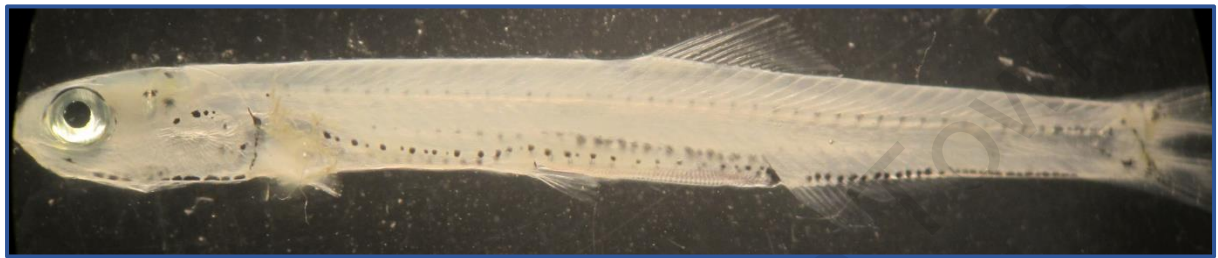


Investigating the trophic ecologies of early life stages of small pelagic fishes in the Benguela upwelling ecosystem



Thesis Presented for the Degree of
DOCTOR OF PHILOSOPHY
In the Department of Biological Sciences
UNIVERSITY OF CAPE TOWN
February 2023

Submitted by
Matthew Christopher Horton

Supervised by
Dr (Professor) Lynne J. Shannon
Dr Carl D. van der Lingen

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

Declarations

I declare that this thesis is my work and has been written in the full support of both supervisors: Dr (Professor) Lynne J. Shannon and Dr Carl D. van der Lingen. I certify that this work has not been submitted wholly or partially for any other degree of examination in any other University, and each contribution to or quotation in this thesis has been properly acknowledged, cited, and referenced.

The Ecopath with Ecosim model, which is a direct modification of the original model and used previously provided fitting data subject to agreed PIAI conditions, will not be made publicly available. The model presented herein refines the original model which is the intellectual property of the original author and their funders.

Signature

Matthew C. Horton

Date: 08/02/2023

Contents

Abstract	6
Acknowledgements	8
List of Figures	9
List of Tables	12
List of Acronyms	14
Chapter 1	17
1.1. Small Pelagic Fishes	17
1.2. Benguela Upwelling System	20
1.2.1. Environmental Changes in the Benguela	21
1.2.2. Primary and Secondary Production Changes in the Benguela.....	23
1.3. Small Pelagic Fishes Distribution and Ecology.....	25
1.3.1. Sardine <i>Sardinops sagax</i>	25
1.3.2. Anchovy <i>Engraulis encrasicolus</i>	28
1.3.3. West coast round herring <i>Etrumeus whiteheadi</i>	30
1.4. Small Pelagic Fishes Trophic Ecologies	31
1.5. Small Pelagic Fishes Recruitment Variability	36
1.5.1. Early Life Stage Mortality	39
1.5.2. Ontogenetic Shifts in Feeding Success	41
1.6. Ecopath for the Southern Benguela	42
1.7. Objectives of this Thesis	43
1.8. Outline of Thesis Structure.....	44
Chapter 2	46
2.1. Introduction	46
2.2. Methods	46
2.2.1. Collection.....	46
2.3. Results	49

2.4.	Discussion	58
Chapter 3		61
3.1.	Introduction	61
3.2.	Methods	64
3.3.	Results	73
3.4.	Discussion	80
Chapter 4		87
4.1.	Introduction	88
4.2.	Methods	90
4.3.	Results	100
4.4.	Discussion	117
Chapter 5		126
5.1.	Introduction	127
5.2.	Methods	130
5.3.	Results	136
5.4.	Discussion	150
Chapter 6		158
6.1.	Introduction	159
6.2.	Methods	161
6.3.	Results	166
6.4.	Discussion	180
Chapter 7		190
7.1.	Overview	190
7.2.	Ontogenetic Development.....	191
7.3.	Sources of Trophic Partitioning.....	195
7.4.	Recruitment and Climate Changes	197
7.5.	Comparative Trophic Ecology of Clupeoids.....	201

7.6.	Effects of Including Early Life Stages in Models.....	209
7.7.	Limitations and Future Work.....	212
7.8.	Conclusion	214
References		216
Supplementary Information		263
	PREBAL Diagnostics.....	263

Abstract

The Benguela upwelling system, located on the west coast of southern Africa, harbours large biomasses of three small pelagic fishes; anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and west coast round herring *Etrumeus whiteheadi*. Despite fisheries management interventions, stocks of sardine have been low for the past decade following consecutive years of poor recruitment. This has highlighted that despite low fishing mortality, variance in recruitment may be largely governed by fluctuations in early-stage mortality rates. Therefore, examining early life traits that may explain a fraction of this mortality could be fundamental to understanding the underlying mechanics of recruitment. This study seeks to investigate the ontogenetic development in morphology and trophic ecology of early life stages of these three small pelagic fish species in the Benguela, and how they compare interspecifically and spatially. Increasing our temporal resolution of the ecological ontogeny of a species will enable accurate future analysis of trophic pathways and linkages within ecosystems and their feedback to vital ecosystem services such as fisheries.

Results show that there is a high likelihood of trophic partitioning between sardine and anchovy larvae through distinct differences in their ecomorphology. Sardines exhibit traits in their development such as increased relative gut length, that would suggest a higher degree of herbivory compared to anchovy. Contrastingly, anchovy display positive allometric growth patterns in their cranial development at a younger age, suggesting a greater importance of particulate feeding on larger prey. These results provide an anatomical basis of how both the feeding ability and behaviour of these two species may differ which would predispose them to distinct diets.

Both species exhibited trophic progression inferred through (a) a ^{15}N enrichment and (b) an increase in carnivory fatty acid trophic markers. Interspecific partitioning is facilitated through distinctions in prey-size composition, with anchovy consuming comparatively larger prey than sardine. Surprisingly, sardine exhibit a higher $\delta^{15}\text{N}$, arising from the increased presence of smaller carnivorous copepods in their diet, which highlights the complexity of the food web dynamics in the Benguela. Prey-size selection is an important regulator of both intra- and interspecific competition in these species.

Round herring pre-recruits are further trophically disassociated from sardine than anchovy, consuming on average larger particles with very little herbivory compared to sardine and anchovy. This was corroborated by (a) a ^{15}N enrichment from sardine to anchovy to round herring indicative of feeding at higher trophic levels, and (b) ^{13}C depletion in the opposite order, indicative of a reduced dependence on autotrophic components. Stomach content analysis suggested substantial filter-feeding for anchovy and sardine, but relatively little for round herring. Therefore, the compounding effect of the feeding mode with the functional traits provides potential answers for variances seen in their trophic ecology.

The Ecopath model that included a finer life history of anchovy, sardine and round herring exhibited substantially more small pelagic fish-centred trophic pathways that were previously grouped into plankton groups than the model that did not. As a consequence, there was an improvement in model fit of 14 out of the 19 functional group time series analysed. In terms of overall model function, there was no change in biomass or system variability. However, there was a significant change in the trophic level estimation of functional groups, that had system-wide ramifications. This study has shown that despite the relative mass insignificance of small pelagic larvae in the system, they still have a considerable effect on the ecosystem dynamics. However, it seems that when disaggregating functional groups into life history stanza, if the same increase in resolution is not reflected in their prey, then vital trophic relationships can be lost.

This research has highlighted crucial distinctions between the ecology of anchovy and sardine early life stages that may give rise to differences in condition and starvation and hence mortality in the face of varying prey compositions. The foundational work detailed here will contribute to future studies aimed at understanding the population dynamics of these species, and so contribute to the already multi-faceted toolkit that aims to sustainably manage the small pelagic fisheries of the Benguela.

Acknowledgements

There have been a lot of people who have pivotal to this thesis, and I want to express a massive thank you to all of you. Although I unfortunately won't be able to thank you all, there are a few that deserves a special mention.

I am entirely grateful to both the scientific staff and boat crew aboard the M153 research cruise. To the crew of the Mesozoo- and Ichthyoplankton group, Dr Werner Ekau, Dr Tim Dudeck, Dr Caroline Müller and Stefanie Bröhl, thanks so much for the hard hours you all put in on the cruise, tirelessly taking net samples and helping me understand German nautical vocabulary. Sir Hans Verheye, I am forever grateful for you transporting my precious samples on dry ice back to UCT.

To the colleagues that selflessly took the time to teach me new scientific methods; Lisa Mansfield from the Sea Point DFFE aquarium, thank you for teaching me phytoplankton taxonomy and how to use inverted microscopes. Raika, Connie and Steffi from the ZMT, thank you for taking the time to re-teach me basic biology and chemistry!

It goes without saying that this project would not have been possible without the calm and consistent guidance of my fantastic supervisors. Your overarching perspective on the position of this thesis really developed it into a complete, conceptual piece of work. Carl's attentiveness, eye for detail and encyclopaedic knowledge on small pelagic fish have been invaluable throughout this entire project, and I could not be without. Lynne's cheerful delivery of corrections, willingness to talk and incredible modelling tuition has given me a quiet, but necessary confidence throughout this journey.

The Horton's - I could not have asked for a more supportive family. Mum and Dad, thank you for giving me the support and opportunity to do exactly what I wanted to do, and for making me totally fish mad. It is safe to say that this thesis is a result of this madness. To Gramps, you have helped me produce this work through your unwavering support, and I cannot thank you enough. This piece of work is mostly for you all.

Lastly to Mia. You've encouraged, motivated, comforted and even consoled me through this whole process, and I can't even start to express my gratitude. Your own motivation and dedication have inspired me to finish this. You mean the world to me.

List of Figures

Chapter 1	Page
Figure 1.1. Descriptive fishery statistics of the small pelagic fishery in South Africa	19
Figure 1.2. Historical catches of sardine <i>Sardinops sagax</i> and anchovy <i>Engraulis encrasicolus</i> in Namibia.....	20
Figure 1.3. Small pelagic fish specific coastal areas in Namibia	27
Figure 1.4. Small pelagic fish specific coastal areas in South Africa	28
Figure 1.5. Spawner-recruitment relationship of anchovy, sardine and round herring in the southern Benguela	37
 Chapter 2	
Figure 2.1. Sampled stations during the M153 research cruise	48
Figure 2.2. Density of sardine and anchovy during the M153 research cruise	50
Figure 2.3. The length frequency of (a) nBUS anchovy, (b) sBUS anchovy and (c) nBUS sardine, caught at different depths.....	51
Figure 2.4. Distribution of pre-recruit samples from DFFE	52
Figure 2.5. Length-frequencies of fish samples	52
Figure 2.6. Spatial distribution of pre-recruit samples in accordance with SST (°C), Dissolved oxygen (ml l ⁻¹) and Chl content (mg m ⁻³)	54
Figure 2.7. Spatial distribution of M153 samples in accordance with SST (°C)	55
Figure 2.8. Depth and dissolved oxygen concentration (ml l ⁻¹) of M153 samples	56
Figure 2.9. Depth and chlorophyll- <i>a</i> concentration (mg ml ⁻³) of M153 samples	57
 Chapter 3	
Figure 3.1. Stations sampled from the M153 cruise, and the samples supplied by the SHARP DFFE program	66
Figure 3.2. Schematic of the left, lateral gill arch	67
Figure 3.3. Morphometric measurements taken of larvae	68
Figure 3.4. The relationship between gape size and caudal length for anchovy and sardine	74
Figure 3.5. The relationship between relative gut length and caudal length for anchovy and sardine	75

Figure 3.6.	The relationship between (a) the number of- and (b) the initial growth of pyloric caeca and caudal length for anchovy and sardine	75
Figure 3.7.	The relationship between the branchial basket measurements and caudal length for anchovy and sardine	77
Figure 3.8.	The piecewise regression of the PC2 scores from the separate principal component analyses fitted to the species-specific covariance matrix of log-transformed morphometric data, against the caudal length (mm) for both anchovy and sardine	78
Figure 3.9.	PC1 scores of the separate PCAs fitted to the pre- and post-metamorphosis individuals for both anchovy and sardine	80

Chapter 4

Figure 4.1.	Stations sampled in the southern and northern Benguela aboard the M153 cruise	92
Figure 4.2.	Quantile regression on the maximum prey size for anchovy and sardine larvae	101
Figure 4.3.	Contribution to dietary carbon by prey taxa for anchovy and sardine	105
Figure 4.4.	Contribution to dietary carbon by prey size for anchovy and sardine taxa	106
Figure 4.5.	Isotopic biplot for sardine and anchovy	108
Figure 4.6.	The effects of the independent variables included in both the isotope GLMs ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$)	109
Figure 4.7.	$\delta^{15}\text{N}$ GLM model output of caudal length (mm) for both anchovy and sardine.....	110
Figure 4.8.	The principal component analysis performed on the fatty acid data for anchovy and sardine	113
Figure 4.9.	Results of the GLMs fitted to the fatty acid trophic markers and ratios for anchovy and sardine	115
Figure 4.10.	Plots of the mean ($\pm$ SE) of the $\delta^{15}\text{N}$ (‰) and (a) PUFA/SFA ratio, (b) EPA/DHA ratio, (c) Carnivory ratio and (d) Diatom ratio for the three species groups split into separate ontogenetic stages (5 – 15mm, 15 – 25 mm and 25 – 35 mm), with the output of the linear model fitted	117

Chapter 5

Figure 5.1.	Total biomass and recruitment of anchovy, sardine and round herring in the southern Benguela	128
-------------	--	-----

Figure 5.2.	Distribution of small pelagic pre-recruit samples	131
Figure 5.3.	Schematic of the left, lateral gill arch	132
Figure 5.4.	The relationship of relative gut length and pyloric caeca counts to caudal length for the three small pelagic species	137
Figure 5.5.	The gape size relative to caudal length for the three small pelagic species	138
Figure 5.6.	The relationship between the branchial basket measurements and caudal length for the three small pelagic species	140
Figure 5.7.	Quantile regression on the maximum prey size for the three small pelagic species	141
Figure 5.8.	Contribution to dietary carbon by prey taxa for the three small pelagic species	145
Figure 5.9.	Contribution to dietary carbon by prey size for the three small pelagic species	146
Figure 5.10.	The isotopic biplot of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the three pre-recruit species .	148
Figure 5.11.	Shows (a) the difference in mean $\delta^{15}\text{N}$ (‰) with standard deviation bars between the three species, and (b) the effects of the independent variables (Caudal length [mm] and species) in the GLM used to explain the variation within the $\delta^{13}\text{C}$ (‰) data	149

Chapter 6

Figure 6.1.	The environmental anomaly fitted to the small-celled phytoplankton group for the disaggregated and original model.....	167
Figure 6.2.	Standardised predicted biomass from the disaggregated model for life history stages of anchovy and sardine	172
Figure 6.3.	The forcing functions (FF) applied to (a) large-celled phytoplankton and (b) juvenile and adult sardine, and the model predicted biomass of (c) the three zooplankton groups and (d) adult sardine.	172
Figure 6.4.	Model fits of anchovy and sardine comparing both the original model (Shannon et al., 2020) and the new disaggregated model	174
Figure 6.5.	Model fits of anchovy and sardine predators comparing both the original model (Shannon et al., 2020) and the new disaggregated model	176
Figure 6.6.	The calculated indices for both the disaggregated and original model over the modelled time series.....	179

Chapter 7

Figure 7.1.	Combined gape size and relative gut length analysis from Chapters 3 and 5	192
Figure 7.2.	The combined branchial basket analyses from Chapters 3 and 5	194
Figure 7.3.	Combined analyses of contribution to dietary carbon by prey size from Chapters 4 and 5	196
Figure 7.4.	The combined stable isotope analysis from Chapters 4 and 5; represents the isotopic biplot of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the three species	197
Figure 7.5.	Stable isotope ratios of N^{15} and C^{13} for the three small pelagic species in southern Africa from the following studies: this study, Geist (2013), Sholto-Douglas (1992), Sholto-Douglas et al. (1991) and van der Lingen and Miller (2011)	205
Figure 7.6.	The contribution to dietary carbon (%) of site-categorised prey items for anchovy, <i>sardine</i> , and round herring in the Benguela from the following studies: this study, James (1987) and van der Lingen (2002)	206
Figure 7.7.	Branchial basket measurements for anchovy <i>Engraulis encrasicolus</i> in southern Africa	207
Figure 7.8.	Branchial basket measurements for sardine <i>Sardinops sagax</i> in southern Africa	208
Figure 7.9.	Branchial basket measurements for round herring <i>Etrumeus whiteheadi</i> in southern Africa	209

List of Tables

Chapter 1		Page
Table 1.1.	Ecological and life history characteristics of the three-study species.....	32
Chapter 2		
Table 2.1.	Descriptive statistics of the caudal length (mm) of the samples obtained for this thesis	53
Chapter 3		

Table 3.1.	Results from the multivariate general linear model applied on the branchial basket characteristics for larval anchovy and sardine	76
Table 3.2.	Results of the fit piecewise regression fit on the PC2 and caudal length data for both anchovy and sardine.	79
Chapter 4		
Table 4.1.	Regressions used to calculate the dry weight and carbon content of prey items described from the stomach content analysis	93
Table 4.2.	Summary of FATM and FA ratios.....	100
Table 4.3.	The feeding incidence in larval species caught in the nBUS and sBUS	101
Table 4.4.	Prey index values by prey category for the two larval species	103
Table 4.5.	Stable isotope indices calculated for the three species groups	108
Table 4.6.	Results of the two GLMs fitted for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with unique explanatory variables.....	109
Table 4.7.	Sensitivity analyses results showing the GLMs fitted for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to fish under 20 mm in caudal length.....	110
Table 4.8.	Fatty acid composition of tissue samples taken from both anchovy and sardine from the southern and northern Benguela.	112
Table 4.9.	Results from the multivariate GLMs applied for specific fatty acid trophic markers and ratios for anchovy and sardine larvae	114
Chapter 5		
Table 5.1.	Results from the multivariate general linear model applied to the branchial basket measurements for anchovy, sardine and round herring	139
Table 5.2.	Prey index values by assigned prey category, for the stomach content results of anchovy, sardine and round herring juveniles	143
Table 5.3.	Stable isotope indices calculated or the three juvenile species	147
Table 5.4.	Results of the two GLMs fitted to both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with unique explanatory variables	149
Chapter 6		
Table 6.1.	The number of functional groups included in a selection of Ecopath model case studies over periods of their development	160

Table 6.2.	Shows the age (months) and length (mm) of the different life history stages represented for the three small pelagic species in the new disaggregated model	162
Table 6.3.	Justification of the new predator-prey interactions involving larval small pelagic fish, included in the new disaggregated model.....	164
Table 6.4.	New diet parameters calculated for the disaggregated functional groups based on the 1978 model, based on dietary information from Chapter 4 and 5.....	167
Table 6.5.	New model parameters for the disaggregated functional groups based on the 1978 model	168
Table 6.6.	Model comparisons between the Ecopath and Ecosim model produced by Shannon et al. (2020) and the disaggregated model produced in this study	170
Table 6.7.	The differences in both predator consumption (ΣQ) and number of predator pathways (total pathways [unique pathways]) for the two models	171
Table 6.8.	Model indicator mean and standard deviation for the entire time series of estimates of both models for the indices utilised	180

List of Acronyms

ABFZ	Angola-Benguela Frontal Zone
AIP	Allometric Inflection Point
ANOSIM	One-Way Analysis of Similarity
BD	Body Depth
BUS	Benguela Upwelling System
CL	Caudal Length
CpD	Body Depth at Caudal Peduncle
DFFE	Department of Forestry, Fisheries and the Environment
DHA	Docosaheptaenoic Acid
EBFM	Ecosystem-Based Fishery Management
EBUS	Eastern Boundary Upwelling Systems
EEZ	Economic Exclusion Zone
EFA	Essential Fatty Acids

EPA	Eicosapentaenoic Acid
EwE	Ecopath with Ecosim
FA	Fatty Acids
FAMEs	Fatty Acid Methyl Ester Derivatives
FATM	Fatty Acid Trophic Markers
FF	Forcing Function
FL	Fork Length
GLM	Generalised Linear Model
HD	Head Depth
HDo	Head Depth at the Operculum
IRI	Indices of Relative Importance
L	Prosome Length
HL	Head Length
MidL	Mid Lateral Line Length
MPA	Marine Protected Area
MUFA	Monounsaturated Fatty Acids
nBUS	Northern Benguela
OMZ	Oxygen Minimum Zone
PCA	Principal Component Analysis
PostAFL	Posterior Anal Fin Margin Length
PostAL	Post- Anal Fin Length
PostDFL	Post-Dorsal Fin Length
PP	Primary Productivity
PreAFL	Pre-Anal Fin Length
PreDFL	Pre-Dorsal Fin Length
PUFA	Polyunsaturated Fatty Acids
sBUS	Southern Benguela
SE	Standard Error
SEA	Standard Ellipses Area
SFA	Saturated Fatty Acids
SIA	Stable Isotope Analysis
SHARP	Sardine, Hake and Anchovy Recruitment Programme
SNL	Snout Length

SS	Residual Sum of Squares
SST	Sea Surface Temperature
TAC	Total Allowable Catch
TAB	Total Allowable Bycatch
TFA	Total Fatty Acids
TL	Total Length
TRAFFIC	Trophic tRansfer eFFICIency in the Benguela Current
W	Width or Prosome Width
%N_p	Percentage Number of Prey Item <i>p</i>
%CC_p	Percentage Contribution to Dietary Carbon of Prey Item <i>p</i>
%F_p	Frequency of Occurrence of Prey Item <i>p</i>

Chapter 1

Introduction

1.1. Small Pelagic Fishes

Small pelagic fishes (e.g., sardines, anchovies and herrings) have great ecological and commercial importance. They perform crucial intermediary roles within an ecosystem, enforcing both regulatory top-down and bottom-up control (Cury et al., 2000), demonstrated through studies highlighting the population changes in dependent species, such as seabirds (Crawford et al., 2011; Cury et al., 2011), predatory fish (Muck, 1989; Parker et al., 2020) and crustacean zooplankton (Verheye et al., 1998). Since the onset of industrial fishing, small pelagic fishes have dominated the global catch, for example in 2018, 23% was attributed to the small pelagic sector (FAO, 2020). They are typified by exhibiting large decadal and interannual variations in biomass, stimulating the ongoing discussion to whether anthropogenic impacts or natural environmental variations have provoked such fluctuations (Cochrane & Hutchings, 1995; Richardson et al., 1998; Essington et al., 2015; Szuwalski & Hilborn, 2015; Costalago et al., 2018). They often occupy highly variable environments such as eastern boundary upwelling systems, making it challenging to disentangle the contributing factors that explain these complex population dynamics.

The Benguela upwelling system (BUS), located on the west coast of southern Africa (Cury & Shannon, 2004; Hutchings et al., 2009; Kirkman et al., 2016), is divided into three distinct regions; the northern BUS (nBUS), the southern BUS (sBUS) and the Lüderitz upwelling cell that divides the two. It harbours large biomasses of three small pelagic fishes; anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and west coast round herring *Etrumeus whiteheadi* (hereafter referred to as round herring). These are short-lived, early maturing, serial broadcast spawners (Blaxter & Hunter, 1982; Roel & Melo, 1990; Melo, 1994a; b; Akkers et al., 1996; Beckley & van der Lingen, 1999; Geja et al., 2016) that primarily feed on phytoplankton and zooplankton (Blaxter & Hunter, 1982; James, 1988; Garrido & van der Lingen, 2014). These species exhibit large variations in recruitment success and subsequent population size (Checkley et al., 2009; DEFF, 2020).

The sBUS located in South Africa supports the two largest South African fisheries: in terms of catch, the small pelagic purse seine fishery predominantly targeting anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi*, and in value, the hake fishery targeting the shallow-water *Merluccius capensis* and deep-water hake *M. paradoxus* (DEFF, 2020). Initially, the purse-seine fishery targeted predominantly sardine and horse mackerel *Trachurus capensis*. Catches for both species curtailed through the mid/late 1960s, with peaks in sardine catches at 400,000 tons in the early 1960s (van der Lingen et al., 2006c). As a consequence of dwindling catch, an exploratory fishery for anchovy was established in the early 1970s by implementing smaller mesh sizes (Newman et al., 1979). Anchovy then became the dominant catch of the purse seine fishery with catches averaging at 200,000 tons, whilst sardine fell dramatically to averaging 50,000 tons during the 70s and 80s (van der Lingen et al., 2006c). Anchovy catches briefly fell during the mid-1990s, from its peak of 600,000 tons in the late 1980s to 40,000 tons in 1996. However, both species made a substantial return during the early 2000s accumulating in a combined catch in excess of 500,000 tons during the early and mid-2000s (Figure, 1.1.; DEFF, 2020). Following these successful years of recruitment, sardine catches, and biomass fell again due to successive years of poor recruitment. The fishery has returned to its previous state, with anchovy being the dominant catch averaging around 200,000 tons and sardine contributing approximately 50,000 tons (DEFF, 2020).

Round herring catches were first recorded in the late 1950s and have since never exceeded 100,000 tons (Roel & Armstrong, 1991; DEFF, 2020). Despite biomass being greater than the long-term average, catches have remained stable at approximately 50,000 tons, half of the implemented precautionary upper catch limit (DEFF, 2020). As an underexploited resource, attempts are being made to increase catches through other forms of fishing (DEFF, 2020). Despite fisheries management interventions, stocks of sardine have been low for the past decade following consecutive years of poor recruitment (de Moor, 2019).

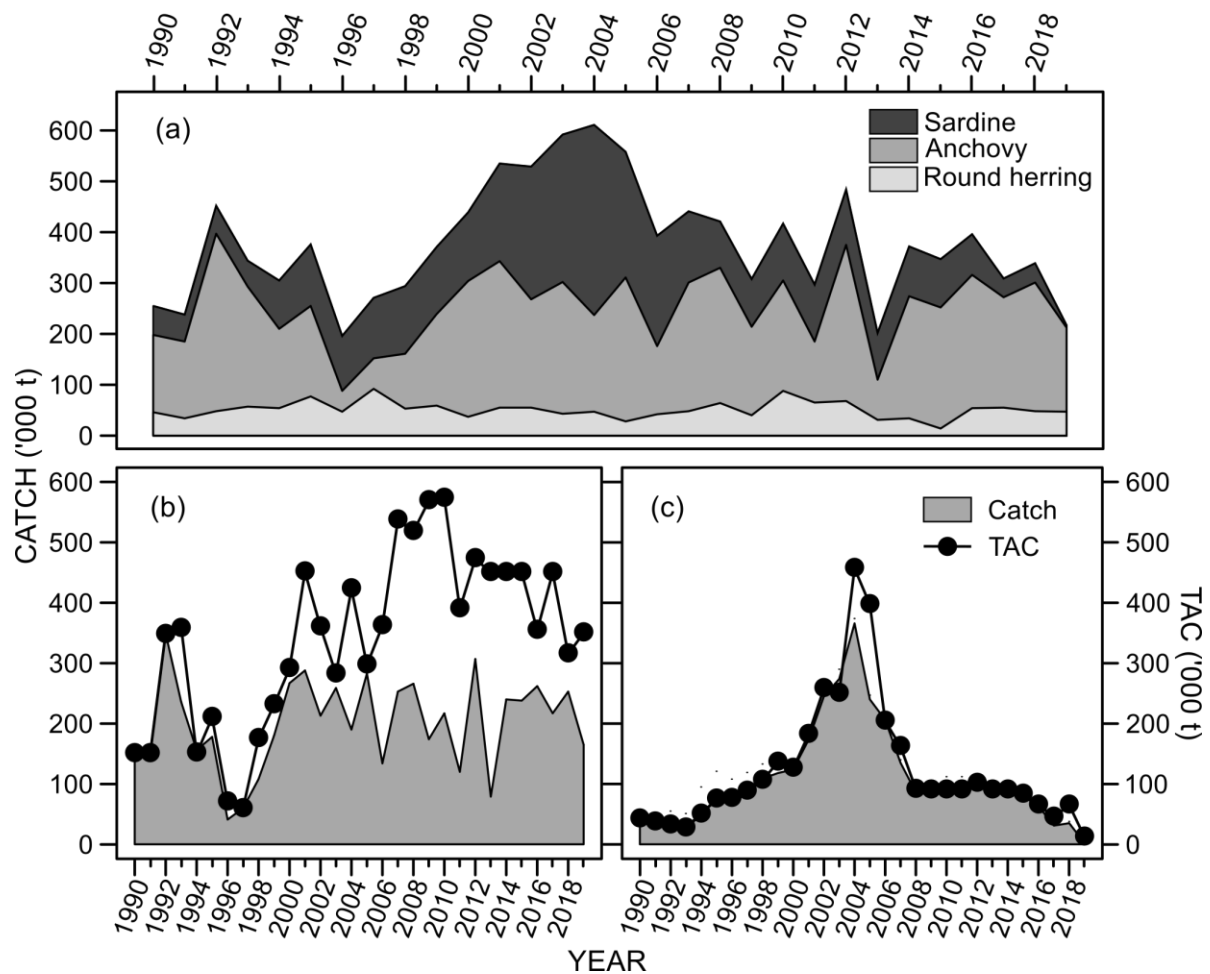


Figure 1.1. Descriptive fishery statistics of the small pelagic fishery in South Africa, (a) the annual combined catch of anchovy, sardine and round herring, (b) the annual catch and final TAC of anchovy, (c) the annual catch and final TAC of sardine from 1990 – 2019/20

Industrial purse seine fishing commenced in nBUS, located in Namibia, during the 1940s and was centred from Walvis Bay. Initially targeting sardine, the fishery grew in catches from 50,000 tons in 1950 to 1400,000 tons in 1968 (Figure 1.2.; Crawford et al., 1987). Unsurprisingly, the fishery collapsed shortly after, sustaining only 11,000 tons in 1980. Hereafter, catches have fluctuated around 50,000 tons (Crawford et al., 1987; Boyer & Hampton, 2001; Kirchner et al., 2009). During the collapse, the fishery began to heavily target anchovy using smaller mesh sized nets, initially as a competitive exclusion tactic to aid the collapsed sardine's recovery (Butterworth, 1983). However, it was soon realised that anchovy was also an important economical resource and that it was imperative to avoid anchovy meeting the same demise as sardine, thus a quota was implemented during the 1980s (Butterworth, 1983). Unfortunately, management tactics

were not sufficient and anchovy catches decreased dramatically. Since the 1990s, catches have remained at approximately 50,000 tons, with biomass surveys estimating the stock as severely depleted (Boyer & Hampton, 2001). Following these declines, the dominating intermediate trophic level species have changed from primarily anchovy and sardine to horse mackerel (*Trachurus capensis*), pelagic gobies (*Sufflogobius bibarbatus*) and gelatinous plankton (Salvanes et al., 2011, 2018; Flynn et al., 2012). Juvenile round herring are caught in the nBUS as bycatch in the horse mackerel and sardine fisheries, but catches remain small at around 1,000 tons (Boyer & Hampton, 2001). Currently, small pelagics contribute a severely reduced proportion to the countries total catch (van der Lingen et al., 2006c; FAO, 2020). With persisting unfavourable environmental conditions and continual fishing pressure, both stocks have seen poor annual recruitment and adult biomass (Boyer et al., 2001b).

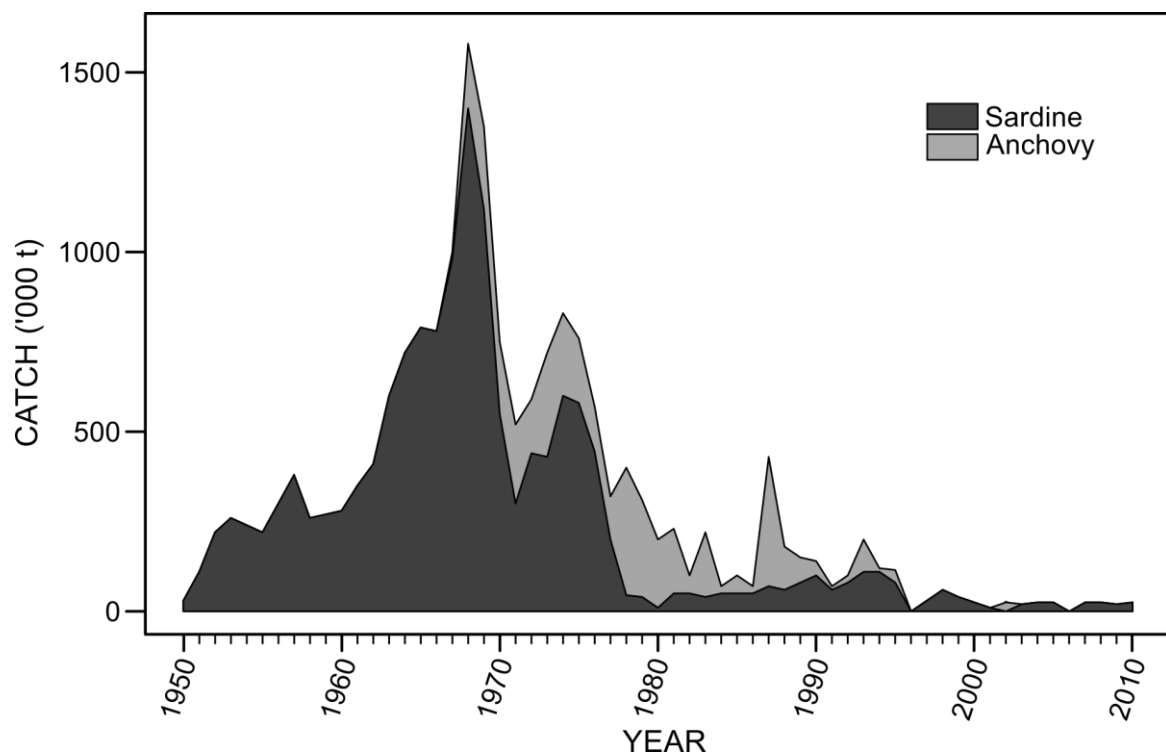


Figure 1.2. Historical catches of sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* in Namibia.

1.2. Benguela Upwelling System

Eastern boundary upwelling systems (EBUS) are characterised by very high primary productivity and short food chains. Although these systems only constitute approximately 2% of the oceans area, the four major currents, the Humboldt, California, Benguela and Canary, provide 25% of the primary productivity needed to support the catch from global capture fisheries (Pauly & Christensen, 1995). The BUS is located on the west coast of southern Africa, from Namibe, Angola (15.20 °S) to Cape Agulhas, South Africa (34.83 °S, Kirkman et al., 2016). The BUS is unique in comparison to other EBUS in the fact that it is bounded at both its equatorward and poleward ends by warm water regimes; the Angolan and Agulhas currents, in the north and south respectively (Shannon & Nelson, 1996). Upwelling is governed by three features: the south Atlantic high-pressure cell, eastward moving cyclones across the southern part and a low-pressure cell on the southern African continent (Nelson & Hutchings, 1983). These features produce favourable alongshore, south easterly winds that induce coastal upwelling. The coastal cyclonic wind-stress tends to have its most limited poleward extent during austral winters. Its southern most boundary extends during spring, peaking just south of the Cape of Good Hope during late spring, before retreating equatorward (Bakun & Nelson, 1991). Both the nBUS and Lüderitz cell lack seasonality with upwelling occurring for more than 95% of the year on average, and although upwelling also occurs perennially in the sBUS, it does however display strong seasonal trends with peaks in austral summer (Lamont et al., 2018a).

1.2.1. Environmental Changes in the Benguela

Due to strong interannual and decadal variations in upwelling systems, it is inherently difficult to disentangle genuine long-term environmental changes attributable to climate change. However, with the increasing accumulation of long-term data sets, decadal trends are beginning to be teased out.

The subtropical waters off Angola are characterised by the convergence of cold, nutrient rich equatorward water from the nBUS and warm, oligotrophic poleward water from the Angolan current, namely the Angolan Benguela Frontal Zone (ABFZ). This dynamic zone extends poleward during austral summer and autumn, before retreating equatorward during winter (Veitch et al., 2006). Despite this seasonal variation, there has been an average poleward shift over the last three decades (Vizy et al., 2018). This shift

was likely provoked by the average poleward movement of the South Atlantic high-pressure cell, which was estimated at a rate of 0.22 – 0.34 degrees per decade (Vizy et al., 2018). Furthermore, the Angolan coastal waters that bound the system have warmed by between 0.23 °C (Jarre et al., 2015) and 0.8 °C per decade (Potts et al., 2014). The nBUS has seen a relative warming (Rouault et al., 2007), most likely due to the relative reduction in upwelling and increased intensity of Benguela Niño events.

The nBUS is characterised by having a large oxygen minimum zone (OMZ). Low oxygenated waters (<1 ml O₂ l⁻¹) from the Angolan Gyre are transported via a poleward undercurrent onto the Namibian shelf during austral summer (Mohrholz et al., 2008). It is anticipated that these low OMZ will expand (Diaz & Rosenberg, 2008; Monteiro et al., 2008; Stramma et al., 2010), resulting in substantial constriction of tolerable habitat ranges for hypoxic intolerant species such as anchovy and sardine (Ekau & Verheye, 2005; Kirchner et al., 2009). This may be a partial explanation for the absence of their stock recovery in the nBUS, as both are principally distributed in waters > 2 ml O₂ l⁻¹ (Ekau & Verheye, 2005; Kirchner et al., 2009). The system is now dominated by the bearded goby *Sufflogobius bibarbatus* and horse mackerel *Trachurus capensis*, which have a greater hypoxic tolerance in comparison (Salvanes et al., 2011, 2018; Geist, 2013; Geist et al., 2014). Conversely, the sBUS is characterised by seasonal hypoxic events north of the Cape Columbine upwelling cell (Penven et al., 2001), however, there has been no long-term trend in deteriorating conditions (Hutchings et al., 2012).

Rouault et al. (2010) found significant cooling within the sBUS of up to 0.5 °C per decade during austral summer and spring on the west coast, and 0.4 °C per decade during austral spring on the south coast. Although, it was later uncovered that the initial cooling trend was significantly restricted, and only present on the west coast between Cape Columbine and Cape Point (Dufois et al., 2012). Using *in situ* South African Weather Service sites, (Blamey et al., 2015) later corroborated this trend by finding significant warming north of Cape Columbine.

Upwelling in the region has shown strong interannual and decadal variation, yet although not statistically significant, there has been an overall increase in upwelling in the sBUS, notably on the Agulhas Bank (Lamont et al., 2018a). Total cumulative upwelling in the sBUS has been correlated with the meridional position of the South Atlantic high-pressure cell, with a more poleward extent increasing upwelling at the southern extremes of the system (Blamey et al., 2012; Jarre et al., 2015; Lamont et al., 2018a). For

example, Lamont et al. (2018a) found an increase in total upwelling days on the Agulhas Bank during the period of 1979 – 2014. This was substantiated by Duncan et al. (2019) highlighting localised cooling on the south coast at Tsitsikamma Marine Protected Area (MPA) due to an increased number of extreme upwelling events.

Overall, there has been a general trend of upwelling increasing towards its poleward extent, which fits the predicted trends of upwelling in these systems (Sydeman et al., 2014; Rykaczewski et al., 2015; Wang et al., 2015), warming at its extremes and increasing OMZ. The formation of the South Atlantic high-pressure cell is dependent on the subsidence of the Hadley Cell which is predicted to extend poleward (Lu et al., 2007). It is therefore anticipated that the meridional position of the South Atlantic high-pressure cell will follow a similar fate. So, considering that the upwelling in the Benguela is intimately linked to its position and intensity (Jarre et al., 2015; Lamont et al., 2018a), we would expect that current oceanographic trends will likely continue. With primary production and the support of subsequent trophic levels being so dependent on oceanographic functions in the Benguela, it would be expected that we would see changes in the biology of this system.

1.2.2. Primary and Secondary Production Changes in the Benguela

Fluctuations in primary productivity (PP) in the BUS are driven by a multitude of environmental variables, such as temperature, nutrients and available light (Platt & Jassby, 1976; Falkowski, 1981; Gallegos, 1992; Lamont et al., 2014), consequently, there are large variations in biomass, species composition and size. Although productivity differs between both systems, times of highest PP tend to coincide with peak upwelling months (Verheye et al., 1992; Martin et al., 2015).

The primary productivity and phytoplankton biomass follow a shelf-ward increasing trend until it reaches a mid-shelf peak (Barlow, 1982; Hansen et al., 2014; Lamont et al., 2014). Freshly upwelled water has a low PP, but as it warms and moves across the shelf, PP increases. Beyond the mid-shelf, PP starts decreasing as the water approaches the shelf edge. (Barlow, 1982; Lamont et al., 2014; Hansen et al., 2014). The optimal temperature for phytoplankton productivity in the sBUS is between 12 and 15 °C (Lamont et al., 2014). Temperature plays a crucial role in the size and species composition of primary producers, with warmer waters tending to be characterised by

smaller phytoplankton and a lower PP. This is corroborated by the smaller size classes of phytoplankton found in the south of the sBUS, corresponding to the warm Agulhas Current retroflection area (Lamont et al., 2014).

Upwelling provides valuable nitrates that are utilised by autotrophs in the euphotic zone. These autotrophs utilise this nitrogen from either (a) recycled nitrogen, ammonium through heterotrophic metabolism, or (b) new nitrogen, nitrates from upwelling (Dugdale & Goering, 1967). The source nitrogen plays a crucial role in the size and species composition of autotrophs. Nano- and pico- plankton production both depend largely on assimilating recycled nitrogen, whereby larger net-plankton depend on new nitrogen (Probyn, 1985). This has resulted in a spatial organisation of phytoplankton by size within the system, with larger microphytoplankton dominating inshore areas and smaller nanophytoplankton more commonly found offshore (Lamont et al., 2018b). Thus, changes in coastal wind stress that promote upwelling and colder temperatures will likely result in substantial changes in both the size and spatial organisation of the phytoplankton community (Probyn, 1985, 1992).

Many studies have tried to calculate total phytoplankton productivity in both the sBUS and nBUS, yet there seems to be an element of disagreement. Using satellite derived chlorophyll-*a* data sets (1998 – 2007/2010), trends in the nBUS have exhibited increasing PP (Demarcq, 2009; Jarre et al., 2015), conversely, *in situ* studies in Walvis Bay during the same period have highlighted declining phytoplankton concentrations but with marked changes in community structure (Hutchings et al., 2009; Jarre et al., 2015). The sBUS has shown no long-term shift in PP, with both *in situ* and satellite derived studies agreeing (Hutchings et al., 2012; Jarre et al., 2015; Verheye et al., 2016a).

Secondary production, specifically copepods, has drastically changed in the sBUS over the past 70 years. Larger copepods are presently relatively less abundant than smaller copepods and biomass is significantly higher than historical levels (Verheye et al., 2016a). The increase in biomass is likely concomitant with the onset of industrial fishing, causing a relaxation of top-down control. This situation is corroborated by an observed decrease in biomass of copepods in the sBUS when the biomass of small pelagics increased after the 1990s (Jarre et al., 2015). Furthermore, with the relative warming and reduced upwelling observed north of Cape Columbine (Dufois & Rouault, 2012), the relative depletion of larger copepods in the St Helena Bay region described by Verheye et al. (2016) is expected. The nBUS has also experienced both a drastic increase

in zooplankton abundance, with a ten-fold increase in copepods since the 1970s, and a reduction in copepod average size (Verheye et al., 2016a), with a reduction in top-down predation pressure and environmental perturbations having significant impacts (Hampton, 2012).

It is evident that the system has undergone changes in its physical and biological dynamics. Considering that the physical are likely to continue (Sydeman et al., 2014; Rykaczewski et al., 2015; Wang et al., 2015) and small pelagic fish are so tightly linked to these processes, it will be important to understand and monitor the effects of these on the ecological community.

1.3. *Small Pelagic Fishes Distribution and Ecology*

Small pelagic fishes are generally distributed in coastal waters and are seldom found beyond the shelf edge. Broadly, they are short-lived, early maturing, serial broadcast spawners (Blaxter and Hunter, 1982; Roel and Melo, 1990; Geja et al., 2016) that primarily feed on phytoplankton and zooplankton (Blaxter and Hunter, 1982; James, 1988; Garrido and van der Lingen, 2014). They exhibit wasp-waist control in performing crucial roles of transferring energy from primary producers to higher trophic levels while also exerting top-down control on their prey (Cury et al., 2000).

1.3.1. *Sardine *Sardinops sagax**

Southern African sardine *Sardinops sagax* are found in both the sBUS and nBUS, as well as eastwards as far as Durban, South Africa. They are early maturing (length-at-50% maturity of 17 - 19 cm caudal length; Davies, 1954, 1956; Matthews, 1964; van der Lingen et al., 2006b), fast growing and short-lived species (Thomas, 1984). Sardine stocks in the nBUS and sBUS have long been considered as two distinct stocks, due to the presence of the environmental barrier caused by the perennial upwelling cell at Lüderitz (Lett et al., 2007). However, more recently, scientific evidence has strongly supported the division of the sBUS stock into two separate stocks, with overwhelming evidence of phenotypic and genetic distinction between the two sub-areas (Hampton, 2014; Weston et al., 2015; Idris et al., 2016; Sakamoto et al., 2020; Teske et al., 2021). The stocks are described as

cold-temperate sardine that predominate on the west coast and warm-temperate sardine that are found on the south coast (Teske et al., 2021).

In Namibia, spawning of sardine during high biomass periods was either on the shelf off Walvis Bay or in the mixing zone south of the Angola Benguela Frontal Zone (ABFZ) near Palgrave Point (Figure 1.3; O'Toole, 1977; Le Clus, 1990a; Checkley et al., 2009b). Spawning locations varied between the northern region in the 1980s (van der Lingen & Durholtz, 2003) and the southern region of Walvis Bay in the 2000s (Kreiner et al., 2011). Spawning eggs and larvae tend to drift poleward along the coast and recruit as 0-year fish to the fishery ground off Walvis Bay. Juveniles and young adults then typically return north to the northern spawning region off Palgrave Point, to spawn as young adults (Boyer & Hampton, 2001).

In South Africa, sardine distribution extends from Hondeklip Bay (30° 3 S, 17° 3 E) on the west coast, to Durban (29.9 ° S, 31.0 ° E) on the east coast. From 1984 to early 2000s sardine biomass steadily rose from 50 thousand to 4 million tons, with most residing on the west and southwest coast (Figure 1.4; Coetzee et al., 2018; DEFF, 2020). Following this increase in biomass, the stock expanded east with a large proportion moving east of the Cape Agulhas (van der Lingen et al., 2005; Coetzee et al., 2008). This spatial reorganisation has persisted with biomasses east and west of Cape Agulhas approximately equating each other (Coetzee et al., 2018). It is thought that a combination of disproportionate fishing effort, relative reproductive output due to difference in stock structure, environmentally-induced changes and recruit survival have likely defined the observed geographic reorganisation (Coetzee et al., 2008).

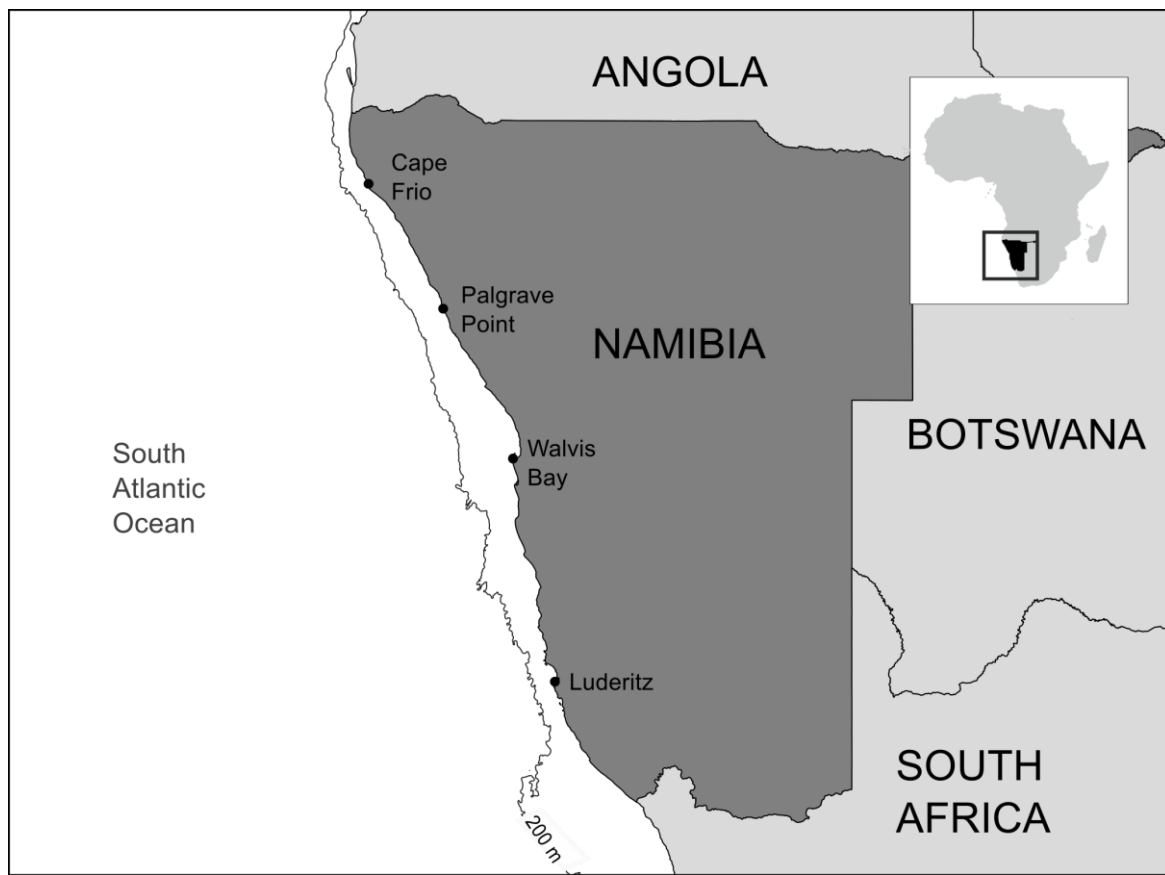


Figure 1.3. Marine coastal regions specific to the small pelagic distribution in the northern Benguela of the coast of Namibia, South Africa.

Off South Africa, nursery and spawning grounds are principally distinct. Spawning peaks bimodally during austral spring and summer, with the first peak in August/September and followed by a second peak in February (Fowler, 1998; Huggett et al., 1998; Checkley et al., 2009b). Spawning areas are predominantly focussed on the west and south coast, specifically the western Agulhas Bank (Figure 1.4; van der Lingen et al., 2001, 2005; Twatwa et al., 2005; Mhlongo et al., 2015). Yet spawning does occur at lower levels on the central and eastern Agulhas Bank, and off the coast off the east coast during the sardine run (Checkley et al., 2009b). Since the 1960s, there has been significant oscillation in spawning between the west coast, southwest coast and western, central and eastern Agulhas Bank (Fowler & Boyd, 1998; Beckley & van der Lingen, 1999; van der Lingen et al., 2001, 2005; Twatwa et al., 2005; Mhlongo et al., 2015). It is thought that environmental conditions have likely played a role, but moreover stock size and structure have had the most dominant influence on the spatial organisation of spawning (Mhlongo et al., 2015), which is evident from the large surge of recruits in the early 2000s resulting

in an eastward expansion of both the stock and the spawning habitat (van der Lingen et al., 2005).

It is hypothesised that the two stocks, cold-temperate and warm-temperate sardine, tend to spawn in separate areas, which effects the location of recruitment. Eggs spawned on the southwest coast and western Agulhas Bank are transported via the strong shelf-edge frontal jet, downstream to the west coast nursery ground (Figure 1.4; Shelton & Hutchings, 1982). The further east eggs are spawned on the Agulhas Bank the lower the likelihood of successful transportation to the west coast nursery. Eggs spawned on the central and eastern Agulhas Bank predominately recruit inshore onto the south coast (Miller et al., 2006; McGrath et al., 2020). Juveniles then migrate to their principal spawning locations as young adults (Crawford, 1980), and large adults (>18 cm total length) disperse west and east of the Agulhas Bank (Barange et al., 1999).

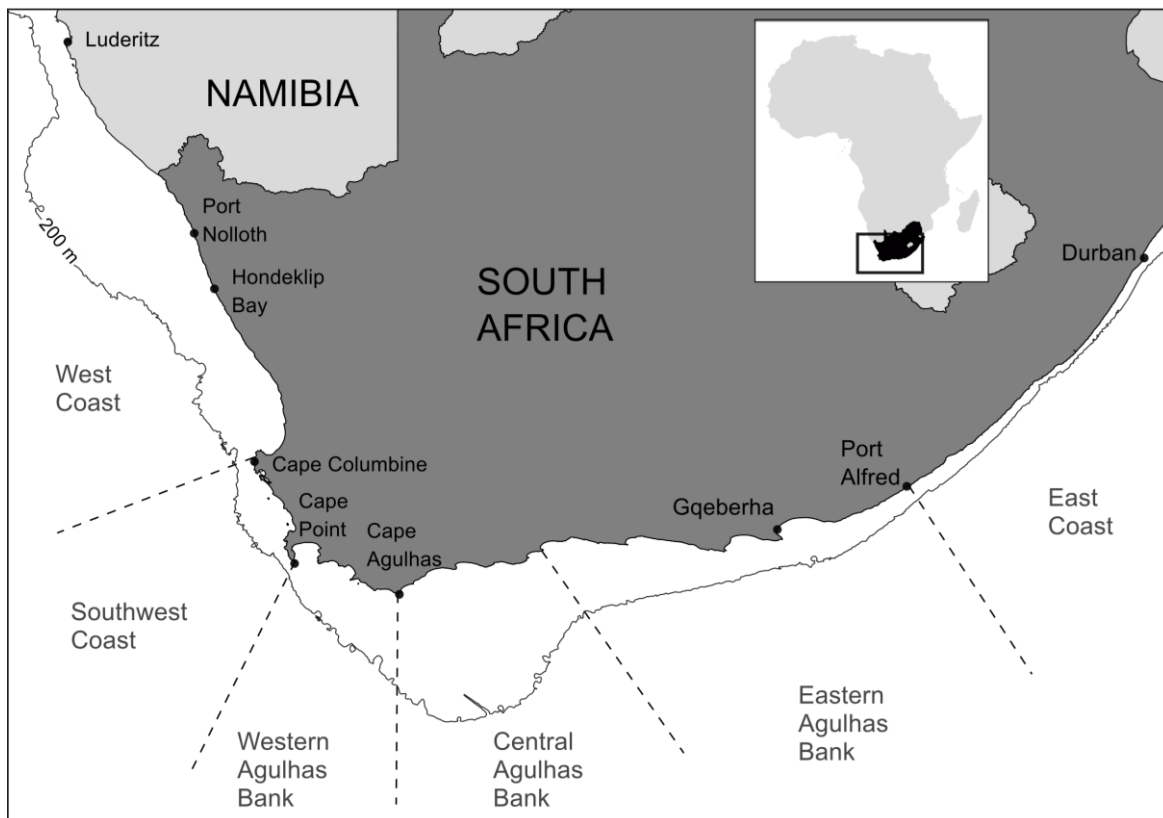


Figure 1.4. Marine coastal regions specific to small pelagic fish distribution in the southern Benguela and South African sovereign waters.

1.3.2. Anchovy *Engraulis encrasicolus*

The Cape anchovy *Engraulis encrasicolus* is also a short-lived, fast-growing species (Table 1.1) that is found in both systems, with a similar distribution to that of the sardine. Spawning in Namibian anchovy occurs primarily during summer and early autumn, with a peak in December – March (O’Toole, 1977; Le Clus, 1985; Checkley et al., 2009b). Prior to the 1970s it was thought that anchovy spawning was concurrent with sardine, occurring in both the spawning regions. However, from the early 1970s, egg abundance was only found in significant quantities in the north, with 90% of larvae found between Cape Frio and Palgrave Point (Figure 1.3; O’Toole, 1977). This trend persisted into the early 2000s (Cruickshank, 1987; Tjizoo, 2008). Once hatched, the larvae are advected offshore to warmer waters where zooplankton availability is greater. Juveniles then migrate southwards, via the coastal counter-current, and begin to form large shoals south off Walvis Bay (Cruickshank, 1987). Adults then return north to their spawning grounds to spawn as young adults (Boyer & Hampton, 2001).

The stock in the sBUS has a similar extent and spatial structure to that of the sardine (DEFF, 2020), and to a degree share much of their early life history. Anchovy primarily spawn over the Agulhas Bank and their eggs and larvae are transported via the strong shelf-edge frontal jet current, downstream to the primary west coast nursery grounds in St Helena Bay (Shelton & Hutchings, 1982; Checkley et al., 2009b). Juveniles then move inshore and migrate poleward, returning to their spawning grounds on the Agulhas Bank ready to spawn as they mature at the age of one. In the late 1980s, the majority of the spawner biomass resided west of Cape Agulhas, on the southwest coast and the western Agulhas Bank (Figure 1.4). During the early and mid-1990s, the anchovy stock underwent a drastic reorganisation, with 80% of the spawner biomass residing east of the Cape Agulhas in 1996 (van der Lingen, 2002). This has persisted, with the central and eastern Agulhas Bank being the favoured spawning habitats (Roy et al., 2007). This abrupt shift was likely environmentally mediated through a 0.5 °C cooling on the inner shelf of the central and eastern Agulhas Bank, and has persisted due to potential biological effects of “extended natal homing” and hypothesised increased ambient food conditions (van der Lingen, 2002; van der Lingen & Huggett, 2003; Roy et al., 2007).

Anchovy spawn multiple times during the spawning season, which tends to occur during austral spring and summer with a primary peak in late/spring/summer (Melo, 1992, 1994a; Fowler, 1998; Richardson et al., 1998). The optimum environmental window for spawning is smaller than sardine, typically spawning in warmer (17 – 23 °

C), less turbulent waters during periods of reduced wind speed (Twatwa et al., 2005; Mhlongo et al., 2015). This provides convincing evidence to why spawning is largely restricted to the Agulhas Bank, bolstered by greater thermal stability (Richardson et al., 1998). During the 1970s, their principal spawning habitat has been on the western Agulhas Bank (Shelton, 1986), and seemingly remained relatively spatio-temporally stable. However, egg samples have highlighted a shifting importance of spawning grounds east of Cape Agulhas, likely concomitant with the abrupt shift in adult spawner biomass (van der Lingen et al., 2001; Twatwa et al., 2005). It is worth noting that despite the shift in adult biomass and preferred spawning habitats, the west coast is still believed to be the primary nursery ground (Roy et al., 2007), regardless of a significant reduction in successful egg transport from the central and eastern Agulhas Bank (Mullon et al., 2003).

1.3.3. West coast round herring *Etrumeus whiteheadi*

Information regarding the life history of the round herring *Etrumeus whiteheadi* is not as comprehensive as its sympatric heterospecifics. The species is endemic to southern Africa, almost exclusively to the sBUS (Roel & Armstrong, 1991). In the sBUS, the species is found between Port Nolloth on the west coast to Port St Johns on the east coast (Roel & Armstrong, 1991). Through the biannual acoustic surveys, round herring were distributed comprehensively around the coast up to the shelf edge (Armstrong et al., 1991; Roel & Armstrong, 1991), with estimated biomass being relatively stable at approximately 1.5 million tons since the late 1990s (DEFF, 2020). Fish are commonly found within the inshore and mid-shore region during austral summer, with adults migrating offshore during the winter (Roel & Armstrong, 1991). Juveniles are largely inshore residents, migrating offshore during their ontogeny (Roel & Armstrong, 1991).

Round herring are fast growing and short-lived species that at 50% maturity reach lengths of 13.1 cm (1.2 years) and 12.2 cm (0.8 years) caudal length for females and males respectively (Table 1.1). Both growth and maturity have shown significant variation in estimates between studies and years (Geldenhuys, 1978; Roel & Melo, 1990; Waldron et al., 1991; Geja et al., 2016), which could either be a product of inter-study differences or autoregulatory compensation due to density-dependent effects as seen in sardine (van der Lingen et al., 2006b).

Spawning occurs during a prolonged spawning season that peaks during July – November (Shelton, 1986; Roel & Melo, 1990; Roel & Armstrong, 1991), but there are several additional spawning events throughout the year, detailed by strong, yearly multi-modal size classes of length-frequencies (Durholtz et al., 2010). It is anticipated that eggs spawned west of Cape Agulhas follow similar trends to those of anchovy and sardine, transported via the shelf-edge frontal jet current to the west coast nursery ground (Shelton & Hutchings, 1982; Roel & Armstrong, 1991). Eggs spawned east of the Cape Agulhas are likely transported shelf-wards, as juveniles and larvae are often found and caught inshore of the south and east coast (Roel & Armstrong, 1991; Beckley & Hewitson, 1994).

1.4. *Small Pelagic Fishes Trophic Ecologies*

Initially it was thought that large biomass levels of small pelagic fish were a consequence of their phytophagy, feeding directly on large-celled phytoplankton which increased the trophic transfer efficiency (Ryther, 1969). This hypothesis was originally supported (Loukashkin, 1970; King & Macleod, 1976), yet modern studies have shown that despite a few obligate herbivorous species, the majority of small pelagic fishes are considerably more zooplanktivorous than once thought (Cushing, 1978; James, 1987; van der Lingen, 2002).

The trophic ecologies of adults, and to a lesser extent juveniles, of small pelagic fishes in the Benguela upwelling ecosystem are relatively well documented and understood (Garrido & van der Lingen, 2014). However, information regarding the trophic ecology of larval stages of small pelagic fish in the Benguela is extremely limited. To quote Garrido and van der Lingen (2014) “*The diet of larval Engraulis encrasicolus has been poorly studied [both] in the Benguela system, where it is limited to the diet of only three individuals (King and Macleod, 1976)*”. Therefore, we must currently depend on information from conspecifics.

Table 1.1. Ecological and life history characteristics of the three-studied species. Bold font indicates characteristics from the southern Benguela, italics indicate northern Benguela and normal font indicates general species characteristics.

Species	Growth		Maturity		Reproduction		Trophic ecology	
	L_{∞} (cm)	K	t_0 (cm)	Length-@-50% (cm)	Technique	Frequency	Egg size (mm) and shape	Spawning time
Anchovy	14.0	1.59	0.00 ¹	9.5 (C) ⁹	Serial	7 - 8 days ¹³	1.17 - 1.44	October - March ¹⁷
	<i>12.1</i>	<i>0.97</i>	<i>-1.32</i> ²		Broadcast ¹²		Oval ¹⁶	<i>October - March</i> ¹⁸
	<i>13.0</i>	<i>1.33</i>	<i>-0.17</i> ²					
	14.8	1.37	0.03 ³					
Sardine	29.9	0.36	0.25 ⁴	19.0 (C) ¹⁰	Serial	15 days ¹⁴	1.17 - 1.91	September - February ¹⁹
	<i>21.2</i>	<i>1.19</i>	<i>-0.38</i> ⁵		Broadcast ¹²		Spherical ¹⁶	<i>September - March</i> ²⁰
	<i>22.6</i>	<i>1.09</i>	<i>0.00</i> ⁵					
	21.4	0.95	-0.17 ⁶					
Round herring	30.1	0.71	-0.28 ⁷	13.1 (F) ¹¹	Serial	> 2 days ¹⁵	1.32 - 1.47	Yearly
	20.4	0.41	1.92 ⁸	12.2 (M) ¹¹	Broadcast ¹²		Spherical ¹⁶	July - November (peak) ²¹
Feeding	Diet		Feeding mode	Morphology (mm)		Flexion development	Max length	Trophic level
Diel rhythm				Metamorphosis			$\delta^{15}N$ (‰, SE)	
Nocturnal ²²	Zooplankton		Particulate ¹²	35 ²⁵	7.5 - 8.7 ¹⁶		200 ²⁷	3.54 ²⁸
	< Phytoplankton ¹²		Filter feeding					2.70 ²⁹
							12.90 (0.40) ³⁰	
Continuous ²³	Zooplankton		Particulate ¹²	35 ²⁵	7.4 - 11.3 ¹⁶		280 ²⁷	2.99 ²⁸
	< Phytoplankton ¹²		Filter feeding					2.00 ²⁹
							12.70 (0.40) ³⁰	
Diurnal ²⁴	Zooplankton ¹²		Particulate ¹²	35 ²⁶	8.4 - 11.6 ¹⁶		220 ²⁷	3.64 ²⁸
			Filter feeding					3.10 ²⁹

Prosch (1986)¹, Melo (1984)², Waldron et al. (1989)³, Nawratil (1962)⁴, Thomas (1984)⁵, Kerstan (*pers. Comm.* In Shin et al., 2004)⁶, Waldron et al. (1991)⁷, Geja et al. (2016)⁸, Le Clus (1979)⁹, Davies (1954, 1956)¹⁰, Roel & Melo (1990)¹¹, Blaxter & Hunter (1982)¹², Melo (1994)¹³, Akkers et al. (1996)¹⁴, Nyuji et al. (2022)¹⁵, Olivar & Fortuño (1991)¹⁶, Melo (1992)¹⁷, Le Clus (1991)^{18, 20}, Davies (1954, 1956)¹⁹, Roel & Melo (1990)²¹, James (1987)²², Coetzee (1997)²³, Roel & Armstrong (1991)²⁴, Hunter (1975)²⁵, Armstrong & Thomas (1989)^{26, 27}, van der Lingen & Miller (2011)²⁸, Iitembu et al. (2012)²⁹

1.4.1. Sardine

Sardines are predominately filter feeders yet food particles exceeding 1200 μm can elicit a particulate feeding response (van der Lingen, 1994). Their branchial basket has five pairs of cartilaginous gill arches and both gill arches and rakers increase in size and number during their ontogeny. Gillrakers increase in number linearly with size translating to a small gillraker gap in comparison to anchovy and round herring, that facilitates sardines to retain smaller particles ($> 10 \mu\text{m}$; van der Lingen, 1994). Sardines undergo a less defined vertical migration, fish in the sBUS can be observed throughout the water column during the day, but then scatter near the surface at night (Coetzee, 1997). In the nBUS, there is no depth difference, instead shoals scatter near the surface at night and then form dense shoals throughout the day (Thomas & Schüle, 1988). Feeding periodicity is high during development as juveniles, with peak feeding at sunset (van der Lingen, 1998), although adults tend to feed continuously throughout the day (van der Lingen, 1998).

Sardine diet is often numerically dominated by phytoplankton (King & Macleod, 1976), and the ability to utilise phytoplankton as a prey source becomes of great importance during certain times of the year (van der Lingen, 2002). However, in terms of dietary carbon, zooplankton are a much more important dietary component (van der Lingen, 2002). Sardines obtain the bulk of their carbon from smaller particles ($< 1200 \mu\text{m}$), typically calanoid and cyclopoid copepods, anchovy and crustacean eggs, and copepods nauplii (van der Lingen, 2002).

During first feeding the European (*Sardina pilchardus*), Common (*Strangomera bentincki*), Japanese (*Sardinops melanostictus*) and Pacific sardine (*Sardinops sagax*) are all primarily zooplanktivorous, selecting for copepod nauplii and eggs (Muck et al., 1989; Conway et al., 1994; Voss et al., 2009; Morote et al., 2010; Contreras et al., 2014; Hirai et al., 2017). Protists such as tintinnids play important roles in early larval sardine diets (Conway et al., 1994; Morote et al., 2010). Throughout their ontogeny, younger copepod stages and nauplii become a less important part of their diet with adult copepods, of calanoid, *Corycaeus*, *Oncaea* in the Japanese sardine (Watanabe & Saito, 1998; Yasue et al., 2011), and *Arcatia*, *Oithona* and *Clausocalanus* in the European sardine (Conway et al., 1994; Morote et al., 2010), begin to fill this energetic space.

1.4.2. Anchovy

Anchovies are omnivorous clupeoids that possess the feeding apparatus that facilitates the exploitation of both phytoplankton and zooplankton. Anchovies are primarily particulate feeders but can switch to filter-feeding when the size-composition of prey items declines below 700 μm (James and Findlay, 1989). Similar to sardine both gill arches and rakers increase in size and number during their ontogeny. In juvenile anchovy the number of gillrakers increase until approximately 80 mm caudal length, where after the number of gillrakers cease to increase (King & Macleod, 1976). Therefore, gillraker gap increases allometrically in anchovy and is comparatively bigger than that of sardine (King & Macleod, 1976). James (1987) concluded that anchovy formed dense midwater and demersal shoals during the day. After dusk these shoals migrate to the surface layers and disperse, which is concurrent with peak feeding times (James, 1987).

Dietary studies have shown that anchovies are primarily zooplanktivorous (James, 1987; Louw et al., 1998; Plounevez & Champalbert, 2000; Mketsu, 2008; Raab et al., 2011). A global similarity in their diet is the large contribution of copepods, primarily calanoids (James, 1987; Plounevez & Champalbert, 2000; Mketsu, 2008; Raab et al., 2011). Smaller copepods, such as cyclopoids and poecilostomatoids, are frequently found in stomachs, yet make up a smaller contribution to dietary carbon (Plounevez & Champalbert, 2000; Mketsu, 2008). The other spatially dependent major dietary constituents are fish eggs (James, 1987; Mketsu, 2008), brachyuran larvae (Plounevez and Champalbert, 2000), euphausiids (James, 1987; Plounevez & Champalbert, 2000) and crustacean eggs (Louw et al., 1998; Mketsu, 2008). Phytoplankton was seldom found in notable quantities (James, 1987) other than by King and Macleod (1976).

The European (*Engraulis encrasicolus*), Japanese (*Engraulis japonicus*) and Argentinean (*Engraulis anchoita*) anchovy larvae all rely heavily on zooplankton. Major components of their diet were copepod eggs, nauplii and early copepodite stages (Ciechomski, 1966; Hirakawa et al., 1997; Tudela et al., 2002; Catalán et al., 2010). During their ontogeny, their maximum prey size and width dramatically increase, increasing their trophic niche breadth. Young copepod stages remain a valuable source of energy, however they become increasingly less important as fish begin selecting for larger adult stages of copepods, such as *Acartia*, *Paracalanus*, *Oithona* and *Oncaea* in Japanese anchovy in the south (Islam & Tanaka, 2009; Yasue et al., 2011), and calanoid and

cladocerans in Japanese anchovy in the central regions (Hirakawa et al., 1997). In some juvenile anchovy, phytoplankton plays an important role, for instance the Argentinean anchovy was found to have stomachs full of diatoms (*Conscinodiscus* and *Triceratium*) and dinoflagellates (*Exuviaella*; de Ciechowski, 1966).

1.4.3. West coast round herring

Similarly, round herrings are omnivorous (Whitehead & Wongratana, 1986). It is assumed that round herrings can both filter- and particulate feed, with the latter being the primary feeding mode. Most studies highlight an importance of particles > 1500 μm (Wallace-Fincham, 1987; Mketsu, 2008; Vorsatz et al., 2015), implying a smaller dependence on filter feeding compared to its intraguild interspecifics. Similar to anchovy, the number of gillrakers cease to increase past fish of 50 mm (King & Macleod, 1976; Wallace-Fincham, 1987), therefore the gillraker gap also increases with length (Wallace-Fincham, 1987). Round herring has the largest gillraker gap out of the three species (Vorsatz et al., 2015). The species undergoes diel vertical migrations, spending daylight hours at depths and then migrating to the surface at night. Their main prey items, euphausiids and large copepods (Wallace-Fincham, 1987), also undergo these migrations, therefore it is postulated that round herring synchronise their migration patterns to have opportunity to continually feed (Roel and Armstrong, 1991). However, through feeding periodicity analysis, Wallace-Fincham (1987) concluded that peak feeding likely occurred during daylight hours- consequently at depth.

Wallace-Fincham (1987) produced a comprehensive dietary analysis highlighting a clear ontogenetic shift in prey items. Copepods, euphausiids and decapods were all important in terms of mass, however during development, copepod abundance decreased whereas euphausiids and decapods increased. Other prey items included; chaetognaths, cladocerans, ostracods, fish eggs, pteropods, bivalve larvae, squid and juvenile fish. Mketsu (2008) analysed their dietary components on the east coast, the largest contributors to dietary carbon were fish eggs and large calanoid copepods (>1000 μm). The large contribution from eggs likely reflected the well-known spawning ground of many species on the Agulhas Bank (Hutchings et al., 2002). In terms of size distribution of ingested prey, both Mketsu (2008) and Vorsatz et al. (2015) concluded that round herring ingested larger prey items on average in comparison to sardine and anchovy.

Phytoplankton was found in negligible proportions, and primarily only in the west coast population (Wallace-Fincham, 1987), none in east coast individuals (Mketsu, 2008).

Larval herring species follow a similar trajectory of dietary progression. Newly exogenous feeding Atlantic herring (*Clupea harengus*) are largely dependent on copepod nauplii, eggs and copepodite stages (Bjørke, 1976; Checkley, 1982; Arula et al., 2012). As seen in both sardine and anchovy larvae, adult stages of copepods begin to replace younger stages, such as cyclopoid and calanoid copepods in the round herring (*Etrumeus teres*, Chen et al., 1992), and *Acartia*, *Eurytemora*, *Pseudocalanus* and *Calanus* copepods in the Atlantic herring (Checkley, 1982; Cohen & Lough, 1983; Arrhenius, 1996; Pedersen & Fossheim, 2008; Arula et al., 2012). Interestingly, large particles such as bivalve larvae, played an important role for early Atlantic herring larva (Checkley, 1982; Friedenberg et al., 2012).

1.5. *Small Pelagic Fishes Recruitment Variability*

Stock-recruitment models, such as Ricker's and Beverton-Holt (Beverton & Holt, 1954; Ricker, 1954), have been fundamental for forecasting the response of a species biomass under varying scenarios of fishing mortality. These models assume that (a) recruitment is constant, and (b) is a function of the previous year's biomass. However, it is apparent that recruitment is a function of multiple variables and is not solely dependent on the reproductive output of the stock (Figure 1.5). This is evident from fisheries where biomass has fluctuated significantly whilst fishing mortality has remained constant. For example, the South African anchovy population has shown large population variations since the early 2000s, with a peak of 6.5 million tons in 2001 to a low of 0.8 million tons in 2011 regardless of relatively constant fishing mortality (DEFF, 2020). Spawner biomass does play a role in recruitment, but natural mortality of pre-recruit stages may help explain a significant portion of the varied recruitment success.

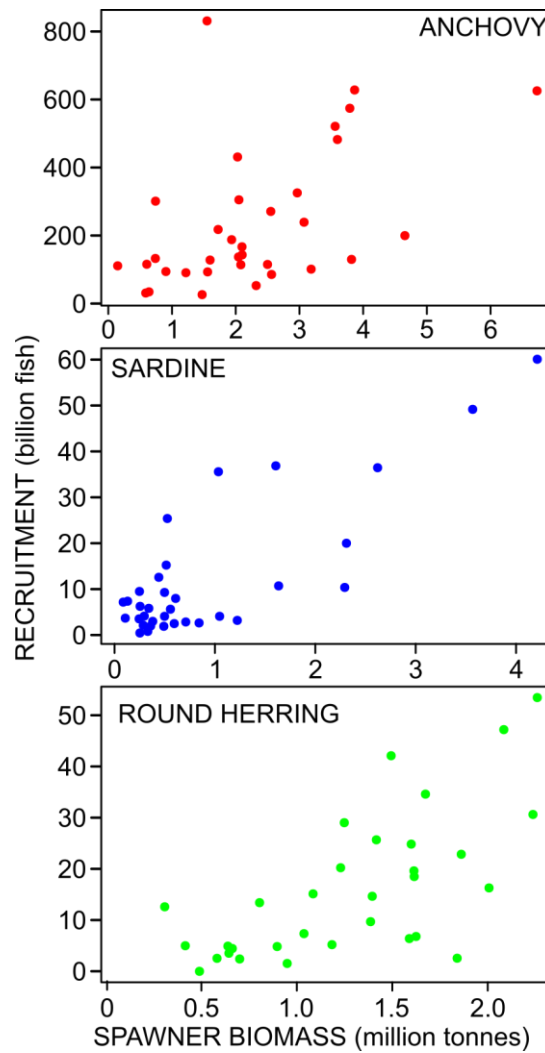


Figure 1.5. Spawner biomass (million tons) and recruitment (billion fish) relationship of anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi* in the southern Benguela (data supplied by DFFE).

Discovering potential environmental correlates that provide the power to increase our predictive ability of recruitment has its obvious benefits, although it has many inherent difficulties (Haltuch et al., 2019). For instance, many fish species have complex, multi-staged, early life histories that possess stage-dependent rates of natural mortality, thereby simplifying these processes to often one or two variables is difficult and littered with mathematical pitfalls (Haltuch et al., 2019). Regardless, many studies have empirically shown the significance of environment – recruitment relationships (Cochrane & Hutchings, 1995; Beaugrand et al., 2003; Olsen et al., 2011), yet it has been difficult to include them in formal stock assessment models. A meta-analysis by Skern-Mauritzen et al. (2016) found that out of 1250 marine fish stock studies only 24 of them

had included environmental indices as recruitment drivers that were used in management.

For species that have a longer pre-recruit stage, useful environmental-recruitment dynamics are even more difficult to prove (Subbey et al., 2014; Haltuch et al., 2019), which has been shown for cod and walleye pollock (Basson, 1999; Zhang et al., 2010). However, for short lived species, such as anchovy and sardine, recruitment functions show considerable promise in supporting fisheries management (Cochrane & Starfield, 1992; Hill et al., 2017; van der Sleen et al., 2018). Out of the 24 marine fish stocks outlined by Skern-Mauritzen et al. (2016), nine are clupeoids. One of these is the Pacific sardine, where recruitment is influenced by ocean temperatures (Jacobson & MacCall, 1995). This led to including average SST in the assessment and harvest guidelines in 2010 (Hill et al., 2008b). Yet, in the light of new data the plasticity of these relationships was recognised, and an update to the harvest guidelines was conducted in 2017 (Lindegren et al., 2013a; Hill et al., 2017).

For obvious reasons, accurate recruitment forecasting could be the holy grail for fisheries management. The ability to predict incoming recruitment would hopefully maximise the industry's catch with minimal risk, a challenge that the South African small pelagic fishery currently faces for two separate reasons. Firstly, the TAC for the sardine-directed fishery is currently recommended following the results of the adult biomass hydro-acoustic surveys in November. Typically, there would be a mid-year revision of the TAC following the recruitment surveys, however this does not currently occur as the recruitment estimates are particularly unreliable when adult biomass is at such low levels (DEFF, 2020).

Secondly, the directed-anchovy fishery predominantly targets (70%) fish that are young-of-the-year. In this fishery initial total allowable catch (TAC) and bycatch (TAB) levels (for anchovy and juvenile sardine, respectively) are set at the beginning of the fishing season (January) following the total biomass hydro-acoustic survey conducted the preceding November (Coetzee et al., 2018; DEFF, 2020). The anchovy stock assessment is based on a spawner biomass-recruit relationship and the initial anchovy TAC is set assuming historical average recruitment. Given uncertainty in the spawner biomass-recruit relationship, there are challenges to accurately predicting recruitment at the beginning of the year. Therefore, management implements a precautionary approach whereby the initial TAC is subjected to a scale-down factor of 0.85, which aims to

minimise risk to the stock (de Moor, 2018). The initial TAC is then revised following the recruitment hydro-acoustic survey conducted in May/June, with the final TAC either remaining the same as the initial (below average or average recruitment) or increasing (above average recruitment; de Moor, 2018). If the TAC is increased, there is often little time for industry to catch recruits off the west coast before they move onto the western Agulhas Bank (van der Lingen pers. comm.). Consequently, if management was better informed and the scaling factor could reflect anticipated above- or below-average (good and bad) recruitment years, there would be a better chance for the industry to catch their quota, something rarely met by the anchovy-directed fishery (DEFF, 2020). A simple ordinal method of “good”, “normal” and “bad” recruitment conditions could theoretically accrue a 16 % increase in total catch (Cochrane & Starfield, 1992). Recently, van der Sleen et al. (2018) investigated the relationship between anchovy recruitment and upwelling off the west coast and found that a threshold-generalized additive model that included information on the relative distribution of anchovy spawners of the preceding year accounted for 82% of observed recruitment variation.

Whilst providing evidence of such relationships is of great importance, this study does not seek to document significant relationships between the trophic ecology of small pelagic early life stages and their survival. Rather, it aims to add vital ecological and biological information to our limited knowledge about these pre-recruits in the Benguela, that will inform our decisions on selecting and exploring potential recruitment drivers and will hopefully assist in avoiding erroneous identification of environment-recruitment relationships.

1.5.1. Early Life Stage Mortality

Szuwalski & Hilborn (2015) showed that although fishing mortality exacerbated small pelagic fish stock declines, the onset was due to recruitment failure, independent of fishing. This led the authors to conclude that variance in recruitment of small pelagic fishes is largely governed by fluctuations in early-stage mortality rates due to environmental conditions. Evasion of mortality, primarily from predation, starvation and physical processes, is ultimately defined by the combination of a larva’s morphology, physiology and behaviour. These undergo significant transformation up until metamorphosis whereby notable ontogenetic processes cease (Fuiman & Higgs, 1997).

Therefore, examining early life history traits that may explain a fraction of this mortality could be fundamental to understanding the underlying mechanics of recruitment.

Fish often have complex life cycles that contain an early life, planktonic stage. These stages tend to depend on a multitude of physical factors for their successful transportation to and retention in suitable nursery grounds. Pinpointing the primary contributors to the loss of early life history stages, such as sea surface temperature (Houde, 1974; Bradbury et al., 2001), winds (Lough et al., 1994) and upwelling (Bakun & Parrish, 1982), is challenging. Successful recruitment hinges on the temporal alignment of these physical factors during specific life history stages. This has been highlighted through the multiple theoretical hypotheses trying to explain optimal environmental conditions needed for successful small pelagic recruitment (Lasker, 1981; Cushing, 1990; Roy, 1993; Bakun, 1997).

As components of the planktonic community and having limited locomotor function, fish larvae are vulnerable to high levels of predation by a multitude of invertebrates (Lillelund & Lasker, 1971) and fishes (Cushing, 1974; Colin, 1976; Bailey & Houde, 1989). For example, in clupeoid species, there is a significant amount of cannibalism, contributing up to as much as 70% of total egg mortality (Valdés et al., 1987; Valdés-Szeinfeld & Cochrane, 1992). Mortality rates decline with size due to reduction of predatory species and increased predator avoidance ability, providing explanation for why faster growing larvae may have better chances of survival due to spending less time in stages with higher predation (Houde, 1989; Takahashi & Watanabe, 2004).

