



The effect of progressive hypoxia on swimming activity and schooling in Atlantic herring

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Schools of herring exposed to progressive hypoxia show a peak in velocity during severe hypoxia, at 15–34% oxygen saturation, followed by a decrease in swimming speed until school disruption occurred. The observed increase in swimming speed during severe hypoxia reveals a graded response, since the lower the fish's swimming speed prior to severe hypoxia (U_{95-50} , the speed at oxygen saturations between 95 and 50%), the greater the relative increase in swimming speed. The oxygen saturations at which both peak velocity and school disruption occurred were lower for fish with lowest U_{95-50} , suggesting that the fish with the slowest speed U_{95-50} reach their critical P_{O_2} (at which there is respiratory distress) last, i.e. at lower oxygen saturation. At a functional level, it is suggested that herring encountering hypoxia increase their speed in order to find more favourable conditions, and the magnitude of this increase is modulated by their respiratory distress. It is also hypothesised that the observed increase in speed may be related to an increase in the rate of position shifting within the school. Since the oxygen saturation at which the response to hypoxia occurs and the magnitude of the response are related to the fish's preferred speed prior to severe hypoxia, it is suggested that such a preferred speed should be measured in experiments testing the effect of hypoxia on fish behaviour.

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INTRODUCTION

Oxygen availability is one of the main factors affecting the swimming activity of fish (Randall, 1970; Bryan *et al.*, 1990). The occurrence of hypoxic events in coastal environments has increased in recent years, due to the continual development of human activities along the coasts (Orel *et al.*, 1986; Baden *et al.*, 1990). Although hypoxic conditions are found usually in coastal areas, both benthic and pelagic fish may be subject to hypoxia at certain times of their lives or during certain seasons. For instance, herring *Clupea harengus* L., a pelagic species, may experience hypoxia in Norwegian fjords (Dommasnes *et al.*, 1994) and in the Kattegat and the Baltic Sea (J. F. Steffensen, pers. obs.). In addition, pelagic species may experience large reductions in oxygen availability when swimming in the centre-back region of a large school (McFarland & Moss, 1967).

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Although most authors have found an effect of hypoxia on the swimming activity of fish, results on various species have demonstrated both increases (Dizon, 1977; Bejda *et al.*, 1987) and decreases in swimming activity (Metcalf & Butler, 1984; Fisher *et al.*, 1992; Schurmann & Steffensen, 1994). In addition, it is unclear whether fish can recognize hypoxic water. Some early laboratory studies on stickleback *Gasterosteus aculeatus* L. (Jones, 1952) and on roach *Rutilus rutilus* (L.) (Hoeglund, 1961) suggest that hypoxia avoidance by fish was due to oxykinesis alone (i.e. unidirectional, increased activity level in hypoxic water resulting in the movement of the fish to higher-oxygenated water), and not because they were able to recognize hypoxic water. On the other hand, experiments on salmon *Oncorhynchus tshawytscha* (Walbaum) and *O. kisutch* (Walbaum), bass *Micropterus salmoides* (Lacépède) and bluegill *Lepomis macrochirus* Rafinesque have not supported this view, and suggest that fish could sense hypoxia as they had an immediate avoidance of hypoxic water (Whitmore *et al.*, 1960). Studies using oxygen gradients showed that roach (Stott & Cross, 1973) and brook trout *Salvelinus fontinalis* (Mitchill) (Spoor, 1990) spent less time in the deoxygenated region of the gradient than in the normoxic area. There is also evidence from various field studies that oxygen availability can affect the distribution of various species of fish (Congleton, 1980; Matthews *et al.*, 1985; Suthers & Gee, 1986).

