

**Fish ecology in a low oxygen environment: a case study
from the Arabian Sea**



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WESTERN AUSTRALIA**

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This thesis is presented for the degree of doctor of Philosophy of

The University of Western Australia

School of Animal Biology

The University of Western Australia

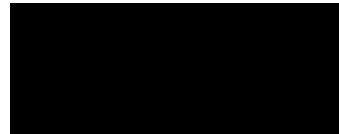
2017

Statement of contributions to thesis

This thesis contains a General Introduction (Chapter 1), three data chapters (Chapters 2-4) arranged in journal format and a General Discussion (Chapter 5). I personally participated in the survey activity during the preparation for the stock assessment survey and was a member of the scientific team on the third voyage. I processed all datasets and performed all the data analyses featured in this thesis. I wrote all the chapters with feedback from Professor Jessica Meeuwig (all chapters) and Dr. Michel Claereboudt (Chapters 2-4).



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Abstract

Climate change is having an enormous effect on global oceans. Climate scientists predict that, in association with ocean warming and acidification, the extent of oxygen minimum zones (OMZs) will expand globally. Low levels of dissolved oxygen associated with OMZs are predicted to impact fish communities both in terms of diversity and growth. Patterns in marine biodiversity may vary as species range-shift or are reduced in abundance due to sub-optimal conditions in relation to their dissolved oxygen level tolerances. Low dissolved oxygen concentrations in OMZs may also influence important aspects of fish populations including size structure and condition. The response to reduced oxygen concentration is generally size-specific with smaller individuals found in shallow waters and larger individuals found in deeper waters. Fish condition, as quantified by weight at a given length, may be negatively impacted if reduced oxygen concentration via influence on metabolism and behaviour such as movement and foraging.

One of only three globally existing permanent OMZs is found in the Arabian Sea. This OMZ provides a natural laboratory in which fish responses to low levels of dissolved oxygen can be observed, with implications for future effects of globally expanding OMZs evaluated. I analysed data from a large-scale demersal fisheries survey undertaken over 33,200 km² across four regions and a depth range from 20 to 250 m to assess fish response to an OMZ. Surveys were undertaken at four periods during the Southwest Monsoon (SWMon) and the Northeast Monsoon (NEMon), and during inter monsoonal periods, both pre (PreMon) and post (PostMon) Southwest Monsoon. Recorded data included species abundance and size. Environmental data included bottom temperature (°C), salinity (ppt), dissolved oxygen (ml l⁻¹), and depth (m). The survey generated data for 99,319 individuals representing 445 species and 164 families from 764 research trawls.

I quantified variation in species diversity and total abundance as a function of region, season, and depth strata. I also considered how these attributes of the fish diversity were associated with seabed temperature, salinity and dissolved oxygen levels. Finally, as a measure of fish condition, I compared the length-weight relationships (LWR) of 53 species generated within the OMZ to those for the same species from non-OMZ regions. Within the Arabian Sea, I also compared the LWRs of seven species (*Drepane. longimana*, *Pagellus affinis*, *Pomadasys commersonnii*, *Argyrops spinifer*, *Carangoides equula*, *Cheimerius nufar* and *Plectorhinchus schotaf*) in relation to region. Finally, I tested the effects of region, season and depth on length distributions for five economically important demersal species found regionally (*A. spinifer*, *D. longimana*, *Epinephelus diacanthus*, *Lethrinus nebulosus* and *P. commersonnii*) and explored the relationship between length distributions and the environmental variables.

Fish richness was greatest during the Northeast Monsoon and in shallow waters. No differences in biodiversity were found between regions. The biodiversity indices were poorly explained by the environmental variables. I found that *A. spinifer*, *E. diacanthus*, and *P. commersonnii* length varied significantly among regions and seasons but not depth, and that *D. longimana* and *L. nebulosus* varied only by depth strata. Temperature was the main environmental variable that explain the variation in length distribution for *A. spinifer*, *E. diacanthus*, *L. nebulosus* and *P. commersonnii*. I found that the fish in the Arabian Sea had significantly higher body condition coefficients than their conspecifics in non-OMZ regions; essentially, they were heavier at length. There was no significant difference in allometric growth rates between the Arabian Sea OMZ and conspecifics elsewhere. Within the Arabian Sea, of the seven species evaluated, two species grew faster and three species slower towards the south, whereas the remaining two species showed no regional effect on their allometric growth rate.

My results suggest that there is an effect of the OMZ on diversity, length and condition but that this effect is species-specific. Generally, biodiversity was greatest and size largest during the NEMon at which point, the influence of the distribution of the OMZ is relatively weak and offset by moderate upwelling. Fish condition in the Arabian Sea was generally higher than conspecific elsewhere which may reflect the overall high productivity of the region with the capacity of individual fish to “head start”, regardless of the presence of the OMZ. However regional analysis suggests that species can respond either positively or negatively to the OMZ and it remains unclear what drives these differential responses.

As OMZs are predicted to expand globally, understanding their impacts on economically important fisheries is critical. The Southwest Monsoon, which determines the extent of the Arabian Sea OMZ, strongly impacts the socioeconomic life of more than 60% of the world’s population including those of India, Pakistan, Iran, Bangladesh and other close by countries, with many of these people reliant on fishing. Although fish condition in the Arabian Sea was high relative to non-OMZ regions, this reflects upwelling-driven productivity. Other regions in which OMZs expand that lack upwelling may be more negatively impacted in terms of fisheries productivity. As such, expanding OMZs may well reduce fisheries productivity globally and these impacts need to be incorporated into ocean management.

Table of Contents

Abstract	ii
Table of Contents	v
List of Tables	vi
List of Figures	vii
Appendix A	viii
Publication arising from this thesis	ix
Acknowledgements	x
Chapter 1- General Introduction	1
1.1 Climate Change	1
1.2 Oxygen and Fish	3
1.3 Biodiversity	4
1.4 Length distribution	4
1.5 Fish condition	5
1.6 Fisheries independent data.....	5
1.7 The Arabian Sea	6
1.8 Objectives and Aims.....	10
1.9 Thesis Outline.....	10
1.10 References	12
Chapter 2- Influence of climate-driven low oxygen zones on fish biodiversity: a case study from the Arabian Sea.....	19
2.1 Abstract.....	19
2.2 Introduction	20
2.3 Methods	24
2.4 Results	27
2.5 Discussion.....	29
2.6 References	32
Chapter 3- The influence of oxygen minimum zone and some oceanography parameters on the length distribution of five fish species in the Arabian Sea	45
3.1 Abstract.....	45
3.2 Introduction	48
3.3 Methods	51
3.4 Results	53
3.5 Discussion.....	54
3.6 References	57
Chapter 4- Low oxygen zones predict future condition of fish under climate change ...	67
4.1 Abstract.....	67
4.2 Introduction	68
4.3 Methods	71
4.4 Results	73
4.5 Discussion.....	75
4.6 References	79
Chapter 5- General Discussion	93
5.1 Learnings with regard to OMZs	95
5.2 Limitations.....	96

5.3 Future research	97
5.4 Conclusions	97
5.5 References	97

List of Tables

Table 2.1. Sampling effort in each level of the three factors included in this study during the fisheries-independent survey in the Arabian Sea coast of Oman (2007 – 2008).	38
Table 2.2. Variation in estimated species richness between regions, seasons, and depth based on goodness of fit by Chi-square analysis strata. Chi-square contingency tests were used to determine if variation in estimated species richness were similar across region by season, region by depth, and season by depth. The numbers in bold were significant probability at 0.05 level.....	38
Table 2.3. PERMANOVA results of three biodiversity indices across region, season and depth strata. Chao and Shannon refers to a combined metric of the Chao1 and Shannon indices. NS: not significant.	39
Table 2.4. The Biological-Environmental correlation analysis used to extract the best correlations between fish biodiversity attributes and environmental variables based on general additive models (GAM).	39
Table 3.1. Statistics of length measurements for the five focal species from the Omani coast of the Arabian Sea (2007–2008 SE: standard error of the mean.	62
Table 3.2. GAM results for the five focal species mean length from Omani coast of the Arabian Sea, (2007–2008).	62
Table 4.1. Descriptive statistics for environmental variables of the Northwest Arabian Sea (n=38928) and by region.	84
Table 4.2. Paired t-tests performed for the length-weight regression parameters for 53 species of fish from the Northwest Arabian Sea oxygen minimum zone (OMZ) and non-OMZ regions.	85
Table 4.3. <i>P</i> values for the slopes of the regressions of analysis of covariance (ANCOVA) of log (W) on with log (L) with region as covariate.	85
Table 4.4. Length-weight relationships parameters of the five species across the studied regions in Northwest Arabian Sea. R ² = coefficients of determination, a= intercept, b = slope and SE = standard error.	86

List of Figures

Figure 2.1. Classification of the regions in the study area. A: Ra's al Hadd to Masirah Island; B: Masirah Island to Ra's Al Madrasah, C: Ra's Al Madrasah to Ra's Hasik; D: Ra's Hasik to Yemen border.	40
Figure 2.2. Estimated cumulative number of fish species as a function of sampling effort. The bounds are the 95% Confidence intervals.	41
Figure 2.3. Number of species by depth strata of the four regions in the Omani coast of the Arabian Sea.	42
Figure 2.4. Biodiversity indices using PCA for fish species from the Omani coast of the Arabian Sea; Chao1 and Shannon were combined to create an index that reflects richness and evenness.	43
Figure 2.5. Mean value of observed Chao and Shannon combined index, species richness and total abundance by Regions, Seasons and Depth with significant differences ($p < 0.05$) indicated. Standard error (SE) are also indicated... ..	44
Figure 3.1. Classification of Regions across the study area. A: Ra's al Hadd to Masirah Island; B: Masirah Island to Ra's Al Madrasah, C: Ra's Al Madrasah to Ra's Hasik; D: Ra's Hasik to Yemen border.	63
Figure 3.2. Mean length of fishes in each trawl sample from a different region, stratum and season in the Omani coast of the Arabian Sea (2007–2008). For all figures horizontal axis presents the factors, the vertical axis presents the mean length (cm) and bars present the standard error of the mean. Letters inside the bars (a, b and c) indicate the Post-hoc test results of significant differences otherwise they were equal.	64
Figure 3.3. Comparison of kernel density estimate (KDE) probability density functions for mean length of each trawl sample (of each trawl sample) frequency distribution of fishes from a different region, stratum and season in the Omani coast of the Arabian Sea (2007–2008). For all figures, horizontal axis presents the mean length and the vertical axis presents the probability density.	65
Figure 3.4. Response curves of oceanographic variables in the Generalised Additive Models (GAM) for four species from the Omani coast of the Arabian Sea(2007–2008). The Y-axis represents the partial residuals (logarithm value) and dashed lines represent 95% confidence intervals.	66
Figure 4.1. Study area and regions where A: Ra's al Hadd to Masirah Island; B: Masirah Island to Ra's al Madrasah, C: Ra's alMadrasah to Ra's Hasik; D: Ra's Hasik to Yemen border.	91
Figure 4.2. Slopes of the regressions \pm standard errors of the slopes for <i>Argyrops spinifer</i> , <i>Carangoides equula</i> , <i>Drepane longimana</i> , <i>Pagellus affinis</i> and <i>Pomadasys commersonnii</i> across the four regions in the northwest Arabian Sea. Y axis for all plots represent the b value (slope).	92

Appendix A

Length-weight regression coefficients for 94 species of fishes, sharks and rays of the Northwest Arabian Sea. Species for which LWR are presented for the first time are in bold. FL = Fork length, a = intercept, b = slope and R² = coefficients of determination.

a. Disk diameter was used to quantify size for rays. b. For this species without fork, total length was used instead fork length.. 87

Appendix 1. Biological data from the trawl sampling in the Omani coast of the Arabian Sea (2007-2008) used in this thesis. NEMon; Northeast Monsoon; PreMon; Pre-Southwest Monsoon; SWMon: Southwest Monsoon; PostMon: Post-Southwest Monsoon..... 100

Appendix 2. Vertical reading of environmental data from the trawl sampling in the Omani coast of the Arabian Sea (2007-2008) used in this thesis. NEMon; Northeast Monsoon; PreMon; Pre-Southwest Monsoon; SWMon: Southwest Monsoon; PostMon: Post-Southwest Monsoon. No.: Number of samples. 111

Publication arising from this thesis

This thesis is submitted as a series of data investigation chapters which will be submitted to international peer-reviewed journals as manuscripts. The chapters (Chapters 2 to 4) were formatted in accordance to the requirement of each journal:

Al-Rasady, I., Meeuwig, JJ., and Claereboudt, M. Anticipating the influence of climate-driven low oxygen zones on fish biodiversity: a case study from the Arabian Sea. *Marine Ecology Progress Series*. In preparation. (Chapter 2).

Al-Rasady, I., Meeuwig, JJ., and Claereboudt, M. The influence of oxygen minimum zone and some oceanography parameters on the length distribution of five fish species in the Arabian Sea. *Fisheries Research*. In preparation. (Chapter 3).

Al-Rasady, I., Meeuwig, JJ., and Claereboudt, M. Low oxygen zones predict future condition of fish under climate change. *Environmental Biology of Fish*. In preparation. (Chapter 4).

Chapter 2- Issam overall contribution: 70%. Prof. Jessica assisted with the data analysis, structure and content editing of the chapter (20%). Dr. Michel assisted with the data analysis, structure and content editing of the chapter (10%).

Chapter 3- Issam overall contribution: 70%. Prof. Jessica assisted with the data analysis, structure and content editing of the chapter (20%). Dr. Michel assisted with the data analysis, structure and content editing of the chapter (10%).

Chapter 4- Issam overall contribution: 70%. Prof. Jessica assisted with the data analysis, structure and content editing of the chapter (20%). Dr. Michel assisted with the data analysis, structure and content editing of the chapter (10%).

Acknowledgments

The great acknowledgement is to whom deserve all the praise in the first life and in the hereafter.

I want to thank my supervisors Professor Jessica Meeuwig and Dr. Michel Claereboudt. They have been supportive throughout the study. They were always on my side whenever I needed help. I spent many hours in their offices discussing my study and they were always supportive. Their critical thinking and wide experience have helped me to look at my results from different angles.

This thesis would not have come into existence without the valuable help from various people and organizations. It is impossible to mention them all. I would like to thank all of them who have helped me during the study and during the production of the thesis. The next thanks are to those who pray for me to success especially my parents, brothers, sisters, my relatives, friends and others.

The great thanks are to His Excellence Dr. Hamed Al-Oufi for his enormous support for my study. I would like to thank the Ministry of Higher Education in Sultanate of Oman for the scholarship they offer for me. Thanks to the Consulate General of the Sultanate of Oman in Melbourne and the Omani student society in WA.

I want to thank the following for the technical support. David Tickler and Dr. Phil Bouchet for assistance in R language and Yqoop Al-Gabre for Annual Fish Statistics data.

Last but not least, my special thanks goes to my wife and her brothers Ibrahim and Ahmed, who took full responsibility for my children while I was busy in my study. Their generosity, unselfishness, confidence and support are nothing short of overwhelming.

Chapter 1- General introduction

1.1 Climate Change

Climate change is having dramatic effects on the planet (IPCC 2014). The oceans, comprising some 71% of the earth's surface, are particularly vulnerable to climate change (Rogers and Laffoley 2011; Ashkenazy et al. 2013; Jungclaus et al. 2013). Since 1978, both the Arctic and Antarctic ice caps have experienced substantially increased rates of melting (Richter-Menge et al. 2006) causing sea level to rise globally (Alley et al. 2005), but at different rates regionally (Nicholls and Cazenave 2010). Many islands in the Pacific Ocean are now facing the threat of disappearing from the global map as consequence of sea level rise (Hughes et al. 2003) and on continents, sea level rise is causing increased flooding in river deltas (Wassmann et al. 2004). Melting polar ice caps may also shift the axis on which the Earth spins (Adhikari and Ivins 2016). Such changes to the Earth's axis of spin are thought to cause shifts in seasons. For instance, the onset of snowfall in Europe was delayed in 2015. More generally, other regions of the world are facing increasingly heavy rains and considerable increases in the frequency and strength of hurricanes (Hanna et al. 2013).

The most pervasive impacts of climate change on the world's oceans are warming (Sarmiento et al. 2004), lowered salinity (Doney et al. 2012), acidification (Hoegh-Guldberg and Bruno 2010) and expansion of low oxygen zones (Cheung et al. 2012). Between 1880 and 2012, the average global sea water temperature rose by 0.9 °C and the projection for the year 2100 predicts a possible 5.4 °C increase if carbon emissions are not reduced (Rose et al. 2016). Warming has accelerated over the last three decades; the global average sea water temperature has increased by 0.2 °C per decade which corresponds to an increase in energy of 14×10^{22} J in the upper 700 m depth strata of the world's oceans (Hoegh-Guldberg and Bruno 2010). During the 1990s, the Southern

Ocean temperature also increased by 0.17 °C between the 700 m to 1100 m depth stratum (Gille 2002).

Ocean temperature and salinity are strongly correlated, as warming temperatures increases salinity (Levitus et al. 2000). Ocean salinity is controlled by the water cycle which includes fluxes of fresh water, precipitation levels and the amount of water that has evaporated (Yu, 2011). Ocean salinity is affected by climate change through the amplification of the water cycle (Williams et al. 2007). For instance, an increase in atmospheric temperature of 1 °C will amplify the water cycle rate by 8±5%, which in turn will increase the amount of rainfall in wet areas of the world by 16-24% (Durack et al. 2012). The relationship between salinity and temperature is one of the most fundamental physical oceanographic inputs for modelling ocean and climate variability (Katsura et al. 2013) with salinity used as an indicator for water mass formation (Yan et al. 2013) and as a dynamic tracer for geostrophic circulation (Qiu and Chen 2012).

In addition to driving a general warming of the oceans and increased salinity, climate change reduces the concentration of dissolved oxygen (Koslow et al. 2011; Long et al. 2016). As oceans warm, dissolved oxygen decreases due to the reduction in oxygen solubility gained from the mixing with the contacting air layer just above the seawater surface (Matear et al. 2000). Specifically, increasing ocean temperature has increased ocean stratification, preventing the mixing of the oxygen in the water column (Deutsch et al. 2011). It is calculated that with a 1 °C increase in ocean temperature, dissolved oxygen levels will decrease by two percent (Long et al. 2016). The reduction in dissolved oxygen level is increasingly pronounced since the 1950s, especially in so-called Oxygen Minimum Zones (OMZs), areas defined as having dissolved oxygen levels less than 0.5 ml⁻¹ and currently present in the southern Indian, Pacific and Atlantic Oceans (Helm et al. 2011; Xu et al. 2015).

1.2 Oxygen and Fish

The concentration of dissolved oxygen is fundamentally important to marine life with each species having its own oxygen tolerance limits (Crain and Bertness 2006). During the different life stages of fish, adults are more tolerant to low levels of dissolved oxygen than early life stages, with juveniles more tolerant than individuals at the larval pelagic stage (Miller et al. 2002). Fish, like other living organisms, need oxygen for respiration and this is obtained from the seawater as dissolved oxygen. Fish obtain energy for respiration through metabolism (Li and Yakupitiyage 2003) that requires adequate amounts of oxygen to convert glycogen to glucose (Polakof et al. 2012). Changes in dissolved oxygen can lead to impacts on fishes that change marine species distributions (Shultz et al. 2011). For instance, since 1951, 20% of 24 taxa of mid-water fishes have declined due to the expansion of an OMZ toward the surface of the California Current, increasing fish mortality via asphyxia, predation or fishing (Koslow et al. 2011). The seasonal shoaling of OMZs extends to the seabed and has the potential to influence socioeconomically important demersal fish and reduce the landings of artisanal fisheries (Piontkovski and Al-Oufi 2014) which comprised mostly of demersal fish (Mathews et al. 2001).

As such, expanding OMZs may affect biodiversity patterns through changes in distribution. As tolerance to oxygen concentration varies with fish body size, OMZs may alter length distribution of fishes. Finally, growth of fish is affected by oxygen in the different growth process and this will likely be reflected in fish condition. This study will cover these three matters: fish biodiversity, length distribution and fish growth condition, in an existing OMZ in the Arabian Sea.

1.3 Biodiversity

Fish biodiversity is a measure of the variety of fish present in a specific ecosystem, frequently quantified as the number of species (Cappo 2004). Oxygen minimum zones affect marine biodiversity through climate change that alters the environmental characteristics that drive species to move to different habitats or reduce abundance (Thomas et al. 2004). Expanded OMZs can affect fish biodiversity by shifting fish distributions poleward (Cheung et al. 2009). Hypoxia can also force fish to shift from preferred habitats and create gaps in the community structure and lead to alterations in community structure (Ives and Cardinale 2004). Frequent mass mortality caused by the declines in dissolved oxygen level can also lead to changes in biodiversity indices (Diaz and Rosenberg 2008). Low oxygen concentration can reduce fish activity and as a result may affect predation patterns (Scott and Helfman 2001).

1.4 Length distribution

Length distributions of fishes are influenced by the environment in which they are found. For instance, within species, as individuals grow larger they tend to move to deeper water (Fitzpatrick et al. 2012; Nilsson and Ostlund-Nilsson 2008) and the environmental physical parameters also differ between coastal and offshore waters (Smit et al. 2013). Increases in low dissolved oxygen zone lead to change in the species-specific length distribution in the coastal and offshore waters (Rijnsdorp et al. 2009), however, no single environmental variable could explain the distribution of fish in space or time in the coastal waters (McIlwain et al 2011). It is also important to note that fishing can strongly influence length distributions, with disproportionate reductions in large species and individuals (refs).

1.5 Fish condition

Fish condition is predicted to be reduced due to the effect of the climate change (Walters and Hassall 2006). Reduction in dissolved oxygen can influence the condition of fish by affecting metabolism, growth, feeding and energy expenditure (Buentello et al. 2000). Anabolic processes in fish use dissolved oxygen for healing, growth and reproduction (Lei et al. 2016). Besides the amount of dissolved oxygen in the environment, anabolism also depends on the quality and the quantity of food intake (Li and Yakupitiyage 2003). Reduction in dissolved oxygen causes stress to the fish hence the food intake is negatively affected as consequently are the anabolic processes (Portz et al. 2006). The study of fish condition is fundamental for fisheries ecology (Jorgensen et al. 2007), with condition often defined morphometrically in terms of body weight relative to length. Heavier fish at a given length are assumed to be in a better condition with consequent benefits for reproduction. Eight different indices can be used to quantify fish condition (Bolger and Connolly 1989), including parameters from length-weight relationships (Froese 2006).

1.6 Fisheries independent data

Assessing the effect of climate-driven OMZs on fish biodiversity, size structure and condition can be explored using large sets of fisheries-independent data. Fisheries-independent data have been widely used to assess stock size and to quantify fish abundance and distribution (Booth 2000; Hsieh et al. 2006). For instance, distribution of pelagic sharks in the western North Atlantic between 1977 and 1994 was studied using fisheries-independent data and led to an improved understanding of species biology and management measures (Simpfendorfer et al. 2002). Key species distributions have also been described using fisheries-independent data, for instance, in the Benguela ecosystem (Pecquerie et al. 2004). This type of data is well trusted because of the standard of the method used to estimate fish distributions (Chen et al. 2003). Nevertheless, bias in fish

distribution estimations has occurred even in fisheries-independent data studies due to fish behavior (Irwin et al. 2008). Fish gather during spawning seasons or in a feeding grounds and this aggregation can lead to over- or under- estimates of fish distribution and abundance (Paradinas et al. 2015). Moreover, not all areas may be accessible to sampling because of the geographical characteristics of the seabed (Williams et al. 2010). Fisheries independent sampling also requires considerable amounts of capital and manpower (Smith and Addison 2003). However, in the case of the predicted climate-driven expansions in OMZs, fisheries-independent sampling of existing OMZs holds potential to provide insight into how marine systems may respond.

1.7 The Arabian Sea

The Arabian Sea has one of the most extreme climate regimes globally because of the influence of the Southwest monsoon (Herring et al 1998). The regional oceanography of the Arabian Sea has been the subject of a number of surveys. Seasonal variability in oceanography has been surveyed by the US Joint Global Ocean Flux Study (JGOFS) between 1994 and 1996 (Morrison 1997 1998; Morrison et al. 1998 1999; Shi et al. 2000) and the International Indian Ocean Expedition (IIOE) between 1973 and 1974 (Qasim 1982). Both surveys described the oceanography in terms of dissolved oxygen, temperature and salinity at the sea surface, between 50 to 100 m, and at depths greater than 1000 m during the different seasons in the Arabian Sea. The JGOFS survey route involved two parallel lines from the Omani coast of the Arabian Sea to the deep central parts of the Arabian Sea It focused on the mixed layer in the Arabian Sea (Morrison et al. 1998). The IIOE survey covered a wider area of the Arabian Sea, with sampling stations located along the coastal areas of the northwest coast of Indian, Pakistan, Iran, the Omani coast on the Sea of Oman and the Arabian Sea, and the center of the Arabian Sea. This survey in particular considered how the oxygen minimum zone depth varies in location,

size, depth and season (Qasim 1982).

The OMZ in the Arabian Sea varies in its location and depth both seasonally and between years, largely as a function of the strength of the monsoon (Naqvi 1991). Typically, dissolved oxygen varies from 4.2 to 5.2 ml l^{-1} at the surface of the Arabian Sea during the Southwest Monsoon and declines with depth from between 0.9 and 4.5 ml l^{-1} at 100 m and 0.3 to 1 ml l^{-1} at 1000 m (Qasim 1982). Generally, the OMZ is found in the northern region of the Arabian Sea, with dissolved oxygen increasing from the north region of to the south regions of Arabian Sea (Qasim 1982). Morrison et al. (1999) located the OMZ in the Arabian Sea as areas where dissolved oxygen concentration was less than 4.5 ml l^{-1} and they found these low levels at depths of 150 m. In particular, the Ras al Hadd region had dissolved oxygen levels less than 0.2 ml l^{-1} (Morrison et al. 1999). However, Morrison et al. (1998) correlated the concentration of dissolved of oxygen with oceanographic variables such as salinity and temperature, suggesting temporal and spatial variability in its strength and location, confirming the conclusion of Qasim (1982) that “the oxygen minimum zone depth that vary in area, depth and from season to season.”

