type DEB model for organisms with metabolic acceleration during larval stage
APECOSM	Apex Predators ECOSystem Model
BA	Bad/limited adult food condition
BL	Bad/limited larval food condition
BR	Bad/limited recruit food condition
CBA	Cool bad/limited adult food condition
CBL	Cool bad/limited larval food condition
CBR	Cool bad/limited recruit food condition
CGA	Cool good/unlimited adult food condition
CGL	Cool good/unlimited larval food condition
CGR	Cool good/unlimited recruit food condition
DAFF	Department of Agriculture, Forestry and Fisheries (now DFFE)
DEFF	Department of Environment, Forestry and Fisheries (formerly DAFF, now DFFE)
DFFE	Department of Forestry, Fisheries and the Environment (formerly DAFF or DEFF)
DEB	Dynamic Energy Budget
Eqn.	Equation
FAO	Food and Agriculture Organization of the United Nations
GA	Good/unlimited adult food condition

GL	Good/unlimited larval food condition
GR	Good/unlimited recruit food condition
NEMURO	North Pacific Ecosystem Model for Understanding Regional Oceanography
NEMURO.FISH	North Pacific Ecosystem Model for Understanding Regional Oceanography For Including Saury and Herring
SL	Standard length
std	standard DEB model
WBA	Warm bad/limited adult food condition
WBL	Warm bad/limited larval food condition
WBR	Warm bad/limited recruit food condition
WGA	Warm good/unlimited adult food condition
WGL	Warm good/unlimited larval food condition
WGR	Warm good/unlimited recruit food condition

Chapter 1 Introduction: Bioenergetic modelling and small pelagic fish in the Southern Benguela ecosystem

1.1 The importance of understanding the physiology of organisms

Marine fishes, as water-breathing ectotherms, have complex life cycles which often comprise several distinct life-history stages including egg, larval, juvenile, and adult stages (Rijnsdorp *et al.* 2009). Fish display a large diversity in their morphology, physiology, and behaviour adaptations, as well as the habitats that they occupy (Talbot 1993). They are among the animals that are most efficient in converting food into body tissue and show a large diversity in their source of nutrition (Talbot 1993). Ecological energetics of fish, which includes how energy is acquired, retained, and transferred between trophic levels in an ecosystem, is affected by the energy availability during a fish's life cycle (Albo-Puigserver *et al.* 2017). This in turn influences the nutritional conditions during key periods of their development and is important in determining an individual's subsequent life-history trajectory (Metcalf & Monaghan 2001). Fishes typically increase their body size as they grow and may require spatially separate habitats for successive life history stages, allowing each stage to mature and subsequently return to spawning grounds for successful reproduction (Rijnsdorp *et al.* 2009). Growth rates of fishes are set by both temperature and prey availability, both of which play a critical role in understanding foraging dynamics and feeding behaviour that influences growth physiology (Peck *et al.* 2013). There is a growing belief among scientists that studying ecophysiology, which is defined as the relationship between an individual's physiology and their physical and biological environmental characteristics, is important as it could give a cause-and-effect understanding of how climate-driven changes in marine environments affect fish survival (Peck *et al.* 2013).

The value of analysing fish growth in terms of rates of energy intake, transformation, and losses, as well as the energetic resource partitioning within the fish have been well established (Talbot 1993). Physiology-based models of fish life cycles is an exciting and swiftly emerging field; models that incorporate physiology will typically focus on bioenergetics due to the inherent link to ecological performance (McKenzie *et al.* 2016, Peck *et al.* 2018). To this end, balanced bioenergetics budgets provide a useful framework to facilitate the study of physiological (energy gained from prey consumption and energy loss through metabolism and assimilation efficiency of food) and environmental factors (such as temperature and prey availability) that determine fish growth, and have played a central role in understanding fish biology (Talbot 1993, Peck *et al.* 2018). Establishing programs to study ecophysiology, especially how fishes function during various life stages, could

make a significant contribution to the resolution of management and conservation issues for marine fishes, and may improve the ability to accurately project potential impacts of environmental pressures as well as allowing the development of species-specific parameterisations of physiology-based (mechanistic) models (McKenzie *et al.* 2016, Peck *et al.* 2021).

1.2 Bioenergetic models

Simple bioenergetic models traditionally have been used to address questions regarding physiological and behavioural properties, and dynamics of single organisms, populations, and communities. Models are required because, in many cases, empirical data alone do not offer a practical way to understand how environmental changes could impact the physiology or viability of organisms (Nisbet *et al.* 2012). In these circumstances there are three main reasons why models are used: 1) there are unknown numbers of different organism-environment interaction combinations to be considered (especially some for which experimentation is impractical, unethical, species are rare or endangered, or sampling is too expensive) (Petersen *et al.* 2008, Pecquerie *et al.* 2011, Nisbet *et al.* 2012); 2) experimental studies yield restricted results that may be specific to certain populations, species, ecosystems or conditions (Petersen *et al.* 2008, Nisbet *et al.* 2012); and 3) climate change can cause persistent changes in environmental variables (e.g. temperature and upwelling) (Bakun *et al.* 2015), and alter the frequency of extreme situations (Nisbet *et al.* 2012) in the system which could have fundamental (and non-linear) impacts on fish physiology (Rijnsdorp *et al.* 2009, Peck *et al.* 2013). These circumstances can alter the time history of events, making measurements that give average conditions or current levels of variability limited predictive value (Petersen *et al.* 2008, Pecquerie *et al.* 2011, Nisbet *et al.* 2012).

Traditionally, bioenergetic models have been powerful data-synthesising tools, with strong empirical foundations that described how the energy acquisition from feeding gets partitioned among growth, maintenance, reproduction, respiration, excretion, or activity processes that were commonly defined operationally (Hansen *et al.* 1993, Nisbet *et al.* 2012). These bioenergetics models compared energy consumed with energy expended and gained through energy balance equations (Hansen *et al.* 1993). Examples of these type of budget models are carbon and nitrogen budget models developed for anchovy (James *et al.* 1989) and sardine (van der Lingen 1998, van der Lingen 1999) to examine the effects of trophic condition on the energetics of these species in the Southern Benguela. Other traditional bioenergetics models focussed mainly on allometric relationships to describe the full lifecycles of fish species. Examples of these models are based on work by Kitchell *et al.* (1977) on

energy partitioning and fish growth of yellow perch (*Perca flavescens*) and walley (*Stizostedion vitreum vitreum*), as well as work by Stewart & Binowski (1986) to investigate the dynamics of consumption and food conversion of Lake Michigan alewives (*Alosa pseudoharengus*). These models formed the bases for a bioenergetics model developed by Rudstam (1988) for Atlantic herring (*Clupea harengus*). These models have been successfully used to describe full life cycles of several small pelagic fish species all over the world (Ito *et al.* 2004, Oguz *et al.* 2008, Okunishi *et al.* 2009, Politikos *et al.* 2011, Politikos *et al.* 2015, Gkanasos *et al.* 2019) (see more on these models in Chapter 5).

In contrast, Kooijman (2000, 2001, 2010) developed a theoretical approach to bioenergetics modelling known as dynamic energy budget (DEB) theory. DEB theory started its development in 1979 on the effect of toxicants on the reproduction of waterflea (*Daphnia magna*) and included consequences for populations (Kooijman & Metz 1984, Marques *et al.* 2018). This theory is based on well-defined assumptions that provide a description of the complete life cycle of single organisms from embryo to adult (Kooijman 2000, Nisbet *et al.* 2000, Kooijman 2010, Marques *et al.* 2018, Peck *et al.* 2018). One of the assumptions that the DEB model makes is that a range of energetic processes, including assimilation and maintenance, depend on an organism's body volume or surface area (Kooijman 2000, Pecquerie 2008). A basic DEB model consists of an isomorphic organism with one substrate, namely food, and one type of reserve which can then be systematically generalised to describe multiple substrates and numerous types of reserves (Kooijman 2000, Nisbet *et al.* 2000, Sousa *et al.* 2008). A basic DEB model incorporates a standard 12-parameter model that can predict both inter- and intraspecific variations in many mass and energy fluxes in any appropriate biological environment (Freitas *et al.* 2011, Nisbet *et al.* 2012), DEB models are assumed to be appropriate for the majority of heterotrophic unicellular organisms and animals (Sousa *et al.* 2008, Kooijman 2012, Kooijman 2014).

Small pelagic fish are difficult to model using traditional population dynamic models because of their short life expectancies, characteristic aggregative behaviour, rapid response to climate and environmental signals, and large variable natural mortality (Barange *et al.* 2009). An advantage of applying DEB theory to small pelagic fish species is that a species-specific set of parameters can be used to reconstruct and simulate the growth of fish over time (Freitas *et al.* 2011, Sarà *et al.* 2013) and under a variety of temperature and food conditions, based on first-principles understanding of physiology, biology, and ecology.

Dynamic energy budgets (DEBs) are useful for describing the flow of energy from food assimilation to maintenance, growth, development, and reproduction as a function of the environment (i.e., food density and temperature) for individual organisms (Nisbet *et al.* 2000, van der Veer *et al.* 2006, Pecquerie 2008, Nisbet *et al.* 2012). The standard DEB model ('std') describes three life stages during a heterotrophic organism's life cycle, namely the embryonic stage, juvenile (including larvae) stage (Figure 1.1a) and adult stage (Figure 1.1b) (Nisbet *et al.* 2012, Pethybridge *et al.* 2013, Marques *et al.* 2018). Maternal reserve (in the form of energy contained in the yolk sac) is used by the embryo for development, growth and maintenance until the individual is sufficiently developed (by achieving a particular energy threshold invested in development) to start exogenous feeding. This is marked as the 'birth' of the individual (Nisbet *et al.* 2012). 'Puberty' is the second transition, when the organism starts committing energy to reproduction, which happens after further energy investment into development (Nisbet *et al.* 2012).

In the standard DEB model, an organism's state can be completely described by contributions from: 1) the volume of the structure (V), defined as the biomass requiring energy expenditure for maintenance; 2) the amount of energy in the reserve (E), defined as biomass that does not require maintenance; and 3) the energy invested into maturation (E_H) or energy invested into reproductive reserve in adults (E_R) (Sousa *et al.* 2008, Nisbet *et al.* 2012). The structure and reserve of the organism are generalized compounds, with mixtures of many compounds making up the biomass of an organism (Sousa *et al.* 2008). An organism is characterised by four state variables, which include the above three components (structure, reserve, and reproduction) and a 'maturation' variable that describes the increase in organism complexity through embryonic and juvenile development (Kooijman 2010, Sousa *et al.* 2008, Nisbet *et al.* 2012). The standard DEB model is based on a simplified rule for the division of resources; the κ -rule states that a fixed fraction (κ) of mobilized energy is allocated to growth and somatic maintenance, with priority given to maintenance, and $1-\kappa$ is allocated to development and maturity maintenance in embryos and juveniles or to reproduction and maintenance of maturity in adults (Kooijman 2000, Pecquerie 2008, Kooijman 2010, Freitas *et al.* 2011).

Initially the focus of DEB theory was on the development of a consistent theory, but this focus subsequently shifted to the development of parameter estimation methods (van der Meer *et al.* 2014). Based on DEB theory, several databases and tools have been developed since 2000 to facilitate the

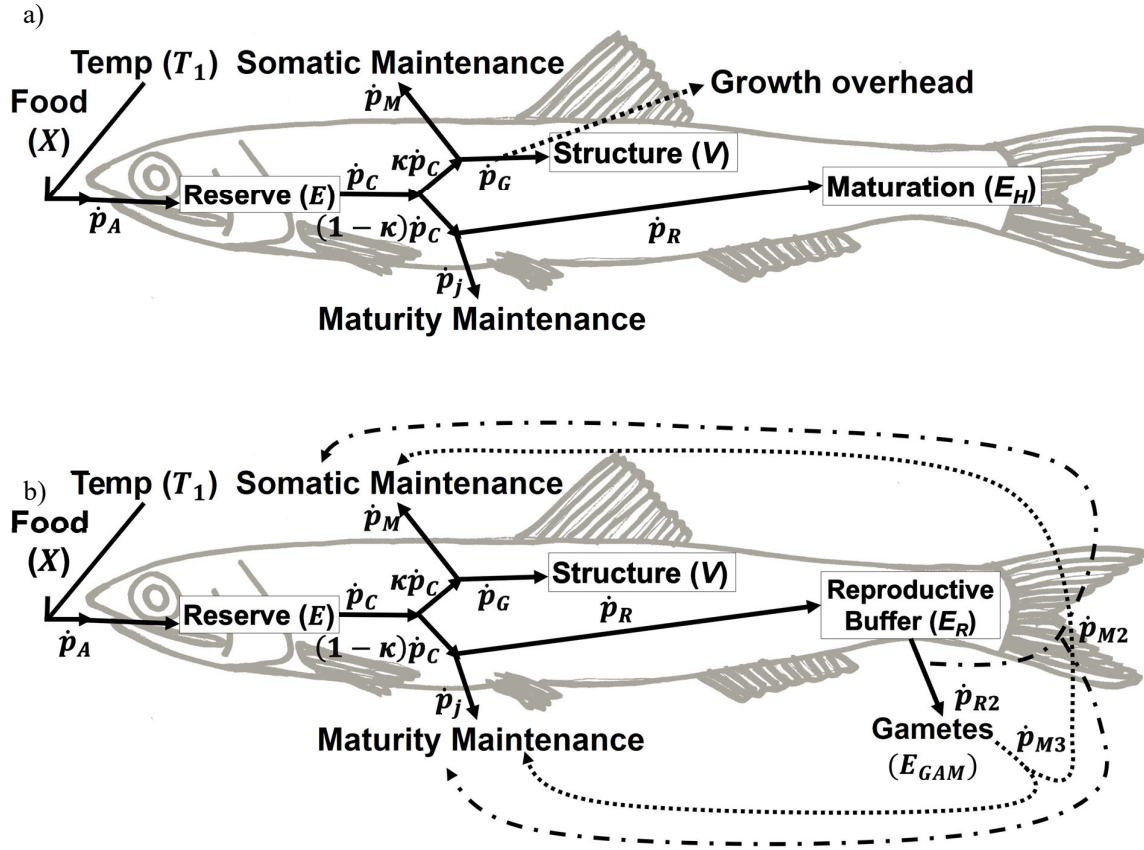


Figure 1.1 A schematic illustration of a standard DEB model showing two of the life history stages (adapted from Nisbet *et al.* (2012) and Pethybridge *et al.* (2013)): a) juvenile stage and b) adult stage, where $\dot{p}_A$ is the assimilation rate, $\dot{p}_C$ is the mobilization, $\dot{p}_G$ is the energy allocated to growth, $\dot{p}_M$ is the somatic maintenance rate, $\dot{p}_j$ is the maturity maintenance rate, $\dot{p}_R$ is the reproductive flux, $\dot{p}_{R2}$ is the energy mobilized to the gametes, $\dot{p}_{M2}$ is the flux for emergency somatic maintenance and $\dot{p}_{M3}$ is the flux for gonad resorption or atresia.

estimation of parameters on a rapidly growing number of species (Kooijman 2000, Lika *et al.* 2011a, Lika *et al.* 2011b). These tools include DEBtool, a software package written in Matlab with functions that can be used to illustrate the implications of DEB theory as well as the applications of this theory in the analysis of ecophysiological behaviour of animals, plants, algae, and microorganisms (DEBtool 2021). The Add_my_Pet (AmP) collection and AmPtool are extensions of the DEBtool software, dealing exclusively with animals and using the covariation-method (Lika *et al.* 2011a, Lika *et al.* 2011b) for parameter estimation (AmP 2021, AmPtool 2021).

As the collection of species which DEB models were applied to grew, it became clear that the standard DEB model needed simple extensions to accommodate specific taxa to account for e.g., larval stages, fetal development, metabolic acceleration in various forms, etc., which led to DEB models being classified according to the mode of metabolic acceleration as s-models, a-models, and h-models (Kooijman 2014, Lika *et al.* 2014, Marques *et al.* 2018).

The s-models apply to many animal species without larval stages and assume isomorphic growth over all life stages (Marques *et al.* 2018). In the case of isomorphic growth, organisms experience a constant surface-area to volume ratio, meaning growth slows down because incoming energy comes in faster than it can be burned for maintenance (Lika *et al.* 2014, Marques *et al.* 2018). These models include, among others, the ‘std’ DEB model, which is the standard DEB model with egg development (Marques *et al.* 2018). The a-models apply to most species with a larval stage where organisms show metabolic acceleration during this stage (Kooijman 2014, Lika *et al.* 2014, Marques *et al.* 2018). In a-models metabolic acceleration occurs at or soon after birth and frequently continues until the organism undergoes morphological metamorphosis (Lika *et al.* 2014, Marques *et al.* 2018). In a-models organisms increase their surface-area proportionally to volume, known as V1-morphy, which impacts how fast food is assimilated and energy mobilized (Marques *et al.* 2018). This means that assimilation would continue to increase with volume and mobilization would continue to increase due to reserve mobilization being proportional to the surface-area of the reserve to structure interface (Marques *et al.* 2018). These models include the ‘abj’ DEB model, which is similar to the ‘std’ model but accounts for metabolic acceleration between birth and metamorphosis, with isomorphic growth before and after acceleration; it is a one-parameter extension of the ‘std’ model (Marques *et al.* 2018). The ‘abj’ DEB model has previously been applied to several fish species, including European anchovy (*Engraulis encrasicolus*) (Pecquerie *et al.* 2009), Pacific bluefin tuna (*Thunnus orientalis*) (Jusup *et al.* 2011), zebrafish (*Danio rerio*) (Augustine *et al.* 2011), several European Perciformes (Lika *et al.* 2014) and European sea bass (*Dicentrarchus labrax*) (Stavrakidis-Zachou *et al.* 2019). The h-models mostly apply to hexapods (insects). They are like a-models but include extra life stages that are triggered by the reproduction buffer density (Marques *et al.* 2018).

Existing, successful DEB models for small pelagic fishes include one for European anchovy (*Engraulis encrasicolus*) in the Bay of Biscay, developed to simulate growth and reproduction (Pecquerie *et al.* 2009). That study found that DEB models could be used realistically to predict

spawning in spatially and temporally varied environments by this species and could also provide initial conditions for bio-physical models used to predict larval survival in the Bay of Biscay. Pethybridge *et al.* (2013) used a size-structured DEB model to examine the effects of short-term environmental changes on *E. encrasicolus* in the North-western Mediterranean Sea. They found that the model successfully replicated seasonal and ontogenic growth patterns, including spring and summer active growth, autumn and winter weight loss, and the amplitude and timing of multi-batch spawning events. Gatti *et al.* (2017) used length and mass at age and energy density to calibrate and parameterize DEB models for European anchovy and sardine (*Sardina pilchardus*) in the Bay of Biscay and found that these species have specific approaches to the acquisition of energy, and allocation specifically to spawning. Gatti *et al.* (2017) found that anchovy are characterised by high metabolic rates and requirements and would benefit from periods of increased resource availability for growth and spawning, so called income spawning, whereas sardine have less demanding food requirements and metabolic costs. Sardine used their large reserve storage to lengthen their spawning periods and spawn when food availability was not high, thereby decoupling their spawning from prey bloom availability, known as capital spawning behaviour. These examples demonstrate the utility of DEB models in increasing understanding of population drivers of small pelagic fishes.

Kooijman and Lika (2014) considered DEB parameters to be species-specific because they are indicators of a species' biological and physiological traits. Because of this, DEB models assume that growth differences among species from different locations are due to differing environmental conditions (Pecquerie 2008). Core parameters for European anchovy *E. encrasicolus* from the Bay of Biscay and the North-western Mediterranean could be compared to each other to assess whether this assumption is true, but expanding the comparison to include other regions, for example the Southern Benguela upwelling ecosystem off southwestern Africa, would strengthen any inferences made. The anchovy populations from these areas have different life-history traits and adaptations to niche environments, which may be reflected in their estimated parameters. This can in turn cause trade-offs in their energy allocation.

This study aims to investigate the intraspecific variability in parameters and to challenge the hypothesis that parameters are species-specific. At present, little is known about intraspecific variability in parameter values and, if such variability exists, whether it is related to environmental variability, genetic variability, or phenotypical plasticity (van der Veer *et al.* 2006). Van der Veer *et*

al. (2001) were the first to compare intraspecific (between males and females) and interspecific energy flow in North Atlantic flatfish species (plaice, flounder, dab and sole) through dynamic energy budgets. They found that intraspecific differences in growth between sexes were mainly due to differences in one core parameter, the maximum surface area-specific ingestion rate. This could be attributed to female flatfishes growing to much larger size (and thus body volume) than males and is reflected in differences in food intake (van der Veer *et al.* 2001). Interspecific differences were reflected in two core parameters (surface area-specific maximum ingestion rate and fraction allocated to growth and reproduction) as well as egg volume (van der Veer *et al.* 2001).

Marn *et al.* (2019) were the first to compare population-specific DEB parameters sets of loggerhead turtles from the Mediterranean and the North Atlantic. They identified three core parameters that captured most of the differences in growth, maturation, and reproduction in the two populations, and found higher somatic maintenance and lower cumulative investments into maturation for the Mediterranean population. This could be interpreted as environmental adaptations to factors, such as high salinity and low food availability, favouring smaller sizes at sexual maturation.

Guillaumot *et al.* (2020) investigated the metabolic differences in DEB models between intertidal and subtidal morphotypes of the Antarctic limpet (*Nucella concinna*). They observed only minimal energetic contrasts between intertidal and subtidal morphotypes in two core parameters (small differences in assimilation rate and their ability to store reserves). Since minor differences existed between temperature-corrected parameter values of the two populations, the observed differences could be best explained by differences in environmental conditions (temperature and food availability).

Models in this study were developed in the context of DEB theory for three small pelagic species from the Southern Benguela; European (locally known as Cape) anchovy (*Engraulis encrasicolus*), redeye round herring (*Etrumeus whiteheadi*), and sardine (*Sardinops sagax*). The principal reason for model development was to enable inter-specific comparisons of parameter values and to examine how short-term variability in environmental conditions would likely affect competition for resources between these species and, in turn, how they would grow and reproduce. These models can be upscaled for populations (Maury & Poggiale 2013) and should be useful for incorporation into larger ecosystem models, such as predator-prey and end-to end ecosystem models (Shannon *et al.* 2000,

Shin *et al.* 2004, Travers *et al.* 2006, Shannon *et al.* 2020), since small pelagic fish are important prey species in the Southern Benguela ecosystem in addition to being commercially exploited.

1.3 Small Pelagic Fish

The Clupeiformes are an order of typically cool-water schooling fish that occur in most of the world's oceans and seas. These are typically coastal fish, occurring in shoals in the upper levels of the water column and hence are epipelagic fish, although they are more commonly known as small pelagic fish. Members of this order typically occur in high abundance in upwelling regions around the world (Whitehead 1985, Armstrong & Thomas 1989), and the relatively narrow continental shelves off the four eastern boundary currents i.e. California (United States of America), Humboldt (Peru and Chile), Canary (North-West Africa), and Benguela (west coast of southern Africa) and the western boundary current system off Japan (i.e. the Kuroshio Current Ecosystem, the Kuroshio Current Extension and the Oyashio Current) support some of the largest populations of clupeoids in the world (Alheit *et al.* 2009, Checkley *et al.* 2009b). This means that these clupeoid species have habitats that can be influenced by coastal and oceanic upwelling and freshwater (Checkley *et al.* 2009b). Their habitats can also be characterised not only by geography, such as the properties of the coast and bottom, but also by the hydrography, such as the properties of the water (Checkley *et al.* 2009b). In most of these areas, clupeoid populations are dominated by anchovy and sardine (Armstrong & Thomas 1989, Jarre-Teichmann *et al.* 1998). The upwelling in eastern boundary currents is driven by the physical environment, which enriches the supply of nutrients in the upper layers of the ocean and stimulates phytoplankton growth, which supports zooplankton and, in turn, clupeoid populations, creating productive populations that are targeted for exploitation by fisheries (Armstrong & Thomas 1989, Grémillet *et al.* 2008, Checkley *et al.* 2009b).

Small pelagic fish are fast-growing, short-lived, highly fecund, and often characterised by variable and high levels of natural mortality. This means their stock size is dependent on recruitment, making populations of these fish species variable, unpredictable and not as responsive to management measures as other longer-lived species (Barange *et al.* 2009). Poor larval nutritional condition caused by starvation can decrease their ability to avoid attacks by predators and hence increase their vulnerability to predation. This leads to hampered growth rates, which increases the time of exposure in small, vulnerable size classes (Garcia *et al.* 1998, Santos *et al.* 2007, Chicharo & Chicharo 2008).

Studies have shown that the assessment of larval growth and nutritional condition are integral to understanding recruitment dynamics in small pelagic fish (Costalago *et al.* 2020). Food availability and physical environmental factors such as turbulence and upwelling intensity are important factors that influence early larval survival and small pelagic fish recruitment, which have an important effect on fisheries and their management (Cury & Roy 1989).

1.4 Small pelagic fishes in the southern Benguela

Fisheries

Small pelagic fish are captured in large quantities typically by purse-seine fisheries in several regions around the world (Barange *et al.* 2009) including the Benguela (Beckley & van der Lingen 1999). In terms of global landed mass, herrings, sardines, and anchovies are among the most important groups of fish caught, and contributed 20.6% of the global fisheries catch in 2018 and 18% in 2017 (FAO 2020). Fisheries for small pelagics in the Benguela started in the late- 1940s, with three species making up the majority of small pelagic catches around South Africa: anchovy, *Engraulis encrasicolus* (formerly known as *E. capensis*); redeye round herring, *Etrumeus whiteheadi* (formerly known as *E. microps* or *E. teres*); and sardine, *Sardinops sagax* (formerly known as *Clupea ocellatus*, *S. ocellatus* or *S. ocellata*) (Whitehead 1985, Prosch 1986, Whitehead *et al.* 1988, Grant & Bowen 1998, Beckley & van der Lingen 1999, van der Lingen *et al.* 2009). Catches of sardine were historically (1960s and 1970s) high in the northern Benguela but dwindled since and have been negligible since the late-1990s (Kainge *et al.* 2020).

Sardine catches in the Southern Benguela showed a rapid increase from less than 200 000 t in the 1950s to over 400 000 t in the early 1960s, after which catches declined during the mid-1960s (Figure 1.2) and remained low for the next 30 years (de Moor *et al.* 2017, van der Lingen 2021). Sardine catches increased to a second peak after fisheries started targeting the species off the South Coast (around Mossel Bay and Port Elizabeth) of South Africa, and peaked mid-2000s before declining again to very low levels in recent years (Figure 1.2) (van der Lingen 2021). After the collapse of sardine stocks in the 1960s the South African purse-seine fishery switched to smaller meshed nets and started targeting anchovy (van der Lingen 2021). Anchovy catches peaked in the 1980s at 600 000 t then declined before reaching a second peak in the mid-2000s (Figure 1.2) (van der Lingen

2021). Redeye round herring have been caught in the South African purse-seine fishery since the 1960s but to a lesser extent than anchovy and sardine. Catches have never exceeded 100 000 t (Figure 1.2), even though attempts have been made by the fishery to increase catches of this species (van der Lingen 2021).

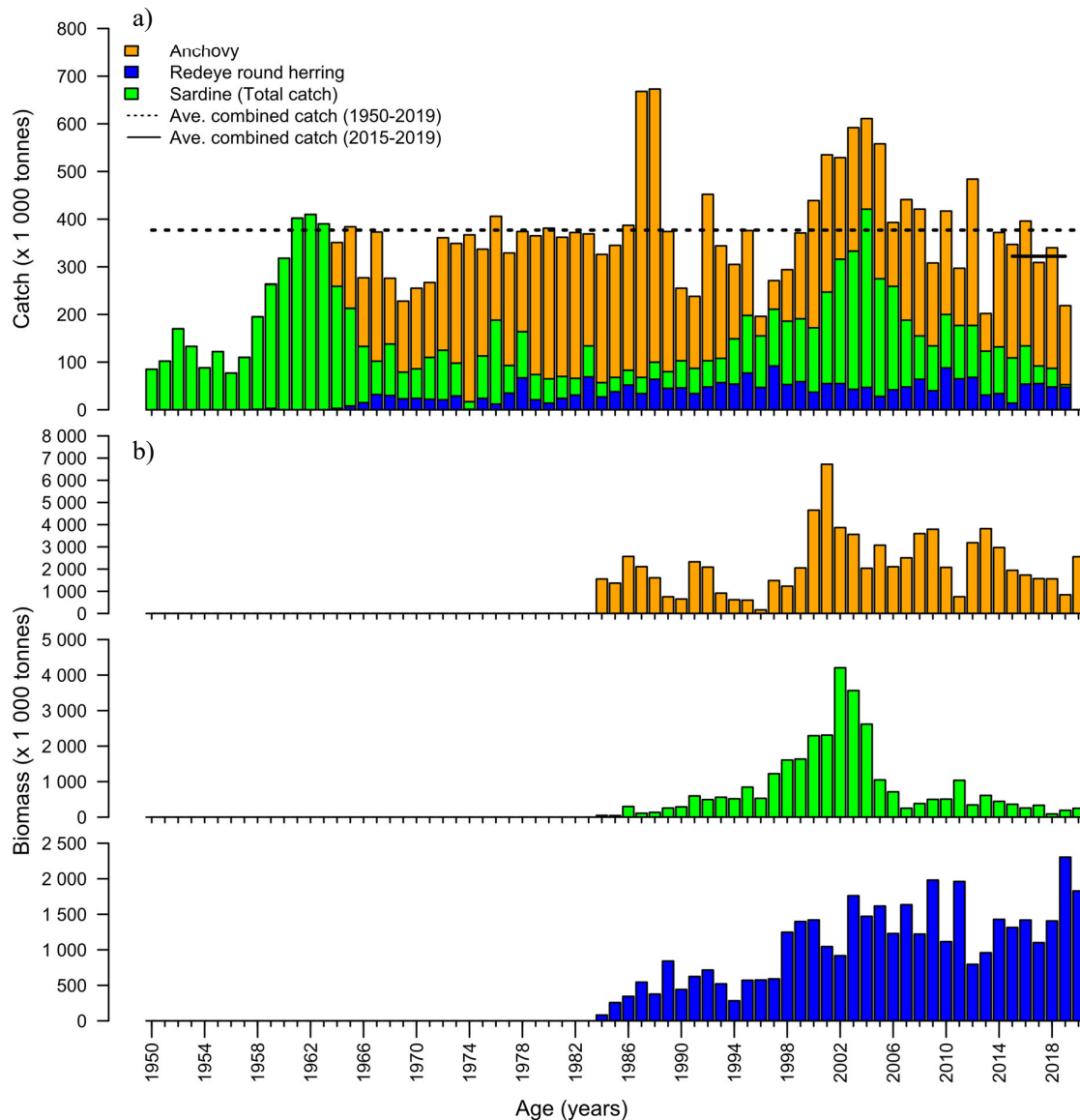


Figure 1.2 a) The annual combined catch of anchovy, redeye round herring and sardine around the coast of South Africa from 1950 to 2019. The dotted line represents the average combined catch of small pelagic fish from 1949 to 2019. The solid black line shows the average combined catch of small pelagic fish from 2015 to 2019. b) Time series of survey estimated total biomass of anchovy (top panel), sardine (centre panel) and redeye round herring (bottom panel) from 1984 to 2020. Redrawn from DEFF (2020) and van der Lingen (2021).

In terms of landed catch, the small pelagic fishery is the largest in South Africa (van der Lingen 2021). The long term average annual catch for small pelagic fish over the last seventy years (1950-2019) since the fishery started is 377 000 t ($\pm$ 113 000 t), which is only marginally higher than the average combined catch over the last five years (2015-2019) of 322 000 t (Figure 1.2a) (van der Lingen 2021). Together, anchovy and sardine (from both directed and bycatch) comprised 79% ($\pm$ 12%) of the average annual catch taken by the small pelagic fishery during the period 1950 to 2019 (van der Lingen 2021). Of the total annual catch, 70-80% comprises juvenile anchovy, while mostly adults of redeye round herring and sardine are targeted by the fishery, with by-catch of juvenile redeye round herring and sardine with anchovy due to small pelagic fish in the Benguela forming mixed schools (DEFF 2020, van der Lingen 2021).

These three small pelagic fish species are processed differently, with anchovy and redeye round herring being reduced to fishmeal and oil, while sardine is frozen or canned for human consumption, pet food and bait (van der Lingen 2021). In terms of unit landed mass, sardine is approximately five times more valuable than the other two species (van der Lingen 2021). The small pelagic fishery is also South Africa's second most valuable fishery, with an estimated wholesale value of R 1.6 billion in 2013 (Brick & Hasson 2016, van der Lingen 2021).

At present, anchovy and redeye round herring are abundant in terms of estimated biomass (Figure 1.2b), but anchovy biomass is still substantially lower than during their peak years in the early 2000s (DAFF 2016, Coetzee *et al.* 2020, DEFF 2020, van der Lingen 2021). In contrast, the sardine population around South Africa is depleted (Figure 1.2b), with estimated biomass from DEFF pelagic surveys remaining low (Coetzee *et al.* 2020, DEFF 2020, van der Lingen 2021).

Habitat, distribution, and spawning

The southern Benguela is a cool, temperate, coastal upwelling system, and is separated from the northern Benguela along the Namibian coast by an intense year-round upwelling cell off Lüderitz (26-27.5°S) (Hutchings *et al.* 2009, Kirkman *et al.* 2016). The intermingling of small pelagic fish stocks between the northern and southern Benguela, despite their extensive migrations, is thought to be prevented by a surface hydrodynamic and subsurface thermal barrier caused by the Lüderitz upwelling cell (Lett *et al.* 2007, Coetzee *et al.* 2008, Checkley *et al.* 2009b). The distribution of

anchovy, redeye round herring and sardine in South Africa extends from the Orange River south and eastwards towards East London, with sardine distribution further extending as far as Durban in KwaZulu-Natal (Armstrong & Thomas 1989, Hampton 1992, Beckley & Hewitson 1994, Hutchings *et al.* 1998, Beckley & van der Lingen 1999, Kreiner *et al.* 2001, Coetzee *et al.* 2008).

Small pelagic fish spawning, and early larval development occur in regions of high plankton production associated with wind-driven upwelling, and rivers and are associated with a wide range of salinities and temperatures between 12°C and 26°C (Checkley *et al.* 2009b). Habitat for small pelagic fishes in the Benguela tends to be confined to the continental shelf but does extend for short distances beyond the continental shelf in a few areas where there is strong advection (e.g., the southern tip of the Agulhas Bank) (Checkley *et al.* 2009b). Globally, sardine tend to be more oceanic, making long migrations between spawning and feeding regions, while anchovy tend to be more coastal and less migratory (Checkley *et al.* 2009b). Off South Africa in the Southern Benguela all three species occur coastally and offshore (especially at high densities), with juveniles (and often adults) occurring inshore, while adults mostly occur offshore in deep water towards the shelf edge (Armstrong *et al.* 1991, Roel & Armstrong 1991, Barange *et al.* 2005).

Various factors restrict small pelagic fish habitats to the continental shelf of South Africa, including the strong Agulhas Current on the east and south coasts, the west coast jet current, and low phytoplankton concentrations offshore on both coasts (Checkley *et al.* 2009b). Mesozooplankton communities throughout the Benguela range from moderate to high concentrations, with a peak on the west coast near St. Helena Bay (33°S), decreasing in warmer waters off the boundary zones (Hutchings *et al.* 1991, Checkley *et al.* 2009b) and eastwards off the south coast. Small pelagic fish in the Southern Benguela typically spawn off the southwest coast and south coast and use the northwest coast (north of Cape Columbine) as their primary nursery ground (Hutchings *et al.* 2002). Anchovy, redeye round herring and sardine in the Southern Benguela tend to school together as juveniles, diverging in their distribution, habitat, and behaviour as they grow (Armstrong *et al.* 1991). This means that small pelagic fish in this region migrate against food gradients when they move from the west coast nursery to spawn in locations upstream of the main nursery grounds (on the western Agulhas Bank and south coast), which may account for the poor fish yield relative to primary production in the Benguela when compared to a system like the Humboldt (Hutchings *et al.* 2002, Checkley *et al.* 2009b).

All three small pelagic fish species are serial spawners. Anchovy spawn mainly over the Agulhas Bank, producing eggs between Cape Point and Port Elizabeth, extending to the outer edge of the central Agulhas Bank in most years (Figure 1.3a). Their distribution tends to narrow towards the east of the Agulhas Bank, coinciding with the narrowing of the continental shelf in that area (Hampton 1992, Shannon 1998, Checkley *et al.* 2009b). The spawning season is during spring and summer and can start with low levels in September and extend to the end of March. Peak spawning occurs between October and January/February (Shannon 1998, Huggett *et al.* 2003, Barange *et al.* 2009). Eggs and larvae are rapidly transported from the spawning grounds (Agulhas Bank) to a nursery area along the west coast by frontal jet currents, which are found on the boundaries of upwelling centres (Hutchings *et al.* 1998). Eggs spawned east of Cape Agulhas have a substantially lower probability of being transported to this west coast nursery area than those spawned to the west of Cape Agulhas (Huggett *et al.* 2003). Young anchovy start appearing in the west coast fishery when they are between six and nine months old (8-10 cm standard length), usually starting in April each year and peaking between May and July. Anchovy recruit into the spawning population when they are approximately one year old (> 10 cm standard length). One year old anchovy adults mostly congregate on the western Agulhas Bank for spawning, while older anchovy appear to shift their distribution to the central and eastern Agulhas Bank to spawn (Roel *et al.* 1994, Hutchings *et al.* 2002, Huggett *et al.* 2003, Checkley *et al.* 2009b)

Redeye round herring do not strictly conform to the epipelagic classification. The adult fish spend the day close to the seabed and rise to the surface at dusk (Armstrong & Thomas 1989), and this extensive vertical migration (more than shown by anchovy and sardine) is characteristic of mesopelagic fish species. Spawning takes place during a relatively long season since redeye round herring eggs are found year round, all around the South African coast (Roel *et al.* 1994). Eggs are concentrated where most of the adults are found, near the 200 m isobath (Figure 1.3b) (Beckley & Hewitson 1994). Spawning seems to peak during the late winter and spring, from approximately August to October (Shelton *et al.* 1985, Roel & Armstrong 1991, Beckley & Hewitson 1994). During this period, shoreward drift of eggs and larvae can be favoured by reduced alongshore advection, the passage of cyclones causing a reversal in the wind directions or the prolonged drift in only one direction on the south coast (Roel & Armstrong 1991). In summer, eggs and larvae spawned on the western Agulhas Bank are transported to the west coast by strong northward-flowing currents over the outer shelf. Eggs and larvae are retained along the entire west coast. Zero- to one-year old fish aggregate close

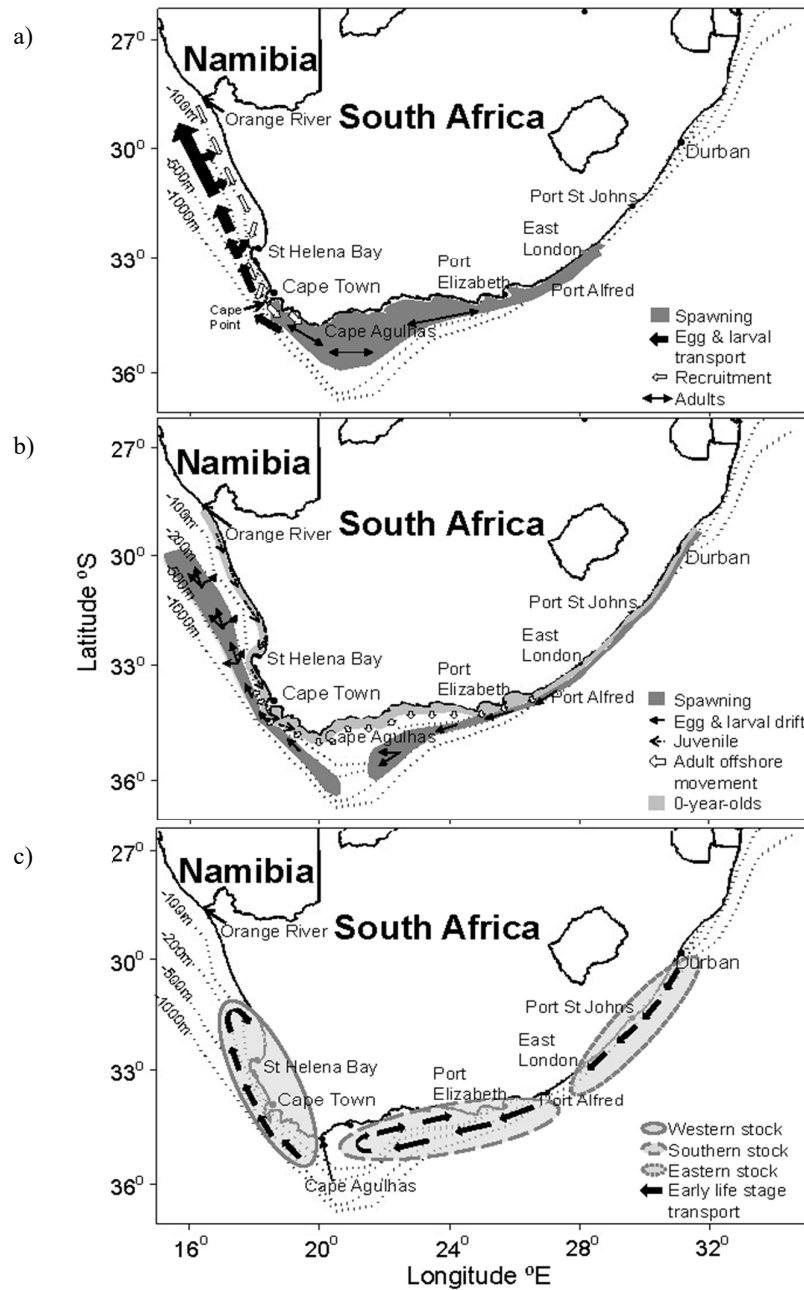


Figure 1.3 Distribution and movement of a) anchovy (*E. encrasicolus*), b) redeye round herring (*E. whiteheadii*) and c) sardine (*S. sagax*) around the coast of South Africa. Spawning indicates spawning grounds. Solid black arrows represent distribution and drift of eggs and larvae. Recruitment represents movement of one-year old fish towards the Agulhas Bank to spawn. Dashed black arrows indicate movements of adults. Light grey indicates juvenile redeye round herring distribution (zero-year olds). Dashed line arrows show movement of juveniles on the west coast. Solid white arrows represent offshore movement of one- to two-year old fish.

inshore along the west coast, moving south during autumn and winter with the inshore, southward water movement and, consequently, becoming distributed along the south coast. Larvae that have been transported shoreward to the east coast can be retained there (Roel & Armstrong 1991, Hampton 1992).

Sardine in the Southern Benguela has historically been managed as a single population, but it has been hypothesized that this sardine population consists of three stocks (Sakamoto *et al.* 2020), semi-discrete western and southern stocks (de Moor & Butterworth 2015) and an eastern stock (Fréon *et al.* 2010). This hypothesis has been well supported by numerous avenues of evidence, including non-continuity in distribution patterns (Coetzee *et al.* 2008), separation of spawning areas with different but overlapping spawning periods around the coasts of South Africa (van der Lingen *et al.* 2015, McGrath *et al.* 2020), as well as spatial variability in several characteristics, including; morphometric and meristic characters (van der Lingen *et al.* 2010b, Idris *et al.* 2016, Groenewald *et al.* 2019), parasite loads (van der Lingen *et al.* 2015, Weston *et al.* 2015), genetic characters (Teske *et al.* 2018), otolith $\delta^{18}\text{O}$ microstructure (Sakamoto *et al.* 2020), and various contaminants (Uren *et al.* 2020, Wu *et al.* 2020).

Adult sardine on the South African coast are distributed mainly to the west of Cape Agulhas (20°E) for the western subpopulation and to the east of 22°E for the eastern subpopulations, with the area to the east of Cape Agulhas (20-22°E) acting as a mixing area between the two subpopulations (Coetzee *et al.* 2008, Sakamoto *et al.* 2020). The western and southern subpopulations spawn year-round from mid-shelf to offshore, peaking from spring (September/October) to summer (February/March) off the west coast (van der Lingen *et al.* 2001, van der Lingen & Huggett 2003, Barange *et al.* 2009) and winter to spring off the south coast (Sakamoto *et al.* 2020) (Figure 1.3c). IBM particle tracking studies representing the early life history stages of sardine investigated three main spawning and nursery grounds for the western and southern stocks (Miller *et al.* 2006, McGrath *et al.* 2020). They found that particles spawned on the west coast, west of Cape Agulhas (20°E), would be retained on the west coast or advected offshore, particles spawned on the east coast would be retained on the south coast, and < 20% of particles spawned on the south coasts would be transported to the west coast (Miller *et al.* 2006, McGrath *et al.* 2020), with eggs seldom found on the central Agulhas Bank (mixing area between 20 and 22°E) (van der Lingen *et al.* 2015). Sardine larvae and juveniles tend to recruit inshore in all regions; however, the nursery areas and growth of the early life stages are not well understood,

especially for the southern and eastern subpopulations (Sakamoto *et al.* 2020). The sardine run is an annual winter occurrence of shoals of similar-sized, two-year old fish that come close inshore off the Eastern Cape and KwaZulu-Natal coast (van der Lingen *et al.* 2010a), and is hypothesized to be the winter spawning migration of a third subpopulation off South Africa (Fréon *et al.* 2010). The third eastern subpopulation is believed to use the KwaZulu-Natal coast as a nursery area, with eggs in that region occurring between winter and spring (Connell 2010).

Life stages of small pelagic fishes in the Southern Benguela

1.4.1.1 Eggs

The small pelagic fishes under investigation are oviparous, producing planktonic eggs that are pelagic and range in size from 0.044-0.190 cm, with shapes from spherical to elliptical (Olivar & Fortuno 1991, Watson & Sandkop 1996a, Watson & Sandkop 1996b). Anchovy eggs are typical of Engraulid eggs in that they are oval in shape with a smooth outer membrane (chorion), a narrow perivitelline space (fluid-filled space between the chorion and the egg cell), a segmented yolk and no oil globule (King *et al.* 1978). They tend to have a maximum diameter of 0.13 cm and a minimum diameter of 0.06 cm (Figure 1.4a) (Olivar 1987, Olivar & Fortuno 1991). King *et al.* (1978) found an exponential relationship between incubation temperature and incubation time, with hatching taking 108 and 21 hours, respectively, at their coolest and warmest incubation temperatures (11.9°C and 23.2°C). Below 13.6°C, even though the eggs developed to hatching, the larvae had a pronounced spinal curve and were abnormally developed (King *et al.* 1978, Shelton & Hutchings 1990). At hatching, normally-developed larvae measured between 0.25 and 0.32 cm in length (Figure 1.4d) (King *et al.* 1978).

Redeye round herring eggs are smooth and spherical with a large, lightly segmented yolk. They have a narrow perivitelline space measuring between 0.013 and 0.017 cm, no oil globule, and a smooth chorion (Figure 1.4b) (O'Toole & King 1974, Olivar & Fortuno 1991). The average egg diameter measured for this species was 0.14 cm (range 0.13 -0.15 cm) (O'Toole & King 1974, Olivar 1987). Incubation time increased with decreasing temperature from 36 hours at 20.5°C to 135 hours at 11.0°C (O'Toole & King 1974). Newly hatched larvae measured between 0.39 cm and 0.45 cm (Figure 1.4e) (O'Toole & King 1974).

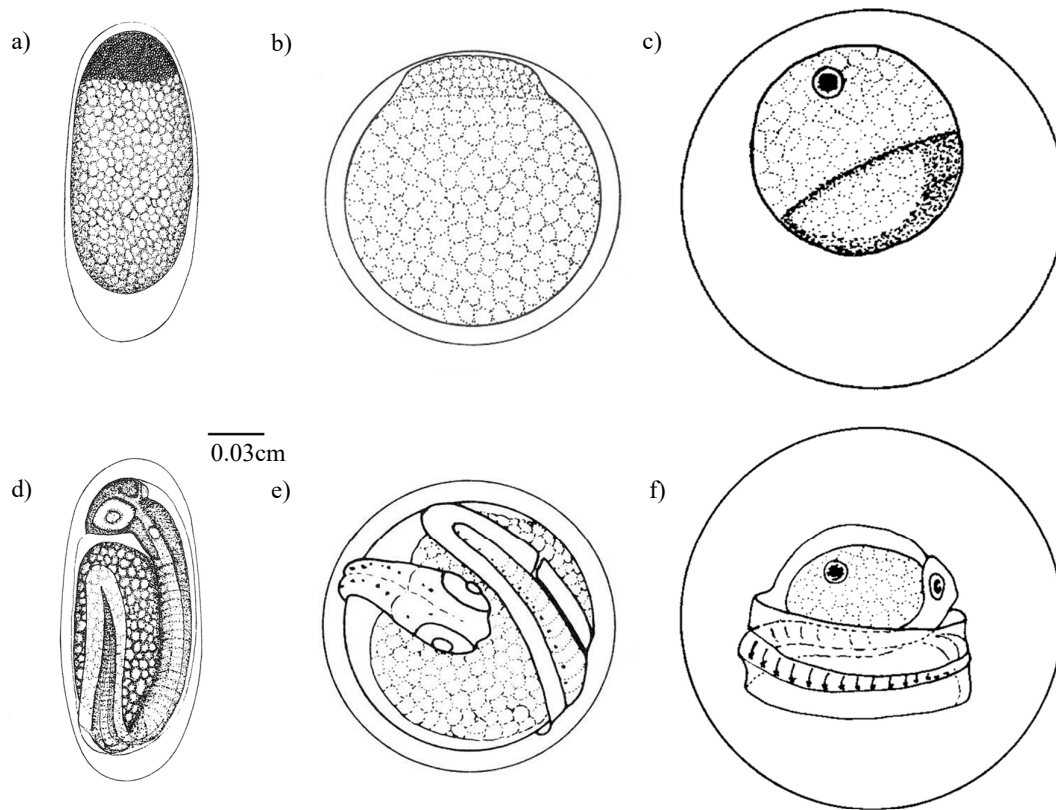


Figure 1.4 Small pelagic fish eggs, showing blastula stage of, a) anchovy adapted from King *et al.* (1978), b) redeye round herring from O'Toole & King (1974) and c) sardine from King (1977), and the shape of final stage eggs showing larvae just before hatching for: d) anchovy adapted from King *et al.* (1978), e) sardine from King (1977) and f) redeye round herring from Olivar & Fortuno (1991).

Sardine eggs are spherical in shape, have smooth, thin chorions, wide perivitelline spaces and a single oil globule at the vegetative pole that measures, on average, 0.018 cm (King 1977, Olivar 1987, Olivar & Fortuno 1991). The eggs have a diameter range between 0.13 and 0.19 cm (average diameter 0.18 cm) and contain yolk that is yellowish-brown and segmented, with an average diameter of 0.10 cm (Figure 1.4c) (King 1977, Olivar 1987). Sardine egg development and time to hatch also showed an exponential relationship with temperature. At 13°C development took, on average, 66 hours, with an incubation time at 22°C of 23 hours (King 1977). It was found that, even though full term incubation of eggs was possible at cooler temperatures, below 13°C the fish did not develop full eye pigmentation or a functional jaw (King 1977). Newly hatched normally developed sardine larvae measured between 0.28 and 0.30 cm (Figure 1.4f).

1.4.1.2 Larvae

Early larvae of small pelagic fishes are slender and elongated and are fed by reserve yolk in a large sac connected to the gut, which is straight and extends more than 70% of the fishes' standard lengths. Once the yolk is exhausted the larvae, which only have a limited swimming capability, must find their own food (Olivar & Fortuno 1991). Newly hatched anchovy larvae are virtually transparent since they do not develop pigmentation during the egg phase and have an undeveloped mouth (King *et al.* 1978). When anchovy larvae reach a length between 0.37-0.39 cm, their eyes become functional and fully pigmented, and the yolk has been almost completely absorbed (King *et al.* 1978). At 0.43 cm anchovy larvae develop a functional jaw and can start feeding exogenously (Konè *et al.* 2013). One distinctive character for differentiating between anchovy, redeye round herring and sardine throughout larval development is the length of the gut (Olivar & Fortuno 1991). For the genus *Engraulis* it is characteristic for the end of the gut to be situated below the midpoint and the end of the dorsal fin after the larvae reach 0.60 cm in length (Figure 1.5b) (Olivar & Fortuno 1991). Notochord flexion (where the dorsal bending develops into dorsal fin rays) in anchovy takes place between 0.75 and 0.86 cm (Figure 1.5a-b) (Olivar & Fortuno 1991). In anchovy, the shape of the head is similar to that of sardine since the eyes are round and slightly elongated (Figure 1.5c) (Olivar & Fortuno 1991).

Redeye round herring larvae are slender, with sparse pigmentation on their bodies and a posteriorly placed anus. At 0.50 cm the mouth is formed, and the jaws become functional, but the eyes remain unpigmented until the larvae reach a size between 0.55 cm and 0.60 cm, at which stage the yolk-sac is almost completely absorbed (O'Toole & King 1974, Olivar & Fortuno 1991). After 0.60 cm length, the gut extends three myomeres beyond the dorsal fin (Figure 1.6a-b) (Olivar & Fortuno 1991). Notochordal flexion in redeye round herring takes place between 0.84 and 1.16 cm (Olivar & Fortuno 1991). Redeye round herring larvae have a snout that is elongated and flattened, and slightly oval eyes (Figure 1.6b-c) (Olivar & Fortuno 1991). Redeye round herring larvae are slender, with sparse pigmentation on their bodies and a posteriorly placed anus. At 0.50 cm the mouth is formed, and the jaws become functional, but the eyes remain unpigmented until the larvae reach a size between 0.55 cm and 0.60 cm, at which stage the yolk-sac is almost completely absorbed (O'Toole & King 1974, Olivar & Fortuno 1991). After 0.60 cm length, the gut extends three myomeres beyond the dorsal fin (Figure 1.6a-b) (Olivar & Fortuno 1991). Notochordal flexion in redeye round herring takes

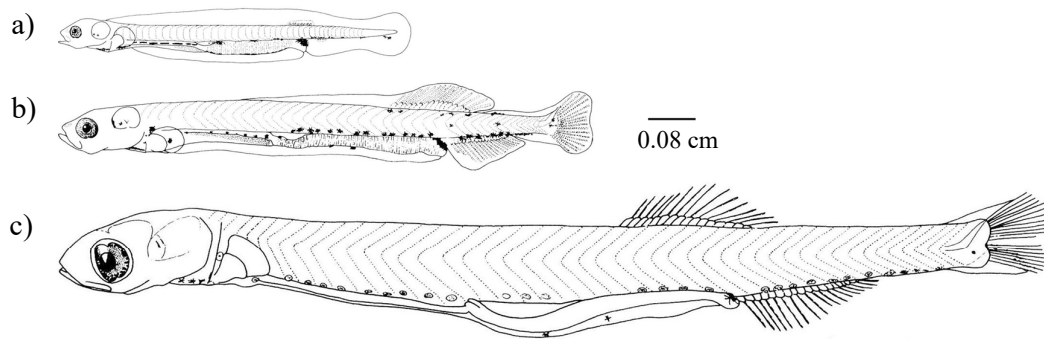


Figure 1.5 Larvae of anchovy at different sizes, a) 0.59 cm larva, b) 0.90 cm larva and c) 1.67 cm larva (from Olivar & Fortuno (1991)).

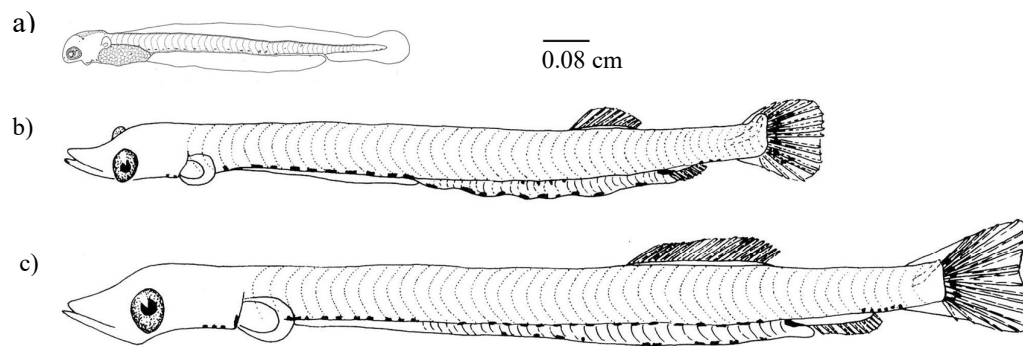


Figure 1.6 Larvae of redeye round herring at different sizes, a) 0.60 cm larva (from O'Toole & King (1974)), b) a 1.3 cm larvae and c) a 1.65 cm larvae (b-c from Olivar & Fortuno (1991)).

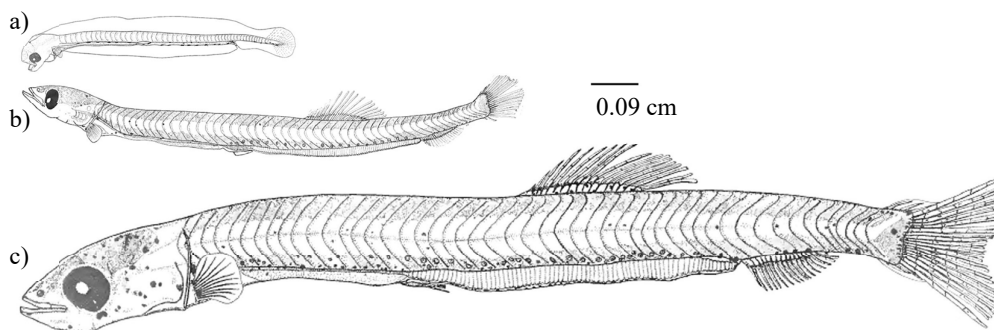


Figure 1.7 Larvae of sardine at different sizes, a) five- to six-day old larva at 0.51 cm (from Louw & O'Toole (1977)), b) 0.93 cm larva from Olivar & Fortuno (1991) and c) 1.81 cm larva (from Louw & O'Toole (1977)).

place between 0.84 and 1.16 cm (Olivar & Fortuno 1991). Redeye round herring larvae have a snout that is elongated and flattened, and slightly oval eyes (Figure 1.6b-c) (Olivar & Fortuno 1991).

Sardine larvae are slender and more elongate than the other two species. They have a non-functioning mouth, digestive and optic system at hatching and measure 0.28-0.30 cm in length (King 1977, Louw & O'Toole 1977, Olivar & Fortuno 1991). At approximately 0.5 cm notochord length, the eyes become pigmented, the head is no longer flexed, and the yolk sac has almost disappeared (Figure 1.7a) (Louw & O'Toole 1977, Olivar & Fortuno 1991). In sardine larger than 0.60 cm, the gut extends between five and seven myomeres past the dorsal fin (Olivar & Fortuno 1991). Notochord flexion in sardine occurs between 0.74 and 1.13 cm and fin development progresses fairly quickly from 0.90 cm (Figure 1.7b) (Louw & O'Toole 1977, Olivar & Fortuno 1991). In sardine, the head is slightly elongated with the snout pointed (Figure 1.7c), and they have round eyes that are slightly elongated (Olivar & Fortuno 1991). Basic post larval features are established when retinal pigmentation is completed, and a functional jaw is formed (King 1977).

Metamorphosis is the transitional stage between larvae and juveniles, characterised by a change from a larval body shape to a juvenile-adult body shape (Kendall *et al.* 1984). This transition brings about ontogenetic processes, which include the loss of specialized larval characters and the attainment of juvenile-adult characters, which include changes in pigment pattern, body shape, and fin migration (Kendall *et al.* 1984). At the end of metamorphosis, the only difference between juveniles and adults are the pigmentation patterns (Kendall *et al.* 1984). Certain characteristics change during the metamorphosis stage in sardine, including the depth of the body, length of the head and the positions of the dorsal, anal, and pelvic fins (Figure 1.8) (Louw & O'Toole 1977). In anchovy, metamorphosis takes place between 3.0 to 3.5 cm (King *et al.* 1978). Redeye round herring metamorphosis starts around 3.0 to 3.5 cm (Armstrong & Thomas 1989). Sardine metamorphosis starts at approximately 2.2 cm standard length and lasts until 3.2 cm standard length (Louw & O'Toole 1977). The juvenile stage starts when the metamorphic changes are complete, and the young fish look like the adults with regards to shape and fin position (Louw & O'Toole 1977).