Starvation contributes significantly to the total mortality of early life history stages. Hjort's (1914) Critical Period Hypothesis describes the importance of the availability of appropriate food particles to newly exogenously feeding larvae. Once yolk reserves have been depleted, the first-feeding larvae have a very limited timeframe to feed successfully before the onset of irreversible starvation or the "point of no return". Successful feeding is the result of an individual's intrinsic characteristics combined with extrinsic factors such as density of suitable prey (Hunter, 1975; Lasker & Zweifel, 1978; McClatchie et al., 2007).

In the Benguela, efforts to quantitatively explain the observed variance in recruitment of small pelagics has been an ongoing challenge. Substantial attention has been directed at the natural mortality caused by physical processes (Boyd et al., 1998; Huggett et al., 2003; Parada et al., 2003). However, regardless of its obvious importance

highlighted through intraguild predation and cannibalism (Valdés et al., 1987; Valdés-Szeinfeld & Cochrane, 1992), inherent challenges make the quantification of predation difficult. Similarly, quantifying starvation is challenging as estimates commonly rely on the use of condition indices (Wilhelm et al., 2005; Grote et al., 2012) and an awareness of the point of irreversible starvation. However, in order to predict the onset of starvation, it is imperative to consider the factors that initially induce starvation in early life history stages, namely planktonic food production and the trophic ecology of small pelagic fishes. While the former is well documented (Verheye et al., 1998, 2016a; Lamont et al., 2014), as previously mentioned our knowledge of the trophic ecologies of small pelagic fish in the Benguela is currently limited to juvenile and adult stages (van der Lingen et al., 2006c).

1.5.2. Ontogenetic Shifts in Feeding Success

Starvation from insufficient external food occurs after the depletion of the yolk sac, which depending on the species, quality and size of the egg can happen up to 30 days post-hatching (Blaxter & Hunter, 1982). Following this point there are many physiological, behavioural and morphological milestones during the ontogeny of small pelagic larvae that are influential on their ability to feed successfully.

Firstly, the development of their locomotor ability is an important period. Newly hatched pelagic larvae are equipped with a continuous median finfold (Kendall et al., 1981) and a single layer of red aerobic muscle fibres (Batty, 1984). This enables them to engage in burst swimming, facilitating the adjustment of their position in the water column, feeding, and evading predation. Major milestones of development such as gaining midlateral red muscle, development of the caudal and dorsal fins, and flexion of the notochord (Batty, 1984; Nikolioudakis et al., 2010), increases a larvae's cruising speed and subsequently the volume of water searched (Blaxter, 1986). Initially, larvae have extremely limited scotopic vision restricting them to diurnal feeding (Blaxter, 1968). They possess effective binocular vision allowing perception of depth, yet vision is initially restricted to close objects (Blaxter & Staines, 1971). Both optic and spectral ability are enhanced throughout their early life, increasing their perception field and spectral optimums (O'Connell, 1981).

Certain characteristics of the feeding apparatus, such as mouth size and gape, influence prey acquisition directly. Mouth gape in feeding larvae sets the upper limit on size of prey attainable by the individual (Schmitt & Holbrook, 1984; Karpouzi & Stergiou, 2003). Allometric increases in gape size are diet specific, e.g., carnivorous fish exhibit the highest allometric increase, as their prey size is generally the largest (Scharf et al., 2000; Karpouzi & Stergiou, 2003). For lower trophic level fish, alternative feeding appendages become of increasing importance. For instance, in clupeoids, gillrakers become the most significant determinant of prey capture. During their early ontogeny, the feeding apparatus of small pelagic fish develops with growth, significantly altering both their ability to attain prey and the prey size-composition (Blaxter & Hunter, 1982).

To conclude, there are many factors that both indirectly and directly affect the capability of an individual larva to obtain prey, all of which change significantly throughout the early life history stages. It is therefore reasonable to assume that whilst individuals are undergoing such morphological transformations, their diet would likely follow a similar transformation.

1.6. Ecopath for the Southern Benguela

Increasing our temporal resolution of the dietary ontogeny of a species will enable accurate future analysis of trophic pathways and linkages within ecosystems and their feedback to vital ecosystem services such as fisheries. Currently, there are several popular methods that quantitatively model entire ecosystems such as ATLANTIS (Fulton et al., 2004), Ecopath with Ecosim (EwE, Christensen & Walters, 2004) and to a lesser extent OSMOSE (Shin & Cury, 2001; Shin et al., 2004). EwE is one of the most widely used and has been applied to all four of the major EBUS (Jarre et al., 1991; Jarre-Teichmann et al., 1998; Heymans & Baird, 2000; Shannon, 2000; Amorim et al., 2004; Field, 2004; Neira & Arancibia, 2004; Moloney et al., 2005; Koehn et al., 2016; Chiaverano et al., 2018; Shannon et al., 2020). EwE is a tool that facilitates the quantitative parameterisation of an entire ecosystem. Functional groups within the model are defined either by specific species or groups of species with similar life history traits. Most importantly, the model adheres to one core fundamental; that both the energy input and output of a functional group must balance. Since its conception (Polovina, 1984; Christensen & Pauly, 1992), the tool has undergone a series of sequential developments, incorporating both temporal

(Ecosim) and spatial (Ecospace) components (Walters et al., 1997, 1999; Christensen & Walters, 2004).

Modellers attempt to quantify ecological interactions as accurately as possible, striving to replicate reality. Incorporating the option of multi-stanza specification into Ecopath has allowed the user to break down species into discrete age/length categories, providing the opportunity to include a more detailed age structure (Christensen & Walters, 2004). Few models in any of the four major EBUS have included more than one life history stage (stanza) for any of the small pelagic species present (Field et al., 2006; Tam et al., 2008; Watermeyer et al., 2008a; b; Neira et al., 2014; Shannon et al., 2014b; Chiaverano et al., 2018). The most recently published Ecopath model of the sBUS represents multiple stages for anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*, although these are only represented as juveniles and adults, and round herring are not split into stanzas (Shannon et al., 2020). This therefore poses the question, of whether there would be a benefit in our ecosystem understanding and model capabilities from including a higher resolution of life history stages for small pelagic fish in ecosystem models.

1.7. Objectives of this Thesis

This study seeks to investigate the ontogenetic development in morphology and trophic ecology of early life stages of small pelagic fishes in the Benguela, and how they compare interspecifically and between northern and southern sub-systems. In this study, the term "early life stages" is defined to include all larval stages as well as juveniles, consistent with modern definitions (Catalán et al., 2020). Increasing our temporal resolution of the ecological ontogeny of a species will facilitate accurate future analysis of trophic pathways and linkages within ecosystems and their feedback to vital ecosystem services such as fisheries. This study aims to document the trophic ecology of early life stages of Benguela small pelagic fishes which are not known, in order to address the following two questions:

1. Is there an ontogenetic shift in trophic ecology attributable to key morphological milestones during the early life stages of sardine *Sardinops*

sagax, anchovy *Engraulis encrasicolus* and round herring *Etrumeus whiteheadi*?

2. Does increasing the life history resolution of the trophic ecology of these species in ecosystem models provide us with new information on trophic transfer efficiencies and species interactions of pelagic fish – centred pathways?

This is facilitated through the following aims:

- I. Identify key morphological milestones during the ontogeny of the three small pelagic fish species that would promote significant feeding success or dietary shifts;
- II. Investigate whether these milestones correspond to significant shifts in trophic ecology through a multi-faceted approach of stomach content, stable isotope and fatty acid analyses;
- III. Disaggregate the most recent Ecopath model to include increased life history resolution of small pelagic fishes in the Benguela;
- IV. Investigate the model fit of small pelagic dependent species following the increased small pelagic trophic pathways;
- V. Investigate overall model function following disaggregation of small pelagic fishes.

1.8. *Outline of Thesis Structure*

This thesis presents four key data chapters (3 – 6) with two introductory Chapters (1-2) and a final synthesis Chapter that highlights the main conclusions. Chapters 3 – 6 are prepared with the intent to publish them separately.

The samples used in this thesis came from multiple sources and therefore, their distribution, density and the environmental conditions are described in Chapter 2.

The trophic ecology, described through both ecomorphological traits and traditional stomach content and biochemical analyses, of larval anchovy *Engraulis encrasicolus* and

sardine *Sardinops sagax* is presented in Chapters 3 and 4. These Chapters discuss the trophic partitioning among these two species at this life history stage.

Using samples obtained from routine small pelagic recruit and spawner biomass surveys, the trophic ecology of pre-recruit and juvenile anchovy, sardine, and round herring *Etrumeus whiteheadi* are explored. Similarly, the predisposition for trophic partitioning at this stage is discussed and compared to the larval stage.

The results from Chapters 3 – 5 are synthesised and utilised by disaggregating these species into increased life history stages in the most recent Ecopath with Ecosim model of the southern Benguela in Chapter 6. The results from this Chapter discuss the benefit of including a finer life history resolution and provides modelling recommendations for future studies.

The results from the data Chapters are discussed and synthesised in Chapter 7.

Chapter 2

Spatial and temporal occurrence of fish larvae in the BUS

2.1. Introduction

Data for this thesis was obtained from an array of sources, however the core of the thesis was built around larval and juvenile samples collected from the M153 RV Meteor research cruise, and provided by the Department of Forestry, Fisheries and the Environment (DFFE, previously DEFF) from biannual hydro-acoustic surveys. The Benguela exhibits substantial physical and biochemical variance, and because small pelagic fishes are so tightly coupled with these processes, it is essential that these samples are described in terms of their bio-physical environment. It is worth noting that supporting data used in the subsequent Chapters of this thesis not mentioned here, will be described chronologically as and when it is implemented throughout the thesis.

The M153 RV Meteor cruise was an international research effort contributing towards the TRAFFIC project (Trophic tRANSfer eFFICIency in the Benguela Current), aiming to expand our knowledge on the processes that drive the trophic structures of both the northern and the southern Benguela. Different gears were deployed to assess and measure both biophysical properties and biological components, such as phyto-, zooplankton and fish. The DFFE biannual hydro-acoustic surveys were performed during austral summer and winter, to assess biomass of small pelagic spawners and recruits, respectively. Conducted since 1984, these surveys were conducted along cross-shelf transects from Hondeklip Bay to Port Alfred. Trawls were conducted throughout these surveys, which provided this thesis with pre-recruits.

2.2. Methods

2.2.1. Collection

Larvae and early juveniles of sardine and anchovy were collected from the northern and southern Benguela upwelling system during the austral summer (February/March 2019) research cruise M153 aboard the RV Meteor. Two sampling grid boxes were

designed in both systems to facilitate comparable sampling stations, which consisted of at least three transects both perpendicular and parallel (50 m, 100 m and ~ 1000 m isobaths) to the coast. Both grid boxes also had two 48-hour stations to assess vertical migrations (Figure 2.1). A MultiNet Maxi rigged with eight nets equipped with 300 μm and one net with 500 μm mesh size was used to sample ichthyoplankton. The net was routinely towed obliquely at 2 knots between approximately 10 m from the ocean floor (or 200 m maximum depth) and the surface. A total of 62 hauls were made over 44 stations (nBUS = 24, sBUS = 20). The neuston was sampled using a modified catamaran that had two 500 μm mesh nets vertically stacked that sampled the surface (0 – 0.15 m) and the near-surface (0.15 – 0.30 m) water layers. The nets were towed horizontally through the water at 4 knots. A total of 47 hauls were made covering 28 stations (nBUS_n = 15, sBUS_n = 13). Not every scheduled station was sampled using both samplers due to time and weather constraints. Following each haul, the contents of the nets were emptied into individual white sorting trays where larvae were identified. Once clupeoids were identified, they were further described to species level (*Engraulis encrasicolus*, *Sardinops sagax* and *Etrumeus whiteheadi*) under a microscope (Olivar & Fortuño, 1991). Individuals were then quickly measured (caudal length) using a graticule and frozen in individual cryotubes at -80 °C.

Temperature, oxygen and chlorophyll-*a* were measured at the beginning of every station using a CTD equipped with an SBE 43 Oxygen sensor. CTD casts were deployed down to a maximum depth of 800 m or 5 m from the ocean floor. Dissolved oxygen content was then calibrated using the Winkler titration method calculated from 38 Niskin bottle samples taken during the cruise. For each larval sample, the environmental data from the corresponding depth was used.

Early and late juveniles were obtained from midwater trawls made during routine small pelagic total biomass (November) and recruitment (May - June) surveys performed by the DFFE of South Africa. Samples were frozen at -20 °C aboard immediately after capture and kept frozen until further analysis at the University of Cape Town. Due to the indiscriminate procurement of these samples, biophysical inferences and spatial descriptions made from the data can only be qualitative.

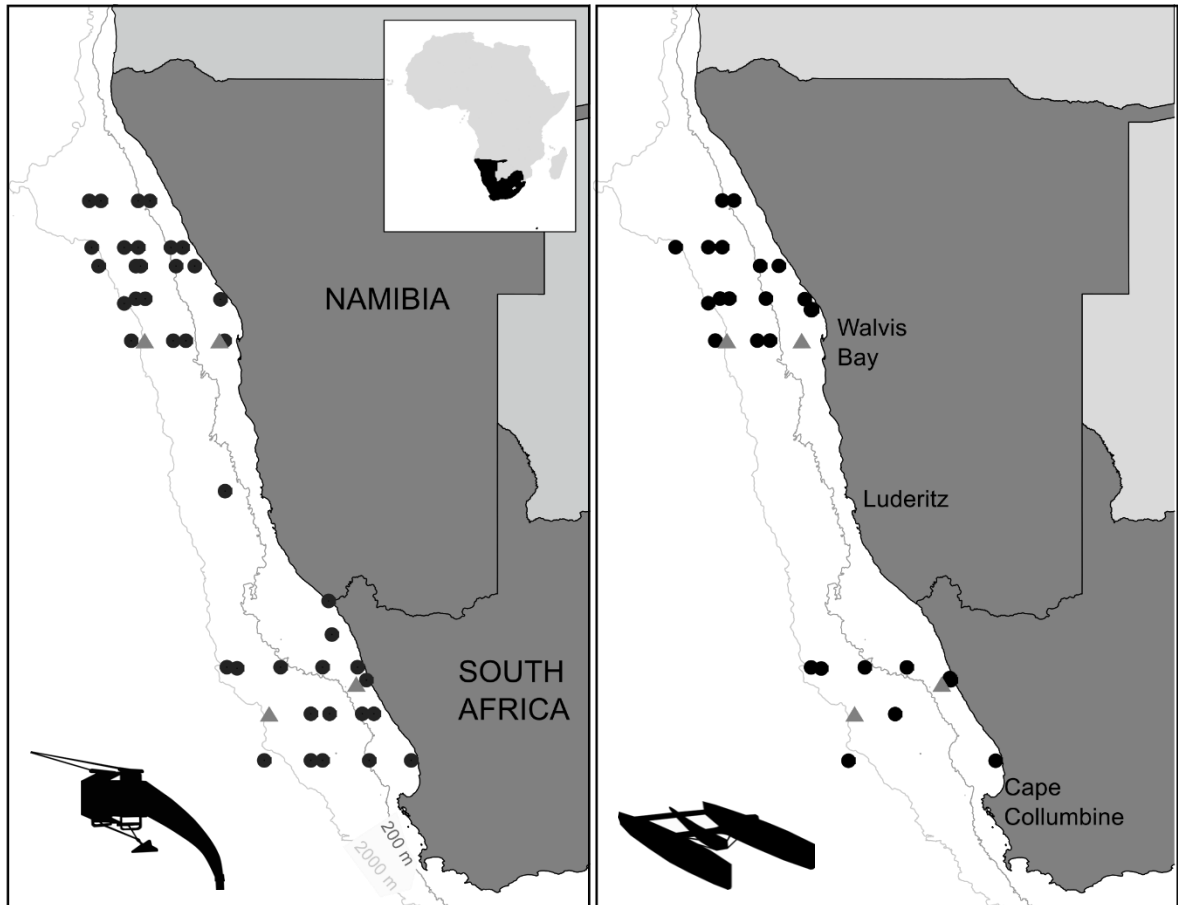


Figure 2.1. Stations sampled in the southern and northern Benguela aboard the M153 cruise in February and March 2019. The left panel shows stations sampled by the MultiNet Maxi and the right panel shows the stations sampled by the modified neuston catamaran. ▲ depict 24-hour stations where multiple hauls were made.

For maps and qualitative purposes, satellite derived data was obtained for the three environmental variables. Firstly, sea surface temperature (SST) was obtained from the Global Ocean 1/12° Physics analysis and forecast product output provided by Copernicus Marine (CMEMS, 2020). Dissolved oxygen content was obtained from the Global Ocean Biogeochemistry Hindcast model output by Copernicus Marine. Finally, chlorophyll-*a* data was provided by OceanColor, using the Modis Aqua 4km L2SMI daily data (NASA Ocean Biology Processing Group, 2015). Daily data was used for all three environmental variables and averaged over the sampling timeframe. For the juvenile samples provided by DFFE, ambient environmental data was derived from the corresponding grid cell of the satellite data.

2.2.2. Description of Samples; Length-Frequencies, Station Depth and Environmental Variables

Both pieces of sampling equipment used on the M153 research cruise were fitted with a mechanical flowmeter, facilitating the calculation of volume of water (m^3) sampled during each haul. This was then used to calculate density of fish larvae per station.

Length-frequencies of the three species from the separate systems from both the M153 RV Meteor cruise and DFFE data was investigated to illustrate the different life stages represented in this thesis.

In order to analyse station depth, temperature, oxygen and chlorophyll-*a* for larval samples, a separate one-way ANOVA was implemented between species using the *in situ* environmental data. Post-model validation was examined to assess homoscedasticity and normality of residuals. If these assumptions were violated a one-way Kruskal-Wallis was implemented instead. The species and systems were grouped together in order to analyse differences; anchovy from the nBUS (hereafter nBUS anchovy), sardine from the nBUS (hereafter nBUS sardine) and anchovy from the sBUS (hereafter sBUS anchovy). Sardine from the sBUS was removed from the analysis due to the very small sample size ($n=2$).

2.3. Results

2.3.1. Description of Samples

In total there were 1,054 individual larval samples collected, 604 anchovy and 451 sardine; round herring larvae were completely absent from the samples.

Of the 50 hauls completed by both the neuston catamaran and MultiNet Maxi in the nBUS only 14 hauls over 9 stations contained fish samples. A total of 429 larvae were caught, 333 sardine and 96 anchovies, with a co-occurrence of both species in 8 hauls over 6 stations. The majority of sardine were caught on the shelf, with > 90% of the catch being caught in waters < 200 m deep, however there were samples collected with a max depth of 450 m deep (Figure 2.2). The highest density of sardine was found at the shelf edge with 170 larvae 100 m^{-3} . Conversely, anchovy were distributed equivalently both on the shelf (55 %) and off the shelf (45 %, Figure 2.2). Anchovy wasn't as frequently encountered as sardine, and its largest density was found at inshore with a density of 15 larvae 100 m^{-3} .

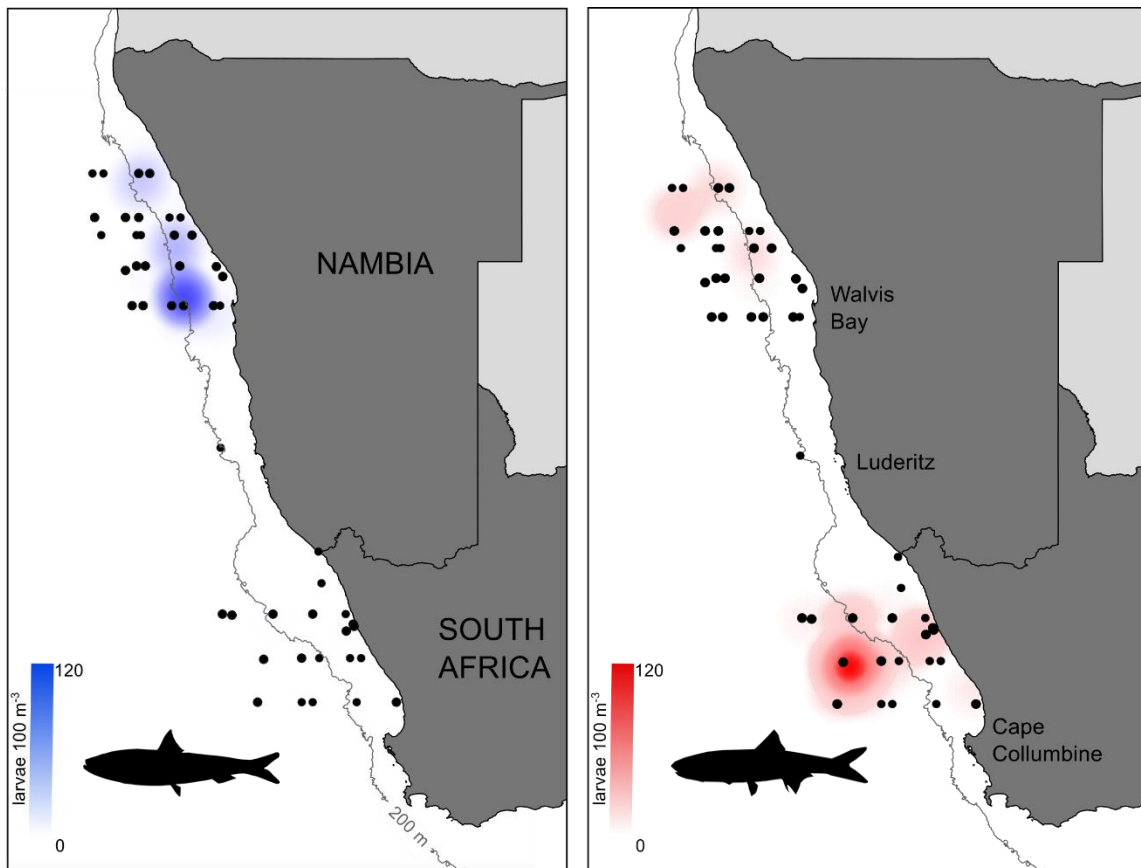


Figure 2.2. Density of larvae (100 m^{-3}) of sardine (left panel) and anchovy (right panel) caught during the M153 cruise in February and March 2019, from both the MultiNet Maxi and Neuston Catamaran.

Out of the total 47 hauls made in the sBUS only 27 hauls across 13 stations resulted in a positive catch. There was an almost complete absence of sardine, with only two specimens being collected at the shelf edge ($30^{\circ}40 \text{ S}$, $17^{\circ}00 \text{ E}$) and at the coast ($30^{\circ}01 \text{ S}$, $15^{\circ}36 \text{ E}$).

There was a total of 504 anchovy caught in the sBUS, and anchovy were caught at both stations where sardine were caught. Similar to the nBUS, the largest proportion of anchovy were caught off the shelf, with 80% caught between 200 – 2500 m isobaths. There was a high density of anchovy caught at the 2500 m isobath during a multi haul 24-hour station ($121 \text{ larvae } 100 \text{ m}^{-3}$). However, the highest density recorded was during station 8 at the 350 m isobath of $321 \text{ larvae } 100 \text{ m}^{-3}$ (Figure 2.2).

In both the nBUS and sBUS, the majority of fish caught were found in the top 30 meters of the water column. Specifically, 90% of sardines and 77% of anchovies in nBUS, and 67% of anchovies in sBUS were caught in this upper depth range (Figure 2.3).

Additionally, there was a noticeable difference in the size of fish caught at different depths, with larger fish being caught progressively shallower (Figure 2.3).

A total of 292 juvenile samples were provided and processed, comprising of 106 anchovy, 98 sardine and 88 herring (Table 2.1). Samples were provided from two separate dates. Firstly, there were anchovy and sardine samples provided from spring 2018, these were caught coastally in St Helena Bay (Figure 2.4) and represent a smaller size class to that of individuals caught further south, indicated by the two smaller frequency peaks in Figure 2.5c. The second batch of samples were provided from late spring/early summer 2019, as shown in Figure 2.4, which represent the larger dominant peaks in their size frequency distribution in Figure 2.5c. All samples were caught coastally, within the 100 m isobath.

Length frequencies taken during the cruise differ between both species and system (Figure 2.5a & b). The length frequencies of anchovy caught within the nBUS shows a bimodal distribution, with two peaks at 7 mm and at 19 mm. Notably, the peak of anchovy within the sBUS is different to that of anchovy in the nBUS, with a peak at 14 mm. Sardine in the nBUS had one peak, slightly smaller than the dominant peak to that of anchovy in the system. However maximum and minimum of both species in the system were similar (Table 2.1). It is difficult to make any inferences from the sample of sardine taken from the sBUS due to the small sample size ($n = 2$).

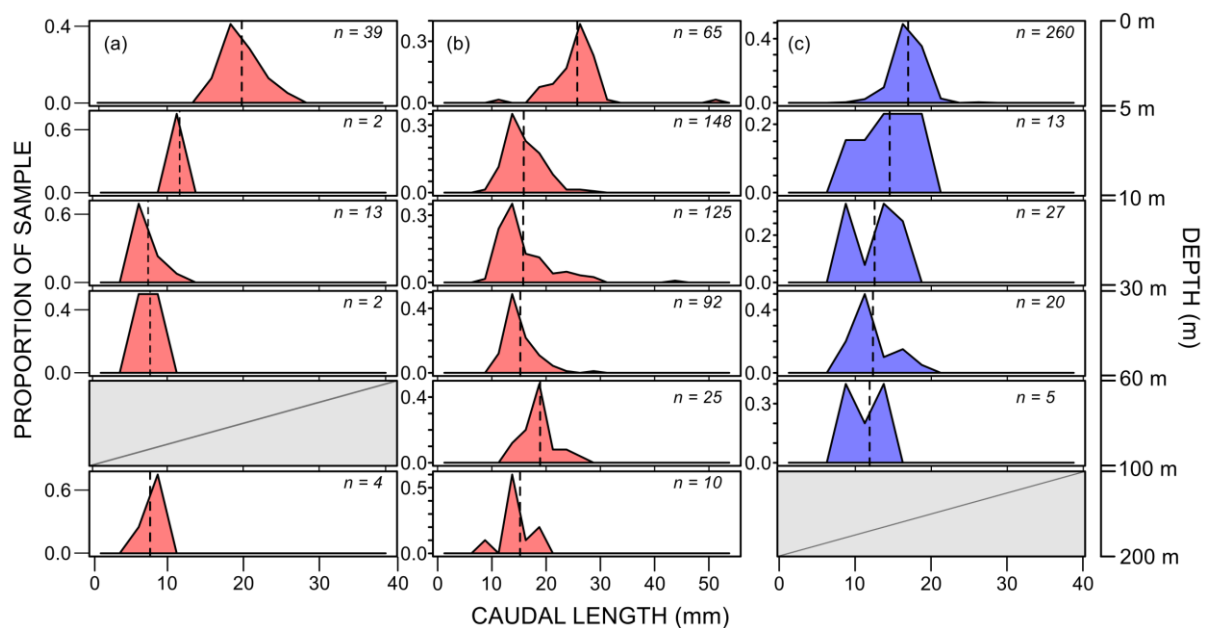


Figure 2.3. The length frequency of (a) nBUS anchovy, (b) sBUS anchovy and (c) nBUS sardine, caught at different depths from the samples collected during the M153 cruise. Vertical lines represent the mean caudal length of the depth specific sample.

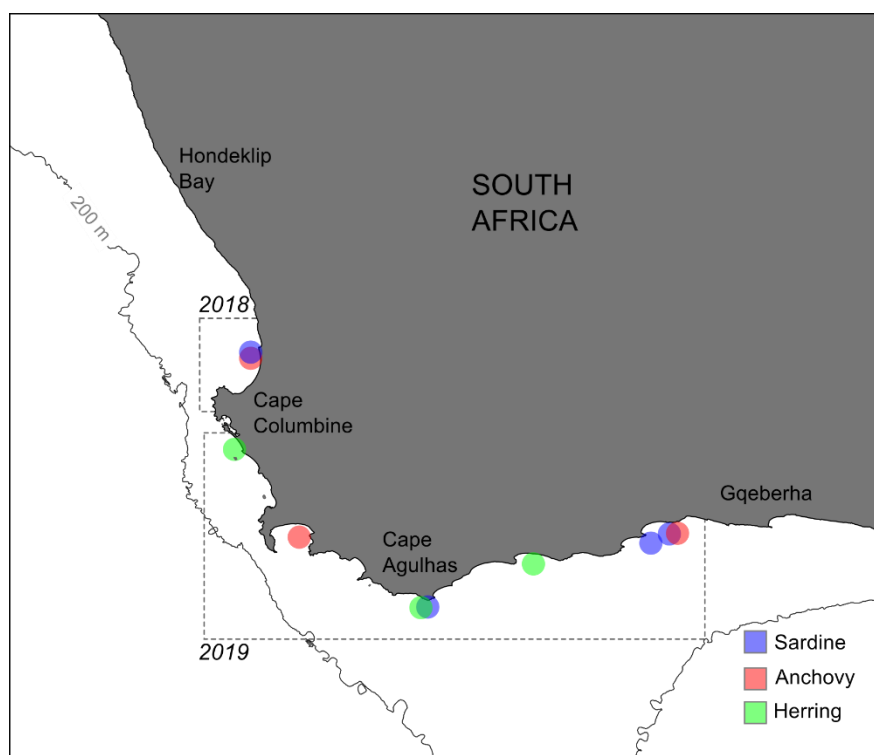


Figure 2.4. Depicts the spatial distribution of the juvenile samples provided by DFFE from the annual biomass survey. The years in which the samples were taken are depicted by each time box; “2018” and “2019”.

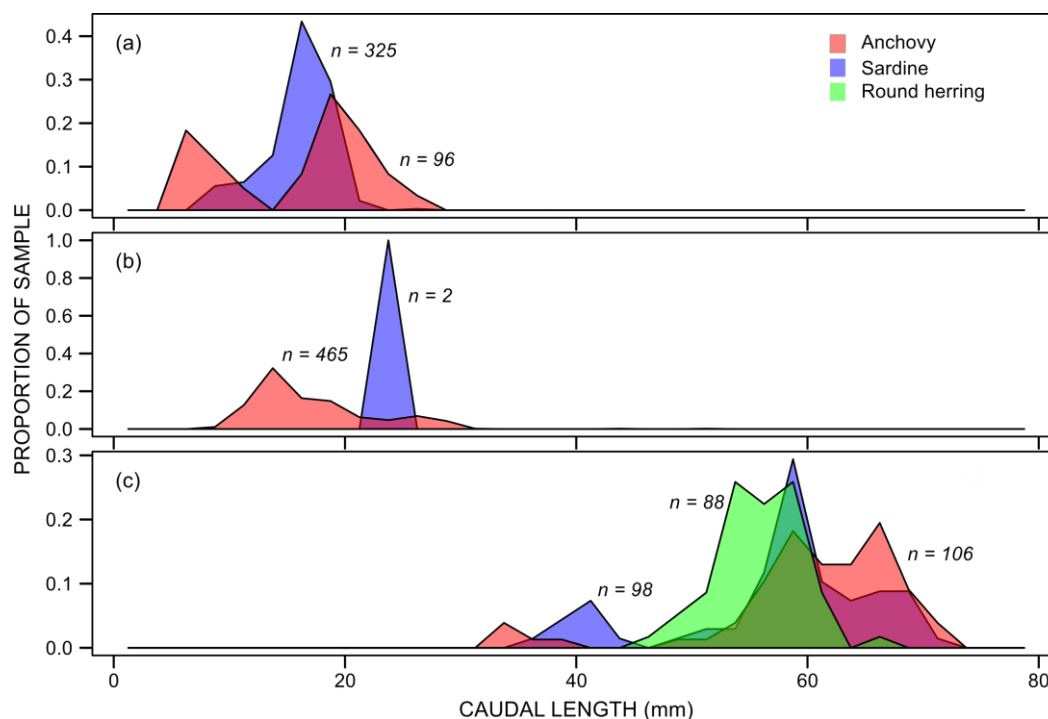


Figure 2.5. Shows the length-frequencies as proportion of the total number sampled for samples taken during the M153 cruise from the (a) nBUS and (b) sBUS, and (c) juvenile samples provided by DFFE during their annual biomass survey.

Table 2.1. Descriptive statistics of the caudal length (mm) of the samples obtained for this thesis. Larvae were obtained from the M153 cruise and juveniles were obtained from the DFFE annual biomass survey. $\bar{x}$ is the sample mean (mm), s is the standard deviation of the sample mean (mm), Max and Min are the maximum and minimum values (mm), giving the range, and n is the sample size.

	nBUS Larvae					sBUS Larvae				
	$\bar{x}$	s	Max	Min	n	$\bar{x}$	s	Max	Min	n
Anchovy	15.937	6.308	27.29	5.50	60	17.253	5.301	52.00	9.81	465
Sardine	16.131	2.727	25.90	7.58	325	23.977	0.032	24.00	23.96	2
Herring	-	-	-	-	-	-	-	-	-	-

	sBUS Juveniles				
	$\bar{x}$	s	Max	Min	n
Anchovy	60.609	8.184	72.00	33.60	106
Sardine	57.711	8.532	70.75	36.00	98
Herring	55.823	3.717	65.95	45.36	88

2.3.2. Station depth

Differences in spatial organisation between the three larval groups by station depth (m) was tested using a one-way ANOVA, post model residuals showed homoscedasticity and were normal. The results showed that there was a statistical difference between the mean depths that the two species were caught ($F_s = 190.1$, $df_1 = 3$, $df_2 = 934$, $p = <0.0001$). A Tukey HSD test was used to explore the intergroup differences and showed a significant difference between all three groups. Anchovy were comparatively further offshore compared to sardine (Figure 2.2), with sBUS anchovy having the largest mean ($\pm$ SD) station depth of 617.96 ($\pm$ 594.48) m, then nBUS anchovy (mean [$\pm$ SD] = 267.82 [$\pm$ 359.42]) and finally nBUS sardine (mean [$\pm$ SD] = 162.43 [$\pm$ 58.32]).

Juvenile samples obtained from the South African west and southwest coasts (Figure 2.6) were caught in waters of comparably lower SST (16.46 – 16.53 °C) than the larval samples (18.38 – 20.24 °C).

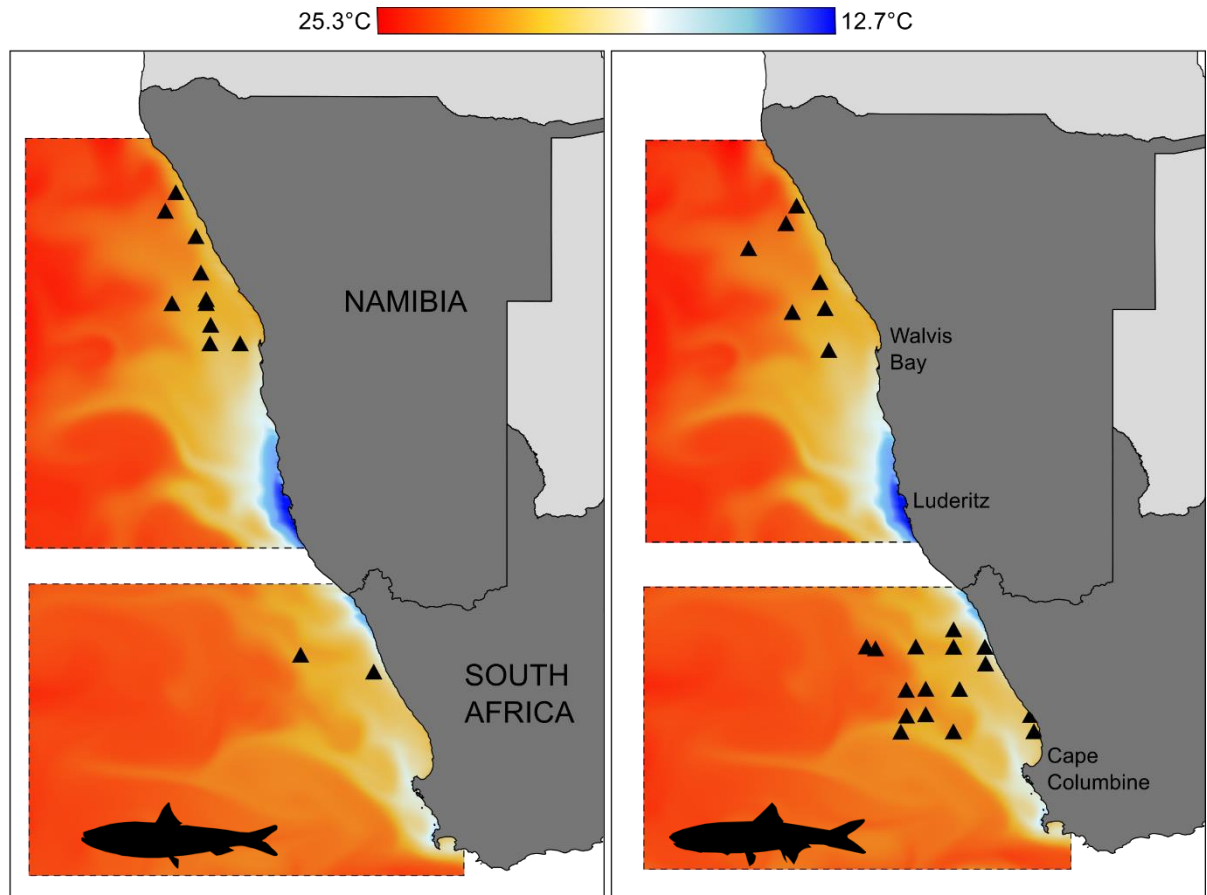


Figure 2.7. Depicts the positions of larval catches during the M153 cruise in February and March 2019 for sardine (left panel) and anchovy (right panel). Mapped sea surface temperature (°C) data were obtained from the Global Ocean 1/12° Physics analysis and forecast product output provided by Copernicus Marine and averaged for the sampled two-week time frame in each system.

2.3.4. Dissolved Oxygen

A one-way ANOVA was applied, and post-model residuals satisfied the assumptions of homoscedasticity and normality. There was a significant difference in mean dissolved oxygen content (ml L^{-1}) between all three ($F_s = 405.3$, $df_1 = 2$, $df_2 = 947$, $p = <0.0001$), with a Tukey HSD post-hoc test showing significance between all three groups. Anchovy caught in the sBUS were found at significantly higher dissolved oxygen

levels (mean [SD] = 5.2831 ml L⁻¹ [$\pm$ 0.4345]), than both nBUS anchovy (mean [SD] = 4.462 ml L⁻¹ [$\pm$ 0.9571]) and nBUS sardine (mean [SD] = 3.9705 ml L⁻¹ [$\pm$ 0.7991], Figure 2.8).

Juveniles of all three species were obtained from areas with comparable dissolved oxygen content (ml L⁻¹), ranging from 5.21 to 5.92 ml L⁻¹ (Figure 2.6).

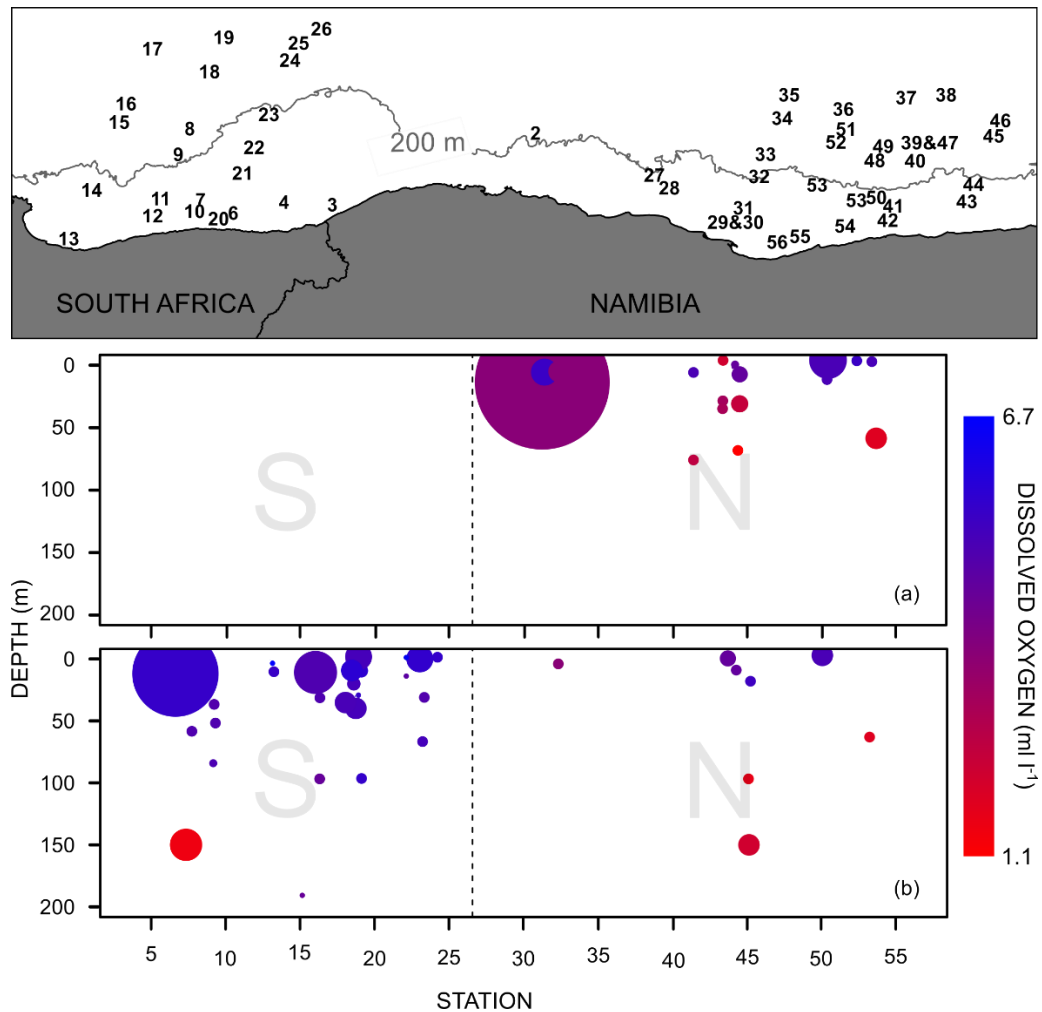


Figure 2.8. Depth and dissolved oxygen concentration of both (a) sardine and (b) anchovy at each station of the M153 cruise in February and March 2019. Top panel shows the numbered stations of the M153 cruise. Size of points are proportion of catch of the specific species within the subsystem.

2.3.5. Chlorophyll-*a*

A Kruskal-Wallis was applied as the data was not-normal, but variances were similar. The ambient chlorophyll-*a* concentrations were not equal between the three

groups ($\chi^2 = 74.16$, $df = 2$, $p < 0.0001$). Following the post-hoc multiple comparison test there was a significant difference in ambient chlorophyll-*a* between nBUS sardine and both anchovy groups (nBUS sardine – nBUS anchovy: $z = 4.19$, $p\text{-value} = < 0.001$, nBUS sardine – sBUS anchovy: $z = 8.44$, $p\text{-value} = < 0.001$). However, there was no intraspecific difference between anchovy groups. Anchovy were found in comparatively higher chlorophyll areas (nBUS anchovy mean [$\pm$ SD]: 1.0844 mg m^{-3} [0.9372], sBUS anchovy mean [$\pm$ SD]: 1.2228 mg m^{-3} [1.7013]) compared to sardine (nBUS sardine mean [$\pm$ SD]: 0.8947 mg m^{-3} [1.1909], Figure 2.9).

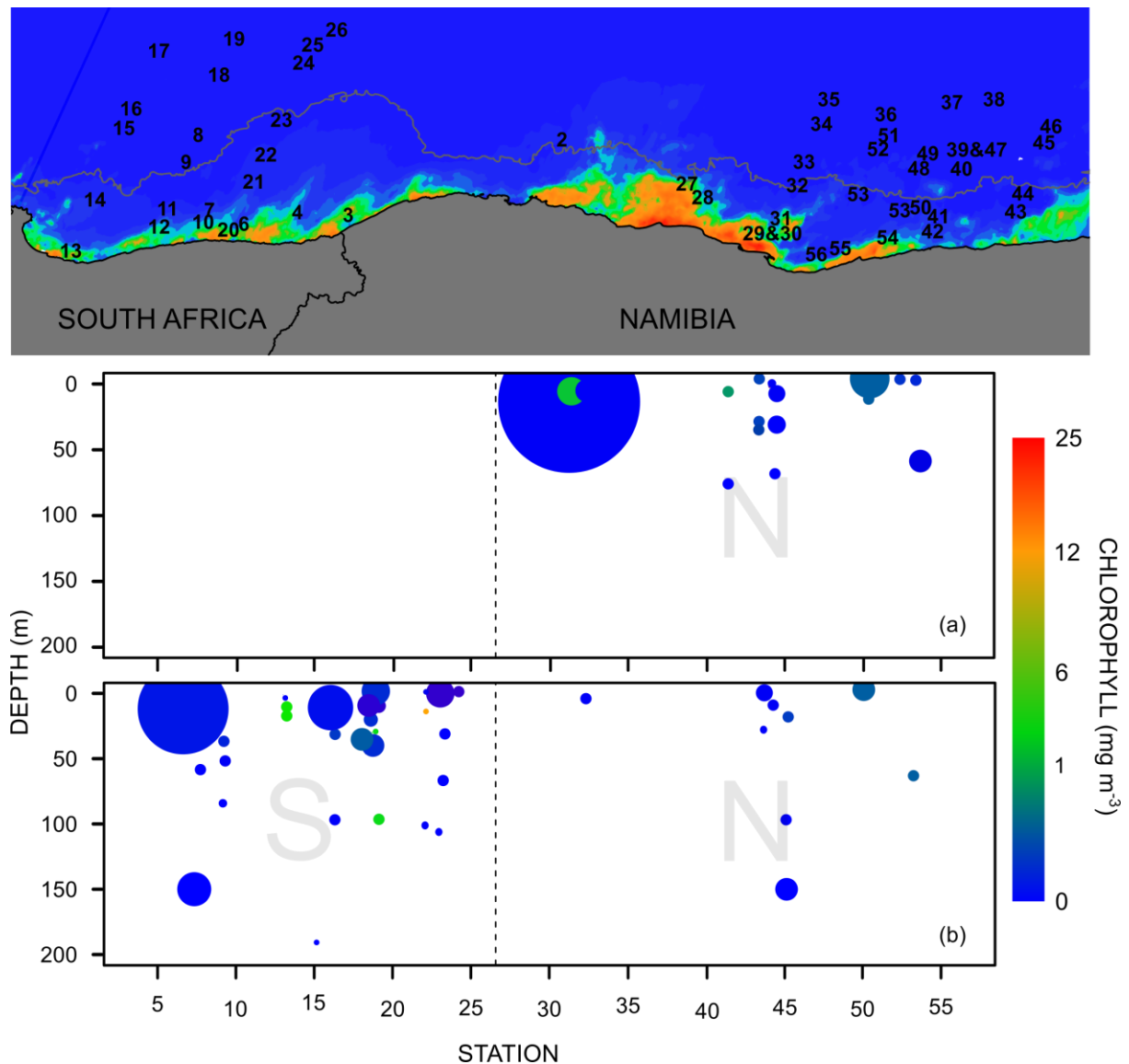


Figure 2.9. Depth and chlorophyll-*a* concentration of both (a) sardine and (b) anchovy at each station of the M153 cruise in February and March 2019. Top panel shows the numbered stations of the M153 cruise and the Modis Aqua 4km L3SMI daily chlorophyll-*a* data obtained from OceanColor and averaged for the sampled time period.

Juvenile samples obtained from both east of- and at Cape Agulhas had comparable chlorophyll-*a* concentrations, ranging from 0.48 – 1.91 mg m⁻³ whereas, samples collected from the west and southwest coasts (Figure 2.6) were caught in areas with considerably higher concentrations, ranging from 4.58 mg m⁻³ to 31.84 mg m⁻³.

2.4. Discussion

Larval samples collected during the M153 cruise showed significant difference between the systems and species over the tested environmental variables. Anchovy larvae were found in higher concentrations offshore (> 200 m isobath), in warmer waters, with higher dissolved oxygen and chlorophyll-*a* concentrations compared to sardine.

Sardine larvae were almost completely absent from the sBUS. This is unexpected for February, since sardine tend to have a spawning peak during austral summer, typically in February (Fowler, 1998; Huggett et al., 1998). It was therefore expected to observe newly hatched larvae in the west coast nursery area. As seen in historical ichthyoplankton surveys, showing peak sardine larvae abundances during August-October and January-February (Fowler, 1998). This lack of larval sardine density was likely a factor in the severely reduced recruits detected by the June 2019 hydroacoustic recruitment survey, which only recorded 3.54 billion recruits- a third of the previous 10-year average (10.03 billion, de Moor et al., 2020).

Anchovy larvae were found at their highest concentrations at deeper isobaths compared to sardine. There are strong cross-shelf trends in the community structure and biomass of phyto- and zooplankton within the Benguela, with spatially distinct offshore and inshore plankton assemblages divided by the frontal zone (Gibbons & Hutchings, 1996a). Principally, offshore plankton communities have lower levels of abundance and are characterised by smaller celled phytoplankton and a higher diversity of copepods (Dickerson Hopson, 1983; Gibbons & Hutchings, 1996a; Crichton et al., 2013; Mushanganyisi, 2019). Whilst shelf communities exhibit a pronounced peak in plankton biomass at the shelf edge during upwelling seasons, and a concentrated peak inshore during autumn and winter (Verheye et al., 1992). It would be therefore safe to deduce that the ambient prey assemblages available for the samples collected in this study would be characteristically different between the two larval species.

The length-frequencies of larval anchovy caught within the nBUS and sBUS differ, as they show a bimodal and unimodal distribution, respectively, which may be indicative of multiple spawning events within the nBUS and a single in the sBUS. Anchovy have two spawning peaks in the nBUS, firstly in the south during late spring and then in the north during summer (Le Clus, 1990a), conversely anchovy in the sBUS tend to have a single peak during summer (Fowler, 1998). Sardine in the nBUS follow a similar spawning pattern to that of anchovy, with two separate events. The peak observed may temporally match the spawning of the second peak in the anchovy length-frequency, with a difference in length arising from different growth rates or sardine and anchovy.

The juvenile samples from DFFE were caught over two separate periods, early summer 2018 and 2019. Judging from the length-frequency plots it is plausible that the juveniles caught in early summer 2019 are the same year-class as the larvae caught on the west coast during the M153 cruise. Their location of capture may indicate that they are migrating back to the Agulhas Bank to initiate spawning as adults (Figure 2.4). The first two small peaks in length-frequency of sardine and anchovy ($\sim 35 - 40$ mm) represent the samples taken from the St Helena Bay area during 2018 (Figure 2.4), potentially a size class about to embark upon their migration south.

As pre-recruits move south towards the Agulhas Bank, waters tend to warm and become increasingly oligotrophic, as observed here: samples collected from the south coast are from considerably warmer waters with lower chlorophyll-*a* concentrations compared to their west coast counter parts. It must be restated that conclusions mentioned about the juvenile distribution are only qualitative.

Temperature has always been established as an important environmental characteristic that significantly alters a species physiological ecology. There are many significant roles it plays during the early life stages of fish, impacting behaviour, metabolism and growth rate (Somarakis et al., 2018), and as a consequence, it is constantly being investigated to help explain variation in recruitment (e.g., Takasuka et al., 2008; Lindegren et al., 2013; Garrido et al., 2017). Both anchovy and sardine successfully spawn at different thermal optimums in the Benguela, with sardine possessing a larger thermal range but preferring cooler waters (van der Lingen et al., 2001; Mhlongo et al., 2015). This is somewhat in agreement with the thermal distribution of the observed larval density. Sardine were found at lower temperatures on average, however the thermal range of anchovy found in the sBUS was larger. The upper edge of

their thermal tolerance may be indicative of their optimal growth temperature (Takasuka et al., 2007), as growth rates of laboratory-reared larval anchovy are higher at higher temperatures than that of sardine (Brownell, 1983).

Dissolved oxygen is critical for many physiological processes, and with global dissolved oxygen concentrations decreasing (Schmidtke et al., 2017) and oxygen minimum zones increasing globally (Stramma et al., 2010), species with high physiological demands will encounter decreasing favourable conditions. The nBUS has an extensive oxygen minimum zone (OMZ), largely attributed to extreme upwelling and the addition of warm, low oxygenated, equatorial water from the Angolan Gyre, which is expected to expand due to climate change (Monteiro et al., 2008; Ekau et al., 2018). The sBUS doesn't have a defined OMZ, rather seasonal hypoxic and anoxic conditions in St Helena Bay, that haven't showed any long-term change (Hutchings et al., 2012; Pitcher et al., 2014). Both anchovy and sardine in this study were found in well oxygenated waters ($> 2.5 \text{ ml l}^{-1}$), with only three sardines in the north found in hypoxic conditions ($< 2 \text{ ml l}^{-1}$). This is consistent with previous ichthyoplankton surveys performed in the nBUS, whereby both species have been shown to be vertically stratified largely by the presence of the OMZ (Ekau & Verheye, 2005; Kirchner et al., 2009).

In this study, sardines were found in waters having significantly lower chlorophyll-*a* concentrations compared to that of both anchovy groups. Although phytoplankton dynamics are complex, peaks in primary production tend to correspond to peaks in secondary production (Verheye et al., 2016a). Therefore chlorophyll-*a* is commonly used as a proxy for ambient zooplankton (Shannon et al., 1984), which itself may be an indication of productive feeding grounds for small pelagic fish. Therefore, anchovy in this study may have the opportunity for faster growth and better condition, which has been indicated for both larval anchovy and sardine (Basilone et al., 2004; Costalago et al., 2020; Véron et al., 2020).

With distinct interspecific differences across depth, temperature, dissolved oxygen content and chlorophyll-*a*, the distribution of larval samples in this study have provided evidence supporting a difference in trophic ecology between the two larval species presented in this Chapter. Furthermore, it is indicated that as individuals move in a coastal and poleward direction during their early stage ontogeny, there is changing environmental conditions between stages. These differences described in this Chapter have established a firm foundation for the remainder of this thesis.

Chapter 3

The ecomorphology of small pelagic fish larvae in the Benguela upwelling system.

Abstract

Recruitment variability in small pelagic fishes is largely governed by fluctuations in pre-recruit mortality rates, primarily through predation, advective loss and starvation. However, our knowledge of the trophic ecology of early life stages of these species in the Benguela is extremely limited. Morphological variables that have a functional relationship to resource use through feeding behaviour and ability can be used as indicators of trophic ecology and can identify intra- and inter-specific differences. This study examines and compares multiple aspects of the ecomorphology (allometric growth, alimentary and branchial basket development) of larval sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* in the Benguela, and how ontogenetic changes may affect trophic partitioning within and between these species. Results show a high likelihood of trophic partitioning between these species through distinct differences in their ecomorphology. Sardines exhibit traits in their development such as increased relative gut length, that would suggest a higher degree of herbivory throughout their early life stages compared to anchovy. Contrastingly, anchovy display positive allometric growth patterns in their cranial development at a younger age, suggesting a greater importance of selective feeding on larger prey. These results provide an anatomical basis of how both the feeding ability and behaviour of these two species may differ during their larval phase which would predispose them to distinct diets. This information will be utilised in addition to both traditional and modern dietary tools to create a comprehensive description of the trophic ecologies of small pelagic fish larvae in the Benguela.

3.1. Introduction

Competitive interactions between cohabitating species organises a system through resource utilisation (Schoener, 1983). The ability of several intraguild species to coexist together largely depends on how resources are shared and allocated inter- and intraspecifically. Resource partitioning between species or life history stages can be facilitated through the divergent evolution of morphological characteristics (Taper & Case, 1985; Nagelkerke et al., 1995), as successful feeding in fish larvae is largely determined by the development of functional morphological traits and the availability of suitable food sources (Rønnestad et al., 2013). Many functional morphological attributes have been correlated with distinctions in feeding behaviour and diet, primarily relating to feeding apparatus (Tanaka et al., 2006; Spiegel et al., 2011; Wittenrich & Turingan, 2011; Vorsatz et al., 2015), mouth morphology (John Gatz, 1979; Wainwright & Richard, 1995; Piet, 1998; Scharf et al., 2000; Davis et al., 2012), fin formations (Nunn et al., 2007) and digestive tract developments (Ciechomski, 1966; Smith, 1989; Paugy, 1994; Ward-Campbell et al., 2005; Davis et al., 2012). This interdependence has led to the use of ecomorphological attributes as indicators of trophic ecology in certain species.

There are several useful ecomorphological characteristics that can be applied to elucidate broad trophic information. Firstly, the morphology and development of the alimentary tract. Newly hatched altricial larvae possess rudimentary alimentary canals that are commonly undifferentiated, straight tubes (Ciechomski, 1966; Govoni et al., 1986). Prior to the onset of exogenous feeding, larval guts tend to convolute and coil to increase surface area and food residence time for successful assimilation (Govoni et al., 1986; Hunt von Herbing et al., 1996; Rønnestad et al., 2013). Coiling progresses throughout ontogeny with the further addition of appendages such as the pyloric caeca (Govoni et al., 1986). It is theorised that gut morphology is indicative of principal diet, specifically with longer intestinal lengths implying a higher degree of herbivory (Smith, 1989; Paugy, 1994; Elliott & Bellwood, 2003). In clupeoids, the rudimentary straight and undifferentiated gut is present far past the onset of exogenous feeding and may only convolute and coil late into the larval stage (Ciechomski, 1966; Hunt von Herbing et al., 1996). Late differentiation of the stomach could indicate a shift in diet by either increasing the volume of prey (Reifel & Travill, 1978) or increasing the protein content (O'Connell, 1981), which would likely coincide with a shift in diet.

Secondly, the development of feeding apparatus. Gape size is a common trait that influences diet by setting the maximum prey size (Blaxter, 1963; Scharf et al., 2000;

Morote et al., 2010). Other traits, such as dentition (Stoner & Livingston, 1984) and gillrakers (Tanaka et al., 2006; Spiegel et al., 2011; Vorsatz et al., 2015) provide valuable information on the feeding technique and minimum prey size. It is well defined that for adult clupeoids their gillrakers and mouth gape set minimum and maximum limits on their ingestible prey. Their branchial basket morphology, specifically the gillraker spacing, plays a defining role in the facilitation of resource partitioning between sympatric interspecifics (Tanaka et al., 2006; van der Lingen et al., 2006b). In pre-recruit's however, the development of the branchial basket and gape is relatively unknown, yet it likely plays a significant role in the diet of early life stages.

Aside of specific characteristics, allometric growth patterns can be a useful indicator of ecology. Growth during the larval stage is an obviously important process that mitigates size-dependent and growth-dependent mortality (Takasuka et al., 2003; Meekan et al., 2006). However, relative growth rates are not uniform across all morphological characteristics (Fuiman, 1983; Blaxter, 1988). Depending on the species, growth is relatively accelerated in certain areas, prioritising specific morphological characteristics that are considered of higher importance for survival (Fuiman, 1983). For example, in a lot of species somatic growth is focussed at the anterior and posterior end of the larvae (Fuiman, 1983), advancing morphological characteristics that will aid in increased feeding and locomotor ability. The timing of these focussed growth patterns elucidates important information about dietary niches during a species ontogeny.

As size can range over several orders of magnitude over the life of a fish, it is very common for dietary shifts to occur during their ontogeny. These shifts in diet are often obvious in species where metamorphosis is coupled with dramatic life history changes. For instance, in flatfishes, whilst advancing into a juvenile stage the laterally symmetrical, pelagic larvae develop into laterally asymmetrical, benthic adults (Moser et al., 1984; di Pane et al., 2019): both their morphology and environment dramatically change. Contrastingly, clupeoids undergo a subtle, albeit distinct, transformation, with all life history stages remaining in the pelagic habitat. Yet, subtlety does not equate to insignificance. Development is most pronounced prior to metamorphosis, with most morphological characteristics increasing considerably in count or size with body length. It is therefore highly probable that the diet of clupeoid larvae changes throughout their ontogeny.

Due to very strong upwelling and Ekman transport at the Lüderitz upwelling cell, there is minimal mixing of epipelagic species between the northern and southern Benguela (Lett et al., 2007). Therefore, the small pelagic stocks from the northern and southern Benguela are considered distinct and are managed as separate stocks (Hutchings et al., 2009). Morphological traits of conspecifics in either system may differ due to the differences in spatial environmental conditions resulting in genetically or phenotypically distinct characteristics. These differences have been well documented in adult clupeoids, with spatial distinctions in branchial basket morphology of subpopulations of sardine *Sardinops sagax* around the coast of southern Africa (Idris et al., 2016), with these observed differences being the likely consequence of differences in ambient prey assemblages. Therefore, with distinct environmental conditions in the nBUS and sBUS it would be interesting to investigate the potential divergence in ecomorphological characteristics of small pelagic fish larvae.

In South Africa and Namibia, the local clupeoids, sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*, occupy the same nursery grounds, and likely begin to form mixed schools from an early age (Isaacs, 1963). Therefore, the aim of this Chapter is to test the hypothesis that there is trophic partitioning between these species, facilitated through differences in ecomorphological traits. This will be performed by describing the broad trophic ecology of the larvae of both sardine and anchovy in the Benguela through the application of several pre-correlated ecomorphological traits.

3.2. Methods

3.2.1. Data Collection

Samples of larvae from the northern and southern Benguela upwelling system were collected during the austral summer research cruise (M153) aboard the RV Meteor. Two sampling grids (one per sub-system) were used to facilitate comparable sampling stations. Each sampling box consisted of at least three transects parallel to the coast at isobaths of 50 m, 100 m and 1000 m, and two 48 hours stations conducted to assess vertical migrations (Figure 3.1). A MultiNet Maxi rigged with eight nets equipped with 300 µm mesh size and one net with 500 µm was used to sample ichthyoplankton. The net was routinely towed obliquely at 2 knots between approximately 10 m from the ocean

floor (or 200 m maximum depth) and the surface. A total of 62 hauls were made over 44 stations (nBUS n = 24, sBUS n = 20). The neuston was sampled using a modified catamaran that had two 500 µm mesh nets vertically stacked that sampled the surface (0 – 0.15 m) and the uppermost water layer (0.15 – 0.30 m). The nets were towed horizontally through the water at 4 knots. A total of 47 hauls were made covering 28 stations (nBUS n = 15, sBUS n = 13). Following each haul, the contents of the nets were emptied into individual white sorting trays where larvae were identified to species level (*Engraulis encrasicolus* and *Sardinops sagax*) under a microscope. Individuals were then quickly measured using a graticule and frozen in individual cryotubes at -80 °C.

Missing length categories of sardine larvae from the sBUS were supplemented from historical ichthyoplankton samples collected by the Department of Forestry, Fisheries and Environment (DFFE) from the Sardine, Hake and Anchovy Recruitment Programme (SHARP) monitoring line located off Scarborough (Figure 3.1). Samples were only used from the same season as those from the M153 cruise (February and March), to reduce any interseasonal differences. Historical samples were scanned for clupeoid larvae chronologically, beginning at the 2019 February and March samples. The most recent samples containing sardine larvae of correct size samples were from the 2012 and 2013 SHARP project. Those samples were stored in formalin and were only used in the multivariate allometry section of this study.

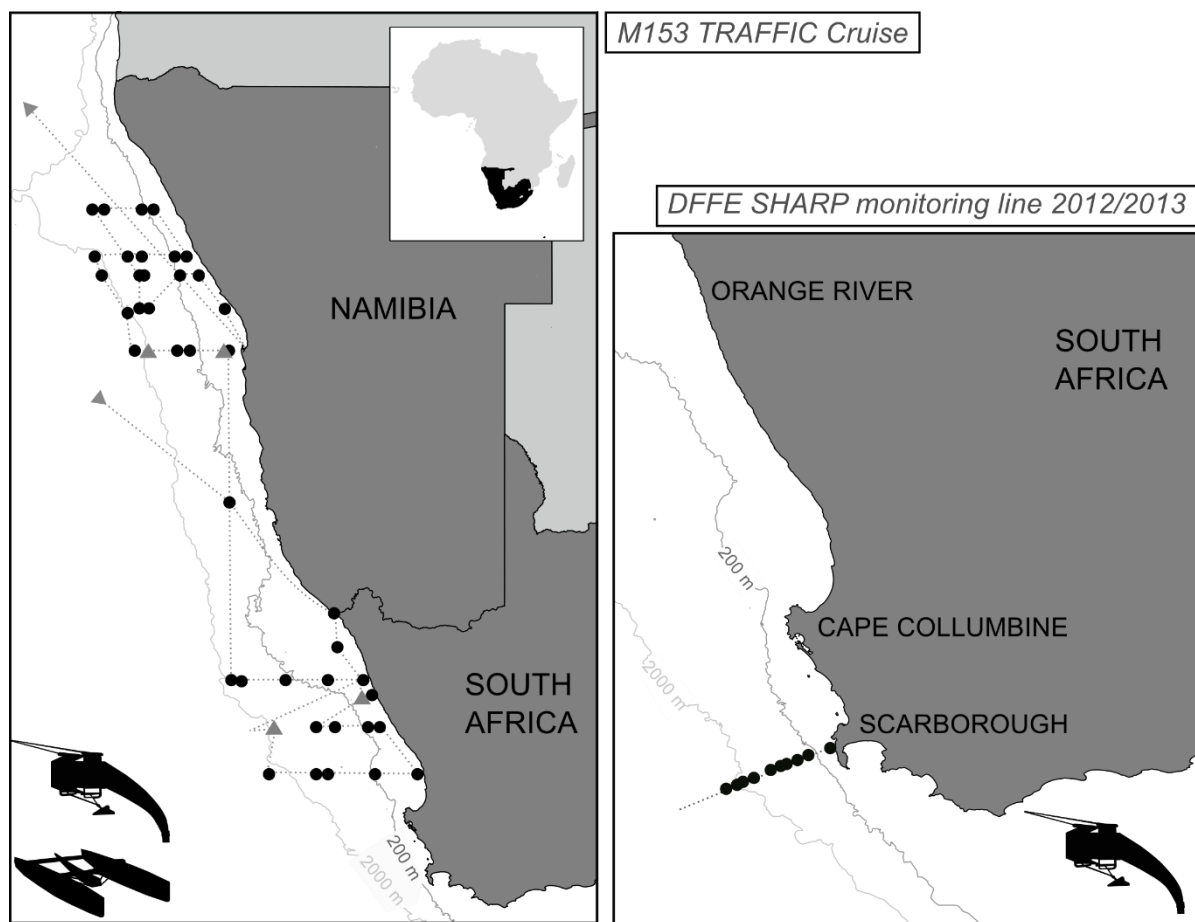


Figure 3.1. Depicts the stations sampled in this study. The left panel shows the stations sampled by both a MultiNet Maxi and Neuston catamaran in the northern and southern Benguela from the M153 cruise. The right panel depicts the stations sampled by DFEE using a MultiNet Midi for the sardine, hake and anchovy recruitment programme (SHARP) in 2012 and 2013. ▲ depict 24-hour stations where multiple hauls were made.

Fish from the M153 cruise were thawed and then the caudal length (mm) and wet weight (mg) of all fish were taken in the laboratory. Each individual was placed on a graticule accurate to 0.01 mm and viewed underneath a Nikon SMZ800 microscope under a magnification of x40. Several morphological measurements were made. The gape size was measured as the maximum distance between the upper and lower jaws at maximum stretch. Both larval species possessed straight guts that were clearly differentiated into a fore- and hindgut due to striation of the hindgut. There was no clear definition between the oesophagus and the foregut, therefore for the purpose of this study the straight, direct

gastrointestinal tract from the mouth to the anus was classed as the gut length. Development of pyloric caeca were monitored and counted.

The measurements of the branchial basket morphology were performed using the same Nikon SMZ800 microscope. Measurements and counts of the gill arch length, gillraker spacing and total number of gillrakers were taken. All measurements were made from the first gillraker on the left lateral side. The gill arch length was comprised of the total length of the epibranchial, ceratobranchial and hypobranchial arch, as seen in Figure 3.2. The total number of gillrakers was the sum of all gillrakers present on the epi-, cerato- and hypobranchial arch. The gillraker spacing was measured following the methods presented by Tanaka et al. (2006), whereby five gillraker spacings were measured from the middle of the ceratobranchial arch and averaged (Figure 3.2).

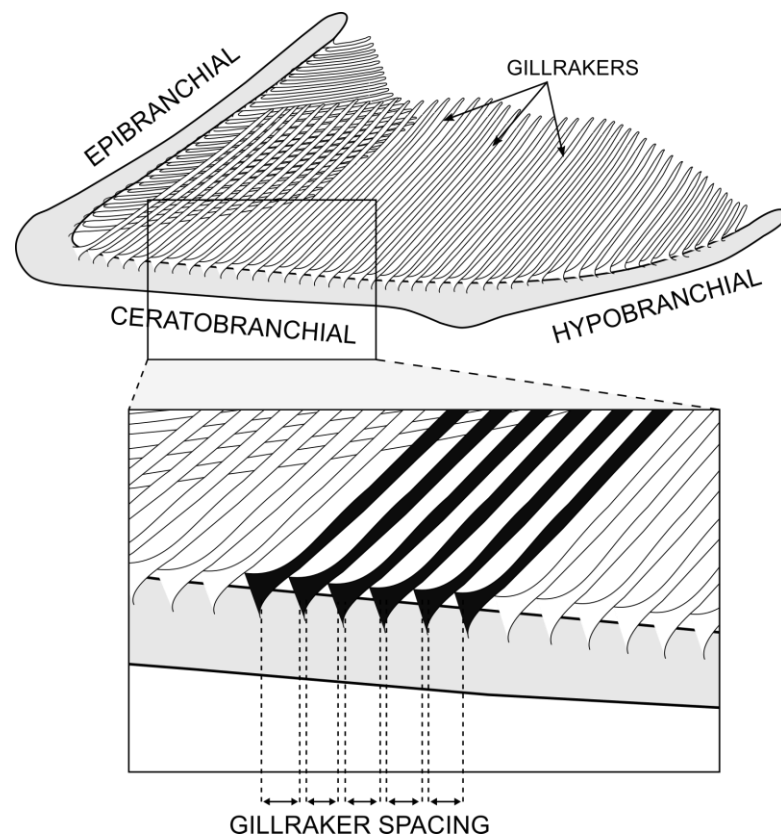


Figure 3.2. A schematic of the first, left lateral gill arch from the larval anchovy and sardine taken in this study, depicting the position of the epi-, cerato-, and hypobranchial arch, as well as the method for calculating the gillraker spacing from Tanaka et al. (2006).

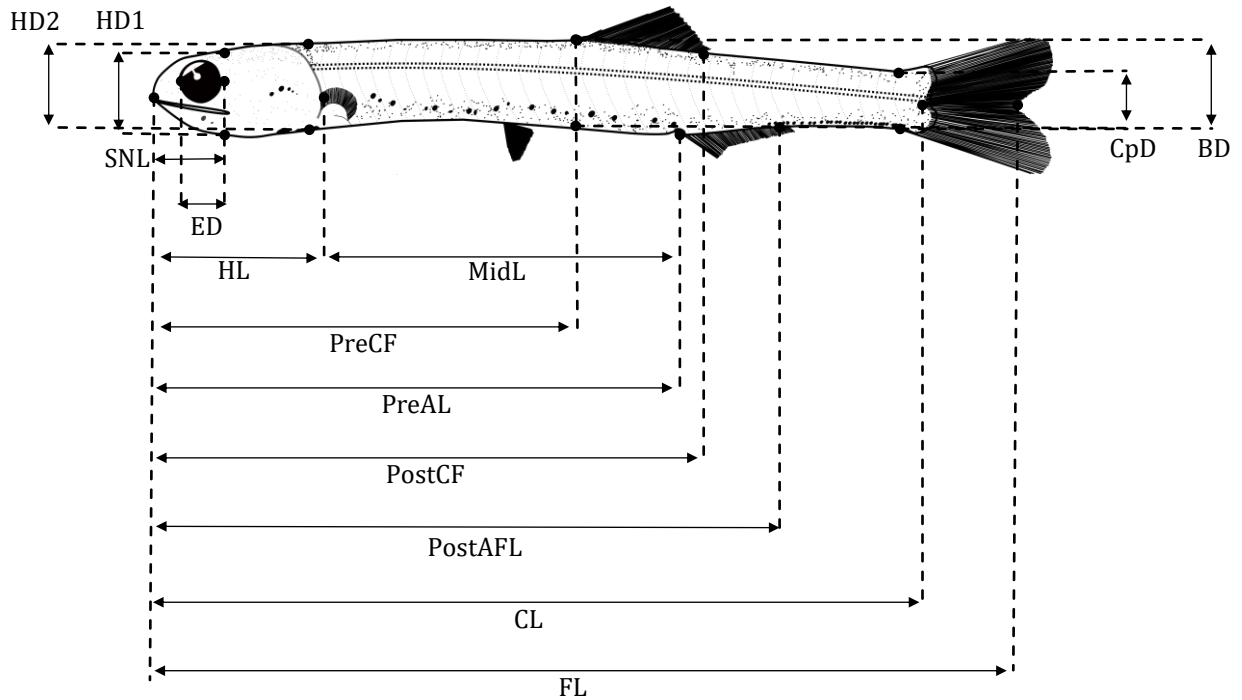


Figure 3.3. The morphometric linear measurements taken from each larva for the multivariate allometry analysis (drawing depicts a 35 mm anchovy larva).

Individuals from both the M153 cruise and the SHARP monitoring line were placed on a graticule accurate to 0.01 mm and viewed underneath a Nikon SMZ800 microscope under a magnification of x40, and photographs of the lateral side of each fish were taken using a Canon EOS 650D camera. From these photographs several morphometrics were measured for the multivariate allometry using ImageJ (Schneider et al., 2012); (a) snout length was taken from the snout of the fish to the anterior edge of the eye (SNL), (b) head length was from the snout to the operculum (HL), (c) pre dorsal fin length was taken from the snout to the anterior margin of the dorsal fin (PreDFL), (d) pre anal fin was taken from the snout to the anterior margin of the anal fin (PreAFL), (e) post anal fin was taken from the snout to the posterior edge of the anal fin (PostAFL), (f) post dorsal fin was taken from the snout to the posterior edge of the caudal fin (PostDFL), (g) caudal length was taken from the snout of the fish to the base of the caudal fin or the end of the notochord in fish with post- or pre- caudal fin development (CL), (h) fork length was taken from the snout of the fish to the fork of the caudal fin or the end of the notochord in fish with post- or pre- caudal fin development (FL), (i) the mid lateral line between the operculum and anus was taken (MidL), (j) the mid lateral line between the

anus and the posterior margin of the caudal fin was taken (PostAL), (j), head depth at the posterior margin of the eye (HD1), (k) head depth at the operculum (HD2), (l) body depth at the anterior margin of the caudal fin (BD), and (m) body depth at the caudal peduncle (CpD; Figure 3.3).

3.2.2. Statistical Analyses

All statistics in this study were performed on the statistical platform R Version 3.5.1 (R Core Team, 2018) using a significance threshold of 0.05.

3.2.2.1. Gape Size

Gape was individually analysed to assess both ontogenetic developments and interspecific differences using General Linear Models (GLMs) on log-log transformed data. The initial model included *Species*, *Caudal Length* and *Region* as explanatory variables. Model simplification was performed using the F-test and model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

3.2.2.2. Stomach and Pyloric Caeca

Relative gut length was calculated and then modelled using a GLM. The initial covariates used were *Species*, *Caudal Length* and *Region*. Model simplification was performed using the F-test and model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

The development of pyloric caeca was explored using a GLM applied to the semi-log transformed data, using *Species*, *Caudal Length* and *Region* as explanatory variables to investigate interspecific and system differences. Model simplification was performed using the F-test and model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

Furthermore, the length-where-50% have ≥ 1 pyloric caecum was determined by fitting the following logistic function with binomial distribution to the proportional data:

$$\frac{\exp(x)}{1 + \exp(x)} \quad (1)$$

using an ogive where x is the proportion of individuals that have ≥ 1 pyloric caecum, in order to find the length where pyloric caeca begin to develop for each species.

3.2.2.3. Branchial Basket Morphology

Branchial basket morphology was compared between the two species of varying CL using Multivariate GLMs to test for significant differences in the dependent variables total number of gillrakers, gill arch length and gillraker spacing of the two species from both systems varying in CL. For both gill arch length and gillraker spacing data were log-transformed prior to analysis in order to normalise residuals. The GLMs had the following form:

$$B_{dfs} = e^{(\beta_0 + \beta_1 \times \log_e(CL)_{fsb} + \beta_2 \times Species_{fb} + \beta_3 \times Region_{ds} + \log_e(CL)_{fsb} \times Species_{fb} + \varepsilon_{dfs})} \quad (2)$$

whereby B_{dfs} is the dependent variable d of the f^{th} fish of the s^{th} species from the b^{th} Region, β_0 is the intercept value, β_1 is the level of influence that $\log_e(CL)_{fs}$ has on the dependent variable d , $\log_e(CL)_{fsb}$ is the log-transformed caudal length (mm) of the f^{th} fish, β_2 is the level of influence that $Species_{fb}$ has on the dependent variable d , $Species_{fb}$ is the parameter describing the influence that each species has on each dependent variable d , β_3 is the level of influence that $Region_{ds}$ has on the dependent variable d , $Region_{ds}$ is the parameter describing the influence that the location (either nBUS or sBUS) has on each dependent variable d , $\log_e(CL)_{fsb} \times Species_{dsb}$ is the interaction term and ε_{dfs} are the residuals that are normally distributed with equal variance. The relationship of total number of gillrakers to CL follows an exponential function, as shown by Gibson (1988) and Costalago & Palomera (2014). Therefore, the GLM fitted to the total number of gillrakers data follows the following form:

$$B_{dfsb} = \beta_0 + \beta_1 \times \log_e(CL)_{fsb} + \beta_2 \times Species_{fb} + \beta_3 \times Region_{ds} + \log_e(CL)_{fsb} \times Species_{fb} + \epsilon_{dfsb} \quad (3)$$

Model simplification was performed using the F-test and model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

3.2.2.4. Multivariate Allometry

The morphometric variables shown in Figure 3.3 were analysed using a principal component analysis (PCA) to investigate differences in growth allometry (Jolicoeur, 1963; Shea, 1985). Univariate analysis showed no significant differences between anchovy from the nBUS and sBUS therefore they were modelled as a single group. The ontogenetic morphometric data were log-transformed before calculating the covariance matrix and performing the PCA. When implementing a PCA on log-transformed ontogenetic morphometric data from groups of individuals with diverging growth, the first principal component encapsulates the variation in body shape and size due to sharing common patterns in growth allometry, whilst the second principal component (and all subsequent components) encapsulates the variation in body shape and size from divergent growth trajectories due to either slope differences or vertical shifts in the bivariate relationships (Shea, 1985). Therefore, with ontogenetic data, shifts in divergent growth from subsequent early life stages could be visualised by divergent PC2 loadings when plotted against caudal length (Nikolioudakis et al., 2010). Subsequently, this was used in this study to quantitatively locate the shift in allometric growth (hereafter referred to as the allometric inflection point) that is associated with early life stages.

The allometric inflection point (AIP) was estimated by fitting a piecewise regression using maximum likelihood to the second principal component loadings and CL (mm), which can be written as:

$$y_i = \beta_0 + \beta_1 x + \beta_2 (x - L)k + \epsilon \quad (4)$$

where y_i is principal two component loadings, β_0 is the y intercept, β_1 is the slope of the relationship between CL and PC2 loadings for pre-AIP larvae ($x < AIP$), β_2 is the slope of

the relationship for post-AIP larvae ($x > AIP$), x is the CL (mm), L is the estimated species specific AIP (mm), ε are the residuals and k denotes breakpoint constant whereby;

$$k = \begin{cases} 0 & ; x \leq L \\ 1 & ; x > L \end{cases} \quad (5)$$

Post-model validation was examined to assess homoscedasticity and normality of residuals.

According to Jolicoeur (1963) and Shea (1985) the principal loadings of the first component from a group that share the same growth trajectories are correlated with the morphometric specific allometric growth coefficient (v) represented in Huxley (1932) bivariate function of relative growth:

$$y = bx^v \quad (6)$$

where x and y are two measurable traits. Hence, a PCA was fitted to both species pre- and post-AIP ($< L$ and $> L$, respectively). The PC1 loadings of each pre- and post-AIP stage was then compared to the theoretical isometry loading outlined by Jolicoeur (1963) as:

$$I_s = \frac{1}{\sqrt{n}} \quad (7)$$

where n is the number of morphometric variables included in the analysis. The variability of the PC1 loadings was estimated by a non-parametric bootstrapping technique, with 1000 iterations (Efron, 1981).

3.3. Results

3.3.1. Gape Size

The gape morphology of both larval species was largely similar. Both species initially exhibited an elongated, posterior directed mouth that developed into a superior directed mouth. Gape size was different during larval development between the species. The GLM fitted to the data included *Caudal Length*, *Species* and their interaction term ($F_{(3, 933)} = 1613, p\text{-value} < 0.001$). Sardines have a significantly smaller gape size that is more isometric compared to anchovy (Figure 3.4). There was no significant difference between gape size of anchovy in the northern and southern Benguela and *Region* was therefore dropped from the model.

3.3.2. Stomach and Pyloric Caeca

There was no significant difference in relative gut length between anchovy from the northern and southern Benguela, therefore *Region* was removed from the model. The model that contained *Species*, *Caudal Length* and their interaction term as explanatory variables was significant ($F_{(3, 496)} = 483.7, p\text{-value} < 0.001$). As seen in Figure 3.5, sardine have a larger relative gut length compared to anchovy of similar length.

Pyloric caeca did not develop in either species until there was visible convolution at the intersection of the fore- and hindgut, as the adult stomach began to develop. The final simplified model fitted to the counts of pyloric caeca contained *Caudal Length* and *Species* as significant explanatory variables, *Region* was not significant and was dropped from the model. The final model showed a significant difference between sardine and anchovy ($F_{(3, 85)} = 706, p\text{-value} < 0.001$). Sardine develop considerably more pyloric caeca

than anchovy: for larvae of 25 mm CL, sardine have 24 pyloric caeca whereas anchovy have 6 (Figure 3.6). The logistic curves fitted to the pyloric caecum data for both anchovy and sardine show that 50 % of anchovy had at least one pyloric caecum at a length of 24.43 mm, whereas this occurred at a size of 19.78 mm for sardine.