The temperature in the Arabian Sea varies from season to season and from location to another (Naqvi 1991). In the Arabian Sea, the sea surface temperature varied between 28 and 29 °C at the time of the JGOFS survey (Morrison 1997 1998; Morrison et al. 1998). During the Southwest Monsoon the seawater temperature can decline from between 24 and 28 °C to as low as 16 to 18 °C, but generally averages 20 °C (Sheppard et al. 2000; Wilson et al. 2002). Sea surface temperature ranges between 22.5 and 28.5 °C at depths between 20 and 60 m to less than 15 °C at 1000 m (Qasim 1982). Temperature generally increases from north to south in the Arabian Sea (Qasim 1982).

Temperature and salinity are strongly correlated. The wind during the Northeast Monsoon drives low temperatures and produces a well-ventilated salinity maximum at about 36.8

ppt at the sea surface of the Arabian Sea (Naqvi 1991). The average salinity in the Arabian Sea during the US JGOFS was between 36.2 to 36.5 ppt (Morrison 1998). At the sea surface, the salinity concentration near the coast was between 35.3 and 36.8 ppt and increased during the Northeast Monsoon 36.9 ppt (Morrison et al. 1998). The salinity was between 35.4 to 36.6 ppt at the sea surface and between 35.3 to 35.5 ppt at 1000 m depth and decreased from north to south in the Arabian Sea region (Qasim 1982).

The oceanography of the Arabian Sea is strongly affected by the Southwest monsoon which upwells high levels of nutrients to the surface water, resulting in frequent brown, red and green tide events as a result of phytoplankton blooms (Sherr and Sherr 2002). Harmful plankton bloom causes severe impact on coastal resources. Fish kill incidents have been regularly reported in the Arabian Sea because of the bloom of the most common dinoflagellate species *Noctiluca scintillans* (Al-Gheilani et al. 2011). The OMZ and harmful plankton blooms are a major threat to marine ecosystems of the Arabian Sea.

The marine ecosystem of the Arabian Sea includes a wide range of habitat and associated flora and fauna. These habitats include coral reefs, sandy and rocky bottom support wide diversity of marine fauna (McIlwain et al. 2011). For instant, over 100 species of corals are known from the ergion (Rezai et al. 2004) and estimates of fish fauna vary between 300 (Fouda and Hermosa 1998) and 579 (Siddeek et al. 1999). Charismatic mega fauna include dugong, turtles, whales and dolphins (Mikhalev 1997). Seagrass, Kelp and macroalgae grow on the substrate of the Arabian Sea reaching a size of 1.5 m (Schils and Coppejans 2003).

The Arabian Sea also experiences one of only three permanently existing Oxygen Minimum Zones globally, with the other two located in the Eastern Pacific Ocean and off of West Africa (Levin et al. 2000). Two semi-annual monsoons in the Arabian Sea drive one of the most energetic current systems in the world with the greatest seasonal

variability of environmental parameters observed in any ocean basin (Schott and McCreary 2001). The Southwest Monsoon, occurs during the boreal summer when a hot Asian land mass and Tibetan Plateau result in low pressure over Asia and high pressure over the Indian Ocean (Shi et al. 2000). The geostrophically balanced airflow results in a strong topographically steered southwesterly wind and the formation of a low-level atmospheric feature called the Findlater Jet (Goes et al. 2005). The Southwest Monsoon causes large nutrient upwellings in the Arabian Sea parallel to the Omani coastline (Honjo et al. 1999). The upwelling event during the Southwest Monsoon makes the Arabian Sea one of the most biologically productive seas globally (Ryther and Menzel 1965) which causes the depletion of oxygen ($O_2 \leq 4.5 \mu M$) and formation of one of the largest-in-size oxygen minimum zones (OMZ) on the planet between depths of 50 and 1000 m (Morrison et al. 1998; Levin et al. 2000). During the boreal winter, the Northeast Monsoon in the Arabian Sea forms from the cooling of the Eurasian continent which results in and increase in high pressure zones over land and low pressure zones over the Indian Ocean (Shi et al. 2000).

The Arabian Sea represents a significant opportunity to study the influence of climate change on fish biodiversity, length distribution and growth with respect to the role of OMZs. Most of our understanding with respect to the influence of oxygen on fish is from models, lab experiments or lethal events such as fish kills (Diaz and Rosenberg 2008). (Diaz and Rosenberg 2008). While studies have demonstrated or modelled the temperature-driven shifts in the distribution of fish species with latitude and depth (Cheung et al. 2009), the influence of a persistent low oxygen environment on fish biodiversity, length distributions and condition have yet to be explored on large, natural spatial scales. Natural factors such as environmental parameters and anthropogenic factors such as fishing influence the diversity, length distribution and condition of the fish (Cheung et al. 2012). Permanent OMZs in the Arabian Sea provide an opportunity to

study the effect of natural and artificial factors regionally, seasonally and at depth on fish diversity, length distribution and condition.

1.8 Objectives and Aims

A challenge for science lies in anticipating how predicted environmental changes will influence marine ecosystems and the organisms inhabiting them. This thesis will address this challenge by (1) modelling fish species biodiversity across regions of the Arabian Sea varying in their exposure to monsoonal influences, and across regions and depth strata; (2) quantifying the relationship between length distributions and seasons, regions and depth, and oceanographic conditions for five focal fish species; and (3) comparing length-weight relationships of fish sampled from the OMZ region in the Arabian Sea with those of their conspecifics from non-OMZ regions. Combined, these analyses will be used to predict the influence of the OMZ on the fish assemblage.

1.9 Thesis Outline

This thesis is divided into three data chapters. All analyses are based on a large fisheries-independent dataset acquired in the Northwest Arabian Sea off the coast of Oman between September 2007 and September 2008. The survey was conducted from the Al Mustaqila 1, a 45.2 m long modern commercial fishing vessel designed to operate efficiently under a wide variety of conditions in both inshore and offshore environments. The bottom trawl was configured with a 70 m sweep length and 9 m bottom backstop length. The mouth area of the trawl was 308 m of minimum circumference and used 800 mm mesh in the fore part of the net. The cod-end was 20 meters long and used a 16 mm liner. The headline height averaged by survey ranged from 9 to 12.7 m. The net was rigged with standard Thyboron Type 7 trawl doors and 150 m bridles. The survey covered the continental shelf across the 20–250 m depth range across four regions: Ra's al Hadd to Masirah Island (Region A), Masirah Island to Ra's al Madrasah (Region B), Ra's al Madrasah to Ra's

Hasik (Region C), and Ra's Hasik to the Yemen border (Region D). Sampling occurred throughout the year, during the four major seasons of the Arabian Sea; the Northeast Monsoon (NEMon; January - March), the Pre-Southwest Monsoon season (PreMon; April - June), the Southwest Monsoon (SWMon; July -September), and the Post-Southwest Monsoon season (PostMon: October - December). The region was also subdivided into four depth strata: DS1 (20 to 50 m); DS2 (51 to 100 m); DS3 (101 to 150 m); and DS4 (151 to 250 m). For a total of 764 demersal trawls, fish specimens were classified to genus and species using the FAO species catalog (Cohen et al. 1999) with key environmental measurements taken for each trawl including bottom temperature (°C), salinity (ppt), dissolved oxygen (mll^{-1}), and depth (m). At sea, fork length of sampled fish was measured to the nearest millimeter, and the weight was recorded to the nearest gram.

In Chapter 2, I determine how indicators of diversity such as species richness vary with region, season and depth strata and how these varied as a function of the environmental variables (temperature, salinity and dissolved oxygen). In Chapter 3, I investigate the effect of region, season, and depth strata on the length distribution of five economically important species (*Argyrops spinifer*, *Drepane longimana*, *Epinephelus diacanthus*, *Lethrinus nebulosus* and *Pomadasys commersonnii*). I also explore the relationship between the length distribution of the fish and environmental variables (temperature, salinity and dissolved oxygen). In Chapter 4, I test how fish condition varies between fish from the Arabian Sea's OMZ relative to conspecifics from non-OMZ region using length-weight relationships. I also compare the effect of regions on the condition of seven species (*A. spinifer*, *D. longimana*, *Carangoides equula*, *Cheimerius nufar*, *Pagellus affinis*, *Plectorhinchus schotaf* and *P. commersonnii*).

Climate change will alter environmental variables in the ocean including dissolved oxygen, with OMZs predicted to expand. The general discussion of my thesis integrates

the results from the three data chapters to consider how expanding OMZs may influence patterns of biodiversity, change in size distributions and fish condition in these areas. Such potential impacts have both global implications, particularly with respect to food security of an ever-increasing world population. Studying the regional impact of a potentially expanding OMZ in the Arabian Sea is also important. Climate change scenarios predict a strengthened Southwest Monsoon which in turn will bring more low dissolved oxygen water to the Arabian Sea. As the Southwest Monsoon affects the socioeconomic life of 60% of the world's population that occupying Pakistan, India and other close by countries (Zhou et al. 2010), many of whom depend on fishing as a source of income and protein, negative impacts of expanding OMZs have important regional implications. As existing OMZs expand and new OMZs form, the implications for food security become global.

1.10 References

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Chapter 2- Influence of climate-driven low oxygen zones on fish biodiversity: a case study from the Arabian Sea

Target Journal: Marine Ecology Progress Series

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2.1 Abstract

Fish biodiversity is at risk globally due to the climate-driven expansion of areas of low dissolved oxygen. The Arabian Sea is one of three regions globally with a persistent oxygen minimum zone (OMZ). The Arabian Sea OMZ is a consequence of the high productivity associated with the Southwest Monsoon (SWMon). During the Northeast Monsoon (NEMon), the OMZ is also present but tends to be found in deeper water (> 200 m). I examined patterns in fish biodiversity across the Arabian Sea with respect to region, season and depth strata, and in relation to environmental conditions, including bottom sea temperature, salinity and dissolved oxygen. Analyses were based on 764 trawl samples collected as part of a stock assessment survey conducted between 2007 and 2008. A total of 99,319 fish were collected, representing 207 species. There was no variation in the estimated total species diversity by region, and the number of species was highest during the NEMon and decreased with greater depth. The average species richness per trawl also did not vary with region and was highest during the NEMon and lowest in the post-Southwest Monsoon (PostMon) period and was greatest in the shallowest depth strata. The Chao1 and Shannon indices of biodiversity showed no regional patterns but were highest in the NEMon and lowest in the SWMon. The analysis also showed declines in

these two indices with increasing depth. The total abundance was significantly higher during the PreMon and was invariant in three depth strata 1, 2 and 4 and low in depth strata 3. Biodiversity indices were poorly explained by the environmental variables. Climate change is expected to strengthen the SWMon, which will expand the OMZ. As the SWMon period and its expanded OMZ is associated with lower species richness, biodiversity is likely to be negatively affected by climate change. The generality of this prediction should be evaluated by exploring patterns in biodiversity associated with other OMZs globally, and as these features expand through time.

Keywords: Biodiversity, OMZ, South West monsoon, North East monsoon, species richness, abundance.

2.2 Introduction

Patterns in fish biodiversity and distribution are underpinned by habitat and environmental conditions which may be modified by anthropogenic factors such as climate change, fishing, habitat fragmentation and pollution (Raffaelli 2004). The presence of the OMZ in the Arabian Sea however provides a rare opportunity to specifically consider how changing environmental conditions associated with the OMZ, both regionally, seasonally and at depth, affect fish biodiversity, acknowledging that these activities such as fishing may also influence these patterns and cannot be excluded (Catalan et al. 2006). Climate change is expected to influence the patterns of fish biodiversity with respect to alterations in distribution and abundance by changing the marine ecosystem hydrography (Cheung et al. 2009). Fish communities are closely linked to their environment (Jones et al. 2004) and respond differentially to changes in ambient conditions. Such responses can include changes in horizontal (Perry et al. 2005) and vertical distribution (Dulvy et al. 2008). For instance, with ocean warming, fishes have shown pole-ward movements escaping from warming water to water bodies where

temperature falls within their range of tolerance (Nye et al. 2009). Additionally, distribution may deepen as fishes migrate vertically to maintain preferred temperature ranges (Pörtner and Knust 2007). Such changes can yield overall shifts in species composition with both local losses and additions (Hiddink and Hofstede 2008; Cheung et al. 2009).

Sea surface temperature (SST) has increased globally by 0.2 °C in the last 30 years (Hansen et al. 2006). Temperature strongly influences fish through impacts on physiology, metabolism, growth, reproduction and behaviour (Pauly 1980). Such impacts can result in range shifts either through migration (Pörtner and Knust 2007) or reduced productivity of affected populations (Brander et al. 2003). Indeed, while fish can positively react to increases in temperature, with for instance, enhanced growth, such benefits are constrained by limits with respect to temperature tolerances (Pörtner 2001) as temperature beyond these limits force fish to utilize more of its energy budget in the form of carbohydrates (Hemre et al. 2002) and reduce the amount of food intake (Handeland et al. 2008) hence negatively affecting fitness and growth. Increases in temperature can also lead to a greater risk of disease, mass fish mortalities and thus contribute to biodiversity loss (Harvell et al. 2002).

Associated with climate driven increases in temperature is the reduction in dissolved oxygen levels in the global seas (Matear and Hirst 2003). Stratification prevents mixing of water masses between surface and deep layers, reducing the dissolved oxygen in the deeper layer (Pörtner and Knust 2007). Oxygen minimum zones (OMZs), defined as regions with permanent dissolved concentrations less than 0.5 ml⁻¹, are expected to expand in area and volume across oceans globally, but especially in tropical regions (Matear and Hirst 2003; Stramma et al. 2008). Increasingly, the influence of oxygen on patterns in fish biodiversity is being recognised (Jackson and Mandrak 2002; Worm et al. 2006; Vaquer-Sunyer and Duarte 2008). Persistent OMZs increase the risk of hypoxia

(<0.5 mll⁻¹) and can influence biodiversity by causing mass mortality of marine fishes (Gray et al. 2002). At non-lethal levels, OMZs can influence biodiversity by altering fish behaviour and fitness (Kramer 1987). Persistent OMZs can also affect the metabolic rate through oxygen blood pressure, limiting the energy used in reproduction, growth and other vital rates (Pörtner and Knust 2007). Low oxygen can lead to migration to new areas which in turn, may increase predation risk for migrating individuals (Harley et al. 2006) with subsequent reductions in fitness and consequences for biodiversity (Vinebrooke et al. 2004). Persistent OMZs can cause physiological stress to non-migrating individuals, with impacts on growth, reproduction, age at maturity (Vaquer-Sunyer and Duarte 2008; Pauly 2010). These sub-lethal affects may also affect biodiversity by reducing, through time, the number of species able to occupy OMZs (Doney et al. 2012).

The effects of persistent OMZs on biodiversity are, however, unclear as fish species respond differentially to conditions in relation to their specific tolerances. The effects of low levels of dissolved oxygen are dependent on size, life history stage, and metabolic rate. For instance, small species and individuals are more affected by low levels of dissolved oxygen than large species and individuals because they have lower energy budgets (Staples and Nomura 1976). This constrains their search for suitably oxygenated water, making behavioral change more difficult and increasing their vulnerability to predation and mortality (Rijnsdorp et al. 2009). For early life history stages, demersal and pelagic species appear similarly affected by low oxygen concentration through increased mortality that reduces recruitment (Walther et al. 2002). In later life history stages, demersal species are more greatly affected by low oxygen concentrations as they tend to have less capacity for migration compared to pelagic species (Barbaro et al. 2009).

The influence of changing environmental conditions, such as reductions in dissolved oxygen concentration, occurs against a backdrop of large-scale biogeography (Willig et al. 2003). For instance, fish diversity tends to decline with depth (Nye et al. 2009) and

increase towards the equator (Perry et al. 2005). Deeper water is also typically characterised by low dissolved oxygen concentration (Schmittner et al. 2007) which may not suit smaller species, and if further deoxygenation of deep water occurs, small species may be locally extirpated (Nilsson and Ostlund-Nilsson 2008). Additionally, expanding OMZs near the equator may also lead to pole-ward range shifts of affected species (Pörtner and Knust 2007), counterbalancing the current trend towards greater equatorial diversity.

The Arabian Sea provides an important model system in which to study the effects of persistent OMZs on fish diversity. It is characterised by permanent, shallow (<50 m) low dissolved oxygen concentration water (Helly and Levin 2004) and is one of only three OMZs globally (Arabian Sea, Eastern Pacific Ocean, and off West Africa) where oxygen is consistently less than 0.5 ml⁻¹ (Levin et al. 2000). The Southwest Monsoon drives vertical nutrient fluxes via coastal upwelling that enhance pelagic productivity along the Omani coastline, followed by deoxygenation as the organic material is respired (Brock and McClain 1992; Honjo et al. 1999; Sheppard et al. 2000). The Northeast Monsoon season also brings high nutrients and increased primary production to the Arabian Sea. It occurs during the winter as a result of cool, dry continental air brought by prevailing Northeast trade winds but is less intense than the Southwest Monsoon (Kumar et al. 2001).

Against this environmental background, the Arabian Sea's fish fauna is both diverse and representative of the Indo-Pacific. The 166 families recorded from the Arabian Sea represent 92.6% of the families recorded in the Indo-Pacific Ocean (Fouad et al. 1998), Al-Jufaili et al. (2010) recorded a total of 1176 marine fish species, 1138 species were identified by Fouad et al. (1998) 930 described by Randall (1995), 280 were described by Al-Abdessalaam (1995). Manilo and Bogorodsky (2003) present a list of 1769 from all coasts of the Arabian Sea to a depth up to 500 m, include India, Oman, Yemen and the

East coast of Africa. Over 364 marine species support the commercial fisheries in the Arabian Gulf, Oman Sea and the Arabian Sea (Siddeek et al. 1999).

In this study, I use data from a research survey across the Northwest Arabian Sea off the coast of Oman between September 2007 and September 2008 to quantify patterns in demersal fish biodiversity by region, season and depth strata given measured differences in dissolved oxygen. I further consider the relationship between dissolved oxygen and other environmental variables with respect to their influence on fish biodiversity.

2.3 Methods

A research survey across the Northwest Arabian Sea off the coast of Oman was carried out by the New Zealand National Institute of Water and Atmospheric Research (NIWA) for the government of the Sultanate of Oman between September 2007 and September 2008 using a two-phase stratified random survey design (McKoy et al. 2009). The survey was conducted from the Al Mustaqila 1, a 45.2 m long modern commercial fishing vessel designed to operate efficiently under a wide variety of conditions in both inshore and offshore environments. The bottom trawl was configured with a 70 m sweep length and 9 m bottom backstop. The mouth area of the trawl had a 308 m minimum circumference and used 800 mm mesh in the fore part of the net. The cod-end was 20 m and used a 16 mm liner. The headline height ranged from 9 to 12.7 m when averaged by survey. The net was rigged with standard Thyboron Type 7 trawl doors and 150 m bridles. The sampling effort was stratified randomly for the three factors included in this study: Region; Season and Depth Strata (Table 2.1). The survey covered the continental shelf across the 20–250 m depth range across four regions: Ra's al Hadd to Masirah Island (Region A), Masirah Island to Ra's al Madrasah (Region B), Ra's al Madrasah to Ra's Hasik (Region C), and Ra's Hasik to the Yemen border (Region D) (Figure 2.1). Sampling occurred throughout the year, allowing data to be allocated to one of the four

major seasons of the Arabian Sea (Piontkovski et al. 2011): the Northeast Monsoon (NEMon; January - March), the Pre-Southwest Monsoon season (PreMon; April - June), the Southwest Monsoon (SWMon; July -September), and the Post-Southwest Monsoon season (PostMon: October - December). The four depth strata were: DS1 (5 to 50 m); DS2 (51 to 100 m); DS3 (101 to 150 m); and DS4 (151 to 250 m).

Samples from a total of 764 demersal trawls were collected across the region, with key environmental measurements taken for each trawl. These included bottom temperature ($^{\circ}\text{C}$), salinity (ppt), dissolved oxygen (ml l^{-1}), and depth (m). At sea, fish were classified to genus and species using the FAO species catalogue (Cohen et al. 1999) and counted. The records were stored in the database of the Fish Resources Assessment Survey of the Northwest Arabian Sea Coast of Oman (McKoy et al. 2009).

In this study the species richness is estimated as the number of fish species in each region, season and depth stratum. Abundance is the total number of each fish species in each region, season and depth stratum. To assess the adequacy of sampling effort in capturing the biodiversity of the region, fish species richness was computed using EstimateS program (Version 9, Colwell et al. 2004). The program estimates species richness by extrapolating the asymptote of species accumulation curves i.e. plotting the cumulative species richness against sampling effort at each level of sampling effort using various models of rarefaction. Estimated species richness was calculated for each region, season and depth stratum. Chi-square Goodness-of-Fit tests were run in Excel software to test the null hypotheses that species richness is evenly distributed as a function of (1) region, (2) season and (3) depth strata. Additionally, Chi-square contingency tests were calculated to determine whether patterns of species richness across region were independent of season and depth, and likewise whether patterns of species richness across season were independent of depth, thereby capturing any potential interactions between the factors (Zar 1999).

Twelve biodiversity indices were calculated for each of the 764 trawls conducted during the survey using the "diversity" option in Past software v2.17c (Hammer et al. 2001). These included: Dominance D, Berger-Parker, Evenness e^H/S , Menhinick, Equitability J, Fisher alpha, Chao1, Taxa S, Simpson 1-D, Margalef, Brillouin and Shannon index '. These continuous indices were first normalised to address differences in variable scales, with resemblance then calculated based on a Euclidean distance matrix. Two-dimensional ordinations were created by Principal Component Analysis (PCA) using Primer to visualise the contributions of both richness and equitability to the overall biodiversity patterns. The null hypothesis is that the species richness had the same biodiversity patterns. Single indices from opposing clusters were chosen to represent patterns in biodiversity amongst the samples and avoid redundancy of these related metrics and a new Euclidean distance matrix calculated on to normalised values of the twelve biodiversity indices.

Observed species richness and total abundance for each trawl was also calculated. Euclidean distance matrices were calculated for each of these variables given their continuous nature. Data were not normalized prior to the permutational ANOVA as the analyses are a univariate application of permutational methods (Wood 2009). The null hypothesis is that the mean of observed species richness and total abundance were the same for all factors (region, season and depth strata). Finally, the fish community composition data (abundance by species) were transformed via square root to down-weight and up-weight common and rare species, respectively. This transformation was followed by calculation of the Bray-Curtis resemblance matrix given the presence of joint-zeros in the abundance data and their non-informative nature. The overall statistical design for these univariate biodiversity metrics consisted of testing the influence of region, season and depth strata using a three-way permutational ANOVA with interactions. Non-significant interactions were sequentially removed, beginning with the

3-way interaction, and followed by the 2-way interactions with the highest p -values, following Underwood (1981). Tukey Post-hoc pairwise tests using R software (Wood 2009) where significant main effects were indicated. Effects were visualised with bar charts, including interactions where present.

As region, season and depth strata are to some degree proxies for environmental conditions, general additive models (GAMs) were used to investigate the relationships between environmental characteristics of the sampling station (i.e. temperature, salinity, dissolved oxygen and sea bottom depth) as explanatory variables with patterns in fish biodiversity (Chao1, Species richness and Abundance) as response variables. General additive models were built using the package ‘mgcv’ of R software (Wood 2009) at the significant difference at $\alpha = 0.05$ with parameter estimation by residual maximum likelihood (REML). The maximum bias dimension was set to $k = 4$ as suggested by (Hastie and Tibshirani 1990) to minimise over fitting and preserve biological realism.

2.4 Results

The fitted species accumulation curve suggests that our overall 764 sampling effort was reasonable with approximately 207 species predicted to be present (Figure 2.2). The species accumulation curve increased rapidly up to point of approximately 300 samples, at which point the rate of species accumulation decelerated. The curve did not reached a plateau at 764 samples. Chi-square goodness of fit tests indicate that the number of estimated species were evenly distributed across regions (χ^2 : $p = 0.40$; Table 2.2) but unevenly distributed among seasons (χ^2 : $p < 0.001$; Table 2.2) and by depth strata (χ^2 : $p < 0.001$; Table 2.2). Specifically, the estimated species pool was highest during the NEMon season and lowest in the PostMon season (χ^2 : $p < 0.001$; Table 2.2), highest in depth strata 1 and lowest in the deepest strata 4 (χ^2 : $p < 0.001$; Table 2.2). The contingency Chi-square tests indicate that the way in which the species pool varies by depth depends on the region and the season but that seasonal variations in estimated species richness do

not vary with region (Table 2.2). The number of estimated species decreased with depth from strata 1 to 4 in all regions and during all seasons (χ^2 : $p < 0.05$; Table 2.2), except in region C where the number of species was higher in stratum 2 than stratum 1 (Figure 2.3). The twelve observed biodiversity indices largely separated into indicators of diversity and indicators of evenness (Figure 2.4). Of these, I chose Chao1 and Shannon as these had the least collinear with the samples. The variance in region factor was not significantly different in Chao-Shannon, species richness and total abundance, but season factor was significant in Chao-Shannon, species richness and total abundance ($p < 0.01$; Table 2.3 and figure 2.5). Pairwise tests for both Chao-Shannon and species richness show that these metrics were significantly lower in the SWMon season relative to the other seasons ($p < 0.01$; Table 2.3 and figure 2.5). A combination of Chao1 and Shannon (hence Chao-Shannon) and species richness were significantly higher during the NEMon season relative to the other seasons ($p < 0.01$; Table 2.3 and figure 2.5). The total abundance was highest during the PreMon ($p < 0.01$; Table 2.3 and figure 2.5). Chao-Shannon, species richness and total abundance were significantly higher in the shallowest depth strata and decreased as the depth increase ($p < 0.01$; Table 2.3 and figure 2.5). In Chao and Shannon, the diversity during the SWMon was approximately a third lower than the PreMon and the PostMon seasons and half of that observed during the NEMon season (Figure 2.4). The only significant interaction between the factors was between region and season in their impact on total abundance ($p < 0.01$; Table 2.3).

