SPONTANEOUS SWIMMING ACTIVITY OF ATLANTIC COD *GADUS MORHUA* EXPOSED TO GRADED HYPOXIA AT THREE TEMPERATURES

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Summary

The spontaneous swimming activity of Atlantic cod *Gadus morhua* was investigated at graded levels of hypoxia at three temperatures (5, 10 and 15 °C) by using a computerized system monitoring animal activity. The fish were tested individually, and swimming distance was used as a measure of activity. No significant effect of temperature on swimming distance in normoxic water was found. At all temperatures, activity level decreased with decreasing oxygen saturation. Swimming behaviour at normoxia and 50 % and 25 % oxygen saturation is described. No apparent avoidance of hypoxic water was found based on the distribution of swimming speeds and turning angles. The possible benefits of a decreased activity level in a hypoxic environment are discussed.

Introduction

The activity level of fish is, among other factors, influenced by temperature (Sullivan, 1954; Bryan *et al.* 1990) and oxygen availability (Randall, 1970; Metcalfe and Butler, 1984; Kutty, 1968; Fisher *et al.* 1992; Nilsson *et al.* 1993). The swimming activity of red hake *Urophycis chuss* (Bejda *et al.* 1987) and skipjack tuna *Katsuwonus pelamis* (Dizon, 1977) has been reported to increase when the fish are exposed to hypoxia. However, a decrease in activity has been reported for both dogfish *Scyliorhinus canicula* (Metcalfe and Butler, 1984) and eelpout *Zoarces viviparus* (Fisher *et al.* 1992) when exposed to hypoxic water. When fish swim from normoxic to hypoxic water, the behavioural responses immediately after encountering hypoxic water vary from violent burst swimming in speckled trout *Salvelinus fontinalis* (Sheppard, 1955) to no response in sticklebacks *Gasterosteus aculeatus* (Jones, 1952). From experiments with sticklebacks (Jones, 1952) and roach *Leuciscus rutilis* (Höglund, 1961), it was concluded that fish were unable to recognize hypoxic water and that avoidance movements induced by respiratory distress led them to water with higher oxygen availability. Experiments with chinook salmon *Oncorhynchus tshawytscha*, coho salmon *Oncorhynchus kisutch*, largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus* (Whitmore *et al.* 1960), however, have not supported this view, since an immediate avoidance of

hypoxic water was found for these fishes. Other investigations with roach *Rutilus rutilus* (Stott and Cross, 1973) and brook trout *Salvelinus fontinalis* (Spoor, 1990) in oxygen gradients showed that these fish did not avoid hypoxic water completely but spent less time in the deoxygenated region of the gradient. The different responses reported in these studies may partly be due to the different experimental methods and conditions, but may also be ascribed to different strategies used by fish under hypoxic conditions. While an increase in activity level enhances a fish's probability of encountering better-oxygenated water, it also increases its oxygen requirements. Conversely, a reduction in activity in response to hypoxia, while decreasing the fish's oxygen requirements, also reduces its chances of reaching a more favourable environment.

A more favourable environment, in this case, does not necessarily mean better-oxygenated water, but could also include regions at lower temperatures. Temperature is an important environmental factor influencing the survival of fish in a hypoxic environment as shown by the lethal oxygen level of speckled trout *Salvelinus fontinalis* (Graham, 1949) and Atlantic cod *Gadus morhua* (Schurmann and Steffensen, 1992), which decreases with a reduction in water temperature. In their natural environments, e.g. the Baltic Sea, hypoxic conditions often prevail during the spring and autumn months. Over the same period, these waters are thermally stratified. It was therefore of interest to investigate how swimming activity of Atlantic cod is influenced by hypoxia and temperature. The present investigation describes the swimming activity, measured as actual swimming distance, of Atlantic cod exposed to graded hypoxia at three temperatures. Furthermore, to elucidate the influence of hypoxia on swimming behaviour, a more detailed description of the swimming behaviour of these fish at normoxia and at two levels of hypoxia is presented.

Materials and methods

Experimental animals

Atlantic cod *Gadus morhua* (L.) (body length 30±2 cm, mass 200–300 g) were caught by trawling in Øresund (Helsingør, Denmark). They were held in recirculated sea water (30‰) at 5, 10 or 15 °C for several months prior to the experiment. The fish acclimated to 10 and 15 °C were caught during the summer months of 1992 at ambient water temperatures of approximately 12 °C, while the fish acclimated to 5 °C were caught in autumn 1992 at water temperatures of approximately 8 °C. They were fed on commercial trout pellets and frozen mussels 2–3 times a week and were in good condition. The fish were starved for at least 3 days prior to the experiment.

