Low Oxygen Zones Predict Future Condition of Fish Under Climate Change

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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

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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 conditions 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

1 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 (CO_2) (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 km^2 with depths ranging to 2990 m. Mean environmental conditions are 24 °C temperature and 4 ml^{-1} O_2, 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 ml^{-1} (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 1327 $mgCm^{-2}$ day^{-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 (Reichart et al. 1997; Schulz et al. 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 dial 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 mll^{-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. A spatially extensive and fisheries-independent data were analyzed 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.

2 Data Resources and Analysis

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 backstrop. 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 Madrakah (Region B), Ra’s al Madrakah to Ra’s Hasik (Region C), and Ra’s Hasik to the Yemen border (Region D) (Fig. 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 (20–50 m); DS2 (51–100 m); DS3 (101–150 m); and DS4 (151–250 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 (°C), dissolved oxygen (mll^{-1}), salinity (ppt), and depth (m). At sea, specimens were classified to genus and species using the FAO species catalog (Nielsen 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). 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

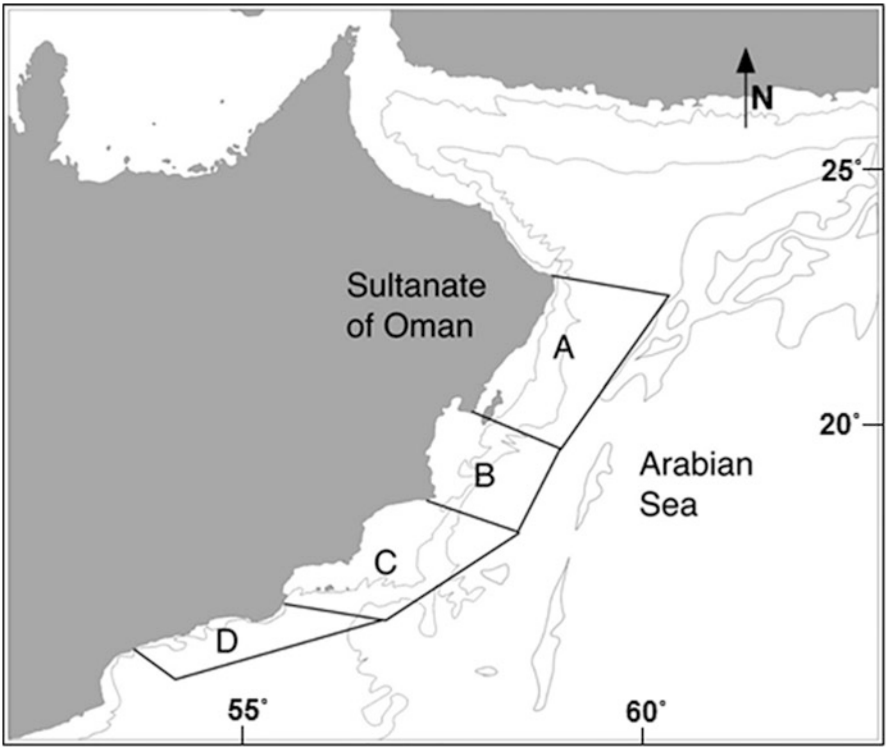

Fig. 1 Study area and regions where A: Ra's al Hadd to Masirah Island; B: Masirah Island to Ra's al Madrakah, C: Ra's alMadrakah to Ra's Hasik; D: Ra's Hasik to Yemen border

from the survey database. Length and weight were $\log_{10}$ transformed, and regression coefficients (R^2) were estimated for $\log_{10}$(weight) as a function of $\log_{10}$(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 Wilcoxon signed-rank test 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).

3 Results Obtained

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 °C ± 3.87 SD (Table 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 ppt ± 0.66 SD, and mean bottom dissolved oxygen was 0.41 mll^{-1} ± 0.25 SD (Table 1). The minimum surveyed depth was 13 m in region A, and the maximum depth was 814 m in region C (Table 1), with a mean value of 63.6 ± 95.7 SD across all samples. Depths sampled were similar in regions B and C and substantially deeper in region D (Table 1).