The GAMs demonstrated that salinity and dissolved oxygen explained a significant amount of variation in Chao1 and species richness ($p < 0.01$; Table 2.4) and that temperature significantly explained variation in Chao1 ($p = 0.03$; Table 2.4). However, despite the statistical significance of the tests, the deviance explained by the models was very low for all variables in Chao1, species richness and total abundance (Table 2.4). The

highest deviance explained was 2.7% by salinity with respect to species richness (Table 2.4).

2.5 Discussion

Accurate estimates of species richness and abundance are necessary to understand the status and trends of fish assemblages in the aquatic environment (Cappo et al. 2004). Species accumulation curves are typically used to estimate the rate of new species discovery under increased sampling effort (Thompson et al. 2003). The species accumulation curve did not reach a plateau however, even a doubling of the effort would generate only approximately 15-20% additional species. This pattern of species accumulation suggests that either the sampling effort was insufficient (Thompson and Withers 2003), there was high fish diversity with complex geographic distribution (Magurran and Henderson 2003), or species were highly patchy (Cappo et al. 2004). For instance, in the Chilean OMZ, fish were not evenly distributed, resulting in an underestimation of species richness (Quiroga et al 2009). However, even though a plateau was not reached, the species pool estimated from the accumulation curves can be compared with other curves in non OMZ areas (Soberón and Llorente 1993; Colwell et al. 2004).

The univariate biodiversity metrics of Chao1, the Shannon Index, the combined Chao Shannon species richness and total abundance showed similar patterns across region and depth, with the exception of the presence of an interaction between region and depth on total abundance. The general effects of region and depth may be attributed to either of two possible reasons. These consistent patterns in biodiversity across region and depth reflect species-specific environmental preferences (Piontkovskie et al. 2011) and depth preferences (Collie et al 2000). Seasonal differences may reflect adaptive strategies to variation in environmental conditions with respect to growth and survival (Brönmark et al. 2008). Finally, movement between seasons may also reflect differential reproduction

and feeding and changes in physical oceanographic parameters that alter patterns in the biodiversity indices (Brönmark et al. 2008).

During the Northeast Monsoon, nutrients upwell into surface waters at a time when cooling conditions in the surface water trigger phytoplankton production which is then widely spread over whole Arabian Sea (Madhupratap et al. 1996; Raghukumar and Anil 2003). The abundance of phytoplankton causes an increase in zooplankton biomass and hence, an increase in fish production across the shelf marine ecosystem (Ware and Thomson 2005). All fishes sampled in this study are piscivorous and their diversity and abundance is generally limited by the abundance of planktivorous fishes which in turn depend on zooplankton that rely on phytoplankton (Sala and Knowlton 2006). The summer upwelling in the Arabian Sea during the SWMon is most pronounced off the coasts of Oman and Somalia (Burkill et al. 1993) and plays a great role in the fish community structure in the Arabian Sea (Bianchi et al. 2000). This strong upwelling brings large concentrations of nutrient from the bottom of the ocean to the surface and leads to increased productivity but creates OMZs in different parts in Arabian Sea parallel to the Omani coastline (Levin et al. 2000). The presence of these monsoon-enhanced OMZs may explain the generally reduced biodiversity during the SWMon compared to other seasons because the fish try to avoid occurring in the low oxygen areas (Worm et al. 2006).

Species diversity metrics generally decreased with increasing depth in this study, consistent with patterns observed elsewhere (Fitzpatrick et al. 2012). The high diversity in the shallow depth strata may reflect the tendency for many smaller fish species tend to avoid predators when searching for food to support adequate growth and reach maturity stages (Linehan et al. 2001). In contrast, large fish species tend to occupy deeper water for the metabolic benefit of living in cooler water and the longer lifespan this supports (Blaber and Blaber 1980; Linehan et al. 2001). This may explain the lower species

number recorded in the deeper depth strata. Also, the coastal habitat provides juveniles and small fish with food and refuges from piscivorous fishes in the shallow areas (Paterson and Whitfield 2000). Predation risk is also higher in shallow water for larger fish species because there no shelters to hide from predators (Blaber and Blaber 1980) whereas deeper water can present a higher risk predation for small fish species because of high number of large predators (Breitburg 1992). Fish that have escaped predation or fishing mortality in shallow waters grow and move to deeper water, characterised by low dissolved oxygen, because they have the physiological ability to tolerate the low oxygen concentrations better than smaller fish species (Nilsson and Ostlund-Nilsson 2008). Heavy fishing throughout the year by foreign trawlers between 1980 and 2010 (Anon 2013) could also explain high fish diversity in the shallow depth strata relative to the deeper strata. Trawlers typically fished in areas more than 20 km from the shore and in water depths greater than 50 m (McIlwain et al. 2006). Trawling causes physical destruction of marine habitats that causes biodiversity loss (Watling 1999) and as such may be implicated in our patterns. However, the effect of depth on biodiversity was consistent across the regions despite trawling being concentrated in regions B, C and D. The variation in the distribution of fish species in different part of the global oceans remains a fundamental issue in aquatic ecology (Sosa-López et al. 2007). Although the deviance explained by GAMs for all indices was poor (<2.7%), salinity was the best predictor of fish biodiversity. Similar results were found in the Great Barrier Reef in Australia where, among the different oceanographic parameters variables, salinity was most significantly related to fish species richness for coral reef fishes (Mellin et al. 2010). The relationship between environmental variables and biodiversity were difficult to model because they remain poorly understood (Mora and Robertson 2005). There was a significant reduction in fish diversity during the Southwest Monsoon, associated with the strongest OMZ along the Omani coast of Arabian Sea. With the

increasing OMZs because of the climate change fish biodiversity in the Arabian Sea and other parts of the globe is in threat. Immediate action should be implemented to protect the global fish biodiversity by creating marine protected areas. Further studies should be undertaken to detect the most sensitive fish and habitat to OMZ. Although the sample size was adequate to generate results for a general assessment of the effect of the OMZ on biodiversity, conclusions need to be considered in light of the uneven distribution of sampling effort between the factors. Further analyses should also include the effect of fishing effort in the last decades on the fish biodiversity of the Arabian Sea. Environmental variables, fishing effort and the biodiversity indices should be modelled to acquire more understanding of the effect of OMZ on biodiversity.

2.6 References

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Table 2.1. Sampling effort in each level of the three factors included in this study during the fisheries-independent survey in the Arabian Sea coast of Oman (2007 – 2008).

Region	No.	Season	No.	Depth	No.
A	187	NEMon	265	1	293
B	243	PreMon	173	2	285
C	236	SWMon	211	3	130
D	98	PostMon	115	4	56

Table 2.2. Variation in estimated species richness between regions, seasons, and depth based on goodness of fit by Chi-square analysis strata. Chi-square contingency tests were used to determine if variation in estimated species richness were similar across region by season, region by depth, and season by depth. The numbers in bold were significant probability at 0.05 level.

Factor	χ^2	Df	<i>p</i> -value
<i>Goodness of Fit</i>			
Season	20.956	3	< 0.001
Region	2.94	3	0.401
Stratum	111.05	3	< 0.001
<i>Contingency</i>			
Region x Season	16.19	9	0.063
Region x Depth	18.62	9	0.029
Season x Depth	19.02	9	0.025

Table 2.3. PERMANOVA results of three biodiversity indices across region, season and depth strata. Chao and Shannon refers to a combined metric of the Chao1 and Shannon indices. NS: not significant.

	Season	Stratum	Region : Stratum
Chao and Shannon	<0.01	<0.01	NS
Species richness	<0.01	0.01	NS
Total abundance	<0.01	<0.01	<0.01

Table 2.4. The Biological-Environmental correlation analysis used to extract the best correlations between fish biodiversity attributes and environmental variables based on general additive models (GAM).

Index	Temperature		Salinity		Dissolved Oxygen	
	<i>P</i>	Deviance explained	<i>P</i>	Deviance explained	<i>P</i>	Deviance explained
Chao1	0.03	0.7%	<0.01	1.9%	<0.01	2.2%
Species richness	0.12	0.3%	<0.01	2.7%	<0.01	2.4%
Abundance	0.37	0.0%	0.05	0.9%	0.32	0.0%

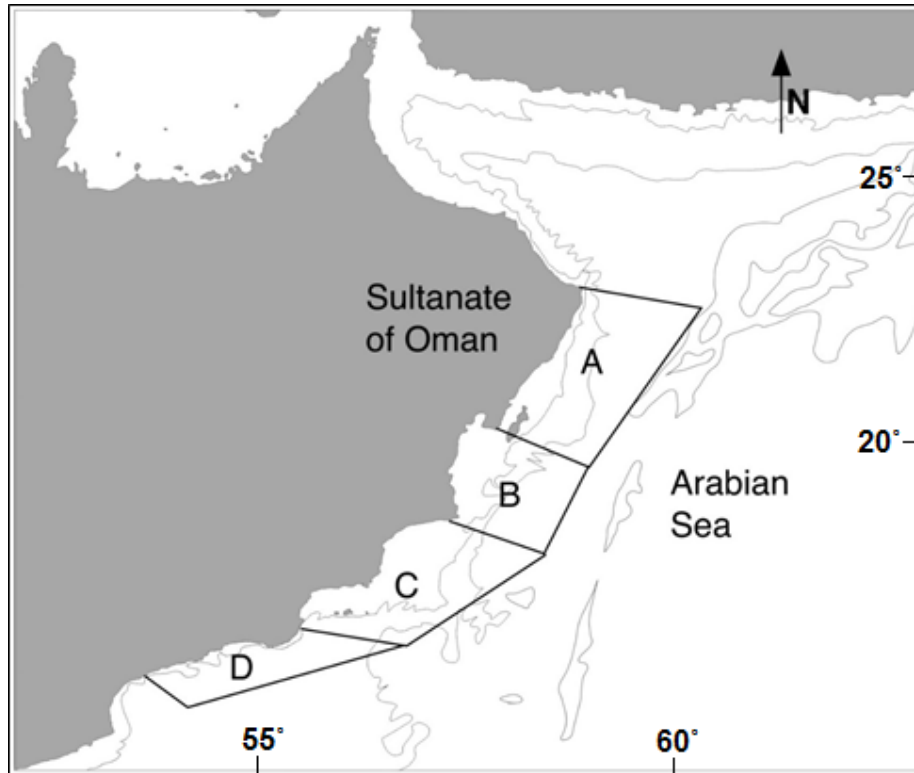


Figure 2.1. Classification of the regions in the study area. A: Ra's al Hadd to Masirah Island; B: Masirah Island to Ra's Al Madrasah, C: Ra's Al Madrasah to Ra's Hasik; D: Ra's Hasik to Yemen border.

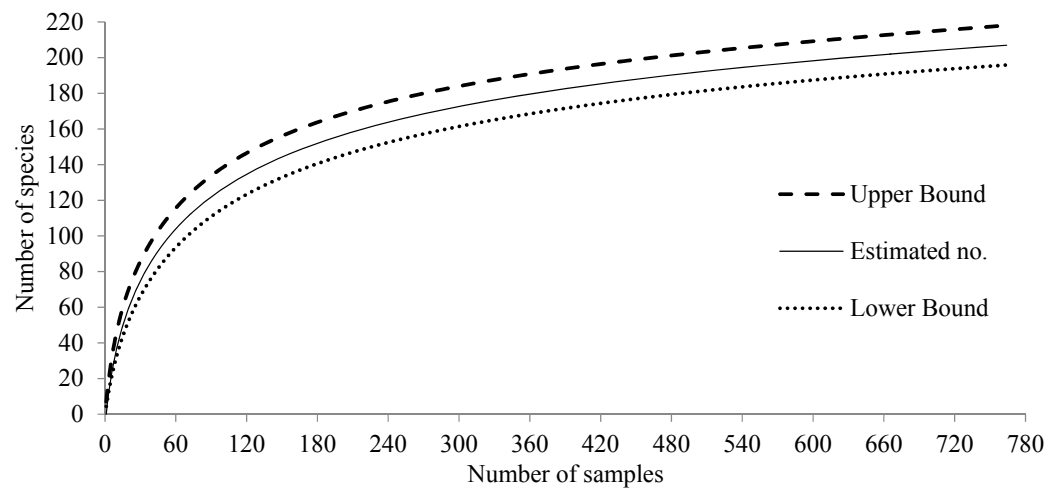


Figure 2.2. Estimated cumulative number of fish species as a function of sampling effort. The bounds are the 95% Confidence intervals.

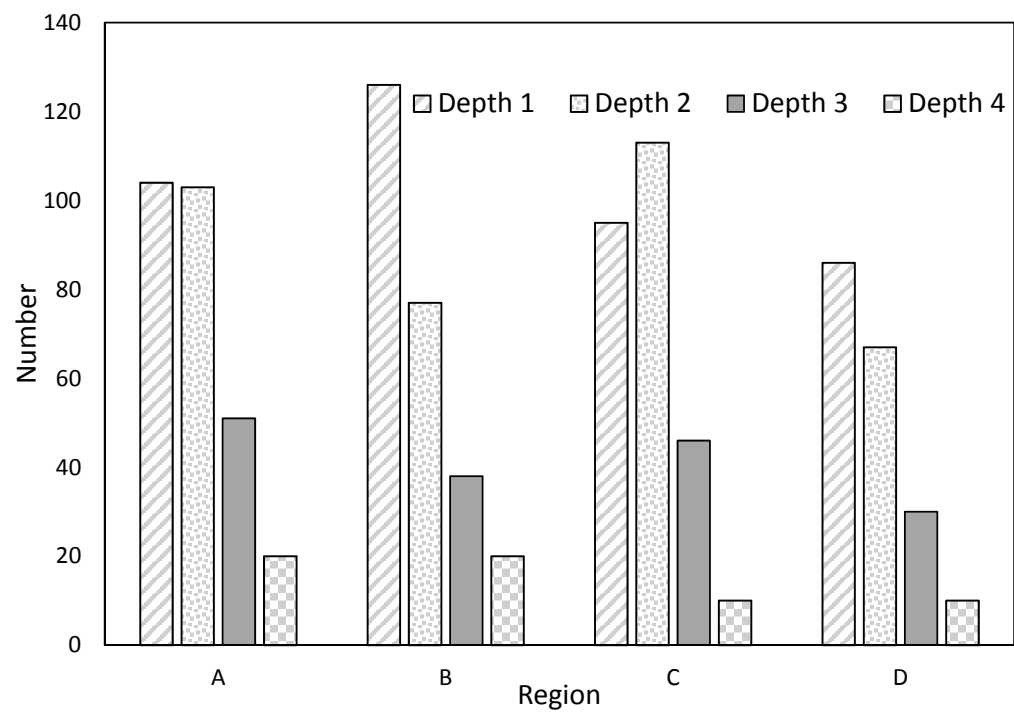


Figure 2.3. Number of species by depth strata of the four regions in the Omani coast of the Arabian Sea.

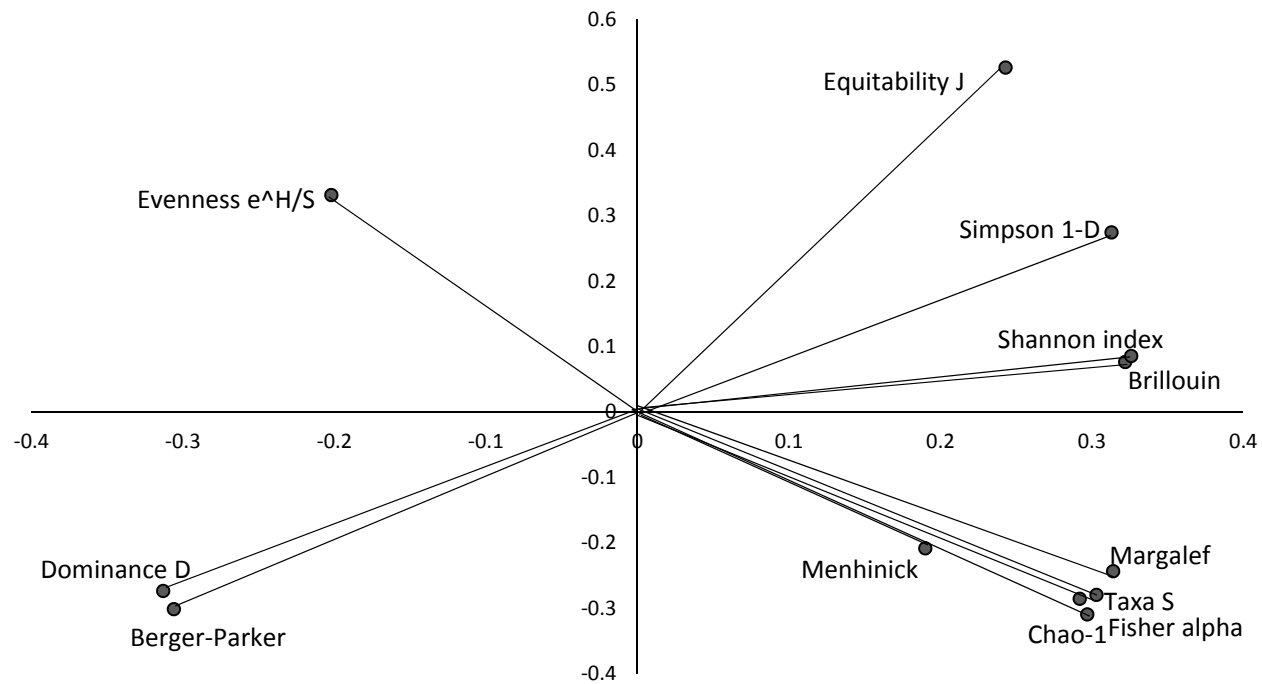


Figure 2.4. Biodiversity indices using PCA for fish species from the Omani coast of the Arabian Sea; Chao1 and Shannon were combined to create an index that reflects richness and evenness.

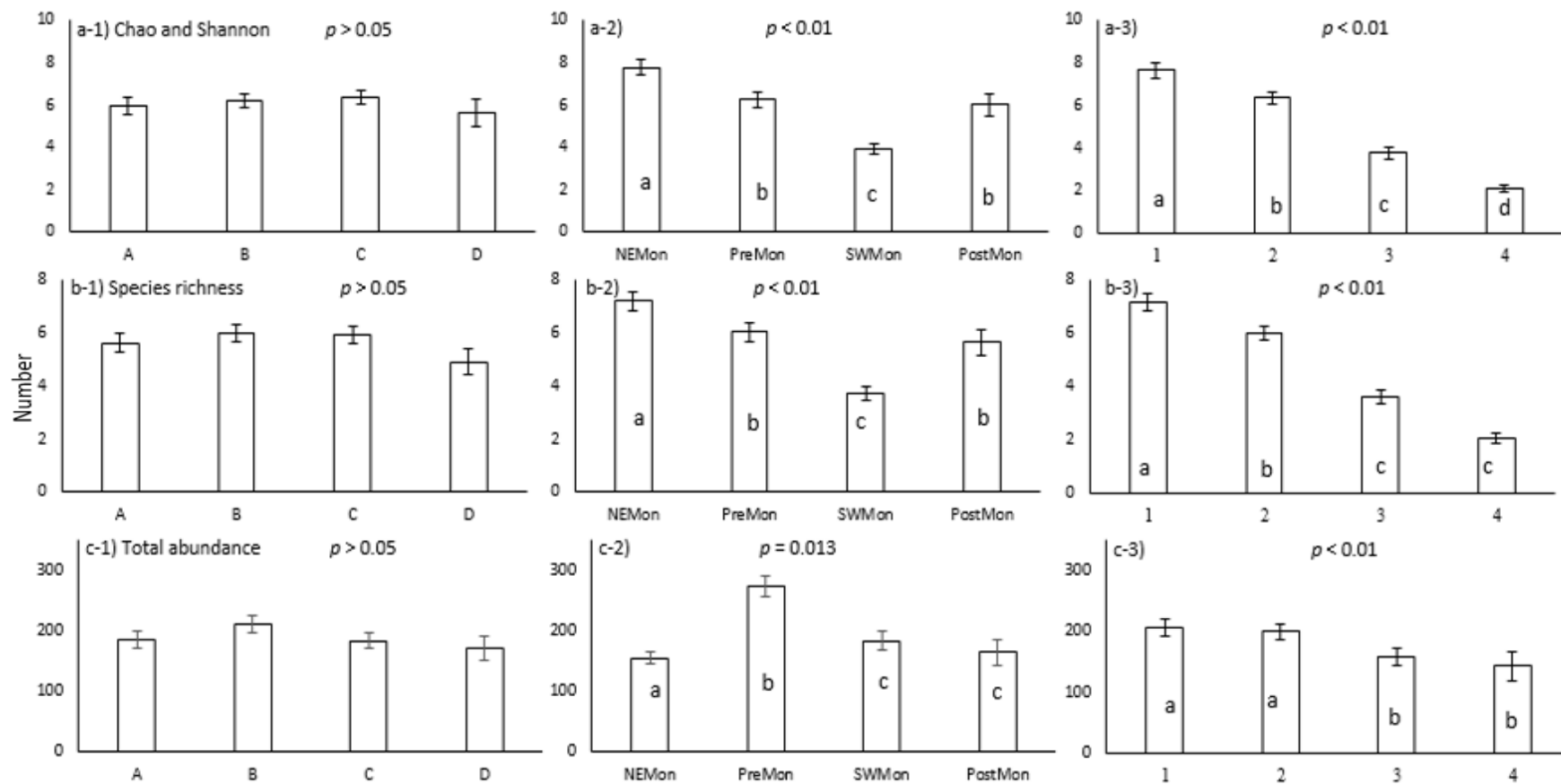


Figure 2.5. Mean value of observed Chao and Shannon combined index, species richness and total abundance by Regions, Seasons and Depth with significant differences ($p < 0.05$) indicated. Standard error (SE) are also indicated.

Chapter 3- The influence of oxygen minimum zone and oceanographic parameters on the length distribution of five fish species in the Arabian Sea

Target Journal: Fisheries Research

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3.1 Abstract:

Environmental conditions strongly influence fish growth and size. Temperature, salinity and oxygen can have negative effects on growth and size when species' tolerances are exceeded. Climate modelling predicts that persistent oxygen minimum zones (OMZs), where dissolved oxygen concentration is less than 0.5 ml⁻¹, will expand globally, in addition to increases in ocean temperature. The persistent oxygen minimum zone in a warming Arabian Sea is one of only three in the world, and as such, provides a window into the potential responses of fish fauna to decreasing oxygen levels in the global seas. Fork lengths for 19,633 fish of five economically important species (*Argyrops spinifer*, *Drepane longimana*, *Epinephelus diacanthus*, *Lethrinus nebulosus* and *Pomadasys commersonnii*) were measured in four regions, during four seasons and at four depth strata in the Arabian Sea in order to test the influence of these factors, as proxies for the OMZ, on mean length and length frequency distributions. The five species showed three general responses. The first group includes *E. diacanthus* and *P. commersonnii* which were largest in the south, largest during the Northeast Monsoon and did not vary in size with depth, possibly taking advantage of rich food sources for recruits but with southern populations associated with the OMZ comprised of larger individuals. The second group was comprised of *D. longimana* and *L. nebulosus* which were smaller in shallow depths and showed no influence of region or season and appear relatively insensitive to the OMZ.

These two species show typical distribution in relation to depth, with larger individuals found in deeper waters. Finally, *A. spinifer*, was smallest in the south and in deep waters but showed no effect of season. This may indicate a sensitivity to the OMZ where larger individuals are neither found in the south nor at depth. The results of kernel density estimates largely mirrored these results. The environmental variables were significant but explained little of the deviance in fork length, with the exception of temperature which explained approximately 40% and 26.9% of the variation in length of *E. diacanthus* and *A. spinifer* respectively. These groupings may reflect differential species sensitivities to the OMZ which is strongest in the southern regions during the SW Monsoon. This highlights the need for careful consideration of responses to expanding OMZs, particularly with how this translates into fisheries productivity.

Keywords: dissolved oxygen, temperature, salinity, kernel density estimate

3.2 Introduction

Length is an important attribute of fish for a range of reasons. Length distribution data are regularly used to assess the structure of fish populations with great accuracy (Gabelhouse 1984). Age and growth parameters are derived from length-frequency data (Fournier et al. 1990). Natural mortality is one of the most essential life history parameters and scales with fish length (Gislason et al. 2010). Length at first capture and length at first maturity are also important parameters underpinning fisheries management (Froese 2006). Patterns in fish length distribution affected by natural factors such as environmental parameters and anthropogenic factors such as fishing and pollution (Berkeley et al. 2004a). The permanent existing of the OMZ in the Arabian Sea however provides an opportunity to closely look at changing environmental conditions associated with the OMZ, both regionally, seasonally and at depth, affect fish length distribution besides the effect of fishing which may also influence these patterns.

The size structure of fish populations is often closely linked to latitude, depth (Benoît and Swain 2003) region, habitat (Friedlander and Parrish 1998), season (Francis 1990) and can be further influenced by activities such as fishing (Shin et al. 2005). Fish length tends to increase with depth (Fitzpatrick et al. 2012), both reflecting ontogenetic movements within species and the presence of larger species in deeper waters (Roberts 2002). This may in part reflect physiology, with larger fish having a larger gill surface area able to tolerate lower dissolved oxygen concentrations in deep water (Nilsson and Ostlund-Nilsson 2008). Smaller fish may also occupy shallower waters to avoid predators when searching for food and large fish occupying deep water for the metabolic benefit and longer lifespan (Linehan et al. 2001).

Season may influence length distributions through the reproduction process that drives larval production and the entrance of small recruits to the population (Moutopoulos and

Stergiou 2002). Larvae survival and hence the abundance of recruits will also depend heavily on food availability which differs seasonally and annually (Hinrichsen et al. 2003). Additionally, fishing influences length distributions by truncating them through selective removal of larger size fish and hence reducing the mean size through time (Jennings and Dulvy 2005; Pauly and Palomares 2005).