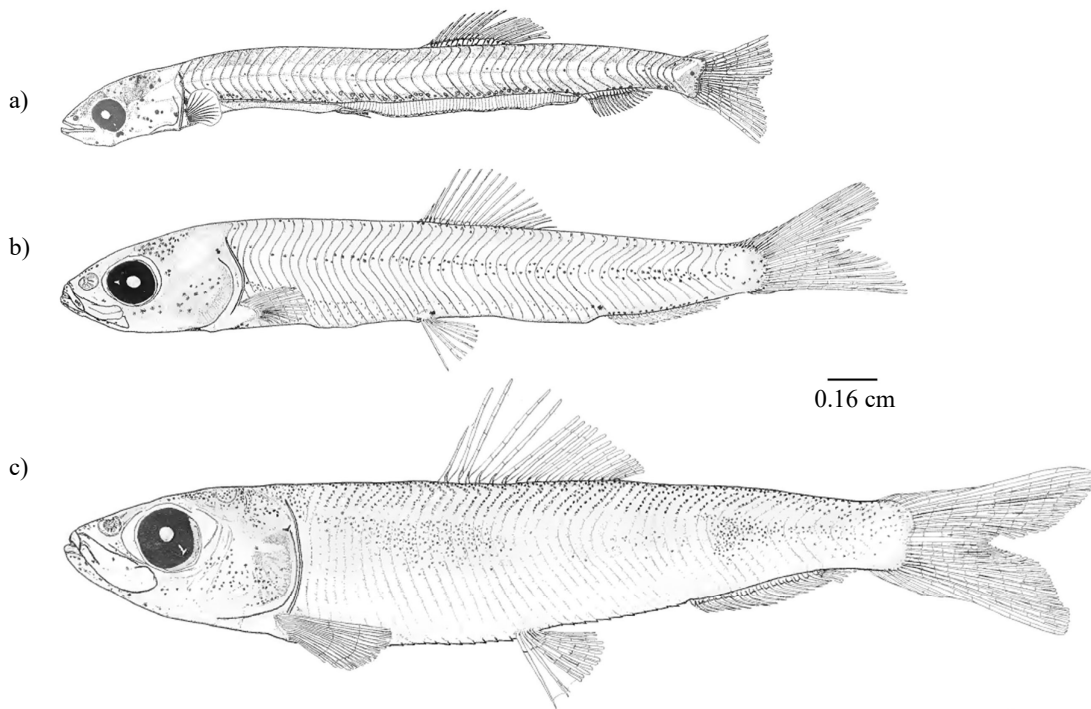


Figure 1.8 Metamorphic stage larvae of sardine (*S. sagax*) showing altered fin positions during growth from: a) 2.32 cm larva to b) 2.77 cm metamorphic stage larva and c) 3.37 cm early juvenile fish, with complete fin migration and considerable dorsal pigmentation (from Louw & O'Toole (1977)).

1.4.1.3 Juveniles and Adults

Fish of the family Engraulidae, like anchovy, are usually slender and long with an oval cross-section (Figure 1.9a) (Whitehead *et al.* 1988). One of their most distinguishing features is the prominent snout that projects beyond the tip of the lower jaw (Whitehead *et al.* 1988). Anchovy have short dorsal fins near the midpoint of the body with the anal fins positioned well behind the base of the last dorsal fin ray (Whitehead *et al.* 1988). They have a silver stripe along their sides that usually disappears with age (Whitehead *et al.* 1988). Anchovy first start reproducing around 8.0cm standard length (SL) (approximately one year old), attain 50% maturity at 9.5 cm SL and are all considered mature between 11 and 12 cm SL (Le Clus 1979, Melo 1992). Anchovy reach a maximum size of 16 cm SL and a maximum age of four years (Prosch 1986, Waldron *et al.* 1989, Barange *et al.* 2009).

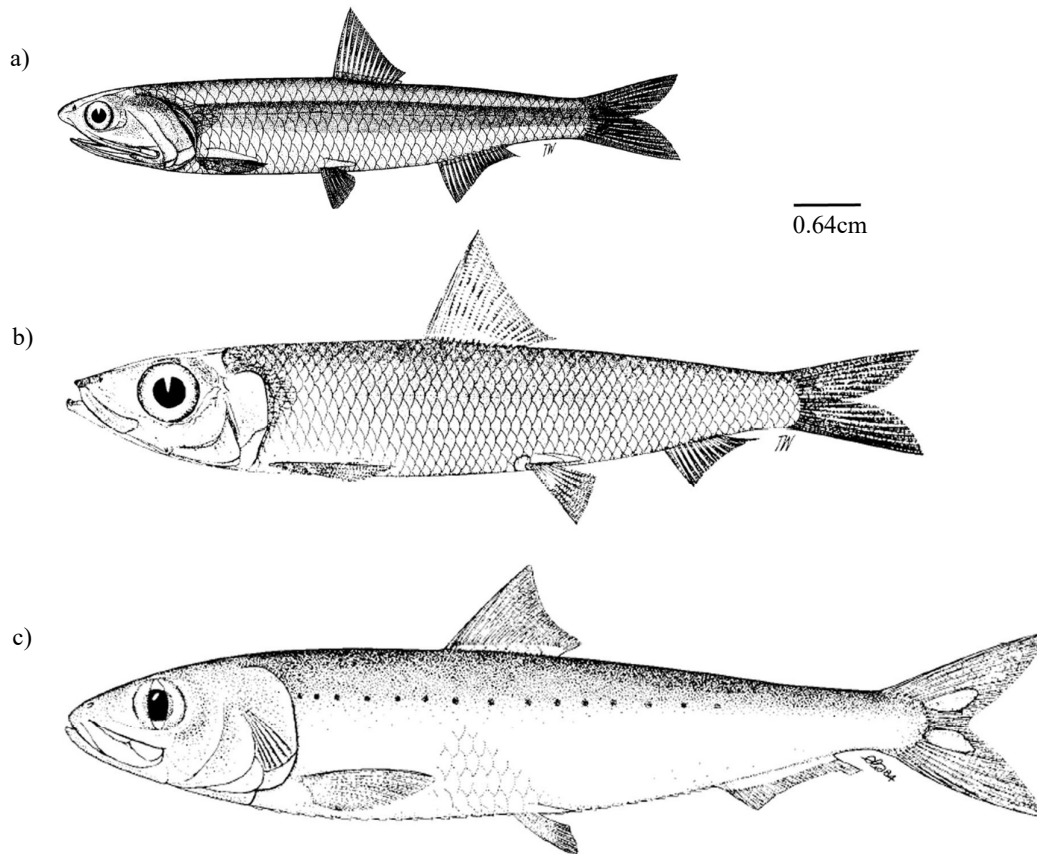


Figure 1.9 Adult fish of a) anchovy (*E. encrasicolus*) from Whitehead *et al.* (1988), b) redeye round herring (*E. whiteheadi*), and c) sardine (*S. sagax*) from Whitehead (1985).

Fish of the Clupeidae family (herrings and sardines) are fusiform shaped (long and tapered at the ends) and oval in cross-section. They are characterised by a terminal mouth and a dorsal fin that is short and near the midpoint of the body (Whitehead 1985). Redeye round herring have a slender body shape with rounded bellies, and whereas they possess a W-shaped pelvic scute they have no pre- or post-pelvic scutes (Whitehead 1985). They have a pelvic fin base positioned below or just before the base of the last dorsal fin ray (Whitehead 1985). Redeye round herring first start to mature around 12 cm SL, with 50% maturity at approximately 13 cm SL and approximately one year old (0.8 years for males and 1.2 years for females) (Geja *et al.* 2016). All fish of this species are considered mature at 18.0 cm SL at an age of approximately three years old (Roel & Melo 1990, Geja *et al.* 2016). Redeye round herring reach a maximum length at 20 cm SL, at an age between 6 and 7 years (Figure 1.9b) (Geja *et al.* 2016).

At 3.30 cm, the top of the body in juvenile sardine is covered by closely arranged melanophores, which give sardine the appearance of a dark dorsal surface and a light ventral surface (Louw & O'Toole 1977). The heads of juvenile fish have extensive pigmentation, their opercular bones have visible radial ridges and the entire body is covered in scales (Louw & O'Toole 1977). As the juveniles grow, the dorsal pigmentation increases and from 4.50 cm a row of dark spots, characteristic of the adult fish, starts to develop along the ventral surface (Louw & O'Toole 1977, Olivar 1987). Sardines are distinguished from the herrings by radiating bony striae on the operculum of the fish and dark spots along their sides (Whitehead 1985). They have a complete series of scutes along their bellies, with a pelvic scute present (Whitehead 1985). Sardine start reproducing later than anchovy, at around 17 cm SL, and reach the age at 50% maturity around 19 cm SL at approximately two years old (van der Lingen *et al.* 2006a). All sardine are considered to be mature at 21 cm SL (Beckley & van der Lingen 1999). Sardine reach a maximum size at 23 cm SL at an age between 8 and 10 years (Figure 1.9c) (Kerstan 2000, Barange *et al.* 2009).

Feeding ecology

Small pelagic fish are ecologically important, being major constituents of marine food webs, where phytoplankton are consumed by herbivorous zooplankton, which are consumed by larvae, and in turn are preyed upon by carnivorous zooplankton or larger fish (Pepin & Dower 2007). Small pelagic fish occupy a mid-level trophic niche, regulating the transfer of energy from lower to higher trophic levels (Jarre-Teichmann *et al.* 1998, Cury *et al.* 2000, Fairweather *et al.* 2006). Determining the composition of the diets of predators is fundamental to delineating food webs in traditional ecology, making knowledge about small pelagic fish ecology vital since they are an important food source for higher trophic predators, including seabirds, marine mammals, and other fish (Jarre-Teichmann *et al.* 1998, Cury *et al.* 2000, Fairweather *et al.* 2006, Wan *et al.* 2010). Studies have suggested that clupeoid fish consume both phytoplankton and zooplankton, with significant phytoplankton feeding taking place in areas where strong upwelling is persistent (such as Namibia and Peru), and zooplankton being more dominant in the diet of fish living in areas where upwelling is weaker and less persistent (Blaxter & Hunter 1982). Most clupeid fish are omnivorous microphagists that get most of their energy from feeding on zooplankton (van der Lingen *et al.* 2009, Garrido & van der Lingen 2014). The observed trophic ecology, especially the differential feeding strategies, of co-occurring anchovy and sardine, led to the development of the trophic dissimilarity hypothesis (van der Lingen *et al.* 2006b) for

variable upwelling intensity in the Benguela (this hypothesis will be discussed in more detail in Chapter 4). The spatio-temporal match of consumers like small pelagic fish and their resources ensures the continuity and resilience of food webs (Cushing 1990, Grémillet *et al.* 2008). Environmental unpredictability and strong variability in ecosystems can often cause a mismatch between predators and their prey; this can have profound effects on the energy flow between trophic levels, the population dynamics and ecosystem structure (Grémillet *et al.* 2008)

In the southern Benguela ecosystem, the trophic ecology of adult and juvenile small pelagic fishes (anchovy, redeye round herring and sardine) are moderately well understood (Roel & Melo 1990, van der Lingen *et al.* 2006b, van der Lingen *et al.* 2009). Adult anchovy are primarily particulate-feeders and specialist planktivores that are strongly selective in the range of sizes of prey they capture. Anchovy are unable to retain prey of $< 200 \mu\text{m}$, hence phytoplankton is not generally an important dietary component for this species, which mostly consumes large zooplankton (large calanoid copepods and euphausiids) (van der Lingen *et al.* 2006b). The largest contribution to adult redeye round herring diets comes from euphausiids and large copepods, which also perform daily vertical migrations through the water column, allowing the redeye round herring to feed on them throughout the day and night (Wallace-Fincham 1987, Roel & Armstrong 1991). Adult sardine are considered generalist planktivores and are primarily filter-feeders (van der Lingen 2002) and have a capacity to ingest a wide range of prey sizes, from small phytoplankton to large macrozooplankton. They do not seem to be selective in the prey size they prefer (van der Lingen *et al.* 2006b).

Newly-hatched small pelagic larvae sustain themselves with yolk from the yolk-sac connected to the gut, but once the yolk is exhausted the larvae, which have only a limited swimming capability, must find their own food (Olivar & Fortuno 1991). In the Benguela, food for fish larvae is produced almost year round, but the environment is so variable that many individuals in the early life history stages die because they occur in unfavourable (temperature, dissolved oxygen, etc.) oceanographic conditions, are eaten by predators or are swept offshore by unfavourable currents, where they starve (Armstrong & Thomas 1989, Olivar & Fortuno 1991, Cury *et al.* 2000). To avoid starvation and to ensure growth, fish larvae and juveniles must depend on their ability to find, capture, and ingest sufficient amounts of appropriate prey (Morote *et al.* 2010). Hence, this ability to find sufficient food is also a major determinant of recruitment success. Therefore, knowledge about the feeding ecology

of larvae is essential for understanding their recruitment variability and their early life-histories (Young & Davis 1990).

Aspects of the trophic dynamics of anchovy and sardine have been compared to those across a range of ecosystems, including those from other upwelling regions (the Benguela, California and Humboldt Currents) as well as the North-western Pacific, North-eastern Atlantic and Mediterranean regions, by van der Lingen *et al.* (2009), who found that the trophic dynamics of these two species showed developmental changes. Typically, the larvae and juveniles of sardine and anchovy were almost exclusively zooplanktivorous (feeding on copepod eggs, nauplii and copepodites), with phytoplankton gaining increased importance with fish size, due to elaboration of the brachial basket (van der Lingen *et al.* 2009). An exception was for anchovy larvae in the northern Humboldt Current system, which fed on phytoplankton (centric diatoms) and zooplankton (van der Lingen *et al.* 2009). A study on round herring *Etrumeus teres*, a sister species of *E. whiteheadi*, in the Gulf of Mexico found that round herring larvae also ate predominantly zooplankton (in this case pteropods, cycloid copepods and calanoid copepods) (Chen *et al.* 1992). However, there is a lack of information on the diet and trophic position of larvae and post-larvae of anchovy, redeye round herring and sardine in the entire Benguela ecosystem, representing a significant gap in the knowledge of these economically and ecologically important species (van der Lingen *et al.* 2006b, van der Lingen *et al.* 2009, Garrido & van der Lingen 2014). This gap limits understanding of how survival and growth variation in the early life history stages could influence subsequent recruitment success in the Southern Benguela ecosystem.

1.5 Aims, objectives and structure of the thesis.

The main aims of this study were to investigate: 1) whether core DEB parameters for *E. encrasicolus* are species-specific between the Southern Benguela and other regions; and 2) the extent to which the main three small pelagic fishes (anchovy, redeye round herring and sardine) in the Southern Benguela ecosystem would grow and survive under different environmental conditions, in isolation and together from larvae to adults, as an exploration of how niche differences among bioenergetic strategies for the three species allow them to co-occur. This would be accomplished by creating a DEB model for growth representing the full life history of each of the three species.

Chapter 2 describes the development of an anchovy DEB model (with equations and a full set of parameters), with the aim of creating a framework to represent the entire life cycle in the Southern Benguela of anchovy *E. encrasicolus*, including growth and reproduction. One of the objectives of this chapter was to investigate differences among core parameters, identifying five important missing parameters (the fraction allocated to growth and maintenance κ , maximum storage density $[E_m]$, volume-specific maintenance rate $[\dot{p}_M]$, surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ and volume-specific cost for structure $[E_G]$), their effects on growth and reproduction in the anchovy model, and comparing their values to those from other regions where *E. encrasicolus* have been modelled. The key hypothesis being investigated in this chapter was that not all core DEB parameters may be species-specific and that the environment should also influence parameter values. A second objective was to investigate the effects on anchovy growth and reproduction of environmental inputs such as: a) scaled functional responses (f) as a function of food density and b) temperature. In addition, the chapter aimed to assess c) the effects of temperature and food inputs on anchovy during starvation scenarios.

In Chapter 3, the parameters from the general anchovy model were adapted to develop DEB models comprising complete life cycles and a full parameter set for redeye round herring *Etrumeus whiteheadi* and sardine *Sardinops sagax*, for which there are fewer empirical data in the Southern Benguela. Development of DEB models for these species would enable an interspecific comparison of the five important core parameters (identified in Chapter 2) of small pelagic fishes in this region. As in Chapter 2, the effect of these parameters on the redeye round herring and sardine modelled growth would be shown and compared to results from other regions where DEB models for sardine have been developed (none presently exist for *Etrumeus* spp.), as well as to results from the anchovy model. It was hypothesised that, even if DEB core parameters may not be interchangeable between ecosystems, as has been shown in Chapter 2, there may be general trends in the differences between anchovy and sardine parameters that may be helpful in core parameter estimations. A second objective was to investigate the influence of environmental inputs such as those described in Chapter 2, on the growth and reproduction of sardine and redeye round herring as well as the effect of starvation on these species during different scenarios.

Feeding linkages in marine organisms are determined by both the species and their life stages, since organisms cover a range of sizes through their life span and will typically change their diet as they

grow (Moloney *et al.* 2011). The aim of Chapter 4 was to investigate the trade-offs between temperature and feeding condition on the growth and reproductive outputs of small pelagic fish in the Southern Benguela. The objectives for this chapter were to investigate the effect of temperature, feeding conditions, and a combination of the two effects on the length of time it would take to reach metamorphosis in small pelagic fish larvae, the time taken to reach age at recruitment, and the effects of these conditions on the growth and reproductive output of adult small pelagic fish. It is hypothesised that, with increased upwelling in a cooling environment, more large prey items would be prevalent favouring anchovy and redeye round herring populations. Sardine on the other hand, would be less favoured due to the lack of small prey items on which they thrive. The DEB models of these small pelagic species, which are key food species in the Southern Benguela ecosystem, can be upscaled for populations and incorporated into predator-prey and larger ecosystem models. This could be useful for generating insights and projections of the effect of short-term environmental change and food availability on long-term population dynamics of small pelagic fish in a changing climate.

Chapter 5 discusses the niche adaptation of each species and how differences among bioenergetic strategies for the three species allow them to co-exist and how these adaptations tie into the main findings of the thesis. In addition to showing new understanding resulting from application of the DEB models, it also touches on some of the advantages and disadvantages of using models developed by other scientists.

Chapter 2 A Dynamic Energy Budget (DEB) model of anchovy *Engraulis encrasicolus* growth and reproduction in the Southern Benguela ecosystem.

Abstract

The Dynamic Energy Budget (DEB) model is a useful tool for describing the energy flow in individual organisms, from food assimilation to maintenance, growth, development, and reproduction as functions of environmental drivers such as temperature and food availability. DEB models have successfully described the growth and reproduction of European anchovy *Engraulis encrasicolus* in the northern hemisphere by allowing for the identification of the specific and common processes during each life stage. This study developed a DEB model for *E. encrasicolus* in the Southern Benguela, where this species plays an economically and ecologically important role. Model development will improve understanding of how environmental variability is likely to impact the growth and reproduction of anchovy in this region, which is critically needed given present and future impacts of climate change on marine ecosystems. Additionally, model development will enable the investigation of the DEB theory assumption that core model parameters are species-specific, by comparing differences (if any) in DEB model core parameters between *E. encrasicolus* in the Southern Benguela and elsewhere. Growth and reproduction of anchovy were simulated by a DEB model, estimating core parameters, and exploring the effects of varied environmental conditions (food density, including zero food, and temperature) on an individual anchovy in terms of their energy available for growth throughout their life cycle and reproduction. The model was calibrated using published literature and survey-derived estimates of recruitment strength and total biomass for the period 2012-2016. For five core model parameters, best visual fit values were estimated from von Bertalanffy growth models and length-weight relationships of anchovy. Southern Benguela anchovy had slower growth rates, higher reserve storage capacity ($[E_m]$), invested less energy into reproductive reserve storage capacity (κ), had lower maintenance costs and assimilated rates but had smaller structural growth costs than anchovy in other regions. These differences were attributed to cooler temperatures, higher but less visible food availability and slower growth rates of anchovy in the Southern Benguela, indicating that these parameters are influenced by the environment. Hence, caution should be exercised before assuming that DEB parameters are species-specific and transferable between regions. The DEB model for Southern Benguela anchovy required a scaled functional response (f) of at least 0.6 to enable fish to reach sexual maturity and be able to reproduce. Higher growth rates were observed at warmer temperatures but increasing temperature decreased

survival of anchovy during starvation, whereas increasing the initial f increased their survival. The anchovy DEB model can be incorporated into ecosystem models to investigate the effects of potential ecosystem changes on this species and to better understand the interaction between this ecologically important species and its predators.

Introduction

Anchovy *Engraulis encrasicolus* has been a primary target of a valuable small pelagic fishery in South Africa since the mid-1960s (Crawford 1987, Lluch-Belda *et al.* 1989, DAFF 2016). This species is of great ecological importance because it occurs in high abundance, occupies an intermediate level between lower (plankton) and upper (predatory fish, marine mammals, and seabirds) trophic levels in marine food webs, and has good nutritional value (Pethybridge *et al.* 2013). Anchovy have an r-selected life history strategy, which means they are fast growing and mature early, have a short life span of approximately three to four years and are quick to respond to environmental variability (Somarakis *et al.* 2004, Pethybridge *et al.* 2013). This leads to large interannual fluctuations in population size that can be up to several orders of magnitude, which may negatively impact fisheries as well as creating difficulty in stock assessments (Field *et al.* 2009, Alheit *et al.* 2009, Barange *et al.* 2009, Pethybridge *et al.* 2013, Katara 2014).

Due to their economic and ecological importance, the biology, ecology, and population dynamics of anchovy in the Southern Benguela ecosystem have been well studied, which means empirical data are available to create bioenergetic models for this species. In contrast to empirical approaches of more traditional bioenergetic models (Nisbet *et al.* 2012), Kooijman (2000, 2001, 2010) and van der Meer (2006) developed a more theoretical approach to bioenergetics in the form of dynamic energy budget (DEB) models. The standard DEB model can be used to describe an organism's rate of assimilation and energy utilization for maintenance, reproduction, and growth as a function of its environment (food density and temperature) (Pecquerie *et al.* 2009).

The standard 'std' DEB model can be divided into four metabolic processes (Figure 2.1). The first metabolic process, 'ingestion', assumes that food caught by an anchovy is assimilated and enters the reserve, from where it is allocated to maintenance, growth, and reproduction (Kooijman 2000, Kooijman 2010, Nisbet *et al.* 2000). 'Dissipation', the second metabolic process, is characterised as metabolic work or maintenance that does not lead to the production of new biological material and

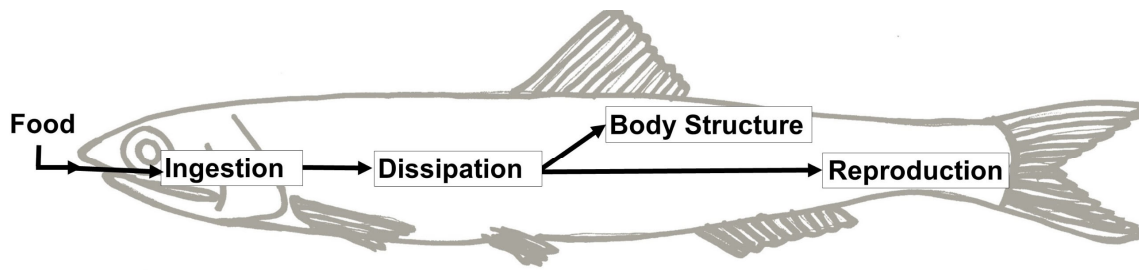


Figure 2.1 A simple representation of the four main metabolic processes included in the standard Dynamic Energy Budget (DEB) model.

includes somatic and maturity maintenance as well as the overheads of growth and reproduction (Kooijman 2000, Kooijman 2010, Nisbet *et al.* 2000). The third metabolic process, ‘body structure’, is where part of the reserve is assigned to elaborating somatic structures (Kooijman 2000, Kooijman 2010, Nisbet *et al.* 2000). In ‘reproduction’, the fourth metabolic process, part of the reserve is assigned to maturation in juveniles and the reproductive buffer in adults (Kooijman 2000, Kooijman 2010, Nisbet *et al.* 2000). In adults, if there is no food assimilation because of starvation the reproductive buffer is utilized to pay maintenance costs (Pethybridge *et al.* 2013). Since its development the ‘std’ DEB model has been extended to accommodate larval stage metabolic acceleration (Kooijman 2014, Lika *et al.* 2014, Marques *et al.* 2018). One of these extended models is called the ‘abj’ DEB model, this model is similar to the ‘std’ model but accounts for metabolic acceleration during the larval stage between birth and metamorphosis (Marques *et al.* 2018). Where the ‘std’ model assumes isomorphic growth throughout the lifecycle of the fish, the ‘abj’ model assumes metabolic acceleration in the larval stage, with isomorphic growth after metamorphosis (Kooijman 2014, Lika *et al.* 2014, Marques *et al.* 2018). This study did not consider acceleration during the larval stage and applied the ‘std’ DEB model to the full life cycle of anchovy. This is sufficient for this study as the ‘std’ DEB model can be used to model the entire lifecycle of organisms with egg development and the larval acceleration in growth of anchovy in the Southern Benguela is slower than in the anchovy studies in Europe (Pethybridge *et al.* 2013, Gatti *et al.* 2017).

DEB theory has been successfully used to describe the life cycle dynamics of European anchovy *Engraulis encrasicolus* in the Bay of Biscay (Pecquerie 2008, Pecquerie *et al.* 2009, Gatti *et al.* 2017) and in the North-western Mediterranean Sea (Pethybridge *et al.* 2013). DEB parameters are

considered to be species-specific; therefore, core parameters for anchovy from these regions can be compared to each other and to those from the Southern Benguela, since the parameter values of this species should indicate their biological and physiological traits (Pecquerie 2008, Kooijman & Lika 2014, Gatti *et al.* 2017). Pecquerie (2008) speculated that growth differences in the DEB models among anchovy populations of the same species would be caused mainly by environmental influences.

This study aims to assess whether DEB theory would be suitable for developing a framework for a ‘generalized’ anchovy model that can describe the life cycle, including growth and reproduction, of female anchovy in the Southern Benguela. The objectives of the study were to 1) estimate values of core parameters for *E. encrasicolus* in the Southern Benguela and compare them to parameter values estimated for this species in other parts of the world; 2) investigate the effect of varied environmental conditions, such as in food density and temperature, on individual female anchovy in the Southern Benguela in terms of the energy available for growth and reproduction throughout their life cycle; and 3) investigate the reaction of simulated anchovy to starvation. It was hypothesised that not all core parameters utilized in the DEB model are interchangeable for *E. encrasicolus* from different regions, and that the varied environmental conditions in which the species occurs also influences their values.

Methods

2.1 The model

Individual anchovy are represented in the standard dynamic energy budget (DEB) model by the energy content (J) of three state variables: 1) the reserve (E); 2) the structure (V); and 3) gonads, which are affected by maturation in juveniles (E_H), gamete production (E_{GAM}), and reproduction in adults (E_R) (Pecquerie *et al.* 2009, Pecquerie *et al.* 2011, Pethybridge *et al.* 2013, Gatti *et al.* 2017). The DEB model assumes that the reserve will be used continuously and refilled, while somatic maintenance will continuously reduce and rebuild structural material throughout the life of the individual (Kooijman 2000, Pecquerie *et al.* 2009). In DEB models, priority is given to the metabolic cost of survival of the individual (through somatic maintenance), rather than to growth and reproduction, meaning that energy will only be allocated to the structure and maturation/reproduction once the maintenance costs have been allocated (MacDonald *et al.* 2018).

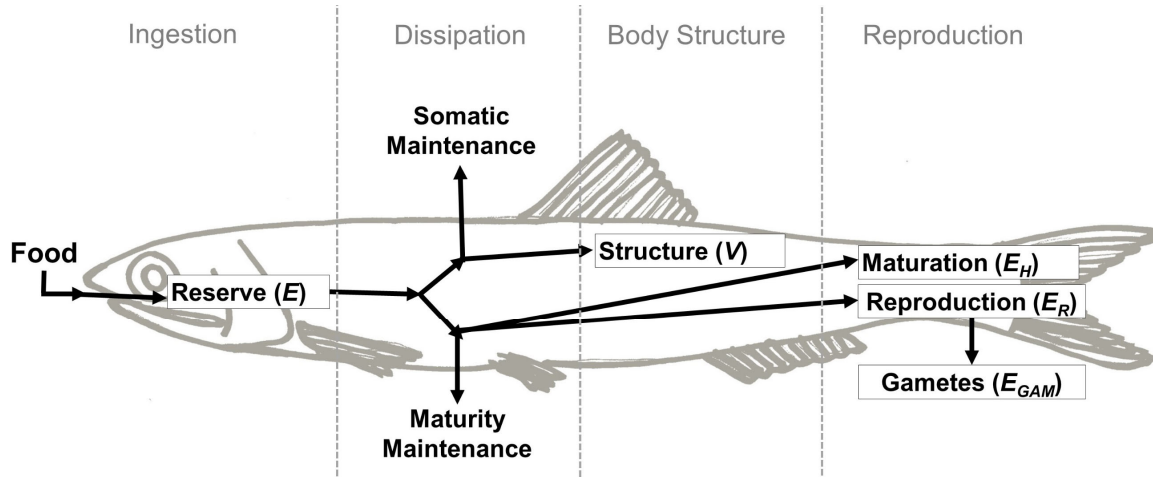


Figure 2.2 A simple conceptual diagram of the standard dynamic energy budget (DEB) model showing the state variables and maintenance modelled for an individual anchovy.

The following assumptions are used to model the main processes underpinning these concepts: 1) during ‘ingestion’ all energy that is assimilated enters the reserve (E) (Figure 2.2); 2) during ‘dissipation’, energy for metabolic maintenance can be subtracted from the reserve; 3) during ‘body structure’ and following the allocation of maintenance cost, a fraction of the remaining assimilated energy can be allocated to the structure (V); and 4) during ‘reproduction’, the remaining energy is allocated to maturation (E_H) or reproduction (E_R), and the energy that is allocated to reproduction in adults is assigned to gamete production (Pecquerie *et al.* 2009, Pecquerie *et al.* 2011, Gatti *et al.* 2017, MacDonald *et al.* 2018).

The DEB model in this study is non-spatial and time is represented continuously, based on a daily time step using ordinary differential equations (Pethybridge *et al.* 2013). The rate of change in the energy content of the reserve ($J.d^{-1}$) is given by:

$$\frac{d}{dt}E = \dot{p}_A - \dot{p}_C \quad 1$$

where $\dot{p}_A$ is the rate at which anchovy assimilate energy ($J.d^{-1}$) and $\dot{p}_C$ is the rate that anchovy lose energy to mobilization ($J.d^{-1}$) into different processes (Pecquerie 2008, Pethybridge *et al.* 2013, MacDonald *et al.* 2018).

The rate of change of the structural volume ($\text{cm}^3 \cdot \text{d}^{-1}$) is given by:

$$\frac{d}{dt}V = \frac{\dot{p}_G}{[E_G]} \quad 2$$

where $\dot{p}_G$ is the fraction of the mobilized energy remaining after maintenance cost that is allocated to form the structure ($\text{J} \cdot \text{d}^{-1}$) (Pecquerie 2008, Pethybridge *et al.* 2013, MacDonald *et al.* 2018) and $[E_G]$ is the energy needed for one unit of growth to occur in structural body volume ($\text{J} \cdot \text{cm}^{-3}$) (van der Meer 2006).

The rate of change of the energy allocated to maturation (E_H , $\text{J} \cdot \text{d}^{-1}$) or reproduction (E_R , $\text{J} \cdot \text{d}^{-1}$) is given by:

$$\text{if } L_v < L_{vp} \quad \frac{d}{dt}E_H = \dot{p}_R \text{ else } \frac{d}{dt}E_H = 0 \quad 3$$

$$\text{if } L_v < L_{vp} \quad \frac{d}{dt}E_R = 0 \quad 4$$

$$\begin{aligned} \text{else if } & L_v \geq L_{vp} \\ & \& E_{GAM} \geq 2 \cdot E_{batch}^* \\ & \& O_{Dev} \geq O_{DevTime} \end{aligned} \quad \frac{d}{dt}E_R = \dot{p}_R - \dot{p}_{R2} - \dot{p}_{M2} - E_{batch}^*$$

$$\text{else} \quad \frac{d}{dt}E_R = \dot{p}_R - \dot{p}_{R2} - \dot{p}_{M2}$$

where L_v is the volumetric length (cm), L_{vp} is the volumetric length at puberty (cm), $\dot{p}_R$ is the fraction of the mobilized energy remaining after maintenance cost that is allocated to maturation or reproduction ($\text{J} \cdot \text{d}^{-1}$), $\dot{p}_{R2}$ is the energy needed to start producing gametes ($\text{J} \cdot \text{d}^{-1}$), $\dot{p}_{M2}$ is energy needed for emergency somatic maintenance ($\text{J} \cdot \text{d}^{-1}$) and E_{batch}^* is the energy content of one batch of eggs (J) released during the timestep (d^{-1}) when conditions $E_{GAM} \geq 2 \cdot E_{batch}^* \& O_{Dev} \geq O_{DevTime}$ are met. E_{GAM} is the energy allocated to the gametes (J), O_{Dev} is oocyte development time (d), and $O_{DevTime}$ is the time taken to reach full oocyte development (d). Once the eggs are released the energy for that one egg batch is removed from E_R for the next timestep.

The rate of energy change allocated to the gametes ($J.d^{-1}$) is given by:

$$\begin{aligned} \text{if } E_{GAM} \geq 2.E_{batch}^* \& O_{Dev} \geq O_{DevTime} \quad \frac{d}{dt}E_{GAM} = \dot{p}_{GAM} - \dot{p}_{M3} - E_{batch}^* \\ \text{else} \quad \frac{d}{dt}E_{GAM} = \dot{p}_{GAM} - \dot{p}_{M3} \end{aligned} \quad 5$$

where $\dot{p}_{GAM}$ is the energy from the fraction allocated to reproduction that is allocated to gamete growth ($J.d^{-1}$), $\dot{p}_{M3}$ is the energy for gonad resorption or atresia if the fish is starving ($J.d^{-1}$) and E_{batch}^* is the energy content of one batch of eggs (J) released during the timestep (d^{-1}) where E_{GAM} has enough energy for one batch of eggs (Pecquerie 2008, Pethybridge *et al.* 2013). Once the eggs are released the energy for that one egg batch is removed from E_{GAM} for the next timestep.

The core DEB model is illustrated in Figure 2.3a, and the equations are given in Table 2.1 with their corresponding equation numbers illustrated in Figure 2.3b. In the model, parameters framed in curly brackets are surface-area specific rates, while parameters framed by square brackets are volume-specific rates (Kooijman 2000, Sarà *et al.* 2013). In the model, $\dot{p}_M$ is the energy allocated to somatic maintenance ($J.d^{-1}$) (Table 2.1; Eqn. 9) and $\dot{p}_j$ is the energy allocated to maturity maintenance ($J.d^{-1}$) (Table 2.1; Eqn. 11) (Pecquerie 2008, Pethybridge *et al.* 2013).

From the model, certain outputs can be calculated (Table 2.1; Eqns. 16-20). The structure V can be used to calculate the volumetric length L_v , which in turn can be used to determine L_C , the standard (caudal) length of the organism (cm). W_{dw} is the total dry weight of the organism (g), W_{ww} is the total wet weight of the organism (g) and W_{GON} is the gonad weight (g).

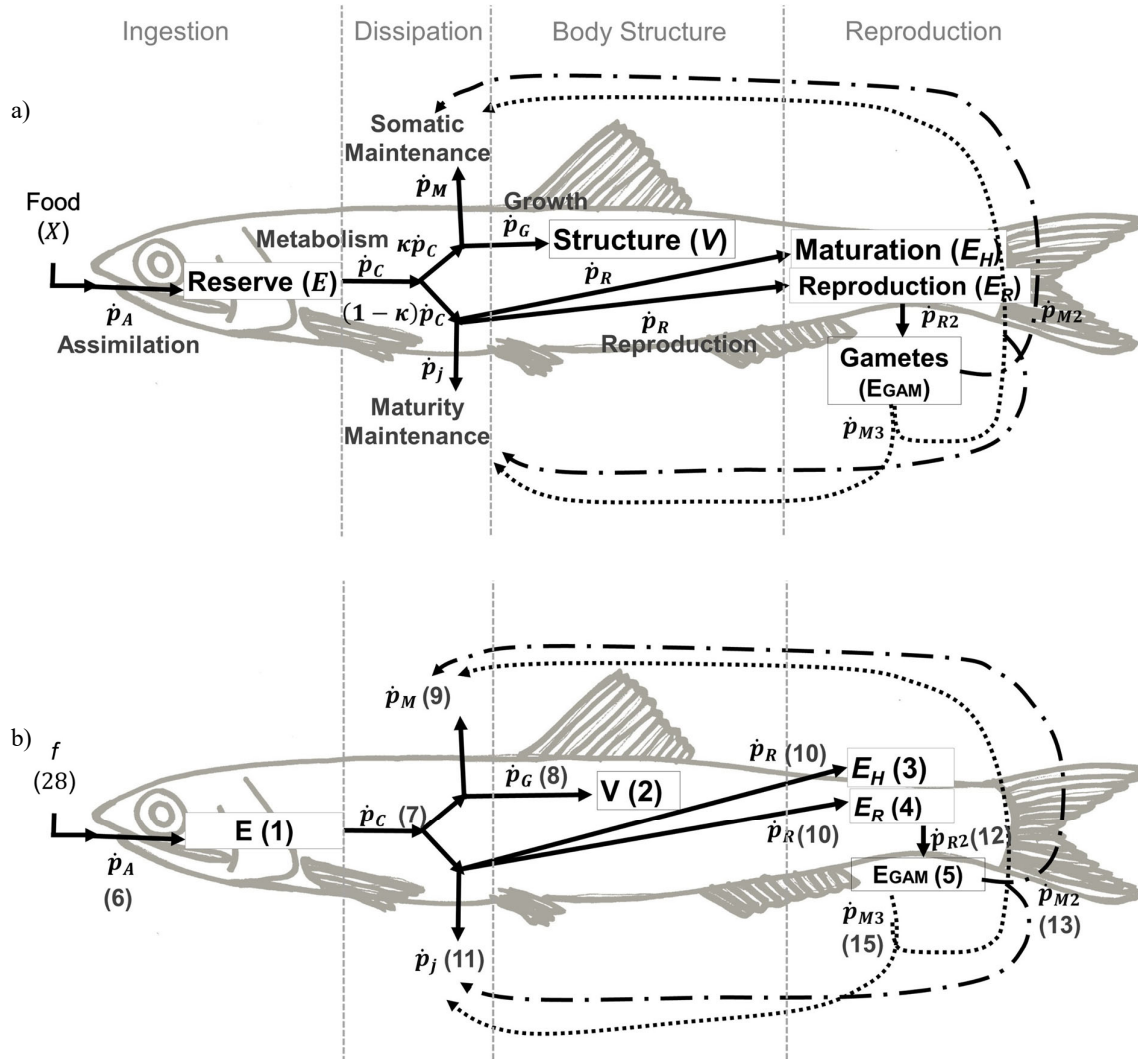


Figure 2.3 a) A conceptual diagram of the dynamic energy budget (DEB) model showing the fluxes of an individual anchovy. During the juvenile stage, the reproductive buffer (E_R) is zero and during the adult stage maturation (E_H) is zero. b) The DEB model showing the state variables and fluxes of an individual anchovy with their corresponding model equation number.

Table 2.1 Dynamic energy budget (DEB) model equations showing the model fluxes and state variables (from Pethybridge *et al.* 2013, Gatti *et al.* 2017). A conceptual diagram of these processes can be found in Figure 2.3b. The model parameters used in these equation are explained and defined in Table 2.4.

Description	Symbol.	Formula	Eq.
STATE VARIABLES (AND THEIR RATE OF CHANGE)			
Reserve (J)	E	$\frac{d}{dt}E = \dot{p}_A - \dot{p}_C$	1
Structure (cm ³)	V	$\frac{d}{dt}V = \frac{\dot{p}_G}{[E_G]}$	2
Maturity (J)	E_H	If $L_v < L_{vp}$ $\frac{d}{dt}E_H = \dot{p}_R$ else $\frac{d}{dt}E_H = 0$	3
Reproduction (J)	E_R	If $L_v < L_{vp}$ $\frac{d}{dt}E_R = 0$ Else if $L_v \geq L_{vp}$ & $E_{GAM} \geq 2.E_{batch}^*$ & $O_{Dev} \geq O_{DevTime}$ $\frac{d}{dt}E_R = \dot{p}_R - \dot{p}_{R2} - \dot{p}_{M2} - E_{batch}^*$ else $\frac{d}{dt}E_R = \dot{p}_R - \dot{p}_{R2} - \dot{p}_{M2}$	4
Gametes (J)	E_{GAM}	If $E_{GAM} \geq 2.E_{batch}^*$ & $O_{Dev} \geq O_{DevTime}$ $\frac{d}{dt}E_{GAM} = \dot{p}_{GAM} - \dot{p}_{M3} - E_{batch}^*$ else $\frac{d}{dt}E_{GAM} = \dot{p}_{GAM} - \dot{p}_{M3}$	5
FLUXES (J.d ⁻¹)			
Assimilation	$\dot{p}_A$	$\dot{p}_A = \{\dot{p}_{Am}\} \cdot f \cdot V^{2/3}$	6
Mobilization	$\dot{p}_C$	$\dot{p}_C = \frac{[E]}{[E_G] + \kappa[E]} \cdot \left([E_G] \cdot \frac{\{\dot{p}_{Am}\}}{[E_m]} \cdot V^{2/3} + [\dot{p}_M] \cdot V \right)$	7
Growth	$\dot{p}_G$	$\dot{p}_G = \max(\kappa\dot{p}_C - \dot{p}_M, 0)$	8
Somatic Maintenance	$\dot{p}_M$	$\dot{p}_M = [\dot{p}_M] \cdot V$	9
Reproduction	$\dot{p}_R$	$\dot{p}_R = (1 - \kappa)\dot{p}_C - \dot{p}_J$	10
Maturity Maintenance	$\dot{p}_J$	$\dot{p}_J = \frac{1 - \kappa}{\kappa} [\dot{p}_M] \cdot \min(V, V_p)$	11
Gamete (energy mobilization)	$\dot{p}_{R2}$	$\dot{p}_{R2} = E_R \left(\frac{\{\dot{p}_{Am}\}}{[E_m] \cdot V^{1/3}} + \frac{[\dot{p}_M]}{[E_G]} \right) \left(1 - \kappa \frac{E}{[E_G] \cdot V + \kappa \cdot E} \right)$	12
Emergency Somatic Maintenance	$\dot{p}_{M2}$	$\dot{p}_{M2} = \min(-\dot{p}_G, \dot{p}_{R2})$	13
Gamete Allocation (synthesis)	$\dot{p}_{GAM}$	$\dot{p}_{GAM} = \max(0, K_R(\dot{p}_{R2} - \dot{p}_{M2}))$	14
Atresia (resorption of gonads)	$\dot{p}_{M3}$	$\dot{p}_{M3} = \max\left(\dot{p}_M - \frac{(\kappa\dot{p}_C + \dot{p}_{M2})}{[E_G]}, 0\right)$	15

E_{batch}^* , once E_{GAM} has enough energy for two egg batches, one of the egg batches are released during that timestep (d⁻¹) and the energy for that egg batch is removed from E_R and E_{GAM} for that timestep.

Table 2.1 (cont.) Dynamic energy budget (DEB) model equations showing the model fluxes and state variables (from Gatti *et al.* 2017). A conceptual diagram of these processes can be found in Figure 2.3b. The model parameters used in these equation are explained and defined in Table 2.4.

Description	Symbol	Formula	Eqn.
MODEL OUTPUT			
Volumetric Length (cm)	L_V	$L_V = V^{1/3}$	16
Standard Length (cm)	L_C	$L_C = L_V/\delta$	17
Dry Weight (g)	W_{dW}	$W_{dW} = d_v \cdot V + \frac{E}{\mu_E} + \frac{E_R}{\mu_R}$	18
Wet Weight (g)	W_{ww}	$W_{ww} = W_{dW} \cdot \gamma$	19
Gonad Weight (g)	W_{GON}	$W_{GON} = \left(0.015 \cdot d_v \cdot V + \frac{E_{GAM}}{\mu_G} \right) \cdot \gamma$	20

2.2 Parameter estimation

2.2.1 Data collection

Length and weight data were collected from individual anchovy sampled during pelagic biomass and pelagic recruitment surveys conducted over the period 2012-2016 by the Department of Agriculture, Forestry and Fisheries (DAFF, now DFFE). Pelagic biomass surveys are undertaken during October/November, to cover the peak anchovy spawning season, and recruitment surveys are undertaken during May/June when juvenile anchovy recruit to the population and fishery. In total, 25 887 anchovy were sampled during the 2012-2016 surveys with L_C ranging between 3.0 and 14.7 cm and W_{ww} ranging between 0.1 and 35.6 g.

2.2.2 Life cycle parameters

Anchovy life cycle parameter were mostly assembled from published field and laboratory studies, with some unpublished data used in the study (Table 2.2). For the sake of comparison, all anchovy total length (L_T) values were converted to standard length (L_C) values (Table 2.3, Eqn. 23) (DAFF 2018).

For this study birth signifies hatching, so length at birth corresponds to the length at hatching. Puberty signifies length at first allocation to reproduction, a value that is smaller than the length at maturity (i.e., length at first reproduction); meaning that female anchovy first fill the reproductive buffer and then convert it into eggs (Pecquerie 2008).

2.2.3 von Bertalanffy growth curve

To compare model results in this study with empirical results, a von Bertalanffy equation fitted to observations (Waldron *et al.* 1989) was used:

$$L_C = L_\infty (1 - e^{-k(a-a_0)}) \quad 21$$

where standard (caudal) length L_C (cm) is calculated using the maximum asymptotic length L_∞ (cm), k is the growth rate (year^{-1}), a is the age (year) at that length and a_0 is the hypothetical age (year) at length zero (Table 2.2).

2.2.4 Length-weight relationship

The length-weight relationship, calculated from the 2012-2016 survey data, for generating weights at length that could be compared, as ground-truthing to the results of the anchovy DEB model:

$$W_{ww} = 0.00595 \cdot L_c^{3.186} \quad 22$$

where W_{ww} was the wet weight (g) and L_c was the standard (caudal) length (cm) from survey data ($R^2 = 0.95$).

Table 2.2 Life cycle parameters for the Southern Benguela anchovy *Engraulis encrasicolus* DEB model based on laboratory and field data from various authors at a reference temperature T_{ref} of 20°C.

Description	Symbol	Value	Units	Reference
Age at birth	a_b	1.33	days	King <i>et al.</i> (1978)
Age at metamorphosis	a_j	67	days	Brownell (1983)
Age at puberty	a_p	1	years	Le Clus (1979)
Life span of fish	a_m	4	years	Barange <i>et al.</i> (2009)
Standard length at birth	L_b	0.30	cm	Armstrong & Thomas (1989)
Standard length at metamorphosis	L_j	3.5	cm	Armstrong & Thomas (1989)
Standard length at puberty	L_p	8.0	cm	Le Clus (1979)
Maximum standard length	L_m	16	cm	Barange <i>et al.</i> (2009)
Wet weight at birth	W_{wb}	0.000128	g	DAFF data (2012-2016)
Wet weight at metamorphosis	W_{wj}	0.123	g	DAFF data (2012-2016)
Wet weight at puberty	W_{wp}	4.485	g	DAFF data (2012-2016)
Maximum wet weight	W_{wm}	40.817	g	DAFF data (2012-2016)
REPRODUCTIVE PARAMETERS				
Energy content of 1g egg	E_{egg}	0.720	J.egg ⁻¹	Szeinfeld (1993) ; Hunter & Leong (1981)
Full oocyte development time (peak season)	$O_{DevTime}$	9	days	Melo (1994a)
Full oocyte development time (end of season)	$O_{DevTime}$	12	days	Melo (1994a)
Relative batch fecundity	RF_{batch}	530	eggs.g ⁻¹	van der Lingen & Durholtz (2003)
Egg batches per year	N_{batch}	14-21	batch.y ⁻¹	Melo (1994b)
VON BERTALANFFY PARAMETERS				
Maximum asymptotic length	L_{∞}	14.80	cm	Waldron <i>et al.</i> (1989)
Growth rate	k	1.370	y ⁻¹	Waldron <i>et al.</i> (1989)
Age at length zero	a_0	-0.030	y	Waldron <i>et al.</i> (1989)

Table 2.3 Equations used to estimate parameters in Table 2.4 used as an input for the Southern Benguela anchovy *Engraulis encrasicolus* DEB model at a reference temperature T_{ref} of 20°C.

Description	Symbol	Formula	Eqn.
LENGTH EQUATIONS			
Standard length	L_C	$L_c = 0.8949 \cdot L_T - 0.5385$	23
Shape coefficient	δ	$\delta = \frac{W_W^{1/3}}{L_C}$	24
DEB PARAMETERS			
Water temperature	T_1	$T_1 = T + 273$	25
Temperature correction	$c(T_1)$	$c(T_1) = \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T_1}\right)$	26
Volume-specific maintenance cost	$[\dot{p}_M]$	$[\dot{p}_M] = [\dot{p}_M]_{ref} \cdot c(T_1)$	27
Surface-area-specific assimilation rate	$\{\dot{p}_{Am}\}$	$\{\dot{p}_{Am}\} = \{\dot{p}_{Am}\}_{ref} \cdot c(T_1)$	28
Functional response	f	$f = \frac{X}{X + K}$	29
Energy per batch of eggs	E_{batch}	$E_{batch} = E_{egg} \times (RF_{batch} \times W_W)$	30
Age-specific batch fecundity	F_{batch}	$F_{batch} = E_{batch}/E_{egg}$	31
Fraction of energy fixed into eggs	K_R	$K_R = \mu_R/\mu_E$	32

2.3 DEB parameter estimation

2.3.1 Shape coefficient (δ)

According to Pecquerie (2008), it is assumed that: 1) anchovy display isomorphic growth (i.e., the overall shape does not change through the life cycle); and 2) the reserve contributes little to standard length, so the physical length quantifies structural length. In this study the length-weight relationship was used to calculate an approximate value for the shape coefficient δ that is dimensionless if it is assumed that $1 \text{ g} = 1 \text{ cm}^3$ (Table 2.3; Eqn. 24) (Pecquerie 2008). Fitting a non-linear model to the length and weight data resulted in a heteroscedastic pattern in the residuals, hence the length and

weight data were log transformed and a linear regression model was fitted to the transformed data to calculate the shape coefficient. The linear regression model of the log transformed data for length and weight gave $\delta = 0.209$ ($t = -4\,758$, $n = 25\,887$, $p < 0.001$) (Table 2.4). All statistical analyses were performed using R for windows (R Core Team 2021).

2.3.2 Volumetric length (L_V)

In the standard DEB model, the surface area, and the body volume of the animal play important roles in energy exchange and fluxes (Sarà *et al.* 2013), with assimilation assumed to be proportional to the structural volume's surface-area, while maintenance is proportional to structural volume (Pecquerie *et al.* 2009, Sarà *et al.* 2013). In DEB models a shape coefficient (δ) is used to calculate standard length (L_c) of individuals from the volumetric length (L_V or $V^{1/3}$) or vice versa (Table 2.1, Eqn. 16) (Pecquerie 2008).

2.3.3 Water temperature (T_l)

For use in the DEB model, all water temperatures in degrees Celsius (T °C) were converted to water temperature T_1 in Kelvin (K) (Table 2.3, Eqn.25)

2.3.4 Arrhenius temperature (T_A)

The Arrhenius temperature T_A (K) is an alternative to the Q_{10} temperature function, and has been used to show the effects of temperature on biological rates, assuming that all rates were affected in the same way (Kooijman 2000, van der Veer *et al.* 2006, Pecquerie *et al.* 2009, Chowdhury *et al.* 2018). The Arrhenius temperature T_A (K) was calculated from observed values of metabolic rate according to Kooijman (2010) and Pecquerie (2008). King *et al.* (1978) described the relationship between egg development time D (h) and water temperature T_1 (K) for anchovy from the Northern Benguela as:

$$D = 43787.93 (T_1 - 273)^{-2.41} \quad 33$$

To calculate the Arrhenius temperature, $\ln(1/D)$ was plotted against $1/T_1$ to obtain a straight line with slope $T_A = 12\,026$ K ($n = 14$, $r^2 = 0.99$) for a temperature range from 284 K (11°C) to 297 K (24°C).

Table 2.4 DEB model parameters and, where applicable, the values and references for anchovy *Engraulis encrasicolus* in the Southern Benguela ecosystem used in the equations in Tables 2.1 and 2.3 for a reference temperature T_{ref} of 293 K (20°C). The half saturation constant (K) under the feeding parameters has the same unit as food density (X) (not given).

Description	DEB Parameter	Value	Units	Reference
FEEDING PARAMETERS				
Half saturation constant	K		As for food density	
Maximum assimilation rate	$\{\dot{p}_{Am}\}$		J.cm ⁻² .d ⁻¹	
Scaled functional response	f		-	
ENERGY PARAMETERS				
Fraction allocated to growth and maintenance	κ		-	
Maximum storage density	$[E_m]$		J.cm ⁻³	
Volume-specific maintenance cost	$[\dot{p}_M]$		J.cm ⁻³ .d ⁻¹	
Volume-specific cost for structure	$[E_G]$		J.cm ⁻³	
VOLUMETRIC PARAMETERS				
Volumetric length at puberty	L_{vp}	1.37	cm ³	
Maximum volumetric length	L_{Vm}	3.34	cm	
TEMPERATURE PARAMETERS				
Arrhenius Temperature	T_A	12 026	K	
Reference temperature (or 20°C)	T_{ref}	293	K	
Water Temperature	T_1		K	
CONVERSION PARAMETERS				
Density of the structure	d_V	0.11	g.cm ⁻³	Gatti <i>et al.</i> (2017)
Dry Weight to Wet Weight conversion	γ	4.1	-	Pethybridge <i>et al.</i> (2013)
Energy density of 1g of gametes	μ_G	23 880	J.g ⁻¹	Gatti <i>et al.</i> (2017)
Energy density of 1g of reproductive buffer	μ_R	24 937	J.g ⁻¹	Gatti <i>et al.</i> (2017)
Energy density of 1g of reserve	μ_E	31 332	J.g ⁻¹	Gatti <i>et al.</i> (2017)
Shape coefficient	δ	0.209	-	DAFF data (2012-2016)

2.3.5 Temperature correction $c(T_1)$

Body temperature affects all physiological and metabolic rates of anchovy, including the maximum assimilation rate $\{\dot{p}_{Am}\}$ and the somatic maintenance rate $[\dot{p}_M]$ (Pethybridge *et al.* 2013). The Van't Hoff-Arrhenius equation is used in DEB theory to describe the influence of temperature on physiological rates (van der Meer 2006). The equation for the effect of temperature on metabolic rates is given by a correction equation $c(T_1)$ (Table 2.3; Eqn. 26), where T_1 was the water temperature in Kelvin (K), the reference temperature in this case T_{ref} was set at 293 K (or 20°C) and T_A was the Arrhenius temperature (K) calculated for anchovy.

2.3.6 Reserve density [E]

DEB theory describes the reserve density ($[E]$, J.cm⁻³) as the energy reserves (E , J) per unit volume (V , cm³) (van der Meer 2006) and assumes that, during constant environmental conditions, the reserve density is constant (Pecquerie 2008) and is given by:

$$[E] = E/V \quad 34$$

The change in reserve density under changing environmental conditions (Pecquerie 2008) is given by:

$$\frac{d}{dt}[E] = \frac{\{\dot{p}_{Am}\}}{V^{1/3}} \left(f - \frac{[E]}{[E_m]} \right) \quad 35$$

where $\{\dot{p}_{Am}\}$ is the maximum assimilation rate (J.cm⁻².d⁻¹), V is the structure (cm³), f is the functional response and $[E_m]$ is the maximum storage density (J.cm⁻³).

2.3.7 Reproduction

The Southern Benguela anchovy spawning season falls between spring and summer (October to March), with peak spawning occurring between October and January/February (Shannon 1998, Huggett *et al.* 2003, van der Lingen & Huggett 2003, Barange *et al.* 2009). Anchovy have a spawning temperature tolerance range between 17°C and 23°C and an optimum temperature range for spawning between 18 and 20°C (Mhlongo *et al.* 2015). According to King *et al.* (1978), 14°C is the coolest water temperature needed for successful development of anchovy eggs. In this model only adult anchovy ($L_v > L_{vp}$) were able to spawn.

Two alternative conditions were applied for producing a single batch of gametes following Pethybridge *et al.* (2013) and Gatti *et al.* (2017). Firstly, $E_{GAM} \geq 2 \cdot E_{batch}^*$ (E_{batch}^* was calculated using Table 2.3; Eqn. 30). This means that a batch of eggs is released when the energy mobilized to the gametes (E_{GAM}) is more than or equal to the energy content of two egg batches (Gatti *et al.* 2017). The energy content of one egg E_{egg} (Table 2.4) was estimated by multiplying the mean caloric value of one egg ($5\,600\text{ J.g}^{-1} \cdot W_w\text{ egg}^{-1}$) (Szeinfeld 1993) by the mean wet weight of a recently-spawned anchovy egg ($1.286 \times 10^{-4}\text{ g.W}_w\text{ egg}^{-1}$) (Hunter & Leong 1981). The relative batch fecundity RF_{batch} (Table 2.4) was set to 530 eggs.g^{-1} for each spawn (range 481-624 eggs.g^{-1} per spawn) (Alheit 1993, Shelton *et al.* 1993, van der Lingen & Durholtz 2003).

For the second condition, a batch of oocytes must reach full development before they are spawned, i.e., $O_{Dev} > O_{DevTime}$. In the Benguela it takes 9-14 days for anchovy oocytes to reach full development ($O_{DevTime}$) (Szeinfeld 1993, Melo 1994a). The spawning interval was calculated by dividing 100 by the percentage of the spawning fraction (calculated by Melo 1994a) (e.g., for a spawning fraction of 0.07 the spawning interval would be $100/(0.07 \cdot 100) = 14$ days). For this study, $O_{DevTime}$ was set to 9 days during the peak spawning season and 12 days at the end of the spawning season. The implementation of these rules meant that the mother's size, caloric intake, and external temperatures would limit the frequency, amplitude, and intensity of anchovy spawning events (Pethybridge *et al.* 2013). Melo (1994a) estimated that anchovy could release between 14 and 21 egg batches per year (average of 17 egg batches per year), and an age-specific batch fecundity F_{batch} (J) was calculated using Pethybridge *et al.* (2013) (Table 2.3; Eqn. 31). The number of egg batches released per year was calculated by adding the number of egg batches spawned during the peak and end of the spawning season. This was calculated by dividing the number of days in a season by the spawning interval (e.g. the number of days in the peak spawning season (92 days) divided by the average spawning interval during peak season (8.33 days between batches) to get 11 batches spawned during peak season, add those for the end of the spawning season (6 batches) to get the average number spawned per year of 17 egg batches).

2.3.8 Energy density in the buffers (d_V, μ_E, μ_R, μ_G)

Various energy densities were used for the weight calculations. In the model, d_V was the density of the structural volume (g.cm^{-3}), μ_E was the energy density of one gram of reserve (J.g^{-1}), μ_R was the energy density of one gram of reproductive reserve (J.g^{-1}) and μ_G was the energy density of one gram

of gametes (J.g^{-1}) (Gatti *et al.* 2017). For the purpose of this study, the energy density in the buffers and the density of the structure were fixed using Gatti *et al.* (2017) (Table 2.4), since it is assumed that the chemical composition was the same for the same species.

2.4 Missing DEB parameters

Five parameters were identified within the DEB model that influence model outputs of length and weight but are difficult to estimate. These parameters are: i) the fraction allocated to growth and maintenance (κ); ii) the maximum storage density [E_m]; iii) the volume-specific maintenance rate [$\dot{p}_M$]; iv) the surface-area-specific assimilation rate [$\dot{p}_{Am}$]; and v) the volume-specific cost for structure [E_G]. Each parameter was separately varied in the model to find the optimum value that provided the closest visual fits to three growth curves for anchovy in the Southern Benguela. The three growth curves were: 1) length-at-age from the von Bertalanffy growth curve for anchovy; 2) weight-at-age generated by the model; and 3) the length-weight relationship calculated from the 2012-2016 survey data. These growth curves were generated for different values of the five parameters for a constant environment with a reference temperature T_{ref} of 293 K (20°C) and unlimited food ($f = 1.0$).