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

Table 1 Descriptive statistics for environmental variables of the Northwest Arabian Sea (n = 38,928) 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^{-1})	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 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	*P*
a	0.037	0.023	0.028
b	0.293	0.299	0.11

Table 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	*P*
Cheimerius nufar	2321	0.17
Plectorhinchus schotaf	120	0.28
Drepane longimana	2257	0.0001
Pagellus affinis	1014	0.026
Pomadasys commersonnii	4131	0.0001
Argyrops spinifer	4271	0.0009
Carangoides equula	271	0.025

to three species. The sparid *Argyrops spinifer* and the haemulid *Pomadasys commersonnii* were the most abundant species, with 4130 (10.3%) and 4110 (10.2%) individuals, respectively, followed by 3171 (7.9%) individuals of the lethrinidae, *Lethrinus nebulosus*. Only nine elasmobranch species (2504 individuals) were included in the analysis based on abundance (Appendix). 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). 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 2). However, there was no difference in the slopes (Wilcoxon signed test, $P = 0.11$; Table 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 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 (Fig. 2; Table 4). Three out of five (*Drepane longimana*, *Pagellus affinis*, and *Pomadasys commersonnii*) showed lower allometric coefficients with lower latitude (Fig. 2),

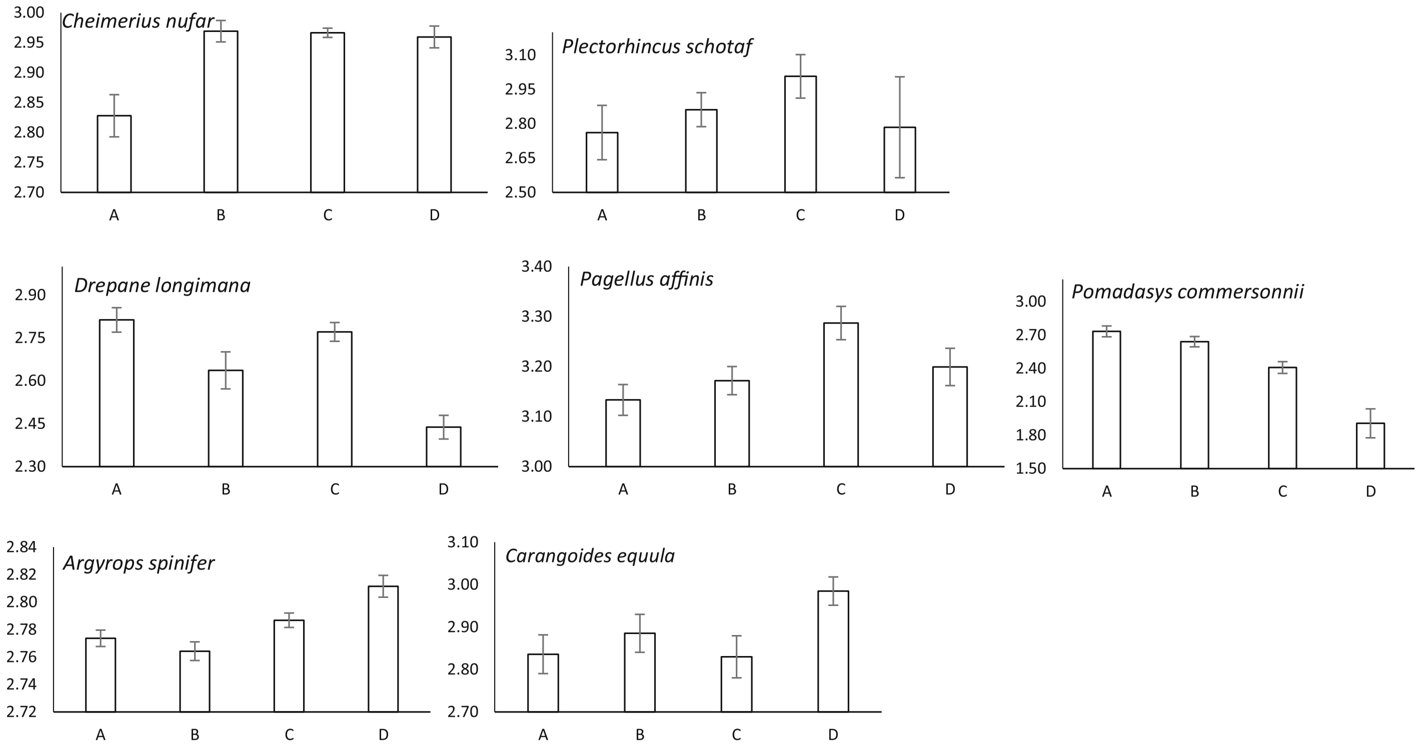

Fig. 2 Slopes of the regressions ± standard errors of the slopes for *Argyrops spinifer*, *Carangoides equula*, *Drepane longimana*, *Pagellus affinis* and *Pomadasys commersonnii* across the four regions in the Northwest Arabian Sea. Y axis for all plots represent the *b* value (slope)

Table 4 Length–weight relationships parameters of the five species across the studied regions in Northwest Arabian Sea

Species	Region	*N*	R^2	*p*	*a*	SE	*b*	SE
Argyrops spinifer	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
Carangoides equula	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
Drepane longimana	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
Pagellus affinis	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
Pomadasys commersonnii	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

R^2 = coefficients of determination, a = intercept, b = slope, and SE = standard error

whereas the remaining two (*Argyrops spinifer*, *Carangoides equula*) showed an increase of the allometric coefficient at lower latitudes.