These contrasting observations suggest that there may be species-specific differences in the reaction to and recognition of hypoxic water. The response to hypoxia is likely to be related to the fish's lifestyle and the characteristics of its habitat. For instance, schooling fish may have a tendency to increase in speed as a response to hypoxia, in order to increase the reshuffling of individuals in the school. Similarly, active pelagic fish may behave differently from sluggish benthic species. Skipjack tuna *Katsuwonus pelamis* (L.) (Dizon, 1977) are active pelagic species and their first response to progressive hypoxia is an increase in swimming speed. On the other hand, Fisher *et al.* (1992) found that the swimming activity of the eelpout *Zoarces viviparus* (L.), a benthic species, decreased when exposed to hypoxia, possibly due to its lower escape capacity, and suggests that such a behaviour can be advantageous in an environment where hypoxic conditions are of short duration. Similarly, Dallavia *et al.* (1998) found that the spontaneous swimming activity of the sole *Solea solea* L., a benthic species, was lowered when exposed to gradual hypoxia, and burst activity occurred only as a last response at oxygen saturation close to lethal, i.e. <5%. It is also possible that previous contradictory results may be due to different experimental methods. Among these, the rate of deoxygenation seems to be a relevant factor. Moss & McFarland (1970), for instance, found that the swimming speed of schooling anchovies *Engraulis mordax* Girard did not vary in response to a slow reduction in hypoxia, but increased suddenly in response to a rapid reduction of oxygen.

In addition, at least from a theoretical point of view, it is unclear whether it would be advantageous for a fish to increase or decrease its speed in reaction to hypoxia. An increase in activity may increase the fish's probability of finding a more suitable environment, although it would also increase the risk of exhaustion. On the other hand, decreasing swimming speed may be in accordance with the reduced metabolic scope (the ratio of maximum metabolic rate to basal

metabolic rate) caused by hypoxia (Fry, 1971), but it would also reduce the chances of reaching a more favourable environment. This is not necessarily only represented by better oxygenated water, but also by lower temperature, which decreases the metabolic activity and the lethal oxygen level of the fish (Schurmann & Steffensen, 1994). As shown in various animals, a response to hypoxic stress can be the selection of cooler environment, the so-called behavioural hypothermia response (Wood, 1995).

This dilemma may give rise to two alternative strategies, one implying an increase and the other implying a decrease in swimming activity (Schurmann & Steffensen, 1994), which may be species- or context-specific. Here, the hypothesis is tested that the fish's activity (speed) prior to severe hypoxia may modulate the occurrence of school disruption and variations in swimming speed during severe hypoxia. It is shown that the reaction of schooling herring to hypoxia may be more complex than suggested by the two-alternative hypothesis, since it entails a graded response that depends on the fish's activity level prior to severe hypoxia.

MATERIALS AND METHODS

EXPERIMENTAL ANIMALS

Atlantic herring (L_T 12.3 ± 0.65 cm; mean \pm s.e.; n of sub-sample=20) were caught locally by beach seine in the Dunstaffnage Bay, Scotland. They were held in recirculated sea water in circular tanks (2 m diameter; 90 cm depth) at the local conditions of temperature and salinity for several months before the experiments. The experiments were performed during August, at a water temperature of $15 \pm 1^\circ$ C.

EXPERIMENTAL APPARATUS

A school of 19–22 herring was exposed to progressive hypoxia, from normoxia to when they stopped schooling behaviour *sensu stricto* (Pitcher, 1983). School disruption was defined as the break up of the school, when fish do not show uniform orientations and are swimming in different directions. The experimental tank measured 2 m in diameter and was 1 m high. The water level was kept *c.* 60 cm. A CCD video camera was mounted 2 m above the tank and connected to a computer equipped with a video frame-grabber (Visionetics VFG-512 BC) that digitized single video frames with a resolution of 256×256 pixels at 25 frames s^{-1} . The position of the school was determined by calculating its geometric centre. The x - y coordinates of the geometric centre of the school were transmitted *via* an RS-232 port to a second computer with a data acquisition program (Labtech Notebook) which calculated the cumulative distance swum by the fish within successive 10-s periods, and stored it on disk for later analysis. The values of the distance were smoothed over 5-min periods using a moving average procedure. These values were used to calculate speed.

Temperature and % oxygen saturation were recorded using a combined temperature sensor and oxygen electrode (WTW Oxi196 Microprocessor Oximeter), placed by the tank wall at 20 cm above the bottom, and connected to the second computer *via* an AD/DA interface board (Data translation DT2801).

