Influence of Climate-Driven Low Oxygen Zones on Fish Biodiversity: A Case Study from the Arabian Sea

Issam Humaid Al-Rasady, Jessica J. Meeuwig, and Michel R. Claereboudt

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 the 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

---

I. H. Al-Rasady (✉)
School of Biological Sciences and the UWA Oceans Institute, The University of Western Australia, Perth, WA, Australia

Marine Sciences and Fisheries Centre, Ministry of Agriculture and Fisheries Wealth, Muscat, Sultanate of Oman

J. J. Meeuwig
School of Biological Sciences and the UWA Oceans Institute, The University of Western Australia, Perth, WA, Australia

M. R. Claereboudt
Department of Marine Science and Fisheries, College of Agriculture and Marine Sciences, Sultan Qaboos University, Al-Khod, Sultanate of Oman

L. A. Jawad (ed.), *The Arabian Seas: Biodiversity, Environmental Challenges and Conservation Measures*, https://doi.org/10.1007/978-3-030-51506-5_29

environmental variables. Climate change is expected to strengthen the SWMon, which will expand the OMZ. As the SWMon period and its expanded OMZ are 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

1 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 poleward 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 forces fish to utilise 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 and 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 l^{-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 ml l^{-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 and age at maturity (Vaquer-Sunyer and Duarte 2008; Pauly 2010). These sublethal effects 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 behavioural 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 poleward 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 l^{-1} (Levin et al. 2000). The Southwest Monsoon drives vertical nutrient fluxes via coastal upwelling that enhances 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 (Fouda et al. 1998), Al-Jufaili et al. (2010) recorded a total of 1176 marine fish species, 1138 species were identified by Fouda et al. (1998), 930 described by Randall (1995), and 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, which include India, Oman, Yemen and the East coast of Africa. Over 364 marine species support the commercial fisheries in the Arabian Gulf, Oman and the Arabian Sea (Siddeek et al. 1999).

In this study, the data from a research survey across the Northwest Arabian Sea off the coast of Oman were used 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. Further, the relationship between dissolved oxygen and other environmental variables were considered with respect to their influence on fish biodiversity.

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 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 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

Table 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

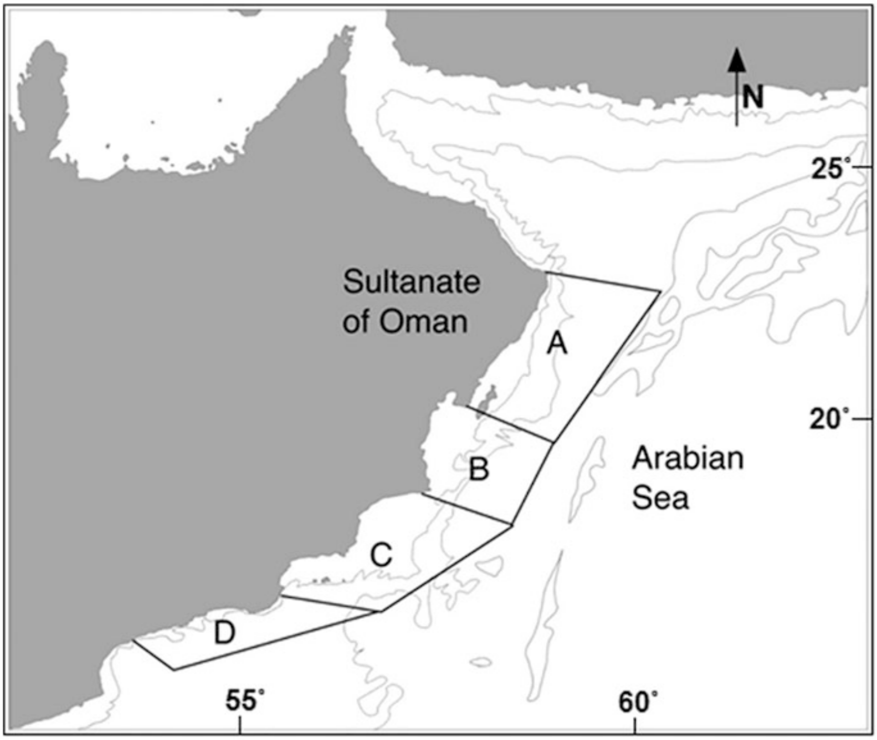

Fig. 1 Classification of the regions in the study area. A, Ra's al Hadd to Masirah Island; B, Masirah Island to Ra's Al Madrakah, C, Ra's Al Madrakah to Ra's Hasik; D, Ra's Hasik to Yemen border

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 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 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 four depth strata were DS1 (5–50 m), DS2 (51–100 m), DS3 (101–150 m) and DS4 (151–250 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 (°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 programme (Version 9, Colwell et al. 2004). The programme 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 among the samples and avoid redundancy of these related metrics and a new Euclidean distance matrix calculated on to normalised values of the 12 biodiversity indices.