Determination of the effects of climate change on fish populations is complicated (Harley et al. 2006) because climate change influences many environmental variables that directly affect fish populations (Rijnsdorp et al. 2009). In particular, climate-driven changes in environmental variables such as temperature, salinity and dissolved oxygen can affect the distribution of fish populations (Lehodey et al. 2006). Fish species vary in the range of environmental conditions they tolerate (Nye et al. 2009) and fish size distribution will change in response to changes in environmental variables (Perry et al. 2005). For instance, sea water temperature increases driven by climate change are largely in the shallows (<50 m water depth) with stratification preventing mixing of water between warming shallows and deeper, cooler water masses (Walther et al. 2002). As such, the distribution of fish in warming shallow waters may decline as individuals either migrate to escape warm tropical water (Perry et al. 2005) or experience reduced reproductive output (Rijnsdorp et al. 2009).

Climate change is also expected to affect the level of dissolved oxygen in global oceans (Matear and Hirst 2003) but less attention to date has been paid to how this affects fish length. Climate change is expected to increase the extent of persistent oxygen minimum zones (OMZs), areas defined as where dissolved oxygen concentration is less than 0.5 ml l^{-1} on a global scale, but especially in tropical oceans (Matear and Hirst 2003; Stramma et al. 2008). In effect, OMZs may reduce the amount of suitable habitat by changing the dissolved oxygen concentration (Diaz and Rosenberg 2008). Dissolved oxygen concentration is directly related to food intake, the efficiency of food intake, and hence

the growth of the fish will be affected if the concentration of dissolved oxygen declines (Buentello et al. 2000). Climate-driven changes in dissolved oxygen concentration may also lead to alterations in the behaviour of the fish, for instance, increasing predation rates (Burleson et al. 2001).

The Arabian Sea provides a model system to study the effect of climate change, and in particular the effect of OMZs, on fish length. The Arabian Sea is characterised by a persistent shallow OMZ (Helly and Levin 2004). The region experiences two extreme seasonal changes in atmospheric forcing, driven by the Southwest Monsoon and the Northeast Monsoon with two inter-monsoon periods, the Pre-Southwest Monsoon and the Post-Southwest Monsoon (Morrison et al. 1998). During the boreal summer months, the northwest of the Arabian Sea is a region of active upwelling and enhanced biological activity driven by the Southwest Monsoon (Izumo et al. 2008). High biological production is also brought by the Northeast Monsoon during much of the boreal winter months in the northern region of the Arabian Sea (Madhupratap et al. 1996; Rostek et al. 1997). Both of these seasons can reduce shallow water oxygen concentrations to hypoxic levels as the pulses of organic material resulting from increased primary production decay (Ivanova et al. 2003). The timing of the two monsoons vary from year to year (Qasim 1982) producing dramatic changes to the biological and oceanographic conditions of the Arabian Sea (Qasim 1982; Morrison 1997; Morrison et al. 1998, 1999). The region is also characterised by artisanal and industrial fishing sectors that have the potential to affect the distributions of fish length. These fisheries include the traditional sector in fiberglass boats using hand line and synthetic fiber nets (Al-Oufi et al. 2004) and the industrial sector operating on factory trawlers between 1980 and 2010 (Anon 2013).

This study aims to investigate the fish length distribution of five economically important species in the Arabian Sea in relation to OMZ and some oceanographic parameters. I consider the effect of the persistent oxygen minimum zone on fish length by quantifying

differences in length distribution in relation to region, season and depth strata. Additionally, I explore the relationships between length and dissolved oxygen, salinity and temperature.

3.3 Methods

A research survey across the Northwest Arabian Sea off the coast of Oman was carried out by the New Zealand National Institute of Water and Atmospheric Research (NIWA) for the government of the Sultanate of Oman between September 2007 and September 2008 using a two-phase stratified random survey design (McKoy et al. 2009). The research vessel used the same rigged trawl gear and deployed in the same manner for all the demersal tows across all surveyed station to avoid any bias and selectivity in the data collection (McKoy et al. 2009). Tow duration was typically approximately 30 minutes at a speed of 2–3 knots. The survey was conducted from the Al Mustaqila 1, a 45.2 m long modern commercial fishing vessel designed to operate efficiently under a wide variety of conditions in both inshore and offshore environments. The bottom trawl was configured with a 70 m sweep length and 9 m bottom backstop. The mouth area of the trawl had a 308 m minimum circumference and used 800 mm mesh in the fore part of the net. The cod-end was 20 m and used a 16 mm liner. The headline height ranged from 9 to 12.7 m when averaged by survey. The net was rigged with standard Thyboron Type 7 trawl doors and 150 m bridles. The survey covered the continental shelf across the 20–250 m depth range across four regions: Ra's al Hadd to Masirah Island (Region A), Masirah Island to Ra's al Madrasah (Region B), Ra's al Madrasah to Ra's Hasik (Region C), and Ra's Hasik to the Yemen border (Region D) (Figure 3.1). Sampling occurred throughout the year, allowing data to be allocated to one of the four major seasons of the Arabian Sea (Piontkovski et al. 2011): the Northeast Monsoon (NEMon; January - March), the Pre-Southwest Monsoon season (PreMon; April - June), the Southwest Monsoon (SWMon; July -September), and the Post-Southwest Monsoon season (PostMon: October -

December). Samples were also assigned to one of four depth strata: DS1 (5 to 50 m); DS2 (51 to 100 m); DS3 (101 to 150 m); and DS4 (151 to 250 m).

A total of 764 demersal trawls was completed across the region with key environmental measurements taken for each trawl. These included bottom temperature (°C), salinity (ppt), dissolved oxygen (mll⁻¹), and depth (m). Fork length (FL), to the nearest millimetre, was measured for all individuals, with the estimates for five economically important species extracted from the database for this analysis. The focal species are: *Argyrops spinifer*, *Drepane longimana*, *Epinephelus diacanthus*, *Lethrinus nebulosus* and *Pomadasys commersonii*.

The overall statistical design consisted of testing the influence of Region, Season and Depth Strata using a three-way permutational parametric ANOVA with interactions for the mean length of the five selected species in each trawl sample. Where insufficient sample sizes existed within a Region, Season or Depth strata ($n < 200$). Non-significant interactions were sequentially removed, beginning with the 3-way interaction, and followed by the 2-way interactions with the highest p -values, following Underwood (1981). Post-hoc pairwise tests were then conducted for each significant main effect. Differences were visualised with bar charts. The frequency distributions were also contrasted using Kernel density estimates (KDE) in R language for statistical computing by the function 'sm.density.compare' (100 permutations) in the package 'sm' which also produces a plot to accompany each test (Bowman and Azzalini 2010). To study the effect of oceanographic variables (i.e. temperature, salinity, dissolved oxygen and sea bottom depth) as explanatory variables on the mean of the five species length distribution as response variables, general additive models (GAMs) were evaluated using the package 'mgcv' of R software (Wood 2009) at the significance level of $\alpha = 0.05$ with parameter estimation by residual maximum likelihood (REML). The maximum bias dimension was

set to $k = 4$ as suggested by (Hastie and Tibshirani 1990) to minimise over fitting and preserve biological realism.

3.4 Results

Length measurements of 19,633 individuals from the five focal species collected from each of four different regions during four seasons and in four different depth strata in the Arabian Sea were analysed. The most abundant species was *P. commersonnii* (6,110) while the least abundant species was *E. diacanthus* (1,181) (Table 3.1). The five focal species ranged in mean size from the relatively small *A. spinifer* (33.5 cm \pm 0.16 cm SE) to the relatively large *P. commersonnii* (60.8 cm \pm 0.07 cm SE). The sampled individuals generally included representatives of the largest reported size classes in Fishbase (Froese and Pauly 2015), however, smaller individuals were less consistently sampled (Table 3.1).

Permutational 3 way parametric analysis of variance suggests that mean length of the five species reflects three patterns with respect to their response to the three different factors. The first group, comprised of *E. diacanthus* and *P. commersonnii*, tends to respond to region and season (Figure 3.2). *E. diacanthus* and *P. commersonnii* are largest in the south during the NEMon (Figure 3.2). The second group including *A. spinifer* tends to be larger in north regions and in the shallows depth (Figure 3.2). In contrast, *D. longimana* and *L. nebulosus* show little effect of region or season but are both larger with increased depth (Figure 3.2).

The KDE analyses generally mirrored those of the ANOVA on mean lengths. While *E. diacanthus* and *P. commersonnii* tend to be larger in south, *A. spinifer* is smaller in south (Figure 3.3). KDE analysis reflect the same results of analysis of variance for the season factor for *E. diacanthus* and *P. commersonnii* (Figure 3.3). Regarding the depth factor,

the KDE analyses exclude *D. longimana* and reflect the same results for *L. nebulosus* as in the analysis of variance.

The Generalised Additive Models (GAM) investigating the effects of oceanographic variables (temperature, salinity and dissolved oxygen) on the distribution of fish fork length were significant (Table 3.2 and Figure 3.4). The highest levels of deviance explained were 40.2% and 26.9% for *E. diacanthus* and *A. spinifer* in relation to temperature (Table 3.2). However, the deviance explained by the remaining models was generally low, especially for *P. commersonnii* and *L. nebulosus* (4.3%) for temperature (Table 3.2). Similarly, dissolved oxygen contributed to low levels of deviance explained for *P. commersonnii* and *L. nebulosus* (6.5%; Table 3.2) and salinity for *L. nebulosus* (6.5%; Table 3.2).

3.5 Discussion

The strength of the data in this study lie in the wide range of size classes that are included, both within and among species (Gabelhouse 1984). The length distribution of five species in this study were tested by KDE which provided comparable length-based evidence on year class strength for individual species prior to recruitment to the fishery (Sheather and Jones 1991; Miranda 2007; Langlois et al. 2012). The KDE analysis compared the whole length distribution in different factors not just as a central point as in the ANOVA. The results of this study (ANOVA and KDE) classified the five species mean length into three groups according to their significant response to the different factors, and were largely consistent.

ANOVA test results suggested variation in fish length in response to the factors may reflect biological and ecological aspects (Logerwell et al. 2005) as was also observed for condition (Chapter 4). *A. spinifer* and *P. commersonnii* occur over a wide range of sea bottoms whereas *E. diacanthus* is found almost exclusively, on muddy sand bottoms

(Froese and Pauly 2015). Habitat differences in the studied regions in the Arabian Sea (McKoy et al. 2009) may provide preferable habitat for *E. diacanthus* and *P. commersonnii* such that larger lengths are achieved in the south and larger *A. spinifer* in the north (Rijnsdorp et al. 2009). These distributions also reflect different recruitment patterns in relation to species preferences (Cury and Roy 1989). *A. spinifer* seems to be sensitive to the OMZ as it is less distributed in the southern regions of the Arabian Sea (Qasim 1982; Morrison et al. 1998). Fishing cannot however be excluded as having an effect on length, particularly as the truncation of size distributions is a well-recognised outcome of exploitation (Shin et al. 2005). In particular, *A. spinifer* is typically smaller in region C where it was subjected to heavy fishing pressure between 1980 and 2010 (Anon 2013). However high fishing pressure also occurs in Regions B and D yet no comparable reductions in size are observed here. Foreign owned trawlers fish around the year retaining valuable fish in the Asian markets such as *A. spinifer* and discarding any other fishes which not valuable (Mathews et al. 2001). *D. longimana* and *L. nebulosus* are found in wide variety of habitats (Froese and Pauly 2015), and this may reflect why their length distribution were not affected by Region (Vivier et al. 2010).

Timing of recruitment differs among fish species resulting in variation in length distributions (Berkeley et al. 2004a). KDE for mean length distribution found that *E. diacanthus* and *P. commersonnii* differed significantly between seasons. As most of the demersal fish in the Arabian Sea spawn during the SW Monsoon (McIlwain et al. 2006), this may explain the occurrence of the small and medium sized *E. diacanthus* and *P. commersonnii* at this time. During the SW Monsoon, the Omani coast receives an enormous amount of primary productivity and organic matters brought by upwelling (Peeters et al. 2002). Fish tend to spawn in this time of year to ensure that their offspring find enough food to survive (Berkeley et al. 2004b). Moreover, fish tend to spawn in time where the oceanographic variables are suitable for their larvae and juveniles to grow in a

better condition (Shoji et al. 2011). The reduction in seawater temperature during the upwelling event in SW Monsoon season induce the fish with a thermal shock that promotes spawning (Al-Rasady et al. 2011).

Depth influenced the length distributions of *A. spinifer*, *D. longimana* and *L. nebulosus* , reflecting the great role that depth plays in the distribution of fish (Benoît and Swain 2003). *A. spinifer* is a relatively deep sea fish found in depths greater than 250 m (Froese and Pauly 2015). This species aggregates in deep water to spawn and their larval settlement and recruitment also occur in deep water (Devine et al. 2006) which may explain the small size length and length distribution of smaller size of *A. spinifer* in deep strata up to 150 m. Larger *A. spinifer* can move to shallow water to search for food or to seek a refuge to hide from predators (Gratwicke and Speight 2005). As *D. longimana* and *L. nebulosus* grow larger as they move to deeper sea bottoms, it remains unclear how this pattern relates to changes in their diet (Corten 2001) and predator avoidance (Miner and Stein 2011). *Lethrinus nebulosus* and *D. longimana* are typically found in depths less than 80 m (Froese and Pauly 2015) but this study recorded *L. nebulosus* and *D. longimana* in depths up to 150 m. It is unclear whether this is an effect of the OMZ, driving shifts to deeper water (Pörtner and Knust 2007).

Change in oceanographic variables leads to change in the distribution of body length of the fish in different parts of the global oceans (Law 2000). General additive models were used to predict the effect of oceanographic variables on the length distribution of the fish in the Arabian Sea. General additive models are effective in predicting relationships between species and environment (Meynard and Quinn 2007). The GAM models presented here indicated that the key environmental variable that explains the deviance in the length distribution was temperature. This is consistent with other studies that identify temperature as the ecological master variable for fish (Lee et al. 2003) because of its effect on oxygen (Rijnsdorp et al. 2009) and salinity (Schouten et al. 2002). The

maximum deviance explained by temperature was 40.2% for *E. diacanthus*. This level of predictive power is consistent with previous studies that also used GAM to compare the effect of oceanographic variables with blue shark catch (Walsh and Kleiber 2001) and juvenile abundances, finding similar levels of deviance explained (Pasquaud et al., 2012). These studies also identified the need for other parameters to be included to increase the deviance explained.

In conclusion, length distributions of the five fish species studied in the Arabian Sea were to varying degrees influenced by region, season and stratum. The occurrence of *L. nebulosus* and *D. longimana* in depths greater than 150 may make them more vulnerable to OMZ expansion in the Arabian Sea. The results are important for regional fisheries management in the Sultanate of Oman given the need to consider the fisheries exploitation in the face of climate change.

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Table 3.1. Statistics of length measurements for the five focal species from the Omani coast of the Arabian Sea (2007–2008 SE: standard error of the mean.

<i>Species</i>	No.	Mean (FL cm)	SE	Min (FL cm)	Max (FL cm)	Max estimated from Fishbase (FL cm)
<i>Argyrops spinifer</i>	5511	33.5	0.1572	5.6	62.1	70
<i>Drepane longimana</i>	2881	34.9	0.0491	22.1	43.8	50
<i>Epinephelus diacanthus</i>	1181	36.3	0.2573	15.3	55.4	55
<i>Lethrinus nebulosus</i>	3950	43.1	0.1598	18.4	74.2	87
<i>Pomadasys commersonnii</i>	6110	60.8	0.0713	33.2	78.3	80

Table 3.2. GAM results for the five focal species mean length from Omani coast of the Arabian Sea, (2007–2008).

<i>Species</i>	Variable	<i>p</i> -value	Deviance explained
<i>Argyrops spinifer</i>	Temperature	2.71×10^{-12}	26.9%
<i>Epinephelus diacanthus</i>	Temperature	2.02×10^{-13}	40.2%
<i>Pomadasys commersonnii</i>	Temperature	2.13×10^{-2}	4.3%
	Dissolved oxygen	7.71×10^{-3}	6.5%
<i>Lethrinus nebulosus</i>	Temperature	2.13×10^{-2}	4.3%
	Dissolved oxygen	7.71×10^{-3}	6.5%
	Salinity	8.19×10^{-3}	6.5%

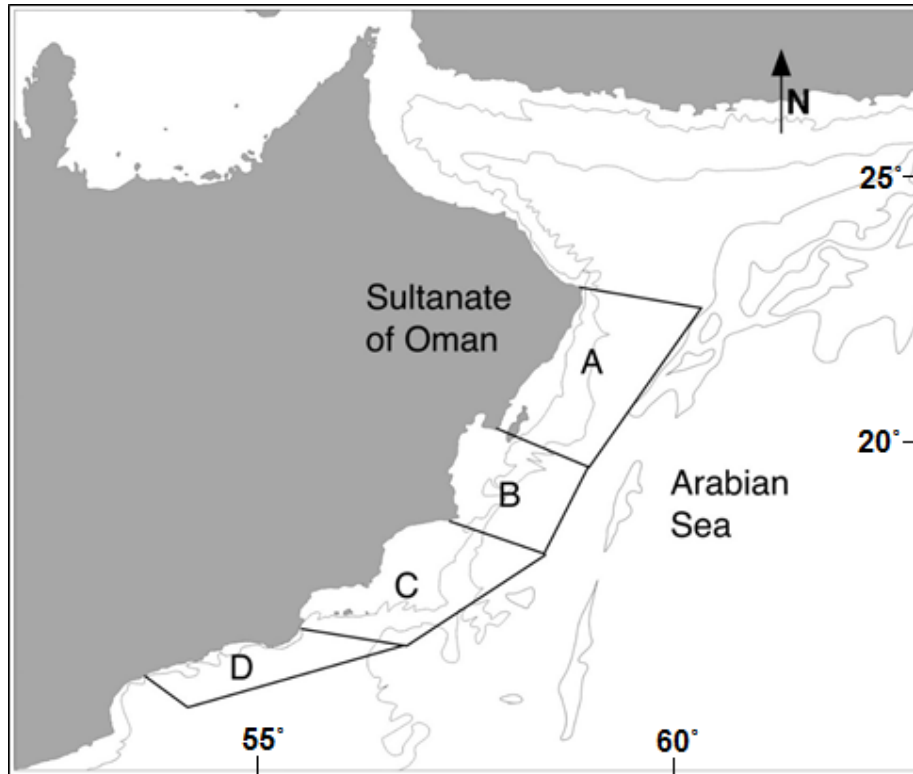


Figure 3.1. Classification of Regions across the study area. A: Ra's al Hadd to Masirah Island; B: Masirah Island to Ra's Al Madrasah, C: Ra's Al Madrasah to Ra's Hasik; D: Ra's Hasik to Yemen border.

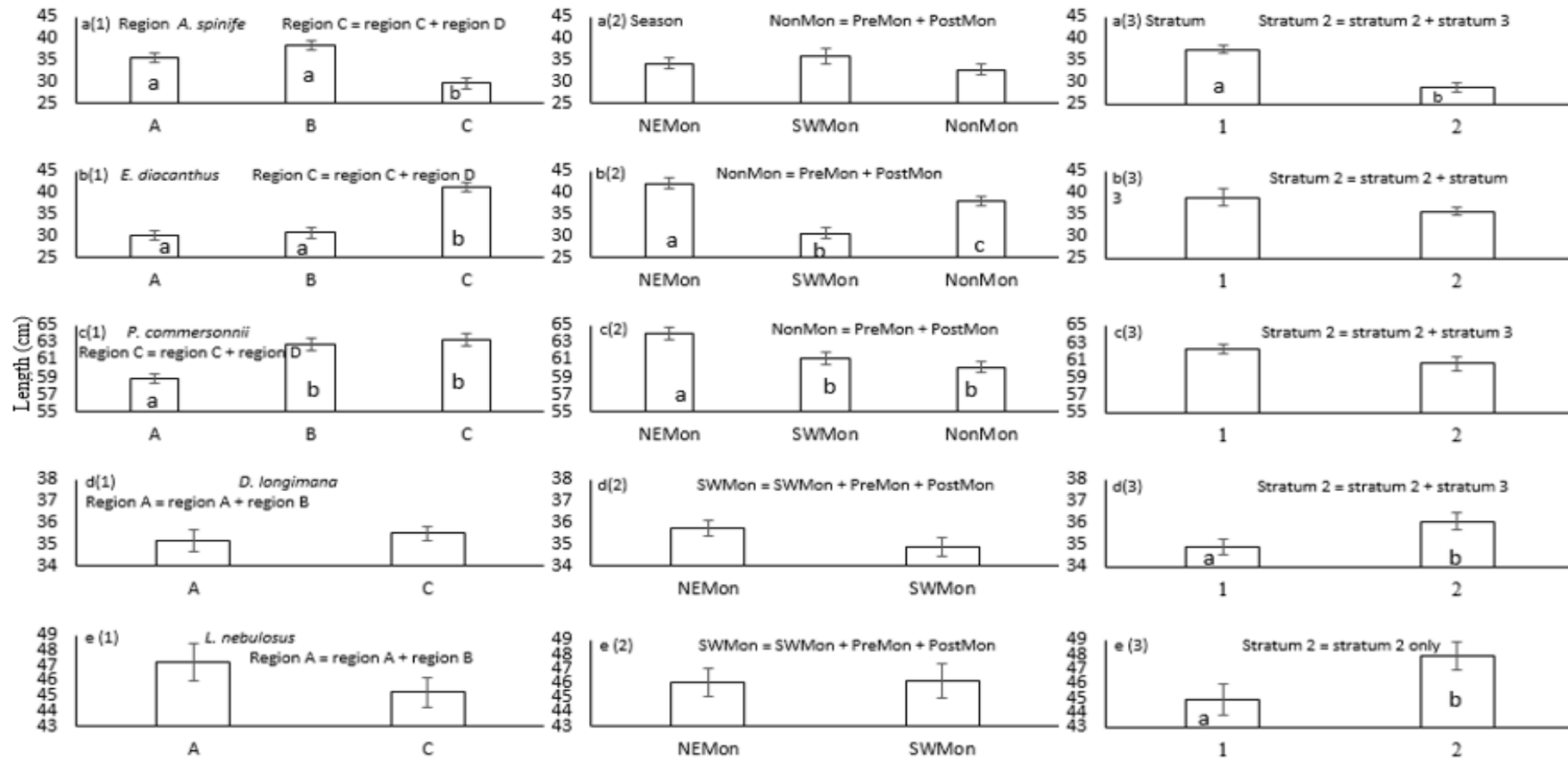


Figure 3.2. Mean length of fishes in each trawl sample from a different region, stratum and season in the Omani coast of the Arabian Sea (2007–2008). For all figures horizontal axis presents the factors, the vertical axis presents the mean length (cm) and bars present the standard error of the mean. Letters inside the bars (a, b and c) indicate the Post-hoc test results of significant differences otherwise they were equal.

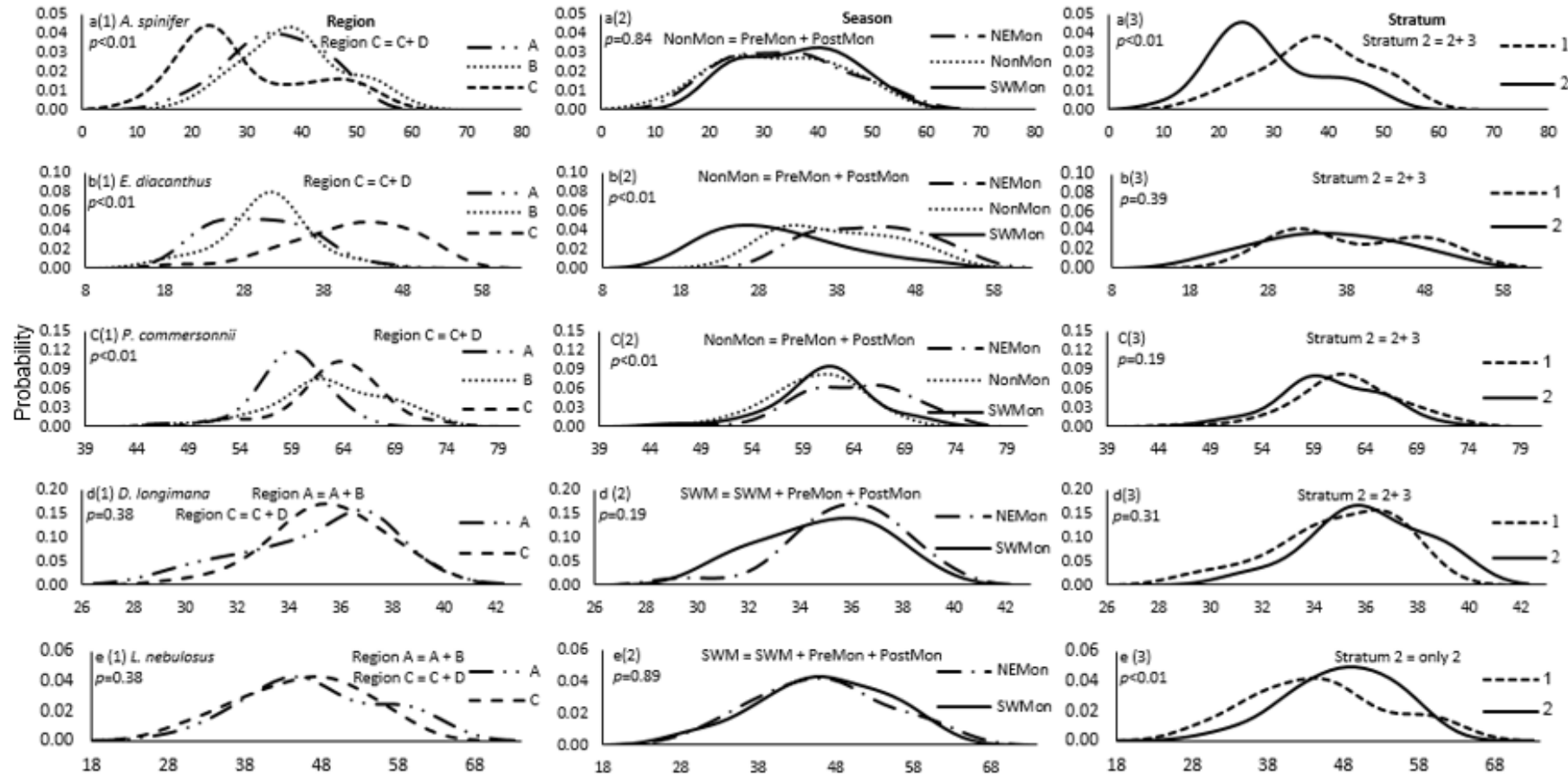


Figure 3.3. Comparison of kernel density estimate (KDE) probability density functions for mean length of each trawl sample (of each trawl sample) frequency distribution of fishes from a different region, stratum and season in the Omani coast of the Arabian Sea (2007–2008). For all figures, horizontal axis presents the mean length and the vertical axis presents the probability density.