Experimental apparatus

The tank in which the observations were made (Fig. 1) measured 120 cm×60 cm and had a water depth of 25 cm. The water temperature in the tank was kept constant (±0.2 °C) using a HETO thermostatted cooling system.

A CCD video camera mounted above the tank was connected to an Olivetti M24 computer (computer 1, Fig. 1) equipped with a video frame-grabber (Visionetics VFG-512 BC) that digitized single video frames with a resolution of 256×256 pixels at a speed
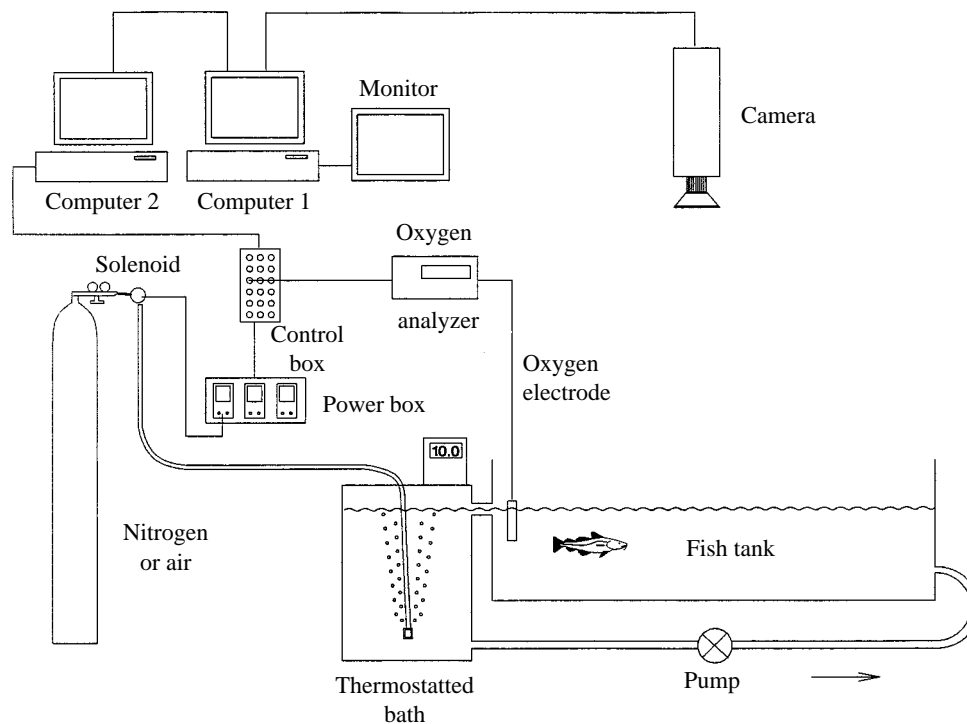
Fig. 1. The experimental apparatus used to record the activity of fish under different conditions. Computer 1 determined the position of the fish by digitizing video frames recorded by a CCD camera. The positions were collected in computer 2 every second and stored for later analysis. Computer 2 was also used to control the oxygen saturation of the water. Refer to text for more details.

up to real time ($25\,\text{frames}\,\text{s}^{-1}$). The tank was illuminated by two 60 W light bulbs, one at each end, to ensure uniform illumination. Under these lights, the fish had a silhouette that enabled the custom-designed software program to detect its position. The position of the fish was determined by calculating its geometric centre. The precision of the position determination was calculated by dividing the area covered by the camera by the number of pixels in this area. The area covered by the camera was $120\,\text{cm} \times 60\,\text{cm} = 7200\,\text{cm}^2$ and the number of pixels was $240 \times 150 = 36\,000$. Every pixel thus represented an area of $7200\,\text{cm}^2/36\,000 = 0.2\,\text{cm}^2$. The *x,y*-coordinates of the position of the fish were transmitted *via* an RS-232 port to a second computer (Olivetti M300) with a data acquisition program (Labtech Notebook) and an AD/DA interface board (Data Translation DT2801), which calculated instantaneous swimming speed, distance travelled and position every second and stored them on disk for later analysis. This computer also monitored and regulated the oxygen level at pre-set levels by controlling solenoid valves adding either nitrogen or air to the recirculating water.

Oxygen saturation was measured using a WTW OXI 92 with a WTW EO 96 electrode. Oxygen saturations above 80 % were considered normoxic.