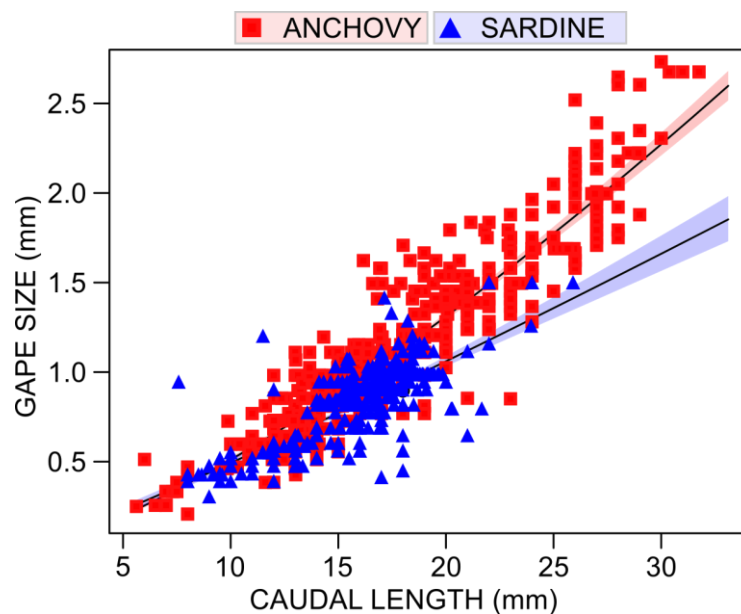


Figure 3.4. The relationship between gape size (mm) and caudal length (mm) from the linear models fitted for both anchovy and sardine, with shaded areas representing 95 % confidence intervals.

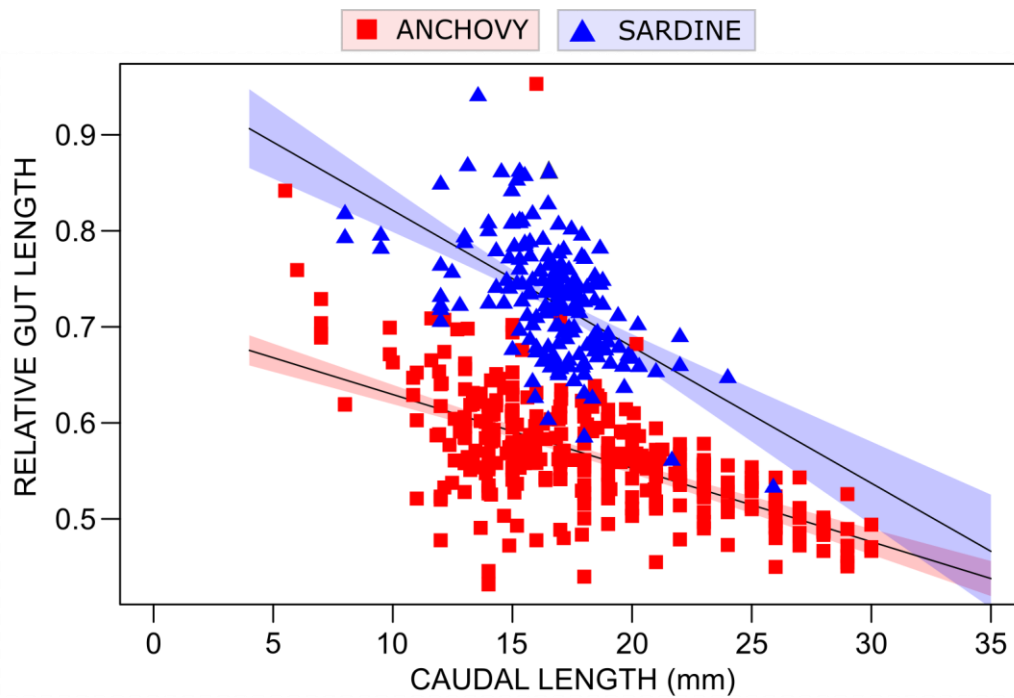


Figure 3.5. The relative gut length against caudal length (mm) for both larval species. Lines are the linear model output, with shaded areas representing 95% confidence intervals.

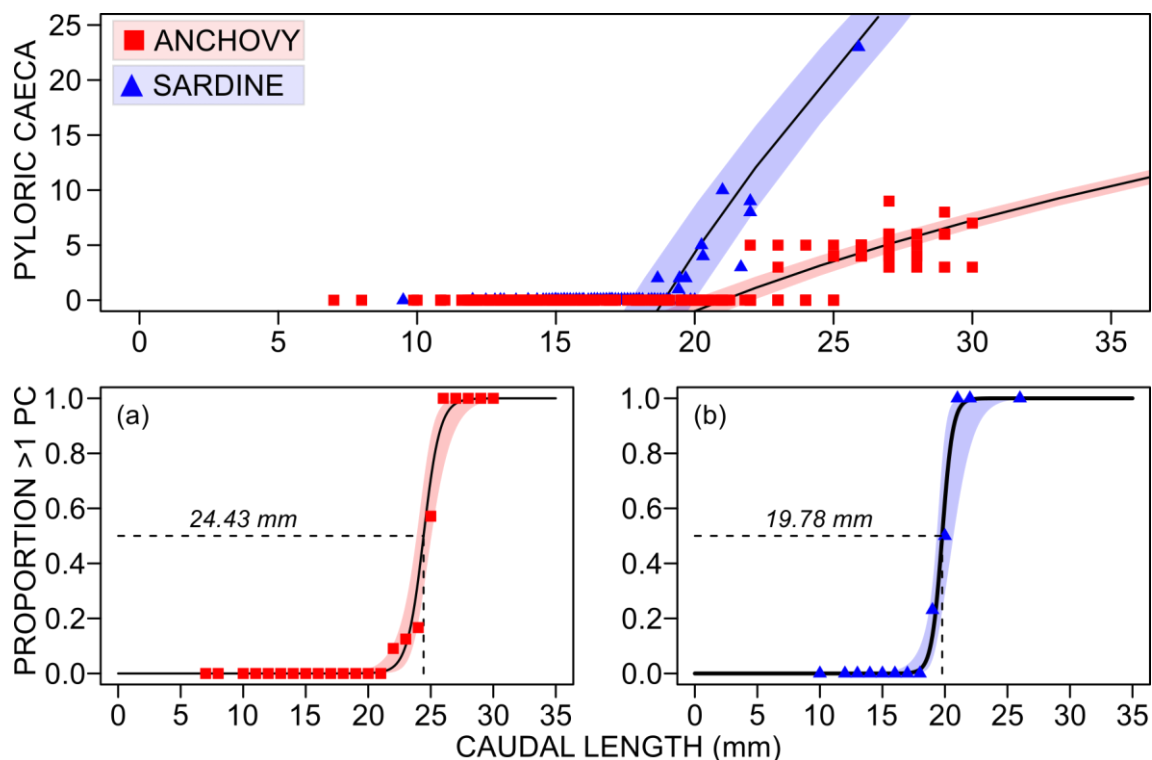


Figure 3.6. The top plot shows the pylori caeca count of both species; the lines represent the GLM model output with 95% confidence intervals. The bottom two plots represent the ogives fitted to the proportion data for (a) anchovy and (b) sardine that have at least one pyloric caecum.

3.3.3. Branchial Basket Morphology

The branchial baskets from both larval sardine and anchovy from both systems were measured from specimens ranging between 7.00 – 34.46 mm (nBUS anchovy [min, max]: 7.00, 25.00; sardine [min, max]: 9.00 – 22.00 mm; sBUS anchovy [min, max]: 11.61 – 34.46 mm). After model simplification, all three dependent variables (gill arch length, total number of gillrakers and gillraker spacing) were significantly correlated with caudal length (Table 3.1). For all models, *Region* was not significant and was therefore dropped. Models for gill arch length and total gillrakers, both showed a significant difference between species, although there was no interaction term for the total gillraker model (Table 3.1). For the gillraker spacing model *Species* did not explain any variation in the data and was dropped from the model. The models explained a substantial amount of the variation within the data (Adjusted R^2 : gill arch length = 0.8761, total gillrakers = 0.8225, gillraker spacing = 0.7709, Table 3.1). There was an indiscernible difference in gill arch length between the two species shortly after hatching, however, a difference was detected by the late larval stage (15 – 20 mm), with anchovy having larger gill arch lengths. There was a significant difference in total gillrakers between the two species, with anchovy having significantly more (Figure 3.7). There was no difference in gillraker spacing between the two species (Figure 3.7).

Table 3.1. Results from the multivariate general linear model, displaying the statistics for both the response and explanatory variables for pre-recruit anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*, obtained from the west coast of South Africa.

Model variable	Explanatory variables	F statistic	Effect df	Error df	Adjusted R^2	p -value
$\ln(\text{Gill-arch length})$	$= \ln(CL) * \text{Species}$	482.0	3	201	0.8761	***
Total Gillrakers	$= \ln(CL) + \text{Species}$	473.6	2	202	0.8225	***
$\ln(\text{Gillraker spacing})$	$= \ln(CL)$	653.8	1	203	0.7709	***

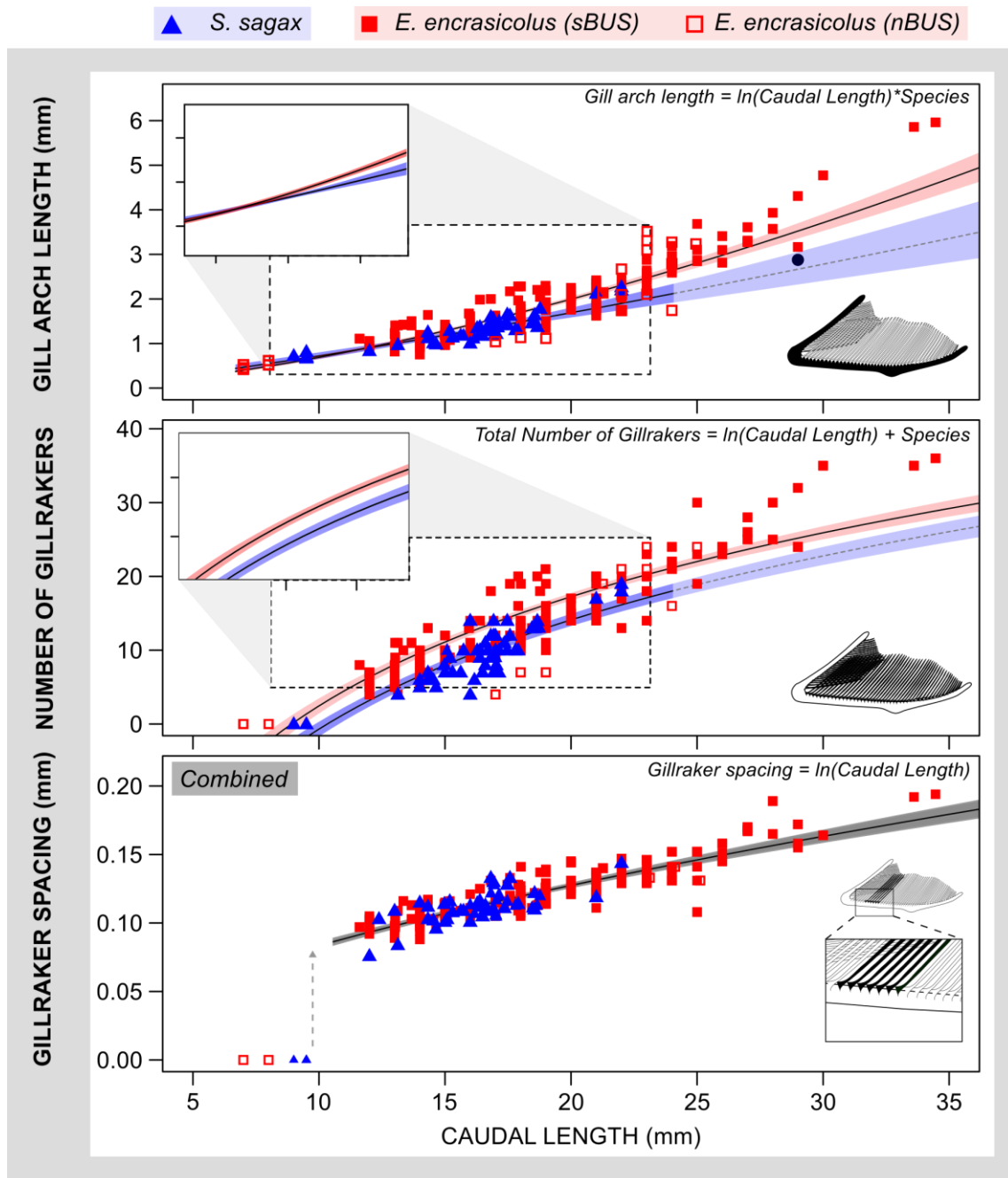


Figure 3.7. The relationship between caudal length (mm) and three branchial meristic measurements (a) gill arch length, (b) total gillrakers and (c) gillraker spacing of the three groups (sBUS anchovy, nBUS anchovy and nBUS sardine). The predicted relationships were calculated from the multivariate general linear model results, with gill arch length and gillraker spacing calculated from the inverse natural log of the results. Shaded areas depict the 95% confidence intervals.

3.3.4. Multivariate Allometry

The principal component analysis of the log-transformed covariance matrix exhibited a clear shift in ordinal orientation for both species when the PC2 scores were plotted against caudal length (Figure 3.8). The results of the piecewise regression on the data using equation (4) gave an estimate of the AIP at 12.20 and 14.48 mm for anchovy and sardine, respectively (Table 3.2).

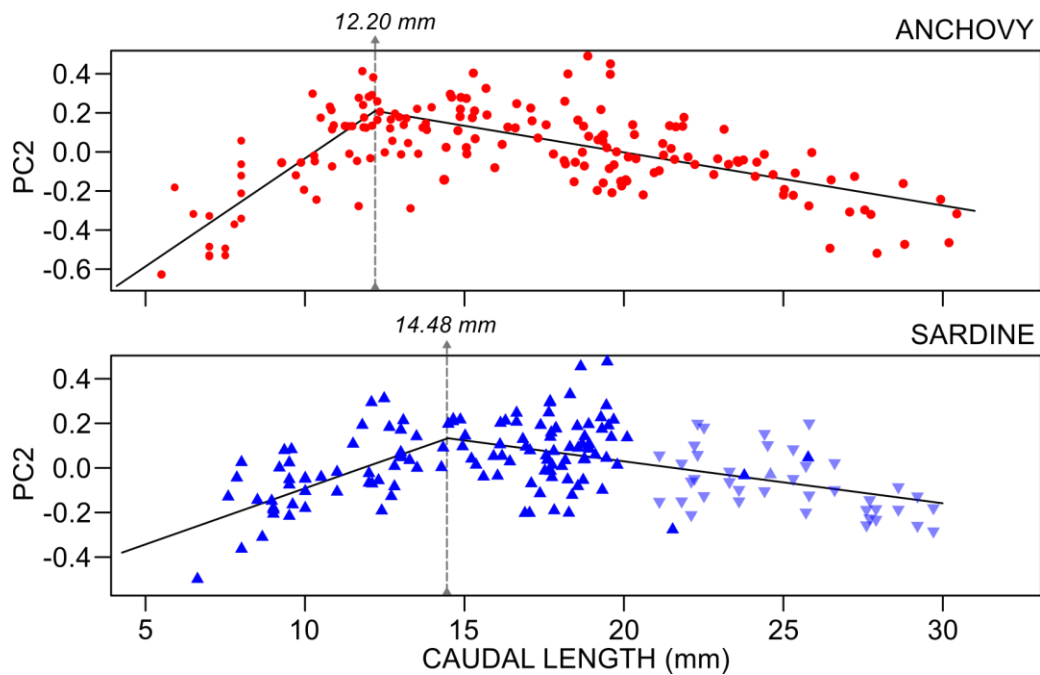


Figure 3.8. The piecewise regression of the PC2 scores from the separate principal component analyses fitted to the species-specific covariance matrix of log-transformed morphometric data, against the caudal length (mm) for both anchovy and sardine caught in the Benguela. ▼ Depicts the sardine samples that were obtained from historical SHARP samples.

The allometric PC1 scores were compared against the theoretical score of isometry (0.258; Figure 3.9). For anchovy, the most profound difference between pre- and post-AIP larvae was the significantly positive allometry for HL and SNL, and negative allometry for HD1 and HD2. Post-AIP larval scores for these were closer to isometry for HL and SNL, and then positively allometric for HD and HDo. Variables relating largely to fish length and somatic growth were approximately isometric for both groups (CL, FL, PosDFL, PostAFL, PostAL). Both EyeD and BD remained isometric for both groups, whereas CpD was positively allometric for both groups (Figure 3.9).

Sardine showed a different trend to anchovy. The greatest differences between pre- and post-AIP sardine was the greater positive allometry observed in SNL, EyeD, HL and CpD in post-AIP individuals. There was a greater positive allometry in HD2 and BD in pre-AIP individuals. For most of the measurements relating to somatic growth and length, namely PreDFL, PreAL, PostAFL, PostDFL, CL, FL and MidBL, all measurements were negatively allometric, with pre-AIP individuals showing a greater isometry (Figure 3.9).

Table 3.2. Results of the fit piecewise regression fit on the PC2 and caudal length data for both anchovy and sardine.

Parameters	Estimates	
	Anchovy	Sardine
β_0	-1.139	-0.955
β_1	0.111	0.092
β_2	-0.138	-0.108
Allometric inflection point	12.20 mm	14.48 mm
95% C.I.	11.07- 15.12	9.84 – 16.63
R ²	0.524	0.288

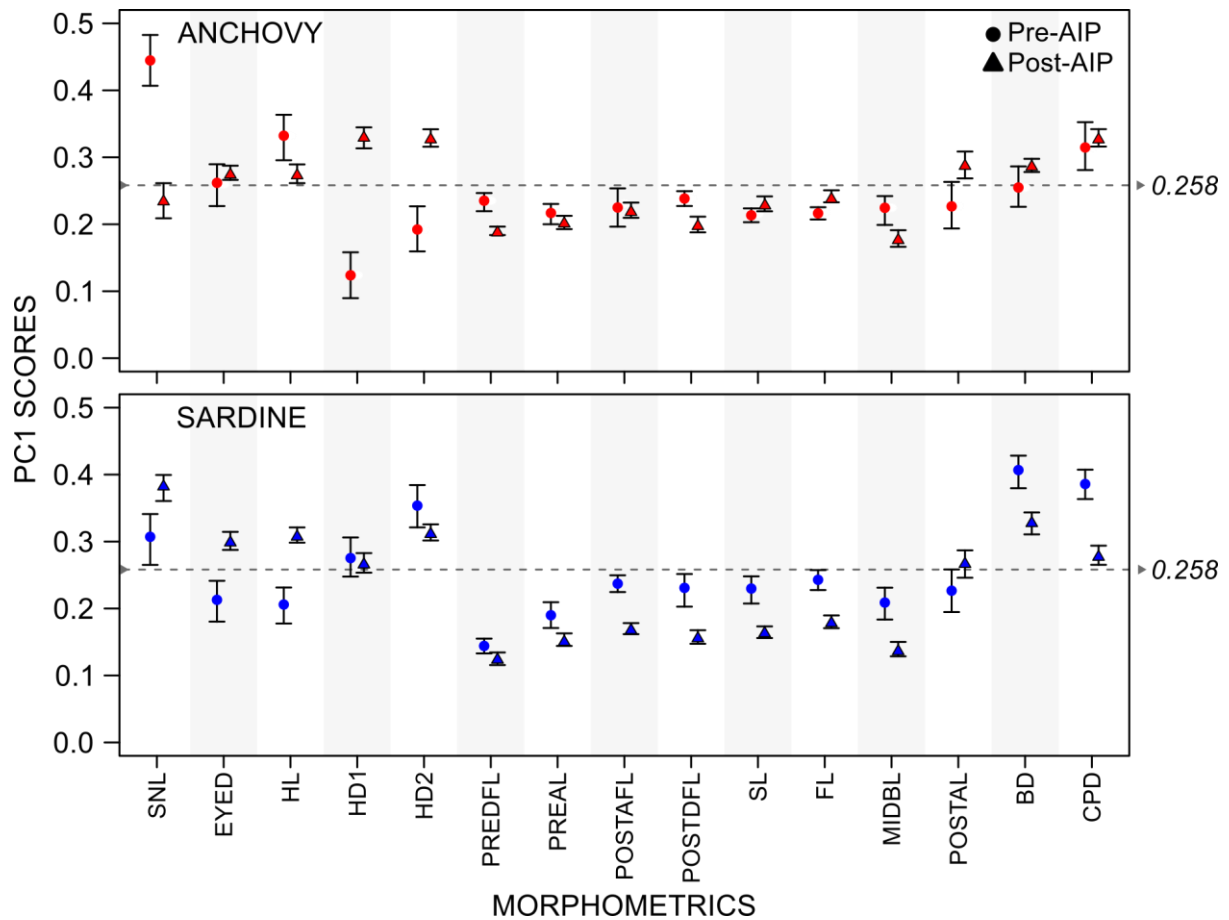


Figure 3.9. PC1 scores (with bootstrapped confidence intervals) of the separate PCAs fitted to the pre- and post-AIP (allometric inflection point) individuals for both anchovy and sardine, for the morphometric variables (see methods for variable descriptions), compared against the line of isometry (0.258).

3.4. Discussion

This study has highlighted several important differences in ecomorphological traits between sardine and anchovy larvae. It is likely that there is a degree of size-partitioning in their diet facilitated through differences in gape size, with anchovy having a significantly larger gape that develops allometrically. Anchovy direct initial growth at morphometrics that aid in feeding, whereas sardine develop these characteristics later. This delayed growth may imply a potentially higher dependency on smaller, non-mobile prey items for sardine during their early larval stages. This is corroborated further by the pronounced distinction in alimentary morphology between the species, which would

suggest a higher degree of herbivory and detritivory in sardine due to a greater relative gut length and increased pyloric caeca.

There were no discernible differences in ecomorphological characteristics between anchovy from the northern and southern Benguela. Spatial distinctions in morphology have been used as additional tools for stock delineation in semi-sympatric conspecifics, with the basis that distinct stocks would show different morphological attributes (Swain & Foote, 1999). A primary cause for this deviation in morphology is the spatial differences in ambient prey items, which then leads to divergent trophic morphologies such as mouth gape and gillrakers (Turan, 2004; Costalago et al., 2015; Idris et al., 2016; Groenewald et al., 2019). These distinctions have been described in a wide variety of fish species (Silva, 2003; Turan, 2004; Turan et al., 2006), and more specifically, the sardine and anchovy stocks around southern Africa. It has been established that the small pelagic stocks of the northern and southern Benguela are principally distinct (Armstrong & Thomas, 1989; Cloete et al., 1997), which is reflected in the morphological distinctions in the branchial baskets between sardine in the nBUS and sBUS (Idris et al., 2016). These spatial differences were not observed for the early life stages, and therefore may only diverge later during development. Further analysis of larger size classes would be needed to investigate at what point phenotypic divergence occurs in small pelagic fish species.

Despite significant interspecific differences in both gill arch length and total number of gillrakers, there was no difference in the gillraker spacing observed between species. A disparity in branchial basket morphology has been well established as a source of trophic niche partitioning between intraguild species for both marine (Tanaka et al., 2006; van der Lingen et al., 2006b; Rohan & Buckley, 2018) and freshwater species (Spiegel et al., 2011). Differences in gillraker spacing generates a size-partitioned diet reducing competitive interactions. Evidence of a divergence in gillraker spacing between adult and juvenile clupeoids and between species in the southern Benguela is comprehensive (van der Lingen et al., 2006b; Vorsatz et al., 2015; Idris et al., 2016; Horton & van der Lingen, 2019), with sardine having the smallest gillraker spacing compared to anchovy and then round herring *Etrumeus spp.* Yet this was not observed in this study. The trends in both gill arch length and total gillrakers found in this study match those reported by King & Macleod (1976), however they described a difference among species in gillraker spacing, with sardine having a larger gap. They did not sample fish smaller than 27.9 mm, and trends for early larval sizes were extrapolated from larger

individuals, this may have caused the discrepancy. The convergence of gillraker spacing from divergent gill arch lengths and number of gillrakers for both species in this study would suggest an optimum spacing for these species at these lengths. The results here indicate that branchial morphology does not facilitate resource partitioning between these species as described in their adult stages.

There was a significant difference in gape size between the two species, anchovy had a larger gape that increased allometrically. Tanaka et al. (2006) investigated the trophic partitioning between adult Japanese anchovy *Engraulis japonicus*, Pacific round herring *Etrumeus teres* and Japanese jack mackerel *Trachurus japonicus*, and summarised that, although gillraker morphology was partially responsible, the divergence in diet observed was largely due to difference in feeding habits, e.g. filter- and particulate-feeding. Hence, as clupeoid larvae are particulate feeders and have not started filter feeding yet, niche partitioning may occur through alternative characteristics. A larger gape size observed in anchovy would facilitate the exploitation of larger prey items compared to sardine. This was observed by Morote et al. (2010) who noted a greater gape size in anchovy larvae, along with a preference for progressively larger prey items when compared to European sardine *Sardina pilchardus*. This provides evidence that resource partitioning between clupeoid larvae in the Benguela may likely be through maximum prey size rather than minimum.

This study highlighted significant differences in relative gut length, and the initial growth and numbers of pyloric caeca between sardine and anchovy. Sardine had a longer relative gut length, developed pyloric caeca earlier and possessed significantly more than anchovy. Relative gut length is often utilised as an index of feeding habit; generally speaking, relative gut length increases from carnivorous to herbivorous diets (Smith, 1989; Paugy, 1994; Elliott & Bellwood, 2003). This is due to the greater digestive processing required for autotrophic components. Therefore, this slight difference in relative gut length between the two species, may be indicative of a higher importance of phytoplankton and detritus in the diet of sardine. It is worth noting that the relative gut lengths for both species are still less than one, which would still imply carnivorous feeding (Ward-Campbell et al., 2005). This is not uncommon for larvae, as their diets are often dominated by early life stages of pelagic crustaceans such as copepod nauplii (Hirakawa et al., 1997; Tudela et al., 2002; Voss et al., 2009; Catalán et al., 2010; Morote et al., 2010; Contreras et al., 2014; Hirai et al., 2017).

Despite this interspecific difference, both species exhibited a decrease in relative gut length, indicative of a reduced dependency of autotrophic components in their diet. This is consistent with dietary studies of small pelagic fish larvae, where there is a total dependency on consumers (e.g., Tudela et al., 2002; Catalán et al., 2010; Morote et al., 2010; Contreras et al., 2014). It is interesting to note that the guts of both species were straight tubes and had yet to form convoluted loops as seen in the adult forms, at which point the relative gut lengths of these species increase dramatically. This is indicative of an increased dependency on phytoplankton which is corollary of the widely observed herbivorous behaviour seen in adult clupeoids (King & Macleod, 1976; van der Lingen, 2002).

The function of pyloric caeca is primarily to increase the gut surface area for dietary absorption (Buddington & Diamond, 1986, 1987). Although there is a large variability in both count and size of pyloric caecum between species, evidence for corollary dietary differences is disputed (Delariva & Neves, 2020; Moreira et al., 2020). However, some studies have shown that increased pyloric counts are a characteristic of increased herbivory in fishes (Delariva & Neves, 2020). Additionally, if one employs the notion that an increased intestinal length is symptomatic of greater herbivory due to the extended retention time of prey and gut absorption surface, then the increased pyloric count would likely act in a similar process. Consequently, it is likely that sardine larvae have a higher dependency on phytoplankton and detritus comparatively to anchovy due to combination of a relatively larger intestine length and more pyloric caeca.

In this study the overall growth trends for both species were relatively focussed at the anterior and posterior ends, with positive allometric growth observed in the cranial and caudal fin development. This U-shaped growth pattern in early larvae is not uncommon, especially in clupeoids (Fuiman, 1983; Blaxter, 1988; Hunt von Herbing, 2001; Nunn et al., 2012). It highlights the importance of successful feeding in newly exogenous feeding larvae coupled with the advanced locomotor ability to obtain more mobile prey and mitigate predation. Despite the overall similar trends for both species, there were interspecific distinctions in temporal allometry. For both sardine and anchovy there were divergent growth characteristics found at similar inflection points of 12.20 mm and 14.48 mm, respectively (Figure 3.8). For anchovy, the greatest difference between pre- and post-AIP individuals was that during pre-AIP, growth was focussed on several cranial characteristics, with SNL and HL having positive allometric growth. The

gillrakers had not developed prior to the inflection point for anchovy (Figure 3.7), so increasing the opercula chamber by elongating the head would allow the gape to increase and facilitate the elaboration of the branchial apparatus. An increase in these characteristics is linked to an increase in prey size (Wainwright & Richard, 1995; Piet, 1998; Davis et al., 2012), therefore implying a significant importance of obtaining larger prey items for early larval stages of anchovy. Post-AIP individuals showed an increase in the allometric growth of the depth of the fish, with HD, HDo, BD and CpD showing a positive allometric trend. The development of the trunk and tail is indicative of increased locomotor activity, by increasing red musculature and fin development (Blaxter & Hunter, 1982). Increased swimming speeds substantially reduces mortality through improving predator evasion (Bailey & Batty, 1984), but also increases the searching activity for feeding (Hunter, 1972). Hunter (1972) showed that the litres per hour of water searched by anchovy larvae increased exponentially with larval length, which a substantial increase in larvae > 10 mm likely a result of the increased allometric growth as seen in this study.

Unlike anchovy, the pre-AIP group for sardine tended to have comparatively isometric or negative allometric growth trends for cranial characteristics, such as SNL, ED, HL and HD1, and positively allometric growth of somatic growth characteristics such as SL, PreAL, PostAFL, FL and BD. Directing less at the development of feeding characteristics initially could be indicative of a greater dependence on smaller prey items during sardine early larval stages. A higher dependency on phytoplankton and smaller protists in smaller (< 9 mm) sardine larvae compared to anchovy was observed in the Mediterranean (Morote et al., 2010). This is corroborated by the greater isometry seen in the gape size of sardine larvae, indicating that increasing prey size may not be as important as for anchovy (Figure 3.4). There was an increased importance of somatic growth seen in sardine during initial stages, which is in support of the Müller & Videler (1996) hypothesis, that larvae immediately grow in length as fast as possible to exit the viscous flow regime, which significantly increases a larvae's survival (Yavno & Holzman, 2018).

Freezing has a well described shrinking effect on fish samples (Fowler & Smith, 1983; Wessels et al., 2010). However, this study is comparative, and all samples were frozen therefore the shrinkage effect from freezing is standardised among samples. That said, it is worth mentioning that these measurements are relative and not absolute, which may

lead to erroneous conclusions if compared to other studies. The multivariate allometry analyses utilised samples that had been either frozen or fixed in formaldehyde, and the fixation and preservation of samples in formaldehyde also leads to shrinkage (Fowler & Smith, 1983; Hjörleifsson & Klein-MacPhee, 1992; Fox, 1996). The degree of shrinkage difference between freezing and formaldehyde is size-dependent in larval fish, with small, newly hatched larvae being more susceptible to increased shrinkage, and formaldehyde having the most significant affect (Hjörleifsson & Klein-MacPhee, 1992). However, as larval size increase, the difference in shrinkage between freezing and formaldehyde becomes indiscernible. Therefore, for the larvae used from the historical SHARP samples that were all > 20 mm it likely means the level of morphological distortion between them and the M153 samples would theoretically be minimal.

A second potential limitation of the study is the likelihood of decadal differences in the morphology of sardine larvae between the SHARP and M153 samples. Historical DFFE samples were chronologically scanned for sardine larvae starting from the 2019 February and March samples and then working backwards annually. However, more recent samples utilised vertical bongo nets for ichthyo- and zooplankton sampling, which larger larvae (> 20 mm) evade. Therefore, these larger size categories were only found in the samples that utilised MultiNets that were towed obliquely, which were the SHARP 2012/13 samples. It is understandable that there may be morphological differences between these samples. van der Lingen et al. (2006c) analysed the morphological condition factor of sardine in the sBUS between 1953 – 2004 and observed interannual and decadal variation which they suggested could be partially explained by density-dependent effects, with sardine in poorer condition during times of high biomass and vice versa. Adult biomass of sardine between 2011-2012 (1.0 and 0.3 million tons) and 2019 (0.2 million tons) were similarly low compared to historical highs of 4.2 million tons in the early-2000s (DEFF, 2020; de Moor et al., 2021). Hence, these density-dependent effects between these dates may be similar, and as morphometric factors reflect condition (Nelson et al., 1994), major changes in the morphology of sardine larvae would likely be reduced.

Overall, there was a large degree of agreement between the multiple ecomorphological characteristics within each species used in this study. The combination of the isometric gape, larger intestine, greater pyloric caecum count and delayed development of the cranial area observed in sardine larvae provides morphological

evidence that would predispose them to a diet comprised of comparatively smaller particles and a possibly greater dependence on phytoplankton and detritus. However, ecomorphological traits only provide broad information on the trophic ecology of individuals, and the results of this study will be complemented with traditional and modern dietary analyses of these larval species in the following Chapter so that a holistic picture of their trophic ecology can be attained.

Chapter 4

Ontogenetic changes in the diets of larval sardine and anchovy in the Benguela upwelling system inferred from stomach content and biochemical analyses.

Abstract

Variance in recruitment of small pelagic fishes is largely governed by fluctuations in pre-recruit mortality rates; primarily through predation, advective loss and starvation. Limited attention has been directed at larval starvation and our knowledge of their trophic ecology is extremely limited. This study examines and compares the trophic ecology of larval sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* in the Benguela Current ecosystem through a multi-faceted approach combining stable isotope, fatty acid and stomach content analyses, and assesses how ontogenetic changes may affect trophic partitioning between the two. Intraspecific competition appears to be reduced through increased prey-size consumption by larger larvae for both species. This ontogenetic shift in prey-size consumption is manifested in both species displaying significant ^{15}N enrichment during their early life, indicating trophic progression. This was further corroborated through the fatty acid trophic markers, that showed clear increases in carnivory and consumption at higher trophic levels. Interspecific partitioning is facilitated through distinctions in prey-size composition, with anchovy consuming comparatively larger prey than sardine. Surprisingly, sardine exhibit a higher $\delta^{15}\text{N}$, considered to arise from the increased presence of smaller carnivorous copepods in their diet, which highlights the complexity of the food web dynamics in the Benguela. Prey-size selection is an important regulator of both intra- and interspecific competition, and the information documented here will be useful in ecosystem models that predefine primary and secondary production by size class. Such information will also provide the opportunity to include a finer life history resolution of these small pelagic species in ecosystem models.

4.1. Introduction

Small pelagic fishes (e.g. sardines, anchovies and herrings) have great ecological and commercial importance (Cury et al., 2000; FAO, 2020). They perform crucial links between autotrophs and higher trophic levels whilst supporting substantial fisheries- 23 % of the total global fisheries catch in 2018 was from the small pelagic sector (FAO, 2020). These species are characterised by large decadal and interannual fluctuations in their recruitment and biomass, which makes forecasting and management often difficult. Despite conservative fishing management interventions in South Africa, both local clupeoids, anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*, have exhibited large variations population size (Checkley et al., 2009; DEFF, 2020). It is theorised that this variation in recruitment may be explained by fluctuations in mortality exhibited during early life stages.

Since Hjort (1914) conceptualised the “Critical Period” hypothesis to explain the variability in recruitment of fishes through early life history stage mortality, there has been a lot of scientific attention directed at untangling the problem (Lasker, 1981; Cushing, 1990; Roy, 1993; Bakun, 1997). A common theme among hypotheses is the great importance placed upon successful feeding of newly exogenous-feeding larvae. It is the contribution of multiple biotic and abiotic factors, but ultimately it is the consequence of sufficient prey densities and an individual’s ability to successfully forage (Lasker, 1975; Ware et al., 1981; Rilling & Houde, 1999). Feeding success is not independently culpable for induced mortality; rather it is one of the primary variables that indirectly contributes to mortality through decreased growth, size, and reduced predator avoidance through starvation (Miller et al., 1988; Bailey & Houde, 1989; Meekan et al., 2006; Tanaka et al., 2006). Size- and growth-dependent mortality are significant sources of mortality in early life stages, with mortality decreasing with increasing size and growth (Miller et al., 1988; Bailey & Houde, 1989), and both have been empirically validated by a number of studies (Cowan & Houde, 1992; Meekan & Fortier, 1996; Takasuka et al., 2003; Meekan et al., 2006; Tanaka et al., 2006). This would therefore highlight the importance of understanding the trophic ecology of larval fishes, in hope of broadening our understanding of potential sources of starvation that will ultimately lead to mortality.

Competitive interactions between species organises a system through resource utilisation (Schoener, 1983). The ability of several intraguild species to coexist largely

depends on how resources are shared and allocated. Intraspecific competition is often limited via dietary shifts during the ontogeny of fish (Winemiller, 1989; Post, 2003; Graham et al., 2007). Size is an important factor regulating these dietary shifts, as individuals of the same species can span several orders of magnitude in size (Werner & Gilliam, 1984). Size and growth of specific characteristics can dictate the feeding ability and behaviour of an individual (Werner, 1974), ultimately changing prey species and size during a species' ontogeny. These shifts provide a competitive release (Amundsen et al., 2003), access to energetically rich food sources (Sánchez-Hernández et al., 2019a) and an increase in niche breadth (Llopiz, 2013; Egan et al., 2018). Development is most pronounced prior to metamorphosis; therefore, we would expect dietary changes throughout the pre-metamorphosis stages of clupeoids.

The trophic ecology of adult clupeoids in the Benguela has been very well described (King & Macleod, 1976; James, 1987; Wallace-Fincham, 1987; van der Lingen, 1994, 2002; Louw et al., 1998; Mketsu, 2008), with juveniles to a lesser extent (Louw et al., 1998). These sympatric species, sharing remarkably similar life histories, commence the formation of interspecific schools at a young age (Isaacs, 1963). Consequently, competitive interactions during both adult and recruit stages have led to well-documented trophic partitioning, primarily driven by distinctions in morphological attributes, particularly in branchial basket development (van der Lingen et al., 2006c and references therein). Size-based partitioning is evident, with prey items progressively increasing in size from sardine to anchovy and then to round herring. This pattern is supported by stable isotope studies, indicating ^{15}N enrichment across the mentioned species. (Sholto-Douglas et al., 1991; van der Lingen & Miller, 2011; Iitembu et al., 2012). It therefore leads to the question whether there is partitioning during the early stages of these species, and if so at what point during their ontogeny do they diverge and develop their own distinct diets.

Studying the trophic ecology of larval fish is a difficult task due to a very low feeding incidence (Blaxter et al., 1963), hence studying stomach contents can be an arduous task. This study will use a multi-faceted approach of stable isotope, fatty acid and stomach content analyses. Stable isotope (SIA) and fatty acid analysis can be beneficial tools by providing valuable information about the long term trophodynamics of a species (Post, 2002; Dalsgaard et al., 2003; Fry, 2006). Commonly investigated isotopes in ecology are ^{12}C and ^{13}C , and ^{14}N and ^{15}N . Enriched $\delta^{15}\text{N}$ (‰) values are indicative of

species occupying higher trophic levels. Marine isotopic ecology has shown a general trend of $\delta^{13}\text{C}$ (‰) offshore depletion (Hobson & Welch, 1992; France, 1995), which is also a consistent trend in South African waters (Hill et al., 2006). Furthermore, enriched $\delta^{13}\text{C}$ (‰) is common in species deriving their carbon from diatom-based production (Fry & Wainright, 1991). Specific fatty acids, present in the lipid profiles of fish, can provide a precise means to elucidate the dietary habits of consumers. By analysing these specific trophic markers, it is possible to link specific fatty acids to certain types of prey or food sources, such as 18:1n-7 fatty acid for diatoms and both 20:1n-9 and 22:1n-11 for calanoid copepod consumption (Graeve et al., 1994; Auel et al., 2002; Dalsgaard et al., 2003). At higher trophic levels these trophic markers are difficult to distinguish, yet for plankton and lower trophic levels they are particularly valuable (Dalsgaard et al., 2003).

The absorption and assimilation rate of dietary components into identifiable markers is contingent upon the species' turnover rate, which is intricately linked to their metabolic rate (Dalsgaard et al., 2003; Fry, 2006). Larval organisms exhibit a notably elevated metabolic rate in proportion to their body mass (Peck and Moyano, 2016). Consequently, the incorporation of dietary items into their tissues occurs at an accelerated pace. Sholto-Douglas (1992) conducted a study revealing noticeable changes in the isotopic signature of sardine larvae under *ex vivo* conditions within 1-3 weeks following a dietary shift. Likewise, lipid deposition into fatty tissues reached equilibrium within 2 weeks after a dietary shift in fish larvae, as demonstrated by Rainuzzo et al. (1997).

The aim of this Chapter is to determine whether trophic partitioning occurs between larvae of small pelagic fish. This will be performed by using the multi-faceted approach of stomach content, stable isotope and fatty acid analyses in order to (a) study the trophic ecology and (b) to investigate and document ontogenetic dietary shifts in larval anchovy and sardine. The results of this Chapter will be utilised with the results from Chapter 3 to create a comprehensive description of the trophic ecologies of small pelagic fishes in the Benguela.

4.2. Methods

4.2.1. Data collection

Samples of larvae were collected during the M153 cruise (Figure 4.1) as described in Chapter 3. Fish were thawed and then the caudal length (mm) and wet weight (mg) of all fish were taken in the laboratory. Stomachs were then excised, blotted dry and then measured to the nearest 0.0001 g. They were then opened, and their contents extruded into a petri dish containing 20 ml of Milli-Q water (Millipore). Emptied stomachs were again blotted dry and weighed to provide information on the wet weight of stomach contents. This was then converted to dry weight using the ratio of five to one (Yamaguchi & Ikeda, 2000). Large prey items were identified to the lowest taxonomic level possible, and then grouped into the following 13 taxonomic groups: Brachyuran, Foraminifera, Fish eggs, Tintinnids, Euphausiids, Diatoms, Dinoflagellates and then copepods split into Calanoid, Cyclopoid, Harpacticoid, Nauplii, Copepod eggs and Unidentified copepods. Each prey item was then measured (total length [TL], width or prosome width [W] and prosome length [L], where applicable and all measurements in μm). Then dry weight (μg) and carbon content (μg) were estimated using prey-taxon specific length – weight and weight – carbon content regressions (Table 4.1). These identified prey items were removed from the sample and the remaining smaller and unidentified stomach contents were then transferred into a 20ml sedimentation chamber. These were allowed to settle over night before implementing the Utermöhl method as described by Hasle (1978) to identify phytoplankton and estimate their total abundance in the sample.

Dorsal muscle tissue samples for stable isotope and fatty acid analyses were taken from thawed samples. Samples for stable isotope analysis were oven dried at 60 °C for 24 – 48 hours and then homogenised into a fine powder using a pestle and mortar. Subsample aliquots of approximately 400 μg were weighed into tin cups on a microbalance accurate to 1 μg , where the individual weight of the entire dried muscle sample was < 400 μg , similar samples were combined (same station, species and size) to make up this mass. Samples were then combusted in a Flash elemental analyser 1112 (Thermo Finnigan, Bremen, Germany) and the gases were directed to a Delta V Plus isotope-ratio mass spectrometer via a ConFlo IV gas control unit (Thermo Scientific, Bremen, Germany). Samples were not lipid-extracted prior to analysis due to the low muscle mass of small larvae but because lipids can cause a depletion in ^{13}C , the lipid

normalisation equation of Post et al. (2007) for aquatic animals was used when the C:N ratio of individual samples was > 3.5 .

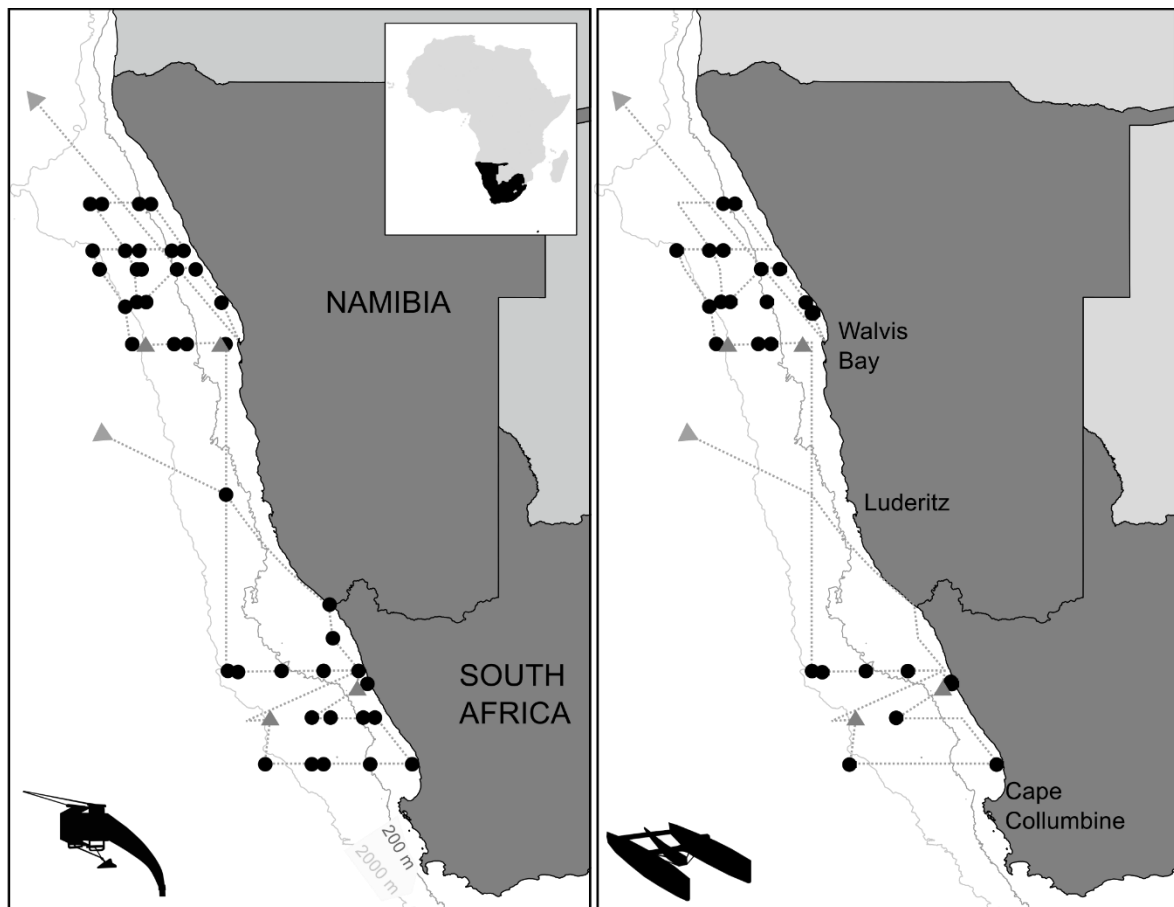


Figure 4.1. Stations sampled in the southern and northern Benguela aboard the M153 RV Meteor cruise in February and March 2019. The left panel shows stations sampled by the MultiNet Maxi and the right panel shows the stations sampled by the modified neuston catamaran. ▲ depict 24-hour stations where multiple hauls were made

Table 4.1. Regressions used to calculate the dry weight (DW) and carbon content (CC) of prey items described from the stomach content analysis of larval sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* caught in the northern and southern Benguela.

Prey Category	Included major taxa	Measurements	Length (µm) - weight (µg) regression	Weight (µg) - Carbon content (µg)	Reference
Calanoid	Acartia Heterohabdus Pleuramamma Paracalanus Calanoides Paracartia	TL – Total Length PL – Prosome Length PW – Prosome Width	${}^1\text{Ln}(\text{DW } \mu\text{g}) = 2.74(\text{PL } \mu\text{m}) - 16.41$	${}^20.424 * \text{DW } \mu\text{g} = \text{CC } \mu\text{g}$	¹ Chisholm & Roff, (1990) ² van der Lingen (2002)
Cyclopoid	Oithona	TL – Total Length PL – Prosome Length PW – Prosome Width	${}^1\text{Ln}(\text{DW } \mu\text{g}) = 1.96\text{Ln}(\text{PL } \mu\text{m}) - 11.64$	${}^20.424 * \text{DW } \mu\text{g} = \text{CC } \mu\text{g}$	¹ Chisholm and Roff (1990) ² van der Lingen (2002)
Harpacticoid	Microsetella	TL – Total Length PL – Prosome Length PW – Prosome Width	${}^1\text{Ln}(\text{DW } \mu\text{g}) = 1.96\text{Ln}(\text{PL } \mu\text{m}) - 11.64$	${}^20.424 * \text{DW } \mu\text{g} = \text{CC } \mu\text{g}$	¹ Chisholm and Roff (1990)- modified as in van der Lingen (2002) ² van der Lingen (2002)
Decapod	Brachyura larvae	TL – Total Length CL – Carapace Length CW- Carapace Width	$\text{ln}(\text{DW } \mu\text{g}) = 2.58\text{ln}(\text{CL } \text{mm}) + 2.04$	$0.349 * \text{DW } \mu\text{g} = \text{CC } \mu\text{g}$	Lindley, (1998)
Euphausiid	Euphausiid larvae	TL – Total Length	${}^1\text{Ln}(\text{DW } \mu\text{g}) = 0.456 + 0.8\text{ln}(\text{TL } \mu\text{m})$	${}^20.424 * \text{DW } \mu\text{g} = \text{CC } \mu\text{g}$	¹ Lindley et al., (1999) ² van der Lingen (2002)
Copepod egg	-	DM	${}^1\text{Ln}(\text{DW } \mu\text{g}) = 0.0143(\text{DW}) - 3.381$	${}^20.4 * \text{DW } \mu\text{g} = \text{CC } \mu\text{g}$	¹ van der Lingen (2002) ² Huntley and Lopez (1992)
Fish egg	Sardinops eggs	TL – Total Length TW – Total Width	${}^1\text{DW } \mu\text{g} = 0.093(\text{vol}) + 0.0012$ ${}^2\text{vol} = 4/3\pi(\text{TW } \mu\text{m})^3 + \pi r^2 (\text{TL } \mu\text{m} - 500)$	${}^30.457 * \text{DW } \mu\text{g} = \text{CC } \mu\text{g}$	^{1,2} van der Lingen (2002) ³ Napier, (1993)
Foraminifera	-	W - Width		$\text{Vol} = 4.3 * \pi * (W (\text{mm})/2)^3$ $0.061 * \text{vol } (\mu\text{m}^3) = \text{CC } \mu\text{g}$	Caron et al., (1995)
Tintinnid	-	W -Width		$\text{Vol} = \pi * (W \mu\text{m}/2)^2$ $0.000053 * \text{vol} + 444.5 = \text{CC } \mu\text{g}$ $11389 \text{ pg C cell}^{-1}$	Verity & Lagdon, (1984)
Diatom	Coscinodiscus Chaetceros			$3247 \text{ pg C cell}^{-1}$	Diatom Database
Dinoflagellate	Protoperdinium Ceratum	a – Length b - Width		$\text{Vol} = \pi/12 * a * b^2$ $0.760 * \text{vol}^{0.819} = \text{CC } (\text{pg C cell}^{-1})$	Menden-Deuer & Lessard, (2000)

Lipid extraction for fatty acid analysis of muscle tissue was performed using a modified Folch et al. (1957) method, outlined by Peters et al. (2007). Samples were freeze dried for 72 hours and then their dry weights were taken. Subsequently, dichloromethane:methanol (CH₂Cl₂:MeOH, 2:1, v/v) and the first internal standard (23:0) were added to the dried sample and left at -80 °C overnight. The sample was then homogenised using a twice repeated sequence of a Potter Elvehjem (1200 rpm) and a sonicator (0.2 second pulse with an amplitude of 20%). The homogenized sample was then transferred to a pre-rinsed centrifuge tube and 2ml of 0.88% KCl was added. Centrifuge tubes were shaken vigorously for 30 seconds before being placed in the centrifuge for 10 minutes at 3000 rpm and 2°C. Using a pre-heated Pasteur pipette, the upper aqueous phase was removed. The lower, lipid containing phase was then evaporated under N₂. At this point 200µl of the second internal standard (19:0) was added, so that loss of fatty acids from the extraction process could be calculated.

The lipids in the solvent were hydrolysed and then the fatty acids were converted to their fatty acid methyl ester derivatives (FAMES) by adding both 250 µl of hexane and 1ml of 3% H₂SO₄/MeOH. The air was then replaced by N₂ and samples were then stored in a heating block at 80°C for four hours. FAMES were then extracted using hexane in a four-part process; 4 ml of distilled water and 1.5 ml of hexane were added, then the centrifuge tubes were shaken vigorously for 30 seconds and placed in the centrifuge for 10 minutes and 3000 rpm at 2 °C. The upper hexane phase was then removed, transferred to glass tubes, evaporated under N₂ and then stored on ice. This four-step process was repeated three times (without the addition of distilled water) to maximise the transfer of fatty acids. The final solvent was evaporated completely, 1 ml of hexane was added and then all air was replaced with N₂, with samples then finally stored at -80 °C until analysis. The FAMES were then analysed using a GC-FID (Agilent Technologies 7890B) with an OPTIMA 225 column, 25 meters in length and 0.32 mm in diameter. The process was initiated at 50 °C with a temperature ramp of 6 °C/min.

4.2.2. Statistical Analyses

All statistical analyses were performed using the platform R 4.1.2 (R Core Team, 2018) and a threshold significance value of $p < 0.05$ was applied.

4.2.2.1. Stomach Content Analysis

Samples were separated into the following categories depending on their time of capture and based on the daylight hours from the 1st of March 2019; night (20:45 – 05:15), dawn (05:15 – 06:30), day (06:30 – 19:20) and dusk (19:20 – 20:45). Diel feeding rhythm was then investigated for all larval species using a Pearson's chi-squared test.

Ontogenetic shifts in larval prey size were investigated by fitting quantile regressions to prey size (μm) and caudal length (mm) with fitting at the 99 % and 1% quantile regressions to identify the maximum and minimum prey size, respectively (Scharf et al., 1998).

The dietary composition was described using three prey indices outlined by Hyslop (1980); the percentage number of prey item p ($\%N_p$), the percentage contribution to dietary carbon of prey item p ($\%CC_p$) and the frequency of occurrence of prey item p ($\%F_p$), these are calculated in the following manner;

$$\%N_p = \frac{\text{total number of prey item } p}{\text{total number of all prey items}} \times 100 \quad (1)$$

$$\%CC_p = \frac{\text{total contribution to dietary carbon of prey item } p}{\text{total contribution to dietary carbon of all prey items}} \times 100 \quad (2)$$

$$\%F_p = \frac{\text{frequency of prey item } p \text{ found in stomachs}}{\text{Total number of stomachs containng food items}} \times 100 \quad (3)$$

These three indices were then subsequently combined to calculate an index of relative importance (IRI) for each individual prey item p (Pinkas et al., 1971; Cortés, 1997) using the following equation;

$$IRI_p = (\%N_p + \%CC_p) \times \%F_p \quad (4)$$

The IRI_p was then totalled for all prey items p for each species of fish f , and then made into a percentage, so that comparisons between f and p were possible.

$$\%IRI_{pf} = \frac{IRI_p \times 100}{\sum_1^n IRI_p} \quad (5)$$

where n is the total number of prey categories and p is the specific individual prey category found in the sample of stomachs.

Fish were grouped into 5 mm length-bins so that ontogenetic changes in the diets of the two species could be analysed. Prey were categorised in two ways; firstly, by taxonomy and secondly, by size (here forward referred to as prey-species and prey-size datasets respectively). Prey-sizes were grouped into 200 μ m bins, and the contribution to dietary carbon (%) for both prey-species and prey-size categories were calculated per 5 mm length-bin of fish, following the same equation as (2). However, prey item referred to either prey-species or prey-size category.

4.2.2.2. *Stable Isotope Analyses*

Stable isotope metrics described by Layman et al. (2007) were calculated using methods outlined by Jackson et al. (2011). Inferring information from isotopic indices can be biased by sample sizes, therefore using a Bayesian approach minimises sensitivities to biases corresponding to small sample sizes. The *SIBER* R package was used (Jackson & Parnell, 2023).

In order to explore the relationship between the isotopic signatures and caudal length, general linear models (GLMs) were implemented with additional independent variables. Both models (one each for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) initially included the following independent variables; *log(Caudal Length)* (mm), *Distance to Shore* (km), *Species* and *Region* (nBUS or sBUS). Significant independent variables were determined by F-tests. The final GLM model for $\delta^{15}\text{N}$ contained three of the original independent variables (*log(Caudal Length)*, *Distance to Shore*, *Species*). The final GLM model for $\delta^{13}\text{C}$ contained only *log(Caudal Length)* and *Species* as significant independent variables. Model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

The caudal length range of anchovy and sardine stable isotope samples differed slightly, consequently a sensitivity test was run whereby only samples less than 20 mm

in length were included in the stable isotope GLM analyses. The same protocol was performed and the results were compared.

4.2.2.3. *Fatty Acid Analyses*

Fatty acid data were analysed using a Principal Component Analysis (PCA), to explore primary differences in fatty acid profiles of larvae of the two larval from the two systems. The fatty acid matrix, consisting of 19 fatty acids, was transformed into proportions and then arcsine-square root transformed to normalise the data. There is debate around this transformation of proportions (Warton and Hui, 2011; Happel et al., 2017), yet it is still widely used in modern fatty acid analyses (e.g., Boissonnot et al., 2019; Mathiske, 2020; Massing et al., 2022).

A one-way analysis of similarity (ANOSIM) was then used to test for significant differences in fatty acid composition between the species and systems.

To assess historical diet from the fatty acid signatures of the samples, specific fatty acid trophic markers (FATM) and FA ratios were applied. Ratios are often used to help discriminate diet by normalising FATMs relative to specific markers. As both species are known to be omnivorous, with both phytoplankton and zooplankton contributing significant amounts of dietary carbon, FATM were used to determine the level of both phytoplanktophagy and zooplanktophagy. Both 16:1n-7 and 18:1n-7 fatty acids were used to identify diets derived from a diatom source. The fatty acid 18:1n-9 was utilised as a marker of carnivory (Graeve et al., 1994; Auel et al., 2002), along with both 20:1n-9 and 22:1n-11 that are commonly used as indicators of the consumption of calanoid copepods (Sargent & Falk-Petersen, 1988).

The use of fatty acid ratios, derived from well-known fatty acid trophic markers, to elucidate further information regarding diet has become commonplace in trophic studies. Four ratios were utilised in this study that help describe the degree of carnivory and herbivory in the larval diets. Firstly, the ratio:

$$\frac{\text{eicosapentaenoic acid (EPA, 20: 5n - 3)}}{\text{docosahexaenoic acid (DHA, 22: 6n - 3)}} \quad (6)$$

was used as an index of trophic feeding. In obligate herbivores this ratio is commonly used as a degree of diatom- vs. dinoflagellate-based diet (Auel et al., 2002) - however in omnivores, which is suspected for clupeoid larvae, the EPA/DHA ratio can be used as an index of carnivory, with lower ratios indicating feeding higher up the food chain (Dalsgaard et al., 2003). Secondly, the ratio:

$$\frac{\text{palmitoleic acid (16: 1n - 7)}}{\text{palmitic acid (16: 0)}} \quad (7)$$

was implemented as an index of diet derived from a diatom source (from here referred to as the Diatom ratio). As mentioned, 16:1n-7 is a common fatty acid accumulated from a diet of diatoms, whereas elevated 16:0 is associated with a dinoflagellate-based diet (Dalsgaard et al., 2003). Therefore, the index is used to determine the level of diet based on diatoms, with a ratio >1 indicating a diet with significant diatom consumption (Dalsgaard et al., 2003). An additional index of carnivory (from here referred to as the Carnivory ratio) was used in parallel to equation (6), this is the modified equation from Bode et al. (2015):

$$\frac{18: 1n - 9}{16: 1n - 7 + 16: 4n - 1 + 18: 1n - 7 + 18: 4n - 3 + 18: 1n - 9} \quad (8)$$

whereby, 16:1n-7, 16:4n-1, 18:1n-7 and 18:4n-3 are commonly used for herbivory and 18:1n-9 is a marker of carnivory. Lastly, a third index of carnivory was utilised:

$$\frac{\sum PUFA}{\sum SFA} \quad (9)$$

where the sum of polyunsaturated acids (PUFA) over the sum of saturated fatty acids (SFA) is used as an indicator of recent carnivory (Cripps & Atkinson, 2000; Dalsgaard et al., 2003), with higher values indicating increased carnivory (Table 4.2 for summary of FATM and ratios).

General Linear Models were fit to the FATM and FA ratio data, initially including *log(Caudal Length)*, *Species*, *Region* and *Chlorophyll-a* as explanatory variables, in order to assess the ontogenetic, inter and intra-specific, and habitat differences. Significant

independent variables were determined by F-tests. Model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

4.2.2.4. *Condition Indices*

Both morphometric and biochemical condition indices were calculated to assess the condition of individual larvae. Firstly, the morphometric condition factor was calculated using the following equation:

$$CF = \frac{\text{Observed wet body mass}}{\text{Expected wet body mass}} \quad (10)$$

whereby the expected wet body mass is the fitted linear regression of the log-log transformed observed wet-weight and caudal length data. The biochemical condition indices used were the residuals of the simple linear regression of the following equation:

$$\frac{n-3}{n-6} = m \ln(\text{Caudal length mm}) + c \quad (11)$$

with the residuals used to remove the allometric affect as previously described by Suthers (1988) and Teodósio et al. (2017). Both n-3 and n-6 PUFA are important to marine fish, however marine fish have a much higher requirement for n-3 (Sargent et al., 1995). Consequently, higher ratios of n-3/n-6 is indicative of better nutrition through better feeding conditions (Tocher and Harvey, 1988; Lytle et al., 1990). A simple ANOVA was used to test for significance difference in morphological and biochemical condition between the species and systems. The multiple-pairwise comparison Tukey HSD test was then implemented to elucidate differences between groups.

4.2.2.5. *Biochemical Comparison*

Data from both fatty acid trophic ratios and stable isotope analysis were pooled into the three caudal length bins (5 – 15, 15 – 25 and 25 – 35 mm) for the two species and systems. The mean $\delta^{15}\text{N}$ (‰) of each bin was then plotted against the PUFA/SFA and

EPA/DHA ratios, and the Carnivory and Diatom markers, and linear models were fitted to assess the relationship between the two biochemical (stable isotope and fatty acid analysis) methods. Model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

Table 4.2. Summary of the fatty acid trophic markers (FATM) and fatty acid (FA) ratios used to assess the historical diet of the two species.

	Eq.	Description
FATM		
16:1n-7		Diatom marker
18:1n-7		Diatom marker
18:1n-9		Carnivory marker
20:1n-9		Calanoid marker
22:1n-11		Calanoid marker
FA ratio		
EPA/DHA	(6)	Carnivory index
Diatom Marker	(7)	Diatom relative to dinoflagellate index
Carnivory Marker	(8)	Carnivory relative to herbivory index
PUFA/SFA	(9)	Indicator of recent carnivory

4.3. Results

4.3.1. Stomach Content Analysis

In total, 697 stomachs were analysed. Feeding incidence in larval species between the two systems were similar (sBUS anchovy = 5.3%, nBUS anchovy = 4.2 %, nBUS sardine = 7.8%), sBUS sardine was left out of calculations due to only one individual analysed (Table 4.8). There was no diel feeding rhythm for anchovy from either system (sBUS anchovy; $\chi^2 = 5.99$, $df = 2$, $p = 0.112$, nBUS anchovy; $\chi^2 = 0.24$, $df = 2$, $p = 0.889$), yet nBUS sardine had a higher feeding incidence during the day than at night and dawn ($\chi^2 = 17.23$, $df = 2$, $p < 0.001$).

Table 4.4. The feeding incidence in larval anchovy and sardine caught in the nBUS and sBUS. Times were split into night (20:45 – 05:15), dawn (05:15 – 06:30), day (06:30 – 19:20) and dusk (19:20 – 20:45).

Species			Night	Dawn	Day	Dusk	Total
Anchovy	sBUS	<i>Contained food</i>	7	5	7	0	19
		<i>Empty</i>	191	39	119	9	358
		<i>Total</i>	198	44	126	9	377
	nBUS	<i>Contained food</i>	0	0	3	0	3
		<i>Empty</i>	4	1	66	0	71
		<i>Total</i>	4	1	69	0	74
Sardine	sBUS	<i>Contained food</i>	0	0	0	0	0
		<i>Empty</i>	0	0	1	0	1
		<i>Total</i>	0	0	1	0	1
	nBUS	<i>Contained food</i>	5	1	13	0	19
		<i>Empty</i>	157	14	55	0	226
		<i>Total</i>	162	15	68	0	245

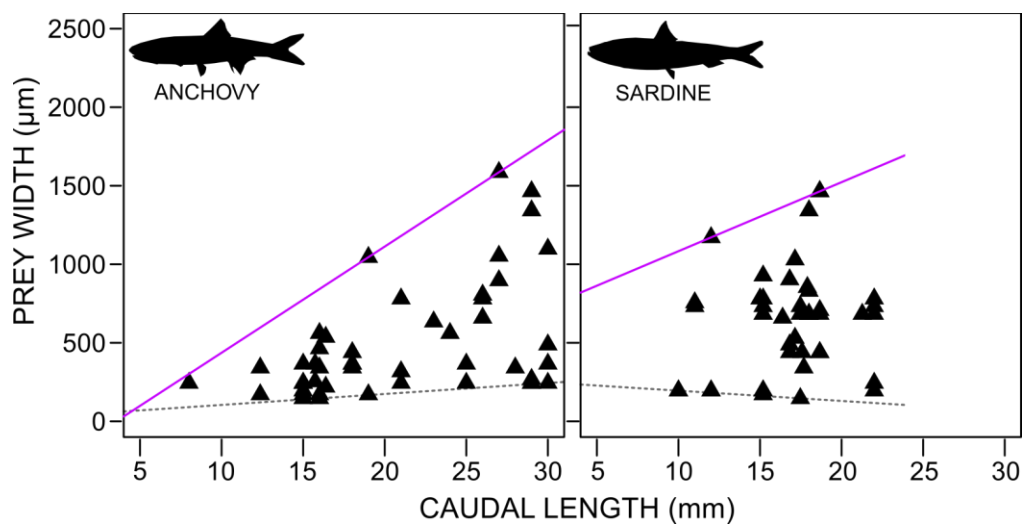


Figure 4.2. Scatter plots of the prey size (width of individual prey items; μm) against caudal length (mm) for anchovy and sardine larvae, with the 99% quantile regression line in purple representing the maximum and the 1% quantile regression in dotted grey representing the minimum prey width.

Both 99% and 1% quantile regressions were fit to the species-specific prey width (μm) scatter plots (Figure 4.2). The 99 % quantile regressions fit for anchovy; $\text{Prey Width } (\mu\text{m}) = 69.52 \times \text{Caudal Length } (\text{mm}) + 107.50 (\mu\text{m})$, was significant ($p\text{-value} < 0.001$) showing a positive increase in maximum prey width during their ontogeny. For sardine, the 99% quantile regression equation; $\text{Prey Width } (\mu\text{m}) = 25.48 \times \text{Caudal Length } (\text{mm}) + 476.16 (\mu\text{m})$, showed a slight increase in prey maximum width, albeit the equation was not significant ($p\text{-value} = 0.384$). Minimum prey width did not increase for anchovy ($\text{Prey Width } (\mu\text{m}) = 0.65 \times \text{Caudal Length } (\text{mm}) + 146.40 (\mu\text{m})$, $p\text{-value} = 0.977$) and slightly decreased (but not significantly) for sardine ($\text{Prey Width } (\mu\text{m}) = 256.95 (\mu\text{m}) - 6.18 \times \text{Caudal Length } (\text{mm})$, $p\text{-value} = 0.557$).

Due to the low (4 - 8 %) feeding incidence in the larvae, there was only a total of 41 positive stomachs out of 697 analysed stomachs. Anchovy from the sBUS contained prey from five major prey categories, with copepods being the greatest dietary contributor. Copepod nauplii made up the largest proportion of their diet (% IRI 71.98), with adult cyclopoid (% IRI 12.12, primarily *Oithona similis*) and adult calanoid (% IRI 5.20, primarily *Calanoides carinatus*) copepods contributing the next most (Table 4.8). For sardine from the nBUS similarly, copepods were the greatest dietary component, with nauplii contributing the most (% IRI 83.15), and other adult stages of calanoid (% IRI 5.22, primarily *Pleuromamma abdominalis*) and harpacticoid (% IRI 3.95, primarily *Microsetella* sp.) copepods contributing significant proportions. Phytoplankton, both diatoms (*Coscinodiscus* sp.) and dinoflagellates (*Protoperidinium* and *Ceratium* sp.), were found in larger quantities in the few anchovy with food from the nBUS (% IRI 10.10) compared to both sBUS anchovy (% IRI 1.55) and nBUS sardine (% IRI 4.33). Similar to both sBUS anchovy and nBUS sardine, the nBUS anchovy stomach contents were comprised almost entirely of copepods (nauplii % IRI 55.44 and cyclopoid % IRI 19.95), with dinoflagellates also contributing to the diet (IRI % 10.10).

Table 4.4. Prey index values by assigned prey category, taxon to species level are also names, for sBUS anchovy (A_s), nBUS anchovy (A_n) and nBUS sardine (S_n), caught off the west coast of South Africa and Namibia, %N – percentage number, %CC – percentage of contribution to dietary carbon, %F – frequency of occurrence, and %IRI – indices of relative importance. The highest values in each category are in bold, underlined text.

Prey category			Taxon			% N			% CC			% F			% IRI		
						A_s	A_n	S_n	A_s	A_n	S_n	A_s	A_n	S_n	A_s	A_n	S_n
FISH EGGS	Fish eggs	<i>Sardinops sagax</i>	9.52	0.00	0.00	0.01	0.00	0.00	15.79	0.00	0.00	1.95	0.00	0.00			
ZOOPLANKTON	Brachyuran		0.00	0.00	1.43	0.00	0.00	0.22	0.00	0.00	5.26	0.00	0.00	0.09			
	Foraminifera		6.35	0.00	2.86	0.50	0.00	0.14	15.79	0.00	5.26	1.40	0.00	0.17			
	Tintinnid		0.00	0.00	1.43	0.00	0.00	3.92	0.00	0.00	5.26	0.00	0.00	0.31			
	Euphausiid		0.00	0.00	2.86	0.00	0.00	0.03	0.00	0.00	5.26	0.00	0.00	0.17			
COPEPODS	Calanoid	<i>Pleuromamma abdominalis</i> , <i>Paracartia africana</i> , <i>Paracalanus sp.</i> , <i>Paracalanus parvus</i> , <i>Acartia sp.</i> , <i>Calanoides carinatus</i> , <i>Heterohabdus sp.</i>	9.52	0.00	8.57	15.90	0.00	14.08	15.79	0.00	21.05	5.20	0.00	5.22			
	Cyclopoid	<i>Oithona similis</i> , <i>O. atlantica</i> ,	11.11	9.09	5.71	24.48	46.12	2.48	26.32	33.33	15.79	12.12	19.95	1.42			
	Harpacticoid	<i>Microsetella sp.</i>	12.70	9.09	10.00	1.65	1.38	3.71	21.05	33.33	26.32	3.91	3.78	3.95			
	Copepod		<u>31.75</u>	<u>45.46</u>	<u>37.14</u>	<u>56.31</u>	<u>31.24</u>	<u>73.86</u>	<u>63.16</u>	<u>66.67</u>	<u>68.42</u>	<u>71.98</u>	<u>55.44</u>	<u>83.15</u>			
	Nauplii																
	Copepod egg		7.94	0.00	4.29	0.76	0.00	0.22	15.79	0.00	5.26	1.78	0.00	0.26			
	Copepod	<i>Unidentified copepods</i>	1.59	9.09	4.29	0.21	20.58	1.16	5.26	33.33	15.79	0.12	10.72	0.94			
PHYTOPLANKTON	Diatom	<i>Coscinodiscus sp.</i> , <i>Chaetoceros sp.</i>	3.18	0.00	11.43	0.03	0.00	0.06	5.26	0.00	15.79	0.22	0.00	1.99			
	Dinoflagellate	<i>Protopteridinium sp.</i> , <i>Ceratium sp.</i>	6.35	27.27	10.00	0.16	0.67	0.14	15.79	33.33	21.05	1.33	10.10	2.34			

There was a clear change in the diets of sBUS anchovy and nBUS sardine during their ontogeny. The most distinct change in diet was the progression from nauplii to adult stages of copepods, such as *Calanoides carinatus* and *Oithona similis*. Although nauplii remained a key component of the diet of both species in all size classes, adult copepods contributed to ca 80 % and 30 % of total dietary carbon for anchovy and sardine, respectively, in the largest studied size classes (Figure 4.3). A key prey-species difference between the two species was that anchovy consumed larger calanoid copepods, specifically *Calanoides carinatus*, whereas sardine consumed the smaller *Paracartia africana* and *Heterohabdus* spp. The cyclopoid species were similar between the two small pelagic fish.

The contribution to dietary carbon (%) from different size classes of prey changed throughout the ontogeny of sBUS anchovy (Figure 4.4). Smaller prey items were important to smaller individuals, with 100 % of their dietary carbon coming from prey items smaller than 800 μm for individuals smaller than 25 mm. As sBUS anchovy grew in size there was a sudden progression in the dependency of larger prey size classes, with larger individuals (> 25 mm) obtaining more than 60 % of their dietary carbon from prey larger than 800 μm . Despite a low sample size for nBUS anchovy, there is a similar pattern for the two size classes observed. This pattern was different for sardine, where items smaller than 800 μm were important for all the studied size classes, with at least 80 % of their dietary carbon coming from items less than this size (Figure 4.4).

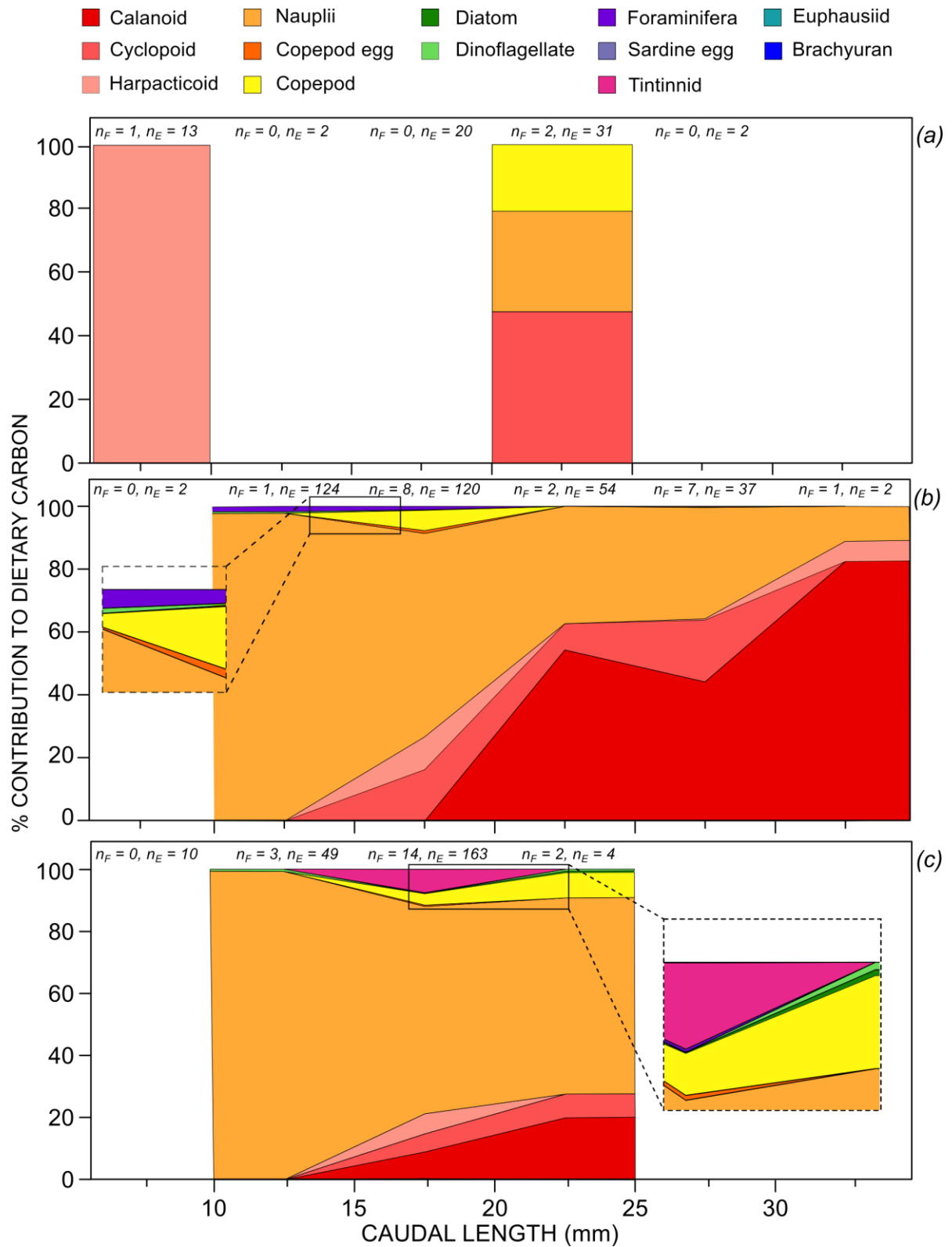


Figure 4.3. The contribution to dietary carbon (%) of specific prey taxa for (a) nBUS anchovy, (b) sBUS anchovy and (c) nBUS sardine, for 5 mm length bins of larvae. n_F is the number of stomachs containing food, n_E is the number of empty stomachs.

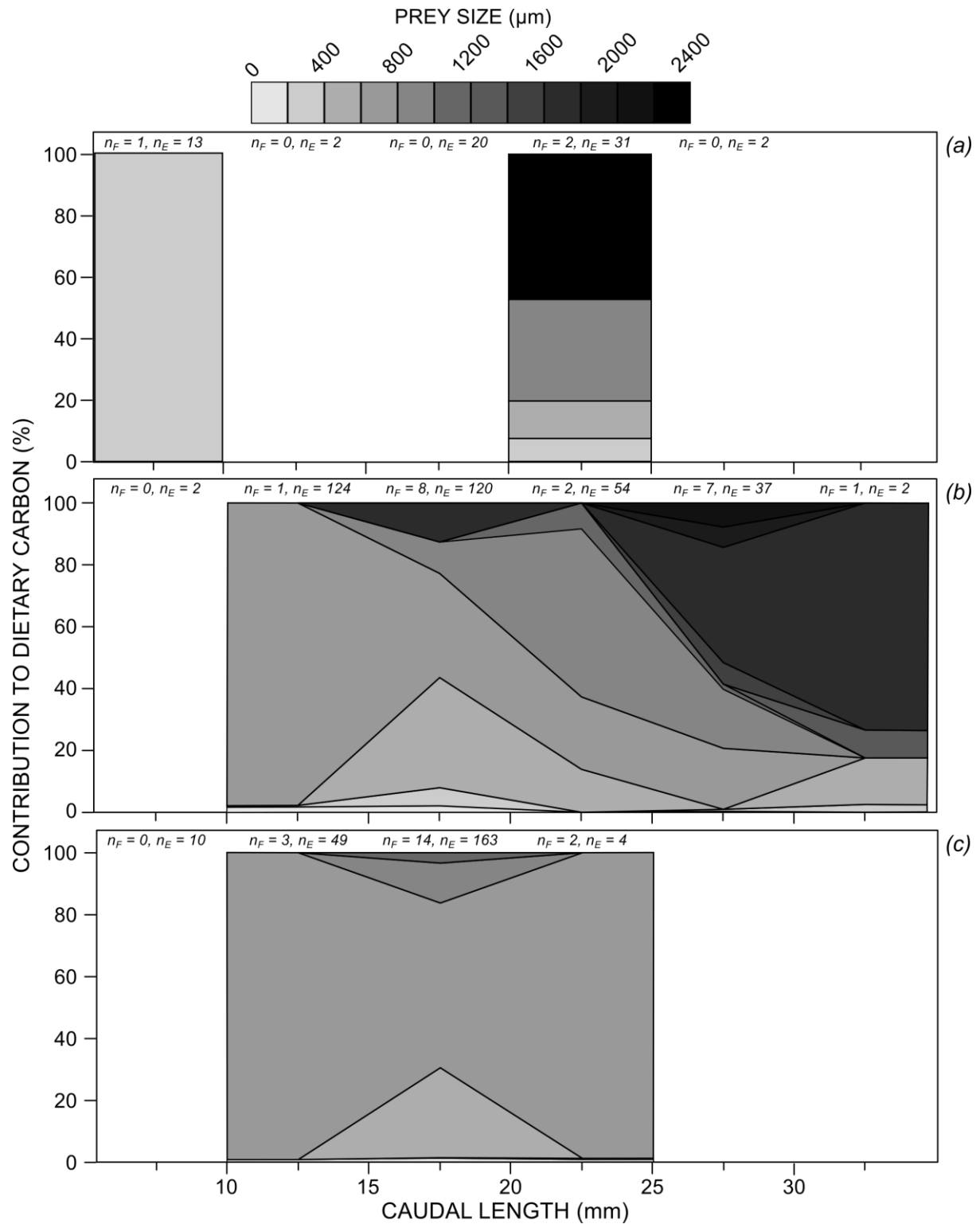


Figure 4.4. The contribution to dietary carbon (%) of prey size class categories for (a) nBUS anchovy, (b) sBUS anchovy and (c) nBUS sardine, for 5 mm length bins of larvae. n_F is the number of stomachs containing food, n_E is the number of empty stomachs.

4.3.2. Stable Isotope Analysis

Stable isotope indices were calculated from the isotopic data for each of the three species groups of larvae as shown in Table 4.8. As seen in Figure 4.5, the three larval groups occupy a similar isotopic niche space. The three larval groups had comparatively similar standard ellipse areas (SEA) and isotopic ranges, however there was a slight dissimilarity in the trend of confidence ellipses. Sardines with higher $\delta^{15}\text{N}$ values had comparatively lower $\delta^{13}\text{C}$ values than individuals with a lower $\delta^{15}\text{N}$, where this trend was the opposite for anchovy individuals.

