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IFMA Module 1b Ocean Chemistry: Fisheries and Low Oxygen

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Executive Summary

As a result of climate change, low oxygen conditions are predicted to occur more frequently and over a much greater geographic extent in the near future. Oxygen is essential for aerobic metabolism of marine organisms and oxygen availability affects habitat suitability for all fish species, yet little research has focused on the availability of oxygen in relation to climate change. Much work has been carried out with regard to the effects of acute hypoxia on the physiology of marine species, but far less on long-term, chronic effects and especially concerning commercially important fish and shellfish. The experimental results produced under this work contribute to filling that gap, by furthering our understanding of the effects of low oxygen conditions on sea bass in a warming climate. We have carried out experiments on sea bass (*Dicentrarchus labrax*) to determine their metabolic scope and critical oxygen tension at realistic future UK sea temperatures.

All fish showed very similar maximum and standard metabolic rates at each temperature. The metabolic rates increased with increasing temperature, and the metabolic scope also increased. This suggests that temperatures were not high enough to limit the metabolic scope, and that temperatures higher than those likely to occur in the North Sea this century are required to limit this. However temperatures were high enough to affect the metabolic rates of the fish, which used more oxygen for the same metabolic processes at 21°C and 23°C than at the lower temperature of 19°C.

The critical oxygen experiments were less straightforward to interpret because there was insufficient mixing in the respirometer chamber, which meant that oxygen consumption was overestimated. Initial analysis has been carried out to try to correct for this mixing effect, but more work is needed to give accurate oxygen consumption values. The data however did vary across the different temperature treatments, and there was an observed difference in the oxygen concentration at which the oxygen consumption starts to reduce at different temperatures. This indicates that oxygen concentration is more limiting to sea bass at the higher temperatures, however further work is required to produce robust results.

The results will be analysed in detail, in combination with a meta-analysis from the wider literature, as part of Cefas' internal investment project DP329 "Fisheries, Low Oxygen and Climate Change (FLOX)", in which the results will be used to model the potential effects of projected low oxygen and increased temperature conditions in the North Sea. The utility of these experimental results within FLOX will mean that they are not only a 'means to an end', but that they will be applied in a meaningful way to scale up to ecosystem-wide consequences for commercial fisheries. Within IFMA we have demonstrated that Cefas has the capability to perform metabolic scope and critical oxygen measurements, which have until now, have not been performed at either Lowestoft or Weymouth.

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1 Introduction

Oxygen availability is a key factor that determines habitat suitability for marine fish. As a result of climate change, low oxygen conditions are predicted to occur more frequently and over a much greater geographic extent in the near future. Low oxygen was among the 75 risks considered in the 'Marine & Fisheries' sector report of the UK CCRA in January 2012, but the potential threat could not be adequately quantified at that time. Similarly, oxygen concentrations are specifically mentioned in the EU Marine Strategy Framework Directive (under descriptor 3), which states that governments should take action such that *"reductions of oxygen concentrations do not constitute an undesirable disturbance to the balance of organisms present in the water and to the quality of the water concerned"*. This work also fits with the NAP action on Good Environmental Status (listed on page 161 of the 2013 NAP document).

Persistent low oxygen regions (such as the Oyster Grounds in the North Sea) have already been recorded (Figure 1) as a result of a previous Defra-funded research project ('Marine Ecosystem Connections'). In this region, oxygen conditions are projected to reduce further in the coming century (van der Molen *et al*., 2013). A review paper has been submitted to the *Journal of Fish Biology* (Townhill *et al*., submitted) which argues that much research has already been conducted with regard to the effects of acute hypoxia on the physiology of marine species, but far less on long-term, chronic effects and especially concerning commercially important fish and shellfish. The review concludes that more work needs to be done, to integrate experimental results with modelling techniques, particularly around the UK. The experimental results produced under this work package contribute to filling this gap, by furthering our understanding of the effects of low oxygen conditions on sea bass in a warming climate.