Observed species richness and total abundance for each trawl were also calculated. Euclidean distance matrices were calculated for each of these variables given their continuous nature. Data were not normalised 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 was 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 three-way interaction, and followed by the two-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 between the different variables in the factors.

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 overfitting and preserve biological realism.

3 Results Obtained

The fitted species accumulation curve suggests that our overall 764 sampling effort was reasonable with approximately 207 species predicted to be present (Fig. 2). The species accumulation curve increased rapidly up to point of approximately

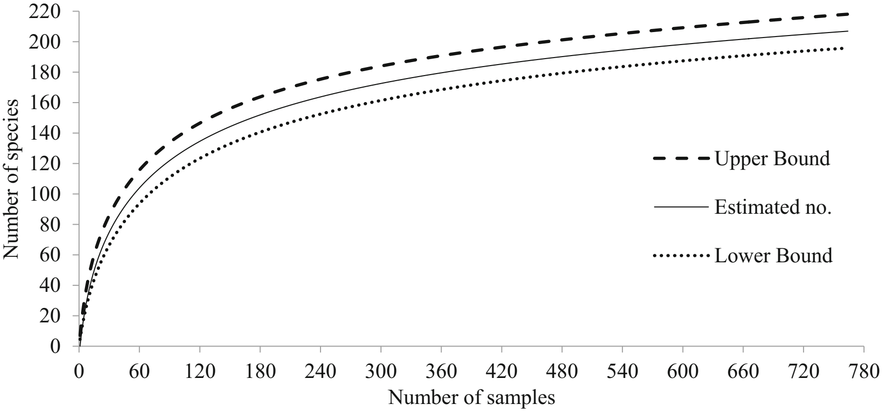

Fig. 2 Estimated cumulative number of fish species as a function of sampling effort. The bounds are the 95% confidence intervals

Table 2 Variation in estimated species richness between regions, seasons and depth based on goodness of fit by Chi-square analysis strata

Factor	χ^2	Df	p-Value
Goodness of fit			
Season	20.956	3	<**0.001**
Region	2.94	3	0.401
Stratum	111.05	3	<**0.001**
Contingency			
Region × season	16.19	9	0.063
Region × depth	18.62	9	**0.029**
Season × depth	19.02	9	**0.025**

Chi-square contingency tests were used to determine if variation in estimated species richness was similar across region by season, region by depth and season by depth. The numbers in bold were significant probability at 0.05 level

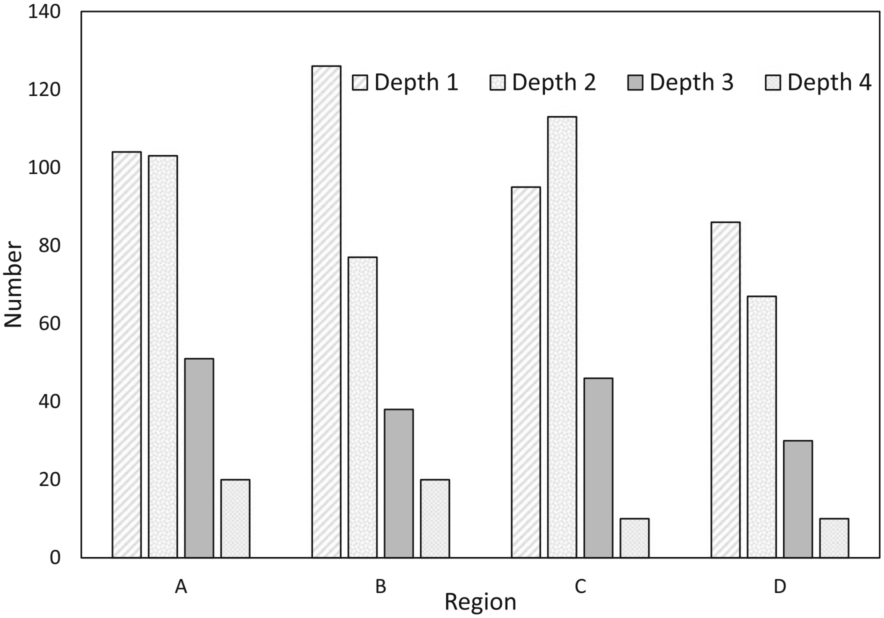

Fig. 3 Number of species by depth strata of the four regions in the Omani coast of the Arabian Sea