EXPERIMENTAL PROCEDURE

Herring were transferred from the holding tank to the experimental tank containing normoxic water (96–100% oxygen saturation) 1 day prior to the experiment. A total of 206 herring was used in 10 replicate experiments. All experiments were conducted in the afternoon. A cylinder of compressed nitrogen was connected to an air stone which was placed at the bottom of a cylindrical tank (50 cm in diameter, 2 m high) filled with water. This water was used as recirculating water for the experimental tank. Water was

deoxygenated in this separate cylindrical tank so that bubbles of gas would not disturb fish behaviour or obscure the video image. Water was pumped constantly from the bottom of the experimental tank to the bottom of the deoxygenation cylinder and overflowed from an outlet near the top of the deoxygenating cylinder back into the experimental tank. This resulted in a gradual decrease of the % oxygen saturation within the experimental tank. At the beginning of the experiments oxygen saturation was 96–100%. The experiment was stopped when school disruption occurred, i.e. at an oxygen saturation of 12–25%. No fish died during the experiments or subsequently. Oxygen saturation decreased from 95 to 25% in 219 ± 9 min (mean \pm s.e.; $n=10$). A minimal water circulation assured oxygen level to be uniform in different positions of the tank. At the end of the experiments, differences in % oxygen saturation between the centre of the tank, midway between centre and wall, and 5 cm from the wall (all measurements made immediately below the surface, midwater and bottom of the tank) were $<1\%$. Before and during the experiments, fish schools were swimming in a circular clockwise manner, at a distance of *c.* 10–30 cm from the wall, until school disruption occurred.

PARAMETERS ANALYSED

To test the hypothesis that the fish's activity prior to severe hypoxia may have an effect on swimming speed and schooling behaviour during severe hypoxia, the relationships between the activity prior to severe hypoxia (U_{95-50} , the mean speed between 95 and 50% oxygen saturation) and peak speed during severe hypoxia (U_M , maximum speed at $<50\%$ oxygen saturation), the last recorded value of speed just before school disruption occurred (U_D), the oxygen saturation at the time of U_M (O_M) and the oxygen saturation just before school disruption occurred (O_D) were analysed.

RESULTS

As a general qualitative rule, the swimming speed observed was relatively constant from the beginning of each run until about 50% oxygen saturation. At lower oxygen saturation, speed appeared to increase in most runs albeit to different degrees [Fig. 1(a)]. With even lower oxygen saturation, speed decreased in all runs until school disruption occurred. School disruption occurred as a sudden process. Surfacing occurred rarely, and usually at the time of school disruption. This pattern of the swimming speed was also shown in the averaged curve of all runs at 5% oxygen saturation intervals [Fig. 1(b)]. The mean swimming speed at the highest (U_{95} , swimming speed at 95% oxygen saturation) and lowest (U_{25} , swimming speed at 25% oxygen saturation) values of oxygen saturation available for all runs were compared. U_{95} was 0.30 ± 0.02 m s⁻¹ (corresponding to 2.5 ± 0.1 L s⁻¹) and U_{25} was 0.33 ± 0.1 m s⁻¹ (corresponding to 2.7 ± 0.1 L s⁻¹), respectively. These two values did not differ (paired *t*-test, $P>0.05$; $t=2.12$; d.f.=9; *n* of pairs=10). Although this result would suggest no effect of hypoxia on speed, there appeared to be, in most runs, an increase in speed during hypoxia, which varied considerably in extent and % oxygen saturation at which it occurred [Fig. 1(a)]. The peak in swimming speed occurred at different oxygen saturations, ranging from *c.* 15 to 34% [Fig. 1(a)]. Such a range may have masked any significant increase of speed at any given % of oxygen saturation. Similarly to peak speed, school disruption occurred at different % oxygen saturation for each run, ranging 12–25%. Therefore, the response to hypoxia was not stereotypical in terms of the oxygen saturation at which it occurred.