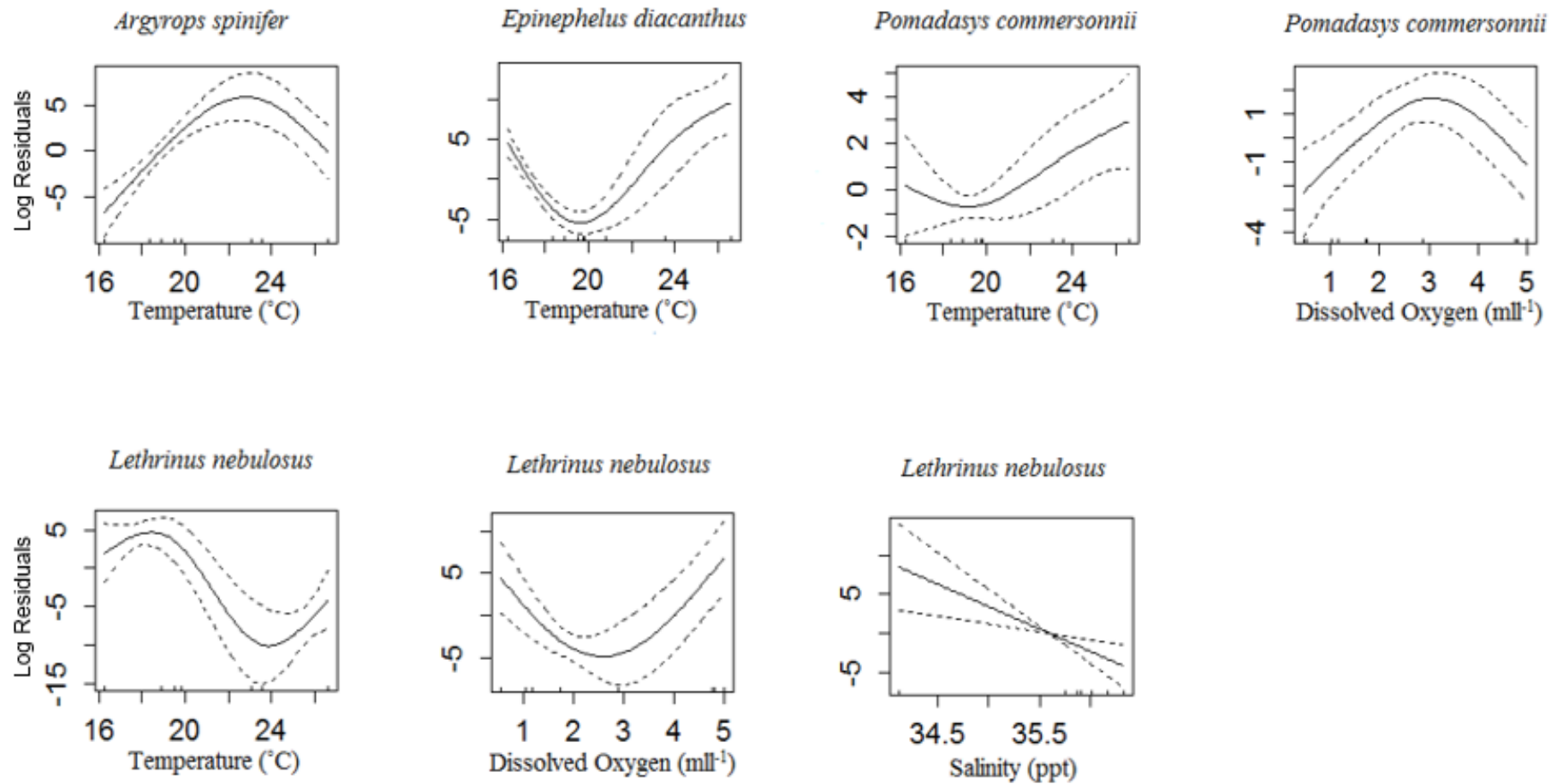


Figure 3.4. Response curves of oceanographic variables in the Generalised Additive Models (GAM) for four species from the Omani coast of the Arabian Sea(2007–2008). The Y-axis represents the partial residuals (logarithm value) and dashed lines represent 95% confidence intervals.

Chapter 4- Low oxygen zones predict future condition of fish under climate change

Target Journal: *Environmental Biology of Fish.*

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4.1 Abstract

Oxygen concentrations are predicted to decline under climate change scenarios. To assess the possible effect of low dissolved oxygen levels on fish condition, we evaluated the condition of fish in the Northwest Arabian Sea, a region of persistent oxygen minimum zones (OMZs). Condition of fish was inferred from the coefficients of length-weight relationships (LWR), comparing LWR coefficients for 53 species sampled across the northwest Arabian Sea OMZ to the coefficients reported for these species from non-OMZ regions. Regional effects of oxygen depletion were also examined by comparing coefficients from LWR of seven fish species in four different regions of the Northwest Arabian Sea across a latitudinal gradient. The estimated values of a , the body form coefficient, were significantly higher in the northwest Arabian Sea than in non-OMZ regions. However, there was no significant difference in b , the allometric growth rate, observed in the northwest Arabian Sea with those observed elsewhere. Regions showed significant difference in allometric growth rates for five of seven investigated fish species, with *Drepane longimana*, *Pagellus affinis*, and *Pomadasys commersonnii* showing decreasing trends from north to south, while *Argyrops spinifer* and *Carangoides equula* showed the opposite trend and *Cheimerius nufar* and *Plectorhinchus schotaf* showed no discernable trend. Fishes from the northwest Arabian Sea had larger body forms (as indicated by the LWR coefficient a) compared to conspecifics in non-OMZ regions, but showed increased allometric growth rates (as indicated by the LWR coefficient b) with declining oxygen on a regional basis. Climate models predict expansion of OMZs

globally and fishes in the Arabian Sea showed unexpected responses in relation to the OMZ. Consequently, the condition of the fishes need to be studied in Arabian Sea using empty weight during different seasons, regions and depth strata and configure its relation to the environmental factors and compare the results with same fishes from non-OMZ.

Keywords: Length-weight relationship, northwest Arabian Sea, body form, allometric growth rate

4.2 Introduction

Climate change is predicted to have significant consequences for marine ecosystems and the fisheries they support (Brander 2010; Cheung et al. 2009), with oceans functioning as a natural carbon sink, absorbing approximately half of all anthropogenic carbon dioxide (CO₂) (Le Quéré et al. 2007). Analysis of available time series has revealed changes in distribution, abundance and production of fish species that correlate with climate-related environmental variables (Rijnsdorp et al. 2009). There is also evidence suggesting that species change the timing of their life cycles in response to ocean warming, and have shifted their geographic distributions toward higher latitudes (Chen et al. 2011). Moreover, climate change may also lead to a reduction in mean body size as predicted by the temperature-size rule, under which individuals experiencing higher temperatures will have smaller body sizes (Walters and Hassall 2006; Feary et al. 2010). The synergistic effects of climate change on fish are also driving concern with respect to fisheries production (Halpern et al. 2008).

One predicted impact of climate change is increased areal extent of persistent oxygen minimum zones (OMZs) (Diaz and Rosenberg 2008). Of particular concern are the substantial reductions in formation rate and/or density of certain key water masses that lead to changes in the dissolved oxygen levels via reduction in the ventilation rate and biogeochemical cycling and changes in overturning timescales (Matear 2003). Climate

change scenarios also predict outgassing of oxygen from the ocean into the atmosphere and large declines in the dissolved oxygen concentrations in the ocean by the end of this century (Keeling et al. 2010).

The Arabian Sea covers an area of approximately 3,862,000 km² with depths ranging to 2990 m. Mean environmental conditions are 24 °C temperature and 4 m/l O₂, but these conditions vary strongly by season, and are driven by the monsoon. For instance, during periods when the OMZ occurs, oxygen levels typically decline to < 0.2 m/L (Kumar et al. 2009). The Arabian Sea fish fauna includes representative species from all marine families found in the Indian Ocean, and 93% of the marine fish families found across the Indo-Pacific (Fouda et al. 1998; Siddeek et al. 1999; Henderson et al. 2007). The region supports both artisanal and industrial fisheries that use a variety of fishing gear including gillnets, traps, lines and hooks, and bottom trawls (Al-Oufi et al. 2000; Al-Masroori et al. 2004; McIlwain et al. 2006).

The Arabian Sea has one of the only three permanently existing Oxygen Minimum Zones globally, with the other two located in the Eastern Pacific Ocean and off West Africa, and as such provides a natural experiment where the effects of low oxygen levels on fish can be examined. The Arabian Sea OMZ is driven by large scale forcing factors such as monsoons that strongly affect oxygen levels (Von Rad et al. 1999). Additionally, aeolian forcing, fluvial inputs from the surrounding land masses, and upwelling of nutrient-rich water to the surface by the Southwest Monsoon make the Arabian Sea one of the most productive oceanic areas in the world (Brink et al. 1998), with reported mean primary productivity in Oman's Economic Exclusive Zone of 1,327 mgCm⁻²day⁻¹ (Khalfallah et al. 2015). The region is also characterized by slow water circulation and a high salinity current exists at 200–350 m water depth, forming the upper limit of the OMZ (Reichert et al. 1997; Schulz 1998; Von Rad et al. 1999). A strong thermocline further prevents

downward mixing of oxygenated surface water (Altabet et al. 1995; Brink et al. 1998; Von Rad et al. 1999). Consequently, a persistent OMZ is located along the Omani coast in the Arabian Sea (Morrison et al. 1999).

Dissolved oxygen concentration is important to fish as it underpins the physiological basis for fish growth (Breitburg 2002). Dissolved oxygen concentration can influence feeding, metabolic rate and energy expenditure of fish (Buentello et al. 2000; Borsuk et al. 2001). When dissolved oxygen concentration decreases, respiration and feeding activities also decline causing reduced growth rates (Wu et al. 2003) with implications for reproductive output (Wu 2002). Additionally, behavioral changes such as changes in diel vertical migration can occur in response to reduced oxygen levels (Diaz and Rosenberg 2008; Gibson and Atkinson 2003). Finally, low oxygen levels can increase the risk of disease (Pichavant et al. 2001) and lead to acute responses such as mass mortalities (Peterson et al. 2000; Naqvi et al. 2010). Indeed, expanding hypoxia and anoxia have been blamed for the replacement of economically important demersal fish species with less valued planktonic omnivores in the Black Sea where oxygen levels have fallen from 2 to 0.5 ml l^{-1} , and only six of 26 commercial fisheries remain viable (Mee 1992; Diaz 2001).

Changes in growth and behavior in response to reduced oxygen levels may manifest in changes to fish condition (Wu 2002). Fish condition can be quantified by length-weight relationships (LWR) in terms of whether individuals are at a predicted weight at a given length (Murphy et al. 1991; Koops et al. 2004). Length-weight relationships are characterized by a non-linear model that estimates the coefficients a and b , where the intercept a reflects body form, and the slope b is the allometric growth rate. These coefficients are species-specific (Piet and Jennings 2005) and can be used to compare populations across habitats and regions (Gonçalves et al. 1997; Petrakis and Stergiou 1995). The use of LWRs as an indicator of condition is based on the assumption that greater weight at a length indicates better condition (Froese 2006). Moreover, as body

weight is positively correlated with reproductive output (Wootton 1985) and the quality of offspring (Venturelli et al. 2009), there are multiple benefits to greater weight at length. While previous studies have assessed a wide range of climate-driven impacts on fish and fisheries, the influence of a persistent low oxygen environment in the Arabian Sea on fish condition has yet to be explored. I here analyse a spatially extensive and fisheries-independent data on fish lengths and weights from the Arabian Sea comparing species-specific LWR in the Arabian Sea to those generated for these species in non-OMZ regions. As the Arabian Sea also shows gradients in oxygen, generally decreasing from north to south (Madhupratap et al. 2001), I also tested intraspecific patterns in length-weight relationships along this latitudinal gradient

4.3 Methods

A research survey across the Northwest Arabian Sea off the coast of Oman was carried out by the New Zealand National Institute of Water and Atmospheric Research (NIWA) for the government of Oman between September 2007 and September 2008 using a stratified random survey design (McKoy et al. 2009). The survey was conducted from the Al Mustaqila 1, a 45.2 m long modern commercial fishing vessel designed to operate efficiently under a wide variety of conditions in both inshore and offshore environments. The bottom trawl was configured with a 70 m sweep length and 9 m bottom backstop. The mouth area of the trawl had a 308 m minimum circumference and used 800 mm mesh in the fore part of the net. The cod-end was 20 m and used a 16 mm liner. The headline height ranged from 9 to 12.7 m when averaged by survey. The net was rigged with standard Thyboron Type 7 trawl doors and 150 m bridles. The survey covered the continental shelf in the 20–250 m depth range across four regions: Ra's al Hadd to Masirah Island (Region A), Masirah Island to Ra's al Madrasah (Region B), Ra's al Madrasah to Ra's Hasik (Region C), and Ra's Hasik to the Yemen border (Region D) (Figure 4.1). Sampling occurred throughout the year, allowing data to be allocated to one

of the four major seasons of the Arabian Sea (Piontkovski et al. 2011): the Northeast Monsoon (NEMon; January - March), the Pre-Southwest Monsoon season (PreMon; April - June), the Southwest Monsoon (SWMon; July -September), and the Post-Southwest Monsoon season (PostMon: October - December). The region was also subdivided into four depth strata: DS1 (20 to 50 m); DS2 (51 to 100 m); DS3 (101 to 150 m); and DS4 (151 to 250 m).

A total of 764 demersal trawls were completed across the region with measurements of key environmental parameters taken for each trawl. These included bottom temperature ($^{\circ}\text{C}$), dissolved oxygen (mll^{-1}), salinity (ppt) and depth (m). At sea, specimens were classified to genus and species using the FAO species catalog (Cohen et al. 1999), the fork length was measured to the nearest millimeter, and the weight was recorded to the nearest gram for a subset of individual fish across a range of sizes (Appendix A). These data were stored in the database of the Fish Resources Assessment Survey of the Northwest Arabian Sea Coast of Oman (McKoy et al. 2009).

To test whether LWR for populations in this OMZ differed from those derived for non-OMZ regions, we first extracted the length and weight data for individual fishes from the survey database. Length and weight were \log_{10} transformed and regression coefficients (R^2) were estimated for $\log_{10}(\text{weight})$ as a function of $\log_{10}(\text{length})$ for each species with a minimum of 30 individuals, as suggested by Froese (2006). Ordinary least squares regression was used with residuals assessed to evaluate the appropriateness of model fit (Zar 1999). We also extracted the length-weight coefficients for each of these species from Fishbase (Froese and Pauly 2015) for non-OMZ regions. Where multiple equations existed in Fishbase, we chose the equation based on sample size, sex and size range, and strength of the coefficient of determination (R^2). Because the statistical distribution of the regression coefficients is unknown, the intercept ($\log_{10}(a)$) and slope (b) of the length-weight regressions were compared using a paired non-parametric rank test (Wilcoxon

matched pair signed test (Siegel, 1956) in which each species included a paired set of estimates for the OMZ and non-OMZ relationships. Length-weight relationships with R^2 values less than 0.8 were excluded from the comparison because of the relatively large uncertainty.

To assess, overall changes in conditions as a function of latitude (Regions A-D), a non-parametric ANOVA (Friedman's two way analysis of variance by rank; Siegel 1956) was used. We selected all species in which a common range of sizes was represented in the four regions given the allometric influence of size on growth, and for which there was at least 20 individuals. For these seven species, the intraspecific changes in condition as a function of region were compared using analysis of covariance (ANCOVA) (Zar 1999).

4.4 Results

Environmental conditions of 38,928 measurements of temperature, salinity, dissolved oxygen and depth were obtained across the study region. The mean bottom sea temperature during the study period was $20.21\text{ }^{\circ}\text{C} \pm 3.87\text{ SD}$ (Table 4.1), with the mean temperature generally increasing from north to south. However, none of the other environmental variables showed directional trends with latitude. Mean bottom salinity was $35.7\text{ ppt} \pm 0.66\text{ SD}$ and mean bottom dissolved oxygen was $0.41\text{ ml l}^{-1} \pm 0.25\text{ SD}$ (Table 4.1). The minimum surveyed depth was 13 m in region A and the maximum depth was 814 m in region C (Table 4.1), with a mean value of $63.6 \pm 95.7\text{ SD}$ across all samples. Depths sampled were similar in regions B and C, and substantially deeper in region D (Table 4.1).

A total of 40,032 fish representing 94 species and 39 families were included in our analysis (Appendix A). The family Carangidae was the most speciose with 17 representatives, followed by the Haemulidae with 8 species and 5 species each in the Nemipteridae and Sparidae. The remaining 35 families were represented by one to three

species. The sparid *Argyrops spinifer* and the haemulid *Pomadasys commersonnii* were the most abundant species, with 4,130 (10.3%) and 4,110 (10.2%) individuals respectively, followed by 3,171 (7.9%) individuals of the lethrinid, *Lethrinus nebulosus*. Only 9 elasmobranch species (2504 individuals) were included in the analysis based on abundance (Appendix A). For the 94 included species, the mean coefficient of variation (R^2) was 0.95 (± 0.005 SD), with 60% of LWR having coefficients of determination greater than 0.95.

This study provided the first published records of LWR for 27 species (see Appendix A). These 27 species belonged to 20 families (over half of the sampled families), included five species of rays and two shark species, and comprised approximately 22.7% of the sampled individuals. Nine species were endemic to the Arabian Sea, and comprised 22.8% of the individuals for which our analysis presented the first published records. As these were the first published records for these species, no comparisons could be made to relationships developed for conspecifics in non-OMZ regions.

Of the remaining 66 species, 53 species-specific LWR based on fork length from non-OMZ regions were available in FishBase. There was a significant difference for the intercept with values of the intercept a derived from individuals in the Northwest Arabian Sea typically greater than the values reported for the same species in non-OMZ regions (Wilcoxon signed test, $P = 0.028$; Table 4.2). However, there was no difference in the slopes (Wilcoxon signed test, $P = 0.11$; Table 4.2).

Seven species had a minimum of 20 individuals with similar size ranges across the four regions. There was no effect of region on the LWR for two of these species (*Cheimerius nufar* and *Plectorhinchus schotaf*) while region did influence the LWR of the remaining five species (Table 4.3). There was no significant effect of region on the intercept value ("a") for any of the five species. The slopes for each of the five species did not show consistent patterns across the four regions (Figure 4.2; Table 4.4). Three out of five

(*Drepane longimana*, *Pagellus affinis*, and *Pomadasys commersonnii*) showed lower allometric coefficients with lower latitude (Figure 4.2), whereas the remaining two (*Argyrops spinifer*, *Carangoides equula*) showed an increase of the allometric coefficient at lower latitudes.

4.5 Discussion

We established LWR for 94 species of fish found in the Northwest Arabian Sea. The strength of these relationships reflects, in part, the large sample sizes underpinning them (Taylor 1990). Moreover, these data were collected throughout the year across a wide range of sizes (Appendix A Table 1; McKoy et al. 2009), thus increasing their reliability (Chu et al. 1995). Finally, our estimates of the LWR coefficients are very similar to those previously reported from the Northwest Arabian Sea for *A. spinifer* and *L. nebulosus* (Al-Mamry et al. 2009) *Carangoides chrysophrys* (Al-Rasady et al. 2011) and several other species (Human and Al-busaidi 2008). These indicators of reliability suggest that differences in LWR between OMZ and non-OMZ regions should be detectable if present.

The body form coefficients, a , were on average significantly higher in the OMZ when compared to those estimated from non-OMZ regions. This suggests that across the length ranges observed, fish are consistently heavier at length in the OMZ region than in non-OMZ regions. This result was unexpected as I had predicted that the negative consequences of low oxygen levels would reduce growth. One possible explanation is high regional productivity offsetting negative impacts of low oxygen levels and perhaps providing a head start for recruit growth. The region is amongst the most productive globally in terms of primary productivity (Barber et al. 2001). Due to the summer Southwest Monsoon and winter Northeast Monsoon, winds that induce the coastal upwelling affects the shallow hydrography up to depths of about 400 m and along some 1000 km of the northern Arabian Sea in a region extending from the coast to 150 km offshore (Goes et al. 2005). Both monsoons bring nutrients to the photic zone which

triggers spectacular phytoplankton blooms (Kumar et al. 2009). The summer and winter productivity enhance the food web (Levin 2003), thereby favoring the establishment of fish juvenile individuals that may be able to take advantage of seasonal high periods of productivity to pack on weight acting as an effective “head start”. Both the NE monsoon and SW monsoon seem to drive spawning with large numbers of species observed to spawn in both periods (McIlwain et al. 2006; McKoy et al. 2009) a time when large scale increase in biological production take place in most of the Arabian Sea (Madhupratap et al. 1996), possibly enhancing larval growth and survival of fish larval and juveniles (Grimes and Finucane 1991).

Behavioral adaptations in fish may also explain the occurrence of fish in OMZ. Fishes are known to migrate to OMZs to exploit abundant food and escape from predators and competitors (De Robertis et al. 2001; Gibson and Atkinson 2003). For instance, myctophids in the Arabian Sea stay in a deep layer with an extremely low oxygen level of $< 0.1 \text{ ml l}^{-1}$ during the day time to escape from predators and search for food at night at high oxygen level at the surface water (Kinzer et al. 1993). The same behavior has also been recorded for the large population of photichthyid fishes, gelatinous animals and swimming crabs in the Arabian Sea and Oman Sea (Herring et al. 1998). Larger fish are more mobile and may more easily be able to show behavioral adaptations by, for instance, moving vertically from deoxygenated waters into oxygenated waters to recover oxygen debt (Koslow et al. 2011; Jutfelt and Hedgärde 2013). Some fishes also have adaptive strategies such as increasing their gill surface (Childress and Seibel 1998; Gibson and Atkinson 2003) and modifying respiratory pigments (i.e. haemoglobins or haemocyanins) to increase oxygen affinity (Childress and Nygaard 1974; Sanders and Childress 1990; Levin 2003) and hence counterbalance the negative long duration effects of low oxygen. The allometric coefficient of the fish collected in the OMZ was not significantly different than those associated with their counterparts in non-OMZ regions. The lack of a

significant difference implies that the regional effect on fish weight as a function of length was independent of fish length. This is in contrast to laboratory studies that show hypoxia induces size-specific reductions in fish growth due to decreases in the rate of food intake (Pichavant et al. 2001). Our result was also unexpected because large fish are more susceptible to oxygen stress (Nilsson and Ostlund-Nilsson 2008) and thus growth might be expected to slow with increases in length. Non-significant difference between allometric growth coefficients may also reflect the high primary production in the Arabian Sea which enriches the food web in the region and leads to flourishing growth of different fish species (Pauly and Palomares 2005). As such, high productivity may allow fish to grow at optimal rates regardless of size and reflective of optimal growth rates in non-OMZ regions.

In OMZs, some fish could be found in all regions and other are limited to specific regions according to the characteristics of the region depth and oxygen level (Quiroga et al 2009). ANCOVA results showed significant differences in the patterns of LWR across the regions for five of the seven species however these were not related to clear latitudinal gradients nor were they correlated to environmental parameters. They do however reflect habitat and life-history differences among the three groups of species. The two species that showed no regional affects are *C. nufar* and *P. schotaf*. These are both strongly reef-associated species although *P. schotaf* can be found in brackish waters (Froese and Pauly 2015). The three species that showed increases in allometric growth rate as moving south were *A. spinifer*, *C. equula* and *P. affinis*. These three species are all demersal species found on the continental shelf and slopes of Indo-Pacific oceans (Froese and Pauly 2015). The remaining two, *Drepane longimana* and *Pomadasys commersonnii*, showed decrease in allometric growth rate as moving south. Both species are migratory and amphidromous and oceanadromous respectively (Froese and Pauly 2015). The same distribution were

found for Macrouridae which found in all regions whereas, Ipnopidae and Squalidae scartarted in the Chilean OMZ (Quiroga et al 2009).

Coefficients of LWRs may also be influenced by fishing pressure, as fishing influences demographic traits of fishes, such as growth and reproduction (Jennings et al. 1995). However, this is an unlikely explanation for our results. The highest fishing pressure over the last 30 years has been in the area between Masirah Island and Halaniyat Island (regions B to D), with overfishing by foreign trawlers driving decreases in landings (McIlwain et al. 2006) pecies such as kingfish, *Scomberomorus commerson*, show spatial variation in growth in the coastal waters of the Sultanate of Oman in relation to fishing effort (McIlwain et al. 2005). However, decreasing trends from north to south for *D. longimana*, *P. affinis*, and *P. commersonnii* could be attributed to the fishing effort. In addition, simple indices such as catch per unit effort reflect size structure, density and the rate functions (Willis et al. 1993). The catch statistic data in the Arabian Sea showed that the relative catch per unit effort for fishes caught in the studied regions decrease as moving to the south regions (MAFASR 2012).