The overall $\delta^{15}\text{N}$ GLM was significant ($F = 36.98$, $df_1 = 3$, $df_2 = 133$, $p < 0.001$) with the three explanatory variables; $\log(\text{Caudal Length})$, *Distance to Shore*, and *Species* being significant and accounting for 44.3 % of the variability in the data (Table 4.6). There was a positive exponential correlation with *Caudal Length*, with ^{15}N enrichment during their ontogeny for both species (Figure 4.6 & 4.7). There was a negative relationship with *Distance to Shore*, showing that samples were generally ^{15}N depleted offshore vs inshore. Interestingly, there was a significant difference between sardine and anchovy larvae in terms of $\delta^{15}\text{N}$ values; sardine had a higher $\delta^{15}\text{N}$ value than anchovy (Figure 4.6). There was no difference in $\delta^{15}\text{N}$ values between anchovy from the northern and southern Benguela.

The $\delta^{13}\text{C}$ GLM was also significant ($F = 7.17$, $df_1 = 3$, $df_2 = 133$, $p < 0.001$) with the two explanatory variables; $\log(\text{Caudal Length})$ and *Species*, and their interaction term, accounting for 12.0 % of the variation seen in the data. There was a small enrichment in $\delta^{13}\text{C}$ with *Caudal Length* in anchovy (Figure 4.6). Contrastingly for sardine, there was a $\delta^{13}\text{C}$ depletion with *Caudal Length*. This difference is likely the cause of the difference in the isotopic space as seen in Figure 4.5.

Following the model fitting procedure, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ GLM in the sensitivity analysis had the same explanatory variables as the models with the full isotopic data set. Furthermore, the explanatory variables for both GLMs in the sensitivity analysis had very similar slopes to the GLMs using the full data set (Table 4.7).

Table 4.5. Stable isotope indices calculated for the three species groups (S = sBUS and N = nBUS), showing the mean (‰), range (‰) and SEA which is the standard ellipses area which has been corrected for small sample size bias.

Isotope Indices	Larvae		
	Anchovy S	Anchovy N	Sardine N
Mean $\delta^{15}\text{N}$ ($\pm$ SD ‰)	10.546 (0.556)	10.422 (0.688)	10.891 (0.480)
Mean $\delta^{13}\text{C}$ ($\pm$ SD ‰)	-18.617 (0.456)	-18.351 (0.625)	-18.731 (0.474)
Range $\delta^{15}\text{N}$ (‰)	2.25	2.06	2.31
Range $\delta^{13}\text{C}$ (‰)	3.23	1.74	2.50
SEA	0.740	0.752	0.667

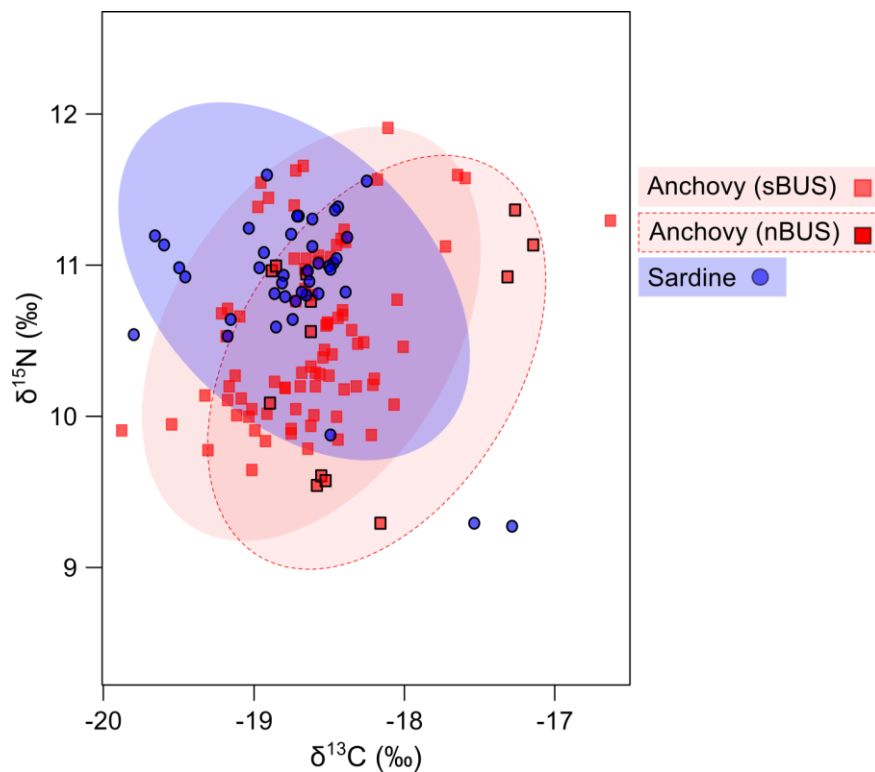


Figure 4.5. Represents the isotopic biplots for the three species groups with 95% confidence ellipses.

Table 4.6. Results of the GLMs fitted for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with unique explanatory variables showing the estimates of the parameters with their associated standard error (Std. err), t -statistic and p -value.

$\delta^{15}\text{N}$	Estimate	Std. err	t -value	p -value
Intercept	7.846	0.478	16.422	< 0.001 ***
$\log(\text{Caudal Length [mm]})$	1.042	0.151	6.883	< 0.001 ***
Species	0.199	0.086	2.318	0.022 *
Distance to shore (km)	-0.002	0.001	-2.899	0.004 **
$\delta^{13}\text{C}$				
Intercept	-19.810	0.429	-46.202	< 0.001 ***
$\log(\text{Caudal Length [mm]})$	0.436	0.151	2.892	0.005 **
Species	7.344	1.995	3.681	< 0.001 ***
$\log(\text{Caudal Length [mm]})$	-2.602	0.691	-3.765	<0.001 ***
* Species				

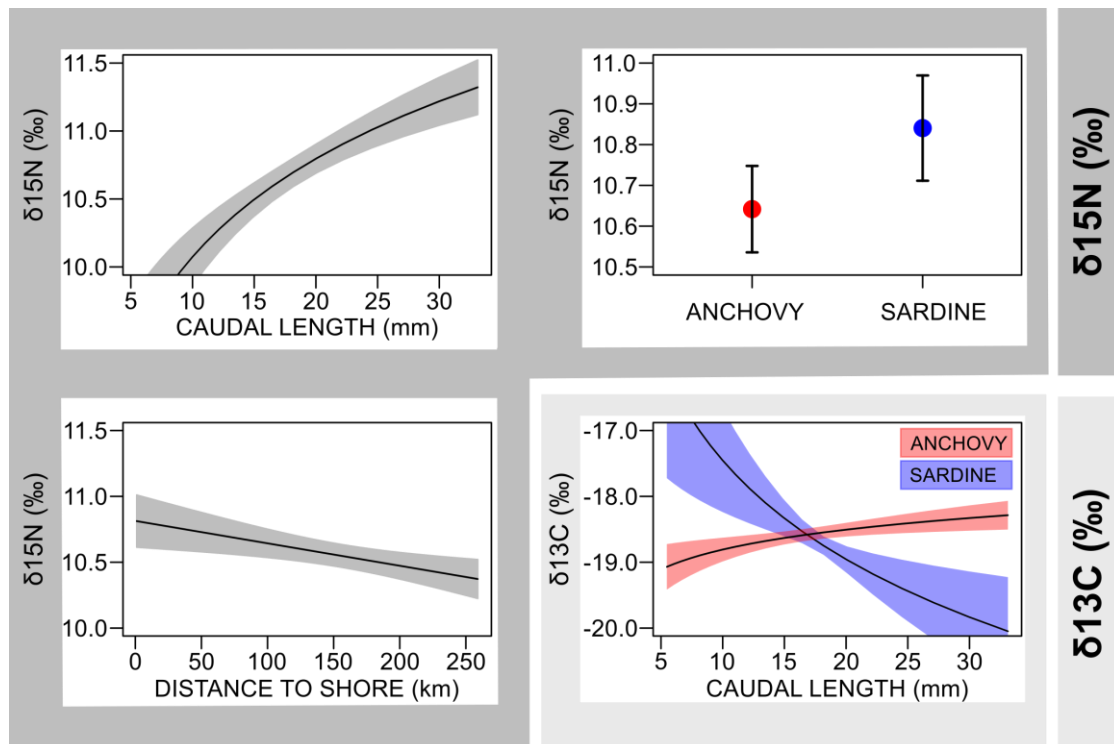


Figure 4.6. The effects of the independent variables included in both the GLMs ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) used to explain the variation seen within the isotopic data. Bars and shaded areas represent 95% confidence intervals.

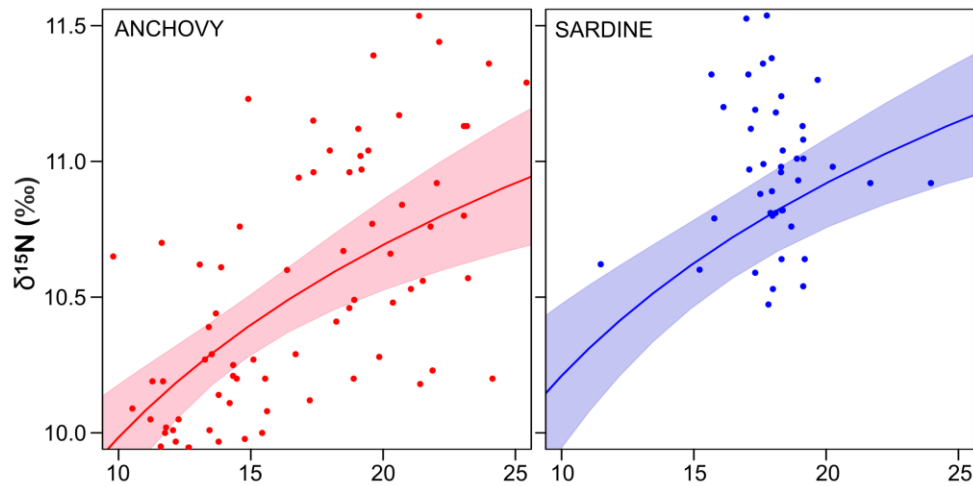


Figure 4.7. $\delta^{15}\text{N}$ GLM model output for both anchovy and sardine, shaded areas represent 95% confidence intervals.

Table 4.7. Sensitivity analyses results showing the GLMs fitted for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to fish under 20 mm in caudal length, with unique explanatory variables showing the estimates of the parameters with their associated standard error (Std. err), t -statistic and p -value.

$\delta^{15}\text{N}$	Estimate	Std. err	t -value	p -value
Intercept	7.906	0.604	13.079	< 0.001 ***
$\log(\text{Caudal Length [mm]})$	1.023	0.210	4.884	< 0.001 ***
Species	0.227	0.108	2.097	0.038 *
Distance to shore (km)	-0.002	0.001	-2.434	0.012 *
$\delta^{13}\text{C}$				
Intercept	-19.625	0.516	-38.046	< 0.001 ***
$\log(\text{Caudal Length [mm]})$	0.360	0.192	1.869	0.012 *
Species	8.874	1.963	4.520	< 0.001 ***
$\log(\text{Caudal Length [mm]})$	-3.126	0.687	-4.551	< 0.001 ***
* Species				

4.3.3. Fatty Acid Analysis

There were 19 fatty acids detected in appreciable quantities in all three species groups (Table 4.8). Unfortunately, the dry weights of samples were erroneous due to a calibration error with the scales. Therefore, fatty acids will be described as the percentage of total fatty acids per sample. Polyunsaturated fatty acids (PUFAs) were the major constituents of the total fatty acids (TFA) in all three groups, with similar proportions between them (53.38 – 56.43 % TFA). Docosahexaenoic acid (22:6n-3, DHA) was found in the highest proportion in all three groups, with the lowest in nBUS sardine (36.95 %) and highest in sBUS anchovy (39.04 %). Eicosapentaenoic acid (20:5n-3, EPA) was also found in appreciable quantities in all three groups (12.34 – 14.52 %). Saturated fatty acids (SFAs) were dominated by short-chain fatty acids, with large proportions of 16:0 (20.71 – 21.63 %) and smaller proportions of 14:0 (3.60 – 4.46 %) and 18:0 (4.47 – 6.46 %). The monounsaturated fatty acids (MUFAs) were observed in the smallest proportions, with the largest contribution from the fatty acids 18:1n-7 and 18:1n-9.

A principal component analysis was performed to analyse the fatty acid composition between the three species groups. The first three principal components (PC) explained 77.3% of the variance in the data, with the first two components explaining accumulatively 65.7 % (Figure 4.8a). PC1 was mainly represented by positive eigenvectors of 22:6n-6, 24:1n-9 and 20:4n-6, and negative eigenvectors of 18:1n-9, 18:0 and 18:1n-7, all values are represented in decreasing order of explanatory power (Figure 4.8 (b)). PC2 was largely represented by positive eigenvectors of 22:6n-6, 18:0 and 18:1n-9, and negative eigenvectors of 20:1n-9, 20:4n-6 and 22:1n-11, similarly, all values are represented in decreasing order of explanatory power (Figure 4.8b).

Table 4.8. Fatty acid composition of tissue samples taken from both anchovy and sardine from the southern and northern Benguela. Numbers are represented as % of total fatty acids ($\pm$ standard deviation).

Fatty Acid (% TFA)	Anchovy sBUS Total <i>n</i> = 39	Anchovy nBUS Total <i>n</i> = 13	Sardine nBUS Total <i>n</i> = 40
SFA	30.88	30.47	30.95
14:0	4.02 $\pm$ 0.7	4.46 $\pm$ 0.7	3.60 $\pm$ 0.9
16:0	21.63 $\pm$ 1.1	21.08 $\pm$ 1.3	20.71 $\pm$ 1.3
18:0	4.79 $\pm$ 2.1	4.47 $\pm$ 1.2	6.46 $\pm$ 1.4
20:0	0.17 $\pm$ 0.1	0.22 $\pm$ 0.2	0.13 $\pm$ 0.2
24:0	0.27 $\pm$ 0.2	0.25 $\pm$ 0.2	0.05 $\pm$ 0.1
MUFA	13.64	13.10	15.67
14:1n-5	0.04 $\pm$ 0.0	0.05 $\pm$ 0.0	0.02 $\pm$ 0.1
16:1n-7	3.33 $\pm$ 0.9	3.69 $\pm$ 0.8	3.22 $\pm$ 0.8
18:1n-9	6.53 $\pm$ 3.1	5.57 $\pm$ 1.6	8.16 $\pm$ 2.6
18:1n-7	2.59 $\pm$ 0.8	2.41 $\pm$ 0.4	2.73 $\pm$ 0.9
20:1n-9	0.07 $\pm$ 0.1	0.11 $\pm$ 0.2	0.60 $\pm$ 1.3
22:1n-11	0.01 $\pm$ 0.0	0.04 $\pm$ 0.0	0.07 $\pm$ 0.3
24:1n-9	1.07 $\pm$ 0.5	1.24 $\pm$ 0.4	0.87 $\pm$ 0.7
PUFA	55.48	56.43	53.38
18:2n-6	1.49 $\pm$ 0.5	1.42 $\pm$ 0.2	1.50 $\pm$ 0.5
18:3n-3	0.79 $\pm$ 0.6	0.88 $\pm$ 0.3	1.25 $\pm$ 0.6
20:2n-6	0.22 $\pm$ 0.1	0.24 $\pm$ 0.1	0.12 $\pm$ 0.2
20:4n-6	0.95 $\pm$ 0.5	1.75 $\pm$ 0.4	1.21 $\pm$ 0.9
20:3n-6	0.02 $\pm$ 0.0	0.02 $\pm$ 0.1	0.01 $\pm$ 0.1
20:5n-3	12.98 $\pm$ 2.1	14.51 $\pm$ 1.9	12.34 $\pm$ 1.8
22:6n-3	39.04 $\pm$ 8.1	37.60 $\pm$ 3.9	36.95 $\pm$ 7.8
FA ratio			
EPA/DHA	0.37 $\pm$ 0.2	0.39 $\pm$ 0.1	0.36 $\pm$ 0.1
Diatom marker	0.15 $\pm$ 0.0	0.18 $\pm$ 0.0	0.16 $\pm$ 0.0
Carnivory Marker	0.51 $\pm$ 0.1	0.47 $\pm$ 0.1	0.57 $\pm$ 0.0
PUFA/SFA	1.82 $\pm$ 0.3	1.86 $\pm$ 0.2	1.75 $\pm$ 0.3

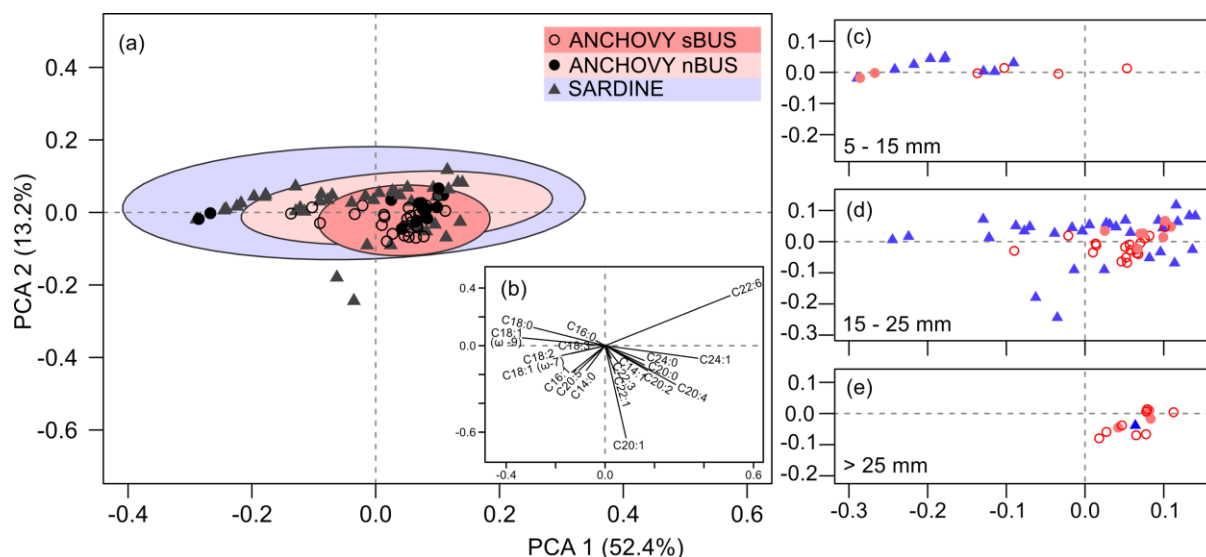


Figure 4.8. The principal component analysis performed on the fatty acid data of the three separate species groups, showing (a) the scores with 95% confidence ellipses, (b) the loadings of the individual fatty acids and (c - e) the size (caudal length mm) categorised scores of PC2 (y axis) against PC1 (x axis).

The three species groups occupy a similar space represented by their PCA scores, however, the confidence ellipses calculated for the three species groups differ. Both confidence ellipses from the northern components are larger. Similarly, both anchovy components have smaller ellipses than sardine, due to differences in variation of fatty acid composition of the species. These differences are largely seen in PC1 and are primarily caused due to differences in proportions of 18:1n-9 and the increase in PUFAs, primarily 22:6n-3, during their ontogeny. These differences were corroborated by a significant result from the ANOSIM analyses, showing that there was a significant difference in the fatty acid composition between the three species groups ($R = 0.224$, $p\text{-value} = 0.001$).

Interestingly, as seen in Figure 4.8 (c – e), when categorised into ontogenetic stages by 10 mm length bins, there is a clear positive trend in PC1 scores during their early life. This positive shift in PC1 scores during their ontogeny is due to positive eigenvectors of longer chained fatty acids, such as 22:6n-3, 24:1n-9, 20:4n-6, and 20:2n-6 (Figure 4.8 (b)).

Table 4.9. Results from the multivariate GLMs, displaying the *F statistic*, response and explanatory variables, degrees of freedom (df), adjusted R² and *p-value*, for specific fatty acids and ratios for anchovy and sardine larvae collected from the west coast of southern Africa.

Model variable	Explanatory variables	F statistic	Effect df	Error df	Adjusted R ²	<i>p-value</i>
16:1n-7 Diatom	= log(<i>CL</i>) * <i>Species</i>	8.55	3	78	0.219	***
18:1n-9 Carnivory	= log(<i>CL</i>) * <i>Species</i> + <i>Chlorophyll a</i>	38.86	4	77	0.652	***
18:1n-7 Diatom	= log(<i>CL</i>) * <i>Species</i>	16.80	3	78	0.369	***
EPA/DHA	= log(<i>CL</i>) * <i>Species</i>	11.66	3	78	0.283	***
Carnivory	= log(<i>CL</i>) + <i>Region</i> + <i>Chlorophyll a</i>	20.59	3	78	0.421	***
Diatom	= log(<i>CL</i>) + <i>Species</i>	8.52	2	79	0.152	***
PUFA/SFA	= log(<i>CL</i>) * <i>Species</i>	19.84	3	78	0.411	***

GLMs fit to the FATM and FA ratio data (see Table 4.2 for summary) initially included *Caudal Length (mm)*, *Species*, *Region* (nBUS or sBUS) and *Chlorophyll-a* as explanatory variables, in order to assess ontogenetic and species differences.

For both diatom markers (16:1n-7 and 18:1n-7) there was a significant negative exponential relationship for both species (Table 4.9). There was a similar %TFA for both markers over the observed species-specific size classes, but both markers showed a sharper decrease with increasing size in sardine (Figure 4.9).

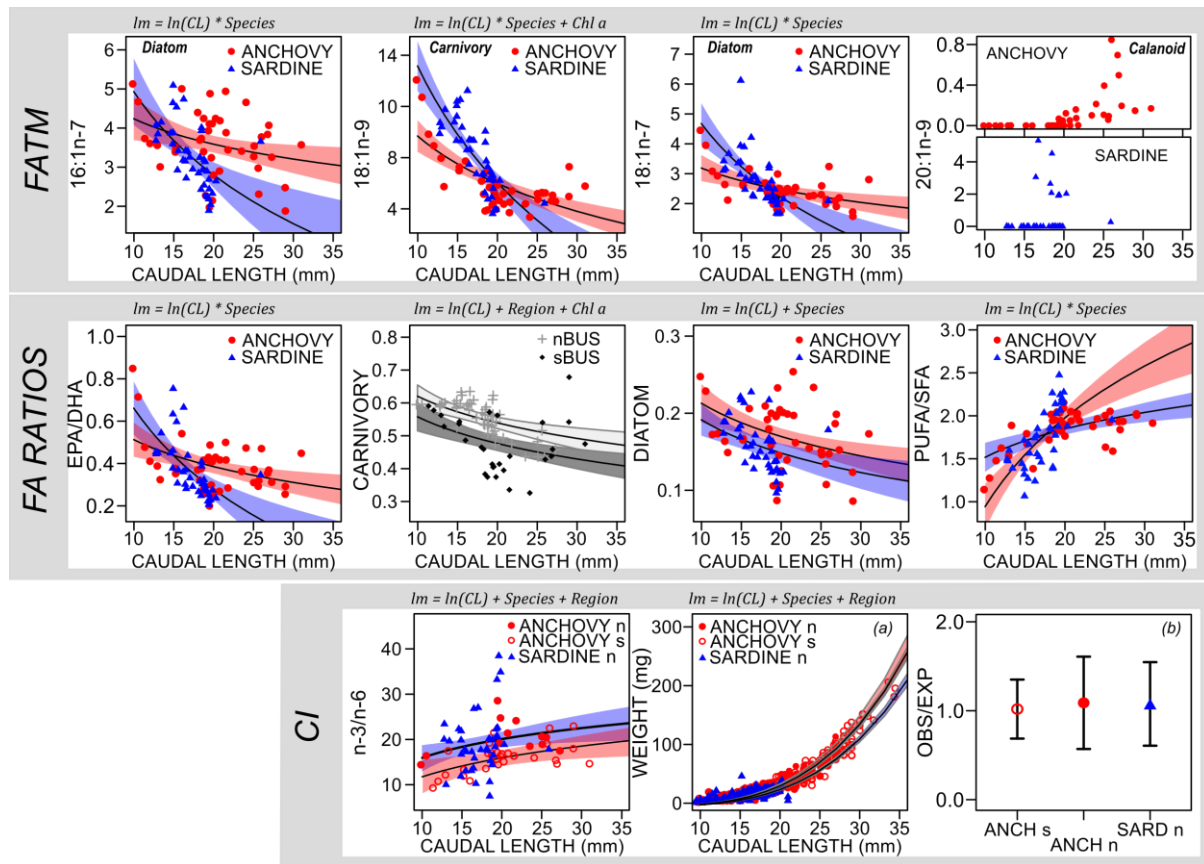


Figure 4.9. The results of the GLMs fitted to both the specific fatty acid trophic markers and ratios plotted against larval caudal length (mm). Condition indices (CI) models are shown for both the biochemical model n-3/n-6 and morphology model, with the means of the observed/expected weight for the three species groups. Shaded areas represent the 95 % confidence area.

The same trend was observed in the carnivory marker 18:1n-9, with an exponential decrease in the marker for both species with size (Table 4.9). Again, the decrease was steeper for sardine than observed in anchovy (Figure 4.9). For the calanoid markers, 20:1n-9 and 22:1n-11, models could not be fitted due to high zero inflation. However, it is worth noting that for 20:1n-9 there is a sudden presence of this marker during the ontogeny of both species, it is more pronounced in anchovy, but found in substantially larger quantities in sardine (Figure 4.9).

A significant decrease in the EPA/DHA ratio with size was found for both species, with a steeper reduction for sardine compared to anchovy (Table 4.9 and Figure 4.9). The carnivory ratio also decreased with size but showed no significant difference between

the two species, although there was a significant difference between the two systems indicating that northern Benguela larvae were more carnivorous than those in the southern Benguela (Figure 4.9). The Diatom marker showed a significant difference between the species, with anchovy exhibiting higher diatom ratios compared to sardine of the same size. Both species exhibited a decrease in the Diatom marker during their ontogeny (Figure 4.9). Lastly, the PUFA/SFA GLM showed a significant increase in the ratio for both species, which increased with size rapidly for sardine than for anchovy (Table 4.9 and Figure 4.9).

4.3.4. *Condition indices*

There was no significant difference between the mean morphological condition factor of each species group ($F = 2.853$, $df = 2$, $p\text{-value} = 0.06$).

However, there was a significant difference in n-3/n-6 residuals between the three species groups (F value = 5.973, $df = 2$, $p\text{-value} = 0.004$). A post-hoc Tukey HSD test showed a significant difference between both nBUS anchovy (mean = 1.79) and sBUS anchovy (mean = -2.49, $p\text{-value} = 0.03$), and nBUS sardine (mean = 1.32) and sBUS anchovy (mean = -2.49, $p\text{-value} = 0.006$).

4.3.5. *Comparison of Biochemical Methods*

Linear models fitted to the means estimated from the stable isotope and fatty acid analyses show that there are negative correlations between the Carnivory, Diatom and EPA/DHA trophic markers and $\delta^{15}\text{N}$, and a strong positive correlation between the PUFA/SFA ratio and $\delta^{15}\text{N}$ (Figure 4.10). From the plots, it appears that the smallest length-category of both sardine and anchovy from the nBUS are having the largest effect on the models.

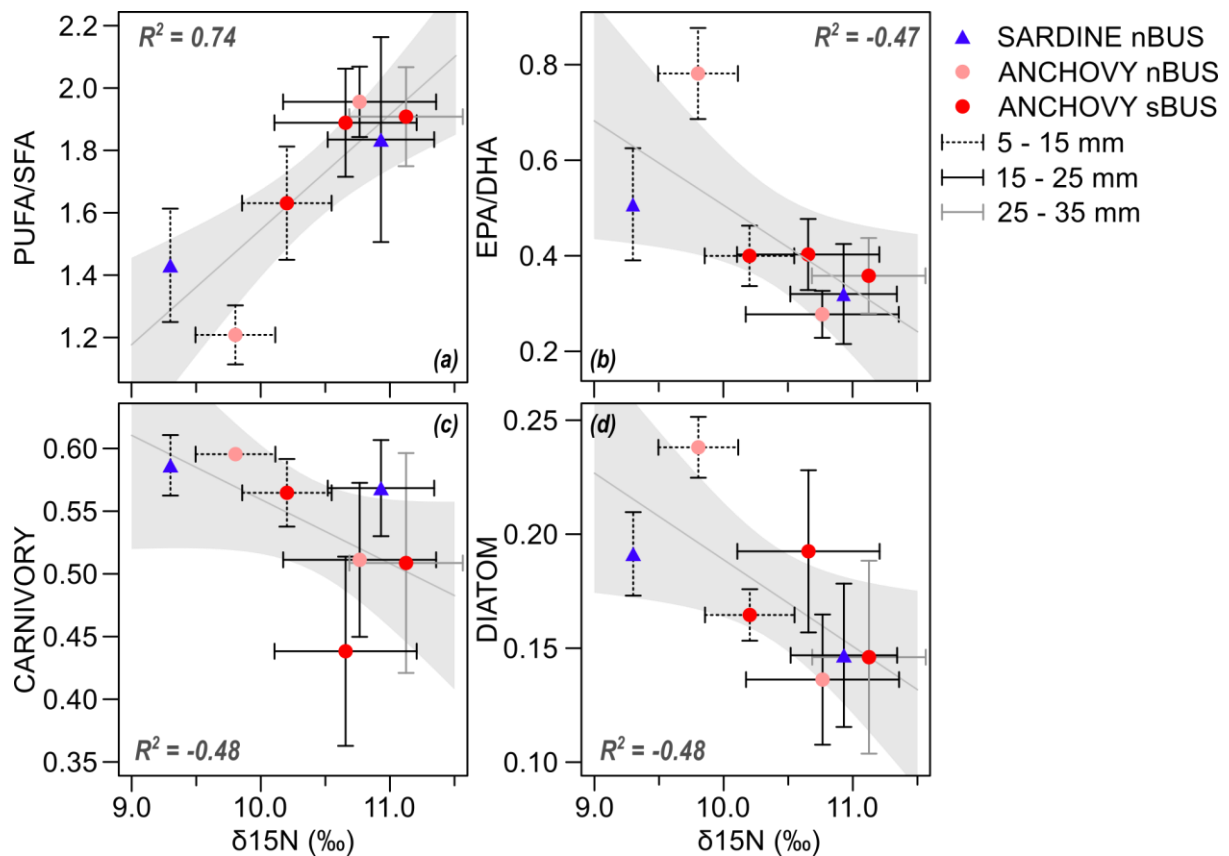


Figure 4.10. Plots of the mean ($\pm$ SD) of the $\delta^{15}\text{N}$ (‰) and (a) PUFA/SFA ratio, (b) EPA/DHA ratio, (c) Carnivory ratio and (d) Diatom ratio for the three species groups split into separate ontogenetic stages (5 – 15mm, 15 – 25 mm and 25 – 35 mm), with the output of the linear model fitted to the means with the 95 % confidence interval (grey shaded area).

4.4. Discussion

Anchovy and sardine larvae studied in the southern and northern Benguela exhibit strong ontogenetic shifts in diet, primarily through increased prey size and trophic niche breadth observed for larger individuals. There was a slight, albeit significant, difference between the two species in maximum prey size. However, distinctions elucidated by biochemical methods may suggest further dissimilarities deserving of future investigation.

4.4.1. Trophic Ontogeny

There was a clear ^{15}N enrichment with caudal length (mm) for both species, with a maximum increase in $\delta^{15}\text{N}$ of 2.06 – 2.31 ‰ between the smallest and largest size classes of anchovy and sardine (Table 4.4). It is understood that the trophic fractionation of ^{15}N is not constant between trophic levels (TL), instead it progressively narrows up the food web (Hussey et al., 2014), and therefore using a fixed value of 3.4 ‰ per trophic level can greatly underestimate higher trophic levels (Post, 2002). However, for lower trophic level species (TL 2 and 3) 3.4 ‰ proves to be consistent. Hence, if we implement 3.4 ‰ in this study, then during the early development of these larvae their trophic position increases by around two thirds of a trophic level. The biggest trend observed was the increasing contribution to dietary carbon from adult stages of copepods and decreasing contribution from nauplii (Figure 4.3). This is a common result found in many other studies of the trophic ecology of small pelagic fish early life stages (Tudela et al., 2002; Voss et al., 2009; Morote et al., 2010; Arula et al., 2012), primarily due to changes in morphological characteristics that facilitate predation on larger prey items (Tudela et al., 2002; Karpouzi & Stergiou, 2003; Morote et al., 2008). Similar to most intraguild species, copepods also exhibit both intra- and interspecific niche partitioning. Research exploring the ontogenetic development of copepod species' diets indicates a trend in size-dependent prey-size preference, whereby older stages incorporate larger prey items into their diet (Saiz et al., 2014; Im et al., 2015; Im & Suh, 2019). Corroborated by size fractionated particulate organic matter (< 2 – 200 μm) showing a consistent enriching trend of ^{15}N (Park et al., 2011; Im et al., 2015; Im & Suh, 2019). Therefore, this large increase in $\delta^{15}\text{N}$ observed in the studied larval fishes presented here likely represents the increasing importance of larger, older ontogenetic stages of copepods in their diet.

The fatty acid composition and ratios of anchovy found in this study are similar to results from studies performed on conspecifics locally (Mathiske, 2020) and globally (Rossi et al., 2006; Costalago et al., 2011; Teodósio et al., 2017). There was an increased importance of long-chain MUFAs and PUFAs during their ontogeny, which is corroborated with the size-specific means (% TFA) found in conspecifics (Rossi et al., 2006; Costalago et al., 2011; Teodósio et al., 2017; Mathiske, 2020). The same importance of long-chain MUFAs and PUFAs was observed during the ontogeny of sardine larvae.

The Diatom trophic marker decreased for both species with size, indicating reduced herbivory during their ontogeny. This would be expected during their early larval stages, as with certain morphological developments such as increased gape size

(Chapter 3) and locomotor ability (Blaxter and Hunter, 1982), the capture of larger mobile prey becomes an option. To a degree, this is corroborated by the stomach content analysis that showed whilst the contribution to dietary carbon from phytoplankton was similar for sardine of the studied size classes, there was a decrease found in anchovy. Phytoplankton was also found in seemingly negligible quantities in other dietary studies of anchovy (Hirakawa et al., 1997; Islam & Tanaka, 2009; Yasue et al., 2011) and sardine larvae (Conway et al., 1994; Watanabe & Saito, 1998; Morote et al., 2010; Yasue et al., 2011). Interestingly, Ciechomski (1966) observed an opposite trend in the Argentine anchovy, with autotrophic components increasing in abundance with size of larvae. Spatio-temporal differences in ambient prey composition could be the source of the variation, yet it does highlight the potential for dietary flexibility in small pelagic larvae.

Both EPA/DHA and PUFA/SFA ratios highlighted an ontogenetic increase in carnivory and feeding at a higher trophic level for both species. This matches the increase in adult copepods and carnivorous species found in the diet of larger larvae. Furthermore, as previously mentioned, the Diatom marker decreased with size for both species and phytoplankton remained relatively low throughout the studied size classes. Increasing consumption of secondary consumers such as carnivorous copepods would likely cause the observed increase in carnivorous markers. Furthermore, the fatty acid 20:1n-9 is an important component of the wax esters biosynthesised *de novo* by calanoid copepods and therefore acts as a marker of calanoid consumption (Dalsgaard et al., 2003). This marker only becomes traceable at ~ 16 and 18 mm for sardine and anchovy respectively, which supports an increase in carnivory during their ontogeny.

Smaller individuals of both sardine and anchovy have very high levels of 18:1n-9, at around 12 and 11 % TFA respectively. This then decreases dramatically throughout their ontogeny. This fatty acid (18:1n-9 - Oleic acid) has commonly been implemented as a fatty acid trophic marker that implies carnivorous feeding (Sargent & Falk-Petersen, 1988; Dalsgaard et al., 2003; Schukat et al., 2014; Bode et al., 2015). Initially devised through the trophic interactions of copepods, it is thought that since it is a major FA in most marine animals it will therefore be accumulated through diet. Additionally, high levels of 18:1n-9 have also been associated with both Prymnesiophyceae (Coccolithophores) and Dinophyceae (Dinoflagellates; see Dalsgaard et al., 2003). This leads to a degree of ambiguity and uncertainty when inferring conclusions from these results. Similarly high levels of this carnivory marker was found in other small clupeoid

larvae and the authors to concluded that due to a high ambient density of Prymnesiophyceae it likely reflected a herbivorous diet (Rossi et al., 2006; Garrido et al., 2012). Furthermore, studies have shown that eggs and newly hatched endogenous feeding larvae in both clupeoids and other teleosts' are heavily enriched with this fatty acid (Laurel et al., 2010; van der Bank, 2010; Garrido et al., 2012). This strongly suggests that these high levels of 18:1n-9 in early life stages may not be representative of their trophic ecology but rather of their non-genetic maternal inheritance.

All vertebrates, including fish, are capable of biosynthesizing short chain SFA, especially 16:0 and 18:0. These are then readily desaturated to short chain MUFAs such as 18:1n-9 that are essential for energy sources (Dalsgaard et al., 2003; Tocher, 2003). Many studies have described teleosts' limited capabilities to desaturate and elongate short chain SFAs and MUFAs to long chain PUFAs such as DHA and EPA (Olsen et al., 1990; Dalsgaard et al., 2003; Tocher, 2003; Laurel et al., 2010). To what extent this happens is largely unknown, but it is thought that these capabilities are often largely suppressed due to a diet heavily enriched with these essential fatty acids (Olsen et al., 1990; Tocher, 2003). Consequently, these EFAs are heavily conserved through the diet of developing fish, whereas short chain SFAs and MUFAs are readily mobilised and metabolised for energy (Tocher, 2003). During their development, short chain fatty acids decrease with increasing sized individuals (e.g., Figure 4.9), whereas long-chain fatty acids generally increase. Therefore, it is plausible that both larval species are conserving valuable long chain PUFAs from their diet for somatic growth and metabolising shorter chain fatty acids for energy. Hence, the use of trophic indices using shorter chained fatty acids may need to be re-addressed, certainly for early stages of fish. As it is difficult to discern between diet and somatic growth patterns in the shorter chain fatty acid composition of developing larvae. This is corroborated by the biochemical method comparison between fatty acid and stable isotope signatures. Enrichment of ^{15}N is a widely accepted standard for increasing trophic levels, and when plotted against trophic indices using shorter chain fatty acids there is a negative relationship (Figure 4.10), this has also been the case for other species including lower trophic levels (Mathiske, 2020). Therefore, conclusions about diet using short-chain fatty acid data could be erroneous.

4.4.2. *Interspecific Comparisons*

There was a clear interspecific difference in prey-size consumption inferred from the stomach content analysis with anchovy consuming larger prey than sardine. Increasing prey width during ontogeny is not uncommon in fish (Scharf et al., 2000; Nunn et al., 2007; Wittenrich & Turingan, 2011), as selected prey particle size is a consequence of several morphological traits that develop during growth. Minimum size classes in clupeoids are dictated via the gillraker spacing in their branchial baskets (van der Lingen et al., 2006b) whereas maximum particle size would be limited by the mouth gape (Ciechomski, 1966; Scharf et al., 2000). From the results of Chapter 3, there was no difference in gillraker spacing between the two species, however there was a large difference in gape size between the two species. Gape size was much larger in anchovy larger than sardine and increased allometrically. Therefore, the prey size range selected by clupeoid larvae in the Benguela appears to be size limited, which could be a mechanism of resource partitioning between these species.

At initial inspection there was a degree of discord between the stomach content and stable isotope analyses. Anchovy showed an increase in prey size with caudal length where sardine did not, yet this was coupled with anchovy having a lower ^{15}N in comparison to sardine. This may be explained by the differences in the prey-species composition of their diet. In terms of adult copepod consumption, anchovy consumed primarily large *Calanoides carinatus* compared to the smaller *Paracartia* and *Heterohabdus* species preyed on by sardine. It has become increasingly obvious that the trophic dynamics of copepods are far more dynamic than previously thought. For example, calanoids were traditionally described as primary herbivores performing the crucial link between autotrophs and carnivores in marine systems (Verheye et al., 1992). However, more recent studies have shown the complexity of their omnivory (Schukat et al., 2014; Bode et al., 2015; Benedetti et al., 2016), with sympatric calanoids having a range of 1.8 trophic levels deduced from stable isotope analysis (Schukat et al., 2014). With such variation amongst species, it is not surprising to see such differences between anchovy and sardine. *Calanoides carinatus* was described through both stable isotope and fatty acid analysis to have the highest degree of herbivory and the lowest trophic level out of the calanoid species studied by Schukat et al. (2014). These larger more herbivorous copepods ingested by anchovy may contribute to the difference in $\delta^{15}\text{N}$ values between anchovy and sardine larvae.

Both species from the different systems exhibit similar isotopic niche areas (~ 0.7 , Table 4.9), yet the orientation of the standardised ellipses is different between the species. Sardine enriched in ^{15}N are comparatively ^{13}C depleted, whereas anchovy show a positive relationship between the two isotopes (Figure 4.5). This is also seen in the negative relationship with ^{13}C with size for sardine. This ^{13}C isotopic ecology differs within systems due to differences in source production. Diatom- and benthic-based production is typically ^{13}C enriched, whereas pelagic phytoplankton, such as dinoflagellate-based, is depleted (Fry & Wainright, 1991). This spatial trend has been corroborated around the South African coast showing an offshore depletion trend in ^{13}C (Hill et al., 2006). Therefore, this difference in ^{13}C isotopic signature, would imply a difference in dietary carbon. This is interesting as both anchovy from the nBUS and sBUS were found further offshore (average station depth; 267 and 617 m, respectively) in comparison to sardine from the nBUS (average station depth; 162.4 m). Therefore, the data has showed the opposite trend of what would be expected.

There may be two explanations for this. Firstly, the observed diet species-composition concluded that dinoflagellates were consistently found and numerically more important in sardine in the later larval stages (Figure 4.3). Hence, the higher contribution by dinoflagellates to sardine diet during the larger size classes may explain this depletion trend observed. Secondly, one of the benefits of using biochemical methods to study trophic ecology is that it provides information on assimilated diet components that may be missed through traditional stomach content analyses. This may be extremely important for larvae due to a combination of a very low feeding incidence and a high frequency of stomach evacuation. Consequently, this deviation in isotopic signatures between the two species, may be representative of important prey items that have been missed such as protozooplankton (Bils et al., 2022). This would need further attention through investigation of stable isotopes of fine size-fractionated or species separated samples of ambient plankton, or metabarcoding of stomach content DNA (Albaina et al., 2016; Bachiller et al., 2020; Kume et al., 2021; Novotny et al., 2022).

4.4.3. Trophic Ecology Differences Between the Northern and Southern Benguela

The low feeding incidence observed in this study was similar to others of clupeoids (Tudela et al., 2002; Geist, 2013). Hence, commenting on differences in stomach contents between northern and southern Benguela anchovy is challenging, given only three positive stomachs in the nBUS. There was no difference in isotopic signatures of both ^{13}C and ^{15}N of anchovy between the two systems. Considering the observed changes in the food web structure of the northern Benguela (Heymans et al., 2004), one would anticipate the possibility of detecting a difference in trophic ecology between the distinct small pelagic fish stocks. Mathiske (2020) performed a comparative study of the trophic ecology of major planktonic species between the southern Benguela and the northern Benguela, previously analysed by Schukat et al. (2014), using biochemical methods. The author showed a slight, albeit insignificant, difference, whereby nBUS anchovy were ^{15}N depleted in comparison to sBUS anchovy. The $\delta^{15}\text{N}$ data for nBUS anchovy used from Schukat et al. (2014), showed an average of 7.3 ‰. There was no specification of the length of the larvae analysed which is unfortunate as the results here have shown a large ontogenetic effect on the isotopic signatures. Therefore, this small value may rather be indicative of a smaller fish used. Additionally, given the observed changes in the food web in the nBUS, we would anticipate a higher ^{15}N signature due to the presence of the larger oxygen minimum zone (OMZ). These OMZs are areas of strongest anammox and denitrification which causes ^{15}N enrichment (Espinoza et al., 2017). Despite this, anchovy from the separate systems occupy a similar trophic level.

Anchovy from both systems had similar length-specific values of the carnivory and herbivory trophic markers and ratios. This indicates that they share the same degree of omnivory and ontogenetic progression of diet. Despite the drastic changes observed in the higher trophic levels in the nBUS, there are still similarities in the major zooplankton assemblages and biomass in both systems (Gibbons & Hutchings, 1996b; Huggett et al., 2009). Therefore, as anchovy in both systems have yet to diverge in terms of their ecomorphological traits (Chapter 3) and in combination with similar prey assemblages, it is unsurprising that their isotopic signatures and feeding behaviour are similar.

The PCA analysis and ANOSIM results revealed a significant difference in the fatty acid composition of anchovy between the nBUS and the sBUS. This discrepancy was predominantly associated with two small individuals from the nBUS, depicted as the two furthest left-hand points in Figure 4.8. These two individuals, being the smallest in the analysis, exhibited a fatty acid composition primarily composed of shorter-chained

saturated and monounsaturated fatty acids, with a notable absence of long-chain polyunsaturated acids. Consequently, this disparity is likely attributable to ontogenetic effects. This interpretation is further supported by the analysis of FATM and ratios with caudal length (mm), wherein the difference between the species in the two systems is not statistically significant.

There was a notable difference in biochemical condition indices between the two systems, with anchovy in the sBUS being in worse condition than either species in the nBUS. A similar trend was observed in adult sardine during the period from 1984 to 1999 (Kreiner et al., 2001). The authors hypothesised that the better condition observed in the nBUS was partially due to density -dependent effects and an effect of the drastically reduced sardine stock in the region. To some degree, this may account for the observed difference in condition in this study, considering the stability and health of the anchovy stock in the sBUS (Coetzee et al., 2020) in contrast to the sustained depletion of the nBUS stock since the 1990s (Boyer & Hampton, 2001; Kainge et al., 2020). Furthermore, Costalago et al. (2020) conducted a comparative analysis of the condition of anchovy *Engraulis encrasicolus* larvae between Algoa Bay and the west coast of South Africa. Surprisingly, the larvae exhibited better condition in Algoa Bay, despite its status as a more oligotrophic area. The authors concluded that despite the productivity differences, the observed improvement in condition could be attributed to density-dependent effects. A similar trend was also highlighted in the anchovy *Engraulis anchoita* in the southwest Atlantic (Diaz et al., 2018). Productivity obviously plays an important role due to increased prey availability (Teodósio et al., 2017; do Souto et al., 2019), however, the anchovy larvae in this study from both systems were sampled from similar *chlorophyll-a* and temperature conditions (Chapter 2). This may suggest that density-dependent effects could play an important role and provides the basis for future work.

.

4.4.4. Conclusion

Through a multifaceted approach this study has provided evidence of inter- and intraspecific differences in the trophic ecology of these commonly schooling intraguild species. Prey-size selection is an important regulator of both intra- and interspecific

competition, with anchovy selecting and ingesting larger particles than sardine. This will be useful information in ecosystem models that predefine primary and secondary production by size classes and will therefore hopefully provide the opportunity to include a finer life history resolution of these small pelagic fish species. This study has corroborated findings from many other trophic studies, in which the trophodynamics of marine species are not as straightforward as once thought. The use of biochemical methods has aided in untangling the Gordian knot of food web dynamics. Yet, this study has highlighted potential inconsistencies regarding the utility of using shorter chained MUFAs as carnivory indices that may lead to erroneous conclusions. Therefore, future work must be directed at the review of fatty acid trophic markers for fish and higher trophic levels.

Chapter 5

*The trophic ecology of juvenile anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi* in the southern Benguela.*

Abstract

The biomass and recruitment trajectories of the three abundant clupeoids in the southern Benguela (anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi*) have been drastically different. There has been a steady and significant increase in both recruitment and biomass of round herring since the late 1980s. The recruitment of small pelagic fishes is predominantly influenced by fluctuations in pre-recruit mortality rates, yet limited attention has been directed at early life stages of round herring in the Benguela, specifically round herring. Therefore, this study employs a comprehensive approach, utilising ecomorphology, traditional and biochemical methods, to examine and compare the trophic ecology of pre-recruit round herring, sardine, and anchovy in the southern Benguela. Several ecomorphologic and trophic distinctions between the three species that would imply a degree of trophic separation between them were observed. Despite having ecomorphological traits more similar to sardine, round herring exhibit greater trophic dissimilarity from sardine than anchovy. Round herring, on average, consumed larger prey items, while anchovy and sardine fed substantially on large-celled phytoplankton, a dietary component entirely absent from the guts of round herring. These dietary differences were corroborated by the stable isotope analysis that detailed (a) a ^{15}N enrichment from sardine to anchovy to round herring indicative of feeding at higher trophic levels, and (b) ^{13}C depletion in the opposite direction, indicative of a reduced dependence on autotrophic components. Stomach content analysis suggested substantial filter-feeding for anchovy and sardine, but relatively little for round herring. Therefore, the compounding effect of the feeding mode with the functional traits provides potential answers for variances seen in their trophic ecology. These trophic differences are akin to the trophic separation described for adults of these species.

5.1. Introduction

The southern Benguela upwelling system (sBUS) harbours large biomasses of three small pelagic fishes; anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi*. All species exhibit large variations in recruitment success and subsequent population size (Checkley et al., 2009; DEFF, 2020). Dissimilar to anchovy and sardine, there has been a significant increase in both recruitment and biomass of round herring since the late 1980's (Figure 5.1; Coetzee et al., 2020). Round herring catches were first recorded in the late 1950s and have since never exceeded 100,000 tons (Roel & Armstrong, 1991; DEFF, 2020). Despite increasing round herring biomass, catches have remained stable at approximately 50,000 tons. This is due to (a) the difficulties in catching them through purse seines and (b) only targeting them early in the year before anchovy become available (DEFF, 2020).

Despite temporal differences in spawning, whereby anchovy and sardine exhibit peak spawning during austral spring and summer (Melo, 1992, 1994b; Fowler, 1998; Huggett et al., 1998; Richardson et al., 1998; van der Lingen & Huggett, 2003), and round herring have peaks in July – November (Shelton, 1986; Roel & Melo, 1990; Roel & Armstrong, 1991), the recruit and pre-recruit life history of the three species is similar. Spawning primarily happens on the Agulhas Bank for all three species, and depending on the location, eggs and larvae will either be transported downstream to the west coast nursery ground via a strong shelf-edge frontal jet current (Shelton & Hutchings, 1982; Roel & Armstrong, 1991), or if they are spawned on the central and eastern Agulhas Bank (i.e. east of Cape Agulhas) they will be mostly retained inshore on the south coast (Roel & Armstrong, 1991; Beckley & Hewitson, 1994; Huggett et al., 1998; Miller et al., 2006; McGrath et al., 2020). Juvenile round herring are largely inshore residents, migrating offshore during their ontogeny (Roel & Armstrong, 1991), and as juveniles they are commonly found in mixed schools with sardine and anchovy. Consequently, both young sardine and round herring (< 1 year) are caught as bycatch in the anchovy recruit (6 – 9 months) directed fishery (Painting, 1993; Coetzee et al., 2018; de Moor, 2022).

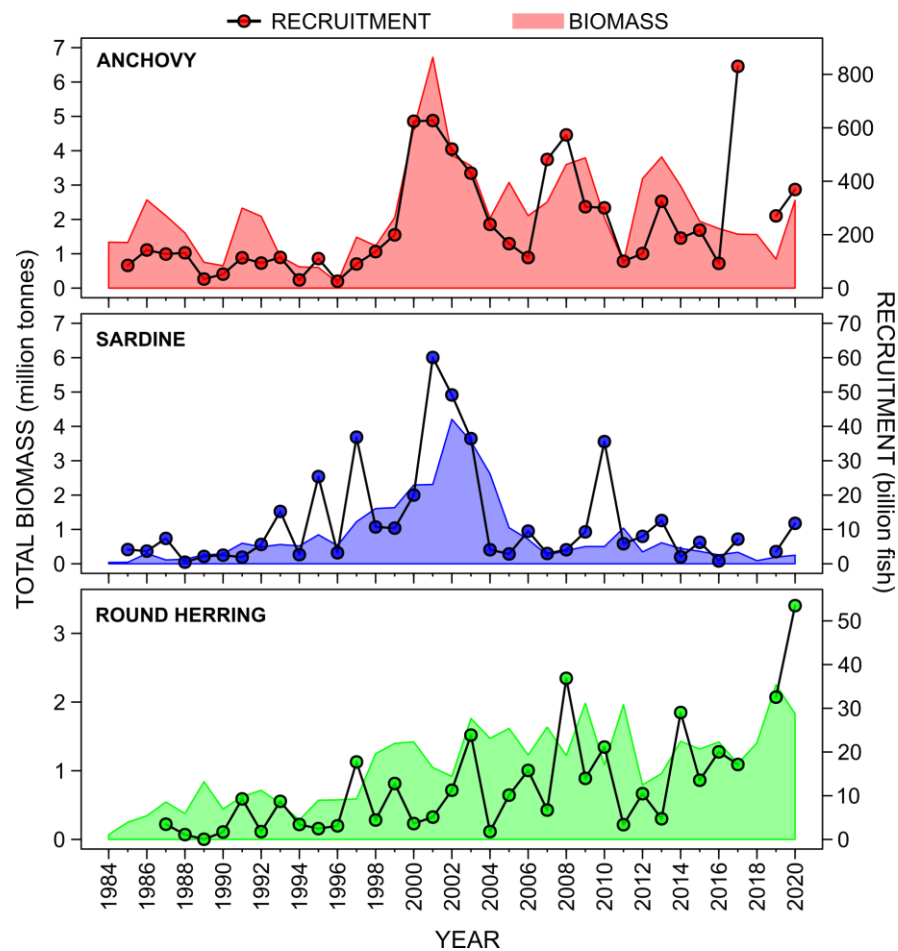


Figure 5.1. Total biomass (million tonnes) and recruitment (billion fish) of anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi* in the southern Benguela.

Knowledge of the ecology of juvenile stages is crucial to understanding the recruitment dynamics of small pelagic species, as mortality during pre-recruit stages largely dictates recruitment. Yet despite their importance, they lack significant scientific attention (Peck et al., 2013). Despite spatial synchronicity during their pre-recruit stages, the recruitment and biomass trajectories of the three abundant clupeoids in the southern Benguela have been drastically different over the past decades. Takahashi et al. (2008) showed that the observed species alternations between Japanese sardine *Sardinops melanostictus* and Japanese anchovy *Engraulis japonicus* may have arisen from a change in the environmental conditions in their nursery area that led to more favourable temperature conditions and prey-size compositions for anchovy than sardine. Therefore, differences in the trophic ecology between the local clupeoids in South Africa may have influenced these differing trends of recruitment and biomass.

Understanding the trophic dynamics of small pelagic fishes in the southern Benguela has received considerable attention. The trophic ecology of these species has been described for adults (King & Macleod, 1976; James, 1987; Wallace-Fincham, 1987; van der Lingen, 2002), recruits on the east coast (Mketsu, 2008), and recruits of sardine and anchovy on the west coast (Louw et al., 1998). Throughout the size classes in the above studies, there were clear differences in the diet of the three species primarily facilitated through size-based partitioning, with sardine consuming the smallest prey. Despite this extensive coverage however, no description of the diet of round herring pre-recruits and juveniles on the west and south coast has yet been conducted.

The importance of understanding the trophic ecology of different life history stages of ecologically and commercially important fish species becomes explicitly clear when creating biological and ecological models. Currently, there is only information for the diet of adult round herring on the west coast. As a result, the most recent Ecopath with Ecosim (EwE) model of the southern Benguela incorporates a single age group (one stanza) for round herring. Both anchovy and sardine are divided into recruits and adults (i.e., two stanzas) in the same model, ensuring the comprehensive inclusion of their ecological and commercial interactions. As morphological development is greatest during early life stages which diet is so inherently linked, it could be assumed that the diet of juvenile round herring differs greatly to their adult counterparts. If so, it would be beneficial to disaggregate round herring further in ecosystem models.

Given the current depletion of the sardine stock and the anticipated uncertainty surrounding the future of small pelagic stocks in the face of climate change, it is evident that diversifying target species in the South African small pelagic sector is essential. This approach is crucial for ensuring economic stability and alleviating fishing pressure on vulnerable stocks (van der Lingen, 2021a). There is a precautionary upper catch limit of 100,000 tonnes for round herring, yet in recent years the average catch has remained at ca. 50,000 tonnes. There is a difficulty in the fishery to catch round herring due to the species being further offshore and stronger swimmers. Yet despite this, an increase in the exploitation of this species is an attractive alternative to relieve pressure from sardine and anchovy. Before this occurs, it is imperative to understand their ecosystem role in the southern Benguela ecosystem. Therefore, the aim of this Chapter is to investigate interspecific differences in trophic niche and breadth that would facilitate trophic partitioning between pre-recruit and juvenile round herring *Etrumeus whiteheadi*, sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*. This will be performed by

providing a holistic description of the trophic ecology of the three species through a multifaceted approach including both ecomorphological traits and traditional trophic analyses such as stomach contents and stable isotopes.

5.2. Methods

5.2.1. Data Collection

Pre-recruit and juvenile samples of round herring, anchovy and sardine were obtained from routine small pelagic total biomass surveys conducted by the Department of Forestry, Fisheries, and the Environment (DFFE) of South Africa in November 2018 and 2019 (Figure 5.2). Samples were collected from midwater trawl catches and immediately blast frozen at -20 °C aboard for further analysis at the University of Cape Town.

In the lab, fish were thawed and then their caudal length (mm) and wet weight (g) were taken. A 1 cm² of muscle tissue from the left lateral side of the fish was removed and stored in a - 20 °C freezer for stable isotope analysis. The first left lateral gill arch was then removed for branchial basket analysis. The alimentary tract was excised for various measurements, and then placed in formalin for stomach content analysis.

Several morphometric measurements were taken from each sample using a Nikon SMZ800 microscope under x40 magnification and a graticule accurate to 0.01 mm. Firstly, the alimentary tract was analysed, with gut length measured as the stretched length from the posterior sphincter of the stomach to the anus and the total number of pyloric caeca counted. Secondly, the gape size was measured as the distance between the upper and lower jaws at maximum stretch.

The following branchial basket morphological measurements and counts from the first left lateral gill arch were taken; gill arch length, gillraker spacing and total number of gillrakers. The gill arch length comprised of the total length of the epibranchial, ceratobranchial and hypobranchial arches combined, as seen in Figure 5.3. The total number of gillrakers was the sum of all gillrakers present on the epi-, cerato- and hypobranchial arches. The gillraker spacing was measured following the methods presented by Tanaka et al. (2006), whereby five gillraker spacings were measured from

the middle of the ceratobranchial arch and an average value was then calculated (Figure 5.3).

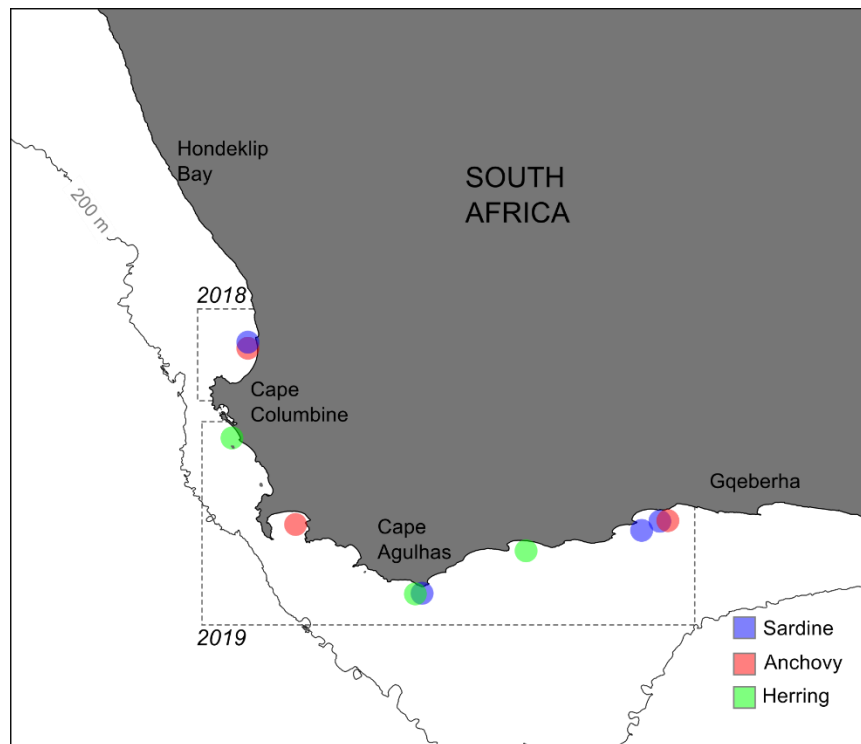


Figure 5.2. Distribution of the anchovy, sardine and herring pre-recruit and juvenile samples obtained from the DFFE small pelagic spawner biomass surveys conducted around the coast of South Africa in 2018 and 2019.

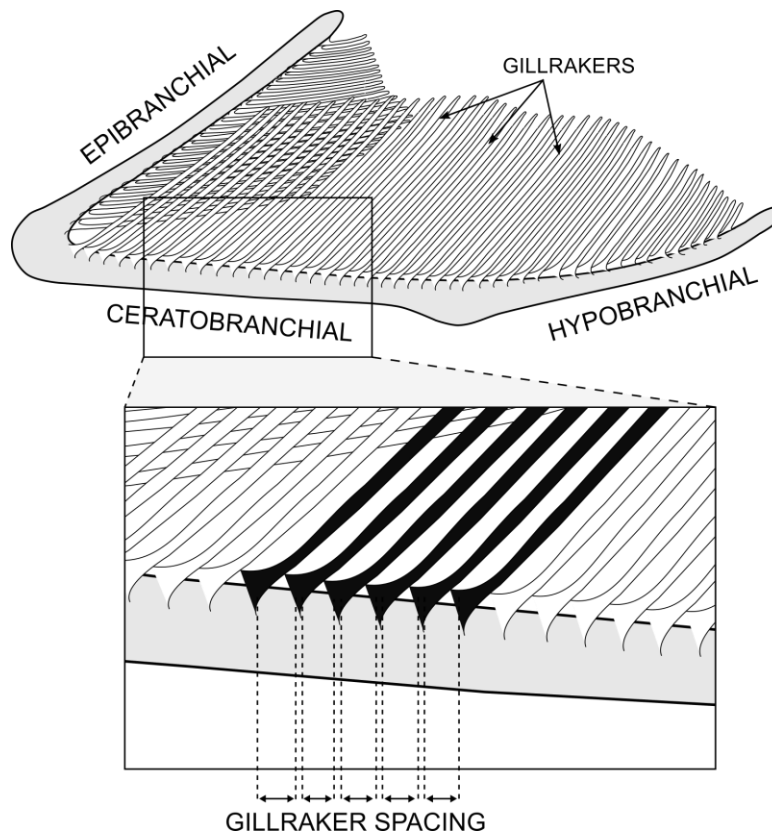


Figure 5.3. Drawing of the first left lateral gill arch of a small pelagic fish representing the specific branchial measurements used in this study.

Excised stomachs were blotted dry and then weighed to the nearest 0.0001 g. Their contents were emptied into a petri dish containing 20 ml of Milli-Q water (Millipore), and empty stomachs were again blotted dry and weighed to provide information on the wet weight of stomach contents. This was then converted to dry weight using a ratio of five to one (Yamaguchi & Ikeda, 2000). Stomach contents were examined under a microscope and large prey items were identified to the lowest taxonomic level possible, and then grouped into the following 24 taxonomic groups: Amphipoda, Brachiopoda, Decapoda, Diphyidae, Echinodermata, Fish eggs, Tintinnids, Euphausiids, Ostracods, Dinoflagellates, Diatoms, which were further split into *Coscinodiscus*, *Chaetoceros*, *Skeletonema*, *Stephanopyxis*, *Thalassiosira*, *Thalliacea* and *Pseudo-nitzschia*, and Copepods, which were further split into Calanoid, Cyclopoid, Harpacticoid, Poecilostomatoid, Nauplii, Copepod eggs and Unidentified copepods. Each prey item was then measured (total length [TL], prosome width or width [W] and prosome length [L], where applicable and all measurements in μm). The dry weight (μg) and carbon content (μg) were estimated using prey-taxon specific length – weight and

weight - carbon content regressions (Table 5.1). These identified prey items were removed from the sample and the remaining unidentified stomach contents were then transferred into a 20ml sedimentation chamber. These were allowed to settle over night before implementing the Utermöhl method as described by Hasle (1978) to identify smaller phytoplankton and estimate their total abundance in the sample.

Frozen muscle tissue samples were thawed and then oven dried at 60 °C for 24 – 48 hours. Following desiccation, the muscle samples were homogenised into a fine powder using a pestle and mortar. Subsample aliquots of approximately 400 µg were weighed into tin cups on a microbalance accurate to 1 µg. Samples were then combusted in a Flash elemental analyser 1112 (Thermo Finnigan, Bremen, Germany) and the gases were directed to a Delta V Plus isotope-ratio mass spectrometer via a ConFlo IV gas control unit (Thermo Scientific, Bremen, Germany). As lipids can cause a depletion in ¹³C, the lipid normalisation equation of Post et al. (2007) for aquatic animals was used when the C:N ratio of individual samples was > 3.5. This was performed to standardise methods between studies to enable comparison.

Fatty acid analyses were not performed on pre-recruit and juvenile samples for two reasons, (1) samples were obtained from the DFFE hydroacoustic surveys and frozen onboard at -20°C, not -80°C which is standard protocol for fatty acid analysis, and (2) there was limited funding.

5.2.2. Statistical Analyses

All statistics in this study were performed on the statistical platform R Version 3.5.1 (R Core Team, 2018) using a significance threshold of $p < 0.05$.

5.2.2.1. Relative Gut Length and Pyloric Caeca

Relative gut length was calculated as *Gut Length/Caudal Length*, and then modelled using a general linear model (GLM) with *Species* and *Caudal Length* as initial covariates. Model simplification was performed using the F-test and post model residuals were analysed to check that the assumptions of normality and homoscedasticity were satisfied.

The change in number of pyloric caeca was explored using a GLM applied to the semi-log transformed data, using *Species* and *Caudal Length* as explanatory variables to investigate interspecific differences. Model simplification was performed using the F-test and model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

5.2.2.2. *Gape Size*

Gape was analysed to look for both ontogenetic developments and interspecific differences using GLMs on the log-log transformed data. The initial model included *Species* and *Caudal Length* as explanatory variables. Model simplification was performed using the F-test and model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

5.2.2.3. *Branchial Basket Morphology*

Branchial basket morphology was analysed between the three species of varying size using multivariate GLMs to test for significant differences in total number of gillrakers, gill arch length and gillraker spacing. For both gill arch length and gillraker spacing, data were log-transformed prior to analysis to normalise residuals. The GLM had the following form;

$$B_{dfs} = e^{(\beta_0 + \beta_1 \times \log_e(CL)_{fs} + \beta_2 \times Species_f + \log_e(CL)_{fs} \times Species_f + \epsilon_{dfs})} \quad (1)$$

whereby B_{dfs} is the dependent variable d of the f^{th} fish of the s^{th} species, β_0 is the intercept value, β_1 is the level of influence that $\log_e(CL)_{fs}$ has on the dependent variable d , $\log_e(CL)_{fs}$ is the log-transformed caudal length (mm) of the f^{th} fish, β_2 is the level of influence that $Species_f$ has on the dependent variable d , $Species_f$ is the parameter describing the influence that each species has on each dependent variable d , $\log_e(CL)_{fs} \times Species_f$ is the interaction term and ϵ_{dfs} are the residuals that are normally distributed with equal variance. The relationship of total number of gillrakers to CL follows an exponential function, as corroborated by Gibson (1988) and Costalago et al. (2014). Therefore, the GLM fitted to the total number of gillrakers data has the following form;

$$B_{dfs} = \beta_0 + \beta_1 \times \log_e(CL)_{fs} + \beta_2 \times Species_f + \log_e(CL)_{fs} \times Species_f + \varepsilon_{dfs} \quad (2)$$

Model simplification was performed using the F-test and model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

5.2.2.4. Stomach Content Analysis

Shifts in diet during the pre-recruit and juveniles ontogeny were investigated by fitting 99% and 1% quantile regressions to prey size (μm) and caudal length (mm), to determine maximum and minimum prey size, respectively (Scharf et al., 1998).

The dietary composition was described by using three prey indices outlined by Hyslop (1980); the percentage number of prey item p ($\%N_p$), the percentage contribution to dietary carbon of prey item p ($\%CC_p$) and the frequency of occurrence of prey item p ($\%F_p$), calculated in the following manner;

$$\%N_p = \frac{\text{total number of prey item } p}{\text{total number of all prey items}} \times 100 \quad (3)$$

$$\%CC_p = \frac{\text{total contribution to dietary carbon of prey item } p}{\text{total contribution to dietary carbon of all prey items}} \times 100 \quad (4)$$

$$\%F_p = \frac{\text{frequency of prey item } p \text{ found in stomachs}}{\text{Total number of stomachs containng food items}} \times 100 \quad (5)$$

These three indices were then subsequently combined to calculate the indices of relative importance (IRI) for each individual prey item p (Pinkas et al., 1971; Cortés, 1997) using the following equation;

$$IRI_p = (\%N_p + \%CC_p) \times \%F_p \quad (6)$$

The IRI_p was then totalled for all prey items p for each species of fish f , and then expressed as a percentage, so that comparisons between f and p were possible.

$$\%IRI_{pf} = \frac{IRI_p \times 100}{\sum_1^n IRI_p} \quad (7)$$

where n is the total number of prey categories found in the sample of stomachs.

Fish were grouped into 5 mm length-bins so that the diet of the three species could be analysed during their ontogeny. Prey were categorised in two ways; firstly, by taxonomy and secondly by size (hereafter referred to as prey-species and prey-size datasets respectively), with sizes grouped into 200 μ m bins. The contribution to dietary carbon (%) for both prey-species and prey-size categories were calculated per 5 mm length-bin of fish, following the same equation as (4). However, prey item refers to either prey-species or prey-size category.

5.2.2.5. *Stable Isotope Analysis*

Stable isotope metrics including $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ range, and standard ellipse area described by Layman et al. (2007) were calculated using methods outlined by Jackson et al. (2011). Inferring information from isotopic indices can be biased by sample sizes, therefore using a Bayesian approach minimises sensitivities to biases corresponding to small sample sizes. The *SIBER* R package was used (Jackson & Parnell, 2023).

To explore the relationship between the isotopic signatures and caudal length, GLMs were implemented with additional independent variables. Both models ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) initially included the following independent variables; *log(Caudal Length)* (mm), *Distance to Shore* (km), *Location* (west or south coast) and *Species*. Significant independent variables were determined by F-tests. The final GLM model for $\delta^{15}\text{N}$ contained only one of the original independent variables, namely *Species*, whereas the final GLM model for $\delta^{13}\text{C}$ contained *log(Caudal Length)* and *Species* as significant independent variables. Model residuals were analysed to ensure that the assumptions of normality and homoscedasticity had been satisfied.

5.3. *Results*

5.3.1. *Relative Gut Length and Pyloric Caeca*

The model for relative gut length that contained *Species*, *Caudal length* and their interaction term as explanatory variables was significant ($F_{(5,115)} = 83.52$, $p\text{-value} < 0.001$). Sardine have a significantly larger relative gut length compared to both anchovy and round herring (Figure 5.4), and round herring had the smallest relative gut length for the studied size classes. The final pyloric caeca model, that contained *Species*, *Caudal Length* and their interaction term as explanatory variables, was also significant ($F_{(5,99)} = 304.1$, $p\text{-value} < 0.001$). There was a significant difference in pyloric counts between the three small pelagic fish, being lowest in anchovy, followed by sardine and then substantially higher in round herring (Figure 5.4).

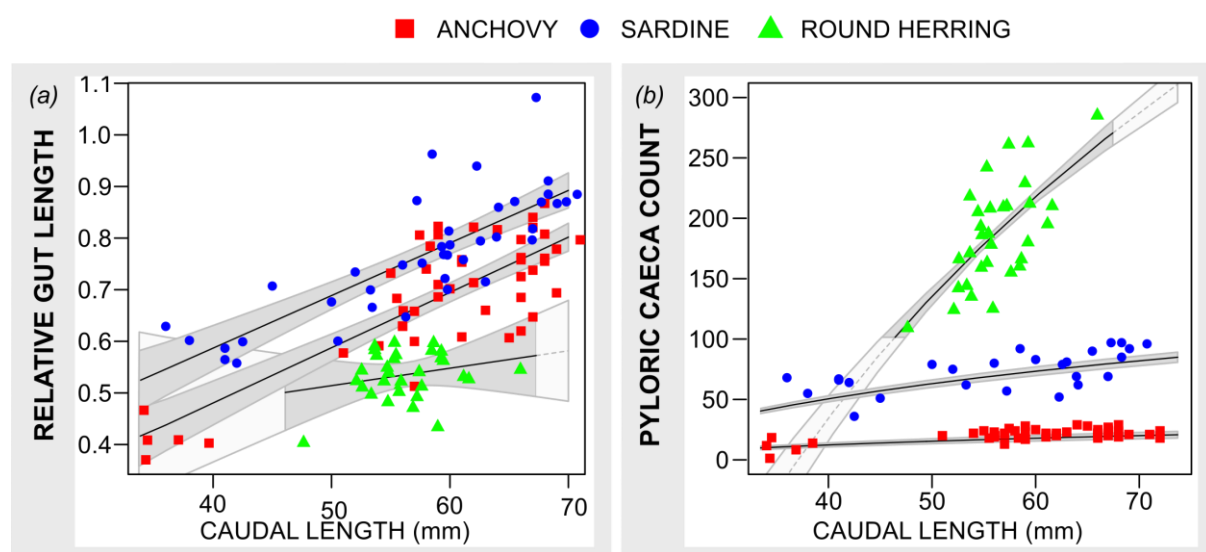


Figure 5.4. The relative gut length and pyloric caeca count for anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi*, representing (a) the pylori caeca count against caudal length (mm), and (b) the relative gut length against caudal length (mm) for each species. The symbols indicate observations, and the lines are the linear model outputs, with 95% confidence intervals shown in grey shading.

5.3.2. Gape Size

The final gape size model contained *Species*, *Caudal Length* and their interaction term and was significant ($F_{(5,180)} = 449.5$, $p\text{-value} < 0.001$). The gape size of anchovy was significantly larger and clearly differentiated from both sardine and round herring (Figure 5.5). Although round herring have a slightly larger gape for the studied size

classes compared to sardine, the gape size is less differentiated between the two species and has significantly more overlap than either with anchovy.

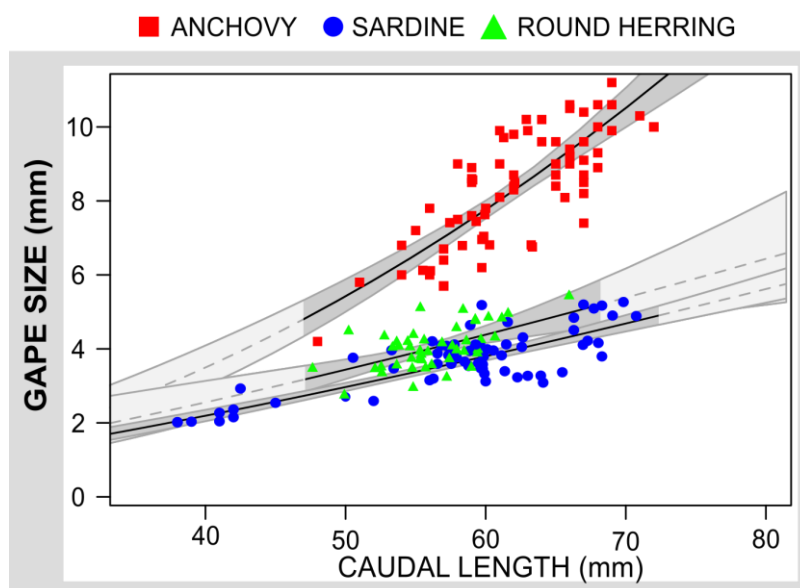


Figure 5.5. Gape size for anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi*. Symbols indicate observations and the lines represent the GLM model outputs with 95% confidence intervals in grey shading.

5.3.3. Branchial Basket Morphology

Branchial baskets were measured from specimens ranging between 37 – 72 mm for anchovy; 36 – 70 mm for sardine; and 53 – 62 mm for round herring. All three dependent variables, gill arch length ($F_{(5, 171)} = 913.2, p\text{-value} < 0.001$), total gillrakers ($F_{(5, 171)} = 89.0, p\text{-value} < 0.001$) and gillraker spacing ($F_{(5, 171)} = 510.6, p\text{-value} < 0.001$) were significantly correlated with caudal length (Table 5.1). *Species* also had a significant influence on all three of the dependent variables, and together these explained a large amount of the variation seen in the data, with R^2 values of 0.96, 0.72 and 0.94 for the gill arch, total gillraker and gillraker spacing models, respectively (Table 5.1). Gill arch length increases with caudal length for all species but there is a discernible difference between the three species, with the longest gill arch for anchovy and then shorter arches for round herring and then sardine (Figure 5.6). The number of gillrakers increased with caudal length for all three species. Larger sardine had clearly more gillrakers compared to anchovy and round herring, however there was an overlap between anchovy and sardine

for smaller size classes (36 – 45 mm, Figure 5.6). Anchovy had more gillrakers compared to round herring, but there was a high degree of overlap. These differences resulted in clear differences in gillraker spacing between the three species. Anchovy had the largest gillraker spacing followed by round herring, and then sardine (Figure 5.6).

Table 5.1. Results from the multivariate general linear models for branchial basket characteristics, displaying the statistics for both the response and explanatory variables for pre-recruit anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi*, obtained from the west and south coast of South Africa. The results of Wilks and Pillai multivariate statistical tests for the explanatory variables are also shown.

Model variable	Test statistic	Value	Effect df	Error df	Adjusted R ²	<i>p</i> -value
<i>ln</i> (gill-arch length)	<i>F</i>	913.2	5	171	0.9628	***
total gillrakers	<i>F</i>	89.0	5	171	0.7154	***
<i>ln</i> (gillraker spacing)	<i>F</i>	510.6	5	171	0.9354	***
Constant (β_0)	Wilks	0.00049	3	168		***
	Pillai	0.99951	3	168		***
Species	Wilks	0.01801	6	336		***
	Pillai	1.51526	6	338		***
<i>ln</i> (caudal length)	Wilks	0.08283	3	168		***
	Pillai	0.91717	3	168		***
<i>ln</i> (caudal length) *	Wilks	0.5731	6	336		***
Species	Pillai	0.42737	6	338		***

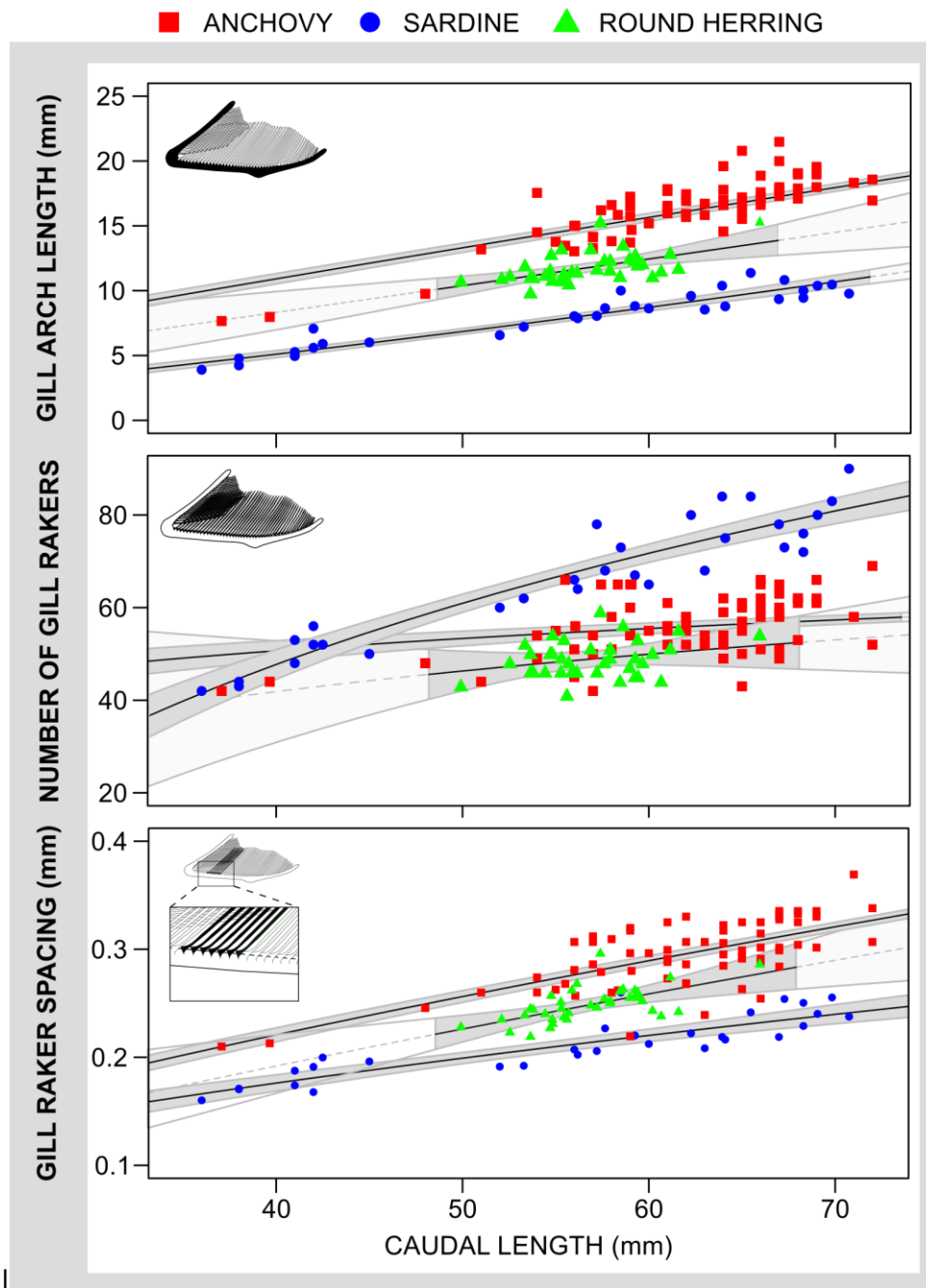


Figure 5.6. The relationships between the three branchial basket measurements (a) gill arch length (mm), (b) total number of gillrakers and (c) gillraker spacing (mm) and caudal length (mm) for pre-recruits and juveniles of anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*) and round herring (*Etrumeus whiteheadi*). The predicted relationships (lines) were calculated from the multivariate general linear model results, shaded areas depict the 95% confidence intervals, and unshaded areas depict the predicted 95% confidence intervals outside the range of the data

5.3.4. Stomach Content Analysis

A total of 219 stomachs were analysed (anchovy, 89; sardine: 70; round herring = 60), with 139 stomachs containing food (anchovy, 55; sardine: 44; round herring = 40). Feeding incidence was similar between all species with round herring slightly higher than the others (anchovy: 61.8%; sardine: 62.9 %; round herring: 66.7%).