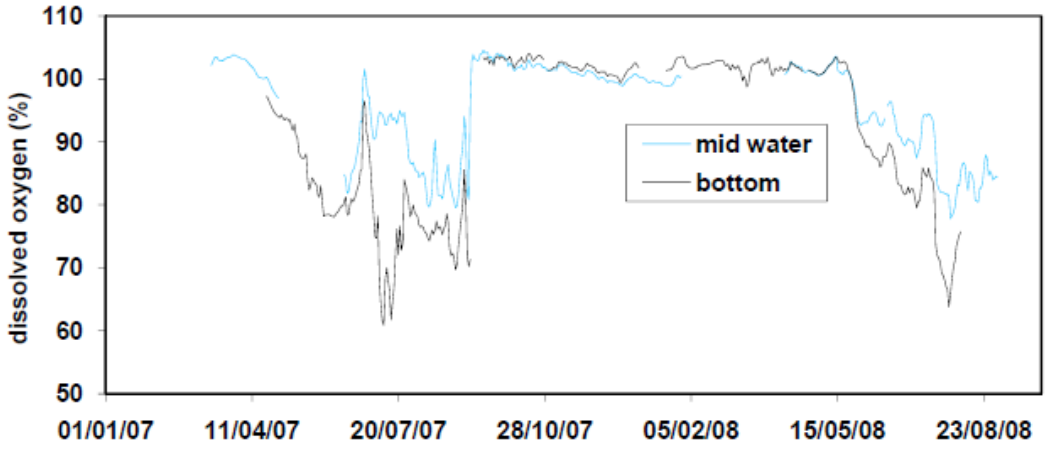

Figure 1. Oxygen saturation data at 35 m (mid water) and 45 m (bottom) depth within the Oyster Grounds region of the central North Sea in 2007 and 2008 (taken from Greenwood *et al*., 2010).

Metabolic or aerobic scope is a good measure of the capacity of fish to grow, feed and reproduce (Fry, 1971). Temperature and oxygen levels both limit the metabolic scope of fish (Fry, 1947), as illustrated in Figure 2, the rationale being that the physiological evolution of fish has resulted in maximised metabolic scope within a certain temperature range within which performance (growth, feeding, reproduction, movement etc.) is optimised (Clark *et al*., 2013). Some argue that maximum metabolic scope is not a good measure of a fish's optimum water temperature (Clark et al., 2013), however changes in metabolic scope over a realistic environmental temperature range can give insights into the ability of a fish to perform its necessary behaviours.

The concept of metabolic scope developed by Fry (1971) can be most easily explained diagrammatically (Figure 2). Metabolic scope is the difference between the maximum metabolic rate and the standard metabolic rate – that is the range of metabolic rates within which a fish can perform its physiological and behavioural functions such as swimming, feeding, reproducing. Standard metabolic rate increases more than maximum metabolic rate with increasing temperature, and maximum metabolic rate decreases with lower oxygen levels. This therefore causes a narrowing of the metabolic scope within which a fish can perform its necessary functions. Metabolic scope measurements are relatively straightforward in the laboratory and in the study of Cucco *et al*. (2012), have been combined with outputs from hydrodynamic models to predict suitable habitats for flathead grey mullet in the Mediterranean.