2.4.1 Fraction allocated to growth and maintenance κ

The maintenance ratio is part of the κ -rule, which states that a fixed fraction (κ) of the reserve (E) was allocated to somatic maintenance ($\dot{p}_M$) and growth ($\dot{p}_G$) (priority was given for maintenance), while the remaining fraction ($1-\kappa$) was allocated to development or reproduction ($\dot{p}_R$) and maturity maintenance ($\dot{p}_J$) (van der Meer 2006, Pecquerie 2008). Pecquerie *et al.* (2009) assigned a κ -value between 0.6 and 0.65 and Gatti *et al.* (2017) assigned a κ -value of 0.71 for anchovy in the Bay of Biscay. Pethybridge *et al.* (2013) assigned a κ -value of 0.7 for anchovy in the North-western Mediterranean. To find the optimum κ -value for anchovy in the Southern Benguela it was varied between 0.1 and 0.99, increasing by steps of 0.01 to see which fraction allocated to growth and maintenance would be optimal for the anchovy DEB model.

2.4.2 Maximum storage density $[E_m]$

Maximum storage density $[E_m]$ (J.cm^{-3}) was defined as the difference in energy content between an individual with unlimited resources (i.e., well-fed) and an individual that has depleted their entire reserve (i.e., starved) (Lavaud *et al.* 2017). DEB theory assumes that $[E_m]$ is proportional to the volumetric maximum length (van der Veer *et al.* 2006). For anchovy, the estimate of $[E_m]$ was varied between 1 000 and 8 000 J.cm^{-3} to find the optimum value of $[E_m]$ for the model.

2.4.3 Volume-specific maintenance rate $[\dot{p}_M]$

The volume-specific maintenance rate $[\dot{p}_M]$ ($\text{J.cm}^{-3}.\text{d}^{-1}$) represents the maintenance cost needed to build one unit of volume per unit time (van der Meer 2006) and is assumed to be a major part of the maintenance of the whole individual (van der Veer *et al.* 2006). It is affected by temperature and is scaled by the temperature correction factor $c(T_1)$ (van der Meer 2006) (Table 2.3; Eqn. 27). The volume-specific maintenance rate for reference conditions $[\dot{p}_M]_{ref}$ was varied between 20 and 140 $\text{J.cm}^{-3}.\text{d}^{-1}$ to find the optimum value for $[\dot{p}_M]_{ref}$ at a reference temperature T_{ref} of 293 K (20°C).

2.4.4 Surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$

The surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ ($\text{J.cm}^{-2}.\text{d}^{-1}$) is dependent on the animal's diet and the efficiency with which the animal converts food that has been ingested into assimilated energy (van der Meer 2006). This rate was also affected by temperature (van der Meer 2006) so the surface-area-specific assimilation rate for reference conditions $\{\dot{p}_{Am}\}_{ref}$ was scaled by the temperature correction factor $c(T_1)$ for different water temperatures (Table 2.3; Eqn. 28). To find the optimum values for the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$ at reference conditions the value was varied between 100 and 470 $\text{J.cm}^{-2}.\text{d}^{-1}$.

2.4.5 Volume-specific cost for structure $[E_G]$

The volume-specific cost for structure $[E_G]$ (J.cm^{-3}) was defined as the energetic cost needed for one unit of growth to occur in structural body volume (van der Meer 2006). To find the optimum value for $[E_G]$ at reference conditions, it was varied between 100 and 7 000 J.cm^{-3} .

2.5 Description of experiments

2.5.1 Varying the scaled functional response (f)

The functional response (f) (Table 2.3; Eqn. 29) was the ingestion rate of anchovy as a fraction of the maximum possible ingestion of an individual of a given size. It is a function of food density (X) and a half saturation constant (K); this parameter was dimensionless and has values ranging from zero (starving) to one (unlimited food intake) (Pethybridge *et al.* 2013).

In this experiment the fish experienced constant temperature at a reference temperature T_{ref} of 293 K (20°C). The functional response (f) was assigned values between 0.1 and 1.0 that increased sequentially by 0.1, with $f=1.0$ signifying an unlimited food supply and $f=0.1$ signifying near starvation. Von Bertalanffy growth curves and the length-weight relationships at different functional response levels were then compared to observed growth curves to assess how the functional response influenced anchovy growth patterns.

2.5.2 Varying the water temperature (T)

In this experiment anchovy experienced constant unlimited food ($f=1.0$), while the water temperature (T) was varied between 12°C and 26°C in 2°C increments to assess how temperature affected the growth and reproduction of anchovy by changing the parameters affected by temperature (Table 2.8). Von Bertalanffy growth curves and the length-weight relationships at different temperatures were then compared to observed growth curves.

2.5.3 Starvation study

Standard DEB theory allows for storage dynamics to be modified during starvation (Pecquerie 2008). This happens when maintenance costs cannot be paid from the reserve due to a lack of assimilation. In this case growth ceases and the reproductive buffer (E_R) is utilized to pay the maintenance costs and the gametes are absorbed through atresia ($\dot{p}_{M3}$) (Figure 2.4) (Pecquerie 2008). If starvation occurs and the reproductive buffer is empty, either because the fish is a juvenile or because the fish is in poor condition, the individual dies (Pecquerie 2008).

Atresia is a process that occurs naturally in spawning populations and progressed from a few females showing atresia during the peak spawning to over 50% of females near the end of the spawning season

for northern anchovy *Engraulis mordax* (Hunter & Macewicz 1985). In Southern Benguela anchovy *E. encrasicolus*, instances of gonad atresia during peak spawning are typically low, although occasional high levels attributed to poor food availability have been reported (Melo 1994a). Low values were typically observed in February and March, close to the end of the spawning season (Melo 1994a, Painting *et al.* 1998).

To simulate the amount of time it would take anchovy in the model to starve to death (reproductive buffer $E_R = 0$) at different stages of reproductive development, they were placed into different starvation scenarios. These were timed to occur just before spawning started or at the middle of the spawning season and persisted for the remainder of an individual's life. The time to starvation was assessed under varied temperature and food regimes. In the first instance, anchovy would have unlimited food ($f = 1$) until they reached the desired start or middle of the spawning season, after which starvation would occur ($f = 0$). The number of days taken for the reproductive buffer (E_R) to reach zero was recorded for water temperatures (T) ranging between 12 and 26°C in 2°C increments. In the second instance, anchovy experienced different constant scaled functional responses ($f = 0.1, 0.9, 0.8, 0.7$ or 0.6) at a constant reference temperature $T_{ref} = 293$ K (20°C) until they reach the desired start or middle of the spawning season, after which starvation would occur ($f = 0$). The number of days taken for the reproductive buffer (E_R) to reach zero was recorded at that temperature.

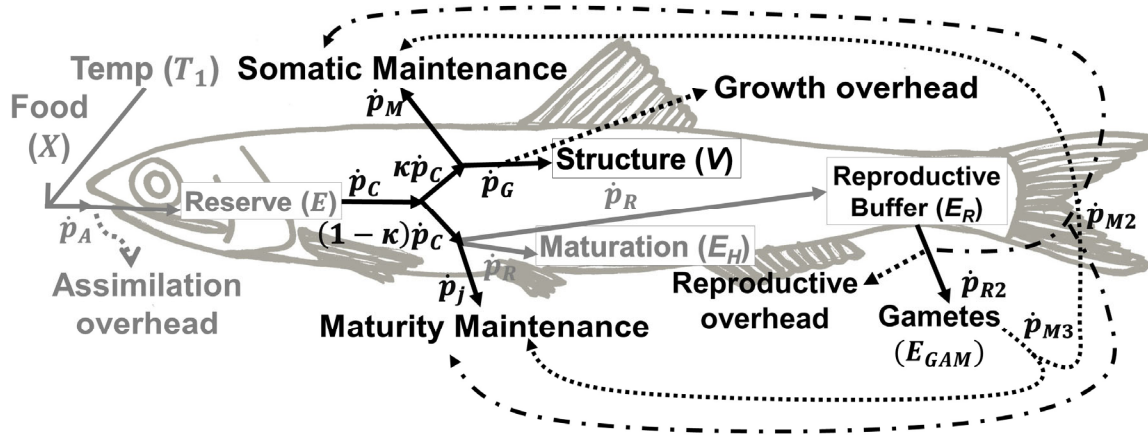


Figure 2.4 A conceptual diagram of the standard dynamic energy budget (DEB) model showing the route of fluxes of an anchovy during starvation. The grey pathways are the processes that cease during starvation and the black pathways are how maintenance are paid during starvation.

All anchovy (*Engraulis encrasicolus*) model code for the Southern Benguela can be accessed at: <https://doi.org/10.25375/uct.16802584> (Groenewald *et al.* 2021a)

Results

Estimated missing DEB parameters.

The five missing anchovy DEB parameters were estimated at reference conditions where the functional response f was 1.0 and the reference temperature T_{ref} was 293 K (20°C). The values of these parameters that provided the closest visual fits to the von Bertalanffy growth curve and the length-weight relationship from the survey data are shown in Table 2.5. The model calculated the number of days taken to reach sexual maturity as 205 days (approximately 0.6 years), the maximum length and weight values as 14.68 cm and 59.545 g, respectively, and the number of egg batches spawned throughout the anchovy's lifetime as 49 batches (approximately 14-15 egg batches per year) (Table 2.6).

2.4.1 Fraction allocated to growth and maintenance κ

Simulated length-at-age growth curves for anchovy, under stable environmental conditions, followed a von Bertalanffy growth curve, with lower values of κ resulting in reduced length-at-age (Figure 2.5a). Lower values of κ decreased the variability in the weight-at-age, leading to smaller peaks in weight-at-age during the spawning season when egg batches were produced and released (Figure 2.5b). The increased variability in weight at higher values of κ meant there was increased variability

Table 2.5 Optimum estimated DEB model parameters values used in the equations in Tables 2.1 and 2.3 for a reference temperature T_{ref} of 293 K (20°C) and a functional response f of 1.0.

Parameter	Symbol	Min	Max	Value	Units
Fraction allocated to growth and maintenance	κ	0.1	0.99	0.35	-
Maximum storage density	$[E_m]$	1 000	8 000	2 800	J.cm ⁻³
Volume-specific maintenance cost	$[\dot{p}_M]_{ref}$	20	140	25	J.cm ⁻³ .d ⁻¹
Maximum assimilation rate	$\{\dot{p}_{Am}\}_{ref}$	105	470	220	J.cm ⁻² .d ⁻¹
Volume-specific cost for structure	$[E_G]$	100	7 000	1 200	J.cm ⁻³

Table 2.6 The effects of changing (Shift; arrow indicated increase or decrease) each parameter individually on the anchovy model output at reference conditions (temperature T_{ref} of 293 K (20°C) and a functional response f of 1.0). Where a_p is age at puberty (days; brackets are in years), L_p is standard length at puberty (cm), L_m is maximum standard length (cm), W_{wp} is wet weight at puberty (g), W_{wm} is wet weight (g) at maximum length and N_{batch} is the number of egg batches produced by an anchovy as predicted by the model during a four year lifespan. Optimum model output is highlighted in bold.

Parameters	Symbol	Shift	Value	a_p (days (years))	L_p (cm)	L_m (cm)	W_{wp} (g)	W_{wm} (g)	N_{batch}
Model				205 (0.6)	8.02	14.68	3.870	59.545	49
Fraction allocated to growth and maintenance	κ (-)	↓ ↑	0.25 0.45	324 (0.9) 163 (0.4)	8.01 8.03	10.51 18.81	3.849 3.885	22.466 106.310	46 36
Maximum storage density	$[E_m]$ (J.cm ⁻³)	↓ ↑	800 4 800	140 (0.4) 269 (0.7)	8.02 8.01	14.73 14.52	2.644 5.073	53.054 64.403	61 34
Volume-specific maintenance cost	$[\dot{p}_M]_{ref}$ (J.cm ⁻³ .d ⁻¹)	↓ ↑	15 35	172 (0.5) 266 (0.7)	8.02 8.00	23.70 10.52	3.878 3.836	201.960 21.015	36 45
Maximum assimilation rate	$\{\dot{p}_{Am}\}_{ref}$ (J.cm ⁻² .d ⁻¹)	↓ ↑	120 320	1 392(3.8) 124 (0.3)	8.00 8.04	8.01 21.36	3.821 3.911	3.838 196.230	0 58
Volume-specific cost for structure	$[E_G]$ (J.cm ⁻³)	↓ ↑	200 2 200	113 (0.3) 296(0.8)	8.01 8.01	14.74 14.42	3.845 3.864	58.839 56.711	58 42

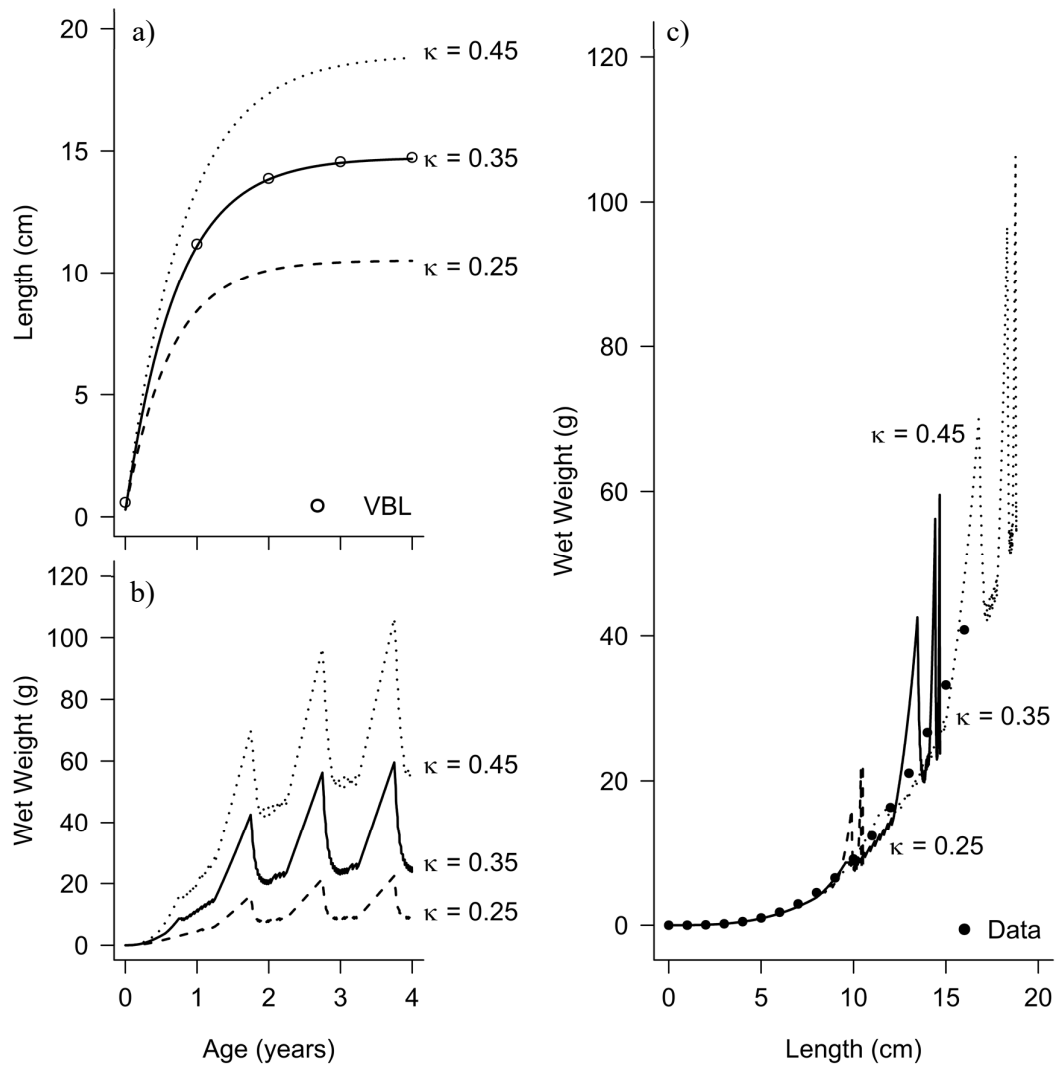


Figure 2.5 Effect of the fraction allocated to growth and maintenance (κ) on anchovy growth curves in the Southern Benguela at reference conditions (temperature T_{ref} of 293 K (20°C) and functional response f of 1.0). The effect of differing κ is shown in model output of a) length-at-age, b) weight-at-age, and c) length-weight relationship. Lines represent different values of fractions allocated to growth and maintenance (κ) indicated next to each line, $\circ$ VBL represents the von Bertalanffy growth curve and $\bullet$ Data represents the length-weight relationship from survey data.

in the length-weight relationship. The slopes of the length-weight curves did not change for different values of κ (Figure 2.5c). The fraction allocated to growth and maintenance (κ) markedly influenced the number of egg batches spawned by anchovy. A decrease in κ of 0.1 decreased the number of egg batches spawned by 3, while an increase of 0.1 decreased the number of egg batches spawned by 13 (Table 2.6).

Changing the fraction allocated to growth and maintenance (κ) influenced two of the other important missing parameters. To achieve a von Bertalanffy growth curve for anchovy with a decrease in κ , there would have to be an increase in the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$, and a decrease in the volume-specific cost for structure $[E_G]$.

2.4.2 Maximum storage density $[E_m]$

The maximum storage density $[E_m]$ influences both the shape and slope of the anchovy length-weight relationship. To show the influence of $[E_m]$ on the anchovy growth curves, the optimum value of $2\,800\text{ J.cm}^{-3}$ was varied by increasing and decreasing $[E_m]$ by $2\,000\text{ J.cm}^{-3}$ (Figure 2.6). The decrease in $[E_m]$ increased the maximum length by 0.05 cm, while the increase in $[E_m]$ decreased the maximum length by 0.16 cm (Table 2.6). Thus changing $[E_m]$ does not markedly change the maximum length but it does change the rate at which anchovy reach their maximum length. At lower values of $[E_m]$ anchovy reached their maximum length faster than at higher values (Figure 2.6a). The maximum storage density $[E_m]$ also influenced the weight output of the anchovy model. The decrease in $[E_m]$ decreased the maximum weight by 6.491 g, while the increase in $[E_m]$ increased the maximum weight by 4.858 g (Table 2.6). Thus, increasing the value for $[E_m]$ increased the maximum weight as well as the length of time it took to reach that maximum weight (Figure 2.6b). Higher values of $[E_m]$ gave a steeper slope to the length-weight curve (Figure 2.6c). Increasing $[E_m]$ by $2\,000\text{ J.cm}^{-3}$ decreased the number of egg batches anchovy produced in their lifetime by 12 egg batches, while decreasing $[E_m]$ increased the number of egg batches by 15 (Table 2.6).

Changes to $[E_m]$ also influenced the volume-specific cost for structure $[E_G]$. Thus, to achieve a von Bertalanffy growth curve consistent with anchovy growth, if $[E_m]$ is decreased the corresponding $[E_G]$ value would have to be increased.

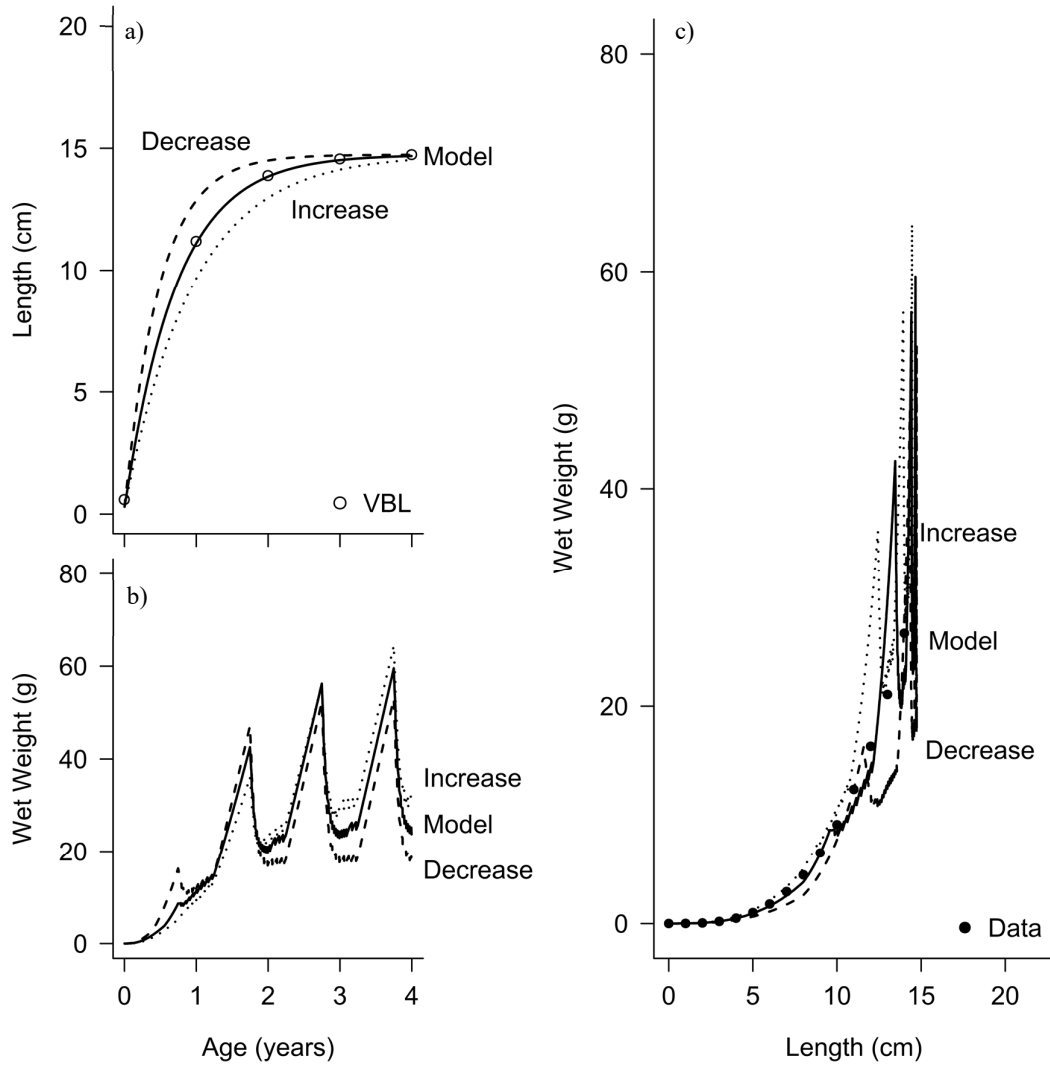


Figure 2.6 The influence of the maximum storage density $[E_m]$ (J.cm⁻³) on the anchovy DEB model length, weight, and age at reference conditions (temperature T_{ref} of 293 K (20°C) and functional response f of 1.0). The influence of $[E_m]$ on the model output is illustrated in a) the length-at-age curve, b) the weight-at-age curve and c) the length-weight relationship. Model (—) represents the model output for the optimum value of $[E_m]$ (2 800 J.cm⁻³). Increase (...) and decrease (---) shows how an increase and decrease to 4 800 J.cm⁻³ and 800 J.cm⁻³, respectively, influences the shape of the model output, ○ VBL represents the von Bertalanffy growth curve and ● Data represents the length-weight relationship from survey data.

2.4.3 Volume-specific maintenance rate $[\dot{p}_M]_{ref}$

The volume-specific maintenance rate $[\dot{p}_M]_{ref}$ ($\text{J.cm}^{-3}.\text{d}^{-1}$) affects both the length and weight output of the model. To show the influence of $[\dot{p}_M]_{ref}$ on the growth curves, the optimal value of $[\dot{p}_M]_{ref}$ ($25 \text{ J.cm}^{-3}.\text{d}^{-1}$) was varied by increasing and decreasing the value by $10 \text{ J.cm}^{-3}.\text{d}^{-1}$ (Figure 2.7).

The decrease in $[\dot{p}_M]_{ref}$ increased the maximum length by a substantial 9.02 cm, while the increase in $[\dot{p}_M]_{ref}$ decreased the maximum length by 4.16 cm (Table 2.6). Thus, an increase in $[\dot{p}_M]_{ref}$ resulted in a decrease in the maximum length and the shape of the length-at-age curve, with anchovy weight-at-age curves, with the decrease in $[\dot{p}_M]_{ref}$, increasing the maximum weight by 142.415 g, while reaching a plateau faster at larger values of $[\dot{p}_M]_{ref}$ (Figure 2.7a). The same pattern was seen in the increase in $[\dot{p}_M]_{ref}$, which decreased the maximum weight by 38.530 g (Table 2.6). Thus larger $[\dot{p}_M]_{ref}$ values led to smaller weights and maximum weights (Figure 2.7b). Changing $[\dot{p}_M]_{ref}$ changed length and weight values in such a way that the slope of the length-weight relationship remained unchanged (Figure 2.7c). Increasing $[\dot{p}_M]_{ref}$ decreased the number of egg batches anchovy produced in their lifetime by 4 egg batches, while decreasing $[\dot{p}_M]_{ref}$ decreased the number of egg batches by 13.

Changing the volume-specific maintenance rate $[\dot{p}_M]_{ref}$ influenced three of the missing parameters. So, to achieve the desired von Bertalanffy growth curve by decreasing $[\dot{p}_M]_{ref}$ there would have to be a decrease in both the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$, and a decrease in the volume-specific cost for structure $[E_G]$ or an increase in the maximum storage density $[E_m]$. The volume-specific maintenance rate $[\dot{p}_M]_{ref}$ also played an important role in the time it would take for anchovy to starve to death, with an increase in $[\dot{p}_M]_{ref}$ leading to a decrease in the survival of starved anchovy.

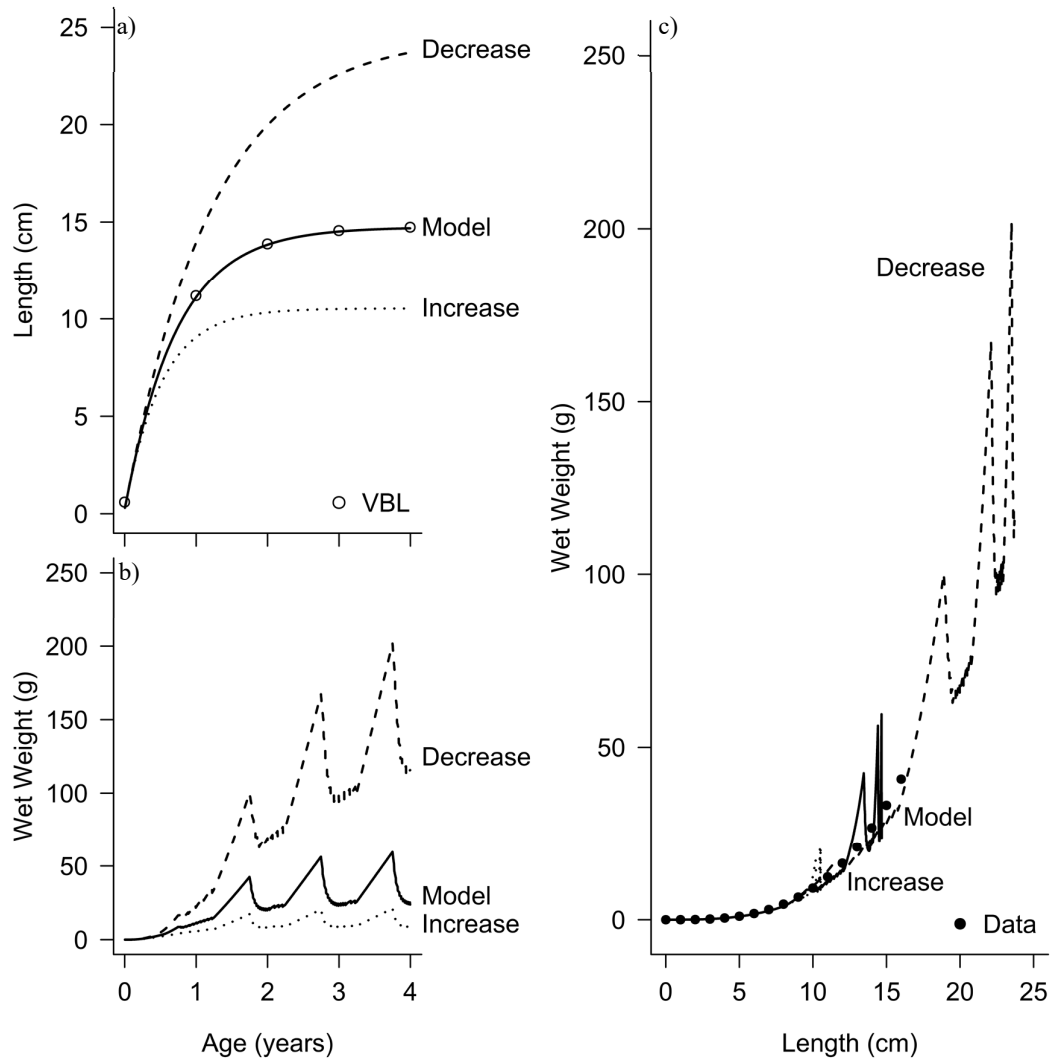


Figure 2.7 The influence of the volume-specific maintenance rate $[\dot{p}_M]_{ref}$ ($\text{J} \cdot \text{cm}^{-3} \cdot \text{d}^{-1}$) on the anchovy DEB model length, weight and age at reference conditions (temperature T_{ref} of 293 K (20°C) and functional response ($f=1.0$)). Where the influence of $[\dot{p}_M]_{ref}$ on the model output is illustrated in a) length-at-age curve, b) weight-at-age curve and c) length-weight relationship of the anchovy model. Model (—) represents the model output for the optimum value of $[\dot{p}_M]_{ref}$ of $25 \text{ J} \cdot \text{cm}^{-3} \cdot \text{d}^{-1}$. Increase (...) and decrease (---) represents an increase to $35 \text{ J} \cdot \text{cm}^{-3} \cdot \text{d}^{-1}$ and decrease to $15 \text{ J} \cdot \text{cm}^{-3} \cdot \text{d}^{-1}$ and how that influenced the shape of the model output, ○ VBL represents the von Bertalanffy growth and ● Data represents the length-weight relationship from survey data.

2.4.4 Surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$

The surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ is affected by temperature and is scaled by the temperature correction factor $c(T_1)$ for different water temperatures. To show the influence of $\{\dot{p}_{Am}\}_{ref}$ on the growth of anchovy in the model the optimum value for $\{\dot{p}_{Am}\}_{ref}$ ($220 \text{ J.cm}^{-2}.\text{d}^{-1}$) was varied by increasing and decreasing the value by $100 \text{ J.cm}^{-2}.\text{d}^{-1}$ (Figure 2.8).

The surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$ ($\text{J.cm}^{-2}.\text{d}^{-1}$) affected both the length and the weight outputs of the anchovy model. Varying $\{\dot{p}_{Am}\}_{ref}$ by $\pm 100 \text{ J.cm}^{-2}.\text{d}^{-1}$ varied the maximum length by $\pm 6.67 \text{ cm}$ (Table 2.6). An increase in $\{\dot{p}_{Am}\}_{ref}$ led to anchovy having faster growth rates so they reached their maximum length faster and at larger maximum lengths (Figure 2.8a). Changing $\{\dot{p}_{Am}\}_{ref}$ values had a marked effect on anchovy weight; decreasing this decreased the maximum weight by 55.707 g , while the increase in $\{\dot{p}_{Am}\}_{ref}$ increased the maximum weight by 136.685 g (Table 2.6). Thus, higher values of $\{\dot{p}_{Am}\}_{ref}$ lead to anchovy achieving heavier weight values faster (Figure 2.8b). The influence of $\{\dot{p}_{Am}\}_{ref}$ was such that an increase in $\{\dot{p}_{Am}\}_{ref}$ led to increases in both length and weight in such a way that the slope of the length-weight relationship did not change (Figure 2.8c). Changing $\{\dot{p}_{Am}\}_{ref}$ also affected the number of egg batches produced during the anchovy's life cycle. The decrease in $\{\dot{p}_{Am}\}_{ref}$ reduced the total number of egg batches produced by 49 (Table 2.6), while increasing $\{\dot{p}_{Am}\}_{ref}$ increased the total number of egg batches produced by nine.

Changing the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$ influenced most of the missing parameters. To attain the desired von Bertalanffy growth curve by decreasing $\{\dot{p}_{Am}\}_{ref}$, there would have to be a decrease in both the volume-specific maintenance rate $[\dot{p}_M]_{ref}$ and either a decrease in the volume-specific cost for structure $[E_G]$ or an increase in the maximum storage density $[E_m]$.

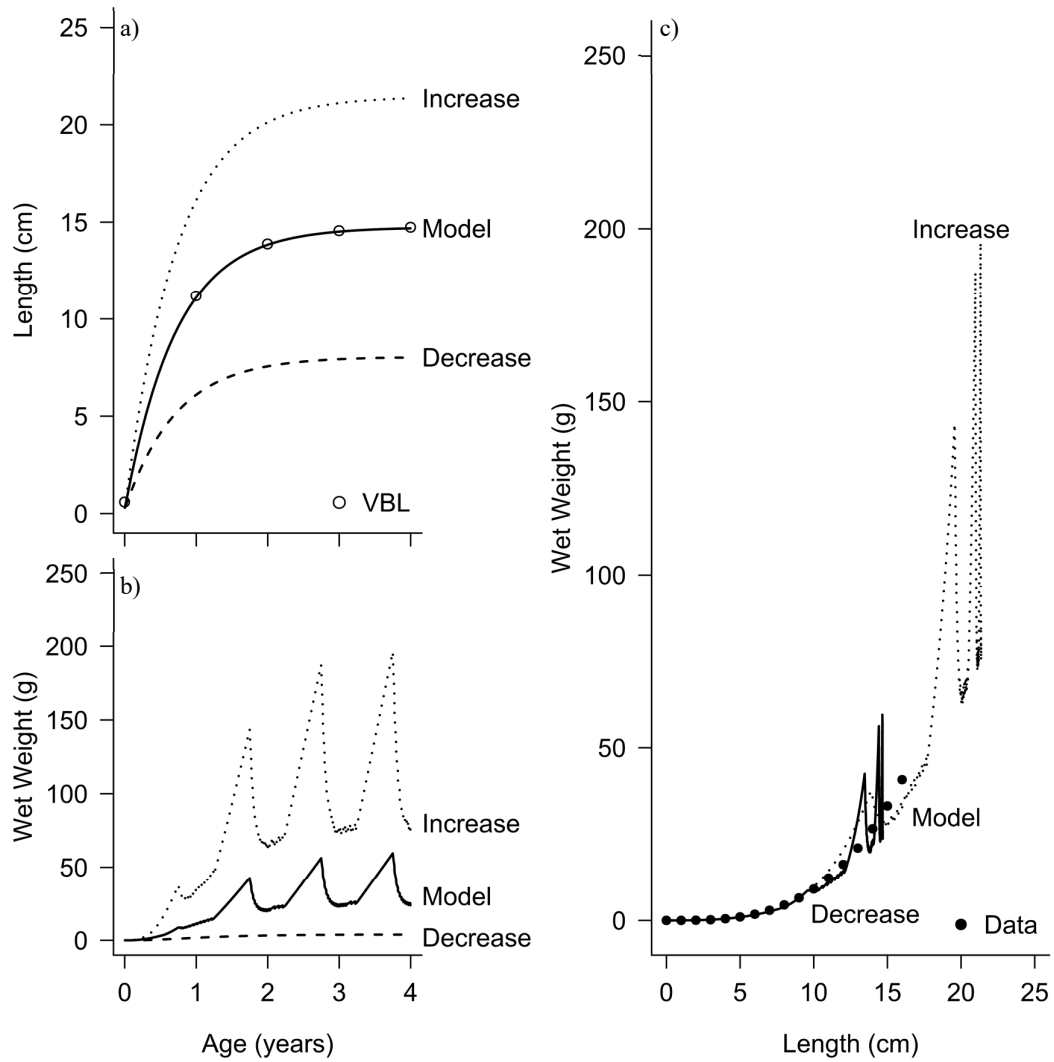


Figure 2.8 The influence of the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$ ($\text{J}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) on the anchovy DEB model length, weight and age at reference conditions (temperature T_{ref} of 293 K (20°C) and functional response ($f=1.0$)). Where the influence of $\{\dot{p}_{Am}\}_{ref}$ on the model output is illustrated on the a) at age curve, b) weight versus age curve, and c) length-weight curve of the anchovy model. Model (—) represents the model output for the optimum value of $\{\dot{p}_{Am}\}_{ref}$ of $220 \text{ J}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$. Increase (...) and decrease (---) shows how an increase to $320 \text{ J}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ and a decrease to $120 \text{ J}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ influences the shape of the model output, ○ VBL represents the von Bertalanffy growth and ● Data represents the length-weight relationship from survey data.

2.4.5 Volume-specific cost for structure $[E_G]$

To show the influence of the volume-specific cost for structure $[E_G]$ on the model output, the optimum value for volume-specific cost for structure $[E_G]$ ($1\,200\text{ J.cm}^{-3}$) was varied by $\pm 1\,000\text{ J.cm}^{-3}$ (Figure 2.9). The volume-specific cost for structure $[E_G]$ (J.cm^{-3}) influenced the shape of both length- and weight-at-age curves.

The decrease in $[E_G]$ increased the maximum length by 0.06 cm, while the increase in $[E_G]$ decreased the maximum length by 0.26 cm (Table 2.6). Thus changing $[E_G]$ changed the slope of the length-at-age curves, with anchovy showing faster growth rates at lower values of $[E_G]$, even if there was not a big difference in the maximum length values (Figure 2.9a). A different pattern was seen in the weight-at-age curves, with the decrease in $[E_G]$ decreasing the maximum weight by 0.706 g, while the increase in $[E_G]$ decreased the maximum weight by 2.834 g (Table 2.6), most likely due to the slower growth rate. If the model run was extended the increase in $[E_G]$ would have led to higher maximum weights. The weight-at-age curve reached the maximum weight faster at lower values of $[E_G]$, even though the maximum weight-at-age did not change by a large amount (Figure 2.9b). Changes in $[E_G]$ also affected the shape and maximum value of the length-weight relationship curve for adult anchovy but not juveniles (Figure 2.9c). The decrease in $[E_G]$ increased the number of egg batches produced by nine in anchovy; with the increase in $[E_G]$ decreasing the total number of egg batches produced by seven (Table 2.6).

Changing the volume-specific cost for structure $[E_G]$ influenced three of the missing parameters. A decrease in $[E_G]$ would have to be compensated for by a decrease in both volume-specific maintenance rate $[\dot{p}_M]_{ref}$ and the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$, or an increase in the maximum storage density $[E_m]$, to get the desired anchovy von Bertalanffy growth curve.

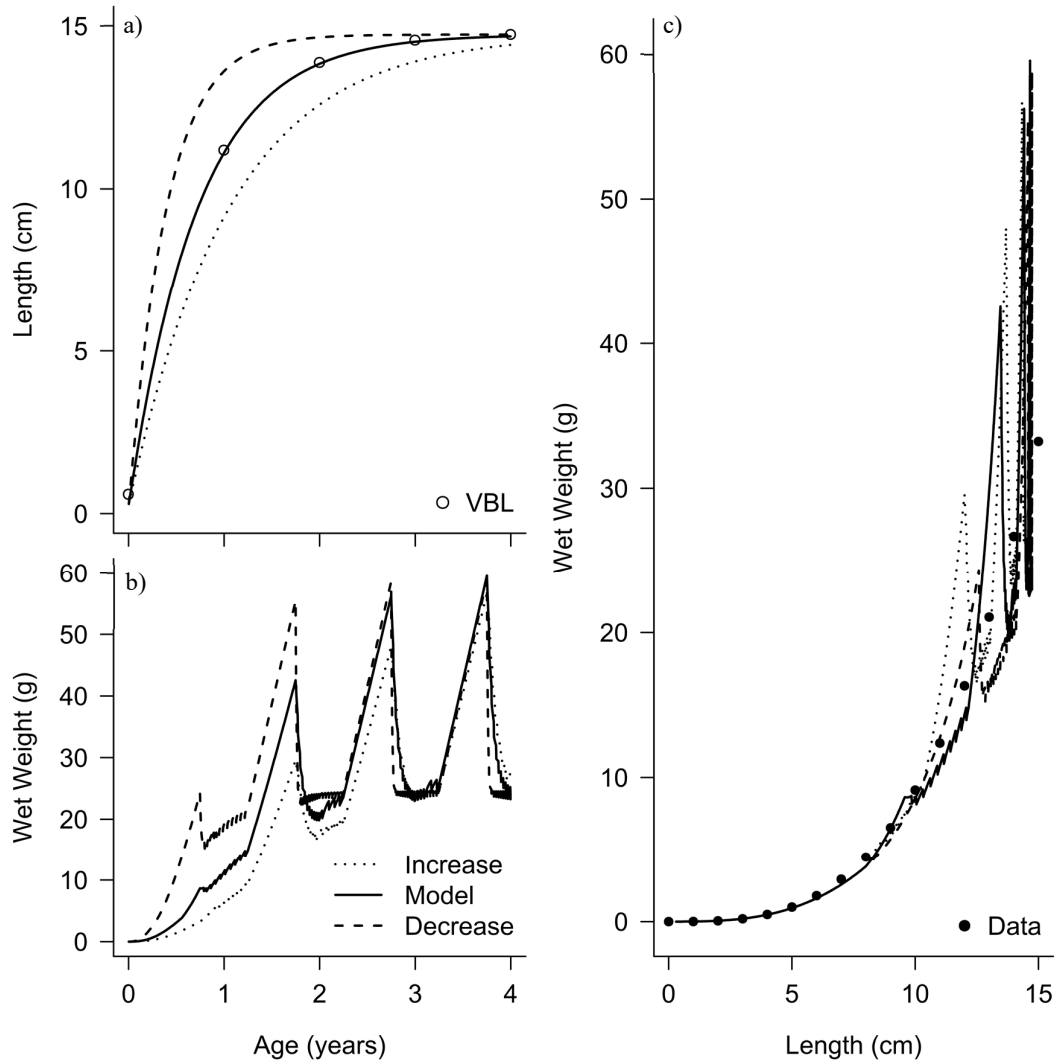


Figure 2.9 The influence of the volume-specific cost for structure $[E_G]$ (J.cm⁻³) on the anchovy DEB model length, weight, and age at reference conditions (temperature T_{ref} of 293 K (20°C) and functional response ($f=1.0$)). Where the influence of $[E_G]$ on the model output is illustrated in a) the length-at-age curve, b) the weight-at-age curve, and c) the length-weight relationship of the anchovy model. Model (—) represents the model output for the optimum value of $[E_G]$ of 1 200 J.cm⁻³. Increase (...) and decrease (---) shows how an increase to 2 200 J.cm⁻³ and a decrease to 200 J.cm⁻³ influences the shape of the model output, ○ VBL represents the von Bertalanffy growth and ● Data represents the length-weight relationship from survey data.

Experimental results for the anchovy model

2.5.1 Varying the scaled functional response (f)

A decrease in the functional response caused a reduction in both the size and reproductive rates of anchovy. At constant reference temperature $T_{ref} = 293$ K (20°C) and optimum conditions with unlimited food ($f = 1.0$), anchovy reached a maximum length of 14.68 cm and a maximum weight of 59.545 g (Table 2.7). At low food conditions ($f \leq 0.5$) anchovy did not reach sexual maturity (puberty), their maximum lengths only reached 7.36 cm and weight only reached 2.311 g at an f of 0.5 (Table 2.7). The length of time taken to reach sexual maturity increased with a decrease in f . At unlimited food anchovy reached sexual maturity in 205 days (0.6 year) compared to the 502 days (1.4 years) at an f of 0.6 (Table 2.7). The number of egg batches anchovy spawned in their four-year lifespan ranged between 13 and 49 egg batches for functional response values between 0.6 and 1.0.

Food availability and thus the functional response affected the growth curves of anchovy. At higher functional response (f) values, anchovy reached larger maximum lengths (L_m) (Figure 2.10a). Higher f values affected the wet weight curves as well, with heavier maximum wet weights at higher f values (Figure 2.10b). The functional response f affected the length-weight relationship in such a way that smaller f values generated a decrease in the slope of the length-weight relationship curve because of a slower growth rate (Figure 2.10c).

2.5.2 Varying the water temperature (T)

Two of the rates estimated for the DEB model are affected by temperature and are scaled by the temperature correction factor $c(T_1)$. Table 2.8 shows the values for the volume-specific maintenance costs $[\dot{p}_M]$ and the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ calculated for each water temperature (T) between 12 and 26°C using Eqn. 27 and 28, respectively. An increase in temperature from 12 to 26°C increased the volume-specific maintenance cost from 8 J.d⁻¹.cm⁻³ to 57 J.d⁻¹.cm⁻³ and the surface-area-specific assimilation rate from 70 J.cm⁻².d⁻¹ to 501 J.cm⁻².d⁻¹.

The model showed that water temperatures between 16 and 20°C resulted in slightly smaller ages at puberty (between 205 and 358 days or 0.5 to 1.0 years) than those reported in the literature (Table 2.9). Temperature also affected the number of egg batches that anchovy produced throughout their life cycle, with more egg batches being produced at warm than cool temperatures (Table 2.9).

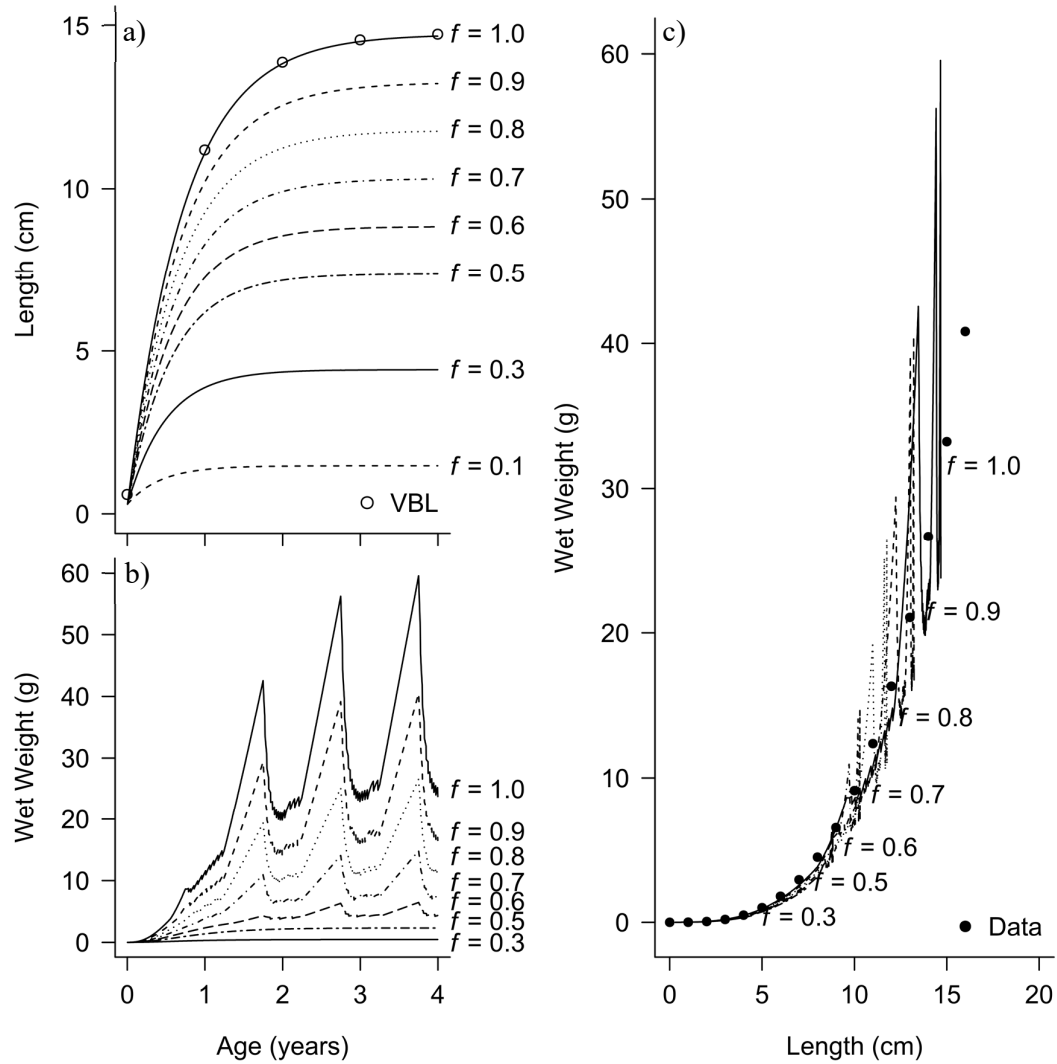


Figure 2.10 The effect of the change in functional response (f) on the growth curves of anchovy in the Southern Benguela under constant reference temperature T_{ref} of 293 K (20°C). The effect of changing the f is shown in a) the length (cm) versus age (years) curves, b) the weight (g) versus age (years) curve and c) the length(cm) versus weight (g) curve. The lines indicate the different values of f , ○ VBL is the growth according to the von Bertalanffy growth equation for anchovy and ● Data represents the length-weight relationship from survey data.

Table 2.7 Effect of varying the scaled functional response (f) on the model output of anchovy for a constant reference temperature T_{ref} of 293 K (20°C). Lit is the observed values from literature. Where a_p is age at puberty (days) with the age in years in brackets, L_p is standard length at puberty (cm), L_m is maximum standard length (cm), W_{wp} is wet weight at puberty (g), W_{wm} is wet weight (g) at maximum length from the length-weight relationship with the maximum length from the survey data in brackets and N_{batch} is the number of egg batches produced by an anchovy as predicted by the model during a four year lifespan.

	a_p (days (years))	L_p (cm)	L_m (cm)	W_{wp} (g)	W_{wm} (g)	N_{batch} (egg batches)
Lit	365 (1.0)	8.00	16.00	4.485	40.817 (35.6)	60
$f=1.0$	205 (0.6)	8.02	14.68	3.870	59.545	49
$f=0.9$	230 (0.6)	8.00	13.22	3.667	40.493	47
$f=0.8$	269 (0.7)	8.01	11.76	3.496	26.591	41
$f=0.7$	336 (0.9)	8.00	10.3	3.320	14.825	31
$f=0.6$	502 (1.4)	8.00	8.83	3.143	6.462	13
$f=0.5$	-	-	7.36	-	2.311	0
$f=0.3$	-	-	4.42	-	0.442	0
$f=0.1$	-	-	1.47	-	0.014	0

The number of egg batches produced increased from 15 to 49 egg batches as temperature increased from 14°C to the reference temperature of 20°C (Table 2.9).

Temperature affected the growth rate of anchovy in the DEB model. Anchovy grew faster at warm temperatures and reached their maximum length (Figure 2.11a) and maximum weight (Figure 2.11b) faster than at cool temperatures. Temperature did not, however, change the values of maximum length or weight by much, with the maximum lengths only differing by between 0.01 and 0.75 cm and the maximum weights differing by between 10.630 and 19.064 g between 14 and 26°C (Table 2.9). Temperature changed the length-weight relationship in a consistent way, so Figure 2.11c shows no real difference in the slope of the length-weight relationship for different temperatures.

Table 2.8 Changes in dynamic energy budget model parameters affected by water temperature (T), where T is the water temperature ($^{\circ}\text{C}$), T_1 is the water temperature in Kelvin (K), $c(T_1)$ is the temperature correction, $[\dot{p}_M]$ is the volume-specific maintenance costs and $\{\dot{p}_{Am}\}$ is the surface-area-specific assimilation rate.

T ($^{\circ}\text{C}$)	T_1 (K)	$c(T_1)$ (-)	$[\dot{p}_M]$ ($\text{J}\cdot\text{cm}^{-3}\cdot\text{d}^{-1}$)	$\{\dot{p}_{Am}\}$ ($\text{J}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$)
12	285	0.32	8	70
14	287	0.42	11	93
16	289	0.57	14	125
18	291	0.75	19	166
20	293	1.00	25	220
22	295	1.32	33	291
24	297	1.74	43	382
26	299	2.28	57	501

Table 2.9 The effect of different water temperatures (T , $^{\circ}\text{C}$) on the model output at a constant functional response ($f = 1.0$). Lit is the observed values from literature, a_p is age (days) at puberty with the age in years in brackets, L_p is standard length (cm) at puberty, L_m is maximum standard length (cm), W_{wp} is wet weight (g) at puberty, W_{wm} is wet weight (g) at maximum length from the length-weight relationship with the maximum length from the survey data in brackets and N_{batch} is the number of egg batches produced by an anchovy as predicted by the model during a four year lifespan.

T ($^{\circ}\text{C}$)	a_p (days (years))	L_p (cm)	L_m (cm)	W_{wp} (g)	W_{wm} (g)	N_{batch} (egg batches)
Lit	365 (1.0)	8.00	16.00	4.485	40.820 (35.6)	60
12	638 (1.7)	8.01	12.24	3.836	18.821	8
14	476 (1.3)	8.00	13.37	3.830	27.694	15
16	358 (1.0)	8.01	14.12	3.854	38.324	22
18	270 (0.7)	8.01	14.52	3.853	48.417	34
20	205 (0.6)	8.02	14.68	3.870	59.545	49
22	156 (0.4)	8.02	14.73	3.865	71.478	59
24	120 (0.3)	8.04	14.74	3.900	86.656	61
26	92 (0.3)	8.00	14.74	3.865	105.720	61

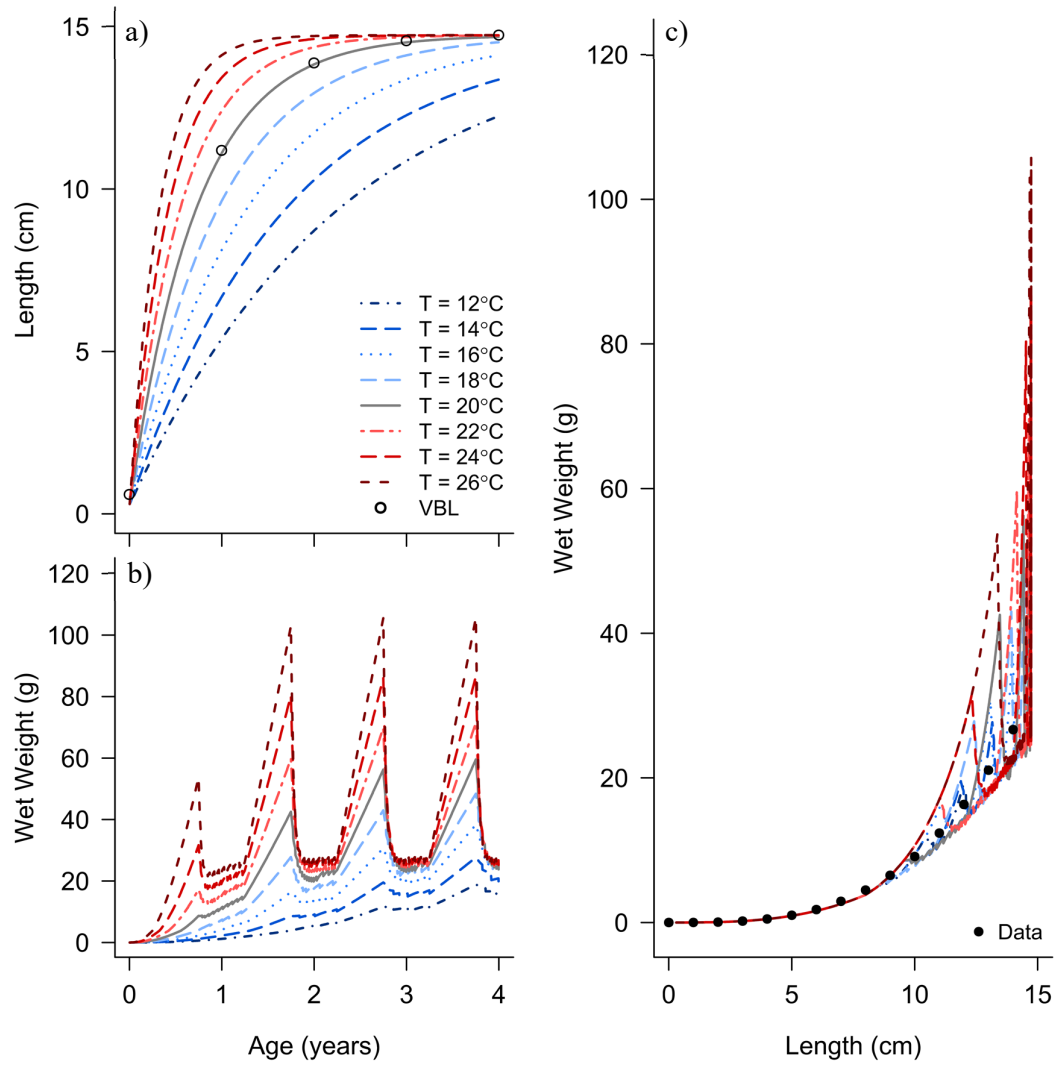


Figure 2.11 The effect of temperature (T , $^{\circ}\text{C}$) on the growth curves of anchovy in the Benguela at a constant functional response ($f = 1.0$), where the effect of changing T is shown on the a) length (cm) at age (years) curves, b) weight (g) at age (years) curve, and c) length-weight relationship. The lines indicate the model results for different values of T , $\circ$ VBL is the growth according to the von Bertalanffy growth equation and $\bullet$ Data represents the length-weight relationship from survey data.

2.5.3 Starvation study

Simulations of anchovy starvation showed that anchovy took longer to starve to death at the start of the spawning season compared to the middle of the spawning season, both for differing water temperatures (T) and for a differing functional response (f) (Figure 2.12). Anchovy did not reach sexual maturity for temperatures between 12 and 14°C until their second year and, therefore, there are no data points for their first year at these temperatures. Starvation simulations were excluded for anchovy aged four years due to simulation runtime concluding before $E_R = 0$. During all spawning seasons and at all points during the spawning season there was a decrease in the number of days that anchovy survived at temperatures warmer than 20°C (Figure 2.12a). Survival during the first and, to a lesser extent, second spawning season differed in trend from the other spawning seasons; survival period increased in as temperature increased after which survival decreased. Anchovy survived between 39 and 40 days during the start of their first spawning season and between 0 and 59 days during the middle of their first spawning season. Further spawning seasons showed a general negative relationship between survival period and temperature (Figure 2.12a). Anchovy survival was higher during the start (137 to 88 days) than the middle (125 to 3 days) of the second and the start (212 to 33 days) and middle (215 to 3 days) of the third spawning season when moving from 12 to 26°C. During their fourth spawning season, however, anchovy survival period decreased from 90 to 33 days as temperature increased past 18°C. For temperatures under 18°C the model simulation reached maximum age before the reproductive buffer reached zero and these results were, therefore, omitted.

Simulations of anchovy starvation for different functional responses showed that there was a positive relationship between anchovy survival and functional response, with fish lasting longer at higher functional response levels. Anchovy only started spawning in the second year of their lifecycle at $f = 0.6$. The number of days that anchovy survived when moving from limited food ($f = 0.8$) to unlimited food ($f = 1.0$) during the start of their first spawning ranged between 21 and 52 days, compared to between 16 and 59 days during their middle of the first spawning season when moving from $f = 0.7$ to $f = 1.0$ (Figure 2.12b). Larger anchovy during subsequent spawning seasons tended to survive for longer periods without food, fish at the start of the spawning season living much longer than at the middle of the spawning season. Survival during the second spawning season differed between the start (32-137 days) and middle of the season (1-26 days) when moving from $f = 0.6$ to $f = 1.0$. The same trend was observed in starvation for start (43-154 days) and middle (5-31 days) spawning season during the third spawning.