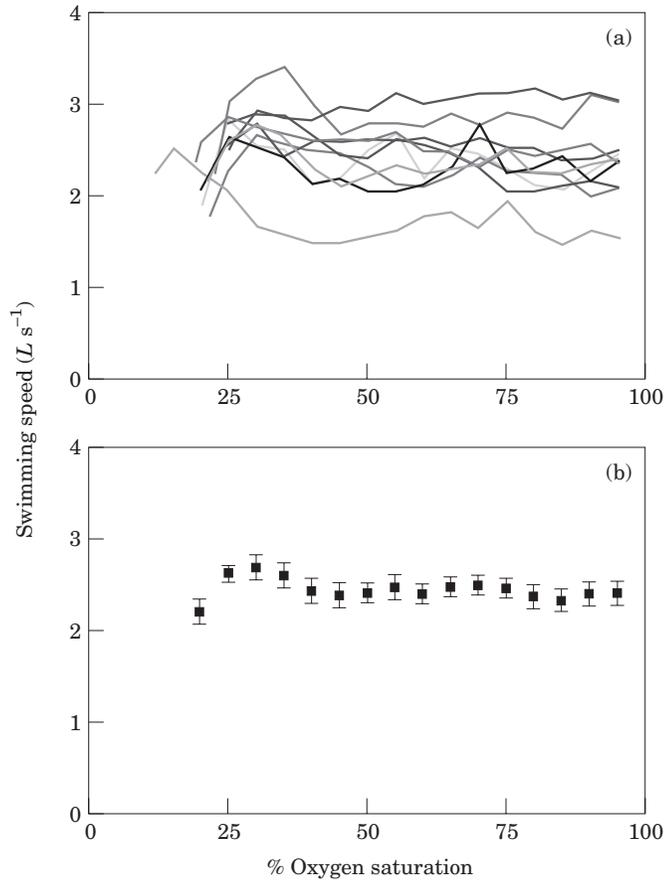


FIG. 1. (a) The swimming speeds of herring schools for each run at 5% intervals of oxygen saturation (10 runs total). (b) The average swimming speed at 5% intervals of oxygen saturation. Vertical bars indicate S.E.

Since comparison of swimming speeds at different fixed levels of hypoxia [as made by Moss & McFarland (1970), Dizon (1977) and Schurmann & Steffensen (1994)] may not reveal any significance in speed increase, as the speed increase occurred at various oxygen saturations, a new analysis is introduced that takes into account swimming speeds prior to severe hypoxia. This permits testing the hypothesis that the swimming activity level (speed) preceding severe hypoxia (i.e. U_{95-50} , the average speed between 95 and 50% oxygen saturation) modulates the herring response to hypoxia in terms of swimming speed and schooling behaviour (i.e., U_M , maximum speed at <50% oxygen saturation; O_M , the oxygen saturation at the time of U_M ; U_D , the last recorded value of speed just before school disruption occurred; O_D , the oxygen saturation just before school disruption occurred).

U_M increased with increasing U_{95-50} ($r^2=0.59$; $P<0.01$; d.f.=1.8; $F=11.36$; $n=10$) [Fig. 2(a)]. The regression line approached the line of identity at the highest values of U_M and U_{95-50} . This was also shown by the slope of this regression line, which differed significantly from unity (t -test; $P<0.01$; $t=3.7$; d.f.=8), i.e. the increase in speed ($U_M - U_{95-50}$) was not constant, but decreased