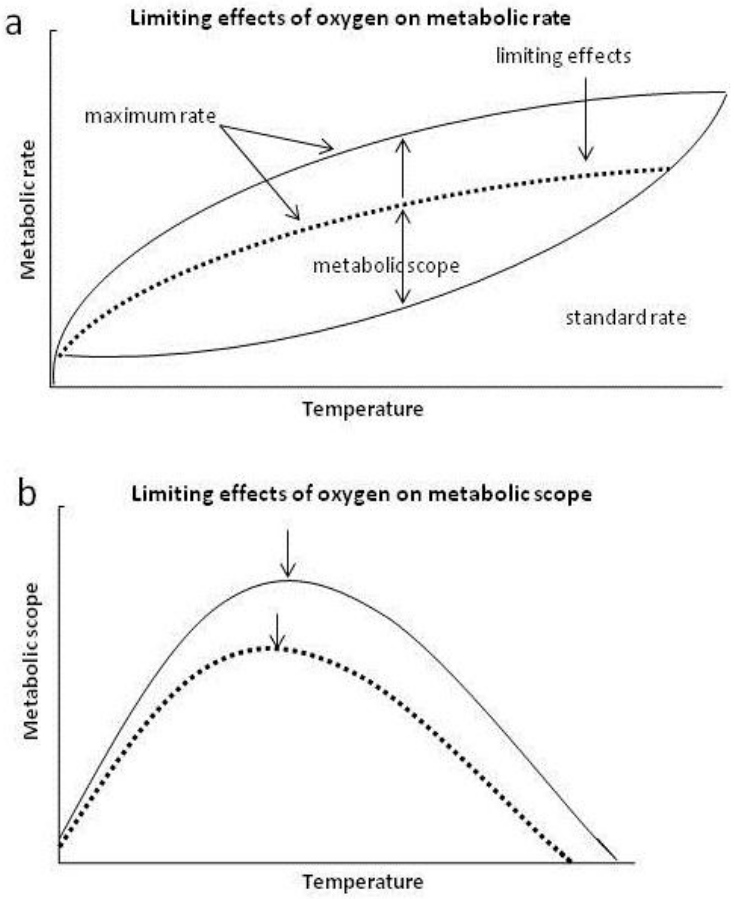

Figure 2. (a) The limiting effects of reduced oxygen on maximum metabolic rate. Increasing temperatures narrow the gap between maximum and standard metabolic rates, and so reducing metabolic scope. Reduced dissolved oxygen will also cause limiting effects on the maximum metabolic rate (dotted line), again reducing the metabolic scope. (b) The limiting effects of reduced oxygen on metabolic scope. Reduced oxygen causes a reduction in metabolic scope (dotted line) compared with full oxygen (solid line), and displaces the optimum temperature for scope (arrows). Adapted from Fry (1947).

Another way of characterising the hypoxia tolerance of fish is the critical oxygen tension or threshold (P_{crit}). This is the lowest partial oxygen pressure that enables the fish to maintain its resting (routine) oxygen consumption (Nilsson and Randall, 2010). To measure this, the resting rate of oxygen consumption is measured at different oxygen levels, and the P_{crit} is the oxygen concentration at which oxygen consumption begins to drop. At oxygen concentrations below the P_{crit}, oxygen delivery can't meet demand and a fish is unable to perform its resting metabolic processes aerobically and will eventually die (Schurmann and Steffensen, 1997). Some species are more tolerant of hypoxia than others and have a lower P_{crit}. Basal metabolic rate rises with temperature, and so with climate

change, the oxygen concentration required to maintain resting metabolic processes may be increased (Nilsson and Randall, 2010).

1.1 Aims

Within IFMA, we have carried out similar experiments to Cucco *et al*. (2012), on sea bass (*Dicentrarchus labrax*) to determine metabolic scope and critical oxygen tension at realistic future UK sea temperatures, in order to determine whether future oxygen and temperature conditions in this region will be limiting to this species. Fish respiration was examined at different temperatures and ambient oxygen concentrations, using equipment and animals already available at the Cefas Lowestoft laboratory, yielding both metabolic scope and critical oxygen threshold data.

2 Methods

All experiments were carried out under the authority of the UK Home Office project licence PPL 70/8027 and regulated by the UK Animals (Scientific Procedures) Act 1986.

2.1 Approach

Sea bass (n=6) were pit-tagged and held in the Lowestoft aquarium facility in a tank supplied with aerated sea water at a temperature of 19°C. Fish lengths ranged from 31 to 38 cm. The bass had been captive bred also at the Lowestoft aquarium. The experimental method was to carry out metabolic scope experiments overnight, and critical oxygen experiments the next day with the same fish, initially at 19°C. This was then repeated the next evening with the next fish, and when the experiments had been completed with all 6 fish, the temperature of the holding tank was increased to 23°C and fish were left to acclimate for 2 days. The experiments were then repeated in the same manner, with the respirometer temperature also increased to 23°C.