4 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, Table 5; 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 among 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 affect 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 mll^{-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., hemoglobins or hemocyanins) 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 others 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 was found for Macrouridae which found in all regions, whereas Ipnopidae and Squalidae scatarted 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 Hallaniyat Island (regions B–D), with overfishing by foreign trawlers driving decreases in landings (McIlwain et al. 2006) species 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 N_2O, 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.

Appendix

Table 5 Length–weight regression coefficients for 94 species of fishes, sharks, and rays of the Northwest Arabian Sea

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

(continued)

Table 5 (continued)

Family	Species	Sample size	Min FL (cm)	Max FL (cm)	*a*	*b*	R^2
Carcharhinidae	*Rhizoprionodon acutus*	292	35.5	89	0.0071	2.8926	0.9424
Clupeidae	***Sardinella albella***	30	9.7	13.8	0.0139	2.8731	0.9698
	Sardinella longiceps	82	13.4	20.4	0.0005	4.1468	0.8184
	Sardinella sindensis	401	6.1	19.8	0.0062	3.2405	0.9798
Cynoglossidae	***Cynoglossus carpenteri***[a]	51	15.7	21.8	0.029	2.4361	0.8757
Dasyatidae	***Himantura gerrardi***[a]	355	17.2	95	0.0424	2.9337	0.9918
	Himantura uarnak[a]	66	22.6	146	0.1127	2.7023	0.9883
Drepanidae	***Drepane longimana***	2257	22	43.2	0.0795	2.7554	0.8984
Dussumieriidae	*Dussumieria elopoides*	249	4.8	19.6	0.0041	3.3196	0.9764
	Etrumeus sadina	150	11.7	21.1	0.0076	3.1385	0.9073
Engraulidae	*Encrasicholina heteroloba*	56	4.9	8.9	0.0129	2.8124	0.8094
	Thryssa vitrirostris	66	9.1	15.2	0.0135	2.8115	0.924
Gerreidae	*Gerres filamentosus*	85	14.4	22.3	0.0664	2.6037	0.9266
Gymnuridae	***Gymnura poecilura***[a]	301	27.8	95	0.0044	3.1768	0.9888
Haemulidae	*Diagramma pictum*	251	10.9	73	0.0244	2.875	0.9959
	Plectorhinchus flavomaculatus	35	39.3	51.1	0.0254	2.8747	0.9572
	Plectorhinchus pictus	35	29.2	65.2	0.0118	3.1507	0.9827
	Plectorhinchus schotaf	120	21.4	61.9	0.0087	3.2006	0.9309
	Pomadasys commersonnii	4110	33	78	0.1081	2.4841	0.9074
	Pomadasys kaakan	43	33.6	58.7	0.0225	2.9023	0.9669
	Pomadasys maculatus	83	14.4	57.9	0.0414	2.7443	0.9914
	Pomadasys stridens	167	15.6	22.5	0.0427	2.6932	0.898
Leiognathidae	*Equulites elongates*	131	5	9.9	0.0124	2.9464	0.8715
	Leiognathus oblongus	200	3.5	11.8	0.005	3.6028	0.9411
Lethrinidae	*Lethrinus lentjan*	107	10.4	41.1	0.0277	2.8953	0.9785
	Lethrinus microdon	99	25.6	58.9	0.0172	2.9684	0.9793
	Lethrinus nebulosus	3171	22.2	67.8	0.0274	2.8849	0.9901