Experimental procedure

The experiments were carried out from July to November 1992. The fish were kept at a photoperiod of 16 h:8 h light:dark. Twenty-four fish, eight at each temperature (5, 10 and 15 °C), were used. Each fish was transferred to the experimental tank containing normoxic water at a temperature similar to that of the acclimation tank, at least 1 day prior to the experiment. During experiments, there was no human activity in the experimental room. The duration of each experiment was 7.5 h. Over the experimental period, each fish was exposed to the following oxygen saturations: 100, 80, 70, 60, 50, 40, 30, 25, 20 and 15 % for 45 min periods. The change in oxygen saturation from one level to the next was achieved in approximately 5 min. To ensure stable experimental conditions, only data from the last 30 min of the 45 min period, at each level of oxygen saturation, were used for calculation of the swimming activity.

Pilot studies were carried out to determine appropriate sampling periods and to ensure that there was no influence of diel activity over the course of the experiment.

Analysis of results

The swimming distance, velocity and turning angle distribution of the fish were calculated from the *x,y*-coordinates collected every second. The actual swimming distance covered by the fish during the 30 min periods was calculated at each oxygen saturation and was used as a measure of activity. The distance between the *x,y*-coordinates was used to calculate the distribution of swimming velocities. The change in direction from one second to the next was used to calculate the turning angle of swimming fish (for velocities exceeding $0.25\,BL\,s^{-1}$, where BL is body length). The effect of a reduction in oxygen saturation on swimming activity was evaluated by comparing the swimming activity during and immediately after the deoxygenation period with the swimming activity prior to this period.

The effects of hypoxia on swimming behaviour were investigated by comparing behavioural variables at normoxia, 50 % and 25 % oxygen saturation. Behavioural variables, such as the distribution of swimming speeds, the distribution of turning angles at swimming speeds exceeding $0.25\,BL\,s^{-1}$, the maximum swimming speed and the number of swimming speeds exceeding $1\,BL\,s^{-1}$, were used. Values from normoxia, 50 % and 25 % oxygen saturations only were selected to simplify the analysis.

To evaluate the effects of hypoxia on swimming distance, the incipient oxygen-dependent activity level (IODAL) was determined for each fish using the following criteria. A horizontal line was drawn through the mean swimming distance between normoxia and 80 % oxygen saturation. A regression line of the values for the swimming distance at the five lowest oxygen saturations was also determined. The intercept between these two lines was considered to represent the IODAL (Fig. 2).

Turning angles were calculated for swimming speeds exceeding $0.25\,BL\,s^{-1}$. No distinction was made between right and left turns. Since the number of swimming speeds exceeding $0.25\,BL\,s^{-1}$ decreases with decreasing oxygen availability, so do the number of observations from which turning angles could be calculated. To compare the distribution of turning angles for swimming fish ($>0.25\,BL\,s^{-1}$) at different oxygen
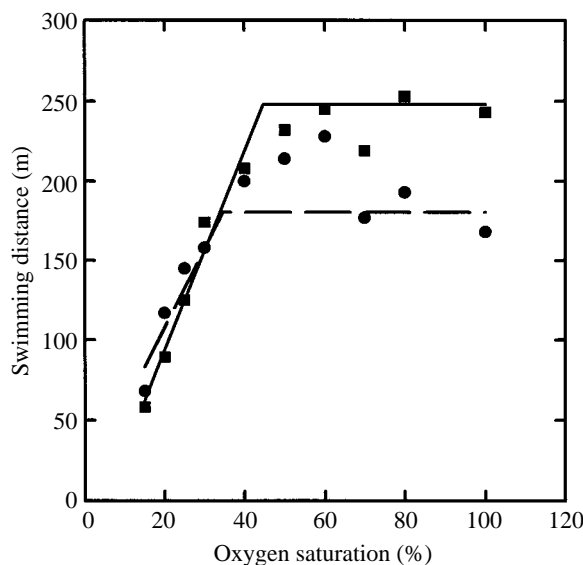
Fig. 2. An example of the incipient oxygen-dependent activity level (IODAL) determination in two fish (squares and circles) at 10 °C. The horizontal lines represent the mean swimming distances at 100 and 80 % oxygen saturation. The lines are linear regressions of oxygen saturation against the swimming distance at the five lowest oxygen saturations.

levels, therefore, the turning angles were recalculated to give relative values by dividing the number of observations in a specific angle interval (e.g. 0–10 °) by the total number of observations in that period, for each fish.

Mann–Whitney tests (Siegel and Castellan, 1988) were used to test for significance at the $P<0.05$ level.

Results

Effects of temperature and hypoxia on swimming distance

Swimming distances at 5, 10 and 15 °C at each of the 10 oxygen saturations are shown in Fig. 3. At all temperatures, there was pronounced individual variation and, consequently, the differences in the average swimming distance observed at normoxia were not significant.