Quantile regressions were fit to the stomach content data for the three species, to investigate the minimum and maximum prey size, and niche breadth of each species (Figure 5.7). The 99 % quantile regressions that represents the maximum prey width for both anchovy ($y = 138.3 \times \text{Caudal Length (mm)} - 6002.4 (\mu\text{m})$) and round herring ($y = 145.7 \times \text{Caudal Length (mm)} - 5656.8 (\mu\text{m})$) were significant ($p\text{-value} = 0.006$ and $p\text{-value} = 0.009$, respectively), and shows that both species increase their maximum prey width throughout their juvenile stage. The 99 % quantile regression fit for sardine was not significant, with the slope not differing from zero. The 1 % quantile fit for both anchovy and round herring were insignificant with their slopes not differing from zero ($p\text{-value} > 0.05$ for both), whereas the minimum quantile regression fit for sardine was significant ($y = -1.9 \times \text{Caudal Length (mm)} + 173.1 (\mu\text{m})$, $p\text{-value} = 0.009$), indicating that minimum prey width gets smaller during their juvenile ontogeny.

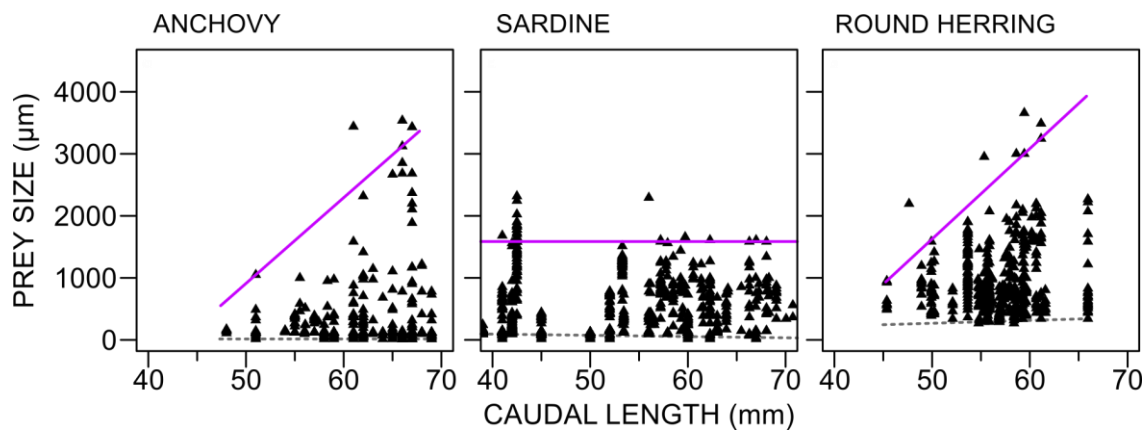


Figure 5.7. Scatter plots of the width of prey items (μm) against caudal length (mm) for anchovy, sardine and round herring pre-recruits and juveniles, with the 99% quantile regression line in purple representing the maximum and the 1% quantile regression in grey representing the minimum prey width.

Anchovy stomachs contained a total of 21 different prey groups. The most important in relation to IRI were diatoms (IRI % = 65.55 %), and of these the most important was *Skeletonema* (IRI % = 22.65 %). Copepods, excluding copepod eggs, were also important dietary components (IRI % = 19.1 %), with calanoids contributing the most to this (17.28 %). However, in terms of their contribution to dietary carbon, diatoms contributed considerably less (4.49 % CC), whereas larger crustaceans such as amphipods (33.75 % CC), euphausiids (19.32 % CC) and calanoids (33.06 % CC) contributed the majority to dietary carbon content. Sardine contained prey items from 18 prey groups with copepods being the most important prey (IRI % = 68.50 %) of which calanoids were the most dominant (IRI % = 33.48 %). Other important prey items were copepod eggs (IRI % = 24.52 %), ostracods (IRI % = 6.58%) and diatoms (IRI % = 22.61). The most abundant diatom found was *Skeletonema* which contributed 53.69 % of prey items numerically. Round herring had a less diverse diet than anchovy and sardine, with only 10 prey groups found in their stomachs. The most important prey were copepods (IRI % = 75.47 %), with calanoids (IRI % = 42.45 %) and poecilostomatoids (IRI % = 30.56 %) being the most important. In terms of contribution to dietary carbon, calanoid and poecilostomatoid copepods were again the most important, but larger crustaceans like amphipods (4.59 % CC) and euphausiids (11.90 % CC, Table 5.2) also contributed significantly.

In terms of anchovy ontogeny during their juvenile stage, there was a slight dietary shift with diatoms becoming less important with increasing fish size and calanoid and other larger crustaceans such as amphipods, decapods, euphausiids and ostracods becoming more important. Throughout the studied size classes copepods remained important dietary components (Figure 5.8a). Sardine also showed a slight dietary shift in terms of the species ingested, with harpacticoid copepods decreasing and poecilostomatoids increasing with fish size. Copepods and their eggs remained valuable dietary components in terms of their contribution to dietary carbon (Figure 5.8b), with the addition of ostracods, diphyidae and diatoms throughout their ontogeny. For round herring, the most profound change in prey species composition was the reduced ingestion of poecilostomatoid copepods and the increased ingestion of calanoids and euphausiids (Figure 5.8c). Copepods, specifically calanoids, were always extremely important, contributing on average 61.95 % CC. Round herring diet was often supplemented by other large crustaceans such as euphausiids, decapods and amphipods (Figure 5.8c).

Table 5.2. Prey index values by assigned prey category, taxon to species level are also names, for pre-recruit anchovy (A), sardine (S) and round herring (RH), caught off the west and south coasts of South Africa. % N – percentage number, % CC – percentage of contribution to dietary carbon, % F – frequency of occurrence, and % IRI – percentage of summed indices of relative importance. The highest values in each category are in bold, underlined text

	Prey category	Taxon	% N			% CC			% F			% IRI		
			A	S	RH	A	S	RH	A	S	RH	A	S	RH
FISH EGGS	Fish eggs	<i>Engraulis encrasicolus</i>	0.00	0.36	0.00	0.00	0.57	0.00	0.00	18.61	0.00	0.00	0.24	0.00
		<i>Sardinops sagax</i>	0.00	0.26	0.00	0.00	0.01	0.00	0.00	13.95	0.00	0.00	0.05	0.00
ZOOPLANKTON	Amphipod	<i>Themisto gaudichaudii</i>	0.02	0.00	0.18	33.75	0.00	4.59	7.69	0.00	2.50	6.41	0.00	0.12
	Brachiopoda	<i>Cladoceran</i>	0.01	0.01	7.00	0.02	0.10	3.15	3.85	4.65	37.50	0.01	0.01	3.44
	Decapod	<i>Lucifer sp., Brachyuran sp.</i>	0.00	0.00	8.44	0.00	0.00	2.10	0.00	0.00	47.50	0.00	0.00	4.53
	Diphyidae	<i>Dolilium sp.</i>	0.01	0.20	0.00	1.71	6.79	0.00	1.92	20.93	0.00	0.08	1.99	0.00
	Echinodermata	<i>Pluteus larva</i>	0.01	0.00	0.00	1.02	0.00	0.00	1.92	0.00	0.00	0.05	0.00	0.00
	Euphausiid	<i>Calytopes, furcillia</i>	0.01	0.02	1.98	19.32	0.01	11.90	3.85	4.65	20.00	1.83	0.01	2.51
	Ostracod		0.19	1.03	23.70	0.86	8.02	3.17	32.69	53.49	57.50	0.84	6.58	13.96
	Tintinnid		0.19	0.00	0.00	0.03	0.00	0.00	3.85	0.00	0.00	0.02	0.00	0.00
COPEPODS	Calanoid	<i>Pleuromamma abdominalis, Paracartia africana, Paracalanus sp., Paracalanus parvus, Acartia sp., Calanoides carinatus, C. natalis, Heterohabdus sp.</i>	0.05	0.41	19.75	33.06	41.92	61.95	21.15	58.14	57.50	17.28	33.48	42.45
	Cyclopoid	<i>Oithona similis, O. atlantica</i>	0.06	0.28	1.62	2.67	6.83	1.05	26.92	37.21	12.50	1.82	3.60	0.30
	Harpacticoid	<i>Microsetella sp.</i>	0.00	0.11	3.59	0.00	3.04	0.42	0.00	25.58	37.50	0.00	1.09	1.36
	Poecilostomatoid	<i>Oncaea mediterranea,, Oncaea sp., Corycaeus affinis, C. agilis and Corycaeus sp.</i>	0.01	0.36	31.24	0.34	7.97	9.76	5.77	51.16	82.50	0.05	5.80	30.56
	Nauplii		0.01	0.03	2.51	0.06	0.24	1.93	3.85	6.98	20.00	0.01	0.02	0.80
	Copepod egg		0.92	11.20	0.00	2.24	22.49	0.00	75.00	53.49	0.00	5.83	24.52	0.00
	Copepod	<i>Unidentified copepods</i>	0.01	0.00	0.00	0.04	0.00	0.00	1.92	0.00	0.00	0.01	0.00	0.00
DIATOMS	Coscinodiscus	<i>Coscinodiscus gigas</i>	19.74	11.69	0.00	2.81	1.28	0.00	23.08	20.93	0.00	12.84	3.69	0.00
	Chaetoceros	<i>Chaetoceros sp.</i>	8.05	5.11	0.00	0.80	0.39	0.00	21.15	18.61	0.00	4.61	1.39	0.00
	Skeletonema	<i>Skeletonema sp.</i>	27.93	53.69	0.00	0.16	0.24	0.00	32.69	18.61	0.00	22.65	13.65	0.00
	Stephanopyxis	<i>Stephanopyxis sp.</i>	0.13	0.00	0.00	0.02	0.00	0.00	1.92	0.00	0.00	0.01	0.00	0.00
	Thalassiosira	<i>Thalassiosira sp.</i>	3.09	7.95	0.00	0.02	0.04	0.00	13.46	18.61	0.00	1.03	2.02	0.00
	Thalliacea	<i>Thalliacea sp.</i>	0.01	0.00	0.00	0.19	0.00	0.00	1.92	0.00	0.00	0.01	0.00	0.00
	Pseudo-nitzschia	<i>Pseudo-nitzschia sp.</i>	39.16	7.27	0.00	0.49	0.07	0.00	25.00	18.61	0.00	24.44	1.86	0.00
DINOFLAG-ELLATE	Dinoflagellate	<i>Protoperidinium sp., Ceratium sp.</i>	0.44	0.03	0.00	0.40	0.40	0.00	9.62	6.98	0.00	0.20	0.01	0.00

There was a clear dietary progression in prey size for anchovy (Figure 5.9a), with larger prey items becoming more important for larger fish. Items < 800 μm became less important to their diet, accounting for 4 % CC and 29 % CC in the two larger size classes (65 – 70 and 70 – 75 mm, respectively). The largest prey ingested by anchovy was 6700 μm . For sardine, there was no clear progression in size classes of prey ingested (Figure 5.9b), with both smaller and larger fish ingesting prey of > 1000 μm . The maximum size of prey ingested by sardine was 1610 μm , but on average 60 % of their dietary carbon was obtained from prey < 800 μm throughout their ontogeny. Round herring showed an ontogenetic increase in the size of dietary components. Smaller components (< 800 μm) occurred in consistently small quantities, ranging between 3 % CC and 20 % CC between the size classes. Larger prey components became increasingly more important, with prey items larger than 2000 μm contributing only 12 % CC in the smaller size class compared to 87 % CC in the largest size class (Figure 5.9c).

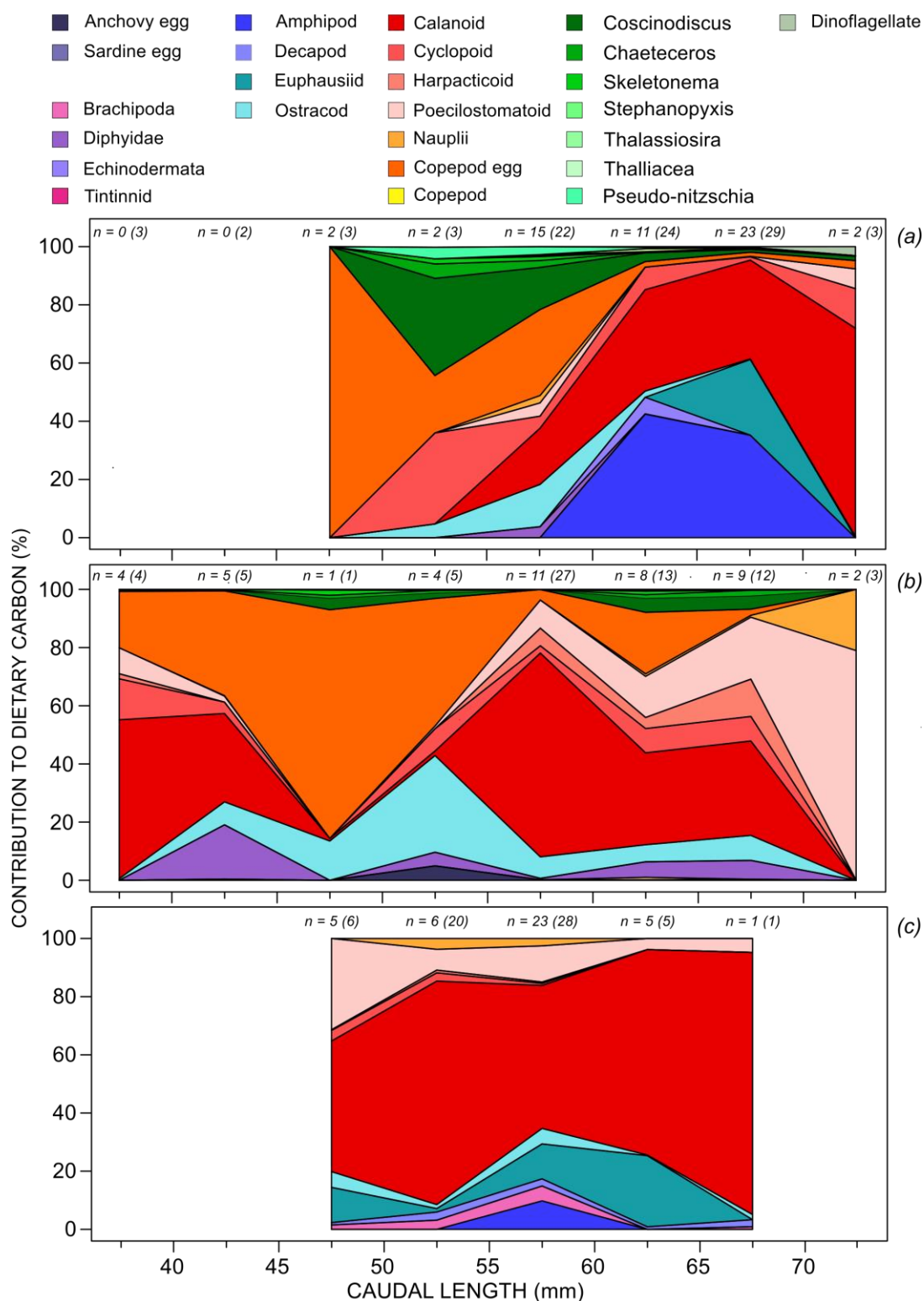


Figure 5.8. The contribution to dietary carbon (%) of each prey groups averaged for 5 mm caudal length bins of pre-recruits of (a) anchovy, (b) sardine and (c) round herring. Italic numbers above each plot represents the number of full stomachs, numbers in parentheses represents empty stomachs.

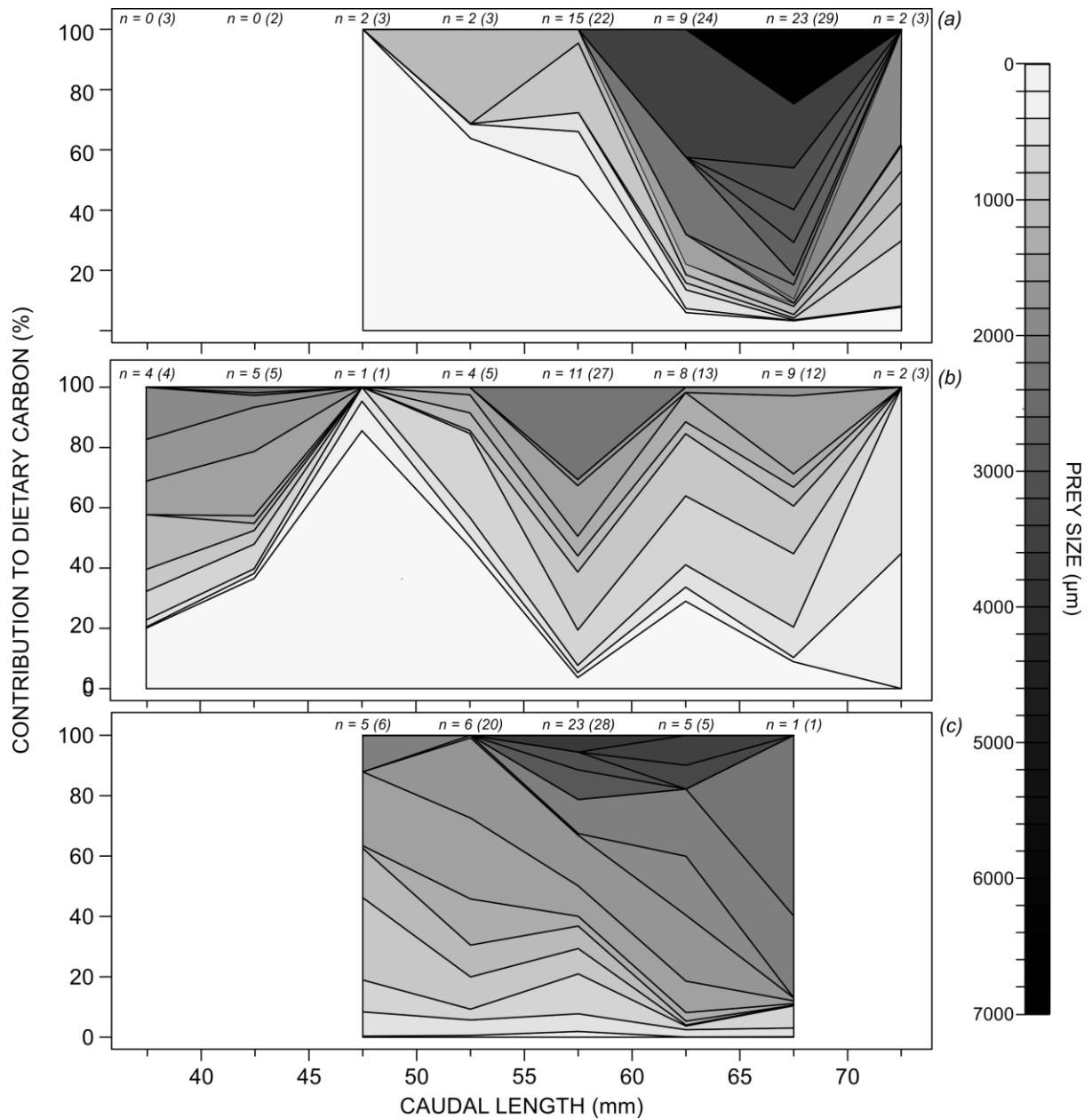


Figure 5.9. The contribution to dietary carbon (%) of each prey-size category (200 μm size bins) averaged for 5 mm caudal length bins of pre-recruits of (a) anchovy, (b) sardine and (c) round herring. Italic numbers above each plot represents the number of full stomachs, numbers in parentheses represents empty stomachs.

5.3.5. Stable Isotope Analysis

As seen in the isotopic biplot in Figure 5.10, the three species occupy mostly distinct isotopic niche spaces. There was a clear enrichment of ^{15}N from sardine to anchovy to round herring (Table 5.3), as well as an enrichment of ^{13}C in the reverse order. Furthermore, there was a difference in standard ellipse areas (SEA, Table 5.3) between the three species, with sardine having the largest, then anchovy and then round herring. Lastly, there was an overlap in the standard ellipses for sardine and anchovy, whilst that for round herring was completely distinct.

Table 5.3. Stable isotope indices calculated for pre-recruit and juvenile anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi* from the west and south coasts of South Africa, showing the mean (‰), range (‰) and SEA (SEA was corrected for small sample size bias).

Isotope Indices	Pre-recruits & Juveniles		
	Anchovy	Sardine	Round herring
Mean $\delta^{15}\text{N}$ ($\pm$ SD ‰)	12.074 (0.220)	11.235 (0.338)	12.901 (0.215)
Mean $\delta^{13}\text{C}$ ($\pm$ SD ‰)	-16.881 (0.432)	-16.458 (0.467)	-18.517 (0.240)
Range $\delta^{15}\text{N}$ (‰)	0.67	1.12	0.86
Range $\delta^{13}\text{C}$ (‰)	1.87	1.53	0.85
SEA	0.316	0.506	0.168

The $\delta^{15}\text{N}$ GLM was significant ($F = 204.8$, $df_1 = 2$, $df_2 = 56$, $p < 0.001$) with just one explanatory variable (*Species*) accounting for 87.54 % of the variation seen in the data (Table 5.4). There was a significant enrichment in ^{15}N from sardine to anchovy to round herring (Figure 5.11a).

The $\delta^{13}\text{C}$ GLM was significant ($F = 88.26$, $df_1 = 5$, $df_2 = 53$, $p < 0.001$) with the two explanatory variables (*Caudal Length* and *Species*) and their interaction term, accounting for 88.3 % of the variation seen in the data (Table 5.4). There was a small, but significant, enrichment of ^{13}C for both anchovy and round herring with increasing caudal length (mm). Contrastingly, there was a ^{13}C depletion with increasing caudal length in sardine (Figure 5.11b). There is a substantial overlap in ^{13}C between anchovy and sardine, whereas round herring has a more distinct signature.

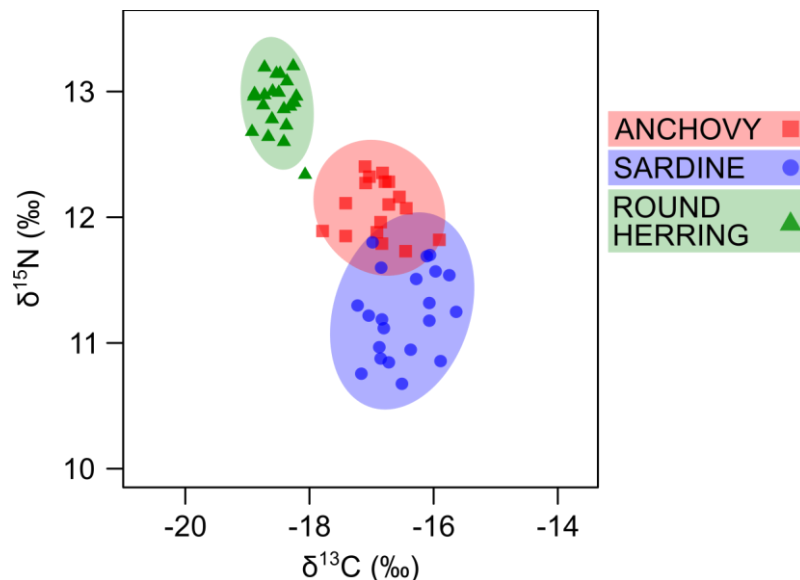


Figure 5.10. Isotopic biplot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*) and round herring (*Etrumeus whiteheadi*) caught in the southern Benguela.

Table 5.4. Results of the GLMs fitted for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with unique explanatory variables and showing the estimates of the parameters with their associated standard errors (Std. err), t -statistic and p -value.

$\delta^{15}\text{N}$	Estimate	Std. err	t -value	p -value
Intercept	12.07	0.07	184.64	< 0.001
Species (Round herring)	0.82	0.09	9.50	< 0.001
Species (Sardine)	-0.84	0.09	-9.64	< 0.001
$\delta^{13}\text{C}$				
Intercept	-20.81	4.04	-5.15	< 0.001
$\log(\text{Caudal Length [mm]})$	0.95	0.98	0.97	0.335
Species (Round herring)	-2.98	5.47	-0.54	0.589
Species (Sardine)	10.31	4.29	2.40	0.019
$\log(\text{Caudal Length [mm]})$	0.36	1.34	0.27	0.787
* Species (Round herring)				
$\log(\text{Caudal Length [mm]})$	-2.44	1.04	-2.35	0.023
* Species (Sardine)				

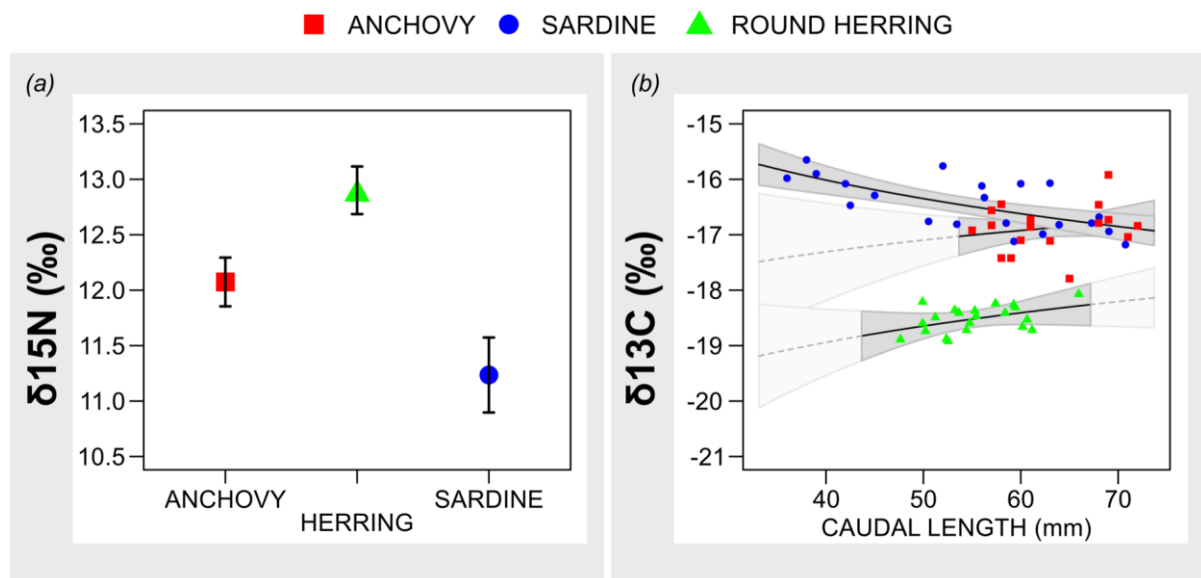


Figure 5.11. Shows (a) the mean $\delta^{15}\text{N}$ (‰) with standard deviation bars of each species, and (b) the effects of the independent variables (*Caudal Length* and *Species*) in the GLM used to explain the variation within the $\delta^{13}\text{C}$ (‰) data, shaded areas represent 95% confidence intervals and unshaded areas represent confidence intervals predicted outside of the data range.

5.4. Discussion

This study has described distinct ecological characteristics for the three species studied that likely facilitate trophic partitioning between the pre-recruit stages. Similar trends to their previously described adult trophic ecologies were observed, with a clearer trophic similarity between anchovy and sardine, than between either of these species and round herring.

5.4.1. Ecomorphological Characteristics

Ecomorphological characteristics can be a good indication of diet due to the convergent evolution and phenotypic expression of diet and morphology. Larger relative gut length has been correlated with herbivory in fish (Smith, 1989; Paugy, 1994; Elliott & Bellwood, 2003). Therefore, sardine displays the highest degree of herbivory among the three clupeoids, as evidenced by its larger relative gut length compared to anchovy and round herring. This observation aligns with previous literature, which consistently reports adult sardine as the most herbivorous, while round herring and anchovy exhibit little to no herbivory. (James, 1987; Wallace-Fincham, 1987; Plounevez & Champalbert, 2000; Mketsu, 2008; Raab et al., 2011). Furthermore, the results from the stomach contents in this study showed an absence of herbivory by round herring pre-recruits, but a substantial degree of herbivory by both anchovy and sardine.

Pyloric caeca exhibit a large variation between species in terms of their counts and size (Delariva & Neves, 2020; Moreira et al., 2020). Increased numbers of pyloric caeca have been used to indicate herbivory in certain fishes (Delariva & Neves, 2020). As the caeca primarily increase gut surface area for absorption and assimilation, increased numbers may (akin to relative gut length) indicate increased digestion of an autotrophic diet. Yet, in this study round herring had significantly more pyloric caeca compared to both anchovy and sardine, suggesting higher herbivory by the former. This contradicts inferences made from both the relative gut length and the stomach content analyses which indicated no herbivory. This discordance highlights the ambiguity around the function of pyloric caeca, and other studies have highlighted their importance regarding

the quantity of food (Reifel & Travill, 1978) and an increased protein content (O'Connell, 1981). This suggests that it would be advisable to perform a meta-analysis on the interdependence between diet and pyloric caeca in fishes to distinguish specific relationships before future use.

As seen in this study, there were notable differences in gape size among the three species, with anchovy having the largest gape, followed by round herring and sardine. This likely creates the possibility for size-based partitioning of diet through maximum prey dimensions. The gape size results imply that anchovy has the capacity to consume the largest prey items among the three pre-recruit clupeoids. This inference is supported by the stomach content analysis, where, despite round herring consuming the largest particles on average, the largest prey item was found in the stomach of an anchovy. A similar trend was also observed by Mketsu (2008), where round herring recruits in mixed-species shoals consumed the largest prey on average although anchovy and round herring had similar maximum prey sizes.

Differentiation of the gillraker spacings has been described as a source of resource partitioning between sympatric clupeoids. This study found clear distinctions in gillraker spacing between the three studied species; anchovy had the largest gillraker spacing followed by round herring and then sardine. Vorsatz et al. (2015) compared the branchial morphology of four southern African clupeoids east coast round herring *Etrumeus wongratani*, west coast round herring, sardine and anchovy, and reported no difference in gillraker spacing between anchovy and west coast round herring, which contrasts the results of this study. However, the branchial data of anchovy and sardine was from Namibian stocks (King & Macleod, 1976). There is a well-documented spatial variation in the phenotypic expression of branchial morphology in clupeoids. Idris et al. (2016) demonstrated this by describing significant differences in sardine gillraker spacing within South African and Namibian waters, with greatest differences observed between Namibian and South African sardine. Therefore, the comparison of Vorsatz et al. (2015) may not be representative of the actual association observed in South African clupeoids.

The difference between anchovy and round herring gillraker spacing contrast with the expected results predicted from trophic studies (van der Lingen & Miller, 2011) and global studies on branchial morphology (Tanaka et al., 2006). Tanaka et al. (2006) found that the local round herring (*Etrumeus teres*) had a greater gillraker spacing compared to the local anchovy (*Engraulis japonicus*) species. However, the gillraker spacing of round herring in this study was comparable to the results presented by Wallace-Fincham

(1987), suggesting that the results presented here are truly representative of the association between round herring and anchovy in the southern Benguela.

5.4.2. Ecological Analyses

Anchovy have the largest gillraker spacing and gape size of the three clupeoids, suggesting their capability to consume the largest prey items. Yet, this was not supported by either the stomach content or stable isotope analyses; round herring consumed the greatest average prey size and occupied the highest trophic level. Tanaka et al. (2006) compared the diet and branchial basket morphology of three planktivorous fish species from the East China Sea and suggested that feeding behaviour (i.e., filter- or particulate-feeding) was a larger determinant of diet than morphology was. Sardine are primarily filter-feeders that switch to particulate-feeding when prey items are $> 1200\ \mu\text{m}$ maximum dimension (van der Lingen, 1994). Conversely, anchovy are primarily particulate feeders that switch to filter-feeding when prey items are $< 700\ \mu\text{m}$ (James & Findlay, 1989). The ability to filter-feed for both species is available in high concentrations of smaller prey items. Unfortunately, little is known about the feeding behaviour in relation to particle size and concentration for *Etrumeus* species, however it is speculated that like other round herring species *E. whiteheadi* has the ability to do both. Based on the stomach content data, both sardine and anchovy consumed a significant number of small particles ($< 400\ \mu\text{m} = 5 - 94\ \text{CC } \%$, $< 400\ \mu\text{m} = 4 - 100\ \text{CC } \%$, respectively), which would likely indicate that they spent more time filter feeding. In contrast, round herring had a minimal proportion of their dietary carbon derived from prey items smaller than $400\ \mu\text{m}$ ($< 2\ \%$ for all studied size classes, Figure 5.9), which indicates very little filter-feeding. This difference in feeding behaviour likely compounds the distinctions in gillraker spacing and gape size between these species.

Round herring stomachs were numerically dominated by large calanoid copepods, contributing 66 % to their dietary carbon. This exclusive diet was also observed in adult round herring on the south coast of South Africa, where Wallace-Fincham (1987) observed entire gut contents made up solely of large calanoid copepods. A similar observation was reported by Mketsu (2008) looking at mixed shoals of juvenile clupeoids on South Africa's east coast. Similar to previous studies phytoplankton was completely absent from the stomachs of round herring pre-recruits examined here (Wallace-

Fincham, 1987; Mketsu, 2008). In terms of dietary progression there was no considerable change in species composition and calanoids were consistently the primary food source that contributed the most dietary carbon for round herring. This was supplemented by other crustaceans such as euphausiids and ostracods. Interestingly, despite no change in prey species composition, there was a clear increase in average prey size consumed. For the smaller fish, 90 % of their dietary carbon was sourced from prey smaller than 1600 μm . This progressively decreased in larger fish, resulting in fish greater than 60 mm only obtaining 20 % of their dietary carbon from prey less than 1600 μm . A similar trend was found by Wallace-Fincham (1987) for round herring between 50 mm and 229 mm caudal length.

The largest and most important contributor to the dietary carbon of anchovy was copepods, more specifically calanoids. This dependency on copepods has been seen in juvenile (Mketsu, 2008; Borme et al., 2009) and adult anchovy (James, 1987; Plounevez & Champalbert, 2000; Raab et al., 2011). Other larger crustaceans such as amphipods and euphausiids were rarer but contributed significantly to their dietary carbon, as found in previous studies (James, 1987; Plounevez & Champalbert, 2000). It is well known that in terms of dietary carbon, anchovy are zooplanktivorous, deriving the bulk from zooplankton (James, 1987; Louw et al., 1998; Plounevez & Champalbert, 2000; Mketsu, 2008; Raab et al., 2011). Yet, phytoplankton were found in both considerable quantities (e.g., *Skeletonema* species = 28 % N) and consistently between individuals (*Skeletonema* species = 33 % F). Therefore, despite their lack of contribution to dietary carbon (*Skeletonema* species = 0.16 % CC), they are important dietary components. For anchovy there is a slightly clearer pattern during their ontogeny, whereby copepod eggs and phytoplankton become less important as the fish get larger and are replaced by larger crustaceans such as calanoid copepods and amphipods. This is also represented clearly in the prey-size progression, where the size of prey increases with the size of the fish. Fish smaller than 60 mm obtained 70 % of their dietary carbon from prey smaller than 800 μm , where fish larger than 60 mm obtained 70 % of their dietary carbon from prey larger than 800 μm .

Likewise, phytoplankton played a significant and frequent role in the diet of pre-recruit sardine. The largest contributors were the large-celled diatoms such as *Coscinodiscus*, *Skeletonema* and *Thalassiosira* species, which are common in upwelling systems. Although numerically important, they contributed very little to overall to dietary carbon, as found in previous studies (van der Lingen, 2002). In accordance with

both local (Louw et al., 1998; van der Lingen, 2002) and global (Costalago et al., 2015) studies of sardine diet, crustacean eggs and ostracods were also important prey items in terms of contribution to dietary carbon. In terms of dietary progression there was not a significant change in the species composition of prey items for sardine. Copepods, mostly calanoids and poecilostomatoids, provided the majority of dietary carbon throughout most size classes. There were exceptions where a large amount of dietary carbon was sourced from copepod eggs and phytoplankton (45 – 50 mm), yet this size class was represented by one positive stomach, and therefore unlikely represents the entire diet of this ontogenetic stage. It does however provide interesting evidence of an individual that derived its entire dietary carbon from filter-feeding. There was an increase in the dietary carbon sourced from prey items < 1200 μm . For individuals less than 45 mm < 50% of their dietary carbon was obtained from items < 1200 μm , yet for individuals larger 45 mm > 70% of their dietary carbon was sourced from items < 1200 μm . This could suggest that smaller individuals are still developing the ability to successfully filter-feed.

In terms of diet, there was a degree of overlap between the three species, with some similarities in species and size composition. Sardine and anchovy were the most similar in terms of both species and size composition. Both species exploited small prey and phytoplankton implying a greater readiness to employ filter-feeding behaviour. A similar trend was observed both by Louw et al. (1998) and Mketsu (2008). With little exploitation of autotrophic components, round herring are further disassociated from anchovy and sardine despite greater similarities in their ecomorphological traits. This likely arises from their feeding behaviour. Inferring from the stomach content data, round herring are less prone to switching to filter-feeding compared to both anchovy and sardine.

Stomach content analysis provides a snapshot of the diet of an individual and often misses out small, delicate, and easily digestible food items. Stable isotope use facilitates analysis of the assimilated diet and a better estimate of trophic position. Larval and juvenile individuals exhibit a notably elevated metabolic rate in proportion to their body mass, particularly when compared to their later life history stages (Peck and Moyano, 2016). Consequently, the incorporation of dietary items into their tissues occurs at an accelerated pace. Sholto-Douglas (1992) conducted a study showing that the isotopic signature of sardine larvae experienced noticeable changes within 1-3 weeks under *ex vivo* conditions.

There was a high degree of distinction between the isotopic signatures of juveniles of the three species in this study. Firstly, there was an enrichment of ^{15}N from sardine to anchovy and then round herring, with a greater distinction observed in round herring. This implies that round herring occupy the highest trophic level (Post, 2002). A similar relationship is found in adults (van der Lingen & Miller, 2011). These results corroborate the stomach content analysis, with the highest similarity between anchovy and sardine—likely a result of the increased direct foraging of phytoplankton and smaller zooplankton.

Sardine had the largest standard ellipses area (Figure 5.10), which is indicative of increased trophic flexibility in comparison to both anchovy and round herring. This contrasts the stomach content data, whereby anchovy showed the largest niche breadth. This discrepancy could be attributable to the smaller and often missed prey groups, and also small sample sizes. Modern stomach analysis techniques using metabarcoding have shown the presence of fragile, soft bodied tunicates and protists in the stomachs of larval and adult sardine (Albaina et al., 2016; Hirai et al., 2017). It is likely that this observed increase in trophic flexibility implied through the $\delta^{15}\text{N}$ ratios is likely due to the increased breadth of the sardine's diet extending into smaller organisms that are not visible via microscopic gut content analyses.

There was a distinction in the $\delta^{13}\text{C}$ ratios, with round herring significantly ^{13}C depleted compared to its heterospecifics. There is a well described spatial variation in marine $\delta^{13}\text{C}$ ratios, with both offshore and cross-shore trends. This spatial trend has been corroborated around the South African coast showing a general offshore and cross-shore eastward depletion trend in ^{13}C (Hill et al., 2006, 2008a). Diatom- and benthic-based production is typically ^{13}C enriched, whereas pelagic phytoplankton, such as dinoflagellate-based is depleted (Fry & Wainright, 1991). Neither of these spatial distinctions were observed in the small pelagic pre-recruits in this study, as both location and distance to shore did not help explain any of the variation in the data. This significant depletion in the $\delta^{13}\text{C}$ ratio of round herring is likely indicative of the reduced dependency of direct-diatom consumption as seen in sardine and anchovy. Furthermore, medium to large calanoid copepods were the primary source of dietary carbon for round herring and studies have shown that local calanoid copepods can be ^{13}C depleted in comparison to autotrophic components of the food web (Mathiske, 2020).

This study includes samples from separate years and different localities, therefore potential spatio-temporal variance must be mentioned. There are clear temporal trends in environmental conditions in the southern Benguela. As the southern Benguela displays

strong seasonal trends in coastal upwelling, with peaks in austral summer (Lamont et al., 2018a), seasonality has been described as the dominant cause of variation in environmental conditions (Demarcq et al., 2007; Huggett et al., 2009). These seasonal trends are also reflected in the isotopic signatures of the suspended particle matter in South Africa (Holmes et al., 2002; Hill et al., 2008a). Despite, clear interannual trends in phytoplankton (Demarcq et al., 2007) there seems to be very little in terms of the secondary production (Huggett et al., 2009). Therefore, it was assumed that the seasonality component was the largest contributor to variation in secondary production. Samples for this study were collected in subsequent years (2018 and 2019), potentially introducing interannual variability, but all samples were taken during austral late spring/summer. There are spatial differences between the west and south coast both in terms of primary and secondary production (Huggett et al., 2009; Lamont et al., 2014) and in isotopic baselines (Hill et al., 2006; van der Lingen & Miller, 2014). These spatial differences may be manifested in the isotopic signatures of the samples in this study. To minimise this potential spatial effect, multiple samples were taken around the coast for each species with the objective of standardising the spatial variation. It is worth noting, that for the stable isotope analysis *Location* was initially included in the model but did not describe any of the variation in the data and was therefore removed. Hence this reported spatial variation was not evident in the data analysed in this study.

5.4.3. Conclusion

This study has shown a substantial degree of agreement between both ecomorphological and ecological analyses, providing a holistic depiction of the trophic ecology of the pre-recruit phase of these three species. Although the functional feeding traits explain a large amount of the variation seen in the diet between the species, it seems that the compounding effect of feeding behaviour provides potential answers for variances seen in the stomach content analysis. Despite sharing greater ecomorphological similarities with sardine, round herring is further trophically separated from sardine compared to anchovy. This distinction primarily results from round herring's lack of direct exploitation of autotrophic components. van der Lingen & Miller (2011) also observed a similar trophic separation in adults but were concerned with the higher degree of similarities between anchovy and sardine than round herring, due to the zooplanktivorous nature of both anchovy and round herring. Therefore, this

study proposes that the herbivorous and filter-feeding nature of anchovy is more important than previously thought despite the absence of phytoplankton in some studies.

Chapter 6

Implications of increasing life history resolution of small pelagics in a trophic model of the southern Benguela.

Abstract

Ecosystem models have been often implemented as strategic and scientific tools to advise on an ecosystem approach to fisheries management. Modellers attempt to quantify ecological interactions as accurately as possible, striving to replicate reality. Increasing complexity can introduce more uncertainty, but there is a growing emphasis on including species-specific details and temporal dynamics for improved modelling of vital life history phases. Therefore, this study aimed to further disaggregate the small pelagic functional groups of the southern Benguela into a finer representation of life history stages that included larvae and pre-recruits as additional stages to juveniles and adults. This development provided an opportunity to gauge whether increased resolution would provide new information on trophic transfer efficiencies and species interactions of pelagic fish-centred pathways. The developed model exhibited substantially more small pelagic fish centred trophic pathways that were previously grouped into plankton groups than the model without larvae/pre-recruits. There was an improvement in model fit of 14 out of the 19 functional group time series. In terms of overall model function there was no change in biomass or system variability, however, there was a significant change in the trophic level estimation of functional groups that had system wide ramifications. This study has shown that despite the relative insignificance of small pelagic larvae in terms of mass in the system, they still make an important contribution to the ecosystem dynamics. However, it seems that when disaggregating functional groups into life history stanzas, if the same increase in resolution is not reflected in their prey, then vital trophic relationships can be lost.

6.1. Introduction

The repercussions of extensive fishing in marine systems have become increasingly apparent, motivating the move from traditional single-species management towards an ecosystem-based approach (Pauly et al., 2002; Pikitch et al., 2004; Smith et al., 2011). With an emphasis on both ecosystem and target species health, ecosystem-based fishery management aims to replace conventional fishing targets such as maximum sustainable yield with holistic catch quotas, aiming to support a healthy ecosystem that ensures sustainable fishing. Modelling is a key tool in understanding the ecosystem dynamics under exploitation, that helps produce scientific and strategic advice for management (Plagányi et al., 2007; Smith et al., 2007, 2011).

A disputed topic is the sustainability of small pelagic fishing in eastern boundary upwelling systems (EBUS). Since the onset of industrial fishing, small pelagic fish have dominated the global catch, for example in 2018 23% was attributed to the small pelagic sector (FAO, 2020). Ecologically, they perform crucial intermediary roles, enforcing both regulatory top-down and bottom-up control (Cury et al., 2000), which is demonstrated through studies highlighting the dramatic population changes emulated in dependent species, such as sea birds (Crawford et al., 2011, 2018; Cury et al., 2011) and predatory fish (Muck, 1989; Parker et al., 2020). Consequently, how the commercial and ecological dynamics of these species' affects trophically dependent species is of particular curiosity.

There has been considerable attention directed at the use of EwE models in the southern Benguela (Shannon, 2000; Shannon et al., 2004, 2007, 2008, 2020; Watermeyer et al., 2008a; Smith et al., 2015), with many specifically focusing on the small pelagic fish centred pathways under varying scenarios of harvest control strategies (Shannon et al., 2000, 2007; Smith et al., 2015) and biomass scenarios (Shannon & Cury, 2003; Shannon et al., 2004). They will remain integral components of the modern fisheries management toolkit and will continue to be developed in the face of new developments and data.

There is a trade-off between realism and uncertainty in large ecosystem models. It is well known that one of the biggest issues with ecosystem models is that when increasing complexity through a higher resolution, one is at risk of introducing a higher degree of uncertainty in the output, reducing the reliability of conclusions (Plagányi & Butterworth, 2004; Heymans et al., 2016; Koehn et al., 2016). Despite this, models are increasing in size and complexity to include the essential ecosystem components (Table 6.1). The

realisation to at least separate small pelagics into distinct species was exclaimed by Koehn et al. (2016), stating that the roles and influences of key predator-prey relationships can be overlooked if these species are grouped together in small pelagic fish-centred ecosystems. Essington & Plagányi (2014) also highlighted the importance of including sufficient detail regarding the species of interest and, if possible, to include temporal dynamics that facilitate the modelling of critical periods during their life history. This alludes to the question whether ecosystem models would benefit from further disaggregation of small pelagic fishes.

Table 6.1. The number of functional groups included in a selection of Ecopath model case studies over periods of their development, where case studies were selected based on importance of small pelagics in the modelled ecosystems.

Model area	Functional groups per model												
	2000	2001	2002	2003	2004	2008	2009	2012	2016	2017	2018	2020	
Bay of Biscay		38 ¹								43 ²			
Southern Benguela				31 ³		32 ⁴						48 ⁵	
California Current					63 ⁶				83 ⁷				
Northern Humboldt						32 ⁸					41 ⁹		
Northern Benguela	22 ¹⁰						32 ¹¹		32 ¹²				
Baltic Sea				15 ¹³				22 ¹⁴					

¹Ainsworth et al. (2001), ²Moullec et al. (2017), ³Shannon et al. (2003), ⁴Shannon et al. (2008), ⁵Shannon et al. 2020, ⁶Field (2004), ⁷Koehn et al. (2016), ⁸Tam et al. (2008), ⁹Chiaverano et al. (2018), ¹⁰Heymans and Baird (2000), ¹¹Heymans et al. (2009), ¹²Heymans and Tomczak (2016), ¹³Harvey et al. (2003), ¹⁴Tomczak et al. (2012)

The application of multiple stanzas in an Ecopath model is beneficial when there are either trophic distinctions during the ontogeny of a species or discrete fishery interactions between life history stages. For example, sardine and anchovy in the most recent southern Benguela model were separated into recruits and adults so that the fishery interactions could be correctly modelled (Shannon et al., 2020). The rationale for disaggregating recruits further would predominantly be to (a) model the trophic dissimilarities observed between life history stages, and (b) to include additional trophic pathways of larval predators that have been overlooked or grouped into other functional groups. Development is most pronounced prior to metamorphosis and, as shown in

Chapters 3, 4 and 5, is reflected in their ecomorphology and trophic ecology. It appears that intraspecific competition is reduced through differences in prey-size composition during their ontogeny.

This Chapter aims to assess whether an increased resolution of small pelagic functional groups in an ecosystem model will provide new information on trophic transfer efficiencies and species interactions of pelagic fish-centred pathways. This will be performed by further disaggregating the small pelagic functional groups of the southern Benguela into a finer representation of life history stages via the inclusion of a larval stage. The information gained will provide future recommendations and advice for the benefit of including increased life history stanzas in future EwE models. This is necessary as information regarding early life stages is lacking and studies investigating these stages are laborious and time consuming, therefore the benefit should be ascertained prior to their conception.

6.2. Methods

6.2.1. Ecopath with Ecosim

Ecopath with Ecosim (EwE) is a tool that facilitates the quantitative parameterisation of an entire ecosystem (Polovina, 1984; Christensen & Pauly, 1992; Walters et al., 1997, 1999; Christensen & Walters, 2004). Functional groups are defined either by specific species or groups of species with similar life history traits. The model adheres to one core fundamental; that both the energy input and output of a functional group must balance (see Chapter 1 for more details). This study utilised the previously published EwE model of the southern Benguela (Shannon et al., 2020). The model encapsulates the southern Benguela stretching from the Orange River mouth on the west coast, to East London on the south east coast of South Africa. It captures the years between 1978 – 2015. The model has been repeatedly developed from its initial construction (Shannon et al., 2004, 2008, 2020), and now contains 48 living functional groups of which 26 are fish and 7 are top predators (Table 6.1). As mentioned previously, five species are represented by multiple stanzas: anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax*, horse mackerel *Trachurus capensis*, shallow-water Cape hake *Merluccius capensis* and deep-water Cape hake *Merluccius paradoxus*. Each species is represented as both adults and either juveniles or recruits (Shannon et al., 2020).

Shannon's et al. (2020) model (hereafter referred to as the original model) was fit implementing four factors to improve the model fit to the time series. Firstly, a forcing function was applied to the large-celled phytoplankton to emulate the upwelling processes observed in the southern Benguela (named *upwell*) as derived from Lamont et al. (2018a). Secondly, a forcing function was applied to the relative availability of both juvenile and adult sardine east or west of Cape Agulhas to their predators (named *FF on sardine*). Through stepwise fitting, the 40 most vulnerable predator-prey interactions were estimated (named *40vs*) and then lastly, an environmental anomaly was fitted to the small-celled phytoplankton group including 18 spline points. The model was fit to the same suite of time series fitted in the original model (for more details see Shannon et al., 2020), and all-time series used in the model fitting had equal weightings.

Table 6.2. Age (months) and length (mm) of the different life history stages represented for the three small pelagic species in the new disaggregated model.

	Life history stage (months [length mm])			
Species	Larvae	Pre-recruit	Recruit	Adult
Anchovy	0 [0]	2 [35]	4.5 [65]	12[110]
Sardine	0 [0]	2 [35]	3.7 [65]	12[120]
West coast round herring			1.6 [20]	12.7 [140]

6.2.2. Functional Group Disaggregation

In the original model, the larval stages of fish are incorporated into the macrozooplankton (2 – 20 mm) functional group, and therefore species-specific predator-fish larvae dynamics are currently grouped with zooplankton. Following the development of increased dietary information regarding the early life stages of anchovy and sardine in the Benguela, the life stages of these species were separated. For anchovy and sardine, they were split into the following groups: larvae, pre-recruits, recruits, and adults (Table 6.2). For round herring, they were simply split into juveniles and adults, due to a lack of dietary information regarding early life stages (Table 6.2). Recruits less than 20 mm in length were grouped with the zooplankton. It is pertinent to note that diets of stages that are split, i.e., anchovy and sardine recruits, and round herring adults, will be altered as they will no longer include the diets of smaller life history stages.

Diet for each stage was deduced from the results of Chapters 4 and 5. The dietary results from these Chapters were re-categorised into the specific life history stages as outlined in Table 6.2. Prey items were then categorised into the following five functional groups as determined by the original Ecopath model: small phytoplankton ($< 10 \mu\text{m}$), large phytoplankton ($>10 \mu\text{m}$), microzooplankton ($2 - 200 \mu\text{m}$), mesozooplankton ($200 - 2000 \mu\text{m}$) and macrozooplankton ($2 - 20 \text{mm}$). The diet for each life history stage was then calculated using the Dirichlet distribution and maximum likelihood estimation (Ainsworth et al., 2010; Masi et al., 2014). The benefit of using this method is that firstly it refrains from over estimation of the proportion of rare dietary items and secondly it provides an estimate of error of each dietary proportion (Ainsworth et al., 2010).

The new predator-prey interactions for the new life history stanzas were categorised from literature, previous studies, and expert input. Further rationale and information for these interactions can be found in Table 6.3.

6.2.3. Model Comparisons

For the purpose of this study, the same model fitting procedure described for the original model was used for the revised model in order to standardise the fitting procedure and allowing a direct comparison. However, due to new trophic linkages and functional groups in the disaggregated model (hereafter referred to as the disaggregated model), a search was performed to estimate the vulnerability parameters of the 40 most sensitive predator-prey interactions in the disaggregated model. Searching and fitting vulnerabilities to predator-prey interactions is the process of adjusting these parameters to align model predictions with observed ecological data. Vulnerability represents the susceptibility of prey species to predation, for example a high vulnerability occurs when increased predator biomass leads to a substantial rise in predation mortality for a specific prey species, whereas a low vulnerability corresponds to a predator being strongly constrained by prey availability. Following this, the environmental anomaly applied to the small-celled phytoplankton was re-fit to the new predator-prey vulnerabilities. The 1978 model from Shannon et al., (2020) corresponds to the initial conditions of both models.

Table 6.3. Justification of the new predator-prey interactions involving larval small pelagic fish, included in the new disaggregated model.

Species		Justification	Source
Predator	Prey		
Gelatinous zooplankton	Anchovy/sardine larvae	Clupeid larvae are commonly found in the stomachs of jellyfish globally, with up to 45% of their diet being contributed to fish larvae.	Möller (1980); Purcell et al., (1994); Purcell et al., (2014); Tilves et al., (2016)
Anchovy adults	Anchovy/sardine larvae	<i>Engraulis</i> spp. have been shown to consume fish larvae through in vivo experiments	Folkvordi and Hunter, (1986); Takasuka et al., (2007)
Round herring adults	Anchovy/sardine larvae	<i>Etrumeus</i> spp. have been shown to consume other clupeoid larvae.	Takasuka et al., (2007)
Round herring adults	Anchovy/sardine pre-recruits	Anchovy pre-recruits have been observed in the stomach of Redeye round herring stomachs (van der Lingen pers. comms.). It is thought that this is why they are at a higher trophic level than anchovy.	van der Lingen (pers. comms.)
Horse mackerel adults	Anchovy/sardine larvae	Global <i>Trachurus</i> spp. have been found to have up to 7 local clupeoid larvae in their stomachs.	Takasuka et al., (2007)
Horse mackerel adults	Anchovy/sardine pre-recruits	South African <i>Trachurus</i> ssp. commonly consumed clupeoid recruits. 10 % (in terms of frequency) of their diet was made up by pre-recruits. Furthermore, there is a considerable overlap in their spatial distribution.	Pillar and Barange (1998); Le Roux (2013)
Chub mackerel	Anchovy/sardine larvae	Global <i>Scomber</i> spp. are known to feed on local clupeoid larvae. This has been found in both stomach content analysis and lab studies.	Folkvordi and Hunter, (1986); Robert et al., (2010)
Chub mackerel	Anchovy/sardine pre-recruits & Round herring juveniles	The stomach content of chub mackerel in the Canary Islands comprised of 17% of sardine pre-recruits. Length frequency of consumed fish covered pre-recruits and juveniles.	Castro (1993)
Shallow water hake (small & large)	Anchovy pre-recruits	For small hake - the size of anchovy in the guts doesn't change between small and large hake. Pre-recruits for small and large hake are around 5 % by frequency	Pillar and Wilkinson (1995)
Shallow water hake (small & large)	Round herring juveniles	There is a similar trend for round herring- although there is more of a positive relationship between prey and predator size. Hake smaller than 30 cm only consume herring recruits (smaller than 131)	Pillar and Wilkinson (1995)
Snoek	Anchovy/sardine larvae	It is likely that there is consumption of larvae by snoek- their nursery ground where juveniles are often found are in St Helena Bay and Cape Agulhas. High degree of overlap with larvae spatial distribution. Anchovy and sardine form a large part of their diet. Although life history stages of them are not disclosed.	Griffiths (2002); McQueen, (2002)

As the models are fitted to the same set of time series data ($n = 73$), the predicted fits obtained from the Ecosim outputs provide an objective criterion that facilitates direct comparison. Ecosim calculates the fit of the model output for the functional groups compared to the time series data via residual sum of squares (RSS). Therefore, changes in the RSS between both models can be directly assessed to elucidate a negative or positive change in fit. Secondly, the ability for either model to correctly predict the observed data was assessed by fitting linear models to the observed and predicted biomass data for each functional group – time series pairing. The R^2 value from the regression was also used as an assessment of model fit improvement. The differences in both RSS and R^2 between the two models were assessed to conclude whether the increased life history resolution in the disaggregated model helped to increase the fit of the predicted output to the time-series data.

Although both models were fit to 73 different time series, this study is interested in the direct effects of including additional life history stanzas, so the model fits were only explored for the small pelagics and their predators.

6.2.4. Overall Model Function

The PREBAL diagnostic criteria outlined by Link (2010) and Heymans et al. (2016) was applied. This technique is applied to check that model assumptions have been satisfied. The criteria used are founded on ecological and fisheries principles, for instance biomass estimates should not span 5-7 orders of magnitude, see Link (2010) for more criteria.

Several indices were chosen from those proposed in the IndiSeas project (Shin et al., 2010). These indices were compared between the models to assess whether the disaggregation of small pelagic fishes changes the overall output of the disaggregated model. The indices used were (a) *Total biomass of surveyed species*, (b) *Trophic Level (TL) of landings*, (c) *proportion of predatory fish*, (d) *mean lifespan*, (e) *1/CV of total biomass*, (f) *1/(Landings/Biomass)* and (g) *mean length of fish*. Total biomass reflects the overall production capacity and resource potential of the system (Bundy et al., 2010). $1/(\text{Landings}/\text{Biomass})$ is an index that highlights the resource potential dedicated to fisheries (Shin et al., 2010). Trophic Level of landings represents the trophic level of the whole catch (Shannon et al., 2014a). Mean length of fish in the community is an index that

reflects the direct effects of fishing on the community (Shin et al., 2005). Proportion of predators in the system is a measure of diversity and shows the effects of fishing in the system (Shin et al., 2010). Mean lifespan this index is related to the stability of the system- the smaller the index the less stable, as individuals with shorter life spans are more directly affected by environmental perturbations (Shin et al., 2010). $1/CV$ of total biomass is the measure for stability of the ecosystem, as it is an index for the degree of interannual and decadal fluctuations in biomass in the system (Fulton et al., 2004). A decrease means a reduction in stability. For all indices except $1/CV$ of total biomass, a student t-test was applied to compare the means of each indicator between the original and disaggregated model.

6.3. Results

6.3.1. The Balanced Model

The new dietary parameters for the disaggregated life history stages of the small pelagics and the small pelagic predators can be found in Table 6.4 and Supplementary Table S.2 respectively. The new disaggregated model parameters are shown in Table 6.5, all other initial inputted parameters remained the same as in the original model of Shannon et al. (2020). In accordance with the PREBAL diagnostic criteria established by Link (2010) and Heymans et al. (2016), the disaggregated model adhered to general ecological principles (Supplementary Figure S.1). Consequently, the model was ecologically and thermodynamically balanced in accordance with the logical constraints as outlined by Darwall et al. (2010).

The environmental anomaly that was fitted to the small-celled phytoplankton group deviated slightly from the environmental anomaly fitted in the original model (Figure 6.1). The most pronounced differences were (a) during the early 2000s where there was a larger forcing in the disaggregated model and (b) from 2013 – 2016 where there was a much larger variation seen in the original model.

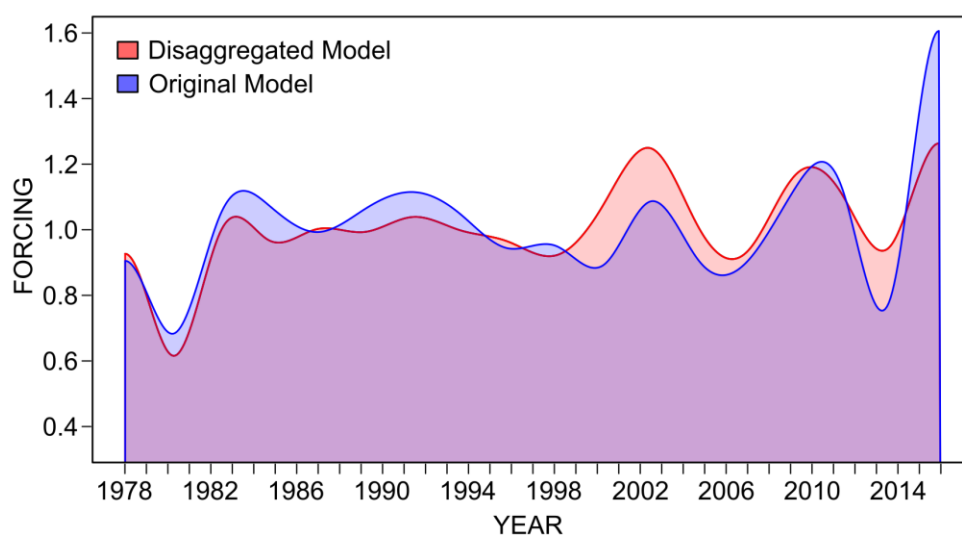


Figure 6.1. The environmental anomaly fitted to the small-celled phytoplankton group for the disaggregated and original model.

Table 6.4. New diet parameters calculated for the disaggregated functional groups based on the original model, based on dietary information from Chapter 4 and 5. Values are presented as the composition of diet in terms of live weight fractions.

Group name	Small phytoplankton ($< 10 \mu\text{m}$)	Large phytoplankton ($>10 \mu\text{m}$)	Micro- zooplankton ($2 - 200 \mu\text{m}$)	Meso- zooplankton ($200 - 2000 \mu\text{m}$)	Macro- zooplankton ($2 - 20 \text{ mm}$)
Anchovy					
<i>Larvae</i>		0.0970	0.197	0.706	
<i>Pre-recruit</i>	0.135	0.147	0.345	0.373	
<i>Recruit</i>		0.100	0.300	0.500	0.100
<i>Adult</i>		0.0500	0.0400	0.570	0.340
Sardine					
<i>Larvae</i>		0.138	0.122	0.740	
<i>Pre-recruit</i>	0.0880	0.100	0.245	0.567	
<i>Recruit</i>	0.250	0.150	0.500	0.100	
<i>Adult</i>	0.320		0.320	0.290	0.0700
Round herring					
<i>Juvenile</i>				0.748	0.252
<i>Adult</i>				0.600	0.400

There was a discrepancy between the predicted trophic position and stable isotope-derived estimates for both anchovy and sardine larvae. They exhibited a higher relative trophic position compared to their older life history stages in the disaggregated model (Table 6.5). This contradicts the stable isotope analysis of these species, which shows a clear trophic progression during their early life stages (Chapter 4). The same is also seen in the sardine pre-recruits, with larger predicted trophic positions compared to both recruits and adults (Table 6.5). Round herring shows a slight ontogenetic progression in their trophic position as reflected in the data (Chapter 5).

Table 6.5. New model parameters for the disaggregated functional groups based on the original model.

Group name	Trophic level	Biomass (tons km ⁻²)	Total mortality (y ⁻¹)	Q/B (y ⁻¹)	EE	P/Q (y ⁻¹)
Anchovy						
Larvae	3.36	0.0189	2.4	72.41	0.94	0.03
Pre-recruit	2.93	0.2910	1.6	32.80	0.96	0.05
Recruit	3.27	4.2410	1.2	17.94	0.96	0.08
Adult	3.55	7.0630	1.2	14.40	0.32	0.08
Sardine						
Larvae	3.26	0.0004	2.4	119.1	0.95	0.02
Pre-recruit	3.12	0.0088	1.6	48.59	0.96	0.03
Recruit	2.68	0.2190	1.4	20.60	0.98	0.07
Adult	2.91	0.6000	1.2	12.37	0.98	0.10
Round herring						
Juvenile	3.61	0.8370	1.4	30.04	0.66	0.05
Adult	3.66	5.5550	1.3	13.00	0.68	0.10

6.3.2. *Flow Control/Vulnerabilities*

Following the protocol outlined by Scott et al. (2015), and adopting the same parameters as Shannon et al. (2020), the 40 most vulnerable predator-prey interactions were searched for to increase the model fit to the time series. There were no vulnerable interactions highlighted for any of the four life history stanzas of anchovy, or either of the two-life history stanza for round herring. Of the 40 most sensitive predator-prey interactions estimated, 20 % (8/40) were attributed to the life history stanzas of sardine. These interactions were a mix of both bottom-up and top-down interactions. There were large top-down forcing from yellowtail, small hake and sea birds. Conversely, bottom-up forces influenced anchovy spawners, chub mackerel, small hake, cetaceans, and sea birds (exact vulnerabilities can be found in the Supplementary Table S.3).

Due to the disaggregation of the small pelagics, the disaggregated model had considerably more small pelagic centred trophic pathways compared to the original model, although total consumption of the three small pelagics was similar to the original model (Table 6.7).

Table 6.6. Model comparisons between the Ecopath and Ecosim model produced by Shannon et al., (2020) and the disaggregated model produced in this study. Shaded boxes show an increase in the model fit (Δ ; This study – Shannon et al. (2020) for each time series), the RSS% is the percentage contribution of the overall model RSS.

	Shannon et al., (2020)		This study		Δ
Factors fitted					
<i>Upwell</i>	X		X		
<i>FF on sardine</i>	X		X		
<i>40vs</i>	X		X		
<i>Equal weightings</i>	X		X		
	RSS		RSS		$\Delta\%$
Overall model fit	1368		1220		-11
	R^2	RSS%	R^2	RSS%	ΔR^2
Small pelagic time series					
<i>Round herring November biomass</i>	+0.022	1.29	+0.100	1.23	0.077
<i>Anchovy May recruit biomass</i>	+0.115	1.40	+0.120	1.61	0.005
<i>Sardine May recruit biomass</i>	+0.092	2.65	+0.378	2.82	0.287
<i>Anchovy model predicted Nov biomass</i>	+0.162	0.88	+0.263	0.94	0.101
<i>Sardine model predicted Nov biomass</i>	+0.510	0.94	+0.348	1.25	-0.162
Predator time series					
<i>Chub mackerel west coast biomass</i>	+0.061	4.92	+0.004	4.70	-0.057
<i>Chub mackerel south coast biomass</i>	+0.058	2.99	+0.092	3.17	0.033
<i>Penguin breeders</i>	+0.047	0.80	+0.002	0.55	-0.045
<i>Gannet breeders</i>	+0.564	0.41	+0.639	0.31	0.075
<i>Squid south coast biomass</i>	+0.007	0.35	+0.011	0.30	0.003
<i>Horse mackerel west coast biomass</i>	+0.001	1.94	+0.198	1.48	0.196
<i>Horse mackerel south coast biomass</i>	+0.034	0.21	+0.045	0.20	0.011
<i>M. capensis modelled spawner SPB</i>	+0.103	0.23	+0.015	0.41	-0.088
<i>M. capensis modelled recruitment</i>	+0.146	0.61	+0.131	1.15	0.015
<i>Pelagic feeding demersal biomass</i>	+0.001	1.14	+0.074	0.96	0.074
<i>Sciaenid's CPUE west coast</i>	+0.467	0.10	+0.032	0.18	-0.436
<i>Sciaenid's CPUE south coast</i>	+0.318	0.08	+0.032	0.14	-0.286
<i>Snoek CPUE west coast</i>	+0.393	0.10	+0.520	0.08	0.127
<i>Yellowtail CPUE west coast</i>	+0.089	0.23	+0.537	0.29	0.448
<i>Thunnus alalunga CPUE</i>	-0.029	0.97	-0.010	0.28	0.019

Table 6.7. Differences in consumption of small pelagics by their predators, and number of predator pathways (total pathways [unique pathways]) summed for all the life history stanzas within each species, between the two models.

Model	Species	Σ Consumption (t km ⁻² yr ⁻¹)	Number of pathways
Shannon et al., (2020)	Anchovy	7.098	35 [21]
	Sardine	0.577	22 [18]
	Round herring	5.378	19 [-]
This study	Anchovy	7.141	62 [24]
	Sardine	0.578	47 [22]
	Round herring	5.379	32 [20]

6.3.3. Population Dynamics

Model predicted biomass for the separate life history stages was standardised to the mean of the corresponding stanza, so that meaningful comparisons could be made. There were interesting dynamics observed in the biomass for the separate life history stages of anchovy and sardine. For anchovy, contrary to what one would expect, there was increasing interannual variation in abundance from larvae to recruits (Figure 6.2a-c left hand panel). This interannual variation is dampened for the adult stage (Figure 6.2d left hand panel). All stages of anchovy followed a similar decadal variation in biomass. For sardine the early life stages followed a similar pattern, with interannual variation increasing from larvae to recruits (Figure 6.2a-c right hand panel). Modelled sardine adults exhibit an out of series oscillation, with a shift in biomass from recruits to adults (Figure 6.2d right hand panel). This is likely the effect of both the sardine FF and the large-celled phytoplankton FF. The large-celled phytoplankton FF has clearly contributed to the modelled peak in meso- and macrozooplankton observed in the late 1990s and early 2000s (Figure 6.3a and c), that likely contributes to the population growth of modelled pre-recruits and recruits as shown in Figure 6.2. This cohort develops into the modelled adult peak during the early 2000s, which is also partly driven by the sardine FF creating a reduction in the availability of modelled adult sardine to predators during the same period (Figure 6.3b and d). It is worth noting that the interannual variation observed in the early life stages was far more prominent in anchovy rather than sardine.

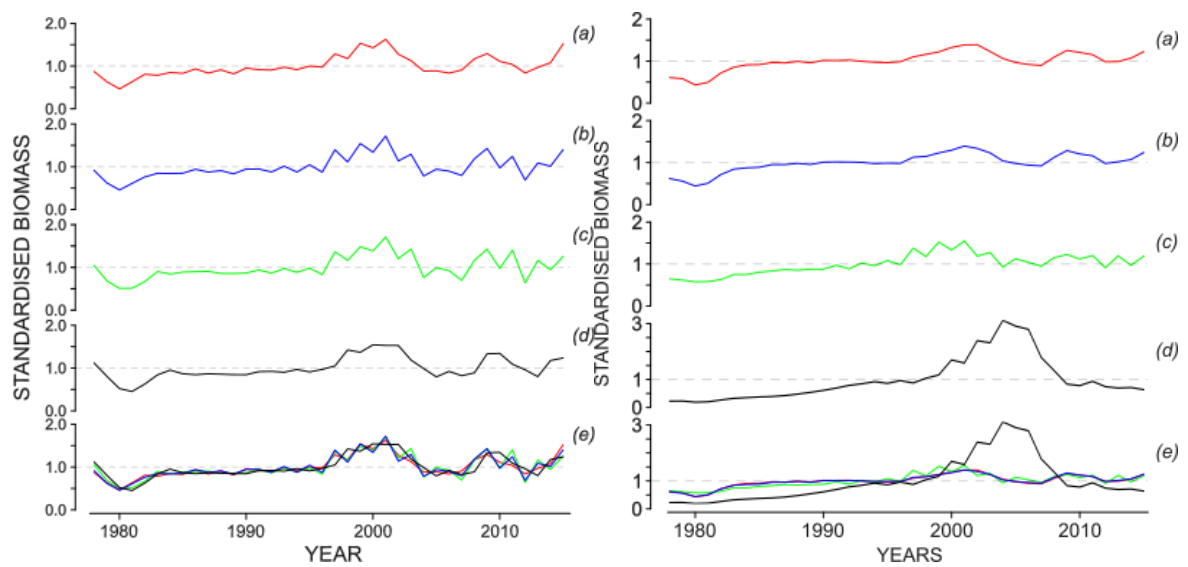


Figure 6.2. Standardised predicted biomass from the disaggregated model for anchovy (left) and sardine (right) larvae (a), pre-recruits (b), recruits (c), adults (d) and combined (e).

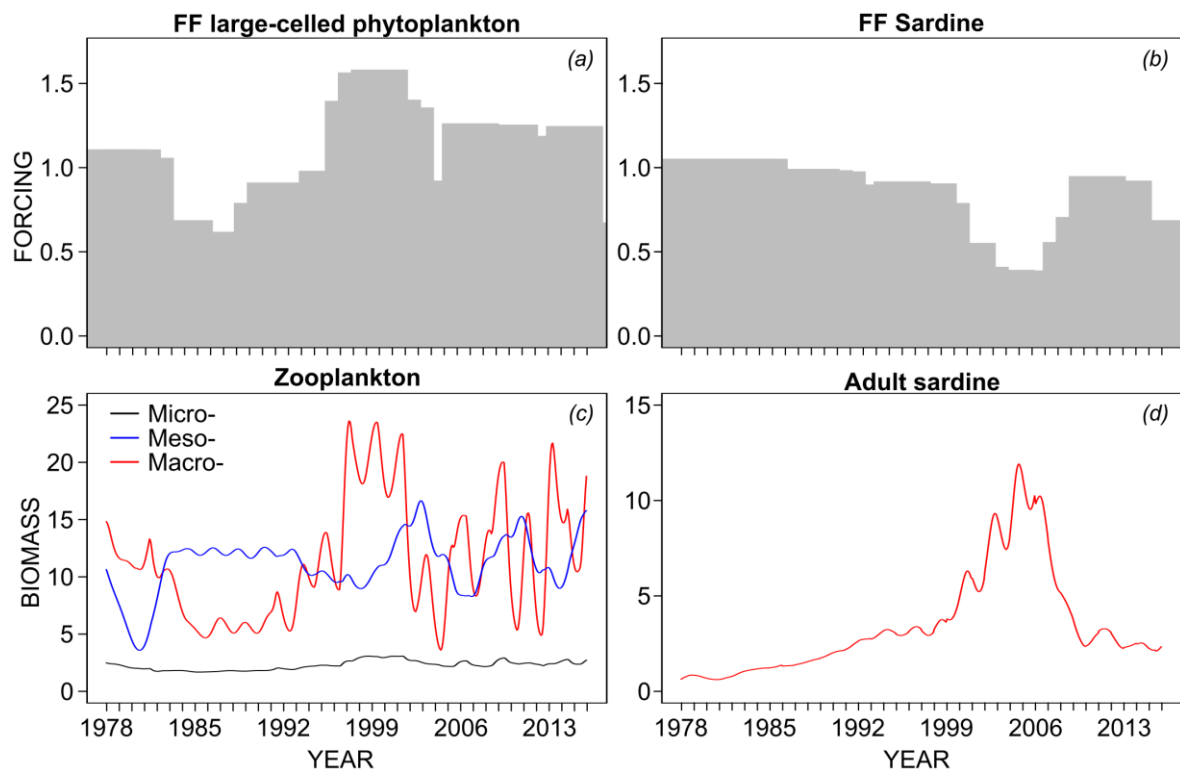


Figure 6.3. The forcing functions (FF) applied to (a) large-celled phytoplankton and (b) juvenile and adult sardine, and the model predicted biomass of (c) the three zooplankton groups and (d) adult sardine.

6.3.4. Model Fit Comparison

There was an overall increase in the fit of the disaggregated model compared to the original model by a decrease in residual sum of squares of 10.82 % (Table 6.6). Out of the total 73 time series that were used to fit the model, the sum of squares was improved for 44. The best improvement was for the “Yellowtail CPUE west coast” with a $0.448 \Delta R^2$, and the worst change in fit was for the “Sharks and Rays CPUE SC” time series of a $-0.342 \Delta R^2$.

As the system is characterised by small pelagic fish, it is important to assess the fit of the disaggregated model to the small pelagic time series. Out of the five small pelagic time series, there was an improvement in the model prediction for four of them, albeit slight in some cases; “Round herring November biomass”, “Anchovy May recruit biomass”, “Sardine May recruit biomass” and “Anchovy model predicted November biomass” (Table 6.6, Figure 6.4). For anchovy, with an improved R^2 for both time series, the disaggregated model encapsulated the general fluctuations in the observed biomass over the original model (Figures 6.4a-b). For sardine there was an increase in model fit for the recruits (Figure 6.4c), although overall still a poor fit to the observed data. Large increases in recruitment throughout the late 1990s and early 2000s were not modelled well. For the sardine adults, the disaggregated model showed a reduction in R^2 , displaying a much poorer fit to the observed data (Figure 6.4d). Lastly, the disaggregated model fit of round herring was improved, although the model still poorly predicted the observed high and low values (Figure 6.4e).

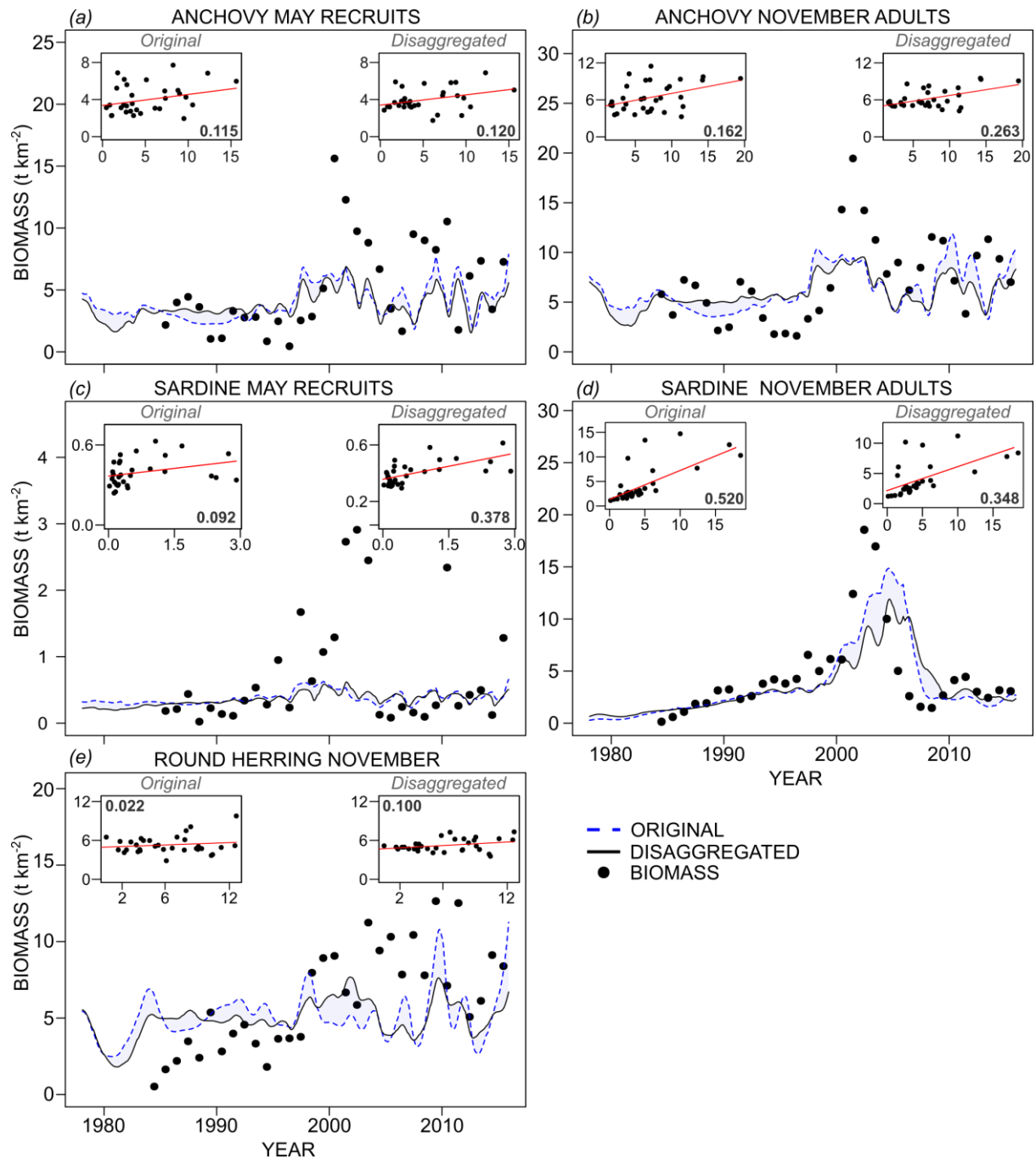


Figure 6.4. Model fits of anchovy and sardine comparing both the original model (Shannon et al., 2020) and the new disaggregated model. Plots show the observed biomass from each time series, the predicted biomass from the two models, and the model specific modelled-observed scatter plots with the R^2 value.