(continued)

Table 5 (continued)

Family	Species	Sample size	Min FL (cm)	Max FL (cm)	*a*	*b*	R^2
Lutjanidae	*Lutjanus lutjanus*	295	16.9	33.8	0.0169	2.9817	0.9482
	Pristipomoides filamentosus	129	10.1	71	0.0081	3.1692	0.988
Mullidae	*Parupeneus rubescens*	50	14.6	34.7	0.018	3.026	0.9844
Myliobatidae	***Aetomylaeus nichofii***[a]	180	22.8	61.1	0.0054	3.2198	0.9794
	Rhinoptera jayakari[a]	194	52.7	87	0.0144	3.0448	0.8739
Nemipteridae	*Nemipterus japonicus*	220	9.5	33.4	0.0182	2.9952	0.9923
	Nemipterus rally	1704	6.1	20.2	0.0038	3.5779	0.9262
	Parascolopsis aspinosa	196	5.1	20.5	0.067	2.508	0.9223
	Parascolopsis eriomma	36	13.6	30.6	0.0148	3.0878	0.988
	Scolopsis taeniata	98	7.3	30.9	0.0133	3.0896	0.9926
Ostraciidae	*Tetrosomus gibbosus*	45	15.8	23.6	0.0635	2.7452	0.8301
Paralichthyidae	*Pseudorhombus arsius*	150	9.1	39.4	0.0084	3.0459	0.9838
Pinguipedidae	***Parapercis alboguttata***	67	7.2	18	0.0073	3.0877	0.9637
Platycephalidae	***Kumococius rodericensis***	1009	6.6	32.2	0.013	2.851	0.9456
Plotosidae	*Plotosus limbatus*	42	41.5	58.1	0.0312	2.5644	0.8013
Priacanthidae	*Priacanthus hamrur*	96	16.3	24.8	0.0011	3.845	0.8722
Psettodidae	*Psettodes erumei*	82	11.9	63.9	0.0033	3.3746	0.986
Rhinobatidae	***Rhinobatos punctifer***[a]	311	24.3	91	0.0078	2.8112	0.9911
Sciaenidae	***Argyrosomus heinii***	134	16.6	73.8	0.0299	2.7599	0.9542
	Otolithes ruber	321	27.9	52.5	0.0157	2.8748	0.9771
Scombridae	*Rastrelliger kanagurta*	117	8.2	28.7	0.0061	3.3155	0.9966
	Scomber japonicus	290	18.9	40.4	0.0074	3.1573	0.9909
Serranidae	*Epinephelus diacanthus*	868	19.1	55.4	0.0104	3.0766	0.9882
	Epinephelus polylepis	99	19.9	121	0.0036	3.3317	0.988
	Epinephelus radiates	42	13.8	60.1	0.0063	3.2158	0.994

(continued)

Table 5 (continued)