At all temperatures, there was a significant decrease in swimming distance with decreasing oxygen level. This was not related to diel variation in the activity level (swimming distance), since pilot experiments showed that the activity level was relatively constant during the hours of daylight. The IODALs were 39.6±11.8, 51.7±10.0 and 42.7±11.4 % oxygen saturation (mean ± S.D., N=8) at 5, 10 and 15 °C, respectively. The value at 5 °C was significantly lower than that at 10 °C, while no significant differences were found between values at 5 and 15 °C or between values at 10 and 15 °C.

Swimming speed and avoidance reactions

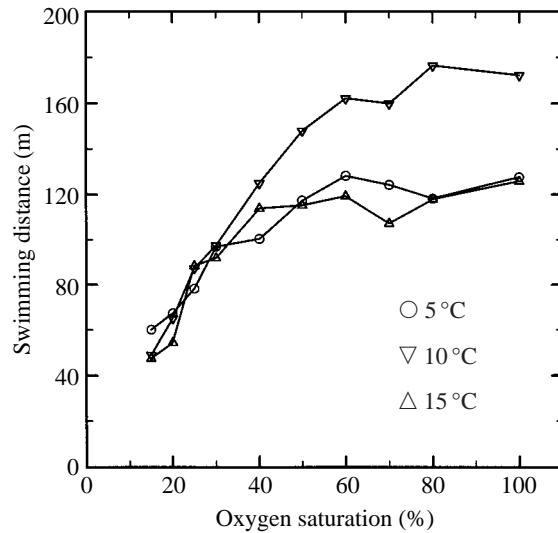The mean swimming speeds at each temperature and oxygen saturation are given in

Fig. 3. Swimming distance of cod at 5, 10 and 15 °C at different oxygen saturations. Each point represents the mean distance (m) covered by eight cod during 30 min. At all oxygen saturations, the activity levels (swimming distance) at 5 and 15 °C are similar and there is a tendency for cod at 10 °C to be more active at higher oxygen saturations. At oxygen saturations below 30 %, the activity levels are similar at all temperatures and decrease with decreasing oxygen saturation.

Table 1. A detailed analysis of the distribution of swimming speeds at 5, 10 and 15 °C and 100, 50 and 25 % oxygen saturations is shown in Fig. 4. The observed swimming speeds rarely exceeded $1\,BL\,s^{-1}$. The swimming speed at 10 °C was usually higher than those at 5 and 15 °C, and the frequency of 'high-speed' swimming decreased with decreasing oxygen saturation at all temperatures. The maximum swimming speed observed and the number of swimming speed measurements exceeding 0.25 and $1\,BL\,s^{-1}$ are given in Table 2.

The relative turning angle distribution for swimming fish is shown in Fig. 5. There was no difference in the distribution of turning angles between normoxia, 50 % and 25 % oxygen saturation at any of the temperatures.

The effect of deoxygenation on the swimming activity, calculated as percentage change in the mean speed, is shown in Fig. 6. The changes in the mean speed during and immediately after a deoxygenation period are shown relative to the swimming activity during the 30 min prior to deoxygenation. There were no significant changes in the mean swimming speed in response to a change in oxygen saturation.

An example of the swimming behaviour of one fish as the oxygen saturation was changed from 50 % to 40 % is given in Fig. 7

Discussion

The lethal oxygen saturations for cod at 5, 10 and 15 °C were recently reported to be 5,

Table 1. *The mean, maximum and minimum swimming distances at 5, 10 and 15 °C at different oxygen levels*

% Oxygen saturation	5 °C				10 °C				15 °C			
	Swimming distance (m)			Mean speed $(BL\,s^{-1})$	Swimming distance (m)			Mean speed $(BL\,s^{-1})$	Swimming distance (m)			Mean speed $(BL\,s^{-1})$
	Mean	Max.	Min.		Mean	Max.	Min.		Mean	Max.	Min.	
100	128	222	32	0.24	172	243	78	0.32	126	219	82	0.23
80	118	205	48	0.22	176	253	74	0.33	118	208	58	0.22
70	124	222	51	0.23	160	219	84	0.30	107	236	54	0.20
60	128	224	48	0.24	162	228	77	0.30	119	227	73	0.22
50	117	212	65	0.22	148	232	66	0.27	115	193	64	0.21
40	100	147	65	0.19	125	208	64	0.23	114	143	58	0.21
30	97	161	32	0.18	97	174	33	0.18	92	155	47	0.17
25	78	150	33	0.14	87	145	48	0.16	88	150	55	0.16
20	67	121	33	0.12	65	117	39	0.12	54	90	14	0.10
15	60	78	30	0.11	49	83	27	0.09	48	89	26	0.09

Values are the mean swimming distance (in m) covered in 30 min by eight fish.
BL is body length.

