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Original Article

Ocean biogeochemical models as management tools: a case study for Atlantic wolffish and declining oxygen

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Society is moving towards a no-analogue climate that will fundamentally affect ocean ecosystems and the socio-economic activities that depend on them. Warming has led to displacements of various populations, calling for an adaptation of fisheries management plans and Species at Risk recovery strategies. Dissolved oxygen (DO) has declined, but its impacts on habitat are much less studied. Severe hypoxia is lethal, but even sublethal hypoxia can trigger species displacements. We use Atlantic wolffish (*Anarhichas lupus*) as a case study to investigate the impact of DO on optimal habitat on the Socian Shelf, Canada, considering that their habitat becomes suboptimal at DO lower than \sim 65% saturation. First, we demonstrate that DO has decreased using two observational climatologies before and after 1980, and that the spatial pattern of the associated expansion of low oxygen waters (DO < \sim 65% saturation) over the shelf is consistent with the observed contraction of Wolffish population. Then, we use a spatially explicit regional ocean model that couples physical and biological processes to simulate a scenario in which a continued decline of DO in the open ocean leads to a further expansion of low oxygen waters over the shelf. The future low DO extends to regions that currently have high Wolffish biomass, and likely other species as well. While fishing pressure likely drives the observed decline in Wolffish, both observations and model scenario suggest that DO can further constrain habitat. We argue that management/recovery plans should consider DO as one of the potential stressors of not just Atlantic wolffish but any oxygen-sensitive species. Finally, we emphasize that biogeochemical ocean models can inform management by elucidating the direction and ranges of future changes in ocean environmental conditions.

Keywords: Atlantic wolffish, dissolved oxygen, marine habitats, Northwest Atlantic, regional ocean models, Scotian Shelf.

Introduction

Anthropogenic carbon emissions and climate change modify the ocean's temperature, acidity, and oxygen concentrations (Rhein *et al.*, 2013), and thus directly affect the habitat and ecophysiology of marine organisms (e.g. Pauly, 2010; Pörtner, 2010; Cheung *et al.*, 2011). Marine species will need to adapt or migrate in response to their changing habitats, with uncertain and potentially undesired ecological and economic consequences. Global model projections predict lower estimated catch potentials and smaller maximum body weight in marine fish by 2050 (Cheung *et al.*, 2011, 2013a), while shifts in the distributions of marine species are projected (Shackell *et al.*, 2014) or already being observed (Pinsky *et al.*, 2013). As environmental

changes affect the suitability of marine habitats (i.e. some regions may become less or not suitable, while some others may become more suitable), animals' responses may vary from migrations within or outside present habitats to increased mortality. Therefore, identifying optimal fish habitat with explicit consideration of various environmental stressors, including low dissolved oxygen (DO) and low pH, and creating or updating management tools have become essential but not straightforward tasks for managers and policy-makers (Hartman *et al.*, 2014; Shackell *et al.*, 2014). These tools are especially needed for the hydrographically complex coastal regions, which hold a significant fraction of the world's fisheries (Pauly and Christensen, 1995) and where future changes are even more difficult to predict.

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Species habitat is traditionally defined as a function of substrate, depth, and temperature (Mahon and Smith, 1989). The inclusion of DO in definitions of optimal or suitable habitat is not as common, due both to lack of data and because the scientific focus on coastal hypoxia is relatively recent (e.g. Grantham et al., 2004; Diaz and Rosenberg, 2008; Gilbert et al., 2010). In the context of climate change, substrate and depth can be assumed to remain unperturbed, but temperature, DO, and pH are expected to change, the latter not only because of the increased diffusion of atmospheric carbon dioxide (CO₂) into the oceans, but also because the processes that remove oxygen from water also produce CO₂ (Burnett, 1997; Melzner et al., 2012). From these three environmental variables, only temperature is likely to produce new opportunities (i.e. some habitats that are too cold may become more suitable). As will be detailed later, the expected declines in DO and pH would only deteriorate habitat suitability.