The method of measuring oxygen consumption followed that of Wright *et al*. (2014). A Brett-type swim tunnel respirometer (Brett 1965) using intermittent flow (Melzner *et al*., 2009) was used. The respirometer (swim chamber section of 25 × 25 × 87 cm) was submerged in an outer tank, which measured 232 × 95 × 70 cm having a total water capacity of 187 l (Loligo Systems, ApS). After each measuring phase, the outer tank provided the source of aerated water which was used to flush the inner swim chamber (flush pump, Eheim, 20 l min^{-1}). The outer tank was filled with an inflow (1 lmin^{-1}) of fresh seawater (from an in-shore well) throughout to ensure high water quality. The water in the outer tank was kept fully aerated during the metabolic scope experiments, or the oxygen level controlled during the critical oxygen experiments, and temperature maintained using a temperature regulator (Loligo Systems). Water velocity in the swim chamber was maintained at

22.146 cms^{-1}. The constant movement of the water aimed to ensure that the oxygen tension remained fully mixed throughout the chamber to obtain as accurate a measurement as possible.

Each experiment was broken down into 'measurement', 'flush' and 'wait' phases. During the measurement phase, the swim chamber was completely shut off from the outer tank, and the oxygen tension of the water chamber recorded using a galvanic oxygen electrode. Mass-specific oxygen consumption (MO_2) was calculated from the rate of decrease in oxygen tension. During the flush phase, the swim chamber was flushed with aerated seawater from the outer tank to either replenish oxygen levels (during the metabolic scope experiments) or to decrease the oxygen levels in the chamber (critical oxygen experiments). A wait phase enabled the oxygen levels to stabilise within the chamber before the next measurement phase, ensuring accurate consumption measurements.

The phases of the experiments were automatically controlled through an interface (DAQPAC- G1X, Loligo Systems) connected to a PC with AutoResp™ software (Version 1.6, Loligo Systems). A mini-DO galvanic cell oxygen probe suspended into the water current of the respirometer, connected to the DAQ interface, was used to measure oxygen tension within the swim chamber. Oxygen saturation data was calculated using Auto - Resp™. In a previous study within the same respirometer, Wright *et al*. (2014) had created a visual cue for orientation to encourage the fish to maintain position toward the front of the swim chamber (following Griffiths & Alderdice 1972) using strips of black electrical tape spaced 1 cm apart, fixed vertically to the outer wall at the front of the chamber. This was left in place for these experiments.

On completion of the critical oxygen experiment, the swim chamber was completely flushed with fully aerated water until the fish returned to resting metabolic rate and then the fish were returned to the holding tank.

2.2 Metabolic scope

At the start of each experimental procedure, one fish was captured from the holding tank at approximately 5pm, its pit-tag read, and then transferred to a large bucket. It was then chased with a wooden stick for 3 minutes to increase its activity levels as much as possible. It was immediately placed in the swim chamber of the fully aerated respirometer. The outer tank was set to continuously flush (to maintain aeration). MO_2 in the swim chamber was measured for 300 seconds

at 185 second intervals (180 second flush, 5 second wait) overnight, with the fish's metabolic rate gradually decreasing from being chased to swimming gently in the respirometer.

2.3 Critical oxygen threshold

The morning following the metabolic scope experiments, the phase period of the respirometer was changed to 600 seconds flush, 5 seconds wait and 300 seconds measure. At the same time, the oxygen levels in the outer tank were steadily lowered at a rate of between 2-3 kPa per hour by bubbling nitrogen gas through an air stone. This was continued throughout the day until an oxygen level of approximately 30% was reached, at which point the nitrogen flow to the air stone was replaced with air and the respirometer set to continuous flush, to ensure that the fish recovered quickly and fully from the low oxygen conditions. Once the fish behaviour was back to normal (swimming normally, no longer sluggish), the fish was returned to the holding tank.

A nitrogen test run was also carried out using the same methodology, but without a fish in the respirometer.