This study demonstrates the potential of LWR as an indicator of environmental change, in addition to its more traditional role in fisheries management (Froese 2006). In particular, it allows comparisons between OMZ and non-OMZ regions which can form a basis for ongoing monitoring as OMZs expand globally. Changes to condition in response to OMZ expansion have direct implication for food security and the economic productivity of fisheries. It also allows for regional differences in condition to be detected and if applied over time, would allow exploration of how condition is varying with any intensification of the OMZ within the Arabian Sea. The primary production in the Northwest Arabian Sea seems to positively affect condition in the OMZ region despite low oxygen levels but also that responses on a regional basis are species-specific. The Northwest Arabian Sea is the source of 2–35% of global oceanic N₂O, a key greenhouse

gas (Bange et al. 2001), and is also particularly sensitive to climate change (Owens et al. 1991). It is also home to approximately more than 60% of the world population in India, Pakistan, Iran and other close by countries, many of whom depend on regional fisheries (Zhou et al. 2010). Monitoring how expanding and potentially intensifying OMZs affect fish condition is thus both of environmental and economic importance.

4.6 References

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Table 4.1. Descriptive statistics for environmental variables of the Northwest Arabian Sea (n=38928) and by region.

Variable	Statistics	Arabian Sea	Region			
			A	B	C	D
Temperature (°C)	Mean	20.21	19.11	19.76	21.13	21.19
	SD	3.87	3.03	3.71	4.02	5.12
	Min	15.38	16.79	17.58	15.80	15.38
	Max	26.66	19.52	19.82	26.66	23.54
Salinity (ppt)	Mean	35.70	36.07	35.79	35.12	36.22
	SD	0.66	0.79	0.79	0.37	0.37
	Min	34.13	36.01	35.75	34.13	35.94
	Max	36.50	36.50	36.22	36.06	36.33
Dissolved Oxygen (mg/l)	Mean	0.41	0.38	0.33	0.55	0.38
	SD	0.25	0.19	0.20	0.35	0.18
	Min	0.01	0.01	0.01	0.01	0.01
	Max	1.72	1.72	0.60	1.12	0.47
Depth (m)	Mean	63.6	69.6	38.53	57.63	147.43
	SD	95.7	84.8	115.58	61.54	112.97
	Min	13	13	17	17	31
	Max	814	429	381	814	480

Table 4.2. Paired t-tests performed for the length-weight regression parameters for 53 species of fish from the Northwest Arabian Sea oxygen minimum zone (OMZ) and non-OMZ regions.

L-W parameter	OMZ	non-OMZ	<i>P</i>
<i>a</i>	0.037	0.023	0.028
<i>b</i>	0.293	0.299	0.11

Table 4.3. *P* values for the slopes of the regressions of analysis of covariance (ANCOVA) of log (W) on with log (L) with region as covariate.

Species	No	<i>P</i>
<i>Cheimerus nufar</i>	2321	0.17
<i>Plectorhincus schotaf</i>	120	0.28
<i>Drepane longimana</i>	2257	0.0001
<i>Pagellus affinis</i>	1014	0.026
<i>Pomadasys commersonii</i>	4131	0.0001
<i>Argyrops spinifer</i>	4271	0.0009
<i>Carangoides equula</i>	271	0.025

Table 4.4. Length-weight relationships parameters of the five species across the studied regions in Northwest Arabian Sea. R^2 = coefficients of determination, a= intercept, b = slope and SE = standard error.

Species	Region	N	R2	p	a	SE	b	SE
<i>Argyrops spinifer</i>	A	1739	0.994	< 0.05	0.0294	0.019	0.275	0.005
	B	853	0.996	< 0.05	0.0321	0.022	0.283	0.006
	C	958	0.995	< 0.05	0.0303	0.022	0.278	0.006
	D	721	0.993	< 0.05	0.0300	0.031	0.277	0.009
<i>Carangoides equula</i>	A	72	0.985	< 0.05	0.0299	0.135	0.272	0.040
	B	136	0.992	< 0.05	0.0358	0.071	0.290	0.022
	C	21	0.988	< 0.05	0.0415	0.234	0.308	0.078
	D	42	0.967	< 0.05	0.0357	0.257	0.287	0.084
<i>Drepane longimana</i>	A	244	0.914	< 0.05	0.0325	0.208	0.296	0.058
	B	696	0.829	< 0.05	0.0174	0.156	0.253	0.044
	C	917	0.921	< 0.05	0.0265	0.096	0.279	0.027
	D	400	0.908	< 0.05	0.0280	0.160	0.283	0.045
<i>Pagellus affinis</i>	A	407	0.968	< 0.05	0.0434	0.080	0.313	0.028
	B	180	0.950	< 0.05	0.0458	0.146	0.324	0.056
	C	306	0.977	< 0.05	0.0423	0.079	0.307	0.027
	D	121	0.991	< 0.05	0.0441	0.079	0.316	0.027
<i>Pomadasyys commersonnii</i>	A	1755	0.897	< 0.05	0.0324	0.091	0.273	0.022
	B	821	0.959	< 0.05	0.0324	0.081	0.272	0.020
	C	855	0.870	< 0.05	0.0234	0.137	0.250	0.033
	D	700	0.893	< 0.05	0.0284	0.142	0.264	0.034

Appendix A. Length-weight regression coefficients for 94 species of fishes, sharks and rays of the Northwest Arabian Sea. Species for which LWR are presented for the first time are in bold. FL = Fork length, a = intercept, b = slope and R^2 = coefficients of determination. a. Disk diameter was used to quantify size for rays. b. For this species without fork, total length was used instead fork length.

Family	Species	Sample size	Min FL (cm)	Max FL (cm)	a	b	R^2
Ariidae	<i>Netuma bilineata</i>	527	22.2	68	0.0258	2.8906	0.9819
	<i>Plicofollis dussumieri</i>	187	22.9	65.2	0.0499	2.7128	0.9655
	<i>Plicofollis tenuispinis</i>	151	25.7	43.6	0.0182	2.9449	0.939
Balistidae	<i>Sufflamen fraenatum</i>	85	13.8	34.7	0.0327	2.9278	0.993
Carangidae	<i>Alectis ciliaris</i>	31	19.5	73	0.0653	2.6529	0.9965
	<i>Alectis indica</i>	160	21.2	102	0.0069	3.145	0.9871
	<i>Alepes djedaba</i>	163	23.6	37.1	0.0245	2.8564	0.9377
	<i>Carangoides armatus</i>	30	10.4	61.3	0.0017	3.5601	0.9936
	<i>Carangoides chrysophrys</i>	2036	17.6	73	0.0518	2.7265	0.9948
	<i>Carangoides coeruleopinnatus</i>	39	20.1	31.7	0.0812	2.5765	0.9678
	<i>Carangoides equula</i>	271	13.6	45.1	0.0336	2.8368	0.9899
	<i>Carangoides fulvoguttatus</i>	60	25.5	85	0.0485	2.713	0.992
	<i>Carangoides malabaricus</i>	364	16.3	36.1	0.0401	2.7772	0.9746
	<i>Decapterus russelli</i>	1271	4	24.3	0.0044	3.3485	0.9646
	<i>Gnathanodon speciosus</i>	116	46.4	85	0.0476	2.8026	0.9745
	<i>Megalaspis cordyla</i>	44	40	53.4	0.0107	3.0148	0.8981
	<i>Parastromateus niger</i>	60	26.4	48	0.048	2.8181	0.8412
	<i>Scomberoides commersonianus</i>	34	35	96.8	0.064	2.6153	0.9831
	<i>Selar crumenophthalmus</i>	167	17.8	24	0.0255	2.8324	0.8378
	<i>Trachurus indicus</i>	1750	3.5	36.2	0.0111	3.0557	0.9786
	<i>Uraspis helvola</i>	285	16.4	42	0.0616	2.7286	0.9839
Carcharhinidae	<i>Rhizoprionodon acutus</i>	292	35.5	89	0.0071	2.8926	0.9424
Clupeidae	<i>Sardinella albella</i>	30	9.7	13.8	0.0139	2.8731	0.9698
	<i>Sardinella longiceps</i>	82	13.4	20.4	0.0005	4.1468	0.8184
	<i>Sardinella sindensis</i>	401	6.1	19.8	0.0062	3.2405	0.9798

Cynoglossidae	<i>Cynoglossus carpentieri</i> ^a	51	15.7	21.8	0.029	2.4361	0.8757
Dasyatidae	<i>Himantura gerrardi</i> ^a	355	17.2	95	0.0424	2.9337	0.9918
	<i>Himantura uarnak</i> ^a	66	22.6	146	0.1127	2.7023	0.9883
Drepanidae	<i>Drepane longimana</i>	2257	22	43.2	0.0795	2.7554	0.8984
Dussumieriidae	<i>Dussumieria elopoides</i>	249	4.8	19.6	0.0041	3.3196	0.9764
	<i>Etrumeus sadina</i>	150	11.7	21.1	0.0076	3.1385	0.9073
Engraulidae	<i>Encrasicholina heteroloba</i>	56	4.9	8.9	0.0129	2.8124	0.8094
	<i>Thryssa vitrirostris</i>	66	9.1	15.2	0.0135	2.8115	0.924
Gerreidae	<i>Gerres filamentosus</i>	85	14.4	22.3	0.0664	2.6037	0.9266
Gymnuridae	<i>Gymnura poecilura</i> ^a	301	27.8	95	0.0044	3.1768	0.9888
Haemulidae	<i>Diagramma pictum</i>	251	10.9	73	0.0244	2.875	0.9959
	<i>Plectorhinchus flavomaculatus</i>	35	39.3	51.1	0.0254	2.8747	0.9572
	<i>Plectorhinchus pictus</i>	35	29.2	65.2	0.0118	3.1507	0.9827
	<i>Plectorhinchus schotaf</i>	120	21.4	61.9	0.0087	3.2006	0.9309
	<i>Pomadasys commersonnii</i>	4110	33	78	0.1081	2.4841	0.9074
	<i>Pomadasys kaakan</i>	43	33.6	58.7	0.0225	2.9023	0.9669
	<i>Pomadasys maculatus</i>	83	14.4	57.9	0.0414	2.7443	0.9914
	<i>Pomadasys stridens</i>	167	15.6	22.5	0.0427	2.6932	0.898
	<i>Equulites elongates</i>	131	5	9.9	0.0124	2.9464	0.8715
	<i>Leiognathus oblongus</i>	200	3.5	11.8	0.005	3.6028	0.9411
Lethrinidae	<i>Lethrinus lentjan</i>	107	10.4	41.1	0.0277	2.8953	0.9785
	<i>Lethrinus microdon</i>	99	25.6	58.9	0.0172	2.9684	0.9793
	<i>Lethrinus nebulosus</i>	3171	22.2	67.8	0.0274	2.8849	0.9901
Lutjanidae	<i>Lutjanus lutjanus</i>	295	16.9	33.8	0.0169	2.9817	0.9482
	<i>Pristipomoides filamentosus</i>	129	10.1	71	0.0081	3.1692	0.988
Mullidae	<i>Parupeneus rubescens</i>	50	14.6	34.7	0.018	3.026	0.9844
Myliobatidae	<i>Aetomylaeus nichofii</i> ^a	180	22.8	61.1	0.0054	3.2198	0.9794
	<i>Rhinoptera jayakari</i> ^a	194	52.7	87	0.0144	3.0448	0.8739
Nemipteridae	<i>Nemipterus japonicus</i>	220	9.5	33.4	0.0182	2.9952	0.9923
	<i>Nemipterus rally</i>	1704	6.1	20.2	0.0038	3.5779	0.9262
	<i>Parascolopsis aspinosa</i>	196	5.1	20.5	0.067	2.508	0.9223

	<i>Parascolopsis eriomma</i>	36	13.6	30.6	0.0148	3.0878	0.988
	<i>Scolopsis taeniata</i>	98	7.3	30.9	0.0133	3.0896	0.9926
Ostraciidae	<i>Tetrosomus gibbosus</i>	45	15.8	23.6	0.0635	2.7452	0.8301
Paralichthyidae	<i>Pseudorhombus arsius</i>	150	9.1	39.4	0.0084	3.0459	0.9838
Pinguipedidae	<i>Parapercis alboguttata</i>	67	7.2	18	0.0073	3.0877	0.9637
Platycephalidae	<i>Kumococius rodericensis</i>	1009	6.6	32.2	0.013	2.851	0.9456
Plotosidae	<i>Plotosus limbatus</i>	42	41.5	58.1	0.0312	2.5644	0.8013
Priacanthidae	<i>Priacanthus hamrur</i>	96	16.3	24.8	0.0011	3.845	0.8722
Psettodidae	<i>Psettodes erumei</i>	82	11.9	63.9	0.0033	3.3746	0.986
Rhinobatidae	<i>Rhinobatos punctifer^a</i>	311	24.3	91	0.0078	2.8112	0.9911
Sciaenidae	<i>Argyrosomus heinii</i>	134	16.6	73.8	0.0299	2.7599	0.9542
	<i>Otolithes ruber</i>	321	27.9	52.5	0.0157	2.8748	0.9771
Scombridae	<i>Rastrelliger kanagurta</i>	117	8.2	28.7	0.0061	3.3155	0.9966
	<i>Scomber japonicas</i>	290	18.9	40.4	0.0074	3.1573	0.9909
Serranidae	<i>Epinephelus diacanthus</i>	868	19.1	55.4	0.0104	3.0766	0.9882
	<i>Epinephelus polylepis</i>	99	19.9	121	0.0036	3.3317	0.988
	<i>Epinephelus radiates</i>	42	13.8	60.1	0.0063	3.2158	0.994
Siganidae	<i>Siganus canaliculatus</i>	166	23.8	41.2	0.0488	2.7104	0.9407
Sparidae	<i>Argyrops spinifer</i>	4130	8.8	62.1	0.0443	2.8004	0.9949
	<i>Boops lineatus</i>	64	7.5	21.4	0.0036	3.5163	0.9669
	<i>Cheimerius nufar</i>	2297	10.4	59.3	0.0321	2.8489	0.9819
	<i>Pagellus affinis</i>	887	6.3	30.7	0.02	2.9834	0.9731
	<i>Rhabdosargus sarba</i>	411	15.8	40.8	0.0513	2.7559	0.9491
Sphyraenidae	<i>Sphyraena acutipinnis</i>	122	21.6	60.7	0.0086	2.8734	0.9463
	<i>Sphyraena flavicauda</i>	110	9.2	30	0.0125	2.8255	0.9528
	<i>Sphyraena putnamae</i>	152	59.6	121	0.0289	2.6181	0.8754
	<i>Sphyraena qenie</i>	100	40.1	101.2	0.03	2.6002	0.978
Synodontidae	<i>Saurida tumbil</i>	297	8	57.1	0.0126	2.9502	0.9916
	<i>Saurida undosquamis</i>	626	6.5	38.8	0.0039	3.2583	0.9839
	<i>Synodus dermatogenys</i>	72	8	14.1	0.0008	4.0426	0.8965
	<i>Trachinocephalus myops</i>	48	7.6	15.4	0.0045	3.3585	0.9397

Terapontidae	<i>Terapon jarbua</i>	58	16.2	31.9	0.0133	3.0854	0.9707
Trachichthyidae	<i>Hoplostethus mediterraneus mediterraneus</i>	178	10.9	17.6	0.0686	2.6253	0.8381
Triakidae	<i>Iago omanensis</i>	579	18.4	80	0.0021	3.1116	0.9801
	<i>Mustelus mosis</i>	175	65.5	105	0.0001	3.866	0.9264
Trichiuridae	<i>Trichiurus lepturus^b</i>	816	35.9	119	0.0001	3.5812	0.9364
Triglidae	<i>Lepidotrigla omanensis</i>	120	10.4	16.5	0.0105	3.0751	0.8357
	<i>Pterygotrigla hemisticta</i>	1025	6.8	25.1	0.0091	3.1367	0.9343

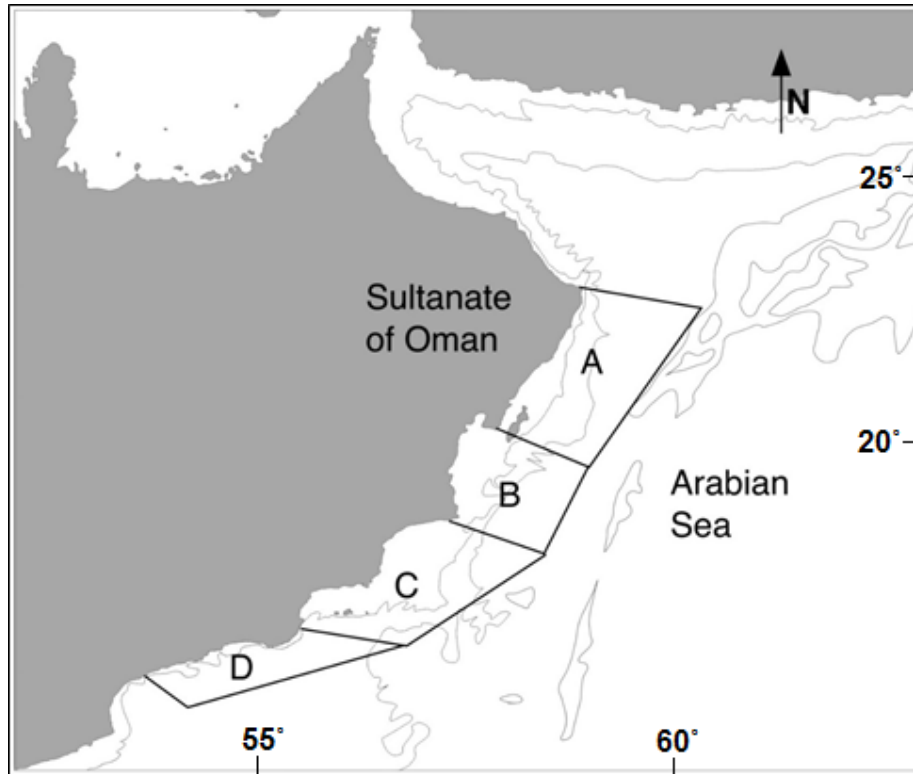


Figure 4.1. Study area and regions where A: Ra's al Hadd to Masirah Island; B: Masirah Island to Ra's al Madrasah, C: Ra's alMadrasah to Ra's Hasik; D: Ra's Hasik to Yemen border.

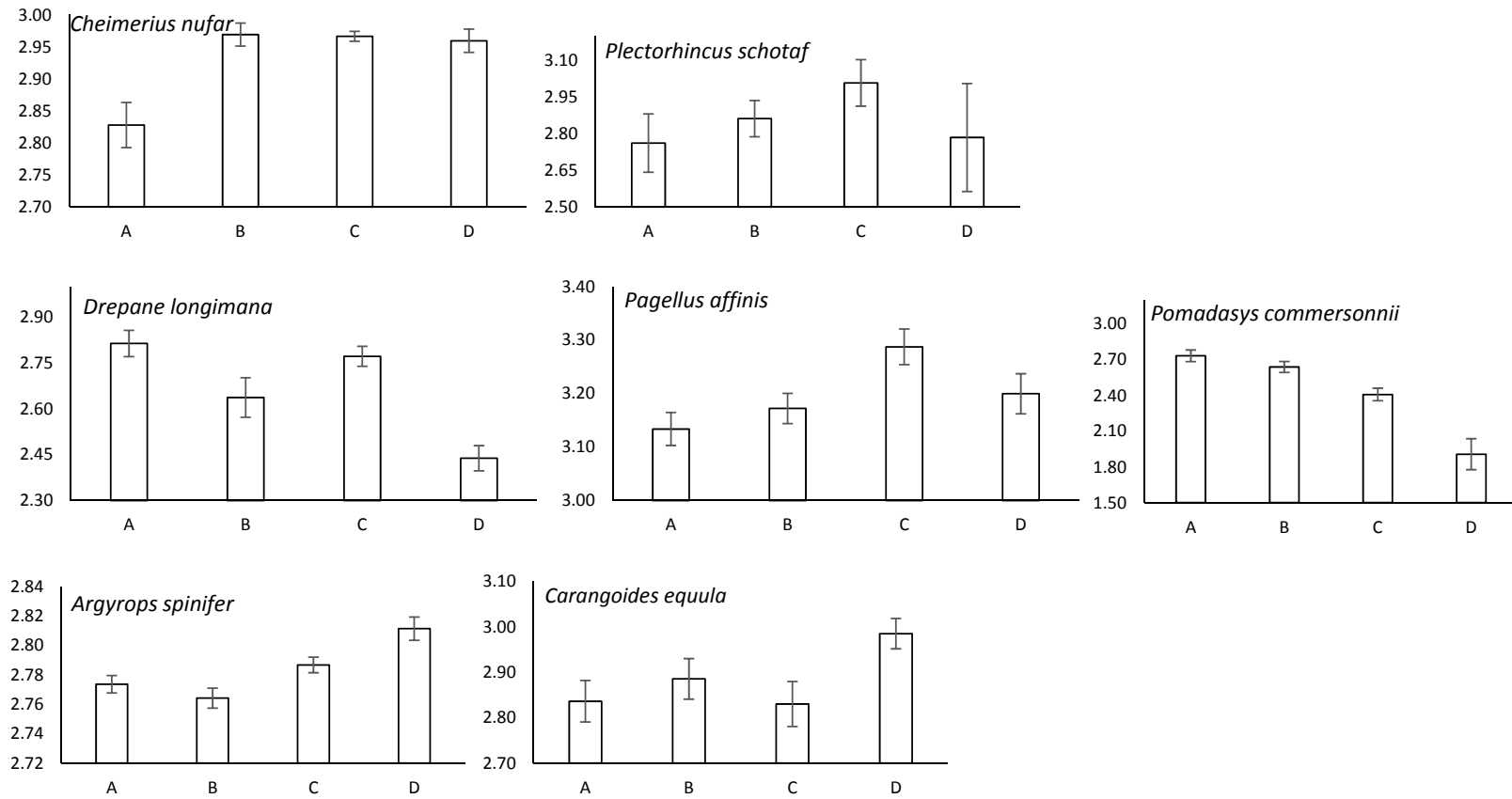


Figure 4.2. Slopes of the regressions \pm standard errors of the slopes for *Argyrops spinifer*, *Carangoides equula*, *Drepane longimana*, *Pagellus affinis* and *Pomadasys commersonnii* across the four regions in the northwest Arabian Sea. Y axis for all plots represent the b value (slope).

Chapter 5- General Discussion

In this thesis, I used a large scale dataset collected from a fisheries-independent survey conducted in the Arabian Sea between 2007 and 2008 to explore the effect of one of only three persistent oxygen minimum zones (OMZ) globally on fish biodiversity, length and condition. Both relatively high biodiversity and larger fish size were associated with the NE Monsoon, a period when the OMZ is relatively weak (Chapters 2 and 3). However, overall high fish condition was associated with the OMZ region compared to non-OMZs (Chapter 4). This latter result was unexpected as low oxygen levels are predicted to reduce growth (Long et al. 2016). One possible explanation is high regional productivity that offsets negative impacts of low oxygen levels, perhaps providing a head start for recruits growth (Chapter 4). The combination of these results suggest that the effects of the OMZ on fish assemblages are highly nuanced, and can be both positive and negative.

Region had no effect on patterns in biodiversity (Chapter 2) but was associated with fish length distributions and condition in the Arabian Sea on a species-specific basis (Chapter 3 and 4). Species-specific responses may reflect strong habitat preferences (Rijnsdorp et al. 2009). Alternatively, regional differences in length distribution may reflect food availability and refuges from larger predators (Cury and Roy 1989). Season had a stronger effect on diversity, length and condition than did region and again, for the latter two attributes, these influences were species-specific. The high biodiversity in the Northeast Monsoon may reflect the ample food available at that time (Raghukumar and Anil 2003) which contrasts to the poorer conditions during the Southwest Monsoon given the stronger OMZ (Levin et al. 2000) (Chapter 2). All of the five species that were generally larger during the NE Monsoon, *A. spinifer*, *E. diacanthus* and *P. commersonnii*. *E. diacanthus* and *P. commersonnii*, also gather during the SW season and NE monsoon seasons to spawn (Berkeley et al. 2004). The differential regional effects on the five species (*Drepane longimana*, *Pagellus affinis*, *Pomadasyd commersonnii*, *Argyrops*

spinifer and *Carangoides equula*) in terms of allometric growth coefficients suggest that life history and habitat preferences are relevant to increasing OMZs (Rijnsdorp et al. 2009).

Depth was an important factor for the biodiversity indices and the length distributions of the fish in the Arabian Sea. Biodiversity was significantly higher in the shallow waters than in the deeper water (Chapter 2) and the fish with large length found significantly more in the deeper water (Chapter 3) as oxygen concentration decrease as the depth of the water increase. *D. longimana* and *L. nebulosus* were significantly smaller in shallow water and as these species show ontogenetic variation where they move to deeper water as they grow larger (Corten 2001).

Environmental variables (temperature, salinity and dissolved oxygen) were generally poor predictors of the fish assemblage. Although environmental conditions vary among seasons in the Arabian Sea (Naqvi et al. 2006), and such variation may lead fish to moving among regions and depths (Brönmark et al. 2008), these variables generally did not explain much of the variation in biodiversity and length (Chapter 2 and 3). The environmental factors were poorly related to the biodiversity indices (Chapter 2), possibly because the indirect effect of the environmental variables on the fish biodiversity are not well studied and modeled (Mora and Robertson 2005). On the other hand, temperature explained 40% of the relation of the fish length distribution of *E. diacanthus* (Chapter 3). While temperature is considered an ecological master variable for the fish (Lee et al. 2003), including with regard to its influential interaction with dissolved oxygen consumption (Rijnsdorp et al. 2009) and salinity concentration (Schouten et al. 2002), it remains unclear why environmental factors were weak in their capacity as predictors. High fishing pressure between 1980 and 2010 could explain the low fish biodiversity in deep strata (Chapter 2) and the less distribution of *A. spinifer* in region C (Chapter 3) and

the variation in growth parameters in region C of *A. spinifer*, *C. equula*, *P. affinis*, *D. longimana* and *P. commersonnii* (Chapter 4).