Many efforts have been focused on understanding the effect of warming temperatures on marine life, investigating the effect of temperature on survival, metabolism, reproduction, growth, thermal habitat, etc. (Fry, 1971; Wood and McDonald, 1997; Pörtner, 2001; Mohseni et al., 2003; Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Cheung et al., 2013b, and many others). However, as the ocean surface becomes warmer and more stratified, both oxygen solubility and ventilation of subsurface layers are reduced, leading to a decline in subsurface oxygen concentrations (Brewer and Peltzer, 2009; Keeling et al., 2010). Furthermore, the metabolic rate and oxygen consumption of fish, invertebrates, and even bacteria increase with temperature (Fry, 1971), increasing the rate of oxygen depletion (Genovesi et al., 2011). Observations show that DO is declining both in the open ocean and on continental shelves (e.g. Gilbert et al., 2005, 2010; Stramma et al., 2008). For instance, oxygen in the upper water mass of the North American Basin has decreased by 6 μ mol kg⁻¹ (~6.15 μ M) between 1960 and 2009 (Stendardo and Gruber, 2012, their Supplementary Table S1). On the Scotian Shelf in the northwest North Atlantic, observations indicate an oxygen decline of 1.06 μ M year⁻¹ from 1961 to 1999 at 150 m depth in Emerald Basin (Petrie and Yeats, 2000). Because respiration is the privileged method of energy production in most marine organisms (Nelson and Chabot, 2011), severe hypoxia is lethal to many species, causing mass mortality or migration, a decrease in productivity, biomass, and biodiversity (Tyson and Pearson, 1991; Diaz and Rosenberg, 1995, 2008; Rabalais et al., 2002, 2010; Montagna and Ritter, 2006; Pollock et al., 2007). Even intermediate (sublethal) hypoxia can be sufficient to trigger avoidance and displacements in marine fish (Whitmore et al., 1960; Claireaux et al., 1995; Herbert and Steffensen, 2005; Herbert et al., 2011). For marine fish and invertebrate that stay and face sublethal hypoxia, low oxygen concentrations can affect metabolic capacity or scope (the difference between the maximum rate of oxygen extraction and the rate required for survival, Fry, 1971), behaviour, habitat choice, growth, and development (e.g. Herrmann et al., 1962; Bejda et al., 1992; Neill et al., 1994; Chabot and Dutil, 1999; Claireaux et al., 2000; Pichavant et al., 2001; Foss et al., 2002; Chabot and Claireaux, 2008; Ekau et al., 2010; Pörtner, 2010).

To investigate potential future distributions of DO, we currently rely on biogeochemical ocean models that couple physical, chemical, and biological processes. High-resolution regional models are best suited to address changes in the coastal ocean, since global models still lack sufficient resolution to represent continental shelf processes properly, particularly in the Scotian Shelf area (Lavoie *et al.*, 2013). Regional ocean models can simulate past and present conditions,



Figure 1. Map showing the domain of the Atlantic Canada Model (black box). Contours depict 200 and 1000 m isobaths. Text labels show the location of the Scotian Shelf, Grand Banks, Gulf of Main (GoM), Gulf of St Lawrence (GoSL), and Laurentian Channel.

for which they can be validated against observations from ships, moorings, buoys, satellites, etc. For projecting future conditions with these models, there are two main options: one is to force the regional model with output from global climate model projections (i.e. downscaling); the other is to perform scenarios or sensitivity experiments where idealized changes in the model forcing and/or boundary and initial conditions are applied. Sensitivity experiments are especially useful for evaluating the consequences of changes in a single variable.

Here, we apply a regional ocean model to investigate potential changes in optimal habitat with respect to DO to demonstrate that our approach of combining observations and numerical models can become a useful tool for the management of marine species and their habitats (e.g. by helping to identify regions where a species recovery is likely to be more successful). We focus our study on the Scotian Shelf, which belongs to the continental shelf of Atlantic Canada, and use a regional model developed for this region (Figure 1). The model has previously been described in Brennan et al. (2015) and is subsequently referred to as Atlantic Canada Model or ACM. We chose Atlantic wolffish (Anarhichas lupus) as the species for our case study. This long-lived, late maturing species tolerates relatively cold temperatures in the range of -1 to 10° C and, on the Scotian Shelf, has a temperature preference between 3 and 6°C (Scott, 1982; O'Dea and Haedrich, 2002). As a demersal species, Atlantic wolffish is found in deep continental shelf waters, between 73 and 126 m on the Scotian Shelf (Scott and Scott, 1988) and 40 and 240 m in the Gulf of Maine (Rountree, 2002). In the Northwest Atlantic, they feed primarily on a variety of bottom invertebrates (echinoderms, molluscs, and crustaceans; Scott and Scott, 1988; Rountree, 2002). Wolffish abundance has experienced a significant decline on the Scotian Shelf (Shackell et al., 2012) and is currently listed as a species of Special Concern in this region under both the Species at Risk Act and the Committee on the Status of Endangered Wildlife in Canada (SARA and COSEWIC, respectively). In the Gulf of Maine and Georges Bank area, Wolffish is considered a Species of Concern under the US Endangered Species Act. Atlantic wolffish is sensitive to declining oxygen, with negative effects (decreased heart rate) occurring at concentrations below 60-70% saturation (K. Gamperl, pers. comm.), although hypoxia becomes lethal only at \sim 20% saturation in juveniles (Le François et al., 2001). Juveniles of a related species, the Spotted Wolffish, exhibit declines in specific growth rate below 70% oxygen saturation (Foss et al., 2002; Simpson et al., 2013). Furthermore, many species begin to exhibit lower metabolic capacity (aerobic scope), locomotor activity, food consumption, and/or growth rates at DO levels of \sim 60–70% saturation, e.g. Atlantic cod (Gadus morhua; Chabot and Dutil, 1999; Claireaux et al., 2000), turbot (Scophthalmus maximus; Pichavant et al., 2000, 2001), sea bass (Dicentrarchus labrax; Pichavant et al., 2001), common sole (Solea solea; Lefrançois et al., 1998; Lefrancois and Claireaux, 2003) and Chinese shrimp (Fenneropenaeus chinensis; Wei et al., 2009). In this study, we will use an incipient limiting oxygen threshold (sensu Fry, 1971) of 65% saturation for Atlantic wolffish, considering habitat as optimal in those regions where oxygen is above 65% saturation and suboptimal otherwise.