2.4 Data analysis

As with Wright *et al.* (2014), in order to take into account size differences in fish, MO_2 was calculated from raw oxygen consumption values (Fonds *et al*., 1992, Clarke & Johnston 1999, Sloman *et al*., 2006) using:

$$MO_2 = V \times \left(\frac{\delta pO_2}{\delta t}\right) \times \alpha M^{-1} \qquad (1)$$

where V is the volume of the swim tunnel, pO_2 is the partial pressure of oxygen, t is time, α is the oxygen solubility and M is the wet weight of the fish. The MO_2 values were standardised to 800 g using an allometric scaling exponent of 0.8 (Fry, 1971, Edwards *et al*., 1972). Those results with an R^2 of less than 0.7 were discarded.

The maximum MO_2 value recorded for each fish over the metabolic scope experimental period was taken as the maximum metabolic rate, and the mean of the lowest 10% of values taken as the standard metabolic rate. The difference between these two was the metabolic scope.

For the critical oxygen P_{crit}, the MO_2 was plotted for the duration of the experiment. In a well-mixed respirometer, the critical oxygen threshold was taken as the oxygen concentration at which the MO_2

began to drop. However, on analysing the results, it was discovered that in this experiment, oxygen use within the chamber was overestimated because there was insufficient mixing as the water became de-oxygenated. To correct for this over-estimation of oxygen use, the difference between the ambient and chamber oxygen content at the start of the measuring phase in the nitrogen test run was compared to the amount of erroneous oxygen use - measured as the difference from the start and end of the trial (Figure 3). The linear correlation between the two components provides a means to correct for the over-estimated oxygen use within the chamber.

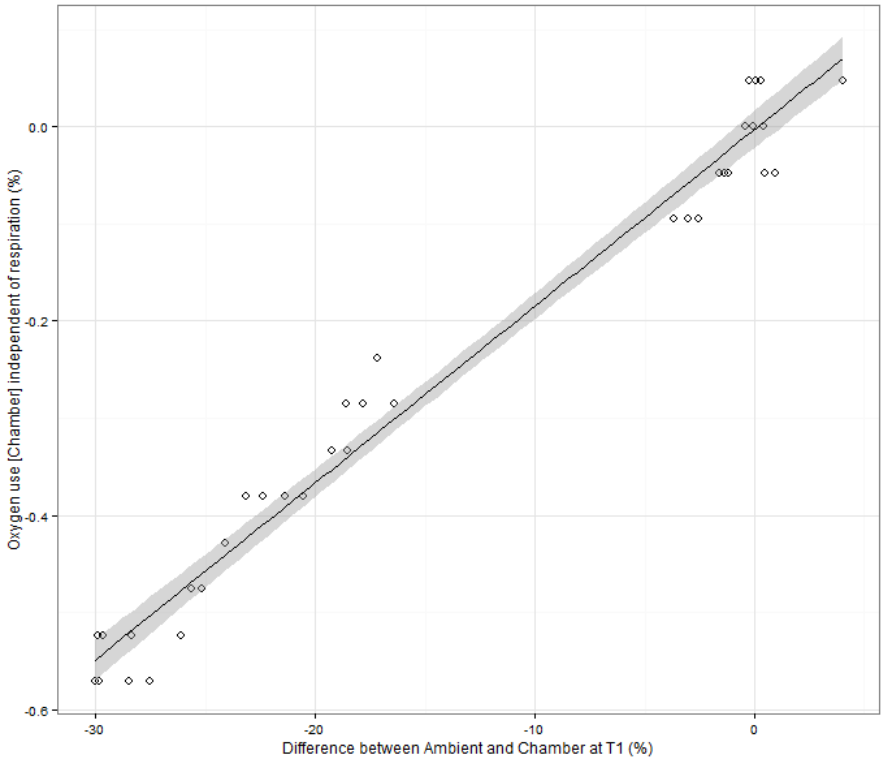

Figure 3. Difference between the ambient and chamber oxygen content of the water (%) at the beginning of the experiment (T1) in relation to the oxygen use recorded in the chamber as a result of insufficient mixing, for the nitrogen test run. The linear regression corresponds to y=x*0.018174-0.002678.