5.1 Learnings with regard to OMZs

Climate change is predicted to increase the distribution of the OMZs globally (Stramma et al. 2012). My results suggest that overall, fish biodiversity will be negatively affected under expanding OMZs (Chapter 2) but that this may be offset by increased productivity for some species (Chapters 3 and 4). The latter is likely to occur where expanded OMZs remain associated with upwelling. In cases where there is no additional nutrient input into the system, additional OMZ-associated productivity may not occur as a result of global warming. The predicted shift in the Earth's axis of spin (Adhikari and Ivins 2016) may lead to shifts in seasons and strengthen the wind stress which will negatively affect the Arabian Sea. Shifting the seasons may reduce the productivity of the Arabian Sea, affecting the head start growth and reducing its condition (Levin 2003). Increasing wind stress will strengthen the upwelling to bring more low dissolved oxygen to the surface in the Arabian Sea enlarging the OMZ distribution in the Arabian Sea. In other regions which are expected to have new or expanding OMZs in the future, the impact may be significant, particularly in areas which lack upwelling. The productivity will be less and hence the fish biodiversity and the condition will be reduced.

The potential negative impact of a growing OMZ on fish will be significant because it can lead to reduced habitat quality for fish (Ekau et al. 2010). On the other hand, previous studies showed that fish respond to OMZs. Mobile fish, especially larger individuals, show behavioral adaptations such as moving vertically from deoxygenated waters into oxygenated waters to recover oxygen debt (Koslow et al. 2011; Jutfelt and Hedgärde 2013). Other fish species increase their gill surface (Childress and Seibel 1998; Gibson and Atkinson 2003) and modify respiratory pigments (i.e. haemoglobins or haemocyanins) to increase oxygen affinity (Childress and Nygaard 1974; Sanders and

Childress 1990; Levin 2003), hence overcoming the negative effect of low oxygen. Some fishes also benefit from migration to OMZs to exploit abundant food and escape from predators and competitors (De Robertis et al. 2001; Gibson and Atkinson 2003).

Of concern is the degree to which expansion of OMZs changes the biology, behavior and exploitation rate of species. For instance the size at which the fish start to reproduce could be modified because of the effect of low oxygen on the food intake by the fish and hence the growth will change (Mallekh and Lagardere 2002). Feeding behavior could also be affected by OMZs when fish move to new regions of ample dissolved oxygen concentration levels and then start to feed on a new prey (Diaz and Rosenberg 1995). The effect of OMZs may expand to increased overexploitation when fish move from OMZ areas (Jackson et al. 2001).

5.2 Limitations

Although the sample size was adequate to generate results for a general assessment of the effect of the OMZ, sampling effort was not evenly distributed between the factors. For instance, the number of samples collected during the PreMon and PostMon was less than the two main seasons (SWMon and NEMon). Also, region D was the less sampled compared to the other regions and depth strata 3 and 4 were also less sampled relative to shallower strata. Dietary studies could not be conducted from this survey because of the stomach content of the fish were not taken. However, this survey should be continued every year to reflect the variation in species richness abundance and to correlate the results with the environmental variables to insure of the sustainability of the fish stock in OMZ and detects OMZ effects on this region.

5.3 Future research

Fish condition is a very important index and could be used to compare the fitness of the status of fish between different regions. I suggest this study be replicated in other OMZs to compare the results and gather more scientific evidence on the effect of the OMZ on fish assemblages. Upwelling areas also should be included in this study to see the effect of the productivity on the fish condition. Also, there is a need to expand the number of species to look at the generalities of the OMZ effect and link it to the biology of the fish and to the environmental variables.

Gill surface area is very important as it functions to exchange gases in fish. The gill surface area of fish should be compared between fishes from OMZ with the same fishes in non-OMZ to see if there is any modification or adaptation of fish to overcome the effect of OMZ.

Fishing activity could have an effect on the fish diversity, distribution and condition, so including the fishing effect in the future study will be useful.

5.4 Conclusions

Climate change is a serious issue because it will fundamentally alter the environmental variables in the ocean. Alteration in environmental variables is likely to strongly affect fish populations because fish species have specific limits. As a result, fish may shift from their original habitat to another habitat consequently biodiversity, distribution and fish growth will be affected. The climate change will increase the OMZs and its effect will be enormous especially when the SWMon is going to strengthening, which will bring more low oxygen from deep water. The SWMon affect the socioeconomic life of 60% of the world population occupying India, Nepali, Bangladesh and nearby countries (Zhou et al. 2010), whom most depend on fishing as a source of income.

5.5 References

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Appendix 1. Biological data from the trawl sampling in the Omani coast of the Arabian Sea (2007-2008) used in this thesis. NEMon; Northeast Monsoon; PreMon; Pre-Southwest Monsoon; SWMon: Southwest Monsoon; PostMon: Post-Southwest Monsoon.

Season	Species	Length (cm)					Weight				
		No.	Mean	SE	Min	Max	No.	Mean	SE	Min	Max
NEMon	<i>Acanthopagrus bifasciatus</i>	7	32.03	2.05	27	37.8	7	863.57	149.05	535	1285
	<i>Albula argentea</i>	19	62.69	0.87	56.6	73.3	19	3055.26	129.17	2240	4525
	<i>Alectis ciliaris</i>	13	45.45	2.80	30.2	58.8	13	1791.92	257.38	610	3250
	<i>Alectis indica</i>	81	49.99	1.97	21.2	83	81	2179.69	177.66	190	6945
	<i>Alepes djedaba</i>	150	30.65	0.21	24.4	37.1	150	444.27	9.41	205	715
	<i>Argyrops spinifer</i>	1725	33.87	0.27	13.2	61.8	1725	1064.32	21.74	60	5075
	<i>Argyrosomus heinii</i>	135	54.39	0.80	41.5	73	135	2100.30	96.14	835	5295
	<i>Argyrosomus hololepidotus</i>	91	77.77	2.00	28	110	91	5721.10	347.77	235	12700
	<i>Bodianus macrognathos</i>	4	47.40	1.50	44.8	50	4	2020.00	190.53	1690	2350
	<i>Caesio lunaris</i>	19	27.94	0.31	26.5	30.6	19	459.21	13.23	370	570
	<i>Carangoides armatus</i>	55	56.29	1.28	10.4	64	55	3097.84	104.94	26	4030
	<i>Carangoides bajad</i>	9	29.88	0.28	29	31	9	525.56	27.81	455	665
	<i>Carangoides chrysophrys</i>	1290	40.63	0.38	17.6	73	1290	1595.60	34.05	110	5750
	<i>Carangoides coeruleopinnatus</i>	39	27.01	0.52	20.1	30.9	39	414.23	18.59	180	560
	<i>Carangoides equula</i>	153	25.79	0.60	13.6	41.7	153	412.91	28.59	55	1365
	<i>Carangoides ferdau</i>	10	45.41	5.53	23.6	79	10	2370.00	676.39	280	6955
	<i>Carangoides fulvoguttatus</i>	59	41.94	2.34	25.2	91.7	59	1816.27	283.72	320	10700
	<i>Carangoides malabaricus</i>	118	26.06	0.43	16.3	36.1	118	371.48	15.01	85	980
	<i>Cheimereus nufar</i>	896	32.13	0.24	12.6	57.5	896	704.48	16.63	35	3255
	<i>Chlorurus strongylocephalus</i>	12	45.41	2.62	32.5	58.1	12	2227.50	370.44	600	4275
	<i>Cookeolus japonicus</i>	45	27.62	0.13	26	30	45	390.00	5.70	325	490
	<i>Decapterus macarellus</i>	16	25.94	0.65	20.5	30.4	16	216.19	21.20	102	480
	<i>Decapterus russelli</i>	745	21.59	0.44	8.2	58.5	745	294.18	21.02	5	2365
	<i>Diagramma pictum</i>	384	41.03	0.71	19.3	73	384	1375.66	58.41	100	4895
	<i>Drepane longimana</i>	1065	35.59	0.08	22	42	1065	1508.26	9.38	365	2565
	<i>Dussumieria elopoides</i>	125	14.81	0.13	12.8	19.6	125	33.06	1.23	21	88

<i>Echeneis naucrates</i>	8	59.23	3.19	46.4	68	8	1000.00	206.15	335	1720
<i>Epinephelus coioides</i>	2	68.45	29.55	38.9	98	2	8357.50	7642.50	715	16000
<i>Epinephelus diacanthus</i>	104	42.36	0.67	29.3	53.8	104	1086.06	52.84	330	2070
<i>Epinephelus indistinctus</i>	5	99.00	2.43	90	103	5	14280.00	978.98	11200	16400
<i>Epinephelus polylepis</i>	18	57.68	6.14	28.4	121	18	5191.67	2209.47	295	32300
<i>Epinephelus radiatus</i>	5	49.54	2.59	43.9	56	5	1643.00	250.38	940	2235
<i>Epinephelus tukula</i>	11	90.73	2.17	74	98	11	10944.09	783.46	5185	14000
<i>Etrumeus teres</i>	249	16.09	0.09	12.6	21.1	249	47.74	1.00	25	110
<i>Gerres filamentosus</i>	175	19.38	0.10	15.1	22.3	175	154.31	1.83	70	215
<i>Gerres longirostris</i>	4	27.25	0.23	26.7	27.8	4	490.00	11.73	460	515
<i>Gnathanodon speciosus</i>	72	62.35	0.99	46.4	85	72	5380.49	258.23	2285	11800
<i>Kumococius rodericensis</i>	40	19.29	0.83	13.5	29.1	40	63.38	7.66	15	180
<i>Lepidotrigla bispinosa</i>	241	17.73	0.11	9.5	21.6	241	74.27	1.41	10	145
<i>Lethrinus lentjan</i>	120	30.04	0.43	19.8	41.1	120	569.25	21.83	150	1270
<i>Lethrinus microdon</i>	294	43.67	0.37	25.6	65	294	1349.61	32.73	290	3820
<i>Lethrinus nebulosus</i>	2178	43.49	0.22	22.3	66	2178	1679.86	22.40	205	4940
<i>Lutjanus bengalensis</i>	10	21.45	0.67	17.1	23.5	10	157.00	13.17	70	235
<i>Lutjanus coeruleolineatus</i>	14	25.51	1.36	16.3	32.4	14	300.71	43.36	60	555
<i>Lutjanus lutjanus</i>	334	24.90	0.20	16.9	33.8	334	249.90	6.42	70	610
<i>Megalaspis cordyla</i>	24	47.87	0.64	43.7	53.4	24	1305.00	51.25	1015	1740
<i>Nemipterus japonicus</i>	158	22.37	0.23	18.3	33	158	204.46	7.20	85	550
<i>Nemipterus randalli</i>	110	13.72	0.14	10.6	18.5	110	39.47	1.32	17	95
<i>Netuma bilineata</i>	125	33.80	0.80	23.7	61.1	125	829.84	68.04	230	3935
<i>Otolithes ruber</i>	307	36.58	0.35	27.2	50.8	307	525.33	15.58	195	1380
<i>Pagellus affinis</i>	463	17.37	0.21	9.2	31.5	463	121.25	5.15	15	585
<i>Parascolopsis eriomma</i>	12	20.00	1.42	13.6	30.5	12	176.67	37.67	50	495
<i>Parastromateus niger</i>	56	30.09	0.61	26.4	48	56	751.16	64.13	455	3140
<i>Plectorhinchus flavomaculatus</i>	31	45.59	0.65	39.3	51.1	31	1519.35	62.97	955	2065
<i>Plectorhinchus pictus</i>	15	50.08	2.32	30.6	60	15	2935.00	328.34	630	5150
<i>Plectorhincus schotaf</i>	73	33.52	0.61	21.4	61.9	73	641.71	39.67	180	2930
<i>Plicofollis dussumieri</i>	9	54.64	2.45	44.5	65.2	9	2528.33	266.85	1405	3780

<i>Plicofollis tenuispinis</i>	12	36.05	0.56	32.8	38.7	12	714.17	36.38	480	885
<i>Polydactylus sextarius</i>	8	22.61	0.87	18.5	26.6	8	208.75	20.24	120	295
<i>Pomacentrus caeruleus</i>	4	49.30	2.54	44.9	53.7	4	167.50	1.44	165	170
<i>Pomadasys argenteus</i>	17	42.42	1.63	34.9	52.7	17	1231.18	145.15	615	2360
<i>Pomadasys commersonnii</i>	828	62.45	0.21	39.9	78	828	3070.27	25.52	920	5300
<i>Pomadasys kaakan</i>	35	47.05	1.11	33	57.6	35	1779.00	114.97	625	2950
<i>Pomadasys maculatus</i>	14	39.83	3.81	22.2	57.9	14	1297.86	288.52	230	3310
<i>Pomadasys stridens</i>	96	19.20	0.15	15.6	22.5	96	125.42	2.62	70	185
<i>Priacanthus hamrur</i>	11	22.50	0.46	20.2	24.8	11	187.55	11.13	133	260
<i>Pristipomoides filamentosus</i>	8	28.05	6.84	13.5	51.4	8	875.63	408.23	35	2270
<i>Psettodes erumei</i>	45	47.37	1.13	38	63.9	45	1634.22	138.76	740	4195
<i>Pseudorhombus arsius</i>	32	33.10	0.77	22.3	40.7	32	361.72	24.82	110	700
<i>Pterygotrigla hemisticta</i>	145	18.81	0.22	12.1	25.1	145	100.48	3.52	25	240
<i>Puerulus sewelii</i>	77	7.94	0.09	6.2	9.6	77	99.03	3.12	50	160
<i>Rachycentron canadum</i>	40	64.34	2.99	33.8	96	40	3266.00	418.24	250	9900
<i>Rhabdosargus sarba</i>	179	29.50	0.36	21	43.2	179	576.56	21.37	200	1605
<i>Sardinella albella</i>	73	12.92	0.11	9.7	14.9	73	22.41	0.53	9	34
<i>Sardinella longiceps</i>	47	16.69	0.16	13.2	19.3	47	59.45	1.65	24	93
<i>Sardinella sindensis</i>	185	13.99	0.07	11.3	16.7	185	31.52	0.50	16	56
<i>Sargocentron rubrum</i>	11	21.15	0.35	19.3	22.8	11	250.00	12.92	205	315
<i>Saurida tumbil</i>	188	37.28	0.43	15.8	57.6	188	582.90	21.99	30	2320
<i>Saurida undosquamis</i>	214	22.33	0.41	11.1	37.4	214	123.46	7.73	15	455
<i>Scolopsis taeniata</i>	159	24.69	0.32	10.9	30.9	159	289.62	10.15	35	515
<i>Scomber japonicus</i>	27	24.41	0.14	23.1	26	27	182.22	3.02	145	205
<i>Scomberoides commersonianus</i>	7	66.51	3.94	58.1	89.5	7	3401.43	741.83	2155	7805
<i>Scomberoides tol</i>	7	41.27	0.83	37.8	44.2	7	528.57	32.73	425	650
<i>Scomberomorus commerson</i>	15	66.71	1.21	56.5	77	15	2316.00	129.10	1175	3455
<i>Selar crumenophthalmus</i>	52	19.61	0.14	17.6	21.3	52	112.19	2.39	75	144
<i>Seriola dumerili</i>	4	60.55	4.30	53.1	68	4	3572.50	668.28	2415	4730
<i>Seriola rivoliana</i>	2	91.25	9.55	81.7	100.8	2	11350.00	2550.00	8800	13900
<i>Seriolina nigrofasciata</i>	10	37.29	2.87	26.9	48.2	10	1066.50	223.71	335	2120

	Siganus canaliculatus	114	32.39	0.36	23.8	41.2	114	611.14	19.69	210	1150
	Sphyraena acutipinnis	153	43.44	0.42	26.2	60.7	153	449.23	14.19	115	1110
	Sphyraena flavicauda	86	24.72	0.18	21.3	30	86	89.88	3.00	50	220
	Sphyraena jello	20	96.69	8.04	22.2	138.9	20	6569.00	966.58	70	13900
	Sphyraena putnamae	165	75.04	0.72	43.4	94	165	2394.79	63.22	475	4475
	Sphyraena qenie	95	67.28	2.07	40.1	125	95	2086.47	206.38	330	10200
	Sufflamen fraenatum	3	27.17	2.86	22.2	32.1	3	506.67	132.80	275	735
	Terapon jarbua	58	27.70	0.34	21.3	34.3	58	389.22	14.32	130	685
	Trachinotus africanus	46	43.58	1.41	34.1	63.9	46	1862.50	152.56	980	4280
	Trachinotus blochii	11	55.76	1.53	49.8	63.7	11	3599.09	240.76	2620	4900
	Trachurus indicus	191	14.71	0.37	9.5	35.7	191	58.05	6.21	3	625
	Trichiurus lepturus	899	78.92	0.38	53	119	899	457.95	9.40	130	1715
	Umbrina ronchus	4	31.50	0.64	30.4	32.6	4	402.50	24.54	360	445
	Uraspis helvola	199	26.99	0.35	16.4	41.5	199	539.12	22.91	130	1635
	Velifer hypselopterus	9	34.52	0.32	33.2	35.8	9	1026.67	29.18	940	1165
PreMon	Acanthopagrus bifasciatus	3	33.83	0.22	33.4	34.1	3	1105.00	16.07	1080	1135
	Alectis ciliaris	10	48.50	5.57	21.9	73	10	2407.00	627.33	270	5905
	Alectis indica	33	57.91	1.42	36.7	74	33	2553.79	147.91	945	4305
	Alepes djedaba	3	31.60	1.38	29.5	34.2	3	511.67	73.11	415	655
	Argyrops spinifer	1443	34.78	0.31	8.8	59.7	1443	1200.64	25.48	15	4295
	Argyrosomus heinii	115	59.47	0.81	43.3	72.3	115	2358.74	76.72	890	3740
	Argyrosomus hololepidotus	22	77.41	4.85	39.7	105.3	22	5593.64	804.62	570	11100
	Atule mate	2	29.60	3.50	26.1	33.1	2	375.00	161.00	214	536
	Auxis thazard thazard	7	37.04	0.37	35.8	38.9	7	828.57	23.85	745	930
	Carangoides chrysophrys	281	42.60	0.57	25.3	62.5	281	1597.42	52.27	300	3885
	Carangoides equula	44	19.86	0.78	14.2	45.1	44	188.61	32.38	63	1430
	Carangoides ferdau	8	47.40	0.87	44.1	50.3	8	2290.00	106.81	1880	2595
	Carangoides fulvoguttatus	4	80.63	4.38	67.5	85	4	7420.00	880.00	4780	8300
	Carangoides malabaricus	145	27.06	0.23	19.7	32.3	145	385.45	8.19	155	595
	Cheimerus nufar	561	29.81	0.39	12.9	54.3	561	641.71	20.76	35	2825
	Cookeolus japonicus	9	29.99	0.29	28.2	30.8	9	462.22	16.65	390	530

<i>Decapterus russelli</i>	353	17.58	0.16	11.2	23.4	353	75.29	1.78	19	140
<i>Diagramma pictum</i>	216	49.34	0.75	22	68	216	2065.81	72.50	170	4345
<i>Diplodus cervinus omanensis</i>	6	31.87	1.41	29.2	36.3	6	1001.67	133.72	690	1405
<i>Drepane longimana</i>	485	36.05	0.12	25.7	43.2	485	1591.91	15.14	655	2680
<i>Echinorhinus brucus</i>	4	59.50	5.14	50.6	68.4	4	1017.50	209.29	655	1380
<i>Epinephelus diacanthus</i>	67	44.83	0.81	29.9	55.2	67	1307.27	63.91	350	2215
<i>Epinephelus epistictus</i>	3	29.70	6.90	22.8	43.5	3	440.67	294.67	146	1030
<i>Epinephelus gabriellae</i>	4	41.45	1.41	39	43.9	4	997.50	99.59	825	1170
<i>Epinephelus indistinctus</i>	4	107.00	0.58	106	108	4	19500.00	173.21	19200	19800
<i>Epinephelus polylepis</i>	22	42.10	2.73	25.5	62	22	1322.00	233.26	192	3405
<i>Epinephelus radiatus</i>	3	40.57	3.45	33.8	45.1	3	951.67	229.93	540	1335
<i>Etrumeus teres</i>	246	19.10	0.05	16.7	21.6	246	81.53	0.56	52	107
<i>Kumococius rodericensis</i>	37	19.89	0.87	13.1	32.2	37	81.76	11.86	18	270
<i>Lagocephalus guentheri</i>	4	38.25	1.65	35.4	41.1	4	1005.00	167.43	715	1295
<i>Lepidotrigla bispinosa</i>	73	16.27	0.14	13	19.5	73	56.23	1.51	25	95
<i>Lepidotrigla omanensis</i>	34	13.26	0.17	11.3	15	34	31.53	1.34	16	45
<i>Lethrinus lentjan</i>	35	33.90	0.77	26.2	42.3	35	761.43	50.92	380	1440
<i>Lethrinus microdon</i>	52	45.39	0.60	28.6	51.2	52	1501.08	51.25	471	2340
<i>Lethrinus nebulosus</i>	478	44.24	0.43	22.2	62.7	478	1759.54	41.81	210	4805
<i>Lutjanus lutjanus</i>	246	24.56	0.28	17.2	33.3	246	281.20	8.67	90	625
<i>Megalaspis cordyla</i>	57	43.81	0.33	36.4	49.4	57	945.79	20.75	550	1435
<i>Nemipterus japonicus</i>	126	15.38	0.35	10	27.6	126	80.99	7.63	15	390
<i>Nemipterus randalli</i>	86	13.75	0.23	8.9	18.5	86	44.65	2.08	8	105
<i>Neopinnula orientalis</i>	11	18.65	0.53	15.8	20	11	50.82	4.18	28	62
<i>Netuma bilineata</i>	119	46.38	0.92	28.8	67	119	1848.87	105.96	375	5065
<i>Netuma thalassina</i>	5	58.08	7.90	35.6	76.1	5	3408.00	1160.52	750	6200
<i>Otolithes ruber</i>	186	41.82	0.30	32.7	56.2	186	735.99	14.64	330	1730
<i>Pagellus affinis</i>	319	16.91	0.15	11	27.6	319	97.53	3.10	25	466
<i>Parascopopsis eriomma</i>	12	22.62	1.33	18.2	30.6	12	263.75	53.40	125	610
<i>Parastromateus niger</i>	4	38.70	1.07	35.7	40.7	4	1306.25	110.71	1085	1610
<i>Parupeneus rubescens</i>	40	24.95	0.92	14.6	34.7	40	353.63	33.95	65	840

<i>Plectorhinchus pictus</i>	27	50.74	0.97	42.5	61.2	27	2706.30	153.87	1475	4695
<i>Plectorhincus schotaf</i>	39	32.17	0.22	29	34.4	39	582.44	11.62	460	700
<i>Plicofollis dussumieri</i>	127	48.82	0.59	31.7	61.8	127	1973.82	60.41	530	3885
<i>Plicofollis tenuispinis</i>	11	39.05	1.26	29.7	43.6	11	904.09	68.92	410	1145
<i>Pomadasys commersonnii</i>	1021	61.98	0.17	39.9	74.3	1021	3005.84	21.99	865	4645
<i>Pomadasys maculatus</i>	56	20.65	0.42	14.4	37.8	56	192.86	14.34	75	925
<i>Pomadasys olivaceus</i>	15	20.79	0.46	18.5	24.5	15	173.33	12.07	120	270
<i>Pomatomus saltatrix</i>	6	65.55	6.24	51.6	79.5	6	3495.00	854.18	1585	5405
<i>Priacanthus hamrur</i>	17	20.19	0.57	17.8	28.1	17	113.76	15.15	75	344
<i>Pristipomoides filamentosus</i>	109	22.46	0.99	15.4	71	109	338.17	88.77	55	5995
<i>Psettodes erumei</i>	4	46.23	2.77	41.7	53.7	4	1461.25	297.75	1035	2320
<i>Pseudorhombus arsius</i>	4	32.18	4.14	20.1	38.1	4	387.50	113.18	70	555
<i>Pterygotrigla hemisticta</i>	259	18.48	0.15	9.9	24	259	90.10	2.22	11	195
<i>Rachycentron canadum</i>	4	76.68	21.90	53.4	142.3	4	9535.00	8055.13	1415	33700
<i>Rhabdosargus sarba</i>	121	33.37	0.19	27.7	37.3	121	815.29	13.28	415	1075
<i>Sarda orientalis</i>	6	45.35	1.18	42.7	51	6	1385.83	133.70	1150	2045
<i>Saurida tumbil</i>	74	43.44	0.70	34.8	57.1	74	892.97	44.99	440	1835
<i>Saurida undosquamis</i>	26	22.50	0.42	17.6	25.7	26	92.27	4.73	45	135
<i>Scolopsis taeniata</i>	62	25.79	0.58	12.3	30.7	62	361.37	18.29	30	565
<i>Scomber japonicus</i>	21	26.65	0.20	25.2	28.3	21	245.48	7.22	210	315
<i>Seriola dumerili</i>	13	38.21	0.42	36.5	41.1	13	872.31	24.01	745	1065
<i>Seriola rivoliana</i>	3	76.67	5.67	71	88	3	6953.33	1523.33	5430	10000
<i>Seriolina nigrofasciata</i>	15	40.89	1.76	33.6	49.4	15	1282.67	164.37	700	2210
<i>Siganus canaliculatus</i>	187	30.38	0.14	25.3	35.1	187	522.78	7.00	315	785
<i>Sphyraena acutipinnis</i>	144	42.45	0.54	20.6	56.2	144	435.42	17.62	45	885
<i>Sphyraena jello</i>	7	105.69	2.95	97.4	115	7	6009.29	492.26	4365	7600
<i>Sphyraena putnamae</i>	21	77.01	5.77	37.6	121	21	3229.05	570.50	275	8100
<i>Sphyraena genie</i>	31	74.00	2.47	49.8	97	31	2344.19	185.47	805	4065
<i>Sufflamen fraenatum</i>	4	34.05	0.20	33.7	34.4	4	895.00	34.64	835	955
<i>Terapon jarbua</i>	8	26.26	0.69	22.6	27.9	8	365.63	30.38	200	455
<i>Trachinotus africanus</i>	6	62.53	0.26	61.9	63.3	6	3775.00	129.67	3415	4125