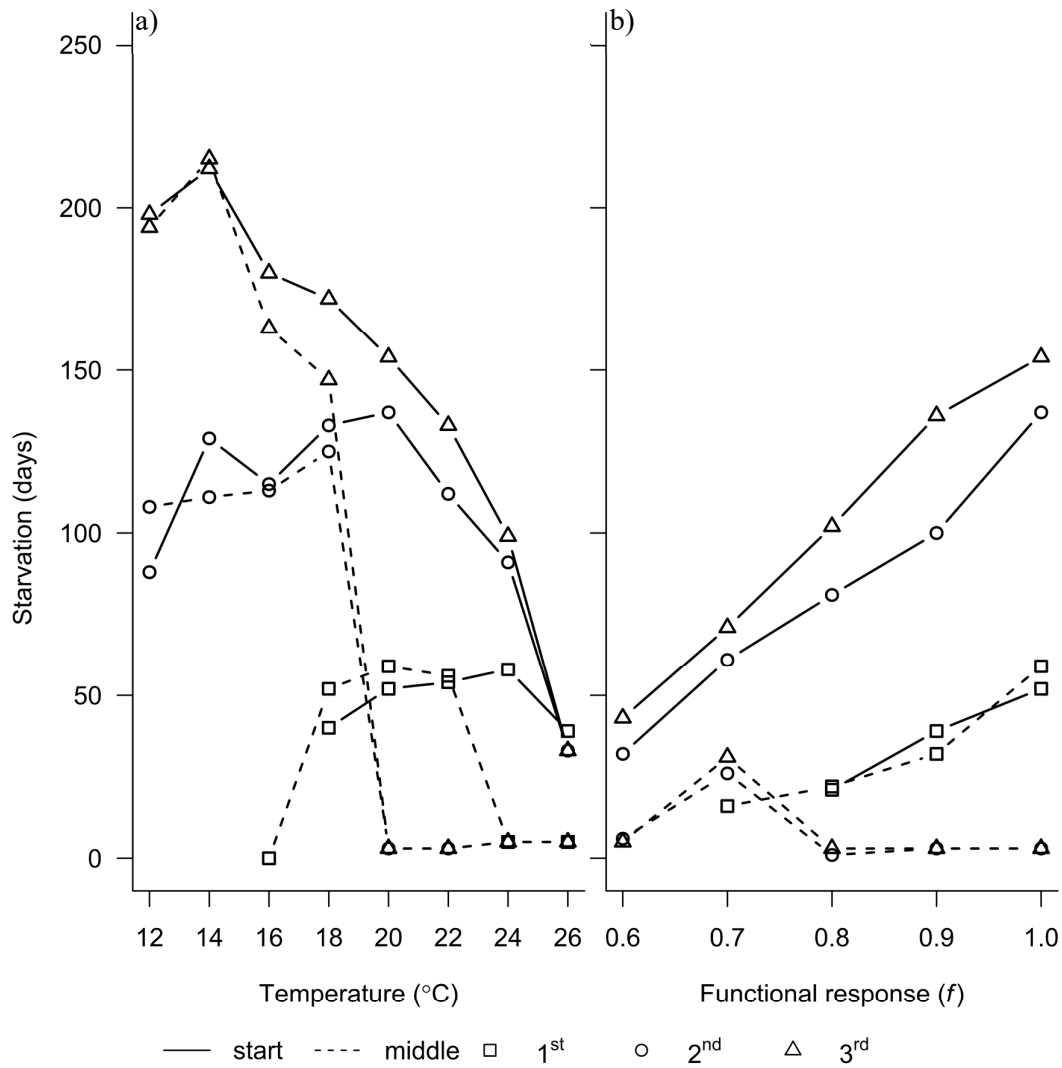


Figure 2.12 Simulated time in days since starvation was initiated as a function of spawning season (i.e., for anchovy of different ages). Comparing starvation and a) different water temperatures (T , $^{\circ}\text{C}$) with a constant initial functional response of ($f = 1$), and b) different initial functional responses at reference temperature $T_{ref} = 293 \text{ K}$ (20°C). Starvation was initiated at the start of spawning seasons (—) or in the middle of the spawning season (---) for the duration of the anchovy lifespan (1st to 3rd year of life).

Discussion

The physiological response of organisms to environmental conditions and the inter-relationships between environmental factors and body size, and growth rate, have been documented for both wild and captive fish populations (Talbot 1993, Marn *et al.* 2019). For instance, a reduction in food availability reduces the maximum size a fish can reach, and growth rate of the fish is directly affected by temperature (Talbot 1993, Marn *et al.* 2019). The sensitivity of individual physiological variation within a given species to environmental conditions, including the variation among populations in different geographical locations because of local adaptation, is of particular interest to scientists (McKenzie *et al.* 2016). However, present knowledge has a few studies comparing the intra-specific variation in DEB parameter within different populations. Van der Veer *et al.* 2001 identified a single DEB parameter (the maximum specific assimilation rate $\{\dot{p}_{Am}\}$) that lead to the intraspecific differences in growth between female and male flatfishes in the North Atlantic. Marn *et al.* (2019) identified three DEB primary parameters (the maximum specific assimilation rate $\{\dot{p}_{Am}\}$, volume-specific somatic maintenance $[\dot{p}_M]$ and maturity at puberty) that captured the most differences in growth, maturation, and reproduction between two loggerhead turtle populations from the Mediterranean and North Atlantic. Guillaumot *et al.* (2020) identified two core parameters (small differences in assimilation rate and their ability to store reserves) that accounted for minor differences between the intertidal and subtidal morphotypes of the Antarctic limpet (*Nucella concinna*).

A DEB model was used to investigate the similarities and differences in energetic strategies of anchovy *Engraulis encrasicolus* in the Southern Benguela compared to the Bay of Biscay and the North-western Mediterranean Sea. These comparisons were based on DEB model parameter estimates, growth, and spawning simulations in response to environmental inputs, and survival during starvation during different environmental conditions. The model parameters were adjusted for anchovy in the Southern Benguela because they had different growth rates and spawning intervals than anchovy in other areas. The anchovy DEB model matched empirical data and growth curves well for both juveniles and adults, with an over estimation in the maximum weight for scenarios with large functional response values ($f = 0.9-1.0$). The model also matched the empirical data well for the number of egg batches spawned per year by anchovy (average 15 egg batches).

Table 2.10 Comparison of core DEB model parameter values for anchovy *Engraulis encrasicolus* from the Southern Benguela (this study), Bay of Biscay (Pecquerie 2008, Pecquerie *et al.* 2009, Gatti *et al.* 2017) and the North-western Mediterranean Sea (N-W Med. Sea) (Pethybridge *et al.* 2013)

Parameter	Symbol	Units	Southern Benguela	Bay of Biscay	N-W Med. Sea
Fraction allocated to growth and maintenance	κ	-	0.35	0.65-0.7	0.7
Maximum storage density	$[E_m]$	J.cm ⁻³	2 800	1 815	2 700
Volume-specific maintenance cost	$[\dot{p}_M]_{ref}$	J.cm ⁻³ .d ⁻¹	25	158	48
Maximum assimilation rate	$\{\dot{p}_{Am}\}_{ref}$	J.cm ⁻² .d ⁻¹	220	884	230.75
Volume-specific cost for structure	$[E_G]$	J.cm ⁻³	1 200	3 725	4 000

Several anchovy *Engraulis encrasicolus* DEB parameters in the Southern Benguela differed from parameters for anchovy in the Bay of Biscay (Pecquerie 2008, Pecquerie *et al.* 2009, Gatti *et al.* 2017) and in the North-western Mediterranean Sea (Pethybridge *et al.* 2013) (Table 2.10).

Differing DEB parameters

A value of 0.35 for the fraction allocated to growth and maintenance (κ , the fraction of energy that each anchovy spent on somatic growth and maintenance) was found to give the best visual model fit to observed Southern Benguela anchovy growth curves (length- and weight-at-age and length-weight relationship; Table 2.5). This value is low compared to the 0.65 and 0.7 found by Pecquerie *et al.* (2009) and Gatti *et al.* (2017), respectively, for this species in the Bay of Biscay and to the 0.7 reported by Pethybridge *et al.* (2013) for the North-western Mediterranean Sea (Table 2.10). According to the κ -rule, the fraction that is allocated to reproduction (1- κ) in the anchovy model means that, in the Southern Benguela, 65% of assimilated energy would be allocated to reproduction compared to the 30-35% for anchovy in European waters. In the Benguela it takes 14 days at the start of the spawning season and 9 days during peak spawning season to achieve full oocyte development (Melo 1994a). Anchovy in the Bay of Biscay have an oocyte development time of between three and five days at the beginning of the spawning season and one to two days during peak spawning (Motos 1996).

Anchovy in the Benguela have a relative batch fecundity (RF_{batch}) value of between 481 and 624 eggs.g⁻¹ female weight per spawn (Alheit 1993, Shelton *et al.* 1993, van der Lingen & Durholtz 2003), while anchovy in European waters have a RF_{batch} of between 226 and 646 eggs.g⁻¹ of female weight per spawn (Somarakis *et al.* 2004). This could be an indication that anchovy in the Southern Benguela show a more “income” breeding strategy by using more of their concurrent intakes of energy to pay for a reproductive attempt than in the Bay of Biscay. This model did not consider seasonal influence of food availability (plankton production) and temperature. Organisms move along a capital-income breeding continuum (see Chapter 5) in response to a match-mismatch between their food and egg production, and their physiological condition (McBride *et al.* 2015, Gkanasos *et al.* 2019). Studies have found that a more capital breeding response was promoted at high latitudes where there was strong seasonal fluctuation in food availability, while a more income breeding response was promoted at low latitudes where there were more moderate or prolonged seasonal cycles (Shultz & Conover 1997, McBride *et al.* 2015). The model also showed that higher values of κ generated faster juvenile growth rates in Southern Benguela anchovy (Figure 2.5).

The maximum storage density [E_m] influenced the shape of the length-weight relationship (Figure 2.6). The [E_m] value for anchovy in the Southern Benguela was standardised to 2 800 J.cm⁻³ (Table 2.5), which was much higher than the 1 815 J.cm⁻³ found by Gatti *et al.* (2017) and close to the 2 700 J.cm⁻³ found by Pethybridge *et al.* (2013) (Table 2.10). The model indicated that higher values for [E_m] resulted in slower anchovy growth rates (Figure 2.6).

The volume-specific cost for maintenance at reference temperature or $[\dot{p}_M]_{ref}$ was standardised to 25 J.cm⁻³.d⁻¹ (Table 2.5) for anchovy in the Southern Benguela, a value that was lower than the 158 J.cm⁻³.d⁻¹ estimated by Gatti *et al.* (2017) and the 48 J.cm⁻³.d⁻¹ estimated by Pethybridge *et al.* (2013) (Table 2.10). The maximum assimilation rate at reference temperature or $\{\dot{p}_{Am}\}_{ref}$ for anchovy in the Southern Benguela was standardised to 220 J.cm⁻².d⁻¹, a value much lower than the 884 J.cm⁻².d⁻¹ found by Gatti *et al.* (2017) but close to the 230.75 J.cm⁻².d⁻¹ found by Pethybridge *et al.* (2013) (Table 2.10). However, $[\dot{p}_M]$ and $\{\dot{p}_{Am}\}$ are influenced by temperature, and the reference temperature of anchovy in the North-western Mediterranean Sea was calculated at 289 K (16°C). Therefore, these values could not accurately be compared to those in the Southern Benguela, which was calculated at a reference temperature of 293 K (20°C). Given that these parameters are influenced by temperature, it stands to reason that anchovy in the Bay of Biscay would have higher values for $[\dot{p}_M]_{ref}$ and $\{\dot{p}_{Am}\}_{ref}$ since they experience higher ambient temperatures during spawning, 15-18°C

in May to 20-24°C in July (Motos 1996). Comparatively, anchovy in the Southern Benguela typically spawn in waters between 17 and 23°C but mostly in waters between 18 and 20°C (Shannon 1998, Richardson *et al.* 1998, Mhlongo *et al.* 2015); therefore, smaller values for $[\dot{p}_M]_{ref}$ and $\{\dot{p}_{Am}\}_{ref}$ are anticipated. The shorter oocyte development time and larger relative batch fecundity in Bay of Biscay anchovy means more energy needs to be assimilated over shorter periods of time to attain enough energy to produce fully developed oocytes. Therefore, larger values of $\{\dot{p}_{Am}\}_{ref}$ could be expected for anchovy in the Bay of Biscay. According to the anchovy DEB model, lower values of $[\dot{p}_M]_{ref}$ (Figure 2.7) and $\{\dot{p}_{Am}\}_{ref}$ (Figure 2.8) indicated slower growth rates.

The volume-specific cost for structure or $[E_G]$ of Southern Benguela anchovy was standardised as 1 200 J.cm⁻³, which is less than the 3 725 J.cm⁻³ found by Gatti *et al.* (2017) and the 4 000 J.cm⁻³ found by Pethybridge *et al.* (2013) (Table 2.10). The volume-specific cost for structure was defined as the energetic cost needed for one unit of growth to occur in structural body volume (van der Meer 2006) and is dependent on the complexity of the cell (Kooijman 2000, van der Meer 2006). This implied that the $[E_G]$ value would be similar for species that are phylogenetically related (Sarà *et al.* 2013).

The estimated core parameters discussed indicate that anchovy in the Southern Benguela have slower growth rates than the same species in the Bay of Biscay and the North-western Mediterranean Sea. This finding is supported by the literature. Brownell (1983) reared Southern Benguela anchovy in captivity and found a growth rate of between 0.15 and 0.60 mm.day⁻¹ between temperatures of 18.5 and 19.5°C. Field studies by Prosch (1986) estimated a growth rate of 0.50 mm.day⁻¹ in larval anchovy and 0.40 mm.day⁻¹ in juvenile anchovy in 1983/84, while Waldron (1995) estimated a growth rate of 0.32 mm.day⁻¹ for juvenile anchovy in 1991 in the Benguela. Wilhelm (2002) estimated a mean growth rate for larval anchovy between 0.33 and 0.36 mm.day⁻¹ and a juvenile growth rate between 0.22 and 0.24 mm.day⁻¹ during 2000, when large areas of the Benguela experienced warm water temperatures (19 - 26°C) during the 1999/2000 spawning season (Wilhelm *et al.* 2005). Costalago *et al.* (2020) sampled anchovy larvae in February 2014 in two locations off South Africa and found that their average individual growth rates for larvae of length 1.07 cm was 0.49 mm.day⁻¹ in Algoa Bay and 0.46 mm.day⁻¹ for larvae of length 0.96 cm on the west coast. Comparatively, juvenile *E. encrasicolus* in the Bay of Biscay showed considerably faster growth rates of 0.88 mm.day⁻¹, probably because of warmer waters during their spring and summer season and/or because high prey visibility compensated for their low food concentrations (Motos 1996, Pecquerie

2008, Aldanondo *et al.* 2010). Juvenile anchovy in the Western Mediterranean Sea have a growth rate of 0.89 mm.day^{-1} at a temperature of 20°C (Palomera *et al.* 1988, Palomera *et al.* 2007), while larval anchovy in the North Aegean Sea (eastern Mediterranean) had a growth rate in summer of 0.80 mm.day^{-1} and a slower growth rate of 0.63 mm.day^{-1} in winter (Schismenou *et al.* 2013).

Environmental effects on growth

Environmental factors such as temperature and food availability can lead to large variations in growth rates of anchovy larvae and juveniles (Aldanondo *et al.* 2010). DEB theory states that an individual's maximum volumetric length is dependent on processes such as energy allocated to growth and energy required by maintenance; however, actual assimilated energy is represented by the functional response (f) (Pecquerie 2008). Anchovy require continual ingestion of food because of their serial spawning reproductive strategy, which is very energy intensive and makes food availability essential for successful reproduction (Melo 1994a, Richardson *et al.* 1998). According to the model a functional response value of at least 0.6 is needed for anchovy to reach sexual maturity (Table 2.7, Figure 2.10). The model also captured that at lower functional responses mature anchovy would produce fewer egg batches in their lifetime.

DEB theory also states that, for different water temperatures in the same constant food environment, anchovy would have the same asymptotic size (Pecquerie 2008). Model results indicated that even though anchovy had the same maximum length values at different water temperatures (Table 2.9), water temperature affected maximum weight and the growth rate of anchovy (Figure 2.11). Anchovy would grow faster at warmer temperatures because this increased metabolic demand through increased activity (Hunter 1977). This is reflected by the increase in the maximum assimilation rate $\{\dot{p}_{Am}\}$, which increased with increasing temperature (Table 2.8). Mhlongo *et al.* (2015) investigated whether anchovy spawning patterns had changed in recent years when compared to changes in sea surface temperature and found that anchovy tended to spawn in water between 17°C and 23°C , but preferred waters with temperatures between 18 and 20°C . According to the model, anchovy could spawn between 34 and 49 egg batches throughout their lifetime between 18°C and 20°C , which is close to estimates by Melo (1994a) (14-21 egg batches a year or 42-63 batches in total assuming three spawning seasons). If anchovy grow faster at warm temperatures, this could theoretically increase the fecundity of individuals in these warmer waters as well as decreasing the exposure of larvae to predation (Hunter 1977).

King *et al.* (1978) reported that larval anchovy in the Northern Benguela could tolerate temperatures between 11.9°C and 23.21°C, but they failed to develop eye pigmentation or a working jaw in temperatures below 14°C. If this also applies in the Southern Benguela then even if anchovy could spawn up to 8 egg batches at 12°C the resulting larvae would not be viable in this colder water.

These environmental factors are interconnected, with temperature affecting the activity of anchovy which in turn increases the metabolic demand at higher temperatures, which would affect feeding demand. Feeding and temperature effects on the anchovy model are discussed in more detail in Chapter 4.

Starvation

Starvation simulations in the Southern Benguela indicated that survival of anchovy decreased when temperature increased (Figure 2.12a). This can be attributed to temperature affecting the volume-specific cost for maintenance [$\dot{p}_M$] with an increase in temperature increasing [$\dot{p}_M$] (Table 2.8), which means that the anchovy must expend more energy for maintenance at higher temperatures. Since this cost can only be paid by the reproductive buffer (E_R) during starvation, higher maintenance would deplete the reproductive buffer faster so the survival period will decrease compared to that of fish at lower temperatures.

The survival period in anchovy increased for fish with a higher functional response (f) before starvation (Figure 2.12b). A higher functional response meant that there would be more food available when initially building the reproductive buffer (E_R). Thus, when the anchovy are starved and atresia starts, there would be higher reserves in the reproductive buffer to pay the maintenance.

The starvation study also indicated that anchovy survived for shorter periods when food was limited before the onset of starvation (5 - 43 days at a f of 0.6 and 26 – 71 days at an f of 0.7). This is reflected by Painting *et al.* (1998), who measured gonad atresia in anchovy and found that in 10% of the stations on the western Agulhas Bank, anchovy were unable to meet their maintenance requirements during November when food was limited. This meant that if anchovy stopped feeding during the start of the peak spawning season, there would be high levels of atresia at the end of the spawning season. This is supported by high levels of gonad atresia being noted towards February and March by Painting *et al.* (1998), coinciding with the end of the anchovy spawning season.

It should be noted that starvation survival was much higher than anticipated at the start compared to the middle of the spawning season. This is most likely due to the reproductive buffer being filled during the non-spawning season without having losses due to spawning. One would therefore expect more energy in the reproductive buffer before the spawning season than in the middle.

In all cases larger and older anchovy survived for longer during starvation, as can be seen from the results for the third and fourth year of spawning (Figure 2.12). This correlates with findings by Hunter and Macewicz (1985) for northern anchovy *Engraulis mordax*, where small (standard lengths of ≤ 10 cm) females consistently had higher rates of atresia than larger females.

In conclusion, both temperature and food availability influence the growth, reproduction, and survival of anchovy *E. encrasicolus* in the Southern Benguela. One of the assumptions of DEB theory is that the core parameters are species-specific, since they are indicators of the biological and physiological traits of that species (Pecquerie 2008, Kooijman & Lika 2014, Gatti *et al.* 2017). Comparing the five missing core parameters for the same species of anchovy *E. encrasicolus* in the Southern Benguela to those in the Bay of Biscay and the North-western Mediterranean Sea, it was apparent that growth differences in anchovy populations are influenced by their environment. These growth differences in turn influence the core DEB parameters. Therefore, care should be exercised before assuming that all core DEB parameters are species-specific and thus transferable between populations in different regions. It is important to look at environmental, biological, and physiological characteristics and how they compare to other areas where that same species occurs, before creating a DEB model for that species from a new region. It is also important to ensure that intra-specific comparisons are made between parameters that have been calculated at the same reference temperature, since temperature plays such an important role in influencing parameter values.

Chapter 3 Using dynamic energy budget (DEB) theory to simulate life cycles of redeye round herring (*Etrumeus whiteheadi*) and sardine (*Sardinops sagax*) in the Southern Benguela ecosystem.

Abstract

Limited resource availability for empirical work has created the necessity for investigating the extent to which bioenergetics models and model parameters are transferable among species and subpopulations that are exploited by fisheries and/or are ecologically important. To that end, a Dynamic Energy Budget (DEB) model developed for anchovy in the Southern Benguela was adapted to estimate parameters through visual fits and explore the effects of environmental conditions on the growth and reproduction of individual redeye (also known as west coast) round herring (*Etrumeus whiteheadi*) and a generic (*i.e.* not taking account of the population structure shown by this species with two subpopulations documented) sardine (*Sardinops sagax*), two ecologically and economically important species in the Southern Benguela ecosystem. To investigate the energy accessible for growth and reproduction during their life cycle and their response to starvation, the model was adjusted using data collected during surveys from 2012-2016 and published empirical data. Best fit values were estimated for five core parameters using von Bertalanffy growth models and length-weight relationships of redeye round herring and sardine separately. Redeye round herring had lower structural growth and maintenance costs than sardine. Sardine invested more in reproductive reserve storage capacity and structural growth than redeye round herring. Redeye round herring required a scaled functional response (f) of at least 0.7, while sardine required an f value of at least 0.8 during feeding to reach sexual maturity and reproduce. Warmer temperatures produced increased growth rates in both species but decreased survival during starvation, and survival of both species decreased with decreasing f during starvation. No published DEB models have been developed for *S. sagax* elsewhere, so the Southern Benguela sardine DEB model could only be compared with one developed for European sardine (or pilchard) *Sardina pilchardus* from the Bay of Biscay, which despite being a different genus within the Clupeidae is ecologically and functionally similar to *S. sagax*. Differences in core parameters of sardine between the two regions were observed, most likely due to the influence of environmental inputs. However, general trends in the differences between sardine and anchovy parameters were similar in both regions. Thus, even though parameters may not be transferable between ecosystems and species, trends in this species pair in other regions (*e.g.*, California and Japan) could be useful for core parameter estimation. No DEB models have been developed for any *Etrumeus* species; hence no comparisons could be done for redeye round herring.

These DEB models can be useful in investigating the potential impacts of ecosystem changes on small pelagic fishes, such as are likely to arise from climate change, by linking the DEB models to biophysical ecosystem models like the Apex Predators ECOSystem Model (APECOSM).

Introduction

Small pelagic fish make up a large component of catches in several of the world's fisheries (Beckley & van der Lingen 1999, Barange *et al.* 2009). Sardine (*Sardinops sagax*) has been exploited by the South African small pelagic fishery since the 1930s with annual catches peaking during the 1960s at just over 400 000 t (Beckley & van der Lingen 1999, van der Lingen & Durholtz 2003); sardine is frozen or canned for human consumption, pet food, or bait. Redeye round herring (*Etrumeus whiteheadi*) has been exploited as bycatch in the South African small pelagic fishery since the 1950s and has primarily been used for fishmeal, fish oil and fish paste (Geja *et al.* 2016), although canning of this species for human consumption has recently been initiated (van der Lingen 2021). Small pelagic fish are often characterised as fast-growing, fast maturing, short-lived, and highly fecund organisms with high and variable natural mortality (Barange *et al.* 2009), also known as an r-selected life history strategy. These traits mean that their stock size depends on recruitment, which make these small pelagic fish populations variable, unpredictable and not as responsive to management measures as long lived species (Barange *et al.* 2009).

There is a need in fisheries science to investigate the extent to which models and model parameters are transferable among species and subpopulations, due to limited resources for empirical work (Pecquerie *et al.* 2011). This could ensure that the focus of research is on parameters of species and habitats that are unique and thus non-transferable, making such research more cost effective (Pecquerie *et al.* 2011). Redeye round herring have fewer empirical data available on their dynamics than anchovy in the Southern Benguela. Sardine, on the other hand have been well studied as a single panmictic population, which has led to an abundance of empirical data available on the dynamics of this species in the Southern Benguela. However, the hypothesis of semi-discrete subpopulations of sardine in the Southern Benguela (de Moor & Butterworth 2015, van der Lingen *et al.* 2015, de Moor *et al.* 2017, Sakamoto *et al.* 2020) has meant that the exact dynamics of each semi-discrete subpopulation are not well known. Small pelagic fish dynamics have been notoriously difficult to model using traditional population dynamic models and assumptions, because of their r-selected life history strategies and aggregative behaviour (Barange *et al.* 2009).

The very characteristics that make small pelagic fish difficult to model traditionally make them good candidates for the use of the more theoretical approach to bioenergetics modelling known as dynamic energy budget (DEB) theory, developed by Kooijman (2001, 2010). These DEB models are used to describe the energy flow from food through assimilation to the maintenance, development, growth, and reproduction of individual organisms as a function of their environment (van der Veer *et al.* 2006, Pecquerie 2008, Nisbet *et al.* 2012). Gatti *et al.* (2017) successfully used DEB models to compare biological traits between anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus* in the Bay of Biscay, finding that the two species show different approaches to the acquisition and storage of energy and specifically, to the allocation of energy to spawning.

This study aims to adapt the ‘generalised’ Southern Benguela anchovy energetics model and parameters, developed using DEB theory for a standard (‘std’) DEB model and described in Chapter 2, to redeye round herring and generalised (i.e., not stock-specific) sardine in the Southern Benguela upwelling system, as there are fewer empirical data for these two species than for anchovy. These DEB models described the life cycle, including growth and reproduction for females of these two species in the Southern Benguela. The objectives of the study were to: 1) estimate core DEB parameters for redeye round herring and sardine in the Southern Benguela, and compare them to parameters estimated for anchovy in the Southern Benguela (Chapter 2) as well as to those for sardine in the Bay of Biscay; 2) investigate the effects of food (through the functional response) and temperature in terms of energy available for growth and reproduction, for individual redeye round herring and sardine in the Southern Benguela; and 3) investigate the response of the DEB models to starvation at different temperatures and food conditions. It was hypothesised that, even if DEB core parameters are not interchangeable between ecosystems, as has been shown in Chapter 2, there may be general trends in the differences between sardine and anchovy parameters that may be helpful in core parameter estimations for these or similar species elsewhere.

Methods

3.1 The model

The models for both redeye round herring and sardine were based on the ‘std’ DEB model developed for anchovy in Chapter 2. The model equations given in Table 2.1 were used to model the growth and reproduction of female redeye round herring and sardine separately.

3.2 Parameter estimation

3.2.1 Data collection

Length and weight data for redeye round herring and sardine were collected for the period 2012-2016 during annual DAFF (now DFFE) spawner and recruitment surveys. Spawner biomass surveys are undertaken during October/December, close to the peak spawning seasons for redeye round herring (August to October; Roel & Armstrong 1991, Beckley & Hewitson 1994) and sardine (September/October; van der Lingen *et al.* 2001, van der Lingen & Huggett 2003). Recruitment surveys are undertaken during May/June when juvenile small pelagic fish aggregate on the west coast nursery grounds and juvenile anchovy recruit into the fishery. In total, 22 930 redeye round herring were measured, with standard (caudal) lengths ranging from 1.8 to 22.6 cm and wet weights from 0.1 to 120.3 g. A total of 11 163 sardine were measured and their standard lengths ranged between 4.0 and 22.3 cm and wet weights between 0.3 and 158.6 g.

3.2.2 Life cycle parameters

The life cycle parameters for redeye round herring and sardine were assembled from published field and laboratory studies and unpublished data (Table 3.1). For the comparisons, all redeye round herring and sardine total length (L_T , cm) values were converted to standard length (L_C , cm) values using DAFF (2018):

Redeye round herring	$L_C = 0.8357L_T - 0.1002$	36
Sardine	$L_C = 0.8471L_T - 0.2501$	37

Hatching in this study signified “birth”, meaning that length at birth corresponds to length at hatching, while puberty signified length at first allocation to reproduction. This value was smaller than the length at maturity (i.e., length at first reproduction), meaning redeye round herring and sardine first filled the reproductive buffer then converted it into eggs (Pecquerie 2008).

Table 3.1 Life cycle parameters for redeye round herring *Etrumeus whiteheadi* and sardine *Sardinops sagax* in the Southern Benguela based on laboratory, field and unpublished data from various authors. All values are expressed at a reference temperature T_{ref} of 293 K (20°C).

Description	Symbol	Units	Redeye round herring		Sardine	
			Value	Reference	Value	Reference
Age at birth (hatching)	a_b	days	1.60	O'Toole & King (1974)	1.55	King <i>et al.</i> (1978)
Age at metamorphosis	a_j	days	68	Waldron <i>et al.</i> (1991)	62	Brownell (1983)
Age at puberty	a_p	years	0.8-1.2	Geja <i>et al.</i> (2016)	1-3	Barange <i>et al.</i> (2009)
Life span of fish	a_m	years	7	Geja <i>et al.</i> (2016)	10	Kerstan (2000)
Standard length at birth (hatching)	L_b	cm	0.385	O'Toole & King (1974)	0.258	Armstrong & Thomas (1989); King <i>et al.</i> (1978)
Standard length at Metamorphosis	L_j	cm	3.5	Wallace-Fincham (1987)	3.2	Louw & O'Toole (1977)
Standard length at puberty	L_p	cm	12	Geja <i>et al.</i> (2016)	17	Beckley & van der Lingen (1999)
Maximum standard length	L_m	cm	20.41	Geja <i>et al.</i> (2016)	23	Kerstan (2000)
Wet weight at birth	W_{wb}	g	0.0004	DAFF data (2012-2016)	0.00009	DAFF data (2012-2016)
Wet weight at metamorphosis	W_{wj}	g	0.248	DAFF data (2012-2016)	0.307	DAFF data (2012-2016)
Wet weight at puberty	W_{wp}	g	23.065	DAFF data (2012-2016)	57.551	DAFF data (2012-2016)
Maximum wet weight	W_{wm}	g	87.366	DAFF data (2012-2016)	151.087	DAFF data (2012-2016)

Table 3.1 (cont.) Life cycle parameters for redeye round herring *Etrumeus whiteheadi* and sardine *Sardinops sagax* in the Southern Benguela based on laboratory, field, and unpublished data from various authors. All values are expressed at a reference temperature T_{ref} of 293 K (20°C).

Description	Symbol	Units	Redeye round herring		Sardine	
			Value	Reference	Value	Reference
REPRODUCTIVE PARAMETERS						
Energy content of 1 g egg	E_{egg}	J.egg ⁻¹	0.720	Szeinfeld (1993)	1.26	Lasker (1965)
Full oocyte development time (peak season)	$O_{DevTime}$	d	6	Roel & Melo (1990)	11	Akkers <i>et al.</i> (1996)
Full oocyte development time (end of season)	$O_{DevTime}$	d	15	Roel & Melo (1990)	18	Akkers <i>et al.</i> (1996)
Relative batch fecundity	RF_{batch}	eggs.g ⁻¹	118	Roel & Melo (1990)	215	Akkers & Melo (1996)
Egg batches per year	N_{batch}	batch.y ⁻¹	24-33	Roel & Melo (1990)	20-29	Akkers <i>et al.</i> (1996)
VON BERTALANFFY PARAMETERS						
Maximum asymptotic length	L_{∞}	cm	20.41	Geja <i>et al.</i> (2016)	21.4	Shin <i>et al.</i> (2004)
Growth rate	k	year ⁻¹	0.41	Geja <i>et al.</i> (2016)	0.95	Shin <i>et al.</i> (2004)
Age at length zero	a_0	years	-1.92	Geja <i>et al.</i> (2016)	-0.17	Shin <i>et al.</i> (2004)

3.2.3 von Bertalanffy growth curve

A von Bertalanffy equation (Chapter 2, Eqn. 21) was fitted to observations from the model for comparison with empirical results. The von Bertalanffy equation described by Geja *et al.* (2016) for redeye round herring and Shin *et al.* (2004) for sardine was used in this case. The standard length L_C (cm) of the fish is calculated using the maximum asymptotic length L_{∞} (cm), the growth rate k (year⁻¹), the age at that length a (year) and the hypothetical age at length zero a_0 (year) (Table 3.1).

3.2.4 Length-weight relationship

The length-weight relationships were calculated from the 2012-2016 survey data, and used to generate weight at length values that could be compared to the DEB model results of redeye round herring and sardine:

$$\text{Redeye round herring} \quad W_{ww} = 0.00712 \cdot L_c^{3.146} \quad 38$$

$$\text{Sardine} \quad W_{ww} = 0.00678 \cdot L_c^{3.193} \quad 39$$

where W_{ww} is the wet weight (g) and L_c is the standard length (cm) from survey data ($R^2 = 0.98$ for both redeye round herring and sardine).

3.3 DEB Parameter estimation

3.3.1 Shape coefficient δ

It is assumed that redeye round herring and sardine display isomorphic growth, so the overall shape does not change through the life cycle of the fish and the reserves contribute little to standard length, so the physical length quantifies structural length. The same method was used to calculate the shape coefficient (δ) for the redeye round herring and sardine models as described for anchovy in Chapter 2. In both species a non-linear model was first fitted to the length and weight data, resulting in a heteroscedastic pattern in the residuals. To reduce this, the length and weight data were log transformed and a linear regression model was fitted to the transformed data to calculate the shape coefficient. The regression model gave a shape coefficient for redeye round herring of $\delta = 0.218$ ($t = -5\,755$, $n = 22\,930$, $p < 0.001$) and for sardine of $\delta = 0.224$ ($t = -3\,386$, $n = 11\,243$, $p < 0.001$) (Table 3.2). All statistical analyses were performed using R for windows (R Core Team 2021).

3.3.2 Volumetric length L_v

In the DEB models for redeye round herring and sardine the shape coefficient (δ) is used to calculate standard length (L_c) of individuals from the volumetric length (L_v or $V^{1/3}$) (Pecquerie 2008) (Table 2.1, Eqn. 16).

Table 3.2 DEB model parameters for redeye round herring and sardine in the Southern Benguela ecosystem (used in equations from Chapter 2, Table 2.3) at a reference temperature T_{ref} of 293 K (20°C). Where applicable, values and reference sources are shown.

	DEB		Redeye round herring		Sardine	
Description	Parameter	Units	Value	Reference	Value	Reference
FEEDING PARAMETERS						
Maximum assimilation rate	$\{\dot{p}_{Am}\}$	J.cm ⁻² .d ⁻¹				
Scaled functional response	f	-				
ENERGY PARAMETERS						
Fraction allocated to growth and maintenance	κ	-				
Maximum storage density	$[E_m]$	J.cm ⁻³				
Volume-specific maintenance cost	$[\dot{p}_M]$	J.cm ⁻³ .d ⁻¹				
Volume-specific cost for structure	$[E_G]$	J.cm ⁻³				
VOLUMETRIC PARAMETERS						
Volumetric length at puberty	L_{Vp}	cm	2.62		3.81	
Maximum volumetric length	L_{Vm}	cm	4.45		5.15	
TEMPERATURE PARAMETERS						
Arrhenius temperature	T_A	K	11 263	O'Toole & King (1974)	9 651	King (1977)
Water temperature	T_1	K				
Reference temperature (20°C)	T_{ref}	K	293		293	
CONVERSION PARAMETERS						
Shape coefficient	δ	-	0.218	DAFF data (2012-2016)	0.224	DAFF data (2012-2016)

3.3.3 Water temperature T_1

The redeye round herring and sardine DEB models used water temperature T_1 in Kelvin (K) in the equations, so all water temperatures in degrees Celsius ($T^{\circ}\text{C}$) were converted to Kelvin (K) (Table 2.3, Eqn. 25).

3.3.4 Arrhenius temperature T_A

The Arrhenius temperature T_A (K) was calculated from observed values of metabolic rate according to Kooijman (2010) and Pecquerie (2008). The relationships between egg development time D (h) and temperature T_1 (K) for redeye round herring (O'Toole & King 1974) from the Southern Benguela and for sardine (King 1977) from the Northern Benguela was described as:

Redeye round herring	$D = 21\,018 (T_1 - 273)^{-2.1051}$	40
Sardine	$D = 12\,218.058 (T_1 - 273)^{-1.934}$	41

To calculate the Arrhenius temperature for redeye round herring and sardine, $\ln(1/D)$ was plotted against $1/T_1$ to obtain a straight-line slope that represented the Arrhenius temperature T_A . The Arrhenius temperature for redeye round herring was calculated as $T_{A_redeye} = 11\,263\text{ K}$ ($n = 1, r^2 = 0.99$) spanning a temperature range between 284 K (11°C) and 294 K (21°C). The Arrhenius temperature for sardine was calculated as $T_{A_sardine} = 9\,651\text{ K}$ ($n = 12, r^2 = 0.99$) for a temperature range 284 K (11°C) to 295 K (22°C).

3.3.5 Temperature correction $c(T_1)$

Redeye round herring and sardine metabolic rates were affected by temperature. Therefore, metabolic rates were scaled by a correction equation $c(T_1)$ (Table 2.3; Eqn. 26), where T_1 was the water temperature, T_{ref} was the reference temperature (set at 293 K (or 20°C)) and T_A was the respective Arrhenius temperature (K) for redeye round herring or sardine.

3.3.6 Reserve density $[E]$

The reserve density $[E]$ ($\text{J}\cdot\text{cm}^{-3}$) for redeye round herring and sardine was calculated using the method described in Chapter 2 for constant environmental conditions (Eqn. 34) and changing environmental conditions (Eqn. 35).

3.3.7 Reproduction

Redeye round herring spawn year-round, with peak spawning during the spring from August to October (Shelton *et al.* 1985, Roel & Armstrong 1991, Beckley & Hewitson 1994, Roel *et al.* 1994). O'Toole & King (1974) conducted hatching experiments on redeye round herring and successfully hatched eggs between 11.5 and 20.5°C. The spawning season for sardine in the Southern Benguela also occurs year-round, with peak spawning occurring between August and March (spring and summer) (Barange *et al.* 2009). Sardine have a temperature tolerance range for spawning between 13 and 22°C, with 13°C being the coolest temperature that led to successful development of eggs (King 1977, Shannon 1998). The optimal temperature range for spawning is between 16 and 22°C (King 1977, Shannon 1998, Mhlongo *et al.* 2015). In both DEB models only adult ($L_v \geq L_{vp}$) redeye round herring and sardine can spawn.

Two subsequent spawning conditions were applied to the redeye round herring and sardine models for producing a single batch of gametes (Pethybridge *et al.* 2013, Gatti *et al.* 2017). The first condition, $E_{GAM} \geq 2 \cdot E_{batch}^*$ (E_{batch}^* was calculated using Table 2.3; Eqn. 30), ensures there would be enough energy available for gamete production. The energy content of one redeye round herring egg E_{egg} was set as 0.720 J (Table 3.1). This was the same as an anchovy egg, since both species have a narrow perivitelline space and the exact energy content of redeye round herring eggs is unknown (O'Toole & King 1974, King *et al.* 1978, Hunter & Leong 1981, Olivar & Fortuno 1991, Szeinfeld 1993). Assuming that a Southern Benguela sardine egg has the same energy content as a Pacific sardine (also *Sardinops sagax*) egg, the energy content of one egg E_{egg} (Table 3.1) of 0.56 mm³ was calculated as 1.26 J (Lasker 1962, Lasker 1965, Gatti *et al.* 2017). The relative batch fecundity RF_{batch} (Table 3.2) for redeye round herring was set to 118 eggs.g⁻¹ per spawn (Roel & Melo 1990), while relative batch fecundity for sardine was set to 215 eggs.g⁻¹ per spawn (Le Clus 1988, Akkers & Melo 1996, van der Lingen & Durholtz 2003).

The second condition requires that a batch of oocytes had to reach full development before spawning or $O_{Dev} > O_{DevTime}$. Redeye round herring $O_{DevTime}$ was set to 6 days for peak spawning season and 15 days for the rest of the spawning season (Roel & Melo 1990). The number of egg batches that redeye round herring produced varied between 24 and 44 egg batches per year, with an average of 34 batches per year (Roel & Melo 1990). Sardine in the Southern Benguela take between 11 and 18 days for oocytes to fully develop ($O_{DevTime}$) (Akkers *et al.* 1996). In this study the $O_{DevTime}$ for

sardine was set to 11 days for peak spawning season and 18 days for the rest of the spawning season (Akkers *et al.* 1996). The number of egg batches that sardine produced a year varied between 21 and 30 egg batches per year, with an average of 25 egg batches per year (Akkers *et al.* 1996). The age-specific batch fecundity F_{batch} (J) for each species was calculated using Pethybridge *et al.* (2013) (Table 2.3; Eqn. 31). Spawning interval and number of egg batches spawned was calculated as for anchovy in Section 2.3.7 using Roel & Melo (1990) (redeye round herring) and Akkers *et al.* (1996) (sardine).

3.3.8 Energy density in the buffers (d_V , μ_E , μ_R , μ_G)

For the purpose of this study the energy density in the buffers (μ_E , μ_R , μ_G) and the density of the structure (d_V) for both species were fixed to values used for anchovy by Gatti *et al.* (2017) (Table 3.3). It is assumed that the reserve, maturation, and reproductive buffers have the same energy content for similar species, since they have the same chemical composition.

3.4 Missing DEB parameters

Five parameters (κ , $[E_m]$, $[\dot{p}_M]$, $\{\dot{p}_{Am}\}$ and $[E_G]$) were identified within the anchovy DEB model as parameters that influence model outputs of length and weight and are difficult to measure (van der Veer *et al.* 2006). These parameters were altered separately under constant environments (reference temperature $T_{ref} = 293$ K (20°C) and $f = 1$) for each species to find the optimum parameter value that

Table 3.3 DEB model parameters that were assumed to be the same for anchovy (Chapter 2), redeye round herring and sardine.

Description	DEB Parameter	Value	Units	Reference
CONVERSION PARAMETERS				
Density of the structure	d_V	0.11	g.cm^{-3}	Gatti et al. (2017)
Dry weight to wet weight conversion	γ	4.1	-	Pethybridge et al. (2013)
Energy density of 1 g of gametes	μ_G	23 880	J.g^{-1}	Gatti et al. (2017)
Energy density of 1 g of reproductive buffer	μ_R	24 937	J.g^{-1}	Gatti et al. (2017)
Energy density of 1 g of reserve	μ_E	31 332	J.g^{-1}	Gatti et al. (2017)

showed the best visual model fit to their three growth curves. These growth curves were: 1) the length-at-age from the von Bertalanffy growth curve for redeye round herring and sardine; 2) the weight-at-age curves generated by the model; and 3) the length-weight relationships calculated using the 2012-2016 survey data.

3.4.1 Fraction allocated to growth and maintenance κ

A fraction allocated to growth and maintenance κ of 0.35 was estimated for anchovy in the Southern Benguela (Chapter 2). Gatti *et al.* (2017) estimated κ -values between 0.42 and 0.67 for sardine *Sardina pilchardus* under different modelling scenarios in the Bay of Biscay. To find the optimum κ -value for redeye round herring and sardine, κ was varied between 0.1 and 0.99.

3.4.2 Maximum storage density [E_m]

The maximum storage density [E_m] for anchovy was set as 2 800 J.cm⁻³ (Chapter 2). To find the best estimates for redeye round herring and sardine, [E_m] was varied between 1 000 and 8 000 J.cm⁻³ for each species separately.

3.4.3 Volume-specific maintenance rate [$\dot{p}_M$]

The volume-specific maintenance rate [$\dot{p}_M$] is affected by temperature and is scaled by the temperature correction factor $c(T)$ (Table 2.3; Eqn. 28). The volume-specific maintenance rate at reference temperature [$\dot{p}_M$]_{ref} for anchovy was set to 25 J.cm⁻³.d⁻¹ (Chapter 2). To find the best estimates for redeye round herring and sardine at reference temperature T_{ref} of 293 K (20°C), [$\dot{p}_M$]_{ref} was varied between 50 and 140 J.cm⁻³.d⁻¹.

3.4.4 Surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$

The surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ is also affected by temperature. Table 2.3, Eqn. 28 was used to scale the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ with the temperature correction factor $c(T)$ for different water temperatures. The surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ _{ref} for anchovy was set to 220 J.cm⁻².d⁻¹ (Chapter 2). To find the optimum value for the surface-area-specific assimilation rate for redeye round herring and sardine at reference conditions, $\{\dot{p}_{Am}\}$ _{ref} was varied between 100 and 1 500 J.cm⁻².d⁻¹.

3.4.5 Volume-specific cost for structure [E_G]

The volume-specific cost for structure [E_G] for anchovy was set to 1 200 J.cm⁻³ (Chapter 2). To find the optimum value for [E_G] at reference conditions it was varied between 100 and 16 000 J.cm⁻³ for both species.

3.5 Description of experiments

3.5.1 Varying the scaled functional response (f)

In this experiment the modelled redeye round herring and sardine were exposed to a constant reference temperature T_{ref} of 293 K (20°C). The scaled functional response (f) was assigned values between 0.1 (signifying near starvation) and 1.0 (unlimited food supply), stepping by 0.1. The resulting lengths and weights of redeye round herring and sardine were compared to those predicted from the von Bertalanffy model and their length-weight relationships, to illustrate how the functional response influenced their growth patterns.

3.5.2 Varying the water temperature (T)

In this experiment redeye round herring and sardine experienced constant unlimited food ($f = 1.0$), while the water temperature (T) was varied between 12°C and 26°C. The aim was to see how temperature affected the growth and reproduction of redeye round herring and sardine by changing the parameters affected by temperature ($\{\dot{p}_{Am}\}$ and $[\dot{p}_M]$) (Table 2.8). The resulting length and weights were compared to those predicted from the von Bertalanffy growth curve and the length-weight relationships for the two species, to illustrate how temperature influenced their growth patterns.

3.5.3 Starvation study

Atresia is the resorption of gametes for maintenance payment and is a natural occurrence in spawning small pelagic fish populations (Hunter & Macewicz 1985). Roel and Melo (1990) found atresia in oocytes throughout the redeye round herring spawning season but mainly in May, which they interpreted as coinciding with the end of the spawning season. Akkers *et al.* (1996) found high incidences (38 - 39%) of atretic stage 3 ovaries in sardine in September and March, coinciding with the start and end of the peak spawning season.

To simulate the length of time it would take redeye round herring and sardine in the model to starve to death (reproductive buffer $E_R = 0$) at different stages of development, they were placed into different starvation scenarios. These were set to occur at the start of the peak spawning season and at the middle of the spawning season for the duration of the life cycle of both species. In the first instance, redeye round herring and sardine would have unlimited food ($f = 1.0$) until they reached the desired start or middle of the spawning season, after which starvation would occur ($f = 0$). The number of days it took for the reproductive buffer (E_R) of each species to reach zero was recorded for different water temperatures (T) ranging between 12 and 26°C at 2°C increments. In the second instance, different constant scaled functional responses were set for redeye round herring ($f = 0.1, 0.9, 0.8$ or 0.7) and sardine ($f = 0.1, 0.9$ or 0.8) at constant reference temperature $T_{ref} = 293$ K (20°C) until they reached the desired start or middle of the spawning season, after which starvation occurred ($f = 0$). The length of time taken for the reproductive buffer (E_R) to reach zero was then recorded.

Redeye round herring (*Etrumeus whiteheadi*) model code for the Southern Benguela can be accessed at: <https://doi.org/10.25375/uct.16802629> (Groenewald *et al.* 2021b). Sardine (*Sardinops sagax*) model code for the Southern Benguela can be accessed at: <https://doi.org/10.25375/uct.16802611.v1> (Groenewald *et al.* 2021c).

Results

Estimated missing DEB parameters.

Simulations of redeye round herring using parameters estimated at reference conditions (functional response $f = 1.0$ and the reference temperature $T_{ref} = 293$ K (20°C)) found that a fraction allocated to growth and maintenance κ of 0.54, a maximum storage density $[E_m]$ of 3 000 J.cm⁻³, a volume-specific maintenance cost $[\dot{p}_M]_{ref}$ of 25 J.cm⁻³.d⁻¹, a maximum assimilation rate $\{\dot{p}_{Am}\}_{ref}$ of 203 J.cm⁻².d⁻¹ and a volume-specific cost for structure $[E_G]$ of 5 000 J.cm⁻³ showed the closest visual correspondence to the von Bertalanffy growth curve and the length-weight relationship from the survey data (Table 3.4, Figure 3.1). The length of time redeye round herring took to reach sexual maturity was calculated as 711 days (approximately 1.9 years), the maximum length and weight values, respectively, as 19.32 cm and 87.924 g, and the number of egg batches spawned throughout

the redeye round herring's lifetime as 170 egg batches (between 33 and 34 egg batches per year) (Appendix A, Table A.1).

Simulations of sardine parameters estimated at reference conditions ($f = 1.0$ and $T_{ref} = 293$ K (20°C)) found that a fraction allocated to growth and maintenance κ of 0.42, a maximum storage density $[E_m]$ of 4 300 J.cm⁻³, a volume-specific maintenance cost $[\dot{p}_M]_{ref}$ of 84 J.cm⁻³.d⁻¹, a maximum assimilation rate $\{\dot{p}_{Am}\}_{ref}$ of 956 J.cm⁻².d⁻¹ and a volume-specific cost for structure $[E_G]$ of 8 000 J.cm⁻³ showed the closest visual correspondence to von Bertalanffy growth and the length-weight relationship from the survey data (Table 3.4, Figure 3.1). The length of time taken by sardine to reach sexual maturity was calculated as 559 days (approximately 1.5 years), the maximum length and weight values, respectively, as 21.34 cm and 158.73 g, and the number of egg batches spawned throughout the sardine's lifetime as 209 egg batches (between 24 and 25 egg batches per year) (Appendix A, Table A.2).

3.4.1 Fraction allocated to growth and maintenance κ

At stable environmental conditions DEB models tended towards von Bertalanffy growth and the developed DEB models for redeye round herring and sardine came close to matching the growth curves from the literature. Changing the allocation to growth and maintenance changed the weights of redeye round herring and sardine, which changed the growth rate in juveniles. At smaller values for κ , the growth rate for juvenile fish in the model increased and the number of egg batches produced increased, illustrated in Appendix A (1). The optimum allocation to growth and maintenance κ was taken as 0.54 for redeye round herring and 0.42 for sardine (Table 3.4), values that gave the closest visual fit to the length-weight relationships from survey data and the best estimate of numbers of egg batches.

3.4.2 Maximum storage density $[E_m]$

The optimum estimate for the maximum storage density $[E_m]$ was set for redeye round herring as 3 000 J.cm⁻³ and for sardine as 4 300 J.cm⁻³ (Table 3.4). The effects of changing $[E_m]$ on the redeye round herring and sardine growth curves are illustrated in Appendix A (2).

3.4.3 Volume-specific maintenance rate $[\dot{p}_M]_{ref}$

The volume-specific maintenance rate for reference conditions $[\dot{p}_M]_{ref}$ was estimated as 25 J.cm⁻³.d⁻¹ for redeye round herring and 84 J.cm⁻³.d⁻¹ for sardine (Table 3.4). Illustrations of how changing $[\dot{p}_M]_{ref}$ affected the growth curves for both species are presented in Appendix A (3).

3.4.4 Surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$

The surface-area-specific assimilation rate under reference conditions $\{\dot{p}_{Am}\}_{ref}$ was set to 203 J.cm⁻².d⁻¹ for redeye round herring and to 956 J.cm⁻².d⁻¹ for sardine (Table 3.4). The effect of changes in $\{\dot{p}_{Am}\}_{ref}$ on the growth curves of redeye round herring and sardine are illustrated in Appendix A (4).

3.4.5 Volume-specific cost for structure $[E_G]$

The volume-specific cost for structure $[E_G]$ was set to 5 000 J.cm⁻³ for redeye round herring and to 8 000 J.cm⁻³ for sardine (Table 3.4). The effect of changes in $[E_G]$ on the growth curves of redeye round herring and sardine are illustrated in Appendix A (5).

Table 3.4 Optimum estimated DEB model parameters used in the equations in Tables 2.1-2.3 (Chapter 2) for a reference temperature of 293 K (20°C) for redeye round herring and sardine.

Parameter	Symbol	Min	Max	Redeye round herring	Sardine	Units
Fraction allocated to growth and maintenance	κ	0.5	0.99	0.54	0.42	-
Maximum storage density	$[E_m]$	1 000	8 000	3 000	4 300	J.cm ⁻³
Volume-specific maintenance cost	$[\dot{p}_M]_{ref}$	50	140	25	84	J.cm ⁻³ .d ⁻¹
Maximum assimilation rate	$\{\dot{p}_{Am}\}_{ref}$	100	600	203	956	J.cm ⁻² .d ⁻¹
Volume-specific cost for structure	$[E_G]$	1 000	16 000	5 000	8 000	J.cm ⁻³

Experimental results for redeye round herring and sardine models

3.5.1 Scaled functional response (f)

Redeye round herring reached a maximum length of 19.32 cm and a maximum weight of 87.924 g at a functional response of 1.0. These values showed a difference to the maximum length and weight observed from literature, indicating an underestimation of the length values in the model. It was found that redeye round herring needed an f value of at least 0.7 to reach sexual maturity ($L_p > 12$ cm). Redeye round herring would produce a maximum of 170 egg batches at unlimited food ($f = 1.0$) throughout their lifecycle and would produce 59 egg batches at an f of 0.7 (Table 3.5). Sardine growth reached a maximum length at $f = 1.0$ of 21.34 cm and a maximum weight of 158.730 g (Table 3.5). These maximum lengths and differed from the observed maximum length values from literature, indicating an underestimation in the model results, especially for the length values. It was found that sardine needed a consistent functional response (f) larger or equal to 0.8 for sardine to reach sexual maturity ($L_p > 17$ cm) and be able to reproduce (Table 3.5). At unlimited food ($f = 1.0$) sardine produced 209 egg batches though their life cycle, with 4 egg batches being produced at an f of 0.8 (Table 3.5).

Changes in f did not change the slope of the length-weight curves of redeye round herring or sardine by much, only the maximum length and weight reached (Figure 3.1c & f). A decrease in f increased the length of time taken for redeye round herring to reach sexual maturity from 711 days (1.9 years) at an f of 1.0 to 1 392 days (3.8 years) at an f of 0.7 and increased the length of time taken for sardine to reach sexual maturity from 559 days (1.5 years) at an f of 1.0 to 1 843 days (5.0 years) at an f of 0.8. These ages at sexual maturity for sardine fell within estimates of sexual maturity from literature for $f = 0.9$ to 1.0. However, in redeye round herring the age at sexual maturity was later than values from literature, showing that redeye round herring in the model reached sexual maturity later than would be expected.

3.5.2 Varying the water temperature (T)

Temperature affected the volume-specific maintenance rate [$\dot{p}_M$] and the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$. Thus, these parameters are scaled for temperature with the temperature correction factor $c(T_1)$ for both species (Table 3.6). For a temperature range between 12 and 26°C the temperature correction ranged between 0.34 and 2.16 for redeye round herring and between 0.40

Table 3.5 Model results for redeye round herring and sardine for different functional responses (f). Lit is the observed values from literature, where a_p is age at puberty, L_p is standard length at puberty, L_m is maximum length, W_{wp} is wet weight at puberty, W_{wm} is wet weight at maximum length from the length-weight model with maximum wet weight measured from surveys in brackets and N_{batch} is the number of egg batches produced by an individual during its lifespan.

	a_p (days)	L_p (cm)	L_m (cm)	W_{wp} (g)	W_{wm} (g)	N_{batch} (egg batches)
REDEYE ROUND HERRING						
Lit	365	12.00	20.41	23.065	87.366 (120.3)	177
$f=1.0$	711	12.00	19.32	15.100	87.924	170
$f=0.9$	832	12.01	17.44	14.478	61.356	152
$f=0.8$	1 022	12.00	15.55	13.745	39.648	115
$f=0.7$	1 392	12.00	13.65	12.993	23.268	59
$f=0.6$	-	-	11.74	-	11.497	0
$f=0.5$	-	-	9.81	-	6.327	0
$f=0.3$	-	-	5.92	-	1.221	0
$f=0.1$	-	-	1.99	-	0.040	0
SARDINE						
Lit	365 – 1 095	17.00	23.00	57.550	151.090 (158.6)	240
$f=1.0$	559	17.01	21.34	56.443	158.730	209
$f=0.9$	744	17.00	19.20	53.088	96.110	135
$f=0.8$	1 843	17.00	17.07	48.812	51.284	4
$f=0.7$	-	-	14.94	-	31.648	0
$f=0.6$	-	-	12.80	-	18.603	0
$f=0.5$	-	-	10.67	-	9.998	0
$f=0.3$	-	-	6.40	-	1.828	0
$f=0.1$	-	-	2.13	-	0.055	0

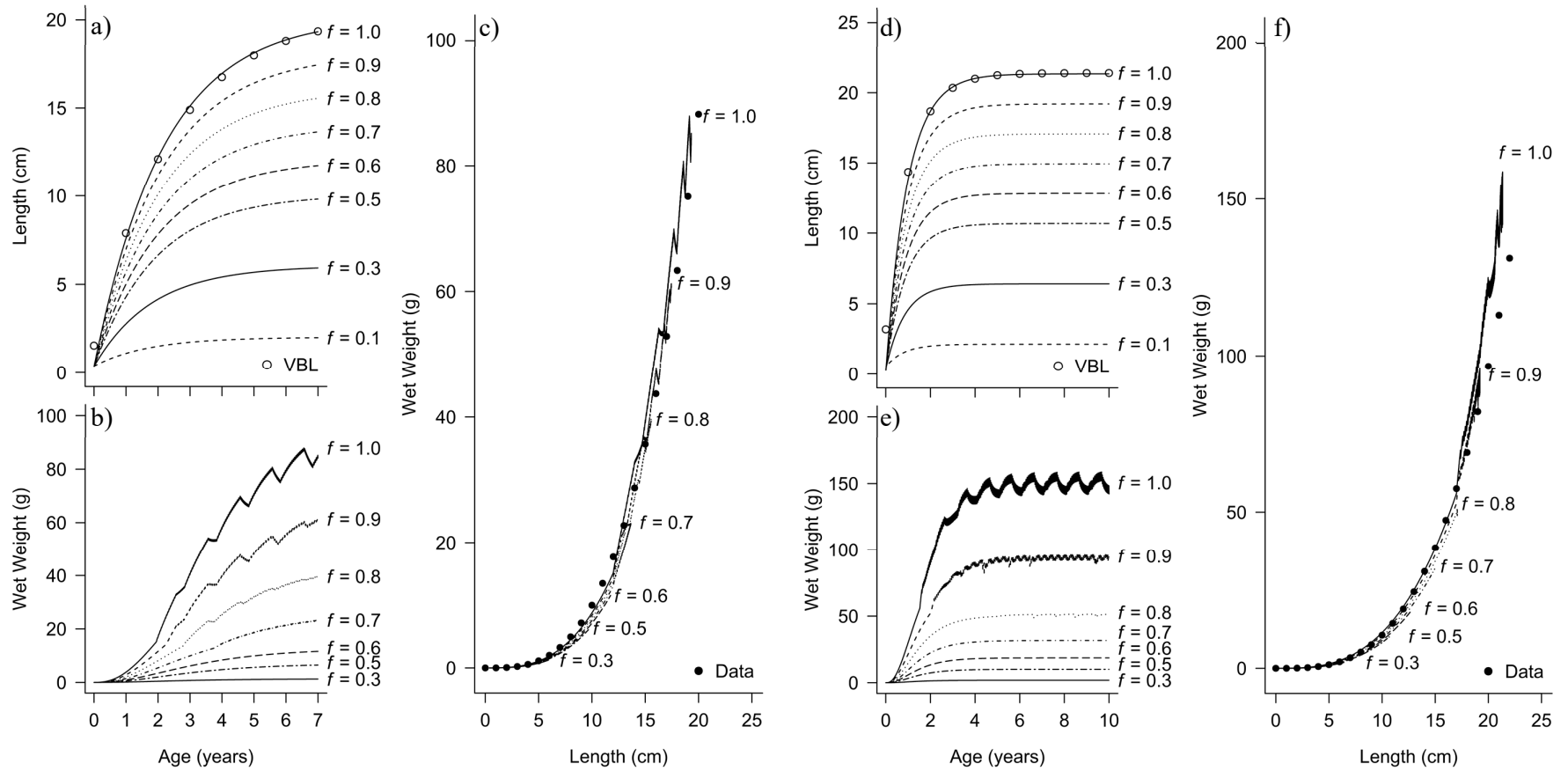


Figure 3.1 The effect of the change in functional response (f) on the growth curves of redeye round herring (a-c) and sardine (d-f) in the Southern Benguela where the effect of changing f is shown on, a & d) the length (cm) at age (years) curves, b & e) the weight (g) at age (years) curve, and c & f) the length-weight relationship. The lines indicate different values of f , $\circ$ VBL is the von Bertalanffy growth and $\bullet$ Data represents the length-weight relationship from survey data.

and 1.94 for sardine (Table 3.6). For this temperature range the $[\dot{p}_M]$ ranged between 8 and 54 J.d⁻¹.cm⁻³ for redeye round herring and between 69 and 439 J.d⁻¹.cm⁻³ for sardine, while $\{\dot{p}_{Am}\}$ ranged between 103 and 655 J.cm⁻².d⁻¹ for redeye round herring and between 379 and 1 852 J.cm⁻².d⁻¹ for sardine (Table 3.6).