By correcting for this difference using the nitrogen test run, the oxygen consumption measurement was corrected to close to 0 $mgO_2/kg/hr$ (Figure 4). This correction was therefore applied to all of the results, in order to show the oxygen consumption due only to the fish, and not to the mixing oxygen.

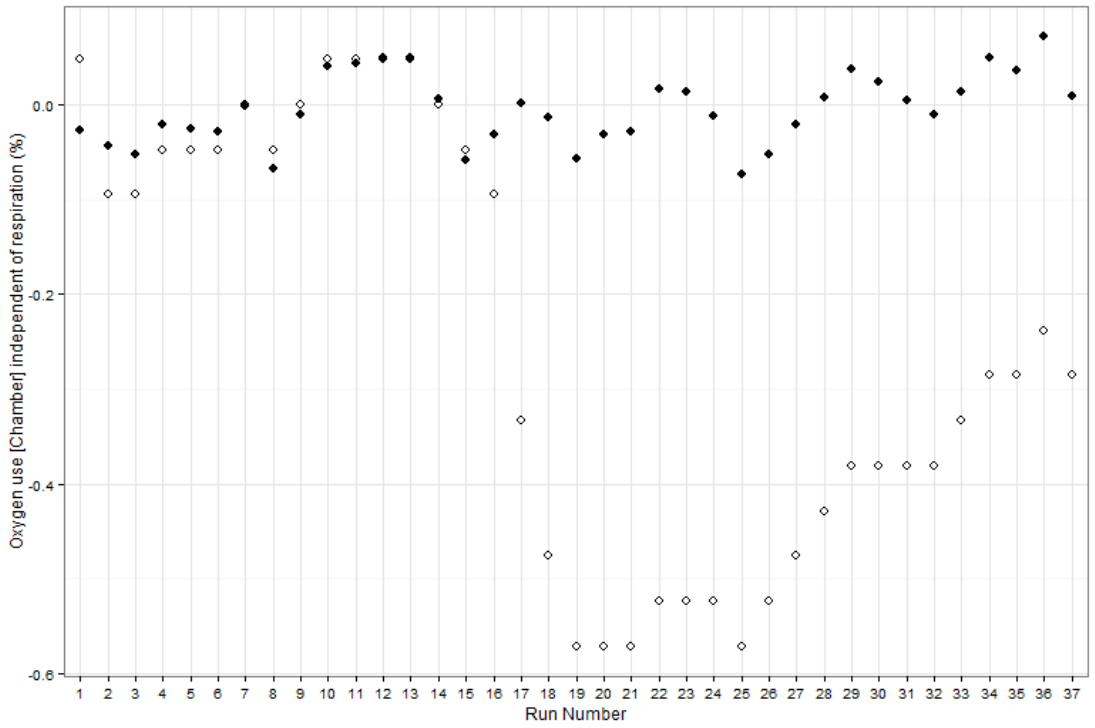

Figure 4. Oxygen use recorded in the chamber as a result of insufficient mixing before (hollow circles) and after correction (black circles). The rate of nitrogen inflow was increased at around run 14, where the sudden increase in oxygen use is seen. Each run number is one measuring phase, beginning when the nitrogen gas is switched on.

3 Results and Discussion

3.1 Metabolic scope

All fish showed very similar maximum and standard metabolic rates at each temperature. The metabolic rates increased with increasing temperature (example of one fish shown in Figure 5), and the metabolic scope also increased (as the gap between maximum and standard metabolic rate increased) (Table 1). This suggests that these temperatures were not high enough to limit the metabolic scope, and that temperatures higher than those likely to occur in the North Sea this century are required to limit this. They are high enough however to affect the metabolic rates of the fish, with fish using more oxygen for the same metabolic processes at 21°C and 23°C than at the lower temperature of 19°C.