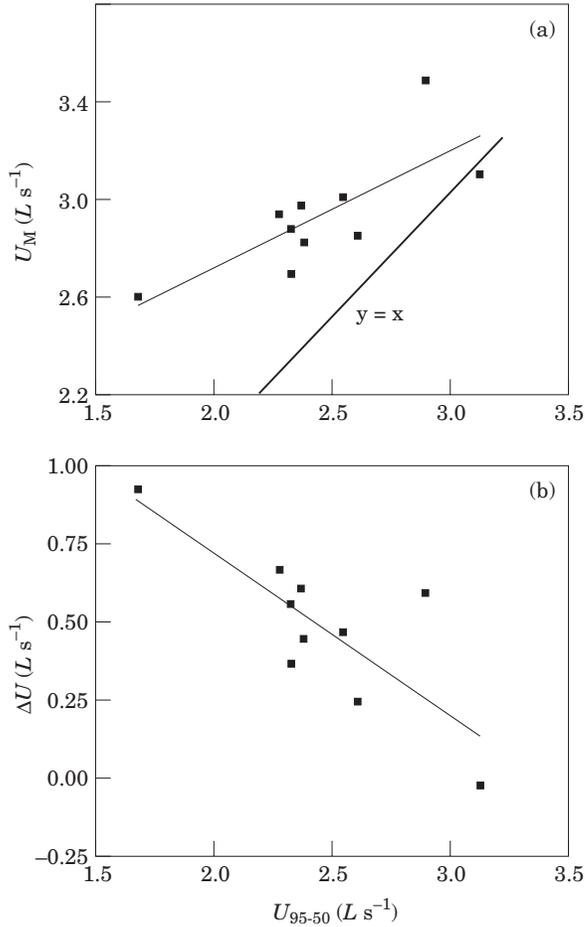


FIG. 2. (a) The linear relationship between U_M (maximum speed at <50% oxygen saturation) and U_{95-50} (the mean speed between 95 and 50% oxygen saturation) ($y = 0.48x + 1.8$; $r^2 = 0.59$; $P < 0.01$; $n = 10$). The regression line converges with the line of identity ($y = x$), meaning that at the highest values, U_M and U_{95-50} tend to converge. (b) The relationship between the increase in speed, ΔU (the absolute increase in speed for U_M relative to U_{95-50}) and U_{95-50} ($y = -0.5x + 1.8$; $r^2 = 0.63$; $P < 0.01$; $n = 10$).

linearly with increasing U_{95-50} . This pattern can be visualized by looking at the relationship between ΔU (the absolute increase in speed for U_M relative to U_{95-50}) and U_{95-50} [regression line in Fig. 2(b); $r^2 = 0.63$; $P < 0.01$; d.f. = 1.8; $F = 13.71$; $n = 10$]. In percentage terms, the increase of U_M relative to U_{95-50} corresponded to *c.* 50% for the lowest U_{95-50} ($1.6 L s^{-1}$), while it approached zero at U_{95-50} beyond $3.0 L s^{-1}$. The speed at which school disruption occurred (U_D) was not significantly related to U_{95-50} (non-significant regression; $P = 0.17$ d.f. = 1.8; $F = 2.23$; $n = 10$).

In terms of oxygen saturation, both O_M and O_D were related to U_{95-50} [regression lines on Fig. 3(a); $r^2 = 0.49$; $P < 0.05$; d.f. = 1.8; $F = 7.80$; $n = 10$ and Fig. 3(b), $r^2 = 0.78$; $P < 0.001$; d.f. = 1.8; $F = 27.79$; $n = 10$, respectively], in such a way that U_M and school disruption both occurred at higher oxygen saturations when U_{95-50} was higher. Therefore, the faster the herring swam prior to severe hypoxia, the higher the % oxygen saturation at which the increase in speed, and

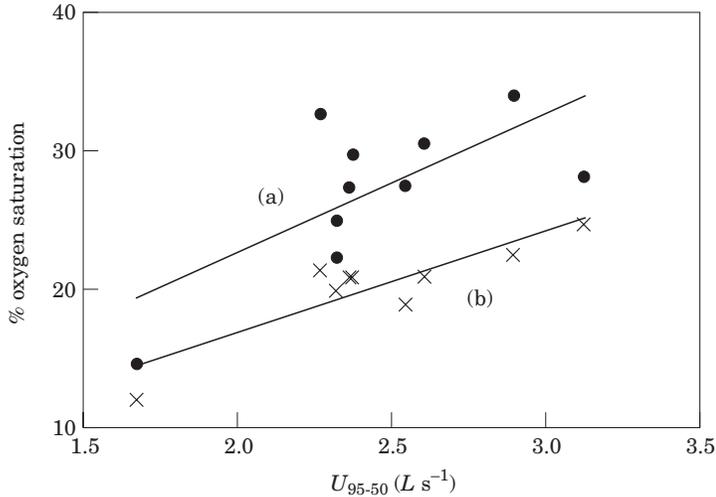


FIG. 3. (a) The relationship between O_M (●, the oxygen saturation at the time of U_M) and U_{95-50} (the mean speed between 95 and 50% oxygen saturation) ($y=10.2x+2.3$; $r^2=0.49$; $P<0.05$; $n=10$), and (b) O_D (×, the oxygen saturation just before school disruption occurred) and U_{95-50} ($y=6.6x+1.8$; $r^2=0.78$; $P<0.001$; $n=10$).

subsequent school disruption, occurred. In addition, as expected since both O_M and O_D were related to U_{95-50} , the correlation between them was significant (Pearson $r=0.82$; $P<0.01$; $n=10$).