Temperature affected the growth rates of both redeye round herring and sardine, with fish reaching their maximum lengths and weights faster at warmer temperatures (Figure 3.2). The maximum lengths and weights for redeye round herring differed for different temperatures, with the maximum length ranging between 13.48 and 20.09 cm and maximum weights ranging between 26.110 and 113.750 g (Table 3.7). In sardine, changes in temperature changed the slopes of the length-at-age (Figure 3.2d) and the weight-at-age (Figure 3.2e) curves. However, temperature did not influence the maximum length values in sardine. All the maximum lengths between temperatures of 12 and 26°C ranged between 21.00 and 21.34 cm and weights ranged between 144.04 and 170.78 g (Table 3.7).

The model maximum length values for both redeye round herring and sardine showed lower values than what is expected from literature, indicating there may be an underestimation in the models for length of the fish. Temperature affected the length and weight values of redeye round herring and

Table 3.6 Redeye round herring and sardine DEB parameters that are affected by water temperature, where T is the water temperature in °C, T_1 is the water temperature in K, $c(T_1)$ is the temperature correction, $[\dot{p}_M]$ is the volume-specific maintenance costs and $\{\dot{p}_{Am}\}$ is the surface-area-specific assimilation rate.

		Redeye round herring			Sardine		
		$c(T_1)$	$[\dot{p}_M]$	$\{\dot{p}_{Am}\}$	$c(T_1)$	$[\dot{p}_M]$	$\{\dot{p}_{Am}\}$
T (°C)	T_1 (K)	(-)	(J.d ⁻¹ .cm ⁻³)	(J.cm ⁻² .d ⁻¹)	(-)	(J.d ⁻¹ .cm ⁻³)	(J.cm ⁻² .d ⁻¹)
12	285	0.34	8	69	0.40	33	379
14	287	0.45	11	91	0.50	42	480
16	289	0.59	15	119	0.63	53	606
18	291	0.77	19	156	0.80	67	762
20	293	1.00	25	203	1.00	84	956
22	295	1.30	32	263	1.25	105	1 195
24	297	1.68	42	341	1.56	131	1 490
26	299	2.16	54	439	1.94	163	1 852

Table 3.7 Model results for redeye round herring and sardine for different temperatures (T , °C). Lit is the observed values from literature. Where a_p is age at puberty, L_p is standard length at puberty, L_m is maximum length, W_{wp} is wet weight at puberty, W_{wm} is wet weight at maximum length from the length-weight relationship with the maximum wet weight from the survey data in brackets and N_{batch} is the predicted number of egg batches produced by the model during their individual lifespans.

	a_p (days)	L_p (cm)	L_m (cm)	W_{wp} (g)	W_{wm} (g)	N_{batch} (egg batches)
REDEYE ROUND HERRING						
Lit	438	12.00	20.41	23.065	87.366 (120.3)	177
$T = 12$	2 084	12.00	13.48	15.127	26.110	21
$T = 14$	1 584	12.00	15.42	15.147	41.938	56
$T = 16$	1 208	12.00	17.12	15.151	59.701	93
$T = 18$	925	12.00	18.44	15.161	76.412	133
$T = 20$	711	12.00	19.32	15.100	87.924	170
$T = 22$	549	12.00	19.81	15.200	100.480	190
$T = 24$	426	12.01	20.02	15.261	108.740	198
$T = 26$	331	12.00	20.09	15.255	113.750	204
SARDINE						
Lit	365 – 1 095	17.00	23.00	57.550	151.090 (158.6)	240
$T = 12$	1 401	17.00	21.00	56.147	144.040	60
$T = 14$	1 108	17.01	21.23	56.221	149.710	86
$T = 16$	879	17.01	21.31	56.279	152.810	118
$T = 18$	699	17.00	21.33	55.974	153.560	159
$T = 20$	559	17.01	21.34	56.443	158.730	209
$T = 22$	448	17.01	21.34	56.580	163.440	224
$T = 24$	360	17.01	21.34	56.702	167.520	231
$T = 26$	290	17.01	21.34	56.799	170.780	237

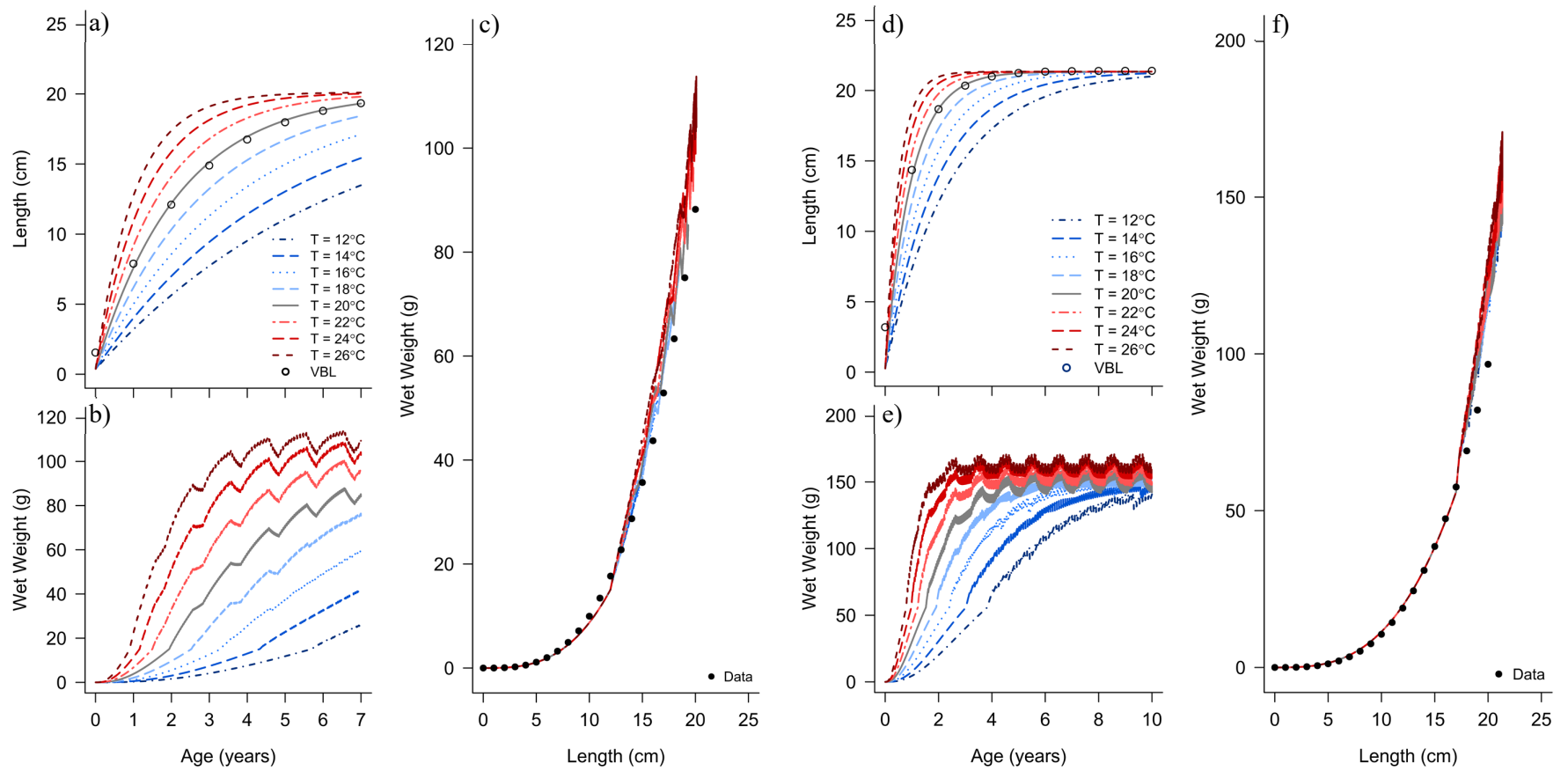


Figure 3.2 The effect of temperature (T) on the growth curves of redeye round herring (a-c) and sardine (d-f) in the Southern Benguela where the effect of changing T is shown for a & d) the length (cm) at age (years) curves, b & e) the weight (g) at age (years) curve, and c & f) the length-weight relationship. The lines indicate different values of T ($^{\circ}\text{C}$) with blue indicating temperatures below and red indicating temperatures above the reference temperature, $\circ$ VBL is the von Bertalanffy growth and $\bullet$ Data represents the length-weight relationship from survey data.

sardine in such a way that there is little difference in the length-weight relationship for different temperatures in either of the two species (Figure 3.2c & f).

Since temperature affected the growth rate it would also affect the length of time it takes redeye round herring and sardine to reach sexual maturity. Age at puberty ranged between 2 084 days (5.7 years) and 331 days (0.9 years) for redeye round herring and between 1 401 days (3.8 years) and 290 days (0.8 years) for sardine for temperatures between 12 and 26°C (Table 3.7).

The number of egg batches produced by redeye round herring and sardine differed for different temperatures, with more being produced in warmer waters. The number of egg batches produced for temperatures between 14 and 20°C for redeye round herring ranged between 56 and 170 egg batches, and for sardine ranged between 86 and 209 egg batches (Table 3.7).

3.5.3 Starvation study

Redeye round herring and sardine starvation simulations showed that for differing water temperatures (T), fish survived longer when food was removed in the middle of the spawning season than at the start, with older fish in general surviving longer (Figure 3.3). Redeye round herring of all ages showed first an increase and then a decrease in survival when moving along the temperature gradient from 12 to 26°C, with the maximum survival occurring at colder temperatures for older fish (Figure 3.3a). In general redeye round herring survived for longer without food than sardine at differing water temperatures. Sardine younger than six years old showed first an increase then a decrease in survival when moving along the temperature gradient from 12 to 26°C (Figure 3.3b). In contrast, sardine of six years and older had a negative relationship between survival and temperature, with sardine surviving for longer at colder temperatures. Older sardine showed overlap in their survival at different temperatures.

Starvation simulations for redeye round herring and sardine for differing functional responses (f) showed fish survived longer when food was removed in the middle of the peak spawning season than at the start, with older fish, in general, surviving longer (Figure 3.4). Starvation simulations of both redeye round herring and sardine showed a positive relationship between survival and functional response, with survival increasing as the scaled functional response increased. In general redeye round herring survived for longer without food than sardine at differing scaled functional responses.

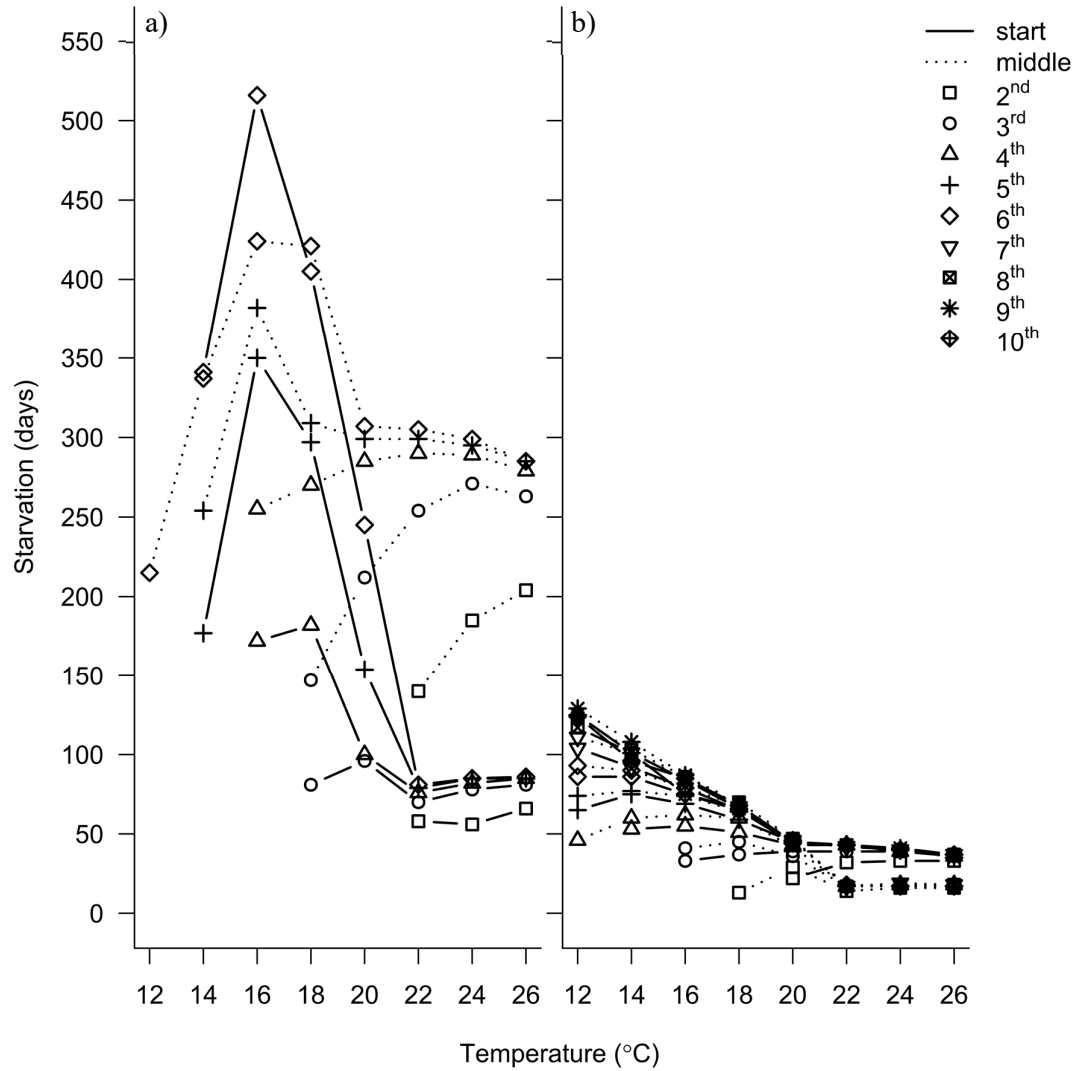


Figure 3.3 Simulated time in days since starvation was initiated as a function of spawning season. Comparing starvation in different water temperatures (T , °C) with a constant initial functional response of ($f = 1.0$) for a) redeye round herring and b) sardine. Starvation was initiated at the start of spawning seasons (—) or middle of the spawning season (---) for duration of the lifespan of the fish. The 2nd to 10th represents the year of life in which spawning occurred.

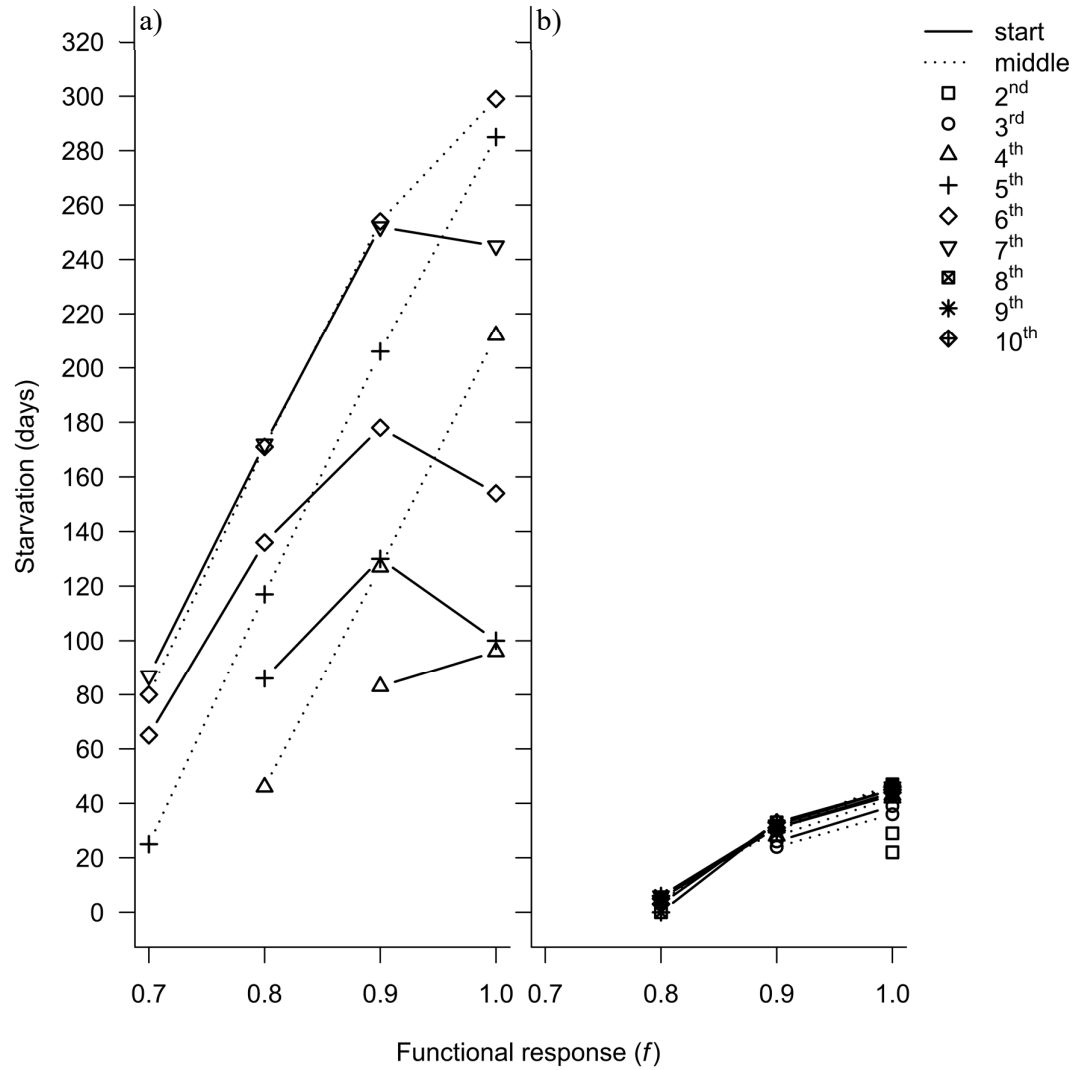


Figure 3.4 Simulated time in days since starvation was initiated as a function of spawning season. Comparing starvation for a) redeye round herring and b) sardine for different initial functional responses at reference temperature $T_{ref} = 293$ K (20°C). Starvation was initiated at the start of spawning seasons (—) or middle of the spawning season (---) for duration of the lifespan of the fish. The 2nd to 10th represents the year of life in which spawning occurred.

Discussion

Anchovy, redeye round herring, and sardine in the Southern Benguela have different life history characteristics. Anchovy is the shortest lived of the three species and reach their maximum length within 4 years. They spend approximately 5% of their lifespan as larvae and 20% of their life span as juveniles, and are reproductively active for 75% of their lifespan (Table 3.8). They are highly fecund, releasing almost twice as many eggs per spawn as redeye round herring and sardine over a shorter spawning season (Table 3.8). Redeye round herring reach their maximum length within 7 years, are the slowest growing species of the three as early larvae (30 days post first feeding), and spend 3% of their lifespan as larvae, between 11 and 17% of their lifespan as juveniles and are reproductively active between 80 and 86% of their lifespan. They have the lowest batch fecundity of the three species, spawning only a quarter the number of eggs of anchovy per spawn and half the number of eggs of sardine. They do, however, have the fastest oocyte development time of the three species, so they can spawn more often than anchovy and sardine, and over a longer period than anchovy but not sardine. Sardine are the longest living of the three small pelagic fish, reaching their maximum length within 10 years, spending approximately 2% of their lifespan as larvae, between 8 and 28% of their lifespan as juveniles and are reproductively active between 70 and 90% of their lifespan (Table 3.8). Larval sardine grow the fastest of the three small pelagic species during the 30 days post first feeding. Sardine release less than half the number of eggs of anchovy per spawn, yet they produce more egg batches yearly over a longer spawning period.

These small pelagic fish have different size preferences for apportioning food, with anchovy and redeye round herring feeding preferentially on larger food particles than sardine (Table 3.8). The three species have different von Bertalanffy growth curves, anchovy, and sardine both have very fast growth in their larval and juvenile phase in their first year, while redeye round herring are slower growing, only having their fastest growth rate in their second year of life (Figure 3.5). DEB models were used to investigate similarities and differences in the energetic strategies between redeye round herring and sardine and then compared to anchovy (Chapter 2). These comparisons were based on model parameter estimates, growth and spawning simulations and responses to environmental inputs from food and temperature.

Table 3.8 Main life history characteristics of the three small pelagic fish species in the Southern Benguela. The reference list at the bottom of the table is linked to the superscript next to each value.

Characteristic	Unit	Redeye round		
		Anchovy	herring	Sardine
Age at birth	days	1.33 ¹	1.60 ²	1.55 ¹
Age at Metamorphosis	days	67-78 ³	68 ⁴	52-76 ³
Age at puberty	years	0.5-1 ⁵	0.8-1.2 ⁶	1-3 ⁷
Life span	years	4 ⁷	7 ⁶	10 ⁸
Length at hatching	cm	0.248-0.32 ⁹	0.39-0.45 ²	0.275-0.295 ¹
Length at metamorphosis	cm	3.0-3.5 ⁹	3.5 ¹⁰	2.2-3.2 ¹¹
Length at puberty	cm	8 ⁵	12 ⁶	17 ¹²
Maximum length	cm	16 ⁷	20.41 ⁶	23 ⁸
Growth rate (larvae 30 days post first feeding)	mm.day ⁻¹	0.48 ¹³	0.37 ¹³	0.58 ¹³
Growth rate (juveniles < 0.5 years)	mm.day ⁻¹	0.46-0.49 ¹⁴	0.44 ⁴	0.55-0.60 ¹⁵
Spawning interval	days	9-12 ¹⁶	6-15 ¹⁷	11-18 ¹⁸
Egg batches	batch.year ⁻¹	14-21 ¹⁶	24-33 ¹⁷	20-29 ¹⁸
Relative batch fecundity	eggs.g ⁻¹ per spawn	530 ¹⁹	118 ¹⁷	215 ²⁰
Spawning season		October to March ⁷	Year-round ²¹	Year-round ⁷
Peak spawning season		October - January/February ⁷	August – October ²¹	August - March ⁷
Spawning temperature	°C	17-23 ²²	11.5-20.5 ²	13-22 ²³
Feeding type		Intermediate mixed feeding ²⁴	Particulate feeding ²⁵	Intermediate mixed feeding ²⁴
Particle size preference	mm	0.5-2.0 Particulate ²⁴	>1.5 Particulate 0.20-0.25 Filter ²⁵	0.01-1.2 Filter >1.2 Particulate ²⁴
Diet		Larger zooplankton & phytoplankton ²⁴	Larger zooplankton ²⁵	Smaller zooplankton & phytoplankton ²⁴

- ¹ King *et al.* (1978) ² O'Toole & King (1974) ³ Brownell (1983) ⁴ Waldron *et al.* (1991) ⁵ Le Clus (1979)
⁶ Geja *et al.* (2016) ⁷ Barange *et al.* (2009) ⁸ Kerstan (2000) ⁹ Armstrong & Thomas (1989)
¹⁰ Wallace-Fincham (1987) ¹¹ Louw & O'Toole (1977) ¹² Beckley & van der Lingen (1999)
¹³ Thomas (1986) ¹⁴ Costalago *et al.* (2020) ¹⁵ Kerstan *et al.* (1996) ¹⁶ Melo (1994a)
¹⁷ Roel & Melo (1990) ¹⁸ Akkers *et al.* (1996) ¹⁹ van der Lingen & Durholtz (2003)
²⁰ Akkers & Melo (1996) ²¹ Roel *et al.* (1994) ²² Mhlongo *et al.* 2015 ²³ King 1977
²⁴ van der Lingen *et al.* (2006b) ²⁵ Wallace-Fincham 1987

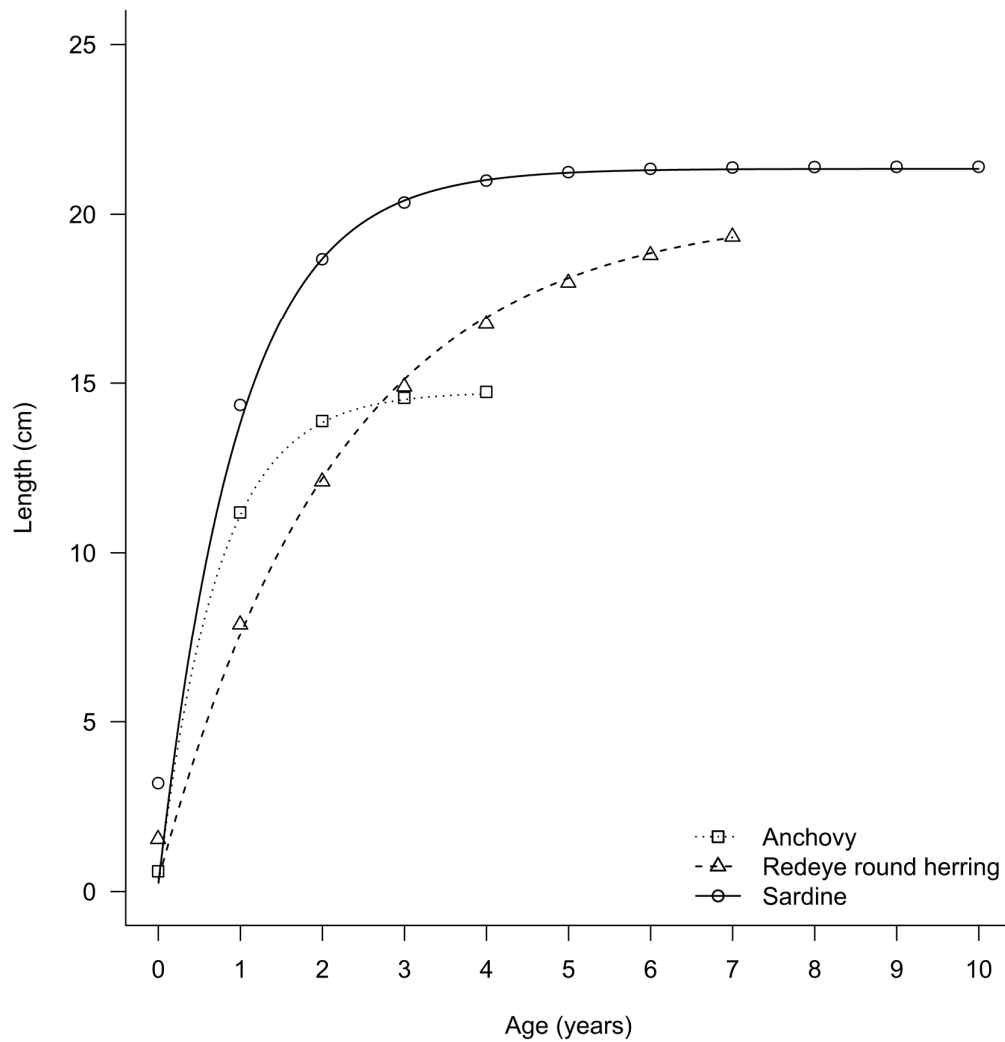


Figure 3.5 von Bertalanffy growth curves for three small pelagic fish in the Southern Benguela. The lines represent the model output for the small pelagic fish and points represents growth from empirical data.

The parameters from the anchovy model (Chapter 2) had to be adjusted for redeye round herring and sardine since they had different growth rates, spawning intervals, and energy requirements. Redeye round herring had slower growth rates, lower structural growth and maintenance costs, while sardine showed faster growth rates and invested more in reproductive reserve storage capacity. Redeye round herring required a lower minimum scaled functional response value ($f=0.7$) than sardine ($f=0.8$) to reach sexual maturity and reproduce. Warmer temperatures increased the growth rates of juveniles in both species but decreased their survival during starvation scenarios. Survival in

redeye round herring and sardine decreased with a decrease in the scaled functional response (f) during starvation.

Model performance will be discussed separately for: 1) how models performed in comparison to model-independent, empirical data collected from surveys and/or the literature; 2) how estimated DEB parameters for sardine in the Southern Benguela differed from the functionally similar European sardine *Sardina pilchardus* in the Bay of Biscay, and how DEB parameters estimated for redeye round herring and sardine differed from those for anchovy in the Southern Benguela; 3) how the models performed in response to environmental fluctuations in temperature and functional response; and 4) how the DEB models responded to different starvation scenarios.

Model evaluation

In both redeye round herring and sardine the DEB model outputs followed the empirical data well, especially for the von Bertalanffy growth curves and, to a lesser degree, the length-weight relationships. Discrepancies between DEB model outputs and empirical and/or literature values were limited to an underestimation of the adult maximum length. Sardine, and to a lesser extent redeye round herring, had greater weight values in the DEB model after fish reach sexual maturity, than is observed in empirical data, as was shown by the deviation in the adult length-weight relationships (Figure 3.1c). This could be due to the model being constrained to one temperature for most of these experiments i.e., the reference temperature (20°C). The difference could also be an indication that the volume-specific cost for structure [E_G], needs to have separate values for juvenile and adult fish, as it seems that adult redeye round herring and sardine invest more into their volume-specific cost for structure than juveniles (Figure A.2). It is also worth noting that the fraction allocated to growth and maintenance had a large impact on the energy accumulated for spawning frequency and the number of egg batches that the fish produced in both species.

There is an indication that redeye round herring store more energy than is needed before spawning. One of the conditions in the model was that twice the energy of a batch of eggs ($2 * E_{batch}$) had to be stored before spawning could begin. Forcing the model redeye round herring to spawn based on just this condition produced many more egg batches per year than should be possible. Therefore, the spawning interval was also enforced as a condition in the model, to reduce the number of egg batches produced in a year to between 33 and 34, which was similar to the observed average of 34 egg batches

per year (Roel & Melo 1990). A contributing factor to this discrepancy with spawning frequency may be the lack of information on the energy content of a redeye round herring egg.

Differing DEB parameters

Comparisons between sardine *Sardinops sagax* in the Southern Benguela and sardine *Sardina pilchardus* in the Bay of Biscay (Gatti *et al.* 2017) showed differences in their core DEB parameters. Redeye round herring and sardine core parameters also differed from those estimated for anchovy in the Southern Benguela.

The fraction allocated to growth and maintenance (κ), known as the fraction of energy that an individual spent on somatic growth and maintenance, was set to 0.42 for sardine in the Southern Benguela (Table 3.4). This was at the lower end of the κ value range found by Gatti *et al.* (2017) for sardine in the Bay of Biscay, which ranged between 0.42 and 0.67. Southern Benguela sardine tend to have higher κ values than anchovy in this system (0.35, see Chapter 2), which is inconsistent with findings from the Bay of Biscay by Gatti *et al.* (2017). This low κ means that sardine in the Southern Benguela would allocate 58% of assimilated energy ($1-\kappa$) to reproduction, according to the κ -rule. Interestingly, sardines around the world show remarkably similar spawning intervals for their peak spawning seasons. In the California Current and the Mediterranean ecosystems, sardine have spawning intervals of between 9 and 11 days (Macewicz *et al.* 1996, Ganas *et al.* 2014), while sardine in the Bay of Biscay have a spawning interval of 12 days (ICES 2015, Gatti *et al.* 2017) and sardine in the Southern Benguela have a spawning interval of 10.5 days during peak spawning and 17.5 days at the start of the spawning season (Akkers *et al.* 1996). Relative batch fecundity (RF_{batch}) of sardine in the Southern Benguela was found to be 215 eggs.g⁻¹ per spawn (Le Clus 1988, Akkers & Melo 1996, van der Lingen & Durholtz 2003). Comparatively, sardine in the Bay of Biscay have a higher relative batch fecundity of 336-462 eggs.g⁻¹ per spawn (Nunes *et al.* 2011, Gatti *et al.* 2017). Therefore, sardine in the Bay of Biscay would allocate less assimilated energy to reproduction (between 33% and 58% in this case), to build more reserves in the same spawning interval as sardine in the Southern Benguela this may indicate that sardine in the Bay of Biscay have a more capital breeding strategy than in the Southern Benguela.

Redeye round herring *Etrumeus whiteheadi* had a fraction allocated to growth and maintenance κ value of 0.54 (Table 3.4). This was larger than that of anchovy (0.35) and sardine (0.42) in the

Southern Benguela and means that redeye round herring would direct 46% of assimilated energy into reproduction storage capacity, compared to the 65% and 58% that anchovy and sardine invest, respectively. This indicates that redeye round herring is showing a more “capital breeding” strategy than the other species, storing reproductive capital to finance each reproductive attempt (Stephens *et al.* 2009). Anchovy and sardine, on the other hand, show a more “income breeding” strategy, using concurrent intakes of energy to pay for a reproductive attempt (Stephens *et al.* 2009). Redeye round herring in the Southern Benguela had a spawning interval of 6 days during peak spawning season and 15 days during off-peak spawning (Roel & Melo 1990), which is shorter than anchovy (9-14 days) and sardine (10.5-17.5 days). The relative batch fecundity (RF_{batch}) of redeye round herring in the Southern Benguela was found to be 118 eggs.g⁻¹ female weight per spawn (Roel & Melo 1990). Comparatively, anchovy have an RF_{batch} value of between 481 and 624 eggs.g⁻¹ female weight per spawn (Alheit 1993, Shelton *et al.* 1993, van der Lingen & Durholtz 2003) and sardine have an RF_{batch} of 215 eggs.g⁻¹ female weight per spawn (Le Clus 1988, Akkers & Melo 1996, van der Lingen & Durholtz 2003). Therefore, redeye round herring do not have to allocate as much assimilated energy to reproduction as the other two species, since they produce fewer eggs per batch spawn. Since the models were run under constant environmental conditions, they did not consider the seasonality (influence of temperature and plankton production) or the degree of overlap between the periods of high food concentrations and spawning, or how it would affect the breeding strategy of each species (i.e., their positions along the capital-income continuum). Fishes move along the capital-income breeding continuum in response to several conditions such as a fish’s physiological condition or the match-mismatch between food production and egg production (McBride *et al.* 2015, Gkanasos *et al.* 2019). According to research by Shultz & Conover (1997) and McBride *et al.* (2015), fish in higher latitudes would show a more capital breeding response in response to strong seasonal fluctuation in food availability, while fish in low latitudes would show a more income breeding response in response to a more moderate or prolonged seasonal cycle.

The volume-specific cost for maintenance at reference temperature $[\dot{p}_M]_{ref}$ was standardised to 84 J.cm⁻³.d⁻¹ (Table 3.4) for sardine in the Southern Benguela, a value that was lower than the 100 to 142 J.cm⁻³.d⁻¹ estimated by Gatti *et al.* (2017) for European sardine. The $[\dot{p}_M]_{ref}$ value for redeye round herring was set to 25 J.cm⁻³.d⁻¹ (Table 3.4), the same value as that of anchovy (25 J.cm⁻³.d⁻¹) but lower than sardine in the Southern Benguela. The maximum assimilation rate at reference temperature $\{\dot{p}_{Am}\}_{ref}$ for sardine in the Southern Benguela was standardised to 956 J.cm⁻².d⁻¹. This

value was lower than the 987 to 1 186 J.cm⁻².d⁻¹ found by Gatti *et al.* (2017) for sardine in the Bay of Biscay, but higher than the $\{\dot{p}_{Am}\}_{ref}$ of anchovy (220 J.cm⁻².d⁻¹) and redeye round herring (203 J.cm⁻².d⁻¹) in the Southern Benguela. Redeye round herring and anchovy in the Southern Benguela feed in cold upwelled intermittent mixed waters (12-15°C) on large prey items (Wallace-Fincham 1987, van der Lingen *et al.* 2006b, Mketsu 2008), and spawn in warm waters, with redeye round herring preferring slightly cooler waters (14-24°C) (Roel & Armstrong 1991, van der Lingen *et al.* 2005). Sardine, on the other hand, feed in highly stable warm water (> 15°C) on small prey items (van der Lingen *et al.* 2006b) and prefer to spawn in waters between 16 and 22°C (Mhlongo *et al.* 2015). Larger values for $\{\dot{p}_{Am}\}$ would be anticipated for sardine (Table 3.6) since they feed on smaller food particles than the other two species, and a study by Queiros *et al.* (2019) on sardine (*S. pilchardus*) in the Western Mediterranean Sea showed that individuals that feed on small food particles had to consume twice as much food as those feeding on large food particles to achieve the same growth and condition. One would expect $[\dot{p}_M]$ and $\{\dot{p}_{Am}\}$ values for sardine in the Bay of Biscay to be lower than in the Southern Benguela since these rates are influenced by temperature and sardine *S. pilchardus* preferred a temperature range between 12 and 15°C in the Bay of Biscay and between 12 and 19°C in the North-west Mediterranean (Planque *et al.* 2007, Palomera *et al.* 2007, Peck *et al.* 2013). However, Gatti *et al.* (2017) acknowledged that their estimates were high compared to other authors and attributed it in large part to the addition of energy density in their calibration procedure, which significantly affected their parameter estimates by imposing more constraints. The DEB model results estimated for sardine and redeye round herring in this study indicated that lower values of $[\dot{p}_M]_{ref}$ (Figure A.3) and $\{\dot{p}_{Am}\}_{ref}$ (Figure A.4) could result in slower growth rates for both species.

The volume-specific cost for structure $[E_G]$ for sardine was set to 8 000 J.cm⁻³, which was higher than the 2 800 to 2 860 J.cm⁻³ estimated by Gatti *et al.* (2017). The $[E_G]$ value for redeye round herring was set to 5 000 J.cm⁻³, which was lower than that of sardine. The DEB model results indicated that higher values of $[E_G]$ indicated slower growth rates (Figure A.5). The $[E_G]$ value was defined as the energetic cost needed for one unit of growth to occur in structural body volume (Kooijman 2000, van der Meer 2006). Since $[E_G]$ is dependent on the complexity of the cell and is similar for phylogenetically related species (Kooijman 2000, van der Meer 2006, Sarà *et al.* 2013), it stands to reason that these values would differ not only between the small pelagic fish in the Southern Benguela but also between the two sardine species. From the results it is apparent that sardine have higher costs for structural growth and needed more energy for growth to occur than either anchovy or redeye round

herring in the Southern Benguela. The faster growth of the former compared to the latter is evident in the von Bertalanffy growth curves for their first three years of life (Figure 3.5).

The maximum storage density or $[E_m]$ of redeye round herring was set to 3 000 J.cm⁻³ and $[E_m]$ for sardine in the Southern Benguela was set at 4 300 J.cm⁻³ (Table 3.4). This was higher than the $[E_m]$ range for European sardine found by Gatti *et al.* (2017) of between 2 054 and 2 772 J.cm⁻³. The values for $[E_m]$ of redeye round herring and sardine were higher than the 2 800 J.cm⁻³ estimated for anchovy in the Southern Benguela. This indicated that these three pelagic species in the Southern Benguela have slower growth rates than anchovy (see comparison in Chapter 2) and sardine in the Bay of Biscay.

This slower growth rate of small pelagics in the Southern Benguela compared to the Bay of Biscay was supported by other missing core parameters discussed above and by the literature. Larval redeye round herring grew at 0.37 mm.day⁻¹ in their first 30 days after first-feeding, slower than sardine (0.58 mm.day⁻¹) and anchovy (0.48 mm.day⁻¹) during the same time frame (Thomas 1986, Wallace-Fincham 1987). Waldron *et al.* (1991) estimated growth rates in juvenile redeye round herring as 0.44 mm.day⁻¹ at 0.5 years, 0.22 mm.day⁻¹ at 1.5 years, 1.26 mm.day⁻¹ at 2.5 years, 0.13 mm.day⁻¹ at 3.5 years, 0.11 mm.day⁻¹ at 4.5 years and 0.09 mm.day⁻¹ at 5.5 years. Sardine *Sardinops sagax* reared in captivity had a larval growth rate between 0.2 and 1.0 mm.day⁻¹ in their third and fourth week of growth, after which growth stabilised at 0.42 mm.day⁻¹ between 20 and 23°C (Brownell 1983). Kerstan *et al.* (1996) estimated the growth of sardine juveniles aged 0.5 years to be between 0.55 and 0.60 mm.day⁻¹ (Beckley & van der Lingen 1999). Comparatively, juvenile sardine *Sardina pilchardus* in the Bay of Biscay had a faster daily growth rate of 1.91 mm.day⁻¹ for seven day old larvae, after which the growth rate decreased (Dulčić 1995). Silva *et al.* (2015) found an instantaneous mean growth rate for juvenile sardine *S. pilchardus* in northern Portugal between 124 days (0.3 years and 7.9 cm) and 272 days (0.7 years and 13.7 cm) to be 0.77 mm.day⁻¹. Therefore, sardine in the Bay of Biscay have faster growth rates for juveniles than redeye round herring and sardine in the Southern Benguela.

There are clear differences between the DEB parameters for the three small pelagic species in the Southern Benguela, which may be linked to their trophic strategies. This echoes trends in the differences in parameters between anchovy and sardine in the Bay of Biscay observed by Gatti *et al.*

(2017). Kooijman (2013) described a ‘waste to hurry’ strategy in small organisms that exhibit r-selected life history patterns and suggested that these organisms waste resources to remain small (Somarakis *et al.* 2004, Pethybridge *et al.* 2013, Gatti *et al.* 2017). This was seen as a survival strategy because the amount of food needed to cover maintenance costs would increase with structural body length, meaning that fast growth would need large $\{\dot{p}_{Am}\}$ values and in turn moderate to large $[\dot{p}_M]$ values due to the interaction between the two variables (Kooijman 2013, Gatti *et al.* 2017). The r-endpoint in the r-selected life history strategy represents the quantitative extreme where the optimal strategy is to put all available matter and energy into reproduction, and the least viable amount of matter and energy into each individual offspring to produce as many offspring as possible; therefore, r-selection gives rise to high productivity (Pianka 1970, Jones 1976). The K-endpoint represents the qualitative extreme where the optimal strategy is to put all available matter and energy into maintenance and the production of a few very fit offspring, therefore, K-selection gives rise to increased efficiency in utilizing environmental resources (Pianka 1970, Jones 1976). No organism falls completely at the extremes of a r-selected or K-selected strategy but tends to fall at different points along the r-K continuum (Pianka 1970, Jones 1976). All three Southern Benguela species display a more r-selected life history strategy, with anchovy life history strategy the most extreme (closest to the r-end) along the r-K continuum, while sardine places furthest away from the r-end on the r-K continuum (still r-selected but a little closer to the K-end) than the other two species.

Anchovy have the shortest life span and earliest maturation of the three species. They achieve their growth and reproduction needs (with high egg batch fecundity) during zooplankton blooms, which matches the ‘waste to hurry’ strategy described by Kooijman (2013). This strategy also relates to the ‘feast or famine’ pattern of anchovy described by van der Lingen *et al.* (2006b), where anchovy show rapid growth in food environments of large zooplankton as a result of fast metabolic rates. In poor food environments with small zooplankton, however, growth is likely to be minimal to negligible (van der Lingen *et al.* 2006b). A similar strategy has been described for northern anchovy *Engraulis mordax* in the California Current upwelling ecosystem (Rykaczewski 2009).

Redeye round herring are particulate-feeding microphagists and principally consume large zooplankton but can supplement their diet with alternative food sources by being facultative planktivores that eat phytoplankton and pelagic fish eggs, larvae and even juveniles on occasion (Wallace-Fincham 1987, James 1988a, Mketsu 2008, C. D. van der Lingen, DFFE, personal

communication). This means that they can decouple their food dependence during spawning, so they can spawn at a reduced batch fecundity, more frequently and over a longer period. Sardine have evolved more of a 'steady state' pattern in life history characteristics, where they feed on the fraction of zooplankton that is continually available (i.e., small copepods which show little population variability) (van der Lingen *et al.* 2006b), a strategy also used by this species in the California Current system (Rykaczewski 2009). This means, like redeye round herring, they are able to decouple their food dependence during spawning, so they can spawn at a reduced batch fecundity over a longer period of time (van der Lingen *et al.* 2006b, Gatti *et al.* 2017). There is a trade-off between batch fecundity and the length of the spawning season. By increasing their spawning season, redeye round herring and sardine decrease their batch fecundity, therefore spawning fewer eggs per batch, but they can spawn more batches per year in a longer spawning season. This means that of all three species, redeye round herring would spawn more eggs per year than anchovy and sardine, even though they have the smallest relative batch fecundity.

Environmental effects on growth

Changing sea surface temperatures are likely to result in ecological changes in productivity patterns and shifts in distribution of small pelagic fishes (Fréon *et al.* 2009, Mhlongo *et al.* 2015). There is evidence of long-term changes in the physical characteristics of the southern Benguela, with a trend of cooling of 0.55°C per decade being recorded in coastal waters mainly on the west and south coasts of South Africa over a 25 year period from the 1980s (Rouault *et al.* 2010, Blamey *et al.* 2015, Mhlongo *et al.* 2015, Augustyn *et al.* 2017). There also has been a decreasing trend in chlorophyll *a* in the entire southern Benguela of 0.5 mg.Chl.m⁻³ per decade (Demarcq 2009, Mhlongo *et al.* 2015). Thus, future change in the environment could lead to a decrease in the amount of food available to small pelagic fishes. The functional response (*f*) represents energy assimilated from the ingestion of food as a function of food density (Pecquerie 2008). Redeye round herring and sardine are serial spawners, a characteristic shared by anchovy in the Southern Benguela. This spawning strategy is very intensive, since it requires almost continual food ingestion by organisms (Roel & Melo 1990, Melo 1994a, Akkers *et al.* 1996, Richardson *et al.* 1998), but to different degrees between the three species. The DEB model indicated that redeye round herring required an *f* value of not less than 0.7 to reach sexual maturity, whereas sardine required a functional response *f* value of not less than 0.8 (Table 3.5, Figure 3.1). As the functional response (*f*) is the ingestion rate of the fish as a fraction of the maximum possible ingestion of an individual of a given size, this indicated that, of the three small

pelagic species, sardine needed to ingest larger fractions of food than anchovy and redeye round herring to survive. The DEB models also show that, under unfavourable food conditions, both redeye round herring and sardine produced fewer egg batches in their lifetime; therefore, decreased food availability can lead to a decrease in fecundity.

According to DEB theory, redeye round herring and sardine would show little variability in their asymptotic sizes for maximum length and weight for different water temperatures in constant food environments (Pecquerie 2008). This was reflected, to a certain extent, in the sardine model where results indicated similar maximum length but not weight over temperatures between 14 and 26°C (Table 3.7). Temperature affected the growth rates of juvenile sardine, with slower growth rates at colder temperatures causing fish to reach asymptotic length and weight later than at warmer temperatures (Figure 3.2d-e). However, this pattern did not hold for redeye round herring, which had very different maximum lengths and weights at different temperatures, even though they did show the fastest growth rates at warmer temperatures (Table 3.7, Figure 3.2a-b). This difference may be due to redeye round herring having a quite different von Bertalanffy growth curve than either anchovy or sardine. Redeye round herring do not completely reach an asymptotic length before the end of their lifespan and have fast growth rates between ages two and three years, before growth slows down again. In contrast, anchovy and sardine have fast growth in the first year after which it slows down. The DEB models also showed that redeye round herring and sardine produced fewer egg batches at cooler temperatures. Small pelagic fish experience a decrease in activity at colder temperatures because of a decrease in metabolic demands (Hunter 1977). This was reflected by the decrease in the maximum assimilation rate $\{\dot{p}_{Am}\}$ and volume-specific cost for maintenance $[\dot{p}_M]$, which decreased with decreasing temperature (Table 3.6).

Redeye round herring preferred water with sea surface temperatures between 10 and 20°C for spawning (Roel & Armstrong 1991). The DEB model for redeye round herring found that they would produce between 21 and 170 egg batches between 12 and 20°C, giving an average of between 19 and 34 egg batches a year. This is close to estimates by Roel and Melo (1990) of an average of 34 egg batches a year. Mhlongo *et al.* (2015) investigated egg occurrence in the Benguela over a 21-year period and found that sardine eggs occurred in temperatures ranging from 16 to 22°C, with the main sea surface temperatures for spawning between 17.0-17.3°C and 18.0-19.5°C. According to the DEB model, sardine would produce between 118 and 209 egg batches between 16 and 20°C, giving an

average of between 15 and 25 egg batches a year, which is close to estimates by Akkers *et al.* (1996) of around 25 egg batches a year.

Incubation studies have shown that redeye round herring were successfully hatched at temperatures between 11.5 and 20.5°C (O'Toole & King 1974). Sardine, in contrast, could tolerate temperatures between 11 and 22°C for spawning but at temperatures colder than 13°C larvae failed to develop a functional jaw or pigmented eyes (King 1977). Thus, even if sardine produced 60 egg batches at 12°C they would not be viable, unless the eggs were moved into temperatures warmer than 13°C during development.

Increases in temperature could lead to increased growth rates, which could lead to an increase in fecundity, since larger females are known to have higher batch fecundity and also more prolonged spawning seasons (Le Clus 1988, Le Clus 1989), and this was shown to be the case for redeye round herring and sardine. Slower growth rates at colder temperatures and, in turn, decreased metabolic demands, would likely lead to greater predation exposure during larval phases (Hunter 1977). The effects of temperature and feeding on the redeye round herring and sardine models will be dealt with in more detail in Chapter 4.

Starvation

Starvation simulations showed positive and then negative relationships between temperature and survival of both redeye round herring (Figure 3.3a) and sardine (Figure 3.3b) (aged five years and younger), with survival first increasing and then decreasing over the temperature range assessed. Sardine older than five years have a negative relationship between temperature and survival. That temperature affected rates in the DEB models is illustrated by an increase in the volume-specific cost for maintenance [$\dot{p}_M$] at warmer temperatures. During starvation, the maintenance costs to both redeye round herring and sardine could only be paid by utilizing the reproductive buffer (E_R). Therefore, survival decreased at warmer temperatures because high maintenance costs depleted the reproductive buffer faster than at colder temperatures. In general, redeye round herring survived longer without food than sardine, probably because they had lower maintenance costs than sardine.

There was a positive relationship between survival and the functional response (f) when moving from a food-unlimited to a food-limited environment in both redeye round herring (Figure 3.4a) and sardine (Figure 3.4b). Higher f values resulted in faster ingestion rates, making more food available to initially build the reproductive buffer. This, in turn, resulted in increased reserves in the reproductive buffer for the payment of maintenance during atresia. According to the DEB model results, redeye round herring could survive for longer (65-100 days at a functional response of 0.7) at lower functional response values than sardine (3-6 days at a functional response of 0.8).

It is worth noting that the number of days that redeye round herring and sardine can survive in the model are quite high, which may be due to the spawning condition $E_{GAM} \geq 2 \cdot E_{batch}^*$, since this condition means that even if the fish spawn there will still be enough energy in the reproductive buffer for a second spawn. In real life conditions, fish would probably spawn when they have enough energy in the reproductive buffer for one batch of eggs, thereby resetting the reproductive buffer to zero after each spawn. It also assumes that fish would have unlimited food available every day of their lifecycle in a constant temperature environment, which could also be skewing the results.

Roel and Melo (1990) observed incidences of atresia year-round for redeye round herring. For unlimited initial food intake ($f = 1.0$) at 20°C (the reference temperature), redeye round herring could survive between 96 and 154 days (for 2 to 4 year). when feeding ceased, whereas sardine could only survive between 22 and 48 days. Therefore, if sardine stopped eating at the start of the spawning season in August, there would be atretic ovaries in September. This matches well with observations by Akkers *et al.* (1996), who found high incidences of atretic Stage 3 ovaries in sardine in September.

Both redeye round herring and sardine showed higher survival rates in older fish under differing temperatures (Figure 3.3) and functional responses (Figure 3.4). This is due to larger fish having a larger reproductive buffer, which would allow them to pay maintenance for longer during atresia.

Conclusion

Environmental factors such as temperature and food availability influenced growth, reproduction, and survival of redeye round herring *E. whiteheadi* and sardine *S. sagax* in the Southern Benguela. Comparisons with the anchovy model (Chapter 2) showed an overall difference in the biological

characteristics and bioenergetic strategies between these three small pelagic species in the Southern Benguela. The biggest difference between the three was related to their spawning strategy and growth rates. Redeye round herring displayed lower investments than anchovy and sardine in reproductive storage capacity (κ) and assimilation rates $\{\dot{p}_{Am}\}$. The reserve storage capacity of redeye round herring was higher than that of anchovy but lower than sardine, and they had much higher structural growth costs than anchovy but less than sardine. Sardine displayed lower investments than anchovy in reproductive reserve storage capacity, but higher maintenance costs, assimilation rates, reserve storage capacity $[E_m]$ and cost for structural growth $[E_G]$.

Comparisons between sardine in the Southern Benguela and the Bay of Biscay showed that parameter values differed between the two regions, even for species of the same genus, because they are influenced by temperature and food availability. The same general trend in differences between anchovy and sardine held for both the Southern Benguela and Bay of Biscay. For example, the reserve storage capacity was higher in sardine than anchovy in both regions. The one difference was that the fraction allocated to growth and maintenance was smaller in anchovy in the Benguela than in sardine. Thus, even though the core parameters are not transferable between regions, this apparent general trend could be helpful in making parameter estimation easier and deepening understanding of the life history strategies of different fishes in different environments.

Chapter 4 Investigating the trade-offs between temperature and food in three life stages of small pelagic fishes in the Southern Benguela

Abstract

Climate change is influencing ecosystem productivity in the Benguela upwelling system by causing coastal cooling in some areas and warming in others. Anchovy, redeye round herring and sardine are short-lived fishes that are quick to respond to environmental variability, with temperature and food playing important roles in the development of early life stages and reproduction in adults. Coastal cooling and intensified upwelling on the west and south coast of South Africa provide increased nutrients and better food environments for small pelagic fishes, thereby increasing larval and juvenile growth rates, while concomitant cool water associated with upwelling decreases growth rates and affects reproductive output in adults. This study aimed to investigate the trade-offs between temperature and food effects on the growth and reproductive output of these three small pelagic fish species in the Southern Benguela. Dynamic energy budget (DEB) models developed for anchovy, redeye round herring and sardine were used to model the effects of changing environments by comparing growth during the larval and recruit stages and reproductive output during the adult stage under different temperature and food scenarios. Both temperature and food affected growth rates of small pelagic fish. All three species had slower growth rates at colder temperatures within their specified temperature range. However, whereas larvae showed a trade-off between temperature and feeding effects, with slow growth rates due to cool temperatures counterbalanced by fast growth rates from enhanced food availability, this trade-off was not apparent in recruits and adults. Feeding conditions had the largest influence on growth rates of recruits and reproductive output of adults, with faster growth rates and more egg batches produced in good food conditions. Small pelagic fish produced more egg batches if good recruitment conditions were followed by good adult feeding conditions. Understanding small pelagic fish responses to environmental changes provides important information on the variable population dynamics of these fish species, hence providing insight and helping to predict the impacts of climate change on these ecologically and economically important species.

Introduction

Understanding the growth of small pelagic fishes and their physiological responses to environmental factors, such as temperature and food, is fundamental in understanding biological processes that link population dynamics to climate variability (Takasuka 2018, Peck *et al.* 2021). Feeding connections in marine organisms like small pelagic fish are determined by both the species and their life stage, since inter-specific differences in trophic ecology are observed (van der Lingen *et al.* 2009, Garrido & van der Lingen 2014), and these fishes span a range of sizes throughout their life cycle and will typically change their diet as they grow (Moloney *et al.* 2011). Temperature and food play a major role during the early life stages of small pelagic fish in determining their growth rate and in turn influencing when larvae reach metamorphosis (Hunter 1977, Takasuka 2018). Cold temperatures can lead to increased food resources for the larvae (e.g., in upwelling systems), allowing them to reduce their metabolic demand by decreasing larval activity (Hunter 1977, Peck *et al.* 2013, Garrido *et al.* 2015, Somarakis *et al.* 2019). However, colder temperatures result in slower growth and development rates, leading to increased exposure to predation during the larval stage (Hunter 1977, Volkoff & Rønnestad 2020, van Denderen *et al.* 2020). Recruitment success is affected by physical processes such as upwelling intensity, wind speed, turbulence, and water temperature, and biological processes like food availability (Cury & Roy 1989, Katara 2014, Takasuka 2018, Peck *et al.* 2021). Temperature (as a physical process) and food (as an energy gain process) also affect reproductive parameters and outputs in adult small pelagic fish (Peck *et al.* 2013, Garrido *et al.* 2015, Takasuka 2018, Volkoff & Rønnestad 2020).

Considerable research has been conducted in the Benguela ecosystem, both in laboratories and in the field, to study the feeding ecology of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) (van der Lingen *et al.* 2006b). There also has been limited research on the feeding ecology of redeye round herring (*Etrumeus whiteheadi*) (Wallace-Fincham 1987, Mketsu 2008). Anchovy are intermediate mixed feeders, preferentially particulate-feeding on larger zooplankton like calanoid copepods and euphausiids (particles > 0.7 mm) and filter-feeding on small zooplankton and phytoplankton (particles 0.20 - 1.5 mm) (James 1988b, van der Lingen *et al.* 2006b). Redeye round herring are particulate-feeders, preferring large zooplankton like large calanoid copepods, euphausiids and decapods, and fish eggs (particles 0.5 - 2.0 mm) (Wallace-Fincham 1987, Mketsu 2008). Sardine are also intermediate mixed feeders, using non-selective filter-feeding to feed on small phytoplankton (like dinoflagellates and diatoms) and zooplankton (like crustacean eggs, cycloid

copepods and calanoid copepods) (particles 0.01 - 1.2 mm). In addition, sardine can switch to particulate-feeding for particles > 1.2 mm at reduced food concentrations, although they filter-feed on large particles when present in high concentrations (van der Lingen 1994, van der Lingen *et al.* 2006b, van der Lingen *et al.* 2009). Young life stages of small pelagic fish also show this size-based apportioning of zooplankton in their diet (Louw *et al.* 1998, van der Lingen *et al.* 2009). Unfortunately, little to no information is available at present on larval small pelagic fish diet in the southern Benguela but studies on anchovy/anchoveta and sardine larvae in the California, Humboldt and Peruvian upwelling systems have shown that, after reaching about 9 mm length, anchovy/anchoveta start to prefer larger prey than sardine larvae (Cole 1999, van der Lingen *et al.* 2009). Small pelagic fish juveniles shoal together in the southern Benguela, and studies have found that, even though these juveniles consume similar types of food like copepods, crustacean eggs and nauplii, juvenile sardine ingest smaller prey items than juvenile anchovy if a large range of prey sizes are available (Louw *et al.* 1998, van der Lingen *et al.* 2009).

Studies on changing climate in the Benguela between 1982 and 2009 showed a cooling trend on the South African west coast which falls in the southern Benguela, and a cooling trend for the south coast of South Africa on the Agulhas Bank (although south coast data requires further investigation) (Rouault *et al.* 2010, Blamey *et al.* 2015). The cooling trends are consistent with an intensification of upwelling along the Agulhas Bank on the south coast and increased upwelling in the southern Benguela (Lamont *et al.* 2018). Intensified physical forcing, such as winds favourable to upwelling, would increase the rate of upwelling, which would cause turbulence in the upper layers of the water column and faster transport of surface waters offshore, causing intermittent mixing in the water column (Bakun *et al.* 2015).

There are two main food-based hypotheses that are applicable to small pelagic fishes; 1) the optimal environmental window hypothesis (applying generally to all small pelagics within upwelling ecosystems), and 2) the trophic dissimilarity hypothesis (species-specific hypothesis applying to anchovy and sardine), which arguably falls within the optimal environmental window. The “optimal environmental window” hypothesis was developed by Cury & Roy (1989) to explain recruitment dynamics of clupeid fish, in the context of physical processes brought about by wind-induced upwelling (Figure 4.1) (Cury & Roy 1989, Cole & McGlade 1998). This hypothesis states that there is a dome shaped relationship between upwelling and recruitment. The recruitment success of small pelagic fish increases with upwelling intensity, when cold nutrient rich water is brought to the surface,

increasing plankton production and food availability for small pelagic fish. Recruitment success, however, decreases when upwelling intensity gets too high, since too much turbulence disrupts their feeding success and increases offshore advection, leading to high losses of eggs and larvae (Cury & Roy 1989, Takasuka 2018). There is evidence of this optimal environmental window operating for both anchovy and sardine in the southern Benguela (Waldron *et al.* 1997, Skogen 2005).