Family	Species	Sample size	Min FL (cm)	Max FL (cm)	*a*	*b*	R^2
Siganidae	*Siganus canaliculatus*	166	23.8	41.2	0.0488	2.7104	0.9407
Sparidae	*Argyrops spinifer*	4130	8.8	62.1	0.0443	2.8004	0.9949
	Boops lineatus	64	7.5	21.4	0.0036	3.5163	0.9669
	Cheimerius nufar	2297	10.4	59.3	0.0321	2.8489	0.9819
	Pagellus affinis	887	6.3	30.7	0.02	2.9834	0.9731
	Rhabdosargus sarba	411	15.8	40.8	0.0513	2.7559	0.9491
Sphyraenidae	***Sphyraena acutipinnis***	122	21.6	60.7	0.0086	2.8734	0.9463
	Sphyraena flavicauda	110	9.2	30	0.0125	2.8255	0.9528
	Sphyraena putnamae	152	59.6	121	0.0289	2.6181	0.8754
	Sphyraena qenie	100	40.1	101.2	0.03	2.6002	0.978
Synodontidae	*Saurida tumbil*	297	8	57.1	0.0126	2.9502	0.9916
	Saurida undosquamis	626	6.5	38.8	0.0039	3.2583	0.9839
	Synodus dermatogenys	72	8	14.1	0.0008	4.0426	0.8965
	Trachinocephalus myops	48	7.6	15.4	0.0045	3.3585	0.9397
Terapontidae	*Terapon jarbua*	58	16.2	31.9	0.0133	3.0854	0.9707
Trachichthyidae	*Hoplostethus mediterraneus mediterraneus*	178	10.9	17.6	0.0686	2.6253	0.8381
Triakidae	***Iago omanensis***	579	18.4	80	0.0021	3.1116	0.9801
	Mustelus mosis	175	65.5	105	0.0001	3.866	0.9264
Trichiuridae	*Trichiurus lepturus*[b]	816	35.9	119	0.0001	3.5812	0.9364
Triglidae	***Lepidotrigla omanensis***	120	10.4	16.5	0.0105	3.0751	0.8357
	Pterygotrigla hemisticta	1025	6.8	25.1	0.0091	3.1367	0.9343

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

References

Al-Mamry JM, McCarthy ID, Richardson CA, Ben Meriem S (2009) Biology of the king soldier bream (*Argyrops spinifer*, Forsskål 1775; Sparidae), from the Arabian Sea, Oman. J Appl Ichthyol 25:559–564

Al-Masroori H, Al-Oufi H, McIlwain JL, McLean E (2004) Catches of lost fish traps (ghost fishing) from fishing grounds near Muscat, Sultanate of Oman. Fish Res 69:407–414

Al-Oufi H, McLean E, Palfreman A (2000) Observations upon the Al-Batinah artisanal fishery, the Sultanate of Oman. Mar Policy 24:423–429

Al-Rasady I, Govender A, Al-Jufaili SM (2011) Reproductive biology of longnose trevally (*Carangoides chrysophrys*) in the Arabian Sea, Oman. Environ Biol Fish 93:177–184

Altabet MA, Francois R, Murray DW, Prell WL (1995) Climate-related variations in denitrification in the Arabian Sea from sediment 15N/14N ratios. Nature 373:506–509

Bange HW, Andreae MO, Lal S, Law CS, Naqvi SWA, Patra PK, Rixen T, Upstill-Goddard RC (2001) Nitrous oxide emissions from the Arabian Sea: a synthesis. Atmos Chem Phys Discuss 1:167–192

Barber RT, Marra J, Bidigare RC, Codispoti LA, Halpern D, Johnson Z, Latasa M, Goericke R, Smith SL (2001) Primary productivity and its regulation in the Arabian Sea during 1995. Deep-Sea Res II Top Stud Oceanogr 48:1127–1172

Borsuk ME, Higdon D, Stow CA, Reckhow KH (2001) A Bayesian hierarchical model to predict benthic oxygen demand from organic matter loading in estuaries and coastal zones. Ecol Model 143:165–181

Brander K (2010) Impacts of climate change on fisheries. J Mar Syst 79:389–402

Breitburg D (2002) Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries 25:767–781

Brink K, Arnone R, Coble P, Flagg C, Jones B, Kindle J, Lee C, Phinney D (1998) Monsoons boost biological productivity in Arabian Sea. EOS Trans Am Geophys Union 79:165–165

Buentello JA, Gatlin DM, Neill WH (2000) Effects of water temperature and dissolved oxygen on daily feed consumption, feed utilization and growth of channel catfish (*Ictalurus punctatus*). Aquaculture 182:339–352