CONSIDERATIONS ON SWIMMING SPEEDS AND PATH CURVATURE

The path curvature of fish swimming around a circle generates a swimming disadvantage when compared to a straight course. Circular tanks introduce an additional factor not encountered by fish swimming along a straight path (Weihs, 1981). This is the centripetal force required for continuous motion in a curved path. This force is proportional to the fish mass and inversely proportional to the path radius. The principles to be considered have been modelled by Weihs (1981) and applied to herring swimming around a circular path by He & Wardle (1988). Using equation 11 and Table I from He & Wardle (1988), and substituting values for path radius of 80 cm (present tank radius being 100 cm, and the approximate distance of the centre of the school from the wall being 20 cm) and herring length of 12.3 cm, it was calculated that, along a straight course, these herring might have swum 16% faster than the recorded values.

DISCUSSION

ALTERNATIVE STRATEGIES *V.* GRADED RESPONSE TO HYPOXIA

The effect of hypoxia on swimming activity has been the subject of a number of investigations (with contrasting results) in which the fish's response to severe hypoxia was an increase (Dizon, 1977; Bejda *et al.*, 1987) or a decrease in swimming speed (Metcalf & Butler, 1984; Fisher *et al.*, 1992; Schurmann & Steffensen, 1994). Schurmann & Steffensen (1994) suggested that such different responses may be ascribed to different strategies employed by the fish. Both

strategies, given certain conditions, may pay off. An increase in activity may increase the fish's chances of escaping from the hypoxic waters, although it would also shorten the time to exhaustion. On the other hand, a decrease in activity (and therefore oxygen demand) may be caused by hypoxia, but it would also reduce the chances of reaching better-oxygenated water or a cooler environment. It is possible that such alternative strategies may exist in different species or different experimental conditions.

The idea of two alternative strategies usually implies a bimodal pattern in the variable in question across individuals or species (McLaughlin, 1989), in the present case speed. However, present results show that the first response of herring to hypoxia is graded, i.e. it involves a range of responses from >50% increase between U_{95-50} and U_M , for the lowest U_{95-50} , to virtually no increase for the highest U_{95-50} . This first response was followed by a decrease in speed until school disruption occurred. This suggests that the herring response to hypoxia is more complex than previously assumed for other fish. The complexity of the response has implications both for the significance of the response itself and for the mechanisms producing it.

At the functional level, such a graded response may correspond to a continuous trade-off between the fish's respiratory distress at the given conditions of oxygen content in the water, and its need to find a more favourable environment by increasing swimming speed. In addition, the rise in speed is not sudden, but gradual. Such a gradual rise may have the benefit of delaying exhaustion. It is suggested that herring encountering hypoxia increase their speed to find more favourable conditions, but they do so according to their respiratory distress. This suggests a compromise between the two above-mentioned strategies.

Environmental oxygen concentration can be affected by the presence of large schools (Dommasnes *et al.*, 1994) and can vary within the school itself, with lower oxygen concentration in the centre-back of the school than in the front (McFarland & Moss, 1967). An increase in speed in fish that are experiencing low oxygen saturation may be related to an increase in the rate of position shifting within the school. This would not prevent hypoxia in the present study, since the small schools of *c.* 20 individuals were likely to experience similar hypoxic conditions at any given time during the experiment. However, in nature such a response to hypoxia may prevent the breaking up of a large school which would occur if the back of the school experienced the respiratory distress caused by hypoxia without a speed-increase reaction. Adaptively, such a behaviour corresponds to limiting the respiratory distress on each individual member of the school, as the negative effects (i.e. hypoxia) of being in the back of the school would be experienced only for a brief period of time by each fish periodically, in accordance with the relative repositioning of each individual. While being in the back of the school may be disadvantageous from a respiratory point of view, being in the front implies significantly higher predation risk (Bumann *et al.*, 1997). Therefore, in nature, shuffling of school positions may be related to a number of biotic and abiotic factors.