For the predator time series there was an improvement in the R^2 for 8 out of the 14 biomass time series (Table 6.6, Figure 6.5). There was an increase in the R^2 value for the west coast chub mackerel, yet it still exhibited a relatively poor fit (west coast Figure 6.5a). There was a new vulnerability for chub mackerel in the disaggregated model, with top-down control exerted by sciaenids. This may help explain the persistent suppressed biomass following the early 2000s as there was a corresponding increase in the biomass of sciaenids. Squid also showed a slight improvement in the predicted biomass (Table 6.6). The disaggregated model predicted biomass showed reduced amplitude of fluctuations in squid biomass on the south coast compared to the original model, which better reflects the observed biomass (Figure 6.5o). Similar to the original model there were no vulnerabilities for this functional group. There was an improvement for model fit for both time series for horse mackerel (west and south coast). Although there was a marginal increase for the south coast time series, there was a significant increase for the west coast time series, with the R^2 improving greatly (Figure 6.5c-d). In the original model there was very large top-down control by adult horse mackerel on juvenile sardine, whereas in fitting of the new disaggregated model, this was not identified as one of the most sensitive interactions for vulnerability estimation. There was an overall increase in the disaggregated model fit of pelagic-feeding demersals after the early 2000s compared to the original model ($\Delta R^2 = 0.074$). Similar to the original model, there was no predator-prey vulnerability attributed to this group. Snoek showed an improvement in the new model, with an increase in R^2 by 0.127 (Figure 6.5h). The original model fit top-down control of juvenile sardine by pelagic-feeding demersals, whereas this was not estimated as a sensitive interaction in the fitting routine for the new disaggregated model. Yellowtail exhibited an increase in predicted biomass compared to the original model, with a significant increase in R^2 of 0.448 (Figure 6.5g). The original vulnerability of a top-down forcing of juvenile sardine remained in the disaggregated model. There was an increase in the model fit for the Tunas and Swordfish group to the “*Thunnus alalunga* CPUE” timeseries, with a reduction in R^2 (Table 6.6, Figure 6.5f). The large vulnerability on adult sardine was removed in the disaggregated model following the fitting procedure.

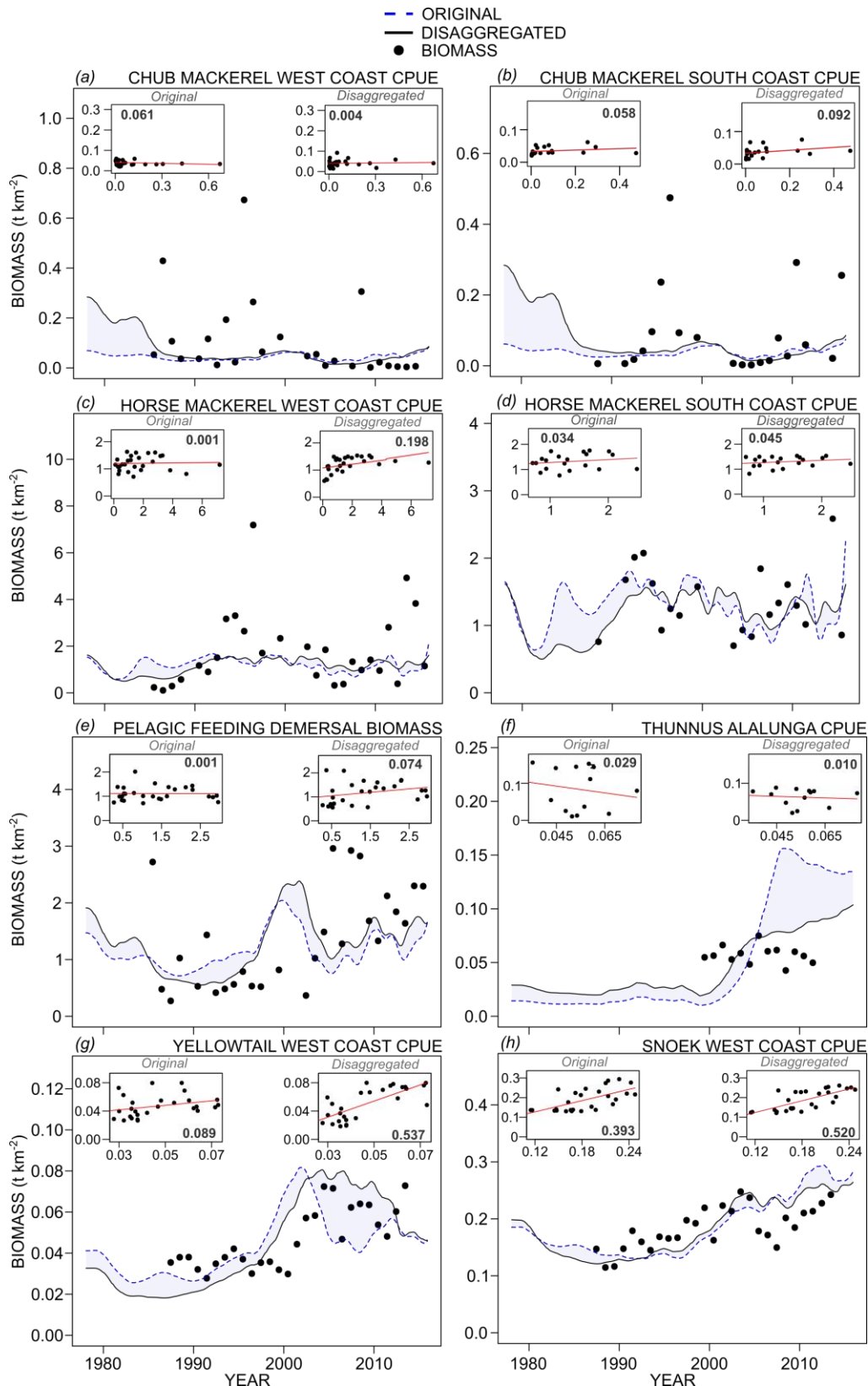


Figure 6.5. Model fits of anchovy and sardine predators comparing both the original model (Shannon et al., 2020) and the new disaggregated model. Plots show the observed biomass from each time series, the predicted biomass from the two models, and the model specific modelled-observed scatter plots with the R^2 value.

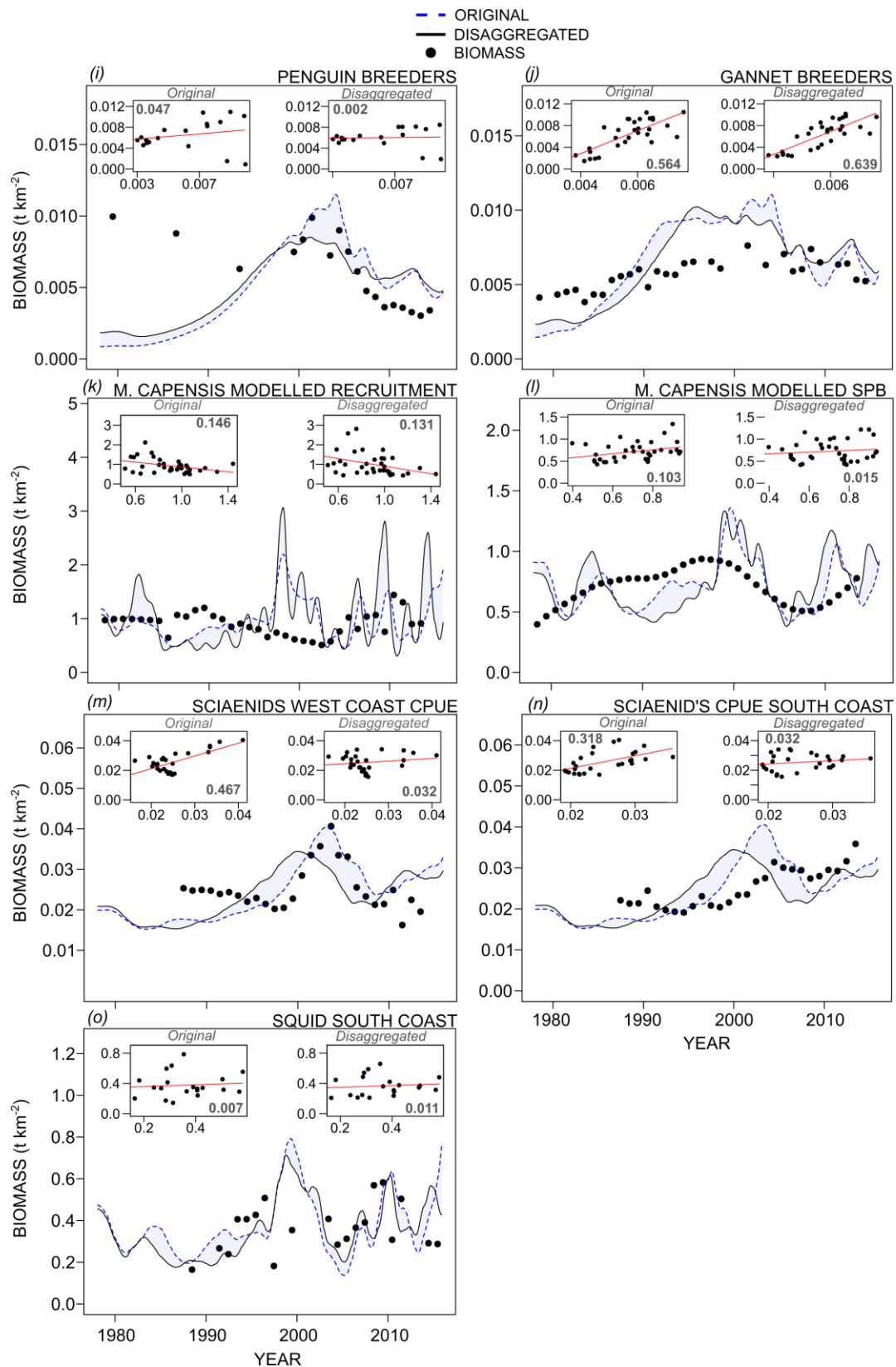


Figure 6.5. *Continued.*

The disaggregated model showed an increase in R^2 for just the “Cape gannet breeder” time series. Penguins showed a decrease in overall R^2 in the disaggregated model fit ($\Delta R^2 = -0.045$). The bottom-up vulnerability for adult sardine was removed in the disaggregated model. The model fit is still very poor at the beginning and end of the time series (Figure 6.5i). The predicted model fit for Cape gannets was improved ($\Delta R^2 = 0.075$, Figure 6.5j, Table 6.6). Both models have a similar bottom-up control by adult sardine, therefore this improved fit may have manifested from the interdependence of small pelagic consumption.

There were some pelagic-centred time series that saw a decrease in disaggregated model fit. Firstly, there was a decrease for shallow water cape hake, both recruits ($\Delta R^2 = -0.015$) and adults ($\Delta R^2 = -0.088$). The disaggregated model biomass prediction for recruits showed a much greater interannual fluctuation in biomass than the original model. In the disaggregated model there were vulnerabilities attributed to macrozooplankton, pre-recruit sardine (bottom-up) and juvenile sardine (top-down), compared to only juvenile sardine (top-down) and other cephalopods (bottom-up) in the original model. Lastly, there was a drastic reduction in the disaggregated model fit for sciaenids (both west and south coast time series). The original model fitted both the west and south coast time series very well, predicting the observed peak in biomass in the early 2000s. This peak was shifted earlier in the disaggregated model, likely as a result of the removal of the top-down control on juvenile sardine in the disaggregated model. Therefore, the peak is asynchronous with the sardine peak.

6.3.5. Overall Model Function

For the indices, *Proportion of Predators* and *Total Biomass*, the trajectory over the projected time period for both model predictions followed a very similar pattern and there was no discernible difference (Figure 6.6). For the other four indices there are clear differentiations during the modelled time periods between the two models. Both *Mean Length*- and *Mean Lifespan of Fish* shared a similar trajectory, where in the original model there was a large peak in the indices during the early 2000s, but this was completely non-existent in the new disaggregated model. The *Trophic Level of Catch* showed an interesting change, the two trajectories of the index split in the late 1980s, with the trophic level being considerably larger in the new disaggregated model for the remainder

of the time series. Lastly, the index $1/(\text{Landings}/\text{Biomass})$ exhibited a more intricate difference, the index for both models tended to show a similar trajectory except during the late 1990s to 2000s whereby there was a significant increase in the index in the new disaggregated model (Figure 6.6).

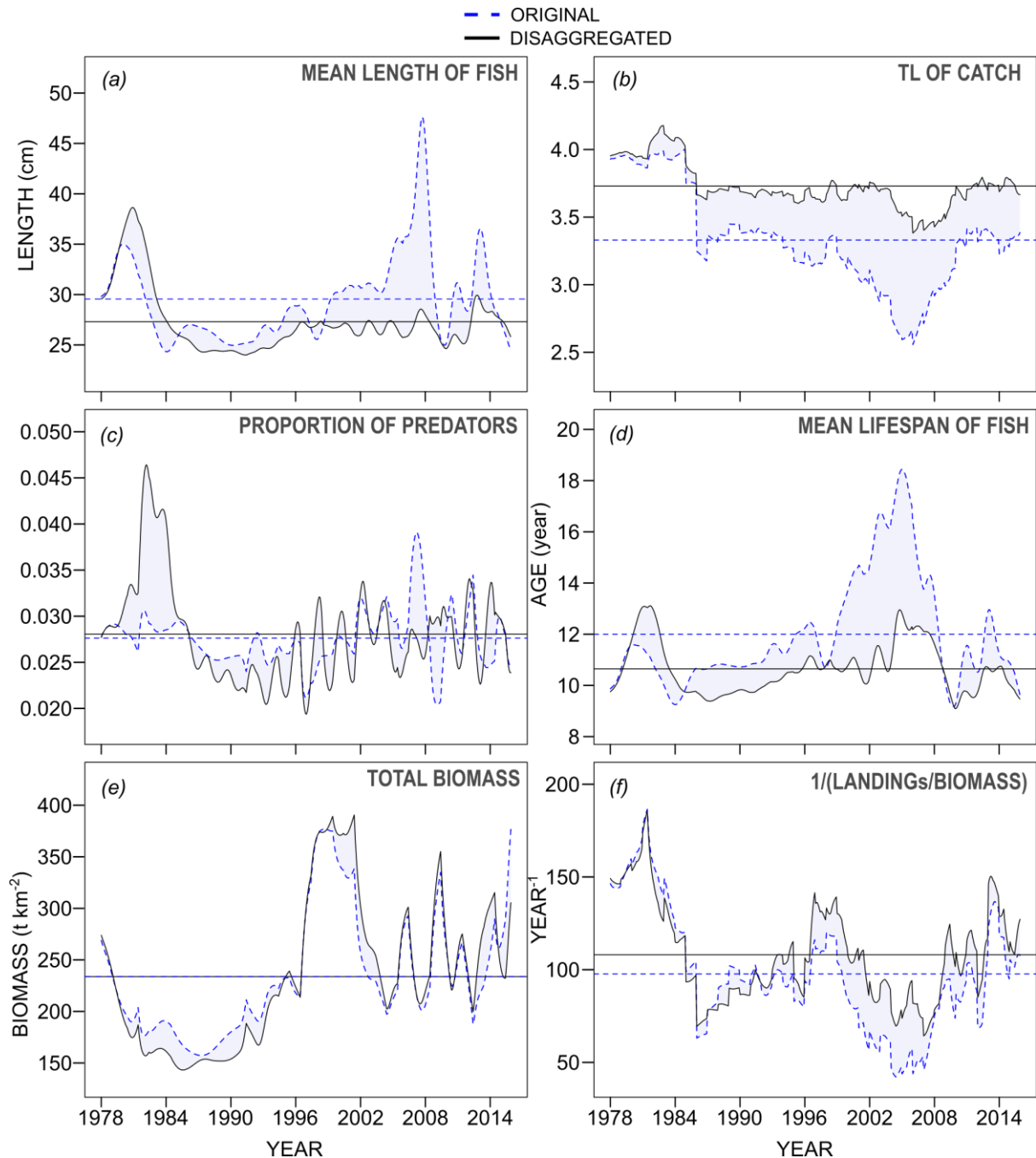


Figure 6.6. The calculated ecological indicators for both the disaggregated and original model over the modelled time series. The colour specific horizontal dotted lines are the means for that indicator for the specific model.

There was a significant difference in four of the 6 indices that were tested. *Mean fish length* was significantly larger in the original model, by 2.05 cm ($t = -8.86$, $df = 838.08$, $p\text{-value} < 0.001$). There was a significant difference in the *Trophic Level of the Catch* between the two models, with a significantly larger trophic level observed in the disaggregated model ($t = 20.98$, $df = 635.12$, $p\text{-value} < 0.001$). The *Mean Lifespan of Fish* in the new model was significantly smaller than the original model, by over two years ($t = -8.86$, $df = 838.08$, $p\text{-value} < 0.001$). There was a significant difference in the $1/(\text{Landings}/\text{Biomass})$ index between the two models, with the new disaggregated model having a larger index in comparison ($t = 5.37$, $df = 875.58$, $p\text{-value} < 0.001$).

There was no significant difference in the *Proportion of Predatory Fish* between the models ($t = 1.54$, $df = 720.40$, $p\text{-value} = 0.123$). There was also no significant difference in *Total Biomass* between the two models ($t = -0.02$, $df = 878.34$, $p\text{-value} = 0.96$). No statistical test was used to compare the $1/\text{CV of Total Biomass}$ index, yet qualitatively they were not dissimilar (Table 6.8).

Table 6.8. Model indicator mean and standard deviation for the entire time series of estimates of both models for the indices utilised.

Indicators	Shannon et al., (2020)	This model
Mean fish length (cm)	29.56 [4.37]	27.31 [3.23]
TL of landings	3.33 [0.37]	3.73 [0.17]
Proportion of predatory fish	0.028 [0.003]	0.028 [0.005]
Mean lifespan (years)	12.00 [2.17]	10.65 [0.99]
1/CV of total biomass	0.0074	0.0061
Total biomass ($t \text{ km}^{-2}$)	233.85 [58.03]	233.77 [70.33]
$1/(\text{Landings}/\text{Biomass})$ (year^{-1})	97.73 [31.87]	108.09 [26.07]

6.4. Discussion

This study re-developed the EwE model of the southern Benguela produced by Shannon et al. (2020) to investigate whether including a finer life history resolution of small pelagic fishes would provide beneficial changes to the model fit. It was shown here

that disaggregating small pelagic fish further in a system where they perform pivotal roles showed a degree of improvement in model fit. The disaggregated model exhibited substantially more small pelagic fish centred trophic pathways that were previously grouped into plankton groups. As a consequence of this, it had a diverse set of results in terms of overall ecosystem output, which will be discussed.

6.4.1. Model Fit to Time Series

Out of the five small pelagic time series, there was an improvement in model fit for four; “Round herring November biomass”, “Anchovy May recruit biomass”, “Sardine May recruit biomass” and “Anchovy model predicted November biomass”. Adult sardine biomass decreased in its overall model fit (Figure 6.4). Interestingly, a key finding from the conception of the original model by Shannon et al. (2020) was reiterating the pivotal role played by sardine in the southern Benguela. This was emphasised by the increased model fit after implementing the sardine forcing function and the high level of sardine related predator-prey sensitivities (40%). Yet, following the fitting routine for the disaggregated model, many of the sardine centred predator-prey sensitivities were removed, leaving only 20%. This reduction may be a more real representation of the modern system, where sardine have been reduced to historically low levels that have persisted since the mid-2000s (DEFF, 2020). There were still no sensitive predator-prey interactions involving anchovy or round herring. Although the fit increased, round herring still had a relatively poor fit to the observed time series (Figure 6.4). This could be a consequence of the underrepresentation of this functional group in the disaggregated model. The ecotrophic efficiency of both juvenile and adult round herring in the disaggregated model is < 0.7 , which is certainly low for juveniles (Table 6.5). This indicates that a large proportion of energy is lost between trophic levels, suggesting an inefficient energy flow within the system. Hence this warrants the updated diet studies of potential predators as currently the disaggregated model may underestimate the trophic role of round herring in the southern Benguela.

There was an overall improvement in the fit of the disaggregated model predicted biomass of chub mackerel compared to the time series data. Originally, chub mackerel exerted top-down control on juvenile sardine. However, following the model fitting routine, in the disaggregated model the juvenile sardine predator-prey sensitivity was

changed to a bottom-up forcing. Chub mackerel caught in South Africa tend to migrate south from Namibian waters to the South African west coast during austral spring and summer. This is when the upwelling is strongest and food is abundant (Crawford & de Villiers, 1984). With catches remaining low since the 1960s in South Africa, indicating a reduction in total biomass (Villacastin-Herrero et al., 2010; DEFF, 2020), coupled with their highly diverse diet (Castro, (1993) and abundant feeding grounds, bottom-up control of sardine by chub mackerel may be more likely, supporting the change in vulnerabilities between the models.

The biomass prediction of squid from the disaggregated model was improved, albeit not greatly. Similar to the original model, there were no vulnerabilities fitted for the predator-prey interactions involving squid. There is a high degree of spatial overlap between squid and early life stages of small pelagic fishes. The largest proportion of biomass is found on the south coast (DEFF, 2020), and although not the primary nursery ground for small pelagics, it still plays an important role (Miller et al., 2006; Teske et al., 2021). Therefore, this spatial overlap coupled with their dependency on small pelagics in their diet (Augustyn, 1991; Augustyn et al., 1994), provides rationale for the inclusion of these additional pathways that have helped increase the model fit.

The disaggregated model output for Cape horse mackerel was fitted to both the west coast and south coast biomass time series (Figure 6.5). Interestingly, the spatial distribution of Cape horse mackerel is primarily inshore from the northwest South African EEZ border to Port Alfred on the East coast (DEFF, 2020). There was a reduction in the model fit in the disaggregated model for the south coast time series, but an improved model fit of horse mackerel to the west coast time series. This may reflect the importance of early life stages of small pelagics in the diet of horse mackerel on the west coast.

Pelagic-feeding demersals is a functional group that is comprised of eight species. There was an overall increase observed in the disaggregated model fit, yet the model fit was still poor (Figure 6.5). Despite some overlap in diet between the species, there are clear dietary distinctions between them. Out of the eight, Cutlass fish and Cape Dory predate significantly on anchovy, with prey lengths as small as 10 mm (Meyer & Smale, 1991). Therefore, it is likely that early life stages play a role in their diet. Conversely, the other six species infrequently feed upon small pelagics and exhibit significant ontogenetic changes in their prey selection (Meyer & Smale, 1991). Therefore, it is understandable

that when attempting to simplify and aggregate these species into a single group, some additional trophic pathways may not be beneficial to certain species within the group.

Both bird groups, African penguins, and Cape gannets, showed a general improvement in the model fit to the time series. The intimate relationship between the breeding success of African penguins and the availability of sardine and anchovy has been repeatedly proven (Crawford, 1998; Crawford et al., 2006, 2011b; Sydeman et al., 2021). Shannon et al. (2020) investigated this relationship via implementing the Food Availability Index forcing function outlined by Crawford et al. (2019), and although the fit to penguins was greatly improved there was a predominant reduction for most other functional groups. Yet it provided evidence that including a form of vulnerability index on penguins was beneficial and needed future work. This was corroborated by African penguin-sardine interactions being among the 40 most sensitive predator-prey interactions in the original model. Interestingly, these were removed in the disaggregated model fitting process. Yet, the inclusion of early life stages in the diet of African penguins did improve the fit to data. Fish larvae have often been found in the stomach of African penguins, especially those neighbouring the west coast small pelagics nursery ground. It is thought that they opportunistically fill an energetic void whilst there is a lack of adult anchovy and sardine (Crawford et al., 2011). Furthermore, these early life stages play an important role for fledglings to hone their predatory skills (Wilson, 1985). Despite the improved model fit, the increase in breeding pairs of penguins during the early 2000s, that coincided with the boom of small pelagics, was modelled poorly in the disaggregated model (Figure 6.5). This potentially highlights the importance of having a bottom-up control exerted by sardine to this functional group (as was the case in the original model).

The model fit for snoek and yellowtail were both significantly improved through the additional small pelagic trophic pathways. Residing inshore from the west to the south coast of South Africa, snoek are important predators of small pelagics (Griffiths, 2002). Their primary nursery ground is on the west coast, synchronising with the nursery area of small pelagics. As they are retained inshore until around 30 – 40 cm long, it is highly likely that early life stages of small pelagic fish play a vital role in their ecology (Griffiths, 2002; Mcqueen, 2002). Yellowtail are described to have a broader diet, with sardine contributing significantly (Dunn, 2014). Both models fitted bottom-up control of yellowtail by juvenile sardine. This fits with the diet described by Dunn (2014), who reports a high importance of sardine in their diet. However, Parker et al. (2020)

highlighted a dependency on anchovy east of Cape Agulhas. This discrepancy could highlight the effects of interannual plasticity in their diets, since Dunn (2014) studied fish during 2011-2012, when anchovy biomass was considerably lower than long term averages and sardine slightly higher than previous years. The model has shown that yellowtail have benefited from disaggregation of small pelagics to include early life stages, yet it would be worthwhile in the future to explore an increased dietary dependency of anchovy.

Despite the relatively poor fit, there was an improvement of the predicted biomass of the tuna and swordfish functional group using the “*Thunnus alalunga* CPUE” as a proxy of biomass. As is the case for most piscivorous fish, this functional group undergo drastic ontogenetic development in their diet. Small scombrids and tunas exhibit strong piscivory from a very early age, with the striped bonito *Sarda orientalis* consuming mainly fish larvae by day 4 post hatching (Kaji et al., 2002). Furthermore, with the reduced sardine peak in the early 2000s compared to the original model (Figure 6.4), adult sardine contributed less to their diet in the disaggregated model (Figure 6.5f), which likely contributed to the decline in the peak of the Tuna & Swordfish functional group.

There were two functional groups for which model fit declined with the addition of multiple life history stages of small pelagic fish; shallow water cape hake and sciaenids. The original model proved a good fit for the predicted sciaenids time series data, which was greatly diminished following the disaggregation and the refitting. The original prediction encapsulates the increase in biomass during the early 2000s. This is due to the dependency of sciaenids on sardine which was modelled through a vulnerability in the original model. However, after the new disaggregated model fitting, this vulnerability was removed, manifesting in the shifted peak. In the model, anchovy contribute to a larger proportion of sciaenids diet to sardine, which may be the cause of this shifted peak. As seen in Figure 6.4b, the modelled biomass of anchovy adults increases earlier than that of sardine, just before the 2000s. This harmonises with the earlier peak observed in the disaggregated model predicted biomass for sciaenids. This reduction in fit highlights the importance and dependency of sciaenids on sardine, corroborated by Parker et al. (2020) whereby Geelbeck *Atractoscion aequidens* CPUE was significantly matched with sardine biomass. Therefore, a revision of their modelled diet and the vulnerability parameter is warranted for this functional group.

There was a decrease in the disaggregated model fit for both juveniles and adults of shallow water Cape hake. Following the model fitting routine, shallow water Cape hake were the only functional group to have a vulnerability (bottom-up) to one of the early life histories stages; sardine pre-recruits. This is likely the reason we see an increased interannual variability in the biomass of Cape hake juveniles- as the predicted biomass of sardine pre-recruits exhibits significant interannual variability (Figure 6.2). The amount of variability in the juveniles of the new model is substantial, and although studies have shown that there can be variability in hake recruitment (Kainge et al., 2013), it is unlikely to be this much. This proves to be an important warning for further studies whereby setting vulnerabilities to lower trophic level functional groups that have significant amounts of fluctuation may manifest in corresponding consumers.

Often stable isotope studies that estimate the trophic positioning of functional groups can be used to ground truth the estimates within the model. There is a large discrepancy between the model estimates of trophic positioning of the early life stages and the stable isotope estimates from previous studies. The size-based dietary information used for the early life stages was drawn from Chapter 4, which also shows that for both sardine and anchovy there is a clear enrichment in ^{15}N during their ontogeny, with the largest during the larval stanza between 0 – 35 mm (Chapters 4 and 5). However, the disaggregated model estimated the trophic positioning of larvae and pre-recruits for both species to be larger than the recruits and adults (Table 6.5). This difference likely arises from the fact that the model groups phyto- and zooplankton by size classes. It has been widely shown that even within just copepods of similar sizes, the degree of omnivory can vary wildly (Schukat et al., 2014; Bode et al., 2015; Benedetti et al., 2016). For example, the $\delta^{15}\text{N}$ signature of calanoid copepods can vary by the equivalent of 1.8 trophic levels (Schukat et al., 2014). Consequently, for the model to correctly estimate the trophic positioning of early life stages, the modelled dietary components, primarily zooplankton, should be based on functional traits such as feeding strategies rather than size.

The disaggregated model exhibited increased variability in the predicted biomass of functional groups and life history stages of small pelagic fishes. Firstly, there is an observable increase in biomass variability among anchovy life history stages over time, aligning with findings suggesting higher recruitment variance for small pelagics in recent years (DEFF, 2020). Small pelagic fish are intricately interconnected with the underlying physical processes in their ecosystem. Research has shown temporal (Blamey et al., 2012;

2015) and spatial (Lamont et al., 2018a) increases in environmental variability within the southern Benguela, which is likely manifested in the life history stages of anchovy. Secondly, the disaggregated model predicts a greater interannual oscillation in the biomass of species when compared to the original model. This variability is likely attributed to the inclusion of larvae as a distinct life history stage. As previously noted, lower trophic levels mirror environmental conditions, and this heightened variability propagates downstream to affect consumer species.

6.4.2. Overall Model Function

A model with the aim to be used as a specific tool must be constructed for the specific topic and question. However, first it is important to conceptualise models that encompass a fine taxonomic resolution of functional groups, that can then be adapted to address the specific question. Therefore, it is important to understand if including a finer life history resolution of species is necessary for future ecosystem models. Despite the significant changes in the ecosystem fit to specific time series data, there was no system change in the overall productivity of the new disaggregated model compared to the original model, with both having a similar total biomass. Furthermore, despite differences in the predicted biomass of specific functional groups, the overall system variability was equal, as inferred from the $1/CV$ of biomass index. This implies that, overall, the ecosystem is functioning similarly, but there are more nuanced differences in the details of the model.

As a consequence of disaggregating the small pelagic groups further, there was a significant change in the overall trophic level estimation of the entire food web. The *TL of the catch* was significantly higher in the disaggregated model (Figure 6.6). In the original model, anchovy and sardine recruits encompassed the entire diet for all life history stages prior to adults, hence their trophic level was weighted lower. Following the disaggregation, the diet of sardine and anchovy recruits were revised and included less prey items from lower trophic levels. Subsequently, there was an increase in the overall trophic position of sardine and anchovy. The original model estimated the trophic position of sardine and anchovy recruits at 2.526 (see Shannon et al., 2020), whereas the disaggregated model estimated them at 2.679 and 3.266 respectively. Consequently, these increases caused enrichment in their predators, which is reflected in the increase in the *TL of the catch*. Additionally, as previously stated, the modelled trophic positions

of the early life stages in the disaggregated model were overestimated in comparison to trophic studies. Therefore, this may also add to the increase in *TL of the Catch* index, as it would have enriched all subsequent consumers.

There was a notable decrease in both the mean length and lifespan of the fish community in the disaggregated model (Figure 6.6). These indices are indicative of the ecosystem's stability and regenerative capacity. The most significant change occurred during the early 2000s, likely corresponding to a decline in sardine abundance (Figure 6.4). This shift in biomass dynamics of small pelagic fish in the disaggregated model likely reduced the biomass available for downstream piscivores. Several large piscivorous groups in the model experienced a concurrent reduction in predicted biomass, including tuna, swordfish, sciaenids (Figure 6.5), and pelagic chondrichthyans (not shown here, but exhibiting a peak biomass reduction of 60%). These groups are trophically linked to small pelagics both directly, as predators, and indirectly, through prey-species that rely on small pelagics. Although the accuracy of this change is challenging to justify, there is supporting evidence from the improved model fit of the Tuna and Swordfish functional group to the "*Thunnus alalunga* CPUE" timeseries.

Interestingly, despite the reduction in large piscivores such as *Tuna and swordfish*, *Pelagic- and Benthic feeding chondrichthyans* observed in the new disaggregated model, there was no significant difference in the *Proportion of predatory fish* between the disaggregated and original model (Figure 6.6). There may be two explanations for this change. Firstly, there were increases in the biomass of smaller piscivorous predators such as chub mackerel, yellowtail, and pelagic feeding demersals. Secondly, the model categorises functional groups as "predators" if their TL is greater than four. As a consequence of the observed increase in TL of the system due to the revised diet of the anchovy and sardine recruits, there were several species that were promoted into the > 4 TL group, such as Chub mackerel and Cape hake recruits.

The reduction in the peak in the mean length and lifespan of fish during the early 2000s (Figure 6.6), may be indicative of a higher fishing pressure on small pelagics during this time. In the early 2000s during the high biomass years, the stock assessment and the operational management procedure for the South African sardine fishery both operated under the premise of a single sardine population, disregarding spatial distribution and fishing effort considerations (De Oliveira and Butterworth, 2004). This led to a spatial

disparity between fishing effort, resulting in an elevated level of exploitation, especially on spawning adults west of Cape Agulhas (Coetzee et al., 2008).

6.4.3. Limitations

It is worth touching on the limitations of the model. Firstly, increasing parameterisation of more life history stages of functional groups will inherently increase the uncertainty of the output of the model. The uncertainty surrounding the static parameters used in this study were deemed as adequate via implementing the PREBAL technique outlined by Link (2010). To address uncertainty in the model further, tools such as Ecosampler that measure the sensitivity of results to input parameter uncertainty, should be applied before strategic use (Steenbeek et al., 2018). Secondly, the data used to devise the diet for the newly disaggregated early life stages was used from a single cruise, and therefore may miss out on seasonal and interannual differences in diet. However, it has been shown that larval anchovy and sardine are largely size-selective feeders that are limited by their mouth gape (Chapters 3 and 4). Therefore, if there were seasonal differences it would be most notable in the species composition rather than size composition, i.e., the ambient species composition may change but the size of selected particles would not. Subsequently, as the model groups phyto- and zooplankton groups by size and not species, this aseasonality in the diet data should not be an issue. Nevertheless, as with all species included in the model, increasing the data for dietary studies will reduce the uncertainty, and therefore replicate studies would be beneficial for improved model parameterisation in the future.

This study only used R^2 as a comparative index to evaluate the two models. However, it is important to also consider the value of the slope when assessing model performance. Relying solely on R^2 may not identify situations where model predictions are negatively correlated with observed data, as demonstrated by the *M. capensis* modelled recruitment. Additionally, R^2 alone may not provide enough information to determine whether the relationship between the predicted and observed data is statistically significant. Therefore, it is recommended that future studies consider both R^2 and the slope value in order to comprehensively evaluate the model's performance, especially since many R^2 values in this study indicate poor relationships.

Limitations associated with the original model are outlined in Shannon et al. (2020) and are not within the scope of this study. This study does not seek to improve all aspects of the model, rather question whether increasing the number of life history stages represented in the model of small pelagic fishes is beneficial.

6.4.4. Conclusion

This study has provided evidence that increasing early life stages of pivotal species in a trophic model can (a) increase the model fit to observational data by increasing the trophic pathways within the modelled system, and (b) have meaningful ramifications for the overall model representation of ecosystem functioning. It has been shown that despite the relative mass redundancy of small pelagic larvae in the system, they still have a considerable effect on the ecosystem dynamics. Consequently, is the inclusion of increased life history stages in ecosystem models beneficial? Unfortunately, as with many complex systems, the answer is not straight forward. However, as with any study, the trade-offs between precision and time and resources are undeniable. Understanding and appropriately quantifying the trophic ecology of early life stages can be extremely time consuming. Consequently, despite the increase in model performance, the utilisation of time and resources to disaggregate these functional groups needs to be considered when developing a specific model to address one's research question. Nevertheless, this study emphasizes that various functional groups in an upwelling system, like the southern Benguela, have crucial interactions with small pelagic fish. For future modelling efforts, disentangling and thoroughly investigating the consumption of these species to better represent early life stages could enhance the overall utility of the model. Lastly, this study has highlighted that it may be worthwhile for future models to consider the re-organisation of the phyto- and zooplankton prey functional groups according to traits rather than size. For instance, delineating functional groups based on feeding strategies, such as filter feeders, predators, and omnivores, could provide a more ecologically informative framework for understanding trophic interactions in the ecosystem.

Chapter 7

Synthesis and Conclusion

7.1. Overview

Small pelagic fish in upwelling systems perform crucial ecological roles (Cury et al., 2000) and have great commercial importance. They have dominated global catches since the onset of industrial fishing (FAO, 2020). Therefore, safeguarding these species is crucial in order to meet both their socio-economic and ecological demands. This requires a comprehensive understanding of their ecological and life history processes, neither of which are mutually exclusive. Often, the life history and population dynamics of these species are tightly coupled to environmental processes, yet detecting these environmental relationships can be incredibly difficult. Many hypotheses spanning decades have postulated that processes operating during early life stages could help elucidate information for resolving the problem (Hjort, 1914; Lasker, 1981; Cury & Roy, 1989; Cushing, 1990; Roy, 1993; Bakun, 1997; Swalethorp et al., 2022). This study has aimed at addressing some knowledge gaps of early life stages, by using modern analytical methods and ecosystem modelling to describe the ecological role of small pelagic fishes in the Benguela.

This thesis comprises of four data Chapters; Chapter 3 analyses several ecomorphological traits for larval sardine and anchovy in both the northern and southern Benguela, Chapter 4 investigated the trophic ecology of larval stages of sardine and anchovy through a multifaceted approach and Chapter 5 investigated the combination of ecomorphological traits and trophic ecology of pre-recruit stages of sardine, anchovy and round herring in the southern Benguela. Finally, Chapter 6 utilised this information to further refine an already-developed ecosystem model of the southern Benguela in Ecopath to assess the benefit of including a finer life history resolution. This is the most comprehensive analysis on the trophic ecology of early life stages of small pelagic fishes in the Benguela upwelling region, and here its importance is discussed.

7.2. Ontogenetic Development

Significant shifts in ontogeny are often associated with obvious distinct changes in diet or habitat use. More gradual changes are often overlooked in importance (Sánchez-Hernández et al., 2019b). Unlike other species that undergo clear shifts in diet, such as piscivores, or habitat use, such as flat fishes (Moser et al., 1984; di Pane et al., 2019), most clupeoids remain pelagic planktivores for the entirety of their life history. Yet this study has shown that despite no great saltatory change, there are subtle developments in the trophic ecology of small pelagics in the Benguela upwelling region during their early life stages. Synthesised from the conclusions of Chapters 3, 4 and 5, there is a clear species-specific progression in both diet and associated morphology for sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*.

The majority of ontogenetic changes in diet tend to be size related changes (Werner & Gilliam, 1984). Without any appendages to grab and manipulate prey, feeding in fish is largely dependent on mouth morphology and apparatus (Sánchez-Hernández et al., 2019b). As detailed in Chapters 3 and 4, size-based diet progression is the mode of ontogenetic change for the larval phase of sardine and anchovy. Allometric increases in gape size for both species facilitated an increase in prey maximum, in turn increasing their niche breadth (Figure 7.1a). This ecomorphological relationship is commonly found in small pelagic fish larvae and has been observed in many species (Tudela et al., 2002; Karpouzi & Stergiou, 2003; Morote et al., 2008). There may be many applicable explanations for this observation, such as intraspecific competition (Schoener, 1983) and increased calorific quality of prey. However, synchrony with the ambient prey field may also help describe the observed subtle trend. As highlighted in Chapter 4, early naupliar and copepodite stages are crucial dietary components of larvae, with later copepod life history stages becoming of increasing importance with increasing fish size. Therefore, for newly exogenously feeding larvae to successfully forage within a patch of early life history stages of copepods, it is important to match their gape size to the dominant copepod stages. Evidence suggests that although cohorts are likely being continuously produced, there are still clear highs and lows of age-specific abundance of copepods. Verheye (1991) studied the short-term variations in abundance of *Calanoides carinatus* life history stages at a station in the southern Benguela. It was evident that there was continuous low recruitment of copepodite stages throughout the study period (ca. one

month), but there was a single clear high-density event during the period. Monthly peaks in density are evident for dominant copepod species in other Eastern Boundary Upwelling Systems (Hidalgo et al., 2005; Hidalgo & Escribano, 2008). Therefore, if larvae increase their gape size at a rate matching that of copepod growth, they will be able to continually feed on the same patch and cohort of copepods.

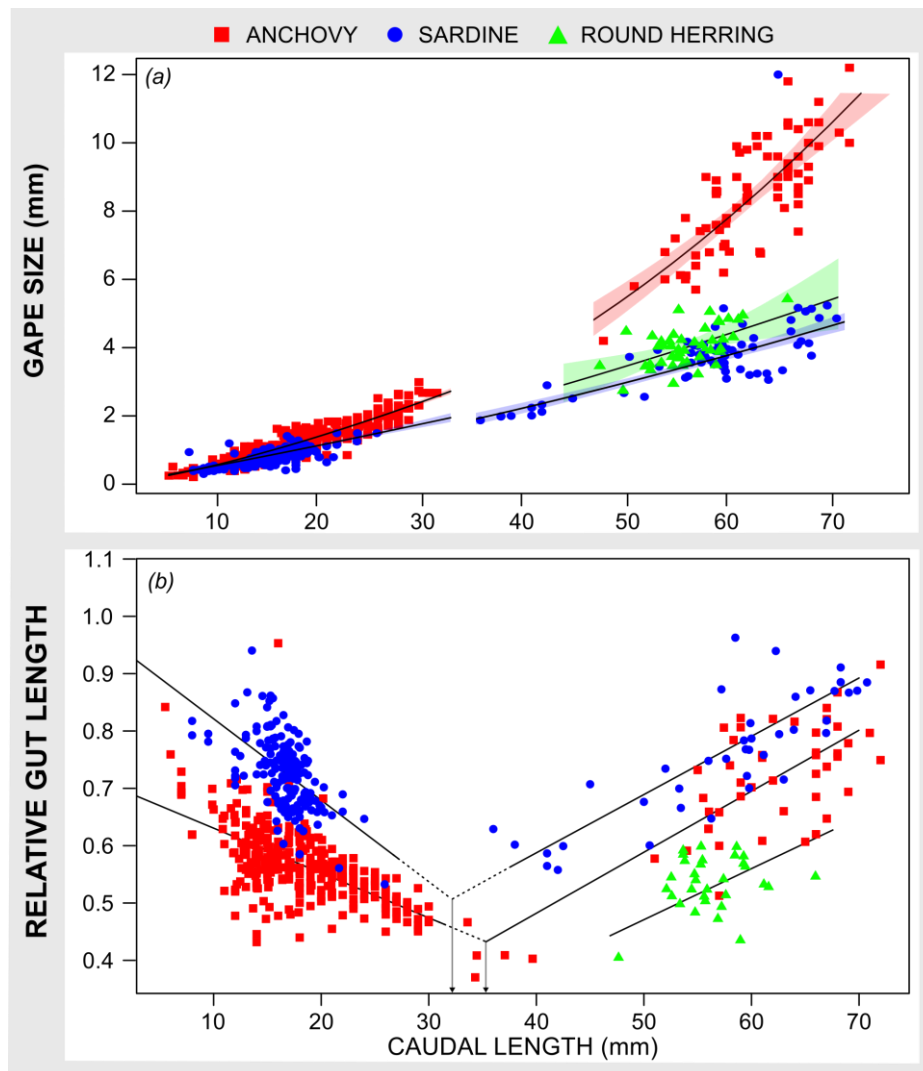


Figure 7.1. The gape size and relative gut length against caudal length (mm) of the three studied species combining the separate analyses of the larval stages from Chapter 3 and the juvenile stages from Chapter 5. The shaded areas depict 95 % confidence intervals.

The majority of ontogenetic changes in diet tend to be size related changes (Werner & Gilliam, 1984). Without any appendages to grab and manipulate prey, feeding in fish is largely dependent on mouth morphology and apparatus (Sánchez-Hernández et al., 2019b). As detailed in Chapters 3 and 4, size-based diet progression is the mode of ontogenetic change for the larval phase of sardine and anchovy. Allometric increases in gape size for both species facilitated an increase in prey maximum, in turn increasing their niche breadth (Figure 7.1a). This ecomorphological relationship is commonly found in small pelagic fish larvae and has been observed in many species (Tudela et al., 2002; Karpouzi & Stergiou, 2003; Morote et al., 2008). There may be many applicable explanations for this observation, such as intraspecific competition (Schoener, 1983) and increased calorific quality of prey. However, synchrony with the ambient prey field may also help describe the observed subtle trend. As highlighted in Chapter 4, early naupliar and copepodite stages are crucial dietary components of larvae, with later copepod life history stages becoming of increasing importance with increasing fish size. Therefore, for newly exogenously feeding larvae to successfully forage within a patch of early life history stages of copepods, it is important to match their gape size to the dominant copepod stages. Evidence suggests that although cohorts are likely being continuously produced, there are still clear highs and lows of age-specific abundance of copepods. Verheye (1991) studied the short-term variations in abundance of *Calanoides carinatus* life history stages at a station in the southern Benguela. It was evident that there was continuous low recruitment of copepodite stages throughout the study period (ca. one month), but there was a single clear high-density event during the period. Monthly peaks in density are evident for dominant copepod species in other Eastern Boundary Upwelling Systems (Hidalgo et al., 2005; Hidalgo & Escribano, 2008). Therefore, if larvae increase their gape size at a rate matching that of copepod growth, they will be able to continually feed on the same patch and cohort of copepods.

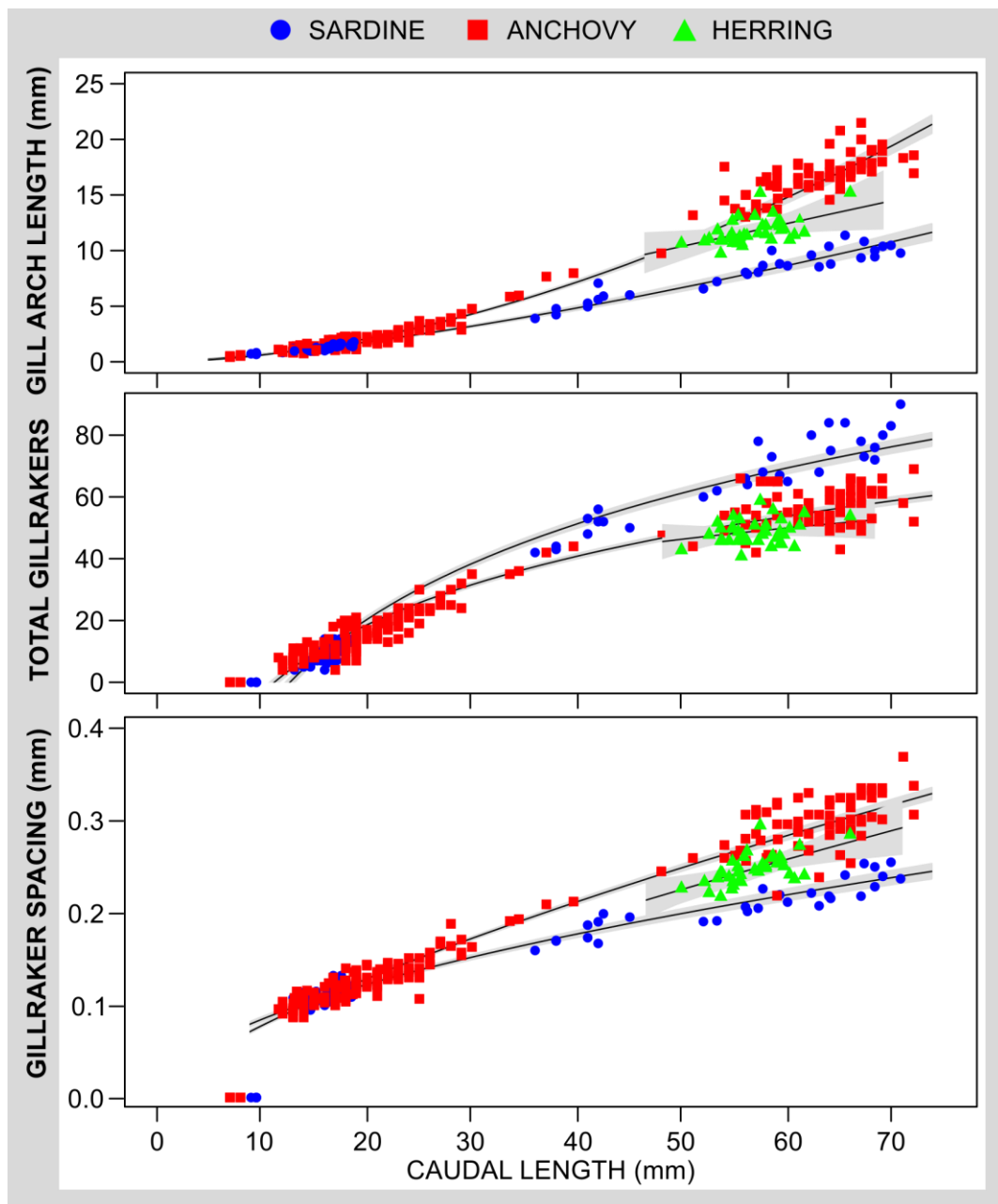


Figure 7.2. The relationship between caudal length (mm) and the three branchial basket meristic measurements of the three studied species combining the separate analyses of the larval stages from Chapter 3 and the juvenile stages from Chapter 5. The shaded areas depict 95 % confidence intervals.

There was also a likely change in the feeding mode during the studied clupeoids trophic ecology. Development of the branchial apparatus that facilitates filter feeding in both species is a big step. It is not sure at what point exactly filter feeding is initiated in clupeoids, and estimates seem to vary quite significantly. De Ciechomski (1966) found phytoplankton to be numerically dominant in the gut of the Argentine anchovy *Engraulis anchoita* at around 38 mm, implying filter feeding. Yet, King & Macleod (1976) estimated that filter-feeding occurred much later at around 80 and 100 mm for Namibian anchovy and sardine respectively (King & Macleod, 1976). From the results in Chapter 5, it was clear that active filter feeding was present in the pre-recruits of both anchovy and sardine (40 – 70 mm). Yet, for the larval size classes, the combination of their diet and lack of developed branchial baskets implied strictly particulate feeding. Consequently, filter-feeding likely initiated at some point between late-larvae and early pre-recruits. This was further corroborated from the relative gut length, as there seems to be an inflection point close to metamorphosis (~35 mm; Hunter, 1975; Armstrong & Thomas 1989) for both anchovy and sardine (Figure 7.1b). The relative gut length begins to increase in length, implying higher importance of autotrophic components that would be acquired through filter-feeding. Unfortunately, there was a lack of data in this study for the size of individuals during metamorphosis (~35 mm), and therefore the exact period cannot be concluded and would need further attention.

7.3. Sources of Trophic Partitioning

In addition to the ontogenetic change in diet for the three small pelagic species, this study has highlighted potential sources of niche partitioning between them during both larval and pre-recruit stages. For the larvae, there was a large degree of dietary overlap, however a degree of trophic partitioning was observed through a divergence in gape size-facilitating the consumption of larger prey by anchovy (Chapters 3 and 4). For pre-recruit stages, the trophic partitioning had become far more apparent, with species-specific distinct dietary components and isotopic signatures (Chapter 5). Dissimilar to larvae, this was likely facilitated through the compounding effects of gape size, branchial basket apparatus and feeding mode (Figure 7.1a, 7.2). This is more akin to the trophic separation described for adult anchovy, sardine, and round herring (van der Lingen et al., 2006c; van der Lingen & Miller, 2011). The trophic separation observed among all life stages of these

intraguild species serves as evidence that food limitation and interspecific competition for food resources exist. These trophic differences in adults have been proposed as a potential contributing factor for the differences observed in adult biomass (van der Lingen et al., 2006c; van der Lingen, 2021). Consequently, could this also be the case for the early life stages, where mortality is much higher? An ambient prey field better suited to early stages of one species over the other could have substantial effects on recruitment through differences in feeding success.

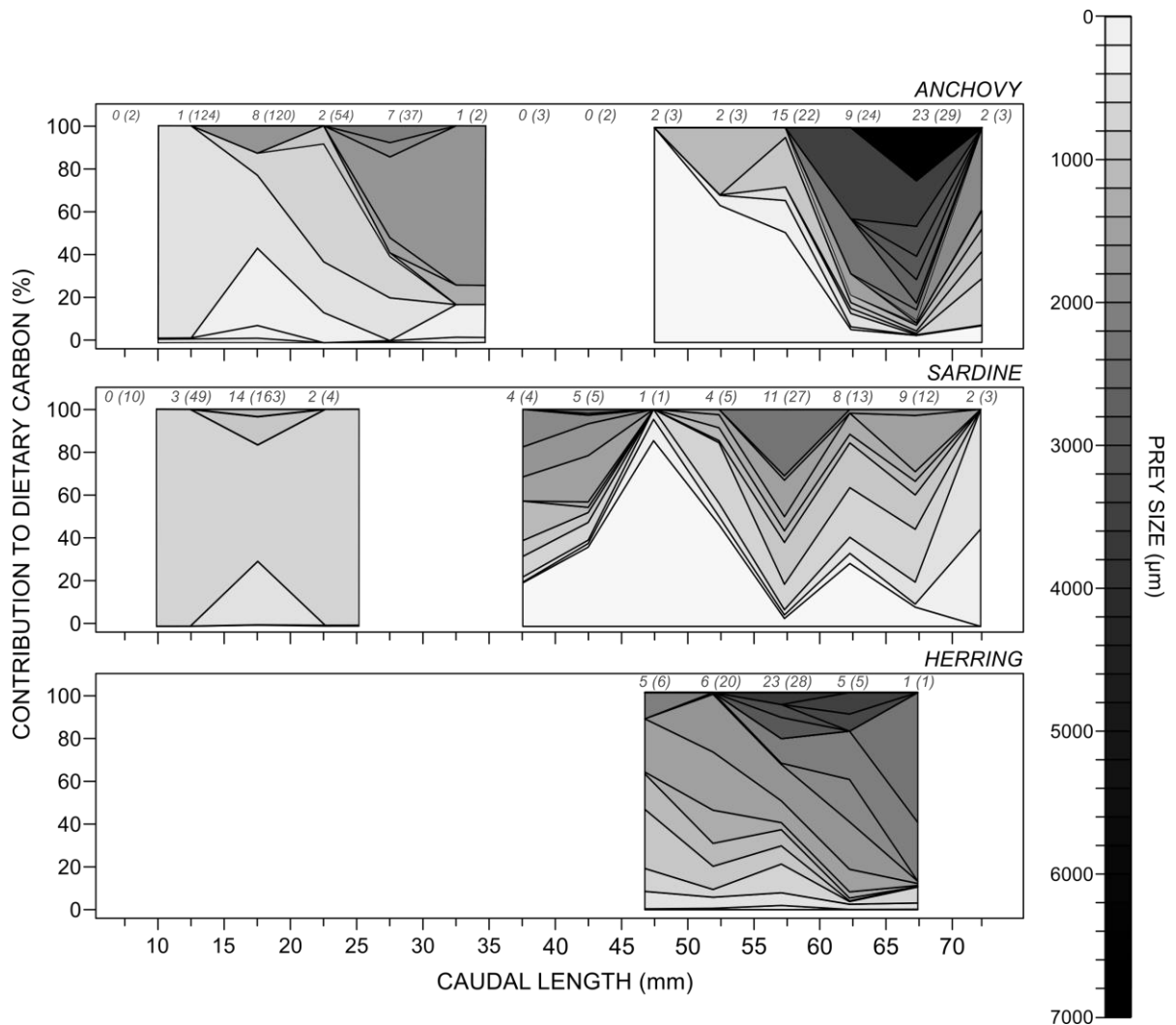


Figure 7.3. The contribution to dietary carbon (%) of each prey-size category (200 µm size bins) averaged for 5 mm length bins of larvae and pre-recruits of (a) anchovy, (b) sardine and (c) round herring. Italics numbers above each plot represents the number of full stomachs, numbers in parentheses represents empty stomachs. Results combined from Chapters 4 and 5.

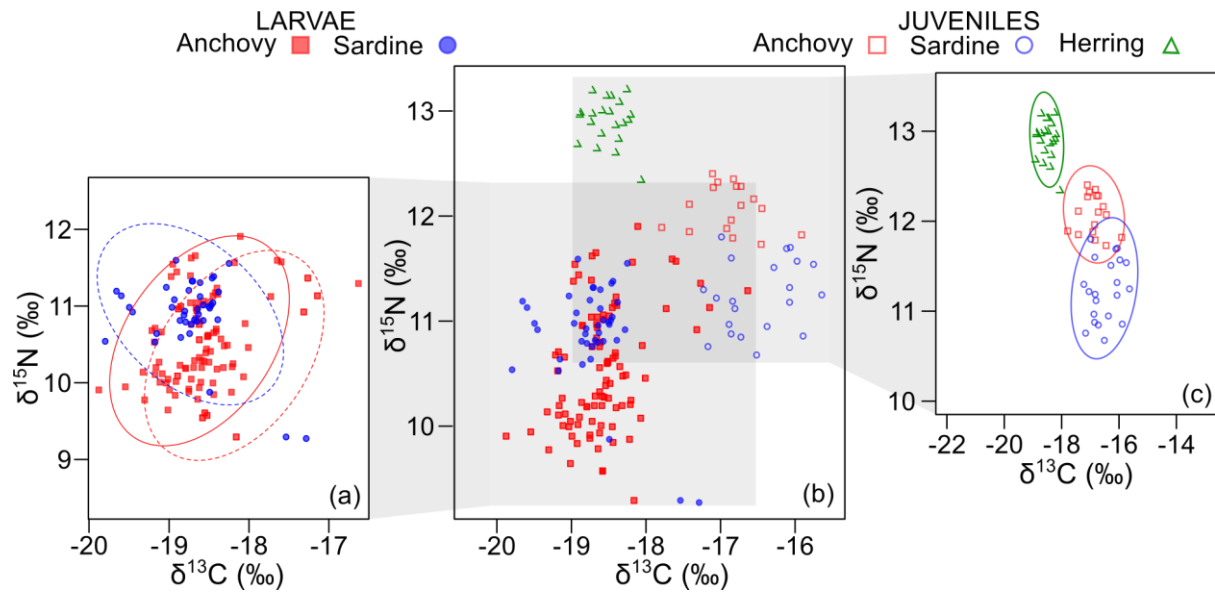


Figure 7.4. The combined (b) stable isotope analysis from Chapters 4 (a) and 5 (c); represents the isotopic biplot of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the three species, anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi* caught in the Benguela.

7.4. Recruitment and Climate Changes

Small pelagic fishes are characterised by a large variability in recruitment success, with mortality during early life stages being a common theory to explain these fluctuations (Hjort, 1914; Lasker, 1981; Cushing, 1990; Roy, 1993; Bakun, 1997; Swalethorp et al., 2022). As previously mentioned, starvation is a large contributor to mortality, and therefore having the appropriate ambient prey composition for first feeding and older larvae can have significant ramifications for overall recruitment. Many studies have linked increased recruitment with the increased provision of food, with many specifically mentioning the survival of early life stages (Beaugrand et al., 2003; van der Sleen et al., 2018; Brosset et al., 2020; Yu et al., 2020). Hence, given the observed trophic differences between larval sardine and anchovy, a change in ambient prey conditions favouring one species over the other could potentially lead to a disparity in survivorship. Examples of this have been highlighted for adult stages of small pelagic fish, for example, sticklebacks have increased in biomass significantly over the last couple of decades in the Baltic Sea. Rotifers, a key prey component of the stickleback's diet (Novotny et al., 2022), have significantly increased in abundance since the 1970s due to

anthropogenic induced environmental changes (Suikkanen et al., 2013). This has allowed sticklebacks to drastically increase in abundance. It is therefore not farfetched that there may be a similar process operating in the Benguela for early life stages of small pelagic fishes considering the observed climatic changes.

Due to strong natural interannual and decadal fluctuations in environmental conditions in the Benguela upwelling system, it is difficult to discern any strong environmental change. Yet, with the increasing presence of long-term data sets and satellite imagery, trends are being teased out in the Benguela upwelling system. As highlighted in Chapter 2, the system is experiencing a warming in the equatorward and poleward bounding waters (Rouault et al., 2009, 2010; Potts et al., 2014), a poleward shift in upwelling (Blamey et al., 2012; Jarre et al., 2015; Lamont et al., 2018a; Vizzy et al., 2018; Duncan et al., 2019), increased oxygen minimum zones in the northern Benguela (Diaz & Rosenberg, 2008; Monteiro et al., 2008; Stramma et al., 2010), and localised cooling and warming (Rouault et al., 2007; Dufois et al., 2012; Blamey et al., 2015; Jarre et al., 2015; Duncan et al., 2019). The newly documented trophic differences highlighted in this study pose the question of how small pelagic species will react in response to these environmental changes.

Primary and secondary production are closely linked to both large and local-scale environmental conditions (e.g., Lamont et al., 2014; Louw et al., 2016). Consequently, climatically induced environmental changes are likely to impact the productivity, biomass, or community structure of these lower trophic levels. Verheye et al. (2016) reviewed the productivity changes in both the nBUS and sBUS over the last 5 – 6 decades. To synthesise, primary productivity has increased in the nBUS (Demarcq, 2009), but not the sBUS (Hutchings et al., 2012; Jarre et al., 2015), and both systems have exhibited a substantial increase in total biomass of copepods with a relative increase in small over large individuals (Verheye et al., 2016a). Now, these changes are not what one might expect if we hypothesise that the differences in larval trophic ecology can impact the population trajectories of small pelagic fish species. Firstly, one would assume that if competition was a probable cause, then resources would be limiting, restricting the proliferation of either or both species simultaneously. However, the large increase in observed copepod biomass coupled with an overall reduction in fish stocks, would suggest that competition between these intraguild species has been reduced. Secondly, as described in this thesis, the trophic partitioning between sardine and anchovy early

life stages is size based, with sardine consuming smaller prey items on average (Figure 7.3, Chapters 4 and 5). Hence, with an increased relative biomass of smaller copepods we would expect that the ambient prey size composition would benefit sardine rather than anchovy. Yet, the relative adult biomass of both species over the last two decades in the southern Benguela suggests the opposite trend. Therefore, if trophic partitioning between the species was to contribute to the differences in recruitment and adult biomass, then there must be other contributing factors such as spatio-temporal variation in prey availability (Hjort, 1914; Cushing, 1990).

The majority of literature describes system changes either in reference to satellite derived indices, such as chlorophyll-a, or as bulk adult zooplankton biomass, such as copepods (Verheye et al., 2016). It is well documented in both literature and the results of this study, that smaller zooplankton such as heterotrophic protists (Kume et al., 2021) and early life history stages of copepods make up the majority of fish larvae diet (Chapter 4; e.g., Catalán et al., 2010; de Ciechomski, 1966; Hirakawa et al., 1997; Tudela et al., 2002). Therefore, using indices that relate to bulk biomasses of zooplankton may not be indicative of the actual prey environment for early life stages. For example, Bils et al. (2017) showed that the abundance of round herring larvae was better predicted by the abundance of dinoflagellates and copepodites rather than adult copepods. Similar studies have supported this, concluding that fish larval density was better correlated to small/micro zooplankton and early life history stages of copepods (Yu et al., 2020; Huang et al., 2021). Consequently, despite significant changes in bulk zooplankton, specifically copepods, in the Benguela upwelling system, there could be different trends in small zooplankton taxa which may have an effect on the survival of early life stages on small pelagic fish.

Cushing's (1990) Match-Mismatch Hypothesis is founded on the synchrony of phenology between predator and prey. The importance of suitable prey items available to first feeding larvae is crucial to mitigate starvation. Small pelagic fishes in the Benguela have a strict spawning schedule that facilitates the recruitment of eggs and newly hatched larvae to recruit into productive nursery grounds, such as Walvis Bay, Namibia (Boyer & Hampton, 2001) and St Helena Bay, South Africa (Shelton & Hutchings, 1982), during peak productivity. As demonstrated in Chapters 3 and 4, both sardine and anchovy larvae are constrained by prey size, determined by their maximum gape width. This limitation primarily directs their diet toward small zooplankton, with a focus on the early life

history stages of copepods. Therefore, the synchrony of first feeding small pelagic larvae with the developmental stages of copepods is crucial. The phenology and growth of lower trophic levels are tightly coupled with environmental conditions, especially temperature (Huntley & Lopez, 1992; Edwards & Richardson, 2004; Mackas et al., 2012). Therefore, in the face of the environmental changes observed over the last 5 decades in the Benguela, it would not be contrived to believe that there are phenological ramifications which may reduce the temporal synchrony of predator and prey.

There are two elements to this potential discord, firstly, divergence of phenological relationships between sensitive trophic interactions, and secondly changes in growth rates. Growth rates of copepods are tightly coupled to temperature, with temperature explaining 90 % of the variance between species (Huntley & Lopez, 1992). Hence, with the decreasing temperature in St Helena Bay (Dufois et al., 2012; Blamey et al., 2015) and increasing in the nBUS (Rouault et al., 2007), we would expect to see a change in the growth rate of individual copepods. Depending on the change, this may cause divergence in the previously described synchrony between predator and prey. Changes in phenology are becoming increasingly apparent (e.g., Asch, 2015; Régnier et al., 2019; Weigel et al., 2021; Wilson et al., 2018). Asch (2015) showed that almost 60 % of the studied fish larvae (43 species) in the California Current had shifted in their seasonal peak abundance. This adaptation to a changing climate will be significant if the species constituting important trophic interactions change at a different rate. Unfortunately, this seems to be the case. Significant differences in both the rate and direction of change are observed across trophic levels and functional groups, leading to phenological asynchrony (Thackeray et al., 2010; Régnier et al., 2019; Brosset et al., 2020). This issue has been highlighted as a key cause to the observed decline in Western Baltic Spring Spawning herring. With temperatures rising earlier in spring due to climate change, spawning occurs earlier which causes a mismatch in the larvae and the peak plankton boom (Moyano et al., 2022). These conspicuous implications of climate change could be manifested in the Benguela upwelling system, creating a mismatch for larvae of small pelagic fishes. Furthermore, with the described trophic differences between sardine and anchovy larvae in Chapters 3 and 4, how these changes in ambient prey conditions will affect either species is unknown and warrants attention. Very little is known about the phenological changes and peak abundances of early life history stages of copepods in the Benguela. Understanding their dynamics in relation to small pelagic larvae may elucidate important

information regarding the differences in adult biomass trajectories of the two species in the southern Benguela.

In addition to synchrony between predator and prey, Lasker's Stable Ocean Hypothesis (1981) proposes that during periods of calm waters, sufficient densities of plankton are produced, which in turn facilitate successful larval feeding. On the other hand, turbulent mixing during periods of rough waters may significantly reduce prey densities, leading to a decrease in larvae-prey encounter rates. This theory is supported by Cury and Roy's Optimal Environmental Window Hypothesis (1989), which suggests that areas with strong wind and upwelling experience reduced recruitment success due to physical constraints on larval mortality rates. In the Benguela region, upwelling has been increasing towards its poleward extent, especially on the south coast (Lamont et al., 2018a; Duncan et al., 2019). Since the spatial reorganisation of the sardine stock in the early 2000s, the south coast has become an important nursery ground for warm temperate sardines (McGrath et al., 2020; Teske et al., 2021). As a result, successful feeding in warm temperate sardine larvae may be hampered by an increase in turbulent water events, leading to a decrease in prey availability.

7.5. Comparative Trophic Ecology of Clupeoids

The trophic ecologies of the early life stages of the three small pelagic fish species in this study are consistent with previously described literature. Dietary composition for larvae is dominated by early life history stages of copepods. Broadly speaking global both anchovy and sardine have (a) similar dietary preferences, with nauplii and early copepodite stages dominating their diet, and (b) a similar dietary progression. The anchovy in the study were akin to other anchovy larvae such as the European anchovy (*Engraulis encrasicolus*) from the North Atlantic and Mediterranean, Japanese anchovy (*Engraulis japonicus*) and Argentinean (*Engraulis anchoita*) anchovy, with nauplii and early copepodite stages being the most important source of dietary carbon (de Ciechomski, 1966; Hirakawa et al., 1997; Tudela et al., 2002; Catalán et al., 2010). A similar progression in prey width was highlighted throughout their early life ontogeny, with old copepodite stages and adult copepods becoming increasingly more important. A similar trend is apparent for other sardine larvae: European sardine (*Sardina pilchardus*), Common sardine (*Strangomera bentincki*), Japanese sardine (*Sardinops melanostictus*)

and Pacific sardine (*Sardinops sagax*) feed almost exclusively on nauplii and copepod eggs, which then progresses into adult stages of copepods (Watanabe & Saito, 1998; Muck et al., 1989; Conway et al., 1994; Voss et al., 2009; Morote et al., 2010; Yasue et al., 2011; Contreras et al., 2014; Hirai et al., 2017).

The interspecific difference arises from prey size rather than prey species. This study highlighted a divergence in gape size between anchovy and sardine larvae, with anchovy having a larger gape. This was manifested in the dietary analysis, with a larger prey size on average in anchovy than sardine. Morote et al. (2010) highlighted similar dynamics in sympatric clupeoids, where a larger average prey size was consumed due to a larger gape in Mediterranean anchovy. This appears to be an important competitive dynamic for larvae, as larval clupeoids have not yet developed their operational branchial baskets that facilitate adult filter-feeding methods (Hunter & Thomas, 1974; Blaxter & Hunter, 1982).

Garrido and van der Lingen (2014) summarised the gaps and limitations in our current understanding of the trophodynamics of small pelagics. The work presented here directly addresses several of their key points. To put the work in perspective, several of the key areas identified by the authors, namely stomach contents, stable isotopes, and branchial morphology, have been plotted with similar studies of the adult stages of southern African clupeoids. It is clear from Figures 7.5 – 7.9 that in terms of trophic development, the most exaggerated change is during the early life stages.

For all three species there are defined enrichment trends in stable isotope ratios. There is a clear ontogenetic trend of ^{13}C enrichment for all three species. It is well described that diatom- and benthic-based production is typically ^{13}C enriched, whereas pelagic phytoplankton, such as dinoflagellate-based is depleted (Fry & Wainright, 1991). Therefore, this enrichment of ^{13}C throughout the ontogeny of all species is likely due to an increased dependence on coastal phytoplankton derived food webs. There is a general enrichment of ^{15}N for all species during their ontogeny, though it appears that there is greater variance between studies during the adult stage. (Figure 7.5). It would be difficult to discern if this was a result of temporal differences or from the trophic flexibility exhibited by adults. This would need to be explored via monitoring studies of these species.

There are not many dietary studies that have analysed stomach contents by contribution to dietary carbon for the three study species, yet the foundational papers by

James (1987) and van der Lingen (2002) give detailed stomach analysis of anchovy and sardine adults. As seen in Figure 7.6, the trend in prey size consumption observed in anchovy larvae and pre-recruits continues into adulthood with an increase in the prey size selected with fish size. For sardine, there is little difference between the prey size composition of diet pre-recruits (this study) and adults (Figure 7.6; van der Lingen, 2002). The only study that looks specifically into the trophic ecology of round herring was that by Wallace-Fincham (1987), which despite its thoroughness, did not include contribution to dietary carbon, and therefore not used here as a comparison.

Branchial basket data was collected from the following studies: Idris et al. (2016), King and Macleod (1976), Horton and van der Lingen (2019), Wallace-Fincham (1987) and this study. Previously published data shows that for anchovy and sardine there were no previous estimates of branchial morphology for individuals smaller than approximately 60 mm. In this study, gillraker spacing increases the greatest during the early stages of both sardine and anchovy, which is supported by the stable isotope results.

Interestingly there appears to be a clear difference in gillraker spacing for anchovy between regions (Figure 7.7). These distinctions have been used in the past for sardine to support the hypothesis of spatially distinct stock structure (Idris et al., 2016). It is obviously difficult to identify whether this difference is genetically or phenotypically driven. Even if environmentally-mediated phenotypic plasticity is occurring, regional differences in anchovy gillraker spacing offer foundational insights into the potential existence of sub-populations of anchovy around the southern African coast. The eastward increase in gillraker spacing from Namibia to the East Coast of South Africa is consistent with academic theory, suggesting that due to an eastward decrease in large-celled phytoplankton, planktivorous clupeoids become primarily zooplanktivorous. van der Lingen (2002) studied the diet of sardine around the coast of South Africa and showed that the relative contribution of phytoplankton to their diet was far smaller on the east coast than the west coast. Therefore, this environmental effect may be causing the observed difference gillraker spacing in anchovy.

Despite the same general methodology, there is a marked difference between the gillraker spacing of sardine pre-recruits from this study and from Idris et al. (2016; Figure 7.8). This difference may have arisen from two distinctions. Firstly, this study used Imaging software to compute gillraker spacing via pixels which has a higher accuracy and precision than reading from a graticule. Secondly, the methods by Tanaka et al. (2016)

described measuring the width of five gillraker spacings “*in the middle of the gill arch*”; this study took this to mean the centre of the ceratobranchial arch, which may have been different to Idris et al. (2016). It is difficult to understand the source of this difference exactly, and therefore this comparison should be made with caution.

Wallace-Fincham (1987) documented the branchial morphology of round herring, and it seems that the pre-recruits of this study had a similar morphology (Figure 7.9). It is evident that there has been a scarcity of scientific study on the trophic ecology of round herring in South Africa (Figures 7.5, 7.6 & 7.9). Prior to an exploratory expansion in the round herring directed fishery, it is key to understand their ecological role in the system. This was further supported by the results of Chapter 6, indicating that the data presently utilised to describe the ecology of round herring in the model substantially underestimates their role, particularly as prey, in the system. Therefore, future studies should be directed at round herring in the southern Benguela.

The trophic ecology of anchovy and sardine larvae highlighted in this study, is similar to that of small pelagic fish in the other cold water upwelling systems namely the California, Humboldt and Canary Current (see earlier in this section for comparison). This study has highlighted the role of the trophic ecology of these species as potential drivers of recruitment variability through changes in food availability and therefore feeding success. Utilising an end-to-end model, Sánchez-Garrido et al. (2019) explored the population dynamics of local clupeoids through the control of environmental conditions in the Canary Current. Using a comparable diet parameterisation for both anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), where anchovy preys upon larger items than sardine, the authors demonstrated that the primary driver of recruitment fluctuations during years of high variability was the survival and feeding of age-0 individuals. Similarly, in the Californian Current, variability was largely correlated to prey availability for anchovy *Engraulis mordax* and age-0 survival in sardine *Sardinops sagax* (Fiechter et al., 2015). Finally, Crus et al. (2022) utilising similar methods in the Humboldt Current provided evidence that recruitment strength was strongly correlated to larval mortality and zooplankton abundance in anchovy *Engraulis ringens*. It is clear that the predator-prey dynamics of small pelagic fish larvae in these systems warrants further attention to characterise the exact trophic links that undermine these key relationships.

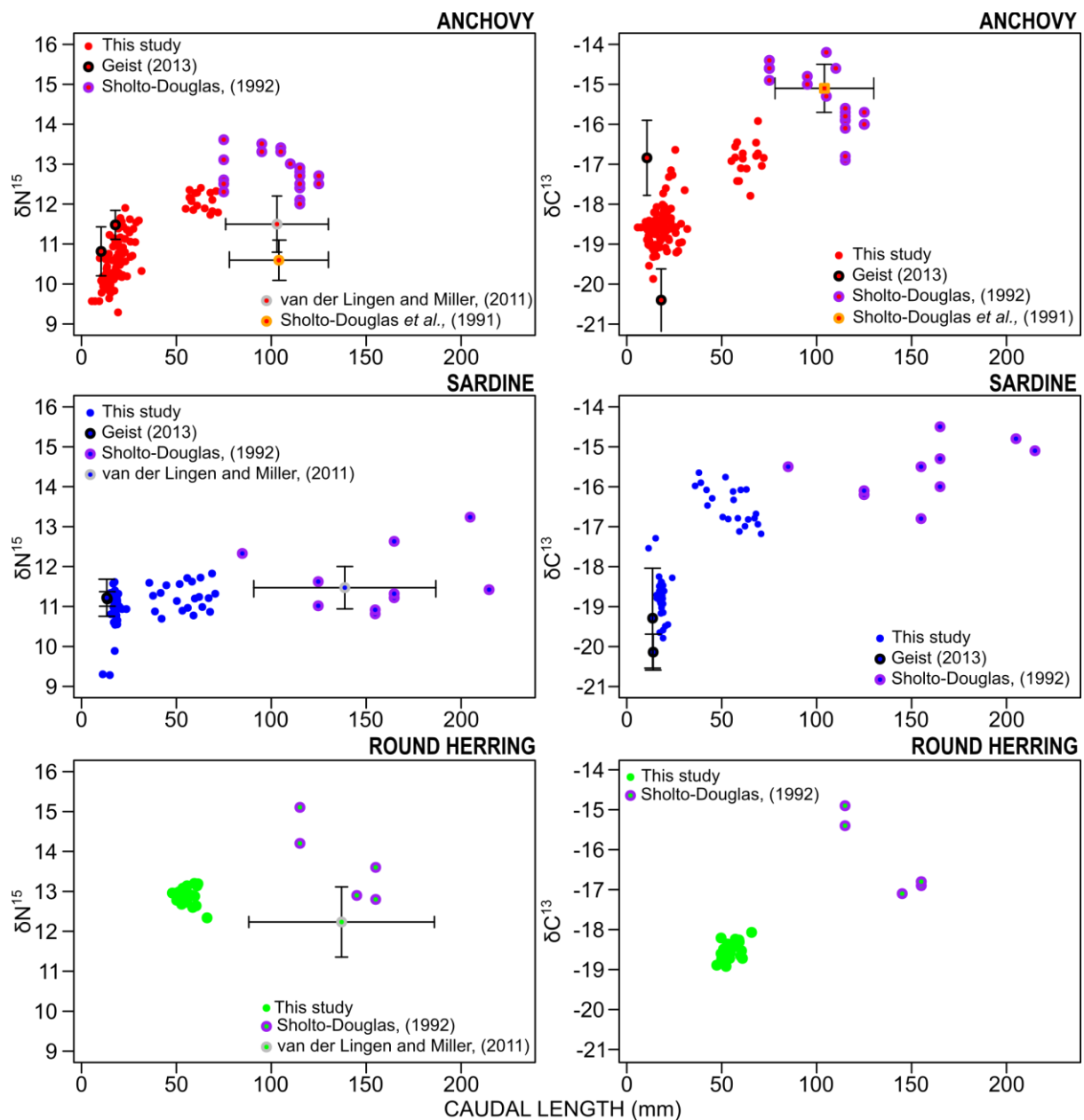


Figure 7.5. Stable isotope ratios of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the three small pelagic species in southern Africa from the following studies: this study, Geist (2013), Sholto-Douglas (1992), Sholto-Douglas et al. (1991) and van der Lingen and Miller (2011). Error bars represent standard deviation where appropriate for mean values.

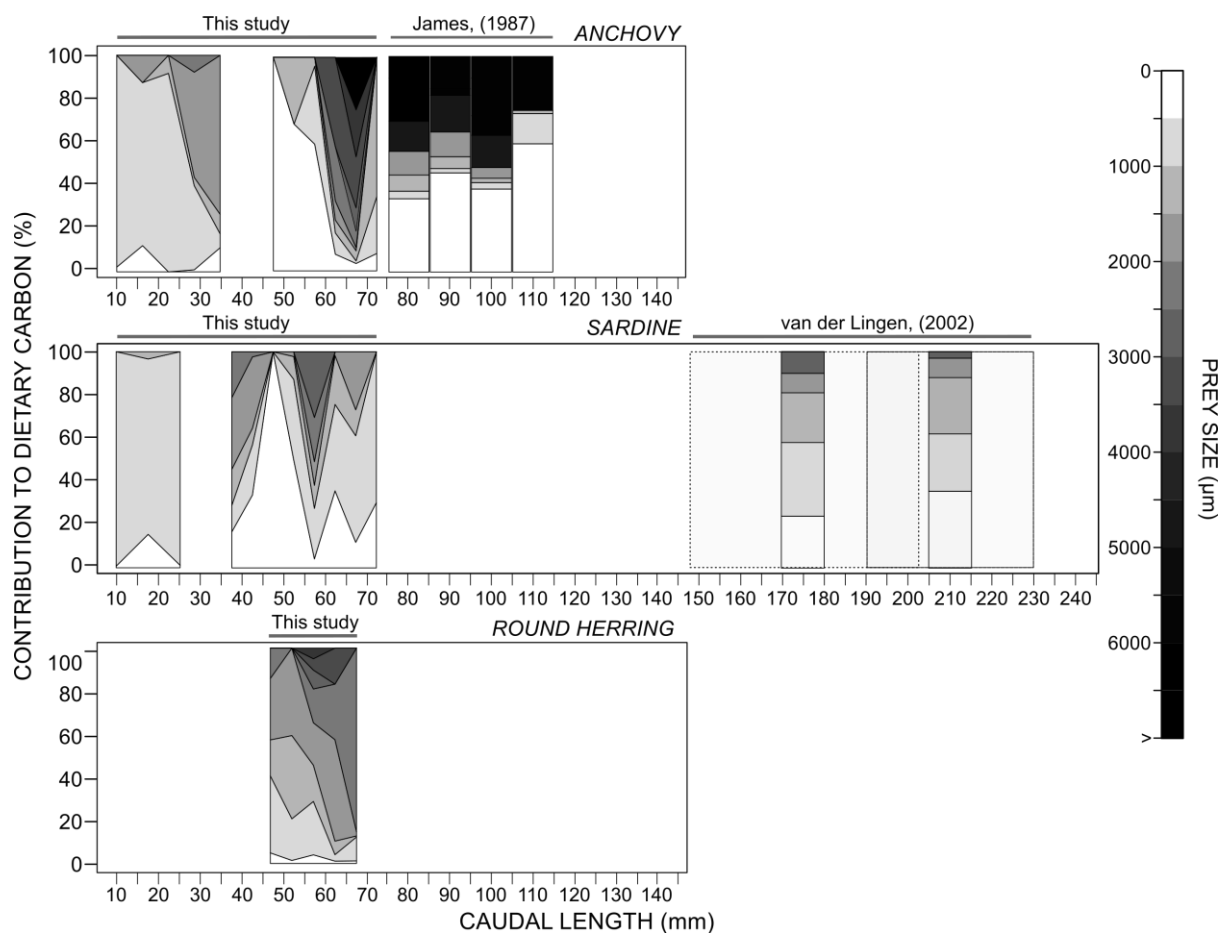


Figure 7.6. The contribution to dietary carbon (%) of site-categorised prey items for anchovy, sardine, and round herring in the Benguela from the following studies: this study, James (1987) and van der Lingen (2002). The grey boxes for the sardine from van der Lingen (2002) study represent the length range of the samples used for the mean diet values depicted.