This paper is organized as follows. We start by describing the datasets and numerical model used in this study (Material and methods). Then, we identify optimal and suboptimal regions for Atlantic wolffish according to two oxygen climatologies (pre- and post-1980) and investigate the changes in the species' biomass in those areas (Oxygen subhabitats and Atlantic wolffish in the three subhabitats, respectively). In the Atlantic wolffish and oxygen: past, present, and futuristic scenario section, we compare the spatial and temporal variability of Atlantic wolffish with that of the suboptimal habitat and, using a model scenario, evaluate whether future suboptimal habitats are likely to expand. Finally, we discuss how this methodology could be used to inform managers and decision-makers, for instance, when designing recovery strategies for species at risk and designating marine protected areas (MPAs; see the Discussion section).

Material and methods

Atlantic wolffish abundance and distribution

Observations of Atlantic wolffish distribution and abundance from 1970 to 2009 are available from summer research vessel surveys on the Scotian Shelf by the Department of Fisheries and Oceans Canada (Simon and Comeau, 1994; Horsman and Shackell, 2009). We interpolated the weight per tow (hereafter referred to as biomass) onto a grid using the inverse distance weighting (IDW) technique with a fixed search radius of 0.15° (same procedure as Horsman and Shackell, 2009). IDW was selected because this interpolation technique fits the source data accurately and preserves local anomalies in the interpolation grid. For our interpolation, we divided the dataset in five periods of 8 years each (Table 1) following the same rationale as Horsman and Shackell (2009).

We also followed Horsman and Shackell's procedure for creating "ranked maps". First, we classified the interpolated biomass into ten percentile classes (or deciles). Then, the maps of deciles were ranked with values from 1 to 10, where 1 was assigned to locations that fell in the first decile (1–10th percentile), 2 to locations in the 2nd decile (11–20th percentile), etc. up to 10, which represents locations in the 91–100th percentile.

Observation-based oxygen climatology and oxygen subhabitats

We created two oxygen climatologies for the Scotian Shelf region (horizontal resolution ~ 10 km, Figure 2) using observations from the BioChem database until 2010 (Devine *et al.*, 2014; DFO, 2014) and from the World Ocean Database until 2006 (Boyer *et al.*, 2009),

Table 1. Study periods and rationale.

Period	Description
1970 – 1977	Period when foreign fleets were active in Canadian waters
1978 – 1985	Establishment of the 200 mile limit (exclusive economic zone) and subsequent recovery of domestic stocks before domestic fisheries were fully engaged
1986 – 1993	Domestic fleets increased fishing pressure, which combined with colder waters on the eastern Scotian shelf, led to a decline in growth rate and collapse of some fish stocks
1994 – 2001 2002 – 2009	Horsman and Shackell (2009) considered the period 1994 – 2006 to represent the collapse and non-recovery of several groundfish species on the eastern Scotian shelf. Here, since we have more years of data, we created two periods of 8 years each

with observations dating as early as 1922. The climatologies were prepared using oxygen concentrations in micromolar. The WOD09 values were converted from millilitre per litre to micromolar using the factor 44.659. One climatology used observations averaged over the 1922–1980 period, while the other was for 1980–2010 (we refer to them as "pre-1980" and "post-1980", respectively). The reference year 1980 was chosen to reflect two periods of different states of the system (pre- and post-strong anthropogenic influence), with more than 30 years worth of observations in each.