The mechanisms resulting in the observed response are unclear. It is interesting to notice that the speed increase response occurred at different oxygen saturations, depending on U_{95-50} . Assuming that fish in different runs had

similar sensitivity to hypoxia, this may imply that the response is not governed by a given hypoxic level, but rather by an internal balance between the hypoxic level and the respiratory distress of the animals. This would explain why slow swimming herring start increasing their speed at lower % oxygen saturation than fast swimming fish. This would be in accordance with Jones's (1952) hypothesis that it is the respiratory distress rather than the recognition of hypoxic water that triggers hypoxia avoidance.

The magnitude of the increase is not constant but depends on U_{95-50} . It could be expected that fish swimming with the lower U_{95-50} show the highest speed increase (ΔU), since having a lower activity prior to severe hypoxia may imply lower respiratory distress. Indeed, ΔU is inversely related to U_{95-50} . However, the peak velocity (U_M) of fish with the lowest U_{95-50} is the lowest in absolute value [Fig. 2(a)], possibly because O_M is lowest for fish with the lowest U_{95-50} . Therefore, the U_M of fish with low U_{95-50} may be limited by low oxygen saturation at the time of the speed increase (O_M). There is probably a critical P_{O_2} for respiratory distress, which is likely to change with U_{95-50} , since V_{O_2} at a given speed does not vary with P_{O_2} (Bushnell *et al.*, 1984). O_M and O_D vary with U_{95-50} (Fig. 3), suggesting that the fish with the slowest U_{95-50} would reach their critical P_{O_2} (at which there is respiratory distress) last.

The increase in speed in all runs is a gradual rather than a sudden response. The resulting peak speed may therefore depend on the length of time during which such an increase persists. While the increase is likely to be a behavioural response of hypoxia avoidance, the end of the increasing phase and the subsequent decrease in speed may occur in accordance with the physiological limits imposed by the combination of increasing speed and increasing hypoxia.

PREFERRED SWIMMING SPEEDS

The preferred speeds in this experiment should be viewed in the context of relevant reference values such as the calculated U_{opt} (the speed at the minimum cost of transport, Weihs, 1973) and the maximum sustained speed (U_{ms} , Videler, 1993) of herring. It should be taken into account that, while U_{opt} should not vary with the amount of oxygen dissolved in the water (since the relationship between V_{O_2} and speed does not vary with oxygen saturation; Bushnell *et al.*, 1984), U_{ms} should be related to it, and therefore would have varied during the experiment.

The calculated U_{opt} for a 15 g (the approximate weight of a 12.3 cm herring, based on Coull *et al.*, 1989) generic fish is around $2 L s^{-1}$ (Videler, 1993). He & Wardle (1988) found that the U_{ms} of 25-cm herring was $4.1 L s^{-1}$ at 14°C. Given that maximum sustained swimming speed in $L s^{-1}$ is inversely related to fish size (He & Wardle, 1988) we can expect 12-cm herring to have a U_{ms} slightly $>4 L s^{-1}$. The mean U_{95-50} in the present experiments was $2.4 L s^{-1}$ and ranged *c.* $1.5-3 L s^{-1}$ (Fig. 1). The observed variation in U_{95-50} can be ascribed to natural variation, as fish can choose their swimming speed although their preferred speeds are expected to be below U_{ms} and around U_{opt} . The U_{95-50} recorded is similar to the U_{opt} expected ($2 L s^{-1}$, see above), in accordance with previous results on fish preferred speeds (e.g. Weihs *et al.*, 1981) and is lower than the expected U_{ms} at normoxia, based on He & Wardle's results.