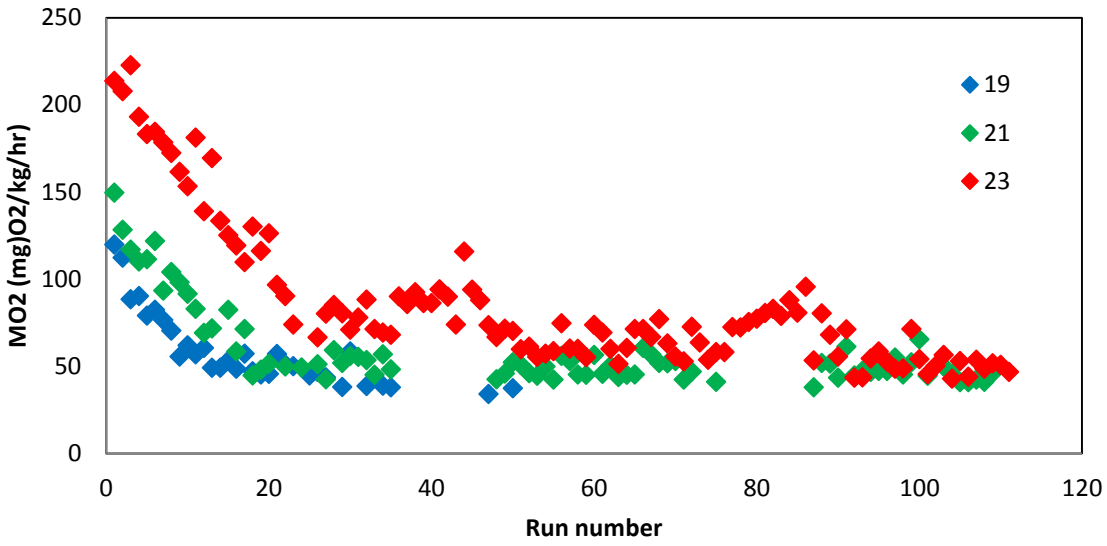

Figure 5. The metabolic rate decrease at different temperatures of fish number 6223 after being chased at run 0, to being left to rest overnight. Temperatures shown in °C. The highest (maximum) and lowest (standard) metabolic rates increase with increasing temperature. Each measurement phase is one run. Results with an $R_2 > 0.7$ were discarded and so are not shown.

Table 1. Summary of results for all fish at different temperatures.

Temperature (+-0.5) (°C)	Maximum Metabolic Rate ($mgO_2/kg/hr$)		Mean Standard Metabolic Rate ($mgO_2/kg/hr$)		Mean Metabolic Scope ($mgO_2/kg/hr$)	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
19	138.6	18.0	45.26	8.7	84.73333	24.7
21	205.14	67.7	49.6	9.1	155.54	64.8
23	208.4833	62.1	55.88333	4.7	152.6	61.0

3.2 Critical oxygen threshold

Critical oxygen threshold experiments were somewhat less straightforward and more complex to interpret than metabolic scope experiments. The insufficient mixing problem that was found in the respirometer during the critical oxygen experiments make the oxygen results less robust than those for metabolic scope. In the raw data there is overestimation of the oxygen consumption, because the water in the chamber was still mixing with the lower oxygen water during the measuring phase. Having applied the correction for this mixing, using the nitrogen test run, there are still

unexplainable trends in the oxygen consumption of the fish, which may be a result of artefacts. Therefore more work is required to remove the mixing effect of the chamber with the ambient water, in order to extract the actual oxygen consumption of the fish. Future experiments must consider the problems experienced here, and ensure that the flow rate, the flush, wait and measurement periods are sufficient to ensure that water is sufficiently mixed and the oxygen consumption measurements are true representations. Different methods of reducing the oxygen levels could also be considered, such as using step-wise reductions instead of the gradual reductions used here.

Even without having fully corrected the data for the lack of mixing however, there are still interesting trends which can be noted between temperatures. All of the fish at each temperature showed a similar pattern of oxygen consumption, with the consumption starting to decrease around 40-50% at 19°C, approximately 60% at 21°C, and around 70% at 23°C (example of one fish shown in Figure 6). These initial results indicate that as temperature increases the fish are limited by the oxygen content of the water at a higher oxygen concentration, however further investigation is needed to fully interpret these results.