Given that Atlantic wolffish is a demersal fish, we used bottom oxygen concentrations from these climatologies to identify regions of different suitability for this species: optimal habitat where oxygen is above a defined threshold (65% saturation, see the Introduction section) and suboptimal habitat where oxygen is below the threshold. Since oxygen saturation depends on temperature and salinity, the 65% saturation threshold cannot be directly compared with our climatologies in micromolar. The 65% saturation threshold implies a range of oxygen concentrations in a region with varying temperature and salinity fields as the Scotian Shelf. Using temperature and salinity climatological values from Geshelin et al. (1999) for the bottom waters of the Scotian Shelf ($\sim 0.8-9.5^{\circ}$ C, 31–35), the oxygen concentrations at 65% saturation range from \sim 185 to 234 μ M, where the lower values are found on the warmer, western Scotian Shelf (including Emerald Basin). For the annual mean bottom temperature and salinity on the Scotian Shelf (5.23°C, 33.5), 65% saturation corresponds to 206 µM. Therefore, we used this value as a conservative oxygen threshold, noting that parts of the eastern Scotian Shelf may drop below the 65% saturation threshold at higher oxygen concentrations.

Biogeochemical model scenario

To evaluate the effect of future oxygen conditions, we combined the results of a numerical biogeochemical model and our oxygen climatologies. Our model, the Atlantic Canada Model (ACM; Brennan *et al.*, 2015), is based on the Regional Ocean Modelling System (ROMS, version 3.5, http://myroms.org). The model domain comprises the continental shelf and adjacent deep ocean of the northwest North Atlantic from Cape Cod in the south to north of Newfoundland, including the Grand Banks (Figure 1). The model is nested within the regional ocean-ice model of the northwest North Atlantic from Urrego-Blanco and Sheng (2012) and is forced with atmospheric reanalysis fields (winds, specific humidity, air temperature, precipitation, and short- and long-wave radiation) from Large and Yeager (2004). The biological module tracks and outputs eight state variables: chlorophyll, phytoplankton,



Figure 2. Distribution of bottom DO conditions in the pre-1980 and post-1980 climatologies. (a and b) Oxygen concentrations in micromolar. (c and d) Optimal (oxygen \geq 206 μ M) and suboptimal (oxygen < 206 μ M) habitats in black and red, respectively. (e) Combination of subhabitats discussed in the text: regions that have oxygen \geq 206 μ M in both periods ("always optimal", black), regions with oxygen < 206 μ M in both periods ("always suboptimal", black), regions with oxygen < 206 μ M in both periods ("always suboptimal", black), regions with oxygen < 206 μ M in both periods ("always suboptimal", blue). And regions that are optimal in the pre-1980 climatology and suboptimal in the post-1980 climatology ("optimal-to-suboptimal", blue). Maps show the 150, 200, and 1000 m isobaths. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

zooplankton, large and small detritus, nitrate, ammonium, and DO. The biological sources of DO in the model are new and regenerated primary production, while the sinks are remineralization of detritus, respiration by zooplankton, nitrification, and sediment oxygen consumption. Furthermore, the model includes air-sea gas exchange of oxygen following García and Gordon (1992) and Wanninkhof (1992) parameterizations, and mixing and advective transport of oxygen through coupling with the ocean circulation



Figure 3. Box plot of oxygen concentrations in the three subhabitats on the Scotian Shelf (see inset): "always suboptimal" (red), "optimal-to-suboptimal" (blue), and "always optimal" (black). The lower and upper limits of each box represent the 25 and 75% percentiles, respectively; the horizontal line within each box indicates the median oxygen concentration in the subhabitat; the dashed, vertical lines indicate the range in each subhabitat. The dashed, horizontal line indicates the DO threshold (206μ M) and the *x*-axis labels indicate the pre-1980 (grey boxes) and post-1980 (white boxes) climatologies. The inset shows the areas used for the boxplots of each subhabitat (the total area corresponds to the region with Atlantic wolffish biomass observations from 1970 to 2009 summer surveys). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

model. More details on the biological module of the ACM can be found in Fennel *et al.* (2006, 2013).

We performed a baseline simulation that represents current oxygen conditions (1999–2003) and a scenario simulation where we projected the effect of an assumed further oxygen decline in deep ocean waters. For the latter, we extrapolated the observed rate of oxygen decline in Emerald Basin (-1.06μ M year⁻¹, Petrie and Yeats, 2000) forward by 50 years (i.e. 53 μ M). We modified the model's initial and boundary conditions by reducing the oxygen concentration of subsurface water (below 100 m) by 53 μ M in the deep ocean (i.e. offshelf regions where the bottom depth is 200 m or deeper). The baseline simulation was then redone with these modified initial and boundary oxygen conditions.