	Trachinotus blochii	7	50.14	2.02	44	57.6	7	2527.14	251.80	1940	3455
	Trachurus indicus	165	17.27	0.25	13.1	27.7	165	72.82	3.72	26	260
	Trichiurus lepturus	188	87.10	0.83	68	119	188	620.72	19.04	230	1585
	Umbrina ronchus	34	36.44	1.70	27.6	62.5	34	768.82	122.59	260	2745
	Uraspis helvola	16	35.28	1.13	25.5	42	16	1016.19	81.88	464	1400
SWMon	Alectis indica	8	60.10	1.44	56.3	65.6	8	2635.00	101.22	2340	3070
	Alepes djedaba	12	28.23	0.67	25.1	29.9	12	353.33	26.29	230	415
	Argyrops spinifer	520	34.71	0.57	10	62.1	520	1278.29	49.21	30	5380
	Argyrosomus heinii	88	59.29	0.94	28.9	70	88	2496.82	85.16	240	3905
	Argyrosomus hololepidotus	7	71.84	3.28	64.4	86.5	7	4037.86	575.14	2625	7100
	Boops lineatus	43	17.35	0.26	15.5	22.5	43	95.35	4.86	72	195
	Carangoides chrysophrys	138	42.17	0.77	28.9	60.2	138	1571.88	77.67	380	3855
	Carangoides equula	73	29.98	0.41	19.7	38.1	73	544.73	20.09	145	1125
	Carangoides malabaricus	16	20.55	0.23	19.5	21.5	16	160.00	4.38	135	180
	Cheimerius nufar	673	26.45	0.34	10.4	59.3	673	478.82	21.09	55	3135
	Decapterus russelli	168	19.02	0.21	14.7	24.5	168	93.51	3.80	35	200
	Diagramma pictum	28	31.54	2.07	18.8	57.6	28	660.89	144.76	100	3120
	Drepane longimana	470	34.05	0.10	28.5	39.8	470	1320.14	11.79	720	2085
	Epinephelus diacanthus	284	34.97	0.59	19.1	54.1	284	765.32	37.85	75	2375
	Epinephelus epistictus	2	61.85	0.85	61	62.7	2	3732.50	562.50	3170	4295
	Epinephelus gabriellae	7	45.51	0.47	43.7	46.4	7	1212.14	29.34	1115	1305
	Epinephelus polylepis	27	36.62	1.59	19.9	53.1	27	819.26	113.60	100	2245
	Epinephelus radiatus	24	38.80	2.82	13.8	59.4	24	1171.04	192.16	30	3175
	Epinephelus stoliczkae	4	28.80	0.29	28.3	29.3	4	350.00	11.55	330	370
	Equulites elongatus	60	8.63	0.11	7.3	9.9	60	7.45	0.33	3	12
	Etrumeus teres	38	16.35	0.23	14.2	19	38	54.47	2.43	35	80
	Hoplostethus mediterraneus	603	14.55	0.05	11	17.6	603	71.16	0.92	30	135
	Kumococius rodericensis	106	15.20	0.26	11.3	28.8	106	34.67	1.53	15	95
	Lethrinus lentjan	9	33.34	1.20	30.5	40	9	747.22	92.21	555	1280
	Lethrinus nebulosus	280	44.44	0.42	25.6	62	280	1638.43	42.32	315	4195

Megalaspis cordyla	4	51.13	1.03	48.4	53	4	1358.75	108.27	1125	1605
Nemipterus japonicus	36	26.58	0.62	15.5	33.4	36	360.56	20.56	70	635
Nemipterus randalli	38	14.65	0.23	11.5	16.4	38	49.47	2.40	20	75
Neopinnula orientalis	8	17.03	0.65	14.5	19.6	8	40.63	4.71	24	59
Netuma bilineata	9	43.46	1.27	38.9	47.9	9	1298.89	103.80	850	1650
Otolithes ruber	50	38.05	0.51	31.8	49.6	50	589.50	26.12	315	1360
Pagellus affinis	202	17.43	0.24	11.6	26.9	202	118.86	5.69	27	420
Pelates quadrilineatus	65	18.84	0.11	17.4	21.7	65	107.54	2.20	85	160
Plectorhinchus flavomaculatus	4	49.05	1.11	45.9	50.9	4	1831.25	151.96	1390	2085
Plectorhinchus pictus	4	43.20	8.00	29.2	65.2	4	2273.75	1279.63	410	6000
Plectorhincus schotaf	6	33.87	0.72	31.9	36.8	6	697.50	54.54	555	940
Plicofollis dussumieri	22	36.84	1.25	32.5	54.6	22	882.95	121.17	590	2700
Plicofollis tenuispinis	3	37.90	1.37	35.2	39.7	3	880.00	87.61	705	975
Pomadasys commersonnii	1733	61.11	0.11	42.3	73.6	1733	3114.67	14.93	1055	5355
Pomadasys olivaceus	4	23.65	0.78	22.3	25	4	237.50	27.42	190	285
Pomadasys stridens	71	20.48	0.13	17.2	22.5	71	144.37	3.20	70	195
Pristipomoides filamentosus	5	21.58	0.21	21	22.1	5	147.00	7.52	135	170
Pterygotrigla hemisticta	2	18.80	0.90	17.9	19.7	2	95.00	5.00	90	100
Rastrelliger kanagurta	114	26.23	0.10	22.7	28.7	114	313.77	4.13	190	420
Rhabdosargus sarba	157	29.65	0.29	15.8	36.4	157	619.33	14.05	95	970
Sardinella longiceps	65	18.26	0.10	16.9	20.4	65	84.75	1.50	70	130
Saurida tumbil	139	41.59	0.36	29.2	54.7	139	790.43	23.04	210	2035
Scolopsis taeniata	6	29.07	0.51	27.5	30.2	6	450.00	31.14	355	520
Scomber japonicus	7	27.89	0.79	25.7	30.7	7	288.57	31.09	220	405
Scomberoides commersonianus	21	80.77	1.35	63	90.2	21	6400.00	262.04	4700	8800
Scomberomorus commerson	5	88.66	3.62	79.8	95	5	4577.00	470.27	3700	6275
Selar crumenophthalmus	26	24.80	0.44	21	27.7	26	249.62	13.51	145	355
Sphyraena acutipinnis	87	51.57	0.41	45	61.3	87	831.03	21.29	525	1330
Sphyraena flavicauda	5	23.48	0.17	23.2	23.9	5	88.60	2.20	85	94
Sphyraena jello	4	125.70	3.55	116	131	4	9500.00	722.26	7800	10700
Sphyraena putnamae	27	63.35	1.28	53.3	84	27	1597.41	79.61	885	2870

	Sphyraena qenie	2	101.50	18.50	83	120	2	4355.00	1845.00	2510	6200
	Trachinotus africanus	4	48.63	2.27	44.2	53.8	4	2273.75	273.17	1680	2980
	Trachurus indicus	936	22.71	0.09	17.7	27.6	936	169.97	1.56	75	285
	Trichiurus lepturus	37	90.81	2.91	35.9	118.7	37	876.35	65.73	30	1785
	Umbrina ronchus	26	29.25	0.61	24.2	34.7	26	322.50	20.48	170	545
	Uraspis helvola	6	25.13	2.96	20.1	35.4	6	480.00	153.89	230	1070
PostMon	Alectis ciliaris	15	52.37	1.52	45.6	64.5	15	2780.00	226.09	1975	3965
	Alectis indica	47	54.93	1.21	47.5	102	47	2344.79	296.87	1280	15600
	Alepes djedaba	133	29.23	0.21	24.9	34.8	133	424.62	9.35	245	675
	Argyrops spinifer	583	36.17	0.42	15.8	60	583	1255.69	39.13	90	4160
	Argyrosomus heinii	32	63.13	0.88	45	70	32	3108.59	106.57	1125	4090
	Carangoides chrysophrys	335	46.76	0.42	23	65	335	1910.04	43.25	300	4105
	Carangoides gymnostethus	18	51.30	1.81	36.9	61.3	18	2678.33	214.04	1165	4170
	Carangoides malabaricus	88	27.60	0.32	19.2	33.8	88	422.78	13.73	125	730
	Caranx sexfasciatus	4	67.30	1.85	64.1	70.5	4	4162.50	261.25	3710	4615
	Cheimerius nufar	191	33.12	0.48	19.4	52.5	191	757.15	35.30	130	2715
	Chlorurus strongylocephalus	3	52.37	4.67	47.7	61.7	3	2976.67	1086.67	1890	5150
	Decapterus russelli	222	19.16	0.08	17.2	23.2	222	84.69	0.96	65	150
	Diagramma pictum	204	48.29	0.62	25.7	67	204	1962.03	69.26	265	4850
	Drepane longimana	237	34.68	0.18	29.1	40.7	237	1423.06	18.84	860	2340
	Dussumieria elopoides	5	19.34	0.29	18.2	19.7	5	82.00	4.36	65	90
	Epinephelus coioides	3	106.73	9.27	88.2	116	3	23300.00	5600.00	12100	28900
	Epinephelus diacanthus	414	33.86	0.37	22.3	55.4	414	605.17	23.89	155	2260
	Epinephelus epistictus	4	39.18	4.78	34.4	53.5	4	1007.50	457.50	550	2380
	Epinephelus indistinctus	2	104.50	0.50	104	105	2	17400.00	500.00	16900	17900
	Epinephelus polylepis	4	51.03	9.12	41.9	78.4	4	2773.75	1618.75	1155	7630
	Gnathanodon speciosus	7	61.31	1.93	54.1	67.1	7	4834.29	359.30	3415	5900
	Kumococius rodericensis	21	14.34	0.42	11.8	18.5	21	26.19	2.67	15	55
	Lethrinus lentjan	20	29.85	1.05	19.4	37.1	20	528.00	49.57	155	945
	Lethrinus nebulosus	275	46.59	0.64	26.4	67.8	275	1999.05	68.46	335	4960
	Lutjanus lutjanus	31	31.38	0.42	23	34.8	31	526.77	18.92	185	760

Megalaspis cordyla	9	45.20	0.44	43.5	47.3	9	1037.78	31.63	960	1260
Moolgarda pedaraki	8	49.76	0.66	47	52.4	8	2095.63	75.58	1750	2420
Nemipterus japonicus	40	25.19	0.82	11.4	31	40	334.50	25.50	30	575
Nemipterus randalli	299	12.33	0.08	9.9	17.4	299	31.70	0.68	14	84
Netuma bilineata	9	47.09	0.86	43.5	50.7	9	1700.00	95.25	1315	2160
Pagellus affinis	30	13.63	0.29	10.9	16.1	30	47.67	3.52	25	80
Plectorhinchus pictus	18	52.82	1.71	42.1	63	18	3315.28	313.00	1510	5440
Plectorhincus schotaf	2	39.00	0.20	38.8	39.2	2	927.50	87.50	840	1015
Plicofollis dussumieri	34	54.26	0.46	50	61.9	34	2543.53	66.74	1965	3740
Plicofollis tenuispinis	195	30.53	0.19	26	42.5	195	451.97	9.82	255	1260
Polydactylus sextarius	2	46.60	0.90	45.7	47.5	2	1442.50	212.50	1230	1655
Pomadasys argenteus	3	50.13	1.01	48.2	51.6	3	1803.33	103.94	1625	1985
Pomadasys commersonnii	549	60.21	0.28	33	71.3	549	2819.48	30.42	470	4350
Pomadasys kaakan	35	46.93	1.08	33.6	58.7	35	1641.29	107.99	590	3065
Pristipomoides filamentosus	7	14.07	3.44	10.1	34.7	7	107.43	85.45	13	620
Psettodes erumei	13	45.71	1.90	34.4	54.3	13	1493.46	191.66	550	2370
Pseudorhombus arsius	13	33.62	0.92	27.7	37.8	13	370.77	33.24	185	565
Pterygotrigla hemisticta	84	16.18	0.34	10.6	24.1	84	63.75	4.92	10	225
Rachycentron canadum	5	70.00	1.34	67	73	5	3414.00	265.36	2890	4050
Rhabdosargus sarba	33	29.25	0.48	24.5	35.8	33	582.12	20.39	400	890
Saurida tumbil	44	40.95	0.76	30.2	55.7	44	760.23	46.10	280	1870
Saurida undosquamis	37	29.26	0.90	15	39.7	37	254.73	17.51	35	580
Scolopsis taeniata	74	23.41	0.38	13.9	29.1	74	242.91	10.00	50	415
Scomber japonicus	261	28.75	0.35	18.9	40.4	261	335.38	11.02	80	985
Scomberoides commersonianus	11	75.35	2.16	66.6	88	11	4880.45	371.37	3450	6970
Scomberoides tol	4	37.40	0.62	36.4	39.1	4	405.00	32.47	330	475
Scomberomorus commerson	4	56.05	0.55	55.1	57	4	1495.00	51.96	1405	1585
Sphyraena acutipinnis	17	48.14	1.77	38.9	65	17	687.94	77.92	320	1570
Sphyraena putnamae	69	80.10	0.48	71.6	87.6	69	2876.81	43.07	2275	3645
Sphyraena qenie	21	92.81	3.79	72	134	21	4099.76	542.25	2060	10500
Trachinotus africanus	54	47.94	0.80	39.5	58.4	54	2268.52	110.31	1235	4150

Trachurus indicus	379	23.83	0.16	13	38.6	379	210.04	4.97	31	825
Trichiurus lepturus	73	91.14	2.30	43.2	117	73	868.77	58.74	55	1810
Uraspis helvola	65	22.00	0.40	18.7	31.4	65	297.15	17.45	175	740

Appendix 2. Vertical reading of environmental data from the trawl sampling in the Omani coast of the Arabian Sea (2007-2008) used in this thesis. NEMon; Northeast Monsoon; PreMon; Pre-Southwest Monsoon; SWMon: Southwest Monsoon; PostMon: Post-Southwest Monsoon. No.: Number of samples.

Season	Temperature (°C)					Salinity (ppt)					Dissolved Oxygen (mll ⁻¹)				
	No.	Mean	SE	Min	Max	No.	Mean	SE	Min	Max	No.	Mean	SE	Min	Max
NEMon	493	20.57	2.17	18.31	23.38	493	36.56	0.18	36.35	36.86	493	1.73	2.28	0.02	9.89
	166	23.50	0.12	22.39	23.58	166	36.60	0.17	34.94	36.78	166	4.82	0.22	4.39	5.91
	239	23.54	0.01	23.51	23.56	239	36.75	0.08	36.42	36.84	239	4.37	0.26	4.15	5.35
	102	23.92	0.21	23.59	24.12	102	36.58	0.12	36.08	36.76	102	4.44	0.54	3.53	4.90
	230	23.52	1.00	17.72	24.09	230	36.51	0.59	27.90	37.26	230	2.74	1.09	0.22	6.09
	148	23.71	0.15	23.53	23.87	148	36.63	0.02	36.55	36.66	148	3.92	0.32	3.65	6.92
	159	23.40	0.12	23.14	23.51	159	36.56	0.03	36.46	36.61	159	4.56	0.18	4.48	5.83
	134	23.51	0.06	23.38	23.57	134	36.49	0.43	32.94	36.58	134	4.46	0.45	4.30	8.12
	329	21.19	1.87	18.86	24.09	329	36.42	0.13	36.24	36.79	329	1.34	1.73	0.00	6.23
	46	23.38	0.01	23.36	23.39	46	36.41	0.02	36.35	36.43	46	4.55	0.60	3.58	6.73
	54	22.78	0.01	22.75	22.78	54	36.49	0.18	35.29	36.54	54	4.81	0.43	4.55	6.68
	67	22.38	0.42	21.81	22.72	67	36.63	0.15	36.33	36.85	67	4.77	0.52	4.17	7.05
	134	22.74	0.41	22.02	23.09	134	36.56	0.24	34.35	36.85	134	5.19	0.35	4.45	7.15
	154	23.17	0.30	22.54	23.35	154	36.49	0.09	36.30	36.70	154	4.97	0.37	3.80	6.83
	312	23.46	0.12	23.12	23.57	312	36.58	0.05	36.27	36.68	312	4.54	0.32	3.22	7.04
	233	22.17	1.56	19.61	23.57	233	36.47	0.14	36.18	36.67	233	3.11	1.86	0.38	5.17
	282	22.09	1.50	19.67	24.39	282	36.41	0.14	36.12	36.65	282	2.44	1.90	0.13	8.02
	575	21.54	2.06	17.65	24.57	575	36.40	0.16	36.11	36.64	575	2.34	1.91	0.04	7.57
	143	22.18	1.60	19.04	24.36	143	36.37	0.19	35.19	36.57	143	3.09	1.67	0.23	5.08
	1000	17.16	2.65	13.62	22.54	1000	36.46	0.17	36.09	36.82	1000	1.10	2.18	0.02	7.95
	982	16.46	3.70	13.06	24.41	982	36.14	0.17	35.92	36.51	982	0.63	0.99	0.09	4.43
	18	24.31	0.54	23.76	25.21	18	35.99	1.45	30.18	36.39	18	4.74	0.04	4.69	4.87
	126	23.84	0.44	23.05	24.44	126	36.30	0.04	35.97	36.35	126	4.68	0.10	4.53	4.84
	258	24.64	0.79	23.54	25.78	258	36.24	0.43	31.36	36.33	258	4.60	0.15	4.37	4.83
	616	20.10	3.15	15.38	25.24	616	36.09	0.12	35.81	36.34	616	2.77	1.38	1.08	4.80

	344	21.19	3.81	15.01	25.46	344	36.07	0.20	35.77	36.35	344	1.10	0.80	0.45	2.91
	656	15.75	3.94	12.74	25.60	656	35.94	0.18	34.31	36.42	656	3.00	1.20	1.35	4.92
PostMon	453	23.41	1.81	21.40	27.54	453	35.77	1.09	33.51	37.73	453	2.56	1.48	0.58	4.59
	436	23.13	2.43	20.63	27.34	436	35.82	1.41	33.03	40.37	436	2.33	1.71	0.51	4.80
	111	26.88	1.54	23.54	28.09	111	34.96	1.51	32.67	36.83	111	3.86	0.76	1.89	4.53
	80	23.49	0.82	23.02	25.68	80	36.93	1.61	35.74	39.91	80	2.00	0.60	1.67	3.66
	428	24.87	1.42	23.75	27.82	428	35.97	0.82	34.48	38.18	428	2.50	1.02	1.41	4.51
	139	27.37	0.03	26.98	27.39	139	36.13	1.00	25.94	36.33	139	5.57	1.59	4.29	9.79
	296	27.49	0.25	27.14	27.77	296	36.43	0.49	28.00	36.54	296	6.52	1.80	4.38	10.00
	57	27.91	0.07	27.83	28.14	57	36.24	0.27	34.24	36.32	57	4.50	0.24	4.34	5.34
	273	26.85	0.26	26.49	27.62	273	36.30	0.04	36.25	36.41	273	3.72	0.48	2.80	4.73
	192	27.29	0.13	27.13	27.65	192	36.23	0.06	35.96	36.28	192	4.09	0.45	3.64	5.68
	163	27.47	0.11	27.27	27.61	163	36.21	0.11	35.74	36.33	163	4.14	0.36	3.66	4.88
	372	25.01	2.12	22.46	27.72	372	36.22	0.14	35.90	36.46	372	2.57	1.46	0.68	5.10
	236	21.36	3.72	17.30	28.07	236	36.27	0.13	36.10	36.53	236	0.61	0.71	0.19	2.77
	342	24.76	3.10	20.99	29.45	342	36.24	0.17	35.27	36.67	342	2.86	1.36	1.05	4.57
	355	23.86	3.47	19.74	29.23	355	36.18	0.18	33.83	36.44	355	2.68	1.48	0.75	4.63
	67	28.59	0.08	28.27	28.69	67	36.40	0.02	36.32	36.42	67	4.47	0.07	4.34	4.61
PreMon	277	17.24	0.16	17.08	18.00	277	36.23	0.08	36.02	36.31	277	0.11	0.01	0.12	0.07
	723	21.24	5.23	13.64	26.60	723	36.28	0.09	36.02	36.52	723	2.18	2.28	0.18	4.68
	307	20.29	3.18	16.16	26.06	307	36.13	0.10	35.91	36.44	307	1.26	1.67	0.00	4.56
	688	21.95	2.20	19.75	24.40	688	36.11	0.04	35.63	36.35	688	2.38	2.04	0.36	4.79
	5	22.04	0.00	22.04	22.05	5	36.11	0.00	36.11	36.12	5	7.57	1.15	6.32	9.23
	897	20.14	1.48	17.98	25.20	897	36.04	0.03	35.82	36.29	897	1.13	1.02	0.18	4.66
	103	29.55	0.03	29.47	29.62	103	36.31	0.02	36.21	36.35	103	4.35	0.01	4.31	4.36
	654	25.59	2.54	23.17	28.52	654	36.17	0.05	35.89	36.53	654	3.57	0.80	2.74	4.53
	346	27.02	3.35	18.26	28.80	346	36.23	0.16	33.67	36.32	346	3.77	1.43	0.20	4.57
SWMon	652	19.68	2.40	17.75	25.40	652	36.74	1.16	34.74	39.21	652	1.27	1.53	0.03	4.55
	1219	21.28	3.12	18.31	26.92	1219	35.64	1.03	33.69	39.99	1219	1.28	1.70	0.04	5.03
	446	22.57	2.73	19.52	26.30	446	35.50	1.40	32.96	40.16	446	2.25	1.83	0.45	4.85
	439	22.37	2.96	19.28	26.83	439	35.43	1.43	32.77	40.39	439	2.04	1.77	0.17	4.66

172	26.35	0.63	24.51	26.99	172	35.88	0.94	33.89	37.55	172	4.43	0.36	3.36	4.77
66	21.92	0.37	21.66	23.18	66	36.03	1.34	34.87	38.55	66	2.05	0.36	1.72	3.28
243	22.59	0.90	21.39	24.40	243	35.48	0.42	34.80	38.25	243	2.84	1.66	0.80	5.18
691	19.89	2.07	17.07	23.36	691	35.54	0.45	34.21	36.67	691	1.52	1.85	0.05	5.79
29	21.42	0.60	20.57	22.41	29	38.13	0.33	37.28	38.57	29	1.55	0.82	0.71	3.22
244	22.56	1.39	20.74	24.21	244	35.56	0.88	33.88	38.20	244	2.49	2.15	0.19	5.24
295	21.66	1.41	20.18	24.56	295	35.29	0.61	34.23	37.47	295	1.93	2.03	0.09	5.00
241	22.67	1.55	20.64	24.78	241	35.21	0.84	33.89	38.73	241	2.46	2.20	0.07	5.07
191	23.54	1.39	20.87	24.68	191	35.16	0.75	33.10	35.81	191	3.58	1.79	0.17	4.96
149	21.15	0.39	20.76	22.09	149	35.45	0.32	34.76	36.34	149	2.72	0.95	2.11	5.04
226	21.73	0.95	20.72	24.54	226	35.16	0.53	33.43	36.58	226	3.40	1.41	1.82	5.88
259	21.79	1.77	19.81	25.58	259	35.03	0.83	33.82	37.76	259	2.34	1.94	0.29	5.70
213	21.53	1.06	20.43	24.05	213	35.37	0.67	34.55	37.12	213	2.42	1.55	0.83	6.61
153	21.67	0.89	20.32	23.53	153	34.98	0.28	34.10	35.38	153	3.61	1.58	0.86	5.19
73	21.03	0.08	20.92	21.20	73	35.78	0.45	35.47	37.26	73	0.87	0.09	0.82	1.39
340	21.68	1.31	20.02	23.34	340	35.65	0.61	34.54	37.39	340	2.58	1.98	0.31	8.38
587	20.20	2.59	18.35	25.77	587	35.53	0.77	33.31	38.93	587	1.04	1.60	0.01	5.10
372	19.86	1.23	18.07	23.43	372	36.49	0.47	35.90	38.02	372	0.57	0.90	0.01	4.41
510	22.04	1.80	19.82	24.70	510	35.81	0.67	34.67	37.50	510	2.06	1.93	0.17	5.28
118	23.36	0.93	21.33	24.24	118	35.21	0.53	34.45	36.38	118	3.51	1.50	0.82	7.33
186	22.54	1.50	21.59	25.95	186	36.30	0.12	35.17	36.39	186	1.98	0.89	1.47	4.51
744	24.43	3.13	20.55	28.02	744	36.27	0.09	35.66	36.54	744	2.96	1.44	0.91	4.60
70	28.21	0.04	28.15	28.29	70	36.22	0.02	36.06	36.23	70	4.44	0.02	4.38	4.47
162	24.04	1.46	22.08	27.29	162	36.35	0.09	36.19	36.51	162	2.98	1.13	1.28	5.02
810	21.18	3.40	16.79	27.36	810	36.37	0.11	36.02	36.67	810	1.46	1.65	0.02	4.64
28	23.42	1.73	21.92	26.14	28	36.28	0.59	33.49	36.67	28	3.33	1.30	1.82	4.95
13	23.02	0.38	22.06	23.25	13	36.28	0.06	36.23	36.47	13	0.26	0.52	0.23	1.26
987	20.94	1.93	18.88	23.45	987	36.14	0.06	35.05	36.31	987	1.77	2.39	0.23	5.03
694	17.29	0.82	16.68	20.46	694	36.14	0.34	35.44	37.73	694	0.30	0.74	0.06	3.80
306	17.65	1.91	15.80	22.27	306	35.31	0.61	33.73	35.87	306	0.76	1.33	0.11	4.95
305	16.39	0.19	16.25	17.08	305	35.91	0.21	35.55	36.53	305	0.32	0.43	0.09	2.10

509	16.80	0.54	16.46	19.27	509	35.74	0.43	34.36	36.74	509	0.45	0.98	0.07	5.25
186	17.81	0.71	17.23	19.89	186	35.37	0.42	34.50	35.80	186	0.96	1.45	0.13	5.20
439	18.37	2.10	15.49	23.41	439	36.66	0.33	36.35	38.31	439	0.76	1.41	0.05	4.94
561	15.86	3.06	12.96	25.57	561	35.25	0.65	32.62	35.98	561	0.45	0.94	0.11	4.70
1000	16.63	1.49	14.64	19.57	1000	35.85	0.51	34.26	36.79	1000	0.91	0.63	0.31	2.63