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish 10:235–251

Childress JJ, Nygaard M (1974) Chemical composition and buoyancy of midwater crustaceans as function of depth of occurrence off Southern California. Mar Biol 27:225–238

Childress JJ, Seibel BA (1998) Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. J Exp Biol 201:1223–1232

Chu KH, Chenb QC, Huangb LM, Wong CK (1995) Morphometric analysis of commercially important penaeid shrimps from the Zhujiang estuary, China. Fish Res 23:83–93

De Robertis A, Eiane K, Rau G (2001) Eat and run: anoxic feeding and subsequent aerobic recovery by Orchomene obtusus in Saanich Inlet, British Columbia, Canada. Mar Ecol Prog Ser 219:221–227

Diaz RJ (2001) Overview of hypoxia around the world. J Environ Qual 30:275–281

Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. Science 321:926–929

Feary DA, Burt JA, Bauman AG, Usseglio P, Sale PF, Cavalcante GH (2010) Fish communities on the world's warmest reefs: what can they tell us about the effects of climate change in the future? J Fish Biol 77:1931–1947

Fouda MM, Hermosa GV Jr, Al-Harthi SM (1998) Status of fish biodiversity in the Sultanate of Oman. Ital J Zool 65:521–525

Froese R (2006) Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. J Appl Ichthyol 22:241–253

Froese R, Pauly D (eds) (2015) FishBase. World Wide Web electronic publication. www.fishbase.org. (10/2015)

Gibson R, Atkinson R (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanogr Mar Biol Annu Rev 41:1–45

Goes JI, Thoppil PG, Gomes H do R, Fasullo JT (2005) Warming of the Eurasian landmass is making the Arabian Sea more productive. Science 308:545–547

Gonçalves JMS, Bentes L, Lino PG, Ribeiro J, Carkrio AVM, Erzini K (1997) Weight-length relationships for selected fish species of the small-scale demersal fisheries of the south and south-west coast of Portugal. Fish Res 30:253–256

Grimes CB, Finucane JH (1991) Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. Mar Ecol Prog Ser 75:109–119

Halpern BS, McLeod KL, Rosenberg AA, Crowder LB (2008) Managing for cumulative impacts in ecosystem-based management through ocean zoning. Ocean Coast Manag 51:203–211

Henderson AC, McIlwain JL, Al-Oufi HS, Al-Sheili S (2007) The Sultanate of Oman shark fishery: Species composition, seasonality and diversity. Fish Res 86(2-3):159–168

Herring PJ, Fasham MJR, Weeks AR, Hemmings JCP, Roe HSJ, Pugh PR, Holley S, Crisp NA, Angel MV (1998) Across-slope relations between the biological populations, the euphotic zone and the oxygen minimum layer off the coast of Oman during the southwest monsoon (August, 1994). Prog Oceanogr 41:69–109

Human BA, Al-busaidi H (2008) Length and weight relationships for 31 species of fishes caught by trawl off the Arabian Sea coast of Oman. Agric Mar Sci 13:43–52

Jennings S, Grandcourt EM, Polunin NVC (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles? Reef fish communities. Coral Reefs 14:225–235

Jutfelt F, Hedgärde M (2013) Atlantic cod actively avoid CO2 and predator odour, even after long-term CO2 exposure. Front Zool 10:81

Keeling RE, Körtzinger A, Gruber N (2010) Ocean deoxygenation in a warming world. Annu Rev Mar Sci 2:199–229

Khalfallah M, Zylich K, Zeller D, Pauly D (2015) Fisheries Centre. In reconstruction of marine fisheries catches for Oman (1950–2010). Fisheries Centre working paper #2015-89, University of British Columbia, Vancouver, 11p

Kinzer J, Böttger-Schnack R, Schulz K (1993) Aspects of horizontal distribution and diet of myctophid fish in the Arabian Sea with reference to the deep water oxygen deficiency. Deep-Sea Res II Top Stud Oceanogr 40:783–800

Koops MA, Hutchings JA, McIntyre TM (2004) Testing hypotheses about fecundity, body size and maternal condition in fishes. Fish Fish 5:120–130