Our next step was to compute the difference between the scenario and the baseline simulation and to add this difference to the oxygen climatology post-1980. The resulting oxygen field was used as the scenario to investigate the effect of a decline in offshore oxygen concentrations on Atlantic wolffish populations over the Scotian Shelf.

Results

Oxygen subhabitats

The climatological distribution of DO in bottom waters on the Scotian Shelf shows a decrease in concentrations from the pre-1980 to the post-1980 periods (Figure 2a and b). On average, the decrease was ~5%, with larger changes in Emerald Basin and along the shelf break of 10%. Using these climatologies to investigate the changes in optimal (DO $\geq 206 \ \mu$ M) and suboptimal (DO < 206 $\ \mu$ M) habitats for Atlantic wolffish, we find that suboptimal habitat expanded by 85% after 1980 (Figure 2c and d). In Figure 2d, suboptimal (red) areas expand roughly to the 150 m isobath. We can distinguish three different subhabitats (Figure 2e): areas that were optimal before



Figure 4. Time-series of mean Atlantic wolffish biomass in three subhabitats of the Scotian shelf (see inset in Figure 3): "always suboptimal" (red), "optimal-to-suboptimal" (blue), and "always optimal" (black). Biomass was previously interpolated in five periods (8 years each). The horizontal lines show the mean biomass for each period and the vertical lines show the associated standard error. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

and after 1980 ("always optimal"), areas with suboptimal conditions before and after 1980 ("always suboptimal"), and areas that were optimal before 1980 and became suboptimal after 1980 ("optimalto-suboptimal"). A box plot summarizes the climatological bottom oxygen concentrations found in each subhabitat on the Scotian Shelf for both periods (Figure 3). In the pre-1980 climatology, DO in the "optimal-to-suboptimal" subhabitat (blue) shows values above but close to the threshold. In other words, the region that became suboptimal in the post-1980 climatology was barely optimal before 1980. All three subhabitats show a decrease in DO from the pre-1980 to post-1980 periods, but the declines are larger in the "always suboptimal" and "optimal-to-suboptimal" subhabitats (e.g. medians decreased by 8 and 9% in these two subhabitats, respectively, while the decrease in the median DO in the "always optimal" subhabitat was 3%).

Atlantic wolffish in the three subhabitats

After dividing the region in three oxygen subhabitats, we followed the procedures described in the Atlantic wolffish abundance and distribution section to interpolate Atlantic Wolfish biomass on the Scotian Shelf and then calculated the mean biomass in each subhabitat at each of the five periods (time-series in Figure 4). The mean biomass is the highest in the "always optimal" subhabitat (black), followed by the "optimal-to-suboptimal" subhabitat (blue). Note that the peak in the latter subhabitat corresponds to the period when the Exclusive Economic Zone was established (Atlantic wolffish abundance and distribution), leading to a temporary recovery of domestic stocks. The "always suboptimal" subhabitat (red) shows the lowest mean biomass, reaching very low levels (<0.2 kg) as early as the 1986-1994 period. All subhabitats show declining biomass trends and by 2002-2009, the mean biomass drops below 0.35 kg in all subhabitats (0.34, 0.28, and 0.06 kg for the "always optimal", "optimal-to-suboptimal", and "always suboptimal" subhabitats, respectively). The rate of decline in biomass was fastest in the "always optimal" subhabitat.

Atlantic wolffish and oxygen: past, present, and futuristic scenario

The ranked maps described in the Atlantic wolffish abundance and distribution section show both the temporal and spatial variability of Atlantic wolffish biomass (Figure 5a, c, and e). Regions with high biomass (red areas in ranked maps) become scarcer and contract over time; moreover, regions without observed Wolffish (dark blue areas) become more widespread. The latter regions expand by 10% from 1970-1977 to 1986-1993, and then by a further 31% from 1986-1993 to 2002-2009. By superimposing the suboptimal habitats onto the ranked maps, we analyse the connection between biomass and DO (Figure 5b, d, and f). The overlap of biomass in 1970-1977 with pre-1980 suboptimal habitat (grey areas, Figure 5b) shows that suboptimal areas were on top of small regions in the western Scotian Shelf and Emerald Basin, where no Atlantic wolffish were observed. Approximately 13% of the pixels shown in Figure 5b had both suboptimal DO conditions and no Wolffish biomass, while <3% of the pixels presented both suboptimal DO and observed biomass (i.e. suboptimal areas were characterized mainly by a lack of Atlantic wolffish). There were some regions with DO above the threshold that also presented no animals. When we overlap biomass for 1986-1993 with the post-1980 suboptimal area (Figure 5d), the expansion of the suboptimal (grey) area is highly co-located with areas where no Atlantic wolffish was observed, especially in the Emerald Basin and western Scotian Shelf. In this case, 24% of the pixels had both suboptimal conditions and no observed biomass and 6% had suboptimal DO and biomass in or above the first percentile.