Table 2. *The number of observed swimming speeds exceeding 0.25 and 1 BL s^{-1} and the maximum observed velocity at normoxia (=100% oxygen saturation) and oxygen saturations of 50% and 25% at temperatures of 5, 10 and 15 °C, during 30 min (=1800 observations) of measurements*

Temperature (°C)	Number of observations >0.25 $BL\,s^{-1}$			Number of observations >1 $BL\,s^{-1}$			Maximum velocity ($BL\,s^{-1}$)		
	100%	50%	25%	100%	50%	25%	100%	50%	25%
5	679	593	340*	20	15	4	1.8	2.3	1.7
10	929	814	400*	26	14	4*	2.7	1.7*	2.2
15	601	617	333*	9	5	7	2.1	2.1	1.8

Values are means for eight fish.
Asterisks indicate that a value is significantly ($P<0.05$) different from the normoxic condition
BL, body length.

14 and 16.5%, respectively (Schurmann and Steffensen, 1992). The lowest oxygen saturation used in the present investigation (15%) was at the previously reported lethal level. However, no fish died during these experiments. Schurmann and Steffensen (1992) determined the lethal oxygen saturation for cod at different temperatures by gradually decreasing the oxygen saturation of 125 l of water containing six fish at a rate of 0.5% min^{-1}. The lethal level was reached in approximately 3 h compared with 7.5 h in the present investigation. One possible explanation of why all the fish in this investigation survived could be the difference in the rate of deoxygenation. Alternatively, fish in groups may be more sensitive to hypoxia than is an individual alone. The fish in the present study were also allowed access to the surface, in contrast to the earlier work, and aquatic surface-breathing at low oxygen saturations, as described by Kramer (1987), may have been possible. In a pilot experiment, it was observed that cod occasionally swam at the surface with an open mouth, presumably taking in water mixed with air. On these occasions, the inspired P_{O_2} would have been higher than the ambient water oxygen saturation. This behaviour, however, was not observed frequently and was not considered to have influenced the results reported here.

The metabolic rate of fish is known to be temperature-dependent. As temperature rises, the metabolic rates of the fish increase and the solubility of oxygen in water decreases. The IODAL would therefore be predicted to be highest at 15 °C, as the metabolic rate is at its highest and the oxygen content of the water is at its lowest at this temperature. In this study, however, the IODAL was highest at 10 °C (although there was no significant difference between values at 10 °C and 15 °C). This discrepancy can be explained by the tendency towards a higher activity level at 10 °C than at 15 °C. A high activity level with a concurrently higher oxygen demand could not be maintained with a reduced availability of oxygen. At 5 °C and at 15 °C, the normoxic activity level could be maintained at a lower oxygen saturation because the initial activity level, and hence the rate of oxygen consumption, was lower.
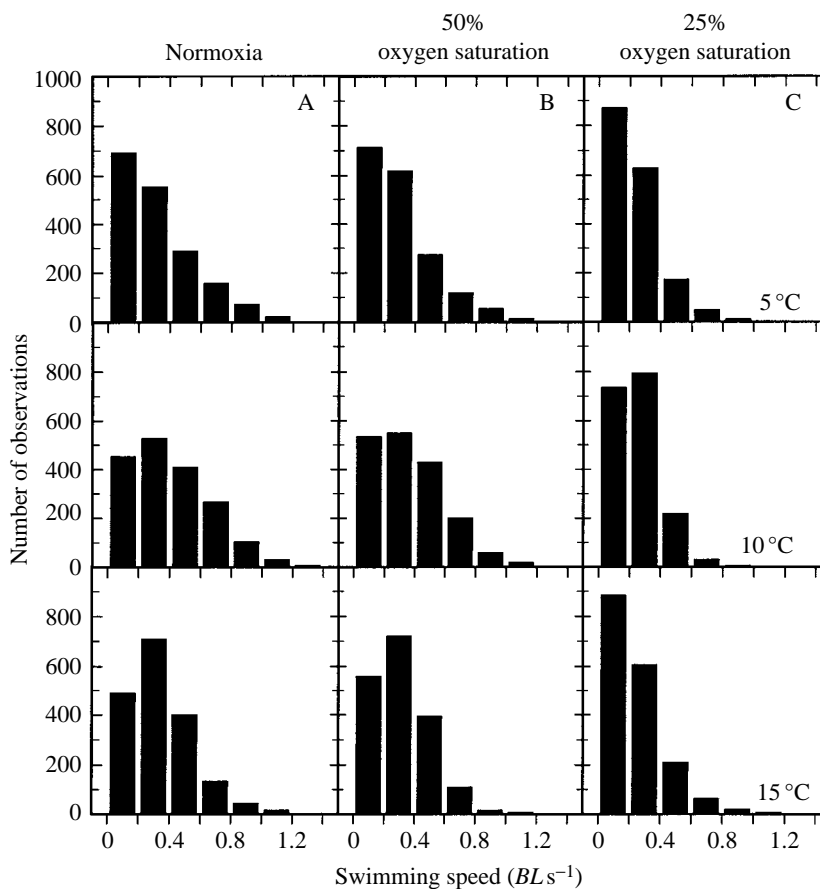
Fig. 4. The distribution of swimming speeds at 5, 10 and 15 °C at oxygen saturations of 100 %, (A) (=normoxia), 50 %, (B) and 25 % (C). Values are means for eight cod at each temperature and oxygen saturation during 30 min of measurements. The swimming speed at 10 °C is usually higher than those at 5 or 10 °C, and the frequency of higher swimming speeds decreases with decreasing oxygen level.