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 indicates that the number of estimated species was evenly distributed across regions (χ^2: $p = 0.40$; Table 2) but unevenly distributed among seasons (χ^2: $p < 0.001$; Table 2) and by depth strata (χ^2: $p < 0.001$; Table 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), highest in depth strata 1 and lowest in the deepest strata 4 (χ^2: $p < 0.001$; Table 2). The contingency Chi-square tests indicate that the

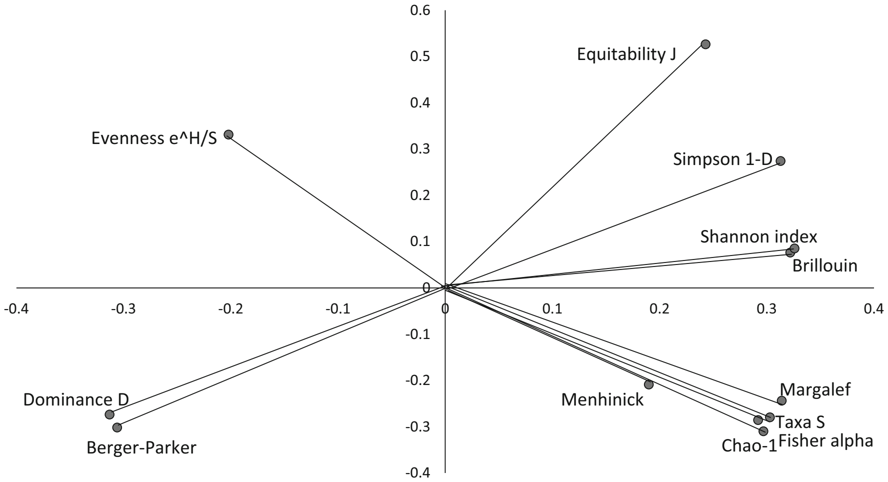

Fig. 4 Biodiversity indices using PCA for fish species from the Omani coast of the Arabian Sea; Chao1 and Shannon were combined to create an index that reflects richness and evenness

Table 3 PERMANOVA results of three biodiversity indices across region, season and depth strata

	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

Chao and Shannon refers to a combined metric of the Chao1 and Shannon indices
NS not significant

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). 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), except in region C where the number of species was higher in stratum 2 than stratum 1 (Fig. 3).

The 12 observed biodiversity indices largely separated into indicators of diversity and indicators of evenness (Fig. 4). Of these, I chose Chao1 and Shannon as these had the limit 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 3; Fig. 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 3; Fig. 5). A combination of Chao1 and Shannon (hence Chao-Shannon) and species richness was significantly higher during the NEMon season relative to the other seasons ($p < 0.01$; Table 3; Fig. 5). The total abundance was highest during the PreMon ($p < 0.01$; Table 3; Fig. 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 3;