What could happen under future climates? Using the future scenario described in the Biogeochemical model scenario section, we found that a decrease in DO in the open ocean could lead to a further expansion of the suboptimal habitats for Atlantic wolffish (a 55% increase with respect to the post-1980 climatology; Figure 5f). The largest decreases in DO concentrations between the post-1980 climatology and the future scenario occurred in the deeper waters of the shelf, i.e. those connected to the open ocean, such as Emerald Basin, Gulf of Maine, and the Laurentian Channel (Figure 5g vs. h). On average, DO concentrations on the Scotian Shelf decreased by $\sim 10\%$ (the maximum decrease was 21%).

To assess the impact of such an expansion of suboptimal habitat, we quantified whether the affected regions have high or low biomass at present. We looked at the biomass in the latest period (2002–2009, ranked map in Figure 5e) and analysed how much of it is found in areas that remain optimal under the future scenario (i.e. the region of the ranked map in Figure 5f that did not overlap with the grey, suboptimal area). Figure 6a and b shows the histograms for both biomass maps, and the difference between both histograms (Figure 6c) emphasizes that most of the regions affected by low oxygen in the model scenario were in the highest deciles (5-10th, yellow to red bars). In other words, an expansion of low oxygen water as shown by our future scenario would affect regions where high biomass is currently observed.

Discussion

Previous studies have shown declining long-term oxygen trends on the Scotian Shelf (Petrie and Yeats, 2000; Gilbert *et al.*, 2010) and our climatologies pre- and post-1980 also show a clear decrease in oxygen (Figure 3). We find that deeper areas of the shelf, where oxygen is either below or barely above the threshold in the pre-1980 climatology, became suboptimal habitats for Atlantic wolffish (DO < 206 μ M) in the post-1980 period. Moreover, Wolffish biomass was higher in the regions with more oxygen (Figure 4). Our analysis shows that the observed contraction of Atlantic wolffish distribution is consistent with the expansion of areas with DO < 206 μ M in the two climatologies (Figure 5). Moreover, the geographical expansion of low oxygen areas in deep basins over the shelf suggests that low DO waters are coming from offshore, rather than being generated by local biological processes.

In a model-based future scenario that assumes a continuation of the observed oxygen decline in subsurface open-ocean waters, DO further declines over the shelf and further decreases the optimal habitat for Atlantic wolffish. This simple simulation of a future scenario shows how, holding everything else constant, an oxygen decrease in offshore waters can lead to lower oxygen concentrations over Emerald Basin, the western Scotian Shelf, and the eastern Scotian Shelf close to the Laurentian Channel. The impact of climate change will certainly be more complex than just an offshore DO decrease. While some effects of a warmer climate on DO are easy to predict (e.g. decrease in oxygen solubility, the enhancement of organic matter decomposition below the pycnocline and associated DO consumption), others are less straightforward. For instance, warmer surface waters and modified wind patterns could lead to changes in ocean stratification, which could lead to alterations in productivity and consequently, in DO dynamics.

Nevertheless, we note that this scenario is an underestimation of the expected impact of lowering DO in a warmer climate. For instance, the standard metabolic rate (SMR), which is the rate of oxygen consumption for an inactive post-absorptive fish (Frappell and Butler, 2004; Chabot *et al.*, 2016), increases with temperature. As a result, the minimum DO level required by the fish to fulfil its SMR increases, leading to a reduction in its hypoxia tolerance (Fry and Hart, 1948; Schurmann and Steffensen, 1997; Hicks and McMahon, 2005; Shimps *et al.*, 2005; Collins *et al.*, 2013).



Figure 5. Left (a, c, and e): Ranked maps showing the distribution of Atlantic wolffish biomass in terms of percentiles for the periods 1978 – 1985, 1986 – 1993, and 2002 – 2009. "None" indicates that no wolffish was observed. Right (b, d and f): Same maps, overlapped with suboptimal habitat in terms of oxygen (grey mask). Suboptimal habitats for the pre-1980 climatology, post-1980 climatology, and model-scenario are on top of each of the three periods mentioned before, respectively. Ranked maps are described in more detail in the Atlantic wolffish abundance and distribution section. (g) DO climatology post-1980 and (h) future DO scenario.