Koslow J, Goericke R, Lara-Lopez A, Watson W (2011) Impact of declining intermediate-water oxygen on deepwater fishes in the California current. Mar Ecol Prog Ser 436:207–218

Kumar SP, Roshin RP, Narvekar J, Kumar PKD, Vivekanandan E (2009) Response of the Arabian Sea to global warming and associated regional climate shift. Mar Environ Res 68:217–222

Le Quéré C, Rödenbeck C, Buitenhuis ET, Conway TJ, Langenfelds R, Gomez A, Labuschagne C, Ramonet M, Nakazawa T, Metzl N et al (2007) Saturation of the Southern Ocean CO$_2$ sink due to recent climate change. Science 316:1735–1738

Levin LA (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanogr Mar Biol Annu Rev 41:1–45

Madhupratap M, Kumar SP, Bhattathiri PMA, Kumar MD, Raghukumar S, Nair KKC, Ramaiah N (1996) Mechanism of the biological response to winter cooling in the northeastern Arabian Sea. Nature 384:549–552

Madhupratap M, Gopalakrishnan TC, Haridas P, Nair KKC (2001) Mesozooplankton biomass, composition and distribution in the Arabian Sea during the Fall Intermonsoon: implications of oxygen gradients. Deep-Sea Res II Top Stud Oceanogr 48:1345–1368

MAFASR (2012) Catch statistics of the year 2012 in the Sultanate of Oman. Ministry of Agriculture and Fisheries

Matear RJ (2003) Long-term changes in dissolved oxygen concentrations in the ocean caused by protracted global warming. Glob Biogeochem Cycles 17:1125

McIlwain JL, Claereboudt MR, Al-Oufi HS, Zaki S, Goddard JS (2005) Spatial variation in age and growth of the kingfish (*Scomberomorus commerson*) in the coastal waters of the Sultanate of Oman. Fish Res 73:283–298

McIlwain J, Hermosa GV, Claereboudt M, Al-Oufi HS, Al-Awi M (2006) Spawning and reproductive patterns of six exploited finfish species from the Arabian Sea, Sultanate of Oman. J Appl Ichthyol 22:167–176

McKoy J, Bagley N, Gauthier S, Devine J (2009) Fish resources assessment survey of the Arabian sea coast of Oman. Technical report 1. Fish resources of the Arabian Sea coasts of Oman: project summary. Final report prepared for the Ministry of Fish Wealth, Sultanate of Oman. Bruce Shallard and Associates, Wellington, 177 pp

Mee LD (1992) The Black Sea in crisis: a need for concerted international action. Ambio 21:278–286

Morrison J, Codispoti L, Smith SL, Wishner K, Flagg C, Gardner WD, Gaurin S, Naqvi SW, Manghnani V, Prosperie L et al (1999) The oxygen minimum zone in the Arabian Sea during 1995. Deep-Sea Res II Top Stud Oceanogr 46:1903–1931

Murphy BR, Willis DW, Springer TA (1991) The relative weight index in fisheries management: status and needs. Fisheries 16:30–38

Naqvi SWA, Moffett JW, Gauns MU, Narvekar PV, Pratihary AK, Naik H, Shenoy DM, Jayakumar DA, Goepfert TJ, Patra PK et al (2010) The Arabian Sea as a high-nutrient, low-chlorophyll region during the late Southwest Monsoon. Biogeosciences 7:2091–2100

Nielsen JG, Cohen DM, Markle DF, Robins CR (1999) FAO species catalogue. Ophidiiform fishes of the world (*Order Ophidiiformes*)

Nilsson GE, Ostlund-Nilsson S (2008) Does size matter for hypoxia tolerance in fish? Biol Rev Camb Philos Soc 83:173–189

Owens NJP, Law CS, Mantoura RFC, Burkill PH, Llewellyn CA (1991) Methane flux to the atmosphere from the Arabian Sea. Nature 354:293–296

Pauly D, Palomares M (2005) Fishing down marine food web: it is far more pervasive than we thought. Bull Mar Sci 76:197–211