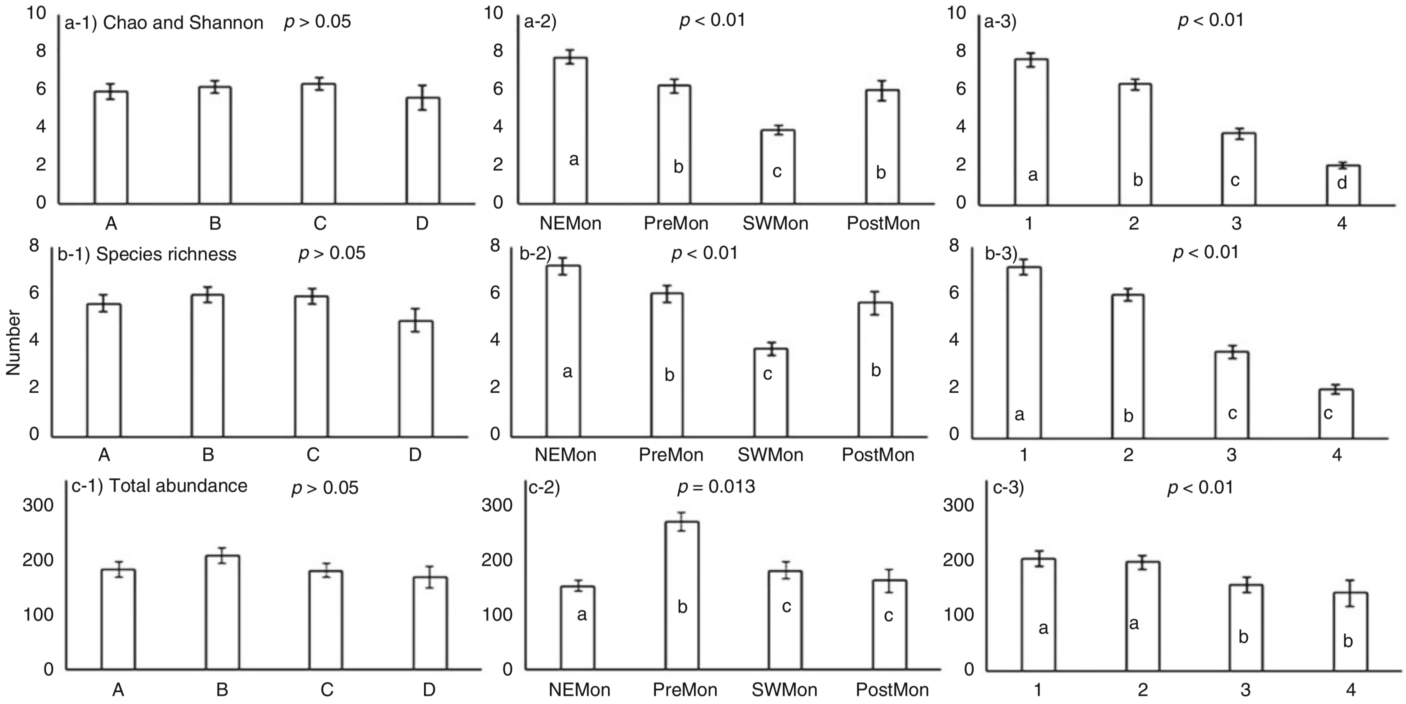

Fig. 5 Mean value of observed Chao and Shannon combined index, species richness and total abundance by regions, seasons and depth with significant differences ($p < 0.05$) indicated. Standard error (SE) are also indicated

Table 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)

	Temperature		Salinity		Dissolved oxygen	
Index	*p*	Deviance explained	*p*	Deviance explained	*p*	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%

Fig. 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 (Fig. 4). The only significant interaction between the factors was between region and season in their impact on total abundance ($p < 0.01$; Table 3).

The GAMs demonstrated that salinity and dissolved oxygen explained a significant amount of variation in Chao1 and species richness ($p < 0.01$; Table 4) and that temperature significantly explained variation in Chao1 ($p = 0.03$; Table 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 4). The highest deviance explained was 2.7% by salinity with respect to species richness (Table 4).

4 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 and 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 are 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 are 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 parts 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 was 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.

References

Al-Abdessalaam T (1995) Marine species of the Sultanate of Oman. An identification guide. Ministry of Agriculture and Fisheries, Sultanate of Oman, Publication no. 46/95

Al-Jufaili S, Hermosa G, Al-Shuaily S, Al-Mujaini A (2010) Oman fish biodiversity. Mar Sci 21:3–51

Anon (2013) Fisheries statistical yearbook 2013. Ministry of Agriculture and Fisheries, Muscat, Oman, 240 pp

Barbaro A, Einarsson B, Birnir B, Sigurthsson S, Valdimarsson H, Palsson OK, Sveinbjornsson S, Sigurthsson T (2009) Modelling and simulations of the migration of pelagic fish. ICES J Mar Sci 66:826–838

Bianchi G, Gislason H, Graham K, Hill L, Jin X, Koranteng K, Manickchand-Heileman S, Paya I, Sainsbury K, Sanchez F, Zwanenburg K (2000) Impact of fishing on size composition and diversity of demersal fish communities. ICES J Mar Sci 57:558–571

Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. J Fish Biol 17:143–162

Brander K, Blom G, Borges MF, Erzini K, Henderson G, MacKenzie BR, Mendes H, Ribeiro J, Santos AMP, Toresen R (2003) Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature. ICES Mar Sci Symp 219:261–270

Breitburg D (1992) Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behaviour, and physical disturbance. Ecol Monogr 62:525–546

Brock J, Mcclain C (1992) Interannual variability in phytoplankton blooms observed in the northwestern Arabian Sea during the southwest monsoon. J Geophys Res 97:733–750

Brönmark C, Skov C, Brodersen J (2008) Seasonal migration determined by a trade-off between predator avoidance and growth. PLoS One 3:e1957

Burkill PH, Mantoura RFC, Owens NJP (1993) Biogeochemical cycling in the northwestern Indian Ocean: a brief overview. Deep Sea Res Part II Top Stud Oceanogr 40:643–649

Cappo M, Speare P, De'Ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. J Exp Mar Biol Ecol 302:123–152

Catalan IA, Jimenez MT, Alconchel JI, Prieto L, Munoz JL (2006) Spatial and temporal changes of coastal demersal assemblages in the Gulf of Cadiz (SW Spain) in relation to environmental conditions. Deep-Sea Res 53:1402–1419

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

Cohen DM, Markle DF, Robins CR (1999) FAO species catalogue

Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. J Anim Ecol 69:785–798

Colwell RK, Chang XM, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85:2717–2727

Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, English CA, Galindo HM, Grebmeier JM, Hollowed AB, Knowlton N et al (2012) Climate change impacts on marine ecosystems. Annu Rev Mar Sci 4:11–37

Dulvy NK, Rogers SI, Jennings S, Stelzenmller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. J Appl Ecol 45:1029–1039

Fitzpatrick BM, Harvey ES, Heyward AJ, Twiggs EJ, Colquhoun J (2012) Habitat specialization in tropical continental shelf demersal fish assemblages. PLoS One 7:e39634

Fouda M, Hermosa G Jr, SM AH (1998) Status of fish biodiversity in the Sultanate of Oman. Ital J Zool 65:521–525

Gray J, Wu R, Or Y (2002) Effects of hypoxia and organic enrichment on the coastal marine environment. Mar Ecol Prog Ser 238:249–279

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Palaeontological Statistics Software Package for education and data analysis. Palaeontol Electron 4:1–9

Handeland SO, Imsland AK, Stefansson SO (2008) The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. Aquaculture 283:36–42

Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M (2006) Global temperature change. Proc Natl Acad Sci U S A 103:14288–14293

Harley CD, Randall Hughes A, Hultgren KM, Miner BG, Sorte CJ, Thornber CS, Rodriguez LF, Tomanek L, Williams SL (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD (2002) Climate warming and disease risks for terrestrial and marine biota. Science 296:2158–2162

Hastie TJ, Tibshirani RJ (1990) Generalized additive models, vol 43. CRC Press

Helly JJ, Levin LA (2004) Global distribution of naturally occurring marine hypoxia on continental margins. Deep Sea Res Part I Oceanogr Res Pap 51:1159–1168

Hemre GI, Mommsen TP, Krogdahl A (2002) Carbohydrates in fish nutrition: effects on growth, glucose metabolism and hepatic enzymes. Aquac Nutr 8:175–194

Hiddink J, Ter Hofstede R (2008) Climate induced increases in species richness of marine fishes. Glob Chang Biol 14:453–460

Honjo S, Dymond J, Prell W, Ittekkot V (1999) Monsoon-controlled export fluxes to the interior of the Arabian Sea. Deep Sea Res Part II Top Stud Oceanogr 46:1859–1902

Jackson D, Mandrak N (2002) Changing fish biodiversity: predicting the loss of cyprind biodiversity due to global climate change. In: American Fisheries Society Symposium. American Fisheries Society, pp 89–98

Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. Proc Natl Acad Sci U S A 101:8251–8253

Kramer DL (1987) Dissolved oxygen and fish behaviour. Environ Biol Fish 18:81–92

Kumar S, Ramaiah N, Gauns M, Sarma VV, Muraleedharan P, Raghukumar S, Dileep Kumar M, Madhupratap M (2001) Physical forcing of biological productivity in the Northern Arabian Sea during the Northeast Monsoon. Deep Sea Res Part II Top Stud Oceanogr 48:1115–1126