Figure 6. (a) Histogram of the ranked map for the period 2002 – 2009 (Figure 5e). (b) Histogram for the same period, only considering the regions within the optimal area in the model scenario (Figure 5f). (c) Difference between (a and b). Colour scale as in ranked maps of Figure 5. Note that "rank" from 1 to 10 corresponds to 1st to 10th decile and that the locations with no observations were not included in the histograms (dark blue colour in Figure 5). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Similarly, the incipient limiting oxygen threshold, where DO begins to affect aerobic scope, increases with temperature (Fry, 1971; Cech *et al.*, 1984; Claireaux *et al.*, 2000; Lefrançois and Claireaux, 2003). Therefore, a greater proportion of the Atlantic wolffish population could live in suboptimal conditions due to the combined effects of warmer temperatures and lower DO in the future. For a species like Atlantic wolffish, currently considered as Species of Special Concern, such deterioration of habitat would not only be detrimental for its recovery but could even jeopardize its survival.

In this study, we considered the incipient limiting oxygen threshold for Atlantic wolffish to be 65% saturation and assumed it to be \sim 206 μ M, based on the annual mean bottom temperature and salinity of the Scotian Shelf. On colder, less saline areas of the shelf (e.g. eastern region), a saturation of 65% would represent oxygen concentrations $>206 \mu$ M. Therefore, our analysis underestimates the effect of oxygen changes in these regions, leading to classify these colder waters as optimal habitats, when their oxygen saturation levels could be below 65%. Conversely, the warmer, more saline regions of the shelf (e.g. western region and Emerald Basin) could be above the 65% threshold at DO $< 206 \,\mu$ M, overestimating the effect of DO. However, we believe that the latter does not affect our conclusions, since Wolffish will be more sensitive to hypoxia in warmer water and the exact incipient limiting level is not fully known for this species. Thus, 65% is a conservative estimate, potentially being as high as 70%.

Using two oxygen categories (optimal and suboptimal) is a simplification. Suboptimal habitat does not mean unavailable habitat. In contrast, areas that are close to or below the lethal DO level are unavailable to fish. For instance, the lethal DO level for cod in the Gulf of St Lawrence is 21% saturation, but the risk of mortality becomes significant at 28% (Plante *et al.*, 1998). Cod are virtually absent from parts of the Estuary and Gulf of St Lawrence with <30% saturation (Chabot, 2004). Atlantic wolffish have a similar hypoxia tolerance (Le François *et al.*, 2001) and therefore likely cannot inhabit regions with <30% saturation. Such severe hypoxia is not found (nor projected in our scenario) in the study area. Nevertheless, while fish can survive and grow at DO levels below the incipient limiting oxygen threshold, their aerobic scope is reduced, and the reduction is proportional to the severity of

hypoxia. A reduced aerobic scope means that there is less energy available for digesting food, which impacts food consumption and growth (Herrmann et al., 1962; Cech et al., 1984; Bejda et al., 1992; Secor and Gunderson, 1998; Chabot and Dutil, 1999; Thetmeyer et al., 1999; Buentello et al., 2000; Pichavant et al., 2001; Foss et al., 2002; Jordan and Steffensen, 2007; Chabot and Claireaux, 2008; Zhang et al., 2010a; Yang et al., 2014), and activity (Chabot and Dutil, 1999; Dutil et al., 2007; Zhang et al., 2010b). A possible improvement to this study would be to also consider a second oxygen threshold below which growth would be greatly compromised and have "barely usable" and "suboptimal" categories. As the exact hypoxia level that would separate the two categories is unknown for this species and Atlantic wolffish biomass was low in the suboptimal habitat, our understanding of wolffish habitat would gain little from using more subhabitat categories. Moreover, despite the two-category simplification, we were able to show a relationship between contraction of Atlantic wolffish biomass and declining oxygen concentrations.

Under density-dependent habitat selection, animals occupy optimal (most suitable) habitat first, and then move to marginal habitat as per capita resources decline in optimal habitat (e.g. Shackell et al., 2005). Consistent with this theory, Atlantic wolffish biomass is higher in the regions with higher DO (Figure 4), indicating that those regions are indeed more suitable than the regions with lower DO. In particular, decreasing DO and deterioration of habitat is of concern for sedentary animals such as Atlantic wolffish, which undergo limited migration (Templeman, 1984), since they might be forced to stay in suboptimal habitat. The consequences of the latter can range from low production to increased mortality (as described above when discussing the impact of a decreased aerobic scope). Furthermore, DO decline could also affect Wolffish indirectly by altering its food supply; however, echinoderms, molluscs, and crustaceans (the main food sources of Atlantic wolffish) are more tolerant to low DO conditions than sensitive species like wolffish and cod (Vaquer-Sunyer and Duarte, 2008; Dupont-Prinet et al., 2013).