On the other hand, all values of U_M observed (range 2.6–3.5 $L s^{-1}$) are higher than U_{opt} . It appears that while the U_M is higher than the optimal speed such as that used in migrations, it does not exceed the maximum sustained speed, i.e. the speed beyond which fatigue would occur in normoxic conditions. While U_M is lower than the U_{ms} at normoxia, it may approach U_{ms} values for the oxygen saturation at which it occurs. The increase in speed observed does not correspond to a startle reaction at the burst swimming speed typical of fast-starts (maximum speed in fast-starts ranges between 7.4–13.6 $L s^{-1}$ in fish with lengths ranging between 10–14 cm; Domenici & Blake, 1997), but it appears to be a slight increase which may not imply a major recruitment of fast glycolytic (white) fibres. On the other hand, anaerobic metabolism within slow oxidative (red) fibers may occur due to hypoxia (as shown in salmonids, Farrell *et al.*, 1998).

SCHOOL DISRUPTION

Like U_M , school disruption occurs at a different oxygen saturation levels depending on U_{95-50} , so that fish with the lowest U_{95-50} show school disruption at the lowest oxygen saturations. This result is in line with the relationship between O_M and U_{95-50} and the significant correlation between O_M and O_D . School disruption is probably a result of the respiratory distress imposed on the fish. Fish that have swum at higher speeds must experience higher stress and exhaustion. The sensory capabilities needed for proper schooling, such as lateral line and vision (Partridge & Pitcher, 1980), may be affected by these conditions lowering the fish's general sensory awareness. In addition, when school disruption occurred, there were a few surface-gasping events, which may, in part, have been the indirect causes of school disruption by altering the speed coordination among school members. School disruption occurred at 12–25% oxygen saturation. Prior to such saturations, herring did not show any sign of distress although they increased their swimming speed, peaking between 15 and 34% oxygen saturation. Field data suggest that herring can tolerate oxygen saturations of *c.* 30% for long periods of time (2 ml l⁻¹ at around 7° C and 35% salinity in Dommasnes *et al.*, 1994).

Unlike all other variables, U_D (the swimming speed at school disruption) was not related to U_{95-50} . Assuming that school disruption is related to the respiratory distress experienced by the fish, this result suggests that, at the time of school disruption, fish with different U_{95-50} may have similar levels of respiratory distress, due to the compensatory effect of their different responses to severe hypoxia. School disruption in the field may depend on other factors such as the acuity of the hypoxic event. If hypoxia occurred gradually within a similar time frame as in the present experiments, school disruption would occur around 18–20% oxygen saturation, which corresponds to O_D at speeds near their optimal (estimated at *c.* 2 $L s^{-1}$ for the herring used in this experiment, see above) as wild fish may be expected to swim at when undisturbed (Weihs, 1973; Weihs *et al.*, 1981; Videler, 1993).

CONCLUSIONS

Although it is possible that present results are specific to herring and to these conditions of progressive hypoxia, a similar pattern may be present in other

species. Previous studies (Moss & McFarland, 1970; Dizon, 1977; Schurman & Steffensen, 1994) tested differences in speed attained at given oxygen concentrations during progressive hypoxia experiments. In the present experiments, the peak in speed (U_M) occurred at different oxygen saturations for each run, depending on U_{95-50} . Therefore, in experiments conducted using progressive hypoxia, measuring swimming speed at a given oxygen saturation may not result in significant values of increase in swimming speed, since the oxygen saturation at which the peak in speed occurs depends on activity prior to hypoxia (U_{95-50} in the present experiment). This may explain why some previous studies (e.g. Moss & McFarland, 1970) found no effect of progressive hypoxia on speed.

Also, after its peak, swimming speed decreased until school disruption occurred. This decrease was measured only until school disruption because of the methodology. In fish tracked singly, such a trend in decreasing speed may be monitored until the fish stopped swimming altogether, and may result in a major decrease in activity measured at a given oxygen level. Therefore, depending on the oxygen saturation at which speed is taken in experiments using progressive hypoxia, an increase or decrease in activity in response to hypoxia, or no effect at all, may be found, masking the complexity of the response. In conclusion, measuring fish activity at given oxygen saturations in progressive hypoxia experiments may not reveal the effect of hypoxia on activity. It is suggested that the response to hypoxia in terms of oxygen saturation at which the response occurs and the magnitude of the response are related to the fish's preferred speeds prior to hypoxia, and such activity should be measured in order to allow testing the effect of hypoxia on fish behaviour.

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