Levin LA, Gage JD, Martin C, Lamont PA (2000) Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. Deep Sea Res Part II Top Stud Oceanogr 47:189–226

Linehan J, Gregory R, Schneider D (2001) Predation risk of age-0 cod (Gadus) relative to depth and substrate in coastal waters. J Exp Mar Biol Ecol 263:25–44

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

Magurran AE, Henderson PA (2003) Explaining the excess of rare species in natural species abundance distributions. Nature 422:714–716

Manilo LG, Bogorodsky SV (2003) Taxonomic composition, diversity and distribution of coastal fishes of the Arabian Sea. J Ichthyol 43:S75–S149

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

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

Mellin C, Bradshaw CJ a, Meekan MG, Caley MJ (2010) Environmental and spatial predictors of species richness and abundance in coral reef fishes. Glob Ecol Biogeogr 19:212–222

Mora C, Robertson DR (2005) Causes of latitudinal gradients in species richness: a test with fishes of the tropical eastern pacific. Ecology 86:1771–1782

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

Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Mar Ecol Prog Ser 393:111–129

Paterson AW, Whitfield AK (2000) Do shallow-water habitats function as refugia for juvenile fishes? Estuar Coast Shelf Sci 51:359–364

Pauly D (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES J Mar Sci 39:175–192

Pauly D (2010) Gasping fish and panting squids: oxygen, temperature and the growth of water-breathing animals. Excell Ecol 22:1–247

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915

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

Pörtner H (2001) Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. Naturwissenschaften 88:137–146

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95–97

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

Raffaelli D (2004) How extinction patterns affect ecosystems. Science 306:1141–1142

Raghukumar S, Anil A (2003) Marine biodiversity and ecosystem functioning: a perspective. Curr Sci 84:884–892

Randall J (1995) Coastal fishes of Oman. University of Hawaii Press

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

Sala E, Knowlton N (2006) Global marine biodiversity trends. Annu Rev Environ Resour 31:93–122

Schmittner A, Galbraith ED, Hostetler SW, Pedersen TF, Zhang R (2007) Large fluctuations of dissolved oxygen in the Indian and Pacific oceans during Dansgaard-Oeschger oscillations caused by variations of North Atlantic Deep Water subduction. Paleoceanography 22

Sheppard C, Wilson S, Salm R, Dixon D (2000) Reefs and coral communities of the Arabian Gulf and Arabian Sea. Coral Reefs Indian Ocean: their ecology and conservation. Oxford University Press, Oxford, NY, pp 257–293

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

Soberón MJ, Llorente BJ (1993) The use of species accumulation functions for the prediction of species richness. Conserv Biol 7:480–488

Sosa-López A, Mouillot D, Ramos-Miranda J, Flores-Hernandez D, Do Chi T (2007) Fish species richness decreases with salinity in tropical coastal lagoons. J Biogeogr 34:52–61

Staples DJ, Nomura M (1976) Influence of body size and food ration on the energy budget of rainbow trout *Salmo gairdneri* Richardson. J Fish Biol 9(1):29–43

Stramma L, Johnson GC, Sprintall J, Mohrholz V (2008) Expanding oxygen-minimum zones in the tropical oceans. Science 320:655–658

Thompson GG, Withers PC (2003) Effect of species richness and relative abundance on the shape of the species accumulation curve. Austral Ecol 28:355–360

Thompson GG, Withers PC, Pianka ER, Thompson SA (2003) Assessing biodiversity with species accumulation curves; inventories of small reptiles by pit-trapping in Western Australia. Austral Ecol 28:361–383

Underwood AJ (1981) Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr Mar Biol Annu Rev 19:513–605

Vaquer-Sunyer R, Duarte CM (2008) Thresholds of hypoxia for marine biodiversity. Proc Natl Acad Sci U S A 105:15452–15457

Vinebrooke RD, Cottingham KL, Norberg M, Scheffer J, Dodson SI, Maberly SC, Sommer U (2004) Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. Oikos 104:451–457

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395

Ware DM, Thomson RE (2005) Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science 308:1280–1284

Watling LES (1999) Impacts of mobile fishing gear: the biodiversity perspective. In: American Fisheries Society Symposium, vol 22, pp 31–40

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst 34:273–309

Wood SN (2009) Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation. R Packag Version 1.7-27

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR et al (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790

Zar JH (1999) Biostatistical analysis. Prentice Hall