The “trophic dissimilarity” hypothesis was developed by van der Lingen *et al.* (2006a, 2009) to show differential feeding strategies between anchovy and sardine, under variable upwelling intensity in the Benguela (Figure 4.2). Under intermittent mixing conditions, as occur during upwelling, nutrients are brought to the surface periodically, enriching the surface waters and lowering the water temperatures to between 12 and 15°C (van der Lingen *et al.* 2006b). These mixed surface waters promote the growth of high biomass phytoplankton populations dominated by large chain-forming diatoms (Figure 4.2) (Mitchell-Innes & Pitcher 1992), which in turn support the enhanced growth rates of

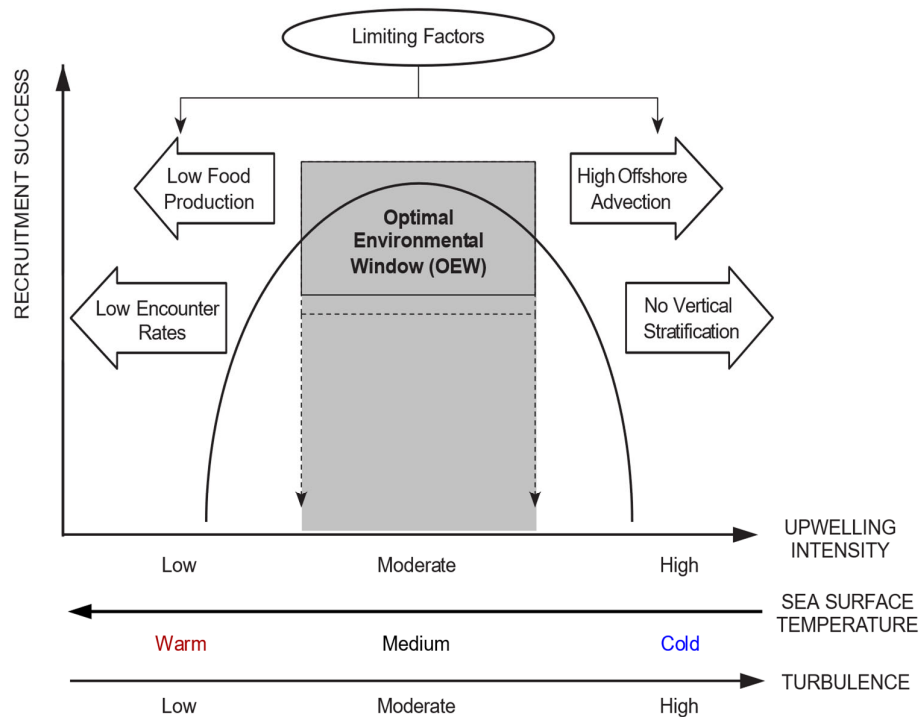


Figure 4.1 Schematic of the optimal environmental window hypothesis developed by Cury & Roy (1989) to show how coastal upwelling influences clupeid recruitment success. Adapted and redrawn from Cole & McGlade (1998).

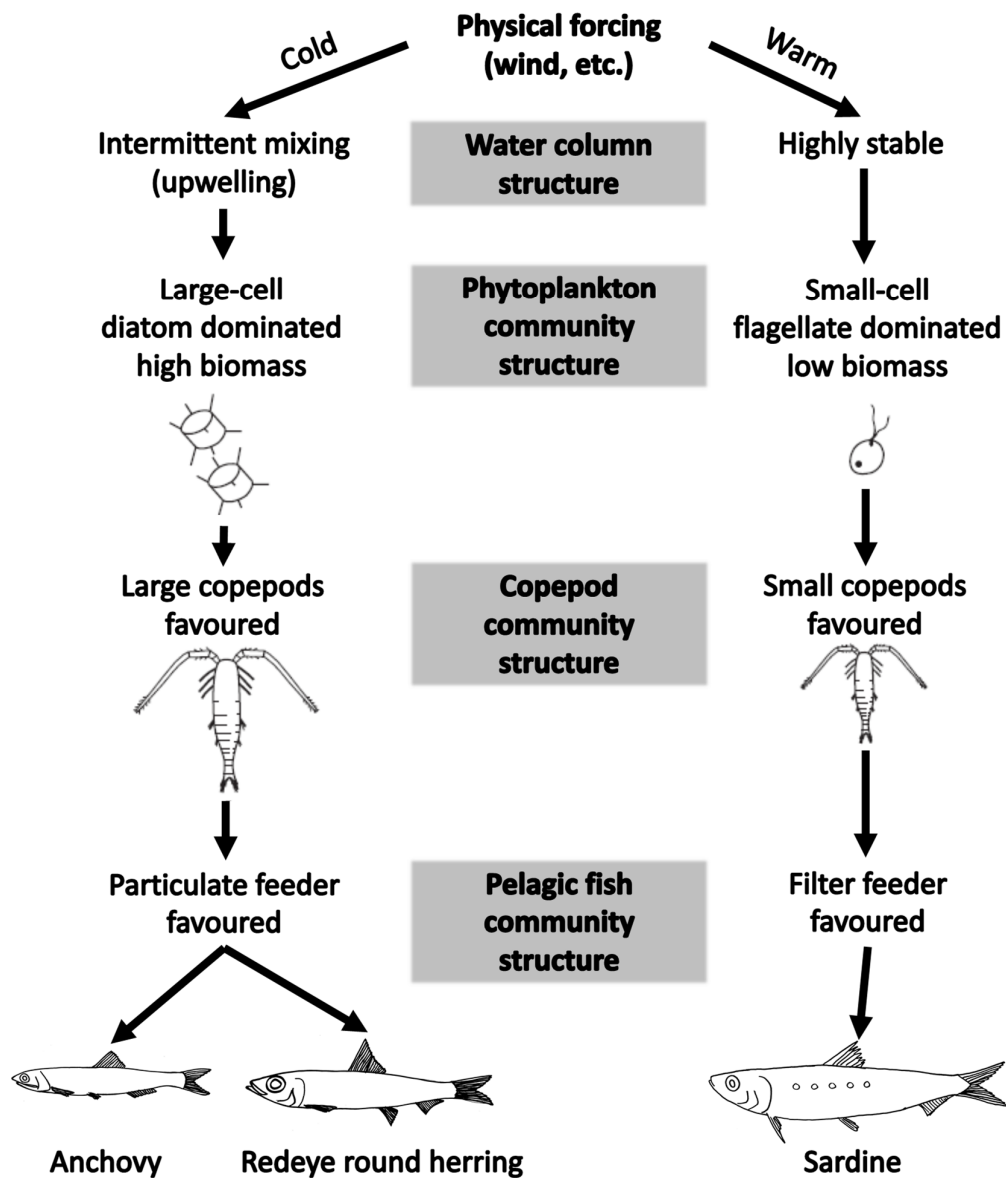


Figure 4.2 A conceptual framework illustrating the trophic dissimilarity hypothesis for anchovy and sardine, with redeye round herring included. Physical forcing influences phytoplankton and differential feeding of zooplankton, differentially favouring anchovy, redeye round herring or sardine in the Benguela. Redrawn from van der Lingen *et al.* (2006b) and adapted by adding redeye round herring to the anchovy partitioning side.

large copepods like *Calanoides* and *Calanus* (van der Lingen *et al.* 2006b). Under a cool upwelling regime, there is increased abundance of large prey items to small pelagic fish communities favouring size-selective particulate-feeders like anchovy (van der Lingen *et al.* 2006b) and redeye round herring (Wallace-Fincham 1987, Mketsu 2008) (Figure 4.2). During the quiescent phase between upwelling events or when upwelling does not occur, the water column is stable, water temperatures are warm ($> 15^{\circ}\text{C}$), and nutrients are limited in the upper layers, allowing small nanoflagellate populations to thrive at low biomass levels (Figure 4.2) (Mitchell-Innes & Pitcher 1992). These small-cell phytoplankton communities support small copepods that favour non-selective filter-feeders like sardine (Figure 4.2) (van der Lingen *et al.* 2006b).

The aim of this chapter was to investigate the trade-offs between temperature and food effects on three life history stages (larvae, juveniles, and adults) of anchovy, redeye round herring and sardine. The objectives for this chapter were to investigate the effects of: 1) temperature; 2) feeding conditions; and 3) a combination of temperature and feeding conditions on: a) the growth rate of larval small pelagic fish, by assessing how long it would take to reach metamorphosis; b) the growth rates of recruits, by investigating the time taken to reach recruitment age; and c) the effects of these conditions on the growth and reproductive output of adults. The null hypothesis to be tested is that in a cool environment with increased upwelling and more large-celled prey items, anchovy and redeye round herring populations would be favoured whereas sardine, which thrive in warm stable environments, would be constrained.

The results of this study could be incorporated into population and ecosystem models and may be useful for generating insights and projections of the effect of short-term environmental change (including food availability) arising from environmental variability as well as longer-term change anticipated from climate change, on the long-term population dynamics of these small pelagic fishes.

Methods

4.1 Modelling life stages

The dynamic energy budget (DEB) models developed for anchovy in Chapter 2, and for redeye round herring and sardine in Chapter 3, were used to model the growth and reproduction of each species separately under different temperature and feeding scenarios using the model equations given in Table 2.1. The life cycle parameters for anchovy are given in Table 2.2 and the anchovy DEB parameters

are given in Tables 2.4 - 2.6, whereas those for redeye round herring and sardine are given in Tables 3.1 - 3.4. Model code used for all experiments for anchovy can be found at Groenewald *et al.* (2021a), redeye round herring at Groenewald *et al.* (2021b) and sardine at Groenewald *et al.* (2021c).

For this study, three life history stages were defined for each of the three small pelagic fish species: 1) the larval stage, between length at birth (L_b) and length at metamorphosis (L_j), 2) the recruit stage, between length at metamorphosis and length at puberty (L_p) (when small pelagics reach sexual maturity), and 3) the adult stage between length at puberty and the end of the lifespan of the fish (a_m).

4.2 Description of experiments

4.2.1 Temperature experiments

The aim of the temperature experiments was to investigate the effects of differing water temperatures ($^{\circ}\text{C}$) on each of the three life history stages in all three species of small pelagic fish. The temperature ranges over which small pelagic fishes (all three species) in each life stage are found in the Southern Benguela have been documented (D. Yemane, DFFE, personal communication 2020, October 16), and the temperature at which each species is most abundant in that range was defined as the “natural” temperature for these experiments (Table 4.1). This natural temperature was taken as a baseline for ‘ideal growth’ during that life stage for each of the three small pelagic species. For each life stage the natural temperature was decreased by 2.0°C in 0.5°C increments to simulate colder temperatures and increased by 2.0°C in 0.5°C increments to simulate warmer temperatures (Table 4.1).

All these temperature experiments had a functional response (f) of 1.0 to simulate good food conditions. The flow of the experiments is illustrated in Figure 4.3. For recruit experiments the growth during the preceding larval stage took place at the larval natural temperature, but once the length at metamorphosis was reached the temperature scenarios for recruits were used. For the adult experiments, growth during the larval and recruit stages took place at larval and recruit natural temperatures, but once length at puberty was reached the temperature scenarios for adults were used for the remainder of the life cycle of the fish.

Table 4.1 Temperature (°C) and functional response (*f*) values used in the temperature, food and combined temperature/food experiments illustrated in Figures 4.3 - 4.5 for each life stage of the three small pelagic fishes. Size range is the length of each species in that stage (cm). Natural is the temperature where fish are most abundant, cold (blue) is the cold range and warm (red) is the warm range for each species. Bad (orange) and good (green), respectively, represent bad/limiting and good/unlimiting food environments.

Life Stage	Size Range (cm)	Temperature (°C)			Functional response (f)	
		Natural	Cold (C)	Warm (W)	Bad (B)	Good (G)
ANCHOVY						
Larvae	0.0-3.5	20.5	18.5-20.0	21.0-22.5	0.6	1.0
Recruits	3.6-8.0	15.5	13.5-15.0	16.0-17.5	0.6	1.0
Adults	8.1-16.0	19.5	17.5-19.0	20.0-21.5	0.6	1.0
REDEYE ROUND HERRING						
Larvae	0.0-3.5	17.5	15.5-17.0	18.0-19.5	0.7	1.0
Recruits	3.6-12.0	16.5	14.5-16.0	17.0-18.5	0.7	1.0
Adults	12.1-20.4	19.5	17.5-19.0	20.0-21.5	0.7	1.0
SARDINE						
Larvae	0.0-3.2	21.0	19.0-20.5	21.5-23.0	0.8	1.0
Recruits	3.3-17.0	15.5	13.5-15.0	16.0-17.5	0.8	1.0
Adults	17.1-23.0	21.5	19.5-21.0	22.0-23.5	0.8	1.0

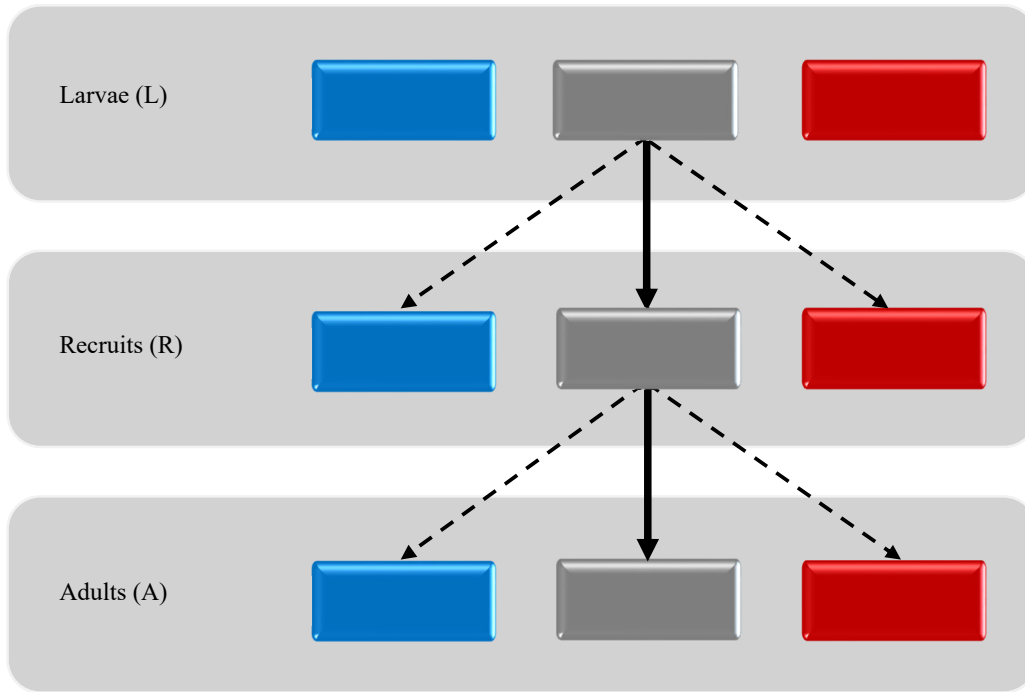


Figure 4.3 Flow diagram in the temperature experiments for each stage of anchovy, redeye round herring and sardine. Grey represents the natural temperature where the species are most abundant; blue represents the cooler temperatures and red represents the warmer temperatures given in Table 4.1.

4.2.2 Food experiments

The aim of the food experiments was to investigate the effects of the food environment, as a function of the scaled functional response (f), on each of the life history stages in all three species of small pelagic fish. A good unlimited/food-rich condition is represented by $f = 1.0$ (Table 4.1). DEB models of small pelagic fish indicated that anchovy required a functional response $f \geq 0.6$, redeye round herring required $f \geq 0.7$ and sardine required $f \geq 0.8$ to reach sexual maturity and be able to reproduce during limited food conditions, hence these values were used to represent the food-limited scenarios (Table 4.1). The water temperature ($^{\circ}\text{C}$) for each stage was set at the natural temperature from the temperature experiments.

The flow of the experiments is illustrated in Figure 4.4. There were two experiments for each species in the larval stage i.e., bad larval limited/food-poor condition (BL) and good unlimited/food-rich

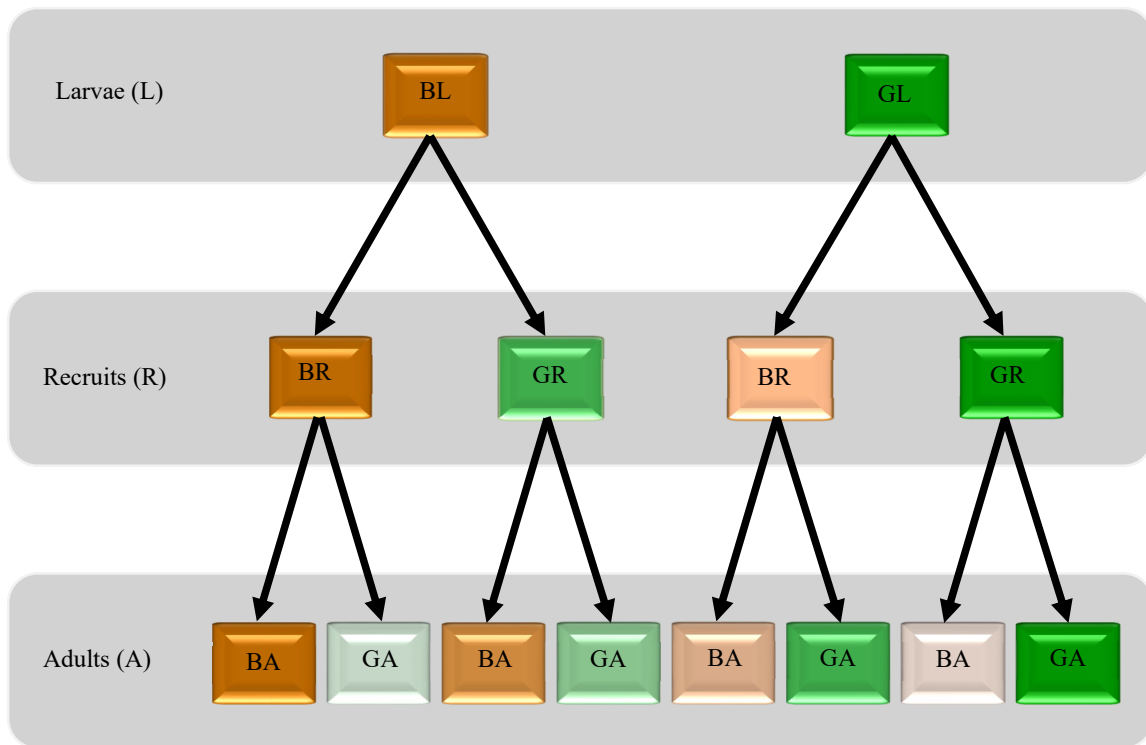


Figure 4.4 Flow diagram for the food experiments for each life stage of anchovy, redeye round herring and sardine. Orange represents a limiting bad food environment (B), and green represents an unlimited good food environment (G) (Table 4.1). The code in each block represents food environments for each stage e.g., BL = bad larval food environment and GL = good larval food environment.

condition (GL). There were four experiments in the recruit stage; each experiment takes the letters of the previous condition (larvae) and current condition (recruits), e.g., a combination of BLGR would simulate recruit growth after a bad larval food condition (BL) in a good recruit food condition (GR). There were eight experiments during the adult stage, each simulating different larval and recruit conditions and the adult growth response to those conditions, e.g., a combination of BLGRGA would simulate adult growth after a bad larval food condition (BL) and good recruit food condition (GR) during a good adult food condition (GA).

4.2.3 Combined temperature/food experiments

The aim of these experiments was to investigate the combined effects of temperature (°C) and food on each of the life history stages for all three small pelagic fish species. In these experiments the

coolest (C) and warmest temperatures (W) in the temperature range (Table 4.1) for each life stage of each species were taken in combination with bad/limiting food conditions (B) and good/unlimiting food environments (G) under different scenarios.

The flow of the experiments is illustrated in Figure 4.5. There were four experiments for each species in the larval stage i.e., bad larval food conditions at the coldest temperature (CBL), good larval food conditions at the coldest temperature (CGL), bad larval food conditions at the warmest temperature (WBL), and good larval food conditions at the warmest temperature (WGL). There were 16 experiments in the recruit stage; each experiment takes the letters of the previous condition (larvae) and current condition (recruits), e.g., WBLCGR would simulate recruit growth after a warm bad larval food conditions (WBL) in a cool good recruit food condition (CGR). There were 64 experiments during the adult stage each simulating different larval and recruit conditions and the adult growth response to those conditions, e.g., WBLCGRCGA would simulate adult growth after a warm bad larval food condition (WBL) and cool good recruit food condition (CGR) during a cool good adult food condition (CGA).

Results

4.2.1 Temperature experiments

Larval anchovy and sardine occur most frequently in warmer waters than redeye round herring (Table 4.1). Temperature affected the growth rates of larvae of anchovy, redeye round herring and sardine (Figure 4.6a-c). All three species reached their length at metamorphosis (Figure 4.6a-c) and their weight at metamorphosis (Figure 4.6d-f) faster at warmer temperatures. Sardine larvae reached their age at metamorphosis faster (41-63 days) than anchovy (53-86 days) and redeye round herring (151-254 days). (Figure 4.6g-i). Anchovy larvae took 6-7% longer and quicker to reach age at metamorphosis for every 0.5°C cooling and warming relative to their natural temperature. Larvae of redeye round herring took 6-7% longer and quicker for every 0.5°C cooling and warming, and sardine larvae took 5-6% longer and 4-7% quicker for every 0.5°C cooling and warming, respectively, relative to their natural temperatures.

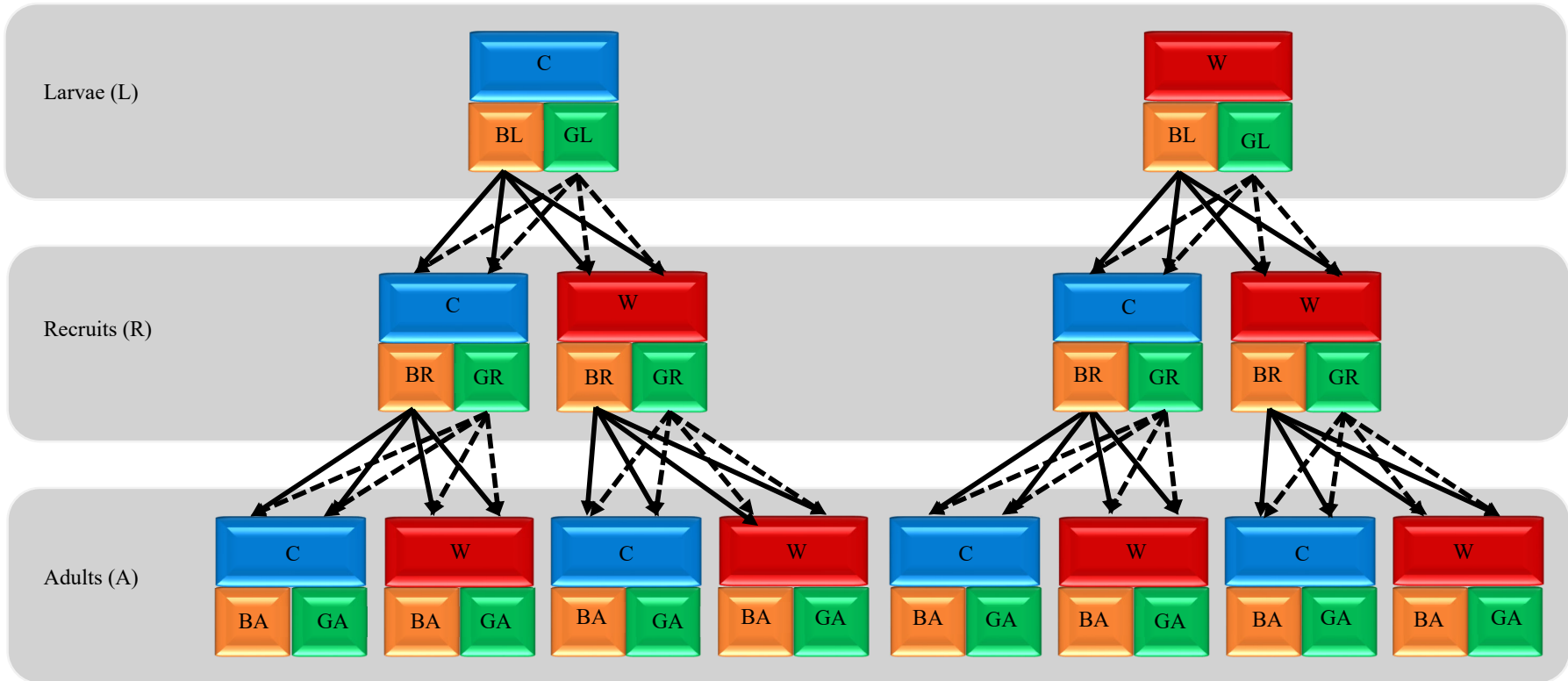


Figure 4.5 Flow diagram for combined temperature/food experiments for each stage of anchovy, redeye round herring and sardine. Blue represents coldest (C) and red represents warmest (W) temperatures, orange represents a bad/limiting food environment (B), and green represents a good/unlimiting food environment (G) (Table 4.1). The code in each block represents food environments for each temperature combination in each stage e.g., CBL = cool bad larval food environment and WGL = warm good larval food environment.

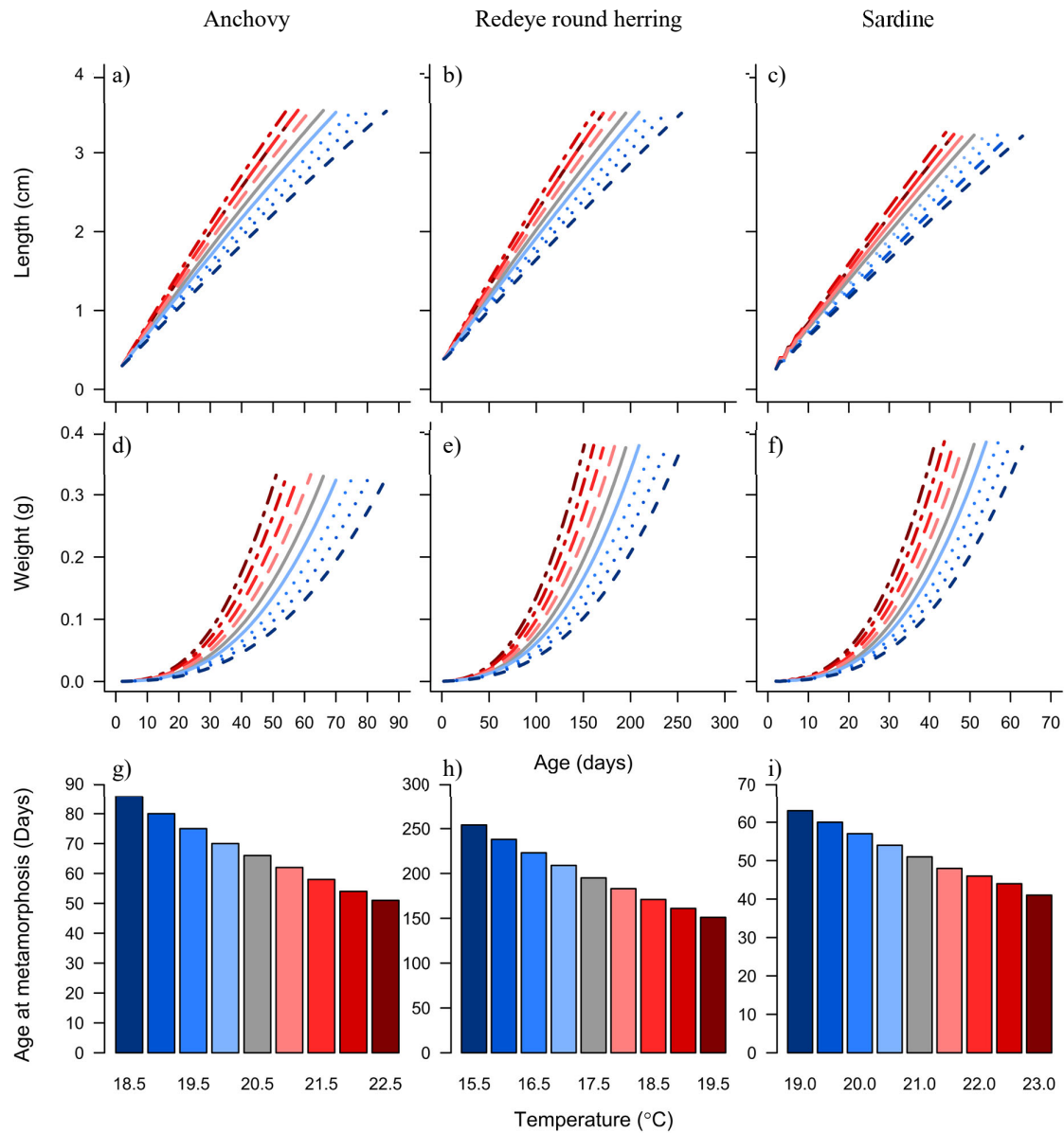


Figure 4.6 The effect of water temperature (°C) on the larval stages of anchovy (left panel), redeye round herring (central panel), and sardine (right panel). (a-c) Length (cm) at age (days), (d-f) weight (g) at age, and (g-i) age at metamorphosis (days) for larval small pelagic fishes. The nine temperature experiments are scaled to the natural temperature (grey), with colours from blue (coldest) to red (warmest). The temperature values for each species are shown in the bottom row.

Small pelagic recruits frequently occur in similar temperatures in the environment and hence have similar natural temperatures (Table 4.1). Variations in temperature affected recruit growth rates (Figure 4.7), with all three species reaching their length (Figure 4.7a-c) and corresponding weight at recruitment (Figure 4.7d-f) faster at warmer temperatures. Anchovy reached their age at recruitment (0.7-1.1 years) faster than the other species (Figure 4.7g), and redeye round herring took the longest (2.4-3.8 years, Figure 4.7h). Sardine took between 2.0 and 3.0 years (Figure 4.7i) to reach their age at recruitment. Anchovy recruits took 6% longer and 5-6% quicker to reach their age at recruitment, respectively, for every 0.5°C cooling and warming relative to the natural temperature of 15.5°C. Redeye round herring and sardine recruits took 6% longer and 5-6% quicker to reach their age at recruitment, respectively, for every 0.5°C cooling and warming relative to the natural temperatures of 16.5°C and 15.5°C, respectively.

Adult anchovy and redeye round herring are most abundant in cooler water, with natural temperatures of 19.5°C, while sardine occur in warmer water with a natural temperature of 21.5°C. Temperature affected the growth and condition of adult small pelagic fishes (Figure 4.8). In adult anchovy and sardine, fish reached their asymptotic maximum length (Figure 4.8a & c) and weight (Figure 4.8d & f) faster at warmer temperatures. Redeye round herring grew to their largest maximum lengths (Figure 4.8b) and weights (Figure 4.8e) at warmest temperatures. Temperature had little effect on the total number of egg batches produced by small pelagic fishes, with all three species producing fewer eggs at colder temperatures in the spectrum.

4.2.2 Food experiments

Food conditions affected the growth rates of larval anchovy, redeye round herring and sardine (Figure 4.9). Small pelagic larvae in a good food conditions (GL) with unlimited food availability reached their maximum length at metamorphosis (Figure 4.9a-c) faster than in bad food conditions (BL) with limited food availability. The larvae also attained a larger maximum weight at metamorphosis in a GL condition (Figure 4.9d-f). The age at metamorphosis was reached faster in during GL condition, with anchovy reaching their age at metamorphosis 32 days faster, redeye round herring 75 days faster, and sardine 11 days faster than in a BL condition (Figure 4.9g-i).

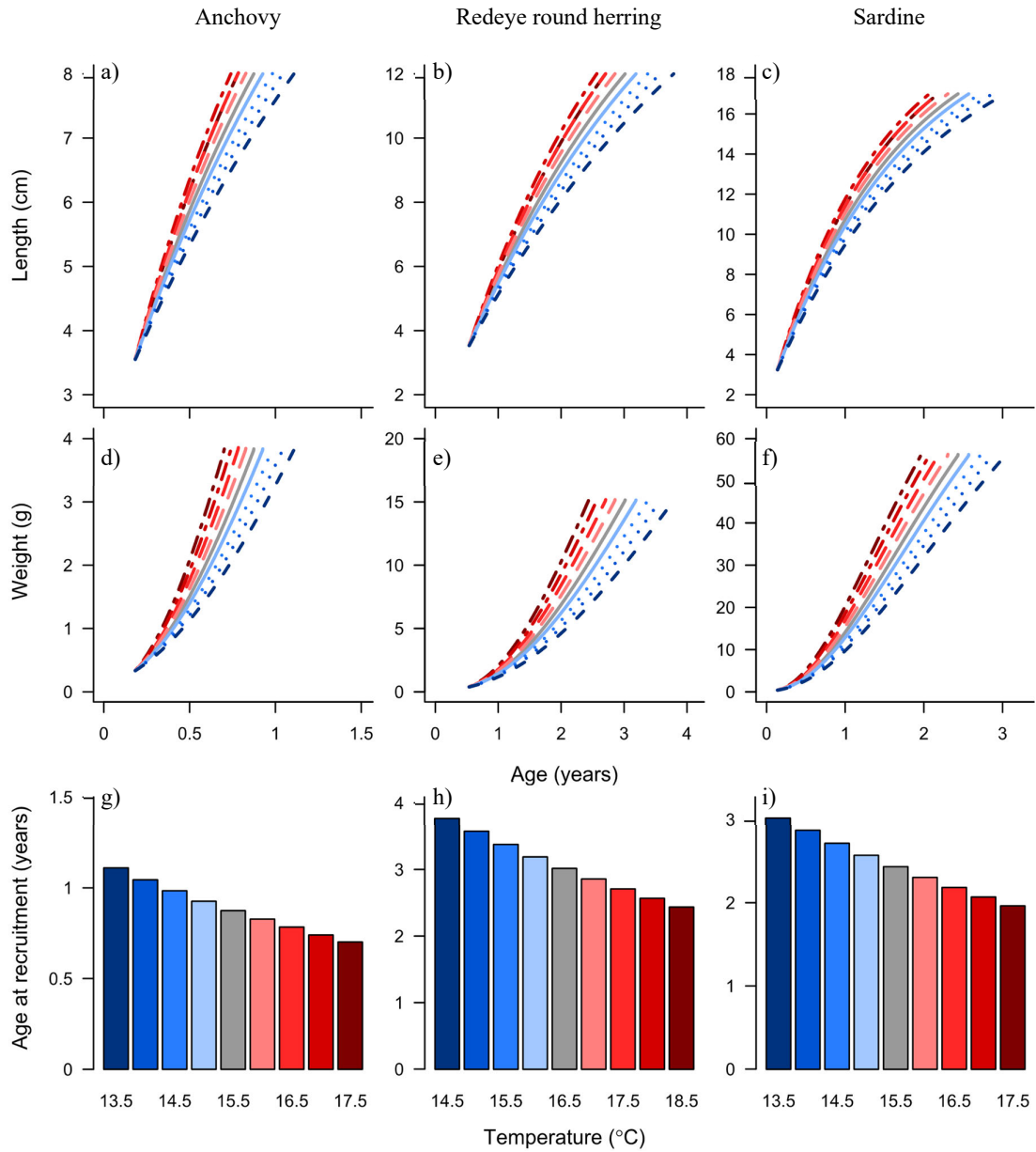


Figure 4.7 The effect of water temperature (°C) on the recruitment stages of anchovy (left panel), redeye round herring (central panel), and sardine (right panel). (a-c) Length (cm) at age (years), (d-f) weight (g) at age, and (g-i) age at recruitment (years) for recruit small pelagic fishes. The nine temperature experiments are scaled to the natural temperature (grey), with colours from blue (coldest) to red (warmest). The temperature values for each species are shown in the bottom row.

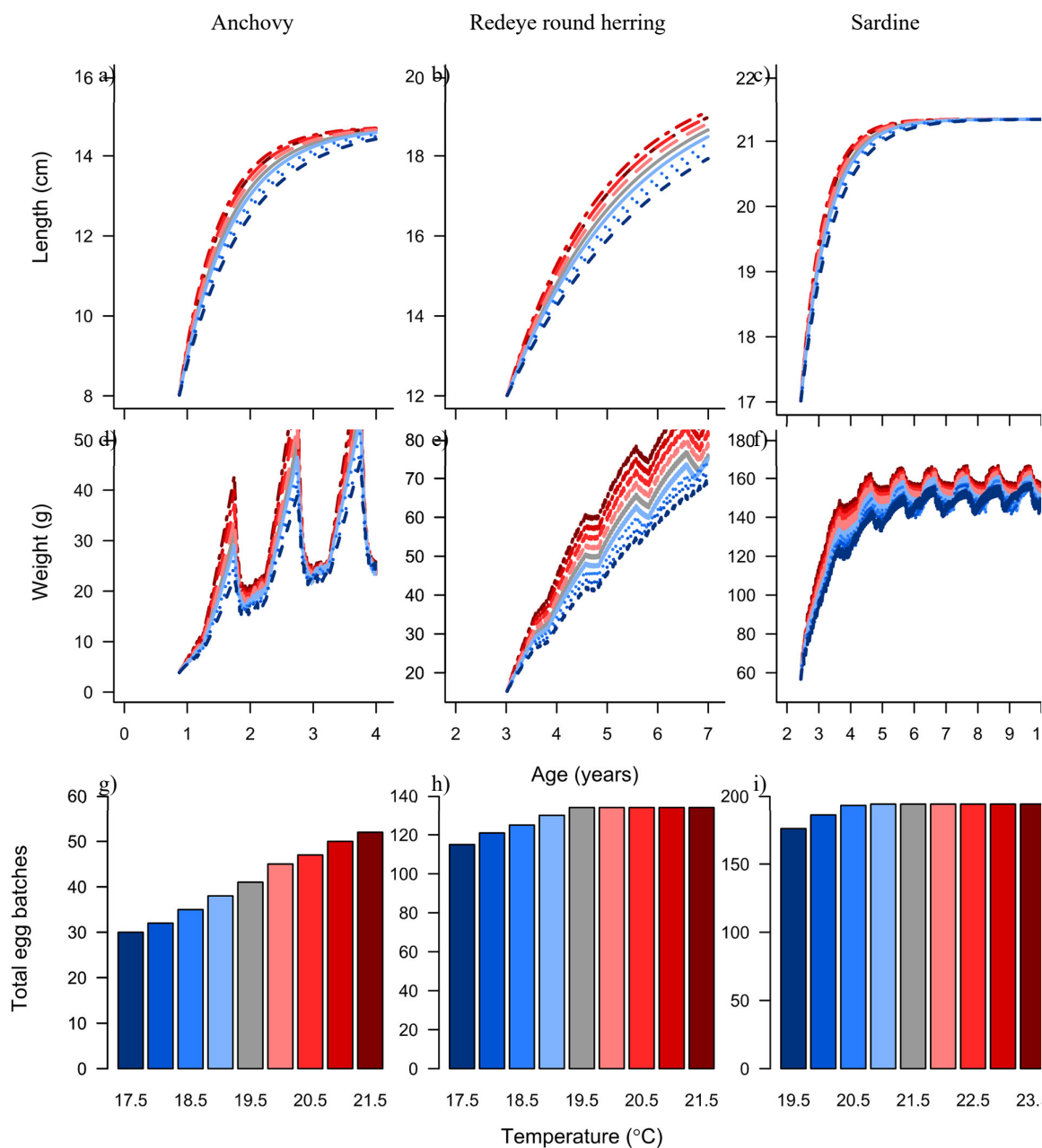


Figure 4.8 The effect of water temperature on adult anchovy (left panel), redeye round herring (central panel), and sardine (right panel). (a-c) Length (cm) at age (years), (d-f) weight (g) at age (years), and (g-i) the total number of egg batches produced for adult small pelagic fishes. The nine temperature experiments are scaled to the natural temperature (grey), with colours from blue (coldest) to red (warmest). The temperature values for each species are shown in the bottom row.

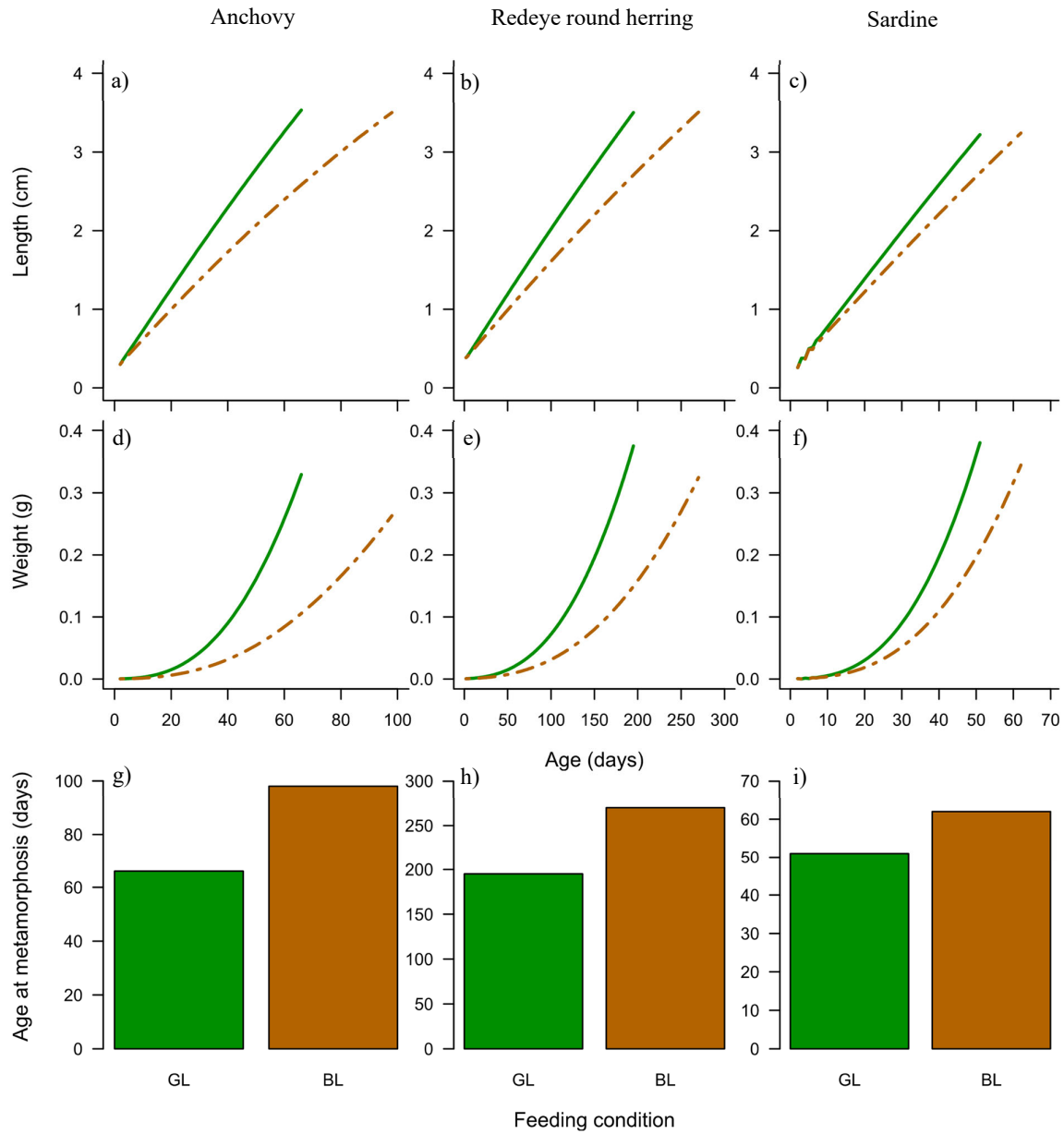


Figure 4.9 The effect of food environment on the larval stages of anchovy (left panel), redeye round herring (central panel) and sardine (right panel). (a-c) Length (cm) at age (days), (d-f) weight (g) at age, and (g-i) the age at metamorphosis (days). The two larval food experiments are represented by colours and symbols; the colours are defined on the bottom row; the symbols represent either good (G) or bad (B) food environments for larvae (L).

Food conditions had a large impact on small pelagic fish recruits (Figure 4.10). In the four feeding experiments illustrated in Figure 4.10, good food conditions during the recruit stage (GR) are illustrated in green and bad food conditions for recruits (BR) in orange. Recruits reached their length at recruitment (Figure 4.10a-c), maximum weight (Figure 4.10d-f) and age at recruitment (Figure 4.10g-i) faster under GR (green) conditions than in the BR (orange) conditions for all species. Regardless of the food conditions during the larval stage, the time spent in the recruit stage increased substantially under BR conditions. For anchovy it more than doubled, for redeye round herring it was 1.8 to two times longer, and for sardine it tripled. The legacy of bad larval food conditions (comparing BLGR to GLGR) was to increase the time in the recruit stage by 42 days for anchovy and 81 days for redeye round herring, but only by 12 days for sardine.

Adult small pelagic fishes showed interspecific similarities and differences in their responses to different feeding conditions during the three life cycle stages (Figure 4.11). All three species showed greater maximum lengths (Figure 4.11a-c) and maximum weights (Figure 4.11d-f) at the end of their lifetimes under GA environments (green curves). Similarly, under BA food conditions all three small pelagic fishes grew to lengths that were not much greater than their length at recruitment (Figure 4.11a-c). Anchovy and sardine adults in a GA condition recovered well from BR conditions with small differences in their maximum lengths (difference < 0.6-0.7 cm) and larger differences in weights (difference < 13 and < 25 g for anchovy and sardine respectively) under -BRGA and -GRGA scenarios. In contrast, redeye round herring did not recover, with a difference of 3.4-5.7 cm in maximum length and 32-51 g in maximum weight between fish recovering from a BR condition and fish that had experienced a GR condition.

Different feeding conditions during the three life stages affected the number of egg batches produced by the small pelagic fishes (Figure 4.11g-i). In all three small pelagic species most egg batches were produced if fish had good recruit (GR) and adult (GA) food conditions. Anchovy recovering from BR conditions in a GA condition produced between 19 and 20 fewer egg batches during their lifetime (Figure 4.11g), while sardine recovering from BR conditions produced 152 fewer egg batches than under GR conditions (Figure 4.11i). Redeye round herring did not follow the same trend; the number of egg batches produced during their lifetime depended on the feeding conditions experienced by the recruits more than the adults. Redeye round herring would produce more egg batches during GA than

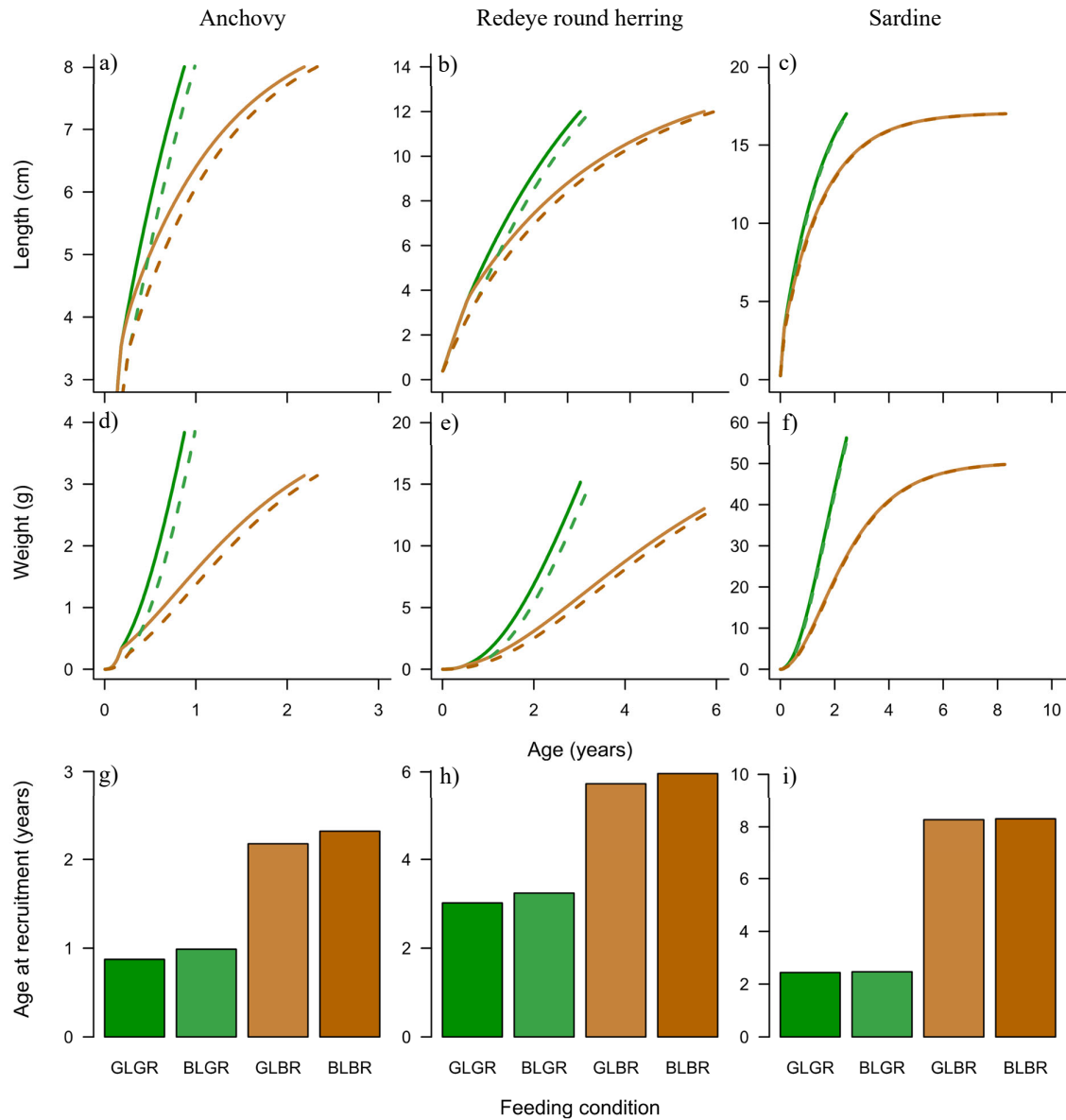


Figure 4.10 The effect of food environment on the recruit stages of anchovy (left panel), redeye round herring (central panel), and sardine (right panel). (a-c) Length (cm) at age (years), (d-f) weight (g) at age, and (g-i) age at recruitment (years). The four recruit food experiments are represented by colours and symbols; the colours are defined on the bottom row, the symbols represent either good (G) or bad (B) food environments sequentially for larvae (L), then for recruits (R).

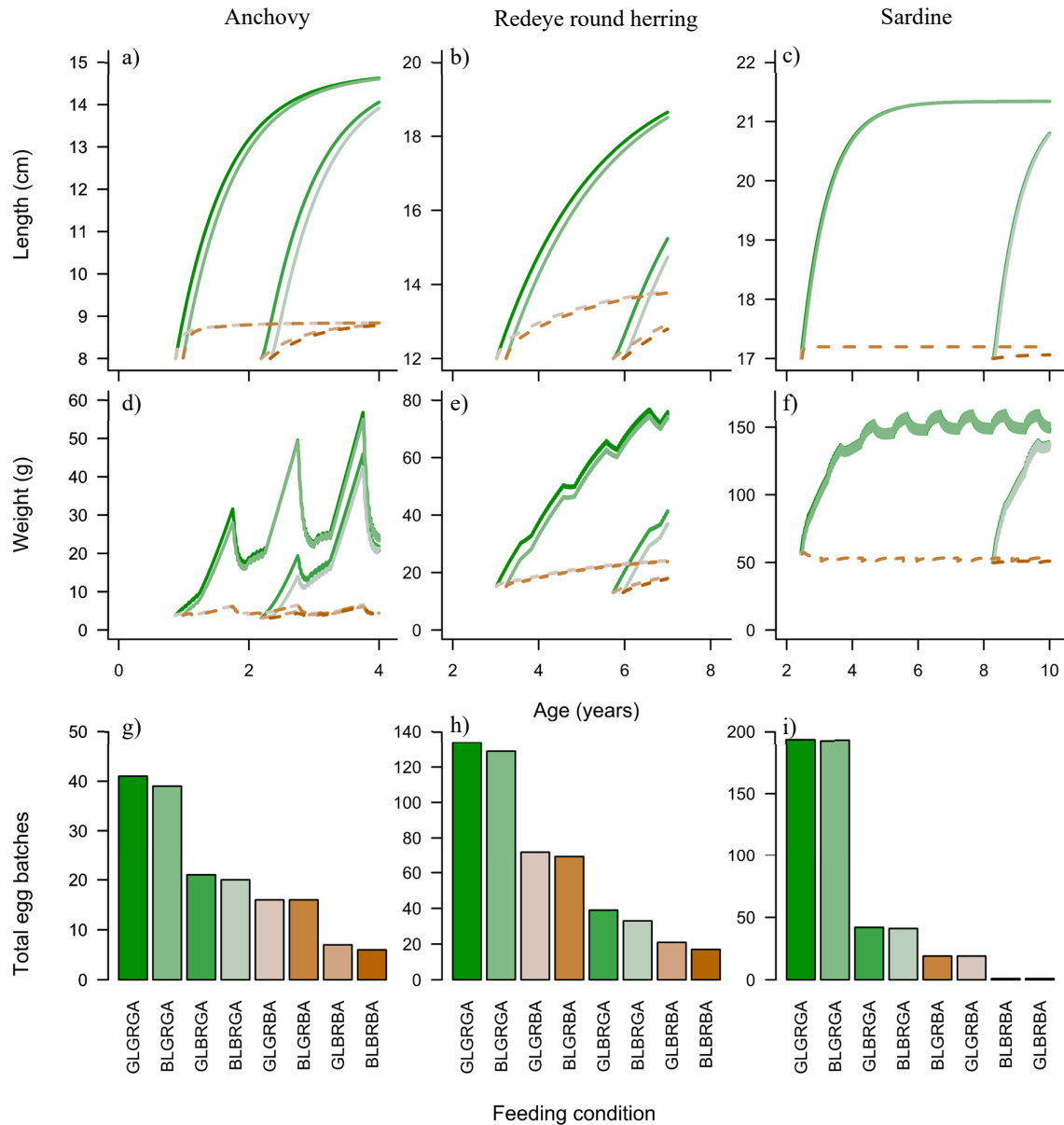


Figure 4.11 The effect of food environment on the adult stages of anchovy (left panel), redeye round herring (central panel), and sardine (right panel). (a-c) Length (cm) at age (years), (d-f) weight (g) at age, and (g-i) the total number of egg batches produced. The eight adult food experiments are represented by colours and symbols; the colours are defined on the bottom row, the symbols represent either good (G) or bad (B) food environments sequentially for larvae (L), then for recruits (R), then for adults (A).

BA conditions if they experienced the same recruit conditions but would produce 33 and 36 more egg batches in GRBA conditions than in BRGA conditions (Figure 4.11h).

4.2.3 Combined temperature/food experiments

Temperature and food both influence the growth rate of small pelagic fish larvae (Figure 4.12). In anchovy, and to a lesser extent redeye round herring larvae, in warm, bad/limiting food environments (WBL, light red) the growth curves for length-at-age (Figure 4.12a-b) and weight-at-age (Figure 4.12d-e) showed little difference from cool good/unlimiting food environments (CGL, dark blue). Sardine differed in that their warm water experiment results (WGL, dark red & WBL) for length-at-age (Figure 4.12c) and weight-at-age (Figure 4.12d) showed a close association in the growth curves, with a similar trend for cool water experiments (CGL & CBL, light blue). In all three species, larvae in GL environments reached larger maximum weights than in BL environments (Figure 4.12d-f). Larvae reached their length at metamorphosis faster in W experiments in all three species (Figure 4.12g-i). Sardine showed the smallest difference in the time (8 days) taken to reach metamorphosis between WGL and WBL conditions, while anchovy and redeye round herring showed a difference of 25 days and 57 days, respectively. Anchovy showed only a 10 day difference in the time taken to reach metamorphosis between WBL and CGL condition (Figure 4.12g), while redeye round herring and sardine showed differences of 46 days and 14 days, respectively. Anchovy and redeye round herring larvae showed large differences in the time taken to reach metamorphosis between CGL and CBL conditions (Figure 4.12g-h) at 43 and 98 days, respectively. Sardine larvae, in contrast, only showed a difference of 14 days in time taken to reach metamorphosis between CGL and CBL conditions.

Small pelagic recruit growth rate is affected by both temperature and food condition (Figure 4.13). In all three species, recruits reached their length (Figure 4.13a-c) and weight (Figure 4.13d-f) at recruitment faster in warm good/unlimiting food environments (WGR, dark red), followed by cool good/unlimiting food environments (CGR, dark blue), warm bad/limiting food environments (WBR, light red), and cool bad/limiting food environments (CBR, light blue). Redeye round herring recruits showed little difference in the growth curves between CGR and WBR conditions (Figure 4.13b). Sardine recruits showed a close association in the growth curves for length (Figure 4.13c) and weight (Figure 4.13f) in each condition, unlike anchovy and redeye round herring recruits. All three species had greater maximum weights at recruitment for GR conditions (Figure 4.13d-f). In a comparison

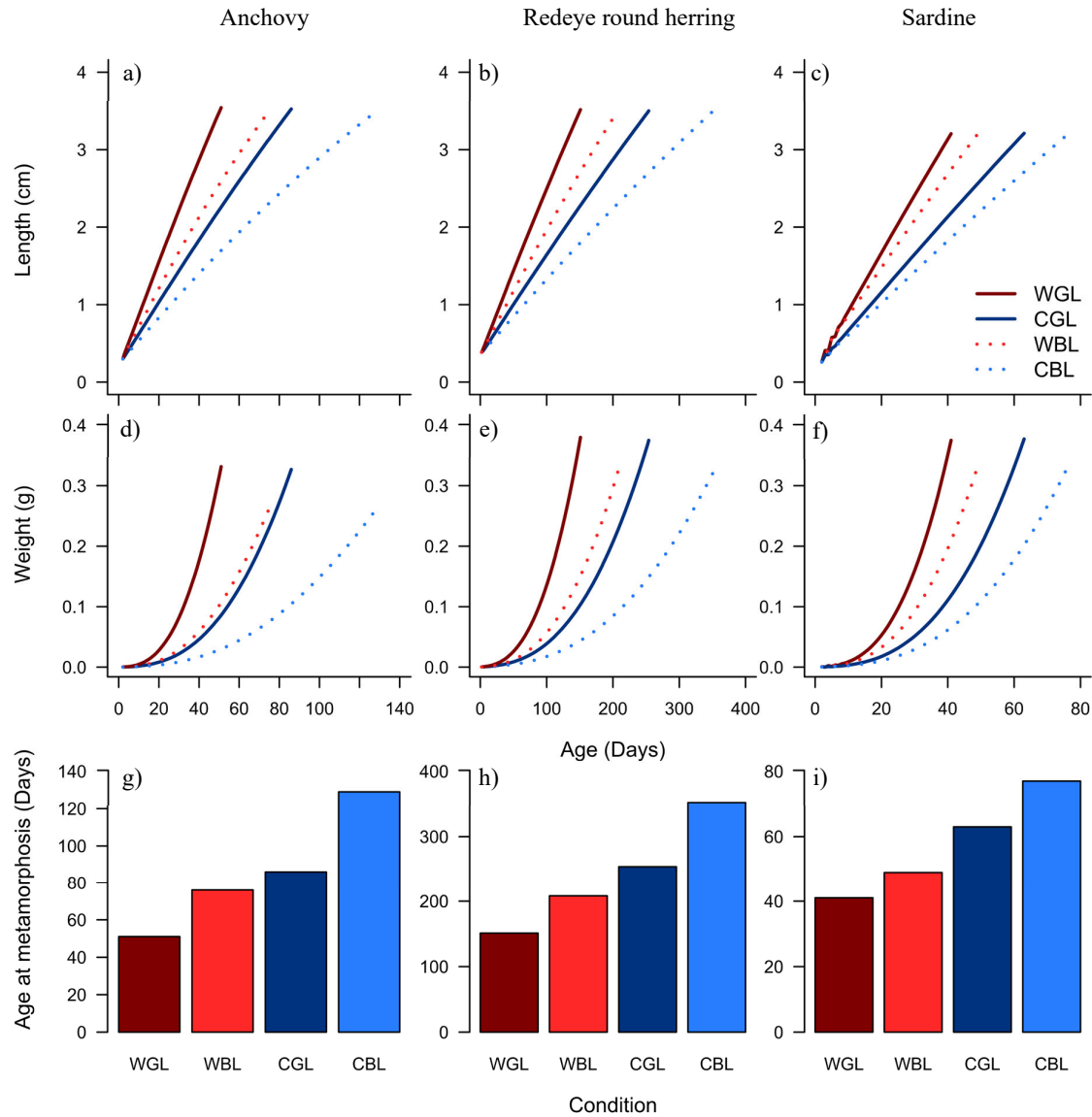


Figure 4.12 The effects of a combined temperature/food environment on the larval stages of anchovy (left panel), redeye round herring (central panel) and sardine (right panel). (a-c) Length (cm) at age (days), (d-f) weight (g) at age, and (g-i) the age at metamorphosis (days). The four larval food experiments are represented by colours, lines, and symbols; the colours are defined on the bottom row, the symbols represent either cool (C, blue) or warm (W, red) water temperatures and good (G, dark colours) or bad (B, light colours) food environments for larvae (L). Solid lines represent GL and dotted lines represent BL conditions.