All subhabitats showed declining biomass trends (Figure 4; the steepest decline occurred where biomass was the greatest), consistent with previous reports of trends of mature individuals on the Scotian Shelf (Simon *et al.*, 2011). The decline in Wolffish



Figure 7. Box plot of bottom temperature (as measured in the Atlantic wolffish surveys) in the three subhabitats on the Scotian Shelf, per 8-year period (see inset in Figure 3): "always suboptimal" (red), "optimal-to-suboptimal" (blue), and "always optimal" (black). The lower and upper limits of each box represent the 25 and 75% percentiles, respectively; the horizontal line within each box indicates the median bottom temperature in the subhabitat; the dashed, vertical lines indicate the range in each subhabitat. The dotted, horizontal line indicates the 6°C temperature. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

abundance in this region, as well as in the Gulf of St Lawrence and off Newfoundland and Labrador, has been attributed to fishing activity (O'Dea and Haedrich, 2002). Our analysis suggests that the change in DO may be a further stress on recovering Wolffish populations. Temperature, depth, and substrate type are other important factors influencing distribution (Keats et al., 1985; O'Dea and Haedrich, 2002). Depth and sediment type have not changed in the different subhabitats, except for possible habitat damage by trawling (O'Dea and Haedrich, 2002). Remarkably, temperature does not show a warming trend in our survey data from 1970 to 2009 (Figure 7). The median temperature in the "always optimal" subhabitat (black box plots in Figure 7) is around the upper limit of preferred temperatures for Atlantic wolffish (6°C, Scott, 1982; O'Dea and Haedrich, 2002), while "always suboptimal" regions are generally warmer than 6°C (red box plots in Figure 7). In contrast, oxygen is decreasing and could play a role in the contraction of optimal habitat. It is not known if the suboptimal habitat identified in this study was characterized by a greater fishing intensity than the "always optimal" subhabitat. Estimates of fishing pressure or fishing mortality would help elucidate the role of this anthropogenic factor. However, these calculations are complex, requiring information like age structure and natural mortality, and are beyond the scope of this study.

The management plan for Atlantic wolffish and recovery strategies for Spotted and Northern Wolffish in Canada only considered oxygen depletion as a problem related to the eutrophication resulting from dumping of fish waste (Kulka et al., 2007). However, the report on the progress of the implementation of this plan and its strategies did include issues related to hypoxia in the Gulf of St Lawrence and studies on the effects of DO on growth in some species (DFO, 2013). We believe this is a step in the right direction. Following the precautionary principle, we argue that management and policy should take DO into consideration as a potential stressor of Atlantic wolffish and other marine animals. In times of unprecedented change and on the doorstep of no-analogue climates, society, managers, and policy-makers need to use available information, although incomplete, to plan for the future. In particular, present and future DO levels should be considered when deciding the location of MPAs. Current MPAs may become ineffective if the marine species

that they intended to protect shift their location due to environmental changes (Hartman *et al.*, 2014). Model sensitivity studies like the one presented here could help establish a more dynamical definition for any given MPA (e.g. using temperature, oxygen, and/or any other appropriate variables instead of just latitude, longitude, and bathymetry ranges).

Conclusions

We show that DO is related to Atlantic wolffish suitable habitat and suggest that the contraction of Wolffish distribution is consistent with the expansion of low oxygen areas. Furthermore, since the deeper areas of the shelf are connected to the open ocean through upwelling, these areas are vulnerable to a continued decline in offshore oxygen conditions. While we do not suggest that oxygen drives the observed decline in Atlantic wolffish populations, the hypothesis that oxygen affects Wolffish habitat in this region is plausible and consistent with the available observations. Therefore, we argue that management and policy should consider oxygen as one of the potential stressors of Atlantic wolffish and other oxygen-sensitive marine animals.

Here, we highlighted how the combined use of observations and numerical models provides a powerful tool to study optimal habitats of marine species in past, present, and future conditions. Moreover, we note that while our model and analysis is region-specific, the methodology could be applied to any given region and to different species (and of course, it could be applied to other stressors, like temperature and/or pH). In particular, the design of future policies, recovery strategies, and MPAs can benefit from using numerical models as a tool to constrain or elucidate the direction and likely ranges of future changes in ocean conditions. Mills et al. (2013) already recommended the use of coupled models linking physical changes to biological outcomes and economic impacts to help sustain fisheries and fishing communities in a warmer and more variable climate. While the future will always remain uncertain and present knowledge will always have gaps, the precautionary principle urges to use the best available information during planning and decision-making to provide the necessary protection to marine ecosystems and the many socio-economic sectors that depend on them.

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