There are relatively few investigations of spontaneous swimming activity available in the literature. Clark and Green (1990) tracked Atlantic cod with acoustic tags; four individuals were followed in detail, with positional information recorded every 2 min. The average swimming speed of these individuals was approximately $0.36\,BL\,s^{-1}$, slightly higher than the swimming speeds observed in the present study (Table 1). In their natural environment, the activity levels of fish are influenced by many factors, such as the presence of predators, ambient temperature, day length, light intensity, territorial behaviour, feeding activity and the availability of oxygen. In a laboratory situation, as in this study, most of these factors have been eliminated, although other factors may be introduced by the unnatural environment.

A reduction in the activity level of cod in hypoxic water might increase their chances of survival. By reducing the activity level before the situation becomes lethal, the cod will
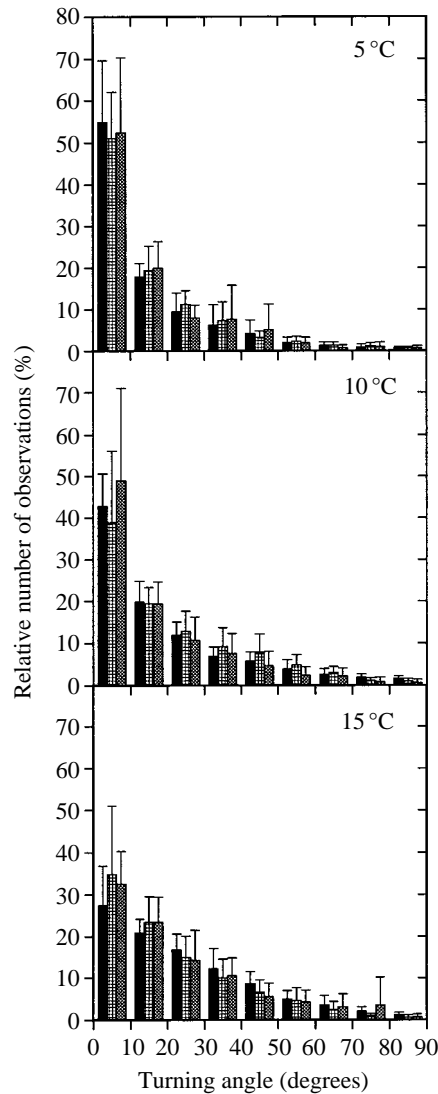
Fig. 5. The frequency of different turning angles at swimming speeds exceeding $0.25\,BL\,s^{-1}$ at 5, 10 and 15 °C, where *BL* is body length. The three columns for each turning interval represent the relative numbers of observations at normoxia (filled bar), 50 % saturation (squared bar) and 25 % saturation (cross-hatched bar). Values are the mean + S.D. for eight fish. There is no difference in the frequency of different turning angles between normoxia, 50 % and 25 % oxygen saturation at any of the temperatures.