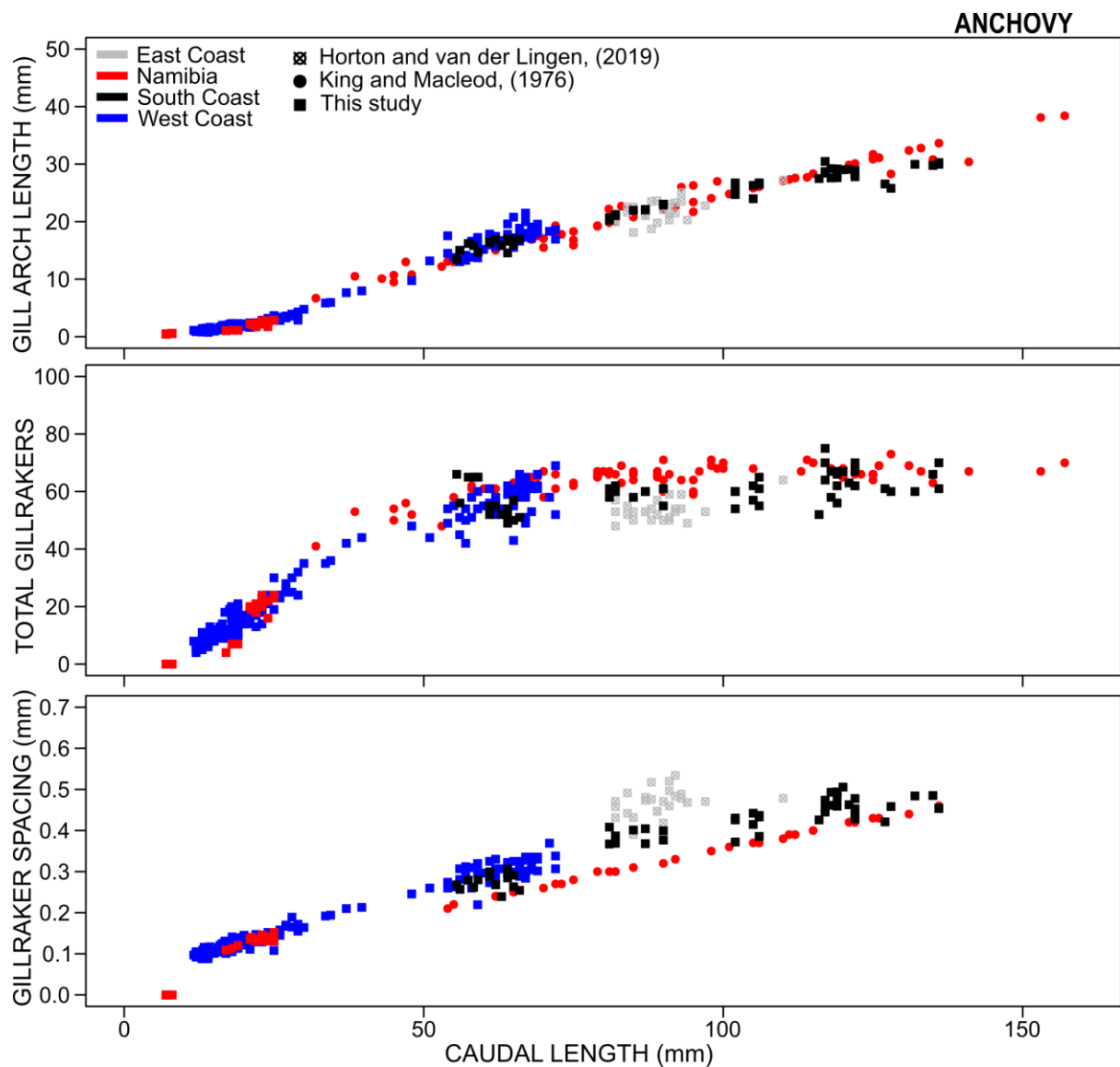


Figure 7.7. The relationship between caudal length (mm) and three branchial meristic measurements (a) gill arch length (mm), (b) total gillrakers and (c) gillraker spacing (mm) for all stages of anchovy *Engraulis encrasicolus* in southern Africa. Data are taken from the following studies: this study, Horton and van der Lingen (2020) and King and Macleod (1976).

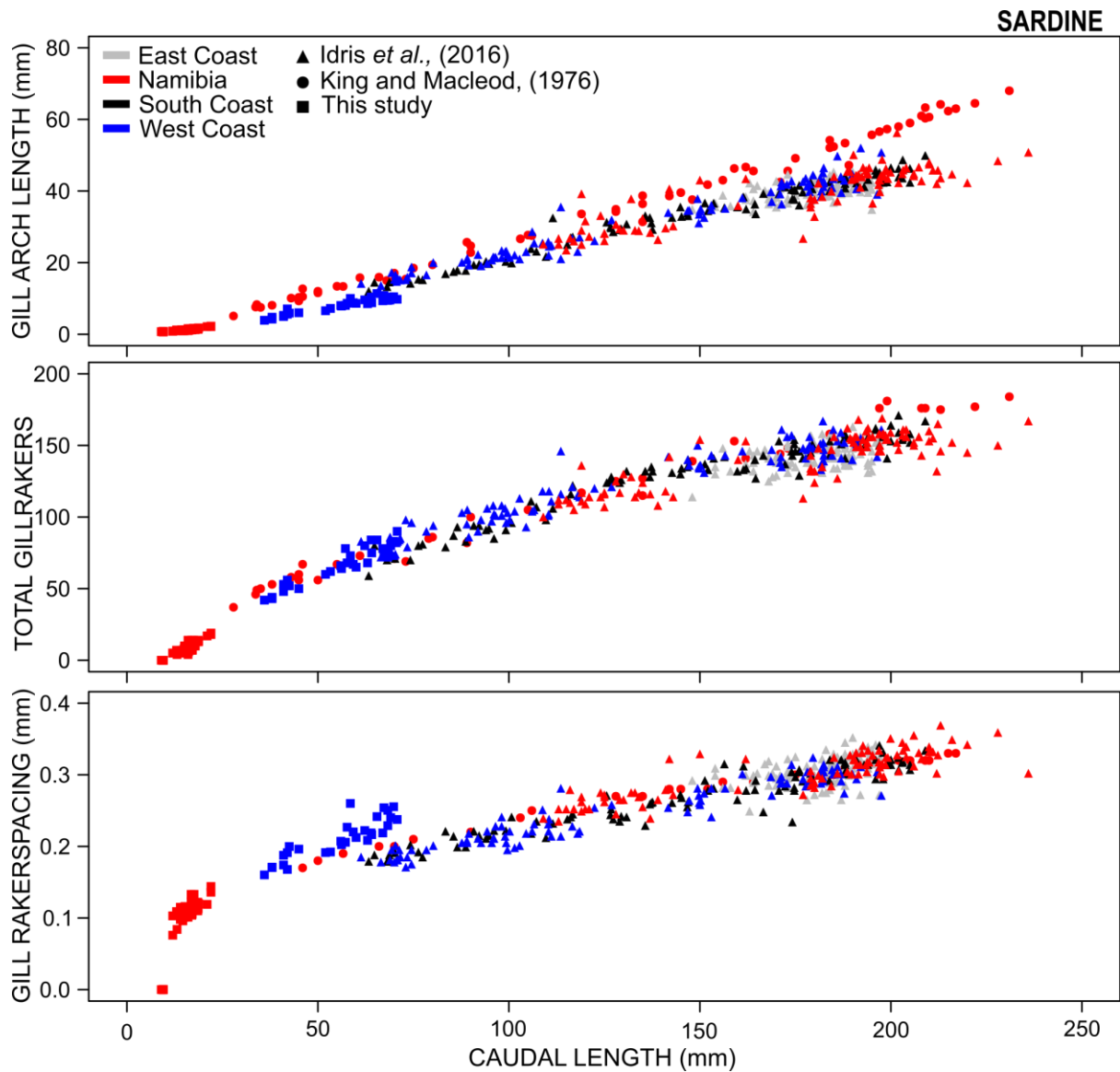


Figure 7.8. The relationship between caudal length (mm) and three branchial meristic measurements (a) gill arch length (mm), (b) total gillrakers and (c) gillraker spacing (mm) for all stages of sardine *Sardinops sagax* in southern Africa. Data are taken from the following studies: this study, Idris *et al.* (2016) and King and Macleod (1976).

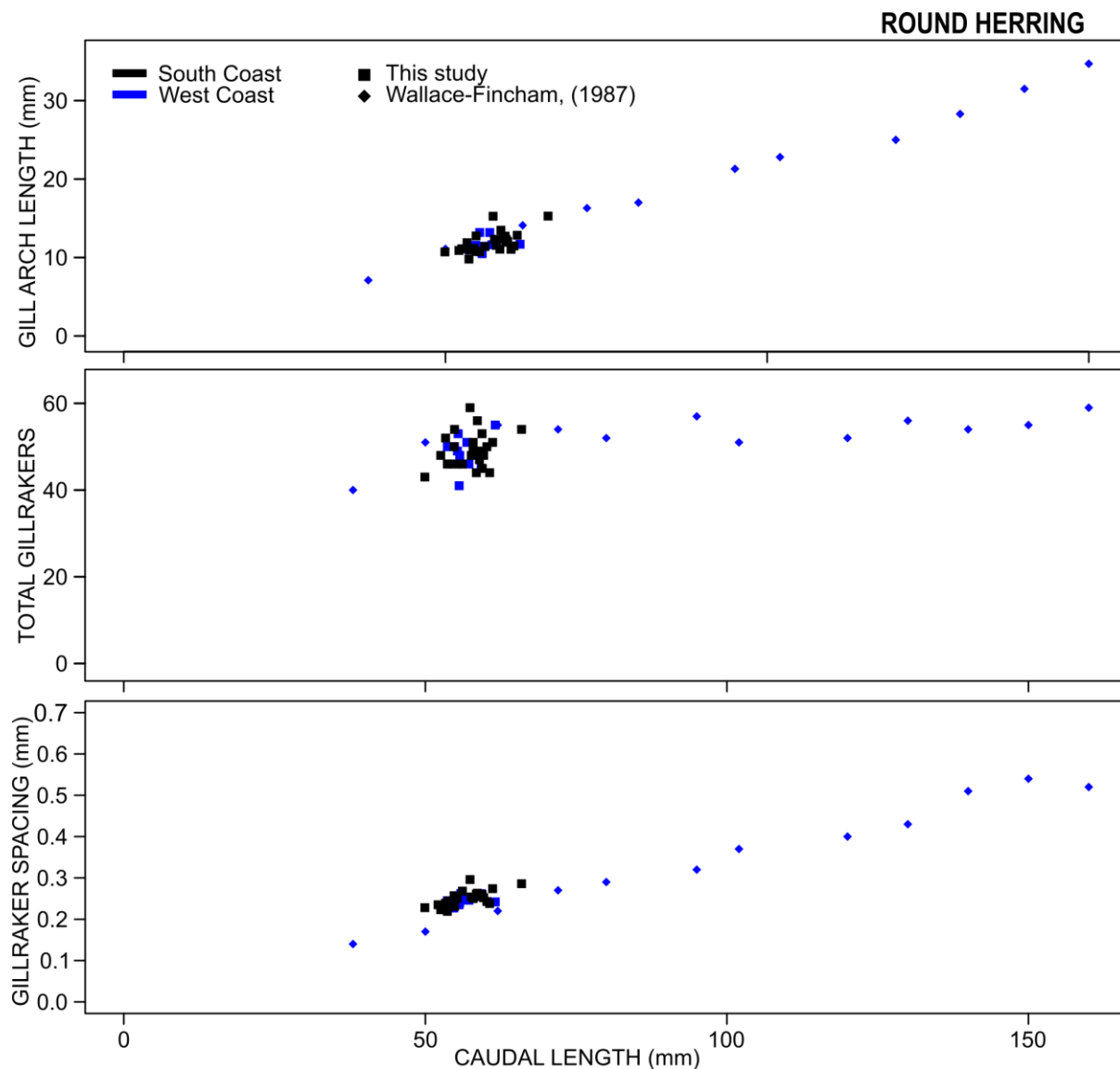


Figure 7.9. The relationship between caudal length (mm) and three branchial meristic measurements (a) gill arch length (mm), (b) total gillrakers and (c) gillraker spacing (mm) for all stages of round herring *Etrumeus whiteheadi* in southern Africa. Data are taken from the following studies: this study and Wallace-Fincham (1987).

7.6. Effects of Including Early Life Stages in Models

Conservation of marine ecosystems, whilst providing sustainable socio-economic growth and exploitation, is the basic principle of the South African Marine Living Resource Act of 1998. It requires the constant endeavour to manage the country's marine resources in a way that is both integrative and holistic whilst balancing the trade-offs between ecosystem services and the demands of stakeholders. Fundamentally this a

challenging and demanding task. The fisheries sector has long understood that it cannot continue utilising a traditional single-species management model - rather it must understand the ecosystem ramifications of exploitation and set catches according to ecosystem health rather than stock status, i.e., Ecosystem-Based Fisheries Management (EBFM, Pikitch et al., 2004). To implement EBFM, ecosystem models have become crucial tools to help strategically advise stakeholders and managers on the trade-offs between ecological and socio-economic demands. They are increasingly being applied to address questions of broad ecosystem change in the face of anthropogenic impacts, such as climate change (Marshall et al., 2017; Serpetti et al., 2017; Sánchez-Garrido et al., 2021), and management strategy evaluations such as MPAs (Olsen et al., 2018; Ortega-Cisneros et al., 2022) and changing fishing pressures (Olsen et al., 2018).

Following a workshop on “Modelling ecosystem interactions for informing an ecosystem approach to fisheries” that included the input of many different modelling experts, the FAO published a guide to the best practises of ecosystem modelling (FAO, 2008). There are two points in that document that are pertinent to this thesis. Firstly, when developing a model, the best practise is to initially include a fine resolution of taxonomic groups. Subsequently, this model can then be altered and specified to meet management questions and objectives. Secondly, the age, size or stage structure of species should be included if they are of particular interest. This study developed an already taxonomically extensive ecosystem model (Shannon et al., 2020) to include a finer resolution of life history stages for small pelagic fishes.

There were marked changes in both the species-specific function and the overall model function following the disaggregation. Firstly, regardless of overall model function, this study highlighted several predator-prey interactions that were affected by increased small pelagic pathways. Additionally, 11 out of 15 small-pelagic predators exhibited an improvement of the fit between model predicted biomass and the observed biomass, which amalgamated to an overall decrease in RSS of 11 % compared to the original model. Therefore, against the single criteria of reduction in RSS, the disaggregation of small pelagic fishes benefited the model. Disaggregation also results in significant decreases in the *Mean Length* and *Lifespan of fish*- this largely arose from reductions in the biomasses of large piscivorous species. It would be difficult to say that there has been an overall improvement, as ultimately the best model is specific to the intended management

objective. Yet, what we can conclude is that by introducing a finer life history stage resolution of small pelagic fishes, several aspects of the model are altered.

Although there were changes in the overall model function, there was one key issue that arose which had marked ramifications on subsequent model function. It seems that when disaggregating functional groups into life history stanza, if the same increase in resolution is not reflected in their prey, then vital trophic relationships can be lost. This became poignantly clear through an increase in a key model index; *Trophic Level of catch*. It is difficult to discern the exact manifestation of this change, however, a likely contributor was the inaccurate estimation of the trophic level of the small pelagic life history stages. As a consequence of primary and secondary production in the model being grouped into size-based fractions, the intricate trophic interactions of zooplankton, which are often not size based, are lost. It is apparent that the trophic level of copepods can vary drastically (Schukat et al., 2014) and these intricacies are absent in the current functional groupings. This has had ramifications in the model, by producing higher estimations of trophic levels for fish larvae, and then all subsequent consumers. Therefore, if using a model of higher life history resolution of small pelagics was to be continued, thought would need to be applied into the further disaggregation of their prey.

Walters (1986, page 189) described trophic models on a scale of complexity and uncertainty, whereby increasing parameterisation results in increasing uncertainty, and simplicity results in model bias (Collie et al., 2016). Consequently, there is no “one size fits all”, yet this does not stop the constant criticism of “omission” or “commission” in contrasting models. The most prominent part of the discussion in any modelling paper will be the caveats and limitations, whether this is omitting or simplifying specific groups (e.g., Fiechter et al., 2015) or the uncertainty arising from the degree of parameterisation (e.g., Ortega-Cisneros et al., 2022; Surma et al., 2021). Hence, if one was to be critical, it could be argued that despite seeing changes in the model output described in this thesis, the increased parameterisation will likely increase the uncertainty of the output. Yet, it seems that model conclusions tend to go missing in the crux of uncertainty, which can often lead to inaction of management inferences. Walters (1986) stated “*that resource managers must learn to live with some very substantial uncertainties*” and although we must acknowledge and be cognizant of uncertainty, it will likely always be significant in large, parameterised models. Therefore, it is becoming commonplace for these models to be utilised in conjunction with a suite of models varying in complexity. This is being

performed in both the Californian Upwelling System (Kaplan et al., 2019) and the Benguela Upwelling System (Smith et al., 2015; Ortega-Cisneros et al., 2017; Shannon et al., 2020).

During the original conception of this thesis, there was a clear order of research. Firstly, conduct field studies to gather ecological information on small pelagic fish, and secondly, utilise this information by developing corresponding life history stages in an ecosystem model. Yet, with hindsight, preliminary investigations utilising the EwE model would have greatly benefitted this study. As mentioned, trophic studies of larval fish can be laborious, time-consuming, and expensive. Exploring certain diet composition scenarios of life history stages in Ecopath with Ecosim first could have provided clear direction for subsequent field studies. Key parameters could have been identified facilitating targeted sampling and better use of resources. For example, the diets described in Chapters 3, 4 and 5 are meticulously detailed yet this was unmatched in the planktonic groupings of the ecosystem model. Time could have been saved by focusing on a similar taxonomic resolution. Conversely, running scenarios before going into the field would have highlighted the need for a functional grouping of zooplankton, which may have provided an alternative direction for the thesis. Obviously, there are other reasons for gaining a fully integrated picture of the trophic ecology of these stages, however from a modelling point of view this may have been unnecessary. The strategic use of ecosystem models goes beyond informing high level management or policy, as there is obvious value in using them as a tool to help design more focused and targeting field studies.

This model is not intended to be used strategically for management purposes and it would need further work analysing sources of uncertainty to meet critic's standards. However, it has illustrated that despite the relevant insignificance in terms of mass, small pelagic larvae can have system wide effects in an ecosystem model. Yet, more importantly, this study has provided a valuable lesson for future studies looking to disaggregate groups further, that the resolution of prey model groups needs to complement the resolution of predator model groups.

7.7.Limitations and Future Work

There are several limitations of this study that are a product of both temporal and financial constraints, which were compounded by the global Covid-19 pandemic. There were several data issues in this study the first being the issue of missing fish size classes. It was obviously an aim of the study to sample across all size classes from newly exogenously feeding larvae through metamorphosis to pre-recruits. As highlighted, the period of metamorphosis was marked as a potentially important period for development of alternative feeding modes. Secondly, the aseasonality and lack of interannual representation in the data was not the original intention. With seasonal trends seen in primary and secondary production (Louw et al., 2016; Lamont et al., 2018b) there are obvious temporal trends in the trophic ecology of fish (e.g., Costalago et al., 2012; Holt et al., 2019). Thirdly, there was a total absence of both round herring and sardine larvae sampled in the southern Benguela, precluding a full ontogenetic comparison between the three species. Unfortunately, with any marine study, one is at the mercy of the ocean, and can only sample what is there at that time. Additional planned cruises were hindered due to the pandemic. Therefore, future data contributions of these species are warranted.

With any scientific conclusion, many other questions arise. The conclusions from the stable isotope and stomach content analysis in Chapter 4 described potential missing prey items from the stomach contents. Modern ecological methods that have a high taxonomic resolution of prey from stomach contents, such as DNA metabarcoding and qPCR (Kume et al., 2021; Novotny et al., 2022), should be employed to gain an understanding of the microscopic, soft bodied individuals that are likely important prey items but rapidly digested and not identified. Obviously, it is problematic that the feeding incidence of larvae is very low (Chapter 4), so even employing these methods may still be an arduous task due to very high sample sizes. Therefore, the use of modern biochemical analyses will remain extremely useful. However, as shown in Chapter 4, the use of specific fatty acid trophic markers will need to be revisited specifically for fish larvae. Ground-truthing of specific markers, in particular the trophic markers utilising short chain saturated fatty acids, is imperative before any further application.

In the EwE model, species are primarily categorised based on their functional traits, yet phytoplankton and zooplankton are sorted by size. Size has been a common trait to aggregate plankton as it is inherently linked to broad functional and physiological traits (Andersen et al., 2016; Litchman et al., 2017). However, the results from this study suggest that having them as size fractionated components might miss key trophic

interactions. Additionally, it has been observed zooplankton responses to climate change vary among functional groups (Pecuchet et al., 2020; Venello et al., 2021; Heneghan et al., 2023). Therefore, segregating zooplankton into functional groups can help understand the trophic pathways and predict how these systems will react under climate change. Heneghan et al. (2020) applied a functional size-spectrum model (Zooplankton Model of Size Spectra version 2) that groups zooplankton into nine functional groups on freely available global data sets. Model predictions were consistent with observed patterns and results provided interesting insights into the key supporting roles of specific functional zooplankton groups on fish biomass. Using these emerging models to aid in segregating zooplankton biomass in the Benguela into model functional groups could be a promising future direction.

Another avenue of interest highlighted by this study is round herring. As shown in the EwE model in Chapter 6, the ectotrophic efficiency for both juveniles and adults was < 0.7 . This shows that from the given data available, this species was underutilised in the ecosystem model. Given that there are recommendations to diversify catches in the small pelagic sector in South Africa (van der Lingen, 2021b), and round herring is an attractive alternative to sardine, it would be necessary to better understand their ecological importance in the southern Benguela before increased exploitation is considered. The contribution of round herring to diets of predators needs closer attention and diets of predators in recent years need quantifying (most studies are now decades old – Wallace-Fincham, 1987; Roel & Armstrong, 1991). Lastly, as highlighted in this chapter, the potential for phenological divergence between small pelagic early life stages and their prey is an area of interest that has been identified in this study. We know of system changes in both abundance and average size of copepods in the southern Benguela, however it is unknown whether there have been temporal shifts in their phenology or changes to their growth rate. This is something that warrants attention and may add to the explanation of the lack of recovery seen in South African sardine stocks.

7.8. Conclusion

The research presented in this thesis provides valuable knowledge on the early ontogenetic development of the trophic ecology of commercially important small pelagic fishes in the Benguela. Yet, whilst the information gained is pertinent to understanding

their role in the ecosystem, it has generated further questions. The ecology of fish larvae has been an area of peaked interest, and with the development of novel modern analytical tools we have begun to decode the black box of larval dynamics. This information is crucial to start testing the decades of theories and hypotheses concerning the key recruitment and ecosystem processes that are dependent upon these stages. The work detailed here has provided additional information that will hopefully contribute to the already multi-faceted toolkit that aims to sustainably manage the small pelagic fishery.

References

- Ainsworth, C.H., Kaplan, I.C., Levin, P.S. & Mangel, M. (2010). A statistical approach for estimating fish diet compositions from multiple data sources: Gulf of California case study. *Ecological Applications*. 20(8):2188–2202.
- Akkers, T.R., Melo, Y.C. & Veith, W. (1996). Gonad development and spawning frequency of the South African pilchard *Sardinops sagax* during the 1993-1994 spawning season. *South African Journal of Marine Science*. 17:183–193.
- Albaina, A., Aguirre, M., Abad, D., Santos, M. & Estonba, A. (2016). 18S rRNA V9 metabarcoding for diet characterization: A critical evaluation with two sympatric zooplanktivorous fish species. *Ecology and Evolution*. 6(6):1809–1824.
- Amorim, P., Duarte, G., Guerra, M., Morato, T. & Stobberup, K.A. (2004). Preliminary Ecopath model of the Guinea-Bissau continental shelf ecosystem (NW-Africa). In *West African coastal ecosystems: models and fisheries impacts*. 7th ed. Palomares & D. Pauly, Eds. Vancouver: Fisheries Centre Research Reports. 95–112.
- Andersen, K. H., Berge, T., Gonçalves, R. J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N. S., Lindemann, C., Martens, E. A., Neuheimer, A. B., Olsson, K., Palacz, A., Prowe, A. E., Sainmont, J., Traving, S. J., Visser, A. W., Wadhwa, N., & Kiørboe, T. (2016). Characteristic sizes of life in the oceans, from bacteria to whales. *Annual review of Marine Science*, 8:217-241.
- Armstrong, M.J., Chapman, P., Dudley, S.F., Hampton, I. & Malan, P.E. (1991). Occurrence and population structure of pilchard *Sardinops ocellatus*, round herring *Etrumeus whiteheadi* and anchovy *Engraulis capensis* off the East Coast of Southern Africa. *South African Journal of Marine Science*. 11(1):227–249.
- Armstrong, M.J. & Thomas, R.M. (1989). Clupeoids. In *Oceans of Life off Southern Africa*. A.I.L. Payne & R.J.M. Crawford, Eds. Cape Town. 105–121.
- Arrhenius, F. (1996). Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* (L.)) in the northern Baltic Sea. *ICES Journal of Marine Science*. 53(4):701–712.

- Arula, T., Kotta, J., Lankov, A., Simm, M. & Põlme, S. (2012). Diet composition and feeding activity of larval spring-spawning herring: Importance of environmental variability. *Journal of Sea Research*. 68:33–40.
- Asch, R.G. (2015). Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*. 112(30):4065–4074.
- Auel, H., Harjes, M., Da Rocha, R., Stübing, D. & Hagen, W. (2002). Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. *Polar Biology*. 25(5):374–383.
- Augustyn, C.J. (1991). The biomass and ecology of chokka squid *Loligo vulgaris reynaudii* off the West Coast of South Africa. *South African Journal of Zoology*. 26(4):164–181.
- Augustyn, C.J., Lipinski, M.R., Sauer, W.H.H., Roberts, M.L. & Mitchell-Innes, B.A. (1994). Chokka squid on the Agulhas Bank: life history and ecology. *Suid-Afrikaanse Tydskrif vir Wetenskap*. 90:143–154.
- Bachiller, E., Albo-Puigserver, M., Giménez, J., Pennino, M. G., Marí-Mena, N., Esteban, A., Lloret-Lloret, E., Jadaud, A., Carro, B., Bellido, J. M. & Coll, M. (2020). A trophic latitudinal gradient revealed in anchovy and sardine from the Western Mediterranean Sea using a multi-proxy approach. *Scientific Reports*, 10(1):17598.
- Bailey, K.M. & Batty, R.S. (1984). Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. *Marine Biology*. 83(3):287–291.
- Bailey, K.M. & Houde, E.D. (1989). Predation on Eggs and Larvae of Marine Fishes and the Recruitment Problem. *Advances in Marine Biology*. 25(C):1–83.
- Bakun, A. (1997). Patterns in the ocean: ocean processes and marine population dynamics. *Oceanographic Literature Review*. 44(5):1–530.
- Bakun, A. & Nelson, C.S. (1991). The seasonal cycle of wind-stress curl in subtropical eastern boundary current regions. *Journal of Physical Oceanography*. 21(12):1815–1834.
- Bakun, A. & Parrish, R.H. (1982). Turbulence, transport, and pelagic fish in the California and Peru current systems. In *CalCOFI report*. V. XXIII.
- van der Bank, M. (2010). Studies on the integrated feeding of *Sufflogobius bibarbatus* (von Bonde, 1923) in the Northern Benguela ecosystem using fatty acid biomarkers and stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$). MSc Thesis. University of the Western Cape.

- Barange, M., Hampton, I. & Roel, B.A. (1999). Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from acoustic surveys. *South African Journal of Marine Science*. (21):367–391.
- Barlow, G.W. (1961). Causes and significance of morphological variation in fishes. *Systematic Zoology*. 10(3):105–117.
- Barlow, R.G. (1982). Phytoplankton ecology in the Southern Benguela current. III. Dynamics of a bloom. *Journal of Experimental Marine Biology and Ecology*. 63(3):239–248.
- Basilone, G., Guisande, C., Patti, B., Mazzola, S., Cuttitta, A., Bonanno, A. & Kallianiotis, A. (2004). Linking habitat conditions and growth in the European anchovy (*Engraulis encrasicolus*). *Fisheries Research*. 68(1–3):9–19.
- Basson, M. (1999). The importance of environmental factors in the design of management procedures. *ICES Journal of Marine Science*. 56(6):933–942.
- Batty, R.S. (1984). Development of swimming movements and musculature of larval herring (*Clupea harengus*). *Journal of Experimental Biology*. 110:217–229.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S. & Reid, P.C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*. 426(6967):661–664.
- Beckley, L.E. & Hewitson, J.D. (1994). Distribution and abundance of clupeoid larvae along the East Coast of South Africa in 1990/91. *South African Journal of Marine Science*. 14(1):205–212.
- Beckley, L.E. & van der Lingen, C.D. (1999). Biology, fishery and management of sardines (*Sardinops sagax*) in southern African waters. *Marine and Freshwater Research*. 50(8):955–978.
- Begg, G.A. & Waldman, J.R. (1999). An holistic approach to fish stock identification. *Fisheries Research*. 43(1–3):35–44.
- Benedetti, F., Gasparini, S. & Ayata, S.D. (2016). Identifying copepod functional groups from species functional traits. *Journal of Plankton Research*. 38(1):159–166.
- Beverton, R.J.H. & Holt, S.J. (1954). On the Dynamics of Exploited Fish Populations. 11th ed. R.J.H. Beverton & S.J. Holt, Eds. HMSO.
- Bils, F., Moyano, M., Aberle, N., Hufnagl, M., Alvarez-Fernandez, S. & Peck, M.A. (2017). Exploring the microzooplankton–ichthyoplankton link: a combined field and modeling study of Atlantic herring (*Clupea harengus*) in the Irish Sea. *Journal of Plankton Research*. 39(1):147–163.

- Bils, F., Aberle, N., van Damme, C.J.G., Peck, M.A. & Moyano, M. (2022). Role of protozooplankton in the diet of North Sea autumn spawning herring (*Clupea harengus*) larvae. *Marine Biology*. 169(7):1–16.
- Bjørke, H. (1976). Food and feeding of young herring larvae of Norwegian spring spawners. *Fisk. Dir. Skr. Ser. HavUnders.*, 16:405-421.
- Blamey, L.K., Howard, J.A.E., Agenbag, J. & Jarre, A. (2012). Regime-shifts in the southern Benguela shelf and inshore region. *Progress in Oceanography*. 106:80–95.
- Blamey, L.K., Shannon, L.J., Bolton, J.J., Crawford, R.J.M., Dufois, F., Evers-King, H., Griffiths, C.L., Hutchings, L., Jarre, A., Rouault, M., Watermeyer, K.E. & Winker, H. (2015). Ecosystem change in the southern Benguela and the underlying processes. *Journal of Marine Systems*. 144:9–29.
- Blaxter, J.H.S. (1963). The Feeding of Herring Larvae and Their Ecology in Relation to Feeding. *California Cooperative Oceanic Fisheries Investigations*. 10:79–88.
- Blaxter, J.H.S. (1968). Visual Thresholds and Spectral Sensitivity of Herring Larvae. *Journal of Experimental Biology*. 48(1):39–53.
- Blaxter, J.H.S. (1986). Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society*. 115:98–114.
- Blaxter, J.H.S. (1988). 1 Pattern and Variety in Development. In *The Physiology of Developing Fish. Part A. Eggs and Larvae*. V. 11. W.S. Hoar & D.J. Randall, Eds. London: Academic Press. 1–58.
- Blaxter, J.H.S. & Hunter, J.R. (1982). The Biology of the Clupeoid Fishes. *Advances in Marine Biology*. 20:1–223.
- Blaxter, J.H.S. & Staines, M.E. (1971). Food searching potential in marine fish larvae. In *Fourth European Marine Biology Symposium*. D.J. Crisp, Ed. Cambridge, UK: Cambridge University Press. 467–485.
- Bode, M., Hagen, W., Schukat, A., Teuber, L., Fonseca-Batista, D., Dehairs, F. & Auel, H. (2015). Feeding strategies of tropical and subtropical calanoid copepods throughout the eastern Atlantic Ocean - Latitudinal and bathymetric aspects. *Progress in Oceanography*. 138:268–282.
- Booi, K. (2000). Characterization and comparison of diets of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) pre-recruits from mixed shoals in the southern Benguela ecosystem. MPhil Thesis. University of Bergen.

- Boissonnot, L., Niehoff, B., Ehrenfels, B., Søreide, J. E., Hagen, W. & Graeve, M. (2019). Lipid and fatty acid turnover of the pteropods *Limacina helicina*, *L. retroversa* and *Clione limacina* from Svalbard waters. *Marine Ecology Progress Series*, 609:133-149.
- Borme, D., Tirelli, V., Brandt, S.B., Fonda Umani, S. & Arneri, E. (2009). Diet of *Engraulis encrasicolus* in the northern Adriatic Sea (Mediterranean): Ontogenetic changes and feeding selectivity. *Marine Ecology Progress Series*. 392:193–209.
- Boyd, A.J., Shannon, L.J., Schulein, F.H. & Taunton-Clark, J. (1998). Food, transport and anchovy recruitment in the southern Benguela upwelling system of South Africa. *From local to global changes in upwelling systems*. 196–209.
- Boyer, D.C., Boyer, H.J., Fossen, I. & Kreiner, A. (2001). Changes in abundance of the northern Benguela sardine stock during the decade 1990-2000, with comments on the relative importance of fishing and the environment. *South African Journal of Marine Science*. (23):67–84.
- Boyer, D.C. & Hampton, I. (2001). An overview of the living marine resources of Namibia. *South African Journal of Marine Science*. (23):5–35.
- Bradbury, I.R., Snelgrove, P.V.R. & Fraser, S. (2001). The influence of temperature on advective loss of Atlantic cod (*Gadus morhua*) eggs from the inshore environment. *Fisheries Oceanography*. 10(4):342–352.
- Brewer, G.D. (1976). Thermal tolerance and resistance of the northern anchovy, *Engraulis mordax*. *Fisheries Bulletin*. 74(2).
- Brosset, P., Smith, A.D., Plourde, S., Castonguay, M., Lehoux, C. & van Beveren, E. (2020). A fine-scale multi-step approach to understand fish recruitment variability. *Scientific Reports*. 10(1):1–14.
- Brownell, C.L. (1983). Laboratory rearing of Cape anchovy *Engraulis capensis* and South African pilchard *Sardinops ocellata* through metamorphosis. *South African Journal of Marine Science*. 1(1):181–188.
- Buddington, R.K. & Diamond, J.M. (1986). Aristotle revisited: The function of pyloric caeca in fish. *Physiological Sciences*. 83:8012–8014.
- Buddington, R.K. & Diamond, J.M. (1987). Pyloric ceca of fish: a “new” absorptive organ. *Gastrointestinal and Liver Physiology*. 252:65–76.
- Bundy, A., Shannon, L.J., Rochet, J., Neira, M.-J., Shin, S., Hill, Y.-J. & Aydin, L. (2010). The good(ish), the bad, and the ugly: a tripartite classification of ecosystem trends. *ICES*. 67(4):745–768.

- Butterworth, D.S. (1983). Assessment and management of pelagic stocks in the southern Benguela region. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources*. G.D. Sharp & J. Csirke, Eds. San José, Costa Rica: FAO Fish Report. 329–405.
- Caron, D.A., Michaels, A.F., Swanberg, N.R. & Howse, F.A. (1995). Primary productivity by symbiont-bearing planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda. *Journal of Plankton Research*. 17(1):103–129.
- Castro, J.J. (1993). Feeding ecology of chub mackerel *Scomber japonicus* in the Canary Islands area. *South African Journal of Marine Science*. 13(1):323–328.
- Catalán, I.A., Folkvord, A., Palomera, I., Quílez-Badía, G., Kallianoti, F., Tselepides, A. & Kallianotis, A. (2010). Growth and feeding patterns of European anchovy (*Engraulis encrasicolus*) early life stages in the Aegean Sea (NE Mediterranean). *Estuarine, Coastal and Shelf Science*. 86(2):299–312.
- Catalán, I. A., Reglero, P. & Álvarez, I. (2020). Research on early life stages of fish: a lively field. *Marine Ecology Progress Series*, 650:1-5.
- Checkley, D. (1982). Selective Feeding by Atlantic Herring (*Clupea harengus*) Larvae on Zooplankton in Natural Assemblages. *Marine Ecology Progress Series*. 9:245–253.
- Checkley, D.M., Alheit, J., Oozeki, Y. & Roy, C. (2009a). *Climate Change and Small Pelagic Fish*. Cambridge University Press.
- Checkley, D.M., Ayon, J.R.P., Baumgartner, T.R., Bernal, M., Coetzee, J.C., Emmett, R., Guevara, R., Hutching, L., Ibaibarriaga, L., Nakata, H., Oozeki, Y., Planque, B., Schweigert, J., Stratoudakis, Y. & van der Lingen, C.D. (2009b). Habitats. In *Climate Change and Small Pelagic Fish*. D.M. Checkley, J. Alheit, Y. Oozeki, & C. Roy, Eds. 64–147.
- Chen, W., Govoni, J.J. & Warlen, S.M. (1992). Comparison of feeding and growth of larval round herring *Etrumeus teres* and gulf menhaden *Brevoortia patronus*. *Fishery Bulletin*. 90(1):183–189.
- Chiaverano, L.M., Robinson, K.L., Tam, J., Ruzicka, J.J., Quiñones, J., Aleksa, K.T., Hernandez, F.J., Brodeur, R.D., Leaf, R., Uye, S., Decker, M.B., Acha, M., Mianzan, H.W. & Graham, W.M. (2018). Evaluating the role of large jellyfish and forage fishes as energy pathways, and their interplay with fisheries, in the Northern Humboldt Current System. *Progress in Oceanography*. 164:28–36.
- Chisholm, L.A. & Roff, J.C. (1990). Size-weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. *Marine Biology*. 106(1):71–77.

- Christensen, V. & Pauly, D. (1992). ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*. 61(3-4):169-185.
- Christensen, V. & Walters, C.J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*. 172(2-4):109-139.
- Ciechomski, J. D. (1966). Investigations of food and feeding habits of larvae and juveniles of the Argentine Anchovy *Engraulis anchoita*. *California Cooperative Oceanic Fisheries Investigations*. 11:72-81.
- Cloete, R., Boyer, H. & Boyer, D. (1997). Notes on research and management of the northern Benguela pilchard. In *Proceedings of an International Workshop on the Research and Management of Pilchard in Namibia*. Namibia: Ministry of Fisheries and Marine Resources. 107-117.
- Le Clus, F. (1979). Fecundity and maturity of anchovy *Engraulis capensis* off South West Africa. *Fisheries Bulletin (South Africa)*. 11:26-38.
- Le Clus, F. (1985). The spawning of anchovy, *Engraulis capensis* Gillchrist, off South West Africa. PhD Thesis. University of Port Elizabeth.
- Le Clus, F. (1990a). Spatial variability in the seasonal trends of ovary weight in the Namibian pilchard population, 1965-1979. *South African Journal of Marine Science*. 9(1):69-83.
- Le Clus, F. (1990b). Impact and implications of large-scale environmental anomalies on the spatial distribution of spawning of the Namibian pilchard and anchovy populations. *South African Journal of Marine Science*. 9(1):141-159.
- Le Clus, F. (1991). Hydrographic features related to pilchard and anchovy spawning in the Northern Benguela system, comparing three environmental regimes. *South African Journal of Marine Science*. 10(1):103-124.
- Cochrane, K.L. & Hutchings, L. (1995). A structured approach to using biological and environmental parameters to forecast anchovy recruitment. *Fisheries Oceanography*. 4(2):102-127.
- Cochrane, K.L. & Starfield, A.M. (1992). The potential use of predictions of recruitment success in the management of the South African anchovy resource. *South African Journal of Marine Science*. 12(1):891-902.
- Coetzee, J.C. (1997). Acoustic investigation of the shoaling dynamics of sardine *Sardinops sagax* populations: Implications for acoustic surveys. MSc Thesis. University of Cape Town.

- Coetzee, J.C., van der Lingen, C.D., Hutchings, L. & Fairweather, T.P. (2008). Has the fishery contributed to a major shift in the distribution of South African sardine? *ICES Journal of Marine Science*. 65(9):1676–1688.
- Coetzee, J.C., de Moor, C.L. & Butterworth, D.S. (2018). A summary of the South African sardine (and anchovy) fishery. In *MARAM Report: MARAM/IWS/2018/Sarine/BG1*. 1–14.
- Coetzee, J.C., Shabangu, F.W., Geja, Y., Merkle, D., Maliza, L., Ntiyantiya, D., Bali, A., Peterson, J., Jarvis, G., Mxunyelwa, N., Mahlati, O., Mhlongo, J., Mabali, A., Fono, A., Chauke, V., April, W., Johnson, M., Williams, M., Engel, H. & Rademan, J. (2020). Results of the 2020 Pelagic Biomass survey. DEFF report: FISHERIES/2020/DEC/SWG-PEL/130rev2.
- Cohen, R.E. & Lough, R.G. (1983). Prey Field of Larval Herring *Clupea harengus* on a Continental Shelf Spawning Area. *Marine Ecology Progress Series*. 10(3):211–222.
- Colin, P.L. (1976). Filter feeding and predation on the eggs of *Thallasoma* sp. by the Scombrid fish *Rastrelliger kanagurta*. *Copeia*. 596–597.
- Collie, J.S., Botsford, L.W., Hastings, A., Kaplan, I.C., Largier, J.L., Livingston, P.A., Plagányi, É., Rose, K.A., Wells, B.K. & Werner, F.E. (2016). Ecosystem models for fisheries management: finding the sweet spot. *Fish and Fisheries*. 17(1):101–125.
- Contreras, T., Castro, L.R., Montecinos, S., Gonzalez, H.E., Soto, S., Muñoz, M.I. & Palma, S. (2014). Environmental conditions, early life stages distributions and larval feeding of Patagonian sprat *Sprattus fuegensis* and common sardine *Strangomera bentincki* in fjords and channels of the northern Chilean patagonia. *Progress in Oceanography*. 129:136–148.
- Conway, D.V.P., Coombs, S.H., Fernández de Puelles, M.L. & Tranter, P.R.G. (1994). Feeding of larval sardine *Sardina pilchardus* (Walbaum) off the north coast of Spain. *Boletín del Instituto Español de Oceanografía*. 10:165–175.
- Copernicus Marine Service Information (CMEMS, 2020). Global Ocean Physics Analysis and Forecast. E.U. Marine Data Store (MDS). DOI: 10.48670/moi-00016 (Accessed on 06-MAR-2020).
- Cortés, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*. 54(3):726–738.
- Costalago, D., Tecchio, S., Palomera, I., Álvarez-Calleja, I., Ospina-Álvarez, A. & Raicevich, S. (2011). Ecological understanding for fishery management: Condition and growth of anchovy late larvae during different seasons in the Northwestern Mediterranean. *Estuarine, Coastal and Shelf Science*. 93(4):350–358.

- Costalago, D., Navarro, J., Álvarez-Calleja, I. & Palomera, I. (2012). Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. *Marine Ecology Progress Series*. 460:169–181.
- Costalago, D., Strydom, N. & Frost, C. (2014). Nutritional condition of fish larvae in South African estuaries: an appraisal of three biochemical methods. *African Journal of Marine Science*. 36(3):377–386.
- Costalago, D., Strydom, N., Frost, C. & Clemmesen, C. (2015). Preliminary insight into the relationship between environmental factors and the nutritional condition and growth of *Gilchristella aestuaria* larvae in the upper reaches of South African estuaries. *Environmental Biology of Fishes*. 98(12):2367–2378.
- Costalago, D., Potter, P., Pattrick, P. & Strydom, N.A. (2018). Influence of environmental variables on the larval stages of anchovy, *Engraulis encrasicolus*, and sardine, *Sardinops sagax*, in Algoa Bay, South Africa. *Environmental Biology of Fishes*. 101(2):225–236.
- Costalago, D., Kisten, Y., Clemmesen, C. & Strydom, N.A. (2020). Growth and nutritional condition of anchovy larvae on the west and southeast coasts of South Africa. *Marine Ecology Progress Series*. 644:119–128.
- Costalago, D. & Palomera, I. (2014). Feeding of European pilchard (*Sardinia pilchardus*) in the northwestern Mediterranean: from late larvae to adults. *Scientia Marina*. 78(1):41–54.
- Cowan, J.H. & Houde, E.D. (1992). Size-dependent predation on marine fish larvae by Ctenophores, Scyphomedusae, and Planktivorous fish. *Fisheries Oceanography*. 1(2):113–126.
- Crawford, R. (1998). Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. *African Journal of Marine Science*. 19(0).
- Crawford, R.J.M. (1980). Seasonal patterns in South Africa's Western Cape purse seine fishery. *Journal of Fish Biology*. 16(6):649–664.
- Crawford, R.J.M., Shannon, L. V. & Pollock, D.E. (1987). The Benguela ecosystem. Part IV. The Major Fish and Invertebrate Resources. In *Oceanography and Marine Biology Annual Review*. V. 25. H. Barnes & M. Barnes, Eds. Aberdeen University Press. 305–457.
- Crawford, R.J.M., Barham, P.J., Underhill, L.G., Shannon, L.J., Coetzee, J.C., Dyer, B.M., Leshoro, T.M. & Upfold, L. (2006). The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation*. 132(1):119–125.

- Crawford, R.J.M., Altwegg, R., Barham, B.J., Barham, P.J., Durant, J.M., Dyer, B.M., Geldenhuys, D., Makhado, A.B., Pichegru, L., Ryan, P.G., Underhill, L.G., Upfold, L., Visagie, J., Waller, L.J. & Whittington, P.A. (2011). Collapse of South Africa's penguins in the early 21st century. *African Journal of Marine Science*. 33(1):139–156.
- Crawford, R.J.M., Makhado, A.B. & Oosthuizen, W.H. (2018). Bottom-up and top-down control of the Benguela ecosystem's seabirds. *Journal of Marine Systems*. 188:133–141.
- Crawford, R.J.M., Sydeman, W.J., Thompson, S.A., Sherley, R.B., Makhado, A.B. & Votier, S. (2019). Food habits of an endangered seabird indicate recent poor forage fish availability off western South Africa. *ICES Journal of Marine Science*. 76(5):1344–1352.
- Crawford, R.J.M. & de Villiers, G. (1984). Chub mackerel *Scomber japonicus* in the South-East Atlantic-its seasonal distribution and evidence of a powerful 1977 year-class. *South African Journal of Marine Science*. 2(1):49–61.
- Crichton, M., Hutchings, L., Lamont, T. & Jarre, A. (2013). From physics to phytoplankton: Prediction of dominant cell size in St Helena Bay in the Southern Benguela. *Journal of Plankton Research*. 35(3):526–541.
- Cripps, G.C. & Atkinson, A. (2000). Fatty acid composition as an indicator of carnivory in Antarctic krill, *Euphausia superba*. *Canadian Journal Fisheries and Aquatic Science*. 57(3):31–37.
- Cruickshank, R.A. (1987). Ecology of the Migration and Distribution of the Anchovy *Engraulis capensis* off Namibia. MSc Thesis. University of Cape Town.
- Cruz, M. H., Frenger, I., Getzlaff, J., Kriest, I., Xue, T., & Shin, Y. J. (2022). Understanding the drivers of fish variability in an end-to-end model of the Northern Humboldt Current System. *Ecological Modelling*, 472:110097.
- Cury, P.M., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñ, R.A., Shannon, L.J., Verheye, H.M., Cury, P., Crawford, R.J.M., Shannon, L.J. & Verheye, H.M. (2000). Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*. 57:603–618.
- Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., Murphy, E.J., Österblom, H., Paleczny, M., Piatt, J.F., Roux, J.P., Shannon, L. & Sydeman, W.J. (2011). Global seabird response to forage fish depletion - One-third for the birds. *Science*. 334(6063):1703–1706.

- Cury, P. & Shannon, L.J. (2004). Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Progress in Oceanography*. 60:223–243.
- Cushing, D.H. (1974). The Possible Density-Dependence of Larval Mortality and Adult Mortality in Fishes. *The Early Life History of Fish*. 103–111.
- Cushing, D.H. (1978). Upper Trophic Levels in Upwelling Areas. In *Upwelling Ecosystems*. R. Boje & M. Tomczak, Eds. New York: Springer, Berlin, Heidelberg. 101–110.
- Cushing, D.H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology*. 26:249–293.
- Dalsgaard, J., St. John, M., Kattner, G., Müller-Navarra, D. & Hagen, W. (2003). Fatty acid trophic markers in the pelagic marine environment. *Advances in Marine Biology*. 46:225–340.
- Darwall, W.R.T., Allison, E.H., Turner, G.F. & Irvine, K. (2010). Lake of flies, or lake of fish? A trophic model of Lake Malawi. *Ecological Modelling*. 221(4):713–727.
- Davies, D.H. (1954). The South African pilchard (*Sardinops ocellata*). Development, occurrence and distribution of eggs and larvae, 1950-1951. *Invstl. Rep. Div. Sea Fish*. 15:1–26.
- Davies, D.H. (1956). The South African pilchard (*Sardinops ocellata*). Sexual maturity and reproduction; 1950-1954. *Invstl. Rep. Div. Sea Fish*. 22:1–155.
- Davis, A.M., Pusey, B.J. & Pearson, R.G. (2012). Trophic ecology of terapontid fishes (Pisces: Terapontidae): the role of morphology and ontogeny. *Marine and Freshwater Research*. 63:128–141.
- DEFF. (2020). Status of the South African Marine Fishery Resources 2020. Cape Town.
- Delariva, R.L. & Neves, M.P. (2020). Morphological traits correlated with resource partitioning among small characin fish species coexisting in a Neotropical river. *Ecology of Freshwater Fish*. 29(4):640–653.
- Demarcq, H. (2009). Trends in primary production, sea surface temperature and wind in upwelling systems (1998-2007). *Progress in Oceanography*. 83(1–4):376–385.
- Demarcq, H., Barlow, R. & Hutchings, L. (2007). Application of a chlorophyll index derived from satellite data to investigate the variability of phytoplankton in the Benguela ecosystem. *African Journal of Marine Science*. 29(2):271–282.
- De Oliveira J. A. A. & Butterworth D. S. (2004). Developing and refining a joint management procedure for the multispecies South African pelagic fishery, *ICES Journal of Marine Science*. 61:1432-1442.

- Diaz, M. V., Marrari, M., Casa, V., Gattás, F., Pájaro, M. & Macchi, G.J. (2018). Evaluating environmental forcing on nutritional condition of *Engraulis anchoita* larvae in a productive area of the Southwestern Atlantic Ocean. *Progress in Oceanography*. 168:13–22.
- Diaz, R.J. & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*. 321(5891):926–929.
- Dickerson Hopson, S. (1983). The Pelagic Copepods of Lambert's Bay: An Ecological Study of a West Coast Fishing Ground. MSc Thesis. University of Cape Town.
- Dufois, F., Penven, P., Whittle, C.P. & Veitch, J. (2012). On the warm nearshore bias in Pathfinder monthly SST products over Eastern Boundary Upwelling Systems. *Ocean Modelling*. 47:113–118.
- Dufois, F. & Rouault, M. (2012). Sea surface temperature in False Bay (South Africa): Towards a better understanding of its seasonal and inter-annual variability. *Continental Shelf Research*. 43:24–35.
- Dugdale, R.C. & Goering, J.J. (1967). Uptake of new and regenerated forms of nitrogen in primary production. *Limnology and Oceanography*. 12(2):196–206.
- Duncan, M.I., James, N.C., Bates, A.E., Goschen, W.S. & Potts, W.M. (2019). Localised intermittent upwelling intensity has increased along South Africa's south coast due to El Niño–Southern Oscillation phase state. *African Journal of Marine Science*. 41(3):325–330.
- Dunn, K. (2014). The diet, reproductive biology, age and growth of yellowtail, *Seriola lalandi*, in South Africa. MSc thesis. University of Cape Town.
- Durholtz, D., de Moor, C. & Geja, Y. (2010). Examination of redeye round herring size and age data – towards developing a growth curve for the redeye stock assessment. *MARAM Report: MCM/2010/SWG-PEL/49*. 1–10.
- Edwards, M. & Richardson, A.J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*. 430(7002):881–884.
- Efron, B. (1981). Nonparametric estimates of standard error: The jackknife, the bootstrap and other methods. *Biometrika*. 68(3):589–599.
- Ekau, W., Auel, H., Hagen, W., Koppelman, R., Wasmund, N., Bohata, K., Buchholz, F., Geist, S.J., Martin, B., Schukat, A., Verheye, H.M. & Werner, T. (2018). Pelagic key species and mechanisms driving energy flows in the northern Benguela upwelling ecosystem and their feedback into biogeochemical cycles. *Journal of Marine Systems*. 188:49–62.

- Ekau, W. & Verheye, H.M. (2005). Influence of oceanographic fronts and low oxygen on the distribution of ichthyoplankton in the Benguela and southern Angola currents. *African Journal of Marine Science*. 27(3):629–639.
- Elliott, J.P. & Bellwood, D.R. (2003). Alimentary tract morphology and diet in three coral reef fish families. *Journal of Fish Biology*. 63(6):1598–1609.
- Espinoza, P., Lorrain, A., Ménard, F., Cherel, Y., Tremblay-Boyer, L., Argüelles, J., Tafur, R., Bertrand, S., Tremblay, Y., Ayón, P., Munaron, J.M., Richard, P. & Bertrand, A. (2017). Trophic structure in the northern Humboldt Current system: new perspectives from stable isotope analysis. *Marine Biology*. 164:86.
- Essington, T.E., Moriarty, P.E., Froehlich, H.E., Hodgson, E.E., Koehn, L.E., Oken, K.L., Siple, M.C. & Stawitz, C.C. (2015). Fishing amplifies forage fish population collapses. *Proceedings of the National Academy of Sciences of the United States of America*. 112(21):6648–6652.
- Essington, T.E. & Plagányi, É.E. (2014). Pitfalls and guidelines for “recycling” models for ecosystem-based fisheries management: evaluating model suitability for forage fish fisheries. *ICES Journal of Marine Science*. 71(1):118–127.
- Falkowski, P.G. (1981). Light-shade adaptation and assimilation numbers. *Journal of Plankton Research*. 3(2):203–216.
- FAO. (2008). Fisheries Management 2. The ecosystem approach to fisheries 2.1 Best practices in ecosystem modelling for informing an ecosystem approach to fisheries. Rome.
- FAO. (2020). *The State of World Fisheries and Aquaculture 2020. Sustainability in action*. Rome.
- Fiechter, J., Rose, K.A., Curchitser, E.N. & Hedstrom, K.S. (2015). The role of environmental controls in determining sardine and anchovy population cycles in the California Current: Analysis of an end-to-end model. *Progress in Oceanography*. 138:381–398.
- Field, J. (2004). Application of ecosystem-based fishery management approaches in the Northern California Current. PhD Thesis. University of Washington.
- Field, J.C., Francis, R.C. & Aydin, K. (2006). Top-down modelling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Progress in Oceanography*. 68(2–4):238–270.
- Flynn, B.A., Richardson, A.J., Brierley, A.S., Boyer, D.C., Axelsen, B.E., Scott, L., Moroff, N.E., Kainge, P.I., Tjizoo, B.M. & Gibbons, M.J. (2012). Temporal and spatial patterns in the abundance of jellyfish in the northern Benguela upwelling ecosystem and their link to thwarted pelagic fishery recovery. *African Journal of Marine Science*. 34(1):131–146.

- Folch, J., Lees, M. & Sloane Stanley, G.H. (1957). A simple method for the isolation and purification of total lipides from animal tissues. *Journal of Biological Chemistry*. 226(1):497–509.
- Folkvord, A. & Hunter, J. (1986). Size-specific vulnerability of Northern anchovy, *Engraulis mordax*, larvae to predation by fishes. *Fishery Bulletin*. 84(4):859–869.
- Fowler, J.A. (1970). Control of vertebral number in teleosts- an embryological problem. *The Quarterly Review of Biology*. 45(2):148–167.
- Fowler, J.L. (1998). Egg and Larval Ecology of Anchovy (*Engraulis capensis*) and Sardine (*Sardinops sagax*) in the southern Benguela Ecosystem. MSc Thesis. University of Cape Town.
- Fowler, J.L. & Boyd, A.J. (1998). Transport of anchovy and sardine eggs and larvae from the western Agulhas Bank to the West Coast during the 1993/94 and 1994/95 spawning seasons. *South African Journal of Marine Science*. (19):181–195.
- Fowler, G.M. & Smith, S.J. (1983). Length Changes in Silver Hake (*Merluccius bilinearis*) Larvae: Effects of Formalin, Ethanol, and Freezing. *Canadian Journal of Fisheries and Aquatic Sciences*. 40(7):866–870.
- Fox, C.J. (1996). Length changes in herring (*Clupea harengus*) larvae: effects of capture and storage in formaldehyde and alcohol. *Journal of Plankton Research*. 18(4):483–493.
- Friedenberg, L.E., Bollens, S.M. & Rollwagen-Bollens, G. (2012). Feeding dynamics of larval Pacific herring (*Clupea pallasii*) on natural prey assemblages: The importance of protists. *Fisheries Oceanography*. 21(2–3):95–108.
- Fry, B. & Wainright, S.C. (1991). Diatom sources of ¹³C-rich carbon in marine food webs. *Marine Ecology Progress Series*. 76(2):149–157.
- Fuiman, L.A. (1983). Growth gradients in fish larvae. *Journal of Fish Biology*. 23(1):117–123.
- Fuiman, L.A. & Higgs, D.M. (1997). Ontogeny, growth and the recruitment process. In *Early Life History and Recruitment in Fish Populations*. R. C. Champers and E. A. Trippel, Ed. Chapman & Hall, New York.
- Fulton, E.A., Fuller, M., Smith, A.D.M. & Punt, A.E. (2004). *Ecological indicators of the ecosystem effects of fishing: final report*. Hobart, Tasmania.
- Gallegos, C.L. (1992). Phytoplankton photosynthesis, productivity, and species composition in a eutrophic estuary: comparison of bloom and non-bloom assemblages. *Marine Ecology Progress Series*. 81:257–267.

- Garrido, S., Saiz, E., Peters, J., Ré, P., Alvarez, P., Cotano, U., Herrero, D.L., de Murguía, A.M. & Irigoien, X. (2012). Effect of food type and concentration on growth and fatty acid composition of early larvae of the anchovy (*Engraulis encrasicolus*) reared under laboratory conditions. *Journal of Experimental Marine Biology and Ecology*. 434–435:16–24.
- Garrido, S., Silva, A., Marques, V., Figueiredo, I., Bryère, P., Mangin, A. & Santos, A.M.P. (2017). Temperature and food-mediated variability of European Atlantic sardine recruitment. *Progress in Oceanography*. 159:267–275.
- Garrido, S. & van der Lingen, C.D. (2014). Feeding Biology and Ecology. In *Biology and Ecology of Sardines and Anchovies*. K. Ganas, Ed. CRC Press. 122–189.
- Geist, S.J. (2013). Early life history traits of coastal pelagic fishes in the northern Benguela Current ecosystem off Namibia. PhD Thesis. Universität Bremen.
- Geist, S.J., Ekau, W. & Kunzmann, A. (2013). Energy demand of larval and juvenile Cape horse mackerels, *Trachurus capensis*, and indications of hypoxia tolerance as benefit in a changing environment. *Marine Biology*. 160(12):3221–3232.
- Geist, S.J., Kunzmann, A., Verheye, H.M., Eggert, A., Schukat, A. & Ekau, W. (2014). Distribution, feeding behaviour, and condition of Cape horse mackerel early life stages, *Trachurus capensis*, under different environmental conditions in the northern Benguela upwelling ecosystem. *ICES Journal of Marine Science*. 72(2):543–557.
- Geja, Y., Durholtz, M.D. & Moloney, C.L. (2016). Age and growth of redeye round herring *Etrumeus whiteheadi* off the South African coast. *African Journal of Marine Science*. 38(4):493–501.
- Geldenhuys, D. (1978). Age Determination of the South African Round Herring, *Etrumeus micropus* and Length and Age Composition of the Commercial Catches, 1965–1973. South Africa Department of Industries, Sea Fisheries Branch, Cape Town.
- Gibbons, M.J. & Hutchings, L. (1996a). Zooplankton diversity and community structure around southern Africa, with special attention to the Benguela upwelling system. *South African Journal of Marine Science*. 92:63–76.
- Gibbons, M.J. & Hutchings, L. (1996b). Zooplankton diversity and community structure around southern Africa, with special attention to the Benguela upwelling system. *South African Journal of Science*. 92(2):63–76.
- Gibson, R.N. (1988). Development, morphometry and particle retention capability of the gill rakers in the herring, *Clupea harengus* L. *Journal of Fish Biology*. 32(6):949–962.

- Govoni, J.J., Boehlert, G.W. & Watanabe, Y. (1986). The physiology of digestion in fish larvae. *Environmental Biology of Fishes*. 16(1–3):59–77.
- Graeve, M., Hagen, W. & Kattner, G. (1994). Herbivorous or omnivorous? On the significance of lipid compositions as trophic markers in Antarctic copepods. *Deep Sea Research*. 41:915–924.
- Griffiths, M.H. (2002). Life history of South African snoek, *Thyrsites atun* (Pisces: Gempylidae): a pelagic predator of the Benguela ecosystem. *Fisheries Bulletin*. 100:690–710.
- Groenewald, G., Moloney, C.L. & van der Lingen, C.D. (2019). Spatial variation in meristic and morphometric characteristics of sardine *Sardinops sagax* around the coast of southern Africa. *African Journal of Marine Science*. 41(1):51–60.
- Grote, B., Ekau, W., Stenevik, E.K., Clemmesen, C., Verheye, H.M., Lipinski, M.R. & Hagen, W. (2012). Characteristics of survivors: Growth and nutritional condition of early stages of the hake species *Merluccius paradoxus* and *M. capensis* in the southern Benguela ecosystem. *ICES Journal of Marine Science*. 69(4):553–562.
- Haltuch, M.A., Brooks, E.N., Brodziak, J., Devine, J.A., Johnson, K.F., Klibansky, N., Nash, R.D.M., Payne, M.R., Shertzer, K.W., Subbey, S. & Wells, B.K. (2019). Unraveling the recruitment problem: A review of environmentally-informed forecasting and management strategy evaluation. *Fisheries Research*. 217:198–216.
- Hampton, I. (2012). Biophysical features and trends in the Benguela Current Large Marine Ecosystem (rapporteurs). In *Proceedings of the FAO/Benguela Current Commission Workshop on Climate Change Implications for Fisheries of the Benguela Current Region: Making the Best of Change*. FAO Fisheries and Aquaculture Proceedings. 79–125.
- Hampton, S.L. (2014). Multidisciplinary investigation into stock structure of small pelagic fishes in southern Africa. PhD Thesis. University of Cape Town.
- Hansen, A., Ohde, T. & Wasmund, N. (2014). Succession of micro- and nanoplankton groups in ageing upwelled waters off Namibia. *Journal of Marine Systems*. 140(PB):130–137.
- Hasle, G.R. (1978). The Inverted-Microscope Methods. In *Phytoplankton Manual*. A. Sournia, Ed. Paris: United Nations Educational, Scientific, and Cultural Organisation. 88–96.
- Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Suthers, I. M., Blanchard, J. L., & Richardson, A. J. (2020). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. *Ecological Modelling*, 435:109265.

- Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. *Nature*, 13(5):470-477.
- Heymans, J.J., Shannon, L.J. & Jarre, A. (2004). Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s, and 1990s. *Ecological Modelling*. 172(2-4):175-195.
- Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C. & Christensen, V. (2016). Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling*. 331:173-184.
- Heymans, J.J. & Baird, D. (2000). Network analysis of the Northern Benguela ecosystem by means of NETWRK and ECOPATH. *Ecological Modelling*. 131(2-3):97-119.
- Hidalgo, P., Escribano, R. & Morales, C.E. (2005). Annual life cycle of the copepod *Eucalanus inermis* at a coastal upwelling site off Mejillones (23°S), northern Chile. *Marine Biology*. 146(5):995-1003.
- Hidalgo, P. & Escribano, R. (2008). The life cycles of two coexisting copepods, *Calanus chilensis* and *Centropages brachiatus*, in the upwelling zone off northern Chile (23°S). *Marine Biology*. 155(4):429-442.
- Hill, J.M., McQuaid, C.D. & Kaehler, S. (2006). Biogeographic and nearshore-offshore trends in isotope ratios of intertidal mussels and their food sources around the coast of southern Africa. *Marine Ecology Progress Series*. 318:63-73.
- Hill, J.M., McQuaid, C.D. & Kaehler, S. (2008a). Temporal and spatial variability in stable isotope ratios of SPM link to local hydrography and longer term SPM averages suggest heavy dependence of mussels on nearshore production. *Marine Biology*. 154(5):899-909.
- Hill, K., Dorval, E., Lo, N., Macewicz, B., Show, C. & Felix-Uraga, R. (2008b). Assessment of the Pacific sardine resource in 2007 for U.S. management in 2008. US Department of Commerce, La Jolla, California.
- Hill, K., Crone, P.R. & Zwolinski, J. (2017). U.S. Pacific Marine Mammal Stock Assessments: 2016. *NOAA Technical Memorandum*. 1-134.
- Hirai, J., Hidaka, K., Nagai, S. & Ichikawa, T. (2017). Molecular-based diet analysis of the early postlarvae of Japanese sardine *Sardinops melanostictus* and Pacific round herring *Etrumeus teres*. *Marine Ecology Progress Series*. 564:99-113.
- Hirakawa, K., Goto, T. & Hirai, M. (1997). Diet composition and prey size of larval anchovy, *Engraulis japonicus*, in Toyama Bay, southern Japan Sea. *Bulletin of the Japan Sea National Fisheries Research Institute*. 47:67-78.

- Hjörleifsson, E. & Klein-MacPhee, G. (1992). Estimation of live standard length of winter flounder *Pleuronectes americanus* larvae from formalin-preserved, ethanol-preserved and frozen specimens. *Marine Ecology Progress Series*. 82(1):13–19.
- Hjort, J. (1914). Fluctuations in the great fisheries of Northern Europe. *Rapports et Procès-Verbaux*. 20:1–228.
- Holmes, E., Lavik, G., Fischer, G., Segl, M., Ruhland, G. & Wefer, G. (2002). Seasonal variability of $\delta^{15}\text{N}$ in sinking particles in the Benguela upwelling region. *Deep-Sea Research Part I: Oceanographic Research Papers*. 49(2):377–394.
- Holt, R.E., Bogstad, B., Durant, J.M., Dolgov, A. v, Ottersen, G. & Barents, G. (2019). Barents Sea cod (*Gadus morhua*) diet composition: long-term interannual, seasonal, and ontogenetic patterns. *ICES Journal of Marine Science*. 76(6):1641–1652.
- Horton, M. & van der Lingen, C.D. (2019). Comparative trophic ecology of Cape anchovy *Engraulis encrasicolus* and Natal anchovy *Stolephorus holodon* off South Africa's east coast. *African Journal of Marine Science*. 41(3):269–279.
- Houde, E.D. (1989). Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fishery Bulletin*. 87(3):471–495.
- Huang, Y.H., Tao, H.H., Gong, G.C. & Hsieh, C.H. (2021). Importance of prey size on investigating prey availability of larval fishes. *PLOS ONE*. 16(5):1–8.
- Huggett, J., Verheye, H., Escribano, R. & Fairweather, T. (2009). Copepod biomass, size composition and production in the Southern Benguela: Spatio-temporal patterns of variation, and comparison with other eastern boundary upwelling systems. *Progress in Oceanography*. 83:197–207.
- Huggett, J.A., Boyd, A.J., Hutchings, L. & Kemp, A.D. (1998). Weekly variability of clupeoid eggs and larvae in the Benguela jet current: Implications for recruitment. *South African Journal of Marine Science*. (19):197–210.
- Huggett, J.A., Fréon, P., Mullon, C. & Penven, P. (2003). Modelling the transport success of anchovy *Engraulis encrasicolus* eggs and larvae in the southern Benguela: The effect of spatio-temporal spawning patterns. *Marine Ecology Progress Series*. 250:247–262.
- Hunt von Herbing, I. (2001). Development of feeding structures in larval fish with different life histories: Winter flounder and Atlantic cod. *Journal of Fish Biology*. 59(4):767–782.
- Hunt von Herbing, I., Boutilier, R.G., Miyake, T. & Hall, B.K. (1996). Effects of temperature on morphological landmarks critical to growth and survival in larval Atlantic cod (*Gadus morhua*). In *Marine Biology*. V. 124. Springer-Verlag. 593–606.

- Hunter, J.R. (1972). Swimming and feeding behaviour of larval anchovy *Engraulis mordax*. *Fishery Bulletin*. 70(3):821–838.
- Hunter, J.R. (1975). Behavior and survival of Northern anchovy *Engraulis mordax* larvae. *California Cooperative Oceanic Fisheries Investigations Report*. 19:138–146.
- Hunter, J.R. & Thomas, G.L. (1974). Effect of prey distribution and density on the searching and feeding behaviour of larval Anchovy *Engraulis mordax* Girard. *The Early Life History of Fish*. 559–574.
- Huntley, M.E. & Lopez, M.D.G. (1992). Temperature-Dependent Production of Marine Copepods: A Global Synthesis. *The American Naturalist*. 140(2):201–242.
- Hutchings, L., Beckley, L.E., Griffiths, M.H., Roberts, M.J., Sundby, S. & van der Lingen, C.D. (2002). Spawning on the edge: Spawning grounds and nursery areas around the southern African coastline. *Marine and Freshwater Research*. 53(2):307–318.
- Hutchings, L., van der Lingen, C.D., Shannon, L.J., Crawford, R.J.M., Verheye, H.M., Bartholomae, C.H., van der Plas, A.K., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R.G., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J.C. & Monteiro, P.M.S. (2009). The Benguela Current: An ecosystem of four components. *Progress in Oceanography*. 83(1–4):15–32.
- Hutchings, L., Jarre, A., Lamont, T., van den Berg, M. & Kirkman, S.P. (2012). St Helena Bay (southern Benguela) then and now: Muted climate signals, large human impact. *African Journal of Marine Science*. 34(4):559–583.
- Huxley, J.S. (1932). Problems of Relative Growth. First Edit ed. London: Methuen & Co.
- Hyslop, E.J. (1980). Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology*. 17(4):411–429.
- Idris, I., Moloney, C.L. & van der Lingen, C.D. (2016). Spatial variability in branchial basket meristics and morphology of southern African sardine *Sardinops sagax*. *African Journal of Marine Science*. 38(3):351–362.
- Iitembu, J.A., Miller, T.W., Ohmori, K., Kanime, A. & Wells, S. (2012). Comparison of ontogenetic trophic shift in two hake species, *Merluccius capensis* and *Merluccius paradoxus*, from the Northern Benguela Current ecosystem (Namibia) using stable isotope analysis. *Fisheries Oceanography*. 21(2–3):215–225.
- Im, D.H., Wi, J.H. & Suh, H.L. (2015). Evidence for ontogenetic feeding strategies in four calanoid copepods in the East Sea (Japan Sea) in summer, revealed by stable isotope analysis. *Ocean Science Journal*. 50(3):481–490.

- Im, D.H. & Suh, H.L. (2019). Evidence for resource partitioning by ontogeny and species in calanoid copepods. *Progress in Oceanography*. 176:1–9.
- Isaacs, J.D. (1963). Larval sardine and anchovy interrelationships. CalCOFI Reports Volume X. San Diego, CA.
- Islam, M.S. & Tanaka, M. (2009). Diet and prey selection in larval and juvenile Japanese anchovy *Engraulis japonicus* in Ariake Bay, Japan. *Aquatic Ecology*. 43(2):549–558.
- Jackson, A.L., Inger, R., Parnell, A.C. & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*. 80(3):595–602.
- Jackson A. & Parnell A (2023). SIBER: Stable Isotope Bayesian Ellipses in R. R package version 2.1.9, <https://CRAN.R-project.org/package=SIBER>.
- Jacobson, L.D. & MacCall, A.D. (1995). Stock recruitment models for Pacific sardine *Sardinops sagax*. *Canadian Journal Fisheries and Aquatic Science*. 52:566–577.
- James, A.G. (1987). Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. *South African Journal of Marine Science*. 5(1):673–692.
- James, A.G. (1988). Are clupeid microphagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *South African Journal of Marine Science*. 7(1):161–177.
- James, A. & Findlay, K. (1989). Effect of particle size and concentration on feeding behaviour, selectivity and rates of food ingestion by the Cape anchovy *Engraulis capensis*. *Marine Ecology Progress Series*. 50(3):275–294.
- Jarre, A., Muck, P. & Pauly, D. (1991). Two approaches for modelling fish stock interactions in the Peruvian upwelling ecosystem. In *ICES Marine Science Symposium*.
- Jarre, A., Hutchings, L., Kirkman, S.P., Kreiner, A., Tchpalanga, P.C.M., Kainge, P., Uanivi, U., van der Plas, A.K., Blamey, L.K., Coetzee, J.C., Lamont, T., Samaai, T., Verheye, H.M., Yemane, D.G., Axelsen, B.E., Ostrowski, M., Stenevik, E.K. & Loeng, H. (2015). Synthesis: climate effects on biodiversity, abundance and distribution of marine organisms in the Benguela. *Fisheries Oceanography*. 24:122–149.
- Jarre-Teichmann, A., Shannon, L.J., Moloney, C.L. & Wickens, P.A. (1998). Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. *South African Journal of Marine Science*. (19):391–414.

- Gatz, A. (1979). Community Organization in Fishes as Indicated by Morphological Features. *Ecology*. 60(4):711–718.
- Jolicoeur, P. (1963). The Multivariate Generalization of the Allometry Equation. *Biometrics*. 19(3):497–499.
- Kainge, P., Bahamon, N., Bartholomae, C.H., Kathena, J.N., van der Plas, A.K. & Gordo, A. (2013). Stock-environment recruitment analysis for Namibian Cape hake *Merluccius capensis*. *African Journal of Marine Science*. 35(4):555–564.
- Kaji, T., Kodama, M., Arai, H., Tagawa, M. & Tanaka, M. (2002). Precocious development of the digestive system in relation to early appearance of piscivory in striped bonito *Sarda orientalis* larvae. *Fisheries Science*. 68(6):1212–1218.
- Kaplan, I.C., Francis, T.B., Punt, A.E., Koehn, L.E., Curchitser, E., Hurtado-Ferro, F., Johnson, K.F., Lluch-Cota, S.E., Sydeman, W.J., Essington, T.E., Taylor, N., Holsman, K., Maccall, A.D. & Levin, P.S. (2019). A multi-model approach to understanding the role of Pacific sardine in the California Current food web. *Marine Ecology Progress Series*. 617:307–321.
- Karpouzi, V.S. & Stergiou, K.I. (2003). The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology*. 62(6):1353–1365.
- Kendall, A.W., Ahlstrom, E.H. & Moser, H.G. (1981). Early Life History Stages of Fishes and Their Characters. *Ontogeny and Systematics of Fishes*. 1–12.
- King, D.P.F. & Macleod, P.R. (1976). Comparison of the food and the filtering mechanism of Pilchard *Sardinops ocellata* and Anchovy *Engraulis capensis* off South West Africa, 1971 - 1972. *Sea Fisheries Branch Investigational Report*. 3:1–29.
- Kirchner, C.H., Bartholomae, C.H. & Kreiner, A. (2009). Use of environmental parameters to explain the variability in spawner-recruitment relationships of Namibian sardine *Sardinops sagax*. *African Journal of Marine Science*. 31(2):157–170.
- Kirkman, S.P., Blamey, L., Lamont, T., Field, J.G., Bianchi, G., Huggett, J.A., Hutchings, L., Jackson-Veitch, J., Jarre, A., Lett, C., Lipiński, M.R., Mafwila, S.W., Pfaff, M.C., Samaai, T., Shannon, L.J., Shin, Y.J., van der Lingen, C.D. & Yemane, D. (2016). Spatial characterisation of the Benguela ecosystem for ecosystem-based management. *African Journal of Marine Science*. 38(1):7–22.
- Koehn, L.E., Essington, T.E., Marshall, K.N., Kaplan, I.C., Sydeman, W.J., Szoboszlai, A.I. & Thayer, J.A. (2016). Developing a high taxonomic resolution food web model to assess the

- functional role of forage fish in the California Current ecosystem. *Ecological Modelling*. 335:87–100.
- Kreiner, A., van der Lingen, C.D. & Fréon, P. (2001). A comparison of condition factor and gonadosomatic index of sardine *Sardinops sagax* stocks in the northern and southern Benguela upwelling ecosystems, 1984-1999. *South African Journal of Marine Science*. 23:123–134.
- Kreiner, A., Yemane, D., Stenevik, E.K. & Nadine, E. (2011). The selection of spawning location of sardine (*Sardinops sagax*) in the northern Benguela after changes in stock structure and environmental conditions. *Fisheries Oceanography*. 20(6):560–569.
- Kume, G., Kobari, T., Hirai, J., Kuroda, H., Takeda, T., Ichinomiya, M., Komorita, T., Aita-Noguchi, M. & Hyodo, F. (2021). Diet niche segregation of co-occurring larval stages of mesopelagic and commercially important fishes in the Osumi Strait assessed through morphological, DNA metabarcoding, and stable isotope analyses. *Marine Biology*. 168(1):1–14.
- Lamont, T., Barlow, R.G. & Kyewalyanga, M.S. (2014). Physical drivers of phytoplankton production in the southern Benguela upwelling system. *Deep-Sea Research I*. 90:1–16.
- Lamont, T., García-Reyes, M., Bograd, S.J., van der Lingen, C.D. & Sydeman, W.J. (2018a). Upwelling indices for comparative ecosystem studies: Variability in the Benguela Upwelling System. *Journal of Marine Systems*. 188:3–16.
- Lamont, T., Brewin, R.J.W. & Barlow, R.G. (2018b). Seasonal variation in remotely-sensed phytoplankton size structure around southern Africa. *Remote Sensing of Environment*. 204:617–631.
- Lasker, R. (1975). Field Criteria for Survival of Anchovy Larvae: the relation between Inshore Chlorophyll Maximum Layers and Successful first Feeding. *Fishery Bulletin*. 73(3):453–462.
- Lasker, R. (1981). The Role of a Stable Ocean in Larval Fish Survival and Subsequent Recruitment. In *Marine fish larvae: morphology, ecology and relation to fisheries*. R. Lasker, Ed. University of Washington press. 80–89.
- Lasker, R. & Zweifel, J.R. (1978). Growth and Survival of First-Feeding Northern Anchovy Larvae (*Engraulis mordax*) in Patches Containing Different Proportions of Large and Small Prey. In *Spatial Pattern in Plankton Communities*. Springer US. 329–354.
- Laurel, B.J., Copeman, L.A., Hurst, T.P. & Parrish, C.C. (2010). The ecological significance of lipid/fatty acid synthesis in developing eggs and newly hatched larvae of Pacific cod (*Gadus macrocephalus*). *Marine Biology*. 157:1713–1724.

- Layman, C.A., Albrey Arrington, D., Montaña, C.G. & Post, D.M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*. 88(1):42–48.
- Le Roux, J. L. (2013). Parasite assemblages of Cape horse mackerel (*Trachurus capensis* *Castelnau*, 1861) from the northern and southern Benguela. MSc Thesis. University of Cape Town.
- Lett, C., Veitch, J., van der Lingen, C.D. & Hutchings, L. (2007). Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystems. *Marine Ecology Progress Series*. 347:247–259.
- Lillelund, K. & Lasker, R. (1971). Laboratory studies of predation by marine copepods on fish larvae. *Fishery Bulletin*. 69(3):655–667.
- Lindgren, M., Checkley, D.M. & Quinn, T. (2013a). UC San Diego Oceanography Program Publications Title Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised. *Canadian Journal of Fisheries and Aquatic Sciences*. 70(2).
- Lindgren, M., Checkley, D.M. & Quinn, T. (2013b). Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised. *Canadian Journal of Fisheries and Aquatic Sciences*. 70(2).
- Lindley, J.A. (1998). Dry Weights, Carbon and Nitrogen Content of Decapod Larvae from the Plankton. *Journal of the Marine Biological Association of the United Kingdom*. 78(1):341–344.
- Lindley, J.A., Robins, D.B. & Williams, R. (1999). Dry weight carbon and nitrogen content of some euphausiids from the north Atlantic Ocean and the Celtic Sea. *Journal of Plankton Research*. 21(11):2053–2066.
- Litchman, E., Klausmeier, C. A., Schofield, O. M., & Falkowski, P. G. (2007). The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. *Ecology letters*, 10(12):1170-1181.
- Lytle, J. S., Lytle, T. F. & Ogle, J. T. (1990). Polyunsaturated fatty acid profiles as a comparative tool in assessing maturation diets of *Penaeus vannamei*. *Aquaculture*, 89:287–299.
- van der Lingen, C.D. (1994). Effect of particle size and concentration on the feeding behaviour of adult pilchard *Sardinops sagax*. *Marine Ecology Press Series*. 109:1–13.
- van der Lingen, C.D. (1998). Gastric evacuation, feeding periodicity and daily ration of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *African Journal of Marine Science*. 19:305–316.