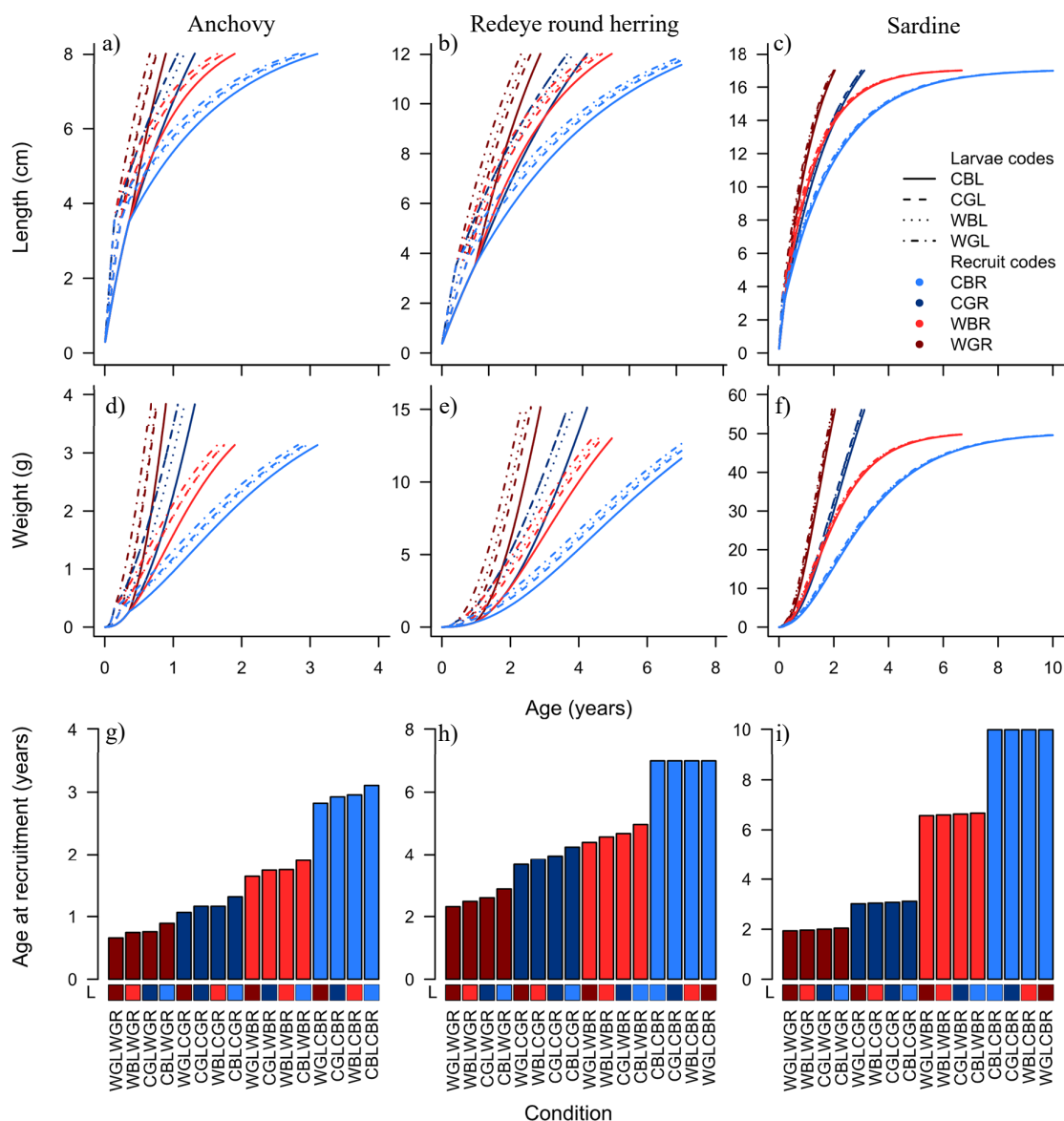


Figure 4.13 The effects of a combined temperature/food environment on the recruit stages of anchovy (left panel), redeye round herring (central panel) and sardine (right panel). (a-c) Length (cm) at age (days), (d-f) weight (g) at age, and (g-i) the age at recruitment (years). The sixteen temperature/food experiments are represented by colours, lines, and symbols; the colours are defined in the legend and the bottom row, the symbols represent either cool (C, blue) or warm (W, red) water temperatures and good (G, dark colours) or bad (B, light colours) food environments for recruits (R) and larvae (L). Solid lines represent GL and dotted lines represent BL conditions. Colours in the top row of age at recruitment plots (g-i) represent recruit conditions, while colours on the bottom row represents larval conditions.

between GR and BR conditions, anchovy weighed 0.7 g less, redeye round herring weighed 2.1 g less and sardine weighed 6.4 g less.

All three species showed the same trend in the grouping of conditions for the time taken to reach age at recruitment. Recruits in GR conditions spent less time in the recruit stage than in BR conditions (Figure 4.13d-f). In all three species the experimental conditions grouped in the order of WGR, CGR, WBR and CBR for their time taken to reach age at recruitment. Anchovy and redeye round herring showed steady increases when comparing WGR to CGR conditions (Figure 4.13g), while sardine showed big increases in time spent in the recruit stage when comparing conditions (Figure 4.13h-i). All three species showed a large increase in the time spent in the recruit stage in CBR conditions. When comparing WR conditions to CR conditions, all three species spent between 1.5 and 1.6 times longer in the recruit stage. Food condition had a large effect on the time spent in the recruit stage, with anchovy spending almost 2.5 times longer, redeye round herring spending twice as long and sardine spending three times as long in the recruit stage during BR conditions (Figure 4.13g-i). Larval conditions (L) also influenced the time fish spent in the recruit stage (Figure 4.13g-i, colour bar under the histogram). In all three species, recruits in WL conditions reached recruitment faster than in CL conditions.

Weights of anchovy aged two years, redeye round herring aged three years and sardine aged four years were compared to see how the different temperature/food conditions would affect the weights of adult fish. Recruit food conditions played a large role in the weight-at-age of adult small pelagic fishes (Figure 4.14a-c). In all three species their largest weight values were reached under conditions where GA followed GR conditions and smallest weights after BR conditions (Figure 4.14a-c, centre row of each panel). Larval conditions also affected the weight that small pelagic fish reached. Anchovy larvae reached larger weights under conditions where they experience GL conditions initially, while redeye round herring and sardine reached larger weights at WL conditions (Figure 4.14a-c, bottom row of each panel).

Temperature and food conditions influenced the reproductive output of all three small pelagic species (Figure 4.15). All three species produced more egg batches at good/unlimiting adult food (GA) conditions (Figure 4.15, dark colours in top row). Anchovy had a reduction of 2 egg batches, redeye round herring a reduction of 7 and sardine a reduction of 52 when comparing GA to BA conditions. All three species produced more egg batches if the adult stage followed from GR conditions. All three species produced their lowest number of egg batches if adult conditions followed BR conditions.

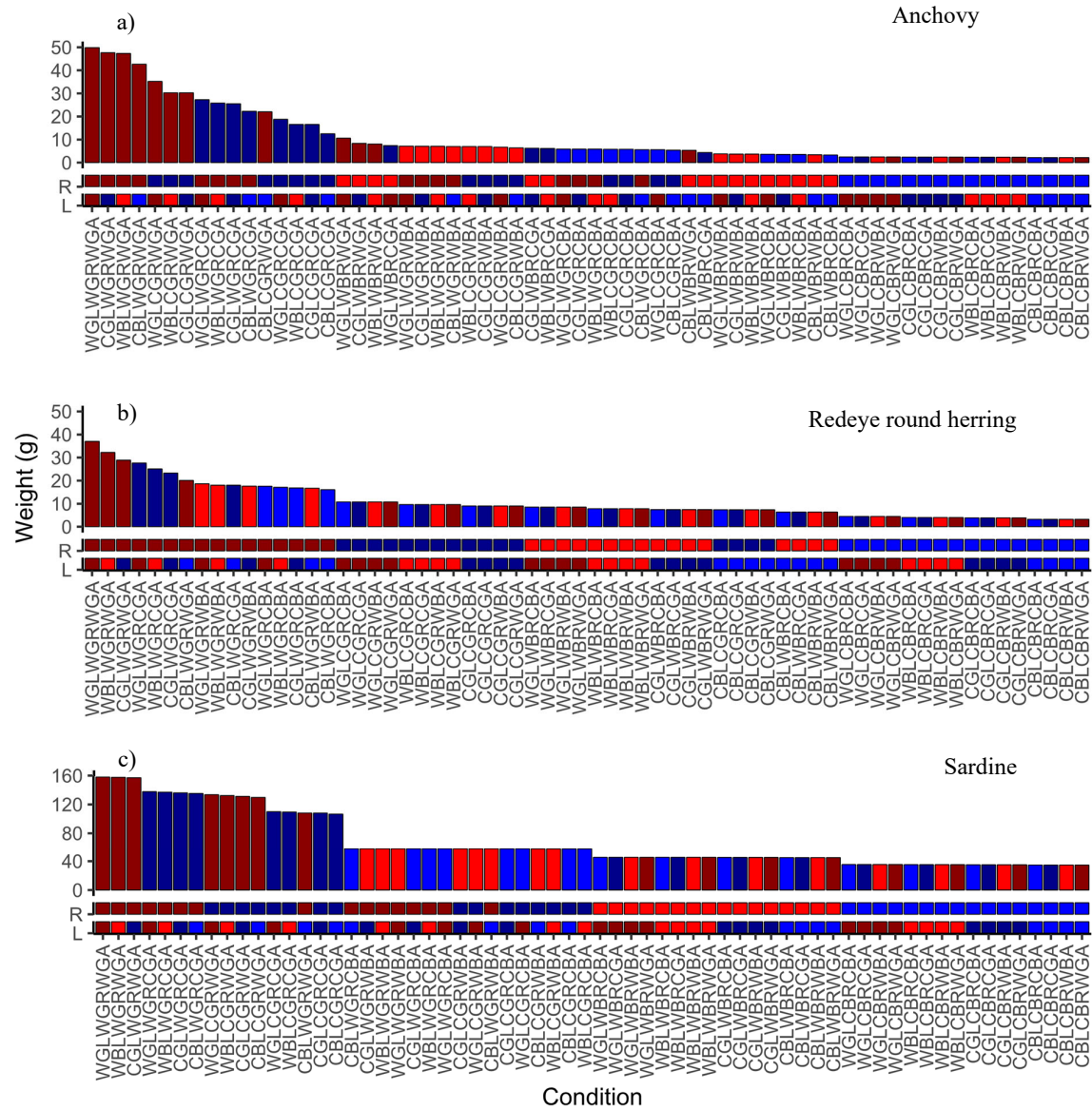


Figure 4.14 The effects of a combined temperature/food environment on the weight (g) at age (years) of adults from a) anchovy aged two years, b) redeye round herring aged three years, and c) sardine aged four years. The 64 temperature/food experiments are represented by colours which in combination represent either cool (C, blue) or warm (W, red) water temperatures and good (G, dark blue and red) or bad (B, light blue and red) food environments for adults (A), recruits (R) and larvae (L). In each panel the colours in the top row represents adult conditions, the centre row represents recruit conditions, and the bottom row represents larval conditions.

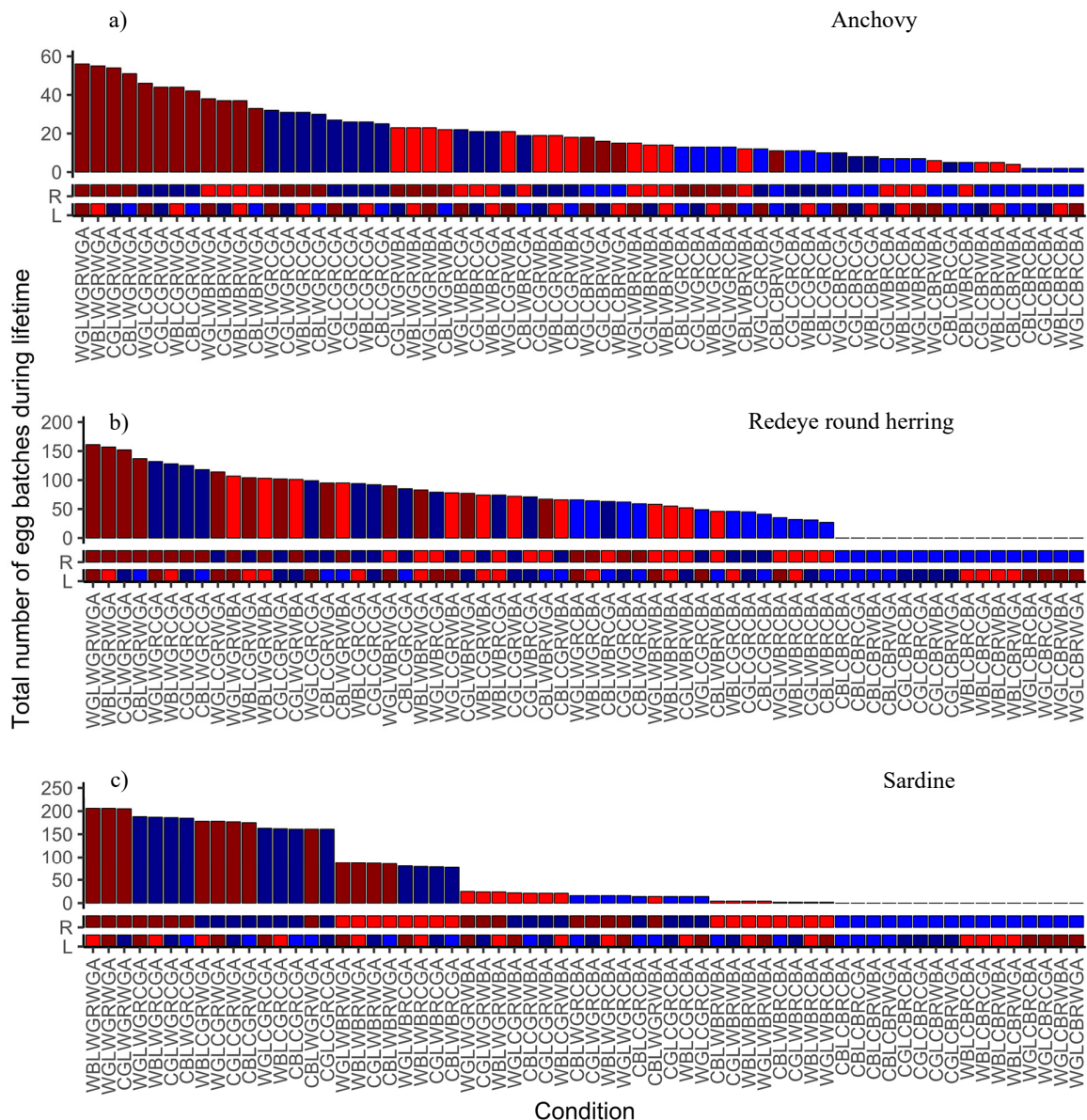


Figure 4.15 The effects of a combined temperature/food environment on the total number of egg batches produced by adults of a) anchovy, b) redeye round herring, and c) sardine during their lifetime. The 64 temperature/food experiments are represented by colours that in combination represent either cool (C, blue) or warm (W, red) water temperatures and good (G, dark colours) or bad (B, light colours) food environments for adults (A), recruits (R) and larvae (L). In each panel the colours in the top row represents adult conditions, the centre row represents recruit conditions, and the bottom row represents larval conditions.

Redeye round herring produced zero egg batches if the adult stage followed CBR conditions, a reduction of 27 egg batches (Figure 4.15b), while sardine produced few to no egg batches if they experience BA conditions after experiencing BR conditions, a reduction of 2 egg batches (Figure 4.15b). Larval conditions also affected egg production, with all three species producing more egg batches if they experience initial WL conditions (Figure 4.15a-c, bottom row of each panel).

Discussion

One of the most important findings from this study is the importance of good recruit body condition for adult body condition and reproductive output in small pelagic fishes. Results are consistent with other studies of small pelagic fishes that recognise environmental factors and food availability as factors that determine recruitment success (Cury *et al.* 2000). This in turn sets up length, weight (an approximation of fish body condition) and the reproductive potential of adult small pelagic fish and their capacity to produce viable and good quality eggs and larvae (Garrido *et al.* 2008, Somarakis *et al.* 2019, Peck *et al.* 2021). Silva *et al.* (2006) looked at fish condition and fat reserves related to length-at-maturity of European sardine *Sardina pilchardus* in the northeastern Atlantic and western Mediterranean and found that mean sardine weight and percentage fat at length correlated significantly with length at first maturity, and that regional changes in sardine condition could be caused by changes in food availability. Morimoto (1991) looked at the relationship between nutritional body condition and the reproductive ability of Japanese sardine (*Sardinops melanostictus* now *S. sagax*) and found a strong correlation between fat reserves (i.e., spawner condition), and the quantity and quality of eggs those fish produced. Brosset *et al.* (2016) examined maternal effects of adult European anchovy (*Engraulis encrasicolus*) and sardine in the Gulf of Lions and found that egg quantity in both species increased with the size of the fish, and egg quality increased with larger lipid reserves.

This study aimed to investigate the trade-offs between temperature and food conditions on three life history stages, i.e., larval, recruit and adult stages, of anchovy, redeye round herring and sardine in the Southern Benguela. The lengths- and weights-at-age were obtained from model outputs of dynamic energy budget (DEB) models created for each species individually. The results indicated that both temperature and food affected the growth rates of small pelagic fishes, with food seeming to have the largest influence on recruit growth and adult reproduction. Temperature plays a large role in larval development, since temperature drives energetic processes (Somarakis *et al.* 2019) and warmer temperatures mean faster hatching and faster development rates of the feeding apparatus. The

DEB models were effective in showing the effect of temperature and food condition on the growth and reproduction of all three stages of the three small pelagic fishes; however, there was an underestimation in the length-at-age. One drawback of the DEB models was that they represent food condition through the functional response (f), which is the ingestion rate of the organism as a function of available food density; therefore, the model considers the quantity of food but not the food quality in the various food condition scenarios. This could be a limiting factor since a small quantity of high quality food could give the same amount of energy as a large quantity of poor quality food. To mitigate this issue, the functional response was used as an approximation, with $f = 1.0$ representing a food condition with good quality food in the concentrations needed to reach age at maturity and maximum length, while the lower f value in the “bad food condition” represented a food environment that may have just enough good quality food or high concentrations of bad quality food to reach age at maturity and be able to reproduce.

Environmental effects on growth and reproduction

For larvae especially, temperature drives energetic processes, since food consumption, metabolism, and activity levels such as swimming speed and encounters with predators show a strong temperature dependence (Somarakis *et al.* 2019). Larvae in the temperature (Figure 4.6) and temperature/food combined (Figure 4.12) experiments for all three species reached age at metamorphosis faster in warm water conditions. These findings are consistent with larval growth experiments that found a positive correlation between recent daily growth rate and temperature in small pelagic fish larvae (Thomas 1986, Sakamoto *et al.* 2020). Similar results were found by Costalago *et al.* (2020), where anchovy larvae had higher individual growth rates in the warmer waters of the southeast coast than in the cooler waters of the west coast in conditions where high food density was available. Sardine larvae showed little difference in the time taken to reach age at metamorphosis between good and bad food conditions within each temperature of the temperature/food experiment (Figure 4.12i). This indicated that, for sardine, water temperature played a more important role in larval growth than food condition. Similar results were found by Sakamoto *et al.* (2020), where sardine in warmer waters off the south and east coast of South Africa had faster early growth rates than west coast sardine in cooler water. Warmer temperatures increase the growth rate of small pelagic fish larvae, decreasing the time spent in the larval stage, thereby expediting development of larvae, and increasing their chances of survival by decreasing their exposure to predators and increasing their ability to find food post hatching (King 1977, Peck *et al.* 2013, Somarakis *et al.* 2019). Slower growth rates at cooler temperatures decrease

metabolic demands, meaning that at low temperatures fish can ingest less food per unit time and still survive (Hunter 1977, van Denderen *et al.* 2020)

Within food (Figure 4.9) and temperature/food combined (Figure 4.12) experiments, small pelagic fish larvae reached their age at metamorphosis faster in good food conditions within temperatures. Anchovy showed the smallest difference between the warm-bad food condition and cold-good food condition for temperature/food experiment (Figure 4.12g). This is consistent with findings for northern anchovy (*Engraulis mordax*) by Hunter (1977), who identified high food density (good food conditions) and cool temperatures as mechanisms that would reduce larval activity and conserve energy of larval fish. Reducing their activity would also decrease the metabolic demand on larvae so they need less food per unit time to survive to metamorphosis (Hunter 1977). Takahashi & Watanabe (2005) observed similar results for Japanese anchovy (*Engraulis japonicus*) larvae in the Kuroshio-Oyashio transition region. They observed slower growth rates in late larvae living in colder waters because of a reduction in the amount of food ingested, even in high food density (good food conditions). In all the larval experiments, redeye round herring larvae took the longest time to reach age at metamorphosis, followed by anchovy and sardine. This is consistent with results from field studies and rearing experiments, which found redeye round herring grew slowly during the larval stage, especially in the first 30 days from first feeding (Thomas 1986, Wallace-Fincham 1987).

Therefore, experiments indicated that, for larval small pelagic fish, temperature played a more important role than food condition during this stage of development. Small pelagic fish larvae are visual feeders, so prey needs to be sufficiently close to be seen, hence the volume of water they are able to search for food is small and larvae can cover only short distances to find food (Hunter 1984). It has been estimated that pilchard *Sardina pilchardus* larvae (5–7 mm) could search only 0.1–0.2 l/hr (Blaxter & Staines 1971 in Hunter 1984), while anchovy *Engraulis mordax* larvae (6–10 mm) could search 0.1–1.0 l/hr (Hunter 1984). It was also found that food search abilities in small pelagic fish improve with growth, since perceptive distance, swimming speed and capture success rates are all functions of length or age (Hunter 1984). Therefore, the longer it takes for small pelagic fish larvae to reach length at metamorphosis, the greater the chances of not finding food and starving to death (Hunter 1984) as well as of being preyed upon. This also means that food will become more accessible to larger larvae, as swimming speed improves and develops. Small pelagic recruitment into viable

populations often depends on the conditions and growth rates of their individual larvae (Costalago *et al.* 2020).

Temperature sets the upper limit to growth rates within all fish species, meaning that the water temperatures an individual experiences within its lifespan would influence the size (length and weight) and the age at maturity (or in this case recruitment) (Peck *et al.* 2013). Temperature experiments for recruits (Figure 4.7) showed faster growth rates for all three species in warmer waters. In the recruit food (Figure 4.10) and temperature/food (Figure 4.13) experiments, recruit food condition had a large influence on small pelagic fish growth, after which temperature influenced growth i.e., fish from warm good food recruit conditions had younger ages at maturity (where they get recruited into the population) than fish from cool good food recruit conditions. As juveniles, small pelagic fishes transition to continuous intermittent swimming typical of recruits and adults, which means that they can search larger volumes of water for food and can increase the frequency of prey encounters, and hence are more actively finding food than larvae (Hunter 1977). Food experiments (Figure 4.10) showed that if small pelagic fish experience good food conditions during the recruit stage, they recover from bad feeding conditions during the larval stage, with anchovy, redeye round herring and sardine all spending only 1% longer in the recruit stage than they would if they experienced good recruit feeding conditions after good larval feeding conditions (GLGR).

In all three species, a good food condition during the recruit stage led to small pelagic fish recruits being in much better condition (larger weights at age) than in bad food conditions (Figure 4.10d-f & Figure 4.13d-f). Sardine recruit length (Figure 4.13c) and weight (Figure 4.13f) at age curves for each recruit condition (lines per colour type grouping) showed almost no difference, indicating that initial larval conditions had almost no effect on sardine recruit growth. In contrast, anchovy and redeye round herring did show differences, indicating that initial larval condition did influence the recruit curves. In anchovy recruits, good larval food conditions had a larger influence on the recruit age grouping than temperature, while temperature had a larger influence on redeye round herring and sardine recruit age groupings than larval food condition (Figure 4.13g-i). Comparisons between good and bad food conditions within the same temperature showed that recruits in all three species would spend much longer (anchovy and redeye round twice as long and sardine three times longer) in the recruit stage during bad food conditions. This would have a knock on effect as small pelagic fish cohorts would take longer to recruit into the population and would be in poorer condition going into the adult stage, translating into reduced reproductive potential for adults in the next stage of the lifecycle (Somarakis *et al.* 2019).

Once small pelagic fish reach their age at maturity, they are recruited into the population. Small pelagic body conditions play an important role in the reproductive output and the condition of eggs and larvae (Garrido *et al.* 2008, Somarakis *et al.* 2019, Peck *et al.* 2021). Adult anchovy and sardine reached their asymptotic length and weight slower at colder temperatures, while redeye round herring had smaller maximum lengths and weights at colder temperatures (Figure 4.8). Adult small pelagic fish from good adult food conditions were shown to be in much better condition with larger weights at age (Figure 4.11d-f & Figure 4.14), than those in bad adult food conditions. However, the weight-at-age of adults of all three species were influenced by their recruit conditions (Figure 4.14). Small pelagic fish adults that experienced good recruit food conditions reached larger weights at age in the adult stage whereas those in cool bad recruit conditions consistently had the lowest weights in all three species. Therefore, it can be concluded that recruit condition has a large influence on the conditions of adult small pelagic fish. Anchovy and redeye round herring showed better condition during warm recruit conditions, which in some cases was better than in cool good food conditions. This could be due to the upper limit of the preferred recruit temperature range for both species showing overlap with the adult preferred temperature range. In contrast, sardine showed clear separation between good and bad food conditions in the recruit stage, which carried over into the adult stage with good food conditions showing higher adult weights than bad food conditions. This is consistent with studies that found that sardine show reduced specificity in spawning habitat selection, selecting their habitat over a broad range of environmental variables, but tended to time their spawning events to maximize larval food availability (Twatwa *et al.* 2005). Small pelagic larval condition also played a role in determining weight-at-age in adults but to a much smaller extent (Figure 4.14). In all anchovy and redeye round herring, temperature conditions during the larval stage played a large role in determining adult weight (Figure 4.14).

Adults of all three small pelagic fish species showed a decrease in the number of egg batches produced at cooler temperatures in temperature experiments (Figure 4.8), while redeye round herring and sardine showed no changes in the number of egg batches spawned at warmer temperatures. This may be an indication that adult anchovy spawn in warmer temperatures. These results are consistent with those found on spawning habitat preferences for small pelagic fish in the Benguela, where anchovy are selective in their spawning habitats, preferring warmer waters (Twatwa *et al.* 2005, Mhlongo *et al.* 2015), while redeye round herring (Roel & Armstrong 1991) and sardine (Twatwa *et al.* 2005, Mhlongo *et al.* 2015) spawn over a wide range of temperatures.

Food (Figure 4.11g-i) and food/temperature (Figure 4.15) experiments showed that anchovy, redeye round herring, and sardine produced more egg batches if fishes had good food conditions during the adult and recruit stages. Anchovy would produce 32-39% fewer egg batches, redeye round herring would produce 69-74% fewer egg batches and sardine 52-58% fewer egg batches during their lifetime if they had bad food conditions during the recruit stage and good food conditions during the adult stage. Anchovy would produce 59-70% fewer egg batches and sardine 90% fewer egg batches if they experienced bad adult food conditions compared to good adult food conditions (Figure 4.15). This is consistent with good spawner body conditions influencing the energy available for egg batch production (van der Lingen *et al.* 2006b, Ndjaula *et al.* 2013). Changing the prey biomass available to adults would have an effect on spawner body condition; better condition of adults in good rather than those in bad food conditions would likely have a positive effect on the quantities of eggs spawned in each batch as well as the energy available per egg (quality of eggs) (Garrido *et al.* 2008, Peck *et al.* 2013, Brosset *et al.* 2016, Peck *et al.* 2021 and references therein). This translates into changes in larval survival, since larvae from larger eggs tend to be able to feed off yolk for longer after hatching than those from smaller eggs, which gives the former greater reserves for metabolism, so they have more time to find food (Hunter 1984).

Redeye round herring egg batch production, in contrast, did not show this trend but showed that, regardless of adult temperature or feeding condition, they would produce the same number of egg batches if the temperature were kept constant (Figure 4.11). Redeye round herring produced 100% fewer egg batches in a cool bad recruit food condition than in a warm bad recruit food condition and producing 2% fewer egg batches in bad recruit food conditions than in good recruit food conditions. Differing feeding conditions in adults would affect the body condition of the adult redeye round herring as shown in the larger maximum weights for redeye round herring in good adult food conditions (Figure 4.11e & Figure 4.14b). Therefore, even though they may produce the same number of egg batches they would possibly produce more, better quality eggs in each batch for good adult feeding conditions (Garrido *et al.* 2008, Peck *et al.* 2013, Brosset *et al.* 2016).

Foraging dynamics in a changing climate

It has been shown that temperature and food availability contribute to growth rates in small pelagic fish. Thus, when examining growth physiology in small pelagic fish it is important to understand their foraging dynamics and feeding behaviour (Peck *et al.* 2013). Anchovy (James & Findlay 1989, van der Lingen *et al.* 2006b), redeye round herring (Wallace-Fincham 1987, James 1988a, Mketsu 2008)

and sardine (van der Lingen 1994, van der Lingen *et al.* 2006b) in the Benguela have the ability to adapt their feeding behaviour to whatever prey resources are available and can change their prey fields within different size spectra, independent of prey concentration, to increase their food intake while reducing energy expenditure in changing food environments (Peck *et al.* 2013).

Changes in upwelling off the west and south coast of South Africa can have different effects on small pelagic fish survival and their feeding environment, depending on upwelling intensity and the knock-on effects from physical forcing. If the upwelling intensity is too strong then it will have a negative effect on small pelagic fish production due to a disruption of their feeding strata and/or excessive offshore transport of planktonic larvae of small pelagic fish and their prey items away from favourable environmental conditions (Cury & Roy 1989, Bakun *et al.* 2015).

Small pelagic fish are quick to respond to environmental changes, characterizing them as ‘excellent bio-indicators of climate-driven changes in marine systems’ (Peck *et al.* 2013). Changing climate in the Southern Benguela could impact small pelagic fish recruitment success by changing small pelagic fish distributions, changing lower trophic level (phytoplankton and zooplankton) species compositions and productivity, and changing the overall circulation patterns experienced by these species (Fréon *et al.* 2009, van der Lingen 2021). However, the trophic dissimilarity (Figure 4.2) and resource partitioning of the different small pelagic species means that changes in plankton compositions would affect the species differently (van der Lingen *et al.* 2006b, van der Lingen 2021). Within increased upwelling events we would expect colder nutrient rich water and development of larger species of phytoplankton and in turn zooplankton communities (van der Lingen *et al.* 2006b, van der Lingen 2021). In these conditions anchovy and redeye round herring would be favoured since they preferentially particulate-feed on larger food items (Wallace-Fincham 1987, van der Lingen *et al.* 2006b, van der Lingen 2021). Sardine are less efficient at removing large food items and favour small-food item environments where they employ energy efficient filter-feeding to efficiently remove these food items (van der Lingen *et al.* 2006b, van der Lingen 2021). In environments dominated by large plankton species they would have to resort to more expensive particulate-feeding (van der Lingen *et al.* 2006b). Recruitment strength and total biomass of anchovy and redeye round herring have shown higher numbers since 2000 than before, while sardine has not (van der Lingen 2021). This could be indicative that climate change-driven enrichments to the trophic environment for anchovy and redeye round herring led to these species responding favourably (van der Lingen 2021). However, these developments should be interpreted cautiously, since it is based on a comparatively

short (35 years) time series and small pelagic fish populations can fluctuate on a range of time scales (Field *et al.* 2009).

Conclusion

Both temperature and feeding conditions influence the growth and reproduction of small pelagic fishes in the Southern Benguela, with cooler temperatures decreasing the growth rate of all three species in all three life stages. In larvae, especially anchovy and sardine, there is almost a net trade-off between temperature and feeding environment effects, where decreased growth rates from cool waters are mitigated by increased growth rates from good food conditions. In small pelagic fish recruits the increased growth rates from good food conditions far outweighed the decreased growth rates from cooler temperatures and had a big influence on the reproductive output of adults, particularly redeye round herring. Small pelagic fish in warm good food conditions would also be in better body condition for reproduction, leading to more, better quality eggs and giving post-yolk sac larvae a better chance of surviving by giving them more time to develop before they must find food after hatching.

Chapter 5 Niche dynamics of small pelagic fishes in the Southern Benguela

Three species of small pelagic fishes co-occur in large abundance in the Southern Benguela: anchovy (*Engraulis encrasicolus*), redeye round herring (*Etrumeus whiteheadi*) and sardine (*Sardinops sagax*). These fishes have adopted different life history strategies to enable them to exploit different niches in the ecosystem. The main aim of this study was to develop full life cycle, dynamic energy budget (DEB) models for each of the three species, with the key hypothesis being that they would utilize differences in their environment and adopt bioenergetic strategies that matched their different niches, allowing them to compete and co-occur. Potential niche adaptations for small pelagic fishes include breeding strategies, spawning habitat, egg transport and hatching, larval and juvenile growth rates, schooling behaviour, vertical migrations, and trophic dynamics (Checkley *et al.* 2009a, Peck *et al.* 2013, Somarakis *et al.* 2019, Peck *et al.* 2021). This chapter will give an overview of these niche adaptations in these fishes in the Southern Benguela, linking them to some of the major results from this study. This will include comparisons to other ecosystems where these or similar species or species pairs co-occur, either separately or concurrently.

Three similar species occur in the North-western Pacific, namely Japanese anchovy (*Engraulis japonicus*), Pacific round herring (*Etrumeus teres*) and Japanese sardine (*Sardinops melanostictus*) (Oozeki *et al.* 2007, Takasuka *et al.* 2008a), and in many other ecosystems there are anchovy/sardine pairings, for example: European anchovy (*E. encrasicolus*) and European sardine (*Sardina pilchardus*) in the Bay of Biscay (Planque *et al.* 2007, Checkley *et al.* 2009b) and the eastern Mediterranean Sea (Giannoulaki *et al.* 2006, Checkley *et al.* 2009b, Somarakis *et al.* 2019); northern anchovy (*E. mordax*) and Pacific sardine (*S. sagax*) in the California Current system (Lluch-Belda *et al.* 1991, Checkley *et al.* 2009b); Peruvian anchovy/anchoveta (*E. ringens*) and Pacific sardine (*S. sagax*) in the Humboldt Current system (Gutiérrez *et al.* 2007, Checkley *et al.* 2009b); and Australian anchovy (*E. australis*) and Pacific sardine (*S. sagax*) in South Australian waters (Ward *et al.* 2001).

This chapter will indicate how the niche adaptations of anchovy, redeye round herring and sardine in the Southern Benguela may have affected the values of key model parameters compared to those for similar species in other ecosystems. The pitfalls and lessons learned from using existing models will be discussed, and future work will be suggested that can move these studies forward.

Niche dynamics of small pelagic fishes

5.1 Capital versus income breeding strategies

Different organisms, including fishes, tend to show pronounced variation in their life histories, including the way they finance their growth and reproduction (Stephens *et al.* 2009, McBride *et al.* 2015). This has led to many models describing life history that focus on patterns of energy allocation to growth and reproduction (Stephens *et al.* 2009). The relationship between somatic growth energy allocation and reproductive energy allocation, and how they relate to the timing of breeding and the division between capital and income breeding, has garnered keen interest from scientists (Stephens *et al.* 2009). This is largely due to the capital and income categorization having the potential to integrate basic physiology and environmental drivers, also known as ecophysiology (McBride *et al.* 2015). Organisms often exhibit one of two methods for financing their reproduction: “income breeding” where they use the simultaneous intake of food to pay for a reproductive attempt, or “capital breeding” where they finance their reproduction through stored energy (Stephens *et al.* 2009, McBride *et al.* 2015).

McBride *et al.* (2015) looked at the different breeding patterns in fish, including Clupeiformes, and found that breeding patterns in multiple spawning clupeoids are not limited to extreme forms of capital or income breeding, but rather a range over a complete continuum of intermediate breeding strategies. Many clupeoid species have developed a mixed capital-income breeding strategy where, in response to its own physiological condition and the environment, an individual’s genotype can move along the capital-income continuum (Ganias *et al.* 2014, McBride *et al.* 2015, Somarakis *et al.* 2019).

Model parameter estimation in Chapter 2 and Chapter 3 indicated that, of the three small pelagic species in the Southern Benguela, redeye round herring exhibits an extreme capital breeding strategy by only investing 46% of assimilated energy into reproduction. Redeye round herring and sardine also show elements of a capital breeding strategy by decoupling their dependence on food during spawning by reducing their batch fecundity and spawning more frequently over longer periods of time (van der Lingen *et al.* 2006b). Reducing secondary oocytes through atresia also reduces the final egg count during the spawning season (a particular strategy of capital breeders) (McBride *et al.* 2015), and since atresia has been observed in redeye round herring year round (Roel & Melo 1990) it is also an indication that they fall more to the capital breeding side of the continuum. Anchovy, on the other

hand, show the most extreme income breeding strategy of the three species by investing 65% of assimilated energy into reproduction, showing rapid growth and high egg batch fecundity in good (large zooplankton-dominated) food environments due to fast metabolic rates, and almost negligible growth in poor (small zooplankton-dominated) food environments. These results support the hypothesis that this species operates under a “feast or famine” scenario, whereas sardine employ a steady-state trophic ecology as suggested by van der Lingen *et al.* (2006b).

Similar patterns have been observed in co-occurring small pelagics in other ecosystems (Ganias *et al.* 2014, Queiros *et al.* 2019). In the North-western Mediterranean Sea and the Bay of Biscay, European anchovy (*E. encrasicolus*) are mixed income-capital breeders, relying more on income energy for reproduction, while European sardine (*Sardina pilchardus*) are more mixed capital-income breeders, relying mostly on capital from energy stored during their resting period (McBride *et al.* 2015, Gatti *et al.* 2017, Albo-Puigserver *et al.* 2020). This is also the case for Japanese anchovy (*E. japonicus*) and Japanese sardine (*Sardinops melanostictus*) in the Kuroshio Current system (North-western Pacific): the former are typical income breeders requiring food at the time of spawning almost throughout the year (McBride *et al.* 2015, Tanaka *et al.* 2016, Takasuka *et al.* 2019), whereas the latter are more capital-income breeders that feed intensively prior to their winter spawning season even though they continue feeding at the time of spawning (Morimoto 1996 in Takasuka *et al.* 2019). Pacific round herring (*Etrumeus teres*) off southern Japan exhibited an inverse relationship between reproduction and body condition, producing large pelagic eggs over a protracted spawning season, and exhibited a lower batch fecundity compared to Japanese sardine when co-occurring in the same spawning ground (Plaza *et al.* 2007). Therefore, *E. teres* also show a more capital-income breeding strategy (Plaza *et al.* 2007), like redeye round herring (*E. whiteheadi*) in the Southern Benguela.

5.2 Adult spawning habitat selection

Small pelagic fish habitats are characterized by geography, i.e., the fixed properties of the ocean bottom and coast, and hydrography, i.e., the variable sea water properties, the latter of which provides these fishes with options for moderating the effects of changing climate by moving elsewhere (Checkley *et al.* 2009b). Small pelagic fish habitat in the Southern Benguela tends to be restricted to the continental shelf, only extending a short distance beyond the shelf in a few areas with strong advection, like the southern tip of the Agulhas Bank (Checkley *et al.* 2009b). The oceanographic features that constrain small pelagic fish to the continental shelf in this region include the Benguela jet current on the southwest coast of South Africa, the strong Agulhas Current on the east and south

coasts of South Africa, and low phytoplankton concentrations offshore on both coasts (Checkley *et al.* 2009b). In the Southern Benguela, the South African coast west of 20°E is a wind-driven, coastal upwelling system whereas, in contrast, the south coast of South Africa, also considered to be part of the Southern Benguela, has characteristics of both an upwelling and a temperate shallow shelf system, showing both seasonal coastal, shelf-edge and dynamic upwelling (Hutchings *et al.* 2009, Kirkman *et al.* 2016, Peck *et al.* 2021).

In general, when taking temperature alone into account, anchovies (engraulids) tend to utilize a wider range of spawning temperatures than sardines (Oozeki *et al.* 2007, Peck *et al.* 2013). Anchovy in the Southern Benguela are particular in their spawning habitat selections, preferring warm water between 17°C and 23°C, but mostly between 18°C and 20°C (Richardson *et al.* 1998, Twatwa *et al.* 2005, Barange *et al.* 2005, Mhlongo *et al.* 2015). These temperatures are often associated with high copepod production and create a reliable, good-food environment for anchovy (Richardson *et al.* 1998, Twatwa *et al.* 2005). This was consistent with this study's findings (Chapter 4), which indicated that anchovy in good (especially warm) food environments would be in better condition and produce more egg batches than in cold, bad-food environments. Redeye round herring is a more temperate species and does not appear to be as selective as anchovy in their temperature preferences, spawning over a wide range of temperatures from 14-24°C (van der Lingen 2005). However, even though they spawn all along the coast of South Africa they concentrate mainly near the 200 m isobath (Roel & Armstrong 1991), with their eggs and those of anchovy and sardine principally found from mid-shelf to offshore of the shelf edge (van der Lingen 2005). Sardine are also less selective in their spawning habitat selection than anchovy, occurring in habitats that have a broad range of environmental variables and spawning mostly in slightly cooler (16°C to 22°C) waters than anchovy (Twatwa *et al.* 2005, Barange *et al.* 2005, Mhlongo *et al.* 2015). Studies have found a positive relationship in the Southern Benguela between sardine egg abundance and chlorophyll *a* concentration; i.e., phytoplankton biomass, as well as production of the copepod *Calanus agulhensis*, indicating that sardine time their spawning events to maximize larval food availability (Richardson *et al.* 2003, Twatwa *et al.* 2005). This is consistent with results in Chapter 4, where redeye round herring and sardine in good-food conditions would have better body conditions (weight-at-age) and produce more egg batches (50 - >75% more in the case of sardine) than in bad food conditions, with temperature during those conditions playing a minimal role. A similar interspecific difference in temperature ranges was found in the northwest Mediterranean for European anchovy and sardine (Palomera *et al.* 2007) and the North-western Pacific for Japanese anchovy and sardine (Oozeki *et al.* 2007, Takasuka *et al.* 2008b), with anchovy

preferring warmer waters and sardine colder waters. In contrast, Pacific round herring in the North-western Pacific had a broader spawning temperature range (10-30°C) (Oozeki *et al.* 2007) than redeye round herring in the Southern Benguela. Northern anchovy and Pacific sardine in the eastern North Pacific differed from the pattern shown in the Southern Benguela, with anchovy preferring to spawn in cold water and sardine in warm water (Lluch-Belda *et al.* 1991, Takasuka *et al.* 2008b, Takasuka 2018).

In general, anchovy are most often associated with coastal upwelling regions or regions with freshwater influence, while sardine typically occur further offshore (Checkley *et al.* 2009b). In the southern Benguela all three species occur both in coastal waters and offshore, with adults mostly spawning offshore in deeper water over the continental shelf, although they do also spawn inshore, especially when the population is at high abundance (Roel & Armstrong 1991, Armstrong *et al.* 1991, Hutchings *et al.* 2002, Barange *et al.* 2005). Even though the inshore west coast appears an ideal spawning ground for small pelagic fish, being characterised by a broad shelf, sluggish currents, high productivity, and moderate stratification, most spawning by small pelagic fish in the Southern Benguela occurs on the south coast (Hutchings *et al.* 2002), where the waters are warmer and more stable but also more oligotrophic than on the west coast (Hutchings *et al.* 2002). Offshore losses may be greater on the south coast but spawning there is ultimately more successful, since eggs and larvae, particularly from the south-west coast, are transported by the Benguela jet to a nursery ground on the upper west coast where they benefit from the higher productivity there (Hutchings *et al.* 1998, 2002). Since egg development times and larval growth rates (Chapter 4) are faster in warmer waters, this may contribute to the success of spawning in warmer waters on the south coast because temperature plays a more important role than feeding in larval growth. Japanese anchovy and sardine at high abundance show similar patterns, spawning both inshore and offshore, with anchovy being able to tolerate low-salinity and high-temperature coastal waters while sardine avoid spawning in coastal waters (Oozeki *et al.* 2007). In contrast, Pacific round herring are limited to inshore spawning, avoiding both low salinity coastal waters, and offshore surface waters (of areas deeper than 3 000 m) due to a narrow salinity tolerance (Oozeki *et al.* 2007, Peck *et al.* 2021).

In the Southern Benguela the peak spawning of anchovy and sardine (west coast subpopulation) is timed to coincide with the upwelling season (Andrews & Hutchings 1980, Sakamoto *et al.* 2020). Anchovy spawn during spring and summer, peaking in October and January/February (Huggett *et al.* 2003). The sardine western and southern subpopulations spawn year-round, but their peak spawning is concentrated in spring and summer off the west coast and winter to spring off the south coast of

South Africa (van der Lingen *et al.* 2001, van der Lingen & Huggett 2003, Barange *et al.* 2009, Sakamoto *et al.* 2020). Redeye round herring, like sardine, spawn year-round, with peak spawning in winter and spring (between August and October), when the predominant wind direction is reversed by the regular passage of cyclones past the South African coast (Andrews & Hutchings 1980, Roel & Armstrong 1991). In this case, peak spawning seasons for anchovy and west coast spawning sardine are in phase with each other, while spawning season for south coast sardine and redeye round herring are in phase with each other. In the California Current, Bay of Biscay, and Tsushima Current, spawning seasons for anchovy and sardine are slightly out of phase, and completely out of phase in the Kuroshio Current and the Gulf of Cadiz (Checkley *et al.* 2009b).

In the Southern Benguela, anchovy spawning preferences also extend to spawning in stable habitat conditions, with weak winds and strongly stratified water column conditions (in the quiescent phase of upwelling events), and eggs mainly being restricted to the warm, upper-mixed layer of the water column (Shelton & Hutchings 1990, Twatwa *et al.* 2005). Because redeye round herring spawn in winter and spring, when the predominant wind direction is reversed, water temperatures are cooler than 20°C, and there is a stratified and stabilized water column (Andrews & Hutchings 1980, Roel & Armstrong 1991). During these periods alongshore advection of the eggs is reduced, and shoreward drift of eggs and larvae are favoured (Roel & Armstrong 1991). Sardine prefer to spawn in areas with strong winds and fast current speeds and seem to prefer spawning in well-mixed water masses (Twatwa *et al.* 2005).

Because anchovy are very specific in their habitat selections, spawning anchovy are more likely to be affected by changing ocean climate conditions, since changing environmental variables such as the cooling water in the Southern Benguela and increased upwelling (Rouault *et al.* 2010, Blamey *et al.* 2015) can modify their spawning habitats (Twatwa *et al.* 2005). Sardine spawning habitats, in contrast, are less likely to be affected by changing climate conditions, due to their less specific habitat selection and their ability to change their habitats when the conditions are unsuitable for successful spawning (aided by their larger size and better swimming ability) (Twatwa *et al.* 2005). Unfortunately, there is little to no information available as to the effect of recent changing climate on the habitat selection of redeye round herring. However, since they spawn outside the upwelling season in cooler water than the other two species, and prefer to spawn in more stratified water (Roel & Armstrong 1991), their spawning habitat may be less likely to be affected by cooling and increased upwelling (Rouault *et al.* 2010, Blamey *et al.* 2015) observed in the Southern Benguela and. Roberts *et al.* (2020) analysed the impacts of climate change on a similar species of round herring (*Etrumeus*

teres) in the North Atlantic, and found that this species has shifted its distribution over the last 30 years, as their distribution is strongly influenced by bottom temperature and salinity. Therefore, further studies are necessary to understand the potential impacts of climate change on redeye round herring spawning habitats in the Southern Benguela.

5.3 Egg transport and hatching

Studies have shown that female fish that produce eggs with higher yolk reserve would have larger larvae at time of hatching, leading to increased chances of survival (Garrido *et al.* 2015). As has been shown above, female fish do not partition resources in a fixed manner; partitioning of resources is dynamic and dependent on recent feeding conditions (Peck *et al.* 2021). Brosset *et al.* (2016) investigated reproductive allocation and performance in female European anchovy and sardine in the Northwest Mediterranean and found both species had a positive link between fish size and egg quantity, while lipid reserves had a positive relationship with egg quality but not quantity. There was also preferential allocation towards reproduction, even if the fish were in low body condition (length- and weight-at-age) (Brosset *et al.* 2016). Similar results were shown in Chapter 4 for all three species, where adults would produce egg batches even if they were in poor condition with smaller lengths-at-age and weights-at-age.

The spatial distribution of fish eggs is dependent on the location where they were spawned, their physical properties (buoyancy and dimension) and the ambient water properties, including density, currents (whose direction and velocity have strong links to depth), and wind-induced turbulence (Sundby 1991, Osman *et al.* 2010). Pelagic fish eggs tend to rise towards the surface due to their specific density being lower than that of the surrounding upper mixed layer of the water column (Sundby 1991). However, due to the turbulent forces of wind-induced mixing counteracting the eggs' buoyancy forces, only a small fraction of eggs is found at the surface (Sundby 1991). Thus, pelagic fish eggs concentrate at various depths from the surface dependent on the extent of the counteracting forces (Sundby 1991).

All three species of small pelagic fishes in the Southern Benguela utilize the Agulhas Bank as their principal spawning area (van der Lingen *et al.* 1998). Small pelagics tend to spawn their eggs above the thermocline at different depths to help retention and transport to nursery areas (Dopolo *et al.* 2005, Osman *et al.* 2010). The highest concentrations of eggs and larvae from all three species are found in the upper layers of the water column (< 100 m, with only a few eggs found > 80 m) (Olivar & Fortuno

1991, Dopolò *et al.* 2005, Osman *et al.* 2010). On the western Agulhas Bank, eggs and larvae were distributed deeper than on the eastern and central Agulhas Bank, most likely due to the deeper thermocline on the western Agulhas Bank (Osman *et al.* 2010). On the western Agulhas Bank the highest egg abundance was in the upper 20 m, with anchovy, redeye round herring and sardine showing relative (% of total) egg abundances of 65%, 49% and 47%, respectively (Dopolò *et al.* 2005). Anchovy early-stage eggs were distributed in the upper 40 m, while early-stage eggs of redeye round herring and sardine were distributed in the upper 80 m and 60 m, respectively (Dopolò *et al.* 2005). Egg distribution on the western Agulhas Bank is facilitated by the spawning depth of the adults, with anchovy spawning in warm well-mixed water above the thermocline (Dopolò *et al.* 2005). Sardine tend to spawn under the Ekman transport layer (water layer that is moved offshore by wind-driven upwelling, extending from ~ 40-60 m) (Stenevik *et al.* 2001, Dopolò *et al.* 2005). Redeye round herring, in contrast, spawn deeper than the other two species (Dopolò *et al.* 2005). On the eastern Agulhas Bank, anchovy and sardine eggs were concentrated in the upper 10 m of the water column (Osman *et al.* 2010). Anchovy spawning in the shallower warmer layers than the other two species decrease their risk of predation by decreasing the time they spend in the embryonic stages. This is reflected in results in Chapter 4, which showed that warmer temperature played a more important role in anchovy spawning than for redeye round herring or sardine. Redeye round herring, in contrast, spawn in deeper water than the other two species, placing their eggs in cooler waters, which likely increase their risk of predation, by resulting in longer embryonic duration (Dopolò *et al.* 2005). Similar spawning depths were reported for anchovy in Japan (*E. japonicus*: upper 20m, Matsuoka *et al.* 2002) and southern California (*E. mordax*: upper 30 m, Moser & Pommeranz 1999 in Dopolò *et al.* 2005). Round herring eggs off the Japanese coast also had a deeper distribution than sardine eggs (Konishi 1980 in Dopolò *et al.* 2005). Sardine *S. sagax* off Namibia in the Northern Benguela (Stenevik *et al.* 2001) and in Australian waters (Fletcher 1999) also spawned at depths between 40 and 60 m.

Clupeiform fish as a group show impressive ranges in egg development rate (5 -100% d⁻¹) and the time taken for eggs to hatch (between 20 days and < 1 day), with both conditions depending on the species and their temperature tolerance at the extremes (Peck *et al.* 2013). This means there are large inter-specific differences in the temperature ranges that support the viable development of fertilized eggs and their hatching into yolk sac larvae (Peck *et al.* 2013). Anchovy eggs in the Southern Benguela took between 21 and 108 hours to hatch at temperatures of 23°C and 12°C, respectively, during hatching experiments, but larvae from eggs that hatched at temperatures less than 14°C were not

viable and/or were deformed (King *et al.* 1978). Sardine took between 30 and 118 hours to hatch during hatching experiments at temperatures between 22°C and 11°C, respectively, and failed to develop viable larvae at temperatures less than 13°C (King 1977). Redeye round herring, in contrast, spawn and can develop viable larvae at colder temperatures than either anchovy or sardine and take between 36 and 135 hours to hatch at temperatures of 20.5°C and 11.0°C, respectively, during hatching experiments (O'Toole & King 1974). These development rates are likely a reflection of spawning depth and spawning habitat. On the western Agulhas Bank late-stage eggs for all three species are most abundant in the upper 20 m of the water column (Dopolo *et al.* 2005), this places them in the Ekman layer in warmer waters (Andrews & Hutchings 1980). Since temperature drives energetic processes in early development (Somarakis *et al.* 2019), egg development times and following early-larval growth rates (Chapter 4) would increase when developing and hatching in warmer waters, as well as increasing the chances of developing viable larvae.

5.4 Larval growth rates

Growth rates in most marine fishes are positively correlated with survival during early life stages, as faster growth rates mean that individuals spend less time in stages where they are particularly vulnerable to predation and starvation; larger larvae are more proficient in feeding and predator avoidance (Kanstinger & Peck 2009). As has been stated before, growth rates in small pelagic fish are set both by temperature and prey availability (Peck *et al.* 2013, Katara 2014). In the Southern Benguela sardine larvae have the fastest growth rates over the first 30 days post first-feeding, followed by anchovy and then redeye round herring (Thomas 1986, Wallace-Fincham 1987); this is consistent with the results in Chapter 4. Anchovy and sardine show fast growth rates in their first six months post-hatching (Brownell 1983, Beckley & van der Lingen 1999, Costalago *et al.* 2020, Sakamoto *et al.* 2020), while redeye round herring show their fastest growth rates between two and three years old (Waldron *et al.* 1991). Temperature has important effects on stage duration, since it affects all component rates of the energy budgets, with cooler temperatures leading to longer larval durations, potentially wider dispersal distances (away from the spawning population) and higher cumulative mortalities (O'Connor *et al.* 2007, Somarakis *et al.* 2019). This was also consistent with findings in Chapter 4, which showed that, in the larval stage, temperature played a more important role than food in the larval stage duration of small pelagic fish in the Southern Benguela, while food played a more important role in determining recruit growth rates.

Peck *et al.* (2013) reviewed the thermal niches (optimal and sub-optimal temperature ranges) for European anchovy and sardine and found that thermal niches for these species are not only species- and stage-specific, but that growth rates for the same species in other systems also differed, depending on the region or system, year of study and/or study type. Comparisons of results from this study with anchovy (Chapter 2) and sardine (Chapter 3) in warmer systems, like the Bay of Biscay and the North-western Mediterranean, showed faster growth rates in these fishes there than in the colder Southern Benguela, which is consistent with Peck *et al.* (2013).

5.5 Schooling behaviour and vertical migration

Schooling behaviour in gregarious fish has been established as an important life history characteristic that influences how fish breed, feed, rest and flee (Peck *et al.* 2021). Clupeid fish schools are highly adaptive structures, in that their sizes, shapes and dynamics relate to abundance, feeding, migration, predator avoidance, conservation of energy and reproduction (Blaxter & Hunter 1982, Cury *et al.* 2000). Similar sized small pelagic fish with similar body forms tend to school together regardless of species (Cury *et al.* 2000, Louw *et al.* 2014), with schooling behaviour commencing just after notochord flexion in larvae (Peck *et al.* 2021). Studies have shown that the schooling transition corresponds to the start of vertical migration and changes in diet (Peck *et al.* 2021). This is an important shift that facilitates escape from the viscous flow regime and modifies the effects of bottom up forcing, changing the capacity of the fish to reach prey and to interact with currents (Peck *et al.* 2021). This change in capacity to reach prey (after notochord flexion and the start of metamorphosis) through schooling and diel vertical migrations is consistent with findings in Chapter 4, where the feeding environment starts playing a more important role than temperature in fish growth rates after fishes reach metamorphosis.

In the Southern Benguela, anchovy, redeye round herring and sardine school together in their first year, diverging in their behaviour and distribution as they grow (Armstrong *et al.* 1991, Roel & Armstrong 1991, Louw *et al.* 2014). Juveniles of the three species aggregate inshore during autumn and winter within the upwelling region of the west coast before moving to the south and south-west coasts to spawn (Armstrong *et al.* 1991). Anchovy mature faster than redeye round herring and sardine; therefore, adult anchovy are often caught with juvenile redeye round herring and sardine. Anchovy adults and juvenile sardine (between one and two years old) tend to aggregate over the mid-shelf and offshore areas towards the eastern boundary of the Southern Benguela, where cold upwelled water mixes with warm Agulhas Current water (Armstrong *et al.* 1991, Mhlongo *et al.* 2015). Redeye

round herring and sardine exhibit similar size-related distribution patterns in the Southern Benguela since they are not as selective as anchovy in their temperature preferences. They show an extended range within their habitat, with adults occurring more frequently towards the shelf-edge (Armstrong *et al.* 1991).

Diel vertical migration is a prevalent behaviour, observed in both marine and freshwater fish and plankton, where animals occur in the deeper layers of the water column during the day and the shallow surface layers during the night, ascending and descending at dusk and dawn, respectively (Wurtsbaugh & Neverman 1988, Mehner & Kasprzak 2011, Brierley 2014). Changing light intensity at twilight is considered an important trigger for vertical migrations, with feeding opportunities, predator avoidance, bioenergetic efficiency or a combination of these being the factors influencing the adaptive value of diel vertical migrations (Mehner & Kasprzak 2011).

In the Southern Benguela, anchovy form dense schools in the midwater and demersal layer during the day (James 1987, van der Lingen *et al.* 2006b) and redeye round herring typically school in the demersal layer during the day, often occurring within 15-20 m of the seabed (Roel & Armstrong 1991, Armstrong *et al.* 1991). A few hours before sunset, these two species start migrating towards the surface and then disperse into the surface scatter layers at night. At sunrise, they migrate back down to the deeper layers and come back together into schools (James 1987, Roel & Armstrong 1991, Armstrong *et al.* 1991, van der Lingen *et al.* 2006b). Juvenile round herring in mixed schools do not perform large-scale vertical migrations (Roel & Armstrong 1991). Sardine in the Southern Benguela show highly variable vertical migration. They are observed throughout the water column during the day, often on or near the bottom. At night they migrate to form a scattering layer close to the surface (Coetzee 1997, van der Lingen *et al.* 2006b).