save energy. This 'sit and wait' strategy may have been beneficial to the cod in the present study, since none of the fish died, although the lowest oxygen saturations were at levels previously found to be lethal (Schurmann and Steffensen, 1992). In a recent study, Nilsson *et al.* (1993) concluded that crucian carp *Carassius carassius* exposed to anoxia save energy by reducing their spontaneous swimming activity to about 50 % of that at
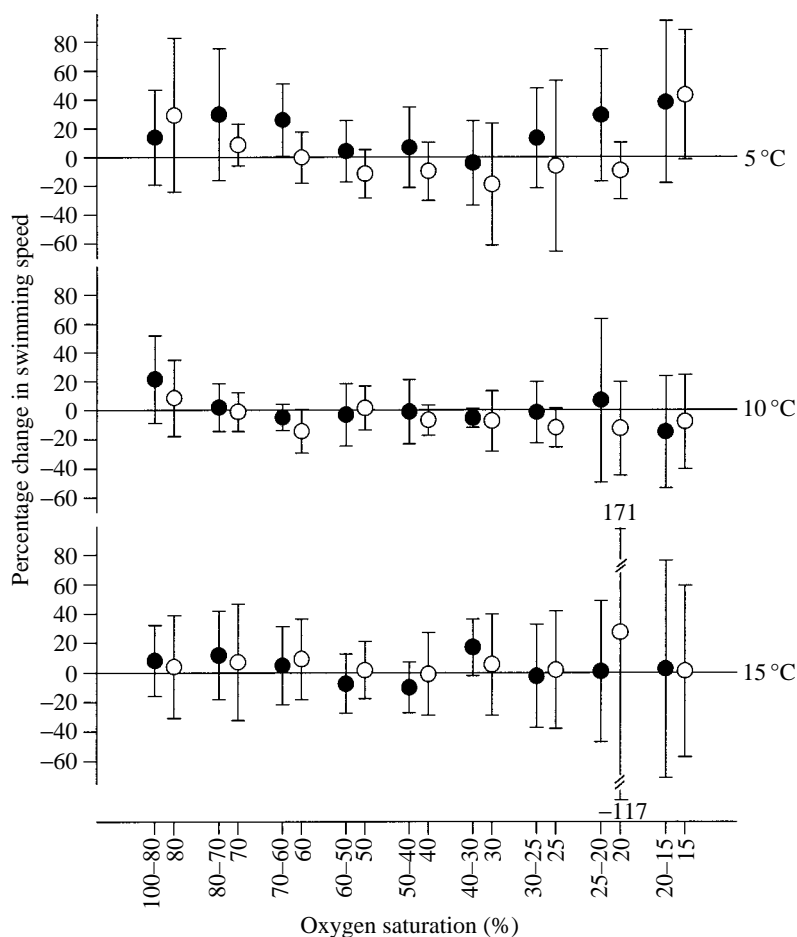
Fig. 6. The percentage change in mean swimming speed as the oxygen saturation was reduced at 5, 10 and 15 ˚C. Filled symbols represent the relative change in swimming speed during the 5 min period when the oxygen was reduced from one level to another compared with the mean swimming speed in the 30 min period immediately preceding the reduction in oxygen saturation. The open symbols to the right of the filled symbols represent the relative change in swimming speed during the first 5 min after the new oxygen level had been established compared with the same 30 min period. Values are mean ± S.D. for eight fish. None of the changes in swimming speeds is significantly different from those prior to the deoxygenation.

normoxia. If the fish had used an alternative strategy, for example stayed active or even increased their activity level in order to search for a more favourable environment, the low oxygen saturation could have been lethal.

Behaviour in hypoxic water

Experiments with chinook salmon, coho salmon, largemouth bass, bluegill (Whitmore *et al.* 1960) and brook trout (Spoor, 1990) in oxygen gradients have demonstrated that these species avoid water with an oxygen saturation below a certain level, whereas they
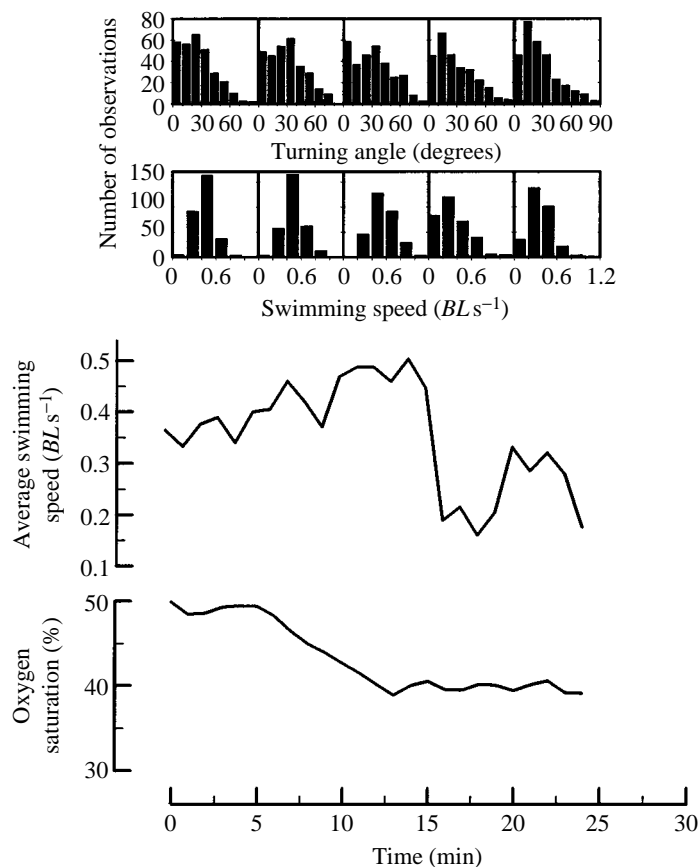
Fig. 7. An example of the behaviour of an individual cod when the oxygen saturation was reduced from 50 % to 40 %. The bottom panel is a continuous recording of the oxygen saturation. A moving average (*N*=5) of the swimming speed as the oxygen saturation decreases is also shown. The two panels at the top show the distribution of the turning angles and swimming speeds of the cod divided into 5 min intervals over the same time axis. Initially, the swimming speed increases slightly as oxygen saturation decreases, but when the oxygen saturation reaches 40 %, the swimming speed decreases. The frequency of high-angle turns increases as oxygen saturation decreases.