- van der Lingen, C.D. (2002). Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *South African Journal of Marine Science*. 24:301–316.
- van der Lingen, C.D. (2021a). Adapting to climate change in the South African small pelagic fishery. In *Adaptive management of fisheries in response to climate change*. T. Bahri, M. Vasconcellos, Welch, D, J. Johnson, R.I. Perry, X. Ma, & R. Sharma, Eds. FAO Fisheries and Aquaculture. 177–194.
- van der Lingen, C.D. (2021b). Chapter 10: Adapting to climate change in the South African small pelagic fishery. In *Adaptive management of fisheries in response to climate change: FAO Fisheries and Aquaculture Technical Paper No. 667*. T. Bahri, M. Vasconcellos, D. Welch, J. Johnson, R.I. Perry, X. Ma, & R. Sharma, Eds. Rome: FAO. 177–194.
- van der Lingen, C.D., Hutchings, L., Merkle, D., Van Der Westhuizen, J.J. & Nelson, J. (2001). Comparative Spawning Habitats of Anchovy (*Engraulis capensis*) and Sardine (*Sardinops sagax*) in the Southern Benguela Upwelling Ecosystem. In *Spatial Processes and Management of Marine Populations*. G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, & D. Witherell, Eds. 185–211.
- van der Lingen, C.D., Coetzee, J.C., Demarcq, H., Drapeau, L., Fairweather, T.P. & Hutchings, L. (2005). An eastward shift in the distribution of southern Benguela sardine. *GLOBEC International Newsletter*. 11(2):17–22.
- van der Lingen, C.D., Shannon, L.J., Cury, P.M., Kreiner, A., Moloney, C.L., Roux, J.P. & Vaz-Velho, F. (2006a). Resource and Ecosystem Variability, including Regime Shifts, in the Benguela Current System. In *Large Marine Ecosystems*. L. V. Shannon, G. Hempel, P. Malanotte-Rizzoli, C.L. Moloney, & J. Woods, Eds. Elsevier B.V. 147-.
- van der Lingen, C.D., Fréon, P., Fairweather, T.P. & van der Westhuizen, J.J. (2006b). Density-dependent changes in reproductive parameters and condition of southern Benguela sardine *Sardinops sagax*. *African Journal of Marine Science*. 28(3 & 4):625–636.
- van der Lingen, C.D., Hutchings, L. & Field, J.G. (2006c). Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: Are species alternations between small pelagic fish trophodynamically mediated? *African Journal of Marine Science*. 28(3–4):465–477.
- van der Lingen, C.D. & Durholtz, M.D. (2003). Review of variability in Biomass, Growth, and other characteristics of Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax* in the Benguela Current Upwelling Ecosystem. Marine and Coastal Management, South Africa.

- van der Lingen, C.D. & Miller, T.W. (2011). Trophic Dynamics of Pelagic Nekton in the Southern Benguela Current Ecosystem: Calibrating Trophic Models with Stable Isotope Analysis. In *Interdisciplinary Studies on Environmental Chemistry—Marine Environmental Modeling & Analysis*. K. Omori, X. Guo, N. Yoshie, N. Fujii, I.C. Handoh, A. Isobe, & S. Tanabe, Eds. TERRAPUB. 85–94.
- van der Lingen, C.D. & Miller, T.W. (2014). Spatial, ontogenetic and interspecific variability in stable isotope ratios of nitrogen and carbon of *Merluccius capensis* and *Merluccius paradoxus* off South Africa C. *Journal of Fish Biology*. 85:456–472.
- Link, J.S. (2010). Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: A plea for PREBAL. *Ecological Modelling*. 221(12):1580–1591.
- Lough, R.G., Smith, W.G., Werner, F.E., Loder, J.W., Page, F.H., Hannah, C.G., Naimie, C.E., Perry, R.I., Sinclair, M. & Lynch, D.R. (1994). Influence of wind-driven advection on interannual variability in cod egg and larval distributions on Georges Bank: 1982 vs 1985. *ICES Marine Science Symposia*. 198(January):356–378.
- Loukashkin, A.S. (1970). On the diet and feeding behavior of the northern anchovy, *Engraulis mordax* (Girard). *Proceedings of the California Academy of Sciences, 4th series*. 37:419–458.
- Louw, D.C., van der Plas, A.K., Mohrholz, V., Wasmund, N., Junker, T. & Eggert, A. (2016). Seasonal and interannual phytoplankton dynamics and forcing mechanisms in the Northern Benguela upwelling system. *Journal of Marine Systems*. 157:124–134.
- Louw, G.G., van der Lingen, C.D. & Gibbons, M.J. (1998). Differential feeding by sardine *Sardinops sagax* and anchovy *Engraulis capensis* recruits in mixed shoals. *South African Journal of Marine Science*. 19(19):227–232.
- Lu, J., Vecchi, G.A. & Reichler, T. (2007). Expansion of the Hadley cell under global warming. *Geophysical Research Letters*. 34(6):1–5.
- Mackas, D.L., Greve, W., Edwards, M., Chiba, S., Tadokoro, K., Eloire, D., Mazzocchi, M.G., Batten, S., Richardson, A.J., Johnson, C., Head, E., Conversi, A. & Peluso, T. (2012). Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology. *Progress in Oceanography*. 31–62.
- Marshall, K.N., Kaplan, I.C., Hodgson, E.E., Hermann, A., Busch, D.S., McElhany, P., Essington, T.E., Harvey, C.J. & Fulton, E.A. (2017). Risks of ocean acidification in the California Current food web and fisheries: ecosystem model projections. *Global Change Biology*. 23(4):1525–1539.

- Martin, B., Eggert, A., Koppelman, R., Diekmann, R., Mohrholz, V. & Schmidt, M. (2015). Spatio-temporal variability of zooplankton biomass and environmental control in the Northern Benguela Upwelling System: Field investigations and model simulation. *Marine Ecology*. 36(3):637–658.
- Masi, M.D., Ainsworth, C.H. & Chagaris, D. (2014). A probabilistic representation of fish diet compositions from multiple data sources: A Gulf of Mexico case study. *Ecological Modelling*. 284:60–74.
- Massing, J. C., Schukat, A., Auel, H., Auch, D., Kittu, L., Pinedo Arteaga, E. L., Acosta, J. C. & Hagen, W. (2022). Toward a solution of the “Peruvian puzzle”: Pelagic food-web structure and trophic interactions in the northern Humboldt current upwelling system off Peru. *Frontiers in Marine Science*, 8: 759603.
- Mathiske, A. (2020). Food Web Analysis of the Southern Benguela Upwelling System by Means of Trophic Biomarkers (Stable Isotopes, Fatty Acids). MSc Thesis. University of Bremen.
- Matthews, J.P. (1964). The pilchard of South West Africa (*Sardinops ocellata*). Sexual development, condition factor and reproduction 1957–1960. *Investigational Report of the Marine Research Laboratory of South West Africa*. 10.
- McClatchie, S., Rogers, P.J. & McLeay, L. (2007). Importance of scale to the relationship between abundance of sardine larvae, stability, and food. *Limnology and Oceanography*. 52(4):1570–1579.
- Mcqueen, N.J. (2002). Temporal Variation in the Diet and Feeding Intensity of Snoek (*Thyrssites atun*) in the Southern Benguela Upwelling System. MSc Thesis. University of Cape Town.
- Meekan, M.G., Vigliola, L., Hansen, A., Doherty, P.J., Halford, A. & Carleton, J.H. (2006). Bigger is better: size-selective mortality throughout the life history of a fast-growing clupeid, *Spratelloides gracilis*. *Marine Ecology Progress Series*. 317:237–244.
- Meekan, M.G. & Fortier, L. (1996). Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. *Marine Ecology Progress Series*. 137(1–3):25–37.
- Melo, Y.C. (1984). Age studies on anchovy *Engraulis capensis* Gilchrist off South West Africa. *South African Journal of Marine Science*. 2(1):19–31.
- Melo, Y.C. (1992). The biology of the anchovy *Engraulis capensis* in the Benguela Current region. PhD Thesis. University of Stellenbosch.
- Melo, Y.C. (1994a). Multiple spawning of the anchovy *Engraulis capensis*. *South African Journal of Marine Science*. 14(1):313–319.

- Melo, Y.C. (1994b). Spawning frequency of the anchovy *Engraulis capensis*. *South African Journal of Marine Science*. 14(1):321–331.
- Menden-Deuer, S. & Lessard, E.J. (2000). Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology and Oceanography*. 45(3):569–579.
- Meyer, M. & Smale, M.J. (1991). Predation patterns of demersal teleosts from the Cape south and west coasts of South Africa. 1. Pelagic predators. *South Africa. 1. Pelagic predators, South African Journal of Marine Science*. 10(1):173–191.
- Mhlongo, N., Yemane, D., Hendricks, M. & van der Lingen, C.D. (2015). Have the spawning habitat preferences of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) in the southern Benguela changed in recent years? *Fisheries Oceanography*. 24:1–14.
- Miller, D.C.M., Moloney, C.L., van der Lingen, C.D., Lett, C., Mullon, C. & Field, J.G. (2006). Modelling the effects of physical-biological interactions and spatial variability in spawning and nursery areas on transport and retention of sardine *Sardinops sagax* eggs and larvae in the southern Benguela ecosystem. *Journal of Marine Systems*. 61(3–4):212–229.
- Miller, T.J., Crowder, L.B., Rice, J.A. & Marschall, E.A. (1988). Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences*. 45(9):1657–1670.
- Mketsu, Q.K. (2008). Comparative dietary analysis of four small pelagic fish species from presumed mixed shoals off South Africa's east coast. MSc Thesis. University of Cape Town.
- Mohrholz, V., Bartholomae, C.H., van der Plas, A.K. & Lass, H.U. (2008). The seasonal variability of the northern Benguela undercurrent and its relation to the oxygen budget on the shelf. *Continental Shelf Research*. 28(3):424–441.
- Moloney, C.L., Jarre, A., Arancibia, H., Bozec, Y.M., Neira, S., Roux, J.P. & Shannon, L.J. (2005). Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models. *ICES Journal of Marine Science*. 62(3):493–502.
- Möller, H. (1980). Scyphomedusae as predators and food competitors of larval fish. *Meeresforsch.* 28:90–100.
- Monteiro, P.M.S., van der Plas, A.K., Mélice, J.L. & Florenchie, P. (2008a). Interannual hypoxia variability in a coastal upwelling system: Ocean-shelf exchange, climate and ecosystem-state implications. *Deep-Sea Research Part I: Oceanographic Research Papers*. 55(4):435–450.

- de Moor, C.L. (2018). Considering alternative constraints to the anchovy Harvest Control Rule. In *MARAM Report: FISHERIES/2018/APR/SWG-PEL/06*. 1–7.
- De Moor, C.L. (2019). Initial sardine projections based on constant catch scenarios. In *MARAM Report: FISHERIES/2019/FEB/SWG-PEL/05rev. 1 - 40*.
- de Moor, C.L., Merkle, D. & Coetzee, J. (2020). The data used in the 2020 anchovy assessment. In *MARAM Report: FISHERIES/2020/JAN/SWG-PEL/02*. 1–17.
- de Moor, C.L., Merkle, D. & Coetzee, J. (2021). The data used in the 2021 sardine assessment. In *MARAM Report: FISHERIES/2021/SPR/SWG-PEL/22*. 1 – 27.
- de Moor, C.L. (2022). Finalised assessment of South African round herring, using data from 1987 to 2021. In *MARAM Report: FISHERIES/2022/OCT/SWG-PEL/34*. 1–33.
- Moreira, E., Novillo, M., Eastman, J.T. & Barrera-Oro, E. (2020). Degree of herbivory and intestinal morphology in nine notothenioid fishes from the western Antarctic Peninsula. *Polar Biology*. 43(5):535–544.
- Morote, E., Olivar, M.P., Pankhurst, P.M., Villate, F. & Uriarte, I. (2008). Trophic ecology of bullet tuna *Auxis rochei* larvae and ontogeny of feeding-related organs. *Marine Ecology Progress Series*. 353:243–254.
- Morote, E., Olivar, M.P., Villate, F. & Uriarte, I. (2010). A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the Northwest Mediterranean: Influence of prey availability and ontogeny. *ICES Journal of Marine Science*. 67(5):897–908.
- Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, A.W. & Richardson, S.L. (1984). Ontogeny and systematics of fishes. In *An International Symposium Dedicated to the Memory of Elbert Halvor Ahlstrom*. H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, & S.L. Richardson, Eds. La Jolla, California: The American Society of Ichthyologists and Herpetologists. 1–778.
- Moyano, M., Illing, B., Akimova, A., Alter, K., Bartolino, V., Börner, G., Clemmesen, C., Finke, A., Gröhsler, T., Kotterba, P., Livdane, L., Mittermayer, F., Moll, D., von Nordheim, L., Peck, M.A., Schaber, M. & Polte, P. (2022). Caught in the middle: bottom-up and top-down processes impacting recruitment in a small pelagic fish. *Reviews in Fish Biology and Fisheries*. 4:1–30.
- Muck, P. (1989). Major Trends in the Pelagic Ecosystem off Peru and Their Implications. In *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. D. Pauly, P. Muck, J. Mendo, & J. Tsukayama, Eds.

- Muck, P., Rojas de Mendiola, B. & Antonietti, E. (1989). Comparative Studies on Feeding in Larval Anchoveta (*Engraulis ringens*) and Sardine (*Sardinops sagax*). In *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. D. Pauly, P. Muck, J. Mendo, & I. Tasukayana, Eds. Callao, Peru: International Centre for Living Aquatic Resources Management (ICLARM). 86–96.
- Müller, U.K. & Videler, J.J. (1996). Inertia as a “safe harbour”: Do fish larvae increase length growth to escape viscous drag? *Reviews in Fish Biology and Fisheries*. 6(3):353–360.
- Mullon, C., Fréon, P., Parada, C., van der Lingen, C.D. & Huggett, J. (2003). Modelling the transport success of anchovy *Engraulis encrasicolus* eggs and larvae in the southern Benguela: the effect of spatio-temporal spawning patterns. *Marine Ecology Progress Series*. 250:247–262.
- Mushanganyisi, K.S. (2019). Seasonal and spatial variability of pelagic fishes in relation to environmental variability in St Helena Bay. MSc Thesis. University of Cape Town.
- Myers, R.A. (1998). When do environment-recruitment correlations work? *Reviews in Fish Biology and Fisheries*. 8(3):285–305.
- Nagelkerke, L.A.J., Sibbing, F.A. & Osse, J.W.M. (1995). Morphological Divergence during Growth in the Large Barbs (*Barbus spp.*) of Lake Tana, Ethiopia. *Netherlands Journal of Zoology*. 45(3–4):431–454.
- NASA Ocean Biology Processing Group. (2015). MODIS-Aqua Level 2 Ocean Color Data Version 2014. NASA Ocean Biology Distributed Active Archive Center. https://doi.org/10.5067/AQUA/MODIS_OC.2014.0
- Napier, I.R. (1993). The Organic carbon content of gravel bed herring spawning grounds and the impact of herring spawn deposition. *Journal of the Marine Biological Association of the United Kingdom*. 73(4):863–870.
- Nawratil, O. (1962). The pilchard of South West Africa (*Sardinops ocellata*). Age composition of *Sardinops ocellata* in the commercial catches 1958 and 1959 with reference to a change in rate of growth. *Investigational Report Marine Research Lab SW Africa*. 6:1–33.
- Neira, S., Moloney, C.L., Shannon, L.J., Christensen, V., Arancibia, H. & Jarre, A. (2014). Assessing changes in the southern Humboldt in the 20th century using food web models. *Ecological Modelling*. 278:52–66.
- Neira, S. & Arancibia, H. (2004). Trophic interactions and community structure in the upwelling system off Central Chile (33–39°S). *Journal of Experimental Marine Biology and Ecology*. 312(2):349–366.

- Nelson, K., Hutchinson, E.S., Li, G., Sly, F.L. & Hedgecock, D. (1994). Variation in Life-History and Morphology in Northern Anchovies (*Engraulis mordax*). *California Cooperative Oceanic Fisheries Investigations Reports*. 35:108–120.
- Nelson, G. & Hutchings, L. (1983). The Benguela upwelling area. *Progress in Oceanography*. 12(3):333–356.
- Newman, G.G., Crawford, R.J.M. & Centurion-Harris, O.M. (1979). Fishing effort and factors affecting vessel performance in the South African purse-seine fishery, 1964-1972. *Investigational Report of the Sea Fisheries Branch South Africa*. 120:1–34.
- Nikolioudakis, N., Koumoundouros, G., Kiparissis, S. & Somarakis, S. (2010). Defining length-at-metamorphosis in fishes: A multi-character approach. *Marine Biology*. 157(5):991–1001.
- Novotny, A., Jan, K.M.G., Dierking, J. & Winder, M. (2022). Niche partitioning between planktivorous fish in the pelagic Baltic Sea assessed by DNA metabarcoding, qPCR and microscopy. *Scientific Reports* 2022 12:1. 12(1):1–11.
- Nunn, A.D., Harvey, J.P. & Cowx, I.G. (2007). The food and feeding relationships of larval and 0+ year juvenile fishes in lowland rivers and connected waterbodies. I. Ontogenetic shifts and interspecific diet similarity. *Journal of Fish Biology*. 70(3):726–742.
- Nunn, A.D., Tewson, L.H. & Cowx, I.G. (2012). The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries*. 22(2):377–408.
- Nyuji, M., Takasuka, A. & Okada, M. (2022). Variation in reproductive parameters of round herring in the Pacific coastal waters of Japan. *Journal of Sea Research*. 187:102247.
- O'Connell, C.P. (1981). Development of Organ Systems in the Northern Anchovy, *Engraulis mordax*, and Other Teleosts. *American Zoologist*. 21(2):429–446.
- Olivar, M. & Fortuño, J. (1991). Guide to Ichthyoplankton of the Southeast Atlantic (Benguela Current Region). *Scientia Marina*. 55(1):1–384.
- Olsen, E., Kaplan, I.C., Ainsworth, C., Fay, G., Gaichas, S., Gamble, R., Girardin, R., Eide, C.H., Ihde, T.F., Morzaria-Luna, H.N., Johnson, K.F., Savina-Rolland, M., Townsend, H., Weijerman, M., Fulton, E.A. & Link, J.S. (2018). Ocean futures under ocean acidification, marine protection, and changing fishing pressures explored using a worldwide suite of ecosystem models. *Frontiers in Marine Science*. 5(64):1–23.
- Olsen, E.M., Ottersen, G., Llope, M., Chan, K.S., Beaugrand, G. & Stenseth, N.C. (2011). Spawning stock and recruitment in North Sea cod shaped by food and climate. *Proceedings of the Royal Society B: Biological Sciences*. 278(1705):504–510.

- Olsen, R.E., Henderson, R.J. & McAndrew, B.J. (1990). The conversion of linoleic acid and linolenic acid to longer chain polyunsaturated fatty acids by *Tilapia (Oreochromis nilotica)* in vivo. *Fish Physiology and Biochemistry*. 8(3):261–270.
- Ortega-Cisneros, K., Cochrane, K. & Fulton, E.A. (2017). An Atlantis model of the southern Benguela upwelling system: Validation, sensitivity analysis and insights into ecosystem functioning. *Ecological Modelling*. 355:49–63.
- Ortega-Cisneros, K., Weigum, E., Chalmers, R., Grusd, S., Lombard, A.T. & Shannon, L. (2022). Supporting marine spatial planning with an ecosystem model of Algoa Bay, South Africa. *African Journal of Marine Science*. 44(2):189–204.
- O'Toole, M. (1977). Investigations into some important fish larvae in the South East Atlantic in relation to the hydrological environment. MSc Thesis. University of Cape Town.
- di Pane, J., Joly, L., Koubbi, P., Giraldo, C., Monchy, S., Tavernier, E., Marchal, P. & Loots, C. (2019). Ontogenetic shift in the energy allocation strategy and physiological condition of larval plaice (*Pleuronectes platessa*). *PLOS ONE*. 14(9):1–17.
- Painting, S. J. (1993). Sardine and anchovy recruitment prediction–South Africa. *US Globec News*, 5, 1-2.
- Parada, C., van der Lingen, C.D., Mullon, C. & Penven, P. (2003). Modelling the effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: An IBM approach. *Fisheries Oceanography*. 12(3):170–184.
- Park, J.I., Kang, C.K. & Suh, H.L. (2011). Ontogenetic diet shift in the euphausiid *Euphausia pacifica* quantified using stable isotope analysis. *Marine Ecology Progress Series*. 429:103–109.
- Parker, D., Coetzee, J.C., Winker, H. & van der Lingen, C.D. (2020). Accounting for linefish dependency in management of the South African small pelagic fishery. *African Journal of Marine Science*. 42(3):183–194.
- Paugy, D. (1994). Écologie des poissons tropicaux d'un cours d'eau temporaire (Baoulé, haut bassin du Sénégal au Mali): adaptation au milieu et plasticité du régime alimentaire. *Revue d'Hydrobiologie Tropicale*. 27(2):157–172.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R. & Zeller, D. (2002). Towards sustainability in world fisheries. *Nature*. 418(6898):689–695.
- Pauly, D. & Christensen, V. (1995). Primary production required to sustain global fisheries. *Nature*. 374(6519):255–257.

- Peard, K.R. (2007). Seasonal and interannual variability of wind-driven upwelling at Lüderitz, Namibia. MSc Thesis. University of Cape Town.
- Peck, M.A., Reglero, P., Takahashi, M. & Catalán, I.A. (2013). Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. *Progress in Oceanography*. 116:220–245.
- Pedersen, T. & Fossheim, M. (2008). Diet of 0-group stages of capelin (*Mallotus villosus*), herring (*Clupea harengus*) and cod (*Gadus morhua*) during spring and summer in the Barents Sea. *Marine Biology*. 153(6):1037–1046.
- Penven, P., Roy, C., Brundrit, G.B., Colin de Verdière, A., Fréon, P., Johnson, A.S., Lutjeharms, J.R.E. & Shillington, F.A. (2001). A regional hydrodynamic model of upwelling in the Southern Benguela: research letter. *South African Journal of Science*. 97(11):472–475.
- Peters, J., Dutz, J. & Hagen, W. (2007). Role of essential fatty acids on the reproductive success of the copepod *Temora longicornis* in the North Sea. *Marine Ecology Progress Series*. 341:153–163.
- Pecuchet, L., Lindegren, M., Kortsch, S., Całkiewicz, J., Jurgensone, I., Margonski, P., Otto, S. A., Putnis, I., Strāķe, S., & Nordström, M. C. (2020). Spatio-temporal dynamics of multi-trophic communities reveal ecosystem-wide functional reorganization. *Ecography*, 43(2):197-208.
- Piet, G.J. (1998). Ecomorphology of a size-structured tropical freshwater fish community. *Environmental Biology of Fishes*. 51(1):67–86.
- Pillar, S. C. & Barange, M. (1998). Feeding habits, daily ration and vertical migration of the Cape horse mackerel off South Africa. *South African Journal of Marine Science*, 19(1): 263-274.
- Pillar, S. C. & Wilkinson, I. S. (1995). The diet of Cape hake *Merluccius capensis* on the south coast of South Africa. *South African Journal of Marine Science*. 15(1): 225-239.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D. & Link, J. (2004). Ecosystem-Based Fishery Management. *Policy Forum Ecology*. 305:346–348.
- Pinkas, L., Oliphant, M.S. & Iverson, I.L.K. (1971). Food Habits of Albacore, Bluefin Tuna, and Bonito in California Waters. *State of California the Resources agency: Department of Fish and Game. Fish Bulletin*. 157:1–105.
- Pitcher, G.C., Probyn, T.A., du Randt, A., Lucas, A.J., Bernard, S., Evers-King, H., Lamont, T. & Hutchings, L. (2014). Dynamics of oxygen depletion in the nearshore of a coastal

- embayment of the southern Benguela upwelling system. *Journal of Geophysical Research: Oceans*. 119:2183–2200.
- Plagányi, É.E., Rademeyer, R.A., Butterworth, D.S., Cunningham, C.L. & Johnston, S.J. (2007). Making management procedures operational—innovations implemented in South Africa. *ICES Journal of Marine Science*. 64(4):626–632.
- Plagányi, É.E. & Butterworth, D.S. (2004). A critical look at the potential of ECOPATH with ECOSIM to assist in practical fisheries management. *African Journal of Marine Science*. 26:261–287.
- Platt, T. & Jassby, A.D. (1976). The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. *Journal of Phycology*. 12(4):421–430.
- Plounevez, S. & Champalbert, G. (2000). Diet, feeding behaviour and trophic activity of the anchovy (*Engraulis encrasicolus* L.) in the Gulf of Lions (Mediterranean Sea). *Oceanologica Acta*. 23(2):175–192.
- Polovina, J.J. (1984). Model of a coral reef ecosystem. I. The ECOPATH model and its application to French frigate shoals. *Coral Reefs*. 3(July):1–11.
- Pörtner, H.O. & Peck, M.A. (2010). Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *Journal of Fish Biology*. 77(8):1745–1779.
- Post, D.M. (2002). Using Stable Isotopes to estimate trophic position: model, methods and assumptions. *Ecology*. 83(3):703–718.
- Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J. & Montaña, C.G. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*. 152(1):179–189.
- Potts, W.M., Henriques, R., Santos, C. V., Munnik, K., Ansorge, I., Dufois, F., Booth, A.J., Kirchner, C.H., Sauer, W.H.H. & Shaw, P.W. (2014). Ocean warming, a rapid distributional shift, and the hybridization of a coastal fish species. *Global Change Biology*. 20(9):2765–2777.
- Probyn, T.A. (1985). Nitrogen uptake by size-fractionated phytoplankton populations in the southern Benguela upwelling system. *Marine Ecology Progress Series*. 22:249–258.
- Probyn, T.A. (1992). The inorganic nitrogen nutrition of phytoplankton in the southern Benguela: new production, phytoplankton size and implications for pelagic foodwebs. *South African Journal of Marine Science*. 12:411–420.
- Prosch, R.M. (1986). Early growth in length of the anchovy *Engraulis capensis* Gilchrist off South Africa. *South African Journal of Marine Science*. 4(1):181–191.

- Purcell, J. E., Nemazie, D. A., Dorsey, S. E., Houde, E. D. & Gamble, J. C. (1995). Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. *Oceanographic Literature Review*, 5(42): 383.
- Purcell, J. E., Tilves, U., Fuentes, V. L., Milisenda, G., Olariaga, A. & Sabatés, A. (2014). Digestion times and predation potentials of *Pelagia noctiluca* eating fish larvae and copepods in the NW Mediterranean Sea. *Marine Ecology Progress Series*, 510: 201-213.
- R Core Team. (2018). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Raab, K., Nagelkerke, L.A.J., Boerée, C., Rijnsdorp, A.D., Temming, A. & Dickey-Collas, M. (2011). Anchovy *Engraulis encrasicolus* diet in the North and Baltic Seas. *Journal of Sea Research*. 65(1):131–140.
- Rainuzzo, J. R., Reitan, K. I. & Olsen, Y. (1997). The significance of lipids at early stages of marine fish: a review. *Aquaculture*, 155(1-4): 103-115.
- Régnier, T., Gibb, F.M. & Wright, P.J. (2019). Understanding temperature effects on recruitment in the context of trophic mismatch. *Scientific Reports 2019 9:1*. 9(1):1–13.
- Reifel, C.W. & Travill, A.A. (1978). Structure and carbohydrate histochemistry of the stomach in eight species of teleosts. *Journal of Morphology*. 158(2):155–167.
- Richardson, A.J., Mitchell-Inne, B.A., Fowler, J.L., Bloomer, S.F., Verheye, H.M., Field, J.G., Hutchings, L. & Painting, S.J. (1998). The effect of sea temperature and food availability on the spawning success of Cape anchovy *Engraulis capensis* in the southern Benguela. *South African Journal of Marine Science*. 19(19):275–290.
- Ricker, W.E. (1954). Stock and Recruitment. *Journal of the Fisheries Research Board of Canada*. 11(5):559–623.
- Rilling, G.C. & Houde, E.D. (1999). Regional and temporal variability in growth and mortality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay. *Fisheries Bulletin*. 97:555–569.
- Roel, B.A. & Armstrong, M.J. (1991). The round herring *Etrumeus whiteheadi*, an abundant, underexploited clupeoid species off the coast of southern Africa. *South African Journal of Marine Science*. 11(1):267–287.
- Roel, B.A. & Melo, Y.C. (1990). Reproductive biology of the round herring *Etrumeus whiteheadi*. *South African Journal of Marine Science*. 9(1):177–187.

- Robert, D., Takasuka, A., Nakatsuka, S., Kubota, H., Oozeki, Y., Nishida, H. & Fortier, L. (2010). Predation dynamics of mackerel on larval and juvenile anchovy: is capture success linked to prey condition? *Fisheries Science*. 76: 183-188.
- Rohan, S.K. & Buckley, T.W. (2018). Trophic Niche separation between sympatric sibling flatfishes in relation to gill raker morphology. *Transactions of the American Fisheries Society*. 147(3):431-443.
- Rønnestad, I., Yúfera, M., Ueberschär, B., Ribeiro, L., Saele, Ø. & Boglione, C. (2013). Feeding behaviour and digestive physiology in larval fish: current knowledge, and gaps and bottlenecks in research. *Reviews in Aquaculture*. 5:59-98.
- Rossi, S., Sabatés, A., Latasa, M. & Reyes, E. (2006). Lipid biomarkers and trophic linkages between phytoplankton, zooplankton and anchovy (*Engraulis encrasicolus*) larvae in the NW Mediterranean. *Journal of Plankton Research*. 28(6):551-562.
- Rouault, M., Illig, S., Bartholomae, C., Reason, C.J.C. & Bentamy, A. (2007). Propagation and origin of warm anomalies in the Angola Benguela upwelling system in 2001. *Journal of Marine Systems*. 68(3-4):473-488.
- Rouault, M., Penven, P. & Pohl, B. (2009). Warming in the Agulhas Current system since the 1980's. *Geophysical Research Letters*. 36(12):L12602.
- Rouault, M., Pohl, B. & Penven, P. (2010). Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. *African Journal of Marine Science*. 32(2):237-246.
- Roy, C. (1993). The Optimal Environmental Window Hypothesis: a non-linear environmental process affecting recruitment success. *ICES Statutory Meeting*. 76.
- Roy, C., van der Lingen, C.D., Coetzee, J.C. & Lutjeharms, J.R.E. (2007). Abrupt environmental shift associated with changes in the distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela. *African Journal of Marine Science*. 29(3):309-319.
- Rykaczewski, R.R., Dunne, J.P., Sydeman, W.J., García-Reyes, M., Black, B.A. & Bograd, S.J. (2015). Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. *Geophysical Research Letters*. 42(15):6424-6431.
- Ryther, J.H. (1969). Photosynthesis and fish production in the sea. *Science*. 166(3901):72-76.
- Saiz, E., Griffell, K., Calbet, A. & Isari, S. (2014). Feeding rates and prey: predator size ratios of the nauplii and adult females of the marine cyclopoid copepod *Oithona davisae*. *Limnology and Oceanography*. 59(6):2077-2088.

- Sakamoto, T., van der Lingen, C.D., Shirai, K., Ishimura, T., Geja, Y., Peterson, J. & Komatsu, K. (2020). Otolith $\delta^{18}\text{O}$ and microstructure analyses provide further evidence of population structure in sardine *Sardinops sagax* around South Africa. *ICES Journal of Marine Science*. 77(7):2669–2680.
- Salvanes, A.G. v., Utne-Palm, A.C., Currie, B. & Braithwaite, V.A. (2011). Behavioural and physiological adaptations of the bearded goby, a key fish species of the extreme environment of the northern Benguela upwelling. *Marine Ecology Progress Series*. 425:193–202.
- Salvanes, A.G. v., Christiansen, H., Taha, Y., Henseler, C., Seivåg, M.L., Kjesbu, O.S., Folkvord, A., Utne-Palm, A.C., Currie, B., Ekau, W., van der Plas, A.K. & Gibbons, M.J. (2018). Variation in growth, morphology and reproduction of the bearded goby (*Sufflogobius bibarbatus*) in varying oxygen environments of northern Benguela. *Journal of Marine Systems*. 188:81–97.
- Sánchez-Garrido, J. C., Werner, F. E., Fiechter, J., Rose, K. A., Curchitser, E. N., Ramos, A., García Lafuente, J., Arístegui, J., Hernández-León, S., & Santana, A. R. (2019). Decadal-scale variability of sardine and anchovy simulated with an end-to-end coupled model of the Canary Current ecosystem. *Progress in Oceanography*, 171, 212–230.
- Sánchez-Garrido, J.C., Fiechter, J., Rose, K.A., Werner, F.E. & Curchitser, E.N. (2021). Dynamics of anchovy and sardine populations in the Canary Current off NW Africa: Responses to environmental and climate forcing in a climate-to-fish ecosystem model. *Fisheries Oceanography*. 30(3):232–252.
- Sánchez-Hernández, J., Nunn, A.D., Adams, C.E. & Amundsen, P.A. (2019). Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. *Biological Reviews*. 94(2):539–554.
- Sargent, J.R. & Falk-Petersen, S. (1988). The lipid biochemistry of calanoid copepods. *Hydrobiologia*. 167–168(1):101–114.
- Sargent, J. R., Bell, J. G., Bell, M. V., Henderson, B. J. & Tocher, D. R. (1995). Requirement criteria for essential fatty acids. *Journal of Applied Ichthyology*, 11:183–198.
- Scharf, F. S., Juanes, F. & Sutherland, M. (1998). Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology*, 79(2): 448–460.
- Scharf, F.S., Juanes, F. & Rountree, R.A. (2000). Predator size - Prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series*. 208:229–248.

- Schmidtke, S., Stramma, L. & Visbeck, M. (2017). Decline in global oceanic oxygen content during the past five decades. *Nature*. 542(7641):335–339.
- Schmitt, R.J. & Holbrook, S.J. (1984). Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. *Oecologia*. 63(1):6–12.
- Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012). NIH Image to ImageJ. *Nature Methods*. 671–675.
- Schoener, T.W. (1983). Field Experiments on Interspecific Competition. *The American Naturalist*. 122(2):240–285.
- Schukat, A., Auel, H., Teuber, L., Lahajnar, N. & Hagen, W. (2014). Complex trophic interactions of calanoid copepods in the Benguela upwelling system. *Journal of Sea Research*. 85:186–196.
- Scott, E., Serpetti, N., Steenbeek, J. & Heymans, J.J. (2016). A Stepwise Fitting Procedure for automated fitting of Ecopath with Ecosim models. *SoftwareX*. 5:25–30.
- Serpetti, N., Baudron, A.R., Burrows, M.T., Payne, B.L., Helaouët, P., Fernandes, P.G. & Heymans, J.J. (2017). Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. *Scientific Reports*. 7(1):1–15.
- Shannon, L.J. (2000). Trophic models of the Benguela upwelling system: an ecosystem approach to fisheries management. PhD Thesis. University of Cape Town.
- Shannon, L., Coll, M., Neira, S., Cury, P. & Roux, J.P. (2007). Exploring the ecological role of small pelagic fish using trophic models: what can be learnt from fishing impacts about the possible impacts of climate change? In *SPACC, Chapter 2*.
- Shannon, L., Coll, M., Bundy, A., Gascuel, D., Heymans, J.J., Kleisner, K., Lynam, C.P., Piroddi, C., Tam, J., Travers-Trolet, M. & Shin, Y. (2014a). Trophic level-based indicators to track fishing impacts across marine ecosystems. *Marine Ecology Progress Series*. 512:115–140.
- Shannon, L. v., Hutchings, L., Bailey, G.W. & Shelton, P.A. (1984). Spatial and temporal distribution of chlorophyll in southern African waters as deduced from ship and satellite measurements and their implications for pelagic fisheries. *South African Journal of Marine Science*. 2(1):109–130.
- Shannon, L. V., Boyd, A.J., Brundrit, G.B. & Taunton-Clark, J. (1986). On the Existence of an El Nino-Type Phenomenon in the Benguela System. *Journal of Marine Research*. 44(3):495–520.
- Shannon, L.J., Cury, P.M. & Jarre, A. (2000). Modelling effects of fishing in the Southern Benguela ecosystem. *ICES Journal of Marine Science*. 57(3):720–722.

- Shannon, L.J., Field, J.G. & Moloney, C.L. (2004). Simulating anchovy-sardine regime shifts in the southern Benguela ecosystem. *Ecological Modelling*. 172(2–4):269–281.
- Shannon, L.J., Neira, S. & Taylor, M. (2008). Comparing internal and external drivers in the southern Benguela and the southern and northern Humboldt upwelling ecosystems. *African Journal of Marine Science*. 30(1):63–84.
- Shannon, L.J., Osman, W. & Jarre, A. (2014b). Communicating changes in state of the southern Benguela ecosystem using trophic, model-derived indicators. *Marine Ecology Progress Series*. 512:217–237.
- Shannon, L.J., Ortega-Cisneros, K., Lamont, T., Winker, H., Crawford, R.J.M., Jarre, A. & Coll, M. (2020). Exploring temporal variability in the Southern Benguela Ecosystem over the past four decades using a time-dynamic ecosystem model. *Frontiers in Marine Science*. 7(540).
- Shannon, L.J. & Cury, P.M. (2003). Indicators quantifying small pelagic fish interactions: Application using a trophic model of the southern Benguela ecosystem. *Ecological Indicators*. 3(4):305–321.
- Shannon, L. V. & Nelson, G. (1996). The Benguela: Large Scale Features and Processes and System Variability. In *The South Atlantic*. 1st ed. G. Wefer, W.H. Berger, G. Siedler, & D.J. Webb, Eds. Berlin: Springer, Berlin, Heidelberg. 163–210.
- Shea, B.T. (1985). Bivariate and multivariate growth allometry: statistical and biological considerations. *Journal of Zoology*. 206(3):367–390.
- Shelton, P.A. (1986). Fish spawning strategies in the variable southern Benguela Current region. PhD Thesis. University of Cape Town.
- Shelton, P.A. & Hutchings, L. (1982). Transport of Anchovy, *Engraulis capensis* Gilchrist, Eggs and Early Larvae By A Frontal Jet Current. *ICES Journal of Marine Science*. 40(2):185–198.
- Shin, Y.J., Shannon, L.J. & Cury, P.M. (2004). Simulations of fishing effects on the southern Benguela fish community using an individual-based model: Learning from a comparison with ECOSIM. *African Journal of Marine Science*. 26:95–114.
- Shin, Y.J., Rochet, M.J., Jennings, S., Field, J.G. & Gislason, H. (2005). Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science*. 62(3):384–396.
- Shin, Y.-J., Shannon, L.J., Bundy, A., Coll, M., Aydin, K., Bez, N., Blanchard, J.L., de Fatima Borges, M., Diallo, I., Diaz, E., Heymans, J.J., Hill, L., Johannesen, E., Jouffre, D., Kifani, S., Labrosse, P., Link, J.S., Mackinson, S., Masski, H., Möllmann, C., Neira, S., Ojaveer, H., Ould Mohammed Abdallahi, K., Perry, I., Thiao, D., Yemane, D., Cury Shin, P.M., Mohammed Abdallahi, Ould

- & Masski, H. (2010). Using indicators for evaluating, comparing, and communicating the ecological status of exploited marine ecosystems. 2. Setting the scene. *ICES Journal of Marine Science*. 67(4):692–716.
- Shin, Y.J. & Cury, P.M. (2001). Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquatic Living Resources*. 14(2):65–80.
- Sholto-Douglas, A. D. (1992). The use of stable isotope ratios of carbon and nitrogen to elucidate pelagic marine foodwebs of the Benguela and Agulhas Bank regions of South Africa. MSc thesis, University of Cape Town.
- Silva, A. (2003). Morphometric variation among sardine (*Sardina pilchardus*) populations from the northeastern Atlantic and the western Mediterranean. *ICES Journal of Marine Science*. 60(6):1352–1360.
- Skern-Mauritzen, M., Ottersen, G., Handegard, N.O., Huse, G., Dingsør, G.E., Stenseth, N.C. & Kjesbu, O.S. (2016). Ecosystem processes are rarely included in tactical fisheries management. *Fish and Fisheries*. 17(1):165–175.
- van der Sleen, P., Rykaczewski, R.R., Turley, B.D., Sydeman, W.J., García-Reyes, M., Bograd, S.J., van der Lingen, C.D., Coetzee, J.C., Lamont, T. & Black, B.A. (2018). Non-stationary responses in anchovy (*Engraulis encrasicolus*) recruitment to coastal upwelling in the Southern Benguela. *Marine Ecology Progress Series*. 596:155–164.
- Smith, L. (1989). Digestion in Teleost Fishes. In *Fish Nutrition*. 2nd ed. J.E. Halver, Ed. San Diego, CA: Academic Press. 331–421.
- Smith, A.D.M., Fulton, E.J., Hobday, A.J., Smith, D.C. & Shoulder, P. (2007). Scientific tools to support the practical implementation of ecosystem-based fisheries management. *ICES Journal of Marine Science*. 64(4):633–639.
- Smith, A.D.M., Brown, C.J., Bulman, C.M., Fulton, E.A., Johnson, P., Kaplan, I.C., Lozano-Montes, H., Mackinson, S., Marzloff, M., Shannon, L.J., Shin, Y.J. & Tam, J. (2011). Impacts of fishing low-trophic level species on marine ecosystems. *Science*. 333(6046):1147–1150.
- Smith, M.D., Fulton, E.A., Day, R.W., Shannon, L.J. & Shin, Y.J. (2015). Ecosystem modelling in the southern Benguela: comparisons of Atlantis, Ecopath with Ecosim, and OSMOSE under fishing scenarios. *African Journal of Marine Science*. 37(1):65–78.
- Somarakis, S., Tsoukali, S., Giannoulaki, M., Schismenou, E. & Nikolioudakis, N. (2018). Spawning stock, egg production and larval survival in relation to small pelagic fish recruitment. *Marine Ecology Progress Series*. 2018:113–136.

- Do Souto, M., Brown, D.R., Leonarduzzi, E., Capitanio, F.L. & Diaz, M. V. (2019). Nutritional condition and otolith growth of *Engraulis anchoita* larvae: The comparison of two life traits indexes. *Journal of Marine Systems*. 193:94–102.
- Spiegel, J.R., Quist, M.C. & Morris, J.E. (2011). Trophic ecology and gill raker morphology of seven catostomid species in Iowa rivers. *Journal of Applied Ichthyology*. 27(5):1159–1164.
- Steenbeek, J., Corrales, X., Platts, M. & Coll, M. (2018). Ecosampler: A new approach to assessing parameter uncertainty in Ecopath with Ecosim. *SoftwareX*. 7:198–204.
- Stoner, A.W. & Livingston, R.J. (1984). Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia*. 1:174–187.
- Stramma, L., Schmidtko, S., Levin, L.A. & Johnson, G.C. (2010). Ocean oxygen minima expansions and their biological impacts. *Deep-Sea Research Part I: Oceanographic Research Papers*. 57(4):587–595.
- Subbey, S., Devine, J.A., Schaarschmidt, U. & Nash, R.D.M. (2014). Modelling and forecasting stock–recruitment: current and future perspectives. 71(8):2307–2322.
- Suikkanen, S., Pulina, S., Engström-Öst, J., Lehtiniemi, M., Lehtinen, S. & Brutemark, A. (2013). Climate change and eutrophication induced shifts in northern summer plankton communities. *PLOS ONE*. 8(6):e66475.
- Surma, S., Pitcher, T.J. & Pakhomov, E.A. (2021). Trade-offs and uncertainties in Northeast Pacific herring fisheries: ecosystem modelling and management strategy evaluation. *ICES Journal of Marine Science*. 78(6):2280–2297.
- Suthers, I.M. (1988). The use of condition indices in larval fish. *Bureau of Rural Resources Proceedings*. 15(15):49–55.
- Swain, D.P. & Foote, C.J. (1999). Stocks and chameleons: The use of phenotypic variation in stock identification. *Fisheries Research*. 43(1–3):113–128.
- Swalethorp, R., Landry, M., Semmens, B., Ohman, M., Aluwihare, L. & Chargualaf, D. (2022). Anchovy booms and busts linked to trophic shifts in larval diet. *CalCOFI Report*.
- Sydeman, W.J., García-Reyes, M., Schoeman, D.S., Rykaczewski, R.R., Thompson, S.A., Black, B.A. & Bograd, S.J. (2014). Climate change and wind intensification in coastal upwelling ecosystems. *Science*. 345(6192):77–80.
- Sydeman, W.J., Hunt, G.L., Pikitch, E.K., Parrish, J.K., Piatt, J.F., Boersma, P.D., Kaufman, L., Anderson, D.W., Thompson, S.A. & Sherley, R.B. (2021). South Africa’s experimental

- fisheries closures and recovery of the endangered African penguin. *ICES Journal of Marine Science*. 78(10):3538–3543.
- Szuwalski, C.S. & Hilborn, R. (2015). Environment drives forage fish productivity. *Proceedings of the National Academy of Sciences*. 112(26).
- Takahashi, M., Nishida, H., Yatsu, A. & Watanabe, Y. (2008). Year-class strength and growth rates after metamorphosis of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific Ocean during 1996 - 2003. *Canadian Journal Fisheries and Aquatic Science*. 65:1425–1434.
- Takahashi, M. & Watanabe, Y. (2004). Growth rate-dependent recruitment of Japanese anchovy *Engraulis japonicus* in the Kuroshio - Oyashio transitional waters. *Marine Ecology Progress Series*. 266:227–238.
- Takasuka, A., Aoki, I. & Mitani, I. (2003). Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. *Marine Ecology Progress Series*. 252:223–238.
- Takasuka, A., Oozeki, Y. & Aoki, I. (2007). Optimal growth temperature hypothesis: Why do anchovy flourish and sardine collapse or vice versa under the same ocean regime? *Canadian Journal of Fisheries and Aquatic Sciences*. 64(5):768–776.
- Takasuka, A., Oozeki, Y., Kubota, H. & Lluch-Cota, S.E. (2008). Contrasting spawning temperature optima: Why are anchovy and sardine regime shifts synchronous across the North Pacific? *Progress in Oceanography*. 77(2–3):225–232.
- Tam, J., Taylor, M.H., Blaskovic, V., Espinoza, P., Michael Ballón, R., Díaz, E., Wosnitza-Mendo, C., Argüelles, J., Purca, S., Ayón, P., Quipuzcoa, L., Gutiérrez, D., Goya, E., Ochoa, N. & Wolff, M. (2008). Trophic modeling of the Northern Humboldt Current Ecosystem, Part I: Comparing trophic linkages under La Niña and El Niño conditions. *Progress in Oceanography*. 79(2–4):352–365.
- Tanaka, H., Aoki, I. & Ohshimo, S. (2006). Feeding habits and gill raker morphology of three planktivorous pelagic fish species off the coast of northern and western Kyushu in summer. *Journal of Fish Biology*. 68(4):1041–1061.
- Taper, M.L. & Case, T.J. (1985). Quantitative genetic models for the coevolution of character displacement. *Ecological Society of America*. 66(2):355–371.
- Teodósio, M.A., Garrido, S., Peters, J., Leitão, F., Ré, P., Peliz, A. & Santos, A.M.P. (2017). Assessing the impact of environmental forcing on the condition of anchovy larvae in the

- Cadiz Gulf using nucleic acid and fatty acid-derived indices. *Estuarine, Coastal and Shelf Science*. 185:94–106.
- Teske, P.R., Emami-Khoyi, A., Golla, T.R., Sandoval-Castillo, J., Lamont, T., Chiazzari, B., McQuaid, C.D., Beheregaray, L.B. & van der Lingen, C.D. (2021). The sardine run in southeastern Africa is a mass migration into an ecological trap. *Science Advances*. 7(38):4514–4529.
- Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I.J. & Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*. 16(12):3304–3313.
- Thomas, R.M. (1984). A method of age determination for the south west African pilchard *Sardinops ocellata*. *South African Journal of Marine Science*. 2(1):63–70.
- Thomas, R.M. & Schülein, F.H. (1988). The shoaling behaviour of pelagic fish and the distribution of seals and gannets off Namibia as deduced from routine fishing reports, 1982–1985. *South African Journal of Marine Science*. 7(1):179–191.
- Tjizoo, B. (2008). Characterizing and comparing the spawning habitats of Sardine (*Sardinops sagax*) and Anchovy (*Engraulis encrasicolus*) in the Northern Benguela. MSc Thesis. University of Cape Town.
- Tilves, U., Purcell, J. E., Fuentes, V. L., Torrents, A., Pascual, M., Raya, V., Gili, J. M. & Sabatés, A. (2016). Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs and larvae in the NW Mediterranean. *Journal of Plankton Research*, 38(5): 1243-1254.
- Tocher, D. R. & Harvey, D. G. (1988). Fatty acid composition of the major phosphoglycerides from fish neural tissues, (n-3) and (n-6) polyunsaturated fatty acids in rainbow trout (*Salmo gairdneri*) and cod (*Gadus morhua*) brains and retinas. *Fish Physiology and Biochemistry*, 5:229–239.
- Tocher, D.R. (2003). Metabolism and Functions of Lipids and Fatty Acids in Teleost Fish. *Reviews in Fisheries Science*. 11(2):107–184.
- Tudela, S., Palomera, I. & Quílez, G. (2002a). Feeding of anchovy *Engraulis encrasicolus* larvae in the north-west Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*. 82(2):349–350.

- Turan, C. (2004). Stock identification of Mediterranean horse mackerel (*Trachurus mediterraneus*) using morphometric and meristic characters. *ICES Journal of Marine Science*. 61(5):774–781.
- Turan, C., Oral, M., Öztürk, B. & Düzgüneş, E. (2006). Morphometric and meristic variation between stocks of Bluefish (*Pomatomus saltatrix*) in the Black, Marmara, Aegean and northeastern Mediterranean Seas. *Fisheries Research*. 79(1–2):139–147.
- Twatwa, N.M., van der Lingen, C.D., Drapeau, L., Moloney, C.L. & Field, J.G. (2005). Characterising and comparing the spawning habitats of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *African Journal of Marine Science*. 27(2):487–499.
- Valdés, E.S., Shelton, P.A., Armstrong, M.J. & Field, J.G. (1987). Cannibalism in South African anchovy: Egg mortality and egg consumption rates. *South African Journal of Marine Science*. 5(1):613–622.
- Valdés-Szeinfeld, E.S. & Cochrane, K.L. (1992). The potential effects of cannibalism and intraguild predation on anchovy recruitment and clupeoid fluctuations. *South African Journal of Marine Science*. 12(1):695–702.
- Veitch, J.A., Florenchie, P. & Shillington, F.A. (2006). Seasonal and interannual fluctuations of the Angola-Benguela Frontal Zone (ABFZ) using 4.5 km resolution satellite imagery from 1982 to 1999. *International Journal of Remote Sensing*. 27(5):987–998.
- Venello, T. A., Sastri, A. R., Galbraith, M. D., & Dower, J. F. (2021). Zooplankton functional group responses to environmental drivers off the west coast of Vancouver Island, Canada. *Progress in Oceanography*, 190:102482.
- Verheye, H.M., Hutchings, L. & Huggett, J.A. (1992). Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. *South African Journal of Marine Science*. 12(1):561–584.
- Verheye, H.M., Richardson, A.J., Hutchings, L., Marska, G. & Gianakouras, D. (1998). Long-term trends in the abundance and community structure of coastal zooplankton in the southern Benguela system, 1951-1996. *South African Journal of Marine Science*. (19):317–332.
- Verheye, H.M., Lamont, T., Huggett, J.A., Kreiner, A. & Hampton, I. (2016a). Plankton productivity of the Benguela Current Large Marine Ecosystem (BCLME). *Environmental Development*. 17:75–92.

- Verheye, H.M., Lamont, T., Huggett, J.A., Kreiner, A. & Hampton, I. (2016b). Plankton productivity of the Benguela Current Large Marine Ecosystem (BCLME) Environmental Development. *Environmental Development*. 17:75–92.
- Verity, P.G. & Lagdon, C. (1984). Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids In Narragansett Bay. *Journal of Plankton Research*. 6(5):859–868.
- Véron, M., Duhamel, E., Bertignac, M., Pawlowski, L. & Huret, M. (2020). Major changes in sardine growth and body condition in the Bay of Biscay between 2003 and 2016: Temporal trends and drivers. *Progress in Oceanography*. 182:102274.
- Villacastin-Herrero, C.A., Crawford, R.J.M. & Field, J.G. (2010). Statistical correlations between purse-seine catches of chub mackerel off South Africa and selected environmental parameters. *South African Journal of Marine Science*. 12(1):157–165.
- Vizy, E.K., Cook, K.H. & Sun, X. (2018). Decadal change of the south Atlantic Ocean Angola–Benguela frontal zone since 1980. *Climate Dynamics*. 51(9–10):3251–3273.
- Vorsatz, L.D., van der Lingen, C.D. & Gibbons, M.J. (2015). Diet and gill morphology of the East Coast redeye round herring *Etrumeus wongratanai* off KwaZulu-Natal, South Africa. *African Journal of Marine Science*. 37(4):575–581.
- Voss, R., Dickmann, M. & Schmidt, J.O. (2009). Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the German Bight, North Sea. *Oceanologia*. 51(1):117–138.
- Wainwright, P.C. & Richard, B.A. (1995). Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes*. 44:97–113.
- Waldron, M., Armstrong, M.J. & Prosch, R.M. (1989). Aspects of the variability in growth of juvenile anchovy *Engraulis capensis* in the southern Benguela system. *South African Journal of Marine Science*. 8(1):9–19.
- Waldron, M., Prosch, R.M. & Armstrong, M.J. (1991). Growth of juvenile round herring *Etrumeus whiteheadi* in the Benguela system. *South African Journal of Marine Science*. 10(1):83–89.
- Wallace-Fincham, B.P. (1987). The Food and Feeding of *Etrumeus whiteheadi* Wongratana 1983, off the Cape Province of South Africa. MSc Thesis. University of Cape Town.
- Walters, C. (1986). *Adaptive Management of Renewable Resources*. New York: Macmillian Publishing Company.

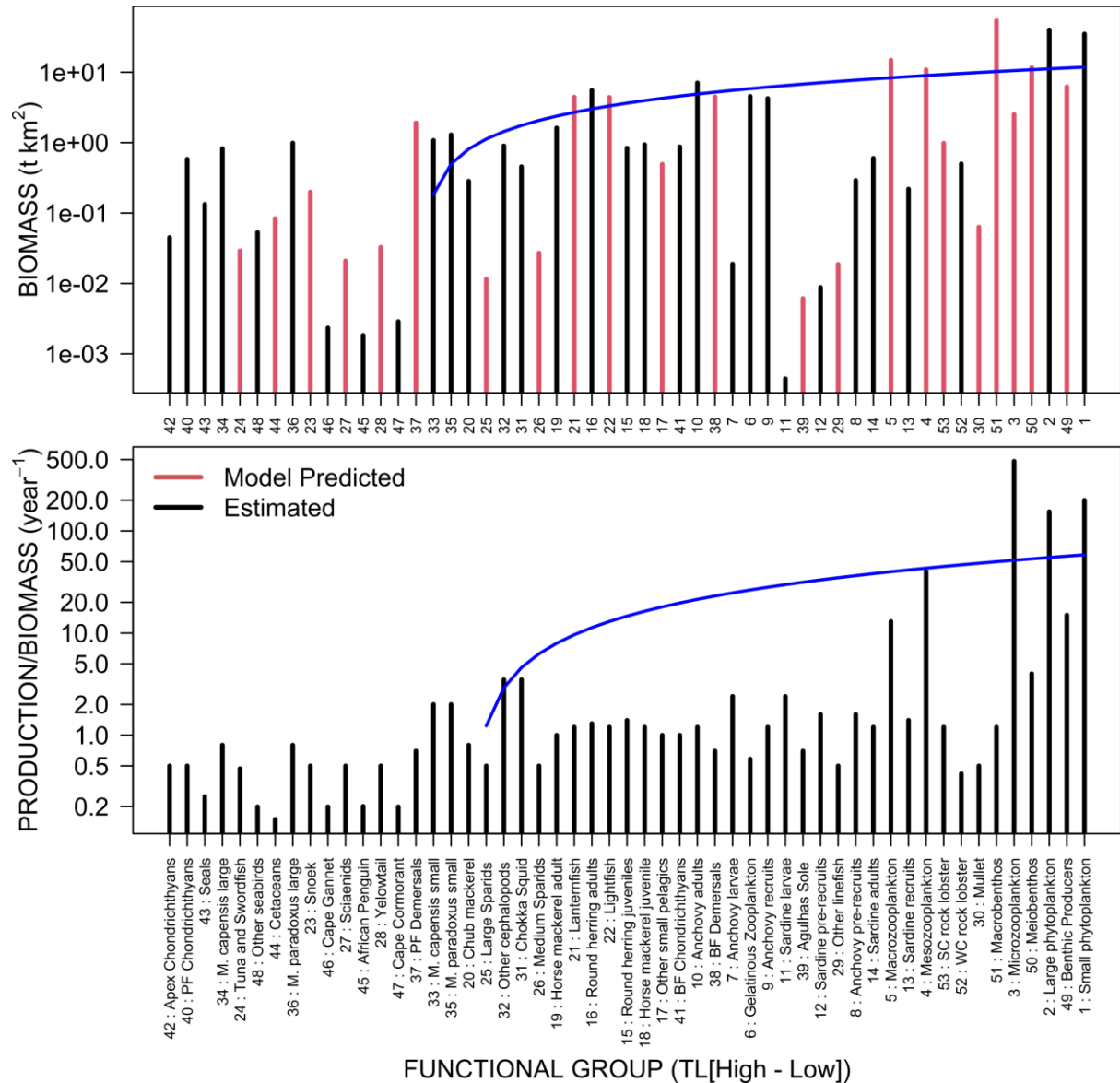
- Walters, C.J., Christensen, V. & Pauly, D. (1997). Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries*. 7(2):139–172.
- Walters, C.J., Pauly, D. & Christensen, V. (1999). Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems*. 2(6):539–554.
- Walters, C.J., Pauly, D., Christensen, V. & Kitchell, J.F. (2000). Representing Density Dependent Consequences of Life History Strategies in Aquatic Ecosystems: EcoSim II. *Ecosystems*. 3:70–83.
- Wang, D., Gouhier, T.C., Menge, B.A. & Ganguly, A.R. (2015). Intensification and spatial homogenization of coastal upwelling under climate change. *Nature*. 518(7539):390–394.
- Ward-Campbell, B.M.S., Beamish, F.W.H. & Kongchaiya, C. (2005). Morphological characteristics in relation to diet in five coexisting Thai fish species. *Journal of Fish Biology*. 67(5):1266–1279.
- Ware, D.M., de Mendiola, B.R. & Newhouse, D.S. (1981). Behaviour of first-feeding Peruvian anchoveta larvae, *Engraulis ringens* J. *Investigacion Cooperativa de la Anchoveta y su Ecosistema-Icane-entre Peru y Canada Callao Peru*. 80–88.
- Watanabe, Y. & Saito, H. (1998). Feeding and growth of early juvenile Japanese sardines in the Pacific waters off central Japan. *Journal of Fish Biology*. 52(3):519–533.
- Watermeyer, K.E., Shannon, L.J., Roux, J.P. & Griffiths, C.L. (2008a). Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. *African Journal of Marine Science*. 30(2):383–403.
- Watermeyer, K.E., Shannon, L.J. & Griffiths, C.L. (2008b). Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. *African Journal of Marine Science*. 30(2):351–382.
- Weigel, B., Mäkinen, J., Kallasvuo, M. & Vanhatalo, J. (2021). Exposing changing phenology of fish larvae by modeling climate effects on temporal early life-stage shifts. *Marine Ecology Progress Series*. 666:135–148.
- Werner, E.E. & Gilliam, J.F. (1984). The Ontogenetic Niche and Species Interactions in Size-Structured Populations. *Annual Review of Ecology and Systematics*. 15:393–425.
- Wessels, G., Moloney, C.L. & van der Lingen, C.D. (2010). The effects of freezing on the morphometrics of sardine *Sardinops sagax* (Jenyns, 1842). *Fisheries Research*. 106(3):528–534.

- Weston, L.F., Reed, C.C., Hendricks, M., Winker, H. & van der Lingen, C.D. (2015). Stock discrimination of South African sardine (*Sardinops sagax*) using a digenean parasite biological tag. *Fisheries Research*. 164:120–129.
- Whitehead, P.J.P. & Wongratana, T. (1986). Family no. 55: Engraulidae. In *Smiths' Sea Fishes*. M.M. Smith & P.C. Heemstra, Eds. Johannesburg: Macmillan South Africa. 204–207.
- Wilhelm, M.R., Painting, S.J., Field, J.G., Kerstan, M. & Durholtz, M.D. (2005). Impact of environmental factors on survival of larval and juvenile Cape anchovy *Engraulis encrasicolus* (G.) in the southern Benguela upwelling region, determined from hatch date distributions: Implications for recruitment. *Marine and Freshwater Research*. 56(5):561–572.
- Wilson, R.P. (1985). The Jackass Penguin (*Spheniscus demersus*) as a pelagic predator. *Marine Ecology Progress Series*. 25(3):219–227.
- Wilson, C.J., Murphy, H.M., Bourne, C., Pepin, P. & Robert, D. (2018). Feeding ecology of autumn-spawned Atlantic herring (*Clupea harengus*) larvae in Trinity Bay, Newfoundland: Is recruitment linked to main prey availability? *Journal of Plankton Research*. 40(3):255–268.
- Wittenrich, M.L. & Turingan, R.G. (2011). Linking functional morphology and feeding performance in larvae of two coral-reef fishes. *Environmental Biology of Fishes*. 92(3):295–312.
- Yamaguchi, A. & Ikeda, T. (2000). Vertical distribution, life cycle, and developmental characteristics of the mesopelagic calanoid copepod *Gaidius variabilis* (Aetideidae) in the Oyashio region, western North Pacific Ocean. *Marine Biology*. 137(1):99–109.
- Yasue, N., Takasuka, A. & Shirakihara, K. (2011). Interspecific comparisons of growth and diet among late larvae of three co-occurring clupeoid species in the Kii Channel, Japan. *Marine Biology*. 158(8):1709–1720.
- Yavno, S. & Holzman, R. (2018). Do viscous forces affect survival of marine fish larvae? Revisiting the 'safe harbour' hypothesis. *Reviews in Fish Biology and Fisheries*. 28(1):201–212.
- Yu, H., Yu, H., Ito, S. Ichi, Tian, Y., Wang, H., Liu, Y., Xing, Q., Bakun, A. & Kelly, R.M. (2020). Potential environmental drivers of Japanese anchovy (*Engraulis japonicus*) recruitment in the Yellow Sea. *Journal of Marine Systems*. 212:103431.

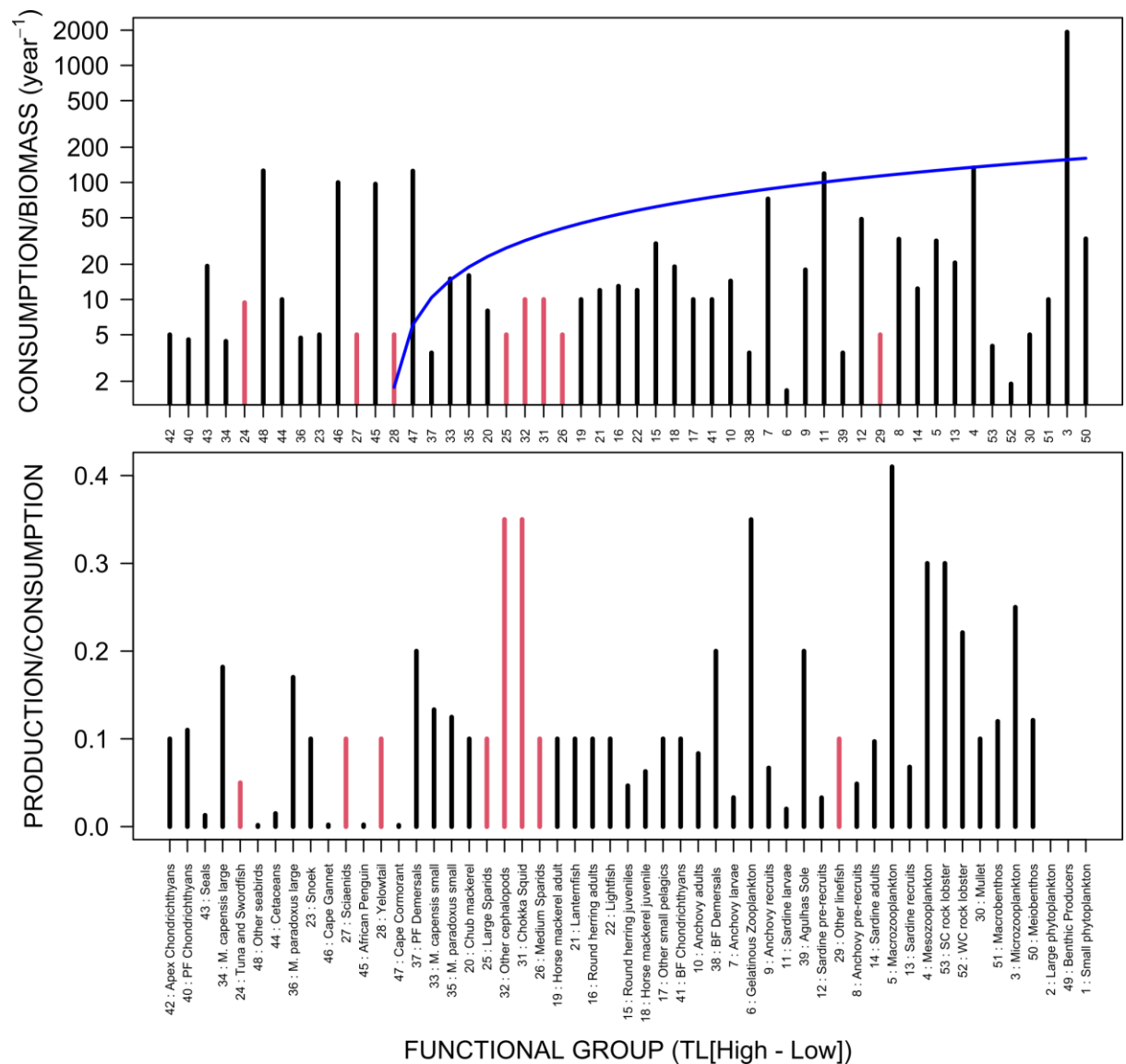
Zhang, T., Bailey, K.M. & Chan, K.S. (2010). Recruitment forecast models for walleye pollock *Theragra chalcogramma* fine-tuned from juvenile survey data, predator abundance and environmental phase shifts. *Marine Ecology Progress Series*. 417:237–248.

Supplementary Information

PREBAL Diagnostics



Supplementary Figure S.1. The PREBAL diagnostics are plotted for various Ecopath parameters as a function of functional group. Functional groups on the x-axis are plotted by trophic level in descending order. Lines depict the outcome of the linear model fit to $\log(y \text{ axis}) \sim x \text{ axis}$.



Supplementary Figure S.1. *Continued.*

The PREBAL technique for model diagnostics was implemented following the methods outlined by Link (2010). Firstly, biomass should span between 5 – 7 orders of magnitude between the highest and the lowest trophic level. In this model there was 5 orders of magnitude difference from the base trophic level to the top level (Supplementary Figure 7.1). This is within the acceptable range. Secondly, the slope of biomass decline between trophic levels on a log scale must be between 5 – 10 %. The decline shown in the biomass (from low to high trophic levels) is less than the 5 – 10 % level, as shown in Supplementary Figure 7.1. Similar to Shannon et al. (2020), the slope is relatively flat which is largely a consequence of the importance of mid-level trophic

levels in the southern Benguela. The detritus is at a similar order of magnitude in terms of biomass as the primary productivity.

The vital rates (P/B , Q/B and P/Q) across taxa and trophic levels were investigated as shown in Supplementary Figure 7.1. c The P/B was high for primary and secondary production, and squid and cephalopods. This high turnover rate is expected. For the new functional groups, they remained within the flat spread of P/B rates for the other functional groups. The Q/B rates express the same trend as shown in Shannon et al., (2020), with the avian groups having comparatively large Q/B s. This is due to them being homeothermic and requiring an increased consumption rate (Link, 2010). There is a generally decreasing trend from low trophic levels to high trophic levels if one was to remove the avian groups. Some of the new functional groups, especially larval anchovy and sardine, had higher levels of Q/B . This is expected as growth rates are highest during early development stages of fish. These levels, however, do sit very close to the trend line (Supplementary Figure 7.1). Finally, the P/Q rates for the modelled groups were the same for the functional groups used in the original model. For the new functional groups (early life history stages of anchovy, sardine and herring), the P/Q fell just below 0.1. This was the same for anchovy and sardine adults in the original model.

Supplementary Table S.2. The dietary composition of all the functional groups that prey on small pelagic fish as inputted into the 1978 Southern Benguela model.

Prey \ predator	Microzooplankton	Mesozooplankton	Macrozooplankton	Gelatinous Zooplankton	Anchovy larvae	Anchovy pre-recruits	Anchovy recruits	Anchovy adults	Sardine larvae	Sardine pre-recruits	Sardine juveniles	Sardine adults	Round herring juvenile	Redeye adults	Other small pelagics	Juvenile Horse mackerel	Adult Horse mackerel	Chub mackerel	Lanternfish	Lightfish	Snoek	Tuna & Swordfish	Large Sparids	Medium Sparids	Sciaenids	Yellowtail	Other linefish
Small Phytoplankton	0.400	0.500	0.000	0.000	0.000	0.135	0.000	0.000	0.000	0.088	0.250	0.320	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Large Phytoplankton	0.000	0.000	0.330	0.000	0.097	0.147	0.100	0.050	0.138	0.100	0.150	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Microzooplankton	0.050	0.500	0.330	0.000	0.104	0.345	0.300	0.040	0.122	0.245	0.500	0.320	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mesozooplankton	0.000	0.000	0.340	0.640	0.706	0.373	0.500	0.570	0.740	0.567	0.100	0.290	0.748	0.600	0.810	0.750	0.390	0.010	0.400	0.670	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Macrozooplankton	0.000	0.000	0.000	0.120	0.093	0.000	0.100	0.340	0.000	0.000	0.000	0.070	0.252	0.400	0.160	0.250	0.524	0.799	0.600	0.330	0.170	0.150	0.000	0.000	0.200	0.200	0.000
Gelatinous Zooplankton	0.000	0.000	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Anchovy larvae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Anchovy pre-recruits	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.003	0.000	0.000	0.050	0.005	0.000	0.000	0.004	0.016	0.000
Anchovy recruits	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.017	0.000	0.000	0.100	0.055	0.000	0.000	0.046	0.084	0.000
Anchovy adults	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.277	0.200	0.000	0.000	0.050	0.050	0.000
Sardine larvae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sardine pre-recruits	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.005	0.007	0.000
Sardine juveniles	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.010	0.000	0.000	0.029	0.010	0.000	0.000	0.095	0.143	0.000
Sardine adults	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
Round herring juvenile	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.002	0.000	0.000	0.025	0.002	0.000	0.000	0.002	0.023	0.000
Round herring adults	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.046	0.008	0.000	0.000	0.085	0.008	0.000	0.000	0.000	0.077	0.000
Other small pelagics	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.098	0.100	0.000

Supplementary Table S.2. *Continued.*

Prey \ predator	Mullet	Chokka Squid	Other cephalopods	Small <i>M. capensis</i>	Large <i>M. capensis</i>	Small <i>M. paradoxus</i>	Large <i>M. paradoxus</i>	PF Demersals	BF Demersals	Agulhas Sole	PF Chondrichthyans	BF Chondrichthyans	Apex Chondrichthyans	Seals	Cetaceans	African Penguin	Cape Gannet	Cape Cormorant	Other seabirds	Meiobenthos	Macrobenthos	WC rock lobster	SC rock lobster
Small Phytoplankton	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Large Phytoplankton	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Microzooplankton	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mesozooplankton	0.000	0.020	0.020	0.000	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000
Macrozooplankton	0.050	0.270	0.290	0.792	0.046	0.769	0.255	0.648	0.050	0.000	0.000	0.000	0.000	0.000	0.040	0.000	0.000	0.000	0.080	0.000	0.000	0.000	0.000
Gelatinous Zooplankton	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.060	0.000	0.000	0.000	0.000
Anchovy larvae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Anchovy pre-recruits	0.000	0.005	0.005	0.002	0.008	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.080	0.005	0.100	0.000	0.000	0.000	0.000	0.000
Anchovy recruits	0.000	0.025	0.025	0.028	0.091	0.077	0.001	0.001	0.003	0.000	0.000	0.000	0.000	0.092	0.150	0.320	0.059	0.600	0.029	0.000	0.000	0.000	0.000
Anchovy adults	0.000	0.000	0.000	0.000	0.200	0.000	0.002	0.001	0.002	0.000	0.020	0.000	0.000	0.150	0.150	0.190	0.200	0.214	0.100	0.000	0.000	0.000	0.000
Sardine larvae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sardine pre-recruits	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.005	0.000	0.000	0.000	0.000	0.000
Sardine juveniles	0.000	0.001	0.001	0.006	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.004	0.019	0.062	0.000	0.000	0.000	0.000	0.000
Sardine adults	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.007	0.070	0.200	0.300	0.000	0.014	0.000	0.000	0.000	0.000
Round herring juvenile	0.000	0.011	0.011	0.007	0.020	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Round herring adults	0.000	0.039	0.039	0.024	0.067	0.054	0.028	0.085	0.025	0.000	0.049	0.000	0.000	0.019	0.030	0.050	0.019	0.000	0.023	0.000	0.000	0.000	0.000
Other small pelagics	0.000	0.000	0.000	0.000	0.010	0.001	0.002	0.000	0.000	0.000	0.020	0.000	0.000	0.003	0.020	0.002	0.234	0.000	0.039	0.000	0.000	0.000	0.000

Supplementary Table S.3. Vulnerabilities of the 40 most sensitive predator-prey interactions (40vs) following the model fitting routine after disaggregating the life history stages of small pelagics in the 1978 Ecopath model developed by Shannon et al., (2020). >> depict very large sensitives $\sim 1 \times 10^6$, neutral vulnerabilities are 2.

Prey \ predator	Microzooplankton	Mesozooplankton	Macrozooplankton	Gelatinous Zooplankton	Anchovy larvae	Anchovy pre-recruits	Anchovy recruits	Anchovy adults	Sardine larvae	Sardine pre-recruits	Sardine juveniles	Sardine adults	Round herring juvenile	Redeye adults	Other small pelagics	Juvenile Horse mackerel	Adult Horse mackerel	Chub mackerel	Lanternfish	Lightfish	Snoek	Tuna & Swordfish	Large Sparids	Medium Sparids	Sciaenids	Yellowtail	Other linefish
Small Phytoplankton	1	2				2				2	2	2															
Large Phytoplankton			1		2	2	2	2	2	2	2																
Microzooplankton	2	2	1.8		2	2	2	2	2	2	2	2															
Mesozooplankton			2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	17.3							
Macrozooplankton				2	2		2	2				2	2	2	2	2	2	2	>>	>>	2	2			2	2	
Gelatinous Zooplankton				2											2												
Anchovy larvae				2				2						2			2	2			2	2				2	
Anchovy pre-recruits																	2	2			2	2			2	2	
Anchovy recruits																	2	2			2	2			2	2	
Anchovy adults																					2	2			2	2	

Supplementary Table S.3. *Continued.*

Prey \ predator	Microzooplankton	Mesozooplankton	Macrozooplankton	Gelatinous Zooplankton	Anchovy larvae	Anchovy pre-recruits	Anchovy recruits	Anchovy adults	Sardine larvae	Sardine pre-recruits	Sardine juveniles	Sardine adults	Round herring juvenile	Redeye adults	Other small pelagics	Juvenile Horse mackerel	Adult Horse mackerel	Chub mackerel	Lanternfish	Lightfish	Snoek	Tuna & Swordfish	Large Sparids	Medium Sparids	Sciaenids	Yellowtail	Other linefish
Sardine larvae				2				1						2			2	2			2	2				2	
Sardine pre-recruits																	2	2			2	2			2	2	
Sardine juveniles																	2	1			2	2			2	>>	
Sardine adults																						2					
Round herring juvenile																	2	2			2	2			2	2	
Round herring adults																	2	2			2	2				2	
Other small pelagics																					2	2			2	2	
Juvenile Horse mackerel																					2	2			2	2	
Adult Horse mackerel																					2	2					
Chub mackerel																					2	2			>>		
Lanternfish																		>>			2	2					
Lightfish																		2			2	2					
Snoek																											
Tuna & Swordfish																											

Supplementary Table S.3. *Continued.*

Prey \ predator	Microzooplankton	Mesozooplankton	Macrozooplankton	Gelatinous Zooplankton	Anchovy larvae	Anchovy pre-recruits	Anchovy recruits	Anchovy adults	Sardine larvae	Sardine pre-recruits	Sardine juveniles	Sardine adults	Round herring juvenile	Redeye adults	Other small pelagics	Juvenile Horse mackerel	Adult Horse mackerel	Chub mackerel	Lanternfish	Lightfish	Snoek	Tuna & Swordfish	Large Sparids	Medium Sparids	Sciaenids	Yellowtail	Other linefish
Large Sparids																											
Medium Sparids																											
Sciaenids																											
Yellowtail																									2		
Other linefish																											
Mullet																							2	2	2		
Chokka Squid																						2				2	
Other cephalopods																					2	2	2			2	
Small <i>M. capensis</i>																					2	2					
Large <i>M. capensis</i>																											
Small <i>M. paradoxus</i>																					2	2					
Large <i>M. paradoxus</i>																											
PF Demersals																					2	2					
BF Demersals																							2	2			
Agulhas Sole																											
PF Chondrichthyans																											
BF Chondrichthyans																											

Supplementary Table S.3. *Continued.*

Prey \ predator	Microzooplankton	Mesozooplankton	Macrozooplankton	Gelatinous Zooplankton	Anchovy larvae	Anchovy pre-recruits	Anchovy recruits	Anchovy adults	Sardine larvae	Sardine pre-recruits	Sardine juveniles	Sardine adults	Round herring juvenile	Redeye adults	Other small pelagics	Juvenile Horse mackerel	Adult Horse mackerel	Chub mackerel	Lanternfish	Lightfish	Snoek	Tuna & Swordfish	Large Sparids	Medium Sparids	Sciaenids	Yellowtail	Other linefish
Apex																											
Chondrichthyans																											
Seals																											
Cetaceans																											
African Penguin																											
Cape Gannet																											
Cape Cormorant																											
Other seabirds																											
Benthic Producers																											2
Meiobenthos																											2
Macrobenthos																							2.06	2			2
WC rock lobster																											
SC rock lobster																											
Detritus	1			2																							

Supplementary Table S.3. *Continued.*

Prey \ predator	Mullet	Chokka Squid	Other cephalopods	Small <i>M. capensis</i>	Large <i>M. capensis</i>	Small <i>M. paradoxus</i>	Large <i>M. paradoxus</i>	PF Demersals	BF Demersals	Agulhas Sole	PF Chondrichthyans	BF Chondrichthyans	Apex Chondrichthyans	Seals	Cetaceans	African Penguin	Cape Gannet	Cape Cormorant	Other seabirds	Benthic Producers	Meiobenthos	Macrobenthos	WC rock lobster	SC rock lobster	Detritus
Small Phytoplankton																									
Large Phytoplankton	2																								
Microzooplankton																									
Mesozooplankton		2	2					2	2						2				2						
Macrozooplankton	2	2	2	1	2	1	2	2	2						2				2						
Gelatinous Zooplankton																			2						
Anchovy larvae		2	2					2																	
Anchovy pre-recruits		2	2	2	2	2		2						2		2	2	2							
Anchovy recruits		2	2	2	2	1	2	2	2					2	2	2	2	2	2						
Anchovy adults					2		2	2	2		2			2	2	2	2	2	2						
Sardine larvae		2	2					2																	
Sardine pre-recruits		2	2	1	2	2											2	2	2						
Sardine juveniles		2	2	>>	2	2								2		2	2	2							
Sardine adults											2			2	1	2	1.25		>>						
Round herring juvenile		2	2	2	2			2						2			2								
Round herring adults		2	2	2	2	2	2	2	2		2			2	2	2	2		2						
Other small pelagics					2	2	2				2			2	2	2	2		2						
Juvenile Horse mackerel					2									2		2	2	2	2						

Supplementary Table S.3. *Continued.*

Prey \ predator	Mullet	Chokka Squid	Other cephalopods	Small <i>M. capensis</i>	Large <i>M. capensis</i>	Small <i>M. paradoxus</i>	Large <i>M. paradoxus</i>	PF Demersals	BF Demersals	Agulhas Sole	PF Chondrichthyans	BF Chondrichthyans	Apex Chondrichthyans	Seals	Cetaceans	African Penguin	Cape Gannet	Cape Cormorant	Other seabirds	Benthic Producers	Meiobenthos	Macrobenthos	WC rock lobster	SC rock lobster	Detritus
Adult Horse mackerel					>>						2	2	2	2	2										
Chub mackerel					2						2		2	>>		2	2								
Lanternfish		2	2	2	2	2	1	2	2		2	2		2	2	2	2		2						
Lightfish		2	2	2	2	2	1	2	2		2	2		2	2	2	2		2						
Snoek					2		2				2		2			2	2								
Tuna & Swordfish													2												
Large Sparids											2		>>												
Medium Sparids											2		2												
Sciaenids											2		2												
Yellowtail													2												
Other linefish											2		2	2											
Mullet											2								2						
Chokka Squid			2	2	2	2	2	2	2		2	2	2	2	2	2			2						
Other cephalopods		2	2	2	2	2	2	2	2		2	2	2	2	2				2						
Small <i>M. capensis</i>		2	2		2			2	2				2	2	2		2		2						
Large <i>M. capensis</i>					2				2		>>	>>		2	2		2								
Small <i>M. paradoxus</i>		2	2	2	2		2	2	2				2	2	2		2	2							

Supplementary Table S.3. *Continued.*

Prey \ predator	Mullet	Chokka Squid	Other cephalopods	Small <i>M. capensis</i>	Large <i>M. capensis</i>	Small <i>M. paradoxus</i>	Large <i>M. paradoxus</i>	PF Demersals	BF Demersals	Agulhas Sole	PF Chondrichthyans	BF Chondrichthyans	Apex Chondrichthyans	Seals	Cetaceans	African Penguin	Cape Gannet	Cape Cormorant	Other seabirds	Benthic Producers	Meiobenthos	Macrobenthos	WC rock lobster	SC rock lobster	Detritus
Large <i>M. paradoxus</i>							2		2		2			2	2		2								
PF Demersals				2	2		2	2	2		2	2	2	2		2	2		2						
BF Demersals				2	2		2	2	2	2	2	3.19	2	2											
Agulhas Sole													2												
PF Chondrichthyans											2		2												
BF Chondrichthyans									2		2	1	2												
Apex Chondrichthyans																									
Seals													>>						2						
Cetaceans													2												
African Penguin													2												
Cape Gannet													>>												
Cape Cormorant													2												
Other seabirds																			2						
Benthic Producers	2																			2	2	2	2		
Meiobenthos	2	2								1											>>	2	2		
Macrobenthos		2	2						2	1		>>	2	2							>>	1	2		
WC rock lobster			2									2	2	2					2						
SC rock lobster			2									2	2												
Detritus	2																			1	1	2	2		