Most clupeoids and other small pelagic fish species undergo vertical migrations towards surface layers at night (Zwolinski *et al.* 2007). In the Northern Benguela similar vertical migration patterns and differences in shoal depth have been observed for anchovy (Thomas & Schülein 1988), while sardine formed small, scattered schools, and showed no significant differences in shoal depth between night and day (generally remaining in the top 20 m of the water column) (Thomas & Schülein 1988, van der Lingen *et al.* 2006b, van der Lingen *et al.* 2009). Northern anchovy and Pacific sardine off the Washington and Oregon coast (California Current System) followed similar vertical migrations, and schooling patterns also showed a diel pattern, with schools dispersing at night and reforming rapidly into discrete schools at sunrise (Kaltenberg & Benoit-Bird 2009).

Planktivores, in general, display a diel feeding cycle, foraging during either the day or at twilight and by night (James 1988a). Pelagic particulate-feeders in general require light above a certain threshold for visual predation, in which case migrating upwards at dusk increases feeding opportunities at twilight (Blaxter & Hunter 1982, Zwolinski *et al.* 2007). Filter-feeders can feed on abundant or small prey even in darkness (Zwolinski *et al.* 2007). The vertical migrations allow late juvenile and adult redeye round herring and sardine to feed on migrating zooplankton continuously through the day and night (Roel & Armstrong 1991, van der Lingen *et al.* 2006b), although smaller sardine peak in their feeding activity around sunset (van der Lingen *et al.* 2006b). Anchovy, in contrast, show a marked feeding periodicity and are nocturnal foragers; feeding peaked for recruits at dusk and for adults at dawn (James 1987, van der Lingen *et al.* 2006b). These diel vertical migrations facilitate the capacity of these fishes to reach and stay in good feeding environments, which is more important than temperatures experienced, especially post-metamorphosis (Chapter 4).

Sardine in the Humboldt Current and north-eastern Atlantic system show a similar lack of feeding periodicity as those in the Benguela, feeding throughout the diel cycle, whereas anchovy in most other systems show strong feeding periodicity, feeding primarily during daylight hours (van der Lingen *et al.* 2009).

5.6 Feeding dynamics

When examining growth physiology, an understanding of foraging dynamics and feeding behaviour is critical, since growth rates in fish are set by both temperature and prey availability (Peck *et al.* 2013). Some small pelagic fish species can adapt their feeding behaviour to prey resources that are readily available, while other species are more rigid in their feeding behaviour (Peck *et al.* 2013). The ability of microphagous clupeoids to switch between filter-feeding on smaller food items and particulate-feeding on larger food items makes them flexible and highly opportunistic foragers, able to employ the feeding mode that maximizes energy intake in particular environments (van der Lingen *et al.* 2009).

In the Southern Benguela all three species utilize zooplankton as their dominant food source but appear to partition their trophic resources based on particle size (van der Lingen *et al.* 2009). Adult anchovy (James 1987, van der Lingen *et al.* 2006b) and redeye round herring (Wallace-Fincham 1987, Mketsu 2008) preferentially particulate-feed on large zooplankton, although anchovy will switch to filter-feeding for small zooplankton and phytoplankton. Sardine, in contrast, non-selectively

filter-feed on small phytoplankton and zooplankton but can switch to particulate-feeding for large particles at reduced food concentrations (van der Lingen 1994, van der Lingen *et al.* 2006b, van der Lingen *et al.* 2009). These three small pelagic fish species in the Benguela have the ability to adapt their feeding behaviour to increase their food intake while reducing their energy expenditure, independent of prey concentration, to prey fields that are available, or to change their prey fields within their different size spectra (Peck *et al.* 2013). As has been shown in Chapter 4, and stated above, adult small pelagic fish in good body condition from good food environments produce more egg batches. Therefore, by increasing food intake and reducing energy expenditure these fishes would be in better body condition and hence able to spawn more egg batches and better quality eggs (Brosset *et al.* 2016).

Small pelagic fish in other systems similarly showed resource partitioning of food sources. Off northern and western Kyushu (Japan) co-occurring Pacific round herring particulate-fed on large zooplankton and selected large prey items in the water, despite a high abundance of small prey items, while Japanese anchovy preferentially filter-fed on small prey items (Tanaka *et al.* 2006). In most other systems where sardine and anchovy co-occur, adults show size-based partitioning of zooplankton resources (van der Lingen *et al.* 2009 and references therein). In these co-occurring species pairs, sardine generally feed on small zooplankton, often including small calanoid, cyclopoid and poecilostomatoid copepods, and phytoplankton is generally more important in their diet, while anchovy feed on large zooplankton like large calanoid copepods and euphausiids (van der Lingen *et al.* 2009). Peruvian anchoveta and Pacific sardine in the Humboldt Current System similarly feed mainly on zooplankton but forage on larger prey items (e.g., euphausiids) to a greater degree than in other systems (Peck *et al.* 2021).

In the majority of ecosystems where clupeids occur, small pelagic fish larvae and juveniles feed predominantly on zooplankton, with the exception of first-feeding Humboldt anchovy larvae which feed almost exclusively on phytoplankton (van der Lingen *et al.* 2009). Anchovy and sardine recruits in the Southern Benguela have also shown indications of size apportioning when there is a wide range of prey sizes available, with juvenile anchovy ingesting larger copepods than juvenile sardine when these two species shoal together. However, if only small prey sizes are available, no difference is found in their diets (Louw *et al.* 1998). Unfortunately, there is little to no diet information available at present for larval and juvenile redeye round herring and larval anchovy and sardine in the Southern Benguela. In the Californian and Peruvian upwelling systems, however, it has been shown that

anchovy/anchoveta larvae feed preferentially on larger prey items than sardine larvae (Cole 1999, van der Lingen *et al.* 2009).

The adult trophic partitioning mentioned above, in combination with phytoplankton being more important in the diet of sardine than anchovy, leads to sardine consistently feeding at a lower trophic level than anchovy in most systems (van der Lingen *et al.* 2009). In the Southern Benguela redeye round herring feed at a higher trophic level than anchovy and sardine, while sardine feed at a lower trophic level than anchovy (Watermeyer *et al.* 2008, Shannon *et al.* 2020), as evidenced by their Nitrogen isotope ratios (van der Lingen & Miller 2011).

Changing climate and increased upwelling in systems can change the phytoplankton and zooplankton (i.e., lower trophic level) species composition and productivity as well as changing the overall circulation that small pelagic fish experience (Fréon *et al.* 2009, van der Lingen 2021). Increased upwelling in the Southern Benguela would increase the nutrient rich cold water in the region, leading to the development of planktonic communities dominated by large organisms (van der Lingen *et al.* 2006b, van der Lingen 2021). Due to the trophic dissimilarity and resource partitioning of the three species in the Southern Benguela, changing plankton composition would affect the species differently. Anchovy and redeye round herring would likely be favoured during increased upwelling events, since these species preferentially particulate-feed on large prey items (Wallace-Fincham 1987, van der Lingen *et al.* 2006b, Mketsu 2008, van der Lingen 2021). Sardine, on the other hand, are less efficient at removing large particles and would have to switch to particulate-feeding (a feeding strategy that is more energy intensive) to be able to thrive in plankton communities dominated by large organisms and would, therefore, likely be negatively affected should the changing climate in the Southern Benguela lead to large-particle dominated food environments (van der Lingen *et al.* 2006b, van der Lingen 2021).

A summary of all the niche adaptation discussed above for anchovy, redeye round herring and sardine in the Southern Benguela is given in Table 5.1.

Table 5.1 Summary of niche adaptations of anchovy (*Engraulis encrasicolus*), redeye round herring (*Etrumeus whiteheadi*), and sardine (*Sardinops sagax*) in the Southern Benguela.

Adaptation	Anchovy	Redeye round herring	Sardine
Capital vs income breeding	Most extreme income breeder of the three species; invests 65% of assimilated energy into reproduction; shows rapid growth and high batch fecundity in good food environments & negligent growth in poor food environments; highest relative batch fecundity of the three species; with the least number of egg batches spawned per year; shows a “feast or famine” trophic ecology	Most extreme capital breeder of the three species; invests only 46% of assimilated energy into reproduction; shows decoupled dependence on food during spawning season by reducing relative batch fecundity & spawning more frequently over longer periods; lowest relative batch fecundity of the three species; atresia found year-round; with the most egg batches spawned per year; shows a steady state trophic ecology	More to the capital-income side of the continuum; invests 58% of assimilated energy into reproduction; shows decoupled dependence on food during spawning season by reducing relative batch fecundity & spawning more frequently over longer periods; intermediate relative batch fecundity; intermediate number of egg batches spawned per year; shows a steady state trophic ecology
Adult spawning habitat selection	Preferentially spawn in warmer waters (18-20°C); in waters where is temperature associated with copepod abundance; peak spawning during spring & summer; spawns in stable conditions, weak winds, strongly stratified water, in the warm upper mixed layer; cooling climate & increased upwelling likely to affect spawning habitat negatively	Temperate species; spawn over wide range of temperatures; mainly near 200 m isobath; peak spawning during winter & spring; spawns in cooler water temperatures (< 20°C), at time of reversed wind direction, in a stratified & stable water column; spawning habitat less likely to be affected by cooling in region and increased upwelling	Spawns over a wide range of environments; in slightly cooler water than anchovy; time spawning for max. larval food availability; west coast spawning peaks during spring & summer; south coast spawning peaks during winter & spring; spawn in well-mixed layers, with strong winds and fast current speeds; spawning habitat less likely to be affected by changing climate

Table 5.1 (cont.) Summary of niche adaptations of anchovy (*Engraulis encrasicolus*), redeye round herring (*Etrumeus whiteheadi*), and sardine (*Sardinops sagax*) in the Southern Benguela.

Adaptation	Anchovy	Redeye round herring	Sardine
Egg transport and hatching	Spawn in warm well-mixed layer above thermocline; early-stage eggs concentrated in the upper 40 m of the water column on western Agulhas Bank, and upper 10 m on the eastern Agulhas Bank; late-stage eggs concentrated in upper 20 m in warmer waters; fastest hatching time in warmer waters; only develop viable larvae in waters > 14°C	Spawn deeper in cooler water than other two species; early-stage eggs concentrated in the upper 80 m of the water column on western Agulhas Bank; late-stage eggs concentrated in upper 20 m in warmer waters; slowest hatching time of the three species; able to hatch viable larvae in cooler waters (11°C)	Spawn under the Ekman transport layer; early-stage eggs concentrated in the upper 60 m of the water column on western Agulhas Bank; upper 10 m on the eastern Agulhas Bank; late-stage eggs concentrated in upper 20 m in warmer waters; intermediate hatching time between other two species; only develop viable larvae in waters > 13°C
Larval growth rates	Larvae show fastest growth rate 30 days post first-feeding; have their fastest growth rates in the first six months	Larvae show slowest growth rate 30 days post first-feeding; have their fastest growth between age two and three years	Intermediate growth rate 30 days post first-feeding; between other two species; have their fastest growth in first six months
Schooling behaviour and vertical migration	School with other two species in first year; adults are often caught with juveniles of other two species; adults & juvenile sardine aggregate over mid-shelf and offshore; in region where cold upwelled water mix with warm Agulhas Current water	School with other two species in first year; juveniles often caught with adult anchovy & juvenile sardine; shows a similar size-related distribution as sardine due to less selective temperature preferences	School with other two species in first year; juveniles often caught with adult anchovy and juvenile redeye round herring; shows a similar size-related distribution as redeye round herring due to less selective temperature preferences

Table 5.1 (cont.) Summary of niche adaptations of anchovy (*Engraulis encrasicolus*), redeye round herring (*Etrumeus whiteheadi*), and sardine (*Sardinops sagax*) in the Southern Benguela.

Adaptation	Anchovy	Redeye round herring	Sardine
Schooling behaviour and vertical migration (cont.)	Diel vertical migration; occupies the midwater/demersal layer during the day, migrating to surface layer at dusk, occupies surface layer at night and migrate to deeper waters at dawn; nocturnal foragers with marked feeding periodicity; recruit feeding peaks at dusk, while adult feeding peaks at dawn	Diel vertical migration; occupies the demersal layer during the day, migrating to surface layer at dusk, occupies the surface layer at night and migrate to deeper waters at dawn; juveniles in mixed schools do not show large-scale migrations; vertical migrations allow late juveniles & adults to feed continuously throughout the day & night	Vertical migration: distributed throughout water column during day and occupies the scattering layer close to surface at night; vertical migrations allow late juveniles & adults to feed continuously throughout the day & night; with smaller juveniles feeding activity peaking around sunset
Feeding dynamics	Adults preferentially particulate-feed on large zooplankton; can switch to filter-feeding for small phytoplankton & zooplankton at reduced food concentrations; recruits feed on larger prey than sardine when wide range of prey available, otherwise no difference in diets; feeds at an intermediate trophic level between the other two species; likely to be favoured by increased upwelling bringing about an increase in larger prey items	Adults preferentially particulate-feed on large zooplankton; feeds at highest trophic level of the three species; likely to be favoured by increased upwelling bringing about an increase in larger prey items	Adults non-selectively filter-feed on small phytoplankton and zooplankton; can switch to particulate-feeding for large prey at reduced food concentrations; recruits feed on smaller prey than anchovy when wide range of prey available, otherwise no difference in diets; feeds at lowest trophic level of the three species due to small item food preference; likely to be negatively affected by increased upwelling bringing about an increase in larger prey items

Good practice for using pre-existing DEB models.

As the world's fish stock decline, there is a trend in conservation and ecology of increasing reliance on computer models and software to answer pertinent questions, especially in cases where there are limited resources for empirical work (Kettenring *et al.* 2006, Pecquerie *et al.* 2011). This has included investigating the extent to which models and model parameters are transferable among species and subpopulations in fisheries (Pecquerie *et al.* 2011). These trends have the potential to fill gaps in empirical data and have the capacity to improve ecological understanding for conservation and management (Kettenring *et al.* 2006). However, researchers making use of “community” models often do not fully understand basic information about these models, such as the objectives, assumptions, scale, data requirements, outputs, or programming language, unless the information is explicitly outlined (Kettenring *et al.* 2006). This could limit their ability to understand the complexities of the model and could lead to inappropriate use of models (Kettenring *et al.* 2006). Thus, it is essential that researchers invest time to explore potential models they intend to use and try to fully understand the models, to tease out assumptions, objectives, and any other important elements (Kettenring *et al.* 2006).

As has been shown for anchovy (Chapter 2), redeye round herring and sardine (Chapter 3) in the Southern Benguela, dynamic energy budgets (DEBs) are useful tools for describing the flow of energy from food assimilation to maintenance, growth, development, and reproduction as a function of food density and temperature (van der Veer *et al.* 2006, Pecquerie 2008, Nisbet *et al.* 2012), especially where explicit feeding information for larval stages are lacking. This section aims to convey lessons learned in this study that may be useful when planning to use existing DEB models.

One important conclusion from Chapter 2, where anchovy *Engraulis encrasicolus* parameters were compared among populations in the Southern Benguela, Bay of Biscay and North-western Mediterranean Sea, was that care should be taken in assuming that all core DEB parameters are species-specific and thus transferable between regions. It is important to look at environmental (temperature and food availability), biological, and physiological characteristics (growth rates of larvae and recruits) and how they compare to other areas where that same species occurs before creating a DEB model for that species. It is also important to make sure that parameters for species are compared only if they have been calculated at the same reference temperature, since temperature plays such an important role in influencing DEB model parameter values.

Even though DEB parameters may not be species-specific and transferable between regions (Chapter 3), it was shown that the general trend in differences between sardine and anchovy held for both the Southern Benguela and Bay of Biscay. Thus, comparisons between similar groups of species in other regions could be helpful in parameter estimation, as well as deepening understanding of the life history of different fish species in different environments.

As has already been discussed (Chapters 2 - 4), water temperature plays an important role in DEB models, since the body temperature of small pelagic fish affected physiological (growth rates) and metabolic rates (maximum assimilation rate $\{\dot{p}_{Am}\}$ and the somatic maintenance rate $[\dot{p}_M]$) (Pethybridge *et al.* 2013). The reference temperature (T_{ref}) for DEB models is set to 293 K or 20°C. So, when estimating core parameters, the temperature ranges that species are most abundant at needs to be considered, as well as whether the species experience different temperature ranges during different life stages.

Future work

This thesis has highlighted several issues that would need further research to improve DEB models and better resolve the impacts of changing environments on small pelagic fishes in the Southern Benguela. These include:

- 1) Quantification of the energy content of a redeye round herring egg, to better simulate the reproductive dynamics of the species in the DEB model. This is especially important if they are mostly capital breeders (like round herring off Japan) and invest much energy into producing few eggs.
- 2) Modification of the sardine model to consider the western and southern sardine subpopulations. This may include quantifying the energy content of eggs for each subpopulation and investigating whether the spawning interval differs for the two subpopulations. Since the two subpopulations have different peaks in spawning season, this would also need to be modified in the model to make it more subpopulation specific.
- 3) Linking the scaled functional response to feeding environments for the three species. This would include linking not just food quantity but food quality, as that would affect the energy intake. Queiros *et al.* (2019) showed that food size, even without modifying its energy content, is as important for body condition, growth, and lipid reserves as food quantity. As an example, sardines

feeding on small particles had to consume twice as much food to achieve the same growth and condition as those feeding on large particles.

- 4) One of the most important results from this study was the importance of larval and pre-recruit condition on adult small pelagic fish body condition and reproductive output. However, there is little known about the feeding dynamics of early life history stages of these small pelagic fish. Therefore, attempts to estimate food types and whether there is resource partitioning in early life stages could be helpful in linking models to the feeding environment.
- 5) Further interrogation of the larval stage of the models should be pursued by implementing an ‘abj’ DEB model. Existing literature indicated that the length-to-age curve of the larval stage did not follow the von Bertalanffy curve, but that larval growth started slow and accelerated as they grew. This has an impact on the time taken to reach metamorphosis and can be captured well with an ‘abj’ DEB model. This will need to be differently adapted for redeye round herring since they have their accelerated growth in their second year, unlike anchovy and sardine.
- 6) The model parameters should be fitted to the model differential equations using a numerical fitting scheme for differential equations (such as deSolve in R, ode in Matlab or Automatic Differentiation Model Builder (ADMB). This will not only give more accurate estimates of the parameters but can identify possible covariance between the parameters. This will facilitate investigating whether possible trade-offs (caused by the covariance) could account for the difference between the fitted values in the model and those in other studies.

Incorporating individual small pelagic models in population scale models

The main aim of this study was to develop full life cycle models for anchovy, redeye round herring and sardine. This study has primarily focussed on DEB theory and models; however, it is not the only energy model that can be used to describe the full lifecycle of small pelagic fish. Energetics models that focus mainly on allometric relationships (sometimes referred to as ‘Wisconsin type models’ Campos-Candela *et al.* 2019) are based on the pioneering work of Kitchell *et al.* (1977) for modelling fish growth in yellow perch (*Perca flavescens*) and walley (*Stizostedion vitreum vitreum*). Kitchell *et al.* (1977) built their model on earlier work concerning energy partitioning in fish (Deslauriers *et al.* 2017 and references therein). Rudstam (1988) developed a bioenergetics model for Atlantic herring (*Clupea harengus*) in the Baltic where components of energy budgets were modelled as functions of temperature and fish weight and structured after bioenergetic models by Kitchell *et al.* (1977) and

Stewart & Binowski (1986). These models have also successfully been used to model full life cycles of small pelagic fish (Oguz *et al.* 2008, Politikos *et al.* 2011, Politikos *et al.* 2015, Gkanasos *et al.* 2019).

Ito *et al.* (2004) coupled a bioenergetics model (based on the energetics model proposed by Rudstam (1988)), with ecosystem model to investigate the relationship between the growth of Pacific saury (*Cololabis saira*), prey zooplankton density and sea surface temperature (Ito *et al.* 2004). The basic fish bioenergetic/ecosystem coupled model became known as the ‘North Pacific Ecosystem Model for Understanding Regional Oceanography For Including Saury and Herring’ or NEMURO.FISH, was developed by the North Pacific Marine Science Organization (PICES) model task team (Megrey & Kishi 2002) and is composed of a lower level ecosystem model (NEMURO) and a fish bioenergetics model (Ito *et al.* 2004, Okunishi *et al.* 2009, Hamza *et al.* 2021). The NEMURO.FISH model is useful for studying the population dynamics and growth of a variety of commercially important small pelagic species (Ito *et al.* 2004, Megrey *et al.* 2007, Okunishi *et al.* 2009, Okunishi *et al.* 2012a, Hamza *et al.* 2021)

Integrating the information from the individual DEB models for anchovy, redeye round herring and sardine in the Southern Benguela could be scaled up to population level through individual-based models (IBMs). Full-life-cycle energetic IBMs can be coupled with hydrodynamic or physical-biogeochemical models (external forcing) to bring about a mechanistic understanding of how the variability patterns of growth, egg production, recruitment and spawning stock biomass are affected by the physics, biogeochemistry, and biology experienced by fish populations (Gkanasos *et al.* 2019, Bueno-Pardo *et al.* 2020). Coupling energetic IBMs in 1-D configurations (lacking a horizontal dimension for movement/migration) with hydrodynamic or physical-biogeochemical models provides a useful step for calibrating the average trophic and thermal conditions of an ecosystem to growth, egg production and/or population biomass (Gkanasos *et al.* 2019). These 1-D IBMs also provide ways to accurately test the outcomes of management measures, including the reduction of fishing mortality and the effect of temporal fishing bans (Gkanasos *et al.* 2019). Bueno-Pardo *et al.* (2020) used an energetic coupled IBM to hindcast a period of population collapse and recovery for Bay of Biscay anchovy at the beginning of the century, allowing them to study the effects of environmental and human pressures on the population.

Coupled bioenergetic models have been successfully implemented in several studies for European anchovy (*Engraulis encrasicolus*) in the Black Sea (Oguz *et al.* 2008), Bay of Biscay (Pecquerie *et*

al. 2009, Gatti *et al.* 2017, Bueno-Pardo *et al.* 2020), the North Aegean Sea (Politikos *et al.* 2011, Politikos *et al.* 2015, Gkanasos *et al.* 2019) and the Gulf of Lions (Pethybridge *et al.* 2013), as well as for Peruvian anchovy (*Engraulis ringens*) in Peru (Xu *et al.* 2013) and Japanese anchovy (*Engraulis japonicus*) from the East China Sea to Taiwan (Tu *et al.* 2012). Coupled bioenergetic models have also successfully been implemented for several sardine and sardinella studies namely European sardine (*Sardina pilchardus*) in the Bay of Biscay (Gatti *et al.* 2017) and the North Aegean Sea (Gkanasos *et al.* 2019), Japanese sardine (*Sardinops melanostictus*) in the western North Pacific (Okunishi *et al.* 2009, Okunishi *et al.* 2012a, Okunishi *et al.* 2012b), as well as round sardinella (*Sardinella aurita*) off northwest Africa (Brochier *et al.* 2018). Based on either energetic frameworks, the models were either online or offline coupled with regional hydrodynamic and/or biogeochemical models and generally implemented in 1-D configurations for European small pelagic models (Gkanasos *et al.* 2019), 2-D configuration (including fish movement) for Japanese sardine in the western North Pacific (Okunishi *et al.* 2009, Okunishi *et al.* 2012a, Okunishi *et al.* 2012b) and Japanese anchovy in the East China Seas to Taiwan model (Tu *et al.* 2012), and 3-D configurations to the North Aegean (Politikos *et al.* 2015), and Peruvian (Xu *et al.* 2013) anchovy stock and northwest African round sardinella (Brochier *et al.* 2018).

Conclusions

The key hypothesis of this study was that anchovy, redeye round herring and sardine in the Southern Benguela would exploit environmental differences and would adopt different bioenergetic strategies to match these different niches, allowing them to compete and co-occur. Comparisons of some of the niche dynamics of these species showed they have adapted different strategies to best utilize their environment and resources (Table 5.1). These included adults having different breeding strategies (either more capital or more income breeding), spawning habitats (being selective versus not being selective), peaks in spawning season (either in phase or out of phase with each other and the upwelling season) and spawning depths (shallower in warmer water or deeper in cooler water). These three species also adopted similar but slightly different diel vertical migrations for feeding as well as clear patterns in resource partitioning (particle-feeding on large prey and filter-feeding on small prey) to best utilize the food that is available in their environment.

Comparisons with other ecosystems where these species co-occur showed that in many instances thermal and feeding niches are species- and stage-specific, but growth rates especially, depend on region or system and are heavily influenced by temperature and feeding environment. Therefore,

careful consideration is needed when adapting existing DEB models for the same or similar species in different ecosystems.

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Appendix A. Influence of missing DEB parameters on redeye round herring and sardine growth curves

This appendix shows how differing the five missing core parameters from Chapter 3 for redeye round herring and sardine, one at a time influences the growth rates and maximum length and weight values, and the number of egg batches produced during their lifetime.

1. Fraction allocated to growth and maintenance κ

Decreasing the fraction allocated to growth and maintenance (κ) of redeye round herring (0.54) to 0.44 decreased the maximum length by 3.48 cm and increasing κ to 0.64 increased the maximum length by 3.43 cm (Table A.1). The maximum weight decreased by 41.714 g ($\kappa = 0.44$) and increased by 62.256 g at a κ of 0.64. Increasing and decreasing the fraction allocated to growth and maintenance (κ) of sardine by 0.1 increased and decreased the maximum length by 5.08 cm, while a 0.1 increase in κ increased the weight by 175.830 g ($\kappa = 0.52$) and a decrease in κ of sardine to $\kappa = 0.32$ decreased the maximum weight by 109.767 g (Table A.2).

In redeye round herring the number of egg batches produced would decrease by 28 ($\kappa = 0.44$) and by 7 ($\kappa = 0.64$) at higher values of the fraction allocated to growth and maintenance. Increasing κ by 0.1 decreased the number of egg batches produced by sardine by five, while sardine with a $\kappa = 0.35$ would not reach sexual maturity so no egg batches would be produced.

The fraction allocated to growth and maintenance for redeye round herring and affected the growth rate in both species. Increasing κ increased the maximum length achieved in the model and increased the growth rate, meaning that they reached their plateau maximum length faster (Figure A.1 a & d). A change in κ affected the length-weight relationship in such a way that the height of the length-weight curve increased with an increase in κ , however, the shape of the length-weight curve did not change for either species (Figure A.1 c & f).

Table A.1 The effects of changing each parameter on the model output of redeye round herring. Where a_p is age at puberty (days) and in brackets the age in years, L_p is standard length at puberty (cm), L_m is maximum length (cm), W_{wp} is wet weight at puberty (g), W_{wm} is wet weight (g) at maximum length and N_{batch} is the number of egg batches produced by a redeye round herring as predicted by the model during a seven year lifespan.

Parameters	Symbol	Change	Value	a_p (days (years))	L_p (cm)	L_m (cm)	W_{wp} (g)	W_{wm} (g)	N_{batch} (egg batches)
Model				711 (1.9)	12.00	19.32	15.224	87.924	170
Fraction allocated to growth and maintenance	κ	↓	0.44	987 (2.7)	12.01	15.84	15.168	46.210	142
	(-)	↑	0.64	573 (1.6)	12.00	22.75	15.101	150.180	163
Maximum storage density	$[E_m]$	↓	500	553 (1.5)	12.01	19.77	9.347	74.377	189
	(J.cm ⁻³)	↑	5 500	856 (2.3)	12.00	18.74	21.023	103.340	126
Volume-specific maintenance cost	$[\dot{p}_M]_{ref}$	↓	15	577 (1.6)	12.00	28.69	15.224	291.690	183
	(J.cm ⁻³ .d ⁻¹)	↑	35	1 013 (2.8)	12.00	14.21	15.137	30.734	101
Maximum assimilation rate	$\{\dot{p}_{Am}\}_{ref}$	↓	103	-	-	9.81	-	8.249	-
	(J.cm ⁻² .d ⁻¹)	↑	303	401 (1.1)	12.02	28.83	15.326	318.630	199
Volume-specific cost for structure	$[E_G]$	↓	1 000	285 (0.8)	12.01	20.11	15.188	78.948	207
	(J.cm ⁻³)	↑	9 000	1 138 (3.1)	12.00	17.45	15.191	74.743	132

Table A.2 The effects of changing each parameter on the model output of sardine. Where a_p is age at puberty (days) and in brackets the age in years, L_p is standard length at puberty (cm), L_m is maximum length (cm), W_{wp} is wet weight at puberty (g), W_{wm} is wet weight (g) at maximum length and N_{batch} is the number of egg batches produced by a sardine as predicted by the model during a ten year lifespan.

Parameters	Symbol	Change	Value	a_p (days (years))	L_p (cm)	L_m (cm)	W_{wp} (g)	W_{wm} (g)	N_{batch} (egg batches)
Model				559 (1.5)	17.01	21.34	56.443	158.730	209
Fraction allocated to growth and maintenance	κ	↓	0.32	-	-	16.26	-	48.963	0
	(-)	↑	0.52	394 (1.1)	17.01	26.42	56.740	334.560	204
Maximum storage density	$[E_m]$	↓	300	330 (0.9)	17.01	21.34	27.562	108.560	234
	(J.cm ⁻³)	↑	8 300	654 (1.8)	17.01	21.34	85.300	211.810	141
Volume-specific maintenance cost	$[\dot{p}_M]_{ref}$	↓	74	482 (1.3)	17.01	24.22	56.590	255.340	222
	(J.cm ⁻³ .d ⁻¹)	↑	94	696 (1.9)	17.01	19.07	56.231	97.725	141
Maximum assimilation rate	$\{\dot{p}_{Am}\}_{ref}$	↓	856	772 (2.1)	17.00	19.11	56.168	98.538	124
	(J.cm ⁻² .d ⁻¹)	↑	1 056	449 (1.2)	17.02	23.57	56.701	235.450	224
Volume-specific cost for structure	$[E_G]$	↓	3 000	277 (0.8)	17.02	21.34	56.477	131.870	235
	(J.cm ⁻³)	↑	13 000	840 (2.3)	17.00	21.32	56.435	180.670	168

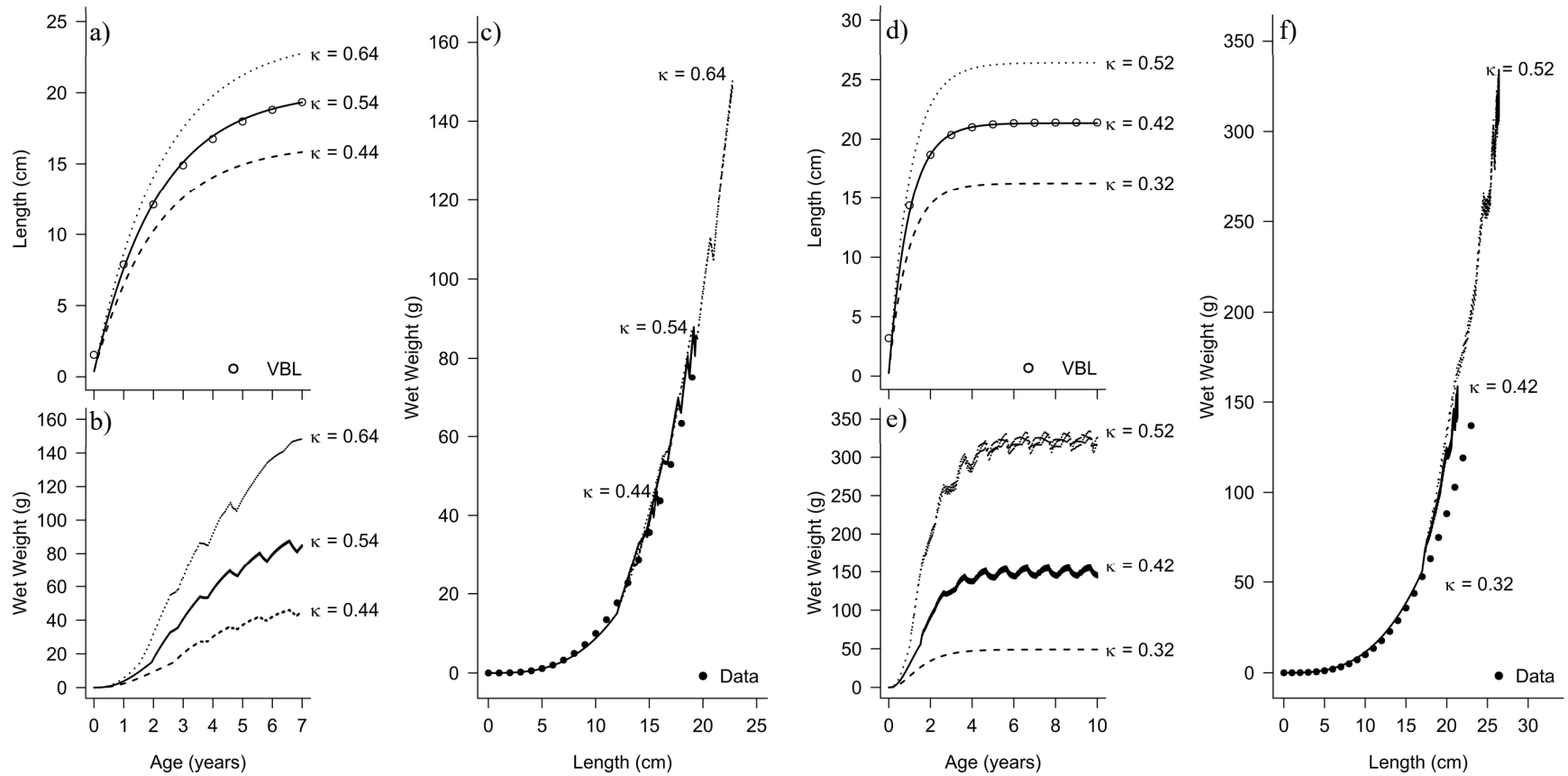


Figure A.1 Effect of different fractions allocated to growth and maintenance (κ) on redeye round herring and sardine growth curves in the Southern Benguela. The effect of κ on the length-at-age of a) redeye round herring and d) sardine. The effect of differing κ on the weight-at-age results of b) redeye round herring and e) sardine. The effect of differing κ on the length-weight relationship of c) redeye round herring and f) sardine. Where the lines represent different values of fractions allocated to growth and maintenance (κ) indicated next to each line, $\circ$ VBL represents the von Bertalanffy growth and $\bullet$ Data represents the length-weight relationship from survey data.

2. Maximum storage density [E_m]

The maximum storage density [E_m] affected the growth rate and weight of redeye round herring and sardine. To illustrate this the optimum [E_m] was varied by $\pm 3\,000\text{ J.cm}^{-3}$ for each species separately (Figure A.2). The increase in [E_m] for both species, showed a slowing in the growth rate, so it would take them longer to reach their plateau maximum lengths (Figure A.2 a & d). Changing [E_m] did, however, not affect the value of the maximum length that redeye round herring and sardine reached by much. In redeye round herring maximum length increased by 0.45 cm with a decrease in [E_m] and decreased by 0.58 cm with an increase in [E_m] (Table A.1). For sardine, increasing and decreasing [E_m] had to no effect of the maximum length (Table A.2).

Increasing [E_m] led to an increase in the maximum weight that redeye round herring and sardine reached, as well as the growth rate, with animals reaching their maximum weight faster at lower values of [E_m] (Figure A.2 b & e). Decreasing [E_m] in redeye round herring decreased the maximum weight by 13.547 g, while increasing [E_m] increased the maximum weight by 15.416 g (Table A.1). Sardine maximum weight decreased by 50.17 g with a decrease in [E_m] and increased by 53.080 g with an increase in [E_m] (Table A.2).

Since [E_m] influenced the growth rate and the maximum weight but not the maximum length of the species, it caused [E_m] to influence the slope of the length-weight relationship of both species (Figure A.2 c & f). Changing [E_m] also lead to a change in the number of egg batches that redeye round herring and sardine produced. For redeye round herring the decrease in [E_m] led to an increase in egg batches of 19 and an increase in [E_m] led to a decrease in the number of egg batches of 44 (Table A.1). The decrease in [E_m] led to an increase in the number of egg batches by 25 in sardine, while the increase of [E_m] led to a decrease of 68 (Table A.2).

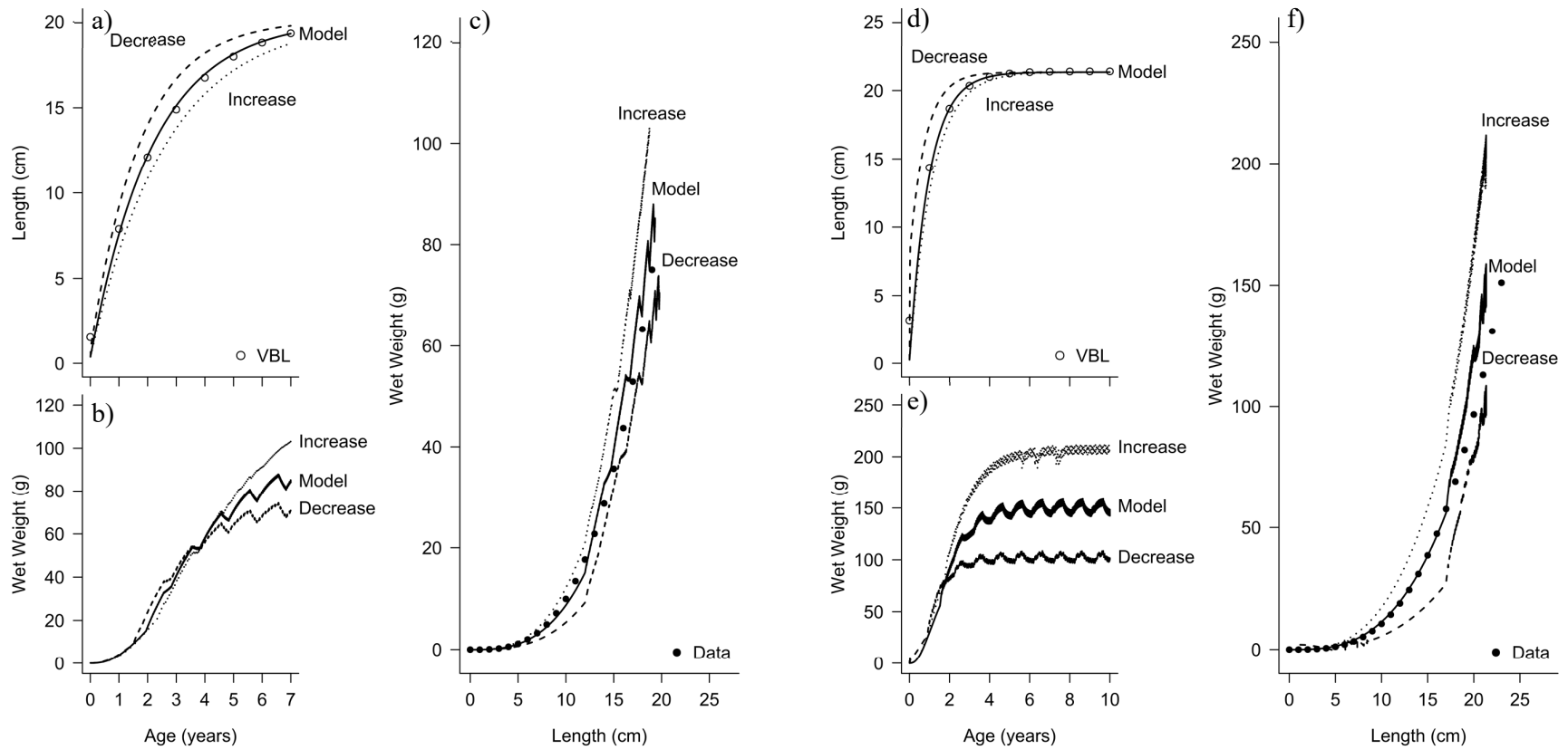


Figure A.2 The influence of the maximum storage density $[E_m]$ ($\text{J}\cdot\text{cm}^{-3}$) on the redeye round herring and sardine DEB model length, weight and age. Where a) and d) illustrates the influence of $[E_m]$ on the length-at-age curve of redeye round herring and sardine, respectively, b) and e) illustrates the influence of $[E_m]$ on the weight-at-age of redeye round herring and sardine, respectively, and c) and f) illustrates the influence of $[E_m]$ on the length-weight relationship of redeye round herring and sardine, respectively. The solid (—) line represents the model output for the optimum value of $[E_m]$, the dotted line (...) shows how an increase in $[E_m]$ influences the shape of the model output, the dashed line (---) shows how a decrease in $[E_m]$ influences the shape of the model output, $\circ$ VBL represents the von Bertalanffy growth and $\bullet$ Data represents the length-weight relationship from survey data.

3. Volume-specific maintenance rate $[\dot{p}_M]_{ref}$

To illustrate how changing $[\dot{p}_M]_{ref}$ would affect the growth curves for both species the $[\dot{p}_M]_{ref}$ values were varied by $\pm 10 \text{ J.cm}^{-3}.\text{d}^{-1}$. The volume-specific maintenance rate $[\dot{p}_M]_{ref}$ influenced both the shape and size of the redeye round herring and sardine growth curves. An increase in $[\dot{p}_M]_{ref}$ led to both species reaching their plateau of maximum length and weight faster and at lower maximum length and weight values (Figure A.3 a-b). The decrease in $[\dot{p}_M]_{ref}$ in redeye round herring led to an increase in the maximum length of 9.37 cm, while an increase in $[\dot{p}_M]_{ref}$ led to a decrease in the maximum length of 5.11 cm (Table A.1). The decrease in $[\dot{p}_M]_{ref}$ in sardine increased the maximum length by 2.88 cm and the increase in $[\dot{p}_M]_{ref}$ decreased the maximum length by 2.27 cm (Table A.2).

Changes in $[\dot{p}_M]_{ref}$ had a large effect on the weight output of the model. Redeye round herring maximum weight increased by 203.766 g with the decrease in $[\dot{p}_M]_{ref}$ and decreased by 57.190 g with the increase in $[\dot{p}_M]_{ref}$ (Table A.1). In sardine the decrease in $[\dot{p}_M]_{ref}$ increased the maximum weight by 96.610 g and an increase in $[\dot{p}_M]_{ref}$ decreased the maximum weight by 61.005 g (Table A.2).

A change in $[\dot{p}_M]_{ref}$ affected the length-weight relationship in such a way that the height of the length-weight curve decreased with an increase in $[\dot{p}_M]_{ref}$, however, the shape of the length-weight curve did not change for either species (Figure A.3 c & f). Changes in $[\dot{p}_M]_{ref}$ also influenced the number of egg batches produced by redeye round herring and sardine. For redeye round herring the decrease in $[\dot{p}_M]_{ref}$ increased the number of egg batches produced by 13, while the increase in $[\dot{p}_M]_{ref}$ decreased the number of egg batches by 69 (Table A.1). The decrease in $[\dot{p}_M]_{ref}$ in sardine increased the number of egg batches produced by 13 and an increase in $[\dot{p}_M]_{ref}$ decreased the number of egg batches by 68 (Table A.2).

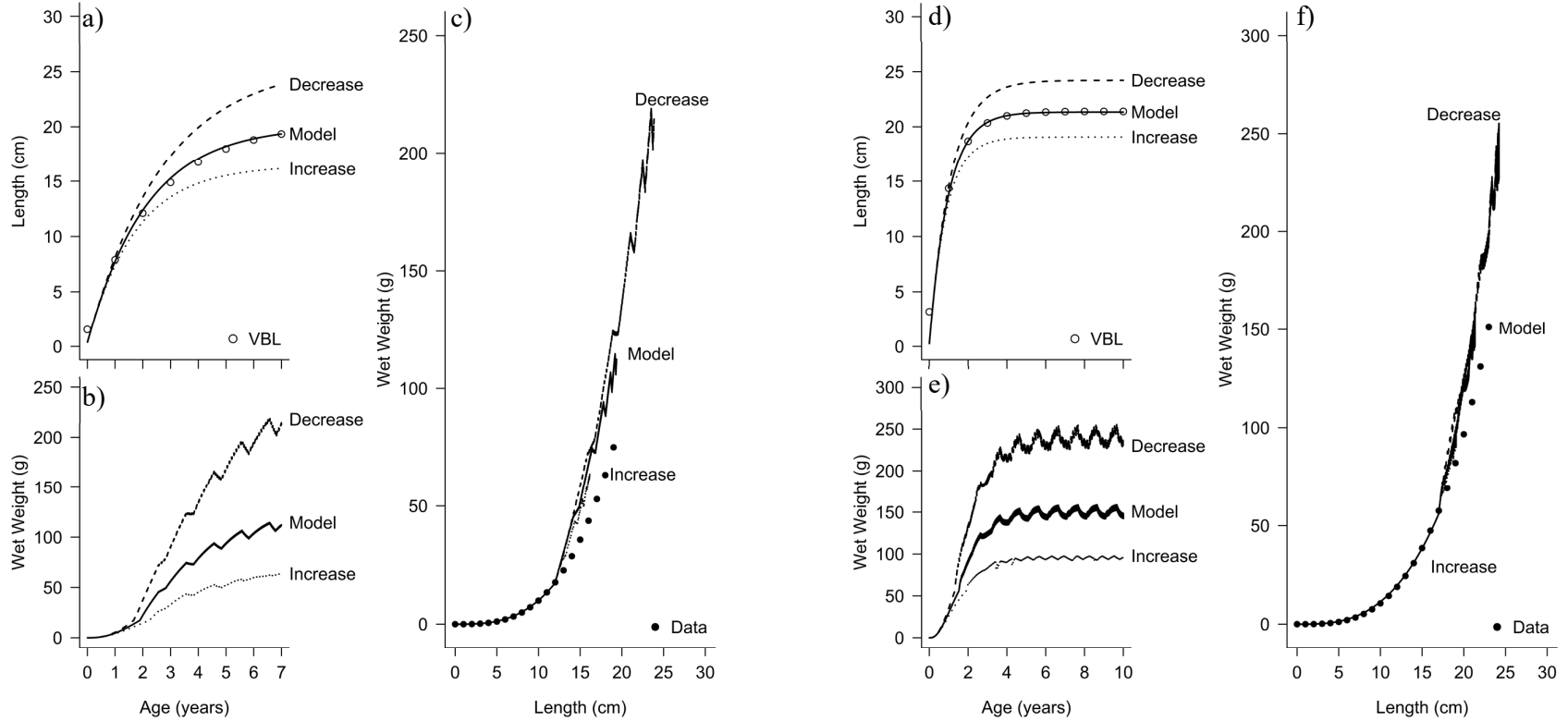


Figure A.3 The influence of the volume-specific maintenance rate $[\dot{p}_M]_{ref}$ ($\text{J} \cdot \text{cm}^{-3} \cdot \text{d}^{-1}$) on the redeye round herring and sardine DEB model length, weight and age. Where a) and d) illustrates the influence of $[\dot{p}_M]_{ref}$ on the length-at-age curve of redeye round herring and sardine, respectively, b) and e) illustrates the influence of $[\dot{p}_M]_{ref}$ on the weight-at-age of redeye round herring and sardine, respectively, and c) and f) illustrates the influence of $[\dot{p}_M]_{ref}$ on the length-weight relationship of redeye round herring and sardine, respectively. The solid (—) line represents the model output for the optimum value of $[\dot{p}_M]_{ref}$ the dotted line (...) shows how an increase in $[\dot{p}_M]_{ref}$ influences the shape of the model output, the dashed line (---) shows how a decrease in $[\dot{p}_M]_{ref}$ influences the shape of the model output, ○ VBL represents the von Bertalanffy growth and ● Data represents the length-weight relationship from survey data.

4. Surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$

The surface-area-specific assimilation rate $\{\dot{p}_{Am}\}_{ref}$ influences both the length and weight variables in the redeye round herring and sardine model. To illustrate how changing $\{\dot{p}_{Am}\}_{ref}$ would affect the growth curves for redeye round herring and sardine the $\{\dot{p}_{Am}\}_{ref}$ values were varied by $\pm 100 \text{ J.cm}^{-2}.\text{d}^{-1}$. An increase in $\{\dot{p}_{Am}\}_{ref}$ led to an increase in the maximum length both species reached in the model, the model also took longer to reach its plateau for the maximum length (Figure A.4 a & d). The increase and decrease in $\{\dot{p}_{Am}\}_{ref}$, respectively, increased and decreased the maximum length of redeye round herring by 9.51 cm (Table A.1) and sardine by 2.23 cm (Table A.2).

An increase in $\{\dot{p}_{Am}\}_{ref}$ led to an increase in the time it took for weight to reach its plateau, as well as the maximum weight reached by both species (Figure A.4 b & e). In redeye round herring the decrease in $\{\dot{p}_{Am}\}_{ref}$ decreased the maximum weight by 79.675 g, while the increase in $\{\dot{p}_{Am}\}_{ref}$ increased the maximum weight by 230.706 g (Table A.1). The decrease in $\{\dot{p}_{Am}\}_{ref}$ decreased the maximum weight in sardine by 60.192 g, while the increase in $\{\dot{p}_{Am}\}_{ref}$ increased the maximum weight by 76.720 g (Table A.2).

Changing $\{\dot{p}_{Am}\}_{ref}$ changed the height but not the slope of the length-weight relationship of both species (Figure A.4 c & f). Changing $\{\dot{p}_{Am}\}_{ref}$ also changed the number of egg batches produced by redeye round herring and sardine.

The number of egg batches was decreased by 170 (fish did not reach sexual maturity) for the decrease in $\{\dot{p}_{Am}\}_{ref}$ in redeye round herring, while the increase in $\{\dot{p}_{Am}\}_{ref}$ increased the number of egg batches produced by 29 (Table A.1). In sardine the decrease in $\{\dot{p}_{Am}\}_{ref}$ decreased the number of egg batches produced by 85, while the increase in $\{\dot{p}_{Am}\}_{ref}$ for sardine increased the number of egg batches produced by 15 (Table A.2).

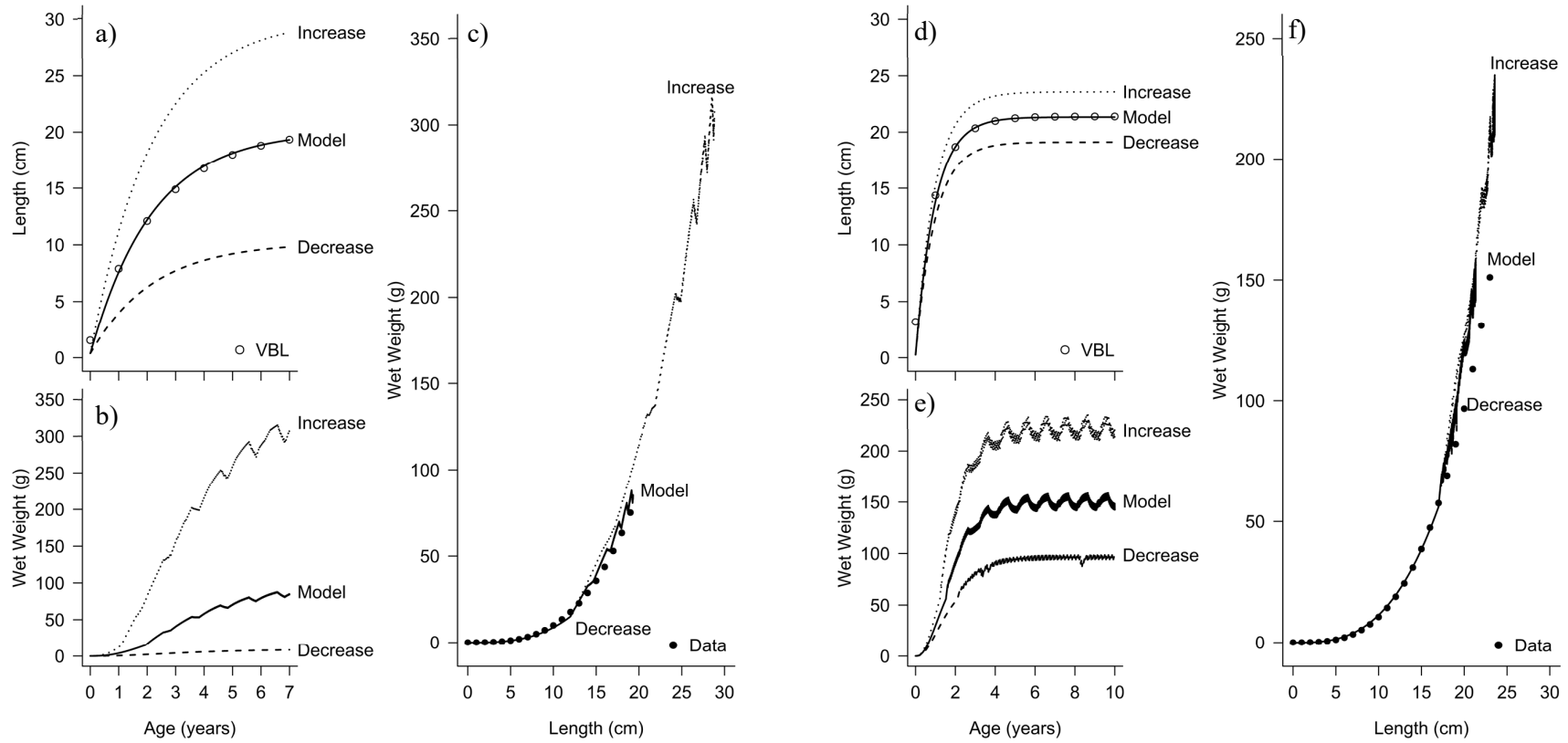


Figure A.4 The influence of the surface-area-specific assimilation rate $\{p_{Am}\}$ ($\text{J} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$) on the redeye round herring and sardine DEB model length, weight and age. Where a) and d) illustrates the influence of $\{p_{Am}\}$ on the length-at-age curve of redeye round herring and sardine, respectively, b) and e) illustrates the influence of $\{p_{Am}\}$ on the weight-at-age of redeye round herring and sardine, respectively, and c) and f) illustrates the influence of $\{p_{Am}\}$ on the length-weight relationship of redeye round herring and sardine, respectively. The solid (—) line represents the model output for the optimum value of $\{p_{Am}\}$, the dotted line (...) shows how an increase in $\{p_{Am}\}$ influences the shape of the model output, the dashed line (---) shows how a decrease in $\{p_{Am}\}$ influences the shape of the model output, $\circ$ VBL represents the von Bertalanffy growth and $\bullet$ Data represents the length-weight relationship from survey data.

5. Volume-specific cost for structure [E_G]

To illustrate how changing [E_G] would affect the growth curves of both species, [E_G] was varied by $\pm 4\,000\text{ J.cm}^{-3}$ for redeye round herring and $\pm 5\,000\text{ J.cm}^{-3}$ for sardine. The volume-specific cost for structure [E_G] influenced the growth rate of redeye round herring and sardine and thus the shape of the length-at-age (Figure A.5 a & d) and the weight-at-age curves (Figure A.5 b & e). Increasing [E_G] increased the time it took for both species to reach their maximum length and weight plateau but did not change the value of the maximum length reached by much. In redeye round herring the decrease in [E_G] increased the maximum length by 0.79 cm and the decreased the maximum weight by 8.976 g, while the increase in [E_G] decreased the maximum length by 1.87 cm and the maximum weight by 13.181 g (Table A.1). In sardine the decrease in [E_G] did not change the maximum length and the increase in [E_G] only decreased the maximum length by 0.02 cm, while the decrease in [E_G] decreased the maximum weight by 26.86 g and the increase in [E_G] increased the maximum weight by 21.94 g (Table A.2).

Changing [E_G] change the height or slope of the length-weight relationship for both species, but only after the fish reached sexual maturity (Figure A.5 c & f). In redeye round herring the decrease in [E_G] increased the number of egg batches by 37, while the increase in [E_G] decreased the number of egg batches by 38 (Table A.1). Decreasing [E_G] in sardine increased the number of egg batches produced by 26, while increasing [E_G] decreased the number of egg batches produced by 41 (Table A.2).

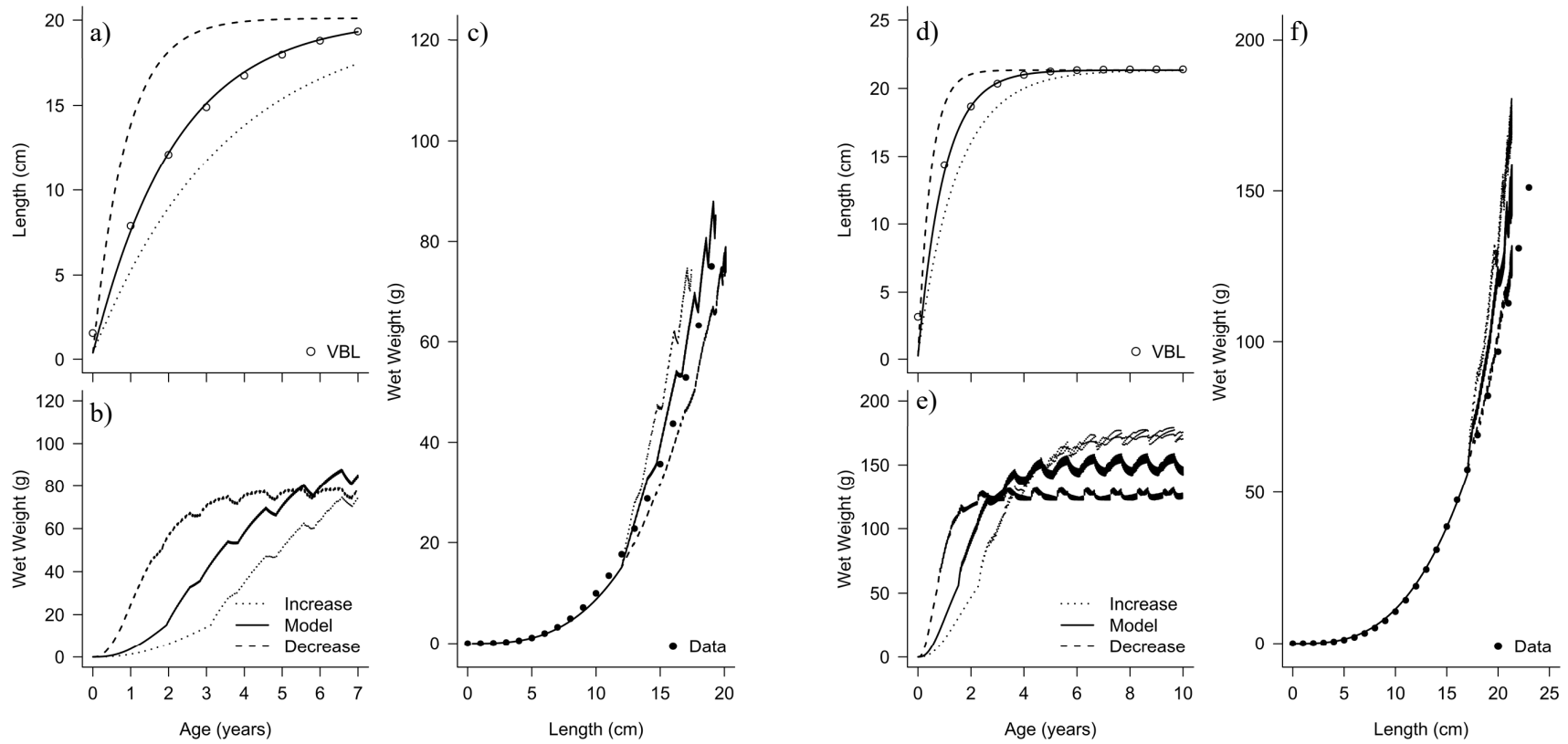


Figure A.5 The influence of the volume-specific cost for structure $[E_G]$ ($\text{J} \cdot \text{cm}^{-3}$) on the redeye round herring and sardine DEB model length, weight and age. Where a) and d) illustrates the influence of $[E_G]$ on the length-at-age curve of redeye round herring and sardine, respectively, b) and e) illustrates the influence of $[E_G]$ on the weight-at-age of redeye round herring and sardine, respectively, and c) and f) illustrates the influence of $[E_G]$ on the length-weight relationship of redeye round herring and sardine, respectively. The solid (—) line represents the model output for the optimum value of $[E_G]$ the dotted line (...) shows how an increase in $[E_G]$ influences the shape of the model output, the dashed line (---) shows how a decrease in $[E_G]$ influences the shape of the model output, $\circ$ VBL represents the von Bertalanffy growth and $\bullet$ Data represents the length-weight relationship from survey data.