show no apparent oxygen level preference above that limit. Stott and Cross (1973) conditioned roach to utilize the upper section of a laboratory channel as a 'home range'. When this upper section was deoxygenated, the fish swam out of their 'home range', but quickly returned when oxygen was reintroduced. Even when the oxygen saturation in the 'home range' was lower than 10 %, the roach made occasional excursions into and out of the 'home range'. Field data also support the observation that fish avoid hypoxic waters. In a study covering 42 species, Coble (1982) concluded that both species number and density were greater at sites with a high oxygen concentration than at sites with a low oxygen concentration. Furthermore, Suthers and Gee (1986) showed that the distribution of yellow perch *Perca flavescens* was limited by hypoxia. Trawling data collected on spot

Leiostomus xanthurus, hogchoker *Trinectes maculatus* and croaker *Micropogonias undulatus* by Pihl *et al.* (1991) showed that the reaction to hypoxia was dependent upon the hypoxic tolerance of the species. In stratified water, where the lower part of the water column becomes increasingly hypoxic, fish may move to shallow water areas or closer to the surface to avoid hypoxic conditions. The most hypoxia-tolerant species are the last to move (Pihl *et al.* 1991).

While it seems to be generally accepted that fish avoid areas with low oxygen saturation, there is some disagreement in the literature on the mechanisms involved (Doudoroff and Shumway, 1970). From experiments with roach, Höglund (1961) described hypoxia-avoidance as oxykinesis alone; that is, the result of a unidirectional, but increased, activity level in hypoxic water resulting in the movement of the fish back to better-oxygenated water. An opposite conclusion was reached by Whitmore *et al.* (1960), who described this avoidance reaction as a direct response to hypoxia; that is, that the fish were able to sense hypoxia and to return directly to water with more oxygen. Höglund's (1961) oxykinetic hypothesis is not supported by the present study as there was no increase in the activity level with decreasing oxygen saturation (Fig. 6) and the swimming pattern (described by the turning angles) did not differ between normoxic and hypoxic water (Fig. 5). However, the conclusions of Whitmore *et al.* (1960) are not supported either, since fish do swim into water with low oxygen saturation and the avoidance reaction does not seem to be instantaneous (Stott and Cross, 1973; Spoor, 1990).

The Øresund (the Sound) that connects Kattegat and the Baltic Sea is characterized by a thermocline and a halocline. In summer, there is a flow of cold marine water south from Kattegat along the bottom. At the surface, however, warmer brackish water from the Baltic Sea flows towards Kattegat. During the autumn, the benthic waters are commonly hypoxic (20–25 % oxygen saturation) (Nielsen and Gargas, 1984; H. Schurmann and J. F. Steffensen, personal observations). The cod that inhabit these waters are therefore faced with a dilemma. To avoid the hypoxic deep water, the cod can move up the water column, as observed by Pihl *et al.* (1991). Here, however, they have to cope with higher, potentially lethal, temperatures as well as a lower salinity. As shown in this study and in previous work (Schurmann and Steffensen, 1992), cod are able to survive low oxygen saturations if the water is cold and the activity level is reduced. Whether cod in a stratified environment, where the water is separated into a cold hypoxic lower layer and a warm normoxic upper layer, inhabit the bottom area at a relatively low activity level or whether they move away is not known. If they do leave, they may seek out a more favourable environment either by following gradients in temperature or oxygen or by following the preferred combination of these two factors (Schurmann and Steffensen, 1992). Field studies of cod equipped with a transmitter relaying information on temperature, oxygen saturation and depth should resolve this question.

position of animals. Constructive criticism from two anonymous referees is gratefully acknowledged.

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