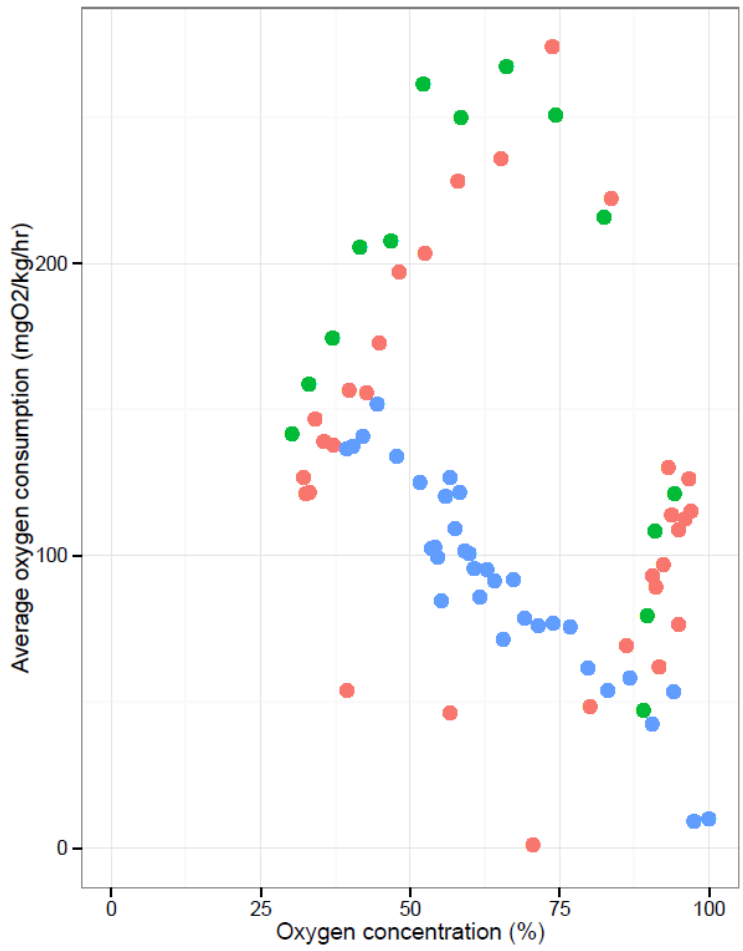

Figure 6. The critical oxygen threshold experiment raw (uncorrected) data for fish number 6223. Red = 23°C, green = 21°C, blue = 19°C. It can be seen that the peaks in oxygen consumption appear at higher oxygen concentrations as temperature increases.

4 Conclusions

The results will be analysed in detail as part of Cefas's internal investment project DP329 "Fisheries, Low Oxygen and Climate Change (FLOX)". These results, and those from a metadata analysis, will be used to spatially model the potential effects of projected low oxygen and increased temperature conditions in the North Sea. The critical oxygen threshold results will be further scrutinized and if possible, the mixing effect removed to produce values for the P_{Crit} for sea bass. If suitable, these experimental results, and those from the published literature, will be combined directly with historic oxygen measurements (Queste *et al*., 2012) and/or future projections from the GOTM-ERSEM coupled model (and by van der Molen *et al.,* 2013). The results will then be used to discuss whether

different species of commercial fish will be negatively affected by predicted future changes in oxygen and temperature in this region. This analysis will be based on metabolic scope, P_{Crit} and other oxygen threshold values and metrics available in published work.

Within IFMA Cefas has undertaken the preliminary work to perform metabolic scope and critical oxygen experiments, which have until now, not been performed at either the Cefas Lowestoft or Weymouth laboratories. Lessons have been learnt from problems in the mixing, and consequently experiments in the future will benefit from this. Further experiments in this area on different species will be of benefit to further understanding of how commercially important fish, and shellfish, are able to cope with decreasing oxygen around the UK. Further experiments could include investigating the effect of low oxygen on the response of prey species to predators, predators to prey, and egg and larval growth rates. Being able to use these experimental results within FLOX will mean that they are not themselves a 'means to an end', but that the values can be applied in a meaningful way to give further insights into how commercially valuable fish species may be affected by climate change in the future, i.e. to answer the 'so what?' question of relevance to policy making and the fishing industry.

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