Peterson CH, Summerson HC, Thomson E, Lenihan HS, Grabowski J, Manning L, Micheli F, Johnson G (2000) Synthesis of linkages between benthic and fish communities as a key to protecting essential fish habitat. Bull Mar Sci 66:759–774

Petrakis G, Stergiou KI (1995) Weight-length relationships for 33 fish species in Greek waters. Fish Res 21:465–469

Pichavant K, Person-Le-Ruyet J, Bayon NL, Severe A, Roux AL, Boeuf G (2001) Comparative effects of long-term hypoxia on growth, feeding and oxygen consumption in juvenile turbot and European sea bass. J Fish Biol 59:875–883

Piet G, Jennings S (2005) Response of potential fish community indicators to fishing. ICES J Mar Sci 62:214–225

Piontkovski S, Al-Azri A, Al-Hashmi K (2011) Seasonal and interannual variability of chlorophyll-a in the Gulf of Oman compared to the open Arabian Sea regions. Int J Remote Sens 32:7703–7715

Quiroga E, Sellanes J, Arntz WE, Gerdes D, Gallardo VA, Hebbeln D (2009) Benthic megafaunal and demersal fish assemblages on the Chilean continental margin: the influence of the oxygen minimum zone on bathymetric distribution. Deep-Sea Res II Top Stud Oceanogr 56:1112–1123

Reichart GJ, Den Dulk M, Visser HJ, Van Der Weijden CH, Zachariasse WJ (1997) A 225 kyr record of dust supply, paleoproductivity and the oxygen minimum zone from the Murray Ridge (Northern Arabian Sea). Palaeogeogr Palaeoclimatol Palaeoecol 134:149–169

Rijnsdorp AD, Peck MA, Engelhard GH, Mollmann C, Pinnegar JK (2009) Resolving the effect of climate change on fish populations. ICES J Mar Sci 66:1570–1583

Sanders NK, Childress JJ (1990) Adaptations to the deep-sea oxygen minimum layer: oxygen binding by the hemocyanin of the bathypelagic mysid, *Gnathophausia ingens* Dohrn. Biol Bull 178:286

Schulz H, von Rad U, Erlenkeuser H (1998) Correlation between Arabian Sea and Greenland climate oscillations of the past 110,000 years. Nature 393:54–57

Siddeek MSM, Fouda MM, Hermosa GV (1999) Demersal fisheries of the Arabian Sea, the Gulf of Oman and the Arabian Gulf. Estuar Coastal Shelf Sci 49:87–97

Siegel S (1956) Nonparametric statistics for the behavioural sciences. McGraw-Hill, Sidney Siegel

Taylor R (1990) Interpretation of the correlation coefficient: a basic review. J Diagnostic Med Sonogr 6:35–39

Venturelli PA, Shuter BJ, Murphy CA (2009) Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. Proc Biol Sci 276:919–924

Von Rad U, Schulz H, Riech V, Den Dulk M, Berner U, Sirocko F (1999) Multiple monsoon-controlled breakdown of oxygen-minimum conditions during the past 30,000 years documented in laminated sediments off Pakistan. Palaeogeogr Palaeoclimatol Palaeoecol 152:129–161

Walters RJ, Hassall M (2006) The temperature-size rule in ectotherms: may a general explanation exist after all? Am Nat 167:510–523

Willis DW, Murphy BR, Guy CS (1993) Stock density indices: development, use, and limitations. Rev Fish Sci 1:203–222

Wootton RJ (1985) Energetics for reproduction. In: Tytler P, Calow P (eds) Fish energetics new perspectives. Croom Helm, London, pp 231–254

Wu RSS (2002) Hypoxia: from molecular responses to ecosystem responses. Mar Pollut Bull 45:35–45

Wu RSS, Zhou BS, Randall DJ, Woo NYS, Lam PKS (2003) Aquatic hypoxia is an endocrine disruptor and impairs fish reproduction. Environ Sci Technol 37:1137–1141

Zar JH (1999) Biostatistical analysis. Prentice Hall, Upper Saddle River

Zhou X, Guo Z, Qin L (2010) Natural and anthropogenic impacts on the Asian monsoon precipitation during the 20th century. Sci China Earth Sci 53:1683–1688